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Selective Transmission of Light in the Ocean Waters and its Relation to Phytoplankton Photosynthesis*

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Abstract: Occurrence of the depth differences in pigment composition and photosynthetic properties of marine phytoplankton were examined in relation to the spectral changes of light with depth. Phytoplankton were taken from various depths in the northwestern North Pacific, and their absorption spectra were determined with intact cells and in 90% acetone extract. The photosynthetic activities of phytoplankton were concurrently measured under blue, green, red and white light. The difference in absorption spectra for the surface and deeper samples was considerably small, indicating that the prevailing green or blue light in the deeper layers may have little significance for depth-variations of the pigment composition in marine phytoplankton. The depth differentiation in the shape of the light-photosynthesis curve was marked in a well stratified water column but no active response of deeper phytoplankton to green light could be confirmed. The photosynthetic efficiencies of phytoplankton for blue and green light were approximately 105-115% and 80-90% of white light, respectively, irrespective of sampling depth.

1. Introduction

Light, one of the crucial environmental factors, affects the process of photosynthesis in both quality and quantity, and therefore the growth of plants. On the other hand, it has been well known that the light penetrating into the water column changes remarkably its spectral composition as well as intensity (cf. JERLOV, 1968). These phenomena lead to the classical theory of chromatic adaptation or light adaptation of algae in relation to their vertical distributions in aquatic environments. Studies in this field, however, have mainly dealt with seaweeds and surprisingly little information is available for phytoplankton. As far as we know, photosynthetic adaptation of natural phytoplankton to light intensity has been investigated by several investigators (TALLING, 1957; STEEMANN-NIELSEN and HANSEN, 1959; RYTHER and MENZEL, 1959; ICHIMURA, 1960; JØRGENSEN, 1969), but our knowledge of the chromatic adaptation still remains far from being understood. The adaptability of phytoplankton to light conditions at which they live is not only a fascinating subject in the study of primary production in the sea but also important from eco-physiological viewpoint.

Some properties of photosynthetic adaptability of phytoplankton to light environments especially in relation to the spectral changes of underwater light were pursued on several cruises during the period of 1967 to 1969 in the North Pacific.

2. Methods

Light attenuation in seawater was measured by a selenium underwater photometer in conjunction with neutral and colored glass filters. The relative sensitivities of a photodetector fitted with each of filters are shown in Figure 1. Water temperature was measured with reversing thermometers. For measurement of *in situ* photosynthesis, water samples were taken from various depths with twin 20-l Van Dorn samplers made of plastic and they were poured into clear bottles made of Pyrex glass, 100 ml in capacity. After adding each

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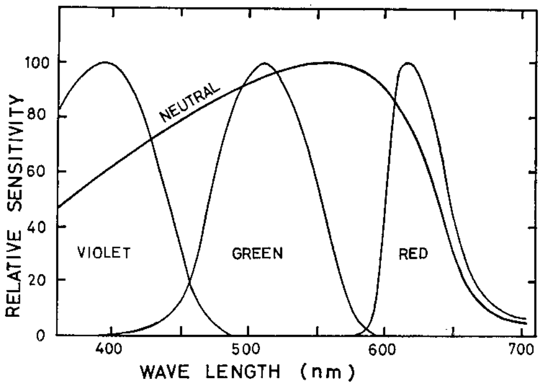

Fig. 1. Spectral sensitivity of an underwater photometer fitted with neutral or colored glass filters.

one ml of 10μCi/ml $NaH^{14}CO_3$ solution to the bottles, a series of bottles were covered with aluminium foil for simultaneous determination of the dark carbon fixation. The bottles were suspended from a buoy at the respective depths from which the water samples had been taken. The water samples from the surface and the depths of 50, 75 and 100 m were also suspended at the depths in parallel with those of the ordinary *in situ* experiment. After exposure for midday 3 hours the bottles were taken up and each of the water samples was filtered through a sheet of HA Millipore filter. Filters were dried in a desiccator and their radioactivity was measured with a 2π gas-flow counter (Aloka TDS-1). The value of the dark fixation was subtracted from that of the light bottle to obtain a corrected light value.

In the laboratory on shipboard, photosynthesis of phytoplankton was measured by the light and dark bottle method using ^{14}C technique. The water samples in glass bottles were incubated in a water bath at *in situ* temperature for 2 hours under various light intensities regulated by varying the distance from the light sources. The light sources used were the following lamps; ordinary incandescent lamp (WL, 3,200 °K, white light), daylight fluorescent lamp (FL-20-D, white light), blue fluorescent lamp (FL-20-B, blue light), green fluorescent lamp (FL-20-GF, green light) and red fluorescent lamp (FL-20-RF, red light). The spectra of radiation energy with various lamps are given

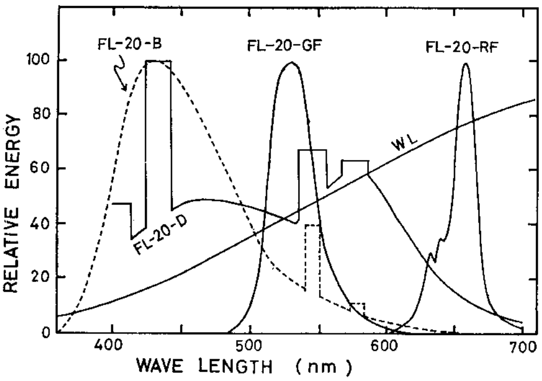

Fig. 2. Spectral energy distributions of five lamps used in the present work. Fl-20-B, FL-20-GF and FL-20-RF are colored fluorescent lamps and FL-20-D is a daylight-type fluorescent lamp. WL is usual incandescent lamp (3,200°K).

in Figure 2. Light intensity was measured with a selenium photometer and converted to radiation flux density ($erg/cm^2 \cdot sec$). The conversion factors used were obtained for individual light sources by the intercalibration of light measured with the photometer and the thermopile, after cutting off the thermal radiation through a water filter of 5 cm. The concentration of phytoplankton in the water sample was assessed by chlorophyll measurement. The water samples of 5 to 10 l were filtered through HA Millipore filters and kept in the cold and dark until analysis. The chlorophyll *a* concentration was measured according to the method recommended by SCOR-UNESCO W. G. 17 (1966).

3. Results

1. Selective transmission of light in seawater

The field measurements of light penetration in the water were made at several geographic locations in the northwestern North Pacific (Figure 3). Figure 4 illustrates the light penetration measured in three spectral regions (red, green and violet) and in the entire visible light range for the following water masses; the Subtropical Countercurrent, the Kuroshio, the Kuroshio Extension and the Oyashio. The green region of the spectrum was the most transmissive, the violet was somewhat less transmissive, and the red region was rapidly absorbed. It is evident that the features of selective transmission of light vary considerably with water masses. Table 1 shows the mean attenuation coefficient for neutral, violet, green and red light calculated from the transmission curves in Figure 4. The table also presents attenuation coefficients of incident solar radiation in a pure water column calculated using the data on spectral distribution of incident light on clear day presented by WALSH (1961) and those on transmission coefficients for pure water by CLARKE and JAMES (1939). The values quoted varied in the range of 0.169 in the red region to 0.009 in the green region according to the water masses. In the Subtropical Countercurrent, the values were minimal for each waveband and they were roughly the same as in the pure water. The geographic difference in the attenuation coefficients was relatively small for the red region but was noticeable in the green and violet regions; the values in the Oyashio were about 2.5 times larger than those in the subtropical clear water.

The vertical gradient of light intensity was slight in clearest oceanic water of the Subtropical Countercurrent and the depth at which the visible light reduced to 1 % of the surface was

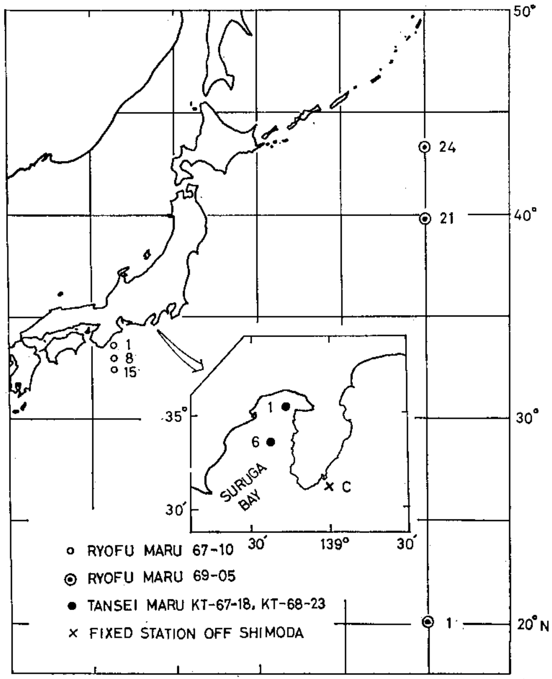

Fig. 3. Map of the northwestern Pacific showing the location of sampling stations.

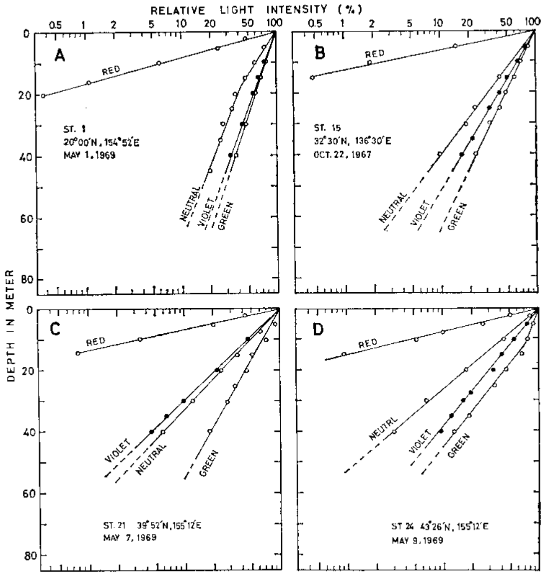

Fig. 4. Depth profiles of different spectral regions in percent of surface light intensity. A, the Subtropical Countercurrent; B, the Kuroshio; C, the Kuroshio Extension; D, the Oyashio.

Table 1. Attenuation coefficients per meter for different wave length regions obtained in the northwestern North Pacific and pure water.

	Subtropical Countercurrent	Kuroshio Current	Kuroshio Extension	Oyashio Current	Pure water
N	0.014	0.025	0.031	0.038	0.012
V	0.010	0.019	0.033	0.026	0.011
G	0.009	0.016	0.018	0.024	0.012
R	0.125	0.169	0.148	0.129	0.096

N, neutral; V, violet; G, green; R, red.

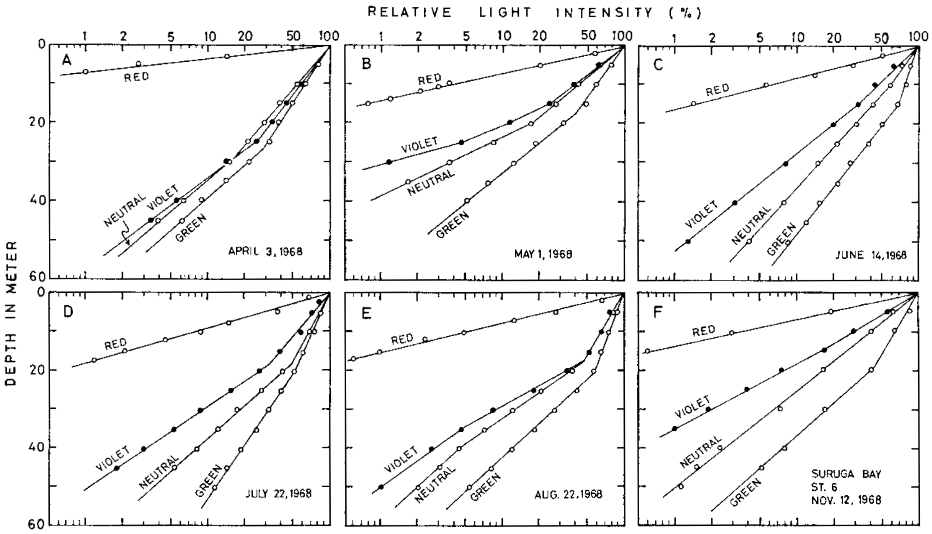

Fig. 5. Seasonal changes of light penetration at Station C in neritic water off Shimoda (34°36′N, 138°59′E).

estimated to be 120–150 m. In somewhat clear oceanic water of the Kuroshio the light attenuation was still gradual and an approximate depth of 1 % light extended to 80–100 m. At further north latitudes relatively rapid attenuation of light was measured, particularly in the Oyashio regions, where 1 % of the surface visible light penetrated to a depth of 69–70 m in turbulent water masses and 40–50 m in stable water masses.

The light attenuation in the sea varies widely with a combining function of such agents as absorption and scattering of light by water molecules, dissolved organic matter and suspended particulate matter. Thus it varies seasonally, especially in coastal waters, from month to month or one day to another. Figure 5 shows the light penetration measured in a near-shore water adjacent to the Kuroshio, 5 miles off the Shimoda Marine Biological Station, Tokyo Kyoiku University. The depth of 1 % light level varied from the lowest 40 m in late spring and autumn to twice as much the depth of 80 m in midsummer. These variations are probably attributed in the former case to the vigorous growth of phytoplankton and in the latter case to the temporal replenishment of the relatively clear oceanic water from the Kuroshio which occasionally prevails near this site.

2. Depth-profiles of photosynthetic rate of phytoplankton

For measuring the photosynthetic response of phytoplankton to light intensity in the water column, the *in situ* experiments were made at several stations in the northwestern North Pacific. Results are shown in Figure 6, where open circles were obtained by the usual *in situ* method, and solid circles, oblique crosses and squares, with a series of water samples suspended at various depths. Photosynthetic rate was expressed in terms of mg C/(mg chl·h). In most cases, the samples gave profiles with a light inhibition in the surface layer and one maximum in the subsurface layer. The photosynthetic rate measured at the optimal light depth varied markedly with samples from large values in the surface samples to lower ones in deeper samples. It may be fairly asserted that the photosynthetic rates measured in the layers below the middle depth of the euphotic zone are similar for various samples. This may suggest that there is no appreciable occurrence of photosynthetic adaptation in deeper phytoplankton. As seen in Figure 6(A), however, the photosynthetic rate measured at the depth of 60 m was higher for *in situ* sample compared with those for the samples from the surface and the depth of 50 m and 75 m in the Kuroshio

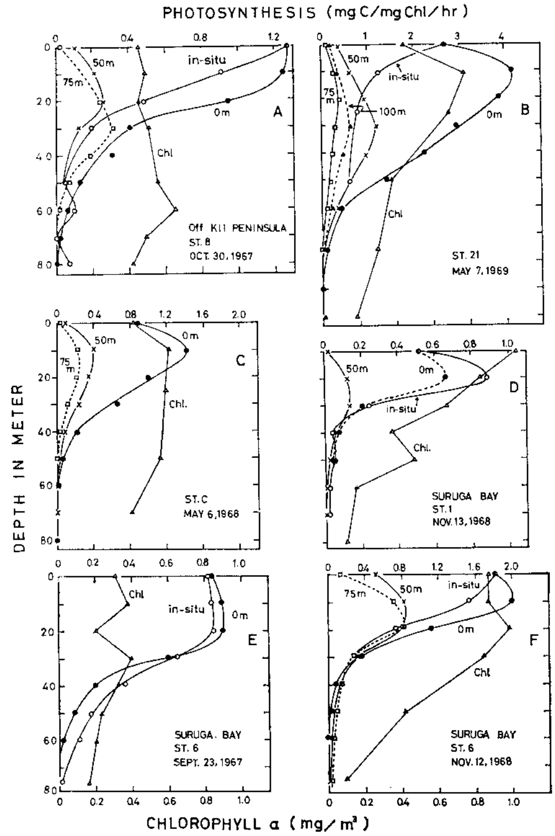

Fig. 6. Vertical profiles of photosynthetic rate of phytoplankton and chlorophyll *a* concentration in the Kuroshio (A), the Kuroshio Extension (B) and coastal waters (C-F). Further explanations are in text.

off Kii Peninsula. The same penomenon was also observed in neritic waters adjacent to the Kuroshio. Charts D, E and F in Figure 6 show the results obtained in Suruga Bay as part of JIBP-PM studies. In this area diatoms were dominant phytoplankton throughout a year. Dinoflagellates were also predominant in deeper layers. From the depth profiles of photosynthetic rate in charts E and F, it will be seen that photosynthetic rate of deeper phytoplankton is higher in deeper layers compared with the surface phytoplankton. In November, however, all samples of Station 1 (D) showed a considerably similar response to light intensity below middle layer of the euphotic zone.

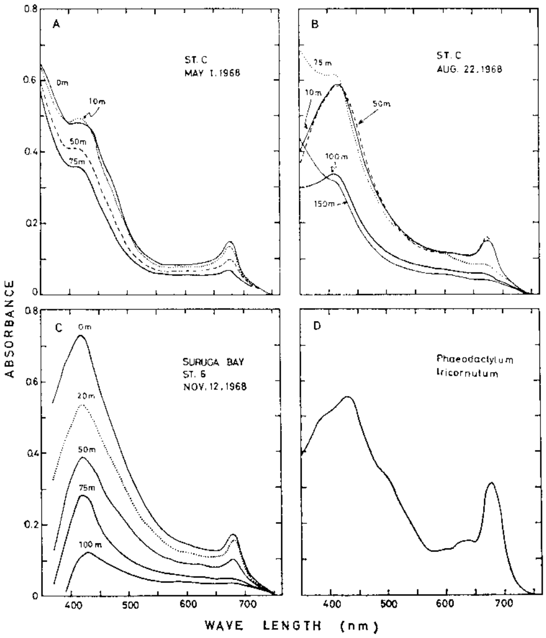

Fig. 7. Absorption spectra for particulate organic matter collected on a 47-mm HA Millipore filter. A-C; neritic water off Shimoda. D; *Phaeodactylum tricornutum* at early exponential growth phase under white light of 1,500 lux.

3. Depth difference in pigment composition of phytoplankton

To examine roughly the changes in pigment composition of phytoplankton with depth, the absorption spectrum of particulate organic matter was measured by the following procedure. The particulate organic matter in sample water was retained on a Millipore filter and the filter was set just before the photoreceptor of a Shimadzu Multipurpose Recording Spectrophotometer (MPS-50L). An untreated filter was used as a reference. Using the spectrophotometer and the Millipore filter, a strong scatterer, the effect of scattering on absorption measurement of the particulate organic matter was minimized. The curve was normalized to zero at 750 nm of the spectrum. The absorption curves for the samples collected from neritic waters adjacent to the Kuroshio and the cultured diatom *Phaeodactylum tricornutum* are shown in Figure 7. From these curves, it is apparent that the suspended matter attenuates considerably the short wave length light. The two peaks (or bumps) at 410–440 nm and 670–680 nm were found in all samples but their magnitude varied considerably from sample to sample. This optical property is similar to that reported by YENTSCH (1962), and he suggests that the contribution of the chloroplastic pigments to the absorption of light changes with depth and water masses. Furthermore, the ratio of absorbance at the two peaks is considerably high compared with that for young culture of the diatom *Phaeodactylum tricornutum* (Figure 7-D). These facts suggest that some components of suspended matter other than chloroplastic pigments contribute considerably to the absorption of shorter wave lengths. All samples on May 1 (Figure 7-A) showed a monotonic increase in absorption towards shorter wave lengths. This is probably due partly to the dissolved organic substances such as "yellow substance" associated with the particulate organic matter or adsorbed on the filter.

Figure 8 shows the absorption spectra in 90 % acetone extracts of the particulate organic matter. Measurement of absorption was made at wave length intervals of 5 or 10 nm and log E-spectrum was normalized to −1.20 at 663 nm. Besides large absorption peaks at 430 nm and 663 nm, there were appreciable absorption peaks at about 580 nm and 620 nm. These are probably due to the addition of the small bands of chlorophyll *a* and chlorophyll *c*. A shoulder of fucoxanthin at 480 nm was not clear in most of the samples. Since the difference in the shape of absorption spectra for the surface and deeper samples was relatively small, the effect of profuse blue green light in the deeper layer may be of little significance for the pigment formation of phytoplankton. This conclusion might not be applied to the water mass where phytoplankton consists mainly of blue-green algae.

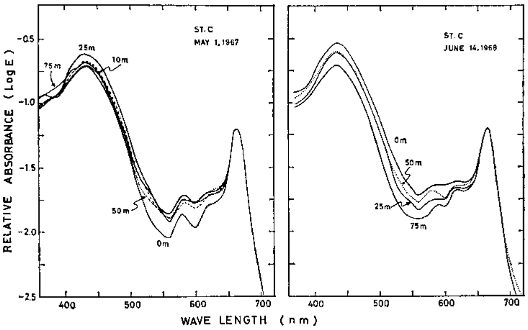

Fig. 8. Absorption spectra for 90 % acetone extracts of particulate organic matter collected from various depths at Station C.

4. Depth difference in photosynthetic properties of phytoplankton

The shape of light-photosynthesis curve was examined for understanding the photosynthetic response of phytoplankton to light intensity. Some results measured under the ordinary incandescent lamp (WL, 3,200 °K, white light) are shown in Figure 9. The depth differentiation of the curve was noticeable for the samples from the highly stratified water masses (B, C, D), in which the curve was differentiated from the sun type of the surface sample to the shade one of the deeper samples. The differentiation was slight in the turbulent water masses (A). However, exceptional examples deviated far from this general pattern were sometimes observed. As has been shown in Figure 9-A

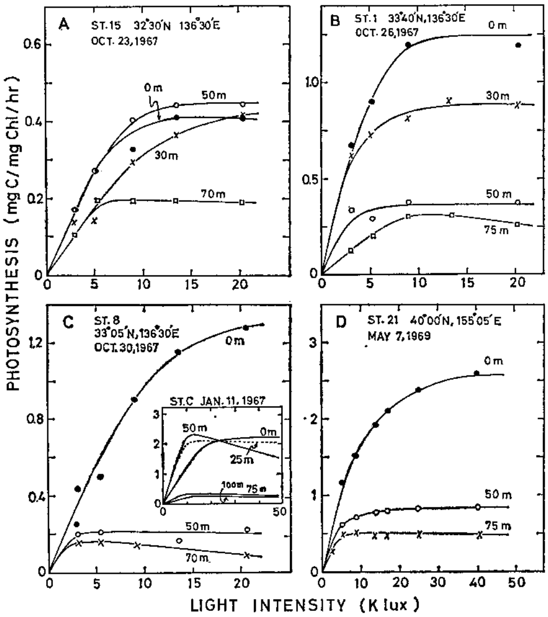

Fig. 9. Light-photosynthesis curves for samples from different depths in various water masses. A–C; the Kuroshio. D; the Kuroshio Extension. Figure inserted in C; coastal water.

and the figure set in chart C, the initial slope ($\Delta P/\Delta I$) of the curve and the photosynthetic rate at light saturation of subsurface samples (25 and 50 m) were comparable to those of the surface sample. As had already been discussed in the previous papers (TAKAHASHI *et al.*, 1971; SHIMURA and ICHIMURA, 1972), this photosynthetic nature of deeper phytoplankton has probably resulted from specific physiological properties peculier to algal species and/or growth conditions.

The effect of the quality of light on photosynthesis was examined in a series of experiments. Photosynthetic rate was measured under illumination of different qualities described in the method, and light intensity was expressed in terms of radiation flux density within the given waveband (erg/cm^2·sec). Figure 10 shows the light-photosynthesis curves of the phytoplankton from the depths of 0, 25, 50 and 75 m in the neritic water off the Shimoda Marine Biological Station in May 1968. A moderately significant difference was noticed in apparent photosynthetic efficiency for different wavebands. It is difficult to conclude, however, with definite precision that deeper phytoplankton utilize more effectively the green light compared with the surface phytoplankton. Similar experiments were made at several stations in the northwestern North Pacific. The apparent photosynthetic efficiency of phytoplankton for different wavebands was deduced from the initial slope of the curve obtained from 2-hour incubation (mg C/mg Chl/hr/10^4 ergs·cm^{-2}·sec^{-1}). As seen in Figure 11, except for a few data, the apparent photosynthetic efficiency was in order of blue>white (fluorescent light)>red>green. The apparent efficiency of green light was 80-90 % and that of blue light was 105-115 % of the white light, irrespective of sampling depth. An active response of deeper phytoplankton to green light could not be confirmed in the present study.

4. Discussion

One of the essential problems in the study of phytoplankton ecology in the ocean is to make clear the photosynthetic responses of phytoplankton to spectral changes of light in the water column. On this line, pigment composition and photosynthetic properties of phytoplankton were examined on samples taken

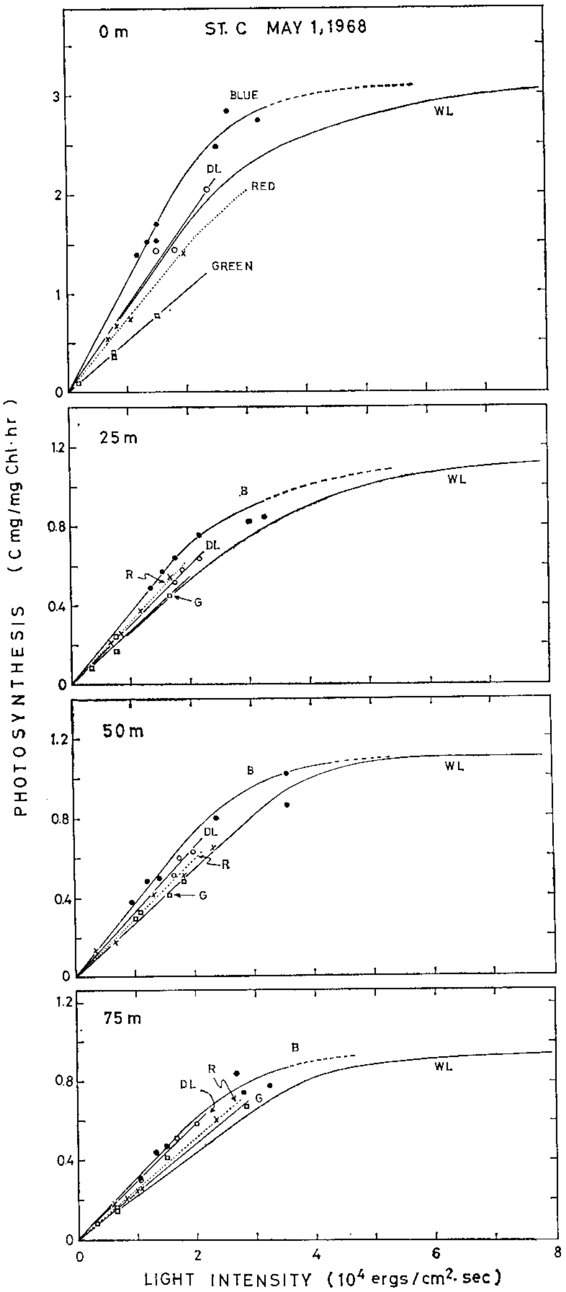

Fig. 10. Light-photosynthesis curves obtained under different qualities of light for phytoplankton collected from various depths in neritic water off Shimoda.

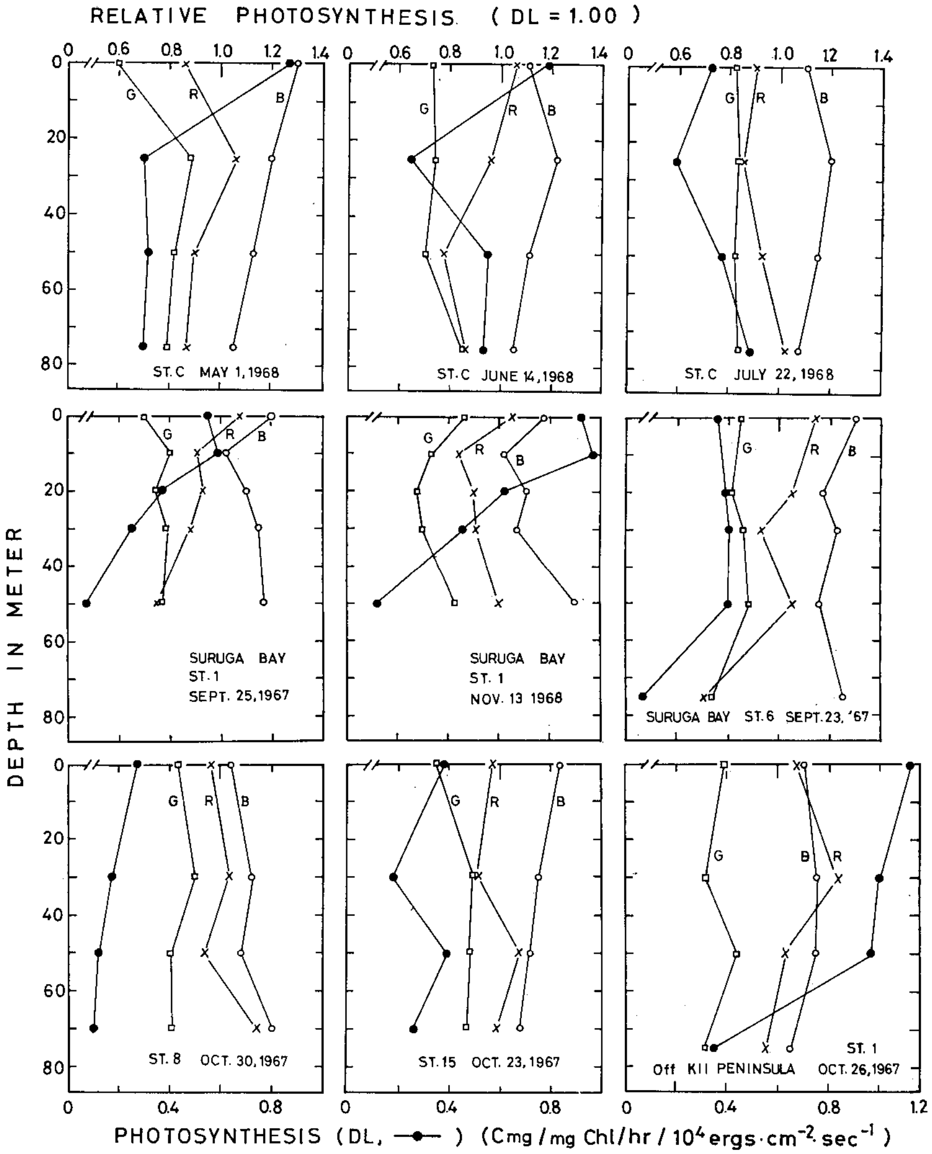

Fig. 11. Efficiency of different qualities of light for photosynthesis of phytoplankton collected from various depths. Photosynthetic rate per unit energy of white light (FL-20-D) (C mg/mg Chl/hr/10^4 ergs·cm^{-2}·sec^{-1}) is indicated with solid circles and other symbols are for relative photosynthetic efficiency of colored light to white light.

from various depths in the northwestern North Pacific.

The apparent photosynthetic efficiencies of phytoplankton for blue and green light were approximately 105-115 % and 80-90 % of white light, respectively, without regard to sampling depth. The high efficiency of diatoms for green light is probably explained by a large contribution of fucoxanthin in photosynthesis (TANADA, 1951).

The results obtained in the present study could not provide any definitive proof to the occurrence of chromatic adaptation in phytoplankton populations. Pigment composition and the apparent photosynthetic efficiency of phytoplankton grown under different quality of light at different depths were not variable but rather similar. This has been ascertained by several laboratory experiments. MANN and MYERS (1968) could not observe any considerable differences in absorption spectrum of *Phaeodactylum* grown under red (>650 nm) and white light. WALLEN and GEEN (1971 a, b) showed that the ratio of carotenoids to chlorophyll *a* in *Cyclottela nana* and *Dunaliella tertiolects* was higher to some extent in cells grown under green light than under blue light or white light, but the increase of carotenoids did not improve photosynthetic rate in green light. Their results may indicate that the increased carotenoids were photosynthetically in a nonfunctional state in cells, although the absorption spectra of intact cells were not presented. From these facts the adaptive photosynthetic response of phytoplankton to chromatic light is probably negligible in diatoms. The results of our study may be a general tendency in the sea, where diatoms are dominant among numerous phytoplankton species. However, some groups of blue-green algae (FUJITA and HATTORI, 1960, 1962; JONES and MYERS, 1965) and red algae (BRODY and EMERSON, 1959) show a considerable change in pigment composition by the quality of light under which they have been grown, and the difference in pigment compositions brings about the differences in photosynthetic action spectrum. This may be true for marine blue-green algae such as *Trichodesmium*, which is distributed widely in tropical and subtropical oceans.

On the other hand, it has been shown that blue light stimulates the incorporation of fixed carbon atoms into amino acids and protein, while red light into carbohydrates and sugars (PIRSON and KOWALLIK, 1964; OGASAWARA and MIYACHI, 1970). WALLEN and GEEN (1971c) examined the photosynthate in phytoplankton population in relation to light quality under natural conditions. They found that the distribution of ^{14}C in newly formed organic compounds is large in carbohydrate fraction in near surface layer and the distribution in amino acid increases with depth, and these changes are in response to light quality rather than intensity. Further studies are needed to make clear the effect of the spectral changes of light on the pigment system and the photosynthetic products of phytoplankton in the sea.

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海中における光の選択的透過と植物プランクトンの光合成

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要旨：海中光の深度に伴う，強度及び波長組成の変化に対応した植物プランクトンの光合成的適応を明らかにする目的で，北部北太平洋の数測点で採取した植物プランクトンについて，色素組成と光合成特性の深さによる変化を調べた．植物プランクトンの色素組成は生細胞及び 90％ アセトン抽出液の吸収スペクトルから調べたが，生育深度による相違は顕著でなく，生産層深部で優占的である緑色青色光の植物プランクトンの色素組成に対する効果は小さいものと考えられる．光合成特性は青色光，緑色光，赤色光及び白色光を用いて調べた．よく成層した水塊中の植物プランクトンの光－光合成曲線は表層の陽生型から深層の陰生型へと顕著な分化を示したが，深層の植物プランクトンの緑色光に対する光合成的適応は確認できなかった．植物プランクトンの青色光下と緑色光下での光合成効率は生育深度に関係なく，それぞれ白色光下のそれの 105～115％ と 80～90％ であった．