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Regional variations in the winter chlorophyll *a* and primary productivity of micro-, nano- and pico-phytoplankton fractions in the Bering Sea basin

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Abstract: Regional variations in chlorophyll *a* concentrations and primary productivity of micro-(10–200 μm), nano-(2–10 μm) and picophytoplankton($<2\mu$m) fractions were measured at the surface in the Bering Sea basin from January to March 1993. Chlorophyll *a* concentrations of micro-, nano- and pico-phytoplankton fractions were 0–0.3, 0–0.09 and 0.1–0.4 μg l^{-1}, respectively. Primary productivity of the three phytoplankton fractions was respectively 0–0.45, 0–0.53 and 0.04–0.37 μg C l^{-1} h^{-1}. In the eastern region, chlorophyll *a* concentration of the three fractions was more than 0.2, 0.06 and 0.3 μg l^{-1}, and primary productivity more than 0.2, 0.4 and 0.3 μg C l^{-1} h^{-1}, respectively. The chlorophyll *a* concentration and primary productivity of the three fractions were lower in the western and central regions than in the eastern region, and rather uniform in the western and central regions. We conclude that for the eastern region, their growth rates, nutrient availability and zooplankton grazing pressure were unlikely to be related to their high chlorophyll *a* concentrations and primary productivity. In the eastern region, the Alaskan Stream with water of a low density flowed into the upper layer across the Aleutian Islands. The inflow formed a shallower upper mixed layer in the eastern region and this shallower upper mixed layer leads to a net positive production of the three phytoplankton fractions. We therefore suggest that the inflow of the Alaskan Stream causes an increase of micro-, nano- and pico-phytoplankton and hence their high chlorophyll *a* concentrations and primary productivity in the eastern region.

1. Introduction

Regional variations in chlorophyll *a* concentration and primary productivity have been observed in the summertime Bering Sea basin and shelf break areas (KAWAMURA, 1963 ; TANIGUCHI, 1969 ; MCROY *et al.*, 1972 ; SAINO *et al.*, 1979) and the high values were observed in the eastern region and the shelf break front. TANIGUCHI (1969) suggested that sporadic water turbulence and vertical mixing induced by storms play an important role in the high values. On the contrary, wintertime chlorophyll *a* concentration and primary productivity were measured in the eastern region (MCROY *et al.*, 1972). Primary productivity was one order of magnitude smaller in the winter than in the summer, whereas chlorophyll *a* concentration in the winter was about 20% of that in the summer on average. Little is known about regional variations in the biomass and productivity of the phytoplankton community in the wintertime Bering Sea basin.

The phytoplankton community is composed of various size fractions and the size structure has a marked influence on the ecosystem (e.g., PARSONS *et al.*, 1984b). Moreover, each size fraction has specific controlling factors for fluctuation in biomass (HARRISON and TURPIN, 1982). It is thus necessary to determine the biomass and

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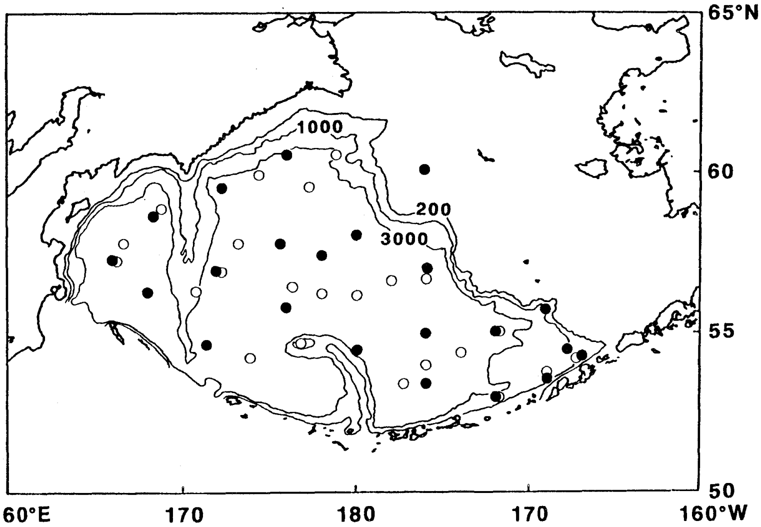

Fig. 1. Location of the sampling stations in the Bering Sea from January to March 1993. Open circles indicate the stations for measuring chlorophyll *a* concentration and primary productivity at the surface and solid circles, the stations for the CTD casts. Numbers indicate the depth in meters.

productivity of size-fractionated phytoplankton, and examine the controlling factors for each fraction to explain the controlling factors for fluctuations in the phytoplankton community. Sieburth *et al.* (1978) divided phytoplankton into three size fractions : microplank ton >20 μm, nanoplankton 2–10 μm and picoplankton <2 μm. Here, we reter to the 10–200, the 2–10 and the<2 μm size fractions as micro-, nano- and pico-phytoplankton, respectively. We determined the regional variations in chlorophyll *a* concentration and primary productivity of these phytoplankton fractions in the wintertime Bering Sea basin and examined the factors causing their regional variations.

2. Materials and methods

This study was carried out from January to March 1993 during a cruise of the Kaiyo Maru of the Fisheries Agency of Japan (Fig. 1). Surface seawater was collected 8–10 a.m. using an acid-cleaned plastic bucket. Samples were sieved through a 200 μm mesh screen to remove large zooplankton.

Chlorophyll *a* concentration was determined by fluorometry according to Parsons *et al.* (1984a). Total chlorophyll *a* was determined in samples filtered through 47mm Whatman GF/F filters. Size-fractionated chlorophyll *a* was measured in samples obtained as follows : seawater samples were filtered through 2 and 10 μm pore size Nuclepore filters and then the filtrates were refiltered onto 47 mm Whatman GF/F filters(<2 and <10 μm fractions). The filters were stored frozen at −20℃ until analysis ashore. Pigments were extracted in 90% acetone and fluorescence was measured with a Hitachi F−2000 fluorophotometer. Calibration of the fluorophotometer was performed with commercially prepared chlorophyll *a* standards from Wako Pure Chemical Industries, Ltd. (Tokyo). Chlorophyll *a* concentrations of the 2–10 and 10−200 μm fractions were obtained from the differences between the <10 and <2 μm fractions and between the total and <10 μm fraction, respectively.

Primary productivity was determined by the ^{13}C method (Hama *et al.*, 1983). The tracer experiments were started within 1 h after sample collection. The seawater samples (1–l) were dispensed into six acid-cleaned 1-l polycarbonate bottles and enriched by an addition (1−ml) of Nah $^{13}CO_3$ (99 atom% ^{13}C ; Shoko Co., Ltd., Tokyo)to about 10% of the total inorganic carbon in ambient water. Incubations were conducted under sunlight and cooled with near-

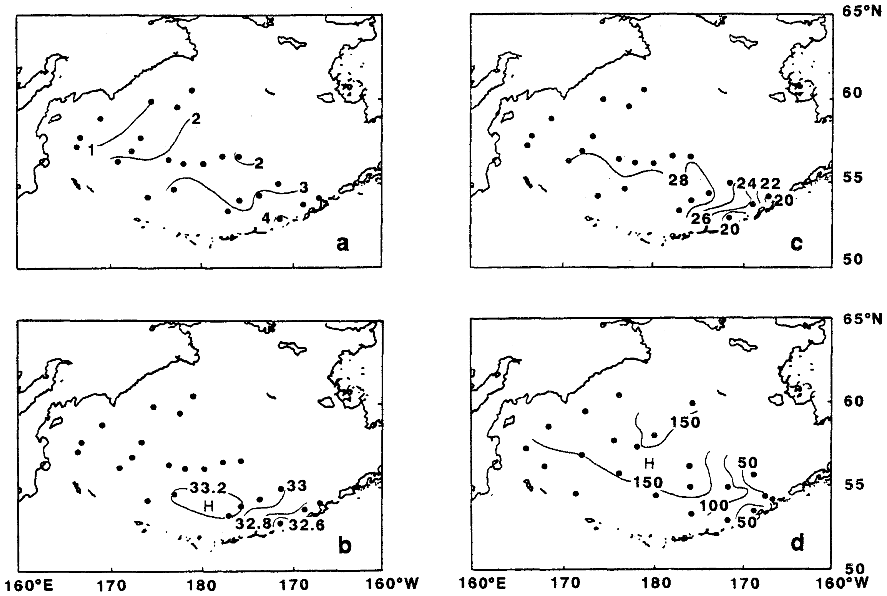

Fig. 2. Regional variations in temperature (℃) (a), salinity (b) and nitrite+nitrate concentration (μM) (c) at the surface and the depth of upper mixed layer (m) (d).

surface seawater for 3–4 h. Fractionation of size classes was carried out immediately after incubation. Two samples were directly filtered through precombusted (450℃ for 4 h) 47mm Whatman GF/F filters(total). Two of the remaining four samples were filtered through Nuclepore filters with a pore size of 2 μm and the other two with pore size of 10 μm. The filtrates were refiltered onto 47mm Whatman GF/F filters (<2 and <10 μm fraction). Particulate matter on the Whatman GF/F filters was rinsed with prefiltered seawater. Filters were stored frozen at −20℃ until analysis ashore. They were treated with HCl fumes for 4 h to remove inorganic carbon and completely dried in a vacuum desiccator. The isotopic ratios of ^{13}C to ^{12}C and particulate organic carbon were determined through infrared absorption spectrometry using a JASCO EX−130 $S^{13}CO_2$ analyzer (Japan Spectroscopic Co., Ltd., Tokyo; cf., Satoh *et al.*, 1985). Total inorganic carbon in the water was measured with an infrared analyzer (Shimadzu TOC 5000). Primary productivity was calculated according to the ezuation described by Hama *et al.*(1983). Sizefractionated primary productivity was estimated in the same manner as the chlorophyll *a* concentration. Repeatability of the tracer experiment was 7.3% as the coefficient of variation for nine replications.

Surface temperature and salinity were measured with a thermometer and with an Auto Lab salinometer. Surface nutrient concentrations were immediately determined using a Bran and Luebbe Auto Analyzer II. Vertical profiles of temperature and salinity down to 1000 m were measured using a Neil Brown CTD Mark II at different station locations from the stations for measuring chlorophyll *a* concentration and primary productivity (Fig.1). The depths of water at all stations except one CTD station were deeper than 500 m (Fig. 1).

3. Results

A high-east and low-west trend was observed in the surface temperature (Fig. 2a). Surface salinity was relatively low in the eastern region and nearly uniform in the western and central regions (Fig. 2b). Surface nitrite+nitrate concetration were relatively low in the eastern region (Fig. 2c). Water with a relatively high temperature, low salinity and low nutrient concentration was found in the eastern region. Based on temperature, salinity and

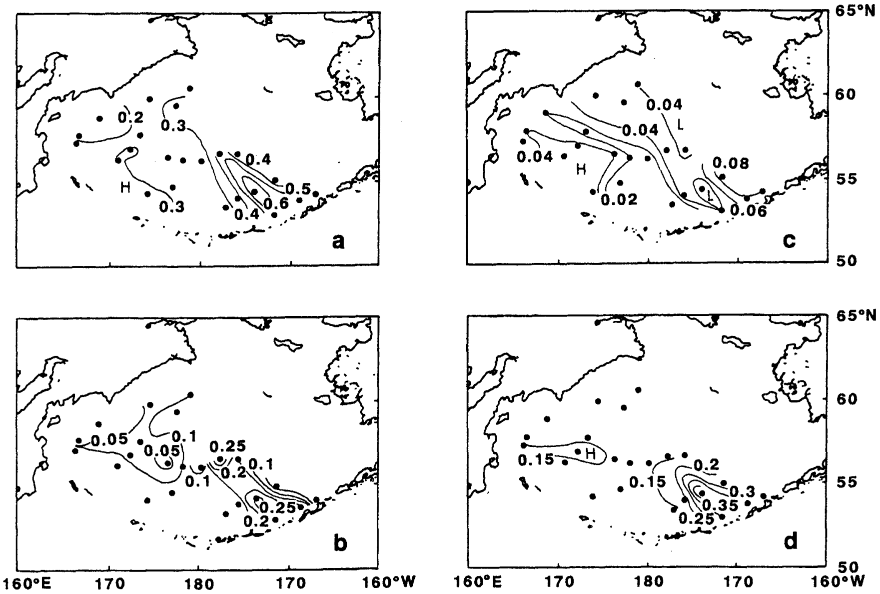

Fig.3. Regional variations in chlorophyll *a* concentrations (μg l^{-1}) of the total (a), micro- (10–200 μm) (b), nano- (2–10 μm) (c) and pico-phytoplankton (<2 μm) (d) fractions at the surface.

nutrient horizontal distributions (Fig. 2a, b, c), this water originates from the direction of the Aleutian Islands. The depth of the upper mixed layer is defined as the depth where the vertical sigma-t gradient was maximum. In the eastern region mixed layer depths were shallower than 100 m, whereas 100–200 m in the western and central regions (Fig. 2d).

Total chlorophyll *a* concentration at the surface ranged from 0.12 to 0.70 μg l^{-1} throughout the stations (Fig. 3a). The chlorophyll *a* concentrations were more than 0.5 μg l^{-1} in the eastern region. The concentrations were lower than 0.4 μg l^{-1} in the western and central regions and generally 0.2–0.3 μg l^{-1}. Chlorophyll *a* concentrations were rather uniform in these regions. The chlorophyll *a* concentrations of the micro-, nano- and pico-phytoplankton fractions were 0–0.3, 0–0.09 and 0.1–0.4 μg l^{-1}, respectively (Fig. 3b, c, d). The concentrations of the three phytoplankton fractions exceeded 0.2, 0.06 and 0.3 μg l^{-1}, respectively, in the eastern region, while they were generally lower than 0.15, 0.06 and 0.15 μg l^{-1}, respectively, in the western and central regions ; ranging generally 0.05–0.15, 0.02–0.05 and 0.1–0.15 μg l^{-1}, respectively. The chlorophyll *a* concentrations of all three fractions were rather uniform in the western and central regions, while the concentrations of the total and the three phytoplankton fractions were higher in the eastern region.

Total primary productivity at the surface ranged from 0.30 to 1.2 μg C l^{-1} h^{-1} throughout the stations (Fig. 4a). The primary productivity values were more than 1 μg C l^{-1} h^{-1} in the eastern region. The values were lower than 1 μg C l^{-1} h^{-1} in the western and central regions and generally 0.3–0.5 μg C l^{-1} h^{-1}. Primary productivity was rather uniform in these regions. The primary productivity of the three phytoplankton fractions was 0–0.45, 0–0.53 and 0.04–0.37 μg C l^{-1} h^{-1}, respectively (Fig. 4b, c, d). In the eastern region values of the three phytoplankton fractions were more than 0.2, 0.4 and 0.3 μg C l^{-1} h^{-1}, respectively. In the western and central regions values of the three fractions were generally lower than 0.3, 0.2 and 0.2 μg C l^{-1} h^{-1}, respectively, ranging generally 0.1-0.3, 0.1–0.2 and 0.05–0.2 μg C l^{-1} h^{-1}, respectively ; and for each fraction the primary productivity was rather uniform. The primary

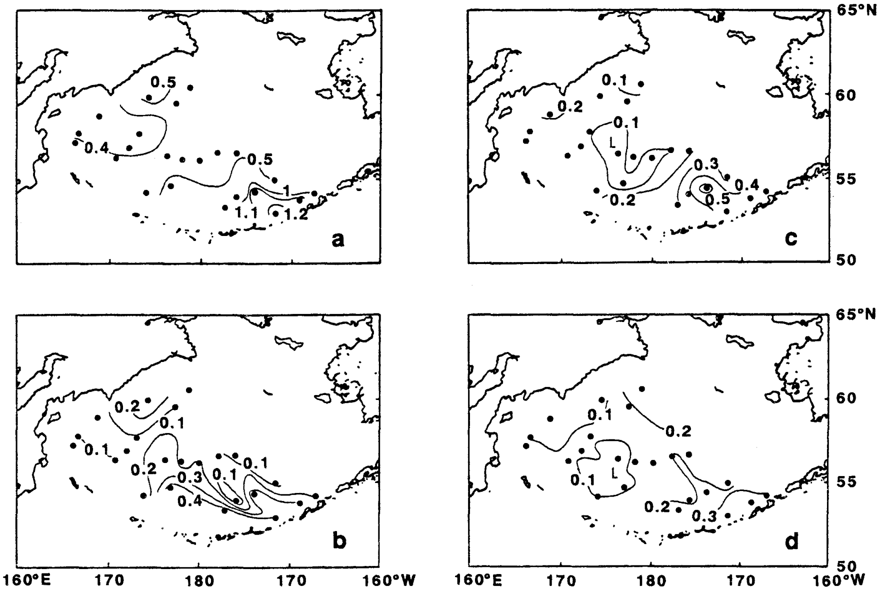

Fig. 4. Regional variations in primary productivity (μg C l^{-1} h^{-1}) of the total (a), micro- (10–200 μm) (b), nano- (2–10 μm) (c) and pico-phytoplankton (<2 μm) (d) fractions at the surface.

productivity of the total and each of the three fractions was higher in the eastern region than in the western and central regions, a pattern similar to that of the chlorophyll *a* concentration.

The biomass of phytoplankton may have much influence on regional variations in primary productivity of the three phytoplankton fractions. Using chlorophyll *a* concentration as an index of the phytoplankton biomass, primary productivity per unit of chlorophyll *a* may be taken as an indicator of activity for phytoplankton productivity. Values of the total phytoplankton ranged from 0.96 to 3.6 μg C μg Chla^{-1} h^{-1} (Fig. 5a). The values were not higher in the eastern region than in the western and central regions, a pattern dissimilar to those for chlorophyll *a* concentration and primary productivity. Values for the micro-, nano- and pico- phytoplankton fractions were 0–13, 0–18 and 0.36–2.7 μg C μg Chla^{-1} h^{-1}, respectively (Fig. 5b, c, d). Values for each of the three phytoplankton fractions were not higher in the eastern region than in the western and central regions, as found for the total phytoplankton. Remarkably high and low values were found for the micro- and nano-phytoplankton fractions at a few stations. The value of the pico-phytoplankton fraction was rather uniform throughout the stations.

4. Discussion

Results show that the biomass and productivity of the phytoplankton community were relatively high in the eastern Bering Sea in winter. Results further show that the micro-, nano- and pico-phytoplankton fractions were responsible for the relatively high biomass and productivity. One might expect the occurrence of factors in the eastern region that led to the increase of these phytoplankton. We discuss possible factors below.

Primary productivity per unit of chlorophyll *a* for the three fractions did not tend to be higher in the eastern region than in the western and central regions (Fig. 5b, c, d). Primary productivity per unit of chlorophyll *a* is a measure of the growth rate of phytoplankton (LALLI and PARSONS, 1993). Growth rates of these phytoplankton fractions are unlikely to be higher in the eastern region than in the western and central regions.

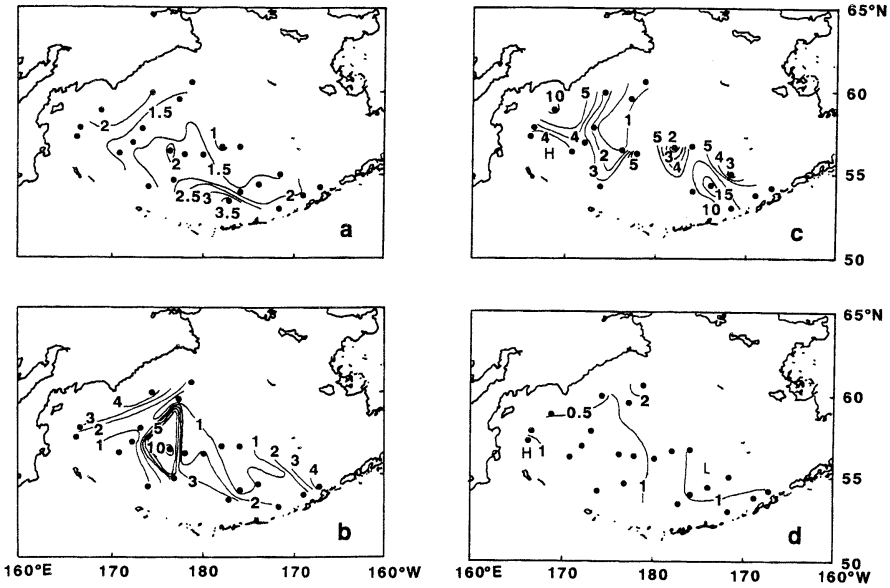

Fig. 5. Regional variations in primary productivity per unit of chlorophyll *a* (μg C μg Chla^{-1} h^{-1}) of the toal (a), micro- (10–200 μm) (b), nano- (2–10 μm) (c) and pico-phytoplankton (<2 μm) (d) fractions at the surface.

Larger phytoplankton have a higher half-saturation constant (Ks) for macronutrients (Malone, 1980). Parsons *et al.* (1984b) showed that Ks may determine the minimum concentration at which a species can grow. The Ks for nitrate uptake of large phytoplankton (10–100 μm cell size) is less than 5 μM (Malone, 1980). Ambient concentrations of nitrite+nitrate at the surface were more than the Ks value at all stations (Fig. 2c) and thus macronutrients are unlikely to limit the growth of the three phytoplankton fractions in the Bering Sea basin in winter.

Iron is an important micronutrient for phytoplankton (e.g., Martin and Fitzwater, 1988). The stations in the eastern region were located near the Aleutian Islands (Fig. 1), and thereby iron may have been a limiting factor for phytoplankton in the western and central regions but not in the eastern region. Iron limitation lowers primary productivity per unit of chlorophyll *a* (Greene *et al.*, 1991 ; Barber and Chavez, 1991)and growth rate (Coale *et al.*, 1996a ; Boyd *et al.*, 1996), and establishes a phytoplankton community dominated by small cells (Martin *et al.*, 1989 ; Boyd *et al.*, 1996 ; Coale *et al.*, 1996b). However, primary productivity per unit of chlorophyll *a* for the three fractions was not lower in the western and central regions than in the eastern region (Fig. 5b, c, d), and the percentage contribution of pico-phytoplankton did not tend to be higher in the western and central regions than in the eastern region (Fig. 6). Iron may thus fail to be a limiting factor for phytoplankton in the Bering Sea basin in winter.

Odate (1994) showed a possible top-down controlling system in the northern North Pacific. According to Odate (1994), when the macrozooplankton grazing impact is intense, the biomass of microzooplankton and net phytoplankton (>10 μm cell size) is low, whereas the biomass of pico-phytoplankton (<2 μm cell size) is high. Therefore, even though zooplankton grazing impact is weak in the eastern regin, the weak impact of zooplankton grazing is not likely to cause a high biomass of all three phytoplankton fractions simultaneously.

According to Sverdrup's (1953) critical depth model, net positive production of phytoplankton will occur in the water column if the

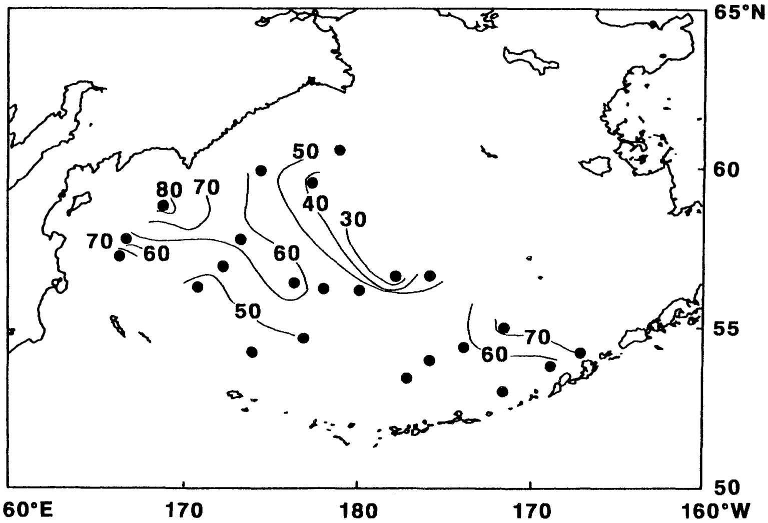

Fig. 6. Regional variation in the percentage contribution of pico-phytoplankton(<2 μm) fraction to the total chlorophyll *a* concentration at the surface.

critical depth is greater than the depth of mixing, whereas no net production can take place if the critical depth is less than the depth of mixing. This model can be applied to fluctuation of phytoplankton regardless of cell size. The three fractions therefore will increase simultaneously if the upper mixed layer depth is shallower than the critical depth.

OBATA *et al.* (1996) estimated the critical depth to be shallower than 100 m in the Bering Sea basin in winter. In this study, the upper mixed layer depth was shallower than 100 m in the eastern Bering Sea, whereas the depth was 100–200 m in the western and central regions (Fig. 2d). According to SVERDRUP's (1953) critical depth model, it is expected that phytoplankton biomass will be increased in the upper layer in the eastern region. As high chlorophyll *a* concentrations of micro-, nano- and picophytoplankton fractions were observed at the surface in this region (Fig. 3b, c, d), we suggest that the shallower upper mixed layer depth in the eastern region leads to an increase of the three phytoplankton fractions.

Warm (>3℃) and low saline (<33) water was observed at the surface in the eastern Bering Sea (Fig. 2a, b). The Alaskan Stream which flows westward along the southern side of the Aleutian Islands flows into the upper layer in the Bering Sea across the straits and passes of the Aleutian Islands (OHTANI, 1965, 1970). The winter surface temperature and salinity of the Alaskan Stream are 3–4℃ and lower than 33.0 (OHTANI, 1970). In this study, the surface temperature and salinity in the eastern region were almost equal to the surface temperature and salinity of the Alaskan Stream. Moreover, the surface water of the Aaskan Stream has a high temperature and low salinity, in other words, a low density compared with the upper water in the wintertime Bering Sea (OHTANI, 1970). Accordingly, the upper mixed layer in the eastern region was of water from the Alaskan Stream. We therefore suggest that the flow of the Alaskan Stream into the upper layer in the eastern Bering Sea caused the shallower upper mixed layer in this region, and thereby an increase in the micro-, nano- and picophytoplankton fractions and hence their chlorophyll *a* concentrations and primary productivity.

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