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Changes in Photosynthetic Pigment Concentration in Seaweeds as a Function of Water Depth

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Abstract

We conducted a study of the relationship between changes in photosynthetic pigment content and water depth in Great Harbor near Woods Hole, Massachusetts, USA, on the green algae *Ulva lactuca* and *Codium fragile* and the red algae *Porphyra umbilicalis* and *Chondrus crispus*. A calibrated underwater photometer equipped with spectral band filters measured light attenuation by the water column. The depth required for a 10-fold diminution of photon flux was 3.6, 5.3, 6.0 and 6.0 m for red, blue, yellow and green light, respectively. Seaweeds were attached to vertically buoyed lines and left to adapt for 7 days; then, with their positions reversed, they were allowed to readapt for 7 days. All species showed greater photosynthetic pigment content with increased depth. Further, the ratio of phycobiliproteins and chlorophyll *b* to chlorophyll *a* increased with depth. Changes in pigment content were reversible and occurred in the absence of cell division. There was a net loss of pigments near the surface (high irradiance), and subsequent synthesis when seaweeds were transferred to a position deep in the water column (low irradiance). In contrast, seaweeds which were found in intertidal habitats changed only their pigment concentration, and not pigment ratio, a phenomena analogous to higher plant sun and shade adaptation. Therefore, seaweeds modify their photon-gathering photosynthetic antennae to ambient light fields in the water column by both intensity adaptation and complementary chromatic adaptation.

Introduction

Trends observed in the vertical distribution of seaweeds correlated with their photosynthetic pigment content led to the concept of a phylogenetic adaptation to the prevailing color(s) of light at the depths where the seaweeds occurred (see Rabinowitch, 1945, for discussion). (We define "seaweeds" here exclusively as benthic thalloid marine algae.) That is, green seaweeds (Chlorophyceae) were presumed to predominate in shallow waters, red seaweeds (Rhodophyceae) in deep waters, and brown seaweeds (Phaeophyceae) in intermediate depths. All these seaweeds contain the green chlorophyll *a*, and accessory photosynthetic pigments which, when present in sufficient quantities, blend with or mask the visual color of chlorophyll *a*. Specific accessory pigments are diagnostic of each of the three classes of seaweeds, i.e., the red and blue phycobiliproteins of the red algae, the green chlorophyll *b* of the green algae, and the brown xanthophylls of the brown algae.

The various dissolved and particulate substances present in seawater largely determine its optical properties (Jerlov, 1968). There is an absorption and scattering of light in the sea, both of which are wavelength-dependent. Simply stated, there are changes in both light quality and quantity with increasing depth, and the precise characteristics are determined by the particular water column. Sunlight becomes blue-green after passing through several meters of seawater. Consequently, seaweeds living deep beneath the sea receive little light of wave-lengths which are effectively absorbed by chlorophyll (violet and red) to

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"drive" photosynthesis. However, the accessory pigments will absorb the available blue-green light, the red phycobiliproteins better than the brown xanthophylls, and the energy of the absorbed photons is coupled to photosynthesis by resonance transfer from "antenna" (accessory plus most of chlorophyll *a*) to photoactive (species P_{680} and P_{700} of chlorophyll *a*) pigments.

Adaptation of the antenna or light-harvesting pigments is one of many physiological adaptations in the photosynthetic apparatus of seaweeds to the ambient light field. Other components might include both quantitative and qualitative aspects of chloroplast development, capacity of the photosynthetic electron-transport chain, and rate-limiting enzymes in the dark reactions (as RuDP carboxylase) (see Björkman, 1973, for review). However, little data for the physiological-ecology of seaweeds exists, and therefore, we chose to begin with pigment variations. The following is an account of how seaweeds quantitatively adapt their photon-gathering antennae to ambient light fields under natural conditions.

Materials and Methods

Study Site

We conducted this study during the summer of 1974 and 1975 at the Woods Hole Marine Biological Laboratory, Massachusetts, USA, and in the waters immediately adjacent to the Laboratory, especially Great Harbor.

Seaweeds

The seaweeds used for this study were the green algae *Ulva lactuca* and *Codium fragile* and the red algae *Porphyra umbilicalis* and *Chondrus crispus*. The green algae were used to test chlorophyll *b* - chlorophyll *a* photosynthetic pigment systems and the red algae to test phycobiliprotein-chlorophyll *a* systems. We chose *U. lactuca* and *P. umbilicalis* for their optical thinness; both are membranous seaweeds, and light passes through two cell layers and one cell layer, respectively. *Codium fragile* and *Chondrus crispus* were chosen for their optical thickness; both have thick cortical and medullary tissue systems through which little light can pass. All the seaweed species are of economic importance. *U. lactuca* (sea lettuce) and *P. umbilicalis* (laver) are extensively cultivated and eaten in Asia. *Chondrus crispus* (Irish moss) is the source of the phycolloid carrageenan, and is harvested on the northeastern coast of North America for this purpose. *Codium fragile* (dead-man's fingers), a recently introduced component of the southern New England flora, is a nuisance species in shellfisheries (Wassman and Ramus, 1973).

Vertical Suspension of Seaweeds

For a given experiment we collected individuals of a species at the same time and locality to insure physiological uniformity. Seaweeds were held firmly in the turns of a polypropylene line buoyed from a surface float (Fig. 1). A 1 kg weight at the lower end held the line vertical. The lower end of the line was attached to a 2 m link-chain and cement block, allowing the line to rise and fall with the tide without any point on the line changing position with respect to the surface during the tidal cycle. We attached seaweeds to the lines at measured intervals from the surface for the duration of the experiment, usually 7 days.

Vertical Position Reversal

To test pigment-content reversibility, a line which had been in position for 7 days was simply reversed; that is, the bottom became the top and the top became the bottom. Seaweeds were then allowed to adapt to their new light fields for 7 days.

Pigment Analyses

We measured pigment content with a Pye-Unicam (P-1800B) double-beam recording spectrophotometer, either from whole mounted (*in vivo*) or solvent-extracted (*in vitro*) seaweeds. For *in vivo* measurements, a small piece of seaweed was placed on a HAWP Millipore filter, and the two were sandwiched between clear Plexiglass, then all placed in a standard 1 cm cuvette containing filtered seawater. The reference sample contained all components except the seaweed. The cuvettes were placed in an auxiliary position very near to the face of the photomultiplier tube. The seaweeds were then scanned from 350 to 750 nm. The Millipore filters provide a large and constant white-light scattering so that the additional scattering by the seaweed is negligible (Cellarius and Mauzerall, 1966). Seaweeds were mounted whole in this apparatus. For solvent extraction, we ground pieces

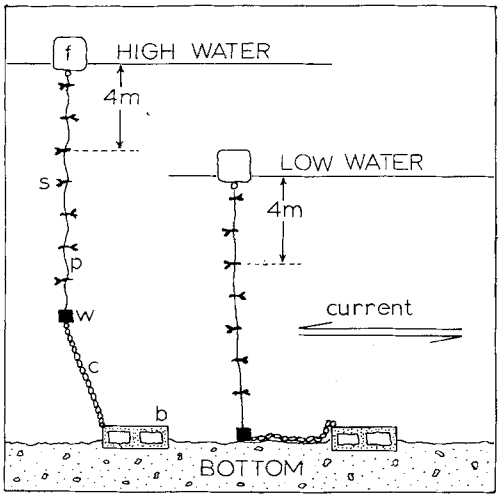

Fig. 1. Apparatus for suspending seaweeds in the water column so that distance of any seaweed relative to water surface remains constant during course of a tidal cycle. f: float; s: seaweed; p: polypropylene line; w: 1 kg weight; c: heavy chain; b: concrete building block

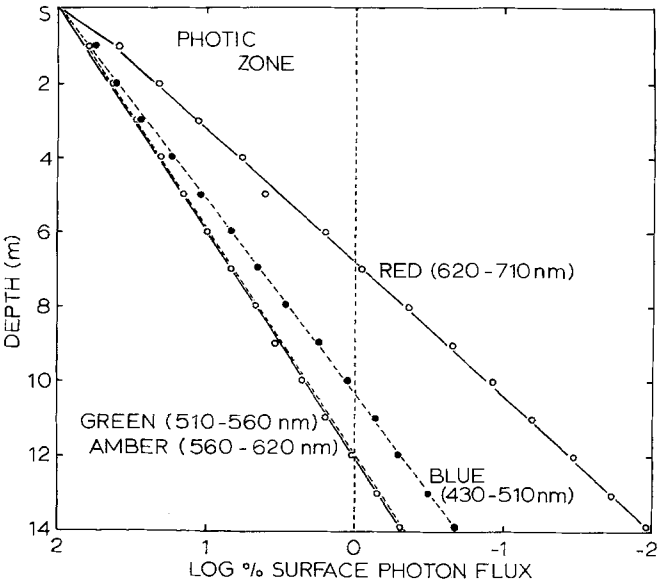

Fig. 2. Specific light-absorption characteristics of waters of Great Harbor as measured with underwater photometer equipped with Plexiglass transmission filters. Appropriate corrections have been made for the sensor sensitivity profile and filter transmission curves. Measurements were made on a clear windless day in July, 1975 at 14.00 hrs. Lower limit of photic zone is marked by vertical dotted line, and is defined as 1% of the surface photon flux

of seaweed in hand-tissue homogenizers and added acetone or methanol to a final concentration of 80 to 90%, plus a few mg of $MgCO_3$. The equations used to calculate chlorophyll concentrations were those of Arnon (1949) for acetone extracts, and those of Holden (1965) for methanol extracts. Pigment contents are given as a mean value ± one standard deviation, and are taken from at least 10 samples.

Light Measurements

Tyler (1973) has been critical of the use of lux measurements for correlation with oceanic productivity. He argues justifiably that spectral irradiance data should be converted from photometric units to quanta or power available. We describe here the methods we developed to meet his criteria.

We measured light attenuation by the water column with a Whitney-Montedoro LMD 8A underwater photometer equipped with both deck and underwater sensors. Spectral band filters were placed over the sensors to isolate spectral regions. The spectrum was divided into the bands 430 to 510 nm, 510 to 560 nm, 560 to 620 nm, and 620 to 710 nm by the use of appropriate combinations of Rohm and Haas Plexiglass filter series, blue (No. 2045), green (No. 2092), amber (No. 2451), red (No. 2444), and an infrared filter with a sharp cut-off at 720 nm. Filter transmission and meter sensitivity factors converted photometer readings to relative photon fluxes, based on the data of Taylor and Kerr (1941) for incident radiation at the surface of the sea.

Results

We determined the specific light-absorption characteristics of the waters of Great Harbor where the experiments occurred (Fig. 2, and Table 1). The water column itself was totally homogeneous due to the thorough mixing caused by rapid tidal currents. Within each of the spectral regions examined, the photon flux decreased exponentially with increasing depth. Although the water column is not a monochromater *per se*, it does serve to enrich the green portion of the spectrum.

Data in this paper comes from spectrophotometric scans of whole (*in vivo*) and solvent-extracted material. The reproduc-

Table 1. Summary of solar insolation attenuation by the water column in which experiments were performed

Spectral region	Wavelength range (nm)	Meters per 10-fold attenuation	Ratio of photon flux 0.5:10 m	Relative photon flux normalized to surface		
				Surface[a]	0.5 m	10 m
Red	620 - 710	3.6	550	0.27	0.18	0.0003
Amber	560 - 620	6.0	27.4	0.26	0.16	0.0058
Green	510 - 560	6.0	31.0	0.26	0.18	0.0060
Blue	430 - 510	5.3	69.0	0.21	0.16	0.0024
				1.00	0.68	0.0145

[a]Calculated from data of Taylor and Kerr (1941).

Table 2. Tissue homogeneity. Data is taken from *in vivo* scans, and is given as mean peak height ± 1 standard deviation at the specified wavelength

Alga and tissue	A_{678}	A_{620}	A_{565}
Porphyra umbilicalis (margins + center)	.320±.013	.215±.006	.252±.006
Chondrus crispus (3 tips)			
1 m	.488±.044	.186±.023	.226±.074
10 m	.983±.066	.566±.060	.921±.101
	A_{678}	A_{653}	
Ulva lactuca (margins + center)	.376±.013	.276±.010	

Table 3. Tissue homogeneity and ranges of chlorophyll concentrations in seaweeds collected from region of Woods Hole. Chlorophyll concentrations were measured in methanol extracts of tissue and are expressed in nmoles/cm^2 seaweed surface ± 1 standard deviation

Alga	Habitat	Chlorophyll
Ulva lactuca	Sun	1.89 ± 0.12
	Shade	17.90 ± 1.14
Codium fragile	Sun	13.83 ± 1.56
	Shade	26.18 ± 2.75
Porphyra umbilicalis	Sun	1.12 ± 0.12
	Shade	3.43 ± 0.23
Chondrus crispus	Sun	3.28 ± 0.61
	Shade	5.80 ± 0.85

Table 4. *Ulva lactuca*. Pigment content of seaweeds collected from intertidal sun and shade habitats, and from position-reversal experiments in the water column. Relative peak heights taken from *in vivo* scans. Chlorophyll concentrations were measured in methanol extracts of tissue, and expressed as nmoles/cm^2 seaweed surface. Pigment ratios are ± 1 standard deviation. Other values are typical for a given experiment. Data for water-column experiments comes from 3 lines, each analyzed after 7 days in position, their position reversed, and analyzed again after 7 days

Habitat	A_{678}	Chlorophyll *a*	Chlorophyll *b*	Chlorophyll *b:a*
Intertidal				
Sun	0.115	1.29	0.68	0.53 ± .04
Shade	0.871	9.98	5.94	0.62 ± .03
Sun:shade	0.13	0.13	0.11	-
Water column				
1 m	-	2.24	1.00	0.44 ± .03
10 m	-	7.68	5.11	0.67 ± .07
1 m:10 m	-	0.29	0.20	-

Table 5. *Codium fragile*. Pigment content of seaweeds collected from intertidal sun and shade habitats, and from position-reversal experiments in the water column. Chlorophyll concentrations were measured in methanol extracts of tissue, and expressed as nmoles/g fresh weight. Pigment ratios are ± 1 standard deviation. Other values are typical for a given experiment. Data for water-column experiments comes from 3 lines, each analyzed after 7 days in position, their position reversed, and analyzed again after 7 days

Habitat	Chlorophyll *a*	Chlorophyll *b*	Chlorophyll *b:a*
Intertidal			
Sun	111	72	0.68 ± 0.02
Shade	302	200	0.72 ± 0.05
Sun:shade	0.37	0.36	-
Water column			
1 m	120	74	0.63 ± 0.07
10 m	275	175	0.67 ± 0.04
1 m:10 m	0.44	0.42	-

Table 6. *Porphyra umbilicalis*. Pigment content of seaweeds collected from intertidal sun and shade habitats, and from position-reversal experiments in the water column. Relative peak heights taken from *in vivo* scans. Chlorophyll concentrations were measured in methanol extracts of tissue, and expressed as nmoles/cm^2 seaweed surface. Pigment ratios are ± 1 standard deviation. Other values are typical for a given experiment. Data for water-column experiments comes from 3 lines, each analyzed after 7 days in position, their position reversed, and analyzed again after 7 days

Habitat	A_{678}	Chloro-phyll *a*	A_{565}:A_{678}	A_{620}:A_{678}
Intertidal				
Sun	0.235	2.30	0.60±0.08	0.56±0.09
Shade	0.345	3.55	0.73±0.06	0.61±0.00
Sun:shade	0.68	0.65	-	-
Water column				
1 m	0.175	1.76	0.47±0.10	0.50±0.07
10 m	0.248	2.49	0.76±0.06	0.66±0.04
1 m:10 m	0.71	0.71	-	-

Table 7. *Chondrus crispus*. Pigment content of seaweeds taken from position-reversal experiments in the water column. Relative peak heights taken from *in vivo* scans. Chlorophyll concentrations were measured in methanol extracts of tissue, and expressed as nmoles/g fresh weight. Pigment ratios are ± 1 standard deviation. Other values are typical for a given experiment. Data for water-column experiments comes from 3 lines, each analyzed after 7 days in position, their position reversed, and analyzed again after 7 days

Position	A_{678}	Chloro-phyll *a*	A_{565}:A_{678}	A_{620}:A_{678}
1 m	0.76	178	0.59±0.04	0.42±0.03
10 m	1.03	254	0.89±0.12	0.51±0.08
1 m:10 m	0.74	0.70	-	-

ibility of such measurements is shown in Tables 2 and 3. We were able to determine absolute concentrations of chlorophylls in every case, because complete extraction was possible in methanol. However, phycobiliproteins could n o t be extracted quantitatively by any method we used, nor is there any report of this having been accomplished by others for s e a w e e d s. Therefore, we used peak heights of *in vivo* scans to determine relative phycobiliprotein content. In our data, the peak heights at a specific wave-length of maximum absorption represent the following pigments: A_{678} = chlorophyll *a*; A_{620} = phycocyanin; A_{565} = phycoerythrin. For *Ulva lactuca, Porphyra umbilicalis* and *Chondrus crispus*, the absorption by chlorophyll *in vivo* is directly porportional to chlorophyll concentration, as determined from methanol extracts (compare A_{678} and chlorophyll *a* columns in Tables 4, 6, and 7). The minimal overlap of phycoerythrin (A_{565}) with chlorophyll (A_{678}) allows us to use the former absorption as a direct measure of phycoerythrin concentration. The greater overlap of phycocyanin absorption (A_{620}) with chlorophyll (A_{678}) allows only a qualitative comparison.

The cylindrical thallus of *Codium fragile* is so thick that A_{678} values are not proportional to chlorophyll *a* concentration. Our data show that the calculated absorption for the red peak is approximately 3 for *C. fragile* from shaded habitats, and 1.5 for *C. fragile* from exposed habitats. These high absorptions cause *in vivo* measurement to fail (0.9 for both), perhaps because of stray light limitations of the spectrophotometer and light "sieving" due to heterogeneous absorption. Therefore, pigment concentrations for *C. fragile* are based on methanol extractions only. In *Chondrus crispus*, the calculated absorptions are 1.0 and 0.6 compared with *in vivo* measurements of 1.0 and 0.8 (Table 7). In the optically thin *Ulva lactuca* and *Porphyra umbilicalis* the *in vivo* measurements correlate well with extraction data (Tables 4 and 6).

Two distinct phenomena are present. First, seaweeds growing in the narrow band delimited by mean low water and mean high water, strictly speaking intertidal seaweeds, exhibited differences only in their pigment concentrations, with no significant differences in pigment ratios (Tables 4, 5 and 6). Here, high concentrations of pigments corresponded with plants in protected (shade) positions.

Second, seaweeds fixed to a vertically suspended line increased total pigment concentration with increasing depth (Tables 4, 5, 6 and 7), and increased the accessory pigment to chlorophyll *a* ratio with increasing depth (Tables 4, 6 and 7), except *Codium fragile* (Table 5). Further, as demonstrated by position-reversal experiments, changes in pigment concentration and ratio are reversible (Tables 4, 5, 6 and 7). There is a net loss of chlorophyll under high light (surface) conditions, and subsequent synthesis when the tissue is placed in dim light (deep) environments.

This appears to occur in the absence of cell division or growth. Pigment changes occurred uniformly throughout the thalli. All the seaweeds used in this study grow distally, i.e., new cells add only to the margins of the thallus, and elongation of existing cells also takes place in peripheral regions. Since no intensity or color banding appeared in the thalli, our results indicate that pigment changes can occur in the absence of cell division or elongation.

Discussion

In order to absorb the light present in the ambient light field efficiently, a pigment must have a color complementary to that of the light field. Engelmann (1883, 1884) attributed the vertical distribution of seaweeds to their ability to produce pigments complementary to the color of the light field, a phenomenon which he called c o m p l e m e n t a r y c h r o m a t i c a d a p t a t i o n. Oltmanns (1892, 1923), on the other hand, proposed that the vertical distribution of seaweeds is determined by intensity rather than the color of the prevailing light, hence i n t e n s i t y a d a p t a t i o n. Harder (1923) suggested that both intensity and color play a part in the adaptation of seaweeds to increasing depths. A discussion of chromatic versus intensity adaptation must include both phylogenetic and ontogenetic considerations. Red algae found near or on the surface can be olive-red whereas those found at depths are deep red, a function of phycoerythrin to chlorophyll *a* ratios. Lubimenko (Table 15, VII, *in* Rabinowitch, 1945) gives figures for phycoerythrin to chlorophyll ratios as a function of water depth, both for inter- and intraspecific comparisons of red algae. An enrichment for phycoerythrin is proportional to increasing depth, thus correlated with enrichment for a complementary light field. Seybold and Egle (Table 15, VIII, *in* Rabinowitch, 1945) found that green algae had the highest chlorophyll *b* to *a* ratios of all green plants, except similarly submersed higher plants. Beale and Appleman (1971) observed that photoautotrophically growing *Chlorella vulgaris* increased its total chlorophyll content when light intensity limited the growth rate. Conversely, when growth was not limited by available light, pigment synthesis ceased while growth continued until the cells diluted out the unnecessary chlorophyll.

Among land plants, intensity adaptation is more important than chromatic adaptation, presumably because there are more pronounced variations in the intensity of light than in spectral composition. This has led to the designation "sun" and "shade" plants, both from the standpoint of phylogenetic and ontogenetic adaptation (see Björkman, 1973 for review).

Critical experiments which distinguish chromatic from intensity adaptation have been successfully completed in the laboratory with algae (see Halldal, 1970, and Bogorod, 1975, for reviews). Further, complementary chromatic adaptation has been convincingly demonstrated, especially for blue-green algae. During these researches, the use of monochromaters and a limited repertoire of planktonic species has narrowed the concept of complementary chromatic adaptation and, in some cases, excluded any consideration of variations in chlorophyll *a*. Here we carry the concept back to the oceans and place it in the context of the sessile plant, which is obliged to adapt physiologically to the ambient light field, by means of intensity and/or color adaptation. The water column is n o t a monochromator; rather, it progressively enriches the spectrum for green light with increasing depth. Accompanying this color shift is a diminution of total photon flux. Therefore, adaptation must be responsive to changes in both light q u a l i t y and q u a n t i t y. Further, we apply the concept to benthic thalloid marine algae (seaweeds, *sensu strictu*) for which Engelmann (1883) originally conceived the term.

We observed two distinct phenomena with respect to pigment changes. First, intertidal seaweeds adapt as "sun" and "shade" species, i.e., total pigment concentrations vary with little or no variation in the ratio of accessory pigment to chlorophyll *a*. The intertidal environment is patchy, due primarily to the ebb and flow of tides, the vertical stacking of seaweeds, and relief in the substratum. The color of shaded and exposed habitats is similar, whereas the light intensity differs radically. We have found that the response of seaweeds to the intertidal light field represents classic intensity adaptation, as discussed first by Oltmanns in 1892 (Tables 3, 4, 5 and 6 of present paper).

The second phenonenon was observed in the vertical suspension and position reversal experiments. Here, the environment is uniformly graded; i.e., both light intensity and color change with depth. The seaweed response is to increase pigment concentrations, as well as to shift ratios of accessory pigment to chlorophyll *a* to higher values, presumably to utilize photons in the "green window". The phycoerythrin to chloro-

phyll *a* ratio shift was most pronounced, followed by the phycocyanin to chlorophyll *a* ratio shift. By contrast, the observed chlorophyll *b* to chlorophyll *a* shift was sometimes within the quantitative range of experimental error, and therefore not as significant (Tables 4 and 6). In addition, it is important that changes in pigment concentrations are reversible, and can occur in the absence of cell division.

Björkman (1973) reported that most higher plant chlorophyll concentrations range from 2.5 to 7.5 mg dm^{-2} leaf area (approximately 30 to 80 nmoles chlorophyll cm^{-2}). The seaweeds tested here range below that value, 1 to 30 nmoles cm^{-2}. However, in the red algae, phycobiliproteins add considerably to the total absorption.

The findings of this study present interesting problems concerning the developmental aspects of intensity and color adaptations in seaweeds. Recently, Columbo and Orsenigo (1976) reported that *Halimeda tuna* (a siphonous green alga related to *Codium fragile*) adapts to increasing depth by enlarging the utricular surface and thinning the cell walls, thus increasing the total area of exposed chloroplasts. However, little change was seen in chloroplast number or thylakoid distribution. Our study does not address anatomical alterations of the thallus, and their study offers no explanation of differences in pigment concentrations.

We believe that the conciliatory view of Harder (1923) prevails over those of Engelmann (1883) and Oltmanns (1892): seaweed adaptation to ambient light fields involves b o t h intensity a n d color adaptations, and these two phenomena are not strictly separable under natural conditions. In the succeeding paper, we demonstrate the effects of intensity and color adaptation on the photosynthetic capacity of these seaweeds.

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