Assessing the impact of temperature on coral bleaching in reef systems

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Abstract

Coral reefs are critical ecosystems that support high biodiversity and provide numerous benefits to both humans and marine ecosystems. However, global climate change, driven by increasing greenhouse gas emissions, poses a significant threat to these ecosystems. Rising ocean temperatures are a primary consequence of climate change and have profound impacts on coral reef systems worldwide. This paper examines the ecological interactions and mechanisms leading to coral bleaching under thermal stress. The symbiotic relationship between corals and zooxanthellae algae is disrupted as elevated temperatures induce heat stress, leading to the expulsion of zooxanthellae and subsequent bleaching. Heat shock proteins and cellular responses provide initial defense mechanisms, but prolonged stress overwhelms these protective processes. Additionally, photodamage and oxidative stress further contribute to coral bleaching. Impaired pH regulation, and decreased carbonic anhydrase activity, hampers coral calcification and vital physiological processes. Understanding these processes is crucial for effective conservation strategies to mitigate the impacts of rising ocean temperatures and protect these coral reef systems against ongoing climate change.

Contents

1 Introduction

Coral reefs, often referred to as the ”rainforests of the sea”, are remarkable ecosystems that harbor immense biodiversity, making them vital hubs of the marine ecosystem. Despite occupying less than 1% of the ocean floor, these coral reefs serve as habitats for approximately a third of marine species (McAllister, 1991). Beyond their ecological significance, coral reefs also hold great cultural, economic, and recreational value for coastal communities around the world (Moberg & Folke, 1999), because of their contributions to tourism, fishing, building materials, coastal protection, and the development of new medications and biochemicals (Carté, 1996).

Coral reefs are important for biodiversity due to their rich and diverse ecosystems. These underwater structures, formed by the accumulation of calcium carbonate secreted by corals, provide a unique habitat that supports a vast array of marine life, including fish, invertebrates, algae, and plants. The complex three-dimensional structure of coral reefs offers microhabitats, creating niches for a variety of organisms. Reef systems are recognized as biodiversity hotspots due to their remarkable concentration of unique species. Many organisms found on coral reefs are endemic, meaning they are found nowhere else in the world. This high level of endemism makes coral reefs particularly valuable in terms of preserving genetic diversity.

Because coral reefs are home to a diverse range of fish and other marine species, making them crucial fishing grounds for coastal communities. Reef-based fisheries provide a significant source of protein, income, and livelihoods for millions of people worldwide. Local fishermen rely on the abundance and diversity of fish species found in coral reefs for their catch. Fishing activities within coral reef ecosystems provide employment opportunities for fishermen and support related sectors, including processing, marketing, and trade (Cinner & McClanahan, 2006). The availability of fish from coral reefs not only ensures food security for these communities but also contributes to local economies and poverty alleviation (Moberg & Folke, 1999). Fish sourced from these coral reefs are a vital source of protein and essential nutrients in the diets of millions of people, particularly in coastal regions where alternative food sources may be limited.

The growth of living corals is a key process in reef-building, which enhances shoreline protection and coastal resilience. Healthy coral reefs help to dissipate the energy of waves approaching the shoreline (Principe *et al.*, 2012). As waves encounter the reef, they break and lose energy, reducing the intensity of the waves before they reach the shoreline. This wave energy dissipation significantly mitigates the erosive power of the ocean and helps protect the coast. According to Costa *et al.* (2016) in Recife, state of Pernambuco, Brazil, continental shelf reefs (>2m depth) were able to reduce wave energy by up to 67%, while fringing reefs during low tides were able to reduce wave energy by up to 99.9%.

Primarily driven by the emission of greenhouse gasses into the atmosphere, global temperatures have been steadily rising over the past century. This alarming rise in global temperatures due to climate change poses a significant threat to the survival and health of these ecosystems. This phenomenon has tremendous consequences for the Earth’s ecosystems, including the delicate balance of coral reef systems. Coral reefs also provide a crucial defense against storm surges, which occur during tropical storms and hurricanes. Storm surges are elevated water levels driven by strong winds and low atmospheric pressure associated with these weather events. Healthy coral reefs can attenuate storm surges by absorbing and dispersing some of the surge’s energy. As waves associated with the storm surge encounter the reef, they are partially deflected and reduced in height, thereby reducing the inundation and potential damage to coastal areas (Elliff & Silva, 2017).

As the Earth’s atmosphere continues to trap more heat, the world’s oceans are absorbing a significant portion of this excess heat (Solomon *et al.*, 2007). The rising ocean temperatures have implications for the health and stability of coral reefs. The effects of rising temperatures on coral reefs extend beyond the corals themselves. The intricate web of ecological interactions within coral reef ecosystems is disrupted, impacting a wide range of organisms, from fish and invertebrates to other symbiotic relationships within the reef community (Hoegh-Guldberg, 1999). As coral reefs provide crucial nursery habitats and feeding grounds for many marine species, the loss of these ecosystems can have cascading effects on the health and productivity of adjacent coastal and oceanic areas.

Corals have a symbiotic relationship with algae called zooxanthellae (Hoegh-Guldberg, 1999). These algae live within the coral tissues and provide the corals with the energy derived from photosynthesis. In return, corals offer shelter and nutrients to the zooxanthellae. This mutually beneficial association forms the foundation of coral reef ecosystems. Zooxanthellae algae belong to the dinoflagellate family and are primarily photosynthetic organisms. They utilize sunlight to convert carbon dioxide and nutrients into organic compounds, providing the corals with a substantial energy source (Allemand & Furla, 2018). The photosynthetic activity of zooxanthellae not only fuels coral growth but also aids in the deposition of calcium carbonate, the building blocks of coral reefs. Additionally, the pigments produced by zooxanthellae give corals their vibrant colors, enhancing their visual appeal.

However, when exposed to high temperatures, corals experience physiological stress, leading to the expulsion of the zooxanthellae and subsequent bleaching. Coral bleaching is a distressing phenomenon where corals lose their vibrant colors and become pale or even white (Warner *et al.*, 1996). This process is not only visually striking but also indicative of severe physiological damage and potential mortality (Spalding & Brown, 2015). Without the symbiotic zooxanthellae, corals struggle to meet their energy requirements and become more vulnerable to disease outbreaks (Brown *et al.*, 1996). Prolonged exposure to elevated temperatures can lead to mass coral mortality, resulting in the degradation and loss of entire reef ecosystems.

The concern is that the current reef-building corals will be unable to adapt to the conditions of such a rapid temperature increase leading to coral bleaching (Pandolfi *et al.*, 2011). Coral bleaching hampers the growth and recovery of corals, limiting their capacity to rebuild and maintain the reef structure. As bleaching events become more frequent and severe, the ability of corals to reproduce, settle, and grow is compromised. The overall reduction in coral growth and reef-building processes further weakens the reef structure. As a result, the three-dimensional structure of the reef weakens, making it less effective in absorbing and dispersing wave energy (Spalding & Brown, 2015).

In light of the escalating threat posed by rising global temperatures, it is imperative to deepen our understanding of the impact of temperature/thermal stress on coral bleaching in coral reef systems. This thesis aims to assess the biological and ecological aspects of coral bleaching, investigating the underlying mechanisms. By gaining insight into the effects of temperature on coral reef systems, the effects of bleaching on coral reef systems and the link between temperature and coral bleaching.

2 Rising Temperatures and Coral Bleaching Events

Global average temperatures have been on the rise. This not only has an effect on land but also in the seas and oceans around the world, resulting in rising water temperatures (fig 1.) (Bâki Iz, 2018; Solomon *et al.*, 2007). Between 1880 and 2013 temperatures on earth have risen by almost 1 °C (Stocker, 2014), this increase in temperature has a direct effect on the the sea surface temperature (SST) (Bâki Iz, 2018).

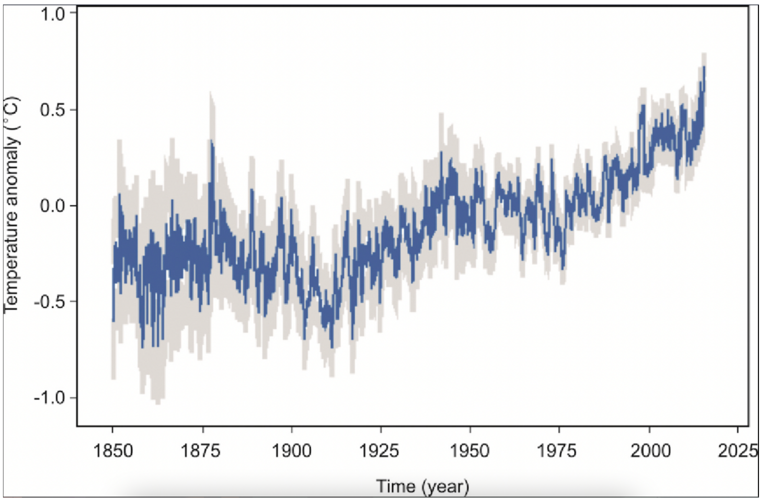

Figure 1: Median global average sea surface temperatures (SST) anomalies between 1850 and 2015 relative to 1961 - 1990 with 95% confidence range. (Bâki Iz, 2018)

The warming of our planet's climate has resulted in rising ocean temperatures, posing a serious threat to the health and survival of coral reefs (Spalding & Brown, 2015). Coral reefs are highly sensitive to these changes in temperature, and they have evolved to survive within temperatures between 23 °C and 29 °C, with most corals living in conditions close to the upper limit of this thermal range (Spalding & Brown, 2015). When ocean temperatures rise beyond this range, corals get a stress response that can cause a phenomenon known as coral bleaching. Coral bleaching occurs when the stressed corals expel their symbiotic algae (zooxanthellae) that live within their tissues (Pandolfi *et al.*, 2011). According to Loya *et al.* (2001), in 1998 at Sesoko Island the SST peaked at 2.8 °C above average, this caused extensive coral bleaching and eventual mortality. This bleaching resulted in a 61% reduction of species richness and 85% reduction of coral cover (Loya *et al.*, 2001).

When corals bleach, they lose their color and appear white, hence the term "bleaching." The loss of the symbiotic algae deprives the corals of their main food source and makes them more susceptible to disease (Spalding & Brown, 2015). If the temperature stress causing the bleaching event persists, the affected corals may eventually die.

In recent years the amount of coral bleaching events have increased with notable mass bleaching events happening in 1997-1998, 2010 and 2014-2017 (van Oppen & Lough, 2018). These mass bleaching events were likely caused by El Niño Southern Oscillation (ENSO) events (Claar *et al.*, 2018; Hughes *et al.*, 2018). ENSO events caused the local SST in 9 sites around Palau, Western Caroline islands to increase by 1.0 - 1.25 °C, leading to a SST of 31 °C (Bruno *et al.*, 2001). ENSO events are predicted to further increase local SST in the future as global warming progresses (Hughes *et al.*, 2018), further increasing the amount of (severe) coral bleaching events (Claar *et al.*, 2018).

According to Hughes *et al.* (2018), "the number of years between recurrent severe bleaching events has diminished fivefold in the past four decades, from once every 25 to 30 years in the early 1980s to once every

5.9 years in 2016” (fig. 2). As figure 2 shows, in most observed sites by Hughes *et al.* (2018) coral bleaching events now repeat after 1 - 6 years after the last bleaching event during 2000 - 2016. While during 1980 - 1999 the return times of bleaching events was about evenly distributed. The increased frequency of coral bleaching events is connected with rising ocean temperatures and is a direct consequence of global warming (Hughes *et al.*, 2018).

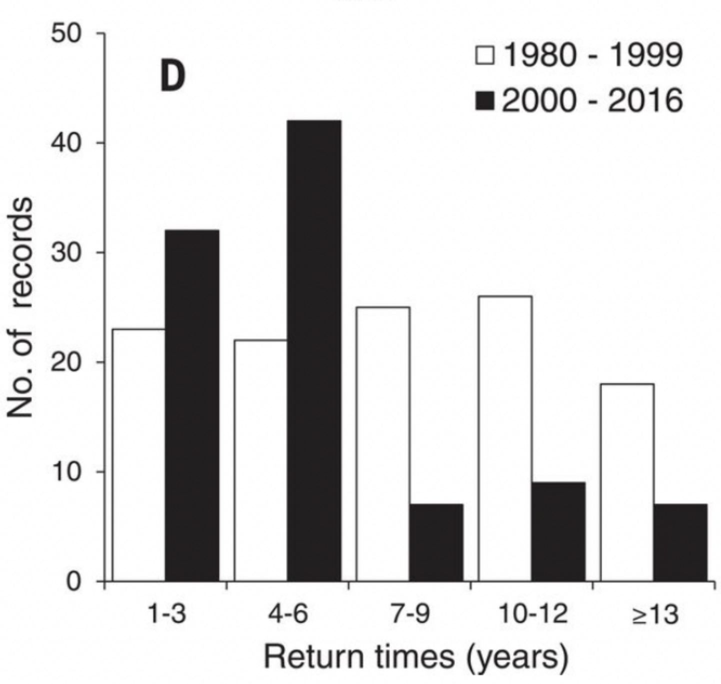

Figure 2: Frequency distributions of the return times in years between severe coral bleach events between 1980-1999 (white bars) and 2000-2016 (black bars) (Hughes *et al.*, 2018).

As the planet’s climate continues to warm, ocean temperatures rise, and the likelihood of prolonged heat stress on coral reefs intensifies. Extended exposure to elevated temperatures can trigger these bleaching events (fig. 3), 2 hours of exposure to temperatures of 36 °C is enough for *G. djiboutiensis* to expel 50% of their Zooxanthellae (Sharp *et al.*, 1997). The thermal stress associated with increased temperatures disrupts the delicate balance of coral-zooxanthellae symbiosis, leading to potential detrimental consequences. The frequency of these bleaching events has been rising globally with a rate of 3.9% yearly, and the frequency of severe bleaching events has been increasing even faster at a rate of 4.3% yearly (fig. 4) (Hughes *et al.*, 2018). Also the number of locations affected by these events has increased (fig. 5). Throughout the years an increasing number of locations have been affected by bleaching events or severe bleaching events, with only 6 out of 100 globally distributed locations not affected by a severe bleaching event (Hughes *et al.*, 2018).

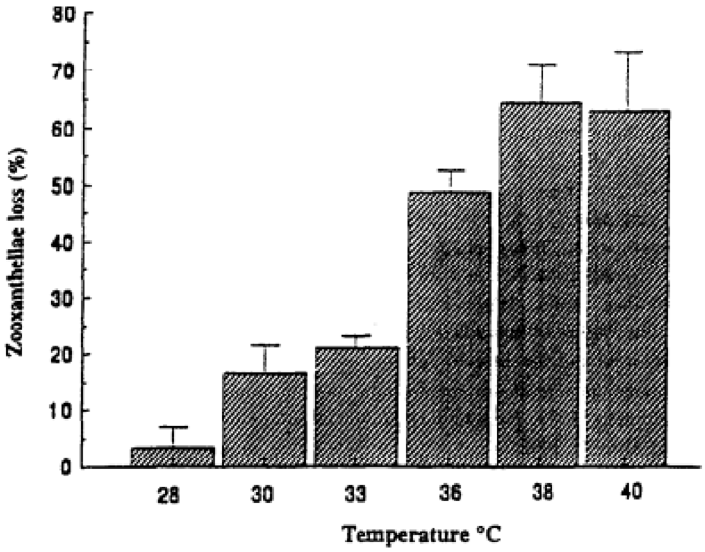

Figure 3: Percentage of zooxanthellae loss after 2 hours of exposure to heat shock temperatures in *G. djiboutiensis*. Error bars represent standard deviation. (Sharp *et al.*, 1997)

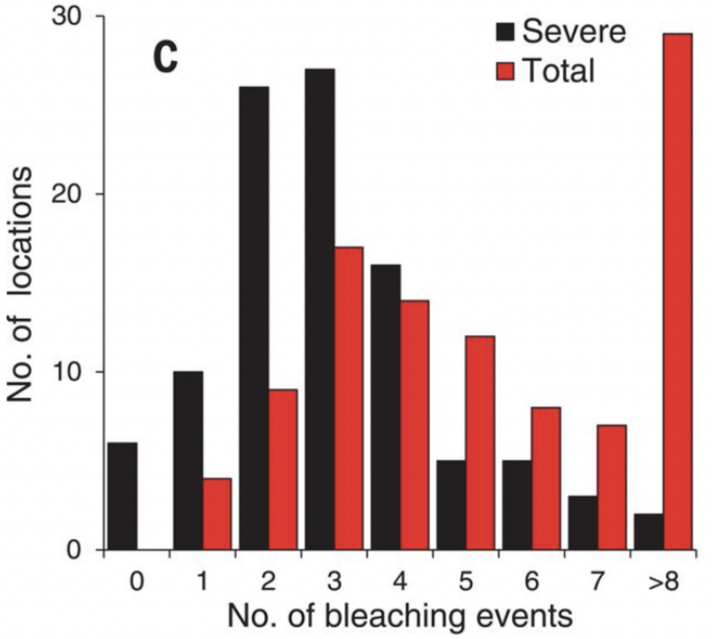

Figure 4: Frequency distributions of the number of severe bleaching events (black bars) and total bleaching events (red bars) per location (Hughes *et al.*, 2018).

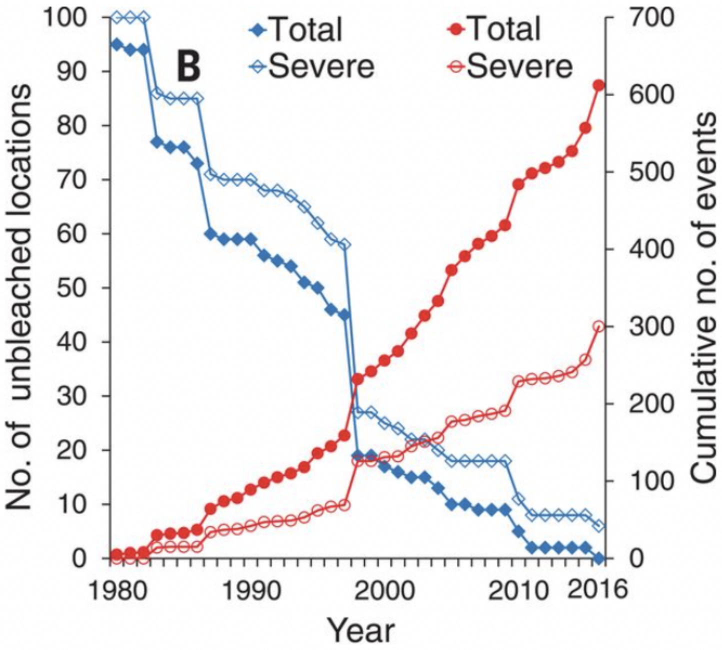

Figure 5: The decreasing number of locations that have not been affected by bleaching or severe bleaching (left axis; blue). The cumulative number of severe bleaching events and total bleaching events (right axis; red) Hughes *et al.* (2018).

3 Mechanisms and Processes Leading to Coral Bleaching

The thermal stress caused by SST ≥ 30 °C (Spalding & Brown, 2015) disrupts the functioning of photosynthetic machinery in zooxanthellae, reducing their ability to generate energy through photosynthesis (Spalding & Brown, 2015; Warner *et al.*, 1996). This leads to a decline in the energy reserves of corals, impairing their growth and reproductive capacities (Brown *et al.*, 1996). Additionally, increased temperatures can cause cellular damage and oxidative stress, compromising the health and survival of corals (Cziesielski *et al.*, 2019; Lesser, 1997).

3.1 Heat Shock Proteins

Heat Shock Proteins (HSPs) play a critical role in the cellular responses of corals and zooxanthellae to thermal stress and are essential components of the mechanisms involved with coral bleaching. These proteins act as molecular chaperones, assisting in the proper folding and stabilization of proteins under normal conditions (Bozaykut *et al.*, 2014). However, when corals are exposed to elevated ocean temperatures, the increased heat disrupts protein structure and can lead to denaturation, rendering proteins non-functional.

Under thermal stress, corals upregulate the production of HSPs as a protective response to maintain cellular homeostasis and prevent protein damage. HSPs are synthesized in higher quantities to refold or remove denatured proteins, ensuring their proper functioning and preventing the accumulation of damaged proteins that could have detrimental effects on cellular processes (Barshis *et al.*, 2010).

The upregulation of HSPs is primarily regulated at the gene expression level (Louis *et al.*, 2017). Heat shock factor (HSF), a transcription factor, plays a central role in activating the genes that encode HSPs. When cells experience heat stress, the HSF is activated and translocates to the nucleus, where it binds to specific DNA sequences known as heat shock elements (HSEs). This binding initiates the transcription of HSP genes, leading to the synthesis of HSPs (fig. 6) (Louis *et al.*, 2017; Stice, J. & Knowlton, 2008).

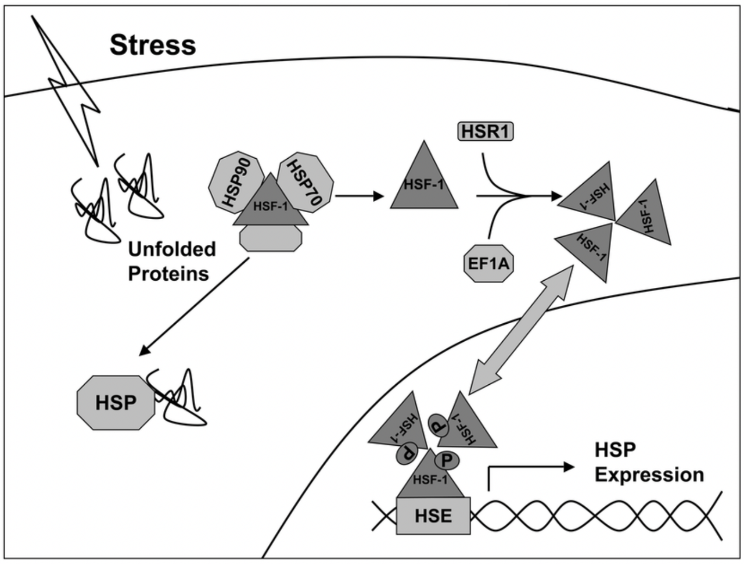

Figure 6: Heat shock leading to HSP detaching from multi-protein complex, releasing HSF-1. HSF-1 translocates to nucleus where it actives HSE which results in HSP production. (Stice, J. & Knowlton, 2008)

In addition to their chaperone function, HSPs also have a broader cellular protective role. They assist in the assembly and disassembly of protein complexes, facilitate the transport of proteins across cellular membranes, and prevent the aggregation of unfolded proteins (Bozaykut *et al.*, 2014). Furthermore, HSPs can interact with other cellular components, such as signaling molecules and enzymes, to regulate various cellular processes and maintain cellular integrity (Louis *et al.*, 2017).

However, despite the crucial role of HSPs in cellular responses to thermal stress, prolonged exposure to high temperatures can overwhelm the cellular defense mechanisms (Jokiel & Coles, 1977). According to Jokiel & Coles (1977), exposure to temperatures of 32 °C caused mortality within days, while corals at 30 °C appeared to remain healthy for several weeks before losing their zooxanthellae and eventually increased mortality after 2 months. Accumulation of damaged proteins caused by prolonged heat stress due to ocean temperatures of 30 °C or higher can exhaust cellular energy reserves, because of the energy requirements needed for sustained production(Sørensen *et al.*, 2003).

It is important to note that the expression and effectiveness of HSPs can vary among different coral species and genotypes. Some corals may exhibit greater resilience to thermal stress due to their ability to produce higher levels of HSPs or possess genetic variations that confer better stress tolerance (Fitt *et al.*, 2009; Seveso *et al.*, 2018, 2014).

According to Loya *et al.* (2001), branched pocilloporids (e.g. *Stylophora pistillata, Pocillopora damicornis, Seriatopora hystrix*), branched porites (e.g. *P. sillimaniani, P. cylindrica, P. horizontalata*) and finely branched *Millepora intricata* were considered the "losers" during a bleaching event in 1998 caused by elevated SST. In 1997 these corals were the locally dominant species, however after the bleaching event they had become locally extinct. Furthermore the soft coral community was reduced by 99% (Loya *et al.*, 2001). The "winners" of this bleaching event were the huge encrusting colonies (e.g. *Leptastrea purpurea, L. transversa, Porites lutea*), because of mortality of previous large colonies, their relative abundance had increased sevenfold in 1999 (Loya *et al.*, 2001).

Loya *et al.* (2001) hypothesize that the reason branched corals were the "losers" was due to morphology. Branched coral species have a relatively surface area compared to encrusting corals and are therefore more susceptible to heat stress.

Moreover research done by Matsuda *et al.* (2020) in Kāneʻohe Bay, Hawaiʻi shows that individuals of *Montipora capitata* and *Porites compressa* that have genotypes that are more resilient to heat stress and therefore less susceptible to bleaching have a lower partial mortality than individuals of the same species that are more susceptible to bleaching. But, individuals of *P. compressa* had greater resilience after being affected by bleaching while being more susceptible to bleaching compared to individuals of *M. capitata.*

3.2 Reactive Oxygen Species

Photodamage and oxidative stress are critical processes influenced by rising ocean temperatures that contribute to coral bleaching (Dykens *et al.*, 1992). As corals experience thermal stress, the excess heat and light energy absorbed by the symbiotic zooxanthellae can disrupt the photosynthesis within the coral tissue (Takahashi *et al.*, 2009).

Under normal conditions, the photosynthetic activity of zooxanthellae provides corals with a reliable energy source in the form of photosynthates. However, when corals are exposed to high temperatures ($\geq$ 32 °C) for 10 days (Louis *et al.*, 2017), the photosynthetic machinery of zooxanthellae becomes impaired. The increased heat disrupts the electron transport chain and other photosynthetic processes, resulting in the overproduction of reactive oxygen species (ROS) (Louis *et al.*, 2017; Nielsen *et al.*, 2018; Szabó *et al.*, 2020).

ROS, including superoxide radicals, hydrogen peroxide, and hydroxyl radicals, are highly reactive molecules that can cause oxidative damage to cellular structures and biomolecules. The overproduction of ROS by zooxanthellae in Photosystem I (Szabó *et al.*, 2020) causes the ROS to leak out and subsequently harms the host cell (Cziesielski *et al.*, 2019; Nielsen *et al.*, 2018). After leaking out of the endosymbionts ROS accumulates and overwhelms the antioxidant defense mechanisms of corals, leading to oxidative stress (Cziesielski *et al.*, 2019). Antioxidant enzymes, such as superoxide dismutase, catalase, and glutathione peroxidase, play a crucial role in neutralizing ROS and maintaining cellular redox balance (Downs *et al.*, 2000). However, under prolonged thermal stress, the production of ROS exceeds the capacity of these antioxidant defenses, resulting in oxidative damage to lipids, proteins, and DNA (Downs *et al.*, 2002).

Oxidative stress can have detrimental effects on coral physiology and health. Lipid peroxidation, caused by the reaction of ROS with unsaturated fatty acids in cell membranes, compromises membrane integrity and disrupts cellular functions (Asada, 1987). Protein oxidation can lead to the misfolding and aggregation of proteins, impairing their function and causing cellular dysfunction. Additionally, DNA damage resulting from oxidative stress can have long-term consequences for cellular integrity and genetic stability. The coral hosts expel the zooxanthellae to protect themselves from oxidative stress caused by ROS (Suwa & Hidaka, 2006).

Zooxanthellae are vulnerable to photodamage and oxidative stress due to their high exposure to light and their photosynthetic activity. Elevated temperatures increase the production of ROS within zooxanthellae, leading to their dysfunction and impaired photosynthetic capacity (Dykens *et al.*, 1992). As a result, the energy transfer from zooxanthellae to the coral host is disrupted. The impaired photosynthesis and reduced energy production by zooxanthellae, coupled with the oxidative damage to cellular structures, create a state of energy deprivation and cellular dysfunction within corals (Liñán-Cabello *et al.*, 2010).

3.3 Carbonic Anhydrase and pH Regulation

Carbonic Anhydrase (CA) and pH regulation are vital for corals and are affected by rising ocean temperatures and are involved in coral bleaching (Moya *et al.*, 2012). Corals and their symbiotic zooxanthellae rely on precise pH regulation to maintain their physiological functions and the integrity of the coral-zooxanthellae symbiosis (Brownlee, 2009).

Carbonic Anhydrase is an enzyme found in corals that catalyzes the interconversion of carbon dioxide (CO2) and bicarbonate ions (HCO3-) in the presence of water. This enzymatic reaction is crucial for the efficient uptake and utilization of dissolved inorganic carbon (DIC) by coral polyps and zooxanthellae (fig. 7). DIC is essential for the process of calcification, which enables corals to build their calcium carbonate skeletons and maintain the structural integrity of coral reefs (Bertucci *et al.*, 2013).

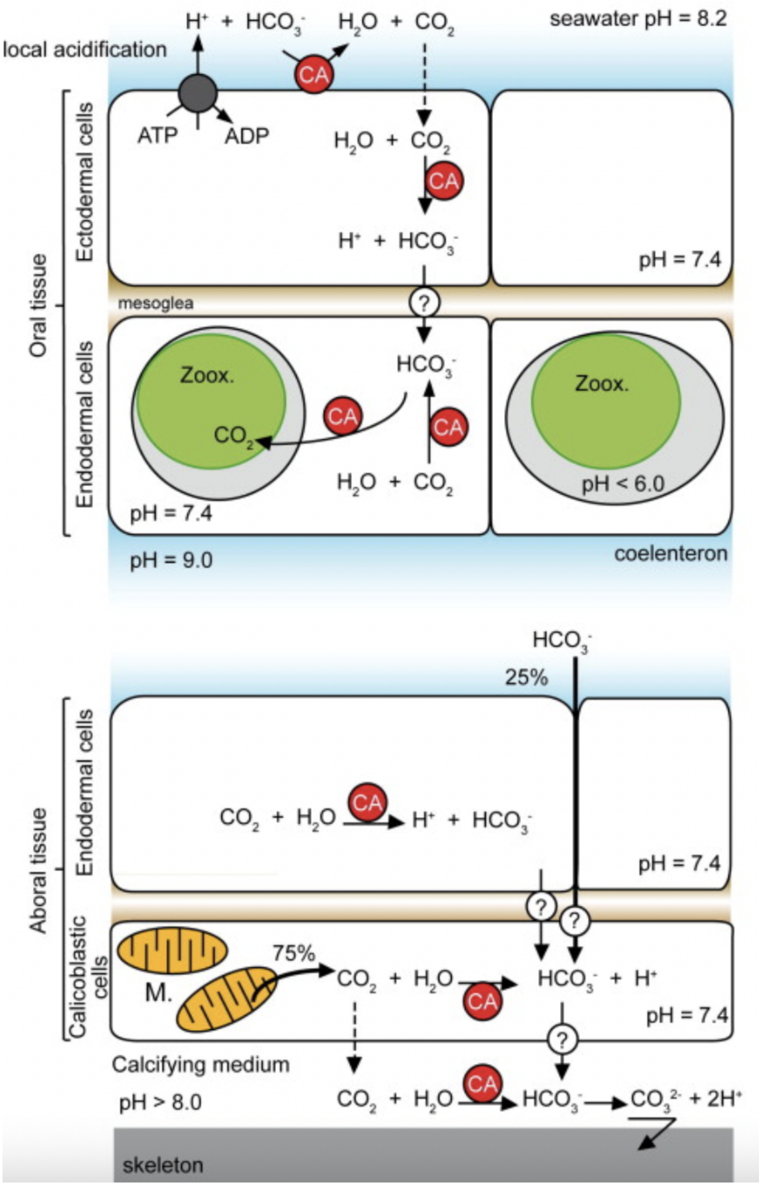

Figure 7: Model of how DICs move through different coral tissues with the help of Carbonic Anhydrase (red circles) (Bertucci *et al.*, 2013).

Under normal conditions, the activity of carbonic anhydrase ensures the conversion of CO2 into bicarbonate ions, which can then be utilized by zooxanthellae for photosynthesis. This process promotes the removal of excess CO2 in coral tissue and helps maintain the carbonate saturation state necessary for coral calcification.

However, under thermal stress, the activity of carbonic anhydrase of corals can be compromised (Moya *et al.*, 2012). Elevated temperatures (≥ 27 °C) for 12 hours (Moya *et al.*, 2012) can disrupt the enzymatic function of carbonic anhydrase, impairing its ability to efficiently catalyze the conversion of CO2 into bicarbonate ions (Bertucci *et al.*, 2013; Moya *et al.*, 2012). This disruption can lead to a decrease in the availability of bicarbonate ions for both coral and zooxanthellae, hindering the coral's calcification and the photosynthetic capabilities of the zooxanthellae further compromising the coral-zooxanthellae symbiosis.

The impaired pH regulation resulting from compromised carbonic anhydrase activity has profound implications for coral health, as shown in figure 7 CA ensures the conversion of $CO2 + H2O \rightarrow H +$

$+HCO3-$ and is important for maintaining steady pH, because of the H+ released in the cytoplasm by this conversion (Bertucci *et al.*, 2013; Capasso *et al.*, 2021). Corals rely on a narrow range of internal pH values, between 8.30 and 7.83 (Wall *et al.*, 2016), for various physiological processes, including the maintenance of proper enzymatic activity. The disruption of pH homeostasis can interfere with essential cellular processes, impair metabolic functions, and lead to cellular dysfunction (Brownlee, 2009).

One significant consequence of impaired pH regulation is the inhibition of calcification. The decrease in the availability of bicarbonate ions, which are essential for coral calcification, can hinder the ability of corals to build and maintain their calcium carbonate skeletons (Brownlee, 2009). Consequently the inability of corals to maintain their calcium carbonate skeletons, harms the structural integrity of coral reefs, making corals more susceptible to physical damage and erosion.

Furthermore, altered pH conditions resulting from impaired carbonic anhydrase activity in coral tissue can affect other vital physiological processes in corals and zooxanthellae. These include nutrient uptake, ion regulation, protein synthesis, and the efficiency of photosynthesis (Bertucci *et al.*, 2013). The disruption of these processes can lead to nutritional deficiencies, reduced energy availability, and an overall decline in coral health and fitness.

3.4 Bacterial bleaching

Higher SST ($\geq$ 30 °C) promotes the growth and proliferation of bacteria, including those associated with coral diseases (i.e. *Vibrio shiloi* and *V. coralliilyticus*) (Banin *et al.*, 2000; Remily & Richardson, 2006). The optimal sea temperatures for the growth of these bacteria is between 30 °C and 35 °C (Remily & Richardson, 2006). But, not only is the growth of these bacteria increased, it also enhances the adhesion to the coral hosts and increases both the toxin production and activity (Remily & Richardson, 2006). The increased bacterial abundance, toxin production and toxin activity all increase the likelihood of corals getting affected by bacterial bleaching.

Research by (Banin *et al.*, 2000), shows that temperature plays an important role in the ability of *V. shiloi* bacteria to infect their host. When the bacteria were grown at 16 °C they were unable to adhere to corals maintained at 16 °C or 25 °C, On the other hand, bacteria grown at 25 °C they adhered to corals at 16 °C and 25 °C. Moreover, toxin production was increased 10 fold in bacteria cultures grown at 29 °C compared to the cultures grown at 16 °C. When the adhesion of *V. shiloi* to corals is successful, the bacteria enters coral tissue where it produces and releases toxins that inhibit the photosynthetic capabilities of the zooxanthellae and leads to lysis (Banin *et al.*, 2000).

Furthermore the weakened state of corals caused by increased SST ($\geq$ 30 °C), makes them more susceptible to bacterial infections and subsequent bleaching. Temperature stress can also weaken the coral's immune response, making it more difficult for corals to fend off bacterial colonization (Traylor-Knowles & Connelly, 2017).

4 Adaptation to Increased Sea Temperatures

While sea temperatures keep rising (Bâki Iz, 2018), corals need to adapt to these increased sea temperatures to avoid extinction (Humanes *et al.*, 2022). According to Humanes *et al.* (2022), "For coral reefs to persist through the coming century, coral adaptation must keep pace with ocean warming".

Corals have shown the ability to undergo genetic adaptation, which allows them to pass down beneficial traits to subsequent generations (Cziesielski *et al.*, 2019). Some corals possess genetic variations that provide increased tolerance to heat stress (Dixon *et al.*, 2015; Howells *et al.*, 2016). When exposed to higher temperatures, these individuals are more likely to survive and reproduce, passing on their heat-tolerant genes to their offspring (Dixon *et al.*, 2015). Over time, this natural selection process enhances the overall resilience of coral populations to warmer conditions.

Coral larvae with parents from warmer locations have up to 10 times higher chance of survival (Dixon *et al.*, 2015). Adult corals of *P. daedalea* growing in the Persian Gulf have adapted to the rising temperatures and after a 6-month acclimation to elevated temperatures of 36 °C (Howells *et al.*, 2016). This resulted in a 66% increase of survival threshold compared to individuals of the same species growing in the Sea of Oman (Howells *et al.*, 2016).

Research done by Berkelmans & van Oppen (2006), shows that corals affected by bleaching could change their dominant symbiont type from C to D. The D type zooxanthellae are a more heat resistant type of symbiont, this process is called symbiont shuffling (Berkelmans & van Oppen, 2006; Cunning *et al.*, 2015). Type D zooxanthellae are able to withstand temperatures 1 - 1.5 °C higher than the type C zooxanthellae. According to Cunning *et al.* (2015), "The proportion of heat-tolerant symbionts dramatically increased following severe experimental bleaching, especially in a warmer recovery environment, but tended to decrease if bleaching was less severe". The type D symbionts might have a better thermal tolerance (Berkelmans & van Oppen, 2006; Cunning *et al.*, 2015), but also have reduced photosynthetic capabilities potentially leading to a reduction of coral growth (Cunning *et al.*, 2015; Ortiz *et al.*, 2013).

Some corals have adapted to gain colorful pigments after being affected by bleaching (fig. 8). About 40% of the shallow water corals in New Caledonia and the great barrier reef that were bleached got these colorful pigments (Bollati *et al.*, 2020). This is an emergency response of the host and symbionts to protect themselves against high light stress (Enríquez *et al.*, 2005) and increase the coral's chance of recovery (Bollati *et al.*, 2020). This coloration happens 2 to 3 weeks after being affected by a bleaching event caused by either mild or temporary heat stress (Bollati *et al.*, 2020).

Figure 8: Coral with colorful pigments after being affected by a bleaching event and losing its symbiotic zooxanthellae (RICHARD VEVERS/THE OCEAN AGENCY, XL CATLIN SEAVIEW SURVEY).

5 Discussion

With global temperatures rising due to climate change, leading to increased ocean temperatures causing an increasing amount of severe mass coral bleaching events happening worldwide (Hughes *et al.*, 2018; van Oppen & Lough, 2018). The mechanisms and processes leading to coral bleaching are intricately tied to the rising of these ocean temperatures. The breakdown of the symbiotic relationship between corals and zooxanthellae, the production of HSPs, the disruption of pH regulation, and the effects of oxidative stress and the increased growth of bacterial pathogens that can cause bleaching are all linked to the rising sea temperatures (Cziesielski *et al.*, 2019; Remily & Richardson, 2006).

To address the challenge of increasing coral bleaching events, urgent global action is needed to mitigate climate change and reduce greenhouse gas emissions. Multiple measures like, transition to renewable energy sources like wind and solar as replacement for fossil fuel-based energy, Forest conservation and restoration as carbon sink to reduce CO2 levels in the atmosphere are needed to slow down global warming.

Efforts should also focus on implementing effective coral reef management and conservation strategies, including the establishment of marine protected areas, restoration initiatives, and the reduction of local stressors such as pollution and overfishing (Ban *et al.*, 2011; Elliff & Kikuchi, 2015) to prevent more stressors harming corals that could further increase risk of mortality (Howells *et al.*, 2016).

However, corals are projected to be lost by approximately 2050. If we succeed in slowing down global warming the subsequent rising of ocean temperatures also slows down. Allowing more time for corals to potentially adapt to these rising temperatures and become more resilient to these temperatures (Cziesielski *et al.*, 2019). Although research and information on how these corals adapted to the rising temperatures and which traits allowed them to adapt is fairly limited (Howells *et al.*, 2016).

Additionally, investigating the genetic and physiological variations in these mechanisms and processes among coral species could provide insights into their susceptibility and resilience to thermal stress. Research done by (Humanes *et al.*, 2022), showed that the 10% most tolerant corals of *Acropora digitifera* required a double dosage (additional 4.8 °C-weeks) of heat stress to induce coral bleaching compared to the 10% least tolerant corals within a population. Predictions of future scenarios, allowed the most heat tolerant corals to survive for an additional 10 years under high CO2 emission scenarios or an additional 17 years in low CO2 emission scenarios.

The loss of coral reef systems would have tremendous consequences for the marine ecosystem, lots of endemic species are dependent on coral reef systems and would likely go extinct without these reef systems. Many fish rely on corals for food sources, shelter, and breeding grounds. According to (Jones *et al.*, 2004), "Over 75% of reef fish species declined in abundance, and 50% declined to less than half of their original numbers" and these numbers will continue to increase. The decline in fish populations due to coral bleaching may lead to increased fishing pressure as fishermen strive to maintain their catch levels. With fewer fish available within the reef ecosystem, fishermen may resort to unsustainable practices, such as overfishing or expanding their fishing efforts to other areas (Elliff & Kikuchi, 2015). This heightened fishing pressure further depletes fish stocks, negatively impacting millions of people worldwide that rely on fishing for food and/or income (Cinner & McClanahan, 2006; Moberg & Folke, 1999).

In conclusion, if we were to lose these coral reef systems, the consequences would be far-reaching beyond the reefs themselves, affecting the entire marine ecosystem and even human populations. Global climate change needs to slow down and much research still needs to be done, to increase our understanding of the mechanisms and processes involved in heat stress of corals if we want to assist corals in adjusting and adapting to this warming ocean environment.

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