Coral and climate change

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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 building of calcareous skeletons of marine organisms, called reef-building corals (Cnidaria Scleractinia). They are cemented together by the biological activity of calcareous organisms (macro-algae, sponges, worms, mollusks, etc.). Coral is referred to as an "ecosystem engineer", while reefs are considered "biogenic" because they result from biological activity. Coral reefs are therefore an ecosystem built by their own inhabitants.

Depending on the calculation method, the total surface area of coral reefs varies from 284,300 km² (Smith, 1978) to 617,000 km² (Spalding *et al.*, 2001), therefore covering between 0.08 and 0.16% of the ocean surface. French reefs alone cover an area of 57,557 km². The largest coral structure is the Great Barrier Reef, which stretches over 2,300 km along the north coast of north-eastern Australia. It is considered to be the only living structure on Earth visible from space. The second-largest reef is New Caledonia's barrier reef, measuring 1,600 km long. These two barrier reefs have been included in the UNESCO World Heritage list (in 1981 and 2008, respectively).

Coral reefs come in different shapes and sizes, and were first described by Charles Darwin during his voyage aboard the HMS Beagle (Darwin, 1842):

- Fringing reefs: These follow coastlines, maintaining an active growth area offshore, and accumulating dead coral inshore, thus 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. As a result, its lagoon expands and the reef extends away from the coast, up to 1 km.
- Atolls: These are the ultimate step in reef evolution, where the island has completely disappeared below the sea surface. Atolls preserve the island's initial circular shape. There are about 400 atolls in the world.

Reef growth is currently of 4 about kg of calcium carbonate ($CaCO_3$) per m² per year (Smith & Kinsey, 1976; Mallela & Perry, 2007) with high values of about 10 kg $CaCO_3$ per m² and per year (Chagos Archipelago, Perry *et al.*, 2015). However, values vary widely from one reef to another and, in some cases, can reach up to 35 kg $CaCO_3$ per m² per year (Barnes & Chalker, 1990), *i.e.* annual vertical growth rates from 1 mm to 20 cm, depending on the species (Tunnicliffe, 1983; Dullo, 2005). Many factors influence these growth rates: light, temperature (optimal between 22° and 29°C), nutrients, sea level, currents, turbidity, pH and calcium carbonate saturation state of seawater (Tambutté *et al.*, 2011, for review).

Calcium carbonate production by reef-building organisms releases carbon dioxide into the marine environment. Hence, contrary to what has long been believed, a reef mainly dominated by coral behaves as a minor source of CO_2, not as a sink (about 1.5 mmol $CO_2/m^2/day$; Gattuso *et al.*, 1993; Tambutté *et al.*, 2011 for review). However, reefs do play a major role as a carbon sink with rates of approximately 70-90 million tonnes of carbon stored annually as $CaCO_3$ (Frankignoulle & Gattuso, 1993).

CORAL, AT THE ORIGIN OF REEFS

Reefs are mainly built by coral. Formerly called zoophyte because of its resemblance to plants, then Madreporaria, reef-building coral is now included in the order Scleractinia (subclass Hexacorallia, class Anthozoa, phylum Cnidaria). Currently, 1,610 valid species have been identified among Scleractinia ("Word List of Scleractinia", Hoeksema & Cairns, 2019; Cairns, 1999), about half of which are involved in reef construction. They are therefore referred to as hermatypic. This coral is composed of polyps of varying size, depending on the species, forming functional units (colonies), that operate as a single organism. For this reason, coral is sometimes referred to as a modular animal. Each polyp has a mouth surrounded by tentacles. Polyps are connected to each other by a network of cavities, called cœlenteron or gastrovascular cavity, running through the coral tissue. Seawater and nutrients circulate in these cavities. Cœlenteron performs many functions, including digestion and fluid circulation for breathing and nutrition.

Tissues are composed of two cell layers, the epidermis (or ectoderm) in contact with seawater and gastrodermis (or endoderm) in contact with the cœlenteron. These two layers are separated by an acellular matrix, called mesoglea. Together, they are shaped like a bag. Coral has a nervous system consisting of nerve fibers, without ganglion formation.

Coral presents various shapes and sizes depending on whether the species is a branching, blade, encrusting or stony coral. For instance, the latter can exceed 10 m in diameter (12 m for "Big Momma", a giant *Porites* discovered in the National Marine Sanctuary of American Samoa in the Pacific Ocean, cf Brown *et al.*, 2009).

The degree of success for a reef to develop and thrive is mainly related to the ability of most scleractinians (just under 900 species, Michel Pichon, pers.comm.) to establish a mutual symbiosis with dinoflagellates — photosynthetic microalgae commonly known as zooxanthellae (*Symbiodinium* sp.). The latter can transfer 75-95% of their photosynthesis products to their animal host for its metabolism (Muscatine & Porter, 1977). Zooxanthellae are located inside coral's gastrodermal cells, isolated from the animal cytoplasm by a perisymbiotic membrane that regulates exchanges between the two partners (Furla *et al.*, 2011). While early research identified only one panmictic[1] zooxanthella species, *Symbiodinium microadriaticum* (Freudenthal 1962), new molecular tools have allowed scientists to discover nine clades in zooxanthellae, referred to as clades A-I (Pochon & Gates, 2010). Each has its own characteristics, suggesting that they could influence coral adaptation to a given environment. New studies in molecular phylogenetics now show that these clades are likely to correspond to different genera (Lajeunesse *et al.*, 2018).

There would thus be: *Symbiodinium* (clade A), *Breviolum* (clade B), *Cladocopium* (clade C), *Durusdinium* (clade D), *Effrenium* (clade E), *Fugacium* (clade F) and *Gerakladium* (clade G). All these genera belong to the family Symbiodiniaceae. This species diversification is thought to have occurred during the Jurassic period (approx. 160 million years ago), which corresponds to adaptive radiation of modern coral. This radiation follows an initial period of coral reef expansion, succeeded by a regression during the Triassic, about 240 million years ago (Muscatine *et al.*, 2005; Frankowiak *et al.*, 2016). This diversification was already linked to a photosynthetic symbiosis (Muscatine *et al.*, 2005), perhaps with Suessiaceae algae — considered to be the ancestors of modern dinoflagellates and now exclusively fossils (Frankowiak *et al.*, 2016; Janouškovec *et al.*, 2017).

The co-evolution between the cnidarian host and its dinoflagellate symbionts shaped the two partners' biology, physiology and morphology. They thus developed unique specific features, such as the

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[1] In population genetics, panmixia is the principle that considers individuals to be evenly distributed within a population and reproduce randomly.

animal host's ability to actively absorb CO_2 to fuel its symbionts' photosynthesis; resist hyperoxia and oxidative stress generated during oxygen production within its tissues; absorb mineral nitrogen compounds; protect itself against ultraviolet rays, etc. (Furla *et al.*, 2005, 2011 for review). Due to the presence of zooxanthellae, coral depth distribution depends on light, availability usually at depths between 0 and 30 m deep. However, some symbiotic coral species can live in very low light conditions down to 150 meters, thus constituting a mesophotic coral ecosystem. Exploration of these environments is just beginning, despite the fact that, they may constitute 80% of total reef habitats (Weiss, 2017). This coral could be a source of larvae to replant damaged surface reefs (Bongaerts *et al.*, 2010).

In addition to zooxanthellae, coral hosts many bacteria, the diversity of which has been highlighted using modern sequencing techniques. These bacteria appear to play a significant physiological role (Thompson *et al.*, 2014 for review).

The entire community of these living organisms forms a functional unit, called a holobiont, often referred to as a super-organism (Rohwer *et al.*, 2002). Symbiont photosynthesis is linked to another coral function, biomineralization, *i.e.* its ability to build a calcareous skeleton (biomineral). This is a composite material, comprising both a mineral and an organic fraction. Even though the latter is minor (< 1 % by weight), it plays a key role in controlling calcium carbonate deposition in the form of aragonite (Allemand *et al.*, 2011; Tambutté *et al.*, 2008, 2011). Using mechanisms that are still debatable, light, via symbiont photosynthesis, stimulates day calcification by a factor of up to 127 compared with night calcification. However, in most cases, this factor varies between 1 and 5, with an average value of 4 (Gattuso *et al.*, 1999).

Coral usually reproduces sexually and involves a larval stage, called planula, which ensures species dispersal. It also has high asexual reproductive capabilities by fragmentation and budding — a property used to develop *ex situ* cultures.

CORAL, CORALS

The word "coral" entails a plurality of species belonging to the phylum Cnidaria and forming the basis of several ecosystems:

- Cold-water corals, also known as deep-water corals: These belong to the same order in the phylum Cnidaria as reef-building corals (Scleractinia). Like them, they are ecosystem engineers, capable of building a rich ecosystem that provides a habitat for many other organisms in the deep waters of the Atlantic and Pacific Oceans, and also the Mediterranean Sea. Unlike their shallow-water cousins, they are acclimatized to cold waters (6°-14°C) and do not host photosynthetic algae. These deep reefs therefore play a significant role as shelters and nursery for many fish species of commercial importance (Roberts *et al.*, 2009).
- Mesophotic corals: These also belong to the order Scleractinia, live at a depth of between 30 and 150 meters and are symbiotic. They form a continuum with surface corals (cf.supra).
- The coralligenous in the Mediterranean Sea:Composed of an assemblage of sessile organisms (*e.g.* sea fans, red coral, encrusting calcareous algae, etc.), this forms a very rich coastal ecosystem built on underwater cliffs. It is of particular interest both for fishing and aquatic tourism (Regional Activity Centre for Specially Protected Areas - RAC/SPA, 2003).

CORAL REEF: A BIODIVERSITY HOTSPOT

The ability to live in symbiosis with dinoflagellates has enabled coral to build large reef structures in usually oligotrophic areas, *i.e.* nutrient-poor waters. Coral reefs have existed in various forms since the Triassic, about 240 million years ago. However, since that time, many phases of disappearance/resurgence have occurred. The construction of the Great Barrier Reef is estimated to have begun 20 million years ago. However, primitive forms, different from modern coral, existed long before the Triassic, during the Devonian, about 400 million years ago.

Coral reefs are home to the greatest biological diversity on Earth, with 32 of the 34 animal phyla known to date, and include one-third of the marine species currently identified, representing nearly 100,000 species (Porter & Tougas, 2001). Hence, 30% of the known marine biodiversity inhabits less than 0.2% of the total ocean surface. In the marine environment, coral reefs are therefore the equivalent of primary tropical forests. As a comparison, the number of mollusk species found on 10 m² of reef in the South Pacific Ocean exceeds the total number of species identified throughout the North Sea. To give another example, in New Caledonia there are over 400 species of coastal nudibranchs, while on mainland France, there is only a dozen species for an equivalent coastline.

However, this biodiversity is not homogeneous between reefs. In fact, there is a skewed distribution of coral diversity and abundance between the Atlantic and Pacific, as well as within these oceans. In both oceans, the diversity and abundance are concentrated in the western parts: the Coral Triangle (also called the "Center for Coral Biodiversity") in the Pacific, including the Malaysia-Indonesia- Philippines-China Sea-Solomon Islands region, and the Caribbean zone in the Atlantic. There is also a strong west-east longitudinal gradient. The fauna and flora associated with reefs generally follow similar gradients.

CORAL REEF: AN EXCEPTIONAL TREASURE FOR HUMANITY

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 in terms of food resources, coastal protection, tourism, etc. 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 (Wilkinson, 2008). On the one hand, economists estimate that the annual value of the services provided by reefs is worth just over 24 billion euros (Chen *et al.*, 2015). On the other hand, the Economics of Ecosystems and Biodiversity report (TEEB, 2010) estimated that the destruction of coral reefs would represent a loss of about 140 billion euros per year.

The ecosystem services provided by coral reefs include:

- Natural resources:
    1. **Food:** Coral reefs provide 9-12% of fish catch worldwide and 20-25% in developing countries ((Moberg & Folke, 1999). This figure reaches 70-90% in South-East Asian countries (Garcia & de Leiva Moreno, 2003). The total estimated income of reef fisheries is 5 billion euros (Conservation International, 2008). Most of these fisheries are traditional, carried out on foot by the local population, mainly women and children collecting fish, mollusks (giant clams), crustaceans (crabs and lobsters) and sea cucumber (also referred to as trepang). A healthy reef is estimated to annually provide 10 to 15 tonnes of fish and invertebrates per km².
    2. **Mineral resources:** Coral reefs provide house building materials (Maldives, Indonesia), sand to build road infrastructure,fertilizers for cropland, etc. Coral reefs in the Maldives thus supply about 20,000 m^3 of material annually (Moberg & Folke, 1999).
    3. **Living resources:** Beyond food fishery, reefs also represent a fishing reserve for coral reef aquariology (15 million fish per year for 2 million aquarists worldwide), pearl farming, etc.
- Conservation:
    1. **Coastal protection:** Coral reefs strongly contribute to protecting coastlines 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 97% of wave impact forces (Ferrario *et al.*, 2014). During the devastating 2004 tsunami in the Indian Ocean, coasts protected by healthy coral reefs were much less affected by the deadly wave (IFRECOR, 2010). The value of coastal

protection against natural disasters has been estimated at between 20,000 and 27,000 euros per year per hectare of coral (TEEB, 2010). The total estimated benefit is 7 billion euros per year (Conservation International, 2008).

- Cultural resources:
    1. **Tourism:** The large number of visitors attracted to the natural beauty of coral reefs (seaside tourism, diving) promotes employment in often poor regions. For example, the Great Barrier Reef attracts some 2 million visitors each year, generating revenues of about 4 billion euros for the Australian economy and supporting 64,000 local jobs (Deloitte Access Economics, 2017). According to estimates compiled in the TEEB report (TEEB, 2010), one hectare of coral reef represents a yearly profit of 64,000 to 80,000 euros from tourism and leisure activities. Ecotourism alone earns 800,000 euros per year in the Caribbean. Approximately 2.5 million visitors per year enjoy the tropical coastal area in Egypt; 23% coming specifically for the coral reefs and 33% engaging in diving activities (Cesar *et al.*, 2003; Hilmi *et al.*, 2018a). Coral reef-related tourism is particularly important for the economy of small island developing States (SIDS). In total, more than 100 countries and territories benefit from coral reef-related tourism and for 23 of them, this income represents more than 15% of their gross domestic product (GDP) (Burke *et al.*, 2011). The total annual income from coral reefs worldwide is estimated to be around 8 billion euros (Conservation International, 2008), and represents about 30% of reef revenues and 9% of the global coastal tourism (Spalding *et al.*, 2017). Coral reef-related tourism is constantly and steadily growing by about 20% per year, *i.e.* four times faster than global tourism (Cesar *et al.*, 2003). However, this sector is very sensitive to reef health, with a fall in revenues of about 20-30% where reefs undergo bleaching episodes (UN Environment *et al.*, 2018; Woodhead *et al.*, 2019).
    2. **Cultural or religious heritage:** Coral reefs sustain many cultural and religious traditions. In southern Kenya, for instance, many religious rituals are organized around coral reefs to appease the spirits (Moberg & Folke, 1999).
    3. **Medical resources and biological models:** The numerous marine invertebrates (sponges, mollusks and soft corals) represent a considerable source of chimiodiversity for future drugs (Bruckner 2002). Coral is also starting to be used as a biological model to better understand immunity or aging mechanisms (Moberg & Folke, 1999).

CORAL REEF: LOCAL AND GLOBAL THREATS

Coral reef ecosystems have been threatened globally since the 1980s (global warming, ocean acidification) and are now also impacted locally (pollution, sedimentation, unsustainable coastal development, nutrient enrichment, overfishing, use of destructive fishing methods, etc.). The Global Coral Reef Monitoring Network (GCRMN) currently estimates that 19% of reefs have been destroyed, 15% are seriously damaged and may disappear within a decade, and 20% are at risk of disappearing within the next 40 years. The rare monitoring studies on reef growth show a clear long-term decrease in coral cover: in an analysis of 2,258 measurements performed on 214 reefs of the Great Barrier Reef during the 1985-2012 period, De'ath *et al.* (2012) highlighted a decline in coral cover from 28% down to 13.8%, and a loss of 50.7% of the initial coral cover.

Among the global events affecting coral reefs, the most significant today is the rising surface water temperature (physical stress factor), causing a widespread phenomenon, known as coral bleaching (see

Ezzat in the present document). This disturbance, the only example, visible to the naked eye of the impact of climate change on an ecosystem is the result of the symbiosis cleavage between coral and its zooxanthellae symbionts. Although they can be reversible during the first few days, bleaching events inevitably lead to coral death within a few weeks of the cleavage (Hoegh-Guldberg, 1999; Weis & Allemand, 2009). This phenomenon, the inner mechanisms of which are still under debate, usually occurs when water temperature exceeds a certain threshold (usually around 28°C) by 0.5°C. However, it very much depends on geographical area (Coles & Riegl, 2013) and species (Loya *et al.*, 2001).

Beyond the direct impacts of bleaching episodes on coral physiology and survival, a recent study showed that the organisms affected by bleaching have a reduced reproductive capacity, making coral reef resilience even more difficult (Hughes *et al.*, 2019).

A second event is just as seriously affecting coral biology: ocean acidification, also referred to as the other CO_2 effect (Doney *et al.*, 2009). This alteration is chemical. Part of the excess carbon dioxide produced by human activities dissolves into the ocean, thus reducing the greenhouse effect (and the rise in global temperature), but also increasing ocean acidity, according to the following reaction: $H_2O + CO_2 \leftrightarrow HCO_3^- + H^+$

To date, seawater pH has decreased by about 0.1 pH units (from 8.2 to 8.1) since the beginning of last century. This corresponds to an increase in water acidity by about 30% (Gattuso & Hansson, 2011). Acidification primarily affects coral calcification rates, and therefore reef growth. However, the effects vary greatly from one species to another, without ever exceeding an inhibition rate of 50% for the same value of CO_2 (Erez *et al.*, 2011). Differences in sensitivity may be due to the differential ability of coral to control pH at the site of calcification (Venn *et al.*, 2013; Holcomb *et al.*, 2014). However, the increase in dissolved CO_2 causes 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 coral physiology is too incomplete to predict whether these organisms will be able to adapt to rapid changes in their environment, especially since earlier studies suggested that the combined effects of decreased pH with temperature rise seem to have cumulative impacts (Reynaud *et al.*, 2003). For some researchers, the rate of climate change is too rapid to enable long-term genetic adaptation in populations with long generation times (Veron *et al.*, 2009). However, signs of physiological acclimatization processes have been identified (Kenkel & Matz, 2016).

The fact that some coral populations are naturally able to withstand much higher temperatures without showing signs of bleaching, such as those of the Persian Gulf which only start bleaching above 34-35°C (Riegl *et al.*, 2011), suggests that adaptation to global warming is possible. Similarly, some coral populations naturally living in more acidic waters than the ocean average, as for instance in Palau (pH=7.8 vs. 8.1), are quite capable of maintaining a high coral cover (Shamberger *et al.*, 2014). Unfortunately, this potential adaptation to ocean acidification is not found on other sites; In Papua New Guinea, for example, branching corals have almost disappeared and a profound alteration of reef functioning can be observed (Fabricius *et al.*, 2011). Recent laboratory studies have shown that coral subjected to a pH of about 7.2 was able to maintain a similar axial growth to control specimens kept at a pH of 8.1. In order to do so, the coral skeleton becomes much more porous (Tambutté *et al.*, 2015). Field observations confirm these experimental results (Rippe *et al.*, 2018). An epigenetic modification of specific gene expression is believed to cause this adaptation (Liew *et al.*, 2018a). As in other organisms, this type of modification can be passed down to future generations (Liew *et al.*, 2018b). This mechanism optimizes gene expression in response to changing environmental conditions. However, this adaptation can have negative consequences, making coral branches more fragile.

Improving our scientific knowledge of coral reefs is therefore necessary to predict their future. Indeed, behind a simple anatomy, coral conceals a high degree of physiological complexity. Isn't the number of their genes actually similar to that of humans?

Without being as pessimistic as the recent IPCC Special Report (IPCC, 2018), which predicts that 2°C warming would destroy almost all coral reefs (99%), it is safe to say that, by 2100, reefs will be different from those existing today.

SOLUTIONS TO ENSURE REEF SURVIVAL IN THE 21ST CENTURY

The scientific community and politicians are now concerned about the future of reefs. This is driving international actions, such as the recent Coral Reef Life Declaration launched in 2017 at the "Our Ocean, an ocean for life" conference by HSH Prince Albert II, HRH the Prince of Wales and HM Queen Noor of Jordan (https://www.fpa2.org/details_actualite.php?idactu=6761&lang=en). The two recent workshops held in Monaco on solutions to save coral reefs (Hilmi *et al.*, 2018b; Allemand & Osborn, 2019) concluded that actions will necessarily require the simultaneous implementation of local and global solutions (including the drastic reduction of greenhouse gas emissions). Among the local solutions, these workshops highlighted:

- **Mitigation**: Mitigation procedures aim to stabilize greenhouse gas concentrations by tackling the causes of climate change, such as reducing carbon dioxide emissions. Most of these solutions are not specific to coral reefs and include seagrass restoration or culture, and mangrove replanting. In fact, these ecosystems are particularly effective CO_2 sinks, locally mitigating the decrease in pH due to ocean acidification (Fourqurean *et al.*, 2012; Howard *et al.*, 2017). Marine geo-engineering solutions have also been proposed, such as adding alkaline materials to seawater (Hilmi *et al.*, 2015 for review) or dispersing on the ocean surface biodegradable biopolymers capable of limiting light penetration.
- **Protection**: The creation of Marine Protected Areas (MPAs) has repeatedly been suggested as an effective way to reduce local stress factors and increase resilience to global changes (Hilmi *et al.*, 2015). The role of MPAs in mitigating, adapting and protecting coral reefs is supported by numerous scientific studies (Ban *et al.*, 2011; Roberts *et al.*, 2017). However, less than 6% of coral species are effectively protected by MPAs today (*i.e.* less than 10% of their distribution area, Mouillot *et al.*, 2016). Furthermore, MPAs do not ensure fully effective protection against global changes. Indeed, the northwest Great Barrier Reef, although protected and far from any direct anthropogenic impact, suffered a significant bleaching event (90%) in 2015-2016 (Hughes *et al.*, 2017). One solution would be to promote the protection of "refuge" areas where corals are stronger than in normal areas, such as the Persian Gulf (Coles & Riegl, 2013; Howells *et al.*, 2016), the Red Sea (Fine *et al.*, 2013, 2019; Osman *et al.*, 2017) or the mesophotic zone at depths between 30 and 150 m (Bongaerts *et al.*, 2010). The creation of a Global Coral Conservatory to preserve species for possible reef restoration or scientific purposes has also been proposed (Zoccola D., pers. comm.), as well as the development of scientific research on coral resistance (Conservation Physiology, Wikelski & Cooke, 2006). A coral conservatory would also help scientists select resistant strains using the assisted evolution method (van Oppen *et al.*, 2015) and artificial reproduction (West & Salm, 2003).
- **Adaptation**: Among the adaptation solutions available to reef areas, promoting a "blue" economy (tourism, fisheries, agriculture) that embodies sustainability principles is essential. In many areas, reducing tourist pressure on reefs, either by regulating diving activities (Hasler & Ott, 2008) or by creating artificial reefs accessible to recreational divers (Kotb, 2016) can also be beneficial. The creation of the Cancún Underwater Museum (MUSA, Mexico), inaugurated in 2010 with 450 underwater sculptures, is a step in the right direction, as is the use of eco-designed mooring buoys (ICRI, 2017) .

- **Restoration**: The final category focuses on restoring deteriorated reef ecosystems, by introducing colonies collected in "refuge" areas, such as the Persian Gulf (see above, Coles & Riegl, 2013) or: *i) ex situ* reared coral using coral fragments resulting from asexual reproduction (Global Coral Conservatory, Rinkevich, 2005, Leal *et al.*, 2014; Allemand, 2014); *ii)* juveniles resulting from sexual reproduction (Nakamura *et al.*, 2011), or *iii)* using *in situ* culture (Kotb, 2016; Rinkevich, 2005, 2014).

While growing, resistant coral strains could be "selected" through an "assisted evolution" process (van Oppen *et al.*, 2015). These authors suggest assisting coral in evolving towards greater resilience. To that end, they propose four options: The first aims to enhance resistance by artificially inducing stress in the laboratory and keeping only the colonies that survive (preconditioning acclimatization). This process is mediated by epigenetic mechanisms (cf. supra). The second option is to actively modify the microbiota associated with coral to select the most resilient community (Peixoto *et al.*, 2017). The third is to select specific organisms to generate resistant phenotypes. The last option is to artificially change the algal component of the coral holobiont by mutation and the genetic selection of zooxanthellae, and inoculate coral with resistant strains of zooxanthellae (Hume *et al.*, 2015). Coral can then be transplanted to natural or artificial reefs. The Reef Ball Foundation, a non-profit organization, has developed specific protocols for deploying, fixing and transplanting coral. Biorock is a patented method that uses electrolytic deposition of calcium carbonate to build artificial structures (Goreau & Hilbertz, 2005). The French NGO Coral Guardian is developing reef restoration programs. While reducing costs, these programs contribute to enhancing local communities' involvement in accelerating sustainable development mechanisms in order to improve their livelihoods.

Coral reefs play a major ecological and socio-economic role. Yet they are currently one of the most threatened ecosystems in the world. The development of original economic, technical and political methodologies is not only necessary to save this iconic ecosystem, but will also provide an action model applicable to other ecosystems.

It is crucial that these methodologies are based on scientific research, developed both in laboratories and *in situ*. The Tara Pacific expedition (https://oceans.taraexpeditions.org/m/qui-est-tara/les-expeditions/tara-pacific/) is an excellent example: dedicated to better understanding the Pacific Ocean reefs, this mission also aims to propose practical solutions to increase their resilience and survival rate.

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