

Subsurface chlorophyll maximum in the Oyashio, Perturbed and Kuroshio waters in August 1999

¹Shinji HASHIMOTO ²Akihiro SHIOMOTO

¹Teikyo University of Science ²Tokyo University of Agriculture

Size-fractionated chlorophyll *a* concentrations in the upper 160 m depth were measured between 43° N and 39° N along 152° E in August 1999. A prominent subsurface chlorophyll maximum (SCM) was found along the transect. The SCM was observed at 20-40 m in the Perturbed waters and 40-60 m in the Kuroshio waters. The depth of the SCM was usually located above nitracline, close to 1% light depth and below the pycnocline in the Perturbed and the Kuroshio waters. On an average, 50 % of the total chlorophyll *a* concentration was constituted by <2 µm fraction of phytoplankton in the SCM of the Perturbed and the Kuroshio waters. The vertical distribution and size composition of biomass were likely positioned by an interplay between light levels and upward nutrient fluxes. In the Oyashio waters, the SCM was located at 10-20 and 50-70 m. The shallow SCM occurred above nitracline and pycnocline. The >10 µm fraction dominated in the shallow SCM whereas the deep SCM was <2 µm fraction.

Keywords : size fraction, subarctic and subtropical North Pacific, subsurface chlorophyll maximum, summer

1. Introduction

Vertical distribution patterns of chlorophyll *a* concentration vary in different seasons and regions. The chlorophyll *a* concentration maximum is not always found near or at the surface but sometimes lies deeper than the bottom of the euphotic zone¹⁾. The presence of a subsurface chlorophyll *a* maximum (SCM) is a common feature during oligotrophic conditions in the ocean. The small cells generally dominate in the SCM environment²⁾. On the contrary, Revelante and Gilmartin³⁾ reported the presence of a higher relative population of large-sized phytoplankton in the SCM. The mechanisms of development and the ecological significance of the SCM have been summarized^{4,6)}. These studies indicate that the mechanisms can differ greatly according to geographical region, season and biological community.

Phytoplankton composition is affected by nitrate + nitrite concentration⁷⁾, iron concentration^{8,9)} and zooplankton grazing^{10,11)}. Generally, the large-sized phytoplankton tends to dominate in nutrient-rich upwelling regions, whereas small-sized phytoplankton is likely to be a characteristic of oligotrophic conditions in the euphotic layer.

Recent mesoscale iron enrichment experiments conducted in the HNLC (high nitrate, low chlorophyll) regions caused a large increase in large-sized phytoplankton biomass¹²⁻¹⁴⁾.

There are three distinct waters masses in the western subarctic Pacific east of Honshu, Japan: Oyashio waters in the subarctic region, Kuroshio waters in the subtropical region and the perturbed waters between the Oyashio waters and Kuroshio waters. Hydrographic condition rapidly varies from the Oyashio waters to the Kuroshio waters. Sasaki *et al.*¹⁵⁾ showed that the chlorophyll *a* concentration in the SCM was relatively higher in the frontal zone between the Perturbed and Kuroshio waters. However, little is known about the vertical distribution of the size structure of phytoplankton from the Oyashio waters to the Kuroshio waters. Investigation of the size structure of phytoplankton community is still lacking. We precisely investigated the vertical distribution of the size structure of phytoplankton community from the Oyashio waters to the Kuroshio waters, and discuss its relation to the physical and chemical structure of the waters column caused the distribution.

2. Material and Methods

Sampling was conducted on board 'Kurosaki' at every 20' (-40km) from 43°N (Stn 1) to 39°N (Stn 13) along 152°E in the North Pacific during August 1999 (**Fig. 1**). Seawater samples were collected at every 10 m from the surface to 100 m depth and at every 20 m from 100 m to 160 m using a Niskin sampler. The samples were filtered separately through Nuclepore filters with pore sizes of 2 and 10 μm and Whatman GF/F filter to determine the size fractions of the chlorophyll *a* concentrations. One liter of seawaters was filtered with vacuum of 150 to 200 mm Hg. The filters were frozen at -20°C until analyses on land. The chlorophyll *a* concentration was measured with a Hitachi F-2000 fluorometer calibrated with commercial chlorophyll *a* (Wako Pure Chemical Industries, Tokyo) after extraction with 90 % acetone¹⁶⁾. The total chlorophyll *a* concentration was obtained from the chlorophyll *a* retained on GF/F filters. The concentration of more than 10 μm fraction was obtained from the chlorophyll *a* retained on the 10 μm filter. The concentration of less than 2 μm fraction was obtained by subtracting chlorophyll *a* retained on the 2 μm filter from the total chlorophyll *a*. The concentration of the 2-10 μm fraction was calculated from the difference

between the $>2\ \mu\text{m}$ and $>10\ \mu\text{m}$ fraction.

The seawater samples for nutrient measurement were frozen at -20°C until analyses. Nitrate+nitrite and silicate concentrations were determined with a Bran and Luebbe TRAACS 800. Temperature and salinity were measured with an Alec STD AST1000PK. Transparency was measured with a Secchi disk in order to calculate the euphotic layer depth

The euphotic layer depth (1% light depth: Z , in m) was estimated using the following simplified equation¹⁷⁾:

$$I = I_0 e^{-kZ} \quad (1)$$

Where I_0 (100%) is the surface light percentage, I (1%) is the light percentage from the surface light and k is the extinction coefficient (m^{-1}). k was calculated from following equation¹⁸⁾:

$$k = 1.45/Tr \quad (2)$$

where Tr is the Secchi disk depth (m). An equation ($kTr=1.7$), which was reported by Poole and Atkins¹⁹⁾, has been generally used to calculate the extinction coefficient. However, Walker¹⁸⁾ reported that the formula, $kTr = 1.45$, is probably the most useful equation to estimate the extinction coefficient from data investigated in various regions and that use of the formula reported by Poole and Atkins¹⁹⁾ will give results that are on average 17 % too high. Therefore, we used the formula, $kTr = 1.45$, to measure k .

3. Results

The Oyashio waters is located the north area of the Perturbed waters in the western North Pacific. The southern and northern boundaries of the Perturbed waters are bordered by the Subarctic Boundary, denoted as a vertical 34.0 isohaline in the surface layers, and by cold waters ($<4^{\circ}\text{C}$) below 100 m, respectively²⁰⁾. Ohtani²¹⁾ noted that the Oyashio waters should be defined as the southern waters from the central Kuril Islands, the Mushiru Channel or the Kita Uruppu Channel, to northeast off Honshu in Japan. In the western

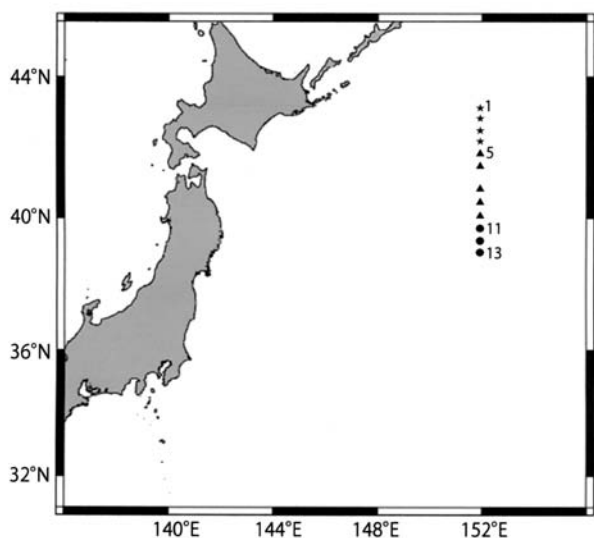


Fig. 1. Location of sampling stations. Solid stars, solid triangles and solid circles indicate stations in the Oyashio waters, Perturbed waters and the Kuroshio waters, respectively.

subarctic regions, the dichothermal layer, which is characterized by a minimum temperature of less than 3 °C, is found in the subsurface layer between 100 and 200 m depths²². In this study, the dichothermal layer was also observed at Stns 1-4 (Fig. 2a). On the other hand, the Kuroshio waters is located the south of the Subarctic Boundary. Thus, Stns 1-4 were located in the Oyashio waters, Stns 5-10 were in the Perturbed waters, and Stns 11-13 were in the Kuroshio waters (Figs. 1 and 2).

The depth of upper mixed layer (pycnocline) was defined as the depth where the vertical variation of sigma-t became maximum at every 1 m. The depths of the upper mixed layer ranged from 26 to 33 m depth in the Oyashio waters, from 8 to 14 m depth in the Perturbed waters and from 9 to 17 m in the Kuroshio waters (Fig. 2c). The mixed layer depths in the Oyashio waters were significantly different from the Perturbed waters and the Kuroshio waters (Mann Whitney U-test, Perturbed waters $U=0$, $p<0.05$; Kuroshio waters $U=0$, $p<0.05$), and were deeper than in the Perturbed waters and the Kuroshio waters. The mixed layer depths were not significantly different in the Perturbed and the Kuroshio waters (U-test, $U=7.0$, $p>0.5$). The depths of the euphotic layer 35-41 m depth in the Oyashio waters, 51-67 m depth in the Perturbed waters and 54-89 m in the Kuroshio waters, respectively (Fig. 2c). The euphotic layer depths in the Oyashio waters were shallower than in the Perturbed waters and the Kuroshio waters (U-test, Perturbed waters $U=0$, $p<0.05$; Kuroshio waters $U=0$, $p<0.05$) and no significant difference was found between the Perturbed and the Kuroshio waters (U-test, $U=3.5$, $p>0.5$). The euphotic layer depths in these three water masses were deeper than the mixed layer depths (U-test, $U=0$, $p<0.05$).

The mean temperature within the upper mixed layer was 14.2, 22.8 and 27.7 °C in the Oyashio, Perturbed and Kuroshio waters, respectively (Fig. 2a). The temperature within the upper mixed layer increased toward the south. The mean salinity within the upper mixed layer was 32.51, 33.24 and 34.18 in the Oyashio, Perturbed and Kuroshio waters, respectively (Fig. 2b). Like temperature, salinity within the upper mixed layer

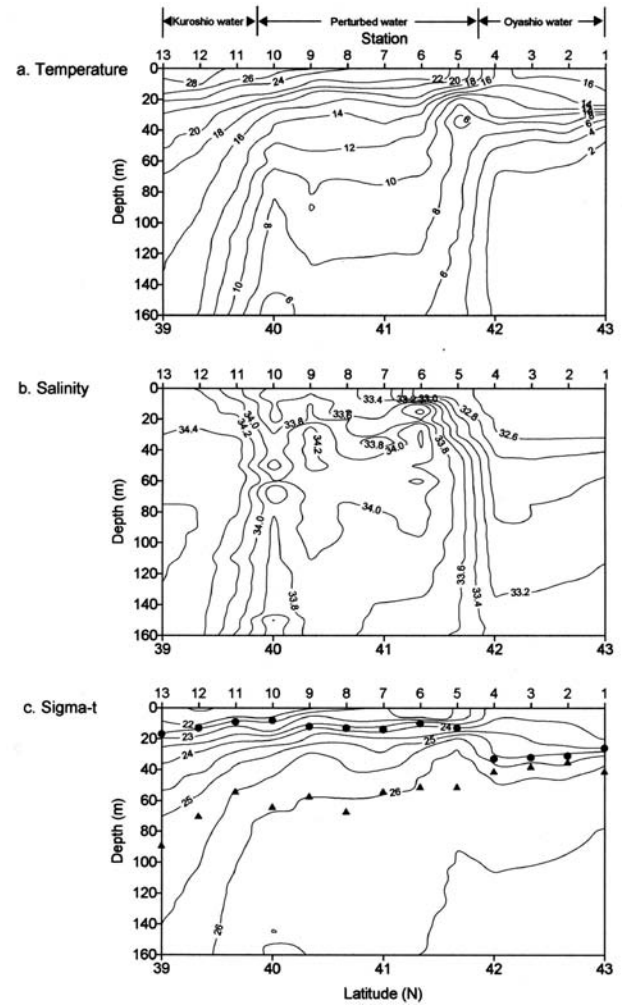


Fig. 2. Spatial variations in (a) temperature (°C), (b) salinity and (c) sigma-t from the Oyashio waters to the Kuroshio waters. Solid circles and solid triangles in (c) sigma-t show the pycnocline and the euphotic layer depth (1 % light level)

also increased toward the south. Salinity maxima (>34.0) can be seen at 40-80 m depth in the Perturbed waters.

The nitrate+nitrite concentrations within the upper mixed layer were more than 1.0 μM in the Oyashio waters and less than 1.0 μM in the Perturbed and Kuroshio waters (Fig. 3a). The concentrations increased with depth in the three water masses (Fig. 3a). The depth of nitracline, determined as the depth of the maximum vertical gradient in nitrate+nitrite concentration, deepened from the Oyashio waters to the Kuroshio waters (Fig. 3a) and was found at 20 m in the Oyashio waters, whereas 20-40 and 30-50 m in the

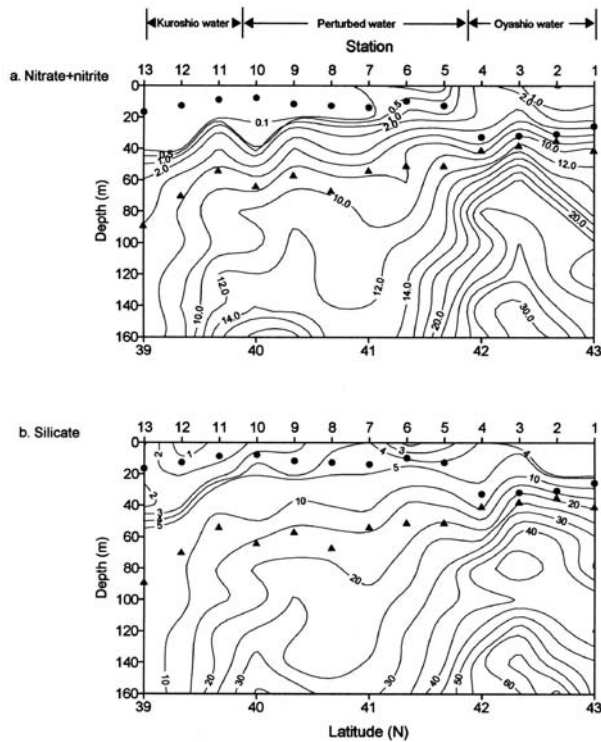


Fig. 3. Spatial variations in (a) nitrate+nitrite concentrations (μM) and (b) silicate concentrations (μM) from the Oyashio waters to the Kuroshio waters. Symbols as in Fig. 2.

Perturbed and Kuroshio waters, respectively. The depth of the nitracline did not correlate with the upper mixed layer depth (t -test, $p > 0.05$). The vertical gradient in nitrate+nitrite concentration tended to be greater in the frontal zone between the Oyashio and Perturbed waters, and between the Perturbed and Kuroshio waters than in the other regions. Silicate mimicked the nitrate+nitrite distribution (Fig. 3b). The concentrations of silicate within the upper mixed layer were found to be less than $5 \mu\text{M}$ at all stations.

The total chlorophyll *a* concentrations within the upper 100 m depth were more than $0.1 \mu\text{g l}^{-1}$ at almost all stations, while the concentrations were below 100 m depth were generally less than $0.1 \mu\text{g l}^{-1}$ (Fig. 4d). The total chlorophyll *a* concentrations within the upper 100 m were 0.04 – $0.93 \mu\text{g l}^{-1}$ in the Oyashio waters, whereas 0.03 – $1.07 \mu\text{g l}^{-1}$ and 0.05 – $1.30 \mu\text{g l}^{-1}$ in the Perturbed and Kuroshio waters, respectively. The subsurface chlorophyll *a* maximum (SCM) was observed at 10–20 m and 50–70 m layer in the Oyashio waters.

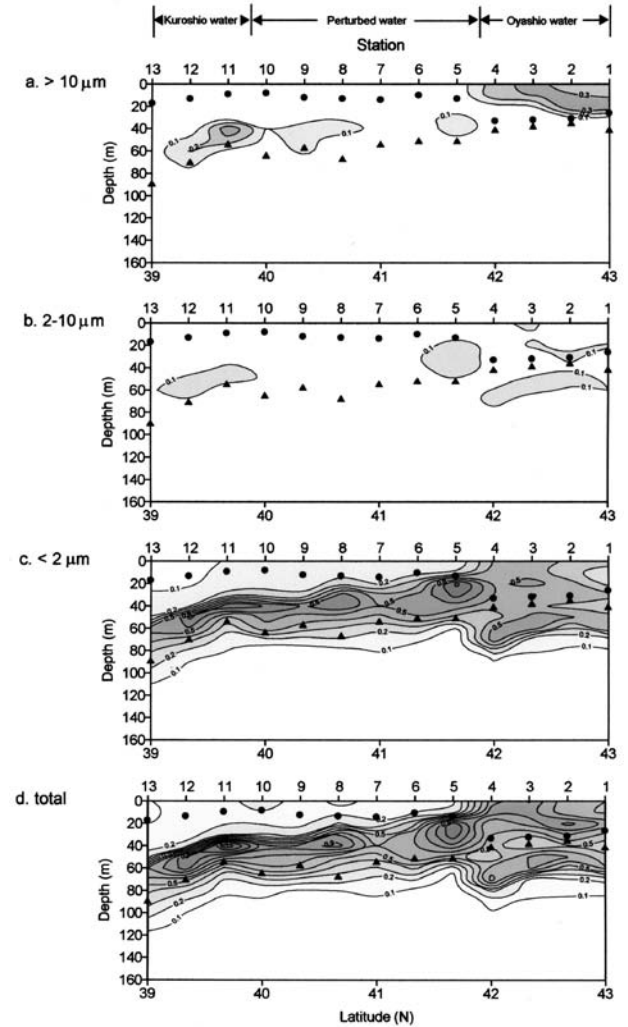


Fig. 4. Spatial variations in chlorophyll *a* concentrations ($\mu\text{g l}^{-1}$) of (a) $>10 \mu\text{m}$ fraction, (b) $2\text{--}10 \mu\text{m}$ fraction, (c) $<2 \mu\text{m}$ fraction and (d) total from the Oyashio waters to the Kuroshio waters. Symbols as in Fig. 2.

As far as we know, the two maximum layers of chlorophyll *a* concentration were observed for the first time in the Oyashio waters. On the other hand, the vertical distributions of the total chlorophyll *a* concentrations showed the SCM in the Perturbed waters (20–40 m) and the Kuroshio waters (40–60 m). No two maximum layer in chlorophyll *a* was found in the Perturbed and Kuroshio waters. The concentrations of the SCM tended to be higher relatively in the frontal zone (Stns 5 and 11) between Oyashio and Perturbed waters, and between Perturbed and Kuroshio waters.

The chlorophyll *a* concentrations of $>10 \mu\text{m}$

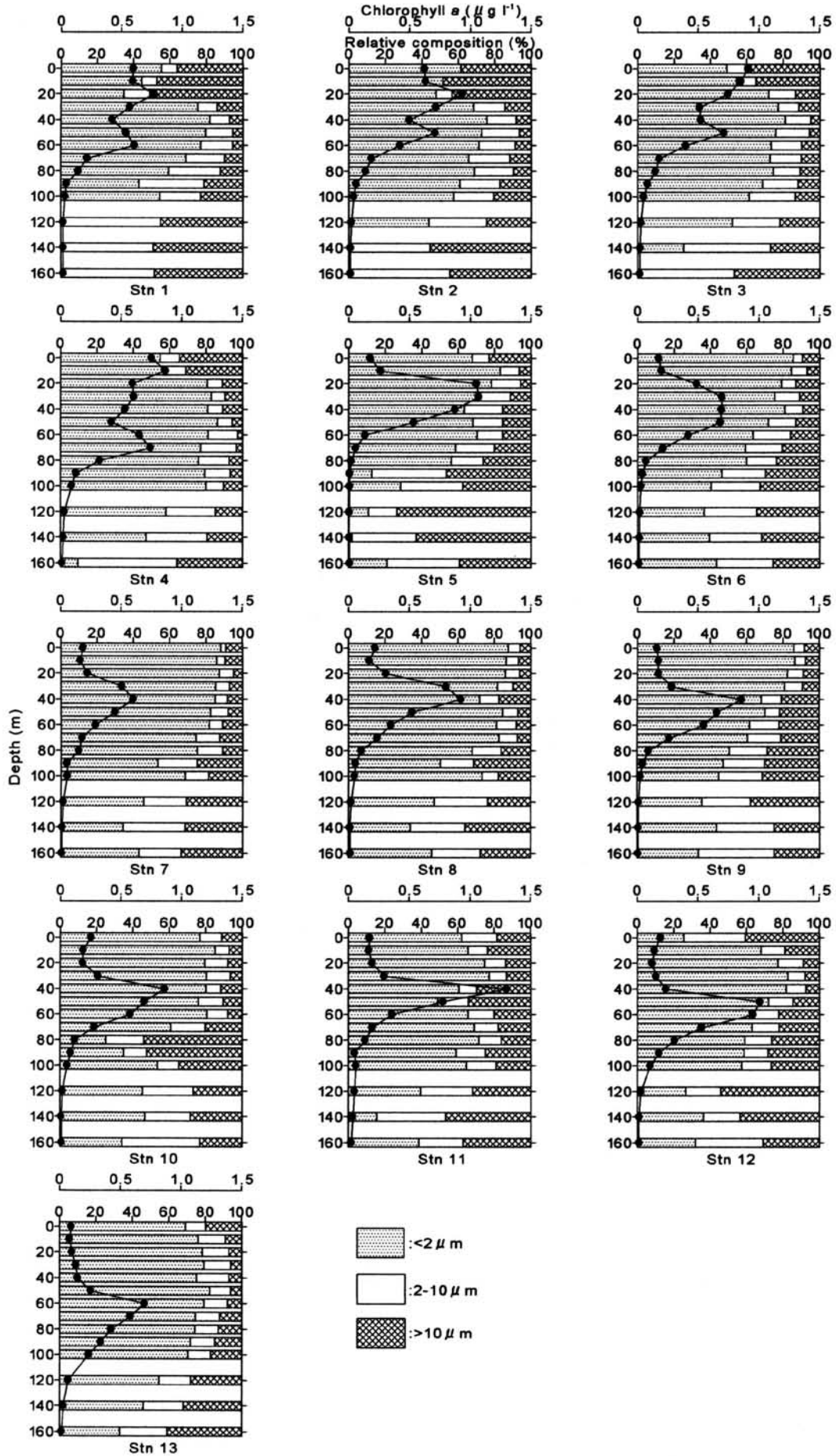


Fig. 5. Vertical profiles of total chlorophyll *a* concentration and its size composition.

fraction in the upper 100 m were 0.01-0.40 $\mu\text{g l}^{-1}$ in the Oyashio waters, 0.01-0.18 $\mu\text{g l}^{-1}$ in the Perturbed waters and 0.01-0.39 $\mu\text{g l}^{-1}$ in the Kuroshio waters (**Fig. 4a**). In the Oyashio waters, the $>10 \mu\text{m}$ fraction tended to be higher in the shallow SCM, whereas it was much lower in deep SCM. Less than 2 and 2-10 μm fraction were 0.02-0.57 $\mu\text{g l}^{-1}$ and 0.01-0.15 $\mu\text{g l}^{-1}$ in the Oyashio waters, 0.01-0.82 $\mu\text{g l}^{-1}$ and 0.01-0.20 $\mu\text{g l}^{-1}$ in the Perturbed waters and 0.03-0.79 $\mu\text{g l}^{-1}$ and 0.01-0.15 $\mu\text{g l}^{-1}$ in the Kuroshio waters, respectively (**Figs. 4b and 4c**). The vertical distributions of <2 and 2-10 μm fractions were higher in the subsurface layer. The concentrations of >10 , <2 and 2-10 μm fractions were found to be higher in the frontal zone (Stns 5 and 11) between the Oyashio waters and the Perturbed waters, and between the Perturbed waters and the Kuroshio waters.

Vertical profiles of the relative compositions in the >10 , 2-10 and $<2 \mu\text{m}$ fraction at each station are shown in Figure 5. The relative percentage of $>10 \mu\text{m}$ fraction within the euphotic layer was 7-51% in the Oyashio waters, 5-23% in the Perturbed waters and 6-41% in the Kuroshio waters. The $>10 \mu\text{m}$ fraction in the Oyashio waters was significantly higher than those of the Perturbed waters and the Kuroshio waters (U-test, Perturbed waters $U=92$, $p<0.05$; Kuroshio waters $U=114$, $p<0.05$). The $>10 \mu\text{m}$ fraction of the shallow SCM at Stns 1 and 2 was predominant. The $>10 \mu\text{m}$ fraction of the deep SCM in the Oyashio waters was less than 10%. The relative percentage of the <2 and 2-10 μm fraction within the euphotic layer was 35-83% and 1-17% in the Oyashio, 63-88% and 3-21% in the Perturbed and 25-83% and 10-34% in the Kuroshio waters, respectively. In general, the relative percentage of the $<2 \mu\text{m}$ fraction was the largest and accounted for an average of 50% of the total chlorophyll *a* concentration at almost stations. The percentage of the $>10 \mu\text{m}$ fraction within the euphotic layer was about three times greater than the 2-10 μm fraction in the Oyashio waters and was approximately equal to the 2-10 μm fraction in the Perturbed waters and the Kuroshio waters. The vertical distribution of the size fraction did not

significantly vary within the euphotic layer in the three water masses and the frontal zone, though the chlorophyll *a* concentrations much varied.

4. Discussion

The SCM usually tends to be associated with the nitracline, thermocline and pycnocline^{23,24}. The occurrence of SCM was observed from the Oyashio waters to the Kuroshio waters (**Fig. 4d**). In the Perturbed and Kuroshio waters, the depth of the SCM was deeper than the upper mixed layer depth, and approximately equal with nitracline and 1% light depth (**Fig. 2c and 4d**). This result coincides with the previous reports²⁵. On the other hand, two layers of the SCM were observed in the Oyashio waters (**Figs. 4d and 5**). As far as we know, this is the first observation in the Oyashio waters. The depths of the shallow SCM corresponded with the nitracline and pycnocline. However, the deep SCM was located below the depths of mixed layer, 1% light and nitracline (**Figs. 2c, 3a and 4d**). The depths of deep SCM were equivalent to about 0.2% light level of surface PAR irradiance and considerably low light condition. Furuya²⁶ reported that the SCM developed at deep layers below 100m where the light intensity was 0.2 to 0.3% level. Therefore, the occurrence of the deep SCM may have been due to an enhanced in situ growth rather than to an accumulation of sinking cells²⁷. It would be possible to evaluate such features using primary productivity and phytoplankton species data to understand the occurrence of deep SCM in the Oyashio waters.

The depths of the nitracline were located at approximately equal depths of the shallow SCM in the Oyashio waters and the SCM in the Perturbed and Kuroshio waters (**Figs. 3a and 4d**). The nutrient concentrations increased immediately below the SCM (**Fig. 3**). This implies that the phytoplankton in the SCM immediately takes up nutrient diffused into the impoverished upper layer²⁸. Consequently, it is likely that the active nutrient uptake plays an important role in the maintenance and development of the SCM²⁹.

The concentrations of the SCM tended to be

relatively higher in the frontal zone (Stns 5 and 11) between the Oyashio and Perturbed waters, and between the Perturbed and Kuroshio waters (**Fig. 4d**). The ambient nutrient concentrations in the frontal zone were not higher than the other regions. However, the vertical gradient in nitrate+nitrite concentration tended to be greater in the frontal zone than in the other regions (**Fig. 3a**). Consequently, the magnitude of the SCM is likely to be affected by the upward nutrient flux rather than the ambient concentrations²⁷⁾.

Large-sized phytoplankton is thought to sink more rapidly from the euphotic layer than small-sized phytoplankton⁷⁾. In the Perturbed and Kuroshio waters, the upper mixed layer was much shallower than the euphotic layer and the nitrate+nitrite concentrations were very low ($<0.1 \mu\text{M}$) (**Fig. 3a**). The relative percentage of the $<2 \mu\text{m}$ fraction accounted for an average of 50% of the total chlorophyll *a* concentration at the SCM of the Perturbed and Kuroshio waters and the deep SCM of the Oyashio waters (**Fig. 5**). The depths of the SCM were equivalent to 4-6% light level in the Perturbed waters and the Kuroshio waters and the deep SCM in the Oyashio waters were about 0.2% light level of surface PAR irradiance. Further, the SCM occurred below the pycnocline. The small-sized phytoplankton can absorb efficiently low levels of light³⁰⁾. Ruiz *et al.*³¹⁾ indicated a higher proportion of small cells in the SCM as a result of favorable light-limited growth conditions. Moreover, the small-sized cells characteristically have low settling velocities³²⁾. Since the SCM was positioned below the upper mixed layer in the Perturbed and Kuroshio waters, most of the $>10 \mu\text{m}$ fraction in the SCM may have sedimented below the euphotic layer. Thus, the relatively high proportion of the $<2 \mu\text{m}$ fraction in the SCM could be due to photoadaptation, low settling velocities of the small-sized phytoplankton and the sinking loss of the $>10 \mu\text{m}$ fraction.

The shallow SCM in the Oyashio waters was dominated by the $>10 \mu\text{m}$ fraction (**Fig. 5**). The nitrate+nitrite concentrations in the Oyashio waters were more than $1.0 \mu\text{M}$ within the upper mixed layer. Oyashio waters are strongly

influenced by Okhotsk Sea²¹⁾. The nitrate+nitrite concentrations at the surface in the Okhotsk Sea are approximately $10 \mu\text{M}$ ³³⁾. Consequently, the concentrations of $>1.0 \mu\text{M}$ in the Oyashio waters may be derived from the Okhotsk Sea. Nishioka *et al.*³⁴⁾ indicated that the iron-rich waters in the Okhotsk Sea are supplied to the surface waters in the Oyashio waters. Therefore, it seems that the large fraction of the $>10 \mu\text{m}$ in the shallow SCM of the Oyashio waters is likely due to not only nitracline and nitrate+nitrite concentration of $>1.0 \mu\text{M}$ but also high iron bioavailability. Further, since the shallow SCM was located above the pycnocline, the sinking loss of the $>10 \mu\text{m}$ fraction may have been reduced.

In spring, remarkably high chlorophyll *a* concentrations, probably due to large diatom blooms, have been reported in the surface layer of the Oyashio regions^{35,36)}. As nutrients become exhausted in the surface layers, however, the depth of the maxima in the phytoplankton biomass deepens. The latter conditions occur in stratified water columns during summer. Therefore, we may have observed the phenomenon of the transition period that chlorophyll maximum layer deepens from shallow depth to deep depth. It will be necessary in the future to accumulate more data on the vertical distribution of the size-fractionated chlorophyll *a* concentration in various seasons in order to clarify the two maximum layer of chlorophyll *a* concentration in the Oyashio waters.

To date, global primary production has been estimated by ocean color sensors (e.g. Sea-viewing Wide Field-of view Sensor, SeaWiFS) combined with satellite derived surface chlorophyll data. The models estimating the chlorophyll *a* biomass integrated in the water column have been considered with only single SCM layer^{37,38)}. If the traditional model on a single SCM from satellite is used for estimation of water-column primary production, the primary production may be underestimated in the Oyashio waters.

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