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Subsurface chlorophyll *a* maximum in the coastal front around St. Paul Island

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Abstract: Size-fractionated primary productivity and chlorophyll *a* (Chl *a*) concentration were measured in the middle domain of the southeastern Bering Sea shelf in summer 2004. A subsurface Chl *a* maximum of 7.9 μg l^{-1} was observed at 20 m depth, around the pycnocline in the coastal front around St. Paul Island. Large phytoplankton exceeding 10 μm in size accounted for about 80% of the primary productivity and Chl *a* concentration at the subsurface Chl *a* maximum. The growth rate of the large phytoplankton was estimated to be 0.09 d^{-1}, which is low compared to previously reported growth rates as well as other rates obtained in this study (0.06–0.56 d^{-1}). More abundant nutrient supply from deeper to upper layers due to the topography of the area is considered the leading factor producing the subsurface Chl *a* maximum. Moreover, ineffective grazing of the large phytoplankton in the middle shelf domain and their accumulation around the pycnocline are thought to be advantageous factors maintaining the subsurface Chl *a* maximum.

key words: the Bering Sea shelf, St. Paul Island, subsurface chlorophyll *a* maximum, large phytoplankton, nutrients

Introduction

The southeastern Bering Sea shelf is one of the most productive regions of the world's oceans (*e.g.* Koblents-Mishke *et al.*, 1970; Berger, 1989; Falkowski and Raven, 1997). Here, the water column over the continental shelf is divided by a series of frontal systems into three distinct water masses: inner, middle and outer (*e.g.*, Coachman, 1986). Coastal fronts have been reported around the Pribilof Islands, situated in the middle shelf domain (Schumacher *et al.*, 1979; Kinder *et al.*, 1983; Flint *et al.*, 2002), and in and around the pycnocline in the coastal fronts around St. Paul Island, a subsurface chlorophyll *a* (Chl *a*) maximum has been observed (Coyle and Cooney, 1993; Hunt *et al.*, 1996; Brodeur *et al.*, 1997). It is suggested that the phytoplankton producing this maximum have a high growth rate; however, this has not yet been confirmed. Nevertheless, the abundant phytoplankton biomass is known to be the base of the abundant biomass of higher trophic levels along with the zooplankton biomass around these fronts (*e.g.*, Hunt *et al.*, 1996; Brodeur *et al.*, 1997; Flint *et al.*, 2002). The composition of the marine ecosystem is greatly influenced by the size structure of the phytoplankton community (*e.g.*,

Parsons *et al*., 1984a; Stocner and Antia, 1986); however, little is known about the size of phytoplankton contributing to the Chl *a* maximum.

I had a chance to measure the growth rates of size-fractionated phytoplankton on the southeastern Bering Sea shelf in summer 2004. This paper shows that large phytoplankton significantly contribute to the subsurface Chl *a* maximum but that their growth rate is not high. It also discusses the factors producing the subsurface Chl *a* maximum.

Materials and methods

This study was conducted at three stations in the middle shelf domain of the southeastern Bering Sea shelf during a cruise of the T/S *Oshoro Maru*, belonging to the Faculty of Fisheries, Hokkaido University, from July 29 to August 10, 2004 (Fig. 1).

The specific growth rate (d^{-1}) of the phytoplankton was calculated by the following equation (*e.g*., Parsons *et al*., 1984b; Furnas, 2002):

$$\text{Growth rate } (d^{-1}) = \ln[(N_0 + \Delta N)/N_0],$$

where N_0 is the initial biomass of the phytoplankton and ΔN is the biomass increased by net photosynthesis per day. The equation was used for estimating the growth rates of <2, 2–10 and >10 μm size fractions of phytoplankton. Biomass is usually expressed as the carbon content (μgC l^{-1}), but here the initial biomass was measured as the Chl *a* concentration (μg l^{-1}). Daily primary productivity was used for the net photosynthesis per day.

Primary productivity was measured by the simulated *in situ* method using the ^{13}C uptake technique (Hama *et al*., 1983). The vertical profiles of PAR (photosynthetically active radiation) were measured using an underwater spectroradiometer (MER 2040/2041; Bioshperical Instruments Inc., San Diego). The three sampling depths corresponded to 100, 30 and 10% of the surface irradiance based on the PAR profiles. Seawater samples were collected using Niskin bottles attached to a CTD system. The samples (2-*l*) were dispensed into two light 2-*l* polycarbonate bottles at each light depth and enriched with ^{13}C-$NaHCO_3$ (99 atom%^{13}C; Shoko Co. Ltd.) to about 10% of the total inorganic carbon in ambient water within 30 min after collection of the samples. Dark bottle uptake is similar to the zero-time blank in the ^{13}C technique (Shiomoto *et al*., 1998), and thus, no dark bottles were used. Bottles of seawater samples inoculated with ^{13}C-$NaHCO_3$ were held in a deck incubator during 6–8 h incubations at a range of irradiances corresponding to the depths at which the samples were taken, obtained using black mesh screens. A constant temperature was maintained in the deck incubator with continuous flowing of near-surface seawater. The experiments were terminated by filtering.

The fractionation of samples into size classes was performed after incubation. Immediately following incubation, 0.5-*l* seawater samples in bottles were directly filtered through precombusted (450°C for 4 h) 47-mm Whatman GF/F filters (*ca*. 0.7-μm pore size: total). The seawater remaining in the bottles after the above filtering was then filtered through Nuclepore filters with pore sizes of 2 and 10 μm, and the filtrate was refiltered through 47-mm Whatman GF/F filters (for the <2 or <10 μm size fractions). The particulate matter on the Whatman GF/F filters was rinsed with prefiltered seawater and the filters were immediately frozen and preserved for isotope analysis ashore, during which they were treated with HCl fumes for 4 h to remove inorganic carbon and com-

pletely dried in a vacuum desiccator. The isotopic ratios of ^{13}C to ^{12}C and particulate organic carbon were determined using a mass spectrometer (ANCA SL, PDZ Europa).

The total inorganic carbon content of the water was measured with an infrared analyzer (Shimadzu TOC 5000). Primary productivity was calculated according to the equation described by Hama *et al*. (1983). Primary productivity of the 2–10 and >10 μm size fractions was obtained from the differences between the <10 and <2 μm size fractions and between the total and <10 μm size fraction, respectively. Primary productivity in the two polycarbonate bottles at each depth was averaged. The daily primary productivity was determined by multiplying the primary productivity during the incubation period by the ratio of the daily integrated photon flux to the photon flux integrated by the incubation period. The primary productivity obtained by the above procedure was almost equal to that obtained using acid-cleaned Teflon-coated 10-*l* Niskin X sampling bottles (General Oceanics) on a Kevlar line (clean technique) for surface seawater on the Bering Sea shelf.

Seawater samples for measuring Chl *a* concentration were obtained from the same seawater samples used for measuring primary productivity. Separate surface seawater samples (0.5-*l*) were filtered through Nuclepore filters with pore sizes of 10 and 2 μm and a Whatman GF/F (total). The filtrate from the Nuclepore filters was refiltered through 47 mm Whatman GF/F filters (for the <2 or <10 μm size fractions). Chl *a* was extracted with N,N-dimethylformamide (Suzuki and Ishimaru, 1990), and Chl *a* concentrations were determined with a Turner Designs 10-AU fluorometer according to Parsons *et al*. (1984b). Calibration of the fluorometer was performed with a commercially prepared Chl *a* standard (Sigma Chemical Co.). Size-fractionated Chl *a* concentrations were estimated in the same manner as the primary productivity. Chl *a* concentration was converted to the carbon content of the phytoplankton by multiplying the slopes between the concentrations of Chl *a* and particulate organic carbon for the three size fractions before incubation. Significant linear regression lines were obtained for the <2 and >10 μm size fractions (p<0.001), with slopes of 92 and 53, respectively. The regression line, however, was not significant for the 2–10 μm size fraction (p>0.1). The average of the slopes of the other two size fractions (73) was used as the slope of the 2–10 μm size fraction. The values were mostly within the range of the carbon to Chl *a* ratios of phytoplankton assemblages in previous culture and field studies (25–100 μgC μgChl a^{-1}; *e.g*., Parsons *et al*., 1984a; Furnas, 2002).

Vertical profiles of temperature and salinity were measured with a CTD-Rosette system (Seabird 9-plus). Vertical profiles of total Chl *a* were obtained from the surface to near the bottom using a Niskin sampler attached to the CTD system. Nutrient concentrations were measured with a Bran and Luebbe Auto Analyser II after storage at −20°C. The physical and chemical data were cited from a data report (Hokkaido University, 2005). On-deck photon fluxes were monitored every two minutes with an Alec model MDS MKV/L quantum sensor on the upper deck during the sampling period.

Results and discussion

The middle shelf domain is characterized by a two-layered water column (*e.g*., Coachman, 1986). The coastal front around St. Paul Island occurs in the vicinity of the

50 m isobath (Schumacher *et al*., 1979; Kinder *et al*., 1983; Coyle and Cooney, 1993; Brodeur *et al*., 1997; Flint and Sukhanova, 2002; Flint *et al*., 2002). The thermocline and halocline, and hence, the pycnocline are vertically gentler in the coastal front around the island than in the surrounding waters in the middle shelf domain. Moreover, the depth of the upper mixed layer is shallower at the fronts than in the surrounding waters. Such characteristics were found at Stn. C situated just southeast of St. Paul Island (Figs. 1 and 2a, b, c), confirming its location in the coastal front.

Pycnoclines were observed at 15–17 m at Stn. A, 19–21 m at Stn. B and 7–16 m at Stn. C (Fig. 2c). The pycnocline was gentler at Stn. C than at Stns. A and B, where they were very steep. The 100 and 30% light depths were within the upper mixed layer (in the upper part of the pycnocline) and the 10% light depth was within the pycnocline at Stns. A and C, whereas all three light depths were within the upper mixed layer at Stn. B (Fig. 2c).

Nitrate was nearly exhausted in the upper mixed layer at every station (Fig. 2d). Nitraclines were observed at 10–20 m at Stns. A and C, and 20–30 m at Stn. B. Moreover, they were observed at nearly the same depths in the pycnoclines at Stns. A and C, and just below the pycnocline at Stn. B. The pycnocline was gentler at Stn. C than at the other two stations (Fig. 2c). As a result, it is suggested that the nutrient supply from the lower to upper layers of the 10% light depth was more abundant at Stn. C than at Stns. A and B, especially at the 10% light depth.

A subsurface Chl *a* maximum represented by a total Chl *a* concentration of 7.9 μg l^{-1} was observed at 20 m depth at Stn. C, whereas no such high subsurface maxima were found at the other two stations (Fig. 2e). This high total Chl *a* concentration was within the range of the values of the subsurface Chl *a* maximum (5–10 μg l^{-1}) re-

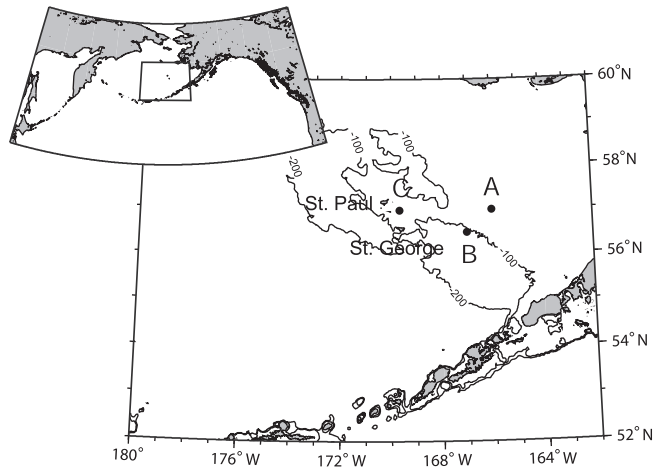

Fig. 1. Location of sampling stations in the middle shelf domain of the southeastern Bering Sea shelf, summer 2004. The depth of the water was 69 m at Stn. A (57°N, 166°W), 101 m at Stn. B (56°30'N, 167°W) and 58 m at Stn. C (57°N, 169°41'W). Stn. C was located just southeast of St. Paul Island.

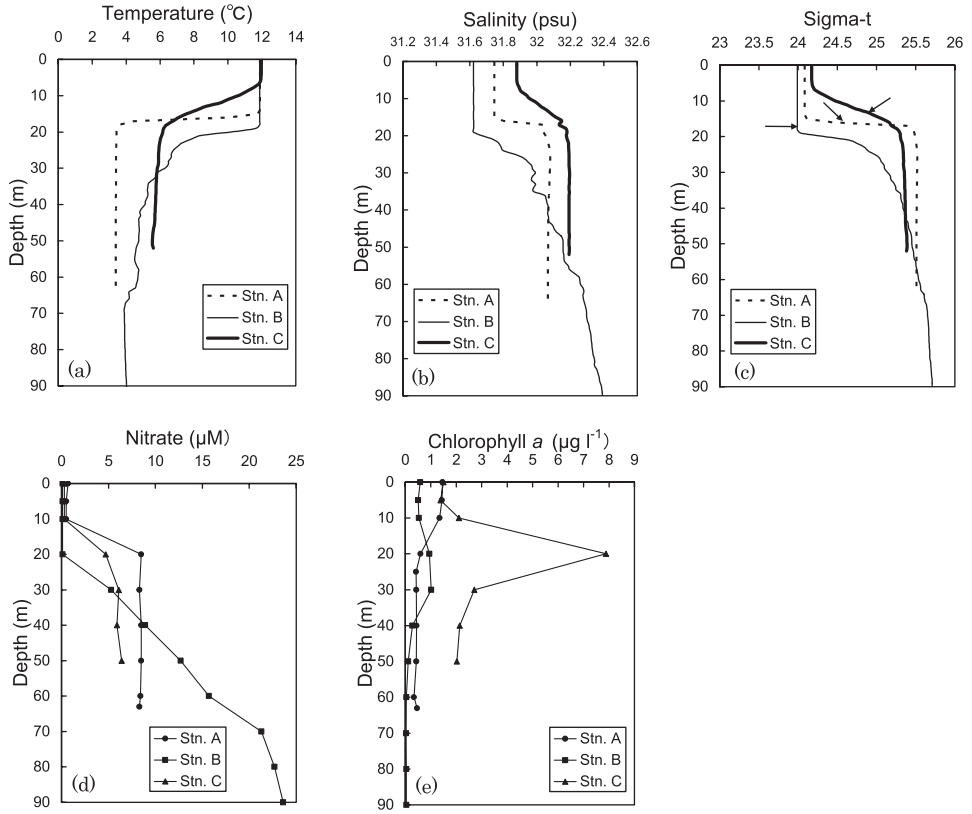

Fig. 2. Vertical profiles of temperature (°C) (a), salinity (psu) (b), sigma-*t* (c), nitrate concentration (μM) (d) and total chlorophyll *a* concentration (μg l^{-1}) (e) at Stns. A, B and C. In (c), the arrows indicate the depths of the 10% light depth.

ported previously in the coastal front around St. Paul Island (Coyle and Cooney, 1993; Hunt *et al*., 1996; Brodeur *et al*., 1997).

In this study, size-fractionated Chl *a* concentration and primary productivity were measured at 100, 30 and 10% light depths. At Stn. C located in the frontal area, the maximum total Chl *a* concentration and primary productivity were observed at the 10% light depth (13 m; Figs. 3a and 4a). The Chl *a* concentration at the 10% light depth was 5.50 μg l^{-1}, representing 70% of the subsurface Chl *a* maximum concentration at the 20 m depth. The phytoplankton community at the 10% light depth at Stn. C was considered to belong to the subsurface Chl *a* maximum in the frontal area. Large phytoplankton of >10 μm size accounted for about 80% of the total Chl *a* and primary productivity at the 10% light depth at Stn. C, *i.e*., at the subsurface Chl *a* maximum (Figs. 3b and 4b). Diatoms are reportedly the dominant large phytoplankton in the middle shelf domain in spring and summer (Goering and Iverson, 1981). It can therefore be said that large phytoplankton, especially diatoms, significantly contribute to the subsurface Chl *a* maximum in the coastal front around St. Paul Island.

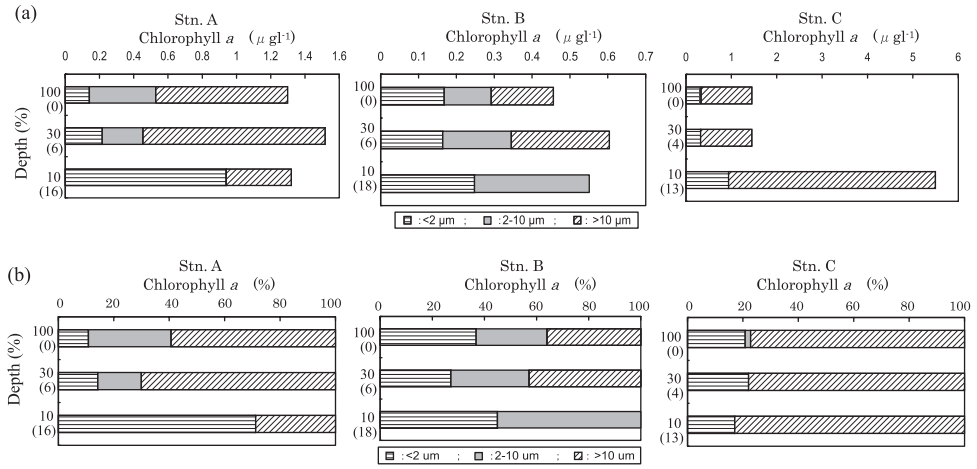

Fig. 3. Size-fractionated chlorophyll *a* concentration ($\mu g\ l^{-1}$) (a) and percentage contribution of the <2, 2–10 and >10 μm size fractions (b) at the 100, 30 and 10% light depths at Stns. A, B and C. The numbers in parentheses indicate the depth in meters.

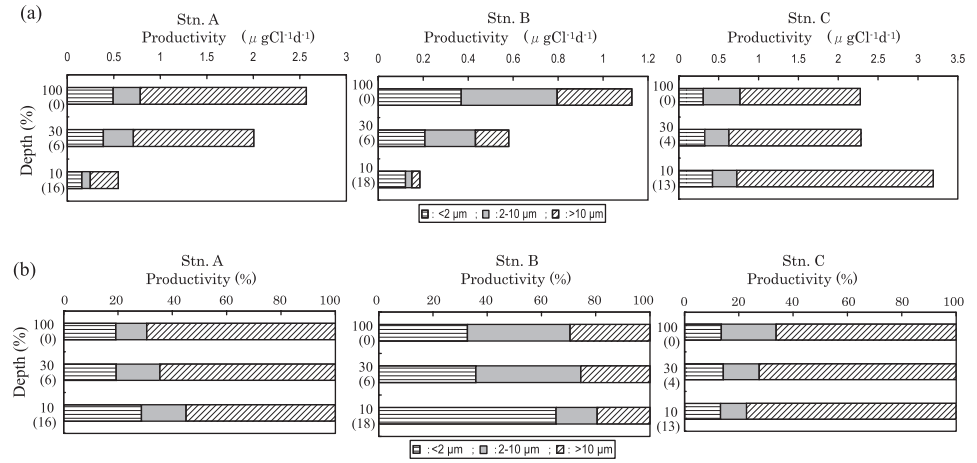

Fig. 4. Size-fractionated primary productivity ($\mu gCl^{-1}\ d^{-1}$) (a) and percentage contribution of the <2, 2–10 and >10 μm size fractions (b) at the 100, 30 and 10% light depths at Stns. A, B and C. The numbers in parentheses indicate the depth in meters.

The growth rates (d^{-1}) of the <2, 2–10 and >10 μm size fractions were 0.02–0.31 d^{-1} (average: 0.12 d^{-1}), 0.09–0.31 d^{-1} (0.16 d^{-1}) and 0.08–0.35 d^{-1} (0.19 d^{-1}), respectively (Table 1). There was no significant difference in the growth rates between the three size fractions (one-way ANOVA, p>0.2), though the average increased with cell size. The maximum values of every size were observed at the 100 or 30% light depth at every station. The growth rate of the large-sized phytoplankton at the 10% light depth at Stn. C,

Table 1. Growth rate (d^{-1}) of the <2, 2–10 and >10 μm size fractions at the 100, 30 and 10% light depths at Stns. A, B and C.

	<2 μm			2–10 μm			>10 μm		
Depth (%)	Stn. A	Stn. B	Stn. C	Stn. A	Stn. B	Stn. C	Stn. A	Stn. B	Stn. C
100	0.31	0.18	0.09	0.09	0.31	nd	0.35	0.27	0.20
30	0.17	0.11	0.09	0.16	0.12	nd	0.20	0.08	0.22
10	0.02	0.04	0.04	nd	0.10	nd	0.13	nd	0.09

nd: no data. The five growth rates indicated by 'nd' were not calculated because chlorophyll *a* concentrations before incubation were almost equal to 0 $\mu g\ l^{-1}$.

i.e., at the subsurface Chl *a* maximum in the coastal front, was estimated to be 0.09 d^{-1} (Table 1). This value is low compared to the growth rates obtained in previous studies (0.06–0.56 d^{-1}; Odate and Saitoh, 2001; Liu *et al.*, 2002) as well as the other rates obtained in this study (Table 1). These findings suggest that the subsurface Chl *a* maximum in the coastal front around St. Paul Island cannot be attributed to the rapid growth of large phytoplankton.

Large-sized phytoplankton prefer higher nutrient concentrations than small-sized phytoplankton (Parsons and Takahashi, 1973; Malone, 1980; Shiomoto, 1997; Shiomoto and Hashimoto, 2001), and hence, a more abundant supply of nutrients should induce an increase in large phytoplankton. In this study, the nutrient supply from deeper layers to upper layers was considered more abundant at Stn. C than at the other two stations, especially at the 10% light depth. A more abundant nutrient supply is thus considered to be the leading factor producing the subsurface Chl *a* maximum in the coastal front of St. Paul Island. The shallower depth of water around the frontal area should cause upwelling of deeper waters rich in nutrients (Fig. 2d; Whitledge *et al.*, 1986; Odate *et al.*, 1999), and thus, the subsurface Chl *a* maximum is ultimately due to the shallower depth.

The mid-shelf group of herbivores consists mostly of small zooplankton, which appear to be ineffective grazers of the large phytoplankton (Goering and Iverson, 1981). On the other hand, large phytoplankton exceeding 10 μm in size sink passively (Takahashi and Bienfang, 1983). However, the subsurface Chl *a* maximum was observed around the pycnocline (Fig. 2c, e), implying an accumulation of the sinking large phytoplankton. Ineffective grazing of the large phytoplankton in the middle shelf domain and their accumulation around the pycnocline are therefore thought to be advantageous factors maintaining the subsurface Chl *a* maximum.

The subsurface Chl *a* maximum was not observed at Stn. A (Fig. 2e); nevertheless, growth rates of the large phytoplankton at the 10% light depth at Stns. A and C were very similar. Ineffective grazing and a subsurface pycnocline are common conditions in the middle shelf domain. In contrast, the nutrient supply from the lower to the upper layer was considered to be less at Stn. A than at Stn. C. Hence, the occurrence of a subsurface Chl *a* maximum somewhere in the middle shelf domain out with the frontal area is possible, if abundant nutrients are supplied.

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