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Climate Change and Coral Reefs. Impacts, Mitigation and Recovery Strategies

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Abstract

Coral reefs are facing an unprecedented threat caused by the increasingly intense effects of global climate change. This endangers their existence and, as a consequence of their weakening and decline, reduces the benefits of all the services they provide, including vital resources for marine biodiversity, protection of the coastal environments and direct sustenance for millions of people. Furthermore, studying the extent and direct effects of this threat is not always straightforward and predicting future consequences is an hard challenge, in addition to the fact that, due to the relatively recent nature of the research on this phenomenon, there is a lack of long-term available data. No less, numerous factors make this challenge difficult to overcome such as the social aspect involved and the complex and different conformations that these ecosystems take on in various parts of the world.

This report investigates the impacts of these stressors on coral ecosystems and their biological and ecological effects on the health and resilience, focusing on the most damaging events, such as coral bleaching, ocean acidification and rising of sea temperatures. It also explores various mitigation and recovery strategies, including coral restoration techniques, the establishment of marine protected areas and innovative and promising approaches such as assisted evolution, genetic engineering and coral gardening. It also highlights the importance of public awareness and empathy and local community engagement as well as more global or circumscribed initiatives.

In doing so, this study’s primary aim is to analyze practical strategies for the preservation and recovery of coral reefs and to highlight their importance across various areas, thanks to a detailed review of current scientific literature and case studies.

Introduction

What would our planet be like without large parts of essential ecosystems that have supported a vast range of life forms for millions of years and play a crucial role in maintaining global balance? Faced with this apparently dystopian question, one might think that the only way to find an answer is through an effort of imagination. The reality, however, is very different. In a few decades the solution to this interrogative could clearly appear before our eyes and have direct or indirect repercussions on our lives. Indeed, numerous important habitats are already being destroyed by anthropic activities, signaling a troubling trend that could soon make this catastrophic scenario a reality. This is the reason why the question I presented is not just an academic curiosity, but a real concern that threatens the balance of nature and, by extension, the existence of many living beings.

Among the others, significat ecosystems facing this problem are the ones composed at the base by corals. Coral reefs are indeed one of the richest in biodiversity and most productive ecosystems of our planet, properties that make them fundamental for the health of the oceans and the whole Earth. In addition to the aforementioned ones, these habitats used to have another feature that made them important for the balance of life: the stability. Indeed, in the last millions of years, coral reefs existed in a state of remarkable stability, largely due to the constant environmental conditions that prevailed in the oceans for geological periods and to the fact that environmental changes, when present, were most of the time slow, allowing the populations of coral polyps to adapt as every living community normally does. The temperature, salinity, and acidity levels of the oceans remained relatively constant in time, creating an ideal environment for these animals to thrive. This property made these complex structures a safe home for a huge number of other living beings, including other animals, plants and algae that rely on this ecosystem for shelter, social interaction, food and other resources. Furthermore, thanks to their characteristics they could ensure protection not only for underwater life, but also for the one on land, due to their action as natural barriers against waves and storms, reducing the impact of these forces on coastlines. This helps prevent coastal erosion, flooding, and habitat loss.

Nowadays, this stability is no longer guaranteed. The corals are very sensitive to different kinds of human disturbance and are currently threatened by overfishing and destructive fishing techniques, different kinds of pollution like nutrient, chemical and plastic pollution, habitat destruction, tourism, invasive species, etc. But in particular, the major threat they face is climate change. This phenomenon is indeed alone responsible for the main conditions that are killing corals and destroying reefs: coral bleaching, due to anomalously high temperature, and the difficulty of building and maintaining their calcium carbonate skeletons, due to acidification of the oceans.

But this trend can be reversed. The scientific community agrees on the fact that there are effective methods useful for significantly reducing carbon dioxide emissions and for restoring a large part of the damaged habitats as well as the fact that, it is important to underline, the sooner we take these measures, the easier and cheaper it will be to intervene and the more damage to the environments we avoid. This obviously also refers to specific habitats such as coral reefs.

This thesis aims to explore in depth the effects of global warming on corals and to examine the most promising methods and technologies available to mitigate these effects, with the aim of contributing to sustainable solutions for their protection, care, conservation and preservation. To do so it focuses on coral anatomy, physiology, ecology, and types of formations, highlighting their importance to ecosystems and human welfare, which underlines the value of preserving them. Subsequently, it delves into the central topic of anthropogenic risk factors and their effects on corals, particularly those related to climate warming, while also mentioning in a less detailed way other factors that can weaken coral structures. A critical chapter evaluates various methods for mitigating damage and recovering coral ecosystems, assessing their effectiveness through case studies, with a focus on strategies related to climate change. Additionally, general approaches to reduce CO_2 emissions are discussed as the most effective means of safeguarding coral reefs. Finally, conclusions are presented, including data analyses, challenges faced during the research, and potential applications.

This study also recognizes the limitations of the research scope. There are many factors that contribute to making it difficult to provide an exhaustive and conclusive investigation of every aspect involved. First of all, the complexity of the ecosystem and the wide range of species that compose it contribute to the elevated complexity found in studying the interactions within it and this difficulty grows even more if the interactions between living beings are abnormal and new due to climate change. Furthermore, different coral species and communities have different responses to changes (that can be both long-term trends and short-term events, which are complicated to distinguish) and this variability makes it difficult to generalize findings across different reef systems, especially since the composition of coral species can vary widely from one location to another. In addition, the effect of global warming on coral reefs is also modulated by local environmental conditions, such as water quality, depth and currents that are different depending on the geographical area. These factors, combined with the limited current documentation and the difficulty in research and monitoring in this regard, make the attempt to predict changes in these ecosystems an arduous challenge, which is already truly complex due to the numerous emerging factors. For these reasons it is also difficult to develop technologies and methods useful for their protection and restoration that are universally effective. Furthermore, there are also social, economic and practical factors that complicate the situation even more. Global warming is indeed a planetary scale problem that requires coordinated international efforts to reduce greenhouse gas emissions, a task that is complicated by varying national interests, economic dependencies and priorities, and political will. In this regard, many of the countries where coral reefs are located are developing ones, where economic resources and capacity for implementing environmental protections are limited. Additionally, the activities that contribute to reef degradation are often economically critical to local populations, making it difficult to impose and enforce restrictions without providing alternative livelihoods. Finally, some of the impacts of global warming on coral reefs are difficult, if not impossible, to reverse and in this case, it usually takes decades to return to the previous situation.

Despite what has been said so far, the aim of the thesis is to offer the most comprehensive and complete vision possible, integrating available data and emerging knowledge.

Exactly for the reasons listed above, it is essential to develop academic literature as quickly as possible regarding the limitations of the loss of this habitat and the prevention of the consequences that would arise from it. It should also be added that the world would lose part of its wonder necessary to develop in people the love for nature and the Earth, which is what shapes scientists and activists and pushes them to preserve such environments and living beings.

Discussion

1 Relevant physical and biological effects of global warming on oceans

According to the AR6 Synthesis Report of the Intergovernmental Panel on Climate Change, biologists, oceanographers and geologists agree that the oceans are changing at a rate never seen in 66 million years (IPCC, 2023) and that, during the time between the previous report in 2014 and the latest in 2023, it has been even faster than what was predicted in the AR5 (IPCC, H. Lee et al., 2023). This change is obviously mainly due to climate warming, which is modifying important parameters of the oceans such as ecology, physics, chemistry and geology (O. Hoegh-Guldberg et al., 2017).

As far as the physical ones are concerned, among the most evident are intensification of upwelling (O. Hoegh-Guldberg et al., 2014) and sea level rise (Church et al., 2013). Upwelling is a process in which deep water rises to the surface, moving organic substances along with it (Bakun et al., 1990). The normal patterns of this phenomenon are modified by the intensification of wind movements and increased water stratification caused by the average rise in temperatures, being especially evident along the coasts (D. Wang et al., 2015). The second phenomenon, sea level rising, instead depends more on the rate of ice melting. As the rate of ice melting increases, the average sea level follows a similar pattern and increases as well (A. Cazenave et al., 2014). However, the alterations most pertinent to coral ecosystems in terms of ocean physics and chemistry are acidification (Rhein et al., 2013), temperature increase (Rhein et al., 2013) and deoxygenation (Pörtner et al., 2014). Each of these phenomena warrants a more thorough elucidation to understand their specific impacts on coral health and resilience. Furthermore, these are not the sole physical and chemical phenomena induced by global warming that contribute to the decline of coral reefs. Changes in the frequency and intensity of tropical storms and cyclones, along with alterations in ocean circulation patterns, also play a significant role in undermining the resilience of these vital ecosystems. Rising temperatures can indeed lead to increased intensity, altered trajectories, modified speeds, and variations in frequency of tropical storms and cyclones that are able to damage corals (K. J. E. Walsh et al., 2019). In contrast, ocean circulation patterns are influenced by a multitude of factors. For instance, the Atlantic Meridional Overturning Circulation (AMOC) is primarily impacted by changes in temperature and salinity, essentially density alterations resulting from freshwater influx due to ice melting (G. Madan et al., 2024). Similarly, the frequency and intensity of El Niño and La Niña events may be exacerbated by rising sea temperatures (W. Cai et al., 2015). Other oceanic circulations, such as wind-driven and coastal currents, may also be modified due to shifting wind patterns (K. McMonigal et al., 2023) and rising sea levels (N. C. Jourdain et al., 2017).

In addition to these changes in the ocean, a broad and intricate array of ecological transformations contributes to the degradation and alteration of coral habitats, warranting comprehensive examination (E. L. Howes et al., 2015).

1.1 Ocean acidification

The oceans, in recent decades, have absorbed a quantity corresponding to approximately 25% of the atmospheric carbon dioxide of anthropogenic origin (T. DeVries et al., 2022). This, on one hand, helps to mitigate the effects of climate warming, but on the other contributes to the increase of water acidification. This phenomenon happens due to an important exchange of carbon dioxide between the atmosphere and the hydrosphere in which CO_2 is absorbed by the oceans in a manner directly proportional to its partial pressure in the air, which in this system increases particularly as the quantity increases (C. Sweeney et al., 2007). Once in the oceans, the dissolved CO_2 changes the chemistry of the water by reacting with the H_2O and forming carbonic acid ($CO_2 + H_2O = H_2CO_3$), a weak acid that in aqueous solution dissociates into bicarbonate ions (HCO_3^-) and hydronium ions (H^+). It is these latter ones that, by increasing in number, decrease the pH of the water and are therefore responsible for acidification (Caldeira and Wickett, 2003). Moreover, the excess of H^+ ions reacts with the carbonate ions (CO_3^{2-}), forming other bicarbonate ions which, in this way, cause the decrease not only of the concentration of CO_3^{2-} ions, but also the decrease of saturation of the level of calcium carbonate ($CaCO_3$) in water (fundamental molecules for life) while the number of bicarbonate ions obviously increases (Rhein et al., 2013). It has been demonstrated that the concentration of carbonate ions has decreased by 10% compared to pre-industrial levels, significantly modifying some processes fundamental to the biology of some living beings. (J. C. Orr, 2011).

Speaking of the surface waters of the epipelagic zone of the oceans, namely between 0 and 200 meters of depth (the ones most affected by this phenomenon and those where the majority of corals are located), their pH is on average basic, remaining mainly between the values of 7.8 and 8.4 as shown in the study by Feely et al. of 2009. In this same paper, it is also reported that since the industrial revolution the pH of the oceans has decreased overall by a value of 0.1, which corresponds to an increase in the concentration of hydrogen ions of 26%. This reduction can vary according to the regions and depends mainly on their buffer capacity, ranging from the largest in the

North Atlantic corresponding to 0.1, to the smallest in the subtropical South Pacific of 0.05 (Egleston et al., 2010).

1.2 Ocean warming

Water temperature is one of the most measured parameters in the oceans (Rhein et al., 2013) for this reason the data in this regard can be considered with greater confidence. The most affected waters are again the superficial ones (due mainly to the fact that the heat exchange between the two media occurs at their point of contact), which represent 64% of the total warming occurring in the ocean (Rhein et al., 2013) with an increase in average temperatures that can be seen across all the globe, but with regional differences (Levitus et al., 2012). In the Northern Hemisphere, for example, there is more pronounced warming and in particular it can be seen in the North Atlantic (Glecklet et al., 2012). Generally speaking, the oceans overall capture 93% of the heat generated by the greenhouse effect (L. Cheng et al., 2019), but, despite this, thanks to the large thermal capacity of water, they can store large quantities of thermal energy without increasing their temperature excessively (G. Boccaletti et al., 2004). Notwithstanding this, warming has been sufficiently high to cause numerous imbalances in the marine biosphere of different places in the world (Pörtner et al., 2014).

Focusing on more regional areas, between 1950 and 2009 the surface water temperatures of the Indian Ocean increased by 0.65ºC, those of the Atlantic Ocean by 0.41ºC (with peaks of 0.54ºC in the equatorial upwelling system) and those of the Pacific by 0.31ºC (with 0.43ºC in the equatorial upwelling system) (Hoegh-Guldberg et al., 2014). Measurements in narrow areas of coral interest show warming of 0.79ºC in the Coral Triangle and of 0.60ºC in the Western Indian Ocean over the same period, while between 1982 and 2006 the Gulf of Mexico warmed by 0.31ºC and the Caribbean Sea by 0.50ºC (Hoegh-Guldberg et al., 2014).

The warming of the ocean surface has initiated or accentuated mechanisms that can also represent examples of positive feedback and therefore accelerate the increase in temperatures, such as melting of ice, stratification of the waters and abnormal absorption and release of CO_2 into the atmosphere. The first is one of the most emblematic cases in this regard. Here is why: that of ice is one of the surfaces with the highest albedo present on the superficial layer of our planet, that means that it is able to reflect a large part of the solar radiation into space and to absorb a minimum percentage of it compared to darker surfaces, which, indeed, have a lower albedo. The rise in both atmospheric and marine temperatures causes the ice to melt faster than normal, thus leaving the surfaces of the soil and water uncovered by it, which absorb more, and thus reflect less, radiation. It is clear that this process causes a further acceleration of ocean warming, which in turn causes faster melting of ice, starting a self-reinforcing cycle (V. Ivanov et al., 2016). Stratification of ocean waters is instead a normal physical phenomenon that refers to the division into layers of the water column, mainly due to their differences in temperature, salinity and density (Sprintall et al., 1992). In recent times, these contrasts between the different layers are exacerbated by climate warming and this, as previously mentioned, initiates a positive feedback process (Ke-xin et al., 2022). This happens because, as the temperature of the surface waters increases, the density decreases and therefore the difference in this physical parameter between the layers increases. This causes less vertical mixing of the waters, further separating the warm surface ones from the cold deep ones, thus causing the upper waters to warm more rapidly, further exacerbating this process (Ke-xin et al., 2022). Furthermore, by slowing this mixing, surface-absorbed CO_2 is prevented from sinking and being stored as it normally would and instead remains at the surface, decreasing the rate at which carbon dioxide is captured by the ocean (T. Bourgeois et al., 2022). Finally, the solubility of CO_2 in water depends among other things on the temperature of the solvent, where the solubility decreases as the temperature increases. This causes not only a lower capacity to absorb carbon dioxide from the atmosphere, but also its faster release into the air, due to the greater kinetic energy of the H_2O molecules which decreases their ability to retain it. For this reason this phenomenon is another example of positive feedback (Bronselaer et al., 2020).

1.3 Ocean deoxygenation

In the 2014 study by Pörtner et al. different terms of oceanic water measurement are presented based on the quantity of dissolved oxygen, in particular there are the hypoxic waters between 60 μmol/kg and 45 μmol/kg, the subtoxic ones under 45 μmol/kg and finally the anoxic ones when the quantity of oxygen is so low that it cannot be measured. This parameter changes over time mainly depending on natural oscillations, but, nowadays, it is abnormally exacerbated by anthropogenic factors, which increase the rate of deoxygenation of the oceans (Rhein et al., 2013). As the name suggests, this refers to the reduction of dissolved oxygen in the marine environment (Keeling et al., 2010). Global warming can increase this phenomenon due to the same physical principles that cause the release of CO_2 into the atmosphere that have been previously explained and that do the same with O_2 molecules, namely the stratification that decreases the mixing of waters and the increase in the kinetic energy of water molecules (A. Oschlies et al., 2018). Furthermore, even in this case we can have examples of positive feedback, of which the most important is the greater production and therefore release into the atmosphere of nitrous dioxide (N_2O), a powerful greenhouse gas (A. Oschlies et al., 2018) that is produced by microorganisms which, with reduced quantities of oxygen, switch their metabolism and consequently increase N_2O secretion (F. Breider et al. 2019). To make matters worse, the deoxygenation of waters is accelerated by other factors of anthropogenic origin, in particular nutrient pollution which causes an increase in algal blooms, a process that consumes further dissolved oxygen (N. N. Rabalais et al. 2014).

It has been measured that 26 Tmol of oxygen per year were lost globally in surface waters (from 0 to 1000 meters) between 1958 and 2015 (Ito et al. 2017), but there are substantial differences if we look specifically at the different geographical regions. This can be particularly seen in coastal areas, especially North American and North European coasts, where increased stratification causes oxygen loss at a rate 10 times faster than in open oceans (Hoegh-Guldberg et al., 2014). More specifically, in the surface waters of the north-eastern Pacific Ocean, a loss of O_2 between 0.4 and 0.7 μmol/kg per year was documented between 1956 and 2006 (F. A. Whitney et al., 2007), quantities similar to those measured between 1955 and 2004 in the west Pacific Ocean, where there had been a loss of 0.45 μmol/kg per year in the Oyashio region (T. Nakanowatari et al., 2007). The equatorial area of this ocean is the place where the highest loss of oxygen has been recorded in the last 50 years, with a decrease in the overall percentage of about 22%, which corresponds to 210 ± 125 Tmol per decade (S. Schmidtko et al., 2017). The most affected regions of the Atlantic Ocean are those of the Caribbean Sea and the western subtropical part, where in the waters above 300 meters, decreases of respectively 0.58 μmol/kg and 0.68 μmol/kg per year were recorded in the period between 1980 and 2013, while the rest of this ocean doesn't appear to have experienced significant oxygen losses (E. Montes et al., 2016), with, instead, an increase in the Gulf of Mexico area (S. Schmidtko et al., 2017). As regards the Indian Ocean, there is little recorded data, but this shows a generic increase in the southern part and a decrease in the northern part (E. L. McDonagh et al., 2005), with a peak in the waters of the Red Sea and the ones of Kenya and Tanzania (S. Schmidtko et al., 2017). Finally, the third largest loss of oxygen in the last 10 years was recorded in the Southern Ocean, with a total of 152 ± 47 Tmol lost per decade, which are approximately 0.06 μmol/kg per year (S. Schmidtko et al., 2017). Curiously, although the equatorial part of the Pacific Ocean is the most affected by this phenomenon, the greatest increase in oxygen concentration was measured in the South China Sea, with an increase reaching up to 10% in the region between mainland Malaysia and the island of Borneo (S. Schmidtko et al., 2017).

1.4 Ocean ecology

There are many complex ecological changes affecting the well-being of coral reefs. The most impactful are those that directly affect the polyps and algae that compose them, putting the ecosystem at risk from the very base of its components and which are mainly caused by the events previously described, but there are phenomena that directly influence the life of other species that can affect these structures indirectly. The most important ones that are linked to climate warming are the increase in algal bloom, arrival of invasive species, greater effectiveness of pathogens and change in biology, distribution and behavior of communities (S. V. Smith and R. W. Buddemeier, 1992).

It has been recorded that algal blooms generally increase as the water temperature increases, with specific differences that depend on the various species that cause them. Ocean acidification, however, does not increase the intensity of the blooms, but increases the production of toxins produced by some species, thus making them more harmful than they would normally be (A. W. Griffith and C. J. Gobler 2020). This worsens a situation which is made serious by a phenomenon not necessarily linked to global warming and that represents the main cause of the intensification of algal blooms, i.e. eutrophication, which can be used as a rich source of useful nutrients by these living beings (P. M. Glibert and J. M. Burkholder 2018). Also regarding the spread of invasive species, global warming can play a key role. Indeed, with the change in water temperature, some species could migrate to areas where the heat is more suitable for them, which can be both warmer or colder, but that have not evolved the adaptations to live in harmony with them (A. Occhipinti-Ambrogi et al., 2007). These species can migrate without external help, but, especially the larvae and other juvenile forms, can also be transported by various factors, including some anthropogenic ones, such as ships or currents that might have changed because of climate change. (J. C. Geburzi et al., 2018).

As regards diseases, climate change can alter the relationship between host and pathogen, changing the biology of one of the two with the possibility of an increase in pathogenicity. Specifically, the change in temperature, the increase in CO_2 concentration, the decrease in pH, the change in salinity and the exposure to extreme climatic events are able on the one hand to weaken the host, change its habits and increase its susceptibility, on the other to increase the activity, infectivity and proliferation of the pathogen (C. A. Burge et al., 2014).

Finally, many effects of global warming can endanger the ecological balance present in coral reefs by altering various aspects of the life of species fundamental for the ecosystem. Indeed, these effects are able to modify important behaviors such as those linked to nutrition and reproduction, as well as distribution, average lifespan and its quality, reproductive success, general health, changes in biological cycles, etc. (IPCC, 2023). The imbalance can result from both an increase and a decrease in the quality of these, as the abnormal proliferation of some species can lead to a change in the trophic chain and it involves animals, plants, algae and microorganisms (K. J. Kroeker et al. 2020).

2 Brief biology and general importance of coral reefs

Understanding the biology and ecological importance of coral reefs is crucial for ensuring the health of marine ecosystems and the well-being of human communities worldwide. Coral reefs support immense biodiversity, providing habitats for countless marine species, including fish, crustaceans, mollusks and algae. With rising threats such as climate change, ocean acidification, and pollution placing immense pressure on these fragile systems, an in-depth understanding of reef biology is essential not only because it enables scientists to develop targeted conservation strategies, enhances public awareness and guides policy decisions that prioritize reef protection, but also because it helps in the understanding of the complex relationships and the life cycles of the species that depend on them. Additionally, coral reefs play essential roles in protecting coastlines from erosion, supporting fisheries that sustain food security and driving tourism in many tropical regions. Recognizing and valuing coral reefs' importance ultimately supports both ecological stability and economic resilience for future generations (Sheppard C. R. C. et al., 2018).

2.1 Distribution

Most coral reefs, due to their physiological functioning, are mainly limited to the shallow waters of the tropical zones of our planet, since their particular temperatures, salinity and substrates coincide with the needs of these biological structures. The total extension of these ecosystems is difficult to calculate, but the most recent measurements presented in the 2024 study by Lyons et al. estimate an extension of approximately 410,285 km^2 of reefs visible from space of which 348,361 km^2 are shallow ones (down to about 15 meters) for a total of 80,213 km^2 of coral habitat (more precisely it ranges from 46,237 to 106,319 km^2 with a 95% confidence interval). This last information indicates that only about a quarter of shallow reefs can support a significant amount of life. The majority of these extend in the Indo-Pacific region, mainly in South East Asia and Oceania with, specifically, a diffusion of approximately 14,173 km^2 in the coasts of Indonesia, 9,416 km^2 in the Australian ones, 7,741 km^2 in the Philippine ones, 3,533 km^2 in those of Papua New Guinea and 2,661 km^2 in those of Fiji. Other important regions are the central Indian Ocean, the Red Sea and the eastern coasts of Africa, where 2,257 km^2 are recorded in Saudi Arabia, 1,508 km^2 in Madagascar, 1,308 km^2 in the Maldives and 1,052 km^2 in Mozambique. Finally, another very significative area is that of the

Caribbean Sea, mainly represented by Cuba and the Bahamas, with an extension of these biomes of 3,536 km^2 and 1,504 km^2 respectively.

Coral reefs can also be found at latitudes greater than the tropics of Cancer and Capricorn, where warm currents arrive from more equatorial areas warming them, just as, if cold currents from temperate zones reach the tropics, decreases in the extension of the reefs can be found. For this reason, these manage to extend north up to Bemuda, the island of Okinawa in Japan and the northern part of the Red Sea, while to the south they exceed notably the Tropic of Capricorn arriving in Australia at Lord Howe Island in the eastern part and Houtman Abrolhos Islands in the western part and in South Africa (Sheppard C. R. C. et al., 2018).

2.2 Types and formation

Three main types of reefs are distinguished, namely fringing, barriers and atolls. The characteristics that distinguish these categories mainly depend on their development and evolution. Indeed, when a reef begins to grow it mainly starts from the edges of an island or land, initially creating a fringing one. With the rise in sea levels or the retreat of the shoreline, the reef separates from the mainland, but continues to grow, creating a barrier when, formally, there is a channel wide enough to allow navigation between the coast and the corals. Finally, when an island completely retreats, we can find the remaining ring of corals that had surrounded it in the past and in this case we define it as an atoll. This is the normal process of reef formation, but there are other cases in which particular forces, especially geological ones, change this trend. In the case in which the mainland pushes towards the sea, there is a continuous formation of fringing reefs and erosion of those exposed to the atmosphere, while in the case in which the sea level relative to that land remains constant for geological times we have the formation of the so-called "patch reefs", a definition also used for all formations that do not fall within the three main ones.

Another important classification is the one that distinguish the reef types based on where their surface faces. When this extends horizontally it is defined as "flat reef" with its exposed surface facing the superficial part of the water, while when it extends more vertically the correct definition is "reef slope" and usually it faces the open sea. The transition zone between these two is usually less extensive and is called "reef crest".

The resources on which the living beings of these ecosystems depend vary according to the different classifications, which is why the different types of reefs have a unique biodiversity (Sheppard C. R. C. et al., 2018).

2.3 Taxonomy and diffusion of reef composers

The main composers of the coral reefs are hard corals, soft corals and sponges with a ratio that vary depending on geographical location, geological characteristics, depth, water composition, and other chemical-physical factors.

As regards the members of the order of *cnidarians* (i.e. corals), there are three groups that are particularly important, the *hexacorals* (stony corals), the *octocorals* (soft corals and sea fans) and a minor group including the black corals and the sea whips. The polyps of the first ones, of which the members of the *scleractinia* order are abundantly present in all types of reefs and responsible for the production of calcium carbonate, always have a number of tentacles equal to six or a multiple thereof; the second ones, instead, always have eight tentacles and they shape is usually taller and more branched in the Caribbean Sea, whereas in Indo-Pacific the dominant forms are lobed, encrusting and less branched.

The two classes of sea sponges (members of the phylum *porifera*) important for these ecosystems are *calcarea* (calcareous sponges) and *demospongiae* (siliceous sponges), which are much more numerous in the Caribbean than in other regions, taking up more space than corals.

An important mention must be made of calcareous red algae, responsible for limestone constructions defined as high-magnesium calcite and that grow mainly in the crest reefs, as they are able to resist the powerful waves that hit this zone. The main genus responsible for these constructions vary depending on the geographical area, with *porolithon* responsible for growth in the Indian and Pacific oceans, while *litophyllum* is the one most present in the Atlantic (Sheppard C. R. C. et al., 2018).

2.4 Biology of reef composers

The single individual that makes up the coral is called "polyp", a 1-2 mm long living being composed of soft tissues constituting one or more rings of tentacles around the mouth that lead to the body cavity. The hard part, called corallite, that they create beneath them is made up of calcium carbonate (of which the principal crystalline form deposited in coral skeletons is the aragonite) and can grow upwards or outwards, so as to surround them. During the night, however, the living part usually comes out of this protection to feed, using particular stinging or hook-shaped cells, the nematocysts, to capture zooplankton.

Their reproduction can be asexual or sexual. In the first case, important examples of cloning are the budding, in which a single individual can divide giving life to two individuals, and the fragmentation, which involves pieces of different sizes broken off due to external events (both of them have a role in the formation of some specific colonies). In the second case, fertilization occurs thanks to the coordinated release into the water of the gametes of either both sexes, in a phenomenon called "broadcast spawn", or only the male ones that will meet the others inside the female's body, in the so-called "brooding". These types of reproduction create planulae larvae that remain in the water for a variable period, usually some days or weeks in the broadcast spawn, whereas in the brooding only few seconds, after which they settle and become true polyps. Among the sexual species, we find a quarter that are hermaphrodites, while the others have distinct sexes with the possibility of changing it with advancing age.

These characteristics are also valid for soft corals, with the only difference that, not having external hard protection, they rely on a skeleton of organic matrix that embeds some spicules made of aggregation of calcite.

The sizes and shapes of sea sponges, instead, vary greatly between the various species, but common characteristics include a unicellular layer called "pinacoderm" that embeds an organic matrix, also known as mesohyl. This part is composed of a skeleton that can be both organic, composed of spongin fibers, and inorganic, composed of mineral spicules, and can contain different types of cells that perform various metabolic functions (such as phagocytosis and contractions for movement), as well as symbiotic bacteria and cyanobacteria. Their reproduction methods are predominantly the same as the ones previously described in corals.

One of the most characteristic features of this phylum is the aquifer system that allows them to feed by filtering small particles present in the water. It is composed of pores into which the fluid enters (ostia), from where it subsequently reaches one or more chambers through various channels and finally it exits from other larger but less numerous pores (oscula). This path is accomplished thanks to special cells, the choanocytes, which, through the movements of their flagellum, create special flows of water. Water filtration is one of the reasons why these animals are important for the coral ecosystem, as well as for the process of bioerosion, sediment consolidation and for providing shelter and food to other living beings (Sheppard C. R. C. et al., 2018).

2.5 Algal symbiosis

The vast majority of corals, the so-called "hermatypic", performs an endosymbiosis with dinoflagellate algae and depends on their photosynthetic activity (the others are the ahermatypics and thanks to their independence from this process they can grow in places where the sun is absent or less intense, such as the poles and vertical slopes). These algae are the zooxanthellae belonging to the genus *symbiodinium*, unicellular organisms contained in the endodermis cells and bound by one or more membranes of animal origin that form a vacuolar compartment known as the "symbiosome".

The symbiosis between them is mutualistic and the advantages are numerous for both parties. The most important one for corals is the possibility of obtaining photosynthetically-fixed carbon organic compounds, better known by the name of "photosynthates" produced by algae both for their own metabolism and for their symbionts. These compounds are fundamental in the calcification of corals and therefore in the formation of their external skeleton, but they also act as nutrients which are in some cases indispensable. This fact is evident especially when we refer to sugars (such as glucose and glycerol) and amino acids, converted from nitrates only by zooxanthellae and then shared with corals, as these ones are not capable of producing them. Other important benefits for corals are the production of oxygen during the photosynthesis of algae, useful for their respiration, and the removal of wastes, such as carbon dioxide and nitrogen compounds. These chemicals are used by zooxanthellae as nutrients for growth and photosynthesis, from which therefore derives this first benefit from the symbiosis with corals, which also offers them shelter and protection, as well as a large and stable support surface (Sheppard C. R. C. et al., 2018).

2.6 Importance of corals for ecosystems and humans

The biodiversity of coral reefs is one of the highest among the various biomes. Indeed, they support an enormous number of living beings which are not only limited to fish and other vertebrates, but also numerous invertebrates. This is immediately noticeable from the fact that, despite making up 1% of the oceans, they are home to 25% of all marine species (Coker et al., 2014) with an estimation of approximately 1 to 9 million species that inhabit both the reefs and surrounding areas (Reaka-Kudla, 1997), many of which have yet to be discovered. The benefits offered to them include shelter, protection, food, breeding ground, symbiosis, social environment and intraspecies opportunities without which they could not live (Allgeier J. E. et al., 2024). Among these species there are also keystone ones which in turn are fundamental for the ecosystem itself, generating a virtuous circle (Cole A. J. Et al., 2008). This characteristic is also reflected in their high commercial value in the fishing industry, which many communities (particularly present in developing nations) rely on not only as a source of income, but also as a primary food stock. (Moberg F. et al., 1999). To give an idea, with more than half of all U.S. fishery species relying on coral reefs for part of their life cycles, the commercial value of fisheries of this country connected to coral reefs exceeds $100 million (Why are corals important?, NOAA National Ocean Service Education et al., 2024).

Another service offered by these structures is the protection of the coasts from storms, tsunamis and wave erosion (managing to reduce wave energy by up to 97%) (Moberg F. el al., 1999). This protection is obviously important in tropical regions with constant incidence of these atmospheric phenomena, such as the Caribbean and South East Asia. Without this natural service, these areas would be forced to invest large amounts of money in artificial protection (Moberg F. el al., 1999).

Another added economic value is that derived from tourism, which thanks to their geographical position, once again brings significant amounts of money to developing countries (Moberg F. el al., 1999). Furthermore, the sequestration of carbon for the formation of their skeleton helps to mitigate climate warming, also avoiding part of the expense necessary to limit or remedy its damage (Shi T. et al. 2021).

Coral reefs also offer remarkable opportunities for scientific research and education. Thanks to these we can indeed increase our understanding of broad spectrums of disciplines such as biology, ecology and geology (Brander L. M. et al., 2007); they can be used as indicators of ongoing climate change (Brander L. M. et al., 2007) and we can even obtain useful information for biomedical research (Bruckner A. W., 2002).

Finally, the cultural and social importance of these ecosystems should also be mentioned. Many coastal communities, especially indigenous peoples, attach spiritual importance to them and all their history is closely linked to coral reefs, not only their current life (Foale S. et al., 2024).

3 Effects of global warming on coral reefs and other risk factors.

It has been seen that no area where coral reefs are present has not been affected by anthropogenic factors and that 41% of these ecosystems have suffered strong repercussions of human origins (Halpern B. S. et al., 2008). Predicting their future condition due to ongoing changes is quite difficult, but most projections agree that these ecosystems are extremely at risk. For instance, Beyer and colleagues in their 2018 study estimate that 70% to 90% of global corals may disappear by mid-century even if the Paris Agreement's emission reduction goals are met; while Wilkinson's team in the study published in 2006 verified that currently 20% of coral reefs have been lost, 24% are at immediate risk of collapse and 26% suffer potentially irreparable damage.

Among the main risks, as has been stated global warming is the most impactful, but there are several others of human origin that contribute to their deterioration, such as pollution, overfishing, habitat loss and invasive alien species. These local factors, despite what was said previously, can have a very strong impact in some geographical areas, such as the Indonesian coral ecosystems present near Jakarta, which have undergone a variation attributable to approximately 80% of local factors (Baum et al., 2015). However, changes in the ecology of these ecosystems, whether due to global or local factors, can harm coral reefs despite not being their direct victims, due to the feedback loops that are initiated as a result (Sheppard C. R. C. et al., 2018).

3.1 Effects of global warming

Global warming, as we have seen, causes various effects on the ocean water and in turn, these have repercussions, often negative, on the biology of corals. These consequences vary not only depending on the effect that causes them, but also on the specific organism that is affected.

3.1.1 Effects of ocean warming

The rise in sea temperatures is one of the main causes of the decline of coral reefs, being the main factor responsible for the bleaching phenomenon (Sheppard C. R. C. et al., 2018). This event is easily visible when a coral colony loses its colors and becomes mostly white, due to the expulsion of the zooxanthellae responsible for photosynthesis and therefore the nutrition of the corals. The corals that show bleaching phenotype are not necessarily dead, in fact it happens that after the expulsion of these symbionts there is a recovery and others return to benefit from the mutualism (National Academies of Sciences et al., 2019). Despite this, it is important to know that large bleaching events are significantly harmful to the ecosystem and difficult to be reversed, with a great deal of time and energy required when possible. (Thomas et al., 2018).

The mechanism at the cellular level that causes this is mostly unknown, but some changes in genes associated with mechanisms responsible for the apoptosis have been seen during it, a factor that could indicate a link (Weis, 2008). In any case, the rise in temperatures is capable of compromising the photosynthesis mechanisms of symbiotic algae, especially the disruption of the electron transport chain delivering the energy of captured photons to carbon-fixing centers in the chloroplast (Weis, 2008), leading also to overproduction of oxygen radicals that damage their hosts and themselves (Riegl et al. 2009).

This process occurs at different thresholds depending in particular on the species of coral and zooxanthellae, but in some cases they can be dissimilar even between different colonies containing the same species (Ainsworth et al., 2016), variation that depends mostly on their genetic differences and their state of acclimatization (Douglas A. E., 2003). However, the events in which bleachings were recorded in the greatest number are the individual extreme ones in which the increase in heat exceeds local summer maximum temperatures by 1 or 2 degrees Celsius, rising in intensity also depending on the duration of the phenomenon (McFarland, 2021). For this reason, time and heat rise are calculated together in an important parameter called Degree Heating Week [ºC-weeks] which shows the accumulated thermal stress that exceeds the bleaching threshold over the previous 12 weeks. In this sense it has been shown that during single events of heat waves an increase between 0 and 3 ºC-weeks causes almost no loss of coral cover because of the bleaching, at 4 ºC-weeks it rises to a loss of 40%, while at 8 ºC-weeks 66% of coverage is lost and finally extreme declines of more than 80% are linked to exposures of 9 °C-weeks or more (Hughes et al., 2018). Moreover, coral reefs that have suffered heavy events of this type have also experienced a reduction in assemblage structure and functional diversity due to the mortality that follows the event, affecting more than 60% of the colonies (Hughes et al., 2018).

Bleachings are mostly local, but there is a history of events of this type on a global scale that have been intensifying in recent times. To be declared as such they must affect 100 square kilometers in the three oceans (Braverman, 2018). The first occurred between 1981 and 1982, followed by the one in 1997-1998 which killed 16% of global corals, "El Niño" then caused the one in 2010 and finally, the longest, between 2014 and 2017, which affected 93% of the Great Barrier Reef (Braverman, 2018).

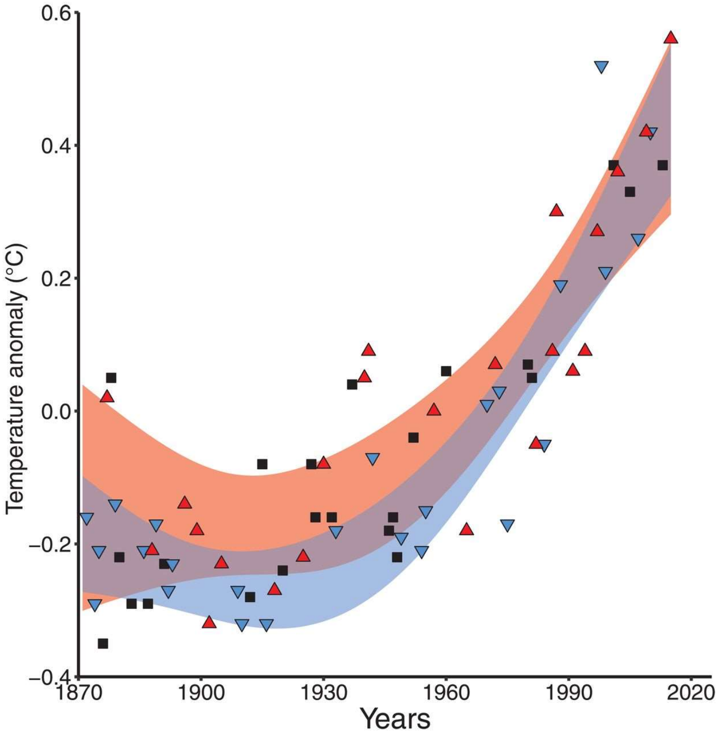

Figure 1. Sea surface temperature anomalies from 1871 to 2016, containing coral reefs between latitudes of 31°N and 31°S. Data points differentiate El Niño (red triangles), La Niña (blue triangles), and ENSO neutral periods (black squares). (Hughes et al. 2018)

The majority of these events occur normally at mid-latitudes (between 15º and 20º north and south), more than at the equatorial ones (despite the equivalent thermal stress in both sites), probably due to lower biodiversity that generally increases the genetic resilience (Sully S. et al., 2019). As regards the future, the predictions made in the 2014 study by van Hooidonk et al. say that there will be severe annual bleachings from 2030, while global ones will start from 2055.

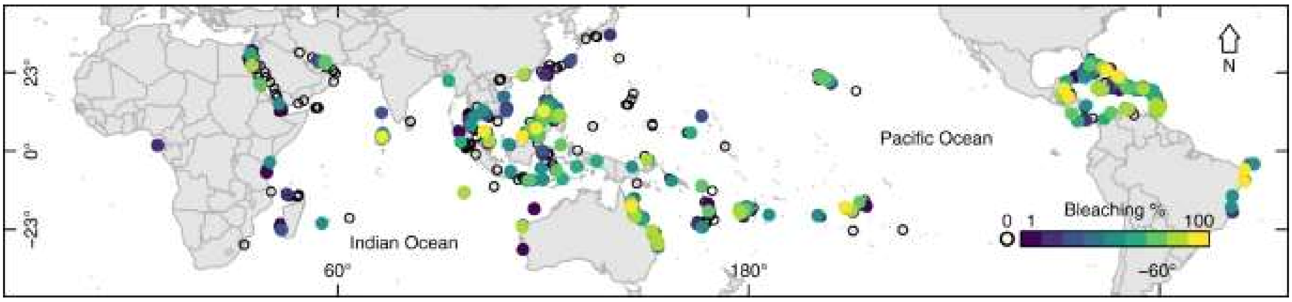

Figure 2. Coral bleaching distribution presented as a percentage of the coral assemblage that bleached at survey, measured at 3351 sites in 81 countries, from 1998 to 2017 (Sully, S. et al. 2019).

In addition, another major phenomenon that contributes to bleaching is exposure to solar radiation, acting both when sea temperatures are elevated and alone at a normal heat level (Brown B. E. et al., 2015).

The rise in temperatures also causes a change in the growth of corals, starting from the larval forms, which grow more allometrically in warmer environments, thus changing their body proportions (Edmunds, 2008). Curiously, a study has shown that in *Porites lutea*, rising temperatures by one degree centigrade increased the skeletal density by 10.5% and the calcification rate by 4.5%, counteracting the effects of the decrease in the pH iin case they have not been bleached (Bessat and Buiges, 2001).

3.1.2 Effects of ocean acidification

Another consequence of the climate change that has a great impact on the coral ecosystem is ocean acidification. The increase in the concentration of carbon dioxide in the water and the consequent decrease in its pH also cause the decrease in the presence of carbonate ions (Caldeira and Wickett, 2003) and, in particular, in the saturation state of aragonite in seawater (Ωa) (Raven et al., 2005). This phenomenon has reached such levels that it has lowered the Ωa by half a unit compared to pre-industrial levels (Cao and Caldeira, 2008), reaching a value of 3.3, capable of not only slowing down growth, but also of extinguish it in certain situations (Hoegh-Guldberg et al., 2007). The reduction in the rate of this physiological phenomenon happens because of the resulting absence of the components necessary for the calcification (which reaches a decrease of 15%-22% per unit decrease in the Ωa) that can cause also their skeleton to become more fragile, even causing in some cases their complete dissolution (Tambutte et al., 2015), as well as a decrease in their general extension rate (Albright et al., 2018). Most studies agree that over the next 30-50 years the level of calcification will decrease by an average of 30%, with estimates varying greatly in ranges (Sheppard C. R. C. et al., 2018), while a recent study has already shown its decline of 14.2% since 1990 in the Great Barrier Reef (Albright et al., 2016), which agrees with the calculations of the average global coral growth reduction corresponding to 15% (Eakin C. M. et al., 2008).

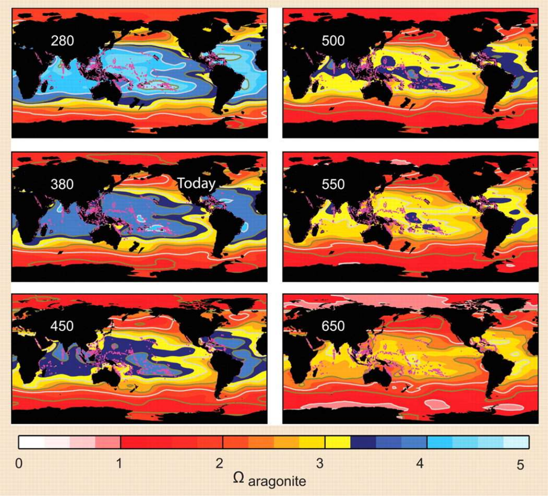

Figure 3. Changes in aragonite saturation predicted to occur as atmospheric CO_2 concentrations (ppm) increase (number at top left of each panel) plotted over shallow-water coral reef locations shown as pink dots (280 ppm indicates the level before the Industrial Revolution) (Hoegh-Guldberg et al., 2007).

Other consequences of ocean acidification for coral reefs include reduced fertilization and recruitment (Albright and Langdon, 2011) and dissolution of the symbiotic zooxanthellae necessary for the normal continuance of coral life (Earle S. A. 2009), therefore contributing to increasing the phenomenon of bleaching (Anthony et al. 2008). In eight weeks of exposure to high concentrations of CO_2, corals of the *acropora* genus lost their algal cover by 50%, while those of the *porites* genus (more resistant to sea acidification) lost 20% of it (Anthony et al. 2008).

Different consequences of these phenomena have been observed and they vary greatly depending on the species affected. The first and most direct consequence is a reduction in both extension rate and skeletal density, of which we have significant evidence in the 16-year study published in 2008 by T. F. Cooper and colleagues, which shows a total reduction of 20.6% in growth rate (the product of linear extension rate and skeletal density) during this period in *porites* corals. This genus is also important in understanding how these phenomena vary depending on the physiological capacities of the various organisms. It has indeed been observed that species of this taxonomic group are the predominant ones around the vents of the seas of Mexico and Papua New Guinea, where therefore the concentrations of CO_2 are naturally high (Fabricius et al., 2011). Indeed, they can resist to them thanks to some adaptations that make them suitable in conditions of reduced calcification (Crook et al., 2013) and that in turn allow them to be able to spread more efficiently also when acidification increases due to anthropogenic causes, as seen in Nikko Bay in Palau. This can be due either to their ability to maintain the pH of the water present at the calcification site at higher levels (McCulloch et al., 2012) or to the ability to absorb enough nutrients to allow them to build their skeletons correctly despite varying environmental conditions (Drenkard et al., 2013). These phenomena were also proven by laboratory experiments done by Shamberger's team in the 2014 study.

Another consequence is the reduction of the skeletal density of corals, while maintaining growth and extension at a normal level. This obviously causes a weakening that is manifested in a higher level of erosion and a more likely breakage, events caused by storms, coral-eating animals such as parrotfish, currents and waves. Furthermore, this causes a decreased capacity to absorb the energy of the waves, also endangering the coastal ecosystem (Hoegh-Guldberg et al., 2007). Finally, there is the case in which both processes are maintained at a normal level by increasing the energy spent on calcification, but at the expense of other physiological processes, in particular reproduction, which could ultimately reduce the larval output (Hoegh-Guldberg et al., 2007).

3.1.3 Global warming related diseases

Several studies demonstrate an increase in the outbreak of coral diseases due to climate warming (Carpenter et al., 2008), especially in the Caribbean, where there has been a decrease in the abundance and diversity of these animals that is unprecedented in geological times. (Weil, 2004). This happens because the threshold relating to their thermal tolerance is exceeded, weakening them and making them more susceptible to infections (Harvell et al., 2002), in addition to the greater proliferation of pathogens that resist higher temperatures better (Randall and van Woesik, 2015). Furthermore, other factors such as nutrient pollution and coastal sediment deposition are associated with an increase in infections, both by compromising the health of the animals (Vega Thurber et al., 2014).

Obviously these events are localized in individual places, depending on which the consequences change significantly. For example, in the Caribbean the most affected groups of living beings are *scleractinian* corals, gorgonians, sea urchins, reef fish, sponges, algae, and other coral reef organisms with symptoms such as tissue-loss and bleachings, changes in reproduction and growth, species diversity, abundance, and size structure (Williams and Bunkley-Williams 2000). The most susceptible genera appear to be *acropora*, *pocillopora*, and *porites* (Riegl et al. 2009).

Globally, between 1972 and 2005, cases of coral diseases were reported on 39 coral genera and 148 species in 63 different countries (Riegl et al. 2009), of which only 14% were from the Indo-Pacific (Sutherland et al., 2004) and the most affected region was the Caribbean. The cases of epizootics in this area began in 1978 mainly affecting *Acropora palmata* and *Acropora cervicornis*, subsequently since 1998 over 30 diseases have been reported affecting 45 species of scleractinian corals, 3 hydrozoans, 10 octocorals, 2 zoanthids, 9 sponges and 2 crustose coral algae (Weil et al. 2006). Among these ones, common documented diseases are dark-spot disease (DSD), yellow-band disease (YBD), white pox disease (WPX), and aspergillosis (ASP) that together with the white plague type II (WP-II) are causing substantial coral mortality (Riegl et al. 2009). Infection has been reported in at least 82% of coral species in the Atlantic Ocean (Goldberg J. and Wilkinson C. 2004), with some susceptible to up to 8 diseases and colonies infected with two or three diseases at the same time (Weil, 2004). In the Indo-Pacific, the same diseases in addition to tumors have been reported in the past (Antonius, 1985) but recently many new ones were identified such as white syndrome, yellow band, skeletal eroding band and Porites ulcerative white spots (Riegl and Antonius 2003).

Diseases affecting other taxonomic groups can also be harmful to corals if the reduction or weakening of their members causes serious ecological consequences. An example is the case that occurred between 1982 and 1984, in which the decimation of a population of *Diadema antillarum* (an herbivorous sea urchin, keystone species for the ecosystem), caused by a disease, triggered increases in fleshy macroalgae and concurrent losses of coral cover, biodiversity and habitat (Aronson and Precht 2001).

3.1.4 Other minor effects of global warming

The rise in sea levels is impactful for the growth of coral reefs, especially those in which it is linked to land submersion, such as atolls (Sheppard C. R. C. et al., 2018). On the ones present in south-east Asia and northern Australia it is particularly significant, where the aforementioned two phenomena add up to reach a relative increase in sea level of 1cm per year (O. Hoegh-Guldberg et al., 2017). This type of coral reefs undergo an alteration in growth due to the changed speed of progression of water inland (Sheppard C. R. C. et al., 2018) which is worsened by abnormal climatic events such as intense cyclones and hurricanes that increase the level of coastal erosion (O. Hoegh-Guldberg et al., 2017). These events do not only cause the rise of the relative level of the sea, but they also cause immediate damage to coral ecosystems when they directly impact the reefs, similarly to what increased energy of storms does. These formations have evolved in environments where such phenomena are common, but the associated abnormalities make them more impactful and long-lasting, creating conditions that are not usually experienced and cause fatal fragmentation. The kinds of coral reefs most affected by cyclones and hurricanes are the superficial branched ones present in the Indian Ocean and the northern and southwestern Pacific Ocean (Sheppard C. R. C. et al., 2018). Examples of these cases that have severely damaged coral ecosystems are those of Cyclone Yasi in February 2011 that hit Australia and Hurricane Dorian in August 2019 that hit the Bahamas (McFarland, 2021). Normally they manage to recover quickly and they would be able to do so even with these abnormal events, but this weakening in combination with the other threats obviously worsens the general situation and can contribute to their mortality (Sheppard C. R. C. et al., 2018).

Regarding water deoxygenation, little is known about its effect on corals and their ways of recovering from this, especially given the fact that these events last only a short period of time and doing research on them is difficult (Johnson M. D. et al., 2021). However, it has been documented that in some reefs acute events of this kind are associated with decimations of their living beings occurred in a few days with consequences proportional to the duration and intensity of the event (Lucey N. M. et al., 2020). Significant is the 2010 episode in Bocas del Toro in Panama, in which the creation of hypoxic conditions caused a mass die-off that killed almost all corals between 10 and 15m (Altieri A. H. et al. , 2017). This happened as a consequence of bleaching and tissue loss, which are the most associated events linked to hypoxic waters that cause their death (Johnson M. D. et al., 2021). Although these events cannot be predicted, it is thought that today 10% of global coral reefs are at risk of hypoxia (Altieri A. H. et al., 2017).

3.2 Other effects not linked to global warming

Effects not directly associated with global warming are important to be understood as they can increase the effects of climate change and worsen the overall situation of coral reefs. Furthermore, in many cases distinguishing the primary cause is not easy and although they apparently do not seem to be linked to global warming, there may be links to this which can only be understood after careful analysis.

In this sense, an emblematic case is that of invasive species. Most of the ones present in the marine environment are transported through commercial ships' ballast waters, but small boat operators, fishermen, divers, pet owners, aquarium owners, travelers and seafood lovers can also contribute (Helvarg D. 2010). During the twentieth century numerous lionfish were released into the southern Floridian waters and managed to proliferate in the Caribbean thanks to the absence of predators causing ecological imbalance due to their nature of voracious predators of juvenile reef fish (Roberts C., 2012). This region isn't the only place affected by invasive species, as evidenced by the 23% of species present at Pearl Harbor in Hawaii which are believed to be potentially non-native in origin (National Academies of Sciences et al., 2019). These may belong to several taxonomic groups, with invasive seaweed recorded in Florida (Lapointe and Bedford, 2010), Hawaii (Martinez et al., 2012) and the Caribbean (Scheibling et al., 2018). Also species of corals or their symbiotic algae that are transported to places where they are not native can become harmful, such as the case of *tubastrea* in the Atlantic (Luz and Kitahara, 2017) and the symbiont *Durusdinium trenchii* in the Caribbean (Pettay et al., 2015). On some islands in the Indian Ocean it has recently been shown that land-based invaders can also damage coral reefs. The rat infestation of these places results in a number of impacts on surrounding coral reefs, including fewer nutrients and fewer fish feeding on algae (Graham et al., 2018). Global warming can be linked to this phenomenon, as it is able to contribute to the arrival and proliferation of these species by creating environmental conditions more suitable for their lifestyle and by weakening their prey or competitors, as it is happening in temperate marine ecosystems due to their tropicalization (Vergés A. et al. 2014).

Another phenomenon that is one of the most harmful ones for coral reefs is that of eutrophication, as it increases the proliferation of fleshy algae. These algae, then compete with corals for space and other resources such as light for the execution of photosynthesis (Sheppard C. R. C. et al., 2018). Furthermore, eutrophication leads to an increase in phosphate ions which causes the reduction of the level of calcification by inhibiting the formation or deposition of aragonite (Muller-Parker and D'Elia, 1997) and additionally it can increase the outbreak of corallivore predators such as the crown-of-thorns starfish (Brodie et al., 2005). Moreover, the health of corals is influenced by other substances that change the quality of water as the latter is significant for their growth, survival, reproduction and recruitment and being these ones susceptible to turbidity, sediments, nutrients, and toxic pollutants present in the water (Duprey et al., 2016). Specifically, sediments cause suffocation, reduced fertilization and juvenile survival of corals and they also inhibite photosynthesis of zooxanthellae (National Academies of Sciences et al., 2019).

In general, other pollutants harmful to these ecosystems include metals, organic compounds, oil and other chemicals such as sunscreen. These primarily affect coral reefs near megacities and areas of coastal resource use which include in particular farming, manufacturing facilities and tourism (McFarland, 2021). The toxic effect of metals differs depending on the compound of origin and mainly affects nerves (i.e. mercury) and the reproductive system (i.e. copper), in addition to the fact that they are among the compounds with the highest capacity to be bioaccumulated and therefore to spread in the food chain (Sheppard C. R. C. et al., 2018). Organic pollutants are more difficult to study and vary greatly in their effects depending on the nature of their compounds. In any case, the most impactful appear to be the herbicides that derive from agricultural processes through rivers and which affect zooxanthellae (Sheppard C. R. C. et al., 2018). As for oil, when it simply floats above the reefs it causes limited damage, whereas when it sinks above them (usually in areas of chronic poisoning by this substance) it causes fatal anoxia, condition associated with reduced reproductive potential and planulae settlement rates (Loya and Rinkevich, 1980). These harmful effects increase with the interaction with other chemicals.

Another serious problem for these ecosystems is habitat loss. Among the most harmful activities in this sense are landfill, dredging and conversion to dry land to build touristic, domestic and industrial structures that cause their burial. The most striking cases in this regard are those of Palm Island and World Island in Dubai which have obviously impacted not only the coral reefs but all the other forms of life present there (Vaughan and Burt 2016). Obviously these effects are increased by the growth of the human population living near the coasts, as it is happening in the underdeveloped countries of Southeast Asia and in tropical islands. In Malé for example, the capital of the Maldives, a portion of the southern coral reef was used in the 80s of the last century to create services needed due to the increase in population that was taking place (Sheppard C. R. C. et al., 2018).

Fishing also constitutes a significant problem for coral reefs, ecosystems that guarantee subsistence for 6.3 million people (Teh L. S. L. et al., 2013). About their slots it has been documented that 90% are fully exploited, overexploited or depleted (FAO, 2018). Here it is important to make a distinction between illegal and legal fishing and the methods that are used. Usually the majority of overexploitation occurs through non-normalized fishing using longlines, seine purses, blast fishing and trawlings, in which the latter two can directly damage corals, while the former damage them indirectly compromising their ecology (Deacon R. T and Parker D. P. 2009). This happens especially when it concerns grazers resulting in a growth in the population of algae that can come to overwhelm corals and potentially to prevent settlement of coral larvae, as is evident in the Caribbean (Avery H., 2018).

Tourism and naval traffic should also be mentioned as harmful agents, being able to weaken these ecosystems both through the release of the pollutants and invasive species mentioned above, and through direct contact and disturbance with the coral environment during activities such as diving, anchoring, mining, dredging, port construction and through shipwrecks (Sheppard C. R. C. et al., 2018).

4 Mitigation and Recovery Strategies

Despite the alarming decline of coral reefs and their associated ecosystems, there are many methods of mitigating this process. Since at the forefront of this crisis there is climate change, widely recognized as the primary driver of coral degradation, the most effective strategies for combating this loss must center around the comprehensive reduction of greenhouse gas emissions (IPCC, 2023). Due to the intricate nature of these issues, a more extensive examination would be required; nonetheless, it is essential to outline the consensus among the scientific community regarding the most promising solutions.

Firstly, a significant proportion of global emissions is attributable to energy production (United Nations Environment Programme, 2023), making it imperative to address this sector in any climate change mitigation strategy. Transitioning to renewable energy sources capable of producing few or no emissions, such as solar, wind, hydro, and geothermal energy, coupled with advancements in energy storage technologies, represents one of the most effective pathways to significantly diminish emissions (United Nations Environment Programme, 2023). However, the emphasis on renewable technologies is not without its challenges. While they offer a crucial means of mitigating climate change, they can inadvertently generate other social and environmental issues, including social inequalities and waste management concerns, often more pronounced than those associated with fossil fuel sources (Volodzkiene L. and Streimikiene D., 2023). In addition, enhancing the efficiency of energy production and spread is a critical aspect of this discourse. Strategies such as optimizing energy distribution and transportation, implementing energy-efficient systems, and refining industrial production processes to minimize energy consumption are vital steps toward achieving a sustainable balance (Liu D., 2023). These dual approaches, renewable energy adoption and increased efficiency, are essential in forging a path toward the reduction of greenhouse gases.

The transport sector plays a pivotal role in exacerbating environmental challenges too, with effective solutions lying in the transition to electric and alternative energy vehicles, enhancing infrastructure for pedestrians and cyclists and expanding public transportation networks (Marzouk O. A., 2023).

Regarding the food sector, widely considered as one of the most significant contributors to greenhouse gas emissions, the adoption of regenerative agriculture and improved livestock management and nutrition practices stands to substantially reduce direct emissions. Furthermore, any approach that mitigates deforestation is critical, as forests serve as vital carbon reservoirs and their destruction releases enormous quantities of stored carbon into the atmosphere (Brennan R. A. et al., 2020). Advocating for reduced meat and dairy consumption is essential, given that extensive deforestation often occurs to create arable land for livestock feed. Overall, fostering a lifestyle that prioritizes low environmental impact, through waste reduction and energy conservation, is vital (Brennan R. A. et al., 2020).

There are also innovative techniques capable of directly addressing carbon dioxide emissions by capturing them during production processes or extracting them from the atmosphere. These methods include Direct Air Capture (DAC), Bioenergy with Carbon Capture and Storage (BECCS), and traditional Carbon Capture and Storage (CCS) systems (United Nations Environment Programme, 2023). Additionally, cost-effective strategies such as recycling, reusing materials, extending the lifespan of products, and converting waste into energy epitomize the principles of the circular economy, thereby minimizing overall environmental impact (Brennan R. A. et al., 2020). Further financial mechanisms, including Carbon Pricing and market-based approaches like Carbon taxes and Cap-and-Trade programs, can incentivize industries to lower their environmental footprints. Lastly, Carbon Offsetting encourages investments in initiatives that actively reduce emissions (United Nations Environment Programme, 2023).

In parallel to these overarching strategies, it is crucial to implement targeted methods for the direct protection of coral ecosystems. Such initiatives can effectively mitigate the adverse effects of climate change and enhance the health and resilience of these vital marine environments (National Academies of Sciences et al., 2019).

4.1 Genetic intervention methods

There are countless methods that act directly on the genetics of corals and associated organisms. Genetics is important to take into consideration since the response to environmental stimuli of these living beings directly depends on the genes (National Academies of Sciences et al., 2019).

Most of these technologies involve cultivating selected or genetically modified coral propagules, which are then introduced into marine environments through techniques like larval seeding or outplanting (coral gardening). Propagules used in these restoration efforts are generated by methods including colony fragmentation, polyp excision, brooded planula larvae collection upon release, and gamete collection from spawning coral species (Harrison, 2011). Fragmentation and excision yield genetically identical clones of the parent colony, while sexually produced planula larvae provide genetic diversity, enabling selection and hybridization for desirable traits (Richmond et al., 2018).

4.1.1 Managed selection

A first approach is that of managed selection. This method consists in the recognition of organisms more suited to new environmental stress conditions and their subsequent use in various interventions such as genetic manipulation, managed breeding, managed relocation and symbiont and microbiome isolation and manipulation. The physiological responses that can be subject to these methods are the ones related to increasing or decreasing of temperature, salinity, sedimentation and light and toxicant exposure (Rose et al., 2018). For example, regarding temperature bearing (one of the most concerned parameters) the differences can be seen by comparing the communities of similar or the same species of Palau capable of living optimally only between 26°C and 30°C (Golbuu et al., 2007) and those of Okinawa, adapted to annual fluctuations between 15°C and 30°C (Nadaoka et al., 2001). The extreme is reached in the Persian/Arabian Gulf, where the corals survive temperatures up to 36°C (Hume et al., 2013). An important community for this method is present in Nikko Bay (Palau) that presents a combination of genes capable of coping with multiple stressors, managing to survive in conditions of temperature (32°C) and acidity (7.9 pH) predicted to be common in coral reefs in 2050 (Camp et al., 2018). Suitable individuals can be either naturally selected by massive bleaching events (that leaves survived corals and the ones that recover in a short amount of time) or can be individuated through molecular techniques before events of this type (National Academies of Sciences et al., 2019). In general, examples of optimal sites for the collection of these individuals include shallow back reef pools, reef flats and patch reefs that heat up during daytime low tides; while geographically the most suitable are found in lower latitude locations along latitudinally lengthy reefs such as the Great Barrier Reef and in equatorial locations with high summer temperatures (National Academies of Sciences et al., 2019). Omic technologies associated with the identification of suitable corals are improving rapidly over time making this method feasible especially when combined with the study of phenotypes in individuals that have been gardened in the laboratory or in the field (Devlin-Durante and Baums, 2017).

Tradeoffs associated with increasing a population's fitness relative to one external stressor may result in a reduction of another. The most famous example is the one that increases the heat tolerance by decreasing the growth speed, qualities conferred by the symbiont genus *Durusdinium*, while the heat-sensitive symbiont genus *Cladocopium* confers a faster growth (Stat and Gates, 2011).

Many of the studies of the process have been done in laboratory, with few results related to its effectiveness in the wild. Despite this, it is known that the scale and limits of use depend primarily on the quantity of suitable colonies found and subsequently on the results of the studies and the consequences of the techniques carried out on them (National Academies of Sciences et al., 2019).

4.1.2 Managed breeding

Regardless of managed selection, conservation methods that concern the genetics of individuals usually involve an active manipulation of genes. For example managed breeding, in which individuals are interbred in such a way as to have offspring with a genome more suited to new environmental conditions and can be done either within individuals of the same species (usually of different populations) or between the ones of different species. Thanks to this method, objectives such as increasing coral cover while preserving local genetics diversity can be achieved by introducing individuals with novel genotypes and higher fitness (National Academies of Sciences et al., 2019).

Specifically, the technique called “supportive breeding within populations” aims to increase population size and genetic diversity, thus improving long-term persistence. It is also effective in maintaining genes in a population that may otherwise lose them following mass die-off events (Schopmeyer et al., 2012). The beneficial outcomes depend on the degree of domestication selection in captivity (Baskett and Waples, 2013); in the Caribbean, for example, it has been associated with significant potential to address problems with low recruitment (Kuffner and Toth, 2016).

"Outcrossing between populations" instead aims to increase fitness and population size by introducing external genetic variation from other communities and it can also be used to increase coral cover (Whiteley et al., 2015). This approach results in the recovery of small and fragmented populations and as consequence it can be used in the ones with limited ability to adapt to an environment that is changing, thanks to the persistent gene flow that increases the effective population size (National Academies of Sciences et al., 2019). However, there are few examples of studies regarding the effectiveness of this technique (Whiteley et al., 2015); although it can be understood in part from studies of natural self-fertilization and inbreeding in corals population, in which inbreeding depression has not been documented (Baums et al., 2010). Despite this, the benefits that can derive from it are practically untested in corals (National Academies of Sciences et al., 2019).

The “hybridization across species” creates new genotypes that can be used in coral reef recovery by increasing coral cover while reducing impacts on local species diversity. In this case infertile hybrids are preferred; while if the goal is to increase coverage and the long term fitness of a community, instead, fertile hybrids may be the most adequate (National Academies of Sciences et al., 2019). Hybridization is usually avoided in conservation strategies, but recently the opinion regarding the fact that it can be effectively used to address problems related to environmental changes in coral ecosystems is growing (Hamilton and Miller, 2016).

To be able to implement the techniques described above, the first fundamental step is to identify the right individuals and this depends on location and local reef restoration goals, as well as on the method intended to be used (National Academies of Sciences et al., 2019). When breeding is done between different populations, the best species for propagation are those that reproduce easily and have a good success rate when reintroduced to their natural environment. Successful outcrossing depends on understanding how well the offspring will perform in the new environment. Additionally, species that can interbreed and produce viable offspring are essential for creating hybrids (National Academies of Sciences et al., 2019).

The effectiveness of these breeding methods also differs depending on which one is implemented. Sexual reproduction carried out in the laboratory, useful for the first technique described, has proven successful in many cases, such as in species like *Acropora tenuis* (dela Cruz and Harrison, 2017), *A. valid* (Villanueva et al., 2012), *A. millepora* (Guest et al., 2014) and *A. digitifera* (Edwards et al., 2015). The resulting release, although studies relating to those carried out on healthy ecosystems have revealed little success (Edwards et al., 2015), is usually effective in ecosystems in precarious health conditions, as highlighted in the 2017 dela Cruz and Harrison study carried out in the northwest of Philippines, where after 3 years from the larval seeding increased coral cover was found. There are however few investigations regarding the fitness of within-species hybrid, but Dixon et al. (2015) demonstrated a rapid response to heat selection within the population created by the introduction of genetic variation into a cold thermal tolerant population of *A. millepora* following crosses with a warm tolerant one that makes the outcrosses between populations promising. Finally, hybridization between different species has not been sufficiently studied, but evidence of its role in coral evolution suggests that it may be an effective way of coral restoration (Arrigoni et al., 2016). This opinion is accentuated by hybrids that are nowadays proliferating naturally following changes in the environment, as happened among Caribbean corals *A. cervicornis* and *A. palmata*, indeed their decline is accompanied by the increase in number of their hybrids *A. prolifera* (Fogarty, 2012). The capacities of producing viable hybrids in artificial settings are different depending on the genera. While experimental crossing of *montipora* and *platygyra* showed success (Willis et al., 1997), hybrids between species within *ctenactis* genus were not viable (Baird et al., 2013). Numerous a*cropora* species have restricted prezygotic and postzygotic isolating mechanisms (Isomura et al., 2016), making them suitable candidates for these studies. A problem linked to this technique is the possible mixing with one or both parent species as it is likely to be possible in *A. prolifera* (Vollmer and Palumbi, 2007), which may result in a change in the desired genome of the individuals of the population. Yet, most of the studies carried out in these cases are aimed at analyzing the fitness of the first generation grown in the laboratory, but to truly understand the effectiveness, more studies are needed regarding the overall state of health after several years and genetic mixing. However, it is agreed that long-term fitness benefits and persistence of populations are dependent on connectivity (National Academies of Sciences et al., 2019).

Depending on the situation, these techniques may lead also to a decrease in fitness (outbreeding depression, figure 4). There are two ways in which it usually occurs: breakdown of co-adapted gene complexes and loss of local adaptation (Templeton, 1986). Individuals produced by hybridization or outcrossing in the former case only receive half of the allelic combinations seen in either parent population and might not be adapted to one or both of the parental environments. In the latter, the result between the combination of loci that are inherited may lead to a breakdown of interactions and influence another fitness trait (National Academies of Sciences et al., 2019). A decline in fitness may become apparent as early as the initial generation of hybridization, however, it could also be delayed until recombination occurs in later hybrid or backcross generations (National Academies of Sciences et al., 2019).

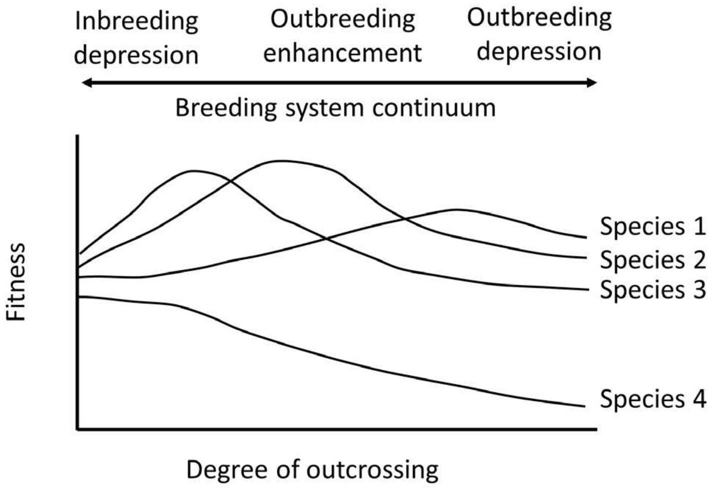

Figure 4. Breeding system continuum describing theoretical fitness outcomes of outcrossing. (Allendorf and Waples, 1996; Edmands, 2007).

Managed breeding infrastructure is essential for selecting and cultivating wild coral propagules, which includes collection vessels, transport facilities, resources for outplanting or larval release and captive breeding and culture facilities. This is generally limited to locations with marine laboratories or private coral husbandry operations. Larval rearing methods using in situ pools and settlement substrates to enhance larval settlement are being developed by organizations such as SECORE (Margaret Miller, presentation to committee, 2018).

4.1.3 Genetic Manipulation

Genetic manipulation is used to modify the genome of various species, which in this case can directly be corals, zooxanthellae or their associated microbiome. Thanks to this technique, the insertion of gene drives can be carried out, which creates a system of inheritance by enhancing passage of a selected genotype to offspring that might be able to increase the levels of stress resilience (National Academies of Sciences et al., 2019). An additional goal can be related to genetic studies that test the susceptibility of corals and algae to stress factors and the identification of the genes responsible for variation in stress tolerance. Anyway, specifically, the most significant intervention for symbiotic algae is the modification of the genes responsible for the reaction with oxygen or those that trigger thermal stress, aiming at the introduction of genetically modified individuals into wild populations, achieving a reduction in bleaching events (National Academies of Sciences et al., 2019).

In practice, the techniques used are genome editing through zinc finger nucleases, transcription activator-like effector nucleases and CRISPR/Cas9 gene editing which are able to remove, add or modify existing genes (Gaj et al., 2013). CRISPR/Cas9 is so far the only method utilized for direct genome editing in corals. This system comprises two essential components: a short noncoding guide RNA (gRNA) and the Cas9 protein, in which the former matches the sequence of the target genomic site, guiding the gRNA/Cas9 protein complex to this precise location. Once there, the Cas9 protein induces a targeted DNA break, enabling insertions or deletions as the cell's repair mechanisms work to mend the break (Li et al., 2013). The process develops in this way: individual colonies or cultures are used for the first tests of genetically altered corals or symbionts, after that, in case of successful completion of a modification, each one would be evaluated separately for resilience gains. Subsequently, it is expected that the alteration would be spread by sexual reproduction or clonal development into a coral population that will be placed into a nursery population. Larger groups can be produced once the spread genetic change is examined for high stress tolerance. Only one altered gene would be affected by these modifications though. If it was determined that more than one gene needed to be modified, and heat tolerance tests indicate that numerous loci are implicated, several alterations may need to be made in succession. Alternatively, the different alterations would have to be merged in a single zygote through rounds of sexual reproduction if carried out in separate lines (National Academies of Sciences et al., 2019).

Actually, there is a single study on this technique in corals (Cleves et al., 2018), providing initial proof-of-concept data using *Acropora millepora* as a model species. In this study, the authors targeted genes encoding fibroblast growth factor 1a, green fluorescent protein, and red fluorescent protein. Fertilized eggs were injected with specific single guide RNA (sgRNA)/Cas9 complexes, resulting in partial deletion mutations in 50% of the larvae. All larvae with successful edits exhibited heterozygous deletion mutations, consisting of a mix of wild-type and various mutated alleles. While generating homozygous mutants through genetic crosses remains challenging, introducing beneficial alleles in heterozygous individuals has the potential to enhance coral resilience when released into wild populations. The study by Levin et al. of 2017 highlights the effectiveness of this technique also on symbiotic algae, suggesting that genetic manipulation offers a promising approach for climate change mitigation. Bleaching susceptibility can be reduced by acting on genes directly responsible for regulating the heat stress response. Finally, CRISPR/Cas9 can also be used in modifying the genome of the microbiome associated with corals, but due to their low efficiency on the repair pathway this method can be fatal for them. Despite this, lately researchers have been working to develop bacteriophage-derived recombination proteins, making this option promising (National Academies of Sciences et al., 2019).

Given the small number of studies in this regard, the ability of this technique of increasing coral resilience has not been documented, but it probably depends on the feasibility of identification of specific gene targets capable of influencing coral tolerance through modifications of one or multiple genes within the same or interconnected pathways. Numerous gene expression changes associated with coral acclimation and adaptation to elevated temperatures have been already documented (Barshis et al., 2013). Additionally, a substantial number of transcription factor modifications have been observed shortly after heat exposure, suggesting potential widespread downstream effects on coral stress response (Traylor-Knowles et al., 2017). However, differences in resilience-related genes across coral populations indicate that heat resistance is likely a multilocus trait governed by dozens or even hundreds of genes (Dixon et al., 2015). Consequently, single target genes with substantial impacts on temperature tolerance have not been identified. Regarding coral dinoflagellate symbionts manipulation, instead, it seems less feasible to be done. Indeed, although genetic transformation of Symbiodinium cells was reported by Ten Lohuis and Miller (1998), this outcome has not been successfully replicated in subsequent attempts (Levin et al., 2017).

Moreover, since each stage of the amplification process takes three to seven years, especially if coral growth and sexual reproduction are involved, the deployment of multigene adaptive manipulations is consequently slowed and the number of modifications that could be rapidly deployed are therefore reduced. For these reasons, this method results as unsuitable in immediate risk situations and is generally less effective in the short-term. However, the amount of time is shortened when asexual proliferation of genetically modified robust corals is used (National Academies of Sciences et al., 2019).

Despite what has been said, there is ongoing debate on the use of gene drives in field settings, because of the risks associated. The introduction of genetically modified organisms may indeed spread undesired features throughout natural populations, raising ethical questions and potentially having an harmful ecological impact (Pugh, 2016). A priori prediction of unintended outcomes is nearly impossible. According to Kuzma and Rawls (2016), the gene drive may unintentionally affect other traits like resistance to viruses or other stressors or the capacity to spread them. Furthermore, resistance that blocks cutting by the CRISPR nuclease can develop as a result from mutations (Noble et al., 2018) and may jeopardize the effectiveness of this method.

4.2 Cryopreservation

There has been much effort in cryopreservation regarding coral conservation. In this process gametes, embryos or other living materials are frozen for later use after thawing as live organisms (Viyakarn et al., 2018). Normally the most used are embryos (Hagedorn et al., 2012), but adult tissues (Feuillassier et al., 2014) and symbiotic algae (Hagedorn et al., 2015) can also be utilized. In the case of sperm and algal symbionts, successful results have been documented in at least 16 coral species (Hagedorn et al., 2017), as well as in embryonic cells (Hagedorn et al., 2012). As regards the larvae (Hagedorn et al., 2006) and the fragments deriving from adults (Feuillassier et al., 2014), only preliminary attempts have been made, without successful outcomes.

Usually this method is used to increase genetic variation in species that may later potentially become critically endangered (Howard et al., 2016), but it can also be used for assisted gene flow, for research purposes and for conserving them for fertilization between species that are distant from each other or that spawn at different times (Hagedorn et al., 2017).

The primary challenge in cryopreservation lies in preventing cellular damage due to ice crystal formation during freezing. To prevent them, cryoprotective agents such as dimethyl sulfoxide and propylene glycol are introduced during the cooling phase. Optimizing this process necessitates empirical evaluation of cooling rates, which may range from slow to ultrafast, alongside controlled thawing rates and precise adjustment of cryoprotectant type and concentration (Viyakarn et al., 2018). A case in which these techniques were successful is that of the study by Hagedorn et al. (2017) in which it was documented that sperm frozen for up to 2 years was as viable as sperm frozen for less than 1 month (although in general fertilization success decreases by about 50% and very long-term tests of storage efficacy have not been done), with the further advantage of being able to easily transport it wherever it is needed.

4.3 Pre-exposure

The term "pre-exposure" is in this case used to indicate the controlled exposure of corals and their symbionts to conditions that might confer some degree of additional tolerance to subsequent re-exposure of the organism or its progeny to the same or similar conditions. A single shock exposure or gradual increases over time may be part of the first exposure, which may be acute or chronic and may involve several stressors. In this way the organism adapts to situations that could be either acute or chronic thanks to the triggered reaction (National Academies of Sciences et al., 2019). This is possible thanks to their normal physiological responses, that allow them to adapt to stress conditions that normally occur in nature. The degree to which these responses prepare the organism for subsequent exposure can be measured by the length of time the response is maintained once the initial exposure ends (National Academies of Sciences et al., 2019).

There is ample evidence that pre-exposure has a positive impact on reef corals, also in the cases in which the underlying mechanism is unknown. It is well documented that corals in lagoons and on reef flats frequently endure high temperatures and high light stress (as well as occasionally high or low salinities and aerial exposure), although it can be challenging to distinguish the relative contributions of local selection versus pre-exposure. Anyway, this results in individuals that are tolerant to thermal bleaching events (Palumbi et al., 2014). Pre-exposure of coral reefs to high irradiance may also help to reduce these episodes thanks to the synthesis of photoprotective fluorescent proteins, which can lessen oxidative stress on corals (Salih et al., 2006).

The effectiveness of this method depends on the mechanisms involved. Among these there are four main types that can be distinguished: acclimatory changes in gene expression, adaptive changes in gene expression, epigenetic modification and changes in holobiont composition. Changes in gene expression adjust how certain genes are expressed and can be either temporary and easily reversible in case they don’t change the gene composition (acclimatation, it operates at the single individual level) or long-lasting and irreversible in case they do it (adaptation). Epigenetic modifications instead, involve chemical changes that affect gene expression without changing the genome which can be either temporary or long-lasting and heritable to the following generations. Finally, changes in holobiont composition involve simply shifts in the microbial species composition that live symbiotically with the host, influencing its health, metabolism, and overall fitness (National Academies of Sciences et al., 2019).

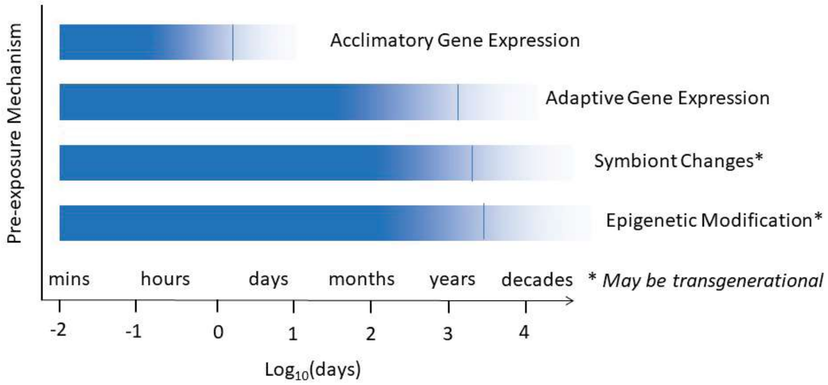

Figure 5. Conceptual representation of variation in the typical longevity of different response mechanisms induced following pre-exposure to stressful conditions. Typical longevity is represented by the vertical blue line within each horizontal bar (National Academies of Sciences et al., 2019)

Despite the mechanisms used, there are three processes for pre-exposure in corals. The first is the acute one that involves short exposure to the stress condition of larvae, recruit or adult in a specific time like gametogenesis or larval development in order to elicit a long-lasting response. The second is the chronic one in which exposure for months or years to particular set of conditions of typically adults are able to trigger long-lasting resilience effects. The third strategy is the identification of corals suitable for restoration by assuming that the natural environmental variety that they have already experienced in the wild produces individuals that have already benefited from a long time of pre-exposure (National Academies of Sciences et al., 2019).

Acute exposure experiments in laboratory environments are technically achievable at reduced scales, but informed considerations regarding life stages, exposure duration, and the level of stress imposed are needed. Establishing coral nurseries in naturally stressed ecosystems is also relatively straightforward, primarily involving the selection of suitable nursery sites. Conversely, the identification of corals that have been naturally "pre-exposed" to stress is more complex, as it demands a comprehensive understanding of coral distribution and environmental variability; however, this process remains entirely feasible (National Academies of Sciences et al., 2019).

Acute pre-exposure methods are relatively practicable regarding tests and implementations on an individual level, however, scaling these methods presents challenges. This is particularly relevant for adult colonies, as each individual must be carefully managed and monitored. This problem can be reduced by conducting pre-exposure in batches and in gravid corals, since the colony could yield hundreds or thousands of pre-conditioned gametes or larvae. Similarly, scaling pre-exposure at the larval or recruit stage is feasible, but generally only if there is an existing infrastructure for active larval rearing and seeding programs. Likewise, strategies that exploit existing environmental conditions to naturally pre-conditioned colonies can be highly scalable (National Academies of Sciences et al., 2019).

The primary risk associated with pre-exposure is that the stressors may weaken, rather than strengthen, the organism, but the release of unsuitable living beings is simple to avoid if the procedure is properly controlled (National Academies of Sciences et al., 2019).

4.4 Artificial cooling

There are two main methods for artificial cooling of coral reef environments able to reduce bleaching, namely shading and mixing with cool water. The first one aims at decreasing the exposure to solar radiation directed to these habitats so that light incidence and water temperatures can be reduced. There are two possible engineered solutions for shading which involve directly the atmosphere and the water column above the reef. In the first case, the method can induce cloud formation and brightening; while in the second increased turbidity and shading layers are considered the most efficient ones. In both cases it is necessary to control the propagation, so as to avoid spreading them outside the area of interest (National Academies of Sciences et al., 2019).

Methods for artificial atmospheric shading include specifically injecting natural aerosols and reflective particles into the various altitude of the atmosphere that encourage clouds and solar reflection, cooling the surface (Latham et al., 2012). Targeted sky brightening may cool specific reef areas, even in regions without abundant clouds, through direct particles termed "marine sky brightenings" for reef protection (Ahlm et al., 2017). Regarding water cooling, induced turbidity caused by suspended particles might lower the light that arrives to coral organisms, but subsequently the energy available decreases and sedimentation increases causing stress (Le Grand and Fabricius, 2011). However, low to moderate levels may reduce coral bleaching risks and provide alternative nutrient sources, aiding the general resilience (Anthony et al. 2009). It has been proven that shading layers, like fixed shade cloths and reflective surface films, are able to decrease light exposure. The former have shown effectiveness in reducing bleaching in certain coral species on the Great Barrier Reef (Coelho et al., 2017), while reflective polymer films, made mainly of calcium carbonate, can reduce sunlight penetration by up to 30% (Rau et al., 2012).

To be suitable for deployment at both regional and local levels, atmospheric techniques still require additional technical improvement (Latham et al., 2012), while on the other hand, it is currently technically possible incorporate increased turbidity and shade layers on a smaller scale (less than one kilometer) (National Academies of Sciences et al., 2019). Though their theoretical efficacy can be deduced, their practicality as solutions has not been tested. However, it is recognized that the marine water cooling methods' primary benefit is their immediate application in regions experiencing extreme heat stress (Frieler et al., 2013). Nevertheless, certain methods might have a too high cost-benefit ratio to be applied to entire reefs or regions and, due to the dissipation, they may also be limited in spatial and temporal scale. Inversely, there are few restrictions on scaling up atmospheric shading to local and regional geographic areas (National Academies of Sciences et al., 2019). In any case, the implementation of these techniques requires a large expenditure of resources and infrastructure, during both implementation and monitoring. (National Academies of Sciences et al., 2019).

As previously stated, thermal stress on coral reefs can be reduced also by replacing warm, surface waters with cooler, deeper waters, consequently reducing bleaching events by offering, like shading techniques, temporary relief focused on high-stress periods. Active cooling methods include using mechanical pumps or utilizing natural temperature and salinity differentials between these two types of waters to create artificial upwelling that brings cool water to shallow, thermally stressed areas (Pan et al., 2016). Although technically feasible, large-scale testing of artificial upwelling for coral bleaching mitigation is still limited. Currently, projects like Reef Havens, which has recently installed underwater fans on the Great Barrier Reef, cover only small areas (a few hectares). While larger systems could theoretically be installed where deep, cooler water is accessible, scaling up remains limited depending on infrastructures and resources. (National Academies of Sciences et al., 2019).

All these techniques have the disadvantage of potentially negatively acclimatizing coral reefs, making organisms less capable of coping with extreme heat events, resulting in greater susceptibility to bleaching (National Academies of Sciences et al., 2019).

4.5 Other methods

Gamete and larval capture and seeding is a particular method of enhancing corals' natural sexual reproductive processes, which uses natural spawning events to provide gametes for later usage or larvae for settlement and lab growth. Since the timing of these episodes is highly predictable, the collection is facilitated and can be done both in situ and in laboratory using containers or nets with fine mesh (e.g., 10 µm) (dela Cruz and Harrison, 2017). The advantages of this procedure include increasing the effectiveness of other techniques previously described when they are combined together (in particular with genetic manipulation techniques), but even alone it is able to increase the degree of fertilization of a population, increasing its size (Williams et al., 2008).

Similarly, other coral restoration methods such as coral gardening and fragmentation can be used independently of genetic manipulation and management techniques to increase the number of individuals in the population. In this case, the most used technique is the so-called "direct transplantation" of coral fragments from one population to another used mainly where construction and other human activities destroy coral reefs or are expected to do so. This method is reported to have a survival rate of 64% of transplanted corals. In general, it has been documented that coral restoration methods involve the creation of artificial reefs in 21% of cases, which are substrates deliberately placed on the seabed for the attachment and growth of corals, useful to mimic characteristics of a natural reef or to increase potential habitat (Boström-Einarsson L. et al., 2020).

Anyway, when managing a coral reef community, there are other possible subjects besides corals. Since the resilience and health of the latter are directly impacted by the diversity and health of other members of the community, other individuals and species may also be the focus of managed relocation (Ladd et al., 2018). In particular, this includes algal competition reduction by controlling herbivorous species such as particular fish and sea urchins, management of fish and invertebrate predation of corals and fish nutrient cycling (Shaver et al., 2018).

Although not directly linked with global warming, the establishment of marine protected areas that include coral reefs is one of the major ways to protect them from human damages. In these areas, it is also important to limit fishing, given that it is often what causes ecological upheavals. There are indeed examples of strategies implemented with more comprehensive attention than simply directly protecting corals that have been effective, with positive effects also in adjacent areas. Since only 6% of coral reefs are effectively protected, the need to increase the number of protected areas is evident, since 21% of these ecosystems are ineffectively protected and 73% do not fall within protected areas (Sheppard C. R. C. et al., 2018). Roberts et al. in this regard stated in a 2006 study that between 20% and 40% of coral reefs must be protected to allow the general conservation of coral ecosystems.

In general, improving the management of fishing in coral reefs with ecological consideration leads to an improvement in the conditions of these habitats (Fenner D., 2012), considering the numerous damages caused by this practice that are illustrated previously. Similarly, the management and reduction of pollutants such as metals, plastics and nitrogenous compounds can be beneficial by decreasing their harmful effects on these living beings (Dubinsky and Stambler 1996).

Finally, education and public awareness are a keypoint of this field, as they are in every conservation program (Morar and Peterlicean 2012). Indeed, they not only convey the scientific significance of protecting coral reefs, but also the appropriate ways in which organizations, governments, and private citizens can accomplish this. They also help people develop empathy for these ecosystems, which makes them more likely to support conservation initiatives and promote sustainable practices. This emotional connection, combined with a clear understanding of the economic advantages, which highlights these actions as a long-term investment, can significantly amplify the impact of conservation education (Ahmed M. et al., 2007).

Conclusions

Climate change poses the most significant threat to coral reefs as the extensive losses they have experienced are primarily attributable to two critical effects that derive from this phenomenon: the increasing sea temperatures lead to coral bleaching, while ocean acidification undermines coral calcification. Heavy bleaching events can cause death, reducing coral assemblage structures and functional diversity and affecting more than 60% of coral colonies; whereas the impairment of calcification directly affects coral growth and skeletal density, with a reduction of extension and hardness corresponding on average to 15%. It is also essential to recognize other significant challenges that coral ecosystems are facing due to climate change, such as sea-level rise, increasingly intense cyclones and new diseases. Furthermore, other anthropogenic factors such as eutrophication, overfishing, invasive species, pollution and habitat loss merit attention since they can exacerbate the adverse impacts of global warming on coral reefs, as they weaken these vital ecosystems further or hinder their recovery.

To effectively address these worrying crises, the most effective solutions must act directly on the comprehensive reductions in greenhouse gas emissions. However, along with these general measures, several innovative interventions specifically targeting coral resilience show promise. Among these, managed breeding, although currently limited in empirical studies, offers great theoretical potential by enhancing genetic diversity and increasing coral adaptability. Similarly, managed selection, which involves interbreeding of coral individuals in order to create resilient strains, has yielded promising data supporting its viability, demonstrating success on certain species in precarious ecosystems. Moreover, pre-exposure techniques, which demonstrated increased tolerance to thermal bleaching and oxidative stress conditions, shape corals to better withstand stressors, representing a cost-effective and straightforward approach that could strengthen coral resilience in a changing climate.

While techniques such as genetic engineering hold the promise of enhanced resilience and adaptability for corals, their complexity, long implementation timescales, and potential unforeseen consequences limit their immediate applicability in light of the urgency posed by climate change. Similarly, cryopreservation methods do not directly address the critical environmental conditions necessary for coral health and survival; while, on the other hand, artificial cooling is not currently feasible given the high cost-benefit ratio, the difficult applicability and the numerous disadvantages.

Furthermore, it is important to consider general ways to decrease coral mortality despite not addressing the effects of global warming (such as coral restoration techniques and the establishment of marine protected areas) and the importance of education and public awareness.

In summary, while the immediate responses to mitigate the effects of global warming on coral reefs must focus on reducing emissions and enhancing resilience through practical interventions like managed breeding, managed selection and pre-exposure strategies, it is vital to simultaneously face the myriad of local and global stressors that could hinder recovery and adaptation. Conservation efforts must be multi-faceted, incorporating, alongside these innovative techniques, public education and the various methods that increase the welfare of corals, even the ones not linked to global warming, in order to ensure the long-term viability of coral ecosystems in a rapidly changing climate.

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