Denis Allemand

Coral Reefs and Climate Change

Coral reefs are found in only a small percentage of global oceans, between 0.08 and 0.16%, but they shelter about one third of the marine species known today. This ecological success is due to a symbiosis between a coral and an intracellular microalga, commonly called zooxanthellae. “Organismic engineers”, they are the source of the largest biological constructions on the planet. Genuine oases of life, they support the direct sustenance of more than 500 million people in the world from fishing, but they engage human interest also for other reasons: protection of coasts against erosion, high value tourist areas... Ecological services from coral reefs are estimated at approximately 30 billion USD per year. Their growth depends on many factors (light, temperature, pH, nutrients, turbidity...). They are therefore extremely sensitive to the current changes in our environment: water temperature variability, ocean acidification, in addition to localized disruptions (pollution, sedimentation, coastal development, overfishing, marine shipping...). An increase of less than 1 degree above a threshold value is sufficient to cause bleaching. It breaks the coral symbiosis with their zooxanthellae throughout the populations, leading to the disappearance of the reef. Similarly, ocean acidification impedes the formation of coral skeleton and many other biological functions such as reproduction. We actually estimate that approximately 20% of the global coral reefs have already disappeared completely; 25% are in high danger; and 25% more will be threatened by 2050 if positive management action is not taken.

WHAT IS A CORAL REEF?

Coral reefs are ecosystems typically found in shallow waters of the intertropical zone (approximately between 33° North and 30° South). The three-dimensional architecture of this ecosystem is formed by the buildup of calcareous skeletons of marine organisms called reef-building corals (Cnidaria, Scleractinia). They are cemented together by the biological activity of calcareous organisms (macroalgae, sponges, worms, molluscs…). Corals are named “engineering organisms”, while the reef is considered “biogenic” because it is the result of biological activity. Coral reefs therefore represent ecosystems that have been built by their own inhabitants.

The total area covered by coral reefs varies, depending on the calculation methods, between 284,300 km² (Smith, 1978) and 617,000 km² (Spalding *et al.*, 2001), therefore covering between 0.08 and 0.16% of the surface of the ocean. French reefs alone cover an area of 55,557 km².

The largest reef is the Great Barrier Reef which runs along the north-eastern coast of Northern Australia over a distance of 2300 km. It is known as the only animal construction visible from space. The second largest reef is French New Caledonia Barrier, which is 1600 km long. These two barrier reefs have been included in the UNESCO World Heritage list (respectively in 1981 and 2008).

Coral reefs come in different shapes and sizes, the first published description dating from Charles Darwin during his voyage on the Beagle (Darwin, 1842):

- Fringing reefs: They follow the coastline, maintaining an active growth area offshore and an accumulation of dead coral inshore, forming a platform reef that over time turns into a lagoon.

- Barrier reefs: the fringing reef becomes a barrier reef subsequent to the progressive sinking of an island. In this way, the lagoon becomes larger and the reef can extend to 1 km from the coast.
- Atolls: these are the ultimate step in the evolution of a reef, where the island has completely disappeared below the sea surface. Atolls preserve the initial circular shape of the island. There are approximately 400 atolls in the world.

Reef growth is approximately 4 kg of calcium carbonate ($CaCO_3$) per m² per year (Smith & Kinsey, 1976), but values can vary considerably from one reef to another, in some cases reaching up to 35 kg $CaCO_3$/m²/year (Barnes & Chalker, 1990), *i.e.* a vertical annual growth rate of 1 to more than 10 cm. Many factors influence these growth rates: light, temperature (optimal between 22° and 29°C), nutrients, currents, turbidity, pH and the saturation state of calcium carbonate in the seawater…

The formation of calcium carbonate by reef-building organisms causes the release of carbon dioxide into the surrounding environment. Hence, contrary to past belief, a reef mainly dominated by coral acts as a minor source and not as a sink of CO_2 (about 1.5mmol CO_2/m² day. Tambutté *et al.*, 2011 for a review). Nevertheless, reefs still do play an important role as a carbon sink (as $CaCO_3$), with rates of the order of 70 to 90 million tonnes of carbon per year (Frankignoulle & Gattuso, 1993).

CORALS, AT THE ORIGIN OF THE REEF

Reefs are mainly built by corals. Formerly known as stony corals, reef-building corals are now included in the Order of Scleractinians (subclass Hexacorallia, class Anthozoa of phylum Cnidaria). Among the Scleractinia, about half the amount of species (about 660 out of 1,482 species known to date, Cairns, 1999) are involved in reef construction. These are called hermatypic. They consist of polyps of variable sizes, depending on the species, and form functional units. Each polyp has a mouth surrounded by tentacles. The polyps are connected to each other by network of cavities, the coelenteron, which covers the coral tissue. The whole assemblage is known as colonial (even though the colony functions as a single organism) while individual corals are called modular animals. They present various shapes and sizes, depending on whether the species are branching coral, blade coral, encrusting, or massive coral for example, and show growth rates that can exceed 15 cm per year of axial growth in their natural environment (Dullo, 2005). The size of certain massive corals may even exceed 6 m in diameter.

The success rate for a reef to develop and to thrive is mainly related to the capability of the majority of scleractinian corals (just under 900 species, Michel Pichon, Comm. Pers.) to establish a mutual symbiosis with photosynthetic dino agellates commonly called zooxanthellae (*e.g.* Symbiodinium sp.). These microalgae reside inside the coral's gastroderm, isolated from the animal's cytoplasm by a perisymbiotic membrane that regulates the exchanges between the symbionts and the host (Furla *et al.,* 2011 for a review). To this day, 9 clades of zooxanthellae, that are potentially different species, exist (Pochon & Gates 2010). Each one presents unique characteristics, which suggests that they could condition the adaptation of corals to a given environment. These two partners have co-evolved since the Triassic (Muscatine *et al.,* 2005), developing unique abilities (*e.g.* the ability for the hosts to actively absorb CO_2 and nutrients and to protect themselves from ultraviolet rays, hyperoxia and oxidative stress; the ability of the algal symbiont to exchange nutrients with its host; Furla *et al.,* 2005, 2011). Due to the presence of zooxanthellae, the distribution of corals at depth is dependent upon light availability (generally between 0 and 30 m depth). By means of modern sequencing techniques, a large diversity in bacteria has been identi ed inside corals. These bacteria appear to play an important physiological role. The entire community of these living organisms forms a functional unit called aholobiont, often referred to as a super-organism.

Symbiont photosynthesis is also related to another function of coral, biomineralization, that is, its ability to build a limestone or biomineral skeleton. The property of a biomineral is that it is a composite material, comprising both a mineral fraction and an organic fraction. Even though the latter is minimal (<1% by weight), it plays a key role in controlling the deposition of calcium carbonate in the form of aragonite (German *et al.*, 2011, Tambutté *et al.*, 2008, 2011). Using mechanisms that are still a matter of debate, light, via symbiont photosynthesis, has been observed to stimulate the calci cation of coral by a factor reaching 127 in comparison to night calci cation. However, in most cases, this factor varies between 1 and 5, with an average value of 4 (Gattuso *et al.*, 1999).

Coral reproduction is typically sexual and involves a larval stage called planula which ensures the species dispersal. They can also have a high asexual reproductive capacity by fragmentation and budding. This capacity is utilized in the development of ex situ cultures.

CORAL AND CORALS

The word Coral entails a plurality of species belonging to the phylum of Cnidaria and forms the basis of several ecosystems:

- Cold-water corals, also called deep-sea corals: these corals belong to the same order of cnidarians as reef-building corals. They are engineering organisms, capable of building a rich ecosystem that provides habitat for many other creatures in the deep waters of the Atlantic, Pacific, as well as the Mediterranean Sea. Unlike their surface water cousins, they are acclimated to cold waters (6°–14°C) and do not host photosynthetic algae. These reefs therefore play a significant role as shelters and nursery areas for many species of fish of commercial interest (Roberts *et al.*, 2009).
- The coralligenous in the Mediterranean: they are formed by an assemblage of stationary creatures (*e.g.* gorgonians, red coral, encrusting calcareous algae…). The coralligenous in the Mediterranean form a very rich coastal ecosystem, especially along underwater cliffs. It is of particular interest both for fishing and aquatic tourism (RAC/SPA 2003).

THE CORAL REEF: A BIODIVERSITY HOT-SPOT

The ability to live in symbiosis with dinoflagellates has allowed coral reefs to build large constructions in usually oligotrophic conditions, that is, nutrient-poor waters. Coral reefs have existed since the Triassic, about 200 million years ago. However, since that time there have been many phases of disappearance/reappearance. The development of the Great Barrier Reef seems to have begun 20 million years ago. However, primitive forms that are different from modern corals, have existed long before the Triassic, during the Devonian about 400 million years ago.

Coral reefs are home to the greatest biodiversity on Earth with 32 of the 34 animal phyla known to date and include a third of marine species known so far, representing nearly 100,000 species (Porter & Tougas, 2001). Hence, 30% of the known marine biodiversity is sheltered in less than 0.2% of the total surface of the oceans! In the marine environment, they therefore represent the equivalent of the primary tropical forests. For comparison, the number of species of molluscs found on 10 m² of reef in the South Pacific is greater than what has been acknowledged throughout the whole North Sea. As another example, in New Caledonia there are over 400 species of coastal nudibranchs while in mainland France there is a dozen species for an equivalent coastline.

This "biodiversity" is however not homogeneous between reefs. In fact, there is a skewed distribution of the diversity and abundance of corals between the Atlantic and Pacific Oceans, as well as within these oceans. In these two oceans, the diversity and abundance are concentrated in the western parts: the Coral Triangle (also called "Centre for Coral Biodiversity") in the Pacific, including the -Indonesia

Malaysia - Philippines - China Sea - Solomon Islands region; the Caribbean in the Atlantic. There is also a strong east-west longitudinal gradient. The fauna and flora associated with reefs generally follow similar gradients.

THE CORAL REEF: AN EXCEPTIONAL WEALTH FOR MANKIND

Coral reefs border the coasts of more than 80 countries across the world (Sheppard *et al.*, 2009) for which they represent an important source of income, just as much in terms of food resources, coastal protection and tourism… Approximately 275 million people worldwide live within 30 km of a coral reef and the livelihood of over 500 million people directly depends on reefs. On one hand economists estimate that the annual value of the benefits provided by the reefs is worth slightly more than 24 billion euros (Chen *et al.*, 2015). On another hand, the TEEB report (TEEB, 2010) has estimated that the destruction of coral reefs would represent a loss of about € 140 billion per year.

The ecosystemic benefits provided by coral reefs include:

1. Natural resources

- Food: coral reefs provide 9 to 12% of the world catch of edible fish and 20 to 25% of the fish catch in developing countries (Moberg & Folke, 1999). This figure reaches 70 to 90% for the South East Asian countries (Garcia & de Leiva Moreno, 2003). The total estimated income of reef fisheries is about 5 billion euros (Conservation International, 2008). Most of these fisheries are traditional, carried out on foot by the local population, especially women and children who collect fish, molluscs (clams), crustaceans (crabs and lobsters) and sea cucumber (also referred to as trepang). A healthy reef is estimated to annually provide 5 to 10 tonnes of fish and invertebrates per km^2.
- Mineral resources: coral reefs provide housing construction materials (Maldives, Indonesia), sand for the construction of roads or fertilizers for agricultural land. Coral reefs in the Maldives thus supply about 20,000 m^3 of material annually (Moberg & Folke, 1999).
- Live Resources: beyond fishing for food needs, reefs also represent a fishing reserve for coral reef aquariology (15 million fish per year for 2 million aquarists in the world) and pearl farming, etc.

2. Conservation

- Coastal Protection: coral reefs have an undeniable role in the protection of coastline from the destructive action of waves and tsunamis. More than 150,000 km of coastline are naturally protected by barrier reefs (http://www.coralguardian.org). A typical coral reef can absorb up to 90% of the impact load of a wave (Wells, 2006). During the devastating 2004 tsunami in the Indian Ocean, coasts protected by healthy coral reefs were much less affected by the deadly wave. The value of coastal protection against natural disasters has been estimated to lie between 20,000 and 27,000 euros per year per hectare of coral (TEEB, 2010). The total profit is estimated at 7 billion euros per year (Conservation International, 2008).

3. Cultural resources

- Tourism: tourists are attracted to the natural beauty of coral reefs (via terrestrial tourism, diving). The large number of visitors promotes employment, a windfall for the poverty-stricken parts of the world. For example, the Australian Great Barrier Reef attracts about 2 million visitors annually, producing an income of around 4 billion Euros for the Australian economy and 54,000 jobs (Biggs, 2011). According to estimates compiled by the TEEB report, one hectare of coral reef represents a yearly profit of 64,000 to 80,000 Euros from tourism and recreational opportunities. Ecotourism alone earned 800,000 euros per year in the Caribbean. The total annual income from coral reefs is estimated around 8 billion euros (Conservation International, 2008).
- Cultural or religious heritage: Coral reefs are at the base of many cultural and religious traditions.

In southern Kenya, for example, many religious rituals are structured around coral reefs in order to appease the spirits (Moberg & Folke, 1999).

- Medical resources: the numerous marine invertebrates (sponges, molluscs or soft corals) represent a potential supply of new drugs for human health. Coral is also starting to be used as a biological model to better understand immunity or aging mechanisms (Moberg & Folke, 1999).

THE CORAL REEF: LOCAL AND GLOBAL THREATS

The coral reef ecosystems are currently threatened both locally (pollution, sedimentation, unsustainable coastal development, nutrient enrichment, over-fishing, use of destructive fishing methods…) and, since the 1980s, globally (global warming, ocean acidification). The Global Coral Reef Monitoring Network (GCRMN) estimates that at present, 19% of reefs have been destroyed, 15% are seriously damaged and may disappear within the next ten years, and 20% could disappear within less than 40 years. The rare monitoring studies on reef growth show a clear long-term decrease in coral cover: in an analysis of 2258 measurements from 214 reefs of the Great Barrier during the 1985-2012 period, De'ath *et al.*, (2012) highlighted a decline in the coral cover from 28.0% to 13.8% as well as loss of 50.7% of initial coral cover.

Among the global events that affect coral reefs, the increasing temperature of surface water is causing a widespread phenomenon, coral bleaching. Unique example, visible to the naked eye, of the impact of climate change on an ecosystem, coral bleaching is the result of the rupture of the symbiosis between corals and zooxanthellae symbionts. Although it can be reversible during the first few days, this bleaching effect inevitably leads to coral death a few weeks after the symbiosis is halted (Hoegh-Guldberg, 1999; Weis & Allemand, 2009). This phenomenon, whose inner mechanisms are still under debate, usually occurs when the temperature exceeds a certain threshold by 0.5°C.

A second event is just as seriously affecting coral biology: ocean acidification, also referred to as the other effect of CO_2 (Doney *et al.*, 2009). Part of the excess carbon dioxide produced by human activities dissolves into the oceans, reducing on one hand the greenhouse effect (and thus reducing the increase in global temperature), but on the other hand causing a increasing acidity of the oceans, according to the following reaction:

$$H_2O + CO_2 \longleftrightarrow HCO_3^- + H^+$$

To date, the pH of seawater has decreased by about 0.1 units since the beginning of last century (from 8.2 to 8.1) which corresponds to an increase in the acidity of the water by about 30% (Gattuso & Hansson, 2011). Acidification primarily affects the calcification rates of corals, and therefore reef growth. However, it appears that the effects vary greatly from one species to another (Erez *et al.*, 2011). The differences in sensitivity may be due to a differential ability of the animal to control the pH of its calcification site (Holcomb *et al.*, 2014; Venn *et al.*, 2013). However the increase in dissolved CO_2 has also been found to cause many other effects on coral physiology, including the alteration of gene expression (Moya *et al.*, 2012; Vidal-Dupiol *et al.*, 2013).

Unfortunately, our present knowledge of the physiology of these creatures is too insufficient to predict whether corals will be able to adapt to rapid changes in the environment, especially since earlier studies suggest that the combined effects of the decrease in the pH with the increase in temperature of the sea seem to have cumulative effects (Reynaud *et al.*, 2003).

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