CURRENT PRIMARY PRODUCTION RATES OF THE WESTERN ARCTIC OCEAN ESTIMATED BY STABLE CARBON AND NITROGEN ISOTOPE TRACERS

By

Sang Heon Lee

RECOMMENDED:

Advisory Committee Chair

Program Head, Marine Science and Limnology

APPROVED:

Dean, School of Fisheries and Ocean Sciences

Dean of the Graduate School

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Sang Heon Lee, B.S., M.S.

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Abstract

Currently, the environments in the Arctic are rapidly changing. These changes of climate and ice conditions may alter the quantity, quality, and timing of production of ice algae and phytoplankton in the Arctic Ocean. The objectives in this study were to detect any change in the carbon production between current and previous studies and lay the groundwork for the future monitoring of ecosystem response to climate change in the different regions of the western Arctic Ocean.

As an arctic ocean mostly covered by multi or first-year ice, the deep Canada Basin had generally low photosynthetic rates and the maximum rates were found between 50 and 60 m in the basin. Based on the percentage of ice cover, the annual production ranged from 3 to 7.5 g C m^{-2} in the basin. Nutrients appear to be a main limiting factor at the surface, whereas the phytoplankton activity might be limited by the low light in the Chl a-max layer. At the surface below the ice, photosynthetic activity might be controlled by both low light and nutrients.

Studies of ice algae and phytoplankton at the first-year sea ice of Barrow in Alaska showed that bottom sea ice algae and phytoplankton are limited mainly by light. Therefore, the current downward trend of sea ice thickness and extent in the Arctic Ocean might cause an increase in primary production or/and change in timing of the production. In addition, the composition in macromolecules of primary producers might be changed under the current ice conditions and thus nutritional status of higher trophic levels might be altered.

As shallow shelf regions, Bering Strait/Chukchi Sea showed that the range of nitrate in the central Chukchi Sea was rather higher whereas the biomass of phytoplankton was lower in this study than in previous studies. Consistently, the mean carbon and nitrogen productivities from this study were almost half of values from previous studies. In conclusion, it appears that

lower phytoplankton biomass in Bering Strait and the Chukchi Sea resulted in the lower carbon and nitrogen uptake rates and consequently more unused nitrate in the regions.

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Chapter 1. General introduction

The arctic seas have not been as intensively studied as the other oceans because of the difficulty imposed by the severe temperatures and ice conditions. Especially, biological oceanographic research has been limited in the arctic oceans. Nansen (1902) and Gran (1904) from the FRAM Expedition found low biomass and few species of phytoplankton in the Arctic Ocean because of low water temperature and illumination through the thick sea ice cover. From IGY Drift Station Alpha in 1957 and 1958, English (1961) found very low primary production in the Arctic Ocean because of the short productivity season and low productivity caused by limiting submarine illumination through the sea ice. After extensive biological field studies were conducted at Fletcher's Ice Island (T3) and main ice camp in the Beaufort Sea during the Arctic Ice Dynamics Joint Experiment (AIDJEX), Pautzke (1979) investigated quantitatively in time and space the physical, chemical, and biological components of the oceanic plankton ecosystem under the ice of the Arctic Ocean and assessed the influence of these components on primary production. Recently, some biological studies were done during the SHEBA ice camp drift from October 1997 to October 1998 (Melnikov et al. 2002). Although recent samplings from icebreakers have enhanced our knowledge of dynamics of the Arctic Ocean, there are still many unknowns about the ecosystems of this remote region.

The combination of cold temperature, occurrence of sea ice and extreme seasonal variations in the light regime controls phytoplankton growth and governs the spatial and temporal patterns of their distributions in polar oceans (Smith and Sakshaug 1990). Because of these extreme conditions, the Arctic Ocean has been generally categorized as a low productivity region (English 1961; Andersen 1989). However, recent primary productivity and DOC measurements have revealed a more active carbon cycling in the surface waters of the Arctic Ocean (Gosselin et al. 1997; Guay et al. 1999; Lee and Whitledge 2005) than previously estimated (English 1961;

Apollonio 1959). Over the past few decades, the environments in the Arctic have been changing at a very rapid rate. The higher temperatures plus a possible increase in ice export have decreased the ice extent and sea-ice thickness in the Arctic Ocean over the past 40 years contributing to more open water, especially in coastal regions (Maslanik et al. 1996; Martin et al. 1997; Rothrock et al. 1999; Rothrock et al. 2003). Laxon et al. (2003) expect additional thinning of Arctic sea ice with the continued increase in melt season length. These changes of climate and ice conditions may alter the relative contributions of sea ice algae and phytoplankton, with respect to the species and/or size composition of primary producers, and the new and total primary production that is occurring. Melnikov et al. (2002) found the physical-chemical characteristics of sea ice and the biological structure of ice communities in 1997-1998 were very different from conditions during the 1970s, based on comparisons of SHEBA results with historical data although it was the spatially restricted sampling (Gradinger et al. 2005). The current environmental changes in the Arctic Ocean might lead to different compositions in photosynthetic-end products of sea ice algae and phytoplankton, which could affect the nutritional status of higher trophic levels. As a consequence, the seasonal distributions, geographic ranges, and nutritional structure of zooplankton and higher trophic levels have been projected to be altered in the Arctic Ocean (Tynan and DeMaster 1997).

Since arctic seas have large geographical variation in the carbon production processes because of different environmental conditions it is important to assess this variability in order to enhance our understanding of responses of the arctic marine ecosystem to the current and future climate changes in the Arctic Ocean. There are few studies on marine primary production that address different regions in the western Arctic Ocean (Cota et al. 1996; Gosselin et al. 1997; Chen et al. 2003). Thus, the basic objectives in this study were to detect differences in carbon production between current and previous studies in the different marine ecosystems and lay the

groundwork for the future monitoring of ecosystem response to climate change in the different regions of the western Arctic Ocean. Our approach is based on the dual label ^{13}C-^{15}N isotope method (Kanda et al. 1985) which measures carbon uptake and simultaneously nitrogen uptake of phytoplankton. We examined carbon and nitrogen uptakes in the Canada Basin, coastal land fast ice of Barrow, Alaska and Bering Strait/Chukchi Sea. The Canada Basin is one part of the western Arctic Ocean which is mostly covered by multi-year or first-year ice. Barrow was chosen for the detailed studies of the ecology of ice algae within sea ice and phytoplankton under the ice, which is difficult to do on the icebreakers. Lastly, Bering Strait and the Chukchi Sea are shallow shelf regions (20-60 m) that are covered by ice for about six months each year. Especially, the Chukchi Sea is the eastern end of the great arctic continental shelf system of the Arctic Ocean (Aagaard 1987; Weingartner 1994) as well as a conduit connecting between the north Pacific and Arctic Oceans.

1.1. Deep Canada Basin

The halocline of the Canada Basin includes Pacific-origin water (McLaughlin et al. 2005), which are a blend of nutrient-rich water originating in the basin of the Bering Sea (Anadyr Water) and fresher, lower nutrient Bering Water and Alaskan Coastal Water. These water masses enter the Chukchi Sea, and eventually the Canada Basin, through Bering Strait (Coachman et al. 1975; Walsh et al. 1989). Coachman et al. (1975) proposed that Anadyr Water enters the Canada Basin by passing west of the Chukchi rise and that Alaska Coastal Water enters directly into the Beaufort Gyre.

Nutrient concentrations are substantially greater in Pacific-origin waters compared to Atlantic-origin waters (McLaughlin et al. 2005) which are important for primary producers in the region. McLaughlin et al. (2002) observed a decrease in thickness of the Pacific-origin water and

an increased volume of Atlantic-origin water in the southern Canada Basin between 1989 and 1995. An unusually fresh surface layer and thin ice was recently observed in the Canada Basin interior (Macdonald et al. 2002). Moreover, the mean ice draft in the basin has decreased from 3.5 m during 1958-1976 to 2.2 m in 1990s (Rothrock et al. 1999). These changes in physical environments might alter the entire ecosystem in the Canada Basin.

1.2. The first-year sea ice of Barrow

Sea ice algae at the ice-water interface provide an additional source of primary production in the arctic seas (Alexander et al. 1974; Horner and Schrader 1982; Demers et al. 1986; Gosselin et al. 1997; Mock and Gradinger 1999; others therein) as well as in the Southern Ocean (Bunt and Lee 1970; Garrison and Buck 1991; Legendre et al. 1992; Arrigo et al. 1997). Ice algae production measurements in Arctic first-year ice are few with reported values ranging from 0.2 to 23 g C m^{-2} $year^{-1}$ (Table 3.4), suggesting strong geographical and annual variations (Horner and Alexander 1972; Alexander 1974; Horner and Schrader 1982; Subba Rao and Platt 1984). Therefore, the estimated contribution of ice algae to yearly production ranges from less than 1 % (Alexander and Chapman 1981) to around 60 % (Horner and Schrader 1982) in the western Arctic Ocean. Although ice algae production seems to vary widely, it has potentially important ecological impact (Alexander 1980) because the ice algae bloom is initiated a couple of months earlier than the phytoplankton bloom in spring (Apollonio 1965; Legendre et al. 1981). Moreover, ice algae might seed the water column bloom after these cells are released from the ice (Schandelmeier and Alexander 1981; Michel et al., 1993). It is also an important source of food for the benthic community and sympagic organisms (such as amphipods) as well as pelagic grazers (Bradstreet and Cross 1982; Michel et al. 2002) before the spring bloom.

The recent reduction of ice-cover is a predominantly spring-summer phenomenon (Chapman and Walsh 1993) and consequently there would be some changes such as the relative amount of primary production, timing of blooms, and physiology of primary producers under the ice cover. However, there have been few recent studies about ice algae or related water column phytoplankton in the western Arctic regions. Barrow was chosen to assess the effects of climate change on the ecosystem of ice algae in the western Arctic first-year fast ice since ice forms and melts completely every year.

1.3. Bering Strait and the Chukchi Sea

1.3.1. Bering Strait

High nutrient waters flowing northward through Bering Strait into the Chukchi Sea are critical in controlling Arctic ocean nutrient budgets (Jones and Anderson 1986; Guay and Falkner 1997; Cooper et al. 1997). Nutrient-rich Anadyr Water and low nutrient Alaskan Coastal Water comprise most of the upper halocline water in the Canada Basin (McLaughlin et al. 2005).

The northward flow of water through the narrow, shallow (< 50 m) Bering Strait results in characteristic water mass distributions of the shelf regions of the southern Chukchi Sea (Coachman et al. 1975; Walsh et al. 1989; Niebauer and Schell 1993). The inflows convey three basically different water masses, Anadyr Water, Bering Shelf Water and Alaskan Coastal Water into the Chukchi Sea (Coachman et al. 1975). These are distinguished primarily by their salinity differences and temperatures in summer (Coachman et al. 1975; Aagaard 1987). Alaskan Coastal Water has a low salinity (< approximately 31.8) due to the influx of freshwater from river discharge along the Alaskan coast (Weingartner 1997). Bering Shelf Water, which is colder (0-3 °C) and more saline (31.8-32.5) than Alaskan Coastal Water, originates on the eastern Bering Sea shelf south of St. Lawrence Island. Anadyr Water originates along the Bering shelf break and is a

high salinity (32.5-33.0) northern branch of the Bering Slope Current (Coachman et al. 1975; Kinder et al. 1975; Coachman and Shigaev 1992; Weingartner 1997). Of these water masses, Anadyr Water supplies the Chukchi continental shelf with high nutrients that promote abundant phytoplankton growth throughout summer and transports oceanic zooplankton onto the shallow northern shelf and into the Chukchi Sea through the western Bering Strait (Sambrotto et al. 1984; Springer et al. 1989; Springer and McRoy 1993).

1.3.2. The Chukchi Sea

The Chukchi Sea extends northward over 1,200 km from Bering Strait to Point Barrow. The Chukchi Sea is the eastern end of the great arctic continental shelf system of the Arctic Ocean (Aagaard 1987; Weingartner 1997). The shelf is remarkably wide (600-800 km) and relatively shallow (20-60 m) (Aagaard 1987; Niebauer and Schell 1993). North of Bering Strait, the Anadyr and Bering Shelf waters mix and flow northward (15-20 cm/sec) into the central and western Chukchi Sea (Weingartner et al. accepted; Woodgate et al. accepted). Alaska Coastal Water also flows northeastward along the Alaska coast (Coachman et al. 1975; Niebauer and Schell 1993). Because the northward flow is warm and of low salinity during summer, the Chukchi Sea becomes ice-free much earlier in the year than it otherwise would (Aagaard 1987). The retreat of sea ice normally begins in early June and the maximum retreat occurs in September (Stringer and Groves 1987; Weingartner 1994). Freeze-up typically begins in October or November (Niebauer and Schell 1993; Weingartner et al. accepted). Ice thickness progressively increases from 0.5-1.0 m in the open Bering Sea to 2 m along the arctic coast (Weeks and Weller 1984).

1.3.3. Previous studies

New data had been acquired on the nutrient dynamics and primary productivity in the Chukchi Sea since the Outer Continental Shelf Environmental Assessment Program (OCSEAP)

managed by NOAA. The Inner Shelf Transfer and Recycling (ISHTAR) project (1983-1989) investigated the transport of water and nutrients through the northern Bering Sea into the Chukchi Sea and measured the primary production related to nutrient dynamics and chl-a concentration (Hansell et al., 1993; Springer and McRoy 1993). The several joint US-USSR Bering and Chukchi Seas Expeditions or Long-term Ecological Research of the Marine Ecosystem in the Arctic and Pacific Oceans (BERPAC) program provided the opportunity to extend the ISHTAR experimental design across the whole northern shelf area, including Russian waters, to examine biological, chemical, and physical fundamental characteristics (Whitledge et al. 1988).

1.3.4. Primary production

Sambrotto et al. (1984) estimated annual production to be 324 g C m^{-2} in the western Bering Strait, based on the nitrate utilization rate, while Hansell et al. (1993) calculated 576-720 g C m^{-2} for the annual production in Bering Sea Water north of Bering Strait based on new production in the region. Based on carbon production and chlorophyll-a concentrations in the region, Springer and McRoy (1993) estimated the annual production to be 470 g C m^{-2}. Recently, Schell (2000) hypothesized that there has been a 30-40 % decrease in seasonal primary productivity in the northern Bering Sea over several decades. However, there has been no direct evidence for the decline in the productivity in this region since the ISHTAR and BERPAC programs in the late 1980s. The only recent production measurements from the Chukchi Sea (Gosselin et al. 1997; Cota et al. 1996) consist of a few stations in the northern Chukchi Sea, which cannot be compared with previous studies because of the large geographical separation. It is therefore particularly important to monitor the Chukchi Sea insofar as processes there both reflect changes in the Bering Sea and regional biological production rates in the western Arctic Ocean (Walsh et al. 1989; Walsh et al. 1997).

1.4. Dissertation

There are many different ways to detect changes in marine ecosystems related to environmental changes caused by climate shifts. Here, a dual ^{13}C-^{15}N stable isotope method for primary production was used as a tool for exploring changes in primary productions in different ecosystems of the western Arctic Ocean. Our measurements are then compared with previous data. Moreover, the physiological statuses of phytoplankton and ice algae indicated by photosynthetic-end products are investigated to provide insight into possible future conditions of phytoplankton and ice algae.

The specific objectives of this study were:

- to quantify the range of nutrients, phytoplankton biomass and productivities in different regions (open ocean, land fast ice at Barrow and continental shelf system) of the western Arctic Ocean.
- to compare contemporary productivity rates with those obtained in the previous decades for assessment of rate changes under present warm temperatures in the regions of the western Arctic Ocean.
- to determine which specific environmental factor exerts the most control on the primary production rates of phytoplankton and ice algae.
- to evaluate possible changes in the physiological conditions of phytoplankton and ice algae within the bottom sea ice in the Arctic Oceans under ongoing environment changes.
- to evaluate the fate of ice algal production to determine the ice algal contribution to the carbon cycle in the coastal fast ice of the Arctic Oceans.

The following chapters describe the pelagic carbon and nitrogen production, size compositions, and physiology status of primary producers under different environment conditions in the western

Arctic Ocean. Chapter 2 describes primary production and new production in the mostly ice-covered Canada Basin, and compares production rates between ice-covered and open-water. Chapter 3 provides detailed characteristics for the ecology of sea ice algae within the sea ice and phytoplankton under the land-fast sea ice at Barrow, Alaska. In-situ carbon production of ice algae and phytoplankton under nutrient and light enrichment conditions provided some insight into primary production and physiological conditions of ice algae related to ongoing and future ice conditions in the Arctic Ocean. Chapter 4 describes current chlorophyll-a concentrations, size compositions of phytoplankton, and primary and new production in different water masses of Bering Strait and the whole Chukchi Sea. Based on the new data from this study in Chapter 4, the primary production rates are compared with the previous estimates to detect any difference in Bering Strait and the Chukchi Sea. Chapter 5 summarizes the results and major conclusions from each chapter in this dissertation.

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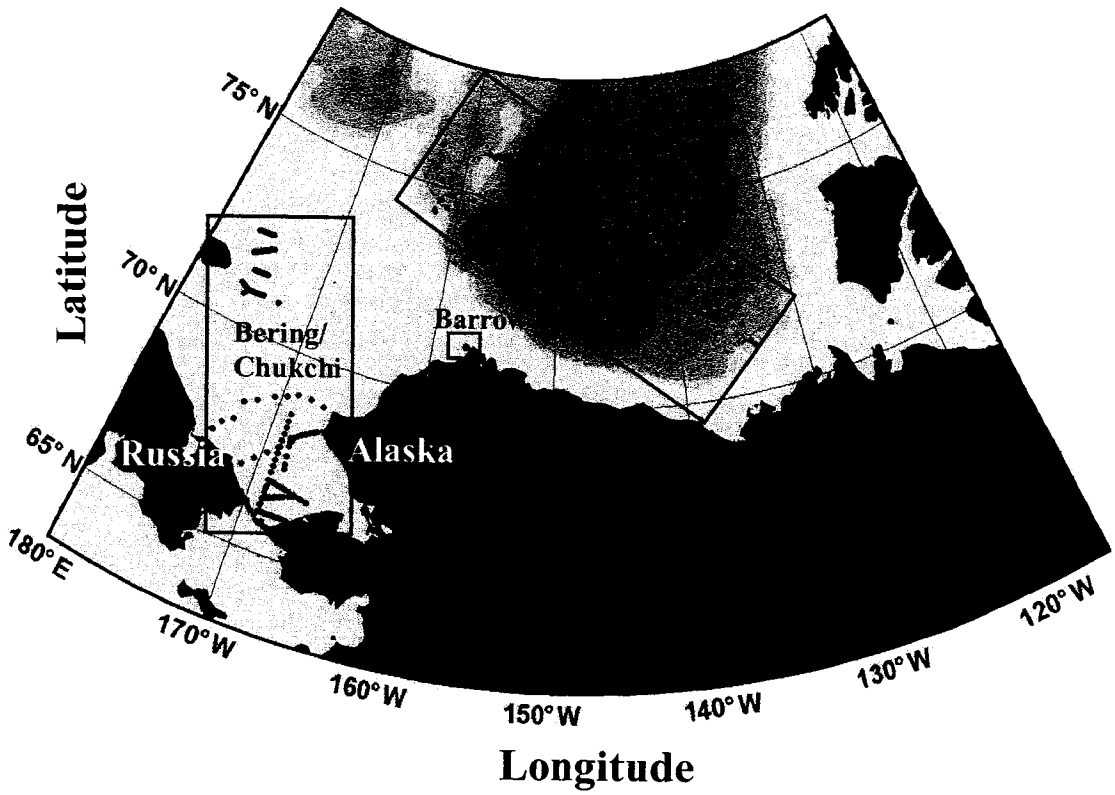

Fig. 1.1. The hydrographic stations of the deep Canada Basin, Barrow, and Bering/Chukchi Seas.

Chapter 2. Primary and new production in the deep Canada Basin during summer 2002*

Abstract

The NOAA Ocean Exploration program provided the opportunity to measure the carbon and nitrogen productivity across the Canada Basin. This research examined the major environmental factors limiting the levels of primary production and possible future climate change on the ecosystems. The vertical distributions of the carbon and nitrogen uptakes of phytoplankton had similar patterns as their respective biomass concentrations which were low at the surface and highest in the chlorophyll-maximum layer. The annual carbon and new production rates of phytoplankton in the Canada Basin were about 5 and 1 g C m^{-2}, respectively. Nutrients were determined to be a main limiting factor at the surface, whereas light may be a major factor to limit phytoplankton productivity in the chlorophyll-maximum layer for open waters. The bottom surface of the ice has a low specific uptake and productivity of phytoplankton, indicating that photosynthetic activity might be controlled by both light and nutrients.

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2.1. Introduction

The combination of cold temperature, occurrence of sea ice and extreme seasonal variations in the light regime controls phytoplankton growth and governs the spatial and temporal patterns of their growth in polar oceans (Smith and Sakshaug 1990). Because of these extreme conditions, the central Arctic Ocean has been generally categorized as a low productivity region (English 1961; Andersen 1989). However, the recent primary productivity and DOC measurements have revealed a more dynamic carbon cycle in the surface waters of the Arctic Ocean (Gosselin et al. 1997; Guay et al. 1999) than previously estimated (English 1961; Apollonio 1959). The deep Canada Basin is the one of the least known areas in the Arctic Ocean. A few measurements of primary production have been determined recently (Gosselin et al. 1997; Cota et al. 1996; Chen et al. 2003) with limited data in the western part of the Canada Basin and an even smaller number of direct measurements of new production have been simultaneously made in this basin. In addition, the Arctic has been changing at a very rapid rate. The higher temperatures have decreased the ice extent and sea-ice thickness in the Arctic Ocean over the past 40 years and have produced more open water, especially in coastal regions (Maslanik et al. 1996; Martin et al. 1997; Rothrock et al. 1999). These changes of climate and ice may alter the relative contributions of sea ice algae and phytoplankton, with respect to the species and/or size composition of primary producers, and the new and total production. As a consequence, the seasonal distributions, geographic ranges, and nutritional structure of zooplankton have been projected to be altered (Tynan and DeMaster 1997). Although phytoplankton and ice algae produce the most basic food source for all the animals that live in the Arctic Ocean, we still do not know if the predicted climate change will provide less or more food in Arctic regions because very little is known about the physical and chemical oceanography and the ecosystem responses of this remote region. The NOAA Ocean Exploration program in collaboration with the JWACS

Ocean Climate supported an oceanographic section across the remote deep Canada Basin between Banks Island and the Northwind Ridge from mid-August to early September 2002 (Fig. 2.1). Measurements include primary production and new production to assess major environmental factors related to present and future climate change on the ecosystems in the area.

2.2. Materials and methods

Daily carbon and nitrogen uptakes were estimated from five light depths (100, 52, 30, 11, and 2 % of surface irradiance), using a ^{13}C tracer and a ^{13}C-^{15}N dual tracer techniques. Each light depth was determined from observed under water radiation with a LICOR 4π light sensor and a surface radiation reference (LI-1400). Water samples from each light depth at open-water stations were inoculated with labeled nitrate ($K^{15}NO_3$), ammonium ($^{15}NH_4Cl$), and carbon ($NaH^{13}CO_3$) substrates. The ^{13}C enrichment was ca. 5-10 % of the total inorganic carbon in the ambient water and an amount equal to 10 % of the ambient nitrate or ammonium concentration was added to each treatment bottle. All incubations were conducted in 600 ml polycarbonate bottles. They were incubated in a deck incubator for the water samples from open water stations or *in situ* incubation under ice floes for ice stations. We have defined on-deck incubations as "open-water" and *in situ* incubations under ice floes as "below ice".

All seawater samples were filtered through 200 μm mesh net to remove large zooplankton (Sakshaug 1980). Since long chain forming diatoms (> 200 μm) are dominant in maximum spring bloom in the Arctic Ocean (Wassmann et al. 1999), we don't expect that they were excluded by the net in the open ocean and late summer. The incubations were terminated by filtration through pre-combusted (450 °C) GF/F glass fiber filters (24 mm) after 3-7 hours depending on weather conditions. The filters were immediately frozen and preserved for mass spectrometric analysis at the stable isotope laboratory of the University of Alaska Fairbanks.

Particulate organic carbon and nitrogen and abundance of ^{13}C and ^{15}N were determined in the Finnigan Delta+XL mass spectrometer after HCl fuming overnight to remove carbonate. *In situ* primary production and nitrogen uptake experiments were conducted on three ice floes with an average thickness of 2.3-m ice. The holes for incubation were made with a SIPRE ice corer (8 cm internal diameter) and the lengths of ice cores were measured. The water from each different light depth below the ice floes was collected by lowering a small water sampler through the hole down to the desired depth. The samples were inoculated with ^{13}C and ^{15}N isotopes, and the incubation water bottles were tied to an anchor rope with a weight at the bottom and then lowered to the depth where they were originally collected. The samples were kept at their *in situ* temperature and light for 3 to 4 hours, retrieved and brought to the ship in a dark insulated box for filtration of the water and phytoplankton through the combusted GF/F glass fiber filters. All carbon and nitrogen uptake rates were corrected by subtraction of dark uptake at each light depth.

Samples for the determination of total chlorophyll a were filtered onto Whatman GF/F glass fiber filters (24 mm). Size-fractionated chlorophyll was determined on samples passed sequentially through 20 μm and 5 μm Nucleopore and 0.7 μm Whatman GF/F filters (47 mm). The filters were kept frozen and returned to the laboratory for analysis. The filters were subsequently extracted in a 3:2 mixture of 90 % Acetone and DMSO (Webb et al. 1992), for 24 hours, and centrifuged based on Parsons et al (1984). Concentrations of chlorophyll a were measured using a Turner Designs model 10-AU fluorometer which had been calibrated with commercially purified Chl a preparations.

The specific growth rates (μ in doublings/day) of phytoplankton based on carbon production was estimated using the equation: $\mu = \log_2 [(POC + \Delta POC)/POC]$

where POC = phytoplankton carbon; ΔPOC = daily photosynthetic rate (Harrison et al. 1982).

To determine which nitrogen form is preferred for phytoplankton growth, a relative preference index (RPI) for nitrate was calculated as

$RPI_{NO3} = \rho(NO_3^-)/ \{\rho(NO_3^-) + \rho(NH_4^+)\}/ [NO_3^-]/ ([NO_3^-] + [NH_4^+])$,

where $\rho(NO_3^-)$ and $\rho(NH_4^+)$ represent the uptake rates and $[NO_3^-]$ and $[NH_4^+]$ are the ambient concentrations (McCarthy et al. 1977).

Salinity, temperature, and nutrient data in every productivity stations were generously provided by Dr. Fiona McLaughlin (IOS).

2.3. Results

2.3.1. Physical and chemical structures in the water column and on the ice floes

General vertical distributions of averaged salinity, temperature, and nutrients from productivity stations in the deep Canada Basin are shown in Figures 2.2 and 2.3. The salinity was low in the upper 20 m layer because of melted sea ice but increased with depth. The salinity in the mixed layer ranged from 26.32 to 32.02 ‰ with a mean of 26.96 ‰. In contrast, the mean temperature was homogeneous from –1.19 °C at the surface to –0.89 °C at the chlorophyll-maximum layer located at about 50-60 m depth. The NO_3^- was almost depleted in the upper mixed layer but the concentration increased below 30 m depth, whereas NH_4^+ had consistently low concentrations down to the chlorophyll-maximum layer. The average snow depth on the surface of ice was approximately 2 to 3 cm. The incident irradiance at the surface right below the snow-covered ice, with an average of 2.3 m thickness, was about 3 % of that radiation at the surface.

2.3.2. Distribution of phytoplankton in the water column

In general, the total phytoplankton biomass represented by chlorophyll was relatively low in the deep Canada Basin. The chlorophyll-maximum layer was prominent between 50 to 60 m at

most of the stations (Fig. 2.4). The phytoplankton biomass ranged from 0.01 to 0.07 mg Chl a m^{-3} in the surface water without ice with an average of 0.04 (± s.d. 0.02) mg Chl a m^{-3}, whereas the mean biomass at the surface below ice was 0.02 mg (± s.d. 0.01) Chl a m^{-3}. The Chl a concentration of the surface layers above 30 m between open and ice-covered waters were statistically significantly different (ANOVA, F; 4.31, p-value < $\alpha = 0.05$). In the chlorophyll-maximum layer, the biomass ranged from 0.27 to 1.08 mg Chl a m^{-3} with an average of 0.60 (± s.d. 0.31) mg Chl a m^{-3}, a value 15 times higher than the surface biomass in open waters. The average integrated chlorophyll above 55 m from all open-water stations was 7.33 (± s.d. 5.03) mg Chl a m^{-2}. Integrated chlorophyll was highest at AG05 (16.74 mg Chl a m^{-2}) in Amundsen Gulf and second highest (13.72 mg Chl a m^{-2}) at NA05 in the end of the transect. For all open-water stations, small phytoplankton (0.7 – 5 μm) represented 69.3 % (± s.d. 10.6 %) of the total phytoplankton biomass at the surface. Small phytoplankton decreased to 44.4 % with high variation (± s.d. 25.9 %) of the total biomass in the chlorophyll-maximum layer (Fig. 2.5). We speculated that relatively high biomass of large phytoplankton (>20 μm) in the layer at NA05 and NW06 stations might be affected by the Bering-Chukchi water mass (Shimada et al. 2001). In comparison, about 50 % was composed of small phytoplankton at the surface under the ice (Table 2.1).

2.3.3. Carbon uptake rate of phytoplankton in the deep Canada Basin

The vertical distribution of rates of phytoplankton primary production in open waters had a similar pattern as their respective biomass concentrations, i.e. low at surface and highest in the chlorophyll-maximum layer depth (Fig. 2.4), whereas the biomass-specific production was highest in the subsurface (about 7 m) and then decreased to the chlorophyll-maximum layer depth. The range of integrated phytoplankton production was from 3.30 to 6.03 mg C m^{-2} h^{-1} with an average of 4.56 mg C m^{-2} h^{-1} in the open water stations. In contrast, the production under ice

was much lower, ranging from 0.11 to 1.12 mg C $m^{-2} h^{-1}$ with an average of 0.47 mg C $m^{-2} h^{-1}$ which was about one order of magnitude lower than that of the open water stations. The carbon specific uptake rates above 30 m were significantly different between open and ice-covered waters (ANOVA, F; 21.3, p-value $< \alpha = 0.01$). The mean growth rate based on carbon production (in Methods) at different depths in open waters varied from 0.04 at surface to 0.19 per day in the chlorophyll-maximum layer, whereas the mean growth rate was 0.01 at the surface below ice (Table 2.1).

2.3.4. Nitrogen uptake rates

The vertical uptake rates of both nitrate and ammonium generally covaried with the carbon uptake in that their uptake rates were relatively constant and low down to about 30 m but increased to a maximum in the chlorophyll-maximum layer (Fig. 2.6). The vertically integrated nutrient uptakes at different stations ranged from 0.10 to 0.54 mg N $m^{-2} h^{-1}$ and from 0.18 to 1.37 mg N $m^{-2} h^{-1}$, respectively for NO_3 and NH_4. The mean uptake rates were 0.25 mg N $m^{-2} h^{-1}$ for nitrate and 1.02 mg N $m^{-2} h^{-1}$ for ammonium, whereas the mean nitrate and ammonium uptakes below ice were 0.01 and 0.02 mg N $m^{-2} h^{-1}$, respectively. In general, ammonium uptake was higher than nitrate uptake for all stations. A relative preference index (RPI) for nitrate was calculated to determine which nitrogen form is preferred for phytoplankton growth in the Canada Basin. If RPI_{NO3} value is less than one, it indicates a preference for ammonium. If RPI_{NO3} is greater than one, it indicates a nitrate preference (McCarthy et al. 1977). The samples from the Canada Basin showed a strong preference for ammonium with a mean of 0.35 (± s.d. 0.12).

2.4. Discussion

2.4.1. Primary production in the water column of deep Canada Basin

In general, the maximum photosynthetic rates were found between 50 and 60 m at most stations. Daily primary production rates in the open water ranged from 79 to 145 mg C m^{-2}, with a mean of 106 mg C m^{-2} in the deep Canada Basin (this was calculated using the assumption of a constant rate of primary productivity and 24 h of sunshine in the summer time). This is much lower than those estimated in the Eastern Canadian Arctic from 227-450 mg C m^{-2} (Grainger 1975; Harrison et al. 1982). However, our range of daily pelagic primary production is comparable with that from the recent study in the Canada Basin. Cota et al. (1996) found 47 to 120 mg C m^{-2} day^{-1} for the range of daily pelagic primary production. If we assume that our mean primary production rate measured is representative of the deep Canada Basin, the estimated annual carbon production for phytoplankton in water column ranged from 9.5 to 17.4 g m^{-2} with a mean of 12.7 g m^{-2}, based on 120 day growth season in the Arctic (Subba Rao and Platt 1984). Our mean annual primary production falls within the range of Cota et al. (1996) which is from 11 to 15 g m^{-2} and is comparable to 9 g m^{-2} of the water column annual carbon production in offshore (> 200 m) regions in the Arctic Ocean (Subba Rao and Platt 1984; Legendre et al. 1992). However, this production is based only on consideration of the open-water in the Canada Basin. In comparison to open-water, the primary production below ice stations was much lower in this study. The range of the daily production below ice stations was from 2.6 to 26.8 mg C m^{-2}, with a mean of 11.3 mg C m^{-2} above ca. 35 m depth. This difference is believed mainly due to low light intensity (about 3 % of surface irradiance) beneath the ice. If we assume an average 70 % minimum ice cover and 30 % open water in the Canada Basin during the summer period (Serreze et al., 2003) and our phytoplankton production estimated below ice is representative for ice-covered waters, then the daily primary production ranges from 25.5 to 62.2 mg C m^{-2}, with a mean 40 mg C m^{-2} for the open and ice-covered waters in the region. Gosselin et al (1997) reported the range of daily primary production from 9 to 73 mg C m^{-2}, with a mean 35 mg C m^{-2}

day^{-1} from the western part of the Canada Basin, which is similar to our range from the eastern part. Based on the assumption of 120 day growth season in the Arctic (Subba Rao and Platt 1984), the annual production ranges from 3 to 7.5 g C m^{-2}, with a mean 5 g C m^{-2}, when transformed in order to take into account of changes in the percentage of ice cover. This mean production value is almost half of other studies (Cota et al. 1996; Subba Rao and Platt 1984; Legendre et al. 1992). Our mean production is even much lower than annual production (around 30 g C m^{-2}) estimated from the slope in Rysgaard et al. (1999) during the 4 months-open water period. This discrepancy is mainly from the difference in the geographical locations where the productivity experiments were executed. Most of productivity data points in Rysgaard et al. (1999) (see Figure 8) are from the coastal areas without multi year ice cover. Our annual production, however, is higher than the estimations by Pautzke (1979) which were 2.1 g C m^{-2} in the southern Canada Basin in 1975 and 3.2 g C m^{-2} for the average of different areas in the Canada Basin during 1971 to 1975 because he measured only the phytoplankton production under drifting pack ice. Our annual production might be still underestimated because of a few factors. The Arctic has distinct seasonal and annual variations in the phytoplankton biomass and in the photosynthetic rate (English 1961; Pautzke 1979) as well as a diurnal cycle (Pautzke 1979). Carbon assimilation is highest in July and declines in August and September in the southern Canada Basin (Pautzke 1979). Our measurements were collected during the end of summer when phytoplankton biomass and activity are relatively low in the Canada Basin. In addition, we did not correct for DOC released from phytoplankton production in our estimates. Recent studies found a high percentage of DOC released by phytoplankton in the Canada Basin (Wheeler et al. 1996; Gosselin et al. 1997). If we assume that DOC released 50 % of the phytoplankton production in the Canada Basin (Gosselin et al. 1997), our estimated annual production would be

double. Moreover, the addition of ice algae production to our estimation would provide better insight into the total annual primary production in the region.

2.4.2. Nitrogen uptake rates and new production of phytoplankton

The average daily total nitrogen ($NO_3^- + NH_4^+$) uptake of phytoplankton was 30.54 (± s.d. 16.19) mg N m^{-2} in open waters whereas it was 0.83 (± s.d. 0.2) mg N m^{-2} below ice. Therefore, annual nitrogen uptake is about 1.17 g N m^{-2} based on the assumption of 70 % of ice cover on average in the Canada Basin during summer. Pautzke (1972) estimated that nitrogen consumption by phytoplankton was 0.45 g N m^{-2} as a mean for 3 years in the northern Canada Basin from 1971 to 1973 using carbon/nitrogen ratio conversions. This is much lower than the nitrogen uptake from this study mainly because they assessed a layer that extended only from 5 to 30 m below ice which is a much smaller euphotic zone than that used for open waters in our study.

The nutrient concentrations are nearly depleted in the upper mixed layer throughout the Arctic Ocean owing to the strong salinity driven stratification, which produces the permanent halocline (Smith and Sakshaug 1990). The physical features (temperature and salinity; Fig. 2.2) and nutrients (Fig. 2.3) in the deep Canada Basin have typical vertical distributions of the Arctic open ocean for summer months (Smith and Sakshaug 1990; Chen et al. 2003). Although some data on nutrient assimilation rates in the Arctic Ocean have suggested that the predominant nitrogen source is nitrate (McRoy et al. 1972; Hattori and Wada 1972), the average f-ratio of NO_3^- uptake/total ($NO_3^- + NH_4^+$) uptake was 0.25 (± s.d. 0.13) in this study. Cota et al. (1996) estimated that the mean f-ratio was 0.12 in the Canadian Basin and Northwind Ridge and Plain, based on an assumption of an ammonium concentration of 0.1 μM. In comparison, the f-ratios were 0.43 in Baffin Bay of the eastern Canadian Arctic during Summer (Harrison et al. 1982) and 0.65 in the Northeast Water Polynya from late May to mid-August (Smith et al. 1997). From the low f-ratio (0.25), the deep Canada Basin appears to have less nitrate available for phytoplankton

growth compared to other Arctic regions. It is noted that ammonium uptake is much higher than nitrate uptake at the depth of 50 m (in Fig. 2.6) even though concentration of nitrate is relatively high at that depth. So, an alternative speculation is that phytoplankton have a strong coupling to light for nitrate uptake and there is a known preference of ammonium rather than nitrate uptake in Fig. 2.6. Corrections for the isotope dilution effect were not applied to the measurement of ammonium uptake rates (Glibert et al. 1982) because the incubation periods were relatively short (3-7 hours) (Dugdale and Wilkerson 1986). However, this protocol might underestimate the uptake rate of ammonium in oligotrophic regions such as the offshore Arctic Ocean (Glibert et al. 1982; Dugdale and Wilkerson 1986; Smith and Sakshaug 1990). We calculated the isotope dilution effect using the equations in Kanda et al. (1987). The average of underestimation for ammonium uptake ranges from 8% to 18% for assuming a=1 and a=2 ("a" is ratio of regeneration and uptake). The f-ratio would be even lower if urea uptake were included in this calculation. If urea uptake is 30 % of total nitrogen uptake in the euphotic zone of the eastern Canadian Arctic (Harrison et al. 1985), then the f-ratio would be 0.18 in the deep Canada Basin. This f-ratio indicates that most of the nitrogen acquired for primary production is regenerated nutrients in the deep Canada Basin. Recent studies have found small plankton (0.7-5 μm) dominate the phytoplankton biomass and production in the Arctic waters (Gosselin et al. 1997; Booth and Horner 1997; Robineau et al. 1994). The small phytoplankton represented about 70 % of the total phytoplankton biomass in the upper mixed layer over all open-water stations in the Canada Basin. Their mean proportion, however, decreased to 44.4 % of the total biomass in the chlorophyll-maximum layer (Fig. 2.5), although there were high variation. The small phytoplankton appear to contribute to more active recycling within the water column than large phytoplankton, due to their slow sinking rates (Grebmeier and Barry 1991) and thus indirectly contribute to regenerated nitrogen for phytoplankton productivity in the nutrient-depleted surface water.

It is important to distinguish between the relative importance of regenerated ammonium and new nitrate as sources of nitrogen for the cell and population because the regenerated nitrogen maintains the cell in a healthy state whereas the new nitrogen increases population size or production passed on to higher trophic levels (Dugdale and Goering 1967). In general, ammonium uptake was higher than nitrate uptake over all stations in the Canada Basin based on f-ratio and RPI_{NO3}. The depleted-nutrient water in the euphotic zone suggested that nutrients are potentially limiting to phytoplankton growth. In addition, the measured particulate and assimilated C/N (Table 2.1) were greater (except the Chl a-max layer) than expected (6.6, the Redfield ratio) and provide more evidence for possible nutrient limitation in this basin (Pautzke 1979).

The average daily NO_3 uptakes of phytoplankton were 5.95 mg N m^{-2} and 0.25 mg N m^{-2} respectively for open-waters and ice-covered waters. Again, if we assumed 70 % of ice cover on average in the region, then the daily NO_3 uptake rate of phytoplankton would be 1.96 mg N m^{-2}. The annual NO_3 uptake would be 235 mg N m^{-2} based on 120 growing days. If the annual NO_3 uptake rate is converted into annual carbon production using the average assimilated C/N ratio (4.4) in the water column observed in this study, the annual new production integrated over the euphotic zone equals 1.04 g C m^{-2} which is about 20.8 % of the total annual primary production (5 g C m^{-2}) in the deep Canada Basin. This percentage is somewhat higher, but not markedly different, than that of Cota et al. (1996). They estimated the mean new production is 16.1 % in the Canadian Basin and Northwind Ridge and Plain.

2.4.3. Major environmental factors limiting phytoplankton productivity

It is difficult to determine which environmental factors control phytoplankton productivity in the Arctic Ocean. The productivity and biomass of phytoplankton, however, are mainly controlled by light and nutrients in the Arctic Ocean (Smith and Sakshaug 1990).

Therefore, we discuss only these two factors. In summer, light is not limited in the surface of open waters in the Arctic. In contrast, it seems to be a limiting factor to phytoplankton under ice-covered waters based on indirect evidence. The chlorophyll a concentration and carbon specific uptake rates are significantly different in surface layer (upper 30 m) between ice-covered and open water regimes. The most distinctive physical difference is light intensity between the two regimes (Table 2.1). The quantity of photosynthetically active radiation at the surface of the water column is markedly reduced by ice and especially snow-covered ice (Andersen 1989; Smith and Sakshaug 1990). Only ca. 3 % of surface irradiance passed through the 2-3 m thickness of ice with light snow cover (2-3 cm) in our study area. The light intensity at Chl a-max layer was about 2 % of surface light which was similar to that at the surface under ice with an average 2.3 m ice thickness. The phytoplankton activity might be limited by the low light intensity in the layer because the specific primary production [mg C (mg Chl)$^{-1}$ h^{-1}] was lowest in the Chl a-max layer (Fig. 2.4). The significant difference between the Chl a-max and the surface below ice is nutrients. Nitrate concentration is much higher in the Chl a-max layer than in surface ice-covered and open waters, although the concentration of ammonium is rather similar between two regimes. The low nitrate concentrations in the upper mixed layer of the basin in 2002 suggest that phytoplankton production may be limited by nutrients (Pautzke 1979).

The various elemental ratios of particulate material have been used as indices of growth rate and/or nutrient status of natural phytoplankton population (Yoder 1979; Goldman et al. 1979), although elemental ratios are simultaneously influenced by a number of factors such as temperature and light (Smith et al. 1995) as well as species composition (Smith and Sakshaug 1990). Assimilated carbon/nitrogen ratios can be 20 in nitrogen-depleted surface waters (Eppley et al. 1979). The mean assimilated C/N ratios at the surface were 15.9 and 13.8 respectively for open and ice-covered waters. In contrast, the mean ratio was 3.6 (± s.d. 9.1) in the Chl a-max

layer in which nutrient concentrations were relatively high. Moreover, the minimum C/Chl a ratio in the Chl a-max layer (Table 2.1) indicates that they are growing at the lower part of the optimum irradiance zone (Smith and Sakshaug 1990; Yoder 1979) with relatively low nutrient stress. The high C/Chl a ratio in the low irradiance-zone below ice is believed mainly due to a pronounced nutrient deficiency (Mikaelyan and Belyaeva 1995; Smith and Sakshaug 1990) although irradiance might also be limiting. It appears that both high irradiance and nutrient deficiency increased the C/Chl a ratio of phytoplankton at the surface in open waters. Therefore, nutrients seem to be a main limiting factor at surface, whereas light may be a major factor limiting phytoplankton productivity in the Chl a-max layer in open waters. At the surface below ice, the low specific uptake and productivity of phytoplankton indicate that photosynthetic activity might be controlled by both light and nutrients.

2.4.4. More food or less in the Arctic Ocean by the climate change in the Arctic Ocean

Direct comparison of rates of primary production between previous and recent years is rather difficult because of seasonal and annual variations in biomass and productivity of phytoplankton as well as interannual differences in areal distribution of phytoplankton. Moreover, a basic difference in the experimental methods between two different time periods makes a comparison more difficult. However, there is some indirect evidence to suggest more food is available to grazing populations in recent years than previous years. Rothrock et al. (1999) found that the mean ice thickness has decreased by about 40 % from 3.1 m in 1958-1976 to 1.8 m in the 1990s over most of the deep water areas of the Arctic Ocean at the end of the melt season. If this decrease is representative in the Arctic Ocean, it would be a tremendous change in light intensity to the phytoplankton below ice and ice algae in ice which are believed to have light limitation (Cota and Smith 1991; Rysgarrd et al. 1999; This study). We found 2-3 times higher specific carbon uptake of ice algae on the bottom of ice and phytoplankton under ice when *in situ*

productivity incubations were executed under 30 % less thickness of the first-year ice in Barrow from early May to early June, 2003 (unpublished data). If snow cover on the ice is similar between the two periods (1960s and 1990s) and light is more limited to phytoplankton productivity than nutrients at the surface in ice-covered waters in the Arctic Ocean, then the primary production would have been increased by the thinner ice thickness and larger amounts of open water.

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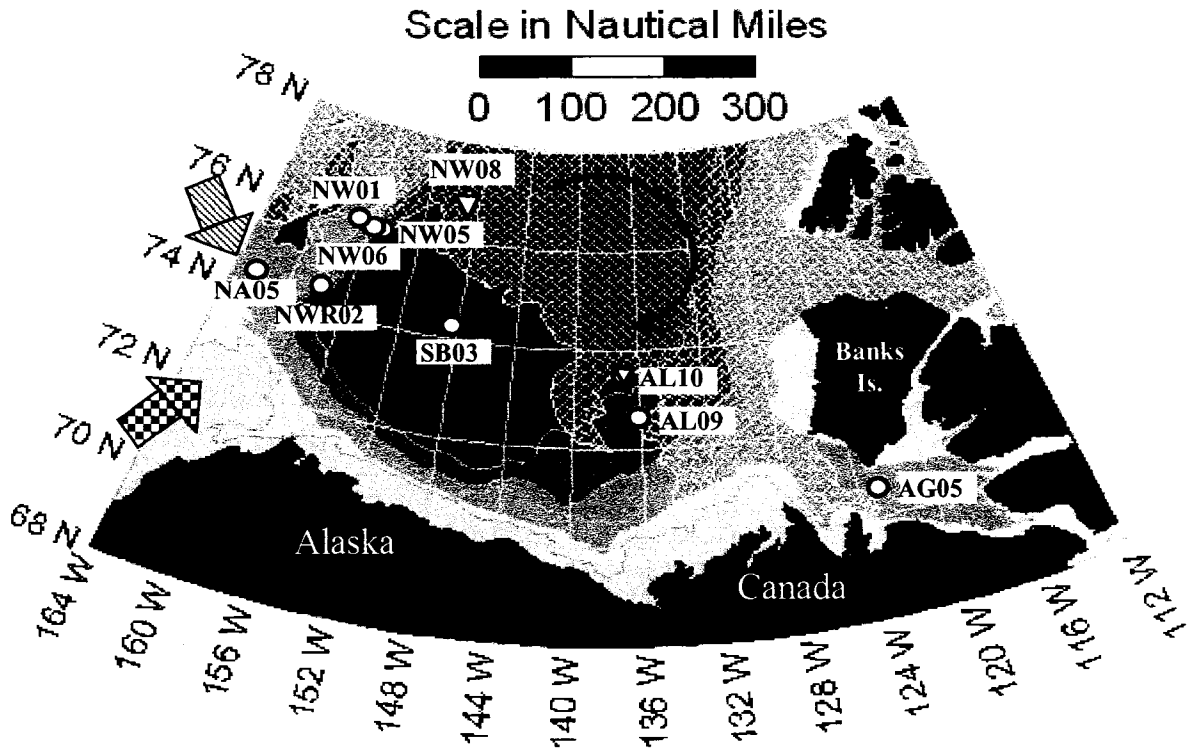

Fig. 2.1. Productivity stations in the Canada Basin during summer 2002. The circles represent water productivity stations and reversed triangles are ice productivity stations. AL10 had two ice stations and one water station and NW08 was third ice station. NW01, NA05, and NWR02 for only surface productivity experiments. White line and hatching: 8/10 ice edge, hatched arrow: Atlantic inflow, dotted arrow: Pacific inflow, black arrow: Ice motion (Map from Fiona McLaughlin, IOS).

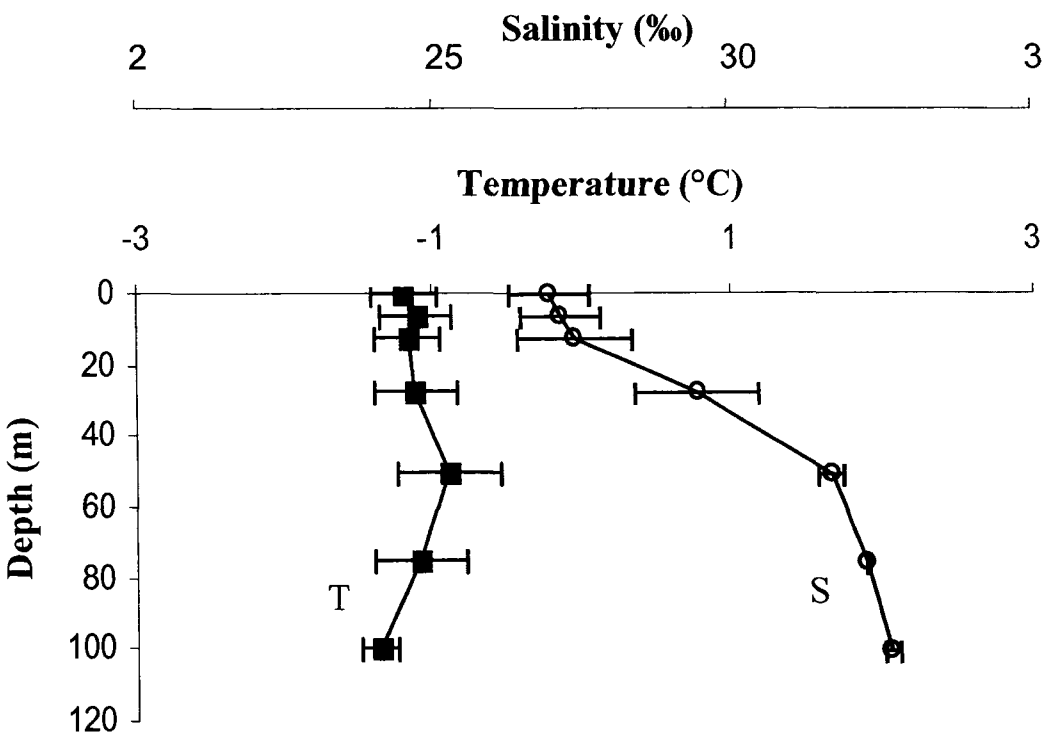

Fig. 2.2. Mean temperature and salinity distributions of the "open-water" productivity stations in the Canada Basin during summer 2002. Standard deviations are shown by bars. Data courtesy of Dr. Fiona McLaughlin (IOS).

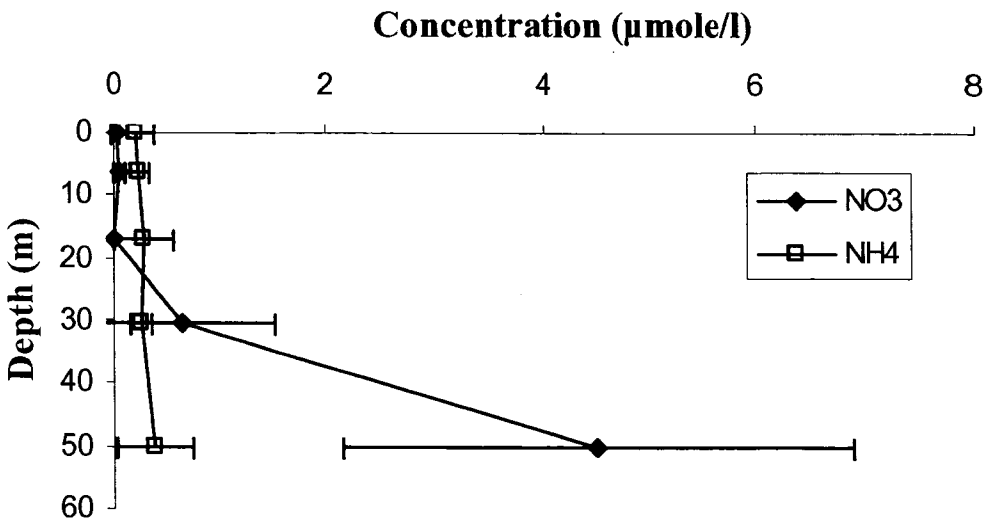

Fig. 2.3. Mean nutrient distributions in the "open-water" productivity stations of the Canada Basin during summer 2002. Standard deviations are shown by bars. Data courtesy of Dr. Fiona McLaughlin (IOS).

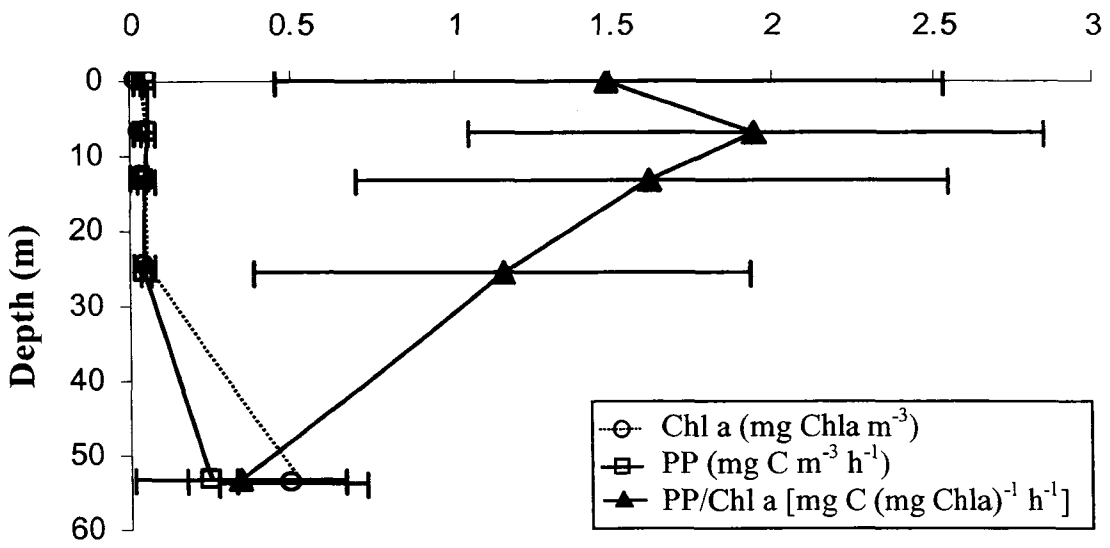

Fig. 2.4. Vertical distributions of mean Chl a, primary production (PP), and biomass-specific production (PP/Chl a) of phytoplankton in the open-water stations. Standard deviations are shown by bars.

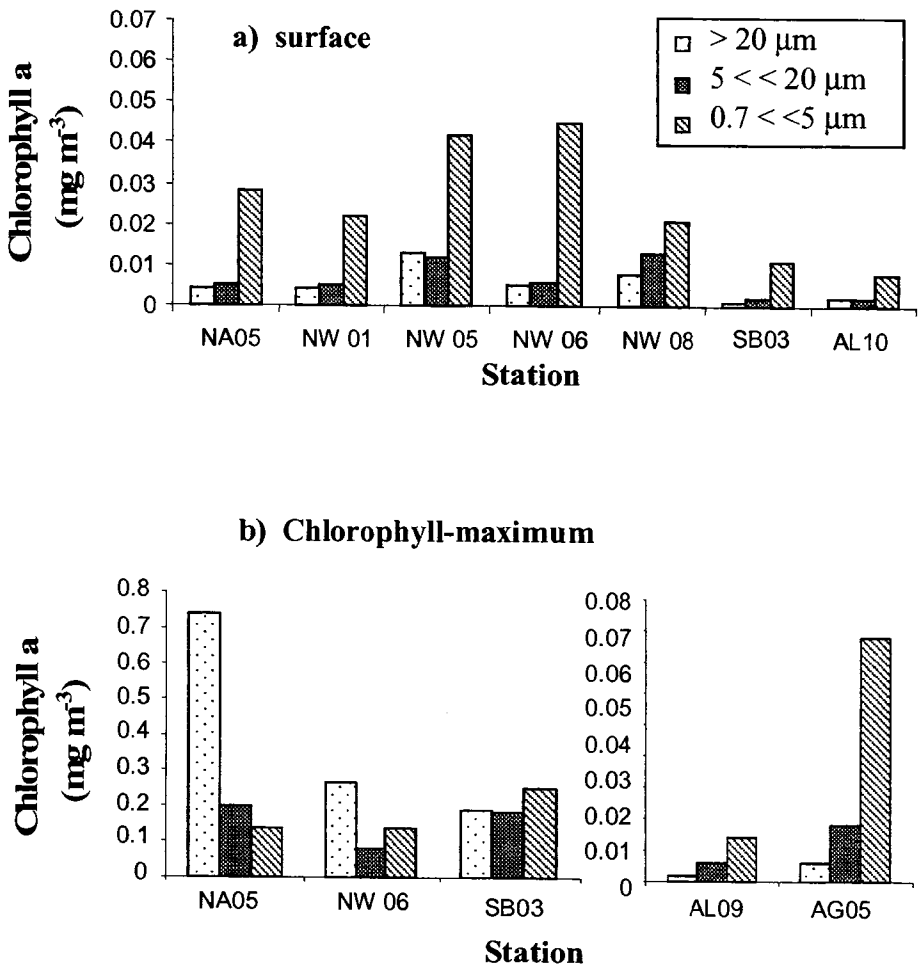

Fig. 2.5. Size-fractionated chlorophyll a; a) in the surface layer, and b) in the chlorophyll-max layer.

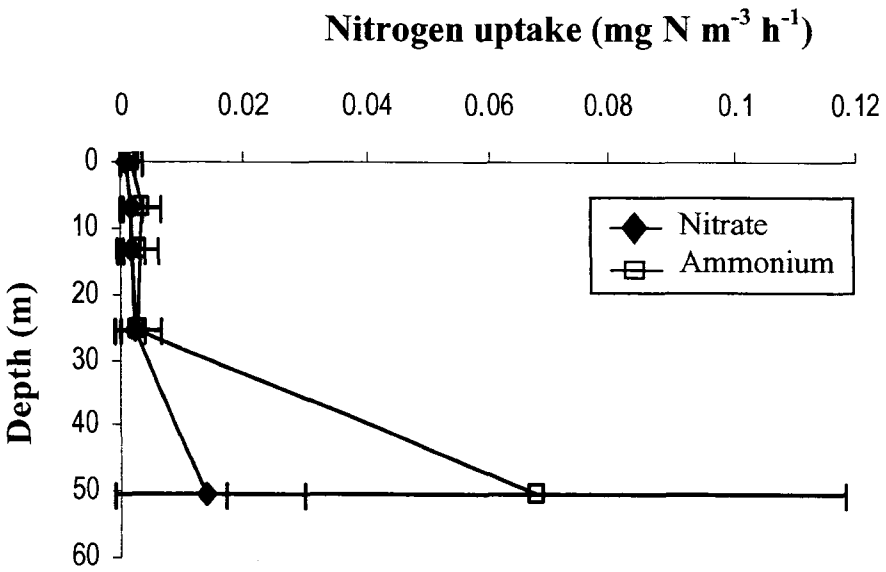

Fig. 2.6. Mean nitrate and ammonium uptake rates for the open-water productivity stations. Standard deviations are shown by bars.

Table 2.1. The comparison of different variables between the surface and chlorophyll a-maximum layer of open-water and the surface below ice at the productivity stations. SD is the standard deviation and n is the number of samples.

	Open Water						Below Ice		
	Surface			Chlorophyll-maximum layer			Surface		
	Mean	SD	n	Mean	SD	n	Mean	SD	n
Temperature (°C)	-1.19	0.22	6	-0.89	0.34	6	-0.62		1
Salinity (‰)	26.96	0.66	6	31.75	0.21	6	26.42		2
Light ($\mu E/m^2 s$)	963	364	8	19	7	8	29	17	3
Nitrate (µmole/l)	0.02	0.04	6	4.52	2.37	6	0	0	3
Ammonium (µmole/l)	0.21	0.16	6	0.40	0.36	6	0.18	0.24	2
Total Chl a (mg Chl a/m^3)	0.04	0.02	8	0.60	0.31	6	0.02	0.01	3
Biomass of large (>20 µm) phytoplankton (%)	13.6	4.9	7	33.7	28	5	21	7.6	3
Biomass of small (0.7-5 µm) phytoplankton (%)	69.3	10.6	7	44.4	26	5	49	13	3
C/N ratio (atom/atom)	8.57	2.53	8	7.86	2.53	5	10.9	0.9	3
Assimilated C/N ratio (atom/atom)	15.9	11	7	3.6	9.1	3	13.8	9.37	3
POC/Chl a (w/w)	314	216	8	16.8	11.2	5	181	25	3
PON/Chl a (w/w)	26	18	8	2.3	2.3	5	14	0.8	3
Carbon specific uptake (h^{-1})	0.000679	0.00037	9	0.0036	0.00034	3	0.000228	0.000161	3
Carbon absolute uptake (mg $C/m^3 h$)	0.040	0.027	9	0.257	0.079	3	0.0125	0.0114	3
Nitrate specific uptake (h^{-1})	0.000291	0.00023	9	0.002354	0.003081	3	0.000084	0.000054	3
Nitrate absolute uptake (mg $NO_3/m^3 h$)	0.001008	0.00118	9	0.0144	0.0153	3	0.000288	0.000209	3
Ammonium specific uptake (h^{-1})	0.001138	0.00047	9	0.006851	0.00704	3	0.000284	0.000031	3
Ammonium absolute uptake (mg $NH_4/m^3 h$)	0.001935	0.00196	7	0.068	0.0503	3	0.000766	0.000281	3
f-ratio	0.24	0.15	8	0.26	0.12	3	0.22	0.09	3
Growth rate (per day)	0.04	0.02	5	0.19	0.02	3	0.014	0.015	3

Chapter 3. Spring time ecology of sea ice algae within the sea ice and phytoplankton under the sea ice at Barrow, Alaska

Abstract

The production of sea ice algae at the ice-water interface is a food source of primary production to herbivores and might be altered by current environmental changes in the Arctic oceans. However, there have been few recent studies of ice algae ecology in the Alaskan Arctic region. *In situ* carbon and nitrogen uptake rates of phytoplankton and ice algae under the ice were measured in the land fast sea ice of Barrow, Alaska by using both ^{13}C isotope tracer and ^{13}C-^{15}N dual isotope tracer techniques. To determine which environmental factor exerts the most control of the production of ice algae and phytoplankton under the ice, light and nutrient increment experiments were executed 3 times during the growing season in 2003. The estimated new and total production rates of ice algae from the bottom ice were ~ 0.8 g C m^{-2} and ~ 2.0 g C m^{-2} respectively, while the new and total production rates of phytoplankton under the ice were ~ 0.15 g C m^{-2} and ~ 0.65 g C m^{-2}. The ice algal total production contributed 80 % of total primary production under the land fast ice at Barrow in 2003 before the phytoplankton bloom. Based on the light and nutrient enrichment experiments, the production of the bottom sea ice algae and phytoplankton at Barrow in 2003 was limited mainly by light which was about 0.3 % of the surface irradiance under the snow-covered sea ice.

3.1. Introduction

In addition to the phytoplankton, sea ice algae at the ice-water interface provide an additional source of the primary production in the Arctic Ocean (Alexander et al. 1974; Horner and Schrader 1982; Demers et al. 1986; Gosselin et al. 1997; Mock and Gradinger 1999; others therein) as well as in the Antarctic oceans (Bunt and Lee 1970; Garrison and Buck 1991; Legendre et al. 1992; Arrigo et al. 1997). Among the various types of sea ice communities, i.e., surface, interior, and bottom (Horner et al. 1992), bottom-ice communities are generally most productive in the fast ice both in the Arctic (Meguro et al. 1967; Alexander et al. 1974; Horner 1985; Smith et al. 1987) and in the Antarctic (Grossi et al. 1987; Arrigo et al. 1990). The contribution of ice algae to total primary production ranges from less than 1 % (Alexander and Chapman 1981) in the coastal regions up to around 60 % (Gosselin et al. 1997) in the central ice covered-ocean for Arctic waters. Although it appears to vary widely from region to region, the ecological impact of ice algal production is potentially important (Alexander 1980) because the ice algae bloom starts a couple of months earlier than the phytoplankton bloom in spring (Apollonio 1965; Legendre et al. 1981). Thus, it is an important food source for sympagic organisms such as amphipods as well as pelagic copepods (Bradstreet and Cross 1982).

Recently, the Arctic has been changing at a very rapid rate. Higher temperatures have decreased the ice extent and sea-ice thickness in the Arctic Ocean over the past 40 years and have produced more open water, especially in coastal regions (Maslanik et al. 1996; Martin et al. 1997; Rothrock et al. 1999; Rothrock et al. 2003). The results from Laxon et al. (2003) suggest that further thinning of Arctic sea ice will continue by increasing melt season length. These changes of climate and ice may alter the relative contributions of sea ice algae and phytoplankton, with respect to the species and/or size composition of primary producers, and the new and total production. As a consequence, the seasonal distributions, geographic ranges, and nutritional

structure of zooplankton have been projected to be altered (Tynan and DeMaster 1997). Although phytoplankton and ice algae produce the most basic food source for all the animals that live in the Arctic oceans, we still do not know if the predicted climate change will provide less or more food in Arctic regions because little is known about the physical and chemical oceanography and the ecosystem responses of this remote region. The recent reduction of ice-cover is a predominantly spring-summer phenomenon (Chapman and Walsh 1993). The change in landfast ice is by increased extent and timing of open water period. However, there have been few recent studies about ice algae in the Alaskan Arctic region. More studies of seasonal and annual production rates and physiological conditions of ice algae and phytoplankton are needed for better understanding the impacts of current and future climate changes on the marine ecosystems in the Arctic communities.

There have been many studies on determining which factors control the production of ice microalgae both in the Arctic and in the Antarctic oceans. A number of factors limit the primary production of phytoplankton in the water column or ice algae within sea ice in the Arctic Ocean. It is difficult to determine the specific environmental factors which control the primary production. However, the production and biomass of phytoplankton or ice algae are mainly controlled by light and nutrients in the Arctic Ocean (Smith and Sakshaug 1990) like other oceans. Some studies suggest that light is a major factor influencing the production of bottom-ice communities in polar oceans (Clasby et al. 1976; Horner and Schrader 1982; Horner 1985; Grossi et al. 1987; SooHoo et al. 1987; Cota and Smith 1991) because of low light intensities that are transmitted through the snow covered sea ice. Less than 2-3 % of the incident irradiation at surface reaches the bottom of the ice (Irwin 1990; Mock and Gradinger 1999; Lee and Whitledge 2005). In contrast, some studies show evidence that the production of ice algae is mainly limited by major macro nutrients such as nitrate and silicate since the production is stimulated by the

addition of nutrients or/and biochemical characteristics and physiological status of ice algae are suggestive of nutrient-limited condition (Demers et al. 1989; Gosselin et al. 1990; Smith et al. 1997). These contrasting reports might be due to regional differences or/and the stage of algae development (Taguchi and Smith, 1997). For example, Gosselin et al. (1990) showed that light was the main limiting factor at the beginning of the growth season and nutrients became limited in later stages. Determining which is a principal factor for the primary production is important to predict how current climate changes in the Arctic Ocean will affect the carbon transport in the marine ecosystems of the Arctic.

The primary objective of this study was to determine which environmental factor exerts the most control on the production rates of ice algae in the bottom layer of sea ice and phytoplankton under the ice to decide the effects of current and future climate changing (especially changes in sea ice thickness) on the total primary production in the Arctic Ocean. The second objective was to evaluate possible changes in physiological condition of sea ice algae under different ice thickness and through the growing season by determining carbon allocation into different macromolecules as photosynthetic end-products.

3.2. Study area

The sampling sites on the sea ice were located approximately 1.0 km offshore from the Naval Arctic Research Laboratory, Barrow, Alaska (Fig. 3.1). The sites were located approximately mid way between the shore and the active pressure ridge. The surface of the sea ice was rather smooth and the water depth at the sampling sites was approximately 4-5 m below the ice. The fast sea ice attached to the coastal land is formed every year. New sea ice usually begins to form in lagoons and shallow protected areas during cold weather in October to early November, and the ice cover grows at a relatively rapid rate (up to 2-3 cm per day depending on

the surface temperature conditions) and gradually slows its growth rate throughout the winter season (Maykut 1985). Sea ice growth in the adjacent coastal ocean is frequently interrupted by strong wind events that blow landfast ice away from the shore. In 2003, all the land fast sea ice around the Naval Arctic Research Laboratory retreated during storms in the middle of December and came back in the late of December and started to grow again. Undeformed first-year ice during the month of December can be of any thickness up to about 1 meter, depending on how long it has been in place and freezing (Richard Glenn, pers. comm.). The ice was about 80 cm thick in the middle of February in 2003. The ice thickness was maximum at around 140 cm in the middle of May and remained so until melt ponds started to form with these refreezing in early June in 2003. In 2004, ice conditions were different from 2003. The ice was 135 and 175 cm respectively in the early March and May in 2004. The land fast ice gradually breaks up by mid-July (Alexander et al. 1974). Currents in this coastal area vary seasonally and the current speed estimated by Alexander et al. (1974) was between 0.5 and 4 knots in summer during ice free periods.

3.3. Materials and methods

Sampling on the fast sea ice at Barrow was done 6 times (12-16 February, 1-6 April, 28 April-1 May, 20-22 May, 27-30 May, and 9-11 June) in 2003 and 2 times (2-4 March and 2-4 May) in 2004. Chlorophyll-a data of phytoplankton and ice algae in 2002 from Dr. Shin (pers. comm., IARC, UAF) were used for comparison.

3.3.1. Temperature and salinity

Temperature and salinity were measured by a portable conductivity meter through the water column under the ice. After a sea ice core was obtained by the ice corer, the ice thickness was measured by a ruler. Next, small holes (diameter = ~ 0.5 cm) for the temperature sensor were

drilled every 10 cm apart from the bottom to the top of the ice. After the temperature measurements, the ice cores were cut off at every 10 cm length (except the bottom 10 cm sections of ice cores which were cut off with 3 cm long bottom and 7 cm section) for bulk salinity, chlorophyll-a and nutrient measurements later in the lab. The ice core sections were stored in dark containers and brought back to the laboratory after the daily sampling was completed on the land fast ice. The samples were thawed in the dark at room temperature. Usually, it took 24 to 36 hrs for the ice cores to thaw completely, which might affect concentrations of chlorophyll-a and inorganic nutrients. After melting was complete, sample aliquots for salinity as well as chlorophyll-a and inorganic nutrients were collected.

3.3.2. Carbon and nitrogen uptake rates

3.3.2.1. Water column productivity under the sea ice

The water was collected by lowering a small water sampler through the ice hole diameter = ~ 9 or 25 cm) down to approximately 2 m water depth under the ice. When the water was distributed into each incubation bottle, we did not use the screened tube for eliminating large zooplankton from the water since the air temperature was so cold that the water froze in the tubing.

Carbon and nitrogen uptake rates were obtained by using both ^{13}C stable tracer and ^{13}C-^{15}N dual stable tracer techniques in 600 ml incubation bottles. Water samples were inoculated with labeled carbon ($NaH^{13}CO_3$) in all the ^{13}C bottles, nitrate ($K^{15}NO_3$) in the $^{15}NO_3 + {}^{13}C$ bottles and ammonium ($^{15}NH_4Cl$) in the $^{15}NH_4 + {}^{13}C$ bottles. After the inoculation of isotopes, three incubation water bottles for each different treatment (^{13}C, $^{15}NO_3 + {}^{13}C$, and $^{15}NH_4 + {}^{13}C$) were tied to an anchor rope with a weight at the bottom and then lowered to three depths (0.5 m, 1.5 m, and 3.5 m from the bottom of the ice) for water column productivity. The incubation ice holes were covered by 3 layers of ice cubes to prevent light transmission through the holes. The samples

were kept at *in situ* temperature and light for 3-4 hrs, retrieved and brought to the lab in a dark insulated box for filtration. The waters of the same isotope treatments from 3 different water depths were mixed well and distributed for total (0.7 μm Whatman GF/F) and size-fractionated (0.7 μm Whatman GF/F and 5 μm Nucleopore) carbon and nitrogen uptake rates. The filters were immediately frozen and preserved for mass spectrometric analysis at the stable isotope laboratory of the University of Alaska Fairbanks. Particulate organic carbon and nitrogen and abundance of ^{13}C and ^{15}N were determined in the Finnigan Delta+XL mass spectrometer after HCl fuming overnight to remove carbonate. Corrections for the isotope dilution effect were not applied to the measurement of ammonium uptake rates (Glibert et al. 1982) because the incubation periods were relatively short (3-4 hours) (Dugdale and Wilkerson 1986). Only for the carbon uptake rates dark uptake rates were subtracted (Li et al. 1993) and then carbon and nitrogen uptake rates were averaged from several identical experiments.

3.3.2.2. Carbon and nitrogen uptake rates of ice algae.

The ice cores were obtained by SIPRE ice corers and the lengths of ice cores were measured. Only 3 cm long sections from several core bottoms (presumed to have most biomass of ice algae) were placed in the productivity bottles (500 ml) inoculated with ^{13}C, $^{15}NO_3$ and $^{15}NH_4$ and filled with filtered seawater (GF/F). After the inoculation of carbon and nitrogen isotopes, the incubation bottles for each different treatment (^{13}C, $^{15}NO_3 + ^{13}C$, and $^{15}NH_4 + ^{13}C$) were tied to an anchor rope with a weight at the bottom and then lowered to the bottom edge of the ice (Fig. 3.2). The incubation holes were covered by 3 layers of ice cubes on top of the holes to prevent light penetration through the ice holes. The samples were kept at its in situ temperature and light for 3-4 hrs, retrieved and brought to the lab in a dark insulated box for filtration. When a brownish color was observed on the bottom of the ice, indicating high biomass of ice algae, each treatment bottle was mixed well and distributed into two filteration sets which were for total (0.7 μm

Whatman GF/F) and size-fractionated (0.7 μm Whatman GF/F and 5 μm Nucleopore) carbon and nitrogen uptake rates. The procedure on handling filters for determining ^{13}C and ^{15}N uptakes of ice algae is identical to those of filters from the water column productivity (previous section 3.4.2.1).

3.3.3. Inorganic nutrient analysis

The water samples from each 1 m water depth in water column (from 0 to 4 m under the ice) were obtained by a small water sampler and frozen until analysis. For nutrients in ice, ice cores were obtained by SIPRE corers and each 10 cm section (except bottom 10 cm which was cut off by 3 and 7 cm length) of 2-3 ice cores was cut off and melted in the dark at room temperature for around 24 hours. Once completely melted, they were mixed and divided for nutrients and chlorophyll-a. The water for nutrient analysis was frozen for the determination of the concentrations of inorganic nutrients (nitrate, silicate, phosphate, ammonium, and nitrite) using an automated nutrient analyzer (ALPKEM) in the laboratory following methods of Whitledge et al. (1981).

3.3.4. Chlorophyll-a analysis for phytoplankton and ice algae

Samples for the determination of total chlorophyll-a concentrations were filtered onto Whatman GF/F filters (24 mm). Size-fractionated chlorophyll-a concentrations were determined on samples passed sequentially through 20 and 5 μm Nucleopore and 0.7 μm Whatman GF/F filters (diameter = 47 mm). The filters were frozen and returned to the laboratory for analysis. The filters were subsequently extracted in a 3:2 mixture of 90 % Acetone and DMSO (Webb et al. 1992) for 24 hours, and centrifuged based on Parsons et al. (1984). Concentrations of chlorophyll-a were measured using a Turner Designs model 10-AU fluorometer which had been calibrated with commercially purified chlorophyll-a preparations. After measuring chlorophyll-a, 100 μl of 10 % HCl solution was added into the extracted solution and stored in a test tube rack

for about 90 seconds to degrade chlorophyll-a into phaeopigments. A final fluorescence reading was taken after the acidification. The methods and calculations for chlorophyll-a and phaeopigments were based on Parsons et al. (1984).

3.3.5. Light increment experiments under different light intensities

The ice algae from the bottom of the ice were obtained by SIPRE corers and sometimes an auger. When holes were drilled using the auger, sometimes broken brown bottom pieces came up on top of the snow or floated in the ice holes. Those bottom pieces were easily discriminated from the sediment-trapped layer in the ice. These pieces were used for productivity experiments under different light intensities since large amounts of ice algae in the bottom of the ice were needed for the different experiments. After filling the sample bottles with measured filtered seawater and inoculating with isotopes (^{13}C and $^{15}NO_3$), another set of bottles for phytoplankton productivity was filled up with water from 2 m water depth under the ice. Two sets of bottles for ice algae and phytoplankton were tied to each anchor line and deployed into the different depths (0.1, 0.5, 1, 1.5, and 4.5 m from the surface of the ice; Fig. 3.3). The different depths of the ice holes provided a natural screen for controlling light intensity. The light intensity through the ice holes was measured for each experiment with a LICOR 4π light sensor and a surface radiation reference (LI-1400). Because ice algae biomass in the melted water of ice productivity bottles was so high, only 10 ml from each bottle was filtered for carbon and nitrogen uptake rates and the rest of the water was filtered for photosynthetic carbon allocation of ice algae under different light intensities. For comparison, α^B (photosynthetic efficiency) and I_k (half saturation constant of light) from the light enhancement experiments were calculated using the equation of the light saturation curve of photosynthesis (Platt et al. 1980) in Figs. 3.19. and 3.20. Some data points at the highest light intensities (at 0.1 m of ice hole depths) from the experiments were excluded for

the regression because there was only one data point and it was not strongly representative for the photoadaptation in the regression.

3.3.6. Nutrient enrichment experiments

To determine effects of varying concentration of ammonium and nitrate on carbon uptake rates of phytoplankton in the water column and ice algae from the bottom of the ice, *in situ* productivity incubations were executed on 28 April, 20 May, and 9 June in 2003. The bottom ice with ice algae was obtained by the auger and/or ice corer. The brown bottom ice filled about one fifth of each productivity bottle and the filtered seawater was used to fill the remaining bottles. The waters for phytoplankton in the water column were taken from the 2 m water depth under the ice. When all productivity bottles were ready, different amounts of concentrated NO_3 solution (10 μmole/ml) were added into 6 productivity bottles for ice algae and 6 bottles for phytoplankton productivity. Different amounts of concentrated NH_4 (5 μmole/ml) were added into another set of bottles for ice algae and phytoplankton productivities. Once all bottles were enriched with inorganic NO_3 or NH_4, ^{13}C isotope tracer was inoculated into the bottles. After the water in each bottle was well mixed, approximately 20 ml water from each bottle was taken for nutrient concentrations before the incubation started and then all the bottles for ice algae were deployed below the ice and the bottles for phytoplankton were deployed at about 2 m water depth below the ice (Fig. 3.4). After 3-5 hrs incubation, the amount of water from each bottle was measured and another 20 ml water was taken for nutrient concentration after the incubation. The rest of the water was filtered for carbon uptake rates.

3.3.7. Photosynthetic carbon allocation in ice algae community

To evaluate the changes in the photosynthetic carbon allocation of ice algae community through the season, the incubations for the macromolecular classes were executed under the ice at 3 different times in 2003. Moreover, ice algae were incubated under different light conditions

on 28 April in 2003. The ^{13}C enrichment was ~ 15 % of the total inorganic carbon in the ambient water. The incubations were terminated by the filtration through pre-combusted (450 °C) GF/F glass fiber filters (diameter = 47 mm) after 4-5 hours depending on weather conditions. The filters were immediately frozen and preserved for analysis in the lab. The differential extraction of macromolecular classes (Low-molecular-weight metabolites, lipids, proteins, and polysaccharides) was performed using the method in Li et al. (1980). The filters with particulate material were cut into small pieces and transferred into test tubes. Three ml of chloroform-methanol (2:1 v/v) were added to the test tube and ultrasonified for 20-30 minutes to extract lipids and LMWM from the ice algae on the filters. After the extraction, the suspension was collected by a Pasteur pipette and stored in a new test tube. The procedure for the extraction was repeated three times. When the extractions were completed, 1.5 ml distilled water was added to the solution in the tube. The mixture was shaken vigorously 3 or 4 times for 2-3 minutes each time and set up for separation of the chloroform phase for lipids and the methanol-water phase for LMWM. The filters were re-suspended in 4 ml of 5 % TCA (trichloroacetic acid) and heated at 95 °C for 20-30 minutes. The suspension was collected for polysaccharides (TCA-soluble) with a Pasteur pipette. The filters with a further 4 ml of 5 % TCA were heated one more time, washed with 5 % TCA solution, and saved for proteins (TCA-insoluble). Abundances of ^{13}C for different macromolecular classes were determined in the Finnigan Delta+XL mass spectrometer, UAF.

3.4. Results

3.4.1. Environmental factors

3.4.1.1. Light intensity

The light intensity through the ice hole (diameter = 9 cm) decreased rapidly from the surface to the 10 cm depth of the ice hole. The mean light level at the 10 cm depth was 13.8 % (S.D. = ± 4.2 %) of the incident light at the surface from 28 April to 9 June in 2003 (Fig. 3.5). Most light was attenuated through the ice (mean thickness ± S.D. = 145 cm ± 11 cm; Table 3.1) with snow cover (mean snow depth ± S.D. = 11.2 cm ± 8.3 cm; Table 3.1). Under the ice, the light intensity in the water column was still slowly decreasing with depth. The light beneath the ice was about 0.3 % of the surface irradiation. This is much lower than the value (about 3 %) of the late summer in the deep Canada basin in 2002 even though the mean ice thickness was higher in the deep basin (Lee and Whitledge 2005; 2.3 m). There are several reasons for less light intensity at Barrow, including different times of year for measurements, higher biomass of algae within ice, and thicker snow cover.

3.4.1.2 Temperature

The temperature distribution in the water column was similar from the 28 April to 9 June, 2003 (Fig. 3.6). The temperatures, however, of the water surface were colder in April and May than in June and the water surface temperature above 2 m depth on 9 June was somewhat colder than below 2 m depth probably because of the melting ice at the surface in this time. The temperature distribution in the ice cores was more variable than that in the water column but the range was not wide. The temperature in the ice cores tended to increase with time except the bottom sections of the ice cores on 20 May. The temperature in the bottom parts of the ice cores was nearly constant at ~ – 1.6 °C during the observation period in 2003 (Table 3.1).

3.4.1.3. Salinity

The salinity distributions within the sea ice and in the water column are presented in Fig. 3.7. Since the water column was shallow and well mixed, the salinity under the ice was homogeneous from the surface to the bottom except the upper 0.5 m water in June, 2003 probably

because of the melting ice. The salinity of the water column decreased from April to June, 2003. Generally, the bulk salinities were higher at the top and the bottom of the ice cores except on 9 June when the snow cover was melted and then frozen on the top of the sea ice. The salinity of the bottom ice cores decreased from April to June in 2003.

3.4.2. Inorganic nutrient concentration

3.4.2.1. Water column

Since the water under the ice was well mixed, the concentration of nutrients was essentially constant in the water column from the surface to the bottom (4 m) at Barrow during the observation period in 2003 (Fig. 3.8). The concentration of SiO_4 at 2 m in the water started to increase as the biomass increased and then decreased after late May. The NO_3 concentration in the water was around 8.4 μmole/l in early April which was identical to that of the early November, 2001 (Shin, IARC, unpublished), suggesting no major uptake by phytoplankton in the water column. There was a slight decrease in the nitrate concentration from early April to late May and then it decreased to 2.2 μmole/l in early June. The NH_4 concentration was 0.5 μmole/l on 1 April and increased until 28 April in 2003 when the biomass of ice algae was highest. After 28 April, it decreased until 9 June. The concentration of PO_4 ranged from 1 to 1.5 μmole/l through the water column but was < 0.5 μmole/l on 9 June.

3.4.2.2. Ice cores

Fig. 3.9 shows the distributions of inorganic nutrients in the ice cores during the observation period from 1 April to 9 June in 2003. On 1 and 28 April, the nitrate concentrations in the ice cores decreased from the top of ice cores toward the bottom and then increased rapidly in the bottom (3cm). By 20 May, nitrate was nearly depleted in the ice cores except in the bottom 3 cm. The nitrate concentration in the bottom remained high (> 3 μmole/l) until 27 May and then decreased to as low as 0.33 μmole/l on 9 June when the sea ice deteriorated. In comparison to

NO_3, NH_4 concentrations were somewhat constant (0-2.5 μmole/l) from the top to the bottom 20 cm of the ice cores during the observation period. The concentrations (1-2.5 μmole/l) within ice cores on 1 and 28 April were higher than those on other periods except in the bottom 20 cm of the ice which had the highest concentrations (> 10 μmole/l) on 27 May and 9 June. The concentration in the bottom 3 cm had an increasing pattern from early spring (3.2 μmole/l) to late spring (> 10 μmole/l) probably caused by high grazing pressure (Horner 1985). Unlike nitrate, NH_4 in the bottom 3 cm was not depleted in any time period. Generally, SiO_4 was not depleted in the ice except the middle part of the ice cores on 20 May and 9 June. PO_4 was generally depleted in the ice cores except the bottom. On 9 June, PO_4 was depleted in the whole section of ice cores even including the bottom section.

3.4.3. Chlorophyll-a concentrations of phytoplankton and ice algae

A relatively high chlorophyll-a concentration of phytoplankton was observed during the ice algae bloom period in 2002, while the chlorophyll-a concentration in the water column under the ice remained low (< 1 μg chl-a l^{-1}) until June, 2003 although the concentrations increased from February to June (Fig. 3.10). In contrast to the water column, the chlorophyll-a concentration in the ice, mostly in the bottom 3 cm part of the ice, increased rapidly before 1 April in 2003 (Fig. 3.11). The chlorophyll-a concentrations of ice algae within the ice were 2.1 μg l^{-1} on 12 February, 126.4 μg l^{-1} on 1 April, 907.8 μg l^{-1} on 28 April, 177.5 μg l^{-1} on 20 May, 561.6 μg l^{-1} on 27 May and 63.9 μg l^{-1} on 9 June in 2003. The concentrations in 2004 were 4.9 μg l^{-1} on 2 March and 31.3 μg l^{-1} on 2 May. More than 95 % chlorophyll-a of ice algae was concentrated in the bottom 3 cm of the ice for April and May and 65 % was in the bottom 3 cm on 9 June in 2003, whereas only 9 % and 74 % were concentrated in the bottom 3 cm of the ice on 2 March and 2 May in 2004, respectively (Fig. 3.12). Large cells (> 5 μm) of phytoplankton in the water

column beneath the ice contributed about 80 % and 50 % of the chlorophyll-a concentrations in 2003 and 2004 respectively (Fig. 3.13). In comparison to phytoplankton, ice algae from the bottom of the ice was mostly composed of large cells (> 5 μm) which represented about 97 % of the total chlorophyll biomass both in 2003 and 2004. In detail, large cells of ice algae > 20 μm comprised about 76 %, middle sized cells (< 20 μm and > 5 μm) contributed 21 %, and small cells (< 5 μm and > 0.7 μm) made up 3 % of the total chlorophyll-a concentrations of ice algae in the bottom ice.

3.4.4. Phaeopigments

The chlorophyll-a/phaeopigments ratio of phytoplankton in the water column kept increasing as the chlorophyll-a concentration of phytoplankton increased except on 20 May when the snow depth on the top of the ice was 10-20 cm. The chlorophyll-a/phaeopigments ratio of the ice algae increased substantially from February to 1 April in 2003 (Fig. 3.14). It is interesting that the ratio increased slightly from 1 April to 28 April even though the biomass of ice algae was maximal during the time. This suggests the presence of increased proportions of senescent algae (Michel et al. 1996). After the first peak of the chlorophyll-a concentration of ice algae on 28 April, the ratio decreased on 20 May and then increased on 27 May. The chlorophyll-a/phaeopigments of ice algal community decreased again at the end of season in 2003.

3.4.5. Carbon uptake rates of phytoplankton and ice algae

Results of the carbon uptake rates of phytoplankton are shown in Fig. 3.15. The uptake rate of phytoplankton in 2003 was 0.01 mg C m^{-2} hr^{-1} on 12 February and increased through time to 0.61 mg C m^{-2} hr^{-1} on 9 June at the end of the season probably in response to increased light. The mean uptake rate of phytoplankton was 0.24 mg C m^{-2} hr^{-1} (S.D. = ± 0.27 mg C m^{-2} hr^{-1}) in 2003. In contrast, the carbon uptake of ice algae was bimodal in 2003. The first peak on 28 April at 0.68 mg C m^{-2} hr^{-1} decreased to 0.09 mg C m^{-2} hr^{-1} on 20 May and increased to the highest

point, 3.51 mg C m^{-2} hr^{-1}, on 27 May then dropped to 0.16 mg C m^{-2} hr^{-1} on 9 June when the ice started to decay. There were many melt ponds on the top of the ice around the sampling location, and they were partially frozen because of a sudden decrease of temperature and there was still 2-5 cm depth of snow on the ice on 9 June 2003. The mean uptake rate of ice algae from the bottom of the ice was 0.75 mg C m^{-2} hr^{-1} with S.D. = ± 1.38 mg C m^{-2} hr^{-1}.

The assimilation ratio of total production (P_T): total biomass (B_T) of phytoplankton increased from 1 April to 27 May and then decreased, while the ratio of ice algae remained low until 20 May and increased rapidly from 20 May to 27 May in 2003 (Fig. 3.16). The assimilation ratio of phytoplankton ranged from 0.04 to 0.26 mg C mg^{-1} Chl-a^{-1} hr^{-1}, whereas the ratio of ice algae was generally lower than that of phytoplankton, ranging from 0.01 to 0.21 mg C mg^{-1} Chl-a^{-1} hr^{-1}. For phytoplankton and ice algae, the mean values were 0.13 (S.D.= ± 0.08) and 0.08 (S.D. = ± 0.08) mg C mg^{-1} Chl-a^{-1} hr^{-1}, respectively but they were not significantly different.

For size-fractionated photosynthetic efficiency, the ratio of large (> 5 μm) phytoplankton ranged from 0.03 to 0.24 mg C mg^{-1} Chl-a^{-1} hr^{-1} with a mean ± S.D.; 0.14 ± 0.09 mg C mg^{-1} Chl-a^{-1} hr^{-1}, whereas the ratio of small (< 5 μm) phytoplankton ranged from < 0.01 to 0.28 mg C mg^{-1} Chl-a^{-1} hr^{-1} with a mean ± S.D.; 0.09 ± 0.11 mg C mg^{-1} Chl-a^{-1} hr^{-1}. In comparison to phytoplankton, the ratios for large ice algae between 0.02 and 0.22 mg C mg^{-1} Chl-a^{-1} hr^{-1} (mean ± S.D. = 0.10 ± 0.10 mg C mg^{-1} Chl-a^{-1} hr^{-1}) were greater than those for small ice algae from 0.01 to 0.09 mg C mg^{-1} Chl-a^{-1} hr^{-1} (mean ± S.D. = 0.03 ± 0.04 mg C mg^{-1} Chl-a^{-1} hr^{-1}), although they were statistically insignificant. The B_L:B_T vs. P_L:P_T relationship of phytoplankton and ice algae was presented in Fig. 3.17. The relative contribution of large (> 5 μm) phytoplankton (P_L) to total primary production (P_T) (mean P_L: P_T ± S.D. = 0.83 ± 0.19) was slightly higher than the contribution of large cell biomass (B_L) to total biomass (B_T) (mean B_L:B_T ratio ± S.D. = 0.78 ±

0.19). Ice algae also had a little higher P_L: P_T ratio (mean ± S.D. = 0.99 ± 0.004) than B_L:B_T ratio (mean ± S.D. = 0.97 ± 0.01). However, there was no significant difference in P_L: P_T ratio between phytoplankton and ice algae.

3.4.6. Nitrogen uptake rates of phytoplankton and ice algae

Results of the ammonium and nitrate uptake experiments in 2003 are shown in Table 3.2. The nitrate uptake rate of phytoplankton in the water column ranged from 0.01 mg N m^{-2} hr^{-1} on 1 April to 0.05 mg N m^{-2} hr^{-1} on 9 June with a mean of 0.02 mg N m^{-2} hr^{-1} (S.D. = ± 0.02 mg N m^{-2} hr^{-1}) and the ammonium uptake rate was from 0.02 to 0.10 mg N m^{-2} hr^{-1} (mean ± S.D. = 0.05 ± 0.03 mg N m^{-2} hr^{-1}) between April and June in 2003. In comparison, the nitrate uptake rate of ice algae ranged from < 0.01 to 0.23 mg N m^{-2} hr^{-1} with an average of 0.08 mg N m^{-2} hr^{-1} (S.D. = ± 0.10 mg N m^{-2} hr^{-1}) and the ammonium uptake rate was from 0.01 to 0.27 mg N m^{-2} hr^{-1} (mean ± S.D. = 0.10 ± 0.11 mg N m^{-2} hr^{-1}) during the same period. The uptake rates of total nitrogen (nitrate and ammonium) (Fig. 3.18) covaried with the carbon uptake rates of phytoplankton and ice algae (Fig. 3.15). The total nitrogen uptake rate of phytoplankton ranged from 0.02 mg N m^{-2} hr^{-1} on 1 April to 0.15 mg N m^{-2} hr^{-1} on 9 June. The mean nitrogen uptake of phytoplankton was 0.07 mg N m^{-2} hr^{-1} with S.D. = ± 0.05 mg N m^{-2} hr^{-1}. The total nitrogen uptake rate of ice algae was bimodally distributed, similar to the carbon uptake rate for ice algae from 1 April to 9 June in 2003. The first peak on 28 April at 0.29 mg N m^{-2} hr^{-1} decreased to 0.07 mg N m^{-2} hr^{-1} on 20 May and increased to the highest point 0.46 mg N m^{-2} hr^{-1} and then dropping to 0.02 mg N m^{-2} hr^{-1} on 9 June at the end of the season. The averaged nitrogen uptake of ice algae over the observation period was 0.17 mg N m^{-2} hr^{-1} with S.D. = ± 0.21 mg N m^{-2} hr^{-1}.

3.4.7. Light increment experiments

3.4.7.1. Carbon uptake rates

To determine how light penetrating different ice thickness affects the carbon uptake rates of phytoplankton and ice algae, *in situ* productivity incubations were executed under different light intensities by putting the incubation bottles at the different depths (0.1, 0.5, 1, 1.5, and 4.5 m) beneath the surface of the ice holes (Fig. 3.3). A few cm bottom parts of ice cores which had most of ice algae in were broken into small pieces to be distributed into 5 different incubation bottles. Phytoplankton was collected from 2 m water depth under the ice and distributed into 5 bottles for comparison. As expected, the uptake rates increased as the incubation depth decreased through the ice hole and consequently light intensity increased. The uptake rates of ice algae peaked at 99 μE m^{-2} s^{-1} on 28 April, 57 μE m^{-2} s^{-1} on 20 May, and 133 μE m^{-2} s^{-1} on June in 2003 (Fig. 3.19). After the peaks, the uptake rates were decreased probably due to the light inhibition. As a comparison, the uptake rates of phytoplankton followed similar patterns as those of ice algae except in June when the phytoplankton uptake rate kept increasing as light increased up to 338 μE m^{-2} s^{-1}. Since the light intensities at the different ice depths were measured one time around at noon each time of the incubations, the light intensities should be considered when they are compared with those from other studies. However, the ranges of α^B and I_k of phytoplankton and ice algae (in Fig. 3.19) were comparable with those from other studies in the Arctic Ocean (Cota and Smith 1991; Johnsen and Hegseth 1991; Rey 1990).

3.4.7.2. Nitrate uptake rates

The nitrate uptake rates of phytoplankton and ice algae generally increased as light intensity increased until light inhibitions (Fig. 3.20). The uptake rate of ice algae peaked at 4 μE m^{-2} s^{-1} on 28 April, 57 μE m^{-2} s^{-1} on 20 May, and 35 μE m^{-2} s^{-1} on 9 June, 2003. As a comparison, the nitrate uptake rate of phytoplankton at the same time peaked at 99 μE m^{-2} s^{-1} on 28 April, 57 μE m^{-2} s^{-1} on 20 May, and 133 μE m^{-2} s^{-1} on 9 June. The peak of nitrate specific uptake rate for ice algae was 2-3 times higher than that of phytoplankton for the 3 observation periods.

3.4.8. Nutrient enrichment experiments

To determine the effects of varying concentrations of ammonium and nitrate on carbon uptake rates of phytoplankton in the water column and ice algae from the bottom of the ice (Fig. 3.4), *in situ* productivity incubations were conducted on 28 April, 20 May, and 9 June in 2003. In general, there were decreases in carbon specific uptake rates of phytoplankton and ice algae after additions of nutrients, although p values were low (Fig. 3.21). It is noted that the concentrations of nitrate and ammonium at the maxima of carbon uptake rates of phytoplankton and ice algae were similar to those of nitrate and ammonium in the water column and the bottom of the ice except the carbon uptake rate in NO_3 enrichment on 28 April because of unusual high NO_3 concentration in the bottom ice.

3.4.9. Photosynthetic carbon allocations of ice algae community

To determine how light through different ice thickness affects the photosynthetic carbon allocations into different macromolecules of bottom ice algae, *in situ* carbon productivity incubations were conducted under different light intensities by putting the incubation bottles at different depths (0.5, 1, and 1.5 m) from the surface of the ice holes (Fig. 3.3) on 28 April in 2003. Photosynthetic carbon allocations into different macromolecules of bottom ice algae from the different depths of the ice holes are shown in Fig. 3.22a. Carbon allocations into LMWM and proteins were much greater than allocations into polysaccharides and lipids under ice of 1.5 m thickness where the bottom ice algae came from. When ice algae were incubated under less ice thickness conditions (1 m and 0.5 m), LMWM and proteins were still predominant macromolecular classes at 1 m ice thickness but LMWM increased somewhat whereas proteins decreased significantly at 0.5 m ice thickness. In comparison, increases in C allocation of lipids were observed at the lower ice thickness of 0.5 m and 1 m ice thickness. The polysaccharide proportion was not significantly changed under the different ice thickness. Photosynthetic C

partitioning into macromolecules through the season is shown in Fig. 3.22b. The predominant macromolecular classes of the bottom ice algae were LMWM (54 %) and proteins (38 %), with lower incorporations into polysaccharides (5 %) and lipids (4 %) on 28 April in 2003. On 20 May, proportions of proteins and lipids increased whereas proportions of LMWM and polysaccharides decreased. The photosynthate partitioning on 9 June was characterized by a high relative C flow into the lipids (62 %). C incorporation into LMWM and proteins were somewhat low (22 % and 15 %, respectively for LMWM and proteins) and polysaccharides attained the lowest allocation with 0.6 % at the end of season on 9 June in 2003.

3.5. Discussion

3.5.1. Chlorophyll-a concentrations of phytoplankton and ice algae

The average amount of chlorophyll-a concentration of phytoplankton in the water under the ice was fairly low (0.4 ± 0.3 μg l^{-1}) during the observation period in 2003 and 2004 (Fig. 3.10), whereas the mean chlorophyll-a concentration of ice algae within the sea ice was 290.5 μg l^{-1} (S.D. = ± 357.2 μg l^{-1}) (Fig. 3.11) which is around seven hundred times greater than that of the sea water. However, since the ice algae community is concentrated in the bottom few cm of the sea ice, the integrated chlorophyll-a concentration of ice algae (8.7 mg m^{-2}) is about 6 times greater than that of phytoplankton in a water depth of 4 m (1.4 mg m^{-2}).

Although the chlorophyll-a concentration patterns were different between 2002 and 2003, it is interesting that the chlorophyll-a concentration of ice algae had a bimodal pattern during the growing season in 2003, which is similar to the descriptions by Alexander et al. (1974) and Horner and Schrader (1982). The plausible explanation of the bimodal ice algal biomass might be active melting of the skeletal layer of the bottom ice and consequent sloughing of algae after they build up high biomass on the first peak because the algal layer absorbs so much of the radiation

that reaches it (Welch and Bergmann 1989). After a fraction of ice algae was sloughed off from the soft bottom ice, they grew back to produce the second peak. In general, the first peak is around late April to early May and the second peak is around late May at Barrow and Narwhal Island of the near shore Beaufort Sea. However, the second peaks from Alexander et al. (1974) and Horner and Schrader (1982) had the highest biomass, whereas the first peak on 28 April at Barrow in 2003 was highest. The maximum values were 23 mg chl-a m^{-2} on 23 May at Barrow in 1973 (Alexander et al. 1974), 27 mg chl-a m^{-2} on 31 May at Narwhal Island of the near shore Beaufort Sea (Horner and Schrader 1982), and 27 mg chl-a m^{-2} on 28 April at Barrow in this study. The data from 2002 (Dr. Shin, IARC, UAF, unpublished) showed that the maximum value of the bottom ice algae was 24 mg chl-a m^{-2} on 1 May although the pattern of ice algal biomass was not apparently bimodal perhaps because of the long interval between observation times of May and June in 2002. Although the sampling of the bottom ice algae with a SIPRE corer might underestimate ice algal biomass at the time of maximum development (Welch et al. 1988), the maximum values at Barrow obtained by the ice corers in 2002 and 2003 are almost identical to that from the plexiglass coring devices of Alexander et al. (1974). It appears the timing of the largest bloom of the bottom ice algae might be shifted into earlier spring season over the last several decades. The historical temperature data at Barrow from 1950 to 2004 shows a trend for increasing average air temperature from January to May in Fig. 3.23. The mean temperature from January to May in early 1970's is – 7.9 °C whereas the temperature in early 2000's is – 3.4 °C. The increase in air temperature was not reflected in the temperature in the water column under the ice during the sampling period. However, it does affect snow melt onset (Lynch et al. 2004). In fact, the snow melt onset at Barrow has a significant trend towards almost one month earlier from 1949 to 2001, although snow cover onset shows very little change (Lynch et al. 2004). The earlier snow melt onset should result in more light through the sea ice which could trigger an earlier

bloom of ice algae since snow-cover is the major factor restricting the penetration of light through ice. The earlier bloom of ice algae due to the earlier snow melt was not detected in 2004. There was no discernible bloom until 3 May (Fig. 3.11) in 2004 primarily because of lower light intensity under the ice than in 2003. There were no distinguishable sediments trapped in the ice in either year, but snow cover and ice thickness were different between the two years. Ice was thinner in 2003 (1.75 m on 3 May 2004, and 1.38 m on 28 April 2003) because the sea ice retreated by strong winds reformed in late December in 2002, and started to grow after thereafter. Furthermore, the snow thickness was lower in 2003 than 2004 (Table 3.1). Although there are no light intensity data under the sea ice, more snow cover and thicker ice before 3 May in 2004 suggests that less light was available to the bottom ice algae (Maykut 1985) in 2004. As a result, the light limitation to the bottom ice algae was more severe in 2004 than in 2003 and consequently there was no discernible bloom until 3 May in 2004.

The maximum chlorophyll-a content per unit area of the bottom ice algae in different locations around the Arctic were compared in Table 3.3. In the Alaskan Arctic, the maximum chlorophyll-a values of ice algal from the bottom few cm ice are similar among the different locations except in the Bering Sea which is located in the sub-Arctic. However, the low chlorophyll-a sample from the Bering Sea might not have been collected at the time of an ice algae maximum for this region. In comparison, although the maximum values of the bottom ice algae in the Canadian Arctic have a wide range regionally and inter-annually, other regions in the Canadian Arctic except Resolute have a similar range (10-25 mg m^{-2}) of the maximum chlorophyll-a concentration of ice algae. The mean maximum chlorophyll-a concentration of the bottom ice algae in the Alaskan Arctic region is 25.8 mg m^{-2} with a small variation (S.D. = ± 2.9 mg m^{-2}), while the average in the Canadian Arctic is 68.4 mg m^{-2} with a wide variation (S.D. = ± 74.0 mg m^{-2}) because of the high variation at Resolute. However, the sampled ice bottom sections

should be considered in comparing the chlorophyll-a values in Table 3.3 since chlorophyll-a concentration might be different depending on the length of the ice bottom section which is sampled.

3.5.2. Light or nutrient limitation

A number of environmental factors may limit the growth rate of ice algae within the sea ice. Like most aquatic environments, temperature, nutrients, and light are generally believed to be the main factors regulating the production and growth of ice algae within the sea ice. In the ice, ice algae might have different factors to control their growth depending on their location of the ice. For example, light may be at the saturation or inhibition level in the upper part of the ice but at less than compensation level at the bottom of the ice (Smith et al. 1988). Cold temperature can inhibit the growth and production of ice algae at the upper part of sea ice depending on air temperature. However, the temperature at the bottom of the ice was relatively constant as around – 2 °C (Table 3.1). Since most of ice algae was concentrated in the bottom of the ice, the temperature effect on the ice algae was not considered to be one of the main controlling factors. Because the intensity of light at the ice-water interface is low compared to the ice surface, light is considered as a critical factor for regulating the growth and biomass of ice algae at the bottom of the ice (Clasby et al. 1976; Horner and Schrader 1982; Demers et al. 1986; Cota and Smith 1991). In contrast, there is biochemical and physiological evidence that the growth of ice algae is limited by nutrients (Demers et al. 1989; Gosselin et al. 1990; Smith et al. 1997), although some studies have concluded that nutrients are not limiting the production of ice algae because the concentrations of dissolved nutrients in the ice are higher than those in the underlying water (Meguro et al. 1967; Alexander et al. 1974; Horner and Schrader 1982). However, it is difficult or inaccurate to decide which factor controls the production at Barrow by interpolating from different locations because there are other different conditions such as brine salinity and nutrients,

temperature, ice thickness, snow cover, sediment trapped in ice and etc. between different locations and times.

Two carbon uptake experiments under light and nutrient enrichment were done to determine the major factors controlling the production of ice algae. The production rates of both ice algae and phytoplankton were evidently enhanced by increased light intensities up to some points before light inhibitions (Fig. 3.19), while the rates were actually decreased by additions of major inorganic nutrients such as nitrate and ammonium (Fig. 3.21). During the observation period, the only nutrient depleted in the melted bottom 3 cm ice cores was PO_4 on June, 2003 (Fig. 3.9). The lowest concentration of nitrate was 0.33 μmole/l while phosphate was totally depleted on 9 June, 2003. However, the concentration in the brine channels where the ice algae live is probably higher than the value from the melted ice cores (Alexander et al. 1974). The concentrations of nutrients at the maxima of carbon uptake rates of ice algae and phytoplankton were slightly higher than those of nutrients measured on water samples and melted samples from the bottom of the ice except on 29 April. At this time, the concentration of NO_3 in the bottom of the ice was 45.8 μmole/l, although this might be a result of or reflect brine drainage or microbial activity (Horner and Schrader 1982). This indicates that phytoplankton and ice algae might not be limited by *in-situ* nutrients and the nutrients are probably sufficient under a light limitation since the carbon uptake rates of phytoplankton and ice algae increased as light intensity increased. The mean assimilated C/N ratios, which are 3.3 and 3.9 for phytoplankton and ice algae, are lower than the Redfield ratio (6.6) and support the idea that these algae are not nutrient-limited, although the particulate C/N ratios are higher (10.5 for phytoplankton and 8.7 for ice algae) than the Redfield ratio probably because of the effect of detritus. If light is limited, the addition of nutrients might not stimulate the carbon uptake of phytoplankton or ice algae because low light intensity suppressed nutrient uptake. Even if growth rates were limited by nutrients and light,

light would be more limiting than nutrients based on the light and nutrient increment experiments (Figs. 3.20 & 21) and determine the total biomass yield of plants like Liebig's law of the minimum (1840). Unfortunately, the experiment on the productivity of ice algae or phytoplankton under increment of both light and nutrients was not performed. However, the nitrate uptake rates under more light showed that nitrate uptake rates of ice algae and phytoplankton were also increased up to light inhibitions (Fig. 3.20). This implies that the production rates were regulated by their limited nitrate uptake in low light conditions under the snow-covered ice since nitrate increases size and/or production of a plant population (Dugdale and Goering 1967).

Numerous studies have shown that light is the major limiting factor in the onset and early development of ice algal blooms at the bottom ice (Horner 1985; Welch and Bergmann 1989; Cota and Smith 1991; Smith et al. 1993). However, in the light increment experiment on 9 June, 2003, the carbon uptake rate of ice algae was still enhanced by increased light intensities. This suggests that the production of ice algae might be light limited through the sea ice season, although the light limitation might hold in different regions and times due to difference in ice thickness and snow cover.

3.5.3. Nitrogen uptake rates of ice algae and phytoplankton

It is important to distinguish between the relative importance of ammonium and nitrate as sources of nitrogen for the cell and population because ammonium maintains the cell in a healthy state whereas nitrate increases population size or production passed on to higher trophic levels (Dugdale and Goering 1967). However, there have been few studies on a time series of nitrogen (nitrate and ammonium) uptake rates of ice algae during the growing season. The ratio of new production (normally NO_3^- uptake) to total primary production (generally $NO_3^- + NH_4^+$ uptake and sometimes urea uptake) is the f-ratio which is an ecologically important parameter of nitrogen uptake (Eppley and Peterson 1979). The mean f-ratios of NO_3^- uptake/total ($NO_3^- +$

NH_4^+) uptake from 1 April to 9 June in 2003 were 0.22 (S.D. = ± 0.06) and 0.34 (S.D. = ± 0.15) for phytoplankton and ice algae respectively (Table 3.4), but they were not statistically significantly different. The mean f-ratio of ice algae was somewhat lower than 0.43 at Barrow on 18 April from Alexander et al. (1974), but their f-ratio was within the range between 0.15 and 0.49 from 1 April to 9 June in 2003. McRoy and Goering (1974) found the f-ratio of ice algae in March was 0.75 in Bering Sea which is much higher than observed in this study. In comparison to ice algae, McRoy and Goering (1974) also found a higher f-ratio of phytoplankton in the Bering Sea (f- ratio = 0.62) than in Barrow (f- ratio = 0.22). However, the mean f-ratio of phytoplankton from this study is rather comparable with that (f = 0.30 without considering dark uptakes) in Prudhoe Bay during summer (Horner et al. 1974) and within the range of 0.05 to 0.38 in the southeastern Chukchi Sea during August (Cota et al., 1996). Furthermore, Lee and Whitledge (2005) found an almost identical f-ratio (= 0.25) of phytoplankton in the deep Canada Basin. The low f-ratios from this study indicate that the total production of phytoplankton and ice algae under the ice at Barrow is fueled largely by regenerated nutrients such as ammonium. However, this does not imply that their production rates are limited by nutrient supply as found for the low f-ratios of oligotrophic oceans. The nitrate concentrations in the bottom 3 cm of the ice and the water column were never totally depleted during the observation period (Fig. 3.9). Ammonium was also not depleted and increased toward the end of season when the concentration was higher than the nitrate concentration. This relatively high ammonium concentration could be an important nitrogen source to ice algae at limiting light levels (Alexander and Chapman 1981). It is well established that the nitrate uptake of phytoplankton can be inhibited by ammonium concentration (Dortch 1990), with the onset of inhibition occurring at as low as 0.1 μM in the subarctic Pacific (Wheeler and Kokkinakis 1990). Furthermore, the uptake of nitrate by phytoplankton is more sensitive to light than ammonium uptake (Dortch and Postel 1989). If the

phytoplankton and ice algae at Barrow are light limited (above section in discussion) during the growing season, they would preferentially utilize more ammonium under low light conditions since ammonium is readily available (Alexander and Chapman 1981). In fact, the nitrate uptake rates of phytoplankton and ice algae were light limited at Barrow during the observation period (Fig. 3.20), although there are no data on ammonium uptake rates under different light intensities. In size-fractionated f-ratios at Barrow, the f-ratio of large cells (> 5 μm) is generally 2 or 3 fold higher than that of small phytoplankton (< 5μm and > 0.7 μm) (Table 3.4), which indicates that large cells depend more on nitrate than ammonium for their photosynthesis. This is also true for the ice algae at the bottom ice. Some studies have shown that photosynthesis by large plankton depends largely on nitrate, whereas small plankton depends on regenerated nitrogen such as ammonium (Probyn 1985; Koike et al. 1986).

A relative preference index (RPI, McCarthy et al. 1977) for nitrate was calculated to determine which nitrogen form is preferred for growths of phytoplankton and ice algae. An RPI_{NO3} less than 1 indicates a preference for ammonium, while an RPI_{NO3} greater than 1 indicates a nitrate preference. The values for phytoplankton show a strong preference for ammonium from February to June in 2003. The mean RPI_{NO3} values are 0.15 (S.D. = ± 0.11) and 0.29 (S.D. = ± 0.12) for small and large phytoplankton indicating a stronger preference for ammonium. In contrast, ice algae have a preference for nitrate. The mean RPI_{NO3} values are 1.27 (S.D. = ± 1.97) and 2.58 (S.D. = ± 3.53) for small and large ice algae from 28 April to 9 June. However, the mean RPI_{NO3} values only between 28 April and 27 May except 9 June are 0.28 (S.D. = ± 0.13) and 0.82 (S.D. = ± 0.37) for small and large cells. The RPI_{NO3} values of ice algae in the bottom ice could be incorrect because the nutrients calculated in the equation are bulk concentrations, not the concentration in the brine channels in which ice algae are living in. There were no statistically significant differences in RPI_{NO3} between small and large cells of phytoplankton and ice algae.

The daily total nitrogen ($NO_3^- + NH_4^+$) uptake rates of phytoplankton ranged between 0.34 and 3.55 mg N m^{-2} with a mean 1.46 mg N m^{-2} (S.D. = ± 1.27 mg N m^{-2}), while the rates of ice algae were from 0.13 to 11.89 mg N m^{-2} with an average 3.95 mg N m^{-2} (S.D. = ± 4.94 mg N m^{-2}) from 1 April to middle of June in 2003. The student t-test showed no significant difference between the nitrogen uptake rates of phytoplankton and ice algae. The averages of only daily nitrate uptake rates were 0.39 mg N m^{-2} (S.D. = ± 1.27 mg N m^{-2}) and 1.79 mg N m^{-2} (S.D. = ± 2.34 mg N m^{-2}) respectively for phytoplankton and ice algae. Based on the assimilated C/N ratios (4.3 ± 2.7 and 5.4 ± 3.9 for phytoplankton and ice algae), the new production rates are estimated 0.20 g C m^{-2} for phytoplankton in the water column and 1.13 g C m^{-2} for ice algae from the bottom 3 cm ice at Barrow during the 117 days observation period in 2003.

3.5.4. Primary production rates of ice algae and phytoplankton

The carbon uptake rate of ice algae from the bottom ice was detectable on 12 February in 2003 when the irradiance at the bottom was about 1.7 µE m^{-2} s^{-1}. Ice algae in the Arctic have a typical critical irradiance threshold of 2.3-9.3 µE m^{-2} s^{-1} (Alexander et al. 1974; Horner and Schrader 1982; Gosselin et al. 1985). However, the critical irradiance threshold for ice algal photosynthesis appears to be well below these in the Arctic (Mock and Gradinger 1999). Since the irradiance at the bottom was measured one time in the middle of the incubation time in this study, it might be not representative as the irradiance during the incubation. Although their activities were so low, they started to grow as early as middle February when the snow cover was 2 cm and ice thickness was about 0.82 m. The assimilation efficiency of the chlorophyll in this study ranged from 0.02 to 0.22 mg C mg^{-1} Chl-a^{-1} hr^{-1} for large ice algae (> 5 µm) and 0.01 to 0.09 mg C mg^{-1} Chl-a^{-1} hr^{-1} for small ice algae (< 5µm and > 0.7 µm) from 1 April to middle June in 2003. In comparison, the assimilation efficiency of the chlorophyll for phytoplankton was between 0.03 and 0.24 mg C mg^{-1} Chl-a^{-1} hr^{-1} for large cells (> 5 µm) and from < 0.01 to 0.28 mg

C mg^{-1} Chl-a^{-1} hr^{-1} for small cells (< 5μm and > 0.7 μm). These ranges are in good agreement with the range of 0.04-0.31 mg C mg^{-1} Chl-a^{-1} hr^{-1} for the bottom ice algae of the first-year ice in Mock and Gradinger (1999) and mean responses from the bottom ice algae of the first-year sea ice at Resolute Bay in high Arctic (Cota and Smith 1991), although a higher P_T:B_T ratio of phytoplankton than ice algae in this study contrasts with that reported by Gosselin et al. (1997). In general, larger (> 5 μm) cells of phytoplankton and ice algae have a higher assimilation number than the small cells found at Barrow in this study. This is contrary to the results from other studies in open oceans (Platt et al. 1983; Joint and Pomroy 1986). However, Hashimoto and Shimoto (2002) observed higher light utilization efficiency of large phytoplankton (> 10 μm) which were dominated by diatoms, in the Pacific in spring. Legendre et al. (1987) also found that higher photosynthetic efficiency in the larger ice algae cells. The higher photosynthetic efficiency in large cells than in small cells indicates a better adaptation of larger cells to low light intensities under the snow-covered ice (Legendre et al. 1987).

In terms of hourly rate per square meter, the range of ice algae carbon production rate was between 0.03 and 3.51 mg C m^{-2} hr^{-1} (average ± S.D. = 0.95 ± 1.45 mg C m^{-2} hr^{-1}) from 1 April to 9 June in 2003. This range is lower than that of ice algae from 6 April to 4 June (from 0.28 to 14.92 mg C m^{-2} hr^{-1}) in Alexander et al. (1974). There are several possible reasons for the lower values of carbon uptake rate in ice algae found here. One might be the inter-annual variation of the ice algal production rate. Alexander et al. (1974) found the highest rate of production, 4.56 mg C m^{-2} hr^{-1}, on 21 May in 1972 which is comparable to the value of this study. However, the incubation methods were different between 1972 and 1973. The SIPRE ice corer was used in 1972, while a plexiglass incubation box was used for the bottom ice algal production in 1973. Another possibility is different incubation methods between this study and that of Alexander et al. (1974). Using a plexiglass incubation box which was attached to the bottom of

the ice, they measured the carbon uptake rate of ice algae at the bottom of the ice where the highest biomass of active ice algae exists (Smith et al. 1990; Palmisano et al. 1985). The SIPRE ice corer was used for getting the bottom ice algae in this study. It might underestimate the production of ice algae since sampling bottom ice algae with a SIPRE corer might underestimate ice algal biomass at the time of maximum development (Welch et al. 1988). However, the maximum biomass of ice algae from the bottom of the ice in 2003 was slightly higher than that in 1973 of Alexander et al. (1974). The other possibility is different light conditions at the bottom of the ice during the observation periods between two studies. The maximum assimilation efficiency of the chlorophyll in ice algae was 0.7 mg C mg^{-1} chl-a^{-1} hr^{-1} with an average of 0.29 mg C mg^{-1} chl-a^{-1} hr^{-1} in 1973 (Alexander et al. 1974), whereas the maximum value of this study was 0.21 mg C mg^{-1} chl-a^{-1} hr^{-1} with an average of 0.08 mg C mg^{-1} chl-a^{-1} hr^{-1} in 2003. The lower assimilation efficiency of the chlorophyll in this study implies that the light limitation of the ice algae is higher in this study than in Alexander et al. (1974). This corresponds with the lower irradiance in 2003. Snow depths were greater on 28 April and 20 May in 2003 than those in the other study and consequently less light reached at the bottom of the ice when the activity of ice algae was presumed to be high. The mean light intensity beneath the ice was 0.32 % (S.D. = ± 0.12 %) of the surface irradiation from February to June in 2003, while the average from Alexander et al. (1974) was 1.03 % (S.D. = ± 0.54 %) from April to June in 1973. Moreover, the sampling time or interval for the ice algal production would be an additional reason for the difference. For example, on 28 April 2003, the ice algal biomass was highest, but the carbon uptake rate was relatively low (0.68 mg C m^{-2} hr^{-1}). This is probably because sampling occurred at the end of bloom when ice algae were senescent. While the chlorophyll-a concentration increased greatly between 1-28 April 2003, the chlorophyll-a/phaeopigments ratio of ice algae was almost the same over this period (Fig. 3.14), suggesting an increase in senescent algae. In addition, the

ice algae on 9 June are believed to be inactive because the chlorophyll-a and chlorophyll-a/phaeopigments ratio of the ice algae decreased from 27 May in 2003.

The annual production of ice algae from the bottom ice is 2 g C m^{-2} at Barrow during the growing season from February to June in 2003 (117 days). This annual production is lower than that from Alexander et al. (1974). If the lower production in this study resulted from lower light intensity as discussed above and the higher (2 or 3 fold) carbon uptake rate at higher light intensity (~ 1.4 % of surface irradiance) from the light increment experiments was used for the production, then the annual production of ice algae from the bottom ice would be 4 or 6 g C m^{-2} which is almost identical to 5 g C m^{-2} at Barrow observed by Alexander et al. (1974). Although the ice algal production of this study is 2 to 3 times less than that of Alexander et al. (1974), this value is comparable to those of others in the Alaskan Arctic (Table 3.5). The annual production of ice algae ranges from as low as 0.22 g C m^{-2} in Bering Sea (Alexander and Chapman 1981) to as high as 5 g C m^{-2} at Barrow (Alexander et al. 1974) in the Alaskan Arctic region. The mean primary production rate in this region is 1.67 g C m^{-2} yr^{-1} which is in good agreement with 2 g C m^{-2} yr^{-1} in this study, although this value might be underestimated because the production rate was calculated based on the biomass and carbon uptake rate of ice algae from the bottom 3 cm of the ice. In contrast, the range of annual production in the Canadian Arctic is from 1 g C m^{-2} (Grainger 1975) to 23 g C m^{-2} (Smith et al. 1988) with an average of 8.1 g C m^{-2}. In comparison to ice algal production, total production of phytoplankton under the ice was 0.65 g C m^{-2} during the course of the sampling period. The ice algae community contributes about 80 % of the total primary production under the land fast ice at Barrow during the spring before the phytoplankton bloom if benthic community contribution were negligible (Horner and Schrader 1982). Horner and Schrader (1982) also found that the ice algae provide about 70 % of the spring primary production in nearshore regions of the Beaufort Sea. This ice algal production provides additional

food source likely important for the herbivores such as amphipods before the phytoplankton bloom.

3.5.5. Photosynthetic carbon partitioning into macromolecules

Fig. 3.22a shows photosynthetic carbon allocations into different macromolecules of the bottom ice algae from the incubations at different ice depths and thus possibly different light intensities. For comparison, the photosynthetic carbon allocations through the season are also shown in Fig. 3.22b.

When the biomass of the bottom ice algae was highest on 28 April in 2003 (Fig. 3.10), the proportion of LMWM was 47-69 % for different ice thickness (Fig. 3.22a). The high proportion of C allocation into LMWM has been reported for the ice algae community (Mock and Gradinger 2000; Smith et al. 1987; McConville et al. 1985) as well as phytoplankton of the Southern Ocean (Barlow and Henry 1982). There are several possible reasons for the high LMWM allocation of ice algae. One might be the accumulation of certain amino acids, sugars, and/or sugar alcohol related to osmo-regulatory or cold resistance functions (Franks 1985; Smith et al. 1987). However, the decrease in the LMWM proportion through the season (Fig. 3.22b) is not explained by the osmo-regulatory or cold resistance functions of LMWM because these was little change in the temperature between April and June in 2003 and the change in the salinity at the bottom ice was not linear in 2003 (Table 3.1). Another explanation is different light intensities during phytoplankton photosynthesis since irradiance is a major factor affecting C allocation into different macromolecules (Suárez and Marañón 2003). Although the proportion of LMWM at 0.5 m ice thickness is higher than that at 1.5 m ice thickness in Fig. 3.22a, the decrease in the LMWM proportion over the season has an opposite trend. The other alternative is that the dominant pathway is the production of LMWM, which is the precursor of macromolecules such as free amino acids and carbohydrates as storage forms, under sufficient nutrient conditions

(Smith et al. 1989; Lindqvist and Lignell 1997; Mock and Gradinger 2000). Conover (1975) and Dortch et al. (1984) described the storage of free amino acids in diatom cells. The predominant ice algae community is believed to be large, chain-forming diatoms (Alexander et al. 1974) under sufficient nutrient conditions (Fig. 3.9) when the biomass of the bottom ice algae was highest on 28 April and then decreased on 20 May and 9 June in 2003. The decrease in the carbon allocation of LMWM from the bottom ice algae along the time might be a result of the decrease in the nutrient concentration available to the bottom ice algae since the nutrient concentration usually decreased over the season in 2003 (Fig. 3.9).

Under increased light conditions (0.5 and 1 m ice thickness), the proportion of proteins decreased whereas the lipid proportion increased. Relative C incorporation into proteins of ice algae tended to decrease with increasing light is consistent with phytoplankton from marine (Morris 1981; Fernández et al., 1994; Suárez and Marañón 2003) and freshwater (Hama et al. 1990) as well as arctic ice algae (Smith et al. 1989). Allocation to lipids is positively related to light intensity as shown for arctic ice algae (Smith et al. 1987; Smith et al. 1989). Over the season, the proportion of lipids increased from 4 % on April to 62 % on June in 2003 (Fig. 3.22b). The proportion of lipids reported for phytoplankton in the literature is mostly 5 to 30 % (Lindqvist and Lignell 1997; Wainman and Lean 1992). There, however, are some measurements of high C allocation into lipids reported for ice algae in the Arctic (Smith et al. 1989; Mock and Gradinger 2000) as well as phytoplankton (Lindqvist and Lignell 1997; Smith and Moris 1980). In general, high C incorporation into lipids is to be expected under physiologically N deficient phytoplankton or during stationary growth phases (Morris 1981; Parrish 1987). High lipid synthesis along with low protein allocation at the end of season might indicate that ice algae at the bottom had a nitrogen limitation or they were presumably in a stationary phase. The nitrogen (nitrate and ammonium) enrichments did not enhance the carbon production of bottom ice algae

(Fig. 3.21). Thus, they were in a stationary phase at the end of season. In fact, the ratio of chlorophyll-a/phaeopigments decreased from 27 May to 9 June in 2003 (Fig. 3.14). However, the carbon allocation into lipids on 20 May was not as high as that on 9 June although the ratio on 20 May was lower than that on 9 June (Fig. 3.22). An alternative explanation for increasing lipid synthesis over the season is increasing light intensity available to the bottom ice algae since lipid allocation is increased by increasing light (Smith et al. 1987; Smith et al. 1989) although it was not large under enriched light intensity (Fig. 3.22a) as the proportion at the end of season. Even though the light intensity under the ice was higher on April than May in Table 3.1, this might not be true for *in situ* conditions because the light was measured after the ice hole was drilled out every time. The biomass of the bottom ice algae was highest on 28 April in 2003 and thus self-shading of the bottom ice algae might be largest so that there could have more overestimation of light intensity through the ice hole on April than on other times. Substantial increased lipid allocation on June at the end of season might be a result of large increase in light penetration through the sea ice with relatively thin snow layer. In any case, higher lipid synthesis of the bottom ice algae under enriched light conditions and at the end of season might be significant to the nutrition of zooplankton and benthos because lipids are the most calorific biomolecules so their production by primary producers are a critical energy source for higher trophic levels (Wainman and Lean 1992).

3.5.6. Ecological significance of changes in sea ice extent and thickness of the Arctic Ocean

Surface and satellite-based observations show the large-scale decrease in sea ice extent from 1953 to 1998 (Vinnikov et al. 1999). They suggested a ~ 20 % reduction in annual mean sea ice extent by the year 2050. This decreasing tendency in ice cover on the Arctic Ocean increased through the late 1980s and mid 1990s partly because of summer and autumn reductions along the Siberian Arctic Coast (Maslanik et al. 1999). In addition to the decrease in sea ice extent,

Rothrock et al. (1999) found substantial reduction in ice thickness in the central Arctic in the 1990s relative to the 1985-1976 climatology because of the positive phases of two modes of natural arctic variability; the decadal-scale Arctic Oscillation and an interdecadal low frequency oscillation (Polyakov and Johnson 2000). Whether thinning of sea ice and less ice extent is a trend or part of a low frequency oscillation remains to be determined, but decreased ice cover might cause an increase in primary production or/and change in timing of the production.

Based on submarine sonar data, Rothrock et al. (1999) found that the mean ice thickness had decreased by about 40 % from 3.1 m in 1958-1976 period to 1.8 m in 1990s over most of the deep water areas of the Arctic Ocean at the end of the melt season. If this decrease is representative throughout the central Arctic Ocean, it would be a tremendous change in light intensity to the phytoplankton and ice algae because the amount of light through the sea ice would increase from ~ 2.2 % up to ~ 12 % of surface irradiance when there is no snow cover on the ice (Andersen 1989). We found 2 or 3 times higher carbon uptake rates of bottom ice algae and underlying phytoplankton, when *in situ* productivity incubations were conducted under ~ 30 % less thickness of the first-year ice in Barrow during the growing season (Fig. 3.24). The averaged amount of light increased from 0.4 % (S.D. = ± 0.4 %) for *in situ* ice thickness to 2.2 % (S.D. = ± 2.0 %) of surface irradiance for 30 % less thickness. If snow cover on the ice is similar between the two periods (1950s and 1990s) and light is a principal factor to control the production in the central Arctic Ocean, then 40 % less ice thickness would cause 2 or 3 times higher production in Arctic Ocean. As well as higher primary production, the bloom patterns of phytoplankton and ice algae might be changed by decreased ice thickness.

Actually, in the central Arctic Ocean, Gosselin et al. (1997) found that the mean ice algal production (30 mg C m^{-2} day^{-1}) is 2 or 3 times higher than those from Apollonio (1959; 17 mg C m^{-2} day^{-1}) and English (1961; 12 mg C m^{-2} day^{-1}) although Pomeroy (1997) has argued that all ^{14}C

production rates from the 1950s were underestimated. Furthermore, Gobeil et al (2001) found that recent solid phase acid volatile sulfide production and a change from oxic to anoxic diagenesis have taken place in Arctic Ocean basin sediments within the past 50 yrs. They concluded that enhanced productivity by thinning sea ice or less snow cover transported more organic carbon from surface to the sea floor and changed conditions in the sediments. In addition to increasing in the production, the composition in different macromolecules of primary producers might be changed under the current ice conditions as shown by the light enrichment experiment. As consequence of changes in amount or/and timing as well as macromolecule composition of primary production, the seasonal distributions, geographic ranges, and nutritional status of higher trophic levels might be altered (Tynan and DeMaster 1997) especially in the coastal areas of Arctic Ocean.

3.6. Summary and conclusions

The maximum biomass of the bottom ice algae was 27 mg m^{-2} on late April in 2003 which is one month earlier than those of previous studies as a result of recent spring earlier snow melt onset because of warmer air temperature (Lynch et al. 2004) and consequently more light through the sea ice The daily total nitrogen ($NO_3^- + NH_4^+$) uptake rates ranged between 0.34 and 3.55 mg N m^{-2} with a mean 1.46 mg N m^{-2} (S.D. = ± 1.27 mg N m^{-2}) and 0.13 to 11.89 mg N m^{-2} with an average 3.95 mg N m^{-2} (S.D. = ± 4.94 mg N m^{-2}), respectively for phytoplankton and ice algae. The averages of only daily nitrate uptakes were 0.39 mg N m^{-2} (S.D. = ± 1.27 mg N m^{-2}) and 1.79 mg N m^{-2} (S.D. = ± 2.34 mg N m^{-2}) respectively for phytoplankton and ice algae. Based on the assimilated C/N ratios, the new production rates are estimated ~ 0.15 g C m^{-2} for phytoplankton in the water column and ~ 0.8 g C m^{-2} for ice algae from the bottom 3 cm ice at Barrow in 2003.

Based on the hourly production rate per square meter, the annual production of ice algae from the bottom ice is 2 g C m^{-2} at Barrow during the growing season from February to June in 2003 (117 days). In comparison to the ice algal production, the total production of phytoplankton under the ice was 0.65 g C m^{-2} during the course of the sampling period. The light and nutrient enrichment experiments showed that these rates of primary production of the bottom sea ice algae and phytoplankton at Barrow were limited mainly by light which was about 0.3 % of the surface irradiance under the snow-covered sea ice although they are believed to adapt to low light intensity. Based on the total carbon production of ice algae and phytoplankton during the observation period in 2003, the ice algae community contributes about 80 % of the total primary production under the land fast ice at Barrow during the spring before the phytoplankton bloom if benthic community contribution were negligible. This ice algal production must be an additional food source which might be important for the herbivores such as amphipods before the phytoplankton bloom.

From the incubations at reduced ice thickness, the bottom ice algae allocated more carbon production into lipids. In addition, at the end of season, increasing light intensity caused the high carbon incorporation into lipids in the bottom ice algae. This high lipid synthesis might be significant to the nutrition of zooplankton and benthos because lipids have the largest caloric content so their production by primary producers is a critical energy source for higher trophic levels (Wainman and Lean 1992).

Sea ice extent as well as sea ice thickness in the Arctic Ocean have decreased over several decades because of warming temperature. Whether thinning of sea ice and less ice extent is a general or temporal downward trend in the Arctic Ocean, these trends might cause an increase in primary production or/and change in timing of the production. In addition to the increasing production, the composition in different macromolecules of primary producers might

change under the current ice conditions. As a consequence of changes in amount or/and timing as well as macromolecule composition of primary production, the seasonal distributions, geographic ranges, and nutritional status of higher trophic levels might be altered (Tynan and DeMaster 1997) especially in the coastal areas of the Arctic Ocean.

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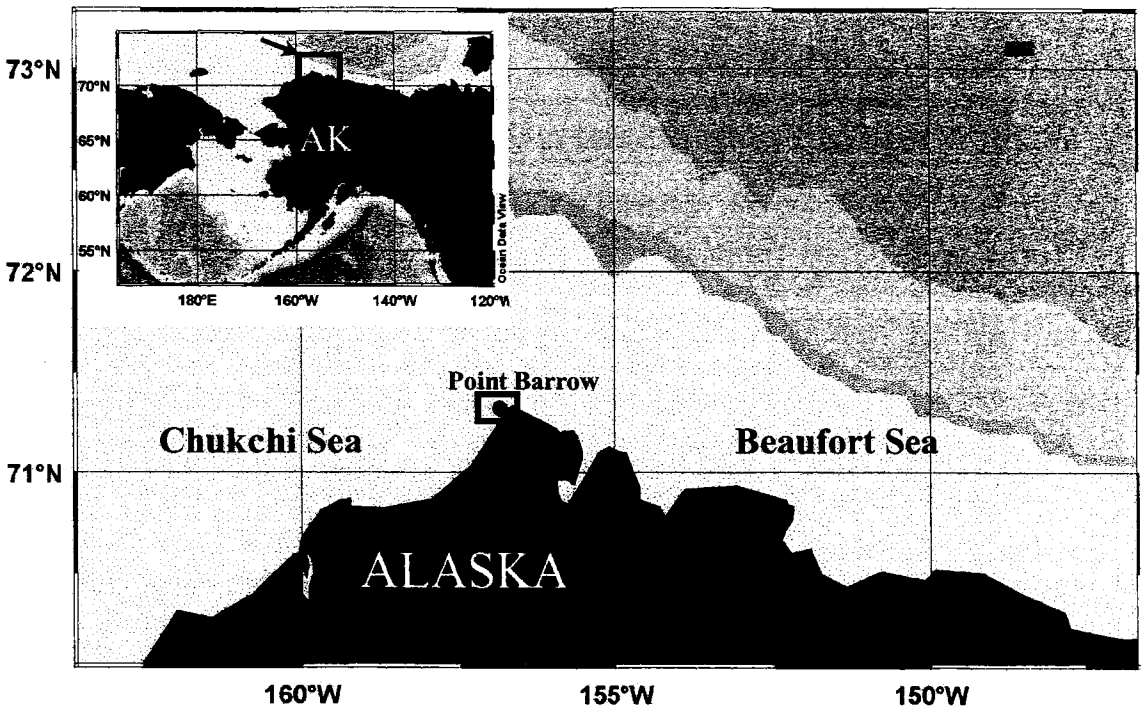


Fig. 3.1. Location of the primary sampling site near the Naval Research Laboratory at Barrow, Alaska.

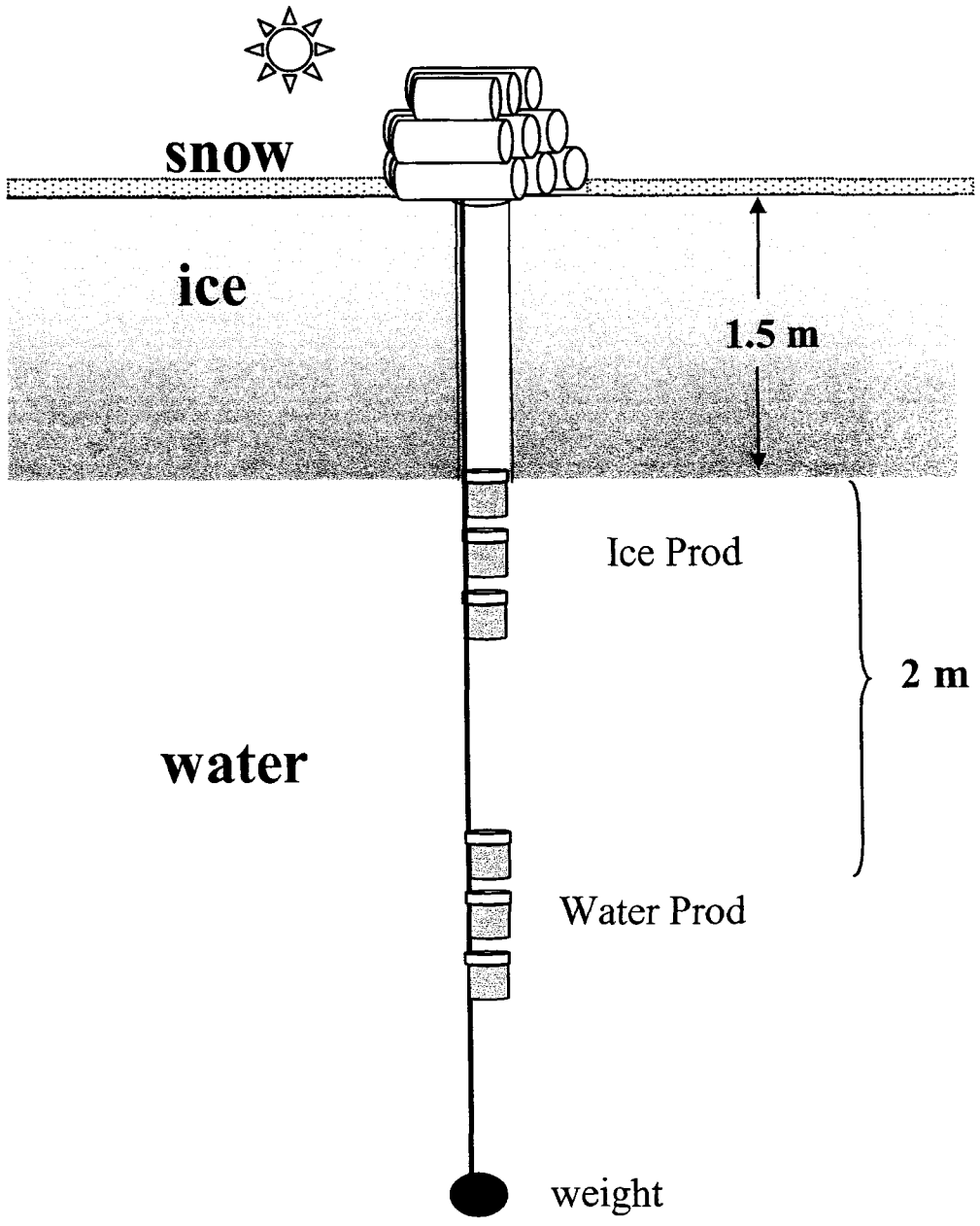


Fig. 3.2. *In situ* productivity experiments of ice algae and phytoplankton under the ice. Ice prod stands for productivity of bottom ice algae and water prod stands for productivity of phytoplankton from water column.

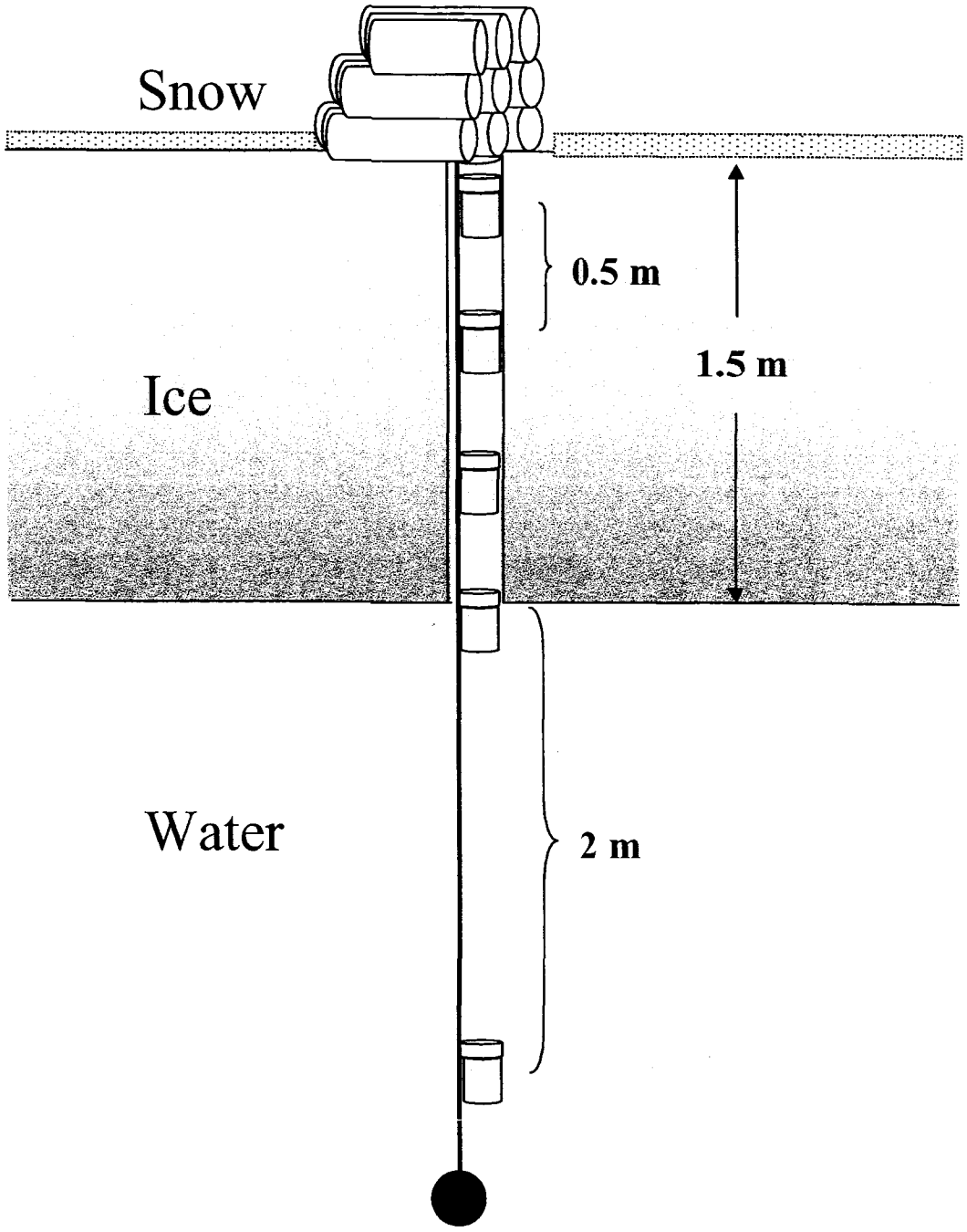


Fig. 3.3. Carbon and nitrogen uptakes of ice algae and phytoplankton under different light intensities at different depths (0.1, 0.5, 1 and 1.5 m) of an ice hole and 2 m water depth under the ice.

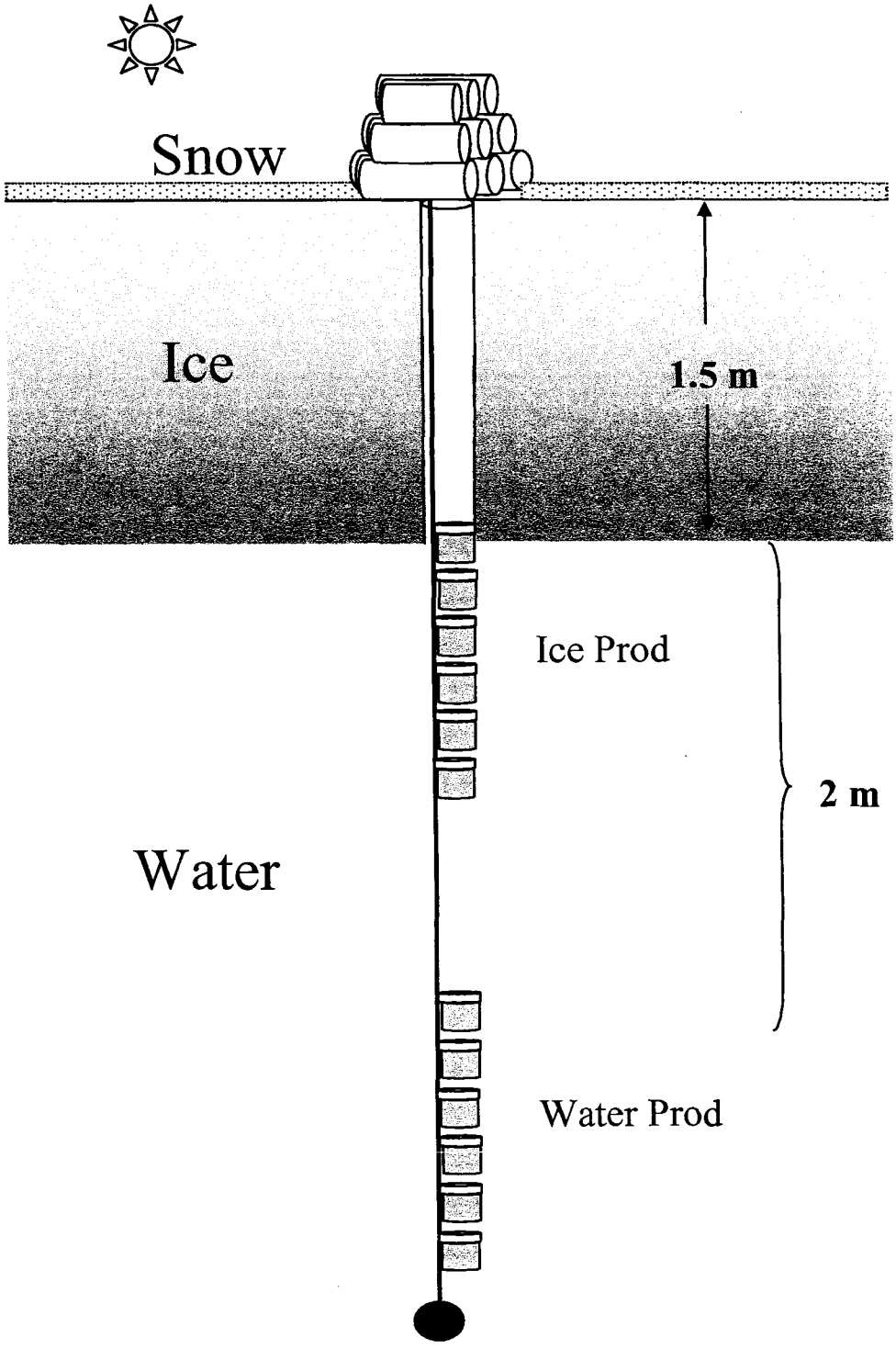


Fig. 3.4. Nutrient enrichment experiments of phytoplankton and ice algae under the ice. The bottles for ice algae were right below the bottom ice and the bottles for phytoplankton were deployed at ~ 2 m water depth under the bottom ice. Ice prod stands for productivity of bottom ice algae and water prod stands for productivity of phytoplankton from water column.

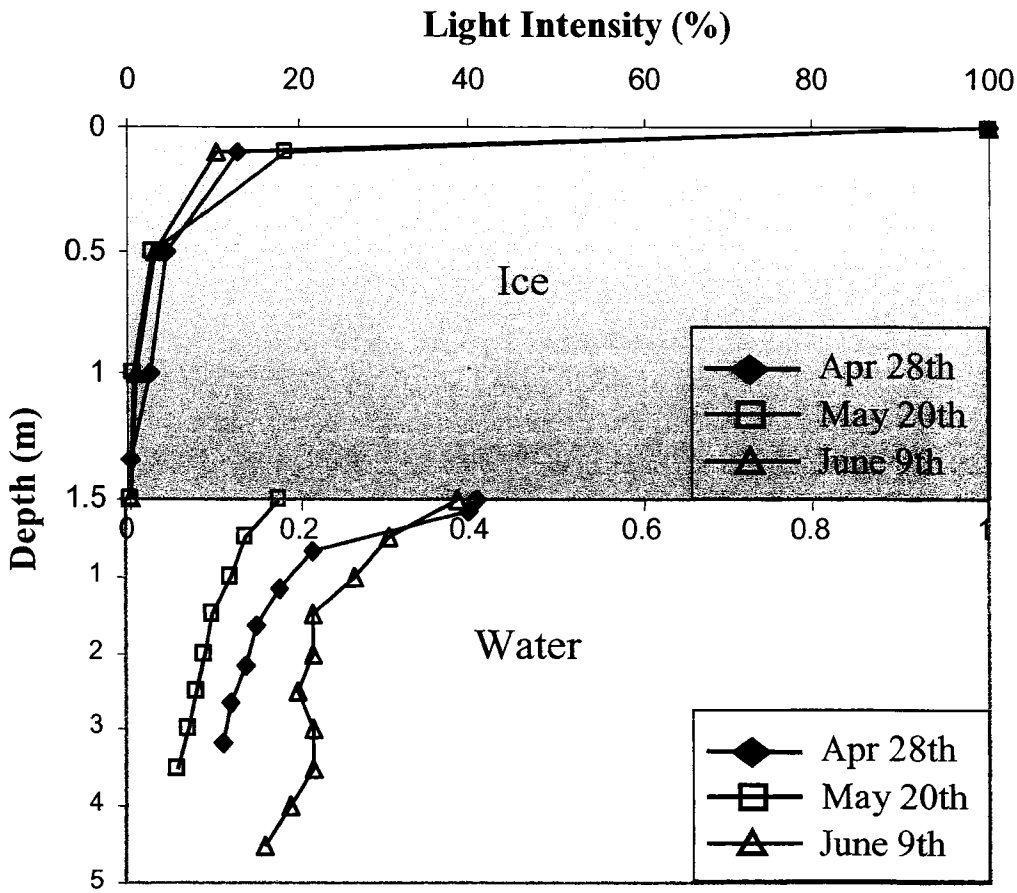


Fig. 3.5. Light intensities through the snow-covered sea ice and water column under the sea ice from 28 April to 9 June in 2003.

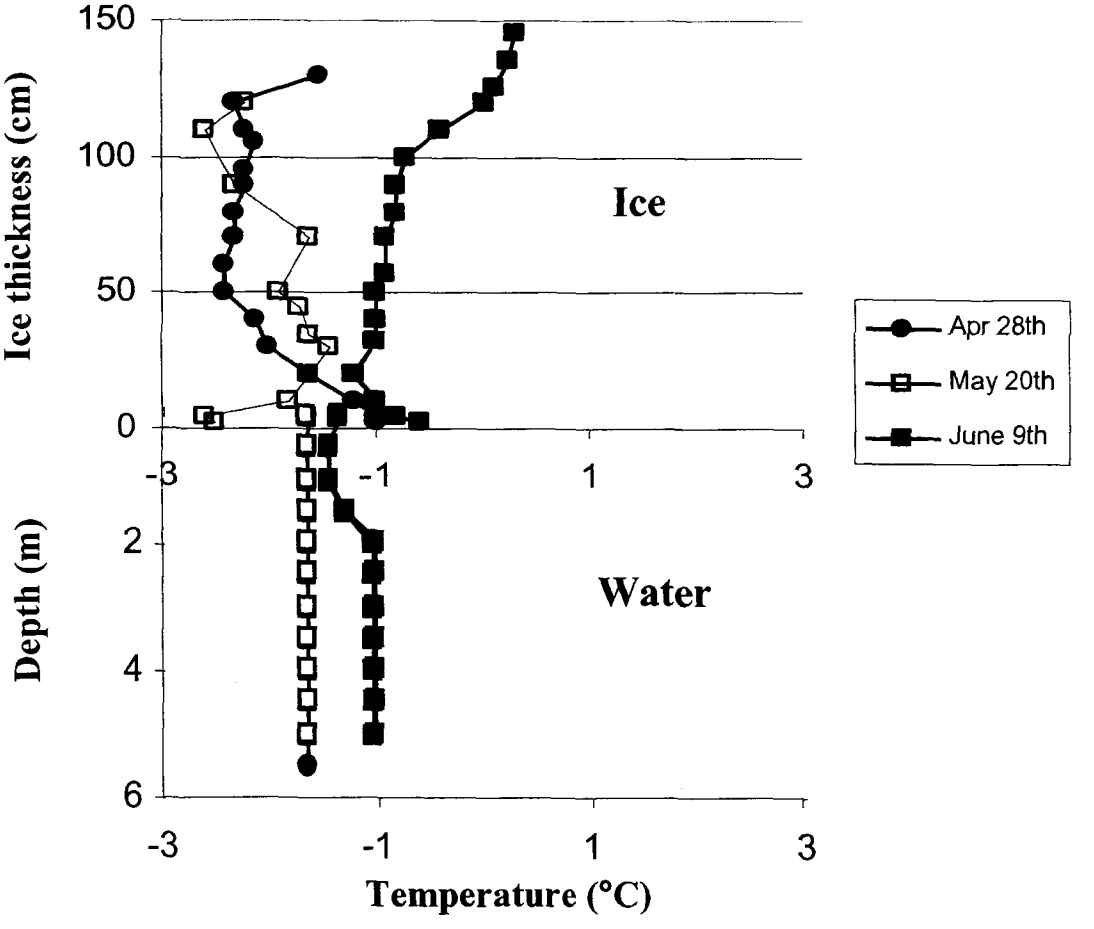


Fig. 3.6. Temperature distributions of sea ice and water column from 28 April to 9 June in 2003. The temperatures in the water column on 28 April and 20 May are identical.

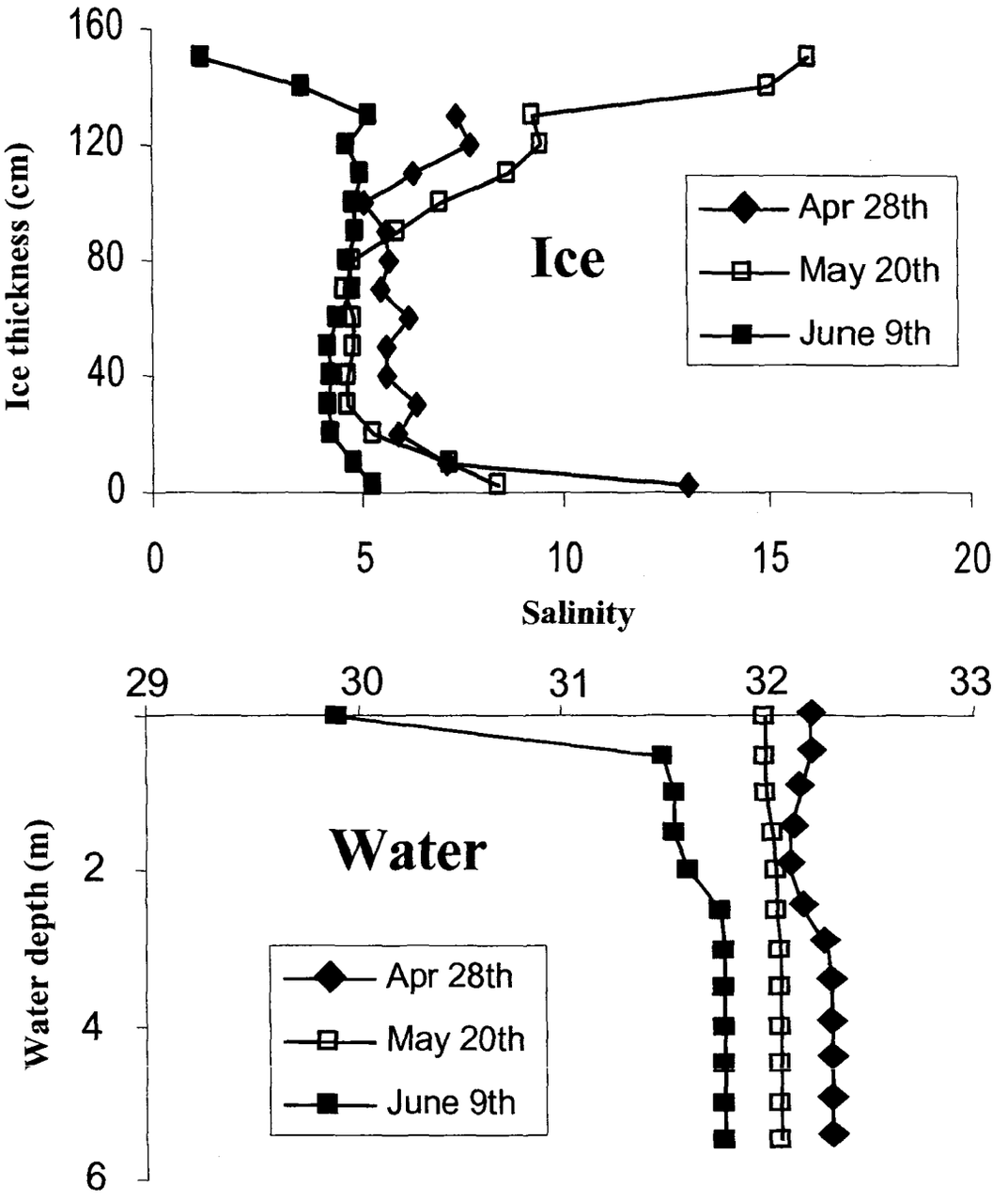


Fig. 3.7. Salinity distributions of sea ice and water column from 28 April to 9 June in 2003. The salinity for sea ice is the bulk salinity. The bottom of the sea ice is 0 cm.

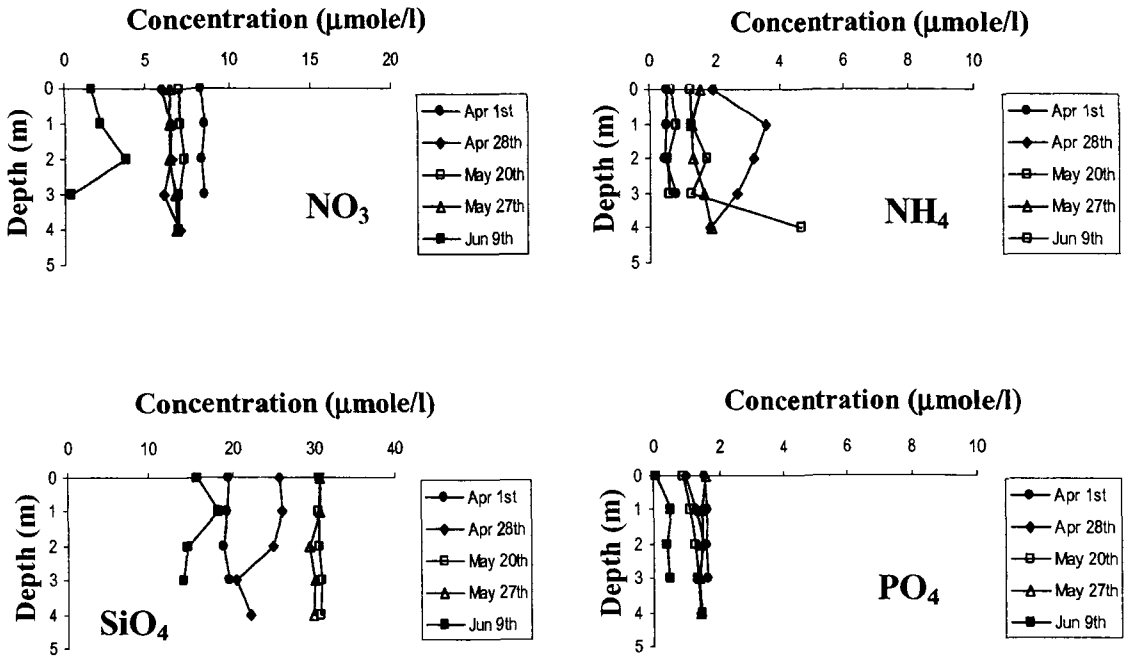


Fig. 3.8. Distributions of inorganic nutrients in the water column from 1 April to 9 June in 2003.

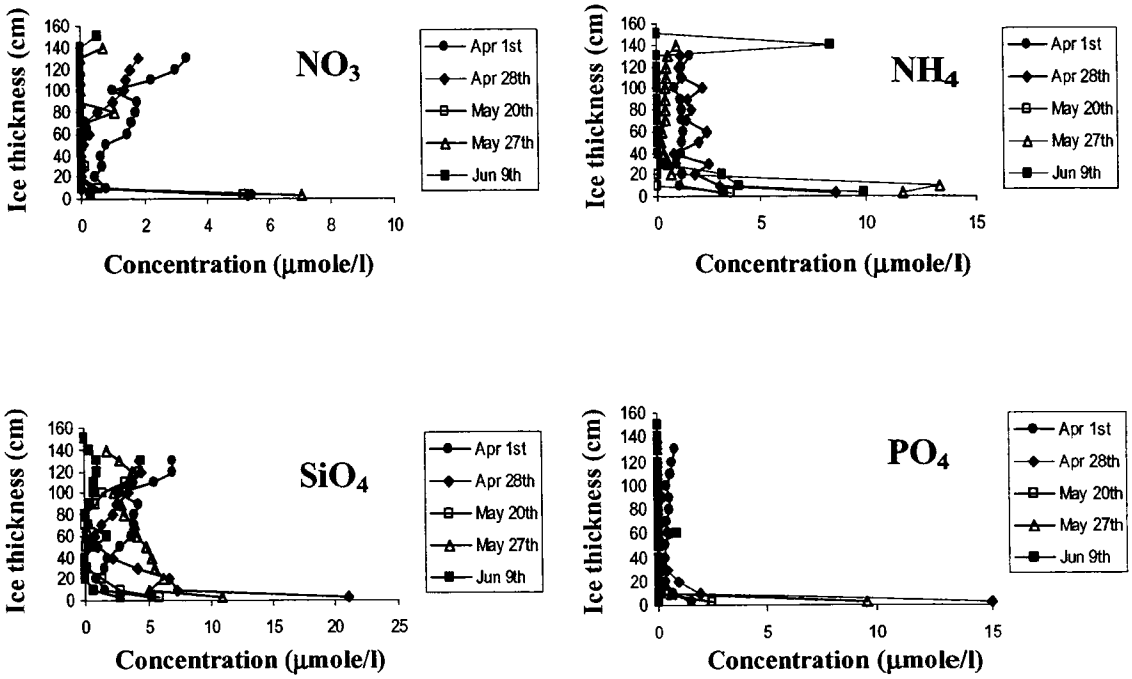


Fig. 3.9. Distributions of bulk inorganic nutrients within sea ice from 1 April to 9 June in 2003.

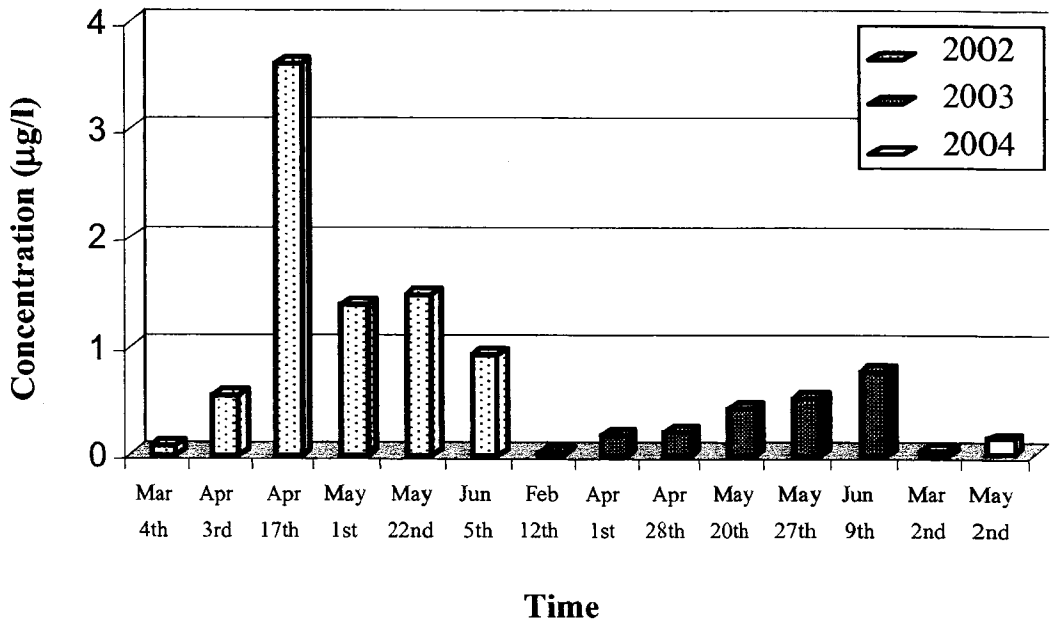


Fig. 3.10. Chlorophyll-a concentration of phytoplankton in the water column at Barrow during spring from 2002 to 2004. 2002 chlorophyll-a data from Dr. Shin (IARC, UAF). The waters were sampled at 2 m under the ice in 2003 and 2004, while the water in 2002 was sampled from the ice holes after they were drilled out.

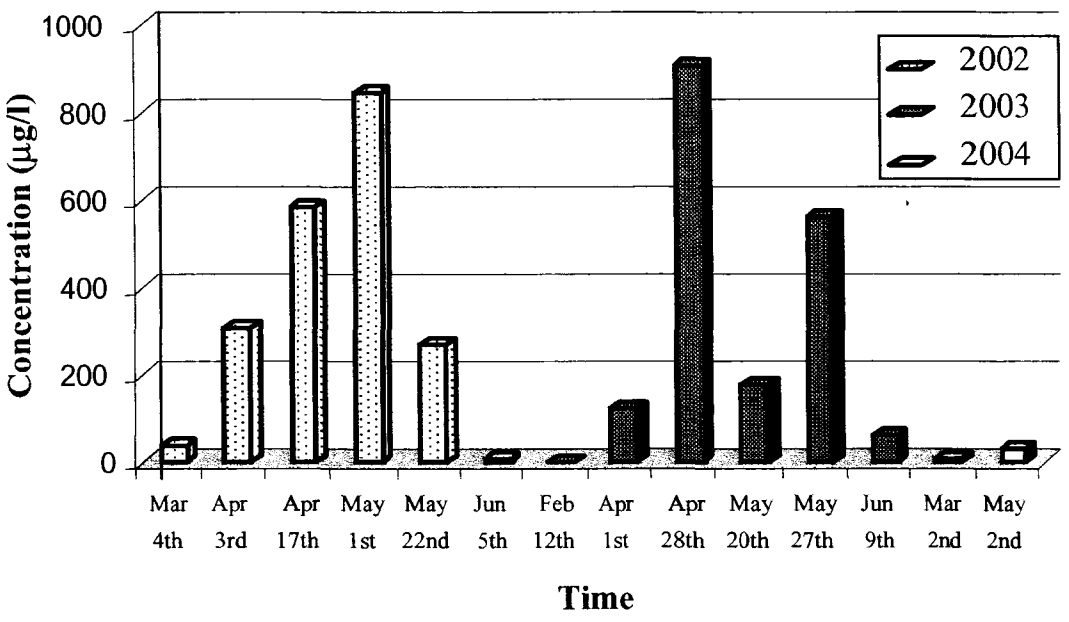
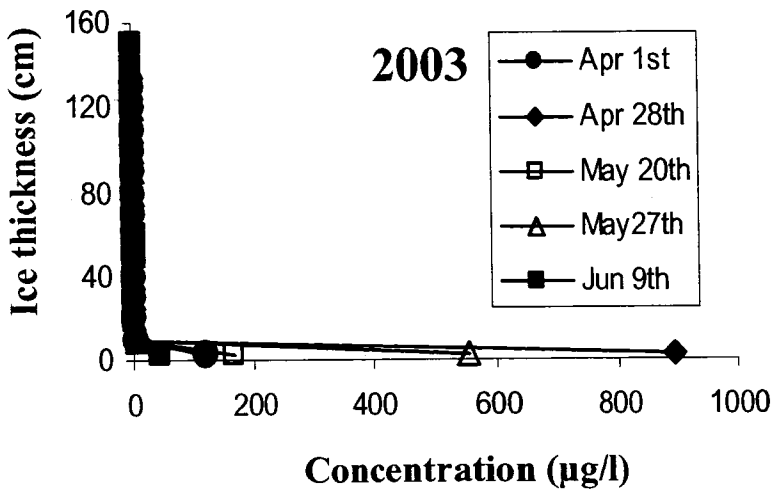


Fig. 3.11. Chlorophyll-a concentration of ice algae within the bottom 3 cm section of the sea ice at Barrow during spring from 2002 to 2004. 2002 chlorophyll-a data from Dr. Shin (IARC, UAF).



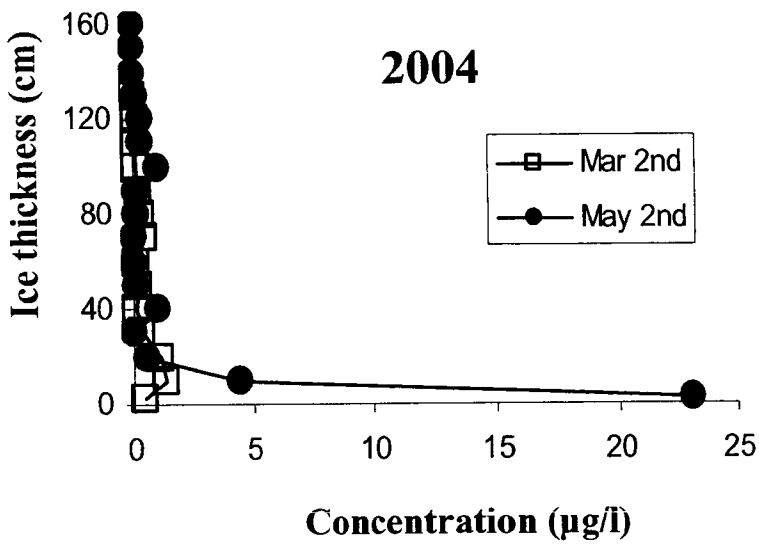


Fig. 3.12. Chlorophyll-a distribution of ice algae within the entire ice cores in different times of 2003 and 2004.

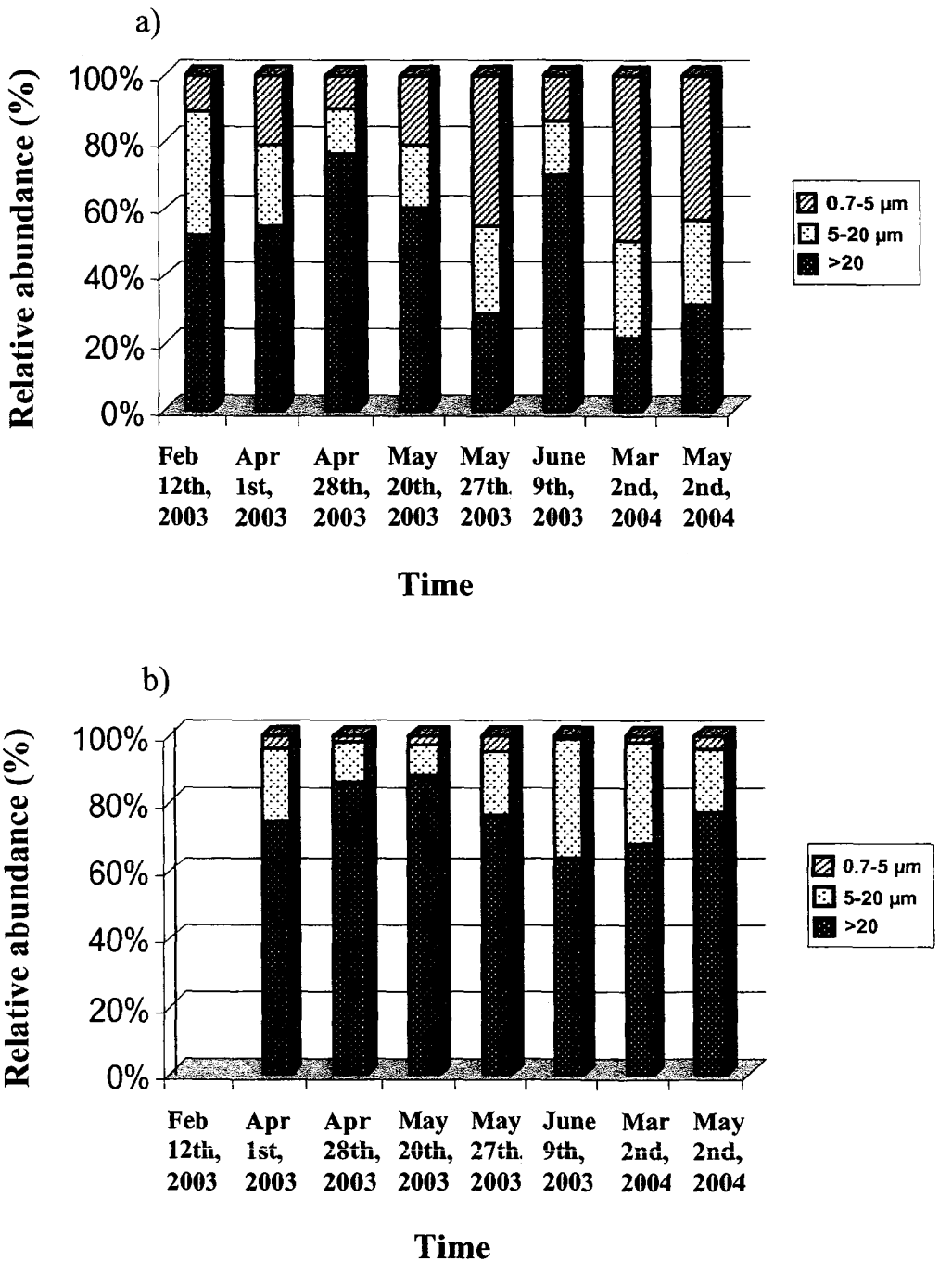


Fig. 3.13. Size fractionation of a) phytoplankton and b) ice algae in 2003 and 2004.

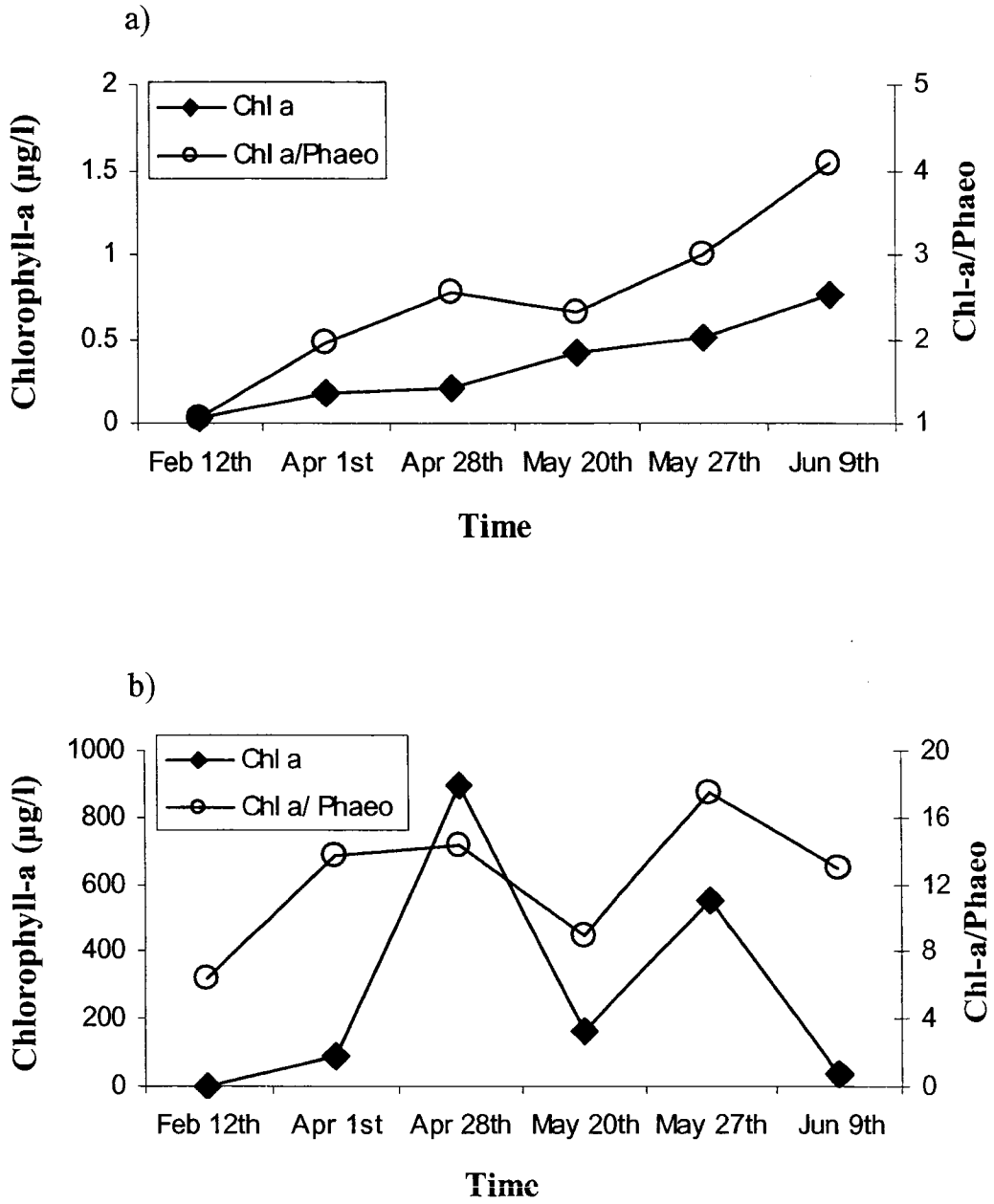


Fig. 3.14. Chlorophyll-a concentration and chlorophyll-a/phaeopigments ratio of a) phytoplankton and b) ice algae in 2003.

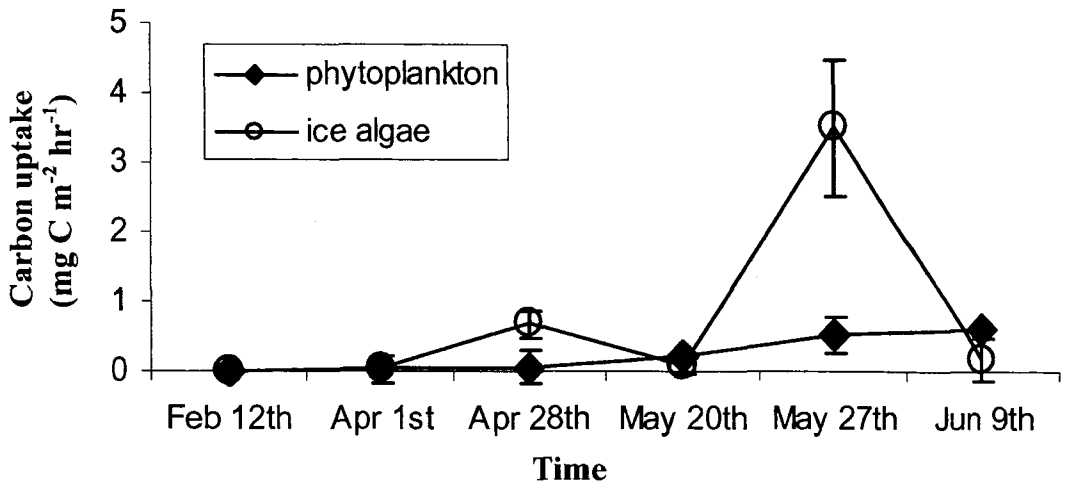


Fig. 3.15. Carbon uptake rates of phytoplankton and ice algae during the observation period from 12 February to 9 June in 2003. Bar stands for the standard deviation for each data point. Some standard deviations are too small to be showed up.

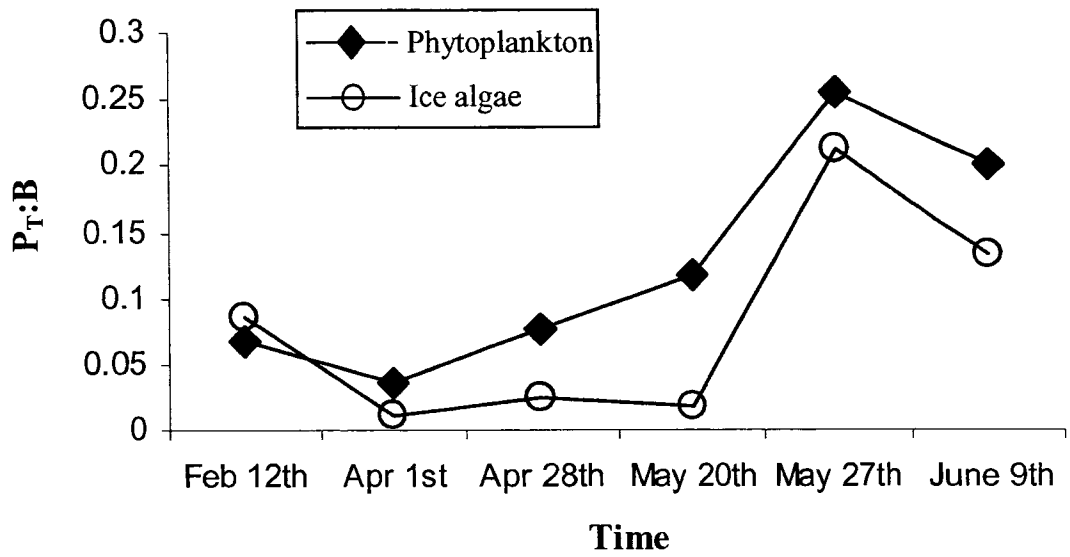


Fig. 3.16. The ratio of total production (P_T): total biomass (B_T) of phytoplankton and ice algae along the time.

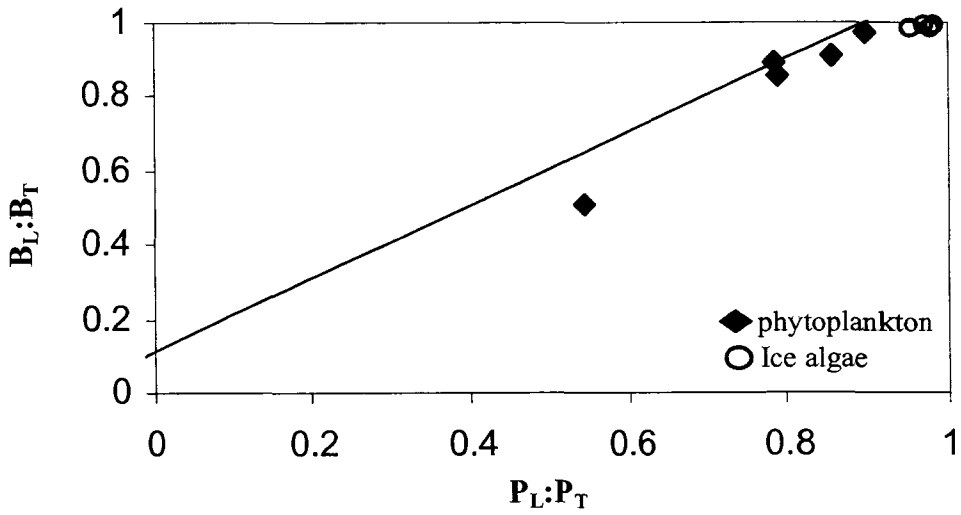


Fig. 3.17. The $B_L:B_T$ vs $P_L:P_T$ relationship of phytoplankton and ice algae. $B_L:B_T$ is a ratio of large cell biomass and total biomass (> 5 μm chlorophyll-a: total chlorophyll-a) and $P_L:P_T$ is a ratio of large cell production and total production (> 5 μm production rate: total production rate).

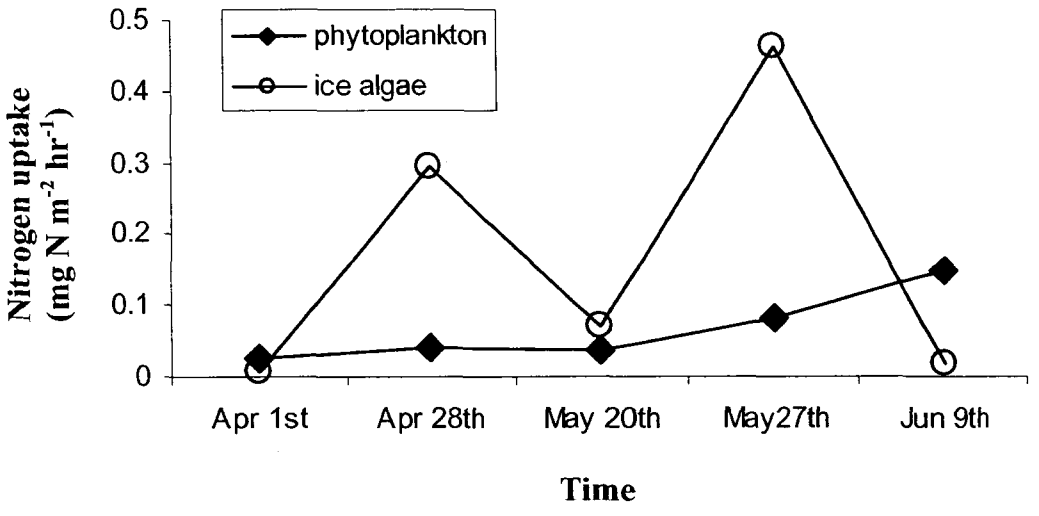


Fig. 3.18. Nitrogen (NO_3 and NH_4) uptakes of phytoplankton and ice algae during the observation period from 1 April to 9 June in 2003.

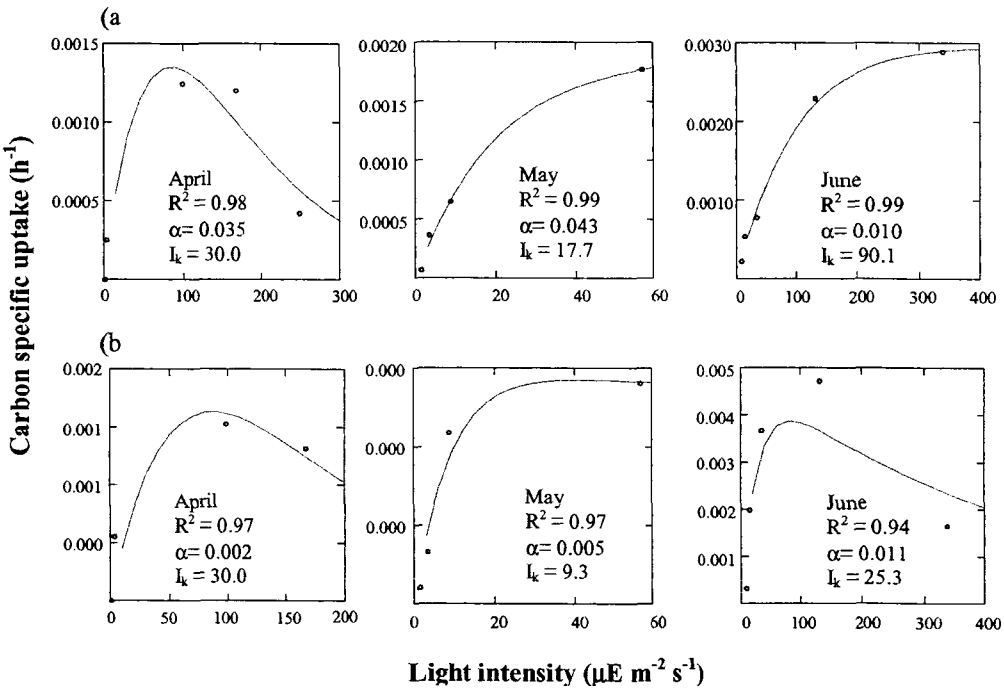


Fig. 3.19. Specific carbon uptakes of (a) phytoplankton and (b) ice algae at different light intensities on 29 April, 20 May and 9 June in 2003. α: photosynthetic efficiency, I_k: half-saturation constant of light (μE m^{-2} s^{-1}).

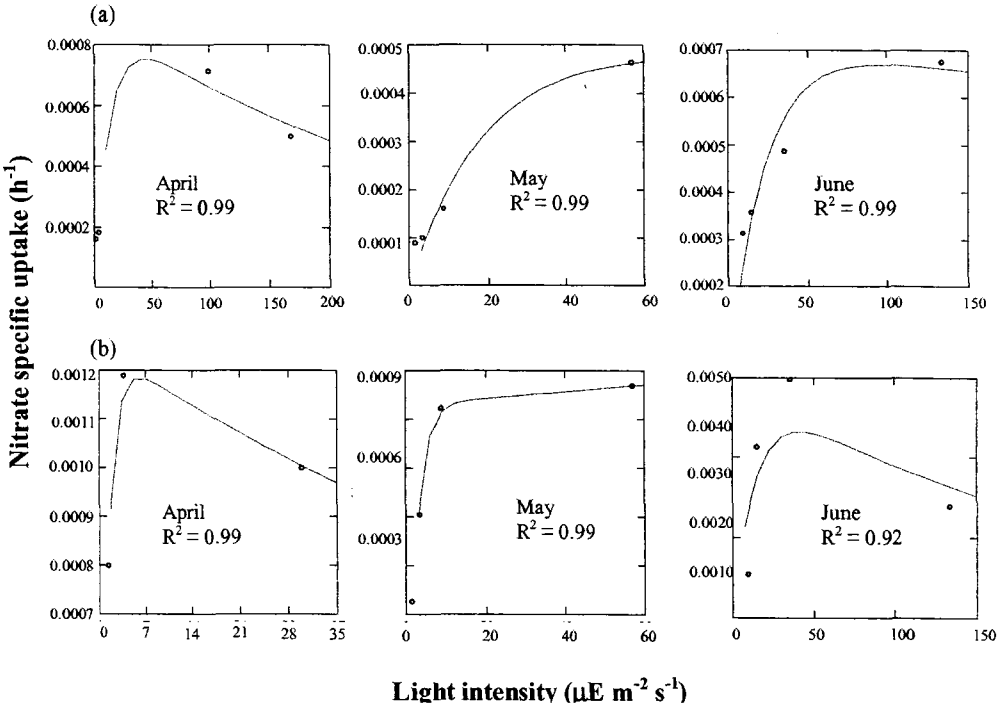


Fig. 3.20. Specific nitrate uptakes of (a) phytoplankton and (b) ice algae at different light intensities on 29 April, 20 May and 9 June in 2003.

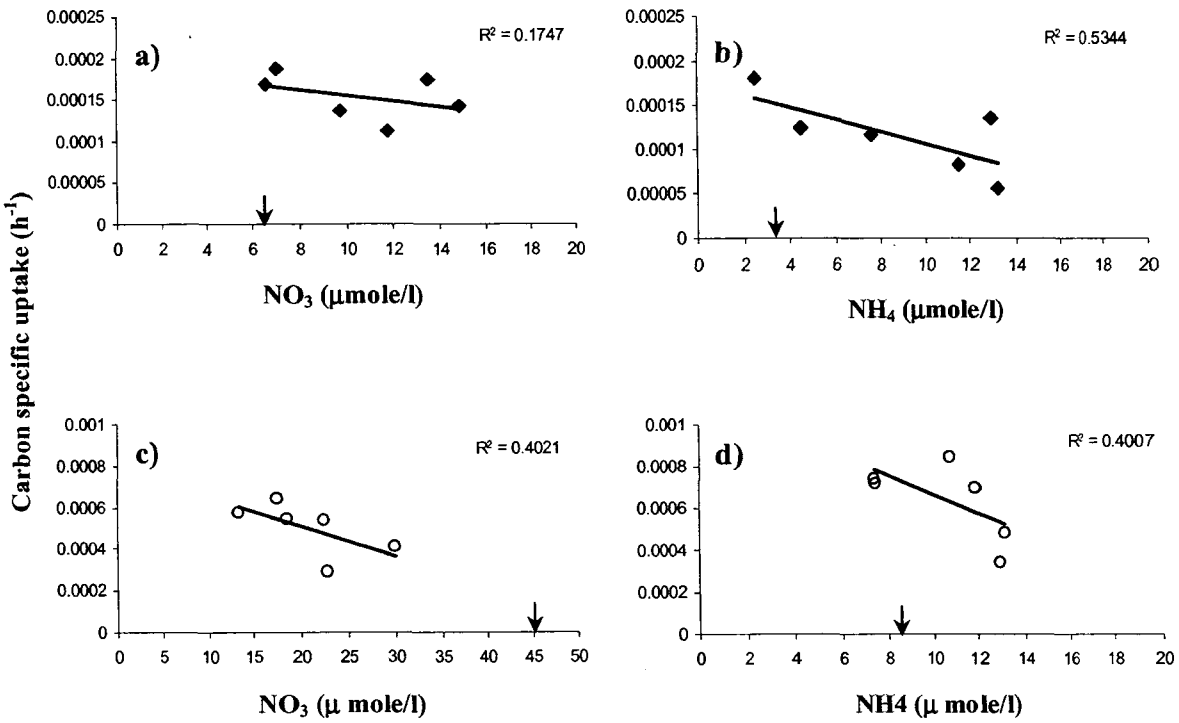


Fig. 3.21-1. Carbon specific uptakes of phytoplankton and ice algae in nitrate and ammonium enrichments on 28 April, 2003. a) and b) are phytoplankton, c) and d) are ice algae. Arrows on the x scale indicate the concentrations at 2 m water depth for phytoplankton and bulk concentrations of nitrate and ammonium in the ice bottom 3 cm sections for ice algae.

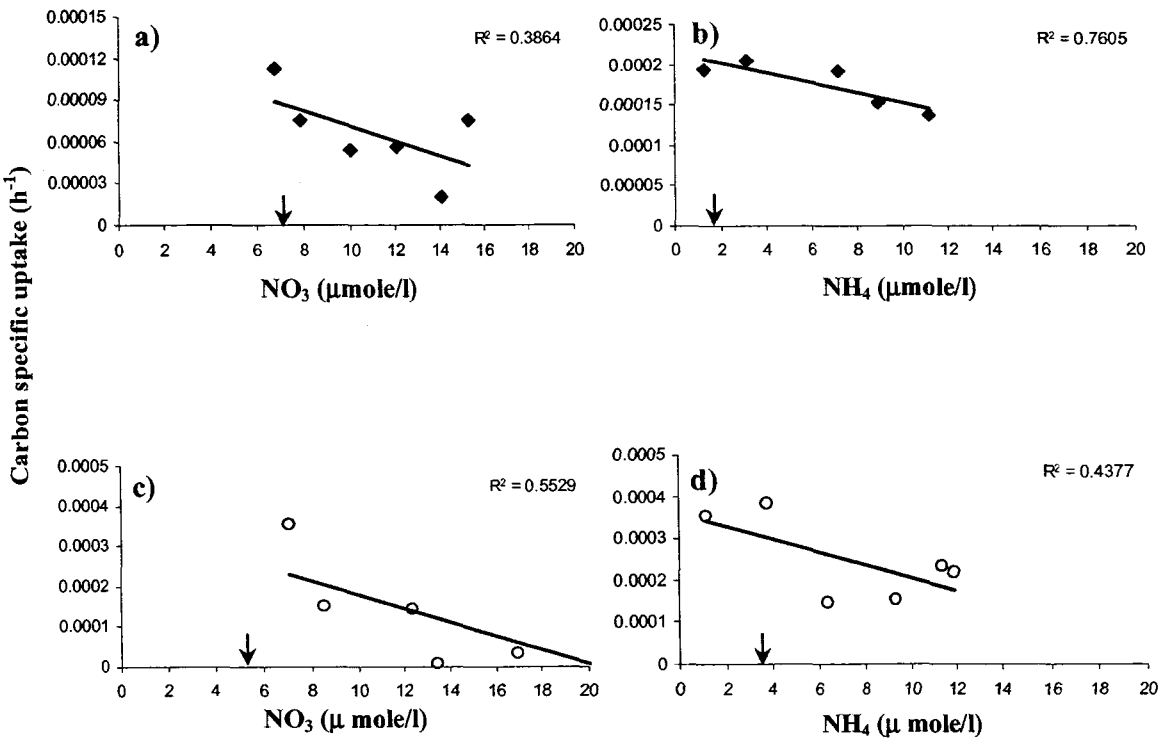


Fig. 3.21-2 Carbon uptakes of phytoplankton and ice algae in nitrate and ammonium enrichments on 20 May, 2003. a) and b) are phytoplankton, c) and d) are ice algae. Arrows on the x scale indicate the concentrations at 2 m water depth for phytoplankton and bulk concentrations of nitrate and ammonium in the ice bottom 3 cm sections for ice algae.

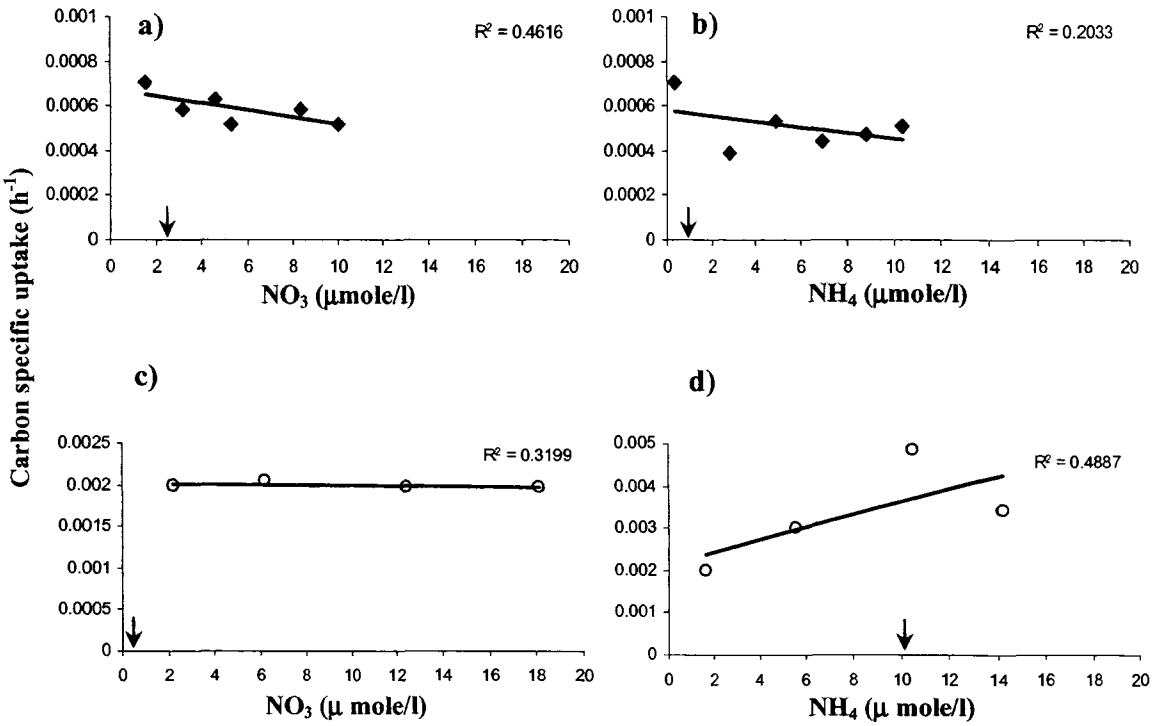


Fig. 3.21-3. Carbon uptakes of phytoplankton and ice algae in nitrate and ammonium enrichments on 9 June, 2003. a) and b) are phytoplankton, c) and d) are ice algae. Arrows on the x scale indicate the concentrations at 2 m water depth for phytoplankton and bulk concentrations of nitrate and ammonium in the ice bottom 3 cm sections for ice algae.

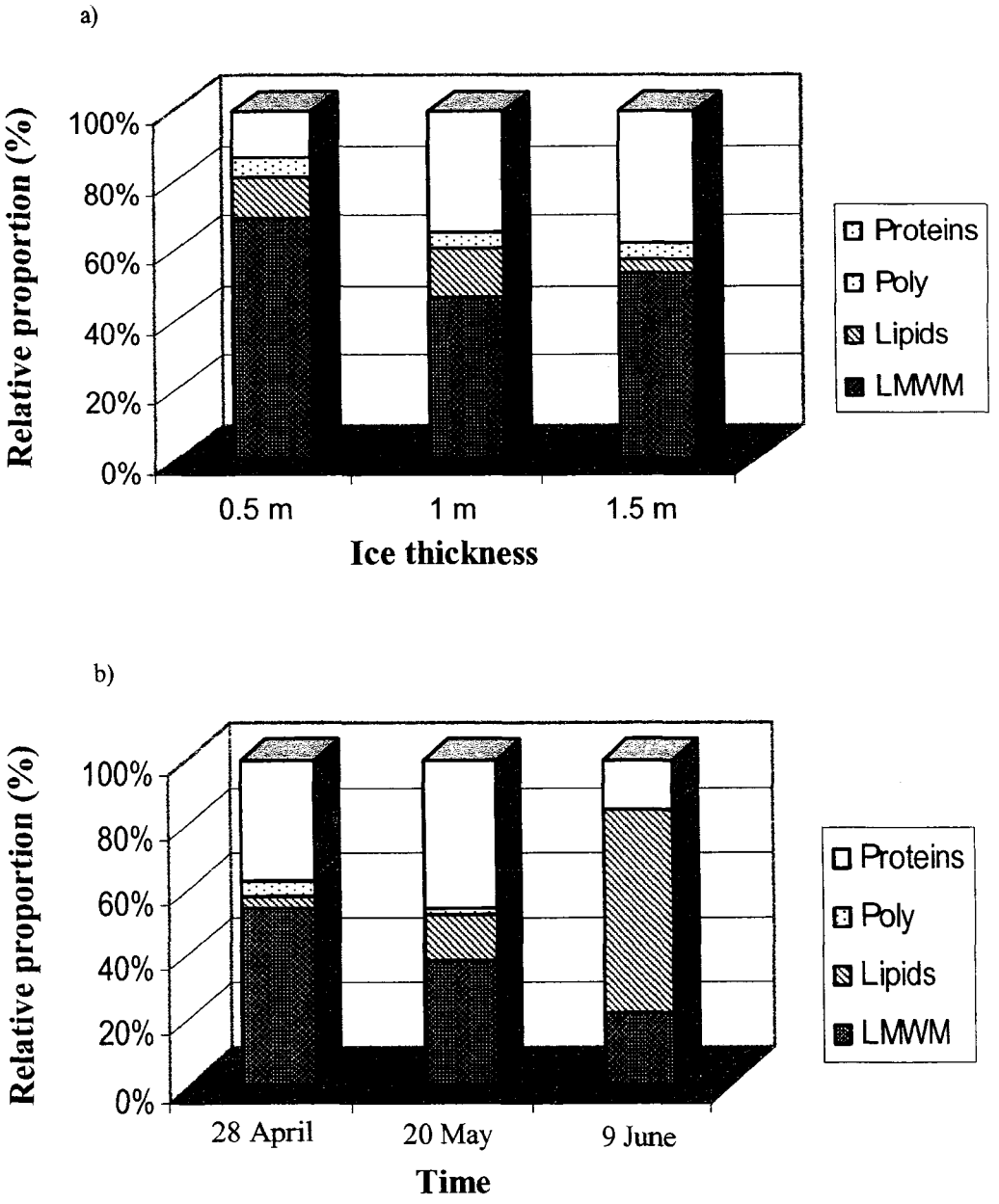


Fig. 3.22. Photosynthetic carbon allocations into different macromolecules of the bottom ice algae a) from different ice thickness on 28 April and b) through the season in 2003. The light intensities at the different ice thickness were 168, 99, and 4 μE m^{-2} s^{-1} for 0.5 m, 1 m, and 1.5 m, respectively. LMWM is low-molecular-weight metabolites and poly means polysaccharides.

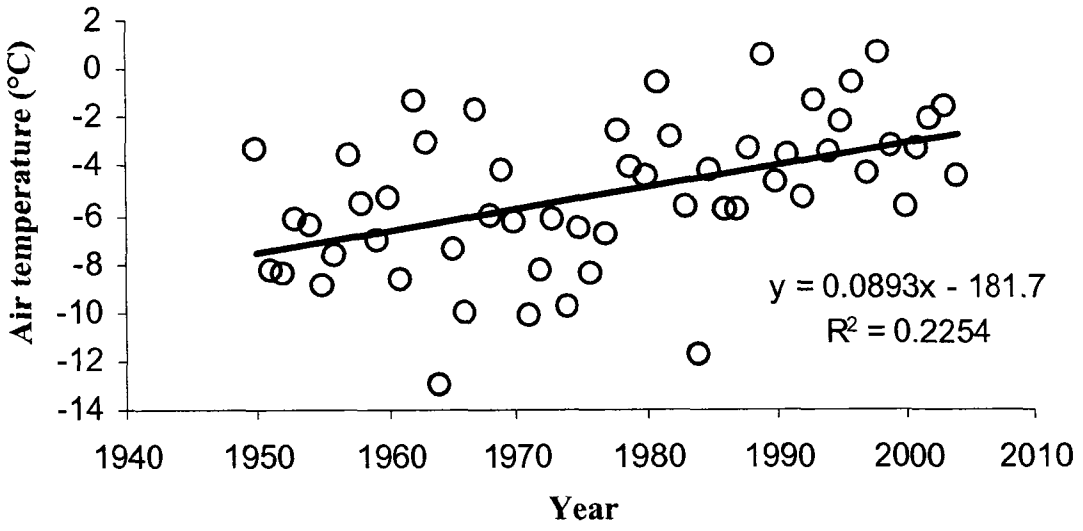


Fig. 3.23. The historical mean air temperature at Barrow from January to May between 1950 and 2004. The data are from the Western Regional Climate Center, US: http://www.wrcc.dri.edu.

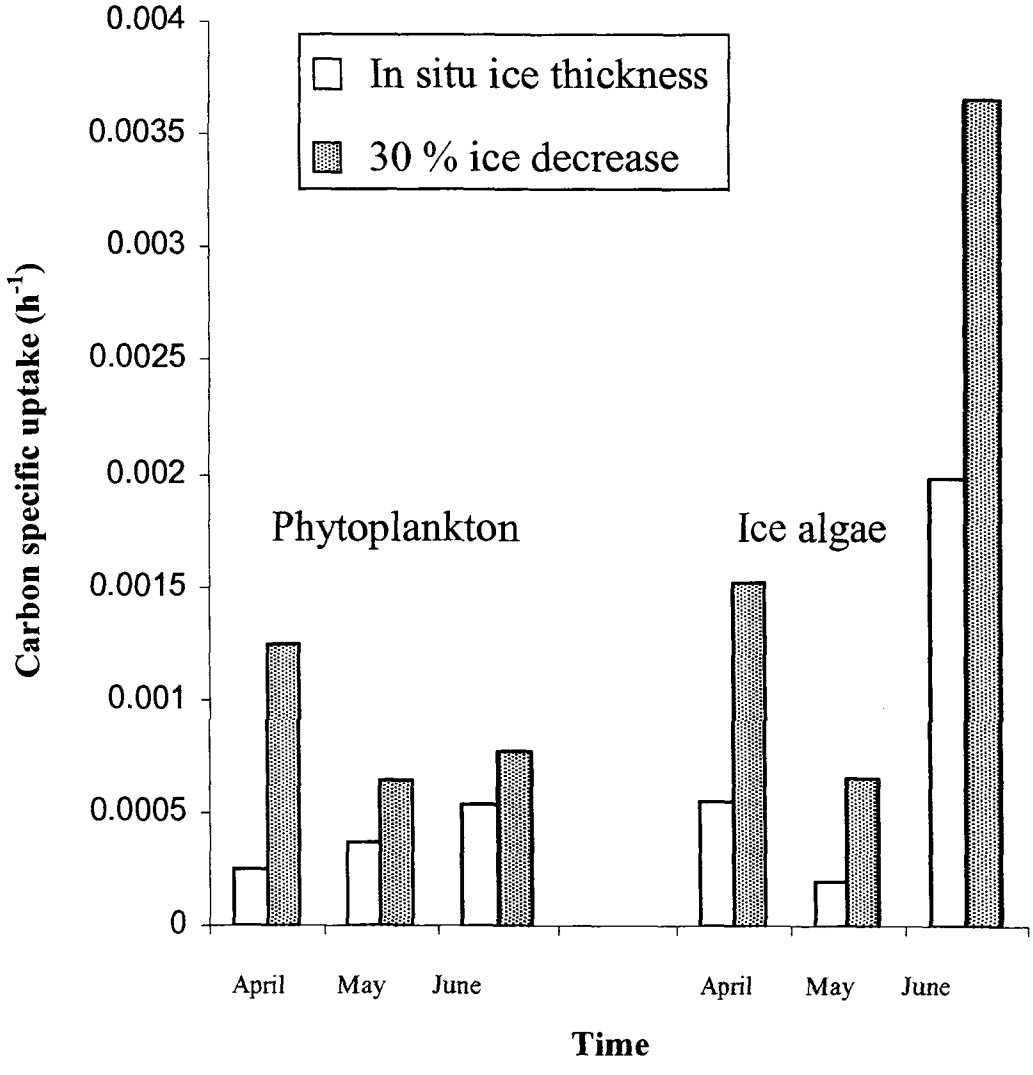


Fig. 3.24. The carbon uptake rates of phytoplankton and bottom ice algae under *in situ* ice thickness and 30 % less ice thickness at the land fast ice of Barrow during the growing season.

Table 3.1. Physical parameters at sampling sites on the fast sea-ice of Barrow in 2003 and 2004. Light intensity beneath the sea ice was measured one time at around 12 P. M. during the productivity experiment.

	2003						2004	
Date	Feb 12th	Apr 1st	Apr 28th	May 20th	May 27th	June 9th	Mar 2nd	May 2nd
Air temperature (°C)	-26	-20	-3	0	1	1	-23	-7
Mean snow depth (cm)	2	2.5	7.5	20	4	3.5	5	7.5
Ice thickness (cm)	82	130	138	140	140	140	135	175
Temperature (°C) in water column (2 m)	-1.6	-1.7	-1.6	-1.6	-1.7	-1.3	-	-
Salinity in water column (2 m)	-	32.4	32	32	31.2	31.4	-	-
Temperature(°C) in bottom ice (3 cm)	-3.4	-2	-1	-2.5	-1.4	-0.6	-	-
Bulk salinity in bottom ice (3 cm)	-	-	13	8.4	-	5.3	-	-
Light intensity (μE m^{-2} s^{-1}) under the ice	1.72	11.5	6.7	3.4	7.7	14.9	-	-

Table 3.2. The uptake rates of nitrate and ammonium of phytoplankton and ice algae. The unit is mg N/m^2 hr. S.D. stands for standard deviation.

Type		1 April	28 April	20 May	27 May	9 June	Average	S.D.
Phytoplankton	NO_3	0.0046	0.0069	0.0080	0.0156	0.0488	0.0168	0.0184
	NH_4	0.0198	0.0352	0.0287	0.0561	0.0991	0.0478	0.0317
Ice Algae	NO_3	0.0013	0.1449	0.0256	0.2279	0.0046	0.0809	0.1012
	NH_4	0.0076	0.1493	0.0452	0.2673	0.0136	0.0966	0.1111

Table 3.3. The maximum chlorophyll-a of the bottom ice algae in land fast ice of different locations of Alaskan and Canadian Arctic. Only Bering Sea from McRoy and Goering (1974) was a seasonal pack ice.

Region	Maximum Chl-a of bottom ice algae (mg m^{-2})	Location	Reference	Ice section
Alaskan Arctic	24	Barrow	Meguro et al. (1967)	colored bottom ice fragments
	23-31	Barrow	Alexander et al. (1974)	interfacial bottom
	26	Beaufort	Horner and Schrader (1982)	interfacial bottom
	27	**Barrow**	**This study (2003)**	**bottom 3 cm section**
	24	Barrow	Shin (2002, unpublished)	bottom 3 cm section
	3	Bering Sea	McRoy and Goering (1974)	bottom 5 cm section
Canadian Arctic	23	Jones Sound	Apollonio (1965)	visually evident chlorophyll section
	10	Robeson Channel	Dunbar and Acreman (1980)	bottom 20 cm section
	19-130	Resolute	Smith et al. (1987, 1989)	bottom 4 cm section
	225	Resolute	Smith et al. (1988)	bottom 3 cm section
	100	Resolute	Welch and Bergmann (1989)	bottom 4 cm section
	160	Resolute	Michel et al. (1996)	bottom 2-4 cm section
	25	Hudson Bay	Dunbar and Acreman (1980)	bottom 20 cm section
	10-30	Hudson Bay	Gosselin et al. (1985, 1986)	bottom 20 cm section
	< 20	Hudson Bay	Tremblay et al. (1989)	interfacial bottom

Table 3.4. f-ratios of size-fractionated phytoplankton and ice algae. Small size represents < 5 µm and > 0.8 µm, and large size is > 5 µm. The f-ratios of large size is estimated, based on biomass. S.D. stands for standard deviation.

Type	Size	1 April	28 April	20 May	27 May	9 June	Average	S.D.
Phytoplankton	total	0.19	0.16	0.22	0.22	0.33	0.22	0.06
	small	0.05	0.04	0.13	0.26	0.12	0.12	0.09
	large	0.23	0.18	0.24	0.18	0.36	0.24	0.08
Ice Algae	total	0.15	0.49	0.36	0.46	0.25	0.34	0.15
	small	0.05	0.18	0.13	0.16	0.14	0.13	0.05
	large	0.15	0.50	0.37	0.48	0.25	0.35	0.15

Table 3.5. Annual production (g C m^{-2} yr^{-1}) of the ice algae in the first-year ice in the Alaskan and Canadian Arctic regions. * represents data from a seasonal pack ice.

Region	Production	Method	Location	Reference
Alaskan Arctic	5	in situ	Barrow	Alexander et al. (1974)
	1	in situ	Prudhoe Bay	Horner et al. (1974)
	1.7	from chl-a	Offshore Beaufort Sea	Schell (1980)
	0.22-1.5	from chl-a	Bering Sea	*Alexander and Chapman (1981)
	0.7	in situ	Narwhal Island	Horner and Schrader (1982)
	0.9	in situ	Stefansson Sound	Horner and Schrader (1982)
	2	in situ	Barrow	**This study**
Canadian Arctic	4.4	estimated	Labrador Shelf	*Irwin (1990)
	5-23	in situ	Resolute Passage	Smith et al. (1988)
	5	estimated	Canadian Archipelago	Bergmann et al. (1991)
	1-10	estimated	Frobisher Bay	Grainger (1975)

Chapter 4. Recent carbon and nitrogen uptake rates of phytoplankton in Bering Strait and the Chukchi Sea

Abstract

Cruises to Bering Strait and the Chukchi Sea in US waters from early September in 2000 to early September in 2004 and a joint US-Russian research cruise (RUSALCA) in 2004 covered all major water masses and contributed to understanding of the regional physics, nutrient dynamics, and biological systems. The integrated concentration of the high nitrate pool in the central Chukchi Sea was greater in this study than in previous studies although the highest nitrate concentration (~ 22 μM) in the Anadyr Water mass passing through the western side of Bering Strait was consistent. The chlorophyll-a near the western side of the Diomede Islands ranged from 200 to 400 mg chl-a m^{-2} and the range in the central Chukchi Sea was 200 to 500 mg chl-a m^{-2} for the 2002-2004 *Alpha Helix* (HX) cruises. Chlorophyll-a concentrations for the 2004 RUSALCA cruise were lower than those from previous studies. Mean annual primary production of phytoplankton from this study was 55 g C m^{-2} for the whole Chukchi Sea and 122 g C m^{-2} for the plume of Anadyr-Bering Shelf Water in the central Chukchi Sea. In contrast, the averages of annual total nitrogen production were 13.9 g N m^{-2} (S.D. = ± 16.2 g N m^{-2}) and 33.8 g N m^{-2} (S.D. = ± 14.1 g N m^{-2}) for the Chukchi Sea and the plume, respectively. These carbon and nitrogen production rates were consistently 2 or 3 fold lower than those from previous studies. I suggest that the lower carbon and nitrogen uptake rates in this study, and consequently more unused nitrate in the water column, were caused by lower phytoplankton biomass in Bering Strait and the Chukchi Sea. However, I do not know if the lower rate of productivity from this study is a general decreasing trend or simply temporal variation in the Chukchi Sea, since temporal and geographical variations are substantially large and presently unpredictable.

4.1. Introduction

Bering Strait is the only conduit of water masses and organic matter between the North Pacific and Arctic Oceans. The mean annual transport through Bering Strait is about 0.8 Sv (Coachman and Aagaard 1988; Roach et al. 1995). The basic driving force of this flow is a ~ 0.5 m height difference between the Bering Sea and the Arctic Ocean (Coachman et al. 1975; Coachman and Shigaev 1992). The transport through the strait has a pronounced seasonal cycle with a summer maximum and a winter minimum and large interannual variations (Coachman and Aagaard 1988). The observed strong variability in the northward flow is caused mainly by the regional wind conditions (Coachman et al. 1975).

The three different water masses passing northward through Bering Strait are Anadyr Water (AW), Bering Shelf Water (BSW) and Alaska Coastal Water (ACW). These are distinguished primarily by their salinity differences (Coachman et al. 1975; Aagaard 1987). ACW has a low salinity (< approximately 31.8) due to fresh water input from rivers flowing into the southeastern Bering Sea. BSW, which is colder (0-3 °C) and more saline (31.8-32.5) than ACW, originates primarily in the middle shelf south of St. Lawrence Island. AW originates along the Bering shelf break and is a high salinity (32.5-33.0) northern branch of the Bering Slope Current (Coachman et al. 1975; Kinder et al. 1975; Coachman and Shigaev 1992; Weingartner 1994). Of these water masses, AW supplies the Chukchi continental shelf with high nutrients that promote abundant phytoplankton growth throughout summer and transports oceanic zooplankton onto the shallow northern shelf and into the Chukchi Sea through the western Bering Strait (Sambrotto et al. 1984; Springer et al. 1989; Springer and McRoy 1993). Usually, the ratio of the three different water masses is 6:3:1, respectively for AW, BSW, and ACW (Coachman et al. 1975). However, the ratio varies seasonally and inter-annually, mostly due to local influences of the wind (Coachman et al. 1975). Consequently, the location and direction of these water masses moving

through Bering Strait have a strong influence on the physical conditions, nutrient concentrations and phytoplankton activity observed in this important gateway to the Arctic Ocean (Springer 1988; Springer and McRoy 1993).

The quantity of nutrients and organic matter flowing through this major passage into the Chukchi Sea and subsequently into the Arctic Ocean must be determined to understand the present functioning of the Arctic system, especially that related to production and biogeochemical processes. Input through Bering Strait is of particular interest as it is the dominant nutrient source and a major source of buoyancy to the upper layer in the Arctic Ocean (Jones and Anderson 1986; Guay and Falkner 1997; Cooper et al. 1997; Coachman and Aagaard 1988). An accurate assessment of nutrient concentrations and fluxes north of Bering Strait in the Chukchi Sea is essential to assessing and understanding the status and health of the Bering and Western Arctic ecosystems, as well as the changing contribution to regional and global issues of production cycles and biogeochemical cycling (Springer and McRoy 1993; Walsh et al. 1997).

Sambrotto et al. (1984) estimated an annual production of 324 g C m^{-2}, based on the nitrate utilization rate, while Hansell et al. (1993) calculated 576-720 g C m^{-2} for the annual production in the western Anadyr flow north of Bering Strait based on new production in the region. Based on ^{14}C uptake and chlorophyll-a concentration in the region, Springer and McRoy (1993) estimated annual production of 470 g C m^{-2}. These annual estimated pelagic production rates are unusually large considering its Arctic location (Sambrotto et al. 1984). Based on the recent decline from 1977 to 1997 in average $\delta^{13}C$ values on the baleen plates of bowhead whales, which reflects their food sources, Schell (2000) suggested that seasonal primary productivity has decreased by 30-40 % in the northern Bering Sea and presumably the Chukchi Sea over several decades.

The Bering Strait region and Chukchi Sea are important feeding grounds for the western Arctic bowhead whale population, as indicated by stable carbon isotope ratios (Schell et al. 1989; Lee et al. 2005), as well as for many seabird populations (Springer et al. 1987). The extremely high pelagic primary productivity provides the basis for enhanced local secondary production, and the huge biomass of zooplankton advected into the region in the Anadyr Current contributes a major portion of the energy used at higher trophic levels (Springer et al. 1989). Thus, transport to the Chukchi Sea via Bering Strait could play an important role in bowhead feeding opportunities in the northern Chukchi Sea (Moore 2000).

In addition to the pelagic environment, a strong pelagic-benthic coupling of biological processes sustains some of the highest benthic faunal biomass in the Arctic, and consequently supports large populations of benthic-feeding marine mammals and seabirds at higher trophic levels in the food chain (Grebmeier and McRoy 1989; Highsmith and Coyle 1992; Springer et al. 1986; Springer and McRoy 1993).

We continued the long-term monitoring of the effect of inflow into the Arctic Ocean via Bering Strait from early September 2000 to early September 2004 to advance our understanding of physical structures, nutrient dynamics, and biological systems in Bering Strait and the Chukchi Sea (Fig. 4.1). This study covered mainly US waters in those regions, however, the RUSALCA program, which is a joint US-Russian research program, provided the ideal sampling across all major water masses including territorial waters of the Russian Federation in Bering Strait and the Chukchi Sea in 2004 (Fig. 4.2). In this paper we report results of this work in 2000-2004. Our primary objective was to quantify the contemporary ranges of nutrients, phytoplankton biomass and primary productivity in different water masses distributed in Bering Strait and the Chukchi Sea. The second objective was to compare contemporary ranges with those obtained in the

previous decade for assessment of rate changes under the current conditions in the Bering Sea and Chukchi Sea.

4.2. Study areas

The Chukchi Sea extends northward over 1,200 km from Bering Strait to Point Barrow, and is the eastern end of the great arctic continental shelf system of the Arctic Ocean (Aagaard 1987; Weingartner 1997). The shelf is remarkably wide (600-800 km) and relatively shallow (20-60 m) (Aagaard 1987; Niebauer and Schell 1993). North of Bering Strait, the Anadyr and Bering Shelf waters mix and flow northward (15-20 cm/sec) into the central and western Chukchi Sea (Weingartner et al. accepted; Woodgate et al. accepted). ACW also flows northeastward along the Alaska coast (Coachman et al. 1975; Niebauer and Schell 1993). Because the northward flow is warm and of low salinity during summer, the Chukchi Sea becomes ice-free much earlier in the year than it otherwise would (Aagaard 1987). The retreat of sea ice normally begins in early June and the maximum retreat occurs in September (Stringer and Groves 1987). Freeze-up begins in October or November (Niebauer and Schell 1993; Weingartner et al. accepted). Ice thickness progressively increases northward from 0.5-1.0 m thickness in the open Bering Sea to 2 m along the arctic coast (Weeks and Weller 1984).

4.3. Materials and Methods

The data were collected from 5 different cruises during 2000 to 2004 aboard the R/V *Alpha Helix* (HX) and 1 cruise in 2004 aboard on R/V *Professor Khromov* (RUSALCA program). For the HX cruises, data were collected only in US territorial waters of Bering Strait and the Chukchi Sea. More extensive sampling of Bering Strait and the Chukchi Sea was conducted in 10-22 August 2004 from the R/V *Professor Khromov* cruise. The dates of the HX cruises were 31

August-3 September 2000, 8-12 September 2001, 21-29 June 2002, 30 June-8 July 2003, and 29 August-6 September 2004.

4.3.1. Inorganic nutrient analysis

Water samples for inorganic nutrients (nitrate, nitrite, ammonium, silicate, phosphate) were obtained from the Niskin bottles mounted on CTD/rosette samplers and were analyzed on shipboard using an automated nutrient analyzer (ALPKEM RFA model 300) following methods of Whitledge et al. (1981). The accuracy for the nutrients of water samples is ± 0.2 % with a full-scale range of 5 volts.

4.3.2. Chlorophyll-a analysis

Samples for the determination of total chlorophyll-a were filtered onto Whatman GF/F glass fiber filters (24 mm). Size-fractionated chlorophyll-a was determined on samples passed sequentially through 20 µm and 5 µm Nucleopore filters (47 mm) and 0.7 µm Whatman GF/F filters (47 mm). The filters were kept frozen and returned to the laboratory for analysis. The filters were subsequently extracted in a 3:2 mixture of 90 % Acetone and DMSO in a freezer for 24 hours and centrifuged (Shoaf and Lium 1976). Concentrations of chlorophyll-a were measured using a Turner Designs model 10-AU fluorometer which had been calibrated with commercially purified chlorophyll-a preparations. After measuring total fluorescence, 100 µl of 10 % HCl solution was added into the extracted solution and stored in a test tube rack for about 90 seconds to degrade chlorophyll into phaeopigments. A final fluorescence reading was taken after the acidification. The methods and calculations for chlorophyll-a and phaeopigments were based on Parsons et al. (1984).

4.3.3. Inorganic nutrient amendments

Surface water samples from the Niskin bottles were placed in a 4 L plastic jug after screening through a 300 µm mesh net and the jug was stored in a cold and dark refrigerator. After

the jug was rolled and mixed to homogenize the sample, the prescreened surface sea water (50 ml) was distributed into 40 pre-washed amendment tubes. Stock nutrients were added into different tubes as in Table 4.1 and each tube was capped and well mixed. The rack of 40 tubes was placed in the deck incubator with tube bottoms pointing toward the light, and incubated in natural light similar to ambient conditions. After one hour, initial fluorescence values were determined after it was well mixed by inversion and cleaned with kimwipes. Once all vials were read, the rack was returned to the incubator on the deck. Daily fluorescence values for each vial were measured at about the same time of day for 5-9 days.

4.3.4. Carbon and nitrogen uptakes of phytoplankton

Daily carbon and nitrogen uptakes were estimated from six light depths (100, 50, 30, 12, 5 and 1 % penetration of the surface photosynthetically active radiation, PAR), using a ^{13}C-^{15}N dual isotope tracer technique. Each light depth was determined from an underwater PAR sensor lowered with CTD/rosette samplers on the HX cruises, while a LICOR 4π light sensor (LI-193SB model) was used for the light depth determinations on the *Professor Khromov* cruise. Seawater samples of each light depth were transferred from the Niskin bottles to 1L polycarbonate bottles through a 300 μm mesh net to remove large zooplankton from the incubation. The incubation bottles were covered with stainless steel screens for each light depth. Water samples were inoculated with labeled nitrate ($K^{15}NO_3$), ammonium ($^{15}NH_4Cl$), and carbon ($NaH^{13}CO_3$) substrates. The ^{13}C enrichment was ca. 10 % of the total inorganic carbon in the ambient water, and an amount estimated to be 10 % of the ambient nitrate or ammonium concentration was added to each treatment bottle. Bottles were incubated in a deck incubator cooled with surface seawater. Although the running surface seawater in the incubator was 2-3 °C warmer than temperatures at *in situ* depths below the surface, the influence of the warmer temperature on the carbon and nitrogen uptakes of phytoplankton from lower euphotic water depths is generally

considered to be small (Dunbar 1968). The 4-7 hour incubations were terminated by filtration through pre-combusted (450 °C) GF/F glass fiber filters (24 mm). The filters were immediately frozen and preserved for mass spectrometric analysis at the stable isotope laboratory of the University of Alaska Fairbanks. Particulate organic carbon and nitrogen and abundance of ^{13}C and ^{15}N were determined in the Finnigan Delta+XL mass spectrometer after HCl fuming overnight to remove carbonate. ^{13}C and ^{15}N uptake rates were calculated based on Hama et al. (1983) and standard JGOFS procedures (UNESCO 1994), respectively.

Corrections for the isotope dilution effect were not applied to the measurement of ammonium uptake rates (Glibert et al. 1982) because the incubation periods were relatively short (4-7 hours) (Dugdale and Wilkerson 1986). However, this protocol might underestimate the uptake rate of ammonium. The isotope dilution effect was calculated by using the equations in Kanda et al. (1987). The average underestimation for ammonium uptake ranges from 5 % (S.D. = ± 0.1 %) to 12 % (S.D. = ± 0.2 %), assuming a = 1 and a = 2 ("a" is the ratio of regeneration and uptake), since the value of "a" is reasonably assumed to be in the range of 1-2 (Glibert 1982; Glibert et al. 1985). The isotope dilution effect on NH_4^+ uptake was somewhat small at productivity stations in the Chukchi Sea probably because of relatively brief incubations and high ammonium concentration in the water column.

4.3.5. Photosynthetic carbon allocations of phytoplankton

To evaluate the photosynthetic carbon allocations of phytoplankton in different water masses, the incubations for the macromolecular classes were accomplished at 3 light depths (100, 30, and 1 % of PAR) at two stations which were distinctly different in salinity, temperature, and nutrient concentrations. The ^{13}C enrichment for photosynthetic carbon allocations of phytoplankton was ~ 15 % of the total inorganic carbon in the ambient water. The incubations were terminated by filtration through pre-combusted (450 °C) GF/F glass fiber filters

(47 mm) after 7-10 hours, depending on weather conditions. The filters were immediately frozen and preserved for analysis in the lab. The basic method for differential extraction of macromolecular classes (low-molecular-weight metabolites, lipids, proteins, and polysaccharides) is identical to the method in Chapter 3.

4.4. Results

4.4.1. Salinity and temperature structures in Bering Strait

Temperature and salinity structures in the water column of Bering Strait were different among seasons and years (Figs. 4.3-7). In 2000, relatively low salinity water (< 31.8), which is believed to be ACW, occupied the entire western part of the U.S. side of Bering Strait (Fig. 4.3). In 2001 and 2003, salinity was somewhat higher (32-32.5) and the water column was well mixed from surface to the bottom except the top layer on the western side. In 2004, the structures of salinity and temperature were rather similar to those in 2003, except high salinity (> 32.5) existed in the bottom layer of the western side in 2004 (Fig. 4.7). In contrast, the physical structure was unusual in 2002 (Fig. 4.5) due to wind and current flows to the south. As a result, lower salinity and higher temperature water from the ACW spread westward on top of more saline and colder Anadyr-Bering Shelf water that extended eastward on the bottom. The temperature in 2002 was somewhat lower than those from other years. This water column structure provided an unusual nutrient supply to a greater extent on the eastern side of the transect (Fig. 4.11). This will be discussed later in the nutrient and chlorophyll-a sections.

4.4.2. Salinity structure on an areal basis

In general, the low salinity ACW (< 31.8) was located along the eastern coastline and higher salinity water (> 32.5) was found on the western side of the southern Chukchi Sea (Figs. 4.8-10). However, the surface current flows tended to be displaced by local wind conditions of

the southern Chukchi Sea in 2002 and 2004 (Figs. 4.8a and 4.10a). The structure of surface salinity in 2004 showed a rather similar pattern to 2002, whereas the bottom salinity distributions were quite similar in 2002, 2003, and 2004 (Figs. 4.8b, 4.9b, and 4.10b).

4.4.3. Vertical structure of NO_3 in Bering Strait.

NO_3 concentrations varied with water mass in Bering Strait. That is, the concentration of NO_3 was almost depleted (< 1 μM) in ACW whereas the AW had relatively high NO_3 concentrations (Fig. 4.3-7). When there was a strong ACW flow at least as far west as the central Bering Strait in 2000, NO_3 was almost depleted across the whole transect (Fig. 4.3). In contrast, when there was a strong AW flow in the strait in 2002, high NO_3 concentrations existed in the water column, although most of the NO_3 at the surface was still depleted due to high uptake of phytoplankton (Fig. 4.5c and d). In the intermediate conditions between those two cases in 2000 and 2002, there existed a strong vertical salinity front separating the two different water masses which were well mixed from surface to bottom. As a result, NO_3 was observed only on the western side of the strait, where the AW existed, in 2001, 2003, and 2004 (Figs. 4.4, 4.6, and 4.7).

4.4.4. Integrated NO_3 concentration in Bering Strait

The interannual variation of integrated nitrate concentration in the water column of the Bering Strait Line (BSL) in Bering Strait was large between years even when the seasonal differences were taken into account (Fig. 4.11). For example, at BSL 1 integrated nitrate concentrations ranged from approximately 2 to 653 mg-at NO_3-N m^{-2} over the 5 year-observation period. Especially in 2002, the enhanced nitrate concentrations continued up to BSL 3 because of higher nutrient concentrations in the AW lying below the ACW (Fig. 4.5b). In contrast, integrated nitrate concentrations were very low (< 13 mg-at NO_3-N/m^2) in 2000 when ACW was present at all stations. In 2004, integrated nitrate was highest (653 mg-at NO_3-N m^{-2}) at BSL 1 probably because the influence of Anadyr water was strongly felt on the western side of the strait. The

highest nitrate concentration was 21.5 μM near the bottom at BSL 1 in 2004. In comparison, the highest integrated nitrate concentration from the RUSALCA cruise was 826 mg-at NO_3-N m^{-2} at station 9, which is markedly higher than that from BSL 1 from the HX cruise in 2004. However, the maximum nitrate concentration was 21.8 μM near the bottom of station 9 in the RUSALCA cruise, which was almost identical to the concentration at BSL 1 on the HX cruise in 2004.

4.4.5. Integrated NO_3 concentration in the Chukchi Sea

There were three distinct regions of particularly high nitrate concentrations in the water column of the Chukchi Sea. One was just north of Little Diomede Island and another was in the central Chukchi Sea (Fig. 4.12a, b, and c), and the last was in Herald Canyon near Wrangell Island (Fig. 4.12d). The maximum values of integrated nitrate in those pools were 681 mg-at NO_3-N m^{-2} in the Chukchi pool in 2003, 858 mg-at NO_3-N m^{-2} near Little Diomede Island in 2004, and 1328 mg-at NO_3-N m^{-2} in Herald Canyon in 2004 from the RUSALCA cruise. Although the size of the high nitrate pool (400-500 mg-at NO_3-N m^{-2}) in the central Chukchi Sea was somewhat different among years, the location and nitrate concentration were quite similar among years for the HX cruises. However, the lateral extent of the high nitrate region in the central Chukchi Sea was larger and the concentration was somewhat higher (600-800 mg-at NO_3-N m^{-2}) from the RUSALCA cruise than from the HX cruises (Figs. 4.9d vs. 4.9a, b, and c). The low nitrate concentrations (< 50 mg-at NO_3-N m^{-2}) were located on the eastern side of the Chukchi Sea, where the typical nitrate-depleted ACW mass occurred throughout the water column.

4.4.6. Areal distributions of inorganic nutrients in Bering Strait and the Chukchi Sea

The nitrate concentration of the surface water was mostly depleted where the water was vertically stratified (Figs. 4.8a, 4.9a, and 4.10a). There was residual nitrate content at the surface in the western part of Bering Strait, which had an origin from AW and the water column was well

mixed (Figs. 4.4b, 4.6b, and 4.7b). The near bottom layer provided a substantial amount of nitrate from the western to the eastern side during a northward flow of water (Figs. 4.8b, 4.9b, and 4.10b). Ammonium was found to have low concentrations in surface water in 2002 and 2003, while it was relatively high in 2004. In contrast, the bottom ammonium concentrations were generally high, especially on the western side of the Chukchi Sea. The bottom concentrations in 2004 were higher than those in 2002 and 2003, which might be seasonal variation, since the sampling time in 2004 was late August to early September, unlike 2002 and 2003: relatively higher ammonium concentrations accumulated over the summer months due to high production and remineralization. The surface silicate concentrations were not as depleted as nitrate, although the silicate concentrations were much lower in surface water than in bottom water. The silicate concentrations decreased from the east to the west in the surface as well as in bottom water in 2002 and 2004. In 2003, the trend of the surface silicate concentration was very interesting in that it increased from the east to the west.

4.4.7. Chlorophyll-a concentration in Bering Strait and the Chukchi Sea

The chlorophyll-a concentrations were high at the surface on the western side of Bering Strait where nitrate concentrations were generally highest (Figs. 4.3-7). This is true for different seasons and different years. The maximum value of chlorophyll-a for the years 2000-2004 was 13.3 mg chl-a m^{-3} at BSL 1, which was located near the Diomede Islands. In comparison, the highest chlorophyll-a value from the RUSALCA cruise in 2004 was 19.6 mg chl-a m^{-3} at station 10 at the western end of the Bering Strait section. There were no chlorophyll-a concentrations higher than 1 mg chl-a m^{-3} on the eastern side of the strait occupied by nitrate-depleted ACW. Generally, integrated chlorophyll concentrations ranged from approximately < 50 mg chl-a m^{-2} at the eastern end of the transect to > 300 mg chl-a m^{-2} at the western end where AW was present (Fig 4.13).

Cross sections from the BSL to the Point Hope Line (PHL) in the Chukchi Sea (see the Map in Fig. 4.1) are shown in Fig. 4.14 and revealed that high chlorophyll-a was limited to the western side of the basin as expected because the AW carries large amounts of phytoplankton and nutrients (Robie et al., 1992; Springer and McRoy 1993). The western sides of the BSL and A3 Line (A3L) had notably high chlorophyll-a, whereas CHUK line had low chlorophyll-a over most of the section. Station CCL 14 at the western end of the PHL had conditionally high chlorophyll-a depending on the current directions. For example, low chlorophyll-a near the western end of the PHL in 2002 was may have resulted from southward winds and current flows that moved the high chlorophyll-a pool from near CCL 14 southward. As a result, lower chlorophyll-a values (< 1 mg chl-a m^{-3}) characterized the majority of the PHL, whereas relatively higher chlorophyll-a concentrations occurred at the surface in the western parts of BSL and A3L in 2002 than in 2003 and 2004 (Fig. 4.14). A pronounced subsurface chlorophyll-a maximum was observed in most sections in 2002 and 2003 cruises, whereas the chlorophyll-a maximum existed in surface water in 2004 (Fig 4.14). The maximum chlorophyll-a values in the Chukchi Sea were 13.3 mg chl-a m^{-3} in BSL 1, 17.6 mg chl-a m^{-3} in CCL 14 (the end of the western PHL section), and 7.8 mg chl-a m^{-3} in A3L 1 for 2002, 2003, and 2004, respectively.

The highest integrated chlorophyll-a concentrations found during the cruises were 734 mg chl-a m^{-2} at station CCL 4 north of the Diomede Islands in 2002, 509 mg chl-a m^{-2} at CCL 13 in 2003, and 492 mg chl-a m^{-2} at CCL 15 from the HX cruise and 450 mg chl-a m^{-2} at station 74 from the RUSALCA cruise in 2004. The distribution of chlorophyll-a closely matched the distribution of nitrate concentrations in the Chukchi Sea (Figs. 4.12 and 4.15). That is, there were three distinct areas of high nitrate and chlorophyll-a concentrations in the Chukchi Sea as compared to the low chlorophyll-a (< 50 mg chl-a m^{-2}) in the nitrate-depleted water mass on the eastern side of the Chukchi Sea.

4.4.8. Size-fractionated chlorophyll-a in Bering Strait and the Chukchi Sea

The phytoplankton community in the Bering Strait water column was generally dominated by the large size fraction (> 5 μm). It is interesting that the composition of the different sizes was nearly identical in Bering Strait in different seasons of years (Fig. 4.16) even though the distributions of integrated chlorophyll-a were different in 2003 (30 June-8 July) and 2004 (29 August-6 September). Large phytoplankton (> 5 μm) comprised 95.8 % of the chlorophyll biomass in the water column at station BSL 1 and 75.8 % of the chlorophyll biomass at station BSL 6 in 2003. In 2004, it was 94.9 % and 69.4 %, respectively for the western and eastern part of Bering Strait in US territorial waters. In comparison, the western part (Station 10) of the whole Bering Strait from the RUSALCA cruise in 2004 had 95.8 % of phytoplankton > 5 μm (Fig. 4.17) which was identical to those from the station BSL 1 in 2003 and 2004. The > 5 μm size class was 70.1 % of the chlorophyll biomass for station 6 from the RUSALCA cruise which is a location similar to BSL 6 from the HX cruises in the eastern part of the strait.

Fig. 4.18 shows the two distinctly different phytoplankton communities in the two different water masses (determined by bottom salinities at 40 m) in Bering Strait and the Chukchi Sea. Phytoplankton > 20 μm contributed about 46 % and 94 % of biomass in the water column of ACW and AW, respectively. The cells < 20 μm and > 5 μm contributed 18.2 % (S.D. = ± 5.5 %) and small cells (< 5 μm and > 0.7 μm) made up 40.4 % (S.D. = ± 19.2 %) in ACW. In contrast, intermediate and small size cells comprised 3.2 % (S.D. = ± 2.6 %) and 3.1 % (S.D. = ± 3.1 %), respectively, of the phytoplankton in AW.

4.4.9. Inorganic nutrient amendment experiments in the Chukchi Sea

To evaluate effects of inorganic macronutrients and the micronutrient iron on phytoplankton growth, three nutrient amendment experiments from the RUSALCA cruise in 2004 were done for the surface phytoplankton community at different stations which were assumed to

have different physical, chemical, and thus biological conditions. The chlorophyll fluorescence was assumed to be representative of the growth of phytoplankton, although this parameter depends sometimes on species and physiology of phytoplankton. After a one day incubation, the phytoplankton from NO_3, NH_4, PO_4+NO_3, SiO_4+NO_3, and Fe+NO_3 treatments started to grow faster than those of the rest of the treatments at station 10 (Fig. 4.19). At the end of the incubation, the fluorescence from NO_3, NH_4, PO_4+NO_3, SiO_4+NO_3, and Fe+NO_3 treatments was 6 to 9 times higher than that of control samples that had no additions. At station 14 (Fig. 4.20), phytoplankton from five treatments (NO_3, NH_4, PO_4+NO_3, SiO_4+NO_3, and Fe+NO_3) grew faster than those from other treatments after day one, but the growth of phytoplankton from only NO_3, Fe+NO_3, and PO_4+NO_3 treatments was significantly different from other treatments at the end of incubation (t-test, $p < 0.01$). The fluorescence from NO_3, Fe+NO_3, and PO_4+NO_3 treatments was slightly higher (~ 2 times) than that of the control. The growth pattern from station 27 (Fig. 4.21) was rather different from those at stations 10 and 14. They grew slowly even after addition of inorganic nutrients and started to grow slightly in NO_3, NH_4, PO_4+NO_3, SiO_4+NO_3, and Fe+NO_3 treatments after day 3. At the end of the incubation, day 6, the fluorescence from NO_3, NH_4, PO_4+NO_3, SiO_4+NO_3, and Fe+NO_3 treatments was 3.5 to 5 times higher than that of control sample.

4.4.10. Carbon uptake rates of phytoplankton in the Chukchi Sea

The carbon uptake rates for the RUSALCA productivity stations were collected only during the summer of 2004, while the uptake rates of A2, A3 and CCL 15 from the HX cruises were mean values from 2002 to 2004. The carbon uptake from the surface to 1 % light depth ranged from 0 to 25.4 mg C m^{-3} h^{-1} with a mean of 2.5 mg C m^{-3} h^{-1} (S.D. = ± 4.8 mg C m^{-3} h^{-1}) in the Chukchi Sea (Table 4.2). Daily integrated rates ranged from 45 to 1496 mg C m^{-2} d^{-1} with a mean of 552 mg C m^{-2} d^{-1} (S.D. = ± 619 mg C m^{-2} d^{-1}), based on a 15 hour photo period in the

Chukchi Sea (Hansell and Goering 1990). Generally, the maximum carbon uptake from the RUSALCA cruise occurred at the 100 % light depth except stations 10, 89 and 73B in the Chukchi Sea. The maximum uptakes at those stations occurred at subsurface. From the HX cruises, only A3 had a subsurface maximum of carbon uptake rate. The depth of the euphotic zone from 100 % to 1 % light depth was 23 m for productivity stations from the RUSALCA cruise in 2004 and averaged 33 m from the HX cruises for 3 years from 2002 to 2004.

4.4.11. Nitrogen uptake rates of phytoplankton in the Chukchi Sea

Generally, there were no discernable trends for nitrate and ammonium uptake rates of phytoplankton with decreasing light intensity at depth (Table 4.3). The nitrate uptake rates of phytoplankton ranged from undetectable to as high as 4.40 mg N m^{-3} hr^{-1} at station 14 with a mean of 0.24 mg N m^{-3} hr^{-1} (S.D. = ± 0.60 mg N m^{-3} hr^{-1}). Ammonium uptake rates ranged from 0.01 to 8.34 mg N m^{-3} hr^{-1} (mean ± S.D. = 0.47 ± 1.37 mg N m^{-3} hr^{-1}) for the RUSALCA and HX cruises in the Chukchi Sea. The range of vertically integrated nutrient uptake rates at different stations was from 0.14 to 15.95 mg N m^{-2} hr^{-1} and from 0.95 to 34.45 mg N m^{-2} hr^{-1}, respectively for nitrate and ammonium in the Chukchi Sea.

To determine which nitrogen form is preferred for phytoplankton growth, a relative preference index (RPI) for nitrate was calculated as

$RPI_{NO3} = \rho(NO_3^-)/ \{\rho(NO_3^-) + \rho(NH_4^+)\}/[NO_3^-]/([NO_3^-]+[NH_4^+])$,

where $\rho(NO_3^-)$ and $\rho(NH_4^+)$ represent the uptake rates and $[NO_3^-]$ and $[NH_4^+]$ at the observed ambient concentrations (McCarthy et al. 1977). If an RPI_{NO3} value was less than one, it indicated a preference for ammonium. If an RPI_{NO3} was greater than one, it indicated a nitrate preference (McCarthy et al. 1977). When the ratios of NO_3 and NH_4 uptake rates were compared with the ratios of these nutrients dissolved in the water (Fig. 4.22), most samples showed a strong NO_3 preference except the samples from 1 % light depths.

4.4.12. Photosynthetic carbon partitioning into macromolecules

Photosynthetic carbon partitioning into macromolecules at two different stations is shown in Fig. 4.23. The photosynthate partitioning at station 14 from the RUSALCA cruise was characterized by a high relative C flow into the low-molecular-weight metabolites (LMWM) at 100 % and 30 % light depths. The C incorporation into proteins tended to increase with light depths from 17.4 % up to 76 %. As a result, carbon to nitrogen uptake ratios of phytoplankton were lower at depth at both stations (Fig. 4.25). The compositions of LMWM and proteins at the 1 % light depth were totally opposed to those at 100 % light depth at station 14. Percentages of C incorporation into polysaccharide and lipid fractions were usually low at different depths. In comparison to station 14, predominant macromolecular classes at PHL 12 were LMWM and proteins at 100 % and 30 % light depths. The production fractions of LMWM were 43 % and 47 %, respectively for 100 % and 30 % light depths, whereas protein productions were 39 % at 100 % light depth and 48 % at 30 % light depth. For the 1 % light depth, the production of proteins was dominant with 70 % of the total particulate production. C incorporation into lipids was low (< 4 %) at different depths while polysaccharides attained the maximal relative proportion with 20.7 % at the 1 % light depth at PHL 12. The macromolecular compositions were averaged across the different depths (Fig. 4.24) to reduce the environmental differences from the each depth. At station 14, LMWM was predominant (53.1 %) followed by proteins (40.3 %). In contrast, proteins were predominant (52.2 %) and followed by LMWM (31.6 %) in the water column of station PHL12.

4.5. Discussion

4.5.1. Inorganic nutrient content in the Chukchi Sea

The highest observed nitrate concentration was ~ 22 μM in the western side of Bering Strait and the central Chukchi Sea. This high nitrate concentration is consistent with that reported from Whitledge et al. (1992). The presence of these high bottom nitrate concentrations may indicate that some nitrification occurs in the Chirikov Basin and Chukchi Sea (Whitledge et al. 1992). The range of the high nitrate pool was from 400 to 500 mg-at NO_3-N m^{-2} in the central Chukchi Sea for 2002 and 2003 HX cruises (Figs. 4.12a and b). Springer (1988) reported between 200-400 mg-at NO_3-N m^{-2} from 1985 to 1987 and Hansell and Goering (1990) reported nitrate concentrations < 500 mg-at NO_3-N m^{-2} in the same region. A somewhat higher range (600-800 mg-at NO_3-N m^{-2}) was found from the HX and RUSALCA cruises in 2004 (Figs. 4.12c and d). The high nitrate concentrations observed in this study might be due to seasonal and/or interannual variations in nitrate concentrations or lower nitrate uptake by reduced phytoplankton biomass (this point is discussed in more detail later).

In contrast, ammonium in surface waters was generally found to be at very low concentrations (< 1 μM; Figs. 4.8a and 4.9a) because of the high affinity of phytoplankton for ammonium. However, there were some locations near Bering Strait with high ammonium in the surface water in 2004 (Fig. 4.10a). These high concentrations might reflect active ammonium regeneration in the near bottom waters and sediments rather than in surface water since the bottom is quite shallow (< 50 m) and the water is well mixed by passing through Bering Strait (Coachman and Shigaev 1992). Relatively high bottom ammonium concentration (Figs. 4.8b-10 b) indicates active ammonium regeneration in the near bottom waters and sediments. A large amount of ammonium is usually released from decomposition of organic matter, especially where high primary production deposition is occurring such as in the central Chukchi Sea (Whitledge et

al. 1992). The highest range of silicate concentration through western Bering Strait was generally 20-34 μM from the HX and RUSALCA cruises between 2002 and 2004. This high silicate is generally associated with AW.

The highest concentration of silicate in the central Chukchi Sea was 20-30 μM in 2002 and 2003 (Figs. 4.8b and 4.9b), while it was 40-50 μM from both cruises in 2004. Higher concentrations (> 60 μM) were found in the water mass with low temperature (< – 1.6 °C) and high salinity (> 33) below the surface water in Herald Canyon near Wrangell Island in the 2004 RUSALCA cruise. The maximum value was ~ 92 μM at 30 m of at station 49 in the canyon (Fig. 4.10b) which is much higher than the highest silicate concentrations from Cooper et al. (1997) and Cooper et al. (1999). The temperature and salinity of the water mass associated with this high silicate concentration in Herald Canyon near Wrangell Island in the 2004 are similar to the description of Weingartner et al. (1999). This water mass forms in the polynya that develops along the south coast of Wrangell Island in winter (Weingartner et al. 1999; refs therein). The high silicate and nitrate concentrations might result from regeneration in the water mass over summer months since high phytoplankton biomass exists in polynya regions during the winter-spring period. There were high chlorophyll-a concentrations in the bottom layer in the region but phytoplankton was inactive based on the ratio of chlorophyll-a/phaeopigments and carbon uptake rates. Silicate is mainly utilized by diatom populations which are dominant in the Chukchi Sea during midsummer (Bidigare et al. 1992) and it appears that there are sufficient quantities of nutrients for them to grow at maximal rates over most of the region.

4.5.2. Chlorophyll-a concentration in Bering Strait and the Chukchi Sea

The chlorophyll-a concentrations at the stations in Bering Strait varied as the result of chemical abundance, which was driven by the physical processes in the region (Figs. 4.3-7). In 2002 when AW extended further east, more nitrate was available to phytoplankton on the BSL

and thus more phytoplankton was observed than in other years. In contrast to that, when ACW extended farther west on the BSL in 2000, integrated nitrate concentration was very low (Fig. 4.11), and subsequently low chlorophyll-a occurred at all stations of the transect. Overall, the fertilization by AW enhanced nutrients and chlorophyll biomass at the western end of US territorial waters in Bering Strait. The distribution of integrated chlorophyll-a concentrations in the Chukchi Sea displayed no large differences among years in this study (Fig. 4.15). Normally, high levels of chlorophyll-a occurred in the western part whereas low values (< 50 mg chl-a m^{-2}) occurred in the eastern part as a result of the different nutrient concentrations in the different water masses. There were three distinct regions of particularly high chlorophyll-a concentrations in Bering Strait and the Chukchi Sea. One was located west of the Diomede Islands, another one was in the central Chukchi Sea (Figs. 4.15a-d) and the final one was in Herald Canyon in the northwestern part of the Chukchi Sea (Fig. 4.15d). The high chlorophyll near the Diomede Islands ranged from 200 to 400 mg chl-a m^{-2} and the pool in the central Chukchi Sea ranged from 200 to 500 mg chl-a m^{-2} for the 2002-2004 HX cruise and 2004 RUSALCA cruise. The chlorophyll-a pool ranged from 200 to 400 mg chl-a m^{-2} in Herald Canyon where high chlorophyll-a concentrations were present below the surface layer (~ 30 m) in 2004.

The range of integrated chlorophyll-a in the pool near the Diomede Islands is somewhat lower in this study than in previous studies, whereas the highest range from the central Chukchi Sea pool is much lower. In the mid-1980s chlorophyll-a ranged from 400 to 600 mg chl-a m^{-2} and 600 to over 1500 mg chl-a m^{-2} for the pools near the Diomede Islands and the central Chukchi Sea, respectively (Robie et al. 1992; Springer 1988; Springer and McRoy 1993). This difference might be caused by the interannual variation in chlorophyll-a concentrations as reported previously (Springer and McRoy 1993). For example, it might be a result of slower growth rates of phytoplankton transported into these regions due to nutrient or light limitation. Nitrate and

ammonium were nearly depleted in the euphotic layers of most of the productivity stations. Moreover, phytoplankton might have more light limitation in this study than previous studies, since the maximum carbon uptakes occurred mostly at the surface (0 m) in this study (Table 4.2) whereas the maximum uptakes were usually found at the depths between 5 and 15 m in Korsak (1992). An alternative explanation is that less phytoplankton biomass was transported through Bering Strait during the years of this study. The flow of AW into the Chukchi Sea carrying high nutrients and phytoplankton biomass from the productive regions upstream in the Chirikov Basin creates the large chlorophyll pool in the central Chukchi Sea (Robie et al. 1992; Springer and McRoy 1993). Thus, lower chlorophyll-a concentrations reported here might indicate lower phytoplankton biomass transported through Bering Strait. Actually, the highest value of chlorophyll-a at the end of the western Bering Strait was somewhat lower in 2004 than in Robie et al. (1992) who reported values of ~ 20 mg chl-a m^{-3} in 2004 and > 30 mg chl-a m^{-3}. However, the large interannual variation of the chlorophyll-a concentrations in this region (Springer 1988; Fig 4.13) makes it difficult to conclude if the lower chlorophyll-a concentrations in this study are from a few observations at different times during an annual variation or from a longer term decreasing trend in phytoplankton biomass of the Chukchi Sea.

4.5.3. Areal distribution of size-fractionated chlorophyll-a.

There are some implications for marine ecosystems from the size composition of phytoplankton at the base of the food web. For example, the different size compositions could influence the number of trophic levels in pelagic food-chains and thus transfer efficiency in the food-chains (Malone 1980), the extent of coupling between pelagic and benthic environments (Grebmeier and McRoy 1989; Joint et al., 1993), and the relative partitioning of nitrate or ammonium utilization in the ecosystem.

Generally, large cells (> 5 μm), which grow best under eutrophic conditions, were dominant in Bering Strait and the Chukchi Sea. Even in ACW where nitrate is normally depleted, large cells dominated (~ 60 %). The dominance of larger phytoplankton in Bering Strait and the Chukchi Sea indicates a shorter, and consequently, more efficient food chain (Parsons 1972). However, because of their fast sinking rate in this shallow basin, these large cells are an advantageous to the benthic food web (Grebmeier and McRoy 1989). A major vertical flux of carbon to the bottom occurs when the food web is based on large phytoplankton cells (Joint et al., 1993). Grebmeier et al. (1988) found low C/N ratios (5.8 to 7.6) at the surface sediment under Anadyr-Bering Shelf Water, indicating a high quality, nitrogen-rich marine carbon supply to the benthos. In contrast, they found lower quality organic matter (higher C/N ratios = 7.7 to 14.0) and much lower benthic biomass in sediment under ACW. The quality and quantity of organic matter that sinks to the bottom as potential food for the benthos depend on a number of major factors such as the rate of primary production, sinking rate of phytoplankton, zooplankton grazing rate, and overall water column depth and proximity to land runoff sources (Grebmeier et al., 1988). Because the zooplankton grazing rate is low (~ 1 % of the daily phytoplankton production) here (Shuert and Walsh 1993), grazing might be ruled out as the reason for the different productions and qualities in sediments under the two different water masses. The water column depth is shallower under the ACW than under Anadyr-Bering Shelf Water and there are more effects of land runoff sources on the sediment under the ACW (Naidu et al., 1993). Therefore, primary productivity and thus cell size structure of phytoplankton community (presumably different sinking rates) are believed to be a major reason for two distinct benthic ecosystems in the Chukchi Sea.

4.5.4. Inorganic nutrient enrichment

Station 10, which was located at the western end of the Bering Strait, showed statistically significantly different growths of phytoplankton in NO_3, NH_4, PO_4+NO_3, SiO_4+NO_3, and Fe+NO_3 treatments after 5 days incubation (t-test, $p < 0.01$). There was no significant difference among those treatments that had nitrogen additions. Since growths of phytoplankton from PO_4, SiO_4, and Fe treatments were not different from the control, it appears that NO_3 and NH_4 are major nutrients supporting the growth of phytoplankton even though the concentrations of PO_4 and SiO_4 were relatively higher than those of NO_3 and NH_4. RPI_{NO3} (= 2.89) indicates a strong preference for NO_3, while the f-ratio (= 0.43) in Table 4.4 shows a community fueled by slightly more NH_4 than NO_3 at station 10. At station 14, only NO_3, Fe+NO_3, and PO_4+NO_3 were significantly different at the end of the incubation (t-test, $p < 0.01$). Since there was no significant growth of phytoplankton from only Fe and PO_4 treatments, NO_3 appears to be the major limiting nutrient in the phytoplankton community even though it was not depleted (~ 1 μM) at the surface. In fact, both the f-ratio (= 0.89 in Table 4.4) and RPI_{NO3} (= 2.63) show a strong affinity of phytoplankton for NO_3 at this station.

The growth pattern from station 27 (see the map in Fig. 4.2) was somewhat different from those of other stations. The growths of phytoplankton from treatments started to differ significantly by day 3. The upper surface water (< 10 m) of station 27 had low salinity (< 31.5) and nearly depleted nutrients except SiO_4. Like other stations, however, growth of phytoplankton from NO_3, NH_4, PO_4+NO_3, SiO_4+NO_3 and Fe+NO_3 treatments was significantly different from that of the control at the end of the incubation. NO_3 and NH_4 are probably major nutrients supporting the growth of phytoplankton at the station because of insignificant enhancement of the phytoplankton growths from PO_4, SiO_4, and Fe treatments. At this station, NO_3 was almost depleted while NH_4 was higher at the surface. The RPI_{NO3} from the surface at this station suggests

a slight preference (RPI = 1.12) for NO_3, whereas the f-ratio shows a strong affinity to NH_4 (f-ratio = 0.05), which might indicate that phytoplankton slightly preferred NO_3 but they largely utilized NH_4 because NO_3 was unavailable to them.

In general, there was no demonstrable iron effect on the growth of phytoplankton based on the following assumptions; the increasing fluorescence from the incubation mostly depended on the increasing growth rather than changes in species composition or physiology of phytoplankton during the incubation, and there were no synergistic effects of the combination of Fe + NO_3 (in other words, the enhanced fluorescence from the Fe and NO_3 treatment was the result of NO_3 addition because there was no statistically significant enhancement in the fluorescence from only Fe addition). The iron limitation of the growth of phytoplankton is well documented in open oceans (Martin 1992) rather than coastal environments (Hutchins et al. 1998) because open oceans are remote from terrestrial sources of iron. The Chukchi Sea is a typical shallow shelf (< 50 m) and the water is well mixed from the surface to the bottom in passing through Bering Strait. It has been noted that those areas with iron limitation are dominated by small cells (< 5 μm) (Morel et al. 1991; Hutchins et al. 1998). The predominant (> 97 % of the composition; Fig. 4.18) large size of cells (> 5 μm) in these regions provides indirect evidence against possible iron limitation.

4.5.5. The photosynthetic-end products in two different water masses of the Chukchi Sea

Photosynthetic C partitioning into macromolecules at two different stations is shown in Fig. 4.23. Station 14 was in a cold (< 5 °C) and saline (> 32.7) water mass which is a typical AW, whereas station PHL 12 was in a warmer (> 9.5 °C) and less saline (< 31) ACW. At station 14, NH_4 concentrations were nearly depleted at the surface (100 % light depth) to 3.4 μM at the 1 % light depth while NO_3 concentrations were relatively high from 1.9 to 22 μM. In contrast, PHL 12 had relatively high NH_4 (2-3 μM) and depleted NO_3 (< 0.06 μM) through the euphotic zone. The

carbon allocations between two stations were rather different at each light depth (100, 30, and 1%; Fig. 4.23) and in the water columns averaged by 3 different light depths (Fig. 4.24). The C incorporation into lipids was very low from 1 to 4 % (Fig. 4.24). The proportion of lipids reported in the literature is 5 to 30 % (Lindqvist and Lignell 1997; Wainman and Lean 1992). High incorporation into lipids is to be expected under physiologically N deficient phytoplankton or during stationary growth phases (Morris 1981; Parrish 1987), whereas high incorporation into proteins generally reflects physiologically healthy phytoplankton with high relative growth rates (DiTullio and Laws 1986; Palmisano et al. 1988). Low incorporation into lipids and relatively high incorporation into proteins at PHL 12 (Fig. 4.24) suggest that phytoplankton had no nitrogen limitation at that time. This is an interesting result since phytoplankton from ACW mass has been thought to be nitrogen limited (Hansell and Goering 1990; Hansell et al. 1993). Although NO_3 was nearly depleted, NH_4 was relatively high (2-3 μM) throughout the water column at PHL 12 in 2004. The relatively high ammonium is believed to have provided enough nitrogen for phytoplankton demand at PHL 12 where small cells (< 5 μm and > 0.7 μm) comprised about 50 % of the community.

In contrast, the protein incorporation at 100 and 30 % light depths was somewhat lower at station 14, while the C incorporation into LMWM was considerably higher at station 14 than at PHL 12 (Fig. 4.23). Large allocation to LMWM has been reported for phytoplankton of the Southern Ocean (Barlow and Henry 1982) as well as ice algae (Smith et al., 1987; McConville et al., 1985), but there are no plausible explanations for the high LMWM allocations at 100 and 30 % light depths of both stations. It might be the accumulation of certain amino acids, sugars, and/or sugar alcohols with cold resistance functions (Smith et al., 1987). However, this is not the case, since the LMWM allocations were lowest for the 1 % light depths which had coldest waters among the three light depths. Under sufficient nutrient conditions, the dominant pathway is the

production of LMWM, which is the precursor of macromolecules such as free amino acids and carbohydrates as storage forms (Smith et al., 1989; Lindqvist and Lignell 1997; Mock and Gradinger 2000). Conover (1975) and Dortch et al. (1984) described the storage of free amino acids in diatom cells. The predominant phytoplankton community at station 14 is believed to be large, chain-forming diatoms, whereas diatoms and flagellates are predominant at PHL 12 (Springer and McRoy 1993). However, this explanation either does not explain the lower LMWM productions at the 1 % light depths which had higher nutrients in both stations. The most plausible explanation for the difference of phytoplankton C metabolism at each light depth of both stations is the different light intensity since irradiance is a major factor affecting C allocation into different macromolecules (Suárez and Marañón 2003). However, the observed vertical variability in phytoplankton C allocation could result from the combination of nutrient concentration, temperature and irradiance.

Carbon incorporation into proteins tended to increase with depth at both stations (Fig. 4.23), which is consistent with other marine (Morris 1981; Fernández et al., 1994; Suárez and Marañón 2003) and freshwater (Hama et al. 1990) studies. Carbon allocation into different macromolecules of phytoplankton under different physiological conditions might be part of the reason that the assimilated C/N uptake ratios in Fig. 4.25 deviated from the expected value of Redfield ratio (= 6.6).

4.5.6. Carbon uptake rates in Bering Strait and the Chukchi Sea

Station A2 in the eastern Bering Strait was dominated by ACW which is normally depleted in major nutrients concentrations through the water column so that the production might be limited for nutrients. In contrast, station 10 in the western Bering Strait had salinity > 32.5 which is typical of the AW. Usually, AW has enriched nutrients originating in the deep Bering Sea (Whitledge et al. 1992) but the nutrients at station 10 were low from 0 to 6 m, which was 100

to 12 % light intensity depths. The nutrient amendment experiment indicated that the phytoplankton in the surface water of station 10 might have nutrient limitation in 2004 since the biomass increased with NO_3 and NH_4 additions (Fig. 4.19). Therefore, station 10 might have nutrient limitation for phytoplankton in most of euphotic zone (from 100 to 12 % light depth). After phytoplankton passed through Bering Strait, the production rates were substantially higher at stations 11, 14 and CCL 15 in the central Chukchi Sea (Fig. 4.26) because the strong current from topographic conditions in the strait enhanced mixing of the water column (Coachman and Shigaev 1992; Zeeman 1992). The production rates at these 5 stations where high nutrient concentrations generally dominated ranged from 0.39 g C m^{-2} d^{-1} at station 10 to 1.50 g C m^{-2} d^{-1} at CCL 15 with a mean of 1.22 g C m^{-2} d^{-1} (S.D. = ± 0.47 g C m^{-2} d^{-1}). In comparison, the production rate was 0.07 g C m^{-2} d^{-1} at stations 24 and 27, located in the western central Chukchi Sea, which had two distinct water layers, a warm (4-8 °C) and less saline (< 31.5) surface layer (~ 15 m) and a cold (2–-1 °C) and saline (> 32.9) bottom layer (below 20 m). Most of the euphotic surface layer (up to 5 % light intensity depth) had nearly depleted nutrients, which might cause nutrient limitation for production and consequently low primary production rates at those stations. The cold and saline bottom layer water below 20 m might be Siberian Coastal water, which has higher salinity (> 32.9) than AW (Coachman and Shigaev 1992; Weingartner et al. 1999). This water associated with the Siberian Coastal Current forms in the polynya along the south coast of Wrangell Island in winter (Weingartner et al. 1999; refs therein). The high nutrient concentrations associated with this southward flowing water mass might be an additional nutrient source that combines with the northward flowing water mass through Bering Strait and thus enhances the primary production rates in the central Chukchi Sea (Whitledge et al. 1992). But this hypothesis is not applicable for stations 24 and 27 because warm and less saline surface water which was depleted in nutrients comprised most of the euphotic layer.

Carbon uptake rated in Bering Strait and the Chukchi Sea ranged from 0.1 g C m^{-2} d^{-1} to 1.5 g C m^{-2} d^{-1} with a mean of 0.6 g C m^{-2} d^{-1} (S.D. = ± 0.6 g C m^{-2} d^{-1}) from 2002 to 2004. Because of large differences among water masses in the Chukchi Sea, the production rates within the same water mass should be compared. In addition, the sampling season for the measurements should be considered since productivity has large variations in this region (Springer and McRoy 1993). The average productivity rates in the southern part of the Chukchi Sea during late July to August from previous studies (Table 4.5) were 1.7 g C m^{-2} d^{-1} with a range from 0.39 to 4.7 g C m^{-2} d^{-1} (Korsak 1992) and 1.6 g C m^{-2} d^{-1} with a range from 0.15 to 5.5 g C m^{-2} d^{-1} (Zeeman 1992). The average rate from the stations in the southern Chukchi Sea (excluding st. 73B, 89, 106 and 107) from this study during 10-22 August 2004 was 0.4 g C m^{-2} d^{-1} with the range from 0.05 to 1.49 g C m^{-2} d^{-1} which is less than half of values from previous studies. These values are not statistically different probably because of large geographical variations. The mean productivity for AW of the Chukchi Sea during 10-22 August 2004 is much lower in this study (1.4 g C m^{-2} d^{-1}) than in Springer and McRoy (1993; 4.7 g C m^{-2} d^{-1}) based on the chlorophyll-a concentration from 1-28 July and the ^{14}C uptake from late July to August in 1988. However, the average productivity (1.4 g C m^{-2} d^{-1}) in 2004 from this study is near the range (1.6-1.9 g C m^{-2} d^{-1}) for the central Chukchi Sea during 12-25 July 1986 from Springer (1988), although his measurements were limited only to the U.S. side of the Chukchi Sea and occurred at a different time in the year. Although the range for low to moderate levels of productivity (0.1-1.0 g C m^{-2} d^{-1}) from Hameedi (1978) in Table 4.5 is similar to this study, he measured productivity in the marginal ice zone of the northern Chukchi Sea during summer, thus the comparison might be unreasonable since the physical and chemical structures could be different in the water columns of the two environments.

Based on 100 growing days (Springer and McRoy 1993), the annual production of phytoplankton from this study is between 10 to 150 g C m^{-2} with a mean of 73 g C m^{-2} for the

southern Chukchi Sea, while the mean annual production for the whole Chukchi Sea including the northwestern part (st. 73B, 89, 106 and 107) is somewhat lower (55 g C m^{-2}). In comparison, the estimated averages of annual primary production rates for the whole Chukchi Sea are 148 and 170 g C m^{-2} from Zeeman (1992) and Korsak (1992) respectively, based on their daily measurements. Although the mean of their production rates encompass the highest range of this study, the mean annual production in this study is 2 or 3 fold lower than the production rates from the previous studies. The difference between this and previous studies might be caused by many factors. The lower production in this study might be the result of seasonal, annual, and/or geographical variations in primary productivity in the Chukchi Sea. Those variations are well known in this area and are mostly attributed to different water masses and thus nutrient concentrations, i.e., the meandering nature of the flow field of AW (Springer and McRoy 1993; Springer 1988; Hansell and Goering 1990). Most productivity data in this study were from the 2004 RUSALCA cruise during 10-22 August. However, the daily production rates at stations 11 and 14 from the 2004 RUSALCA cruise were very similar to those at stations A3 and CCL 15 from the HX cruises (Table 4.2) as representative for the "plume" of AW based on salinity, even though the rates at st. 11 and 14 were from the middle of August in 2004 while the rates at A3 and CCL 15 were averaged from the different seasons and years from 2002 to 2004. The average production rate for the central Chukchi Sea is 122 g C m^{-2} y^{-1} from this study, whereas the value from previous studies is 470 g C m^{-2} y^{-1} (Springer and McRoy 1993), based on 100 growing days. In contrast, the production based on 120 days is 144 g C m^{-2} y^{-1} from this study which is still lower than those from Hansell et al. (1993) (576-720 g C m^{-2} y^{-1}) and Sambrotto et al. (1984) (324 g C m^{-2} y^{-1}). When the annual primary production rates for only the plume of AW are compared, the production values from previous studies are about 3 to 5 fold higher than that in this study.

This large difference from the same water regime might result from the different methods to estimate the production. Springer and McRoy (1993) calculated the production from the relationship between chlorophyll-a biomass and productivity of phytoplankton, and Sambrotto et al. (1984) and Hansell et al. (1993) estimated the annual production based on NO_3 utilization in Bering Strait. However, the mean production rates for AW estimated from Springer (1988), Korsak (1992) and Zeeman (1992) using a similar method (^{14}C uptake) are still 2 or 3 fold higher than this study. Their observed mean production rates were 270, 263 and 327 g C m^{-2} y^{-1}, respectively, based on 100 growing days. The production estimates determined by Springer and McRoy (1993) were based on calculations using chlorophyll-a biomass and P/B ratios (production/biomass of phytoplankton). The mean chlorophyll-a concentration from 5 stations for the plume of Anadyr Water in this study is much lower than their result. Moreover, the average P/B ratio from 5 stations in this study was 8.2 whereas their estimated ratio was 16.5, which indicates more production per unit of phytoplankton than in this study. Euphotic layer depths (100 to 1 % light intensity depths) also are different between this and previous studies. The mean euphotic depth in this study was 23 m from the RUSALCA cruise in 2004 and 33 m from the HX cruises for 3 years from 2002 to 2004, whereas the average of euphotic layer was 45-50 m from Korsak (1992). Consequently, the maximum rates of phytoplankton production occurred mostly near the surface (100 % light depth) in this study, while the maximum values were usually found at depths between 5 and 15 m in Korsak (1992).

Three plausible hypotheses are suggested for the difference in the primary production rates between this and previous studies. The first hypothesis is that the composition of the water masses flowing through Bering Strait and their distributions in the Chukchi Sea might differ between years, since the production rates in the Chukchi Sea highly dependent on the types of water masses (Hansell and Goering 1990). ACW normally has low biomass and nutrients whereas

the Anadyr-Bering Shelf water mass, especially the AW, carries high biomass and nutrients (Robie et al. 1992; Springer and McRoy 1993). Usually, the ratio of the three different water masses passing through Bering Strait is 6:3:1, respectively for AW, BSW, and ACW (Coachman et al. 1975). However, their presence is seasonally and inter-annually rather variable mostly due to local influences of the wind (Coachman et al. 1975). Increased amounts of ACW flowing through Bering Strait and into the Chukchi Sea might lead to lower biomass and nutrients causing less primary production in the Chukchi Sea. Woodgate et al. (2005) found that the water column moving through Bering Strait was fresher and warmer during the summer/autumn period of 2000-2004 than previous years.

The second hypothesis is related to temporal variability in transport through the strait especially during summer months. This effect could apply even if the composition of different water masses through Bering Strait was constant. In years of strong summer transport through Bering Strait, the growing phytoplankton might be quickly moved through the system and might be distributed over a much larger area in the Chukchi Sea. The annual transport estimated from geostrophic winds was substantially lower (Roach et al. 1995) and the average euphotic layer was deeper in 1988 than in this study. Most of previous primary production data that cover the entire Chukchi Sea were obtained in 1988 (Korsak 1992; Zeeman 1992; Springer and McRoy 1993). Moreover, Hameedi (1978) observed relatively high productivity in the central Chukchi Sea in 1974 when the annual transport was much lower than the average value (Roach et al. 1995). Since the summer transport through Bering Strait is maximum for a year, the annual transport might be strongly connected with the summer flow. In fact, the transport through Bering Strait in 2004 was somewhat larger (1.0 Sv) than the mean annual transport (0.8 Sv) (Rebecca Woodgate pers. comm.). These two hypotheses are based on the assumption that the different production rates

between this and previous studies resulted from temporal or/and annual variations in physical environmental factors in the Chukchi Sea.

The third hypothesis is that the primary production has decreased in the Bering and Chukchi Seas (Schell 2000). He suggested that the primary production in the northern Bering and Chukchi Seas has decreased by about 30-40 % over several decades based on a decrease in $\delta^{13}C$ in whale baleen. Another retrospective assessment of primary productivity based on evidence from stable carbon isotopes in seabirds supports this decline hypothesis of a decline in the primary production on the Bering/Chukchi shelf (Abromaitis 2000). An overall decline in benthic standing stock from the 1980's to the present that occurred in the Bering Strait region (Grebmeier and Cooper 2004) might also be a result of a decrease in the primary production. This decrease in primary production in the Bering and Chukchi Seas over the past two decades might be due to environmental changes. Schell (2000) hypothesized that the reduced transport through the strait caused less onshelf flow, lower nutrient fluxes, and thus less productivity, since the estimated transport through Bering Strait decreased from 0.85 to 0.6 Sv over the past 40 years (Roach et al. 1995). Because inter-annual variation of the transport is large (Roach et al. 1995) and the primary production depends on water masses in the Chukchi Sea, there can be many processes contributing to a decline in primary production. For example, another mechanism for the decrease in primary production of the Bering and Chukchi Seas over decades could be related to changes in the composition of water masses passing through Bering Strait. Recently, Peterson et al. (2002) found that the mean annual discharge from the six largest Eurasian rivers to the Arctic Ocean has increased and is apparently related to the increase in the global mean surface air temperature. If more terrestrial discharge, especially the Yukon River increased the relative amount of ACW flowing through the strait, it might have carried lower phytoplankton biomass and nutrients causing less production in the Chukchi Sea. Another mechanism would be lower primary

production in the southern part of Bering Strait and thus lower phytoplankton biomass carrying through the strait. The overall conclusion of this study is that the lower productivity observed might be an indication of the long-term decline in primary production of the northern Bering and Chukchi Seas.

If the lower productivity observed from this study was part of a general trend in this region and the production estimated from this study was representative for the current Chukchi Sea, the primary production has decreased by about 60-80 % from the late 1980s to the early 2000s in the Chukchi Sea. This decline is two fold higher than the estimation (30-40 %) from Schell (2000). However, we do not know if the lower productivity rates from this study represent an overall trend or are related to interannual or shorter term variations.

4.5.7. Nitrogen uptake rates in Bering Strait and the Chukchi Sea

The uptake rates of total nitrogen ($NO_3^- + NH_4^+$) in the Chukchi Sea ranged from 1.37 mg N m^{-2} hr^{-1} to 36.47 mg N m^{-2} hr^{-1} with an average of 9.24 mg N m^{-2} hr^{-1} (S.D. = ± 10.68 mg N m^{-2} hr^{-1}). For the uptake rates in different areas, the average uptake rate of total nitrogen from low nutrient areas was 3.41 mg N m^{-2} hr^{-1} (S.D. = ± 3.34 mg N m^{-2} hr^{-1}), whereas the average total nitrogen for the high nutrient AW in the Chukchi Sea was 22.55 mg N m^{-2} hr^{-1} (S.D. = ± 9.42 mg N m^{-2} hr^{-1}). The ranges of total nitrogen uptake rate for the Chukchi Sea are lower than those from previous studies (Hansell and Goering 1990; Sambrotto et al. 1984; McRoy et al. 1972). In particular, the average of total nitrogen uptake for the high nutrient AW from this study is about 4 fold lower than that from Hansell and Goering (1990). The range of mean values reported by Hansell and Goering (1990) for the Chukchi Sea was from 9.10 mg N m^{-2} hr^{-1} to 86.80 mg N m^{-2} hr^{-1} and their mean value of total nitrogen uptake rate only for the central Chukchi Sea was 85.54 mg N m^{-2} hr^{-1}. However, they included the urea uptake in the total nitrogen uptake calculation, and urea contributed was about 27 % to total nitrogen uptake rate in the area of the Chukchi Sea.

If this amount of urea uptake was added to the average of total nitrogen uptake rate for AW calculated in this study, then the new value would be 28.64 mg N m^{-2} hr^{-1} which is still 3 times lower than that reported from Hansell and Goering (1990).

McRoy et al. (1972) observed that the nitrate contribution was 89 % of total nitrogen uptake rate (NO_3^- + NH_4^+) above the 10 % light depth from one station in the western Bering Strait. In addition, Sambrotto et al. (1984) found that the contributions of nitrate were 55 % and 40 % of total nitrogen uptake (NO_3^- + NH_4^+) in the western Bering Strait and southeast Bering Strait, respectively. Based on 3 nitrogen sources (NO_3^-, NH_4^+, and urea), Hansell and Goering (1990) measured a 50 % contribution of nitrate north of Bering Strait, 30 % in modified Bering Shelf Water and 15 % in the ACW. The mean contributions of nitrate from this study were 50 % and 35 %, respectively, for the central Chukchi Sea and the area outside of the central Chukchi Sea, which are similar to those from Hansell and Goering (1990). This was true even though there was no urea uptake included in the total nitrogen uptake for this study. Although total nitrogen uptake is much lower in this study, the mean f-ratio in the high nutrient AW is similar to those from previous studies (Hansell and Goering 1990; Sambrotto et al. 1984). This suggests that the characteristics of nitrogen uptake of phytoplankton have not changed in the Chukchi Sea.

A decreasing trend of the relative preference index for nitrate (RPI_{NO3}) (Fig. 4.22) might be related to a strong coupling between light and nitrate or increased ammonium uptake at deeper depths. However, the fact that the averaged RPI_{NO3} values for each light depth (except 1 % light depth) of all productivity stations were higher than 1 suggests a strong preference for NO_3 of phytoplankton in most of the euphotic layer of the Chukchi Sea although only 4 stations out of the 13 productivity stations in this study had high nitrate contributions greater than 50 % (f-ratios in Table 4.4).

The averages of assimilated C/N ratio at different light depths showed a strong relationship to depth (Fig. 4.25). Except for the value at the surface, the averages of all depths are lower than the Redfield ratio (= 6.6). For most stations, nutrients were nearly depleted at the surface and increased at depth. Thus, higher assimilated C/N values at the surface and lower values at depth than the Redfield ratio might be indicative of nutrient conditions for phytoplankton growth at that time. However, the fact that a higher C/N ratio in the central Chukchi Sea (mean ± S.D. = 5.6 ± 1.3) occurred when there were more nutrients in the water column compared to other stations (mean ± S.D. = 4.2 ± 2.9; Table 4.4) implies that other factors control the ratio. One plausible factor might be assimilated photosynthetic products of phytoplankton. The predominant photosynthetic product was proteins at PHL 12 (Fig. 4.24) which is a good representative location for outside of the plume. In comparison, the predominant photosynthetic product was LMWM in the Bering Strait plume area. More protein synthesis could be a partial reason for the lower assimilated C/N uptake ratio in the lower production regions.

Based on a 15 hour photo period for 100 growing days (Hansell and Goering 1990; Springer and McRoy 1993), the mean annual total nitrogen production rates in this study were 13.9 g N m^{-2} (S.D. = ± 16.2 g N m^{-2}) and 33.8 g N m^{-2} (S.D. = ± 14.1 g N m^{-2}) for the entire and the central Chukchi Sea, respectively. In contrast, the mean annual production rates only for nitrate are 6.2 g NO_3 m^{-2} (S.D. = ± 7.4 g NO_3 m^{-2}) in the entire Chukchi Sea and 14.6 g NO_3 m^{-2} (S.D. = ± 6.3 g NO_3 m^{-2}) in the central Chukchi Sea in this study. If assimilated C/N ratios of the central and entire Chukchi Sea from Table 4.4 are representative for those areas, then the estimated annual new production rates are 81.9 g C m^{-2} and 26.0 g C m^{-2}, respectively for the central and entire Chukchi Sea. Hansell et al. (1993) estimated new production of 2.4 g C m^{-2} day^{-1} in AW north of Bering Strait. Based on their daily rates of new production and a 100 day growing season, the estimated annual production was 240 g C m^{-2} for AW which is about 3 fold

higher than in this study. This is consistent with lower values in the integrated chlorophyll-a concentration, annual carbon uptake and total nitrogen uptake in this study.

4.6. Summary and conclusions

The highest nitrate concentrations in the AW passing through the western side of Bering Strait from this study were consistent with that from previous studies. However, the integrated concentration of the high nitrate pool in the central Chukchi Sea was somewhat higher in this study than those from previous studies. This might be due to seasonal variations in the nitrate concentrations or the lower uptake rates of nitrate related to lower phytoplankton biomass in the area. In general, the chlorophyll-a concentration of Bering Strait varied as the result of nutrient abundance which was driven by the physical processes in the region. The distribution and concentration of integrated chlorophyll-a were similar among years.

There were three distinct high chlorophyll-a areas located near the Diomede Islands, in the central Chukchi Sea, and in Herald Canyon. High composition (94 %) of large cells (> 20 μm) and thus fast sinking rates as well as high primary productivity in AW supply a high quality, nitrogen-rich marine carbon to the benthos at the surface sediment (Grebmeier and McRoy 1989). The range of integrated chlorophyll-a in the area near the western Diomede Islands was somewhat lower in this study than in previous studies whereas the highest range from the central Chukchi Sea was much lower than the lowest range from previous studies. Moreover, the highest chlorophyll-a concentrations in the AW mass of the western Bering Strait was lower in 2004 than in previous decades.

Overall compositions of the photosynthetic-end products averaged by water depths were somewhat different in AW and ACW. LMWM was predominant (53.1 %) followed by proteins (40.3 %) in an AW station, whereas proteins were predominant (52.2 %) followed by LMWM

(31.6 %) in the water column of ACW. Low incorporation into lipids and relatively high incorporation into proteins at both stations suggested that phytoplankton had no nitrogen limitation at that time. Although the station in ACW had nearly depleted NO_3, relatively higher NH_4 concentration in the water column probably provided enough nitrogen for phytoplankton at the time of the incubation since ammonium is a preferred nitrogen source for phytoplankton, especially for small cells.

The average rate of carbon productivity from stations in the southern Chukchi Sea from this study was almost half the values from previous studies although they were not statistically different probably because of the high spatial variability. The average productivity for the central Chukchi Sea was much lower in this study than in Sambrotto et al. (1984) and Springer and McRoy (1993). Three plausible hypotheses are suggested for the difference in the production rates between this and previous studies. The first hypothesis is that more ACW flowed through Bering Strait in this study period, and that it reduced the volume transport of AW. The second is a temporal difference in the transport through Bering Strait especially for summer time. This could be significant even if the composition of different water masses through Bering Strait is the same. In this case a continuous strong summer transport through Bering Strait in this study might quickly move growing phytoplankton through the system and distribute the increasing biomass over a much larger area. The third hypothesis is that the primary production has decreased in the Bering and Chukchi Seas over decades (Schell 2000). The current lower production might be an indication for the long-term decline in primary production of the northern Bering and Chukchi Seas. If the lower productivity from this study were a general trend in this region and the production estimated from this study were representative for the current Chukchi Sea, the primary production rates have decreased by about 60-80 % from the late 1980s to the early 2000s in the Chukchi Sea. In any case, the lower productivity from this study might be caused mainly by

lower phytoplankton biomass arriving in the southern Chukchi Sea to seed the area. Consistent with the lower carbon uptake rate, the total nitrogen uptake rate for the Chukchi Sea, especially the central area from this study, was lower than those from previous studies (Hansell and Goering 1990; Sambrotto et al. 1984; McRoy et al. 1972), although the mean contributions of nitrate for the center and outside of the Chukchi Sea from this study were similar to those from Hansell and Goering (1990).

In conclusion, it appears that lower phytoplankton biomass in Bering Strait and the Chukchi Sea resulted in the lower carbon and nitrogen uptake rates and consequently more unused nitrate in the regions. However, we do not know if the lower productivity from this study is a general trend or simply reflects temporal/annual variations in the Chukchi Sea.

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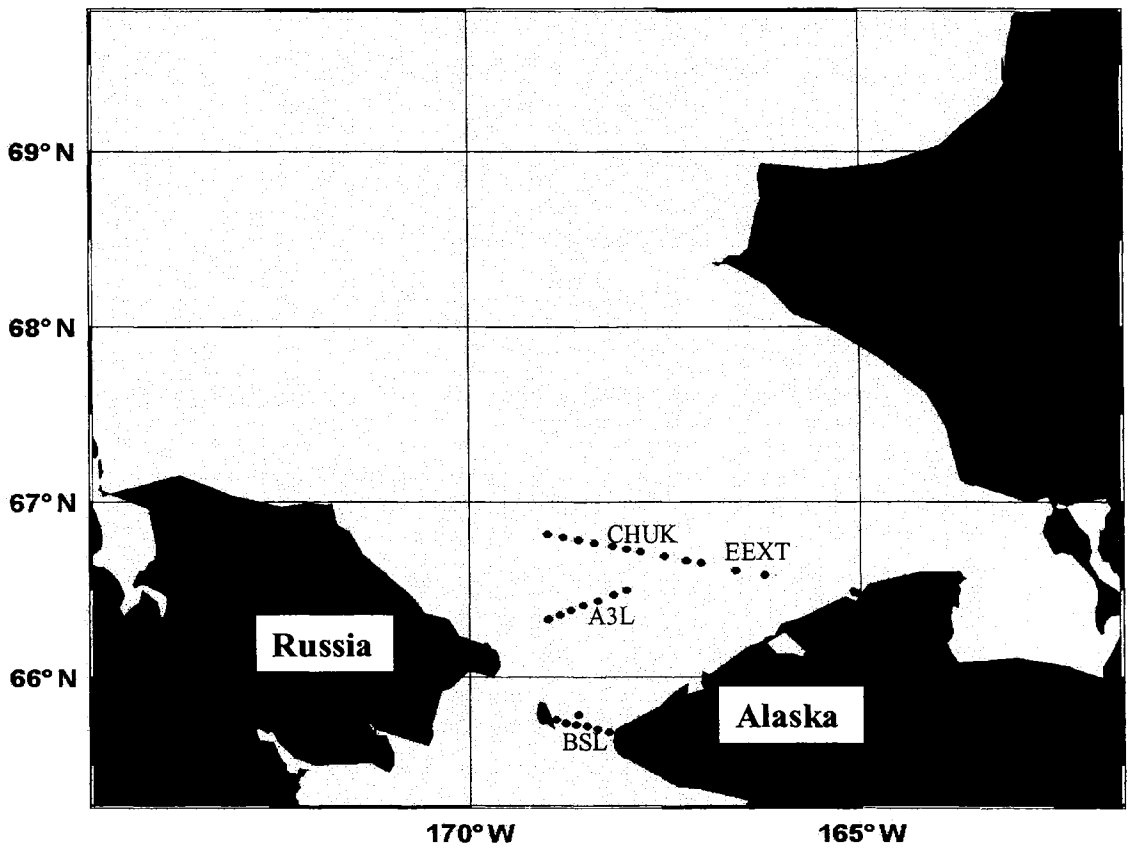

Fig. 4.1a. Sampling locations in Bering Strait and the Chukchi Sea during 31 Aug-3 Sept 2000 *Alpha Helix* cruise.

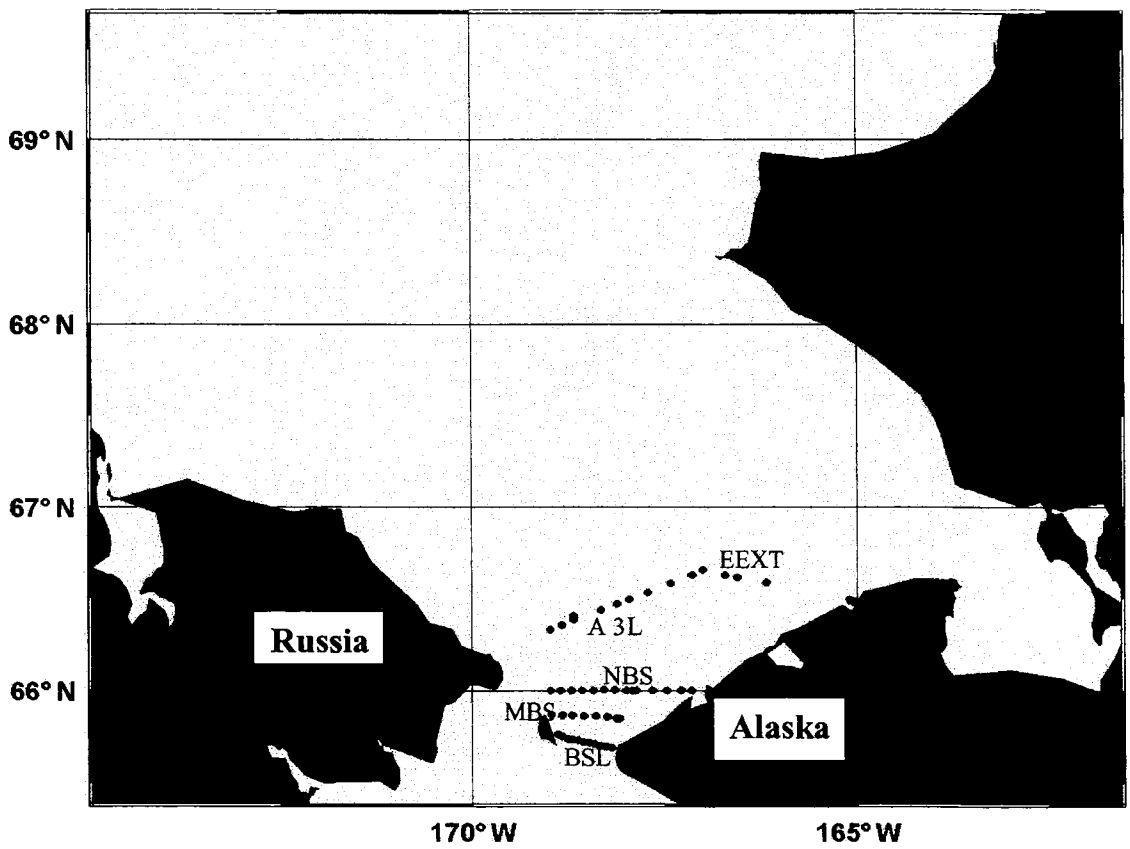

Fig. 4.1b. Sampling locations in Bering Strait and the Chukchi Sea during 8-12 Sept 2001 *Alpha Helix* cruise.

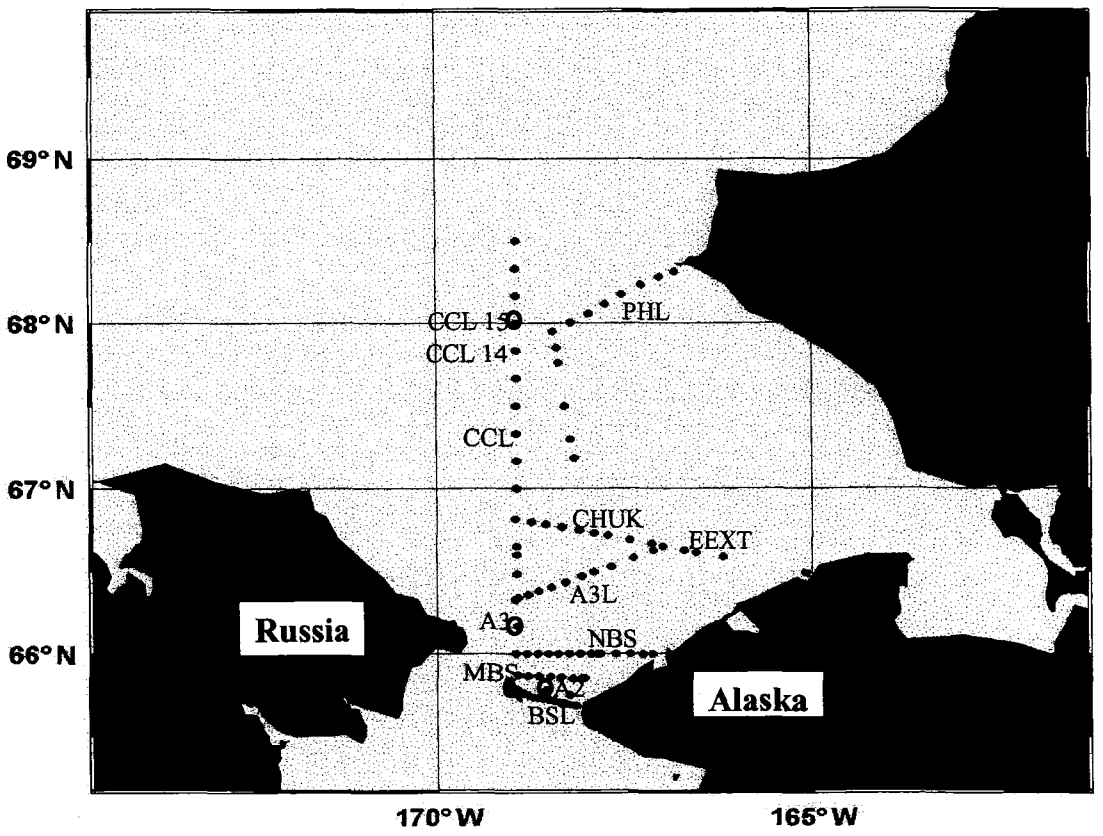

Fig. 4.1c. Sampling locations in Bering Strait and the Chukchi Sea during 21-29 June 2002 *Alpha Helix* cruise. Carbon and nitrogen uptake rates measured at the stations identified by circles.

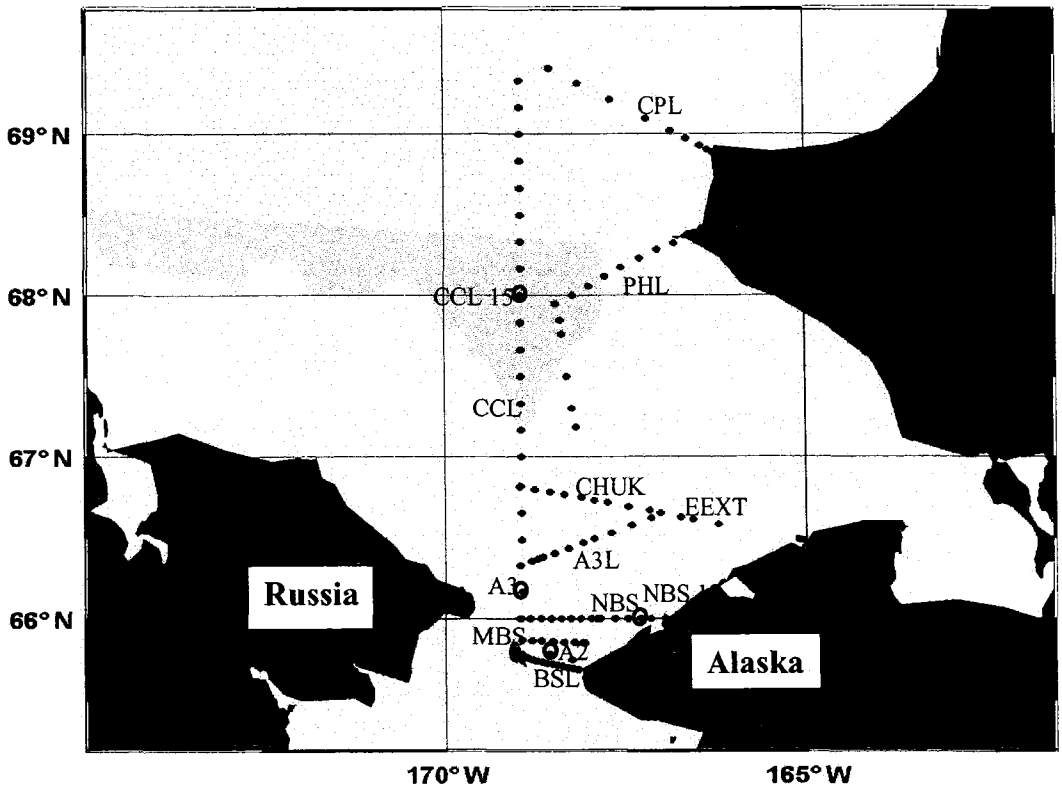

Fig. 4.1d. Sampling locations in Bering Strait and the Chukchi Sea during 30 June-8 July 2003 *Alpha Helix* cruise. Carbon and nitrogen uptake rates measured at the stations identified by circles.

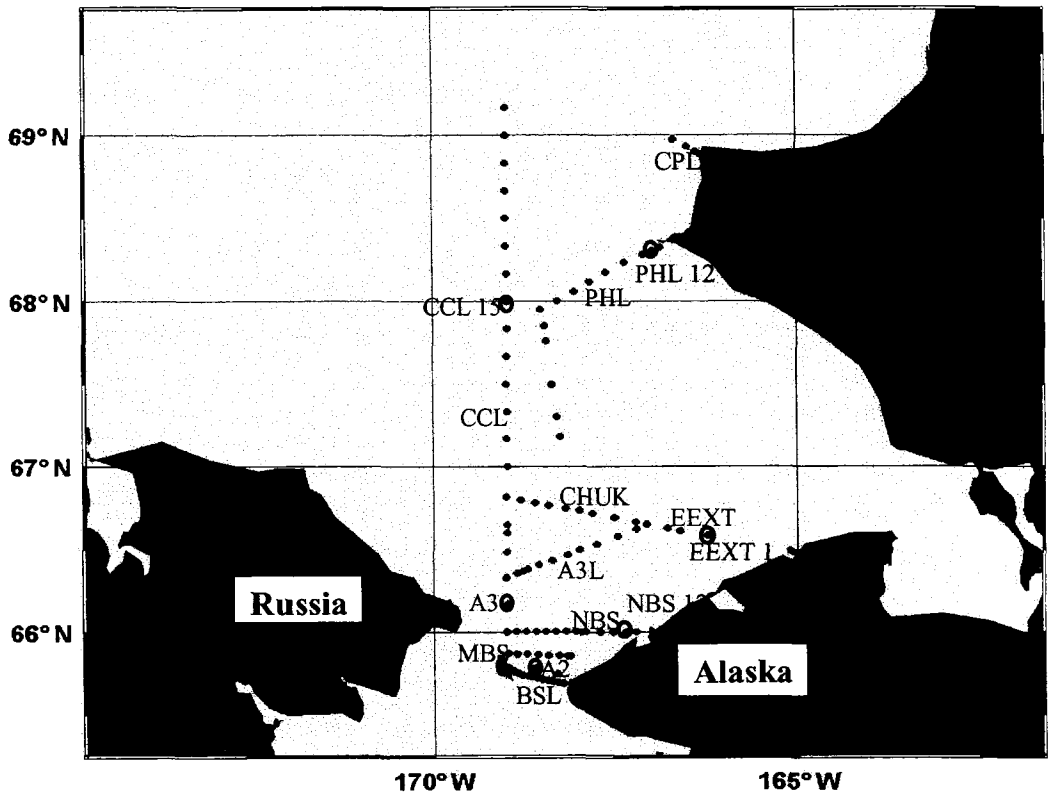

Fig. 4.1e. Sampling locations in Bering Strait and the Chukchi Sea during 29 Aug-6 Sept 2004 *Alpha Helix* cruise. Carbon and nitrogen uptake rates measured at the stations identified by circles.

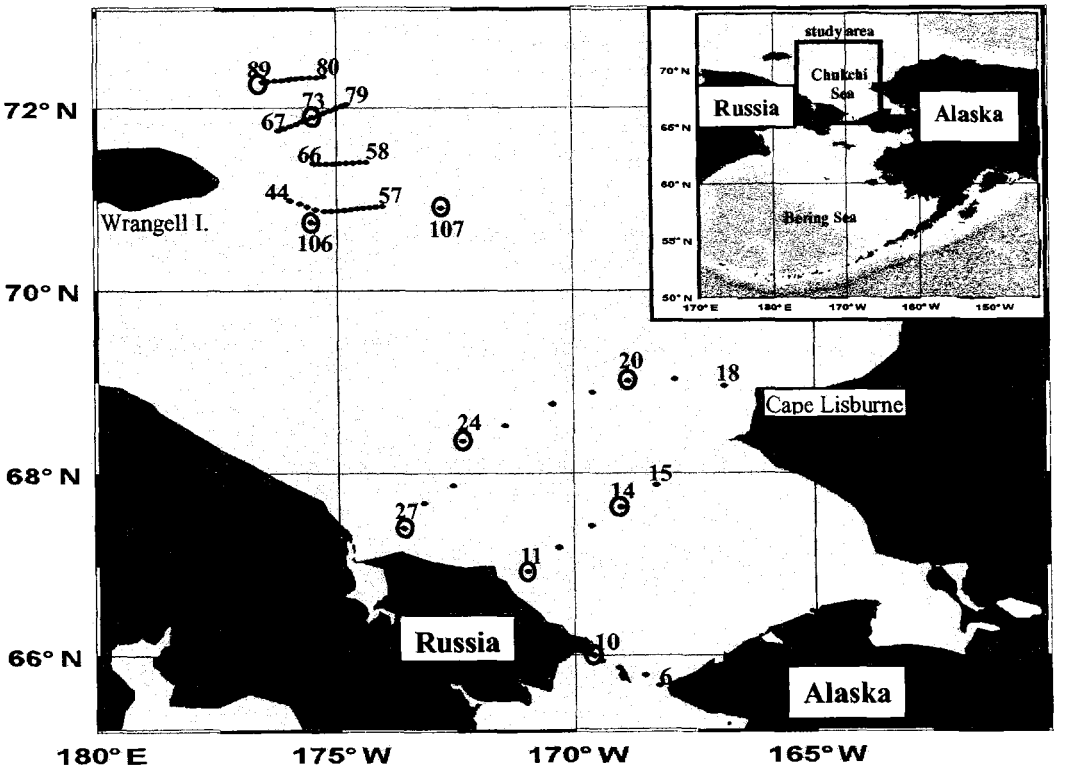

Fig. 4.2. Sampling locations in Bering Strait and the Chukchi Sea during 10-22 Aug 2004 RUSALCA cruise. Carbon and nitrogen uptake rates measured at the stations identified by circles.

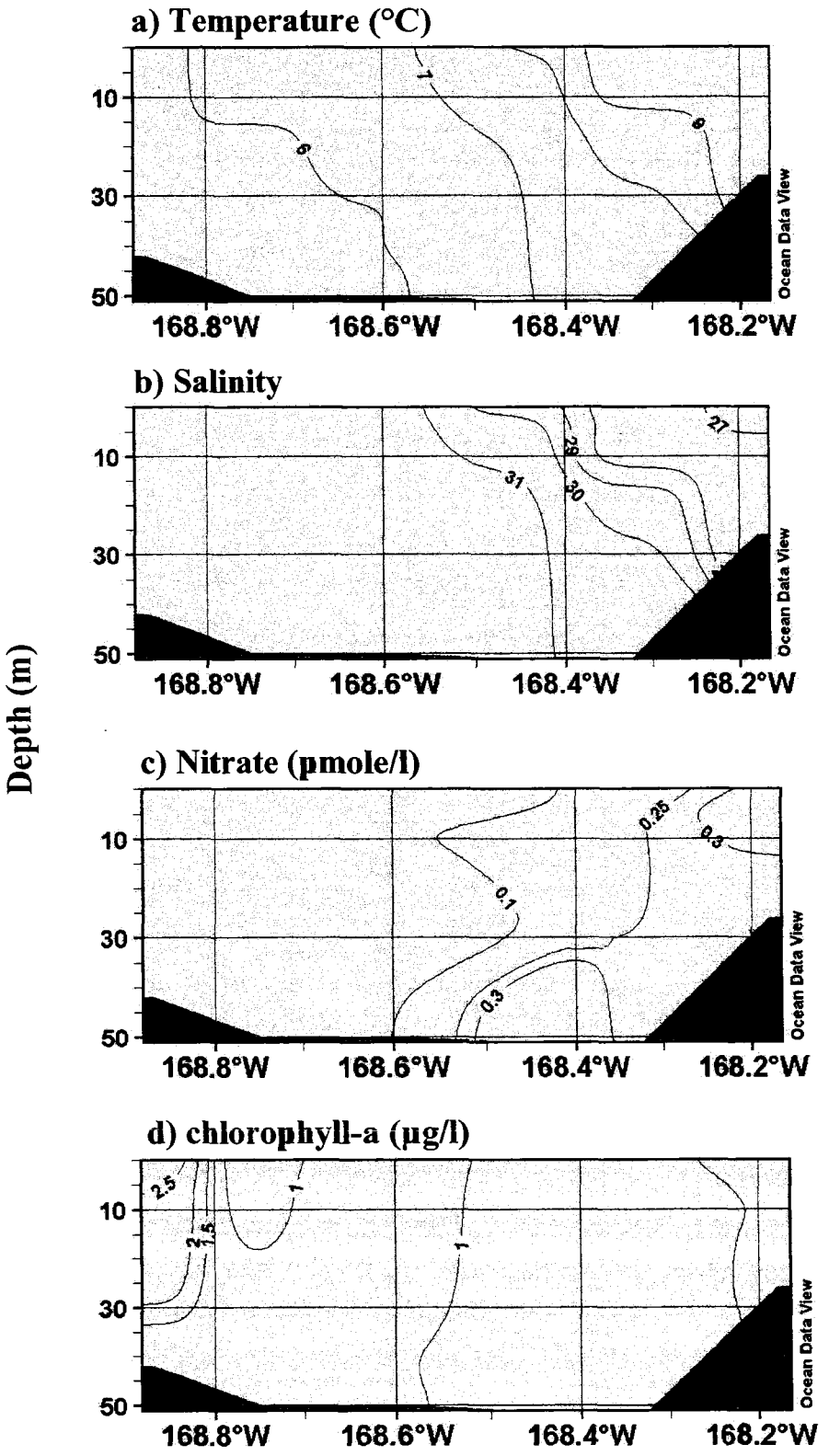

Fig. 4.3. Vertical structures of temperature, salinity, NO_3, chlorophyll-a in Bering Strait (BSL) of US side. 31 Aug-3 Sept 2000 *Alpha Helix* cruise.

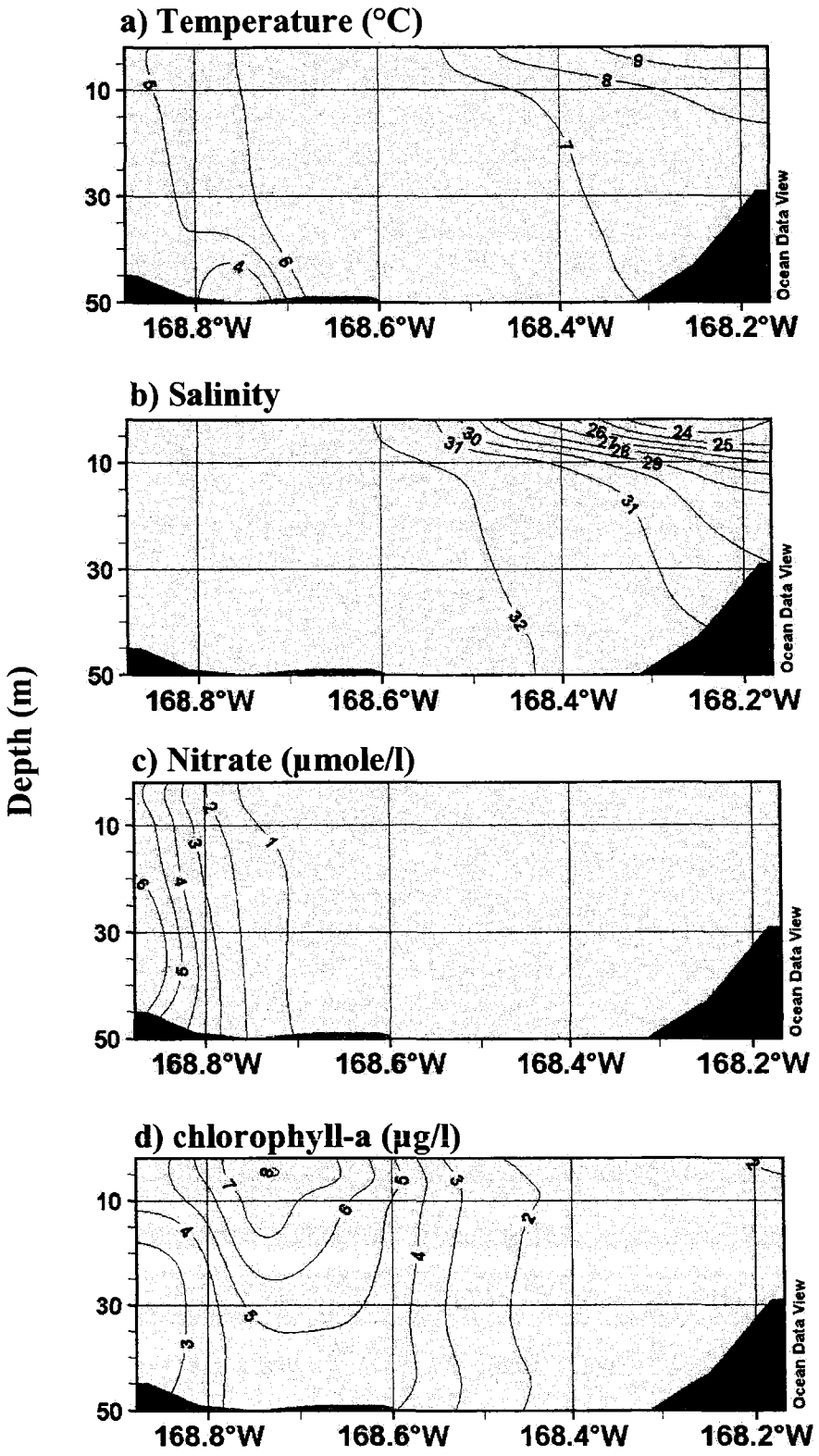

Fig. 4.4. Vertical structures of temperature, salinity, NO_3, chlorophyll-a in Bering Strait (BSL) of US side. 8-12 Sept 2001 *Alpha Helix* cruise.

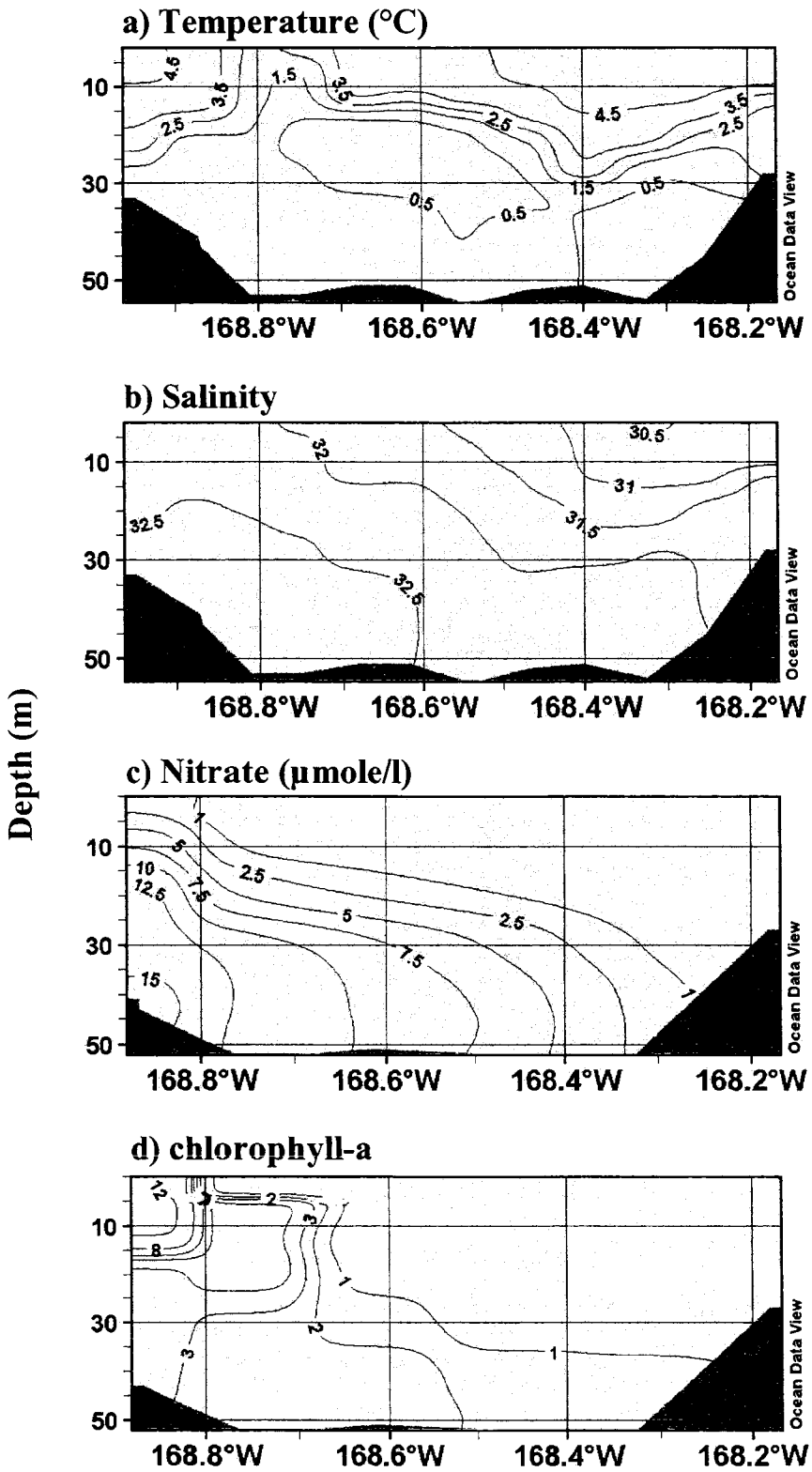

Fig. 4.5. Vertical structures of temperature, salinity, NO_3, chlorophyll-a in Bering Strait (BSL) of US side. 21-29 June 2002 *Alpha Helix* cruise.

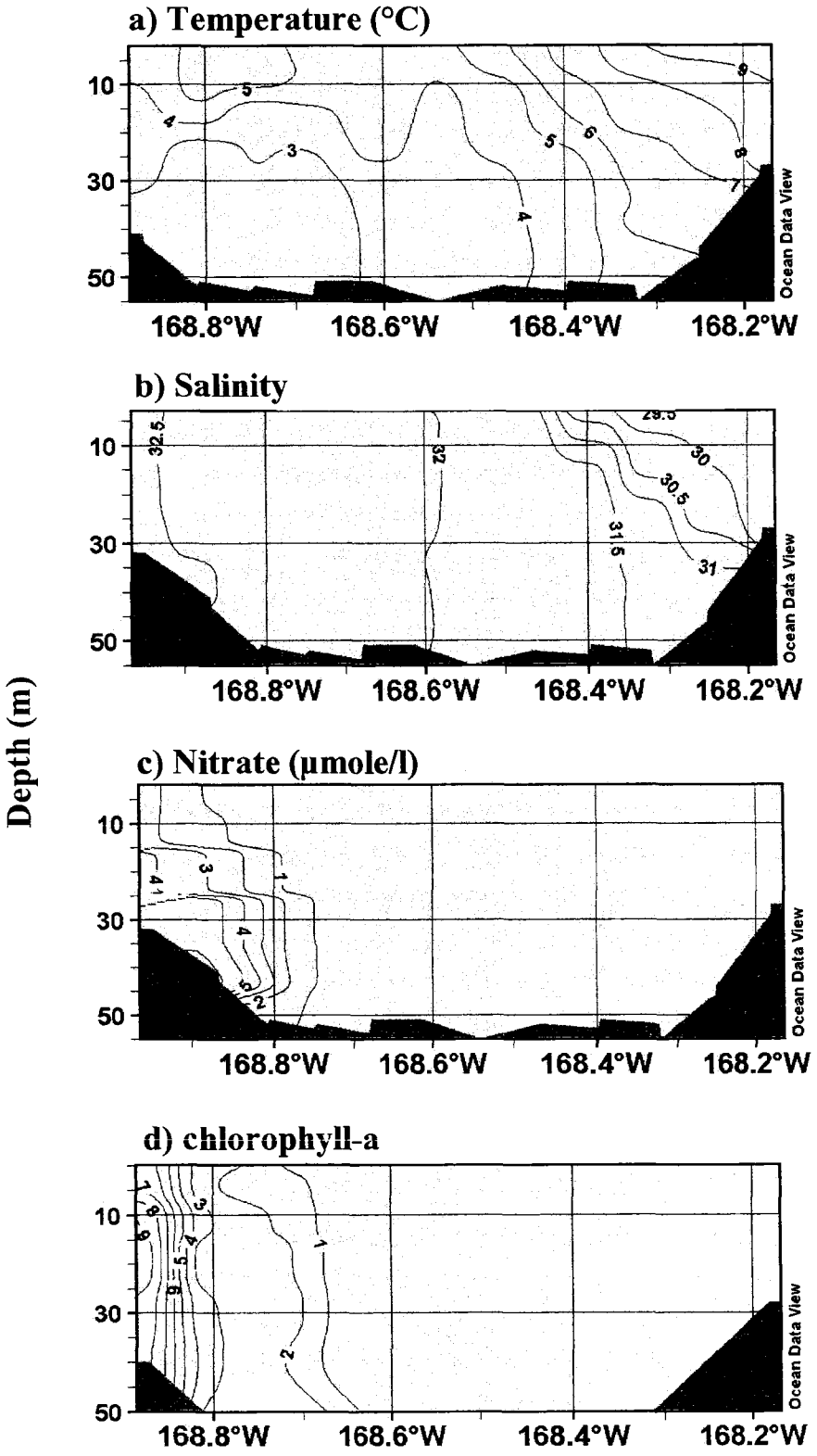

Fig. 4.6. Vertical structures of temperature, salinity, NO_3, chlorophyll-a in Bering Strait (BSL) of US side. 30 Jun-8 July 2003 *Alpha Helix* cruise.

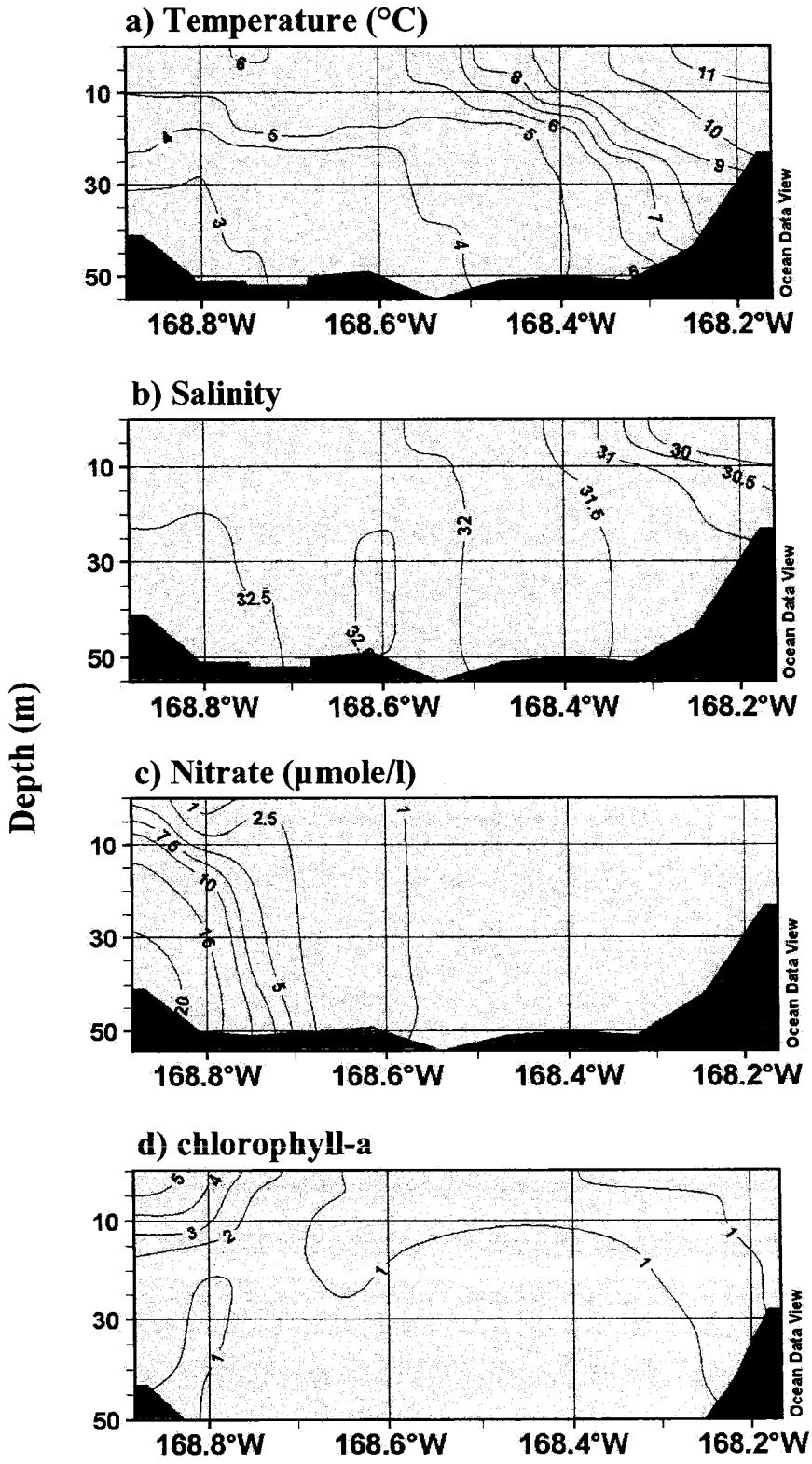

Fig. 4.7. Vertical structures of temperature, salinity, NO_3, chlorophyll-a in Bering Strait (BSL) of US side. 29 Aug-6 Sept 2004 *Alpha Helix* cruise.

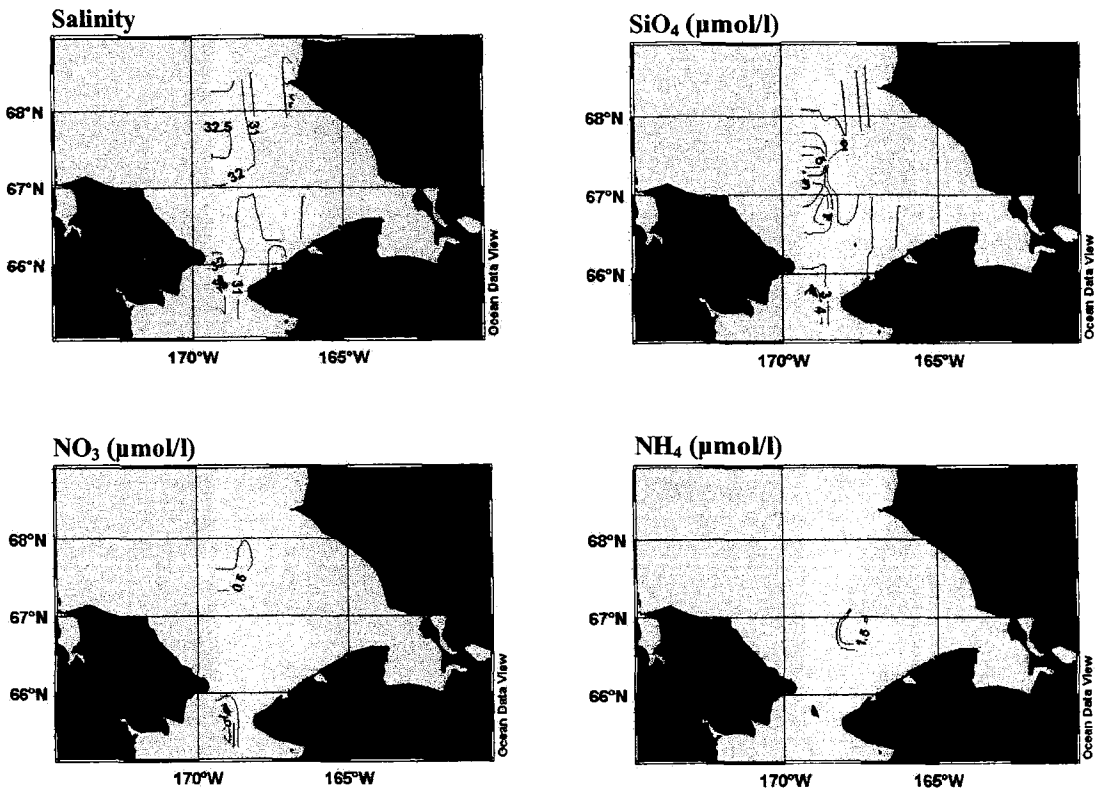

Fig. 4.8a. Areal distributions of salinity and inorganic nutrients at surface of Bering Strait and the Chukchi Sea (US waters). 21-29 June 2002 *Alpha Helix* cruise.

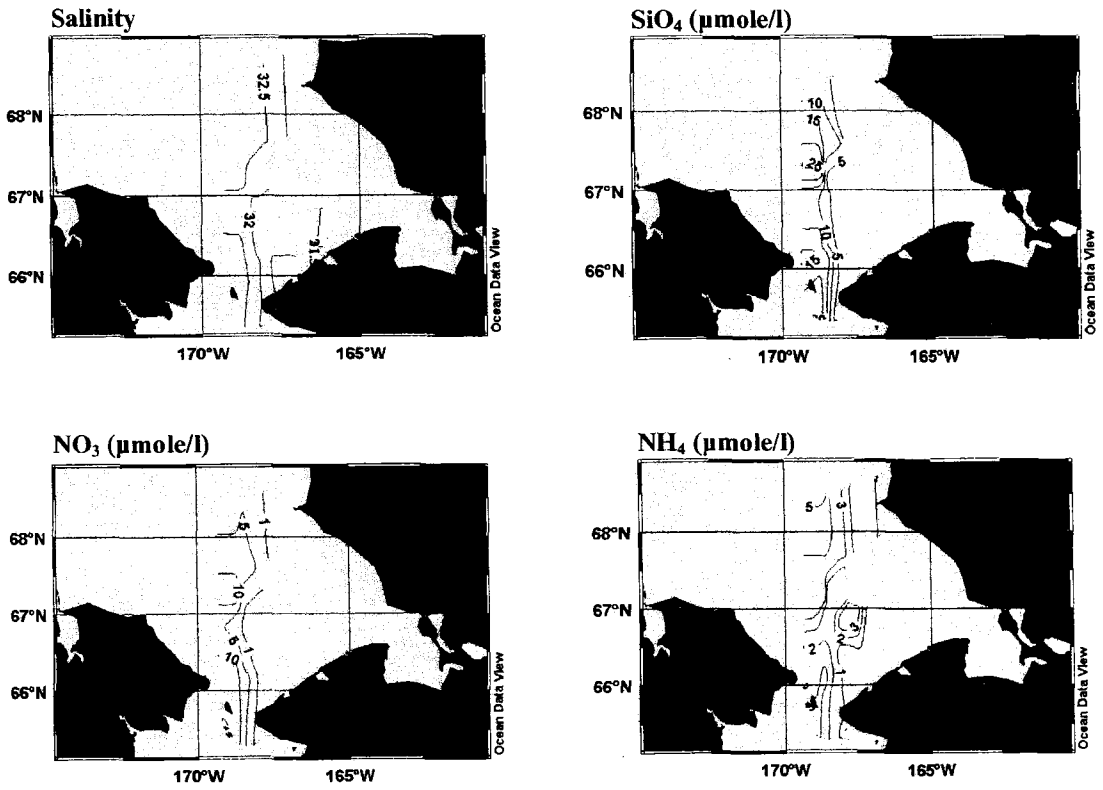

Fig. 4.8b. Areal distributions of salinity and inorganic nutrients at bottom (40 m) of Bering Strait and the Chukchi Sea (US waters). 21-29 June 2002 *Alpha Helix* cruise.

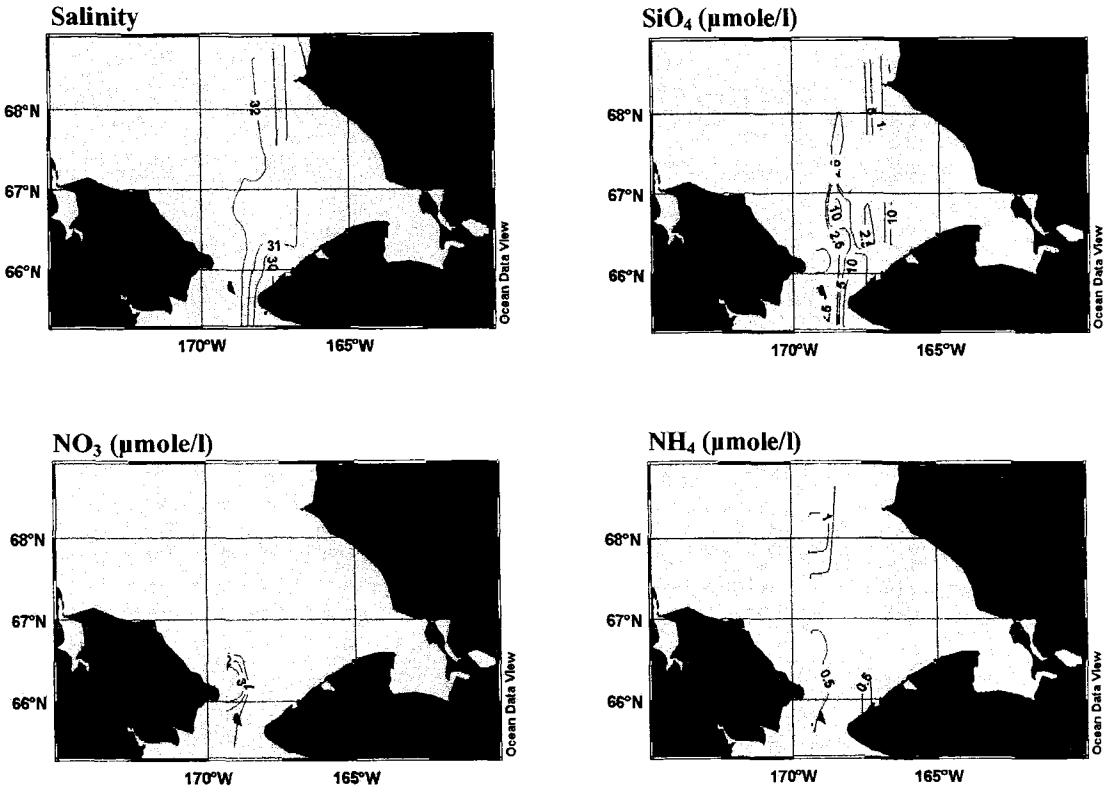

Fig. 4.9a. Areal distributions of salinity and inorganic nutrients at surface of Bering Strait and the Chukchi Sea (US waters). 30 June-8 July 2003 *Alpha Helix* cruise.

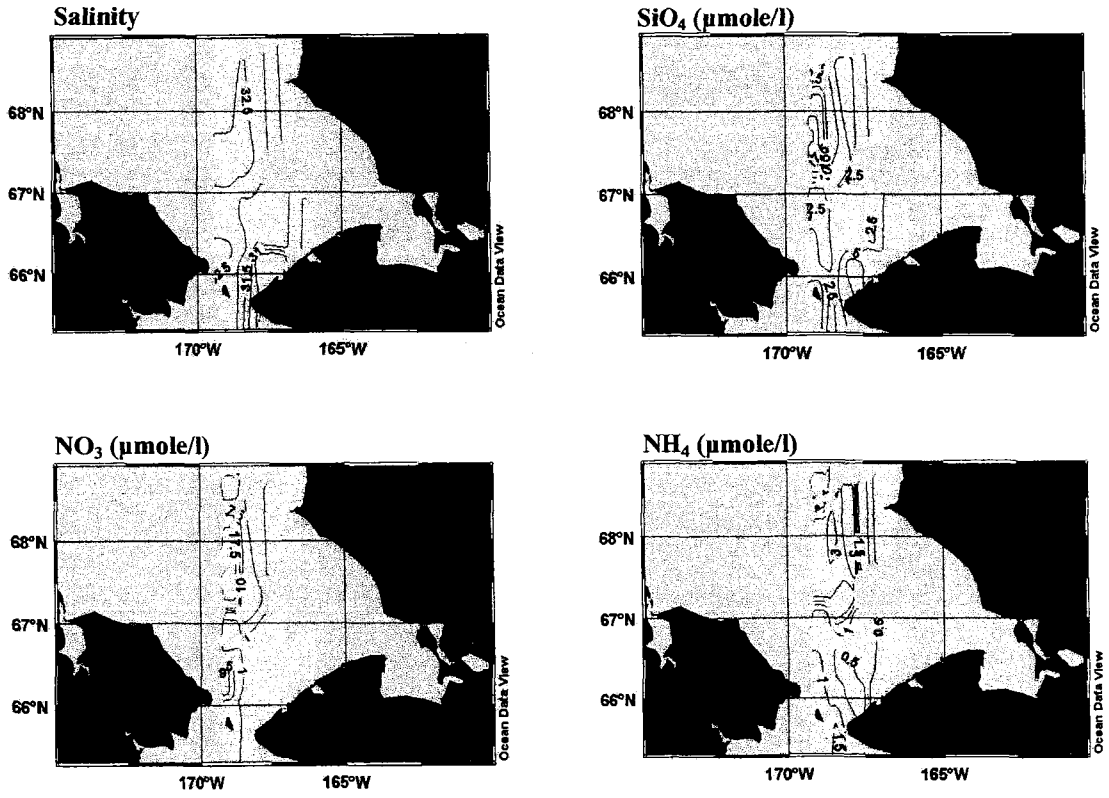

Fig. 4.9b. Areal distributions of salinity and inorganic nutrients at bottom (40 m) of Bering Strait and the Chukchi Sea (US waters). 30 June-8 July 2003 *Alpha Helix* cruise.

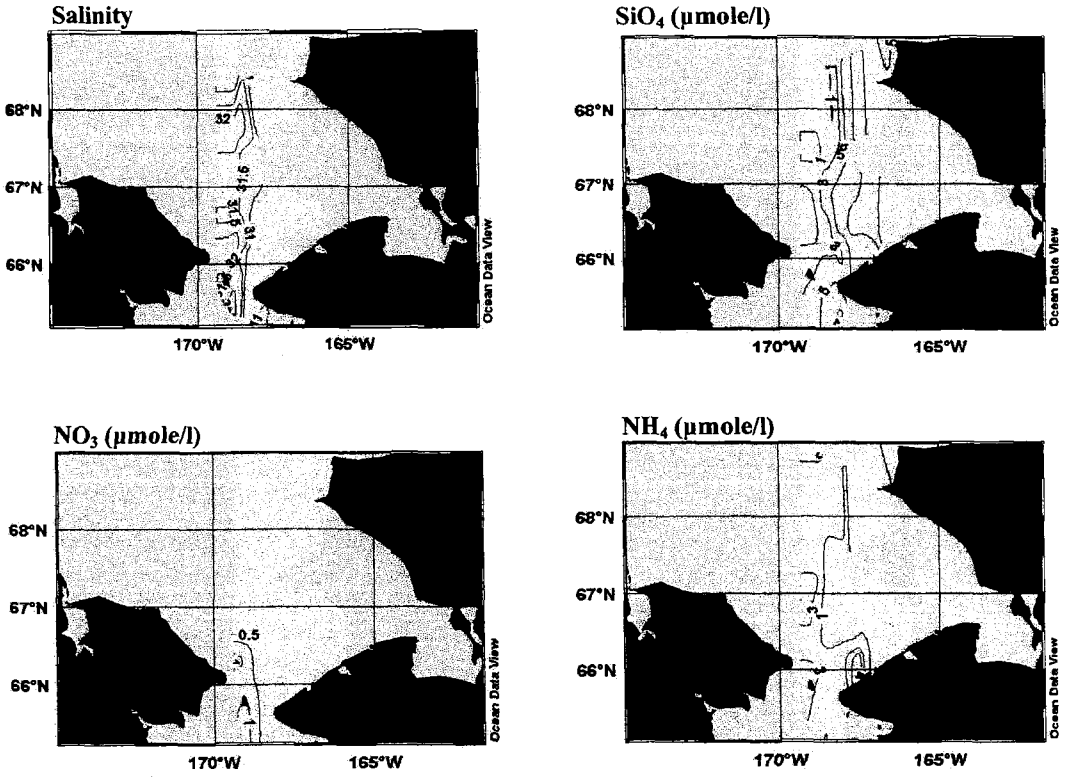

Fig. 4.10a. Areal distributions of salinity and inorganic nutrients at surface of Bering Strait and the Chukchi Sea (US waters). 29 August-6 September 2004 *Alpha Helix* cruise.

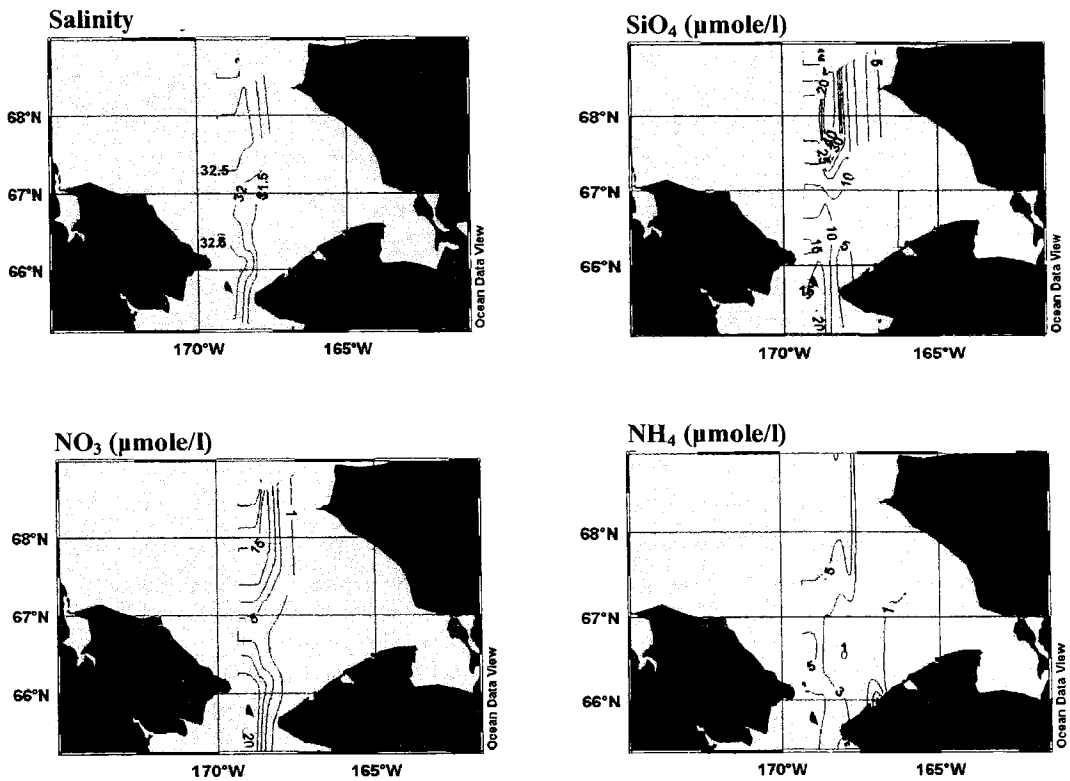

Fig. 4.10b. Areal distributions of salinity and inorganic nutrients at bottom (40 m) of Bering Strait and the Chukchi Sea (US waters). 29 August-6 September 2004 *Alpha Helix* cruise.

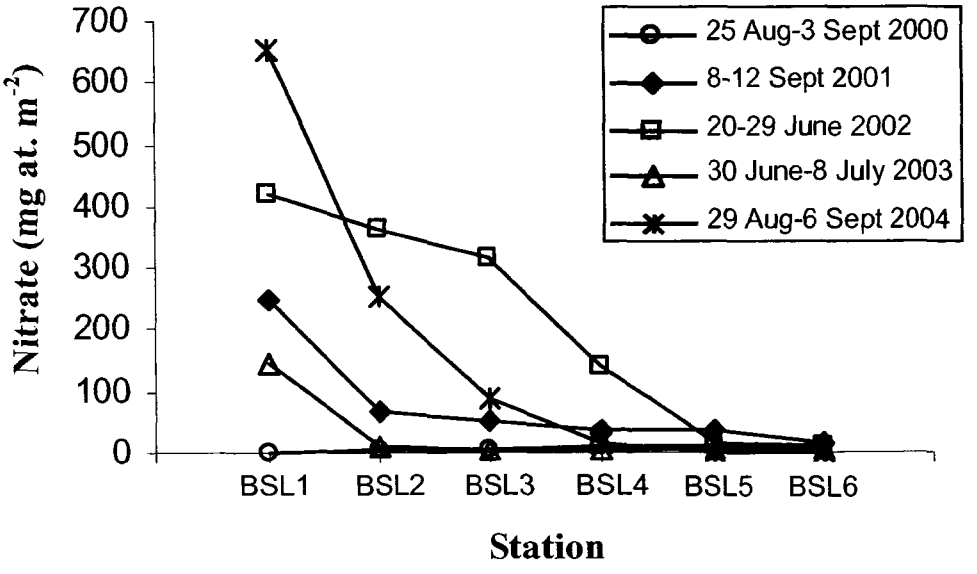

Fig. 4.11. Inter-annual variations of integrated nitrate concentrations (mg at. m^{-2}) at different stations in the Bering Strait Line (BSL) from 2000 to 2004 HX cruises. BSL 1 is the western side of BSL near Diomede Islands and BSL 6 is the eastern side near the Alaska coastal line.

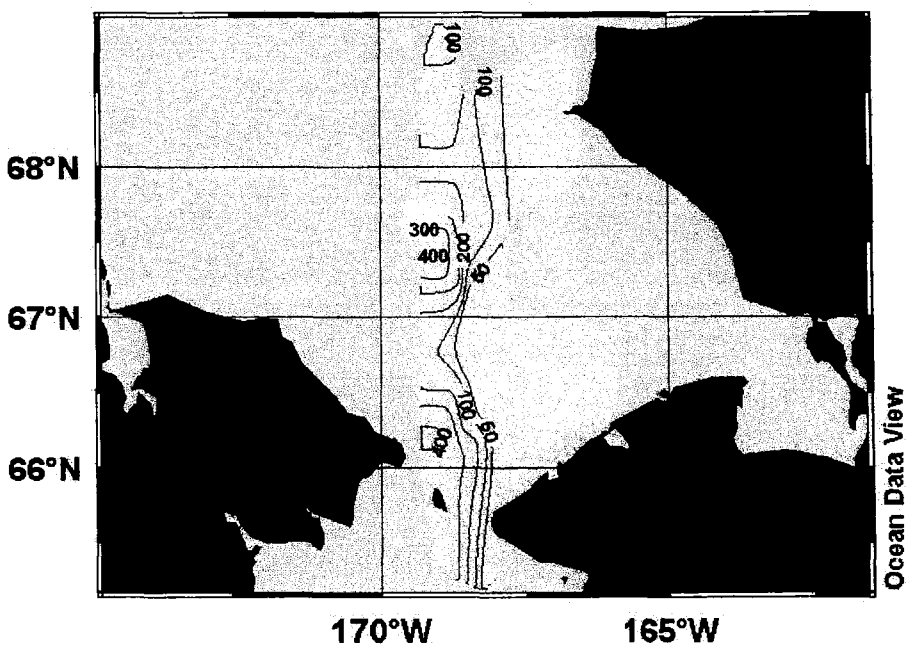

Fig. 4.12a. Areal distribution of integrated nitrate concentration (mg at. m^{-2}) in Bering Strait and the Chukchi Sea (HX cruise). 21-29 June 2002.

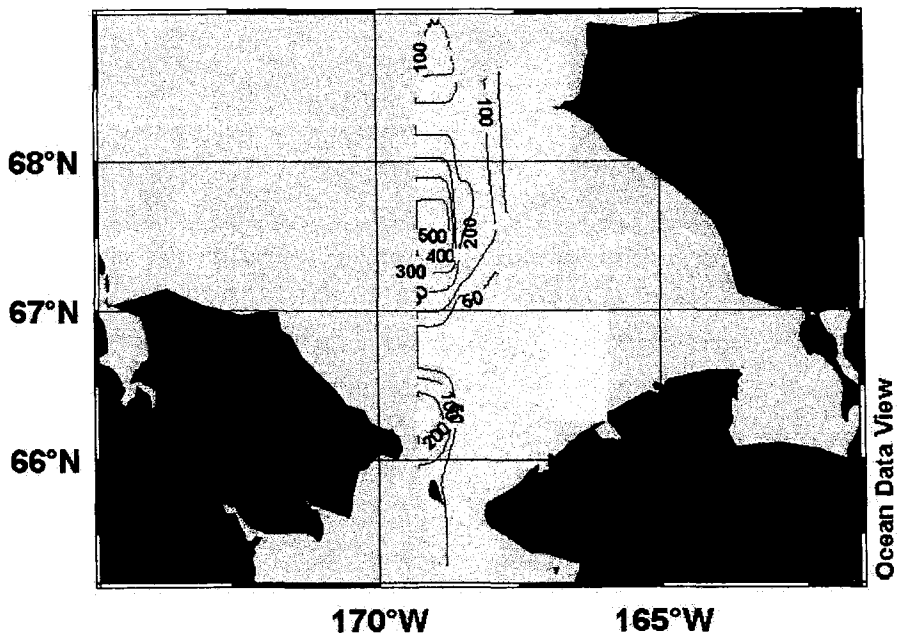

Fig. 4.12b. Areal distribution of integrated nitrate concentration (mg at. m^{-2}) in Bering Strait and the Chukchi Sea (HX cruise). 30 June-8 July 2003.

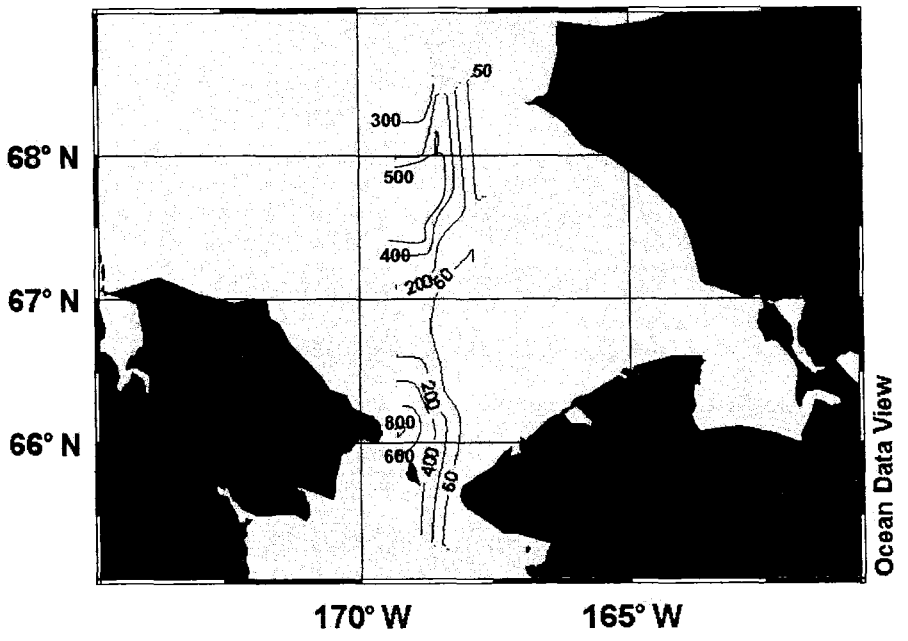

Fig. 4.12c. Areal distribution of integrated nitrate concentration (mg at. m^{-2}) in Bering Strait and the Chukchi Sea (HX cruise). 29 August-6 September 2004.

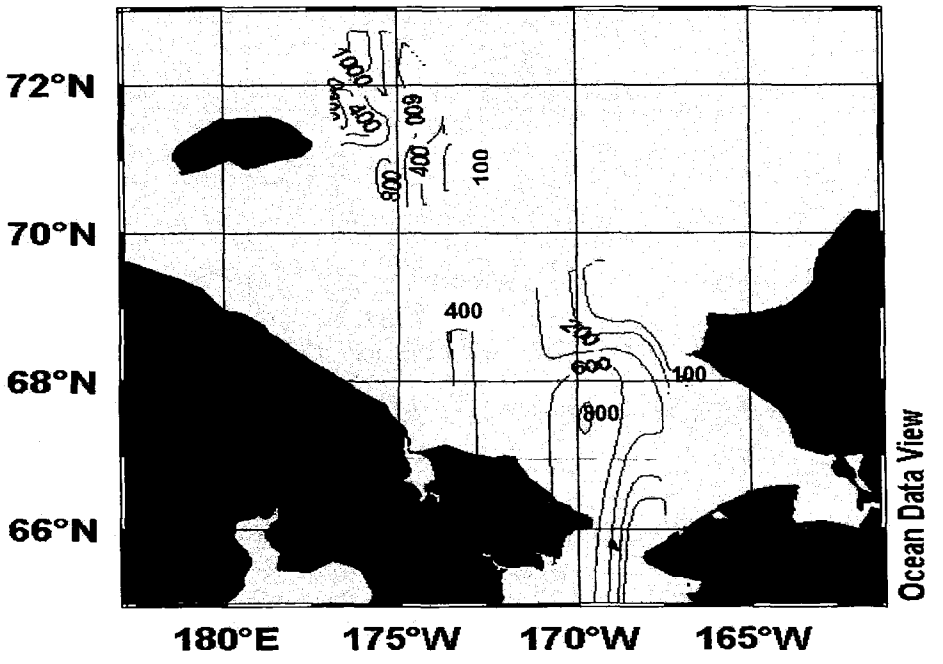

Fig. 4.12d. Areal distribution of integrated nitrate concentration (mg at. m^{-2}) in Bering Strait and the Chukchi Sea (RUSALCA cruise). 10-24 August 2004.

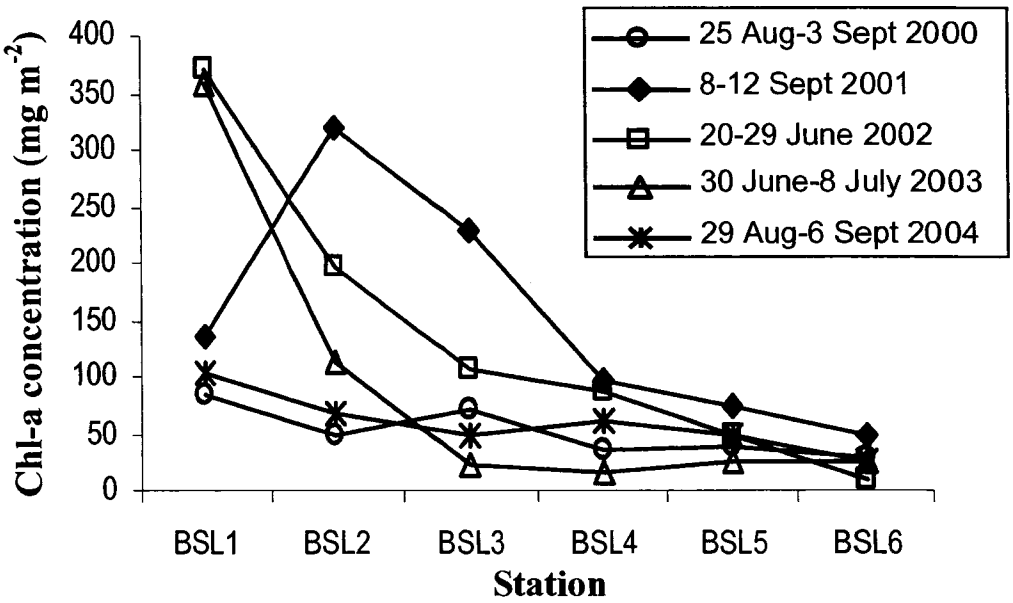

Fig. 4.13. Inter-annual variations of integrated chlorophyll-a concentrations (mg m^{-2}) at different stations in the Bering Strait Line (BSL) from 2000 to 2004 HX cruise. BSL 1 is the western side of BSL near Diomede Islands and BSL 6 is the eastern side near the Alaska coastal line.

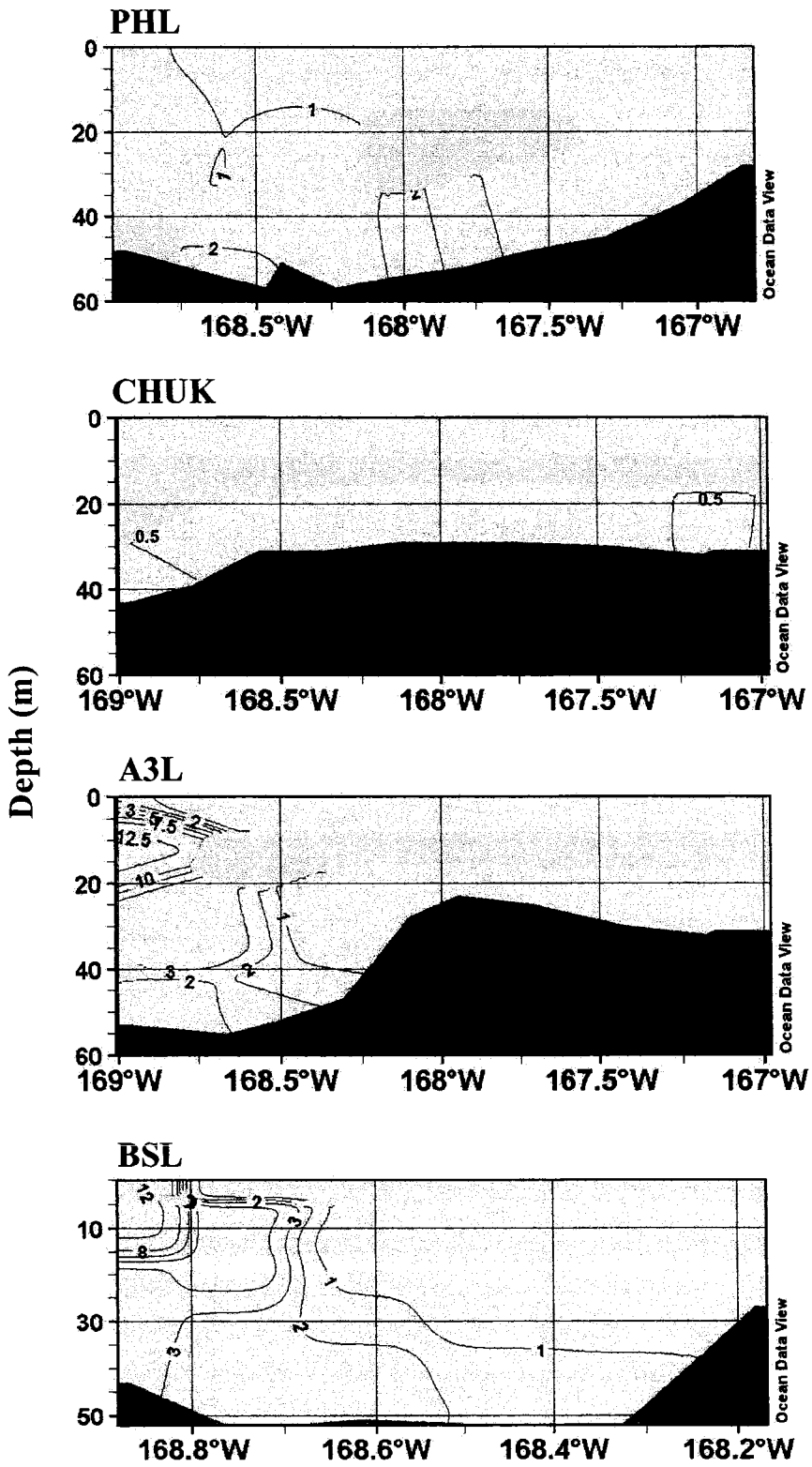

Fig. 4.14a. Vertical distributions of chlorophyll-a concentrations through the different cross sections from BSL to PHL (see the map in Fig. 4.1c). 21-29 June 2002 HX cruise.

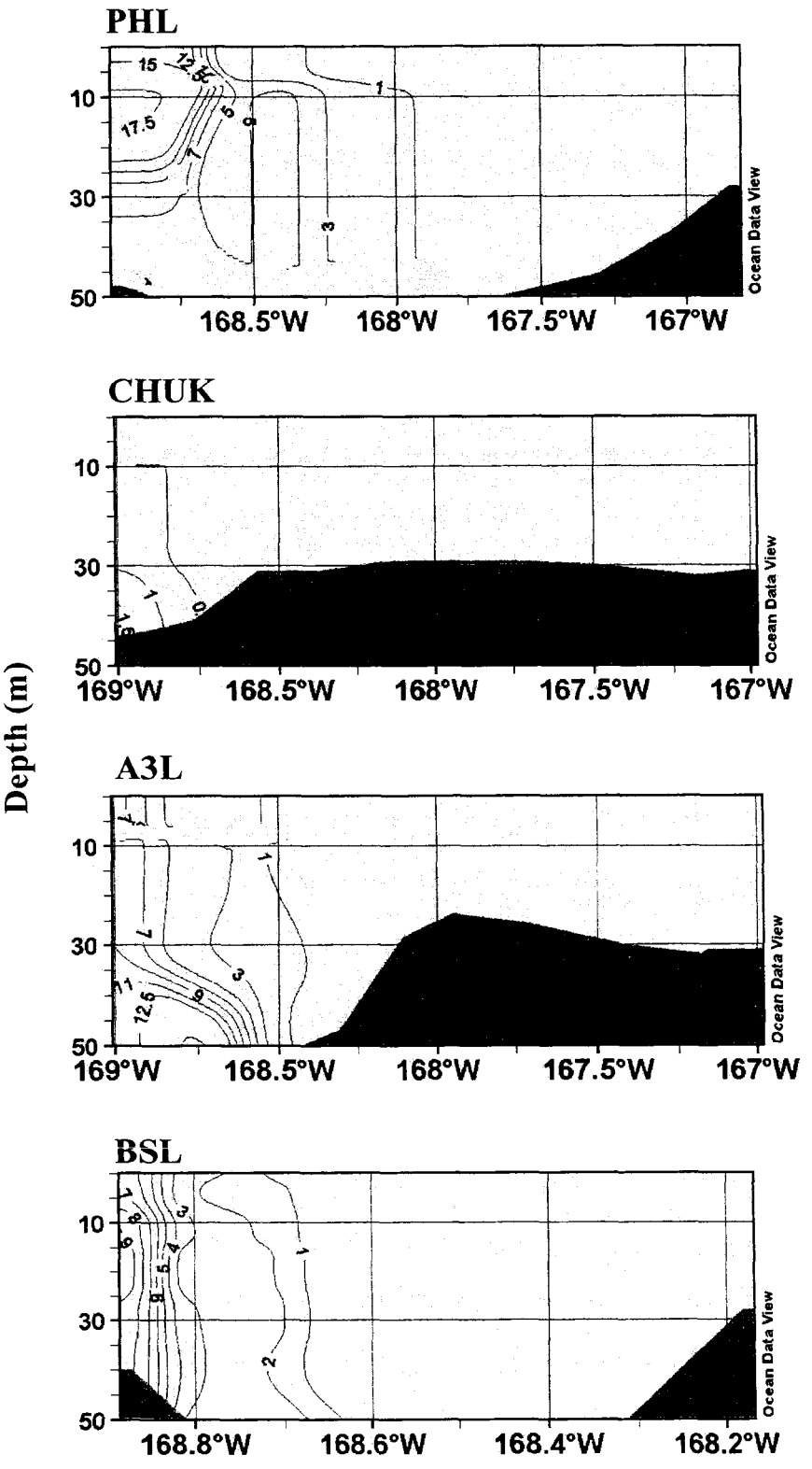

Fig. 4.14b. Vertical distributions of chlorophyll-a concentrations through the different cross sections from BSL to PHL (see the map in Fig. 4.1d). 30 June-8 July 2003 HX cruise.

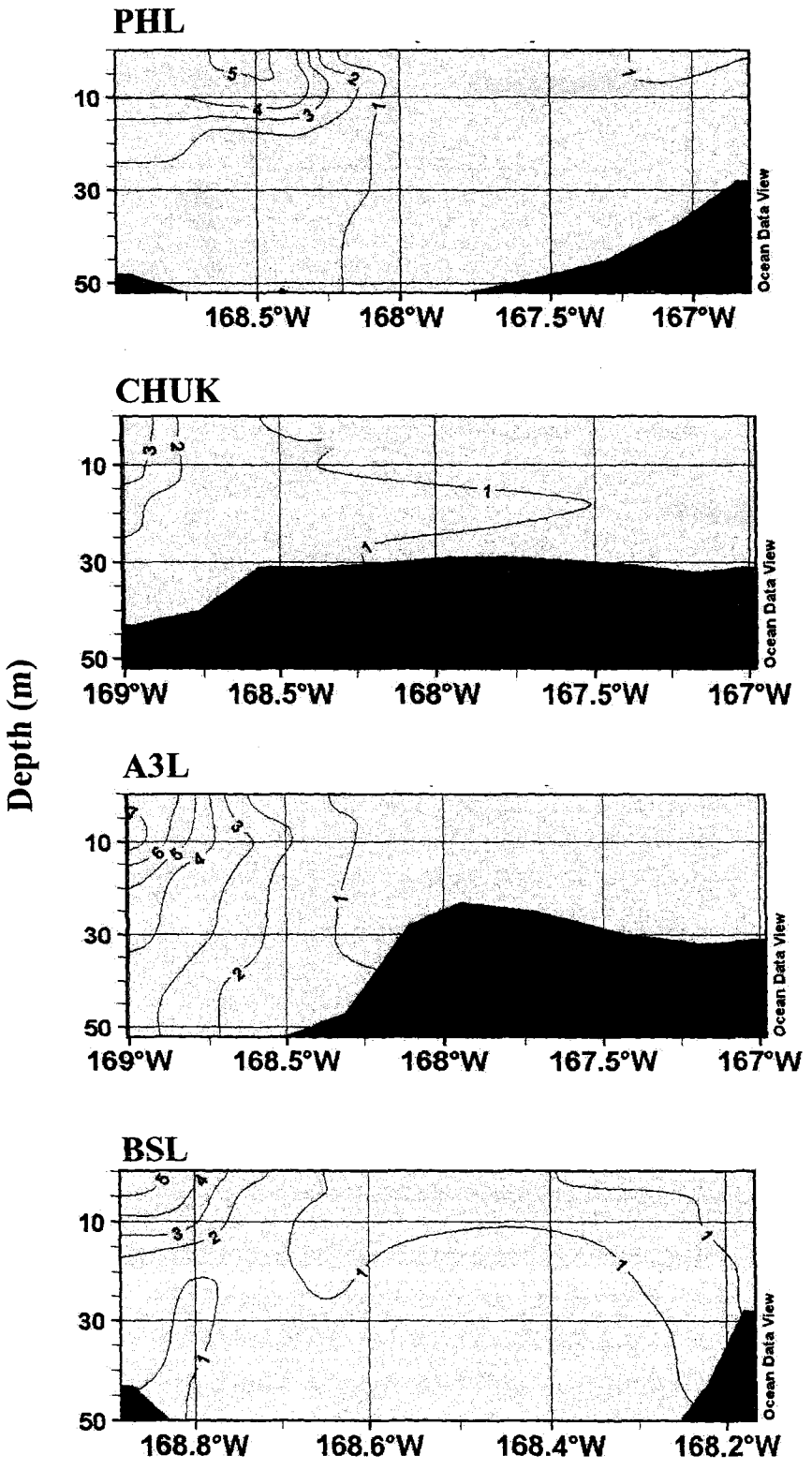

Fig. 4.14c. Vertical distributions of chlorophyll-a concentrations through the different cross sections from BSL to PHL (see the map in Fig. 4.1e). 29 August-6 September 2004 HX cruise.

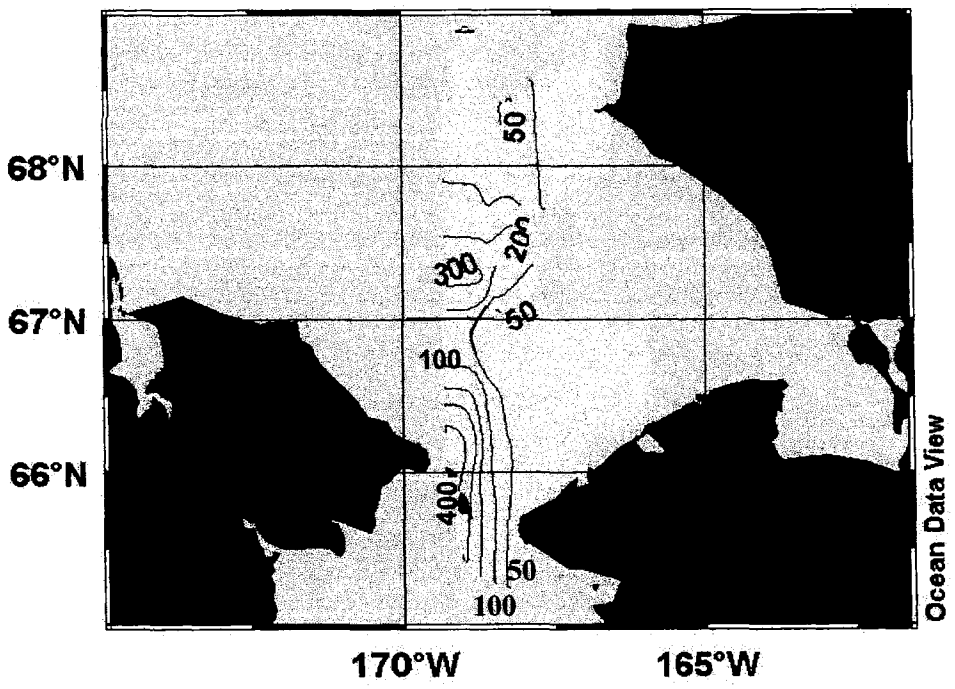

Fig. 4.15a. Areal distribution of integrated chlorophyll-a (mg m^{-2}) in Bering Strait and the Chukchi Sea (HX cruise). 21-29 June 2002.

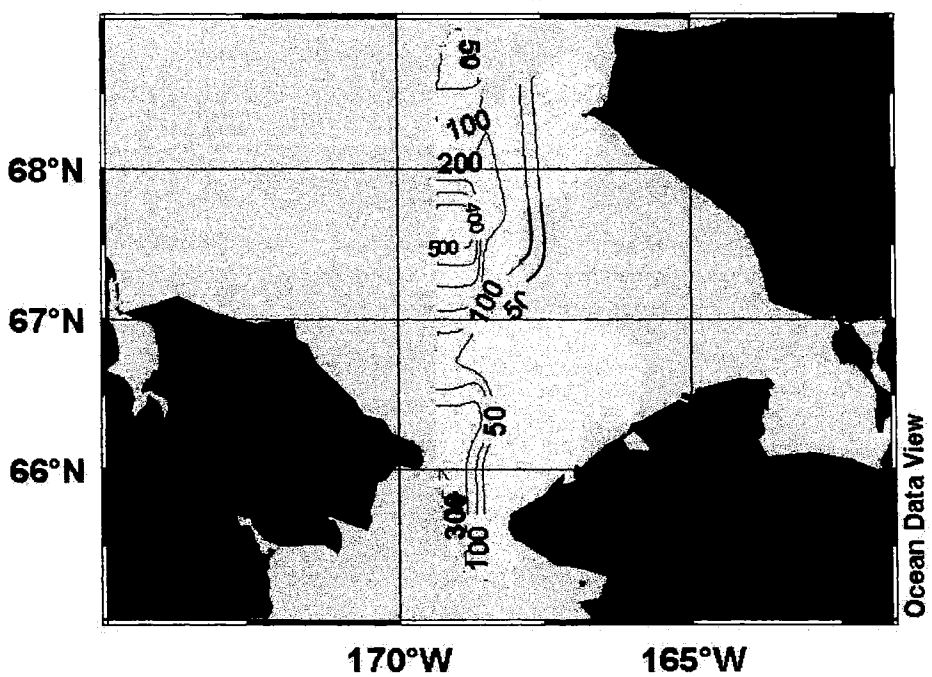

Fig. 4.15b. Areal distribution of integrated chlorophyll-a (mg m^{-2}) in Bering Strait and the Chukchi Sea (HX cruise). 30 June-8 July 2003.

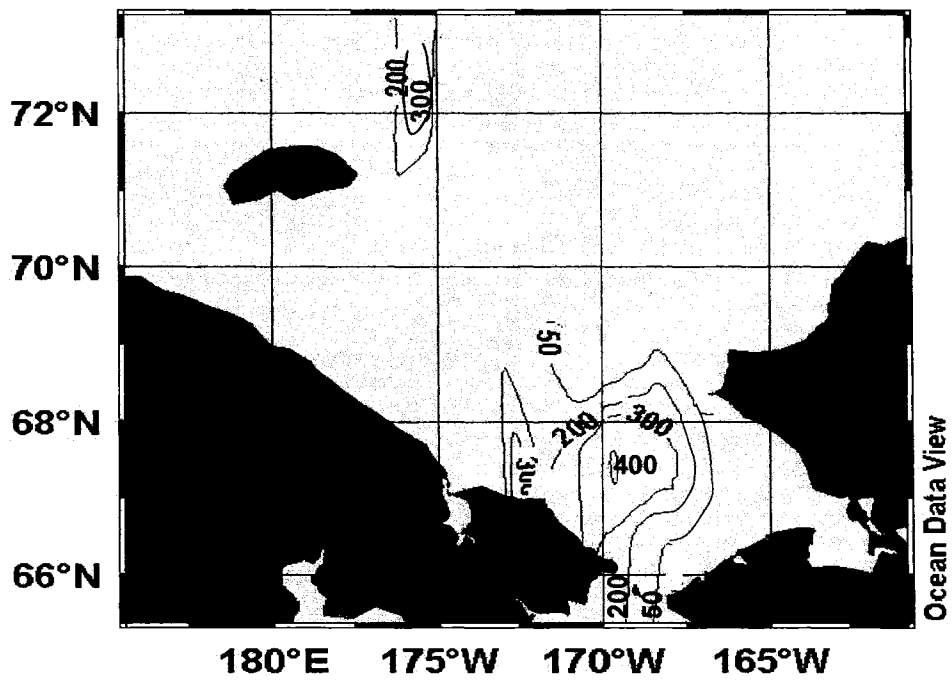

Fig. 4.15c. Areal distribution of integrated chlorophyll-a (mg m^{-2}) in Bering Strait and the Chukchi Sea (RUSALCA cruise). 10-22 August 2004.

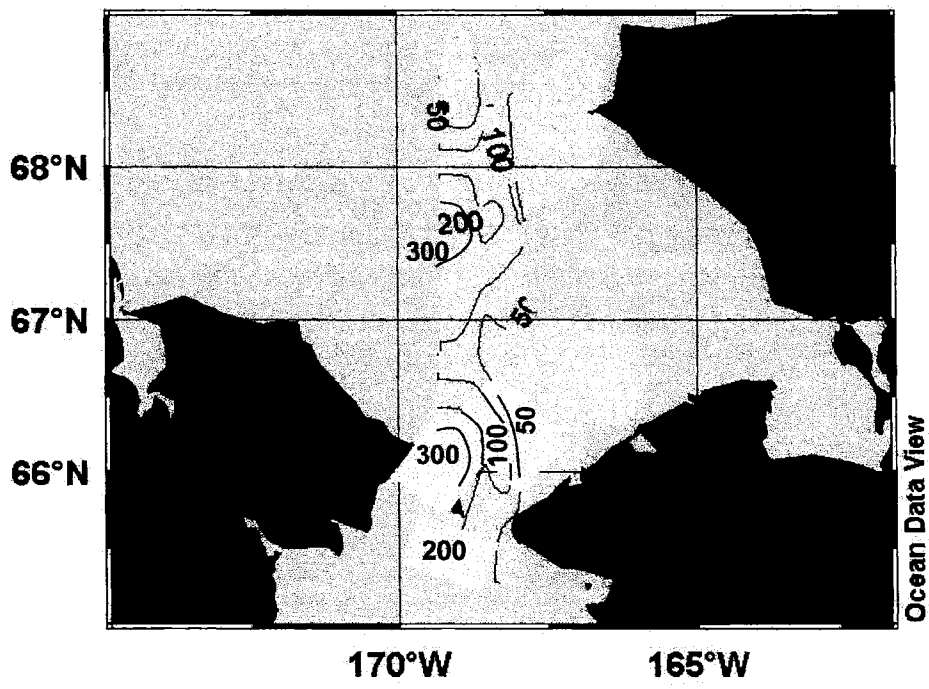

Fig. 4.15d. Areal distribution of integrated chlorophyll-a (mg m^{-2}) in Bering Strait and the Chukchi Sea (HX cruise). 29 August-6 September 2004.

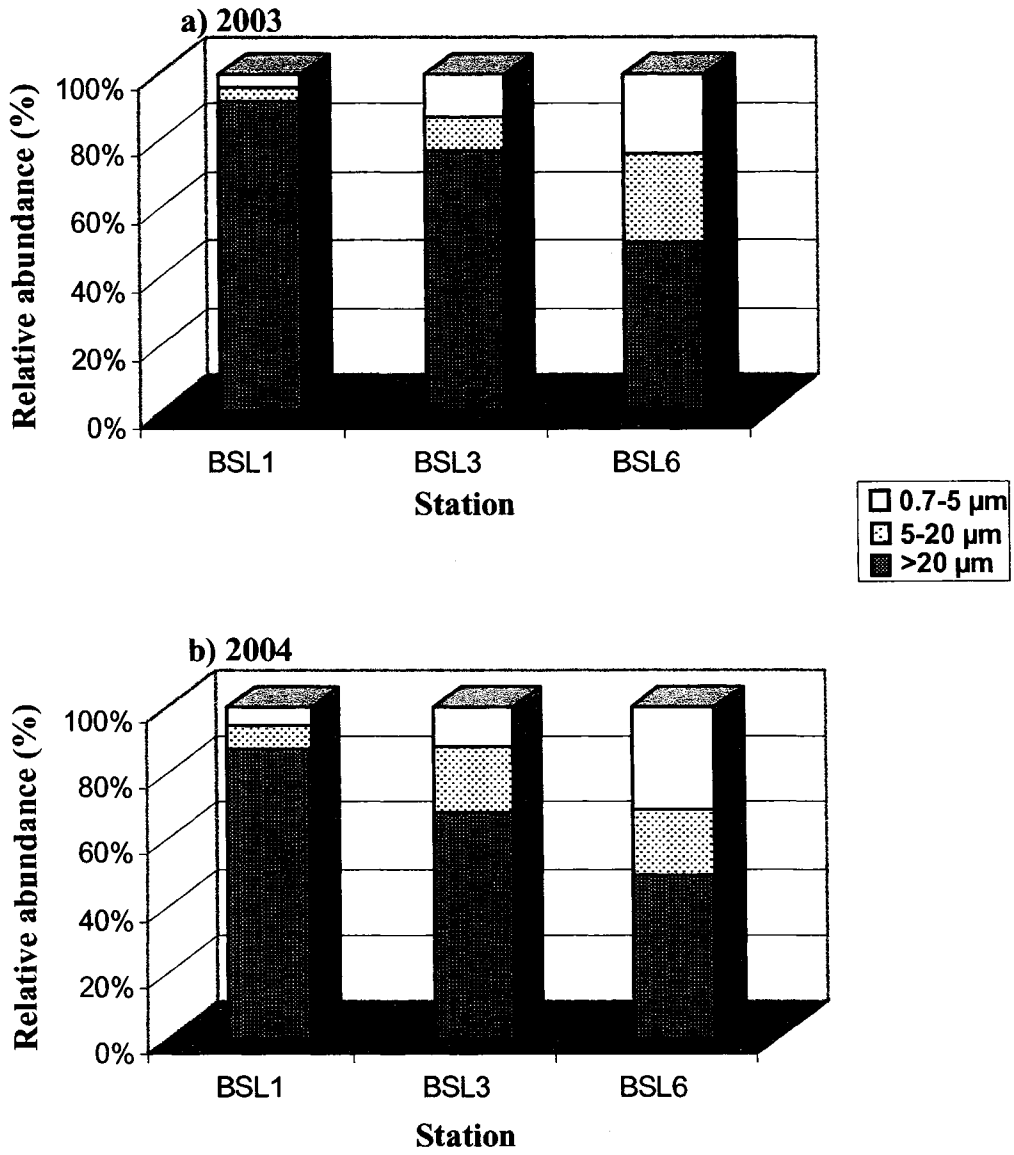

Fig. 4.16. Compositions of different size of chlorophyll-a through the BSL during the 2003 (30 June-8 July) and 2004 (29 Aug-6 Sept) HX cruises. BSL 1 is the western side of BSL near the Diomede Islands and BSL 6 is the eastern side near the Alaska coastal line.

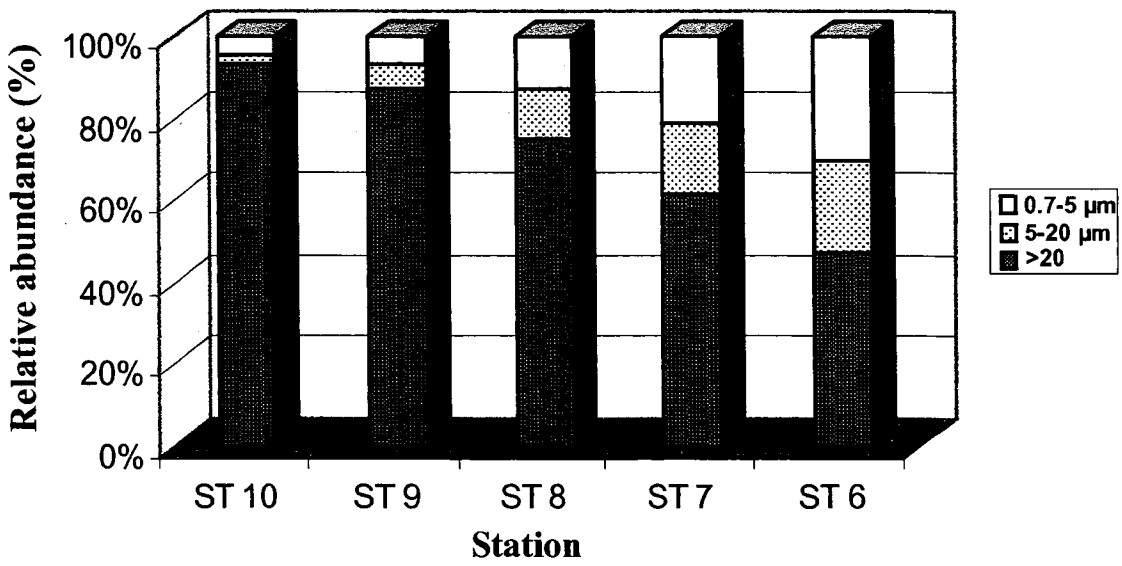

Fig. 4.17. Compositions of different size of chlorophyll-a through Bering Strait during 10-22 Aug 2004 RUSALCA cruise. ST 10 is the western side of Bering Strait and ST 6 is the eastern side near the Alaska coastal line.

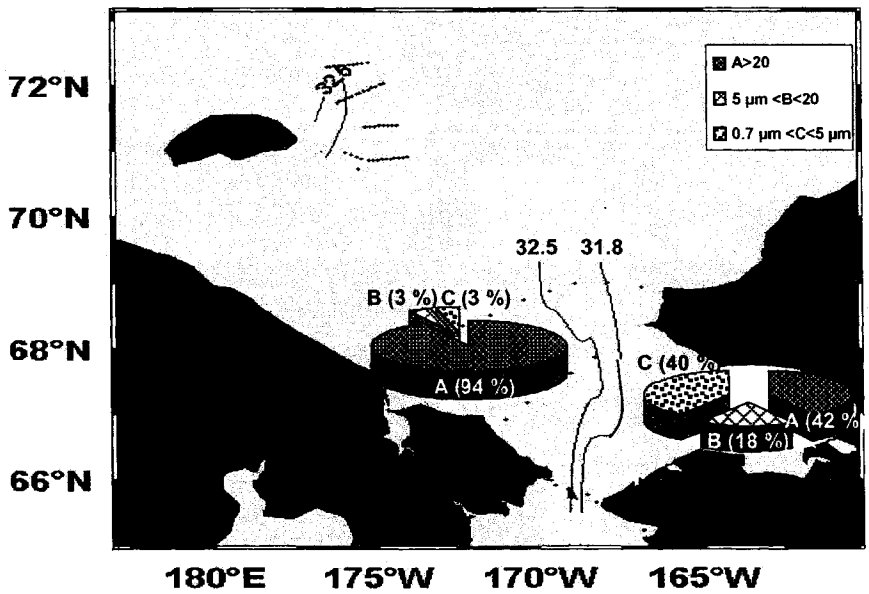

Fig. 4.18. Averaged compositions of different size chlorophyll-a in two different water masses determined by bottom salinities (40 m) in Bering Strait and the Chukchi Sea.

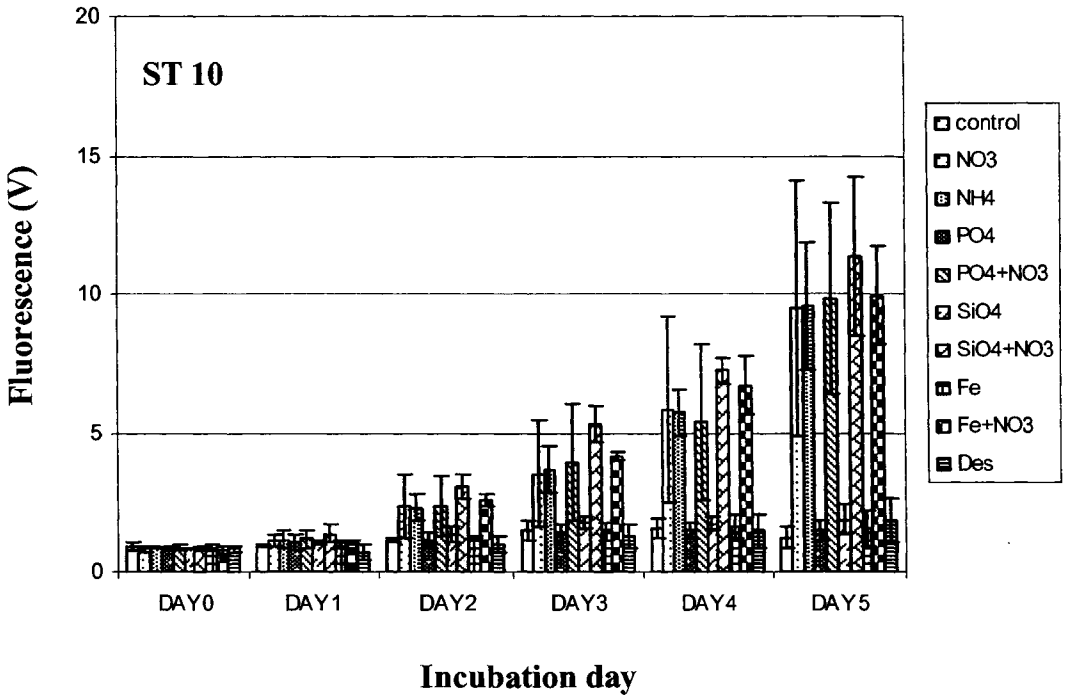

Fig. 4.19. Inorganic nutrient amendments at station 10 in the Chukchi Sea during the 2004 RUSALCA cruise (10-22 Aug). Bars are averages of same treatments and lines are standard deviations for each treatment. Des: Desferol.

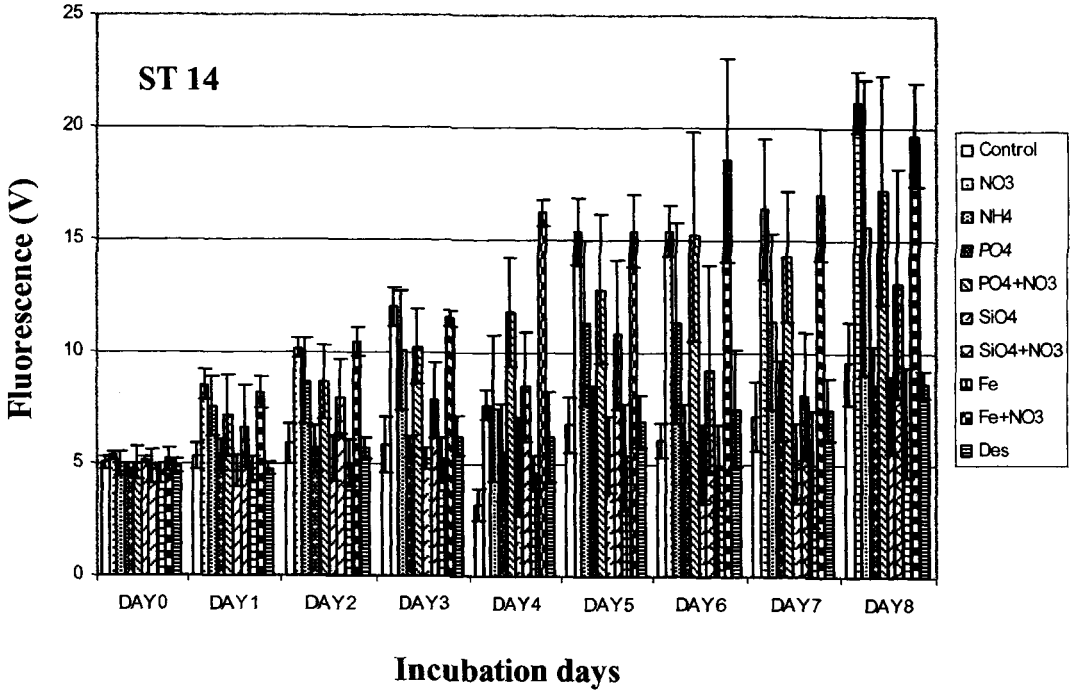

Fig. 4.20. Inorganic nutrient amendments at station 14 in the Chukchi Sea during the 2004 RUSALCA cruise (10-22 Aug). Bars are averages of same treatments and lines are standard deviations for each treatment. Des: Desferol.

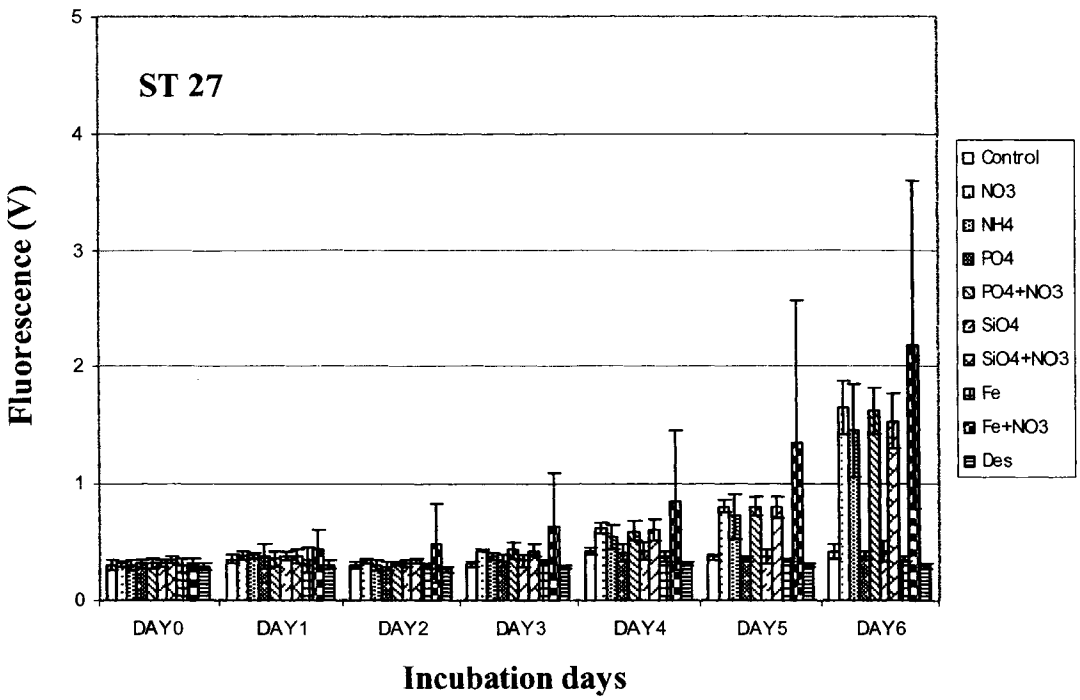

Fig. 4.21. Inorganic nutrient amendments at station 27 in the Chukchi Sea during the 2004 RUSALCA cruise (10-22 Aug). Bars are averages of same treatments and lines are standard deviations for each treatment. Des: Desferol.

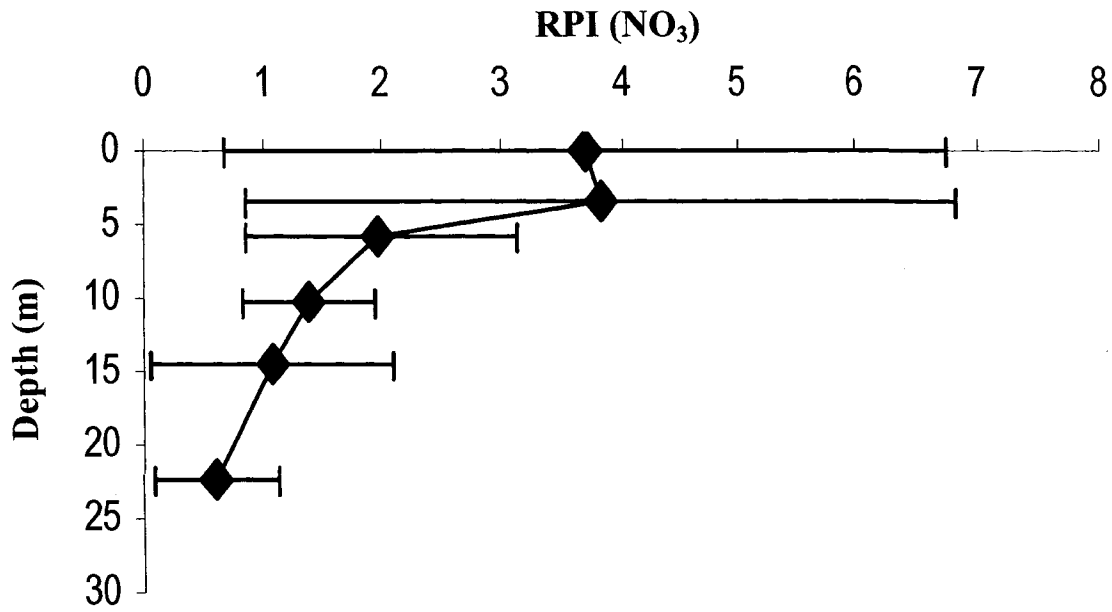

Fig. 4.22. Averaged relative preference index (RPI) for nitrate at different light depths (100, 50, 30, 12, 5, and 1 %) of 10 productivity stations from the 2004 RUSALCA cruise (10-22 Aug) in the Chukchi Sea. Lines stand for standard deviation for each light depth.

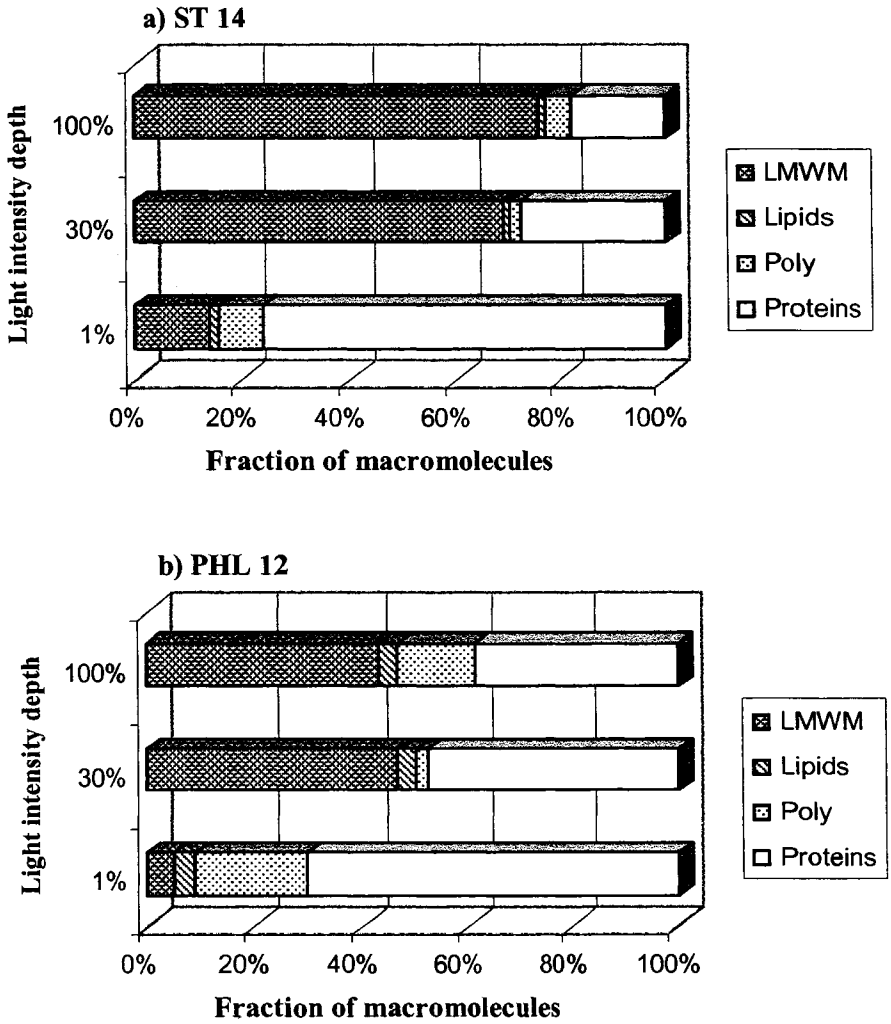

Fig. 4.23. Photosynthetic carbons allocation into macromolecules at three different light depths (100, 30, and 1 %) of the two different stations in 2004. The data for ST 10 and PHL 12 were obtained from the 2004 RUSALCA and 2004 HX cruises, respectively. LMWM is low-molecular-weight metabolites and poly means polysaccharides.

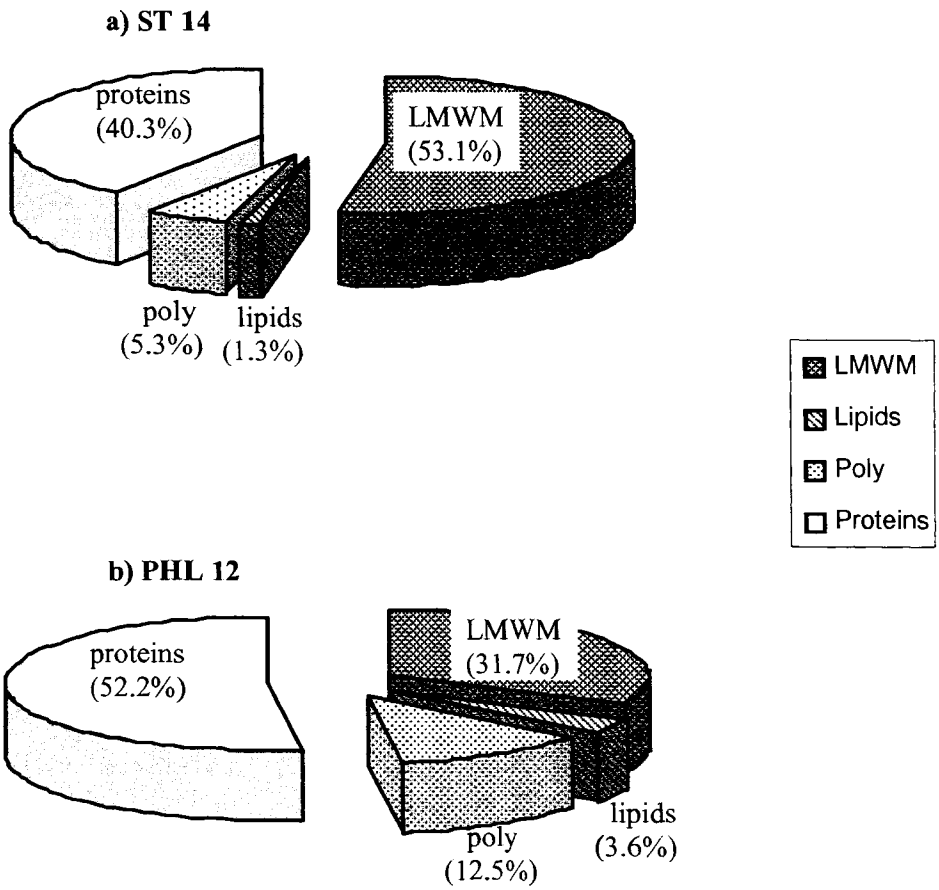

Fig. 4.24. Macromolecular compositions averaged by different light depths (100, 30, and 1 %) in the water columns of the two different stations in 2004. The data for ST 10 and PHL 12 were obtained from the 2004 RUSALCA and 2004 HX cruises, respectively. LMWM is low-molecular-weight metabolites and poly means polysaccharides.

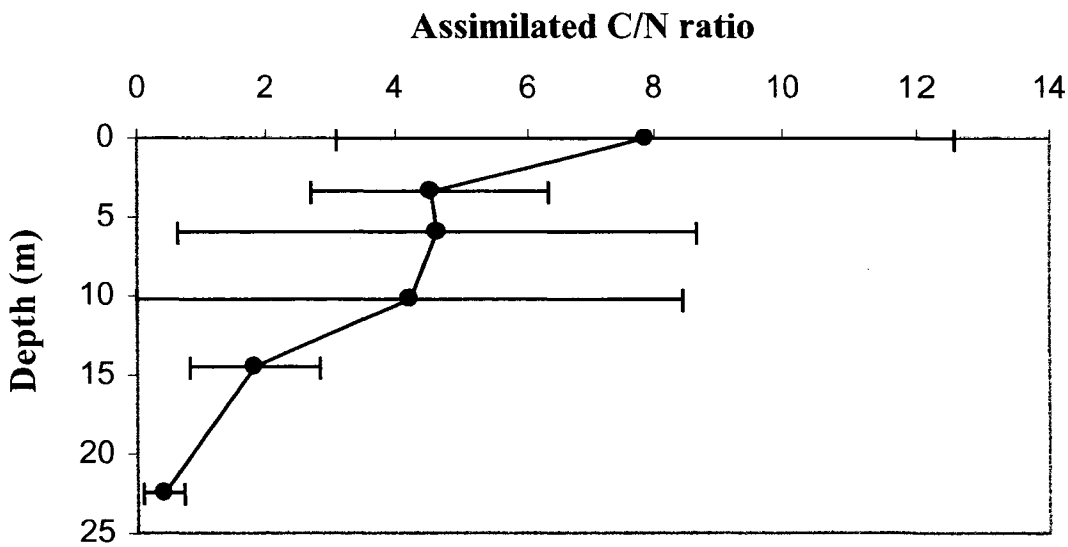

Fig. 4.25. Mean assimilated carbon and nitrogen uptake ratios at the different light depths (100, 50, 30, 12, 5, and 1 %) of the productivity stations during the 2004 RUSALCA cruise (10-22 Aug) in the Chukchi Sea. Lines stand for standard deviation for each light depth.

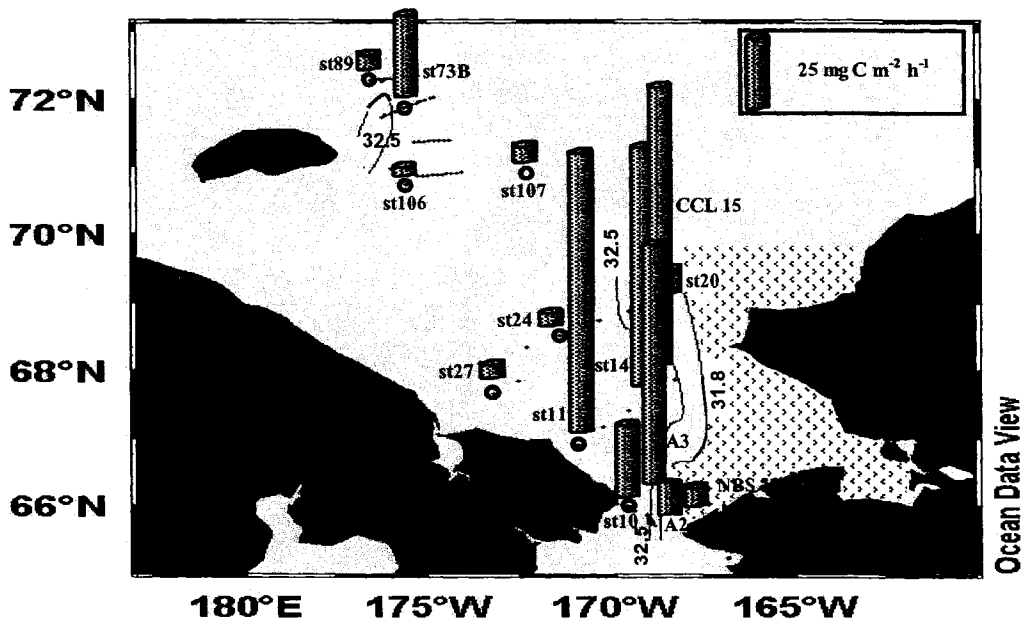

Fig. 4.26. Areal distribution of primary production rates of phytoplankton in Bering Strait and the Chukchi Sea. The production rates at all stations from the RUSALCA cruise were measured in 2004. The rates from A2, A3, NBS 12, and CCL 15 were averaged for the 2002-2004 HX cruises. The shaded area stands for Alaskan Coastal Water mass (< 31.8) determined by the bottom salinities (40 m) in 2004.

Table 4.1. Each treatment for the nutrient amendments and final concentration (µmole/l) in the 2004 RUSALCA cruise.

Treatment	Nutrient amendments	Final concentration
C	No additions	
NO_3	50 µl of stock NO_3 solution (20 µmole/ml)	20
NH_4	200 ul of stock NH_4 solution (5 µmole/ml)	20
PO_4	50 µl of stock PO_4 solution (5 µmole/ml)	5
$NO_3 + PO_4$	50 µl of stock NO_3 solution + 50 µl of stock PO_4 solution	20 + 5
SiO_4	50 µl of stock SiO_4 solution (20 µmole/ml)	20
$NO_3 + SiO_4$	50 µl of stock NO_3 solution + 50 µl of stock SiO_4 solution	20 + 20
Fe	50 µl of stock Fe solution (0.005 µmole/ml)	0.005
NO_3 + Fe	50 µl of stock NO_3 solution + 50 µl of stock Fe solution	20 + 0.005
Desferol	50 µl of working Desferol solution (0.03 µmole/ml)	0.03

Table 4.2. Carbon uptakes (mg C m^{-3} h^{-1}) at different light depths of productivity stations in the Chukchi Sea. The uptakes for all stations from the RUSALCA cruise were one time measurements in 2004, while the uptakes of A3 and CCL 15 from the HX cruises were averaged for 3 years from 2002 to 2004. ± : standard deviations.

Light depth	ST 10	ST 11	ST 14	ST 20	ST 24	ST 27	ST 106	ST 89	ST 73B	ST 107	NBS12	A2
100%	2.54	14.79	25.38	1.46	0.71	0.49	0.30	0.34	0.31	0.9	1.03	0.50
50%	2.10	13.03	17.64	1.04	0.55	0.39	0.26	0.32	0.12	0.57	0.66	0.48
30%	2.60	9.84	12.00	0.62	0.37	0.27	0.16	0.23	0.18	0.34	0.45	0.46
12%	3.80	3.23	2.55	0.22	0.10	0.12	0.07	0.11	0.55	0.13	0.18	0.33
5%	1.04	0.28	0.73	0.03	0.01	0.10	0.05	0.41	1.97	0.03	0.01	0.15
1%	0.06	0.11	0.08	0.01	0.00	0.21	0.08	0.05	0.02	0.00	–	0.05
P*	25.75	99.09	84.55	8.56	4.46	4.79	2.90	5.36	28.77	6.00	6.54	11.90
P	387	1486.5	1269	129	67.5	72	45	81	432	90	98	178.5
B	139	154	170	12	8	73	104	106	282	12	6	34
P/B	2.78	9.65	7.47	10.75	8.44	0.99	0.43	0.76	1.53	7.5	16.35	5.25

Light depth	A3	CCL15
100%	6.97 (±7.81)	14.62 (±20.52)
50%	7.24 (±9.39)	10.63 (±14.82)
30%	7.83 (±6.28)	9.65 (±13.63)
12%	5.33 (±3.89)	3.51 (±3.63)
5%	0.51 (±0.20)	0.68 (±0.61)
1%	0.09 (±0.06)	0.01 (±0.01)
P*	96.29 (±45.86)	99.73 (±120.26)
P	1444.4 (±687.90)	1496 (±1803.92)
B	121 (±68)	408 (±223)
P/B	11.94	3.67

* P*: Integrated hourly primary production (mg C m^{-2} h^{-1})
P: Integrated daily primary production (mg C m^{-2} d^{-1}), based on 15 hrs photo period per one day
B: Integrated chlorophyll-a (mg Chl-a m^{-2}) from 100 % to 1 % light depth

Table 4.3. Nitrate and ammonium uptake rates at different light depths of productivity stations in the Chukchi Sea. The uptakes for all stations from the RUSALCA cruise were one time measurements in 2004, while the uptakes of A3 and CCL 15 from the HX cruises were averaged for 3 years from 2002 to 2004. ± : standard deviations

a) Nitrate uptakes (mg N-NO_3 m^{-3} h^{-1}) in the Chukchi Sea

Light depth	ST 10	ST 11	ST 14	ST 20	ST 24	ST 27	ST 106	ST 89	ST 73B	ST 107	A2	A3	CCL15
100%	0.05	0.39	1.52	0.04	0.01	0.01	0.01	0.06	0.01	0.03	0.06	0.51 (±0.37)	0.44 (±0.46)
50%	0.07	1.46	1.91	0.04	0.01	0.01	0.01	0.06	0.01	0.03	0.05	0.47 (±0.42)	0.48 (±0.59)
30%	0.07	1.08	4.40	0.03	0.01	0.00	0.01	0.04	0.05	0.03	0.04	0.50 (±0.44)	0.50 (±0.64)
12%	0.09	0.13	0.82	0.01	0.01	0.00	0.01	0.03	0.07	0.01	0.02	0.41 (±0.34)	0.40 (±0.42)
5%	0.12	0.10	0.21	0.01	0.00	0.02	0.01	0.23	0.67	0.00	0.04	0.03 (±0.01)	0.22 (±0.35)
1%	0.03	0.09	0.04	0.02	0.01	0.05	0.04	0.10	0.02	0.00	0.01	0.01 (±0.01)	0.17 (±0.29)
P	1.10	8.84	15.95	0.42	0.14	0.39	0.37	2.32	8.49	0.36	1.18	6.85 (±2.69)	7.35 (±8.10)

* P: Integrated hourly production (mg N m^{-2} h^{-1})

b) Ammonium uptakes (mg N-NH_4 m^{-3} h^{-1}) in the Chukchi Sea

Light depth	ST 10	ST 11	ST 14	ST 20	ST 24	ST 27	ST 106	ST 89	ST 73B	ST 107	A2	A3	CCL15
100%	0.09	0.51	0.33	0.10	0.15	0.15	0.04	0.05	0.04	0.06	0.06	0.95 (±1.36)	1.98 (±0.37)
50%	0.16	0.64	0.19	0.21	0.19	0.07	0.04	0.05	0.02	0.08	0.07	0.87 (±1.20)	0.64 (±0.37)
30%	0.08	0.77	0.19	0.09	0.11	0.03	0.03	0.04	0.05	0.08	0.08	0.79 (±1.05)	2.90 (±0.37)
12%	0.12	0.34	0.25	0.06	0.02	0.02	0.02	0.05	0.09	0.04	0.08	0.60 (±0.62)	2.44 (±0.37)
5%	0.10	0.13	0.04	0.07	0.01	0.03	0.01	0.05	0.15	0.01	0.07	0.14 (±0.13)	0.63 (±0.37)
1%	0.11	0.12	0.08	0.02	0.06	0.11	0.27	0.02	0.01	0.01	0.04	0.08 (±0.04)	0.53 (±0.37)
P	1.53	7.15	1.89	1.82	1.61	1.24	1.49	0.95	2.93	1.01	2.98	13.0 (±16.17)	29.11 (±44.39)

* P: Integrated hourly production (mg N m^{-2} h^{-1})

Table 4.4. C/N ratios and f-ratios of different productivity stations in the Chukchi Sea.

Station	Carbon uptake	NO_3 uptake	NH_4 uptake	Total N uptake	f-ratio	C/N ratio
10	25.75	1.10	1.53	2.63	0.428	11.4
11	99.09	8.84	7.15	15.99	0.553	7.2
14	84.55	15.95	1.89	17.84	0.894	5.5
20	8.56	0.42	1.82	2.24	0.188	4.5
24	4.46	0.14	1.61	1.75	0.080	3.0
27	4.79	0.39	1.24	1.63	0.239	3.4
106	2.90	0.37	1.49	1.86	0.199	1.9
89	5.36	2.32	0.95	3.27	0.710	1.9
73B	28.77	8.49	2.93	11.42	0.743	2.9
107	6.00	0.36	1.01	1.37	0.263	5.1
A2	11.90	1.18	2.58	3.76	0.314	3.7
A3	96.29	6.85	13.05	19.90	0.344	5.7
CCL15	99.73	7.35	29.12	36.47	0.202	4.0
average	**36.78**	**4.14**	**5.11**	**9.24**	**0.40**	**4.63**
S.D.	**41.25**	**4.93**	**7.98**	**10.68**	**0.25**	**2.55**

* S.D.: Standard Deviation
* units of NO_3, NH_4, and total N uptakes: mg N m^{-2} h^{-1}
* unit of carbon uptake: mg C m^{-2} h^{-1}

Table 4.5. Comparison of daily primary productivity rates in Bering Strait and the Chukchi Sea. For comparison, the rate from this study is only 2004 RUSALCA data.

Source	Production ($g\ C\ m^{-2}\ day^{-1}$)	Method	Place or Water mass	Season
McRoy et al. (1972)	4.1	^{14}C uptake	western Being Strait	June
Hameedi (1978)	0.1-1.0 > 3.0	^{14}C uptake	Chukchi Sea central Chukchi Sea	July
Sambrotto et al. (1984)	2.7	NO_3^- disappearance	western Being Strait	
Springer (1988)	1.5-16	^{14}C uptake	central Chukchi Sea	11 July-2 Aug.
Korsak (1992)	1.7	^{14}C uptake	Chukchi Sea	28 July-Aug.
Zeeman (1992)	1.6 0.8	^{14}C uptake	Chukchi Sea Bering Strait	28 July-Aug.
Hansell et al. (1993)	4.8- 6.0	NO_3^- disappearance	Anadyr Water in the north of Bering Strait	
Springer and McRoy (1993)	4.7	^{14}C uptake and chl-a concentration	central Chukchi Sea	28 July-Aug.
This study	**0.4** **1.4**	^{13}C uptake	Chukchi Sea central Chukchi Sea	10-22 Aug.

Chapter 5. Conclusions and recommendations

5.1. Conclusions

Over the past few decades, the environment of the Arctic has been rapidly altered due to global change. The higher temperatures plus a possible increase in ice export have decreased the ice extent and sea-ice thickness in the Arctic Ocean over the past 40 years contributing to more open water, especially in coastal regions (Maslanik et al. 1996; Martin et al. 1997; Maslanik et al. 1999; Rothrock et al. 1999; Rothrock et al. 2003). Laxon et al. (2003) expect additional thinning of Arctic sea ice with the continued increase in melt season length. In addition, general circulation models predict an increase in precipitation in the Arctic as the result of increasing atmospheric carbon dioxide concentrations (Phoenix and Lee 2004). In fact, increases in fresh water discharge from the six largest Eurasian rivers to the Arctic Ocean have been observed from 1936 to 1999 (Peterson et al. 2002). These environmental changes in the Arctic are projected to profoundly alter the marine ecosystem of the Arctic Oceans (Melnikov 2000). This study covered 3 different environments in the western Arctic Ocean: the deep Canada Basin, representing the Arctic Ocean which is mostly covered by multi-year or first-year ice (Chapter 2): the land fast sea ice of Barrow (Chapter 3): and Bering Strait and the Chukchi Sea, representing shallow shelf regions covered by seasonal pack ice (Chapter 4). It aimed to provide information on the following 5 issues for these 3 regions.

1. The contemporary range of nutrients concentrations, phytoplankton biomass, and productivity.

In the deep Canada Basin, NO_3^- was almost depleted (< 0.05 μM) in the upper mixed layer, but the concentration increased from 20 m to the chlorophyll-maximum layer (4.52 μM) at around 50 m depth, while NH_4^+ had a consistently low concentration (< 0.40 μM) down to the

chlorophyll-maximum layer. The mean phytoplankton biomass in the surface water without ice was 0.04 mg chl-a m^{-3} (± s.d. 0.02 mg chl-a m^{-3}), whereas the mean biomass at the surface below ice was 0.02 mg chl-a m^{-3} (± s.d. 0.01 mg chl-a m^{-3}). In the chlorophyll-maximum layer, the mean biomass was 0.60 mg chl-a m^{-3} (± s.d. 0.31 mg chl-a m^{-3}).

The annual carbon production rate of phytoplankton in the deep Canada Basin was about 5 g C m^{-2} when transformed in order to take into account the changes in the percentage of ice cover. There was no major depletion of nutrients in the water column under the land fast sea ice and the bottom section of the sea ice at Barrow during the observation period in 2003, except for the low concentration (< 0.5 μM) of PO_4 in the water column and the bottom ice at the end of the season. The chlorophyll-a concentration in the water column under the ice remained low (1 mg chl-a m^{-3}) in 2003 and 2004. The maximum chlorophyll-a concentrations of ice algae were 24 mg chl-a m^{-2} in early May in 2002 and 27 mg chl-a m^{-2} in late April in 2003. Based on the observation period in 2003, the estimated production rates of ice algae on the bottom of the ice and of phytoplankton under the ice were 2.0 g C m^{-2} and 0.7 g C m^{-2}, respectively.

The integrated nitrate concentrations in the central Chukchi Sea, as the most productive region in the Chukchi Sea, were 400-500 mg-at NO_3-N m^{-2} and 600-800 mg-at NO_3-N m^{-2}, respectively for the 2002-2003 *Alpha Helix* cruises and the 2004 *Alpha Helix* and RUSALCA cruises. The integrated chlorophyll-a concentration in the region was 200-500 mg chl-a m^{-2} in this study. Based on 100 growing days (Springer and McRoy 1993), the mean annual production of phytoplankton from this study was 73 g C m^{-2} for the southern Chukchi Sea while the mean annual production for the entire Chukchi Sea was somewhat lower (55 g C m^{-2}).

2. How contemporary productivity rates compare with those obtained in previous decades.

Primary productivity in the deep Canada Basin in this study was higher than the

estimation by Pautzke (1979), mainly because he measured only the phytoplankton production under drifting pack ice. Although the maximum chlorophyll-a concentration of the ice algae was similar to that observed in the previous study at Barrow, the ice algal production in this study was lower than that in Alexander et al. (1974) because of either interannual variation of the ice algal production, different incubation methods, and/or sampling time or interval for the ice algal production. Consistent with this trend of lower chlorophyll-a concentrations in the Chukchi Sea, the carbon and nitrogen uptake rates of phytoplankton were generally lower in this study compared to previous studies. These lower productivity rates from this study represent an overall trend or are related to interannual or shorter term variations.

3. The environmental factor(s) that are most important in controlling productivity of phytoplankton and ice algae.

Nutrients were a main limiting factor for phytoplankton at the surface, whereas light was a major limiting factor in the chlorophyll-maximum layer for open waters. The growth of phytoplankton under the bottom surface of the ice was controlled often simultaneously by both light and nutrients. The primary production rates of phytoplankton and the bottom sea ice algae at the landfast sea ice of Barrow were mainly limited by light through the snow-covered sea ice.

4. Changes in the physiological conditions of phytoplankton and ice algae that might be occurring under ongoing changes in the ice thickness and extent in the Arctic Oceans.

Higher lipid synthesis of the bottom ice algae (possibly phytoplankton) is expected under the reduced ice thickness condition because more light is now available. This might be significant to the nutrition of zooplankton and benthic fauna because lipids are the most energy dense biomolecules (Wainman and Lean 1992).

5. The fate of ice algal production in the coastal fast ice of the Arctic Ocean.

Based on the size composition and physiological condition of ice algae, it appears that the ice algal biomass at the bottom of the sea ice probably rapidly sinks to the sea floor out of the water column especially on the shallow shelf (4-10 m depth), after the ice algae has been released from the bottom ice.

This study in the different regions of the western Arctic Ocean showed that the changes in primary productivity under current environmental changes strongly depend on different parameters for the different locations. The primary productivity in the deep Canada Basin, which is mostly covered by multi-year or first-year ice, would be increased by reduced ice cover and more open water if temperatures continue to warm. Although possible increases of snow due to warming temperatures in the Arctic Ocean might suppress the productivities of phytoplankton and ice algae during the ice-covered period, the overall annual productivity in this region could nevertheless be higher. This would result from an earlier onset of snow melt and open water and thinner sea ice with increased warming that would consequently allow more light to penetrate to the bottom of the ice and into the water column.

In the coastal fast sea ice of Barrow and possibly in the Chukchi Sea, an increase of sediment trapped in the sea ice by greater river discharge due to warming temperature could decrease the productivities of phytoplankton and ice algae during the ice-covered period. However, this could be balanced in the spring and summer by the reduced ice thickness and earlier onset of snow melt that could increase productivities. After the retreat of the sea ice in Bering Strait and the Chukchi Sea, larger freshwater discharge along the coast of Alaska might also decrease the primary production in the Chukchi Sea during the open water period. Generally,

Alaskan Coastal Water carries much less nitrate and chlorophyll-a than Anadyr Water through Bering Strait. If more terrestrial discharge, especially from the Yukon River, were added to Alaska Coastal Water through the strait, and if this led to a proportional reduction in volume transport of Anadyr Water, lower phytoplankton biomass and nutrients and consequently less production in the Chukchi Sea might occur.

5.2. Recommendations

The carbon and nitrogen uptake rates from this study were mostly based on summer measurements. Since the Arctic has distinct seasonal and annual variations as well as a diurnal cycle in the phytoplankton biomass and in the photosynthetic rate, measurements for different seasons and years would be needed to obtain more precise carbon and nitrogen production rates of primary producers. Especially in Barrow, increasing the timing and location of observations would be very important for studying the biomass, primary production, and fate of ice algae since the variations are large. In addition to phytoplankton, ice algae within the sea ice are an important additional food source in the coastal zone near Barrow, Alaska, and thus presumably in Bering Strait and the Chukchi Sea. Improvement of the ice algae production rates would provide better insight into the estimation of total annual primary production in the deep Canada Basin and Bering Strait/Chukchi Sea. Recent studies revealed a high percentage (up to 56 %) of DOC and EPS (Exopolymeric substances) released by phytoplankton and ice algae in the Arctic Ocean (Gosselin et al. 1997; Guay et al. 1999; Krembs et al. 2002). Thus, more research on DOC and EPS productions of producers would be necessary to estimate total primary production and carbon cycling in the Arctic Ocean.

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