Intraspecific color variation in *Porites cylindrica*: the role of color variation in coral resilience

By

Grace McDermott

A thesis submitted in partial fulfillment of the
requirements for the degree of

MASTER OF SCIENCE
IN
BIOLOGY

SUPERVISORY COMMITTEE
Dr. Laurie Raymundo, Chair
Dr. Héloïse Rouzé
Dr. Bastian Bentlage

University of Guam

December 2023

1. Abstract

In an era of rapid environmental change, it is important to consider how intraspecific variation may influence population dynamics when determining the fate of a species. *Porites cylindrica* is an Indo-Pacific coral occurring in two color morphologies on Guam, yellow and brown. This study investigates their current distribution patterns on Guam, their competitive strategies, and their differential responses to selected environmental stressors. Ecological surveys were used to assess colony abundance, competitive dynamics, and disease prevalence in colonies of yellow vs. brown *P. cylindrica*. Disease lesions on colonies of each color morph were monitored photographically *in situ* to further explore differences disease dynamics between morphs. Competitive strategies and heat tolerance of both color morphs were assessed using controlled laboratory assays. Ecological abundance surveys revealed that the yellow color morph was significantly more abundant than the brown morph on Guam (66.5% vs 33.5%, respectively). Yellow morphs were also found to be competitively dominant over brown morphs, in both field surveys (39.8% vs. 29.2%, respectively) and *ex situ* assays (42% vs. 0%, respectively). However, while yellow colonies allocated more energy towards competition, brown colonies recovered significantly faster from heat stress exposure in both symbiont densities and pigmentation. Additionally, disease lesions occurring on brown colonies were significantly smaller and less variable than disease lesions occurring on yellow colonies. Disease prevalence was overall higher among yellow morphs (44%) than brown morphs (29%), however, only between site differences in disease

prevalence were significant. The results of this study indicate that intraspecific differences in color do play a role in a species' resistance and resilience to environmental stress and can help provide insight into future population dynamics and persistence scenarios in the Anthropocene.

Table of Contents

List of figures and tables

Tables:

Figures:

2. Introduction

2.1 Coral Reefs on Guam

The U.S. Territory of Guam, the southern-most Mariana island, lies just outside the Indo-Pacific center of reef biodiversity (Roberts et al. 2002), hosting an estimated 350 species of scleractinian corals (Randall 2003). Guam's coral reefs provide crucial sources of income through their role in tourism, fishing, and coastal protection. In a study published in 2007, the economic value of Guam's reefs was estimated to total US$127 million per year (Van Beukering et al. 2007). However, coral reefs around the globe are deteriorating as a direct result of human influences. The link between increased greenhouse gases, climate change, and anthropogenic pressures is incontrovertible, with mass bleaching events increasing in both frequency and magnitude in recent years (Hoegh-Guldberg 1999; Raymundo et al. 2019). Emerging coral diseases are also a serious threat implicated in extensive reef deterioration, through the disruption of the integrity of the coral holobiont homeostasis between the coral host and the microbiome (Bourne et al. 2009). Evidence from paleontological and ecological monitoring suggest that the occurrence and geographical distribution of coral diseases have also been increasing due to anthropogenic impact (Precht et al. 2002, 2016; Sutherland et al. 2004; Raymundo et al. 2005; Myers and Raymundo 2009; Tracy et al. 2019).

The Indo-Pacific region contains an abundance of scattered, remote islands, often occupied by large coastal populations that have caused the deterioration of reef communities in many areas (Gomez 1988, Hughes et al. 2003). On Guam, repeated *Acanthaster planci* outbreaks, worsening water quality, and high fishing pressure from a growing population have led to the gradual decline in the condition of Guam's reefs since the 1960s (Chesher 1969, Randall and Holloman 1974, Burdick et al. 2008, MacNeil et al. 2015, Raymundo et al. 2019).

The superimposition of elevated sea surface temperatures (SSTs), coupled with increasing bleaching events and disease prevalence, have had devastating effects on Guam's already stressed reefs, and have led to increases in mass mortality events through-out the past decade (Myers and Raymundo 2009; Raymundo et al. 2019).

When predicting the fate of an ecological community, intraspecific variability is an important component to consider, as it comprises the foundation upon which natural selection may function (Violle et al. 2012). Focusing on diversity below the species level provides an additional way to characterize changes in coral communities that might otherwise be obscured in approaches focusing on the species level or higher (Hughes et al. 2018). As climate change continues to decimate coral reefs through mass bleaching and severe weather events (Hughes et al. 2017b, Raymundo et al. 2019), the few resilient species that persist may dominate future communities and subsequently drive future trait shifts (Kubicek et al. 2019). Observing individuals within a species can help identify evolved phenotypes that are more resilient under stressful conditions and could predict the future dynamics of coral reef communities (Kavousi et al. 2020). Therefore, individual coral colony performance is worth focusing on to learn how variation at this level may influence population dynamics in an increasingly stressful environment (Parkinson and Baums 2014, Kavousi et al. 2015).

Variations in coral colony morphology have been correlated with differences in life history strategies, such as growth rate, competition, reproduction, and stress response (Grime and Pierce 2012, Darling et al. 2012, Darling et al. 2013). Coral species have been shown to differ in their susceptibility to bleaching and disease, which may reflect underlying trade-offs in life history traits. A correlative study by Shore-Maggio et al. (2017) observed different color morphs of *Montipora capitata* displaying trade-offs between bleaching and disease resistance in response

to stressors, leading to differences in population dynamics on reef flats in Hawaii. On Guam, variations in color morphology in *Acropora surculosa* have been correlated with differences in resistance to heat stress, with red phenotypes being more sensitive to heat stress than other color phenotypes (Moscato, 2020). These observed variations in coral stress responses within same-species color morphs highlight the need to consider diversity below the species level when predicting future ecological communities.

Guam's shallow reef communities are taxonomically diverse but dominated by the genus *Porites*, which contributes approximately 40% of live coral cover (Myers and Raymundo 2009). However, *Porites* is also the genus with the highest total disease prevalence compared to other coral taxon on Guam, making it a critical genus to focus on in order to better conserve the function and structural integrity of Guam's reefs and their economic value. Of the estimated 13 *Porites* species present on Guam, the branching coral *Porites cylindrica* is highly abundant, contributing to much of the complex structure found on Guam's shallow reef flats. This species exists in two different color morphs, brown and yellow (Fig. 1), which can persist side by side at the same depth and in the same habitats on the reef flats of Guam. The relative differences in abundance, resistance, and/or resilience of the color morphs of *P. cylindrica* have yet to be quantified, and therefore future changes to Guam's reef community structure cannot be accurately predicted.

This study focuses on the intraspecific differences in resistance and resilience to environmental stress between the two color morphs of *P. cylindrica*, through quantification of intraspecific competitive ability, and susceptibility to heat stress and disease. The results of this study can provide a better understanding of the range of stress tolerance within a single species and the role that color variation could play in the tolerance of coral species to environmental

change. Understanding these differences within a species can help make future predictions of community assemblages more accurate, supporting the development of effective management efforts aimed to preserve biodiversity and the economy.

Figure 1. ***P. cylindrica*** **brown and yellow color morphs co-occurring within the same thicket.**

2.2 Biological Strategies

The spatial distribution of sessile marine invertebrates is shaped by the physical, biological, and chemical characteristics of the environment. Reef-building corals require space on the substratum for settlement, growth, and reproduction. Because of their reliance on photosynthetic endosymbionts for energy (Muscatine 1990) and on the consumption of zooplankton for essential nutrients (Ferrier-Pages et al. 2010), corals require a living space exposed to appropriate light levels and water flow carrying prey items (Chadwick and Morrow

2011). Therefore, suitable space is a limiting factor for sessile organisms like corals, resulting in competitive interactions. Because species differ in their competitive ability, species-specific competitive hierarchies result. Preliminary studies have suggested that the development of these competitive hierarchies--or networks--may be associated with high biodiversity in marine communities (Buss and Jackson 1979, Jackson 1979, Buss 1986). Competition among corals for substratum space is a major force on tropical reefs and can contribute to shaping patterns of abundance and distributions of species and their subsequent evolved phenotypes (Rinkevich and Loya, 1985; Connell et al. 2004).

Competition for, and the acquisition of, space by sessile marine organisms usually involve physical mechanisms of interference rather than exploitation (La-Barre et al. 1986). Corals utilize a complex array of competitive mechanisms that include skeletal overgrowth, overtopping/overshading, redirection of growth, extrusion of mesenterial filaments and/or sweeper tentacles, allelopathy, and the physical interception of food particles (Chadwick and Morrow 2011). In terms of competitive traits, a study conducted in Sesoko Island, Okinawa, determined a transitive hierarchy among five *Porites* species *in situ* (*P. rus* > *P. cylindrica* > *P. lobata* > *P. australiensis* > *P. lutea*), where the most common competitive mechanism observed was skeletal overgrowth, with other outcomes being pigmentation response, bleaching, and tissue necrosis. A study by Idjadi and Karlson (2007) demonstrated that skeletal overgrowth was determined to be the most utilized competitive mechanism among two species of *Porites* in Polynesia. However, some corals are less physically aggressive and will instead use tactics to evade and defend from neighboring colonies. For example, many coral species will create skeletal barriers along contact zones of neighboring colonies, leading to competitive stand offs in which neither coral overgrows the other (Chadwick and Morrow 2011). A wide range of

cnidarians also use chemical mechanisms of interference by emitting toxic waterborne allelochemicals to kill larvae, induce tissue necrosis, and inhibit the growth of competing neighbors (Gunthorpe and Cameron 1990a, b; Rinkevich et al. 1992; Aceret et al. 1995). Colonies of *P. cylindrica* have been observed to vary their growth rates depending on the species of neighboring colonies, growing slower but surviving longer when in contact with same species neighbors in comparison to competitive neighbors of different coral species (Dizon and Yap 2005), indicating the possession of an allorecognition system (Rinkevich et al. 1994). In contrast, transplanted colonies of *Porites attenuata* in the Philippines were recorded to have the opposite result when in contact with each other, where their growth rate increased but colonies had overall lower survivorship (Raymundo, 2001). This sort of physiological modification presented in *Porites* indicates an ability to distinguish self from non-self through the recognition of non-self attributes presented in conspecifics, which is the basis of all competitive interactions (Rinkevich et al. 1994).

Intraspecific competition in sedentary organisms is a critical factor in the construction of coral reef communities. Outcomes of same-species interactions can vary from colony fusion and the formation of chimeric colonies to tissue mortality and overgrowth, depending on the maturity of the allorecognition system (Rinkevich et al. 1994), phenotypic variation (Rinkevich and Loya, 1982), and the length of tissue contact time between conspecific corals (Franks and Rinkevich 1994, Frank et al. 1997). In colonies of *Stylophora pistillata*, both color and colony size play a role in competitive aggression (Rinkevich and Loya 1982). *S. pistillata* exhibits hierarchical aggression of color morphs, in which purple colonies are superior to yellow colonies of similar size, and competitively exclude them even when they are not in physical contact. However, previous experimental work has also shown that when coral fragments are exposed to other

genetically identical fragments fusion may occur, resulting in increased survivorship of small colonies through the reduction of size-specific mortality (Raymundo and Maypa, 2004). In contrast, fusion of genetically distinct colonies can significantly lower the growth rates of resultant chimeras (Chornesky, 1991). However, chimerism has been shown to confer some benefits by allowing expression of alternative phenotypes (Rinkevich and Weissman, 1992) and increasing survival chances through larger body size and physical stability (Chornesky 1991).

2.3 Consequences of environmental stressors on the coral holobiont

2.3.1 The Coral Microbiome and Disease

The coral microbiome plays a fundamental role in coral health and is an essential component of the coral holobiont, which includes the coral host, *Symbiodiniaceae*, and associated microorganisms. These associated microorganisms inhabit distinct ecological niches provided by the host, such as the surface, tissue, skeleton, and mucus layers, and are collectively referred to as the microbiome (Bourne and Munn, 2005; Brown and Bythell 2005; Rohwer et al. 2002). The microbiome is composed of an assortment of bacteria, archaea, fungi, and viruses (Bourne et al. 2016; Frade et al. 2016a), which can aid in holobiont stability through the recycling of nutrients, removal of waste products, and providing immune defense against pathogens (Lema, Willis, and Bourne, 2012; Morris et al., 2011; Rosado et al., 2019). Coral microbiomes can be affected by both extrinsic and intrinsic factors; they are specific to a host species but can also be influenced by spatio-temporal conditions. Geography, water quality, depth, seasonality, and the physiological status of the host can all affect coral microbial community composition (Lema, Willis, and Bourne, 2012; Angly et al. 2016; Sweet and Bulling, 2017). The interaction between the environment, disease/pathogenic agents, and the

physiological status of the host is involved in the manifestation of pathogenic diseases (Morris et al., 2011; Sweet and Bulling 2017).

Six disease states have been documented on Guam, affecting eight families of reef-building corals (Myers and Raymundo 2009). Of the disease states recorded, white syndromes are the most prevalent (Fig. 2) (Myers and Raymundo 2009, Sweet et al. 2019). White syndromes represent a significant group of diseases due to their extensive geographical distributions, diverse host ranges, and their ability to cause rapid and often irreversible damage (Aronson and Precht, 2001; Antonius 1985; Pollock et al. 2016). The Indo-Pacific white syndromes are not as extensively characterized as the white diseases of the Caribbean (white band types I and II, white plague, white patch, Serratiosis) and are currently being described under the blanket term "white syndrome" until reliable diagnostic criteria are developed to differentiate potentially etiologically distinct diseases (Ritchie and Smith 1998, Patterson et al. 2002, Pollock et al. 2016; Rogers et al. 2005). White syndromes are characterized by progressing tissue loss that exposes underlying skeleton, manifesting as single to multiple lesions that display~~ing~~ a clear boundary between healthy coral tissue and exposed skeleton (Bourne et al. 2015, Lozada-Misa et al. 2015). Various causal agents have been attributed to tissue loss associated with white syndrome including *Vibrio* and *Rhodobacteracea* bacteria, viruses, helminths, ciliates, and parasites (Bourne et al. 2015). Outbreaks of white syndromes in the Indo-Pacific have also been correlated with environmental factors such as periods of elevated sea surface temperature (Howells et al. 2020). For instance, a 20-fold increase in white syndrome prevalence was recorded in the Great Barrier reef after the anomalously warm summer of 2001-2002 (Willis et al. 2004, Bruno et al. 2007). Howells (2020) tracked outbreaks of white syndrome in the southern Persian Gulf and found that the prevalence of white syndrome

increased exponentially with cumulative heat exposure. However, white syndrome prevalence has no clear link with elevated temperature on Guam, and was even found to be more prevalent during cooler months (Green et al. 2021).

Figure 2. A white syndrome lesion affecting the same branch of a yellow *P. cylindrica*. The same lesion is shown progressing between 6/16/22 (left) and 6/29/22 (middle) and recovering by 8/4/22 (right).

A multitude of taxa are affected by white syndrome, but fast-growing and branching genera are particularly vulnerable (Willis et al. 2004). Broad patterns of differential susceptibility across coral families have been attributed to differing levels of investment in immune parameters, demonstrating a potential phylogenetic basis for coral resilience (Palmer et al. 2010). One previous study has shown that branching *P. cylindrica* accumulates more white syndrome lesions per colony than massive *Porites* spp. (Lozada-Misa et al. 2015). However, *P. cylindrica* lesions were overall much smaller and had a faster healing rate when compared to lesions affecting massive *Porites* colonies. Coral colony size and age have also been determined to factor into disease risk, with larger and older colonies having greater susceptibility to disease infection due to the relationship between surface area and susceptibility, paired with a reduced immune function in older corals (Greene et al. 2019). On Guam, coral host abundance has a

significant link with total disease prevalence, as *Porites* spp. are the most affected by disease states, while acroporids and pocilloporids also show high susceptibility (Myers and Raymundo 2009). These results could be in part due to larger colony sizes associated with some Poritids (i.e. massive *Porites*), correlating with more exposure risk over time and increased susceptibility to injury or pathogen attack with age or time (Greene et al. 2019).

In the study conducted by Lozada-Miza et al. (2015), white syndrome lesions in different *Porites* species were also observed to heal at different rates. Massive and branching *Porites* species displayed different disease dynamics, massive morphologies having larger, more variable, and persistent lesions in comparison with branching morphologies, demonstrating that coral morphology is an important metric of susceptibility. Even within the same species, phenotypic variation can affect disease resistance among corals. *M. capitata* colonies differ in disease resistance, which is driven by both color morph and endosymbiont community clade (Shore-Maggio et al. 2017). While potential differences in disease dynamics have not been studied among color morphs of *P. cylindrica*, low levels of *Vibrio* bacteria are known to occur in healthy colonies of both morphs in similar levels (Lock et al. 2023 in prep, and McDermott et al. in prep), suggesting that the development of *Porites* white syndrome may be a manifestation of stress and consequential dysbiosis. The growing body of evidence supports the idea that intraspecific variations are critical variables in the characterization of disease dynamics (Muller et al. 2018). These findings emphasize the need to consider not only interspecific differences, but also the phenotypic differences within a species when studying the effects of disease on coral reef communities.

2.3.2 Coral bleaching and biological trade-offs

The close association between reef-building corals and symbiotic algae facilitates nutrient cycling, resulting in the high productivity of reefs (Muscatine and Porter 1977). The symbiotic relationship with photosynthetic dinoflagellates is critical to coral function as symbionts provide significant nutrition via photosynthate translocation (Muscatine 1990). Malfunction of the symbiosis can result in bleaching, where photosymbionts are expelled from the coral host, leaving bleached corals nutrient deficient (Hoegh-Guldberg and Smith 1989). Bleached corals that survive have reduced tissue regeneration capacity (Meesters and Bak 1993), decreased calcification (McNeil et al. 2004), and are more susceptible to diseases (Brandt and McManus 2009, Miller et al. 2009). Because bleached corals are in such a vulnerable state, they are at a greater risk of mortality if not repopulated by algal symbionts in a timely manner. Therefore, assessing coral symbiont community characteristics is imperative when conducting studies on resilience and stress response.

Among symbiont community characteristics, chlorophyll content has been shown to be a reliable indicator of physiological stress induced by temperature changes (Glynn-D'Croz, 1990; Jones, 1997 a,b). Chlorophyll *a* concentration of unicellular algae, such as *Symbiodinium*, is an indicator of nutrient status (Rees, 1991) and has been known to have an inverse relationship with symbiont densities (Le Tissier and Brown, 1996). As symbiont density lowers, chlorophyll concentration increases per symbiont, most likely due to a higher availability of nutrients through decreased competition between *Symbiodinium* (Hoegh-Guldberg and Smith 1989b; Jones, 1997). Chlorophyll concentration as well as symbiont density both contribute to chlorophyll density (chlorophyll $a + c_2$ per unit of surface area). Because chlorophyll density is proportional to coral color, color measurements of coral tissue can be used as an indicator of environmental stress

(Winters et al. 2009). The development of inexpensive photographic methods that can successfully estimate chlorophyll density through mathematical normalization of coral color to a reference scale has revolutionized the quantification of coral bleaching.

Both diurnal and seasonal sea surface temperature (SST) fluctuations are generally smaller in the tropics than in higher latitudes, and evidence suggests that mean SSTs in tropical regions have varied by less than 2°C over the past 18,000 years (Thunnell et al. 1994). However, due to anthropogenically enhanced concentrations of atmospheric greenhouse gasses, mean SSTs are currently increasing at a rate of ~2-3°C per century in tropical oceans (Hoegh-Guldberg 1999, Winter et al. 1998). Recent upward trends in SSTs have been correlated with increased frequency and severity of mass coral bleaching events (Hoegh-Guldberg 1999). On Guam, the first recorded island-wide bleaching event was documented in 1994 by Paulay and Benayahu (1999), which resulted in little mortality. More recently, elevated SSTs have induced severe island-side bleaching events in 2013, 2014, 2016, and 2017, causing a significant decline in coral cover (Raymundo et al. 2019). Further mortality was caused by subaerial exposure on shallow reef flats during a major ENSO event beginning in 2014 and extending through 2015, and disease outbreaks in 2016 and 2017. Overall, live coral cover declined by 37% on shallow reef flat zones and 34% at shallow seaward slope sites between 2013 and 2017 as a result of elevated SST induced bleaching events on Guam (Raymundo et al. 2019). (Raymundo et al. 2019). Previous work has shown that less disturbed sites with infrequent extreme warm temperature stresses can be associated with higher populations of sensitive *Acropora* corals while more disturbed sites with more frequent acute heat stress events are usually dominated by stress-resistant *Porites* (McClanahan et al. 2020).

However, while there is variability in thermotolerance present among these two dominant taxa, intraspecific variability is also an important component to consider when comprehending changes in coral assemblages. Less is known about the phenotypic differences within a coral species that correlate with and potentially drive intraspecific differences in bleaching susceptibility. The importance of a coral's genotype in its resistance to thermal stress has been recognized for some time (Edmunds 1994, Fitt et al. 2009). Bleached coral colonies can directly neighbor colonies of the same species that do not exhibit bleaching (Edmunds 1994, Ritson-Williams, and Gates, 2020). Responses to heat stress have so far been unstudied in color morphs of *P. cylindrica*. However, color morphs of *P. cylindrica* on Guam are known to have highly similar symbiont communities, both dominated by *Cladocopium* C15 *Symbiodiniaceae* (Lock et al. 2023). Coral species harboring *Symbiodiniaceae* C15 have been shown to exhibit higher heat resistance in comparison to corals harboring other *Symbiodinium* species, which has been determined through the comparison of photosystem II efficiencies (Fitt et al. 2009). However, bleaching resistance is not solely driven by symbiont communities and has been observed to be highly correlated with characteristics of the host as well. A comparative study on *P. cylindrica* and *S. pistillata* found *P. cylindrica* to be more resistant to thermal stress not only because colonies harbored heat resistant C15 S*ymbiodinium*, but because critical proteins, such as heat-stress protein 70 and superoxide dismutase, were present in significantly higher concentrations in ambient conditions prior to the application of heat stress (Fitt et al. 2009). While this combination provides *P. cylindrica* with greater protection during bleaching events, little is known about potential variation in bleaching resistance and/or resilience in *P. cylindrica* color morphs on Guam.

Variations in color morphology and symbiont community assemblages can be correlated and are often associated with trade-offs among various life history traits. Photodamage to algal symbionts exposed to thermal stress can lead to bleaching and is a major cause of coral reef decline (Hughes et al. 2017). Heat stress inhibits photosystem II repair mechanisms of algal symbionts (Takahashi et al. 2009) resulting in lower photoinhibition (Jones et al. 1998, Warner et al. 1999) and the production of reactive oxygen species that damage cellular components (Lesser 2006). Consequently, corals have evolved photoprotective pigments to reduce stress to symbionts (Salih et al. 2000). Host pigmentation is determined by the sequence of proteins within the host tissue that are homologous to the green fluorescent protein (GFP) from the luminescent jellyfish, *Aequorea victoria* (Matz et al. 1999, Lukyanov et al. 2000). GFP-like proteins can be divided into two major groups based on optical properties: fluorescent proteins (FPs) that produce cyan, green, yellow, and red hues (Alieva et al. 2008) and the non-fluorescent chromoproteins (CPs) that are responsible for pink, purple and blue pigmentation (Dove et al. 2001, Labas et al. 2002, D'angelo et al. 2008). Preliminary studies have suggested that protein pigments in shallow water corals can exert a photoprotective functioning by screening algal symbionts from intense solar radiation (Kawaguti 1944, Salih et al. 1998), while protein pigments in low light habitats optimize light availability for photosynthesis of the symbionts (Schlichter et al. 1985, 1994; Salih et al. 2000; Dove et al. 2001, 2004).

Previous investigations have suggested that both coral color morphology and depth can affect endosymbiont community assemblages in corals and associated trade-offs in life history traits. Differences in symbiont clade distribution among color morphs of *Madracis pharensis* have been observed in one study, with endosymbiont genus *Breviolum* 15 occurring predominantly at deeper reef sites and in green and purple colonies while genus *Breviolum* 7

occurs more often in brown colonies at shallow depths (Frade et al. 2008). In Hawaii, different endosymbiont clades have been observed within different *M. capitata* color morphs and correlate with trade-offs in stress responses. Red morphs are associated with endosymbionts in the *Cladocopium* genus and have been observed to be resistant to disease but have a higher bleaching susceptibility, while orange morphs are associated with clade D Symbiodinium and are more resistant to bleaching but have higher disease susceptibility (Shore-Maggio et al, 2017). Variations in growth rate have also been observed in the different color morphs of *M. capitata*, with faster growth rates occurring in *Cladocopium*-harboring red morphs than in *Durusdinium*-harboring orange morphs at ambient temperature (Shore-Maggio et al. 2017). In Palau, colonies of *Acropora hyacinthus* with lower symbiont densities tended to be more bleaching resistant but had lower growth rates, while the opposite occurred in colonies with higher symbiont densities (Cornwell et al. 2021). Additionally, trade-offs associated with growth rate have been linked to differing levels of FP expression among color morphs of *Hydnophora grandis,* with high FP-expressing color morphs showing higher growth rates under bright light conditions, highlighting the photoprotective function of FPs (Quick et al. 2018).

3. Objectives and Hypotheses

The purpose of this study is to examine whether the two distinct color morphs within *P. cylindrica* correlates with differences in both resistance and resilience from environmental stress. In this study, the term "resistance" refers to the ability of individual colonies to not be impacted by environmental stress or to survive after being exposed to stressful conditions while the term "resilience" refers to the ability of individual colonies to return to a previous state of balance and stability after being exposed to stressful conditions. Currently, not much is known about the

relative abundances of each of the two color morphologies of *P. cylindrica* on Guam, despite the species being a major contributor to much of the complex shallow reef flat structure around the island. Previous studies have shown that phenotypic variation can lead to differences in disease susceptibility (Lozada-Misa et al. 2015, Greene et al. 2019), competitive ability (Rinkevich and Loya 1982), and thermal tolerance (Edmunds 1994, Fitt et al. 2009), and could lead to intraspecific differences and potential trade-offs in both resistance and resilience to environmental disturbances (Shore-Maggio et al. 2017).

When predicting the fate of an ecosystem in an era of rapid climate change, it is important to consider how intraspecific variations may influence population dynamics in an increasingly stressful environment (Fig. 3). This study will utilize both field surveys and laboratory experiments to quantifying physiological responses to thermal stress and pathogenic disease as well as biological life history traits such as symbiont community composition, and competitive ability as a way to determine the resilience of each color morph. Results of experimental assays can be used to better understand differences in relative population abundances and disease and bleaching prevalence of each color morph of *P. cylindrica,* and can be used to help predict future community structure of coral reefs on Guam. Specifically, I will test the following hypotheses:

1. H_0: Color morphs will not differ in their relative abundances on Guam.

   H_a: Color morphs will differ in their relative abundances on Guam.
2. H_0: Color morphs will not differ in competitive ability.

   H_a: Color morphs will differ in competitive ability.
3. H_0: Color morphs will be equally susceptible to pathogenic disease.

H_a: Color morphs will differ in susceptibility to pathogenic disease.

4. H_0: Symbiont densities will vary between color morphs when exposed to heat stress.

   H_a: Symbiont densities will not vary between color morphs when exposed to heat stress.

5. H_0: Color morphs will be equally susceptible to heat stress.

   H_a: Color morphs will differ in susceptibility to heat stress.

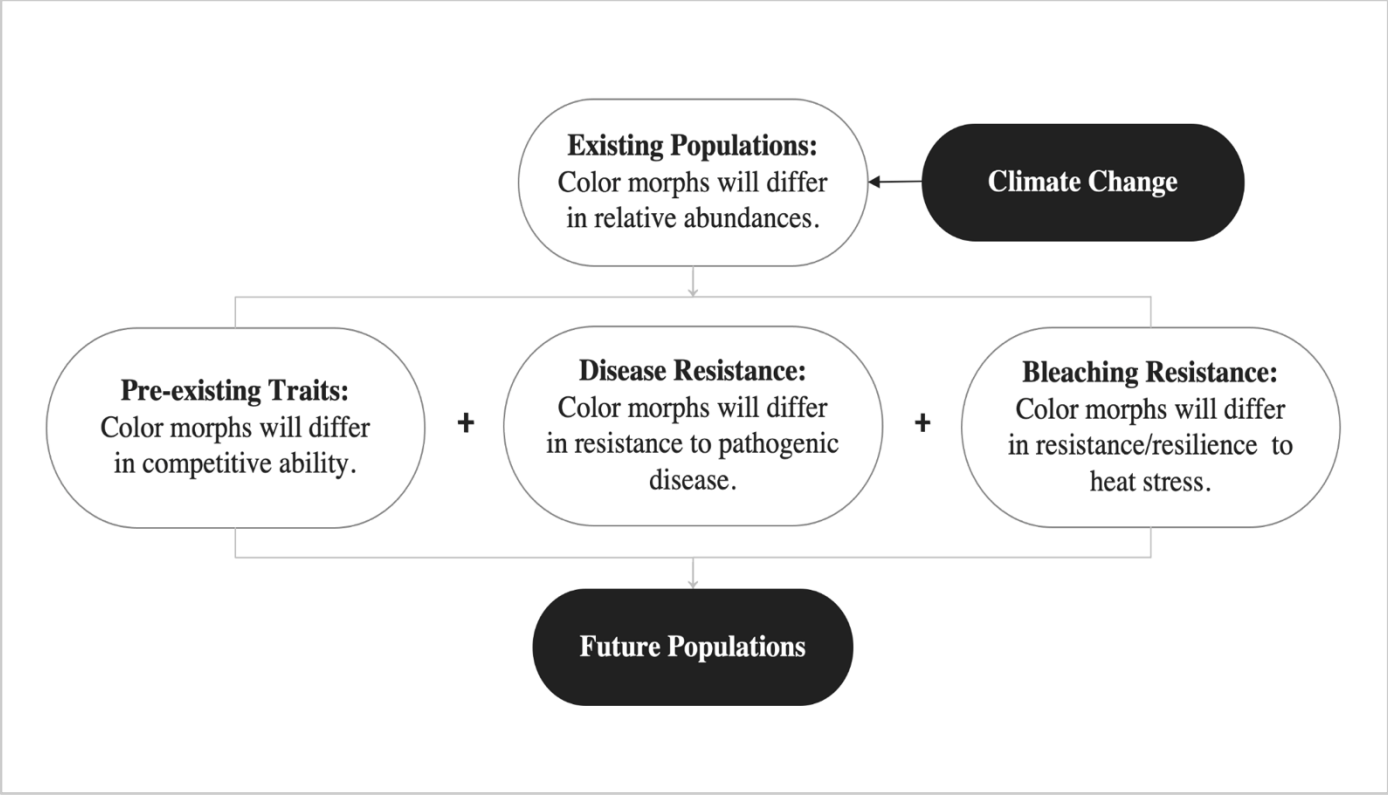

Figure 3. Schematic showing linkages between traits examined in this study. The various life history traits of *P. cylindrica* that have influenced existing population abundances and the biological strategies that will influence future population abundances in an era of rapidly changing climate.

4. Materials and Methods

4.1 *In situ* surveys to characterize relative abundances, disease prevalence, and competitive dynamics

Surveys were conducted at three reef flats (Luminao, Piti East, and Tumon) along the western coast of Guam, which were chosen for their high abundance of *P. cylindrica* (Fig. 4). The objective of these surveys was to look for *in situ* differences between color morphs in: 1) relative prevalence; 2) competitive interactions; and 3) white syndrome severity and prevalence. Corals were surveyed using four 20 x 2 m belt transects laid parallel to shore at two depths (reef flats: 1-3 m, forereefs: 3-5 m). Snorkeler pairs each read a 20 x 1 m belt along opposite sides of the transect, so that the total area surveyed was 160 m^2/transect. Sites were surveyed during October and November 2021 and in May of 2022. Relative Abundance of each morph was calculated per site as the number of colonies per color morph/total number of *P. cylindrica* colonies. The relative abundances of each color morph were then compared statistically using RStudio (Version 2023.06.0+421 (RStudio Team, 2023)). Because data were highly heteroscedastic, a Kruskal-Wallis test (Kruskal and Wallis 1952) was used to compare the prevalence of each color morph. A Pearson chi-square test was also used to compare raw abundances of each morph per site.

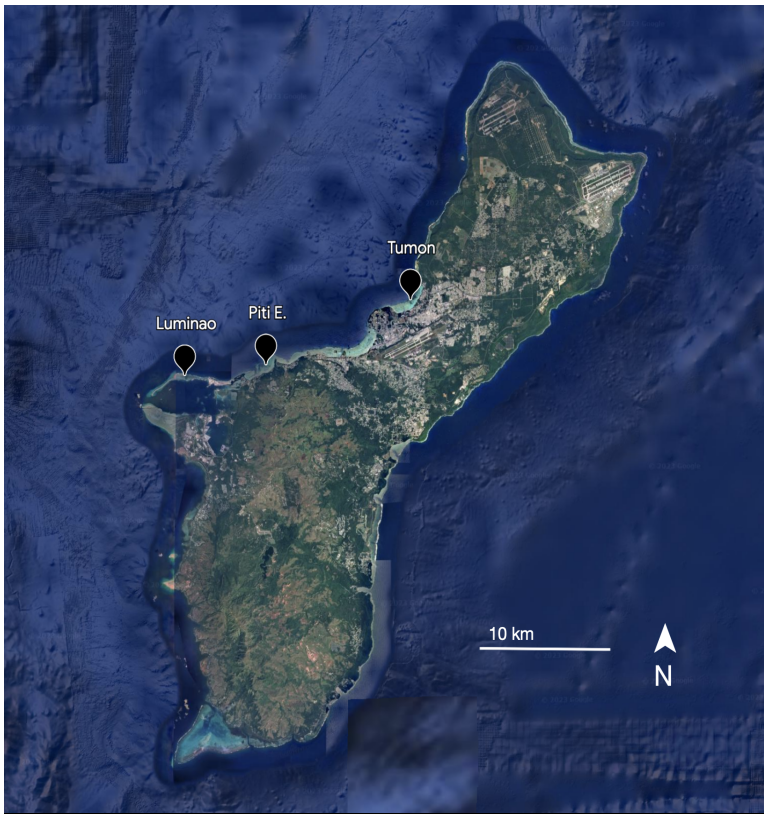

Figure 4. Map of Guam. The location of survey sites, Luminao, Piti East, and Tumon, for the quantification of relative abundances, disease prevalence and severity, and competitive interactions and responses of each color morph of *P. cylindrica*.

White syndrome was chosen to examine, as it is the most prevalent of all coral diseases present on Guam and within the genus *Porites* (Myers and Raymundo 2009). Disease severity was semi-quantitatively assessed along transects as the percent of colony affected and scored from 0-6, where 0 = 0%; 1 = 1-10%; 2 = 11-25%; 3 = 26-50%; 4 = 51-75%; 5 = 76-99%; 6 = 100%. Colonies were measured using a ruler and binned into size classes, however, a linear regression model determined that size did not factor significantly into severity or prevalence, so it was not included during analysis. White syndrome severity was statistically compared between morphs in RStudio (Version 2023.06.0+421 (RStudio Team, 2023)) using a combination of a Kruskall-Wallis testing and Pearson X^2 (Pearson 1900). Kruskall-Wallis was used to compare all

disease prevalence measurements recorded per color morph across each transect per site while Pearson X^2 tested the frequency each disease severity bin occurred per each color morph overall.

White syndrome prevalence was quantified using the following formula: total number colonies of color morph exhibiting white syndrome) / (total number colonies of color morph counted) * 100 and calculated per transect. Transects were then averaged for each site, for an overall site white syndrome prevalence and standard deviations were calculated for prevalence of each color morph per transect and similarly averaged for each color morph per site. Analysis of white syndrome prevalence was completed in RStudio (Version 2023.06.0+421 (RStudio Team, 2023)) using a combination of Kruskall-Wallis tests to compare the differences between color morph and site on prevalence. Pearson X^2 tests were then used to compare raw abundances of each color morph exhibiting white syndrome at each site.

Competitive interactions were assessed between neighboring colonies at Luminao and Piti East. Both intraspecific and interspecific competitive interactions were recorded and categorized as “overgrowing,” “overgrown,” “fusion,” “standoff”. Colonies were classified as “overgrowing” when tissue from one colony directly overtopped tissue from an adjacent colony. Colonies that were “overgrown” exhibited tissue that was being overtopped by a separate colony. When neighboring colonies exhibited physical contact points where there was no border distinguishing the tissue from the separate colonies, they exhibited a “fusion” interaction. The formation of a border line between the tissue of two separate competing colonies in direct contact with each other was classified as a “standoff” interaction. The total number of each interaction type was recorded for each colony observed as present/absent. Interactions were grouped into classes “Competition”, “Fusion”, and “Standoff” for analysis. Pearson X^2 tests were then used to compare the frequency each interaction occurred between different interaction pairs

(yellow-yellow, yellow-brown, brown-brown) within each class. Significance was determined at <0.05.

4.2 Competition assay

To further quantify competitive differences between the two color morphs, a competition assay was carried out in a seawater flow-through system at the University of Guam Marine Lab in Mangilao, Guam. Two colonies of each *P. cylindrica* color morph, two brown (N=2) and two yellow (N=2), were collected from Luminao reef flat (13.464'N and 144.644'E) at the same depths and reef zones as competition surveys and each colony was separated into 15 individual fragments. Colonies were sampled that were a minimum of 10 m apart, to minimize the probability that they were clonal. In total, 60 fragments were prepared and arranged into three different interaction treatments: 1/ intra-colony, same color morph; 2/ inter-colony, same color morph; 3/ inter-colony, different color morph (Fig. 5). Fragments were then affixed on separate tiles and positioned in direct contact with their experimental pair, and randomized within a water table, spaced ≥4 in apart to avoid potential responses elicited by neighboring fragments. Tank maintenance was carried out on a weekly basis and included the removal of algae and predatory nudibranchs.

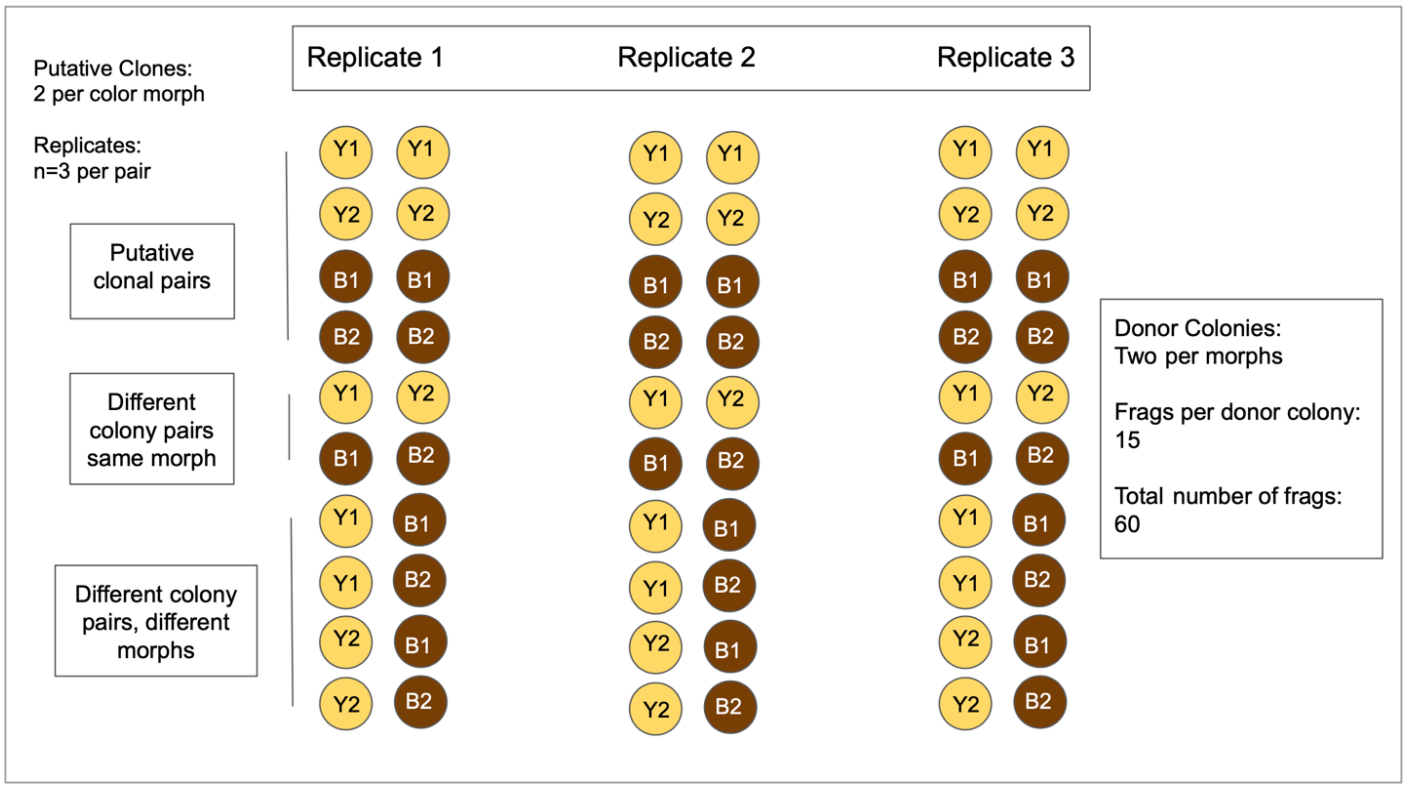

Figure 5. Design schematic for competition assay. Ten pairwise combinations of Y (yellow) B (brown) 1 or 2, and N=3 replicates of each pairing.

Tissue-tissue contact points were monitored photographically on a weekly basis until definitive interactions were observed at 8 wk. A more diverse assortment of interactions was observed in fragments that were observed on a consistent weekly basis over time, in comparison to field survey results. Interactions observed between pairs were scored as fusion, tissue overgrowth by one fragment over the other, or stand-off. An interaction was defined as a stand-off when neither fragment was overgrowing or receding and neither showed signs of tissue damage along the contact margin. Additional responses were observed during *ex situ* experimentation, which included tissue paling, polyp extrusion/retraction, tissue mortality at the contact points, and algal overgrowth. Interactions were determined from visual inspection using a Bausch and Lomb® magnifying lens and documented photographically weekly using an

Olympus Tough TG-5. “Winners” and “losers” of interacting pairs were determined through the visual assessment of photographed contact points. “Losing” coral fragments experienced tissue paling, polyp retraction, tissue mortality at the contact point, and/or overgrowth by their fragment pair. “Winning” fragments were determined by a lack of impacts to healthy tissue and were overgrowing their fragment pair along the contact margin. In cases of fusion or stand-off, there was no definitive winner or loser. Interactions of the color morphs were then compared statistically using Pearson X^2 tests in RStudio (RStudio Team, 2023) to assess significant differences in competitive abilities, where significance is <0.05.

4.3 Resistance and resilience to heat stress

To address potential differences in coral bleaching resistance and resilience in *P. cylindrica* color morphs, a controlled heat stress assay was conducted at the University of Guam Marine Lab from March 10 until April 15, 2022. Twenty donor colonies of *P. cylindrica* were collected (n=10 brown colonies and n=10 yellow colonies) at the same depths and reef zone at the Luminao reef flat as bleaching surveys. Six tanks were utilized and kept at three different temperatures: ~30 ˚C (ambient), 32˚C, and 34 ˚C, with two replicates per temperature (Fig. 6). Each of the twenty donor colonies were separated into six fragments which were then distributed between the six individually heated tanks, so that there were 10 genetically distinct fragments of each color morphs, randomly distributed per tank (Fig. 6). Tanks were heated gradually by ~0.5-1˚C per day over one week. Once signs of bleaching were detected, heaters were shut off to allow a return to ambient temperature for the recovery of fragments. Tank conditions were maintained consistently and included the regular filtering of sea water to 25 µm, bi-weekly water

changes, consistent water motion for homogenous temperature throughout each tank, removal of algae, and temperature adjustments as needed.

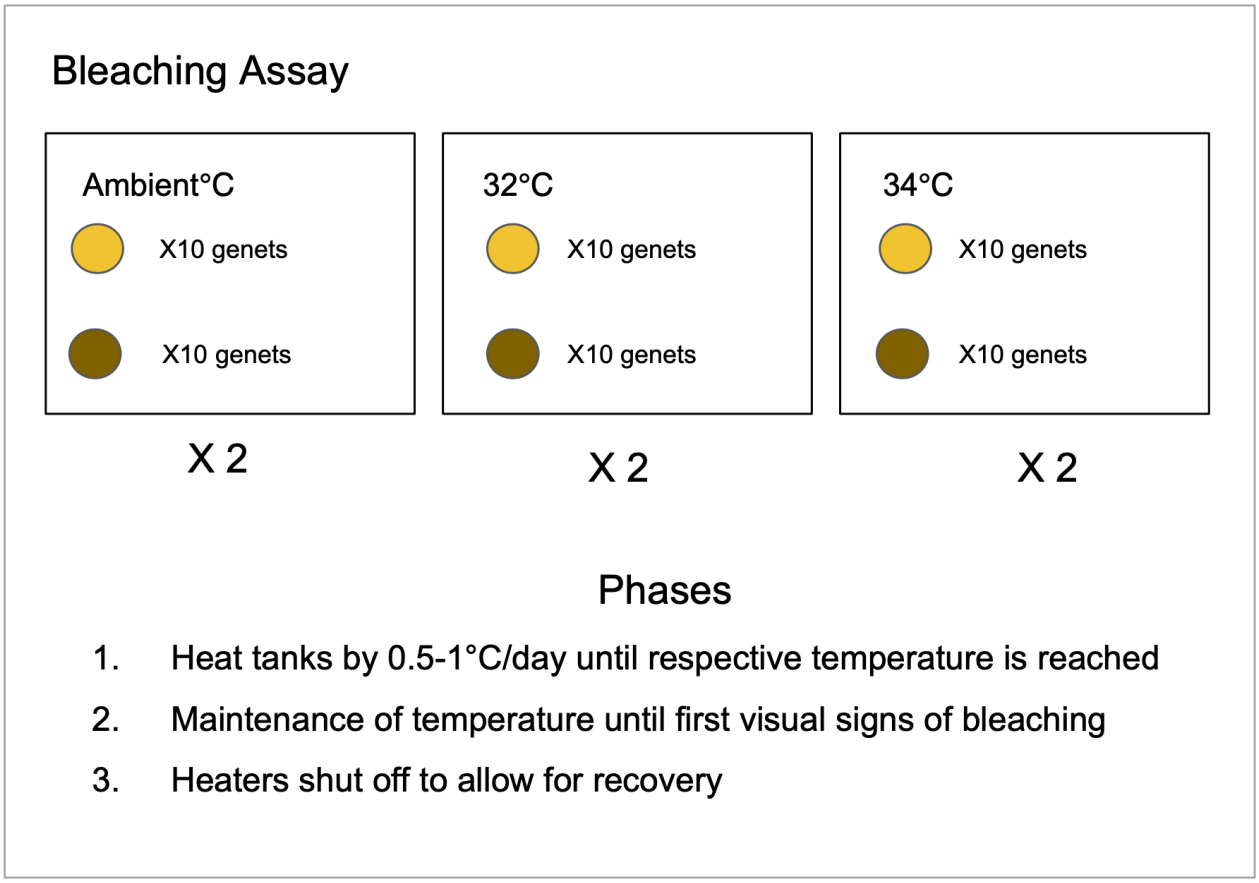

Figure 6. Bleaching assay experimental design. Three treatments were utilized with 10 fragments of each color morph per treatment. Each bin was heated separately and then temperature was maintained until symptoms of bleaching were evident among fragments, at which point heaters were shut off and all tanks returned to ambient temperature.

Tissue samples were collected from fragments in all treatments to determine symbiont density at the start of the experiment, post-bleaching, and post-recovery. Samples were analyzed using flow cytometry following the protocol outlined in the DNeasy Power Kit handbook (Qiagen, 2021) to measure symbiont densities between color morphs and treatments over time. Following collection, each sample was temporarily stored at -80°C until processing and analysis of symbiont densities within *P. cylindrica* color morphs could be conducted. To prepare samples

for flow cytometry, coral tissue was removed using an airbrush compressor containing 0.2 µm filtered sea water, and homogenized. The resulting homogenate was blended using a bead beater for 2 sec and then centrifuged for 4 min at 5000 rpm. The supernatant containing coral tissue was discarded and the pellet resuspended in filtered seawater and repeatedly pelleted and washed until the symbiont cells were free of residual host material. The symbiont suspensions were then analyzed using a flow cytometer with a 15 mW argon ion laser, providing excitation at 488 nm.

Photometric data were collected on a bi-weekly basis using an Olympus Tough TG-6 to document visual signs of heat stress such as changes in pigmentation, and the return of pigmentation post-heat stress. Pigmentation changes of each fragment were photographed alongside a Kodak© gray scale specialized for both color morphs of *P. cylindrica*, which was done using a custom-made macro in MATLAB*,* to detect relative color changes associated with heat stress (Loreto, 2022 in prep). Photos were taken submersed in water in ambient light conditions, in the same tank and location each time. The photos were processed using ImageJ© software (v. 1.53k) and normalized through color correction analysis following the procedure outlined in the UOG Marine Lab Color Photos Protocol (Loreto, 2022 in prep), which utilized the specialized Kodak© gray scales that fragments were photographed with. Following normalization, pigmentation measurements of each fragment were then analyzed statistically.

To determine whether heat stress-related pigmentation change differed between color morphs, fragment color measurements were analyzed statistically in RStudio (Version 2023.06.0+421 (RStudio Team, 2023)) using a fixed linear mixed model with random effects to accommodate repeated measurements. A fixed linear mixed model with random effects was also performed on symbiont cell density data to test for differences between color morphs between temperature treatments and time using the lme4 package (Bates et al. 2015) and the Stargazer

package (Hlavac 2022) was used to view model outputs. Data were transformed, prior to testing, to meet assumptions of normality and equal variances, although data remained heteroscedastic post transformation.

4.4 White syndrome dynamics

To monitor lesion behavior *in situ* on the two color morphs, 10 colonies of brown and yellow *P. cylindrica* morphs haphazardly selected 10 colonies of brown and yellow *P. cylindrica* morphs in Luminao reef flat. Colonies selected were located at least 10 m apart at 1.5 m to 2 m depth and exhibited active white syndrome lesions. Three white syndrome lesions were tagged per colony and photographed bi-weekly from May 26, 2022, to August 4, 2022, using a Canon TG-6. Lesion size was digitally measured from macro-photographs, using Image J© software (v. 1.53k). Lesion status was described each month as one of the following transition states: progressing (acute tissue loss), recovering (tissue resheeting), or in stasis (neither tissue loss nor regrowth along the affected margin). Daily transition rates were calculated as the change in lesion size (cm^2) / the number of days between census dates. Lesions were marked as progressing if the rate of tissue loss was greater than 0.1 and lesions were marked as recovery if the rate of tissue loss was less than -0.1, while lesions were marked as in stasis if the rate of tissue loss was greater than -0.1 but less than 0.1.

To compare the frequency that each transition rate was recorded for each color morph, transition rates from all tagged lesions for every date of data collection were pooled. Transition rate data could not be transformed to meet assumptions of normality and so non-parametric tests were utilized during statistical analysis. Central tendency of the overall distributions of transition rates were compared between color morphs in RStudio using a Kruskall-Wallis test, while variance was compared using an F-Test. Transition rates were then categorized by lesion status:

progressing, stasis, and recovering, and Kruskall-Wallis was employed again to compare the frequency of different transition states per color morph. Additional Pearson X^2 tests were used to compare the proportion of each transition state per color morph, where significance is <0.05.

To analyze lesion dynamics as a function of coral color morphotype, lesions were binned into four size classes based on naturally occurring breaks in the data set (A = 0.01-10.9 cm^2, B = 11-19.9 cm^2, C = 20-39.9 cm^2, D = 40-210 cm^2). Because data were missing for some lesions during May and July sampling dates, May and July data were omitted for this particular analysis. Transition rates of lesions were analyzed for data collected on June 16, 29, and August 4, and therefor there were two transitions from one time point to the next. Possible transitions included progression to a larger size class, recovering to a smaller size class, or staying with in the same size class (stasis). The probability of each lesion transitioning from one size class to the next was calculated per color morph as: number of lesions per size class experiencing each transition state / total number of lesions within that size class. A Markov Chain of probabilities was constructed and used to visually portray these transitions (Grinstead and Snell 1997; Jackson et al. 2003). Pearson X^2 tests were used to compare the proportions of transient rates between size classes of lesions within each color morph as well as the proportion of lesions binned into each size class per color morph, where significance is <0.05.

5. Results

5.1 *In situ* abundance surveys

In situ surveys revealed notable variation in relative abundance between color morphs of *P. cylindrica*. Yellow morphs of *P. cylindrica* displayed considerably higher abundance than brown

morphs at Luminao and Tumon. However, at Piti East, morphs were similarly abundant, although there were almost significantly more brown morphs (Fig.7). A Kruskall-Wallis test across all three sites determined that yellow is overall significantly more abundant than brown ($H = 7.31$, $p < 0.01$). Further analysis comparing abundances of each morph per site using Pearson X^2 tests revealed that yellow was significantly more abundant than brown at Luminao and Tumon., but not at Piti E. (Table. 1).

	Yellow	Brown	X^2	p
Luminao	190	82	22.3	<0.001
Piti E.	388	468	3.75	0.053
Tumon	629	58	286.8	<0.001

Table 1. The abundances of each morph per site. Results of Pearson X^2 tests are shown using X^2 and p values.

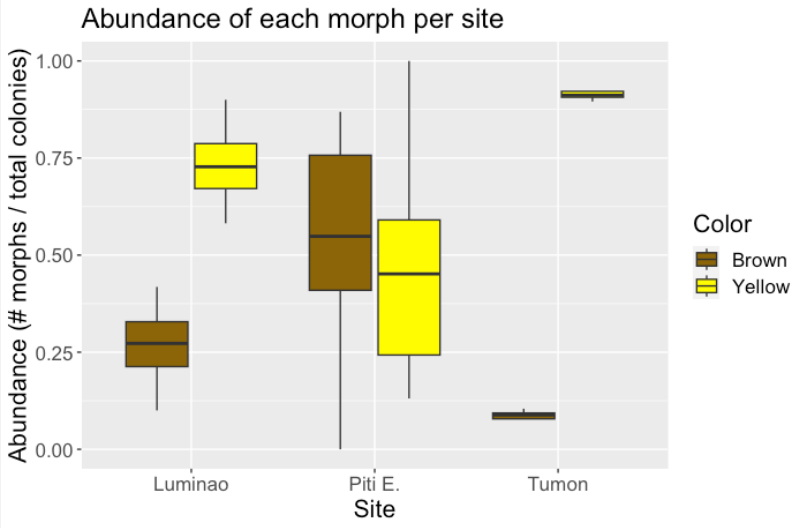

Figure 7. In situ abundance survey results. Total abundance of each color morph per site with abundance being measured as the number of morphs/total colonies. Boxes represent the interquartile range (IQR), which contains the middle 50% of the data, while the line inside each box denotes the median of each data set. Whiskers extend to 1.5 times the IQR.

5.2 Competition dynamics between morphs

5.2.1 *In situ* surveys

Surveys to document *in situ* competitive interactions at Luminao and Piti E. revealed significantly distinct patterns in competitive responses between *P. cylindrica* color morphs. Among the 284 recorded interactions, the most frequent competitive interaction recorded was yellow morphs overgrowing brown, which occurred in 39.8% of all interactions. This was followed by brown overgrowing yellow which occurred in 29.2% of all interactions, and yellow-brown stand-offs which occurred 22.2% of all interactions across all transect surveys (Fig. 8a). Yellow morphs were significantly more competitively dominant than brown morphs, when testing frequencies of only competition interactions ($X^2 = 4.59$; $p = 0.03$).

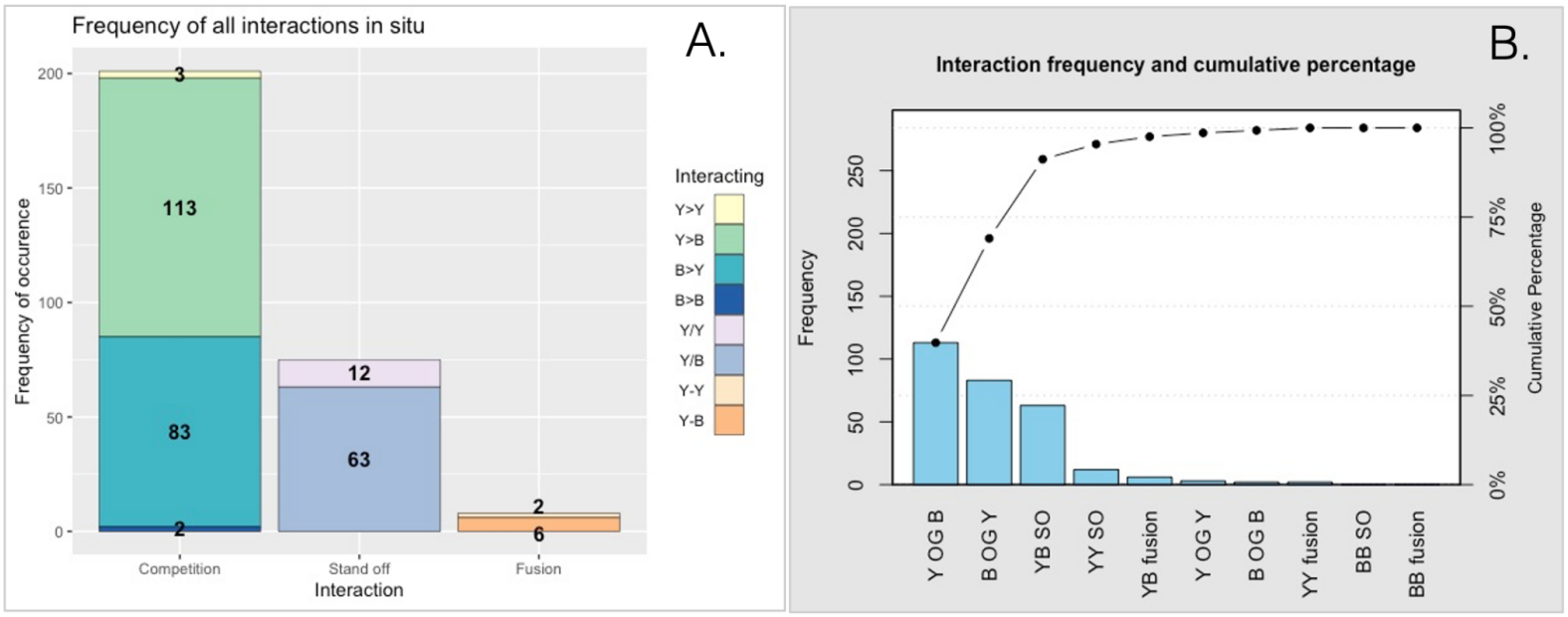

Figure 8. In situ competition survey results. (A) The frequency each pairwise interaction occurred with interaction types being categorized as either "competition," "stand-off," or "fusion." In the legend, “>” indicating “overgrowing” while “/” indicates stand off, and “-” indicates fusion; (B) The occurrence of each pairwise interaction represented as a frequency and a cumulative percentage where “OG” is overgrowth and “SO” is stand-off.

While fusion interactions were rare, yellow-brown fusion was the most common of fusion interactions recorded, when testing only frequencies each fusion interaction between yellow and brown colonies occurred ($X^2 = 4.04$; $p = 0.13$). Stand-offs also occurred significantly more frequently between yellow and brown colonies (Fig. 8), in comparison to stand-offs between yellow colonies and between brown colonies ($X^2 = 24.4$, $p < 0.001$).

5.2.2 Competition assay

The laboratory assay results, which further examined competitive dynamics between *P. cylindrica* color morphs, closely paralleled results obtained from *in situ* competition surveys. Out of the 12 yellow-brown pairs, yellow was observed overgrowing brown a total of 5 times (42% of Y-B interactions), by Week 8. In contrast, no instances were observed where brown fragments overgrew yellow fragments. This was the only significant competitive interaction among all brown-yellow pairs ($X^2 = 10.5$; $p = 0.01$) (Table 2b). However, yellow fragments often became overgrown with algae, even while successfully overgrowing their paired fragment (Table 2.a, b.). Yellow-brown pairs were observed competitively interacting as early as Week 3, where tissue along the contact margin was observed noticeably inflamed and "puffy" in appearance. Two accounts of yellow overgrowing brown occurred during Week 3, and while yellow tissue was observed receding and then spreading along the contact margin of these pairs during the weeks following, yellow morphs were observed to definitively "win" the interaction by Week 8. Among brown fragments in yellow-brown pairs, tissue paling and polyp retraction along the contact margin were common stress responses associated with being overgrown.

Fusion among brown pairs was first recorded in all six clonal brown pairs and in two non-clonal brown pairs during Week 3, so that boundaries separating any two connected brown

fragments were no longer detectable by Week 8. Both fragments deposited coenosteal tissue, which filled in gaps between both fragments so that neither fragment was distinguishable from each other, with very little visual evidence of distress. All 6 clonal brown fragments remained fused as well as the 2 non-clonal fragments for the remainder of the experiment. By Week 7, all 9 brown pairs had fused together. All brown pairs survived and were visually healthy by the end of the experiment. In comparison, only 42% of yellow-yellow pairs fused, which constituted 4 clonal pairs and 0 non-clonal pairs, as 2 clonal pair failed to fuse. Among yellow pairs, two non-clonal fragments were recorded fusing together during Week 3, but gradually unfused and remained separate through Week 7. One non-clonal yellow fused pair suffered total mortality and was overgrown by algae.

A.	Y in Y-B	B in Y-B	Y-Y	B-B
Overgrowing	5	0	0	0
Overgrown	0	5	0	0
Tissue Mortality	3	5	3	0
Algal Overgrowth	6	4	3	0
Fusion	1	1	4	9
Paling	8	10	8	7
Polyps Extended	2	2	0	7
Undetermined Interaction	3	3	0	0

	Frequency
Y overgrowing B	42%
B overgrowing Y	0%
Fusion Y-Y	44%
Fusion B-B	100%
Fusion Y-B	8%
Tissue Mortality Y in Y-B	25%
Tissue Mortality B in Y-B	42%
Tissue Mortality Y-Y	33%
Tissue Mortality B-B	0%
Algal Overgrowth Y in Y-B	66%
Algal Overgrowth B in Y-B	44%
Algal Overgrowth Y-Y	33%
Algal Overgrowth B-B	0%

Table 2. Interaction and response frequencies. (A) The frequency each interaction and response were recorded among all interacting pairs. (B) The frequency each interaction and stress response were recorded as a percentage of interacting pairs. Interactions are classified as occurring between two fragments, like “Overgrowing,” Overgrown,” or “Fusion,” while responses are classified as an observable physical reaction, such as “Algal Overgrowth,” “Tissue Mortality,” “Paling,” or “Polyps Extended.”

With mixed-morph pairs, one yellow-brown pair fused together from Week 6 to 8; however, the yellow fragment in this pair eventually displayed tissue mortality as well as algal overgrowth. Fusion was also observed in a yellow-brown pair, although in a transient pattern. By Week 2 the yellow-brown pair was observed fusing, but notable gaps were observed between fragments during Week 4. However, the following week the same yellow-brown pair was observed to fuse again, where it remained until week 8, where notable gaps were again observed. However, in the week following data collection and the end of the experiment, the same yellow-brown pair was observed fusing again, although accompanied by a large amount of algal overgrowth. It is also noteworthy to include that no stand-off interactions were observed among all interacting pairs.

Tissue paling was the first stress response recorded among fragments, which occurred during Week 1 in all pairs but one clonal brown pair. Tissue mortality was recorded in a non-clonal yellow pair as well as a yellow-brown pair for the first-time during Week 2. Among same color pairings, tissue mortality occurred in 33% of yellow pairs which consisted of only non-clonal, in contrast to 0% of brown pairs. However, among yellow-brown pairs, both tissue mortality and paling occurred more often in brown fragments than in yellow, which could have manifested as a symptom of stress in response to being outcompeted (Table 1). Algal overgrowth first appeared during Week 7, affecting a yellow-brown pair and a non-clonal yellow pair, and spread during the week following. By Week 8, one non clonal and two clonal yellow pairs and six yellow-brown pairs were overgrown with algae, indicating the end of the experiment. Notably, no brown-brown pairs were affected by algal overgrowth and fewer brown fragments were overgrown than yellow fragments among yellow-brown pairs.

5.3 Resistance and resilience to heat stress

After the coral photos were normalized using the kodak gray scale as described in the methods, a linear mixed model with random effects was employed to examine the relationship between temperature, time, color morph, and pigmentation. The model was applied to a dataset comprising 537 observations, grouped by individual IDs. Color morph, as an individual factor of color pigmentation, was found to be significant ($T = 6.4$, $p < 0.01$) across all dates and treatments. Dates 3/21 ($T = -5.4$, $p < 0.01$), 3/24 ($T = -6.4$, $p < 0.01$), and 4/1 ($T = 4.4$, $p < 0.01$) all had highly significant impacts on color pigmentation of both morphs across all treatments. A faster recovery of brown morphs was observed in the photo data (Fig 9), which showed that the surviving brown morphs in the 32°C tanks were significantly more pigmented by April 10 ($T = -0.88$, $p < 0.01$), and continued to recover in pigmentation until the experiment ended (Fig. 9). Yellow fragments in the 34°C tanks were significantly paler than brown fragments at 3/21 ($T = 0.44$, $p < 0.05$) and 3/24 ($T = 0.397$, $p < 0.05$), until April 5 when 100% die off occurred.

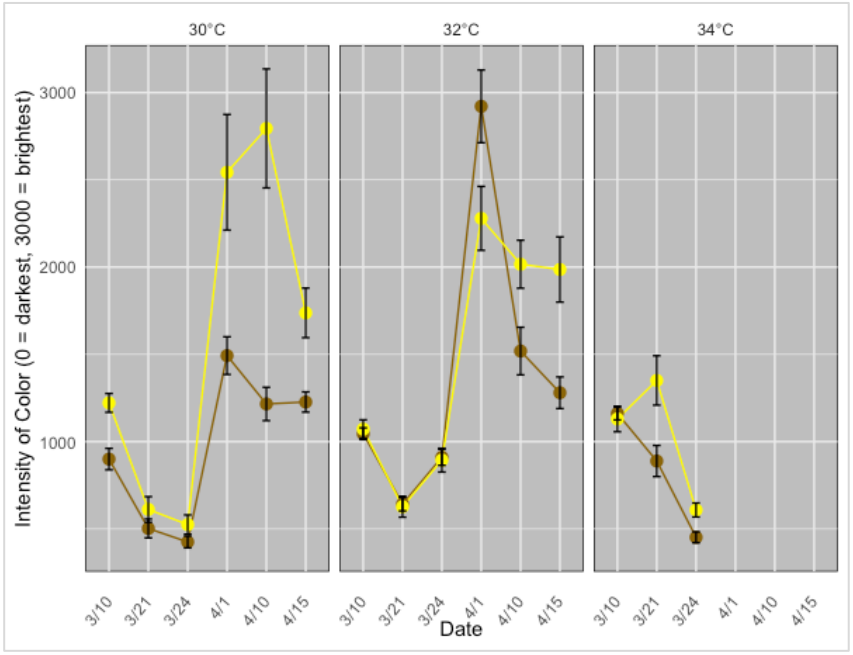

Figure 9. The intensity of color pigment of brown and yellow *P. Cylindrica* color morphs over time. Color pigment is darkest at lower values and lightest at highest values, indicative of bleaching.

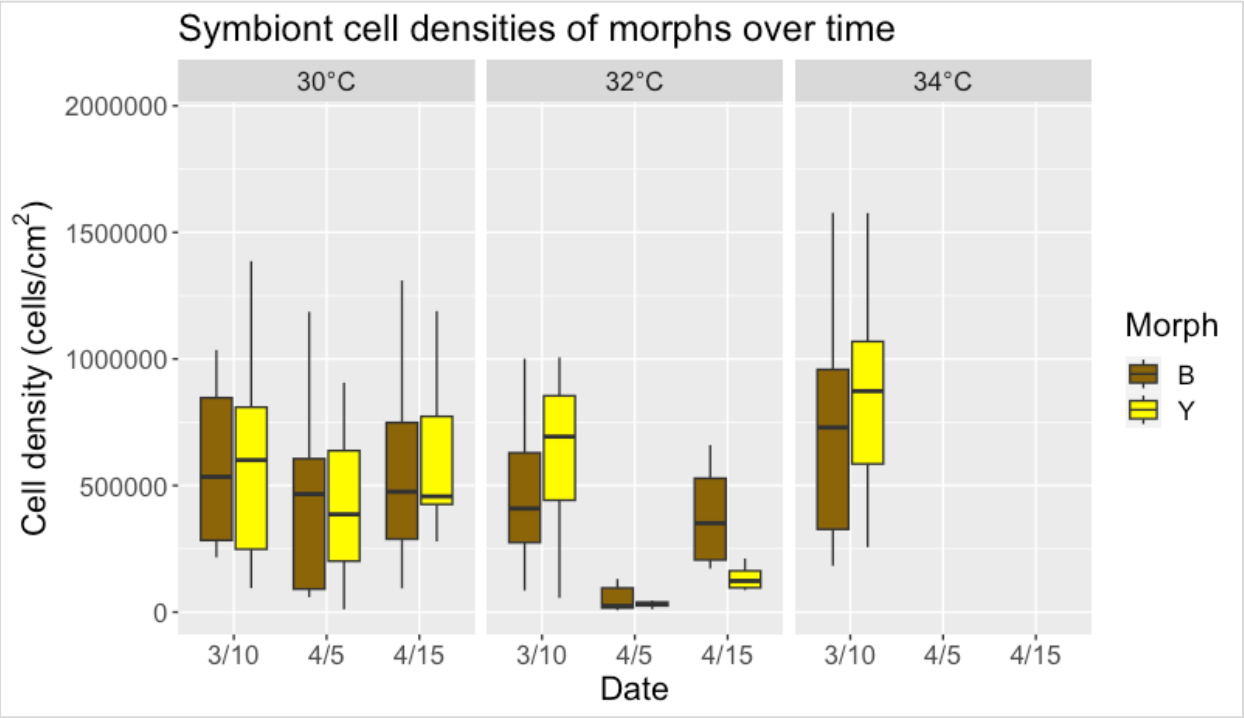

Figure 10. Cell densities of both color morphs exposed to different temperature treatments over time. Cell densities of both color morphs across all temperature treatments and time points measured as cells/cm^2. The boxes represent the interquartile range (IQR), which contains the middle 50% of the data, while the line inside each box denotes the median of each data set. Whiskers extend to 1.5 times the IQR.

Survivorship rates between color morphs were the same at both the middle and end time points among the surviving fragments in the 30℃ and 32℃ tanks. Specifically, 17 fragments of both color morphs survived in the 32℃ tanks by April 5, and both fragment populations decreased to only 4 survivors by the end of the experiment. All fragments of both color morphs were alive in the 30℃ tanks by April 5, and by April 15 both color morphs had only experienced 1 net loss. Overall, survivorship was not significantly different between color morphs. However, both color morphs in 34℃ tanks darkened in color before mortality, similar to fragments in the 30℃ control tank which became darker prior to bleaching on March 24 (Fig. 9). This perceived

increase in pigmentation may be a result of algal overgrowth accumulating on stressed fragments.

A linear mixed model with random effects was employed to examine the relationship between temperature, time, color morph, and symbiont cell densities. The model was applied to a dataset comprising 238 observations, grouped by individual IDs. At the start of the heat stress assay, all corals contained similar symbiont densities, and there were no significant differences between color morphs (Fig. 10). Among fragments exposed to 32℃, brown morph symbiont densities recovered significantly faster than yellow morph symbiont densities ($T = -3.35$, $p < 0.01$). Temperature ($F = 22.97$, $p < 0.01$) and Date ($F = 56.2$, $p < 0.01$) had highly significant impacts on the symbiont cell densities of both morphs across all treatments and time points. Color morph, as an individual factor of symbiont cell density, was not significant on its own ($F = 0.53$, $p > 0.1$). The interaction between Date and Temperature 32℃ had a significant negative effect on cell abundance ($T = -7.06$, $p < 0.01$), specifically during the bleaching phase. Conversely, the interaction between Date and Temperature 32℃ had a significant positive impact on cell densities during the recovery phase ($T = 0.7$, $p < 0.01$). Symbiont cell densities stayed consistently stable among fragments in the 30℃ control tanks (Fig. 10).

5.4 White syndrome dynamics

5.4.1 *In situ* white syndrome prevalence and severity

Color morphs also exhibited variations in the severity and prevalence of white syndrome across different sites (Fig. 11a., b.). The prevalence of white syndrome was overall higher in yellow morphs (44%) than in brown morphs (29%), averaged across all three sites (Fig. 11a), but most notably in Piti East, although there were no significant differences between color morphs

(Kruskal-Wallis H = 0.26, $p > 0.1$). While color morphs did not significantly differ in disease prevalence (Kruskal-Wallis H = 2.77, $p > 0.05$), the prevalence of disease was significantly different between sites (Kruskal-Wallis H = 17.5, $p < 0.001$). White syndrome prevalence was the highest at Luminao, and the lowest at Tumon (Fig. 11a).

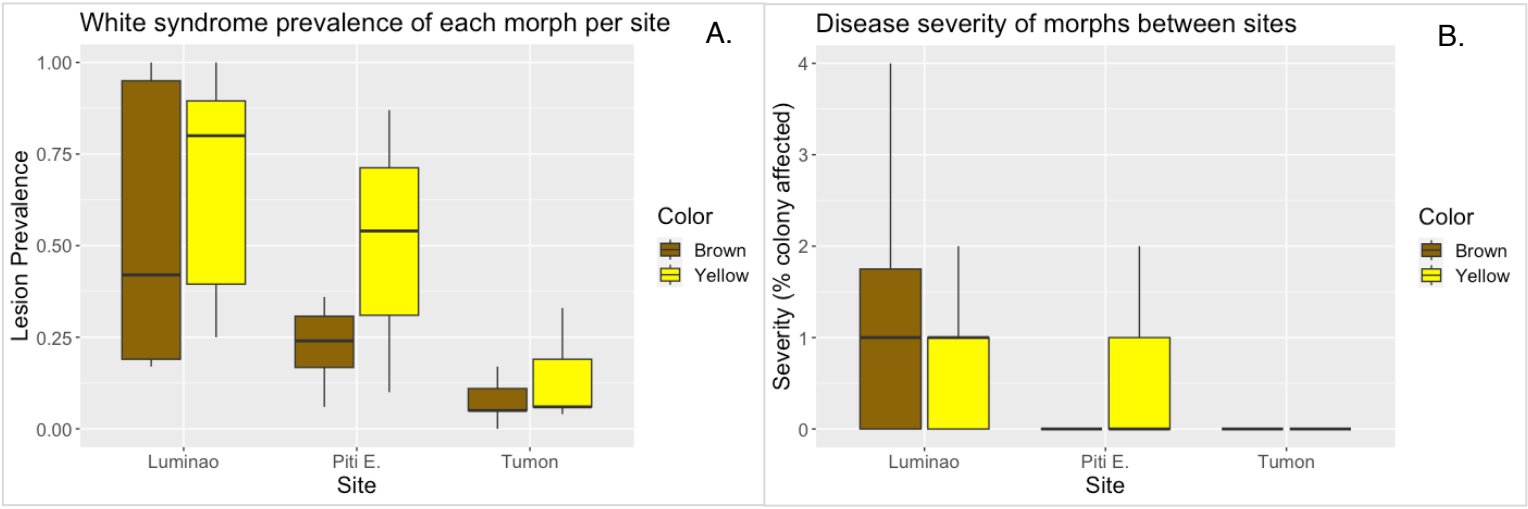

Figure 11. In situ disease survey results. (A) Prevalence of white syndrome on both color morphs per site where prevalence was quantified as the number of colonies affected/total colonies; (B) Disease severity on both color morphs per site where severity is measured as percent of colony affected (0 = 0%, 1 = 1-10%, 2 = 11-25%, 3 = 26-50%, 4 = 51-75%, 5 = 76-99%, 6= 100%). Boxes represent the interquartile range (IQR), which contains the middle 50% of the data, while the line inside each box denotes the median of each data set. Whiskers extend to 1.5 times the IQR.

White syndrome severity ranged from 0% - 75% across color morphs and sites (Fig. 11b), with the majority of colonies visually unaffected by disease. At Luminao, both color morphs displayed similar median severities, whereas in Tumon barely any white syndrome was observed, thus severity was 0 (Fig. 11b). However, at Piti E., yellow morphs exhibited significantly higher white syndrome severity than brown morphs (Kruskal-Wallis H - 14.4, $p <$ 0.001). Comparison of disease severity between brown and yellow morphs across all sites

showed that while the majority of all colonies had a disease severity of 0% (74.5%), significantly more yellow colonies had white syndrome severities of 0% ($X^2 = 78.4$, $p < 0.001$) in comparison to brown colonies. The second most frequented severity class among colonies was 1 (18.8%), with yellow colonies frequenting this disease severity class significantly more than brown colonies ($X^2 = 21.7$, $p < 0.001$). No significant differences were found among color morphs occupying severity class 2 ($X^2 = 3.7$, $p > 0.05$) or 3 ($X^2 = 0.32$, $p > 0.1$). A small minority of colonies experienced white syndrome on >51% of their total colony structure (0.004%), and no significant differences were found between color morphs among this severity class ($X^2 = 0.09$, $p > 0.1$).

5.4.2 Lesion dynamics

The central tendencies of lesion recovery rates were significantly different between color morphs, as yellow displayed a higher frequency of lesions in recovery (Mann-Whitney $W = 182$, $p < 0.05$). The rates of all transitioning lesions on yellow colonies were also significantly more variable than lesions on brown colonies ($F_{66,60} = 0.026$, $p < 0.0001$). Yellow colonies displayed both faster progression and recovery rates (Fig. 12), while 58.9% of all lesions in stasis were found on brown colonies. However, despite statistically significant different variability in progression rates between morphs, there were no significant differences between the mean progression rates of lesions on brown and yellow colonies (Mann-Whitney $W = 232$, $p > 0.1$).

Between the selected subset of timepoints: June 16, June 29, and August 4, differences in the variations of lesion sizes were observed between color morphs. There were 144 total lesions analyzed, which were binned into size classes: small, medium, large, and gargantuan based on their measurements in cm^2 (Fig. 13, Table 3).

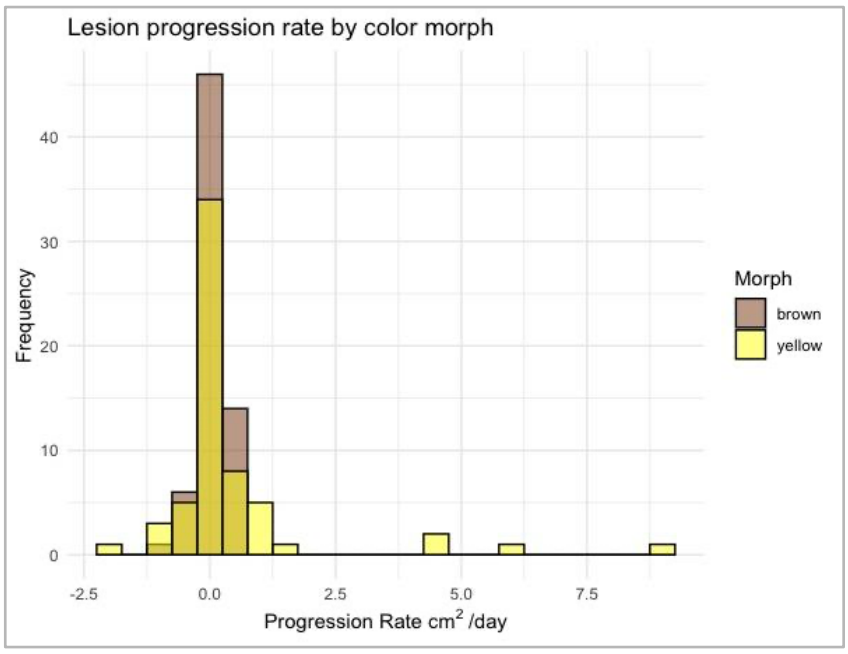

Figure 12. The frequency of lesion progression rates for lesions occurring on yellow and brown morphs. Lesion transient rates were measured as change in cm^2/day. Negative values indicate recovery while positive values indicate progression.

Probabilities of lesions transitioning between size classes were compiled into a Markov model, as shown in Figure 13, although none of the lesions among any of the transition states significantly differed between color morphs. Lesions occurring on yellow colonies exhibited a notably wider size range, ranging from 5.9 to 207.3 cm^2, whereas lesions on brown colonies were comparatively smaller and less variable, spanning from 6.5 to 32.6 cm^2 (Table 3). There was a total of nine observations of lesions on yellow colonies falling into the largest size class, which ranged from 40-210 cm^2, while 0 lesions on brown colonies were observed within the size class (Table 3).

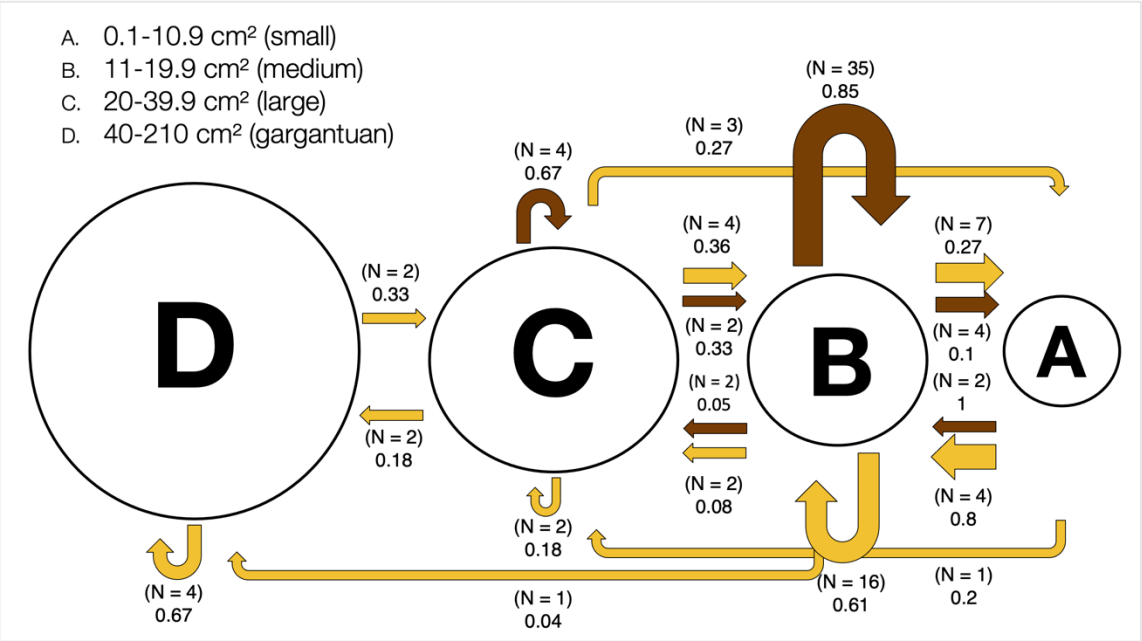

Figure 13. Markov Chain of probabilities for lesions on both color morphs transitioning between size classes. Size class D represents the largest lesions termed "gargantuan", size class C represents large lesions, size class B represents medium size lesions, and size class A represents the smallest sized lesions while arrows represent transition probabilities. Arrow size represents the magnitude of each transition probability while arrow color represents each color morph. Probabilities of each transition are represented as decimals below the total number of lesions transitioning from one size class to the next and were placed next to the corresponding arrow.

The proportion of lesions in the gargantuan size class differed significantly between color morphs ($X^2 = 6$, $p < 0.05$). Lesions affecting yellow morphs occupied a wider range of size classes than lesions on brown morphs and exhibited faster progressions between size classes (Fig. 13). Multiple lesions affecting yellow morphs skipped a size class between census dates, progressing from small to large, medium to gargantuan, or recovering from medium to small, in comparison to brown lesions, which never skipped size classes (Fig. 13). The majority of brown lesions (71.4%) were in a state of stasis in the medium size class, and rarely occupied other size classes.

The most common size class observed in both color morphs was “medium,” which ranged between 11-19.9 cm^2. Although both brown and yellow colonies had the majority of lesions fall into this size class there were relatively more brown lesions that occupied the medium size class (Table 3), however, there were no significant differences in frequencies of medium sized lesions between color morphs ($X^2 = 3.1$, $p > 0.05$). The probability of stasis was the highest among medium-sized brown lesions (0.85), which was greater than the probability of stasis among medium sized yellow lesions (0.61). A greater number of yellow lesions (4) were progressing from small to medium size classes than brown morphs (2), however a greater number of yellow lesions (7) were also recovering from medium size class to small size class than brown (4). Figures 12 and 13 as well as Table 3 demonstrate the variability of lesions affecting yellow morphs of *P. cylindrica* in both size class and progression rates, in comparison to lesions affecting brown colonies.

	Yellow	Brown	X^2	p
Small	12	6	1.03	0.30
Medium	37	58	2.35	0.13
Large	14	8	0.83	0.36
Gargantuan	9	0	6.00	0.01

Table 3. The frequency lesions occurred in each size class for both color morphs. Lesions were censused at three separate time points (6/16, 6/29, 8/4) resulting in three separate size measurements per lesion. Results of Pearson X^2 tests are shown as X^2 and *p* values.

6 Discussion and Conclusion

The present study reports the intraspecific differences between color morphs of *P. cylindrica* on Guam in their relative abundances on reefs and their associated competitive dynamics, and resilience/resistance to environmental stressors, such as bleaching and disease. Yellow morphs were found to be significantly more abundant than brown morphs at two sites on Guam, and were also found to be significantly more competitive than brown morphs, overgrowing colonies more frequently than brown morphs. Brown colonies, however, were observed having a significantly faster recovery in both symbiont cell densities and color pigmentation post bleaching, indicating some level of resilience to heat stress. In terms of disease dynamics, white syndrome was observed being significantly more variable on yellow colonies, with lesions growing significantly larger than lesions on brown colonies, but also recovering faster. The results presented in this study suggest tradeoffs in the resilience/resistance to environmental stress between color morphs of *P. cylindrica*, that may affect future population dynamics on Guam.

Across all sites but Piti E., yellow *P. cylindrica* was significantly more abundant than brown morphs. Yellow morphs of *P. cylindrica* were also significantly more competitive than brown morphs and "won" the majority of yellow/brown interactions, both *in situ* and in the lab competition assay. Because of their greater competitive abilities, yellow colonies are more likely to outcompete brown morphs for space on Guam's reef flats, which may be a contributing factor in the differences in abundances observed. Another potential factor influencing abundance patterns could be the yellow morph's ability to recover after developing white syndrome. White syndrome lesions affecting yellow colonies were observed to recover faster and at a higher frequency than lesions affecting brown morphs, which recovered significantly slower. It's also

possible that yellow color morphs reproduce on a more frequent and/or successful basis than brown morphs, however, reproductive habits of *P. cylindrica* on Guam has yet to be studied.

Although competitive interactions of both color morphs closely mirrored each other in the field and in tank experiments, there were inconsistencies between the pairs that were observed fusing together. Fusion observations were difficult to observe between colonies of the same morph in the field, thus the majority of fusing colonies observed *in situ* were brown and yellow morphs. During *ex situ* experimentation, all brown pairs successfully fused together, with no perceptible boundary between any two fragments, while only 44% of yellow pairs fused. Brown pairs were also notably less susceptible to algal overgrowth, tissue mortality, paling, and were visually healthier looking overall in comparison to yellow pairs. Because brown colonies appeared to be at a competitive disadvantage, it is possible that they allocate more energy towards fusion to increase survivorship through larger colony size and stability (Chornesky 1991). A larger colony size is less easily overgrown and out competed by more aggressive species, and fusion between colonies may function as a defense mechanism against competitors. The brown color morphs success and frequency of fusion between both clonal and potentially non-clonal fragments may have resulted in the absence of brown fusion reports while monitoring *in situ*. However, because no genotyping was performed during this experiment, it is not possible to know for certain whether colonies were non-clonal. A study based on *P. cylindrica* in the Philippines reported colonies as gonochoristic brooders (Abecia et al. 2016), while *P. cylindrica* has been reported broadcast spawning at other locations throughout the Pacific (Kojis & Quinn 1982; Babcock et al. 1986; Tomascik et al. 1997; Itano & Buckley 1988). However, little is known of the reproductive habits of *P. cylindrica* in Guam. It is possible that exposure to

powerful waves due to a high frequency of typhoons and storms in the area could have resulted in increased fragmentation and dispersal, resulting in isolated clonal colonies.

White syndrome occurred in higher proportion and more severely on yellow morphs at Piti E. than on brown morphs, potentially driving a lower abundance of yellow morphs at this site. While white syndrome prevalence did not differ significantly between color morphs, site was a significant factor. Of all three sites, Luminao had the highest prevalence and severity of white syndrome in both color morphs. Luminao reef flats populate the seaward side of the Glass Breakwater, while the sheltered side borders Apra Harbor. Apra Harbor is home to a large, active US Naval base and Guam's commercial port and is a heavily trafficked area by military vessels and shipping carriers. Previous studies have reported high quantities of mercury, copper, lead, tin, and zinc in harbor sediments as well as multiple pollutants resulting from storm water runoff (Belt and Collins 1993; Denton et al. 1999). The close proximity of Luminao to Apra Harbor may have influenced the increased prevalence of white syndrome affecting *P. cylindrica* morphs in this area.

White syndrome lesions occurring on yellow colonies were highly variable and grew to be significantly larger than brown lesions, but also healed at significantly faster rates. The faster recovery rates observed in yellow colonies displaying white syndrome lesions is consistent with the competitive dynamics also observed. It is possible that the fast rate at which lesions on yellow morphs healed as well as the competitive dominance of yellow morphs, are both related to the rate of tissue generation. Yellow morphs were also significantly slower to recover from bleaching, as measured by symbiont cell densities and pigmentation. They became significantly paler than brown morphs in the ambient temperature tank during the bleaching experiment, despite maintaining statistically similar symbiont cell densities from the beginning to the end of

the experiment. The changes in pigmentation that the *P. cylindrica* fragments in the ambient temperature tank experienced are indicative of stress and could be a result of the difference in light and temperature fluctuations that occur in a tank environment compared to *in situ*. However, because symbiont cell densities did not significantly change over time in the ambient temperature fragments, paling could have been a result of changes in FP densities (Baird et al. 2007), reductions in GFP's or GFP- like homologues, or a reduction in Peridinin, xanthophyll pool, chlorophyll c_2 and chlorophyll *a*, as observed in bleached *Montipora monasteriata* colonies that similarly did not lose symbiont densities (Dove et al. 2006). Symbiont communities as well as bacterial communities of samples from both color morphs are also known to be highly similar (Lock et al. 2023 in prep). The microbiomes of both color morph are heavily dominated by C15 *Symbiodinium* and *Endozoicomonas* . The prevalence of vibrio bacteria, which are often defined as pathogens or opportunists, did not differ significantly between color morphs. In addition to the high similarity in microbiome communities between color morphs, they were also found to be genetically similar (Lock et al. 2023 in prep).

As climate change challenges organismal fitness through increasing temperatures and disease prevalence, the fast acclimatization of individuals who can increase their stress tolerance will determine a species' success and survival. Acclimation can lead to variation that results in phenotypic plasticity within a species, through the variability produced in stress responses among clone mates (Durante et al. 2019; Payne and Wagner 2019). This can allow for the flexibility of a single species to produce a range of responses to different conditions (Hochachka and Somero, 2002; Putnam et al. 2016). The mechanism thought to drive phenotypic plasticity and facilitate rapid acclimatization is epigenetics, or the heritable modification of DNA, gene

expression, and associated proteins (Durante et al. 2019; Feil and Fraga 2012; Putnam et al. 2016).

In the case of *P. cylindrica* color morphs on Guam, there are clear trade-offs associated with energy investment. While yellow *P. cylindrica* morphs allocate more energy towards competition and tissue generation, brown morphs invest more in immune response. The associated trade-off for the yellow morphs is a lower resistance to disease and heat stress, while brown morphs are significantly less competitive and heal slower from disease infection. The driver of these trade-offs in biological traits has yet to be determined but could be a result of the development of different photo-protective GFP-like pigments and/or different stress exposure histories. It is possible that the brown phenotype's increased resilience to bleaching and resistance to disease is due to a history of exposure to these stressors, resulting in the heritable modifications of DNA encoding a more robust immune response to environmental stress. In comparison, the yellow phenotype may have a history existing among highly crowded areas requiring a more aggressive competitive ability to obtain space or could even be predated upon on a more frequent basis, requiring faster tissue regeneration for survival. It's easy to speculate on the potential differences in stress exposure histories resulting in the phenotypic differences observed in Guam's *P. cylindrica*, however, both color morphs exist in the same areas of Guam's reef flats and significant differences in environmental stress is probably unlikely. To better understand the trade-offs observed in the life history and biological traits of *P. cylindrica* color morphs on Guam, future molecular work is probably necessary.

The combination of rising sea surface temperatures, increasing disease prevalence, sedimentation, worsening water quality, overfishing, ocean acidification, along with the devastation caused by *Acanthaster plancii,* has put Guam's coral reef ecosystems in increasing

jeopardy. As the rate of extinction rises and susceptible species continue to die off, coral reefs around the globe are shifting so that the few resilient surviving species dominate. As a result of human impacts, coral cover on reefs will continue to decrease and there will be less of a need for species to invest large amounts of energy towards competitive aggression and overgrowth. The species with the most plasticity, that are capable of rapidly evolving to produce phenotypes that can acclimatize to elevated temperatures and the increasing prevalence of pathogenic diseases, are most likely to survive under the future projections of climate change and may constitute the few remaining species among coral reef communities.

While there is still much to understand about phenotypic differences within a species, this study suggests that the diversity of traits, such as color, do play a role in a species success in a changing environment. Future projections of climate change do not bode well for yellow *P. cylindrica* phenotypes, who are highly competitive but have less tolerance of disease and bleaching and have also exhibited an increased susceptibility to algal overgrowth and tissue mortality. Although yellow phenotypes may be more abundant presently, we will most likely observe a shift towards a higher abundance of brown *P. cylindrica* phenotypes, who are less competitive but more resistant to pathogenic disease and heat stress, and therefore have a higher chance of surviving projected environmental conditions. Future genetics work on the color morphs of *P. cylindrica* could advance our understanding of the underlying mechanisms causing the differences in biological and life history traits observed and could help further determine the evolutionary track of these phenotypes.

Because coral reefs around the globe are also threatened by an increasing severity and frequency of bleaching and disease events, it is important to document trade-offs that occur between color morphs of other coral species to further understand the role of color in coral

resilience. Conservation and restoration projects will need to investigate phenotypic differences within coral species in order to outplant the most robust individuals that can withstand an increasingly stressful environment. Trade-offs in biological traits and stress responses observed in this study highlight the need for local and global stressors impacting coral reef ecosystems to be addressed in order to preserve species diversity and global economy.

7 References

Abecia, J.E.D., Guest, J.R. and Villanueva, R.D. (2016), Geographical variation in reproductive biology is obscured by the species problem: a new record of brooding in *Porites cylindrica*, or misidentification?. Invertebr Biol, 135: 58-67. https://doi.org/10.1111/ivb.12116

Acacia J Guest J.R., Villanueva, R.D. (2016) Geographical variation in reproductive biology is obscured by the species problem: a new record of brooding in *Porites cylindrica*, or misidentification?. Invertebr Biol, 135: 58-67. https://doi.org/10.1111/ivb.12116.

Aceret T.L., Sammarco P.W., Coll J.C. (1995) Effects of terpenes derived from the soft coral *Sinularia flexibilis* on the eggs, sperm and embryos of the scleractinian corals *Montipora digitata* and *Acropora tenuis*. Mar Biol 122:317–323.

Alieva N.O., Konzen K.A., Field S.F., Meleshkevitch E.A., Hunt M.E., Beltran-Ramirez V., Miller D.J., Wiedenmann J., Salih A., Matz M.V. (2008) Diversity and evolution of coral fluorescent proteins. PLoS ONE 3:e2680.

Antonius, A. (1985) Coral Diseases in the Indo-Pacific: A First Record. Marine Ecology, 6: 197-218. https://doi.org/10.1111/j.1439-0485.1985.tb00322.x.

Aronson R., Precht W. (2001) White-band disease and the changing face of Caribbean coral reefs. The ecology and etiology of newly emerging marine diseases 159:25-38.

Babcock R.C., Bull G.D., Harrison P.L., Heyward A.J., Oliver J.K., Wallace C.C., Willis B.L. (1986) Synchronous spawnings of 105 scleractinian coral species on the Great Barrier Reef. Mar. Biol. 90:379–394.

Bates D, Mächler M, Bolker B, Walker S (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, **67**(1), 1‑48.doi:10.18637/jss.v067.i01.

Baird A, Bhagooli R, Ralph P, Takahashi S (2008). Coral bleaching: the role of the host. Trends in Ecology & Evolution, 24: 16-20.

Belt Collin Hawaii (1993). Final environmental impact statement of proposed facilities development and relocation of Navy activities to the territory of Guam from the republic of the Philippines. U.S. Navy Pacific Division Naval Activities Engineering Command.

Brandt M.E., McManus J.W. (2009) Disease incidence is related to bleaching extent in reef-building corals. Ecology, 90: 2859-2867 doi: 10.1890/08-0445.1.

Bollati E., Plimmer D., D'Angelo C., Wiedenmann J. (2017) FRETmediated long-range wavelength transformation by photoconvertible fluorescent proteins as an efficient mechanism to generate orange-red light in symbiotic deep water corals. Int. J. Mol. Sci. 18:1174, doi: 10.3390/ijms180 71174.

Bourne D.G., Munn C.B. (2005) Diversity of bacteria associated with the coral *Pocillopora damicornis* from the Great Barrier Reef.*Environmental Microbiology* 7(8):1162-1174.

Bourne D.G., Garren M., Work T.M., Rosenberg E., Smith G.W., Harvell C.D. (2009) Microbial disease and the coral holobiont. Trends Microbiol. 17(12):554-62. doi: 10.1016/j.tim.2009.09.004. Epub 2009 Oct 12. PMID: 19822428.

Bourne D. G., Ainsworth T. D., Pollock F. J., Willis B. L. (2015) Towards a better understanding of white syndromes and their causes on Indo-Pacific coral reefs. Coral Reefs 34, 233–242. doi: 10.1007/s00338-014-1239-x.

Burdick D., Brown V., Asher J., Caballes C., Gawel M., Goldman L., Hall A., Kenyon J., Leberer T., Lundbald E., McIlwain J., Miller J., Minton D., Nadon M., Pioppi N., Raymundo L., Richards B., Schroeder R., Schupp P., Smith E., Zgliczynski B. (2008) Status of the coral reef ecosystems of Guam. Bureau of Statistics and Plans, Guam Coastal Management Program.

Brown B., Bythell J. (2005) Perspectives on mucus secretion in reef corals. *Marine Ecology Progress Series* 296:291-309.

Buss L., Jackson J. (1979) Competitive Networks: Nontransitive Competitive Relationships in Cryptic Coral Reef Environments. The American Naturalist*,* 113(2), 223-234.

Buss L. Somatic cell parasitism and the evolution of somatic tissue compatibility. Proc Natl Acad Sci USA 1982; 79:5337-41.

Buss L. (1986) Competition and community organization on hard surfaces in the sea. In: Diamond J, Case TJ (eds) Community ecology. Harper and Row, New York.

Bruno J.F., Selig E.R., Casey K.S., Page C.A., Willis B.L., Harvell C.D., Sweatman H., Melendy A.M. (2007) Thermal stress and coral cover as drivers of coral disease outbreaks. Plos Biology 5:1220–1227.

Chadwick N., Morrow K. (2011) Coral Reefs: An Ecosystem in Transition || Competition Among Sessile Organisms on Coral Reefs. , 10.1007/978-94-007-0114-4 (Chapter 20), 347–371. doi:10.1007/978-94-007-0114-4_20.

Chesher RH (1969) Destruction of the Pacific corals by the sea star *Acanthaster planci*. Science 165:280–283.

Chornesky E.A. (1991) The ties that bind: inter-clonal cooperation may help a fragile coral dominate shallow high-energy reefs. Mar Biol109:41–51.

Connell J.H., Hughes T.P., Wallace C.C. et al. (2004) A long-term study of competition and diversity of corals. Ecol Monogr 74:179–210.

Cornwell B., Armstrong K., Walker N., Lippert M., Nestor V., Golbuu Y., Palumbi S., (2021) Widespread variation in heat tolerance and symbiont load are associated with growth tradeoffs in the coral *Acropora hyacinthus* in Palau. ELife;10:e64790

D'Angelo C., Denzel A., Vogt A., Matz M.V., Oswald F., Salih A., Nienhaus G.U., Wiedenmann J. (2008) Blue light regulation of host pigment in reef-building corals. Mar Ecol Prog Ser 364:97–106.

Denten G., Concepcion L., Wood R. (1999) Heavy metals, PCBs, and PAHs, in marine ecosystems from four harbor locations on Guam, a pilot study. Water and Environmental

Research Institute of the Western Pacific University of Guam. Guam Environmental Protection Agency.

Dizon R.M., Yap H.T. (2005) Coral responses in single- and mixed-species plots to nutrient disturbance. Mar Ecol Prog Ser 296:165–172.

Dove S., Hoegh-Guldberg O., Ranganathan S. (2001) Major colour patterns of reef-building corals are due to a family of GFP-like proteins, Coral Reefs 19, 197–204, doi:10.1007/PL00006956.

Dove S. (2004), Scleractinian corals with photoprotective host pigments are hypersensitive to thermal bleaching, Marine Ecology Progress Series, 272: 99-116.

Dove S., Ortiz, J. C., Enríquez S., Fine M., Fisher P., Iglesias-Prieto R., Thornhill D., Hoegh-Guldberg O. (2006) Response of holosymbiont pigments from the scleractinian coral *Montipora monasteriata* to short-term heat stress, Limnology and Oceanography, 51, doi: 10.4319/lo.2006.51.2.1149.

Durante M.K., Baums I.B., Williams D.E., Vohsen S., Kemp D.W. (2019) What drives phenotypic divergence among coral clonemates of *Acropora palmata*? *Mol Ecol*. 28: 3208–3224. https://doi.org/10.1111/mec.15140.

Edmunds P. J. (1994) Evidence that reef-wide patterns of coral bleaching may be the result of the distribution of bleaching-susceptible clones. Mar. Biol. 121, 137–142. doi: 10.1007/bf00349482.

Eyal G., Wiedenmann J., Grinblat M., D'Angelo C., Kramarsky-Winter E., Treibitz T., Ben-Zvi O., Shaked Y., Smith T.B., Harii S., Denis V., Noyes T., Tamir R., Loya Y. (2015) Spectral diversity and regulation of coral fluorescence in a mesophotic reef habitat in the Red Sea. PLoS ONE 10:e0128697. doi: 10.1371/journal.pone.0128697.

Fadi G.L., Stephen L.D., Leo W.B. (2008) Allorecognition and chimerism in an invertebrate model organism, Organogenesis, 4:4, 236-240, DOI: 10.4161/org.4.4.7151.

Feil R., and Fraga M. (2012). Epigenetics and the environment: emerging patterns and implications. *Nature Reviews Genetics*13: 97–109.

Ferrier-Pages C., Hoogenboom M., Houlbreque F. (2010) The role of plankton in coral trophodynamics. In: Dubinsky Z, Stambler N (eds) Coral reefs: an ecosystem in transition Springer, Doedrecht.

Fitt W. K., Gates R. D., Hoegh-Guldberg O., Bythell J. C., Jatkar A., Grottoli A. G., et al. (2009) Response of two species of Indo-Pacific corals, *Porites cylindrica* and *Stylophora pistillata*, to short-term thermal stress: the host does matter in determining the tolerance of corals to bleaching. J. Exp. Mar. Biol. Ecol. 373, 102–110. doi: 10.1016/j.jembe.2009.03.011.

Frade, P.R., Englebert, N., Faria, J. et al. (2008) Distribution and photobiology of *Symbiodinium* types in different light environments for three colour morphs of the coral *Madracis pharensis*: is there more to it than total irradiance?. Coral Reefs 27, 913–925 https://doi.org/10.1007/s00338-008-0406-3.

Frade PR, Roll K, Bergauer K, Herndl GJ. (2016a) Archaeal and bacterial communities associated with the surface mucus of Caribbean corals differ in their degree of host specificity and community turnover over reefs. *PLOS ONE* 11(1):e0144702.

Frank U., Rinkevich B. (1994) Nontransitive patterns of historecognition phenomena in the Red Sea hydrocoral *Millepora dichotoma*. Mar Biol 118:723–729.

Frank U., Oren U., Loya Y., Rinkevich B. (1997) Alloimmune maturation in the coral *Stylophora pistillata* is achieved through three distinctive stages, 4 months post-metamorphosis. Proc Roy Soc Lond B 264:99–104.

Fricke H.W. and Schuhmacher H. (1983) The Depth Limits of Red Sea Stony Corals: An Ecophysiological Problem (A Deep Diving Survey by Submersible). Marine Ecology, 4: 163-194, doi:10.1111/j.1439-0485.1983.tb00294.x.

Gilmore A.M., Larkum A.W.D., Salih A., Itoh S., Shibata Y., Bena C., Yamasaki H., Papina M., Van Woesik R. (2003) Simultaneous Time Resolution of the Emission Spectra of Fluorescent Proteins and Zooxanthellae Chlorophyll in Reef-building Corals. Photochemistry and Photobiology, 77: 515-523, doi:10.1562/0031-8655(2003) 0770515STROTE2.0.CO2.

Glynn-D'Croz. (1990) Coral mortality and disturbances to coral reefs in the tropical eastern Pacific: Di dalam: Proc Glob Ecol Conseq 1982-83 El Nino- Southern Oscil: Amsterdam: Elsevier. him 55-126.

Gomez E.D. (1988) Overview of environmental problems in the East Asian Seas region. Ambio 17:166–169.

Greene A., Donahue M.J.,Caldwell J.M., Heron S.F., Geiger E. and Raymundo L.J. (2020) Coral Disease Time Series Highlight Size-Dependent Risk and Other Drivers of White Syndrome in a Multi-Species Model. Front. Mar. Sci. 7:601469. doi: 10.3389/fmars.2020.601469.

Grinstead CM, Snell JL (1997) Chapter 11—Markov Chains. Introduction to Probability. Providence, RI: American Mathematical Society, pp. 405–452.

Grottoli A., Rodrigues L., Palardy, J. (2006) Heterotrophic plasticity and resilience in bleached corals. Nature. 440. 1186-9. doi: 10.1038/nature04565.

Environmental Protection Agency. (2019). EPA Fact Sheet for National Pollutant Discharge Elimination System (NPDES) Permit No. GU0020001 for Guam Power Authority Cabras Power Plant, Route 11 Cabras Island, Municipality of Piti, Guam, 96915.

Gunthorpe L., Cameron A.M. (1990a) Intracolonial variation in toxicity in scleractinian corals. Toxicon 28:1221–1227.

Gunthorpe L., Cameron A.M. (1990b) Widespread but variable toxicity in scleractinian corals. Toxicon 28:1199–1219.

Harvell C. D., Jordan-Dahlgren E., Merkel S., Rosenberg E. (2007) Coral disease, environmental drivers, and the balance between coral and microbial associates. Oceanography 20, 172–195. doi: 10.5670/oceanog.2007.91.

Hlavac M (2022). *stargazer: Well-Formatted Regression and Summary Statistics Tables*. Social Policy Institute, Bratislava, Slovakia. R package version 5.2.3, https://CRAN.R-project.org/package=stargazer.

Hochachka, P.W. and Somero, G.N. (2002) Biochemical adaptation: Mechanism and process in physiological evolution. Oxford University Press, New York.

Hoegh-Guldberg, O., Smith, G.J., (1989) The effects of sudden changes in temperature, light and salinity on the population density and export of zooxanthellae from the reef corals *Stylophora pistillata* Esper and *Seriatopora hystrix* Dana. Journal of Experimental Marine Biology and Ecology 129, 279–303.

Hoegh-Guldberg O., Jones R. (1999) Diurnal patterns of photoinhibition and photoprotection. Marine Ecology Progress Series (in press).

Howells E.J., Vaughan G.O., Work T.M. Burt J.A., Abrego D. (2020) Annual outbreaks of coral disease coincide with extreme seasonal warming. Coral Reefs 39, 771–781. doi: 10.1007/s00338-020-01946-2.

Hughes T.P. et al. (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301: 929–933.

Hughes T., Barnes M., Bellwood D., Cinner J., Cumming G., Jackson J., Kleypas J., Van de Leemput I., Lough J., Morrison T., Palumbi S., Van Nes E., Scheffer M. (2017) Coral reefs in the Anthropocene. Nature 546, 82–90, doi:10.1038/nature22901.

Hughes T.P., Kerry J.T., .lvarez-Noriega M., .lvarez-Romero J.G., Anderson K.D., Baird A.H., Babcock R.C., Beger M., Bellwood D.R., Berkelmans R. (2017b) Global warming and recurrent mass bleaching of corals. Nature 543: 373–377.

Hughes T.P., Kerry J.T., Connolly S.R., Baird A.H., Eakin C.M., Heron S.F., Hoey A.S., Hoogenboom M.O., Jacobson M., Liu G. (2018) Ecological memory modifies the cumulative impact of recurrent climate extremes. Nat Clim Change 9:40.

Idjadi J.A., Karlson R.H. (2007) Spatial arrangement of competitors influences coexistence of reef-building corals. Ecology 88:2449–2454.

Itano D., Buckley T. (1988) Observations of the mass spawning of corals and Palolo (Eunice viridis) in American Samoa. Report to the Department of Marine and Wildlife Resources. Pago Pago, American Samoa. 29 pp.

Jackson J. (1979) Overgrowth Competition Between Encrusting Cheilostome Ectoprocts in a Jamaican Cryptic Reef Environment. Journal of Animal Ecology, 48(3), 805-823. doi:10.2307/4196.

Jerlov N. G. (1968) Optical oceanography. American Elsevier Publ. Co., Inc., New York. 194 p. Limnology and Oceanography, 13, doi: 10.4319/lo.1968.13.4.0731.

Jones R.J., Hoegh-Guldberg O., Larkum A.W.D., Schreiber U. (1998) Temperature induced bleaching of corals begins with impairment of the CO2 fixation mechanism in zooxanthellae. Plant, Cell and Environment 21, 1219–1230.

Jones R. and Randall R. (1971) An Annual Cycle Study of Biological, Chemical, and Oceanographic Phenomena Associated with the Agana Ocean Outfall. Report to the Guam Water Pollution Control Commission, 67 pp.

Jones R., and Yellowlees D. (1997) Regulation and control of intracellular algae (= zooxanthellae) in hard corals*Phil. Trans. R. Soc. Lond. B*352457–468.

Kavousi J., Reimer J.D., Tanaka Y., Nakamura T. (2015) Colony-specific investigations reveal highly variable responses among individual corals to ocean acidification and warming. Mar Environ Res 109:9–20.

Kavousi J., Denis V., Sharp V., Reimer J.D., Nakamura T., Parkinson J.E. (2020) Unique combinations of coral host and algal symbiont genotypes reflect intraspecific variation in heat stress responses among colonies of the reef-building coral, *Montipora digitata*. Mar Biol 167, 23, doi: 10.1007/s00227-019-3632-z.

Kawaguti S. (1944) On the physiology of reef corals. VI. Study on the pigments. Paloa Trop Biol Stn Stud 2: 617-673.

Kojis B.L., Quinn N.J. 1982. Reproductive strategies in four species of *Porites* (Scleractinia). Proc. 4th Int. Coral Reef Symp. 2: 145–151.

Kubicek A., Breckling B., Hoegh-Guldberg O., Reuter H. (2019) Climate change drives trait-shifts in coral reef communities. Sci Rep 9:3721.

Kruskal, W. H., & Wallis, W. A. (1952). Use of Ranks in One-Criterion Variance Analysis. Journal of the American Statistical Association, 47, 583-621. http://dx.doi.org/10.1080/01621459.1952.10483441

Labas,Y. A., Gurskaya N. G., Yanushevich Y. G., Fradkov A. F., Lukyanov K. A., Lukyanov S.A., Matz. M. V. (2002) Diversity and evolution of the green fluorescent protein family. Proc. Natl. Acad. Sci. USA 99: 4256–4261.

La Barre S.C., Coll J.C., Sammarco P.W. (1986) Competitive strategies of soft corals (Coelenterata: Octocorallia). III. Spacing and aggressive interactions between alcyonaceans. Mar Ecol Prog Ser 28:147-156.

Lema KA, Willis BL, Bourne DG. (2012) Corals form characteristic associations with symbiotic nitrogen-fixing bacteria. *Applied and Environmental Microbiology* 78(9):3136-3144.

Lesser M. P. (2006) Oxidative stress in marine environments: Biochemistry and physiological ecology. Annu. Rev. Physiol. 68, 253–278.

Le Tissier M., Brown B. (1996) Dynamics of solar bleaching in the intertidal reef coral *Goniastera aspera* at KO Phuket, Thailand. MEPS 136:235-244.

Lock C., Miller T., Anthony C., Fifer J., McDermott G., Tramonte C., Bentlage B. (2023) In prep.

Loreto P. (2022) Marine Lab Handbook. In prep.

Lozada-Misa P., Kerr A., Raymundo L. (2015) contrasting lesion dynamics of white syndrome among the scleractinian corals Porites spp. PLoS One 10:e0129841. doi: 10.1371/journal.pone.0129841.

Lukyanov K. A., Fradkov A. F., Gurskaya N. G., Matz M.V., Labas Y.A., Savitsky A.P., Markelov M.L., Zaraisky A.G., Zhao X., Fang Y., Tan W., Lukyanov S.A. (2000) Natural animal coloration can be determined by a nonfluorescent green fluorescent protein homolog. J. Biol. Chem. 275: 25879–25882.

MacNeil M.A., Graham N.A.J., Cinner J.E., Wilson S.K., Williams I.D., Maina J., Newman S., Friedlander A.M., Jupiter S., Polunin N.V.C., McClanahan T.R. (2015) Recovery potential of the world's coral reef fishes. Nature 520: 341–344.

Marsh, J.A., and Doty, J.E., Technical Report No. 21, Mangilao, GU. (1975) *Power Plants and the Marine Environments Additional Observations in Piti Bay and Piti Channel, Guam*.

Matz, M., Fradkov, A., Labas, Y., Savitsky, A.P., Zaraisky A.G., Markelov M.L., Lukyanov S.A., (1999) Fluorescent proteins from nonbioluminescent Anthozoa species. Nat Biotechnol 17, 969–973 doi:10.1038/13657.

McNeil B. I., Matear R. J., Barnes D. J. (2004) Coral reef calcification and climate change: The effect of ocean warming, *Geophys. Res. Lett.*, 31, L22309, doi:10.1029/2004GL021541.

McClanahan T.R., Darling E.S., Maina J.M., Muthiga N.A. et al. (2020) Highly variable taxa-specific coral bleaching responses to thermal stresses. Mar Ecol Prog Ser 648:135-151. doi:10.3354/meps13402.

Meesters, E.H., Bak, R.P.M., (1993) Effects of coral bleaching on tissue regeneration potential and colony survival. Marine Ecology Progress Series 96, 189–198.

Miller J., Muller E., Rogers C., Waara R., Atkinson A., Whelan K.R.T., Patterson M., Witcher B. (2009) Coral disease following massive bleaching in 2005 causes 60% decline in coral cover on reefs in the US Virgin Islands. Coral Reefs 28, 925, doi:10.1007/s00338-009-0531-7.

Morris JJ, Johnson ZI, Szul MJ, Keller M, Zinser ER. 2011.Dependence of the cyanobacterium *Prochlorococcus* on hydrogen peroxide scavenging microbes for growth at the ocean's surface.*PLOS ONE* 6(2):e16805.

Muller E. M., Bartels E., Baums I. B. (2018) Bleaching causes loss of disease resistance within the threatened coral species *Acropora cervicornis*. eLife 7:e35066.

Muscatine L., Porter J. W. (1977) Reef corals: mutualistic symbioses adapted to nutrient-poor environments. Bioscience 27(7), 454.60.

Muscatine L. (1990) The role of symbiotic algae in carbon and energy flux in reef corals. In: Dubinsky Z, editor. Coral Reefs Amsterdam: Elsevier. pp. 75–87.

Myers R., Raymundo L. (2009) Coral disease in Micronesian reefs: A link between disease prevalence and host abundance. Diseases of aquatic organisms. 87, 97-104, doi:10.3354/dao02139.

Palmer C. V., Bythell J. C., Willis B. L. (2010) Levels of immunity parameters underpin bleaching and disease susceptibility of reef corals. FASEB J. 24, 1935–1946. doi: 10.1096/fj.09-152447.

Parkinson J.E., Baums I.B. (2014) The extended phenotypes of marine symbioses: ecological and evolutionary consequences of intraspecific genetic diversity in coral-algal associations. Front Microbiol 5:445.

Patterson K.L., Porter J.W., Ritchie K.B., Polson S.W. et al. (2002) The etiology of white pox, a lethal disease of the Caribbean elkhorn coral, *Acropora palmata*. Proc Natl Acad Sci USA 99:8725–8730.

Paulay G., Benayahu Y. (1999) Patterns and consequences of coral bleaching in Micronesia (Majuro and Guam) in 1992–1994. Micronesica 31:109–124.

Payne, J. L., & Wagner, A. (2019). The causes of evolvability and their evolution. *Nature Reviews Genetics*, 20, 24– 38. https://doi.org/10.1038/s41576-018-0069-z.

Pearson, K. (1900). X. On the criterion that a given system of deviations from the probable in the case of a correlated system of variables is such that it can be reasonably supposed to have arisen from random sampling. *The London, Edinburgh, and Dublin Philosophical Magazine and Journal of Science*, *50*(302), 157–175. https://doi.org/10.1080/14786440009463897.

Precht W., Bruckner A., Aronson R., Bruckner R. (2002) Endangered acroporid corals of the Caribbean. Coral Reefs 21, 41–42. doi: 10.1007/s00338-001-0209-5.

Precht W. F., Gintert B. E., Robbart M. L., Fura R., Van Woesik, R. (2016) Unprecedented disease-related coral mortality in Southeastern Florida. Sci. Rep. 6, 1–11.

Pollock F.JLamb J.BField S.NHeron S.F., Schaffelke B., Shedrawi G., et al. (2016) Correction: Sediment and Turbidity Associated with Offshore Dredging Increase Coral Disease Prevalence on Nearby Reefs. PLoS ONE 11(11): e0165541. doi:10.1371/journal.pone.0165541.

Putnam, H.M., Davidson, J.M. and Gates, R.D. (2016), Ocean acidification influences host DNA methylation and phenotypic plasticity in environmentally susceptible corals. Evol Appl, 9: 1165-1178. https://doi.org/10.1111/eva.12408.

Qiagen (2021). DNeasy® Powersoil® Pro Kit Handbook.

Quick C., D'Angelo C., Wiedenmann J. (2018) Trade-Offs Associated with Photoprotective Green Fluorescent Protein Expression as Potential Drivers of Balancing Selection for Color Polymorphism in Reef Corals. Frontiers in Marine Science. 5, 11.

Randall R.H., Holloman J. (1974) Coastal Survey of Guam. UOGML Tech. Rep. No. 14. 404 pp.

Randall R. (2003) An annotated checklist of hydrozoan and scleractinian corals collected from Guam and other Mariana Islands. Micronesica 35–36:121–137.

Raymundo L., Maypa A. (2004). Getting bigger faster: Mediation of size-specific mortality via fusion in juvenile coral transplants. Ecological Applications. 14. 281-295. 10.1890/02-5373.

Raymundo L.J., Rosell K..B, Reboton C.T., Kaczmarsky L. (2005) Coral diseases on Philippine reefs: genus Porites is a dominant host. Dis Aquat Org 64: 181–191.

Raymundo L., Burdick D., Hoot W., Miller R., Brown V., Reynolds T., Gault J., Idechong J., Fifer J., Williams A. (2019) Successive bleaching events cause mass coral mortality in Guam, Micronesia. Coral Reefs, 38, doi: 10.1007/s00338-019-01836-2.

Rees T. (1991) Are symbiotic algae nutrient deficient? *Proc. R. Soc. Lond. B.*243227–233.

Rinkevich B., Loya Y. (1982) Intraspecific competitive networks in the Red Sea coral *Stylophora pistillata*. Coral Reefs 1:161-172.

Rinkevich B., Shashar N., Liberman T. (1992) Nontransitive xenogenic interactions between four common red sea sessile invertebrates. Proc 7th Int Coral Reef Symp Guam 2:833–839.

Rinkevich B., & Weissman I. L. (1992) Chimeras vs Genetically Homogeneous Individuals: Potential Fitness Costs and Benefits. *Oikos*, *63*(1), 119–124. https://doi.org/10.2307/3545520.

Rinkevich B., Frank U., Bak R.P.M. et al. (1994) Alloimmune responses between Acropora hemprichi conspecifics: nontransitive patterns of overgrowth and delayed cytotoxicity. Mar Biol 118:731–737.

Rinkevich B., Sakai K. (2001) Interspecific interactions among species of the coral genus Porites from Okinawa, Japan. Zoology 104:1–7.

Ritchie K.B., Smith G.W. (1998) Type II white band disease. Rev Biol Trop 46 (Suppl 5):199–203.

Ritson-Williams R., Gates R. D. (2020) Coral community resilience to successive years of bleaching in Kane ‘ohe Bay, Hawai ‘i. Coral Reefs 39, 757–769. doi: 10.1007/s00338-020-01944-4.

Roberts C., McClean C.J., Veron J.E.N., Hawkins J.P., Allen G.R., McAllister D.E., Mittermeier C.G., Schueler F.W., Spalding M., Wells F., Vynne C., Werner T.B. (2002) Marine Biodiversity Hotspots and Conservation Priorities for Tropical Reefs. Science 295:1280–1284.

Rogers C.S., Sutherland K.P., Porter J.W. (2005) Has white pox disease been affecting Acropora palmata for over 30 years? Coral Reefs 24:194.

Rohwer F, Seguritan V, Azam F, Knowlton N. (2002) Diversity and distribution of coral-associated bacteria. *Marine Ecology Progress Series* 243:1-10.

RStudio Team. (2023). *RStudio Desktop IDE* (Version 2023.06.0-421) [Computer software]. PBC.

Rosado PM, Leite DCA, Duarte GAS, Chaloub RM, Jospin G, Nunes da Rocha U, Saraiva JP, Dini-Andreote F, Eisen JA, Bourne DG+1 more. (2019) Marine probiotics: increasing coral resistance to bleaching through microbiome manipulation. *The ISME Journal* 13(4):921-936.

Salih A., Hoegh-Guldberg O., Cox G. (1998) Photoprotection of symbiotic dinoflagellates by fluorescent pigments in reef corals. Proceedings of the Australian Coral Reef Society 75th Anniversary Conference School of Marine Science, The University of Queensland, Brisbane, pp 217-230.

Salih A., Larkum A., Cox G., Kuhl M., Hoegh-Guldberg O. (2000) Fluorescent pigments in corals are photoprotective. Nature 408, 850–853.

Salih, A. et al. (2006) The role of host-based color and fluorescent pigments in photoprotection and in reducing bleaching stress in corals. Proc. 10th Int. Coral Reef Symp. 746–756.

Schlichter D., Weber W., Fricke H.W. (1985) A chromatophore system in the hermatypic, deep-water corals *Leptoseris fragilis* (Anthozoan: Hexacorallia). Mar Biol 89: 143-147.

Schlichter D., Meier U., Fricke H.W. (1994) Improvement of photosynthesis in zooxanthellae corals by auto fluorescent chromatophores. Oecologia99: 124-131.

Shore-Maggio, A., Callahan, S.M., Aeby, G.S. (2018) Trade-offs in disease and bleaching susceptibility among two color morphs of the Hawaiian reef coral, *Montipora capitata*.*Coral Reefs* 37, 507–517 https://doi.org/10.1007/s00338-018-1675-0.

Smith E. G., D'Angelo C., Sharon Y., Tchernov D., and Wiedenmann J. (2017) Acclimatization of symbiotic corals to mesophotic light environments through wavelength transformation by fluorescent protein pigments. Proc. Biol. Sci. 284:20170320. doi: 10.1098/rspb.2017.0320.

Sweet M., Burian, A., Fifer J. Bulling M., Elliot D., Raymundo L. (2019) Compositional homogeneity in the pathobiome of a new, slow-spreading coral disease. *Microbiome* 7, 139. https://doi.org/10.1186/s40168-019-0759-6.f.

Sulat D. (2023) Apra Harbor Oil Spill. Pacific News Center.

Sutherland K.P., Porter J.W., Torres C. (2004) Disease and immunity in Caribbean and Indo-Pacific zooxanthellate corals. Mar Ecol Prog Ser 266: 273–302.

Takahashi S., Whitney S.M., Badger M.R. (2009) Different thermal sensitivity of the repair of photodamaged photosynthetic machinery in cultured Symbiodinium species. Proc Natl Acad Sci USA 106:3237–3242.

Thunnell R., Anderson D., Gellar D., Miao Q. (1994) Sea-surface temperature estimates for the tropical western Pacific during the last glaciation and their implications for the Pacific warm pool. Quaternery Research 41, 255.64.

Tomascik T., Mah A.J., Nontji A., Moosa M.K. (1997) The Ecology of the Indonesian Seas. Dalhousie University/ Periplus Editions, Singapore. 1388 pp.

Tracy A. M., Pielmeier M. L., Yoshioka R. M., Heron S. F., Harvell C. D. (2019) Increases and decreases in marine disease reports in an era of global change. Proc. R. Soc. B 286:20191718. doi: 10.1098/rspb.2019.1718.

United States Coast Guard. (2012) Notable Oil Spills in U.S. Waters, Calendar Years 1989 - 2011. Office of Investigation and Analysis (CG-545).

Van Beukering P.J.H., Haider W., Longland M., Cesar H., Sablan J., Shjegstad S., Beardmore B., Liu Y., Garces G. (2007) "The economic value of Guam's coral reefs."

Violle C., Enquist B.J., McGill B.J., Jiang L., Albert C.H., Hulshof C., Jung V., Messier J. (2012) The return of the variance: intraspecific variability in community ecology. Trends Ecol Evol 27: 244–252.

Vogt A., D'Angelo C., Oswald F., Denzel A., Mazel C. H., Matz M. V., Ivanchenko S., Nienhaus G.U., Wiedenmann J. (2008) A green fluorescent protein with photoswitchable emission from the Deep Sea. PLoS ONE 3:e3766. doi: 10.1371/journal.pone.0003766.

Warner M.E., Fitt W.K., Schmidt G.W., (1999) Damage to photosystem II in symbiotic dinoflagellates: a determinant of coral bleaching. Proceedings of the National Academy of Sciences USA 96, 8007–8012.

Willis B.L., Page C.A., Dinsdale E.A. (2004) Coral disease on the great barrier reef. In: Rosenberg E, Loya Y (eds) Coral health and disease. Springer, Berlin, pp 69–104.

Winters G., Holzman R., Blekhman A., Beer S., Loya Y. (2009) Photographic assessment of coral chlorophyll contents: Implications for ecophysiological studies and coral monitoring, Journal of Experimental Marine Biology and Ecology, Volume 380, Issues 1–2, 2009, Pages 25-35.