

Chlorophyll-*a* concentration in the southern Okhotsk Sea in late autumn: a comparison between 1993 and 1996

AKIHIRO SHIOMOTO¹, HITOSHI TANAKA², JIRO SEKI³, IKUTARO SHIMIZU³ & YASUO SHIBUYA²

¹National Research Institute of Far Seas Fisheries, 7-1, Orido 5-chome, Shimizu, Shizuoka 424-8633, Japan

²Hokkaido University, 3-1-1, Minato-cho, Hakodate, Hokkaido 041-0821, Japan

³National Salmon Resources Center, Fisheries Agency of Japan, 2-2 Nakanoshima, Toyohira-ku, Sapporo, Hokkaido 062-0922, Japan

Received 16 January 1998; accepted 6 May 1998

Abstract: The chlorophyll-*a* (Chl-*a*) concentrations in late autumn within the upper mixed layer (generally shallower than 30–50 m) was found to be near homogenous. Chl-*a* concentrations within and below the upper mixed layer were significantly higher in 1996 than in 1993. The Chl-*a* concentrations within the mixed layer was $0.79 \pm 0.29 \mu\text{g l}^{-1}$ (mean $\pm$ 1SD, $n=71$) in 1993 and $1.53 \pm 0.61 \mu\text{g l}^{-1}$ ($n=41$) in 1996, and those below the layer was $0.04 \pm 0.06 \mu\text{g l}^{-1}$ ($n=97$) in 1993 and $0.09 \pm 0.10 \mu\text{g l}^{-1}$ ($n=59$) in 1996. The mean values within and below the upper mixed layer in 1996 were approximately two times higher than in 1993. The difference between the two years, calculated through mean values, was found to be $0.74 \mu\text{g l}^{-1}$ and $0.05 \mu\text{g l}^{-1}$. Possible contributing factors responsible for such differences in Chl-*a* concentrations are discussed. Differences in the grazing impact of macrozooplankton (mainly copepods) were identified as an important factor contributing to the observed difference in Chl-*a* concentrations between the two years.

Key words: chlorophyll *a*, Okhotsk Sea, late autumn, upper mixed layer, macrozooplankton

Introduction

The Okhotsk Sea, like the Bering Sea, is a highly productive marginal sea adjoining the North Pacific Ocean (Koblentz-Mishke et al. 1970). Diatoms have been reported to be a major component of the phytoplankton in this sea (Ohwada 1957; Kawarada 1960; Zenkevich 1963; Hanzawa et al. 1981). However, the importance of diatoms as primary producers may need to be reexamined (Shiomoto 1997). Previous observations have shown that diatom cell numbers are at a maximum in spring and at a minimum in autumn (Ohwada 1957; Kawarada 1960; Hanzawa et al. 1981). Spring maximums (spring bloom) have been confirmed through ship-board chlorophyll-*a* (Chl-*a*) measurements (Watanabe 1989; Nishihama et al. 1989; Mordasova 1997), as well as satellite estimates with the help of the coastal zone color scanner (Saitoh et al. 1996). Minimal concentrations have generally been reported during summer or

winter (Watanabe 1989; Nishihama et al. 1989; Saitoh et al. 1996). Results obtained from shipboard measurements (Mordasova 1997) and satellite imagery (Saitoh et al. 1996; Nezlin et al. 1997) indicates higher Chl-*a* concentrations over the shelves and lower concentrations in the Kuril Basin during summer. In contrast, very little is known about interannual variability in Chl-*a* concentrations in the Okhotsk Sea, although Lapshina (1996) reported a 5-fold change in the year-to-year variation of phytoplankton biomass obtained by vertical plankton net tows.

We have attempted to compare Chl-*a* concentrations between 1993 and 1996 with the help of two sets of cruise data collected from the southern Okhotsk Sea and western Pacific Ocean off the Kuril Islands during the months of October and November (Nat. Res. Inst. Far Seas Fish. 1993, 1997). In this paper we analyse the results obtained from this comparison and discuss the factors influencing interannual variability in Chl-*a* concentrations.

Materials and Methods

This study was conducted during cruises of the R/V *Kaiyo Maru*, Fisheries Agency of Japan. Samplings in the Okhotsk Sea were carried out between 15 and 24 October 1993 and between 22 October and 2 November 1996. All stations were located off the shelf edge. All of the stations at which CTD casts were made were located south of 50°N in 1993, whereas half of the stations for the casts were located south of 50°N and the remaining half between 50 and 52°N in 1996. Observations in 1996 were carried out south of 50°N between 22 and 26 October, and north of 50°N between 27 October and 2 November. Consequently, we used data obtained from all stations in 1993 and only those stations located south of 50°N in 1996 for comparisons (Fig. 1).

Seawater samples for measuring Chl-*a* concentrations were collected from the surface with a plastic bucket and from 10, 20, 30, 50, 75, 100, 125, 150 and 200-m depths using 2.5-liter PVC Niskin bottles mounted on a rosette sampler (General Oceanics) attached to a CTD system. One-liter aliquots of seawater were filtered through a Whatman GF/F filter to determine Chl-*a* concentrations. Concentrations were measured with a Shimadzu F-5100 fluorophotometer according to the method of Parsons et al. (1984a) for samples extracted with 90% acetone. Calibration of the fluorophotometer was performed with commercially prepared Chl-

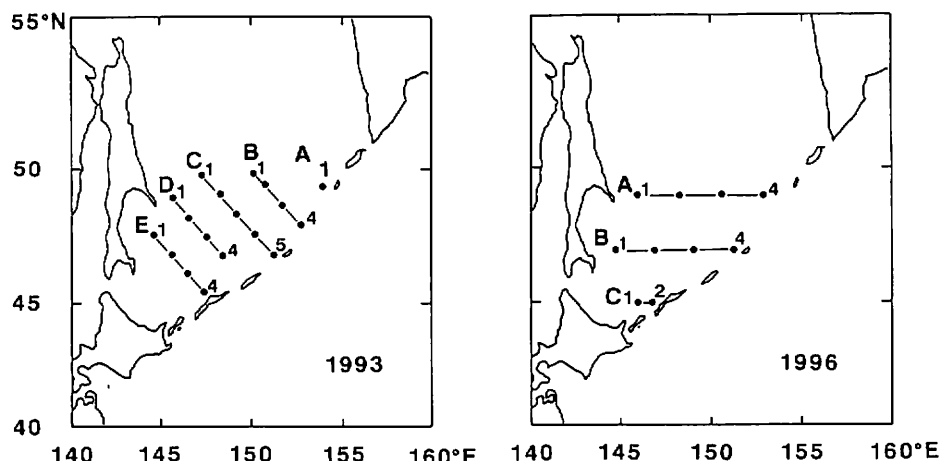


Fig. 1. Location of sampling stations in the southern Okhotsk Sea in late autumn of 1993 and 1996.

a standards from Wako Pure Chemical Industries, LTD. (Tokyo) in 1993 and Sigma Chemical Company (St. Louis) in 1996. The discrepancy between Chl-*a* concentrations obtained by using either standard was 7.7%.

Vertical profiles of temperature and salinity were obtained with a Neil Brown CTD MK-3B in 1993 and a Sea Bird CBE 9 plus in 1996. Seawater samples for measuring nutrient concentrations were collected from the same depths as those for measuring Chl-*a* concentrations. Nutrient concentrations were determined with a Bran & Luebbe Auto Analyzer II immediately after collection. Solar radiation was recorded by an Automatic Meteorological Monitoring System mounted aboard ship. Transparency was measured at the daytime stations using a Secchi disc.

Vertical tows with a Norpac net (mesh size: 100 μm in 1993 and 315 μm in 1996) equipped with a calibrated flowmeter were conducted from a depth of 150 m. Sunrise was at about 0530 h and sunset was at about 1600 h at every station in 1993 and 1996. About half of the tows were made in the daytime and the remaining half at night during both cruises (see Fig. 6B). Twilight observations were treated as nighttime observations because vertically migrating macrozooplankton have been observed in the surface layers in the twilight as well as at midnight in the Okhotsk Sea (Motoda & Sato 1949; Takeuchi 1981) and in the southeastern waters off the Kuril Islands (Taka et al. 1980). Net samples were fixed in 10% formalin seawater neutralized with borax, and the wet weight of macrozooplankton, excluding gelatinous organisms, was determined in the laboratory. Although the mesh size of the net was different in 1993 and 1996, the wet weight of the zooplankton was determined after filtering with a 315- μm mesh size screen in 1993. Hence, we were able to compare wet weights between 1993 and 1996.

Results

In general, temperature, salinity and sigma-*t* were nearly constant within the 30–50 m from the surface in 1993 and 1996 (Figs 2, 3). The depth of the upper mixed layer was defined as the depth where the vertical variation of sigma-*t* for every 1 m was maximum. The depth of the upper mixed layer ranged from 30 to 64 m in 1993 and from 26 to 63 m in 1996. The depths of the upper mixed layer were generally 30–50 m in both years. The temperature values recorded within the upper mixed layer, at 10 m intervals, varied between 3.5 and 12.1°C in 1993 and between 5.1 and 10.8°C in 1996. Similarly salinity within the layer varied between 32.238 and 33.706 in 1993 and between 32.349 and 33.057 in 1996. The Soya Warm Water (temperature: 7–20°C, salinity: 33.6–34.3, Takizawa 1982) was observed around 50 m at Stn E-4 in 1993 (Fig. 2). The upper mixed layer at this station was greatly influenced by its presence. With the exception of Stn E-4, the temperature and salinity within the upper mixed layer ranged from 3.5 to 11.7°C and from 32.238 to 33.338, respectively, in 1993. The 1996 ranges in temperature and salinity closely resembled the ranges in 1993. Vertical mixing of the water-column develops from autumn to winter (Kitani 1973; Aota 1985; Kono & Kawasaki 1995). Judging from the temperatures and salinities within the upper mixed layer, the water within this layer, with the exception of that at Stn E-4 in 1993, was likely to be a mixture of the Okhotsk Surface Water (temperature < 18°C, salinity < 32.5, Takizawa 1982), which is observed in the surface layer during spring and autumn, and the Mixed Water (temperature < 15°C, salinity: 32.4–33.9, Watanabe 1989), which is located between the surface water and the dichothermal water year round. Using the data obtained at 10-m intervals within the upper mixed layer, we conducted tests to determine if there was any significant difference in

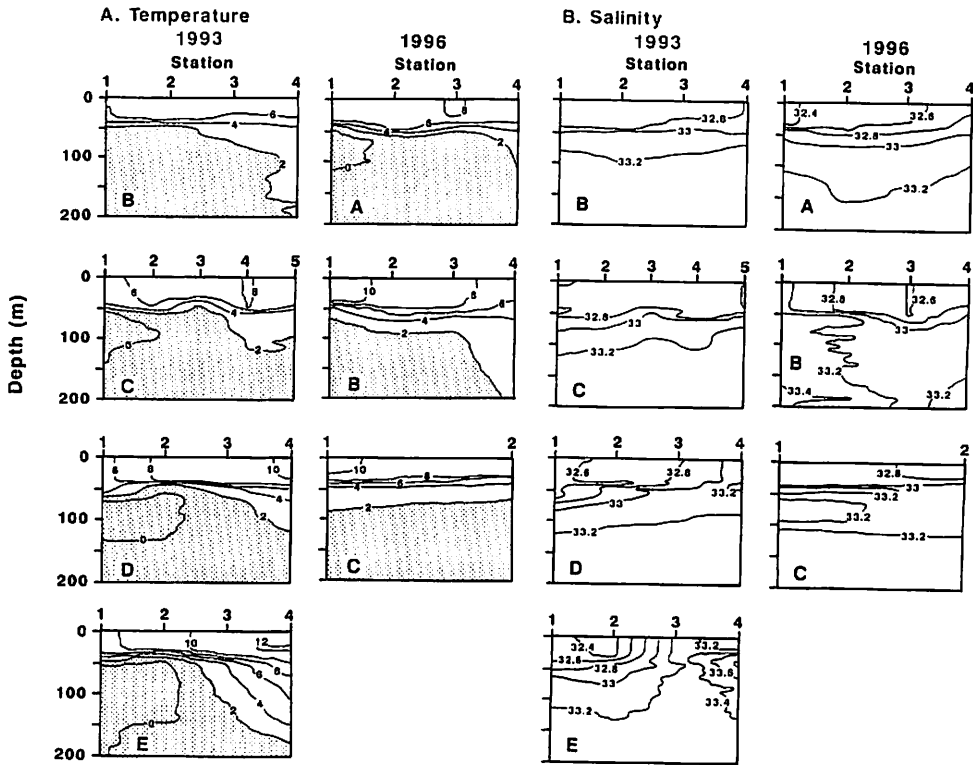


Fig. 2. Vertical sections of temperature (°C) (A) and salinity (B) along lines B, C, D and E in 1993 and along lines A, B and C in 1996 (see Fig. 1). Shaded area indicates dichothermal water with temperatures below 2°C.

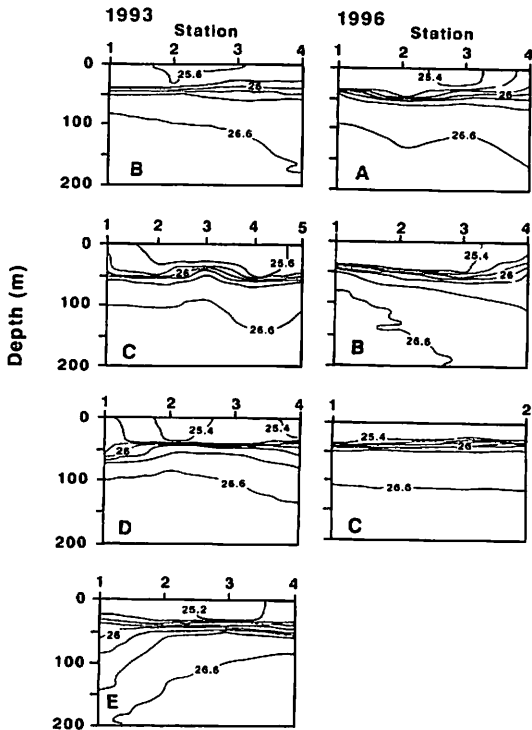
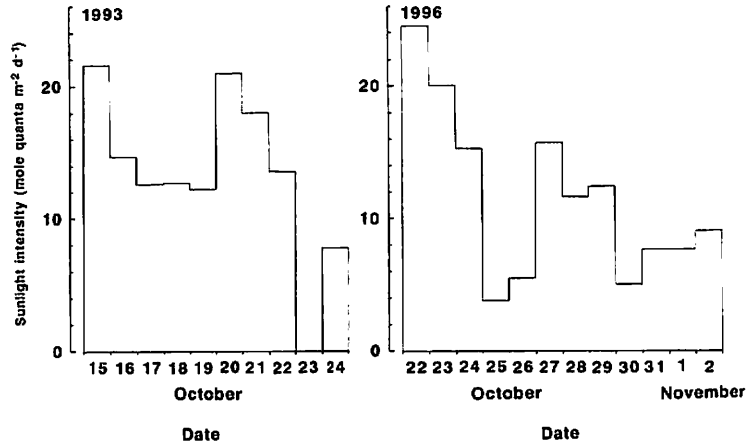


Fig. 3. Vertical sections of sigma- t along lines B, C, D and E in 1993 and along lines A, B and C in 1996 (see Fig. 1).

Fig. 4. Total daily sunlight intensity in 1993 and 1996. Sunlight intensity was monitored at one-hour intervals in lux units. The lux units were then converted to μ einstein $\text{m}^{-2} \text{s}^{-1}$ using the relationship, 1 klux = 16.5μ einstein $\text{m}^{-2} \text{s}^{-1}$ (Richardson et al. 1983).



temperature and salinity between 1993 and 1996. The temperature within the upper mixed layer was found to be significantly different between the two years (Mann-Whitney *U*-test, $p < 0.001$, two-tailed test). The temperatures within the layer was $7.1 \pm 1.9^\circ\text{C}$ in 1993 (mean $\pm$ 1SD, $n = 83$) and $8.3 \pm 1.5^\circ\text{C}$ in 1996 ($n = 46$). The mean temperature was approximately 1°C higher in 1996 than in 1993. In contrast, salinity within the upper mixed layer was not significantly different between the two years (*U*-test, $p > 0.8$). The dichothermal water, ranging from -1.7 to 2.0°C (Kitani 1973), was generally observed below 30–50 m, that is, obviously below the upper mixed layer. We compared Chl-*a* concentrations and physicochemical environmental factors between 1993 and 1996, with the exception of Stn E-4 in 1993.

Sunlight intensity reached a maximum between 1000 and 1200 h. Total daily sunlight intensity was not significantly different between the observation periods in both years (*U*-test, $p > 0.05$): 15–24 October 1993 and 22 October–2 November 1996 (Fig. 4).

Secchi disc depth ranged from 5 to 15 m in 1993 and from 8 to 15 m in 1996. The depth of the euphotic zone is considered to be three times the Secchi disc depth (Parsons et al. 1984b). Hence, the depths of the euphotic zone were calculated to be 15–45 m in 1993 and 24–45 m in 1996. The depth of the upper mixed layer (generally 30–50 m) and the depths of the euphotic zone were nearly equal in both years.

We estimated the critical depth (D_{cr} , in m units) using the following simplified equation (Lalli & Parsons 1993):

$$D_{cr} = I_0 / k I_c \quad (1)$$

where I_0 is the surface light intensity (einstein $\text{m}^{-2} \text{h}^{-1}$), k is the extinction coefficient (m^{-1}) and I_c is the compensation light intensity (einstein $\text{m}^{-2} \text{h}^{-1}$). We calculated k from the following equation (Walker 1980):

$$k = 1.45 / \text{Tr} \quad (2)$$

where Tr is the Secchi disc depth (m). The Secchi disc depth was calculated to be 9 ± 3 m (mean $\pm$ 1SD, $n = 14$) in 1993 and 10 ± 2 m ($n = 10$) in 1996, and we therefore used a value for k of 0.161 m^{-1} in 1993 and 0.145 m^{-1} in 1996. We substituted 0.023 – 0.104 einstein $\text{m}^{-1} \text{h}^{-1}$ converted from 0.002 – 0.009 cal $\text{cm}^{-2} \text{min}^{-1}$ (Parsons et al. 1984b) for I_c . Total daily sunlight intensity was divided by the number of daylight hours between 15 and 24 October 1993 and between 22 October and 2 November 1996, and the daily values were averaged. The mean $\pm$ 1SD was 1.34 ± 0.35 einstein $\text{m}^{-2} \text{h}^{-1}$ ($n = 9$) in 1993 and 1.08 ± 0.50 einstein $\text{m}^{-2} \text{h}^{-1}$ ($n = 10$)

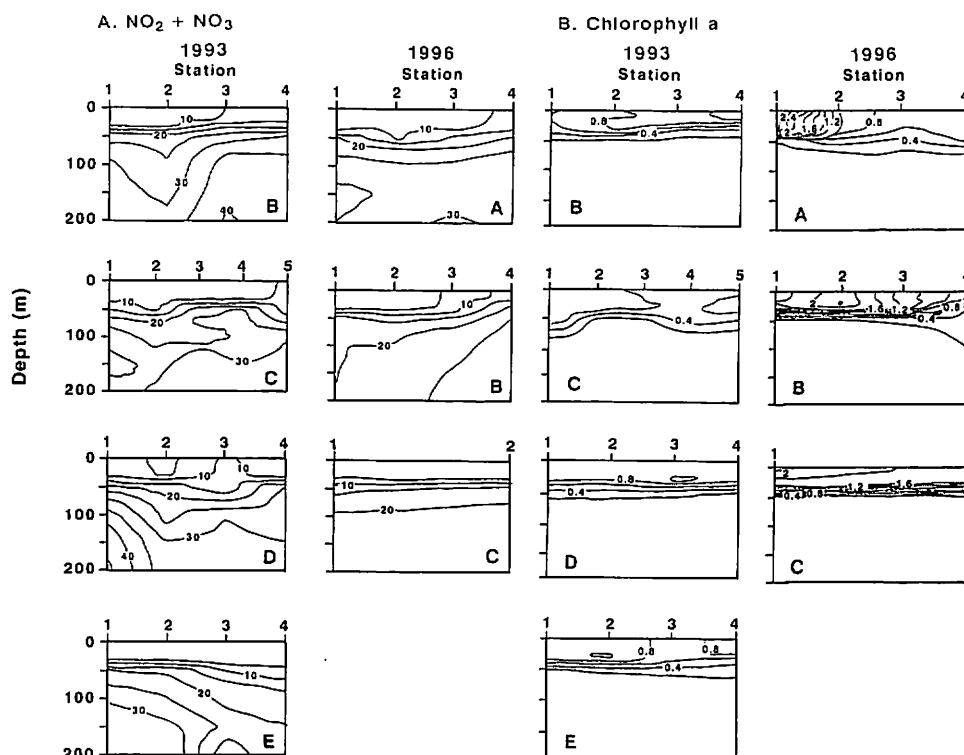


Fig. 5. Vertical sections of nitrite+nitrate concentration (μM) (A) and chlorophyll-*a* concentration ($\mu\text{g l}^{-1}$) (B) along lines B, C, D and E in 1993 and along lines A, B and C in 1996 (see Fig. 1).

in 1996. We used these mean values for I_0 . The minimum critical depth was therefore calculated to be 80 m in 1993 and 72 m in 1996.

Nitrite+nitrate concentration was constant from the surface to 30–50 m depth, the depth of the upper mixed layer (Fig. 5A). The concentration within the mixed layer was not significantly different between the two years (*U*-test, $p > 0.1$). The nitrite+nitrate concentration was calculated to be $7.8 \pm 5.2 \mu\text{M}$ in 1993 (mean $\pm$ 1SD, $n = 71$) and $6.8 \pm 4.7 \mu\text{M}$ in 1996 ($n = 41$). The concentrations below the upper mixed layer and above 200 m were 20–40 μM in both years.

Chl-*a* concentration was also found to be nearly constant within the upper mixed layer (Fig. 5B). The concentrations within the layer ranged from 0.30 to 1.91 $\mu\text{g l}^{-1}$ in 1993 and from 0.24 to 2.78 $\mu\text{g l}^{-1}$ in 1996. The concentration within the upper mixed layer was significantly different between the two years (*U*-test, $p < 0.0001$). The concentration was calculated to be $0.79 \pm 0.29 \mu\text{g l}^{-1}$ in 1993 (mean $\pm$ 1SD, $n = 71$) and $1.53 \pm 0.61 \mu\text{g l}^{-1}$ in 1996 ($n = 41$). The mean in 1996 was about twice as high as that in 1993. The difference between the mean values in the two years was 0.74 $\mu\text{g l}^{-1}$. Below the upper mixed layer, Chl-*a* concentration was generally less than 0.5 $\mu\text{g l}^{-1}$ in both years (Fig. 5B). The concentration below the mixed layer was also significantly different between the two years (*U*-test, $p < 0.0001$). The Chl-*a* concentration was calculated to be $0.04 \pm 0.06 \mu\text{g l}^{-1}$ in 1993 ($n = 97$) and $0.09 \pm 0.10 \mu\text{g l}^{-1}$ in 1996 ($n = 59$). The mean in 1996 was also about twice as high as that in 1993. However, the difference between the mean values for the two years was only 0.05 $\mu\text{g l}^{-1}$.

Chl-*a* standing stock integrated from the surface to 200 m ranged from 27 to 72 mg m^{-2} in 1993 and from 35 to 105 mg m^{-2} in 1996 (Fig. 6A). The standing stock was significantly dif-

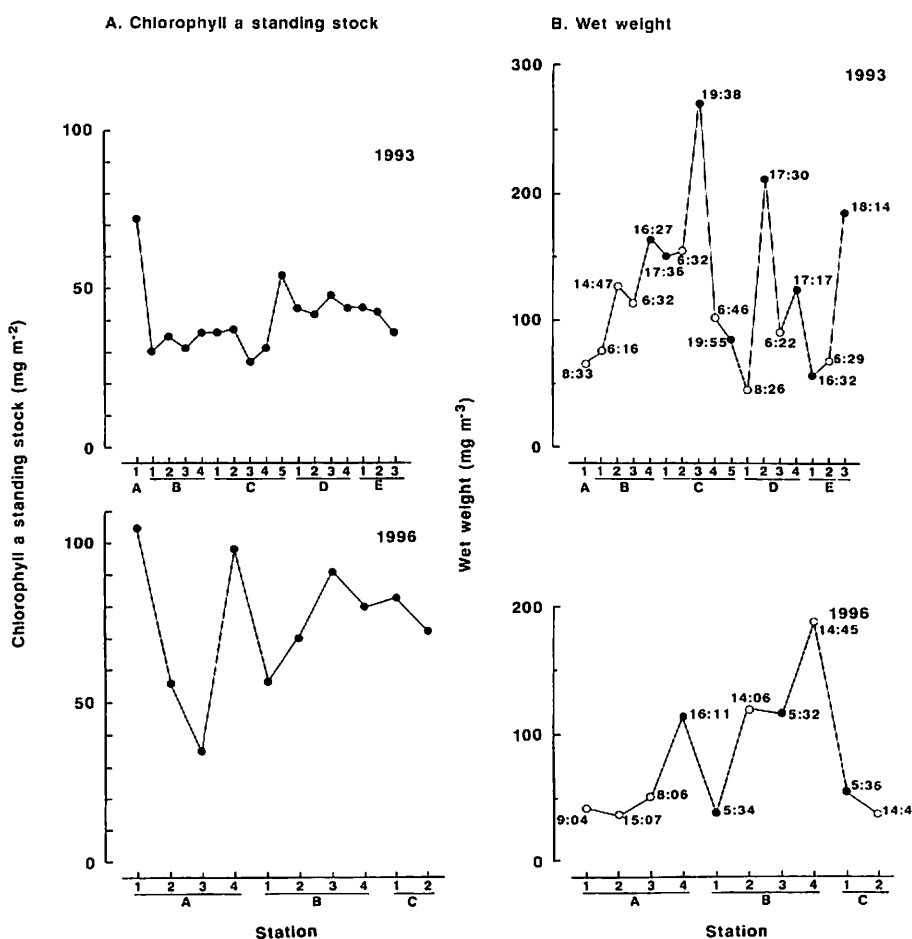


Fig. 6. Variations in chlorophyll-*a* standing stock integrated from the surface to 200 m (A) and the wet weight of macrozooplankton in the upper 150 m of the water column (B) for stations in 1993 and 1996. Open and solid circles in B indicate daytime and nighttime observations, respectively. Figures accompanying the circles in B indicate the starting time of the vertical tows with a Norpac net.

ferent between the two years (*U*-test, $p < 0.001$). The standing stock was $41 \pm 11 \text{ mg m}^{-2}$ (mean $\pm$ 1SD, $n = 17$) in 1993 and $75 \pm 21 \text{ mg m}^{-2}$ ($n = 10$) in 1996. The mean in 1996 was about twice as high as that in 1993. The higher Chl-*a* concentration within the upper mixed layer in 1996 contributed substantially to the higher Chl-*a* standing stock for the upper 200 m.

The wet weight of macrozooplankton obtained with Norpac net tows ranged from 45 to 270 mg m^{-3} in 1993 and from 36 to 187 mg m^{-3} in 1996 (Fig. 6B). Diel vertical migration of macrozooplankton is well known in the Okhotsk Sea (Motoda & Sato 1949; Minoda & Osawa 1967; Takeuchi 1981; Seki et al. 1995). It is thus possible that the wet weights differed substantially between the daytime and nighttime observations at each station for the two years. However, the wet weights of macrozooplankton in the upper 150 m were not significantly different between daytime and nighttime observations for both years (*U*-test, $p > 0.05$). Moreover, the number of stations observed during the day and at night each accounted for approximately 50% in 1993 and 1996 (Fig. 6B). We therefore compared the wet weight of macrozooplankton between 1993 and 1996 using all the data. The wet weights were significantly different be-

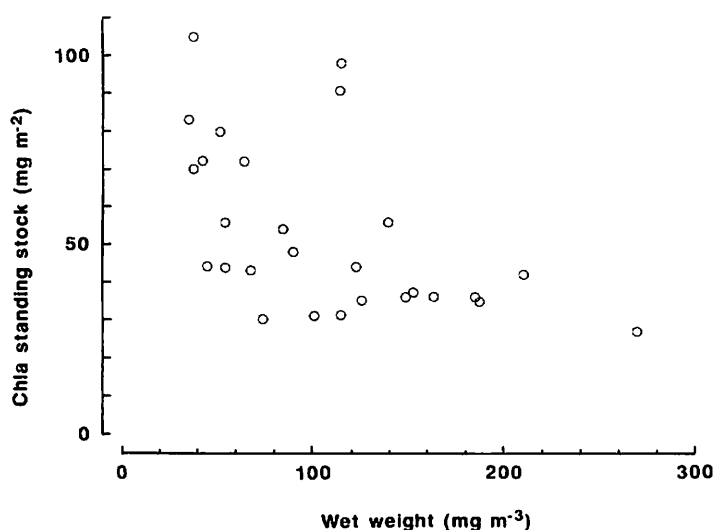


Fig. 7. Relationship between the wet weight of macrozooplankton in the upper 150 m of the water column and the chlorophyll-*a* standing stock integrated from the surface to 200 m in 1993 and 1996. $r_s = -0.62$, $n = 27$, $p < 0.01$ (two-tailed test).

tween the two years (U -test, $p < 0.05$). The mean $\pm$ 1SD was calculated to be $122 \pm 61 \text{ mg m}^{-3}$ in 1993 ($n = 17$) and $80 \pm 51 \text{ mg m}^{-3}$ in 1996 ($n = 10$). The mean value in 1993 was 1.5 times larger than that in 1996. Copepods accounted for the majority of the macrozooplankton abundance in both years. Additionally, we analysed the relationship between macrozooplankton wet weight and Chl-*a* standing stock in the upper 200 m of the water column, using all of the data from 1993 and 1996 (Fig. 7). The Spearman rank correlation showed a significant negative relationship.

Discussion

The Chl-*a* concentration, especially within the upper mixed layer, was higher in 1996 than in 1993. Probable factors causing such interannual variability within the upper mixed layer are addressed below. Results obtained from earlier shipboard measurements (Mordasova 1997) and satellite imagery (Saitoh et al. 1996; Nezlin et al. 1997) show that Chl-*a* concentration is high on the shelves and low in the Kuril Basin. We thus first considered the effect of coastal water advection on Chl-*a* concentrations. In 1996, the stations with lower salinity in the surface layer (Stns A-1, A-2, A-3 and B-3) as shown in Fig. 2B coincided with the stations with higher Chl-*a* concentrations (Fig. 5B). The East Sakhalin Current Water, which is of low temperature and extremely low salinity (temperature $< 7^\circ\text{C}$ salinity < 32.0 , Takizawa 1982) moves south near the coastal area off Sakhalin in autumn and winter (Takizawa 1982). The origin of this water mass is thought to be partly the coastal water off Sakhalin and partly water discharged from Siberian rivers. Thus Chl-*a* concentrations are expected to be higher in waters affected by the East Sakhalin Current Water than in other waters. Hence, the higher Chl-*a* concentration in 1996 could be due to a stronger flow of East Sakhalin Current Water. However, low salinity waters (< 32.6) comparable to those found at Stns A-1, A-2, A-3 and B-3 in 1996 were also observed in 1993 in the surface layer at Stns D-1, E-1 and E-2 (Fig. 2B). These stations may have been affected by the East Sakhalin Current Water. Nevertheless, higher Chl-*a* concentrations were not found in the surface layer at those stations (Fig. 5B). It is evident from the above observation that the East Sakhalin Current Water had little influence on the existence of higher Chl-*a* concentrations in 1996.

The temperature within the upper mixed layer was higher in 1996 than in 1993. The mean temperature was 7.1°C in 1993 and 8.3°C in 1996. The maximum possible growth rate of phytoplankton at these mean temperatures were calculated to be 1.33 d⁻¹ in 1993 and 1.44 d⁻¹ in 1996, using Eppley's (1972) Equation (1). Both rates were similar. The nutrient concentrations within the upper mixed layer were not significantly different between the two years. The depth of the upper mixed layer and the mean total daily sunlight intensity were also not significantly different between the two years. The light extinction coefficients for both years were nearly equal. The average level of photosynthetically active radiation (PAR) in the upper mixed layer is a function of surface PAR, the depth of the mixed layer and the extinction coefficient (Parsons & Lalli 1988). Accordingly, the average PAR in the upper mixed layer was probably nearly equal in 1993 and 1996. Temperature, nutrient concentration and light intensity are factors that regulate phytoplankton productivity. In the absence of any significant difference in any of the above parameters, one might expect the level of phytoplankton productivity in the upper mixed layer to not be significantly different between the two years. Hereafter, we discuss respiratory differences, sinking and zooplankton grazing as possible reasons for the significant difference in phytoplankton concentrations between the years.

According to Sverdrup's (1953) critical depth model, net positive production will occur in the water column if the 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. During the present study, the depth of the upper mixed layer was 64 m at its deepest point in 1993 and 63 m in 1996, whereas the minimum critical depth was 80 m in 1993 and 72 m in 1996. This may have influenced the net production of phytoplankton but it seems safe to infer that the degree of respiration was not the major factor leading to the observed differences in phytoplankton abundances between the two years.

Semina & Tarkhova (1972) showed that the amount of phytoplankton standing stock is proportional to the strength of the density gradient in the main pycnocline. This is probably because a steep gradient favors the retention of phytoplankton cells by halting their sinking below the upper mixed layer. The sigma-*t* gradient at the bottom of the upper mixed layer was not significantly different between the two years (*U*-test, *p* > 0.05). Hence, the level of phytoplankton cell loss through sinking below the upper mixed layer probably did not differ between the two years.

Shiomoto et al. (1997) suggested that zooplankton grazing controls the year-to-year variations in phytoplankton standing stock in the subarctic North Pacific. We did not measure the grazing rates of zooplankton during this study. However, the wet weight of macrozooplankton, as determined from vertical tows with a Norpac net from a depth of 150 m, was found to be significantly larger in 1993 than in 1996 (Fig. 6B). Copepods which feed on phytoplankton (e.g. Parsons & Lalli 1988) accounted for the majority of the macrozooplankton during both years. Vertical migration of copepods up to the surface at night was noticed in the autumn in the Okhotsk Sea (Takeuchi 1981). These results imply a greater grazing impact by macrozooplankton on phytoplankton within the upper mixed layer in 1993 than in 1996. Moreover, the negative correlation between macrozooplankton wet weight and Chl-*a* standing stock strongly implies that zooplankton grazing was of great import (Fig. 7). Consequently, we suggest that differences in the grazing impact of macrozooplankton (mainly copepods) between 1993 and 1996 was the most influential factor causing the observed differences in Chl-*a* concentrations between 1993 and 1996. The effect of zooplankton grazing on phytoplankton biomass in the Okhotsk Sea should be studied in more detail in future investigations.

Acknowledgments

We thank the captain and crew of the R/V *Kaiyo Maru*, Drs Y. Ueno, T. Azuma and M. Ogura of the National Research Institute of Far Seas Fisheries and Drs Y. Kawasaki and T. Kono of Hokkaido National Fisheries Research Institute for their kind help with sampling. We are also grateful to Dr K. Sasaki, National Research Institute of Fisheries Science, for his critical reading and comments on the manuscript. Finally, we express our gratitude to Dr K. Mahapatra, Tokai University, for correcting the manuscript and his helpful comments.

Literature Cited

- Aota, M. 1985. Coastal region of the Okhotsk Sea, p. 7–22. In *Coastal Oceanography of Japanese Islands* (ed. Oceanogr. Soc. Japan). Tokai Univ. Press, Tokyo. (In Japanese.)
- Eppley, R.W. 1972. Temperature and phytoplankton growth in the sea. *Fish. Bull.* **70**: 1063–1085.
- Hanzawa, M., H. Iida, K. Karaushi, M. Matsuzaki, K. Shigehara, S. Kuronuma, M. Akagawa & O. Asaoka 1981. Studies on the mechanism of formation of cold water in the Okhotsk Sea, p. 66–131. In *Report of Joint-Research on the Okhotsk Sea* (ed. Research Coordination Bureau, Science & Technology Agency). Science & Technology Agency, Tokyo. (In Japanese.)
- Kawarada, Y. 1960. A contribution of microplankton observations to the hydrography of the northern North Pacific and adjacent sea—III. Plankton diatoms of the western Okhotsk Sea in the period from June to August 1957. *Mem. Kobe Mar. Obs.* **14**: 73–80.
- Kitani, K. 1973. An oceanographic study of the Okhotsk Sea—Particularly in regard to cold waters. *Bull. Far Seas Fish. Res. Lab.* **9**: 45–77.
- Koblentz-Mishke, O. I., V. V. Volkovinsky & Yu. G. Kabanova 1970. Plankton primary production of the World Ocean, p. 183–193. In *Scientific Exploration of the South Pacific* (ed. Wooster, W.). National Academy of Sciences, Washington D. C.
- Kono, T. & Y. Kawasaki 1995. Development process of the surface mixed layer around the Kuril Islands from October to November, p. 15–22. In *Report on the 1993 R/V Kaiyo-maru Juvenile Salmon Research*, Salmon Report Series No. 40, Nat. Res. Inst. Far Seas Fish., Shimizu. (In Japanese with English abstract.)
- Lapshina, V. J. 1996. Quantitative seasonal and year-to-year changes of phytoplankton in the Okhotsk Sea and off Kuril area of the Pacific, p. 240–246. In *Proceedings of the Workshop on the Okhotsk Sea and Adjacent Area* (convenors: Nagata, Y., Lobanov, V. B. & Talley, L. D.). PICES Scientific Report No. 6, Sidney.
- Lalli, C. M. & T. R. Parsons 1993. *Biological Oceanography: An Introduction*. Butterworth-Heinemann, Oxford, 301 pp.
- Minoda, T. & K. Osawa 1967. Plankton in the sonic scattering layer in the Okhotsk Sea, summer 1963. *Bull. Fac. Fish. Hokkaido Univ.* **18**: 9–19. (In Japanese with English abstract.)
- Mordasova, N. V. 1997. Some peculiarities of chlorophyll distribution in the Sea of Okhotsk. *Oceanology* **37**: 484–491.
- Motoda, S. & S. Sato 1949. A brief observation on the diurnal migration of marine zooplankton of Shiretoko, Hokkaido. *Sci. Pap. Hokkaido Fish. Sci. Inst.* **2**: 72–77.
- National Research Institute of Far Seas Fisheries 1993. *Preliminary Report of the Second Cruise in 1993 of the R/V Kaiyo Maru (data book)*. Salmon Rep. Ser., No. 38, Shimizu, 95 pp. (In Japanese.)
- National Research Institute of Far Seas Fisheries 1997. *Preliminary Report of the Second in 1996 Cruise of the R/V Kaiyo Maru (data book)*. Salmon Rep. Ser., No. 44, Shimizu, 90 pp. (In Japanese.)
- Nezlin, N. P., E. I. Musaeva & V. Yu. D'yakonov 1997. Estimation of plankton stocks in the western part of the Bering Sea and the Sea of Okhotsk. *Oceanology* **37**: 370–375.
- Nishihama, Y., M. Kurata & M. Tada 1989. Seasonal change of chlorophyll concentration lagoon Saroma-ko and Noto-ko and off Abashiri. *Bull. Jpn. Soc. Fish. Oceanogr.* **53**: 52–54. (In Japanese.)
- Ohwada, M. 1957. Diatom communities in the Okhotsk Sea, principally on the west coast of Kamchatka, spring to summer 1955. *J. Oceanogr. Soc. Jpn* **13**: 29–34.

- Parsons, T. R. & C. M. Lalli 1988. Comparative oceanic ecology of the plankton communities of the subarctic Atlantic and Pacific Oceans. *Oceanogr. Mar. Biol. Ann. Rev.* **26**: 317–359.
- Parsons, T. R., Y. Maita & C. M. Lalli 1984a. *A Manual of Chemical and Biological Methods for Seawater Analysis*. Pergamon Press, Oxford, 173 pp.
- Parsons, T. R., M. Takahashi & B. Hargrave 1984b. *Biological Oceanographic Processes*, 3rd ed. Pergamon Press, Oxford, 330 pp.
- Richardson, K., J. Beardall & J. A. Raven 1983. Adaptation of unicellular algae to irradiance: an analysis of strategies. *New Phytologist* **93**: 157–191.
- Saitoh, S., M. Kishino, H. Kiyofuji, S. Taguchi & M. Takahashi 1996. Seasonal variability of phytoplankton pigment concentration in the Okhotsk Sea. *J. Remote Sensing Soc. Jpn* **16**: 86–92.
- Seki, J., I. Shimizu, Y. Ueno, Y. Kawasaki & T. Kono 1995. Composition and distribution of zooplankton in the south Okhotsk Sea and western North Pacific Ocean off the Kuril Islands, p. 45–56. In *Report on the 1993 R/V Kaiyo-maru Juvenile Salmon Research*, Salmon Report Series No. 40, Nat. Res. Inst. Far Seas Fish., Shimizu. (In Japanese with English abstract.)
- Semina, H. & I. A. Tarkhova 1972. Ecology of phytoplankton in the North Pacific Ocean, p. 117–124. In *Biological Oceanography of the Northern North Pacific Ocean* (eds. Takenouchi A. Y. et al.). Idemitsu Shoten, Tokyo.
- Shiimoto, A. 1997. Size-fractionated chlorophyll *a* concentration and primary production in the Okhotsk Sea in October and November 1993, with special reference to the influence of dichothermal water. *J. Oceanogr.* **53**: 601–610.
- Shiimoto, A., K. Tadokoro, K. Nagasawa & Y. Ishida 1997. Trophic relations in the subarctic North Pacific ecosystem: possible feeding effect from pink salmon. *Mar. Ecol. Prog. Ser.* **150**: 75–85.
- Sverdrup, H. U. 1953. On conditions for the vernal blooming of phytoplankton. *J. Cons. int. Explor. Mer* **18**: 287–295.
- Taka, S., M. Kitakata & T. Wada 1980. Food organisms of saury, *Cololabis saira* (Brevoort) and vertical distribution of zooplankton in the southeast waters off Kuril Islands in July, 1976–1978. *Bull. Hokkaido Reg. Fish. Res. Lab.* **45**: 15–41.
- Takeuchi, I. 1981. Characteristics of biological productivity and its change, p. 145–150. In *Report of Joint-Research on the Okhotsk Sea*, (ed. Research Coordination Bureau, Science & Technology Agency). Science & Technology Agency, Tokyo. (In Japanese.)
- Takizawa, T. 1982. Characteristics of the Soya Warm Current in the Okhotsk Sea. *J. Oceanogr. Soc. Jpn.* **38**: 281–292.
- Walker, T. A. 1980. A correction to the Poole and Atkins Secchi disc/ light-attenuation formula. *J. Mar. Biol. Ass. U.K.* **60**: 769–771.
- Watanabe, T. 1989. Environmental characteristics in the Northern Hokkaido. *Bull. Jpn. Soc. Fish. Oceanogr.* **53**: 47–52. (In Japanese.)
- Zenkevich, L. 1963. *Biology of the Seas of the U.S.S.R.* George Allen & Unwin, London, 955 pp.