

Primary production and contribution of "new" production in the warm-core ring and the cold streamer off Sanriku in May 1990

Akihiko SHIOMOTO*, Katsuyuki SASAKI** and Toru SHIMODA**

Abstract: The primary productivity in the warm-core ring ($0.15\text{--}6.89\text{ mgC m}^{-3}\text{ h}^{-1}$) and cold streamer ($2.85\text{--}7.91\text{ mgC m}^{-3}\text{ h}^{-1}$) were roughly equal, and the values were nearly constant shallower than the 10% light level. Daily primary production was estimated to be $930\text{ mgC m}^{-2}\text{ d}^{-1}$ in the warm-core ring and $811\text{ mgC m}^{-2}\text{ d}^{-1}$ in the cold streamer. Chlorophyll *a* concentrations within the euphotic zone were several times higher in the cold streamer ($1.93\text{--}4.23\text{ mg m}^{-3}$) than in the warm-core ring ($0.76\text{--}1.11\text{ mg m}^{-3}$). In contrast, primary productivity per unit chlorophyll *a* was about two times higher in the warm-core ring ($0.15\text{--}7.41\text{ mgC mg Chl. }a^{-1}\text{ h}^{-1}$) than in the cold streamer ($0.63\text{--}3.18\text{ mgC mg Chl. }a^{-1}\text{ h}^{-1}$). The difference was probably because of the differences in size and/or species distributions of phytoplankton. The contribution of "new" production to total production at the surface was estimated to be 43% in the warm-core ring and 31% in the cold streamer, by using maximum uptake rates of nitrate and ammonium. Comparison of the results obtained in this study with the results previously obtained suggested the importance of nutrient flux from deeper layers in regulating primary productivity in the warm-core ring off Sanriku.

1. Introduction

Many observations have been made to elucidate the physical, chemical and biological features in the Kuroshio warm-core rings (e.g. TOMOSADA, 1986; RI and SUGIMOTO, 1989; YASUDA *et al.*, 1992; HAMA, 1992; MATSUO *et al.*, 1993; SASAKI, 1993; YOKOUCHI *et al.*, 1993; CHIANG *et al.*, 1994). Only HAMA (1992) and MATSUO *et al.* (1993), however, reported primary productivity in the warm-core rings and adjacent waters. Outlining HAMA'S results in September 1987, the depth-integrated primary productivity at the warm-core center was about $900\text{ mgC m}^{-2}\text{ d}^{-1}$ and increased to $1,200\text{ mgC m}^{-2}\text{ d}^{-1}$ after a storm. The values at the center were roughly equal to the values in the Oyashio water, whereas the value in the warm streamer, $480\text{ mgC m}^{-2}\text{ d}^{-1}$, was about half that of the center.

The depth-integrated primary productivity in the warm streamer was also measured to be $296\text{ mgC m}^{-2}\text{ d}^{-1}$ in October 1991 by MATSUO *et al.*

Primary production is roughly divided into "new" production and "regenerated" production (DUGDALE and GOERING, 1967). It is essential to estimate the contribution of "new" production to total production to determine the flow of materials to higher trophic levels in the marine ecosystem. The contribution is generally more than 30% in eutrophic region and mostly less than 10% in oligotrophic region (reviewed by SHIOMOTO *et al.*, 1994b). The values obtained in the warm-core rings in the Gulf Stream were roughly within the range of the values in eutrophic region (MCCARTHY and NEVIS, 1986). The contribution, however, was estimated once to be 11% in the warm streamer off Sanriku in October 1991 by MATSUO *et al.* (1993).

In late May 1990, a warm-core ring was observed off Kinka-zan and a cold streamer was observed dragged into the warm-core ring from the east side (Fig. 1a, b). According to

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

**National Research Institute of Fisheries Science, 12-4, Fukuura 2-chome, Kanazawa-ku, Yokohama-shi, Kanagawa, 236 Japan

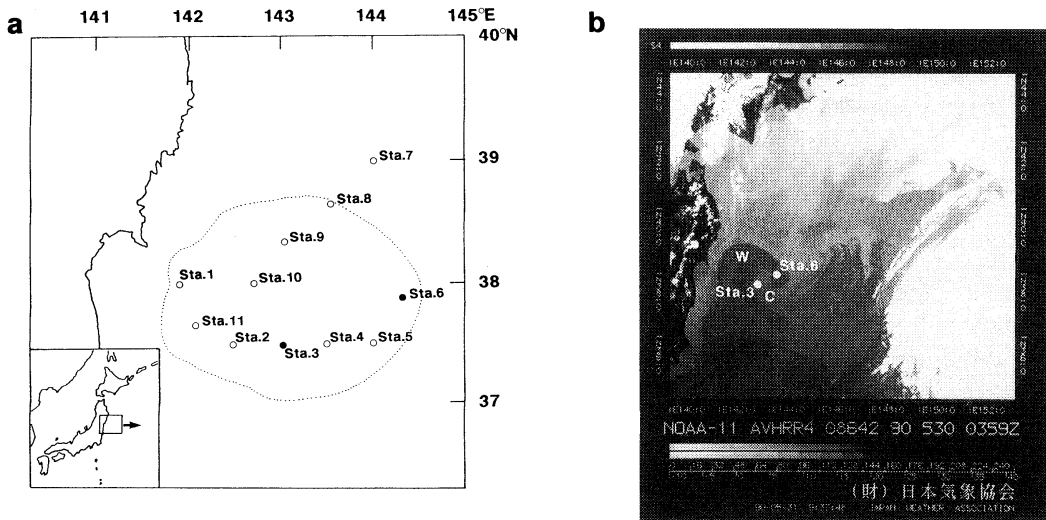


Fig. 1. a: Location of sampling stations off Sanriku in May 1990. Dotted line shows a warm-core ring in May 1990 (YOKOUCHI *et al.*, 1993). Primary productivity and contribution of "new" production to it were measured at solid circles and only CTD casts were done at open circles.
b: NOAA-11 AVHRR infrared image east of Japan on 30 May 1990. W and C shows a warm-core ring and a cold streamer, respectively.

YOKOUCHI *et al.* (1993), the warm-core ring existed from May to September 1990 off Kinkazan. We measured primary productivity and the contribution of "new" production to total production in the warm-core ring and cold streamer. In this paper, we compare the results obtained in the warm-core ring with those obtained in the cold streamer, and also compare the results of this study with those previously gleaned in the warm-core ring off Sanriku.

2. Materials and methods

This study was conducted during the cruise of the R/V "Soyo Maru" of the National Research Institute of Fisheries Science, in 25–29 May 1990 (Fig. 1a). Satellite imagery (NOAA AVHRR) taken on 30 May 1990 indicated that Sta. 6 was located in the Kuroshio warm-core ring and Sta. 3 in the cold streamer originated in the Oyashio water (Fig. 1b). Measurements of primary productivity and the contribution of "new" production to total production were conducted on 28 May at Sta. 6 (warm-core ring) and on 26 May at Sta. 3 (cold streamer).

Primary productivity was measured by the *in situ* method using a ^{13}C -technique (HAMA *et*

al., 1983). Samples were taken from five depths corresponding to 100, 50, 30, 10 and 1% photon fluxes just above the sea surface, using a 10 l Van Dorn sampler. To determine the depths corresponding to these light levels, photon-flux densities in the water column were measured with a flat quantum sensor (LI-COR Model 1000). Water samples were collected between 8 and 10 a.m.

The samples (2 l) were immediately sieved through a 200 μm mesh screen to remove large zooplankton, and then dispensed into 2 l polycarbonate bottles (two light bottles and one dark bottle). Incubations were begun within about one hour after collection. The ^{13}C enrichment was about 10% of the total inorganic carbon in the ambient water. Incubation experiments were conducted for about three or four hours. The experiments were terminated by the samples onto precombusted 47 mm Whatman GF/F filters (450°C for 4 h) with gentle suction. The filters were then rinsed with a 3.5% NaCl solution. The filter papers were immediately frozen and preserved for later isotope analysis ashore. After the filters were treated with HCl fumes for 4 h to remove

inorganic carbon, they were completely dried in a vacuum desiccator. The isotopic ratios of ^{13}C to ^{12}C were determined by quadruple mass-spectrometer (NICHIDEN ANELVA TE-360). Particulate organic carbon was determined simultaneously. Primary productivity was calculated according to HAMA *et al.* (1983). The dark uptake was always corrected for primary productivity.

The contribution of "new" production to total production was estimated as the ratio of the nitrate uptake rate to the total nitrogen uptake rate (nitrate uptake rate + ammonium uptake rate) (EPPLY and PETERSON, 1979). Samples of surface seawater were collected with a submersible pump (Ebara Type DVS-N). These samples were sieved through a $200\ \mu\text{m}$ mesh screen to remove large zooplankton and then used in uptake experiments. Seawater collections were made between 8 and 10 a.m.

The samples (2 l) were dispensed into 2 l polycarbonate bottles and enriched by the addition of either $\text{Na}^{15}\text{NO}_3$ (99.6 atom% ^{15}N) to a final concentration of 0.25 to $8\ \mu\text{mol l}^{-1}$ at Sta. 6 (warm-core ring), and 0.125 to $2\ \mu\text{mol l}^{-1}$ at Sta. 3 (cold streamer), or $\text{d}^{15}\text{NH}_4\text{Cl}$ (99.6 atom% ^{15}N) to a final concentration of 0.125 to $2\ \mu\text{mol l}^{-1}$ at both stations. Incubation experiments were begun within one hour after collection and conducted under simulated surface conditions, being dooled with near-surface seawater for about three to four hours. The experiments were terminated by the samples onto precombusted 47 mm Whatman GF/F filters (450°C for 4 h) with gentle suction. The filters were then rinsed with a 3.5% NaCl solution. The filter papers were immediately frozen and preserved for later isotope analysis ashore. They were completely dried in a vacuum desiccator. The isotopic ratios of ^{15}N to ^{14}N were then determined by quadruple mass-spectrometer (Nichiden Anelva TE-360). Particulate organic nitrogen was determined simultaneously. The nitrogen uptake rate ($\text{mgN m}^{-3}\ \text{h}^{-1}$, denoted as ρ) was computed according to equation (2) described by DUGDALE and WILKERSON (1986).

Temperature and salinity were measured with a Neil Brown Mark III CTD system. On-deck photon fluxes were monitored every fifteen minutes with a flat quantum sensor (LI-

COR Model 1000) on the upper deck during the sampling period. Seawater samples were used to determine the size-fractionated chlorophyll *a* (Chl. *a*) concentrations. The samples were filtered using 10, 2 and $0.4\ \mu\text{m}$ Nuclepore filters. Chl. *a* was determined by fluorometry using a Turner Designs Model 10 fluorometer after extraction with N, N-Dimethylformamide (SUZUKI and ISHIMARU, 1990). Water samples for nutrient determinations were stored frozen, and analyzed ashore with a Technicon Auto Analyzer II or manually according to PARSONS *et al.* (1984). The total carbonate in the seawater was measured with a Beckman Model 365 infrared analyzer.

3. Results

3.1 Physical and chemical environments

The weather was fine during the observation. The mean light intensity during the incubation was about $1,700\ \mu\text{Ein m}^{-2}\ \text{s}^{-1}$, and the total amount of light intensity in a day was about $50 \times 10^6\ \mu\text{Ein m}^{-2}\ \text{s}^{-1}$ at Sta. 6 (warm-core ring) and Sta. 3 (cold streamer).

The vertical profiles of temperature, salinity and nutrient concentrations shallower than 200m at Sta. 6 (warm-core ring) and Sta. 3 (cold streamer) are shown in Fig. 2. At Sta. 6 (warm-core ring) and Sta. 3 (cold streamer) with depth from the surface to 30m, and thermocline was observed between 10 and 30m. Isothermal water that is characteristic of the warm-core ring was observed below 30m. SASAKI (1993) reported that the temperature of isothermal water was about 10°C and that such water extended down to around 300m. Based on the result he judged that the warm-core ring had once passed the winter. Salinity was about 34.25 from the surface down to 200m. At Sta. 3 the temperature decreased with depth from the surface, whereas salinity was about 33.75 at least down to 200m. In addition, the temperature and salinity in the water shallower than 50m at Stas. 3 and 7 were lower than at other stations in the warm-core ring (Table 1). The results obtained in the shipboard observation were consistent with the stellite imagery (NOAA AVHRR) of 30 May 1990 (Fig. 1).

At Sta. 6 (warm-core ring) all nutrient concentrations were very low at the surface. They

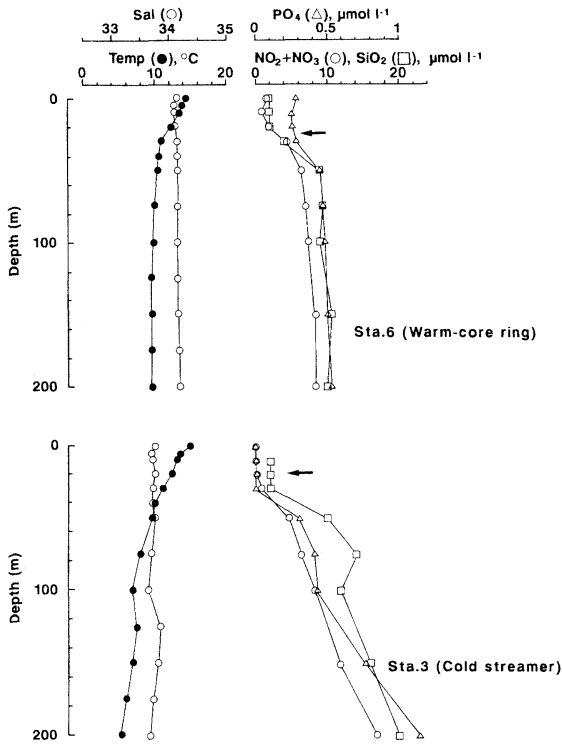


Fig. 2. Vertical profiles of temperature (Temp), salinity (Sal) and concentrations of nutrients (NO_2+NO_3 , SiO_2 , PO_4) shallower than 200m at Sta. 6 (warm-core ring) and Sta. 3 (cold streamer) off Sanriku in May 1990. Arrows indicate the depths of euphotic zone (1% light level).

increased rapidly, however, from 20 to 50m and were nearly constant below 50m. At Sta. 3 (cold streamer), nitrite+nitrate and silicate were nearly exhausted at the surface, whereas phosphate existed minimally. All nutrient concentrations increased dramatically with depth from 30m.

3.2 Chlorophyll *a* and primary productivity

Total Chl. *a* concentration, primary productivity and primary productivity per unit Chl. *a* within the euphotic zone at Sta. 6 (warm-core ring) and Sta. 3 (cold streamer) are summarized in Table 2. Total Chl. *a* concentrations were about 1 mg m^{-3} through the euphotic zone at Sta. 6 (warm-core ring). The concentrations were 2–3 mg m^{-3} shallower than the 10% light level and 4.23 mg m^{-3} at the 1% light level at Sta. 3 (cold streamer). Total Chl. *a*

Table 1. Mean values of temperature and salinity above the depth of 50 m at 11 stations off Sanriku in May 1990

Station	Temperature (°C)	Salinity (Psu)
1	14.38	34.40
2	15.20	34.36
3	11.63	33.73
4	19.39	34.77
5	13.10	34.09
6	11.95	34.12
7	9.62	33.56
8	17.09	34.62
9	19.37	34.74
10	10.32	33.71
11	16.23	34.55

concentrations at Sta. 3 were several times larger than those at Sta. 6. Depth-integrated Chl. *a* at Sta. 3 was about two times larger than that at Sta. 6. The size-fractionated Chl. *a* concentration is shown in Fig. 3. At Sta. 6 every size existed more or less equally at the 100 and 1% light levels, whereas the 2–10 μm fraction dominated and other fractions existed roughly equal at other light levels. At Sta. 3, $>10 \mu\text{m}$ fraction dominated through the euphotic zone and accounted for about 70% of the total Chl. *a* concentration. Other fractions existed more or less equally (about 15%). In addition, $<10 \mu\text{m}$ fraction accounted for 70–80% of total Chl. *a* concentration at Sta. 6, whereas $>10 \mu\text{m}$ fraction accounted for about 70% of total Chl. *a* concentration at Sta. 3.

At Sta. 6, primary productivity shallower than the 10% light level was nearly constant. The mean value \pm SD was calculated to be $5.91 \pm 0.68 \text{ mgC m}^{-3} \text{ h}^{-1}$. The same result was observed at Sta. 3 where the mean value \pm SD was $6.30 \pm 1.44 \text{ mgC m}^{-3} \text{ h}^{-1}$. The mean values at the two stations were nearly equal. Primary productivity differed at these stations' 1% light level, but the values were considerably lower than at shallower than the 10% light level.

The depth-integrated production during the incubation period was estimated by averaging the productivities between two depths, multiplying by the depth interval and summing these values. Multiplying the depth-integrated production by the ratio of the photon flux of a

Table 2. Chlorophyll *a* (Chl. *a*), primary productivity (productivity) and primary productivity per unit chlorophyll *a* (Productivity/Chl. *a*) within the euphotic zone at Sta. 6 (warm-core ring) and Sta. 3. (cold streamer) off Sanriku in May 1990

	Depth		Chl. <i>a</i>	Productivity	Productivity/Chl. <i>a</i>
	%	m	mg m ⁻³	mg m ⁻³ h ⁻¹	mgC mgChl. <i>a</i> ⁻¹ h ⁻¹
Sta.6 (Warm-core ring)	100	0	0.91	5.32	5.85
	50	2.5	0.76	5.63	7.41
	25	6	1.11	6.89	6.19
	10	10.5	1.10	5.81	5.28
	1	25	1.01	0.15	0.15
			(26)	(930)	
Sta.3. (Cold streamer)	100	0	2.73	4.57	1.67
	50	1.5	1.93	5.79	3.00
	25	3.5	2.18	6.91	3.17
	10	7	2.49	7.91	3.18
	1	16.5	4.23	2.65	0.63
			(47)	(811)	

Values in the parentheses indicate chlorophyll *a* for the entire euphotic zone per m² sea surface (mg Chl. *a* m⁻²) and daily primary production for the entire euphotic zone per m² sea surface (mgC m⁻² d⁻¹).

full day to the photon flux during the incubation period gave the daily primary production as reported in Table 2. Daily primary production was 930 mgC m⁻² d⁻¹ at Sta. 6 (warm-core ring) and 811 mgC m⁻² d⁻¹ at Sta. 3 (cold streamer). The former value was about 100 mgC m⁻² d⁻¹ higher than the latter value.

Primary productivity per unit Chl. *a* was nearly constant at shallower than the 10% light level at Sta. 6 (warm-core ring). The mean value \pm SD was calculated to be 6.18 ± 0.90 mgC mgChl. *a*⁻¹ h⁻¹. At Sta. 3 (cold streamer) the values at the 50, 25 and 10% light levels were nearly equal ant the value at the 100% light level (surface) was about half of those. The mean value at shallower than the 10% light level was calculated to be 2.76 ± 0.73 mgC mgChl. *a*⁻¹ h⁻¹. The mean value at Sta. 6 was about two times higher than that at Sta. 3. Primary productivity per unit Chl. *a* at the 1% level of these stations was different, but the values were remarkably lower than those at shallower layers above the 10% light level.

3.3. Nitrogen uptake and contribution of "new" production to total production

The nitrate uptake rates conformed to the Michaelis-Menten equation and saturated within the range of the injected substrate concentration at Sta. 6 (warm-core ring) and Sta. 3

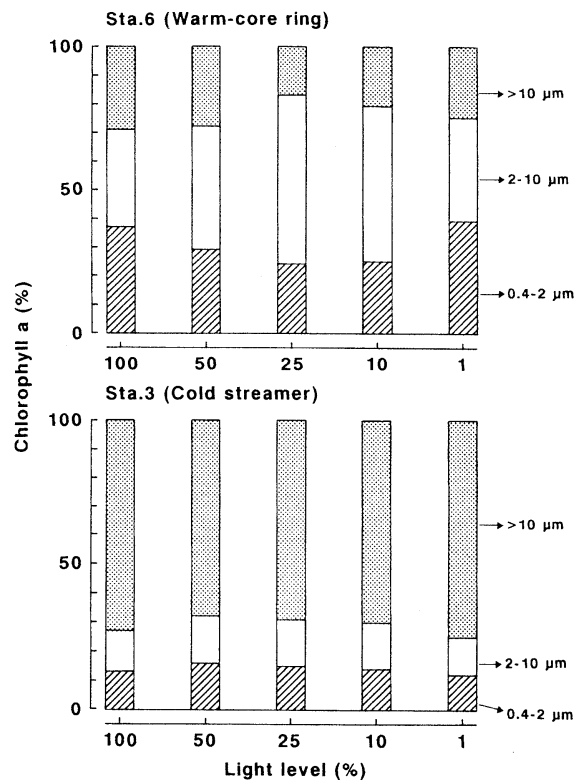


Fig. 3. Vertical changes in relative composition of size-fractionated chlorophyll *a* concentration at Sta. 6 (warm-core ring) and Sta. 3 (cold streamer).

Table 3. Maximum uptake rate (ρ_{\max}), maximum uptake rate per unit chlorophyll *a* ($\rho_{\max}/\text{Chl. } a$), half-saturation constant (Ks) and contribution of "new" production to total production ("new" production/total production) at the surface at Sta. 6 (warm-core ring) and Sta. 3 (cold streamer) off Sanriku in May 1990

		Sta. 6 (Warm-core ring)	Sta. 3 (Cold streamer)
ρ_{\max} (mgN m ⁻³ h ⁻¹)	NO ₃ ⁻	0.456	0.330
	NH ₄ ⁺	0.626	0.736
$\rho_{\max}/\text{Chl. } a$ (mgN mgChl. <i>a</i> ⁻¹ h ⁻¹)	NO ₃ ⁻	0.501	0.121
	NH ₄ ⁺	0.687	0.270
Ks ($\mu\text{mol l}^{-1}$)	NO ₃ ⁻	0.310 [0.7]	0.031 [0]
	NH ₄ ⁺	0.080 [0.16]	-0.044 [0.14]
"new" production/total production	(%) *	43	31

* $\rho_{\max} - \text{NO}_3 / (\rho_{\max} - \text{NO}_3 + \rho_{\max} - \text{NH}_4) \times 100$

[] : Ambient concentration ($\mu\text{mol l}^{-1}$)

(cold streamer). Ammonium uptake rates were nearly constant within the range of injected substrate concentration. The maximum uptake rate (ρ_{\max}), maximum uptake rate per unit Chl. *a* ($\rho_{\max}/\text{Chl. } a$) and half-saturation constant (Ks) of the nitrate and ammonium obtained by concentration dependency experiments are shown in Table 3. The ρ_{\max} of nitrate at Sta. 6 was higher than at Sta. 3, whereas ammonium showed an opposite result. The ρ_{\max} of ammonium was higher than that of nitrate at these stations. The $\rho_{\max}/\text{Chl. } a$ of nitrate and ammonium were several times higher at Sta. 6 than at Sta. 3. The Ks of both nitrogens were lower at Sta. 3, than at Sta. 6, but the values at these stations were roughly equal to the ambient concentrations.

The *in situ* rates of nitrate and ammonium uptake can be calculated using kinetic parameters, ρ_{\max} and Ks, and ambient substrate concentration. We were unable, however, to calculate the rate when the ambient concentrations of nitrogens were close to or beneath the detection limit. Furthermore, the preservation of seawater samples by freezing may have results in uncertainties in ambient concentrations. In this case, the uptake rates calculated were probably far from true values. We therefore estimated the contribution of "new" production to total production using ρ_{\max} for nitrate and ammonium, which is unaffected by the reliability of ambient concentrations of nitrogens. The contribution was estimated to be 43% at Sta. 6 and 31% at Sta. 3. (Table 3).

4. Discussion

The satellite image shows that the warm-core ring originated in the Kuroshio water and the cold streamer in the Oyashio water (Fig. 1b). Daily primary production in the Kuroshio water was 100–300 mgC m⁻² d⁻¹ (e.g. SAIJO *et al.*, 1970). The value in the offshore Oyashio water was 200–800 mgC m⁻² d⁻¹ in non-blooming period and 1,000–2,000 mgC m⁻² d⁻¹ in blooming period (e.g. SHIOMOTO *et al.*, 1994a). In this study, the daily primary production was 930 mgC m⁻² d⁻¹ in the warm-core ring and 811 mgC m⁻² d⁻¹ in the cold streamer (Table 2). The primary productivity in the warm-core ring was consequently higher than in the source water, similar to previous information (e.g. SASAKI, 1993). On the other hand, in the offshore Oyashio, OGISHIMA (1991) reported at spring bloom in May that the total Chl. *a* concentrations attained more than 5 mg m⁻³ in the surface layers, and >10 μm size (large-sized phytoplankton) accounted for more than 80% of the total Chl. *a* concentration. In this study, the total Chl. *a* concentration was 2–4 mg m⁻³ (Table 1) and the Chl. *a* concentration of the >10 μm fraction accounted for about 70% in the cold streamer (Fig. 3). These results suggest that spring bloom occurred in the source water of the cold streamer, the Oyashio water, during our observation. Hence, we can not declare whether primary productivity in the cold streamer is higher than that in the source water.

HAMA (1992) measured primary productivity in the warm-core ring 86B that once passed the

winter, in September 1987; the daily primary production at the center was about $900 \text{ mgC m}^{-2} \text{ d}^{-1}$. The daily primary production in the warm-core ring in this study was estimated to be $930 \text{ mgC m}^{-2} \text{ d}^{-1}$ (Table 2). This value is almost equal to the value in warm-core ring 86B reported by HAMA (1992). The nitrate in warm-core ring 86B was exhausted at the surface layer, whereas the nutricline (about $0.3 \mu \text{ mol l}^{-1} \text{ m}^{-1}$) was noticed from 40 to 60m, and nitrate concentrations were about $10 \mu \text{ mol l}^{-1} \text{ m}^{-1}$ below the nutricline. The same results were found in the vertical profile of nitrite+nitrate concentration in the warm-core ring in this study (Fig. 2). The vertical gradient of the nutrient that was observed between 20 and 50 m was calculated to be about $0.2 \mu \text{ mol l}^{-1} \text{ m}^{-1}$. These facts suggest that a nearly equal supply of nutrient from deeper layers contributed much to the equal daily primary production in both warm-core ring. Thereby nutrient flux from deeper layers probably plays an important role in regulating primary productivity in the warm-core ring off Sanriku.

Conversely, the total Chl. *a* concentration at the surface was more than two times larger in the warm-core ring in this study (about 1 mg m^{-3}) (Table 2) than in warm-core ring 86B (0.2 mg m^{-3}) (HAMA, 1992). Phytoplankton biomass was significantly different between the two warm-core ring although daily primary production was nearly equal. This variance probably reflects the differences in species and size distributions of phytoplankton and grazing pressure by zooplankton between the warm-core ring. Furthermore, considering that the observation seasons of the two warm-core rings were dissimilar, the differences in these biological factors may be the result of seasonal variations in the factors. Seasonal observation of primary productivity and other biological factors is required in the future.

Primary productivity per unit Chl. *a* was about two times higher in the warm-core ring than in the cold streamer (Table 2). Small-sized phytoplankton ($<10 \mu \text{ m}$ fractions) dominated within the euphotic zone in the warm-core ring and large-sized one ($>10 \mu \text{ m}$ fraction) in the cold streamer (Fig. 3). The cell numbers of diatoms was $7.1 \times 10^3 \text{ cells l}^{-1}$ at 0m and 5.7×10^3

cells l^{-1} at 25m, and that of flagellates was $1.3 \times 10^5 \text{ cells l}^{-1}$ at 0m and $2.4 \times 10^4 \text{ cells l}^{-1}$ at 25m in the warm-core ring (NAKATA pers. comm.) The cell numbers of diatoms was $6.7 \times 10^4 \text{ cells l}^{-1}$ at 0m and $6.4 \times 10^4 \text{ cells l}^{-1}$ at 25m, and that of flagellates was $1.5 \times 10^4 \text{ cells l}^{-1}$ at 0m and $9.5 \times 10^3 \text{ cells l}^{-1}$ at 25m in the cold streamer. Flagellates dominated in the warm-core ring and diatoms in the cold streamer. The temperature and nutrient concentrations in the surface layer in the warm-core ring and cold streamer were roughly equal (Table 1; Fig. 2). The primary productivity per unit Chl. *a* of small-sized phytoplankton is generally higher than that of large-sized one under the same environmental conditions (MALONE, 1980; GLOVER *et al.*, 1985). KAWAMURA (1963) and TANIGUCHI (1969) reported that the value was high in the population dominated by flagellates than in the population dominated by diatoms. The difference in primary productivity per unit Chl. *a* between the warm-core ring and cold streamer was thus probably attributed to the differences in size and/or species distribution of phytoplankton.

Nitrite+nitrate concentrations at the surface were very low ($1\text{--}2 \mu \text{ mol l}^{-1}$) in the warm-core ring and were exhausted in the cold streamer (Fig. 2). Were phytoplanktons nitrogen-deficient in both locations for that reason? The atomic ratio of carbon to nitrogen in phytoplankton is nearly equal to the Redfield ratio (6.6) (REDFIELD *et al.*, 1963) when phytoplankton is not nitrogen limited and is growing at or near its maximum rate (GOLDMAN *et al.*, 1979). The ratio increases, however, and rises to above 10 when phytoplankton becomes nitrogen-deficient (DONAGHAY *et al.*, 1978; GOLDMAN *et al.*, 1979). In this study, the atomic ratio of carbon to nitrogen in particulate organic matter at the surface was 7.6 in the warm-core ring and 8.9 in the cold streamer. These values were slightly higher than the Redfield ratio. Furthermore, KANDA and HATTORI (1989) reported that the uptake ratio of carbon to ammonium is remarkably lower than the Redfield ratio when phytoplankton is nitrogen-deficient: 1.8 for *Thalassiosira pseudonana* and 2.0 for *Platymonas* sp. The ratio obtained in this study was 9.9 at the surface in the

warm-core ring and 7.2 in the cold streamer. These values were slightly higher than the Redfield ratio. From these results, we concluded that phytoplankton were not nitrogen-deficient in either location.

The contribution of "new" production to total production obtained in this study (Table 3) were within the range of the values in eutrophic region (>30%: reviewed by SHIOMOTO *et al.*, 1994b) as reported in the warm-core ring in the Gulf Stream (McCARTHY and NEVINS, 1986). The high contribution positively reflects the copious supply of nutrients from the deeper layers (McCARTHY and NEVINS, 1986). This is probably one of the characteristics of warm-core ring.

The diffusional flux of nitrate through the thermocline is an important nitrogen source for supporting "new" production. The flux can be obtained by the equation:

$$F_n = K_z \cdot d_c / d_z$$

where F_n is the diffusional flux of nitrate, K_z is the eddy diffusion coefficient and d_c/d_z is the slope of the nitracline. "New" production can thus be estimated on the basis of the vertical profile of nitrate concentration if K_z has been obtained. K_z , however, has not yet been reported in the warm-core ring off Sanriku. Here, we tried to estimate K_z in the warm-core ring based on several assumptions. Provided that the nitrate is supplied from the deeper layer solely by diffusion and nitrate concentration in the surface layers is in a steady state, F_n is equal to the nitrate amount taken up by phytoplankton within the euphotic zone. Nitracline was noticed from 20 to 30m, and the nitrate (nitrite + nitrate) concentration was $1.9 \mu \text{mol l}^{-1}$ at 20m and $4.5 \mu \text{mol l}^{-1}$ at 30m (Fig. 2). Accordingly, d_c/d_z is calculated to be 0.26 mmol m^{-4} and thereby F_n is $0.26 \text{ mmol m}^{-4} \cdot K_z$. From the daily primary production in the warm-core ring ($930 \text{ mgC m}^{-2} \text{ d}^{-1}$), the nitrate amount taken up by phytoplankton is calculated to be $5.0 \text{ mmol m}^{-2} \text{ d}^{-1}$ by assuming that the uptake ratio of carbon (primary production) to nitrogen is equal to the Redfield ratio (6.6 by atoms), and the contribution of "new" production to total production within the overall euphotic zone is equal to the value at the surface (43%). From

the above, $0.26 \text{ mmol m}^{-4} \cdot K_z$ is equal to $5.0 \text{ mmol m}^{-2} \text{ d}^{-1}$ and thereby K_z is calculated to be $2.2 \times 10^{-4} \text{ m}^2 \text{ s}^{-1}$. The value is nearly equal to the deep-euphoticzone eddy diffusion coefficient in the Gulf Stream warm-core ring in calm conditions prior to a storm: $0.5\text{--}5 \times 10^{-4} \text{ m}^2 \text{ s}^{-1}$ (McCARTHY *et al.*, 1992).

Acknowledgements

We thank the captain and crew of the R/V "Soyo Maru" for the sample collection. We extend our appreciation to Dr. T. SAINO of the Water Research Institute of Nagoya University (former site: Ocean Research Institute, University of Tokyo), for kindly permitting us the use of a mass spectrometer, and to Dr. Y. KATO, Tokai University, for lending an infrared analyzer. We thank Ms. K. NAKATA of the National Research Institute of Fisheries Science for her kind communication on phytoplankton species composition. We are grateful to Dr. K. YOKOHI of the Tohoku National Fisheries Research Institute for his valuable information on the warm-core ring off Sanriku in 1990.

References

- CHIANG, K.P., A. TANIGUCHI and S. KATO (1994): Distribution of diatom assemblages in and around a warm core ring in the North Pacific Polar Frontal Zone. *La mer*, **32**, 195–207.
- DONAGHYA, P.L., J.M. DEMANCHE and L.F. SMALL (1978): On predicting phytoplankton growth rates from carbon: nitrogen ratios. *Limnol. Oceanogr.*, **23**, 359–362.
- DUGDALE, R.C. and J.J. GOERING (1967): Uptake of new and regenerated form of nitrogen in primary productivity. *Limnol. Oceanogr.*, **12**, 196–206.
- DUGDALE, R.C. and F.P. WILKERSON (1986): The use of ^{15}N to measure nitrogen uptake in eutrophic ocean; experimental considerations. *Limnol. Oceanogr.*, **31**, 673–689.
- EPPLEY, R.W. and B.J. PETERSON (1979): Particulate organic matter flux and planktonic new production in the deep ocean. *Nature*, **282**, 677–680.
- GLOVER, H.E., A.E. SMITH and L. SHAPIRO (1985): Photosynthetic characteristics of picoplankton compared with those of larger phytoplankton populations, in various water masses in the Gulf of Maine. *Biol. Oceanogr.*, **3**, 223–248.
- GOLDMAN, J.C., J.J. McCARTHY and D.G. PEAVY (1979): Growth rate influence on the chemical composition of phytoplankton in oceanic waters. *Nature*,

- 279, 210-215.
- HAMA, T. (1992): Primary productivity and photosynthetic products around the Kuroshio warm core ring. *Deep-Sea Res.*, **39**, S279-S293.
- HAMA, T., T. MIYAZAKI, Y. OGAWA, T. IWAKUMA, M. TAKAHASHI, A. OTUKI and S. ICHIMURA (1983): Measurement of photosynthetic production of a marine phytoplakton population using a stable ^{13}C isotope. *Mar. Biol.*, **73**, 31-36.
- KAWAMURA, T. (1963): Preliminary survey of primary production in the northern North Pacific and Bering Sea, June-August 1960. *Inform. Bull. Plantol. Japan*, **10**, 28-35. (in Japanese with English abstract)
- KANDA, J. and A. HATTORI (1988): Ammonium uptake and synthesis of cellular nitrogenous macromolecules in phytoplakton. *Limnol. Oceanogr.*, **33**, 1568-1579.
- MALONE, T.C. (1980): Algal size. *In*, *The Physiological Ecology of Phytoplankton*. I. Morris (ed.), University of California Press, Berkley and Los Angeles, 433-463.
- MATSUO, Y., K. YOKOUCHI and D. INAGAKE (1993): New production in the warm streamer. *In*, Book of Abstracts, 1993 Fall Meeting of The Oceanographical Society of Japan, Oct. 21-25, 1993, Sendai, Japan, p.175. (in Japanese)
- MCCARTHY, J.J. and J.L. NEVINS (1986): Source of nitrogen for primary production in warm-core rings 79-E and 81-D. *Limnol. Oceanogr.*, **31**, 690-700.
- MCCARTHY, J.J., C. GARSIDE and J.L. NEVINS (1992): Nitrate supply and phytoplakton uptake kinetics in the euphotic layer of a Gulf Stream warm-core ring. *Deep-Sea Res.*, **39**, S393-S403.
- OGISHIMA, T. (1991): Distribution of chlorophyll *a* as a phytoplaktonic food for Japanese sardine in the sea area off southeast Hokkaido. *Bull. Hokkaido Nat. Fish. Res. Inst.*, **55**, 173-184. (in Japanese with English abstract)
- PARSONS, T.R., Y. MAITA and C.M. LALLI (1984): *A Manual of Chemical and Biological Methods for Seawater Analyses*. Pergamon Press, Oxford, 173pp.
- REDFIELD, A.C., B.H. KETCHUM and F.A. RICHARDS (1963): The influence of organisms on the composition of sea water. *In*, *The Sea*, Vol.2, M. N. Hill (ed.), Interscience, New York, 26-77.
- RI, K. and T. SUGIMOTO (1989): Distribution and change of nutrient and chlorophyll in water-core ring. *Marine Sciences Monthly*, **21**, 173-178. (in Japanese)
- SAIJO, Y., T. KAWAMURA, S. IZUKA and K. NOZAWA (1970): Primary production in Kuroshio and its adjacent area. *Proc. 2nd CSK Symp.*, Tokyo, 169-175.
- SASAKI, K. (1993): Nutrient supply and production in low trophic levels in warm-core ring off Sanriku. *Marine Science Monthly*, **25**, 87-93. (in Japanese)
- SHIMOTO, A., K. SASAKI, T. SSHIMADA and S. MATSUMURA (1994a): Primary productivity in the offshore Oyashio in the spring and summer 1990. *J. Oceanogr.*, **44**, 150-156.
- SHIMOTO, A., K. SASAKI, T. SSHIMADA and S. MATSUMURA (1994b): Kinetics of nitrate and ammonium uptake by the natural population of marine phytoplankton in the surface water of the Oyashio region during spring and summer. *J. Oceanogr.*, **50**, 515-529.
- SUZUKI, R. and T. ISHIMARU (1990): An improved method for the determination of phytoplankton chlorophyll using N, N-Dimethylformamide. *J. Oceanogr. Soc. Japan*, **46**, 190-194.
- TANIGUCHI, A. (1969): Regional variations of surface primary production in the Bering Sea in summer and the vertical stability of water affecting the production. *Bull. Fac. Fish., Hokkaido Univ.*, **20**, 169-179.
- TOMOSADA, A. (1986): Generation and decay of Kuroshio warm-core rings. *Deep-Sea Res.*, **33**, 1475-1486.
- WRIGHT, R.T., and J.E. HOBBI (1966): Use of glucose and acetate by bacteria and algae in aquatic ecosystems. *Ecology*, **47**, 447-464.
- YASUDA, I., K. OKUDA and M. HIRAI (1992): Evolution of a Kuroshio warm-core ring: variability of the hydrographic structure. *Deep-Sea Res.*, **39**, S131-S161.
- YOKOUCHI, K., D. INAGAKE, Y. MATSUO and M. MURAKAMI (1993): Hydrographic structure and chlorophyll *a* distribution observed during southward movement of a Kuroshio warm-core ring into subtropical waters. *Bull. Tohoku Natl. Fish. Res. Inst.*, **55**, 75-88. (in Japanese with English abstract)

Received January 20, 1995

Accepted September 15, 1995