

Seasonal changes and vertical distributions of chlorophyll *a* and primary productivity at the Yamato Rise, central Japan Sea

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Abstract: Seasonal changes and vertical distribution patterns of chlorophyll *a* (Chl *a*) and primary productivity were investigated in relation to environmental conditions at the Yamato Rise in the central Japan Sea from 1994 to 1997. The maximum biomass and production of phytoplankton was found in spring, with a secondary peak in autumn. In contrast, minimum values were found in winter. Surface Chl *a* and surface primary productivity values in summer and autumn were nearly equal to corresponding values in Kuroshio waters. However, both values were lower than those in Kuroshio waters in winter, while those in spring in the central Japan Sea were considerably higher. Vertical uniformity of assimilation numbers from the surface to near the bottom of the euphotic layer and the existence of a subsurface Chl-*a* maximum in seasons with a stratified water column are notable. Some unique hydrographic features in the Japan Sea include (1) large-scale convectional mixing in winter, (2) abundant supply of nutrients from nutrient-rich subsurface water in winter–spring, and (3) shallow and distinct nutriclines in summer and autumn. These hydrographic features play an important role in determining spatial and temporal variations in phytoplankton biomass and productivity in these waters.

Key words: chlorophyll *a*, Japan Sea, nutrients, primary productivity, subsurface chlorophyll maximum

Introduction

The Japan Sea is located in the subarctic and is one of the marginal seas of the Pacific Ocean. Its hydrography is influenced by both the Tsushima Current Waters and the Northern Cold Waters. A frontal zone exists throughout the year in the central Japan Sea where these two waters meet (Tanioka 1962; Kolpack 1982). The central Japan Sea is also known as an important fishing ground, especially for the Japanese common squid, *Todarodes pacificus* Steenstrup (Ito et al. 1965; Kasahara 1978). This implies that the area is rich in food resources for squid (Okiyama 1965) and therefore, phytoplankton biomass and primary productivity are expected to be high. Consequently, understanding the spatial and temporal changes in these parameters in the central Japan Sea is important from the standpoint of studying fisheries resources.

Measurement of chlorophyll-*a* (Chl-*a*) levels in the Japan Sea have been made routinely since the 1970s by the Maizuru Marine Observatory. Using this data, Ohwada (1971) and

Kano et al. (1984) described general horizontal and vertical distribution patterns of Chl *a* in the Japan Sea. However, these investigations were restricted to particular seasons. Moreover, studies on primary productivity in the Japan Sea are relatively few compared to those in the Pacific (e.g. Ichimura & Saijo 1959; Saijo & Ichimura 1960; Aruga & Monsi 1962; Aruga et al. 1968; Parsons & Anderson 1970; Saijo et al. 1970). Sorokin (1977) examined the relationship between heterotrophic production and primary production in the Japan Sea, while Shim et al. (1985) and Shim & Park (1986) measured primary productivity and other environmental factors in the neritic waters off Korea. Therefore, there is still insufficient information to enable determination of the characteristics of seasonal changes in Chl-*a* levels and primary productivity in the Japan Sea (Nagata 1992).

The objectives of this study are to clarify the seasonal changes and vertical distribution patterns of Chl *a* and primary productivity in the central Japan Sea in relation to the physico-chemical conditions. The reasons as to why these patterns are different from those in other areas, e.g. Kuroshio waters, are also discussed.

Materials and Methods

Seven stations were established near the Yamato Rise in the central Japan Sea (Fig. 1). At each station, vertical profiles of temperature, salinity and fluorescence were measured simultaneously with a CTD (Alec Electronics Co., ACL-208DK), equipped with a fluorometer, to depths of ca. 150 m. Data were obtained from cruises of the R/V *Mizuho Maru* in 1994 (August, October), 1995 (April, August, October), 1996 (April), and the R/V *Kaiyo Maru* in 1997

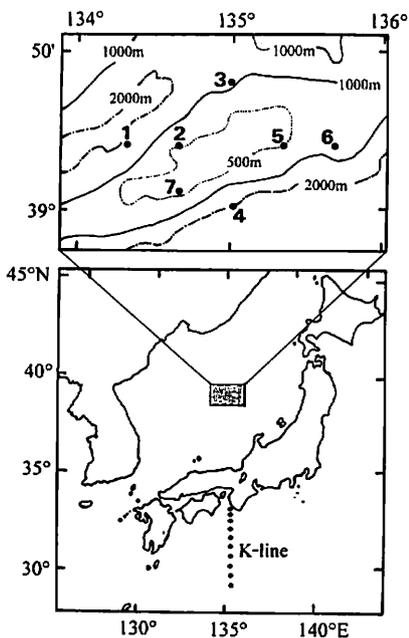


Fig. 1. Seven stations established around the Yamato Rise in the central Japan Sea (upper panel), and station locations in the Pacific Ocean (K-line) where routine observations are conducted by the Kobe Marine Observatory (lower panel).

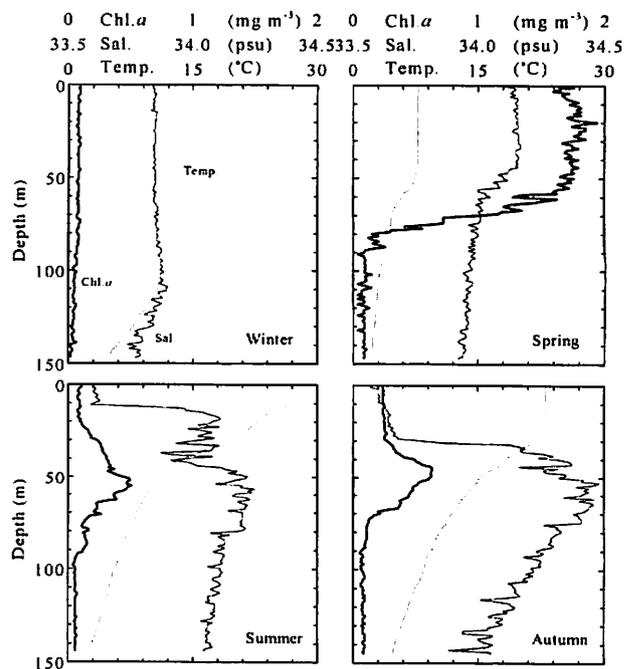


Fig. 2. Vertical profiles of Chl *a* (thick line), temperature (dotted line) and salinity (thin line) from the surface to 150 m in winter (24 Jan. 1997), spring (21 Apr. 1996), summer (24 Aug. 1994) and autumn (9 Oct. 1994) at Stn 4 in the central Japan Sea.

(January). In order to convert all fluorescence readings to Chl-*a* concentrations, Chl *a* was measured from standard hydrographic casts at every station. 260-ml seawater samples, taken from 1.7-liter Niskin sampling bottles from various depths, were filtered onto 25-mm Whatman GF/F filters. These filters and non-filtered seawater were stored at ca. -20°C for a maximum of one month. Determinations of Chl-*a* concentrations were made with a fluorometer (Japan Spectroscopic Inc., FP-777) for samples extracted with *N,N*-dimethylformamide (Suzuki & Ishimaru 1990). Determinations of inorganic nitrogen (nitrite plus nitrate, hereafter referred to as nitrate) and inorganic phosphorus (phosphate) concentrations were carried out using a Bran-Luebbe Autoanalyzer II.

Measurements of primary productivity were carried out using the ^{13}C tracer method according to an in situ incubation technique (Hama et al. 1983) at the stations shown in Fig. 1. Water samples for the incubation experiments were collected with a 15-liter Niskin bottle from the sea surface (ca. 0.5 m), the depth of transparency (Tr) and at a depth of $2\times\text{Tr}$. On the assumption that irradiance decreases exponentially in water and that the extinction coefficient (k) can be estimated using the formula $k=1.45/\text{Tr}$ (Walker 1980), the relative light intensities in these three layers were calculated to be 100, 23 and 6%, respectively. The samples (1000 ml) were immediately sieved through a GG54 net ($334\text{-}\mu\text{m}$ mesh) to remove large zooplankton and dispensed into two clear Pyrex glass bottles. After the addition of $\text{NaH}^{13}\text{CO}_3$ (Sigma Chemical Co., 99 atom% ^{13}C) to 10% of the total inorganic carbon in ambient water, bottles were re-suspended to their respective sampling depths. Incubation experiments were generally started from 1 to 2 h after sunrise and continued for 5–8 h. Immediately following incubation, samples were filtered through precombusted (450°C for 5 h) 25-mm Whatman GF/F filters. These filters were stored at ca. -20°C for later isotopic analysis ashore. They were treated with HCl fumes for 6 h to remove the carbonate, and were completely dried in a vacuum desiccator. The quantity of particulate organic carbon and the isotopic ratios of ^{13}C to ^{12}C were determined using a mass-spectrometer (Europa Scientific Co., ANCA-MS). Primary productivity was calculated according to Hama et al. (1983).

During all cruises, surface levels of photosynthetically active radiation were monitored continuously using a quantum sensor (LI-COR Co., LI-190SA).

Results

Daily photosynthetically active radiation (PAR) readings, taken when measurements of primary productivity were performed, are summarized in Table 1. According to the angle of incidence of light from the sun, PAR was at a minimum in winter and a maximum in summer. Values of PAR during all cruises (mean \pm SD) were 10.0 ± 4.6 (22 d), 31.3 ± 13.4 (13 d), 35.5 ± 16.7 (17 d) and $22.2\pm 6.9\text{ E m}^{-2}\text{ d}^{-1}$ (16 d) in winter, spring, summer and autumn, respectively. Since most of the daily PAR readings taken when measurements of primary productivity were made are within the mean \pm SD, it may be concluded that the values of primary productivity are fairly typical in each season with respect to light conditions.

Since spatial variation of the physical and chemical environment was relatively small within each season, seasonal changes and vertical distributions of Chl *a* and primary productivity in the central Japan Sea were examined with measurements of temperature, salinity and nutrients taken at Stn 4.

Table 1. Transparency (Tr), photosynthetically active radiation (PAR), Chl-*a* concentration, primary productivity and Chl-*a* specific productivity (assimilation number) for the four seasons.

Season	Stn	Date	Tr	Depth* (m)	PAR Quanta** (E m ⁻² d ⁻¹)	Chl <i>a</i> (mg m ⁻³)	Productivity (mgC m ⁻³ h ⁻¹)	Assimilation No. (mgC mgChl <i>a</i> ⁻¹ h ⁻¹)
Winter	4	24 Jan. 1997	19	0 (100)	8.9	0.10	0.14	1.4
				19 (23)	2.0	0.09	0.12	1.3
				38 (6)	0.5	0.07	0.11	1.6
Spring	1	25 Apr. 1995	9	0 (100)	34.6	2.57	4.00	1.6
				9 (23)	8.0	3.15	5.69	1.8
				18 (6)	2.1	2.22	4.28	1.9
	2	25 Apr. 1995	11	0 (100)	34.6	1.82	2.68	1.5
				11 (23)	8.0	1.81	2.55	1.4
				22 (6)	2.1	1.68	2.81	1.7
	5	25 Apr. 1995	—	0 (100)	34.6	1.73	1.50	0.9
					34.6	1.71	1.57	0.9
					38.5	1.75	4.00	2.3
4	21 Apr. 1996	12	0 (100)	38.5	1.75	4.00	2.3	
			12 (23)	8.9	1.80	3.87	2.2	
			24 (6)	2.3	1.82	3.75	2.1	
Summer	4	24 Aug. 1994	20	0 (100)	54.5	0.12	0.23	1.9
				20 (23)	12.5	0.10	0.25	2.5
				40 (6)	3.3	0.29	0.78	2.7
	2	25 Aug. 1994	20	0 (100)	48.9	0.19	0.52	2.7
				20 (23)	11.2	0.17	0.44	2.6
				40 (6)	2.9	0.85	2.75	3.2
	4	26 Aug. 1995	22	0 (100)	32.2	0.12	0.71	5.9
				22 (23)	7.4	0.31	4.50	14.5
				44 (6)	1.9	1.11	12.54	11.3
6	29 Aug. 1995	—	0 (100)	40.3	0.19	0.45	2.4	
				17.9	0.25	0.46	1.8	
				4.1	0.24	0.46	1.9	
Autumn	4	9 Oct. 1994	16	0 (100)	17.9	0.25	0.46	1.8
				16 (23)	4.1	0.24	0.46	1.9
				32 (6)	1.1	0.28	0.30	1.1
	7	28 Oct. 1995	—	0 (100)	20.5	0.57	0.93	1.6
					29.8	0.68	1.42	2.1
					6.8	0.56	6.91	12.3
3	29 Oct. 1995	18	0 (100)	29.8	0.68	1.42	2.1	
			18 (23)	6.8	0.56	6.91	12.3	
				36 (6)	1.8	0.58	0.62	1.1

* Numbers in parentheses show relative light intensity (%) just below the surface.

** On the assumption that surface reflectance is 7% throughout the year (after Campbell & Aarup 1989).

Winter

Chlorophyll-*a* levels and primary productivity were extremely low and did not exceed 0.1 mg m⁻³ and 0.14 mgC m⁻³ h⁻¹, respectively, throughout the water column. Photosynthetic activity per unit of Chl *a*, or the assimilation number, was almost constant at 1.3–1.6 mgC mgChl *a*⁻¹ h⁻¹ throughout the layer above the 6% light level (Table 1). Homogeneous distribution and low concentrations of Chl *a* were also confirmed by the continuous underwater fluorometer measurements (Fig. 2). The 13°C isotherm extended down to around 100 m. Salinity was about 33.85 at least down to 100 m. Concentrations of nitrate and phosphate varied in the top 75 m within a range of 2 μM and 0.4 μM, respectively (Fig. 3). They increased gradually below 75 m. These vertical patterns are considered to be due to intense vertical mixing.

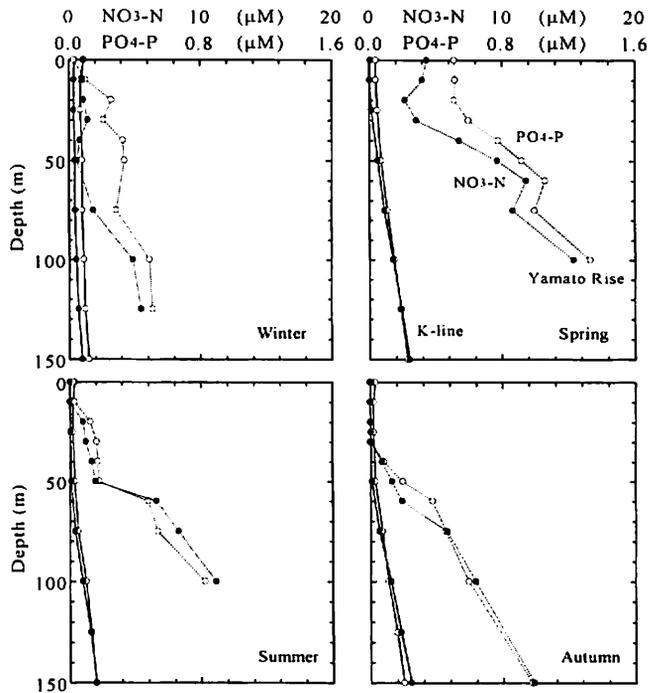


Fig. 3. Vertical distributions of nitrate (closed circles) and phosphate (open circles) at Stn 4 in the central Japan Sea (dotted line) and Kuroshio waters (K-line, see Fig. 1, solid line). Data from the K-line were average values from 1992–1994 and were obtained from the Japan Meteorological Agency (1992–1994).

Spring

The amount of Chl *a* increased markedly to 1.71–2.57, 1.80–3.15 and 1.68–2.22 mg m^{-3} at the 100, 23 and 6% light levels, respectively (Table 1). It was evenly distributed from the surface down to 60 m (Fig. 2). Profiles of primary productivity and assimilation number were similar to those of Chl *a*. Their values at the 100, 23 and 6% light levels were 1.50–4.00 (0.9–2.3), 2.55–5.69 (1.4–2.2) and 2.81–4.28 $\text{mgC m}^{-3} \text{h}^{-1}$ (1.7–2.1 $\text{mgC mgChl a}^{-1} \text{h}^{-1}$), respectively (Table 1). Chlorophyll *a* and primary productivity levels within the euphotic layer were more than ten times those in winter. However, the Chl-*a* concentration below 60 m was rather low, at almost the same level as in winter. Surface temperatures and salinities were higher than those in the deeper waters, and seasonal thermo- and halocline had developed near 60 m depth (Fig. 2). This layer also corresponded to the layer where Chl-*a* concentrations decreased sharply. Dramatic increases in Chl-*a* concentrations and primary productivity in spring were caused by an increase in vertical stability through thermal stratification and high ambient concentrations of surface nitrate ($>4.3 \mu\text{M}$) and phosphate ($>0.5 \mu\text{M}$) (Fig. 3), which had been supplied from the deeper layers by winter convection.

Summer

Chlorophyll *a* and primary productivity decreased throughout the water column as the seasons progressed. However, a noticeable exception was observed at Stn 4 on 26 August 1995, where an extremely high value of primary productivity of 12.54 $\text{mgC m}^{-3} \text{h}^{-1}$ occurred and the assimilation number reached 11.3 $\text{mgC mgChl a}^{-1} \text{h}^{-1}$ (Table 1). According to Falkowski (1981), the assimilation number has a theoretical maximum of 25 $\text{mgC mgChl a}^{-1} \text{h}^{-1}$, however, values reported from open-ocean stations have almost always been less than 5 $\text{mgC mgChl a}^{-1} \text{h}^{-1}$ (Laws et al. 1987). Although the specific source of contamination could

not be determined, these data collected at Stn 4 on 26 August appear to be doubtful. Except for these data, Chl *a* and primary productivity were 0.12–0.19 (0.23–0.52), 0.10–0.17 (0.25–0.44) and 0.29–0.85 mg m⁻³ (0.78–2.75 mgC m⁻³ h⁻¹) at the 100, 23 and 6% light levels, respectively. These parameters were higher at the 6% light level than at the surface. In contrast, assimilation numbers, which were 1.9–2.7, 2.5–2.6 and 2.7–3.2 mgC mgChl *a*⁻¹ h⁻¹ at the 100, 23 and 6% light levels respectively, did not greatly vary with depth.

The vertical profile of Chl *a* determined through discrete sampling was consistent with the values found through continuous observation (Fig. 2). From the continuous measurement, a subsurface Chl-*a* maximum was found between 50 m and 60 m, which corresponds to the bottom of the euphotic zone. In this layer, the concentration of Chl *a* was estimated to be 0.5 mg m⁻³, five times higher than surface concentrations. The vertical distributions of temperature and salinity showed distinct stratification, in contrast to winter and spring, due to the inflow of high-temperature and low-salinity water, called the "Upper Water of the Tsushima Current" (Yasui et al. 1967). Seasonal thermo- and haloclines had formed at approximately 10 m, much shallower than the depth of the Chl-*a* maximum (Fig. 2). The concentrations of nitrate and phosphate were lower than detectable limits in the top 10 m of the water column, probably due to consumption by phytoplankton. Both nitrate and phosphate concentrations increased dramatically from 50 to 60 m, from 2 to 6 μM for nitrate and 0.2 to 0.5 μM for phosphate (Fig. 3). The nutricline depth was 40–50 m deeper than that of the thermo-/halocline, and the subsurface Chl-*a* maximum showed a fairly close correspondence to the nutricline in summer.

Autumn

Chlorophyll *a* and primary productivity increased slightly to 0.25–0.68 (0.46–1.42), 0.24 (0.46) and 0.28–0.58 mg m⁻³ (0.30–0.62 mgC m⁻³ h⁻¹) at the 100, 23 and 6% light levels respectively, except for the 23% light level measurement at Stn 3 on 29 October 1995 (Table 1). This outlying data point may have been due to a contaminated sample, as for the sample discussed previously. Vertical distributions of these factors did not vary with depth, and a similar distribution pattern was observed for the assimilation numbers, which were 1.6–2.1, 1.9 and 1.1 mgC mgChl *a*⁻¹ h⁻¹ at the 100, 23 and 6% light levels, respectively. However, the Chl-*a* maximum was still observed, through continuous measurement, at a depth of 45–50 m (Fig. 2), somewhat shallower than that in summer. Temperature and salinity in the top 30 m were almost homogeneous. The layer was thicker than in summer, which indicated the development of a surface mixed layer. The depth of the Chl-*a* maximum was about 15–20 m deeper than that of the thermo- and halocline which was found at 30 m. This inconsistency was also observed in summer. Though nitrate and phosphate were nearly exhausted in the surface mixed layer from 0–30 m, their concentrations increased rapidly below 30 m (Fig. 3). As in summer, the Chl-*a* maximum layer coincided with the nutricline.

Seasonal changes and vertical distributions of Chl *a* and primary productivity in the Japan Sea can be characterized as follows. There is a typical seasonal change, with maximum values of Chl *a* and primary production occurring in spring, a secondary peak in autumn and minimum values in winter. Further, there is vertical uniformity in the assimilation numbers from the surface down to near the bottom of the euphotic layer and a subsurface Chl-*a* maximum exists in the seasons where stratification occurs.

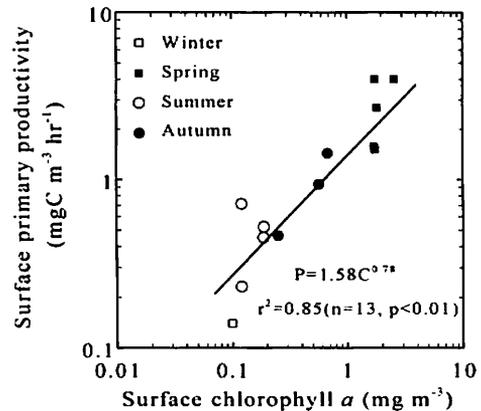


Fig. 4. Relationship between surface Chl *a* and surface primary productivity in the central Japan Sea.

Discussion

Chlorophyll-*a* concentration and primary productivity

A significant positive relationship was observed between log Chl *a* and log primary productivity (Fig. 4). The regression equation is expressed as $P = 1.58C^{0.78}$ ($p < 0.01$), where P is surface primary productivity ($\text{mgC m}^{-3} \text{h}^{-1}$) and C is surface Chl *a* (mg m^{-3}). By using this formula, it is possible to estimate surface primary productivity from surface Chl *a* in the central Japan Sea. In addition, seasonal changes in Chl-*a* concentrations and primary productivity are shown in Fig. 4.

Average surface Chl-*a* concentrations at fixed stations along $135^{\circ}15'E$ from $33^{\circ}40'N$ to $29^{\circ}30'N$ (K-line, Fig. 1) over twelve years (1972–1983) were summarized by the Kobe Marine Observatory (1987). In the northern area of the Kuroshio axis, or the Kuroshio coastal waters, surface Chl-*a* concentrations were 0.4, 0.5, 0.2–0.4 and 0.4–0.6 mg m^{-3} in winter, spring, summer and autumn, respectively. Corresponding values for the southern area of the Kuroshio axis, or the offshore Kuroshio waters, were 0.3–0.4, 0.1–0.3, <0.2 and 0.1–0.3 mg m^{-3} in winter, spring, summer and autumn, respectively (Kobe Marine Observatory 1987). In contrast, there is limited data on seasonal changes in surface primary productivity at fixed stations in Kuroshio waters. In winter, Taniguchi & Kawamura (1970) reported productivities of 0.68 $\text{mgC m}^{-3} \text{h}^{-1}$ south of Kyushu and 1.52 $\text{mgC m}^{-3} \text{h}^{-1}$ offshore of the Boso Peninsula. In the Kuroshio waters off the southern midcoast of Japan, primary productivity was 0.29–4.1 and 0.20–1.32 $\text{mgC m}^{-3} \text{h}^{-1}$ in spring and summer, respectively (Ichimura & Saijo 1959). Saijo & Ichimura (1960) observed productivities of 1–4 $\text{mgC m}^{-3} \text{h}^{-1}$ in the coastal region and 0.1–0.7 $\text{mgC m}^{-3} \text{h}^{-1}$ in the pelagic area of the Kuroshio from spring through summer. In autumn, surface primary productivity in the coastal waters off Shimoda was determined to be 0.8 $\text{mgC m}^{-3} \text{h}^{-1}$ by Hama et al. (1983).

From the results of the present study, Chl-*a* concentrations and primary productivity in the central Japan Sea are nearly equal to those in Kuroshio waters in summer and autumn. However, two features of the central Japan Sea are notable. First, extremely low values of Chl *a* and primary productivity occur in winter. In the Japan Sea, the winter climate is very severe due to the prevalence of strong northwesterly winds blowing over from Siberia. This period of strong winds accelerates cooling and evaporation of the surface waters. Therefore, the development of the surface mixed layer is remarkable, reaching the sea floor in cold years (Nitani 1972). Intense vertical mixing is believed to keep the phytoplankton standing crop and pro-

ductivity at low levels in winter. Akiba & Fukuoka (1976) suggested that the lack of a discontinuous layer in the Japan Sea may result in low productivity during the winter.

The second notable feature of the central Japan Sea is the marked increase in Chl-*a* concentrations in spring. Concentrations of nitrate and phosphate in the surface layer in spring were 4.3 and 0.5 μM , respectively (Fig. 3). Imai et al. (1990) reported that concentrations of surface nitrate and phosphate in winter (February) reach maximum values of 4–10 and 0.4–0.8 μM , respectively, in the offshore waters of the Japan Sea. Vigorous vertical mixing in winter appears to bring an abundant supply of nutrients into the surface layer. In contrast, surface nitrate and phosphate in Kuroshio waters in winter are less than 0.8 (Japan Meteorological Agency 1992–1994) and 0.1–0.4 μM (Kobe Marine Observatory 1987), respectively. Compared to data taken along the K-line (Fig. 1) in Kuroshio waters, the surface waters of the Japan Sea are rich in nutrients in spring (Fig. 3). This results in accelerated phytoplankton production, reflected in the high Chl-*a* values in spring in this area.

In summer and autumn, in spite of complete nutrient depletion, assimilation numbers at the surface were similar to those in spring, when surface nutrients were sufficient. This finding is consistent with that of Goldman et al. (1979), who state that growth rates of phytoplankton in oceanic waters are at a maximum and that nutrient limitation does not occur in the world's oceans. A quantitative study on the ratio of "regenerated" production to "new" production (Dugdale & Goering 1967) in the Japan Sea will be required in the future.

A notable feature described in this study is the relatively small vertical change in assimilation number from the surface down to near the bottom of the euphotic layer. Generally, assimilation numbers are at a maximum at the surface and decrease with depth in stratified waters, as reported for the North Pacific subtropical gyre (Laws et al. 1987; Marra & Heinemann 1987), Kuroshio waters (Shimura & Ichimura 1972) and Oyashio waters (Taniguchi & Kawamura 1972). This indicates that assimilation is limited primarily by surface irradiance. However, relatively high assimilation numbers, which were almost comparable to surface values, were also observed deeper than 40 m in the shelf area of the East China Sea (Hama et al. 1997). Assimilation numbers vary as a function of temperature, nutrient concentrations and phytoplankton cell size, as well as according to the light regime (Falkowski 1981). Therefore, vertical changes in assimilation numbers in the central Japan Sea must be interpreted taking these parameters into account.

Although interactions between temperature and other physico-chemical factors influencing photosynthesis are complicated, assimilation numbers decrease exponentially as ambient temperatures decrease (Eppley 1972; Goldman & Carpenter 1972). However, during this study the assimilation number during summer at 40-m depth, where waters were about 15°C colder than at the surface, was equal to or more than that at the surface (Fig. 2, Table 1). A similar relationship was also observed in autumn. This suggests that neither temperature nor light levels are the primary factors affecting assimilation numbers in the central Japan Sea in summer and autumn.

High assimilation numbers for phytoplankton photosynthesis in nutrient-rich waters are well known (Eppley 1972; Takahashi et al. 1973; Malone 1977). Furthermore, assimilation numbers are generally higher for small-sized rather than large-sized phytoplankton under the same environmental conditions (Eppley et al. 1969; Eppley 1972). In the central Japan Sea, nutrient concentrations near the bottom of the euphotic layer were higher than at the surface (Fig. 3) and the small (less than 10 μm in diameter) diatom, *Thalassiosira* sp., and unidentified microflagellates were dominant in this layer from summer to autumn (Nagata, unpublished data). Vertical uniformity of assimilation numbers in the central Japan Sea is probably attrib-

utable to high nutrient availability and/or the phytoplankton species composition near the bottom of the euphotic layer.

Subsurface chlorophyll-*a* maximum

A remarkable feature of the vertical distribution of Chl *a* in the central Japan Sea is the occurrence of a subsurface Chl-*a* maximum (hereafter referred to as SCM), especially in summer and autumn. SCM has been found to occur in different parts of stratified water columns by a number of different investigators (Longhurst & Harrison 1989). Regarding the mechanism of formation and maintenance of the SCM in the Kuroshio and adjacent areas, Saijo et al. (1969) emphasized the growth of shade-adapted phytoplankton in deep layers and the deterioration of photosynthetic pigments by light in the upper layers. Taniguchi & Kawamura (1972) considered that in the Oyasio region the SCM was formed primarily by the accumulation of phytoplankton sinking from the upper layers to the nutrient-rich discontinuity layer. Takahashi et al. (1985) found that the depth of the SCM shows fairly close correspondence with nutrient levels and the amount of ambient light in and around Kuroshio waters. Longhurst & Harrison (1989) made an extensive literature survey of the vertical profiles of Chl *a* and related factors in the world's oceans, and concluded that the depth of SCMs are determined by the dynamics of algal growth controlled by the supply of nutrients to the mixed layer, the ambient light environment and physiological adaptation. Furuya (1990) suggested that an increase in cellular contents of Chl *a* with depth accentuates the SCM in the tropical and subtropical western Pacific Ocean.

In the central Japan Sea, the SCM formed at 45–60 m depth (Fig. 2). On the assumption that the extinction coefficient is constant throughout the water column, light penetrating to the SCM is 1–3% of that just below the sea surface, a level at which photosynthesis is still possible. Although the physiological state of phytoplankton in the SCM is still unknown, considering the light intensity at the SCM and the fairly close association with the nutricline, the depth of the SCM in the central Japan Sea is likely determined by the ambient light environment and the availability of nutrients.

In this study, grazing of phytoplankton by herbivorous zooplankton was not considered in relation to the vertical distribution patterns of Chl *a* and primary productivity. However, Hobson & Lorenzen (1972) showed that copepod nauplii and copepodids were more abundant in the SCM than in surrounding water. Moreover, Longhurst & Harrison (1989) reviewed the relationship between the vertical distribution of phytoplankton and herbivorous zooplankton, and concluded that where the water column had stabilized and a SCM had developed, the depth of maximum abundance of zooplankton was somewhat shallower than that of the SCM. Longhurst (1976) and Herman et al. (1981) also stated that the upper boundary of the SCM could be maintained by herbivory. Though similar features were observed by Sorokin (1977), limited information exists on the interaction between phytoplankton and zooplankton in the Japan Sea. Therefore, further studies on the grazing impact of zooplankton on the formation and maintenance of the SCM in the Japan Sea are highly desirable.

In conclusion, seasonal changes and the vertical distributions of Chl *a* and primary productivity in the central Japan Sea are due to the unique hydrographic features of the region, particularly, (1) large-scale convective mixing in winter, (2) abundant supply of nutrients from nutrient-rich subsurface water in winter-spring, and (3) shallow and distinct nutriclines in summer and autumn.

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