Spring 2024

Early report of a microcosm of the fourth major global bleaching event: A comprehensive survey of coral bleaching at Chumbe Island Coral Park, Zanzibar

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SIT Study Abroad

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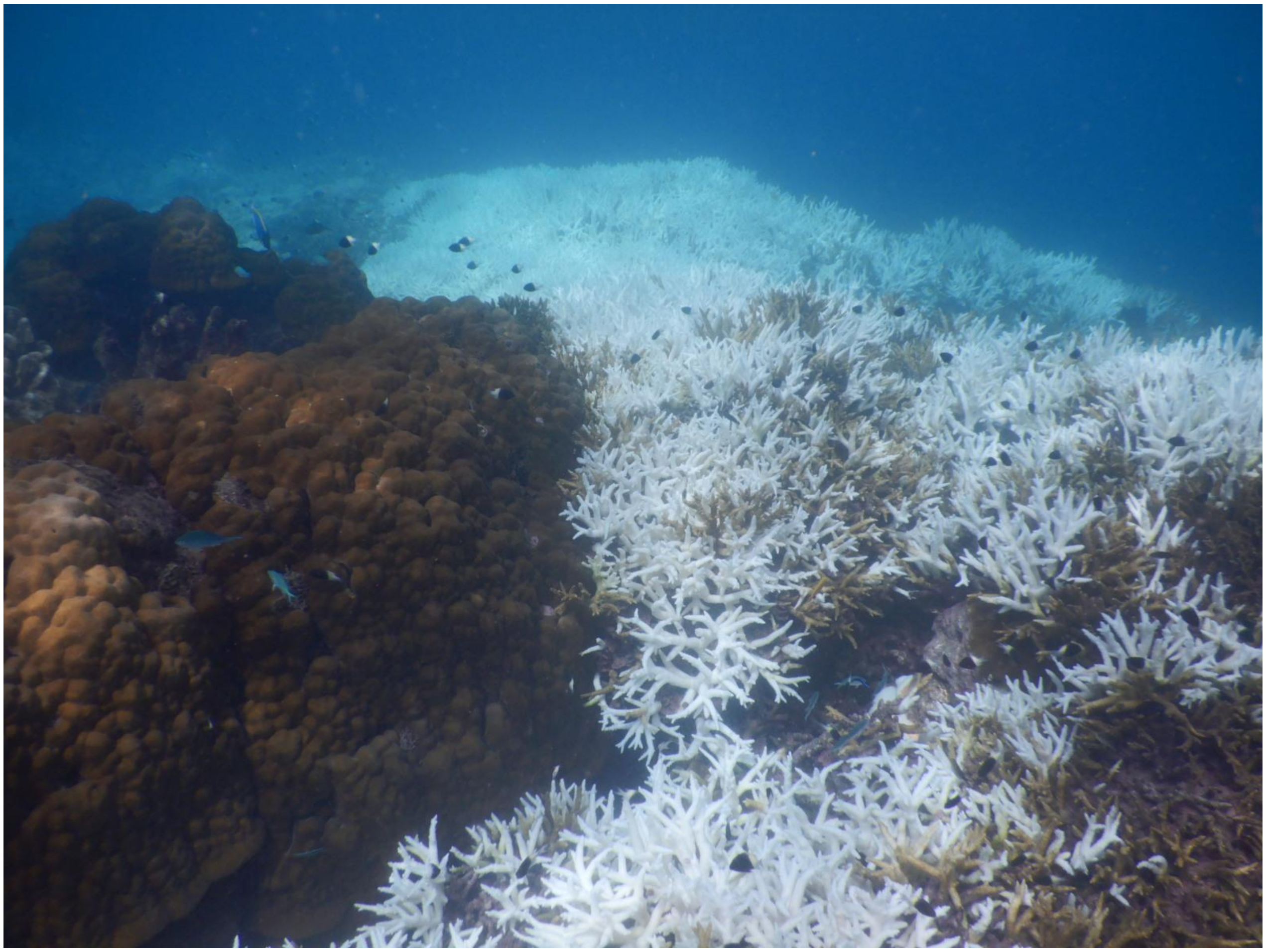

A large *Acropora* colony that has succumbed to bleaching and is beginning to die beside a healthy *Porites* massive coral

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Abstract

Coral reefs harbor a wealth of the biodiversity present in the ocean. They provide an array of ecological and economic services that make them crucial to the function of a healthy ocean and prosperous coastal communities. Due to an array of anthropogenic stressors, including an increase in ocean temperatures as a result of climate change, reefs have been devastated worldwide. This is, in large part, due to the process of coral bleaching, the expelling of symbiont algae which the coral needs to produce energy, for an extended period until death. This study surveyed bleaching and death at a deeper and shallower site along the Chumbe Coral Park reef. Quadrats were thrown along transects within the three principal zones of the reef (back reef, reef crest, and fore reef) to discern the percentage of alive, bleached, dead coral, and coral cover. A multitude of other coral stressors were also examined *ad hoc*. It was found that bleaching and death was widespread across the reef, with the worst death occurring at the reef crest. Bleaching was worst overall in the deeper section of the reef, indicating that the coral morphologies and genera there are more susceptible to thermal stress. The shallower site likely gives an impression of the future of the deeper site under increasingly severe bleaching events, with heartier, more thermally resistant species dominating the north. While local protections can reduce some coral stressors, if steps are not taken to properly address the warming ocean temperatures as a result of

climate change, the collapse of the coral reef ecosystem as a result will mean catastrophic ramifications for the health of the marine environment, a breakdown in global foodways, and the loss of livelihood and nutrition for local communities.

Dhahania

Matumbawe yanajumuisha utajiri wa bioanuai iliyomo katika bahari. Matumbawe yanatoa muunganyiko wa kiikologia pamoja na shughuli za kiuchumi na kufanya bahari iwe na afya pamoja jamii ya watu wa mwambaowa pwania. Anthropogenia tafrani, ikiwemo kuongezeka kwa joto la bahari. Matokeo yake mabadiliko ya tabia nchi, miamba kama inavyoelezewa ulimwenguni kote. Hili ni eneo kubwa, kutokana na kupauka kwa matumbawe eneo hili ni kubwa lenye mwani, pale ambapo matumbawe, yanahitaji kuzalisha nguvu ya muda mrefu mpaka kutoweka. Utafiti huu ulichunguza kupauka kwa matumbawe na kutoweka kwa matumbawe katika kina kikubwa na kina kidogo cha maji. Utafiti huu ulichunguza kupauka kwa matumbawe katika hifadhi ya kisiwa cha Chumbe. "Quadrats" zilirushwa kwenye mistari ya "transects" katika maeneo makuu matatu ya miamba (back reef, reef crest, na fore reef) ili kuweza kujua asilimia ya matumbawe hai, matumbawe yaliyopauka matumbawe yaliofariki pamoja na matumbawe yaliyomo katika hifadhi ya Chumbe. Pamoja uwingi kuchunguza uwingi tafrani za matumbawe ilbainika kuwa kupauka kwa matumbawe pamoja na vifo vilienea kila mahali katika eneo la utafiti. Vifo vingi vilionekana katika eneo la crest. Kupauka kwa matumbawe kulikuwa zaidi kwenye eneo la chini ya mwamba. Hii inaonesha kuwa mophologia na genera zinazoathirika zaidi na tafrani ya hali ya joto. Maji madogo, kupauka kwa matumbawe kuna baadhi ya spesis zinazo himili joto hasa upande wa kaskazini, hata hivyo uhifadhi usiorasmi unapunguza baadhi ya tafrani za spesis za matumbawe. Kupanda kwa joto la bahari pamoja na joto ni matokeo ya mabadiliko ya hali ya tabia nchi, kuporomoka kwa mlolongo wa ikologia ya matumbawe kwa afya ya mazingira ya baharini.

Acknowledgments

I would like to thank Makenna Reilly for her support throughout this project as both my swim partner and closest companion on the island. I would also like to extend my gratitude to the Chumbe main office staff (Helen, Mo, Salim, and any others that were involved) for allowing Makenna and I to stay on the island and conduct our studies as well as checking in on us during our research period. Thank you to my advisor Ulli Kloiber for sharing sea surface temperature data with me and for her advice on all things coral at Chumbe. Additionally, I would like to acknowledge Dr. Christopher Muhando from the Institute of Marine Science for his assistance in collecting sea surface temperature data. I would like to offer my gratitude to the Chumbe staff on the island (Ali and Juma) for arranging our accommodations and helping us with any logistical need that arose. Thank you to the rangers (Kassim, Feisal 'Matatizo', Mkono) for transporting us back and forth between Unguja and Chumbe, as well as to the kayak for helping us at high tide. I appreciate all of the cooking staff (Nasra, Subira, Fatma, and Blandina, to name a few) for all of the wonderful meals. Thank you to the fundi (Husayn, Rama, Omar, Alphizi, Said, Ali and all others) for allowing me to play mpira with them and for their companionship throughout their stay on the island. Thank you to Elis and Lukas for advising me on coral identification and for their friendship. I appreciate Shuwena, Mudi, and Ali for their Swahili instruction that has allowed me to become friends with so many of the wonderful people mentioned here. I would also like to extend my gratitude to all of the office staff (Ali, Zuleikha, Zeinab, and Khamis) as well as to Richard and Said for such a fantastic semester. Finally, thank you to my wonderful cohort for all of the joyful moments I was able to experience with you and for the wonderful memories that I got to make with you.

Introduction

This section gives an overview of coral reef ecosystems, the benefits they offer, and the current threats they are facing, provides a history of coral bleaching at Chumbe Island Coral Park and in the greater Indian Ocean region, and addresses the area of study in which this project will take place.

Goals of this study

This study aims to provide a comprehensive and multifaceted understanding of how Chumbe's fringing reef was and continues to be affected by the mass coral bleaching event that took place from late 2023, into May of 2024. The project seeks to detail the percentage of healthy, bleached, and dead coral along the reef as well as to characterize the reef ecosystem and the threats it faces more generally. The data generated as a part of this study will provide significant positive impacts as it will supplement the monitoring and restoration efforts at Chumbe. The suggestions made as a result of the findings will provide Chumbe Island's management team with a holistic understanding of the effects of this bleaching event and aid them in restoring reef health. This study serves as a microcosm example of greater trends seen throughout the Indian Ocean and the world as reef ecosystems are increasingly subject to anthropogenic, biological, and climactic pressures that threaten their very existence.

Coral reef ecosystems

Corals (known as matumbawe in Kiswahili) belong to the phylum Cnidaria, meaning they have soft bodies and stinging cells. They are typically colonial and made up of a multitude of individual organisms called polyps (National Graphic, 2024). Corals are generally found in warm, shallow ocean waters, with the highest coral diversity and endemism occuring in the Indo-Pacific region (Veron et al., 2016). Scleractinian corals, colloquially referred to as hard corals, are responsible for the ecosystem engineering that results in the physical structure of a coral reef (Wild et al., 2011). These corals produce a hard, calcium carbonate skeleton by utilizing ions in the sea water that surround them (Lippsett, 2018). These skeletons allow Scleractinian corals to grow toward the light, which is necessary due to their symbiotic relationship with a photosynthetic algae called zooxanthellae. This algae lives within the tissue of each coral polyp, where it is provided with both a protected environment and the components necessary for photosynthesis. The coral, in return, receives food and oxygen, as well as aid with waste removal (NOAA, 2019).

Coral reefs tend to develop similar biogeographic zonation (NOAA, 2013), which can be described in various ways but is broadly divided into three primary zones: the reef flat (including the lagoon and the back reef), the reef crest, and the fore reef (including the reef slope) (Figure 1). These zones are defined not only by their location along the reef, but they also have specific defining abiotic factors such as wave energy intensity, depth, light exposure and intensity, and water composition and temperature (Heemsoth et al., 2014). Starting closest to shore and moving out into the ocean, the lagoon is a body of water separated by the natural barrier of the coral reef (NOAA, 2018). Lagoons can contain seagrass beds, coral rubble, and sand. Due to exposure to air and sun at lower tides, it is difficult for many species of coral to survive in this section. The back reef is the start of the reef and is interior to the bulk of the reef structure, so it is sheltered from heavy wave action. This area also tends to be shallower, so the patch reefs that exist within this section can be exposed to air during especially low tide, although not at the same frequency as the lagoon (Heemsoth et al., 2014). Occurring farther out after the back reef is the reef crest, which usually includes the shallowest area of the submerged reef due to the extensive coral growth that occurs there. The maximum absorption of wave energy occurs at the crest and, during low tide, the crest can breach the surface of the water (Kennedy and Roelfsema, 2020). Due to this fact, this zone also receives the greatest amount of light intensity, meaning that corals that live in this section must be resilient enough to withstand intense wave action, increased light intensity, and exposure to air. Furthest from the shore and sloping downward into a greater depth is the fore reef. The degree of the reef slope can vary to different extents, but most corals thrive in the intermediate depth of this zone because there is reduced wave action and less light, but sufficient levels to allow for growth. For these reasons, the greatest coral diversity exists within this zone (Heemsoth et al., 2014).

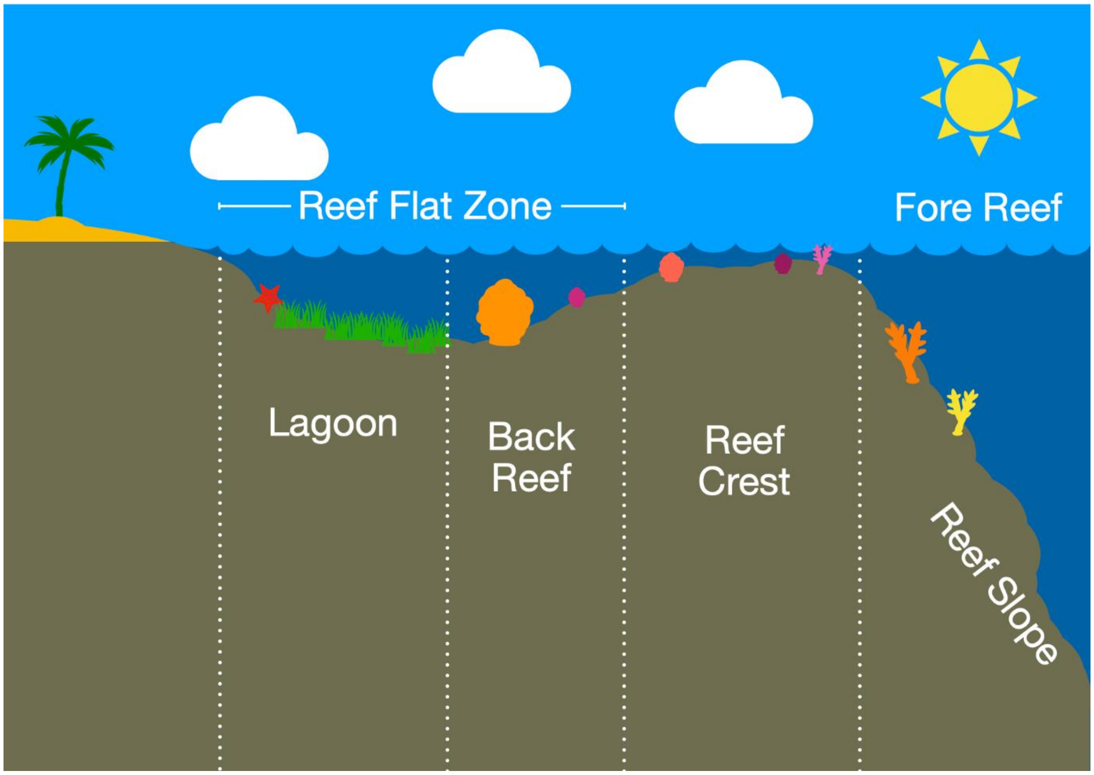

Figure 1. Diagram of the basic zonation of a coral reef. Coral presence depicted is not necessarily accurate.

Ecological and economic benefits of coral reefs

Although coral reefs only constitute 0.2% of the area of the seafloor, they provide the habitat for nearly 25% of the total biodiversity in the ocean (Wagner et al., 2020). Through the three-dimensional reef structure that corals construct, they create the physical habitat to house thousands of fish and other marine species (Hoegh-Guldberg et al., 2017). Reef structures also serve the important function of having the areas necessary to allow a variety of organisms to engage in spawning, feeding, and breeding activities, as well as provide a safe nursery for young (Moberg and Folk, 1999). Coral reefs have been shown to dissipate 97% of the wave energy that, unhindered, would directly impact shorelines, resulting in the reduction of coastal erosion and protection of the coastline from high-energy events, such as storms or hurricanes (Ferrario et al., 2014). Reefs provide additional ecological services such as the production of sand (Perry et al., 2015) and the processing and recycling of biological nutrients (Woodhead et al., 2019).

In addition to ecosystem benefits, coral reefs are also critically important for social and economic reasons. More than 500 million people worldwide depend on coral reefs for fishing and for the harvesting of marine resources, tourism, building materials, and protection from storms and erosion (Harvey et al., 2018; Natural History Museum, 2024). Fishing provides important protein for coastal diets and is necessary for healthy global foodways. A productive, properly-managed reef can produce between 0.2 and 40 tons of seafood per square kilometer annually globally (Reef Resilience Network, 2024a). Additionally, coral reefs and the organisms that live in these ecosystems have potential for biomedical use. These organisms have been used as a source of biological compounds that have been utilized for medicinal or other functional purposes. This includes the case of a compound extracted from a sea hare, described as “one of the most medically valuable natural compounds discovered up to now” that has been shown to treat common tumor cells, such as leukemia cells, small cell lung cancer cells, and human prostate cancer (Bruckner, 2002; Gao et al., 2021). Other species that live along and within reefs potentially contain undiscovered compounds that could form the basis of future treatments for various cancers, HIV, malaria, and other diseases. (Burke et al., 2011) From an economic perspective, a study done in the Asia-Pacific region, which looked at nearly 80% of global reefs, found that corals contributed $25 billion annually on average to the region’s economy from fishing and tourism alone. The majority of this economic value (US$19.5 billion) came directly from reef tourism, while about US$19.5 billion came from both artisanal and industrial fisheries (Bartelet et al., 2024). The combined services and resources generated from these ecosystems are valued at US$350,000 per year per ‘average’ hectare of coral reef (de Groot et al., 2012).

Contemporary threats facing coral reefs

The number one threat to coral reefs is climate change (Environmental Protection Agency, 2024). Climate change results in a multitude of stressors acting on corals, including warming ocean temperatures that cause coral bleaching, sea level rise that causes sedimentation and the smothering of corals, an increase in the frequency and intensity of storms which results in physical destruction of coral colonies, increased runoff and freshwater entering the ocean as a result of shifting precipitation patterns, altered ocean currents that can lead to a lack of nutrients and difficulty dispersing larvae, and ocean acidification, which inhibits the ability of corals to precipitate their calcium carbonate skeleton (NOAA, 2023). Coral bleaching is the process by which healthy coral polyps expel their symbiotic algae due to primarily thermal or light-induced stress, although other stressors can increase the probability of bleaching. Without these algae that give the coral its color, the tissues of the coral become transparent, displaying the white skeleton beneath (Great Barrier Reef Foundation, 2024). Corals do not automatically die from this process and can recover by regaining algae into their tissues in the event that the stress that caused the bleaching is not overly prolonged or severe (Grottoli et al., 2006). Another possibility for recovery is symbiont reshuffling, in which the coral expels algae communities sensitive to heat stress, undergoes the process of bleaching, and recovers as a result of its uptake of heat-resistant colonies of algae (Clarr et al., 2020). Once this algae is expelled, if another population is not re-established within the coral’s tissue within the span of a few days to a few weeks, the coral will starve and die (Sammarco and Strychar, 2013). As a result of these prolonged periods of thermal stress and other factors affecting coral, coverage of living coral worldwide has been reduced by half since the 1950s (Eddy et al., 2021).

Corals suffer from additional biological and anthropogenic stressors that can be additive or synergistic to those caused by climate change (Hughes et al., 2017a). There are a range of coral diseases that have been identified in the Indian Ocean that affect hard corals by eating away at their tissues (Jogee et al., 2023). In addition, corallivores, or coral eaters, can cause damage that results in the removal of either coral tissue or skeletal structures, or both. This has been shown to have negative effects on the growth and fitness of hard coral colonies (Rotjan and Lewis, 2008).

An array of other anthropogenic factors, such as pollution, overfishing, and physical damage to reefs also play a role in added stress and shifting coral assemblages worldwide (Woodhead et al., 2019). Pollution on a reef can take many forms, whether physical debris, chemical waste, or other harmful agents. Agricultural or sewage runoff and the eutrophication that results from the enrichment of nutrients in the water reduces the light that can reach corals. The excessive phytoplankton growth that occurs also causes the rapid consumption of oxygen, creating anoxic water conditions that can negatively impact corals (Dubinsky and Stambler, 1996). Sewage pollution has also been linked to sedimentation that can cause coral death, while the toxic substances that may be present in the pollution are likely to decrease coral cover, affect reef species composition, and negatively impact coral growth and reproduction (Pastorok and Bilyard, 1985). Oil pollution detrimentally impacts reef health (Bak, 1987; Haapkylä et al., 2007) and can cause the complete absence of corals in heavily polluted areas, impaired reproduction and fewer juvenile corals, direct tissue damage, and decreased growth rates, among a variety of other health effects. (Loya and Rinkevich, 1980). Chemical pollution from agents such as pesticides, industrial pollutants, metals, and oil hydrocarbons has been demonstrated to reduce the efficiency and rate of photosynthesis by coral symbionts, diminish coral reproductive output, cause tissue damage, induce bleaching, and result in a multitude of other conditions (Sánchez-Bayo et al., 2011).

A form of pollution that is often overlooked, noise pollution, is impactful to coral reefs as, just as with any other ecosystem, sound is a crucial sensory tool used by the organisms who inhabit the reef to engage with one another and with the environment around them. Anthropogenic noise, such as that from boat motors affects fish physiology and larval movement, impairs nocturnal movement, alters invertebrate larval settlement, anti-predator responses, and also results in impaired movement ability reliant on acoustic cues. These effects have implications on the ecological structure of the reef ecosystem and can cause an imbalance that negatively impacts the health of the reef and its inhabitants (Ferrier-Pagès et al., 2021).

Overfishing and overharvesting of coral reef resources can also lead to an imbalance in the ecosystem that results in its degradation or, in extreme cases, collapse (Roberts, 1995; Gardner et al., 2003). In the case of the overfishing of triggerfish, which predate sea urchins, wide-scale habitat alterations have taken place, as the growth in urchins populations leads to a reduction of fish abundance and diversity as well as the deterioration of corals (McClanahan 1987; McClanahan et al., 1996). Tourism impacts on reefs have also become an increasing concern as development from tourist ventures has damaged inshore reefs through infilling and sedimentation. The desire for tourist recreation and souvenirs has also led to the overharvesting of marine products and damage to the reef via snorkeling and SCUBA diving activities (Hawkins and Roberts, 1996). Additional studies have demonstrated that higher coral cover is found at sites with the least anthropogenic impacts (Crehan et al., 2019).

Coral morphology, life history, and susceptibility to bleaching

Due to their varying life history strategies and environmental conditions, corals take on a range of morphologies and vary in their growth rate. These rates of growth are dependent on a range of environmental factors such as temperature, a sufficient calcium carbonate saturation to facilitate the building of coral skeletons, limited turbidity and sedimentation to allow for sunlight to reach the coral so that it can photosynthesize, salinity, pH, and currents that allow for gas and waste exchange, as well as increased food availability. Corals of the same species can modify their structure into various forms in order to survive in different zones and conditions, such as less light availability or greater wave action. Plate corals, for example, have a larger surface area to allow for a greater absorption of light (Heemsoth et al., 2014). These coral forms can also have ramifications on a coral's vulnerability to disturbance (Cresswell et al., 2020). Life history of coral also has impacts on coral loss and susceptibility, as the areas of the reef under greater pressure from stressors will be comprised of stress-tolerant corals that are more resistant to disturbance and death (Darling et al., 2013).

One such stressor affecting coral reefs is heat stress, that results in coral bleaching (as mentioned previously). While a variety of both host and symbiont characteristics can affect bleaching vulnerability (Dimond et al., 2012), a number of studies have demonstrated the connection between coral morphology and coral bleaching susceptibility (Loya et al., 2001; Dimond et al., 2012; McCowan et al., 2012; Smith et al., 2017; Mizerek et al., 2018). The basic principle is that corals with branching morphologies have thinner layers of tissues covering their skeleton and are typically more thermally sensitive, whereas corals with massive morphologies have thicker layers of tissue and are less sensitive to thermal stress (Wooldridge, 2014). This is partially due to the fact that thicker host tissues provide greater protection from light and moderate the stress experienced by the symbiont housed within them (Dimond at al., 2012). It has also been posited that this phenomenon is due to two contrasting strategies for the host coral to continuously supply the CO_2 necessary for the symbiont to perform photosynthesis. The method employed by thinner-tissue branching corals requires that CO_2 be readily supplemented by surrounding sea water. This strategy requires an efficient cycling of carbon, which is susceptible to collapse under suboptimal environmental conditions, such as periods of excessive light or thermal stress. The method utilized by thicker-tissue massive and encrusting growth forms is less reliant on sea water and is characterized by a lower photosynthetic demand for CO_2, resulting in greater thermal resistance. This decreased necessity for carbon dioxide is achieved as a result of thick tissue layers that have fluorescent pigments that limit the amount of light that reaches their symbionts, as well as a reduced density of those photosymbionts (Wooldridge, 2013). This breakdown in the photosynthetic process resulting in its inhibition, caused by (in this case) the host's failure to supply sufficient CO_2, causes oxidative stress in the tissues of the coral, leading to the expulsion of the symbiont in order to avoid further tissue damage (Lesser, 1996).

While this singular trait of corals having thicker host tissues has been widely demonstrated to provide substantial symbiont photoprotection and reduce bleaching (Dimond et al., 2012), coral morphology does not tell the whole story of bleaching susceptibility. It has been demonstrated that coral taxonomic relationships also play an important role in determining bleaching susceptibility. In a study that examined coral bleaching responses from several thermal stress events, it was found that coral family explained more bleaching variance among species than any other variable studied, including morphological and physiological traits (Mizerek et al., 2018). In another study it was found that while, across all data examined, a greater proportion of branching coral forms bleached as compared to massive coral forms, vulnerability to bleaching and death were not necessarily consistent with this trend within individual families. For example, it was observed that branching species within the family *Faviidae* had a lower rate of bleaching as compared to massive species within the same family (McCowan et al., 2012).

Even among individual coral colonies within the same species, bleaching susceptibility can vary due to genotypic differences in both the host coral and the symbiont that may lead to varying degrees of thermal sensitivity (Sampayo et al., 2008). Coral genotype impacts rates of coral growth and can affect survival under temperature stress (Drury et al., 2017). In addition, it has been demonstrated that certain photosynthetic symbionts are more capable of tolerating stress from excessive heat and light (Robison and Warner, 2006). Certain symbionts are also more conducive to reducing bleaching sensitivity and allowing for coral recovery following a bleaching event (Ulstrup et al., 2006). It is therefore necessary, due to the importance of both the host and the symbiont, to consider the holobiont (the coral and its zooxanthellae together) when considering conservation strategies and thermal stress response (Baird et al., 2009).

Study Area

Chumbe Island Coral Park (CHICOP) is located in the Western Indian Ocean, approximately eight kilometers west of Stone Town, Unguja. Unguja is the principal island in the Zanzibar archipelago and is approximately 37 kilometers off the coast of mainland Tanzania (Figure 2). Chumbe is a low-lying coral island that was established in 1994 as Tanzania's first Marine Protected Area (MPA) and the first privately managed MPA in the world. The island includes both the 55.06 hectare Chumbe Island Reef Sanctuary to the west, recognized as one of the most diverse reefs in East Africa, harboring at least 59 hard coral genera (around 90% of all hard coral species that have been recorded in Eastern African) (CHICOP, 2017) and 514 reef fish species, as well as a 16.64 hectare coral rag forest reserve (Reef Resilience Network, 2022). The well-preserved fringing reef is located on the western side of Chumbe inside of a clearly marked no-take zone, in which no fishing or any other harvesting of marine resources is permitted. Boat traffic, other than that directly affiliated with Chumbe, is also not allowed in the area. The northern portion of the fringing reef is located in shallower waters, while the reef gets deeper the further south it occurs. The northern reef is also more distinctly divided into the three primary reef zones (back reef, reef crest, and fore reef), while the southern portion of the reef has less clear delineation. The eastern side of Chumbe is not protected and CHICOP works with local communities to allow fishing in this area. This provides benefits from a spillover effect that occurs from the healthy reef, creating a more plentiful fish community for fishermen to draw from (CHICOP, 2017).

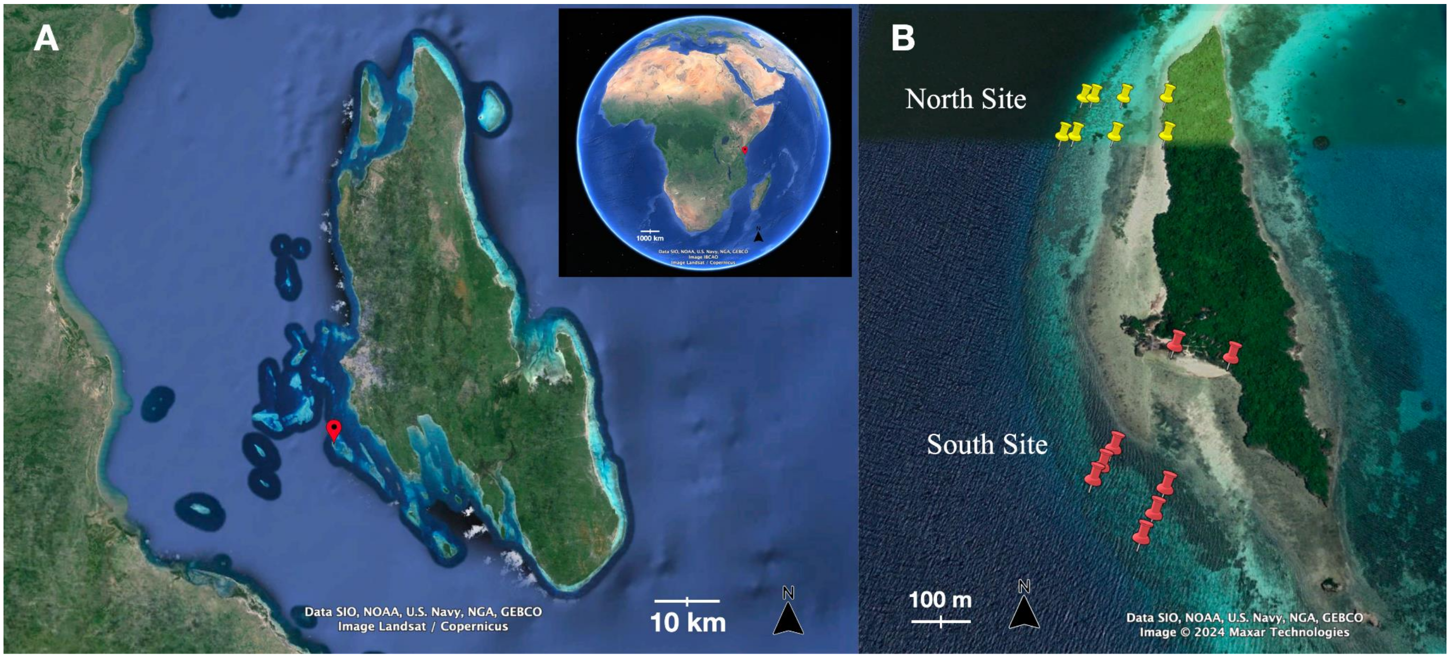

Figure 2. (A) Map of the African continent in the top-right corner with the location of Unguja Island marked with a red pin. The main photo is a map of Unguja Island with the location of Chumbe Island Coral Park marked. (B) Map of Chumbe Island Coral Park with the two sites examined in this study marked by pins, with yellow pins for the northern site and red pins for the southern site. Created in Google Earth (Accessed May 5th, 2024).

Bleaching in the Western Indian Ocean and at Chumbe

Globally, coral bleaching events have increased in frequency and intensity over the last decade. Likely as a result of the more thermally susceptible individuals succumbing to these events and/or local acclimatization, the sea surface temperature (SST) required to initiate bleaching has occurred at a significantly higher threshold (~0.5 °C higher than usual temperatures for the area) than in the previous decade (Sully et al., 2019). The Indian Ocean has not gone unaffected by this bleaching stress, as from January to August of 1998, the largest coral bleaching and mortality event on record occurred in the region, with major ecological impact on reef health and ecosystems (CORDIO, 1999; Quod and Bigot, 2000). In the coastal waters of Tanzania, in areas such as Misali, Mafia, and Pemba 90–100% of corals died after exposure to extreme thermal stress as a result of water temperatures that exceeded 32°C (CORDIO, 1999). This event was the most geographically widespread and significant bleaching of corals ever recorded, occuring in concert with a particularly severe El Niño Southern Oscillation (Wilkinson et al., 1999). The El Niño Southern Oscillation (ENSO) is a naturally occurring climate phenomenon that causes fluctuation in central and eastern equatorial Pacific Ocean temperatures, along with atmospheric changes (WHO, 2023). This phenomenon often significantly raises SST, resulting in considerable coral bleaching and mortality (Brown and Suharsono, 1990). As a response to the catastrophic bleaching and mortality event of 1998, Coastal Oceans Research and Development in the Indian Ocean (CORDIO) was established in 1999. This non-profit research organization has created a network and framework for monitoring bleaching throughout the Indian Ocean, which includes a Google Form for partners and volunteers to report bleaching, an Indian Ocean Bleaching Observations Dashboard, and regularly released bleaching reports (CORDIO, 2024).

In 2016, thermal stress in the Indian Ocean region nearly matched that which was experienced in 1998, with overall hard coral cover declining by 20% and fleshy algae cover increasing by almost 35% as compared to 25% loss of coral cover and a 2.5 times increase in algae as a result of the 1998 event. Notable from this event is that nearly two thirds of corals that bleached were able to recover, indicating an increased resistance to thermal stress as compared to 1998, when warming conditions were largely similar but the coral mortality observed after bleaching was higher (Gudka et al., 2018). This bleaching event resulted in a record high number of bleaching reports submitted to CORDIO for the region (Supplemental Figure 1). This event also coincided with a particularly strong ENSO event, which led to abnormally elevated ocean temperatures in the region (Xie and Fang, 2019). During the period from March to April, SST at Chumbe reached over 30°C, resulting in the bleaching of almost 80% of the hard corals within the protected area. In addition, live hard coral cover decreased by approximately 33% overall, with almost 50% hard coral mortality in the shallower portions of the reef. As a result of Chumbe's regulations to reduce the prevalence of stressors on the reef, its healthy populations of herbivorous fish, and a volunteer effort to remove algae growth, the reef was able to achieve a healthy balance (CHICOP, 2017) and more than 70% of the hard corals recovered (Reef Resilience Network, 2022). In the years with available bleaching data following this event (2017-2018, 2020-2021, 2021-2022, and 2022-2023) bleaching has been at a much more sustainable and less concerning level, not rising above a rate of more than 3% (Kloiber 2018; Kloiber 2022; Kloiber et al., 2023).

As an outcome of these increasingly common and severe bleaching events, resulting in widespread coral mortality, natural selection has selected for higher thermal tolerance (Smith-Keune and van Oppen, 2006). As was demonstrated in the 2016 bleaching event, there are now established populations of corals that are more resistant to thermal stress. This follows trends of coral resilience that were previously documented (Coles and Brown, 2003) and has implications for reef composition and increasing holobiont resilience. Worth noting is that, with the annual bleaching that is predicted to put reefs worldwide at risk later this century (Frieler et al., 2013), certain coral species will not be able to fully recover between events and will experience an increased vulnerability to bleaching (Schoepf et al., 2015). This increasing selective pressure will result in the decline and eventual extinction of certain species, while those coral species capable of high phenotypic plasticity will have the ability to acclimate to increasing thermal stress and survive. This recurring bleaching will likely lead to the selective diversity loss among corals and an overall degradation of coral reef ecosystem health worldwide (Grottoli et al., 2014).

Ongoing monitoring at Chumbe

CHICOP maintains a coral monitoring program that assesses coral health and various factors that influence ecosystem health. Coral monitoring has been conducted from September to March every year since 2006 and, since 2008, it has included the study of a fished reef site located outside of the Chumbe MPA. SSTs around Chumbe have also been recorded daily since 1997. In addition, the monitoring team assesses the prevalence and threat of coral diseases, the population density of fish species that are important to ecosystem health and balance such as triggerfish and herbivorous fish, and closely monitors the presence of coral predators, such as the crown-of-thorns starfish (*Acanthaster planci*), which has been occasionally physically removed from the reef when the species reaches a certain population density threshold or outbreaks occur.

Methods

This section details the methods utilized to accomplish this project.

Transects

A total of 18 transects were performed throughout the study. Nine of these transects occurred along the northern reef site and nine were taken along the southern portion of the reef. These transects were further subdivided into three transects each within the three major zones of the reef: the back reef, reef crest, and fore reef. Transects were 100 m in length and occurred parallel to the shoreline. Prior to data collection, the length of the transect was measured along the shoreline and landmarks were established that were visible from the water. The starting and ending point of each transect was recorded using GPS coordinates. The length of the three reef sections were estimated visually at each site and, in combination with aerial photography of the sites provided by Google Earth, were marked on a map (Figure 3). Transects swims were completed from South to North at each site. Along each transect a one meter by one meter sinking quadrat was randomly thrown a total of ten times and allowed to settle on the substrate. Approximately twelve fin kicks of each foot, depending on strength of the current, occurred between each throw of the quadrat to take data at approximately every ten meters along the transect. Once the transect had settled on the substrate, a picture approximately two meters directly above the quadrat was taken. Additional photos were taken of each individual coral colony in the quadrat, whether alive, bleached, or recently dead. Pictures of any suspected coral disease or other stressor were also taken. Estimated approximate water depth, the time of day, and weather and visibility conditions were recorded for each transect.

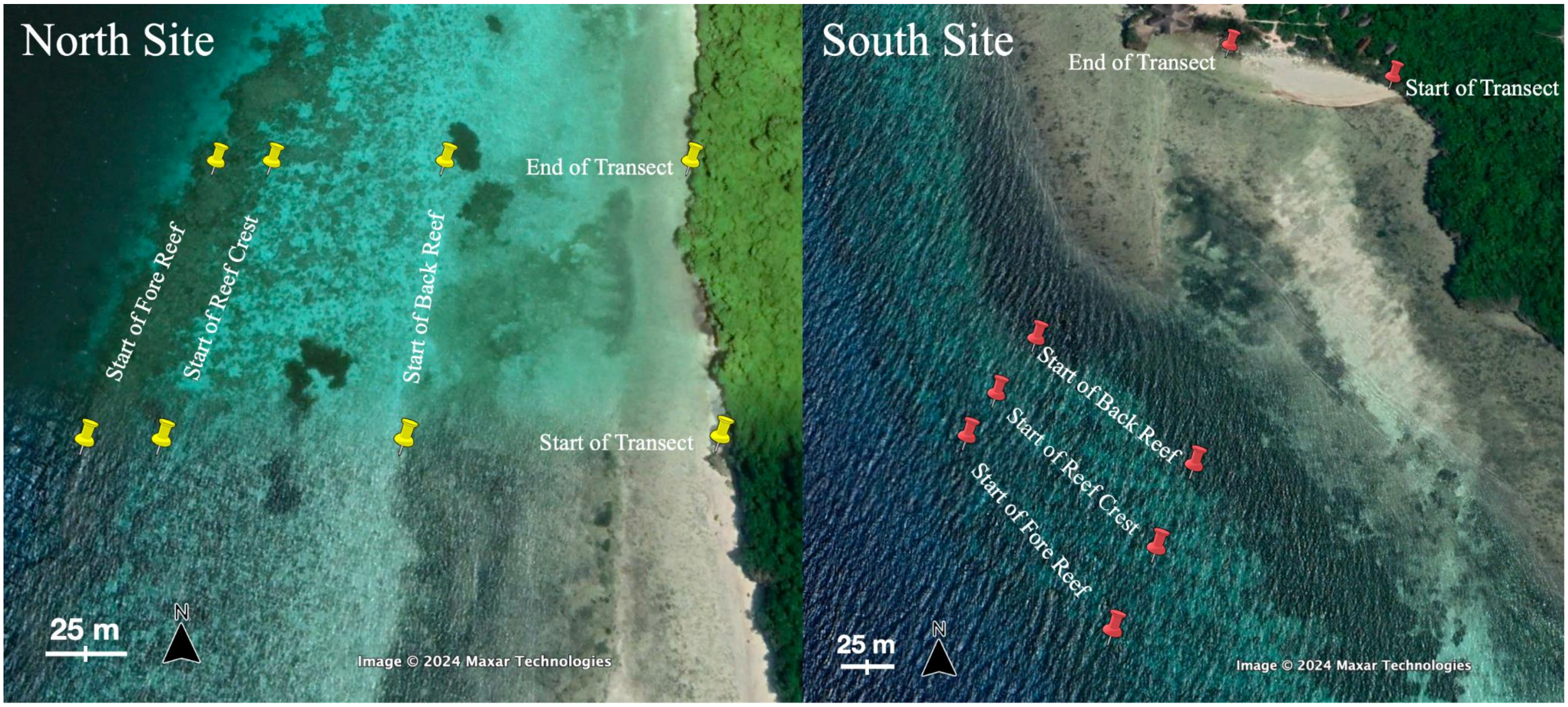

Figure 3. A map of the two sites where data collection occurred. Each section of the reef is also marked with pins at each respective site, with yellow pins used for the northern site and red for the southern site. Coordinates for the location of each pin can be found in Supplemental Table 1. Created in Google Earth (Accessed May 5th, 2024).

Ad hoc data

In order to gain a more comprehensive understanding of the stressors present along the reef at CHICOP, *ad hoc* data was collected throughout the study period. This data generally focused on pollution along the reef and the island itself, fishing pressure exerted on the protected reef, the presence of corallivores, coral disease presence and severity, coral bleaching due to air and/or sun exposure, and the presence of sedimentation. In addition, the coral forms and genera that were most affected by bleaching were identified using The Australian Coral Reef Society Indo Pacific Coral Finder (Kelley, 2009) and recorded. A survey of these factors, while not the primary purpose of this study, can help to understand the factors in addition to heat stress that are present along the reef and that may be contributing to coral bleaching and death.

Reef swims

In an effort to examine the reef as a whole, a total of three reef swims were completed from the beginning of the southern transect to the end of the northern transect. During these swims any *ad hoc* data concerning the categories mentioned above were noted. In addition, the northern, central, and southern sections of the reef were qualitatively compared. Due to time constraints, the central portion of the reef was unable to be surveyed as a part of this study, so these swims allowed for a brief overview of the health of this area of the reef as compared to the study sites. As a whole, these swims provided a more extensive understanding of how the reef ecosystem was being affected by the bleaching event on a broader scale that may not have been as apparent along a single transect. One of these swims occurred after a Category 1 cyclone had passed near the island, causing increased wave action and sediment disruption. The purpose of this final swim was to assess damage to the reef caused by the storm.

Sea surface temperature data

Historic SST data was kindly provided by Chumbe's long term monitoring program. The data was acquired using a Tidbit Stowaway logger, located four meters deep and tied on an anchored rack one meter above the sea floor. Daily temperature readings for the ongoing bleaching event were averaged for each day and compared with historical data from 1998 and 2016.

Image processing

After each transect was completed, photos from the underwater camera used in data collection were transferred to a laptop for processing. Each quadrat along the transect was assessed for healthy coral, bleached coral, and dead coral. Live corals were considered to be those that displayed a healthy color expected of their respective genera. Corals considered to be bleached included both paling and fully bleached corals that had lost their typical color. Dead corals were those that had died relatively recently and displayed algae coverage over an obvious coral skeleton.

ImageJ photo processing software was used to attain the percent coral cover and the percentage of coral in each quadrat that was considered to be alive, bleached, and dead. Photos of the quadrats were opened into the software by selecting file>>>open and choosing the desired file. The scale of one meter was then set within the program using the straight-line tool and the known measurement of the length of the quadrat. This line was drawn over the middle of the quadrat to minimize issues of perspective from the photo. This was achieved by clicking analyze>>>set scale, setting the unit of length to “m”, and establishing the known distance as “1”. Next, a combination of the wand and freehand selection tools were used to select a segment of either alive, bleached, or dead coral. When using the wand tool, the tolerance was adjusted to encompass the entire area of the coral being measured. To record the coral area within the selected area, analyze >>> measure was selected. This process was repeated for each section of coral in the quadrat until all coral was measured. In order to avoid double counting, after measuring a certain section of coral, the selected part of the image was deleted. (Figure 4). Upon measuring all coral areas of a particular category, all measurements for that category were summed. Each category of coral was expressed as a percentage of the overall quadrat. The three categories were summed to obtain coral cover within each quadrat.

In certain situations, such as with finger coral, where corals of each alive, bleached, and dead were interspersed as a kind of mosaic, the larger areas of a particular category were outlined and measured, while the remaining area was measured and estimates were made of what percentage of that area was composed of each category. This estimated percentage was then multiplied by the measured percentage of the area to obtain the overall percentage of the quadrat made up by each group in the mosaic area.

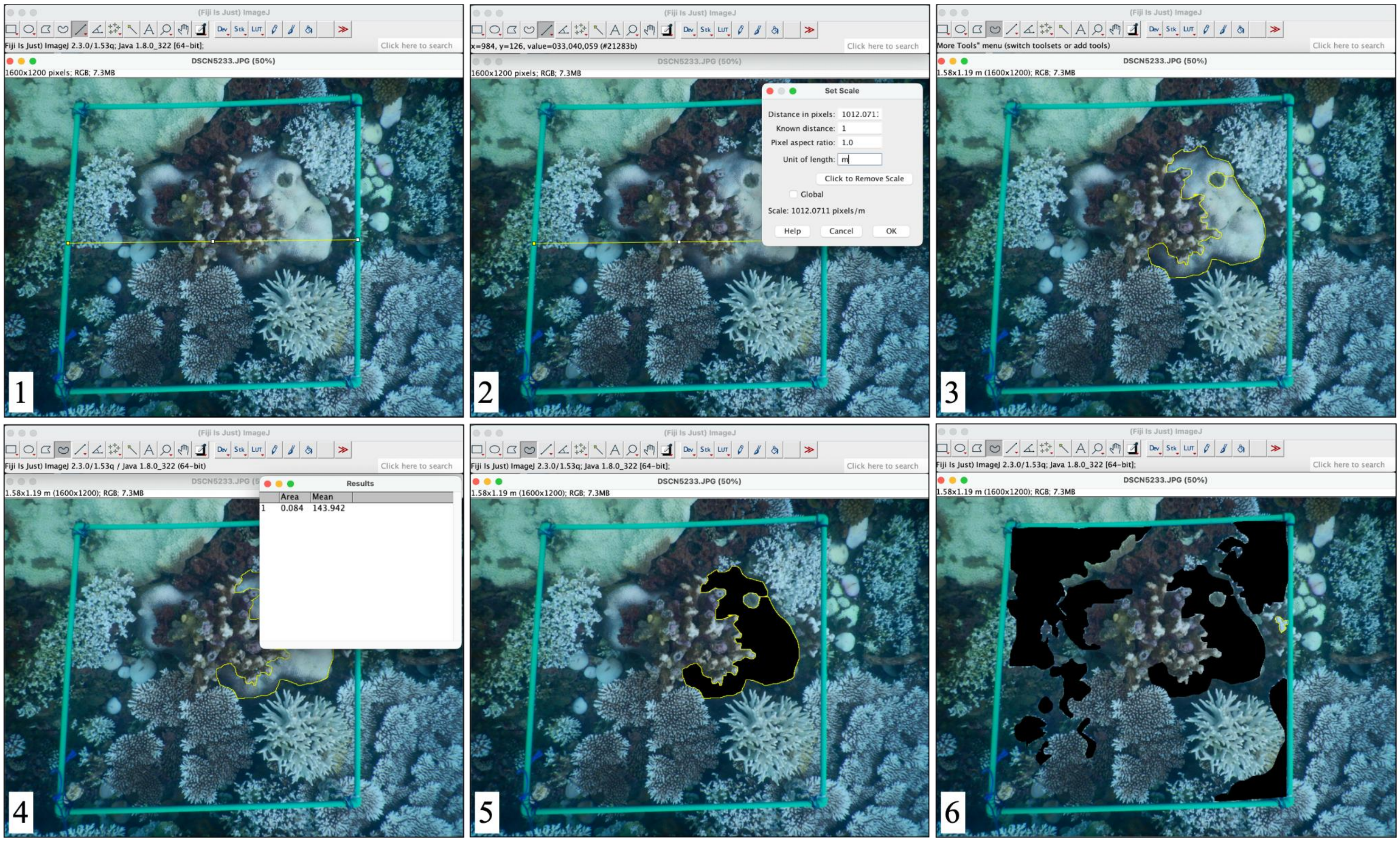

Figure 4. Step by step guide to photo processing. 1) Drawing a line across the middle of the quadrat. 2) Setting the scale of one meter. 3) Outlining the area of a bleached coral. 4) Measuring the area of the outlined coral. 5) Deleting the outlined area to eliminate double counting. 6) Example of a partially processed photo with deleted bleached corals that have been measured.

Data processing

All data collected in this study was compiled in Excel. All statistical tests and graph creation were performed in R 4.2.0. Assumptions of homogeneity of variance and normality of residuals were validated for the one-way ANOVA performed. Tukey HSD post-hoc tests were used to denote a significance of $P \leq .001$. Map creation was performed using Google Earth Pro.

Results

This section provides an overview of the findings of this study.

Coral cover

Average coral cover across all sections of both study sites was 38.65%, with the highest degree of coral cover (by a small margin) occurring along the Southern Reef Crest (52.3%). The southern reef crest and northern and southern fore reef sections had a significantly higher ($P \leq .001$) percentage of coral cover when compared to the northern and southern back reef and the northern reef crest (Figure 5).

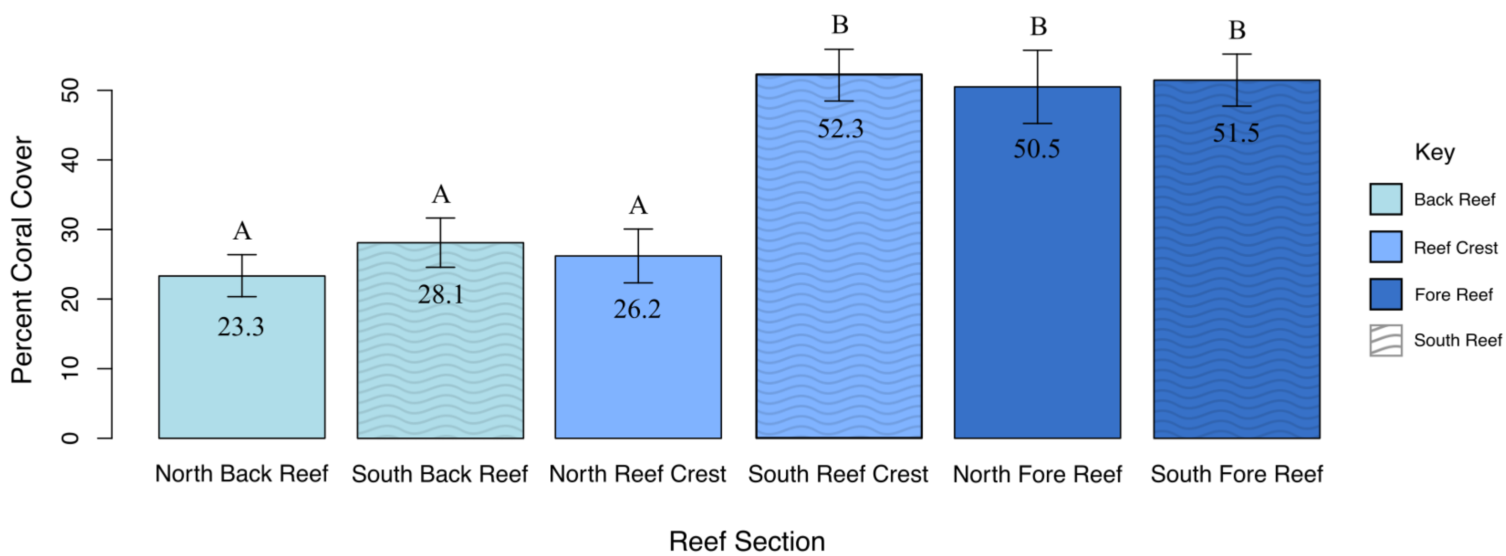

Figure 5. Bar plot depicting coral cover for the reef sections studied in this project. Reef section type is denoted by color and sections from the southern reef site are denoted by waves. Different letters denote significant differences based on Tukey's post hoc tests ($P \leq 0.001$). Error bars show 95% confidence intervals.

Coral condition as a percentage of the reef

With respect to the portion of the reef sampled as a part of this study, coral bleaching and death were lowest within the back reef of both the northern and southern sites. It should be noted that coral cover was also lower in the back reef, so an analysis of coral condition with respect to percent coral cover was also performed (see *Coral condition as a percentage of coral cover*). Bleaching percentages of sample area were highest and comparable along the northern and southern fore reef and the southern reef crest (30.5%, 32.7%, and 30.2%, respectively). In both the northern and southern portions of the fringing reef, death was highest along the reef crest (10.7% and 14.8%, respectively), with the latter being the highest percentage of death across all areas studied. Healthy living coral was at its highest prevalence in the northern back reef and fore reef (12.4% and 11.7%, respectively). In the southern reef, live coral area was comparable among the three reef sections, with the fore reef having the highest percentage of healthy coral at 9.9% (Figure 6).

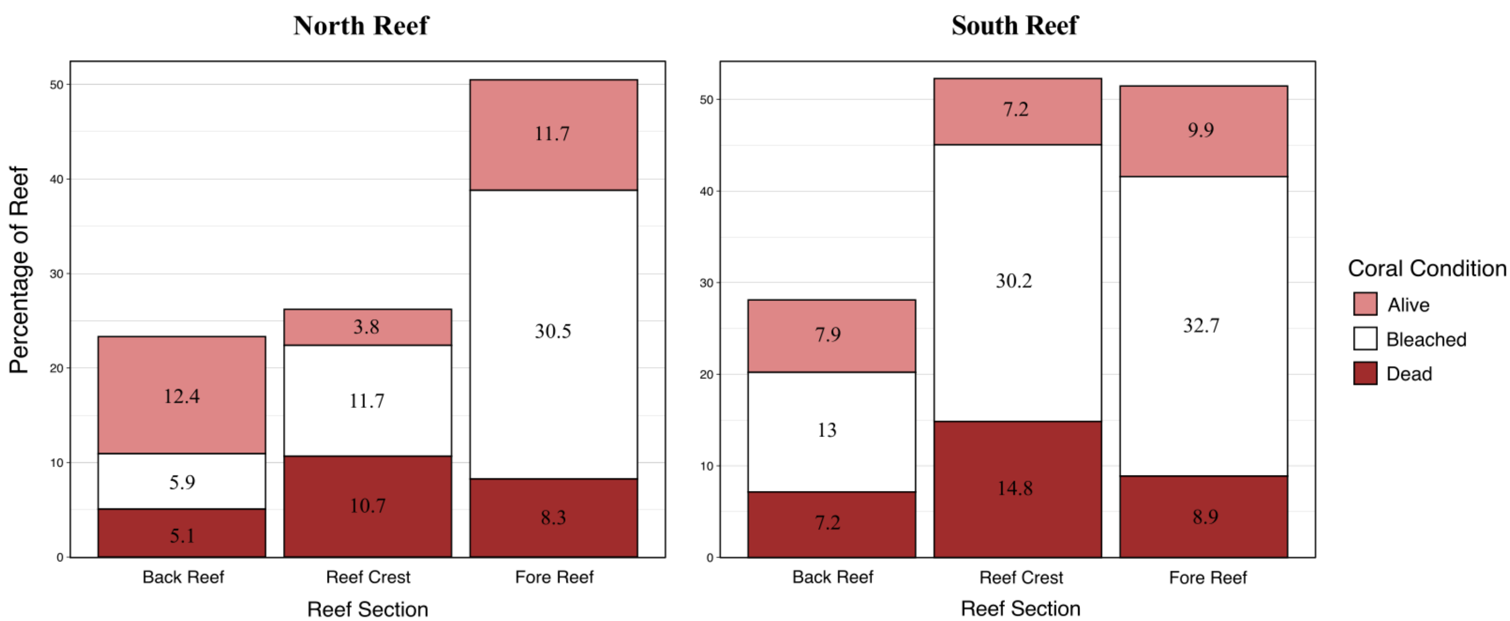

Figure 6. Bar plot depicting coral condition percentages along the reef. The dark red section of bars indicates dead coral area, the white area indicates bleached area, and the light red indicates live coral. Numbers within each section of the bar represent the raw percentage attributed to that respective portion and, summed together, the numbers of any given bar provide the percent coral coverage of that respective section of the reef.

Coral condition as a percentage of coral cover

Examining the coral condition as a percentage of the total coral cover within each respective section yields a slightly different view of coral health along the reef. Portion of coral cover that is bleached shows a consistent pattern between sites, with the fore reef having the highest percentage of bleaching, the reef crest having the intermediary value, and the back reef having the lowest percentage. The highest overall percentage of bleached coral cover was on the southern fore reef, followed closely by the northern fore reef and then southern reef crest (63.5%, 60.5%, and 57.8%, respectively). Death, too, followed a consistent pattern between sites, as it was highest along the northern (40.7%) and southern (28.4%) reef crests. Within each respective study site, death was second highest in the back reef and lowest in the fore reef. It is worth noting that the percentage of dead coral was greater than 16% for all reef sections. The substantially highest percentage of coral cover that was healthy was found within the northern back reef (53.1%), with the next largest percentage of living coral occurring within the southern back reef (28.1%). This coral condition, again, has a consistent pattern across study sites, with the intermediary value of living coral belonging to the fore reef and the lowest occurring along the reef crest (Figure 7).

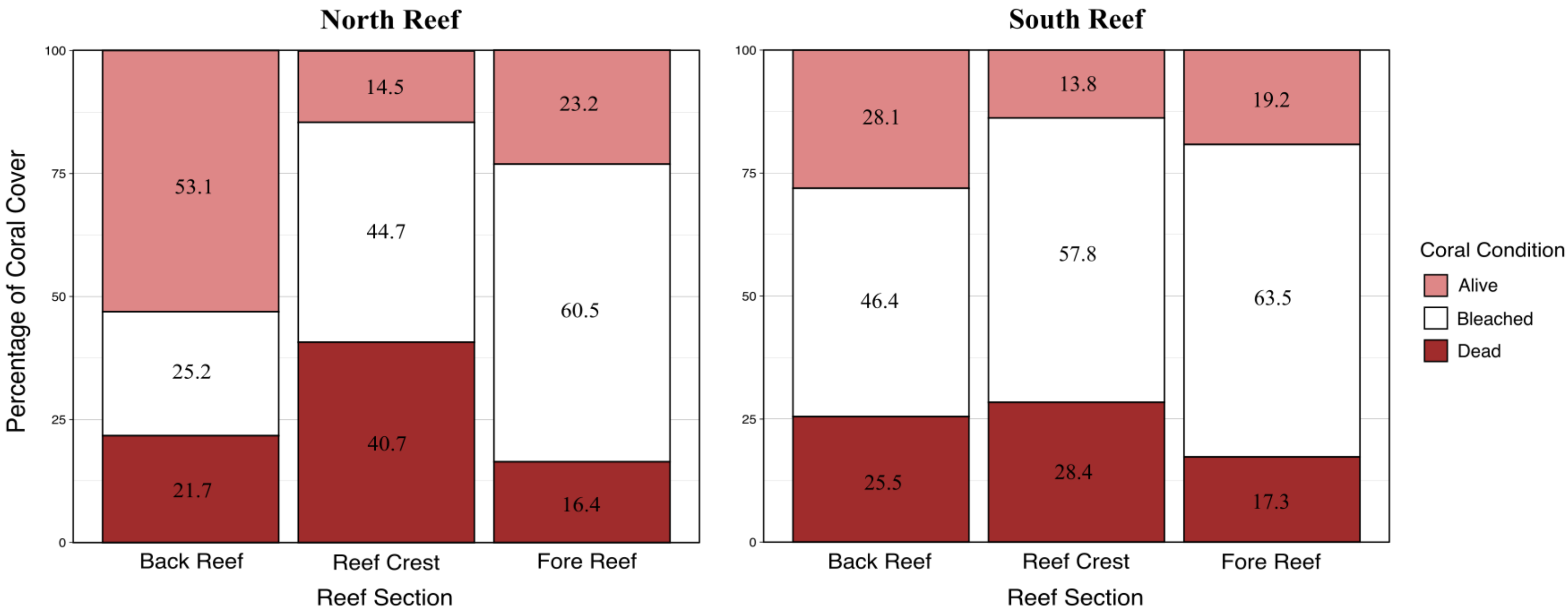

Figure 7. Bar plot depicting coral condition expressed as percentages of the average total coral cover within each respective section and site of the reef. The dark red section of bars indicates dead coral area, the white area indicates bleached area, and the light red indicates live coral. Numbers within each section of the bar represent the raw percentage attributed to that respective portion.

Sea surface temperature

Since the beginning of the calendar year, Chumbe has experienced an average SST of 30°C or more for a total of 65 days. In 2016 SST reached 30°C for 19 days, and in 1998, the worst year of bleaching ever experienced in the Indian Ocean, a total of 42 days of the entire year were above that threshold. SST also rose much earlier in 2024 than in past mass bleaching events and reached a new threshold of 31°C on three occasions (Figure 8).

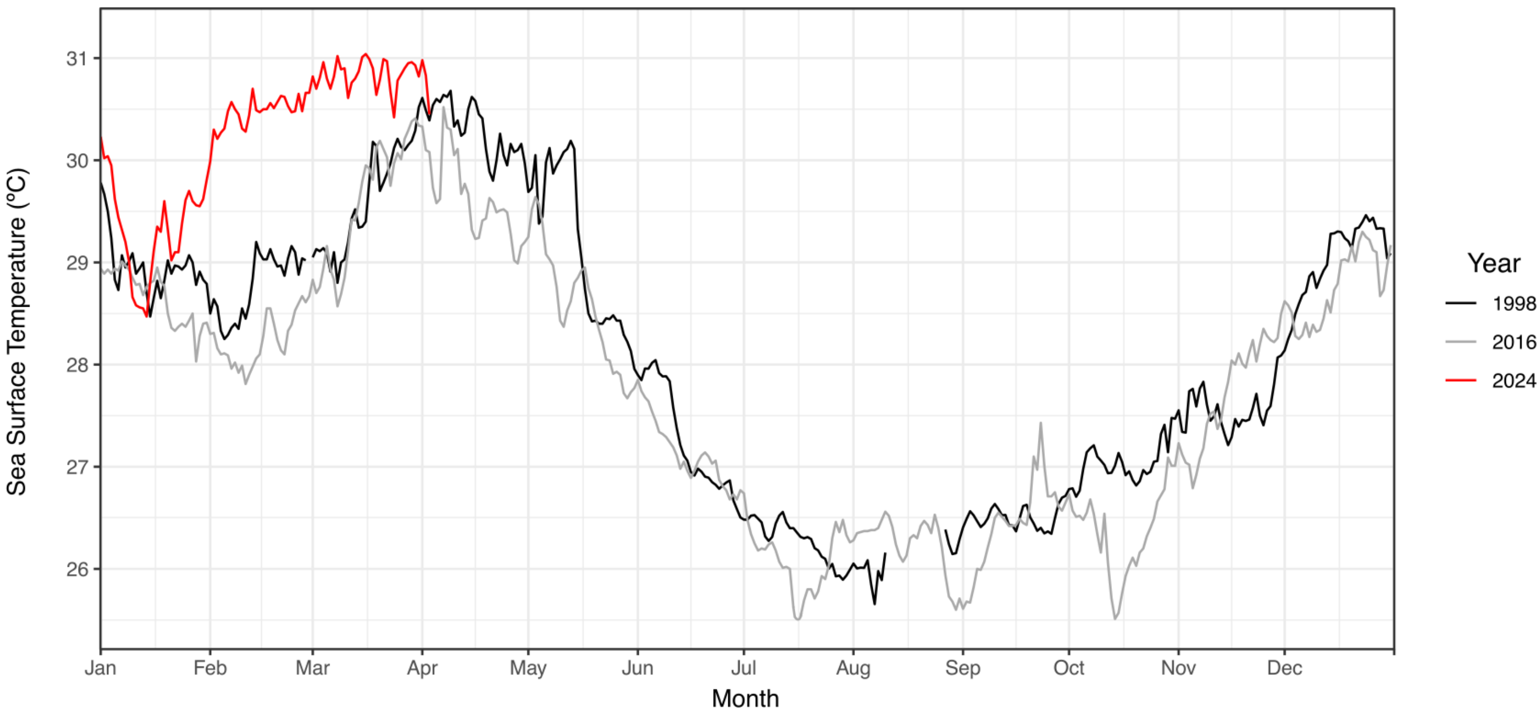

Figure 8. Line graph plotting the SST for the years of most devastating historical bleaching as compared to the 2024 bleaching event observed in this study. The black line indicates data from 1998, while the gray line shows 2016 and the red demonstrates 2024.

Coral forms and genera most susceptible to bleaching

While the reef at CHICOP is constituted by a variety of coral forms and genera, over the course of the study it became apparent that vulnerability to bleaching was not occurring equally, with a few genera and specific coral morphologies bleaching at higher rates than others. *Galaxea* was prevalent in both the north and south with large areas of bleaching. Notably, many of the bleached colonies still possessed their polyps, leaving the possibility of recovery when stress alleviates. Some colonies remained healthy, while others succumbed to death. This genera was most commonly found along the fore reef. Somewhat similarly, *Echinopora*, a lettuce coral, was widespread in both the northern and the southern portions of the reef, but larger areas of bleached *Echinopora* were present in the north and more often along the reef crest. Very little *Echinopora* coral was unbleached and a sizable portion was dead. *Isopora* was perhaps the most widespread genera present across both sites and all reef zones (excepting northern back reef for the most part). A large proportion of *Isopora* colonies, a columnar coral, remained unbleached other than paling at the top. Corals with lesser degrees of branching than *Isopora* typically remained tolerant to thermal stress. Also present throughout the entirety of the reef were free-living *Fungia* corals that were nearly always bleached or dead. The most prominent areas of bleaching in the south were from *Acropora*, a branching coral. Some of the thinnest branching *Acropora* and those in shallower waters, likely those that bleached first, were already dead at the start of the study period. *Seriatopora*, *Stylophora*, and *Pocillopora* were not present as commonly as the rest of the genera mentioned in this section, but these branching corals were almost always bleached when encountered. *Acropora* was also present in the north, but not to the same degree as the south. *Porites* finger corals were prominent primarily in the northern reef in all sections. They were also present at the southern site, but less commonly. Relatively frequently, *Porites* colonies resembled a mosaic of healthy, bleached, and dead coral, but a small portion completely succumbed to the bleaching event (Figure 9). A large number of colonies remained healthy and unbleached. Other *Porites* colonies of massive coral were present throughout the north and south, with a prominent presence in the back reef. These colonies were rarely fully bleached but did occasionally show paling or absence of growth on their upper sections (see *Air and sun exposure*). Another notable observation is that the northern portion of the northern reef site, specifically along the reef crest, was constituted of little other than a large expanse of long-dead coral rubble (Figure 9).

It is worth noting that trends in coral bleaching by genera and morphology were not absolute and varied both across the reef as a whole and within individual areas. There were several instances in which, within the same quadrat, bleaching did not necessarily follow the trends described above. An example of this is a quadrat with a massive coral that has bleached and is expressing fluorescent proteins, while some *Ispopora* colonies and an *Acropora* colony, both with branching morphologies, remain unbleached (Figure 9). Also worth mentioning is that this period of observation occurred toward the end of the bleaching event, capturing only a snapshot of the ongoing process of bleaching and death that can both vary throughout.

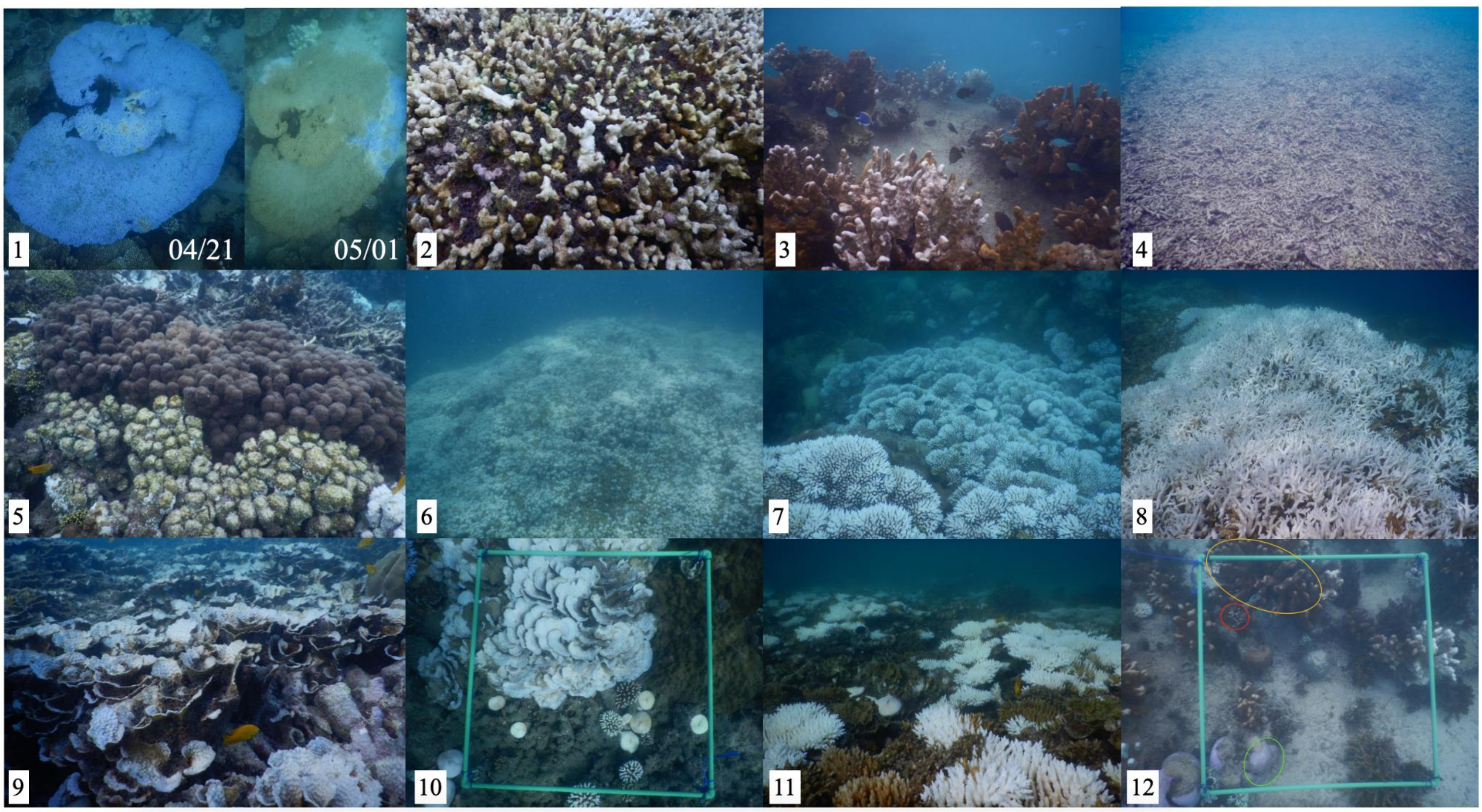

Figure 9. Photos of notable bleaching and death along the reef, including genera observed as most susceptible to thermal stress. 1) Table coral progressing from bleaching to death within the span of ten days. 2) Example of *Porites* finger coral. 3) Several *Isopora* colonies, some healthy and some bleached. 4) Long-dead coral rubble along the northern portion of the north reef site reef crest. 5) Healthy (above) and dying (below) *Galaxea* colonies. 6) Large area of *Galaxea* along the southern fore reef, some of which is bleached and some of which is dead. 7;8;11) *Acropora* colonies at the southern reef site at varying stages of bleaching and death. 9) *Echinopora* colonies at varying stages of bleaching and death. 10) Quadrat containing bleached *Echinopora* (lettuce) and *Fungia* (mushroom) corals. 12) Quadrat showing a bleached and fluorescing massive coral (indicated by green circle), an unbleached *Isopora* columnar coral (indicated by yellow circle), and a mostly unbleached *Acropora* branching colony (indicated by red circle), demonstrating that bleaching trends are not absolute.

Other coral stressors

This section details the range of coral stressors present along the reef.

Corallivores

Drupella snails were not directly observed throughout the study period, but several hermit crabs were observed inhabiting *Drupella* shells, indicating their presence along the reef. Two crown-of-thorns starfish, each smaller than half a meter in diameter, were found on the northern reef (Supplemental Figure 2). A sizable population of butterflyfish and parrotfish were present along the reef. Several butterflyfish were seen consuming coral polyps from both healthy and bleached coral. Large schools of juvenile parrot fish were observed along the northern reef crest consuming the coral rubble present there (Supplemental Figure 2). Larger parrot fish were seen consuming live coral tissue, dead coral skeleton, and algae along the reef as a whole but were present to a greater degree at the southern site.

Disease

Minimal disease was observed during the study period, but several suspected coral diseases were noted. The most commonly encountered disease was *Porites* ulcerative white spots. Additionally, suspected white band disease was observed in several instances during the study period (Supplemental Figure 3). White splotch disease was also encountered a few times.

Air and sun exposure

No living coral was observed exposed to air at low tide throughout the study period, despite the fact that the first day of data collection occurred on a more drastic tidal change (4.24 m) than had occurred for a number of years in the Zanzibar archipelago. During low tide on this day, portions of the northern reef crest were seen breaching the surface, but no live coral was observed in these exposed sections (Supplemental Figure 2).

Effect of sun exposure on bleaching was worst in the northern back reef, where a number of the massive coral colonies present were either bleached or had limited tissue on any horizontal surface that faced up toward the sun. Throughout the reef, coral colonies exhibited paling on their upper portion, with *Isopora* being particularly notable, as the tips of the genera's columns nearly always were paled or bleached (Supplemental Figure 2).

Pollution

Physical pollution along the reef was limited to a tire found lodged in the substrate in the north and a snorkeling mask found resting on a coral in the south. Due to the fact that Chumbe is a protected area, the vast majority of the debris found throughout the study was floating trash that came in with the tides. Despite Chumbe's distinction of the no-take zone, boats were regularly seen within the buoys that denote the protected area. While nothing was directly observed, the presence of these boats likely leads to pollution in the water from gas, oil, and other substances that may come from the vessels. The other major source of pollution was noise pollution as a result of the regular passage of the Zanzibar - Dar Es Salaam ferry (Supplemental Figure 4).

Sedimentation

The most obvious effects of sedimentation occurred in the back reef on the tops of massive corals. Sediment was suspended in the water column as a result of tidal changes, leaving it to settle on the tops of corals. In some cases, the tops of boulder corals no longer had tissues present due to the combined stress of sun exposure and sedimentation. The regular passage of the ferry also created large waves which stirred up settlement in the water column and could contribute to sedimentation on otherwise healthy coral colonies.

Physical damage

At the close of the study period, a Category 1 cyclone (cyclone Hidaya) passed nearby Chumbe and caused particularly strong wave action, as well as increased sediment suspension in the water column. The final reef swim was dedicated to documenting and understanding the extent of the storm damage. At the southern site, damage was worst along the back reef and reef crest, where many coral colonies (almost exclusively *Isopora* and *Acropora*) were fragmented or overturned. Nearly all of the *Isopora* colonies that were fragmented were still living. A majority of the *Acropora* fragments were already bleached or dead, but there were a number that were alive. Across both sites, *Echinopora* and *Galaxea* suffered damage and were strewn across the sea floor. The northern site, which is more protected from winds and wave action due to the typical wind direction and shape of the island, was less affected. A fewer number of *Isopora* colonies were fragmented or overturned. In addition, due to the fact that the north exhibits damage from past bleaching events, areas of widespread coral rubble are somewhat common, so it was more difficult to discern whether damage was historical or from the most recent storm. (Supplemental Figure 5).

Fishing pressures and vessel traffic

As previously mentioned, vessels not affiliated with CHICOP were regularly seen within the protected area. Although many had fishing equipment, no fishing or trapping practice was directly observed. Some traditional vessels that relied on a sail for transport may have been blown into the no-take zone, but others with motors intentionally drove through the area. The only item of marine debris related to fishing observed during the study period was a fishing line with two hooks attached to it encountered in the intertidal area of the southern site.

Fish populations and reef balance

Triggerfish were commonly seen at both the northern and southern reef sites. Very few sea urchins were seen along the reef as a result. As previously mentioned, a large population of parrot fish were present along the reef and were observed eating algae and dead coral, serving to break down old substrate and make it available for the settlement of new coral polyps. Other herbivorous fish, such as rabbit fish were seen along the reef, particularly in those areas where algae was growing following coral death. These fish were observed to eat the algae in these areas.

Miscellaneous observations relevant to reef health

Sea cucumbers were regularly seen feeding on algae in areas where dead coral was prevalent. These organisms were present in moderately high densities across the reef (Supplemental Figure 2). It is important to note that hard corals were not the only organisms bleaching as a part of this event. Bleached soft corals and anemones were regularly encountered during the study. Two Giant tritons (*Charonia tritonis*), which prey on crown-of-thorns starfish, were encountered near one another on the final reef swim (Supplemental Figure 2). Blacktip reef sharks (*Carcharhinus melanopterus*) were observed on two occasions in the water and many more from outside the water. Two sea turtles, likely hawksbill (*Eretmochelys imbricata*), were also observed along the reef. One of these sightings of each the sea turtle and shark occurred along the southern site, while the other occurred along the middle reef area.

Middle reef

The middle reef was observed to be in a condition that was largely in alignment with all of the observations previously described. Given that the southern portion of the reef is in deeper water and the northern portion of the reef is in slightly shallower water, the middle section serves as a gradient connecting the two sites examined in this study. The only stark difference observed in the middle reef section was that the reef crest, similar to the northern edge of the reef crest at the northern study site, was the most expansive area of long-dead coral rubble seen throughout the research period. New coral colonies were observed to be growing on top of this old death, but many were bleached white.

Discussion

This section gives an overview of the most important results and provides context for the significance of this study on a broader scale.

Coral cover

In every section of the reef, the northern site had lower coral cover than the southern site (Figure 5). The difference was most drastic, however, between the northern and southern reef crests. Due to the shallow nature of the north and the elevated location of the reef crest, the northern reef crest has been previously devastated from past bleaching events and large areas of coral rubble are frequent. This reflects a trend witnessed throughout the study period and that is apparent between sites: corals that live in shallow waters are more susceptible to thermal and light stress and, therefore, bleaching and death (Winslow et al., 2024). Much like the southern reef crest during this bleaching event (Figure 7), the northern reef crest likely experienced a high degree of coral death in past events, such as 2016. The time frame since disruptive events like these has not been long enough to allow for repopulation of this section by young corals, so this zone remains at a coral cover similar to that of the northern or southern back reef. Otherwise, the coral cover data follows which would be expected from the various reef zones under healthy conditions. As previously described, it is typical for the lowest coral diversity and density to occur in the back reef and the greatest amount of coral growth to take place at the reef crest, followed closely by the fore reef. (Heemsoth et al., 2014; Kennedy and Roelfsema, 2020).

Coral condition

Due to the fact that the northern site is in shallower water, it has experienced the effects of thermal stress of past events more severely. This has allowed for the proliferation of thermally-resistant corals to exist there, resulting in a higher percentage of live coral cover and lower incidences of bleaching in each section of the north as compared to the south (Figure 7). Despite the fact that the south is in deeper waters, the rate of bleaching and death tends to be more severe because there are vulnerable corals that live there that have not been wiped out by past bleaching events. Due to the nature of the back reef corals having to regularly endure periods of warmer water and sun exposure during low tide, the coral forms and genera found there are more resistant to bleaching and death. For these combined reasons, the heartiest, most thermally-resistant corals are located in the northern backreef, which explains the substantially higher degree of living tissue and lower degree of bleaching encountered there. Death and bleaching were highest on the reef crest in both the north and south due to the zone's shallow nature, leading to light stress in addition to heat stress (Figure 7). This event likely represented the first time that thermal stress was severe enough for a long enough duration that many of the corals along the southern site, those that had been previously safeguarded by the additional depth, were subjected to bleaching and subsequent death.

Sea surface temperature

The SST at which corals begin bleaching varies by region and by individual coral form, genera, or individual. However, it is well-documented that accumulated heat stress is a strong predictor of mass coral bleaching (Skirving et al., 2020). As ocean waters continue to warm, especially earlier in the year and for longer durations, the effects on coral and reef health will be disastrous. The United States National Oceanic and Atmospheric Administration (NOAA) has qualified the most recent bleaching event, and the one reported on in this study, as the fourth global mass bleaching event on record, and the second in the last 10 years (NOAA, 2024). The unprecedented thermal stress experienced by corals during this event led to three new levels being added to the NOAA Coral Reef Watch alerts, which forecast bleaching susceptibility across the world. The new levels allow for the creation of more accurate and detailed alerts, but also extend the bleaching watch from the previous cap of Level 2, which indicates "Risk of Reef-Wide Bleaching with Mortality of Heat-Sensitive Corals," to the new Level 5, which forecasts "Risk of Near Complete Mortality (> 80% of corals)" (NOAA Coral Reef Watch, 2024).

Bleaching trends

Bleaching across the reef as a whole occurred primarily in the most vulnerable of coral morphologies, branching corals. The degree of branching that seemed to be the threshold for this event was that of the columnar coral *Isopora*. While corals with more branching did remain healthy and those with less branching (including massive colonies) did bleach, this susceptibility to bleaching according to morphology remained largely accurate. Coral recruitment in Kenya following the bleaching event in 1998 saw that the fastest growing genera to reestablish on the reef were *Echinopora*, *Acropora*, *Pocillopora*, and *Porites* (Tamelander, 2002). *Galaxea* is also an aggressive competitor with a rapid growth rate that can sting and outcompete surrounding coral colonies (Chalias, 2022). This likely partially explains the expansive colonies of each *Echinopora* and *Galaxea* found along the northern and southern sites, as these corals are able to rapidly take advantage of open space following bleaching events. Given that both were widely bleached and not yet dead, it is likely that many of these colonies will recover and be able to further expand into newly available space. So called “weedy” corals, such as *Acropora* and *Pocillopora,* are fast growing and the first to quickly recolonize a reef following a disturbance (Mangubhai, 2017). This fast-growing nature could mean hope for the reestablishment of these corals if given sufficient time between warming periods. *Porites’* extensive presence in the north is another sign of recovery following bleaching and echoes the fact that heartier, more thermally-resistant corals are those that are surviving and proliferating most.

Other coral stressors

This section describes the impacts of coral stressors on reef health and recovery as well as offers suggestions on how to mitigate stress where possible and practical.

Corallivores

Corallivores do not seem to be an overwhelming threat along the reef at Chumbe. Very few crown-of-thorns starfish were seen throughout the survey period, no living *Drupella* snails were encountered, and fish that prey on coral polyps were not overpopulated along the reef. With that being said, in a previous study at Chumbe, *Drupella* snails were encountered in the majority of sample areas (Turley, 2016). As an added concern, previous studies have demonstrated that *Drupella* are more inclined to prey on stressed corals (Tsang and Ang, 2015), leaving coral colonies especially vulnerable during and immediately following bleaching stress. These snails have been shown to devastate coral reefs, consuming tens of meters of otherwise healthy coral tissue in months and leaving behind areas of coral rubble in their wake (Cumming, 2009). It is, therefore, crucially important that, along with crown-of-thorns, butterflyfish, and parrotfish, these corallivores continue to be monitored. Monitoring and, if necessary, preventative action to cull populations before outbreaks occur could save the reef from the collapse of coral populations and communities, a significant decrease in coral coverage, and cascading detrimental effects on fish populations and benthic communities (Kayal et al., 2012).

Disease

Widespread coral disease was not found in this study, which is consistent with Chumbe's monitoring data that has encountered a low prevalence of coral diseases across the reef (CHICOP, 2017). Another project done on coral disease at Chumbe also concluded that disease occurred in low numbers, but noted that compromised reef health as a result of bleaching events could result in a greater posed threat by disease (Turley, 2016). Rising ocean temperatures have been linked with higher rates of infection within reef ecosystems (Selig et al., 2006). Coral disease rates have tripled over the course of the last 25 years, reaching 9.92% globally in 2023. It has been predicted that the prevalence of coral disease could reach 76.8% globally by 2100 if temperatures continue to rise along their current trajectory (Burke et al., 2023). These findings highlight the importance of continued disease monitoring, especially during periods of high thermal stress, and, if necessary, the use of techniques to alleviate or halt the transmission of infections in the case of an outbreak. There has been success in the past with removing the afflicted area using syringes or pumps, then using clay or underwater epoxy to cover the area and halt cyanobacterial growth. In the event of an outbreak, access to areas with high levels of disease can be altogether restricted to prevent transmission between corals (Reef Resilience Network, 2024b).

Pollution, Sedimentation, Fishing pressures and vessel traffic

A variety of other coral stressors were present along the reef including air and sun exposure, physical trash and noise pollution, sedimentation, and boat traffic. The issue of air and sun exposure is a problem that corals must endure depending on their location along the reef, with the most heat and light resistant coral genera and morphologies, such as massive *Porites* colonies, inhabiting the areas with the most difficult living conditions. Pollution is a region-wide problem across the Zanzibar archipelago that must be addressed more holistically before any significant decrease in floating trash will be seen at Chumbe. In order to limit pollution from vessels and any other debris that may enter into the water as a result, stricter enforcement of no boat passage should be enforced within the protected area.

One of the largest perpetrators of many of these issues, one that actively contributes to noise pollution, heavy wave action, and sedimentation along the reef, is the passage of the Zanzibar - Dar Es Salaam ferry, which, between the two operating ferry companies, travels in waters near Chumbe anywhere from 14 to 18 times each day (Kilimanjaro Fast Ferries, 2024; Zan Fast Ferries, 2024). The observed proximity of the ferry to the protected zone was inconsistent, with some vessels passing by a sizeable distance away from the buoys of the established protected zone and others passing just outside of the markers. Due to this inconsistency in the routing, extending the protected area by a few hundred meters would not significantly impact the ferry route or arrival time, but would allow a greater area over which the wave energy created by the ferry could dissipate before reaching coral colonies. The ferry could also reduce its speed when passing the protected area to reduce wave action. Another possibility for a solution is the construction of a submerged breakwater structure, which is effective in dispersing wave energy and safeguarding reef structures without compromising aesthetics (Nguyet-Minh et al., 2022).

As a means to mitigate negative effects from noise pollution while increasing reef recovery and growth overall, a soundscape of a healthy reef could be utilized at Chumbe. A recent study demonstrated a positive correlation between acoustic enrichment and larval settlement of coral, showing significantly higher settlement rates at a degraded reef site with an enriched soundscape as compared to both healthy and degraded reefs without enriched soundscapes (Aoki et al., 2024). Coral larvae have been found to be particularly attracted to the low-frequency sounds produced by territorial fish, which can protect corals as they grow on the reef. This technique can be further enhanced through the capture and dispersal of “heat-tolerant” larvae from coral that have survived previous bleaching stress. These larvae can be obtained as they float to the top of the water column or by surrounding resistant coral with a cone-shaped net (Ferguson, 2024). This soundscape can also help to counteract the impacts of anthropogenic noise pollution, as it has been demonstrated that coral larvae will move and settle away from areas with high incidence of boat traffic or other polluting sounds (Ferrier-Pagès et al., 2021).

Physical damage

Branching corals were the most impacted from the storm damage, adding another additional pressure to these coral morphologies outside of heat stress. Many of the damaged corals that were overturned or broken by the storm were left resting on other corals, which could not only mean death for the fragmented corals, but also negative health effects for the other colony. This proximity could lead to one colony blocking out the sun from the other colony and preventing it from photosynthesizing, or the two colonies could begin competing for space by stinging and killing one another. Previous studies have demonstrated that the strong wind and wave action caused by tropical cyclones results in a decline in coral cover, specifically in branching corals like *Acropora*, *Stylophora*, and *Pocillopora* (Carter et al., 2022). It has also been demonstrated that the effect of large cyclones with high wind speeds can cause major coral loss at up to 800 km outside of the storm path as a result of the wave energy they generate (Puotinen et al., 2020). It is unclear whether these storms will also increase in frequency or not, as models have shown both scenarios (Lee et al., 2020), but projections show that tropical cyclones will only increase in intensity as the planet continues to warm (Pérez-Alarcón et al., 2023), further amplifying the negative impact and destruction that these weather events will have on coral reef ecosystems. The aforementioned submerged breakwater structure could be a possible mitigation measure that would result in the reduction of wave energy and overall damage to the reef due to storms.

Takeaways

The reef at Chumbe experiences a multitude of stressors, many of which remain at sustainable levels to allow for healthy coral growth, but a severe warming event has caused widespread bleaching and death across the reef. Incidences of both bleaching and death have occurred more frequently along the southern portion of the reef. These conditions are widespread in areas of the reef, such as the southern reef crest and fore reef, that have likely not experienced significant bleaching stress in the past. This event marks the first time that many of the more vulnerable corals in these sections have been impacted by high degrees of thermal stress. The reef crest is the reef zone with the worst incidence of death across both sites, reflecting the high degree of thermal and light stress experienced in this section. The northern site shows evidence of mass mortality from past bleaching events that have led to the proliferation of thermally resistant coral forms and genera. Heavily branching corals are present in a far smaller degree in the north and overall coral cover remains lower. If thermal conditions continue to exacerbate, the northern site likely reflects the future of the southern site as vulnerable coral colonies are selected against by both thermal stress and physical damage from storms and wave action.

Reef recovery

As the reef progresses through the aftermath of this bleaching event and begins the recovery process, several factors are important to consider to facilitate reef restoration. Along the reef, herbivorous fish and sea cucumbers were seen consuming the algae that was starting to form on recently dead coral. Hard coral cover typically recovers best at sites with a higher herbivorous fish abundance and less macroalgae (Evans et al., 2020). Carefully monitoring algal outbreaks following extensive coral death will be crucial to ensuring that the algae does not overtake recovering or otherwise healthy corals. If necessary, steps should be taken to remove excessive algae growth, as was done following the 2016 bleaching event at Chumbe. These events also have ramifications for fish abundance and taxonomic richness, with severe long term effects on coral reef health and ecosystem structure six years after the initial disturbance (Garpe et al., 2006). This change in assemblages not only has an impact on ecosystem health, but also on local communities that rely on fishing for their income and nutrition. Reef health at Chumbe directly impacts these individuals and their livelihoods as the spillover of fish populations and other reef inhabitants outside of the protected area can be sustainably harvested for human consumption and use. It is crucial that the reef at Chumbe continue to be monitored throughout this recovery period so as to best understand how coral repopulation and recovery is progressing. As bleaching events become more frequent and severe, understanding how to best facilitate the recovery process following a bleaching period will be crucial to long-term reef health and resilience.

Future of coral reefs

In the short term, a range of coral conservation strategies are being implemented to restore coral reefs worldwide. These strategies differ in their effectiveness and cost, but some commonly practiced methods are the formation of artificial reef structures and substrate (Bayraktarov et al., 2019), the creation of coral nurseries to farm individual coral colonies that are then transplanted onto reefs (Herlan and Lirman, 2008; Rinkevich, 2014; Ishida-Castañeda, 2019), the use of molecular methods to assess how corals propagate along the reef to inform recovery dynamics and transplantation (Baums, 2008), and the use of soundscapes to increase coral settlement on unhealthy reefs (Aoki et al., 2024). These restoration projects, however, are often costly, occur over a short duration of time, and are implemented in small areas (Bayraktarov et al., 2019). MPAs, such as Chumbe, have been shown to be effective in mitigating multiple forms of coral reef pollution, especially from microbes (Kaimba et al., 2019). While protected status can reduce some of the additive pressures facing corals, these measures are not sufficient to result in differences in bleaching prevalence in protected areas relative to non-protected areas for corals facing thermal stress (Hughes et al., 2017b; Johnson et al., 2022).

If coral reef ecosystems are to be safeguarded in the long-term, no degree of coral restoration effort will be sufficient if ocean conditions are unsuitable for sustainable coral growth and survival. Predictions indicate that as little as 0.2% of global coral will remain at a climate warming of 1.5°C, with 0% at a 2.0°C warming, as corals will experience heat waves that occur at too high an intensity and frequency for recovery to be possible (Dixon et al., 2022). A special report by the IPCC similarly concluded that coral reefs would decline by 70-90% with a global warming of 1.5°C, while virtually all would be lost a rise of 2ºC. The report also warns that limiting global warming to 1.5°C will require “rapid and far-reaching” action, with anthropogenic CO_2 needing to fall by around 45% by 2030 compared to the emission levels from 2010, while reaching net zero emissions by around 2050 (IPCC, 2018). Along with thermal stress, climate change is making storms more severe, causing more intense damage to coral reefs as a result. These selective pressures, which both affect branching corals to a greater degree, as demonstrated in this study, will likely cause the drastic reduction, and possible extinction, of these coral morphologies. In addition, widespread loss in coral diversity and reef health degradation will occur.

There is some cause for hope, however, as bleaching responses from corals have diminished in some areas across major bleaching events, such as the bleaching response in 2016 as compared to that of 1998 (McClanahan, 2017). Additionally, it has been demonstrated that certain coral species are able to recover between bleaching events that occur as frequently as annually (Schoepf et al., 2015). While these factors will not be sufficient for coral survival in a continuously warming climate, they do provide us time to preserve reefs through restoration and rehabilitation efforts while we work to achieve carbon neutrality (Voolstra et al, 2021). It is imperative that we work to both safeguard reefs in the coming decades through local or regional restoration efforts, while working at a global scale to reduce global warming to the greatest extent possible. Failure to do so will result in the collapse of one of the most biodiverse and important ecosystems on the planet.

"People say that coral reefs might be the first ecosystem we could lose, and I like to think that, therefore, they are the first ecosystem we can save. If they're on the brink, and we can save coral reefs, we can save anything. And they become a beacon of hope." - Steve Simpson, professor of marine biology and global change at the University of Bristol (Ferguson, 2024).

Limitations of this study

A number of limitations were encountered throughout the course of the study that affected data collection and processing in various ways. The primary methodology relied on snorkeling, which resulted in limited ability to regularly travel to the depths necessary to properly observe every coral in every quadrat. To mitigate this, pictures were taken of every coral colony, but some misidentification of coral condition may have been made. The methodology used in this study required a picture be taken from above each quadrat to facilitate data processing, but many corals, specifically those of the back reef and reef crest showed signs of bleaching or death at the top, but healthy coral tissue on the sides of the colony, which may have resulted in slightly inflated reporting of bleaching and death, as well as a slight undercounting of healthy tissue. The limited timeframe in which the study took place meant that research could not occur over the entirety of the bleaching event, so valuable context as to how the reef was progressing through the event may have been lost. This project presents a snapshot of the bleaching event as it was observed over the project period and it should be noted that significant changes in living tissue, bleaching, and death can occur both throughout and long after the period of thermal stress. Finally, there was limited training performed prior to the study period in discerning coral bleaching or death by means of thermal stress as opposed to bleaching or death as a result of disease. Consequently, bleaching and death resulting from diseased corals may have been counted alongside bleaching and stress from the bleaching event.

Recommendations Summary

- Careful monitoring of the end of the bleaching event and its aftermath
    - ensuring healthy populations of herbivorous fishes are present along the reef and monitoring to ensure that excessive algae growth does not occur
- Reef restoration
    - implementing a soundscape of a healthy reef to increase larval settlement and
    - counteract the impacts of anthropogenic noise pollution
- Stricter enforcement of no boat passage should be enforced within the protected area.

- Continued coral health monitoring
    - continued disease and corallivore monitoring
        - proper actions to prevent outbreaks before they happen
- Solutions to problems caused by the ferry
    - extending the protected area by a few hundred meters to further dissipate wave energy
    - reduction of ferry speed when passing the protected area
    - installation of a submerged breakwater structure

Conclusion

This study provides a microcosm example of the fourth global bleaching event and the effect that a range of stressors, but primarily thermal stress, have on both shallower and deeper water corals along the Chumbe reef. Bleaching and death was widespread across the reef as a result of thermal stress, with higher degrees of bleaching generally occurring in deeper water. Hard coral cover was lower at the shallower northern site, largely as a result of many areas of coral rubble from past bleaching events. The findings of this study suggest that reef areas impacted by previous bleaching harbor coral forms and genera that are less susceptible to thermal stress, while deeper areas have branching corals and other colonies that are more affected by bleaching conditions. The combined selection pressures of thermal stress and storm damage will continue to select against branching coral forms, which will lead to their decline across the reef. This loss of coral will lead to less diversity along the reef and cascading ramifications for fish communities and reef inhabitants. While efforts can be made to manage stressors at a local level, the vast majority of corals will not survive in a warming climate.

Widespread, significant actions must be taken to address the fundamental problems of global warming and climate change if coral reef ecosystems are going to survive in the long-term.

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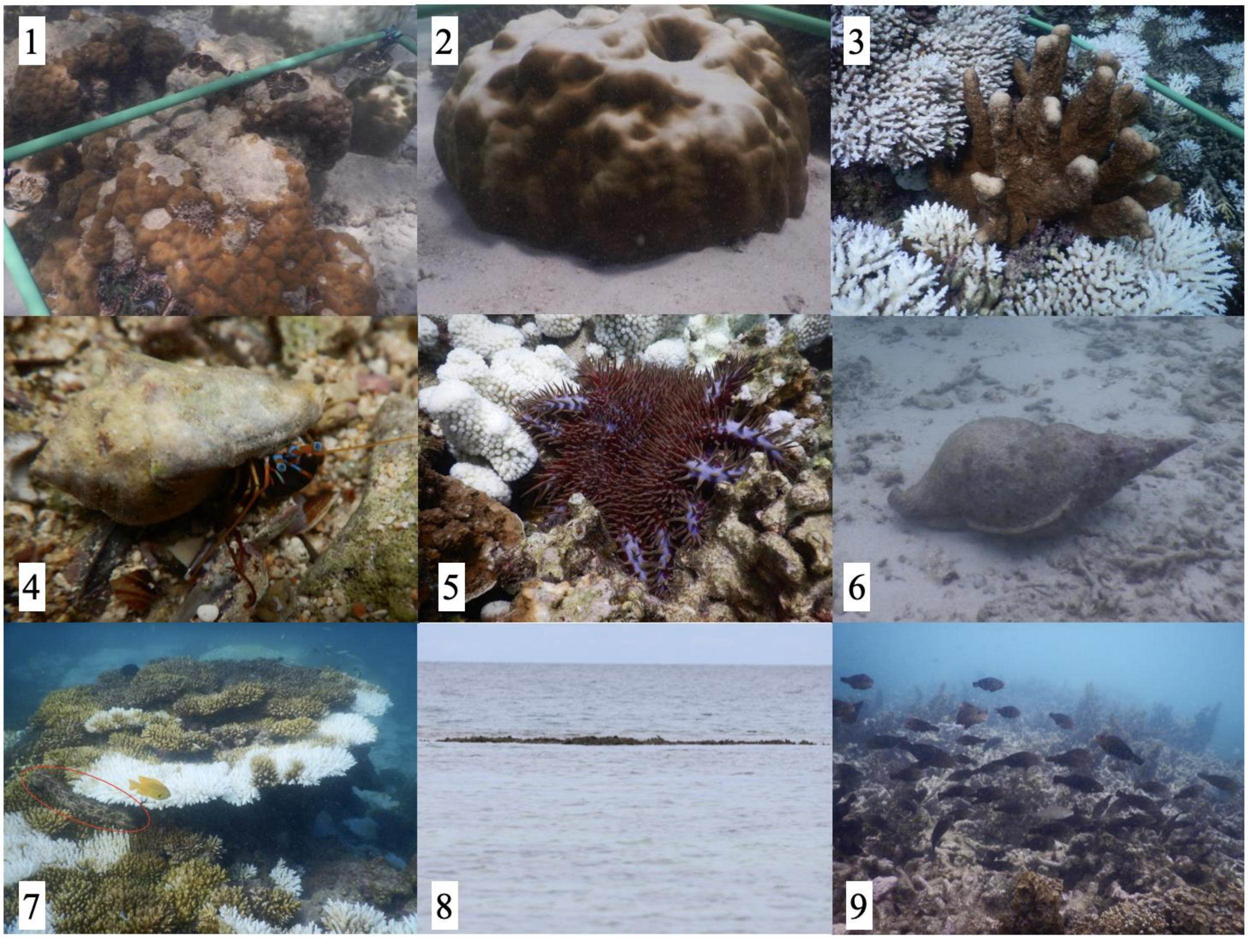
Appendix

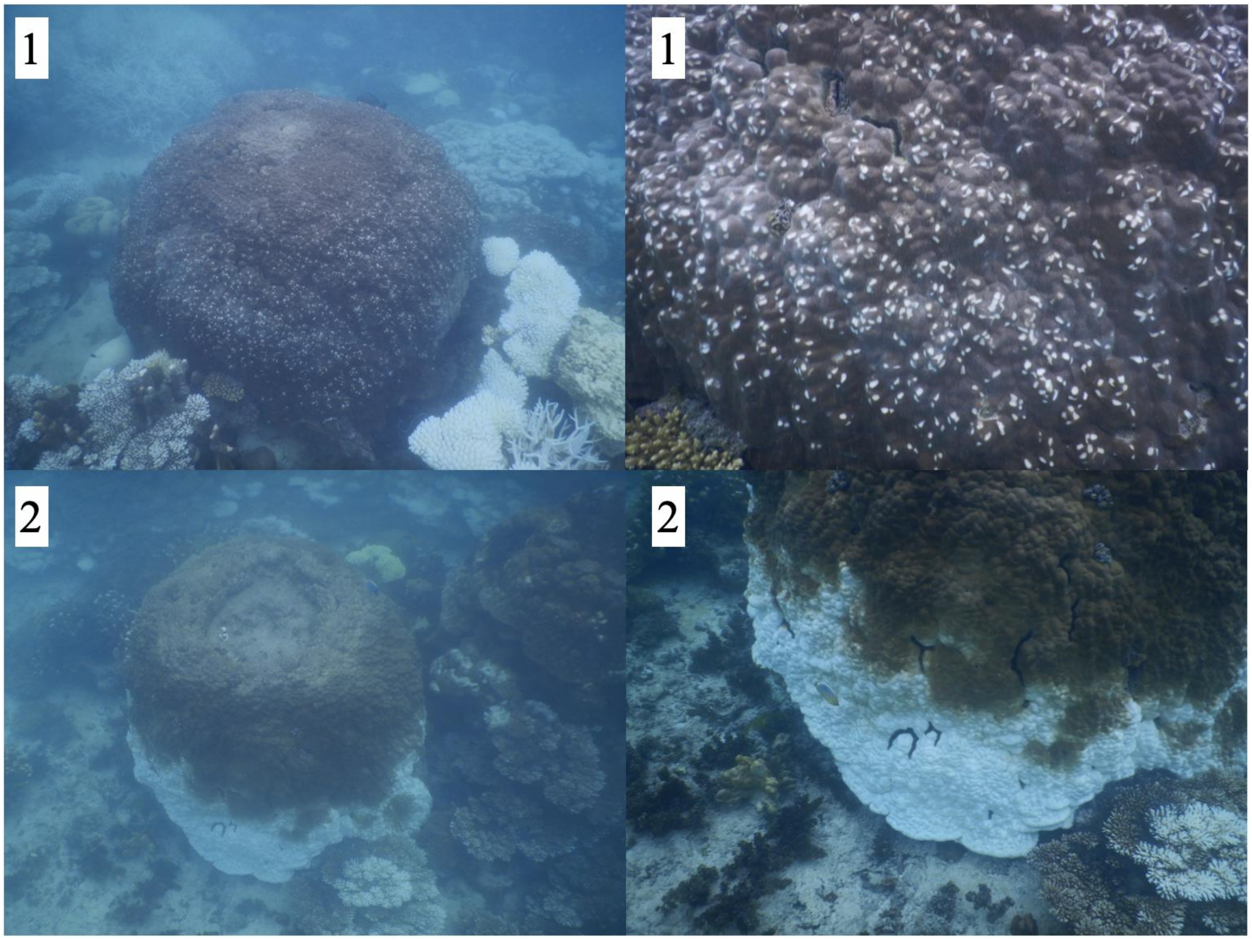
Supplemental Figure 1. Figure from Coastal Oceans Research and Development in the Indian Ocean (CORDIO) depicting the number of bleaching reports spiking in 2016 compared to any other year on record.

Supplemental Table 1. Table of the GPS coordinates for the northern and southern sites utilized in this study. All coordinates are in the World Geodetic System 1984 format.

Label	Coordinates	Label	Coordinates
Northern Transect		**Southern Transect**	
Start of Northern Transect (South)	37 M 0519503 m E	Start of Southern Transect (South)	37 M 0519636 m E
	UTM 9306207 m S		UTM 9305708 m S
End of Northern Transect (North)	37 M 0519500 m E	End of Southern Transect (North)	37 M 0519538 m E
	UTM 9306308 m S		UTM 9305731 m S
South Start of Back Reef	37 M 0519400 m E	South Start of Back Reef	37 M 0519532 m E
	UTM 9306206 m S		UTM 9305471 m S
North Start of Back Reef	37 M 0519412 m E	North Start of Back Reef	37 M 0519444 m E
	UTM 9306308 m S		UTM 9305540 m S
South Start of Reef Crest	37 M 0519321 m E	South Start of Reef Crest	37 M 0519516 m E
	UTM 9306206 m S		UTM 9305429 m S
North Start of Reef Crest	37 M 0519350 m E	North Start of Reef Crest	37 M 0519427 m E
	UTM 9306308 m S		UTM 9305509 m S
South Start of Fore Reef	37 M 0519296 m E	South Start of Fore Reef	37 M 0519498 m E
	UTM 9306206 m S		UTM 9305390 m S
North Start of Fore Reef	37 M 0519350.00 m E	North Start of Fore Reef	37 M 0519415 m E
	UTM 9306308 m S		UTM 9305486 m S

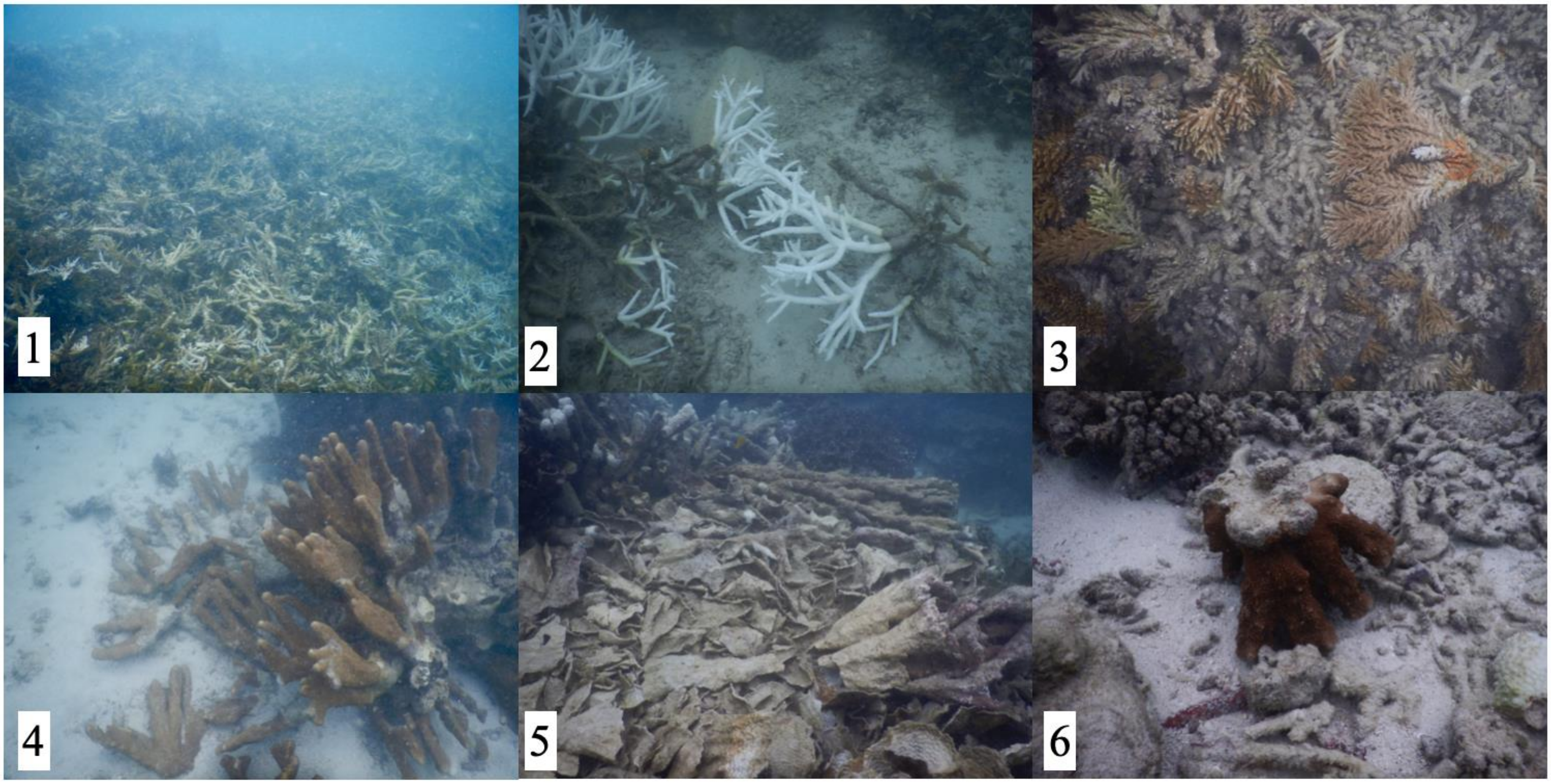


Supplemental Figure 2. Miscellaneous photos of various observations along the reef related to reef health. 1) Massive coral in the northern back reef displaying areas of no tissue on its top surface. 2) Massive northern back reef coral showing bleached areas where it has been exposed to the sun. 3) *Isopora* colony displaying bleached tips. 4) Hermit crab inhabiting a *Drupella* snail shell. 5) Crown-of-thorns starfish. 6) Living giant triton found near another living giant triton. 4) Sea cucumber (indicated by red circle) feeding on algae that has grown over a dead coral skeleton. 8) Exposed reef crest at particularly low tide at the northern site. 9) School of juvenile parrotfish grazing on the coral rubble along the northern reef crest.



Supplemental Figure 3. Instances of coral disease encountered during the study period. 1) A colony overview and close-up picture of suspected *Porites* Ulcerative White Spot. 2) A colony overview and close-up picture of suspected white band disease.

Supplemental Figure 4. Photos of pollution along the reef. 1) Floating debris being deposited onshore. 2) Boat traffic within the protected area. A stream of water can be seen exiting the boat and entering the ocean. 3) Tire integrated into the substrate at the northern site. 4) Ferry that's engine can be heard underwater, creating noise pollution very near the protected area.



Supplemental Figure 5. Photos depicting storm damage to the reef following a Category 1 cyclone. 1;2) Destroyed *Acropora* colonies at the southern reef site. 3) Living *Acropora* colony fragments. 4) Overturned and fragmented *Isopora* colony in the southern back reef. 5) *Echinopora* and *Galaxea* coral rubble at the northern site. It is unclear whether this rubble is from the most recent storm. 6) Overturned *Isopora* colony in the northern back reef.