21. Chemosynthesis: from abysses to mangroves

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CO_2 fixation by the photosynthetic pathway is considered as the main source of energy for ocean ecosystems. However, sunlight is rapidly absorbed by marine waters and, at depths below 200 meters, photosynthesis is no longer possible. The organic matter produced by phytoplankton on the surface is gradually remineralized and only a small part of this resource reaches the obscure regions, which comprise 98% of the volume of the ocean (cf. II.20). As a result, the seabed is considered to be low in energy, especially in places where it lies far from the surface. But in reality this model is not totally relevant. Today, we know that alternative sources of energy are available in the ocean, and represent a mosaic of "chemosynthetic" habitats, in which communities of organisms proliferate through local production of organic matter. For example, deep hydrothermal vents or hydrocarbon seeps can harbor animal communities that are comparable to tropical reefs in terms of biomass.

Symbiotic activity

Deep-sea hydrothermal vents (cf. II.19), which were discovered on oceanic ridges 40 years ago, are emblematic of these environments, where intense microbial production fuels ecosystems identified as being among the most productive marine environments. Chemoautotrophic activity is supported by complex interactions between microorganisms, bacteria and archaea, and the environment chemistry. To date, six metabolic pathways that enable microbes to transform CO_2 into organic molecules have been identified. To 'fix carbon', these microorganisms exploit a variety of chemical compounds, whose reactions release energy. Hydrogen sulfide, abundant in hydrothermal fluids, is the main electron donor used. Its oxidation into sulfate using dissolved oxygen is one of the most energetic reactions available in the mixing zone of the hydrothermal fluid and seawater. Hydrothermal fluids are also rich in iron and dissolved manganese and sometimes in hydrogen, the oxidation of which is another major mode of energy acquisition. Another mode of carbon fixation is used by methanotrophs to produce organic compounds from the methane present in certain hydrothermal fluids, by exploiting the chemical energy of its oxidation.

The fauna that colonize these fluid emission zones therefore depend on these chemoautotrotrophic micro-organisms, and sometimes form close associations with them.

Fig. 1 – **Gills of a giant tubeworm capable of extracting the chemical compounds (CO_2, hydrogen sulfide, oxygen) needed by its endo-symbiotic bacteria.** © Ifremer / MESCAL expedition (UPMC-CNRS). ■

An increasing number of symbioses between invertebrates and one or several bacteria that develop on the surface or inside their host's organs, is being described in these environments. Beyond the emblematic giant tubeworms of the Eastern Pacific off Galapagos, where they were first discovered (Fig. 1), diversified families of bivalves, gastropods, and hydrothermal crustaceans that form symbioses with chemoautotrophic bacteria are now known. These ultra-specialized species and their multiple types of association reflect the optimal utilization of the sources of chemical energy available in environmental conditions that vary extremely over time and in space.

Fig. 2 – **Aggregation of mussels forming symbioses with chemoautotrophic bacteria associated with methane hydrates in a submarine canyon at a depth of 1,600 m, North American margin.** © Deepwater Canyons 2013 – Pathways to the Abyss, NOAA-OER-BOEM-USGS. ■

Unsuspected habitats

The enhanced exploration of the ocean floor in recent decades over regions of high heterogeneous tectonic and magmatic activity, beyond mid-ocean ridge axes, along volcanic arcs and continental margins, including in the most challenging regions of the Antarctic and the Arctic oceans, have progressively revealed the ubiquitous nature of these communities. These findings allow chemosynthesis to be integrated in a wider ecological context, which also includes submarine canyons from which sulfur-rich or methane-rich fluids seep, and faults where alkaline fluids rich in hydrogen and methane are formed by the interaction between seawater and the rocks that form the Earth's mantle.

More ephemeral habitats, such as massive organic substrates, wood or whale carcasses, also harbor communities that exploit chemosynthesis. The end products of organic matter degradation are indeed methane, CO_2 and hydrogen sulfide produced from the conversion of seawater sulfate. Such molecules may in turn serve as a starting point for a chemosynthetic trophic chain. These chemosynthetic symbioses are not limited to great depths. Chemoautotrophy is beginning to be identified as an important component in organic matter-rich marine ecosystems, such as mangrove forests, seagrass or upwelling regions associated with high planktonic productivity in surface waters. The diversity of these associations demonstrates the adaptability of benthic species to the variety of energy sources available *via* different electron donors (sulfide, methane, hydrogen) available, regardless of the geological setting (Fig. 2).

Characterizing the variability of environmental conditions remains a major challenge in deep-sea environments, where limited access to sites constrains monitoring over time. A few sites have benefited from more than 20 years of long-term studies. However, the functioning and dynamics of chemosynthetic ecosystems depend to a large extent on the relations between organisms and, often ephemeral, microenvironments, whose role in the ocean remains difficult to grasp, considering the great diversity of these systems. The extreme variability of physicochemical conditions (temperature, pH, oxygen sulfide toxicity...) and the instability of the habitat that accompanies these resources are essential keys to understanding the relationships that structure communities over time and in space.

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