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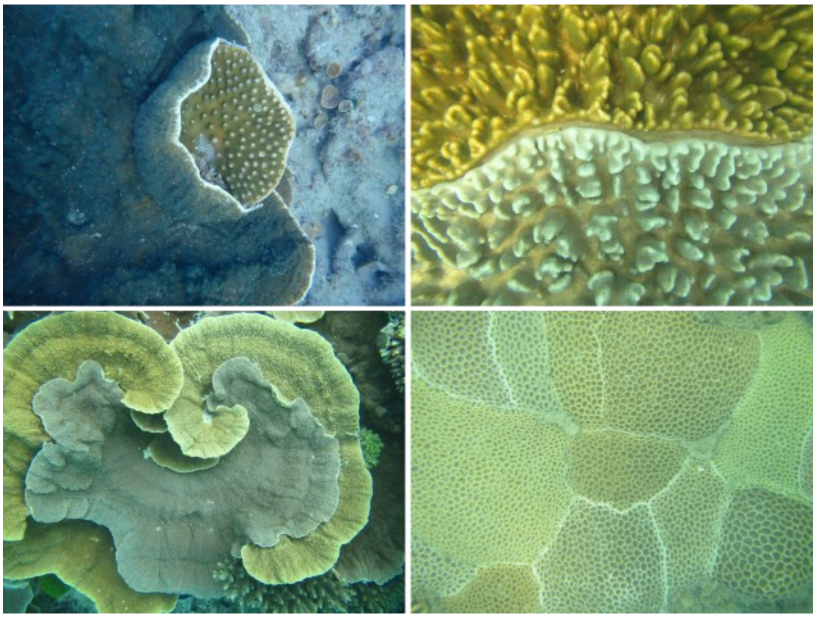
Shifting biotic interactions: the indirect effects of climate change on coral community dynamics



Thesis submitted by Tessa Hill (BSc, MSc)

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In fulfilment of the requirements for the degree of
Doctor of Philosophy in Marine Ecology,
in the College of Science and Engineering, James Cook University, Australia

JAMES COOK
UNIVERSITY
AUSTRALIA

Thesis dedication

For Imogen

"I am speaking of the life of a man who knows that the world is not given by his fathers, but borrowed from his children; who has undertaken to cherish it and do it no damage, not because he is duty-bound, but because he loves the world and loves his children…"
Wendell Berry

"It is the greatest of all mistakes, to do nothing because you can only do little."
Sydney Smith

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Chapter 1 – General Introduction

Written by TH, editorial and intellectual input by MH.

Chapter 2 - Decreased growth in response to thermal stress can alter recovery of coral communities after bleaching events on the Great Barrier Reef

Research question conceived by TH. Video data collected by Hoogenboom lab members, including TH, over a 4-year period. Data extraction by TH and SJ. Statistical support by RJ. Manuscript was written by TH with editorial and intellectual input from MH and MAN.

Chapter 3 - Competition affects bleaching severity, but not bleaching likelihood, in response to thermal stress on reef corals

Research question conceived by TH. Video data collected by Hoogenboom lab members, including TH, over a 4-year period. Data extraction by TH and SJ. Statistical support by RJ and CH. Manuscript was written by TH with editorial and intellectual input from MH and SJ.

Chapter 4 - The indirect effects of ocean acidification on corals and coral communities

Research question was conceived by TH in conjunction with MH. Data collected by TH. Manuscript was written by TH with intellectual input from MH and editorial input from MH and SW.

Chapter 5 - Shifting competitive interactions shape effects of ocean acidification on coral communities

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Predation pilot study (presented within Chapter 6) - Ocean acidification reduces predation pressure from corallivorous butterflyfish

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Chapter 6 - General Discussion. The indirect effects of climate change on coral community dynamics

Written by TH, editorial and intellectual input by MH and SW

Contributor initials:

TH, Tessa Hill; MH, Mia Hoogenboom; SW, Sue-Ann Watson; RMM, Riccardo Rodolfo-Metalpa; SJ, Saskia Jurriaans; MAN, Marina Alvarez-Noriega; RJ, Rhondda Jones; CH, César Herrera; PP, Purva Phaterpekar; GS, Gabriele Sciamma; AS, Andrew Sippel.

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This research was completed under the James Cook University Animal Research Ethics Committee approval number A2453.

Publications arising from this thesis

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Other publications during candidature

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Thesis Abstract

Globally coral reefs have experienced significant declines in recent decades due to climate change and other anthropogenic stressors. On coral reefs, there has been widespread research effort toward quantifying the extent of these environmental changes together with the direct, physiological effects on individual corals. However, less consideration has been given to the indirect effects of environmental change, which are driven by impacts on biotic interactions between individuals and species. Biotic interactions, such as competition and predation, influence the structure and functioning of ecosystems. Therefore, changes to these interactions not only have ecological relevance at a local scale but can also scale up to create phase shifts in benthic assemblages on coral reefs. Despite their importance, there are many knowledge gaps surrounding how the indirect effects of climate change may impact coral reefs. The overall aim of thesis is therefore to deepen our understanding of the indirect effects of climate change on corals and coral communities. In particular, I focus on coral-coral competitive interaction under both ocean warming, and resultant coral bleaching, and ocean acidification.

Chapter 2 assesses impacts of coral bleaching on coral demography on reefs around the Palm Islands, central GBR. I documented the extent and severity of the bleaching, and the impacts on the coral communities, by tracking individual colonies throughout the back-to-back bleaching events of 2016 and 2017. Overall, 1655 individual colonies were monitored and, of these, 73% experienced bleaching, 55% suffered mortality and there was a 6% decrease in average coral cover. However, I also showed that the impact of these bleaching events resulted in more pronounced reef degradation than was evidenced by changes in coral cover alone. This included significant, declines in colony abundance, shifts in community composition and changes in population size structure. This work helps to bridge knowledge gaps between individual and community level effects of bleaching and further evidences the need to use a demography-based approach to coral reef monitoring.

Chapter 3 investigates whether the demographic changes resulting from bleaching subsequently affect competitive interactions. I investigated how competition affects bleaching, and then how bleaching affects competition. Competition and bleaching stress were recorded in 983 colonies between 2015 and 2018. In total, 77% of colonies experienced competition with a total of 1,699 unique competitive interactions identified. Competition did not affect the likelihood of a colony bleaching, however it affected both the bleaching severity and likelihood of subsequent mortality. Following bleaching, both the frequency and

intensity of competition was reduced during the first year of recovery. Combined with the data from **Chapter 2**, I show that coral cover and colony abundance were the likely drivers behind the decrease in the frequency and intensity of competition. This study is the first to consider the bidirectional effects of competition and bleaching on coral communities and demonstrates the complexity of coral responses to climate change.

In **Chapter 4**, I synthesised the direct, physiological effects of ocean acidification, and present a comprehensive review of the indirect effects on coral and coral communities. I show that while acidification tends to have largely sub-lethal effects on individual colonies, there are many small deleterious effects that accumulate to result in increasing prevalence of negative effects at the ecosystem scale. The indirect effects of acidification on coral were numerous and operated through multiple pathways. Of particular concern are the effect of acidification on bioerosion, which may contribute to a shift from net growth to net dissolution, and effects on crustose coralline algae (CCA) which can exacerbate the direct effects of acidification on recruitment through disruption of settlement cues and reduced provision of suitable, stable habitat. Understanding the effect of acidification on the extent, impact and outcome of biotic interactions is critical in our ability to scale up results of single species studies to make predictions about the effect of acidification on reefs in the future.

Ecosystem level processes such as biotic interactions are not easily replicated in experiments or mesocosms. As a result, much ocean acidification research uses naturally acidified sites as natural laboratories. **Chapter 5** replicates the questions and methodologies from **Chapter 3** and similarly aims to establish how the frequency and intensity of competitive interactions vary with ocean acidification, using data from two naturally acidified sites in Papua New Guinea. While the impact of acidification is variable between the two reefs, the frequency and intensity of competition generally declined with acidification. These changes were driven primarily through a decrease in coral cover and lower abundance of colonies. However, aggregated spatial distributions of colonies meant that changes in competition were not as pronounced as anticipated from the changes seen in the community structure. These results highlight that competitive stress for corals may decrease under acidification, however, this is likely to be highly dependent on the spatial distribution of colonies within a community. The extent of the impact of aggregation highlights the potential for ‘ecological surprises’ on reefs under future ocean conditions. While the physiological effect of competition under acidification has previously been investigated, this study is the first to establish a baseline in the amount and intensity of competition in a field setting.

Finally, I synthesise my thesis findings in a **General Discussion Chapter (6)** wherein I integrate the results of this thesis with a pilot study which considered the extent of corallivory from butterflyfish. Data were collected alongside data for **Chapter 5** and show there was a significant decline in overall predation pressure in corals under acidification, indicating a potential reduction in predation stress in the future. In conjunction with the results from competition, I synthesise the results from this thesis to evidence the indirect effects of climate change on coral and coral communities. Using evidence from competition and predation, I consider how changes in the frequency and intensity of these stressors may alter the structure and functioning of coral reefs, and link this with ecological theory of community structuring. I also consider the combination of abiotic, thermal stress, and biotic, competitive stress, in terms of multiple stressors on coral communities. Where possible I draw conclusions about the relative impacts of ocean warming and consequent coral bleaching, and ocean acidification on biotic interactions. Finally, I highlight the relevance of indirect effects for conservation and management of coral reefs.

Overall, I show both ocean warming, and the consequent coral bleaching, and ocean acidification, resulted in notable changes to coral abundance and community composition. These changes were both the cause and consequence of a range of both positive and negative indirect effects on coral demography, abundance, and diversity. In particular, I show that competition and predation may become less prevalent under future climate conditions and therefore that these biotic interactions may become less of a structuring force on coral reefs in the future. Understanding these effects can allow us to understand the mechanisms underpinning community changes with climate change and therefore improves our ability to predict the impact of climate change on coral reefs.

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Chapter 1: General Introduction

1.1 Conceptual Framework

Identifying the factors which govern the biodiversity, abundance and distribution of organisms is one of the fundamental pursuits of ecologists. Traditionally, research on species distributions has tended to focus on patterns of diversity at regional scales, through understanding historical biogeography and the dispersal abilities of organisms (e.g., MacArthur & Wilson, 2001), and on patterns of abundance at local scales, through quantifying physiological tolerances of individuals along local environmental gradients (Edmunds et al., 2018). These distributions represent the 'fundamental niche' of an organism, which is a range of abiotic conditions under which species can survive and reproduce (Hutchinson, 1957). However, the presence and abundance of species within any community is also shaped by biotic interactions (Cornell & Karlson, 2000; Figure 1.1; Morin, 1999). This principle underpins the concept of the 'realised niche', which recognises that all species occur within a complex network of interactions with other species (Darwin, 1859; Tylianakis et al., 2008) such as competition, predation, parasitism, and symbiosis (Cornell & Lawton, 1992; Jordano, 2016; Morin, 1999). These interactions affect biodiversity (Booth & Murray, 2008; Brooker et al., 2009; Jordano, 2016), as well as community structure (Connell, 1975; Cornell & Karlson, 2000) and ecosystem functioning (Harborne et al., 2017; Figure 1.1) and are therefore pivotal to understand the ecology of populations, communities, and ecosystems.

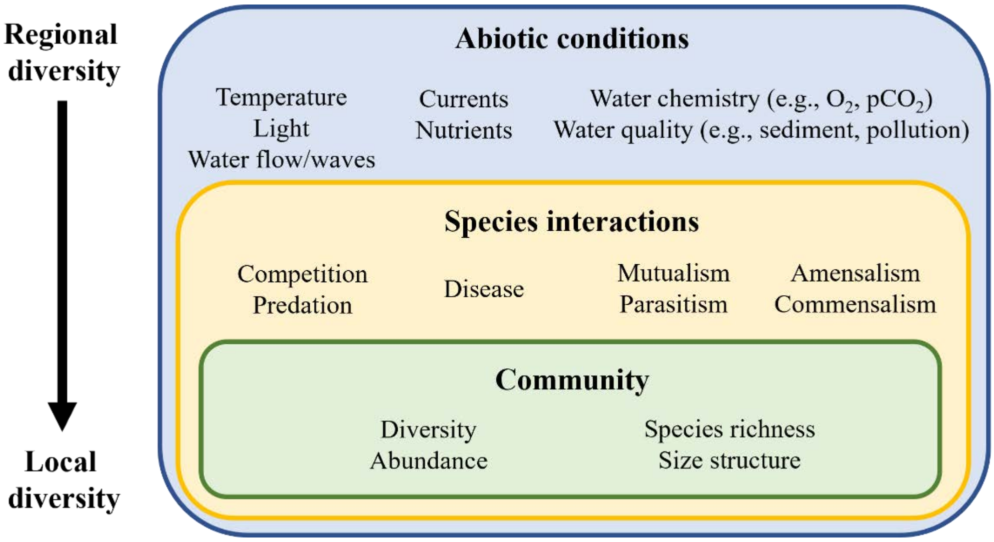

Figure 1.1. A hierarchy of factors which affect community composition at any given time. Adapted from Morin (1999).

Competition is one of the most ubiquitous biotic interactions in ecological communities (Booth & Murray, 2008). Competition occurs "when a number of animals (of the same or of different species) utilize common resources the supply of which is short; or if the resources are not in short supply, when the animals seeking that resource nevertheless harm one or other in the process" (Birch, 1957, p6). By definition, competition generally has negative effects on organism fitness because resource limitation can constrain growth, fecundity, and survival (Morin, 1999). These declines in fitness can scale up to community level impacts through competitive release, competitive exclusion (e.g., Stanley & Newman, 1980), or extinction (Gause, 1934). As such, competition has historically been the primary focus for both ecological theory (Agrawal et al., 2007; Cornell & Karlson, 2000; Gurevitch et al., 2000), and empirical research on biotic interactions (Agrawal et al., 2007; Chesson & Kuang, 2008). However, collecting definitive evidence of competition is challenging (Chornesky, 1989; Cornell & Karlson, 2000; Pianka, 2011), therefore many studies infer competition from the distribution of individuals within a community or competitor removal studies (e.g., Paine, 1966).

The importance of competition is often apparent through biological traits or behaviours that species display to access resources that other species cannot obtain. For example, elongated necks in giraffes allow them to browse the top of canopies and avoid competition with other herbivores for the lower leaves (Cameron & du Toit, 2007). However, investment in biological traits which bring competitive advantage, often result in a trade-off with other biological traits. One example is the competition-colonisation trade-off which reflects observations that organisms which are good competitors are often poor colonisers because they have poor dispersal capability and slow growth rates (Booth & Murray, 2008), while species which invest in colonization traits are often poor competitors. This can result in spatial or temporal zonation within ecosystems between colonisers and slower growing, more competitively dominant species (e.g., Stanley & Newman, 1980). Several other trade-off frameworks, and ecological or life-history strategy systems, have been proposed to capture the processes that create and maintain biodiversity. For instance, the 'r' and 'K' life-history continuum (Pianka, 2011) was an early trade-off model that aligns with competition-colonization theories, wherein 'r' strategists are good colonisers and 'K' strategists are good competitors. Similarly, Grime's C-S-R (competition, stress, ruderal) model, suggest a 'competitive' (C) life history is one of three potential life-history strategies, along with 'stress tolerant' species (S) and fast growing, colonizing, 'ruderal' or weedy species (R; Darling et al., 2012; Grime, 1977). The differences in competitive investment within life history strategies highlights the importance of competition for resources on both an ecological and evolutionary time frame.

Competition, and other biotic interactions, have been widely considered in ecological theory. The Environmental Stress Model (ESM; Menge & Sutherland, 1987) posits that increasing environmental stress drives a decrease in the complexity of species interaction webs. That is, as the environment becomes increasingly harsh, the dominant structuring force shifts from predation, to competition, then to abiotic stress (Figure 1.2). Criticisms of this model highlight the lack of consideration of other biotic interactions (e.g., mutualism, parasitism), with subsequent models also considering the importance of positive biotic interactions (e.g., faciliation; Bertness & Callaway, 1994). Fundamentally, the complexity of many ecosystems means most models are too simplistic (e.g., Smit et al., 2009) to be accurate predictive tools. However, models like the ESM can help to establish the relative impact of biotic and abiotic stressors on biodiversity, structure, and function of ecosystems (Menge & Sutherland, 1987). Evidence in support of the ESM has been found in various habitats, including grassland (Preisser & Strong, 2004)), forest/woodland (Louthan et al., 2013), lakes (Arnott & Vanni, 1993) as well as rocky shores, which was the foundation ecosystem for this model (e.g., Zwerschke et al., 2013). While there is particular support in marine environments (Menge, 2023), only one study has considered coral reefs along a stress gradient, which showed declines in herbivory with environmental stress (wave action; Sjöö et al., 2011).

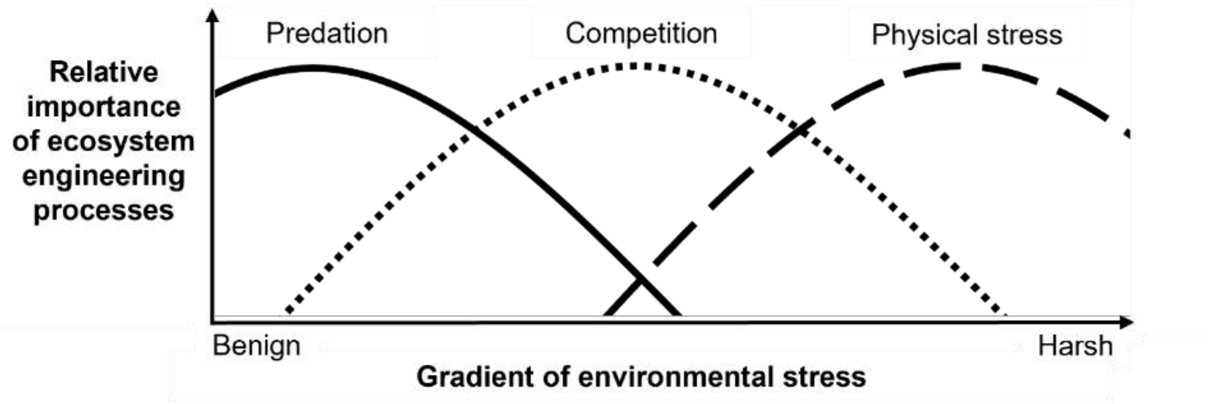

Figure 1.2. A simplified visualisation of the Environmental Stress Model, looking at the structuring processes within a community. Recreated from Crain & Bertness, 2006; Menge & Sutherland, 1987.

1.2 Competition on coral reefs

Coral reefs are highly diverse, at both an ecosystem and a local scale (Booth & Murray, 2008), which creates potential for an enormous number of biotic interactions. Corals are the foundation species of coral reefs and therefore, by definition, are involved in many biotic interactions (Figure 1.3). These include: predatory interactions, both of the corals consuming plankton (Porter, 1976), and corallivorous fishes and invertebrates consuming coral (Cole et al., 2008); symbiotic relationships between corals and *Symbiodiniaceae* and a diverse suite of other microbes (Hernandez-Agreda et al., 2017; Knowlton & Rohwer, 2003); the provision of structural complexity as shelter and habitat for many other reef organisms, which may be either, amensal, commensal or mutually beneficial for the corals (Burkepile & Hay, 2008; Glynn & Manzello, 2015); and competition both between corals and with other sessile benthic organisms, such as macroalgae (Lang & Chornesky, 1990; Figure 1.3). These interactions are a fundamental part of coral reefs, contributing to, and maintaining the structure, function, and high biodiversity of these ecosystems.

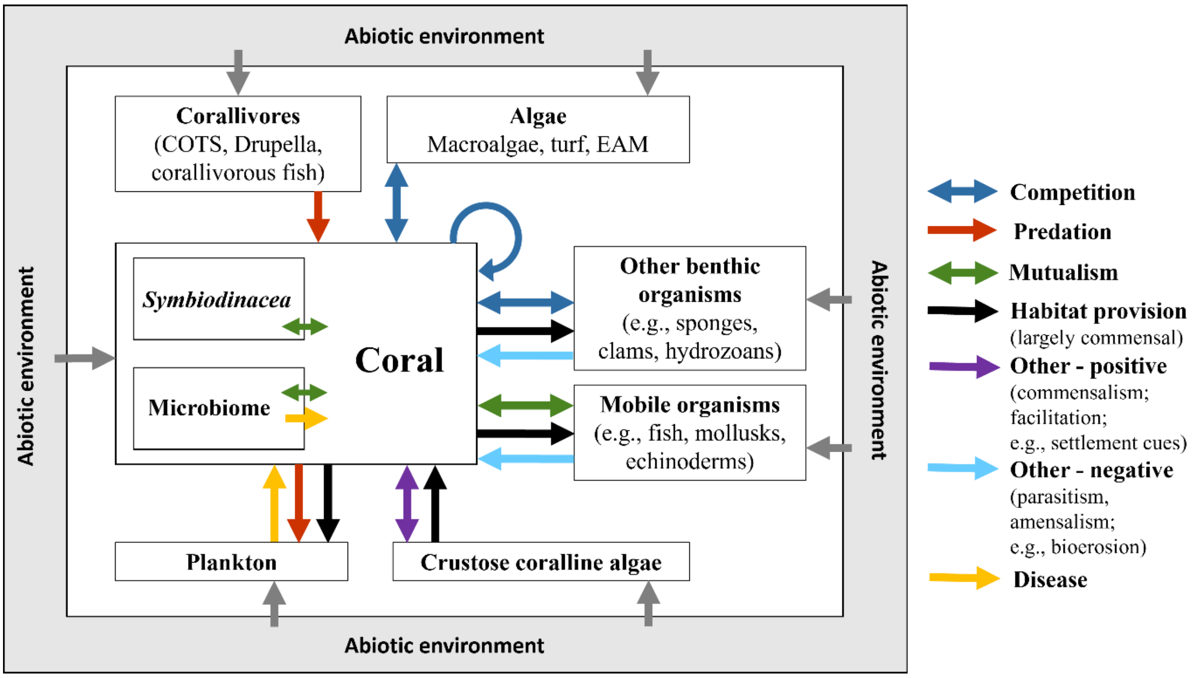

Figure 1.3. Conceptual diagram of the most common coral interactions on a coral reef. Arrows show the direction of effects from each interaction. COTS = crown of thorns starfish; EAM = epilithic algal matrix.

Corals primarily compete for two resources; space for growth, and light for photosynthesis (Jackson, 1977; Lang & Chornesky, 1990). Corals can compete directly for these resources using mesenterial filaments, sweeper tentacles, mucus secretions or allelochemicals which are used to attack and/or digest competitors in close proximity (Dai, 1990; Lang, 1973; Lang & Chornesky, 1990). Alternatively, corals can compete indirectly (interference competition) by monopolising the resources, such as rapid upward growth or having morphologies that result in shading to the colonies below (Connell, 1973; Lang & Chornesky, 1990). In general, it is thought that faster growing and/or branching morphologies such as *Acropora* species tend to rely on interference competition, while slower growing colonies such as *Hydnophora*, which cannot grow away from competition, are thought to invest more heavily in aggressive competitive mechanisms (Connell, 1973; Lang, 1973; Lang & Chornesky, 1990).

Competitive interactions between corals are physiologically costly. Importantly, evidence of this physiological cost is seen for both the dominant ('winner') and subordinate ('loser') competitor (Rinkevich & Loya, 1985; Romano, 1990). For the subordinate competitor this cost arises from the repair and recovery of damaged tissues (Romano, 1990; Figure 1.4). However, for the dominant competitor, the production of specialized tissues like sweeper tentacles can be equally as energetically costly (Chornesky, 1989; Romano, 1990). Evidence of these energetic cost is seen in physiological trade-offs with competing corals found to have slower growth and/or calcification rates (Idjadi & Karlson, 2007; Rinkevich & Loya, 1985; Romano, 1990; Tanner, 1997), reduced investment in reproduction (Rinkevich & Loya, 1985; Tanner, 1997), reduced tissue quality in some species (measured as energetic equivalents of proteins and lipids; Hoogenboom et al., 2011), as well as areas of partial mortality at the site of the competitive encounter (Idjadi & Karlson, 2007; Sheppard, 1985). As a result, corals will attempt to avoid competition where possible, through redirecting growth away from the competitive encounter (Genin et al., 1994; Romano, 1990; Figure 1.4) or, in free living species, actively moving away from a competitor (Chadwick-Furman & Loya, 1992). Despite the potential cost and desire for competitive avoidance, competition largely has sublethal effects on corals with limited evidence of complete mortality (Lapid & Chadwick, 2006; Romano, 1990; Tanner, 1997).

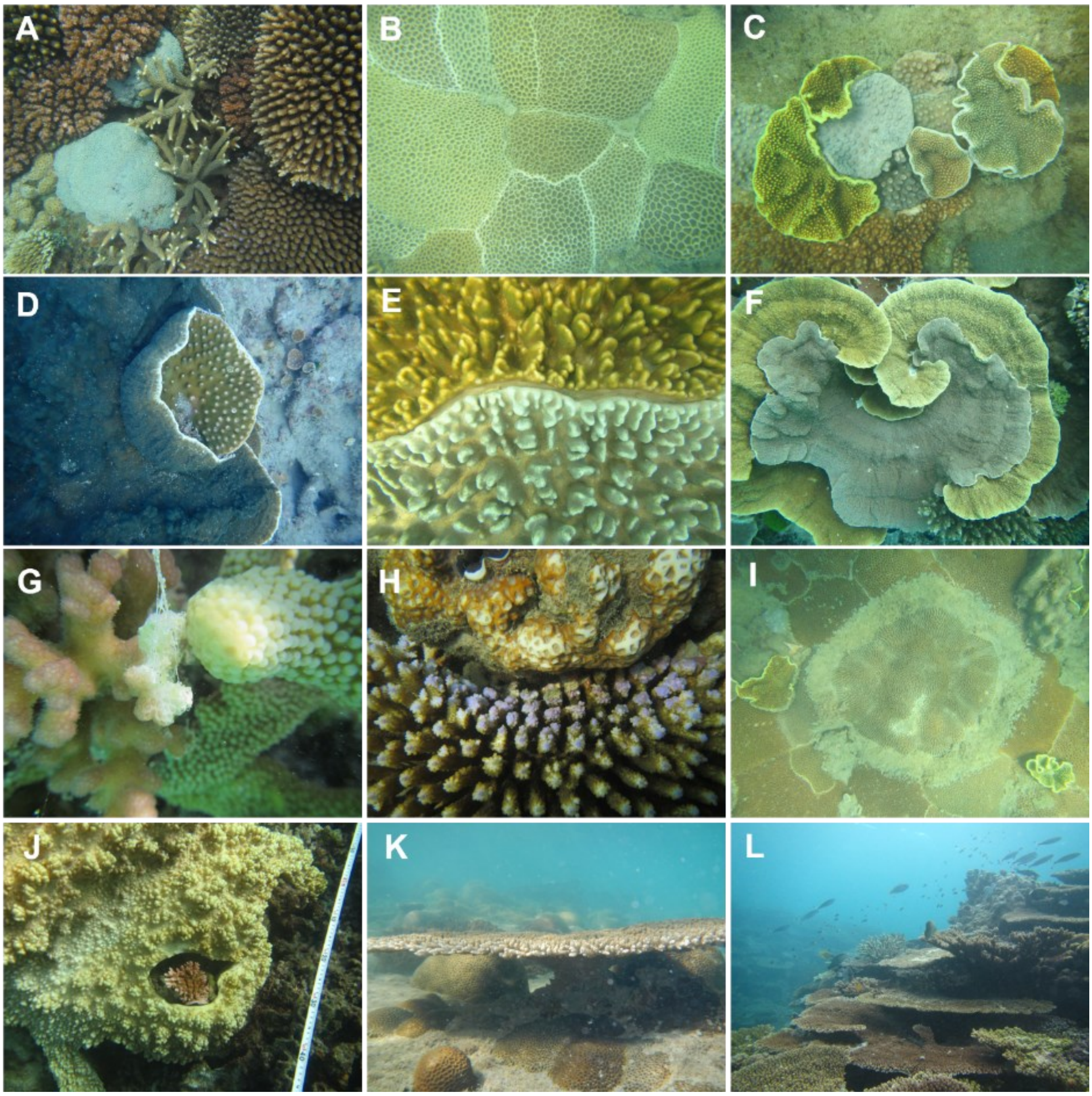

Figure 1.4. Examples of coral-coral competition; competition can be intense when coral cover is high (A, B); competition can also occur at lower coral cover when colonies are aggregated (C); contact competition via overgrowth with a negative effect on one colony (D); contact competition can also occur without aggression between conspecifics (E) and with spatial and temporal reversals in competitive dominance or outcome (F); competition at close proximity resulting in tissue damage from physical aggression (G); evidence of the 'interactive reach' of competition, causing damage and/or preventing growth in competing colonies (H, I); space competition (indirect competition; J); overtopping competition which shades out colonies below (indirect; K, L).

The frequency, intensity, and outcome of competitive interactions between corals, along with their physiological impact, can act as a structuring force in coral communities (Chadwick & Morrow, 2011; Connell et al., 2004). Early investigations presumed competitive interactions were part of a hierarchical network of dominance in corals which, in the absence of disturbance, would ultimately result in the proliferation of the most dominant species (Huston, 1985). However, subsequent investigations have found that coral competitive networks are almost always intransitive, with no overall dominant species, and with both spatial and temporal reversals in competitive dominance, driven by the abiotic and biotic context of an interaction (Bak et al., 1982; Chornesky, 1989; Lang & Chornesky, 1990; Precoda et al., 2017; Figure 1.4). As such, total competitive exclusion of a poor competitor is unlikely, however, competition can still play a role in niche occupancy and resource partitioning among coral species (Porter, 1976). Through these small scale, local impacts, competition has been shown to affect both coral abundance and diversity (e.g., Connell et al., 2004; Genin et al., 1994).

1.3 Abiotic stressors and climate change

In addition to biotic interactions, the abiotic environment has a significant influence on the biodiversity, structure and function of communities. Abiotic impacts are widely included in ecological theory and, historically, have been the primary focus of an extensive body of ecological research (Agrawal et al., 2007). Temperature is one of the most significant abiotic factors for organisms, with most species occurring within a thermal range for survival and with a thermal optima that maximises fitness (Angilletta, 2009). Other abiotic factors which can affect individuals in marine communities can include water chemistry parameters, water flow, light, sedimentation, as well as abiotic disturbance events like cyclones and flood plumes (e.g., Ban et al., 2014; Hughes & Connell, 1999; Tan et al., 2012). The impacts of these abiotic stressors are recognized in the Environmental Stress Model which hypothesizes that in local environments where abiotic stressors are high (i.e., physical conditions are less favourable for growth, reproduction, and survival), physical stressors present the most dominant structuring processes within the community (Menge & Sutherland, 1987). For example, water quality is a critical abiotic factor on coral reefs resulting in strong cross-shelf changes in community between high nutrient, turbid inshore reefs and low nutrient, low turbidity off-shore reefs (Fabricius et al., 2005).

Alongside the physiological effects, the abiotic environment can also affect communities through impacts on biotic interactions. The abiotic context these interactions occur in, can affect the strength of the interaction (Lurgi et al., 2012), as well as the frequency, type, or outcome of an interaction. On coral reefs, increased water temperature can cause a disruption of the symbiotic relationship between corals and their dinoflagellate algae (*Symbiodiniaceae*), resulting in coral bleaching (Glynn, 1996). The dissociation of this relationship not only has significant implications for affected colonies and reefs, but bleaching can subsequently affect other interactions. Bleaching of coral colonies reduces camouflage for site attached damselfish that inhabit the branches of coral colonies, increasing the rate of predation (Coker et al., 2009). Other abiotic factors can also affect interactions. For example, waterflow can disrupt a mutually beneficial relationship between corals and resident damselfish, where the presence of fish under low flow can enhance coral growth but under high flow, the presence of fish reduces growth (Chase et al., 2014). Due to the abundance and diversity of biotic interactions within an ecosystem, how the abiotic context affects biotic interactions is unknown for the majority of interactions in a given location (Jordano, 2016). Furthermore, the outcome of these interactions and their effect on community structure and function, vary dramatically under different abiotic conditions, and so are consequently hard to predict.

The impact of the abiotic environment on both the physiology of individuals, and their biotic interactions, can establish the biodiversity, structure and functioning of ecosystems through evolution and succession over long time periods (e.g., Darwin, 1859). Therefore, our understanding of the effects of the abiotic environment is largely based on historical and/or stable environmental conditions, to which local organisms and communities may well be adapted to. Such adaptation can be seen in the Red Sea where there are high levels of endemism in species and tolerance to physically stressful conditions (Berumen et al., 2019). However, anthropogenic climate change is now resulting in significant changes to the abiotic environment in many ecosystems, often resulting in increased abiotic stress (IPCC, 2023; Figure 1.5). While the Environmental Stress Model was developed to consider communities along a gradient of stress, it can also be applied to temporal gradients in stress as a result of climate change, where abiotic conditions are becoming increasingly stressful (Menge, 2023). The predicted impact would be a community where the dominant structuring force is the abiotic environment, rather than biotic interactions. How a shift in the dominant structuring force may affect community structure and function is largely unknown. Furthermore, the structure and function of a community are often the root of ecosystem services (Tylianakis et al., 2008) and therefore changes within communities may have indirect effects on human populations.

1.4 Indirect effects of climate change

While the direct effects of climate change have been widely investigated for many environments, climate change can also have indirect effects on communities by altering the abiotic context of biotic interactions, or the interactions themselves (Krivtsov, 2009; Figure 1.5). Indirect effects are defined here as, where impacts on one or multiple interacting species, alters the extent, frequency, type, or outcome of a biotic interaction. These indirect effects of climate change can arise from several drivers, which can then subsequently impact the community through various mechanisms (Figure 1.5). For example, climate change is expected to increase the number of pathogens, causing greater disease prevalence (Maynard et al., 2015) and affecting the community through altered mortality rates of susceptible species. Changes in interactions are particularly likely when there is a mismatch in response to climate change between the interacting individuals (Alexander et al., 2016; HilleRisLambers et al., 2013; Lurgi et al., 2012). These differential responses may result in mismatched phenology, altered competitive outcomes, disruption of the food web, or shifts in successional states, which can all subsequently alter the composition and structure of a community (Figure 1.5, and references therein). Because of the secondary nature of indirect effects, their manifestation often has a lag time following the direct effects (Suttle et al., 2007). However indirect effects can be as important for community structure and function as direct effects (Kordas et al., 2011). For the vast majority of biotic interactions, the indirect effect of climate change on those interactions remains a significant knowledge gap.

In recent years, there has been a growing awareness of the impact of multiple, concurrent stressors on communities. Most of this research considers a combination of abiotic, environmental stressors (see: Ban et al., 2014), which can create ‘ecological surprises’ (Paine et al., 1998; Wootton, 1994). These ‘surprises’ result from antagonistic, synergistic, or non-additive impacts of the stressors, i.e., a response which does not equate to the sum of the individual effects of each stressor (Darling & Côté, 2008). These non-additive responses can either mitigate or exacerbate the direct effects of climate change (Figure 1.5) and mean that the effects of climate change cannot be predicted from the direct impacts on individuals alone (Pirotta et al., 2022). The importance of multiple abiotic stressors means they have been highlighted as a significant ecological concern and research priority (Crain et al., 2008; Darling & Côté, 2008) and have had a considerable increase in research effort in the past ~15 years. However, the combination of abiotic and biotic stressors can also impact individuals.

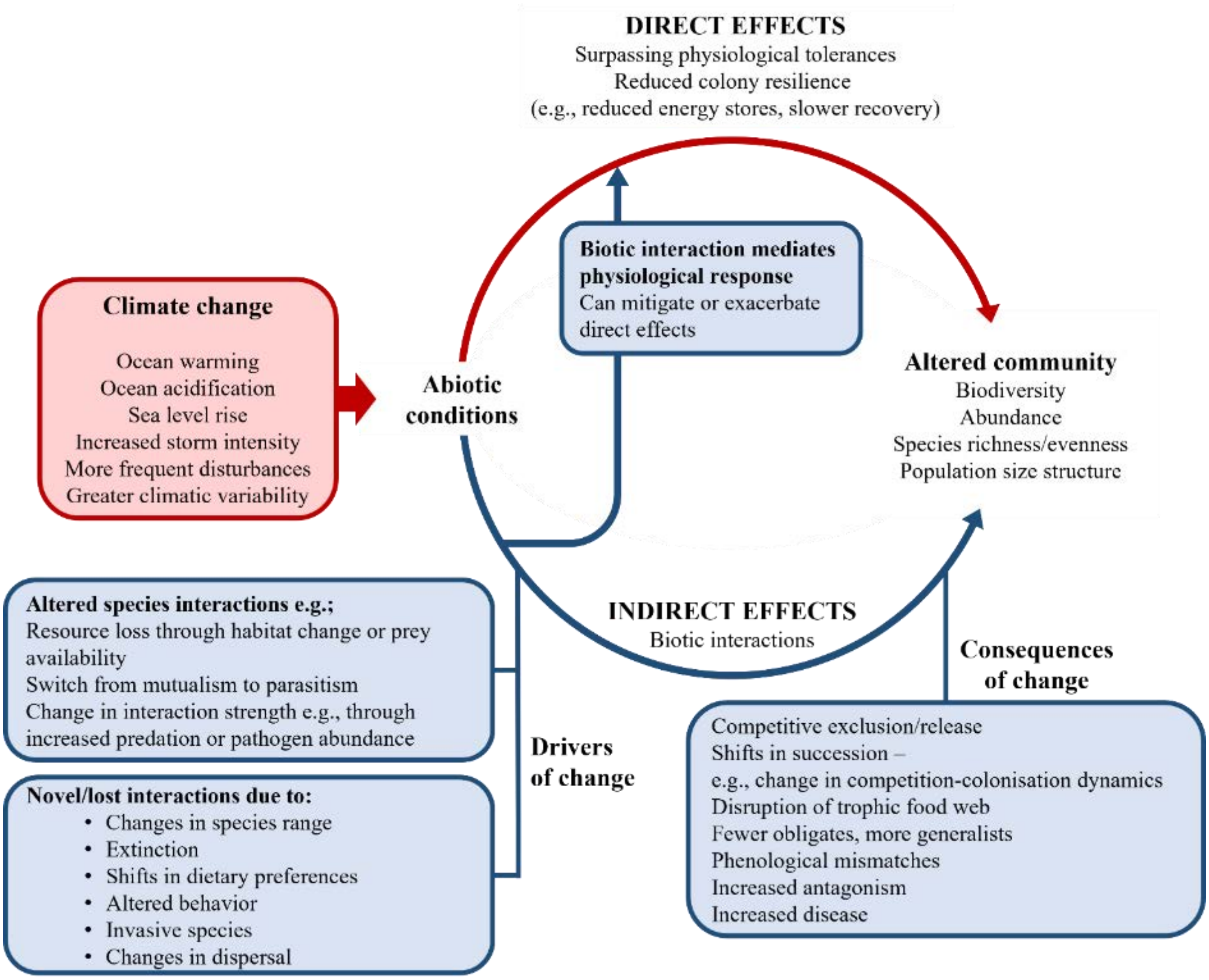

Figure 1.5. The direct (red) and indirect (blue) pathways of climate change impacts. Drivers of change describe how climate change can influence biotic interactions. The consequences of change describe how biotic interactions can determine the impact of climate change on communities. This schematic builds on indirect effects highlighted by Cahill et al., (2013), Gilman et al., (2010) and Lurgi et al., 2012.

Biotic stressors, such as competition and predation, will not only continue to occur as a background stressor as the climate changes but may themselves change in extent or impact. For example, following a thermal stress event in a seagrass community, the fibre content and leaf thickness of seagrass decreased, increasing their susceptibility to grazing by sea urchins (Hernán et al., 2017) and exacerbating the negative effects of the thermal stress. Moreover, exposure to stress from biotic interactions can affect resilience to subsequent stressors (Hughes et al., 2019; Pratchett et al., 2020). Indeed, mortality presumed to have occurred from abiotic stress, may actually have been incited by exposure to a biotic stressor (Teshome et al., 2020). As such, inclusion of biotic stressors has been shown to improve accuracy of models predicting ecosystem functioning under climate change (e.g., Araújo & Luoto, 2007;

Meier et al., 2010). Despite this, few studies to date have considered how biotic stressors could influence the effects of climate change.

1.5 Indirect effects on coral reefs

Significant and rapid increases in sea surface temperatures (SSTs), which are predicted to continue rising in the future, are one of the most significant concerns for coral reefs under global environmental change (Heron et al., 2016; Lough et al., 2018; Sully et al., 2019). These rising sea surface temperatures (SSTs; ocean warming) push corals past their thermal optimal and closer to their thermal limits (Howells et al., 2016; Jurriaans & Hoogenboom, 2019). The critical threat of ocean warming is the risk of coral bleaching, where thermal stress causes a breakdown in the relationship between corals and their symbiotic algae, removing their primary source of energy and increasing the risk of starvation (Anthony et al., 2009; Glynn, 1996). Bleaching events have increased in frequency in the past 20 years (Sully et al., 2019), with the longest and most severe global stress event starting in 2014 and running for 3 years (Eakin et al., 2019). This event resulted in mass bleaching events in 2015, 2016 and 2017 (e.g., Hughes et al., 2017). During this period ~75% of coral reefs globally experienced bleaching with many also experiencing mass mortality (Eakin et al., 2018; Eakin et al., 2019; Hughes et al., 2018). As oceans continue to warm, such bleaching events are predicted to become more frequent and intense, potentially occurring annually by the early 2040s (Heron et al., 2017; Van Hooidonk et al., 2013).

Ocean acidification (OA) is the second major threat of climate change. This occurs when increased atmospheric carbon dioxide (CO_2) drives increased absorption of CO_2 into the ocean, which alters the water chemistry. In addition to becoming more acidic, there is a decrease in bicarbonate ions which are essential for calcification in corals and many other calcifying organisms (Cohen & Holcomb, 2009; Zeebe, 2012). Ocean acidification therefore affects the abilities of corals to calcify and secrete new skeleton, limiting colony growth (Chan & Connolly, 2013). The effects of acidification on corals extends beyond calcification, with negative effects seen on metabolism (Kaniewska et al., 2012), reproduction (Albright, 2011), heterotrophic feeding rates (Houlbrèque et al., 2015), and wound healing/tissue repair (Renegar et al., 2008). These effects can also scale up to changes to a population and community level. At reefs which are naturally acidified from submarine volcanic acidity or hydrogeographic processes, the coral communities have been shown to have lower coral cover (Agostini et al., 2018; Enochs et al., 2015), reduced species diversity (Crook et al., 2012; Fabricius et al., 2011), and be less topographically complex (Fabricius et al., 2011) with some sites shifting towards greater cover of non-reef building soft corals (e.g., Inoue et al., 2013).

The impacts of climate change, in combination with other anthropogenic stressors (e.g., declining water quality) are already apparent. Declines in coral cover, colony abundance and size structure, and topographic complexity have been increasingly reported over the last two decades (Alvarez-Filip et al., 2009; Bruno & Selig, 2007; Dietzel et al., 2020; Sweatman et al., 2011) with reports from 20 years ago already stating that there were no reefs left in a pristine condition (Pandolfi et al., 2003). Similarly, regional impacts of ocean warming, such as changes in the dispersal abilities of organisms or stock recruitment relationships (e.g., Hughes et al., 2019) have been recorded. However, there is a growing understanding that to accurately predict the effects of climate change, including scaling up impacts from organisms to community or ecosystem level, we need to have a more holistic view of the impacts (Gilman et al., 2010; Montoya & Raffaelli, 2010; Tylianakis et al., 2008). This includes understanding how biotic interactions may themselves change as a result of changes in climate, and how they may mediate community response to climate stress (Agrawal et al., 2007; Edmunds et al., 2018; Gilman et al., 2010; Jordano, 2016; Suttle et al., 2007; Tylianakis et al., 2008). Being able to accurately predict the effect of climate change is a critical step in our ability to conserve and protect reefs into the future.

1.6 Research aims and thesis structure

The primary goal of this thesis was to gain new insight into the indirect effects of climate change on corals and coral communities. Specifically, I quantified changes in biotic interactions resulting from coral bleaching due to ocean warming, and ocean acidification. For both climate stressors I strived to first establish the extent of the change in the community resulting from variations in environmental conditions, and second, investigated how these changes affected ecological processes through changes in biotic interactions. I used these to consider how the structure and functioning of reefs may change in the future. I had four overall objectives, each relating to a different chapter.

Chapter 2 established the effect of the 2016-2017 back-to-back bleaching event on the coral population demographics and assemblage structure of the Palm Islands. While previous investigations of the impact of bleaching have focused on coral cover, I explored additional demographic metrics to provide a more in-depth assessment of the impact of these bleaching events on coral communities. **Chapter 3** then quantified how the combined stressors of chronic competitive stress and acute bleaching stress impact coral communities, using the same corals in the same locations as **Chapter 2**. I investigated the bidirectional nature of these stressors where the chronic stress of competition may impact the amount and severity of the acute bleaching stress, and where bleaching may subsequently alter the frequency and intensity of competition. Tracking the fate of coral colonies through time allowed for unique investigations of the impacts of these stressors on these communities. In **Chapter 4,** I synthesised the current evidence of indirect effects of ocean acidification on coral communities. To the best of my knowledge, this is the first published review which focuses on the indirect effects of ocean acidification on coral reefs. In **Chapter 5,** I quantified the frequency and intensity of competition experienced by corals at control and acidified seep sites. This work was completed at naturally acidified sites in Papua New Guinea as an analogue for future environmental conditions under climate change. While volcanic seep sites have been used previously to investigate the physiological effects of acidification on corals, far less attention has been given to the indirect effects on coral species interactions. Finally, in my **General Discussion (Chapter 6)**, I synthesise the evidence of changes in competition with a pilot study which considered changes in predation pressure from corallivorous butterflyfish under acidification. I then considered the evidence to suggest whether the frequency and intensity of competition and predation may vary under future climate conditions, and how any changes fit within the ecological theories of biodiversity maintenance and the impacts of chronic and acute stressors. Overall, I addressed some of the knowledge gaps surrounding the indirect effects of climate change on corals and coral communities. I also highlighted the importance of indirect effects if we wish to scale up findings from single species studies and make accurate predictions about the impact of climate change on corals and coral reefs. Such predictions are essential for conservation and management of coral reefs into the future.

Chapter 2 : Decreased growth following bleaching can alter recovery of coral communities on the Great Barrier Reef

2.1 Abstract

In 2016-2017 the Great Barrier Reef (GBR) experienced its first back-to-back bleaching event, resulting in extensive loss of coral cover. Here I quantify the demography (growth and survival) of the coral communities on the Palm Islands (central GBR), to assess how changes in demography due to the impacts of the 2016-2017 back-to-back coral bleaching events affects recovery of coral cover. I used video data from semi-permanent transects to track individual colonies from before (2015), during (2017) and after (2018), the bleaching events. Coral cover and community composition were measured, together with the abundance, size structure, growth, and mortality for three focal coral genera (*Acropora*, *Pocillopora* and *Porites*). Overall, 73% of colonies bleached and 55% died during the bleaching events or over the following year, and there were significant declines in colony growth in severely bleached corals. Coral cover declined 6.4% after bleaching, with *Acropora* and *Pocillopora* colonies suffering particularly high mortality. *Porites* colonies had lower rates of bleaching and mortality but showed partial mortality and fragmentation following bleaching. The overall effect on communities varied between sites, ranging from declines in colony abundance being masked by the rapid growth of surviving colonies (spatial in-filling that resulted in a 6% increase in coral cover after 1 year), to a shift in community composition due to 98% mortality of *Acropora* colonies. Decreased colony abundance, shifts in community composition due to the almost complete loss of certain genera, high rates of mortality, and decreased growth rates, each have important implications for both the recovery of these populations, and their resistance and resilience to future bleaching. Furthermore, the demographic changes documented here highlight the limitations of quantifying reef condition through coral cover alone and indicate that the overall impact of these back-to-back bleaching events may have been underestimated.

Keywords

Coral bleaching; Population demographics; Mortality; Coral community composition; Resistance; Recovery

2.2 Introduction

Globally, coral reefs are experiencing significant degradation from climate change and a range of other stressors (Hoegh-Guldberg et al., 2007; Hughes et al., 2018; Pandolfi et al., 2003). In recent decades, environmental monitoring of global impacts on reefs have largely used coral cover as a proxy for reef condition (e.g., Bruno et al., 2007; De'Ath et al., 2012; Sweatman et al., 2011), with areas with greater coral cover generally considered to be representative of 'healthier' reefs (Edmunds & Elahi, 2007; Hughes & Tanner, 2000). Although coral cover is undeniably an effective method for quantifying the responses of reefs to a disturbance, the limitations of using coral cover as the only metric of reef health have long been recognized (e.g., Edmunds & Riegl, 2020). This is because measuring coral cover alone can obscure important changes in coral community structure, such as altering the relative abundances of different species, and/or impacts on population dynamics due to changes in colony growth rates, mortality rates or size structure (Baird et al., 2018; Hughes & Tanner, 2000; Richards, 2013). Therefore, there is an increasing need to move beyond coral cover towards a more demographic approach to monitoring coral communities (Cant et al., 2022; Edmunds & Riegl, 2020; Pisapia et al., 2020).

Population demography considers the regulation of a population due to variation in the rates of births and deaths of individuals (and migration in non-sessile organisms). For each species, demographic rates, including fecundity, growth, and mortality, reflect evolutionary drivers and life-history strategies (e.g., Darling et al., 2012; Madin et al., 2016), and affect population growth and replenishment. As different species have different demographic rates and variable susceptibility to stressors like marine heatwaves, disturbances that affect colony abundances (Morais et al., 2021) or population size structure (Brito-Millán et al., 2019; Dietzel et al., 2020; Pisapia et al., 2019) can alter community composition, biodiversity, and functional diversity (Cannon et al., 2021; Loya et al., 2001; McWilliam et al., 2020; Moritz et al., 2021). Moreover, changes in coral diversity and abundance, particularly the loss of erect habitat forming species, can alter ecological processes, including reef accretion, habitat provision and benthic-pelagic coupling, that are critical for reef functioning (Hughes et al., 2018; McWilliam et al., 2020) and reef resilience (Hughes et al., 2019). Understanding how disturbances affect these demographic rates reveals the mechanisms that underpin changes in coral cover and allows us to better assess the impacts of different disturbances.

While the benefits of quantifying coral demographic rates are clear, doing so requires following the fates of individual colonies over time in contrast to less laborious single point-in-time measures like coral cover. Furthermore, corals are modular organisms that can experience growth and whole-colony mortality, as well as shrinkage through fragmentation or partial mortality, and in addition to fission or fusion with other colonies (Hughes, 1984; Hughes & Jackson, 1985). All of these demographic rates can vary among species (e.g., Madin et al., 2020; Pratchett et al., 2015), and can affect both the abundance of colonies and the size structure of the population (e.g., Edmunds et al., 2021; Pisapia et al., 2019). Finally, coral demographic rates are strongly dependent on colony size (e.g., growth rate scales allometrically with colony size at a rate that is generally consistent among species; Dornelas et al., 2017) whereas the relationship between colony size and other demographic rates can be very different for different species (e.g., mortality; Madin et al., 2014). While following the fates of individual colonies through time requires multi-year monitoring, and significant image analysis time, it captures high resolution data to document size-dependent growth and mortality that are required to parameterize models of population and community dynamics. Such models can provide a tool that allows early detection of changes in the status of coral populations and communities before changes in coral cover manifest.

Marine heatwaves due to global climate change are affecting coral reefs around the world (Hughes et al., 2018). Rising sea surface temperatures (SST) are pushing corals beyond their thermal tolerance thresholds often resulting in coral bleaching (Glynn & D'croz, 1990; Hoegh-Guldberg & Salvat, 1995; Jokiel & Coles, 1990). Bleaching is caused by a dissociation of the symbiosis between the corals and their resident *Symbiodiniaceae* population, resulting in pale ‘bleached’ colonies (Glynn, 1996). These photosynthetic *Symbiodiniaceae* are a primary source of energy for corals, without which corals can starve with prolonged exposure to warm waters or when the symbiosis is not re-established (Anthony et al., 2009; Glynn, 1996; McClanahan et al., 2009). Globally, coral bleaching events are becoming increasingly frequent (Sully et al., 2019) with a rapidly decreasing recovery window between disturbances (Hughes et al., 2018). On the Great Barrier Reef (GBR), there have been four mass bleaching events in less than a decade (2016, 2017, 2020 and 2022) following on from the mass bleaching events in 1998 and 2002. These events are predicted to start occurring annually on the GBR from the early 2040s (Heron et al., 2017; Van Hooidonk et al., 2013), with the first back-to-back bleaching events seen in 2016 – 2017. The mass bleaching in 2016 was a major event, with four times more reefs bleaching than either 1998 or 2002 (Hughes et al., 2017). In total 30% of coral cover at shallow locations along the GBR was lost, although this was heavily dominated by loss in the northern sectors of the reef complex (Hughes et al., 2017). The subsequent thermal event in 2017 was more severe across the whole GBR in terms of heat stress, with reefs in the central GBR suffering very high rates of bleaching and mortality (Hughes et al., 2019). Combined, these events reduced mean live coral cover on the central GBR from 22% to 14% (AIMS, 2018).

While the effects of these bleaching events have been catastrophic in many areas, there is a great degree of variability in the response of corals to high SSTs. This includes long recognized, genera specific differences in susceptibility to coral bleaching. For example, while *Acropora* and *Pocillopora* are highly bleaching susceptible, other genera like *Porites*, *Platygyra*, *Galaxea* and *Goniopora* are more bleaching resistant (e.g., Baird & Marshall, 2002; Gleason, 1993; Marshall & Baird, 2000). This has given rise to the concept of thermally tolerant ‘winner’ species and thermally sensitive ‘losers’ species (Loya et al., 2001), with winners less likely to bleach and suffer mortality than losers. The differences in thermal tolerance and bleaching susceptibility are dependent on physiological differences between species such as morphology and tissue thickness (Loya et al., 2001), growth and/or respiration rate (Baird & Marshall, 2002), the ability of polyps to internally shade their *Symbiodiniaceae* (Jones et al., 2000), as well as intrinsic differences in the thermal tolerance of different clades or genotypes of Symbiodiniaceae (Berkelmans & Van Oppen, 2006; Grégoire et al., 2017). This interspecific variability in thermal tolerance is likely associated with among-species variation in demographic rates, and this complex interplay of variation in species tolerances and population dynamics means it is difficult to predict the rates of recovery of coral communities following bleaching events (e.g., McClanahan et al., 2020), and indeed following other disturbances.

Due to the ubiquitous threat of climate change, there has been significant research effort into investigating the effects of bleaching on corals and coral communities. However, monitoring and reporting of coral bleaching impacts are commonly based on overall coral cover with few studies tracking the fate of individual corals through time (but see: Morais et al., 2021; Sakai et al., 2019; Yadav et al., 2023). In this study, I followed coral communities and individual corals over a period of four years spanning both a minor and severe bleaching event. Contextualized by the increasing demand for long-term demographic studies, the overall aim was to document the extent and severity of the 2016-2017 back-to-back bleaching events on the demographics of corals and coral communities at the Palm Islands, central GBR. First, I measured bleaching rates and severity, and how this varies within and between communities. Second, I quantified the demographic impact of this bleaching on individuals, focusing on rates of colony growth and mortality. Finally, I documented the demographic impact of these bleaching events on the local coral community through changes in coral cover, colony abundance, community composition and population size structure. By tracking both coral communities and individuals over time, this study will contribute to knowledge gaps on the links between individual and community level effects.

2.3 Methods

2.3.1 Study site data collection

This study investigated coral communities at three reefs (E Orpheus, SE Pelorus and NE Fantome) on the exposed side of three islands within the Palm Islands group, Queensland (Figure 2.1). Data were collected over four years, spanning a minor (2016) and severe (2017) bleaching event, as part of a chronological study of the demography of these coral communities (Figure 2.2). The coral communities were compared from before (October 2015), during (March 2017) and after (February 2018) the bleaching events to assess the extent of bleaching and mortality, and to identify shifts in population demography and community composition. Other than the bleaching events, there were no major disturbances experienced over this period at the study sites, and all sites were in a similar phase of successional recovery following the impacts of severe tropical cyclone Yasi in 2011.

2.3.2 Data collection and sampling design

Data were collected along semi-permanent transects along the reef crest at a depth equivalent to the lowest astronomical tide (approximately 2 -3 m water depth at high tide). At each survey time point, transects were filmed using a hand-held video camera (GoPro Hero 5), facing the benthos at a height of 0.8 – 1 m. Each transect was divided into replicate 1 m x 5 m quadrats, with five replicates each for E Orpheus and SE Pelorus and three replicates for NE Fantome. These quadrats were revisited at all three survey points, which allowed identification and tracking of individual colonies over time.

The use of videos meant it was not possible to identify colonies to species level and small colonies and/or cryptic colonies were likely to be missed. However, the use of underwater video allowed data collection for a larger sample size and spatial extent, made it easier to relocate colonies across successive years, avoided potential effects on coral growth due to presence of tags, and provided a visual record of the study sites that facilitates reproducible analysis.

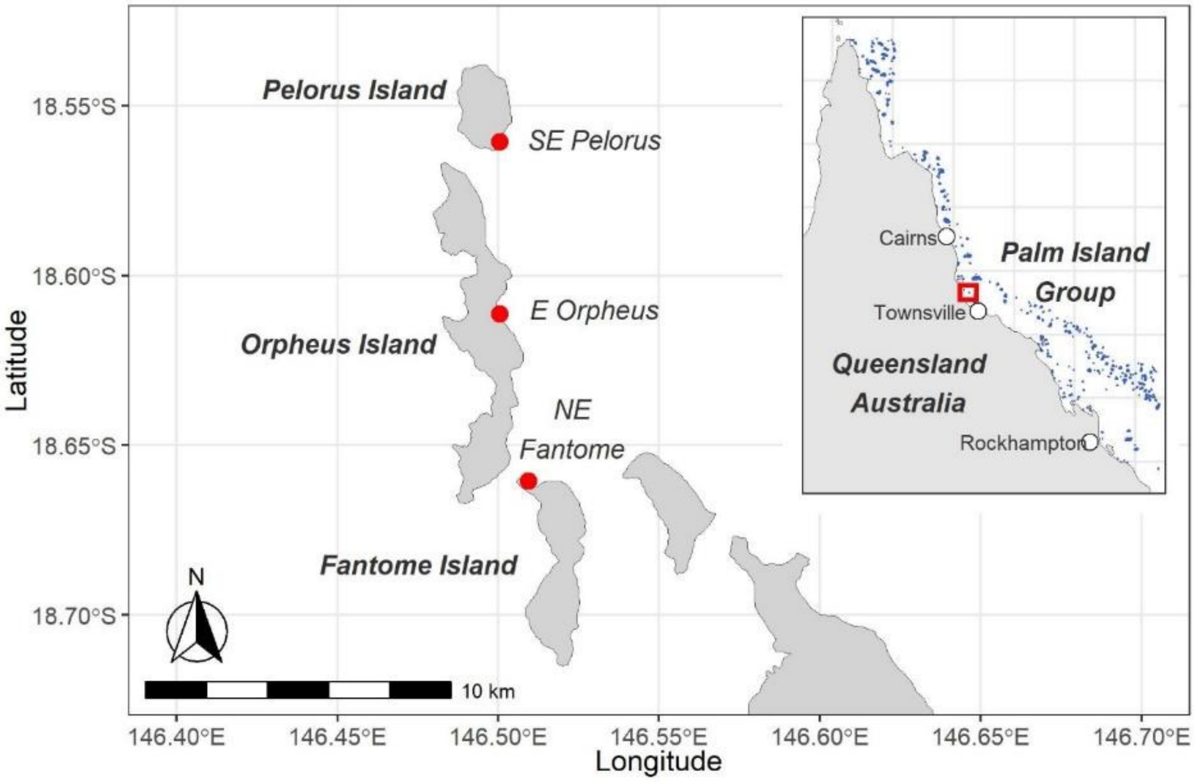

Figure 2.1. Map of survey locations within the Palm Island Group, Queensland.

Overlapping still frames were manually extracted from the videos to create photo-quadrats (1 m x 5 m). These images were analysed in ImageJ (version 1.8.0_112) using the transect tape to scale each photo and identify the quadrat boundary. Within each quadrat, every colony was given a unique reference and details were recorded on genus, size, bleaching presence and severity, and colony outcome (mortality). This study focused on three genera which were easily identifiable in the images: *Acropora*, *Pocillopora* and *Porites*. All remaining colonies were recorded as ‘other hard corals’ or ‘soft corals’.

ImageJ was used to measure colony size for the three focal genera. Colonies less than 5 cm in diameter were recorded as juveniles (Buglass 2016; Pisapia 2019), although I acknowledge that this is a rudimentary estimation which overlooks fast growing recruits and colonies which suffered fragmentation or fission (Hughes and Connell, 1987; Foster 2018). Colonies were grouped into size categories based on 10 cm increments of colony diameter, assuming a circular colony outline (Table A2.1). Colony size was only measured where the complete area was within the quadrat boundary. However, pilot analyses of the data showed that the likelihood of a colony being partially outside the quadrat increased when the colony exceeded 30 cm in diameter. Therefore, all colonies which had an in-quadrat area of over 30 cm were included to prevent misrepresentation of the colony size structure for each population. Colonies in the largest two size classes therefore represent a minimum size, rather than an accurate measurement. Growth was assessed for a subset of 105 colonies which were observed in each of 2015, 2017 and 2018, and where an accurate size measurement was possible at each time point (i.e., colony margin was not obscured in any year). Growth was based on the difference in colony projected area between survey time points. All measurements were standardised to growth per year (change in colony area, cm^2), accounting for the variable time periods between surveys.

During 2016, only mild bleaching was observed for a small number of colonies across the study sites (data not shown). Subsequently, a bleaching rating was given to each colony based on the 2017 survey during the severe bleaching event. In 2017, colonies were rated as ‘not bleached’, ‘mild bleaching’ where colonies were pale or <50% of the colony was bleached, ‘severe bleaching’ where >50% of colony was bleached, there was evidence of fluorescing, or the colony was bright white, and ‘recently dead’. To statistically compare both growth and survival of colonies which did not bleach to those that did, I combined the mild, severe, and recently dead groups to form a ‘bleached’ group. Colony outcome was recorded as ‘survived’, ‘partial mortality’ or ‘mortality’ based on colony condition in 2018. Where colonies were not present in their prior location, or were dead prior to the onset of bleaching, they were recorded as dead and excluded from this analysis.

Coral cover was estimated using a random point sample of the benthos. From a pilot study I found that 50 points per m^2 gave the greatest level of accuracy in coral cover estimates, which resulted in ~230-250 benthic cover records within each quadrat. The small variations in numbers arose from the random positioning of points using a grid overlay on Image J and exclusion of points where the benthos was unclear (<1%). At each point, the benthos was recorded as coral (in *Acropora*, *Pocillopora*, *Porites*, other hard corals, or soft corals categories), as well as algae, sand/sediment, bare rock (hard substrate either with an obvious or presumed epilithic algal matrix) or other (e.g., sponge, ascidians).

2.3.3 Data processing and analysis

All analyses were completed using the statistical software R (version 4.3.0, The R Foundation for Statistical Computing), except the multivariate community analyses which were performed in Primer (version 7, PRIMER-E Ltd., Ivybridge, UK). Coral cover and colony abundance data were analysed using permutational analysis of variance (PERMANOVA) with Bray-Curtis dissimilarities and a square-root transformation and Wisconsin transformation, respectively. These analyses were performed using the ‘vegan’ package. Differences in cover and abundance from before (2015) and after (2018) the bleaching events were compared with site included as an additional factor. Changes in the community composition were visualised using non-metric multidimensional scaling (nMDS) with the similarity percentages routine (SIMPER) identifying the characteristic benthic cover within each site before and after bleaching. The colony size structure for each genus was compared before and after bleaching using two-sample Kolmogorov-Smirnov tests, with data separated both by site and by genus. Comparisons of bleaching proportions and mortality proportions were made using binomial logistic regressions using the package ‘car’. The small number of colonies that underwent partial mortality were grouped with colonies which survived for this analysis. Overall, comparisons of bleaching severity were analysed with an ordinal logistic regression using the ‘ordinal’ package. However, this model was unable to consider an interaction effect between sites and genera due to categories with zero colonies or where 100% of colonies experienced the same level of bleaching. Therefore, Fisher’s exact tests were also performed within each site to compare bleaching severity between genera. The logistic regressions were initially run on the full data set. However, because colony size was only measured for the focal genera, I subsequently repeated the analysis using only these genera, to consider the effect of colony size (in area cm^2) on bleaching severity. Growth rates were compared over time for the 105 colonies which were identifiable in 2015, 2017 and 2018. The change in growth rate (standardised to cm per year) from before (2015-2017) and after (2017-2018) bleaching was analysed using a linear model with a cube-root transformation.

2.4 Results

Overall, this study identified, and tracked the fate of 1,655 unique colonies, of which 984 were recorded both before (2015) and after the bleaching events (2018), and 983 were assessed for bleaching severity (2017; Figure 2.2). In total, 775 (47%) of these colonies were of the three focal genera considered here (*Acropora*, *Pocillopora* and *Porites*).

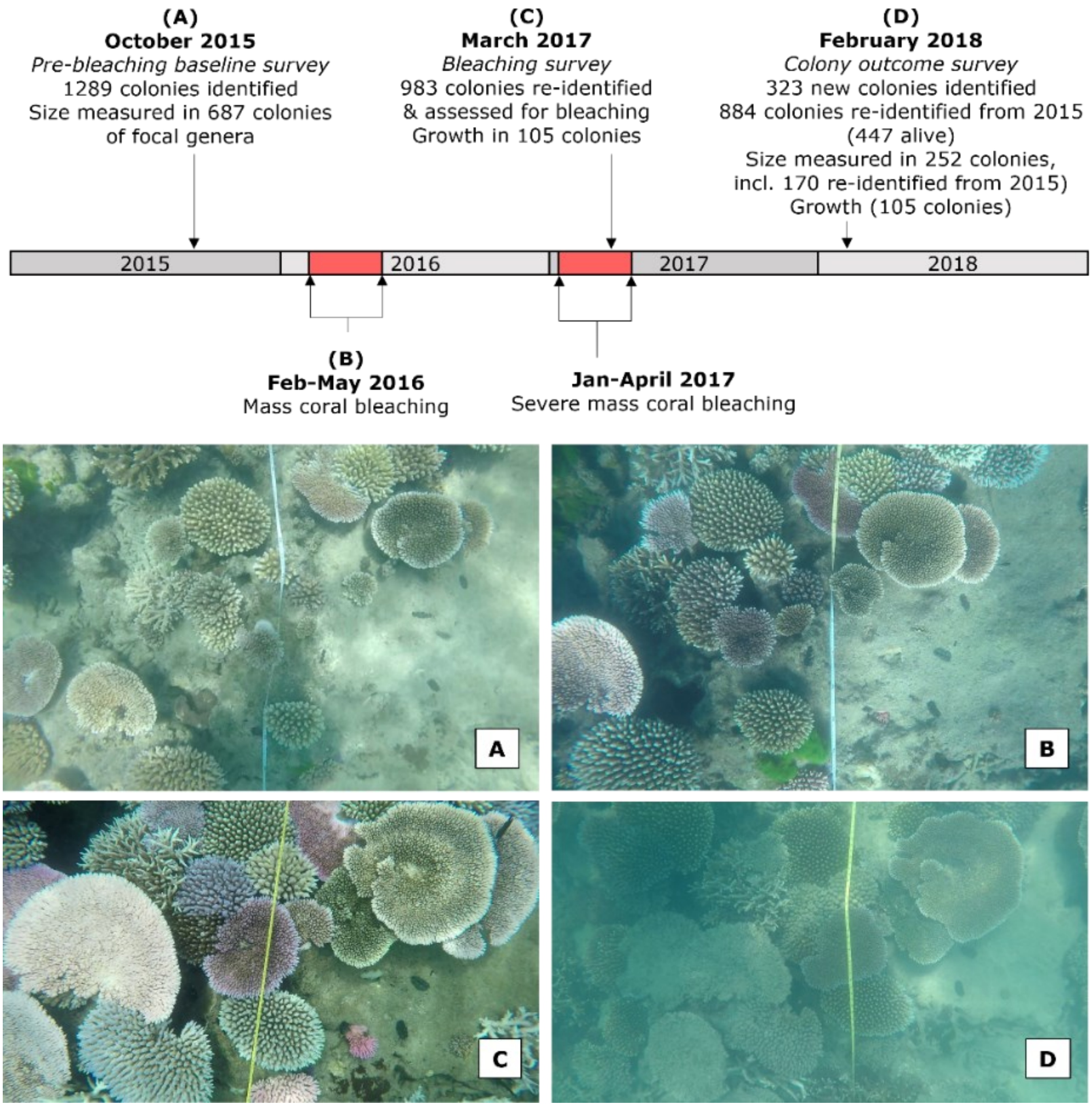

Figure 2.2. Timeline of survey points and mass bleaching events. Photographs show ~1 m section of a quadrat (NE Fantome) at each of the survey times.

2.4.1 Extent and severity of bleaching

In 2017, 73% of colonies showed evidence of bleaching. Of these bleached colonies, 22% had mild bleaching, 44% suffered severe bleaching and a further 8% had already died from severe bleaching at the time of survey (March 2017, Figure 2.2). Both bleaching rates and bleaching severity varied significantly between sites and genera (Table 2.1), with Fisher's exact tests showing significant differences in bleaching severity between genera within each site ($p < 0.01$ for all sites, Table 2.1). *Acropora* and *Pocillopora* had high bleaching prevalence (93% and 100% of colonies, respectively) and were most often recorded as severely bleached (70% and 89% respectively; Figure 2.3b). In contrast, *Porites* colonies had an almost 5-fold lower incidence of bleaching (21%; Figure 2.3b), and only 6% of *Porites* colonies experienced severe bleaching. Bleaching also varied significantly between sites. E Orpheus had almost 30% fewer bleached colonies in comparison to SE Pelorus and NE Fantome (Figure 2.3a, Table 2.1). Bleaching prevalence showed a significant interactive effect between site and genus (Table 2.1) which was driven by differences in bleaching rates in the ‘other hard corals’ which showed more bleaching at SE Pelorus (81%) than E Orpheus (21%), and the soft corals group, which experienced more bleaching at E Orpheus (66%) than the other sites (40% SE Pelorus, 29% NE Fantome). While this effect was not significant for bleaching severity, a similar pattern was found with different responses in ‘other hard corals’ which experienced little bleaching at E Orpheus (79% no bleaching) but were most often severely bleached at SE Pelorus (52% severely bleached). Secondary analyses using just the focal genera found no overall effect of size on either bleaching prevalence or severity (Figure 2.3c, Table 2.1).

Table 2.1. Factors affecting bleaching rate, bleaching severity, and mortality rate for all colonies (left) and focal colonies where the effect of colony size could also be included (right), from binomial logistic regressions (bleaching and mortality rates) and ordinal logistic regressions (bleaching severity).

	Bleaching rate					
Factor	All (n=983)			Focal (n=435)		
	Chisq	*df*	*p*	*Chisq*	*df*	*P*
Site	112.1	2	**<0.01***	31.19	2	**<0.01***
Genus	262.44	4	**<0.01***	94.66	2	**<0.01***
Col. size	-	-	-	2.74	1	0.10
Site * Genus	55.46	8	**<0.01***	3.39	4	0.50
Site * Col. size	-	-	-	14.06	2	**<0.01***
Genus * Col. size	-	-	-	10.31	2	**<0.01***

	Bleaching severity					
Factor	All (n=983)			Focal (n=435)		
	Chisq	*df*	*p*	*Chisq*	*df*	*P*
Site	107.91	2	**<0.01***	35.16	2	**<0.01***
Genus	240.43	4	**<0.01***	83.5	2	**<0.01***
Col. size	-	-	-	2.4	1	0.12

	Mortality rate					
Factor	All (n=791)			Focal (n=375)		
	Chisq	*df*	*p*	*Chisq*	*df*	*p*
Site	14.46	2	**<0.01***	24.18	2	**<0.01***
Genus	57.59	4	**<0.01***	8.26	2	**0.02***
Bleach severity	42.34	2	**<0.01***	22.31	2	**<0.01***
Area	-	-	-	6.43	1	**0.01***
Site * Genus	28.9	8	**<0.01***	3.13	3	0.37
Site * Bleach severity	12.22	4	**0.02***	11.49	4	**0.02***
Site * Col. size	-	-	-	0.79	2	0.67
Genus * Bleach severity	28.77	7	**<0.01***	0	2	1
Genus * Col. size	-	-	-	0.03	2	0.98
Bleach severity * Col. size	-	-	-	3.72	2	0.15

2.4.2 Demographic impact on colonies

2.4.2.1 Growth

Growth rates were recorded for 105 colonies which were observed in all three surveys. Both growth rates and changes in growth rates pre- and post-bleaching were highly variable between colonies. From 2015 to 2017, prior to the severe bleaching event, 79% of colonies had net growth while following bleaching, this fell to 66%. These declines in growth rate were similar between sites (GLM, $F_{(2, 98)} = 0.57$, p=0.57) and genera ($F_{(2, 98)} = 1.48$, p=0.23), however varied significantly with bleaching severity ($R^2=0.11$, $F_{(2, 98)} = 4.42$, p=0.01; Figure

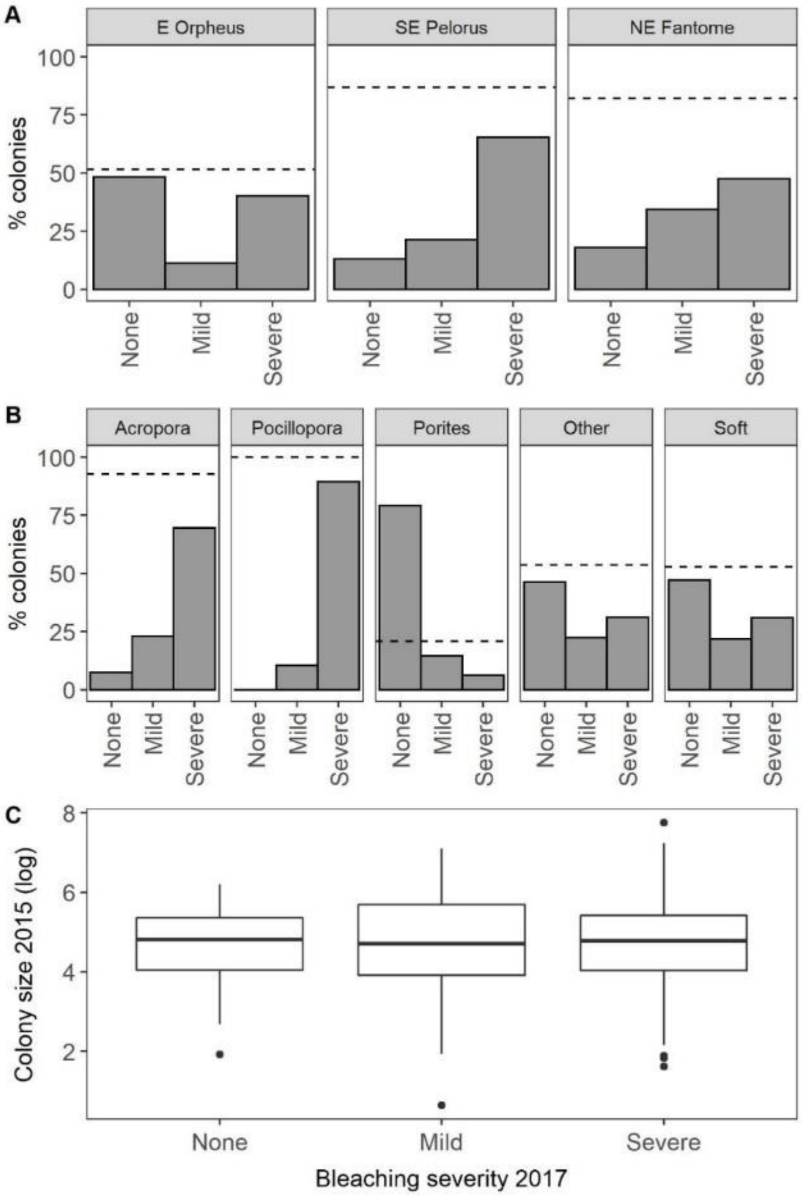

Figure 2.3. The percent of colonies in each bleaching severity category by A) site, B) genus C) size. Dashed horizontal lines shows total percent of colonies with bleaching within category. n= 983 (A, B), 435 (C)

2.4). Across all colonies, mean colony growth rate declined 8% in colonies which did not bleach, 29% in colonies with mild bleaching and 93% in colonies which experienced severe bleaching (Figure 2.4). These reductions resulted in coral cover being 19% lower in 2018 than it would have been if corals had continued to grow at their pre-bleaching rates (based on the total area of the 105 measured colonies). Although not statistically significant, reduced growth rate following bleaching was more prevalent in *Acropora* than in *Porites*. Prior to bleaching, mean colony growth in *Acropora* colonies was 219 ± 32 cm^2 year^{-1} and decreased 68% to 71 ± 41 cm^2 year^{-1}, while mean growth in *Porites* colonies was more consistent at 8.2

± 4 cm^2 $year^{-1}$ before bleaching and 7.7 ± 9 cm^2 $year^{-1}$ after bleaching. Only three Pocillopora colonies survived the 2017 bleaching event and showed no consistent patterns in growth rate. Site, genus, and bleaching severity only partially accounted for the differences in growth rate seen here. Further exploration of within genus differences, showed that effects of bleaching on *Acropora* growth rates were different among different branching morphologies, with bleaching more negatively impacting arborescent and tabular colonies than caespitose and juvenile colonies (Figure A2.1).

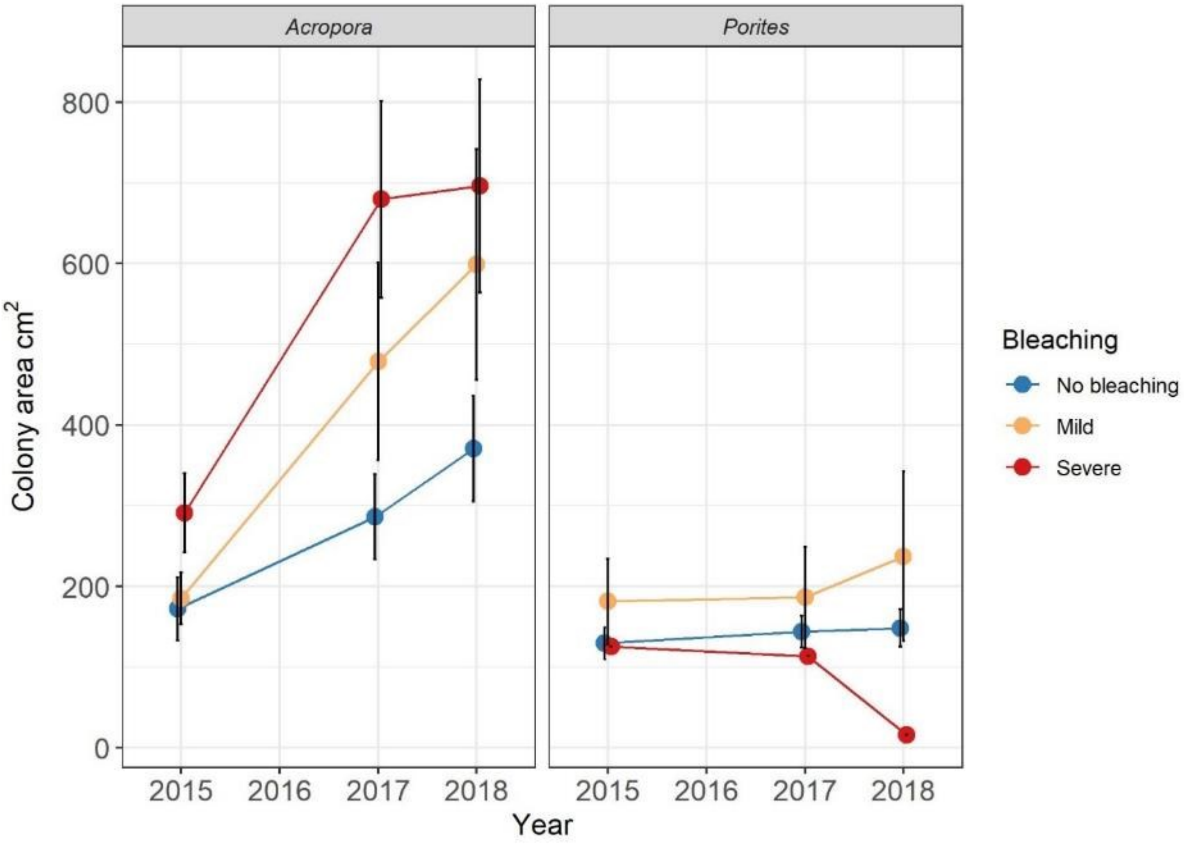

Figure 2.4. Planar colony size, cm^2 (mean ± SE), showing colony growth between 2015 and 2018. n=105 colonies which had a bleaching rating and size measurements at each time point. Pocillopora has been excluded here due to the low number of surviving colonies.

2.4.2.2 Colony outcome (mortality)

Of the 884 colonies identified in both 2015 and 2018, over half (54.9%) had died by the 2018 post-bleaching survey. However, colony outcome varied significantly with site, genus, and bleaching severity, with significant interactions between all the main effects (Table 2.1).

At SE Pelorus and NE Fantome, mortality rates were higher than survival rates (Figure 2.5a). At E Orpheus, survival rates were greater than mortality, however this included moderate levels of partial mortality. Mortality rates between genera were also highly variable, being highest for *Acropora* (73%) and *Pocillopora* (87%), and lower for *Porites* colonies (7%), other hard corals (28%) and soft corals (56%; Figure 2.5b, Table 2.1). Bleaching severity had a significant effect on survival, with colonies with no bleaching or mild bleaching typically surviving (14% and 31% mortality, respectively) while those with severe bleaching typically died (73% mortality; Figure 2.5c, Table 2.1). Of the 414 colonies with severe bleaching, less than one third (27%) survived to the time of the 2018 survey. Partial mortality rates were generally low (8.5% of colonies). However partial mortality was more prevalent in *Porites*, other hard and soft coral genera, and in the larger colonies across all corals surveyed. A secondary analysis of survival of only the focal genera showed generally greater survival in larger colonies (Table 2.1). The mean pre-bleaching colony size of surviving colonies was 234 ± 26 cm^2, compared to 157 ± 9 cm^2 of the colonies which died.

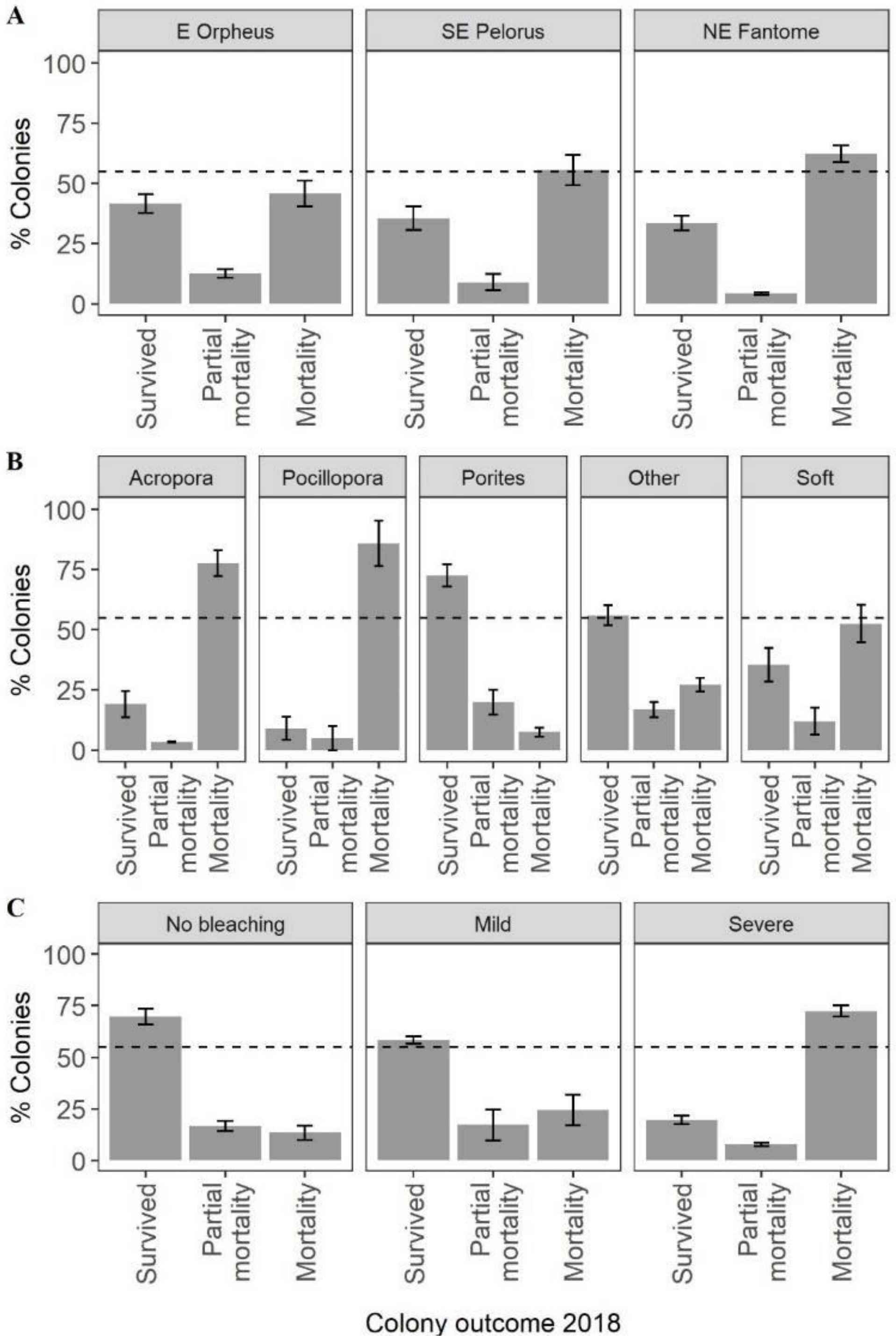

Figure 2.5. Percent of colonies (mean ± SE) that survived, suffered partial mortality or complete mortality between 2015 and 2018 by A) site B) genus and C) bleaching severity. Standard error bars show the variation between quadrats. n = 983 (A, B), 791 (C). Dashed line represents the total % mortality of all colonies re-identified in 2018.

2.4.3 Effects of altered demography on coral community

2.4.3.1 Coral cover and abundance

The bleaching events in 2016 and 2017 resulted in a 6.4% decrease in total live coral cover, from 34% in 2015 to 28% in 2018 (Figure 2.6a), with 91% of the coral mortality recorded occurring following the more severe event in 2017. However, the direction of change differed between sites (Table 2.2). At E Orpheus and SE Pelorus coral cover declined (15% and 5% respectively), whereas coral cover at NE Fantome increased 6% over the same time period (Figure 2.6a). This was driven by an increase in *Acropora* cover at NE Fantome but a decrease of both *Acropora* and other genera at the other two sites (Figure 2.6b).

Due to the high rates of mortality, there was a notable yet not significant decrease in the abundance of coral colonies before and after the bleaching events (Table 2.2). In 2015 the mean number of colonies/m^2 was 19.8 ± 1.9, which declined to 12 ± 0.8 in 2018 (Figure 2.6c). However, the abundance of corals varied significantly between sites (Table 2.2). Bleaching resulted in a 58% decline in colony abundance at NE Fantome, 41% at SE Pelorus and 23% at E Orpheus (Figure 2.6c). These declines were largely driven by substantial declines of *Acropora* colonies (70% decrease in mean colony/m^2). *Pocillopora* abundance similarly decreased (75%) although their lower abundance in 2015 reduced the net impact of this on overall colony abundance. Soft coral and other hard corals had small declines in abundance (25 % and 6 % respectively) while numbers of *Porites* colonies slightly increased (3%; Figure 2.6d).

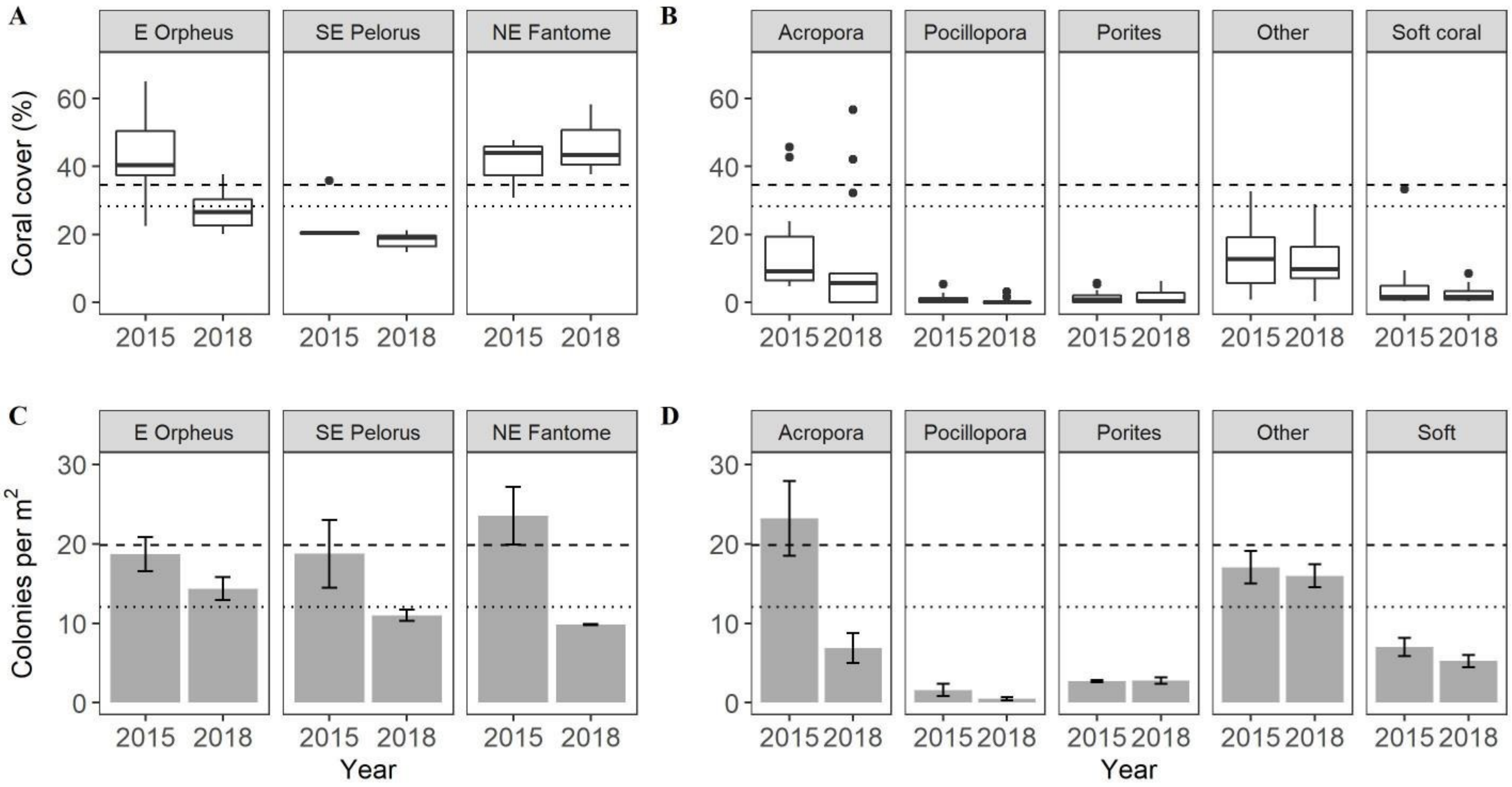

Figure 2.6. Mean (± SE) percent coral cover (A, B) and number of colonies per m^2 (C, D) between sites (A, C) and genera (B, D). Standard error bars show the variation between quadrats (n= 5 $year^{-1}$ for E Orpheus and SE Pelorus, 3 $year^{-1}$ for NE Fantome; n=13 $year^{-1}$ for each genus). Horizontal lines show the mean coral cover (A, B) and mean number of colonies m^2 (C, D) $quadrat^{-1}$ in 2015 (dashed) and 2018 (dotted). Coral cover: n=3231 (2015) and 3222 (2018) random sampling points. Colony abundance: n= 1289 colonies (2015) and 782 (2018).

Table 2.2. The results of PERMANOVA analyses comparing both coral cover and colony abundance from before (2015) and after (2018) the 2016 – 2017 bleaching events.

Coral cover (Square-root transformation) *Stress = 0.14*					
	df	SS	MS	F	*p*
Site	2	0.73	0.36	21.99	**<0.01**
Year	1	0.26	0.26	15.44	**<0.01**
*Site*Year*	2	0.11	0.06	3.42	**<0.01**
Residuals	20	0.33	0.02		
Total	25	1.43			
Abundance (Wisconsin transformation) *Stress = 0.12*					
	df	SS	MS	F	*p*
Site	2	1.91	0.95	22.57	**<0.01**
Year	1	0.11	0.11	2.71	0.06
*Site*Year*	2	0.06	0.03	0.71	0.64
Residuals	20	0.85	0.04		
Total	25	2.93			

2.4.3.2 Community composition

In 2015, there were notable differences in both benthic cover and coral community composition between the sites (Figure 2.7a). The coral assemblage at E Orpheus and SE Pelorus were characterised by other hard corals and *Acropora* as well as 36% macroalgal cover at E Orpheus. At NE Fantome the coral assemblage was heavily dominated by *Acropora* which accounted for 37% of benthic cover and 92% of live coral cover. A SIMPER analysis showed moderate dissimilarity between the sites for benthic cover and colony abundance, with the greatest similarity between E Orpheus and SE Pelorus communities (SIMPER benthic cover = 32, abundance = 32) and the least similarity between E Orpheus and NE Fantome (SIMPER benthic cover = 45, abundance = 48).

By 2018, coral bleaching had resulted in moderate changes in the benthic community compared to 2015 (Figure 2.7b). At E Orpheus, there was a complete loss of *Acropora* and reduced abundance in macroalgae while at SE Pelorus there were large declines in *Acropora, Pocillopora* and soft corals. Finally, there was little change in the dominant benthic cover between years at NE Fantome, but a notable decline in colony abundance. Despite these changes, there was a high degree of similarity within each site from before and after the bleaching events, for both coral cover (SIMPER average similarity = 74 at E Orpheus; 76 at SE Pelorus; 85 at NE Fantome) and abundance (SIMPER average similarity = 79 at E Orpheus; 77 at SE Pelorus; 79 at NE Fantome).

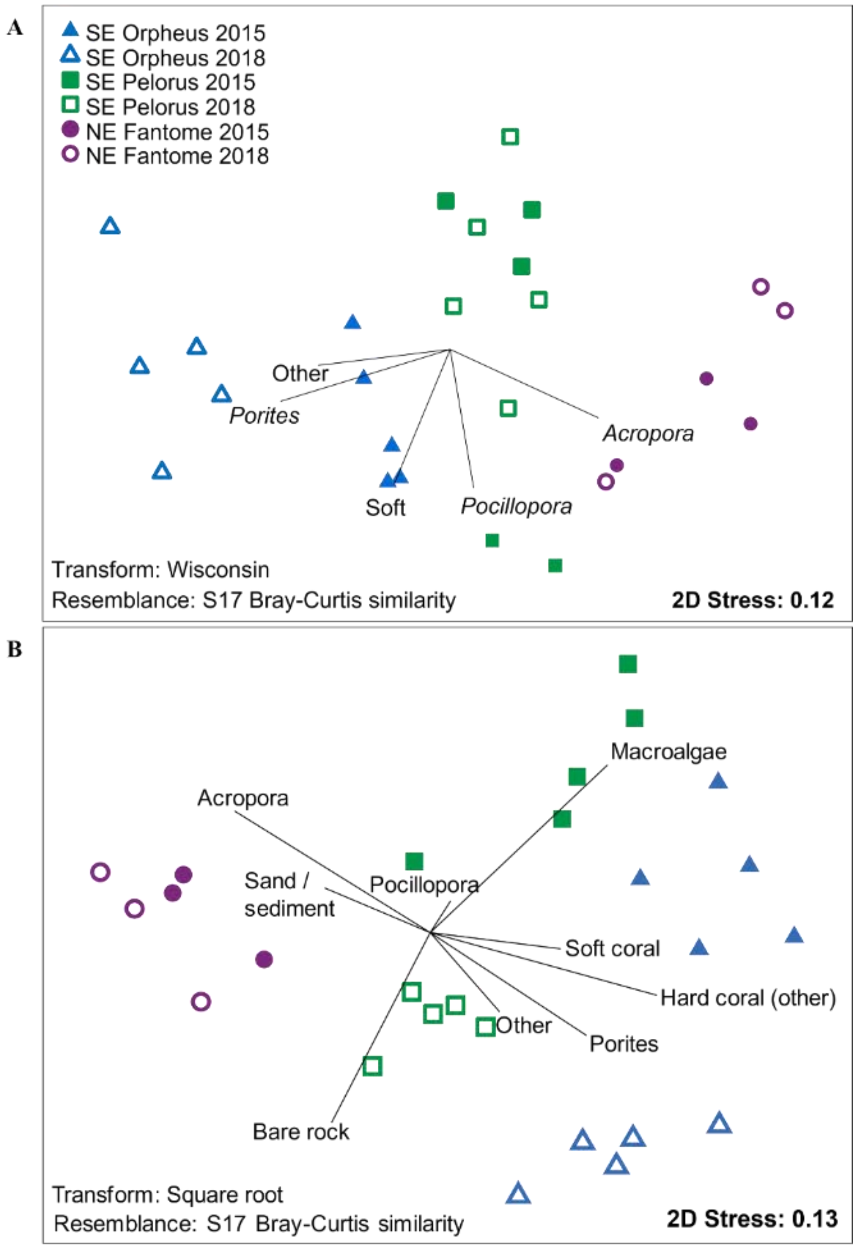

Figure 2.7. Non-metric multi-dimensional scaling plots showing the variation in A) benthic cover and B) colony abundance at three sites from before (2015; closed shapes) and after (2018; open shapes) back-to-back mass bleaching events. Each point reflects a single 1 x 5m quadrat.

2.4.3.3 Size structure

The population size structure of the three focal genera was measured in 526 colonies in 2015 and 265 in 2018. The lower sample size in 2018 was a result of the high rates of mortality seen following bleaching. Coral populations at all sites and within each genus, were skewed towards a dominance of smaller colony sizes (Figure 2.8a,b; Table A2.2). Following bleaching, *Acropora* was the only genus to show a significant change in the population size structure (Table 2.3). In comparison to 2015, by 2018 the mean size of *Acropora* colonies had more than doubled, small colonies were less abundant and there were more colonies in the largest size classes (Figure 2.8b). There was also a notable flattening of the distribution resulting from a large decrease in colony numbers (Table A2.2). These changes are reflected at NE Fantome, which was heavily dominated by *Acropora* colonies and similarly had a significant change in population size structure (Table 2.3). Declines in the abundance of *Pocillopora* resulted in a flattening of the size distribution with a loss of larger colonies and a small decrease in mean colony size, although these changes were not significant. In contrast, the size structure of the *Porites* population remained largely stable over time (Table 2.3).

Table 2.3. Results of two-sample Kolmogorov–Smirnov tests, assessing differences in population size structure before (2015) and after (2018) bleaching, between sites and genera.

		2015 mean colony size +/- SE (cm^2)	*2015 mean colony size class*	*2018 mean colony size +/- SE (cm^2)*	*2018 mean colony size class*	*D*	*p*
Site	*E Orpheus*	132 ± 11	10-20 cm	124 ± 16	10-20 cm	0.08	0.94
	SE Pelorus	151 ± 24	10-20 cm	280 ± 94	10-20 cm	0.08	0.93
	NE Fantome	204 ± 14	10-20 cm	613 ± 84	20-30 cm	0.42	**<0.01**
Genus	*Acropora*	174 ± 11	10-20 cm	507 ± 67	20-30 cm	0.31	**<0.01**
	Pocillopora	147 ± 31	10-20 cm	126 ± 67	10-20 cm	0.48	0.16
	Porites	125 ± 19	10-20 cm	120 ± 15	10-20 cm	0.12	0.85

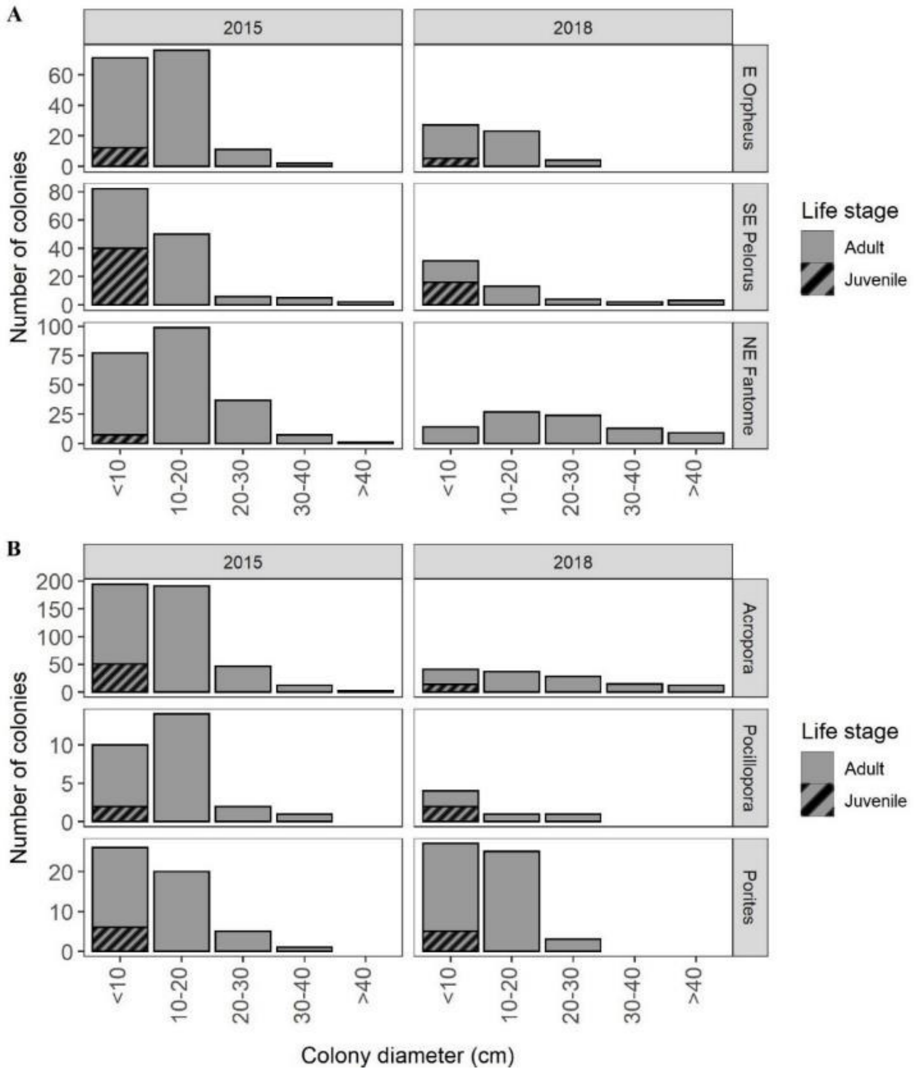

Figure 2.8. Population size histograms from before (2015) and after (2018) the back-to-back bleaching events, by A) site and B) focal genera. The hashed pattern of <10 cm diameter column denotes juvenile colonies (<5 cm diameter). Note the variation in scale between genera due to large differences in abundance. n=720 colonies.

2.5 Discussion

In this study I tracked the fate of coral colonies over four years, spanning a mild and a severe bleaching event, to assess the demographic processes that drive effects of bleaching on coral communities. The results show bleaching prevalence and severity were high over these events, that bleaching resulted in significant mortality and reduced growth in surviving colonies, and that these changes resulted in shifts in the size structure, recovery rates and composition of the coral communities. By tracking individual colonies though time I highlight that the extent of the reef degradation associated with these bleaching events was more pronounced than that evidenced by changes in coral cover alone.

2.5.1 Extent and severity of bleaching

The extent and severity of bleaching, and the consequent declines in coral cover and abundance, varied with genera. Taxonomic variations in bleaching susceptibility have long been recognised (Loya et al., 2001; Marshall & Baird, 2000) and the mortality seen over these bleaching events was largely consistent with the results of previous studies documenting 'winner' and 'loser' species. For example, whole colony mortality was negligible for *Porites* ('winner') but was high for *Acropora* and *Pocillopora* ('losers'). The extent and severity of this bleaching event therefore varied significantly due to site-level differences in pre-bleaching assemblages. Similarly patchy responses to bleaching based on community composition, have previously been seen, both between (Pisapia et al., 2019) and within sites (Edmunds & Elahi, 2007). Such site-specific differences limit our ability to estimate the impact of bleaching events from only a few sites and creates a significant challenge for predicting the impact of future climate change on coral reefs. However, evidence of bleaching even in the more tolerant 'winner' genera highlights the severity of the 2017 event in this region.

In addition to genera-specific differences in bleaching susceptibility, the differences in bleaching rates between the sites highlight more nuanced responses in taxonomic susceptibility with a genus. While *Acropora* cover and colony abundance in 2015 were nearly identical at E Orpheus and SE Pelorus (8.5% cover; 129 and 151 colonies respectively), mortality rates varied notably with 60% mortality at SE Pelorus but 98% mortality at E Orpheus. Such variability is likely to result at least in part from the relative abundance of different species, morphologies, or haplotypes with variable susceptibility to bleaching (Burgess et al., 2021; Gold & Palumbi, 2018). The variation in susceptibility among species within each of the focal genera was not assessed here due to colony identification being limited to genus level. However, during severe events taxonomic differences in susceptibility may become less pronounced with even the more tolerant species bleaching (Hoogenboom et al., 2017). The difference in bleaching susceptibility within genera between sites may be due to differences in environmental conditions. While larger scale environmental factors such as the extent of heat exposure (Hughes et al., 2017) and previous history of stress (Anthony et al., 2009; Pratchett et al., 2020) are likely to be largely similar between these spatially close sites, finer scale differences such as shading between habitats (Hoogenboom et al., 2017) may contribute to some of the variability seen.

2.5.2 Demographics of the individual

In this study, bleaching resulted in significant declines in growth rates, with more severe bleaching resulting in more severe reductions. Similar declines in growth have previously been found for multiple genera, including both *Acropora* and *Porites* (Gold & Palumbi, 2018; Goreau & Macfarlane, 1990; Suzuki et al., 2000) and highlight the physiological cost of bleaching for corals. This slowing of growth following bleaching was particularly evident for *Acropora* colonies and may be anticipated from their fast, weedy growth (Pratchett et al., 2015) and high susceptibility to disturbances (Marshall & Baird, 2000). Declines in growth were also seen for severely bleached *Porites* colonies, however, this was based on a single colony, with the apparent reduction in growth rate actually caused by partial mortality. Furthermore 15% of the colonies measured appeared (visually) unaffected by bleaching but still experienced a slowing of growth greater than 20%. Such declines in growth with exposure to thermal stress but without obvious signs of bleaching have also been shown in the Red Sea (Cantin et al., 2010). Collectively, these results highlight that even when colonies do not bleach and/or die, thermal stress may still result in individual physiological and community level impacts via decreased growth. This observed decline in growth following thermal stress is likely to slow recovery of the coral community. While recovery rates following bleaching have been modelled (e.g., Mumby et al., 2021), where the suppressed growth following bleaching has not been considered, these estimates are likely to have overestimated the recovery of coral cover by failing to consider how high coral cover could have been without the disturbance.

In addition to the slowing of growth following bleaching, the results indicate that pre-bleaching growth rates are associated with bleaching severity. Within the *Acropora* colonies, those which grew fastest prior to bleaching, were also the most likely to experience severe bleaching. This trend has been previously shown in *Acropora*, with pre-bleaching growth in less bleaching tolerant species being twice as high as growth in more bleaching tolerant species (Gold & Palumbi, 2018). This indicates potential trade-offs between bleaching tolerance and growth between colonies (Walker et al., 2023) which is likely driven by multiple factors. For example, corals with low densities of symbionts have been found to be more bleaching tolerant but the lower energy production by the symbiont community also results in slower growth (Cornwell et al., 2021). Interestingly, variations in these trade-offs have been found to occur between individual colonies of the same species (*Acropora hyacinthus*; Cornwell et al., 2021; Gold & Palumbi, 2018; Walker et al., 2023) and as such, the effect of bleaching on coral growth may be very hard to predict based on community composition. However, this has important implications for recovery with these results highlighting that the fastest growing *Acropora* colonies, which are therefore likely to be the drivers in early recovery following disturbance, are also far more susceptible to subsequent bleaching events.

High rates of mortality from bleaching events are well evidenced in the literature (e.g., Morais et al., 2021). Here, just over half of the surveyed colonies died following the 2017 bleaching event. Similar to previous studies I found mortality rates were dependant on genus (Baird & Marshall, 2002; Loya et al., 2001), bleaching severity of individual colonies (Baird & Marshall, 2002), and severity of the thermal anomaly experienced at different reefs (Hughes et al., 2018; Yadav et al., 2023). However, my results show that mortality rates were size dependant with smaller colonies more likely to die than larger colonies. This contrasts with previous studies which have either found no size-dependant mortality (Baird & Marshall, 2002), or higher mortality in larger colonies (Speare et al., 2022). Perhaps more interesting is the disparity that larger colonies tended to bleach more often and more severely, and yet appear to have lower rates of mortality. One explanation for this contrast is that larger colonies also had slightly higher rates of partial mortality and fragmentation, experiencing only patchy tissue loss because of bleaching rather than whole colony mortality. However, overall rates of partial mortality were relatively low and cannot fully explain the disparity between the high bleaching severity and lower mortality rates. Furthermore, many of the largest colonies were *Acropora* which have been shown both in this study and previous work (Baird & Marshall, 2002), to have low rates of partial mortality and largely surviving intact or dying completely. Mortality rates are therefore highly dependent on a number of factors including the genus and size of the colony as well as its bleaching severity and local environmental conditions.

2.5.3 Demographics of the community

In this study I found that total coral cover on three sites in the Palm Island decreased by 6.4% following the back-to-back 2016-2017 bleaching events. However, the inclusion of community demographics as well as tracking individual colonies over time allowed us to provide greater resolution on the extent of the impact of these events. The changes in the abundance of colonies paints a more concerning outlook than coral cover alone. While in E Orpheus and SE Pelorus, declines in coral cover co-occurred with comparable, and expected, declines in colony abundance, at NE Fantome there was a dissociation between coral cover which increased 6% and colony abundance which decreased 58%. These opposing trends were driven by rapid growth in a small proportion of surviving colonies and a significant increase in mean colony size masking the high mortality rates. The surviving colonies that increased in size between 2017 and 2018 were predominately large *Acropora* colonies, which have greater space filling capacity that smaller colonies. While coral cover alone indicates that the corals at NE Fantome were largely unaffected by the bleaching events, decreased colony abundance suggests a greater level of degradation. Colony growth compensating for decreased colony abundance to maintain coral cover has previously been predicted by size class transition models (Foster & Foster, 2018) as well as seen *in situ* following disturbance events (Cannon et al., 2021). However, while quick recovery of coral cover is beneficial, decreased colony abundance is a significant long-term threat to coral populations due to reduced genetic diversity, and because mortality will eventually exceed the ability of the remaining colonies to fill the space through growth (Pisapia et al., 2020). Furthermore, reduced colony abundance affects ecosystem functioning through changes in habitat complexity and altered reef carbonate budgets (Perry & Alvarez-Filip, 2019).

Following the bleaching, the *Acropora* assemblage showed a significant shift in size structure. Although there was a flattening of the size structure resulting from fewer individuals, greater survival of large colonies as well as rapid growth in a small number of surviving or unbleached colonies, meant there was no loss of range in size classes. Maintenance of coral cover and growth into the largest colony sizes is good for structural complexity and maintaining ecosystem functioning (Dietzel et al., 2020). However, it has previously been shown that corals often have notable energy deficit following bleaching which may have implications for other high-energy processes such as recruitment (Baird & Marshall, 2002; Leinbach et al., 2021). As such, while surviving colonies which regrow may be resilient to bleaching (van Woesik et al., 2011), this may be insufficient to maintain a population if recruitment is also impacted.

In contrast, the changes in size structure in *Pocillopora* and *Porites* were not significant. However, there was a trend for the loss of the larger colonies and a shift to smaller mean colony size. Similar shifts towards fewer (Dietzel et al., 2020) and smaller (Pisapia et al., 2020) colonies have previously been shown following bleaching and other disturbance events. The implications of changes in size structure can be important for recruitment because larger colonies contribute disproportionately more to recruitment than smaller colonies (Hall & Hughes, 1996; Sakai, 1998). Therefore, even though the change in size structure was not significantly different following bleaching, losing the largest *Pocillopora* and *Porites* individuals may decrease potential population replenishment, which may ultimately slow recovery. Nevertheless, it is worth noting that the size structure of these communities prior to bleaching was already positively skewed towards smaller colonies sizes, possibly as a result of multiple prior disturbances, including the catastrophic loss of corals during cyclone Yasi in 2011 (Torda et al., 2018). Further studies of bleaching-related changes in reproductive output are required to confirm effects of altered size structure on population replenishment.

2.6 Conclusions and future directions

The unique data set developed here has allowed identification of changes in coral cover and demography by tracking individual colonies over time. I present a high-resolution picture of the extent and severity of coral degradation over a period of back-to-back bleaching events. Results demonstrate significant changes to growth rates during the year following bleaching, which has important implications for reef recovery. Future studies should continue measurements of colony size over longer time periods to quantify how long corals experience a decline in growth and what this may mean for recovery. I also show high spatial variation in bleaching and mortality rates that are more nuanced than simply ‘winner’ and ‘loser’ genera and, consequently, broad categorisation of the presumed bleaching susceptibility coral genera should be interpreted with caution. This study was limited by genera level identification, however greater resolution to species or genotype level, as well as a more detailed environmental assessment, including microhabitat or interactions with other colonies (e.g., shading) may improve our understanding of why bleaching and mortality vary within and between genera. In addition, I show community level changes to demographics including changes in size structure and community composition, and reduced colony abundance. However, recruitment is an important demographic metric which was not measured in this study. Including juvenile recruitment before and after bleaching event in conjunction with other individual and community level demographics, would further deepen our understanding of how bleaching affected these coral communities.

In this study, the inclusion of both individual demography and community dynamics allows a deeper understanding of the true impact of bleaching events on coral communities, and their ability to recover. These demographic assessments provide four indicators that the effect of these bleaching events was more severe than suggested by coral cover alone. First, colony growth masked a significant decline in colony abundance. Second, At E Orpheus, low bleaching rates and severity, and low rates of mortality (compared to other sites) masked a community composition shift driven by an almost complete loss of *Acropora* colonies. Third, partial mortality and fragmentation of some genera, in particular *Porites* colonies, resulted in a reduced mean colony size with the potential for implications on colony fecundity and recruitment. Finally, growth rates were significantly lower in (surviving) bleached colonies compared to before bleaching. The loss of weedy *Acropora* colonies and slower growth in those that survive, as well as potential declines in recruitment from smaller or fragmented colonies, reduce the capacity for those coral communities to recover from these bleaching events. Overall, my results indicate that the 6.4% decline in coral cover found at these study sites after back-to-back bleaching likely underestimates the overall impact of these bleaching events on coral communities and their ability to recover.

Chapter 3 : Competition affects bleaching severity, but not bleaching likelihood, in response to thermal stress on reef corals

3.1 Abstract

Coral bleaching is a direct, acute physiological stressor for corals but can also indirectly affect the structure of coral communities by altering outcomes of species interactions such as competition. Moreover, competition is a chronic stressor for corals that can affect colony vulnerability to thermal stress. In this study I investigate whether and how competition for space on the reef benthos affects the prevalence, severity, or outcome of coral bleaching, and whether coral mortality from bleaching subsequently affects the prevalence and intensity of competition. I tracked the growth and survival of 983 colonies across three locations in the Palm Islands from before, during and after the 2016-2017 back-to-back bleaching events on the Great Barrier Reef. In total 75% of colonies bleached, 55% died and 77% were experiencing competition throughout the 4-year monitoring period. I show that colonies experiencing more intense competition tended to have higher bleaching severity and mortality, and suggest that competition intensity can partially explain within-genus variability in bleaching susceptibility. I also found that following mortality from bleaching, the changes to the coral community meant that competition became less frequent and less intense, and as such, these findings support competitive release during recovery. These findings highlight the importance of considering the indirect effects of bleaching on species interactions when predicting/projecting the effects of climate change on corals and coral communities.

Keywords

Climate change; Marine Heatwaves (MHW); Competition; Community; Bleaching; Indirect effects

3.2 Introduction

Temperature is a fundamental driver of the structure and function of most biological communities and ecosystem (Kordas et al., 2011). It affects not just the physiology, morphology, and survival of individuals but also the global distributions of species, and how species abundances vary among habitats (Angilletta, 2009; Pecl et al., 2017). Although the thermal tolerance ranges of species are highly variable, many species have evolved traits that optimise their fitness within a narrow temperature band. For instance, the compact growth forms and synchronised reproduction of Antarctic flora and fauna allow them to survive extreme low temperatures and scarcity of water (Block et al., 2009). In contrast, reef-building corals have co-evolved nutritional symbiosis with *Symbiodiniaceae*, that enhances calcification and coral growth in warm tropical and subtropical environments. However, global environmental change is causing temperatures in many environments to rise, contributing to a redistribution of species around the globe (Pecl et al., 2017). From the 1980s to mid-2010s, global reef sea-surface temperatures (SSTs) have increased an average of 0.2 ºC per decade (Heron et al., 2016; Lough et al., 2018), and are predicted to increase 0.6 - 2ºC by 2100 (IPCC, 2023; Lough et al., 2018; Sully et al., 2019). On coral reefs, ocean warming is pushing corals closer to the edge of their thermal tolerance (Howells et al., 2016) resulting in more frequent and widespread mass coral bleaching events (Hughes et al., 2018).

Mass coral bleaching events occur when these thermal anomalies, often referred to as marine heatwaves, occur over long durations and large spatial scales. For instance, between 2014 and 2017, a strong El Nino-Southern Oscillation (ENSO) event resulted in prolonged periods of very high sea surface temperatures (Heron et al., 2016), with 2017 presenting the warmest ocean temperatures on record (Eakin et al., 2019), prior to the temperature extremes of 2022 and 2023 (Cheng et al., 2023). Exposure to prolonged periods of above-average summer SSTs can result in a breakdown of the symbiotic relationship between corals and their algal symbionts from the family *Symbiodiniaceae*. Expulsion of the symbionts leaves corals white in appearance and, without their primary source of food, at risk of starvation (Anthony et al., 2009; Glynn, 1996). During the 2014-2017 period of thermal stress, ~75% of coral reefs globally experienced mass coral bleaching (Hughes et al., 2018). This unprecedented bleaching event is the longest and most severe to date (Eakin et al., 2019; Heron et al., 2016) and resulted in substantial coral mortality globally (Hédouin et al., 2020; Hughes et al., 2018; Rodgers et al., 2017). On the Great Barrier Reef (GBR), this marine heatwave resulted in the first back-to-back bleaching event in 2016-2017. While the 2016 event largely impacted the northern section of the GBR and the 2017 event predominately affected the central GBR, together these events resulted in an average 8% decrease in coral cover across the GBR (AIMS, 2018). Although coral mortality is the most significant outcome of coral bleaching, corals also experience other sublethal effects, such as decreased reproduction (Baird & Marshall, 2002; Szmant & Gassman, 1990), slower growth rates (Goreau & Macfarlane, 1990; **Chapter 2**) and reduced/slower recovery from injury (Meesters & Bak, 1993). These sublethal effects, when combined with coral mortality, can cause community level effects such as shifts in diversity (Cannon et al., 2021; Loya et al., 2001; McWilliam et al., 2020) and altered population size structure (**Chapter 2** of this thesis; Brito-Millán et al., 2019; Dietzel et al., 2020; Pisapia et al., 2019).

In addition to the physiological and community level effects of marine heatwaves on corals, changes in several localised processes can also affect the structure of coral communities. These include microhabitat variation, mechanical damage, and biotic interactions like competition and predation. Growth and settlement of corals is constrained by the availability of suitable space on the reef benthos and, therefore, corals compete with diverse benthic taxa primarily for space and light (Chadwick & Morrow, 2011; Lang & Chornesky, 1990). This competition tends to occur only when corals are in close proximity, and is energetically costly, regardless of the outcome (Romano, 1990) and can result in reduced growth rates, altered investment in reproduction and tissue quality (Hoogenboom et al., 2011; Idjadi & Karlson, 2007; Rinkevich & Loya, 1985; Romano, 1990; Tanner, 1997) as well as partial mortality, particularly along the colony margin where competition occurs (Idjadi & Karlson, 2007; Sheppard, 1985). Although competition tends to have primarily sub-lethal effects (Tanner, 1997), it acts as a small disturbance event (Pisapia et al., 2014), opening space on the reef for growth or recruitment. Over time, competition can act as a chronic stressor for corals (see Pisapia et al., 2014), influencing local species diversity and abundances (Chadwick & Morrow, 2011; Connell et al., 2004).

Acute disturbance events that cause widespread mortality, can be beneficial for some species which are resistant to the disturbance, because they experience lower competition after the event (i.e., competitive release). According to ecological theory, organisms do not need to be good competitors if they live in high stress, low diversity habitats, and equally, competitive species in an environment with abundant resources are the least resilient to stress events (Grime 1977). Therefore, environmental shifts resulting from disturbances can impact both organism fitness and competition. The Intermediate Disturbance Hypothesis (IDH; Connell, 1978) extends this principle to address species diversity. It suggests that the greatest diversity of organisms occurs at an intermediate level of disturbance, with high disturbance rates excluding all but the most resistant species, and low disturbance rates excluding poor competitors. While the IDH has been criticised (e.g., Fox, 2012), with fewer empirical studies finding unimodal relationships between disturbance and diversity in recent years (Moi, 2020), the concept of competitive release remains relevant to coral communities where frequent disturbances reduce coral cover. However, ecological models such as the IDH overlook the effect of multiple stressors.

Combined stressors can have surprising outcomes (Darling & Côté, 2008) and/or extreme ecological consequences (Kendrick et al., 2019). For example, seagrass die-offs have resulted from temperature, sedimentation, and predation stress (Buckee et al., 2021). Similarly, mangrove die-offs have been recorded for a combination of predation and disease stress, where predation subsequently increased infection rates (Rossi et al., 2020). On coral reefs, local anthropogenic stressors such as sedimentation, eutrophication and fishing pressure have been shown to reduce coral resilience to bleaching (Brunner et al., 2022; Carilli et al., 2009). To date, however, studies on multiple stressors on reef organisms have focused on abiotic factors (such as sedimentation; Anthony et al., 2007), or contrasts individual stressors with 'combined' stressors consisting of single multivariate groupings (e.g., Osborne et al. 2011). The interaction of chronic biotic stressors like competition with acute disturbances like bleaching has received limited attention. To the best of my knowledge, only one study has considered competition and bleaching *in situ*, which found that bleaching severity during extreme thermal stress was unaffected by competition (Hoogenboom et al., 2017). However, the interaction of multiple stressors likely depends on environmental context, such as the severity of the acute stressor or intensity of the chronic stress. Multiple stressors can create bidirectional affects and as yet, there has been no consideration of whether bleaching subsequently affects the frequency or intensity of competitive stress on corals. Addressing the knowledge gaps surrounding multiple stressors is crucial for predicting and managing the impacts of global environmental change (Bozec & Mumby, 2015; Côté et al., 2016; Darling & Côté, 2008)

The overarching aim of this study was to understand whether and how competition mediates the bleaching responses of reef building corals, and whether bleaching can lead to competitive release during the post-bleaching recovery period. Specifically, I established whether competition affected the likelihood of coral bleaching and colony survival following the 2016-2017 bleaching event. To achieve these aims, I quantified coral bleaching frequency and severity, as well as colony mortality in competing and non-competing corals. In addition, I analysed changes in competition before (2015) and after (2018) the bleaching events, by measuring 1) the proportion of colonies which are competing 2) the competitive intensity and 3) the relative frequency of four different types of competition, (ranging from direct contact competition, to overtopping and proximity competition). Improving our understanding of how bleaching indirectly affects corals through competition changes, will improve our ability to predict how corals and coral communities will be impacted by future bleaching events.

3.3 Methods

3.3.1 Study site data collection

All data for this study were collected from three sites on the exposed side of islands in the Palm Islands group, central Great Barrier Reef (Figure 3.1). These reefs were impacted by a mild bleaching event in 2016, followed by a severe bleaching event in 2017. Each site was surveyed before (2015), during (2017) and after (2018) the 2016-2017 back-to-back bleaching events. I focused on the effects of the 2017 bleaching event which had much higher rates of bleaching and mortality than the 2016 event in Palm Islands.

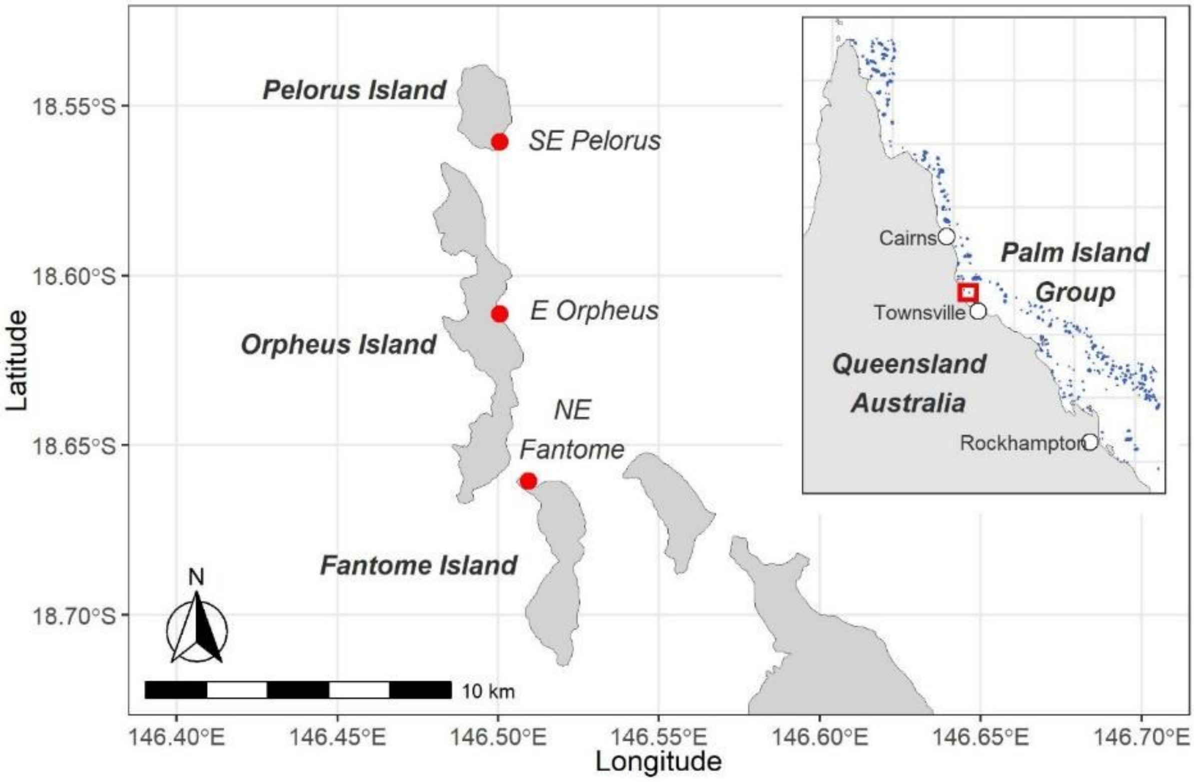

Figure 3.1. Map of survey locations within the Palm Island Group, Queensland.

Prior to bleaching in 2015, semi-permanent benthic transects were established following a depth contour at the lowest astronomical tide along the reef crest and perpendicular to the shore. These transects were marked with transect tape and small stakes, and were revisited, and imaged, in March 2017 and February 2018, allowing individual colonies to be tracked over time (Figure 3.2). Transects were filmed using a hand-held video camera (GoPro Hero 5), facing directly down at the benthos at approximately 0.8 – 1.0 m height. Each transect was 30 – 50 m long and divided into replicate 5m by 1m quadrats. The start of each transect was randomly selected, with at least 1m between transects. In total five replicate transects at E Orpheus and SE Pelorus were filmed and three replicates at NE Fantome.

3.3.2 Image and video data extraction

Overlapping still frames were taken from the videos and analysed using ImageJ (version 1.8.0_112). The images were scaled using the transect tape in each photo, which allowed me to define the 5 x 1 m boundary of each quadrat. Within the quadrats, every colony was identified to genus (*Acropora*', '*Pocillopora*', '*Porites*', 'other hard corals' and 'soft corals') and given a unique ID. Planar surface area was measured for *Acropora*, *Pocillopora* and *Porites* colonies, but only if the entire colony margin was inside the boundary. For colonies identified in 2015, a bleaching severity status was recorded in 2017 and mortality/survival in 2018 (Figure 3.2). Not all colonies were visible at all time points due to minor variations in transect position and changing benthic structures over time.

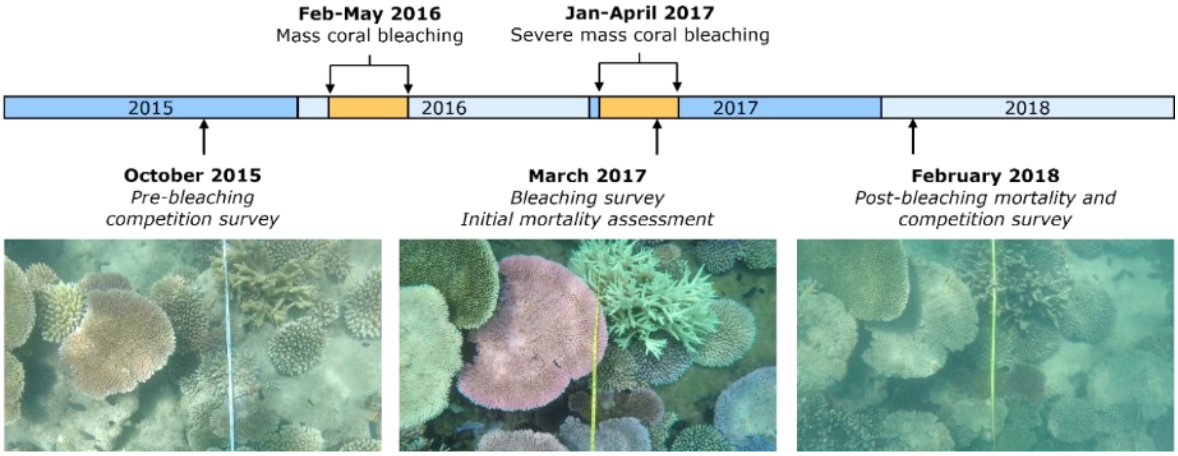

Figure 3.2. Timeline of surveys over the 2016 and 2017 mass bleaching events. Images show the same section of reef over time (NE Fantome) and correspond to the three surveys, before, during and after the bleaching events.

3.3.3 Competition

In 2015 and 2018, all competitive interactions occurring within the transect were identified. In this study, I used spatial proximity as a proxy for competition and defined competition as colonies whose margins were within 5 cm of each other (Lang and Chornesky, 1990; Van Veghel 1996; Hoogenboom et al. 2017). These interactions were classified into four categories: contact, close proximity, space, and overtopping. Contact competition was recorded when colonies were in physical contact with another and a physiological response to competition was almost certain. Competition at this proximity may result in digestion through mesenterial filaments or sweeper tentacles, overgrowth, or negative effects of mucus production (Lang and Chornesky, 1990; Connell, 2004; Elahi 2008). Close proximity competition was recorded when colony margins were ≤ 2 cm of each other. At this distance, corals might interact directly through mesenterial filaments or sweeper tentacles (Bak, 1982; Connell, 2004) but with the likelihood of physical damage diminishing significantly at distances greater than 2 cm (Genin and Karp, 1994). Space competition was recorded where colonies were between 2 and 5 cm apart. Although it has been shown that sweeper tentacles may exceed 5 cm length (Loya 2001), at this distance indirect competition for space (e.g., through resource shading) was presumed to be the dominant effect. Overtopping was recorded when one colony grew above another causing indirect competition for light. These categories were chosen to capture different competitive methods and intensities. While it was common to observe multiple categories of competition for each colony, only most intense form of competition was recorded (wherein contact > proximity > space > overtopping). Competitive interactions were not recorded in cases where colonies within 5 cm were separated by another colony (or part thereof) or by macroalgal stands; or when colonies occurred on different vertical planes separated by a more than 5 cm height (with the exception of overtopping interactions).

Two additional metrics were recorded to estimate competitive intensity. For each colony, the number of competitors within 5 cm of its margin were noted. Additionally, for *Acropora*, *Pocillopora* and *Porites* colonies, the proportion of the margin competing was also recorded. When multiple competing colonies occurred in an aggregation, interaction perimeters overlapped, so competition intensity was measured from only one competitor at any location along the colony margin. For analysis, colonies were grouped into four competitive intensity categories (Table 3.1) based on both the number of competing colonies and the proportion of the margin involved in competition. These two metrics were highly correlated (t=14.1, df = 445, $p < 0.01$) and therefore considered comparable. When both competitive metrics were recorded for a colony, the highest of the two competition ratings was assigned to reflect the maximum competitive stress.

Table 3.1. Competition intensity categories based on both percent of margin competing and the number of competitors. Competing margin was only measured for the three focal genera: Acropora, Pocillopora and Porites.

Competitive intensity	% margin *(Focal genera)*	Number of competitor colonies *(All genera)*
None	0 %	0
Low	1-24.9 %	1-2
Mid	25 – 49.9 %	3-4
High	≥ 50 %	≥ 5

3.3.4 Community changes

To put the changes in competition frequency and intensity into the context of changes to the reef over this time, I also assessed changes in colony abundance and coral cover resulting from the bleaching events (as per **Chapter 2**). Colony abundance was measured using the number of recorded colonies within each of the 5 m by 1 m quadrats. Coral cover was estimated using random point sampling within each quadrat boundary. Benthic cover was recorded at ~250 random points (~50 points per m^2) for each quadrat and categorized into '*Acropora*', '*Pocillopora*', '*Porites*', 'other hard corals' and 'soft corals', as well as macroalgae, turf algae, sand, rubble, and bare rock. The 'bare rock' category encompassed hard substrates without notable algae cover but was presumed to include epilithic algal matrix (EAM) and other benthic encrusting organisms.

3.3.5 Data processing and analysis

All analyses were completed using the statistical software R (version 4.3.0, The R Foundation for Statistical Computing) with model selection based on AICc (Akaike Information Criterion).

To address my first aim, I analysed how the presence and intensity of competition affected bleaching severity. Overall, a chi-square test was used to compare the proportion of bleached colonies between those with and without competition. To analyse the bleaching severity response, I used a multinomial logistic regression (package: 'nnet') because these data did not meet the proportional odds assumption for a cumulative ordinal logistic regression. This analysis allowed me to test for difference among competition categories. The analysis of bleaching severity against competitive intensity was analysed with the cumulative ordinal logistic regression (package: 'VGAM'), however, to meet the proportional odds assumption I combined the 'no competition' and 'low competition' categories which had statistically similar responses in terms of bleaching severity. I also used an ordinal logistic regression to test whether competition type affected bleaching severity. Although four competition types were recorded (contact, close proximity, space, and overtopping) for all competition type analyses, overtopping interactions were excluded due to the clear winner/loser outcomes depending on which colony was overtopping or being overtopped and the resulting small sample size when these competitive pairings were split by competitive outcome.

The second aim considered the impact of competition on mortality. I used three binomial logistic regression analyses (package: 'VGAM'), to test the effects of competition presence, intensity, and type, as well as the impact of bleaching severity, on the proportion of colonies which experienced mortality.

The final aim considered how bleaching events affect the frequency, intensity, and type of competition. To quantify changes in frequency, I first used binomial logistic regression to compare the proportion of competing versus non-competing colonies that bleached. I then compared the number of unique interactions per m^2 from before and after bleaching using a negative binomial generalised linear model (GLM; package: 'pscl'). To analyse changes in the intensity of competition I first used a zero-inflated GLM (package: 'pscl') to compare the number of competitors each colony had before and after the bleaching event. To account for the likelihood that colonies with larger perimeters would have more competitors ($R_{(718)} = 0.35$, $p < 0.01$) colony perimeter was included as an offset within the model. Therefore, only colonies where perimeter was measured (*Acropora, Pocillopora* and *Porites*) were included in the analysis (n=720). I then used a zero-one inflated beta regression (package: 'gamlss') to compare the proportion of the colony margin which was competing before and after bleaching. Colony perimeter was again included as a covariate to account for the impact of perimeter length on the intensity of competition. Finally, to assess changes in the type of competition I used a cumulative ordinal logistic regression to compare the proportion of interactions of each competition type from before and after bleaching. To specifically consider the impact of different types of competition, only colonies with a single competitive interaction were considered, with the exclusion of colonies with multiple interactions and/or competitive types. Coral cover was also included as a covariate- in all competitive analyses, to account for density dependent effects on competition.

3.4 Results

3.4.1 Coral abundance and cover, before and after bleaching

During the surveys, I identified a total of 2071 unique colonies, with 1289 colonies observed in 2015 before the consecutive 2016/2017 bleaching events and 728 colonies observed in 2018 after these events. Of the 1289 colonies I identified in 2015, 983 were re-identified in 2017 and assessed for bleaching, and 983 for survival or mortality in 2018, with a total of 791 colonies identified at all three time points. Overall, 73% of identified colonies bleached in 2017 and 55% suffered mortality by 2018. The average coral cover per quadrat declined 6.9% from 34.3 ± 1.8% before to 27.4 ± 2.0% (mean ± SE) after bleaching. Similarly, colony abundance per quadrat declined 39% from 99 ± 9 to 60 ± 3% (mean ± SE).

3.4.2 The effect of competition on bleaching

Overall, the presence of competition did not affect whether a colony bleached or not (*Chisq* =1.07, df = 1, p = 0.99). However, competition did have a significant effect on the severity of bleaching (*Chisq* =7.6, df = 2, p =0.02). In both competing and non-competing colonies, 73% of colonies bleached (Figure 3.3a), however, colonies experiencing competition had a significantly higher frequency of severe bleaching (53% colonies) than those with no competition (43% colonies). Furthermore, the intensity of competition based on the number of competitors and/or the proportion of the colony margin experiencing competition, also had a significant effect on bleaching severity (*Chisq* =116.3, df = 4, p <0.01; Figure 3.3b). Colonies in the no/low competition category had a lower prevalence of bleaching (64% colonies bleached) and had less severe bleaching (42% colonies) than the mid (78% colonies bleached, 56% severely) and high (86% colonies bleached, 64% severely) competition categories. In contrast, the proportion of colonies that experienced mild bleaching was consistent between the three competition intensity categories (22%, 22% and 21% for none/low, mid, and high respectively).

Bleaching severity also varied significantly with the type of competition (*Chisq* =18.3, df = 4, p <0.001). In general colonies of *Acropora*, ‘other hard coral’ and ‘soft coral’ with contact competition were most likely to severely bleach (68% colonies) while colonies within close proximity to another, and at a greater distance (space competition), had lower rates of severe bleaching (52% and 46% colonies respectively; Figure 3.3c). However, these trends did not hold for *Pocillopora*, where 100% of colonies suffered severe bleaching, and for *Porites*, where 91% of colonies did not bleach. It is worth noting that these two genera had relatively small sample sizes (8 *Pocillopora* colonies and 11 *Porites* colonies). Although this analysis did show that bleaching severity varied significantly between the genera (*Chisq* =89.6, df = 8, p <0.001), these opposing trends in *Pocillopora* and *Porites* did not result in a significant interaction between competition type and genera.

3.4.3 The effect of competition on mortality

Overall, 55% of the colonies identified in 2015 died after the culmination of bleaching events in 2016 and 2017. The likelihood of colony mortality was significantly affected by the presence of competition (Chisq = 7.21, df = 2, p<0.01), with higher mortality rates in colonies experiencing competition (57 %) than those without competition (42 %; Figure 3.4a). Furthermore, presence of competition increased background mortality in corals with no bleaching, from 4 % to 16 %. The intensity of competition also had a significant effect on the likelihood of mortality (Chisq = 56.71, df = 3, p <0.01; Figure 3.4b). While mortality rates were similar between corals with no competition (42%) and those with low competition (40%), those with mid or high competitive intensity had higher rates of mortality (57% and 75% respectively), with this difference statistically significant for colonies experiencing high competition p <0.001). In contrast, the type of competition had no significant effect on the rates of mortality (Chisq = 0.34, df = 2, p =0.84; Figure 3.4c). The mean mortality rate for corals with contact competition, presumed to represent the greatest intensity of competitive stress, was 36%, compared to 33% in proximity competition and 31% with space competition. Bleaching severity also had a significant effect on mortality in all analyses, (Chisq = 263.14, df = 2, p<0.01) with colonies that experienced severe bleaching being significantly more likely to suffer mortality (73% colonies) than those with mild (31%) or no bleaching (14%). Furthermore, the combined effects of bleaching and competition resulted in additive increases in mortality (Figure 3.4b). In the absence of bleaching, 44% of competing colonies died, compared to only 4% of colonies which were not competing (40% increase). For colonies with mild bleaching, there was a comparable increase in mortality of 36% (from 17% in non-competing to 53% in competing) due to the combination of stressors. However, for colonies with severe bleaching, there was a smaller additional increase in mortality from the combination of stressors (increased by 19%, from 64 to 83%; Figure 3.4b).

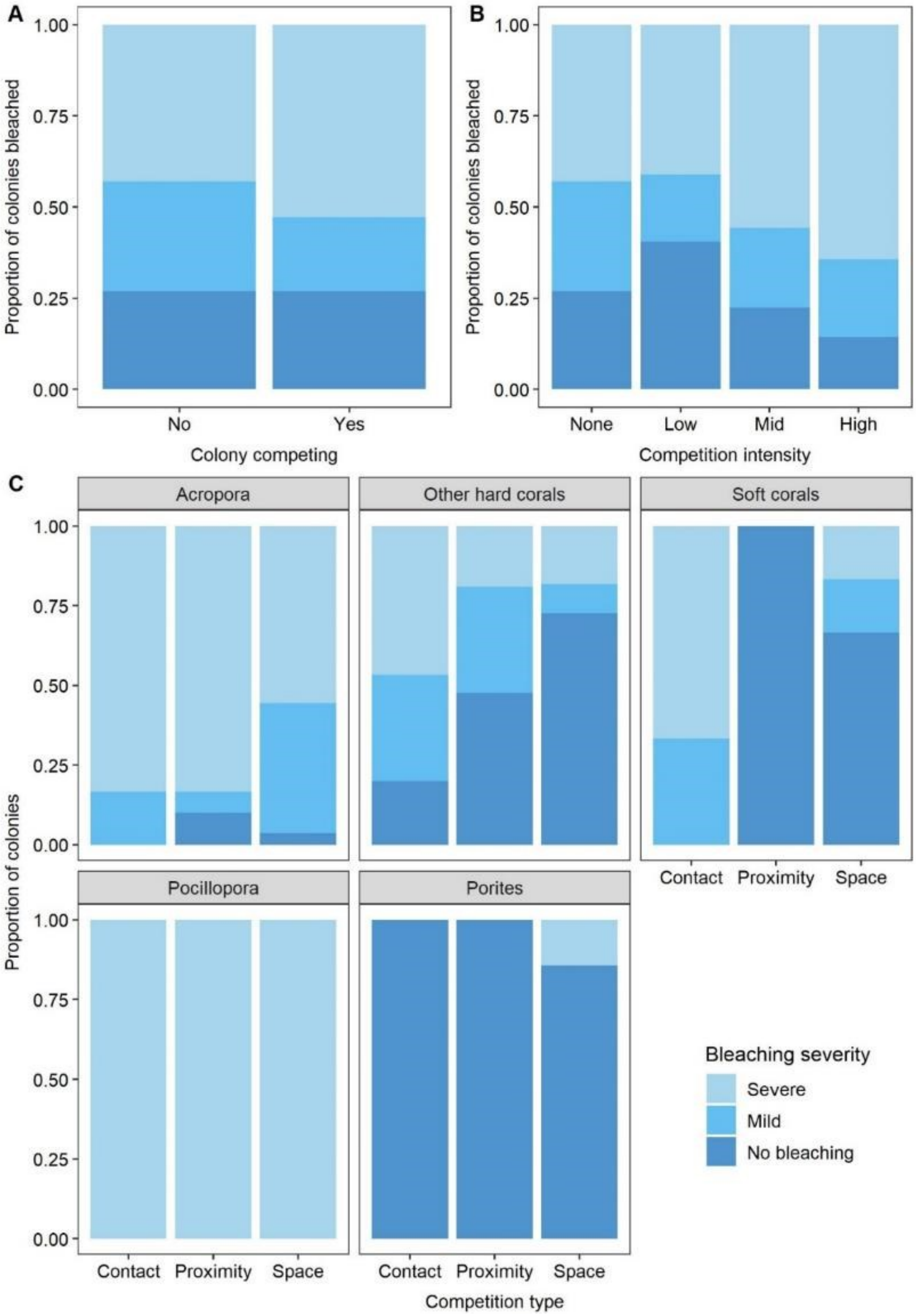

*Figure 3.3. The proportion of colonies in three levels of bleaching severity in relation to; A) presence of competition, n=983 colonies; B) intensity of competition, n=983 colonies; C) competition type (distance), n=163 unique interactions between pairs of colonies, each with a single competitive interaction (*Acropora*-75; other hard corals – 58; soft corals – 11;* Pocillopora *- 8;* Porites *– 11).*

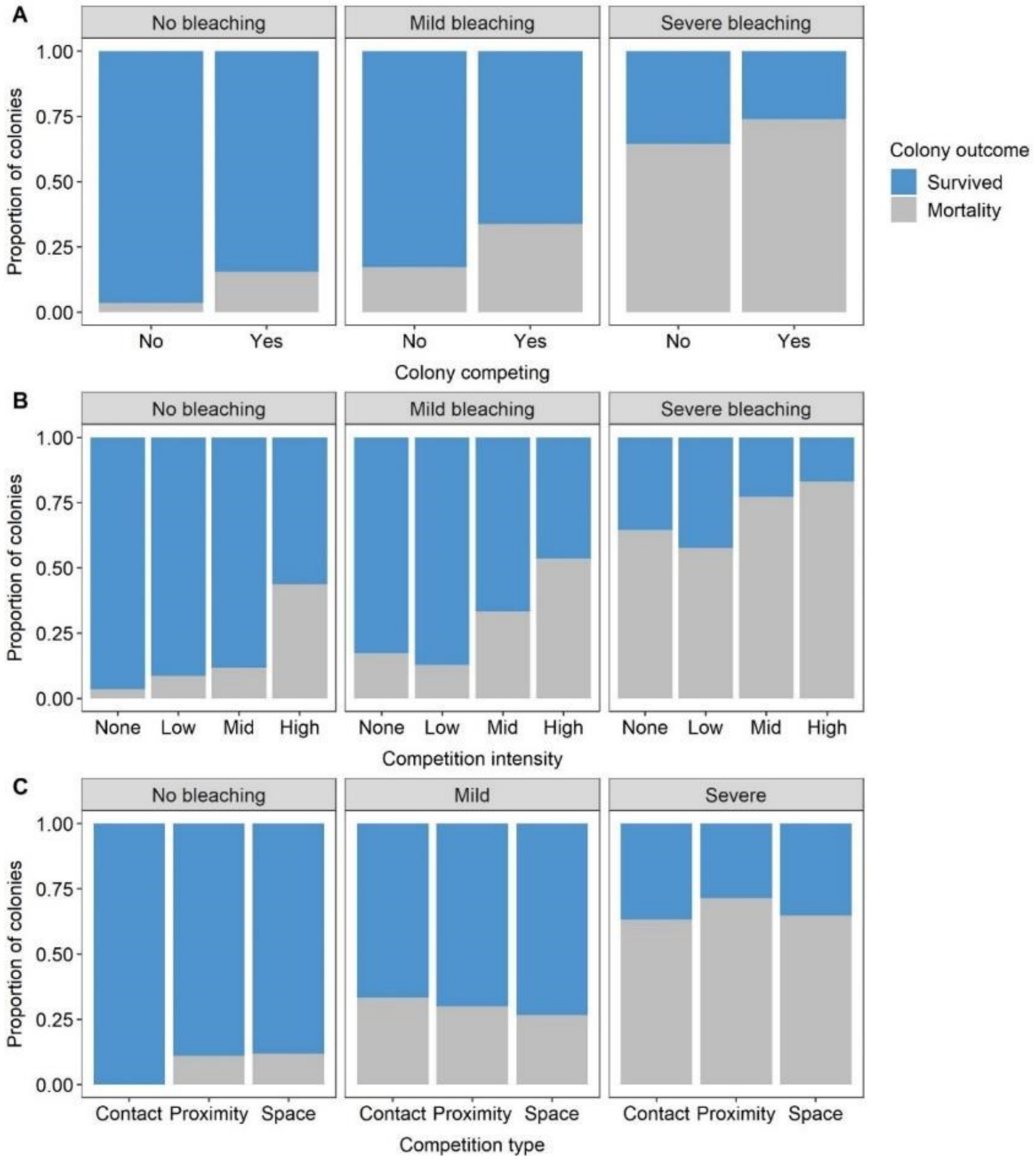

Figure 3.4. The survival or mortality of colonies in 2018 within three bleaching severity categories, by A) the proportion of colonies competing, n= 791 colonies; B) the competitive intensity, n = 791 colonies, and C) the type (distance) of competition, n = 165 unique interactions, each from colonies with a single competitive interaction.

3.4.4 Changes in competition following bleaching

3.4.4.1 Frequency of competition

The back-to-back bleaching events of 2016 and 2017 resulted in a significant decrease in the proportion of colonies that experienced competition (Year effect: *Chisq* =5.17, df = 1, p =0.02; Figure 3.5a). Prior to the 2016-2017 bleaching events, 84 % of colonies were competing but, after bleaching, this declined significantly to 66 %. Colony size also had a significant effect on the proportion of colonies competing, with larger colonies significantly more likely to be competing than smaller colonies (mean colony size of competing corals 247 ± 17.2 cm^2; mean colony size of those which were not competing, 102 ± 16.8 cm^2; size effect: *Chisq* =16.69, df = 1, p <0.01). There was also significant variation in competition rates between sites, with NE Fantome having significantly higher rates of competition (88%) than SE Pelorus (69%; Site effect: *Chisq* =8.94, df = 2, p =0.01; Figure 3.5a). Although there was no significant interaction between site and year, the decline in the proportion of colonies competing from before and after bleaching was lower at NE Fantome (10% fewer colonies competing after bleaching) than at E Orpheus and SE Pelorus (21% and 20% respectively). Finally, pre-bleaching coral cover also had a significant effect on the proportion of colonies competing, with higher coral cover resulting in greater proportion of colonies competing (Coral cover effect: *Chisq* =22.29, df = 1, p <0.001). There was however an interactive effect between site and pre-bleaching coral cover (*Chisq* =7.4, df = 2, p =0.02), with greater effects at E Orpheus than the other sites. At E Orpheus, the mean coral cover of competing corals was 8% higher than non-competing corals, while this difference was much lower at SE Pelorus and NE Fantome (2% and 1% respectively).

In addition to fewer colonies competing, there was also a significant change in the number of interactions before and after bleaching. In total, there were 1699 competitive interactions identified in this study, of which 1237 were recorded in 2015 while only 462 interactions were recorded in 2018. The mean number of interactions decreased significantly between years from 19.0 ± 3.0 interactions per m^2 before bleaching to 7.1 ± 0.8 after bleaching (63% decrease; *Chisq* = 22.36, df = 1, p <0.01; Figure 3.5b). Coral cover also had a significant effect on the number of interactions per m^2 (*Chisq* = 19, df = 1, p <0.01) with greater coral cover resulting in more interactions. A correlation test shows variations in coral cover explained 62% of the variation in number of interactions. There was no significant difference in number of interactions between sites, so this factor was removed in a stepwise regression to achieve the more parsimonious model.

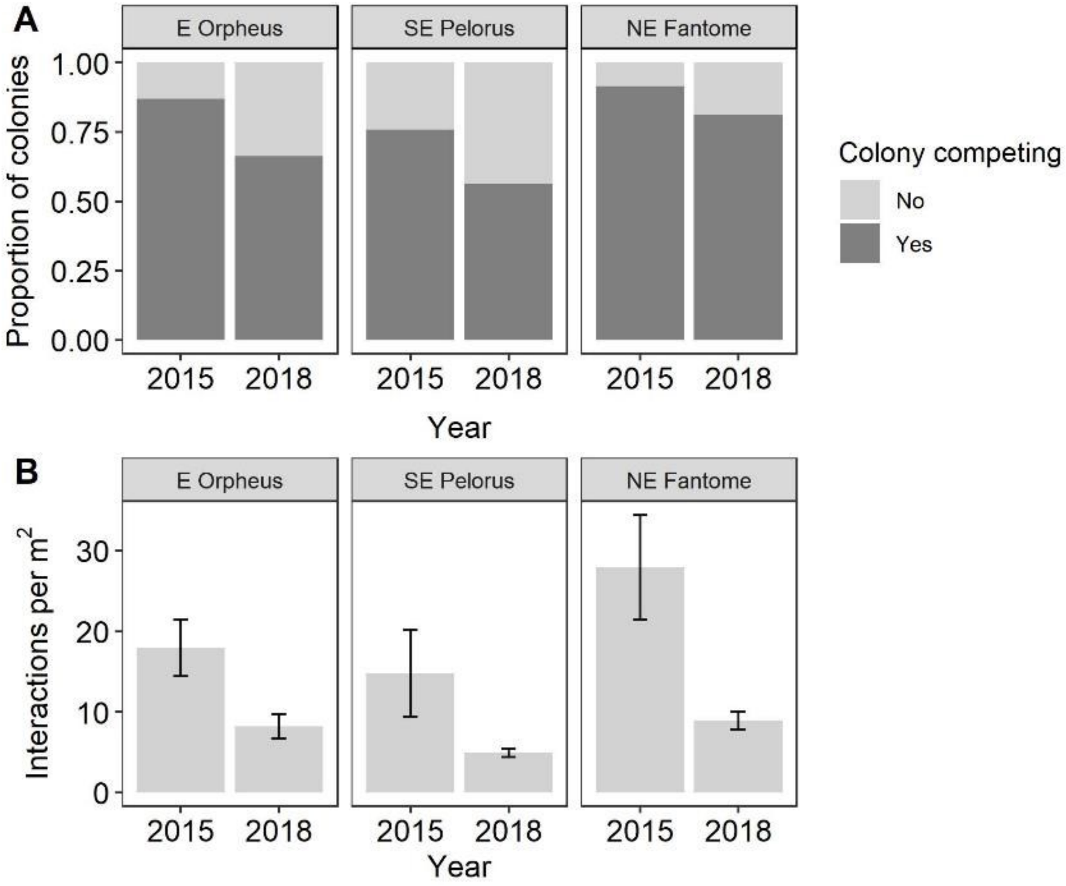

Figure 3.5. The frequency of competition before (2015) and after (2018) bleaching shown through A) the proportion of colonies competing and B) the mean number of interactions per m^2 *of quadrat ± SE. n = 2,071 interactions between pairs of colonies.*

3.4.4.2 Competitive intensity

The bleaching events of 2016/2017 resulted in a significant change in competitive intensity, both in terms of the number of competitors and the proportion of the margin that was competing. Firstly, the number of competitors declined significantly following bleaching from an average of 1.9 ± 0.1 per colony to 1.1 ± 0.1 (*Chisq* = 102.5, df = 1, p < 0.01; Figure 3.6a). There was also a significant difference in the number of competitors between sites (*Chisq* = 18.3, df = 2, p < 0.01), with significantly more competitors at SE Pelorus (2.4 ± 0.1 per colony) than at E Orpheus and NE Fantome (1.8 ± 0.1 and 1.4 ± 0.1, respectively). Coral cover also resulted in significant variations in the number of competitors (*Chisq* = 56.5, df = 1, p < 0.01), with greater coral cover resulting in a greater number of competitors. However, there was a significant interaction between coral cover with both year (*Chisq* = 5.99, df = 1, p =0.01) and site (*Chisq* = 11.9, df = 2, p < 0.01). Second, I found the proportion of the margin competing decreased significantly following bleaching (t=-4.78, df(fit)=24). Prior to bleaching, the mean proportion of the margin experiencing competition was 46 ± 1% (mean ± SE), which decreased to 31 ± 2% (mean ± SE) in 2018 following the bleaching events (Figure 3.6b). This pattern was similar for all sites, however the degree of decline varied. At E Orpheus, the decrease in mean proportion of the margin competing declined 21% (from 43 ± 2 to 22 ± 3%), while at NE Fantome, there was only a 10% decrease in competing margin (from 58 ± 2 to 48 ± 3%). However, the differences among sites were not the same across all years (interactive year*site effect: t=0.01) potentially reflecting variations in the changes of coral cover, and competitive interactions, from before and after bleaching (**Chapter 2**). Overall, the mean proportion of the perimeter competing was far greater at NE Fantome (56 ± 1%) than both other sites (E Orpheus, 37 ± 2%; SE Pelorus, 35 ± 2%).

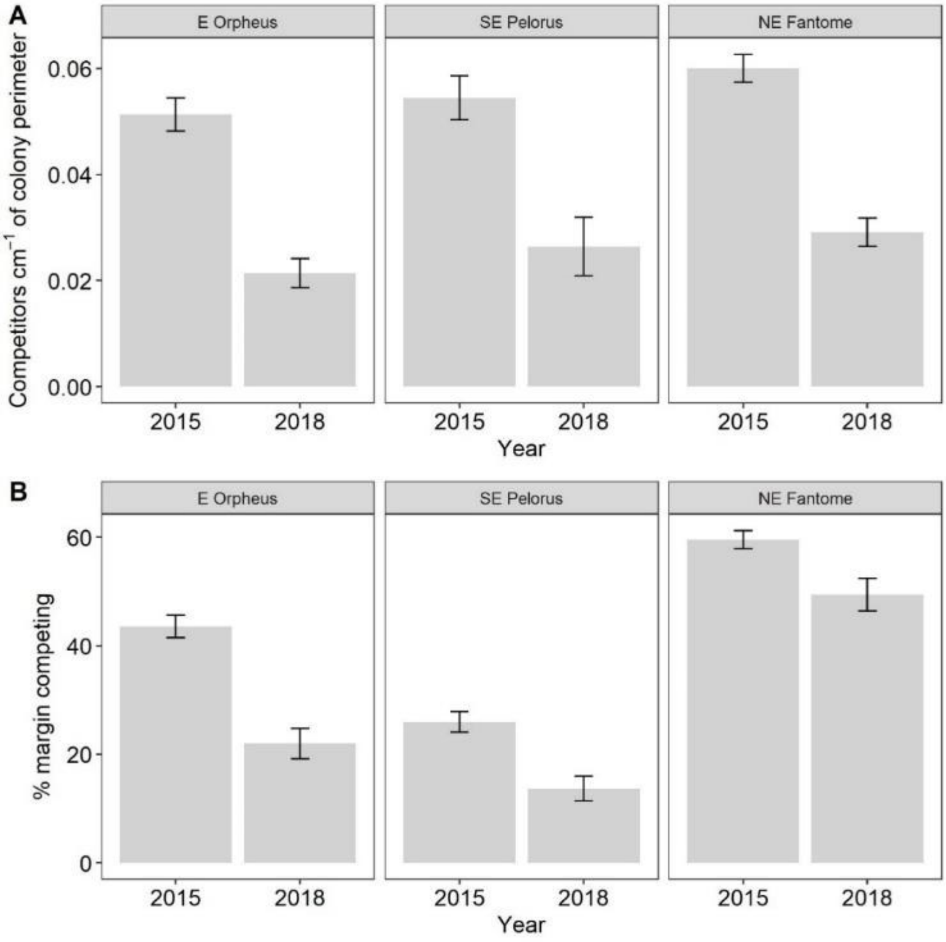

*Figure 3.6. The intensity of competition at each site from before (2015) and after (2018) bleaching, quantified through A) the number of competitors per cm^2 colony area. Competitors was standardized to colony area to account for the likelihood that larger colonies would have more competitors; B) the percent of colony margin competing. n = 720 colonies (*Acropora, Pocillopora *and* Porites *only)*

3.4.4.3 Type of competition

The prevalence of each type of competitive interaction varied significantly from before to after the bleaching event (*Chisq* = 11.72, df = 1, p <0.01; Figure 3.7). Overall, competitive interactions became less intense (i.e., colonies were further apart) after bleaching with a slight decline in the proportion of direct contact interactions from 19 to 16% and an increase in the proportion of space competition from 29 to 33%. This was most prominent at SE Pelorus which had a 13% increase in space competition (Figure 3.7). In contrast, NE Fantome showed the opposite trend with direct contact interactions becoming more frequent after bleaching (13% to 20% of interactions) and space interactions becoming less frequent (30 to 19% of interactions). This variation in response resulted in a significant difference between sites (*Chisq* = 93.26, df = 2, p <0.01), specifically between SE Pelorus and NE Fantome. Overall and individually at each site, the proportion of close proximity interactions remained consistent from before and after bleaching, with the greatest change between years being a 3 % increase after bleaching at E Orpheus.

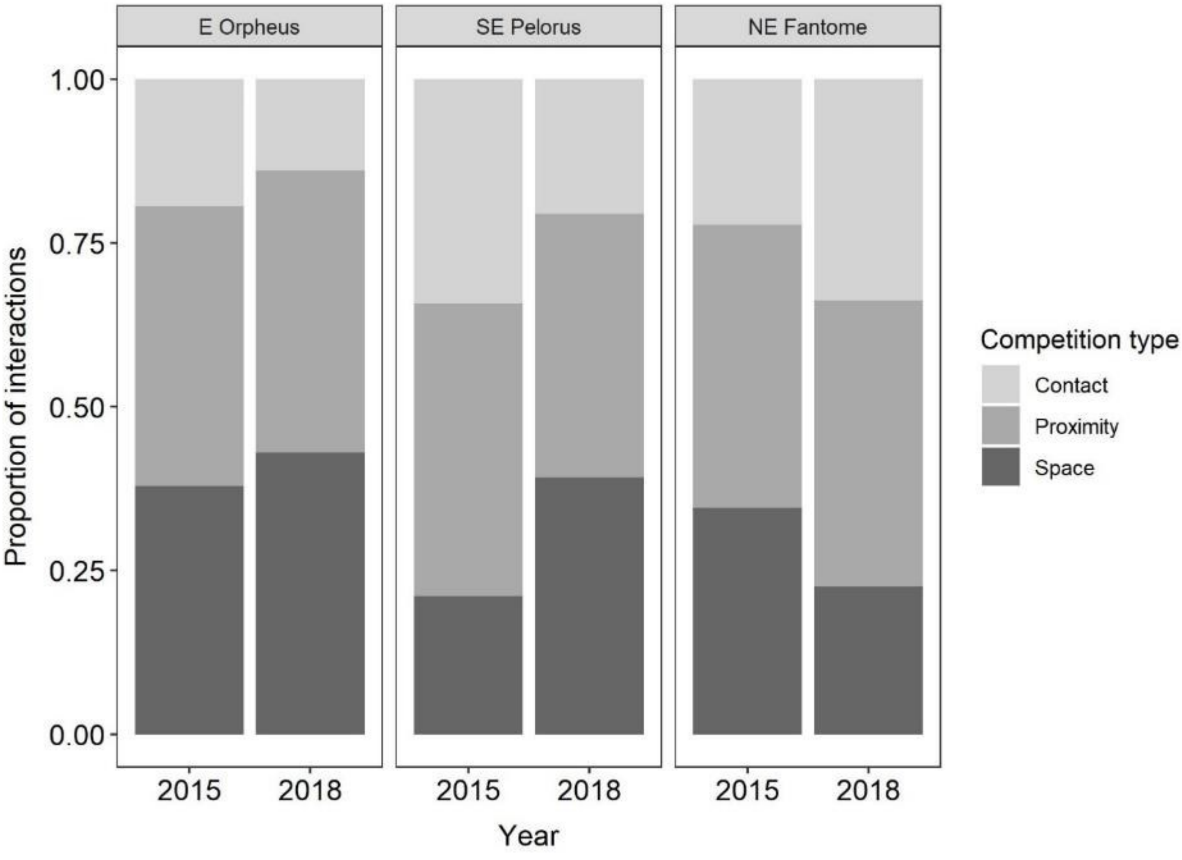

Figure 3.7. The proportion of competitive interactions at each site, of three types (distance) of competition from before (2015) and after (2018) bleaching. n = 1801 unique interactions between pairs of colonies.

3.5 Discussion

The direct effects of marine heatwaves on coral reef communities are well established. However, to date there has been very little consideration of how biotic interactions can shape coral resistance to, and recovery from, bleaching events. This study is the first to consider the bidirectional effects of competition and bleaching on coral communities. In this study I show that the presence of coral-coral competition affected both the severity of coral bleaching and the subsequent likelihood of mortality during the 2016/2017 back-to-back bleaching event on the GBR. Furthermore, I also show that following these bleaching events, there was a reduced level of competition in the first year of recovery. These findings highlight the importance of considering the indirect effects of climate change on corals and demonstrate the complexity in coral responses to multiple stressors.

In this study I showed that coral-coral competition had a significant effect on the severity of bleaching with more intense competition associated with more severe bleaching. I also showed that direct contact competition was more likely to be associated with severe bleaching compared to proximity competition. Finally, competition increased mortality rates, regardless of whether, or how severely, the colonies bleached. Under ambient conditions, competition is energetically costly, reducing the available energy for other biological processes like reproduction and growth (Rinkevich & Loya, 1985; Romano, 1990; Tanner, 1997). Therefore, this study indicates that chronic stress linked to competition can reduce bleaching resistance and increase mortality in some coral species. Conversely, it has also been shown that under environmental stress (combined ocean warming and acidification), corals are less resistant to the effects of competition (Johnston et al., 2020). The combination of temperature and competitive stressors may therefore require either division of limited resources between the stressors, or allocation to a single stressor with consequent increases in vulnerability to the other. While additional research would develop our understanding of resource allocation under multiple stressors, I present clear evidence that competition contributed to the bleaching and subsequent mortality response in coral communities.

To the best of my knowledge, there has been only one other *in situ* study which has considered the impact of competition on coral bleaching. In contrast to my results, this study found that competition had no significant effect on bleaching severity (Hoogenboom et al., 2017). While there were some methodological differences in quantifying competition between our studies, I believe that the primary reason for this contrast is that Hoogenboom et al. (2017) focused on bleaching in *Acropora* colonies only, while this study included all colonies within the transects. *Acropora* are known to be particularly vulnerable to bleaching (Loya et al., 2001; Marshall & Baird, 2000) and it is possible that their susceptibility overrode any minor impacts of competitive stress. Additional interrogation of my data to consider only *Acropora* colonies similarly showed very little difference in bleaching levels resulting from competition (Figure 3; Figure A3.1). While *in situ* evidence of the effect of competition on coral bleaching is limited, evidence of competition altering the response of coral colonies to other environmental stressors, have previously been found. For example, the effect of ocean acidification on coral calcification and growth was exacerbated in corals that also experienced competition (Evensen & Edmunds, 2016; Evensen et al., 2015; Horwitz et al., 2017).

Overall, the evidence presented here suggests that competition exacerbates the impact of thermal stress in terms of both bleaching and mortality. For example, while previous studies have generally found that competition in corals has sublethal effects (Romano, 1990; Tanner, 1997), in this study competition increased mortality rates compared to corals which were not competing. This disparity may result simply from the severity of the 2016/2017 bleaching events and cumulative impacts of back-to-back stressors which can reduced colony resilience (Hughes et al., 2019; Pratchett et al., 2020). In addition, this disparity may in part arise from corals experiencing physiological effects and partial mortality from thermal stress events, even when no visible signs of bleaching are apparent (Hoogenboom et al., 2011; Matsuda et al., 2020). Alternatively, it may indicate that thermal stress heightens the impact of high intensity competition. When multiple stressors occur, the combination of stressors can result in additive, antagonistic or synergistic effects (Côté et al., 2016). The data I present here largely seem to evidence additive effects of the two stressors, which is thought to be the most common type of interaction on coral reefs (Ban et al., 2014). For example, as bleaching severity increased, there was a reduction in the difference in mortality rates between colonies with bleaching as a single stressor, and colonies with the multiple stressors of bleaching and competition. This may indicate that as coral bleaching becomes more severe, any differences in colony tolerance to competition are overshadowed by thermal stress. A similar finding was found for growth in competing corals under ocean acidification. Where coral growth was already suppressed by interspecific competition, there was no additional suppressive effect of acidification (Evensen et al., 2015; Horwitz et al., 2017). While the lack of evidence of synergistic effects benefits corals, the combined effect of multiple stressors varies based on the species involved and the stressors at play (Ellis et al., 2019). This variability in response means that the combined effect of competition and thermal stress cannot be confidently extrapolated from the individual impacts of each stressor. This highlights the importance of multiple stressor research in our ability to predict the effects of climate change on our reefs.

For both bleaching and mortality there was a non-significant but consistent trend for corals with low competition to suffer less bleaching and mortality than those without competition. Competition is a chronic stressor for corals (Pisapia et al., 2014) and this result is therefore unexpected. In general, physiological stress can weaken an individual's response to other stressors, in this case potentially making corals more vulnerable to bleaching. However, environmental stress can also trigger a cellular or immune response in corals (Bellantuono et al., 2012). For example, it has been shown that colonies that were thermally resistant or had thermal pre-conditioning, experienced a 'frontloading' of genetic/immune response which increased resistance to subsequent thermal stress (Barshis et al., 2013; Bellantuono et al., 2012). It is possible that there is a similar immune 'activation' from low competitive stress seen here, which subsequently allows corals to perform better with exposure to thermal stress. However, as competitive intensity increases, this appears to overwhelm the initial immune response, increasing the bleaching severity and mortality rate. While this study investigates the ecological effects of competition, physiological and genetic responses are often what determines an individual's response to stress (Andrade Rodriguez et al., 2021) and future studies might focus on such genetic responses under multiple stressors.

In addition to understanding the effect of competition on bleaching, I also investigated how bleaching subsequently affected competition. High mortality rates meant that the coral communities in 2018 were substantially depleted compared to the pre-bleaching communities in 2015. This resulted in competition becoming less frequent, less intense and occurring at greater distances (i.e., more 'space' competition), likely as a result of fewer coral colonies and lower coral cover and therefore less resource limitation. For surviving corals, this decrease may represent a release from competitive stress. In corals, where competition is rarely lethal (Romano, 1990; Tanner, 1997), this competitive release is likely to manifest in terms of competition having less of an impact on community structure. Therefore, where coral cover is declining as a result of ocean warming and other stressors (AIMS, 2019; Bruno & Selig, 2007; De'Ath et al., 2012; Sweatman et al., 2011), as well as increasing frequency of disturbances and decreasing recovery windows (Hughes et al., 2018), my results suggest that competition becomes less important for coral communities in the future. This finding supports a recent modelling study that showed that as ocean warming continues and bleaching becomes more prevalent, thermal tolerance and to a lesser extent, colony growth rate, will become increasingly important traits for survival and continued existence, with competitive abilities becoming less critical (Kubicek et al., 2019). This change may already be occurring with competition thought to be less prevalent (Johnston et al., 2020) and playing less of a role in structuring reefs than previously thought (Álvarez-Noriega et al., 2018). In this study, coral cover was consistently a significant predictor of the frequency and intensity of competition, however competition has also been shown to occur even when space is not limiting as a result of clustering (Genin et al., 1994). Therefore, any decline in the impact of competition on community structure could be negated if there is high clustering of colonies.

The last survey of these corals was conducted one year after bleaching, and therefore the observed changes in competition are limited to the initial year of recovery. Corals are dynamic ecosystems with frequent disturbances followed by subsequent recovery (Adjeroud et al., 2009; Graham et al., 2011; Torda et al., 2018). Competitive release is therefore likely to be a natural part of the recovery process where the loss of corals creates greater space between colonies. However, continued decline in coral cover was not seen at all sites. At NE Fantome, despite very high mortality, rapid growth of surviving colonies resulted in increased coral cover and only small declines in competitive frequency and intensity, one year after bleaching. Over a longer study duration and in the absence of additional disturbance events, it is plausible that both coral cover and competition may have returned to pre-bleaching levels. Therefore, in reefs where coral cover returns to pre-disturbance levels, the importance of competition may well also recover. Furthermore, the decline in competition (18%) is not equal to the loss of colonies due to mortality (55%). This suggests that most colonies will still experience some competitive stress. This unique dataset which tracked individual colonies from before, during and after the bleaching event meant that our understanding of how competition changes over time could be developed. However, to establish whether this decrease in competitive stress is temporary or part of the ongoing global trend of coral reef decline, longer-term surveys are required following longer recovery periods.

In ecology, definitive evidence of competition is hard to show (Chornesky, 1989; Cornell & Karlson, 2000; Pianka, 2011). In this study, I use distance between colonies as a proxy to infer competition. While this method is common (Connell et al., 2004; Dai, 1990; Hoogenboom et al., 2017) and is likely to be a reasonable assumption, proximity does not always result in competition. Corals may maintain an 'aura' of unoccupied space around themselves which is determined by the interactive reach of their competitive mechanisms (Sheppard, 1985). Therefore, colonies which are greater than 5cm apart may still be competing, in that their growth is restricted by the interactive reach of neighbours.

Subsequent work should therefore include physical evidence of a competitive interaction, such as signs of digestion or injury (Álvarez-Noriega et al., 2018), which would ensure that only active competitive interactions are considered. I also recognise that variations in colony species and morphology may have influenced the measurements of competitive intensity. For example, branching colonies, particularly *Acropora* colonies, have a higher perimeter to surface area ratio than massive or mound shapes colonies. Variations in this ratio with consideration to space-filling capabilities can affect competitive outcomes (George et al., 2021). Further work should therefore consider the ratio between perimeter and surface area to better estimate competitive intensity. The evidence presented here indicate that species specific differences in bleaching susceptibility, mortality and competitive resilience may be interacting. However, these effects are not possible to extract from the genera-level data and future work should consider greater resolution in species ID. Finally, underwater photogrammetry is becoming increasingly employed and allowed us to survey large areas over long time periods and at high resolution. To strengthen these findings, additional *in situ* data collection could provide more detail on competitive interactions, such as capturing outcomes, and competitive interactions that are not visible from above.

The importance of the indirect effects of climate change is increasingly being recognised (Cahill et al., 2013; Hill & Hoogenboom, 2022; Jordano, 2016). My results indicate that reefs with high coral cover or dense colony aggregations, are more likely to suffer severe bleaching and higher subsequent mortality as a result of increased competition, as well as potentially benefit from greater competitive release during recovery. However, by their very nature, indirect effects are highly complex and hard to investigate (Jordano, 2016). For example, occurring within an aggregation where competition is high, can stimulate rapid colony growth (Idjadi & Karlson, 2007; Raymundo, 2001), alter competitive outcomes depending on the species diversity of the aggregation (Hart & Marshall, 2009), or, in contrast to the results seen here, decrease light stress and bleaching (in comparison to being surrounded by sand; Ortiz et al., 2009). Elucidating the true effect of competition amid other environmental influences is highly challenging. Moreover, the impact is likely to vary between colonies, aggregations and sites depending on abundance, morphologies, diversity, and the intensity of interactions. Despite this, my study demonstrates that indirect effects of ocean warming, such as altered competitive interactions, should be accounted for when attempting to scale up individual level bleaching effects to community levels.

3.6 Conclusions

Competition it is an inherent part of all ecosystems, affecting abundance and species diversity, encouraging growth, and creating space for recruitment. Changes in the prevalence and impacts of competition could therefore compound the direct effects of ocean warming and climate change on coral reefs. This study is the first to report on the combined effects of chronic competitive stress and acute bleaching stress in corals, *in situ* and for a variety of genera. The evidence presented here shows that competition can exacerbate the impacts of thermal stress on corals. While the impacts of competition are on a smaller magnitude than the species-specific susceptibilities to bleaching, and of bleaching severity on mortality, competition may contribute to the fine-scale nuances in bleaching responses between colonies. Understanding these indirect effects may help to explain why comparable colonies have variable outcomes under ocean warming and is therefore critical in our ability to scale up findings of bleaching studies to an ecosystem level. Furthermore, I show that during recovery or when coral cover does not return to pre-disturbance levels, competition may become a less dominant structuring force. Collectively, these results highlight the importance of considering the combined effect of acute and chronic stressors for understanding the dynamics of coral communities.

Chapter 4 : The indirect effects of ocean acidification on corals and coral communities

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4.1 Abstract

Ocean acidification (OA) is a major threat to marine calcifying organisms. This manuscript gives an overview of the physiological effects of acidification on reef-building corals from a cellular to population scale. In addition, I present the first review of the indirect effects resulting from altered species interactions. I find that the direct effects of acidification are more consistently negative at larger spatial scales, suggesting an accumulation of sub-lethal physiological effects can result in notable changes at a population and an ecosystem level. I identify that the indirect effects of acidification also have the potential to contribute to declines in coral cover under future acidified conditions. Of particular concern for reef persistence are declines in the abundance of crustose coralline algae (CCA) which can result in loss of stable substrate and settlement cues for corals, potentially compounding the direct negative effects on coral recruitment rates. In addition, an increase in the abundance of bioeroders and bioerosive capacity may compound declines in calcification and result in a shift towards net dissolution. There are significant knowledge gaps around many indirect effects, including changes in herbivory and associated coral-macroalgal interactions, and changes in habitat provision of corals to fishes, invertebrates and plankton and the impact of changes to these interactions for both individual corals and reef biodiversity as structural complexity declines. This research highlights the potential of indirect effects to contribute to alterations in reef ecosystem functions and processes. Such knowledge will be critical for scaling-up the impacts of OA from individual corals to reef ecosystems, and for understanding the effects of OA on reef-dependent human societies.

Keywords:
Coral; Carbon dioxide; Indirect effects; Biotic interactions; Ecosystem; Review

4.2 Introduction

Species interactions occur in every ecosystem and can be pivotal in ecosystem functioning and services (Jordano, 2016). Nevertheless, much of the research that identifies how environmental change affects biological communities is based on the direct physiological and behavioural changes of individuals. While understanding the effects on individuals is important, biological communities can also be indirectly affected by environmental change. This occurs when direct effects on one or more species alter the extent or outcome of interactions between species. Such indirect effects, which affect both individuals and ecosystem functions and processes, can manifest over a far greater scale than that of direct effects (e.g., Alva-Basurto & Arias-González, 2014; Connell et al., 2013) with small changes to an interaction resulting in substantial impacts (Mumby, 2017). Furthermore, ecological interactions can be more vulnerable to environmental change than the biology of individuals (Jordano, 2016). For instance, a recent review of extinctions as a result of climate change concluded that nearly 60% of both extinctions and declines in abundance were the result of a lost interaction rather than physiological tolerances of individuals being surpassed (Cahill et al., 2013). Consequently, understanding how ecosystems are likely to change under future climate scenarios requires understanding alterations in the extent and outcome of ecological interactions.

Ocean acidification (OA) is one component of the ongoing global environmental change resulting from increases in atmospheric carbon dioxide concentrations (Gattuso et al. 2015). These increases are buffered by oceanic absorption of carbon dioxide which result in decreasing oceanic pH (IPCC, 2014; Zeebe, 2012). This uptake of atmospheric carbon dioxide has already caused a 0.1 unit decline in oceanic pH since the industrial revolution and is likely to cause up to an additional 0.3-0.32 unit decline by the end of the century (Gattuso et al., 2015; IPCC, 2014). Changes in pH also result in a change in the concentrations of carbonate and bicarbonate ions in seawater which can affect fundamental organism physiology, such as calcification (Erez et al., 2011). As a result, OA is widely recognised to be a pervasive threat to marine biodiversity (Garrard et al., 2013; Harvey et al., 2013).

While the effects of OA are ubiquitous, they are of particular concern for calcifying organisms such as Scleractinian corals, which use carbonate ions to build their skeleton (Hofmann et al., 2010). This potential for OA to reduce calcification in corals has identified coral reefs as one of the most vulnerable ecosystems to OA (National Research Council 2010). The change in calcification and a suite of other physiological effects on corals, have the potential to result in indirect effects through altered interactions with other reef organisms. This paper provides a short overview of the direct physiological effects alongside a detailed review of the indirect effects of OA on shallow water tropical and temperate corals, to gain new insights about how corals and coral communities may be affected under future acidified conditions. Specifically, I: 1) reviewed the direct, physiological effects of OA on reef building corals across different levels of biological organisation; 2) identified the indirect effects of OA through changes to ecological interactions and provided evidence of how these manifested at an ecosystem level; 3) identified priority areas for future research on indirect effects. While I acknowledge the importance of symbionts and microbial communities in influencing coral responses to environmental change, this review focuses on the responses of, and impacts on, the coral host.

4.3 Methods

I completed a literature search on ISI Web of Science for studies that identified the direct and indirect effects of ocean acidification on corals (completed October 2021). I focused primarily on tropical shallow water corals with some temperate corals included to capture research from naturally acidified field sites in temperate regions. Deep water corals were excluded from this review on the basis that other variables such as temperature and light that also change with depth would confound comparisons of OA effects.

To review the literature on the physiological effects of acidification on corals, papers were selected using search terms for ocean acidification (‘ocean acidification’, ‘$p\mathrm{CO}_2$’ (the partial pressure of CO_2), ‘pH’, ‘carbon dioxide’), ‘coral’ and a direct, physiological metric. These metrics were the eight broad headings presented here (Figure 4.1): ‘tissue biomass’ OR ‘lipid’ OR ‘protein’; ‘calcification’; ‘photosynthesis’; ‘survival’ OR ‘mortality’; ‘growth’ OR ‘skeletal density’ OR ‘porosity’; ‘reproduction’; ‘abundance’; and ‘species richness’ OR ‘species diversity’ OR ‘community composition’. Where possible, all relevant studies found in the search were included with the exception of calcification and photosynthesis due to the vast body of literature on these metrics which have already been the subject of several reviews and meta-analyses (e.g., Erez et al., 2011; Kornder et al., 2018). Therefore, for these metrics, I focused on papers published in the last 10 years. To ensure there was no bias in the data from this particular selection of publications, additional observations of calcification under OA were recorded from studies focusing on another metric where calcification was also measured. Observations were excluded if they considered variations in other environmental variables (e.g., temperature, nutrients, light), although, where possible I included comparisons between ‘ambient’ / ‘control’ conditions with the acidified treatment/s.

For every study selected, the statistical outcomes of comparisons between acidification treatments for each metric, were recorded as ‘significant increase’, ‘significant decrease’, or ‘no significant change’. Effects which were not statistically analysed were excluded. Many studies used $p\mathrm{CO}_2$ treatments or field sites with acidification levels well beyond that expected in the near future (i.e., up to 5000 µatm). To ensure the trends in significance were not driven by these extreme conditions I compared the full dataset to two subsets of the data where I excluded observations involving $p\mathrm{CO}_2$ 1) >1000 µatm; and 2) >2000 µatm. As there were no consistent differences in the proportions of observations reporting positive, neutral, or negative effects of OA among these different datasets, the results presented here include the full range of $p\mathrm{CO}_2$ treatments (N = 902 observations from 93 studies) (Figure 4.1). To account for the often non-linear physiological responses of coral to acidification (e.g., Bove et al., 2019), I included only sequential, non-overlapping comparisons between $p\mathrm{CO}_2$ treatments (e.g., low $p\mathrm{CO}_2$ to mid, mid to high).

Studies on indirect effects were similarly identified using search terms for ocean acidification (‘ocean acidification’, ‘$p\mathrm{CO}_2$’, ‘pH’, ‘carbon dioxide’), ‘coral’ and an indirect effect. The effects considered here were selected using the terms: ‘compet*’; ‘predat*’ OR ‘coralliv*’; ‘crustose coralline algae’ OR ‘CCA’, ‘bioero*’; ‘habitat provision’ then ‘habitat’ AND ‘structural complexity’ and; ‘disease’). An overarching search also included the term ‘indirect’ with the acidification and coral terms. However, as indirect effects are rarely labelled as such, it was necessary to include other broader search methods. Additional searches were therefore conducted around these topics for studies on other marine taxa (e.g., macroalgae and bioeroders) to gain broader understanding of potential non-specified indirect effects of OA. Lastly, the reference section of papers which included relevant information were reviewed for additional studies. All relevant studies found in the search were included however due to the limited recognition of indirect effects, I acknowledge that some relevant studies that did not explicitly refer to indirect effects would not have been captured in this search.

Finally, I reviewed the effects of acidification on the abundance and diversity of corals at naturally acidified reef sites (Table 4.2), as well as evidence of any indirect effects at such sites (Table 4.3). Observations of coral abundance and diversity were only taken from one study per site to avoid over-representation of a limited set of intensively studied locations within the data set. I focused on the effect of $p\mathrm{CO}_2$ as a ‘catch-all’ measure of OA effects.

However, I note that other measures of water chemistry, such as aragonite saturation (Ω) and the relative abundance of carbonate (CO_3^{2-}) and bicarbonate (HCO_3^-) ions, are correlated with pCO$_2$ and that OA effects encompass changes in all of these variables (see Appendix A1).

4.4 Direct effects of OA on coral

Corals employ a range of biological responses to counteract the adverse effects of acidification. These stress responses can manifest at multiple levels of biological organisation ranging from molecular or cellular processes to whole organism responses (Edmunds et al., 2016). The cumulative effect of these physiological responses can translate into effects on populations by altering key demographic rates. This includes population growth through reproduction, recruitment, and colony growth, and population shrinkage through mortality. Ultimately, these demographic parameters then affect coral communities through changes in coral cover, altered community composition and species diversity.

At the molecular and cellular level, corals have a variety of processes that allow them to survive and grow under acidified conditions. While mechanisms such as the ability to internally regulate pH (McCulloch et al., 2012; McCulloch et al., 2017) allow corals to adjust to acidic conditions, they are thought to be energetically costly (Allison et al., 2018). However increased pCO$_2$ does not always result in depletion of energy reserves (measured via tissue biomass; e.g., Strahl et al., 2016; Figure 4.1). This suggests that at least some coral species can maintain growth under OA via regulating pH at the site of calcification (see: Comeau et al., 2022).

At the ‘whole colony’ level, both calcification and photosynthesis can be affected by ocean acidification. For photosynthesis, effects of OA are highly variable among studies (Figure 4.1). The majority of observations considered here showed no significant changes in the rates or efficiency of photosynthesis under OA (e.g., Bahr et al., 2018; Bedwell-Ivers et al., 2017), nor in the density of symbionts or the chlorophyll within each symbiont (e.g., Bedwell-Ivers et al., 2017; Rivest et al., 2017). Changes in photosynthetic acquisition of energy under OA are therefore unlikely to be the limiting factor for coral persistence in the future.

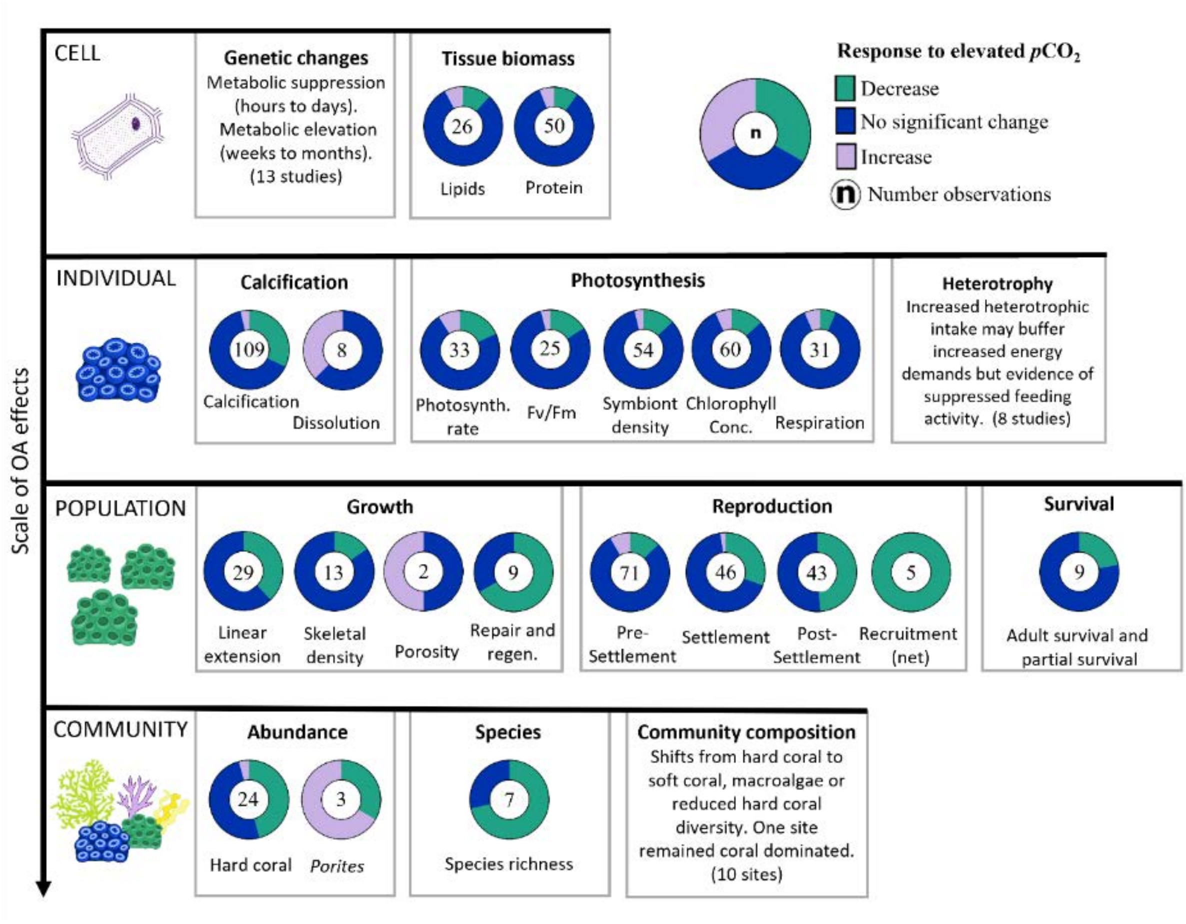

Figure 4.1. A summary of the physiological effects of ocean acidification from a cell to community scale. Pie charts summarise the proportion of observations taken from the literature showing a significant decrease (green), no significant change (blue) or a significant increase (purple) in response to elevated pCO_2. From within any study, only sequential, non-overlapping pCO_2 step comparisons are presented. Number within each pie chart denotes the number of observations for that metric. N = 902 observations from 93 studies.

The effect of acidification on calcification is the most widely recognised threat to corals and there is a substantial body of research showing declines in calcification (Chan & Connolly, 2013; Erez et al., 2011; Kornder et al., 2018), as well as some evidence of increased dissolution (e.g., Fine & Tchernov, 2007; Kline et al., 2019). However, calcification responses are highly variable, and both species and colony specific (e.g., Bahr et al., 2018; Sekizawa et al., 2017), with the overall majority of observations showing no significant effect of acidification (e.g., Carbonne et al., 2021; Figure 4.1). Furthermore, corals continue to calcify and grow in naturally acidified reefs (e.g., Camp et al., 2017; Figure 4.1; Inoue et al., 2013) under conditions far more acidic than the theoretical limits for calcification and net carbonate accretion (2.3 to 3.5 Ω aragonite, Kline et al., 2019; 560 ppm atmospheric CO_2, Silverman et al., 2009; Table 4.2).

At the population level, negative effects of OA are more apparent (Figure 4.1) suggesting that small changes in multiple aspects of physiology might accumulate to comprise a significant impact when summed across all individuals in the population. There is some evidence of a shift in growth strategies under acidification, with some corals maintaining linear extension by building less dense, more porous, skeletons (Mollica et al., 2018; Teixidó et al., 2020). This strategy is unlikely to drive changes in coral cover under acidification, however there may be significant indirect effects through increased vulnerability to breakages in weaker skeletons (Hennige et al., 2015). In contrast, other colonies maintain skeletal density/porosity at the expense of linear extension (Enochs et al., 2015), which can reduce lifetime reproductive because slower growth means corals are more likely to die before reaching the largest, most fecund, colony sizes.

For reproduction metrics, the effect of acidification is again variable among studies. Overall, the early stages of reproduction (production of gametes, fertilisation, and larval development, growth, and survival) appear to largely be unaffected by acidification (e.g., Pitts et al., 2020; Rivest et al., 2018). Conversely, the later stages of reproduction (settlement, metamorphosis, recruit growth and survival) show more consistent negative effects (e.g., Jiang et al., 2018; Yuan et al., 2018), suggesting that recruits are more vulnerable to acidification than gametes or larvae. This is of concern because even a moderate (20%) decline in recruitment was estimated to reduce coral cover by 15% over 7 year period (Evensen et al., 2021). However, declines in recruitment are estimated to potentially rise as high as 52% by mid-century conditions (~560 µatm), and 73-91% by end of century conditions (~800 µatm) (Albright et al., 2010; Fabricius et al., 2017). Such reductions are therefore likely to present a significant threat to the persistence of corals and coral communities under acidified conditions. Finally, despite the described physiological effects, increased $p\text{CO}_2$ does not consistently reduce adult colony survival, under acute experimental or naturally acidified conditions. Rather, OA appears to result in sub-lethal effects, defined here as “physiological effects that reduce coral fitness (e.g., cause slower growth or lower reproductive output) but do not result in mortality”. The accumulation of such sub-lethal effects on growth and reproduction may suppress population growth rates in the future, contributing to changes in abundance, species richness and/or diversity, and community composition at an ecosystem level.

Overall, I find the direct effects of acidification on corals are highly variable. This variation may result from differences in experimental methodology or $p\text{CO}_2$ levels, however it is also likely to represent the significant variation both between individuals, species, and sites. In total across all scales 52% of observations included here found no significant difference with acidification (Figure 4.1). Interestingly however, it appears that consistently negative effects are more often seen at a population level (26% of 274 observations), rather than cell (10% of 80 observations) or colony level (16% of 388 observations). This suggests that while the acidification has largely sub-lethal physiological effects on individuals, coral populations and communities may still be altered. I therefore stress the importance of researching the effects of acidification on coral populations and communities in addition to effects on individual coral colonies.

4.5 Indirect effects of OA on corals

Indirect effects are defined here to be a change in an ecological interaction between species. This may occur when a physiological or behavioural change affects either the extent or outcome of an interaction with another species or taxon. Indirect effects can occur as a result of physiological changes to one or both of the interacting taxa, changes to the interaction itself or changes in environment in which the interaction occurs and, consequently predicting indirect effects is challenging, and requires knowledge of both the stressor and all individuals involved (Connell et al., 2011; Sunday et al., 2016). In the following section I review the indirect effects of OA for reef-building corals, including interactions between corals and between corals and other taxa (see Table 4.1).

Table 4.1. Published studies which consider, or raise the potential for, indirect effects of acidification on corals and coral communities. '-' negative effect, '=' neutral or no effect, '+' positive effect.

Indirect effect	Impact or percent change compared to control	Effect on hard corals	Reference
Coral competition			
Physiological effects of competition	39% (*Montipora aequituberculata*) and 71% (*Porites lutea*) reduction in growth of non-competing corals but in competing corals, there was no additional suppressive effect over that of OA.	-/=	Evensen et al. (2015)
	32% decrease in calcification in corals under paired interspecific competition compared to control. No decrease in calcification in interspecific groups, heterospecific pairs or heterospecific groups.	-/=	Evensen and Edmunds (2016)
	Competition between hard coral *Porites cylindrica* and soft coral *Sinularia* sp. had no significant effect on growth but significant decreased photosynthesis in both species	-/=	Brien et al. (2016)
	Intraspecific competition significantly decreased growth (5 of 6 sp.). No additional suppressive effect of interspecific competition over that of OA (5 of 6 sp.).	-/=	Horwitz et al. (2017)
	Modelled predictions of recovery of coral communities showed 43% recovery under OA when only considering coral growth, but only a 29% recovery when competition was also included. Under OA, coral growth rate decreased exponentially as the proportion of colony competition increased.	-	Evensen et al. (2021)
Competitive capacity	No change in the competitive capacity of *Galaxia fascicularis* under OA, shown through comparable extrusion of mesenterial filaments.	=	Evensen and Edmunds (2018)
Macroalgal interactions			
Physiological effects of coral-algae interactions	2-to-3-fold increase in mortality of *Acropora intermedia* when in contact with *Lobophora papenfusii* macroalgae. Presence of macroalgae had no effect on coral growth but presence of corals significantly reduced macroalgal growth	-/ =/+	Diaz-Pulido et al. (2011)
	Macroalgae (*Dictyota* spp.) and pH individually reduced recruit survival and settlement of *Porites astreoides*, however there was no interactive effect.	-/=	Olsen et al. (2015)
	Porites astreoides recruit survival decreased with *Stypopodium zonale* presence. Settlement was decreased by combination of low pH and *S. zonale* presence.	-	Campbell et al. (2017)
	Competition with *Halimeda heteromorpha* did not affect survival of *Acropora intermedia* but did decrease calcification (includes seasonal temperature effects)	=	Brown et al. (2019)
	Macroalgal (*Dictyota* sp.) presence had no significant effect on *Siderastrea radians* coral growth in paired interactions. Macroalgal biomass decreased with acidification both with and without an interaction with coral.	=/+	Page et al. (2021)

Macroalgal competitive abilities	Mat-forming algae had enhanced productivity and 50% increase in cover. Likely to become competitively superior to corals	-	Connell et al. (2013)
	Altered allelopathy of some macroalgae species (1 of 3), increased rate of tissue death in corals in contact with macroalgae	-	Del Monaco et al. (2017)
Corallivory			
Physiological effects of corallivory	Some evidence of declines in calcification due to damage but no significant difference in wound healing	=	Edmunds and Yarid (2017)
	Acropora spp. were 10 times more likely to suffer mortality following 1 week predation by COTs, but subsequent growth and survival were unaffected by $p\mathrm{CO}_2$.	-/=	Kamya et al. (2018)
Corallivory rate	COTs feeding rate was unaffected by $p\mathrm{CO}_2$.	=	Kamya et al. (2018)
Herbivory			
Herbivore abundance	Increased density of urchins (*Diadema savignyi* and *Echinothrix spp*.)	=/+	Fabricius et al. (2014)
	Decreased density of urchins (*Paracentrotus lividus* and *Arbacia lixula* urchins)	-/=	Hall-Spencer et al. (2008)
CCA			
Induction of coral settlement by CCA	42-63% reduction in CCA cover, resulting in 46-57% reduction in coral settlement	-	Doropoulos et al. (2012)
	Pre-exposure of CCA to high $p\mathrm{CO}_2$ reduced larval settlement success in *Acropora millepora* and *Acropora tenuis* by 54%	-	Webster et al. (2013)
	Larval settlement decreased 87% with *Titanoderma* sp. and 50% with *Porolithon onkodes* and *Sporolithon* sp. due to altered chemical cues	-	Doropoulos and Diaz-Pulido (2013)
	Both CCA cover and the density of juveniles decrease with coastal acidification across the GBR continental shelf. However, there is no evidence that this is causal, as other factors such as suspended sediment also increased along the gradient		Smith et al. (2020)
Habitat provision			
Impact of habitat interactions on coral	The presence of *Trapezia* (crab) and *Alpheus* (shrimp) species reduced calcification in ambient but not in acidified conditions, suggesting a shift from parasitic to mutualistic interactions	+	Doo et al. (2018)
Bioerosion			
Abundance of bioeroders	50-fold increase and 8-fold increase in abundance of boring *Lithophaga* bivalve and Vermetid gastropods respectively (associated with increased abundance of *Porites*)	-	Fabricius et al. (2014)

	No significant difference in external bioeroder abundance in massive *Porites* colonies	=	Valentino (2014)
	Significant increase in presence of macrobioeroders in *Porites* colonies	-	Barkley et al. (2015)
	No significant difference in abundance or community composition of bioeroding endolithic green algae in *Porites* colonies with $p\mathrm{CO}_2$. Endolithic community was less diverse in *Pocillopora damicornis* and *Seriatopora hystrix*, indicating lower buffering potential and resilience to acidification in these species.	= -	Marcelino et al. (2017)
Rate of bioerosion	No significant difference in percent area with internal bioerosion in massive *Porites* colonies	=	Valentino (2014)
	78% increase in erosion and predation by boring organisms in *Porites astreoides*	=	Crook et al. (2013)
	11 fold increase in percent volume of skeleton removed in *Porites* colonies, largely by bioeroding bivalve *Lithophaga*	-	Barkley et al. (2015)
	Skeleton cores from live *Porites* colonies showed significant increase in rate of bioerosion with decreasing aragonite saturation	-	DeCarlo et al. (2015)
	Total bioerosion and chemical bioerosion rates from *Cliona caribbaea* (sponge) increased with $p\mathrm{CO}_2$. No change in mechanical bioerosion.	-	Webb et al. (2017)
Physiological effect of bioeroder on coral	Excavating sponge *Cliona varians* exacerbated declines in calcification in *Porites furcata* resulting from increased $p\mathrm{CO}_2$. No significant effect of *Cliona varians* on *Porites furcata* survival	- =	Stubler et al. (2014)
	Significant increases in net dissolution and bioerosion in *Porites furcata* under high $p\mathrm{CO}_2$ but no further increase with the presence of *Cliona varians.*	-	Stubler et al. (2015)
	Encrusting/excavating sponge did not alter growth rate in *Siderastrea radians* between ambient and acidified conditions.	=	Page et al. (2021)
Coral disease			
Disease virulence	Optimal growth of pathogen *Aurantimonas coralicida* causing white plague type II, was at pH 7, with no growth below pH of 6.	=	Remily and Richardson (2006)
	Black band disease on *Orbicella faveolata* had lower progression rates under acidification	+	Muller et al. (2017)
Abundance of pathogens	Shift in microbiome towards being more pathogenic, with increased abundance of disease associated *Flavobacteria* and fungi under acidification.	-	Vega Thurber et al. (2009)
	Microbial community of *Acropora eurystoma* had increased abundance of *Vibrionaceae* and *Alteromonadacaea* like-pathogens, which are associated with diseased and stressed corals	-	Meron et al. (2011)
	No change in microbial communities between ambient and acidified conditions, with absence of microbial pathogens under acidification	+	Meron et al. (2012)

4.5.1 Competition

For sessile benthic organisms, competition is primarily for resources such as space and light (Lang & Chornesky, 1990) and helps to structure communities and determine species distributions (e.g., Connell et al., 2004). OA may affect competition dynamics through; 1) a change in the frequency of competition as coral cover changes, resulting in either intensification or competitive release (Hofmann et al., 2010); 2) a change in the identity of competitors as species composition changes; 3) an altered outcome of an existing competitive interaction, resulting from differences in the magnitude to which different species are affected by OA; 4) an altered outcome of an existing competitive interaction due to changes in availability of resources, or; 5) novel competitive interactions as a result of shifting distributions (e.g., Alexander et al., 2016).

4.5.1.1 Competition between hard corals

To date, there has been limited investigation of the impact of ocean acidification on competition between hard corals (Table 4.1). However, given the physiological and population-level effects outlined above, I may expect a number of possible changes. Firstly, competitive interactions only occur when colonies are in close proximity (Edmunds et al., 2016) therefore, the occurrence of coral-coral interactions is likely to be lower under acidified conditions if coral cover is reduced. However, lower coral cover does not necessarily correspond to fewer competitive interactions if the remaining colonies are spatially aggregated due microhabitat requirements, or if only a small proportion of free space is actually colonisable. There are currently no studies that demonstrate how the prevalence of competition changes as a result of OA.

Secondly, if there are changes in species richness under OA, different intensity of intra- compared with inter-specific competition may occur in the future (Table 4.1). To date, three studies have examined changes to inter- and intra-specific coral competition under high $p\mathrm{CO}_2$ all of which report that while interspecific competition significantly suppressed growth, the addition of high $p\mathrm{CO}_2$ conditions caused no additional suppression under that kind of competition (Evensen & Edmunds, 2016; Evensen et al., 2015; Horwitz et al., 2017; Table 4.1). However, these studies show different trends for intraspecific competition. One study found no additional suppressive effect of OA above that of intraspecific competition on growth (Evensen et al., 2015), another reported significant declines in growth in five out of the six species (Horwitz et al., 2017). One potential explanation for this difference is the experimental duration, with additional suppressive effects only seen in the longest duration study (1 year; Horwitz et al., 2017). Nevertheless, the scarcity of research on this topic means that it remains unclear whether and how release from interspecific competition will affect coral communities on reefs in the future.

Finally, the physiological cost of competition under OA could be higher in acidified conditions (Table 4.1) if costs of maintaining growth reduce the ability of corals to invest energy in winning competitive interactions. The single study that has investigated this to date found that corals (*Galaxea fascicularis*) responded more rapidly to competition under acidified conditions, but that net tissue necrosis was the same between treatments (Evensen & Edmunds, 2018). While the effect of competition on growth suggests there is a greater physiological cost of competition under OA, the lack of impact on competitive ability potentially indicates a change in allocation of resources to maintain competitive ability. However, while Evensen and Edmunds (2018) focused on mesenterial filaments, these are only one of a number of competitive mechanisms corals use, and the effect of OA on other competitive methods has not been considered as yet.

How the effects of competition under acidification scale up to an ecosystem level is largely unknown. Early evidence of the effect of competition at an ecosystem level found that recovery on coral reefs under the combination of OA and competition reduced recovery an additional 14% compared to OA alone (Evensen et al., 2021). However, competition was found to be less important than coral growth in recovery. therefore, to understand how OA induced changes to coral-coral interactions plays out at an ecosystem level, requires additional research on the extent to which corals compete, their competitive ability or aggression, and the impacts of competition on colony growth and survival.

4.5.1.2 Competition between hard and soft corals

In general, soft corals appear to be more resistant to high $p\mathrm{CO}_2$ than hard corals (Gabay et al., 2014) suggesting that soft corals could win more competitive interactions with hard corals in the future. Under recent historical ambient conditions, adult soft corals were often the subordinate competitors (Dai, 1990), although chemical defences used by soft corals have been shown to affect hard corals through inhibiting recruitment (Atrigenio & Alino, 1996) and growth, as well as causing significant tissue necrosis and mortality (Sammarco et al., 1983). However, ambient oceanic $p\mathrm{CO}_2$ has increased dramatically since these studies were published and it is not known whether these interactions still occur or result in the same outcome under today's or future pCO_2 conditions. Only one study has experimentally tested the physiological effects of competition between hard and soft corals under high pCO_2 conditions. This study found that the presence of a soft coral competitor had a negative effect on photosynthesis but not growth of the hard coral (*Porites cylindrica*), and negligible changes in competitive ability in response to changing pCO_2 conditions (Brien et al., 2016; Table 4.1). In contrast, the cytotoxicity of the soft coral *Sarcophyton* spp. declined with increasing pCO_2 (Januar et al., 2016) potentially indicating a reduced capacity for competition. However, this decline coincided with a decrease in overall coral cover and may therefore represent a decreased need to compete. Similarly, at all three naturally acidified sites that reported abundances for both soft and hard corals, soft corals increased in abundance from ambient to mid pCO_2 before declining again under high pCO_2 (Agostini et al., 2018; Inoue et al., 2013; Januar et al., 2017). However, this result could reflect opportunistic colonisation of space as hard coral abundance declined rather than altered competitive ability. Studies that directly quantify how the prevalence and outcomes of competition changes between corals at natural CO_2 seeps compared to control sites will help to resolve knowledge gaps about how OA will affect reef ecosystems in the future.

4.5.1.3 Competition between hard corals and macroalgae

Competition on reefs also occurs between corals and other sessile benthic organisms such as macroalgae. Calcifying macroalgae (e.g., *Halimeda*) can decline in abundance and diversity under OA in a similar way to corals (Johnson et al., 2014; Zunino et al., 2017). While fleshy macroalgal species (hereafter, macroalgae) can also suffer negative effects of OA on their physiology, diversity, or abundance (e.g., Page et al., 2021), overall, the observed effects on this taxon are predominantly positive (Connell et al., 2013; Johnson et al., 2014; Kroeker et al., 2013; Zunino et al., 2017).

Coral-algal interactions are commonplace, especially in temperate environments, and under ambient conditions are not a significant threat to corals (Vieira, 2020). However, under acidification a disparity between the predominantly negative physiological effect on corals and the predominantly positive effect on macroalgae has the potential to shift this balance, affecting coral-algal competition in two ways. Increases in macroalgae abundance (Connell et al., 2013) are likely to increase the frequency of coral-algal interactions. This increase of interactions has not been explicitly tested under acidification but has been shown under ambient conditions where macroalgae increased in abundance due to fishing pressure removing herbivorous fishes (Bonaldo & Hay, 2014). Furthermore, there is some evidence that coral-algal interactions are more detrimental to corals under high pCO_2 (Table 4.1). For example, direct contact between corals and macroalgae under high pCO_2 conditions results in significantly greater and faster coral mortality than under ambient conditions, in both adult colonies (Del Monaco et al., 2017) and coral larvae (Campbell et al., 2017) . Furthermore, acidification is anticipated to result in smaller colony sizes (e.g., Teixidó et al., 2020) which have been shown to suffer greater mortality than larger corals when interacting with macroalgae under ambient conditions (Ferrari et al., 2012). The mechanisms behind these effects include enhanced macroalgal allelopathy (Del Monaco et al., 2017) and/or elevated production of DOC (dissolved organic carbon) which encourages microbial activity with negative consequences for coral (Diaz-Pulido & Barrón, 2020).

To date, the balance of evidence suggests that algae can often outcompete corals under acidification. At a colony level this may result in an increased likelihood of coral overgrowth (Diaz-Pulido et al., 2011), however there are also wider ecosystem level effects. For example, changes in coral-algal interactions under acidified conditions in favour of macroalgae, can create a density-dependent negative feedback loop where increased macroalgal abundance results in more coral mortality which creates more space for macroalgal colonisation. This can result in ecosystem phase shifts from coral to macroalgal dominated states (Diaz-Pulido et al., 2011), which has been seen in at least one naturally acidified site (Enochs et al. 2015b). However, the maintenance of coral dominance at some naturally acidified sites, despite increased abundance of macroalgae (e.g., Fabricius et al., 2011) suggests that the (chronic) effect of acidification on coral-macroalgal interactions is not sufficient, on its own, to cause this phase shift. There may be a number of explanations for this. Firstly, competition can have negative effects for macroalgae as well as corals (Diaz-Pulido et al., 2011), and the presence of coral-algal competition does not always have additional suppressive effect on growth (Page et al., 2021) or tissue loss from allelopathy (2 out of 3 species; Del Monaco et al., 2017) above that of acidification alone. Secondly, the effect and outcome of coral-algal competition differs between species (e.g., Del Monaco et al., 2017; Vieira, 2020) suggesting phase shifts towards macroalgae are dependent on the macroalgal community composition. Thirdly, other environmental factors such as temperature may play a role. For example, coral-algal interactions vary temporally due to seasonal changes in temperature (Brown et al., 2019). Finally, additional indirect effects, such as decreasing herbivory (see section below), can determine the likelihood of a phase shift (Enochs et al. 2015b). Therefore, I suggest that while altered coral-algae competitive interactions have significant implications for coral communities, broader knowledge of species-specific tolerances to OA for both corals and algae, and better knowledge of the mechanisms and costs of competitive interactions, are required before the outcomes of such encounters can be accurately predicted in the future.

4.5.2 Corallivory

Under ambient conditions (~390-420 µatm pCO_2, based on the approximate global average pCO_2 concentrations from 2010 to 2022), corallivory (predation) of corals can be a chronic stressor to coral communities (Cole et al., 2011), potentially affecting species abundance and diversity (e.g., Lenihan et al., 2011; Littler et al., 1989). Changes in the rate of corallivory under OA are likely based on demonstrated changes in fish behaviour under OA (Ferrari et al., 2011; Munday et al., 2014). Moreover, the potential effect of acidification on fish physiology, such as bone strength/mineralisation (Di Santo, 2019; Mirasole et al., 2021) and skeletal deformities (Pimentel et al., 2014), may alter the impact of corallivory. However, to the best of my knowledge, only two studies have considered how corallivory changes as a result of ocean acidification (Table 4.1). One study found that very high pCO_2 (1608 µatm) conditions did not affect the rate of coral consumption, or further reduce coral survival following predation from Crown-of-Thorns starfish (COTs, Acanthaster plancii; Kamya et al., 2018). A second study showed that injuries made on small corals to simulate bite scars of corallivorous parrotfish healed at the same rate under ambient (420 µatm) and high (1050 µatm) pCO_2 conditions (Edmunds & Yarid, 2017), suggesting acidification does not affect recovery from predation. However, potential changes in rates of predation by different corallivores remains a significant knowledge gap. While as yet untested, acidification could also result in secondary impacts of predation. For example, bite scars from parrotfish are larger on low-density substrate than on high-density substrate (Bruggemann et al., 1994) and, therefore, if coral skeletal density declines as a result of acidified conditions (Mollica et al., 2018; Tambutté et al., 2015) the potential size and impact of predation scars might increase.

Corallivory is an important driver of changes in coral cover. Models of future coral cover on the Great Barrier Reef found managing predation by COTs to be one of the most effective strategies in delaying declines in coral cover (Condie et al., 2021). However, the cumulative impacts of changes to corallivory on coral populations and communities under OA are, as yet, unknown. Despite this, I suggest that predation pressure on individual coral colonies could increase under OA due to potential decreases in coral abundance (Enochs et al. 2015b) reducing food supply, a shift in community composition to a species less preferred for predation (e.g., *Porites* spp.; Fabricius et al. 2011), but little to no change in corallivorous fish community (Munday et al. 2014). Detailed investigation of both the rates and the impact of corallivory, will be important to reveal the implications of changes in predation pressure for corals and coral communities in the future.

4.5.3 Herbivory

Herbivory has been shown to be a critical function in the resilience of coral reefs (Hughes et al., 2007). Under ambient conditions, a loss of herbivory has been noted as significant factor in the occurrence of a number coral to macroalgal phase shifts (Vieira 2020). Fortunately, under acidified conditions, the abundance of herbivores is expected to be equal or greater than ambient conditions, due to the increased availability of food and a simplification of coral reef food webs (Alva-Basurto & Arias-González, 2014; Harvey et al., 2019; Kroeker et al., 2011; Vizzini et al., 2017). Therefore, herbivory is likely to continue being a major benthic structuring process under acidification (Baggini et al., 2015). However, where the herbivores are themselves negatively affected by acidification (e.g., sea urchins; Hall-Spencer et al., 2008) or the algal community becomes less palatable to herbivores (e.g., Harvey et al. 2019), this can reduce the top-down control of macroalgae and result in shifts in the benthic community. These effects are ‘secondary’ indirect effects where the impact on corals occurs via the impact of herbivores on the macroalgal community. In addition, herbivory can also affect corals directly. For example, under acidified conditions coral recruits had significantly higher post-settlement mortality and a higher size-escape threshold from grazing herbivorous fish (Christopher Doropoulos et al., 2012). Although I were unable to find any studies explicitly testing the secondary effects of herbivory on coral communities, I suggest changes in herbivory may be a significant factor in moderating the impacts of acidification on corals and highlight the need for additional research on this topic.

4.5.4 Crustose coralline algae (CCA)

CCA, like corals, are calcifying organisms and are therefore likely to be negatively affected by acidification. For example, increased $p\text{CO}_2$ on CCA has been shown to cause declines in recruitment (Ordoñez et al., 2017), competitive ability (Crook et al., 2016;

Kuffner et al., 2008), growth (Johnson et al. 2014), calcification and recovery following injury (Manning et al. 2019). Ultimately, these changes result in up to 70 to 90% declines in CCA abundance (Fabricius et al., 2015; Kuffner et al., 2008; Vogel et al., 2016), however, these effects are species specific with some species persisting while others suffer reduced abundance or are lost completely (e.g., Peña et al., 2021). Therefore, acidification is also likely to cause shifts in community composition of CCA on reefs.

CCA play a number of vitally important roles for corals. CCA cement and stabilise the reef substratum (Guinotte & Fabry, 2008) which provides stable and suitable habitat for juvenile corals to settle on. However, reef pavement (solid carbonate substratum covered with CCA, turf algae and other sessile invertebrates), has been found to have dissolution rates 86% higher in acidified compared to ambient conditions. Similarly, reefs with low cementation rates under natural acidification suffered an almost complete loss of reef framework following a disturbance, with very low rates of coral recovery (Manzello et al., 2008). Furthermore, like corals, CCA are likely susceptible to increased bioerosion under OA. In addition to reduced abundance, this may contribute to a decrease in reef cementation in the future, reducing the available substrate for settlement of coral recruits.

CCA are often used as a suitable settlement substrate, with declines in CCA abundance therefore reducing available settlement space. For example, during an *in situ* experiment at naturally acidified reefs in Papua New Guinea, 81% of coral recruits settled on CCA, despite it only accounting for 12% of substrate (Fabricius et al. 2017). This will therefore compound the effects of reduced reef cementation, further reducing the availability of suitable space for larval settlement. Finally, CCA act as an important settlement cue for coral larvae (Heyward & Negri, 1999) and increased $p\mathrm{CO}_2$ can disrupt the response of corals to CCA (Table 4.1). For example, when CCA were pre-exposed to high $p\mathrm{CO}_2$, larval settlement declined between 54 to 87% (Doropoulos and Diaz-Pulido 2013; Webster et al. 2013). In addition, a loss of affinity has been shown between coral larvae and the most favourable CCA species (*Titanoderma* sp.) which may further reduce settlement (Doropoulos et al. 2012). To exacerbate this effect, CCA species are differentially affected by increased $p\mathrm{CO}_2$ (see review: Hofmann & Bischof, 2014) resulting in altered community compositions, with preferred settlement species such as *Titanoderma* sp. thought to be less tolerant of acidified conditions (Fabricius et al. 2015). These effects suggest loss of CCA, or changes to the community composition of CCA, are a major pathway of indirect effects of OA on coral communities.

4.5.5 Habitat provision

Corals are ecosystem engineers that build three-dimensional structures that provide habitat, shelter, and food for many other reef organisms. This structural complexity they create affects species richness and abundance of many reef organisms and is a driver of reef ecosystem functioning (Graham & Nash, 2013). Consequently, degradation of structural complexity from acidification (Fabricius et al. 2011; Manzello et al. 2014; Enochs et al. 2015b) can have significant implications for a wide variety of taxa and the functioning of acidified reefs. Here I consider the interactions between corals with fish, invertebrates, and zooplankton.

Under ambient conditions, fish-coral interactions are often mutually beneficial. For example, associations with fish have been shown to benefit corals through enhanced colony growth (Chase et al., 2014) and photosynthesis (Garcia-Herrera et al., 2017), reduced sedimentation and sediment-induced partial mortality (Chase et al., 2018), and protection from predation (Chase et al. 2014). Furthermore, provision of habitat and shelter for herbivorous fishes also benefits corals through maintenance of algae populations. For instance, herbivory pressure was > 7 times higher in high complexity areas compared to low complexity areas (Santano et al., 2021). Moreover, declines in structural complexity at naturally acidified sites can drive a shift in fish community composition (Cattano et al., 2020), and altered abundances of some fish species at acidified compared with ambient areas (Munday et al. 2014). To the best of my knowledge, the effect of ocean acidification on interactions between corals and fishes have not yet been investigated and therefore, how changes in fish abundance or community composition indirectly affect corals ability to persist under acidified conditions, remains unknown.

Many invertebrates use coral for habitat, with almost 1,000 known coral-invertebrate associations (Stella et al., 2011), although this number is likely to have increased over the last decade. This includes species which live in the branches and crevices coral provide, and boring organisms who reside within the coral tissue/skeleton (Stella et al. 2011). Overall, invertebrate communities appear to be negatively affected by acidification and the associated loss in structural complexity (Fabricius et al. 2014). The implications of changes in invertebrate communities or coral-invert interactions depend on the interacting taxa. For example, populations of the herbivorous urchin *Diadema savignyi*, increased dramatically at the acidified site in Papua New Guinea (PNG; Fabricius et al. 2014) which could benefit corals through increased herbivory. In contrast, increased abundance of vermitid gastropods which bore into large *Porites* colonies (Fabricius et al. 2014), may negatively affect corals through weakening their structure. Finally, the mutualistic relationship between the coral host (*Pocillopora verrucosa*), and two ectosymbionts *Trapezia* spp. crabs and *Alpheus*, spp. shrimp reduced the impact of acidification on calcification in the host coral (Doo et al., 2018); Table 4.1). However, it is not clear whether this is because the ectosymbionts reduced the sensitivity of the coral to acidification or provided a resource or service that prevented the reduction in calcification seen in the corals without ectosymbionts. Due to high diversity of coral-associated invertebrates and the range of responses in interactions to acidification, it is hard to predict the potential changes in interactions and what the outcomes of those may be for corals. Furthermore, additional changes in the physical (water flow and temperature) and chemical (e.g., dissolved nutrients and oxygen) conditions of the ocean as a result of acidification and climate change, could further exacerbate changes in interactions between the organisms involved in these symbioses.

Demersal zooplankton use coral to shelter from predation during the day (Alldredge & King, 1977). Similarly to fish, declines in structural complexity under acidified conditions have also been shown to result in reduced biomass and abundance of zooplankton (Allen et al., 2017; Smith et al., 2016). However, zooplankton are an important heterotrophic food source for corals (Houlbrèque & Ferrier-Pagès, 2009) and declines in their abundance has the potential to impact corals, through altered availability of food. The extent of this impact is likely to be species specific, depending on the reliance of each species on heterotrophic food sources. Moreover, some species are capable of mitigating the effects of acidification by increasing heterotrophic energy contributions (Towle et al., 2015). A decline in zooplankton may therefore reduce the resilience of some corals to acidification.

Overall, I suggest that the changes in habitat interactions reviewed here are likely to have only sub-lethal consequences for corals. However, they highlight the possibility of multiple small shifts in the functioning of coral reef ecosystems to accumulate, which may ultimately contribute to a shift in communities greater than that expected from the physiological stressors. This may particularly be the case where changes affect mutually beneficial relationships, creating the possibility of a negative feedback loop. In this case, fewer beneficial habitat associations reduce physiological coral health and/or survival, which further affects habitat associations. Such effects are extremely hard to predict and with the current paucity of data on the indirect effects on corals of changes to habitat associations, this remains a significant knowledge gap.

4.5.6 Bioerosion

Bioeroders are a diverse range of organisms including bacteria, algae, sponges, molluscs, and fishes, which cause erosion through grazing of, attachment to, or embedding in, the coral skeleton (Glynn & Manzello, 2015; Schönberg et al., 2017; Wisshak et al., 2012). There is significant evidence from naturally acidified reefs that bioeroder abundance increases under high $p\mathrm{CO}_2$ (Crook et al. 2013; Enochs et al. 2016b) (Table 4.1). This may be the result of reduced competition for space between settling bioeroders such as sponges (Schönberg & Ortiz, 2008) or an increase in dead coral habitat which supports a high number of invertebrates (Tribollet & Golubic, 2011; Valentino, 2014). Increased bioeroder abundance may have additional indirect effects on coral populations by reducing the available space for settlement. However increased bioeroder abundance is not found for all bioeroding species (e.g., grazers; Schönberg et al. 2017) or where other factors like habitat are limiting (Valentino 2014).

The bioerosive capacity of many species is increased under high $p\mathrm{CO}_2$ (Table 4.1). Chemical bioerosion is less physiologically costly under high $p\mathrm{CO}_2$ (Wisshak et al. 2012) which may increase the bioerosive capacity of boring species. For example, it is estimated that rates of chemical bioerosion by an excavating sponge (*Cliona caribbaea*) could double by the end of the century (Webb et al., 2017). In addition, taxa using mechanical bioerosion may have increased bioerosive capacity where coral skeletons are weaker, less dense/more porous. While corals with lower density were more likely to have evidence of bioerosion than high density corals (Barkley et al. 2015), this correlation has not been explicitly tested under acidification. Furthermore, under ambient conditions, skeletal density does not always result in increased bioerosion. For example, the highest rates of bioerosion were found in the coral genus with the highest skeletal density (Pavona; Cosain-Díaz et al., 2021). These contrasting findings may be explained in part by variable rates of bioerosion between morphologies, with the most dense coral also being the morphology with the highest rates of bioerosion (massive; Cosain-Díaz et al. 2021). However, where density does affect bioerosive capacity, we are likely to underestimate the net effect of OA on coral growth by considering the direct effects in isolation. Finally, bioeroders may have increased biomass and faster growth (Fang et al. 2013; Uthicke et al. 2016), ultimately allowing an individual to have a greater rate of bioerosion or lifetime erosive capacity. The combination of increased bioeroder abundance and bioerosion capacity is expected to result in a large increase in total bioerosion under high

pCO$_2$. By the end of this century, these increases in bioerosion from sponges alone are estimated to be 7% under RCP 4.5, 16% under RCP6 and 31% under RCP8.5 compared to ambient conditions (393 µatm; IPCC, 2014; Wisshak et al., 2012). Similarly, total volume removed by bioerosion under Ω aragonite saturation <2 (comparable to RCP8.5) may increase up to 78% compared to ambient aragonite (Ω aragonite >3.5; Crook et al. 2013). Such increases in bioerosion rates have been shown to result in significant declines in net calcification (Stubler et al. 2014) and even a switch from net calcification to net dissolution (Enochs et al. 2016a). Therefore, in conjunction with the predicted changes in net accretion, bioerosion could be a significant contributor to coral cover declines in the future.

4.5.7 Coral disease

Coral disease results from interactions between the host corals and the pathogen causing the disease. Worldwide, the prevalence of coral diseases has increased in recent decades due to a number of factors, such as rising water temperatures (Tracy et al., 2019) , and decreasing water quality including nutrient enrichment (Vega Thurber et al., 2014), plastic pollution (Lamb et al., 2018) and metal pollution (Tracy et al., 2020). However, the effect of acidification on coral diseases is largely unknown and remains a significant knowledge gap (Vega Thurber et al., 2020). To date, only one study has empirically shown an impact of acidification on disease dynamics, which found that low pH (7.7) decreased the progression of black bank disease on *Orbicella faveolata* under experimental conditions (Muller et al., 2017). This suggests that future acidified conditions may be less favourable to black band disease and result in decreased prevalence and/or progression. However, coral diseases are caused by a range of pathogens including marine and terrestrial bacteria, cyanobacteria, and viruses (Sokolow, 2009; Vega Thurber et al., 2020), meaning the results from Muller et al. (2017) cannot easily be extrapolated to diseases caused by other pathogens.

Despite limited information on coral disease under acidification, there are some indications that pathogen abundance and virulence, and coral susceptibility may change (Table 4.1). Increased abundances of disease-associated bacteria within the coral microbiome have been found experimentally (Grottoli et al., 2018; Meron et al., 2011; Vega Thurber et al., 2020; Table 4.1), and at the seep site in PNG (Morrow et al., 2015), however, this did not result in an increase in infections. Furthermore, microbial pathogens were absent entirely at the seep site in Ishia, Italy (Meron et al., 2012). In addition, there is some evidence that pathogen virulence may be affected by acidification, potentially due to pathogen pH tolerance limits. For example, growth in the bacterium *Aurantimonas coralicida*, which causes white plague type II, was strongly affected by pH with a clear lower limit beyond which no growth occurred (Remily & Richardson, 2006). Finally, corals have shown decreased immunity under acidification, which may result in an increase in susceptibility (see review:Traylor-Knowles & Connelly, 2017). Regardless of this potential decrease in virulence, I note that reduced growth and calcification in corals may reduce the ability of corals to recover if infection does occur and this could heighten the impacts of diseases on coral populations. Additional research is required on the prevalence of disease at naturally acidified sites, as well as both pathogen abundance and virulence, as well as coral susceptibility and recovery, to understand the effect of acidification on coral-pathogen interactions.

4.6 Coral communities under acidified conditions

Ultimately, the coral communities we see in the future will be the result of the combined impacts of both the direct and the indirect effects on corals. With consistent variability in findings between species, location, and experimental studies, as well as the paucity of data on many indirect effects, our ability to accurately scale up our current knowledge to an ecosystem scale is limited. However, globally, there are a number of locations with naturally low pH/high $p\text{CO}_2$ conditions as a result of volcanic gas seeps, hydrographic processes, and localised low pH submarine springs. The natural gradients of $p\text{CO}_2$ around these sites reveal how the direct and indirect effects of OA that are reviewed above could manifest at an ecosystem level. I review the evidence of indirect effects and the result of both direct and indirect effects on ecosystem level metrics, at ten naturally acidified coral communities or coral reefs (Figure 4.2, Table 4.3). Seven of these sites occur around volcanic vents, where gas containing a high percentage of CO_2 seeps through the seafloor and acidifies the surrounding waters. Of these seven, three occur in tropical coral reef ecosystems, in North Sulawesi and Maluku Provinces (Indonesia), Dobu, Esa’Ala and Upa-Upasina (PNG), and Maug (Commonwealth of Northern Mariana Islands [CNMI]), and one on a sub-tropical reef in Iwotorishima (Japan). The remaining three vents are in temperate rocky shore environments where corals occur, in Shikine (Japan), and both Panarea and Ishia (Italy). Carbonate chemistry at vent sites is variable depending on the composition of the vent gases, however $p\mathrm{CO}_2$ conditions close to the vent can be high and well in excess of what is predicted under end of century conditions, particularly in temperate regions (e.g., 5066 µatm in Ishia, Italy; Hall-Spencer et al. 2008). The remaining three sites occur as a result of three different processes. In Rock Island Bays in Palau, acidification occurs in tropical lagoonal reefs where there is restricted circulation of water in semi-enclosed bays (Golbuu et al., 2016). Acidification here is less extreme (~600 µatm) than at some of the vent sites. In Puerto Morelos (Mesoamerica) submarine springs (or 'Ojos') discharge low-pH, low aragonite saturation groundwater, through natural localised springs in close proximity to the tropical Mesoamerican Barrier Reef. This results in high levels of acidity (pH 7.05, $p\mathrm{CO}_2$ data is not stated) as well as reduced salinity and total alkalinity (Crook et al. 2012). Finally, seasonal upwelling results in mild acidification (588 µatm) at the southern-most reefs in the subtropical Galapagos Islands (Eastern Tropical Pacific [ETP]), as well as exposure to cool waters and elevated nutrient levels. Reefs further north are less affected by the upwelling and experience more ambient ocean conditions (Manzello et al. 2014).

A number of other acidified sites have also been described in the literature, however are excluded here because they also experience elevated temperatures and/or deoxygenation (Bouraké, New Caledonia; Mangrove lagoons, northern Great Barrier Reef; Bahia Concepcion, California), or because there are no ecological records of coral communities at those sites, (Ambitle Island, PNG; Mayreau Gardens, Caribbean; White Island, New Zealand) or where the $p\mathrm{CO}_2$ gradient occurs and dissipates daily (Moorea, French Polynesia).

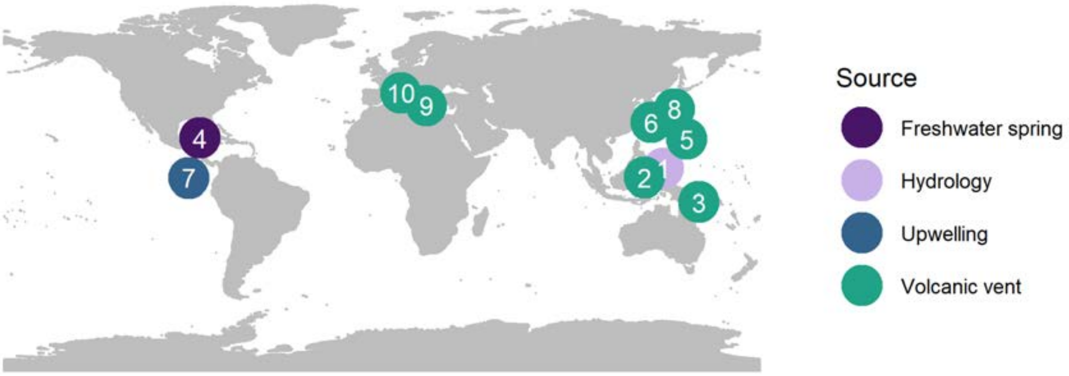

Figure 4.2. The location of the ten natural acidified sites with associated corals which are reviewed here, ordered by smallest to largest decrease in coral cover. 1- Rock Island Bays, Palau; 2- North Sulawesi and Maluku Provinces, Indonesia; 3- Dobu, Esa'Ala and Upa-Upasina, Papua New Guinea (PNG); 4- Puerto Morelos, Mesoamerica; 5- Maug, Commonwealth of Northern Mariana Islands (CNMI); 6- Iwotorishima, Japan; 7- Galapagos, Eastern Tropical Pacific (ETP); 8- Shikine, Japan; 9- Panarea, Italy; 10- Ishia, Italy.

Table 4.2. A summary of the physical site characteristics of the naturally acidified sites in this review '' = data extracted from a figure in source publication, '-' = no data available. Locations are ordered from the smallest to the largest decrease in coral cover. Values presented are means of all sites in each category. 'Control' refers to sites that have ambient water chemistry and are used as reference sites in the source publication.*

		1) Rock Island Bays, Palau		**2) North Sulawesi and Maluku Provinces, Indonesia,**			**3) Dobu, Esa'Ala and Upa-Upasina, PNG**		**4) Puerto Morelos, Mesoamerica**	
Site description	Community type	Tropical coral reef		Tropical coral reef			Tropical coral reef		Tropical coral reef	
	Source	Biological & hydrographic processes		Volcanic seeps			Volcanic seeps		Volcanic seeps	
	Unique/ confounding factors	Semi-enclosed, restricted circulation. Acidified = lagoonal reef, Control = outer reef		Nutrient enrichment/ eutrophication					Decreased salinity and total alkalinity	
	% CO_2 from vent gas	NA		-			>99%		NA	
Physical features	# Site replicates	11 sites along acidification gradient.		Replicate sites at 3 acidified reefs			Replicate sites at 3 acidified reefs		Replicate Ω saturation gradients surrounding 10 springs. No true control site	
	Site	**Control** (Ngaremlengui Barrier)	**High** (Nikko Bay)	**Control (3)**	**Low (3)**	**High (3)**	**Control (3)**	**High (3)**	**Control (10)**	**High (10)**
	Mean pCO_2 (µatm)	392	586	233	409	616	452	748	-	-
	Mean pH	8.03	7.84	8.20	8.01	8.00	8.00	7.83	8.03	7.05
	Mean aragonite saturation (Ω)	3.60	2.34	4.70	3.43	2.60	3.45	2.67	3.6	0.68
Biological features	Dominant reef taxa	Hard coral		Hard coral		Hard coral	Hard coral		Hard coral	
	% change hard coral cover	-	33.9%*	-	-15%*	6.7%*	-	6.5%	-	Signif. Decline
Reference		Shamberger et al 2014; Barkley et al 2015		Januar et al 2016; 2017			Fabricius et al 2011		Crook et al 2012	

		5) Maug, Commonwealth of Northern Mariana Islands			**6) Iwotorishima, Japan**			**7) Galapagos, Eastern Tropical Pacific (ETP)**			
Site description	Community type	Tropical coral reef			Sub-tropical coral reef			Temperate reef/community			
	Source	Low-pH submarine springs			Volcanic seeps			Upwelling			
	Unique/ confounding factors	Decreased salinity and total alkalinity			Semi-enclosed reef, and presence of low salinity hot springs			Exposure to cool, nutrient rich waters. Affected areas are no longer true reefs after failing to recover from El Niño disturbance event (1982-83)			
	% CO_2 from vent gas	61.10%			>40%			NA			
Physical features	# Site replicates	Single vent site			Single vent site			7 sites along acidification gradient			
	Site	**Control (1)**	**Low (1)**	**High (1)**	**Control (1)**	**High (1)**	**Extreme (1)**	**Control** (Darwin)	**Low** (Marchena)	**Mid** (Devil's Crown)	**High** (Urvina)
	Mean pCO_2 (µatm)	401*	442*	502*	225	831	1465	406	468	521	588
	Mean pH	8.04	7.98	7.94	-	-	-	8.02	7.98	7.95	7.90
	Mean aragonite saturation (Ω)	3.84*	3.64*	3.38*	-	-	-	3.28	3.02	2.83	2.42
Biological features	Dominant reef taxa	Hard coral		Macro-algae	Hard coral	Soft coral	Few corals	Hard coral			
	% change hard coral cover	-	-68%*	-99%*	-	-5%*	-10%*	-	-58%	-93%	-97%
Reference		Enochs et al 2015			Inoue et al 2013			Manzello et al, 2008; Manzello et al 2014			

		8) Shikine, Japan					**9) Panarea, Italy**			**10) Ishia, Italy**		
Site description	Community type	Temperate coral community					Temperate coral community			Temperate coral community		
	Source	Volcanic seeps					Volcanic seeps			Volcanic seeps		
	Unique/ confounding factors	Some vents release hydrogen sulphide (H_2S)										
	% CO_2 from vent gas	-					98-99%			90.1–95.3%		
Physical features	# Site replicates	Replicate sites at 2 acidified reefs					Single vent site			Single vent site		
	Site	**Control (3)**	**Low (1)**	**Mid (1)**	**High (1)**	**Extreme (1)**	**Control (1)**	**Mid (2)**	**High (1)**	**Control (2)**	**Low (1)**	**High (1)**
	Mean pCO_2 (µatm)	342	460	714	888	1552	405	684	1110	323	768	10314
	Mean pH	8.22	8.11	7.94	7.9	7.66	8.1	7.9	7.7	8.16	7.9	6.9
	Mean aragonite saturation (Ω)	2.75	2.23	1.6	1.68	0.94	3.6	2.3	1.5	3.99	2.68	0.86
Biological features	Dominant reef taxa	Rocky shores with corals		Rocky shores, no corals, dominated by turf and low profile algae			Rocky shore & cold water corals		Rocky shore, no corals	Rocky shore & cold water corals	Rocky shore, no corals, increased seagrass & macroalgae	
	% change hard coral cover	-	-94%	-100%			-	-41 to 71%	100%	-	100%	100%
Reference		Agostini et al., 2018					Goffredo et al., 2014; Fantazzini et al. 2015			Hall-Spencer et al, 2008		

4.6.1 Changes in coral cover with increasing pCO_2

The effect of acidification on hard coral abundance, with the exception of *Porites* spp., is largely negative (Figure 4.3). Seven of the ten naturally high pCO_2 sites showed reduced hard coral cover compared with adjacent control sites (Figure 4.3, Table 4.2). Nevertheless, the effect is not always negative, and there is limited evidence of a physiological ‘tipping point’ or threshold response to increasing pCO_2. While the three temperate/sub-tropical coral communities, as well as the CNMI and Mesoamerican coral reefs, showed rapid declines in coral cover at ~500 µatm pCO_2, coral cover at similar concentrations increased significantly (~31%) in Palau, was maintained at seep locations in Indonesia (~4% increase) and PNG (~2% increase) and shifted from hard to soft coral cover at Iwotorishima (Figure 4.3, Table 4.2). This suggests that effects of pCO_2 on coral abundance are likely to be influenced by other indirect effects and/or environmental factors, and also by the species composition of coral present at each site (see below). Overall, whereas all of the temperate/sub-tropical coral communities showed a complete loss of corals between control and seep sites, only two of the seven warm water coral reefs showed a significant loss of coral cover across a similar pCO_2 gradient (Inoue et al. 2013; Enochs et al. 2015b; Figure 4.3). Therefore, the high light levels available in warm tropical waters, and the increases in metabolic rates that accompany moderate increases in water temperature, could allow certain species of corals (e.g., *Porites*) to maintain growth rates on tropical reefs despite changes in pCO_2. In contrast, increasing pCO_2 has major effects on coral growth under more marginal conditions.

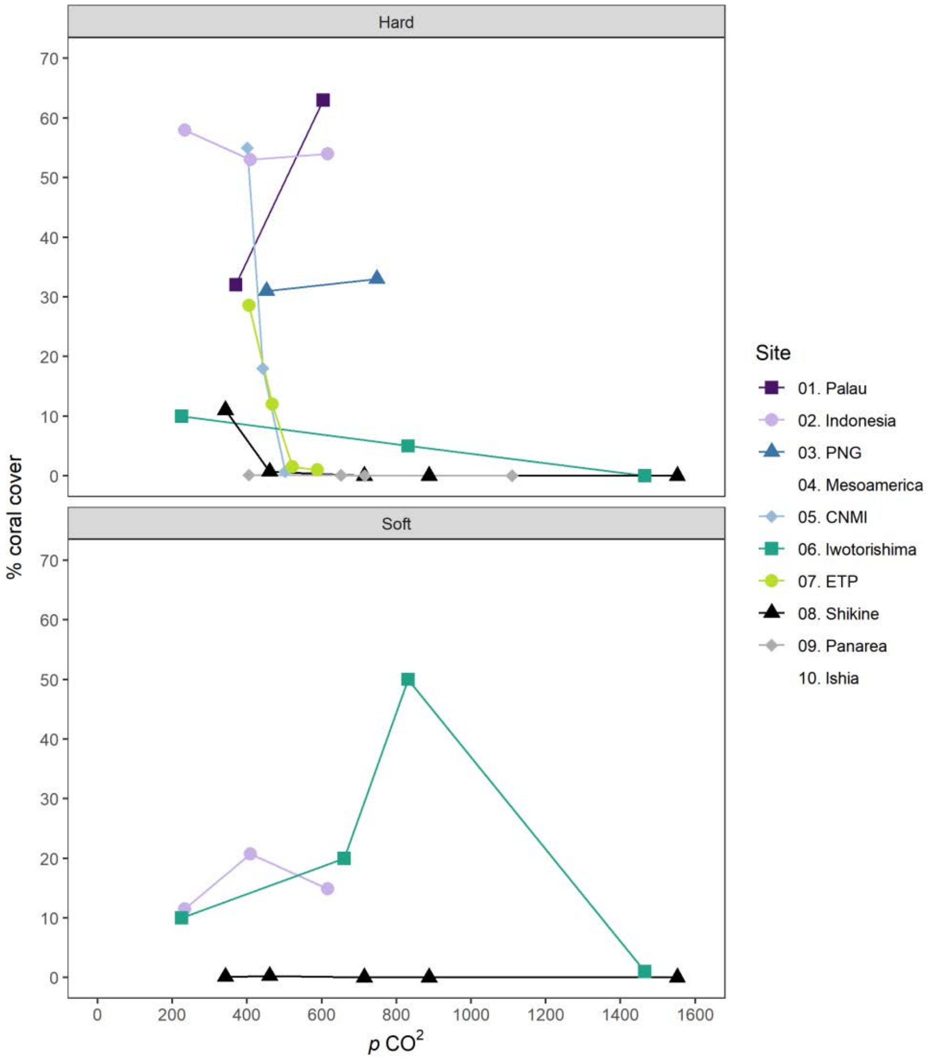

Figure 4.3. The percentage cover of hard corals (top) and soft corals (bottom) along a pCO_2 *gradient at eight of the ten naturally acidified sites reviewed here. Coral cover data are not shown for two sites because of lack of stated* pCO_2 *values (Mesoamerica, site 4) and coral cover (Ishia, site 10), however both studies note significant to total loss of coral cover. Abundances for Iwotorishima (Japan) are approximate, based on broad percentage categories. Site numbers in legend correspond to figure 4.2.*

Differences in local species composition may also influence the impact of $p\text{CO}_2$ on abundance. Among-species variation in sensitivity to acidification has been widely discussed (e.g., Agostini et al., 2021; McCulloch et al., 2012) with the premise that declines in abundance are driven in part by declines in less tolerant, ‘loser’ species. However, ‘winners’ and ‘losers’ are not consistent between sites. For example, the abundance of *Acropora spp.* declined at many of the acidified sites (e.g., Palau) but increased ~65% under high $p\text{CO}_2$ at the Indonesia seep site (Barkley et al. 2015; Januar et al. 2016). Despite the suggested resilience of soft corals to acidification, of the four sites that reported soft coral abundance, only two noted a significant increase in at seep sites with intermediate $p\mathrm{CO}_2$ conditions compared to the control sites. Furthermore, at these locations, soft coral cover subsequently declined at the highest $p\mathrm{CO}_2$ conditions surveyed (Figure 4.3, Table 4.2).

4.6.2 Changes in the coral community with increasing $p\mathrm{CO}_2$

Coral species richness at the ten acidified sites reviewed here consistently declined with increased $p\mathrm{CO}_2$, likely driven by the loss of vulnerable species. Species richness has been reported (or can be inferred) at eight of the ten high $p\mathrm{CO}_2$ sites (Table 4.2), of which seven showed large declines in species richness, from -31% to -100%. The remaining site, Palau, had a 50% increase in species richness and a 10% increase in diversity (Shannon diversity index) between the least and most acidic site (Shamberger et al. 2014; Table 4.2). While this site provides optimistic evidence on the effect of acidification, there are a number of potential reasons for an increase in species richness. For example, the retention of $p\mathrm{CO}_2$ adapted larvae within the semi-enclosed lagoon, the duration and source of acidic exposure (hydrographic processes; Golbuu et al. 2016) which result in alterations to other water chemistry parameters such as low total alkalinity, and habitat differences between the control (outer reef) and acidified (lagoonal) sites reflecting differences in community composition.

A shift in coral community composition has been observed at every naturally acidified site studied to date compared to the control sites. This includes a shift from hard to soft coral (Iwotorishima, Japan), hard coral to macroalgae with corals still present (CNMI) or with corals absent (Shikine, Japan; Ishia, Italy), reduced richness of hard coral (PNG, Indonesia, Mesoamerica and ETP), and increased species richness of hard coral but a shift in dominant species (Palau; Table 4.2). This variety again shows the complexity of predicting the effect of acidification on coral communities but suggests that reefs are unlikely to retain their current composition in the future.

4.6.3 Evidence of indirect effects at naturally acidified locations

By reviewing studies of coral diversity and abundance at naturally acidified locations (Table 4.2), I identify some common indirect effects of OA that structure coral communities. The majority of sites (6 of 10) report an increase in macroalgal abundance as $p\mathrm{CO}_2$ increases. These studies support interpretation of an increase in competitive dominance by algae, and overgrowth of corals (Enochs et al., 2015; Glynn et al., 2018) and of CCA (Kroeker et al.

2013; Crook et al. 2016; Table 4.3) under OA, which in some cases resulted in a complete phase shift to macroalgal abundance (Enochs et al. 2015b). In addition to changes in macroalgae, CCA consistently declines in abundance and diversity as pCO_2 increases (Table 4.3). Evidence from the PNG vents indicates that these declines in CCA abundance were the strongest predictor of recruit density (Fabricius et al. 2017) suggesting a reduction in CCA may have major implications for the long-term persistence of corals at this site. Effects on recruitment have yet to be investigated at any other site. However, acidification also appears to reduce reef cementation in the ETP (Manzello et al. 2008) and at the Shikine vent in Japan where the thick carbonate crusts formed in part by CCA were notably thinner (Peña et al. 2021). This indicates a potential reduction in substrate stability in the future, with further implications for additional declines in recruitment.

Bioerosion tends to be higher at the acidified sites compared to nearby control sites (Table 4.3). This is due to an increase in either the abundance of bioeroders (Enochs et al., 2016; Fabricius et al., 2011) or their bioerosive capacity (Enochs et al., 2016) and potentially exacerbated by decreased coral skeletal density (Manzello et al. 2014; Barkley et al. 2015). The extent of this bioerosion is variable but in the site where corals appear to fare best under acidification (Palau), bioerosion was still 11-fold higher than the control reefs (Barkley et al. 2015). Furthermore, at a reef with lower coral cover in the ETP, bioerosion resulted in the complete loss of the reef framework following a major coral mortality event and prevented recovery back to reef status (Manzello et al. 2014). Consequently, indirect effects of bioerosion on the integrity of coral skeletons and the reef substratum are a significant factor for long term persistence of reefs under acidification.

Linked to changes in coral cover and bioerosion, almost every site (8 of 10) exhibited a decrease in structural complexity with acidification (Table 4.3). These changes have indirect effects on other organisms, for example, changes in abundance within the fish community from PNG were likely driven by changes in structure and habitat provision (Munday et al. 2014). However, the implications of such changes for corals have not been investigated. Without knowing whether the interactions with corals and fishes and/or invertebrates had positive, negative, or neutral effects on corals, it is hard to extrapolate what the impact of these changes might be. However, I stress that as the structural complexity of the reef plays a key role in ecosystem functions and processes, the indirect effects of loss of structural complexity on corals, and many other reef organisms, may be important.

Finally, the among-site differences in responses to changing pCO_2 highlight that there are many potential internal and external factors that moderate indirect effects and therefore may shape how coral communities respond to OA. For example, the indirect effects reported here for PNG and CNMI are similar (increased macroalgal abundance, decreased CCA, increased bioerosion and a decrease in structural complexity) yet in PNG coral cover is maintained and in CNMI coral cover decreases (Table 4.2). This difference may result from both direct physiological effects (calcification declined at CNMI but not at PNG) and indirect effects (in PNG there was evidence of an increase in herbivorous urchin (Fabricius et al. 2014), while in the CNMI, the herbivores avoided predating the dominant algal species (Enochs et al. 2015b). As highly complex environments, the number of potential external factors which may result in indirect effects is significant. For example, reefs are increasingly exposed to other anthropogenic stressors like rising water temperatures and decreasing water quality such as increased turbidity, pollution and/or eutrophication. Similarly, internal factors from within the coral holobiont, such as changes in both the microbial communities and zooxanthellae populations resulting from OA (Biagi et al., 2020; Mason, 2018), may also act as a source of indirect effects on corals and coral communities. In conjunction with OA, these other factors may ultimately exacerbate the extent to which indirect effects affect corals and coral communities, either through compounding the indirect effects highlighted here, or through additional indirect effects not yet considered. Clearly, potential feedbacks between changes in the physical environment as well as the diversity, abundance, and behaviours of species in different coral reef trophic groups will shape coral reef futures.

Table 4.3. Evidence of indirect effects of acidification on corals and coral communities from the naturally acidified sites considered by this review. ***Bold*** *text shows where an indirect effect has been tested. Normal text highlights evidence of a change which may result an indirect effect on corals, but which has not been explicitly tested.*

1. Rock Island Bays, Palau	
Coral-coral competition	The highest coral abundances were in the most acidic sites (1, 2), so competition may also be higher. There were no soft corals in the most acidic sites, so hard-soft competition may be absent. (3)
Coral-algal competition	Macroalgae abundance was low and did not vary with acidity (1, 3)
CCA	CCA cover was low and did not vary with acidity. (1, 3)
Bioerosion	**11 fold increase in bioerosion, primarily from *Lithophaga* bivalve, from least to most acidified site. Likelihood of bioerosion increased as skeletal density decreased (1)**
2. North Sulawesi and Maluku Provinces, Indonesia	
Coral-coral competition	**Cytotoxicity of soft coral *Sarcophyton* sp. decreased with pH but not clear whether this was decreased capability of allelochemical production OR due to decreased demand from lower coral cover (4)**
Coral-algal competition	**Non-calcifying algae did not appear to have a competitive advantage over corals and were more abundance in the control (5)**
Structural complexity and habitat provision	Reduced abundance of framework building corals (4)
3. Dobu, Esa'Ala and Upa-Upasina, Milne Bay, PNG	
Coral-algal competition	Increased macroalgae cover (6)
Corallivory, food webs and herbivory	Little change in fish population but no evidence reported on corallivore abundance (7) Significant increase in herbivorous *Diadema savignyi* urchins (8) Reductions in demersal zooplankton (9, 10)
CCA	CCA cover reduced by 43-85%, including a 60-85% reduction in *Titanoderma* sp., which are the preferred coral settlement substrate (11). 81% of coral recruits settled on CCA, despite it only accounting for 12% of the benthos. (12) This coincides with significant declines in coral recruitment (6, 12) Declines resulted from vulnerabilities in early life stages of CCA, rather than a change in competition, which seems to be weaker with acidification. (11)
Bioerosion	**Visible macrobioeroders were almost twice as abundant (6)** *Echinometra* sp. urchins which are important bioeroders grew fasters and were larger bodied at the vents (13)
Structural complexity and habitat provision	Reduced structural complexity. (6) **Little change in fish population but those seen were driven by change in reef structure and habitat provision (7)**
Coral disease	Increased abundance of disease and stress-associated bacteria (class *Flavobacteria*) (14)
4. Puerto Morelos, Mesoamerica	
Coral-coral competition	Reduced coral cover, smaller and patchier colonies (15)
Coral-algal competition	Fleshy macroalgal abundance was 42% higher that the controls due to altered competitive dynamics (16)
CCA	Acidified sites had 82% less CCA cover than controls. Potential due to CCA being outcompeted by fleshy macroalgae (16)
Bioerosion	Bioerosion was greater in the springs with 78% more volume eroded than the surrounding areas. (17)

Structural complexity and habitat provision	None of three species present are major framework builders so structural complexity is reduced (15)
5. Maug, Commonwealth of Northern Mariana Islands (CNMI)	
Coral-coral competition	Significant reductions in coral cover (18)
Coral-algal competition	Shift to macroalgae dominance, presumed to be in part due to changes in competition (18)
Corallivory, food webs and herbivory	Herbivores tend to avoid the dominant species of macroalgae, potentially explaining the shift to macroalgae abundance (18)
CCA	Reduced CCA abundance and species richness at most acidic site but an increase from control to intermediate (18)
Bioerosion	Greater settlement of microborers and rates of biogenic dissolution on calcite blocks (19)
Structural complexity and habitat provision	Loss of carbonate reef framework near vent (19)
6. Iwotorishima, Japan	
Coral-coral competition	Initial shift to soft coral dominance before almost complete loss of corals (20)
Coral-algal competition	Macroalgae were not observed (20)
Corallivory, food webs and herbivory	Hypothesised control of macroalgae through grazing invertebrates and fishes (20)
Structural complexity and habitat provision	Shift from complex 3D hard corals to less complex softs corals (20)
7. Galapagos, Eastern Tropical Pacific (ETP)	
Coral-coral competition	Significant reductions in coral cover (21)
Coral-algal competition	Possible evidence of *Caulerpa* sp. algae competing and overgrowing corals but no evidence of how this varies along acidification gradient (22)
Corallivory, food webs and herbivory	Sea urchin *Eucidaris galapagensi* predate on corals however fishing is removing their natural predators and resulting in trophic release, with implications for corals. No evidence of how this varies along acidification gradient (22)
CCA	Reefs have low carbonate cementation (23)
Bioerosion	**Bioerosion rates are very high and is a major limiting factor to reef growth. High bioerosion may be due to skeletal density >30% lower in the most acidic reefs, compared to ambient (21)** and very poor rates of reef cementation.(23) Bioerosion contributed to the initial disturbance event resulting in coral mortality, and then removed the reef framework.(22) Bioeroding urchin (*Eucidaris galapagensi*) are predated by fish, however fish abundance is reduced due to fishing resulting in trophic release of urchins (22)
Structural complexity and habitat provision	Complete loss of reef framework in areas most affected by upwelling (21) Coral reef degraded from reef to a coral community (22)
8. Shikine, Japan	
Coral-coral competition	Complete loss of corals (24)
Coral-algal competition	Fleshy and non-calcifying macroalgal abundance increased 53%-98% between ambient and high $p\mathrm{CO}_2$ but with a 56% reduction in diversity (24, 25) Turf-like diatoms were absent in the control but up to 100% of the substate at the acidified site with presumed competitive superiority (26)

Corallivory, food webs and herbivory	Decreased diversity of fishes and community shifts towards species more tolerant of reduced complexity, driven by shifts in algae, corals and CCA. (27) There was no evidence of herbivory on the turf-like diatom mats. Simplification of food web (26)
CCA	Significant decline in % cover and species diversity, thinner crusts with minimal associated faunal communities (24, 25)
Bioerosion	Coral boring serpulids absent in more acidic sites (24)
Structural complexity and habitat provision	6 fold decrease in complexity with acidity, with a shift from corals, calcified organisms and complex CCA structures, to low-profile, turf and non-calcified organism dominance, with low complexity of CCA (24, 25, 27) Decreased diversity of fishes and community shifts towards species more tolerant of reduced complexity, driven by shifts in algae, corals and CCA. (27)
9. Panarea, Italy	
Coral-coral competition	Reduced population density (29)
Corallivory, food webs and herbivory	Significant decline in skeletal density and increase in porosity (29)
Bioerosion	Significant decline in skeletal density and increase in porosity (28, 29)
10. Ishia, Italy	
Coral-coral competition	Complete loss of corals (30)
Coral-algal competition	Increased abundance and biomass of some non-calcifying algal genera (25, 30, 31) at the seep compared to the control, with only 5% of macroalgae unable to tolerate acidified conditions. (32) Reduced cover of erect calcifying algae (32)
Corallivory, food webs and herbivory	Simplification of food web with a decrease in herbivores and heavily calcified invertebrates (31, 33)
CCA	Declines in CCA abundance, from >60% to 0% (30) and diversity. (25) Declines thought to be due to CCA being outcompeted by fleshy macroalgae and altered predation rates/grazing regimes (34).
Bioerosion	Boring microbioeroders were negatively affected by acidification with lower bioerosion on aragonite blocks than in ambient conditions (35)
Structural complexity and habitat provision	Loss of corals (30) and 80% decrease in colony size. (36) Decrease in erect calcifying algae (32) but increase in erect macroalgae (37)
Coral disease	Tissue necrosis increased from <0.5% to 13% under acidified conditions but no evidence this resulted from disease (36) No change in microbial communities with no evidence of microbial pathogens (38)

1. Barkley et al. (2015); 2. Shamberger et al. (2014); 3. Shamberger et al. (2018), 4. Januar et al. (2016); 5. Januar et al. (2017); 6. Fabricius et al. (2011); 7. Munday et al. (2014); 8. Fabricius et al. (2014); 9. Smith et al. (2016); 10. Allen et al. (2017); 11. Fabricius et al. (2015); 12. Fabricius et al. (2017); 13. Uthicke et al. (2016); 14. Morrow et al. (2015); 15. Crook et al. (2012); 16. Crook et al. (2016); 17. Crook et al. (2013); 18. Enochs et al. (2015); 19. Enochs et al. (2016); 20. Inoue et al. (2013); 21. Manzello et al. (2014); 22. Glynn et al. (2018); 23. Manzello et al. (2008); 2. Agostini et al. (2018); 25. Peña et al. (2021); 26. Harvey et al. (2019); 27. Cattano et al. (2020); 28. Goffredo et al. (2014); 29. Fantazzini et al. (2015); 30. Hall-Spencer et al. (2008); 31. Kroeker et al. (2011); 32. Porzio et al. (2011); 33. Foo et al. (2018); 34. Kroeker et al. (2013); 35. Tribollet et al. (2018); 36. Teixidó et al. (2020); 37. Porzio et al. (2013); 38. Meron et al. (2012)

4.7 The future of indirect effects research

In this review I have identified a range of indirect effects which have the potential to have significant impacts on coral and coral communities. Consequently, single-species studies that assess the effects of OA on coral physiology potentially underestimate the effects of OA on coral communities and limit our ability to extrapolate findings to an ecosystem scale. I therefore recommend that the indirect effects of acidification be more widely considered in acidification research.

Indirect effects research can be done using a number of research methods. Small-scale, short-term experiments are the basis of much ocean acidification research and an effective method to establish the impact on simple or paired interactions. Larger-scale, long-term aquaria or mesocosm experiments allow us to potentially include more ecosystem functions/processes such as competition and bioerosion. However, these experimental set-ups are limited in ecological complexity and therefore need to target specific species, interactions, or processes. *In-situ* manipulations are becoming more feasible through the use of FOCE (Free Ocean Carbon Enrichment; Stark et al., 2019) and SCoRE-FOCE (Shallow Coral Reef Free Ocean Carbon Enrichment; Srednick et al., 2020) experimental flumes. *In-situ* flumes use natural communities and therefore have greater ecological complexity, however they may be unable to account for interactions with more mobile taxa such as fishes and can be challenging/expensive to run over ecologically meaningful timescales. FOCE experiments may therefore be useful for research on benthic indirect effects such as bioerosion.

At present, studies using naturally acidified sites remain the only method where it is possible to consider large-scale community and ecosystem level effects, including multi-species interactions and effects on food-webs, using corals which have experienced lifetime exposure to acidification. However, these sites are not perfect analogues of future acidified conditions. For example, these sites often have connectivity to ambient reefs which allows new recruits to arrive from ambient reefs and movement of mobile organisms in and out of the acidified area (Munday et al. 2014). Physically these sites may also differ from future acidified reefs. For example, the source of acidity may also result in other changes to the water chemistry such as elevated levels of DIC (dissolved inorganic carbon; Crook et al. 2012) or other volcanic gases or elements (see review: Gonzalez-Delgado & Hernández, 2018). Nevertheless, these sites are useful proxies to identify indirect effects of potential concern. I suggest that a combination of all research methods will allow us the greatest progression in our understanding of the indirect effects of acidification on corals.

Here I focused specifically on how indirect effects affect corals and coral communities, but the review of the literature illuminates many other potential indirect effects via other taxa, and potentially complex feedbacks among taxa in different trophic groups. For example, the increased competitive success of fleshy algae over CCA (Crook et al. 2016) which may or may not be mediated by herbivory. Interactions such as these equally have the potential to affect structure and function of our future coral reefs and also need to be investigated. Understanding ecosystem trajectories is particularly challenging when ecosystem functioning could change via a cascade of altered interactions, such as what might occur in response to an ecological tipping point or within a trophic chain (e.g., Ferreira et al., 2021). Clearly, however, the ecological impact of these indirect effects can be significant (Mumby, 2017), and therefore identifying and understanding them is vitally important in our ability to scale up direct physiological effects of OA to an ecosystem level.

4.8 Future directions and knowledge gaps

Our review highlights multiple pathways of indirect effects of OA that have the potential to exacerbate the impact of the direct physiological effects on coral colonies (i.e., lower calcification, slower growth, decreased recruitment) and communities (reduced hard coral abundance and species richness). These direct effects, alone, can have flow-on effects to reef ecosystem services like food provisioning and coastal protection. Based on this synthesis of the literature, I propose that the indirect effects of greatest concern are that a decline in CCA, and the settlement cues and habitat they provide, is likely to drive a reduction in recruitment of corals and impede population replenishment after disturbances. I suggest that manipulative field experiments, such as controlled seeding of coral larvae at naturally acidified locations and monitoring of settlement success and post-settlement survival compared with nearby control locations, are needed to resolve existing data gaps. Moreover, declining CCA will lead to diminished levels of reef cementation which can cause coral mortality due to substratum instability (Madin et al., 2012). Detailed monitoring of coral survival after storms at naturally acidified locations compared with nearby control sites, accompanied by measurement of CCA abundance and substratum strength, will provide new insights about how CCA loss affects coral survival.

In addition to changes in CCA, increased bioerosion is likely to compound effects of decreased calcification and increase dissolution, to shift corals from net skeleton accretion towards net skeleton loss. While as yet there is limited evidence of a significant direct effect on coral abundance and diversity resulting from reduced structural complexity, a recent study indicates that coral biodiversity is highest at intermediate roughness (rugosity) of reef substrata (Torres-Pulliza et al., 2020). Field-based observations of the magnitude of bioerosion, and the diversity and abundance of bioeroding taxa, are required to link changes in bioerosion to differences in structural complexity on reefs, and to link these changes to coral diversity. A loss of structural complexity on reefs due to OA (via decreased cementation and increased erosion) is also likely to result in changes to reef functions more broadly. More complex reefs support higher diversity and abundance of fishes and therefore OA could affect the critical reef ecosystem services of food provision.

Our review highlights the need to extend from single species studies to studies that explicitly characterise how species interactions change, and how trophic linkages are altered, as $p\mathrm{CO}_2$ increases. Key knowledge gaps in the literature include the effects of OA on: the prevalence and outcomes of competition between corals and other benthic organisms in the field; the prevalence and impact of predation by corallivores on corals, as well as effects on mutualistic interactions between corals and small fishes that live within their branches; the prevalence and virulence of pathogens that cause coral diseases; and the capacity for herbivorous fishes to reduce coral-macroalgal competition. I recommend that mesocosm experiments that manipulate seawater carbonate chemistry are used alongside field observations at naturally acidified sites to generate new knowledge of OA effects. Understanding how both the direct and indirect effects of OA on the ecosystem engineers of coral reefs, and how these effects propagate throughout the entire reef food web, is critical to predicting coral reef futures as atmospheric and seawater $p\mathrm{CO}_2$ continue to increase.

Chapter 5 : Shifting competitive interactions shape effects of ocean acidification on coral communities

5.1 Abstract

Ocean acidification (OA) resulting from anthropogenic climate change is a chronic stressor for corals, and has a range of direct, physiological effects such as decreases in coral calcification. However, OA can also have indirect effects on the structure and function of coral communities through altering biotic interactions such as competition. Here I assessed how the frequency and intensity of competitive interactions changes with ocean acidification, using two naturally acidified reefs in Papua New Guinea as an analogue for future ocean conditions. In this study I identified 3,941 colonies and analysed 2,222 unique competitive interactions, and related competition prevalence and intensity to coral abundance, population size structure and benthic composition. I show that changes in community composition between acidified seep sites and nearby control sites result in a general trend for decreased frequency and intensity of competition with acidification. In particular, there were fewer competitive interactions per m^2 of reef, and each colony had fewer competitors, likely driven by a decline in both coral cover and colony abundance. However, at one reef these changes were smaller than anticipated due to the spatial aggregation of colonies under acidification which maintained high incidence of competitive interactions. This study is the first to present *in situ* estimates of the frequency and intensity of competition between corals under acidified conditions, and highlights the potential for OA to indirectly affect corals and coral communities via changes in competition.

Keywords
Indirect effects; Competition; Naturally acidified sites; Ocean acidification; Community composition; Aggregation

5.2 Introduction

The oceans and atmosphere of Earth are inextricably linked through processes of evaporation and diffusion. Increasing concentrations of carbon dioxide in our atmosphere result in greater oceanic absorption of this gas and a consequent decrease in pH, referred to as ocean acidification (Zeebe, 2012). This acidification process has been happening since the Industrial Revolution and is projected to result in a 0.06 - 0.32 unit decline in pH, and a corresponding increase in acidity of between 15 and 109 %, by 2100 (Gattuso et al., 2015; IPCC, 2014). In addition to decreasing pH, ocean acidification alters the relative abundance of carbonate and bicarbonate ions (Zeebe, 2012). Many calcifying organisms, like molluscs, calcifying algae, coccolithophores and corals, are reliant on accessible carbonate ions to build skeletons or shells and, therefore, these groups of organisms are particularly vulnerable to OA (Harvey et al., 2013; Kroeker et al., 2010).

The effect of ocean acidification on corals, as the foundation species of coral reefs, is of particular concern (National Research Council, 2010) and consequently has been widely investigated. The primary issue is a decrease in calcification rates in corals because of reduced availability of carbonate ions (Chan & Connolly, 2013; Erez et al., 2011; Kornder et al., 2018). However, declines in calcification have also been shown to affect other parameters of coral growth including reduced skeletal density, porosity, and linear extension (Fantazzini et al., 2015; Mollica et al., 2018; Tambutté et al., 2015; Teixidó et al., 2020). Furthermore, the physiological effect of acidification is not limited to calcification and growth. For example, acidification has been shown to alter colony metabolism (Kaniewska et al., 2012), negatively affect energy stores (in the form of proteins and lipids; Horwitz & Fine, 2014), photosynthesis (Kurihara et al., 2018) and reproduction (see review by Albright, 2011; Yuan et al., 2018), as well as increase colony mortality rates (Kavousi et al., 2016). These changes are likely to arise from the increased energetic demand of survival under acidified conditions (Cohen & Holcomb, 2009; Lin et al., 2018) and therefore consequent energetic trade-offs with other biological processes. These physiological impacts that affect colonies of some species more than others, are likely result in shifts in abundance, diversity, and community composition under acidified conditions (Enochs et al., 2015; Fabricius et al., 2011; Inoue et al., 2013).

In addition to direct physiological impacts, ocean acidification can also affect communities indirectly. Indirect effects can occur when a biotic interaction between species is altered as a result of physiological changes in either (or both) of the interacting taxa, and are expected to have a greater impact at community level than individual physiological responses (Sunday et al., 2016). In coral communities a number of indirect effects of OA have been recorded (see **Chapter 4**). For example, acidification affects the settlement cues for coral larvae from crustose coralline algae (CCA). This occurs both through a change in abundance of CCA (Fabricius et al., 2015), and through disrupting their ability to act as settlement cutes (Doropoulos et al. 2012a; Doropoulos and Diaz-Pulido 2013). Similarly to CCA, interactions between corals and sponges (Wisshak et al., 2012), macroinvertebrates (Fabricius et al., 2014), invertebrate bioeroders (Barkley et al., 2015), herbivores (Doropoulos et al. 2012b), macroalgae (Del Monaco et al., 2017) and other corals (Horwitz et al., 2017) have all been found to be affected by acidification.

Indirect effects are likely to have a more significant effect on communities when the process affected is one that contributes to community structure or functioning (Sunday et al., 2016). For instance, changes in grazing in seagrass communities can result in shifts in seagrass density, size, and species diversity (Burkholder et al., 2013). Similarly, on coral reefs, competition for resources between corals has been shown to affect the abundance, diversity, and structure of coral communities (Chadwick & Morrow, 2011; Connell et al., 2004; Dai, 1990), and predation affects the structure of reef fish communities (Almany & Webster, 2004). Early investigations of how competition between corals may vary under acidified competition has shown the combination of these stressors can result in reduced growth (Horwitz et al., 2017), changes in photosynthesis (Brien et al., 2016) and limit recovery of reefs affected by external stressors (COTS and cyclones; Evensen et al., 2021). In addition, acidification can change the outcome of competitive interactions and cause shifts in competitive hierarchies (Horwitz et al., 2017). These altered species interactions have the potential to cause changes in which species becomes dominant in a particular habitat, and the ability of species to persist and/or colonize new areas.

To date, investigations on the combined stressors of competition and ocean acidification have largely focused on the physiological effect on individual colonies, or on changes in competitive outcomes (Brien et al., 2016; e.g., Evensen et al., 2015; Horwitz et al., 2017). While these investigations are an important step in our understanding of the indirect effects of OA on corals, any extrapolation of the results to a community level does not consider the potential for either the frequency or intensity of competition to also vary as a result of acidification (but see Evensen et al., 2021). Furthermore, many of these investigations have been conducted in controlled laboratory environments, and/or used ecological modelling to scale findings to an ecosystem level based on simplifying assumptions and limited empirical data to parameterize the model. As yet, there has been no assessment of how the frequency or intensity of competition itself may vary in the future as the ocean becomes more acidic. One way of doing this it to use sites which are naturally acidified due to subsurface volcanic activity as an analogue for future water chemistry conditions (Gonzalez-Delgado & Hernández, 2018). Naturally acidified sites yielded important insights about potential effects of OA on reefs but, to date, research has largely focused on physiological impacts on corals and shifts in species composition (e.g., Barkley et al., 2015; Enochs et al., 2015; Fabricius et al., 2011; Noonan et al., 2013), with limited consideration of the indirect effects of OA.

The overall aim of this study was to assess how the frequency and intensity of competitive interactions vary with ocean acidification using naturally acidified reefs as an analogue for future water chemistry. The first objective was to quantify differences in competitive frequency by comparing the proportion of colonies competing between seep sites and nearby control sites at ambient seawater pH and carbonate chemistry. The second objective was to assess differences in competitive intensity with acidification, which was measured through 1) the number of competitors each colony competes with, 2) the proportion of the colony margin experiencing competition, and 3) the relative occurrence of four competitive types that differ in how they affect coral colonies. To put these findings in context with expected differences in coral species composition between the seep and control sites, I also report benthic community metrics including benthic cover, colony abundance and population size structure. This study is the first to report *in situ* prevalence and intensity of competition under acidified conditions. Furthermore, I provide some preliminary insights into the ecology of the coral communities of the naturally acidified reefs at Tutum Bay (Ambitle Island in PNG), which have not been studied to the same extent as other natural analogue sites. These results provide novel insights into how ocean acidification affects the extent to which biotic interactions such as competition have the potential to impact the structure and functioning of reefs in the future.

5.3 Methods

5.3.1 Study site

Data for this study were collected at two naturally acidified reefs in Papua New Guinea, Upa-Upasina (Normanby Island, Milne Bay Province) and Tutum Bay (Ambitle Island, New

Ireland Province) (Figure 5.1). Both reefs are acidified through exposure to submarine volcanic seeps that release high concentrations of CO_2 gas directly into the surrounding seawater, resulting in altered water chemistry (Table 5.1). The effects of these seeps are localised (approx. 700m^2 at Upa-Upasina and 15,000m^2 at Tutum Bay) and control sites were located nearby in areas with ambient water chemistry. Data were collected in January 2017 from Upa-Upasina and September 2017 from Tutum Bay.

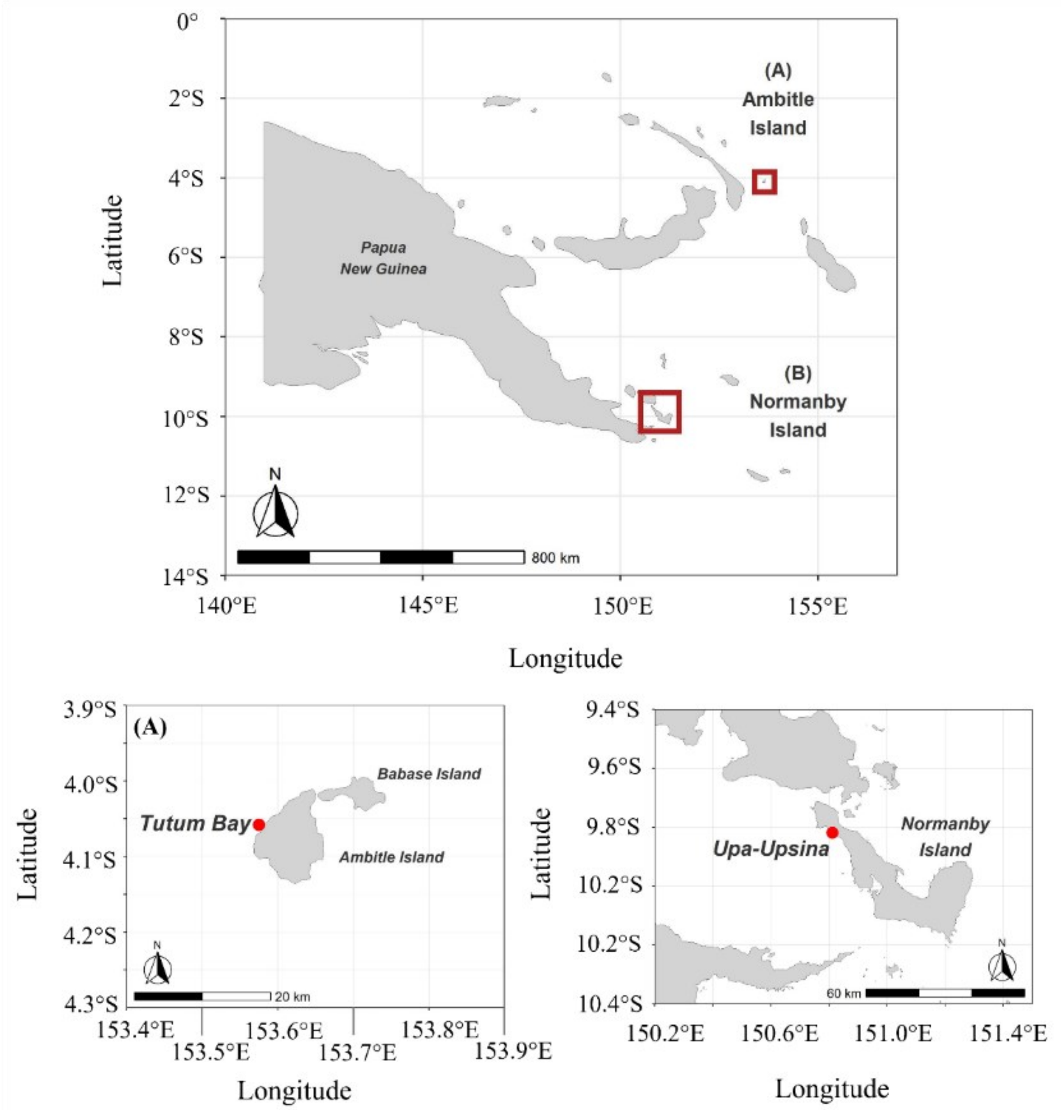

Figure 5.1. Map of study sites situated in Papua New Guinea; A) Tutum Bay, Ambitle Island, New Ireland Province; B) Upa-Upasina, Normanby Island, Milne Bay Province.

Table 5.1. Seawater carbonate chemistry from Upa-Upasina and Tutum bay reefs at the control and seep sites. Data were collected from SeaFET sensors, over the course of multiple trips between 2016 and 2019. Carbonate chemistry was calculated with CO_2SYS using temperature and pH_T data collected from the SeaFETs. All data collected by, and using methods described by, Pichler et al. (2019) and Comeau et al. (2022; see Appendix A1)

Reef	**Site**	**pH_T**	**A_T**	**pCO_2 (μatm)**	**HCO_3^- (μmol kg^{-1})**	**CO_3^{2-} (μmol kg^{-1})**	**CO_2 (μmol kg^{-1})**	**Ω_{arag}**
Upa-Upasina	Control	7.96 ± 0.03	2221.3	469 ± 3	1670 ± 24	198 ± 10	11.69 ± 1	3.25 ± 0.16
	Seep	7.62 ± 0.23	2159.4	1427 ± 1025	1946 ± 105	112 ± 43	36 ± 26	1.83 ± 0.70
Tutum Bay	Control	8.01 ± 0.04	2263.1	434 ± 45	1713 ± 34	224 ± 14	11 ± 1	5.5 ± 0.34
	Seep	7.68 ± 0.12	2314.7	1138 ± 373	2007 ± 72	126 ± 29	28 ± 9	3.1 ± 0.72

5.3.2 Data collection and sampling design

All data from this study were collected from analysis of benthic video transects taken between depths of 3 to 5m and primarily in reef crest and upper reef slope habitats, using the same methods and equipment as described in **Chapter 2**. Raw video transects covered a distance of ~50 m by ~1 m wide, with 3 – 4 replicates at each site. For image analysis purposes, each video was divided into overlapping still frames (as per **Chapter 2**) and the transect tape visible in each still frame was used to scale each image, to enable replicate transects with a fixed area of 5 m^2 to be demarcated (typically with 5 replicate quadrats obtained from each 50 m transect). These scaled transect images were analysed using ImageJ (version 1.8.0_12, U. S. National Institute of Health). From within each of these transects, every living coral colony was identified and recorded as one of five genera/categories: '*Acropora*', '*Pocillopora*', '*Porites*', 'other hard corals' and 'soft corals'. At Upa-Upasina, the size (planar area, cm^2) of colonies of *Acropora, Pocillopora* and *Porites* was measured by tracing the outline of each colony in ImageJ. Size data were not recorded at Tutum Bay due to differences in video quality and transect tape visibility. In total, I analysed eight transects (40 m^2 total area) at each of the control and seep sites at Upa-Upasina, and four control transects (20 m^2 total area) and six seep transects (30 m^2 total area) at Tutum Bay.

5.3.3 Coral community

To contextualise differences in competition, I recorded both colony abundance and coral cover between the two locations and at both control and seep sites. Colony abundance was recorded as the total number of colonies per transect (5 m^2). Coral cover was quantified using a random point sample within each transect boundary (~50 points per m^2). The benthos was recorded using the five coral categories previously identified (‘*Acropora’*, ‘*Pocillopora’*, ‘*Porites’*, ‘other hard corals’ and ‘soft corals’) as well as ‘macroalgae’, ‘turf algae’, ‘calcareous algae’, ‘sand/sediment’, ‘rubble’ and ‘bare rock’. ‘Bare rock’ was used an overarching term to encompass hard substrate with presumed epilithic algal matrix (EAM) and other benthic encrusting organisms, but with no notable macroalgal cover. Due to the limitations of photographs in identifying small areas of crustose coralline algae (CCA), ‘calcareous algae’ refers to upright calcifying algae (e.g., *Halimeda*, *Amphiroa*) and not CCA.

5.3.4 Competition

I recorded every potential competitive interaction observed for each colony identified within each transect. I defined competition as any pair of colonies with all or part of their margin closer than 5cm apart (Hoogenboom et al., 2017; Lang & Chornesky, 1990; Van Veghel et al., 1996). These interactions were further grouped into four categories that reflect a range of competitive intensities: contact, close proximity, space, and overtopping (ordered from most to least intense). Contact competition was defined as colonies which were in direct contact, through overgrowth or where the margins of adjacent colonies met. Competition at this distance is usually through direct or aggressive physiological methods (e.g., digestion through mesenterial filaments; Connell et al., 2004; Elahi, 2008; Lang & Chornesky, 1990) and it was presumed that a physiological effect was present for both colonies. I defined close proximity as colonies < 2cm apart. While these colonies might still be interacting through aggressive or direct methods, the likelihood of injury declines when colonies are more than 2 cm apart (Genin and Karp, 1994). Space competition was defined here as colonies situated between 2 and 5cm apart. At this distance competition shifts to resource pre-emption through space occupancy and alteration of small-scale water flow around colonies and corresponding changes in particle delivery (McWilliam et al., 2018). Finally, overtopping was defined as one colony over shadowing over another in the water column and limiting access to light and other resources. Overtopping typically only has a physiological effect for the shaded ‘understory’ colony. Where a single interaction could be described as more than one competitive type (e.g., close proximity and overtopping), I record only the most intense type of competition to reflect the maximum potential stress due to that interaction. Competition in colonies <5cm apart was not recorded when colonies were separated by another colony, macroalgae, a physical barrier or a difference in height greater than 5cm (with the exception of overtopping interactions).

The potential effects of competition at the reef scale were assessed though differences in both the frequency and intensity of competitive interaction. The frequency of competition was quantified through the proportion of colonies competing, and the number of pairwise competitive interactions per m^2 of reef. Competitive intensity was assessed through the number of competitors each colony encountered, the proportion of the colony margin experiencing competition, and the relative abundance of each competitive type.

5.3.5 Data processing and analysis

All data were analysed using R (version 4.3.0, The R Foundation for Statistical Computing) unless otherwise specified. Analyses tested for differences between reefs (geographic locations) and sites (control or seep), including quadrat as a random effect where relevant to the model. Model selection was based on AICc.

To assess differences in the coral community I compared differences in colony abundance and coral cover using dispersion tests and PERMANOVAs ('vegan' package). Both analyses were run on the raw data using Bray-Curtis dissimilarities. Variations in the community composition between the reefs and acidification states were visualised with nMDS (non-metric multidimensional scaling) and quantified using SIMPER (similarities percentages routine). These community analyses were performed in Primer (version 7, PRIMER-E Ltd., Ivybridge, UK). The size structure of the coral community at Upa-Upasina was analysed using two-sample Kolmogorov-Smirnov tests to compare differences between the control and seep sites for the three genera where colony size was measured (*Acropora*, *Pocillopora* and *Porites*). Skewness and kurtosis were also compared for each population ('moments' package). For this analysis, only colonies with their complete margin within the transect boundary were included, however, this disproportionately excluded the largest colony size class (>40cm diameter). Therefore, to avoid underestimating the size structure of the population, I also included all colonies where the within-transect area was >40cm (12 colonies). To ensure the size structure of this subsample did not significantly vary from the total population, a comparison was made between the two datasets. This analysis showed no significant difference in population size structure.

I used two analyses to assess differences in the intensity of competition among sites and locations. First, I compared the proportion of all colonies which were competing using a binomial linear model with transect included as a random effect (‘lme4’ package). In addition, I considered the correlation between the proportion of colonies competing and coral cover for each transect, using a Pearson product-movement correlation. Second, I compared the number of interactions per transect using a generalised linear mixed model (GLMER) with a Poisson distribution (‘lme4’ package). Changes in the intensity of competition were analysed using three models. I compared the number of competitors per colony using negative binomial GLM (‘MASS’ package). I then used a zero-one inflated beta regression model (‘gamlss’ package) to analyse whether the proportion of the colony margin competing varied between locations or sites. Both models included colony size as an offset (for number of competitors) or covariate (for proportion of margin competing) to account for variations in the intensity of competition in relation to colony size. Colony sizes were only measured at Upa-Upasina. In contrast to the size structure analysis, only colonies with their full margin within the transect were included for the competition analyses. Finally, I also compared the relative abundance of the different competition types using an ordinal cumulative logistic regression (‘VGAM’ package). This analysis included every interaction from all sites and colonies, however, to meet the proportional odds assumption ‘space’ and ‘overtopping’ interactions were combined for the analysis under a combined category of ‘indirect competition’.

5.4 Results

5.4.1 Coral cover and abundance

In this study I identified 3,941 colonies over the two reefs. This included 2,264 colonies at Upa-Upasina and 1,677 colonies at Tutum Bay. A total of 1,451 colonies were of the three focal genera (*Acropora*, *Pocillopora* and *Porites*) and, of those, 610 colonies from Upa-Upasina Reef were measured for colony size. Coral cover varied significantly between the two reefs, with Upa-Upasina having higher average coral cover than Tutum Bay (37% and 26% respectively; Table 5.2; Figure 5.2a). Similarly, coral cover varied significantly between sites, with greater coral cover at the control sites (40%) than the acidified seep sites (26%; Table 5.2; Figure 5.2a). Although not statistically significant, the difference in coral cover due to acidification within each reef varied between locations: 21% lower cover across transects at the seep site in Tutum Bay compared to 7% lower cover at Upa-Upasina. These contrasting effects are likely driven by the increase in *Porites* abundance at seep sites in Upa-Upasina (Figure A5.1). The differences between control and seep sites accounted for 25% of the variation in coral cover, while the differences between reefs accounted for 14% (Table 5.2). Non-significant dispersion tests show that the variation in coral cover was driven by changes in mean cover rather than changes in dispersion (Table 5.2).

Colony abundance varied significantly between reefs and sites, with dispersion tests again confirming that these differences were not driven by differences in variability (dispersion) between the transects (Table 5.2). The mean colony abundance was significantly higher at Tutum Bay (168 ± 34 colonies per m^2) than at Upa-Upasina (142 ±19 colonies per m^2), and at the control sites (220 ± 17 colonies per m^2) than the seep sites (93 ± 17 colonies per m^2; Figure 5.2b). Both reefs showed comparable differences in colony abundance between the control and seep sites. The acidified sites had 57% fewer colonies than the control at Tutum Bay, and 60% fewer colonies at Upa-Upasina. Overall, the impact of acidification had a larger impact on the abundance of corals than the difference between the two reefs (8% of variation was attributed to 'Reef; compared with 39% for 'Site', Table 5.2). Similarly, acidification had a greater impact on abundance of colonies than coral cover.

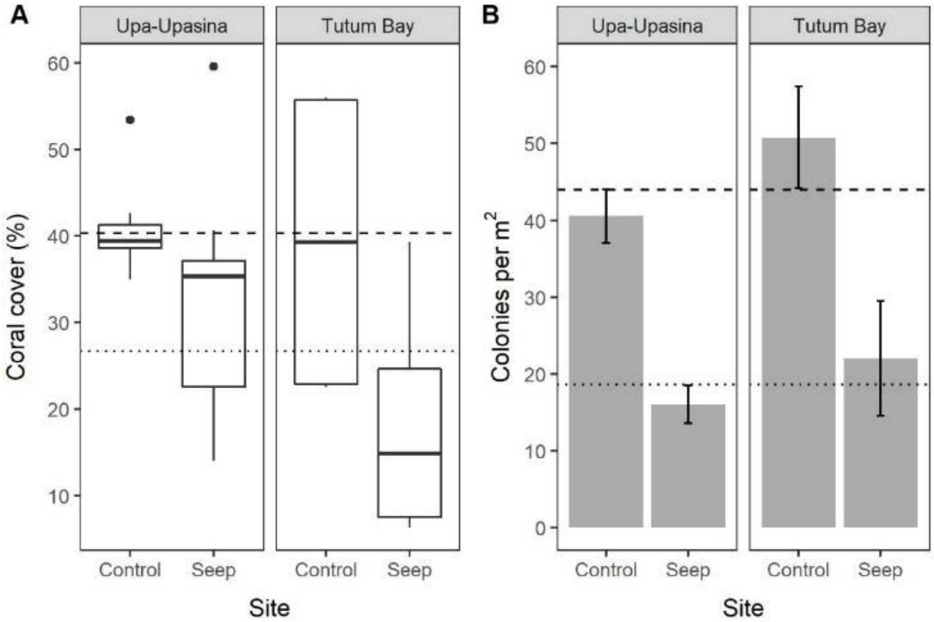

Figure 5.2. Mean (± SE) A) coral cover, and B) colony abundance, under control and seep sites at Upa-Upasina Reef and Tutum Bay. Lines represent the mean coral cover (A) and colony abundance (B) for control (dashed line) and acidified (dotted line) sites.

Table 5.2. The results of PERMANOVA and dispersion analyses comparing both coral cover and colony abundance from Tutum Bay and Upa-Upasina, at both control and seep sites.

Coral cover (raw data - Bray Curtis)							
	PERMANOVA, Stress = 0.136				Dispersion (betadisper)		
	R2	df	F	P	F	df	P
Reef	0.14	1	5.49	**<0.01**	0.43	1	0.52
Site	0.25	1	10.07	**<0.01**	2.49	1	0.13
Reef*Site	0.05	1	2.04	0.07			
Residuals	0.55	22					
Abundance (raw data-Bray Curtis)							
	PERMANOVA, Stress = 0.073				Dispersion (betadisper)		
	R2	df	F	P	F	df	P
Reef	0.08	1	3.63	**0.02**	3.42	1	0.08
Site	0.39	1	17.8	**<0.01**	2.47	3	0.09
Reef*Site	0.04	1	1.79	0.15			
Residuals	0.49	22					

5.4.2 Community composition

The SIMPER analysis showed high similarity between transects for benthic cover (78-80% similarity). The only exception was the Upa-Upasina seep site where the variation among transects was slightly greater (66% similarity). At Tutum bay under control conditions, ‘bare rock’, ‘other hard coral’ and ‘other’ benthic organisms (e.g., sponge, ascidians, zoanthids) were typical of the benthic cover. At Tutum Bay seep site, the typical benthos was also dominated by ‘other hard coral’ as well as a greater abundance of turf- and macro-algae. At the Upa-Upasina control site, the typical benthos included ‘bare rock’, ‘other hard corals’ and sand/sediment, while at the seep site, the benthos shifted to higher cover of turf-algae, *Porites* and ‘bare rock’. Dissimilarity between the control and seep sites was comparable at both reefs and was driven by differences in macro- and calcareous-algae, and sand/sediment, at Tutum Bay (35% dissimilarity) and turf-algae, ‘other hard’ corals and bare rock at Upa-Upasina (35% dissimilarity).

For colony abundance, the SIMPER analysis showed high similarity between the transects within each site (71-89% similarity). A comparison of Tutum Bay and Upa-Upasina reefs also showed the control sites were similar to each other in their abundance of corals (dissimilarity = 18%) which was driven by ‘other hard corals’ and *Porites* at both sites.

Between control and seep sites, dissimilarity was higher at Tutum Bay (38%) and was driven by differences in abundance of ‘other hard corals’, *Porites*, and soft coral. In contrast, dissimilarity between control and seep sites at Upa-Upasina was relatively low (27%), with no change in which genera drove the abundance of corals between the control and seep sites (‘other hard corals’ and *Porites* at both sites).

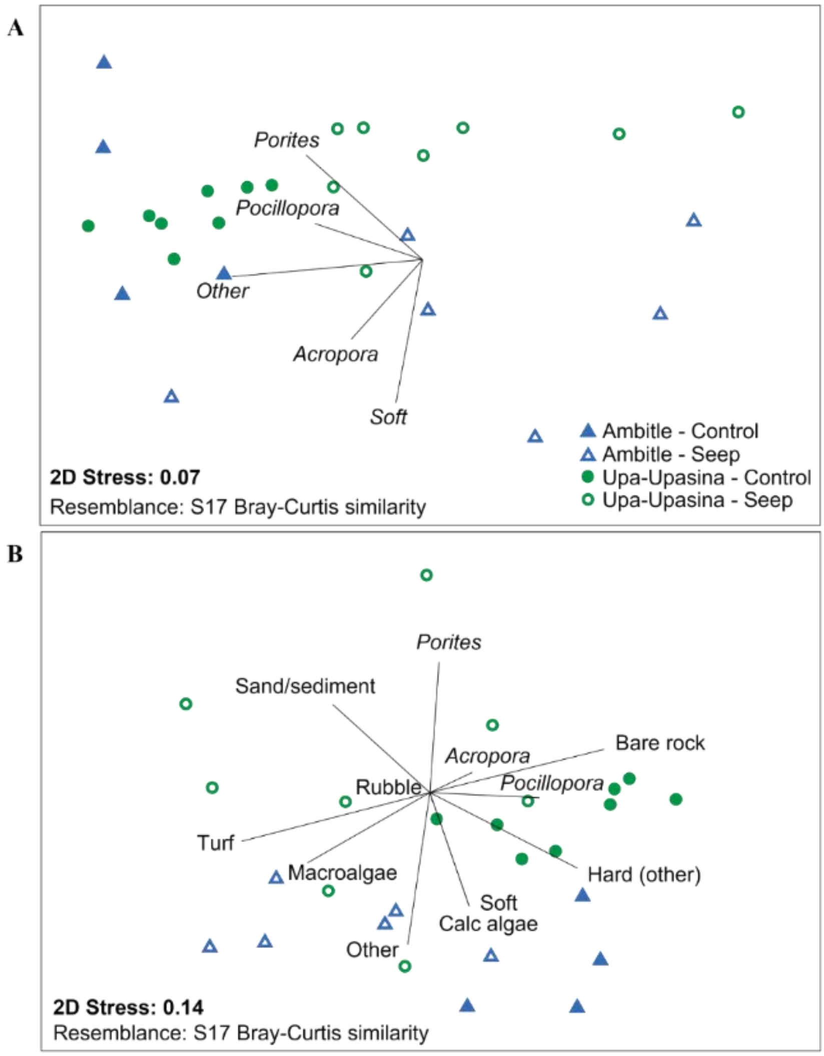

Figure 5.3. Non-metric multi-dimensional scaling (nMDS) plots showing A) colony abundance and B) benthic cover, at Tutum Bay, Ambitle Island (blue triangles) and Upa-Upasina Reef, Normanby Island (green circles) at both control (closed shapes) and seep (open shapes) sites. Each point reflects a single 1 x 5m quadrat.

5.4.3 Population size structure

Overall, the population size structure varied significantly between the control and seep sites at Upa-Upasina (Figure 5.4). At the control reef, the population was dominated by a high abundance of small colonies, with an overall mean colony size of 105 cm^2. At the seep site, the population had a greater abundance of large colonies with an overall mean colony size of 284 cm^2. However, the difference in the size structure for the coral community was driven by a significant difference in the population size structure of *Porites* colonies: for both *Acropora* and *Pocillopora*, colony size distribution was not significantly altered by acidification (Table 5.3). All populations were right skewed and leptokurtic with very high numbers of colonies < 10cm in diameter. However, for all genera, colonies in this size class showed the greatest decrease in abundance with acidification.

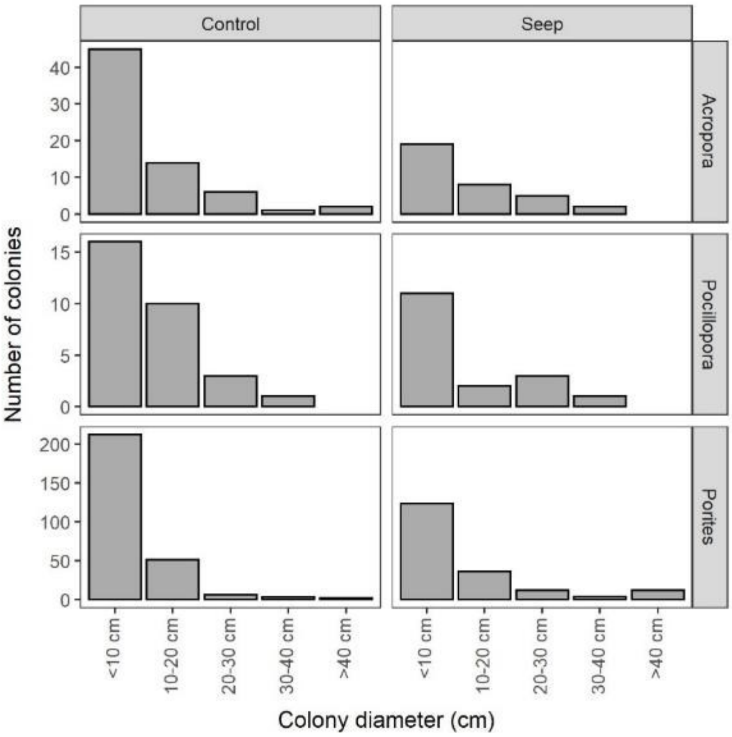

Figure 5.4. Population size histogram of the control (left) and seep (right) communities at Upa-Upasina reef, for the three focal genera. Note the variation in scale between genera due to large differences in abundance. n=372 colonies from control and 238 from seep.

Table 5.3. Results of two-sample Kolmogorov–Smirnov tests, assessing differences in population size structure between control and seep sites, for all colonies and for the three genera where size was measured. This analysis includes colonies with their complete margin within the transect, plus those where the within-transect diameter was > 40cm. n=610 colonies

		Mean colony size ± SE (cm^2)		**KS test**	
		Control	**Seep**	**D**	**p**
Genus	Mean of all colonies	105	284	0.14	0.01
	Acropora	180 ± 64	184 ± 43	0.22	0.22
	Pocillopora	147 ± 37	161 ± 57	0.29	0.33
	Porites	81 ± 13	313 ± 67	0.14	0.02

5.4.4 Competition

From the 3941 colonies identified in this study, I recorded 2,222 competitive interactions between pairs of colonies. Of these interactions, 68% occurred at Upa-Upasina and 32% occurred at Tutum Bay. Similarly, 74% occurred at control sites while 26% were between colonies at seep sites.

Table 5.4. Summary of the frequency and intensity of the competitive interactions between control and seep sites at Tutum Bay and Upa-Upasina Reef.

Reef	**Site**	**Proportion colonies competing**	**Number paired interactions per m^2 ± SE**	**Correlation with coral cover**		**Competitors per cm colony perimeter mean ± SE**	**% Colony margin competing mean ± SE**
				% competing	# interactions per m^2		
Pooled	Control	68 %	27.4 ± 2.5	r = 0.81 **p<0.01**	r = 0.46 p = 0.09	/	/
	Seep	56 %	8.3 ± 1.7	r = 0.73 **p<0.01**	r = 0.67 **p = 0.02**	/	/
Tutum Bay	Control	54 %	23.4 ± 6.1	r = 0.99 **p<0.01**	r = 0.84 p = 0.16	/	/
	Seep	49 %	8.3 ± 3.8	r = 0.74 p= 0.09	r = 0.96 **p<0.01**	/	/
Upa-Upasina Reef	Control	77 %	29.4 ± 2.2	r = 0.68 p=0.06	r = 0.33 p = 0.43	0.07 ± 0.01	34 ± 1.20
	Seep	62 %	8.2 ± 1.3	r = 0.81 **p=0.01**	r = 0.02 p = 0.97	0.03 ± 0.01	25 ± 1.47

5.4.5 Frequency of competition

Of all the variables considered, coral cover had the greatest effect on the proportion of colonies competing (Chisq = 58.46, df=1, p <0.01) with higher coral cover on a transect resulting in a significantly higher proportion of colonies competing ($R_{(1)}$ = 0.83, p <0.01). When analysed separately by reef and site, correlations between the proportion of colonies competing and coral cover were only significantly positive at Tutum Bay control site and Upa-Upasina seep site. While the other sites also showed positive correlations these associations were not statistically significant (Table 5.4). Similarly, genus also significantly affected the proportion of colonies competing, however this was driven only by significant differences between *Acropora* (75% competing) compared to *Porites* (59%) and 'other hard corals' (66%; Genus effect; Chisq = 21.95, df=1, p < 0.01; Figure 5.5b). Finally, there was also a significant interactive effect between reef and site (Chisq = 5.69, df=1, p =0.01) with a notable decrease in the proportion of colonies competing in control compared with seep site only apparent at Upa-Upasina (Figure 5.5a). Here, the proportion of competing colonies was 15 % lower at the seep site than the control, while at Tutum Bay, there were fewer colonies competing at the control site and only a 5% difference between control and seep (Table 5.4; Figure 5.5a).

The number of interactions per m^2 showed notable differences between the two reefs and sites. Overall, Upa-Upasina had a greater frequency of interactions (18.8 ± 2.9 per m^2) than Tutum Bay (14.3 ± 3.9 per m^2; Figure 5.5c). Similarly, there were far more interactions at the control sites compared to seep sites (control, 27.4 ± 2.5 per m^2; seep, 8.3 ± 1.7 per m^2; Figure 5.5c). However, the analysis showed there were interactive effects between reef and site (Chisq = 14.79, df = 1, p < 0.01), as well as between coral cover with reef (Chisq = 20.26, df = 1, p < 0.001) and with site (Chisq = 7.06, df = 1, p < 0.01). These interactive effects were only apparent with inclusion of coral cover in the analysis and reflect the variability in paired responses between coral cover and interactions, both within reef and site. Genus had no significant effect on the number of interactions and was removed from the model during stepwise regression to achieve the most parsimonious model (Figure 5.5d). Further investigation of the effect of coral cover overall showed a significant positive correlation with the number of interactions only at the seep site at Tutum Bay (Table 5.4). While the control site at Tutum Bay also had a positive but non-significant correlation between coral cover and the number of interactions, at both the control and seep sites at Upa-Upasina reef, there was little evidence that coral cover affected the number of interactions (Table 5.4).

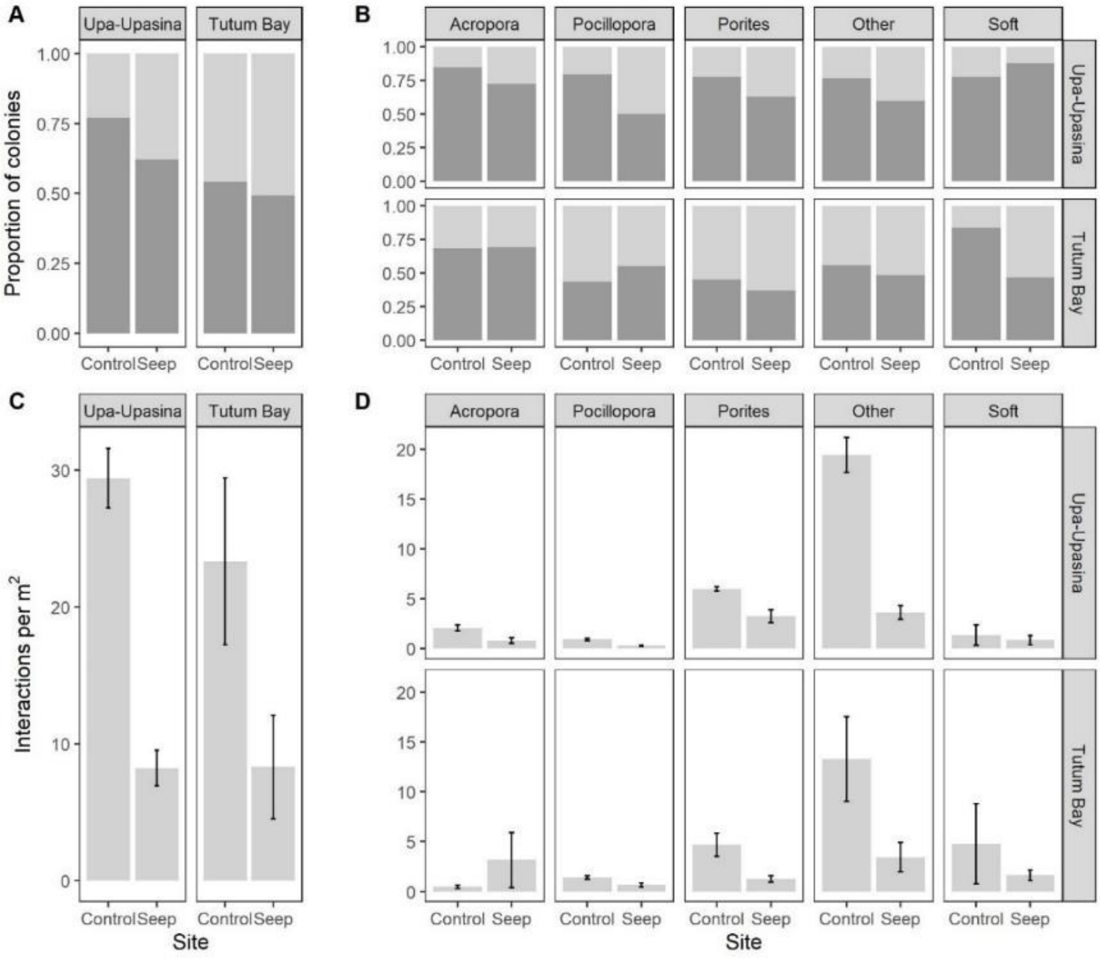

Figure 5.5. The frequency of competition based on the proportion of colonies competing (A, B; n=3,941 colonies) and the number of paired interactions per m^2 of transect (mean ± SE) (C, D; n=2,222 interactions), under both control and seep conditions (A, C) and for each genus (B, D), at Upa-Upasina Reef and Tutum Bay.

5.4.6 Intensity of competition

The number of competitors per cm of colony perimeter was significantly higher at the control sites (0.06 ± 0.01 SE competitors cm^{-1}) compared to the seep sites (0.03 ± 0.01 SE competitors cm^{-1}; Site effect: *Chisq* = 64.73, df = 1, $p < 0.01$; Figure 5.6a). This significant trend for fewer competitors at the seep sites was seen for all three genera, with no significant difference between groups (Genus effect: *Chisq* = 5.7, df = 2, p = 0.06; Figure 5.6b). Although colony size data were unavailable for Tutum Bay, the total number of competitors per colony (not standardized by colony size) also decreased with acidification. However, this decline (18% fewer competitors per colony) was less pronounced than at Upa-Upasina (29%; Figure A5.2)

In contrast to the number of competitors, acidification had no effect on the proportion of the margin competing in colonies with >0 % and <100% of their margin competing (t = -1.236, P=0.22, Figure 5.6c). However, for these colonies, both colony size (area cm^2) and the percent coral cover both significantly affect the proportion of the margin competing (colony size: t = -3.083, p = 0.002; percent coral cover: t = -2.31, p = 0.02). In contrast the likelihood of having 100% of the margin competing was not affected by site, coral cover, or colony size, but was significantly affected genus, with *Porites* having significantly fewer colonies with 100% of the margin competing than *Acropora* (0.9 % compared to 3.9 % for *Acropora*; *Acropora* vs *Porites*: t = -3.76, p < 0.01; Figure 5.6d).

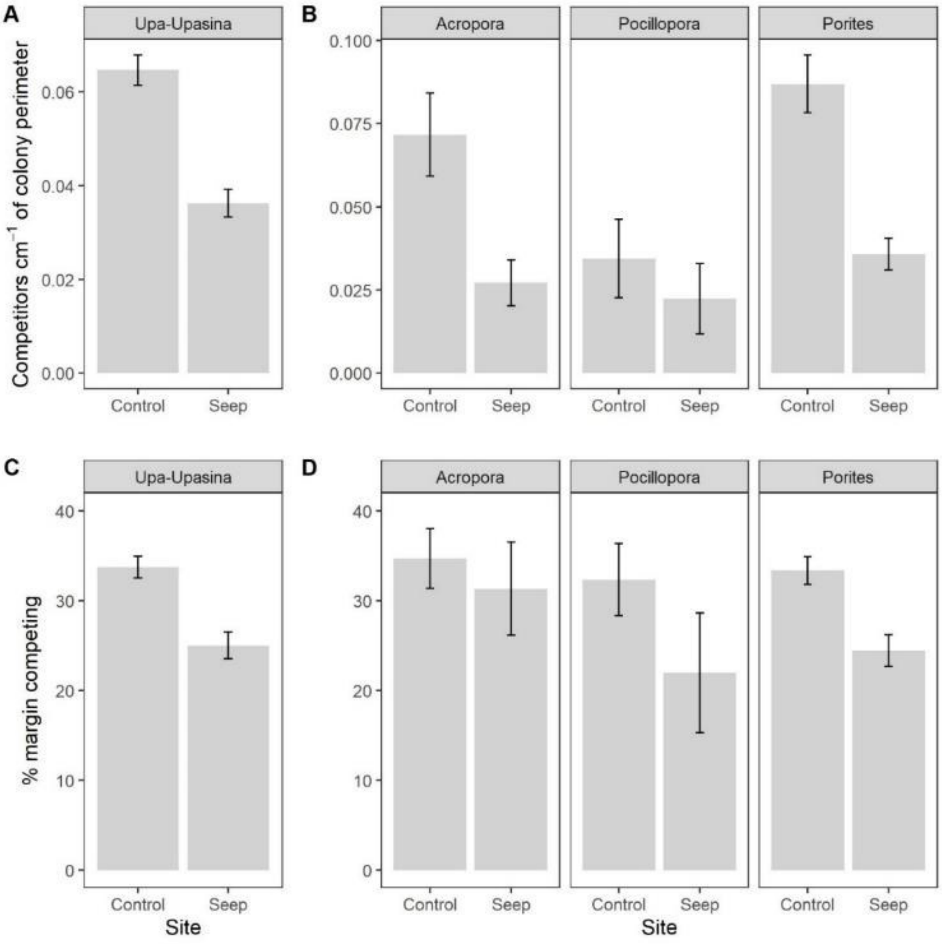

Figure 5.6. The intensity of competition at Upa-Upasina Reef quantified through the mean number of competitors per cm of colony perimeter ± SE (A, B) and the mean (± SE) percent of the colony margin experiencing competition (C, D), by site (A, C) and for the three measured genera; Acropora, Pocillopora *and* Porites *(B, D). N=780 colonies.*

5.4.7 Type of competition

Overall, the majority of the competitive interactions were indirect (52%; Figure 5.7). This included 41% ‘space’ competition (colonies 2-5cm apart) and 11% overtopping. Competition at close proximity accounted for approximately one third of all interactions (37%) with contact competition being the least frequent (11%). Although this pattern was largely consistent between both reefs and sites, differences in frequency of competitive type at the seep site at Tutum Bay lead to a significant interactive effect between reef and site (*Chisq* = 20.35, df = 1, p <0.01; Figure 5.7). At the Tutum Bay seep site, the frequency of contact competition was 10% higher than at the control site (14% control, 21% seep) while indirect competition became less frequent (50% control, 42% seep).

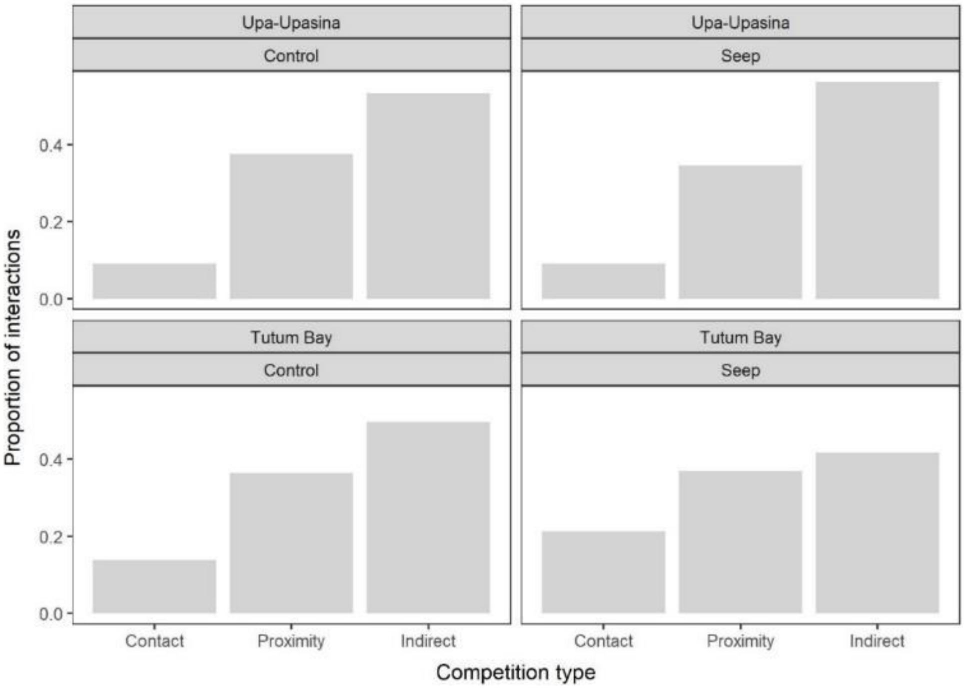

Figure 5.7. The proportion of competitive interactions of three types of competition, from control (left) and seep sites (right) at Upa-Upasina (top) and Tutum Bay reefs (bottom). n = 2,222 paired interactions. Indirect competition includes both competition at distances between 2 and 5 cm and overtopping of one colony by another.

5.5 Discussion

In this study I demonstrated that differences between coral abundance and species composition between control and seep sites affects the frequency and intensity of coral-coral competition. I found that competition generally decreases in frequency and intensity with acidification, however site-specific changes in species composition and spatial distribution of colonies alter the magnitude of this decrease. To the best of my knowledge, this study is the first to present *in situ* estimates of the frequency and intensity of competition between corals under acidified conditions.

5.5.1 The frequency and intensity of competition

Overall, competition was less frequent and less intense at the seep sites. This indicates competition could be less important as a structuring process in coral communities in the future. The differences in competition seen here primarily resulted from fewer interactions per m^2 and fewer competitors per colony, driven by lower coral cover and colony abundance. Ocean acidification can affect coral cover and abundance through slower calcification and growth (Chan & Connolly, 2013; Erez et al., 2011; Kornder et al., 2018) and by reducing recruitment into the population (Albright, 2011; Fabricius et al., 2017). Such declines have also been seen at other naturally acidified reefs (Japan; Agostini et al., 2018; Commonwealth of Northern Mariana Islands; Enochs et al., 2015; e.g., Eastern Tropical Pacific; Manzello et al., 2014). Apart from the effects of space pre-emption at settlement, competition between hard corals only occurs when they are in close proximity (Connell et al., 2004). Therefore, with fewer corals in the environment and lower coral cover, the prevalence and intensity of competition is likely to decrease. As competition is a chronic stressor for corals (Pisapia et al., 2014), reductions in competition stress could result in ‘ecological release’, potentially allowing corals to have greater available resources to counteract stressors due to unfavourable environmental conditions. However, how competition changes if acidification does not result in decreases in coral cover or abundance (e.g., Palau, Barkley et al., 2015; Indonesia, Januar et al., 2016), and whether the effects of competition are smaller or larger under acidification, requires additional investigation.

I also found that acidification resulted in site specific effects on competition. At Upa-Upasina, there was a moderate reduction in the proportion of colonies competing with acidification (15%) but only a small reduction in coral cover (7%). In contrast, at Tutum Bay there was a much smaller difference in the proportion of colonies competing (5% fewer with acidification) and a far greater reduction in coral cover (21%). I suggest that the disparity seen at Tutum Bay was driven by patchiness in colony spatial distribution with greater aggregation in colonies. This is further supported by a disparity in changes in the proportion of competing colonies and the number of competitors per colony. Spatial aggregation of colonies at Tutum Bay maintained high competitive frequency despite reductions in coral cover and abundance. In contrast, large declines in frequency and intensity of competition at Upa-Upasina indicate an overall ‘spacing out’ of colonies with acidification. Broadly, the spatial distributions of corals tend to be non-random (e.g., Bradbury & Young, 1983; Edwards et al., 2017). As sessile organisms, coral spatial distribution is dictated by juvenile settlement, which is affected by the presence of settlement cues, stable substrate, cryptic refugia and larval behaviour, and post-settlement mortality (Carlon & Olson, 1993; Morse et al., 1988; Pedersen et al., 2019), often resulting in aggregated recruitment (Chadwick & Morrow, 2011). With competition only occurring at close proximity, this aggregated distribution of corals can subsequently result in greater frequency and intensity of competition compared to more evenly distributed colonies (Brito-Millán et al., 2019). In addition, when colonies are aggregated, a lower abundance of colonies can result in individuals losing some but not all of their competitors, causing reductions in intensity but not frequency. This suggests that in addition to coral cover and abundance, the spatial structure and distribution of colonies within a community will dictate competitive stress. To the best of my knowledge, changes in the spatial distribution and aggregation of colonies under acidification, are yet to be investigated at naturally acidified sites.

I found no evidence that acidification had a significant effect on the type of competition experienced by colonies on the reef. My initial hypothesis was that indirect forms of competition would become more prevalent due to lower colony abundance and therefore greater spacing between individuals. However, at both reefs, despite significant declines in both abundance and coral cover, there was no change in the proportion of the different types of competitive interactions considered here. However, at Tutum bay, there was a non-significant decrease in the relative proportion of indirect interactions that was driven by a large decrease in the frequency of overtopping interactions (11% of interactions were overtopping in the control, compared to <1% at the seep). This result is likely due to the coral communities at both reefs being less structurally complex, with fewer branching corals (e.g., *Acropora*) and a greater abundance of massive morphologies. Structurally complex, 3-dimensional colonies often result in overtopping of other colonies (Álvarez-Noriega et al., 2018; Baird & Hughes, 2000). Therefore, declines in their abundance and/or colony size may explain the relative decrease in overtopping. Declines in structural complexity were also evident at Upa-Upasina and support previously reported measurements at this reef (Fabricius et al., 2014), yet there was no decline in the proportion of overtopping interactions. This is likely explained by the morphologies present at each seep site, with Tutum Bay having a high abundance of small and low canopy caespitose colonies, while Upa-Upasina maintained larger, canopy creating arborescent, tabular and corymbose morphologies.

In addition to changes in coral cover with acidification, there were also notable differences in the community composition and benthic cover. Differential susceptibility to acidification between species and genera is well established (Fabricius et al., 2011; McCulloch et al., 2012) and is likely to have driven the differences in community composition seen here. Corals occur along a spectrum of life-history strategies, which affect their investment in competition and/or competitive ability (Abelson & Loya, 1999; Darling et al., 2012), with the relative abundance of each coral influencing the amount and outcome of competition within a community. For example, *Acropora* colonies are competitive species (Darling et al., 2012), with rapid growth and 3-dimensional branching and tabular morphologies, which both maximize access to light and overtop nearby colonies (Álvarez-Noriega et al., 2018; Baird & Hughes, 2000). This results in a high number of competitive interactions per colony (Figure S5.2). However, under acidification there was lower coral cover of *Acropora*, which is likely to have contributed to the lower frequency of competitive interactions. Greater resolution in colony taxonomy is required to understand the drivers behind the effects of species composition on competitive frequency and intensity.

5.5.2 Implications of altered competition under acidification

The impact of changes in competition for coral communities clearly requires understanding of whether and how competition results in negative impacts on corals. Do the negative effects of competition arise from the presence of competitors or do effects only manifest when the competition intensity surpasses a threshold? Consistent with the 'threshold' concept, **Chapter 3** of my thesis demonstrated that the intensity of competition had a greater effect on bleaching than the presence of competition. Although I was not able to measure the outcomes of competition in the current study, if similar outcomes are anticipated from bleaching and acidification, the decreased intensity of competition could result in competitive release. The negative effects of competition on corals have been shown in competitive pairings (Rinkevich & Loya, 1985; Romano, 1990; Tanner, 1997), as well as in conspecific and heterospecific aggregations (Elahi, 2008; Idjadi & Karlson, 2007). To the best of my knowledge, only one study has considered the relative impacts of presence versus intensity of competition (Evensen & Edmunds, 2016). In this study the authors found that presence of competition had no effect on growth compared to colonies without competitors, and furthermore that high intensity competition (aggregations) had a similar suppressive effect on calcification than that of the presence of just one competitor. However, in contrast, they found that higher intensity competition under heterospecific aggregations resulted in significantly more rapid vertical growth and a decrease in horizontal growth. Therefore, whether any potential release of competitive stress is biologically significant in terms of community structuring or increasing the resilience of individual colonies corals to acidification, remains a significant knowledge gap.

Spatial distribution appears to play a significant role in the frequency and intensity of competition at Tutum Bay. Growing within an aggregation has both positive and negative impacts on corals. For example, it can result in faster growth rates (Idjadi & Karlson, 2007; Raymundo, 2001), lower juvenile mortality (Rivera & Goodbody-Gringley, 2014) and cause prey dilution, reducing the mortality risk from predation (Kayal et al., 2011). In contrast, aggregations also result in greater disease transmission (Jolles et al., 2002) and increased competition for resources (Kim & Lasker, 1997). These relative costs of growing within an aggregation are likely to vary with acidification. If competition has greater negative physiological impacts under acidification (Brien et al., 2016; Evensen et al., 2015; Horwitz et al., 2017), then occurring within an aggregation may be more stressful under acidification due to higher rates of competition. However, the presence of aggregations at Tutum Bay where acidification has occurred over long time periods, suggests that any increased costs associated with living in an aggregation are not sufficient to result in a shift towards a uniform spatial distribution. While the data presented here, in conjunction with previous studies looking at the physiological impact of competition under acidification (Brien et al., 2016; Evensen & Edmunds, 2016; Evensen et al., 2015; Horwitz et al., 2017), provides the basis for extrapolating the net effect of acidification on corals, I highlight that understanding changes in spatial distribution is required for accurate prediction of how competition may affect coral communities in the future.

In this study, I focused on how changes in coral community under acidification can affect the frequency and intensity of competition. However, changes in the frequency and intensity of competition can subsequently affect the community, via altered competitive outcomes. For example, there was a higher percentage cover of massive *Porites* colonies at Upa-Upasina seep sites compared to the control, which was driven by a significant increase in mean colony size. These increases in cover and colony size are likely due to *Porites* being one of the more tolerant genera to ocean acidification (Barkley et al., 2017; Comeau et al., 2019; McCulloch et al., 2012; Wall et al., 2016). However, *Porites* are also poor competitors under ambient

(Abelson & Loya, 1999) and acidified conditions (Horwitz et al., 2017). It is therefore possible that the increased colony size may have resulted in part from competitive release from stronger competitors. Due to the complex and non-transitive competitive networks in corals, with frequent switches in competitive outcome (Bak et al., 1982; Chornesky, 1989; Lang & Chornesky, 1990; Precoda et al., 2017), competitive release would be challenging to show definitively. However, for some species, even small changes in these networks or outcomes could contribute to changes in their abundance or cover.

In addition to changes in coral cover, there were also notable increase in the abundance and coverage of algae with acidification. At both reefs, the percentage cover of both turf and macroalgae, were between 2- and 10-fold higher at the seep sites. While not considered in this study, coral-algae competition occurs frequently (McCook et al., 2001) with often negative effects on corals (Jompa & McCook, 2003). The abundance of macroalgae is expected to increase with acidification (Fabricius et al., 2011; Kroeker et al., 2013), which may increase the occurrence of coral-algal interactions. Furthermore, the negative effects of coral-algal competition may also be exacerbated under acidification (Del Monaco et al., 2017; Diaz-Pulido et al., 2011). Therefore, to estimate total competitive stress of corals at control and seep sites, additional research is required to quantify both the frequency and impact of interactions with other benthic groups.

The overall impacts of acidification on competition were relatively consistent between Upa-Upasina and Tutum Bay. However, Tutum Bay appeared to have greater differences in coral community between the control and seep sites than Upa-Upasina. This may result in part from the differences in the water chemistry between the sites. At Upa-Upasina, the composition of released volcanic gas is close to pure CO_2 (Fabricius et al., 2011). However, at Tutum Bay the released gas has a slightly lower concentration of CO_2 (~92-98%) and a greater abundance of other trace elements including Silica and Arsenic (Pichler et al., 2019; Pichler et al., 1999). These trace elements have previously been shown to affect coral skeletal chemistry (Pilcher, 2000) and therefore may have resulted in additional, and unaccounted for, impacts on coral colonies. Nevertheless, the effect of competition is hard to empirically test, with many studies relying on inference (Chornesky, 1989). In this study, competition was inferred from spatial proximity of corals. While this method has been widely used (e.g., Connell et al., 2004; Dai, 1990; Hoogenboom et al., 2017), it is not conclusive proof of competition, nor does it allow us to establish the physiological effect of competition on individual colonies. Furthermore, by measuring the proportion of the margin competing on a horizontal plane, I may be underestimating the impacts on massive morphologies, where contact with a competing colony can also frequently affect vertical colony faces.

5.6 Conclusion

Competition, and other biotic interactions, plays a key role in the structure and functioning of ecosystems and, therefore, understanding how these interactions change between locations is critical for our ability to predict the effect of ocean acidification in the future. Here I show that the frequency and intensity of competition may decrease with future acidified conditions. This highlights the potential for competition to become less of a chronic stressor and therefore less of an influence on the structure and function of coral communities. However, I also show that these expected declines in the competition stress may be counteracted by aggregated spatial distribution of colonies which could maintain high competitive stress even as coral cover declines. Coral reefs are ecologically complex ecosystems, and competitive stress in this study was affected by coral cover, abundance, population size structure, community composition and the spatial distribution of colonies. Furthermore, the frequency and intensity of competition need to be quantified alongside an understanding of how such changes may physiologically or ecologically affect corals and coral communities. As such, extrapolation of the species composition on coral reefs of the future based simply on physiological effects from single species studies, are unlikely to accurately predict the extent and effects of competitive stress in the future.

Chapter 6 : General Discussion. The indirect effects of climate change on coral community dynamics

6.1 Thesis summary

Climate change is now the primary driver of coral reef degradation and is likely to result in a significant change to the ecological functioning of coral reefs globally in the coming decades (Baker et al., 2008; IPCC, 2023) To date, most research on the effects of climate change on reefs has focused on the direct physiological effects on corals, resulting from thermally induced coral bleaching and decreases in calcification arising from ocean acidification. However, climate change can also have indirect effects by altering biotic interactions within a community (Gellesch et al., 2013; Jordano, 2016). In this chapter I synthesise the results from each chapter of my thesis to identify how climate change indirectly affects coral reefs through changes in competition, and briefly, predation, the factors influencing changes in those interactions and the implications for coral reefs in the future. I provide novel insights into some of the mechanisms behind community level changes and contribute new insights around significant knowledge gaps on the interactions between abiotic and biotic stressors in high diversity ecosystems.

In my first two data chapters I considered the combination of competition between corals with thermal stress and consequent coral bleaching. In **Chapter 2** I documented the extent and severity of the 2016-2017 bleaching events on coral communities. By tracking individual colonies over time, I identified significant changes in coral population demographics in the Palm Islands, central Great Barrier Reef. Following this, in **Chapter 3** I established how competition affected bleaching rates and severity, and conversely, how bleaching affected the amount of competition. By using the same colonies for both chapters, I was able to connect changes in coral community demographics to understand the drivers of changes in competitive stress. In the next two chapters I then considered the indirect effects of ocean acidification (OA). First, I reviewed the indirect effects of OA on corals and coral communities in **Chapter 4**. I investigated a range of potential indirect effects through changes in biotic interactions and identified two of more significant concern; increased bioerosion and a loss of CCA which facilitates coral recruitment. I also highlight a significant knowledge gap around how the frequency and intensity of many of these interactions change under acidification. In **Chapter 5,** I address that gap for coral-coral competitive interactions under acidified conditions and show that competition might become less of a stressor in the future.

6.2 Indirect effects of climate change via altered biotic interactions

6.2.1 Competition

In this thesis, I demonstrate how climate change indirectly affected the frequency and intensity of competition in coral communities. I showed that both coral bleaching resulting from ocean warming, and ocean acidification, resulted in less frequent and less intense competition in coral communities (**Chapters 3, 5**). These declines were more pronounced with coral bleaching (**Chapter 3**) than with acidification (**Chapter 5**), although with both stressors the results were highly site specific. Competition is a chronic stressor for corals (Pisapia et al., 2014), and can affect community structure and function (Chadwick & Morrow, 2011; Connell et al., 2004). Changes in the frequency and intensity of competition therefore has the potential to alter competitive stress.

Reduced frequency and intensity of competition may result in competitive release for some species. Where the impacts of multiple stressors have varying impacts on different species, it is possible for shifts in community structure to occur. For instance, *Acropora* species tend to be susceptible to climate stress (Baird & Marshall, 2002; Loya et al., 2001) but are considered competitive species through their investment in growth (Darling et al., 2012). In contrast, *Porites* colonies tend to be more resilient to abiotic stress such as acidification (Barkley et al., 2017; Comeau et al., 2019; Wall et al., 2016) but are poor competitors (Abelson & Loya, 1999; Horwitz et al., 2017). Therefore, where the decline or loss of competitively dominant but climate sensitive species occurs, there may be reduced competitive stress on the remaining colonies. However, coral competitive networks tend to be non-transitive, with outcomes varying both spatially and temporally (e.g., Chornesky, 1989; Precoda et al., 2017). So, while competitive release is unlikely to result in significant changes in habitat and geographic distributions of coral species, it may be sufficient to affect colony abundance or size structure and, thereby, influence population dynamics. In **Chapter 5**, the mean colony size of *Porites* increased which may have resulted in part from competitive release under ocean acidification conditions. Competitive release was also shown in **Chapter 3**, where bleaching-induced mortality resulted in rapid growth of the surviving, non-bleached colonies. This growth into recently opened space suggests that prior to bleaching, these colonies were restricted by competition for space.

Competitive release can also result in increased resilience to other stressors. Competition in corals can decrease growth, affect reproductive output, decrease tissue quality, and increase partial mortality (Hoogenboom et al., 2011; Idjadi & Karlson, 2007; Rinkevich & Loya, 1985; Romano, 1990; Tanner, 1997), as well as increase energetic cost to maintain competitive morphologies and repair damage (Chornesky, 1989; Romano, 1990). A decline in competitive stress with climate change therefore has the potential to reduce the prevalence of some of these physiological impacts and increase coral resilience to other stressors. However, despite this potential for decreased competitive stress, competition was still prevalent with both ocean warming and under ocean acidification (at natural seep sites). With both stressors, approximately two-thirds of colonies were competing. Although coral-coral competitive interactions have been predicted to become less frequent in the future (Horwitz et al., 2017), the evidence presented here suggests that competitive stress will not be eliminated because microhabitat variation on reefs can lead to aggregated spatial distributions of colonies, even when coral cover is low.

This thesis largely focused on how climate change indirectly affects communities by altering the frequency and intensity of competition (see Figure 1.5). However, in **Chapter 3** I also considered how competition affects the physiological response to ocean warming, where I showed that exposure to competition increased bleaching severity, and subsequent mortality, following a thermal stress event. While it is widely recognised that species respond differently to bleaching (Baird & Marshall, 2002), there are often fine-scale differences in bleaching severity, with neighbouring colonies of the same species sometimes showing different responses. While this is often attributed to differences in *Symbiodiniaceae* types within colonies (Jones et al., 2008), it is also possible that competition may contribute to some of the fine-scale nuances in bleaching responses between colonies.

Understanding the impact of changes in competition requires an understanding of what drives competitive stress. Where competitive stress arises simply from the occurrence of competition, evidence presented here suggests that moderate reductions in coral abundance and cover may only have minor impacts on coral community dynamics. However, the data presented here suggests that under climate change the intensity of competition may change more rapidly than the occurrence of competition. Declines in abundance and coral cover mean that most corals interact with fewer competitors, and to a lesser extent. Therefore, where the intensity of competition decreases below a currently unknown threshold, a notable decline in competitive stress and subsequent impacts on the community could occur. The prevalence of competitive morphologies, and the diversity of competitive mechanisms (Lang, 1973), suggests that competition has been widespread in coral communities throughout their evolutionary history, and therefore corals may have developed traits that allow them to tolerate the presence of competitors. In contrast, however, most competitive studies show physiological effects of competition in single nubbin-to-nubbin interactions (Romano, 1990; Tanner, 1997), which suggests that the presence of competition alone is enough to result in competitive stress. Elucidating what drives competitive responses will help to interpret how the role of competition in structuring coral communities may change in the future.

6.2.2 Predation

In addition to competition, predation is another biotic interaction that is ubiquitous in all ecosystems, and a form of small-scale biological disturbance (Menge & Sutherland, 1987). Similar to competition, predation is highlighted in ecological theory as a structuring force that affects both abundance (Lotka, 1925; Volterra, 1926) and diversity (Paine, 1966) of species. Predation of corals, or corallivory, is widespread in both fish (Cole et al., 2008) and other taxa (e.g., gastropods, echinoderms; Pratchett, 2010; Stella, 2012) and can exert high levels of predation pressure on corals. Estimates of coral consumption have been shown to be up to 15 g of coral tissue per 200m^2 of reef per day by corallivorous butterflyfish (Cole et al., 2011) and up to 5.7 tonnes of carbonate per year by each individual corallivorous parrotfish, *Bolbometapon muricatum* (Bellwood et al., 2003). The physiological impacts of corallivory include decreases in growth (Lenihan et al., 2011), coral nutritional quality (Rotjan & Dimond, 2010), tissue biomass and lipid content (Cole & Pratchett, 2011), and increases in partial mortality (Welsh et al., 2015) and nematocyst abundance (Gochfeld, 2004). As such, predation can act as a chronic stressor to corals (Cole et al., 2011), and can influence the structure and function of coral communities (Lenihan et al., 2011; Mumby, 2009). For example, intensity of parrotfish feeding can affect zonation in their preferred coral prey species (Littler et al., 1989).

Like competition, the effects of corallivory on individuals and coral communities could vary with climate change. There has already been some consideration of how predation may affect corals under future climate change conditions (Rice et al., 2019). When exposed to thermal stress, corals which have experienced predation have been shown to suffer more frequent and greater severity of bleaching, as well as have slower recovery, compared to corals which have not experienced predation (Madeira et al., 2022; Rotjan et al., 2006; Shaver et al., 2018). Predation on bleached coral is species specific with some corallivores increasing predation rates (Cole et al., 2009) while others actively avoid bleached colonies (MacDonald et al., 2021). However, there has been less consideration of corallivory with acidification. Under OA, predation of juvenile corals by COTS (crown of thorns starfish) resulted in greater subsequent mortality than for corals which did not experience predation (Kamya et al., 2018). To date, there has been no consideration of how the prevalence of corallivory may change under OA. Despite the lack of research in this field, it is hypothesised that changes in predation pressure may arise due to changes in the fish community (e.g., Munday et al, 2014) or changes in coral cover (e.g., Crook et al., 2012; Enochs et al., 2015).

To address this knowledge gap, I planned a field study to compare the intensity of predation pressure from corallivorous butterflyfish (*Chaetodontidae*) on coral communities at multiple naturally acidified reefs. However, due to travel restrictions with COVID-19, this work was unable to be completed in full. Instead, I present here the results of a pilot study on corallivory under OA where I quantified predation pressure at the level of an individual fish, the whole fish population, and the net predation pressure per m^2 of coral cover (Box 6.1). These data were collected at Upa-Upasina (PNG) at the same naturally acidified sites investigated in **Chapter 5** (Box 6.1). Inclusion of these data allows a more complete consideration of how coral communities affected by climate change fit within the environmental stress model (Menge & Sutherland, 1987).

The results indicate that there was significantly lower predation pressure on the acidified coral communities compared to the control communities. However, this net effect was the result of changes at multiple levels. First, although there was no significant difference in the total abundance of butterflyfish, there were significantly fewer obligate corallivores under acidified conditions (Figure 6.1b, Table A6.1). Obligate species are highly dependent on the abundance of their preferred food source. For obligate butterflyfish, this is often *Acropora* and *Pocillopora* colonies (Pratchett, 2005, 2007), both of which can be less abundant under acidified conditions (Barkley et al., 2015; **Chapter 5**; Fabricius et al., 2011). This loss of obligate species aligns with current predictions about the greater vulnerability of specialist species to changes in coral species composition (Binzer et al., 2011; Montoya & Raffaelli, 2010) and a consequent shift towards more generalist species as climate change progresses (Lurgi et al., 2012). Second, individual fish took fewer bites under acidified conditions (Figure 6.2a, Table A6.1). This change was again driven by obligate corallivores with very little change in the number of bites by facultative and non-coral feeders. This is likely due to lower coral availability (Figure 6.1a), meaning more time is spent foraging or swimming between colonies compared to actively feeding (Gunn et al., 2022), but could also be due to shifts in palatability or altered nutritional content of coral. Third, the combination of decreased abundance and fewer bites, resulted in significantly lower predation pressure by the total fish population, again, for obligate corallivores (Figure 6.2b, Table A6.1). This was largely driven by the altered abundance of fish and indicates that factors which affect corallivore abundance may be more critical than physiological or behavioural changes altering predation rate of individuals. Finally, to establish the extent of predation pressure on the coral communities, the population pressure was standardized to the amount of coral cover at each site, which was marginally lower under acidified conditions (Figure 6.1a). The initial hypothesis was that a decrease in coral cover with acidification may increase the amount of predation occurring on any individual colony, resulting from fewer resources supporting the fish community. However, I found that the reductions in predation from fewer obligate species and lower predation rates by individual fish, had a far more significant effect on the predation pressure than the small, reported change in coral cover. This suggests that at the acidified site, corals may have had reduced predation stress and therefore under future ocean conditions, there may be some element of predation release for corals (Figure 6.2c, Table A6.1, Figure A6.1).

Here I show that changes in predation pressure were the result of a combination of both changes in coral cover, fish abundance and predation rates. However, these factors are likely to vary between locations based on community composition, as well as varying across space and over time due to different disturbance histories. In addition, the potential for specialist species to switch to a less preferred food source (Berumen et al., 2005) means predation stress may be shifted to other species of coral. Finally, one of the criticisms of using naturally acidified reefs as a proxy for future ocean conditions is that populations at these sites are open populations, connected to nearby ambient reefs (Fabricius et al., 2014; Shamberger et al., 2014). This is particularly problematic for mobile species such as fish, which move in and out of the seep sites (Munday et al., 2014). Therefore, interpretation of behaviours, such as foraging and diet, may not accurately be extrapolated to future ocean conditions, making it highly challenging to predict both how predation pressure may change, as well as what the outcomes of those changes may be for coral communities. However, the evidence presented here suggests that indirect effects on coral communities through changes in predation pressure have the potential to alter the direct impacts of acidification.

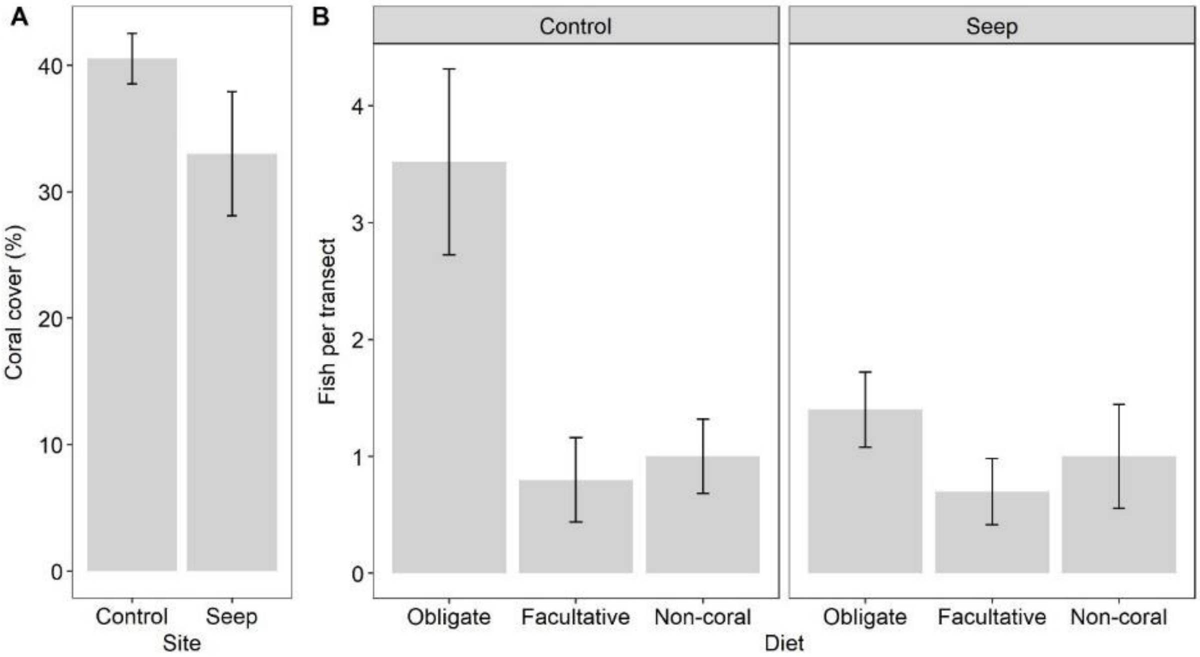

Figure 6.1. A) Mean percent coral cover ± SE. n=8 replicate 5x1m transect per site; B) Mean number of butterflyfish per transect ± SE under acidified seep and control conditions n= 5 replicate 50x4m transects per site. Data were collected at Upa-Upasina reef, PNG. (Coral cover data also presented in ***Chapter 5****)*

Box 6.1.Overview of the methods used to assess predation pressure

Study site

The data were collected from Upa-Upasina, concurrently with data collection for **Chapter 5**.

Fish abundance

The abundance of butterflyfish (Chaetodontidae) was assessed along 5 replicate 50m x 4m belt transects at both the seep and control sites. Transects ran along the reef crest, parallel to the shore and followed a 3-5m depth contour. Fish abundance was measured by visual census of all butterflyfish within 2m of either side of the transect tape, with individuals recorded to species level. Following visual census of the fish population, benthic video transects were taken to analyse coral cover, using the methods outlined in **Chapter 5**.

Feeding observations

Based on the abundance surveys, the six most common species were chosen for feeding observations; *Chaetodon baronessa, C. lunulatus, C. punctatofasciatus* (obligate corallivores), *C. rafflesi*, *Heniochus varius* (facultative corallivores) and *C. vagabundus* (non-coral feeder). Diet type was based on previous butterflyfish feeding studies (Cole et al., 2008; Pratchett, 2005). The inclusion of a non-coral feeder was chosen to act as a control, to establish whether feeding rates change with exposure to high $p\mathrm{CO}_2$ regardless of diet. Feeding observations were completed for a minimum of 10 individuals per species, following the methods described by (Pratchett, 2005). This involved observing an individual for 3 minutes, remaining at a distance of 2-4m and recording all bites taken to pre-determined benthic categories. Best practice was followed such as excluding observations from fish which became unsettled from observer presence, were lost for more than 10 seconds during observation, or engaged in periods of other behaviour (e.g., cleaning). Observations were also excluded if the individuals swam out of the seep area into more ambient pH waters. Where fish were seen in pairs, data were recorded from only one of the pair.

Predation pressure estimates

Predation pressure was estimated at three levels: 1) the number of bites taken by any individual over the observation period; 2) total pressure from the community, where counts from every individual were multiplied by the abundance of that species of fish; 3), the predation pressure of the fish population per m^2, where the total pressure was standardised by the coral cover in m^2. Because fish moved between transect areas, a mean coral cover value was used for each site.

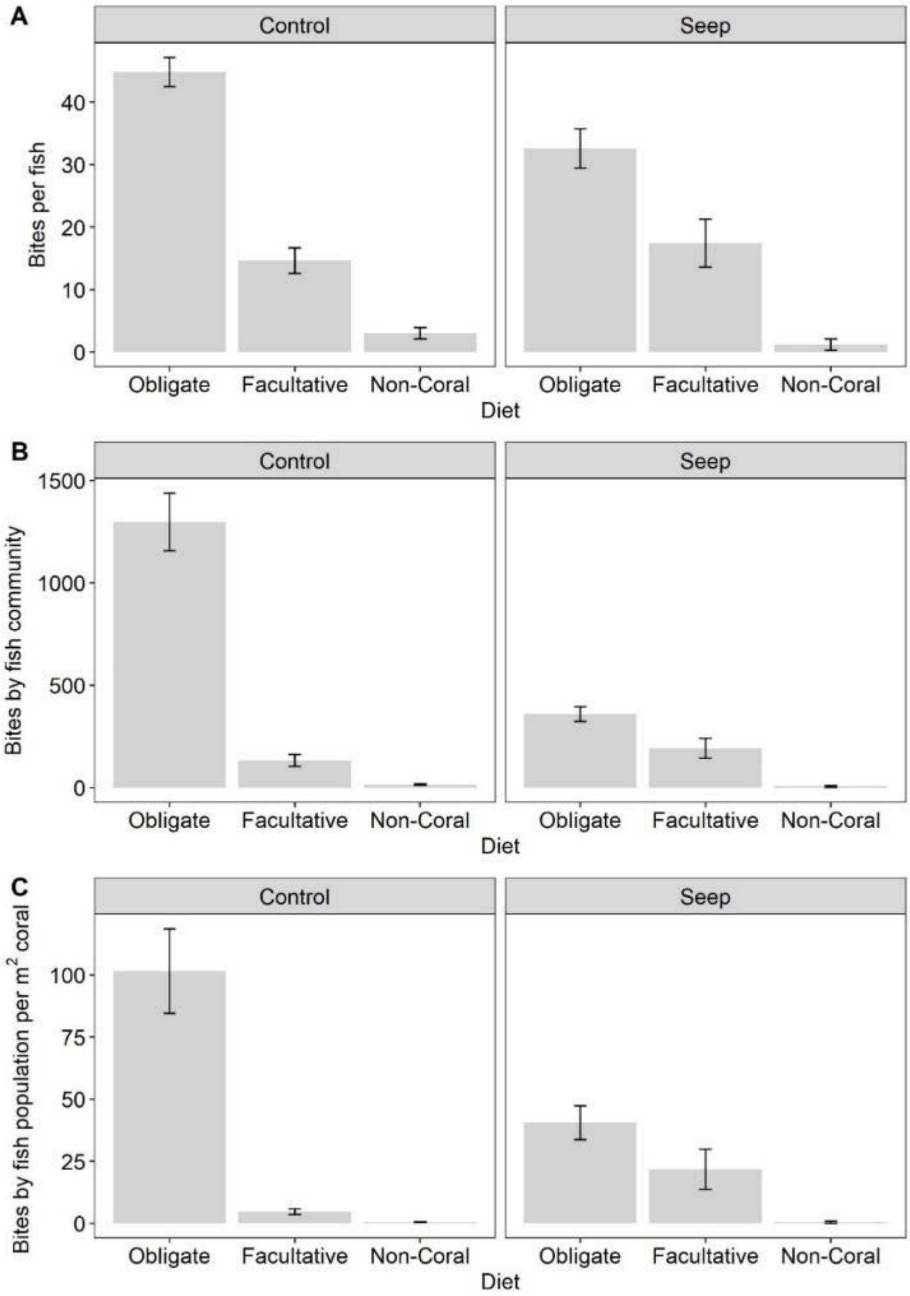

Figure 6.2. Predation pressure from the butterflyfish population under acidified seep and control conditions. Predation pressure was quantified by number of mean bites on coral per 3 minutes, by: A) individual fish; B) the total fish population; C) the total fish population standardized by coral cover at the two sites. Error bars show standard error.

6.3 Other factors influencing how climate change affects biotic interactions

The data collected for this thesis were designed to address the primary aim of investigating the indirect effects of climate change through changes to biotic interactions. However, climate change has a wide range of impacts, including many demographic and community changes which contributed to some of the changes in biotic interactions. Here, I review some of the factors which can co-vary with climate change and can mediate the impact on competition and/or predation.

6.3.1 Site effects

Site specific differences were evident throughout this thesis, in both the coral communities and the indirect effects of climate change on those communities. There were differences in community composition and demographics on a local scale within the Palm Islands (**Chapter 2**), and between islands in PNG (**Chapter 5**). Such differences in communities on small spatial scales are widely reported (e.g., Edmunds & Bruno, 1996) and may result from localised variations in biotic or abiotic factors (Genin et al., 1994; Lenihan et al., 2011). Furthermore, there were site specific differences in competition, both before/outside the stressor and in response to both bleaching and acidification (**Chapter 3, 5**). These differences highlight the significance of the initial state of the community composition in determining both the direct and indirect effects of climate change for a given reef (as per Edmunds & Elahi, 2007). However, this variability means it is extremely challenging to extrapolate findings from any given location to make general predictions about the direct or indirect effects of climate change.

6.3.2 Genus effects and shifts in community composition

Genera specific tolerances to both coral bleaching (ocean warming) and ocean acidification are well established (Fabricius et al., 2011; Loya et al., 2001). The results in this thesis largely corroborates the anticipated findings with decreases in coral cover of the less tolerant *Acropora* and *Pocillopora* colonies, and little change or relative increases in the more tolerant *Porites*, resulting in small shifts in community composition (**Chapter 2, 5**). However, the changes within genera were not consistent between sites. In the Palm Islands, declines in *Acropora* abundance resulted in almost complete loss at some sites but only moderate declines at others (**Chapter 2**). Similarly, at naturally acidified sites *Acropora* tended to decrease in abundance/cover (Barkley et al., 2015) but increased in others (Januar et al., 2017; **Chapter 4**). These inconsistencies may arise from differences in species composition as well as other biotic and abiotic factors.

Genera also had indirect effects on competition. In **Chapter 3**, the genera specific effects on competition were largely not reported because they were overwhelmed by the extent and severity of the coral bleaching response. However, in **Chapter 5**, the frequency and intensity of competition varied significantly between genera. This effect, particularly on intensity, is likely driven by differences in colony morphology between sites. Future research should consider addressing whether genera specific tolerances to the direct effects of climate change, correlate to comparable tolerance to the indirect effects. For example, in **Chapter 3**, bleaching stress overrode competitive stress and therefore the ‘winners’ and ‘losers’ are likely to be largely determined by physiological tolerances to stressors directly. However, under acidification, shifts in competitive hierarchies (Horwitz et al., 2017) along with potential evidence of competitive release (**Chapter 5**) indicate that there may be a mis-match between the ‘winners’ and ‘losers’ based on direct physiological tolerances and indirectly via competition. Similarly, in the **predation pilot study**, the less tolerant genera of *Acropora* and *Pocillopora* may experience a decrease in predation stress. Whether this is sufficient to override direct genera specific effects is unknown.

6.3.3 Coral cover

Lower coral cover was seen both following coral bleaching and with exposure to ocean acidification (**Chapter 2, 5**). These results fit with predictions of lower coral cover under future ocean conditions (Hoegh-Guldberg, 2005; Spalding & Brown, 2015; **Chapter 4**). Coral cover was also consistently significant in analyses of competition under each climate stressor (**Chapter 3, 5**) as well as affected by predation pressure (**predation pilot study**). This highlights the ecological importance of coral cover on reefs and the need for including it in ecological analyses, particularly where those interactions occur in close spatial proximity such as competition. However, the relationship between competition and coral cover was not consistent. In this thesis I showed: significant decreases in coral cover with concomitant declines in competition (E Orpheus, SE Pelorus, **Chapter 2, 3**); significant decreases in coral cover with minor decreases in competition (Tutum Bay, **Chapter 5**); small declines in coral cover with significant decreases in competition (Upa-Upasina, **Chapter 5**); and small increases in coral cover but still with a decrease in competition (NE Fantome, **Chapter 2, 3**). This indicates that while coral cover is important, there must be other factors such as spatial distribution (see section 6.3.6) with potentially more significant impacts on competition.

Coral cover is a quick and effective method to report on reef condition which is widely used as part of reef monitoring (Bruno et al., 2007; De’Ath et al., 2012; Sweatman et al., 2011). However, in this thesis, coral cover masked notable demographic changes such as decreased abundance of colonies, shifts in community composition and changes in the population size structure (**Chapter 2, 5**). These results suggest caution should be taken to not rely on coral cover as the only metric of reef health, nor as an indicator of the frequency or intensity of biotic interactions. Similar concerns about reliance on coral cover have previously been reported (Edmunds & Riegl, 2020; Spalding & Brown, 2015), with a recommendation that we move towards a more demographic approach to monitoring (Cant et al., 2022; Edmunds & Riegl, 2020; Pisapia et al., 2020).

6.3.4 Abundance

Colony abundance decreased with coral bleaching and was lower under ocean acidification. Decreased abundance of corals following the 2016-2017 bleaching event was the result of high rates of colony mortality (**Chapter 2**). While high mortality from bleaching is well established (Eakin et al., 2019; Hughes et al., 2018), the effect on net colony abundance is less often reported (but see: Kuo et al., 2023; Pisapia et al., 2019). Under acidification, lower colony abundance (**Chapter 5**) has similarly been shown at other naturally acidified sites (e.g., Crook et al., 2012) and may result from reduced recruitment (Albright et al., 2010; Fabricius et al., 2017). Colony abundance also had notable effects on competition. While abundance was not included in the analysis, it appeared to have more consistent effects on the intensity of competition than coral cover. Reduced abundance of colonies consistently, and logically, resulted in fewer interactions per m^2 and fewer competitors per colony. Colony abundance is therefore a useful tool in assessing the direct impact of acute stress events like bleaching, as well as in predicting indirect effects through changes in biotic stress. Furthermore, colony abundance is also critical for community resilience to future stressors and provision of ecosystem services (Kayal et al., 2018), and should therefore be included in monitoring more often.

6.3.5 Colony size

Changes in population size structure also occurred under both climate stressors, with a trend for lower abundance of the smallest colonies. This may be driven by reduced resilience of small and/or juvenile colonies, recruitment into the population (Fabricius et al., 2011; 2017) or recruit growth rates (Albright & Langdon, 2011). Interestingly, however, while many studies show a trend toward preponderance of smaller colonies with climate change (e.g., Dietzel et al., 2020; Pisapia et al., 2019), I evidence two examples of increasing frequency of larger colonies. Following the 2016-2017 mass bleaching event, large *Acropora* colonies had proportionally greater survival, followed by rapid growth which resulted in a larger mean colony size than prior to bleaching (**Chapter 2**). This high rate of survival following bleaching is contrary to previous findings (Pisapia et al., 2019). While the reason for these survival rates is unknown, the increase in average colony size was also driven by rapid growth in surviving colonies following mortality of competitors. Under acidification, the mean size of massive *Porites* colonies was more than twice as large as colonies at the control site (**Chapter 5**). This increase in *Porites* abundance and colony size may be driven by greater resilience to unfavourable conditions (McCulloch et al., 2012; Wall et al., 2016) or competitive release. It is interesting to note that changes in population size structure under the different stressors likely resulted from different mechanisms. This highlights the challenges in predicting demographic effects on coral communities, particularly as the severity of ocean acidification continues to increase in the future and will be coupled with additional increases in ocean warming. Furthermore, colony size was intrinsically linked with competition frequency and intensity, with larger colonies or colonies with longer perimeters more likely to be competing and have more competitors (**Chapter 3, 5**). Changes in population size structure is therefore likely to have secondary impacts on the frequency and intensity of competition.

6.3.6 Spatial distribution

In sessile organisms, competition only occurs in close proximity (Connell et al., 2004) with declines in coral cover resulting in fewer potential competitive interactions. However, evidence from thesis suggests any declines may be overridden when corals occur in aggregations, where high competitive intensity was maintained even when cover was low. In this thesis, I did not quantify the spatial distribution of colonies. However, small declines in competitive frequency co-occurring with larger declines in intensity, indicate some level of colony aggregation (**Chapter 3, 5**). Furthermore, the disparity between changes in coral cover and changes in competition with climate stress, also indicate aggregated distribution. Where these aggregations occurred, the effect of spatial distribution overrode the impact of coral cover to maintain higher competitive frequency than anticipated. Occurrence within an aggregation can have positive effects such as increased growth and increased tissue quality in some species (Hoogenboom et al., 2011; Idjadi & Karlson, 2007) and negative effects such as greater competition for resources (Brito-Millán et al., 2019). The relative costs and benefits of aggregated living under climate stress is unknown. However, aggregations within a community can clearly impact the indirect effects of climate change through altered competitive interactions.

6.4 Limitations and future research

In this thesis I have highlighted the importance of the indirect effects of climate change through changes in competition and predation of corals. This work also contributes to the significant knowledge gaps of how biotic interactions may change in the future. Development of the methodologies used here could further aid in our understanding of indirect effects. For example, coral identification in **Chapters 2, 3** and **5** was limited to genera. However, notable differences in bleaching or acidification tolerance have been identified between species and even haplotypes (e.g., Burgess et al., 2021; Gold & Palumbi, 2018). By increasing resolution to species level, our ability to investigate the spectrum of effects on competition and other biotic interactions would also increase. Similarly, the diversity of responses in coral communities to combined climate and competition stress were highly site specific. This variability in response has been highlighted as a significant issue in indirect effect research (Tylianakis et al., 2008). While the results presented here may indicate the general trends of response, there may be challenges in accurately extrapolating these findings to additional locations. Additional research at other sites, with detailed abiotic and biotic exploration of the local environment, may help to establish the mechanisms driving site specific responses. Understanding these effects will further aid in accurate predictions of reefs under future ocean conditions.

To fully explore how climate change indirectly affects coral communities through altered competition, a more in-depth exploration of competition is required. Inclusion of competitive outcome (i.e., ‘win’, ‘lose’, ‘standoff’; e.g., Álvarez-Noriega et al., 2018) and how this varies with ocean warming and acidification is critical to understand. While this was not considered in this thesis, there is evidence from ocean acidification studies that relative competitive success may vary in the future (Horwitz et al., 2017; **Chapter 4**). Similarly, we need to know whether the competitive abilities of corals change. Under ocean acidification the competitive ability of hard corals was unaffected with short term exposure to acidification (Evensen & Edmunds, 2018). In contrast, soft corals showed decreased cytotoxicity, although this could not be conclusively attributed to competitive investment/ability (Januar et al., 2016). However, to the best of my knowledge the competitive abilities of corals during coral bleaching has not been investigated. Finally, if we wish to assess the sum effects of competitive stress on corals, we also need to consider coral-algae interactions and how they may change in prevalence and impact with both bleaching (Jompa, 2001) and acidification (Crook et al., 2016; Enochs et al., 2015).

The impacts of climate change on reefs to date has largely been a result of ocean warming resulting in rising SSTs and increased frequency of marine heatwaves. However, in the future the severity of acidification will increase and further contribute to climate stress on reefs. The combination of ocean warming and acidification is recognized to have significant, and often synergistic, physiological impacts on coral communities (Harvey et al., 2013; Prada et al., 2017), however less is known about the indirect effects. While I do not have the evidence here to discuss whether the combination of these stressors will exacerbate the individual impacts of each climate stress on competition, this has previously been considered in a mesocosm study. This work showed that the combination of thermal stress and acidification exacerbated the impact of competition between colonies, to decrease photosynthesis for the first week of exposure (Johnston et al., 2020). Addressing this knowledge gap would allow for a more realistic understanding of competition under future ocean conditions. Future research may consider addressing this gap at extreme environment reefs, which are affected by both low pH and warm temperatures, and which therefore allow a more accurate assessment of biotic interactions under climate stress (e.g., Bouraké lagoon; Camp et al., 2017).

One of the key findings from the competition analyses was the importance of the spatial distribution of colonies within a community. Aggregated distribution of coral is common on reefs, however to the best of my knowledge changes in spatial distribution have not been considered from either coral bleaching or ocean acidification. We may anticipate increases in coral aggregation under both bleaching, where differences in mortality between microhabitats (Lenihan et al., 2008) can result in the greater survival in more favourable habitats, and under acidification where declines in abundance and calcification in CCA (Anthony et al., 2008; Doropoulos et al., 2012) may result in lower availability of stable settlement habitat. However, in contrast, declines in abundance and coral cover may equally result in decreased aggregation. Additional investigation may consider the balance of these impacts to establish whether the spatial distribution of colonies may change under future ocean conditions.

Darwin hypothesized that the effect of biotic interactions would have different impacts under different abiotic conditions (Darwin, 1859). In particular, the distribution of an organism is limited by the abiotic conditions at cool (high latitude) temperatures and biotic interactions at warm (low latitude) temperatures (Paquette & Hargreaves, 2021). Research in this thesis was conducted at two warm, low latitude reefs and shows that changes in biotic interactions may have significant implications for coral reefs. It is possible therefore that at cooler, higher latitude reefs, the indirect effects of climate change through altered species interactions, may be less significant for corals than the already documented significant direct effects (e.g., Agostini et al., 2018; Hall-Spencer et al., 2008; Manzello et al., 2014). Additional investigations of high latitude/sub-tropical reefs may allow greater investigation of the relative importance of biotic interactions across the geographic distribution of coral reefs and allow more precise predictions of climate change on reefs when adjusted for latitude.

6.5 Implications of thesis

6.5.1 Indirect effects

In this thesis I show that the indirect effects of climate change have important effects on corals. These indirect effects are both mechanisms driving community change (e.g., increased mortality in bleaching corals) and arise due to changes in coral communities (e.g., reduced competitive intensity with lower colony abundance; Figure 6.3). One of the concerns of indirect effects is that they can occur on a greater scale than direct effects (Connell *et al.*, 2013; Alva-Basurto & Arias-González, 2014). While often overlooked, coral bleaching, the primary concern of ocean warming, is in itself, an indirect effect (Figure 6.3), where the relationship between corals and their *Symbiodiniaceae* population is disrupted by thermal stress. The scale upon which coral bleaching can affect corals and coral communities (Eakin et al., 2019; Heron et al., 2016) highlights the potential scope of impact from changes in biotic interactions on reefs. Indeed, the indirect effects of climate change may be more significant than the widely reported direct effects.

Another concern with indirect effects is that species which are initially unaffected from abiotic climate stress, may still be affected indirectly (Crook et al., 2016; Garrard et al., 2013). No definitive evidence was found here to suggest that colonies which tolerated the abiotic stress were subsequently affected by an indirect effect through altered species interactions. However, this may be more apparent for changes in biotic interactions which result in complete mortality, such as through predation (of a non-modular organism) or disease. A higher resolution analysis using species rather than genera would also be required to better establish indirect ‘winner’ and ‘loser’ species, which could be compared with direct/physiological winner and loser species (Fabricius et al., 2011; Loya et al., 2001). However, evidence from **Chapter 4**, highlights bioerosion and changes in CCA as potential mechanisms which may result in acidification tolerant species subsequently being negatively affected by an indirect effect through reduced availability of suitable settlement habitat (Fabricius et al., 2017; Figure 6.3). As such, even climate tolerant species of coral may struggle to find space for settlement which may reduce their future abundance.

In this thesis, only two biotic interactions (competition and predation) are considered in depth. However, a wide range of changes to, and consequences from, these interactions are highlighted. Furthermore, many additional indirect effects of ocean acidification are identified and discussed in **Chapter 4**. Understanding these indirect effects is critical in our ability to scale up findings of impacts to an ecosystem level but can also help to explain why comparable colonies have variable responses to stressors, climate or otherwise. Unfortunately, the breadth of these interactions and the multiple pathways of effects (Figure 1.3; 1.5; 6.3), makes predicting the indirect effects and the outcome of such effects, highly challenging.

6.5.2 Ocean warming compared to ocean acidification

Ocean warming and ocean acidification are very different stressors for corals. Ocean warming is an acute stressor, resulting from rising SSTs and increased frequency and intensity of marine heatwaves. This thesis focused on coral bleaching which is an increasingly common outcome of thermal stress resulting from such warming. In contrast, ocean acidification is a chronic stressor, with most reefs still at a level below that where widespread impacts for corals are anticipated. By comparing the effect on competition of both coral bleaching as a proxy for ocean warming, and the CO_2 seeps as a proxy for ocean acidification, it is possible to consider the relative severity of each climate stressor. Here I refer to the 2016-2017 bleaching event and exposure to the PNG CO_2 seeps as examples of ‘climate stress’. Interestingly, despite the differences in the type (acute vs chronic) and the physiological impacts of stress (bleaching vs altered calcification), both stressors had very similar impacts on the frequency and intensity of competition (Figure 6.4; **Chapter 3, 5**). The similarity in response between climate stressors is likely due to similar responses in the drivers behind the changes; decreased coral cover and abundance. For example, under ocean warming (coral bleaching) the number of colonies decreased 58% after bleaching and the proportion of colonies competing decreased 12%. Under ocean acidification, the number of colonies was 55% lower at the seep site than the control, and the proportion of colonies competing was 18% lower. As such, while the climate stress of ocean warming and ocean acidification appear to be comparable, any stressor or disturbance which affects coral cover or abundance is equally as likely to disrupt competition as the climate stressors considered here. Furthermore, as climate change continues to progress, corals will eventually experiencing concurrent chronic and acute heat stress, as well as chronic acidification stress (see section 6.5.4).

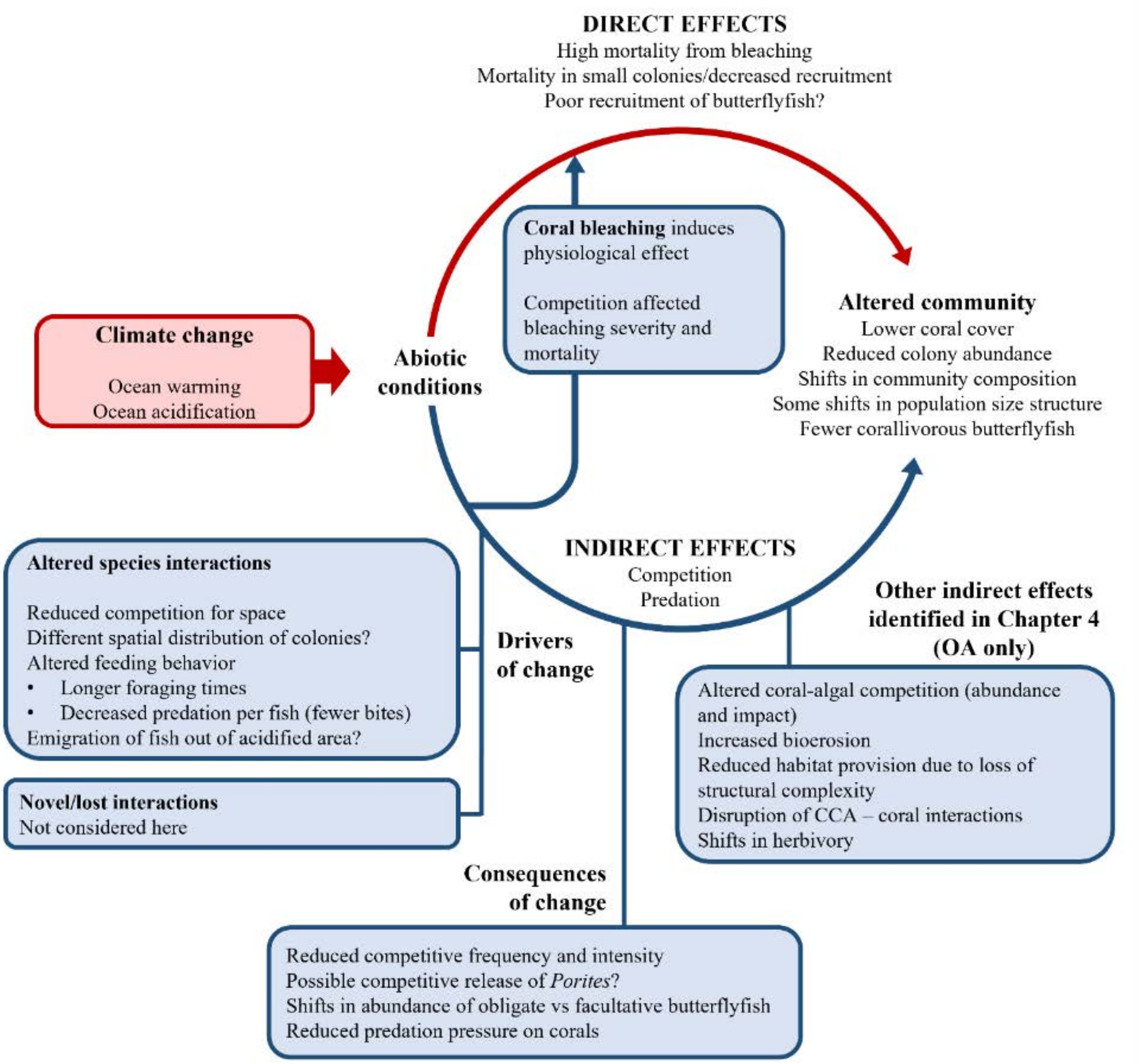

Figure 6.3. The direct (red) and indirect (blue) pathways of climate change impacts seen in this thesis, using the framework set out in Figure 1.5.

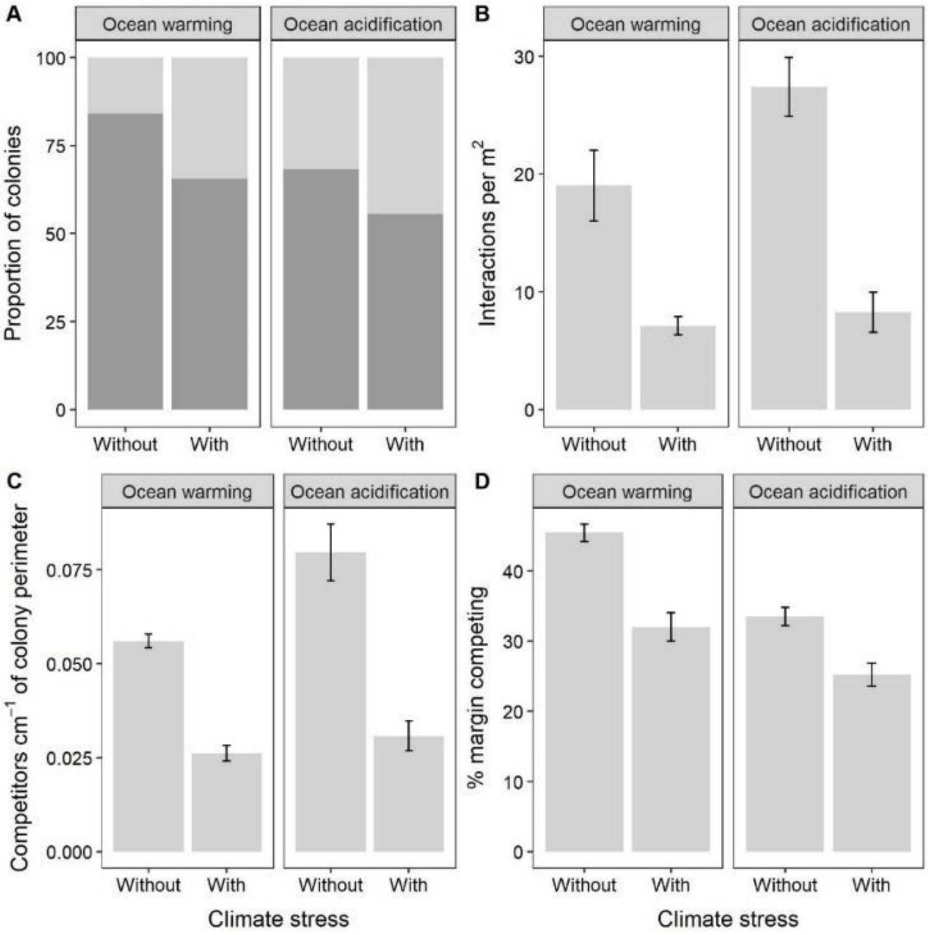

Figure 6.4. A comparison of impact of ocean warming (coral bleaching) and ocean acidification (chronic effects of CO_2 seeps) on the frequency (A) and intensity (B, C, D) of competition. A) the proportion of colonies competing, dark bars = competing, light bars = not competing; B) the number of unique interactions per m^2 (transect mean ± SE); C) the number of competitors (colony mean ± SE) and; D) the percent of the margin competing (colony mean ± SE). 'Without' climate stress refers to before bleaching, and control conditions for acidification; 'With' climate stress refers to after bleaching, and seep sites. Bars show average across all sites/reefs within climate stress categories.

6.5.3 Environmental Stress Model

In this thesis, I aimed to consider how the changes seen in biotic interactions fit with the Environmental Stress Model (ESM), developed by Menge and Sutherland (1987) (Figure 1.2). Traditionally this model considers the relative contribution of biotic and abiotic stressors to community composition, along a gradient of stress. However, it is also possible to apply this model to climate change, which over time is pushing many ecosystems along a gradient of stress towards harsher conditions (Menge, 2023). In this thesis I provide evidence that shows that competition may become less frequent and less intense with climate change (**Chapters 3, 5**). Similarly, I provide early evidence that predation pressure on corals may decrease with acidification. Consistent with ecological theory, together, these results indicate that both predation and competition may become less important as a structuring force as climate change continues to make conditions less favourable for coral survival.

In the ESM, an increase in environmental harshness is when the conditions move away from the optimal conditions towards conditions more likely to result in mortality (Menge & Sutherland, 1987). This definition requires not just understanding the frequency and intensity of the interactions but also the physiological impact or outcome for individuals. The evidence presented here largely considers the prevalence of competition and predation with little evidence of changes in outcome (but see mortality, **Chapter 3**). However, these findings can be combined with previous evidence in the literature to estimate the level of stress from these interactions. For example, under ocean acidification, competition has been shown to cause significantly lower growth in some species compared to ambient conditions (Evensen et al., 2015; Horwitz et al., 2017). With reduced competitive frequency and intensity (**Chapter 5**) competition could become less important to the structure and function of acidified reefs but will likely still play a role. However not all species experience similar declines in growth (Brien et al., 2016) highlighting that the interpretation of the model is likely to be species specific.

Considering the results of this thesis in terms of ecological theory, can help understand potential changes to reefs under future conditions. However, there are a few limitations with the data collected to fully investigate how my results fit within this theory. First, the basis of the ESM is that the relative importance of predation, competition, and physical stress change along a gradient of stress. A comparison of two sites along a gradient (**Chapter 5**), or in the same location but separated by extended periods/with different levels of stress (**Chapter 3**), is sufficient to consider a gradient (Menge, 2023). However, the information we get is a snapshot of two individual times/sites and may not be full representative of any community shifts due to climate change. For example, in **Chapter 2**, I highlight the diversity of community responses to bleaching over a small geographic scale. In addition, to fully consider how climate stress may affect the relative importance of structuring processes, requires both competition and predation to be quantified (Menge, 2023). While I present the results from my pilot study in this discussion, unfortunately replicate analyses at additional sites were not able to be completed due to travel restrictions during COVID-19. Additional evidence is therefore required to adequately report how climate change affects coral community structuring, in terms of the ESM.

6.5.4 Multiple stressors

In **Chapter 3** I consider how the occurrence of competition and bleaching affected colony outcome, including bleaching severity, growth rates and mortality. These data can also be used to consider the type of interaction between the abiotic and biotic stressors. Here I compared the mortality rates of competition alone, bleaching alone and the combined stressors, against an estimated mortality rate, to assess for synergistic interactions (Figure 6.5). This estimate was calculated using the multiplicative model: (A+B)-(A*B). Multiplicative models are useful when the impact from one stressor can probabilistically be compounded by another stress (Folt et al., 1999), and are more appropriate than additive models for mortality rates (Côté et al., 2016). The measured combination of competition and bleaching was extremely close to the predicted combined effect, evidencing a multiplicative or weakly additive interaction (Figure 6.5). The lack of a non-additive (antagonistic or synergistic) response means that the combination of competition and bleaching is unlikely to either mitigate or exacerbate the impacts on mortality rate compared to the sum of the individual stressors. Evidence of non-synergistic interactions have previously been shown on coral reefs under the combination of fishing and coral bleaching which resulted in an antagonistic or weakly additive response on coral cover (Darling et al., 2010). This response was presumed to arise from coral bleaching being a dominant stressor. There is some indication of bleaching being the dominant stressor in this analysis, particularly with severe bleaching (Figure 6.5a, b). The difference in relative impacts between mild and severe bleaching suggests that at mild bleaching, competition is the more dominant stressor. Furthermore, it is worth highlighting that the no-competition, no-bleaching category was not a true control. The corals in this category were exposed to the same thermal stress as the other colonies but did not bleach. Despite maintaining their *Symbiodiniaceae* population, this thermal stress may have cause other physiological effects which decreased resilience to high competitive intensity.

Synergies between stressors are challenging to accurately evidence and are often misidentified (Côté et al., 2016; Dunne, 2010). However, when they occur, they can complicate our ability to predict the impact of stressors in the future because they are not predictable from the impact of the individual stressors (Bruder et al., 2019; Connell et al., 2011) and result in underestimating the net impact (Darling & Côté, 2008). However, the largely predictable response of mortality shown here is a source of optimism for ecological models, allowing mortality rates to be calculated relatively accurately from the sum of two, more easily measured, stressors. The simple multiplicative effect shown here supports more recent work which has highlighted that additive responses are the most common interaction type (Darling & Côté, 2008). Whether such predictable or additive results would also occur with the combination of other stressors, or for other physiological metrics (e.g., growth, recruitment) is not known. Furthermore, while the multiplicative responses provide some optimism for future reefs, multiple stressor research has shown the combined impact of more than two stressors is largely synergistic/non-additive (Crain et al., 2008; Diamant et al., 2023). Therefore, as the combination of ocean warming and ocean acidification occur, we may see greater prevalence of synergies between abiotic and biotic stressors.

6.6 Conclusions and what does this mean for future reefs?

The extent and severity of threats to coral reefs globally mean there is a significant research effort focusing on predicting how coral reefs may change toward the end of the century (Harvey et al., 2013; Kroeker et al., 2013; Van der Zande et al., 2020). One of the greatest challenges to these models is understanding how climate change affects biotic interactions (Tylianakis et al., 2008) as well as understanding how these changes fit within ecological theory. Linking changes in interactions to ecological theory may allow us to better predict the effects of climate change and consequently target our conservation priorities (Montoya & Raffaelli, 2010). Therefore, the primary application of developing our understanding of the indirect effects of climate change is to improve accuracy in predictive models. Furthermore, much of the climate change research to date has used single species studies and then extrapolated these findings to population, community, or ecosystem level. However, the indirect effects presented in this thesis and other studies (e.g., Coker et al., 2009; Evensen et al., 2015) highlight that single species studies are unlikely to scale up accurately without consideration of biotic interactions (Edmunds et al., 2016). Finally, indirect effects have been shown here to affect the reef structure and potentially functioning. The structure and function of reefs are the root of many ecosystem services, and as such are key factors to be targeting conservation effort on. Therefore, understanding the indirect effects of climate change may help to guide conservation efforts.

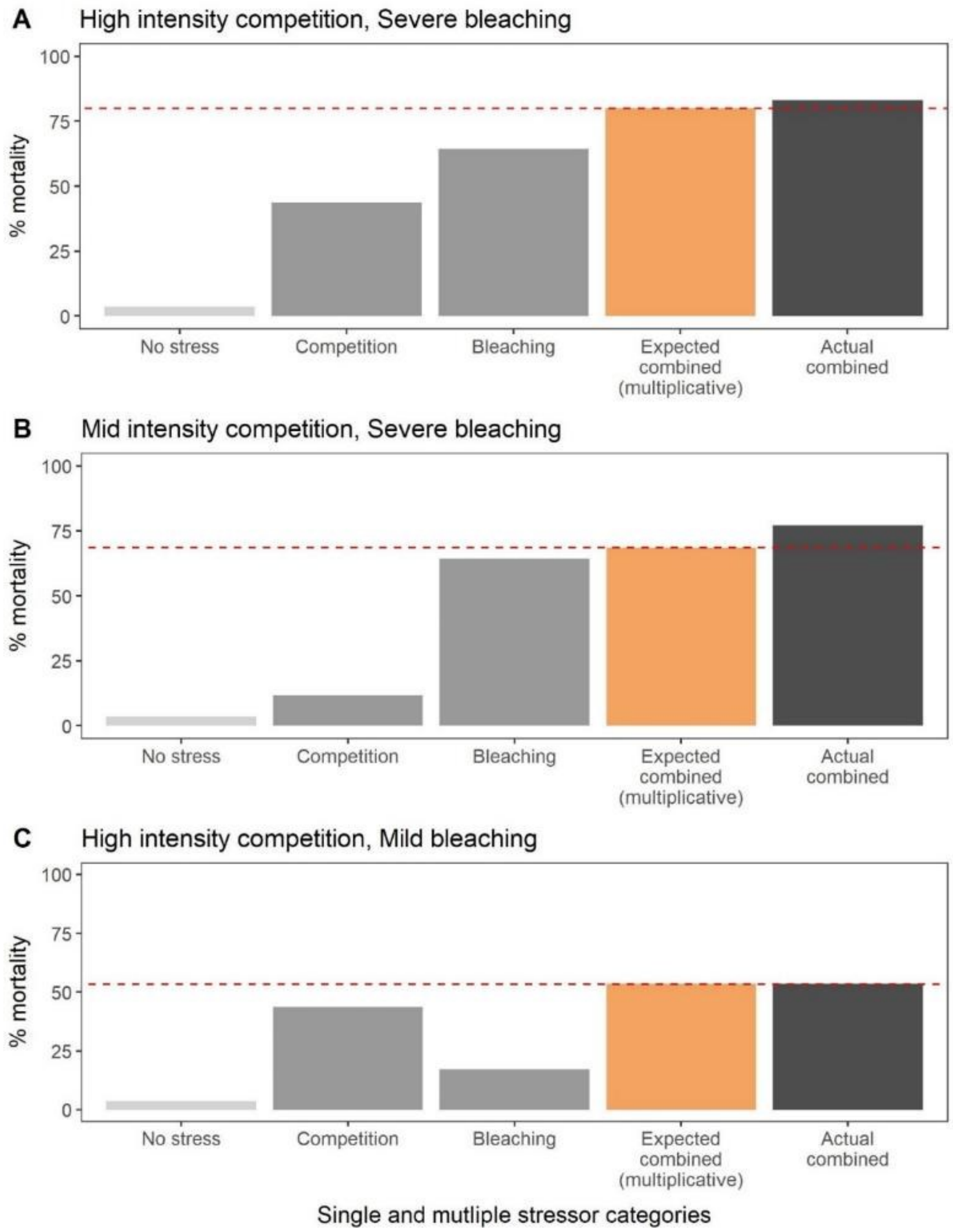

*Figure 6.5. The impact of single (competition; bleaching) and multiple stressors (competition + bleaching) on colony mortality rate following the 2016-2017 bleaching event (**Chapter 3**). Expected combined represents a multiplicative interaction, (A+B)-(A*B); shown by red dotted line to aid comparison. High and mid intensity competition and severe bleaching were defined as per Chapter 3. Graph structure replicated from Côté et al. (2016) to establish multiple stressor response.*

Overall, the results presented here suggest that competition may become a less prevalent stressor on reef in the future. A decrease in the prevalence of these competition and predation stressors under ambient conditions has been shown to affect species diversity or composition. Collectively, these results indicate that competitive release will mean that competition is less of a structuring force for coral communities under future ocean conditions. Although the results are preliminary, my thesis also provides early evidence the predation pressure on corals may be reduced under climate change. However, under thermally stressed or acidified conditions, we may not see comparable changes where corals are already experiencing significant abiotic stress. Therefore, the net effect of coral bleaching and ocean acidification is extremely hard to predict. The evidence presented in this thesis largely supports ecological theory which suggests that the dominant structuring force will shift away from competition and predation and towards abiotic stressors under climate change. However, many of these ecological theories are limited in terms of the breadth of interactions they consider. There may be many other biotic interactions that increase in prevalence, intensity or have altered outcomes which may make them more influential on future reefs. Furthermore, changes in community structure, such as community composition and colony abundance, may result in decreased resilience of coral populations and communities to abiotic stress. Nevertheless, predicting the outcome for coral reefs under climate change requires a new understanding of changes in the physiological impacts of biotic interactions, which is often unknown. As we move into the Anthropocene, seminal ecological theories may need to be revised to consider the net effects of increased levels of abiotic stress on ecosystem functioning, along with the impact of this stress on prevalence and intensity of well-established biotic interactions under novel abiotic conditions.

Glossary

Biotic interactions: The relationship between individuals where the effect of one individual can affect the other. Individuals can be from the same or different species (Brooker, 2006)

Climate change: A change in the state of the climate greater than the anticipated variations, over extended periods, typically decades or longer, and resulting from natural or anthropogenic forcings (IPCC, 2014)

Community: A local assemblage of corals with some degree of structure between individuals or species (Connell, 1975; Done, 1999)

Community structure: Biotic structure or composition of a community, including species richness, diversity and the interactions between individuals and populations within (Morin, 1999)

Community/ecosystem functioning: The storage or movement of energy or material within an ecosystem (Bellwood et al., 2019)

Competition: Occurs when multiple individuals or species have overlapping resource requirements and when that resource is limited in supply, resulting in negative fitness or performance consequences for one, or both, of the competitors (Birch, 1957; Booth & Murray, 2008). In this thesis competition was defined as any pair of colonies with all or part of their margin closer than 5cm apart (Hoogenboom et al., 2017; Lang & Chornesky, 1990; Van Veghel et al., 1996)

Competitive exclusion and release:

Mechanisms driving community or ecosystem species diversity through competitive interactions:

- **Competitive exclusion**: Exclusion of a species from a local community by the presence of a more dominant competitor (Menge & Sutherland, 1987; Segre et al., 2016)

- **Competitive release**: Lack of negative competitive interactions, often through removal or loss of a strong competitor, which results in increased fitness of remaining individuals (Gilman et al., 2010; Segre et al., 2016)

Coral bleaching:
Disruption of the symbiotic relationship between corals and their Symbiodiniaceae, which results in expulsion of the algae and a consequent loss of colour for the coral (hence ‘bleaching’), as well as the loss of their primary energy source. Often results in morbidity or mortality for corals.

Ecosystem: Occurrence of one or more communities along with their abiotic environment (Morin, 1999)

Indirect effects: A change in the physical environment (or other modifying agent) which alters a biotic interaction between two or more individuals (Krivtsov, 2009; Wootton, 1994).

Marine Heatwave:
A prolonged period of anomalously warm ocean temperature (Oliver et al., 2021)

Multiple stressors: The concurrent occurrence of two or more stressors. Outcome of interaction between stressors may be:

- **Additive**: combined stress is equal to the sum of the individual stressors
- **Antagonistic**: combined stress is lower than the sum of the individual stressors
- **Synergistic**: combined stress is higher than the sum of the individual stressors

(Côté et al., 2016; Crain et al., 2008; Darling & Côté, 2008; Folt et al., 1999)

Multiplicative: Type of model to consider multiple stressors, used when one stressor can be further built upon by a second stressor (Côté et al., 2016; Folt et al., 1999)

Ocean Acidification: A reduction in oceanic pH over extended periods, typically decades or longer, largely resulting from increased absorption of atmospheric CO_2 into the oceans (IPCC, 2014)

Ocean Warming: A rise in mean sea surface temperatures (SSTs) over prolonged periods resulting from increasing global surface temperatures (IPCC, 2014).

Population: Group of individuals of a single species occurring within a local area

Predation: An interaction between trophic levels through the consumption of an individual, or part of an individual, by another (Connell, 1975; Lubchenco, 1979). For the data collected in this thesis, predation refers to the consumption of coral tissue by corallivorous butterflyfish, however, predation by Crown of Thorns Starfish (COTS; *Acanthaster planci*) and *Drupella sp.* are also discussed.

Reef: Ecosystem created by the deposition of calcium carbonate by corals and other calcifying organisms. In this thesis, a 'reef' refers to a tropical, shallow water, coral reef, unless otherwise specified.

Stressor: A biotic or abiotic disturbance which exceeds natural levels of variation to cause a sublethal, negative effected on individual performance. May also apply to populations where it describes a decline in the abundance of individuals (Crain et al., 2008; Done, 1999; Hughes & Connell, 1999)

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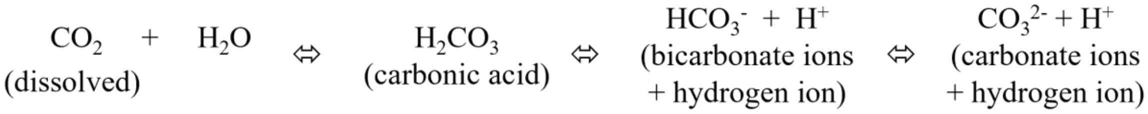
Appendices

Appendix A: Supplementary materials for Chapter 1

A1. Ocean acidification and the effect on seawater carbonate chemistry

Ocean acidification is a reduction in oceanic pH over extended periods, typically decades or longer, largely resulting from increased absorption of atmospheric CO_2 into the oceans (IPCC, 2014). This additional carbon dioxide results in an increase in H^+ ions and therefore a lower total pH (pH_T) which is measures of the abundance of H^+ ions. This change results in a shift in the equilibrium between bicarbonate (HCO_3^-) and carbonate ions (CO_3^{2-}), towards a greater dominance of bicarbonate (Hoegh-Guldberg, 2011; Equation A1.1). Shifts in water chemistry are particularly concerning for calcifying organisms such as corals, which rely on the availability of carbonate ions for calcification (Kleypas et al., 1999). Aragonite is a form of calcium carbonate which often favoured by calcifying organism (Ries et al., 2009). Decreasing ocean pH also causes a decrease in aragonite saturation (**Ω**) which is a measure of how easily aragonite can dissolve into water. With ocean acidification, aragonite saturation is moving from supersaturated conditions (**Ω** >3.5) where it can easily precipitate out of the water by calcifying organisms, towards less saturated conditions (**Ω** <3) where calcification is more costly, and may be counteracted by dissolution (Silverman et al., 2009).



$$\underset{\text{(dissolved)}}{CO_2} + H_2O \Leftrightarrow \underset{\text{(carbonic acid)}}{H_2CO_3} \Leftrightarrow \underset{\substack{\text{(bicarbonate ions}\\ \text{+ hydrogen ion)}}}{HCO_3^- + H^+} \Leftrightarrow \underset{\substack{\text{(carbonate ions}\\ \text{+ hydrogen ion)}}}{CO_3^{2-} + H^+}$$

Equation A1.1. The chemical reactions caused by dissolved carbon dioxide (CO_2) in seawater. Arrows show bidirectional nature of changes, with seawater carbonate chemistry occurring along a spectrum.

Seawater carbonate chemistry can be calculated from water samples based on a few known parameters. These parameters include total alkalinity (TA), total inorganic carbon (TCO_2) which is the sum of bicarbonate and carbonate, pH and pCO_2. Systems such as CO2SYS can use two of these parameters to calculate the remaining carbonate chemistry (Lewis & Wallace, 1998)

Appendix B: Supplementary materials for Chapter 2

Table A2.1. Divisions of colony area (cm^2) used to allocate colonies to size classes, based on diameter of a circular colony structure. Colonies within the smallest size class were divided into juveniles (<20 cm^2 or <5cm in diameter) and small adult colonies.

Area cm^2	**Size category** *Based on diameter of circular colony*
0 – 79 cm^2 *0 – 20 cm^2* *21 -79 cm^2*	0 – 10 cm *<5 cm - Juvenile* *5 – 10 cm*
21 -79 cm^2	5 – 10 cm
80 - 314 cm^2	10 – 20 cm
315 – 707 cm^2	20 – 30 cm
708 – 1257 cm^2	30 – 40 cm
>1258 cm^2	>40 cm

Table A2.2. Skew and Kurtosis analysis of the population size structure before (2015) and after (2018) bleaching

		Skew 2015	***Skew 2018***	***Kurtosis 2015***	***Kurtosis 2018***
Site	*E Orpheus*	2.89	1.54	14.63	4.94
	SE Pelorus	4.63	3.58	29.34	15.08
	NE Fantome	2.03	2.72	8.42	10.59
Genus	*Acropora*	3.8	2.78	26.01	10.76
	Pocillopora	3.09	0.75	13.61	1.71
	Porites	2.33	1.71	10.03	5.89

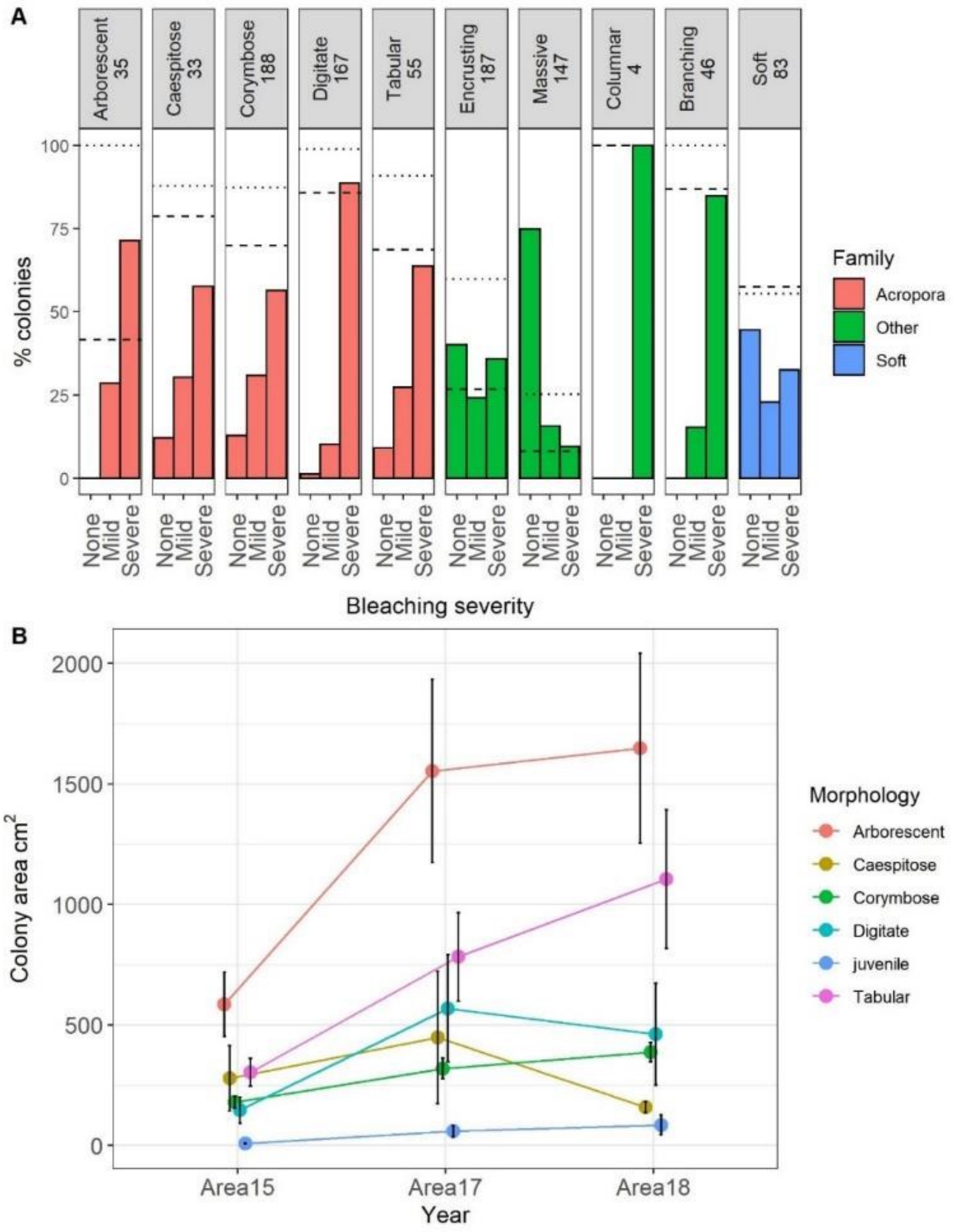


Figure A2.1. A) Total % of colonies in each recorded morphology by bleaching severity. Dotted lines show total % of colonies with bleaching. Dashed line show total % of colonies which died. Juvenile, solitary/free living corals and morphologies recorded as 'other' have been excluded due to lack of certainty in identification and/or small sample sizes. Number of colonies is given in morphology title. B) Growth rates of Acropora *colonies for the 6 morphologies recorded.* Pocillopora *and* Porites *were excluded due to the limited range in morphologies seen. Error bars show the variation between colonies. n=71 colonies*

Appendix C: Supplementary materials for Chapter 3

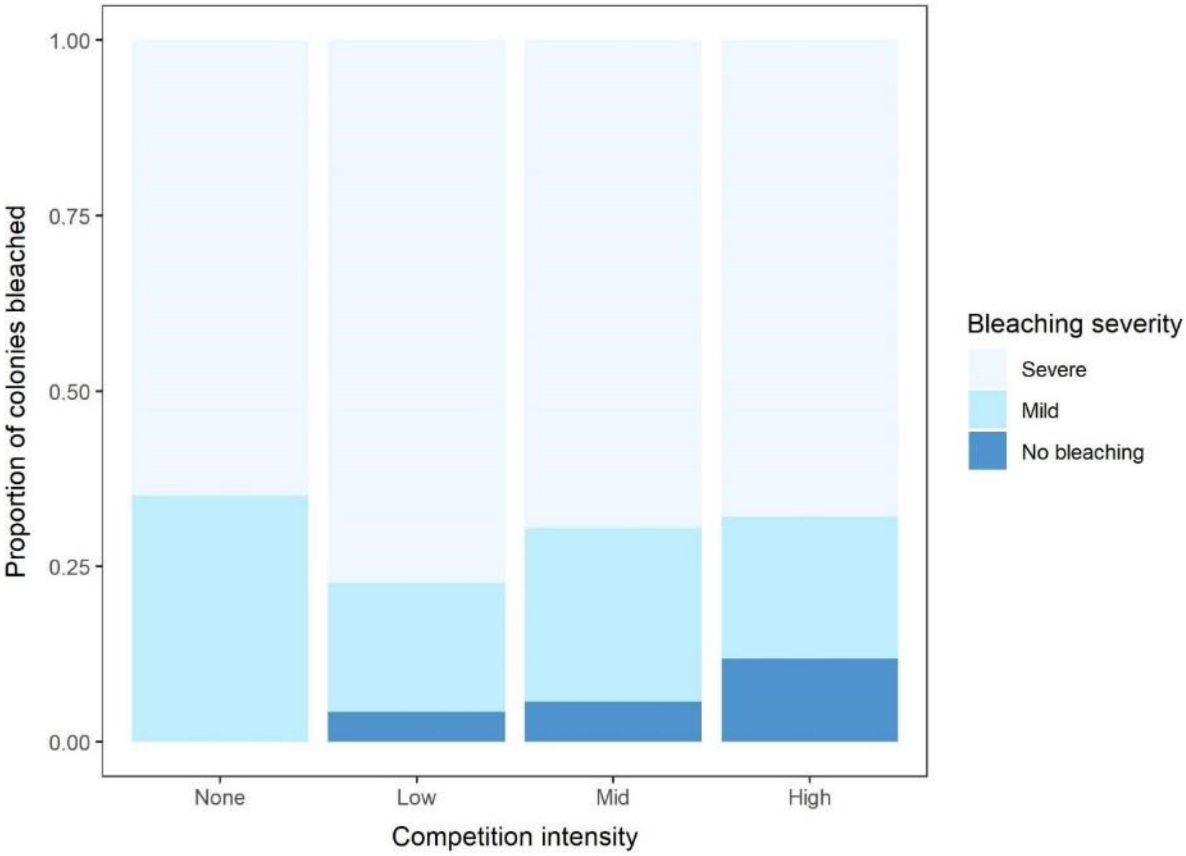


Figure A3.1. The proportion of Acropora *colonies in three levels of bleaching severity in relation to the intensity of competition. n=489 colonies.*

Appendix D: Supplementary materials for Chapter 5

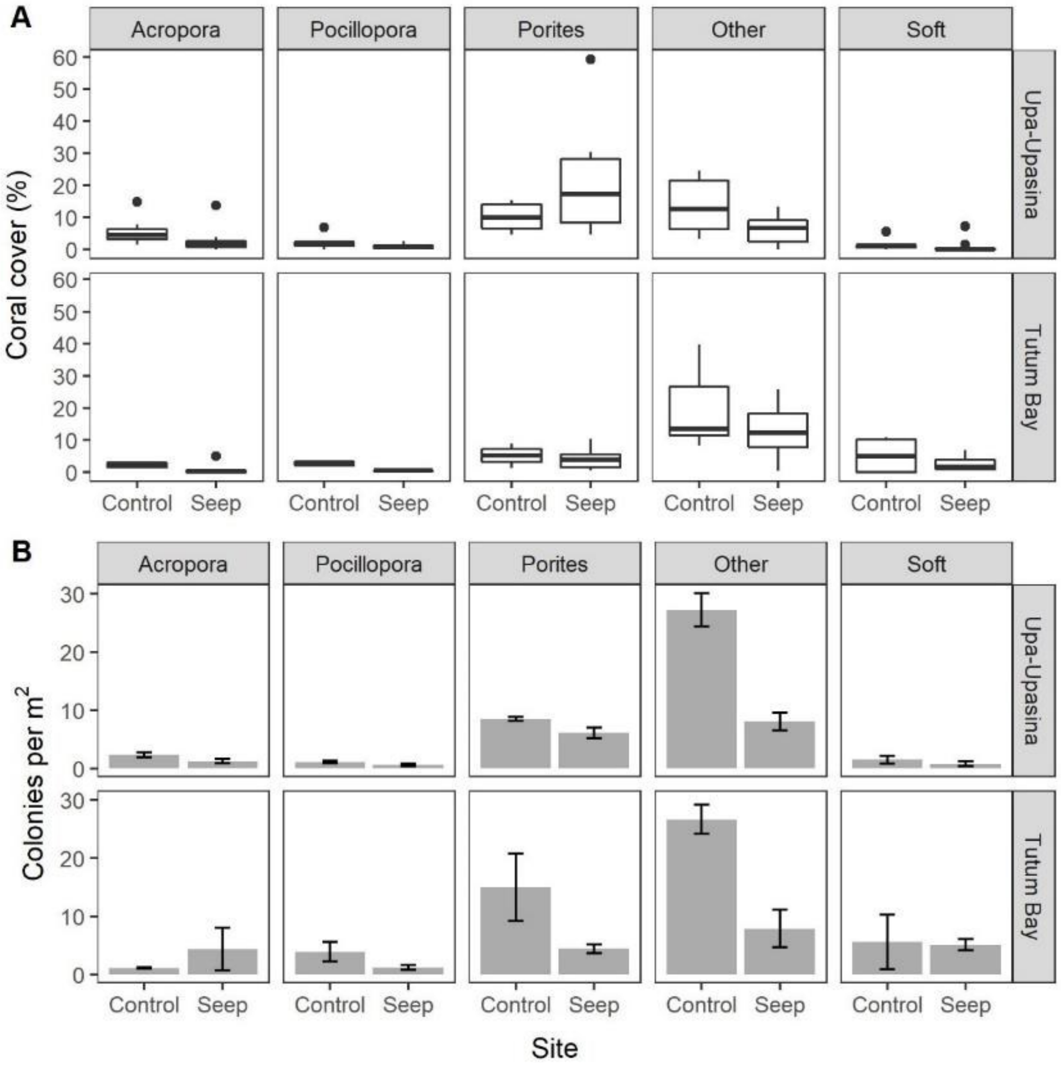


Figure A5.1. Mean (± SE) genus level A) coral cover and B) colony abundance, at control and seep sites at Upa-Upasina Reef and Tutum Bay.

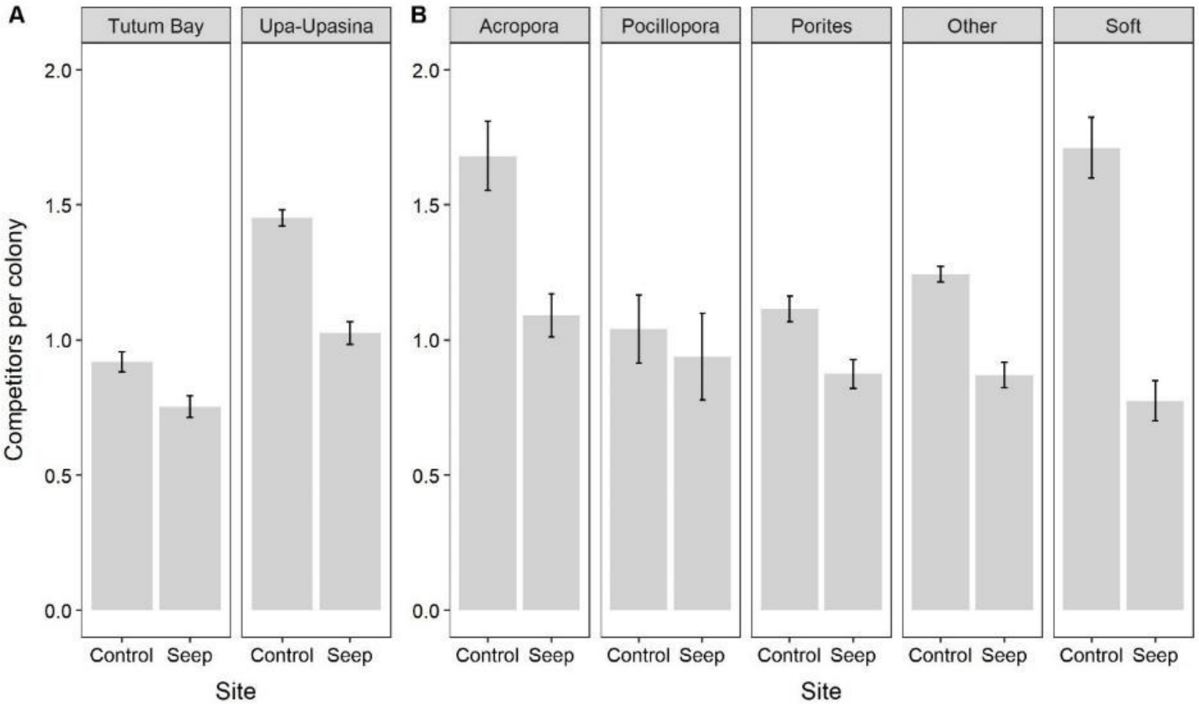


Figure A5.2. The mean number of competitors per colony at control and seep sites, A) at each reef and B) for each genera. Error bars show standard error. These values are based on counts which have not been standardized by colony size.

Appendix E: Supplementary materials for Chapter 6 (General Discussion)

Table A6.1. Statistical analyses on changes in predation pressure by butterflyfish between control and seep sites. Analyses are preliminary and consider only the main effects of acidification and butterflyfish diet.

Fish abundance[1]			
	Chisq	**Df**	**P**
Site	3.65	1	0.06
Diet	12.07	2	<0.01
Site*Diet	1.79	2	0.41
Bites by fish[2]			
	Chisq	**Df**	**P**
Site	8.41	1	<0.01
Diet	184.7	2	<0.01
Site*Diet	0.67	2	0.72
Bites by fish pop[3]			
	Chisq	**Df**	**P**
Site	10.8	1	<0.01
Diet	116.23	2	<0.01
Site*Diet	13.39	2	<0.01
Bites by fish pop standardized to coral cover[4]			
	Chisq	**Df**	**P**
Site	30.62	1	<0.01
Diet	22.66	1	<0.01
Site*Diet	29.8	1	<0.01

(1) Negative binomial GLM; (2) GLM on log-transformed data; (3) Negative binomial GLM; (4) GLM on log-transformed data

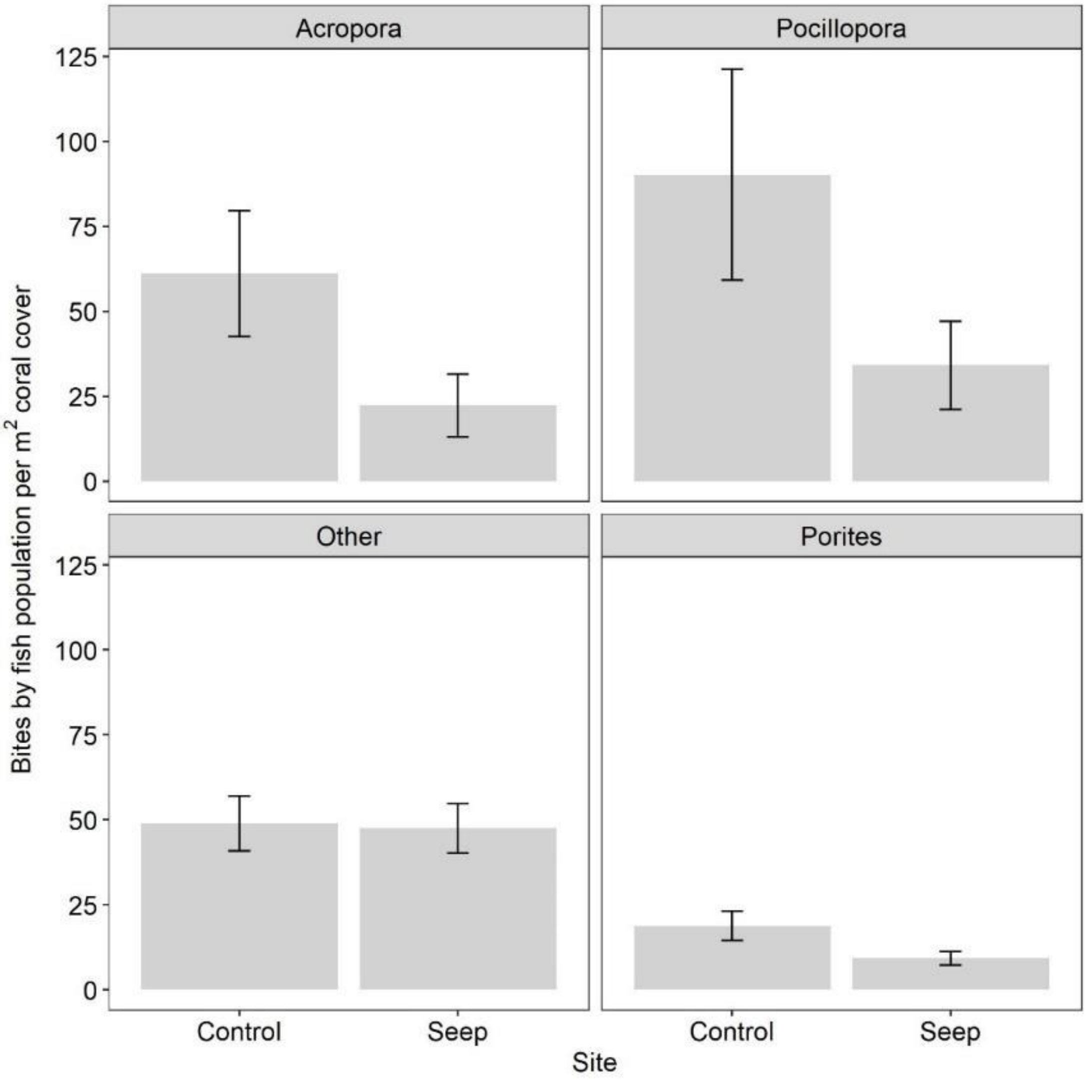


Figure A6.1. Predation pressure from the butterflyfish population on the three focal genera and other hard corals, under acidified seep and control conditions. Predation pressure is quantified by number of bites on coral per 3 minutes, standardized by the abundance of fish and coral cover at each site. Error bars show standard error.