MARINE BENTHIC FLORA

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Summary

The shallow bottom of the sea is the realm of algae and of a few land plants that have returned to the sea, the seagrasses. As light penetrates in the water both its quantity and quality change drastically. The marine benthic flora has acquired, during the course of evolution, a great diversity of characteristic arrays of light harvesting molecules, the accessory pigments, as an adaptation to reduced light availability. The physical forces imposed on marine benthic flora by moving water exert a critical influence on the local scale pattern. Macroscopic marine flora adapt their form to reduce the physical stresses of water motion. Other abiotic and biotic factors such as nutrients and temperature, and competition and herbivory, also contribute decisively to establish the patterns of marine benthic flora.

Short-term changes determine the immediate patterns of production and distribution of marine benthic flora. The seasonal production cycles depend mostly on the seasonal cycles of light, temperature, hydrography and nutrients. Disturbances are a major structuring factor as they alter the outcome of competition and affect both the rates and patterns of succession. A particular case of disturbance is the human exploitation of marine biological resources. Many algae species are exploited as food or for the extraction of phycocolloids and pharmaceutical compounds, but the overharvesting of consumers may also lead to severe alterations of benthic flora due to cascade effects down the food web. Long-term changes in benthic community structure and geographical distribution of flora result from global atmospheric changes. Probably the most compelling global scale change is eutrophication. It can lead to drastic qualitative alterations of the structure and functioning of marine benthic communities. Other important long-term changes are toxic contamination and the human-mediated

introduction of non-indigenous species. The latter is not just speeding up the natural dispersal processes but creating different combinations of species in marine benthic communities. Current levels of human activities have greatly modified marine benthic flora to the point of threatening the sustainability of the ecological goods and services provided by this natural life supporting system. Conservation efforts have led to a new concept of conservation of marine communities, the establishment of marine protected areas.

1. Diversity of benthic marine flora

Plants dominate most terrestrial landscapes. Herbs, shrubs and trees, mostly green, are almost everywhere. But what about the bottom of the sea, the benthic landscapes? For the most part, bare sediments and rocks are what can be seen, unless it is shallow. The shallow bottoms of less than 30 meters are trimmed with “plant” life. This is the realm of algae, not true plants as their cell organization and reproductive structures are less complex, but organisms also using chlorophyll *a* as the main molecule to harvest the light of the sun and transform it into chemical energy and organic matter. In the algae, pigments of distinct color mask the characteristic green color of chlorophyll. The colors of the benthic landscapes are not green, but mostly brown and red because the pigments of marine benthic flora absorb all the light components except the brown and red.

The specific richness of the benthic marine brown algae, Division Heterokontophyta, is very high because they include the microscopic diatoms, the golden-brown algae of the Class Bacillariophyceae with over 100 000 species, most of which are not yet described. The diatoms are like the insects of land habitats—there are many more species than in all the other groups. The specific richness of the marine red algae, Division Rhodophyta, is about 5000 species, the highest of all marine macrophytes. The brown macroalgae, all of them included in the Class Phaeophyceae, are about 1500 species. This is the most important group of marine brown algae, which includes the kelps, the largest, most complex, and most productive macroscopic algae, which dominate the benthic landscapes in temperate and cold waters. Kelp forests create an upper canopy that can be up to 20 m high, with an understory of brown, red and green algae (Figure 1).

The green algae, Division Chlorophyta, are only about 550 marine species, but their evolutionary importance is extraordinary. Circa 500 millions years ago, during the course of evolution, a few of them were able to invade the land margins where the tides did not reach, to become the ancestors of all land plants. Later on, about 100 million years ago, a few complex land plants that produced flowers, returned to the sea. These are the seagrasses (Figure 2), marine flowering plants with about 50 species, mostly tropical, assigned to the Division Magnoliophyta (angiosperms)/Class Liliopsida. Seagrasses develop on shallow coasts on sandy and muddy sediments or, less commonly, on rocky shores.

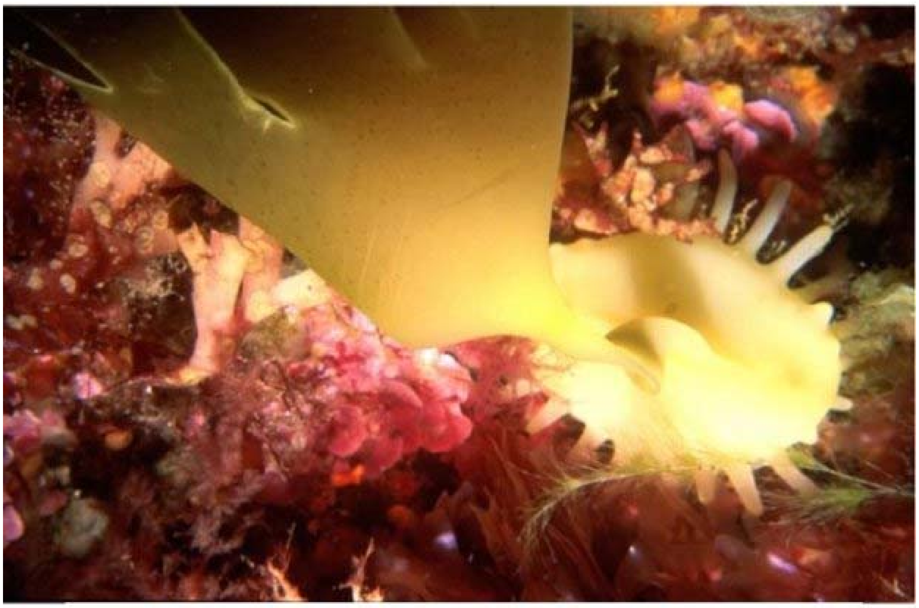

Figure 1. Understory algae under the canopy of the kelp *Saccorhiza polyschides*.

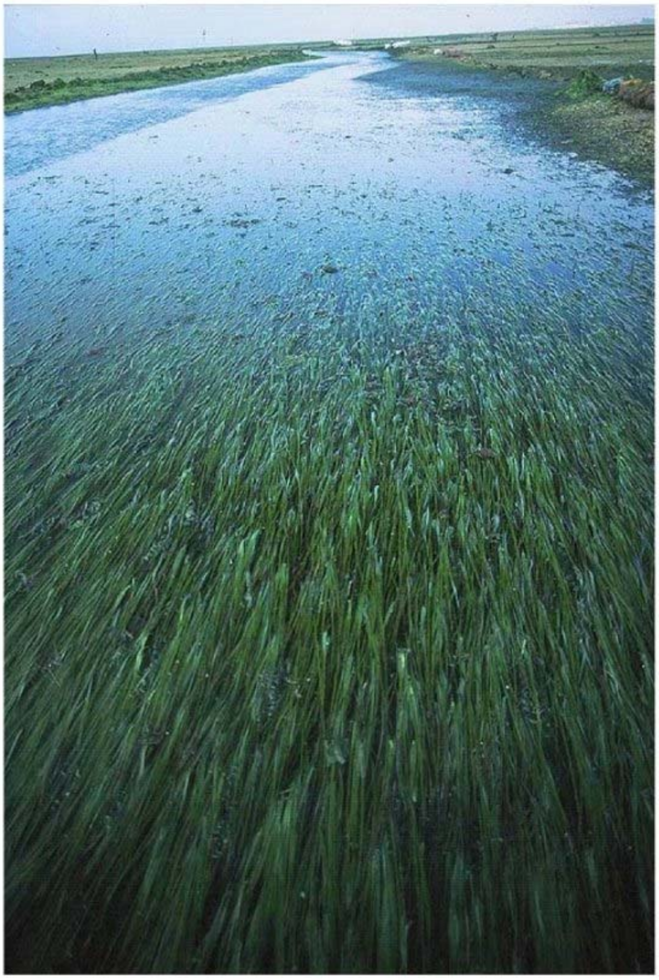

Figure 2. A meadow of the seagrass *Cymodocea nodosa*, Ria Formosa lagoon, Portugal.

The small benthic blue-green algae, which in fact are bacteria (Cyanobacteria), are particularly abundant in warmer seas or on intertidal sediments of confined coastal systems (Figure 3).

Figure 3. Mats of filamentous Cyanobacteria (dark belt) on sediments of Ria Formosa lagoon, southern Portugal. (Photo by the author).

Cyanobacteria are prokaryotic—they lack a membrane-bound nucleus and organelles. They evolved 2 billion years ago and were the dominant life form on earth for more than 1.5 billion years. They were the first organisms containing chlorophyll *a* and using H_2O as the electron donor for photosynthesis, releasing O_2 as a by-product. The same photosynthetic process is found in our time in all eukaryotic algae and plants. In fact, the chloroplasts of all algae and plants are descended from cyanobacteria. The species richness of cyanobacteria is very difficult to evaluate, because they lack the sexual fusion of gametes and thus the biological species concept cannot be used. They can be treated taxonomically like bacteria or like algae, in which case morphological features are used to identify them.

The morphological diversity of the seaweeds that constitute most of marine benthic flora is surprising. The form of algae varies from little single cells, as in diatoms or cyanobacteria, to forests of brown tree-like forms up to 50 meters long, the kelps. Algal morphologies have been interpreted as ecological adaptations to physical resistance, grazer resistance, productivity and role in ecological succession. Seaweeds have been classified into functional-form groups such as sheets (Figure 4a), filamentous (Figure 4b), coarsely branched (Figure 4c), leathery (Figure 4d), articulated calcareous (Figure 4e) and crusts (Figure 4f).

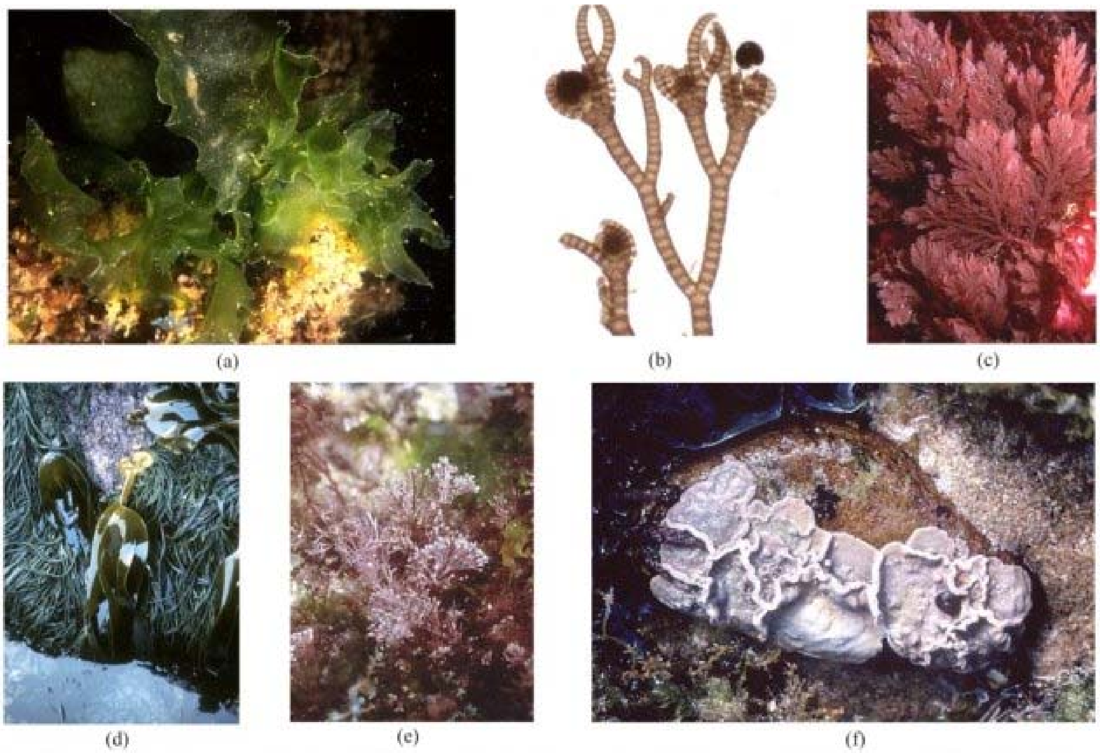

Figure 4. Examples of algal form groups: *Ulva* sheet (a), filamentous *Ceramium* (b), coarsely branched *Plocamium* (c), leathery *Saccorhiza* (d), articulated calcareous *Jania* (e) and *Lithophyllum* crust (f). (Photos by the author).

There is evidence (but also debate) that the resistance to physical factors and to grazing increases within this series, at a trade-off cost of decreased productivity. The cellular organization of highly productive forms is lower; there are no cells with structural functions. All cells of filaments and sheets are photosynthetic, have high energy content, and consequently are a good food source for herbivores. At the other extreme, the calcareous algae are the toughest, but they grow very slowly. Some of them are thought to be hundreds of years old. Every cell of the simple, highly productive, forms originates as reproductive cells, while the more highly structured seaweeds develop special reproductive structures, which can be quite complex. A massive quantity of reproductive spores or gametes is produced by simple forms, which have lower reproductive success than the lower quantity, reproductive bodies of complex forms. The former are the first to develop in new, unoccupied substrates, while the latter are typical of the later stages of ecological succession.

2. Adaptations of benthic marine flora

2.1. Light

Light is a common term used for radiation in that segment of the electromagnetic spectrum, about 400 to 700 nm, to which the human eye is sensitive. But algae and plants are not concerned with vision, but photosynthesis. Nevertheless, by a convenient coincidence, the waveband within which they can perform photosynthesis corresponds approximately to that of the human vision. Light means the same for both the humans and the marine flora.

Those algae that in the course of evolution have remained in, or the higher plants that have returned to, the marine environment have a major disadvantage over their terrestrial counterparts: the medium that surrounds them, water, both absorbs and scatters light. Light availability is the most important limiting factor for primary production by the benthic marine flora. Species must compete for solar radiation not only with each other but also with all the other light-absorbing components of the water column above them.

Light occurs in indivisible units referred to as quanta or photons. The actual numbers of photons that arrive on a horizontal surface on land, in one second of a full summer day is very large: 10^{21}. What happens to them within the water? They are scattered, i.e. they interact with some component of the medium, diverging from their original path, and are eventually absorbed. Scattering does not by itself remove light, but impedes its vertical penetration by increasing the probability of absorption. When a photon passes within the vicinity of a molecule, there is a finite probability that the molecule will capture it, i.e. absorb it. The energy of the molecule increases by an amount corresponding to the energy of the photon. The light absorbing molecules of the aquatic medium, such as the water itself and the particulate matter dissipates this energy mostly as heat energy. A very small amount is dissipated by re-emission of radiation, a phenomenon referred to as fluorescence, being re-absorbed again before it can escape from the system. Absorption and scattering of light under water cause both its intensity and spectral quality to vary markedly with depth (see Figure 5).

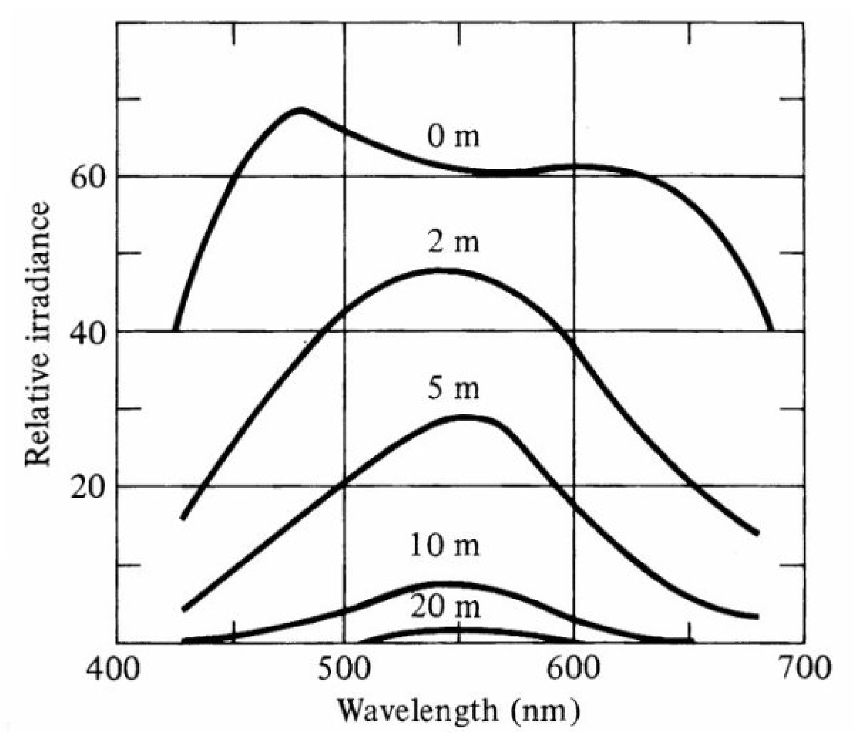

Figure 5. Variation of light intensity and spectral quality with depth. (From Jerlov, NG 1976. Marine Optics, Elsevier Science Publishers, Amsterdam).

As light penetrates the water, both ends of the spectra are absorbed and its intensity decreases drastically. The red and violet wavelengths are the first to be absorbed, in the first few meters. At depths higher than 20 meters the light spectra narrows to 500 to 600 nm, the blue-green color of the spectra.

To adapt to varying light environments, marine flora acquired, during the course of evolution, a great diversity of characteristic arrays of light harvesting molecules, the accessory pigments. They transfer the energy of the photons to the chlorophyll *a* reaction centers where it is used to generate high-energy organic molecules and carbohydrates along the pathways of photosynthesis. There are three chemically distinct types of photosynthetic pigments: the chlorophylls, the carotenoids and the biliproteins with different absorption spectra (see Figure 6).

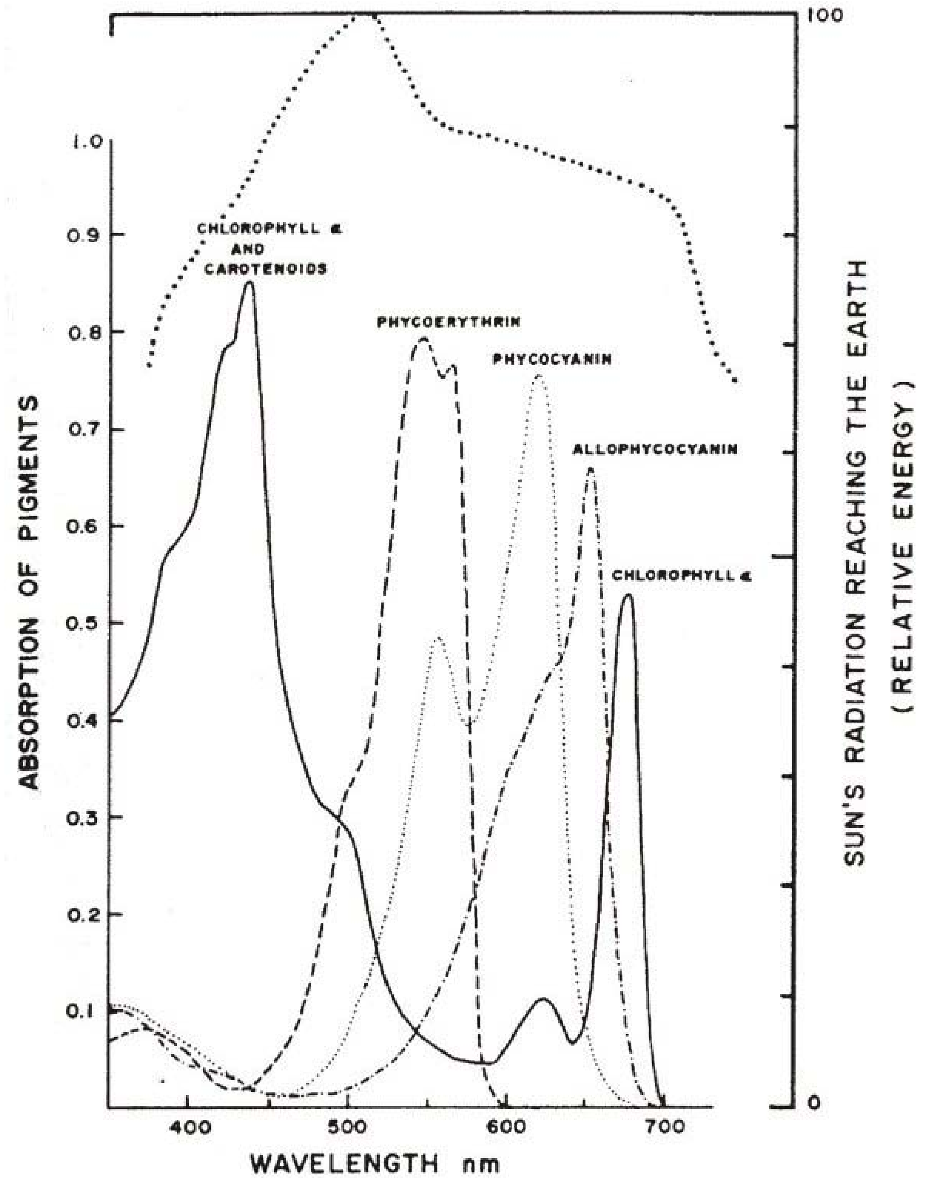

Figure 6. Solar spectrum at the surface of the earth (upper dotted curve) and absorption spectra of algal pigments. (From Grantt 1975, Bioscience 25: 781-788).

All photosynthetic algae and plants contain chlorophyll *a* and βcarotene; three additional chlorophylls occur in the algae, chlorophyll *b* which is found in green algae and also in higher plants, and chlorophylls c_1 and c_2, found only in brown algae. Chlorophylls do not absorb in the 500 to 600 nm spectra window. To adapt to greater depths, accessory pigments are needed.

Algae have a wide variety of carotenoids, of which at least three are involved in light harvesting, in contrast to higher plants. Blue-green and red algae have carotenoids confined to the reaction centers, but they have a protective role against high levels of radiation, which can damage the reaction centers. This is an important adaptation to the intertidal zone, where irradiance is often too high. Green algae have also a similar protection mechanism involving a synthesis cycle between zeaxanthin and violaxanthin (the xantophyll cycle). In most green algae carotenoids play a role in light harvesting, but they are not the predominant pigments. To adapt to higher depths, green algae have specialized carotenoids such as siphonaxanthin, which absorbs around 540 nm. *Valonia macrophysa* (see Figure 7), for example, can develop at depths of more than 40 meters.

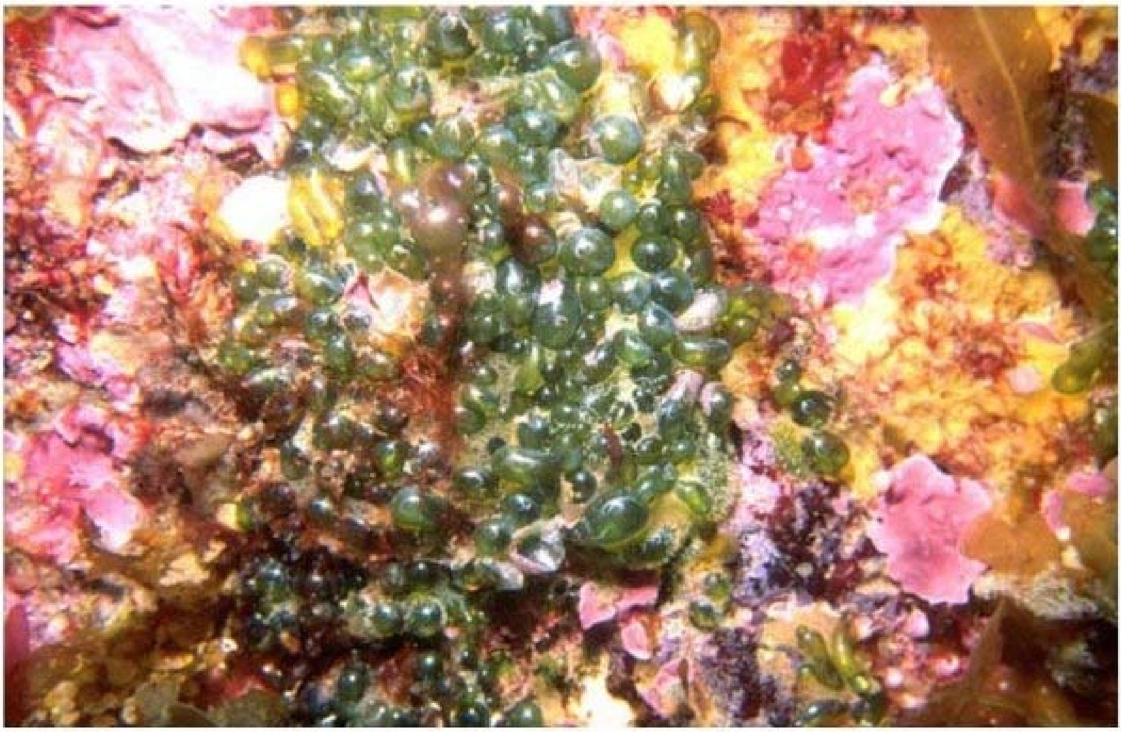

Figure 7. *Valonia macrophysa*, photographed at 40 meters depth at the Ormonde seamount, northeast Atlantic. (Photo by the author).

In brown algae, carotenoids play a major role in light harvesting, particularly fucoxanthin, which with siphonaxanthin are unusual carotenoids absorbing in the green region. Violaxanthin is also an important carotenoid in brown algae, mostly involved in protection against excessive light. Biliproteins are found only in blue-green and red algae. They are either red (phycoerythrins) or blue (phycocyanin, allophycocyanin) in color and play a major role in light harvesting. Phycocyanin is the main biliprotein in the blue-green algae while phycoerythrin is the main component in the red algae.

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Biographical Sketch

Rui O. P. Santos received his B. Sc. and Honors in biology at Faculty of Sciences, University of Lisbon, Portugal, in 1981. From 1981 to 1983 he worked at the National Research Fisheries Institute at Lisbon. He worked as an instructor at the University of Aveiro from 1983 to 1985. From 1985 to 1993 he worked as a Research Scientist at the Engineering and Industrial Technology Laboratory, LNETI. He received his Ph.D. in biology at Dalhousie University, Halifax, Canada in 1993. His thesis research concerned population ecology and resource management of commercial seaweeds. He was appointed Professor Auxiliar at University of Algarve in 1993 and promoted to Professor Associado in 1999. He is the Head of the Department of Ecology and Living Resources of the Faculty of Marine and Environmental Sciences of the University of Algarve. His research interest includes the role of marine vegetation regulating the fluxes and tropho-dynamics of coastal ecosystems, population ecology and ecophysiology of marine plants, marine plant diversity, and economical valorization of marine plants. Santos has 20 peer-reviewed papers published. He is (or was) involved as a co-ordinator or as a participant in five European funded projects and six national funded projects. He participated in the evaluation of projects for EU-FAIR, for NERC, UK and for NSF, USA. He is a member of the Editorial Board of Marine Environment Research.