Coral bleaching, an imminent threat to marine biodiversity

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For thirty years, the ocean mean temperature has been incessantly increasing, which reinforces the intensity and length of coral bleaching. The period between 2014 and 2017 was marked by massive coral mortality in the various ocean basins, with an exceptional decline by more than 50% in the reefs on the Great Barrier Reef – the largest coral structure in existence. Coral resilience was compromised with a low recruitment rate of coral larvae, and the stress experienced was exacerbated by additional anthropogenic factors (pollution, overfishing, urbanization, tourism, ocean acidification, predation by corallivores, etc.). 2018 has been the warmest year for the oceans since records began, suggesting that coral bleaching could become a recurrent phenomenon in the years to come. In order to protect this natural heritage, which is home to more than a third of the global marine biodiversity and on which over 500 million people depend worldwide for their livelihoods, it is necessary and urgent for governments to take action, beyond local measures, towards reducing human impacts on climate.

Despite their ecological and economic importance, coral reefs are affected by many stress factors at both a local level (marine resource overexploitation, destructive fishing methods, tourist pressure, marine pollution, coastal development, predation by corallivores, etc.) and a global level (rising ocean surface temperature, extreme weather events, ocean acidification) [1-4]. Anthropogenic pressure and climate change currently threaten most reef ecosystems around the world. Over time, these stress factors can lead to a rupture between the coral host and its photosynthetic symbionts – a phenomenon referred to as "bleaching" because coral progressively whitens as it loses its symbionts and/or associated photosynthetic pigments [5]. A moderate decrease in the concentration of symbionts and/or associated photopigments is due to a seasonal and natural phenomenon. This occurs when surface water temperature exceeds seasonal mean maximum temperature over a short period of time which varies according to observed sites.

However, for thirty years, the mean ocean temperature has been rising at an abnormal pace, increasing the duration, intensity and extent of coral bleaching [6]. As a result of the loss of its photosynthetic symbionts, which are its main food source, coral is "physiologically" weakened. In the event of an extended bleaching episode, coral dies of nutritional stress, leading to massive mortality in reef ecosystems worldwide, from the Pacific to the Indian Ocean, the Caribbean, and the Red Sea.

HISTORY OF CORAL BLEACHING

The first coral bleaching episode was seemingly reported by Yonge and Nicholls regarding the Great Barrier Reef in the 1930s, when surface water temperature was 35°C [7]. Since the 1980s, scientists have observed an increase in the frequency, intensity and extent of bleaching episodes worldwide [5]. This is caused by a "record" increase in ocean surface temperature due to global warming, combined with the reinforcement of the El Niño phenomenon. Three major bleaching events were reported in 1998-1999, 2010-2011 and 2014-2017. The 1998 episode impacted 60 countries and island nations across the Pacific, Indian and Atlantic Oceans (Caribbean region), the Persian Gulf and the Red Sea [8,9]. The areas covering the Indian Ocean were particularly affected, with over 70% coral mortality observed over a gradient depth up to 50 m [9]. Significant ocean surface temperature anomalies caused a loss of more than 16% of coral reefs around the world [5]. In fact, 1998 was the first "global bleaching episode" declared by National Oceanic and Atmospheric Administration (NOAA).

Again, in 2010, an intense El Niño phenomenon triggered another extreme coral bleaching event, affecting all reefs across the world with, in some regions such as South-East Asia, greater consequences in terms of expansion and mortality.

The 2014-2017 bleaching event was of exceptional and unprecedented magnitude, duration, and extent. This third bleaching episode began in June 2014 in the western Pacific (Guam, the Mariana Islands and Hawaii), then spread to the Marshall Islands and the Florida Keys. In 2015, the phenomenon extended to the South Pacific, the Indian Ocean, the central and eastern regions of the tropical Pacific, and finally the Caribbean. By the end of 2015, when El Niño was reaching its peak, 32% of the world's reefs had been exposed to a temperature anomaly of +4°C, causing coral mortality over more than 12,000 km². In March 2016, the mean seawater temperature in the northern Great Barrier Reef was 1.5 to 2°C higher than the values recorded between 1971 and 2000 at the same time of year. This global bleaching episode affected more reefs than previous events and was particularly damaging in some areas, such as the Great Barrier Reef and the Kiribati and Jarvis Islands in the Pacific Ocean.

More than 70% of coral reefs around the world were affected by the heat wave that led to bleaching and mortality episodes between 2014 and 2017. Historically, coral bleaching has been linked to the natural El Niño cycle – a climate phenomenon characterized by high seawater temperature – in the eastern South Pacific (South America) and to an atmospheric pressure variation cycle in the South Pacific (Southern Oscillation). The last bleaching event (2014-2017) was particularly dramatic, because it was not continuously linked to El Niño episodes (for example, 2017 was a year dominated by La Niña), suggesting that, unlike previous events, the Southern Oscillation had very little impact on coral bleaching.

ALARMING CONSEQUENCES OF THE 2014-2017 BLEACHING EPISODE

Massive coral mortality across the world oceans

In 2016, aerial and underwater exploration programs showed that out of a total of 911 individual reefs observed on the Great Barrier Reef, 93% had been affected, in particular 1,000 km along the coast north of Port Douglas – an area away from human activities, considered perfectly preserved until then [10]. In contrast, in the central region, between Cairns and Mackay, the bleaching was moderate. The southern area was spared due to a drop in seawater temperatures resulting from Cyclone Winston. In 2017, for the second consecutive year, a bleaching episode severely impacted the Great Barrier Reef and more specifically the central area, near Cairns, Townsville and Lizard Island. More than 50% of the reefs composing the Great Barrier Reef died between 2016 and 2017 [11], including centuries-old species, such as *Porites* coral [10]. Guam, the largest island in Micronesia located east-southeast of the Philippine Sea, underwent extreme bleaching episodes for four consecutive years.

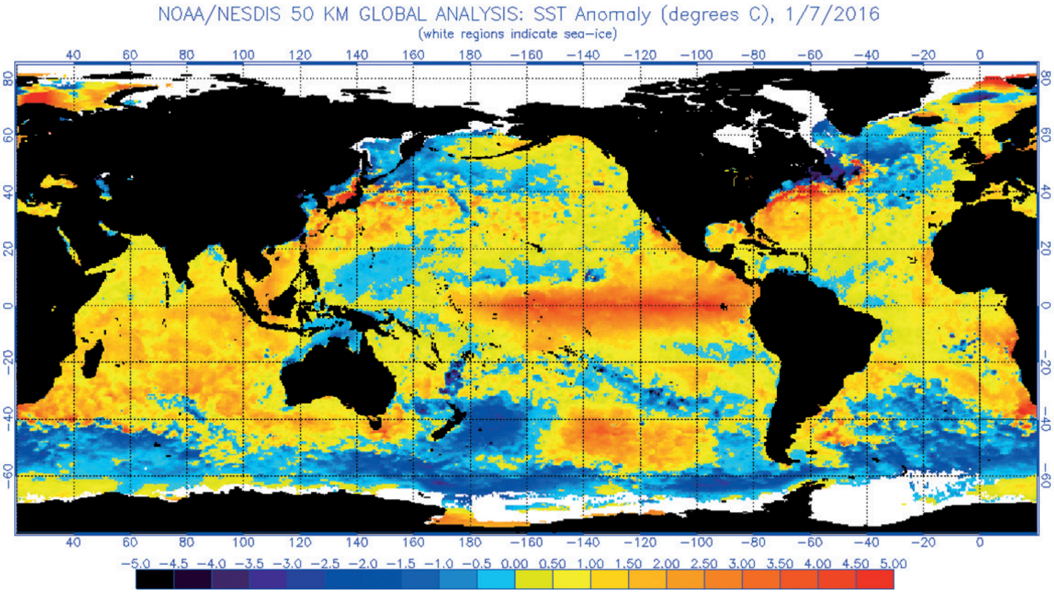

Fig.1 — Sea surface temperature anomalies (°C). The scale ranges from -5°C to +5°C. Positive numbers mean that the temperature calculated on 7/1/2016 was above average.

The phenomenon was severe in the Coral Triangle (Malaysia, Indonesia, the Philippines, and the Solomon Islands), New Caledonia, Fiji and Kiribati, where unusually high seawater temperatures caused more than 80% coral mortality around Christmas Island in 2015-2016. Significant temperature anomalies were also recorded in China, Vietnam, Taiwan, and particularly in Japan, in the Sekiseishoko reef area, where 97% of coral mortality was reported at the end of 2016. Over the past three years, more than 20% of the reefs across the world have disappeared.

Impacts of coral bleaching on the abundance and diversity of reef fish

Coral reefs, often described as cradles of the global marine biodiversity, are home to more than a third of all marine organisms, including 4,000 fish species. However, when reef-building coral undergoes bleaching and dies, a whole biodiversity reservoir is endangered. Following the 2016 heat wave, scientists reported a decrease in the abundance and diversity of herbivorous fish species [12,13], such as damselfish in parts of the Great Barrier Reef [12]. The decline in herbivorous communities is all the more worrying as they play a key functional role in reef development, survival and resilience by consuming the filamentous algae that colonize coral [14].

Nevertheless, it should be noted that the decline in some herbivorous species was not always correlated with a decrease in coral cover [12]. In some areas, experts have observed an increase in the abundance of herbivorous fish, suggesting significant spatial movements and potential short-term "climate refuges".

Compromised recruitment of coral larvae The consequences of recent bleaching events could compromise coral's ability to reproduce. During the 2016-2017 bleaching episodes, the sharp decline in adult individuals of reef-building coral in the northern and central Great Barrier Reef resulted in an 89% drop in larval production compared with the 2016-2017 pre-bleaching periods [15]. Acropora coral – one of the most abundant taxa in the tropics, responsible for the three-dimensional structure of a reef – was the most affected species with a 93% fall in larval production. These observations are alarming, since the quantity of coral larvae produced each year and their dispersal prior to medium/substrate colonization are key elements of reef resilience. The diversity of coral larvae will therefore greatly influence that of future "adult" colonies. "We expect coral recruitment will gradually recover over the next five to ten years as surviving corals grow and more of them reach sexual maturity, assuming, of course, that they do not experience another bleaching event in the coming decade," said Professor Terry Hughes, Director of the Australian Research Council (ARC) – Center of Excellence for Coral Reef Studies.

THE FUTURE OF CORAL REEFS: TOWARDS AN ANNUAL BLEACHING EPISODE?

In February 2019, the global mean ocean surface temperature was 0.7°C higher than the 20th century averages. Climate models predict a short-term extension of the El Niño phenomenon until late spring 2019 (northern hemisphere), thus significantly increasing coral susceptibility to a new bleaching episode and massive mortality. In the event that no action is taken by governments to keep atmospheric temperatures below the +1.5°C threshold in compliance with the Paris Agreement on climate change, experts predict that ocean surface warming could be six times more intense between 2081 and 2100 than the total warming observed over the past 60 years [6]. In fact, until recently, temperatures only rarely and intermittently exceeded the thermotolerance threshold limit above which coral bleaches. However, scientists expect this phenomenon to occur on an annual or biannual basis, thus threatening the survival of coral reefs around the world by 2050. These predictions are alarming because an increase in bleaching intensity, extent and frequency, such as that observed in the Caribbean (1995, 1998, 2005 and 2010) and on the Great Barrier Reef (1998, 2010, 2014-2016 and 2017) for instance, limit reef ecosystem resilience and can lead to higher mortality rates in the long term.

Recent studies have, however, highlighted that some coral species have developed mechanisms and potential for acclimatization to high temperature anomalies. A team of American scientists recently compiled data from the four major bleaching events (1998-2017), encompassing 3,351 sites across 81 countries. They observed that the phenomenon was significantly less pronounced in reefs characterized by a large variation in surface water temperature [16]. Also, some reefs were particularly resistant to the latest heat waves, such as those around the Palmyra Atoll (90% survival rate) in the Northern Line Islands [17], the Indonesian archipelago of Rajat Ampat, or the Gulf of Aqaba in the Red Sea, described as a unique coral refuge [18,19].

From a physiological perspective, some coral species are better able to resist bleaching, such as stony reef-building coral, characterized by slow growth and thick tissue (for instance, taxa from the families Faviidae and Poritidae or Merulinidae). In contrast, branching coral, belonging to the families Pocilloporidae and Acroporidae, is generally more sensitive to strong temperature anomalies [20-22]. Some species may associate with different clades of symbiotic algae to optimize their resistance to thermal stress or regulate their gene expression to strengthen defense mechanisms (genetic diversity) [23-25]. A recent study also demonstrated potential for ecological memory of bleaching, making some coral species potentially more resistant to future events [26]. However, coral resilience remains low and the time required to adapt or acclimatize to thermal stress is too short. These different mechanisms are therefore unlikely to play a major role in reef survival. Finally, other stress factors must be taken into account to accurately predict future development of reef ecosystems. The synergetic effect of some factors (*e.g.* marine pollution and overfishing) can alter trophic relationships between organisms within a reef, increasing coral susceptibility to bleaching, disease, and mortality. For example, during periods of thermal stress, predation by corallivores (*i.e.* sea stars, snails, reef fish) physiologically weakens coral, decreasing its long-term resilience to climate change and other stress factors [27-29].

URGENT NEED FOR ACTION

These recent events have caused concern among the scientific community and heightened collective awareness of the need to act quickly in order to reduce human impact on climate and preserve coral reefs.

In 2016, the Paris Agreement – the first universal agreement on global warming – was signed following the negotiations held at the Paris Climate Change Conference (COP21) in December 2015.

This agreement, which aims to "hold the increase in the global average temperature to below +2°C above pre-industrial levels by 2100" and, if possible, "pursue efforts to limit the temperature increase to 1.5°C", was approved by 196 out of the 197 United Nations (UN) delegations. Moreover, the European Union, in collaboration with the European Environment Agency, set a significant number of environmental and climate objectives encompassing the areas of air and water quality, waste management, energy and transport. At the end of 2018, the Intergovernmental Panel on Climate Change (IPCC) presented a Special Report on "Global Warming of 1.5°C" reminding government authorities of the urgent need for swift action to reduce greenhouse gas emissions. At the current rate, global warming will reach +1.5°C between 2030 and 2052. France alone accounts for 10% of the world's reefs (58,000 km²) and is committed at national level to improving the conservation status of French coral reefs and ensuring their sustainable management through the French Coral Reef Initiative (IFRECOR). At international level, the French government is involved in the International Coral Reef Initiative (ICRI), promoting initiatives and projects to ensure coastal ecosystem protection. Following the signing of the Brussels Declaration "Climate Change and Ocean Preservation" (February 2019), France reiterated its international commitments on sustainable development, climate change and ocean biodiversity preservation.

New techniques and numerous resources have also been implemented to monitor global warming and its impact on coral reefs. For instance, the "Catlin Seaview Survey" expedition, launched in September 2012, monitors the status of coral reefs around the world.

This campaign preceded the production of the documentary "Chasing Corals" (Jeff Orlowski), chronicling the onset and development of the third coral bleaching episode in the various ocean basins, using powerful videos and images that raised awareness among the general public. The Scripps Research Institute in San Diego recently launched the "100 Island Challenge" project, aiming to map 100 coral reefs in order to better understand the impact of climate change and human stressors on this ecosystem. The researchers studied a dataset of thousands of images from the same reef area collected over 8 years. These photographs were assembled using software to create 3D photo mosaics and demonstrated the resilience of Palmyra reefs in the Pacific Ocean following the 2014-2016 bleaching episode. In the same vein, the research schooner Tara sailed more than 100,000 km between 2016 and 2018 as part of the Tara Pacific expedition (led by the CNRS and the Centre scientifique de Monaco – CSM). The aim was to carry out an unprecedented study of reef biodiversity and its "resistance, adaptation, and resilience" abilities in the face of anthropogenic stress factors, using state-of-the-art technology.

These projects also led to numerous conferences and outreach campaigns to inform local populations, and the general public about the challenges facing the oceans. For example, the non-governmental organization "Reef Check" trains volunteer scientific divers to conduct transects in order to monitor the health status of tropical reefs around the world, as well as those stretching along the west coast of California.

The efforts made by these various organizations and governments can lead to the implementation of local actions to reduce human impacts on reef ecosystems. For instance, Mumby & Harborne (2010) [30] proved the effectiveness of marine protected areas (MPAs) for reef resilience in the Caribbean. In 2014, New Caledonia announced the creation of the "Natural Park of the Coral Sea", one of the biggest MPAs in the world (1.3 million km²). According to the Protected Planet Report, 7% of the total ocean surface was classified as "protected" in 2018. MPAs are therefore invaluable refuges to mitigate the decline in biodiversity observed since the 1970s. A recent study also demonstrated the positive effect of the diversity of coral species (polyculture, such as those observed in a healthy reef or a MPA) on coral growth and survival compared with decreasing biodiversity, characterized by a reduction in the number of coral species (monoculture; as observed

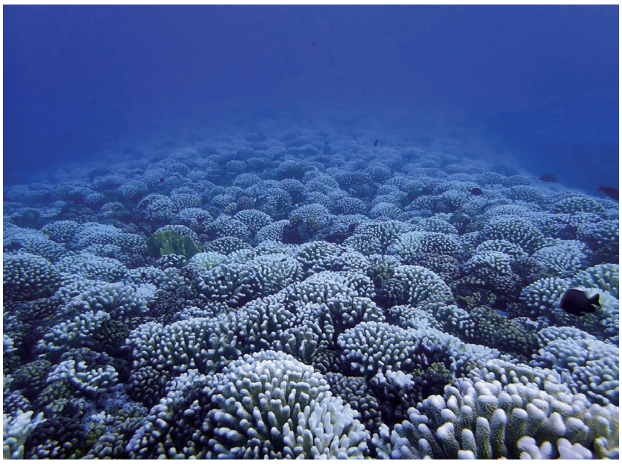

Fig.2 — Coral bleaching in April 2019 in Moorea, French Polynesia. © Kelly Speare, PhD student at the University of California, Santa Barbara.

in a damaged reef) [31]. Moreover, coral planting and reef restoration projects, such as those developed by the NGO "Coral Guardian", both stimulate marine life by promoting the recruitment of coral larvae and create new nurseries for marine organisms.

Biological engineering solutions have also been proposed, suggesting the use of "optimized" coral colonies under new environmental conditions to restore deteriorated reefs. Some scientists suggest using "assisted evolution" techniques to modify coral resilience threshold by performing laboratory artificial selection, which involves exposing coral to various stress factors or selecting thermo-tolerant symbiont stem cells [32].

However, these methods are still very expensive and would be difficult to implement on a large scale, given the enormous area occupied by coral reefs (the Great Barrier Reef alone extends over more than 2,300 km). Finally, at the end of March 2019, in Monaco hosted the first Steering Committee meeting of the World Coral Conservatory project, a program supported by the Prince Albert II of Monaco Foundation, and coordinated by the Centre scientifique de Monaco (CSM) and the Oceanographic Institute, Prince Albert I of Monaco Foundation. This initiative, bringing together research laboratories and public and private aquariums around the world, proposes creating a "Noah's Ark" of most coral species and strains – a way to preserve biodiversity within coral ecosystems by linking scientific research, conservation and awareness-raising.

Coral reefs are currently home to more than a third of the world's marine biodiversity and represent a protein source for more than 500 million people worldwide. According to Professor Terry Hughes, there is only one way to preserve marine life: "[We must] tackle the root cause of global heating by reducing net greenhouse gas emissions to zero as quickly as possible". Designing innovative projects that include scientific, political and social components will reduce our carbon footprint and ensure a future for our planet's ecosystems and for future generations.

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