Biodiversity on rocky coasts: zoning and ecological relationships

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The Atlantic rocky coasts, subject to tidal sway, make it easy to observe the organisms that colonize them. Depending on the level and living conditions, various lichens or large brown algae dominate and form horizontal belts. Less clearly, some fixed or slightly mobile animals are also arranged in belts. Other animals and algae are distributed more irregularly through basins, channels and rocky overhangs. The specific diversity decreases upwards in the emerged area and also when conditions become too difficult: too turbulent, too sunny or with very variable salinity. Organisms on rocky coasts thus have many biological adaptations to emergence or agitation and many specializations and interrelationships related to nutrition.

The Atlantic coasts are subject to the tidal phenomenon; part of the coastline is thus exposed over a variable area that depends on the slope and tidal range. Organisms living in this **tidal balancing zone** and in the surrounding areas therefore have to withstand a very particular and quite variable environment over time. Depending on the characteristics of the mineral substrate, the coastlines are very different in appearance and correspond to distinct ecosystems.

Thus, on **rocky** coasts, the subject of this article, algae, especially brown algae (see focus Algae and their classification), and lichens fixed on the rock most often dominate and are distributed in **horizontal belts**, from the terrestrial environment to the marine environment always immersed; this is why we will insist on these structural species very easy to observe. Some fixed or slightly mobile animals also have such a vertical zoning, while more mobile species (fish, shrimps, various molluscs) follow the movements of the sea or take refuge in basins or sheltered blocks to survive.

Figure 1. Meadows of Zostera marina, eelgrass, a marine flowering plant, on low sandy levels. Due to its habitat and morphology (especially the presence of long ribbon-like leaves), many people think that eelgrass is an algae. In fact, it has roots anchored in the sand. Eelgrass beds have a high biological diversity.

On **sandy or muddy** coasts**,** the zonation is much less clear-cut, as the animals live mainly buried there, especially at low tide [1] . There are fewer plants, apart from local flowering rooted plants: Spartina, Salicornia or other flowering plants in calm high levels and eelgrass (Figure 1) in very low levels. Algae are practically absent due to a lack of stable fixation; the fauna of these environments is very different from that of rocks. An entire article would be needed on these ecosystems, which are organized and function very differently from those of rocky coasts.

1. Ecological factors and their effects

Many ecological factors, and the resulting physico-chemical gradients, directly affect the distribution of living organisms in marine coastlines, and these factors are most often correlated with each other, sometimes complicating interpretation.

1.1. Duration of emergence and dehydration

Figure 2. A rocky coast from Brittany at low tide (A) and high tide, 6 hours later (B).

This factor is essential on the so-called tidal coasts of the Atlantic and the English Channel (and very secondary in the Mediterranean) (see The tides). Twice in about 24 hours, the intertidial zone is alternately submerged at high tide and emerged at low tide (Figure 2). This causes strong constraints on flora and fauna, mainly of marine origin. Moreover, according to the lunar and seasonal cycles, the amplitude of tidal sway varies greatly: important towards the full moon or the new moon and towards the equinoxes, it is quite low in the first and last quarters of the moon and towards the solstices [1] (see Light cycles and living organisms).

Thus, organisms living in the highest levels of the coastline have been selected to resist a long emergence from the marine environment at least 80% of the time. During emergence, they are exposed to direct sunlight, temperature variations, osmotic stress related to fresh rainwater or desiccation. In addition, in the air, marine wildlife can no longer absorb dissolved oxygen from the water; this implies that animals can keep some water around them or, more rarely, change the way they breathe [1]. These conditions are more stable and less constraining for species at the bottom of the foreshore; they are often the same species as those in the permanently submerged area [1].

The **tidal range**, or maximum difference in level between the lowest and highest seas, is typical of a given place and depends on the conformation of the coasts: 14 m in the bay of Mont Saint Michel, 8.50 m in Roscoff, about 6 m in Le Havre and Nantes, just over 4 m in Biarritz. The larger the tidal range, the wider and more diversified tidal swing areas and the wider the belts, thus understanding the interest of the French coasts of the Western Channel, from Cherbourg to Brest.

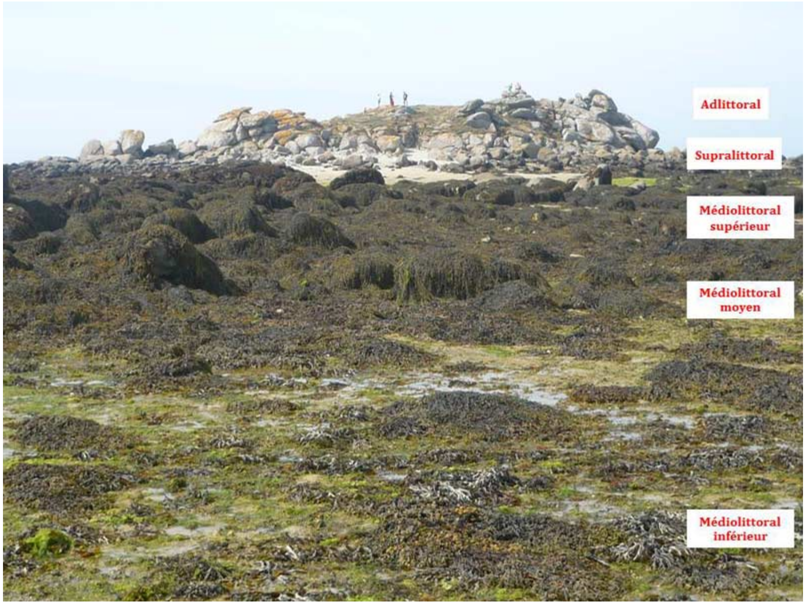

Figure 3. A rocky foreshore at low tide, with its different levels; the infralittoral is not present in this photo.

We therefore define four levels on our marine coasts [1],[2], depending on the marine influence and the duration of emergence (Figures 3 & 7):

the **adlittoral** level in direct continuity with terrestrial ecosystems and subject to salt spray;

the **supralittoral** level, which is only submerged during very high tides and storms;

the **midlittoral** floor constantly swept by the tides and subdivided into three levels;

the **infralittoral** level, the upper level of which only emerged during high tides and for less than an hour at a time. The latter extends up to 10 to 30 m under the sea, depending on the illumination of the sea bed.

The further down the rocky foreshore you go, the larger and more diversified the algae are and the more species there are in the fauna as well; it is for this reason that fishermen on foot wait for the high low tides to hunt or collect lobsters, seeweeds, periwinkles and abalones. Biomass and productivity are also highest in the infralittoral region.

1.2. Water agitation

This factor, linked to currents and waves, depends strongly on the orientation and conformation of the coasts: strong agitation on rocky capes exposed to the west or at the foot of cliffs and little agitation at the bottom of sheltered bays and estuaries. This has a great influence on organisms. Indeed, certain species of algae, in thalle{ind-text}Describes the relatively simple vegetative apparatus of primitive plants (algae, lichens, certain bryophytes...) compared to that of evolved plants that have a cormus with stem, roots and leaves.{end-tooltip} too fragile or very long, are shredded or torn off by strong waves and some animals, poorly fixed or with too soft a body, cannot survive in beaten environments, while others need highly oxygenated beaten water to survive. It should be noted that the same coastal site can be very beaten in the upper mid-coast (by the high tide swell which arrives without obstacles) and relatively calm in the lower mid-coast or the infralittoral (where the waves are slowed down by various obstacles at low tide).

Figure 4. Effects of sea agitation on medium-coastal organisms: A, very beaten mode, without algae and with fixed animals; B, medium beaten mode, with Fucus serratus and various red algae on the shaded edge; C, calm mode, with Ascophyllum nodosum.

Depending on the effects observed on organisms (species present, size and biomass), three **modes of agitation** can be identified, with intermediates: "very beaten", "moderately beaten" and "calm" (Figure 4). We see that the more the midlittoral is beaten, the less algal biomass there is and this can go as far as the bare rock without any organisms.

1.3. Illumination

Figure 5. Overhang of shaded rock with Dendrodoa grossularia or sea gooseberry, social ascidia.

Algae and lichens need light for photosynthesis{ind-text}Bioenergetic process that allows plants, algae and some bacteria to synthesize organic matter from the CO_2 in the atmosphere using sunlight. Solar energy is used to oxidize water and reduce carbon dioxide in order to synthesize organic substances (carbohydrates). The oxidation of water leads to the formation of O_2 oxygen found in the atmosphere. Photosynthesis is at the base of autotrophy, it is the result of the integrated functioning of the chloroplast within the cell and the organism.{end-tooltip}, but too much light is often harmful to organisms used to be protected by a sometimes cloudy water layer. At the mid-coastal level, some species therefore take refuge, to protect themselves from light, under other larger algae - the case of the red alga *Catenella cespitosa* of the upper mid-coastal - at the base of the rocks, which are always wet (Figure 4B) or under rocky overhangs. Many green algae tolerate high levels of light (see Figure 17A below), as well as brown algae at higher levels. Direct sunlight can also be a problem for many animals, such as sponges and ascidians (Figure 5), as it is accompanied by dehydration and heating.

1.4. Other physicochemical factors

With regard to the nature of the **support**, most large algae live on rocks or pebbles, fixed by holdfasts (see below Figure 14B) or false roots, and die fairly quickly if they detach themselves from them. The rocky coasts are therefore their favourite biotope. Granite, gneiss and coarse sandstone, with a rough surface, are the most favourable, while smooth sandstone or marly limestone and chalk, easily broken up by the sea, are less favourable. Some small species of algae are attached to other algae. Many animals survive only by being fixed on various solid supports (Figures 5 & 6 and see below, Figure 19): many gastropods, mussels, barnacles, sea anemones, sponges, ascidians...

During the flood, wide **temperature** variations and freezing are harmful to most marine organisms, which can only live at the bottom of the foreshore. Moreover, the flora and fauna are not identical between Biarritz and Dunkirk, as some species prefer fresh water; this is the case of large brown algae.

In estuaries, water **salinity** is lower and above all much more variable, eliminating many marine species. The water is also **turbid**, as it is loaded with mud, and many algae no longer have enough light in the low levels. Global biodiversity is therefore decreasing sharply, even if productivity remains very high.

1.5. Interspecific competition

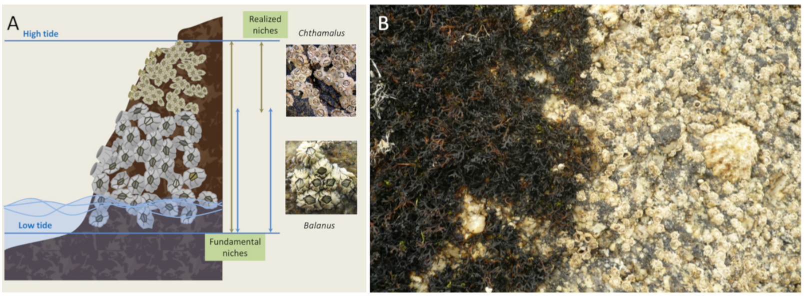

Figure 6. A, Diagram showing an example of competition between two species of barnacles. Although the base niche of Chthamalus stellatus extends over the entire area between high and low tide levels, the effective niche is restricted by the presence of larger Balanus balanoides. [Photo credit: Chthamalus by Michael Maggs (CC BY-SA 3.0) & Balanus, by Auguste Le Roux (CC BY-SA 4.0-3.0-2.5-2.0-1.0), via Wikimedia Commons]. B, Beaten rock, without algae, of the middle coast, housing only a marine lichen in black cushion, Lichina pygmaea, a gastropod, Patella vulgata, and a fixed crustacean, the barnacle Chthamalus stellatus, very abundant here on the right of the picture. These animals have a shell or solid calcareous plates and are well attached to resist waves.

Competition, for place or light, plays an important role in the zoning of organisms; they are the most adapted to local ecological conditions, and sometimes the first to arrive, which dominate leaving little space for others. This is proven by the fact that the presence of a competitive species in a given region forces another to restrict its place on the coast. Figure 6A shows the case of two barnacles species: in the presence of *Balanus balanoides*, *Chthamalus stellatus* is confined to the upper levels, whereas it can live lower; these two species feed by water filtration [3].

Figure 6B illustrates another case of competition in the middle-coastal region: the strong agitation of the environment excluded here seeweeds, which allows the installation of the short cushions of the small *Lichina* who needs light; the barnacle larvae then settle only in areas without lichen; finally, as there are many barnacles fixed, there is little space left for the pads to scrape the rock !

2. Lichen or brown seaweed belts

By combining altitudinal zonation in stages and the various modes of water agitation, we can develop the table below (Figure 7) which presents the various **plant belts** of our rocky coasts [2],[4].

STAGES	Constant disturbance	Moderate disturbance	Disturbance seldom occurs
ADLITTORAL & --100% SUPRALITT. --90%	Wide zones, sometimes up to 20 m high: Various lichens, *VERRUCARIA MAURA*	Rather wide zones, from 0,50 to 2 m high: Various lichens *VERRUCARIA MAURA*	Reduced zone, < 0,50 m high: various lichens, *VERRUCARIA MAURA*
MID-LITTORAL upper --70%	No algae *Lichina pygmaea*	*PELVETIA CANALICULATA* *FUCUS SPIRALIS* *Catenella cespitosa* (shadow)	*PELVETIA CANALICULATA* *ASCOPHYLLUM NODOSUM*
MID-LITTORAL middle --50%	Low algal biomass *Fucus vesiculosus var. linearis* Localy present *Nemalion multifidum*	High algal biomass *FUCUS VESICULOSUS* Few reg algae	*ASCOPHYLLUM NODOSUM* And its parasite, *Polysiphonia lanosa* *Fucus vesiculosus*
--30% MID-LITTORAL lower	*Rivularia bullata* *Fucus serratus* ←←	*FUCUS SERRATUS* Various red algae: *Chondrus crispus,* *Palmaria palmata…*	*ASCOPHYLLUM NODOSUM* *FUCUS SERRATUS* →→→
--10% INFRA- LITTORAL upper --0% middle	*HIMANTHALIA ELONGATA* *Saccorhiza polyschides* *Bifurcaria bifurcata* ←←← *LAMINARIA HYPERBOREA*	*HIMANTHALIA ELONGATA* *Saccorhiza polyschides* *LAMINARIA DIGITATA* Numerous red algae *LAMINARIA HYPERBOREA*	*Sargassum muticum* (introduced) *SACCHARINA LATISSIMA* *LAMINARIA DIGITATA* →→→

Figure 7. Layering of algae and lichens according to average water agitation. The colours of the names correspond to brown algae (brown), red algae (red), cyanobacteria (blue-green) and lichens. The dominant species are in upper case and the others in lower case. The percentages, on the left, correspond to the emergence times of the various levels: 0% at the level of very high seas, 50% in the middle of the shore and 100% at the level of very low seas.

2.1. Lichens at upper littoral stages

Lichens are originally terrestrial organisms. This is why, unlike algae and marine animals, their specific diversity decreases as they descend towards the sea. Many species of lichens can be found on coastal rocks, some of which also live inland *(Xanthoria parietina*) and others are typical of the marine coastline *(Verrucaria maura, Lichina spp.*) [3].

Figure 8. Lichen and algae belts from the adlittoral to the upper midlittoral.

Lichen belts can be seen from afar due to their high contrasted colours (Figure 8). Above, in the **adlittoral** layer, where there are also a few flowering plants that support the salt of the sea spray, the light green tufts of the *Ramalina,* the orange-yellow foliage thallus of the *Xanthoria* and the various crust thallus, ranging from white to dark grey or brown, of many genera of lichens (Figure 9A) are most notable.

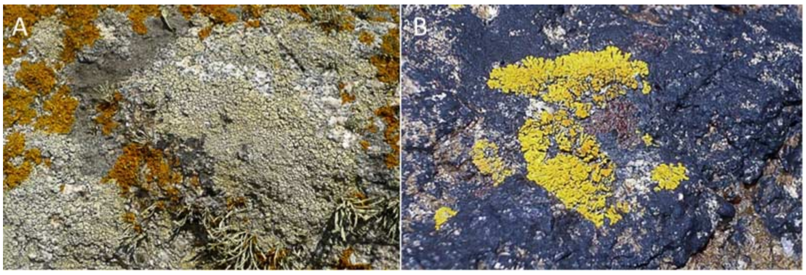

Figure 9. A, Lichens exposed to adlittoral spray: Ramalina spp. in grey-green tuft, Xanthoria spp. in orange patches, Ocrolechia parella in grey crust; B, Lichens of the supralittoral, sometimes covered by the sea: Verrucaria maura in black and Caloplaca spp. in yellow.

The **supra-coastal** layer, covered at very high tides, is colonized by the crusts of *Caloplaca marina* and *C. maritima* scattered in an almost continuous black belt of *Hydropunctaria (= Verrucaria) maura* (Figure 9B). This last fine-crusted lichen is often mistaken for a remnant of oil spills! Among the rare lichens in the **mid-coastal** zone are *Lichina pygmaea*, which live in very beaten environments (Figure 6).

On very rough coasts, the adlittoral and supralittoral levels extend upwards (more than 20 m on the cliffs of Finistère, Quiberon or La Hague) with very wide lichen belts; the very harsh conditions of these coasts favour lichens, whose symbiosis of filamentous fungus, green algae or cyanobacteria makes them more resistant compared to flowering plants. On the other hand, in wave-sheltered estuaries, all these belts together only reach a height of 20 cm; calm conditions even allow oaks to approach the sea and soak their branches at high tide.

2.2. Brown algae of medium and low levels

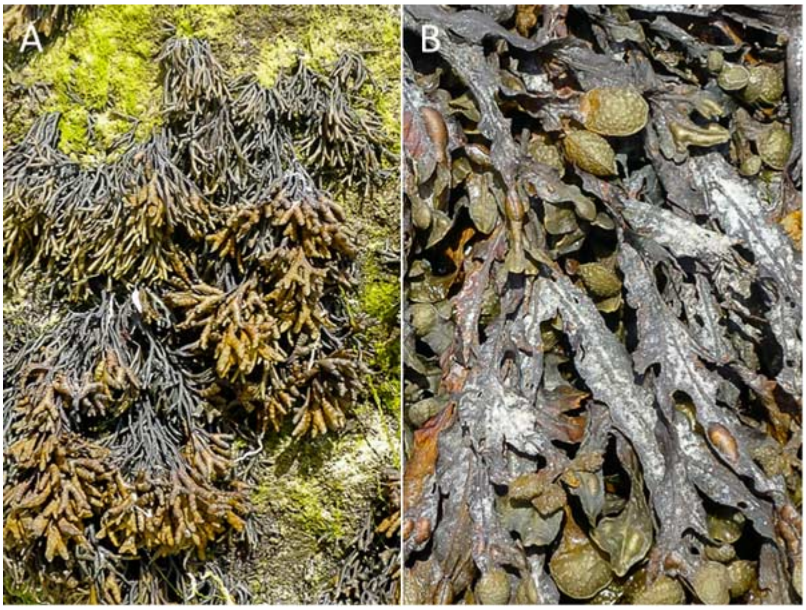

Figure 10. Pelvetia canaliculata (A) and Fucus spiralis (B), of the upper midlittoral not too beaten.

Brown algae or Phaeophycea, Fucales and Laminariales, largely dominate rocky foreshores by their biomass [2]. They were once used to extract soda by burning it in ovens or to fatten fields, under the name of **varech** in Normandy and **goëmon** in Brittany [5] *i.e*. wrach or kelp in english. They therefore form the characteristic belts of the mid- and sub-littoral levels. Their size, as well as their biomass, increases as they descend: 10 cm for *Pelvetia,* about 1 m for *Ascophyllum* and *Sargassum* and up to 5 m for *Himanthalia* and *Laminaria hyperborea*. The floats of some algae allow them to stand vertically at high tide, towards the light, in the case of *Ascophyllum* and *Fucus vesiculosus*.

Figure 11. Ascophyllum nodosum, especially common in the calm midlittoral, and its parasitic red algae Vertebrata lanosa.

The **upper midlittoral** (about 70-80% of the time emerging) consists of two algae belts that can withstand desiccation very well and can lose up to 75% of their water without dying; these are *Pelvetia canaliculata* (Figure 10A) and *Fucus spiralis* (Figure 10B); these algae are absent in very rough environments (Figure 6).

Figure 12. A, Fucus vesiculosus of the middle medolittoral lightly beaten to calm, with floats; B, Fucus vesiculosus var. linearis of the midlittoral well beaten, without floats.

The **average midlittoral** (about 50% of the time emerging) is characterized by *Ascophyllum nodosum* and *Fucus vesiculosus*. The first (Figure 11) is very abundant in calm mode where it forms thick mats and is often parasitized by a red alga, *Vertebrata lanosa*. *Fucus vesiculosus* (Figure 12A) dominates in more beaten environments, but is missing in heavily beaten areas or has a special form of accommodation that is narrower, tougher and without floats (Figure 12B).

Figure 13. Fucus serratus, toothed thallus, of the lower midlittoral.

Finally, most of the **lower midlittoral** (about 30 to 20% of the time emerging) is colonized by *Fucus serratus*, still without floats (Figure 13).

The base of the **lower midlittoral** and **the upper infralittoral** (less than 10% of the time emerging) host the large thalli of *Saccharina latissima* (= *Laminaria saccharina*) (Figure 14A) in a calm environment, from *Saccorhiza polyschides* (Figure 14B) with flattened and soft stipe{ind-text}Stream of algae, which lacks conductive vessels.{end-tooltip}, edible *Himanthalia elongata* (Figure 15) or sea bean, with very long narrow and dichotomous{ind-text}Two-part branching pattern at each growth level. More generally, characterizes the division of something into two clearly opposed elements {end-tooltip} axes, and *Laminaria digitata* (Figure 15) with a smooth and flexible cylindrical stipe, in more or less beaten environments.

Figure 14. A, Saccharina latissima with long undulating thallus, of calm mode; B, Saccorhiza polyschides, attached by bulbous complex holdfast and with flattened stipe, and Palmaria palmata, large red algae at the top right, at the limit of the lower midlittoral rather beaten.

Figure 15. Himanthalia elongata, with narrow dichotomous thallus, and Laminaria digitata, with deeply torn blades and flexible cylindrical stipe, two species typical of the upper infralittoral.

The last belt, in the **infralittoral** never or very rarely emerged, consists of *Laminaria hyperborea*, with a stiff cylindrical stipe. The biomass of these algae is sometimes very high and is said to form "underwater forests". Between Roscoff, Ouessant and Le Conquet, this species forms, with other kelps, the largest and richest algae sector in Europe (the Seaweed Coast), where a semi-industrial exploitation takes place for alginate extraction, among others.

3. Distribution of other organisms

3.1. Red and green algae

Other algae do not form real belts, continuous or regular [2].

Figure 16. A, Sea lettuce, Ulva spp., here fixed on low level rocks; B, Chondrus crispus, red algae of the lower midlittoral

Green algae, or Chlorophyceae, are mostly opportunistic and grow rapidly where there is little competition; they often withstand strong sunlight, variations in salinity or temperature and also the abundance of man-made nitrates. Among them, *Ulva spp.* (Figure16A) or sea lettuce proliferate during the summer on some rocks and then detach from them and accumulate in calm bays where they rot and producing foul smelling decomposing **green tides** (see Nitrates in the Environment).

On the other hand, red algae, or Rhodophyceae, do not tolerate too much light or significant desalination; from dark red to almost black sometimes in winter, they turn green during the summer, because the red pigments are destroyed by UV rays. For this reason, the number of red algae species decreases very rapidly upwards, from the middle mid-coastal. However, from the lower mid-coastal down, they form most of the **specific diversity** (more than half of the more than 500 macroalgae species in the Roscoff region, [6]). As they descend into the ever-submerged infralittoral, these algae benefit from their red pigment, phycoerythrin, which captures the last wavelengths of light transmitted by seawater [7].

The morphological, biological and ecological diversity of Rhodophyceae is very high, but they very rarely exceed 30 cm in length - *Palmaria palmata* (Figure 14B) -, while producing average to low biomass. On the boulders of the *Fucus serratus* belt, large, spots of similarly shaped *Chondrus crispus* (Figure 16B) and *Mastocarpus stellatus* can be observed; these algae, called liken or pioka in Breton, are harvested by hand to extract carrageenans, important industrial and food gelling agents.

In the medium to lower middle coast, **very beaten** and without brown algae, we can observe, only during the summer and in a dispersed way, the small blue-green skins of a cyanobacterium called *Rivularia bullata* or the soft, reddish and slightly branched axes of *Nemalion helminthoides*, a red alga.

3.2. Non-zoning rocky basins

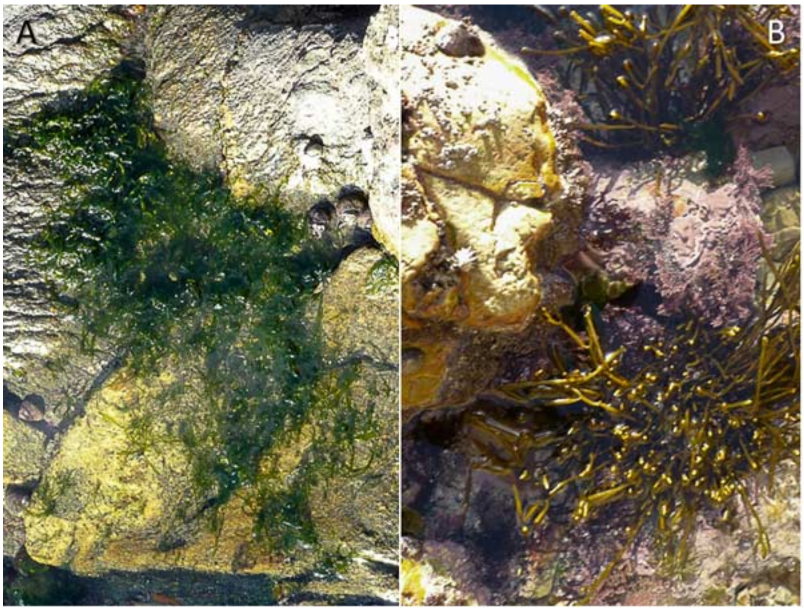

Figure 17. A, Upper midlittoral bowl housing Ulva (= Enteromorpha) compressed, green algae, and the gastropod Monodonta lineata; B, Middle midlittoral bowl with a brown alga, Bifurcaria bifurcate, and various calcified, branched or encrusted Corallinaceae (red algae), pale pink in colour.

The rocky basins, always filled with water, disturb the belt zoning of the foreshore; they offer a favourable biotope for various species that do not tolerate dehydration due to the exposure [1],[2]. Their level on the foreshore, their size, their depth and their illumination will condition their stands. The high level basins, which are desalinated, heated or lose their oxygen quickly, are poor in species, with mostly green algae (Figure 17A). Those below mid-tide level support a variety of animals: sea anemones, shrimps, gastropods, small fish, as well as various algae that normally live below and outside the basins. Figure 17B shows the brown alga *Bifurcaria bifurcata* (15 cm long) and various crustose calcified red algae of the Corallinaceae family; the latter do not leave the bottom of the basin and thus avoid dehydration.

3.3. Stacking and adaptations of fixed or slightly mobile fauna [1]

The gastropods of the **Littorinidae** group are spread as follows (Figure 18): *Melaraphe neritoides* in the supralittoral, *Littorina nigrolineata* and *L. rudis* in the upper midlittoral and *Littorina littoralis* and *L. littorea* (or winkle) from the middle midlittoral to the upper infralittoral; the first one, rarely submerged, has a respiratory and excretory physiology close to land snails. The various **limbs and gibbles**, other gastropods, are also staggered. In addition, *Nucella lapillus*, or dog whelk, has a thicker shell in beaten mode than in quiet mode.

Figure 18. Three examples of rocky foreshore Littorinidae, from left to right: A, Melaraphe neritoides, 5 mm, supralittoral cracks; B, Littorina nigrolineata, 1 to 1.5 cm, on rocks of the upper midlittoral; C, Littorina littoralis, 1 cm, medium to lower midlittoral Fucus grazer.

In the crustacean group, **barnacles** are attached to the rock and protected by solid limestone plates; they also form more or less regular belts: *Elminius modestus* and *Chthamalus stellatus* (Figure 6) at the top, *Balanus balanoides* in the middle and *Balanus perforatus* and *B. crenatus* at the lowest levels.

To avoid being swept away by waves, animals are permanently glued to the rock or algae (Figures 5, 6 and 19), more or less temporarily fixed by filaments for mussels and a suction foot for limbs or stuck in cracks in difficult times (Figure 18A). With few exceptions, most of the animals' biological activity takes place during immersion or when the environment remains wet; at low tide, they live in slow motion, closing their operculum or pressing against the rock, in the case of gastropods.

4. Varied food chains

The plant and animal belts of the rocky coasts form various juxtaposed and interrelated communities, with various food chains operating in an integrated food web. At their base are the **primary producers** of fixed macroalgae, microalgae attached to rocks and also plankton microalgae from the marine flow.

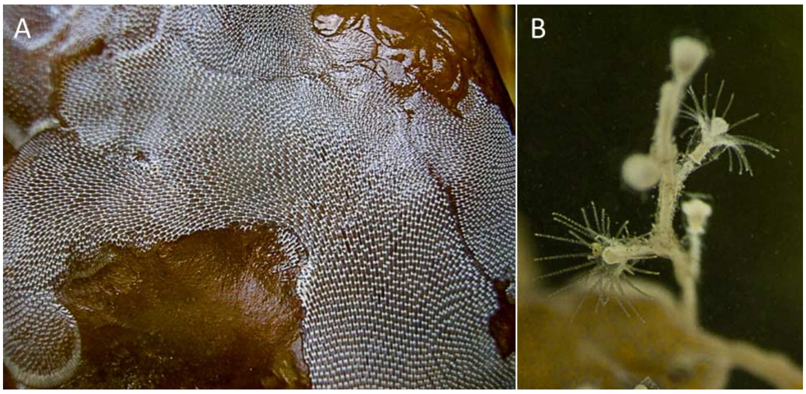

Figure 19. Two examples of animals attached to algae: A, Membranipora membranacea, filter feeder bryozoan; B, Obelia geniculata, predatory hydrarian. Photos: © S. Tanzarella-Paganon.

Secondary animal **producers** are of very varied types:

gastropods, patellae and coastlines (Figures 6 and 18), and sea urchins are fixed **algae grazers**, small or large; sponges, mussels, barnacles (Figure 6), bryozoans (Figure 19A), ascidians (Figure 5) and some worms are plankton and organic debris **filterers**;

many **predators**, anemones and hydrarians (Figure 19B), crustaceans and fishes, catch mobile preys. The dog whelk pierces the fixed barnacles and molluscs. Other gastropods graze on animals fixed on rocks or those stuck to algae;

finally, many crustaceans, such as crabs, are **scavengers** or **detritus feeders** (eaters of corpses or various organic detritus).

Figure 20. Partial view of Sargassum muticum, a large brown alien seaweed from the Pacific and living at the limit of the medium- and infralittoral in calm mode.

In conclusion, it should be noted that the expected rise in sea level could modify both the coasts by erosion and impact the zoning presented here by causing the depletion of some organisms. In addition, many algae or animals have **invaded** the European coasts over the past century, thanks to the exchange of oyster spat or globalized shipping. Examples include the large brown algae *Sargassum muticum* (Figure 20), which arrived from Japan in the late 1970s; it colonizes both calm rocky basins and channels, where it has been able to insert itself into existing belts without causing problems, and muddy sandy areas where it attaches itself to small pebbles or oyster park poles, causing more problems.

References and notes

Cover image. *A rocky coast of Brittany subjected to waves at low tide. [Photo © J. Joyard]. Unless otherwise indicated, photos in this article are by Olivier or Céline Manneville.*

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