1

Algae: Biological and Ecological Characteristics

1.1. The biology of algae

1.1.1. *Definition and taxonomy*

The term “algae” does not correspond to a well-established taxonomic reality; it is used less and less by biologists and has been completely abandoned by phylogeneticists. However, it is still used by naturalists and users of this resource, whether they are harvesters, processors, distributors or consumers. Algae represent a wide variety of photosynthetic organisms that exist in unicellular or multicellular forms. Broadly speaking, a distinction is made between microscopic unicellular algae, or microalgae, and algae that are visible to the naked eye, or macroalgae. Algae consist of eukaryotic cells, which excludes spirulina from this definition, as it is a cyanobacterium with a prokaryotic cell structure. Algae live mainly in aquatic environments, whether marine, brackish or fresh water. Microalgae are present in the aquatic environment but can also be found in particularly humid terrestrial environments such as tree trunks, rocks, glaciers, snowfields and even the walls of certain buildings exposed to the elements. Anecdotally, it should be noted that the purple pigment or B-phycoerythrin secreted by the microalga *Porphyridium cruentum* is believed to be the cause of the reported phenomenon of bleeding statues exhibited in certain particularly humid chapels (personal communication, Gudin Claude). However, another hypothesis based on the involvement of the bacterium *Serratia marcescens*, which produces a brick-red pigment, prodigiosin, is put forward to explain these phenomena (Pitt 1982).

For a color version of all the figures in this chapter, see www.iste.co.uk/fleurence/marinealgae.zip

Marine Algae, A Sustainable Food Resource,
by Joël FLEURENCE.

Microalgae are also present in humid air. This is the case for certain species of Chlorella that have been detected in the atmosphere of the Indian city of Varanasi (Sharma et al. 2006).

Regardless of this morphological distinction between macroalgae and microalgae, it is quite difficult to define algae as a homogeneous plant group from an evolutionary point of view.

The phylogenetic approach has highlighted the evolutionary heterogeneity of algae by distinguishing two taxonomic groups or clades, Rhodobiontes and Chlorobiontes, derived from the same evolutionary sublineage, namely Metabiontes, linked to the green lineage (Lecointre and Le Guyader 2001). From a practical point of view, these two clades include species commonly known as "red algae" (*Palmaria palmata*, *Chondrus crispus*) and "green algae" (*Ulva lactuca, Caulerpa taxifolia*). These two clades share derived characteristics, in other words characteristics inherited from evolution, such as the absence of a peptidoglycan wall at the chloroplast level, the presence of numerous small DNA nucleoids throughout the chloroplast and the ability to form multicellular organisms.

Brown algae, another taxonomic group of algae, have been grouped within the clade Stramenopiles. This clade contains most of the species used for human consumption, such as *Laminaria digitata* (Kombu), *Fucus vesiculosus* (Bladderwrack) and *Himanthalia elongata* (sea beans) (Lecointre and Le Guyader 2001).

Alongside this phylogenetic classification, some authors take a more traditional approach to classifying algae. Thus, green algae are grouped in the phylum Chlorophyta or Charophyta, red algae in Rhodophyta and brown algae in Ochrophyta (Dawes 2016).

The Charophyta phylum consists of the Charophyceae class. These green algae, also known as Charales, are not used for human consumption. Green algae in the Chlorophyta phylum and Chlorophyceae class, on the other hand, are used as food algae. The Rhodophyta and Ochrophyta phyla consist of the Rhodophyceae (red algae) and Phaeophyceae (brown algae) classes, respectively (Dawes 2016). These two classes of algae include many species (*Palmaria palmata, Porphyra tenera, Laminaria japonica, Undaria pinnatifida*) used in human food as sea vegetables.

However, the identification of biological, genetic or molecular characteristics useful for understanding the evolutionary relationship between algae has not changed the biological definition primarily associated with them.

Microalgae, also known as microphytes, are single-celled photosynthetic microorganisms. Depending on the species and conditions, they can, however, assemble to form undifferentiated multicellular aggregates. Some are equipped with flagella for movement, as is the case with algae of the genus *Chlamydomonas* (see Figure 1.1). Others, such as Chlorella, do not have this type of organelle (see Figure 1.2). The microalgae of the two genera mentioned above are freshwater species. Only species of the genus *Chlorella* are currently used as food supplements.

In this area of use, a marine species belonging to the diatom family is currently attracting particular interest. This is the species *Odontella aurita*, which, like *Chlamydomonas reinhardtii*, has a flagellar system for movement (see Figure 1.3).

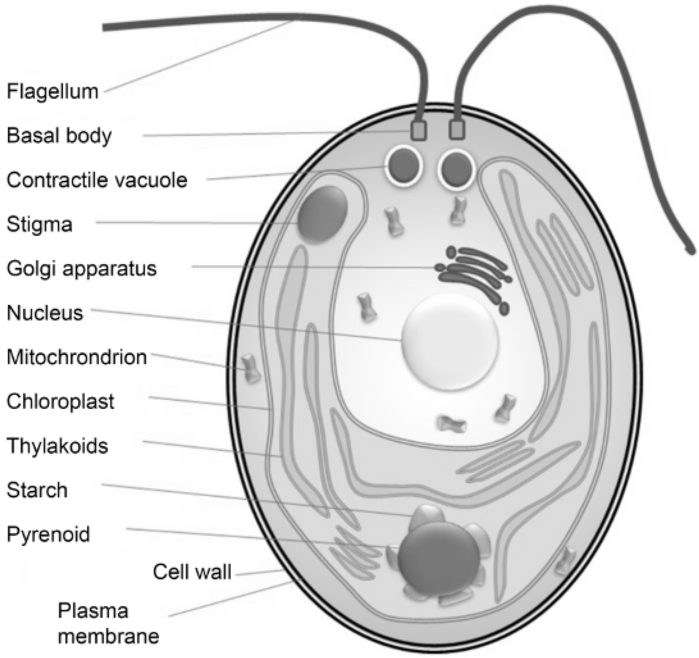


Figure 1.1. *Cellular organization of the microalga* Chlamydomonas reinhardtii *(Fleurence 2021)*

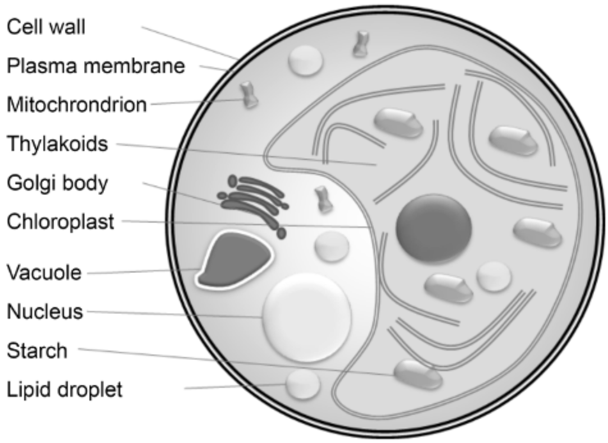


Figure 1.2. *Cellular organization of the microalga* Chlorella vulgaris *(Fleurence 2021)*

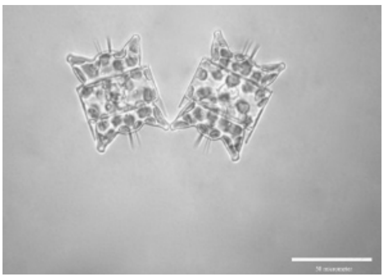


Figure 1.3. Odontella aurita *(see: https://commons.wikimedia.org/wiki/File:Odontella_aurita_cells.jpg)*

Macroalgae, also known as macrophytes or simply "algae", are defined as aquatic plants capable of photosynthesis and those which have a non-vascularized vegetative system called a "thallus" (see Figure 1.4). They share this type of vegetative structure with fungi, which, unlike algae, are unable to perform photosynthesis because they lack chlorophyll pigments. The presence of a thallus initially led botanists to group algae and fungi together in the Thallophytes (lower plants) group. This group was distinguished from the Cormophytes (higher plants), which included plants with a more complex vegetative system consisting of roots, stems, leaves and conducting vessels. This taxonomic classification based on morphological observations is still used today by naturalists. The thallus of an alga, such as *Laminaria digitata*, consists of three distinct morphological parts (see Figure 1.4):

– the upper part called the frond, which consists of multiple blades. These blades constitute the edible part of the algae and are used for food;

– the middle part, or stipe, which enables the algae to stand upright;

– the front part, or haptera, acts as a holdfast, anchoring the algae to its rocky substrate. This organ serves only to anchor the algae and does not absorb minerals, as roots do in cormophytes.

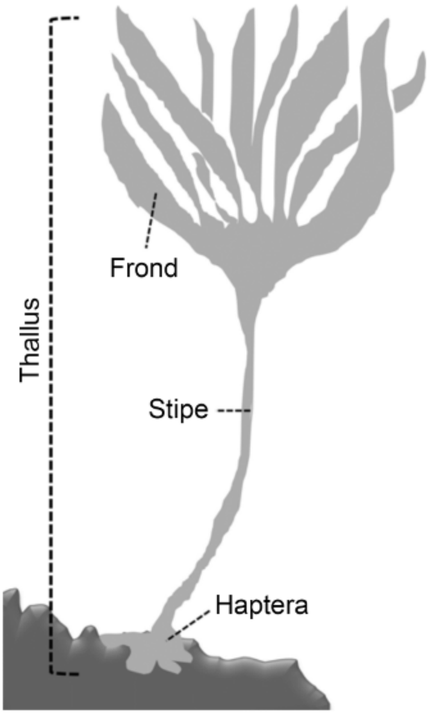


Figure 1.4. *Morphological characteristics of the vegetative apparatus or thallus of the brown alga* Laminaria digitata *(Fleurence 2018)*

Depending on the species, the morphology of the thallus varies greatly, particularly at the stipe level. The latter can be highly developed in brown algae such as *Laminaria digitata* or *Undaria pinnatifida* (see Figure 1.5) or very short in red algae such as *Palmaria palmata* (see Figure 1.6), or even absent in green algae such as *Ulva lactuca* (see Figure 1.7).

Figure 1.5. Undaria pinnatifida *(photo credit © Fleurence J. 2022)*

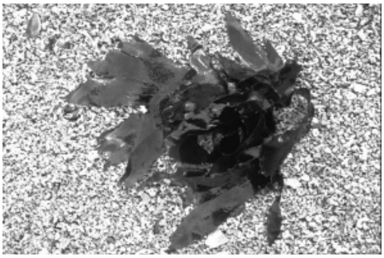


Figure 1.6. Palmaria palmata *(photo credit © Barbaroux O. 2016)*

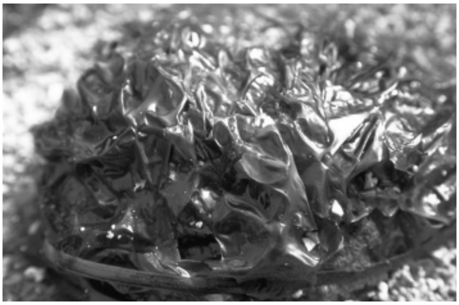


Figure 1.7. Ulva *sp. (photo credit © Barbaroux O. 2016)*

1.1.2. *Development cycles and reproduction*

Algae can reproduce asexually, sexually or even sometimes by cuttings, as is the case with the species *Ulva armoricana*. Knowledge of the life cycle and reproduction of algae is crucial for the development of algaculture in particular. The reproductive cycle of Laminaria (brown algae), and more specifically that of *Laminaria digitata* or *Laminaria japonica*, is currently well understood (see Figure 1.8). During its life cycle, the alga undergoes a heteromorphic digenetic cycle. There is an alternation between a diploid (2n) macroscopic form called sporophyte and a haploid (n) microscopic form called gametophyte. The sporophyte, or asexual form, releases biflagellated, swimming haploid (n) spores from the fertile areas on its frond (sporocysts). These spores develop into microscopic haploid (n) and sexed filaments called gametophytes (n). The gametophytes thus produced release "male" gametes or large "female" gametes called oospheres into the environment. After fertilization and production of the diploid zygote (2n), the latter germinates to produce a seedling or young sporophyte (2n), which will later develop into a mature sporophyte (2n).

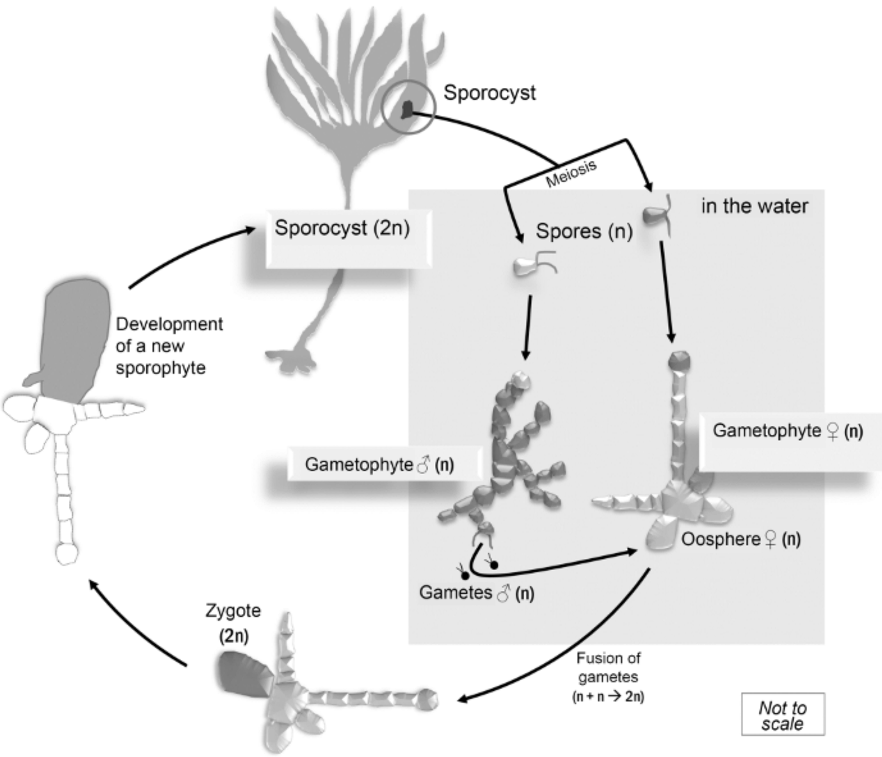


Figure 1.8. *Development and reproduction cycle of brown algae* Laminaria digitata *(Fleurence 2018)*

The life cycle of the brown alga *Undaria pinnatifida* (see Figure 1.9) is also well known and demonstrates many similarities with that of the Laminaria. Like *Laminaria digitata*, this species belongs to the order Laminariales. Its life cycle is, as above, that of a heteromorphic digenetic organism.

However, there are a few differences. In *Undaria* sp., the fertile spore-producing zone is not located at the level of the frond, but at the base of the stipe. This zone is also referred to as the “fertile base” by algae farmers and is characterized by a bulge at the base of the stipe (see Figures 1.4 and 1.5). These fertile bases, known as “Mekabu”, are used in human food, while the frond of the algae is marketed under the name “Wakame”.

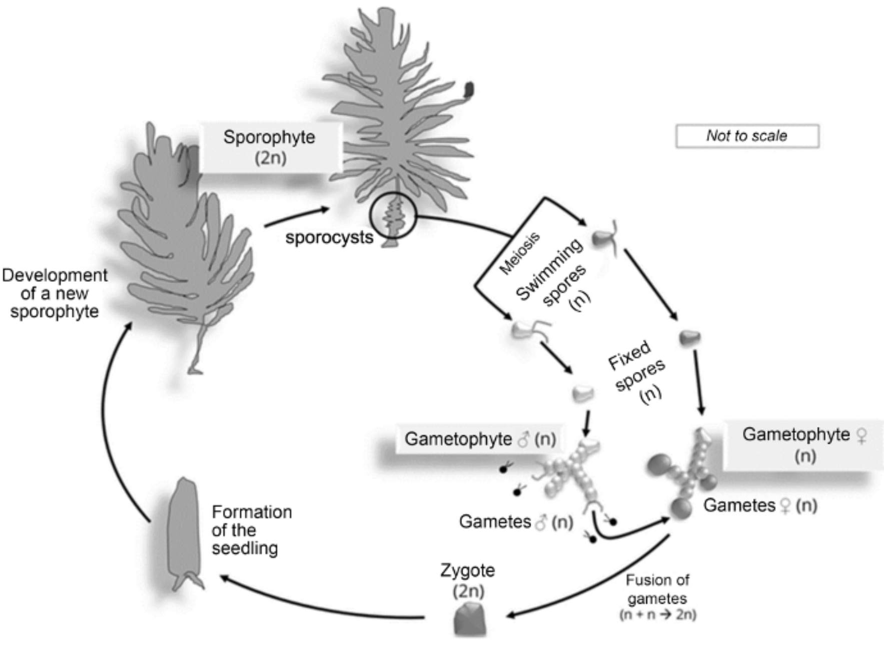


Figure 1.9. *Development and reproduction cycle of brown algae* Undaria pinnatifida *(Wakame) (Fleurence 2018)*

However, other algae species used in human food have very different reproductive cycles. This is particularly true of Ulva, which has an isomorphous digenetic cycle. The diploid sporophyte forms (2n) and haploid gametophyte forms (n) are macroscopic and morphologically similar (see Figure 1.10). This characteristic is a disadvantage in controlling Ulva cultivation, as it is very difficult to distinguish the sporophyte from the gametophyte, unlike Laminariales (*Laminaria* sp., *Undaria* sp.), where the two stages of development are identifiable and easily isolable.

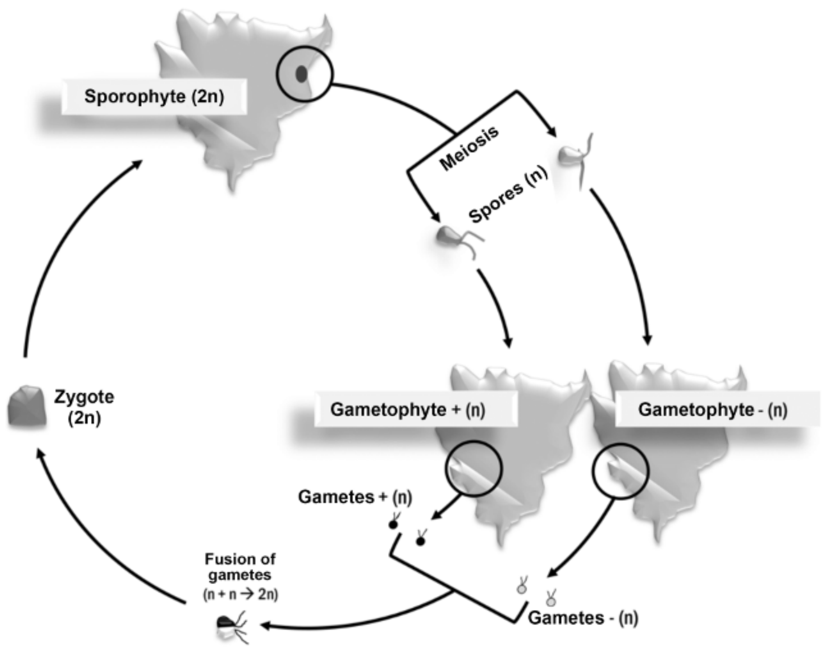


Figure 1.10. *Development and reproduction cycle of the green alga* Ulva *sp. (sea lettuce) (Fleurence 2018)*

In addition to a reproductive cycle based on an asexual pathway (spores) and a sexual pathway (gametes), some species can also reproduce by fragmentation of the thallus. This process of "cutting" is observed in certain Ulvales, such as *Ulva. armoricana* or *Ulva prolifera.* When these species detach from their rocky substrate and become pelagic, they are capable, under certain conditions of temperature and nitrogen nutrient concentrations, of generating new individuals from fragments of their thalli. Thus, the floating biomass of *U. prolifera* can increase by 6.30% per day with only 10 µM of dissolved inorganic nitrogen and a water temperature of 20°C (Keesing et al. 2011). This mechanism is one of the reasons for the proliferative, even invasive, nature of these algae and the onset of green tides.

Other species, such as the red alga *Palmaria palmata,* have a biological cycle that has long been misunderstood. The life cycle of this alga was initially described under in vitro culture conditions by van der Meer and Todd in 1980 (Deniaud 2002). It is described as digenetic and based on the alternation of two generations of individuals. The algae are initially described in a macroscopic diploid (2n) or tetrasporophyte form, producing haploid tetraspores (n) through meiosis, half of which germinate into male gametophytes (n) and the other half into female gametophytes (n). The male gametophytes (n) are macroscopic and morphologically similar to the tetrasporophytes (2n), while the female gametophytes are microscopic. The zygote (2n) resulting from fertilization develops directly into a diploid tetrasporophyte (Cabioc'h et al. 1992). Other authors consider that the cycle of this species is more complex, however, as it is trigenetic. According to these authors, the cycle is based on the succession of three generations during the development of the alga: tetrasporophytes (2n), gametophytes (n) and carposporophytes (2n). The carposporophyte, a diploid individual derived from the development of the zygote, produces diploid spores that generate new diploid tetrasporophytes (De Reviers 2002).

These differences in interpreting the development cycle of the algae *Palmaria palmata* are not conducive to the development of this species' cultivation. In other red algae species, such as those belonging to the genus *Gracilaria,* the presence of a trigenetic cycle involving a carposporophyte generation is, however, well known (Cabioc'h et al. 2006). The cultivation of Gracilaria, particularly for agar production, is therefore common practice.

Knowledge of the biological cycle of algae and, consequently, control of this cycle is one of the conditions for successful algae cultivation. The algacultural development of Laminariales (*Laminaria* sp., *Undaria* sp.) or Gracilariales around the world is a direct result of this observation.

1.1.3. *Pigment composition*

Algae, which have the distinctive feature of living under a layer of water that limits the penetration of light, have developed unique pigments that distinguish some of them from those found in terrestrial plants.

This pigment composition is the basis for their taxonomic classification into green algae (Chlorophyceae), red algae (Rhodophyceae) and brown algae (Phaeophyceae). As seen above, this traditional classification is still used by biologists and is widely used by all actors in the algae industry. While all algae contain chlorophyll a, they differ from one another in their composition of additional pigments known as supernumerary pigments (Table 1.1).

Chlorophyll a, a photosynthetic pigment common to all species of algae and all photosynthetic plants, is characterized by two absorption maxima located at 432 and

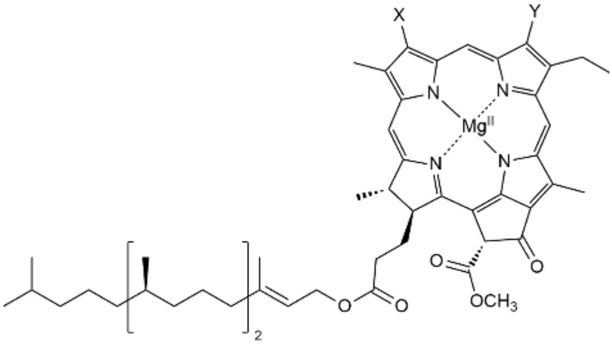
662 nm, respectively (Dumay and Morançais 2016). Chlorophylls b–d have fairly similar chemical structures, but their chromophores are different enough to explain the differences in spectral properties at the light absorption maxima (see Figures 1.11 and 1.12 and Table 1.2). The supernumerary pigments have maximum absorption wavelengths that differ from those of chlorophyll a, and these differ depending on the nature of the pigments (Table 1.2).

Botanical class	Main pigment	Supernumerary pigment
Chlorophyceae (green algae)	Chlorophyll a	Chlorophyll b
Phaeophyceae (brown algae)	Chlorophyll a	Chlorophyll c and an excess of carotenoids (carotene, xanthophyll)
Rhodophyceae (red algae)	Chlorophyll a	Phycoerythrin Phycoerythrocyanin Allophycocyanin Chlorophyll d

Table 1.1. *Pigment composition of different classes of algae (Fleurence 2018)*

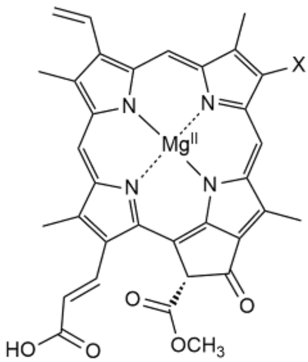
Botanical class	Supernumerary pigment (color)	λ_{max} absorption (nm)
Chlorophyceae (green algae)	Chlorophyll b (olive green)	457
Pheophyceae (brown algae)	α-carotene (yellow) β-carotene (orange-yellow) Chlorophyll c (light green) Fucoxanthin (orange)	447/475 454/484 446/578/627 446/468
Rhodophyceae (red algae)	Phycoerythrin e (purple) Allophycocyanin (blue) Phycoerythrocyanin (orange) Chlorophyll d	540/565 618/671 568/570 401/455/696

Table 1.2. *Spectral characteristics of some supernumerary pigments used in the classification of macroalgae (Dumay and Morancais 2016)*



chl a : X: CH=CH$_2$ Y: CH$_3$
chl b : X: CH=CH$_2$ Y: CHO
chl d : X: CHO Y: CH$_3$

Figure 1.11. *Structure of the chromophores of chlorophylls a, b and d (Fleurence 2018)*



chl c1 : X: CH$_2$-CH$_3$
chl c2 : X: CH=CH$_2$

Figure 1.12. *Structure of the chromophores of chlorophylls c1 and c2 (Fleurence 2018)*

The red, purple and sometimes pink color of red algae is mainly due to phycobilins, chromophores that are constituents of phycobiliproteins and, more specifically, phycoerythrin. These pigments complement the action of chlorophyll a and enable red algae to grow at depths ranging from the intertidal zone (the area affected by tides) to the subtidal zone (the area never uncovered by the tides, including spring tides). Phycobiliprotein pigments are highly unique molecules resulting from the combination of a chromophore, an open tetrapyrrole nucleus, with a protein (see Figure 1.13). In the case of phycoerythrin, this chromophore or phycoerythrobilin restores the absorbed light energy in the form of fluorescence at a specific wavelength ((λ_{max}) fluorescence emission 578 nm for R-phycoerythrin).

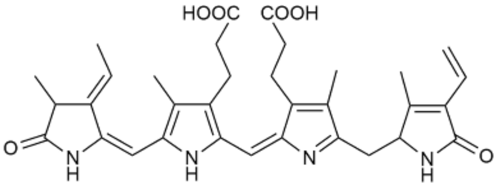
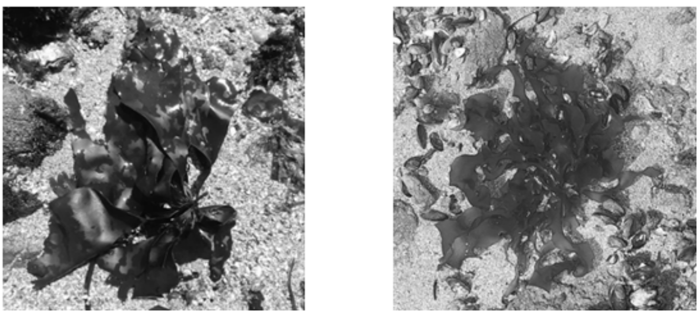


Figure 1.13. *Structure of the chromophore or phycoerythrobilin of phycoerythrin (Fleurence 2018)*

The phycoerythrin and phycocyanin family, original and characteristic pigments of red algae, and even cyanobacteria in the case of C-phycocyanin, is of interest for agri-food applications, particularly as a natural colorant. This pigment diversity, which is responsible for the definition of the different botanical classes of algae, is also responsible for the diversity of colors associated with these marine organisms.

Thus, in red algae or Rhodophyceae, a whole range of hues can be observed, from light pink to dark red. This color variation is the result of the presence of other pigments such as phycocyanin alongside the supernumerary red pigment phycoerythrin (see Figure 1.14).



a) b)

Figure 1.14. *Phenotypic variation in the red color of Rhodophyceae according to species (a)* Palmaria palmata*, b)* Grateloupia turuturu*) (photo credit © Fleurence J. 2022)*

Brown algae (Pheophyceae) have a thallus ranging from dark brown to yellow-brown with orange hues depending on the concentration of carotenoid pigments (see Figure 1.15).

a) b)

Figure 1.15. *Phenotypic variation in the brown color of Phaeophyceae according to species (a)* Undaria pinnatifida*, b)* Fucus vesiculosus*) (photo credit © Fleurence J. 2022)*

Finally, green algae, or Chlorophyceae, due to the simultaneous and predominant presence of chlorophyll pigments of types a and b, have a green thallus (see Figure 1.16).

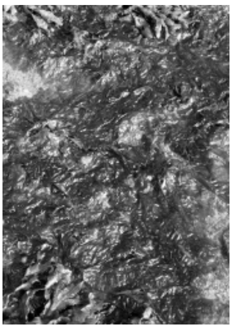


Figure 1.16. Ulva *sp., an alga belonging to the class Chlorophyceae (photo credit © Fleurence J. 2023)*

However, algae color can be misleading, as it can vary depending on environmental conditions for certain species. This criterion can vary depending on whether the algae are submerged under a layer of water of varying depth or exposed on the foreshore (Box 1.1). Other parameters such as the conditions in which the algae develop or are produced (growth in the natural environment or in culture) can also have an impact on the color of the thallus of certain algae. This is the case for red algae, and more particularly for cultivated species belonging to the genus *Porphyra*, whose colors can change from green to brown to red depending on the growing conditions (De Reviers 2002).

In addition to this example, some species classified in the Phaeophyceae family (brown algae) may also have a dark green thallus rather than a brown thallus. This is particularly the case for the species *Himanthalia elongata*, which is valued in human food as a sea vegetable.

Recognition of botanical families of algae on the foreshore. Taxonomic identification

a) b)

Figure 1.17. Fucus *sp. observed under a layer of water (a) and in the open air on the foreshore (b) (photo credit © Fleurence J. 2022)*

The presence or absence of a layer of water during observation may cause variations in color assessment depending on the observer. As a general rule, color should not be used as a taxonomic identification criterion for organisms that have emerged or are emerging from the water.

Box 1.1. *Taxonomic recognition methodology of algae based on color*

1.1.4. *Size*

In addition to color, algae also vary greatly in size, depending on the species and stage of development. A species such as the brown algae *Laminaria japonica*

(*Saccharina japonica*), measures on average 4–6 m in length and 30 cm in width. However, the thallus of the latter can reach 10 m when cultivated (Perez 1997). In contrast, the red alga *Palmaria palmata* has a thallus that rarely exceeds 30 cm in size.

1.2. Ecology of algae

Algae are aquatic plants that are autotrophic for carbon and depend on sunlight for photosynthesis. Their bathymetric distribution is therefore limited by this physiological constraint.

Three bathymetric zones are identified based on light penetration:

– the euphotic zone, where light penetration is sufficient for photosynthesis to occur; this zone can extend to a depth of 200 m;

– the oligophotic zone, where light still penetrates but in insufficient quantities for photosynthesis to occur;

– the aphotic zone, where no light penetrates; this zone corresponds to the abyssal depths.

In terms of the quality of the visible light spectrum (400–700 nm), red radiation is largely blocked at a depth of 10 m, and only blue and green radiation reaches the lower layers of the euphotic zone (< 100 m). This light filtering is responsible for the distribution of algae according to their pigment content. For example, green algae, which, like land plants, only have chlorophylls a and b, are able to absorb red and indigo light, reflecting the rest of the light spectrum, including green, which is responsible for their color. They are found in water layers where red radiation can still penetrate and are therefore located at shallower depths than brown or red algae (see Figure 1.18).

More generally, most algae species used and valued for human consumption are found in the tidal zone. This zone, also known as the foreshore, is accessible on foot and remains the harvesting area for harvesters or seaweed gatherers (see Figure 1.19). Other species, particularly brown algae belonging to the genus *Laminaria*, are found at the lower limit of the intertidal zone and at the upper limit of the subtidal zone, which is never exposed, even during spring tides.

Laminaria are therefore only partially accessible on foot during very high tides, thus limiting their harvest. In Brittany, France, the seaweed field ends at a depth of 30 m, which therefore represents the ecological limit for seaweed harvesting on the Atlantic coast (Quéro and Vayne 1998).

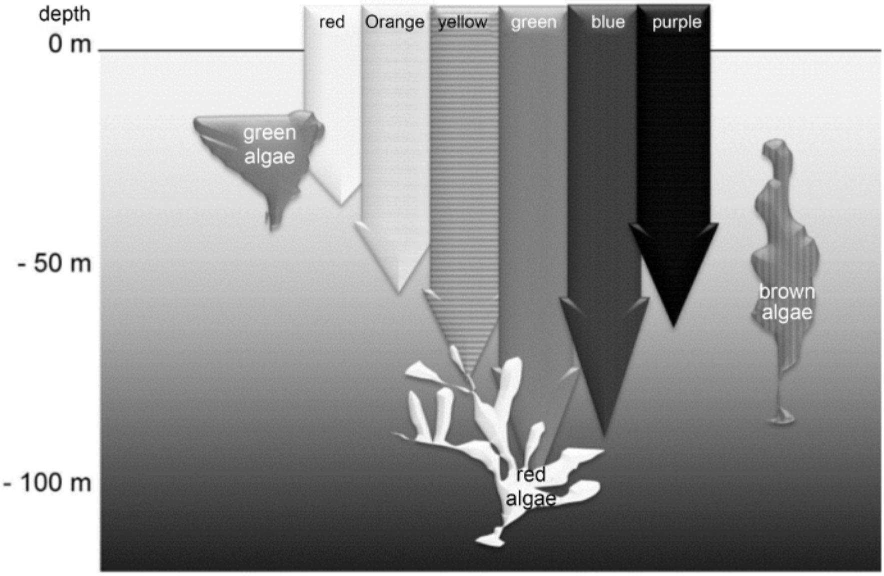


Figure 1.18. *Evolution of light radiation in the visible spectrum as a function of bathymetry (Fleurence 2018)*

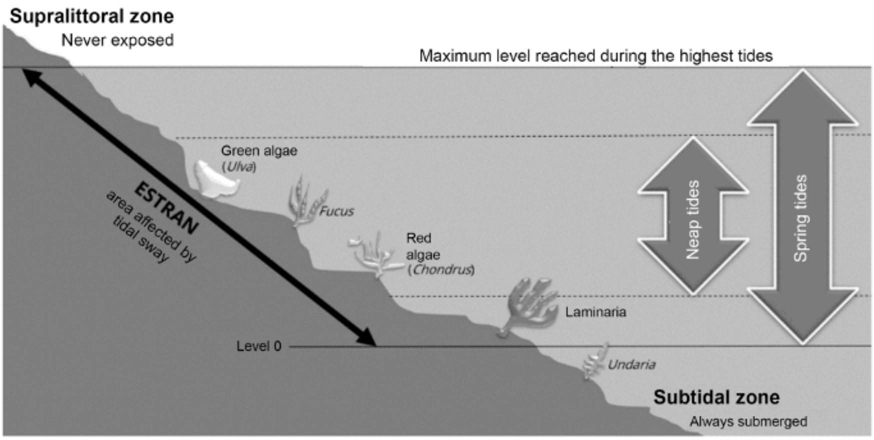


Figure 1.19. *Example of bathymetric distribution of green, red or brown algae used in human food (Fleurence 2018)*

The bathymetric distribution of algal flora can also be influenced by waves. This is particularly observed for species such as *Ascophyllum nodosum* and *Fucus vesiculosus*, which are two brown algae valued as sea vegetables under the respective names of Wrack and Kelp. In sheltered areas, *Ascophyllum nodosum* is found at the same bathymetric level as *Fucus vesiculosus.* In exposed areas, hydrodynamics favor the establishment of *Fucus vesiculosus* at a lower bathymetric level and are not conducive to the colonization of the foreshore by *Ascophyllum nodosum.* This has led some authors to state that *Ascophyllum nodosum* is characteristic of calm waters and *Fucus vesiculosus* of more turbulent waters (Cabioc'h et al. 1992).

Microalgae are present in many aquatic, terrestrial and aerial environments. In the air, they are found in the humid atmosphere thanks to the phenomenon of aerosolization (Box 1.2). In aquatic environments, particularly marine environments, marine microalgae can live in pelagic form in the water column. They then constitute the phytoplankton compartment. They can also develop a benthic lifestyle. In this case, they form part of the microphytobenthos, which combines microalgae and cyanobacteria. The microphytobenthos in the intertidal zone generates a brown-greenish biofilm that is characteristic of mudflats (see Figure 1.21).

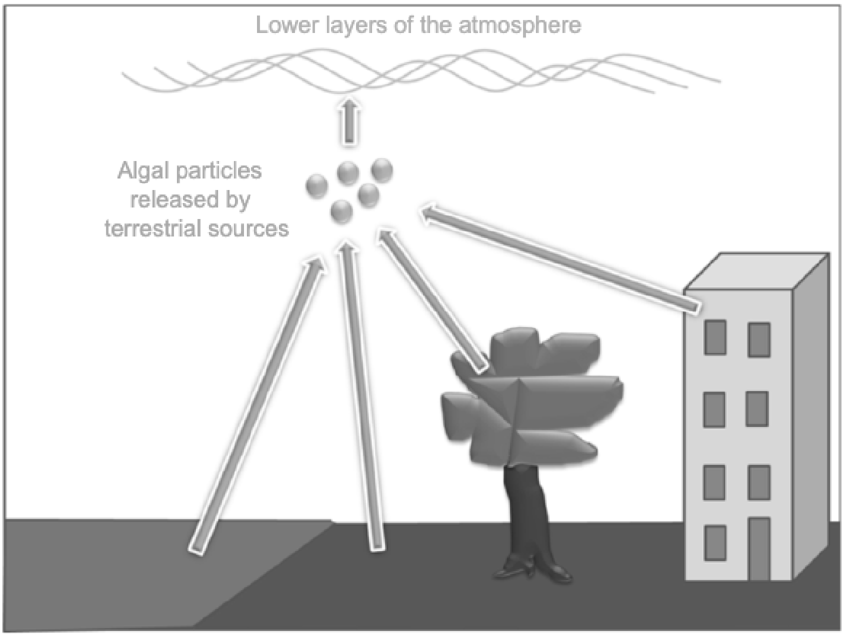


Figure 1.20. *Ecosystems responsible for the release of microalgae in the lower layers of the atmosphere (Fleurence 2021)*

Microalgae are transferred to the lower atmosphere via a process called aerosolization, which transforms them into fine algal particles. They are released from their original environment by wind and upward air currents.

Box 1.2. *Microalgae aerosolization phenomenon*

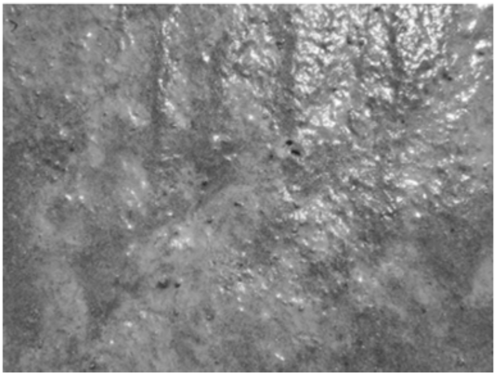


Figure 1.21. *Biofilm forming the colonization of the bottom of a mudflat by microphytobenthos and cyanobacteria (photo credit © Rosa P. 2022)*

All these biological and ecological characteristics of algae and microalgae are essential elements of knowledge about the resource that are necessary for understanding the choice of species exploited and used in human food.

1.3. References

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