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Interannual Variations of Nutrients and Primary Production over the Southeastern Bering Sea Shelf during the Spring of 1997, 1998, and 1999*

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Abstract—The southeastern Bering Sea shelf experienced dramatic changes in large-scale climate conditions and local weather conditions during 1997, 1998, and 1999. We investigated the changes in the nutrient distribution and primary production in response to the changing physical condition over the shelf region. The temperature and salinity profiles showed that sea ice conditions and wind-mixing events strongly influenced the hydrographic conditions. Biological utilization and physical process, such as horizontal advection below the pycnocline, played an important role in the distribution and interannual variation of nutrients. The distribution of temperature and ammonium across the shelf suggested that there was offshore transport of the middle shelf water at mid-depths over the outer shelf, which may export materials from the middle shelf to the outer shelf and shelf break. The distribution of the carbon and nitrogen uptake rates showed large interannual differences due to variations in the development of stratification and nutrient concentrations that resulted from variations in the sea ice dynamics and wind mixing over the shelf region. The occurrence of a high amount of ammonium in the early spring may affect the nitrate utilization and result in an increase of the total primary production.

INTRODUCTION

The fluctuations of atmospheric conditions are closely related to the variations of solar radiation, sea ice cover, and water column temperature, and are very important controlling factors of ecosystem over the southeastern Bering Sea shelf [29]. The strength and position of the Aleutian Low during the winter (storm tracks along the Aleutian Island chain) affect the winds and surface heat flux over the southeastern Bering Sea shelf, which, in turn, control the extent and duration of sea ice [24, 34]. The variations of sea ice and wind influence the development of spring blooms with an early ice-edge bloom occurring in colder years and a later open water spring bloom in warmer years [13, 22]. This further affects the growth and survival of larval and juvenile fish and recruitment of large piscivorous fish [8, 22]. The location of the Aleutian Low is closely related to large-scale atmospheric variations, such as the El Niño/Southern Oscillation (ENSO) and the Pacific Decadal Oscillation (PDO) of the North Pacific sea surface temperature [20, 34].

During the years of 1997, 1998, and 1999, both large-scale atmospheric conditions and local weather conditions showed a strong interannual variation over the southeastern Bering Sea shelf. In 1997, the Aleutian Low was slightly stronger than normal due to the atmospheric teleconnection of ENSO to the southeastern Bering Sea. There were strong positive solar heating anomalies from late May to mid-July and winds were generally weak, except for a severe storm in May [26, 34]. In 1998, the strength of the Aleutian Low was similar to that in 1997, but the solar heating anomalies were near zero and winds were strong into June and after mid-August [34]. In 1999, the 1998/1999 La Nina conditions affected the North Pacific and the southeastern Bering Sea and the pattern and strength of winds were similar to those in 1998 [10, 33].

The interannual variations of physical conditions during the years of 1997, 1998, and 1999 were accompanied by unusual responses of biological and chemical conditions [19, 26, 34]. Several anomalous conditions were observed from lower to higher trophic levels. These include a large decrease of deep nitrate concentrations during June 1997 [27, 37], an unprecedented bloom of coccolithophores (*Emiliania huxleyi*) beginning in July 1997 [12, 38], low returns of sockeye salmon (*Oncorhynchus nerka*) to Bristol Bay during 1997 and 1998 [12] (recurring in 1998 and 1999 [12]), and a massive mortality of short-tailed shearwaters during 1997 [3].

The purpose of this study is to describe the responses of physical (temperature and salinity), chemical (nutrient), and biological (spring primary production) conditions to the observed atmospheric conditions during 1997, 1998, and 1999. The distribution of temperature, salinity, and nutrients was examined across the shelf and along the 70 m isobath of the middle shelf of the southeastern Bering Sea. The total and new production were measured using ^{13}C and ^{15}N dual labeling techniques [30] in order to estimate the spring primary production.

*This article was submitted by the authors in English.

MATERIALS AND METHODS

Data were collected over the southeastern Bering Sea shelf during early May of 1997, 1998, and 1999 (Fig. 1). Water samples for nutrient analyses (nitrate, silicate, phosphate, ammonium, and nitrite) were taken from Niskin bottles mounted on a CTD/rosette sampler and were analyzed on the ship [41]. Water samples for productivity measurements were taken from six depths, which corresponded to the 100, 50, 30, 12, 5, and 1% penetration of the surface photosynthetically active radiation (PAR) at a morning or mid-day station. Each bottle was spiked with 10% additions of ^{13}C ($H^{13}CO_3^-$) and ^{15}N tracers ($^{15}NO_3^-$ or $^{15}NH_4^+$) and then placed in a deck incubator cooled by running surface seawater for 4–6 h. After 4 h, the incubations were terminated by collecting the particulate matter on precombusted GF/F glass fiber filters and were kept frozen until preparation for mass spectrometric analysis. The filters were acid fumed and dried for 24 h at 60°C. The isotopic analysis for the ^{13}C and ^{15}N abundance and the measurements of the quantity of particulate organic carbon (POC) and particulate organic nitrogen (PON) were performed with a CN analyzer coupled to a Europa 20–20 mass spectrometer. The ^{15}N uptake rates were calculated using the following standard JGOFS procedures [39]. The calculation of the carbon uptake rates (h^{-1}) was undertaken with minor modification of the nitrogen equations, such as those for the natural abundance of ^{13}C (atom %) in the particulate phase (1.108%).

RESULTS

Distributions of Hydrographic Properties

Interannual variations of the spring hydrographic conditions were evident in the temperature and salinity distributions of the across-shelf transect and the transect along the 70 m isobath (Fig. 2). During early May 1997, the temperature ranged from ca. –1 to 4°C and the salinity ranged from 31.14 to 32.76 psu. A two-layer structure over the middle shelf region was evident in the temperature profile, while a three-layer system occurred over the outer shelf region and a homogeneous water column occurred on the innermost part of the transect. The influence of ice melt water was evident by the presence of cold (–1 to 2°C) and relatively fresh (<32 psu) water masses over the shelf region where the water column depth was shallower than 100 m, especially at the inner stations of the transect around the M2 station over the middle shelf (Fig. 2). There was a tonguelike feature of the 3°C isotherm over the outer shelf region between 30 and 80 m, which may be related to the export of middle shelf water masses to the outer shelf (Fig. 2). Warmer (>3.5°C) and saltier (>32.6 psu) water masses occurred in the bottom layer over the outer shelf region.

During early May 1998, the water masses over the middle and outer shelf were warmer ($2 < T < 4$°C) and saltier ($32 < S < 33$ psu) than during early May 1997. A homogeneous water mass was distributed at depths shallower than 80 m over the entire shelf area. The minimum temperature over the shelf region was about 2°C, which was ca. 3°C higher than in 1997, while the maximum temperatures in the bottom layer over the outer

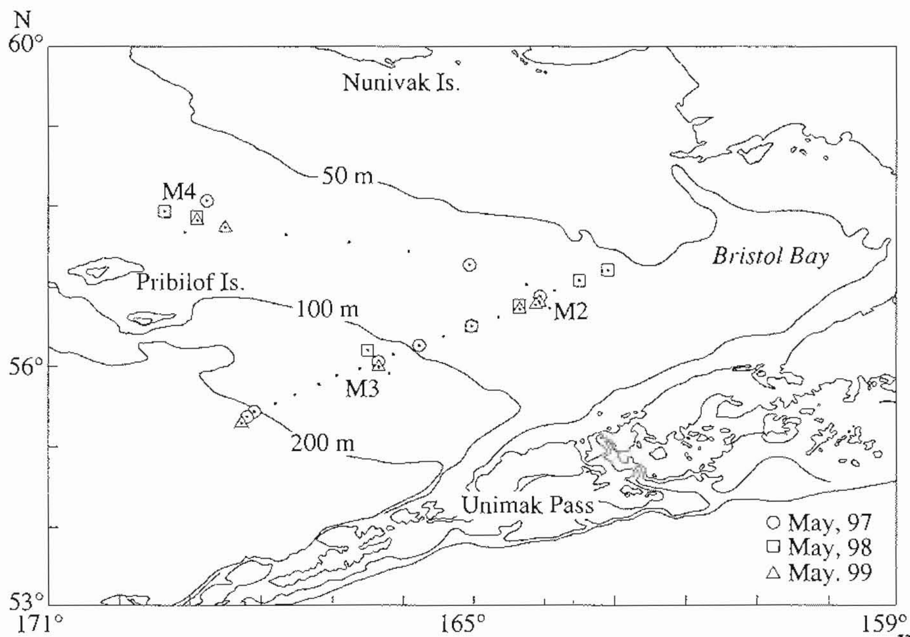

Fig. 1. Locations of hydrographic stations across the shelf and along the 70 m isobath over the southeastern Bering Sea shelf during the spring cruises of 1997, 1998, and 1999.

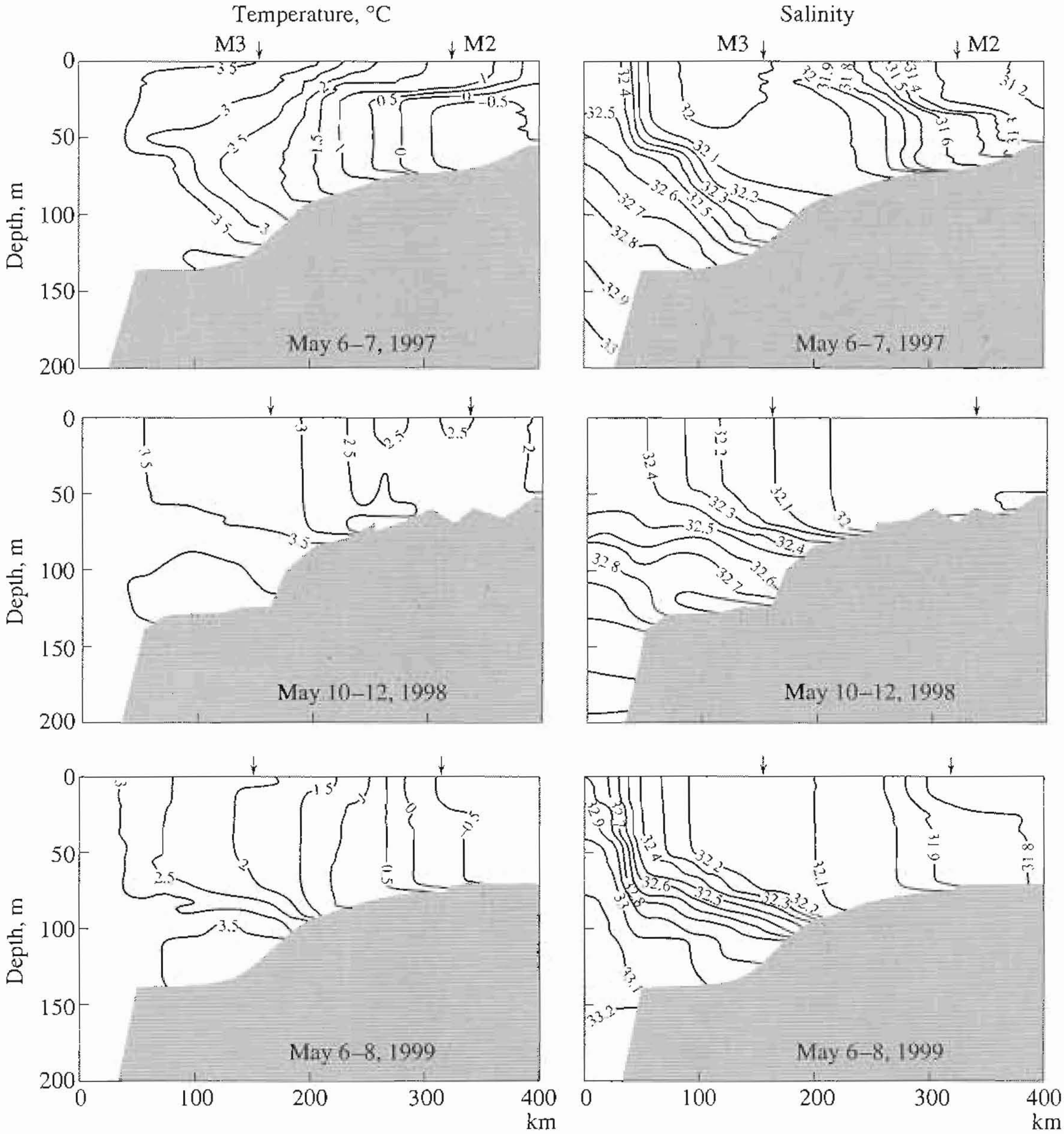

Fig. 2. Distributions of temperature (left) and salinity (right) across the southeastern Bering Sea shelf during the spring cruises of 1997, 1998, and 1999. The locations of mooring stations are marked by arrows.

shelf were similar both in 1997 and 1998. Similar to in early May 1997, warmer and saltier water masses also occurred in the bottom layer over the shelf region. However, the area that was warmer and saltier than the 4°C isotherm and the 32.7 psu isohaline was larger in 1998 than in 1997. The depth of the 33 psu isohaline was slightly shallower in 1998 than 1997. The slope of the shelf-break front was more horizontal in 1998 than in 1997. During early May 1999, the ranges of the temperature ($-1.2 < T < 3.6$°C) and salinity ($31.8 < S < 33.1$ psu) were similar to those in May 1997 but the distributions were more similar to those in May 1998 (Fig. 2). However, there was no temperature signal that would suggest the export of middle shelf water onto the outer shelf. The distributions of the temperature and salinity in the bottom layer over the shelf were slightly cooler (0.4°C) and saltier (0.2 psu), and the 33 psu isohaline occurred farther inshore over the outer shelf region compared with the previous two years. However, the slope of the shelf-break front was similar to that in 1997.

The profiles of the temperature and salinity indicated a strong influence of ice melt water along the

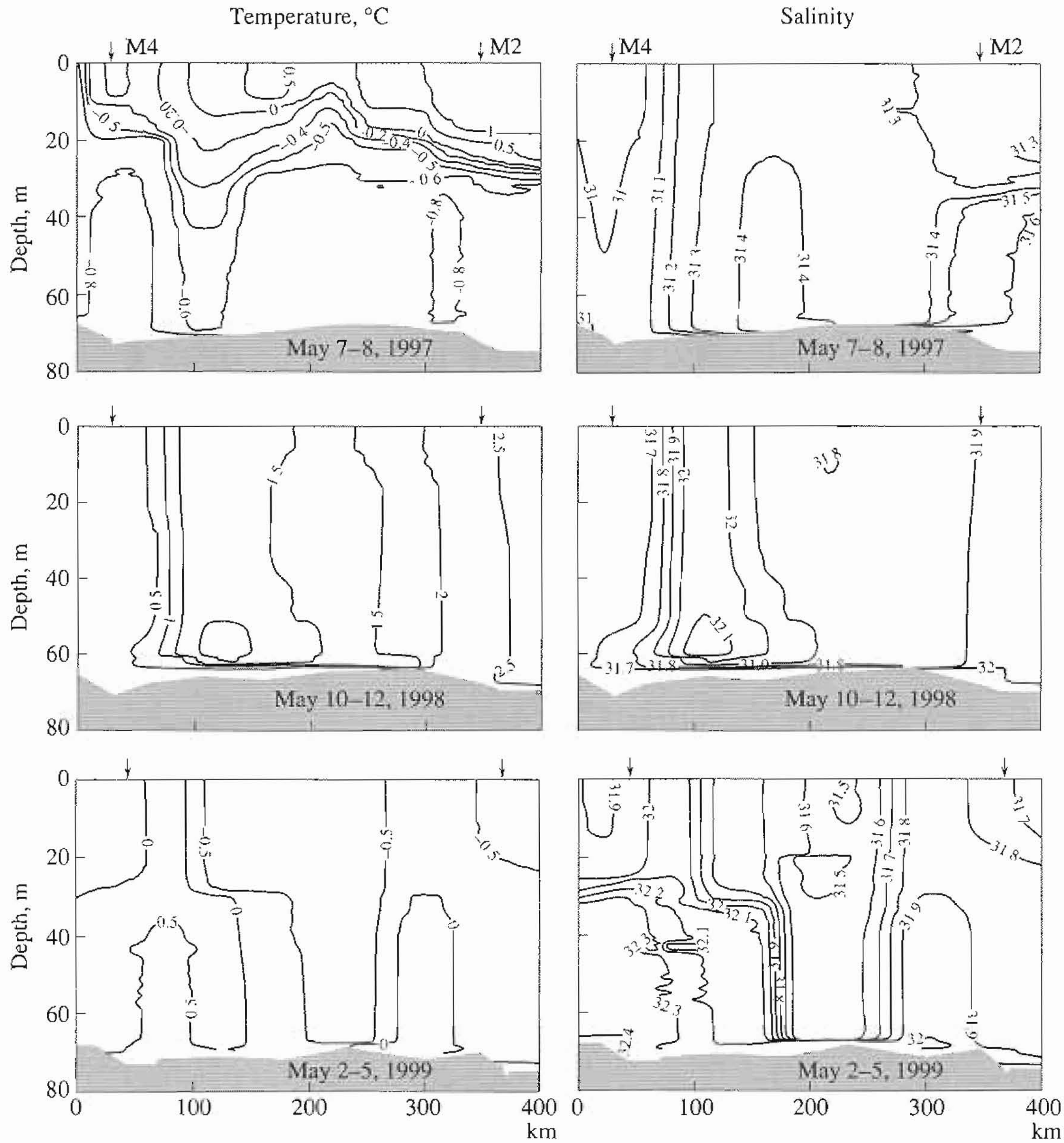

Fig. 3. Distributions of temperature (left) and salinity (right) along the 70 m isobath in the middle domain during the spring cruises of 1997, 1998, and 1999. The locations of mooring stations are marked hy arrows.

70 m isobath transect, which was much more prominent in the northern part than in the southern part of the transect. The properties of the water column were not homogeneous and also showed large interannual variations (Fig. 3). During 1998, a relatively warm (>2°C) and saline (>32 psu) water mass occurred in the water column around the 100 km region of the transect and the temperature and salinity along the transect were slightly higher than in 1997 (Fig. 3). During early May 1999, the distribution of the temperature and salinity clearly showed the intrusion of the warm and saline water masses in the bottom layer of the northern and southern parts of the transect (Fig. 3).

Distribution of Nutrients

During the spring of 1997, 1998, and 1999, the concentrations and the spatial distributions of nitrate and ammonium showed strong variations in the across shelf transects (Fig. 4). During early May 1997, the nitrate concentrations ranged from 0.5 to 22 μM over the shelf region. Low nitrate concentrations (<1 μM) occurred in

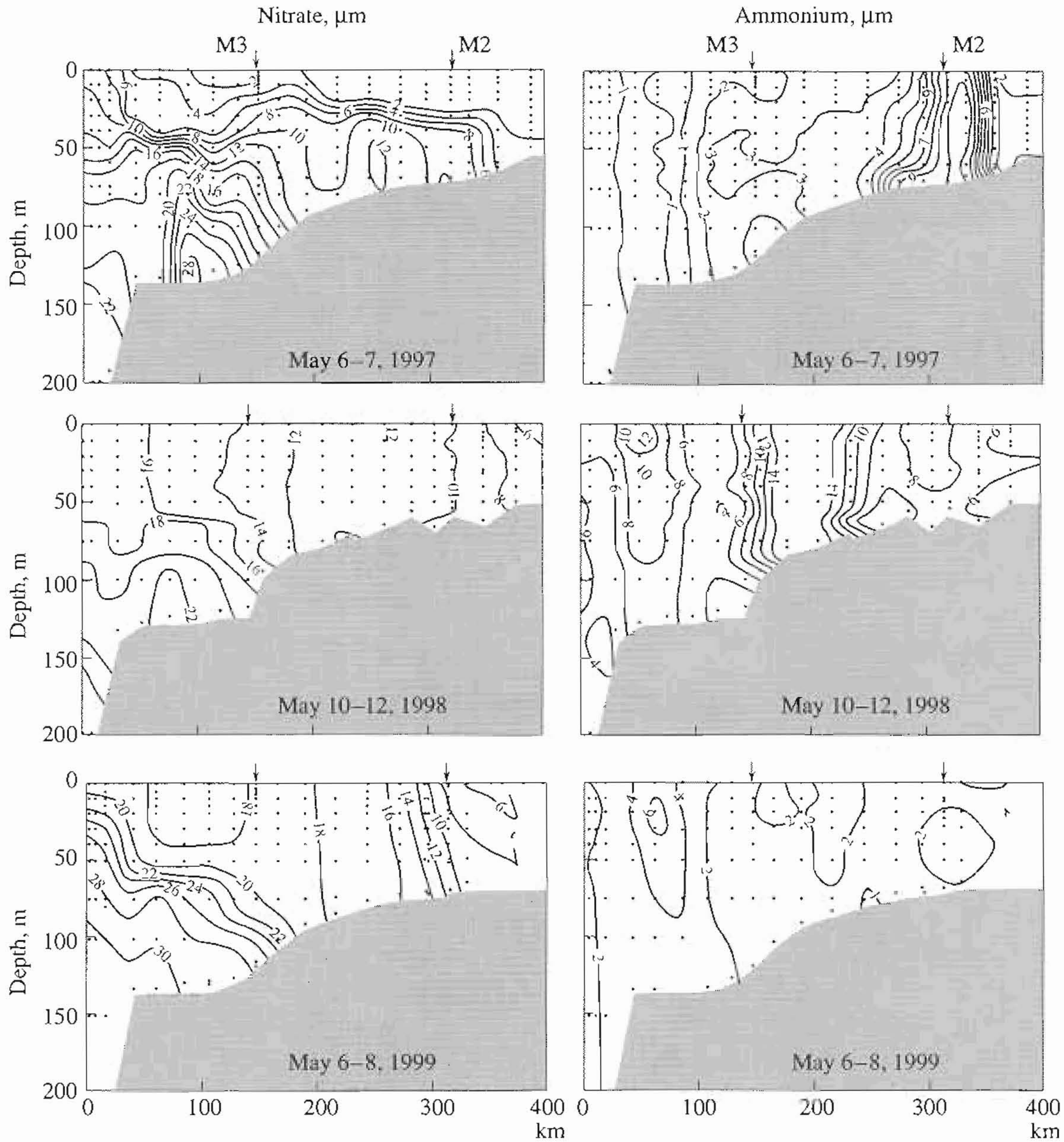

Fig. 4. Distributions of nitrate (left) and ammonium (right) across the southeastern Bering Sea shelf during the spring cruises of 1997, 1998, and 1999. The locations of mooring stations are marked by arrows.

most of the surface layer (<20 m) across the shelf. However, a relatively high nitrate concentration (ca. 9 µM) occurred at the outer shelf station, where a saline water mass outcropped in the surface layer as indicated by the 32 psu isohaline. In the bottom layer of the middle shelf, the nitrate concentrations were still high (>8 µM). There were high nitrate concentrations (>20 µM) in the bottom layer over the outer shelf. A strong gradient of nitrate concentrations, from 10 to 20 µM, occurred at the shelf-break front (Fig. 4). The ammonium concentrations ranged from 0.3 to 14 µM (Fig. 4). The center of the high ammonium concentrations (ca. 8–14 µM) occurred around mooring site M2 and was vertically homogeneous throughout the water column. The ammonium concentrations gradually decreased away from the M2 station and were less than 1 µM over the outer shelf region. A subsurface tongue-like structure of the 3 µM ammonium concentration occurred at about a 75 m depth over the outer shelf region at the 120 m isobath (Fig. 4).

During early May 1998, the nitrate concentrations were slightly higher over the entire southeastern Bering

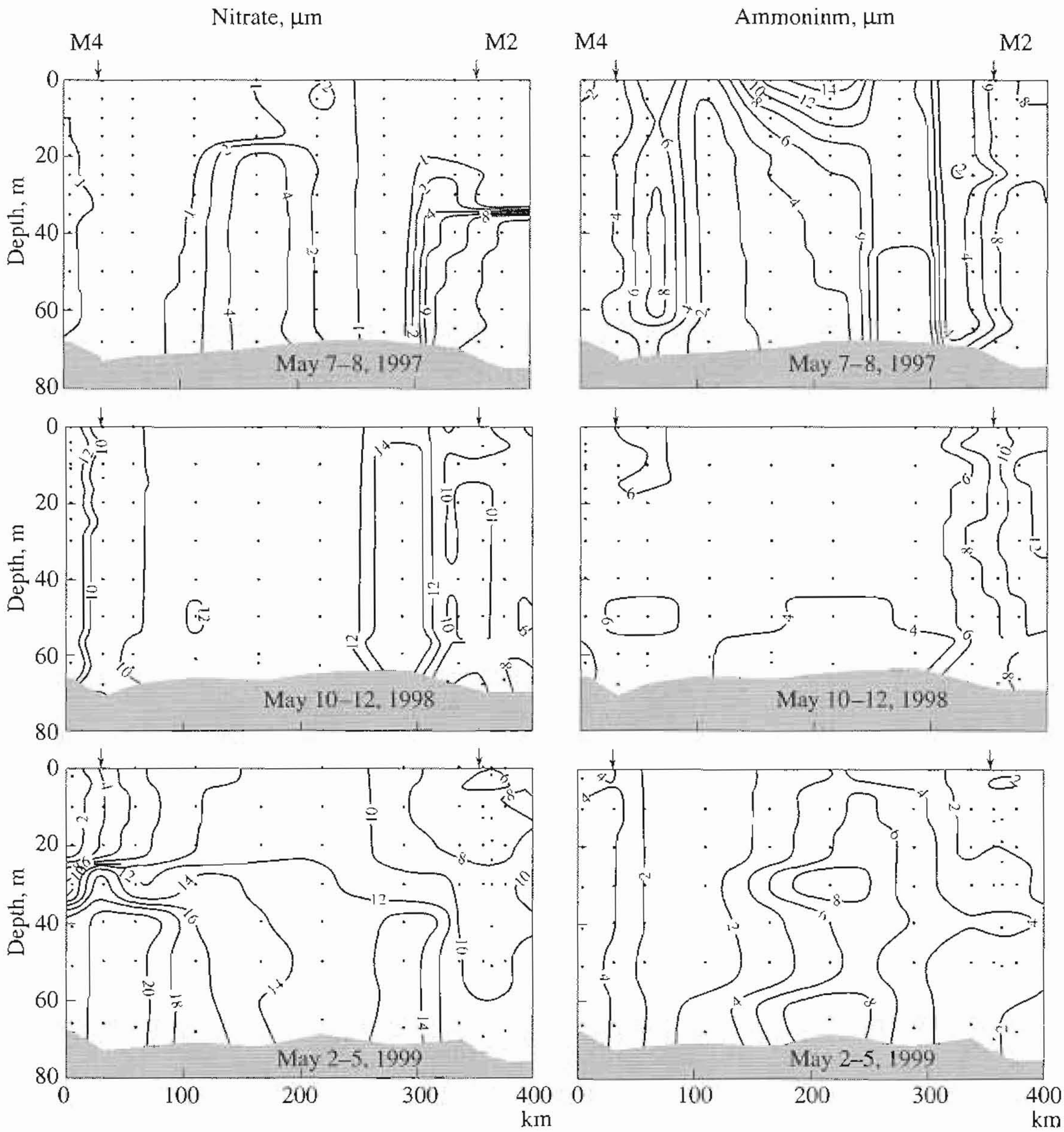

Fig. 5. Distributions of nitrate (left) and ammonium (right) along the 70 m isobath in the middle domain during the spring cruises of 1997, 1998, and 1999. The locations of mooring stations are marked by arrows.

Sea shelf compared with early May 1997 and ranged from 7 to 23 μM (Fig. 4). The nitrate concentrations were vertically homogeneous in the upper 100 m of the water column over most of the shelf region. The nitrate concentrations were low (<8 μM) at the inner end of the across shelf transect and gradually increased toward the offshore stations. The nitrate concentrations were high (>20 μM) in the bottom layer of the outer shelf. The ammonium concentrations were greater (ca. 5–15 μM) during early May of 1998 than during early May of 1997 and were vertically homogeneous. The center of the high ammonium concentrations (7.5–15 μM) occurred around the 100 m isobath. The ammonium concentrations gradually decreased from the center of the high ammonium concentration, except that high ammonium concentrations (ca. 5–10 μM) also occurred over the shelf-break region. There was also an indication of a mid-depth export of high ammonium to the outer shelf over the 100 m isobath (Fig. 4).

During early May 1999, the nitrate concentrations were higher (ca. 9–30 μM) but the ammonium concentrations were lower (ca. 2–6 μM) over the shelf region compared with the previous two years (Fig. 4). The nitrate concentrations rapidly increased from 10 to

16 μM around the M2 station. A water mass containing high nitrate (16–20 μM) occupied most of the shelf region. There was a slight decrease of the nitrate concentration in the surface layer over the outer shelf, where the water column was still well mixed to 70 m. The nitrate concentration in the bottom layer over the outer shelf was higher (≥8 μM) than during the previous two years, and the area with >20 μM nitrate was greater. The ammonium concentrations over most of the shelf region were low (<2 μM) compared to the previous two years. In the surface layer over the outer shelf, the ammonium concentrations were high (ca. 6 μM) and decreased gradually away from that region (Fig. 4).

The concentrations of nitrate and ammonium along the 70 m isobath also showed large interannual variations. During early May, the nitrate concentrations ranged from 0.03 to 11 μM in 1997; 8–15 μM in 1998; and 0.2–21 μM in 1999 (Fig. 5). The nitrate concentration was depleted (<1 μM) at most of the stations along the 70 m isobath over the middle shelf. During 1998, high nitrate concentrations (>11 μM) occurred in the warmer and saltier water masses of the 70 m isobath transect. Relatively low nitrate concentrations (<8 μM) occurred at the southern end. In 1999, at the northern end of the transect, depletion of the nitrate concentration (<1 μM) occurred in the surface layer, while high concentrations (>15 μM) were found in the relatively high salinity bottom layer. The Nitrate concentrations in the bottom layer were generally high in the north and decreased progressively toward the south. At the southern end, the nitrate concentrations were slightly lower in the snrface layer than in the bottom layer.

The ammonium concentrations ranged from 0.3 to 15.4 μM along the 70 m isobath transect during the three years with a general trend of higher concentrations in the south (Fig. 5). Some of the lower ammouium concentrations (<4 μM) occurred around stations with high uitrate concentrations. In 1999, the ammonium concentrations were generally lower (0.3–10.4 μM) than during the previous two years. High ammonium concentrations occurred in the water column between 200 and 300 km from the southern end of the transect; they were coincident with the center of a cold (<–0.5°C) and less saliue (<32 psu) water mass.

Carbon and Nitrogen Uptake Rates

The carbon uptake rates showed interannual variations across the southeastern Bering Sea shelf during early May of 1997, 1998, and 1999 (Fig. 6). During early May 1997, the carbon uptake rates ranged from 0.1 to 42.4 μg C l^{-1} h^{-1} along the across shelf transect. In the middle shelf region, two extreme carbon uptake values were observed. The lowest carbon uptake rates (<0.2 μg C l^{-1} h^{-1}) occurred at M2, while the highest uptake rate (42.4 μg C l^{-1} h^{-1}) was observed at stations between M3 and M2, where high nutrient water outcropped in the surface layer. At the shelf-break and the outer shelf regions, moderate carbon uptake rates (0.2–6.0 μg C l^{-1} h^{-1}) were observed. During early May 1998, the carbon uptake rates ranged from 0.1 to 8.9 μg C l^{-1} h^{-1} across the shelf. Most of the carbon uptake rates were less than 2.5 μg C l^{-1} h^{-1}, except for the high carbon uptake rate (ca. 8.9 μg C l^{-1} h^{-1}) at the innermost station (St. 33) of the transect. The maximum carbon uptake rates in the spring of 1998 were much lower than in 1997. During early May 1999, the carbon uptake rates ranged from 0.1 to 13.5 μg C l^{-1} h^{-1} along the across shelf transect. The carbon uptake rates were generally less than 5.4 μg C l^{-1} h^{-1} but were elevated (up to 13.5 μg C l^{-1} h^{-1}) at the shelf-break station. The carbon uptake rates were lower in 1999 than in 1997 but were slightly higher than in 1998.

The carbon uptake rates of the spring of 1997, 1998, and 1999 varied interannually along the 70 m isobath transect of the middle shelf (Fig. 7). During early May 1997, the carbon uptake rates were generally low over the middle shelf and were similar in both the southern and northern areas. During early May 1998, the carbon uptake rates were slightly greater than during 1997. The carbon uptake was high in the surface layer and decreased with depth. The carbon uptake rates in the surface layer ranged from 0.58 to 8.8 μg C $l^{-1}h^{-1}$. The carbon uptake rates in 1998 were slightly greater in the south than in the north. The highest uptake rate in 1998 occurred at station 32, which is located at the inner end of the transect in the southern part of the middle shelf. During early May 1999, the carbon uptake rates were high in the surface layer and decreased with the depth in the southern part of the transect, while the carbon uptake rates showed a subsurface maximum in the northern part. The carbon uptake rates in 1999 were slightly greater than those of the previous two years. The uptake rates were higher in the north than in the south, in contrast to 1998.

The nitrate uptake rates in the across shelf regions also showed interannual variations during the spring of 1997, 1998, aud 1999 (Fig. 6). During early May 1997, the nitrate uptake rates ranged from 0.01 to 3.8 μg N l^{-1} h^{-1} in the middle shelf region and from 0.1 to 1.4 μg N l^{-1} h^{-1} in the outer shelf and the shelf-break regions. The nitrate uptake rates showed two extreme values in the middle shelf area. The minimum value occurred around station M2, and the maximum value occurred at stations between M3 and M2, where high nutrient water reached the surface. During early May 1998, the nitrate uptake rates were generally less than 0.1 μg N l^{-1} h^{-1} across the shelf, except for the innermost station (0.02–0.46 μg N l^{-1} h^{-1}) of the transect. The nitrate uptake rates were generally lower in 1998 than in 1997 in spite of the higher nitrate concentrations in 1998 compared with 1997. During early May 1999, the nitrate uptake rates were lower in the middle shelf region (0.02–

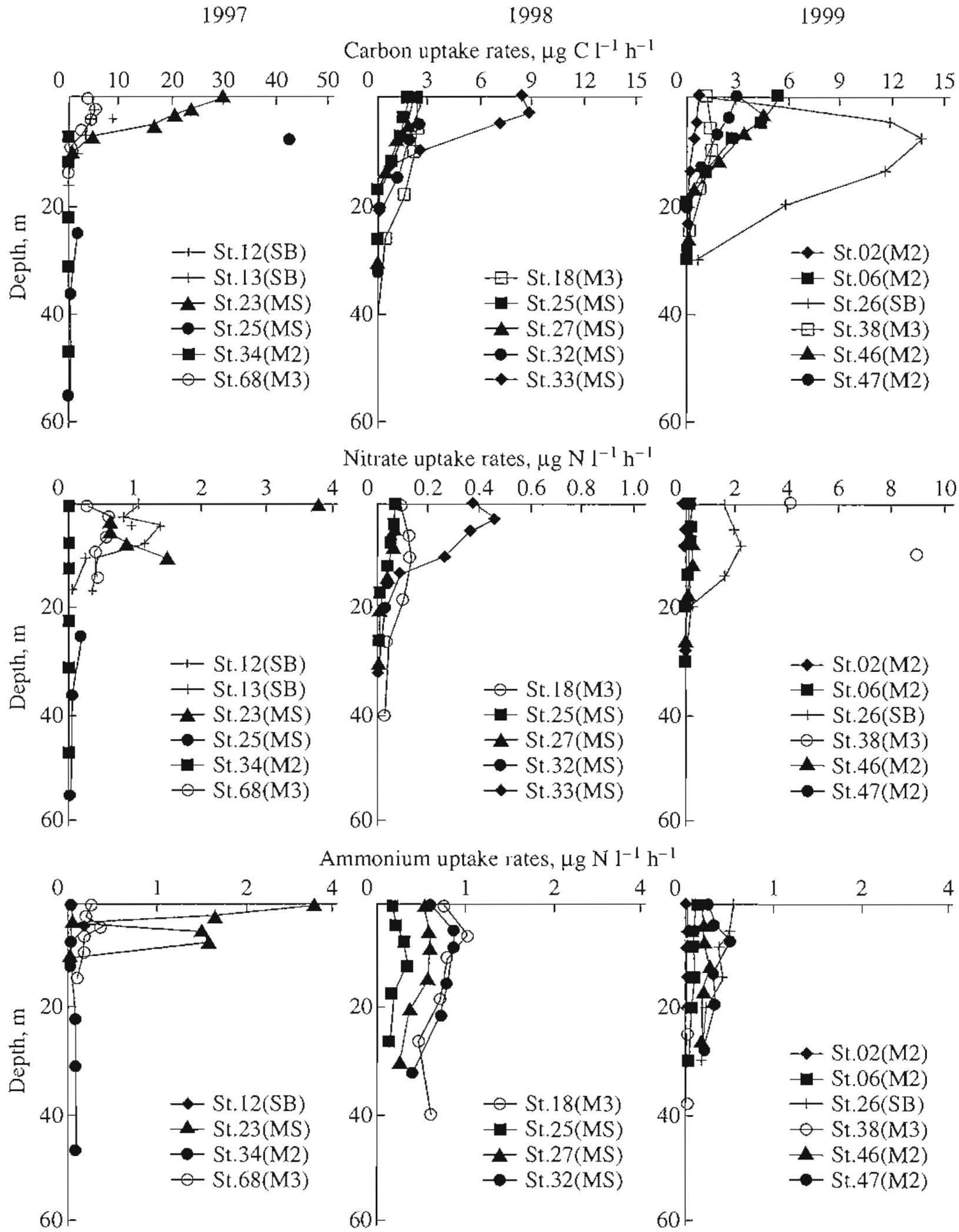

Fig. 6. Vertical profiles of the carbon, nitrate, and ammonium uptake rates from across the shelf over the southeastern Bering Sea during May of 1997, 1998, and 1999. SB indicates the shelf-break region, MS stands for the middle shelf, and M2 and M3 are the locations of moorings over the shelf region.

0.25 μg N l^{-1} h^{-1}) than in the outer shelf and the shelf-break regions (0.02–9.0 μg N l^{-1} h^{-1}). In general, the nitrate uptake rates were higher in the across shelf transect in 1999 than during the previous two years.

Similar to the nitrate uptake rates, the ammonium uptake rates also varied among the years studied. During early May 1997, the ammonium uptake rates were generally less than 0.2 μg N l^{-1} h^{-1}, except at station 23 (0.06–5.54 μg N l^{-1} h^{-1}) over the middle shelf. In the outer shelf and the shelf-break regions, the ammonium uptake rates were 0.1–0.73 μg N l^{-1} h^{-1}. During early May 1998, the ammonium uptake rates were slightly

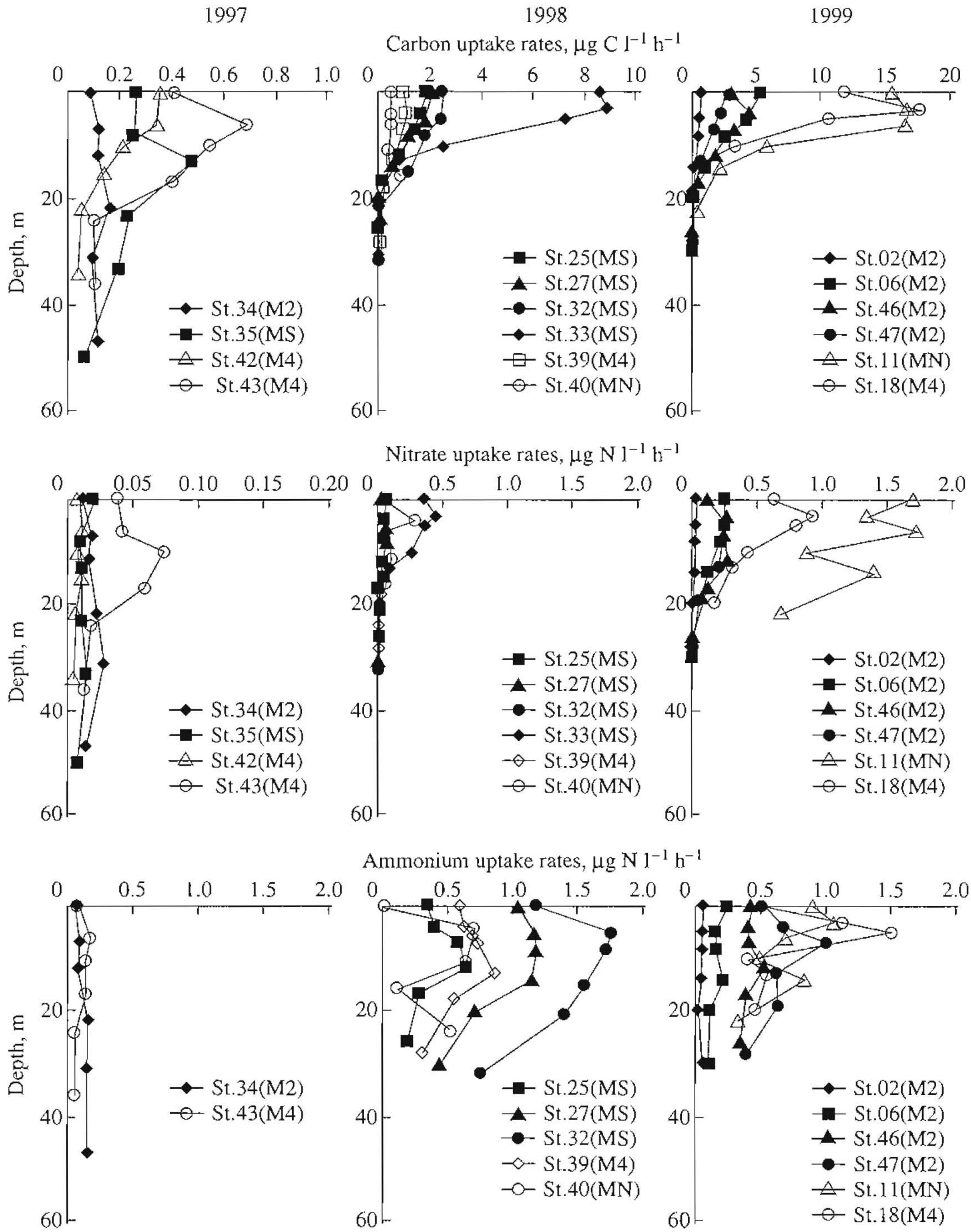

Fig. 7. Vertical profiles of carbon, nitrate, and ammonium uptake rates along the 70 m isobath over the middle shelf transect during May of 1997, 1998, and 1999. M4 and MN are located in the northern part of the middle shelf and M2 and MS are located in the southern part of the middle shelf.

higher across the shelf than during 1997. The ammonium uptake rates over the middle shelf were similar to those over the outer shelf. The ammonium uptake rates ranged from 0.6 to 2.01 μg N l^{-1} h^{-1} along the across shelf transect. During early May 1999, the ammonium uptake rates across the shelf were slightly higher than during 1997 but were lower than those for 1998 (Fig. 6).

Along the 70 m isobath transect, the nitrogen uptake rates were generally similar to those of the middle shelf in the across the shelf transect but showed large interannual variations (Figs. 5, 7). The nitrate uptake rates were slightly high in the southern part of the middle shelf during the spring of 1997 but were much greater in the north than in the south during the spring of 1999. During the spring of 1998, the ammonium uptake rates were slightly higher in the south than in the north (Fig. 7).

DISCUSSION

There were large interannual variations in the physical conditions such as the extent and duration of the sea ice coverage, the sea surface temperatures (SSTs), and the water column average temperatures over the southeastern Bering Sea during 1997–1999 [13, 34]. These were closely related to the variations of the atmospheric conditions and local weather conditions. In 1997, the sea ice conditions were similar to the average of the last three decades except for the timing of the maximum ice extent and retreat [34]. The summer SSTs were among the warmest on record since the 1960s due to the weaker winds than normal during the spring and the summer, but the depth-integrated temperatures were typical of those observed during the last decade [13, 34]. In 1998, ice advanced to M2 and melted in February during a period of weak winds. This prevented the mixing of the fresh cold water to the bottom. After the retreat of the sea ice in late February, the winds were strong enough to mix the fresh cold surface water with the warm saline bottom water, and this resulted in the warmest depth-averaged temperatures observed in the 1990s [34]. In 1999, the extent of the sea ice was not different from that in 1997, but the arrival of the sea ice at M2 was earlier than in 1997 and the retreat of the sea ice was slow compared to the average rates of the last two decades [32]. The sea surface temperature and depth-averaged temperatures were also colder than those of the previous two years [33].

There were strong interannual variations in the distribution of the salinity and temperature over the Bering Sea shelf during early May of 1997–1999 (Figs. 2, 3), which may be related to the variation of the dynamics of the sea ice. The distribution of the salinity over the southeastern Bering Sea shelf in the early spring was largely controlled by the input of freshwater from melting sea ice [34]. In particular, the fresh water supply from the melting sea ice and precipitation is a major source of fresh water over the middle shelf [6]. During the early spring of 1997–1999, the distributions of the salinity and temperature across the shelf and along the 70 m isobath over the middle shelf clearly showed that the locations of the low salinity water masses corresponded well to the locations of low temperature (Figs. 2, 3).

The interannual variations of the onshore fluxes may play a very important role in the hydrographic characteristics over the middle shelf. The salinity was similar in 1998 and 1999 but lower in 1997 (Figs. 2, 3). The maximum ice coverage was similar in 1997 and 1999, but the salinity was higher in 1999 than in 1997. The maximum ice coverage was slightly lower in 1998 than in 1999, but the salinity was similar in both years. Thus, the fresh water input alone cannot explain the interannual variations of the salinity. This may have resulted from the increased onshore transport of the slope water. Stabeno *et al.* [34] observed that the cross shelf transport was reduced in 1997 but enhanced in 1998. The distribution of the salinity in the bottom layer over the outer shelf showed that the locations of the 33 psu isohaline gradually moved onto the shelf from 1997 to 1998 and 1999 (Fig. 2). As discussed later, the location of the 16 μM isopleth of nitrate over the shelf also indicates an increase in the onshore transport of high nitrate slope water in the shelf region (Fig. 4). Our data agreed well with the result from the mooring station over the middle domain on the southeastern Bering Sea shelf (M2) showing greater enhancement of the cross-shelf transport in 1998 than in 1997 [34].

During the early spring of 1997, 1998, and 1999, the concentrations and distributions of nitrates showed large interannual variations in response to the variations in the sea ice and winds, which changed the nutrient utilization (Figs. 4, 5). The fluorescence data from the mooring station indicated the occurrence of an ice related bloom in late April at the M2 site over the middle shelf [34], which presumably resulted in an extensive utilization of nutrients in the surface layer during early May 1997. In the early spring of 1998 and 1999, an early retreat of the sea ice (February) and strong wind mixing prevented the development of density driven stratification, which may cause high nitrate concentrations (Figs. 2–5). Unfavorable physical conditions were responsible for the lack of an obvious spring bloom. The fluorescence data from mooring station 2 clearly show no apparent increase in the early spring of 1998 and 1999, except for an increase in early March 1999 [13].

The interannual variation of the onshore flux of nutrient-rich slope water in the bottom layer over the outer shelf may influence the distribution of nitrates over the shelf. During early May of 1998 and 1999, the strong wind mixing resulted in a vertically homogeneous nitrate distribution over the shelf, but the nitrate concentrations were slightly higher in 1999 than in 1998 as indicated by the location of the 16 μM isopleth across the shelf (Figs. 4, 5). The biological utilization of nitrate was suppressed in both 1998 and 1999 due to the strong wind mixing in the early spring. The nitrate uptake rates were lower both in 1998 and 1999 in spite of the high nitrate concentrations within the water column (Fig. 6). Ammonium inhibition of the nitrate uptake rates by high ammonium concentrations may not be responsible for the slightly lower nitrate concentration in 1998, because the ammonium concentrations were generally higher over the shelf in 1998 than in

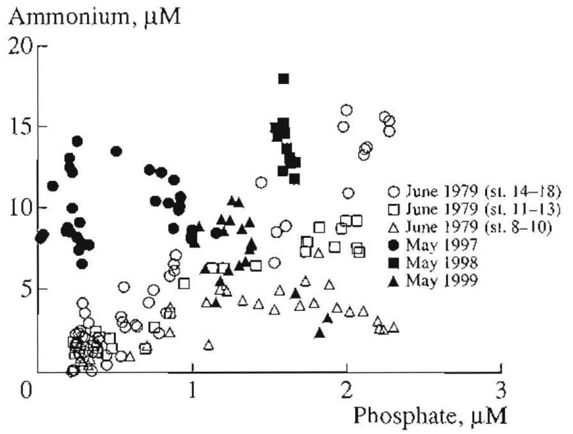

Fig. 8. The relationship between ammonium and phosphate in the high ammonium concentration regions of the southeastern Bering Sea shelf during the PROBES study and this study. During the PROBES study, stations 14–18 were located over the middle shelf, stations 11–13 were located over the middle front, and stations 8–10 were located over the outer shelf region.

1999 (Figs. 4, 5). Therefore, we cannot explain the higher nitrate concentration in 1999 compared with 1998 based on biological consumption alone.

There may be other factors important for regulating the nitrate concentrations over the southeastern Bering Sea shelf such as the interannual variations of the onshore fluxes of slope waters in the bottom layer. As discussed earlier, the distribution of the salinity suggested strong interannual variations of the onshore flux during 1997, 1998, and 1999. In the across shelf transect, the salinity in the bottom layer of the shelf break was higher in 1999 than in 1998, which was deduced by the farther intrusion of the 33 psu isohaline over the shelf region in 1999 than in 1998 (Fig. 2). The salinity profiles along the 70 m isobath transect also showed more extensive intrusion of high salinity and nutrient rich waters in 1999 than in 1998 (Figs. 3, 5).

The mechanisms for the interannual variation of the onshore fluxes are poorly understood. Okkonen *et al.* [25] recently showed how anticyclonic eddies modify the structure of the shelf-break front and enhance the transport of high nutrient and salinity slope water in the shelf regions of the Gulf of Alaska. Stabeno and Van Meurs [36] observed that an episodic event of onshore flow was related to an anticyclonic eddy in the southeastern Bering Sea. Mizobata *et al.* [16] observed the upward transport of nutrient rich water at the edge of anticyclonic eddies in the Bering Sea basin during the summer of 2001. The interannual variation of the eddy activity along the shelf-break region may play an important role in the variation of the onshore transport of nutrient rich slope water in the bottom layer of the shelf.

The occurrence of a high ammonium concentration over the shelf region was one of the interesting characteristics of the nutrient distribution during the early May period of 1997–1999. During the PROBES study, high ammonium concentrations were observed in the bottom layer over the middle shelf as a result of remineralization of the spring phytoplankton bloom during the early summer, but the ammonium concentrations across the shelf were low during the initiation of the spring bloom in April and May [42]. The degradation of organic material produced both phosphate and ammonium concentrations, which resulted in a strong positive relationship between the ammonium and phosphate concentrations. However, this relationship was modified by the low ammonium and high phosphate concentrations of the slope water, which were transported onshore in the bottom layer (Fig. 8). The relationship of the ammonium and phosphate in the center of the high ammonium concentration during early May of 1997 and 1998 showed higher ammonium concentrations than those expected from the remineralization of organic matter. During 1999, most of the ammonium concentrations fit with the positive relationship between ammonium and phosphate but some showed a negative relationship, thus, suggesting strong mixing with slope water containing low ammonium and high phosphate concentrations (Fig. 8). This implies that the water mass before dilution may have a lower phosphate and higher ammonium concentration than those observed. Therefore, the relationship between the ammonium and phosphate during early May of 1997, 1998, and 1999 suggests that the in situ remineralization of the organic matter alone cannot explain the occurrence of the high ammonium concentrations over the shelf, thus, suggesting the existence of other ammonium sources.

The seasonal advance and retreat of sea ice over the shelf region may be related to the high ammonium concentrations observed in the early spring of 1997, 1998, and 1999. Most of the high ammonium concentrations occurred in the low salinity and low temperature waters formed by the ice melt, except for a high ammonium concentration band in the across shelf section during 1999 (Figs. 2, 4). Several studies showed that high ammonium concentrations were observed under the sea ice and in the entire water column following the receding sea ice [1, 17, 21]. Although the source of the ammonium associated with the melting sea ice is not well known, there are several possible processes such as direct release from sea the ice, in situ ammonification, and production from bacteria and protozoans [17, 18, 21]. The high ammonium : phosphate ratio within the brine normalized to the salinity of the underlying water agreed with the slight deficiency of phosphate in our high ammonium area [17]. However, another study suggests that melting sea ice contributes a small proportion of the daily ammonium requirement in spite of the high ammonium concentration [18].

The other possible mechanism is the ammonium production from remineralization of recently settled phytoplankton cells in or close to the sediment. The distribution of the ice edge production showed a highly patchy distribution, which is probably due to the varying light conditions caused by changes in the cloud coverage and/or ice presence [5, 18, 21], which may explain the patchy distribution of the high ammonium concentration areas (Figs. 4, 5). The decomposition of organic matter within the sediment may result in lack of phosphate due to the selective adsorption on ferric oxide under oxic conditions [4]. Mock *et al.* [17] suggested that the equilibrium reaction between the water column and the sediment may be responsible for the high nutrient concentration in Kiel Bight.

The relationship between the ammonium and phosphate in the areas with high ammonium concentrations showed that the phosphate concentrations were higher than those of 1997 at similar ammonium concentrations (Fig. 8). Because of the warm water temperatures, the growth rates of zooplankton may have increased in the early spring in 1998 and resulted in an increase in the ammonium released from metabolic processes or fecal pellet decomposition. Coyle and Pinchuk [9] observed that the abundance and biomass of copepods increased in 1998 due to increases iu the water column temperature on the inner shelf of the southeastern Bering Sea. The sediment traps deployed at M2 collected more organic material in 1998 than during the other two years, and fecal material was the domiuaut component [31].

A tonguelike distribution of the temperature and ammonium concentrations (3°C isotherm and 3 μM ammonium isopleth) at the mid-depths of the outer shelf in the across shelf transect clearly showed the export of middle shelf waters at mid-depths (50–70 m) to the outer shelf (Figs. 2, 4). Whitledge *et al.* [42] observed a tonguelike distribution of high ammonium concentrations at mid-depths (40–60 m) over the outer shelf between May and June of four successive years in the late 1970s and early 1980s. Coachman and Charnell [7] observed net seaward movement of a fine structure across the outer shelf at mid-depth, between the onshore transport in the upper (0–30 m) layer and the bottom layer (below 60 m). They suggested that the seaward movement of the fine structure resulted from differential offshore-directed horizontal pressure gradients produced by a progressive increase of vertical mixing landward in the middle front. The offshore transport at mid-depth may play a very important role in the export of organic material, including regenerated Fe, from the middle shelf to the shelf-break region and beyond during the summer.

Over the southeastern Bering Sea shelf, the annual rates of primary production show large interannual variations depending on the presence or absence of ice-edge blooms and strong wind events [15, 28]. Especially, the times of arrival and retreat of sea ice have been observed to be very important in controlling the occurrence of an early ice-edge related phytoplankton bloom or subsequent open water spring bloom, which in turn may have significant impacts on higher trophic levels [13, 21, 23]. The occurrences of wind mixing events are also very important for the development of the spring phytoplankton bloom and the interannual variation of the annual primary production on the southeastern Bering Sea shelf [28].

Our carbon and nitrogen uptake data agreed well with the prediction of the development of phytoplankton blooms as a function of the timing of the arrival and retreat of sea ice on the middle shelf of the southeastern Bering Sea shelf [2, 13, 23]. During early May of 1997, low carbon and nitrate uptake rates occurred at site M2 and along the 70 m isobath on the middle shelf. The presence of cold and low salinity water and the depletion of the nutrient concentration indicate that an ice-edge phytoplankton bloom occurred along the 70 m isobath on the middle shelf. During early May of 1998 and 1999, the carbon and nitrate uptake rates were slightly higher than those of 1997 but were much lower than those of the spring bloom at station 23 and station 25 of early May 1997 in spite of the high nitrate concentration (Figs. 4–7). In spite of the slight interannual variations, the maximum sea ice extended beyond the M2 mooring site on the middle shelf during 1997, 1998, and 1999. The timing of the advance and retreat of the sea ice was favorable for developing an ice-edge phytoplankton bloom during 1997 but was unfavorable during 1998 and 1999.

The strong spatial variations observed across the shelf and along the 70 m isobath may be related to the dynamics of the sea ice and the particular location of the onshore transport in each of the years. As discussed above, the ice edge phytoplankton bloom resulted in low nutrient concentrations along the 70 m isobath in the middle shelf, which was accompanied by low carbon and nitrate uptake rates. However, high carbon and nitrate uptake rates occurred in the surface layer of station 23 and station 25, where there were high nitrate concentrations, which indicate the development of an open water spring bloom around the 100 m isobath between M2 and M3 (Figs. 4, 6). There were also north–south spatial distributions of the carbon and nitrogen uptake rates along the 70 m isobath. During early May of 1999, there were large differences in the carbon and nitrate uptake rates between the southern and northern parts of the 70 m isobath (Fig. 7). The distributions of the temperature, salinity, and nutrients suggest that the development of strong stratification caused by ice melt waters in the surface layer and the advection of high nitrate and saline waters in the bottom layer may have resulted in an ice related phytoplankton bloom in the northern area. However, the lack of stratification prevented the development of a phytoplankton bloom in the southern area (Figs. 3, 5, 7).

The occurrence of high ammonium concentrations in the early spring may play a very important role in the utilization of nitrate and the control of the total production over the southeastern Bering Sea shelf. In spite of the similar nitrate concentrations and stratification in 1998 and 1999, the nitrate uptake rates were slightly lower in 1998 compared to 1999. The high ammonium concentrations in 1998 may have inhibited the nitrate nptake rates [40]. Rho and Whitledge (in prep) observed that the addition of ammonium in both small and large volume experiments reduced the nitrate uptake rates in samples collected over the southeastern Bering Sea shelf during 2000. However, the carbon uptake rates were not directly affected by the addition of different nitrogen sources. Therefore, the presence of high ammonium concentrations in early spring provides an additional nitrogen source for primary production. Ammonium inhibits nitrate uptake without affecting carbon uptake rates. The overall effect of the high ammonium concentration in the early spring may have resulted in an increase of the total annual primary production. In support of this idea, sediment traps deployed at the M2 site showed that larger amounts of material were collected in 1998 compared with 1999, in spite of similar wind conditions [31].

We were unable to achieve our primary objective of assessing the regional spring primary production rates in relation to different physical conditions. Unlike during the PROBES periods, the development of the spring phytoplankton bloom during the 1997–1999 period showed large interannual variations due to the changing dynamics of the sea ice and wind mixing events. Primary production measurements were conducted over the middle shelf after the spring phytoplankton bloom in 1997 and before the spring phytoplankton bloom in 1998 and 1999. Thus, it is very difficult to extrapolate the observed interannual variation of the carbon and nitrogen uptake rates directly into the interannual variation of the spring primary production.

As an alternative to the direct measurement of the primary production from the uptake rates, the nitrate depletion in the surface euphotic layer can be used to estimate the total primary production combined with the C/N and f ratios [11, 42]. The recent estimate of the total primary production using the nitrate depletion method showed no significant change of the spring phytoplankton bloom during last three decades over the southeastern Bering Sea shelf [27]. However, this method may be inappropriate to use for the estimate of the total annual primary production for several reasons. This method cannot explain primary production utilizing high ammonium concentrations in the early spring. The interannual variations of the onshore flux of high nitrate slope water as observed in 1997, 1998, and 1999 may result in the interannual variation of the maximum nitrate concentration before the start of the spring phytoplankton bloom. The growth of phytoplankton under the sea ice may result in large variations of the prebloom nitrate concentration, which may affect the annual productivity [35]. The nitrate uptake below the thermocline during the summer may also cause uncertainty in the estimate of the primary production using the depletion of the nitrate concentration in the surface euphotic layer [30].

In previous studies, nitrate was the dominant nitrogen source for the growth of the spring phytoplankton over the middle domain of the southeastern Bering Sea shelf, although the maximum nitrate concentrations in the early spring show large interannual variations and the source of the variability was unknown (Sambrotto *et al.* 1986; Whitledge *et al.* 1986). In this study, however, the physical processes such as the onshore transport of nutrient rich slope water in the bottom layer may result in the interannual variation of the nitrate concentrations over the southeastern Bering Sea shelf in the early spring. Likewise, the instantaneous utilization of the nitrate in the spring was quite variable due to the dynamics of the seasonal sea ice and high ammonium concentrations. During the PROBES study, the contribution of new production to the total primary production (f ratio) was high during the peak spring phytoplankton bloom. However, the f ratio gradually decreased as the nitrate concentrations were depleted in the surface euphotic layer. They were usually accompanied by a succession of phytoplankton species from diatom to dinoflagellates that were heavily dependent on ammonium as a nitrogen source (Sambrotto *et al.* 1986). Therefore, the presence of high ammonium concentrations and strong wind mixing in the early spring of 1998 and 1999 may have resulted in favorable conditions for the growth of dinoflagellates and may have caused a change in the ecosystem dynamics over the middle shelf. As an example, Rho (2000) showed a very low value of the f ratio (<0.1) in spite of the high nitrate concentration over the middle and outer shelves during May of 1998. Although there is no study on the species composition of the phytoplankton in the early spring, the unusual appearance of a coccolithopore bloom over the southeastern Bering Sea shelf may be one of the most conspicuous changes in the ecosystem components. However, the mechanisms for the coccolithophore bloom are still unknown.

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