

DISTRIBUTION OF PHYTOPLANKTON ABUNDANCE AND  
PHYSICAL PROPERTIES ON THE SOUTHEASTERN  
SHELF OF THE BERING SEA IN SUMMER

Tsuneo ODATE\*, Naonobu SHIGA, Sei-ichi SAITOH,  
Takako MIYOI\*\* and Shogo TAKAGI

*Faculty of Fisheries, Hokkaido University, 1-1,  
Minato-cho 3-chome, Hakodate 041-0821*

**Abstract:** Oceanographic structure, nutrient concentration, and chlorophyll *a* concentration were surveyed from 55°N to 59°N along 166°W on the southeastern shelf of the Bering Sea during mid to late July of 1994, 1995, and 1996. The present results show a consistent trend that, in every year, high chlorophyll *a* concentration occurred in the outer shelf domain around 55°00'N, as well as the coastal shelf domain, and that the concentrations were usually low in the central shelf domain although large yearly variation occurred. The high phytoplankton abundance in the southern outer shelf domain related to relatively high salinity water, which contained more nitrate than the central shelf domain water. It is suggested that the high abundance is maintained by a continuous supply of nutrients caused by interaction between the ocean current from the open water of the North Pacific and the bottom topography in the vicinity of Unimak Pass. On the other hand, alternative high chlorophyll *a* stock was observed in the coastal shelf domain, where the sea floor depth was about 40 m and vertically homogenous water properties occurred. This suggests that the nutrient supply from the bottom maintains the high phytoplankton abundance. In the central shelf domain, chlorophyll *a* concentrations less than 1.0  $\mu\text{g l}^{-1}$  were usually observed between 55°30'N and 58°30'N in 1995 and 1996. In 1994, however, chlorophyll *a* concentrations of 1.0 to 2.0  $\mu\text{g l}^{-1}$  were widely distributed. The slightly high concentrations coincided with a weak pycnocline and occurrence of cold bottom water, which contained high nitrate. It is suggested that phytoplankton abundance may be low when the pycnocline is well developed or the cold bottom water does not transport a large amount of nutrients in the central shelf domain of the southeastern Bering Sea.

**key words :** Bering Sea shelf, phytoplankton abundance, physical properties

### Introduction

The southeastern Bering Sea shelf is one of the most biologically productive shelves in the world. This shelf region has been the focus of several studies, in particular the

---

\* Present address: National Institute of Polar Research, Kaga 1-chome, Itabashi-ku, Tokyo 173-8515.

\*\* Present address: Hokkaido Fishery Extension Office, Western Kushiro Branch, 2-54, Urami-cho 2-chome, Kushiro 085-0835.

PROBES (Processes and Resources of the Bering Shelf) program (McROY *et al.*, 1986), because highly fertile waters support commercially important walleye pollock and crab fisheries (HOOD, 1983).

The PROBES program led to conceptual models of the Bering shelf ecosystem (COACHMAN, 1986). Three hydrographic domains (coastal, central, and outer shelf domains) on the shelf area and oceanic domain were defined within which phytoplankton seemed to be affected by distinct processes. These domains are separated by fronts, located approximately at the 50 m (inner front) and 100 m (middle front) isobaths, and at the shelf break (shelf break front) (COACHMAN, 1986; COACHMAN and CHARNELL, 1979; KINDER and COACHMAN, 1978; SCHUMACHER *et al.*, 1979). Water column structures of the southeastern shelf have been summarized as follows (COACHMAN, 1986). Vertical mixing caused by tidal currents and wind makes the distribution of water properties uniform in the whole water column in the coastal shelf domain where the sea floor depth is usually less than 50 m. In the central shelf domain a strong pycnocline suppresses turbulence in the whole water column although mixing within the upper and lower layers is caused by wind and tidal currents, respectively. Hence, a two-layered structure is evident in this domain. In the outer shelf domain, however, a two-layered structure is not observed since mixing between the upper and lower layers is enhanced by finestructure, which occurs in the mid-layer.

Primary production on the Bering Sea shelf starts as early as February with algae growing in sea ice (ALEXANDER and CHAPMAN, 1981; McROY *et al.*, 1972). As the ice melts and breaks up from March through May, ice edge blooms develop in the stable, low-salinity, surface water layer (MÜLLER-KARGER and ALEXANDER, 1987; NIEBAUER and ALEXANDER, 1985). In shelf waters not affected by ice, phytoplankton blooms occur in the mixed layer as the water column stratifies due to solar heating. Peak phytoplankton biomass over the shelf typically occurs in mid-May, and the maximum concentration of chlorophyll *a* reaches to more than  $20 \mu\text{g l}^{-1}$  (SAMBROTTO *et al.*, 1986). In June, chlorophyll *a* concentrations returned to early April levels ( $< 2 \mu\text{g l}^{-1}$ ) and nitrate was not observed in the mixed layer (SAMBROTTO *et al.*, 1986). MÜLLER-KARGER *et al.* (1990) revealed the occurrence of fall blooms from August to September based on Coastal Zone Color Scanner images of the shelf. Hence, phytoplankton abundance in summer (July) seems to be the lowest of any season except winter. Although the annual primary production cycle on the Bering Sea shelf is summarized above, there are considerable interannual variations in the distribution of biomass and the magnitude of the blooms (MÜLLER-KARGER *et al.*, 1990; SAMBROTTO *et al.*, 1986).

According to summer hydrographic observations, cold bottom waters are preserved under a sharp thermocline along 50–100 m isobaths from south of St. Lawrence Island to Bristol Bay (COACHMAN, 1986; OHTANI, 1969, 1973; OHTANI and AZUMAYA, 1995). These cold bottom waters are inferred to be the remnants of previous winter cooling and drift ice cover (OHTANI, 1969, 1973; OHTANI and AZUMAYA, 1995). The bottom water temperatures in summer are correlated with the previous winter's freezing degree-days (NIEBAUER, 1980). OHTANI and AZUMAYA (1995) show that the interannual change in the abundance of walleye pollock depends on fecundity and winter conditions at age one.

Organisms at higher trophic levels are extremely dependent upon productivity of phytoplankton through the food web. To study phytoplankton abundance in a similar

area during a similar season is valuable for fully understanding the interannual variability of standing stocks of the higher trophic organisms, including walleye pollock. The previous studies were focused on the spring bloom periods since the spring bloom is the most significant process of the annual production cycle on the Bering Sea shelf (MÜLLER-KARGER *et al.*, 1990; SAMBROTTO *et al.*, 1986; WALSH, 1983). However, episodic inputs of nutrients into the euphotic zone caused by storm events enhance productivity and phytoplankton biomass in stratified shelf waters (IVERSON *et al.*, 1979; WALSH *et al.*, 1978). The purpose of the present study is to consider the relation between the oceanographic conditions and distribution of phytoplankton abundance in the southeastern Bering Sea shelf in three summer periods.

### Methods

Oceanographic observations and seawater samplings were conducted in the southeastern shelf area of the Bering Sea in summer, using the T/S OSHORO-MARU, Faculty of Fisheries, Hokkaido University. The nine stations were occupied from 55°00'N to 59°00'N along the 166°W at 30' intervals (Fig. 1). The observations were carried out from July 17 to 18, 1994, from July 22 to 24 and from July 31 to August 1, 1995, and from July 21 to 26, 1996.

Seawater temperature and salinity were profiled by a CTD-Rosette system (Neil Brown Mark III B). The CTD data were averaged over 1 m intervals. Seawater samples were collected by Niskin bottles on the CTD-Rosette system every 10-20 m from the surface to the bottom. Using aliquots of the seawater samples, concentrations of chlorophyll *a* and nutrient were measured.

One subsample (200-1000 m/l) was filtered with a Whatman GF/F filter. In 1994,

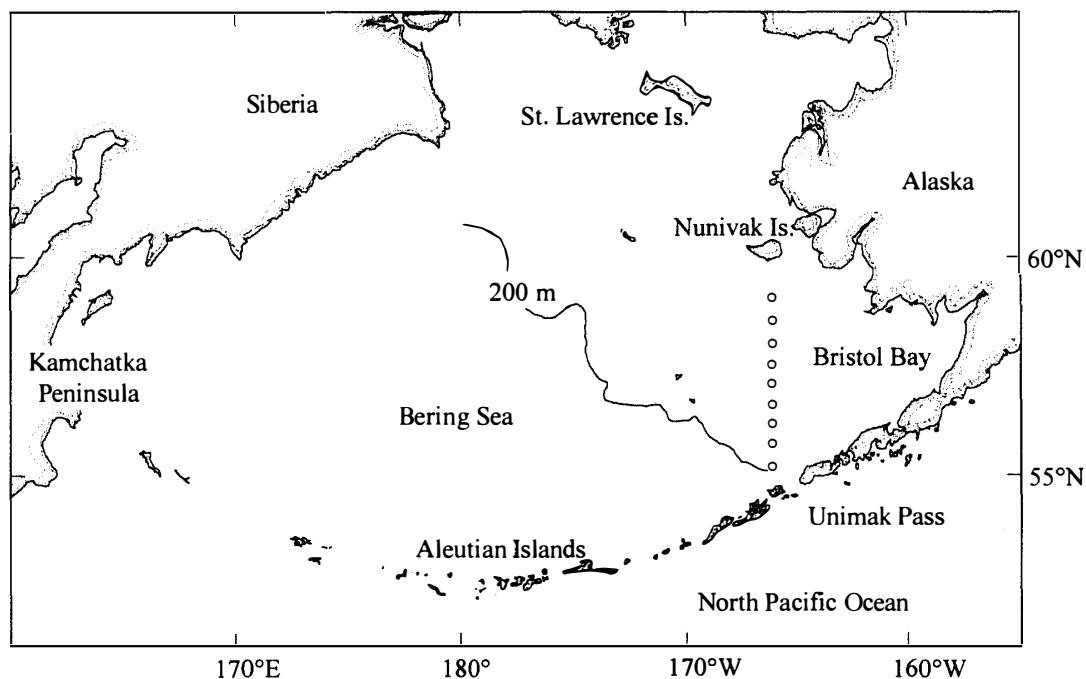


Fig. 1. Sampling stations in the southeastern Bering Sea (open circles).

the filters were kept in a freezer until extraction of pigments with 90% acetone (PARSONS *et al.*, 1984). In 1995 and 1996, the filters were put into a glass vial, which contained N, N-dimethylformamide (SUZUKI and ISHIMARU, 1990), and pigments were extracted in the dark at  $-20^{\circ}\text{C}$ . Concentrations of chlorophyll *a* were determined fluorometrically using a Turner Design Model 10R Fluorometer (PARSONS *et al.*, 1984). The fluorometer was calibrated with pure chlorophyll *a* (Sigma Chemical Co.). The other subsamples were kept in a freezer until later determination of nutrient concentrations using an AutoAnalyzer (STRICKLAND and PARSONS, 1972).

## Results

### Temperature, salinity, and density

Figure 2 shows the vertical distribution of water temperature. Water temperature was between  $0^{\circ}\text{C}$  and  $10^{\circ}\text{C}$ . Water columns were thermally stratified south of  $58^{\circ}00'\text{N}$ , and the vertical difference of water temperature was not large north of  $58^{\circ}30'\text{N}$ .

In 1994, water temperature higher than  $8^{\circ}\text{C}$  was observed in the upper 10 to 30 m south of  $57^{\circ}00'\text{N}$ . In particular, water temperature was higher than  $9^{\circ}\text{C}$  at the surface at  $55^{\circ}30'\text{N}$  and in the upper 23 m at  $56^{\circ}00'\text{N}$ . Water warmer than  $8^{\circ}\text{C}$  was widely distributed in 1995, occupying the top 5 to 30 m of the surveyed area. Surface water temperature was higher than  $9^{\circ}\text{C}$  except at  $55^{\circ}00'\text{N}$ . High water temperature ( $>9^{\circ}\text{C}$ ) was observed in the top 15 to 27 m from  $55^{\circ}30'\text{N}$  to  $57^{\circ}30'\text{N}$ . In 1996, water warmer than  $8^{\circ}\text{C}$  was found in the upper 20 to 30 m south of  $56^{\circ}30'\text{N}$ . Water temperature higher than  $9^{\circ}\text{C}$  occurred in the top 8 to 26 m between  $55^{\circ}30'\text{N}$  and  $56^{\circ}30'\text{N}$ .

Water temperature in the lower layer ( $>30$ – $50$  m) was less than  $3^{\circ}\text{C}$  between  $56^{\circ}30'\text{N}$  and  $58^{\circ}00'\text{N}$  in 1994 and 1995, and between  $56^{\circ}30'\text{N}$  and  $57^{\circ}30'\text{N}$  in 1996. In 1994, the minimum water temperature was about  $0.7^{\circ}\text{C}$  below 30 m at  $57^{\circ}30'\text{N}$  in 1994, and less than  $0.1^{\circ}\text{C}$  below 50 m at  $57^{\circ}00'\text{N}$  in 1995. Water temperature lower than  $2^{\circ}\text{C}$  was not found in the surveyed area in 1996. The minimum bottom water temperature of the central shelf domain was about  $2.2^{\circ}\text{C}$ .

Throughout three years of observations, a similar trend toward higher salinity occurred in the deep layer in the southern part and lower salinity was found in the northern part of the transects (Fig. 3). In the northern part the vertical salinity difference was small as observed in water temperature profiles (Fig. 2). Salinity was higher than 32.0 throughout the water column between  $55^{\circ}00'\text{N}$  and  $55^{\circ}30'\text{N}$  in 1994. Salinity in the top 10 m was less than 32.0 even at the southernmost station in 1995. In 1996, surface salinity higher than 32.0 was only observed at  $55^{\circ}00'\text{N}$ . In the coastal shelf domain, salinity was less than 31.4 (1994), 31.2 (1995), and 31.6 (1996).

Figure 4 shows a temperature-salinity plot based on data collected in the bottom layer. Three domains were recognized. Outer, central, and coastal shelf domains were represented by saline, cold, and less saline-warm waters, respectively. The position of the middle front, which separates the outer shelf domain from the central shelf domain, was located between  $56^{\circ}30'$  and  $57^{\circ}00'\text{N}$  all three years. This front was also visible as horizontally large gradient of bottom salinity (Fig. 3). On the other hand, the position of the inner front, which divides shallower shelf water into central and coastal shelf domains, occurred between  $58^{\circ}00'$  and  $58^{\circ}30'\text{N}$  in 1994 and 1995, and between  $57^{\circ}30'$  and  $58^{\circ}00'\text{N}$  in 1996.

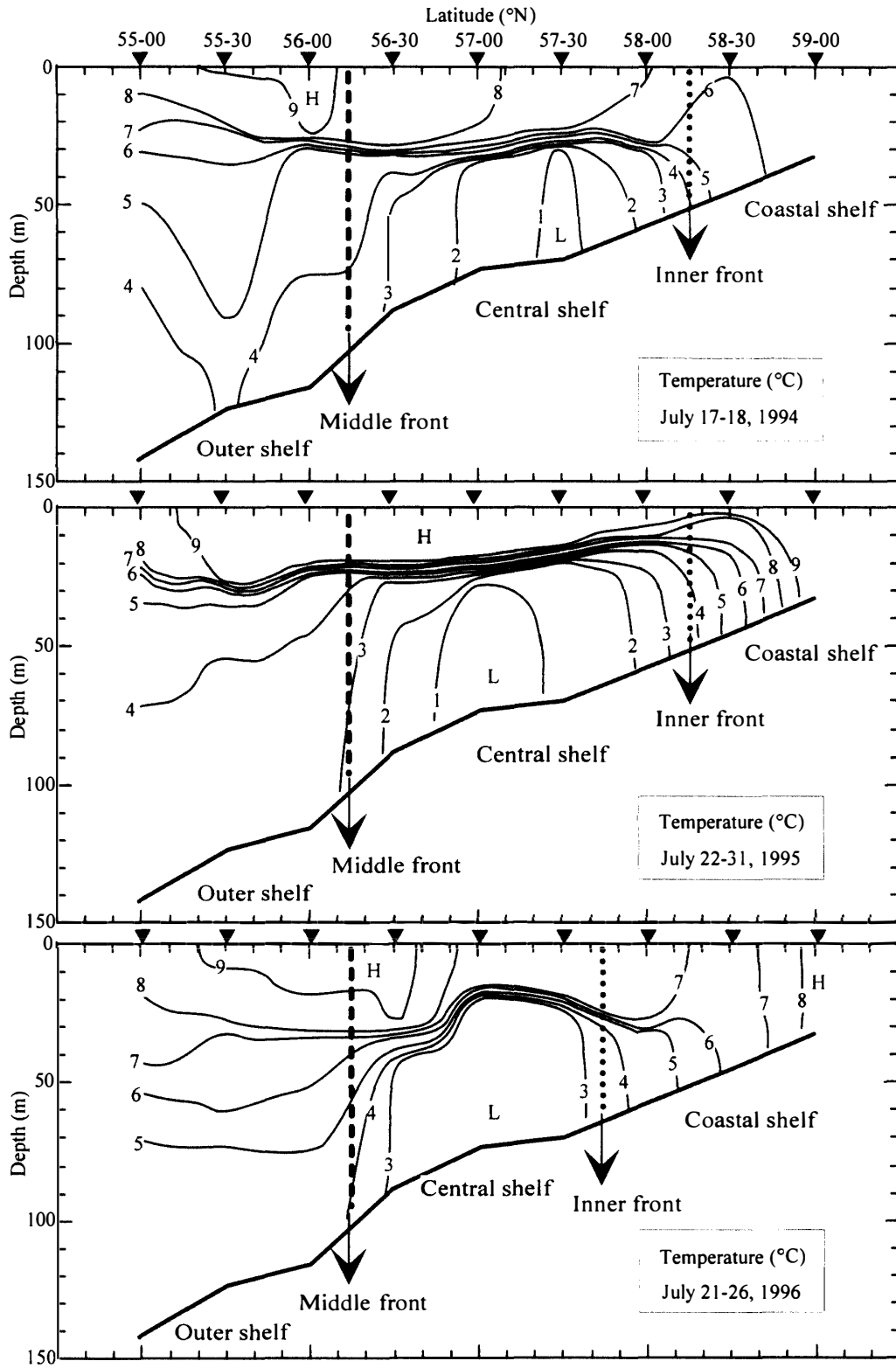


Fig. 2. Vertical section of water temperature from 55°N to 59°N along 166°W in 1994 (top), 1995 (middle), and 1996 (bottom). Inverted triangles show the positions of the CTD observations. Broken and dotted lines are positions of the middle and inner fronts, respectively.

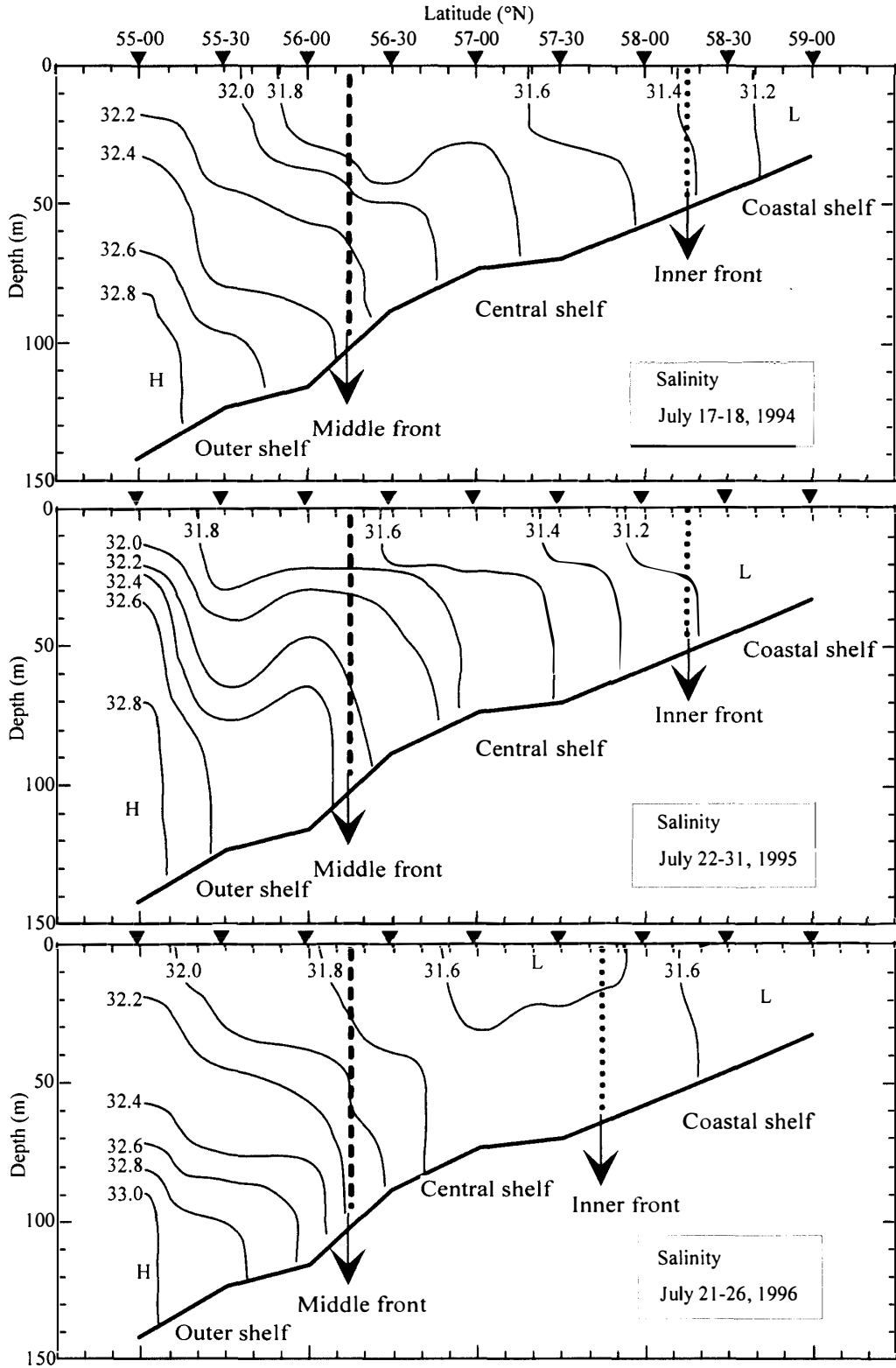


Fig. 3. Vertical section of salinity from 55°N to 59°N along 166°W in 1994 (top), 1995 (middle), and 1996 (bottom). Inverted triangles show the positions of the CTD observation. Broken and dotted lines are positions of the middle and inner fronts, respectively.

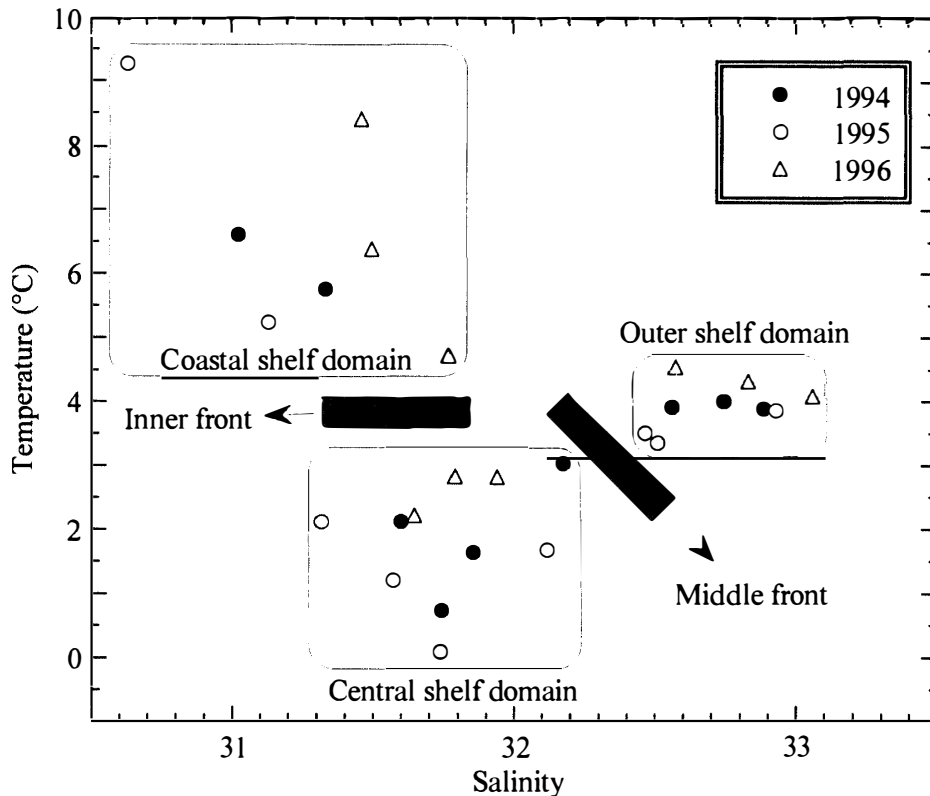


Fig. 4. Temperature-salinity plot based on bottom water. Toned areas indicate the boundary between water masses.

This front corresponded to a horizontally large gradient of bottom temperature (Fig. 2).

The vertical distribution of density is shown in Fig. 5. As observed in the distribution of temperature and salinity, vertically homogeneous density occurred in the coastal shelf domain. A sharp pycnocline occurred in the central shelf domain, in particular between  $57^{\circ}00'N$  and  $57^{\circ}30'N$ . Static stability in the pycnocline, which was defined as the layer in which static stability was higher than  $0.050 \times 10^{-3} \text{ m}^{-1}$ , reached to  $0.930\text{--}0.970 \times 10^{-3} \text{ m}^{-1}$  between  $56^{\circ}30'$  and  $57^{\circ}30'N$ , and was  $0.491 \times 10^{-3} \text{ m}^{-1}$  at  $58^{\circ}00'N$  in 1995. On the other hand, static stability in the pycnocline in the central shelf domain was  $0.376\text{--}0.733 \times 10^{-3} \text{ m}^{-1}$  in 1994 and  $0.377\text{--}0.596 \times 10^{-3} \text{ m}^{-1}$  in 1996.

#### Nitrate concentration

Throughout three years of observations, the concentration of nitrate was high ( $>10 \mu\text{M}$ ) in the deeper layer in the outer shelf domain and was about  $0.1 \mu\text{M}$  in the whole water column of the coastal shelf domain (Fig. 6). Relatively high concentration of nitrate ( $0.8\text{--}4.3 \mu\text{M}$ ) was observed at the surface in the southern outer shelf domain.

In 1994, the surface nitrate concentration was relatively high in the outer shelf domain, and low on the central and coastal shelves. In the central shelf domain, the vertical gradient of nitrate concentration was large in either the 20–30 m or 30–40 m layer, which corresponded to the pycnocline (Fig. 5). The nitrate concentration was lower than  $0.4 \mu\text{M}$  in the top 20 m north of  $55^{\circ}30'N$  in 1995 and in the top 10 or 30 m north of  $55^{\circ}30'N$  in 1996. In the central shelf domain, nitrate concentrations were more than  $1.0 \mu\text{M}$  below

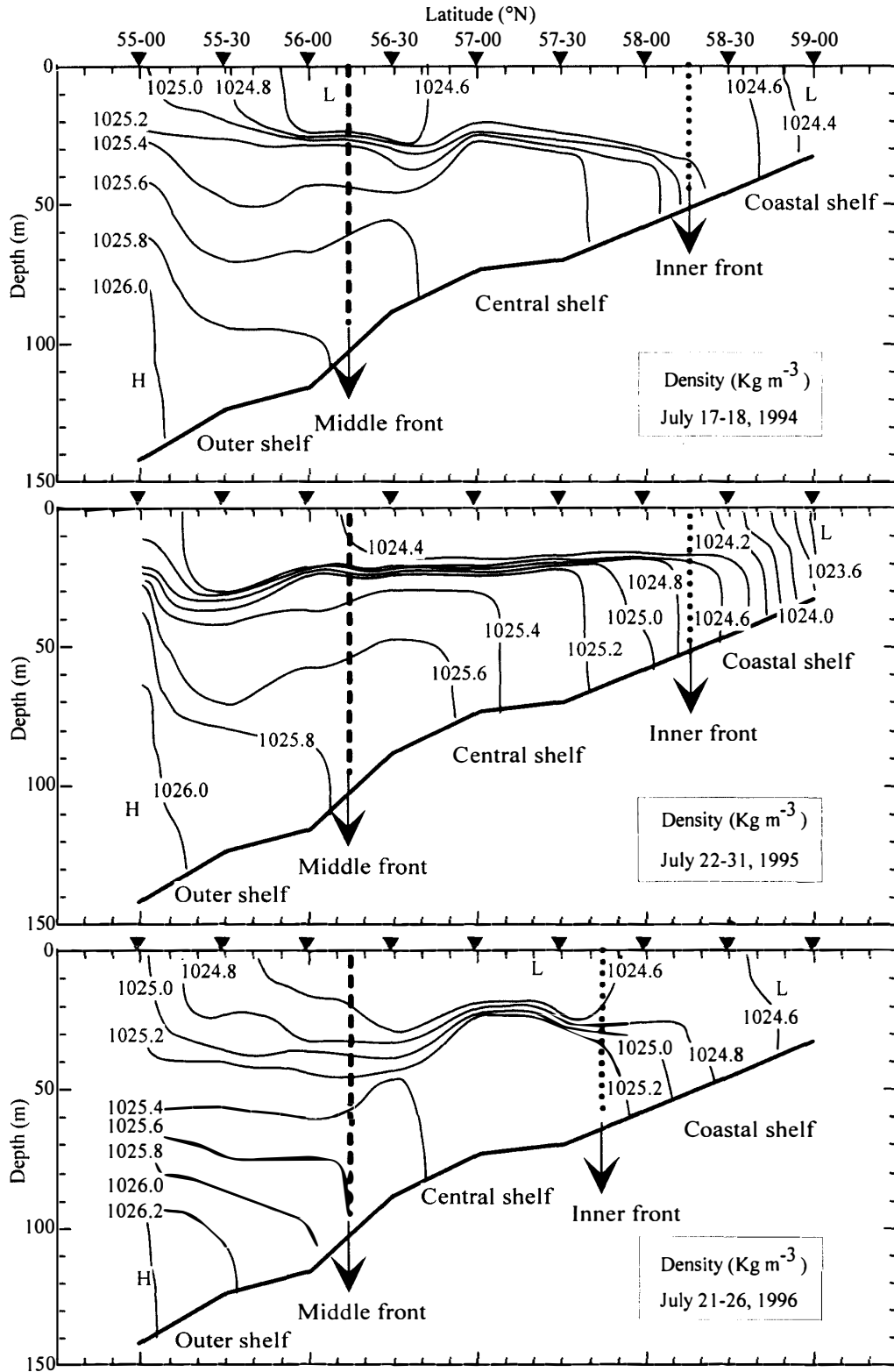


Fig. 5. Vertical section of density from 55°N to 59°N along 166°W in 1994 (top), 1995 (middle), and 1996 (bottom). Inverted triangles show the positions of the CTD observation. Broken and dotted lines are positions of the middle and inner fronts, respectively.



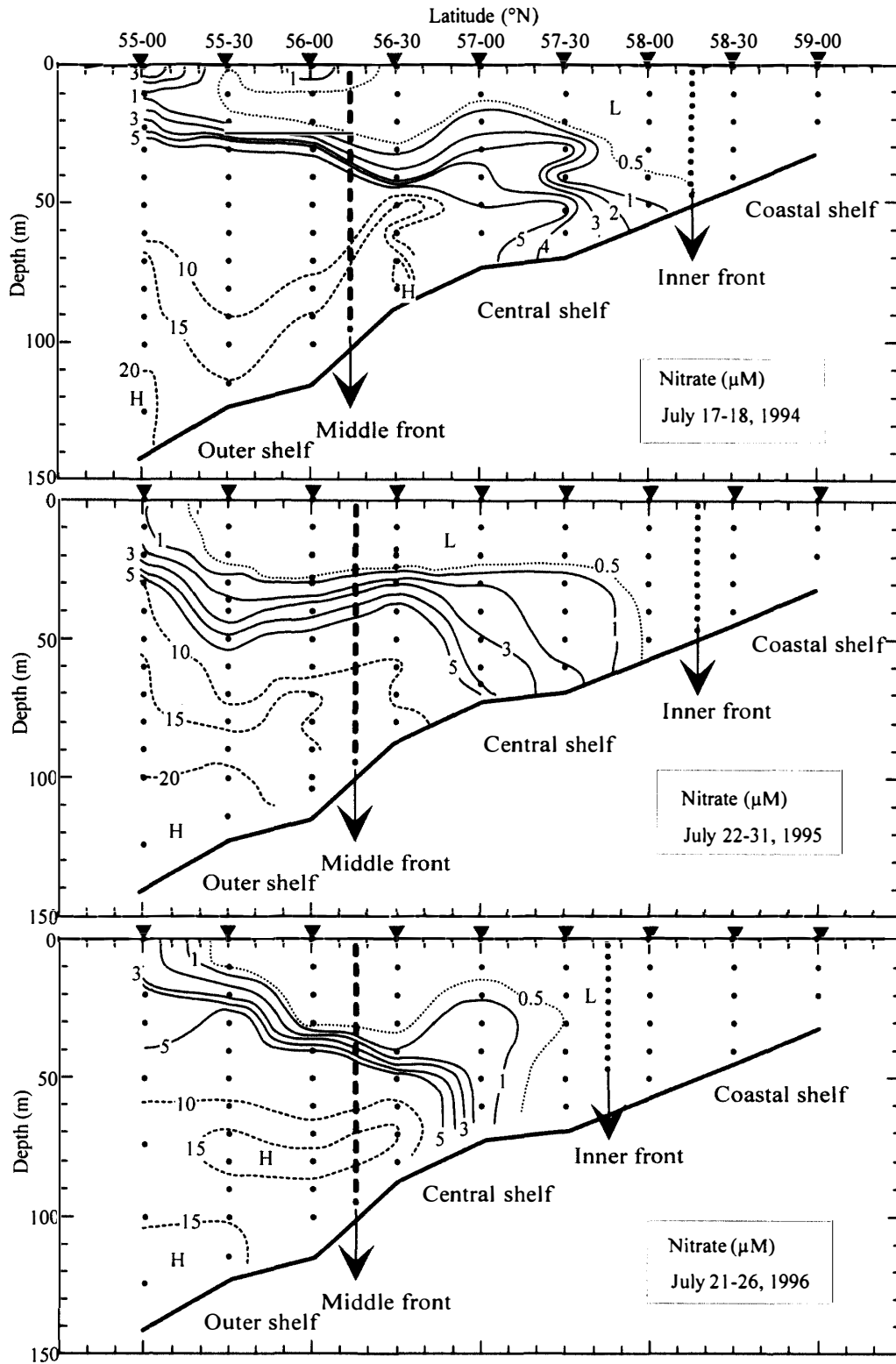


Fig. 6. Vertical section of nitrate concentration from 55°N to 59°N along 166°W in 1994 (top), 1995 (middle), and 1996 (bottom). Inverted triangles show the positions of water samplings. Broken and dotted lines are positions of the middle and inner fronts, respectively.

30 m, which was deeper than the pycnocline (20 m) in 1995. In 1996, relatively high nitrate concentrations occurred below the depth of 30–40 m in the southern central shelf domain (56°30'N and 57°00'N).

#### Chlorophyll *a* concentration

The vertical distribution of chlorophyll *a* concentration is shown in Fig. 7. Three years of observations revealed that the concentration of chlorophyll *a* was relatively high in the southern outer shelf domain and the coastal shelf domain, and relatively low in the central shelf domain.

In 1994, concentration of chlorophyll *a* higher than  $2.0 \mu\text{g l}^{-1}$  occurred in the top 10 m at 55°00'N and in the top 20 m at 55°30'N of the outer shelf domain. The concentration was higher than  $1.0 \mu\text{g l}^{-1}$  at depth 30 m, which coincided with the nitrate gradient layer, at 56°00'N and 56°30'N. The highest concentration of this year,  $4.6 \mu\text{g l}^{-1}$ , was observed at the surface at 55°30'N. Wide distribution of high chlorophyll *a* concentration of more than  $1.0 \mu\text{g l}^{-1}$  was noted north of 57°30'N (northern central shelf and coastal shelf domains). In 1995, chlorophyll *a* concentration was higher than  $1.0 \mu\text{g l}^{-1}$  in the top 20 m at 55°00'N. Between 55°30'N and 56°30'N, the subsurface chlorophyll maximum occurred at depth 20–30 m, in which nitrate concentrations changed. The chlorophyll *a* concentrations were more than  $1.0 \mu\text{g l}^{-1}$  throughout the water column of the coastal shelf domain. The most abundant concentration in this year was  $3.5 \mu\text{g l}^{-1}$  at depth 20 m at 59°00'N. In 1996, the chlorophyll *a* concentrations were 1.6 and  $1.1 \mu\text{g l}^{-1}$  at depths 0 m and 10 m at 55°00'N, respectively. Concentrations of more than  $1.0 \mu\text{g l}^{-1}$  also occurred at 30 m and 40 m at 56°00'N. Chlorophyll *a* concentration was lower than  $1.0 \mu\text{g l}^{-1}$  between 56°30'N and 58°30'N. The highest concentration,  $2.1 \mu\text{g l}^{-1}$ , was noted at 20 m at 59°00'N.

### Discussion

In the present study, oceanographic structure, nutrient concentration, and chlorophyll *a* concentration were surveyed along the same transect on the southeastern shelf of the Bering Sea during the similar period of summer for three years. In general, highly stratified and nutrient limited waters characterize the summer water column on the shelf (SAMBROTTO *et al.*, 1986; WHITLEDGE *et al.*, 1986). As a result, chlorophyll *a* concentrations become relatively low, comparing the bloom periods in spring and fall (MÜLLER-KARGER *et al.*, 1990; SAMBROTTO *et al.*, 1986). The present study, however, showed that the distribution of chlorophyll *a* as well as water column structure was different year to year. We considered the relation between the oceanographic conditions and distribution of phytoplankton abundance in this sea area.

Our results revealed that, in every year, high chlorophyll *a* concentration occurred in the coastal shelf domain (Fig. 7). In this domain, vertical mixing caused by tidal currents and wind makes the distribution of water properties uniform in the whole water column (COACHMAN, 1986). We also showed that fairly homogenous temperature and salinity characterized the water columns of the coastal shelf domain (Figs. 2 and 3). This suggests that nutrient supply from the bottom, which resulted from tidal currents and wind (COACHMAN, 1986), maintained the high phytoplankton abundance since the water column

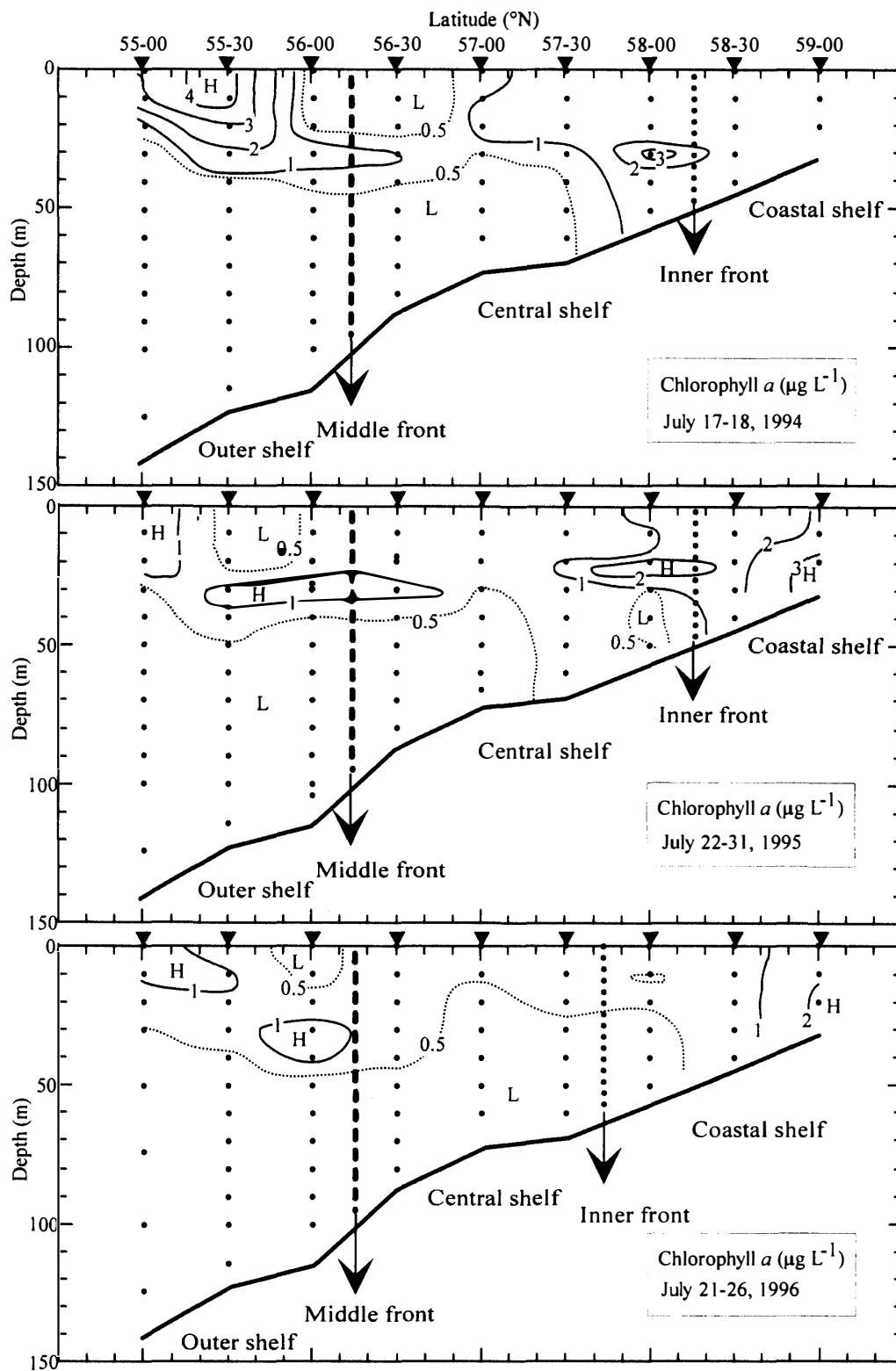


Fig. 7. Vertical section of chlorophyll *a* concentration from 55°N to 59°N along 166°W in 1994 (top), 1995 (middle), and 1996 (bottom). Inverted triangles show the positions of water samplings. Broken and dotted lines are positions of the middle and inner fronts, respectively.

stratification was weak (Fig. 5). Lower vertical difference of chlorophyll *a* concentration also implies active mixing of the water column (Fig. 7).

Alternative high chlorophyll *a* concentration occurred in the outer shelf domain (Fig. 7). In the outer shelf domain, mixing between the upper and lower layers is enhanced by finestructure, which occurs in the mid-layer (*ca.* 30–50 m) (COACHMAN, 1986). Nitrate transported across weak pycnocline seems to support a high abundance of phytoplankton in the subsurface layer. At the southernmost station near Unimak Pass, the chlorophyll maximum layer occurred at the surface. In the vicinity of Unimak Pass, high chlorophyll *a* concentration was frequently observed (McROY *et al.*, 1972; ODATE, 1996). In this sea area, oceanic water comes into the Bering Sea through Unimak Pass from the North Pacific Ocean (COACHMAN, 1986). Interaction between ocean current and bottom topography through the pass enhances water column turbulence, resulting in nutrient rich water. Indeed, nitrate concentrations were higher than  $1 \mu\text{M}$  at the surface of the southernmost station although the surface concentration of nitrate was about  $0.5 \mu\text{M}$  at other stations, excepting at  $55^{\circ}30'\text{N}$  and  $56^{\circ}00'\text{N}$  in 1994 (Fig. 6). The high phytoplankton abundance seems to be maintained by a continuous supply of nutrients, which is transported by the oceanic water.

In the outer shelf domain, the highest concentration of chlorophyll *a* was observed in 1994. Moreover, high chlorophyll water widely occupied the surface layer of the outer shelf domain in 1994, compared to the distributions observed in 1995 and 1996. In 1994, the oceanic water from the North Pacific Ocean indicated by salinity of more than 32.0 reached the surface at  $55^{\circ}30'\text{N}$ . On the other hand, the water did not prevail in the surface at this latitude in the other years. This suggests that the abundance of phytoplankton is likely to be affected by the magnitude of the inflow of the oceanic water.

In the central shelf domain, a well-developed pycnocline suppresses turbulence of the whole water column, although mixing within the upper and lower layers is caused by wind and tidal currents, respectively (COACHMAN, 1986). Hence, a two-layer structure is evident in this sea area. The well-developed pycnocline may prevent supply of nutrients from the bottom water into the euphotic zone so that phytoplankton cannot increase in the surface layer of the central shelf domain (SAMBROTTO *et al.*, 1986). This situation is typical for the water column structure, which was observed at  $57^{\circ}00'\text{N}$  in the central shelf domain in 1995. At this station, water temperatures in the deeper ( $>50$  m) and the surface layer ( $<20$  m) were lower than  $0.1^{\circ}\text{C}$  and higher than  $9^{\circ}\text{C}$ , respectively. The low phytoplankton abundance in the surface of this year seems to result from less supply of nutrients due to the well-developed pycnocline of this domain (SAMBROTTO *et al.*, 1986).

In the central shelf domain, abundance of phytoplankton above the pycnocline was higher in 1994 than in 1995. The relatively high phytoplankton abundance may be explained by the magnitude of the pycnocline since static stability within the pycnocline was smaller in 1994 than 1995, as relatively high abundance was observed at  $58^{\circ}00'\text{N}$  in 1995 where static stability was low.

Static stability within the pycnocline in the central shelf domain was approximately the same in 1994 and 1996. The concentration of chlorophyll *a* in the central shelf domain was, however, lower in 1996 than in 1994. This seems to be correlated with the occurrence of cold bottom water, which contains a large amount of nutrients. It is considered that the low phytoplankton abundance of the central shelf domain in 1996

resulted from low nutrient concentrations in the bottom layer, although the pycnocline was not strong.

The occurrence of cold bottom water seems to be correlated with the previous winter's climate conditions (NIEBAUER, 1980; OHTANI, 1969, 1973; OHTANI and AZUMAYA, 1995). Surface water temperature reflects solar heating in summer. The high surface water temperature in 1995 implies better than average weather conditions in that summer. Consequently, climate conditions are likely to have important influence on biological production through the physical structure on the southeastern Bering Sea shelf.

### Acknowledgments

The authors gratefully acknowledge the captain and crew of the T/S OSHORO-MARU, Faculty of Fisheries, Hokkaido University, and all colleagues involved in this cruise, for their efficient help at sea. Thanks are extended to Mrs. K. SASAOKA and H. KIYOFUJI for their collecting of seawater samples and measurement of chlorophyll *a* concentrations in 1996.

### References

- ALEXANDER, V. and CHAPMAN, T. (1981): The role of euphotic algal communities in Bering Sea ice. The Eastern Bering Sea Shelf: Oceanography and Resources, Vol. 2, ed. by D.W. HOOD and A.J. CALDER. Seattle, Univ. Washington Press, 773-780.
- COACHMAN, L.K. (1986): Circulation, water masses, and fluxes on the southeastern Bering Sea shelf. *Cont. Shelf Res.*, **5**, 23-108.
- COACHMAN, L.K. and CHARNELL, R.L. (1979): On lateral water mass interaction—a case study, Bristol Bay, Alaska. *J. Phys. Oceanogr.*, **9**, 278-297.
- HOOD, D.W. (1983): The Bering Sea. *Estuaries and Enclosed Seas*, ed. by B.H. KETCHUM. Amsterdam, Elsevier, 337-373.
- IVERSON, R.L., COACHMAN, L.K., COONEY, R.T., ENGLISH, T.S., GOERING, J.J., HUNT, G.L., Jr., MCCAULEY, M.C., MCRROY, C.P., REEBURGH, W.S. and WHITLEDGE, T.E. (1979): Ecological significance of fronts in the southeastern Bering Sea. *Ecological Processes in Coastal and Marine Systems*, ed. by J. LIVINGSTON. New York, Plenum, 437-466.
- KINDER, T.H. and COACHMAN, L.K. (1978): The front overlaying the continental slope in the eastern Bering Sea. *J. Geophys. Res.*, **83**, 231-244.
- MCRROY, C.P., GOERING, J.J. and SHIELS, W.E. (1972): Studies of primary production in the eastern Bering Sea. *Biological Oceanography of the Northern North Pacific Ocean*, ed. by A.Y. TAKENOUTI *et al.* Tokyo, Idemitsu Shoten, 199-216.
- MCRROY, C.P., HOOD, D.W., COACHMAN, L.K., WALSH, J.J. and GOERING, J.J. (1986): Processes and resources of the Bering Sea shelf (PROBES): The development and accomplishments of the project. *Cont. Shelf Res.*, **5**, 5-21.
- MÜLLER-KARGER, F.E. and ALEXANDER, V. (1987): Nitrogen dynamics in a marginal sea-ice zone. *Cont. Shelf Res.*, **7**, 805-823.
- MÜLLER-KARGER, F.E., MCCLAIN, C.R., SAMBROTTO, R.N. and RAY, G.C. (1990): A comparison of ship and coastal zone color scanner mapped distribution of phytoplankton in the southeastern Bering Sea. *J. Geophys. Res.*, **95**, 11483-11499.
- NIEBAUER, H.J. (1980): Sea ice and temperature variability in the eastern Bering Sea and the relation to atmospheric fluctuations. *J. Geophys. Res.*, **85**, 7507-7515.
- NIEBAUER, H.J. and ALEXANDER, V. (1985): Oceanographic frontal structure and biological production at an ice edge. *Cont. Shelf Res.*, **4**, 367-388.

- ODATE, T. (1996): Abundance and size composition of the summer phytoplankton communities in the western North Pacific Ocean, the Bering Sea, and the Gulf of Alaska. *J. Oceanogr.*, **52**, 335-351.
- OHTANI, K. (1969): On the oceanographic structure and the ice formation on the continental shelf in the eastern Bering Sea. *Bull. Fac. Fish., Hokkaido Univ.*, **20**, 94-117 (in Japanese with English Abstract).
- OHTANI, K. (1973): Oceanographic structure in the Bering Sea. *Mem. Fac. Fish., Hokkaido Univ.*, **21**, 65-106.
- OHTANI, K. and AZUMAYA, T. (1995): Influence of interannual changes in ocean conditions on the abundance of walleye pollock (*Theragra chalcogramma*) in the eastern Bering Sea. *Climate Change and Northern Fish Populations*, ed. by R.J. BEAMISH. 87-95 (Canadian Special Publication of Fisheries and Aquatic Sciences, **121**).
- PARSONS, T.R., MAITA, Y. and LALLI, C.M. (1984): *A Manual of Chemical and Biological Methods for Seawater Analysis*. Oxford, Pergamon Press, 173 p.
- SAMBROTTO, R.N., NIEBAUER, H.J., GOERING, J.J. and IVERSON, R.L. (1986): The relationship among vertical mixing, nitrate uptake, and growth during the spring bloom on the southeast Bering Sea middle shelf. *Cont. Shelf Res.*, **5**, 161-198.
- SCHUMACHER, J.D., KINDER, T.H., PASHINSKI, D.J. and CHARNELL, R.L. (1979): A structural front over the continental shelf of the eastern Bering Sea. *J. Phys. Oceanogr.*, **9**, 79-87.
- STRICKLAND, J.D.H. and PARSONS, T.R. (1972): *A Practical Handbook of Seawater Analysis*. 2nd ed. *Bull., Fish. Res. Board Can.*, **167**, 311 p.
- SUZUKI, R. and ISHIMARU, T. (1990): An improved method for the determination of phytoplankton chlorophyll using N, N-dimethylformamide. *J. Oceanogr. Soc. Jpn.*, **46**, 190-194.
- WALSH, J.J. (1983): Death in the sea: Enigmatic phytoplankton losses. *Progr. Oceanogr.*, **12**, 1-86.
- WALSH, J.J., WHITLEDGE, T.E., BARVENIK, F.W., WIRICK, C.D. and HOWE, S.O. (1978): Wind events and food chain dynamics within the New York Bight. *Limnol. Oceanogr.*, **23**, 659-683.
- WHITLEDGE, T.E., REEBURGH, W.S. and WALSH, J.J. (1986): Seasonal inorganic nitrogen distributions and dynamics in the southeastern Bering Sea. *Cont. Shelf Res.*, **5**, 109-132.

(Received August 19, 1998; Revised manuscript accepted October 7, 1998)