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Photosynthetic characteristics and primary productivity of phytoplankton in the Arabian Sea and the Indian Ocean during the NE monsoon season

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Abstract: Chlorophyll *a* distribution, photosynthetic characteristics and primary productivity of phytoplankton were investigated in the Arabian Sea and eastern part of the Indian Ocean during the NE monsoon season (January 1994). Concentration of chlorophyll *a* at surface waters varied from 0.05 mg m^{-3} in the South Equatorial Current region to 0.71 mg m^{-3} in the Somali Current region. Standing stock of chlorophyll *a* within the euphotic zone ranged from 7.0 to 20.5 mg m^{-2}. A clear subsurface chlorophyll maximum (SCM) was observed in the layer at depth of 15 to 120 m that was 2–3 % penetration of the incident light. Depth of the SCM varied according to depths of the euphotic zone and mixed layer. The amounts of chlorophyll *a* in the SCM occupied more than 60% of the chlorophyll *a* standing stock within the euphotic zone. Photosynthesis–Irradiance curves illustrated clear differences of photosynthetic characteristics. Initial slope of the curve (α) varied from 0.009 to 0.034 mgC(mg chl. $a)^{-1}h^{-1}(\mu$mol quanta $m^{-2}\,s^{-1})^{-1}$ at the surface and from 0.002 to 0.208 mgC(mg chl. $a)^{-1}h^{-1}(\mu$mol quanta $m^{-2}\,s^{-1})^{-1}$ at the SCM. The maximum value of α (0.208) indicaties the evidence of the dark adaptation of phytoplankton at the most southern site. Both α and maximal photosynthetic rate (P_{max}) were very low at the SCM in the Equatorial Countercurrent region (P_{max}=2.1 mgC (mg chl. $a)^{-1}$ h^{-1}) and the South Equatorial Current(P_{max}=1.2 mgC(mg chl. $a)^{-1}$ h^{-1}). These low values suggested that phytoplankton at the SCM had lost their activity. Primary production varied largely from 0.08 to 0.76 gC m^{-2} day^{-1}. The maximum production was estimated in the Somali Current region, that was attributed to the high ability of photosynthesis as shown on the P–I curve. Light utilization index (Ψ) also indicated the large variance of water column quantum yield within our studied area and high ability of production in the Somali Current region.

1. Introduction

The Arabian Sea and the Indian Ocean were under the influence of monsoons. The monsoons, SW during June–August and NE during December – February, and currents play a very important role in determining the variability of phytoplankton productivity and biomass (KREY, 1973; YENTSCH and PHINNEY, 1993) . Primary productivity and biomass of phytoplankton in these area were measured concentrically during the International Indian Ocean Expedition (IIOE; 1959–1965) by numerous research vessels. The level of primary production as the results of the IIOE were reported by RYTHER *et al.* (1966) in the western part of this region and by SAIJO (1965) in the eastern part, and summarized by KREY (1973) and ARUGA (1973).

After the days of the IIOE, some investigations of photosynthetic characteristics, primary production and chlorophyll *a* standing stocks in the Arabian Sea has been carried out by ship or satellite (e.g. BANSE and MCCLAIN, 1986; BANSE, 1987; YENTSCH and PHINNEY, 1993; GOES *et al.*, 1993; PANT, 1993; BROCK *et al.*, 1993) focused on the interested phenomena such as upwelling and phytoplankton bloom.

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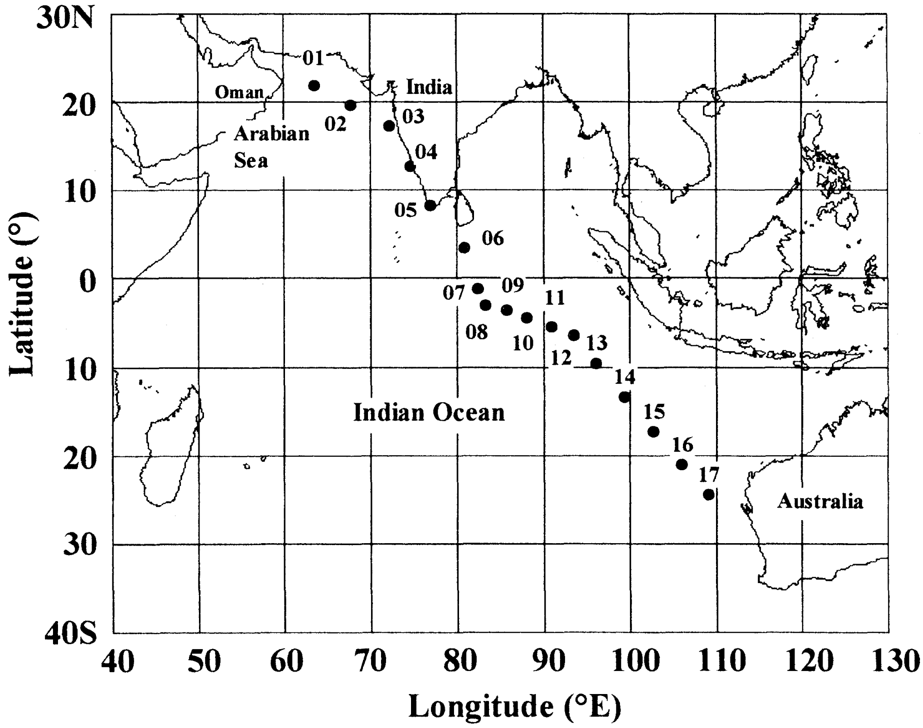

Fig. 1. Map showing the position of sampling stations (●) in the Arabian Sea (Stns. 01–05) and eastern part of the Indian Ocean (Stns. 06–17).

Photosynthetic characteristics shown by Photosynthesis–Irradiance curve (P–I curve) are important factors controlling the photosynthetic activity of phytoplankton in their natural environment (CÔTÉ and PLATT, 1984) and the parameters are being used in models for estimating primary production from remotely sensed data (e.g. PLATT *et al.*, 1988). In the Indian Ocean, however, these parameters have apparently not reported to date. New ocean color sensors such as SeaWIFS and OCTS must need the parameters that are not interpolated.

During the cruise of the T/V Umitaka-Maru III of Tokyo University of Fisheries in January 1994, we made a measurements of primary productivity of phytoplankton in the Indian Ocean included the Arabian Sea. In this paper, the authors present the photosynthetic characteristics and primary productivity of phytoplankton during the NE monsoon season.

2. Material and Methods

A series of investigation was carried out on the cruise from the Gulf of Oman to Fremantle, Australia (Fig. 1).

Water temperature and salinity were measured with a CTD (ICTD, FSI) : OCTOPUS system (OCTO-Parameter Underwater Sensor; ISHIMARU *et al.*, 1984) at 17 stations. The sensor of salinity was calibrated with salinometer.

Primary productivity of phytoplankton was measured at 14 stations except Stns. 05, 06 and 08. Seawater samples for primary productivity were collected using Van Dorn bottles from the sea surface and from the depth of subsurface chlorophyll maximum (SCM) recognized by the data of *in situ* fluorometer equipped with an OCTOPUS system. Additional water samples were collected using a Rossete Multi Water Sampler equipped with an OCTOPUS System for measurement of chlorophyll *a* standing stock of phytoplankton.

For measurement of phytoplankton chlorophyll *a*, 200 ml of water sample was filtered through glass fiber filter (Whatman GF/F, ϕ 25 mm). The filter was immediately soaked in

N, N–Dimethylformamide (DMF) and extracted pigments in the dark (SUZUKI and ISHIMARU, 1990). Concentration of chlorophyll *a* was determined fluorometrically with Turner Designs 10–005R fluorometer within a few days after the soaking (PARSONS *et al*., 1984).

Photosynthetic activity of phytoplankton was measured by the stable ^{13}C isotope method (HAMA *et al*., 1983). Water samples were transferred into 2000 ml clear poly carbonate bottles. After adding $NaH^{13}CO_3$ (approximately 10% of total carbonate, ISOTEC Inc.), the samples were incubated for 4 hours in water bath controlled at surface water temperature under natural light (full sunlight, 46, 21, 11, 6% and dark). After the incubation, the water samples were filtered through glass fiber filters (Whatman GF/F, ϕ 47mm) precombusted at 450℃ for 4 hours. The filters were treated with fume of HCl to remove traces of inorganic carbon, and the isotope ratios of ^{12}C and ^{13}C were determined by infrared absorption spectrometry (SATOH *et al*., 1985) with a ^{13}C analyzer (EX 130, JASCO). The photosynthetic activity was calculated by the equation of HAMA *et al.* (1983), and the rate at each depth was calculated on the basis of P–I curve fit to the model of EILERS and PEETERS (1988) with a nonlinear curve–fitting minimization that uses a Gauss–Newton method. The equation of the model takes the form :

$$p = I/(aI^2 + bI + c)$$

where p is photosynthetic rate, I is irradiance, and a, b, and c are the fitted parameters. Photosynthetic characteristics were calculated with the formulas : initial slope $(\alpha) = 1/c$, optimal intensity $(I_m) = (c/a)^{0.5}$, maximal photosynthetic rate $(P_{max}) = [b + 2(ac)^{0.5}]^{-1}$, and intensity of onset of light saturation $(I_k) = P_{max}/\alpha$.

Photosynthetically available radiation (PAR) was measured with a LI–190SB air quantum sensor and a LI–192SB underwater quantum sensor (LI–COR inc.), and recorded with an LI 1000 (LI–COR inc.) quantum meter.

Primary production in water column was estimated by integrating the value multiplied the photosynthetic rate by chlorophyll *a* concentration at each depth over the entire euphotic zone. Daily value of production was calculated on the basis of integrated PAR during the incubation period and during the whole day (WETZEL and LIKENS, 1991).

3. Results

Hydrographic condition

Based on the surface currents (e.g. MOLINARI *et al*., 1990), studied area was distinguished into total of four regions : Somali Current region (SC, Stns. 01–05); Equatorial Countercurrent region (ECC, Stns. 07–13); South Equatorial Current region (SEC, Stns. 14–16); and West Australian Current region (WAC, Stn. 17).

Spatial distributions of water temperature, salinity and σ–t in the upper 200 m of water column are shown in Fig. 2a, Fig. 2b and Fig. 2c, respectively. Although the salinity was homogeneous vertically, physical features indicated the stratification between 50 and 130 m except in the SC region. Especially, thermocline was developed in the ECC region as illustrated in Fig. 2a. The thermocline weakened at 10 °S where ECC and SEC formed a front. Low salinity band (<35 PSU) was observed at 10 °S (Fig. 2b) and separated the high salinity water mass. In the SC region, water mass was well mixed. In contrast with low temperature (<26 ℃) and high salinity (>36 PSU) near the Gulf of Oman, warm (>28 ℃) and low saline (<34 PSU) water mass was observed along the west coast of India.

Chlorophyll a distribution and photosynthetic characteristics

Spatial distribution of chlorophyll *a* concentration in the upper 200m of water column is shown in Fig. 2d, and the surface values and standing stock of chlorophyll *a* for each region are listed in Table 1. Chlorophyll *a* concentration at the sea surface was low (0.05–0.71 mg m^{-3}). The surface water from the SCC to WAC regions had extremely low (0.05–0.09 mg m^{-3}) chlorophyll *a* concentrations. Although the highest surface value (0.71 mg m^{-3}) was observed at Stn. 01 in the Somali Current region, shallower station of the same region had relatively low values.

Chlorophyll *a* standeng stock within the euphotic zone ranged from 7.0 mg m^{-2} at Stn. 15 in the SEC region to 20.5 mg m^{-2} at Stn. 01 in

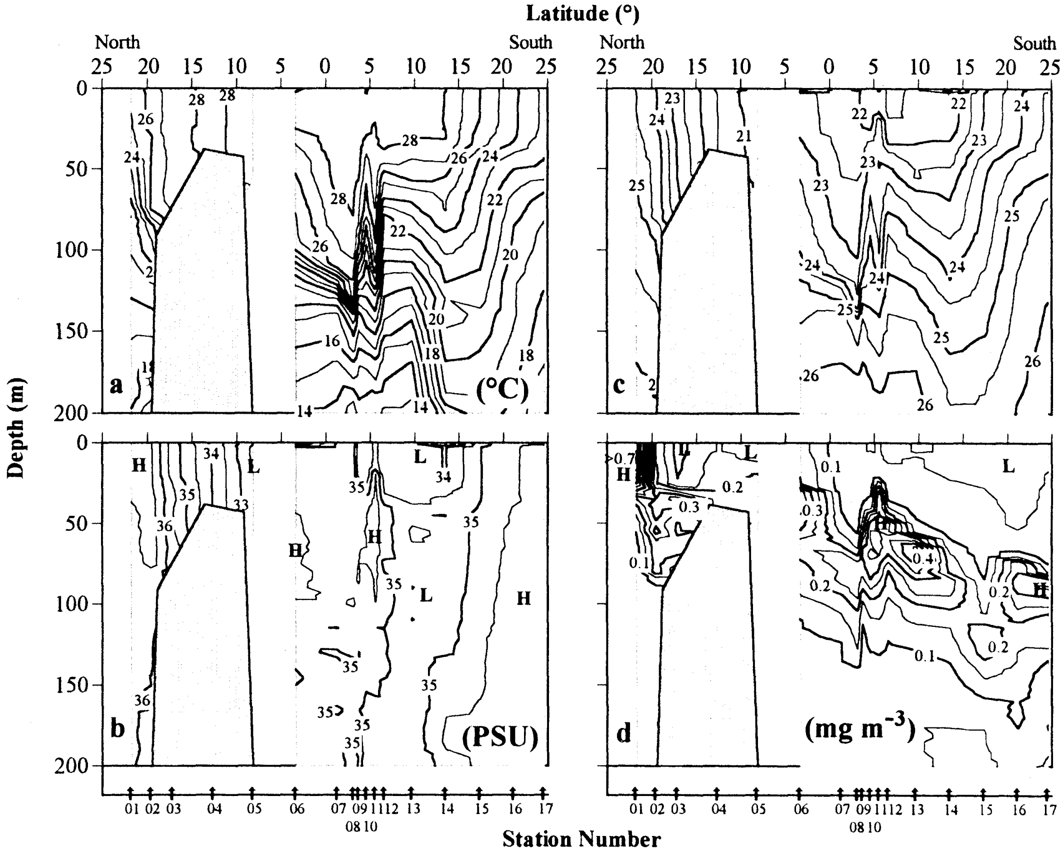

Fig. 2. Vertical sections of (a) water temperature, (b) salinity, (c) σ-t, and (d) chlorophyll *a* concentration in the Arabian Sea and the Indian ocean. Blank area denotes no data.

Table 1. Surface concentration and standing stock within euphotic zone of chlorophyll *a*, primary production, solar radiation incident upon surface, and light utilization index in the different regions showing range and mean. Values in parentheses are mean.

Region	Station	Chlorophyll *a*				
		Surface (mg m^{-3})	Standing Stocks (mg m^{-2})	Primary production (gC m^{-2} day^{-1})	Solar Radiation (mol quanta m^{-2} day^{-1})	Ψ *
Somali Current	01–05	0.19–0.71(0.40)	8.5–20.5(12.7)	0.28–0.76(0.45)	28.0–34.2(30.4)	0.88–1.27(1.06)
Equatorial Countercurrent	07–13	0.09–0.14(0.12)	8.7–15.2(12.4)	0.09–0.20(0.14)	23.9–43.3(35.1)	0.22–0.63(0.36)
South Equatorial Current	14–16	0.05–0.09(0.08)	7.0–13.0(10.1)	0.08–0.11(0.10)	43.1–50.6(45.8)	0.18–0.29(0.22)
West Australian Current	17	0.08	11.8	0.29	35.7	0.69
	Average	0.19	12.0	0.23	36.1	0.55
	C.V.(%)	89.7	27.3	80.8	21.1	67.6

*light utilization index(gC(gchl.*a*)$^{-1}$(mol quanta m^{-2})$^{-1}$)

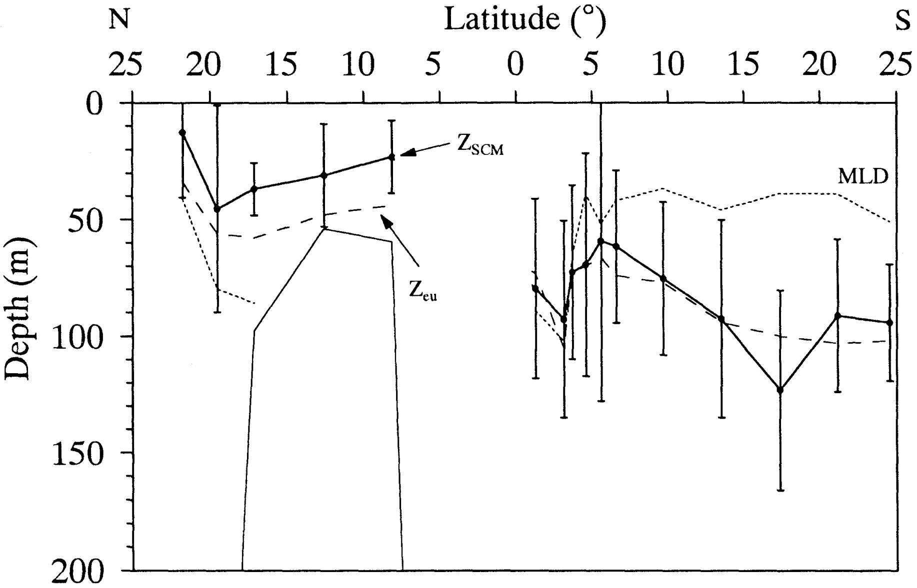

Fig. 3. Depth of subsurface chlorophyll maximum, (Z_{SCM}; —●—), euphotic zone defined as 1% penetration of incident light (Z_{eu}; — —), and mixed layer (MLD; ···). Error bar shows a range of the maximum. Blank area denotes no data.

the SC region. The averaged value in the SC region was relatiely higher (12.7 mg m^{-2}) than those in the other regions. Although surface chlorophyll *a* concentrations had a wide range within the studied area (89.7% C.V.), variation of standing stocks with region was small (27.3% C.V.).

In the layer at depths of 15 to 40 m in the SC region and at 50 to 120 m in the other regions, distinct subsurface chlorophyll maximum (SCM) was observed (Fig. 2d). Maximal concentations at the SCM layer ranged 0.27–0.99 mg m^{-3} in the SC region and 0.25–0.50 mg m^{-3} in the other regons. The SCM occupied more than 60% of the chlorophyll *a* standing stock (Table 1) within the euphotic zone. Comparison of peak depth and range of the SCM, depth where PAR is reduced to 1% of the surface (Z_{eu} : euphotic zone depth), and mixed layer depth (MLD) is shown in Fig. 3. In the present study, range of the SCM is determined on the basis of Gaussian Curve fit (LEWIS *et al.*, 1983; PLATT *et al.*, 1988) modified by MATSUMURA and SHIOMOTO (1993), and MLD is defined as the first depth at which the temperature is 1.0 ℃ less than that at 10 m (RAO *et al.*, 1989). Peaks of the SCM were lower part of the euphotic zone, that were 2–3 % penetration of the surface light except Stn. 15. The SCM changed its vertical distribution according to a relative position of MLD and Z_{eu}. In the SC region, mixed layer (41–86 m) included whole of euphotic zone (34–58 m) and the SCM was approximately within the MLD and/or euphotic zone. MLD in the ECC region was close to Z_{eu} and turned upside-down where top and bottom of the SCM (except Stn. 13 at about 10 °S where is a front as mentioned above) were positioned at above and at below of both depths, respectively. In the SEC and the WAC regions more southern than the front of 10 °S, Z_{eu} was completely lower than MLD. The SCM in these regions was distributed lower than MLD and expanded up to extremely weak light layer deeper than Z_{eu}.

P–I curves at sea surface and SCM in the each region and the parameters of photosynthetic characteristics were shown in Fig. 4 and listed in Table 2, respectively. P–I curves illustrated a clear difference of photosynthetic characteristics between the surface and SCM, and between the regions. All curves at the sea surface show a weak photoinhibition, though, P_{max} of the surface were 1.3–5.4 times as high as for the SCM.

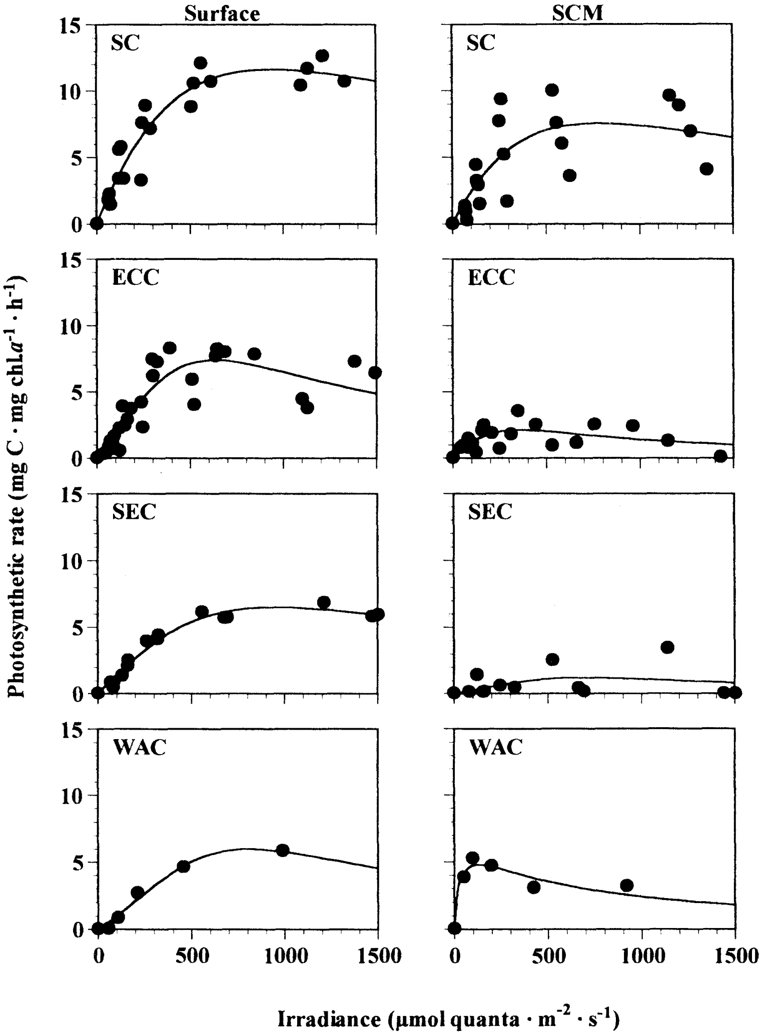

Fig. 4. Photosynthesis–Irradiance curves at surface and SCM fitted to all data in the (SC) Somali Current region, (ECC) Equatorial Countercurrent region, (SEC) South Eauatorial Current region, and (WAC) West Australian Current region.

Table 2. Parameters showing photosynthetic characteristics of phytoplankton in different regions.

Region		Surface				SCM			
	Station	α *	P_{max} **	I_m †	I_k ‡	α *	P_{max} **	I_m †	I_k ‡
Somali Current	01–05	0.034	11.6	938	338	0.027	7.5	780	281
Equatorial Countercurrent	07–13	0.018	7.4	634	412	0.014	2.1	356	156
South Equatorial Current	14–16	0.014	6.5	954	458	0.002	1.2	693	496
West Australian Current	17	0.009	6.0	810	660	0.208	4.8	132	23

*initial slope (mgC(mg chl. a)$^{-1}$h^{-1} (μmol quanta m^{-2} s^{-1})$^{-1}$)
**maximal photosynthetic rate (mgC(mg chl. a)$^{-1}$h^{-1})
†optimal intensity (μmol quanta m^{-2} s^{-1})
‡intensity of onset of light saturation (μmol quanta m^{-2} s^{-1})

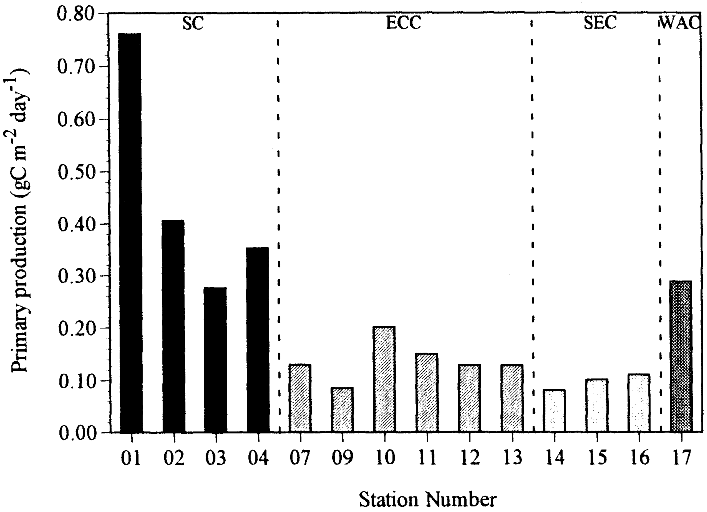

Fig. 5. Primary production at each sampling station. Dashed lines separates the stations into four current regions.

P_{max} was especially high in the SC region that was 1.6–1.9 times at the surface (11.6 mgC (mg chl. $a)^{-1}$ h^{-1}) and 1.6–6.3 times at the SCM (7.5 mgC (mg chl. $a)^{-1}$ h^{-1}) as high as for the others. α of the surface (0.034 mgC (mg chl. $a)^{-1}$ h^{-1} (μmol quanta m^{-2} $s^{-1})^{-1}$) in the SC region is also highest value, that shows most productive surface water. As shown by the values of I_m (634–954 μmol quanta m^{-2} s^{-1}) and I_k (338–660 μmol quanta m^{-2} s^{-1}) of the surface, phytoplankton at the surface was adapted to strong insolation. While at the SCM, photoadaptation to dark was not observed except the WAC region. The SCM in the WAC had high value of an α (0.208 mgC (mg chl. $a)^{-1}h^{-1}$ (μmol quanta m^{-2} $s^{-1})^{-1}$) showing high activity at low light intensity. Although I_k at the SCM in the ECC region was relatively low (156 μmol quanta m^{-2} s^{-1}), low P_{max} (2.1 mgC (mg chl. $a)^{-1}$ h^{-1}) denies a dark adaptation. Phytoplankton at the SCM of the SEC was reduced its activity more than those in the ECC. It appears that high I_m and I_k in this region indicate light adaptation. But this is only a lost of activity because of the remarkably low α (0.002 mgC(mg chl. $a)^{-1}h^{-1}$ (μmol quanta m^{-2} $s^{-1})^{-1}$) and P_{max} (1.2 mgC (mg chl. $a)^{-1}$ h^{-1}).

Primary production and light utilization index

Distribution of daily primary production was shown in Fig. 5, and the values for the each region were shown in Table 1. The studied regions had a widely one order range of primary production (0.08–0.76 gC m^{-2} day^{-1}). The highest value of production was obtained in Stn. 01 in the SC region. Production in the SC region, of which mean production was 0.45 gC m^{-2} day^{-1} with the range of 0.28–0.76 gC m^{-2} day^{-1}, was 1.5–4.5 times in mean value as high as the others. The waters in the ECC region were low productive (0.09–0.20 gC m^{-2} day^{-1}), and more oligotorophic water was observed in the SEC region as shown in the value of primary production (0.08–0.11 gC m^{-2} day^{-1}). Although the WAC region keep close to the SEC region, that had relatively high value (0.29 gC m^{-2} day^{-1}) because of the high photosynthetic activity of phytoplankton in the SCM layer.

Total water column light utilization index (Ψ : FALKOWSKI, 1981) for each region was shown in Table 1. Ψ was estimated from the expression :

$$\Psi = P/(B \cdot I_0)$$

where P is the daily primary production of water column in gC m^{-2} day^{-1}, B is the chlorophyll a standing stock in g chl. a m^{-2}, and I_0 is solar radiation at the sea surface (Table 1) in mol quanta m^{-2} day^{-1}. Averaged value of Ψ for all regions was 0.55 gC (gchl.$a)^{-1}$ (mol quanta $m^{-2})^{-1}$ with 67.6% (C.V.) of variation. In the SC region, mean value of Ψ was 1.06 gC (g chl. a)$^{-1}$ (mol quanta m^{-2})$^{-1}$ with the narrow range (0.88–1.27 gC (g chl. a)$^{-1}$ (mol quanta m^{-2})$^{-1}$) that is 15% in C.V., and the value was the highest within the all studied regions. The index Ψ was fallen into the averaged value of 0.22 gC (g chl. a)$^{-1}$ (mol quanta m^{-2})$^{-1}$ in the SEC region (26% C.V.), and relatively high in the WAC region (0.69 gC (g chl. a)$^{-1}$ (mol quanta m^{-2})$^{-1}$). In the ECC region, the highest variance of Ψ was observed (50% C.V.).

4. Discussion

Distinct physical features in the studied are the front and the low salinity band which had observed also during the IIOE (WYRTKI, 1971; 1973). WYRTKI (1973) suggested that the low salinity band is characteristic of the front formed at 10 °S and separates the high salinity water mass of the northern Indian Ocean from the subtropical high salinity water of the subtropical gyre. Low saline water along the west coast of India is also typical of the SC region. This water mass marks the northward flowing equatorial surface waters (ESW; GOES *et al.*, 1993) from the southwestern Bay of Bengal (BRUCE *et al.*, 1994). Surface salinity maps demonstrated by WYRTKI (1971) also showed the intrusion of low-salinity water from the Bay of Bengal into the Arabian Sea. Moreover, low chlorophyll water mass observed in this region was originated from the Bay of Bengal associated with the ESW (GOES *et al.*, 1993).

Clear differences in chlorophyll distribution, photosynthetic characteristics and primary production were observed, that is according to four regions distinguished by surface currents. In the SC region of the Arabian Sea, these values were distinctly higher than those in the other regions. Moreover α and P_{max} in this region(α =0.034, P_{max} =11.6 at Surface; α = 0.027, P_{max} =7.5 at SCM) was higher than values : α =0.017 mgC (mg chl. a)$^{-1}$h^{-1} (μmol quanta m^{-2} s^{-1})$^{-1}$ (convert watts to mols of quanta assuming 1W=4.6 μmol quanta s^{-1}) and P_{max}=5.37 mgC (mg chl. a)$^{-1}$h^{-1} published by SATHYENDRANATH *et al.* (1996) in the Somali Basin (southwest of Stn. 01). Similar to the conditions in the Somali Basin during the NE monsoon (January 1993) reported by VELDHUIS *et al.* (1997), the MLD exceeded the Z_{eu}. So that, it is considered that the nutrients is supplied enough to keep a high activity compared with it in the other regions. The SC region in this study is including the shallow waters, that is also a reason of high α and P_{max}. However, primary production at the shallow stations (0.28–0.41 gC m^{-2} day^{-1}) was lower than the result of Somali Basin (VELDHUIS *et al.*, 1997) because of the low standing stocks.

In the ECC region, the MLD was closed to the Z_{eu} and almost of the SCM was distributed along the Z_{eu} at depth more than 50m. The SCM in the SEC and the WAC region were also along the Z_{eu} and entirely beneath the MLD situated at approximately 50m. AS long as seen in these results, the SCM was depended on light intensity, but the dark adaptation was observed only in the WAC and activity of phytoplankton were very low as shown in the values of α and P_{max} in the ECC (α =0.014, P_{max}=2.1) and SEC (α =0.002, P_{max}=1.2). The results of JITTS (1965) also illustrated that productivity along the 110° E was infinitesimal at the depth more than about 50m. SAIJO (1965) suggested from the results of the tank experiments that the chlorophyll at the depth of the SCM had almost lost their photosynthetic ability. He more implied that the SCM is not the result of the passive accumulation of senescent phytoplankton but represents an accumulation of actively growing phytoplankton (SAIJO, 1973). The SCM in the ECC and the SEC appeared in our study might avoid the nutrients impoverished surface water mass and strong solar radiation.

Distinct difference and variability in water column light utilization index (Ψ) were appeared in like manners of productivity and P–I curve parameters. The index means water column averaged quantum yield for photosynthesis and has been used as important factor of productivity model estimate the depth-integrated primary production (FALKOWSKI, 1981; PLATT, 1986; MOREL, 1991). The value of Ψ changes with a variety of environments (PLATT, 1986) such as the values of FALKOWSKI (1981)(Ψ =0.43), YODER *et al.* (1985)(Ψ =1.5), CAMPBELL and O'REILLY(1988)(Ψ =1.47), and BALCH *et al.* (1989)(Ψ =0.27). The averaged value obtained of our study ($\Psi = 0.55$) was lower than the world-wide averaged value of 0.96 gC (g chl. *a*)$^{-1}$ (mol quanta m^{-2})$^{-1}$ (BALCH and BYRNE, 1994). However the value in the SC region ($\Psi = 0.88$–1.27) is relatively high within values of the world oceanic waters (e.g. FALKOWSKI, 1981), and same level as much as the values by ^{14}C based experiments in the Somali Basin ($\Psi = 0.84$–1.59; VELDHUIS *et al.*, 1997) in spite of the difference in the technique and method that induces large error (BALCH and BYRNE, 1994). In contrast with the SC region, Ψ in the SEC region ($\Psi = 0.18$–0.29) was one of the lowest value in the world oceans. In case we try to estimate the primary production of water column from satellite derived data, it is difficult to regard our studied regions as only one area where has constant value of Ψ, due to its large variance. In other words, it was appropriate that a variable Ψ and photosynthetic characteristics (α, P_{max}, I_k, I_m) were ramified into four region based on the surface currents.

Although we presented chlorophyll distribution, productivity and photosynthetic characteristics of phytoplankton in the Arabian Sea and the eastern Indian Ocean related to the hydrographic condition and the light penetration, the obtained primary production data are only shipboard estimates that are "point" or "line". It is hoped that the primary production in this area will estimated in more broad-scale from satellite to resolve the global carbon cycle.

It is ideal that simple mathematical model is utilized to estimate the integrate primary production from remotely sensed data. The simplest productivity models estimate primary production as a function of sea surface chlorophyll (e.g. EPPLEY *et al.*, 1985). This simplest relationship for the Arabian Sea and the Indian Ocean (HIRAWAKE *et al.*, 1996) has a strong correlation ($r^2 = 0.90$ for the same dataset as this study), but the model induced a large error in the sites where primary production depends on the standing stock within the SCM layer or chlorophyll concentration was high. It is expected that a more complicated model is attempted for such regions. Although the complex approach also need information on the photosynthetic characteristics, there was very little about these parameters in our studied area, especially from the ECC to WAC region. It is clear that the photosynthetic characteristics presented in this study are very precious data on the next step in the primary producton model.

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References

ARUGA, Y.(1973) : Primary production in the Indian Ocean Ⅱ. *In* Jacobs, J., O.L. LANGE, J.S. OLSON and W. WIESER (Eds.) : The Biology of the Indian Ocean. Springer-Verlag, Berlin. p.127–130.

BALCH, W.M., M.R. ABBOTT and R.W. EPPLEY (1989) : Remote sensing of primary production, I, A comparison of empirical and semi-analytical algorithms. Deep-Sea Res., **36**, 281–295.

BALCH, W.M. and C.F. BYRNE (1994) : Factors affecting the estimate of primary production from space. J.Geophys. Res., **99**, 7555–7570.

BANSE, K.(1987) : Seasonality of phytoplankton chlorophyll in the central and northern Arabian Sea. Deep-Sea Res., **34**, 713–723.

BANSE, K. and C.R. MCCLAIN (1986) : Winter blooms of phytoplankton in the Arabian Sea as observed by the Coastal Zone Color Scanner. Mar. Ecol. Prog. Ser., **34**, 201–211.

BROCK, J., S. SATHYENDRANATH and T. PLATT (1993) : Modelling the seasonality of subsurface light and primary production in the Arabian Sea. Mar. Ecol. Prog. Ser., **101**, 209–221.

BRUCE, J. G., D. R. JOHNSON and J. C. KINDLE (1994) : Evidence for eddy formation in the eastern Arabian Sea during the northeast monsoon. J. Geophys. Res., **99**, 7651–7664.

CAMPBELL, J.W. and J.E. O'REILLY (1988) : Role of satellites in estimating primary productivity on the northwest Atlantic continental shelf. Cont. Shelf Res., **8**, 179–204.

CÔTÉ, B. and T. PLATT (1984) : Utility of the light-saturation curve as an operational model for quantifying the effects of environmenttal conditions on phytoplankton photosynthesis. Mar. Ecol. Prog. Ser., **18**, 57–66.

Eilers, P.H.C. and J.C.H. Peeters (1988) : A Model for relationship between light intensity and the rate of photosynthesis in phytoplankton. Ecol. model., **42**, 199–215.

Eppley, R.W., E. Stewart, M.R. Abbott and U. Heyman (1985) : Estimating ocean primary production from satellite chlorophyll. Introduction to regional differences and statistics for the Southern California Bight. J. Plankton Res., **7**, 57–70.

Falkowski, P.G. (1981) : Light-shade adaptation and assimilation numbers. J. Plankton Res., **3**, 203–216.

Goes, J.I., H.R. Gomes, A. Kumar. A. Gouveia, V.P. Devassy, A.H. Parulekar and L.V.G. Rao (1993) : Satellite and ship studies of phytoplankton along the west coast of India. *In* Desai, B.N. (Eds.) : Oceanography of the Indian ocean. A.A. BALKEMA, Rotterdam. p. 67–80.

Hama, T., T. Miyazaki, Y. Ogawa, T. Iwakuma, M. Takahashi, A. Otsuki and S. Ichimura(1983) : Measurement of photosynthetic production of a marine phytoplankton population using a stable ^{13}C isotope. Mar. Biol., **73**, 31–36.

Hirawake, T., H. Satoh, T. Morinaga, T. Ishimaru, M. Kishino (1996) : In-water algorithms for estimation of chlorophyll *a* and primary production in the Arabian Sea and the eastern Indian Ocean. Ocean Optics XIII, SPIE 2963, 296–301.

Ishimaru, T., H. Otobe, T. Saino, H. Hasumoto and T. Nakai (1984) : OCTOPUS, an octo parameter underwater sensor, for use in biological oceanography studies. J. Oceanogr. Soc. Japan, **40**, 207–212.

Jitts, H.R. (1969) : Seasonal variations in the Indian ocean along 110°E. IV. Primary production. Aust. J. Mar. Freshwat. Res., **20**, 65–75.

Krey, J. (1973) : Primary production in the Indian Ocean I. *In* Jacobs, J., O.L. Lange, J.S. Olson and W. Wieser (Eds.) : The Biology of the Indian Ocean. Springer-Verlag, Berlin. p.115–126.

Lewis, M.R., J.J. Cullen and T. Platt (1983) : Phyto plankton and thermal structure in the upper ocean : Consequences of nonuniformity in chlorophyll profile. J. Geophys. Res., **88**, 2565–2570.

Matsumura, S. and A. Shiomoto (1993) : Vertical distribution of primary productivity function Φ (II)-for the estimation of primary productivity using by satellite remote sensing-. Bull. Nat. Res. Inst. Far Seas Fish., **30**, 227–270. (in Japanese)

Molinari, R. L., D. Olson and G. Reverdin (1990) : Surface current distributions in the tropical Indian Ocean derived from compilations of surface buoy trajectories. J. Geophys. Res., **95**, 7217–7238.

Morel, A. (1991) : Light and marine photosynthesis : a spectral model with geochemical and climatological implications. Prog. Oceanogr., **26**, 263–306.

Pant, A. (1993) : Primary productivity in coastal and off-shore waters of India during two southwest monsoons, 1987 and 1989. *In* Desai B. N. (Ed.) : Oceanography of the Indian Ocean. A. A. BALKEMA, Rotterdam. p.81–90.

Parsons, T.R., Y. Maita and C.M. Lalli (1984) : A manual of chemical and biological methods for seawater analysis. Pergamon Press, Oxford. 173 pp.

Platt, T. (1986) : Primary production of the ocean water column as a function of surface light intensity : algorithms for remote sensing. Deep-Sea Res., **33**, 149–163.

Platt, T., S. Sathyendranath, C.M. Caverhill and M.R. Lewis (1988) : Ocean primary production and available light : further algorithms for remote sensing. Deep-Sea Res., **35**, 855–879.

Rao, R.R., R.L. Molinari and J.F. Festa (1989) : Evolution of the climatological near-surface thermal structure of the tropical Indian ocean. 1. Description of mean monthly mixed layer depth, and sea surface temperature, surface current, and surface meteorological fields. J. Geophys. Res., **94**, 10801–10815.

Ryther, J.H., J.R. Hall, A.K. Pease, A. Bakun and M.M. Jones (1966) : Primary organic production in relation to the chemistry and hydrography of the western Indian Ocean. Limmol. Oceanogr., **11**, 371–380.

Saijo, Y. (1965) : Summary report on photosynthesis and chlorophyll in the eastern Indian Ocean observed by Japanese ships during IIOE. Inform. Bull. Planktol. Japan, **12**, 72–78. (in Japanese)

Saijo, Y. (1973) : The formation of the chlorophyll maximum in the Indian Ocean. *In* Jacobs, J, O.L. Lange, J.S. Olson and W. Wieser (Eds.) : The Biology of the Indian Ocean. Springer-Verlag, Berlin. p. 171–173.

Sathyendranath, S., T. Platt, V. Stuart, B.D. Irwin, M.J.W. Veldhuis, G.W. Kraay and W.G. Harrison (1996) : Some bio-optical characteristics of phytoplankton in the NW Indian ocean. Mar. Ecol. Prog. Ser., **132**, 299–311.

Satoh, H., Y. Yamaguchi, N. Kokubun and Y. Aruga (1985) : Application of infrared absorption spectrometry for measuring photosynthetic production of phytoplankton by the stable ^{13}C isotope method. La mer, **23**, 171–176.

Suzuki, R. and T. Ishimaru (1990) : An improved method for the determination of phytopalnkton chlorophyll using N,N-Dimethylformamide.

J. Oceanogr. Soc. Japan, **46**, 190–194.

VELDHUIS, M.J.W., G.W. KRAAY, J.D.L.V. BLEIJSWIJK and M.A. BAARS (1997) : Seasonal and spatial variability in phytoplankton biomass, productivity and growth in the northwestern Indian Ocean : the southwest and northeast monsoon, 1992–1993. Deep-Sea Res., **44**, 425–449.

YENTSCH, C.S. and D.A. PHINNEY (1993) : The effect of wind direction and velocity on the distribution of phytoplankton chlorophyll in the western Arabian Sea. *In* DESAI B.N.(Ed.) : Oceanography of the Indian ocean. A.A.BALKEMA, Rotterdam. p. 57–66.

YODER, J.A., L.P. ATKINSON, S.S. BISHOP, J.O. BLANTON, T.N. LEE and L.J. PIETRAFESA(1985) : Phytoplankton dynamics within Gulf Stream intrusions on the southeastern United States continental shelf during summer 1981. Cont. Shelf Res., **4**, 611–635.

WETZEL, R.G. and G.E. LIKENS (1991) : Limnological analysis. Springer-Verlag, New York. 391 pp.

WYRTKI, K. (1971) : Oceanographic atlas of the International Indian Ocean Expedition. U.S. Government Printing office, Washington, D.C. 531 pp.

WYRTKI, K. (1973) : Physical oceanography of the Indian ocean. *In* JACOBS, J., O.L. LANGE, J.S. OLSON and W. WIESER (Eds.): The Biology of the Indian Ocean. Springer-Verlag, Berlin. p.18–36.

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