Dynamics of carbonate production and erosion in north-western Australia

Thesis submitted by
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Abstract

Understanding ecological processes that shape contemporary and future communities facilitates knowledge-based environmental management. This thesis investigates key ecological processes shaping coral reef communities across various zones of Ningaloo Reef and Dampier regions in Western Australia, with a focus on providing location-specific data on the abundance and activity level of key producers and/or eroders of calcium carbonate, as well as the environmental conditions which influence them, across multiple reef zones and over extended time periods.

Chapter 2 identifies zone-specific trends in coral populations over a decade at Ningaloo Reef following a heatwave and multiple cyclones. Declines in coral cover on the reef flat corresponded with declines in fast growing corals, particularly *Acropora*. In contrast, reef slope and inshore zones showed little change in total coral cover but exhibited shifts in species assemblages. Importantly, changes in coral cover observed in one reef zone did not necessarily reflect trends across the entire reef, as neighboring locations within different reef zones exhibited contrasting rates of carbonate production, highlighting the need to consider habitat-specific estimates across multiple reef zones when estimating carbonate production at the scale of entire reefs.

Long-term (decadal) carbonate production is closely linked to coral recruitment, as the survival and growth of juvenile corals determine the future composition of adult coral populations and overall coral cover. Coral recruitment patterns in the Dampier Archipelago, were best explained by percent cover of live corals and an oceanographic model that predicted larval dispersal. Despite a 375% difference in recruitment densities between 2015

and 2017, the rank order of coral recruit density among reefs remained similar among years, highlighting potential "recruitment hotspots". Coral populations on reefs with consistently high recruitment rates are likely to recover more quickly following disturbances and sustain higher rates of long-term carbonate production. As a result, future models of carbonate production should aim to incorporate coral recruitment to better capture the contributions of coral recruits to carbonate production over longer timescales.

Chapters 4 and 5 focus on quantification of erosion at Ningaloo Reef, particularly erosion resulting from the activity of both very large and very small bioeroders. Chapter 4 describes the abundance and distribution of *Bolbometopon muricatum* at Ningaloo Reef, the largest species of parrotfish (up to 1.3 m total length), which is able to remove significant amounts of reef carbonates through bioerosion. This species had previously gone undetected in scientific surveys at Ningaloo Reef, and including estimates of bioerosion by *B. muricatum* resulted in total erosion estimates being up to six times higher than previous assessments at the same locations. At the smaller end of the size spectrum, Chapter 5 provides the first empirical estimates of micro and macroborer erosion for Ningaloo Reef. Micro- and macroborer contributions to erosion were estimated to be low (4% and <1% respectively); however, this may be partly attributable to the heavy parrotfish grazing on our experimental blocks. Further research is needed to address methodological issues when measuring micro- and macroborer erosion.

The research presented in this thesis improves our understanding of the abundance and activity levels of key producers and/or eroders, as well as the environmental conditions which influence them, across multiple reef zones in NW Australia. This new data, while not intended to account for the full suite of processes that maintain net carbonate production,

provides for improved net carbonate assessments and the capacity to predict future responses of NW Australian reefs to future climate change scenarios.

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Chapter 1 General Introduction

Coral reefs offer a wide array of crucial ecosystem goods and services including fostering biodiversity (Hoegh-Guldberg, Northrop, and Lubchenco 2019), food security through enhanced fish biomass (Cinner et al. 2009), producing sediment that replenishes shorelines and islands (Dawson, Smithers, and Hua 2014; Cuttler et al. 2019; Morgan and Kench 2016a) and protecting coastlines from wave damage (Sheppard et al. 2005; Ferrario et al. 2014). Additionally, coral reefs are involved in nutrient processing (Fabricius 2005), reducing wave energy which supports the growth of mangroves and seagrasses (James et al. 2023), and in many parts of the world, are a source of building materials (Albert et al. 2015). The financial benefits of just one of these services, coral reef fisheries, has recently been estimated to be valued at over USD 6 billion annually to the global economy (Eddy et al. 2021).

Ecosystem services provided by coral reefs depend heavily on their complex physical structures. This physical structure is the result of the interplay between processes which contribute toward reef growth, and those which contribute toward reef erosion. Organisms which contribute to reef growth include corals and crustose coralline algae, which construct and help to stabilise the reef structure (Stearn, Scoffin, and Martindale 1977a; Hubbard, Miller, and Scaturo 1990; Perry and Hepburn 2008). This reef growth is countered by natural erosive processes which includes biological (Schönberg, Fang, and Carballo 2017; Glynn and Manzello 2015; Bellwood and Choat 1990), physical (Harmelin-Vivien 1994; Cuttler, Hansen, Lowe, and Drost 2018), and chemical mechanisms (Cyronak and Eyre 2016). The net sum of reef growth processes minus those of erosion, determines the net accumulation of calcium carbonate on reefs (termed carbonate budget), and thereby the reefs capacity to maintain its physical structure. The critical importance of maintaining this physical structure

for the provision of a wide range of ecosystem services is now widely recognised, as noted in several recent studies, one of which states, “one of the most ubiquitous features of coral reefs that we want to protect is their physical structure, which is tied to almost every key service that we derive from reefs” (Bellwood et al. 2024, page 284).

In the face of climate change, there is growing concern about the ability of many coral reefs to continue growing and maintaining their physical structure due to a shift in the balance between growth and erosion processes (Hughes et al. 2018). Warming oceans and declining water quality are causing widespread declines in live coral cover and reducing rates of coral recruitment and growth (Hughes et al. 2019; Cornwall et al. 2021). Concurrently, increased rates of chemical dissolution (Cabral-Tena et al. 2018), physical erosion (Puotinen et al. 2020) and biological erosion (Roff, Zhao, and Mumby 2015) are acting synergistically to shift the balance between reef growth and erosion (Perry et al. 2014). Consequently, these changes are reducing the ability of many coral reefs to accrete, maintain their physical structure, and provide services such as shoreline protection and sediment regeneration (Perry et al. 2018; Perry et al. 2015; Perry et al. 2014; Morgan and Kench 2016a). These concerns have lead to a rapid increase in the number of studies assessing rates of net carbonate accumulation on reefs, also known as the carbonate budget (Dee et al. 2023; Stearn, Scoffin, and Martindale 1977b; Scoffin 1980; Sadd 1984; Hamylton, Silverman, and Shaw 2013; Eakin 1996; Morgan et al. 2016; Perry et al. 2014; Perry et al. 2013; Perry et al. 2012; Perry 2011; Lange and Perry 2019). A carbonate budget is the balance between carbonate growth and erosion, providing a useful framework to understand changes in these processes (Perry et al. 2012).

Multiple methods have been developed to quantify carbonate budgets on coral reefs, each tailored to focus on varying temporal and spatial scales. Hydrochemical methods, for instance, provide an indirect assessment of net carbonate production by measuring changes in seawater alkalinity as it flows over a reef (Smith 1981; Muehllehner et al. 2016). In contrast, radiocarbon dating, usually of coral cores, offers a way to measure carbonate production over much longer timescales, from years to centuries (Land 1979; Emery, Tracey Jr, and Ladd 1954; Smith 1970). Most recently, census-based methods have been increasingly used to assess spatial and temporal variability in carbonate budgets over shorter timescales (Januchowski-Hartley et al. 2017; Mallela and Perry 2007b; Perry et al. 2018; Perry et al. 2012; Perry et al. 2014; Perry et al. 2013; Perry et al. 2015; Hart and Kench 2007; Courtney and Andersson 2019).

Censused based techniques offer several advantages over hydochemical or radiocarbon dating methods when estimating carbonate budgets as they provide a rapid "snap-shot" estimate of carbonate production and erosion. Census based methods use data of an organism's relative abundance and distribution, alongside organism-specific activity levels (i.e., rates of growth or erosion), to estimate their relative contribution to carbonate production or erosion at any given location. As such, census based approaches can utilise data that is relatively easy to collect (e.g., live coral cover), use techniques which are both robust and well established (e.g., visual transects and visual estimates of feeding behaviour), and can be applied at both reef system and intra-reef scales to provide an understanding of the relative importance of different processes across varying spatio- temporal scales. Additionally, census-based estimates provide for the rapid assessment of acute and chronic disturbance events on community level rates of carbonate production and erosion (i.e., coral bleaching), and, when

coupled with future climate scenarios, can be used to predict longer-term changes in carbonate budgets and overall reef accretion rates (Perry et al. 2018; Cornwall et al. 2021).

These advantages have contributed to the increase in the number of studies utilising census-based methods for estimating carbonate budgets over the last 25 years (Eakin 1996; Harney and Fletcher 2003; Mallela and Perry 2007a; Lange and Perry 2019; Perry et al. 2018; Januchowski-Hartley et al. 2017; Morgan et al. 2016; Perry et al. 2015; Perry et al. 2014; Perry et al. 2013; Perry et al. 2012). However, census-based methods still have several notable limitations. They are computationally challenging and require data on the local abundance and activity levels of producers and eroders over multiple spatio-temporal scales (Perry et al. 2012). In the absence of this data, many studies rely on estimates from other, often distant locations, with limited consideration for local variations in community composition and environmental factors which influnce reef growth and/or erosion. For example, of the 38 census-based carbonate budget studies pubished since 1977, 28 (73%) utilise coral growth rates derived from different regions and/or coral species (see Browne et al. 2023). These growth rates are then applied to either a subset of coral species (i.e., Stearn 1977; Scoffin 1980; Sadd 1984; Hamylton et al. 2013; Bak 1990; Eakin 1986; Perry 2012, 2013, 2015; Morgan 2014; Browne 2013) or all coral species (i.e., Grigg 1982) to estimate local rates of carbonate production. Similarly, estimates of erosion in many census-based studies utilise rates of biological erosion for fish, urchins and microborers obtained from other locations, and multiply these by local estimates of abundance, to estimate local rates of reef erosion across different substrate types and reef zones (Hubbard, Miller, and Scaturo 1990; Eakin 1996; Edinger et al. 2000; Perry et al. 2018; Perry et al. 2015; Perry et al. 2012; Morgan and Kench 2014; Roik et al. 2018). The consequences of using these estimates of abundance and/or activity levels of carbonate producers and eroders from distant locations is

that these rates may not accurately represent the local abundance and activity of producers or eroders, and thus result in inaccurate estimates.

Further problems arise with using census-based methods to estimate carbonate budgets due to rates of carbonate production and erosion often being non-linear (e.g., Roff et al. 2015), requiring data on the abundance and activity level of producers and eroders to be collected over long-time periods (years) (Pari et al. 1998; Pari et al. 2002; Tribollet 2008; Enochs et al. 2016; Silbiger et al. 2016). Several recent investigations into changes in carbonate budgets on reefs in the central and eastern Indian Ocean (Lange and Perry 2019; Morgan and Kench 2014; Dee et al. 2023), the Caribbean (Manzello, Mark Eakin, and Glynn 2017; Molina-Hernández et al. 2022), and the Indo-Pacific (Perry et al. 2018) have aimed to address these knowledge gaps by incorporating local data on the abundance and activity levels of producers and eroders over extended time periods, However, these studies often lack data on local environmental conditions (e.g., wave exposure, light, nutrients). Consequently, the relationships between environmental variables and rates of reef production and erosion estimated using census-based approaches remain poorly defined (e.g., erosion vs. water movement).

For many coral reefs, such as those in inshore North-West Australia, data on the abundance and activity levels of carbonate producers/eroders and key environmental conditions influencing production and erosion remain limited. Ningaloo Reef, for instance, is one of the world's largest fringing coral reefs, was designated a UNESCO World Heritage site in 2011, and is among the few coral reefs predicted to avoid frequent bleaching events (twice per decade) until after 2041 (Heron et al. 2017). However, most research at Ningaloo has focused on the shallow and wave-sheltered lagoon and reef flat zones, where data is easiest to collect

(see Vanderklift et al. 2021). As a result, there remains a significant gap in our understanding of the abundance and activity levels of key carbonate producers and eroders, particularly within extensive reef slope habitats (although see Perry et al. 2018). Similarly, the Dampier Archipelago region, north of Ningaloo Reef, offers a distinct environmental setting well-suited for studying how coral reef communities respond to factors influencing carbonate production and erosion, however, data on key processes influencing reef growth and erosion remain limited.

To address these knowledge gaps, this thesis aims to provide location-specific data on the abundance and activity level of key producers and/or eroders of calcium carbonate, as well as the environmental conditions which influence them, across multiple reef zones for reefs of NW Australia (Figure 1.1). While creating a complete carbonate budget for reefs of NW Australia is not a specific goal of this thesis, the results in subsequent chapters enhance our understanding of processes contributing to reef growth and erosion at local scales. Specifically, I investigate factors driving carbonate production (i.e., coral recruitment, coral cover, and coral composition: Chapters 2 and 3) and carbonate erosion (i.e., internal and external reef erosion: Chapters 4 and 5), as well as the cause-effect relationship between environmental factors and carbonate budgets (i.e., wave exposure and currents: Chapters 2, 3 and 5).

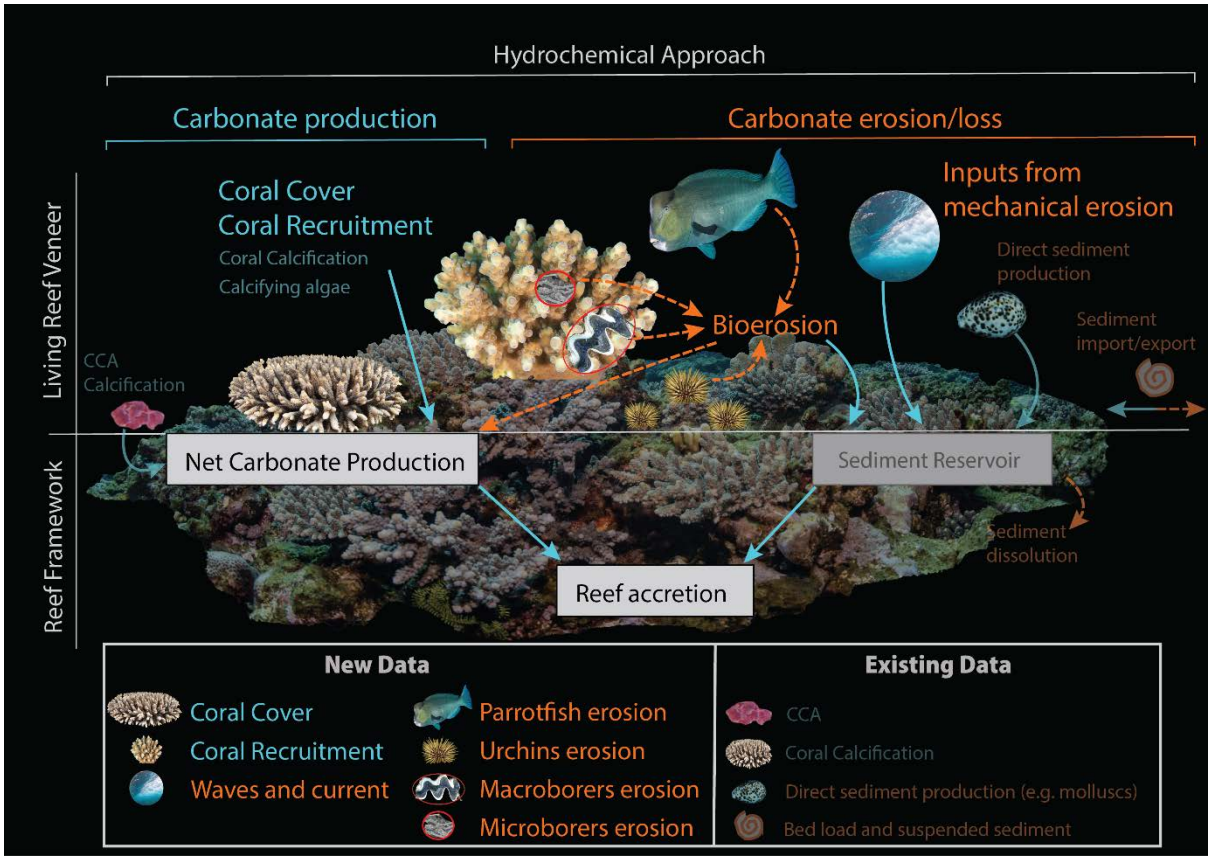

Figure 1.1. Schematic showing the interaction of carbonate production (blue) and erosion (orange) processes typically targeted in census-based carbonate budgets approaches. The taxa I focus on improving estimates of abundance and activity levels for on reefs of NW Australia in this thesis (Chapters 2 to 5) are highlighted.

1.1 Coral reefs of inshore North-West Australia

The Ningaloo and Pilbara regions of north- western Australia lie just north of the Tropic of Capricorn and are characterised by extensive fringing reef development and diverse coral assemblages (Veron and Marsh 1988). Spanning approximately 400 km, the coastal fringing reefs of north-western Australia comprise over 250 species of coral and 500 species of tropical fish. Coral cover and composition vary markedly throughout the region, with the highest cover and diversity on the reef slope at Ningaloo and the mid-shelf reefs of the Dampier Archipelago (Babcock et al. 2020). The continental shelf is narrow at Ningaloo (<10km) but is broader along the north in the western Pilbara coast (>150km), between the Exmouth gulf and the Dampier Archipelago, resulting in stronger tidal currents and increased

turbidity. The western Pilbara coast contains over 1000 islands and fringing reefs, notably the Dampier Archipelago, Montebello and Barrow Islands, and the nearshore islands of the south Pilbara off the coast of Onslow (Figure 1.2).

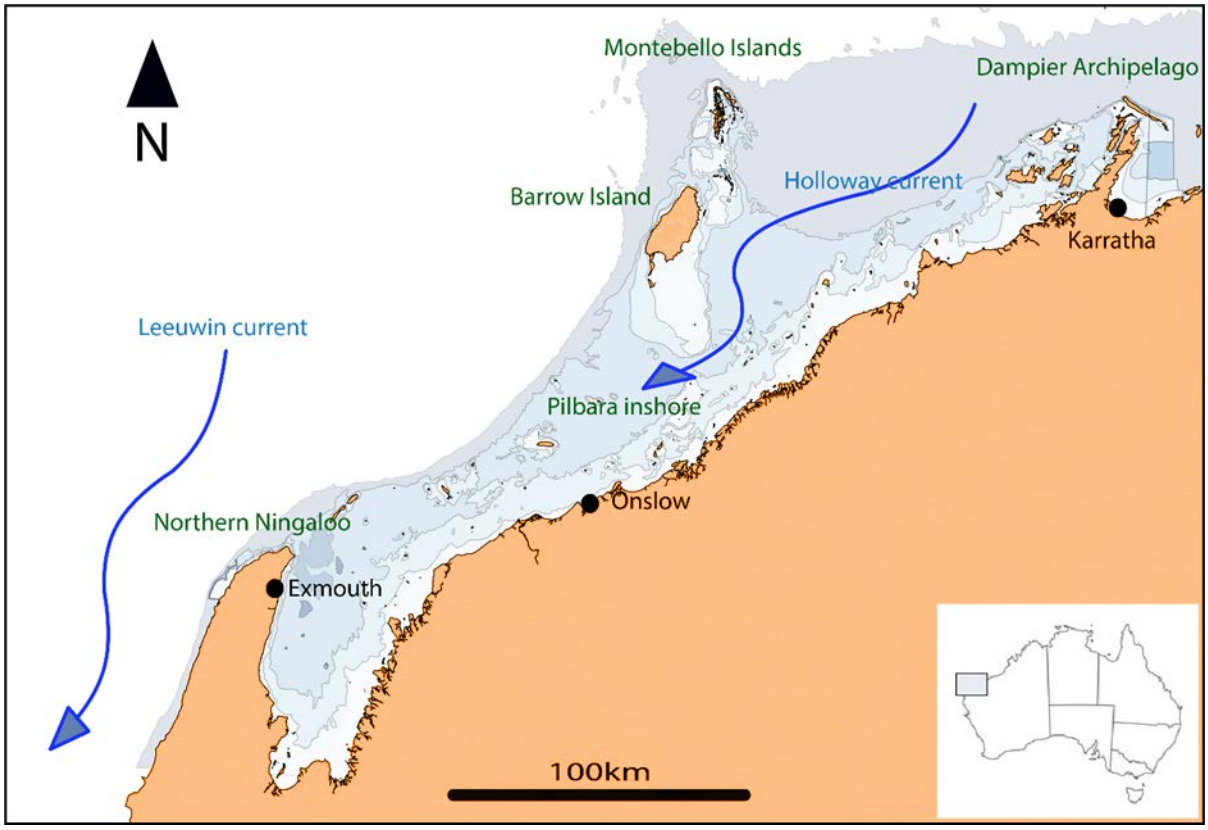

Figure 1.2. Map of the study region showing the location of the study sites at northern Ningaloo Reef and the Dampier Archipelago, the extent of the 100m depth contour (grey) and the flow direction of the Leeuwin and Holloway currents.

Coastal reefs of north-west Australia are influenced by large-scale oceanographic currents, including the south-westerly flowing Leeuwin and Holloway currents, which transport warm, clear, oligotrophic waters to the northernmost reefs of the Dampier Archipelago and northern Ningaloo Reef between March and September (Semeniuk 1982). Here, the influx of clear oceanic waters results in generally low turbidity. In contrast, the nearshore waters surrounding Dampier Islands and inshore Pilbara are characterised by high levels of turbidity and reduced water clarity (Evans et al. 2020; Moustaka et al. 2018). Annual rainfall in the

region is low (averaging <300 mm) (Pearce et al. 2003); however, cyclones are common between November and March (mean = 0.6 cyclones per year) and typically result in dramatic but relatively short-lived (days) increases in freshwater input (Lozano-Montes et al. 2017), turbidity and wave-generated currents (Cuttler et al. 2018; Griffith 2004) and localised impacts of the physical reef structure (Cuttler et al. 2018)

1.2 Ningaloo Reef

Ningaloo Reef, located off the north-west coast of Western Australia, is one of the world's largest fringing coral reefs and was designated as a UNESCO World Heritage site in 2011. A significant portion of Ningaloo, encompassing the coral reef and adjacent marine environments, is safeguarded under marine parks and reserves, overseen by both the state (Department Biodiversity Conservation and Attractions) and federal (Parks Australia) governments. Within these protected areas, there are also designated 'no-take' zones (IUCN Category II reserves), where fishing and extractive activities are prohibited.

Ningaloo Reef's unique ecological dynamics are supported by the juxtaposition of the warm waters of the Leeuwin Current and the nutrient-rich upwelling from the continental shelf (Xu et al. 2016). Northern Ningaloo Reef has well-developed reef slope, reef flat and lagoon reef zones with the reef crest typically 0.2–1.0 km from the shore. As with many coral reef ecosystems, research and monitoring at Ningaloo has focused on the easily accessible sheltered lagoon and reef flat zones, as opposed to the wave exposed reef slope environment (see Vanderklift et al. 2021). As a result, the condition and status of key producers and eroders throughout the extensive reef slope area is poorly understood (however see Perry et al. 2018).

At Ningaloo Reef, oceanic swells—which break on the reef slope and push water across the reef and into the lagoon—are important drivers of local hydrodynamics (Taebi et al. 2012). These swells, which typically reach 2 m in height during afternoon seabreezes and up to 5 m in cyclones, generate currents that travel across the reef flat into the lagoon, eventually leaving the lagoon through reef channels. The speed of these currents is directly related to the height of the waves and is strongest during low tides (0.2–0.4 meters) (Taebi et al. 2012). Wave-driven water flows also affect the temperature of the water over the reef and in the lagoon, channelling cooler, oceanic waters up the reef slope and into the lagoon. Average sea surface temperatures at Ningaloo now range from approximately 24°C to 26°C (Falter et al. 2014), having increased by more than 1°C over the last century (Zinke et al. 2014).

Ningaloo Reef has been exposed to numerous disturbances including tropical cyclones (Cuttler et al. 2018), abnormally high water temperatures (Moore et al. 2012), populations of predatory snails (Bessey et al. 2018), anoxic events (Simpson, Cary, and Masini 1993), coral disease (Onton et al. 2011) and freshwater discharges from floods (Lozano-Montes et al. 2017). Northern Ningaloo has experienced acute heat stress (> 8 DHW) on two occasions since 2007; in March 2011 and February 2013, with declines in coral cover between 14% and 20% (Babcock et al. 2020) Despite these natural disturbances, Ningaloo Reef has largely avoided the severe degradation affecting many of the world's coral reefs due to human activities (Vanderklift et al. 2020). Ningaloo Reef is among the few coral reefs expected to evade frequent bleaching events—at least twice per decade—until after 2041 under current climate projections (Heron et al. 2017). This relative resilience is attributed to the combination of unique weather patterns, oceanography, and comparatively low human impact locally. Ningaloo's unique situation highlights its global significance as an important region

for understanding how coral reef communities are responding to global climate change whilst being relatively free from local pressures.

1.3 Dampier Archipelago

The Dampier Archipelago, to the north of Ningaloo Reef, consists of a group of inshore islands (<20km from the mainland coast) off the north-western coast of Western Australia (Figure 1.1). The 12 large islands and 30 small islands or shoals have well-developed fringing coral reefs (Pearce et al. 2003; Semeniuk 1982) which experience low annual rainfall (Pearce et al. 2003). Accordingly, terrigenous sediment and nutrient input is minimal, due to the absence of significant riverine or freshwater inputs (Wilson et al. 2019a). However, large tidal ranges (max 5.1 m, mean 1.9 m), combined with a wide shallow continental shelf and numerous narrow island passages, can produce tidal currents in excess of 0.5 ms^{-1} (Pearce et al. 2003) which cause sediment to be periodically resuspended (Dufois et al. 2018). As a result, turbidity is variable and is strongly influenced by the prevailing conditions of wind and tide. Coral cover and composition vary markedly throughout the region with the highest coral cover and diversity on mid-shelf reefs of the Archipelago (>35%: Babcock et al. 2020) where there is a greater diversity of habitat types and environmental conditions (Griffith 2004; Moustaka et al. 2019).

1.4 Aims and thesis structure

The aim of this thesis is to investigate how key components of carbonate accretion and erosion vary locally within fringing coral reefs of NW Australia (Figure 1.2). To address this aim, the research within this thesis provides site-specific data on the abundance and activity of key carbonate producers and eroders across multiple reef zones . Specifically, the research

focuses on long-term changes in the abundance and composition of hard corals (Chapter 2), rates of coral recruitment and environmental drivers (Chapter 3), the abundance, distribution and size of a key eroding fish species (Chapter 4), and the abundance and activity levels of internal and external reef eroding taxa (Chapter 5). This new data is then incorporated into revised estimates of net carbonate production, erosion and reef budgets for the study region.

Chapter 2 presents an in-depth analysis of the variations in coral composition and cover across three reef zones on Ningaloo Reef (lagoon, flat and slope) over a decade in which severe heat stress and cyclones occurred. It reveals significant reductions in total coral cover, especially in the *Acropora* species on the reef flat, which is particularly vulnerable to physical damage and bleaching. The chapter highlights the need to recognise changes in coral types specific to each reef zone and the potential effects of environmental stressors like heat stress and cyclones on carbonate production. Unlike most other studies at Ningaloo, this chapter examines the disparities in changes in coral cover among reef zones, shedding light on spatial difference in the temporal dynamics of coral assemblages and identifying areas with greater resilience.

Chapter 3 investigates coral recruitment dynamics within the Dampier Archipelago, revealing spatially consistent patterns in recruitment rates across different reefs. The chapter identifies key predictors of coral recruitment, including percent hard coral cover at varying spatial scales, and assesses the capacity of larval dispersal models, combined with environmental factors, for predicting recruitment. It highlights the ability of models to identify reefs with consistently high rates of recruitment and high reef resilience, which warrant enhanced conservation efforts. This research focuses on the Dampier Archipelago due to its broad spatial variations in turbidity, wave exposure, and ocean temperatures (Moustaka et al. 2019),

providing an ideal setting to explore the effects of meso- and local-scale interactions on coral recruitment. The availability of a high-resolution oceanographic dispersal model for the Archipelago (Feng et al. 2016) provided an excellent opportunity to test the model's accuracy in predicting coral larval dispersal and recruitment.

Chapter 4 focuses on the presence and ecological significance of *Bolbometopon muricatum*, the largest of all parrotfish species, which is found across the Indo-Pacific. The chapter presents novel observations of *B. muricatum* at Ningaloo Reef, indicating its relatively high abundance and frequency of occurrence on the reef crest compared to other zones. These findings represent the first description of this species in the scientific literature at Ningaloo and highlight potential significant contribution of *B. muricatum* to reef erosion at Ningaloo Reef. Furthermore, our results also highlight the limitations in using a single approach to estimate bioeroders with Underwater Visual Census (UVC).

Chapter 5 provides a detailed analysis of erosion rates across multiple habitats within Ningaloo Reef, emphasising the significant role of bioerosion, particularly by parrotfish, in shaping the reef's physical structure. By combining direct measurements of both external and internal erosion with estimates based on parrotfish, urchins, and water velocity, I provide the first partitioned erosion rates for multiple reef zones on an eastern Indian Ocean fringing reef.

Collectively, these chapters contribute insights into the dynamics of coral reef ecosystems in NW Australia, including changes in coral cover, recruitment patterns, the presence of key fish species, and rates of erosion. These studies underscore the complex interactions between environmental factors, species distributions, and ecosystem dynamics within marine environments and provide information on how elements of carbonate erosion and production

differ among sites and zones within a reef system, providing the basis for refined carbonate budgets at the scale of reef zones for these reefs.

Chapter 2 Carbonate production - trends in live coral cover across reef zones

Abstract

Changes in the percent cover of hard corals and in the relative abundance of coral taxa often follow disturbance events on coral reefs. Although the ecological responses of common coral taxa have been well documented, little is known about the ecological responses of uncommon coral taxa or of coral morphological groups across multiple adjacent reef zones. We used Multivariate Auto-Regressive State-Space modelling to assess the rate and direction of change of hard coral cover in relation to coral genera, growth-forms, and susceptibility to bleaching and physical damage across multiple reef zones at northern Ningaloo Reef in Western Australia. Trends were assessed between 2007 and 2016, during which multiple episodic disturbances occurred including cyclones and a heatwave. We provide evidence of zone-specific trends, not only in total hard coral cover, but also in taxonomic and morphological groups of corals at Ningaloo Reef. Declines in coral cover on the reef flat corresponded with declines in fast growing corals, particularly *Acropora spp*. In contrast, coral cover on the reef slope and inshore did not undergo significant change, despite divergent trajectories of individual genera. Importantly, we also show that changes in the composition of coral assemblages can be detected using a morphological based approach when changes are not evident using a taxonomic approach. Therefore, we recommend that future assessments of coral reef trends incorporate not just standard metrics such as total coral cover, but also metrics that provide for detailed descriptions of trends in common and uncommon taxa and morphological groups across multiple reef zones.

2.1 Introduction

Coral reefs are threatened by numerous natural and anthropogenic stressors and many reefs have already lost a high percentage of their living coral (Pandolfi et al. 2003; Hughes et al. 2017). Long-term declines in hard corals have been caused by elevated nutrients (McCook 1999), sedimentation (Fabricius 2005), coral disease (Pollock et al. 2014), elevated water temperatures (McClanahan et al. 2004; Sampayo et al. 2008), physical damage from storms (Harmelin-Vivien 1994; Madin and Connolly 2006) and predation by coral predators (De'ath et al. 2012). The loss of live coral is of concern because the persistent biogenic structures that hard corals create (reefs) are critically important to the functioning of coral reef ecosystems (Hughes and Jackson 1985).

The percentage cover of living hard corals is the most widely used indicator of coral health because it is easily measured and reliably represents changes in the abundance of living hard corals (Osborne et al. 2011). Total coral cover, however, does not provide information on changes in the taxonomic composition of coral assemblages. Importantly, there are substantial differences in the susceptibility of different coral taxa to different types of disturbances, such as heatwaves, cyclones, nutrients, and disease. Strong shifts in taxonomic composition of coral assemblages often follow such disturbances (Persian Gulf—Riegl and Purkis 2015; western Indian Ocean—McClanahan et al. 2007; eastern Indian Ocean—Speed et al. 2013; southern Japan—Hajime et al. 2002; French Polynesia—Pratchett et al. 2011; Great Barrier Reef—Osborne et al. 2011; the Caribbean—Perry et al. 2013). With predictions of increased frequency and intensity of coral bleaching events (Hughes et al. 2017b), cyclones (Elsner et al. 2008), continued ocean acidification (Pachauri et al. 2014) and sea-level rise in the future, shifts in the composition of coral assemblages are likely to continue and may become more prominent.

Our ability to predict future shifts in the composition of coral assemblages is limited by a lack of data on the response of coral taxa in different reef zones with differing environmental conditions. Most assessments of coral cover and composition following coral bleaching events have been done on shallow reefs (< 4m), and few have been done on deeper reefs (>4m) (Baker et al. 2008; Hughes et al. 2017a). Variation in environmental conditions among reef zones including the quantity and quality of light (Dustan 1982; Lesser et al. 2010), wave energy (Done 1982) and temperature (Lesser 2006) can influence rates of coral mortality and recovery following disturbance (Pratchett et al. 2015). As a result, the consequences of disturbance are likely to differ among zones. Improved data on the responses of different coral taxa in different zones is therefore necessary to better predict how coral assemblages will respond to environmental change.

Predicting future shifts in the composition of coral assemblages is further limited by uncertainty around how different coral taxa will respond to disturbance (Hoey et al. 2016). For example, coral genera that are highly susceptible to bleaching (e.g., *Seriatopora*, *Stylophora*, and *Acropora*) can recover rapidly following bleaching due to their generally high rates of recruitment and growth (Trapon et al. 2011; Gilmour et al. 2013). These taxa may increase in abundance on reefs if disturbances are frequent and mild. In contrast, if disturbances are infrequent and severe, widespread mortality of all but the most resistant coral taxa is likely. The ability of coral taxa to respond to disturbance may therefore be greatly influenced by the frequency and severity of disturbances, and their rates of recruitment and growth.

Morphological and trait-based classification of corals has been proposed to offer new insights into patterns of function and diversity on coral reefs (Madin et al. 2016; Wilson et al. 2019b; Zawada et al. 2019). Grouping corals by morphology (referred to as morphs)) can improve the ability to predict the outcomes of disturbance if corals with similar morphs perform a similar ecological function, such as the provision of shelter for small-bodied fishes, irrespective of their taxonomic classification. Branching and bushy coral morphs are more susceptible to bleaching and wave damage than massive corals (due to their lower thermal tolerances and higher drag coefficients) and, as a result, these morphs can dispropportionately influence rates of decline and recovery following bleaching and cyclone disturbance (Pratchett et al. 2015; Wilson et al. 2019b). The abundance of branching and bushy morphs is positively correlated with reef complexity, a significant predictor of fish and invertebrate abundance and diversity (Graham and Nash 2013, Vytopil et al. 2001). Despite the differing responses of various coral growth forms to disturbance, few studies have investigated trends in the abundance of different growth forms across multiple reef zones simultaneously (although see Darling et al. 2017 and McClanahan 2007).

Here, our objectives were to compare decadal trends (2007 to 2016) in taxonomic and morphological coral groups, and groups of corals with differing susceptibility to coral bleaching and physical disturbance, across three major zone types (inshore, reef flat, reef slope). Because different coral taxa and morphs may respond differently to different disturbance types, and coral taxa and morphs with low abundance can have a disproportionately large effect on reef ecology (Kerry and Bellwood 2015), we assessed trends in both common and uncommon genera across multiple reef zones.

2.2 Methods

2.2.1 Study Region

Our study was located along the north-western section of Ningaloo Reef (north-western Australia) between S22°17'00" E113°49'00" and S21°49'00" E114°03'00" (Fig 2.1). This region of Ningaloo Reef has well-developed reef slope, reef flat and lagoon reef zones with the reef crest typically 0.2–1.0 km from the shore. Water depth varies from 1.0 to 3.5 m in the lagoon, 0.1–2.0 m on the reef flat and 3.0–15.0 m on the reef slope. Annual rainfall in the region is low (averaging <300 mm), but the region is subject to frequent tropical cyclones (0.5 per year) during which rainfall can exceed 100 mm in a single day (Lozano-Montes et al. 2017). Since 2007, Ningaloo Reef has been exposed to numerous disturbances including tropical cyclones (Speed et al. 2013; Gilmour et al. 2019), elevated water temperatures (Depczynski et al. 2013), populations of predatory snails (Bessey et al. 2018), anoxic events (Simpson et al. 1993) and freshwater discharges from floods (Lozano-Montes et al. 2017). Our study region at northern Ningaloo has experienced acute heat stress (> 8 DHW) on two occasions since 2007; in March 2011 and February 2013(Gilmour et al. 2019), one freshwater discharge event (250 mm rainfall, March 2014) and one severe tropical cyclone (> Category 2, March 2015) (Figure 2.2a).

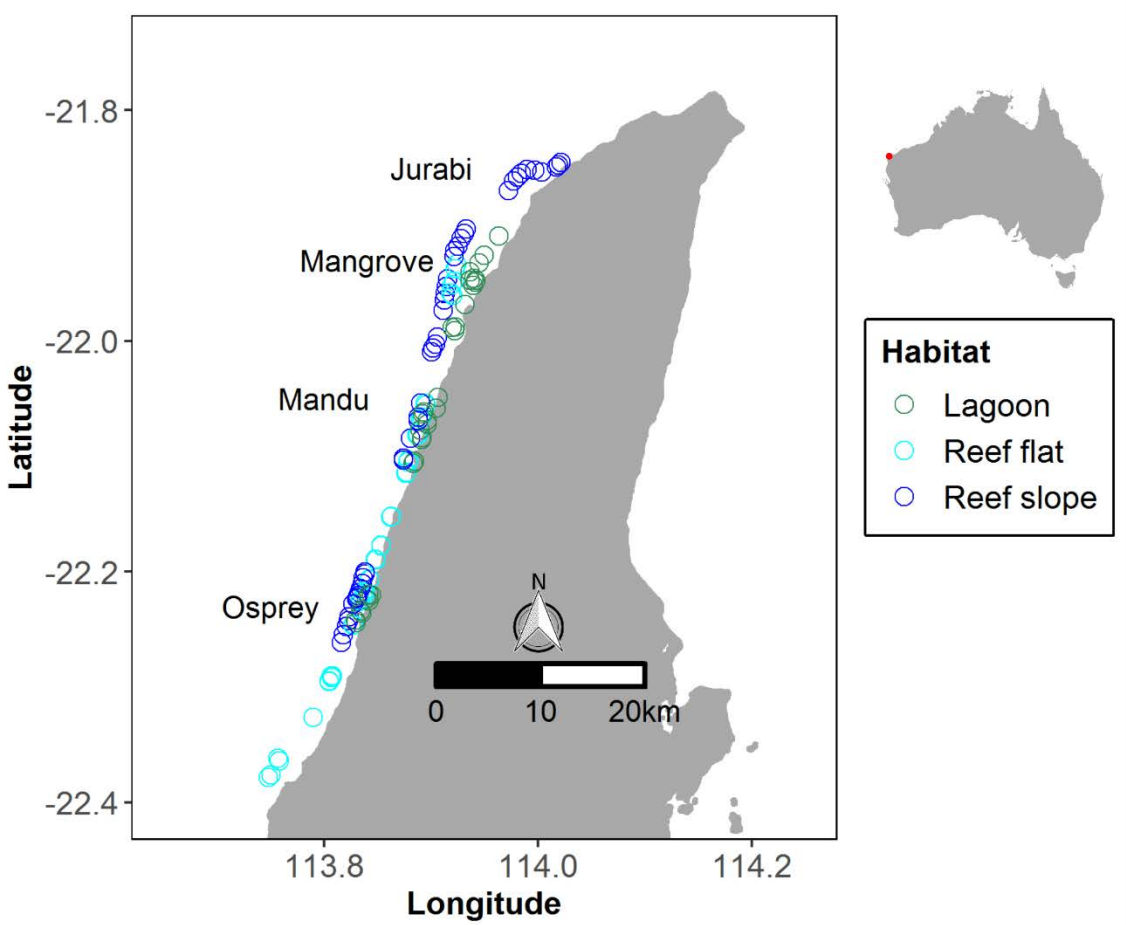

Figure 2.1. Location of the 105 study sites at northern Ningaloo Reef, Western Australia. Colours indicate the three reef zones considered.

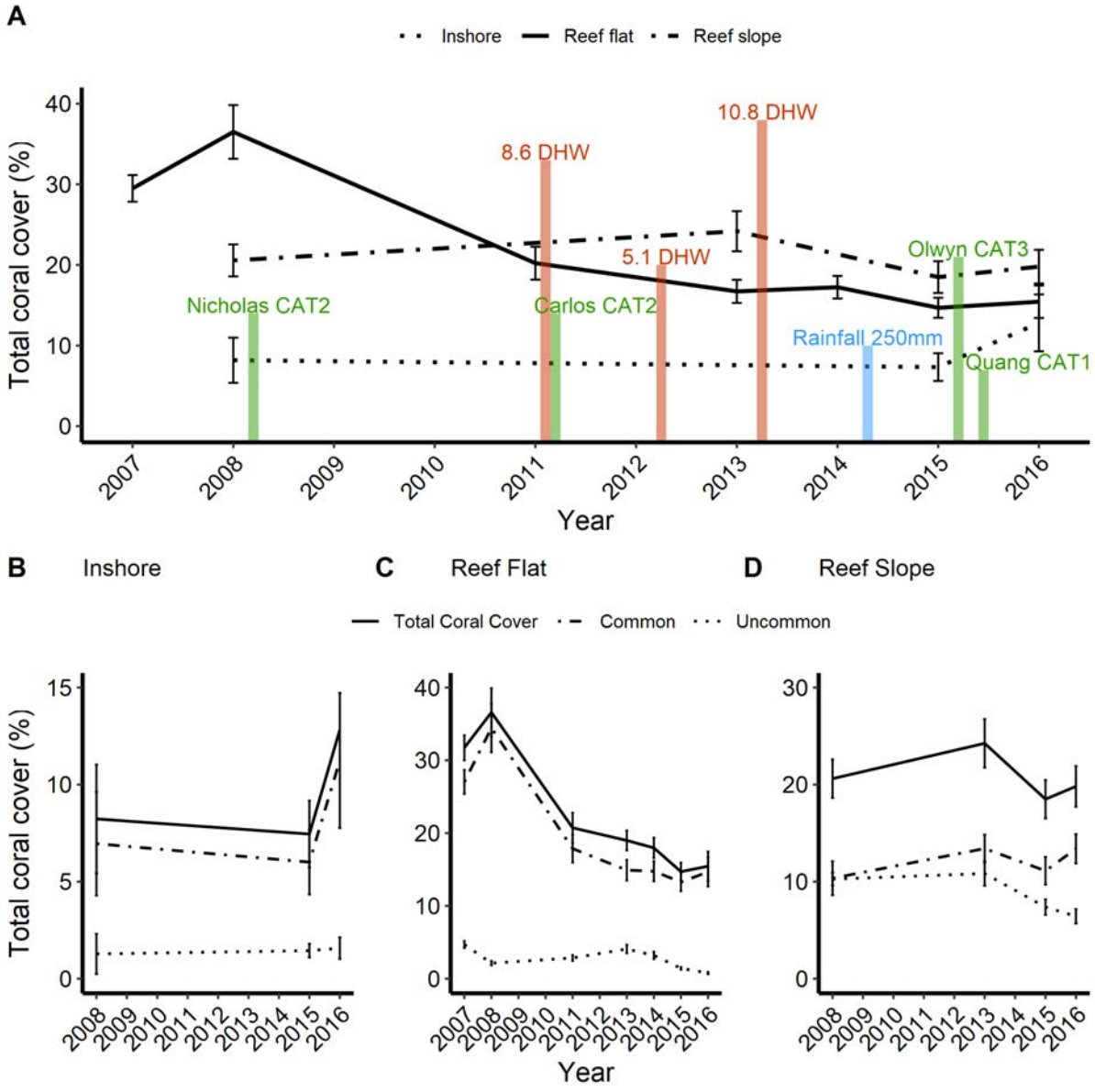

Figure 2.2. (a) Percentage total coral cover (mean ± SE) within the three reef zones and the timing and intensity of cyclone (green), heatwave (orange) and freshwater (blue) disturbances at Northern Ningaloo between 2007 and 2016. CAT = cyclone intensity, DHW = Degree Heating Weeks. (b) Percentage coral cover (mean ± SE) of all corals, common and uncommon coral genera (c) growth forms within inshore, reef flat and reef slope zones between 2007 and 2016.

2.2.2 Benthic surveys and classification of coral genera and growth forms

Coral assemblages were surveyed using photographic line transects of 25–30 m in length, with photographs (0.4 m × 0.5 m) captured approximately 0.5 m above the substrate at 0.5 m intervals. A total of 818 transects were completed across 119 sites between March 2007 and

May 2016 with transects stratified among reef slope, reef flat and inshore (lagoon) reef zones (Table 2.1). Not all sites were surveyed in all years, however, sites included in the analysis were surveyed on at least three occasions between 2007 and 2016 and on at least one occasion before and after the 2011 heatwave (for details see Appendices). Sites were situated at fixed locations (GPS waypoints) with one transect located at each site. Forty photos were randomly selected within each transect and the genus and growth-form of scleractinian (hard) corals was recorded for five (2007 and 2008) or six (2009 to 2016) fixed points per photograph using the software Transect Measure™ (www.seagis.com.au), yielding 200 (2007 and 2008) or 240 (2009 to 2016) points per transect. Points were evenly spaced across the height and width of the image irrespective of coral cover. As the scoring of the earlier collected coral data predated recent coral taxonomy changes (Richards 2018) (i.e., there is no longer a family Faviidae), we used the earlier genera classifications in Veron (2000). Corals were assigned to one of five common growth forms (branching, bushes, massive, encrusting and tabulate) according to Veron (2000).

Table 2.1. Spatial and temporal allocation of transects among years and reef zones. Data are displayed as number of transects/percentage of transects in each reef zone per year.

YEAR	SURVEY MONTH	INSHORE	REEF FLAT	REEF SLOPE	TOTAL
2007	April and May	NA	106/100%	NA	106/100%
2008	Feb and Oct	24/26%	50/54%	18/20%	92/100%
2011	April	6/10%	54/90%	NA	60/100%
2013	May and June	NA	115/79%	29/21%	144/100%
2014	March and May	NA	129/100%	NA	129/100%
2015	April and Oct	54/30%	99/56%	77/24%	184/100%
2016	March and May	17/16%	52/50%	34/33%	103/100%
Total		**84/10%**	**610/74%**	**124/18%**	**818/100%**

2.2.3 Coral susceptibility, life-history and abundance groups

Corals were assigned to three susceptibility groups (low, medium, high) based on susceptibility to physical damage and coral bleaching ratings obtained from the literature ie. coral genera known to be highly susceptible to coral bleaching were assigned a high bleaching rating and genera with low susceptibility to bleaching were assigned a low rating. Similarly, corals were assigned to one of four life-history groups (Competitive, Generalist, Weedy, Stress-tolerant) based on the literature (Table 2.2, Supplementary Table 2; for more detailed information on susceptibility ratings and life-history categories see Madin et al. 2016; Marshall et al. 2000; Darling et al. 2012). Corals were defined as either common or uncommon based on their relative abundance within each reef zone: common coral genera were defined as those which constituted >10% of the coral community in the respective reef zone (mean 2007–2016) and uncommon genera those which constituted <10% of the coral community (Table 2.3, Supplementary Table 3).

2.2.4 Changes in abundance of coral susceptibility, life-history and abundance groups

We used Multivariate Auto-Regressive State-Space modelling (MARSS package in R; Holmes et al. 2012) to assess the rate, direction and statistical significance of trends in coral cover among coral genera, growth forms, life-history traits and the three classes of susceptibility to bleaching and physical damage. MARSS accommodates missing observations and observation error variance that cannot be estimated or known a priori (Holmes et al. 2012) and is well-suited to assessing rates of change. Data were averaged at the level of the transect which served as replicates within reef zones (see Table 2.1). MARSS estimates the annual rate of change (U), with the assumption that the logarithm of the data is approximated by a linear process with Gaussian errors (Holmes 2012). To assess the statistical significance of U we used the parametric bootstrapping routine 'MARSSparamCIs'

(used with the option method="parametric") with 1000 bootstrap runs, which constructs frequentist confidence intervals (95%) on the parameter estimates, including U.

Table 2.2. Biological traits of the 10 most abundant coral genera recorded at Ningaloo Reef between 2007 and 2016. Letters denote data sources. For traits of all 22 genera see Appendix 2.

GENUS	GROWTH FORM[A]	PHYSICAL DAMAGE SUSCEPTIBILITY[B]	BLEACHING SUSCEPTIBILITY[C]	LIFE-HISTORY
Acropora	bushes, branching, tabulate	high	high	Competitive
Porites	massive	low	low	Stress-tolerant
Turbinaria	sheets	high	low	Competitive
Montipora	encrusting	low	high	Generalist
Goniastrea	massive	low	low	Stress-tolerant
Pocillopora	bushes	medium	medium to high	Weedy
Echinopora	branching, bushes	high	low	Generalist
Favites	massive	low	medium	Stress-tolerant
Platygyra	massive	low	medium	Stress-tolerant
Favia	massive	low	medium	Stress-tolerant

Reference sources: *A (Veron 1995; Madin et al. 2016); B (Madin et al. 2016); C (Marshall and Baird 2000; Madin et al. 2016)*

2.3 Results

2.3.1 Trends in percentage cover of total hard coral and coral genera

Temporal patterns in coral cover varied among genera and reef zones (Figures 2.2 and 2.3). There was an overall decreasing trend in percentage cover of hard coral on the reef flat (-0.04 ± 0.03 yr^{-1}, $p < 0.01$) but not on the reef slope (0.02 ± 0.03 yr^{-1}, $p = 0.34$) or inshore (0.01 ± 0.09 yr^{-1}, $p = 0.45$) (Figure 2.3, Appendix 1). Nine of the ten most abundant taxa yielded responses that varied in direction (positive, negative or no-change) among the three reef zones; only one of the 22 taxa (*Pocillopora*) exhibited a consistent, though non-

significant, response across all three reef zones (Figure 2.3, Appendix 1, table 1). For example, rates of change in percentage cover of *Favites* were significantly positive in the inshore zone (1.56 ± 1.15 yr^{-1}, p = 0.01), significantly negative on the reef slope (-0.17 ± 0.05 yr^{-1}, p = 0.01), but had no significant change (-0.12 ± 0.13 yr^{-1}, p = 0.08) on the reef flat (Figure. 2.3, Appendix 1). The magnitude of change was greatest inshore, particularly among corals from the family Faviidae (e.g., *Favia* and *Favites*), which generally increased in percentage cover during the study period. Conversely, all genera on the reef flat declined in percentage cover, though this was only significant for *Acropora* and *Favia*. Although no trends were detected in 13 of the 19 (63%) uncommon genera (Appendix 1), declining trends were detected in six genera, mostly on the reef flat.

2.3.2 Trends in common and uncommon coral genera

There were differences in the number, type and response of common coral genera among reef zones (Figures 2.2 b, c, d and 2.3, Appendix 1). The cover of the most common taxa, *Acropora,* declined on the reef flat at an average rate of 10% (-0.10 ± 0.03 yr^{-1}, p <0.01) per year but we detected no change within inshore and reef slope reef zones. Similarly, the cover of *Porites* increased on the reef slope at an average rate of 6% (0.06 ± 0.01 yr^{-1}, p = 0.01) per year but we detected no change within inshore and reef flat zones. Variable responses were detected for uncommon genera but the most likely response was no change (Figure 2.3, Appendix 1). The mean percent cover of common genera was variable and closely matched that for total hard coral in all reef zones. (Figure 2.2 a, b, c).

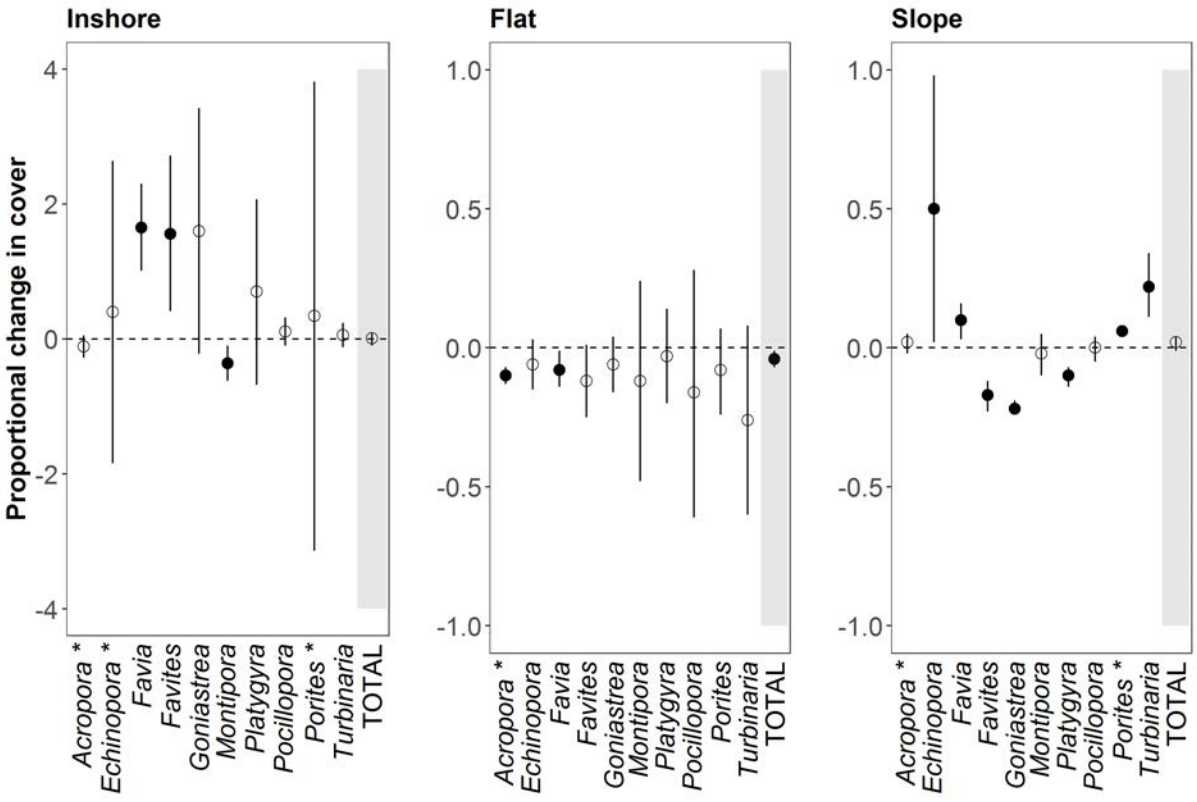

Figure 2.3. Estimated annual change in percentage coral cover (±95% CI) within inshore, reef flat and reef slope zones between 2007 and 2016. Asterisks denote the most abundant (dominant) coral genera for each reef zone (>10% proportional cover). Solid symbols denote statistical significance (p <0.05) ie. the 95% CI does not cross 0 so the annual trend is significant (p <0.05).

2.3.3 Trends in growth-forms and life-history categories.

There were differences in the response of coral growth-forms among reef zones (Figure 2.4, Appendix 1). Declining trends were observed in the *bushes* growth-forms in all three reef zones; however, the magnitude of the declines varied greatly. The largest annual declines in the percentage cover in *bushes* growth forms were observed within the inshore zone (−1.8 ± 1.4 yr^{-1}, p <0.01), followed by the reef flat (−0.27 ± 0.17 yr^{-1}, p <0.01) and the reef slope (−0.13 ± 0.1 yr^{-1}, p <0.01). Percentage cover of *branching* corals also declined within inshore reef zones (−1.21 ± 0.96 yr^{-1}, p <0.01) but no statistically significant change was detected within reef flat and reef slope zones. In contrast, percentage cover of *massive* corals declined on the reef slope (−0.06 ± 0.05 yr^{-1}) but no statistically significant change was

detected within inshore and reef flat zones. Percentage cover of *encrusting* and *tabulate* corals remained stable in all three reef zones (Figure 2.4, Appendix 1).

2.3.4 Trends in coral groups with differing susceptibility to bleaching and physical damage

There were differences in the response of corals with differing susceptibility to *physical damage* and *coral bleaching*, but only for some reef zones. Notably, percentage cover of corals with high susceptibilities to *physical damage* and to *coral bleaching* declined significantly within inshore and reef flat reef zones (inshore −0.63 yr^{-1} and −1.24 yr^{-1} respectively; reef flat −0.07 $yr^{-1}$and −0.06 yr^{-1} respectively; Figure 2.5, Appendix 1), while no change was detected in corals with low susceptibilities to *physical damage* or *coral bleaching.* The percentage coral cover was independent of susceptibility to disturbance within the reef slope zone (Figure 2.5, Appendix table 1), with significant increases in the percent cover of corals with high and low susceptibility to coral bleaching (0.08 yr^{-1} and 0.04 yr^{-1} respectively).

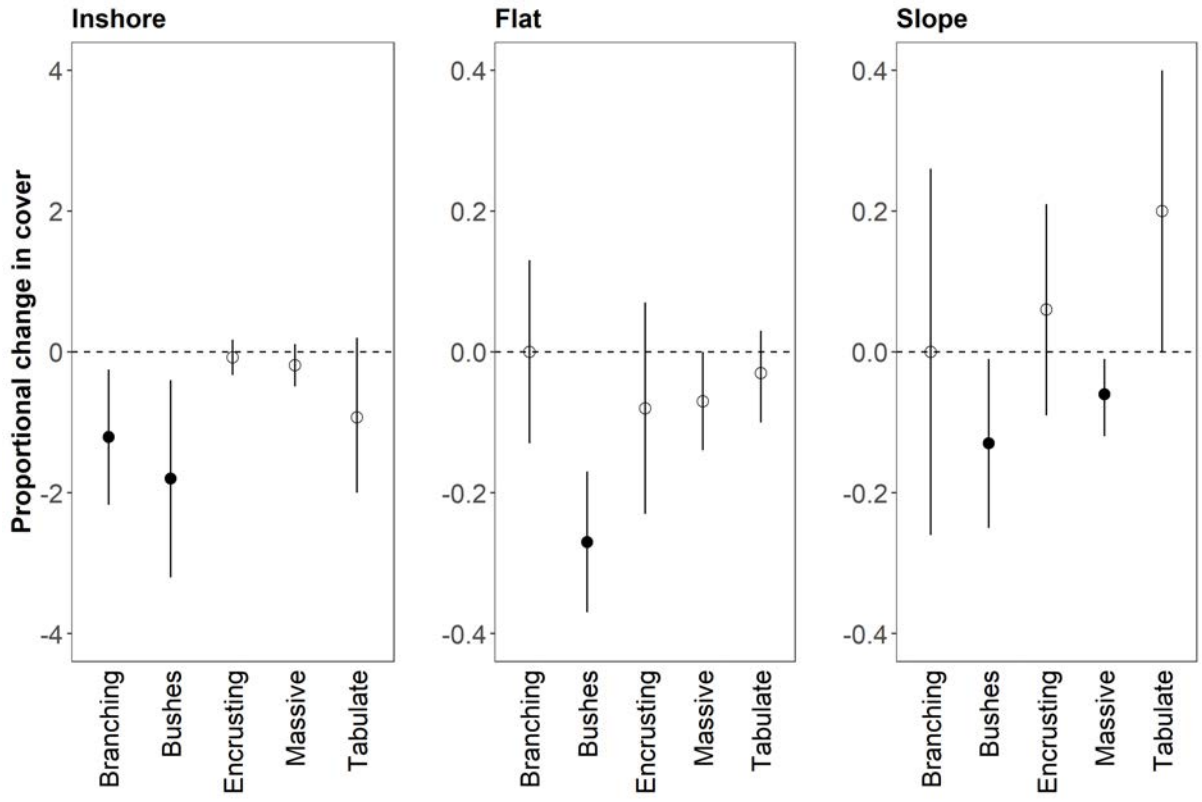

Figure 2.4. Estimated annual change in percentage cover of the dominant five growth-forms (± 95% CI) within inshore, reef flat and reef slope reef zones between 2007 and 2016. Solid symbols denote statistical significance ie. the 95% CI does not cross 0 so the annual trend is significant (p <0.05).

2.4 Discussion

Changes in coral cover at Ningaloo Reef over the 10-year study period were specific to reef zones, with significant declines in total coral cover on the reef flat but not inshore or on the reef slope. Rates of decline in hard coral cover on the reef flat at Ningaloo (4% yr^{-1}) are greater than declines observed on the Great Barrier Reef (0.53% yr^{-1} 1985–2012; De'ath et al. 2012), in the Caribbean (1.3% yr^{-1} 1977–2002; Gardner et al. 2003) and the Indo-Pacific (2% yr^{-1} 1997–2003; Bruno and Selig 2007), which have predominantly been caused by increased physical disturbance and heat stress (De'ath et al. 2012; Hughes et al. 2017a). Although Ningaloo Reef is considered to be largely free of many of the pressures that cause declines in hard coral cover in other locations, such as large-scale terrestrial run-off, high

rates of sedimentation and crown-of-thorns starfish outbreaks (De'ath et al. 2012), the reef has been impacted by coral bleaching and cyclones (Moore et al. 2012; Depczynski et al. 2013; Gilmour et al. 2019) during the last 10 years. Declining trends in hard coral on the reef flat suggest that despite the absence of some of the pressures causing declines in other locations, corals in shallow reef-flat habitats at Ningaloo are undergoing similar or greater declines than elsewhere.

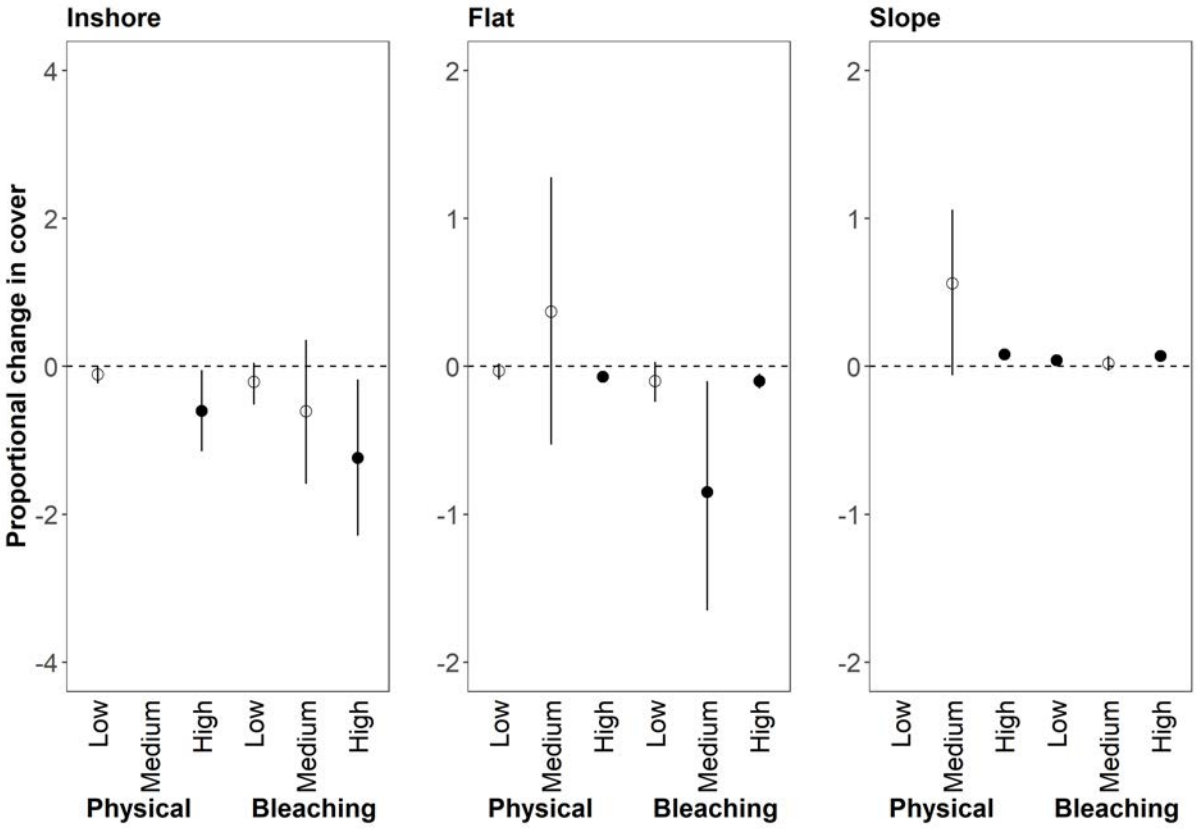

Figure 2.5. Estimated annual percentage change in cover (± 95% CI) within inshore, reef flat and reef slope zones between 2007 and 2016 for each of the three categories of physical damage and bleaching susceptibility. Solid symbols denote statistical significance (p <0.05).

Zone-specific changes observed in coral genera supports the theory that the response of coral taxa differed at small spatial scales. The cover of the most common taxa, *Acropora*, declined on the reef flat at an average rate of 10% (U=0.10) per year, whereas we detected no change within inshore and reef slope reef zones. *Acropora* are fast-growing (Pratchett et al. 2015) but

have a high susceptibility to physical damage (Madin and Connolly 2006), predation (Schoepf et al. 2010) and coral bleaching (Marshall and Baird 2000). Similar rates of decline in the cover of *Acropora* corals have been recorded on the Great Barrier Reef (Hughes et al. 2017c), in the Red Sea (Cantin et al. 2010) and in the Indian Ocean (Wilson et al. 2019b). These declines have been linked with reductions in reef complexity (Graham and Nash 2013), abundance of juvenile and small-bodied fishes (Wilson et al. 2010b), carbonate budgets (Perry et al. 2013; Perry et al. 2018) and availability of food for coral feeding fishes (Cole et al. 2009). A recent study at southern Ningaloo Reef found that *Acropora* is particularly sensitive to small-scale water circulation patterns, with decreases in *Acropora* occurring at locations with long water-residence times (>30 hr) during anoxic events or periods of elevated water temperature (Shedrawi et al. 2017). The lack of strong wave-driven currents and long water residence times during the marine heatwave at our study locations (Pearce and Feng 2013) suggest the observed declines in *Acropora* at reef flat sites may be partially attributable to a combination of reduced flow and heat stress. However, we cannot discount secondary impacts from cyclone damage, which impacted shallow reef and inshore reef zones at Ningaloo during our study period (Speed et al. 2013; Gilmour et al. 2019).

Morphological and trait-based approaches for investigating temporal variability in coral assemblages have been proposed to offer new insights into patterns of function and diversity on coral reefs, particularly when corals with similar morphology perform a similar ecological function, i.e., the provision of shelter for small-bodied fishes (Madin et al. 2016; Darling et al. 2017). We observed declining trends in bushes, branching and massive corals but no trend in either encrusting or tabulate growth-forms. It has been hypothesised that increased physical disturbance can cause declines in the abundance of more fragile coral groups (Pratchett et al. 2011) and there is evidence this may already be happening on many reefs throughout the Indo-

Pacific (McClanahan et al. 2007; Rachello-Dolmen and Cleary 2007; Álvarez-Noriega et al. 2018). Bushy and branching corals tend to have highly porous skeletons (Hughes 1987), low compressive strength and high drag coefficients (Madin and Connolly 2006), making them more susceptible to physical breakage as a result of wave-generated forces. Consistent with these predictions, we found corals with fragile skeletons and high drag coefficients declined in percentage cover within reef flat and inshore reef zones, which may be indicative of the increased frequency of large storms impacting these usually well-protected reef zones in recent years (Gilmour et al. 2019). The disproportionate loss of coral genera with high susceptibility to coral bleaching and physical disturbance within inshore and reef flat reef zones is further evidence that trends in one zone are not always indicative of trends across an entire reef. Disturbance impacts are likely to vary across individual reefs due to differences in the composition of coral assemblages and the differing responses of these assemblages to the prevailing environmental conditions. Indeed, there is often greater dissimilarity in coral assemblages in different reef zones separated by tens of metres, than in assemblages in similar zones separated by thousands of kilometers (Connolly et al. 2009). As a result, monitoring coral reef condition at the scale of a reef requires indicators that capture key processes and early signs of decline across multiple reef zones (Hughes et al. 2011; McClanahan et al. 2011). Most coral reef monitoring programs currently rely on data derived from one single reef zone, due to the need to use limited resources efficiently and to avoid logistical and safety issues associated with sampling wave exposed reef zones. Ningaloo Reef is no exception, with data on coral reef condition in previous studies derived almost exclusively from shallow (<6 m), protected (<2 m mean wave height), accessible, back reef and lagoon zones (see Simpson et al. 1993; Armstrong 2007; Cassata and Collins 2008; Wilson et al. 2010b, 2012; Onton et al. 2011; Moore et al. 2012; Speed et al. 2013; Shedrawi et al. 2017; Lozano-Montes et al. 2017; Bessey et al. 2018, and others). The spatial heterogeneity in the responses of key reef-building corals

observed here highlights the risks in making assumptions regarding trends across an entire reef based on the responses within one reef zone.

Our study indicates zone-specific changes, not only in total hard coral cover, but also in uncommon taxa such as *Pavona* and *Favia*. Notably, these typically uncommon taxa contribute considerably to the overall diversity (number of genera) of the system and can provide important information on changes in community composition (Berumen and Pratchett 2006). The magnitude of trends in uncommon taxa are twice that of common genera (46% versus 18%), suggesting dynamic fluctuations in the abundance of these uncommon taxa may make them more vulnerable to local extinction (Munday 2004). State-space models such as MARSS provide an opportunity to identify underlying trends in uncommon groups by accounting for process error (natural variability) and observation error. The reliable identification of trends in uncommon genera requires intense sampling over small spatial scales. The number of points analysed per image in this study provides a detection probability of approximately 40% for coral genera with a mean percent cover of less than or equal to 0.1%. Given we detected some coral genera with a mean percent cover of less than 0.1%, we acknowledge that genera may have remained undetected. Future studies aiming to identify trends in uncommon coral taxa should therefore consider more intense point sampling of images, or assessments of percent cover over entire images, to improve the probability of detecting uncommon taxa. Importantly, identifying rapid declines in uncommon genera which may be more susceptible to local extinction might assist with predicting the future composition of coral assemblages and associated ecosystem services (TFMPA 1999).

The persistence of coral taxa that are susceptible to coral bleaching on the reef slope (*Acropora*, *Pocillopora*, *Echinopora*) is encouraging given that Ningaloo Reef has experienced two

significant heating events over the past decade (Gilmour et al. 2019). While it remains difficult to ascertain the mechanism by which corals on the slope have survived, greater water flow and lower sea temperatures are typical of reef slope reef zones at Ningaloo (Falter et al. 2014) and, in combination with the transport of cooler water northwards via the Ningaloo current (Woo et al. 2006), may have contributed to the persistence of bleaching sensitive taxa observed here. As we look to identify locations which act as spatial refugia from increasing anthropogenic pressures (West and Salm 2003) and coral taxa with resistance to these pressures (Wooldridge 2014), a better understanding of the responses of a wide range of coral taxa and functional traits across multiple reef zones will become increasingly important. As such, future assessments of coral reef health should aim to provide detailed descriptions of trends in common and uncommon taxa across multiple reef zones.

2.5 Acknowledgements

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Table 2.3. Mean percent cover, proportional cover and dominance category of the 10 most abundant coral genera recorded at Ningaloo Reef between 2007 and 2016. Dominant genera (>10% proportional cover) are shown in red. For a full list of genera see Appendix 3.

GENUS	INSHORE			REEF FLAT			REEF SLOPE		
	PERCENT COVER	PROPORTIONAL COVER	CATEGORY	PERCENT COVER	PROPORTIONAL COVER	CATEGORY	PERCENT COVER	PROPORTIONAL COVER	CATEGORY
*Acropora**	3.6	34.1	Dominant	18.6	85.7	Dominant	9.8	47.8	Dominant
*Porites**	3.4	32.8	Dominant	0.5	2.3	Uncommon	2.4	11.7	Dominant
Turbinaria	0.1	1.0	Uncommon	1.1	4.9	Uncommon	0.3	1.4	Uncommon
Montipora	0.6	6.2	Uncommon	0.5	2.3	Uncommon	1.5	7.5	Uncommon
Goniastrea	0.3	2.6	Uncommon	0.3	1.3	Uncommon	0.7	3.2	Uncommon
Pocillopora	0.1	1.1	Uncommon	0.1	0.5	Uncommon	1.3	6.4	Uncommon
*Echinopora**	1.6	14.9	Dominant	0.1	0.2	Uncommon	0.5	2.5	Uncommon
Favites	0.1	0.8	Uncommon	0.1	0.6	Uncommon	0.8	3.9	Uncommon
Platygyra	0.0	0.4	Uncommon	0.0	0.2	Uncommon	0.6	3.1	Uncommon
Favia	0.1	0.7	Uncommon	0.1	0.4	Uncommon	0.3	1.7	Uncommon

Chapter 3 Carbonate production: patterns in coral recruitment in North-West Australia

Abstract

Understanding ecological processes that shape contemporary and future communities facilitates knowledge-based environmental management. In marine ecosystems, one of the most important processes is the supply of new recruits into a population. Here, we investigated spatiotemporal variability in coral recruitment at 15 reefs throughout the Dampier Archipelago, north-western Australia between 2015 and 2017 and identified the best environmental predictors for coral recruitment patterns over this period. Large differences in recruitment were observed among years, with the average density of recruits increasing by 375% from 0.017 recruits cm^{-2} in 2015 to 0.059 recruits cm^{-2} in 2017. Despite differences in recruitment among years, the rank order of coral recruit density among reefs remained similar among years, suggesting that spatial variation in recruitment within the Dampier Archipelago is partly deterministic and predictable. The density of coral recruits was best explained by percent cover of live corals at both local (within 5 m) and meso-scales (within 15 km), water turbidity and an oceanographic model that predicted larval dispersal. The highest density of coral recruits (~0.13 recruits cm^{-2}) occurred on reefs within sub-regions (15 km) with greater than 35% coral cover, low to moderate turbidity (KD490 < 0.2) and moderate to high modelled predictions of larval dispersal. Our results demonstrate that broad-scale larval dispersal models, when combined with local metrics of percent hard coral cover and water turbidity, can reliably predict the relative abundance of coral recruits over large geographical areas and thus can identify hotspots of recruit abundance and potential recovery following environmental disturbances—information that is essential for effective management of coral reefs.

3.1 Introduction

Recruitment is a key ecological process in the formation and maintenance of populations. For marine organisms with a planktonic dispersive phase, recruitment relies on the supply of larvae and their ability to settle, metamorphose and survive (Connell 1985). Recruitment, defined here as the successful settlement and survival of coral larvae until eight weeks post settlement (Ritson-Williams et al. 2009), is therefore determined by not just the density of incoming larvae (Cameron and Harrison 2020), but also the availability of suitable habitat (Sampayo et al. 2020), larval swimming behaviour during settlement (Gaines and Roughgarden 1985; Gaines et al. 1985) and environmental conditions that influence the early growth and survivorship of larvae (Babcock and Mundy 1996; Gosselin and Qian 1997; Baird and Hughes 2000). Recruitment is typically variable across a range of spatial and temporal scales e.g. among reefs and years, and although patterns established at recruitment may be modified by other demographic processes (e.g., post-settlement survival bottlenecks: Doropoulos et al. 2017), recruitment variability remains a major determinant of the adult assemblage structure (Done 1982; Connell 1985; Connell et al. 1997) that underpins the recovery of many coral populations (Holbrook et al. 2018). Accordingly, understanding causes of recruitment variation remains a priority in marine systems.

On coral reefs, recruitment variability at the reef or local-scale (i.e., <5 km) is particularly important because this is often the scale at which coral reefs are managed, marine reserve boundaries are designated (Sobel and Dahlgren 2004) and larval connectivity is investigated (Cowen and Sponaugle 2009; Hock et al. 2014; Feng et al. 2016; Boschetti et al. 2019). Identifying reefs with consistently high rates of recruitment relevant to other locations (i.e., recruitment hotspots) is important for optimising conservation outcomes because populations

on these reefs will likely recover more quickly following disturbance (Holbrook et al. 2018; Boschetti et al. 2020) and may maintain higher species richness if there is ongoing recruitment of multiple species. From a management perspective, identifying reefs with consistently high and low levels of recruitment is also important because it helps with the prioritisation of reefs for differing conservation outcomes (Sobel and Dahlgren 2004; Game et al. 2008).

Despite considerable effort to understand the role of larval dispersal in driving patterns of coral recruitment among reefs, the relationship is complex due to interactions between environmental variables such as wind, tide and geomorphology (Harrison and Wallace 1990; Banks and Harriott 1996; Connolly and Baird 2010; Feng et al. 2016). The complex nature of these interactions has led to the development of numerical models which aim to predict patterns of larval dispersal and coral settlement over varying spatial scales (Sammarco and Andrews 1989; Crabbe and Smith 2003; Connolly and Baird 2010; Feng et al. 2016). Arguably, one of the most successful attempts to model dispersal of coral larvae was conducted over thirty years ago by Sammarco and Andrews (1989), who accurately predicted high recruitment at sites where eddies were likely to form and persist. However, validation of the model was spatially restricted (5 km) and conducted entirely at off-reef locations (i.e., moorings over sand at depths of 15–18 m); hence, applicability to reef-scale coral recruitment remains equivocal. The lack of suitable field validation of larval dispersal models continues to impede our understanding of the role of mesoscale factors (10s to 100s km) in driving variability in coral recruitment (Crabbe and Smith 2003; Radford et al. 2014; Kool and Nichol 2015).

Our ability to predict reef-scale patterns in coral recruitment is further limited by uncertainty around the relative importance of mesoscale (i.e., hydrodynamics, regional brood stock, temperature) versus local scale factors (i.e., local broodstock, reef complexity, surface orientation, depth) on observed patterns of coral recruitment. Variation in coral recruitment at multiple spatial scales is well documented (Sammarco and Andrews 1989; Fisk and Harriott 1990; Hughes et al. 2000; Turner et al. 2018) and is attributed to complex interactions between factors pre- and post-settlement. Pre-settlement processes typically act at mesoscales and include the abundance and fecundity of broodstock and large-scale hydrodynamics (Sammarco 1994; Eagle et al. 2012). Post-settlement processes typically act at local scales and include light availability, substrate type and orientation (Carleton and Sammarco 1987), turbidity (Fabricius 2005; Evans et al. 2020), competition for space (Bak and Engel, 1979; Mundy and Babcock, 2000), predation (Trapon et al. 2013), and the presence of adult conspecifics (Vermeij 2006). Patterns in recruitment are also likely to vary among corals with different modes of reproduction and/or dispersal. In particular, larvae of brooding corals often have shorter dispersal distances than those of broadcast spawning corals (Vermeij 2005). Accordingly, the scale at which environmental parameters influence supply of recruits is expected to differ among corals with different reproductive strategies. For example, the abundance of adult broadcast spawning corals is often a poor predictor of recruitment over larger scales (>10 km) (Davidson et al., 2019; Eagle et al., 2012; Hughes et al., 1999), whereas the presence of adult conspecifics can promote aggregated recruitment at small scales (<1 m) (Carleton and Sammarco 1987; Mundy and Babcock 2000; Vermeij 2005). Disentangling the relative importance of meso- versus local-scale interactions on patterns of coral recruitment therefore remains a priority to inform predictive modelling (Boschetti et al. 2019; Feng et al. 2016; Kool et al. 2015).

Here, we address this knowledge gap by investigating the relative importance of a range of meso- and local-scale predictors on coral recruitment throughout a coastal archipelago over a three-year period. Specifically, we describe spatio-temporal patterns in coral recruitment throughout the Dampier Archipelago, north-western Australia. The archipelago represents one of the most diverse regions for hard corals in Western Australia and has been identified as an area of high conservation value and a possible World Heritage Area site (CALM 1994). The region is subject to strong cross-shelf gradients in turbidity, wave exposure and ocean temperatures (Moustaka at al. 2019) and, as such, presents a unique opportunity to investigate the importance of meso- versus local-scale interactions on patterns of coral recruitment. Moreover, an oceanographic dispersal model has been developed for the region (Feng et al. 2016), although it is unclear how well this model relates to field estimates of coral recruitment. Our aims were to (1) identify reefs with consistently high or low levels of coral recruitment, (2) identify the best spatial predictors of coral recruitment, (3) assess the importance of mesoscale (i.e., larval dispersal model, regional turbidity and coral cover) versus local scale (reef structural complexity, depth and local coral cover) influences on recruitment, and (4) validate larval dispersal model predictions for the region.

3.2 Methods

3.2.1 Site description

The study region consists of a group of inshore islands (<20 km from the mainland coast) that extends from Cape Preston to Legendre Island off the north-western coast of Western Australia, henceforth referred to as the Dampier Archipelago (Figure 3.1). The Dampier Archipelago is characterised by 12 large islands and 30 small islands or shoals, most with fringing reefs (Semeniuk 1982). The region experiences low annual rainfall (mean =

306 mm.yr^{-1}) and associated terrigenous sediment and nutrient input is minimal, due to the absence of significant riverine or freshwater inputs (Wilson et al. 2019). However, large tidal ranges (max 5.1 m, mean 1.9 m), combined with a wide shallow continental shelf and numerous narrow island passages, can produce tidal currents in excess of 0.5 ms^{-1} (Pearce et al. 2003). Suspended sediment loads are accordingly variable and are strongly influenced by the prevailing conditions of wind and tide. Suspended sediment loads on reefs within the region typically vary from 0.7 mg.L^{-1} (offshore locations) to 2.6 mg.L^{-1} (nearshore locations during large tides) (Pearce et al. 2003). Cyclones are common between November and March (mean = 0.6 cyclones per year) and typically result in dramatic but relatively short-lived (days) increases in freshwater input, turbidity and wave-generated currents (Griffith 2004). The region has significant commercial development, including the world's second largest bulk export port facility, capital and regular maintenance dredging programs, and ongoing commercial vessel traffic for the export of iron ore, salt, natural gas, and cargo (Wilson et al. 2019).

The region is influenced by large-scale oceanographic currents, including the southwesterly-flowing Holloway current, which transports warm, clear, oligotrophic waters to the northernmost reefs between March and September (Semeniuk 1982). These reefs include those adjacent to Kendrew Island, Rosemary Island, Hammersley Shoal and Legendre Island, where the influx of clear oceanic waters results in generally low turbidity (Figure 3.1). In contrast, the nearshore waters surrounding East Lewis, Goodwyn and Regnard islands are characterised by high levels of turbidity and reduced water clarity (Moustaka et al. 2019). Well-developed coral assemblages occur throughout the Dampier Archipelago, with 229 scleractinian coral species from 57 genera and approximately 18,300 ha of suitable reef habitat (Griffith 2004). Coral cover and composition vary markedly throughout the region,

with the highest coral cover and diversity on mid-shelf reefs, and cover of the most common broadcast spawning taxon, *Acropora,* highest on reefs closer to shore (Blakeway et al. 2013; Moustaka et al. 2019). Coral recruitment patterns throughout the region are poorly understood; however, a recent review of coral reproductive patterns in Western Australia suggest that between 60% and 70% of coral species occurring within the Dampier Archipelago spawn during the austral autumn (March–April) (Gilmour et al. 2019).

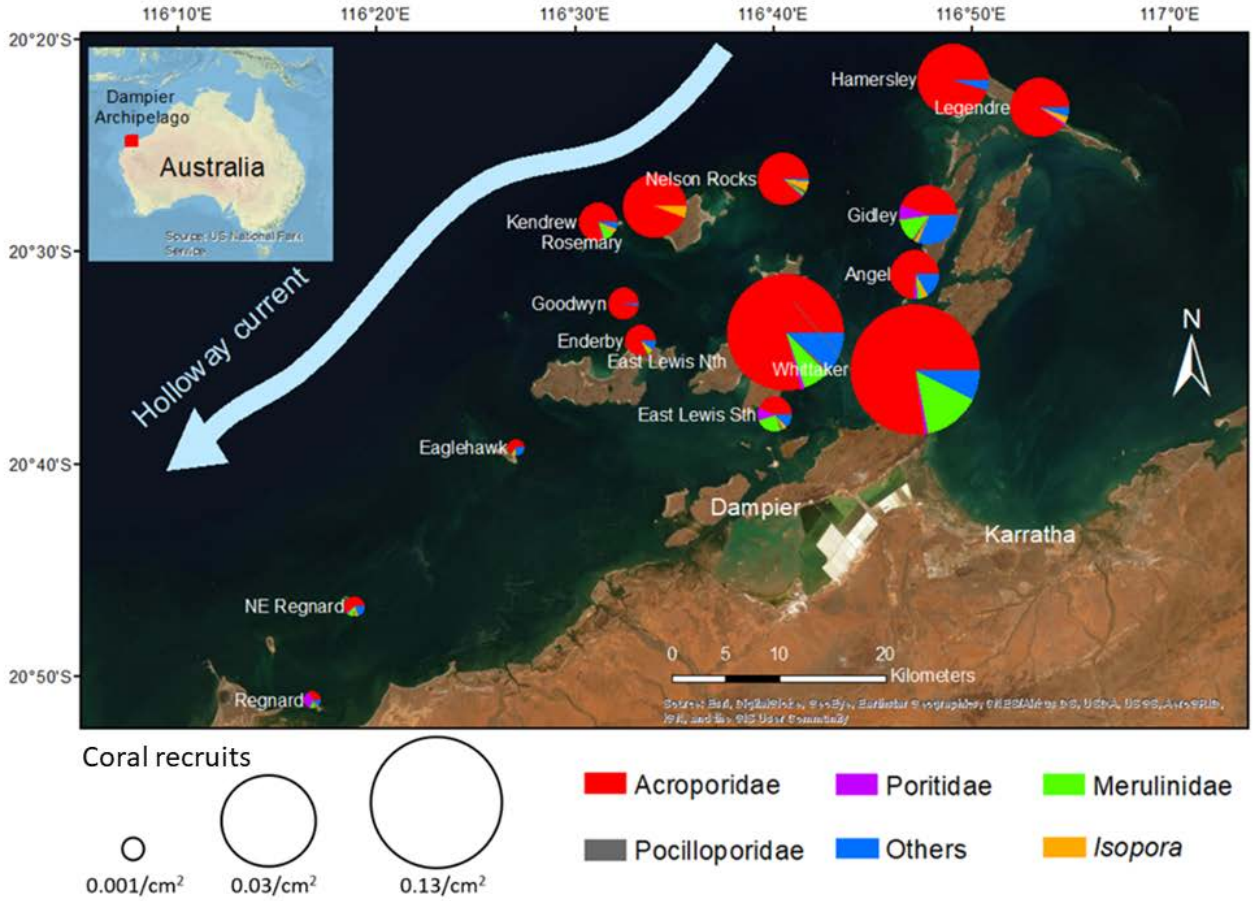


Figure 3.1. Location, mean density, and composition of coral recruits at the 15 reefs within the Dampier Archipelago between 2015 and 2017. Symbol size represents the mean recruitment density (individuals/cm^2) and colours show the different coral groups. The blue arrow represents the predominant flow direction of the Holloway current.

3.2.2 Spatial and temporal patterns in recruit abundance

The abundance of coral recruits was recorded annually from 2015 to 2017 at 15 reefs within the Dampier Archipelago (Figure 3.1). Reefs were selected throughout the Dampier Archipelago such that they were well distributed spatially, encompassed a range of dispersal model predictions (low, medium and high predicted recruitment) (Feng et al. 2016) and supported well-developed coral assemblages (i.e., >10% cover and >10 coral genera; authors pers obs.). At each reef, 15 unglazed terracotta tiles (11 × 11 × 1 cm) were deployed on stainless steel mounting plates (Babcock and Mundy 1996) and distributed randomly within an area of approximately 10 × 10 m. Individual tiles were deployed at a consistent depth range of 6–9 m . However, due to a lack of well-developed coral assemblages at 6–9 m at Enderby Is, Regnard Is, Hammersley, East Lewis South and Nelson Rocks (i.e., > 10% cover and >10 genera), tiles at these reefs were deployed at a depth of 4 m. To minimise movement and/or dislodgement of the tiles, care was taken to ensure the tiles were attached to the solid reef matrix and free from abrasion by macroalgae. Tiles were deployed four weeks prior to the predicted autumn coral spawning (over 4 days in February or March) and then retrieved eight weeks after the spawning period (over 2 days in May or June). On retrieval, organic material was removed from the tiles using chlorine bleach and the tiles were air dried for 24 hours and examined under a stereomicroscope following Mundy (2000). The abundance and family of coral recruits on each tile was recorded, with recruits allocated to one of six groups (Acroporidae, Merulinidae, Pocilloporidae, Poritidae, *Isopora* spp and 'other') based on the distinguishing characteristics described in Babcock et al. (2003). Acroporidae, Merulinidae and Poritidae recruits were classified as spawners and Pocilloporidae and *Isopora* recruits were classified as brooders, as per the dominant reproductive modes described in Gilmour et al. (2016). Due to logistical and weather constraints, all 15 tiles were unable to be retrieved at

several sites (see electronic supplementary material, Table S1). As a result, sites were only included in the analysis if more than 10 tiles were retrieved. .

Spatial and temporal patterns in the abundance of coral recruits were examined using permutational multivariate analysis of variance (PERMANOVA for Primer v7©, Anderson 2008). Differences in total coral recruitment was investigated among reefs and years using a 2-way PERMANOVA. Differences among years (2015, 2016, 2017) for each coral group (spawners, brooders and coral families) were investigated using 1-way PERMANOVAs with pair-wise comparisons to identify in which years recruitment differed for each coral group. *Isopora* were not examined separately due to low numbers. PERMANOVAs were based on a Bray Curtis dissimilarity matrix of square-root transformed abundance data. Differences in the rank order of reefs among years were tested using a Friedman Rank test using the mean density of recruits per reef (cm^{-2}) in XLSTAT 2020.

3.2.3 Predictors of coral recruitment

Generalised additive mixed models were used to assess the relative importance of local (local total hard coral abundance, local brooder abundance, local spawner abundance, reef complexity, substrate type, depth) and mesoscale variables (dispersal model, total hard coral abundance, brooder abundance, spawner abundance, turbidity, mean sea surface temperature (SST)) on coral recruitment (see electronic supplementary material, Table S2). A full-subsets approach was used to fit all possible combinations of variables, while limiting models to three explanatory variables to avoid difficulty in interpreting results (Kleiber and Zeileis 2008; Fisher et al. 2018). Reef and year were included as random effects to increase the inferential power of the model (Harrison 2014). Response data (i.e., density of coral recruits) was not transformed as selecting an appropriate error distribution (in this case a Tweedie

distribution) accounted for non-normal data distribution. Predictor variables were transformed to reduce the skewness where appropriate. Models containing variables with correlations exceeding 0.28 were excluded to avoid issues with collinearity among predictor variables (Graham 2003; Fisher et al. 2018). The model with the lowest Akaike Information Criteria corrected for small sample size (AICc) was selected as the best model and other models within two AICc (ΔAICc<2) of the 'best' model were considered. R^2 values across the full set of models were used to provide an indication of the predictive power of the model and an index of variable importance across the full set of models was calculated by summing the AICc weights for all models containing each variable (Burnham and Anderson 2002). Statistical analyses for identifying predictors of spatial variation in coral recruitment were conducted using the R language for statistical computing (version 3.6.3), and the FSSgam (version 1.11), gamm4 (version 0.2-6) and mgcv (version 1.8-31) packages (Wood 2011; Fisher et al. 2018; Wood and Scheipl 2019).

3.2.4 Larval dispersal model

Predicted numbers of coral larvae that were competent to settle were obtained for the Dampier Archipelago using a two-dimensional larval dispersal model on a 1 × 1 km grid (see Feng *et al*. 2016). The larval dispersal model is based on the three dimensional Regional Ocean Modelling System hydrodynamic model (ROMS; Marchesiello et al. 2003) and provides predictions of the total number of competent coral larvae settling each year across a 1 × 1 km grid by incorporating hydrodynamics with the development and settlement characteristics of larvae from a typical broadcast spawning coral (i.e., *Acropora millepora*; Feng et al. 2016). Coral recruitment predictions, hereafter referred to as dispersal model predictions, were obtained for the 15 study reefs for the years 2015 to 2017 from the grid point closest to the study reef. A known limitation of the dispersal model predictions is the

lack of consideration of variability in coral density on individual reefs, with equal numbers of larvae released on reefs throughout the model domain (see Feng et al. 2016 for details). For this reason, we incorporated coral cover metrics at varying spatial scales in our predictors of coral recruitment.

3.2.5 Percent cover of hard coral and reef complexity

Percent cover of live scleractinian (hard) corals and reef structural complexity were measured annually at increasing distance from the study reefs (3 spatial scales): 5 m, 200 m and 15 km. Within 5 m of the recruitment tiles, estimates of percent coral cover were obtained from high resolution photographic mosaics of the substratum. A GoPro4™ was used to capture overlapping images of the substratum (≈ 200 images per site), which were then combined to construct a two-dimensional photo mosaic with the structure from motion software Agisoft™ (Pedersen et al. 2019). Forty photos were randomly selected from each photomosaic and the percent cover of scleractinian (hard) coral recorded using six fixed points per photograph using the software Transect Measure (www.seagis.com.au). Reef complexity was estimated using the ratio of linear distance to the contoured surface distance of a 10 m length of chain carefully moulded to the reef surface within the 10 × 10m study area (following McCormick 1994).

To estimate percent cover of hard coral at larger spatial scales (i.e., within 200 m and 15 km of the recruitment tiles) coral cover was quantified along replicate 50 m transects. At each reef three transects were situated at fixed locations (permanent markers) with the first transect commencing immediately adjacent the recruitment tiles. Transects were oriented end-to-end (separated by 5 m), parallel to the reef edge and along the same depth contour as the recruitment tiles. Transects were surveyed at least once annually, with transects at six reefs

surveyed twice in the same year (January and May 2015 and 2017) and percent cover and reef complexity of all transects averaged for that year. Photographs were taken by divers at 1 m intervals along each transect (50 photographs per transect) at a height of ~0.5m above the substratum (~0.28m^2 per photo). Forty photos were randomly selected within each transect and the percent cover of scleractinian (hard) coral genera recorded using six fixed points per photograph using the software Transect Measure (www.seagis.com.au). Points were evenly spaced across the height and width of the image to provide a mean point density of approximately 14 points per m^2, sufficient to provide reliable descriptions of percent coral cover from photo transects (Dumas et al. 2009). Corals were assigned to genera using the updated coral taxonomy from Richards (2018) and then assigned as either broadcast spawners or brooders using the dominant reproductive mode described in Gilmour et al. (2016). Percent cover of corals and reef complexity within 200 m and 15 km of recruitment tiles was calculated by averaging all percent cover and reef complexity measurements within 200 m (3–6 transects) and 15 km radius (6–24 transects) of each study reef for each year (see Table S1 for further details).

3.2.6 Environmental data

Environmental data were collected for each reef using a combination of techniques. Mean KD490 (diffuse attenuation coefficient at 490 nm KD2 algorithm; hereafter referred to as turbidity) and degree heating weeks (DHW) were retrieved from NOAA's ERDDAP data server (Dataset ID: nesdisVHNSQkd490Daily and NOAA_DHW respectively; see S5 for details). KD490 represents the MODIS diffuse attenuation coefficient at 490 nm with a KD490 value of 0.1, equating to an attenuation depth of 10 m. Higher KD490 values generally reflect higher turbidity, lower water clarity and more rapid attenuation of light with increasing depth but are susceptible to overestimation in shallow water due to bottom interference (Zhao et al.

2013). Water depth was recorded by divers at each reef to the nearest 0.5 m and adjusted for current tidal conditions using tide tables sourced from the Australian Bureau of Meteorology (http://www.bom.gov.au/oceanography/projects/ntc/wa_tide_tables.shtml).

3.3 Results

3.3.1 Temporal and spatial patterns in recruit densities

Mean densities of coral recruits varied among reefs (PERMANOVA, reef: $p = 0.001$) from a low of 0.0002 recruits cm^{-2} in 2016 at Regnard to a high of 0.273 recruits cm^{-2} at Whittaker Island in 2017 (Figure 3.2; ESM Table S3). Recruit densities varied widely among years (PERMANOVA, year: $p = 0.001$, ESM Table S3), the lowest density occurring in 2015 and the highest in 2017 (Figures 3.2, 3.3a), increases being largely consistent among reefs (PERMANOVA, reef x year: $p = 0.067$, ESM Table S3). Despite the large variability in recruitment among reefs the rank order of recruitment among reefs was consistent among years (Friedman, $\chi 2 = 4.9$, $df = 2$, $p = 0.086$; ESM Table S4). Recruitment was typically highest at Whittaker Island (0.12 recruits cm^{-2}) and East Lewis North, with some of the highest rates of recruitment across the study period recorded at these reefs in 2017 (Figure 3.2). Conversely, coral recruitment at Eaglehawk, Regnard, NE Regnard and Enderby Islands did not exceed 0.008 recruits cm^{-2} across the three years (Figure 3.2).

Temporal differences in coral recruitment among years (Figure 3.3a) were largely driven by increases in broadcast spawning corals (Acroporidae and Merulinidae) that had substantially higher recruitment in 2017 compared to 2015 and 2016 (Figure 3.3c–e). In contrast, brooders and Pocilloporidae groups recruited in highest densities in 2016, while Poritidae recruited in similar densities across all years (Figure 3.3b,f,g; ESM Table S5).

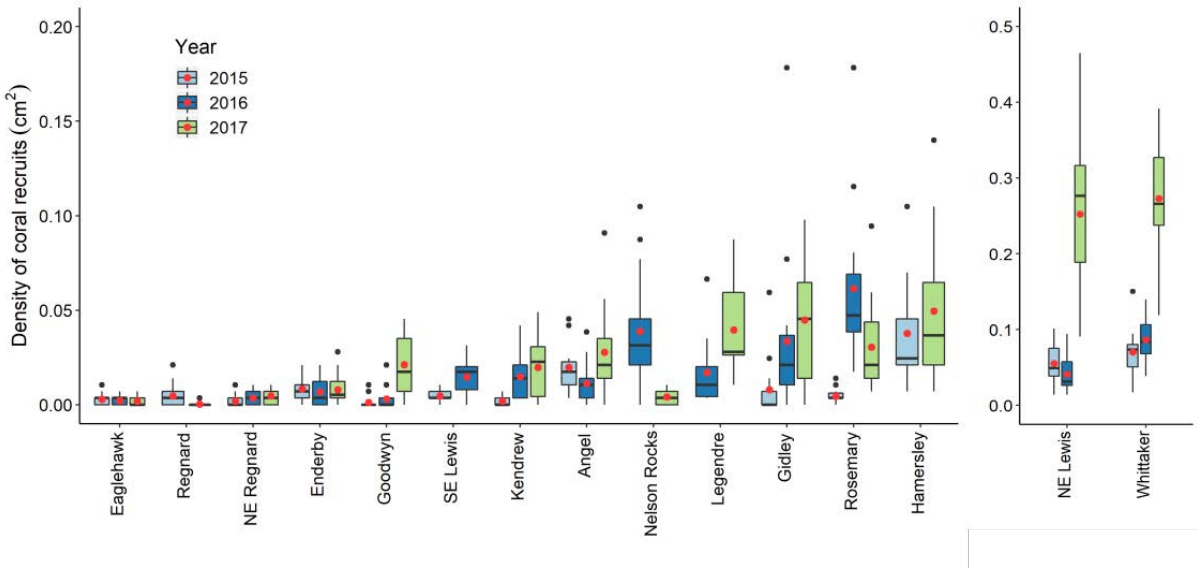


Figure 3.2. Box plots showing the mean (red dot), median (horizontal line), quartiles and outliers (box and black dots) of recruitment density (individuals/cm^2) in 2015, 2016 and 2017 at the 15 reefs throughout the Dampier Archipelago. Reefs are ranked in order from lowest to highest mean recruitment density with NE Lewis and Whitaker shown on a separate y-axis for clarity. Due to logistical and weather constraints, retrieving all 15 tiles was not possible at Regnard Is, South East Lewis Is, Nelson Rocks, Legendre Is. and Hammersley all years, As a result recruitment data is shown for only two years.

3.3.2 Predictors of recruitment

Percent hard coral cover (15 km) and turbidity were the best predictors of total coral recruitment density over the three years, though there were several other models that had similar explanatory power (Figure 3.4, ESM Table S6). Percent hard coral (15 km) was a particularly good predictor of total coral recruitment and was included in all of the top models (ESM Table S6). Highest coral recruitment densities were observed on reefs with greater mesoscale hard coral cover, low turbidity and high dispersal model predictions (ESM Table S6, Figure S1).

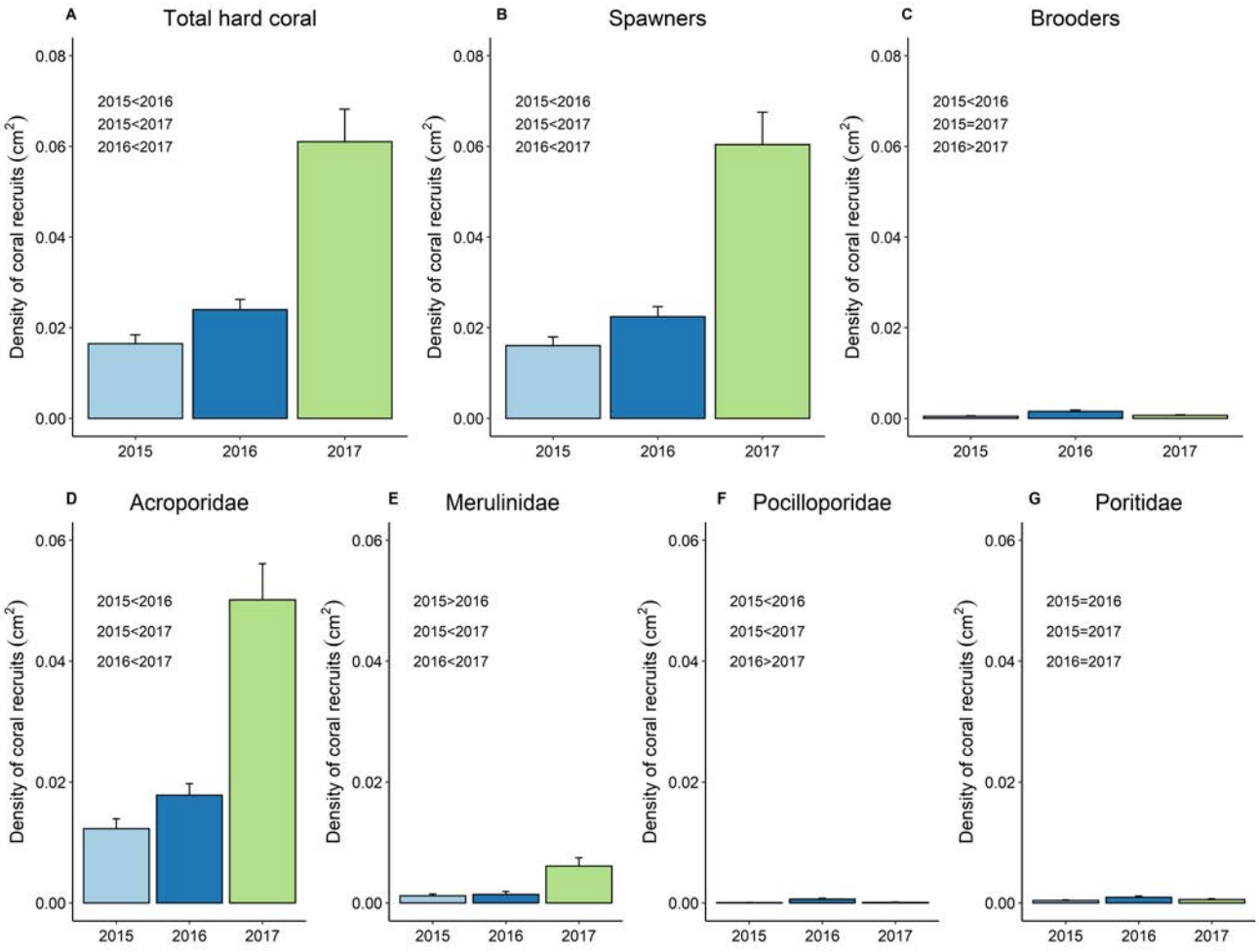


Figure 3.3. Mean density of recruits (+SE) observed in 2015, 2016 and 2017 at the 15 reefs throughout the Dampier Archipelago between 2015 and 2017 for (a) total recruitment (b) total spawners (c) total brooders (d) Acroporidae, (e) Merulinidae (f) Pocilloporidae and (g) Poritidae. Y-axis scales for Acroporidae, Merulinidae, Pocilloporidae and Poritidae are adjusted to illustrate yearly variations.

The best predictors of recruitment for the spawners and Acroporidae were the mesoscale variables hard coral cover (15 km), turbidity and the dispersal model (Figure 3.4), with trends between these groups and best predictors being similar to those observed for total coral recruitment. In contrast, the best predictors of recruitment for brooders, Merulinidae, Poritidae and Pocilloporidae groups were a combination of mesoscale (i.e., dispersal model and turbidity) and local scale (i.e., local hard coral cover, depth and reef complexity) variables (Figure 3.4, ESM Table S6). High recruitment densities of brooders, Merulinidae, Poritidae and Pocilloporidae were observed on reefs with greater than 25% local hard coral

cover (5 m), while recruitment densities at lower coral cover were highly variable (ESM Figure S1). Overall, mesoscale variables explained more variation in coral recruit densities than local scale variables (Figure 3.4), featuring in all top models (ΔAICc<2) for all response variables with the exception of Pocilloporidae (ESM Table S6). Turbidity (i.e., KD490) was included in eight of the fourteen top models (ESM Table S6); however, the relationship between recruitment and turbidity was variable and sensitive to two outlying datapoints which represented reefs with very high turbidity (see ESM Table S6,7 for further details).

Discussion

Despite an almost 4-fold difference in coral recruitment among years, variation in the relative rates of recruitment among reefs was temporally consistent, indicating recruitment in the Dampier Archipelago is partly deterministic and predictable. For example, two reefs in the north-east of the Dampier Archipelago (Whittaker and North East Lewis) had consistently high coral recruitment, while four reefs in the south-west of the archipelago (Eaglehawk, Regnard, North East Regnard and Enderby) had consistently low coral recruitment for all three survey years. These results corroborate previous studies which suggested recruitment patterns recur at the reef scale because oceanographic currents interact with local topography in a seasonally consistent way (Alldredge and Hamner 1980; Wolanski and Hamner 1988; Sammarco 1991; Oliver et al., 1992). Accordingly, we found that the dispersal model explained a moderate amount of the variation in recruitment, particularly for Acroporidae and broadcast spawning corals more generally. Spatially consistent patterns in the recruitment of spawners and brooders have been previously recorded in the central Indian Ocean (Adjeroud et al., 2007), the Great Barrier Reef (Sammarco 1991; Eagle et al., 2012) and the Caribbean (Sammarco 1985), while other studies have recorded congruous spatial patterns only in brooders (Glassom et al., 2004). The limited temporal extent of our study (i.e., 3 years)

prevents us from identifying drivers of variance among years, but identifying reefs with consistently high rates of recruitment relevant to other locations remains a high priority for optimising conservation outcomes, because the regular arrival or recruits to these reefs may promote quicker recovery following disturbance (Boschetti et al., 2020).

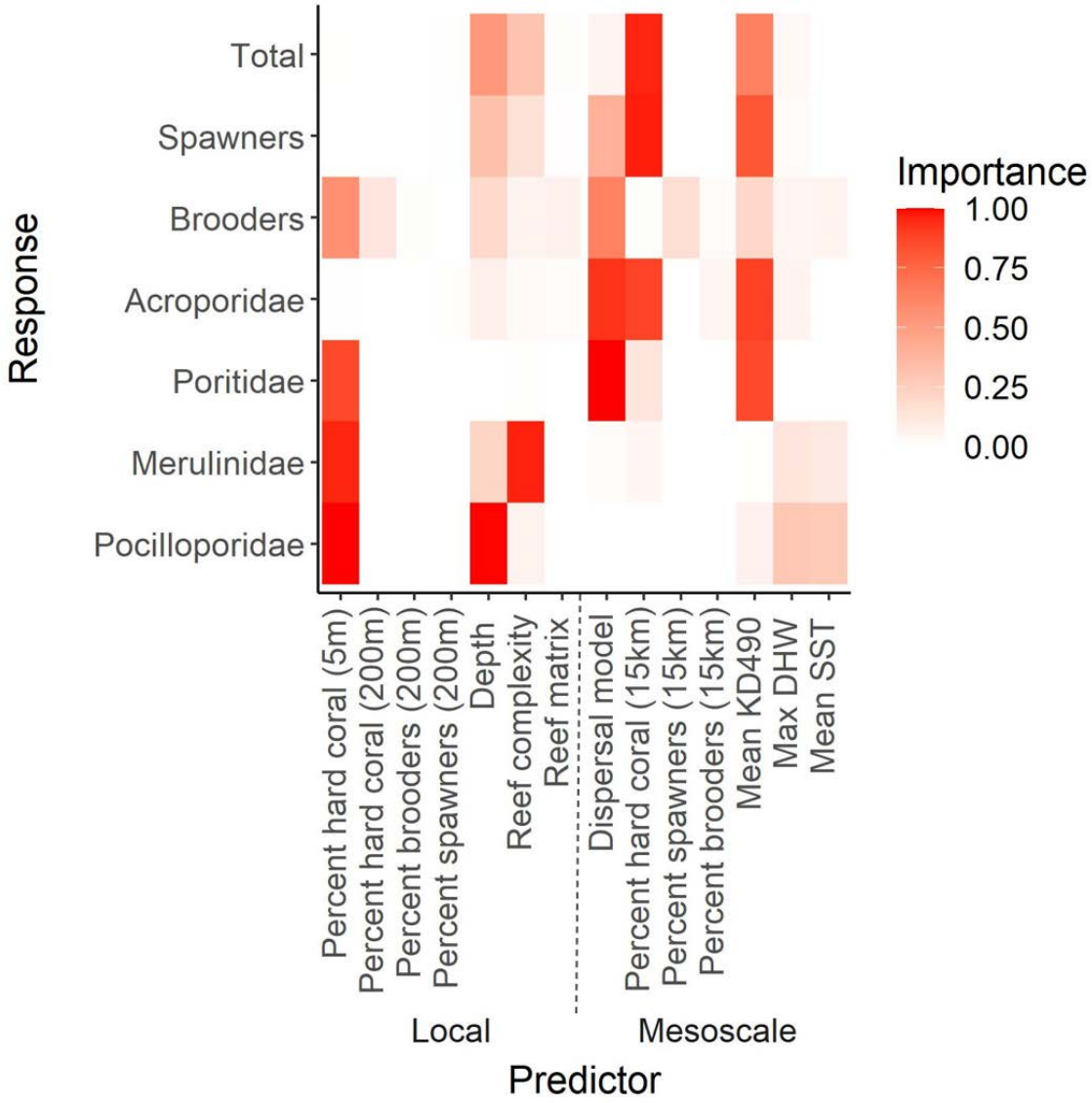


Figure 3.4. Variable importance across the full subset of generalised additive mixed models of coral recruitment in the Dampier Archipelago. DHW = Degree Heating Weeks, SST = Sea Surface Temperature.

The best predictors for coral recruitment over the three years included percent hard coral (at 15 km and 5 m), indicating links between recruitment and adult abundance over different spatial scales for different coral families and reproductive modes. High recruitment of broadcast spawning corals such as Acroporidae and Merulinidae (>0.03 recruits cm^{-2} or 10 recruits per tile) occurred on reefs with greater than 35% mean coral cover within 15 km, while high recruitment of brooders, Pocilloporidae and the broadcast spawning Poritidae occurred when local coral cover (within 5 m) was greater than 25%. The importance of coral cover at differing spatial scales may be driven by the development times of larvae. Local retention of larvae (recruitment) is expected to be high in brooding taxa, as brooded larvae are capable of settlement immediately on release and often settle near conspecifics (Vermeij 2005) and closely related adults (Vermeij and Sandin 2008; Doropoulos et al. 2015). The positive relationship we observed between recruitment of brooders and local coral cover (5 m) supports this hypothesis. Similarly, the positive relationship we observed between recruitment of spawners and coral cover at mesoscales (15 km) suggests mechanisms may operate for more widely dispersed larvae over larger scales.

Positive stock-recruitment relationships have been observed in spawning corals following catastrophic mortality events (Gilmour et al. 2013; Lukoschek et al. 2013) with the recovery of these reefs driven by recruitment of locally sourced larvae (within 15 km). Two additional plausible mechanisms for the positive stock- recruitment relationships in the Dampier Archipelago are enhanced rates of settlement in regions with higher coral cover due to higher larval densities (Heyward et al. 2002; Suzuki et al. 2012; Doropoulos et al. 2018), and/or better post settlement survival of larvae in locations where adults are abundant due to favourable environmental conditions. Regardless of the mechanism, the links between recruitment and adult abundance over different spatial scales suggests high rates of larval

retention within the Dampier Archipelago during our study period. These findings are supported by connectivity models for the region, which found high rates of larval retention within the Dampier Archipelago most years (dispersal distances <10 km) (Kool and Nichol 2015; Feng et al. 2016; Boschetti et al. 2019), and genetic studies which found generally low levels of genetic similarity between corals in the Dampier Archipelago and those located 130 km to the southwest at Ningaloo Reef (Underwood et al. 2013; Evans et al. 2018)

Numerous recruitment models have aimed to disentangle the complex nature of meso- and local-scale interactions on reefs (Connolly and Baird, 2010; Sammarco and Andrews, 1989; Crabbe and Smith, 2003; Feng et al., 2016). Recent advances in hydrodynamic modelling (i.e., reef scale resolution; Feng et al. 2016), bathymetry mapping and the incorporation of larval behaviour characteristics into models (i.e., minimum, peak and maximum competency periods; Connolly and Baird 2010) have resulted in substantial improvements in model predictions of coral recruitment on reefs over the last 30 years. However, our results indicate that adult abundance at both the local and mesoscales were generally better predictors of recruitment than the larval dispersal model. That said, when the larval dispersal model was combined with simple metrics such as percent hard coral cover and water turbidity, it provided good predictions of the relative abundance of coral recruits over large geographical areas. Future dispersal models may be improved through the inclusion of emerging information on the effects of other environmental variables on the behaviour and ecology of coral larvae. For example, temperature can influence pelagic larval duration of marine species, including corals (O'Connor et al. 2006), and is likely to alter dispersal patterns as sea temperatures increase (Figueiredo et al. 2014). Given that post-settlement survival of coral recruits is likely to be dependent on local environmental conditions (Fitzhardinge 1988; Babcock and Mundy 1996; Baird and Hughes 2000; Chong-Seng et al. 2014; Evans et al.

2020), future recruitment models aiming to identify reefs with consistently high (hot-spots) and low recruitment of corals should aim to incorporate a range of local and mesoscale environmental factors.

A 375% increase in the density of recruits between 2015 and 2017 suggests that mesoscale environmental conditions became more favourable for recruitment over the study period. Inter-annual variability in patterns of coral recruitment are well documented (Harrison and Wallace 1990; Harriott and Banks 1995; Harriott et al. 1997; Hughes et al. 1999; Hughes et al. 2019) and are typically attributed to differences in oceanographic conditions (e.g., current patterns, water temperature), adult coral abundance and/or reproductive output (Hughes et al. 2019). Consistent with the influence of large-scale hydrodynamics, we found increases in the dispersal model predictions on most reefs (13 of 15) and a strong shift toward La Niña conditions between 2015 and 2017 (see ESM Table S8). Recruitment rates of some fish, coral and crayfish are positively correlated with the Southern Oscillation Index (SOI) in coastal western Australia, with higher recruitment recorded during La Niña years, when the ENSO-influenced Leeuwin Current is stronger and sea surface temperatures higher (Pearce and Phillips 1988; Lenanton et al. 2009; Wilson et al. 2018). Connectivity models for north-western Australia have also revealed large changes in oceanographic conditions around the same time as the autumn coral spawning period, with the predominant current direction in the dispersal model changing from a north-easterly direction to a south-westerly direction in mid to late March (Feng et al. 2016). Given that the predicted time of spawning between 2015 and 2017 varied by 16 days (14 March to 2 April) it is likely that the predominant current direction differed among years and may have influenced the direction of larval dispersal and/or immediate post-settlement survival of recruits. As a result, changes in mesoscale oceanographic conditions between 2015 and 2017, alongside changes in the fecundity of

corals post bleaching (Babcock et al. 2020), may have contributed to the increased density of recruits observed between 2015 and 2017.

Turbidity (KD490) was among the best predictors of recruitment and showed a weak negative effect on total recruitment and the recruitment of broadcast spawning corals, particularly the Acroporidae. Turbidity is known to be critical during the early lifecycle phases of broadcast spawning corals (Jones et al. 2015), with high turbidity associated with negative impacts on egg fertilisation, settlement and metamorphosis (Babcock and Davies 1991; Humanes et al. 2017). High turbidity is typical on inshore reefs in the Dampier Archipelago (Moustaka et al. 2019) and recent observations of coral recruitment 120 km to the southwest of our study found high recruitment to tiles on turbid inshore reefs (Evans et al. 2020), suggesting that the effect of turbidity on coral recruitment is variable. The lack of a strong relationship between coral recruitment and turbidity in the present study may be due to differences in coral species among sites, the insensitivity or tolerance coral species in this region to turbid water, or the use of KD490 to estimate turbidity. KD490 is a good indicator of water clarity in clear oceanic waters (Zhao et al. 2013) but is susceptible to overestimation in shallow water due to bottom interference (Zhao et al. 2013). KD490 also fails to capture information on the size and/or type of particles in the water column and the intensity of acute turbidity events (https://eastcoast.coastwatch.noaa.gov/cw_k490_hires.php), both of which can influence coral settlement and early survival (Babcock and Davies 1991; Jones et al. 2015). The relationships between coral recruitment and turbidity identified in this study were also heavily dependent on two outlying datapoints (Regnard Is. 2015, 2016). When these two datapoints were removed from the analysis turbidity was no longer included in the top models, suggesting the relationship between turbidity and recruitment was driven by extremes of turbidity. Our results therefore suggest that low to moderate levels of turbidity

are unlikely to be responsible for the observed spatial variation in recruitment observed in the Dampier Archipelago.

3.4 Conclusions

Understanding the processes that influence the replenishment of coral populations and the scales over which they operate remains a research priority. Notable in our study is that coral recruitment followed spatially consistent patterns driven by density dependant relationships between coral recruits and adult coverage. We identified reefs with consistently high rates of recruitment relevant to other locations (i.e., recruitment hotspots), suggesting reefs in the Dampier Archipelago are likely to be both sources and sinks of coral larvae for some taxa. Coral recruit densities in the Dampier Archipelago were generally low (mean = 0.06 cm^{-2}) in comparison to reefs located at similar latitudes on the Great Barrier Reef (e.g., Swains reefs: mean = 0.08 recruits cm^{-2}, Hughes et al. 1999; Keppel Islands: mean = 0.12 recruits cm^{-2}, Davidson et al. 2019); however, they were high in comparison to reefs immediately to the south (Ningaloo Reef 280 km south: mean = 0.01–0.5 recruits cm^{-2}, Turner et al.2018; central Pilbara 50 km south: mean = 0.003 recruits cm^{-2}, Evans et al. 2020). Despite this, our study suggests high rates of larval retention within the Dampier Archipelago and therefore limited capacity for reefs within the Dampier Archipelago to act as occasional sources of larvae to aid in the recovery and resilience of reefs throughout the region (see Boschetti et al. 2019). Our results reaffirm the need for improved models of coral recruitment and to manage coral populations as inter-connected networks of reefs, rather than discrete populations on individual reefs.

3.5 Acknowledgements

I recognise and acknowledge the Yaburrara people, as the traditional custodians of the land and sea country on which this study was conducted. I wish to thank staff at the Department of Biodiversity, Conservation and Attractions for their continued support, in particularly Margaret Mohring, Rachael Marshall and Tim Hunt. I thank Ben Kelly, Nick Mortimer, Nicole Ryan, Cindy Bessey, Marlee Hutton, Monique Grol and the skipper and crew of the *Keshi-Mer* for their valuable field support.

Chapter 4 Carbonate erosion: Bioerosion of carbonate by *Bolbometapon muricatum* at northern Ningaloo

Abstract

Bolbometopon muricatum (bumphead parrotfish, Valenciennes, 1839) is a conspicuous, iconic and ecologically important coral reef fish species. *B. muricatum* plays an important role in the bioerosion of the reef framework and, as a result, has been described as both an ecosystem engineer and keystone species. Despite the complete absence of *B. muricatum* from 32 years of scientific surveys across the Ningaloo Reef World Heritage Area, we recorded a total of 155 individuals of *B. muricatum* across 63.2 ha of reef crest surveys, equating to mean density of 2.38 ind/ha. Our observations represent the first record of this iconic species in scientific surveys at Ningaloo and, in combination with qualitative observations of *B. muricatum* by expert witnesses, indicate *B. muricatum* is likely to have been present in ecologically relevant densities since 2006. The densities of *B. muricatum* observed at northern Ningaloo in 2021 suggest this species is removing an estimated 13.42 tonnes/ha or 1.34 kg/m^2 of calcium carbonate per year, which is broadly comparable with estimates of total parrotfish bioerosion across many reefs in the central Indian and Pacific Oceans. Although not currently afforded elevated conservation status within current management plans, *B. muricatum* possess many life-history characteristics which make them vulnerable to overfishing, which may justify consideration for increased protection within the world heritage listed Ningaloo Reef Marine Park.

4.1 Introduction

Species which create, maintain or modify habitats perform a fundamental role in shaping the physical structure of an area and the species these areas support (Jones, Lawton and Shachak 1996). Such 'ecosystem engineers' change the environment via their own physical structures, i.e., their living tissues and skeletons, or by transforming living or non-living materials from one physical state to another. In some cases these species may alter the availability of energy, food, water or sunlight available to other species, having disproportionately large effects on overall community structure and function (Coleman and Williams 2002). Examples of marine ecosystem engineers include corals, mussels and crustose coralline algae that increase biomass and structural complexity of habitats, seagrasses and kelps—which alter water flows, entrain larvae and provide refuge from predation—and urchins and fish that can cause extensive bioerosion of benthic substrata. Ecosystem engineers are generally considered disproportionately important relative to the rest of the community (Pogoda et al. 2019), often receiving elevated conservation status (Beger et al. 2011; Daling et al. 2019; Jenkins et al. 2010, McClanahan et al. 2011). The impact of ecosystem engineer species, however, depends largely upon the scale of their actions, which can be spatially and temporally variable. Understanding and managing the impact of ecosystem engineer species therefore requires detailed knowledge of their current distribution, abundance and impact.

Bolbometopon muricatum (bumphead parrotfish, Valenciennes, 1839) is a conspicuous, iconic and ecologically important coral reef fish species. *B. muricatum* plays an important role in the bioerosion of the reef framework and has previously been described as both and ecosystem engineer (Hamilton et al. 2016) and a keystone species (Bellwood, Hoey and Choat 2003). Using their large beak-like jaws to feed on reef substrata, large individuals (>100 cm total length; TL) can remove an estimated 5.5 tonnes of reef carbonates annually,

of which approximately 50% can be live coral (Bellwood, Hoey and Choat 2003). On the Great Barrier Reef, it is estimated that bioerosion due to *B. muricatum* accounts for ~85% of bioerosion by parrotfish (Hoes and Bellwood 2008), which was broadly equivalent to the estimated rate of coral reef accretion. Importantly, there are no functionally equivalent species to *B. muricatum* as the three next largest species of parrotfish (*Chlorurus microrhinos*, *Chlorurus strongylocephalus* and *Chlorurus gibbus*) remove an estimated maximum of 1.015 tonnes of carbonates per individual per year, of which only ~5% is live coral (Bonaldo, Hoey and Bellwood 2014). In areas where the abundance of large *B. muricatum* has been removed through fishing, the function of fish bioerosion is essentially lost as smaller species are unable to compensate for the loss of the larger *B. muricatum* (Bellwood, Hoey and Hughes 2012). Therefore, *Bolbometopon muricatum* play a critical role in maintaining the balance between reef erosion and accretion, and thus net carbonate budgets.

Globally, there have been large population declines in *B. muricatum* throughout much of its range (Hamilton et al. 2016). *B. muricatum* lives up to 40 years and attains sexual maturity between 7 and 11 years of age (Choat and Robertson 2002; Choat, Axe and Lou 1996; Choat et al. 2012), approximately twice the maximum age of the next largest parrotfish, *Chlorurus microrhinos* (17 years age; Choat and Robertson 2002; Choat, Axe and Lou 1996). With a habit of sleeping in large groups (>60 individuals) in shallow, sheltered reef locations at night, *B. muricatum* is easily harvested by spearfishers (Hamilton et al. 2016; Dulvy and Polunin 2004, Johannes 1981), making it particularly susceptible to overfishing (Dulvy and Polunin 2004; Donaldson and Dulvy 2004; Kobayashi et al. 2011). In Pacific locations where spearfishing pressure is high, *B. muricatum* populations may have already declined to levels where populations are unsustainable and ecologically irrelevant (Bellwood, Hoey and Choat

2003; Bellwood, Hoey and Hughes 2012). These declines have invoked total fishing bans in some Pacific nations (e.g., Palau) to try and re-establish populations and safeguard reef resilience (Polloi et al. 2014).

Ningaloo Reef on the western Australian coastline (22°S, 113°E) is a fringing reef almost 300 km in length with exceptional cultural, ecological and tourism value. The area was included on UNESCO's World Heritage List in 2011 (Ningaloo Coast World Heritage Area: NCWHA), in part due to recognition of the globally important annual aggregations of whale sharks and the high abundances of manta rays and sharks (http://whc.unesco.org/en/decisions/4278; accessed 20 July 2021). Interactions with these iconic species are tightly regulated (Environment Protection and Biodiversity Conservation Act 1999; Conservation and Land Management and Marine Parks and Reserves Authority 2005) and associated ecotourism activities generate over A$20 million annually for the region (Deloitte Access Economics 2020). However, these iconic species are not considered to be ecosystem engineers or keystone species, nor do they provide services which increase ecological resilience *per se* (i.e., capacity to absorb disturbances and respond to change while retaining essentially the same function) (Scheffer at al. 2001). Despite recent sightings of juvenile *B. muricatum* at Ningaloo Reef (Jenkins and Morrison 2018), there remain no empirical data on its current distribution and/or abundance.

Here, we assess the abundance, density and size structure of *B. muricatum* within Ningaloo Reef, Western Australia. We use data obtained from three sources to assess the spatiotemporal distribution and size structure of *B. muricatum* populations: (1) historical surveys of the abundance and density of reef fish assemblages at northern Ningaloo Reef (1987–2019); (2) qualitative observations of *B. muricatum* at northern Ningaloo by expert

witnesses (2006–2020); and, (3) targeted timed swim surveys of *B. muricatum* abundance and size at northern Ningaloo (2021). We discuss the implications of our findings for the ongoing management of this iconic engineer within the World Heritage listed Ningaloo Reef.

4.2 Materials and Methods

4.2.1 Study location

Our study was focused along the western section of Ningaloo Reef (north-western Australia) along approximately 60 km of coastline (Figure 4.1). Ningaloo Reef is a fringing reef with well-developed lagoon, back reef, reef flat and reef slope zones. The reef crest is typically 0.2–1.0 km from the shore with passages (0.4–1.0 km wide; 2–5 m depth) from the reef slope to lagoon occurring at regular intervals (approximately 10–15 km) along the length of the reef. Fish movement among reef zones is largely unrestricted over the full tidal range, with the exception of shallow reef flat areas which are inaccessible to larger fish (>50 cm TL) during spring low tides (< 0.3m deep: 20–24 hours per month). Live coral cover ranges from 15% to 25% on the reef slope to 25–90% on the reef flat and back reef and 0–5% in the lagoon and within the reef passages (Vanderklift et al. 2020), with Acroporidae and Poritidae corals dominating reef slope and flat zones (Thomson et al. 2020). Ningaloo Reef is relatively isolated from large human populations, with the nearest major town, Exmouth, having a population of less than 2,500. As such, fishing pressure is assumed to be limited. Spearfishing has not been permitted on the reef slope at northern Ningaloo Reef since 2005; however, recreational line fishing is currently permitted within most zones, excluding sanctuary areas (Figure 4.1a). No major commercial fishing activities have occurred within the study area since the 1970s (Conservation and Land Management and Marine Parks and Reserves Authority 2005).

4.2.2 Historic reef fish surveys (1987–2019)

Data from major research and monitoring programs surveying fish at northern Ningaloo Reef over the last 32 years (1987–2019) were examined for records of *B. muricatum* (Table S1). All major tropical marine fishes field guides and online databases were also searched for records of *B. muricatum*. Historical reef fish surveys encompassed three survey methods: Underwater Visual Census (UVC: 1987-2019), Baited Remote Underwater stereo-Video (BRUV:2000-2015) and Diver Operated stereo-Video (DOV:2006-2016) (see Table S1) (Cresswell et al. 2019; Langlois et al. 2010; Murphy and Jenkins 2010). Historical surveys were conducted in four of the five major reef zones at Ningaloo (lagoon, back reef, reef flat, reef slope) ranging from 3 m to 20 m water depth. No historical surveys were conducted within the reef crest zone, most likely due to logistical constraints. Detailed summaries of the time and/or area surveyed within each zone and survey methods are provided in Table 4.1

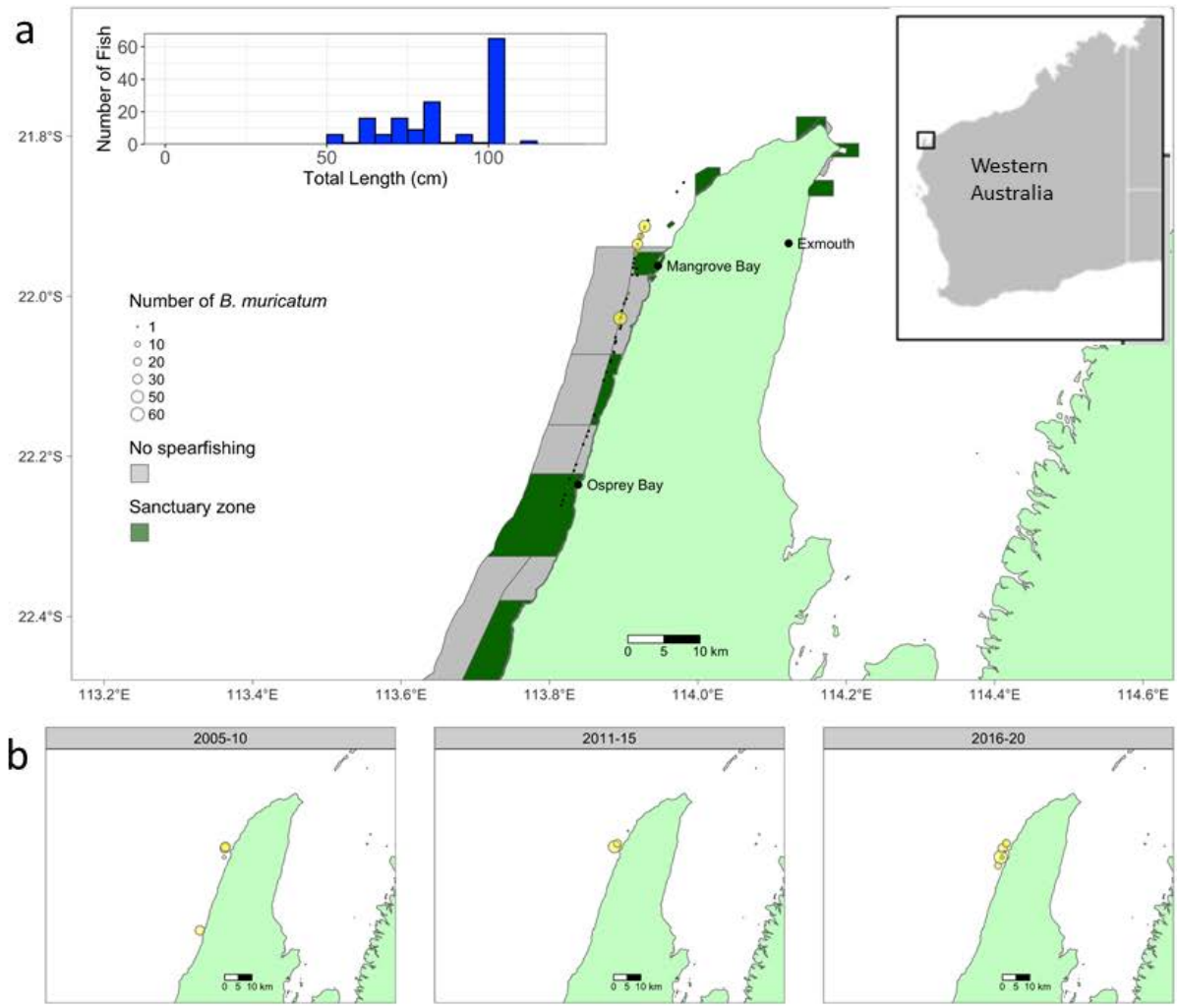


Figure 4.1. (a) Number and size frequency of *B. muricatum* observed during timed swim surveys along the reef crest of Ningaloo Reef between February and May (yellow dots) 2021. Black dots = survey locations, grey regions = no spearfishing zones, green regions = sanctuary zones. (b) Number of *B. muricatum* observed by expert witnesses (yellow dots) between 2005 and 2020 showing the majority of observations were located within 15km of Mangrove Bay.

4.2.3 Qualitative observations of *B. muricatum* at northern Ningaloo (2006–2020) solicited from expert witnesses

Data on the presence and size of *B. muricatum* observed at Ningaloo Reef between 2006 and 2020 were solicited from expert witnesses. Using local community facebook pages (Exmouth, Coral Bay, Ningaloo Whale Shark operators), members were asked to confirm sightings of *B. muricatum* on Ningaloo Reef. Specifically, we asked the following four

questions: “Have you have seen *B. muricatum* (humphead parrotfish) at northern Ningaloo?”; “When have you seen *B. muricatum* at northern Ningaloo?”; “Where have you seen *B. muricatum* at northern Ningaloo (coordinates or reef zone)?”; and, “How many *B. muricatum* were observed and their approximate length?”. If group members responded positively to any of these four questions, they were contacted via phone or email and provided an opportunity to validate their responses and expertise identifying coral reef fish species by answering two further questions: “How confident are you in your response to the previous questions (0–100%)?”; and, “How many years′ experience did they have in identifying coral reef fish species (<5 years, 5–10 years, >10 years)?”. Responses were included if respondents were >80% confident in their response and had more than 5 years experience identifying coral reef fish species. Known experts in surveying fish communities at Ningaloo reef were also contacted directly and asked the same questions with results anonymised and summarised for each habitat (see Table S3 for details)

4.2.4 Observations of *B. muricatum* at northern Ningaloo (2021) from reef crest timed UVC surveys

Data on *B. muricatum* abundance, distribution and size on the reef crest (2–4 m depth) were obtained using a series of 20-minute timed swim surveys between Osprey and Jurabi at northern Ningaloo between February and May 2021 (henceforth called timed UVC surveys). *B. muricatum* are largely restricted to shallow exposed habitats (reef crest and reef flat; Bellwood, Hoey and Choat 2003; Bellwood, Hoey and Hughes 2012) so surveys were targeted within the reef crest (2–4 m depth) on calm days (< 5 knts: 1.5 m swell) when conditions allowed safe access to the surf-zone. Two snorkellers separated by approximately 15 m swam parallel to the reef crest in the direction of the prevailing current for 20 minutes, recording the number and estimated length of each *B. muricatum* within a 10 m wide belt.

Forty-four sites were surveyed with the minimum distance between adjacent surveys approximately 100 m. The start and end points of each survey were recorded using handheld GPS (Garmin eTrex) and the distance swum (metres) and the total survey area (ha) calculated for each survey (Table S2). Prior to conducting surveys observers were trained to identify *B. muricatum* using region-specific field guides (Jenkins and Morrison 2018) and estimate length using calibration models.

4.3 Results

4.3.1 Historic reef fish surveys (1987–2019)

No previous records of *B. muricatum* were recorded in monitoring programs surveying fish at northern Ningaloo Reef over the last 32 years (1987–2019). Three records of *B. muricatum* were recorded in tropical marine fishes field guides between 2011 and 2020. Detailed summaries of the time and/or area surveyed within each habitat and survey methods are provided in Tables 4.1 and S1.

4.3.2 Qualitative observations of *B. muricatum* at northern Ningaloo (2006–2020) solicited from expert witnesses

A total of 27 observations of *B. muricatum* between 2007 and 2020 were solicited from expert witnesses using social media (Figure 4.1b, Table S3). The frequency of observations increased between 2005 and 2020 with ten reported sightings between 2005 and 2015 and seventeen reported sightings between 2016 and 2020 (Figure 4.1b). The mean size of fish in sightings was 80 cm (range = 6–100 cm) and the majority of sightings occurred on the reef flat or reef crest within 15 km of Mangrove Bay (Figure 4.1b).

4.3.3 Observations of *B. muricatum* at northern Ningaloo (2021) from reef crest timed UVC surveys

A total of 155 individuals of *B. muricatum* were recorded across 63.2 ha of reef crest surveys in 2021, equating to mean density of 2.38 ind/ha (Figure 4.1a). This is in contrast to the species' complete absence from 32 years of historical scientific surveys in other reef zones. *Bolbometopon muricatum* distributions at Northern Ningaloo were highly spatially restricted with the majority of individuals located in reef crest habitats adjacent (within 15 km) to Mangrove Bay (Figure 4.1). Maximum densities of *B. muricatum* (42.8 ind/ha) were observed on the reef crest within 10 km of Mangrove Bay, where encounter rates were also high (Figure 4.1a: *B. muricatum* observed on 6 of the total 20 transects adjacent Mangrove Bay). The mean total length of individuals was 80 cm (± 1.6 cm SE) and the range 50–110 cm, with only 7 of the 155 individuals less than 60 cm total length (Figure 4.1a).

Table 4.1. Major research and monitoring programs surveying fish at northern Ningaloo Reef (Cloates to Jurabi; 1987–2019) showing the time (hours) for BRUV surveys, area (ha) for other surveys and number of *B. muricatum* observed across the four major habitats. For a complete list of surveys refer to Tables S1 and S2.

		Reef zone						***B. muricatum***	
Survey method	Years	Lagoon	Back reef	Reef Flat	Reef crest	Reef slope	Total time/area	Number	Density Ind/ha
BRUV (hours)	2000–2015	351.5	34.0	66.0	0	426.0	877.5 hr	0	0
DOV (ha)	2006–2016	13.6	4.0	1.0	0	3.0	21.6 ha	0	0
UVC (ha)	1987–2019	49.9	30.2	28.6	0	35.7	144.4 ha	0	0
This study Timed UVC swim (ha)	**2021**	**0.0**	**0.0**	**0.0**	**63.2**	**0**	**63.2 ha**	**155**	**2.38**

4.4 Discussion

Bolbometopon muricatum was recorded in moderate densities across 63.2 ha of reef crest surveys in 2021, equating to mean density of 2.38 ind/ha (range 0.0–42.8 ind/ha). Its absence from 32 years of historical scientific surveys is likely due to the lack of surveys in the surf/reef crest zone and the sampling biases of historical survey methods (e.g., DOV, BRUV). Regular sightings of *B. muricatum* (up to 100 individuals and up to 120 cm TL) by expert witnesses between 2007 to 2020, in combination with the large size of individuals observed during 2021 surveys (mean ± SE = 80.9 ± 1.2 cm, range = 50–110 cm), indicates *B. muricatum* is unlikely to have recently arrived at northern Ningaloo and may have been present for many years. Furthermore, increased sightings of *B. muricatum* by expert witnesses between 2005 and 2020 suggests it may becoming more abundant at northern Ningaloo. Based on estimates of rates of calcium carbonate bioerosion by individual *B. muricatum* from the Great Barrier Reef (5.69 ± 0.53 tonnes/yr/individual; Hoey and Bellwood 2008), *B. muricatum* at northern Ningaloo is removing up to 13.42 tonnes/ha or 1.34 kg/m^2 of calcium carbonate per year, which is broadly comparable with estimates of parrotfish bioerosion at reefs in the central Indian (i.e., Seychelles, Chagos, Maldives, Mozambique; Perry et al. 2018) and Pacific Oceans (Moorea, Pohnpei, Northern Sulawesi; Bellwood, Hoey and Choat 2003). Although we did not quantify feeding rates during this study, we regularly observed *B. muricatum* feeding scars on live coral colonies during surveys in 2021 (authors pers. obs). *B. muricatum* regularly feeds on living corals (48.2% of bites on outer shelf GBR reefs; [10]), and at northern Ningaloo, is likely to be influencing live coral cover, vertical reef growth, as well as coral growth rates and colony morphologies. Moreover, the redistribution of an estimated 1.34 kg/m^2/yr of reef sediment through *B. muricatum* feeding and excretion at northern Ningaloo would have a marked impact on the

deposition and accumulation of reef sediments. Adult *B. muricatum* are therefore currently present at northern Ningaloo at densities that are likely to be ecologically relevant.

Bolbometopon muricatum distributions at Northern Ningaloo were spatially restricted with individuals observed exclusively in reef crest zones. Moreover, *B. muricatum* was spatially aggregated across just 15 km/26.7 ha of reef crest zone and maximum densities (42.8 ind/ha) were observed within 10 km of Mangrove Bay. Within this area encounter rates were also high (Figure 4.1: *B. muricatum* observed on six of the total 20 transects adjacent to Mangrove Bay) during timed swims and among expert witnesses. The reason for this spatial concentration is not known but may relate to proximity of habitats suitable for juvenile *B. muricatum* and/or adult resting sites. *B. muricatum* typically recruit to branching corals in sheltered lagoons adjacent to mangroves (Hamilton, Adams and Choat 2008), before moving to high-energy forereef foraging habitat as adults (Bellwood, Hoey and Hughes 2012). Adults are also known to seek shelter in deep inter-reef passages at night (Bellwood and Choat 2011, Roff et al. 2017). Reef crest zones at northern Mangrove Bay are characterised by moderate live coral cover (mean ± SE = 19% ± 5.8%; Thomson et al. 2020) and close proximity to the only mangroves stands at Northern Ningaloo. It is therefore possible that the highly restricted spatial extent of observations of *B. muricatum* observed in this study are due to the co-location of ideal habitats for feeding and recruitment, although we are unable to rule other factors such as temperature (see Table S4 for additional factors considered).

The size frequency structure of *B. muricatum* observed at Northern Ningaloo indicates all observed individuals were likely to be reproductively mature adults (>40 cm) (Hamilton, Adams and Choat 2008). Of the 155 individuals observed, the mean total length was 80.9 cm (± 1.6 cm SE) and the range 50–110 cm, with only seven of the 155 individuals less than 60

cm total length (Figure 4.3). Unlike most parrotfishes, *B. muricatum* are gonochoric (single sex), with females reaching sexual maturity at about 55–65 cm TL and 7–9 yrs of age (Hamilton, Adams and Choat 2008). The lack of juvenile-sized *B. muricatum* (<40 cm TL) at Northern Ningaloo is consistent with other studies on the GBR, with Bellwood and Choat (2011) reporting just four juveniles (<35 cm TL) among 664 individuals recorded during >5000 hours of surveys. Noteworthy records of juvenile *B. muricatum* at Ningaloo Reef include those by Denise Jenkins in June 2011 (a single juvenile, 6 cm, 5 km north Mangrove Bay) (Jenkins and Morrison 2018) and Glen Whisson in August 2018 and May 2020 (three juveniles ranging 6–10 cm, 120 km south Mangrove Bay) (iNaturalist.org 2020). Both of these photographic records indicate that juvenile *B. muricatum* do occur at Ningaloo Reef and these juveniles may be recruiting from the populations of reproductively mature local adults observed during the present study.

The absence of *B. muricatum* in historical scientific fish surveys may relate to the methods used being inappropriate for highly mobile, sparsely distributed reef taxa. Alternatively, it may reflect the poleward expansion of this species along the West Australian coast, as has been documented for other tropical reef fish species (Booth et al. 2018). *B. muricatum* is highly gregarious, feeding and sleeping in groups of up to 100 individuals (Domeier and Colin 1997) with spawning aggregations of up to 1200 individuals (Roff et al. 2017). Schools can move up to 6 km per day (Hamilton, Adams and Choat 2008) but they are often sparsely distributed, making them difficult to detect using certain survey techniques (MacKenzie et al. 2004). For example, traditional UVC and DOV techniques generally survey small areas (< 1000 m^2 per survey; Colvocoresses and Acosta 2007) and, as a result, often fail to detect large, highly mobile and/or sparsely distributed fish species. Improved density estimates of sparsely distributed taxa usually require sampling over larger scales (>1000 m^2). The

exclusive observations of *B. muricatum* on the reef crest during our timed swims (>11000 m^2 per survey) suggests *B. muricatum*, like many populations of large-bodied, sparsely distributed reef fishes, is most reliably detected using spatially comprehensive survey techniques conducted within targeted habitats.

4.5 Conclusions

A total of 155 *B. muricatum* were recorded across only 63.2 ha of reef crest surveys, with densities highest in the surf zone of reef crest habitats adjacent Mangrove Bay. By soliciting expert witness observations and combining these with timed swim surveys conducted in the preferred habitats of *B. muricatum*, we were able to provide the first estimate of the distribution, density and size frequency of *B. muricatum* at northern Ningaloo. To our knowledge, these observations represent the first records of adult *B. muricatum* in scientific surveys at Ningaloo Reef. The densities of *B. muricatum* observed at northern Ningaloo in 2021 suggest this species is removing an estimated 13.42 tonnes/ha or 1.34 kg/m^2 of calcium carbonate per year, which is broadly comparable with estimates of total parrotfish bioerosion across many reefs in the central Indian and Pacific Oceans. Regular sightings of adult *B. muricatum* by expert witnesses between 2007 and 2020, in combination with the large size of individuals observed during 2021 surveys, indicates *B. muricatum* may have been present at northern Ningaloo Reef for many years. Although not currently afforded elevated conservation status within current management plans, *B. muricatum* possesses many life-history characteristics that make it vulnerable to overfishing, which may justify consideration for species-specific protection within the world heritage-listed Ningaloo Reef Marine Park.

4.6 **Acknowledgments**

I thank staff from the Department of Biodiversity, Conservation and Attractions for providing access to historical fish datasets, assisting with social media posts and discussions about *B. muricatum*. I thank Brett Molony and Shaun Wilson for helping to improve the manuscript and John (Howard) Choat and Ben Fitzpatrick for providing insights into *B.muricatum* more broadly. I also thank Andrea Asunsolo, Beau DeGroot, Emma Westlake, Natalie Travaglione and Nicholas Gust for field assistance and the expert witnesses who provided information on sightings of *B.muricatum*.

Chapter 5 High rates of erosion on a wave exposed Eastern Indian Ocean fringing coral reef

Abstract

Erosion is a key process in shaping the physical structure of coral reefs, yet due to erosion often being semi-cryptic and difficult to quantify, information remains limited. Here, we investigate erosional processes along Ningaloo Reef, an extensive fringing coral reef in Western Australia. We employed both direct (experimental blocks) and indirect (observation-based estimates) methods to measure erosion in wave-exposed reef slope and protected lagoonal habitats. Direct measurements of erosion on coral blocks were among the highest found globally, with total erosion 3.07 kg/m^2/yr (4% from micro, 0.6% from macro and 94% from external), while indirect rates were estimated at 2.4 ± 0.20 kg/m^2/yr (78% from parrotfish, 22% from urchins). Indirect erosion rates were influenced by the species and size of parrotfish, with *Chlorurus microrhinos* removing 0.44 ± 0.19 kg/m^2/year (22% of parrotfish erosion). Scanning electron microscopy and computed tomography show that micro- and macroborer erosion contributions to direct erosion were low (4% and <1% respectively), most likely due to heavy grazing by parrotfish and the short deployment period of experimental substrates (20 months). A substantial portion of external erosion on blocks (0.53 ± 0.23 kg/m^2/yr) could not be attributed to bioeroders and was poorly correlated with wave exposure, suggesting processes not quantified contribute to this unaccounted aspect of erosion. Our results confirm that bioerosion by parrotfish is especially significant at Ningaloo Reef, and large-bodied individuals of *C. microrhinos* are key in conserving this key ecological process.

5.1 Introduction

The process of erosion plays a crucial role in the maintenance and persistence of coral reefs. The breakdown of reef substrate through physical, biological and chemical processes alters the shape and structural complexity of the reef, which has profound effects on the ecological services it provides. Changes in structural complexity, for example, can affect the diversity of fish assemblages (Graham and Nash 2013) and are an important predictor of reef resilience to disturbance (Perry and Alvarez-Filip 2019). In instances where rates of erosion exceed rates of carbonate production (see e.g., Eakin 1996), the loss of reef structure may also threaten reef capacity to mediate wave exposure, thereby compromising their ability to protect coastlines and inshore habitats (Sheppard et al. 2002; Cuttler et al. 2018; Perry et al. 2018). Conversely, erosion can remove space competitors such as turf and macroalgae, which can free up bare space for coral settlement (McCauley et al. 2014), and generate sediments and rubble that contribute to the stability of shorelines and reef habitats (Bellwood 1996; Perry et al. 2011). Understanding the factors that govern erosion is therefore key to better understanding physical, biological and chemical processes on coral reefs.

Various methods have been established to measure erosion on reefs, leading to greatly improved knowledge of processes that drive both internal and external erosion (Pari et al. 2002; Tribollet and Golubic 2005; Yarlett et al. 2018). However, erosion remains difficult to measure, particularly when it occurs within the reef framework (i.e., internal erosion; Hutchings 1986). Furthermore, the majority of studies that have directly quantified erosion tend to focus on shallow, sheltered reef environments (reviewed in Browne et al. 2021). Given rates of erosion are highly variable across geographic regions and among reef habitats (Silbiger et al. 2017; Browne et al. 2021), it is important to investigate a range of environments to gain insights into the factors driving this variability.

Erosion on coral reefs can be classified into three primary categories: physical, chemical and biological. Physical erosion is primarily caused by hydrodynamic forces leading to dislodgement or abrasion and is positively related to wave exposure and severe storms (Madin and Connolly 2006; Puotinen et al. 2020). Chemical erosion is the dissolution of calcium carbonate; while it typically occurs slowly, it is positively related to factors such as water motion, biological activity and increased ocean acidification (Reyes-Nivia et al. 2013; Glynn and Manzello 2015; Cornwall et al. 2021). Biological erosion is the breakdown of reef carbonates due to the activities of organisms, which may employ both chemical and mechanical processes. Among the three mechanisms of erosion, bioerosion is considered the most significant on coral reefs (Browne et al. 2021), often accounting for the majority reef erosion (Glynn and Manzello 2015).

Bioerosion on coral reefs is attributed to organisms whose actions are categorised as external or internal. External bioerosion occurs when animals scrape the surface of the reef while feeding (Glynn and Manzello 2015). External bioeroders include grazing parrotfish, pufferfish and urchins, which play an important role in creating new substrate for coral recruitment (Mumby and Harborne 2010; McCauley et al. 2014), generating calcium carbonate sediments (Hutchings 1986) and shaping reef structure (Hutchings 1986; Hutchings et al. 2005). Grazing by parrotfish and urchins can contribute up to 90% and 84% of the estimated total bioerosion in the Indo-Pacific and Caribbean respectively (Chazottes et al. 1995; Bellwood 1996; Perry et al. 2014). One-time ‘snapshot’ assessments of grazer abundance and activity have been used to indirectly estimate total rates of erosion (e.g., Graham et al. 2013; Hoey et al. 2016), although this may not adequately capture temporal and spatial variability in grazing pressure (Perry and Hepburn 2008; Johansson et al. 2010; Lange

et al. 2020). Furthermore, long-held empirical relationships between grazer abundance and rates of erosion derived from a limited number of locations are often used to extrapolate across regions or globally (Glynn et al. 2015; Perry et al. 2018), which may not adequately represent local activity of bioeroders.

Like external bioerosion, internal bioerosion of the reef framework by boring organisms can remove substantial amounts of calcium carbonate (Sammarco and Risk 1990; Hutchings et al. 2005; Glynn and Manzello 2015). Internal erosion, however, is logistically challenging to measure as microboring organisms are often small (<10 microns), sparsely distributed (e.g., bivalves) and only detectable using extractive (i.e., collecting and breaking open samples of reef) and/or expensive (i.e., internal scanning) methods (see discussion in Browne et al. 2021). Subsequently, studies have begun utilising a combination of Scanning Electron Microscopy (Grange et al. 2015, Lloyd Newman 2023) and micro computerised tomography (microCT) (Enoch et al. 2016, Dee et al. 2023) to more accurately quantify rates of internal erosion by micro- and macroborers.

There are multiple environmental factors that impact erosion of reef substrates, one of which is wave-driven water movement. Wave-driven water movement can influence rates of physical, chemical and biological erosion (Hutchings 1986), with several studies recording higher rates of (predominantly external) erosion in exposed compared with lagoonal habitats (Tribollet and Golubic 2005; Hoey and Bellwood 2008). Waves generate the physical force needed to break down and dislodge reef framework (Puotinen et al. 2020). This process can promote the growth of micro-algae and macroborers, which, in turn, may accelerate erosion by secreting chemicals that dissolve the reef framework and promote external erosion (Hutchings 1986; Rice et al. 2020). Despite the recognised importance of wave exposure,

most erosion studies using experimental blocks have focused on shallow, sheltered environments (Chazottes et al. 1995; Dee et al. 2023), with notable exceptions (Sammarco and Risk 1990; Kiene and Hutchings 1994; Tribollet and Golubic 2005). As a result, knowledge of how wave exposure influences rates of physical, chemical and biological erosion remains a research priority.

Here, we use high-resolution CT and Scanning Electron Microscope (SEM) scans to measure rates of external and internal erosion of experimental coral (massive *Porites* sp.) blocks deployed for 12–20 months within lagoon and reef slope habitats on a wave-exposed fringing coral reef. By combining direct measurements of external and internal erosion with indirect estimates of parrotfish erosion, urchin erosion and water velocity, we identify the prominent drivers of erosion within the World Heritage-listed Ningaloo Reef. These partitioned estimates of erosion are the first for an exposed, fringing coral reef in the eastern Indian Ocean and provide a basis for understanding and managing spatial variation in a key ecological process.

5.2 Methods

5.2.1 Study region

This study was conducted along the north-western section of Ningaloo Reef (Nyinggulu) between S22°17’00” E113°49’00” and S21°49’00” E114°03’00”. This region of Ningaloo Reef has well-developed fringing reef with a shallow lagoon (max depth: 4 m) extending 1.3–2.0 km from the shore, and a continuous reef slope approximately 2.0–4.0 km from the shore (Thomson et al. 2020; see Supplementary methods, figure 1, table 1).

5.2.2 External and macroborer erosion of coral blocks

A total of 51 blocks (5 × 2 × 1 cm) of dead *Porites* sp. (hereafter referred as blocks) were deployed across 17 sites (10 reef slope, 7 lagoon: n = 3 blocks/site) in September 2020 with 17 blocks retrieved in September 2021 (12 months) and 15 blocks retrieved in May 2022 (20 months). The remaining 19 blocks were unable to be located on retrieval, presumably because they were physically dislodged during the deployment period. Blocks were cut from massive *Porites* sp. cores (75 mm diameter, n = 2) collected from within the study region during a previous study (Müller et al. 2001). Prior to deployment, each block was visually inspected to ensure there were no pre-existing boreholes, density was measured using Archimedes' principle of water displacement (mean density ± SE = 1.44 ± 0.02 g/cm^3) and each block was mounted on an acrylic base (8cm x 2cm x 0.4 cm) using Sikabond 142 epoxy (following Enochs et al. 2016). Blocks were then imaged with a SkyScan 1176 microCT (Bruker-microCT, Kontich, Belgium) at 90 kV and 273 µA (35 µm resolution with a 0.1 mm Cu filter) before being deployed on the reef using stainless mounting plates (Mundy 2000). Blocks were deployed at the start of transects used to record parrotfish and urchins, such that they were located within the transect area (See Supplementary methods). On retrieval, blocks were rinsed in freshwater, oven dried at 60°C for 24h and rescanned with the SkyScan 1176 microCT. Pre- and post-deployment scans were reconstructed using Bruker NRecon software with ring artefact reduction of 20 and beam hardening of 20% (following Dee et al. 2023), then directly compared using Data-Viewer software with a "difference" image stack (.bmp) to identify external erosion (removed exterior pixels), macroborer erosion (removed interior pixels >35 µm) and unchanged material (pixels with no change) (Figure 5.1). Volumetric analysis (cm^3) of external and macroborer erosion for each block was conducted using CTAn software (version 1.18) (see Supplementary methods).

5.2.3 Microborer erosion of blocks

Microborer erosion (<35 μm) was quantified on a subset of coral blocks (n=6) deployed for 12 months using a modified method from Lloyd Newman et al. (2023). Two 1 cm^3 cubes were cut from the upper facing central surface of blocks (3 × lagoon, 3 × reef slope). Cubes were cut ~ 0.5 cm from each edge of the block, soaked in diluted hydrogen peroxide (~6%) for 24h, embedded with low-viscosity resin (Araldite CY212) under vacuum for 3h and cured at 60°C for 24h. One surface of the resin cube was polished using a series of wet/dry paper grits (60 to 2000) until the carbonate material was exposed, then etched for 20 s in 10% HCl, rinsed in distilled water, oven dried and splutter coated with gold for SEM examination. The first cube from each block was used to quantify the mean depth of borers, the second cube used to quantify the surface area removed by microborers (see Supplementary methods).

5.2.4 Parrotfish bioerosion rates

To estimate the bioerosion rates of parrotfishes at each survey site, we used size and species-specific estimates of parrotfish abundance, bite rates, bite volume, and proportion of bites leaving scars. Parrotfish abundance was quantified along a single 100 m × 10 m belt transect at each of 17 sites. Transects were located immediately adjacent to coral blocks (< 1m) with surveys conducted in September 2020, September 2021, and May 2022 (n=3 transects per site) during daylight hours (0700 to 1600), following Sale (1980). Along each 100 × 10 m transect, observers identified and recorded all parrotfishes to species and estimated total length (TL) to the nearest 10 cm. Parrotfish bite rates (bites/min), bite volume (cm^3) and proportion of bites leaving scars were estimated using focal individual observations (following Bellwood 1996; Bruggemann et al. 1996; see Supplementary results). The mean bite mass for each parrotfish species was calculated by multiplying the mean bite volume by the mean substrate density for Indo-Pacific coral reefs (1.47 g/cm^3; Perry at al. 2011).

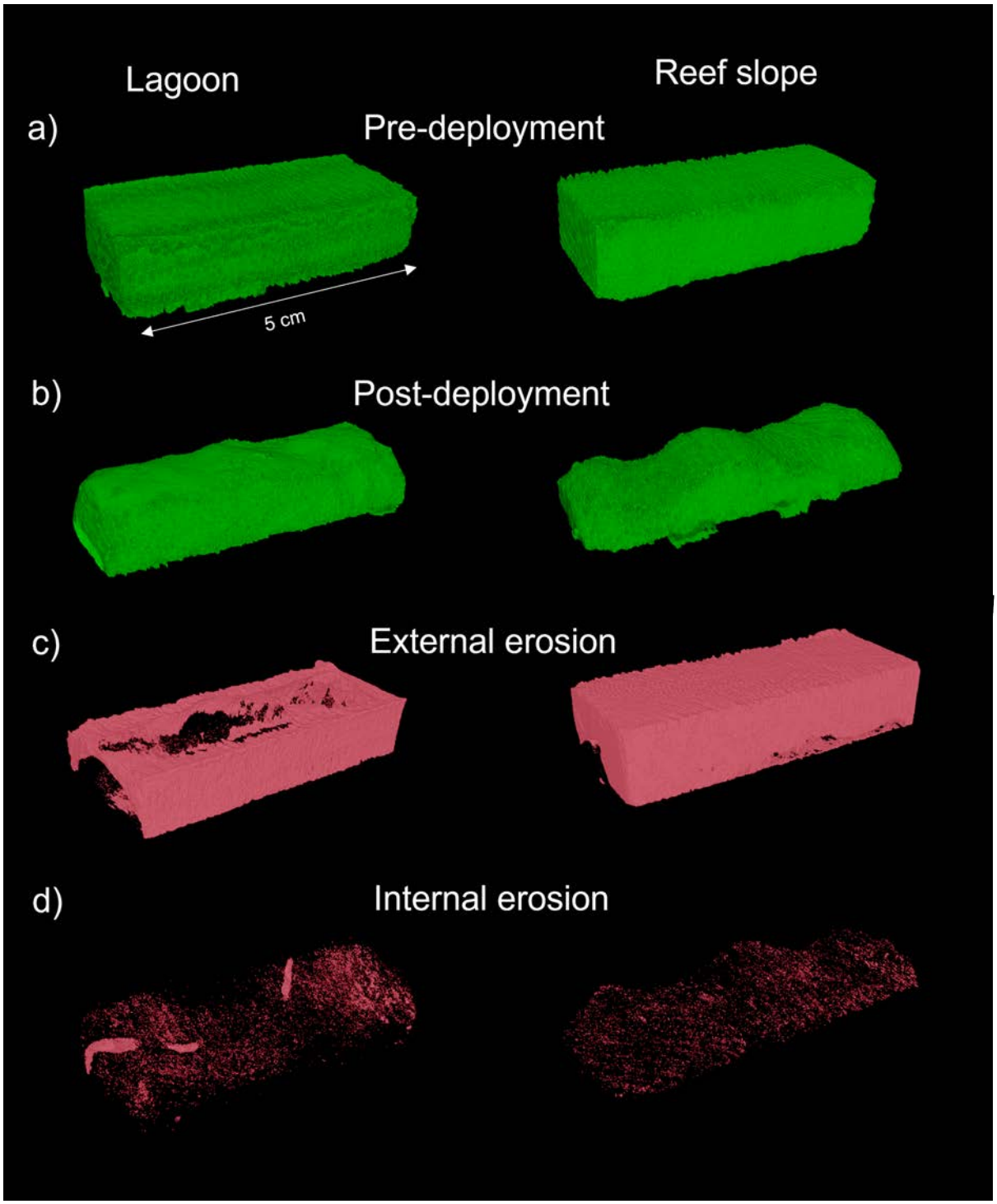


Figure 5.1. Micro computerised tomography (µCT) scans of experimental *Porites* sp. blocks deployed in the lagoon and on the reef slope Ningaloo Reef for 20 months (605 days). Block images show representative scans of two individual blocks pre-deployment (a) post deployment (b) in green, and areas of external (c) and internal (d) erosion recorded post deployment in red.

5.2.5 Urchin bioerosion rates

Urchin bioerosion was based on *Echinometra mathaei*, the most abundant urchin at Ningaloo (Langdon 2012). Bioerosion rates were estimated as the product of average urchin densities and published individual bioerosion rates of *E. mathaei* at Ningaloo (0.13 kg/m^2/yr; Langdon 2012). Urchin densities were quantified using a 25 m photo transect conducted between 0700 and 1600 at each of the 17 sites in September 2020, September 2021, and May 2022 (n=3 transects per site; see Supplementary methods).

5.2.6 Total (net) erosion and unaccounted erosion

To estimate rates of erosion not accounted for by biological processes we combined directly measured rates of internal and external erosion on blocks and subtracted our indirect estimates of biological erosion from parrotfish and urchin surveys.

$$Total\ (net)\ erosion\ =\ internal\ erosion\ +\ external\ erosion$$

$$Unaccounted\ external\ erosion = external\ erosion\ (from\ blocks)\ -\ (parrotfish\ erosion + urchin\ erosion)$$

5.2.7 Structural complexity of reef (rugosity)

Structural complexity of the substrate at each site was estimated using a rugosity index derived from a 10 m chain (chain link dimensions: 22 × 12 mm) laid alongside the transect tape used for surveys of urchins. The chain was placed on the substrate, covering all crevices and gaps within the substrate. We measured the linear distance covered by the chain along the

transect tape and calculated the rugosity index by dividing 10 m by the recorded linear distance (adapted from Risk 1972). Consequently, a higher rugosity index indicated a substrate with greater structural complexity. A mean rugosity was calculated for each site by averaging values from surveys conducted in September 2020, September 2021, and May 2022.

5.2.8 Water velocity estimates

Estimates of wave-induced water velocity at the seafloor (daily mean and max) at each study site were derived using the 'simulating waves near shore' (SWAN) model (Booij et al. 1999) on a 30 × 30 m grid encompassing the study area. To validate model estimates of water velocity, in situ water velocity loggers (Hobo onset Mat-1) were deployed for three months (September 2020–November 2020) at 10 of the 17 sites (6 × reef slope, 4 × lagoon) and the daily mean and maximum water velocities of the model compared with those of the loggers using linear regression. Comparisons between model and in situ logger daily mean and maximum water velocities revealed a high correlation between predicted and observed values (see Supplementary results: Mean water velocity $R^2 = 0.7$, Maximum water velocity $R^2 = 0.9$).

5.2.9 Statistical analyses

Differences in rates of block erosion (microborer, macroborer, external, total), parrotfish (biomass and estimated erosion of six species) and urchin erosion (estimated erosion) among lagoon and reef slope habitats were examined using analysis of variance (ANOVA 'stats' package). ANOVA assumptions of homogeneity of variances and normality were initially tested using Levene's ('car' package) and Shapiro-Wilk tests ('stats' package). In cases

where ANOVA assumptions were not met, data were log transformed. The a priori ANOVA design included deployment length (fixed, 2 levels) × reef position (fixed, 2 levels), with sites a random factor nested within reef position. However, as there were no differences in erosion rates (kg/m^2/yr) between deployment lengths (12 and 20 months), blocks within each deployment length were pooled to improve the level of replication within reef position. To determine the strength and direction of the relationships among erosion sources and environmental variables (water velocity, reef rugosity and visible bite marks), Pearson correlation coefficients were calculated (r^2) and significant relationships visualised ('corrplot' package). Differences in the composition of parrotfish assemblages among habitats was tested using PERMANOVA on log transformed data and a Bray-Curtis similarity matrix. All statistical tests and plots were performed in R version 4.2.2.

5.3 Results

5.3.1 Internal and external erosion of blocks

Overall, rates of external erosion on the blocks were 20 times greater than rates of internal erosion (Figure 5.2, Table 5.1). Rates of external erosion were significantly lower and less variable in the lagoon than on the reef slope ($F_{1,31} = 14.53$, $p < 0.01$; Figures 5.1, 5.2). In comparison, rates of internal erosion (micro- and macroborer) did not differ between the lagoon and reef slope ($F_{1,2} = 0.069$, $p = 0.79$, $F_{1,31} = 0.031$, $p = 0.84$); however, microborer erosion rates were 5 to 6 times higher than macroborer erosion rates (Table 5.1). The number of visible bite marks on blocks was significantly higher on those deployed on the reef slope than the lagoon (slope: 7.23 bites/block versus lagoon: 4.75 bites/block; $F_{1,25} = 4.6$, $p = 0.04$), but did not differ between deployment lengths (12 versus 20 months: $F_{1,31} = 0.31$, $p = 0.59$).

5.3.2 Parrotfish bioerosion

The estimated rate of parrotfish erosion averaged across all locations was 1.88 ± 0.34 kg/m^2/yr. Parrotfish biomass and indirect estimates of parrotfish erosion were 5- to 6-fold greater on the reef slope than the lagoon (biomass: $F_{1,16} = 23.25$, $p < 0.01$; erosion: $F_{1,16} = 23.25$, $p < 0.01$; Figure 5.3, Table 5.1). The composition of parrotfish assemblages differed among habitats ($F_{1,24} = 13.83$, $p < 0.001$; see Supplementary table). with *Chlorurus spilurus* accounting for the majority (40%) of estimated parrotfish erosion within the lagoon and *C. microrhinos* the majority (84%) of estimated parrotfish erosion on the reef slope (Figure 5.3).

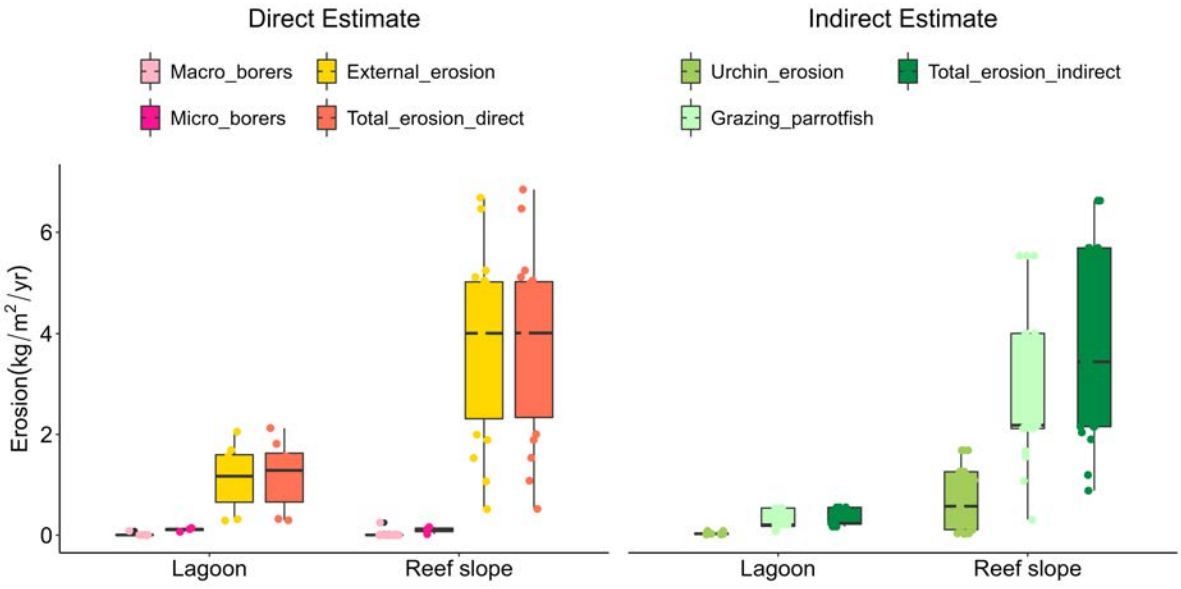


Figure 5.2. Direct estimates of erosion by macroborers (light pink), external erosion of blocks (yellow), microborers (dark pink), total erosion (orange) and indirect estimates of erosion by urchins (green), parrotfish (light green) and total indirect erosion (dark green) (kg$CaCO_3$/m^2/yr) in lagoon and reef slope habitats at Ningaloo Reef. Box panels represent the interquartile range (IQR) and whiskers the range of values.

5.3.3 Urchin bioerosion

The estimated rate of *Echinometra mathaei* erosion averaged across all locations was 0.52 ± 0.11 kg/m^2/yr (Figure 5.2). *E. mathaei* densities and indirect estimates of erosion were 20- and 25-fold higher on the reef slope than the lagoon respectively (density: $F_{1,16} = 9.15$, $p < 0.01$; erosion: $F_{1,16} = 9.15$, $p < 0.01$: Figure 5.2; see Supplementary table). Although not measured, the vast majority of *E. mathaei* were estimated to be of a similar size (30–40 mm test diameter).

5.3.4 Physical environmental variables.

Reef rugosity was significantly higher for reef slope than lagoon sites (Table 5.1; $F_{1,25} = 25.23$, $p < 0.01$). Similarly, both mean water velocity (cm/sec^{-1}; $F_{1,25} = 234$, $p < 0.01$), and max water velocity ($F_{1,25} = 1046$, $p < 0.01$), were greater on the reef slope than in the lagoon (Table 5.1).

Table 5.1. Mean rates of erosion (kg/m^2/yr) and environmental and biological variables (mean ± se) at lagoon (n = 7) and reef slope sites (n = 10) at Ningaloo Reef. Direct and indirect estimates of erosion are shown separately. The percentage of total (net) erosion represented by each erosion source within lagoon and reef slope habitats is shown in brackets.

	Erosion Source	Lagoon	Reef slope	Combined
Direct	Internal macroborers (kg/m^2/yr)	0.01 ± 0.01 (1%)	0.02 ± 0.01 (0.5%)	0.02 ± 0.01 (0.6%)
	Internal microborers (kg/m^2/yr)	0.12 ± 0.04 (9%)	0.11 ± 0.03 (2%)	0.12 ± 0.03 (4%)
	External erosion (kg/m^2/yr)	1.13 ± 0.22 (89%)	3.70 ± 0.41 (97%)	2.93 ± 0.37 (94%)
	Total (direct) erosion (kg/m^2/yr)	1.26 ± 0.25	3.83 ± 0.43	3.07 ± 0.39
Indirect	Grazing parrotfish (kg/m^2/yr)	0.28 ± 0.07 (87%)	2.38 ± 0.35 (76%)	1.88 ± 0.34 (78%)
	Grazing urchins (kg/m^2/yr)	0.04 ± 0.01 (13%)	0.73 ± 0.14 (24%)	0.52 ± 0.11 (22%)
	Total (indirect) erosion (kg/m^2/yr)	0.32 ± 0.04	3.11 ± 0.24	2.4 ± 0.20
	Unaccounted erosion (kg/m^2/yr)	0.81 ± 0.18	0.59 ± 0.33	0.53 ± 0.23
Environmental	Mean water velocity (cm/s)	6.21 ± 2.60	56.83 ± 1.83	41.83 ± 4.76
	Max water velocity (cm/s)	20.05 ± 5.10	155.57 ± 1.66	115.78 ± 12.27
	Depth (m)	3.10 ± 0.06	8.36 ± 0.20	6.96 ± 0.49
	Rugosity ratio	1.19 ± 0.02	1.46 ± 0.03	1.38 ± 0.03

5.3.5 Predictors of erosion

External erosion of blocks was positively correlated ($p < 0.05$) with parrotfish erosion ($r^2 = 0.49$), urchin erosion ($r^2 = 0.50$), maximum water velocity ($r^2 = 0.61$), reef rugosity ($r^2 = 0.47$) and visible bite marks on blocks ($r^2 = 0.44$). Internal erosion was not significantly correlated with any other variable, including external erosion (Supporting Information Figure S3). Results indicated no significant effect of deployment length (12 versus 20 months) on annual rates of external ($F_{1,31} = 1.08$, $p = 0.3$), internal ($F_{1,31} = 0.46$, $p = 0.5$) or total erosion on blocks ($F_{1,31} = 1.14$, $p = 0.29$).

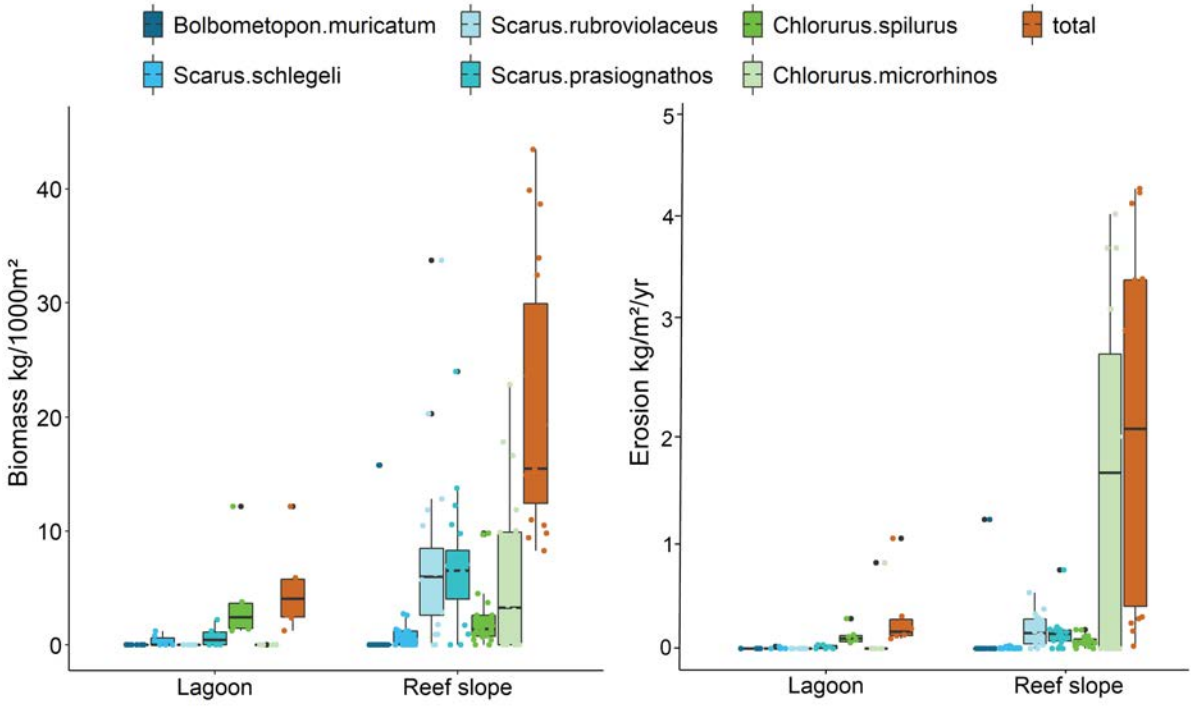


Figure 5.3. Parrotfish biomass (kg/1000m2) and predicted rates of erosion (kg/m2/yr) for the six most abundant species of parrotfish in lagoon and reef slope habitats at Ningaloo Reef. Total represents the sum of erosion by all parrotfish spp. Box panels represent the interquartile range (IQR) and whiskers the range of values.

5.4 Discussion

Accurately measuring erosion across a wide range of coral reefs environments is essential, given rates of erosion are highly variable across geographic regions and among reef zones

(Silbiger et al. 2017; Browne et al. 2021). Here we provide the first partitioned estimates of rates of erosion across multiple reef zones at World Heritage-listed Ningaloo Reef, in the eastern Indian Ocean. Our results emphasise the relevance of external bioerosion relative to other eroding processes. Total mean erosion rates of blocks after 20 months were 2.95 ± 0.37 kg m^2/yr, which is higher than similar length deployments of experimental coral substrates on offshore reefs of the Great Barrier Reef and French Polynesia and more than ten times higher than similar length deployments on turbid inshore reefs of the Great Barrier Reef, Hawaii and nearby Exmouth Gulf (Kiene and Hutchings 1994; Silbiger et al. 2017; Dee et al. 2023) (Table 5.2). Erosion rates are known to exhibit marked regional variability (Bellwood et al., 2003; Brown et al., 2021; Yarlett et al., 2020), with higher rates of erosion characteristic of offshore reefs with high biomass of grazing parrotfish, urchins and high wave exposure (Osorno et al. 2005; Madin and Connolly 2006; Hoey and Bellwood 2008; Cheal et al. 2013). Consistent with this expectation, total erosion on blocks was highest on the reef slope where estimated erosion by parrotfish, grazing urchins and unaccounted erosion were also highest. Hence, the combination of high abundance of excavating parrotfish, urchins and strong wave exposure (reef slope) are likely to have resulted in the high rates of erosion we measured on blocks at Ningaloo reef over 20 months.

Table 5.2. Erosion rates of experimental coral blocks on coral reefs for similar length deployments. Bold values represent the deployment lengths corresponding with erosion rates shown.

Locality	Erosion rate (kg/m^2/yr)	Habitat type	Deployment length (months)	Reference
Lizard Island, Great Barrier Reef, Australia	0.69 to 1.78*	Lagoon, Reef flat, Reef slope, offshore	**12**	Davies and Hutchings 1983
Lizard Island, Great Barrier Reef, Australia	0.30 to 1.96	Lagoon, Reef flat, Reef slope, offshore	12, **24**, 48	Kiene and Hutchings 1994
Northern Great Barrier Reef, Australia	0.46 to 3.6 0.74 to 2.13	Nearshore, midshore, offshore	**12** **36**	Tribollet at al.2002 Tribollet and Golubic 2005

Reunion Is, French Polynesia	1.64 to 4.31	Eutrophic, offshore	**12**	Chazottes et al. 1995
French Polynesia	0.03 – 6.77	Lagoon	**24** 6,**24**, 60	Pari et al.1998 Pari et al. 2002
Inshore, Great Barrier Reef, Australia	0.18 to 0.27	Lagoon, nearshore	12,**24,**48	Kiene and Hutchings 1994
Papua New Guinea,	0.8 to 1.23*	Nearshore, high islands	**24**	Enochs et al. 2016
Hawaii, Kaneohe Bay	0.02 to 0.91	Reef flat, Reef slope nearshore	**12**	Silbiger et al. 2016 Silbiger et al. 2017
Exmouth Gulf, Australia	0.152 ± 0.012	Turbid nearshore	**12**	Dee et al. 2022
Ningaloo Reef	2.95 ± 0.37	Lagoon, Reef slope	**20**	This study

*Erosion estimate did not include external grazers. **Calculation based on substrate density of 1.47g/cm^3

Parrotfish were a key contributor to erosion at Ningaloo, accounting for an estimated 63% of total erosion. Parrotfish are routinely acknowledged as important bioeroders (Bruggemann et al. 1996; Hoey and Bellwood 2008; Ong and Holland 2010; Perry 2011; Kuffner et al. 2019), but estimates of parrotfish erosion often lack context regarding their contribution to total erosion (Bellwood 1995; Bruggemann et al. 1996). Here, we adopt a more comprehensive approach to evaluating erosion by comparing indirect estimates of parrotfish bioerosion with direct quantification of total erosion on experimental blocks, enabling an assessment of parrotfish erosion relative to other external and internal sources of erosion. Estimated parrotfish erosion was 1.88 ± 0.34 kg/m²/yr, which was greater than the combined estimates of the other three sources of erosion in our study: internal borers, grazing urchins and unaccounted erosion (1.62 ± 0.37 kg/m²/yr). This disproportionately large contribution of parrotfish erosion to total erosion was most evident within complex reef slope habitats, where parrotfish erosion was strongly positively correlated with reef rugosity ($r^2 = 0.82$; Supporting Information Figure S3) and accounted for an estimated 63% of total erosion. Our results are consistent with previous studies which found that grazing parrotfish are the primary bioeroders in exposed, complex, shallow reef environments, contributing between 79% and 84% of total bioerosion (Perry, Edinger et al. 2012). Caution is, however, needed when

comparing parrotfish erosion estimates derived from small experimental blocks with those on natural reef surfaces, as likely differences in skeletal density, surface morphologies and the age and composition of the organisms on blocks versus natural surfaces may result in different rates of parrotfish grazing (Molina-Hernández et al. 2022). Nonetheless, the high rates of external erosion on blocks, combined with high estimates of parrotfish erosion and a positive correlation between these two estimates among sites ($r^2 = 0.49$), supports the theory that grazing parrotfish were the dominant source of erosion at Ningaloo.

Parrotfish erosion was only moderately correlated with parrotfish biomass ($r^2 = 0.55$), indicating sites with high parrotfish biomass did not necessarily have a high parrotfish bioerosion rates, or vice versa. Rather, bioerosion rate was determined by the species and sizes of parrotfish present at each site. Highest contributions to bioerosion were found in the 'excavators' *C. microrhinos* (mean ± se = 1.53 ± 0.43 kg/m^2/yr) and *C. spilurus* (mean ± se = 0.08 ± 0.01 kg/m^2/yr) with large individuals of *C. microrhinos* (>60cm TL) and *C. spilurus* (>30cm TL) most common on the reef slope and lagoon respectively. As a result, *C. microrhinos* accounted for approximately 84% of all estimated parrotfish erosion on the reef slope, while in the lagoon, where large individuals of *C. microrhinos* were absent, *C. spilurus* accounted for 40% of estimated parrotfish erosion. There are, of course, other bioeroding groups which may not have been adequately accounted for in our estimates. For example, *B. muricatum*, the largest and potentially most important bioeroding parrotfish (Hoey and Bellwood 2008; Bellwood, Hoey et al. 2012), was rarely encountered in our surveys, and as a result only accounted for approximately 3% of all parrotfish erosion. Large individuals of *B. muricatum* are, however, known to occur in ecologically relevant densities throughout our study area (2.38 ind/ha: Thomson et al. 2021), with potential estimated erosion rates an order of magnitude greater than we have estimated (0.3 kg/m^2/yr). The

comparatively low estimated erosion rates for *B. muricatum* in our study are likely due to the survey method we used (100 × 10m UVC transects), which are less reliable for detecting highly mobile, sparsely distributed reef taxa like *B. muricatum*, than the timed swim surveys that cover larger areas (mean length of timed swim transects in Thomson et al. 2021 = 785 × 20m). In addition, *B. muricatum* is typically found in shallow reef flat and crest habitats (Bellwood, Hoey et al. 2003; Thomson et al. 2021), which were not surveyed during our study. Nevertheless, the combined estimates of erosion by excavating parrotfish (*B. muricatum , C. microrhinos* and *C. spilurus*) in this study ranged from 0.02 kg/m^2/yr to 4.45 kg/m^2/yr (mean ± se = 1.63 ± 0.47 kg/m^2/yr), which is comparable with combined estimates of erosion for *C. microrhinos* and *C. spilurus* in previous studies at Ningaloo Reef (1.18 kg/m^2/yr to 2.30 kg/m^2/yr: Johansson et al. 2012) and suggests most bioerosion in reef slope and lagoon environments at Ningaloo Reef is likely to be due to grazing by just three species of excavating parrotfishes: *B. muricatum* and *C. microrhinos* on the reef slope and *C. spilurus* in the lagoon.

Despite very high densities of urchins at several reef slope sites (range 0.11 to 12.95 ind/m^2, overall mean ± SE = 4.03 ± 0.92 ind/m^2) the relative contribution of grazing urchin *Echinometra mathaei* to total erosion in our study was approximately 17% (0.52 ± 0.11 kg/m^2/yr), which is markedly lower than that of parrotfish at 64% (1.88 ± 0.34 kg/m^2/yr). *E. mathaei* is the most abundant grazing urchin at Ningaloo reef (Babcock et al. 2009; Johansson et al. 2010; Langdon 2012) and on many coral reefs throughout the Indo-Pacific (Keesing 1992; Mokady et al. 1996; Mills et al. 2000; Appana et al. 2003; Langdon 2012). *E. mathaei* has previously been recorded at densities of between 2 and 73 ind/m^2 on reefs in Kenya, Moorea, Eilat and the Marshall Islands, with estimated rates of erosion rates of between 0.01 to 15.3 kg/m^2/yr (Mokady et al. 1996; Peyrot-Clausade et al. 2000). Previous

studies at Ningaloo Reef have estimated erosion rates for *E. mathaei* ranging from 0.00 to 0.55 kg/m^2/yr (Johansson 2012) and as high as 1.00–4.50 kg/m^2/yr (Langdon 2012), which are broadly comparable with our estimates (mean ± SE = 0.52 ± 0.11 kg/m^2/yr). Variation in estimates of erosion by urchins among studies suggests there are spatial and temporal differences in their contribution to erosion budgets, although the consistently low estimates of erosion from *E. mathaei* compared to parrotfish indicate urchins are an important but secondary source of reef erosion at Ningaloo Reef.

Interestingly, we found estimated *E. mathaei* erosion to be positively correlated with reef rugosity ($r^2 = 0.48$), indicating fine-scale reef complexity was higher at sites with high rates of urchin erosion. *E. mathaei* grazing differs from that of parrotfish grazing in that *E. mathaei* prefers to feed on algae within concave reef structures (furrows), moving back and forth along the furrow as it feeds. In contrast, parrotfish tend to preferentially feed on convex surfaces (Bellwood 1996). Due to this unique feeding behaviour, at high densities (>3 ind/m^2) *E. mathaei* can create extensive furrow networks which may enhance small scale reef complexity (Pari et al. 2002; Langdon 2012). The positive correlation we observed between urchin erosion and reef rugosity may then be partially attributable to the extensive furrow networks created by *E.mathaei*, especially at reef slope sites where they were found in high densities (mean ± SE = 5.6 ± 1.12 ind/m^2). Importantly, *E. mathaei*'s preference to feed exclusively within furrows and only leave the protection of these furrows to defend against neighbouring urchins (Langdon 2012), means it was unlikely to have grazed directly on our experimental coral blocks. However, we are unable to completely discount the role of *E. mathaei* as its presence alone indicates it does contribute to erosion on the reef.

The contribution by micro- and macroborers to block erosion was negligible, with rates of internal erosion accounting for only 1% of total erosion. Over short timescales (<3 yrs), bioerosion by internal borers has been shown to undergo ecological succession, with rates of internal erosion increasing as initially microborers, then macroborers, weaken the internal reef structure (Chazottes et al. 1995; Pari et al. 2002). This growing rate of internal erosion is largely attributed to increasing macroborer erosion (Kiene and Hutchings 1994; Pari et al. 2002). Although internal erosion did not increase over the length of our study (12 versus 20 months), macroborer polychaetes were only evident in CT scans of blocks after 20 months. Longer deployment periods blocks may have resulted in greater rates of macroborer erosion (Kiene and Hutchings 1994). Overall, rates of internal bioerosion were likely underestimated during our study, with heavy grazing by parrotfish, potentially removing micro- and macroborers in the outer block layers. Indeed, some scarids appear to preferentially feed on carbonate surfaces with macroborers (Rotjan and Lewis 2005). Hence, what we effectively measured as internal erosion may be better defined as the "residual" borer erosion (as discussed in Chazottes et al. 1995). The lack of micro- and macroboring activity recorded in our study may therefore be due to a combination of heavy grazing by parrotfish and urchins, combined with the relatively short deployment period.

Unaccounted erosion totalled 44% of all erosion (1.62 kg/m²/yr) and is likely to have included components of all three erosion processes: biological, chemical and physical erosion. Using direct estimates of water velocities (daily mean and maximum), we found maximum water velocities were positively correlated with rates of external block erosion (r^2 = 0.61) and parrotfish erosion (r^2 = 0.71) but not the residual unaccounted erosion (non-significant). This suggests that the process by which erosion was enhanced by water velocity was likely through facilitation of biological (i.e., parrotfish grazing), and/or chemical erosion,

rather than through direct physical abrasion. Previous studies have similarly attributed enhanced rates of erosion in exposed reef environments to increased biological and/or chemical erosion (Osorno et al. 2005; Hoey and Bellwood 2008), in particular, grazing by fish and dissolution by sponges. Previous studies have also suggested that increased water velocities may promote the growth of organisms that may further contribute to the process of bioerosion by secreting chemicals that dissolve the reef framework and/or promote increased biological erosion (Hutchings 1986). Storms that generate large waves can, however, have a detrimental effect on corals and reef structure, often resulting in breaking of reef structures and extensive areas of reef rubble (Kenyon et al. 2023). The significance of physical erosion may then become more significant over time scales that incorporate damage to reefs through extreme storms (Scoffin 1993; Perry 2001)

5.5 Conclusion

This study presents in situ measurements of reef erosion rates across multiple reef zones at Ningaloo Reef in the eastern Indian Ocean. The total mean erosion rates on blocks observed after 20 months (2.95 ± 0.37 kg m^2/yr) were higher at Ningaloo Reef than other regions, such as the Great Barrier Reef and French Polynesia. The study highlights the significant role of bioeroding parrotfish, which accounted for approximately 63% of total erosion. Furthermore, erosion rates were influenced by the species and sizes of parrotfish present within each reef zone, rather than the biomass of parrotfish, with one species responsible for most bioeroson (*C. microrhinos*). The grazing urchin *Echinometra mathaei* were found to make a relatively low contribution to erosion (17%) despite their occasional high densities. Moreover, the study indicates that rates of internal erosion by micro and macroborers were almost negligible, likely due to heavy grazing by parrotfish and the relatively short study duration. A substantial portion of external erosion remained unaccounted for (44%), highlighting the importance of improved methods for evaluating erosional processes across different reef environments.

5.6 Acknowledgements

I acknowledge the Jinigudira people, the traditional custodians of the land and sea country on which this study was conducted. I thank staff at the Centre for Microscopy, Characterisation and Analysis at the University of Western Australia for their assistance with microCT scanning, in particular Diana Patalwala, for her endless help with running the scanning software. I thank Malcolm McCulloch for providing *Porites* sp. skeletons and the staff from the from the Department of Biodiversity, Conservation and Attractions for assisting with field logistics. I thank Natalie Travaglione for assisting with data entry and Anna Cresswell, Micheal Haywood, Beau DeGroot, Dan Gorman, Emma Westlake and Nicholas Gust for field assistance.

Chapter 6. General discussion

Understanding the dynamics of reef production and erosion is crucial to predicting how coral reefs will grow and maintain their physical structure, and to providing ecosystem services such as shoreline protection and sediment regeneration (Perry et al. 2014; Perry et al. 2015; Morgan and Kench 2016; Perry et al. 2018). Indirect census-based methods have been widely used for estimating both production and erosion, providing insight into carbonate budgets (Eakin 1996; Harney and Fletcher 2003; Mallela and Perry 2007; Perry et al. 2012; Perry et al. 2013; Perry et al. 2014; Perry et al. 2015; Morgan et al. 2016; Januchowski-Hartley et al. 2017; Perry et al. 2018; Lange and Perry 2019). However, this approach is often based on generalized activity estimates of bioeroding organisms, and/or growth rates of calcifying organisms (Hamylton et al. 2013; Bak 1990; Eakin 1986; Perry 2012; Perry et al. 2018), even though activity levels of producers and eroders may differ across multiple spatial and temporal scales. Subsequently, using rates from varied locations and points in time may not accurately represent the local activity of producers or eroders, resulting in inaccurate estimates.

This thesis addresses the limitations of previous research on reefs in Northwestern Australia by providing new insights into the abundance and activity levels of carbonate producers and eroders over extended time periods. This includes a comparison of direct and indirect methods for quantifying erosion on both wave exposed and sheltered reefs. Further, this thesis offers new knowledge on: (1) hard coral cover, reef rugosity, and the taxonomic and morphological composition of corals across multiple reef habitats over a decade (Chapter 2); (2) spatial patterns of coral recruitment and predictors of recruitment over three years

(Chapter 3); (3) estimates of bioerosion by microborers, macroborers, parrotfish and urchins; and (4) wave-induced water flow across multiple reef habitats (Chapters 4 and 5).

6.1 Dynamics of processes influencing carbonate production

Carbonate production is influenced by a wide range of physical, chemical and biological processes which operate at multiple scales, from individual coral colonies to entire reef systems. Fast-growing corals, such as tabular and branching corals, can produce greater than 25 kg/m^2/yr of carbonate (Pratchett et al. 2020) and consequently hard coral cover is seen as the most critical metric for estimating carbonate production on coral reefs (Chave et al. 1972; Stanley Jr 1981; Perry et al. 2012). However, coral cover varies significantly across locations and over time, often experiencing rapid fluctuations due to changing environmental conditions, biological interactions, and disturbances. Similarly, the growth rates of corals also vary among growth forms and species (Dullo 2005) as well as spatially and temporally due to varying environmental conditions (Pratchett et al. 2015). Consequently, taxa specific data on the abundance and activity of carbonate producers over extended periods and across multiple habitats are required to provide long-term estimates of carbonate production using census-based approaches (Chave et al. 1972)

Using data from Chapter 2, along with new in situ CCA production estimates (unpublished) and percent cover data for Ningaloo reef, I provide updated estimates of long-term carbonate production at Ningaloo reef. These new estimates build on the previous estimates of production for Ningaloo Reef published in Perry et al. (2018) by incorporating (1) mean percent cover of hard corals, CCA and rugosity estimates from annual surveys spanning a decade (2007-2016), (2) new in situ CCA production estimates for reef slope (0.05 ± 0.01

kg/m^2/yr) and reef flat (0.01 ± 0.01 kg/m^2/yr) locations (unpublished), and (3) new estimates of carbonate production across multiple habitats: reef slope (n = 43), reef flat (n = 11) and lagoon (n = 25) locations (Figure 6.1, Table 6.1). Detailed description of production values provided in supplementary material.

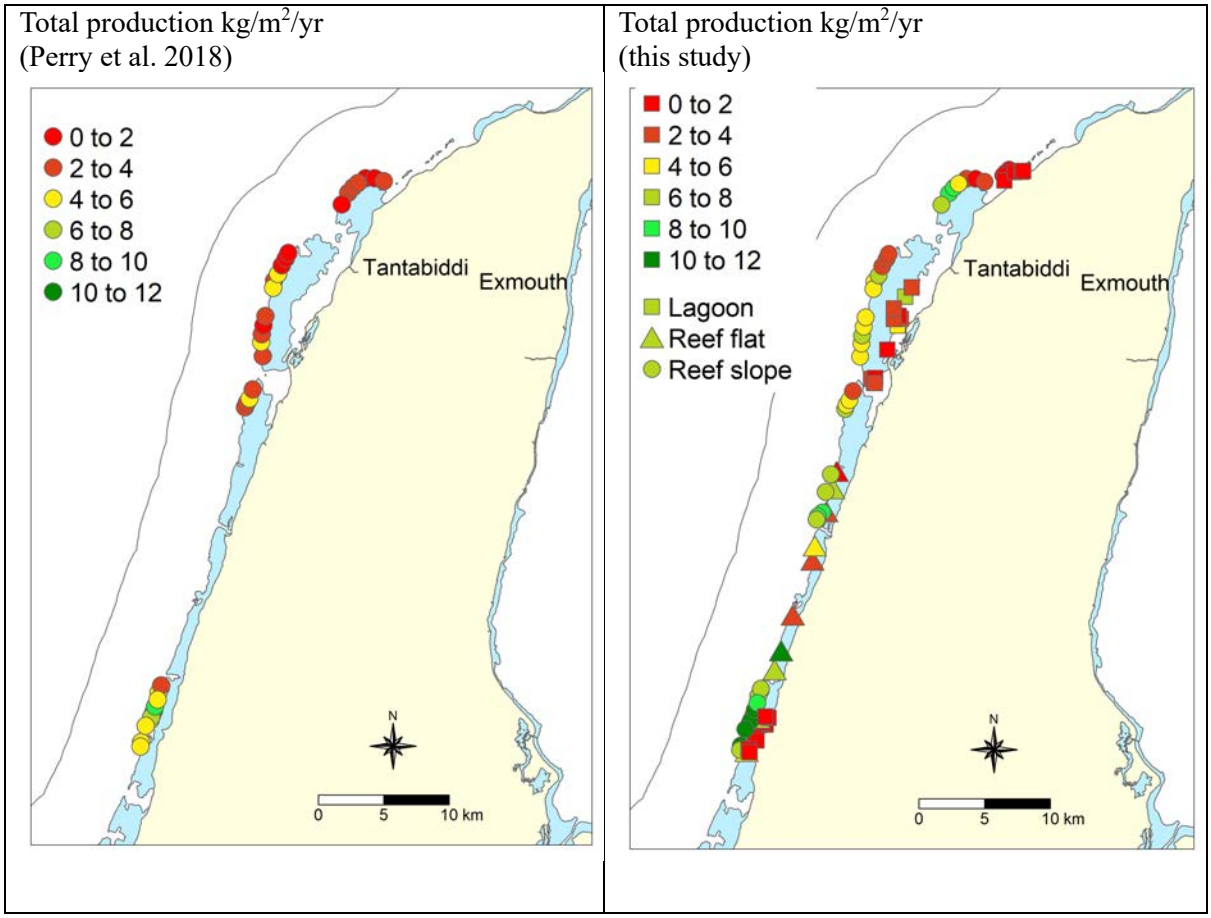


Figure 6.1. Estimated total carbonate production for Ningaloo Reef (kg/m^2/yr) from (a) previous published production rates for reef slope sites from Ningaloo Reef based on 2016 surveys (published in Perry et al. 2018) and (b) this study.

Table 6.1. Comparison of estimated production by hard corals and CCA between previous studies (Perry et al. 2018) and this study at 34 selected reef slope locations at Ningaloo reef.

	Previous estimate kg/m^2/yr (Perry *et al.* 2018)				New estimates kg/m^2/yr (this study)			
	Coral cover	Coral production	CCA production	Total production	Coral cover	Coral production	CCA production	Total production
Mean	19.79	3.62	0.06	3.68	26.63	6.38	0.03	6.41
Min	0.56	0.10	0.01	0.11	0.56	0.01	0.01	0.01
Max	53.33	9.04	0.15	9.11	64.17	21.08	0.24	21.02
SE	9.15	1.55	0.02	1.56	0.78	0.22	0.01	0.22

New estimates of carbonate production for the same 34 reef slope locations were approximately double the previous estimates (Figure 6.1, Table 6.1). The differences between new estimates and those from the previous study (Perry et al., 2018) can be partly explained by the long-term changes in coral cover and composition from 2007 to 2016, as well as the differing lengths of the sampling periods of the two studies (1 versus 10yrs). The earlier study used coral cover data from a single year (2016) to provide a 'snapshot' estimate of carbonate production necessary for comparison with other Indian Ocean locations in the same year (Perry et al. 2018). In contrast, my new estimates incorporate coral cover and composition data collected over the preceding decade (2007–2016) during which significant fluctuations in cover of total and *Acropora* coral were observed (Chapter 2). Census-based methods for estimating carbonate production are particularly sensitive to short-term fluctuations in coral cover, especially in fast-growing, disturbance-sensitive species like *Acropora* (Perry et al. 2012). However, long-term carbonate accumulation may depend less on fast-growing species that wax and wane in abundance and more on slow-growing, massive species (Roff 2020). Therefore, it is important to sample over multiple years when assessing long-term carbonate production and reef accretion potential.

New estimates of carbonate production at Ningaloo Reef reveal habitat-specific differences across multiple reef zones. On average, carbonate production on the reef slope is 1.2 to 4.2 times higher than inshore areas such as the reef flat and lagoon (Figure 6.1). The reef flat, in particular, has experienced a 4% per annual decline in hard coral cover (Chapter 2) – a rate more severe than declines observed on the Great Barrier Reef (0.53% per year from 1985 to 2012; De'ath et al. 2012), in the Caribbean (1.3% per year from 1977 to 2002; Gardner et al. 2003), and in the Indo-Pacific (2% per year from 1997 to 2003; Bruno and Selig 2007). These declines in the GBR, Caribbean and Pacific are mainly attributed to increased physical disturbance and heat stress (De'ath et al. 2012; Hughes et al. 2017). Despite being relatively free from local pressures, such as declining water quality and pollution (Vanderklift et al. 2020), declines in coral cover at Ningaloo Reef suggest coral communities have largely been negatively impacted by coral bleaching and cyclones, with impacts varying among habitats. Moreover, changes in coral cover observed in one reef zone did not necessarily reflect trends across the entire reef, as neighboring locations within different reef zones exhibited contrasting rates of carbonate production (Figure 6.1), highlighting the need to consider habitat-specific estimates across multiple reef zones when estimating carbonate production at the scale of entire reefs.

Carbonate production is influenced not only by existing coral cover but also by the recruitment of new coral colonies. The settlement, survival and growth of juvenile corals shape the future composition, percent cover and overall carbonate production of adult coral populations. In Chapter 3, I identified key spatial predictors of coral recruitment in the Dampier Archipelago from 2015 to 2017, revealing density-dependent relationships between

coral recruits and adult coral cover. The most accurate models for predicting rates of coral recruitment included regional coral cover and hydrodynamics, which together explained up to 65% of the spatial and temporal variability in recruitment over the three survey years.

In Chapter 3, I identified reefs with consistently high recruitment over the three survey years (NE Lewis and Whitaker Island), contributing to a growing body of evidence that recruitment patterns among reefs can be consistent, despite significant variability in recruitment magnitude (e.g., Adjeroud et al. 2022; Beck et al. 2016; Eagle et al. 2012; Edmunds 2021; Wen et al. 2013). Variability in recruitment among reefs is particularly important because individual islands and reefs are the scale at which coral reefs are managed, marine reserve boundaries are designated (Sobel and Dahlgren 2004) and larval connectivity is studied (Cowen and Sponaugle 2009; Hock et al. 2014; Feng et al. 2016; Boschetti et al. 2019). Moreover, persistent patterns in coral recruitment may be particularly relevant for managing coral reef resilience at regional scales. Coral populations on reefs with consistently high recruitment rates, or "recruitment hotspots" are likely to recover more quickly following disturbances (Holbrook et al. 2018; Boschetti et al. 2019), and thereby generally sustain higher rates of long-term carbonate production and, potentially, better adapt to rising sea levels (Doropoulos et al. 2015; Bramanti and Edmunds 2016; Hughes et al. 2019; Gouezo et al. 2021).

For effective coral reef conservation and management, understanding the relationship between the source of coral recruits and their settlement location is important because these relationships can strongly affect recovery times on reefs (Boschetti et al. 2019). The consistent spatial patterns in recruitment identified in Chapter 3 were partly influenced by regional coral cover (within 15 km) as well as local hydrodynamic patterns observed during

the study period (dispersal predictions). Much like the predictable island-wake zones found on some reefs within the Great Barrier Reef (Wolanski and Hamner 1988; Furukawa et al. 1998), the southward-flowing Leeuwin and Holloway Currents appear to have created similar predictable island-wake zones throughout the study area during my study period. These zones, combined with the region's strong tidal eddies and convergence zones (Semeniuk 1982; Feng et al. 2016), likely produced consistent flow patterns in near-reef environments, contributing to the positive stock recruitment relationships documented in Chapter 3.

6.2 Dynamics of processes influencing carbonate erosion

Indirect assessments of erosion on coral reefs often rely on data that is relatively easy to collect, as it requires inexpensive equipment, shorter study durations, and lower levels of expertise (Browne et al., 2021). As a result, some components of erosion that are more challenging to estimate are frequently missed or inadequately measured, leading to inaccurate overall estimates. While previous studies have provided some estimates of bioerosion rates at Ningaloo Reef (Johansson 2012; Langdon 2012; Perry et al., 2018) and the nearby Exmouth Gulf, 80 km west (Dee et al., 2021; Dee et al., 2023), Chapters 4 and 5 expand on this by providing: (1) empirical observations of erosion caused by internal borers (micro- and macroborers) across multiple reef habitats at Ningaloo Reef; (2) empirical observations of erosion caused by parrotfish, urchins and physical factors like wave exposure across various habitats; and (3) a direct comparison between census-based and direct (carbonate-block) estimates of erosion across different habitats. These partitioned erosion estimates are the first of their kind for a wave-exposed, fringing coral reef in the eastern Indian Ocean.

Hidden elements of bioerosion are likely to be present across the full-size spectrum of organisms, particularly at the extremes, where detection and quantification of both very small and very large bioeroders can be challenging. Large-bodied, mobile fish may be underrepresented in bioerosion estimates if the survey methods used are not suitable for detecting their abundance or feeding activity. Although many studies recognise the importance of fish as bioeroders on coral reefs, they often use visual surveys along transects that are 30–50 m in length (Alwany et al. 2009; Perry et al. 2018; Dee et al. 2023). These short belt transects are not suitable for detecting some large, mobile species, such as the bumphead parrotfish, *Bolbometopon muricatum,* which are better surveyed using longer transects or timed swims that cover larger areas of reef (Bellwood et al. 2003; Hoey and Bellwood 2008).

Chapter 4 describes the abundance and distribution of *Bolbometopon muricatum* at Ningaloo Reef, the largest species of parrotfish (up to 1.3 m total length), known for its ability to remove significant amounts of reef carbonates through bioerosion (up to 5.5 tonnes/ind/yr; Bellwood et al. 2003). This species had previously gone undetected in scientific surveys at Ningaloo Reef, leading to an underestimation of its contribution to total erosion, despite its likely presence and estimated removal of up to 13.42 tonnes/ha or 1.34 kg/m² of calcium carbonate per year over the period of my study (Chapter 4). Only by conducting targeted timed swim surveys, covering distances up to 900 m per transect (1.8 ha) (Chapter 4), could I estimate the bioerosion by this large, mobile species (Figure 6.2, Table 6.2). Including the bioerosion rates for *B. muricatum* resulted in parrotfish erosion estimates being six times higher than previous assessments for the same sites at Ningaloo Reef and 13 times more variable (mean ± se: 2.58 ± 3.05 kg/m²/yr vs. 0.42 ± 0.23 kg/m²/yr; Figure 6.2, Table 6.2).

Hence, it is important for erosional studies elsewhere to consider surveys across multiple habitats and at appropriate scales to ensure major contributors to erosion are captured.

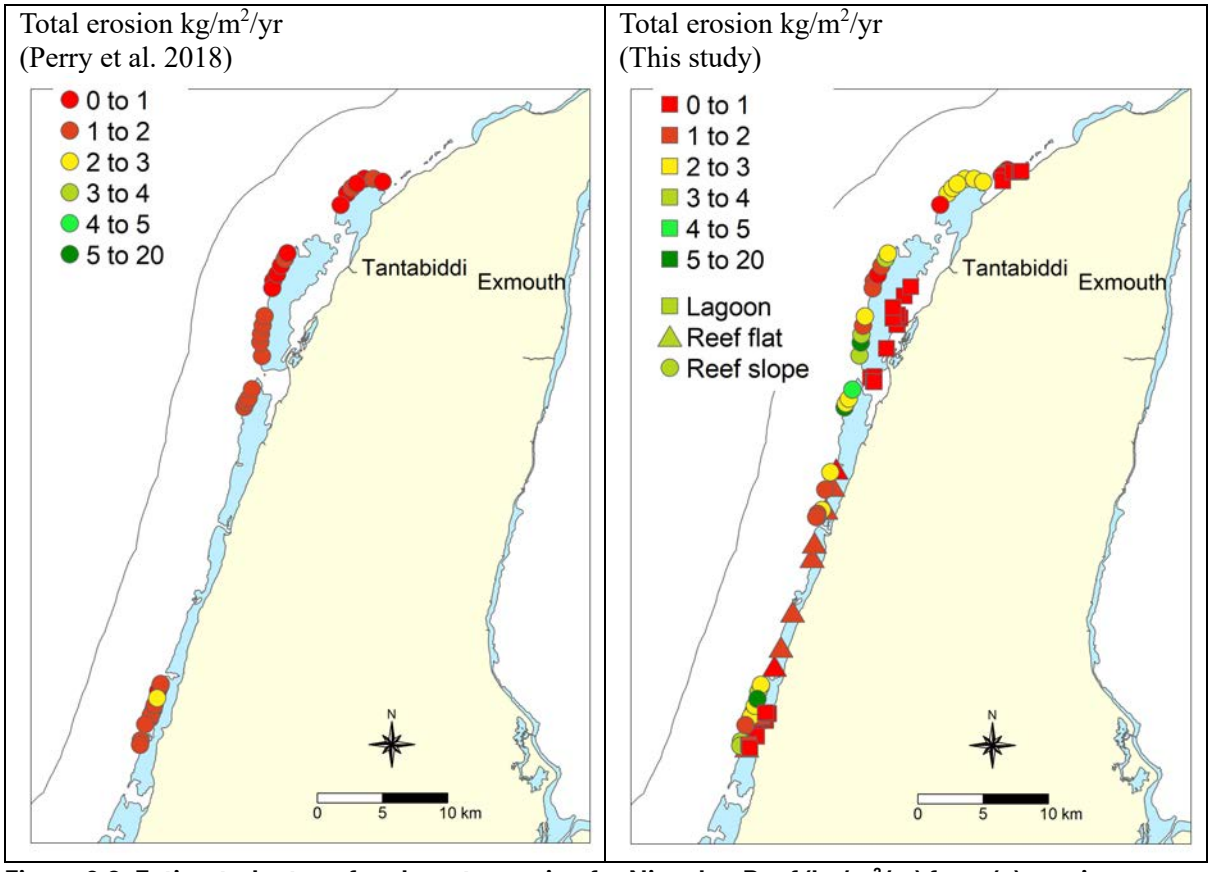


Figure 6.2. Estimated rates of carbonate erosion for Ningaloo Reef (kg/m²/yr) from (a) previous published production rates for reef slope sites from Ningaloo Reef based on 2016 surveys (published in Perry et al. 2018) and (b) this study.

Table 6.2. Comparison of estimated erosion for parrotfish, urchins, micro and macroborers at 34 selected reef slope locations at Ningaloo reef between previous studies (Perry et al. 2018) and this study.

	Previous estimate kg/m^2/yr (Perry et al. 2018)					New estimates kg/m^2/yr (this study)				
	Parrotfish	Urchin	Micro	Macro	Total	Parrotfish	Urchin	Micro	Macro	Total
Mean	0.42	0.13	0.33	0.33	1.21	2.58	0.70	0.11	0.02	3.40
Min	0.02	0.00	0.27	0.27	0.70	0.02	0.03	0.03	0.00	0.73
Max	1.33	1.04	0.48	0.49	2.01	17.80	1.72	0.18	0.02	19.60
SE	0.23	0.18	0.08	0.08	0.34	3.05	0.30	0.04	0.00	3.36

At the smaller end of the size spectrum, quantifying internal erosion of the reef framework presents additional challenges. Micro- and macroborer erosion is particularly difficult to quantify because it occurs beneath the reef surface, requires specialised equipment to visualise, and cannot be captured through rapid-field surveys. This task is further complicated by the need to scale bioerosion estimates from very small measures (e.g., 200 μm) to entire reefs (e.g., hundreds of metres), with subsequent potential for large errors. While many studies recognise the importance of internal borers as significant bioeroders on coral reefs, especially in high-nutrient environments where their diversity and abundance are greatest (Glynn and Manzello 2015; Perry and Harborne 2016; Dee et al. 2021), few employ the specialised techniques needed to accurately quantify both micro- and macroborer activity such as micro-CT and Scanning Electron Microscope imaging. Rather most studies use macro- and micro-erosion rates based on published data that takes limited account of differences in water depth, reef habitat and other environmental drivers on these rates (e.g., Eakin 1996, 2001; Perry et al. 2012).

In Chapter 5, I use micro-CT and Scanning Electron Microscope imaging to present the first in situ measurements of bioerosion by micro- and macroborers at Ningaloo Reef. New in situ estimates of micro- and macroborer erosion were three (micro-erosion) to 16 times (macro-erosion) lower than previous estimates of internal erosion for the same locations (Table 5.2; Perry et al. 2018). The differences between new estimates and those from the previous study (Perry et al., 2018) may be partly explained by the heavy parrotfish grazing on experimental blocks in my study, which likely removed micro- and macroborers from the outer layers of my experimental blocks, resulting in an underestimate in the rates of micro- and macro-erosion for reef slope locations where grazing by parrotfish was high. Nonetheless, these new estimates are the first to use micro-CT and Scanning Electron Microscope to quantify micro- and macro-erosion rates across multiple habitats at Ningaloo Reef and provide a basis for better quantifying micro and macroborer erosion across multiple habitats with a strong wave energy gradient.

6.3 Estimates of net carbonate production

Census-based carbonate budgets are increasingly being used for assessing long-term reef accretion, especially in relation to climate change impacts like sea-level rise and cyclone frequency (e.g., Morgan and Kench 2016; Perry et al. 2018). However, estimates of reef accretion rely on location-specific estimates of net production (total production – erosion), which are scarce for fringing coral reefs in environments with high wave exposure (but see De Bakker et al. 2019). This gap in data means that the connections between carbonate producers and eroders, as well as the effects of wave-driven water flow on net production in fringing reefs, remain poorly understood. In Chapters 2, 4 and 5, I help to address these gaps by providing location-specific data on carbonate erosion and production across reef zones

with varying wave-exposure at Ningaloo Reef. These estimates form the basis for refining net carbonate budget calculations at the scale of individual reef zones (Figure 6.3, Table 6.3).

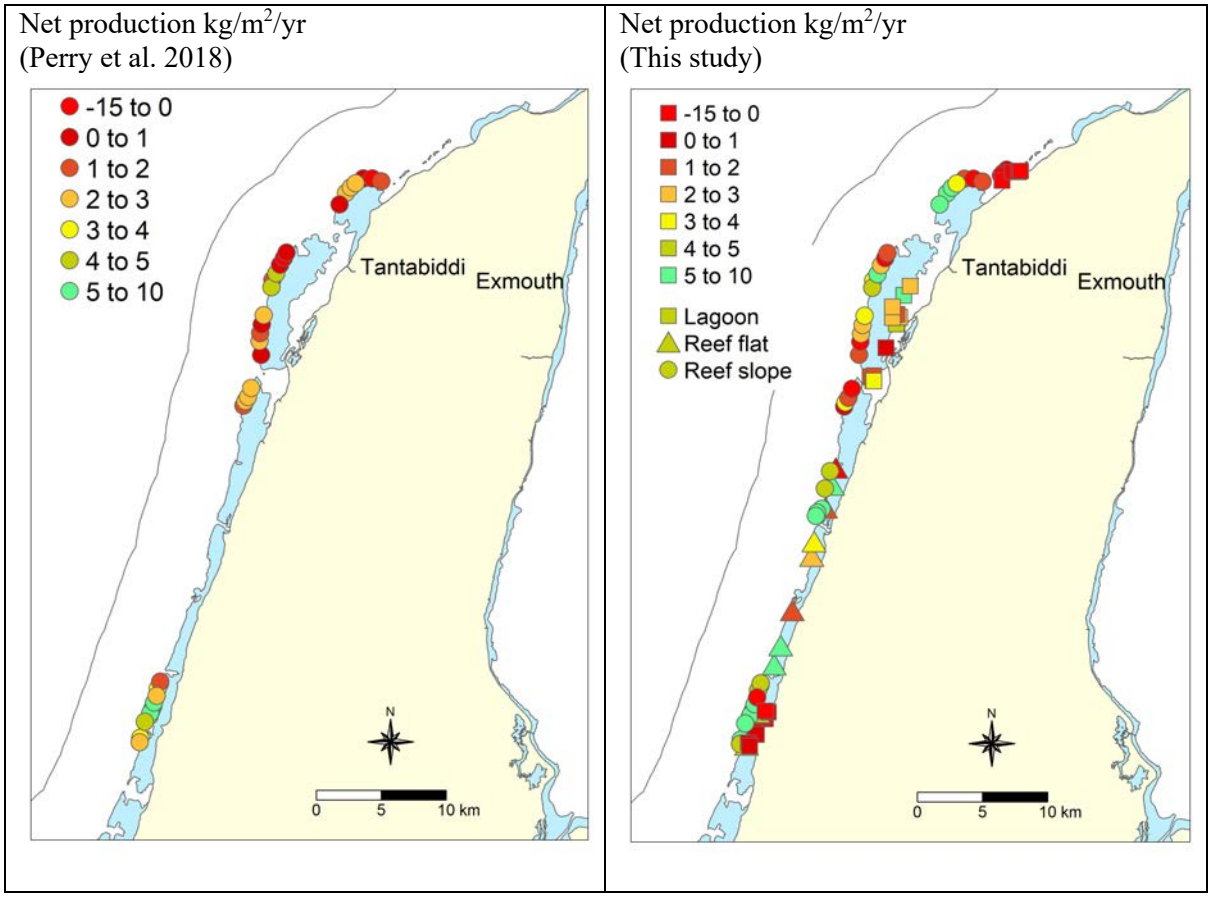


Figure 6.3. Estimated net rates of carbonate production for Ningaloo Reef (kg/m²/yr) from (a) previous published production rates for reef slope sites from Ningaloo Reef based on 2016 surveys (published in Perry et al. 2018) and (b) multiple reef zones incorporating datasets from Chapters 2,4 and 5 in this study).

Estimates of net carbonate production revealed significant habitat-specific differences across reef zones, with the reef flat averaging 4.33 ± 0.83 kg/m²/yr, compared to 3.19 ± 0.59 kg/m²/yr on the reef slope and 1.17 ± 0.37 kg/m²/yr in the lagoon areas (Figure 6.3). Although these estimates do not account for sediment and rubble transport, they highlight that the reef flat and reef slope are the primary sources of carbonate production at Ningaloo Reef. In contrast, the lagoon area exhibited much lower net production due to its low coral cover.

These lagoonal areas likely serve as key depositional environments, where carbonates from the reef flat and slope are deposited as sediment and rubble. This has direct implications for the rate of reef geomorphic development, as spatial variations in net carbonate production and deposition can lead to differences in net reef accretion among reef zones over long time scales. Overall, the carbonate budget at Ningaloo Reef is positive, with biological carbonate production exceeding erosion by an average of 2.63 ± 0.37 kg/m²/yr (Figure 6.3).

New estimates of net carbonate production for reef slope locations averaged 1.25 times higher than those previously reported by Perry et al. (2018) (mean ± SE = 3.09 ± 1.42 vs. 2.47 ± 1.41 kg/m²/yr; Figure 6.4, Table 6.3). Notably, three locations shifted from net positive to net negative budgets, and one location experienced a change of more than 15 kg/m²/yr (Figure 6.4a). These changes in budgetary status were primarily due to the high abundance of *Bolbometopon muricatum* (Chapter 4) at these sites, which led to increased erosion and reduced net production estimates. While the impact of *Bolbometopon* was most pronounced at one site, their bioerosion impacts likely extended more broadly, as schools of this species can travel up to 6 km per day while feeding (Hamilton et al., 2016). Reflecting their broader influence, new estimates of net production across the wider Mangrove Bay region were lower than previous estimates (Figure 6.4), particularly in areas where *B. muricatum* and *C. microrhinos*, the two largest excavating parrotfish species recorded, were most abundant (Chapter 4).

Table 6.3. Comparison of estimated net production (total production – erosion) at 34 selected reef slope locations at Ningaloo reef between previous studies (Perry et al. 2018) and this study.

	Net Production (kg/m^2/yr)	
	Previous estimate (Perry *et al*. 2018)	**New estimate (this study)**
Mean	2.47	3.09
Min	−1.02	−14.61
Max	8.22	8.28
SE	1.41	1.42

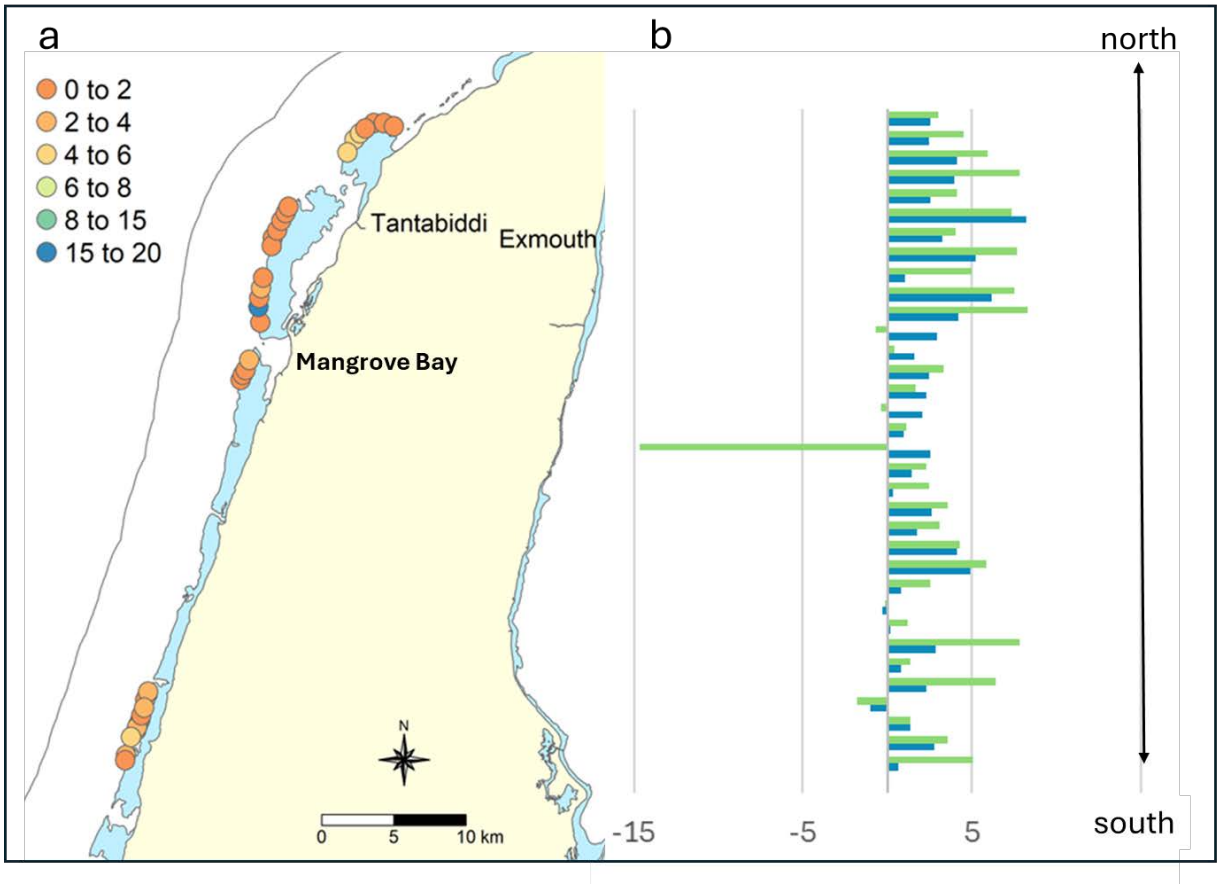


Figure 6.4. (a) Estimated difference in net carbonate production (magnitude in kg/m^2/yr) for 34 selected reef slope locations at Ningaloo reef between previous study (Perry et al. 2018) and this study. (b) Estimated net carbonate production (kg/m^2/yr) in previous study (Perry et al. 2018: blue) and this study (light green). Paired site estimates (6.4b) are ordered from northernmost (top) to southernmost (bottom).

6.4 Conclusions and future research

The aim of this thesis was to improve our understanding of carbonate budgets in Northwestern Australia by providing location-specific data on the abundance and activity levels of key producers and eroders of calcium carbonate across multiple reef zones. Accordingly, detailed information on the relative abundance and distribution of corals and crustose coralline algae (CCA), coral recruitment, and the erosion of carbonate material across different reef habitats was collected. However, collection of location-specific data is time-consuming and labour-intensive, making it prudent to assess how much this local data influences estimates of erosion and production. In this study, local estimates of production and erosion led to revised estimates, showing increases in carbonate production, erosion, and overall net production. The most significant factors driving these changes were changes in the composition of coral communities and the grazing activity of large, excavating parrotfish.

Including local bioerosion rates for parrotfish, particularly *Bolbometopon muricatum*, resulted in average parrotfish erosion estimates that were up to six times higher than previous assessments across the same sites at Ningaloo Reef. Through targeted surveys and detailed in-situ observations of feeding behavior, I was able to account for the broad spatial variations in parrotfish abundance and activity levels at Ningaloo. This approach addressed one of the most challenging aspects of quantifying bioerosion: accounting for the significant spatio-temporal variations in bioeroder populations and their activity levels.

A focus for future work should be to improve our understanding of the movement and feeding activity of *B. muricatum* throughout the day. For example, tracking the movement of individual *B. muricatum* via acoustic tags would provide better understanding of how far they

travel, and therefore the probable area over which their feeding and functional impact (bioerosion) is distributed. If acoustic tags were combined with detachable video-data logging cameras (e.g., crittercams), additional feeding, behavioural and environmental data such as bite frequency, bite rate, preferred feeding substrates and reef zones, alongside the time of day, water depth and water temperature, could also be recorded. This method may be particularly useful for large schooling species such as *B. muricatum*, where the movement and behaviour of a small number of tagged individuals may serve as a reliable proxy for the movement and behaviour of larger schools. This would allow for improved estimates of erosion for many individuals across a full 24-hour cycle.

Scaling bioerosion estimates remains a significant challenge, particularly when using census-based approaches (Browne et al. 2021), which presents an opportunity for further improvement. For example, the current method for estimating microbioerosion, as used in this study, involves scaling measurements obtained at the micron scale (e.g., 200 μm SEM images) and extrapolating them across hundreds of metres of reef. This approach is akin to measuring erosion over a 1 cm section of reef surface and extrapolating it across 10 km of reef and vertically into the reef matrix. Future studies may address this issue by using emerging image recognition technology to automate the identification of microborers and their erosion volumes. This would significantly increase the speed and efficiency of analysing larger substrate volumes and allow for more accurate scaling of measurements.

Long-term (decadal) carbonate production is closely linked to coral recruitment, as the survival and growth of juvenile corals determine the future composition of adult coral populations and overall coral cover. Chapter 3 highlighted that recent advancements in hydrodynamic modelling (e.g., reef-scale resolution), bathymetry mapping and the

integration of larval behaviour into models (e.g., minimum, peak, and maximum competency periods) have significantly enhanced predictions of coral recruitment on reefs, particularly when regional adult coral abundance is included (Chapter 3). However, most census-based estimates of carbonate production remain as 'snapshots' taken at a single point in time, often failing to incorporate estimates of coral recruitment, and hence the contributions of these corals to carbonate production over longer timescales (Browne et al., 2021).

To address this gap, future carbonate production models should incorporate estimates of coral recruitment under different environmental conditions to better understand its influence on long-term carbonate production (Doropoulos et al., 2015; Hughes et al., 2019; Gouezo et al., 2021). Additionally, recent advancements in underwater photogrammetry now enable the accurate three-dimensional measurement of coral recruit growth (Gouezo et al., 2023) and adult coral colonies (Remmers et al., 2024), significantly improving our ability to measure coral growth and estimate carbonate production under varying environmental conditions.

Unravelling erosion and production processes on coral reefs remains extremely challenging. While the overall net carbonate budget at Ningaloo Reef is currently positive, with biological carbonate production exceeding erosion, increasing disturbance intensity and frequency is likely to shift this balance toward more negative budgets. The research presented in this thesis improves our understanding of the abundance and activity levels of key producers and/or eroders, as well as the environmental conditions which influence them, across multiple reef zones in NW Australia. This new knowledge, while not intended to account for the full suite of processes that maintain net carbonate production, provides for improved net

carbonate assessments and the capacity to predict future responses of NW Australian reefs to future climate change scenarios.

Supplementary information to support Chapter 2

Estimated annual change in percentage cover of coral groups (*U*), confidence intervals (CI) and probability (p) that *U* exceeds the distribution of values from a bootstrapping process (1000x) for various groups of corals at Ningaloo Reef. Coral genera are listed in order of abundance from highest to lowest. Coloured rows represent significant trends- gGreen values indicate increasing (positive) trends, red value indicate declining (negative) trends.

Groups		**Inshore**				**Reef flat**				**Reef slope**			
		U	Low CI	High CI	*p*	U	Low CI	High CI	*p*	U	Low CI	High CI	*p*
Total Hard coral	Total hard coral	0.01	-0.10	0.09	0.45	-0.04	-0.07	-0.01	0.00	0.02	-0.01	0.04	0.34
Coral Genera	Acropora	-0.11	-0.28	0.05	0.62	-0.10	-0.13	-0.07	<0.01	0.02	-0.02	0.05	0.34
	Porites	0.34	-3.14	3.81	0.15	-0.08	-0.24	0.07	0.55	0.06	0.05	0.08	0.01
	Montipora	-0.36	-0.62	-0.10	0.01	-0.12	-0.48	0.24	0.25	-0.02	-0.10	0.05	0.38
	Echinopora	0.40	-1.84	2.64	0.24	-0.06	-0.15	0.03	0.18	1.65	0.22	3.08	0.01
	Pocillopora	0.11	-0.10	0.32	0.15	-0.16	-0.61	0.28	0.74	0.00	-0.05	0.04	0.17
	Favites	1.56	0.41	2.72	0.01	-0.12	-0.25	0.01	0.08	-0.17	-0.23	-0.12	0.01
	Goniastrea	1.60	-0.22	3.42	0.48	-0.06	-0.16	0.04	0.14	-0.22	-0.24	-0.19	0.02
	Platygyra	0.70	-0.68	2.07	0.09	-0.03	-0.20	0.14	0.49	-0.10	-0.14	-0.07	0.03
	Turbinaria	0.06	-0.12	0.24	0.78	-0.26	-0.60	0.08	0.44	0.22	0.11	0.34	0.01
	Leptoria	-	-	-	-	-0.07	0.10	-0.28	0.13	-0.10	0.16	-0.43	0.22
	Favia	1.65	1.01	2.30	0.02	-0.08	-0.14	-0.01	0.02	0.10	0.03	0.16	0.03
	Millepora	0.37	-2.48	3.23	0.78	-0.19	-1.30	0.92	0.24	-0.16	-0.41	0.10	0.28
	Cyphastrea	-0.37	0.06	-0.49	0.25	-0.19	0.06	-0.31	0.06	-0.10	0.60	-1.29	1.07
	Galaxea	-	-	-	-	0.13	0.05	0.02	0.24	-0.05	0.06	-0.18	0.07
	Hydnophora	-	-	-	-	-0.06	0.05	-0.18	0.08	-0.33	0.28	-0.89	0.22
	Lobophyllia	-	-	-	-	-0.05	0.07	-0.20	0.09	-0.22	0.04	-0.31	0.12
	Merulina	-0.489	0.168	-0.818	-0.16	-0.12	0.06	-0.24	0.10	-0.23	0.17	-0.57	0.11
	Montastrea	-	-	-	-	-0.16	1.00	-2.12	1.79	-0.58	0.19	-0.96	0.20
	Pavona	-	-	-	-	-0.04	0.03	-0.11	0.02	-0.62	0.10	-0.84	0.41

Groups		Inshore				Reef flat				Reef slope			
	Seriatopora	-	-	-	-	-0.13	0.16	-0.46	0.18	-	-	-	-
	Stylophora	-	-	-	-	-	-	-	-	0.04	0.21	-0.37	0.47
	Leptastrea	-	-	-	-	-	-	-	-	-0.28	0.04	-0.36	0.20
Growth form	Encrusting	-0.08	-0.33	0.17	0.50	-0.08	-0.23	0.07	0.45	0.08	-0.10	0.27	0.76
	Branching	-1.21	-2.17	-0.25	<0.00	0.00	-0.13	0.14	0.69	0.00	-0.11	0.11	0.50
	Bushes	-1.80	-3.20	-0.40	<0.01	-0.27	-0.43	-0.10	<0.01	-0.13	-0.29	0.03	<0.01
	Tabulate	-0.93	-2.03	0.20	0.06	-0.03	-0.10	0.03	0.25	0.23	0.00	0.46	0.90
	Massive	-0.19	-0.49	0.11		-0.07	-0.14	-0.00	0.13	-0.06	-0.12	-0.01	<0.01
Physical susceptibility	Low	-0.11	-0.20	-0.01	0.24	-0.03	-0.09	0.02	0.45	-	-	-	-
	Medium	-	-	-	0.50	0.37	-0.52	1.28	0.84	0.56	-0.06	1.06	0.95
	High	-0.63	-1.42	0.0	0.00	-0.07	-0.11	-0.03	0.02	0.08	0.06	0.11	0.99
Bleaching susceptibility	Low	-0.21	-0.49	0.02	0.09	-0.10	-0.24	0.03	0.12	0.04	0.01	0.08	0.91
	Medium	-0.61	-1.59	0.36	0.27	-0.75	-1.55	0.00	0.01	0.02	-0.03	0.07	0.71
	High	-1.24	-2.29	-0.18	<0.01	-0.06	0.00	-0.11	0.03	0.07	0.03	0.10	0.99

Biological traits of the 29 coral genera recorded at Ningaloo Reef between 2007 and 2016. Letters denote data sources.

GENUS	GROWTH FORM[A]	PHYSICAL DAMAGE SUSCEPTIBILITY[B]	BLEACHING SUSCEPTIBILITY[C]	LIFE-HISTORY[D]
Acropora	bushes, branching, tabulate	high	high	Competitive
Porites	massive	low	low	Stress-tolerant
Turbinaria	sheets	high	low	Competitive
Montipora	encrusting	low	high	Generalist
Goniastrea	massive	low	low	Stress-tolerant
Pocillopora	bushes	medium	medium to high	Weedy
Echinopora	branching, bushes	high	low	Generalist
Favites	massive	low	medium	Stress-tolerant
Platygyra	massive	low	medium	Stress-tolerant
Favia	massive	low	medium	Stress-tolerant
Leptoria	massive	medium	medium	Stress-tolerant
Cyphastrea	massive	low	low	Stress-tolerant
Seriatopora	branching	high	high	Weedy
Merulina	encrusting	medium	medium	Generalist
Hydnophora	branching	high	medium	Generalist
Galaxea	massive	low	medium	Stress-tolerant
Pavona	sheets	medium	medium	Stress-tolerant
Lobophyllia	massive	low	high	Stress-tolerant
Pachyseris	sheets	medium	high	Generalist
Coscinarae	encrusting	low	high	Generalist
Montastrea	massive	low	medium	Stress-tolerant
Heliopora	bushes	high	medium	Competitive
Fungia	massive	medium	low	Stress-tolerant
Leptastrea	massive	medium	low	Weedy
Coeloseris	massive	medium	low	Stress-tolerant
Echinophyllia	encrusting	high	low	Stress-tolerant
Diploastrea	massive	low	low	Generalist

Reference sources: *A (Veron 1995; Madin et al. 2016) B (Madin et al. 2016) C (Marshall and Baird 2000; Madin et al. 2016) D (Darling et al. 2012)*

Mean percent cover, proportional cover and dominance category of the 27 coral genera recorded at Ningaloo Reef between 2007 and 2016. Dominant genera (>10% proportional cover) are shown in red.

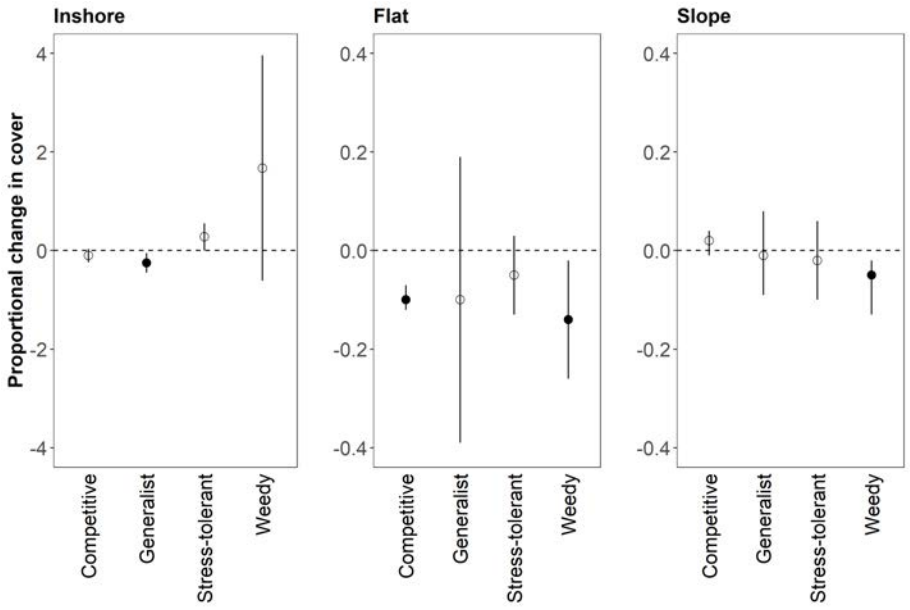
GENUS	INSHORE			REEF FLAT			REEF SLOPE		
	PERCENT COVER	PROPORTIONAL COVER	CATEGORY	PERCENT COVER	PROPORTIONAL COVER	CATEGORY	PERCENT COVER	PROPORTIONAL COVER	CATEGORY
*Acropora**	3.6	34.1	Dominant	18.6	85.7	Dominant	9.8	47.8	Dominant
*Porites**	3.4	32.8	Dominant	0.5	2.3	Uncommon	2.4	11.7	Dominant
Turbinaria	0.1	1.0	Uncommon	1.1	4.9	Uncommon	0.3	1.4	Uncommon
Montipora	0.6	6.2	Uncommon	0.5	2.3	Uncommon	1.5	7.5	Uncommon
Goniastrea	0.3	2.6	Uncommon	0.3	1.3	Uncommon	0.7	3.2	Uncommon
Pocillopora	0.1	1.1	Uncommon	0.1	0.5	Uncommon	1.3	6.4	Uncommon
*Echinopora**	1.6	14.9	Dominant	0.1	0.2	Uncommon	0.5	2.5	Uncommon
Favites	0.1	0.8	Uncommon	0.1	0.6	Uncommon	0.8	3.9	Uncommon
Platygyra	0.0	0.4	Uncommon	0.0	0.2	Uncommon	0.6	3.1	Uncommon
Favia	0.1	0.7	Uncommon	0.1	0.4	Uncommon	0.3	1.7	Uncommon
Leptoria	0.0	0.2	Uncommon	0.0	0.1	Uncommon	0.6	2.8	Uncommon
Cyphastrea	0.1	0.6	Uncommon	0.1	0.5	Uncommon	0.1	0.3	Uncommon
Seriatopora	0.2	2.2	Uncommon	0.0	0.2	Uncommon	0.2	0.7	Uncommon
Merulina	0.1	0.6	Uncommon	0.0	0.1	Uncommon	0.3	1.2	Uncommon

GENUS	INSHORE			REEF FLAT			REEF SLOPE		
	PERCENT COVER	PROPORTIONAL COVER	CATEGORY	PERCENT COVER	PROPORTIONAL COVER	CATEGORY	PERCENT COVER	PROPORTIONAL COVER	CATEGORY
Hydnophora	0.0	0.1	Uncommon	0.0	0.1	Uncommon	0.2	0.9	Uncommon
Galaxea	0.0	0.1	Uncommon	0.0	0.2	Uncommon	0.1	0.5	Uncommon
Pavona	0.1	1.3	Uncommon	0.0	0.0	Uncommon	0.1	0.6	Uncommon
Lobophyllia	0.0	0.1	Uncommon	0.0	0.1	Uncommon	0.2	0.7	Uncommon
Pachyseris	0.0	0.0	Uncommon	0.0	0.0	Uncommon	0.2	0.8	Uncommon
Coscinarae	0.0	0.0	Uncommon	0.0	0.0	Uncommon	0.1	0.7	Uncommon
Montastrea	0.0	0.0	Uncommon	0.0	0.0	Uncommon	0.1	0.5	Uncommon
Heliopora	0.0	0.1	Uncommon	0.0	0.0	Uncommon	0.0	0.2	Uncommon
Fungia	0.0	0.0	Uncommon	0.0	0.0	Uncommon	0.0	0.2	Uncommon
Leptastrea	0.0	0.1	Uncommon	0.0	0.0	Uncommon	0.0	0.2	Uncommon
Coeloseris	0.0	0.0	Uncommon	0.0	0.0	Uncommon	0.0	0.1	Uncommon
Echinophylli	0.0	0.0	Uncommon	0.0	0.0	Uncommon	0.0	0.2	Uncommon
Diploastrea	0.0	0.0	Uncommon	0.0	0.0	Uncommon	0.0	0.1	Uncommon

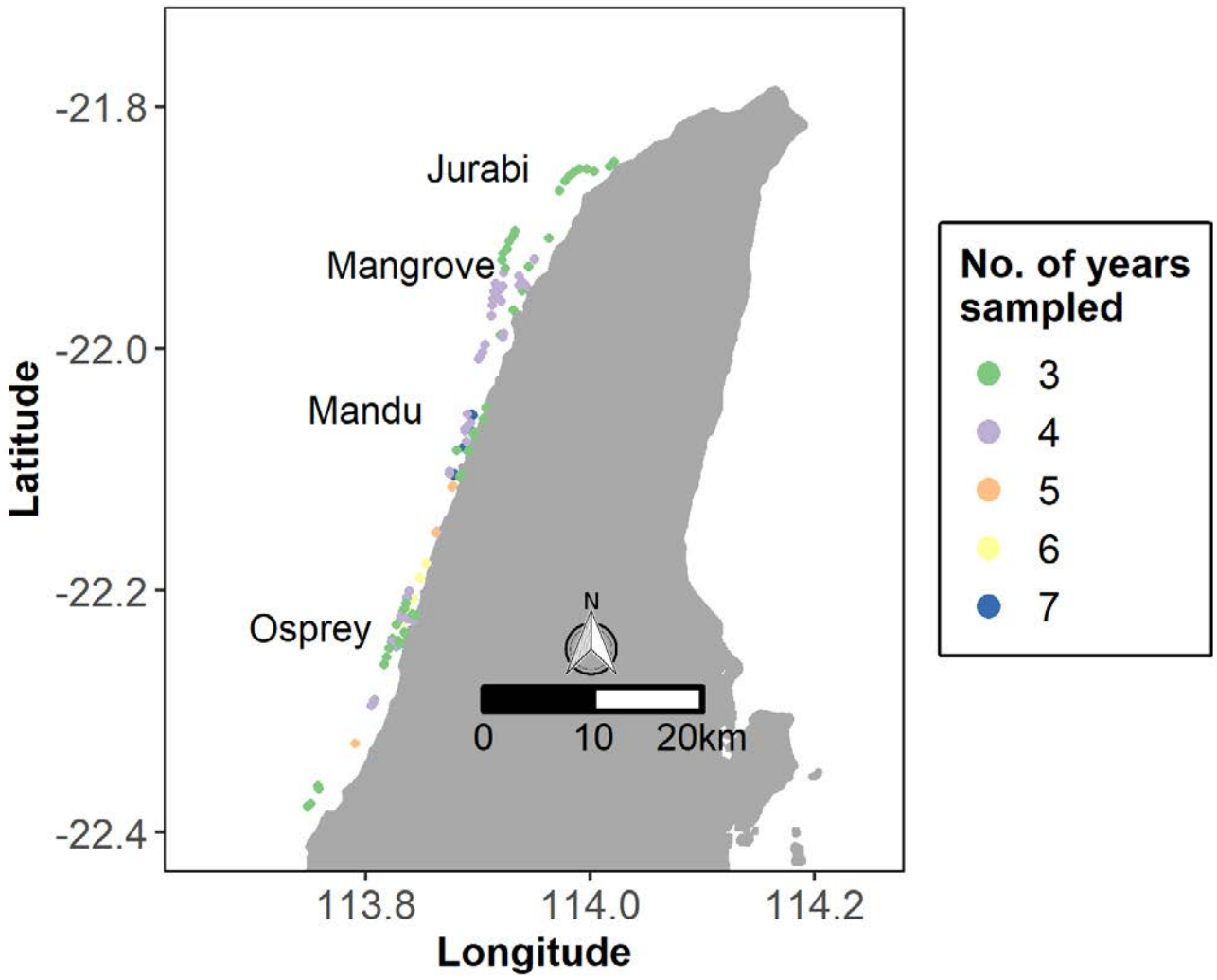
Analysis of trends in four major life-history groups using MARSS

Coral genera were assigned to one of four life-history groups based on the classifications described in Darling et al. (2012): competitive, stress-tolerant, weedy and generalist. Life-history traits were then inferred from the life-history classifications. In the two circumstances where genera contained species which were distributed between to two or more functional groups (i.e., *Acropora* and *Pocillopora*), the genera were assigned to the functional group of the most abundant species within that genus (i.e., *Acropora* = *Acropora spicifera* = Competitive functional group). Competitive corals typically have fast growth rates, reproduce by broadcast spawning and are most abundant at shallow depths. In shallow water, this group can quickly dominate available space. However, this group is also extremely sensitive to physical damage (Madin and Connolly 2006), coral bleaching-induced mortality (McClanahan et al. 2007), predation by crown-of-thorns starfish (De'ath et al. 2012) and *Drupella* spp., and coral disease. In the Indo-Pacific, this group includes the genera *Montipora*, *Pocillopora*, *Turbinaria* and some species of *Acropora*. Stress-tolerant corals typically have slow growth rates, reproduce by broadcast spawning, have high fecundity, form massive-shaped colonies and can attain a large maximum size. These traits are considered advantageous for survival in harsh environments (van Woesik et al. 2012). This group includes *Porites*, *Favia*, *Favites*, *Platygyra* and *Goniastrea* in the Indo-Pacific. **Weedy corals** typically have slow to moderate growth rates, reproduce by brooding larvae, have small colony sizes and are considered to opportunistically colonise recently disturbed habitats more so than other groups (Darling et al. 2012). In the Indo-Pacific, this group includes *Stylophora*, *Seriatopora*, *Leptastrea* and most species of *Pocillopora.* **Generalist corals** typically have moderate growth rates and can attain large maximum colony sizes. This group shares many of the traits exhibited by the other three groups and includes *Echinopora*, *Hydnophora*, *Montipora* and *Pachyseris* in the Indo-Pacific. Coral genera recorded in our

study that had not been assigned to a functional group in Darling et al. (2012) were assigned to one of the four life-history groups based on four of their documented life history traits (Madin et al. 2016), which were considered most important for predicting their response to disturbance: growth form, susceptibility to physical damage, susceptibility to bleaching and reproductive mode (Darling et al. 2012). The below figure shows the estimated annual change in percentage cover of the four life-history categories (± 95% CI) within inshore, reef flat and reef slope reef zones between 2007 and 2016. Solid symbols denote statistical significance ie. the 95% CI does not cross 0 so the annual trend is significant ($p < 0.05$). Significant trends were detected in three of the four life-history groups.



Location and number of years each of the 119 study sites were surveyed northern Ningaloo Reef, Western Australia between 2007 and 2016



Supplementary information to support Chapter 3

Table S1. Details and environmental predictors for the 15 sites where recruitment tiles were deployed between 2015 and 2017. DHW = Degree heating weeks, SST = Sea Surface Temperature.

Reef Name	Location	Depth (m)	Reef matrix	No. transects 2015	No. transects 2016	No. transects 2017	Mean recruits cm^{-2} 2015	Mean recruits cm^{-2} 2016	Mean recruits cm^{-2} 2017	Mean Turbidity 2015	Mean Turbidity 2016	Mean Turbidity 2017	Mean reef complexity	Dispersal model 2015	Dispersal model 2016	Dispersal model 2017	Mean coral cover (5 m)	Mean coral cover (200 m)	Mean coral cover (15 km)	Mean SST (Celsius)	Max DHW
Angel Is	Inshore	6	Volcanic	3	3	3	0.020	0.011	0.028	0.13	0.15	0.14	7.5	274	968	536	23.3	32.7	36.3	28.6	4.8
Eaglehawk Is	Mid-shore	7	Volcanic	6	3	6	0.003	0.002	0.002	0.15	0.17	0.17	7.5	98	216	637	16.7	10	10	28.7	5.3
East Lewis North	Inshore	8	Volcanic	6	3	6	0.055	0.041	0.252	0.17	0.17	0.18	7.9	266	84	533	38.3	41.1	37.4	28.7	4.9
East Lewis South	Inshore	4	Volcanic	6	3	6	0.005	0.015	na	0.08	0.07	0.06	9	249	69	220	5	10.2	27	28.6	4.4
Enderby Is	Mid-shore	4	Volcanic	6	3	6	0.008	0.007	0.008	0.12	0.14	0.12	8.3	390	310	459	16.7	18.7	13	28.7	4.2
Gidley Is	Inshore	6	Volcanic	6	3	6	0.008	0.034	0.045	0.12	0.14	0.12	8.3	94	395	495	33.3	38.3	36.3	28.6	3.4
Goodwyn Is	Mid-shore	7	Limestone	3	3	3	0.001	0.003	0.021	0.09	0.11	0.09	9.5	448	169	460	18.3	26.7	13.3	28.6	2.8
Hamersley Shoal	Offshore	5	Limestone	3	3	3	0.038	na	0.050	0.08	0.09	0.08	9.4	824	807	712	10	9.33	10	28.7	2.4
Kendrew Is	Offshore	9	Limestone	3	3	3	0.002	0.015	0.020	0.08	0.09	0.08	7	81	183	248	6.33	4.73	13	28.5	2.2
Legendre Is	Offshore	6	Limestone	3	3	3	na	0.017	0.040	0.08	0.09	0.08	7	775	729	879	15	11.2	14	28.8	2.3
NE Regnard Is	Mid-shore	6	Limestone	3	3	3	0.002	0.003	0.005	0.18	0.20	0.19	5.5	239	384	304	15	19	17.7	28.7	7.4
Nelson Rocks	Offshore	4	Limestone	3	3	3	na	0.039	0.004	0.10	0.10	0.09	9.7	448	942	512	5	3.9	3.9	28.7	2.3
Regnard Is	Inshore	4	Limestone	3	3	3	0.005	0.000	na	0.37	0.35	0.32	5.5	354	1098	1079	10	25.9	26	28.6	4
Rosemary Is	Offshore	9	Limestone	6	3	6	0.004	0.061	0.031	0.10	0.11	0.09	7.5	372	554	558	5	3.52	13	28.6	2.5
Whittaker Is	Mid-shore	6	Volcanic	3	3	3	0.070	0.086	0.273	0.14	0.15	0.13	5.5	435	899	652	33.3	45.3	37.3	28.7	4

Table S2. Predictor variables included in analysis of coral recruitment in the Dampier Archipelago, Western Australia. All variables were tested for their predictive capability of total recruitment and recruitment of spawners, brooders, Acroporidae, Poritidae, Pocilloporidae and Merulinidae. SST = Sea surface temperature, DHW = Degree heating weeks. References cited: (1) Feng et al. (2016), (2) Boschetti et al. (2019), (3) Vermeij (2005), (4) Hughes et al. (2000), (5) Carleton and Sammarco (1987) (6) Babcock and Davies (1991), (7) Humanes et al. (2017), (8) Evans et al. (2020), (9) Hughes et al. (2019), (10) Baird et al. (2011), (11) Gilmour et al. (2016), (12) Mundy and Babcock (1998), (13) Williams et al. (2018), (14) Harrison and Wallace (1990), (15) Doropoulos et al. (2016), (16) Harrington et al. (2004)

Variable/ Scale/ Transformation	Description	Justification
Dispersal model/ mesoscale/ sqrt	Predictions of the total number of coral larvae arriving at each location. Predictions are based on the larval dispersal model (1 x 1 km resolution) for the Pilbara region (see 1 for details)	Hydrodynamic connectivity influences rates of coral recruitment. Model predictions incorporated large (100 km) and fine scale (1 km) hydrodynamics observed during the autumn mass spawning period each year (March) and provide a relative estimate of total recruitment (1,2).
Percent hard coral (15km)/ mesoscale	Annual estimate of percent coral cover within 15 km of recruitment tiles. Estimates were based on the average coral cover recorded in all 50 m photographic line transects located within 15 km of the recruitment tiles	A positive relationship between adult coral cover and recruit density might be expected if coral larvae settle within 15 km of their parent colonies (3,4)
Percent spawners (15 km) / mesoscale/ sqrt	Annual estimate of percent cover of broadcast spawning corals within 15 km of recruitment tiles. Estimates were based on the average coral cover recorded in all 50 m photographic line transects located within 15 km of the recruitment tiles	A positive relationship between cover of spawning corals and recruit density might be expected if larvae of spawning corals settle within 15 km of their parent colonies (3,4)
Percent brooders (15 km)/ mesoscale	Annual estimate of percent cover of brooding corals within 15 km of recruitment tiles. Estimates were based on the average coral cover recorded in all 50 m photographic line transects located within 15 km of the recruitment tiles	A positive relationship between cover of brooding corals and recruit density might be expected if brooded larvae settle within 15 km of their parent colonies (3,4)
Mean KD490)/ local scale	MODIS diffuse attenuation coefficient at 490 nm. Higher KD490 values reflect high turbidity, lower water clarity and more rapid attenuation of light with increasing depth. A KD490 value of 0.1 equates to an attenuation depth of 10m.	High water turbidity and rates of sedimentation can reduce rates of coral settlement, metamorphosis and early survivorship (5,6,7,8)
Mean SST/ local scale	Mean SST in the 6 months prior to spawning NOAA Dataset ID: dhw_5km	Heat stress can negatively impact coral fecundity and rates of coral recruitment (9)

Variable/ Scale/ Transformation	Description	Justification
Percent hard coral (5 m)/ local scale/ sqrt	Visual estimates of percent coral cover were obtained from high resolution photographic mosaics of the substrate. (10m x 10m).	Adult conspecifics can act as natural settlement inducers in a range of sessile benthic taxa including corals (3,4,5).
Percent hard coral (200 m)/ local scale/ sqrt	Annual estimate of percent coral cover within 200 m of recruitment tiles. Percent coral cover was calculated using mean coral cover from 3 (2016) or 6 (2015, 2017) 50 m photographic line transects along the same depth contour as the recruitment tiles	A positive relationship between adult coral cover and recruit density might be expected if larvae settle within 200m of their parent colonies (3,4)
Percent spawners (200m) / local scale/ log(x+1)	Annual estimate of percent cover of broadcast spawning corals within 200 m of recruitment tiles. Estimates were based on the average coral cover recorded in 3 (2016) or 6 (2015, 2017) 50 m photographic line transects along the same depth contour as the recruitment tiles	Approximately 60% of all corals in Dampier Archipelago are broadcast spawning corals which release larvae in autumn (March – April) (10,11). A positive relationship between cover of spawning corals and recruit density might be expected if larvae settle within 200 m of their parent colonies (3,4)
Percent brooders (200 m)/ local scale/ log(x+1)	Annual estimate of percent cover of broadcast spawning corals within 200 m of recruitment tiles. Estimates were based on the average coral cover recorded in 3 (2016) or 6 (2015, 2017) 50 m photographic line transects along the same depth contour as the recruitment tiles	Approximately 40% of all corals in Dampier Archipelago are brooding corals which release larvae year-round (January - November) (10,11). A positive relationship between cover of brooding corals and recruit density might be expected if brooded larvae settle within 200 m of their parent colonies (3,4)
Depth/ local scale	Depth of site (m)	Light quality and quantity changes with depth and these changes can influence coral settlement orientation, growth and survivorship (12,13)
Max DHW/ local; scale/ sqrt	Maximum DHW in the 6 months prior to spawning NOAA Dataset ID: dhw_5km	Heat stress can negatively impact coral fecundity and rates of coral recruitment (9)
Reef complexity/ local scale	Reef complexity measured using a 10 m length of chain. Estimates represent site averages for the same depth as the recruitment tiles. Lower values represent a higher reef complexity and proportion of uneven surfaces	Increased reef complexity provides a greater microhabitat complexity (exposed and crevice microhabitats) which can influence rates of coral settlement and early survival (15,16)
Reef matrix/ local scale	Classification of underlying reef matrix as either limestone ($CaCO_3$) or volcanic based on the predominant rock type observed by divers.	Substrate type can influence rates of coral settlement and early survival (14,16)

Table S3. PERMANOVA statistics for differences in mean density of recruits between year, reef and year × reef.

All families

Source	df	SS	MS	Pseudo-F	P(perm)	perms
Year	2	16077	8038.7	9.6362	0.001	997
Reef	14	2.9403E+05	21002	25.176	0.001	997
Year x Reef**	23	10038	2331.7	2.7951	0.067	998
Res	399	3.3285E+05	834.22			

Table S4. Friedman rank test for differences in rank order of reefs between years (data = mean density of recruits per reef)

Q (Observed value)	4.909
Q (Critical value)	5.991
DF	2
p-value (one-tailed)	0.086
alpha	0.05

Table S5. PERMANOVA and pairwise post-hoc test statistics for differences in the mean density of recruits among years 2015, 2016 and 2017 for all coral groups. Asterisks denote significance at p < 0.05.

Group	SS	MS	Pseudo-F	P(perm)	Unique perms
Total	182.41	91.205	45.358	0.001*	998
Spawners	191.38	95.688	48.29	0.001*	999
Brooders	1.6372	0.81862	10.359	0.001*	994
Acroporidae	181.66	90.83	52.995	0.001*	999
Merulinidae	10.41	5.205	21.024	0.001*	999
Pocilloporidae	0.77327	0.38664	15.922	0.001*	631
Poritidae	0.23974	0.11987	2.1019	0.12	993

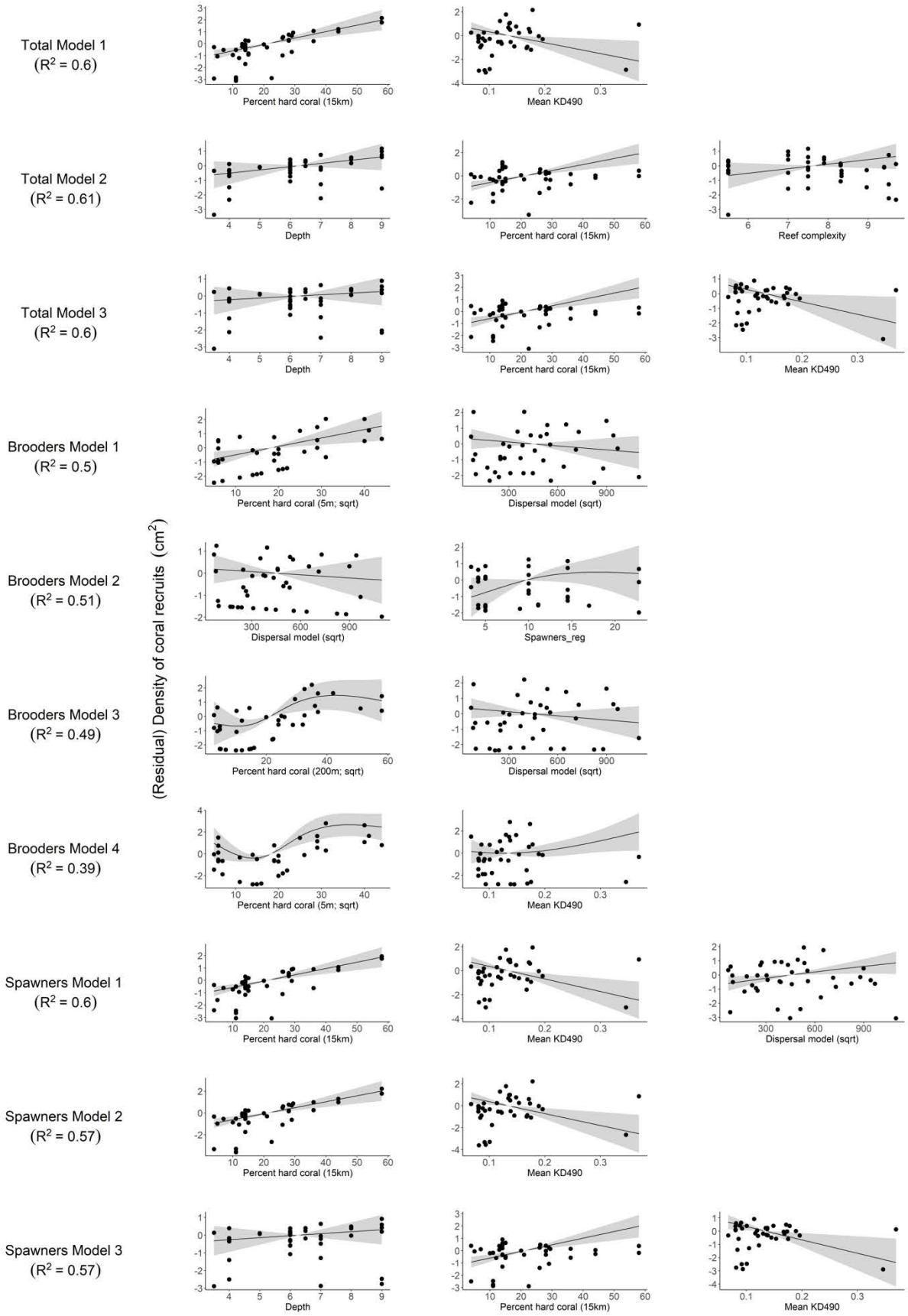
	Groups	t	P(perm)	Unique perms
Total	2015 < 2016	3.695	0.001*	999
	2015 < 2017	8.5668	0.001*	996
	2016 < 2017	5.9844	0.001*	998
Spawners	2015 < 2016	3.2652	0.003	996
	2015 < 2017	8.7011	0.001*	999
	2016 < 2017	6.4735	0.001*	996
Brooders	2015 < 2016	4.0036	0.001*	552
	2015 = 2017	1.0489	0.285	104
	2016 > 2017	3.101	0.001*	572
Acroporidae	2015 < 2016	3.7626	0.001*	996
	2015 < 2017	9.1731	0.001*	998
	2016 < 2017	6.6042	0.001*	998
Merulinidae	2015 > 2016	0.3761	0.684	796
	2015 < 2017	4.8039	0.001*	999
	2016 < 2017	5.1718	0.001*	997
Pocilloporidae	2015 < 2016	4.3874	0.001*	69
	2015 < 2017	0.6864	0.734	9
	2016 > 2017	3.985	0.001*	76

Table S6. Best generalised additive mixed models (GAMMs) for predicting recruitment density between 2015 and 2017 in the Dampier Archipelago, Western Australia. edf = estimated degrees of freedom. Only the top models for each response are reported.

Response	Model	ΔAICc	AICc Weight	R^2	edf
Total recruits	Percent hard coral (15km) + Turbidity	0.00	0.40	0.60	13.97
	Depth + Percent hard coral (15km) + Reef complexity	0.79	0.27	0.61	14.9
	Depth + Percent hard coral (15km) + Turbidity	1.05	0.24	0.60	14.35
Brooders	Percent hard coral (5m) + Turbidity	0	0.17	0.5	17.9
Spawners	Percent hard coral (15km) + Turbidity + Dispersal model	0.00	0.39	0.6	13.99
	Percent hard coral (15km) + Turbidity	0.82	0.26	0.57	14
	Depth + Percent hard coral (15km) + Turbidity	1.54	0.17	0.57	14.37
Acroporidae	Percent hard coral (15km) + Turbidity + Dispersal model	0	0.88	0.57	13.5
Poritidae	Percent hard coral (5m) + Turbidity + Dispersal model	0	0.87	0.42	12.02
Merulinidae	Percent hard coral (15km) + Reef complexity	0	0.47	0.38	6.71
	Depth + Percent hard coral (15km) + Reef complexity	1.59	1.21	0.40	7.72
Pocilloporidae	Depth + Percent hard coral (5m)	0.00	0.30	0.28	0.00
	Depth + Percent hard coral (5m) + MaxDHW	0.07	0.29	0.29	0.07
	Depth + Percent hard coral (5m) + MeanSST	0.16	0.28	0.29	0.16

Table S7. To test the sensitivity of the relationship between turbidity (KD490) and recruitment to outliers we re-ran the GAMM analysis with the two outlying turbidity data points removed. The removal of outliers resulted in turbidity no longer being included as a variable in any of the seven top models. Below we show the best generalised additive mixed models (GAMMs) for total recruitment, spawners and brooders at 15 reefs within the Dampier Archipelago between 2015 and 2017 with turbidity outliers removed. Refer to Methods section for definitions of each predictor variable (x-axis).

Response	Model	ΔAICc	AICc Weight	R^2	edf
Total recruits	Percent hard coral (15km) + Dispersal model	0	0.23	0.65	13.02
	MaxDHW	0.90	0.15	0.49	14.41
	MaxDHW + Reef complexity	1.77	0.10	0.49	14.65
Brooders	Percent hard coral (5m)	0	0.30	0.42	6.63
	Depth + Percent hard coral (5m)	1.66	0.13	0.42	8.34
Spawners	Percent hard coral (15km) + Dispersal model	0	0.25	0.64	12.92
	maxDHW	1.40	0.12	0.48	14.39
	Percent hard coral (15km) + Dispersal model + Reef complexity	1.85	0.10	0.64	13.47
Acroporidae	Depth + Dispersal model	0	0.68	0.49	8.15
Merulinidae	Percent hard coral (5m) + Reef complexity	0	0.47	0.65	6.65
	Percent hard coral (5m) + maxDHW + Reef complexity	1.72	0.20	0.39	7.35
Pocilloporidae	Depth + Percent hard coral (5m) + meanSST	0	0.61	0.29	7.25
	Depth + Percent hard coral (5m)	0.87	0.28	0.30	7.16
	Depth + Percent hard coral (5m) + maxDHW	1.20	0.24	0.30	8.06
Poritidae	Percent hard coral (15km) + Dispersal model	0.00	0.65	0.53	11.12
	Depth + Percent hard coral (5m) + Dispersal model	1.24	0.35	0.46	10.48


Total Model 1
(R^2 = 0.6)
Percent hard coral (15km)
Mean KD490
Total Model 2
(R^2 = 0.61)
Depth
Percent hard coral (15km)
Reef complexity
Total Model 3
(R^2 = 0.6)
Depth
Percent hard coral (15km)
Mean KD490
Brooders Model 1
(R^2 = 0.5)
Percent hard coral (5m; sqrt)
Dispersal model (sqrt)
Brooders Model 2
(R^2 = 0.51)
Dispersal model (sqrt)
Spawners_reg
Brooders Model 3
(R^2 = 0.49)
Percent hard coral (200m; sqrt)
Dispersal model (sqrt)
Brooders Model 4
(R^2 = 0.39)
Percent hard coral (5m; sqrt)
Mean KD490
Spawners Model 1
(R^2 = 0.6)
Percent hard coral (15km)
Mean KD490
Dispersal model (sqrt)
Spawners Model 2
(R^2 = 0.57)
Percent hard coral (15km)
Mean KD490
Spawners Model 3
(R^2 = 0.57)
Depth
Percent hard coral (15km)
Mean KD490
(Residual) Density of coral recruits (cm^2)

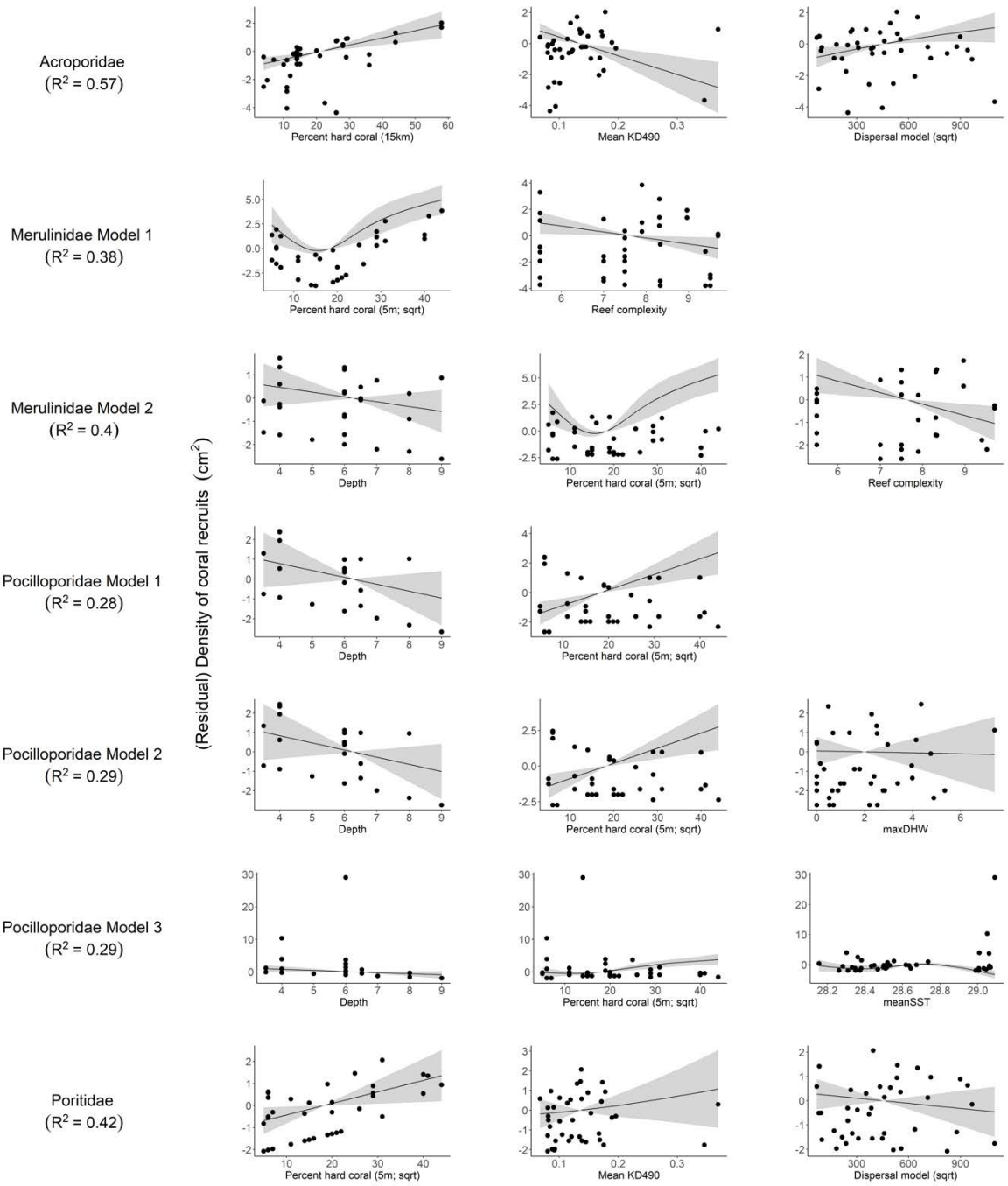


Figure S1. Best generalised additive mixed models (GAMMs) within 2 ΔAICc of the top model for coral recruitment at 15 sites within the Dampier Archipelago between 2015 and 2017 (x-axis). Three models are presented for total coral recruits (rows 1–3), four models for brooding corals (rows 4–7), three models for spawning corals (rows 8–10), one model for Acroporidae (row 11), two models for Merulinidae (rows 12–13), three models for Pocillloporidae (rows 14–16) and one row for Poritidae (row 17).

Spatial and temporal patterns in coral recruitment, coral cover and reef complexity.

Spatial variation in recruitment, coral cover and reef complexity within the Dampier Archipelago was high, with mean recruit densities at Whittaker Island (0.07–0.27 cm^{-2}) and East Lewis North (0.04–0.25 cm^{-2}) approximately 60 times greater than recruit densities observed at Eaglehawk Island (0.002–0.003 cm^{-2}), Regnard Island (0.0002–0.005 cm^{-2}), NE Regnard Island (0.002–0.005 cm^{-2}) and Enderby island (0.007–0.008 cm^{-2}). Reefs with high recruit densities (predominantly in the north-eastern region of the Dampier Archipelago) coincided with locations where live coral cover was greater than 35% and reef complexity was moderate. In comparison, reefs with low recruit densities (predominantly in the south-western region of the Dampier Archipelago) were generally located where coral cover was less than 20%, reef complexity was high and water turbidity was high. The high spatial variation in recruitment, coral cover and reef complexity we observed is likely due to strong cross-shelf gradients in oceanographic currents, turbidity, wave exposure and ocean temperatures throughout the region (CALM 1994; Moustaka et al. 2019.

Temporal variation in recruit densities within the Dampier Archipelago was high with mean recruit densities increasing by 375% between 2015 to 2017. Despite differences in recruitment among years, the spatial variation in relative rates of recruitment among reefs was consistent (i.e., the rank order of reefs was similar among years). The relatively high recruitment at Whittaker Island (mean = 0.07–0.27 cm^{-2}) and East Lewis North (mean = 0.04–0.25 cm^{-2}), combined with high cover of coral (mean >33%) at these reefs, suggests these reefs are likely to be both sources and sinks of coral larvae for some taxa. In comparison, Regnard (mean = 0.0002–0.005 cm^{-2}), North East Regnard (mean = 0.002–0.005 cm^{-2}) and Eaglehawk Islands (mean = 0.002–0.003 cm^{-2}) had consistently low recruitment in all years and low coral cover (mean <25%), suggesting a limited role as a source and/or sink of coral larvae during the study period.

The relative contributions of the different coral taxa to total recruitment were broadly similar among reefs (Acroporidae: mean = 73%, Poritidae: mean = 5%, Merulinidae: mean = 6%, Pocilloporidae: mean = 1%, Isopora: mean = 3%: Figure 1). The only exceptions to this were Acroporidae recruits, which constituted a greater proportion of total recruitment offshore than inshore reefs, and,

conversely, Merilinudae recruits, which were proportionally more abundant at inshore locations (Figure 1). The consistent spatial patterns between recruitment, adult abundance and environmental variables (e.g., reef complexity and water turbidity) observed here provide a better understanding reef-wide persistence and resilience within the Dampier Archipelago which can be used to help prioritise management areas among reefs within the region.

Table S7. Southen Oscillation Index (SOI) values between January 2015 and Dec 2017. SOI data were donwnloaded from: http://www.bom.gov.au/climate/current/soihtm1.shtml

Year	Jan	Feb	Mar	April	May	June	July	Aug	Sept	Oct	Nov	Dec	-SOI months
2017	1.3	-2.2	5.1	-6.3	0.5	-10.4	8.1	3.3	6.9	9.1	11.8	-1.4	4
2016	-19.7	-19.7	-4.7	-22.0	2.8	5.8	4.2	5.3	13.5	-4.3	-0.7	2.6	6
2015	-7.8	0.6	-11.2	-3.8	-13.7	-12.0	-14.7	-19.8	-17.8	-20.2	-5.3	-9.1	11

Supplementary information to support Chapter 4

Table S1. Summary of historical scientific surveys of fish assemblages at Ningaloo Reef (1987 – 2019) AIMS = Australian Institute Marine Science, CSIRO = Commonwealth Industrial and Scientific Research Organisation, RLS = Reef Life Survey, DBCA = Department Biodiversity, Conservation and Attractions, UWA = University Western Australia

Custodian	Year	Method	Reef region	Reef_Zone	Area/time surveyed	Reference
AIMS	1993	UVC-short	Cloates	Back reef	3000m2	Depczynski *et al.*, 2015
AIMS	1993	UVC-short	Maud	Back reef	2250m2	
AIMS	1993	UVC-short	Osprey	Back reef	3000m2	
AIMS	1993	UVC-short	Cloates	Reef slope	3000m2	
AIMS	1993	UVC-short	Osprey	Reef slope	3000m2	
AIMS	1998	UVC-short	Cloates	Back reef	2000m2	
AIMS	1998	UVC-short	Mandu	Back reef	2250m2	
AIMS	1998	UVC-short	Maud	Back reef	2250m2	
AIMS	1998	UVC-short	Osprey	Back reef	2250m2	
AIMS	2014	UVC-short	Cloates	Back reef	15000m2	
AIMS	2014	UVC-short	Maud	Back reef	7500m2	
AIMS	2014	UVC-short	Pelican	Back reef	7500m2	
AIMS	2014	UVC-short	Cloates	Lagoon	6000m2	
AIMS	2014	UVC-short	Mangrove	Lagoon	4500m2	
AIMS	2014	UVC-short	Maud	Lagoon	6000m2	
AIMS	2014	UVC-short	Pelican	Lagoon	7500m2	
AIMS	2014	UVC-short	Tantabiddi	Lagoon	3750m2	
Ayling	1987	UVC-long	Osprey	Back reef	35000m2	Ayling & Ayling, 1987
Ayling	1987	UVC-long	Osprey	Lagoon	25000m2	
Ben Fitzpatrick	2006	BRUV	Mandu	Back reef	1020min	Fitzpatrick *et al.*, 2015
Ben Fitzpatrick	2006	BRUV	Mandu	Back reef	1020min	
Ben Fitzpatrick	2006	BRUV	Osprey	Back reef	660min	
Ben Fitzpatrick	2006	BRUV	Osprey	Back reef	720min	
Ben Fitzpatrick	2006	BRUV	Osprey	Lagoon	720min	
Ben Fitzpatrick	2006	BRUV	Mandu	Reef Flat	1020min	
Ben Fitzpatrick	2006	BRUV	Mandu	Reef Flat	1080min	
Ben Fitzpatrick	2006	DOV	Mandu	Back reef	2500m2	
Ben Fitzpatrick	2006	DOV	Mandu	Back reef	2500m2	
Ben Fitzpatrick	2006	DOV	Osprey	Back reef	3750m2	
Ben Fitzpatrick	2006	DOV	Osprey	Back reef	3750m2	
Ben Fitzpatrick	2006	DOV	Osprey	Lagoon	2500m2	
Ben Fitzpatrick	2006	DOV	Osprey	Lagoon	2500m2	
Ben Fitzpatrick	2006	DOV	Mandu	Reef Flat	2500m2	
Ben Fitzpatrick	2006	DOV	Mandu	Reef Flat	2500m2	

Custodian	Year	Method	Reef region	Reef_Zone	Area/time surveyed	Reference
Ben Fitzpatrick	2007	BRUV	Mandu	Back reef	1080min	
Ben Fitzpatrick	2007	BRUV	Mandu	Back reef	1080min	
Ben Fitzpatrick	2007	BRUV	Osprey	Back reef	660min	
Ben Fitzpatrick	2007	BRUV	Osprey	Back reef	720min	
Ben Fitzpatrick	2007	BRUV	Osprey	Lagoon	600min	
Ben Fitzpatrick	2007	BRUV	Osprey	Lagoon	720min	
Ben Fitzpatrick	2007	BRUV	Mandu	Reef Flat	900min	
Ben Fitzpatrick	2007	BRUV	Mandu	Reef Flat	960min	
Ben Fitzpatrick	2007	DOV	Mandu	Back reef	2500m2	
Ben Fitzpatrick	2007	DOV	Mandu	Back reef	2500m2	
Ben Fitzpatrick	2007	DOV	Osprey	Back reef	3750m2	
Ben Fitzpatrick	2007	DOV	Osprey	Back reef	3750m2	
Ben Fitzpatrick	2007	DOV	Osprey	Lagoon	2500m2	
Ben Fitzpatrick	2007	DOV	Osprey	Lagoon	2500m2	
Ben Fitzpatrick	2007	DOV	Mandu	Reef Flat	2500m2	
Ben Fitzpatrick	2007	DOV	Mandu	Reef Flat	2500m2	
CSIRO	2006	UVC-long	Cloates	Back reef	17000m2	Babcock *et al.*, 2008, 2018
CSIRO	2006	UVC-long	Mandu	Back reef	19000m2	
CSIRO	2006	UVC-long	Pelican	Back reef	13000m2	
CSIRO	2006	UVC-long	Cloates	Lagoon	19000m2	
CSIRO	2006	UVC-long	Mangrove	Lagoon	10000m2	
CSIRO	2006	UVC-long	Mangrove	Lagoon	4000m2	
CSIRO	2006	UVC-long	Mandu	Reef Flat	32000m2	
CSIRO	2006	UVC-long	Mangrove	Reef Flat	11000m2	
CSIRO	2006	UVC-long	Maud	Reef Flat	5000m2	
CSIRO	2006	UVC-long	Osprey	Reef Flat	27000m2	
CSIRO	2006	UVC-long	Pelican	Reef Flat	9000m2	
CSIRO	2006	UVC-long	Lighthouse	Reef slope	31000m2	
CSIRO	2006	UVC-long	Mandu	Reef slope	26000m2	
CSIRO	2006	UVC-long	Osprey	Reef slope	18000m2	
CSIRO	2006	UVC-long	Pelican	Reef slope	23000m2	
CSIRO	2007	UVC-long	Cloates	Back reef	15000m2	
CSIRO	2007	UVC-long	Mandu	Back reef	17000m2	
CSIRO	2007	UVC-long	Cloates	Lagoon	12000m2	
CSIRO	2007	UVC-long	Mangrove	Lagoon	8000m2	
CSIRO	2007	UVC-long	Mangrove	Lagoon	4000m2	
CSIRO	2007	UVC-long	Mandu	Reef Flat	37000m2	
CSIRO	2007	UVC-long	Mangrove	Reef Flat	9000m2	
CSIRO	2007	UVC-long	Maud	Reef Flat	10000m2	
CSIRO	2007	UVC-long	Osprey	Reef Flat	17000m2	
CSIRO	2007	UVC-long	Lighthouse	Reef slope	33000m2	
CSIRO	2007	UVC-long	Mandu	Reef slope	22000m2	
CSIRO	2007	UVC-long	Osprey	Reef slope	9000m2	

Custodian	Year	Method	Reef region	Reef_Zone	Area/time surveyed	Reference
CSIRO	2007	UVC-short	Mandu	Reef flat	7200m2	
CSIRO	2007	UVC-short	Maud	Reef flat	7200m2	
CSIRO	2007	UVC-short	Osprey	Reef flat	7200m2	
CSIRO	2009	UVC-short	Mandu	Reef flat	6000m2	
CSIRO	2010	UVC-short	Mandu	Reef flat	6000m2	
CSIRO	2012	UVC-short	Mandu	Reef flat	6000m2	
CSIRO	2013	UVC-long	Jurabi	Reef slope	14000m2	Vanderklift et al. 2020
CSIRO	2013	UVC-long	Mandu	Reef slope	35000m2	
CSIRO	2013	UVC-long	Osprey	Reef slope	30000m2	
CSIRO	2013	UVC-short	Mangrove	Back reef	2250m2	
CSIRO	2013	UVC-short	Maud	Back reef	2625m2	
CSIRO	2013	UVC-short	Cloates	Reef Flat	6000m2	
CSIRO	2013	UVC-short	Mandu	Reef Flat	6000m2	
CSIRO	2013	UVC-short	Mangrove	Reef Flat	2250m2	
CSIRO	2013	UVC-short	Maud	Reef Flat	3375m2	
CSIRO	2013	UVC-short	Osprey	Reef Flat	6000m2	
CSIRO	2014	UVC-short	Mandu	Reef Flat	6000m2	
CSIRO	2014	UVC-short	Mandu	Reef Flat	6000m2	
CSIRO	2014	UVC-short	Osprey	Reef Flat	6000m2	
CSIRO	2015	UVC-short	Mandu	Reef Flat	6000m2	
CSIRO	2015	UVC-short	Mandu	Reef Flat	5875m2	
CSIRO	2015	UVC-long	Jurabi	Lagoon	4000m2	
CSIRO	2015	UVC-long	Mangrove	Lagoon	8000m2	
CSIRO	2015	UVC-long	Osprey	Reef flat	4000m2	
CSIRO	2015	UVC-long	Jurabi	Reef slope	5000m2	
CSIRO	2015	UVC-long	Jurabi	Reef slope	4000m2	
CSIRO	2015	UVC-long	Osprey	Reef slope	13000m2	
CSIRO	2015	UVC-short	Jurabi	Lagoon	500m2	
CSIRO	2015	UVC-short	Mangrove	Lagoon	1000m2	
CSIRO	2015	UVC-short	Osprey	Reef flat	500m2	
CSIRO	2015	UVC-short	Jurabi	Reef slope	625m2	
CSIRO	2015	UVC-short	Jurabi	Reef slope	500m2	
CSIRO	2015	UVC-short	Osprey	Reef slope	1625m2	
CSIRO	2016	UVC-short	Mandu	Reef flat	5250m2	
CSIRO	2016	UVC-short	Mandu	Reef Flat	750m2	
CSIRO	2016	UVC-short	Mandu	Reef flat	1500m2	
CSIRO	2016	UVC-long	Mangrove	Lagoon	8000m2	
CSIRO	2016	UVC-long	Osprey	Reef flat	3000m2	
CSIRO	2016	UVC-long	Jurabi	Reef slope	5000m2	
CSIRO	2016	UVC-long	Jurabi	Reef slope	1000m2	
CSIRO	2016	UVC-long	Osprey	Reef slope	10000m2	
CSIRO	2016	UVC-short	Mangrove	Lagoon	1000m2	
CSIRO	2016	UVC-short	Osprey	Reef flat	375m2	

Custodian	Year	Method	Reef region	Reef_Zone	Area/time surveyed	Reference
CSIRO	2016	UVC-short	Jurabi	Reef slope	625m2	
CSIRO	2016	UVC-short	Jurabi	Reef slope	125m2	
CSIRO	2016	UVC-short	Osprey	Reef slope	1250m2	
CSIRO	2017	UVC-short	Mandu	Reef flat	1375m2	
CSIRO	2017	UVC-short	Mandu	Reef Flat	375m2	
CSIRO	2017	UVC-long	Mangrove	Lagoon	8000m2	
CSIRO	2017	UVC-long	Osprey	Reef flat	4000m2	
CSIRO	2017	UVC-long	Jurabi	Reef slope	5000m2	
CSIRO	2017	UVC-long	Jurabi	Reef slope	2000m2	
CSIRO	2017	UVC-long	Osprey	Reef slope	13000m2	
CSIRO	2017	UVC-short	Mangrove	Lagoon	875m2	
CSIRO	2017	UVC-short	Osprey	Reef flat	500m2	
CSIRO	2017	UVC-short	Jurabi	Reef slope	625m2	
CSIRO	2017	UVC-short	Jurabi	Reef slope	250m2	
CSIRO	2017	UVC-short	Osprey	Reef slope	1625m2	
CSIRO	2018	UVC-long	Mangrove	Lagoon	8000m2	
CSIRO	2018	UVC-long	Osprey	Reef flat	4000m2	
CSIRO	2018	UVC-long	Jurabi	Reef slope	5000m2	
CSIRO	2018	UVC-long	Jurabi	Reef slope	2000m2	
CSIRO	2018	UVC-long	Osprey	Reef slope	13000m2	
CSIRO	2018	UVC-short	Mangrove	Lagoon	875m2	
CSIRO	2018	UVC-short	Osprey	Reef flat	500m2	
CSIRO	2018	UVC-short	Jurabi	Reef slope	625m2	
CSIRO	2018	UVC-short	Jurabi	Reef slope	250m2	
CSIRO	2018	UVC-short	Osprey	Reef slope	1625m2	
CSIRO	2019	UVC-long	Mangrove	Lagoon	8000m2	
CSIRO	2019	UVC-long	Osprey	Reef flat	4000m2	
CSIRO	2019	UVC-long	Jurabi	Reef slope	5000m2	
CSIRO	2019	UVC-long	Jurabi	Reef slope	2000m2	
CSIRO	2019	UVC-long	Osprey	Reef slope	13000m2	
CSIRO	2019	UVC-short	Mangrove	Lagoon	875m2	
CSIRO	2019	UVC-short	Osprey	Reef flat	500m2	
CSIRO	2019	UVC-short	Jurabi	Reef slope	625m2	
CSIRO	2019	UVC-short	Jurabi	Reef slope	250m2	
CSIRO	2019	UVC-short	Osprey	Reef slope	1625m2	
DBCA	2009	UVC-short	Mandu	Reef flat	5625m2	Wilson *et al.*, 2012; Holmes *et al.*, 2013; Wilson *et al.*, 2018
DBCA	2010	DOV	Maud	Lagoon	3000m2	
DBCA	2010	DOV	Tantabiddi	Lagoon	3000m2	
DBCA	2010	DOV	Lighthouse	Reef slope	1875m2	
DBCA	2010	UVC-long	Jurabi	Lagoon	3000m2	
DBCA	2010	UVC-long	Mandu	Lagoon	3000m2	

Custodian	Year	Method	Reef region	Reef_Zone	Area/time surveyed	Reference
DBCA	2010	UVC-long	Mangrove	Lagoon	3000m2	
DBCA	2010	UVC-long	Jurabi	Lagoon	3000m2	
DBCA	2010	UVC-long	Mandu	Lagoon	3000m2	
DBCA	2010	UVC-long	Mangrove	Lagoon	3000m2	
DBCA	2011	DOV	Cloates	Back reef	3000m2	
DBCA	2011	DOV	Mangrove	Back reef	3000m2	
DBCA	2011	DOV	Maud	Back reef	3000m2	
DBCA	2011	DOV	Osprey	Back reef	3000m2	
DBCA	2011	DOV	Pelican	Back reef	3000m2	
DBCA	2011	DOV	Mangrove	Lagoon	2750m2	
DBCA	2011	DOV	Maud	Lagoon	3000m2	
DBCA	2011	DOV	Tantabiddi	Lagoon	3000m2	
DBCA	2011	DOV	Lighthouse	Reef slope	3000m2	
DBCA	2013	DOV	Mangrove	Back reef	3000m2	
DBCA	2013	DOV	Tantabiddi	Lagoon	3000m2	
DBCA	2013	UVC-short	Cloates	Back reef	2700m2	Wilson et al., 2014
DBCA	2013	UVC-short	Mandu	Back reef	4050m2	
DBCA	2013	UVC-short	Mangrove	Back reef	2700m2	
DBCA	2013	UVC-short	Mangrove	Back reef	2700m2	
DBCA	2013	UVC-short	Maud	Back reef	5400m2	
DBCA	2013	UVC-short	Maud	Back reef	5400m2	
DBCA	2013	UVC-short	Pelican	Back reef	5400m2	
DBCA	2013	UVC-short	Pelican	Back reef	5400m2	
DBCA	2013	UVC-short	Cloates	Lagoon	6750m2	
DBCA	2013	UVC-short	Mangrove	Lagoon	5400m2	
DBCA	2013	UVC-short	Mangrove	Lagoon	5400m2	
DBCA	2013	UVC-short	Maud	Lagoon	6750m2	
DBCA	2013	UVC-short	Maud	Lagoon	6750m2	
DBCA	2013	UVC-short	Pelican	Lagoon	8100m2	
DBCA	2013	UVC-short	Pelican	Lagoon	8100m2	
DBCA	2014	DOV	Cloates	Back reef	10500m2	Wilson *et al.*, 2012; Holmes *et al.*, 2013; Wilson *et al.*, 2018
DBCA	2014	DOV	Mandu	Back reef	4500m2	
DBCA	2014	DOV	Mangrove	Back reef	4500m2	
DBCA	2014	DOV	Maud	Back reef	6000m2	
DBCA	2014	DOV	Osprey	Back reef	4500m2	
DBCA	2014	DOV	Pelican	Back reef	6000m2	
DBCA	2014	DOV	Winderabandi	Back reef	3000m2	
DBCA	2014	DOV	Mangrove	Lagoon	2750m2	
DBCA	2014	DOV	Tantabiddi	Lagoon	3000m2	
DBCA	2014	DOV	Lighthouse	Reef slope	3000m2	

Custodian	Year	Method	Reef region	Reef_Zone	Area/time surveyed	Reference
DBCA	2014	UVC-short	Cloates	Back reef	2700m2	Wilson et al., 2014
DBCA	2014	UVC-short	Mandu	Back reef	4050m2	
DBCA	2014	UVC-short	Mangrove	Back reef	2700m2	
DBCA	2014	UVC-short	Mangrove	Back reef	2700m2	
DBCA	2014	UVC-short	Maud	Back reef	5400m2	
DBCA	2014	UVC-short	Maud	Back reef	5400m2	
DBCA	2014	UVC-short	Pelican	Back reef	5400m2	
DBCA	2014	UVC-short	Pelican	Back reef	5400m2	
DBCA	2014	UVC-short	Cloates	Lagoon	6750m2	
DBCA	2014	UVC-short	Mangrove	Lagoon	5400m2	
DBCA	2014	UVC-short	Mangrove	Lagoon	5400m2	
DBCA	2014	UVC-short	Maud	Lagoon	6750m2	
DBCA	2014	UVC-short	Maud	Lagoon	6750m2	
DBCA	2014	UVC-short	Pelican	Lagoon	8100m2	
DBCA	2014	UVC-short	Pelican	Lagoon	8100m2	
DBCA	2015	DOV	Mandu	Back reef	3000m2	Wilson *et al.*, 2012; Holmes *et al.*, 2013; Wilson *et al.*, 2018
DBCA	2015	DOV	Maud	Back reef	4500m2	
DBCA	2015	DOV	Osprey	Back reef	3000m2	
DBCA	2015	DOV	Tantabiddi	Lagoon	3000m2	
DBCA	2015	DOV	Lighthouse	Reef slope	3000m2	
DBCA	2015	UVC-short	Cloates	Back reef	2700m2	Wilson et al., 2014)
DBCA	2015	UVC-short	Mandu	Back reef	4050m2	
DBCA	2015	UVC-short	Mangrove	Back reef	2700m2	
DBCA	2015	UVC-short	Mangrove	Back reef	2700m2	
DBCA	2015	UVC-short	Maud	Back reef	5400m2	
DBCA	2015	UVC-short	Maud	Back reef	5400m2	
DBCA	2015	UVC-short	Pelican	Back reef	5400m2	
DBCA	2015	UVC-short	Pelican	Back reef	5400m2	
DBCA	2015	UVC-short	Cloates	Lagoon	6750m2	
DBCA	2015	UVC-short	Mangrove	Lagoon	5400m2	
DBCA	2015	UVC-short	Mangrove	Lagoon	5400m2	
DBCA	2015	UVC-short	Maud	Lagoon	6750m2	
DBCA	2015	UVC-short	Maud	Lagoon	6750m2	
DBCA	2015	UVC-short	Pelican	Lagoon	8100m2	
DBCA	2015	UVC-short	Pelican	Lagoon	8100m2	
DBCA	2016	DOV	Mandu	Back reef	3000m2	Wilson *et al.*, 2012; Holmes *et al.*, 2013; Wilson *et al.*, 2018
DBCA	2016	DOV	Mandu	Back reef	3000m2	
DBCA	2016	DOV	Mangrove	Back reef	3000m2	

Custodian	Year	Method	Reef region	Reef_Zone	Area/time surveyed	Reference
DBCA	2016	DOV	Maud	Back reef	4500m2	
DBCA	2016	DOV	Osprey	Back reef	3000m2	
DBCA	2016	DOV	Osprey	Back reef	3000m2	
DBCA	2016	DOV	Tantabiddi	Back reef	3000m2	
DBCA	2016	DOV	Tantabiddi	Lagoon	3000m2	
DBCA	2016	DOV	Lighthouse Bay	Reef slope	3000m2	
DBCA	2016	UVC-long	Mandu	Back reef	3000m2	
DBCA	2016	UVC-long	Mangrove	Back reef	3000m2	
DBCA	2016	UVC-long	Osprey	Back reef	3000m2	
DBCA	2016	UVC-long	Tantabiddi	Back reef	3000m2	
Kathy Cure	2013	DOV	Maud	Back reef	13500m2	na
Kathy Cure	2013	DOV	Pelican	Back reef	7500m2	na
Kathy Cure	2013	DOV	Maud	Reef slope	9000m2	na
Kathy Cure	2013	DOV	Pelican	Reef slope	7500m2	na
Mark Westera	1999	UVC-short	Mandu	Back reef	4000m2	Westera 2003
Mark Westera	1999	UVC-short	Maud	Back reef	4000m2	
Mark Westera	1999	UVC-short	Osprey	Back reef	4250m2	
Mark Westera	2000	BRUV	Mandu	Back reef	750min	
Mark Westera	2000	BRUV	Maud	Back reef	690min	
Mark Westera	2000	BRUV	Maud	Back reef	570min	
Mark Westera	2000	UVC-long	Mandu	Back reef	20000m2	
Mark Westera	2000	UVC-long	Mandu	Back reef	20000m2	
Mark Westera	2000	UVC-long	Maud	Back reef	20000m2	
Mark Westera	2000	UVC-long	Maud	Back reef	25000m2	
Mark Westera	2000	UVC-long	Osprey	Back reef	20000m2	
Mark Westera	2000	UVC-long	Osprey	Back reef	20000m2	
Mark Westera	2000	UVC-short	Mandu	Back reef	3750m2	
Mark Westera	2000	UVC-short	Mandu	Back reef	4000m2	
Mark Westera	2000	UVC-short	Maud	Back reef	4000m2	
Mark Westera	2000	UVC-short	Maud	Back reef	3500m2	
Mark Westera	2000	UVC-short	Osprey	Back reef	4000m2	
Mark Westera	2000	UVC-short	Osprey	Back reef	4000m2	
Reef Life Survey	2010	UVC-short	Cloates	Back reef	1000m2	Edgar GJ, and Stuart-Smith, RD 2014
Reef Life Survey	2010	UVC-short	Maud	Back reef	4250m2	
Reef Life Survey	2010	UVC-short	Pelican	Back reef	1750m2	
Reef Life Survey	2012	UVC-short	Cloates	Back reef	1500m2	
Reef Life Survey	2012	UVC-short	Maud	Back reef	7750m2	
Reef Life Survey	2012	UVC-short	Pelican	Back reef	3000m2	
Reef Life Survey	2015	UVC-short	Cloates	Back reef	1500m2	
Reef Life Survey	2015	UVC-short	Maud	Back reef	11500m2	
Reef Life Survey	2015	UVC-short	Pelican	Back reef	4000m2	

Reef Life Survey	2016	UVC-short	Cloates	Back reef	1500m2	
Reef Life Survey	2016	UVC-short	Maud	Back reef	7500m2	
Reef Life Survey	2016	UVC-short	Pelican	Back reef	1500m2	
Reef Life Survey	2017	UVC-short	Cloates	Back reef	1500m2	
Reef Life Survey	2017	UVC-short	Maud	Back reef	8000m2	
Reef Life Survey	2017	UVC-short	Pelican	Back reef	1500m2	

UWA	2014	BRUV	Cloates	Reef slope	1500min	McLean *et al.*, 2016
UWA	2014	BRUV	Cloates	Reef slope	1500min	
UWA	2014	BRUV	Lighthouse	Reef slope	1200min	
UWA	2014	BRUV	Lighthouse	Reef slope	1200min	
UWA	2014	BRUV	Mandu	Reef slope	960min	
UWA	2014	BRUV	Mandu	Reef slope	960min	
UWA	2014	BRUV	Osprey	Reef slope	900min	
UWA	2014	BRUV	Osprey	Reef slope	900min	
UWA	2014	BRUV	Pelican	Reef slope	1140min	
UWA	2014	BRUV	Pelican	Reef slope	1140min	
UWA	2014	BRUV	Winderabandi	Reef slope	1140min	
UWA	2014	BRUV	Winderabandi	Reef slope	1140min	
UWA	2015	BRUV	Cloates	Back reef	2400min	
UWA	2015	BRUV	Cloates	Back reef	2400min	
UWA	2015	BRUV	Mandu	Back reef	720min	
UWA	2015	BRUV	Mandu	Back reef	720min	
UWA	2015	BRUV	Mangrove	Back reef	720min	
UWA	2015	BRUV	Mangrove	Back reef	720min	
UWA	2015	BRUV	Osprey	Back reef	900min	
UWA	2015	BRUV	Osprey	Back reef	900min	
UWA	2015	BRUV	Pelican	Back reef	600min	
UWA	2015	BRUV	Pelican	Back reef	600min	
UWA	2015	BRUV	Winderabandi	Back reef	720min	
UWA	2015	BRUV	Winderabandi	Back reef	720min	
UWA	2015	BRUV	Cloates	Reef slope	1800min	
UWA	2015	BRUV	Cloates	Reef slope	1800min	
UWA	2015	BRUV	Mandu	Reef slope	1440min	
UWA	2015	BRUV	Mandu	Reef slope	1440min	
UWA	2015	BRUV	Osprey	Reef slope	840min	
UWA	2015	BRUV	Osprey	Reef slope	840min	
UWA	2015	BRUV	Pelican	Reef slope	1200min	
UWA	2015	BRUV	Pelican	Reef slope	1200min	
UWA	2015	BRUV	Winderabandi	Reef slope	660min	
UWA	2015	BRUV	Winderabandi	Reef slope	660min	

Table S2. Summary data from 2021 timed-swim surveys

Month	Latitude	Longitude	Transect length (m)	Surveyed area (ha)	Number fish	Density (ind/ha)
February	-21.8578	113.981	903	1.8	0	0.0
February	-22.218	113.8331	789	1.6	0	0.0
February	-22.0093	113.9007	603	1.2	0	0.0
February	-22.0062	113.9017	598	1.2	1	0.8
February	-22.0031	113.9037	439	0.9	0	0.0
February	-21.9968	113.9063	545	1.1	2	1.8
February	-21.9732	113.9118	561	1.1	0	0.0
February	-21.9644	113.9126	660	1.3	0	0.0
February	-21.9588	113.9131	511	1.0	0	0.0
February	-21.9529	113.9144	388	0.8	0	0.0
February	-21.9465	113.9159	902	1.8	7	3.9
February	-21.8578	113.981	764	1.5	0	0.0
February	-21.8695	113.9718	818	1.6	0	0.0
February	-22.2478	113.8208	695	1.4	0	0.0
February	-22.2612	113.816	688	1.4	0	0.0
February	-22.2549	113.8182	627	1.3	0	0.0
February	-22.2283	113.827	838	1.7	0	0.0
February	-22.2104	113.8358	707	1.4	0	0.0
February	-22.0181	113.8976	609	1.2	0	0.0
February	-22.0263	113.8965	342	0.7	0	0.0
February	-22.037	113.8965	616	1.2	0	0.0
February	-21.9351	113.9187	848	1.7	35	20.6
February	-21.9247	113.9228	874	1.7	11	6.3
February	-21.9126	113.9284	839	1.7	43	25.6
February	-21.9052	113.9329	702	1.4	0	0.0
February	-22.0797	113.8829	810	1.6	0	0.0
February	-22.0696	113.8866	903	1.8	0	0.0
February	-22.0583	113.8886	744	1.5	0	0.0
February	-22.0515	113.8891	776	1.6	0	0.0
February	-21.9655	113.9176	660	1.3	0	0.0
February	-21.974	113.9184	582	1.2	0	0.0
May	-21.9151	113.9278	912	1.8	0	0.0
May	-22.1852	113.8455	618	1.2	0	0.0
May	-22.1751	113.8502	563	1.1	0	0.0
May	-22.1684	113.8528	685	1.4	0	0.0
May	-22.1486	113.8605	606	1.2	0	0.0
May	-21.9151	113.9278	743	1.5	0	0.0
May	-21.9222	113.9243	594	1.2	0	0.0
May	-21.9285	113.9217	912	1.8	1	0.5
May	-22.1051	113.873	668	1.3	0	0.0
May	-22.0948	113.8769	740	1.5	0	0.0

May	-22.082	113.8824	592	1.2	0	0.0
May	-22.0709	113.8871	724	1.4	0	0.0
May	-22.056	113.8895	614	1.2	0	0.0
May	-22.0404	113.8954	530	1.1	0	0.0
May	-22.0352	113.8966	466	0.9	0	0.0
May	-22.0276	113.8954	643	1.3	55	42.8
May	-22.0217	113.8979	545	1.1	0	0.0
TOTAL			31593	63.2	155	

Table S3. Reported sightings of *Bolbometapon muricatum* by expert witnesses between 2007 and 2020 at Ningaloo.

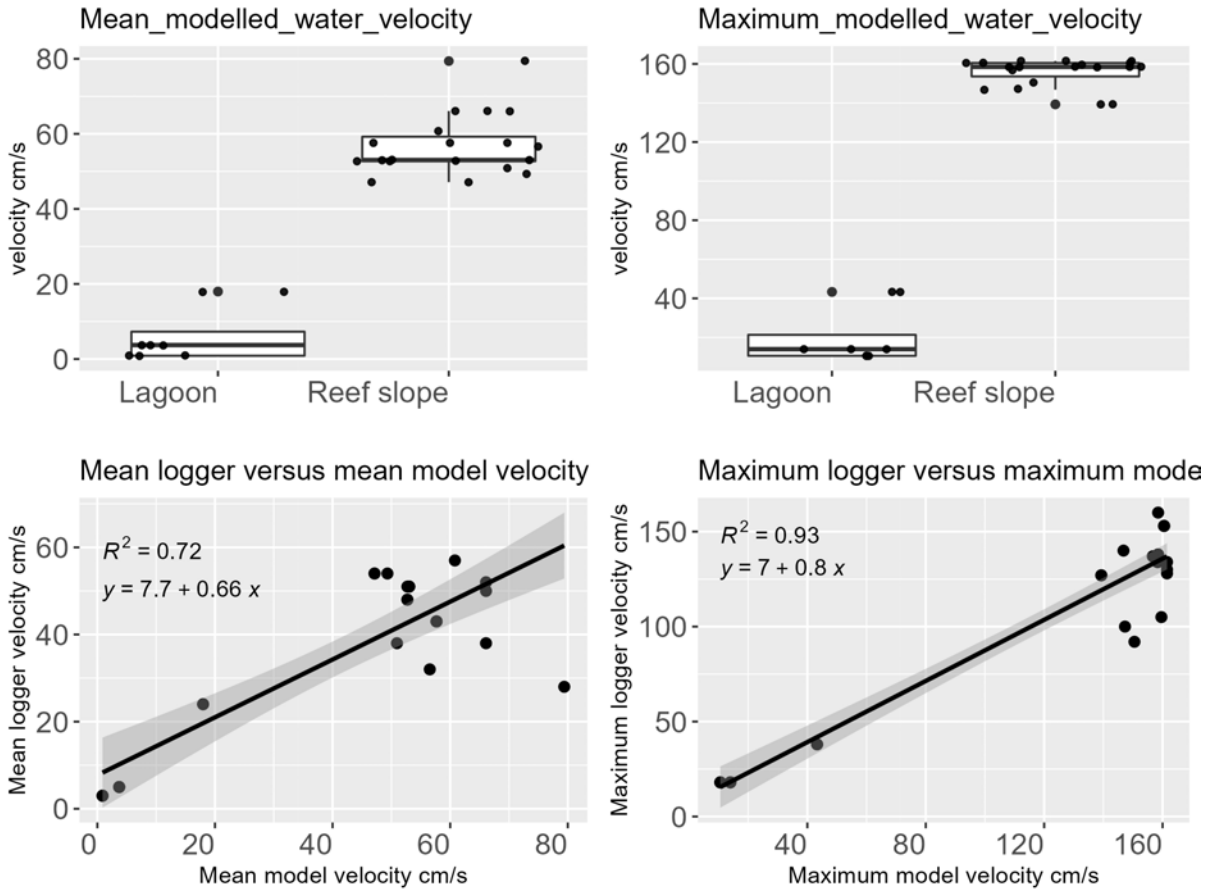
Year	Month	Day	Latitude	Longitude	Number_fish	Length (cm)	Depth (m)	Habitat
2020	-	-	-23.1654	113.7493	15	na	-	Reef slope
2020	-	-	-22.0255	113.8969	15	na	-	Reef slope
2020	10	8	-23.1358	113.7448	15	75	-	Reef slope
2020	9	20	-22.4992	113.6932	10	na	-	Reef flat
2020	10	5	-23.0445	113.7721	1	70	3	Reef flat
2020	9	-	-23.6395	113.6017	15	100	3	Reef slope
2020	2	-	-21.9519	113.9266	20	na	1	Reef flat
2020	9	8	-21.9968	113.9063	60	120	5	Reef slope
2020	5		-23.1729	113.9757	1	6 to 10	5	Lagoon
2020	5		-23.1729	113.9757	1	6 to 10	5	Lagoon
2019	11	-	-21.9519	113.9266	20	na	1	Reef flat
2019	5	-	-21.9974	113.9113	5	70	5	Reef slope
2018	-	-	-21.9778	113.9201	1	na	1	Reef flat
2018	8		-23.1729	113.9757	1	15	5	Lagoon
2017	-	-	-22.4992	113.6932	25	100	5	Reef slope
2016	-	-	-22.4992	113.6932	25	100	5	Reef slope
2016	5	-	-21.9678	113.9131	30	80	1	Reef slope
2015	-	-	-22.4992	113.6932	25	100	5	Reef slope
2015	2	-	-21.9519	113.9266	20	na	1	Reef flat
2014	-	-	-21.9628	113.9157	50	100	1	Reef flat
2011	6		-21.9105	113.9644	1	6	4	Lagoon
2008	-	-	-22.2394	113.8245	30	100	6	Reef slope
2008	2	-	-21.9974	113.9113	5	na	5	Reef slope
2007	11	-	-21.9678	113.9131	30	100	1	Reef slope
2007	11	-	-21.9628	113.9157	30	80	1	Reef slope
2007	-	-	-21.9105	113.9644	1	10	4	Lagoon
2007	-	-	-21.9519	113.9266	1	10	4	Lagoon

Table S4. Assessment of limiting factors on the distribution and abundance of *B. muricatum* at northern Ningaloo (Table adapted from Kobayashi et al. 2011)

Factor considered	Discussion	Plausible limiting factor
Settlement/recruitment	It remains unclear whether any shortages of juveniles at Ningaloo reflect shortages of egg/larval supply or is indicative of bottlenecks in older life history stages. Since recruitment limitation is commonly documented in other reef fish species, this is a plausible limiting factor for this species at northern Ningaloo	Plausible
Juvenile habitat	The juveniles of this species settle/recruit to shallow, low-energy, lagoonal areas within either seagrass, mangroves, or high relief coral formations. This specific habitat requirement is considered to be a plausible limiting factor to their distribution at northern Ningaloo	Plausible
Physical environmental constraints (temperature, salinity, oxygen, light, water clarity)	This species has a wide range and is found throughout the Indo-Pacific from the Red Sea and East Africa as far eastward as the Line Islands and Samoa. The southern extremity of its range in both the Indian and Pacific oceans is approximately 21 degrees south, approximately the same latitude of northern Ningaloo Reef. Extreme environmental conditions are therefore considered a plausible limiting factor for this species at northern Ningaloo	Plausible
Conspecifics	The species displays a relatively complex social behavior. It is possible that density-dependent effects could hinder initial population growth as has been shown in some reef fishes preferentially recruiting to areas with conspecifics.	Possible
Predators	The species is gregarious, grows to a large size, can maneuver adeptly around the benthos, and is likely difficult to prey upon once adult size and behavior are attained. The primary predators of adults would be large sharks, which occur in moderate to high abundance at northern Ningaloo.	Possible
Adult daytime habitat	The species has been shown to have a large home range or territory in the high-energy environment of the forereef and adjacent areas. Space on the reef crest does not seem to be a limiting factor at northern Ningaloo.	Unlikely
Adult sleeping habitat	This species sleeps at night in sheltered areas of the reef, either in caves or in some instances in deeper reef passages. Adequate passages and spur/groove habitat in deeper water is likely necessary for optimal survival while sleeping, all of which are present in habitats adjacent mangrove Bay at Ningaloo.	Unlikely
Adult food	The species is a facultative corallivore and has been observed feeding on algae, sponges, and other benthic organisms. It is an unlikely that food is a limiting factor.	Unlikely

Supplementary information to support Chapter 5

Modelled versus in-situ logger water velocity measurements for (a) mean and (b) maximum daily water velocities as well as mean (c) and maximum modelled water velocities for the lagoon and reef slope.

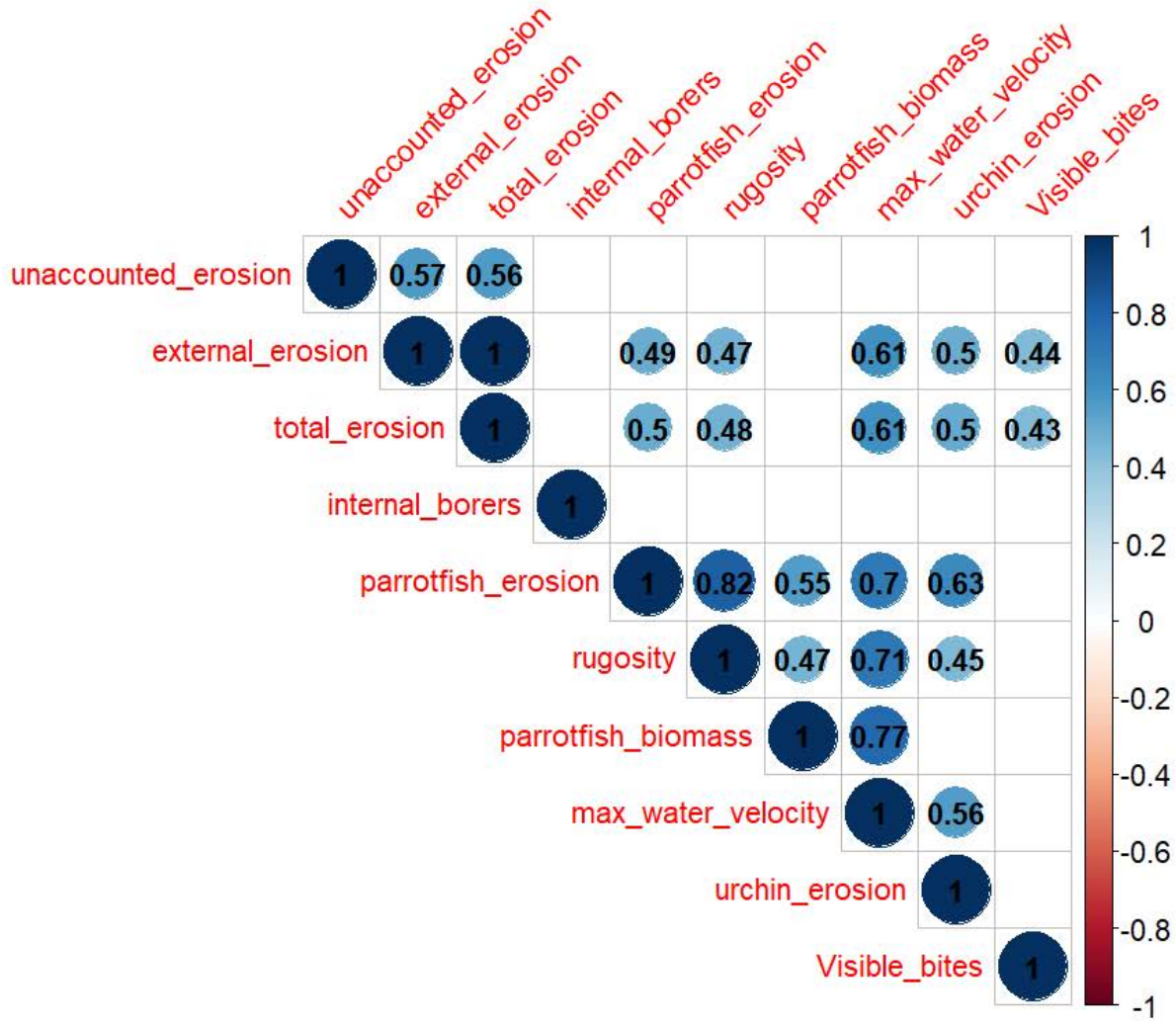


Mean densities of parrotfish and urchins (± se) recorded in lagoon and reef slope habitats at Ningaloo Reef from n=3 surveys at 7 lagoon and 10 reef slope sites

	Lagoon	Reef slope	Combined
Bolbometopon muricatum (ind/1000m^2)	0.00 ± 0.00	0.05 ± 0.05	0.03 ± 0.03
Chlorurus microrhinos (ind/1000m^2)	0.33 ± 0.33	2.35 ± 0.63	1.88 ± 0.51
Chlorurus spilurus (ind/1000m^2)	6.16 ± 1.35	3.30 ± 0.51	3.96 ± 0.54
Scarus prasiognathos (ind/1000m^2)	1.16 ± 0.60	10.2 ± 0.89	8.11 ± 0.81

Scarus rubroviolaceus (ind/1000m^2)	0.00 ± 0.00	4.45 ± 0.82	3.42 ± 0.73
Scarus schlegeli (ind/1000m^2)	0.66 ± 0.49	0.85 ± 0.26	0.80 ± 0.22
Scarus rivulatus (ind/1000m^2)	3.66 ± 1.20	0.15 ± 0.15	0.96 ± 0.40
Scarus ghobban (ind/1000m^2)	2.00 ± 0.73	0.45 ± 0.15	0.80 ± 0.23
Scarus frenatus (ind/1000m^2)	0.00 ± 0.00	2.35 ± 0.53	1.80 ± 0.45
Echinometra mathaei (ind/m^2)	0.28 ± 0.08	5.61 ± 1.12	4.03 ± 0.92

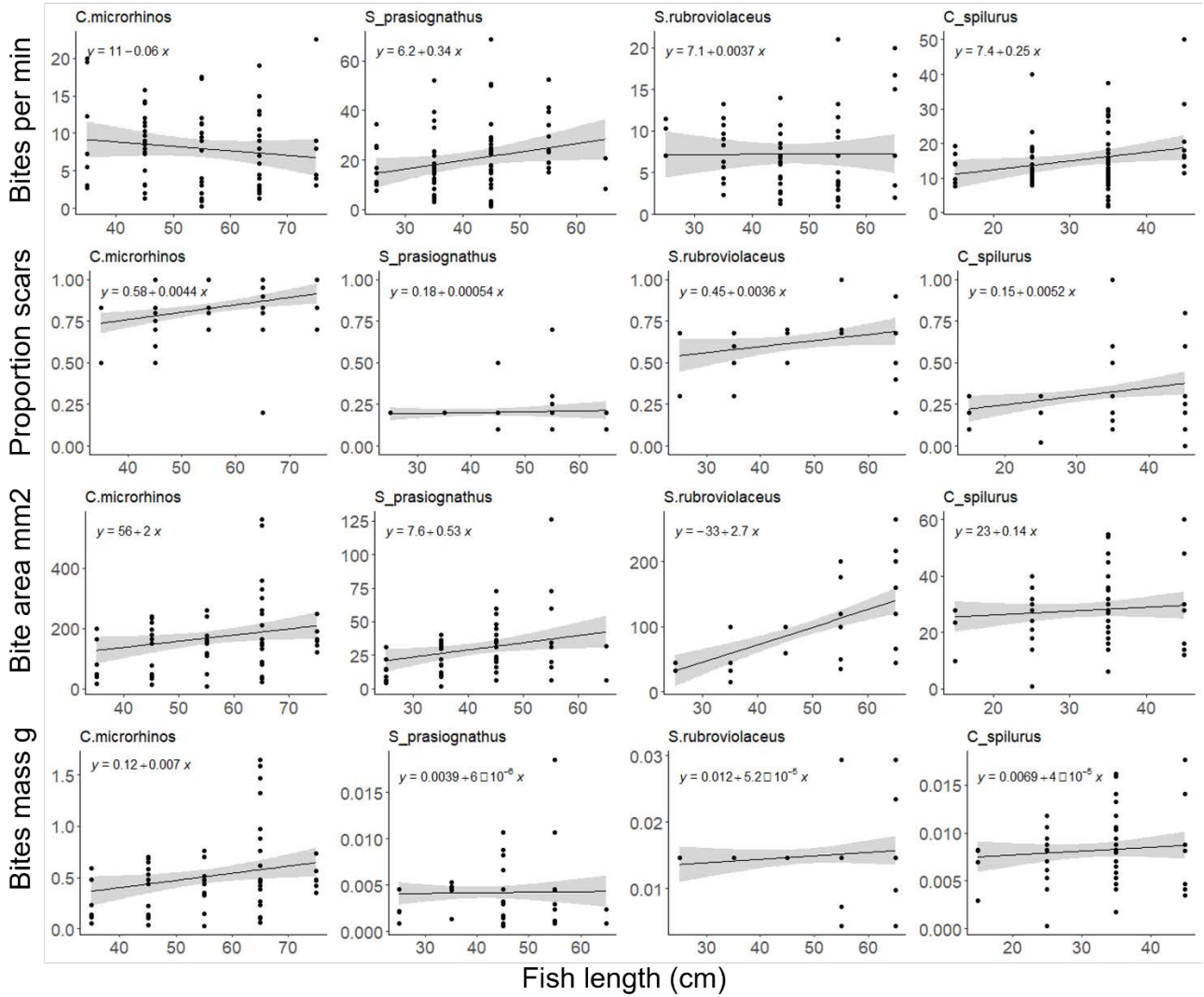
Correlation matrix showing relationships among sources of erosion, visible bite marks on blocks and physical environmental variables (rugosity, water velocity). Coloured circles represent significant correlations ($p < 0.05$) with R^2 values shown.



Feeding metrics used to estimate rate of erosion for the parrotfish *Feeding metrics from this study were compared with those from the literature due to the low numbers of fish observed. ** Feeding metrics obtained from the literature as these species were not observed feeding.

Grazing species	Bite mass (g)	Bites rate (min)	Proportion of bite scars (0-1)	Number of fish observed	Reference
Chlorurus microrhinos	0.17 + 0.006 x length	11 – 0.06 x length	0.58 + 0.0044 x length	79	This study
Chlorurus spilurus	0.0004 + 0.00022 x length	8.4 + 0.22 x length	0.1 + 0.0067 x length	78	This study
Scarus prasiognathos	0.000086 + 0.0001 x length	6.2 + 0.34 x length	0.18 + 0.00054 x length	77	This study
Scarus rubroviolaceus	0.0066 + 0.00042 x length	7.1 + 0.0037 x length	0.45 + 0.0036 x length	59	This study
*Scarus schlegeli**	0.001296 / NA	20.1 / 16.7 to 20.1	0.13 / 0.03	4 / 228	This study / Bellwood and Choat 1990
*Bolbometopon muricatum***	2.3904	2.1	1	0	Bellwood 1996
*Scarus ghobban***	0.07	0.9	0.5	0	Alwany et al. 2009
*Scarus frenatus***	0.007	16.5	0.5	0	Lange et al. 2020
*Scarus rivulatus***	0.001	1.7	0.01	0	Bellwood and Choat 1990

Modelled relationships between fish bite rate, proportion of bites leaving scars mass, bite area and mite mass for the four most abundant excavating parrotfish species observed in this study. *S.schlegeli* relationships were not modelled due to the low numbers of fish observed feeding (n=4)



Supplementary information to support Chapter 6

Production metrics used to calculate new estimates of carbonate production for 14 most abundant taxa ($g/cm^2/yr$)

Taxa	Prodution rate ($g/cm^2/yr$)
Acropora branching	0.82
Acropora corymbose	1.83
Acropora bottlebrush	1.42
Acropora caespitose	1.42
Acropora tabulate	1.42
Porites	0.6
Pocillopora	1.33
Montipora	1.5
Platygyra	1.1
Dipsastrea	2
Paragoniastrea	1.1
Leptoria	1.1
CCA	0.32
Other hard coral	2

References

Adjeroud M, Penin L, Carroll A (2007) Spatio-temporal heterogeneity in coral recruitment around Moorea, French Polynesia: implications for population maintenance, *Journal of Experimental Marine Biology and Ecology* 341:204-218

Adjeroud M, Peignon C, Gauliard C, Penin L, Kayal M (2022) Extremely high but localized pulses of coral recruitment in the southwestern lagoon of New Caledonia and implications for conservation, *Marine Ecology Progress Series* 692:67-79.

Albert JA, Olds AS, Albert S, Cruz-Trinidad A, Schwarz A-M (2015) Reaping the reef: provisioning services from coral reefs in Solomon Islands, *Marine Policy* 62:244-51.

Alldredge AL, Hamner WM (1980) Recurring aggregation of zooplankton by a tidal current, *Estuarine and Coastal Marine Science* 10:31-37

Álvarez-Noriega M, Baird AH, Bridge TCL, Dornelas M, Fontoura L, Pizarro O, Precoda K, Torres-Pulliza D, Woods RM, Zawada K, Madin JS (2018) Contrasting patterns of changes in abundance following a bleaching event between juvenile and adult scleractinian corals, *Coral Reefs* 37:527-532

Alwany MA, Thaler E, Stachowitsch M (2009) Parrotfish bioerosion on Egyptian Red Sea reefs, *Journal of Experimental Marine Biology and Ecology* 371(2):170-176.

Anderson M, Gorley R, Clarke K (2008) *PERMANOVA+ for PRIMER: guide to software and statistical methods*, PRIMER-E.

Appana SD, Vuki VC (2003) A novel method of assessing bioerosion by the sea urchin Echinometra sp. A on a Fijian reef, *The South Pacific Journal of Natural and Applied Sciences* 21(1):25-30.

Ayling T, Ayling AL (1987) *Ningaloo Marine Park: preliminary fish density assessment and habitat survey: with information on coral damage due to Drupella cornus grazing. A report prepared for the Department of Conservation and Land Management, Western Australia*, Department of Conservation and Land Management.

Babcock R, Baird A, Piromvaragorn S, Thomson D, Willis B (2003) Identification of scleractinian coral recruits from Indo-Pacific reefs, *Zoological Studies* 42:211-226

Babcock R, Davies P (1991) Effects of sedimentation on settlement of Acropora millepora, *Coral Reefs* 9:205-208

Babcock R, Mundy C (1996) Coral recruitment: consequences of settlement choice for early growth and survivorship in two scleractinians, *Journal of Experimental Marine Biology and Ecology* 206:179-201

Babcock R, Haywood M, Vanderklift M, Clapin G, Kleczkowski M, Dennis D, Skewes T, Milton D, Murphy N, Pillans R (2008) *Ecosystem impacts of human usage and the effectiveness of zoning for biodiversity conservation: broad-scale fish census. Final analysis*, CSIRO.

Babcock R, Haywood M, Vanderklift M, Murphy N, Clapin G, Limbourn A, Kozak D, Thomson D, McCleod I, Milton D (2009) *Milestone 3.2. 2.26. Lagoon invertebrates final report and monitoring recommendations*, CSIRO Marine and Atmospheric Research/ Australian Institute of Marine Science.

Babcock RC, Thomson DP, Haywood MDE, Vanderklift MA, Pillans R, Rochester WA, Miller M, Speed CW, Shedrawi G, Field S (2020) Recurrent coral bleaching in north-western Australia and associated declines in coral cover, *Marine and Freshwater Research* 72:620-632.

Baird AH, Hughes TP (2000) Competitive dominance by tabular corals: an experimental analysis of recruitment and survival of understorey assemblages, *Journal of Experimental Marine Biology and Ecology* 251:117-132

Baker AC, Glynn PW, Riegl B (2008) Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook, *Estuarine, Coastal and Shelf Science* 80:435-471

Banks SA, Harriott VJ (1996) Patterns of coral recruitment at the Gneering Shoals, southeast Queensland, Australia, *Coral Reefs* 15:225-230

Beck H, Feary D, Nakamura Y, Booth D (2016) Wave-sheltered embayments are recruitment hotspots for tropical fishes on temperate reefs, *Marine Ecology Progress Series* 546:197-212.

Beger M, Babcock R, Booth DJ, Bucher D, Condie SA, Creese B, Cvitanovic C, Dalton SJ, Harrison P, Hoey A (2011) Research challenges to improve the management and conservation of subtropical reefs to tackle climate change threats: findings of a workshop conducted in Coffs Harbour, Australia on 13 September 2010, *Ecological Management & Restoration* 12:e7-e10.

Bellwood DR (1995) Direct estimate of bioerosion by two parrotfish species, Chlorurus gibbus and C. sordidus, on the Great Barrier Reef, Australia, *Marine Biology* 121:419-429.

Bellwood DR (1996) Production and reworking of sediment by parrotfishes (family Scaridae) on the Great Barrier Reef, Australia, *Marine Biology* 125:795-800.

Bellwood DR, Hoey AS, Choat JH (2003) Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs, *Ecology Letters* 6(4):281-285.

Bellwood DR, Hoey AS, Hughes TP (2012) Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs, *Proceedings of the Royal Society B: Biological Sciences* 279(1733):1621-1629.

Bellwood D, Choat J (2011) Dangerous demographics: the lack of juvenile humphead parrotfishes *Bolbometopon muricatum* on the Great Barrier Reef, *Coral Reefs* 30:549-554.

Bellwood DR, Choat JH (1990) A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications, *Environmental Biology of Fishes* 28:189–214.

Bellwood DR, Brandl SJ, McWilliam M, Streit RP, Yan HF, Tebbett SB (2024) Studying functions on coral reefs: past perspectives, current conundrums, and future potential, *Coral Reefs* 43:281-97.

Berumen ML, Pratchett MS (2006) Recovery without resilience: persistent disturbance and long-term shifts in the structure of fish and coral communities at Tiahura Reef, Moorea, *Coral Reefs* 25:647-653

Bessey C, Babcock RC, Thomson DP, Haywood MDE (2018) Outbreak densities of the coral predator Drupella in relation to in situ Acropora growth rates on Ningaloo Reef, Western Australia, *Coral Reefs* 37:985-993

Blakeway D, Byers M, Stoddart J, Rossendell J (2013) Coral colonisation of an artificial reef in a turbid nearshore environment, Dampier Harbour, Western Australia, *PloS One* 8(9):e75281.

Bonaldo RM, Hoey AS, Bellwood DR (2014) The ecosystem roles of parrotfishes on tropical reefs, *Oceanography and Marine Biology: An Annual Review* 52:81-132.

Booij N, Ris RC, Holthuijsen LH (1999) A third-generation wave model for coastal regions: 1. Model description and validation, *Journal of Geophysical Research: Oceans* 104(C4):7649-7666.

Booth DJ, Beretta GA, Brown L, Figueira WF (2018) Predicting success of range-expanding coral reef fish in temperate habitats using temperature-abundance relationships, *Frontiers in Marine Science* 5:31.

Boschetti F, Babcock RC, Doropoulos C, Thomson DP, Feng M, Slawinski D, Berry O, Vanderklift MA (2019) Setting priorities for conservation at the interface between ocean circulation, connectivity, and population dynamics, *Ecological Applications* 30(1):e02011

Bramanti L, Edmunds PJ (2016) Density-associated recruitment mediates coral population dynamics on a coral reef, *Coral Reefs* 35:543-553.

Browne NK, Cuttler M, Moon K, Morgan K, Ross CL, Castro-Sanguino C, ... Zweilfer A (2021) Predicting responses of geo-ecological carbonate reef systems to climate change: a conceptual model and review, *Oceanography and Marine Biology: An Annual Review* 59:229-370.

Bruggemann JH, Van Kessel AM, Van Rooij JM, Breeman AM (1996) Bioerosion and sediment ingestion by the Caribbean parrotfish Scarus vetula and Sparisoma viride: implications of fish size, feeding mode and habitat use, *Marine Ecology Progress Series* 134:59-71.

Burnham KP, Anderson DR, Huyvaert KP (2011) AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons, *Behavioral Ecology and Sociobiology* 65:23-35

CALM (1994) *A representative marine reserve system for Western Australia. Report of the Marine Parks and Reserves Selection Working Group*, Department of Conservation and Land Management.

Cabral-Tena RA, Lopez-Perez A, Reyes-Bonilla H, Calderon-Aguilera LE, Norzagaray-Lopez CO, Rodriguez-Zaragoza FA, Cupul-Magana A, Rodriguez-Troncoso AP, Ayala-Bocos A (2018) Calcification of coral assemblages in the eastern Pacific: reshuffling calcification scenarios under climate change, *Ecological Indicators* 95:726-34.

Cameron K, Harrison P (2020) Density of coral larvae can influence settlement, post-settlement colony abundance and coral cover in larval restoration, *Scientific Reports* 10:1-11

Cantin NE, Cohen AL, Karnauskas KB, Tarrant AM, McCorkle DC (2010) Ocean warming slows coral growth in the central Red Sea, *Science* 329:322-325

Carleton J, Sammarco PW (1987) Effects of substratum irregularity on success of coral settlement: quantification by comparative geomorphological techniques, *Bulletin of Marine Science* 40:85-98

Carlon DB (2001) Depth-related patterns of coral recruitment and cryptic suspension-feeding invertebrates on Guana Island, British Virgin Islands, *Bulletin of Marine Science* 68:525-541.

Chave KE, Smith SV, Roy KJ (1972) Carbonate production by coral reefs, *Marine Geology* 12(2):123-140.

Chazottes, V, Le Campion-Alsumard, T, & Peyrot-Clausade, M (1995) Bioerosion rates on coral reefs: interactions between macroborers, microborers and grazers (Moorea, French Polynesia), *Palaeogeography, Palaeoclimatology, Palaeoecology* 113(2-4):189-198.

Cheal AJ, Emslie M, MacNeil MA, Miller I, Sweatman H (2013) Spatial variation in the functional characteristics of herbivorous fish communities and the resilience of coral reefs, *Ecological Applications* 23(1):174-188.

Choat J, Axe L, Lou D (1996) Growth and longevity in fishes of the family Scaridae, *Marine Ecology Progress Series* 145:33-41.

Choat JH, Klanten OS, Van Herwerden L, Robertson DR, Clements KD (2012) Patterns and processes in the evolutionary history of parrotfishes (Family Labridae), *Biological Journal of the Linnean Society* 107:529-557.

Choat JH, Robertson DR (2002) Age-based studies on ocral reef fishes, in Sale P (ed) *Coral reef fishes: dynamics and diversity in a complex ecosystem*, Academic Press, 57-80.

Chong-Seng K, Graham N, Pratchett M (2014) Bottlenecks to coral recovery in the Seychelles, *Coral Reefs* 33:449-461

Cinner, JE, McClanahan TR, Daw TM, Graham NAJ, Maina J, Wilson SK, Hughes TPJ (2009) Linking social and ecological systems to sustain coral reef fisheries, *Current Biology* 19:206-212.

Cole A, Pratchett M, Jones G (2009) Effects of coral bleaching on the feeding response of two species of coral-feeding fish, *Journal of Experimental Marine Biology and Ecology* 373:11-15

Coleman FC, Williams SL (2002) Overexploiting marine ecosystem engineers: potential consequences for biodiversity, *Trends in Ecology & Evolution* 17:40-44.

Colvocoresses J, Acosta A (2007) A large-scale field comparison of strip transect and stationary point count methods for conducting length-based underwater visual surveys of reef fish populations, *Fisheries Research* 85:130-141.

Connell JH (1985) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities, *Journal of Experimental Marine Biology and Ecology* 93:11-45.

Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time, *Ecological Monographs* 67:461-488

Connolly SR, Baird AH (2010) Estimating dispersal potential for marine larvae: dynamic models applied to scleractinian corals, *Ecology* 91:3572-3583.

Connolly SR, Dornelas M, Bellwood DR, Hughes TP (2009) Testing species abundance models: a new bootstrap approach applied to Indo-Pacific coral reefs, *Ecology* 90:3138-3149.

Conservation and Land Management and Marine Parks and Reserves Authority (2005) *Management plan for the Ningaloo Marine Park and Muiron Islands Marine Management Area 2005–2015*, Government of Western Australia.

Cornwall CE, Comeau S, Kornder NA, Perry CT, van Hooidonk R, DeCarlo TM, ... Lowe RJ (2021) Global declines in coral reef calcium carbonate production under ocean acidification and warming, *Proceedings of the National Academy of Sciences* 118(21):e2015265118.

Courtney TA, Andersson AJ (2019) Evaluating measurements of coral reef net ecosystem calcification rates, *Coral Reefs* 38:997-1006.

Cowen RK, Sponaugle S (2009) Larval dispersal and marine population connectivity, *Annual Review of Marine Science* 1:443-466.

Crabbe MJC, Smith DJ (2003) Computer modelling and estimation of recruitment patterns of non-branching coral colonies at three sites in the Wakatobi Marine Park, S.E. Sulawesi, Indonesia; implications for coral reef conservation, *Computational Biology and Chemistry* 27:17-27.

Cresswell A, Langlois T, Wilson S, Claudet J, Thomson DP, Renton M, Fulton CJ, Fisher R, Vanderklift M, Babcock R (2019) Disentangling the response of fishes to recreational fishing over 30 years within a fringing coral reef reserve network, *Biological Conservation* 237:514-524.

Cuttler MV, Hansen JE, Lowe RJ, Drost EJF (2018) Response of a fringing reef coastline to the direct impact of a tropical cyclone, *Limnology and Oceanography Letters* 3(2):31-38.

Cuttler MVW, Hansen JE, Lowe RJ, Trotter JA, McCulloch MT (2019) Source and supply of sediment to a shoreline salient in a fringing reef environment, *Earth Surface Processes and Landforms* 44:552-64.

Cyronak, T, Bradley D, Eyre J (2016) The synergistic effects of ocean acidification and organic metabolism on calcium carbonate (CaCO3) dissolution in coral reef sediments, *Marine Chemistry* 183:1-12.

Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR, Côté IM (2012) Evaluating life-history strategies of reef corals from species traits, *Ecology Letters* 15:1378-1386.

Darling ES, Graham NAJ, Januchowski-Hartley FA, Nash KL, Pratchett MS, Wilson SK (2017) Relationships between structural complexity, coral traits, and reef fish assemblages, *Coral Reefs* 36:561-575

Darling, ES, McClanahan, TR, Maina, J, Gurney, GG, Graham, NAJ, Januchowski-Hartley, F, Cinner, JE, Mora, C, Hicks, CC, Maire, E, … Mouillot D (2019) Social–environmental drivers inform strategic management of coral reefs in the Anthropocene, *Nature Ecology & Evolution* 3:1341-1350.

Davidson J, Thompson A, Logan M, Schaffelke B (2019) High spatio-temporal variability in Acroporidae settlement to inshore reefs of the Great Barrier Reef, *PloS One* 14.

Dawson JL, Smithers SG, Hua Q (2014) The importance of large benthic foraminifera to reef island sediment budget and dynamics at Raine Island, northern Great Barrier Reef, *Geomorphology* 222:68-81.

de Bakker DM, van Duyl FC, Perry CT, Meesters EH (2019) Extreme spatial heterogeneity in carbonate accretion potential on a Caribbean fringing reef linked to local human disturbance gradients, *Global Change Biology* 25(12):4092-4104.

De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes, *Proceedings of the National Academy of Sciences* 109:17995-17999

Dee S, DeCarlo T, Lozić I, Nilsen J, Browne NK (2023) Low bioerosion rates on inshore turbid reefs of Western Australia, *Diversity* 15(1):62.

Dee S, DeCarlo T, Lozic I, Neilsen J, Browne N (2021) Endolithic borers drive rates of bioerosion among inshore turbid reefs in Western Australia, *Diversity* 15(1):62.

Deloitte Access Economics (2020) *Economic contribution of Ningaloo: one of Australia's best kept secrets*, report commissioned by DBCA.

Depczynski M, Gilmour J, Ridgway T, Barnes H, Heyward A, Holmes T, Moore J, Radford B, Thomson D, Tinkler P (2013) Bleaching, coral mortality and subsequent survivorship on a West Australian fringing reef, *Coral Reefs* 32:233-238.

Domeier ML, Colin PL (1997) Tropical reef fish spawning aggregations: defined and reviewed, *Bulletin of Marine Science* 60:698-726.

Donaldson TJ, Dulvy NK (2004) Threatened fishes of the world: *Bolbometopon muricatum* (Valenciennes 1840)(Scaridae), *Environmental Biology of Fishes* 70:373.

Done TJ (1982) Coral zonation: its nature and significance, in Barnes DJ (ed) *Perspectives on coral reefs*, Australian Institute of Marine Science, 107-147.

Done TJ (1982) Patterns in the distribution of coral communities across the central Great Barrier Reef, *Coral Reefs* 1:95-107.

Doropoulos C, Evensen NR, Gómez-Lemos LA, Babcock RC (2017) Density-dependent coral recruitment displays divergent responses during distinct early life-history stages, *Royal Society Open Science* 4:170082.

Doropoulos C, Gómez-Lemos LA, Babcock RC (2018) Exploring variable patterns of density-dependent larval settlement among corals with distinct and shared functional traits, *Coral Reefs* 37:25-29

Doropoulos C, Ward S, Roff G, Gonzalez-Rivero M, Mumby PJ (2015) Linking demographic processes of juvenile corals to benthic recovery trajectories in two common reef habitats, *PLoS One* 10(5):e0128535.

Dufois F, Lowe RJ, Rayson MD, Branson PM (2018) A numerical study of tropical cyclone-induced sediment dynamics on the Australian North West Shelf, *Journal of Geophysical Research: Oceans* 123:5113-33.

Dullo W-C (2005) Coral growth and reef growth: a brief review, *Facies* 51(1):33-48.

Dulvy NK, Polunin NV (2004) Using informal knowledge to infer human-induced rarity of a conspicuous reef fish, *Animal Conservation* 7:365-374.

Dumas P, Bertaud A, Peignon C, Léopold M, Pelletier D (2009) A quick and clean photographic method for the description of coral reef habitats, *Journal of Experimental Marine Biology and Ecology* 368:161-168.

Dustan P (1982) Depth-dependent photoadaption by zooxanthellae of the reef coral Montastrea annularis, *Marine Biology* 68:253-264.

Eagle JV, Baird AH, Jones GP, Kingsford MJ (2012) Recruitment hotspots: consistent spatial patterns in the relative abundance of coral recruits at One Tree Island, Australia, *Galaxea, Journal of Coral Reef Studies* 14:5-22.

Eakin CM (1996) Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982–1983 El Nino at Uva Island in the eastern Pacific, *Coral Reefs* 15(2):109-119.

Eddy S, Milantara N, Sasmito SD, Kajita T, Basyuni MJ (2021) Anthropogenic drivers of mangrove loss and associated carbon emissions in South Sumatra, Indonesia, *Forests* 12:187.

Edinger EN, Limmon GV, Jompa J, Widjatmoko W, Heikoop JM, Risk MJ (2000) Normal coral growth rates on dying reefs: are coral growth rates good indicators of reef health?, *Marine Pollution Bulletin* 40:404-25.

Elsner JB, Kossin JP, Jagger TH (2008) The increasing intensity of the strongest tropical cyclones, *Nature* 455:92.

Emery KO, Tracey Jr JI, Ladd HS (1954) *Geology of Bikini and nearby atolls*, Geological Survey Professional Paper 260-A, US Government Printing Office.

Enochs IC, Manzello DP, Kolodziej G, Noonan SH, Valentino L, Fabricius KE (2016) Enhanced macroboring and depressed calcification drive net dissolution at high-CO2 coral reefs, *Proceedings of the Royal Society B: Biological Sciences 283*(1842):20161742.

Environment Protection and Biodiversity Conservation Act 1999 (Cth).

Evans RD, Ryan NM, Travers MJ, Feng M, Hitchen Y, Kennington WJ (2018) A seascape genetic analysis of a stress-tolerant coral species along the Western Australian coast, *Coral Reefs* 38:63–78.

Evans RD, Wilson SK, Fisher R, Ryan NM, Babcock R, Blakeway D, Bond T, Dorji P, Dufois F, Fearns P (2020) Early recovery dynamics of turbid coral reefs after recurring bleaching events, *Journal of Environmental Management* 268:110666.

Fabricius KE (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: review and synthesis, *Marine Pollution Bulletin* 50:125-146.

Falter, JL, Zhang Z, Lowe RJ, McGregor F, Keesing J, McCulloch MT (2014) Assessing the drivers of spatial variation in thermal forcing across a nearshore reef system and implications for coral bleaching, *Limnology and Oceanography* 59:1241-55.

Feng M, Colberg F, Slawinski D, Berry O, Babcock R (2016) Ocean circulation drives heterogeneous recruitments and connectivity among coral populations on the North West Shelf of Australia, *Journal of Marine Systems* 164:1-12.

Ferrario F, Beck MW, Storlazzi CD, Micheli F, Shepard CC, Airoldi LJ (2014) The effectiveness of coral reefs for coastal hazard risk reduction and adaptation, *Nature Communications* 5:1-9.

Figueiredo J, Baird AH, Harii S, Connolly SR (2014) Increased local retention of reef coral larvae as a result of ocean warming, *Nature Climate Change* 4:498-502.

Fisher R, Wilson SK, Sin TM, Lee AC, Langlois TJ (2018) A simple function for full-subsets multiple regression in ecology with R, *Ecology and Evolution* 8:6104-6113.

Fisk DA, Harriott VJ (1990) Spatial and temporal variation in coral recruitment on the Great Barrier Reef: Implications for dispersal hypotheses, *Marine Biology* 107:485-490.

Fitzhardinge R (1988) Coral recruitment: the importance of interspecific differences in juvenile growth and mortality, *Proceeding of the Six International Coral Reef Symposium* 2:673-678.

Gaines S, Brown S, Roughgarden J (1985) Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, Balanus glandula, *Oecologia* 67:267-272.
Gaines S, Roughgarden J (1985) Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone, *Proceedings of the National Academy of Sciences* 82:3707-3711.
Game ET, Watts ME, Wooldridge S, Possingham HP (2008) Planning for persistence in marine reserves: a question of catastrophic importance, *Ecological Applications* 18:670-680.
Gardner TA, Côté IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals, *Science* 301:958-960.
Gilmour J, Speed CW, Babcock R (2016) Coral reproduction in Western Australia, *PeerJ* 4:e2010.
Gilmour JP, Cook KL, Ryan NM, Puotinen ML, Green RH, Shedrawi G, Hobbs J-PA, … Oades D (2019) The state of Western Australia's coral reefs, *Coral Reefs* 38:651-667.
Gilmour JP, Smith LD, Heyward AJ, Baird AH, Pratchett MS (2013) Recovery of an Isolated Coral Reef System Following Severe Disturbance, *Science* 340:69-71.
Glassom D, Zakai D, Chadwick-Furman N (2004) Coral recruitment: a spatio-temporal analysis along the coastline of Eilat, northern Red Sea, *Marine Biology* 144:641-651.
Glynn PW, Manzello DP (2015) Bioerosion and coral reef growth: a dynamic balance, in Birkeland C (ed) *Coral reefs in the Anthropocene*, Springer, 67-97.
Gosselin LA, Qian PY (1997) Juvenile mortality in benthic marine invertebrates, *Marine Ecology Progress Series* 146:265-282.
Gouezo M, Wolanski E, Critchell K, Fabricius K, Harrison P, Golbuu Y, Doropoulos CJ (2021) Modelled larval supply predicts coral population recovery potential following disturbance, *Marine Ecology Progress Series* 661:127-145.
Graham MH (2003) Confronting multicollinearity in ecological multiple regression, *Ecology* 84:2809-2815.
Graham NA, Nash KL (2013) The importance of structural complexity in coral reef ecosystems, *Coral Reefs* 32:315-326.
Griffith JK (2004) Scleractinian corals collected during 1998 from the Dampier Archipelago, Western Australia, *Records of the Western Australian Museum Supplement* 66:101-20.
Grigg RW (1982) Darwin Point: a threshold for atoll formation, *Coral Reefs* 1:29-34.
Hamilton R, Adams S, Choat J (2008) Sexual development and reproductive demography of the green humphead parrotfish (*Bolbometopon muricatum*) in the Solomon Islands, *Coral Reefs* 27:153-163.
Hamilton RJ, Almany GR, Stevens D, Bode M, Pita J, Peterson NA, Choat JH (2016) Hyperstability masks declines in bumphead parrotfish (*Bolbometopon muricatum*) populations, *Coral Reefs* 35:751-763.
Hamylton S, Silverman J, Shaw EJ (2013) The use of remote sensing to scale up measures of carbonate production on reef systems: a comparison of hydrochemical and census-based estimation methods, *International Journal of Remote Sensing* 34:6451-65.
Harmelin-Vivien ML (1994) The effects of storms and cyclones on coral reefs: a review, *Journal of Coastal Research* 12:211-31.

Harney JN, Fletcher III CH (2003) A budget of carbonate framework and sediment production, Kailua Bay, Oahu, Hawaii, *Journal of Sedimentary Research* 73:856-68.
Harriott VJ (1985) Recruitment patterns of scleractinian corals at Lizard Island, Great Barrier Reef, *Proceeding of the Fith International Coral Reef Congress* 4:367-372.
Harriott VJ, Banks SA (1995) Recruitment of scleractinian corals in the solitary-islands-marine-reserve, a high-latitude coral-dominated community in eastern Australia, *Marine Ecology Progress Series* 123:155-161.
Harriott VJ, Banks SA (2002) Latitudinal variation in coral communities in eastern Australia: a qualitative biophysical model of factors regulating coral reefs, *Coral Reefs* 21:83-94.
Harriott VJ, Simpson CJ, Lessios HA, Macintyre IG (1997) Coral recruitment on tropical and subtropical reefs in Western Australia, *Proceedings of the Eighth International Coral Reef Symposium, Panama, June 24-29, 1996*:1191-1195.
Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals, *Coral Reefs* 25:133-207.
Harrison XA (2014) Using observation-level random effects to model overdispersion in count data in ecology and evolution, *PeerJ* 2:e616.
Hart DE, Kench PS (2007) Carbonate production of an emergent reef platform, Warraber Island, Torres Strait, Australia, *Coral Reefs* 26:53-68.
Heron SF, Eakin CM, Douvere F, Anderson KL, Day JC, Geiger E, Hoegh-Guldberg O, Van Hooidonk R, Hughes T, Marshall P (2017) *Impacts of climate change on World Heritage coral reefs: A first global scientific assessment*, UNESCO World Heritage Centre.
Heyward A, Smith L, Rees M, Field S (2002) Enhancement of coral recruitment by in situ mass culture of coral larvae, *Marine Ecology Progress Series* 230:113-118.
Hock K, Wolff NH, Beeden R, Hoey J, Condie SA, Anthony KRN, Possingham HP, Mumby PJ (2016) Controlling range expansion in habitat networks by adaptively targeting source populations, *Conservation Biology* 30:856-866.
Hock K, Wolff NH, Condie SA, Anthony KR, Mumby PJ (2014) Connectivity networks reveal the risks of crown-of-thorns starfish outbreaks on the Great Barrier Reef, *Journal of Applied Ecology* 51:1188-1196.
Hoegh-Guldberg O, Northrop E, Lubchenco J (2019) The ocean is key to achieving climate and societal goals, *Science* 365:1372-74.
Hoey A, Howells E, Johansen J, Hobbs J-P, Messmer V, McCowan D, Wilson S, Pratchett M (2016) Recent advances in understanding the effects of climate change on coral reefs, *Diversity* 8:12.
Hoey AS, Bellwood DR (2008) Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef, *Coral Reefs* 27:37-47.
Hoey AS, Feary DA, Burt JA, Vaughan G, Pratchett MS, Berumen ML (2016) Regional variation in the structure and function of parrotfishes on Arabian reefs, *Marine Pollution Bulletin* 105(2):524-531.
Holbrook SJ, Adam TC, Edmunds PJ, Schmitt RJ, Carpenter RC, Brooks AJ, Lenihan HS, Briggs CJ (2018) Recruitment drives spatial variation in recovery rates of resilient coral reefs, *Scientific Reports* 8(1):1-11.
Holmes EE, Ward EJ, Wills K (2012) MARSS: Multivariate autoregressive state-space models for analyzing time-series data, *R Journal* 4:11-19.

Hubbard DK, Miller AI, Scaturo D (1990) Production and cycling of calcium carbonate in a shelf-edge reef system (St. Croix, US Virgin Islands); applications to the nature of reef systems in the fossil record, *Journal of Sedimentary Research* 60:335-60.

Hughes T, Bellwood D, Baird A, Brodie J, Bruno J, Pandolfi J (2011) Shifting base-lines, declining coral cover, and the erosion of reef resilience: comment on Sweatman et al., *Coral Reefs* 30:653-660.

Hughes TP (1987) Skeletal density and growth form of corals, *Marine Ecology Progress Series* 35:259-266.

Hughes TP, Baird AH, Dinsdale EA, Moltschaniwskyj NA, Pratchett MS, Tanner JE, Willis BL (1999) Patterns of recruitment and abundance of corals along the Great Barrier Reef, *Nature* 397:59-63.

Hughes TP, Baird AH, Dinsdale EA, Moltschaniwskyj NA, Pratchett MS, Tanner JE, Willis BL (2000) Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits, *Ecology* 81:2241-2249.

Hughes TP, Barnes ML, Bellwood DR, Cinner JE, Cumming GS, Jackson JBC, Kleypas J, van de Leemput IA, Lough JM, Morrison TH, Palumbi SR, van Nes EH, Scheffer M (2017a) Coral reefs in the Anthropocene, *Nature* 546:82.

Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, Babcock RC, … Wilson SK (2017b) Global warming and recurrent mass bleaching of corals, *Nature* 543:373-377.

Hughes TP, Kerry JT, Baird AH, Connolly SR, Chase TJ, Dietzel A, Hill T, Hoey AS, Hoogenboom MO, Jacobson M, Kerswell A, Madin JS, Mieog A, Paley AS, Pratchett MS, Torda G, Woods RM (2019) Global warming impairs stock–recruitment dynamics of corals, *Nature* 568(7752):387-390.

Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Mark Eakin C, Heron SF, … Torda G (2018) Global warming transforms coral reef assemblages, *Nature* 556:492-96.

Humanes A, Ricardo GF, Willis BL, Fabricius KE, Negri AP (2017) Cumulative effects of suspended sediments, organic nutrients and temperature stress on early life history stages of the coral Acropora tenuis, *Scientific Reports* 7:44101.

Hutchings PA (1986) Biological destruction of coral reefs: a review, *Coral Reefs* 4:239-252.

Hutchings P, Peyrot-Clausade M, Osnorno A (2005) Influence of land runoff on rates and agents of bioerosion of coral substrates, *Marine Pollution Bulletin* 51(1-4):438-447.

James RK, Keyzer LM, Van de Velde SJ, Herman PMJ, Van Katwijk MM, Bouma TJ (2023) Climate change mitigation by coral reefs and seagrass beds at risk: how global change compromises coastal ecosystem services, *Science of the Total Environment* 857:159576.

Januchowski-Hartley FA, Graham NA, Wilson SK, Jennings S, Perry CT (2017) Drivers and predictions of coral reef carbonate budget trajectories, *Proceedings of the Royal Society B: Biological Sciences* 284(1847):20162533.

Jenkins AP, Jupiter SD, Qauqau I, Atherton J (2010) The importance of ecosystem-based management for conserving aquatic migratory pathways on tropical high islands: a case study from Fiji, *Aquatic Conservation-Marine and Freshwater Ecosystems* 20:224-238.

Jenkins D, Morrison S (2018) *Fishes of Ningaloo*, Blue Ocean Publications.

Johannes RE (1981) Working with fishermen to improve coastal tropical fisheries and resource management, *Bulletin of Marine Science* 31:673-680.

Johansson CL (2012) *A functional analysis of herbivory on Ningaloo Reef, Australia* (Doctoral dissertation, James Cook University).

Johansson CL, Bellwood DR, Depczynski M (2010) Sea urchins, macroalgae and coral reef decline: a functional evaluation of an intact reef system, Ningaloo, Western Australia, *Marine Ecology Progress Series* 414:65-74.

Jones R, Ricardo G, Negri A (2015) Effects of sediments on the reproductive cycle of corals, *Marine Pollution Bulletin* 100:13-33.

Jones CG, Lawton JH, Shachak M (1996) Organisms as ecosystem engineers, in Samson FB, Knopf FL (eds) *Ecosystem management: selected readings*, Springer, 130-147.

Keesing JK (1992) Influence of persistent sub-infestation density Acanthaster planci (L.) and high density Echinometra mathaei (de Blainville) populations on coral reef community structure in Okinawa, Japan, *Proceedings of the 7th international Coral Reef Symposium* 2:769-779.

Kenyon TM, Doropoulos C, Wolfe K, Webb GE, Dove S, Harris D, Mumby PJ (2023) Coral rubble dynamics in the Anthropocene and implications for reef recovery, *Limnology and Oceanography* 68(1):110-147.

Kerry JT, Bellwood DR (2015) Do tabular corals constitute keystone structures for fishes on coral reefs?, *Coral Reefs* 34:41-50.

Kiene WE, Hutchings PA (1994) Bioerosion experiments at Lizard Island, Great Barrier Reef, *Coral Reefs* 1*3*:91-98.

Kleiber C, Zeileis A (2008) *Applied econometrics with R*, Springer Science & Business Media.

Kobayashi DR, Friedlander AM, Grimes CB, Nichols RS, Zgliczynski B (2011) Bumphead parrotfish (*Bolbometopon muricatum*) status review, NOAA technical memorandum NMFS-PIFSC.

Kool JT, Nichol SL (2015) Four-dimensional connectivity modelling with application to Australia's north and northwest marine environments, *Environmental Modelling & Software* 65:67-78.

Kuffner IB, Toth LT, Hudson JH, Goodwin WB, Stathakopoulos A, Bartlett LA, Whitcher EM (2019) Improving estimates of coral reef construction and erosion with in situ measurements, *Limnology and Oceanography* 64(5):2283-2294.

Land LS (1979) The fate of reef-derived sediment on the north Jamaican island slope, *Marine Geology* 29:55-71.

Langdon M (2012) *The ecology of the grazing urchin Echinometra mathaei at Ningaloo Marine Park* (Doctoral dissertation, Murdoch University).

Lange ID, Perry CT (2019) Bleaching impacts on carbonate production in the Chagos Archipelago: influence of functional coral groups on carbonate budget trajectories, *Coral Reefs* 38(4):619-624.

Lange ID, Perry CT, Morgan KM, Roche R, Benkwitt CE, Graham NA (2020) Site-level variation in parrotfish grazing and bioerosion as a function of species-specific feeding metrics, *Diversity* 12(10):379.

Langlois TJ, Harvey ES, Fitzpatrick B, Meeuwig JJ, Shedrawi G, Watson DL (2010) Cost-efficient sampling of fish assemblages: comparison of baited video stations and diver video transects, *Aquatic Biology* 9:155-168.

Lenanton R, Caputi N, Kangas M, Craine M (2009) The ongoing influence of the Leeuwin Current on economically important fish and invertebrates off temperate Western Australia-has it changed?, *Journal of the Royal Society of Western Australia* 92:111.

Lesser MP (2006) Oxidative stress in marine environments: biochemistry and physiological ecology, *Annual Review of Physiology* 68:253-278.

Lesser MP, Slattery M, Stat M, Ojimi M, Gates RD, Grottoli A (2010) Photoacclimatization by the coral Montastraea cavernosa in the mesophotic zone: light, food, and genetics, *Ecology* 91:990-1003.

Lozano-Montes HM, Keesing JK, Grol MG, Haywood MDE, Vanderklift MA, Babcock RC, Bancroft K (2017) Limited effects of an extreme flood event on corals at Ningaloo Reef, *Estuarine, Coastal and Shelf Science* 191:234-238.

Lukoschek V, Cross P, Torda G, Zimmerman R, Willis BL (2013) The importance of coral larval recruitment for the recovery of reefs impacted by cyclone Yasi in the Central Great Barrier Reef, *PloS One* 8:e65363.

MacKenzie DI, Royle JA, Brown JA, Nichols JD, Thompson W (2004) Occupancy estimation and modeling for rare and elusive populations, in Thompson W (ed) *Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters*, Island Press,149-171.

Madin JS, Hoogenboom MO, Connolly SR, Darling ES, Falster DS, Huang D, Keith SA, Mizerek T, Pandolfi JM, Putnam HM, Baird AH (2016) A trait-based approach to advance coral reef science, *Trends in Ecology & Evolution* 31:419-428.

Madin JS, Connolly SR (2006) Ecological consequences of major hydrodynamic disturbances on coral reefs, *Nature* 444(7118):477-480.

Mallela J, Perry CJ (2007) Calcium carbonate budgets for two coral reefs affected by different terrestrial runoff regimes, Rio Bueno, Jamaica, *Coral Reefs* 26:129-45.

Manzello DP, Mark Eakin C, Glynn PW (2017) Effects of global warming and ocean acidification on carbonate budgets of Eastern Pacific coral reefs, in Glynn PW, Manzello DP, Enochs IC (eds) *Coral Reefs of the eastern tropical Pacific: persistence and loss in a dynamic environment*, Springer.

Marchesiello P, McWilliams JC, Shchepetkin A (2003) Equilibrium structure and dynamics of the California Current System, *Journal of Physical Oceanography* 33:753-783.

Marshall P, Baird A (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa, *Coral Reefs* 19:155-163.

McCauley DJ, Young HS, Guevara R, Williams GJ, Power EA, Dunbar RB, ... Micheli F (2014) Positive and negative effects of a threatened parrotfish on reef ecosystems, *Conservation Biology 28*(5):1312-1321.

McClanahan TR, Ateweberhan M, Graham NAJ, Wilson SK, Sebastian CR, Guillaume MMM, Bruggemann JH (2007) Western Indian Ocean coral communities: bleaching responses and susceptibility to extinction, *Marine Ecology Progress Series* 337:1-13.

McClanahan TR, Graham NA, MacNeil MA, Muthiga NA, Cinner JE, Bruggemann JH, Wilson SK (2011) Critical thresholds and tangible targets for ecosystem-based management of coral reef fisheries, *Proceedings of the National Academy of Sciences* 108:17230-17233.

McCormick MI (1994) Comparison of field methods for measuring surface-topography and their associations with a tropical reef fish assemblage, *Marine Ecology Progress Series* 112:87-96.

Mills SC, Peyrot-Clausade M, Fontaine MF (2000) Ingestion and transformation of algal turf by Echinometra mathaei on Tiahura fringing reef (French Polynesia), *Journal of Experimental Marine Biology and Ecology* 254(1):71-84.

Mokady O, Lazar B, Loya Y (1996) Echinoid bioerosion as a major structuring force of Red Sea coral reefs, *The Biological Bulletin* 190(3):367-372.

Molina-Hernández A, Medellín-Maldonado F, Lange ID, Perry CT, Álvarez-Filip L (2022) Coral reef erosion: in situ measurement on different dead coral substrates on a Caribbean reef, *Limnology and Oceanography* 67(12):2734-2749.

Moore JAY, Bellchambers LM, Depczynski MR, Evans RD, Evans SN, Field SN, Friedman KJ, Gilmour JP, Holmes TH, Middlebrook R, Radford BT, Ridgway T, Shedrawi G, Taylor H, Thomson DP, Wilson SK (2012) Unprecedented mass bleaching and loss of coral across 12° of latitude in Western Australia in 2010–11, *Plos One* 7:e51807.

Morgan KM, Kench PS (2016) Reef to island sediment connections on a Maldivian carbonate platform: using benthic ecology and biosedimentary depositional facies to examine island-building potential, *Earth Surface Processes and Landforms* 41(13):1815-1825.

Morgan KM, Perry CT, Smithers SG, Johnson JA, Daniell JJ (2016) Evidence of extensive reef development and high coral cover in nearshore environments: implications for understanding coral adaptation in turbid settings, *Scientific Reports* 6:29616.

Morgan KM, PS Kench (2014) A detrital sediment budget of a Maldivian reef platform, *Geomorphology* 222:122-31.

Morgan KM, Kench PS (2016a) Reef to island sediment connections on a Maldivian carbonate platform: using benthic ecology and biosedimentary depositional facies to examine island-building potential, *Earth Surface Processes and Landforms* 41:1815-25.

Morgan KM, Kench PS (2016b) Parrotfish erosion underpins reef growth, sand talus development and island building in the Maldives, *Sedimentary Geology* 341:50-57.

Morgan KM, Perry CT, Smithers SG, Johnson JA, Daniell JJ (2016) Evidence of extensive reef development and high coral cover in nearshore environments: implications for understanding coral adaptation in turbid settings, *Scientific Reports* 6:29616.

Moustaka M, Mohring MB, Holmes T, Evans RD, Thomson D, Nutt C, Stoddart J, Wilson SK (2019) Cross-shelf heterogeneity of coral assemblages in Northwest Australia, *Diversity* 11:15.

Moustaka M, Langlois TJ, McLean D, Bond T, Fisher R, Fearns P, Dorji P, Evans RD (2018) The effects of suspended sediment on coral reef fish assemblages and feeding guilds of north-west Australia, *Coral Reefs* 37:659-73.

Muehllehner N, Langdon C, Venti A, Kadko DJ (2016) Dynamics of carbonate chemistry, production, and calcification of the Florida Reef Tract (2009–2010): evidence for seasonal dissolution, *Global Biogeochemical Cycles* 30:661-88.

Müller A, Gagan MK, McCulloch MT (2001) Early marine diagenesis in corals and geochemical consequences for paleoceanographic reconstructions, *Geophysical Research Letters* 28(23):4471-4474.

Mumby PJ, Harborne AR (2010) Marine reserves enhance the recovery of corals on Caribbean reefs, *Plos One* 5(1):e8657.

Munday PL (2004) Habitat loss, resource specialization, and extinction on coral reefs, *Global Change Biology* 10:1642-1647.

Mundy C (2000) An appraisal of methods used in coral recruitment studies, *Coral Reefs* 19:124-131.

Mundy C, Babcock R (2000) Are vertical distribution patterns of scleractinian corals maintained by pre-or post-settlement processes? A case study of three contrasting species, *Marine Ecology Progress Series* 198:109-119.

Murphy HM, Jenkins GP (2010) Observational methods used in marine spatial monitoring of fishes and associated habitats: a review, *Marine and Freshwater Research* 61:236-252.

O'Connor MI, Bruno JF, Gaines SD, Halpern BS, Lester SE, Kinlan BP, Weiss JM (2007) Temperature control of larval dispersal and the implications for marine ecology, evolution, and conservation, *Proceedings of the National Academy of Sciences* 104:1266-1271.

Oliver J, King B, Willis B, Babcock R, Wolanski E (1992) Dispersal of coral larvae from a lagoonal reef—II. Comparisons between model predictions and observed concentrations, *Continental Shelf Research* 12:873-889.

Ong L, Holland KN (2010) Bioerosion of coral reefs by two Hawaiian parrotfishes: species, size differences and fishery implications, *Marine Biology* 157:1313-1323.

Onton K, Page CA, Wilson SK, Neale S, Armstrong S (2011) Distribution and drivers of coral disease at Ningaloo Reef, Indian Ocean, *Marine Ecology Progress Series* 433:75-84.

Osorno A, Peyrot-Clausade M, Hutchings PA (2005) Patterns and rates of erosion in dead Porites across the Great Barrier Reef (Australia) after 2 years and 4 years of exposure, *Coral Reefs* 24:292-303.

Pachauri RK, Allen MR, Barros VR, Broome J, Cramer W, Christ R, Church JA, Clarke L, Dahe Q, Dasgupta P (2014) *Climate change 2014: synthesis report. Contribution of Working Groups I, II and III to the fifth assessment report of the Intergovernmental Panel on Climate Change*. IPCC

Pari N, Peyrot-Clausade M, Le Campion-Alsumard T, Hutchings P, Chazottes V, Golubic S, Le Campion J, Fontaine MF (1998) Bioerosion of experimental substrates on high islands and on atoll lagoons (French Polynesia) after two years of exposure, *Marine Ecology Progress Series* 166:119-30.

Pari N, Peyrot-Clausade M, Hutchings PA (2002) Bioerosion of experimental substrates on high islands and atoll lagoons (French Polynesia) after 5 years of exposure, *Journal of Experimental Marine Biology and Ecology* 276(1-2):109-127.

Pearce A, Buchan S, Chiffings T, D'Adamo N, Fandry C, Fearns P, Mills D, Phillips R, Simpson C (2003) A review of the oceanography of the Dampier Archipelago, Western Australia, in Wells FE, Walker D, Jones DS (eds) *The marine flora and fauna of Dampier, Western Australia*, Western Australian Museum, 13-50.

Pearce A, Phillips B (1988) ENSO events, the Leeuwin Current, and larval recruitment of the western rock lobster, *ICES Journal of Marine Science* 45:13-21.

Pearce AF, Feng M (2013) The rise and fall of the marine heat wave off Western Australia during the summer of 2010/2011, *Journal of Marine Systems* 111:139-156.

Pedersen NE, Edwards CB, Eynaud Y, Gleason AC, Smith JE, Sandin SA (2019) The influence of habitat and adults on the spatial distribution of juvenile corals, *Ecography* 42:1703-1713.

Perry CT, Murphy GN, Kench PS, Smithers SG, Edinger EN, Steneck RS, Mumby PJ (2013) Caribbean-wide decline in carbonate production threatens coral reef growth, *Nature Communications* 4:1402.

Perry C (2001) Storm-induced coral rubble deposition: Pleistocene records of natural reef disturbance and community response, *Coral Reefs* 20:171-183.

Perry CT, Harborne AR (2016) Bioerosion on modern reefs: impacts and responses under changing ecological and environmental conditions, in Hubbard DK, Rogers CS, Lipps JH, Stanley Jr GD (eds) *Coral reefs at the crossroads*, Springer, 69-101.

Perry CT, Alvarez-Filip L (2019) Changing geo-ecological functions of coral reefs in the Anthropocene, *Functional Ecology* 33(6):976-988.

Perry CT, Hepburn LJ (2008) Syn-depositional alteration of coral reef framework through bioerosion, encrustation and cementation: taphonomic signatures of reef accretion and reef depositional events, *Earth-Science Reviews* 86(1-4):106-144.

Perry CT, Hopley D (2011) Carbonate budgets and reef framework accumulation, in Hopley D (ed) *Encyclopedia of modern coral reefs: structure, form and process*, Springer, 185-190.

Perry CT, Edinger EN, Kench PS, Murphy GN, Smithers SG, Steneck RS, Mumby PJ (2012) Estimating rates of biologically driven coral reef framework production and erosion: a new census-based carbonate budget methodology and applications to the reefs of Bonaire, *Coral Reefs* 31:853-868.

Perry CT, Kench PS, Smithers SG, Riegl B, Yamano H, O'Leary MJ (2011) Implications of reef ecosystem change for the stability and maintenance of coral reef islands, *Global Change Biology* 17(12):3679-3696.

Perry CT, Alvarez-Filip L, Graham NA, Mumby PJ, Wilson SK, Kench PS, Manzello DP, Morgan KM, Slangen AB, Thomson DP (2018) Loss of coral reef growth capacity to track future increases in sea level, *Nature* 558:396-400.

Perry CT, Murphy GN, Kench PS, Edinger EN, Smithers SG, Steneck RS, Mumby PJ (2014) Changing dynamics of Caribbean reef carbonate budgets: emergence of reef bioeroders as critical controls on present and future reef growth potential, *Proceedings of the Royal Society B: Biological Sciences* 281:20142018.

Perry CT, Steneck RS, Murphy GN, Kench PS, Edinger EN, Smithers SG, Mumby PJ (2015) Regional-scale dominance of non-framework building corals on Caribbean reefs affects carbonate production and future reef growth, *Global Change Biology* 21:1153-64.

Perry CT (2011) Carbonate budgets and reef framework accumulation, in Hopley D (ed) *Encyclopedia of modern coral reefs: structure, form and process*, Springer.

Perry CT, Alvarez-Filip L (2019) Changing geo-ecological functions of coral reefs in the Anthropocene, *Functional Ecology* 33:976-88.

Peyrot-Clausade M, Chabanet P, Conand C, Fontaine MF, Letourneur Y, Harmelin-Vivien M (2000) Sea urchin and fish bioerosion on La Reunion and Moorea reefs, *Bulletin of Marine Science* 66(2):477-485.

Peyrot-Clausade M, Hutchings P, Richard G (1992) Temporal variations of macroborers in massive Porites lobata on Moorea, French Polynesia, *Coral Reefs* 11:161-166.

Pogoda B, Brown J, Hancock B, Preston J, Pouvreau S, Kamermans P, Sanderson W, von Nordheim H (2019) The Native Oyster Restoration Alliance (NORA) and the Berlin Oyster Recommendation: bringing back a key ecosystem engineer by developing and supporting best practice in Europe, *Aquatic Living Resources* 32:13.

Polloi K, Golbuu Y, Merep G, Koshiba S, Friedlander A, Koike H (2014) *An assessment of Maml and Kemedukl in Palau and management recommendations*, The Nature Conservancy Micronesia Program Technical Report.

Pratchett MS, Anderson KD, Hoogenboom MO, Widman E, Baird AH, Pandolfi JM, Edmunds PJ, Lough JM (2015) Spatial, temporal and taxonomic variation in coral growth—implications for the structure and function of coral reef ecosystems, *Oceanography and Marine Biology: An Annual Review* 53:215-295.

Pratchett MS, Trapon M, Berumen ML, Chong-Seng K (2011) Recent disturbances augment community shifts in coral assemblages in Moorea, French Polynesia, *Coral Reefs* 30:183-193.

Puotinen M, Drost E, Lowe R, Depczynski M, Radford B, Heyward A, Gilmour J (2020) Towards modelling the future risk of cyclone wave damage to the world's coral reefs, *Global Change Biology* 26(8):4302-4315.

Rachello-Dolmen P, Cleary D (2007) Relating coral species traits to environmental conditions in the Jakarta Bay/Pulau Seribu reef system, Indonesia, *Estuarine, Coastal and Shelf Science* 73:816-826.

Radford B, Babcock R, Van Niel K, Done T (2014) Are cyclones agents for connectivity between reefs?, *Journal of Biogeography* 41:1367-1378.

Reyes-Nivia C, Diaz-Pulido G, Kline D, Guldberg OH, Dove S (2013) Ocean acidification and warming scenarios increase microbioerosion of coral skeletons, *Global Change Biology* 19(6):1919-1929.

Rice MM, Maher RL, Correa AM, Moeller HV, Lemoine NP, Shantz AA, ... Silbiger NJ (2020) Macroborer presence on corals increases with nutrient input and promotes parrotfish bioerosion, *Coral Reefs* 39:409-418.

Richards Z (2018) The Coral Compactus: Western Australia Hard Coral Genus Identification Guide Version 2, Western Australian Museum.

Risk MJ (1972) *Intertidal substrate rugosity and species diversity*, University of Southern California.

Ritson-Williams R, Arnold SN, Fogarty ND, Steneck RS, Vermeij MJ, Paul VJ (2009) New perspectives on ecological mechanisms affecting coral recruitment on reefs, *Smithsonian Contributions to the Marine Sciences* 38:437.

Roff G, Zhao JX, Mumby PJ (2015) Decadal-scale rates of reef erosion following El Niño-related mass coral mortality, *Global Change Biology* 21(12):4415-4424.

Roff G, Doropoulos C, Mereb G, Mumby PJ (2017) Mass spawning aggregation of the giant bumphead parrotfish *Bolbometopon muricatum*, *Journal of Fish Biology* 91:354-361.

Roik A, Röthig T, Pogoreutz C, Saderne V, Voolstra CR (2018) Coral reef carbonate budgets and ecological drivers in the central Red Sea–a naturally high temperature and high total alkalinity environment, *Biogeosciences* 15:6277-96.

Rotjan RD, Lewis SM (2005) Selective predation by parrotfishes on the reef coral Porites astreoides, *Marine Ecology Progress Series* 305:193-201.
Sadd JL (1984) Sediment transport and CaCO3 budget on a fringing reef, Cane Bay, St. Croix, US Virgin Islands, *Bulletin of Marine Science* 35:221-238.
Sale PF (1980) Assemblages of fish on patch reefs—predictable or unpredictable?, *Environmental Biology of Fishes* 5:243-249.
Sammarco PP (1985) The Great Barrier Reef vs. the Caribbean: comparisons of grazers, coral recruitment patterns and reef recovery, *Proceedings of the 5th International Coral Reef Congress, Tahiti, 27 May-1 June 1985* 4:391-398.
Sammarco PW (1991) Geographically specific recruitment and postsettlement mortality as influences on coral communities: The cross-continental shelf transplant experiment, *Limnology and Oceanography* 36:496-514.
Sammarco PW (1994) Larval dispersal and recruitment processes in Great Barrier Reef corals: analysis and synthesis, *The Bio-Physics of Marine Larval Dispersal* 45:35-72.
Sammarco PW, Andrews JC (1989) The Helix experiment: differential localized dispersal and recruitment patterns in Great Barrier Reef corals, *Limnology and Oceanography* 34:896-912.
Sammarco PW, Risk MJ (1990) Large-scale patterns in internal bioerosion of Porites: cross continental shelf trends on the Great Barrier Reef, *Marine Ecology Progress Series* 59:145-156.
Sampayo EM, Roff G, Sims CA, Rachello-Dolmen PG, Pandolfi JM (2020) Patch size drives settlement success and spatial distribution of coral larvae under space limitation, *Coral Reefs* 39:387-396.
Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems, *Nature* 413:591-596.
Schoepf V, Herler J, Zuschin M (2010) Microhabitat use and prey selection of the coral-feeding snail Drupella cornus in the northern Red Sea, *Hydrobiologia* 641:45-57.
Schönberg CH, Fang JKH, Carballo JL (2017) Bioeroding sponges and the future of coral reefs, in Carballo JL, Bell JJ (ed) *Climate change, ocean acidification and sponges: impacts across multiple levels of organization*, Springer, 179-372.
Scoffin TP (1993) The geological effects of hurricanes on coral reefs and the interpretation of storm deposits, *Coral Reefs* 12:203-221.
Scoffin TP (1980) Calcium carbonate budget of a fringing reef on the west coast of Barbados. Part II – Erosion, sediments and internal structure, *Bulletin of Marine Science* 30:475-508.
Semeniuk V (1982) The marine environments of the Dampier Archipelago, *Journal and Proceedings of the Royal Society of Western Australia* 65:97.
Shedrawi G, Falter JL, Friedman KJ, Lowe RJ, Pratchett MS, Simpson CJ, Speed CW, Wilson SK, Zhang Z (2017) Localised hydrodynamics influence vulnerability of coral communities to environmental disturbances, *Coral Reefs* 36:1-12.
Sheppard CR, Spalding M, Bradshaw C, Wilson S (2002) Erosion vs. recovery of coral reefs after 1998 El Niño: Chagos reefs, Indian Ocean, *AMBIO: A Journal of the Human Environment* 31(1):40-48.

Sheppard C, Dixon DJ, Gourlay M, Sheppard A, Payet R (2005) Coral mortality increases wave energy reaching shores protected by reef flats: examples from the Seychelles, *Estuarine, Coastal, and Shelf Science* 64:223-234.

Silbiger NJ, Donahue MJ, Brainard RE (2017) Environmental drivers of coral reef carbonate production and bioerosion: a multi-scale analysis, *Ecology* 98(10):2547-2560.

Silbiger NJ, Guadayol O, Thomas FI, Donahue MJ (2016) A novel μ CT analysis reveals different responses of bioerosion and secondary accretion to environmental variability, *PLoS One* 11(4):e0153058.

Simpson CJ, Cary JL, Masini RJ (1993) Destruction of corals and other reef animals by coral spawn slicks on Ningaloo Reef, Western Australia, *Coral Reefs* 12:185-191.

Smith SV (1970) *Calcium carbonate budget of the southern California continental borderland*, Hawaii Institute of Geophysics.

Smith SV (1981) The Houtman Abrolhos Islands: Carbon metabolism of coral reefs at high latitude 1, *Limnology and Oceanography* 26:612-21.

Sobel J, Dahlgren C (2004) *Marine reserves: a guide to science, design, and use*, Island Press.

Speed CW, Babcock RC, Bancroft KP, Beckley LE, Bellchambers LM, Depczynski M, Field SN, Friedman KJ, Gilmour JP, Hobbs J-PA, Kobryn HT, Moore JAY, Nutt CD, Shedrawi G, Thomson DP, Wilson SK (2013) Dynamic stability of coral reefs on the West Australian coast, *Plos One* 8(7):e69863.

Stanley Jr, GD (1981) Early history of scleractinian corals and its geological consequences, *Geology* 9(11):507-511.

Stearn CW, Scoffin TP, Martindale W (1977) Calcium carbonate budget of a fringing reef on the west coast of Barbados. Part I – zonation and productivity, *Bulletin of Marine Science* 27:479-510.

Suzuki G, Arakaki S, Suzuki K, Iehisa Y, Hayashibara T (2012) What is the optimal density of larval seeding in Acropora corals? *Fisheries Science* 78:801-808.

Taebi S, Lowe RJ, Pattiaratchi CB, Ivey GN, Symonds G (2012 A numerical study of the dynamics of the wave-driven circulation within a fringing reef system, *Ocean Dynamics* 62:585-602.

TFMPA A (Task Force on Marine Protected Areas) (1999) *Strategic plan of action for the national representative system of marine protected areas: a guide for action by Australian governments*, Australia and New Zealand Environment and Conservation Council.

Thomson DP, Babcock RC, Haywood MD, Vanderklift MA, Pillans RD, Bessey C, ... Wilson SK (2020) Zone specific trends in coral cover, genera and growth-forms in the World-Heritage listed Ningaloo Reef, *Marine Environmental Research* 160:105020.

Thomson DP, Cresswell AK, Doropoulos C, Haywood MD, Orr M, Hoey AS (2021) Hidden giants: the story of *Bolbometopon muricatum* at Ningaloo Reef, *Fishes* 6(4):73.

Trapon M, Pratchett MS, Penin L (2011) Comparative effects of different disturbances in coral reef habitats in Moorea, French Polynesia, *Journal of Marine Biology* 2011:807625.

Trapon ML, Pratchett MS, Hoey AS, Baird AH (2013) Influence of fish grazing and sedimentation on the early post-settlement survival of the tabular coral Acropora cytherea, *Coral Reefs* 32:1051-1059.

Tribollet A, Golubic S (2005) Cross-shelf differences in the pattern and pace of bioerosion of experimental carbonate substrates exposed for 3 years on the northern Great Barrier Reef, Australia, *Coral Reefs* 24:422-434.

Tribollet A (2008) The boring microflora in modern coral reef ecosystems: a review of its roles, in Wisshak M, Tapanila L (eds) *Current developments in bioerosion*, Springer, 67-94.

Turner JA, Thomson DP, Cresswell AK, Trapon M, Babcock RC (2018) Depth-related patterns in coral recruitment across a shallow to mesophotic gradient, *Coral Reefs* 37:711-722.

Underwood JN, Wilson SK, Ludgerus L, Evans RD (2013) Integrating connectivity science and spatial conservation management of coral reefs in north-west Australia, *Journal for Nature Conservation* 21:163-172.

Vanderklift MA, Babcock RC, Barnes PB, Cresswell AK, Feng M, Haywood MD, Holmes TH, Lavery PS, Pillans RD, Smallwood CB (2020) The oceanography and marine ecology of Ningaloo, A World Heritage Area, in Hawkins SJ, Lemasson AJ, Allcock AL, Bates AE, Byrne M, Evans AJ, Firth LB, Marzinelli E, Russell B, Smith I, Swearer S, Todd P (eds) *Oceanography and marine biology*, Taylor & Francis.

Vermeij M (2005) Substrate composition and adult distribution determine recruitment patterns in a Caribbean brooding coral, *Marine Ecology Progress Series* 295:123-133.

Vermeij MJ, Sandin SA (2008) Density-dependent settlement and mortality structure the earliest life phases of a coral population, *Ecology* 89:1994-2004.

Vermeij MJA (2006) Early life-history dynamics of Caribbean coral species on artificial substratum: the importance of competition, growth and variation in life-history strategy, *Coral Reefs* 25:59-71.

Veron JEN (2000) *Corals of the world*. Volume 3. Australian Institute of Marine Science.

Westlake EL, Bessey C, Fisher R, Thomson DP, Haywood MD (2021) Environmental factors and predator abundance predict the distribution and occurrence of two sympatric urchin species at Ningaloo Reef, Western Australia, *Marine and Freshwater Research* 72(12):1711-1721.

Wilson S, Fisher R, Pratchett M, Graham N, Dulvy N, Turner R, Cakacaka A, Polunin N (2010) Habitat degradation and fishing effects on the size structure of coral reef fish communities, *Ecological Applications* 20:442-451.

Wilson S, Kendrick A, Wilson B (2019a) The North-Western Margin of Australia, in Sheppard C (ed) *World seas: an environmental evaluation*, Elsevier, 303-331.

Wilson SK, Depcyznski M, Fisher R, Holmes TH, Noble MM, Radford BT, Rule M, Shedrawi G, Tinkler P, Fulton CJ (2018) Climatic forcing and larval dispersal capabilities shape the replenishment of fishes and their habitat-forming biota on a tropical coral reef, *Ecology and Evolution* 8:1918-1928.

Wilson SK, Robinson JPW, Chong-Seng K, Robinson J, Graham NAJ (2019b) Boom and bust of keystone structure on coral reefs, *Coral Reefs* 38:625-635.

Wolanski E, Hamner WM (1988) Topographically controlled fronts in the ocean and their biological influence, *Science* 241:177-181.

Woo M, Pattiaratchi C, Schroeder W (2006) Dynamics of the Ningaloo current off point cloates, Western Australia, *Marine and Freshwater Research* 24:291-301.

Wood S, Scheipl F (2019) *gamm4: generalized additive mixed models using mgcv and lme4, Version 0.5*. https://cran.r-project.org/web/packages/gamm4/gamm4.pdf

Wood SN (2011) Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models, *Journal of the Royal Statistical Society: Series B (Statistical Methodology)* 73:3-36.

Wooldridge SA (2014) Differential thermal bleaching susceptibilities amongst coral taxa: re-posing the role of the host, *Coral Reefs* 33:15-27.

Xu J, Lowe RJ, Ivey GN, Jones NL, Zhang Z (2016) Ocean transport pathways to a world heritage fringing coral reef: Ningaloo Reef, Western Australia, *PLoS One* 11:e0145822.

Yarlett RT, Perry CT, Wilson RW, Philpot KE (2018) Constraining species-size class variability in rates of parrotfish bioerosion on Maldivian coral reefs: implications for regional-scale bioerosion estimates, *Marine Ecology Progress Series* 590:155-169.

Zawada KJA, Madin JS, Baird AH, Bridge TCL, Dornelas M (2019) Morphological traits can track coral reef responses to the Anthropocene, *Functional Ecology* 33:962-975.

Zhao J, Barnes B, Melo N, English D, Lapointe B, Muller-Karger F, Schaeffer B, Hu C (2013) Assessment of satellite-derived diffuse attenuation coefficients and euphotic depths in south Florida coastal waters, *Remote Sensing of Environment* 131:38-50.

Zinke J, Rountrey A, Feng M, Xie S-P, Dissard D, Rankenburg K, Lough JM, and McCulloch MT (2014) Corals record long-term Leeuwin current variability including Ningaloo Niño/Niña since 1795, *Nature Communications* 5:3607.