New Light on Seaweeds

Recent studies have forced reassessment of the role of light-harvesting pigments in depth zonation of seaweeds

Mary Beth Saffo

> **There is one great difficulty with a good hypothesis. When it is completed and rounded, the corners smooth and the content cohesive and coherent, it is likely to become a thing in itself, a work of art. . . . One hates to disturb it. Even if subsequent information should shoot a hole in it, one hates to tear it down because it once was beautiful and whole . . . .**
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> **—John Steinbeck and Ed Ricketts**
> ***The Sea of Cortez***
> **1941**

As every scientist, teacher, and parent knows, the simplest questions are the hardest to answer. In biology, ecological phenomena have a notable way of generating obvious questions that yield complex answers. One such obvious, yet complex, phenomenon is the depth distribution of marine benthic organisms.

There is hardly an example of zonation more striking than the distribution of intertidal organisms on a rocky shore. Even the most casual seashore visitor cannot help but recognize striking horizontal bands of differing colors and densities crossing intertidal rocks, demarcating regions characterized by distinctive assemblages of plants and animals.

The puzzles of such zonation have long enticed biologists. Many detailed, long-term studies underly our current views of the physical and biological factors that affect the distribution patterns of organisms in rocky intertidal habitats. Intertidal zonation in marsh, mudflat, and beach communities, as well as depth zonation in subtidal communities, have also received serious attention. But despite all this work, compelling questions remain. Consider depth zonation in seaweeds.

Seaweed zonation is no longer a neat, simple story linking pigment biochemistry with ecological habitat

Like many other benthic organisms, seaweeds show consistent patterns of depth distribution. Among Northern hemisphere seaweeds, for instance, various species of the stringy green seaweed *Enteromorpha* are typically found on high intertidal rocks, where contact with the ocean may be limited to especially dramatic spring tides or occasional splashing by waves. On many shores, species of the brown rockweeds *Fucus* and *Ascophyllum* dominate regions of the middle intertidal zone, while the large brown seaweeds called kelps are characteristic of the low intertidal zone and subtidal zones.

On a finer taxonomic and spatial scale, seaweeds also show distinctive vertical distributions. Consider two commonplace examples. Five species of rockweed cohabit the same shore in western Scotland, but each occurs at a different intertidal height. One species, *Fucus spiralis*, is most common 2.8–3.4 m above the low tide mark, while another, *Fucus serratus*, is most common at 0.4–1.3 m (Dring 1982, Schonbeck and Norton 1978). In St. Margaret's Bay, Nova Scotia, the kelp *Agarum cribrosum* dominates a distinct subtidal zone, at depths of approximately 15–30 m, while another kelp, *Laminaria longicruris*, is generally found in shallower water, at depths of 4–18 m (Bold and Wynne 1985, Mann 1972).

Why do some seaweed species live only in shallow water, and others live in deeper water? Although this seemingly simple question once had a simple answer, it is now apparent that the simple answer was wrong. This article recounts the development and demise of that attractive, reasonable, and erroneous hypothesis.

Chromatic adaptation: a good hypothesis

In searching for the factors that might determine depth distributions of seaweeds, it makes sense to start—as ecologists often do—by considering those habitat features that vary spatially along with the organisms in question. More than a century ago, German physiologist Theodore Engelmann (1883) suggested that the key variable for seaweed distributions is light.

Since seaweeds need light for pho-

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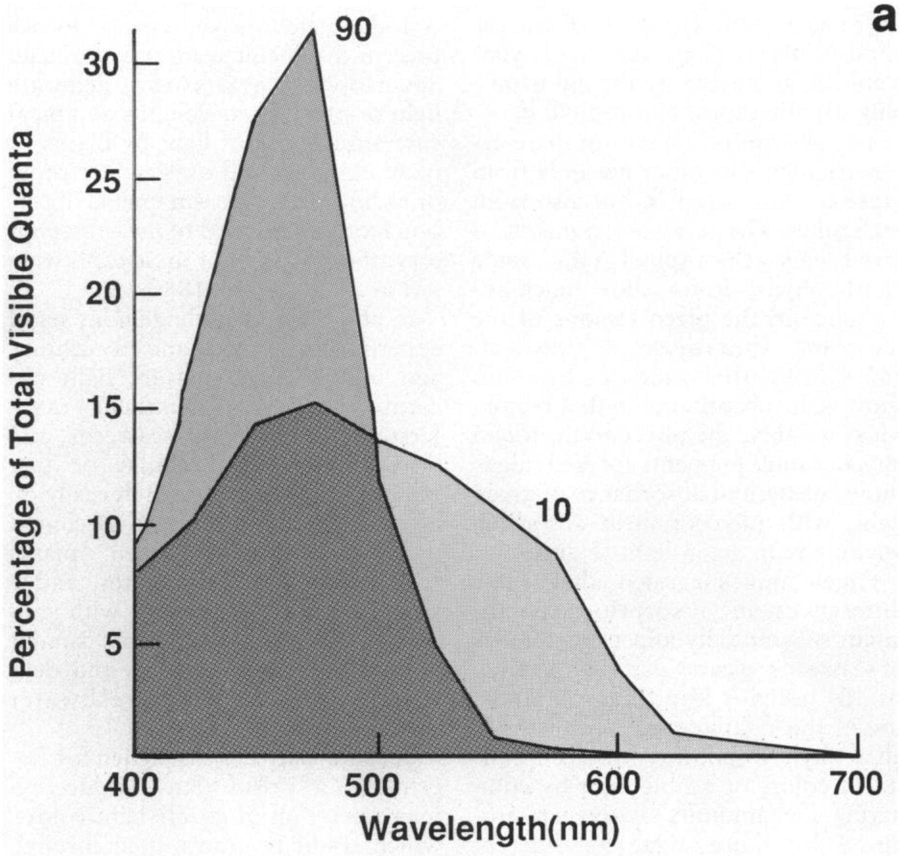

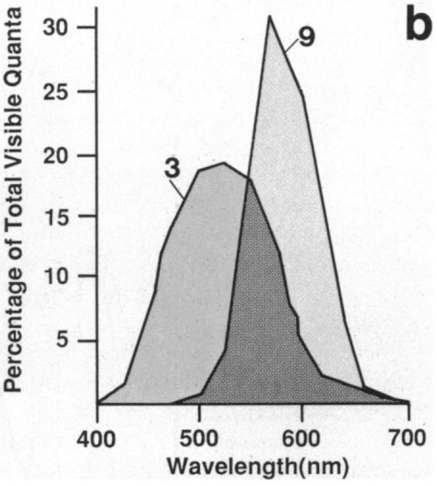

Figure 1. a. (Above) Constriction of spectral range of underwater irradiance with increasing depth, in the clearest (type I) oceanic water. Irradiance at a 10-meter depth still has a fairly broad spectral range; at a 90-meter depth, about 70% of light quanta are at 450–500 nm. After Dring (1981). b. (Right) Spectral changes of underwater irradiance with increasing water turbidity, at 10-meter depths. In coastal water of moderate turbidity (type 3), maximal light transmittance is in green portions of the light spectrum. In coastal water of maximum turbidity (type 9), transmitted light is largely yellow. After Dring (1981).

tosynthesis, their distributions are undoubtedly influenced by the availability of light, which changes drastically with water depth. First, seawater absorbs light strongly, resulting in a marked decrease in irradiance (light flux intercepted per area) with increasing water depth. Even in the clearest ocean waters, the light at 100–140 m depth is much like the deep shade of a dense rain forest—only about one percent of the radiance at the sea's surface.

Most seaweeds cannot live beyond this depth. Only those relatively few seaweeds that can photosynthesize at irradiances as little as 0.05% of surface values are found at greater depths, up to approximately 175–200 m (Lobban et al. 1985). In more turbid coastal and estuarine waters, light is absorbed even faster, such that irradiance may decrease to one percent of surface values at 30, or even 3, meters, resulting in still shallower depth limits for photosynthetic organisms.

As Engelmann noted, light changes not only in quantity, but also in quality, with depth. Seawater absorbs red/infrared (more than 600 nm wavelength) and violet/ultraviolet light (less than 400 nm) much more strongly than it absorbs intermediate wavelengths of light. Therefore light is reduced in spectral range, as well as irradiance, as it passes through water—the bright, full-spectrum white light on the sea surface giving way to blue-green murky dimness. Even in the clearest ocean waters, about 70% of the light reaching a 10-meter depth is in a narrow bluish band of 450–550 nm; and at 90 m it is even more restricted, with about 70% of the light at 450–500 nm , and a peak at about 475 nm (Figure 1a).

In more turbid coastal waters, where most seaweeds live, the spectral range of coastal water is reduced more quickly than that of clear ocean water. Its color also differs from that of ocean water. At 10–100 m depth, it is green rather than blue, with maximum transmittance at 525–550 nm. In the most turbid coastal waters, underwater light is yellow, with maximum transmittance at 575–600 nm (Figure 1b).

Engelmann proposed that the reduction in spectral range of underwater light could pose problems for photosynthesis. As in terrestrial plants, the primary light-absorbing pigment for seaweed photosynthesis is chlorophyll *a*. Chlorophyll *a* absorbs light most strongly in blue-violet (435 nm) and red (680 nm) wavelengths, and most weakly in green wavelengths. Therefore, photosynthesis should be limited when the only light available is green.

But Engelmann noted that seaweeds come in a variety of colors, including green. These colors (or rather the pigments that produce them) are so characteristic of particular algal phyla that they serve as the basis for their taxonomic names. Most seaweeds of the Chlorophyta, the green algae, are green; most species of the Phaeophyta, the brown algae, are brown; and those of the Rhodophyta, the red algae, often are red. These colors are determined in large part by light-harvesting pigments that transfer the light energy they absorb to chlorophyll *a*. Thus the range of light energy available for photosynthesis is greater than what would be predicted by the light-trapping capabilities of chlorophyll *a*.

The absorption spectra of these accessory pigments differ not only from those of chlorophyll *a,* but also from each other. The accessory pigments of green algae (chlorophyll *b* and some xanthophylls) do not show much absorbance in the green regions of the spectrum, while those of brown algae—especially fucoxanthin—do show some absorbance in that region. Most notably, the phycoerythrin and phycocyanin pigments of red algae show substantial absorbance of green light, with phycoerythrin absorbing maximally in green light (Figure 2).

Engelmann suggested that these differences in absorption spectra might substantially affect the abilities of seaweeds to carry out photosynthesis. To test this idea, Engelmann assessed the relative ability of various algal phyla to photosynthesize in different colors of visible light by comparing the amounts of oxygen produced by those algae at different visible wavelengths (Engelmann 1882, 1883, 1884).

Today, such measurements do not present a difficult technical problem. Spectrophotometers can generate light of precise wavelengths and measure absorbance of light by plants or plant extracts; and oxygen electrodes or radioisotopic measurements of carbon fixation are used to measure photosynthetic rates. But these tools were not available in the 1880s.

In an exceptionally ingenious set of experiments, Englemann a century ago managed to measure light absorption and photosynthetic rates. First, he avoided large seaweeds, and instead studied unicellular or tiny multicellular algae, which fit easily on a microscope slide. These specimens included freshwater "green" plants (chlorophytes, euglenophytes, and a moss); freshwater diatoms (with xanthophyll accessory pigments similar to those in brown algae); and delicate, filamentous freshwater rhodophytes.

Second, Carl Zeiss designed for Engelmann a prism that produced a microspectrum of visible light colors, which could be transmitted through algal cells on a microscope slide. Third, Engelmann drew upon his unusually diverse research experience (which embraced muscle physiology, comparative anatomy, and bacterial chemotaxis) in an inventive way. He used aerotactic bacteria as indicators of areas rich in oxygen.

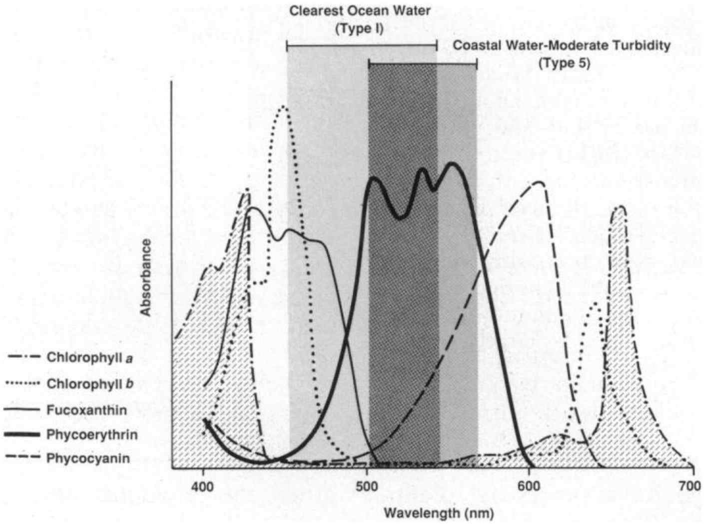

Figure 2. Absorption spectra of photosynthetic pigments compared with spectral range of maximum light transmittance in clear and moderately turbid water at a ten-meter depth. Chlorophyll *a* and *b* show only minimal absorbance at 475–610 nm, where most underwater light is transmitted at a 10-meter depth. In vitro (as shown here), fucoxanthin shows notable absorbance at 475–520 nm, and a still broader in vivo absorbance (475–580 nm) of 475–610 nm light. The absorption spectrum of phycoerythrin (with a characteristic absorption maximum of approximately 550 nm) closely complements the region of maximum light transmittance in moderately turbid coastal waters. With absorption maxima at approximately 618 nm, the absorption spectra of phycocyanins more closely match the transmittance range of underwater light in very turbid coastal waters. Data from Dring (1982), Govindjee and Braun (1974), Haxo and Blinks (1950).

By shining his microspectrum through algal cells mixed with aerotactic bacteria, Engelmann produced a living graph of the relationship between wavelength and photosynthetic rates. The plant filament and the microspectrum marked the horizontal wavelength axis, and accumulations of bacteria provided the vertical axis, representing oxygen production (Figure 3). With green algal cells, Engelmann found that bacterial numbers were greatest in red and blue light and lowest in green light. With diatoms, activity was greatest in red and yellow-green light, while with rhodophytes, activity was greatest in green to yellow-green light.

In an 1844 treatise on marine ecology, the Danish biologist Anders Oersted suggested a pattern of depth distributions for marine plants that assigned green algae to the shallowest waters, brown algae to intermediate depths, and red algae to the deepest waters. In the light of his own experiments, Engelmann (1883) hypothesized that Oersted's patterns of seaweed distributions could be explained by differing photosynthetic capabilities among algal phyla. Since coastal water is more green with increasing depth, the red seaweeds, which can absorb green light the most efficiently, should live deepest. Green algae, with the most limited absorption of green light, should be confined to the shallowest depths. Brown algae, with some absorption of green light, should be found in intermediate depths.

In 1950, F. T. Haxo and Lawrence Blinks of Hopkins Marine Station in Pacific Grove, California, published a classic paper that repeated Engelmann's work, but they studied macroalgae and used more sophisticated and more quantitative methods. Exposing seaweeds to monochromator-generated light of discrete ten-nanometer wavebands (far more precise than that available to Engelmann), they measured light absorption and photosynthetic rates of red, brown, and green algae across the visible-light spectrum. Both the absorption spectra and action spectra of photosynthetic rates were much like those obtained by Engelmann. Red algae showed more absorption of green light, and a greater photosynthetic rate in green light, than green algae (Figure 4).

Further, there was a general correspondence between light absorption and photosynthetic rate at a given wavelength. In green and brown algae, for instance, the action spectrum of photosynthetic rates mimicked closely the absorption spectrum across the entire visible spectrum—the greater the absorption at a particular wavelength, the greater the photosynthetic rate. The action spectra of red algae mimicked absorption spectra at 500–675 nm, but not at the outermost reaches (400–500 nm and 675–750 nm) of the visible spectrum. While the incomplete correspondence between action spectra and absorption spectra in red algae was puzzling (an anomaly that ultimately served as evidence for a two-photosystem electron transfer mechanism in photosynthesis), the work of Haxo and Blinks was generally interpreted as a definitive, modern confirmation of Engelmann's hypothesis.

So compelling is Engelmann's hypothesis, in the elegance of its experimental base, and in the simplicity and clarity of its logic, that for more than 100 years it has remained firmly entrenched in the biological dogma. It was cited, without skepticism, in several classic plant physiology monographs of the 1940s and 1950s (Rabinowitch 1945, 1951). And it is a story that has proved irresistible to textbook writers, biology teachers, and students. An account of Engelmann's ideas, presented as fact, is currently included in at least eight well-known textbooks of introductory biology and plant physiology (Bidwell 1979, Curtis 1983, Jensen et al. 1979, Johnson 1983, Keeton and Gould 1986, Raven and Johnson 1986, Villee et al. 1985, Ward and Hetzel 1984).

I still remember this explanation in detail from my student days in introductory biology; and even now, as a biologist, I continue to hear the story presented by plant physiologist and marine biologist colleagues in undergraduate courses. Engelmann's hypothesis is a teacher's, and a student's, dream. It brings the sometimes overwhelmingly abstract details of the physiology of photosynthesis to the concrete, and fascinating, realm of the seashore, linking physiology to ecology with a memorable story. And it makes sense. But is it true?

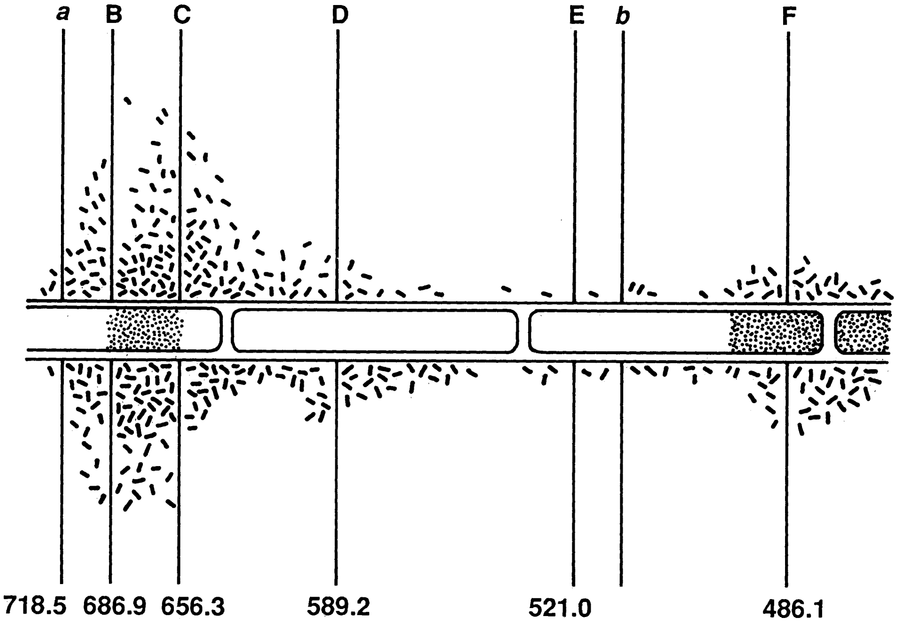

Figure 3. Engelmann's experimental setup. A filament of the chlorophyte *Cladophora* lies along the horizontal axis, through which a microspectrum of visible light is transmitted. *Cladophora* most strongly absorbs red light (left shaded area) and blue light (right shaded area) . Aerotactic bacteria also accumulate preferentially around the plant in red and blue light, suggesting that *Cladophora* is producing oxygen (and thus photosynthesizing) in those parts of the plant that absorb red or blue light. The lettered bands are "Frauenhofer lines," which represent the absorption bands of sunlight. Wavelength equivalents of these lines are noted. After Engelmann (1882).

Tests of Engelmann's theory

From the beginning, there were biologists who questioned Engelmann's conclusions. Friedrich Oltmanns (1892, 1923) maintained that Oersted and Engelmann overstated the differences in depth distribution among chlorophytes, phaeophytes, and rhodophytes, noting that red algae were often found side-by-side with brown and green algae. In culturing green, brown, and red seaweeds under various irradiances and variously colored filters, he also found that growth rates and morphologies of the seaweeds were affected by different irradiances but not by different colors of light. From such data, Oltmanns concluded that vertical distribution of seaweeds was determined chiefly by irradiance, not by spectral quality.

In 1928, two Russian biologists, Vladimir Lubimenko and Z. Tikhovskaya, measured photosynthetic pigment content and photosynthetic rates of chlorophytes, phaeophytes, and rhodophytes in the Black Sea. They found that the ability of seaweeds to photosynthesize at depths of 25 m and 50 m was correlated with amount of total photosynthetic pigment, rather than the kind of pigment or algal phylum. These data led Lubimenko and Tikhovskaya (1929) to the conclusion that "the question of chromatic adaptation in algae is in reality much more complicated than supposed by Engelmann's theory."

Nevertheless, Engelmann's theory continued to prevail. It is only with recent work—especially by Joseph Ramus of Duke University's Beaufort Marine Laboratory and Matthew Dring of the Queen's University of Belfast—that the conceptual and experimental foundations of Engelmann's theory have finally come under serious question.

As Ramus (1981, 1982) noted, Engelmann's hypothesis rests on the validity of three notions, which, until recently, remained deeply engrained,

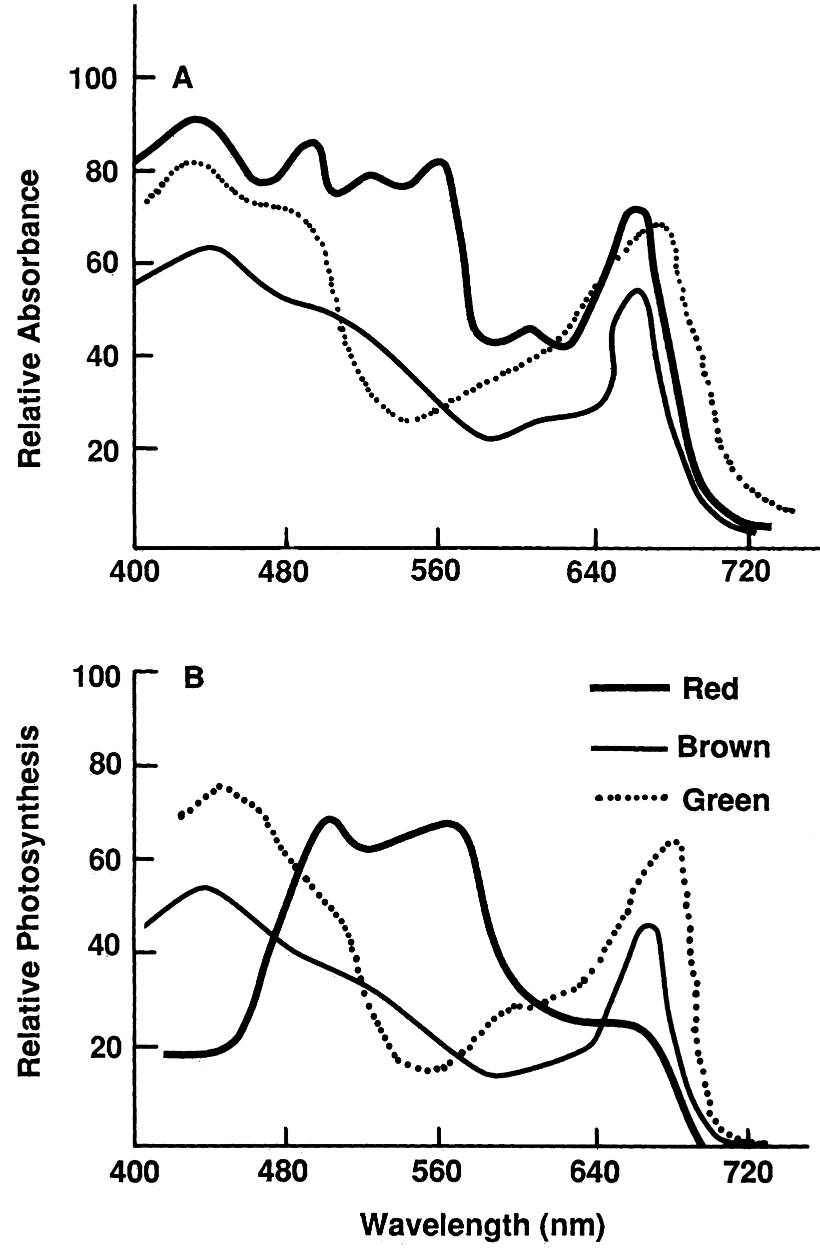

Figure 4. a. Absorption spectra of whole seaweed thalli, comparing absorption patterns of red, green, and brown algae: *Myriogramme spectabilis* (rhodophyte); *Ulva taenita* (chlorophyte); *Coilodesme* (phaeophyte). *Ulva* shows minimal absorbance of green light; *Coilodesme* shows some absorbance; and *Myriogrammme* shows maximal absorbance in green light. After Haxo and Blinks (1950). **b.** Action spectra in red, green, and brown algae. In *Coilodesme* (phaeophyte) and *Ulva taenita* (chlorophyte), absorption spectra closely match action spectra. The absorption spectrum of *Myriogramme* (rhodophyte) matches its action spectrum at 480–600 nm, but not at shorter or longer visible wavelengths. After Haxo and Blinks (1950).

but largely untested, assumptions among biologists:

- The deepest seaweeds are exclusively red algae. Green seaweeds are found only in the shallowest subtidal water, and brown algae inhabit intermediate depths.
- Light is the only, or at least only major, factor that affects seaweed zonation. It is the relative photosynthetic ability of particular seaweeds at different depths (and different light intensities and light spectra) that determines where seaweeds can live.
- Large red seaweeds in the ocean (not just microscopic freshwater red algae on a microscope slide) photosynthesize better in deep water than do green and brown seaweeds. Rhodophytes' superior photosynthetic performance in deep water is due to the presence of phycocyanin and phycoerythrin, which absorb green light more effectively than do the accessory pigments of green algae and brown algae.

Recent studies have questioned each of these assumptions in turn.

Ecological reality

Let's first consider the most straightforward question: where do seaweeds live? Even Engelmann, who accepted Oersted's generalizations, noted (1883) that not all algal distributions correspond to them. A 19th century study of the Gulf of Naples had shown that red algae are found in large numbers not only in deep waters, but also in shady areas of surface waters, where light would be low in intensity, but not necessarily blue. To explain this anomaly, Engelmann suggested that incoming skylight of Naples was bluer than the "white light of the duller skies" of more northern climes, so that even surface algae in the Mediterranean received a high percentage of bluish light. We now know, however, that the percentage of blue light is, if anything, relatively greater, rather than smaller, in incoming light at higher latitudes (Jerlov 1976). It is now also clear that such seaweed distributions, which were considered to be anomalous, are not limited to the Gulf of Naples.

Blinks (1955) noted that the vertical distribution of intertidal seaweeds in central California is the inverse of that predicted by Engelmann. Three of the seaweed species growing highest in the intertidal zone—in the spray zone, where submersion in water is very rare—are red algae; two species of phaeophytes are found lower; and chlorophytes occur below these. This observation certainly calls into question an oversimplified version of Engelmann's hypothesis, one especially favored in introductory texts, that red algae live only in deep water.

Even more compelling, numerous surveys of subtidal waters of tropical, temperate, and boreal regions fail to support the key notion that rhodophytes predominate in the deepest waters. In one such survey, Doty et al. (1974, p. 345) noted: "We suspect that the classical picture was conceived by observers who were reporting what was visible at low tide at hip-boot depths."

Surveying Hawaiian seaweeds from 10 to 165 m depths, Doty and his colleagues found no greater percentage of rhodophytes, compared with green and brown algae, in deep water than in shallow water. In fact, below 90 m depth, the ratio of red to green algal species (2/3) was less than in shallower water (3/1, below 10 m). Comparing the overall distribution of each of the three groups of seaweeds, these investigators found no significant difference in either the minimum or maximum depths inhabited by red, green, and brown algal species (Figure 5).

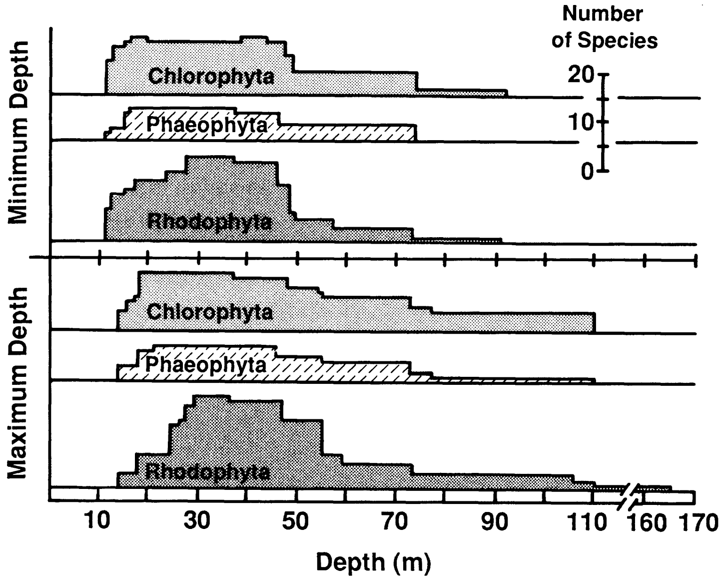

Figure 5. Comparison of the depth distributions of chlorophyte, phaeophyte, and rhodophyte species collected off the coast of the Hawaiian islands, at 10–165-meter depths. There is no significant difference in the overall depth distribution of the 101 species of chlorophytes, phaeophytes, and rhodophytes studied. Although in this collection the one or two deepest-dwelling seaweeds (at 120–165 m) were rhodophytes, earlier collections from Hawaii also yielded two species of green algae from such depths (Doty et al. 1974).

Other surveys, using both dredging and scuba techniques to sample algae, also have failed to confirm the classical picture. In the tropical Atlantic and Pacific Oceans, the Adriatic Sea, the Sea of Japan, and the Arctic Ocean, green algae are among the deepest seaweeds (Gilmartin 1960, Goreau 1963, Lang 1974, Larkum et al. 1967, Wilce 1967). Surveys of seaweeds in the South Pacific, the Caribbean, and the Arctic (Taylor 1961) have found that the numbers of chlorophyte species diminish less rapidly with increasing water depth than do numbers of phaeophyte and rhodophyte species, with the numbers of red species diminishing most rapidly with depth.

A survey off the Carolina coast (Schneider 1976) showed that 28% of red algal species are found at depths greater than 50 m; but 25% of green algal species and 16% of brown algal species are found in those deep waters as well. In the turbid North Pacific waters of the Gulf of Peter the Great, the photic zone is only 30 m deep. But once again, both green algae and red algae penetrate to the maximum 30-meter depth. And once again, the ratio of red algae to green algae does not increase significantly with depth. At depths less than 2 m the red/green algal ratio is 3.4, while at depths greater than 12 m it is 3.7 (Titlyanov 1976).

Finally, biologists (Crossett et al. 1965, Larkum et al. 1967) have assessed the relative biomass of algae at different depths in Mediterranean waters, enlarging the scope of the early study of Naples reported by Englemann. By weight, brown algae dominated the algal communities in shallow waters, above 15 meters. Green algae dominated deeper waters, at depths of 15–75 m, despite the fact that submarine light was spectrally limited (largely blue light, with a peak at about 475 nm) lower than 40 m. Red algae made relatively little contribution to algal biomass at any depth, and even that small contribution did not increase with depth to 75 m, the greatest depth that could be studied with scuba techniques. Encrusting calcareous species of red algae dominated algal cover only in the shadiest walls of a 33-meter-deep grotto. But even in this case, green algal dominance continued part of the way into the cave, well beyond the point where incoming light was narrowed to blue wavelengths.

Complexity of zonation

Why don't red and green seaweeds live where expected? Perhaps traditional views of what determines seaweed distribution are wrong. Let's consider Engelmann's second assumption. Might factors other than relative photosynthetic abilities at different depths affect the distribution of seaweeds? Even a cursory consideration of seaweeds suggests that additional factors must be involved.

First, there are physiological factors that vary with depth. Factors especially relevant to intertidal seaweeds include tolerance of desiccation and of high irradiance (Blinks 1955, Dring 1982, Dring and Brown 1982, Lobban et al. 1985). Other depth-based physiological factors that affect zonation of subtidal algae include temperature, nutrients, and (especially in estuaries) salinity (Gessner and Schramm 1971). Light may also affect seaweeds in a context distinct from its photosynthetic role. Several species of phaeophytes, chlorophytes, and rhodophytes are known to require blue or white light for normal morphology and development (Lobban et al. 1985, Lüning 1981).

The role of other depth-based factors is especially obvious in the many cases where closely related algae differ in depth distribution, despite similar pigmentation (Dring and Brown 1982). Photosynthetic profiles of taxonomically related shallow and deep-water algae provide a further lesson. Many shallow-water seaweeds have higher photosynthetic rates at high irradiances than do deeper-dwelling seaweeds at the same irradiances. Rather than being confined to shallow-water photosynthesis, they are better able to tolerate, and even exploit, intertidal or shallow subtidal conditions in ways that deeper-dwelling seaweeds cannot.

Second, seaweeds may have dependencies on physical factors that do not vary directly with depth. For instance, the vertical range of seaweeds that must attach to a particular substrate—rocks, for instance, or even another alga—will be limited by the vertical range of the substrate. A Mediterranean rhodophyte (*Polysiphonia subulifera*) surveyed by Larkum and colleagues (1967) occurs mainly on a chlorophyte, *Halimeda tuna*. Thus, the upper and lower limits of *P. subulifera's* distribution is limited by the upper and lower limits of distribution of its *Halimeda* substrate.

Finally, seaweeds with similar physiological characteristics may face a different set of biological interactions with other organisms. For instance, the lower depth limit of several seaweeds is determined not by light limitation but by the upper depth limits of particular herbivores or competitors for space (Foster 1982, Lubchenco 1980, 1982, Schonbeck and Norton 1980).

Just as a variety of factors—temperature, soil composition, predation, water availability, and light—affect the distribution of terrestrial plants, so also do many factors affect the vertical distribution of seaweeds. The importance of these additional factors for the distribution of particular seaweed species may explain some of the distribution patterns at odds with Engelmann's and Oersted's predictions.

Physiological relations of pigmentation and light

The effect of additional zonation factors cannot account for all the contradictions between Engelmann's laboratory experiments and the more recent field surveys. Neither laboratory work nor field work alone can resolve the problem. An obvious experimental solution is to blend laboratory and field approaches, in this case to apply Engelmann's experimental questions to seaweeds in the field, rather than to microalgae in the laboratory. However, such field experiments pose special technical difficulties. Engelmann (1883) wanted to measure light absorbances of seaweeds in deep ocean water, but he could not overcome the technical obstacles.

Recently Ramus directly tested the physiological basis of Engelmann's hypothesis—that light-harvesting pigments of a seaweed determine the depth at which a seaweed can live. With a systematic series of physiological experiments in the field and in simulated natural conditions, he compared the photosynthetic abilities, pigment production, and growth rates of differently pigmented seaweeds tested in the same light regimes and at the same water depths. The results of those experiments differed provocatively from those of Engelmann.

First, Ramus and colleagues (1976a,b) compared the photosynthetic ability of two rhodophyte species with that of two chlorophyte species in both shallow water (0.5 m) and deeper water (10 m). Because genetically identical seaweed individuals can differ physiologically if grown at different depths, Ramus studied both seaweeds that had been acclimated to a particular depth and those that had recently been transplanted to that depth.

Surprisingly, the photosynthetic rates of these algae did not appear to be correlated with algal phylum or type of accessory pigment. The data provided instead a correlation of photosynthetic rate with seaweed shape. At a depth of 10 m, for instance, the photosynthetic rate of 10-meter-acclimated green, flat-bladed, sea lettuce (*Ulva lactuca*) was either greater than (per gram of tissue) or comparable with (per gram of chlorophyll *a*) photosynthetic rates for a red, flat-bladed alga, *Porphyra umbilicalis*. Both rates were greater (per gram of tissue) than those of the two thicker seaweeds, the chlorophyte *Codium fragile* and the rhodophyte *Chondrus crispus*.

Ramus and colleagues noted several other differences in the photosynthetic patterns of *Codium* and *Ulva*, similarly pigmented but differently shaped seaweeds, that support the idea that seaweed shape affects photosynthetic abilities. First, when *Ulva* was transplanted from a ten-meter depth to the surface, photosynthetic rates (per gram of tissue) doubled. And when surface-acclimated *Ulva* was transplanted to a ten-meter depth, photosynthetic rates decreased dramatically. In contrast, the photosynthetic rates of *Codium* changed little after transplantation from surface to deep water or vice versa.

Second, *Ulva* grown in ten-meter water showed nearly ten times the chlorophyll *a* concentration, and a notably greater concentration of accessory pigments (chlorophyll *b*) relative to chlorophyll *a,* than surface-grown *Ulva*. However, deeper-grown *Codium* showed chlorophyll *a* concentrations about 1.5 times that of surface-grown plants, but no difference in the ratio of chlorophyll *b* to chlorophyll *a* compared with that of surface-grown *Codium*. Despite apparent lack of *Codium* pigment response to deep water, the photosynthetic rates of *Codium* per gram of chlorophyll *a* or per square centimeter of surface area exceeded those of *Ulva* at low irradiances.

Interpretation of the *Ulva* data is straightforward. *Ulva* that is suddenly transplanted from brighter surface waters to deeper waters will suffer a decrease in photosynthetic rate, because there is less light for photosynthesis in deeper water. But given enough time—seven days or so—*Ulva* can acclimate to life in deeper water by making more of the photosynthetic pigments that better absorb the light available. The photosynthetic rate of *Ulva* that has been growing at a ten-meter depth for a week is about ten times that of surface-grown *Ulva* that has just been transplanted to deeper water. Thus accessory pigments can play an important role in enhancing the ability of some seaweeds to grow in deep water.

But what about *Codium*? To examine possible effects of shape on photosynthetic rates, Ramus (1978) compared the light absorption patterns of *Codium* and *Ulva*. Many published absorption spectra of seaweeds are actually absorption spectra of pigment extracts. But seaweeds absorb light not as pigment solutions, but as structures. Thus, Ramus measured the absorptance (the fraction of incoming light absorbed) of whole seaweeds, with surprising results.

For *Ulva*, which has flat fronds about the thickness and transparency of grass-green cellophane, a plant grown in surface waters absorbs about 19% of incoming light, and shows an absorptance spectrum that closely resembles that of chlorophyll, with little absorption of green light (Figure 6). *Ulva* grown in deeper water absorbs up to 83% of incoming light and has greater amounts of chlorophyll *a* and *b*, a higher ratio of chlorophyll *b* to chlorophyll *a*, and a greater absorptance of green light relative to its surface-grown neighbors. Nevertheless, its absorptance spectrum still shows peaks characteristic of chlorophyll.

But both surface-grown *Codium*, with relatively little chlorophyll (equivalent to that of *Ulva* grown in relatively shady surface waters), and *Codium* from deeper water, with relatively greater chlorophyll, absorb 97–99% of incoming light. Further, *Codium* absorbs strongly across the entire visible spectrum, including green light; optically, *Codium* is black.

Since the absorptance patterns of *Codium* do not change much with amount of pigmentation, the seaweed's opaqueness must arise not so much from greater pigmentation compared with *Ulva*, but rather from its architecture. First, *Codium* is about five times the thickness of *Ulva*. Second, its internal anatomy is quite different. Instead of a thin, double sheet of cells, *Codium* is a spongy mass of fingerlike projections, which are made up of interwoven filaments. These filaments are interspersed with tightly packed arrays of large vacuole-filled bladders (utricles), which are lined with a thin layer of cytoplasm and chloroplasts (Figure 7). Since the chloroplasts are arranged vertically with respect to the exterior utricle tip, one might suppose that the chloroplasts closest to the tip absorb most of the light, with relatively little reaching the interior chloroplasts.

But Ramus (1978) suggested that utricles might operate like a fiber-optics light guide, bouncing light from chloroplast to chloroplast along the membrane-bounded cytoplasm, between the vacuole and utricle wall, all the way down to the base of the utricle. This operation would enhance the probability of capture of each incoming photon by some chloroplast. *Codium* would thus resemble a series of sophisticated solar collectors.

Whatever the detailed mechanism, it is clear that *Codium* maximizes light capture not by possession of phycoerythrin or large amounts of chlorophyll *b*, chlorophyll *a*, or other pigments, but primarily by special structural features. Light absorption is not a matter of pigment biochemistry alone.

Role of phycoerythrin

Whatever structural tricks a green alga may use, it might seem that a red alga's key asset for photosynthesis in deep water is the possession of phycoerythrin, since it absorbs green light. It is upon these absorbance properties that Engelmann's theory is most explicitly and plausibly based. But even for red algae, the role of accessory pigments may not be simply tied to successful photosynthesis in green light.

Gracilaria tikvahiae is a red alga

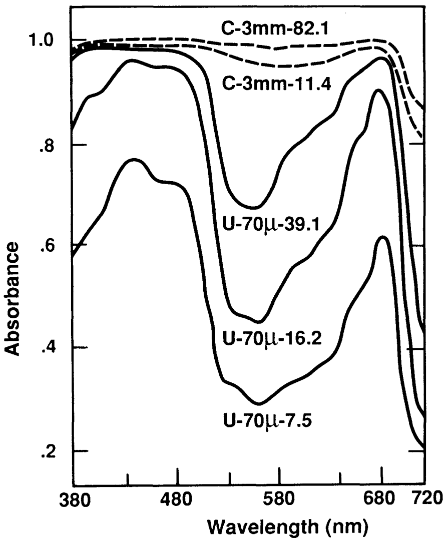

Figure 6. Absorptance spectra of seaweed thalli. C = *Codium fragile*. U = *Ulva lactuca*. Numbers give thallus thickness (in mm or μm), followed by concentration of photosynthetic pigment (nmoles/cm^2). Even at photosynthetic pigment concentrations lower than those of some *Ulva* specimens, *Codium* shows a greater absorptance of green light (Ramus 1978).

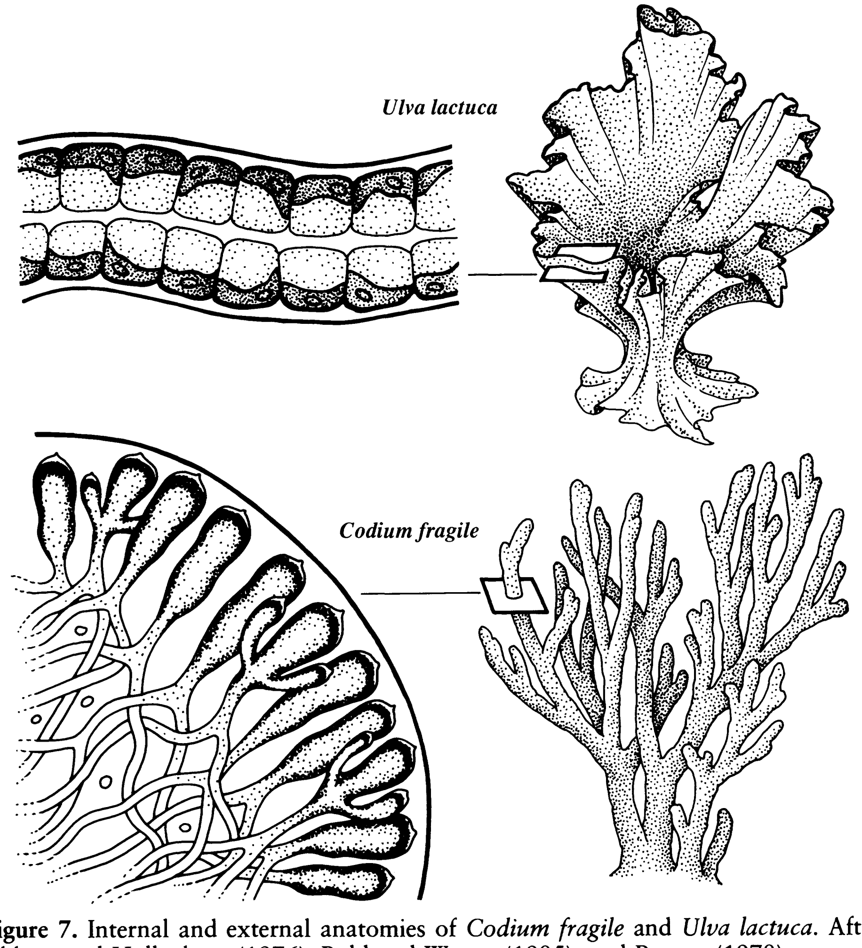

Figure 7. Internal and external anatomies of *Codium fragile* and *Ulva lactuca*. After Abbott and Hollenberg (1976), Bold and Wynne (1985), and Ramus (1978).

found from intertidal waters to 80-meter depths along the southern Atlantic and Gulf coasts of North America. On a granite jetty in Beaufort Inlet, Ramus found a *Gracilaria* frond that was green, rather than red. This genetic variant was successfully cloned in Ramus's laboratory to produce more green plants.

In separate genetic studies of *G. tikvahiae* in Halifax, van der Meer also came across a green variant. Though both green variants had normal concentrations of chlorophyll *a* and phycocyanin, they were strikingly deficient in phycoerythrin compared with their wild-type relatives.

Ramus and van der Meer (1983) used these green variants to explore the effect of phycoerythrin deficiency on photosynthetic rates in three different light regimes: bright, incident sunlight; dim white light (13% of sunlight irradiance, an irradiance that is growth limiting and broadly similar to shaded surface waters); and dim green light (also 13% of sunlight irradiance, similar to deeper coastal water, with a transmittance range of 480–610 nm and a transmittance peak at 550 nm, closely complementing the absorption spectrum of phycoerythrin).

As expected, both the wild type and green variants grew more slowly in the white and the green reduced-intensity light than they did in full sunlight. But surprisingly, the phycoerythrin-deficient mutants showed no significant difference in photosynthetic rate from wild-type *Gracilaria* in any light regime. Ramus and van der Meer concluded that the theory of complementary chromatic adaptation was not supported by their data.

More specifically, such results suggest that the capacity for green light absorption by photosynthetic pigments other than phycoerythrin has been underestimated. Although phycocyanin and fucoxanthin do not absorb maximally in green light, they do have substantial capacity for green light absorption (Figures 2 and 4). So does siphonoxanthin, a xanthophyll found in the deep-water chlorophyte *Ulva japonica* (Lobban et al. 1985). Even chlorophyll *a* and *b* show some absorption of green light, which in certain circumstances can be substantial (Figure 6).

The effect of green-light absorption for an alga lacking phycoerythrin is magnified still further. The monochromicity of light in deep water has been overstated. If, as stated above, 70% of incoming light is restricted to a spectral band of 100–25 nm at depths of 10–90 m, then 30% of the transmitted light is of other wavelengths. Thus, even in deep water, light is not as limited spectrally as in the laboratory experiments of Haxo and Blinks. While elegant laboratory measurements of algal photosynthesis at monochromatic wavebands have contributed much to knowledge of the workings of photosynthetic machinery, they may not be directly relevant to field conditions. For example, the action spectrum/absorption spectra anomaly found in rhodophytes by Haxo and Blinks (1950) disappears when a small amount of 546-nanometer light is added to red light. In addition, the absorption maximum of a seaweed's pigments need not exactly match the transmission maximum of the underwater light for the plant to gather enough light for photosynthesis.

Photosynthesis studies of seaweeds in field conditions pose a very difficult experimental problem, since both the spectral range and irradiance of light are reduced in deep water, and seaweeds normally experience both aspects of light change simultaneously. To separate these variables, Dring (1981) compared published action spectra of many species of red, brown, and green algae with data drawn from both classic and recent work. Combining those data with light transmission values for seawater of various degrees of turbidity, from clear oceanic water to the most turbid coastal waters, Dring predicted the photosynthetic rates of seaweed species in light of different spectral composition but identical irradiance. From his model, Dring suggested that in all water types, red algae should be better adapted chromatically to photosynthesize in depths of 10 m or less, slightly outperforming brown and green algae even at the water's surface.

Dring also predicted high photosynthetic rates for green and brown algae—greater than those of red algae—in clear oceanic waters of greatest depth. He predicted that red algae (such as *Porphyra umbilicalis*) with phycocyanin as a dominant accessory pigment are best adapted for photosynthesis in the most turbid deep water, and that red algae (such as *Chondrus crispus* and the subtidal rhodophyte *Delesseria*) with phycoerythrin as a dominant accessory pigment should be best adapted to photosynthesize in deep waters of intermediate turbidity.

But, once again, seaweed zonation does not correlate well with predictions. In the clearest oceanic water, red algae penetrate as far as green and brown algae, in spite of their predicted poor chromatic adaptation in deep, clear water. At the other extreme, the intertidal *P. umbilicalis* does not penetrate subtidal turbid waters, in spite of its predicted superior photosynthetic ability in deep turbid waters. Dring inferred from his results that "the ecological significance of chromatic adaptation may be far more limited than has often been assumed."

To separate irradiance from spectral quality experimentally, Ramus (1983) grew seven species of red, brown, and green seaweeds in experimental conditions that differed both in irradiance and in spectral composition. He grew seaweeds in running seawater in white light of saturating (full incident) and growth-limiting (13% of incident light) irradiances and in green light at growth-limiting (13%) irradiances. After one to two weeks, Ramus measured pigment densities, growth rates, and photosynthetic rates of these seaweeds. In almost all cases tested (Table 1), seaweed responses to saturating light differed from those to reduced light, whether the reduced irradiance was green or white. Thus, seaweeds responded physiologically to irradiance but not to spectral distribution of light.

Conclusions

The field surveys and experimental work described here have bombarded Engelmann's hypothesis with uncooperative facts. They have forced us to revise three cherished notions of the relationship between light and depth zonation of seaweeds:

- The deepest seaweeds are not exclusively red algae. Green and brown seaweeds can also penetrate the deepest waters of the photic zone. Conversely, there are plenty of red seaweeds in surface waters, and red algae are even found in the highest reaches of the intertidal zone. Systematic surveys have shown that there is no statistically significant difference in the overall depth distribution of red, brown, and green seaweeds. Although most seaweed species do show differing depth ranges in intertidal or subtidal waters, such differences are not correlated directly with algal phylum or with possession or absence of particular light-harvesting pigments.

- Light is only one of the many factors that influence depth zonation of seaweeds. Air exposure, predation, competition for settling space with animals and other plants, substrate, temperature, and salinity may all affect depth zonation. Light plays a role, but not to the extent that we once assumed, and perhaps not even in exactly the way that we once thought self-evident. In the high intertidal regions, excessive light irradiance may play an explicit role in zonation. Even in deep water, seaweeds apparently respond physiologically to the low irradiance of underwater light more than they do to its limited spectral range.
- Red seaweeds do not necessarily photosynthesize better than green and brown seaweeds at great depths. Differential photosynthetic ability of seaweeds in deep and shallow water is often more closely correlated with factors other than algal phylum. There are at least three mechanisms exploited by algae for photosynthesis in dim, spectrally limited deep water, none of which are exclusive to red algae. These mechanisms are: producing more accessory pigment (any accessory pigment, not just phycoerythrin) relative to chlorophyll *a*; producing more photosynthetic pigment generally—accessory pigments and chlorophyll *a*; and possessing special structural features—such as thick fronds and specific chloroplast arrangements—that maximize the efficiency of light absorption.

These revised notions suggest the importance of reconsidering the data that support Engelmann's hypothesis. In many places, as in the Hawaiian survey by Doty and colleagues (Figure 5), the two or three deepest-living algal species are indeed red algae. But given the similarities of overall depth distributions of rhodophytes and other seaweeds, perhaps we should look for features other than the possession of phycoerythrin to explain the success of such algae at the lowest limit of the photic zone. What important role might other morphological and physiological features play in tolerance of low photosynthetic rates, low growth rates, and resistance to predation in deep water?

Table 1. Photosynthetic pigment concentrations (chlorophyll *a* shown here); growth rates; and photosynthetic rates of brown, green, and red seaweeds measured under bright white light and reduced, growth-limiting irradiances of white or green light. Except for photosynthetic responses of the phaeophyte *Sargassum filipendula*, most seaweeds responded physiologically to changes in irradiance but not to changes in spectral distribution of light (abridged from Ramus 1983). *Fuc = Fucus vesiculosus; Sar = Sargassum filipendula; Ulv = Ulva curvata; Cod = Codium decorticatum; Gri = Grinnellia americana; Gra = Gracilaria tikvahiae.*

	phaeophyte		**chlorophyte**		**rhodophyte**	
	Fuc	*Sar*	*Ulv*	*Cod*	*Gri*	*Gra*
GROWTH RATE						
dry wt. biomass doublings/day						
Bright white (I_O)	0.07	0.10	0.43	0.13	0.11	0.18
Dim white (0.13 I_O)	0.02	−0.02	0.16	0.13	0.16	0.05
Dim green (0.13 I_O)	0.02	0.01	0.14	0.13	0.16	0.03
CHLOROPHYLL *a*						
mg/g						
I_O white	1.9	3.7	2.5	2.0	1.1	1.4
0.13 I_O white	3.2	5.2	9.7	4.8	1.9	3.6
0.13 I_O green	3.5	3.8	6.9	5.4	2.4	3.9
PHOTOSYNTHETIC EFFICIENCY						
μmol $O_2 \cdot g^{-1} \cdot h^{-1}/(\text{einstein} \cdot m^{-2} \cdot s^{-1})$						
I_O white	0.69	0.49	1.36	0.39	0.49	0.48
0.13 I_O white	1.05	0.39	3.75	0.90	1.62	0.99
0.13 I_O green	0.95	0.89	3.80	0.79	1.35	0.97

In his classic volumes on photosynthesis (1951, p. 1186), the plant physiologist E. I. Rabinowitch wrote of the then-persuasive evidence in support of Engelmann's theory, "How could it have been otherwise? Would it not be strange if the appearance of orange or red pigments in deep-water algae would be only a coincidence, and these pigments were helpless in performing the task so obviously set to the plants by the character of the 'light field' in which they live—to catch and utilize for their maintenance and propagation radiations in the middle of the visible spectrum which are the only ones to reach them in some intensity?"

Though phycoerythrins and phycocyanins absorb middle-spectrum light, we know now that their significance for the lives of seaweeds in deep water is different from that we once thought so obvious. The significance of these pigments is diminished in a way, but also enlarged by a more complex and more mature understanding of the phenomena involved.

If no longer a neat, simple story linking pigment biochemistry with ecological habit of seaweeds, the history of physiological determinants of seaweed zonation nevertheless serves us still (Dring 1981) "as a cautionary tale illustrating the mean tricks that Nature sometimes plays on us, such as dressing up one form of adaptation to look like another." But nature is not only a repository of tricks, it is also one of answers, for the biologist attentive enough to notice them. Posing the questions that uncover those answers is a biologist's greatest joy and greatest challenge.

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