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Light condition and photosynthetic characteristic of the subsurface chlorophyll maximum at a station in Solomon Sea

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Photosynthetic productivity of phytoplankton was investigated at a station (5°43′S, 153°30′E) in the Solomon Sea, in early December 1989. A pronounced subsurface chlorophyll maximum (SCM) was observed at a layer of 75 m depth, where the relative light intensity was 1.2% of the incident solar radiation at water surface. The chlorophyll *a* concentration at the SCM layer was 0.61 mg m^{-3}. The chlorophyll *a* standing stock at the SCM layer was 46% of the total amount in the water column from surface to 200 m. Photosynthesis-light curve of phytoplankton from the SCM layer indicated shade adaptation. The maximum photosynthetic rate of 0.15 mgC mg·chl·a^{-1} h^{-1} was obtained at 35 μE m^{-2} s^{-1}, which was almost the same light condition at the SCM layer. The photosynthetic efficiencies of phytoplankton from surface, 25 m and the SCM layer for blue light (35 μE m^{-2} s^{-1}) were 57, 56 and 105% of those under daylight, respectively. The primary production in the SCM layer (0.086 mgC m^{-3} h^{-1}) was 17% of that in the 25 m layer (0.50 mgC m^{-3} h^{-1}).

Key Index Words: blue light—photosynthesis—Solomon Sea—subsurface chlorophyll maximum.

A subsurface chlorophyll maximum (SCM) has been often observed in marine environments (e.g. Riley *et al.* 1949, Anderson 1969, Kiefer *et al.* 1976, Yamaguchi and Ichimura 1980, Abbott *et al.* 1982, Takahashi *et al.* 1985). The SCM is commonly found at depths between 30 and 100 m in most areas, which occurred in the lower part of the photic zone where the light level is generally about 1% of the sea surface (Jerlov 1976, Kishino *et al.* 1986). Thus, it is important to know the photosynthetic rate at the light regimes near compensation point for estimating primary production at the SCM layer in the tropical area. During the cruise of the T/V Umitaka Maru III of Tokyo University of Fisheries to Solomon Sea in 1989, we carried out a series of investigations focusing on the photosynthetic characteristics of phytoplankton from the SCM layer. In this paper, we describe the characteristics of the SCM layer with reference to the light conditions.

Materials and Methods

Studying area (5°43′S, 153°30′E) was located in the central part between Bougainville Island and New Ireland (Fig. 1). The depth was approximately 4,500 m. Seawater samples were collected by using Rossete multi samplers equipped with a CTD system (Neil Brown Co. Ltd.). For measurements of size distribution and photosynthetic activity of phytoplankton and nutrients, additional water samples were collected from 0, 25 and 75 m with a Van Dorn sampler. A series of this study was carried out in early December 1989.

For measurement of phytoplankton chlorophyll *a*, seawater samples of one liter were immediately filtered through glass fiber filters (Whatman GF/F) and the filters were kept frozen in a deep freezer at −30°C until analyses. The concentrations of chlorophyll *a* were determined with a Turner Designs 10-005R fluorometer according to the pro-

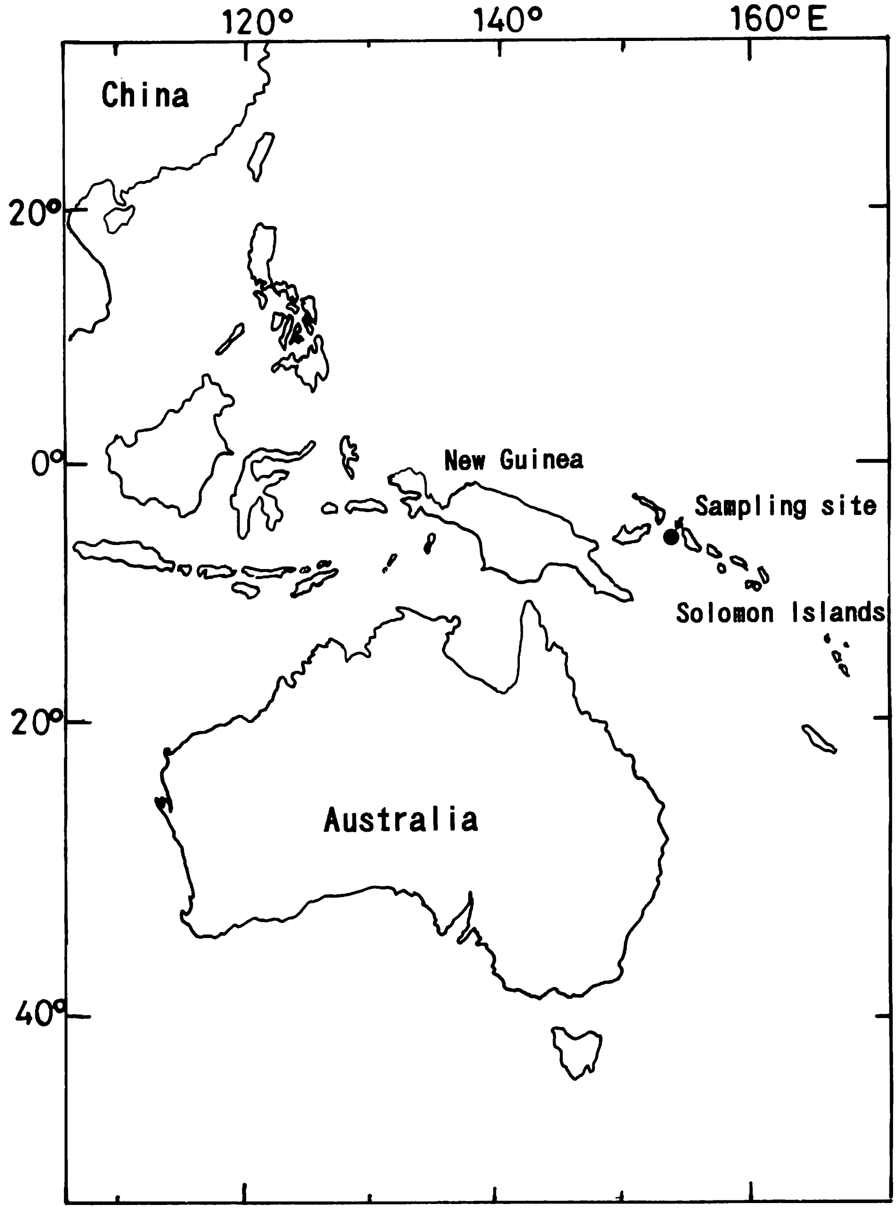

Fig. 1. The map showing location of sampling site (5°43′S, 153°30′E) in Solomon Sea.

cedures of Strickland and Parsons (1972). For determination of size distribution of phytoplankton, aliquots of seawater were filtered through membrane filters (Nuclepore 3 μm, General Electric Ltd.) and plankton nettings (Nitex, mesh size of 10 μm). Chlorophyll *a* concentrations in three fractions were determined fluorometically by the same method mentioned above.

Measurements of photosynthetic activity were made by the stable ^{13}C isotope method (Satoh *et al.* 1985). Water samples collected from 0, 25 and 75 m were transferred into 1000 ml clear polycarbonate bottles. After adding $NaH^{13}CO_3$ (10.7% of the final atom percent of ^{13}C, Prochem Co.) to the bottles, the samples were incubated for 6 hours in water bath controlled at 30°C under 325

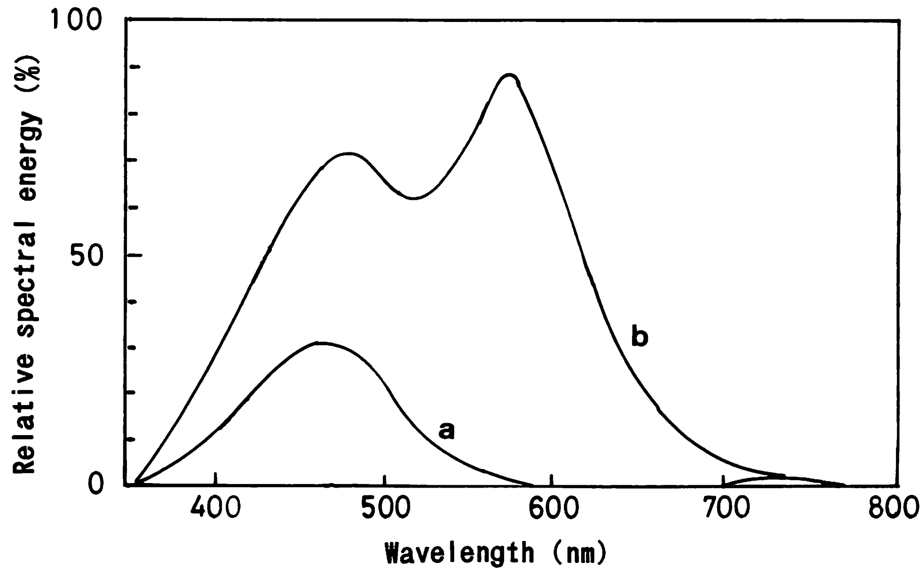

Fig. 2. Spectral energy distributions of blue light (a) and daylight fluorescence lamp (b).

$\mu E\ m^{-2}\ s^{-1}$ of daylight type fluorescence lamps (FL-40SD, Toshiba Co.), which have almost the same spectral irradiance energy as visible light at the range of 400–700 nm (Fig. 2). The light intensity was regulated by changing the number of neutral vinyl sheets wrapped around the bottles. The blue light source was also obtained by placing a blue filter of cellophane sheet in front of the lamps. After the incubation, the samples were filtered through glass fiber filters (Whatman GF/F) precombusted at 450°C for 4 hours. The filters were fumed with HCl for removing inorganic carbon, and the isotope ratios of ^{12}C and ^{13}C were determined by infrared absorption spectrometry with a ^{13}C analyzer (EX-130, JASCO). The photosynthetic rate was calculated by the method of Hama *et al.* (1983). Current velocities were determined with an Acoustic Doppler Current Profiler (CI-20-H ADPC, Furuno Electronic Co.).

Incident and underwater photosynthetically active radiation (PAR, 400–700 nm) was measured with an LI-1000 integrating quantum meter equipped with an LI-190SB air quantum sensor and an LI-192SB underwater quantum sensor, respectively. The underwater spectral irradiance was measured by an underwater irradiance meter (Ishikawa Industrial Co.) with eight interference filters of 422, 481, 513, 552, 599, 661, 682 and 709 nm.

Results and Discussion

Hydrography and light conditions in the study area

The direction of current and velocity of surface water were recorded, the latter being 30–60 cm s^{-1}. The vertical profiles of water temperature, salinity and density (sigma-t) at the study site are shown in Fig. 3a. The water column was well stratified. The water temperature in the mixed layer from surface to 75 m ranged from 30.4 to 29.6°C, and a thermocline developed in the deeper layer of 150–200 m.

A marked subsurface chlorophyll maximum (SCM) was observed at a depth of 75 m (Fig. 3b). The relative light level at the SCM layer was about 1.2% of the incident solar radiation at local noon under clear sky (Fig. 4a). The light penetrating to this depth was so weak that the photosynthesis was strictly restricted by light intensity, as mentioned by Jerlov (1976) and Kishino *et al* (1986). Further, the wavelength distribution of light energy was biased to the range of 481–

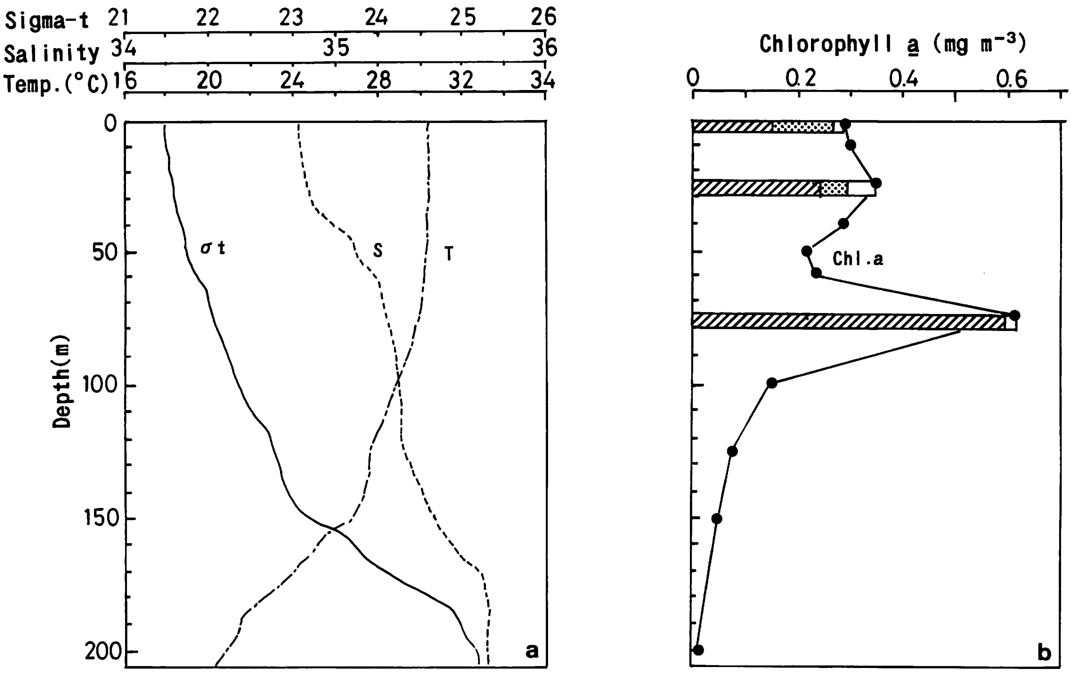

Fig. 3. (a) Vertical distributions of water temperature (T), salinity (S) and density (σt) in the upper 200 m layer. (b) Vertical profile of chlorophyll *a* concentrations (Chl. *a*) and size distribution of phytoplankton at surface, 25 and 75 m layers. The hatched, dotted and white bars indicates the fractions less than 3 μm, between 3 and 10 μm and more than 10 μm, respectively.

552 nm, and the attenuation coefficients at 481, 599 and 682 nm from surface to 10 m depth were 0.096, 0.143 and 0.377 m^{-1}, respectively (Fig. 4b). The light condition in this site was almost similar to those in the western Pacific Ocean (Matsuike 1973). Our results indicated that phytoplankton at the SCM layer could alive under such dim light and restricted wave length conditions.

The concentrations of nitrate, nitrite, phosphate and silicate at each depth are shown in Table 1. The concentrations of nutrients in surface and 25 m depth were extremely low, and increased with the depth around the SCM layer. The nutrient concentration in this area was almost the same as those in the subtropical regions (Yamaguchi and Ichimura 1980, Furuya and Marumo 1983).

In the SCM layer chlorophyll *a* concentration was 0.61 $mg\,m^{-3}$ (Fig. 3b), which was 2.1 times higher than that in the surface water. The integrated chlorophyll *a* concentration from 50 m to 100 m occupied 46% (41.9 $mg\,m^{-2}$) of the total amount of chlorophyll *a* in the water column from the surface to 200 m.

Size distribution of phytoplankton

The pico-plankton (smaller than 3 μm) occupied the large parts of the fraction in every depth as shown in Fig. 3. It constituted 61% of the total chlorophyll *a* concentration, and in the SCM layer more than 90% of the chlorophyll *a* was contained in the pico-plankton. This result was coincident well with those in the tropical regions reported by Takahashi and Hori (1984) and Le Bouteiller and Herbland (1984). Phytoplankton of small size at the SCM layer was mainly composed of flagellates and monads, such as species of *Micromonas*, *Ochromonas* and *Synechococcus* (Johnson and Sieburth 1982, Furuya and Marumo 1983, Takahashi and Hori 1984). Therefore, it is concluded that the difference in vertical distribution of chlorophyll *a* concentration and size distribution of phytoplankton

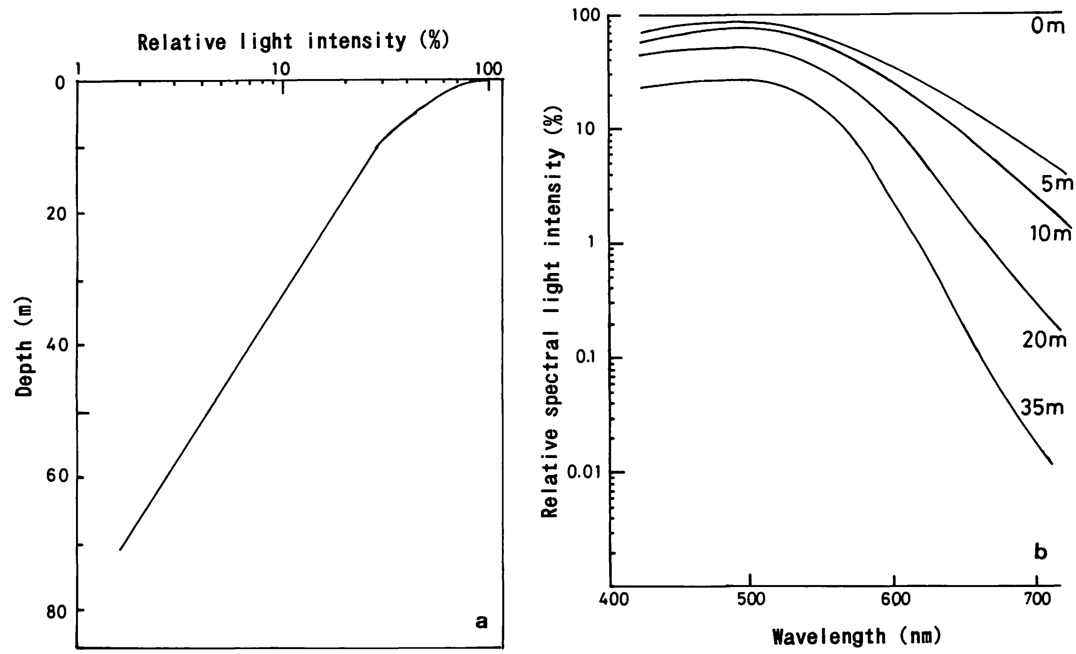

Fig. 4. (a) Relative underwater light intensity in the studying site. (b) Distributions of relative downward underwater spectral irradiance at the other site (7°40'S, 160°30'E) in Solomom Sea.

is due to the difference in species composition between the surface waters and the SCM layer.

Photosynthesis-light curves

Photosynthesis-light curves of phytoplankton from surface, 25 and 75 m layers were shown in Fig. 5a. In the curve of 75 m depth (SCM) the photosynthetic rate was 0.15 mgC mg·chl·a^{-1} h^{-1} at the saturation point of 35 $\mu E\, m^{-2}\, s^{-1}$ which corresponds to 1.0% of downwelling irradiance around noon on a clear day in early December. As can be seen in Fig. 5b, such a low saturating light intensity for photosynthesis of the SCM phytoplankton suggested the shade adaptation of phytoplankton as indicated by several investigators (e.g. Ichimura *et al.* 1962, Shimura and Ichimura 1973). The photoinhibition of photosynthesis was clearly found at the irradiance stronger than 90 $\mu E\, m^{-2}\, s^{-1}$ for the SCM sample. The maximum photosynthetic rate of the surface and 25 m depth samples was 0.75 and 1.1 mgC mg·chl·a^{-1} h^{-1}, respectively. As can be seen in Fig. 5a, high photosynthetic rates at the high saturating light intensities suggest that the phytoplankton at surface and 25 m layers adapted to higher light intensities. The difference in such characteristics as pho-

Table 1. Concentrations of nutrients at surface, 25 m and 75 m depth at the studying station.

Depth (m)	Silicate (μg-at l^{-1})	Phosphate (μg-at l^{-1})	Nitrate (μg-at l^{-1})	Nitrite (μg-at l^{-1})
0	4.79	0.70	0.51	0.024
25	3.52	0.72	0.87	0.027
75	2.91	0.70	0.85	0.025

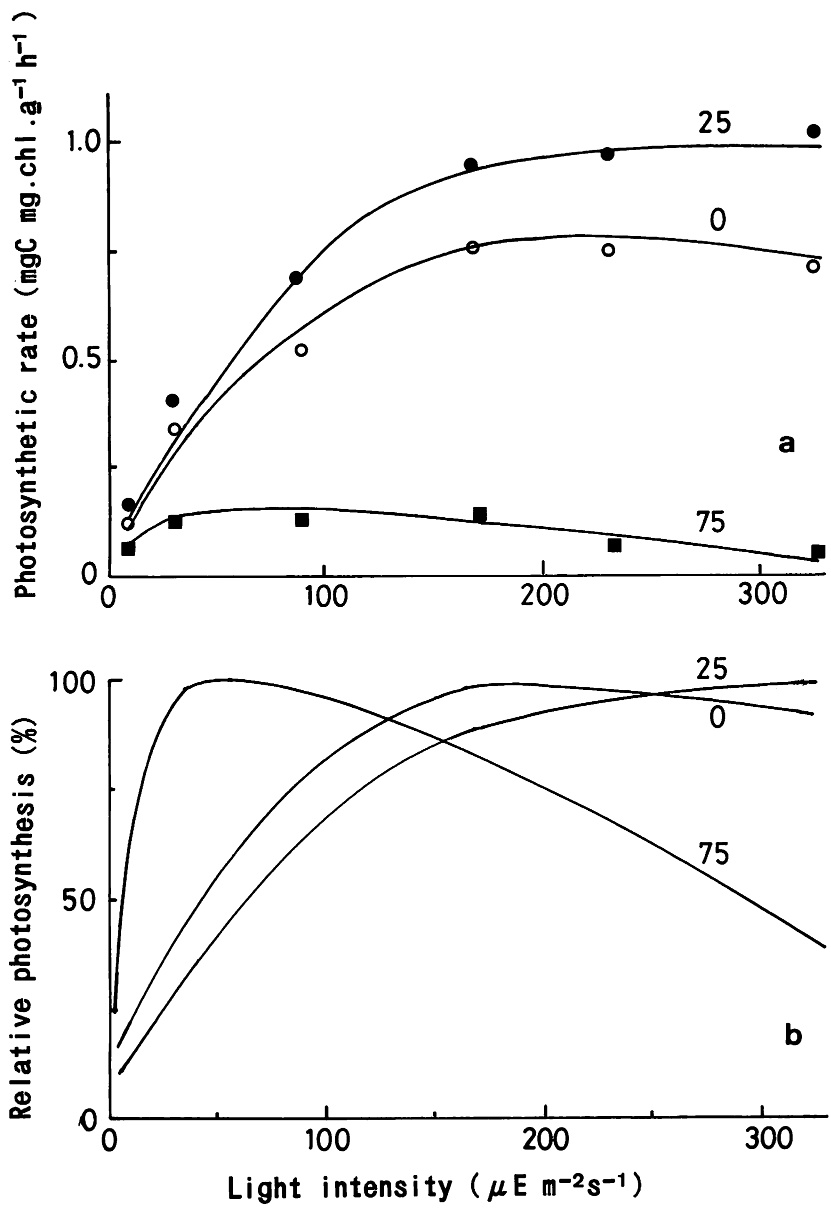

Fig. 5. Photosynthesis-light curves showed by per unit amount of chlorophyll *a* (a) and relative rate (b) of phytoplankton collected from surface, 25 and 75 m depth.

tosynthesis rate and saturation point in photosynthesis-light curves between shallow water and SCM layer phytoplankton may be caused by the light condition at each layer as mentioned above. The maximum photosynthetic production at surface at 25 and 75 m depths was 0.31, 0.50 and 0.086 mgC $m^{-3} h^{-1}$, respectively. These values were higher than those in the subtropical western north Pacific Ocean reported by Yamaguchi and Ichimura (1980), and lower than those in the tropical north Pacific Ocean described by Taguchi (1980).

Water samples from the surface and the SCM layers were incubated under the controlled light intensity of 35 $\mu E\,m^{-2}\,s^{-1}$.

Table 2. Quantum yield for photosynthesis [mgC mg·chl·a^{-1} h^{-1} (μE m^{-2} s^{-1})$^{-1}$] collected from surface, 25 m and 75 m depth under day-light (400–700 nm) and blue-light (400–550 nm) of 35 μE m^{-2} s^{-1}.

Depth (m)	$Q_{day\text{-}light}$	$Q_{blue\text{-}light}$	Q_{blue}/Q_{day}
0	0.015	0.0086	0.57
25	0.014	0.0078	0.56
75	0.0042	0.0044	1.05

Quantum yield of photosynthesis is determined by CO_2 molecules fixed in the biomass per quantum irradiance of light absorbed by phytoplankton (Kirk 1983). Quantum yields of photosynthesis at 35 μE m^{-2} s^{-1} under daylight (Q_{dl}) and under blue light (Q_{bl}) of phytoplankton collected from surface, 25 and 75 m depth were calculated (Table 2). The ratio of Q_{bl}/Q_{dl} is an index of utilization of blue light for photosynthesis (photosynthetic efficiency). Although the quantum yields of photosynthesis in the surface and 25 m layer samples under daylight and blue light were 1.8 times or more higher than those in the SCM, the photosynthetic efficiency of 1.05 for the SCM layer was about two times higher than those for the surface and 25 m samples. This means that the phytoplankton at the SCM layer adapted physiologically to low intensity of blue light by enhancing their photosynthetic activity similar to the cultured SCM microalgae reported by Kamiya and Miyachi (1980). Our result was also supported by the report of Ikeya *et al.* (1991) that the photosynthetic response of cyanophytes isolated from SCM layer in the Kuroshio region of Japan was active for blue-green light. This characteristic might be due to high concentration of phycoerythrin, as described by Ikeya *et al.* (1991). Futher investigations should be done in detail on the photosynthetic pigment system of phytoplankton collected from SCM layer.

In conclusion, the photosynthetic characteristic at the SCM layer was stongly influenced by the light conditions. Standing stock of chlorophyll *a* at the SCM layer was higher than those at the shallow layer, although primary production at the SCM was low because of dim light condition.

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佐藤博雄*・田中英夫*・小池　隆**：ソロモン海における亜表層クロロフィル極大層の光環境と光合成特性

1989年の12月上旬，ソロモン海の1測点 (5°43′S, 153°30′E) において植物プランクトンの生産力を測定した。水深 75 m に表層の約2.1倍の濃度 (0.61 mg・chl・a m^{-3}) をもつクロロフィル極大層 (SCM) が認められ，この層の相対光強度は水面上の日射量の1.2%であった。クロロフィル極大を含む水深 50–100 m のクロロフィル a 積算値は水柱全体（0–200 m の積算値）の46%であった。クロロフィル極大層の植物プランクトンの光合成–光曲線で，光合成速度は 35 μE m^{-2} s^{-1} で最大に達し 0.15 mgC mg・chl・a^{-1} h^{-1} であった。青色光 (35 μE m^{-2} s^{-1}) を照射した場合の 0，25および 75 m 層の植物プランクトンの昼光色光に対する光合成効率は，それぞれ57，56および105%であった。また，水深 75 m のクロロフィル極大層における生産量 (0.086 mgC m^{-3} h^{-1}) は 25 m 層 (0.50 mgC m^{-3} h^{-1}) の17%であった。（*108 東京都港区港南4-5-7　東京水産大学，**514 三重県津市上浜町1515　三重大学生物資源学部）