Size-fractionated chlorophyll *a* and primary productivity in the offshore Oyashio waters in July 1992

Akihiro Shiomoto* and Shinji Hashimoto*

Abstract: Size–fractionated (<2, 2–10 and 10–200 μ m) chlorophyll a (Chl a) concentration and primary productivity were determined at the 100 (surface), 30, 10 and 1% light depths at four stations in the offshore Oyashio waters in July 1992. The share of the <2 or 2–10 μ m fraction was the highest in the total Chl a concentration and primary productivity at all the stations and light depths, except at the 10% light depth at one station. Each of the <2 and 2–10 μ m fractions accounted for 40–50% of the total on average, and the 10–200 μ m fraction accounted for 10–15% of the total on average. The 10–200 μ m fraction accounted for 45% of the total Chl a concentration and primary productivity at the 10% light depth at the one station. Such exception can be attributed to the availability of higher concentration of nitrogenous nutrients (mostly nitrate) and absence of light limited condition for phytoplankton of the 10–200 μ m fraction. We suggest that, in the offshore Oyashio waters in summer, small-sized phytoplankton generally contribute to phytoplankton biomass and productivity, and large-sized phytoplankton contribute likewise when high concentration of nitrate is available at depths with enough light intensity for their growth.

Key words: chlorophyll a, primary productivity, size fractionation, offshore Oyashio waters, nitrate availability, light intensity

1. Introduction

Many shipboard studies have been carried out to determine the total and size-fractionated chlorophyll a (Chl a) concentration and primary productivity in the eastern region of the subarctic North Pacific, the Alaskan Gyre (e.g., BOOTH et al., 1993; Welschmeyer et al., 1993; BOYD and HARRISON, 1999). The results show that small-sized ($\langle 5 \mu m \rangle$) phytoplankton generally contribute to total Chl a and primary productivity. In the Oyashio waters located in the western region of the subarctic North Pacific, total Chl a and primary productivity have been measured in many shipboard observations (e.g., Shiomoto et al., 1994; Kasai et al., 1998; Shiomoto, 2000). However, there are a few measurements of size-fractionated Chl a concentration (MAITA and ODATE, 1988; ODATE and Maita, 1988/89; Taguchi et al., 1992; Shiomoto et al., 1994; Odate, 1996). Size-fractionated primary productivity was reported only in the coastal region in Funka Bay located in the southwestern Hokkaido (MAITA and ODATE, 1988). Results from these studies in the Oyashio waters showed that small-sized phytoplankton ($<2 \mu$ m) contributed significantly to phytoplankton biomass and productivity. The dominant species and size of the phytoplankton have much influence on relationship between different components of marine ecosystem (e.g., Parsons et al., 1984b; STOCKNER and ANTIA, 1986). Hence, it is necessary to investigate further the relative contribution of phytoplankton of different size fractions, for the progress of ecosystem studies in the Ovashio waters.

Under the present investigation, we measured the size-fractionated Chl a and primary productivity in the offshore Oyashio water (salinity \leq 33.4; OHTANI, 1971; KAWAI, 1972) in

^{*} National Research Institute of Far Seas Fisheries, 7–1, Orido 5–chome, Shimizu–shi, Shizuoka, 424–8633 Japan

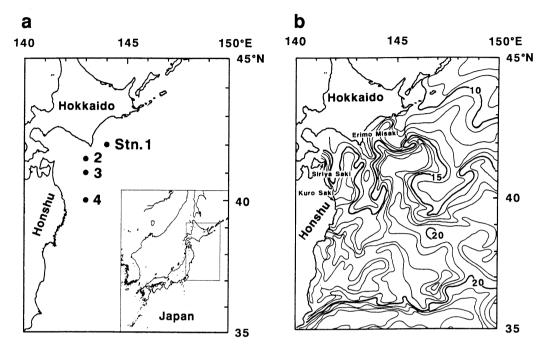


Fig. 1. a: Location of sampling stations in the offshore Oyashio waters, July 1992; b: horizontal distribution of the surface temperature (°C) for 6-10 July 1992 (Japan Fisheries Information Service Center, 1992).

summer. We suggest that small-sized phytoplankton generally contribute to phytoplankton biomass and productivity, and large sized phytoplankton contribute likewise when high concentration of nitrate is available at depths with enough light intensity for their growth.

2. Materials and Methods

This study was conducted during a cruise of the R/V *Shunyo Maru* of the National Research Institute of Far Seas Fisheries in the offshore Oyashio waters in 7–12 July 1992 (Fig. 1a). Seawater samples were collected between 0730 and 0800 hours from four depths corresponding to 100, 30, 10 and 1% light depths using an acid cleaned 30–1 Go-Flo sampler hung on a stainless steel wire. The light depths were determined 30 minutes before sample collection with a cosine response quantum sensor (LI-COR 192SA). The water samples were then sieved through a 200 μ m mesh screen to remove large zooplankton.

The total and size-fractionated Chl a concen-

trations were measured by fluorometry (PARsons et al., 1984a). Total Chl a was determined in samples (0.5-1) filtered through 47 mm Whatman GF/F filters. Size-fractionated Chl a was measured in samples (0.5-1) obtained as follows: seawater samples were filtered through 2 and 10μ m pore size Nuclepore filters and the filtrates were then refiltered onto 47 mm Whatman GF/F filters (<2 and $<10 \,\mu$ m fractions). The filters were then stored frozen at -20° C until analysis ashore. Pigments were extracted in 90% acetone and the fluorescence was measured with a Hitachi F-2000 fluorophotometer. Calibration of the fluorophotometer was performed with commercially prepared Chl a from Wako Pure Chemical Industries, Ltd. (Tokyo). Chl a concentrations for the 2–10 and 10–200 μ m fractions were obtained from the differences between the \leq 10 and \leq 2 μ m fractions and between the total and <10 μ m fraction, respectively.

Total and size – fractionated primary productivity was determined by the ¹³C method

(Hama et al., 1983). The primary productivity experiments were started within 1 hour after sampling. The seawater samples (2-1) were dispensed into two acid-cleaned 2-1 polycarbonate bottles and enriched by the addition (1-ml) of NaH¹³CO₃ (99 atom% ¹³C; Shoko Co., Ltd., Tokyo) to about 10% of the total inorganic carbon in ambient water. Incubations were conducted by the in situ method for 3-3.5 hours. The fractionation of the samples into size classes was carried out after incubation. Immediately after the incubation, an aliquot of 0.5-1 of the seawater samples was filtered directly through precombusted (450°C for 4 hours) 47mm Whatman GF/F filters (total). Aliquots of 0.5-1 of the remaining seawater samples were filtered through Neclepore filters with pore sizes of 2 and 10 μ m. The filtrates were refiltered onto 47 mm Whatman GF/F filters (\leq 2 and \leq 10 μ m fractions) and the particulate matter on the Whatman GF/F filters was rinsed with prefiltered seawater. The filters were then stored frozen at -20° C until analysis ashore. They were treated with HCl fumes for 4 hours to remove inorganic carbon and completely dried in a vacuum desiccator. The isotopic ratios of ¹³C to ¹²C and particulate organic carbon were determined with a mass spectrometer (ANCA SL, PDZ Europa Ltd.). Total inorganic carbon in 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). Size-fractionated primary productivity was estimated in the same manner as the Chl a concentration. Primary productivity obtained in the two bottles was averaged.

Vertical profiles of temperature and salinity were measured using a Neil Brown CTD Mark II. Seawater samples for determing nutrient concentrations were stored frozen until analysis ashore. The concentrations were determined using a Bran and Luebbe Auto Analyser Traccs 800.

3. Results

3.1 General oceanographic conditions

Based on horizontal distribution of the surface temperature in early July 1992 (Fig. 1b), the coastal and offshore regions of the eastern

Hokkaido through Erimo Misaki were occupied by the first Oyashio Intrusion, which was identified as 14°C at the surface, and the southern edge of the water was observed off Sanriku. The extension of the Tsugaru Warm Current, which was identified as 16–17°C at the surface, was observed off Siriya Saki through Kuro Saki.

Vertical profiles of temperature, salinity and density (σ_t) in the upper 100 m are shown in Fig. 2. The temperature was 15–17°C at the surface and decreased with depth at every station. Salinity in the upper 50 m at Stns. 1 and 4. in the upper 30 m at Stn. 2, and in the upper 20 m at Stn. 3 was less than 33.4. The depths of 50 m at Stns. 1 and 4 were located below the depths of the euphotic zone (1% light depth). The depths of 30 m at Stn. 2 and 20 m at Stn. 3 were located below the depths of the 10% light depth. Accordingly, the water mass within the euphotic zone at Stns. 1 and 4 and in the upper 10% light depth at Stns. 2 and 3, belonged to the Oyashio water. All stations were noticed to be located in the first Oyashio Intrusion. Moreover, salinity exceeding 33.5 was observed deeper than 30 m at Stn. 2 and at 20-30 m at Stn. 3. Judging from the surface temperature distribution (Fig. 1b) and salinity, the bottom of the euphotic zone at Stns. 2 and 3 was possibly affected by the Tsugaru Warm Current (salinity >33.7; Ohtani, 1971; Hanawa and MITSUDERA, 1987). The σ_t was almost constant in the top 10 m and increased with depth below 10 m at Stns. 1 and 4, whereas the $\sigma_{\rm t}$ increased with depth at Stns. 2 and 3. The zone where the $\sigma_{\rm t}$ changed markedly with depth, that is, the pycnocline, was between 10 and 30 m at Stns. 1 and 4, and between 0 and 20 m at Stns. 2 and 3.

3.2 Nutrients

The vertical profiles of nutrient concentrations in the upper 1% light depth are shown in Fig. 3. Nitrite + nitrate (NO₂ + NO₃; mostly nitrate) was nearly exhausted in the upper 30 or 10% light depth at Stns. 2, 3 and 4. Nitrite + nitrate concentrations were very low in the upper 30% light depth at Stn. 1, but it was not exhausted. The concentrations increased rapidly from below the 30% light depth at Stns. 1 and 4, and from below the 10% light depth at

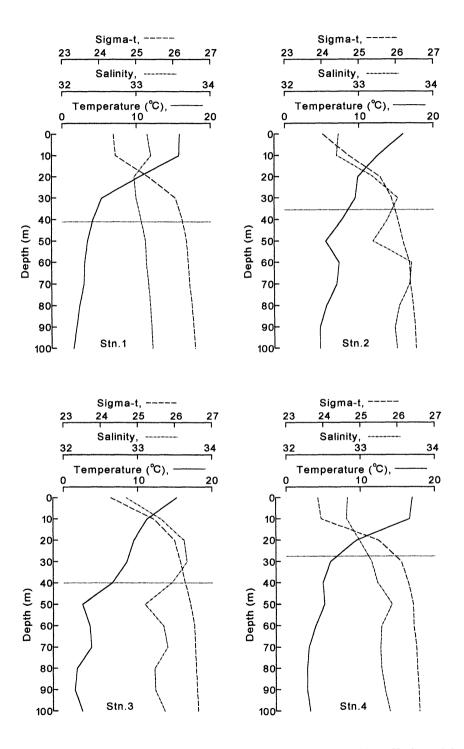


Fig. 2. Vertical profiles of temperature, salinity and sigma-t in the upper 100m. Horizontal dotted lines indicate the bottom of the euphotic zone (1% light depth).

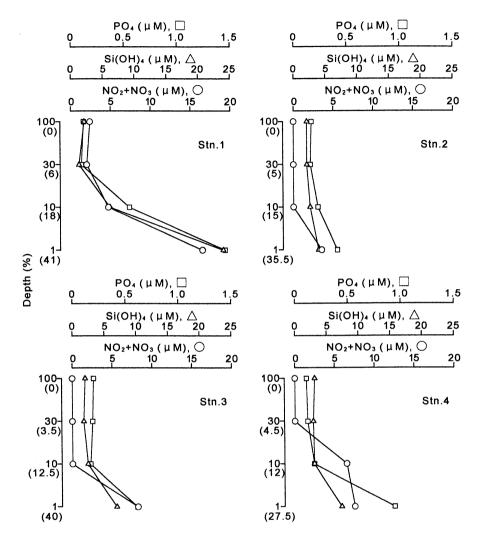


Fig. 3. Vertical profiles of nitrite + nitrate (NO₂ + NO₃), silicate [Si(OH)₄] and phosphate (PO₄) concentrations in the upper 1% light depth. Depths in meters are given in the parentheses.

Stns. 2 and 3. The concentrations below the 1% light depth (30–40 m) were generally between 10 and $20\,\mu$ M in the upper 100 m at Stns. 1, 3 and 4 and between 5 and $10\,\mu$ M at Stn. 2 (not shown). Almost the same trends were observed in vertical profiles of silicate [Si(OH)₄] and phosphate (PO₄) concentrations, though neither nutrient was exhausted even in the upper 10% light depth.

3.3 Chlorophyll a

Total Chl a concentrations were between 0.2

and $0.4\,\mu\,\mathrm{g}$ l⁻¹ at the 100 and 30% light depths, and between 0.5 and $1.5\,\mu\,\mathrm{g}$ l⁻¹ at the 10 and 1% light depths, except the 1% light depth at Stn. 3 (Fig. 4a). Total Chl a concentrations tended to be higher at the 10 and 1% light depths than at the 100 and 30 % light depths. Similar trend was found in the Chl a concentrations of each size fraction.

The relative size composition of Chl a concentration is shown in Fig. 4b. The <2 or $2-10 \mu$ m fraction was the most abundant except at the 10% light depth at Stn. 4, accounting for

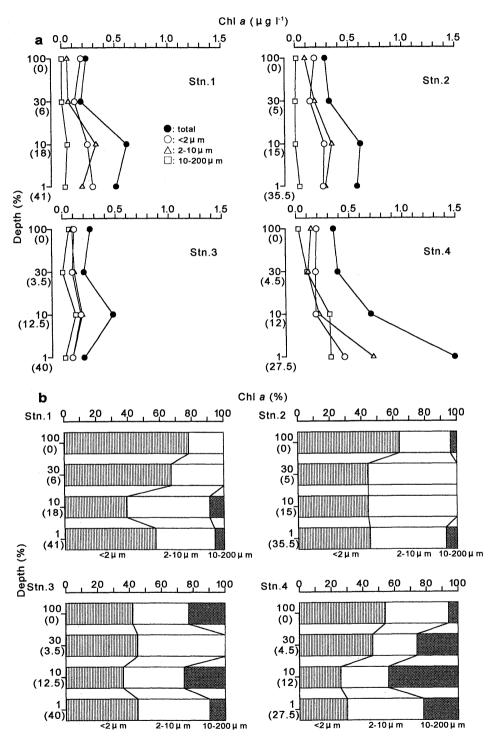


Fig. 4. a: Vertical profiles of total and size-fractionated chlorophyll a (Chl a) concentrations in the upper 1% light depth; b: relative size composition of chlorophyll a concentration in the upper 1% light depth. Depths in meters are given in the parentheses.

38–78% of the total. The sum of the two fractions accounted for 74–100% of the total, except at the 10% light depth at Stn. 4. The 10–200 μ m fraction was the most abundant at the 10% light depth at Stn. 4, accounting for 44% of the total. Mean \pm SD of Chl a concentration of the <2, 2–10 and 10–200 μ m fractions were 48 \pm 14% (n=16), 41 \pm 11% (n=16) and 11 \pm 13% (n=16), respectively, using all of the data.

3.4 Primary productivity

Total primary productivity was between 0.4 and $4.0 \,\mu$ g C l⁻¹ h⁻¹ (Fig. 5a). Maximum productivity was observed at the 10% light depth at Stns. 1 and 4, and at the 30% light depth at Stn. 3. In contrast, productivity was nearly constant in the upper 10% light depth at Stn. 2. Productivity rapidly decreased at the 1% light depth at Stns. 1 and 2. Verical profiles similar to total primary productivity were found in the primary productivity of the 10–200 μ m fraction at Stns. 1, 2 and 4. Distinct increases in primary productivity were found in this fraction at the 10% light depth at Stns. 1 and 4. Primary productivity of the $10-200 \,\mu$ m fraction was almost equal to or higher than those of the other fractions at the 10% light depth at the two stations.

The relative size composition of primary productivity is shown in Fig. 5b. The <2 or 2–10 μ m fraction was the most abundant except at the 10% light depth at Stn. 4, accounting for 37–85% of the total. The sum of the two fractions accounted for 68–100% of the total, except at the 10% light depth at Stn. 4. The 10–200 μ m fraction was the most abundant at the 10% light depth at Stn. 4, accounting for 45% of the total. The same result as Chl a was found in primary productivity. Mean \pm SD of primary productivity of the <2, 2–10 and 10–200 μ m fractions were 38 \pm 16% (n=15), 47 \pm 17% (n=15) and 15 \pm 13% (n=15), respectively, using all of the data.

4. Discussion

Our results show that the share of the <2 or 2–10 μ m fraction was highest in the total Chl a concentration and primary productivity at all the stations and light depths, except at the 10% light depth at Stn. 4. Our results furthermore show that the sum of the two fractions

accounted for more than about 70% of the total Chl *a* concentration and primary productivity. Thus, we noticed that small-sized phytoplankton generally contribute significantly to phytoplankton biomass and productivity. This is consistent with the limited information available regarding the size composition of the phytoplankton biomass and productivity in the Oyashio waters in summer (MAITA and ODATE, 1988; TAGUCHI *et al.*, 1992; ODATE, 1996).

At the 10% light depth at Stn. 4, the large sized phytoplankton contributed more to the phytoplankton biomass and productivity compared to smaller fractions. ODATE and MAITA (1988/89) showed that the variation in Ch1 a concentration of the $>10 \mu$ m fraction depended on that in cell density of the $> 10 \,\mu$ m sized diatoms in the northwestern Pacific. According to Shiomoto et al. (1994, 1996), the cell density of diatoms was more abundant in the case which the $>10 \,\mu$ m fraction dominated the Chl a concentration, compared with the case which the $<10 \,\mu$ m fraction dominated the Chl a concentration in the northwestern Pacific. It is thus highly possible that the high contribution of large-sized phytoplankton to the phytoplankton biomass and productivity at the 10% light depth at Stn. 4 reflected prevalence of large-sized diatoms. What are the factors then that lead to the high contribution of the large-sized phytoplankton (diatoms) to the biomass and productivity?

Large-sized phytoplankton prefer higher nutrient concentrations than small-sized phytoplankton (Parsons and Takahashi, 1973; MALONE, 1980). The concentrations of nitrogenous nutrients (mostly nitrate) were markedly low in the euphotic zone (in the upper 1% light depth) at all stations, and they were nearly exhausted in the upper 30 or 10% light depth (Fig. 3). One possibility, therefore, is that availability of higher concentration of nitrate played an important role leading to the high contribution of large-sized phytoplankton to phytoplankton biomass and productivity at the 10% light depth at Stn. 4. Such assumption can further be supported by the following observation.

Chl a-specific primary productivity is an index of the phytoplankton growth rate (LALLI

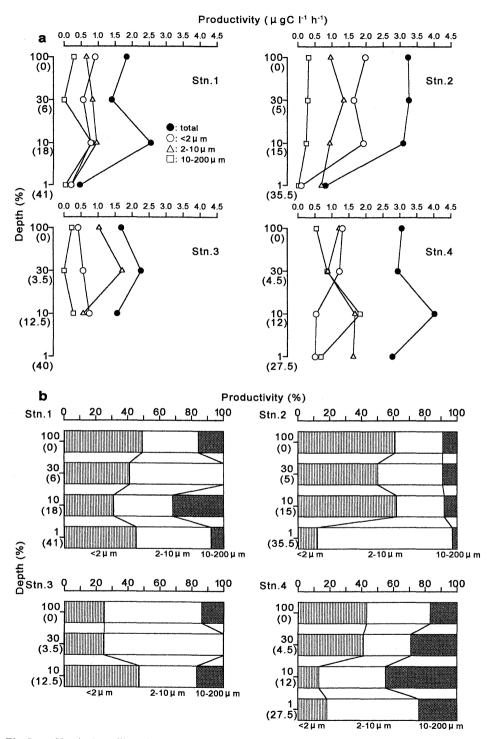


Fig. 5. a: Vertical profiles of total and size-fractionated primary productivity in the upper 1% light depth; b: relative size composition of primary productivity in the upper 1% light depth. Depths in meters are given in the parentheses.

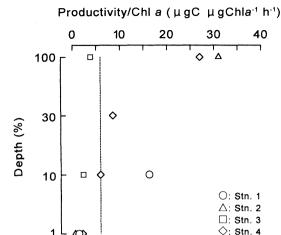


Fig. 6. Chl *a*-specific primary productivity (Productivity/Chl *a*) of the 10–200 μ m fraction at the 100, 30, 10 and 1% light depths at Stns. 1, 2, 3 and 4. The Chl *a*-specific primary productivity could not be calculated at the 100 and 30% light depths of Stn. 1, at the 30 and 10% light depths of Stn. 2 and at the 30% light depth of Stn. 3, because Chl *a* concentartions were almost equal to 0 μ g l⁻¹. The vertical broken line indicates Productivity/Chl *a* at the 10% light depth of Stn. 4.

and Parsons, 1993). The Chl a-specific primary productivity of the $10-200~\mu$ m fraction was markedly lower at the 1% light depth at all stations (Fig. 6), indicating that large-sized phytoplankton growth was limited by light intensity at the 1% light depth but not in the upper 10% light depth. It is thus unlikely that the large-sized phytoplankton contributed to the phytoplankton biomass and productivity at the 1% light depth even if plentiful nitrate was supplied to the light depth.

Ambient nutrient concentration is dependent on the balance between supply and consumption. Total primary productivity at the 10% light depth at Stn. 4 ($4.0\,\mu\,\mathrm{g}$ C l⁻¹ h⁻¹) was higher than the remaining eleven discrete values (1.4– $3.3\,\mu\,\mathrm{g}$ Cl⁻¹ h⁻¹) in the upper 10% light depth at all four stations (Fig. 5). This implis that relatively much nitrate was consumed at the 10% light depth at Stn. 4 compared with the rest. Likewise, ambient nitrate concentration at the 10% light depth at Stn. 4 ($6.5\,\mu$ M) was higher than the remaining eleven values (less than $4.7\,\mu$ M) in the upper 10% light depth

at all stations (Fig. 3). It is thus highly possible that higher concentration of nitrate was available at the 10% light depth at Stn. 4 compared with the rest.

The Chl a-specific primary productivity of the $10-200\,\mu\mathrm{m}$ fraction was $5.9\,\mu\mathrm{gC}\,\mu\mathrm{gChl}$ a^{-1} h⁻¹ at the 10% light depth at Stn. 4 where large sized phytoplankton mostly contributed to the total phytoplankton biomass and productivity. Values exceeding 5.9 μ gC μ gChl a^{-1} h⁻¹ were frequently observed in the upper 10% light depth (Fig. 6), indicating that large-sized phytoplankton have the capacity to contribute to the phytoplankton biomass and productivity in the upper 10% light depth. We therefore suggest that, in the offshore Oyashio waters in summer, small-sized phytoplankton generally contribute to the phytoplankton biomass and productivity, and large-sized phytoplankton contribute likewise when high concentration of nitrate is available at depths with enough light intensity for their growth.

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