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Ocean acidification impacts on coral reefs: From sciences to solutions

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ABSTRACT

Coral reefs distinctly illustrate the close relationship between biodiversity and ecosystem services. They are rich marine ecosystems, hosting extensive biological diversity, and yet that diversity and the ecosystem services provided are among the most endangered because of global changes. By reducing and altering coral reef biodiversity, global changes are endangering the lives of hundreds of millions of people. It was therefore appropriate that the ongoing workshop series "Bridging the gap between Ocean Acidification and Economic Valuation" dedicated, during the International Year of Coral Reefs, its 4th edition in search of solutions inspired by the most recent data of the Natural, Economic and Social Sciences. This article summarizes the ecological and human importance of coral reefs, the reasons for their sensitivity to global changes, and presents the major conclusions of the workshop as well as policy options

0. Introduction

Inspired by HSH Prince Albert II of Monaco and signed by 155 scientists from 26 nations in the wake of the Second Symposium on Ocean Acidification held in 2008, the Monaco Declaration (https://www.gouv.mc/Action-Gouvernementale/L-Environnement/Un-engagement-de-niveau-international/Lutte-contre-l-acidification-des-oceans) called for creating links between biologists and economists to (i) evaluate the socioeconomic impact of ocean acidification and other anthropogenic changes and costs for action versus inaction and (ii) help improve communication between policymakers and scientists. To follow this recommendation, the Centre Scientifique de Monaco (CSM) and IAEA Environmental Laboratories (IAEA-EL) have together organized since 2010, biennial workshops under the banner “Bridging the Gap between Ocean Acidification and Economic Valuation”. The workshops aim to facilitate a multidisciplinary dialogue between natural, economic and social scientists and to provide reliable data to policy makers. The Monegasque Government, the IAEA, the Prince Albert II Foundation, the French Ministry of Ecology and the Oceanographic Museum financially support these workshops.

The first workshop in the series initiated the dialogue between biologists and economists on the socio-economic impacts of ocean acidification. It identified three major socio-economic impacts: fisheries and aquaculture, tourism, and biodiversity (Hilmi et al., 2010). The second workshop focused specifically on the impact of ocean acidification on fisheries and aquaculture with a regional approach (Hilmi et al., 2013b). The third workshop explored the socio-economic impact of ocean acidification on coastal communities, addressing in particular the observed and anticipated threats to the tourism industry (Hilmi et al., 2015).

In a landmark review of the potential impacts of different IPCC scenarios on oceans and associated ecosystem services, Gattuso et al. (2015) demonstrated that coral reefs are the most sensitive marine ecosystems irrespective of the IPCC scenario (RCP2.6/RCP8.5), and are today the most threatened ecosystems globally. Furthermore, coral reef ecosystems distinctly illustrate the close relationship between biology, ecology, human societies and global changes. It was therefore fitting that the theme of the 4th Workshop in the series focused on the biodiversity and ecosystem services of coral reefs, especially when 2018 was the International Year of the Reefs. As with previous workshops, this workshop sought to identify new and trans-disciplinary solutions from the Natural, Economic and Social Sciences. Therefore, the goal of the workshop was to identify at both global and regional level science-based solutions that could improve the resilience of coral reefs threatened by ocean acidification and other global or local stressors.

1. The biological and ecological importance of coral reefs

Coral reefs are biological constructions formed mainly by Scleractinian corals, therefore called “Ecosystem Engineers”

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(Jones et al., 1994). Reef-building corals synthesize a skeleton of calcium carbonate whose accumulation, over millions of years, forms the coral reefs. Such reefs constitute the largest structures built by living organisms: the Great Barrier Reef on the northeast coast of Australia, is 2600 km long and has a total surface area of approximately 344,000 km^2; the New Caledonia barrier reef measures 1600 km. The growth of the coral reef is about 4 kg of $CaCO_3$ deposited per year per m^2 (Smith and Kinsey, 1976) but can in some cases reach 35 kg/year m^2 (Barnes and Chalker, 1990), with linear growth rates of more than 10 cm per year for branched corals. The largest colony of massive corals known to date has a diameter of 12 m and a height of 7 m (the "Big Momma" - a giant *Porites* found in the National Marine Sanctuary of the Samoa Archipelago in the Pacific, see Brown et al., 2009).

The first coral reefs appeared nearly 450 million years ago, whereas the "modern" reefs date from the Triassic, around 237 million years ago (Stanley, 2003; Hoegh-Guldberg, 2014). They are today mainly distributed between 30°N and 30°S in the tropical and subtropical zones around the equatorial belt. They grow on average between 0 and 30 m deep, but can reach more than 100 m deep in some areas (Mesophotic Reefs). Their distribution depends mainly on the light (photic zone) and the temperature of the water (Spalding et al., 2001).

Today, they occupy a total area estimated to be between 284,300 km^2 (Spalding et al., 2001) and 600,000 km^2 (Smith, 1978), i.e. between 0.08 – 0.16% of the sea surface. Indonesia and Australia are the two countries with the most reef surfaces with 17.95 and 17.22% of global reefs respectively, followed by the Philippines (8.8%). Paradoxically, this small area is home to about 30% of the marine species described to date i.e. 93,000 species described in the reefs out of a total of 274,000 known marine species (Porter and Tougas, 2001), including 25% of marine fishes (Allsopp et al., 2009): coral reefs are nearly 400 times richer in species diversity than other ocean areas, which is comparable per square kilometre to large rainforests (Reaka-Kudla, 1997).

This paradox of an oasis in an oceanic desert was noted by Darwin (1842) and was later called the "Darwin Paradox" (Stoddart, 1976; Crossland, 1983). Indeed, tropical waters are very poor in nutrients (oligotrophic environments), making life difficult. The success of coral reefs comes from a key biological process, the symbiosis between coral and unicellular algae, commonly known as zooxanthellae, that live within coral cells (see for review Furla et al., 2005; Stambler, 2011). They are mainly located inside the endodermal cells of coral tissue at a density of about 1 million zooxanthellae per cm^2 of coral tissue. Photosynthesis, carried out by microalgae, produces photosynthates (sugars), the vast majority (up to 95%, Muscatine, 1990; Stambler, 2011) is transferred to the coral host, thus providing most of its food even if the coral remains capable of capturing prey or absorbing dissolved nutrients (Houlbrèque and Ferrier-Pagés, 2009). Symbionts also provide the O_2 needed for coral respiration, while the host provides a stable environment for symbionts, away from grazing. In return, they benefit from nitrogen and phosphorus from the recycling of metabolic waste from the host (Furla et al., 2005), thus avoiding unnecessary waste in a nutrient-poor environment. Nutrients not used for coral metabolism are excreted in the reef environment as mucus at a very high rate, of the order of 5 l per m^2 of reef per year (Wild et al., 2004). This excretion thus allows the coupling between coral/zooxanthellae symbiosis and the nutritive functioning of the reef, while ensuring the recycling of waste. It explains the paradox of Darwin, who contrasted the exuberance of coral reefs with the little food available in tropical seas. This symbiosis is therefore at the origin of the coral reef ecosystem (Allemand and Furla, 2018).

Table 1
Potential net benefits per year of the world's coral reefs (data from Cesar et al., 2003, in billion US$).

Good/Service	Amount (total net benefice/year)
Tourism and recreative activities	9.6
Coastal protection	9.0
Fisheries	5.7
Biodiversity	5,4

Table 2
Potential net benefits per year of some coral reefs (data in billion US$) and percentage of the country's Gross Domestic Product (GDP).

	Net incomes (million US$/year)	% GDP	Reference
Caïcos Islands	17.7	7.8	Carleton and Lawrence (2005)
Guam	127	2.2	Van Beukering et al. (2007)
American Samoa	5.1	1.2	Cesar et al. (2003)
Philippines	1100	0.35	Cesar et al. (2003)
Hawaii	364	0.6	Cesar et al. (2003)
Indonesia	1600	0.2	Cesar et al. (2003)
Great Barrier Reef	6400	1	Deloitte Access Economics (2017)
Bermudes	722	12	Sarkis et al. (2010)

2. The socio-economic importance of coral reefs

As hotspots for biodiversity, coral reefs provide important 'ecosystem services' that generate the conditions for human communities to settle and potentially thrive in coastal areas adjacent to the reefs. Unfortunately, these 'ecosystem services' are most often market externalities and are not factored in to economic policies. Indeed, the concept of environmental economics is relatively recent, this science having really taken off with the publication of Costanza et al. (1997) devoted to determining the economic value of the planet's ecosystems considered as natural capital. It gained further international recognition with the publication in 2005 of the Millennium Ecosystem Assessment (2005).

The main ecosystem services rendered by coral reefs at the global level are, in decreasing order of potential net benefit: incomes from tourism, protection of the coast, production of food for local population (or incomes from the export of these fish) and biodiversity (Table 1; cf. for general discussion Moberg and Folke, 1999; Cesar et al., 2003; David et al., 2007; Hilmi et al., 2017; UN Environment et al., 2018) but these incomes show significant regional disparities (Table 2). The total annual income of global coral reefs is estimated to be between US$ 30 (Conservation International, 2008) and 375 billion/year (Costanza et al., 1997), with huge regional disparities: reef revenues may represent from around 0.2% of the country's GDP (for Indonesia) to 12% (for Bermuda) (Table 3). The total value of the Great Barrier Reef is estimated at US$ 40 billion (Deloitte Access Economics, 2017). They are US$ 197 million for Martinique (Failer et al., 2010).

Among these revenues, the major source comes from tourism and recreational activities: reef tourism accounts for 30% of global reefs and accounts for 9% of coastal tourism worldwide (Spalding et al., 2017). Reef tourism accounts for 90% of Australian reef revenues. This country receives about 2 million tourists per year who come only to visit and dive on the Great Barrier Reef. This represents nearly 60 million overnight stays in 2016 and provides Australia with 64,000 direct and indirect jobs (Deloitte Access Economics, 2017). Approximately 2.5 million visitors a year benefit from Egypt's tropical coastal zone, of which 23% come specifically for coral reefs and 33% participate in diving activities (Cesar et al., 2003; Hilmi et al., 2018). Reef tourism is particularly important for the economies of Small Island Developing States (SIDS). In total, more than 100 countries and territories

Table 3
Coral reef incomes by type of activity and region (data from Cesar et al., 2003).

Million US$	Carribean	Bermudes	Caïcos Islands	Guam	Northern Mariana Islands	American Samoa
Tourism	2100	405	18	94.6	42.3	0.073
Coastal protection	700	265	3,7	8.4	8	0.582
Fisheries	300	4.9	16.9	4	1.3	0.755

benefit from coral reef tourism, and 23 of these countries report that reef-related tourism accounts for more than 15% of their gross domestic product (GDP) (Burke et al., 2011). The annual net benefits from coral reef tourism have been estimated at US$ 2.6 billion for the Caribbean, US$ 364 million for Hawaii, US$ 252 million for the Philippines and Indonesia, between US$ 140 and 182 million for Belize, and US$ 98 million for Guam (Burke et al., 2011). For France, the French Initiative for Coral Reefs (IFRECOR, 2010) has estimated the total number of users of overseas reefs at 780,000, representing on average more than 40% of the total number of tourists in the french overseas territories. Of these, 190,000 are divers. A total of 517 companies are directly linked to coral reef tourism, generating around 1350 direct jobs. The total value of tourism activities supported by coral reefs is estimated at around US$ 207 million for New Caledonia, Martinique, Guadeloupe, St Martin and Moorea in French Polynesia (IFRECOR, 2010). Reef tourism is growing steadily and constantly at around 20% a year, four times faster than world tourism (Cesar et al., 2003). It is, however, very sensitive to the health of the reef with decrease of incomes of about 20 to 30% (UN Environment et al., 2018).

Coral reefs also play a major role as a source of food. It is estimated that 500 million people, mainly in the coral triangle area, depend directly on the reefs for their survival (Wilkinson, 2008). One square kilometre of coral reefs can produce 10–15 tons of fish per year. Revenues from fishing and reef aquaculture represent approximately US$ 126 million/year for the Australian economy or 2% of total reef income. These incomes are all the more important for developing countries. For example, for the Philippines, the value of fisheries is about US$ 45,00000/km^2 of reef per year and about US$ 9000/km^2 per year for export earnings (White et al., 2000). The total global value of reef fisheries would be 5.6 billion US$/year or about 20% of total reef income.

The reefs also protect the coast from erosion by waves. Reefs reduce wave energy by up to 97% (Ferrario et al., 2014). During the Tsunami in Thailand in 2004, the most affected areas were those where reef-associated ecosystems such as mangroves were the most affected by anthropogenic activities (IFRECOR, 2010). Nearly 200 million people worldwide, mainly in Indonesia, India and the Philippines, benefit from this protection by living within 10 m of elevation and less than 50 km from a reef (Ferrario et al., 2014). In the Philippines, for example, reef flood protection is estimated at around US$ 680 million a year (Narayan et al., 2016a,b). Based on the cost of construction of breakwater dikes in a tropical environment that varies from US$ 450/metre to more than US$ 170,000/m in each country, the value of the reefs for the protection of the coasts was the order of US$ 170/ha per year for the Indian Ocean (Wilkinson et al., 1999). It thus appears that the costs of restoration/management of coral reefs were significantly cheaper than the cost of constructing tropical breakwaters (Ferrario et al., 2014).

Apart from these key ecosystem services, reefs are also important reserves for tomorrow's medicines (Bruckner, 2002). They thus contribute significantly to the well-being of man both now and in the future.

3. Coral reefs, a threatened sentinel ecosystem

Unfortunately, the health of reef systems across the globe is highly threatened. De'ath et al. (2009) showed, through the analysis of 328 massive corals of the Great Barrier Reef, that reef growth is presently declining by 14.2% since 1990 while it was stable for the last 400 years. As part of the "Tara Pacific" expedition, the schooner Tara is (2016–2018) conducting a reef-scale analysis of the Pacific Ocean to determine, among other things, the evolution of growth rates during the last century, but predictions for the end of this century, as indicated by the Intergovernmental Panel on Climate Change (IPCC) in its report published in October 2018 (Global warming at 1.5 °C), suggest a loss of 90% of reef-building corals compared to today for a rise in temperature of +1.5 °C and an almost total loss of corals (>99%) for a rise in temperature of +2 °C (IPCC, 2018). Even if these predictions are particularly pessimistic, what is certain is that even if the corals will not disappear, the coral reefs will be deeply modified (Hughes et al., 2018; Moritz et al., 2018). It should be noted however, that detecting the number of coral species may differ between methods, with the quadrat method allowing closer examination of small and cryptic coral species that are not detected by other less accurate methods (Jokiel, 2015).

Threats are of two types: local and global threats. At the local level, the main threats concern overfishing, destructive fishing with dynamite or cyanide, unsustainable tourism, development of coastal infrastructures, pollution (including fertilizers and pesticides from agriculture and the evacuation of wastewater), sedimentation, proliferation of *Acanthaster* starfish or the use of coral skeletons as a building material (Burke et al., 2011). These threats, which could be managed locally, weaken the corals, thus reducing their resilience to global stresses (Carilli et al., 2009).

There are two kinds of global threats:

- A physical modification of the environment caused by the warming of the waters.

This phenomenon is the most immediate and pressing global threat to coral reefs (Hughes et al., 2017). An increase of as little as 1 °C above the normal summer sea surface temperature may impair the symbiosis between coral and its zooxanthellae causing its breakdown. As a result, the coral loses its zooxanthellae, and therefore the intense colours that they gave to the coral, thus revealing through the transparent tissue, their white skeleton, the process is therefore described as "coral bleaching". The cellular mechanisms that cause the breakdown of the symbiosis are still very much discussed (Weis, 2008; Lesser, 2011; Roth, 2014; Bieri et al., 2016), as well as the respective roles of the host and symbionts (Buddemeier and Fautin, 1993; Hoegh-Guldberg et al., 2002). Bleaching can affect a reef of several square kilometres within a few hours, making it a highly visible effect to the naked eye of global warming. Although the first episodes of coral bleaching were described as early as the beginning of the 20th century, we have to wait until the 1980s to see the phenomenon becoming recurrent with mainly three major episodes (Brown, 2015; Donner et al., 2017): the first dates from 1997–1998 and had caused the deaths of 16% of the reefs in the world, mainly in the Indian Ocean, the second took place in 2010 and concerned all the reefs of the planet. The last one took place in 2015–2016, and is to date the longest, largest and most damaging event for coral reefs. Some parts of the Great Barrier Reef, though far from any direct human impact, have bleached by 99%, resulting in 30% mortalities, up to 90% on some areas like Lizard Island (Hughes et al., 2017; Great Barrier Reef Marine Park Authority, 2017). An estimated 29% of shallow-water coral cover was lost during this event across the Great Barrier Reef Marine Park Authority (2017). Colonies of hundreds of years old died, showing the exceptional character of the phenomenon. Death rates of 80% were recorded in Kiribati (Ezzat and Courtial, 2016).

It appears that coral bleaching episodes are becoming more intense and more frequent. Hughes et al. (2017) observed that the length of the period when surface water temperatures exceed the summer average increases as the temperature increases from 1998 to 2016. It is predicted that, in the near future, bleaching episodes will become annual and more than 90% of global reefs will be affected by 2050 (Frieler et al., 2012; Kwiatkowski et al., 2015).

In 2008, the Global Coral Reef Monitoring Network's report estimated that 19% of the surface of the reefs had disappeared and that 15% were threatened in the short term (Wilkinson, 2008). Three years later, the percentage of reefs threatened in the short term was 60% (Burke et al., 2011). To date (2018), the few only regional data showed a global decline. For example, for the Caribbean, the average coral cover for 88 sites declined between 1970 and 2011 from 34.8% to 16.3%, with however a great disparity between the sites (Jackson et al., 2014). During the 2005 bleaching episode, 80% of the Caribbean's reef surface bleached, causing 40% of the reefs to die (Eakin et al., 2015). Twenty-one of the 29 World Heritage listed reefs have experienced severe and repeated bleaching over the last three years, particularly four iconic reefs: the Great Barrier Reef (Australia), the Papahānaumokuākea (Hawaii, USA) sites, and the Lagoons of New Caledonia (France) and Aldabra Atoll (Seychelles). However a recent global survey of Pacific reefs showed that the average live coral cover has been remarkably stable from 1990 to 2016, but species changes were observed with a decrease of *Pocillopora* spp. to the benefit of *Porites* spp. (Moritz et al., 2018), suggesting that, while a relative stability is apparent, the coral community is gradually changing from branched to massive corals. It should also be noted that the traditional metrics used to evaluate ecosystem 'health' and the status of populations is not able to detect a major, yet cryptic, change in community composition (see for a discussion Bellwood et al., 2006).

Predictions are overall pessimistic, and the latest IPCC report estimates, with very high confidence, that bleaching will cause coral mortality in the order of 50% resulting in a reduction in the equivalent reef area (Wong et al., 2014).

- A chemical modification of the environment induced by Carbon Dioxide.

The phenomenon known as 'ocean acidification' results from the dissolution of carbon dioxide in oceanic waters causing a decrease in the pH of the seawater according to the reaction:

$CO_2 + H_2O \rightarrow HCO_3^- + H^+$ (reaction 1)

(where HCO_3^- is bicarbonate and H^+ is the acidic hydrogen ion).

If this phenomenon is beneficial to humanity in the short term by reducing the greenhouse effect and therefore the rise in Earth's average surface temperature, it has led to an increase in the acidity of the oceans by 30% since the beginning of the era with a decrease of pH from 8.2 to 8.1, which could reach 7.8 at the end of this century (Lerman et al., 2011), while the pH remained stable during the last 300 million years. The acidification of the oceans causes a modification of the water chemistry, in particular the carbonate chemistry, a complex chemical system playing a major role in the pH equilibrium both in seawater and in all biological fluids (including plasma) as well as in the formation of sedimentary rocks. In fact, the carbonate ion (CO_3^{2-}) constitutes the essential brick for the formation of shells and other skeletons of invertebrates, including the skeleton of corals when it reacts with calcium (reaction 2) to form calcium carbonate ($CaCO_3$ or limestone):

$CO_3^{2-} + Ca^{2+} \rightarrow CaCO_3$ (reaction 2)

When increasing the acidity of the seawater, protons (H^+) produced in excess will react with the carbonate ion according to reaction 3:

$H^+ + CO_3^{2-} \rightarrow HCO_3^-$ (reaction 3)

Thus, ocean acidification reduces the concentration of carbonate in seawater. These chemical modifications therefore have profound biological impacts by modifying the quantities of carbonate necessary for the formation of the skeletons but especially by modifying the pH, a key parameter in physiology (Comeau et al., 2017). Indeed, the pH regulates a large number of cellular processes, including the activity of many proteins. However, research is still necessary to fully understand all the impacts of ocean acidification on coral reefs (Hilmi et al., 2013a,b, see also Hoegh-Guldberg et al., this issue).

Ocean acidification affects a wide array of species, from corals to bivalves to finfish. Among the many biological effects of ocean acidification, we can mention the reduction of calcification, the disruption of many physiological processes such as reproduction and nutrition, and behavioural changes. Studies show however a great disparity in the sensitivities of organisms. The study of coral reefs naturally submitted to natural sources of carbon dioxide (CO_2 vents), in Papua New Guinea for example, shows that massive corals resist well, at least up to a pH of 7.7, whereas branched corals are very sensitive (Fabricius et al., 2011). If it appears that there will be winners and losers in a more acidic world, the reef morphology and ecology will be strongly disturbed with a decrease in coral biodiversity and an increase in algal cover (Fabricius et al., 2011). However, laboratory studies show that although some coral species appear resistant to acidification, their growth in length is not reduced, these colonies are nevertheless affected by a much greater porosity, making the branches more fragile (Tambutté et al., 2015; Rippe et al., 2018), suggesting a dark future for coral reefs.

To date, if the pulse effects of warm water bleaching events remain the largest – and most catastrophic – impact on coral reefs, the long-term ambient effects of ocean acidification only undermine the resilience of reef ecosystems to such events. The major question is the adaptability of these organizations, which is today at the centre of the debate (see for synthesis, Allemand et al., 2017).

4. The reefs, what solutions for tomorrow?

The only long-term solution for reversing the trend of ocean acidification and its combined effects with rising sea surface temperature is to curtail the increase of atmospheric CO_2, to contain global warming "well below 2 °C compared to pre-industrial levels" and if possible, to aim to "continue efforts to limit the rise in temperatures to 1.5 °C" as expressed at the COP21 in Paris (UNFCCC, 2015). Self-evidently, this solution will take a long time to be implemented and the effects of climate change will have already led to irreversible situations as the impacts of global change on coral reefs have been visible for nearly 40 years. It is therefore necessary to develop solutions to delay the effects of ocean acidification and rising sea surface temperatures.

This inter-disciplinary workshop gathered 62 economic, social and natural science experts from different fields (marine biology, physiology, ecology, zoology, oceanography, genomics, biogeochemistry, macro- and microeconomy, blue finance, anthropology, marine policy, sociology) as well as NGO leaders and decision-makers, from 22 countries. The aim of the 3-day workshop was to stimulate a global discussion on ecological and socio-economic risks and potential solutions for coral reefs in six different regions of the world. From this discussion, both local and global solutions appeared. The solutions discussed during

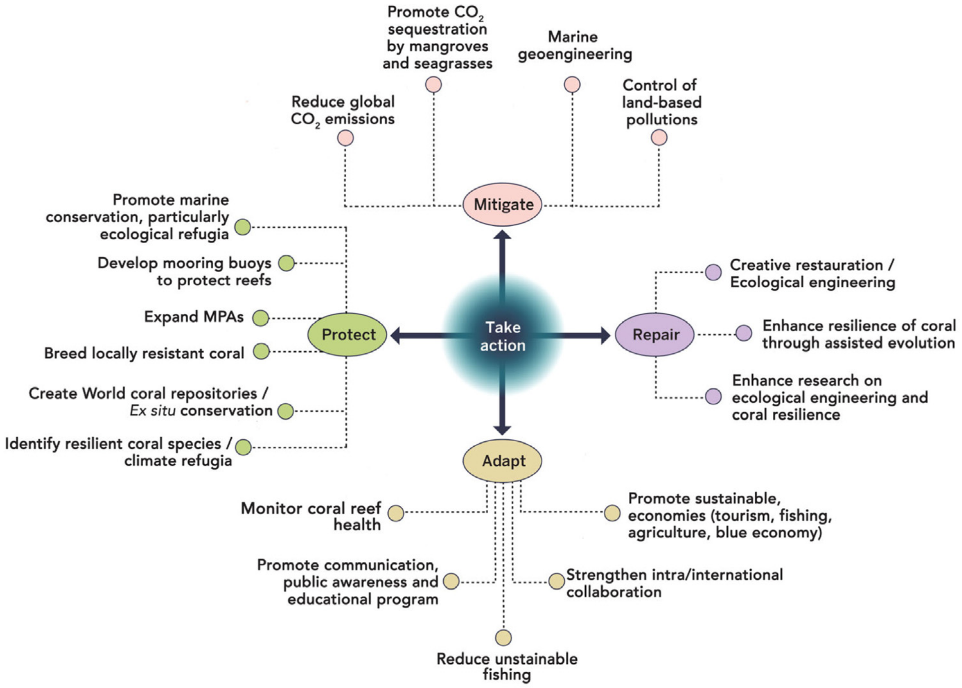

Fig. 1. Solutions for coral reefs against climate change impact. The diagram is based on the four clusters of actions against climate change proposed by Gattuso et al. (2015) and adapted for specific solutions for coral reefs.

this workshop are classified below according to the 4 categories (Fig. 1) proposed by Gattuso et al. (2015):

- Mitigation: Mitigation procedures seek to stabilize greenhouse gas concentrations by addressing the causes of climate change, such as reducing carbon dioxide emissions (Billé et al., 2013). These solutions, most of which are not specific to coral reefs, include the restoration or cultivation of marine phanerogam (seagrass) meadows or the replanting of mangroves. Indeed, these ecosystems constitute particularly efficient "CO_2 sinks" that locally mitigate the pH drop due to ocean acidification (Fourqurean et al., 2012; Howard et al., 2017). Developing phanerogam meadows can help reduce the presence of bacterial pathogens (Lamb et al., 2017). Marine geoengineering has also been proposed as the addition of alkaline materials in seawater (see for a review Hilmi et al., 2015) or the dispersion on the surface of water of biodegradable biopolymers capable of limiting the penetration of light in the water.

- Protection: Local, regional or national regulations, combined with market signals and social campaigns, can be useful in reducing localized pollution that weakens coral reef ecosystems, making them less resilient to climate change (Carilli et al., 2009). Creation of marine protected areas (MPAs) has been repeatedly suggested as an effective way to reduce both local stress and increase resilience to global change (Hilmi et al., 2015). The role of MPAs in coral reef mitigation, adaptation and protection is supported by numerous scientific studies (Ban et al., 2011; Lamb et al., 2015; Roberts et al., 2017), however less than 6% of coral species are effectively protected by MPAs (*i.e.* less than 10% of their distribution range, (Mouillot et al., 2016). On the other hand, MPAs do not provide fully effective protection against global change, since the Northwest of Great Barrier Reef, protected and far from any direct anthropogenic impact, has undergone a significant (> 90%) bleaching phenomenon in 2015–2016 (Hughes et al., 2017). One solution, however, would be to favour the protection of "refuge" areas in which corals are more resilient than in normal areas, such as the Persian Gulf (Coles and Riegl, 2013; Howells et al., 2016) or the Red Sea (Fine et al., 2013; Osman et al., 2017) or the mesophotic zone between 30 and 150 m (Bongaerts et al., 2010). Creation of coral repository in order to preserve coral species for potential reef restoration operation or scientific purpose has also been proposed (Zoccola D., pers. comm.), as well as the development of scientific research on coral resilience (Conservation Physiology, see Wikelski and Cooke, 2006). The coral conservatory could also help in the selection of resistant strains by the method of assisted evolution (van Oppen et al., 2015) and artificial breeding (West and Salm, 2003).

- Adaptation: Among the adaptation solutions available for the reef areas, promoting 'blue' economies (tourism, fisheries, agriculture) that embody sustainability principles is key. In many areas, reducing tourism pressure on reefs either by regulating the dives (Hasler and Ott, 2008) or by creating artificial reefs that could be visited first by amateur divers (Kotb, 2013, 2016) may also be beneficial. The creation of the Underwater Museum of Art (MUSA) at Cancùn (Mexico) inaugurated in 2010 with 450 underwater sculptures goes in the right direction as well as the use of ecological mooring buoys (ICRI, 2017). The workshop also highlighted the merits of strengthening intra/international collaboration, particularly in some areas (like the Red Sea), to develop monitoring programs of coral reef health and to promote communication, educational programs and public awareness. Policy and governance actions may also be applied to promote the adaptation of fisheries and aquaculture (adjustment of fishing pressure to sustainable levels, promotion of more resilient fisheries such as pelagic species, see for example Grafton, 2010; Shelton, 2014).

- Repair: The last category concerns repair and restoration of degraded reef ecosystems. This can be done using colonies taken from "refuge" areas such as the Persian Gulf (see above Coles and Riegl, 2013) or from (i) *ex situ* live coral repository using asexually-produced coral fragments (World coral conservatoire) (Rinkevich, 2005; Leal et al., 2014; Allemand, 2014), (ii) using juveniles obtained from sexual reproduction (Nakamura et al., 2011) or (iii) *in situ* culture (Kotb, 2016; Rinkevich, 2005, 2014). During their culture, the resistant coral strains could be "selected" by an "assisted evolution" process (van Oppen et al., 2015). These authors propose to "evolve" the corals towards greater resilience. For that, they propose four options: the first one aimed to promote resistance by inducing it artificially using laboratory stress and keeping only the colonies that survive (pre-conditioning acclimatization). Such a process is mediated by epigenetic mechanisms as recently demonstrated during lab acidification stress (Liew et al., 2018). The second option suggests to actively modify the coral-associated microbiota again to select the most benefit community (Peixoto et al., 2017). The third method suggests performing selective breeding to generate resistant phenotypes. Finally, the last option is to evolve artificially the algal component of the coral holobiont by mutation and genetic selection of zooxanthellae and inoculate resistant strains of zooxanthellae to coral (Hume et al., 2015). Corals can be transplanted afterwards to natural rocks or artificial reefs. The Reef Ball Foundation, a non-profit organization, has developed specific protocols for the deployment, anchoring and transplantation of corals. Biorock is a patented method using electrolytic deposits of calcium carbonate to construct artificial structures (Goreau and Hilbertz, 2005). If to improve reef restoration, *in situ* or *ex situ* coral culture is required, however, whatever the method, and even if this transplantation is biologically feasible, its cost seems prohibitive, since it can reach up to US$ 15,000/m^2 restored (Ferrario et al., 2014). The French NGO Coral Guardian develops reef restoration programs by closely involving local populations: while reducing costs, these programs help to improve the involvement of local communities in accelerating sustainable development mechanisms in order to improve the livelihoods of the latter.

5. Conclusions

The slow-onset crisis for coral reefs across the globe caused by increasing sea surface temperatures, pollution, over-fishing, habitat destruction and introduced marine pests, is compounded and accentuated by ocean acidification — the other CO_2 problem. The implications for the communities and economic sectors highly dependent on coral reefs are significant and potentially catastrophic. Economic development, safety and public well-being are all threatened by the decline of coral reef systems. For example, a study conducted by the United Nations Environment Programme and the World Conservation Monitoring Center and presented at the 32nd ICRI General Meeting held in Nairobi in December 2017 showed that healthy coral reefs directly contributed to 14 sustainable development goals (SDGs 1, 2, 3, 4, 5, 6, 8, 9, 10, 11, 12, 13, 14 & 16) (Thornton, 2017).

Against this dire backdrop, the objectives of this 4th Workshop in the series were (1) to review the latest scientific findings regarding the biological and ecological impacts of ocean acidification, both spatially and temporally; (2) to better understand the consequences for ecosystem services; and (3) to make the leap from science to solutions. Numerous potential solutions were explored, analysed and debated by experts attending the workshop. They ranged from physical interventions through economic incentives to regulatory instruments at national and local scales.

The workshop illustrated that it is not necessary to define where the science ends and the solutions begin. The two are intrinsically linked. Similarly, the various solutions considered need not be considered in isolation but as part of a flexible and adaptable toolbox. What was absolutely clear from the workshop is that the 'do nothing' option is neither desirable nor palatable.

Urgent action to address ocean acidification is needed simultaneously at the global scale, e.g. mitigation of CO_2, and at local scales, e.g. protection, adaptation and repair. Varying legal, economic and social frameworks, and the complex linkages between the threats to coral reef ecosystems, mean that action by governments and stakeholders to protect a specific coral reef system must respond uniquely to the circumstances and priorities of the community dependent on that system, taking in to consideration national, regional or global commitments related to the reef in question.

No two 'cocktails' for protecting coral reefs from ocean acidification and the other compounding threats will have quite the same appearance, scope or focus. Accelerated effort by a complex and diverse network of government, industry, community groups and research organizations is required to expand the scientific knowledge base on the impacts of ocean acidification, while concurrently implementing targeted, sustained and adaptive solutions…

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