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Correlation of Changes in Pigment Content with Photosynthetic Capacity of 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 photosynthetic capacity as a function of 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*. Seaweeds were attached to vertically buoyed lines at 0.5 and 10 m and were allowed to adapt to the ambient light field. All species showed greater pigment content with depth, and the ratio of accessory pigments to chlorophyll *a* increased with depth. Seaweed samples from 0.5 and 10 m were placed in tandem pairs of stoppered bottles and hung at prescribed depths. The rates of O_2 evolution were calculated from changes in dissolved O_2 content, both as a function of biomass and chlorophyll *a* concentration. Our results indicate that intensity and/or chromatic adaptation enhance the photosynthetic capacity of a seaweed in limiting light conditions. The strategy of seaweeds in manipulating their photon-gathering antennae is not to maximize photosynthetic rate, but rather to optimize the photosynthetic rate. They can change pigment ratios, or simply increase the total amount of pigment, or both. Further, if a seaweed is optically thick, as are *Codium fragile* and *Chondrus crispus*, it does not matter what color it is. We conclude that the red algae are phylogenetically no better adapted to utilize the ambient light at great depth than their green counterparts. The ambient light conditions alone do not determine the limit for the vertical distribution of the red algae relative to the green algae.

Introduction

In a previous paper (Ramus *et al.*, 1976), we demonstrated that seaweeds adapt their photosynthetic "antennae" to both the color and intensity of the natural light field. The natural light field in this case was the waters at Woods Hole, Massachusetts. The seaweeds used were *Ulva lactuca* (sea lettuce), *Codium fragile* (deadman's fingers), *Porphyra umbilicalis* (laver), and *Chondrus crispus* (Irish moss). We used *U. lactuca* and *Codium fragile* to test chlorophyll *b* - chlorophyll *a* pigment systems, and *P. umbilicalis* and *Chondrus crispus* were used to test phycobiliprotein-chlorophyll *a* pigment systems. *U. lactuca* and *P. umbilicalis* are optically thin species, whereas *Codium fragile* and *Chondrus crispus* are optically thick species. We determined the specific light-absorbing characteristics of the water column with an underwater photometer. Seaweeds were buoyed vertically in the water column and in a few days adapted their antennae pigments to the ambient light field. Total pigment concentration increased with depth, as did chlorophyll *b*:chlorophyll *a* and the phycobiliprotein:chlorophyll *a* ratios. Moreover, these intensity and chromatic adaptations were reversible and did not require cell division.

Benthic marine algae - seaweeds - are a significant group of primary producers. Ryther (1963) has suggested that the world-wide production of seaweeds is 10% that of phytoplankton, even though seaweeds inhabit an area only 0.1% of that available to phytoplankton. Mann (1973) concludes from his studies in the coastal waters of Nova Scotia, Canada, that total seeweed production is three times the

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total production of phytoplankton in the same area. Here, the large perennial seaweeds *Laminaria longicruris, L. digitata,* and *Agarum cribosum* , which dominate the seaweed zone, grow rapidly throughout the winter when water temperature is near 0°C and light intensity is low. Winter growth is accompanied by the mobilization of carbon reserves and low respiratory rates; it is also a time of high water transparency and non-limiting nutrient concentrations. Mann's observations stimulate thoughts of other adaptive strategies which seaweeds might employ to maintain high production. In this report, we explore the consequences of intensity and chromatic adaptation (i.e., the shuffling of photosynthetic antenna pigments to complement the ambient light field) for photosynthetic capacity and vertical distribution.

Investigations of seaweed photosynthesis at diverse depths have been conducted in the past, and considering the technologies available, have produced sophisticated data, even by present standards. Notable among these are the works of Gail (1922), Montefort (1929, 1930), Tschudy (1934), and Levring (1947). Although not directed at precisely the same aspects of adaptive physiology, their data and conclusions corroborate and anticipate ours.

Materials and Methods

Rates of photosynthesis are expressed as the net rates in nmoles O_2 evolved/h. The dissolved O_2 was measured directly (as ppm O_2) using a Beckman Fieldlab Oxygen Analyzer equipped with a polarographic electrode, standardized with air-saturated seawater of known temperature and salinity. Standard biological oxygen demand (BOD) bottles enclosed the seaweeds. Each bottle was filled with fresh gravity-filtered (several layers of Whatman No. 1) seawater, and a glass marble was placed in the bottle to enhance mixing. We suspended seaweeds at either 0.5 or 10 m for 7 days prior to each experiment, to adapt their pigment systems to the ambient light field. Several 2 cm diameter discs of *Ulva lactuca* or *Porphyra umbilicalis*, or several excised tips 2 cm in length of *Codium fragile* or *Chondrus crispus* were placed in each bottle. Seaweeds which tended to float were weighted with non-corrosible wire. Bottles containing seaweed samples hung in tandem pairs from a vertically buoyed line at 0.5, 3.5, 6.5, or 9,5 m from the surface. One bottle in each tandem pair contained 0.5 m-adapted seaweed and the other 10 m-adapted seaweed for comparison of net O_2 evolution rates. The bottles remained *in situ* for 3 h, between 11.00 and 14.00 hrs, on calm sunny days only. Bottles used for respiratory rate measurements were made opaque with black plastic tape. At the end of the test period, we placed all bottles in darkness for 30 min to allow internal O_2 in seaweed tissue to come into equilibrium with the external milieu. Continuous monitoring experiments indicated 30 min to be more than adequate time.

For light-saturation experiments, the light source was a 625 W quartz-iodine lamp. Voltage was set at 80 V with a Powerstat Type 116 variable power transformer. The light path was 50 cm from source to sample. Into this path was inserted a 40 cm infra-red filter made of a 10 gallon (38 l) glass-sided aquarium containing 0.37 mM $CuSO_4$ and 10 mM H_2SO_4. A series of Zeiss calibrated half-silvered mirrors and neutral-density filters made of metal screens reduced the irradiance in geometric steps. Irradiance was measured with a Y.S.I. Model 65 radiometer and expressed as mW/cm^2.

For photosynthetic and respiratory rate measurements in the laboratory, we used a water-cooled Plexiglass chamber containing 328 ml of filtered seawater. The seaweed was sandwiched between plastic mesh, and positioned perpendicular to the light path. Water temperature was maintained at 26°C, slightly higher than ambient seawater temperatures at this time. A Clark-type electrode which protruded into the chamber measured oxygen concentration in ppm. The electrode connected to a potentiometric recorder.

To minimize temperature-drift components which are proportional to total O_2 concentration, we bubbled the seawater with N_2 to remove 90% of the O_2 before each experiment began. This is not a sufficiently low oxygen level to cause specific anaerobic effects.

Procedures not mentioned here may be found in the preceding paper (Ramus *et al.*, 1976).

Results

Before attempting field experiments, was carried out several laboratory control experiments to determine the reliability of our methods. In the first, tissue load per bottle over the range used was shown to have little effect on the results. In the second experiment, seaweeds adapted to increasing depths evolved O_2 at increasing rates when exposed to uniform irradiation, results which anticipated our field data.

Net photosynthetic rate (in nmoles O_2 evolved per hour) is expressed as a function of biomass (fresh weight) and chlorophyll *a*. Wet to dry weight ratios are as follows, and are given as mean values ± one standard deviation: *Chondrus crispus* = 4.37 ± 0.39; *Ulva lactuca* = 4.56 ± 0.16; *Porphyra umbilicalis* = 4.99 ± 0.32; *Codium fragile* = 20.57 ± 1.28. These values can be used to convert rates expressed as a function of fresh weight to dry weight. *Chondrus crispus, U. lactuca* and *P. umbilicalis* are comparable using either biomass parameter, whereas *Codium fragile* is not, since its water content is so much higher than the rest.

On a per unit biomass (fresh weight) basis, photosynthetic rate of thin seaweeds (*Ulva lactuca* and *Porphyra umbilicalis*) exceeded that of thick seaweeds (*Codium fragile* and *Chondrus crispus*). In descending order according to average rates at any depth are *U. lactuca* (Fig. 1), *P. umbilicalis* (Fig. 2), *Chondrus crispus* (Fig. 3), and *Codium fragile* (Fig. 4). The photosynthetic rate for deep-water seaweeds invariably exceeded that of surface-water adapted specimens, usually by a factor of two. *Chondrus crispus* exhibited photoinhibition near the surface. Plants adapted at 10 m tended to maintain a more uniform photosynthetic rate with increasing depth than did plants adapted at 0.5 m.

Photosynthetic rates per unit of chlorophyll *a* are also shown (Figs. 1-4). Near the surface, where irradiance is highest, surface-water adapted plants had the lowest pigment concentration and the highest photosynthetic rates per unit of chlorophyll. However, these high rates fell off rapidly with increasing depth, whereas deep-water adapted plants maintained a more uniform photosynthetic rate per unit chlorophyll with increasing depth.

The seaweeds used in these experiments represent natural extremes in pigment concentrations for summer specimens observed in the Woods Hole region. We also tested the effects of natural extremes of solar insolation on the highest primary producer, *Ulva lactuca*. Surface irradiance during a dense fog was about 10 mW/cm^2, and 50 mW/cm^2 on a clear day. As expected, photosynthetic rates dropped accordingly on the overcast day (Figs. 5 and 6) and the compensation depth for *U. lactuca* rose considerably. The compensation depth is here defined as that depth at which the net O_2 evolution rate is zero, during the measurement interval. On clear days, the maximum rate of photosynthesis at the surface was maintained to about 3 m below the surface. On overcast days, the maximum rate of photosynthesis occurred at the surface. We observed a similar pattern for *Codium fragile* and *Porphyra umbilicalis*; and *Chondrus crispus* showed definite inhibition.

We examined the relation of pigment content to light saturation of photosynthesis. In a set of experiments conducted in the laboratory, we compared the rates of O_2 evolution for surface- and deep-water adapted seaweeds under controlled light conditions both approaching and at saturating irradiance. The results for each sample are expressed as rates relative to the maximum at light saturation.

Deep-water specimens of the green algae *Ulva lactuca* and *Codium fragile* saturated at approximately half the irradiance value of surface-water specimens (Fig. 7). Deep- and surface-water specimens of the red algae *Porphyra umbilicalis* and *Chondrus crispus* saturated at the same irradiance value (Fig. 7). Unlike the other species tested, the photosynthetic rate of *C. crispus* exhibited photoinhibition (the rate declined at very high intensities).

We measured absolute photosynthetic rate at saturating irradiance, comparing deep- and surface-water adapted individuals. The gross photosynthetic rate per unit chlorophyll *a* is given in Table 1. The gross rates for deep-water *Codium fragile, Porphyra umbilicalis* and *Chondrus crispus*, were similar to those for surface-water adapted individuals. The gross rate for surface-water *Ulva lactuca* considerably exceeded that for deep-water specimens. The gross rates per unit chlorophyll *a* determined in the laboratory compare favorably with net rates determined in the field at depth of approximately 3.5 m where, on bright days, the irradiance was approximately 10 mW/cm^2, or equivalent to saturating irradiance determined in the laboratory (Fig. 7). Laboratory and field data are comparable. The small differences seen between laboratory and field measurements we attribute to (a) shorter intervals of time where O_2 diffusion rates become limiting, (b) gross rates compared with net rates, (c) ambient temperature differences, i.e., 26° and 23°C, and (d) long-term adaptation effects during the field-data collection.

Field and laboratory measurements were taken during the summers of both 1974 and 1975, and despite some refinement of technique, are comparable. A significant fact is that measurements made with sun- and shade-adapted plants (unpublished data) do not differ significantly from those with surface- and deep-water adapted plants.

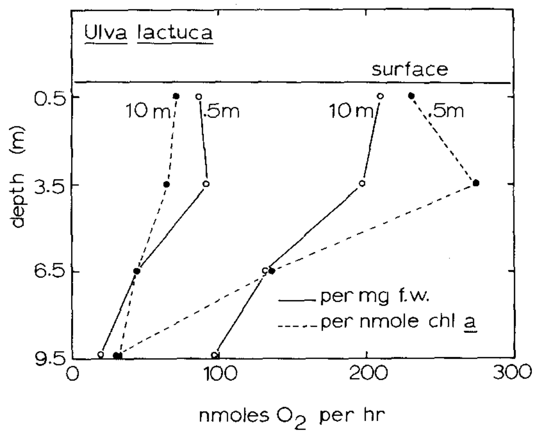

Fig. 1. *Ulva lactuca.* Net photosynthetic rate of seaweeds at prescribed depths, expressed as function of biomass and chlorophyll *a* concentration, comparing surface- with deep-water adapted individuals. Plants were held at 0.5 and 10 m for 7 days prior to experiment, then samples were placed in tandem pairs of BOD bottles and hung at prescribed depths from 11.00 to 14.00 hrs on a clear calm day. Water temperature was 23°C. Pigment data for 0.5 m plants: chlorophyll *b*:*a* = 0.47; chlorophyll *a* = 334 nmoles/g fresh weight (f.w.). For 10 m plants: chlorophyll *b*:*a* = 0.61; chlorophyll *a* = 3061 nmoles/g f.w.

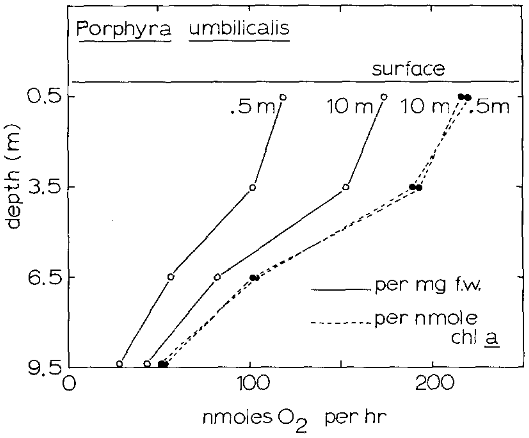

Fig. 2. *Porphyra umbilicalis.* Net photosynthetic rate of seaweeds at prescribed depths, expressed as function of biomass and chlorophyll *a* concentration, comparing surface- with deep-water adapted individuals. Plants were held at 0.5 and 10 m for 7 days prior to experiment, then samples were placed in tandem pairs of BOD bottles and hung at prescribed depths from 11.00 to 14.00 hrs on a clear day. Water temperature was 23°C. Pigment data for 0.5 m plants: A_{565}:A_{678} = 0.42; A_{620}:A_{678} = 0.48; chlorophyll *a* = 538 nmoles/g f.w. For 10 m plants: A_{565}:A_{678} = 0.84; A_{620}:A_{678} = 0.61; chlorophyll *a* = 798 nmoles/g f.w.

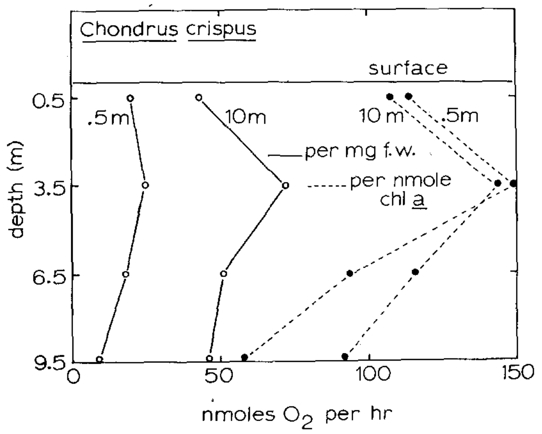

Fig. 3. *Chondrus crispus.* Net photosynthetic rate of seaweeds at prescribed depths, expressed as function of biomass and chlorophyll *a* concentration, comparing surface- with deep-water adapted individuals. Plants were held at 0.5 and 10 m for 7 days prior to experiment, then samples were placed in tandem pairs of BOD bottles and hung at prescribed depths from 11.00 to 14.00 hrs on a clear day. Water temperature was 23°C. Pigment data for 0.5 m plants: A_{565}:A_{678} = 0.44; A_{620}:A_{678} = 0.39; chlorophyll *a* = 174 nmoles/g f.w. For 10 m plants A_{565}:A_{678} = 0.90; A_{620}:A_{678} = 0.58; chlorophyll *a* = 491 nmoles/g f.w.

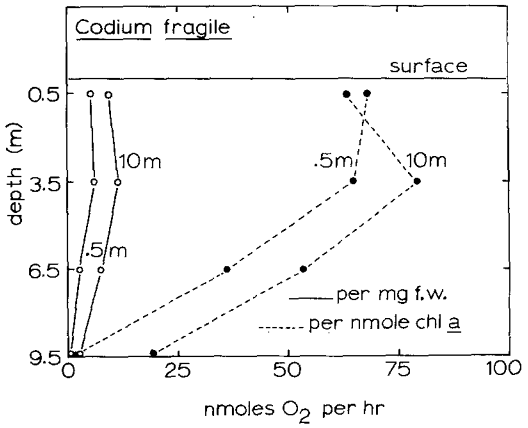

Fig. 4. *Codium fragile.* Net photosynthetic rate of seaweeds at prescribed depths, expressed as function of biomass and chlorophyll *a* concentration, comparing surface- with deep-water adapted individuals. Plants were held at 0.5 and 10 m for 7 days prior to experiment, then samples were placed in tandem pairs of BOD bottles and hung at prescribed depths from 11.00 to 14.00 hrs on a clear day. Water temperature was 23°C. Pigment data for 0.5 m plants: chlorophyll *b*:*a* = 0.65; chlorophyll *a* = 75 nmoles/g f.w. For 10 m plants: chlorophyll *b*:*a* = 0.68; chlorophyll *a* = 124 nmoles/g f.w.

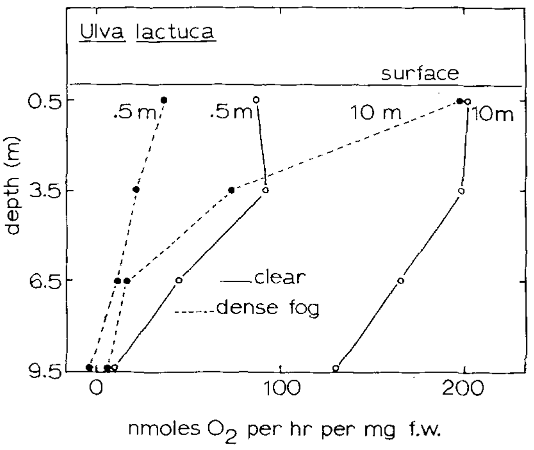

Fig. 5. *Ulva lactuca*. Net photosynthetic rate of seaweeds at prescribed depths, expressed as function of biomass and comparing surface- with deep-water adapted individuals. Measurements were made on both clear (about 50 mW/cm^2 irradiance) and overcast (about 10 mW/cm^2 irradiance) days. Plants were maintained at 0.5 and 10 m for 7 days prior to experiment, then samples were placed in tandem pairs of BOD bottles and hung at prescribed depths from 11.00 to 14.00 hrs. Water temperature was 23°C. Pigment data for clear day - 0.5 m plants: chlorophyll *b*:*a* = 0.47; chlorophyll *a* = 334 nmoles/g f.w.; 10 m plants: chlorophyll *b*:*a* = 0.61; chlorophyll *a* = 3061 nmoles/g f.w. For foggy day - 0.5 m plants: chlorophyll *b*:*a* = 0.47; chlorophyll *a* = 470 nmoles/g f.w.; 10 m plants: chlorophyll *b*:*a* = 0.67; chlorophyll *a* = 1616 nmoles/g f.w.

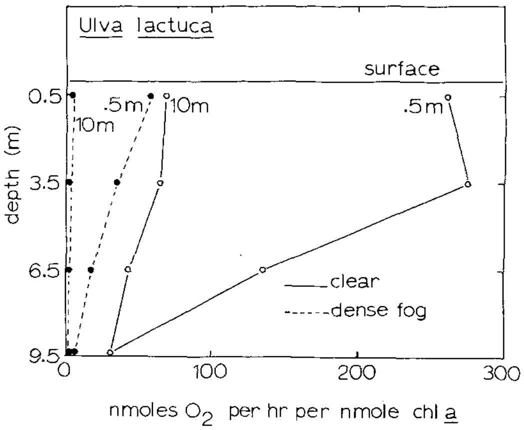

Fig. 6. *Ulva lactuca*. Net photosynthetic rate of seaweeds at prescribed depths, expressed as function of chlorophyll *a* only and comparing surface- with deep-water adapted individuals. Measurements were made on both clear (about 50 mW/cm^2 irradiance) and overcast (about 10 mW/cm^2 irradiance) days. Plants were maintained at 0.5 and 10 m for 7 days prior to experiment, then samples were placed in tandem pairs of BOD bottles and hung at prescribed depths from 11.00 to 14.00 hrs. Water temperature was 23°C. Pigment data for clear day - 0.5 m plants: chlorophyll *b*:*a* = 0.47; chlorophyll *a* = 334 nmoles/g f.w.; 10 m plants: chlorophyll *b*:*a* = 0.61; chlorophyll *a* = 3061 nmoles/g f.w. For foggy day - 0.5 m plants: chlorophyll *b*:*a* = 0.47; chlorophyll *a* = 470 nmoles/g f.w.; 10 m plants: chlorophyll *b*:*a* = 0.67; chlorophyll *a* = 1616 nmoles/g f.w.

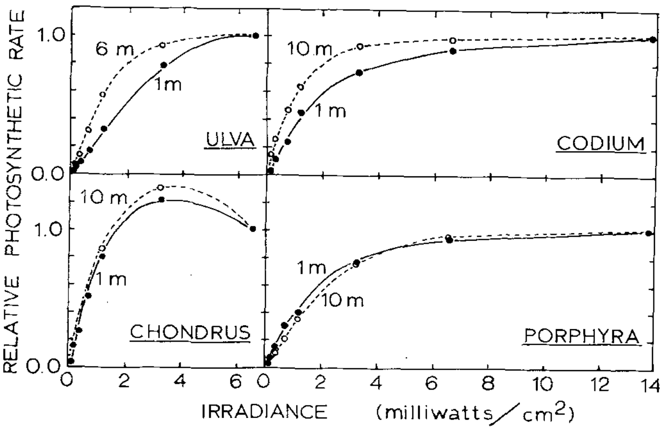

Fig. 7. *Ulva lactuca*, *Codium fragile*, *Porphyra umbilicalis* and *Chondrus crispus*. Relative photosynthetic rates as function of irradiance comparing shallow- with deep-water adapted plants. Absolute net rates were normalized to their respective maxima to give relative rates. Photosynthetic rates were measured as O$_2$ evolution by a Clark-type electrode, using incandescent white-light and water-jacketed Plexiglass chamber at 23°C

Table 1. Gross rates of photosynthesis (nmoles O$_2$ ↑ 20 h/nmoles chlorophyll *a*) determined for surface- and deep-water plants at an irradiance of 10 mW/cm^2 (saturating) in the laboratory at 26°C for a continuous recording period of 15 min. Data taken from slopes during lights on and off, corrected for dark respiration

Species	Surface plants (0.5 m)	Deep plants (10 m)
Ulva lactuca	184	62
Codium fragile	27	21
Porphyra umbilicalis	300	376
Chondrus crispus	146	127

Discussion

We consider here the biological significance of physiological response to environmental change. The environmental change is the gradual diminution of photon flux (light intensity) and shift in wave-length distribution (light color) with increasing water depth. The physiological change is an increase in total antenna-pigment concentration and a shift in antenna-pigment ratio towards green light-absorbing forms. This then is an adaptation, and we are conditioned to believe that adaptations increase the fitness of an individual, from which follows biological significance. We have defined fitness here as a maintenance of photosynthetic capacity, no matter what the ambient light conditions, within reasonable (natural) limits. The primacy of photosynthetic capacity to growth, reproduction – indeed, to survival – is here assumed. Further, the significance of parameters used to express primary production is not clear. As seen from our data, a very different picture of primary production emerges when expressed in terms of biomass (fresh or dry weight), or of chlorophyll *a*. We have asked the question: does intensity and/or chromatic adaptation enhance the photosynthetic capacity of a seaweed in limiting light conditions? Our results indicate the answer to be yes, if we express photosynthetic capacity in units of biomass.

Our data do not distinguish between chromatic and intensity adaptation, because, clearly, both occur simultaneously under natural conditions. We considered the totality of the natural response, no matter the mechanistic questions raised by separating its component parts.

The strategy of seaweeds in manipulating their light-capturing antennae is not merely to maximize photosynthetic rate. Otherwise, all seaweeds would produce maximum antenna (be black in color). Rather, seaweeds maintain an optimal photosynthetic capacity, no matter what the ambient light conditions set by the energy requirement for growth. The result of this effect is to extend vertical distribution, while other factors such as grazing pressure, exposure, and the availability of attachment sites, limit vertical distribution.

The absorption of light by multicellular benthic algae, when the light itself is highly variable, is a complex problem. We sketch here the points necessary to explain the observations of this paper.

In the sea, the solar output is not only attenuated, but the attenuation is wave-length dependent (Jerlov, 1968). Our data, and many similar measurements by others, show that for depths greater than about 1 m, the decrease of intensity (I) with depth (d), at a given wave length is $I = Io\ e^{-xd}$. At a given depth, the distribution of light intensity with wavelength will be denoted $I\ (\lambda)$. It should be noted that I is also an anisotropic function of space: the scatter tends to diffuse the light, but the vertical gradient prevents the approach to total randomness. Over the few square-centimeter dimensions and slowly fluctuating random orientations of the sample, we can assume a simple average intensity of illumination. The total light absorbed over all wave-lengths by the seaweed thallus will be: $I\ (\lambda)[1\text{-}\exp -\alpha\ (\lambda)/A]\ d\ \lambda$, where $\alpha\ (\lambda)$ is the optical cross-section as a function of wave-length and A is the effective area of the sample. We write the absorption in these terms since the usual form of Beer's law is not useful for polychromatic light and complex optical conditions. The parameter σ includes the nonlinear effects of heterogeneous absorption and multiple scatter. This parameter contains all relevant information about the pigments. The limits are set effectively by the overlap of I, and σ, i.e., the light available for absorption and the ability of the plant to absorb light. Although the expression is in general complex, the extremes of small and large $^{\sigma}/A$ are simple:

Case A. If $^{\sigma}/A$ is small (≤ 0.1), i.e., if most of the incident light is not absorbed, the integral reduces to

$$\frac{1}{A} \int_a^b I\ (\lambda)\ \sigma\ (\lambda)\ d\ \lambda,$$

which is just the overlap of the spectral distribution of photons and the absorption cross-section. This is the condition required for "action spectra" measurements. The membranous algae *Ulva lactuca* and *Porphyra umbilicalis* are close to but not at this limit. The absorption of light will increase with increasing pigment content but not necessarily in a linear fashion. The increase will occur throughout the spectrum since the sample is optically thin.

Case B. If $^{\sigma}/A$ is large (≥ 2), i.e., if most of the incident light is absorbed, the integral reduces to

$$\int_d^c I\ (\lambda)\ d\lambda,$$

i.e., simply the light incident on the sample, but over limits set by the sample absorption. If at some wavelengths the sample becomes optically thin, the more general form of the equation must be used in that region. When there is enough pigment to absorb the light completely, further increases in pigment content will not increase the absorption. That is, if one is optically black, it does not matter what color one is. The dense algae *Codium fragile* and *Chondrus crispus* are close to this limit.

In the above discussion we have estimated the light absorbed by a sample. At low light intensities, the rate of photosynthesis is linearly related to the light absorbed and so the above estimates can be written as net rates of photosynthesis. At a sufficiently high intensity, the rate of photosynthesis becomes independent of light intensity, i.e., it saturates. For Case A, the saturation parameter is well defined, since the light is uniform in the sample. For Case B, the saturation curve is "stretched out" by the attenuation of light intensity within the sample.

It seems that there are two strategies open to algae in the response to changes in light intensity and wavelength. They can change pigment ratios, i.e., so-called chromatic adaptation, or they can simply increase the total amount of pigment. Since all pigments have broad bands, absorption occurs throughout the visible spectrum, even for chlorophyll. However, it is only for optically thin algae such as *Ulva lactuca* and *Porphyra umbilicalis* that an increase in pigment will result in a net increase in photosynthesis at low light intensities.

The first strategy implies a shuffling of pigments in the antennae of the photosynthetic unit only. The second strategy, however, could have two methods of implementation. Seaweeds could increase the antenna pigments, or they could make additional photosynthetic units, or both.

The customary plot of the photosynthetic ability of plants as rate of O_2 production versus chlorophyll content can be misleading. This is because only in optically thin specimens can the chlorophyll content be approximately linearly related to oxygen production. In optically thick samples, the chlorophyll must necessarily be heterogeneously illuminated and thus unequally efficient. Moreover, the degree of heterogeneity depends on the incident light intensity.

For optically thick algae such as *Codium fragile* and *Chondrus crispus*, we expect little increase in photosynthesis with increasing light intensity. The fact that a two-fold increase is found in these cases is surprising and suggests that other parameters such as light-induced oxygen uptake and the turnover time are changing. For the green alga *Codium fragile*, however, increased absorption of natural light, particularly deep in the ocean, will occur. However, it will be useful to the seaweed only if the absorbing unit is kept at its surface, otherwise the light is rapidly attenuated. This is in fact the mechanism used by *C. fragile*, and to some extent by all algae. Surface-adapted *C. fragile* appears green whereas deep *C. fragile* appears black, showing that it is the surface-scattered light being absorbed.

The data of Fig. 7 suggest that the green algae *Ulva lactuca* and *Codium fragile* increase the size of their antennae, but that the red algae *Porphyra umbilicalis* and *Chondrus crispus* do not. However, the shape of the saturation curve depends on both the size of the photosynthetic units and their turnover times. Steady-state measurements of the type presented here cannot distinguish between these two constrictions. In any case, we see that the adaptation of algae with depth in the sea may well be richer phenomena than described by experiments on simple laboratory algae.

We conclude, therefore, that the red algae are phylogenetically no better adapted to utilize the ambient light at great depths than their green counterparts. Further, the morphology of the seaweed is at least as important as color, if not more so, in determining the vertical distribution of algae.

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