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Effects of macroalgal removal on inshore coral reef communities and sedimentation dynamics

Thesis submitted by
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Reports

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Abstract

Growing evidence shows some inshore coral reefs of the Great Barrier Reef [GBR] have experienced declines in coral cover and concomitant increases in macroalgal growth. An increasing abundance of fleshy macroalgae is a widely accepted indicator of reef degradation and a recognised threat to coral ecosystem functioning. Removal of macroalgae has been proposed as one approach to assist coral recovery by removing a biological barrier, thereby increasing benthic space for coral recruitment and reducing competition. However, there is limited understanding of the wider ecological impacts of macroalgal removal on benthic reef communities. Alongside increased macroalgal abundance, inshore areas of the GBR are also confronted with higher sedimentation stress than offshore reefs. Sedimentation stress is a major factor influencing the structure of coral communities and post-disturbance recovery. In addition, algal turf communities under high sediment loads can result in substrate unsuitable for coral recovery. Macroalgal removal may eliminate a biological barrier to coral recovery, however it may also affect sedimentation of the benthos, influencing reef recovery capacity. Assessing the relationships between sedimentation of benthic organisms and algal turfs following macroalgal removal on inshore reefs is therefore necessary to evaluate the potential of this technique to assist coral recovery.

The impact of periodic manual removal of macroalgae on percent cover and community composition of benthic organisms was investigated on the fringing reefs of Magnetic Island in the central GBR. Fleshy macroalgae (predominantly *Sargassum* spp.) were removed from 12 established 25 m^2 treatment plots (referred throughout as ‘removal’ plots; n = 6 Arthur Bay, n = 6 Florence Bay) two to three times per year between 2018 and 2021. The percent cover of benthic organisms and community composition was quantified and compared to 12 established 25 m^2 control plots (n = 6 Arthur Bay, n = 6 Florence Bay), not subjected to macroalgal removal. One removal event per year was timed to precede mass coral spawning. Surveys were conducted before and after removal events, as well as during summer to capture seasonal variation. The benthic community composition was quantified by assessing 25 1 m^2 photo-quadrats within each larger 25 m^2 plot. A reduction in macroalgal cover and a rise in hard coral cover was observed in removal plots after three years of periodic macroalgal removal (2018: 81.35% macroalgae, 5.65% coral; 2021: 37.84% macroalgae, 35.09% coral) compared to control plots (2018: 87.04% macroalgae, 7.47% coral; 2021: 83.39% macroalgae, 10.39% coral). Whilst there was strong evidence for an increase in coral cover in removal plots, this result is due not only to the positive effect of macroalgal removal on coral recovery, but also partially due to the sampling artefact of increased visibility of corals in the absence of a macroalgal canopy. The composition of

macroalgal and coral communities was altered through time in removal plots, with reduced *Sargassum* spp. abundance and a greater diversity of other macroalgal genera including *Hypnea, Amphiroa, Padina, Colpomenia,* and *Lobophora*. Coral diversity, however, did not change in response to macroalgal removal.

Sediment deposition and algal turf environments were investigated by deploying SedPods and TurfPods (devices designed to mimic hard coral and algal turf surfaces, respectively). The pods were placed into removal and control plots for one week at a time. The relationships between macroalgal canopies, sedimentation, and turf communities were investigated by measuring sediment deposition, organic content, particle size, and algal turf height in areas where the macroalgal canopy had been manually removed compared to control areas. Removal of fleshy macroalgae (predominantly *Sargassum* spp.) from removal plots was found to have no significant effect on the amount or composition of sediment deposited on proxy coral and algal turf surfaces. In addition, the height of algal turfs was not significantly impacted by the removal of the macroalgal canopy. These results suggest that macroalgal removal is unlikely to expose corals and algal turfs to increased sedimentation, nor alleviate existing sediment-related stress. However, sediment dynamics are complex within reef ecosystems, thus, longer-term studies over a larger area are required to fully determine the impacts of changed benthic composition on sediment dynamics.

Results from this three-year study demonstrate that macroalgal removal may be an effective approach to assist inshore reef ecosystems toward a state more conducive to coral recovery. Periodic removal resulted in less re-growth of macroalgae over time, and, combined with potentially reduced competition with the dominant *Sargassum* spp., coral cover increased significantly. These findings will help to inform decision making by end-users and assist in developing science-based best-practices for localised inshore reef recovery on the GBR.

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Chapter 1: General Introduction

1.1 The Great Barrier Reef – coral reef communities at risk

Coral reefs worldwide are changing rapidly in both structure and function. These changes are primarily attributable to climate change stressors such as increasing sea surface temperatures, ocean acidification, and increasing frequency and severity of cyclones (Hughes et al., 2017). Global changes are exacerbated by local stressors, including overfishing and marine pollution, which have significant consequences for coral reef ecosystem goods and services (Bellwood, Streit, et al., 2019; Hughes et al., 2017). Essential ecosystem goods and services provided by coral reefs include supporting reef biodiversity, providing natural coastline protection, cycling nutrients, and generating income for industry stakeholders like tourism and fisheries (Woodhead et al., 2019). The Great Barrier Reef [GBR], for example, contributes $6.4 billion per year and 64,000 full-time jobs to the Australian economy, generated largely by tourism (Deloitte Access Economics, 2017). Coral reef degradation, therefore, is a serious threat to dependent livelihoods, national economies, and biological diversity.

The GBR comprises almost 3,000 individual reefs spanning over 2,300 km and represents one of the most biodiverse regions in the world, encompassing significant cultural and economic value (Great Barrier Reef Marine Park Authority [GBRMPA], 2019). This is reflected by the long-standing status of the GBR as a World Heritage site since 1981 (GBRMPA, 2019). In the last six years, the GBR has experienced an increasing frequency of thermal bleaching with four mass bleaching events (2016, 2017, 2020, 2022) impacting vast regions of the GBR (ARC Centre of Excellence for Coral Reef Studies, 2020; GBRMPA, 2019, 2020; GBRMPA et al., 2022). Cyclones, crown-of-thorns starfish [CoTS] (*Acanthaster planci*) outbreaks, and chronic poor water quality from sub-optimal land-use practices have also punctuated the disturbance and recovery cycles on the GBR (Haapkylä et al., 2013; Jones et al., 1997; Schaffelke et al., 2017). The combined impact of these stressors have shaped the trajectory of coral reef ecosystems, demonstrated by a decline in coral cover on the GBR by more than 50% between 1985 and 2012 (De'ath et al., 2012), and a loss of 27.6% of all coral between 1996 and 2019 (Abdo et al., 2021). Additional localised declines have occurred in more recent years following the 2016, 2017, and 2020 bleaching events (Abdo et al., 2021; GBRMPA, 2019; Hughes et al., 2018; Thompson et al., 2021). Overall, the GBR has been recovering since cyclone Debbie in 2017, with coral cover increasing on average (GBRMPA et al., 2022). This suggests GBR reef ecosystems are still capable of recovery under chronic stress However, thermal stress induced by the 2022 bleaching event is likely to compromise this recovery period on many GBR reefs, particularly inshore areas (GBRMPA et al., 2022).

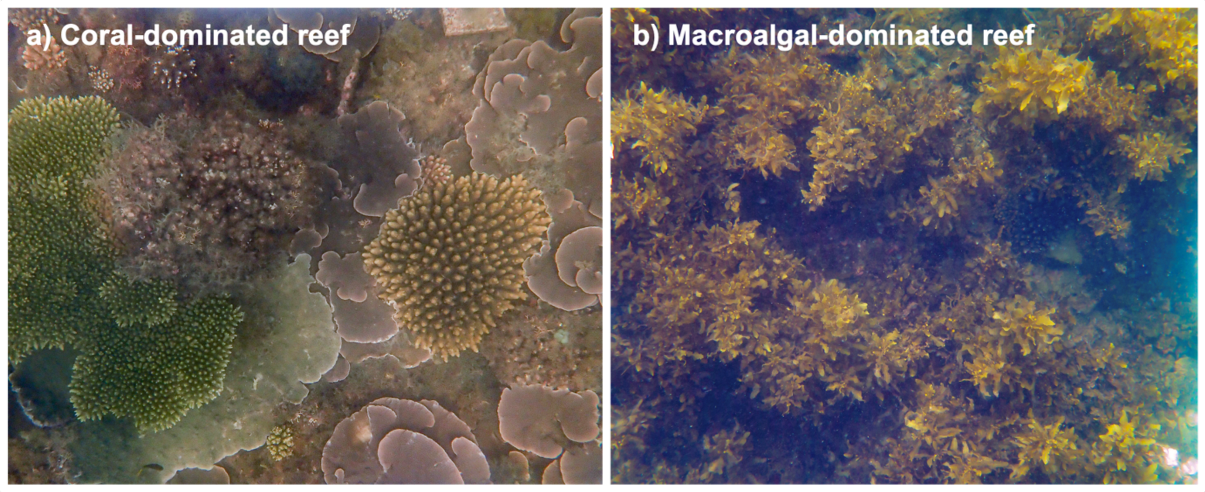


Figure 1.1 *Images of fringing reef at Magnetic Island dominated by **(a)** corals and **(b)** macroalgae*

Inshore reefs of the GBR are impacted to a higher degree by poor water quality relative to reefs further offshore as a result of land-based runoff (Schaffelke et al., 2017). Along with climate change, poor water quality is one of the greatest threats affecting the inner shelf of the GBR (GBRMPA, 2019). Shifts in benthic community composition of many inshore reefs have been characterised by substantial declines in hard coral cover over the last two decades (Ceccarelli et al., 2020). A shift away from coral dominance with concurrent increasing overgrowth by fleshy macroalgae is a generally accepted indicator of coral reef degradation (Birrell et al., 2008; Ceccarelli et al., 2020; Diaz-Pulido & McCook, 2008; Done, 1992; Williamson et al., 2019; Figure 1.1). A higher abundance of macroalgae can be perpetuated via feedback mechanisms which prevent the recovery of coral populations via sexual recruitment or growth (Birrell et al., 2008; Johns et al., 2018). This leads to a loss of reef resilience and potentially a persistent shift of benthic communities which alter the function of coral reef ecosystems (Birrell et al., 2008; Fulton et al., 2019). While macroalgae have an important role in healthy coral reef ecosystems (Fulton et al., 2019), their competitive expansion currently impacts the community composition of some inshore reefs of the GBR (Thompson et al., 2021). This highlights the need to better understand macroalgal dynamics and investigate novel management strategies at a local scale to maintain the ecosystem function of inshore reefs of the GBR (Ceccarelli et al., 2018; Hughes et al., 2017).

1.2 Ecological Succession and Reef Resilience

The concept of ecological resilience requires understanding of ecological succession theory. As ecosystems recover following an ecological disturbance, fast-growing, early-stage successional species are the first to colonise an area, and over time, slower-growing later-stage successional species gradually compete with or are facilitated by the earlier successional stage species (Connell & Slatyer, 1977). Species interactions and environmental conditions influence the process of ecological succession (Doropoulos et al., 2017). On coral reefs, early colonists are generally turf algae, followed by calcareous algae (e.g., *Halimeda),* crustose coralline algae (e.g., *Porolithon*), and fleshy brown algae (e.g., *Sargassum, Padina, Dictyota*), with secondary colonists being sessile invertebrates (e.g., soft and hard corals) (Doropoulos et al., 2017; McClanahan, 1997). If early-stage colonising organisms such as macroalgae, proliferate and inhibit the growth of subsequent colonists due to environmental conditions (e.g., high nutrient levels, thermal stress), then the trajectory of the reef community can shift (Fukunaga et al., 2022). A macroalgal dominated reef community can, therefore, represent a natural, early stage of recovery, or it can signify an altered trajectory in succession, precluding later-stage successional species such as hard corals from becoming established (Dudgeon et al., 2010).

Concepts related to coral reef ecological resilience have been shaped by the influential review on ecological theory by Holling (1973) as the ‘ability to absorb shocks, re-establish functional systems after disturbances, and adapt to change’ (Bellwood et al., 2004; Folke et al., 2004; Hughes et al., 2007, 2010; Mumby & Steneck, 2011; Nyström et al., 2000). The increasing frequency and severity of acute disturbances such as mass bleaching events and tropical storms paired with local stressors is effectively diminishing the resilience of many coral reef ecosystems (Hughes, 2003; Hughes et al., 2010). Coral reef systems with diminished resilience are vulnerable to dramatic and persistent shifts in community composition due to disrupted ecological succession, reduced capacity for recovery and re-organisation following acute disturbances (e.g., cyclone, mass bleaching event), or the inability to adapt to chronic disturbance (e.g., nutrient loading from terrestrial runoff). Persistent shifts from biodiverse communities dominated by reef-building organisms (i.e., scleractinian corals) to monospecific, non-reef building communities (e.g., macroalgae, sponges, corallimorphs) often result in reduced capacity to provide ecosystem goods and services (Alvarez-Filip et al., 2013; Woodhead et al., 2019). Maintaining key processes and functions that promote ecological resilience has been identified as a priority for reef management and essential to preserving coral reef ecosystems into the future (Bellwood, Streit, et al., 2019; Commonwealth of Australia, 2018; Turner et al., 2020).

1.2.1 The ‘phase shift’ phenomenon

Many examples exist globally of coral reefs undergoing a persistent shift in community composition from coral dominance to macroalgal dominance (Done, 1992), or other non-reef building organisms such as sponges or corallimorphs (Norström et al., 2009). This phenomenon has often been referred to in the literature as a ‘phase shift’. However, there has been heated discussion centred on the most appropriate terminology (i.e., phase shift vs.

alternative stable state) due to uncertainties regarding coral reef ecosystem stability (Crisp et al., 2022; Dudgeon et al., 2010; Knowlton, 2004). Strictly speaking, a 'phase shift' is a continuous shift in response to crossing a critical threshold in environmental conditions, from the equilibrium state (e.g., coral dominated community) to a different equilibrium state (e.g., macroalgal dominated community), which may confer more or less stability and resilience than the previous state (Dudgeon et al., 2010). Critically, there exists only one stable equilibrium state for any set of environmental conditions. In contrast, alternative stable states involve a discontinuous 'jump', whereby the new equilibrium state is stable under the same set of environmental conditions as the original equilibrium state. This dynamic can make it more difficult to shift back to the original equilibrium state (Dudgeon et al., 2010; Knowlton, 1992; Petraitis & Dudgeon, 2004). The outcomes underpinning the phenomenon of a persistent shift are clear regardless of the specific terminology used, and manifest as a dramatic change in community structure. Where persistent shifts occur, they are generally a result of diminished resilience within the ecosystem resulting from an external shock (e.g., cyclones or bleaching events), which is usually catalysed by chronic anthropogenic stress (Dudgeon et al., 2010). When coral reefs are functionally dominated by organisms other than hard corals, reinforcing feedback mechanisms can perpetuate a system devoid of biodiversity (van de Leemput et al., 2016). The emphasis on function is critical, because it is important to recognise coral reef ecosystems can take on a variety of forms yet still perform key functions. Recent work has demonstrated the value of different reef states with naturally high levels of macroalgae or non-reef building organisms (Fulton et al., 2019). Despite this, the classic example of a coral-dominated reef shifting to a macroalgal-dominated ecosystem has been heavily studied, most notably in the Caribbean where these shifts have been documented on fringing reef ecosystems dating back half a century (Hughes, 1994). Figure 1.2 illustrates the 'phase shift' phenomenon, which is used throughout to demonstrate the conceptual and theoretical basis of this thesis.

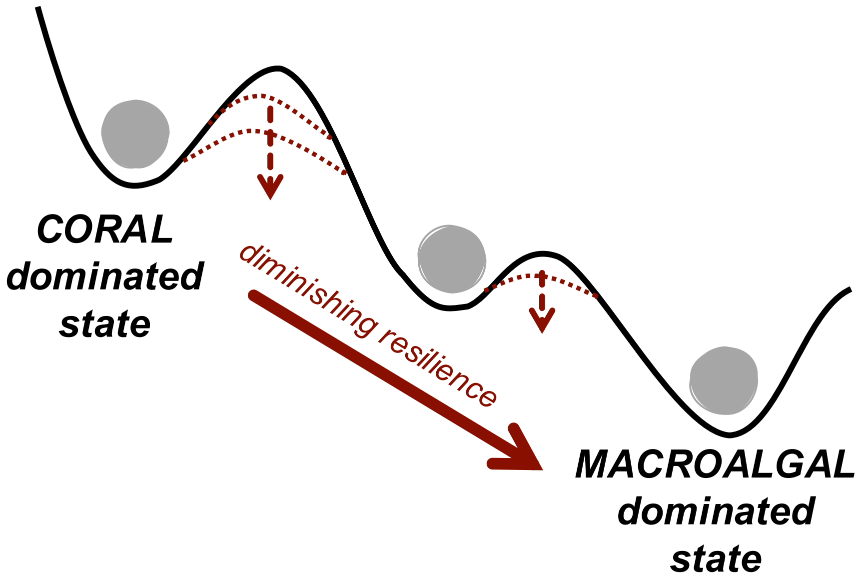


Figure 1.2 *A conceptual representation of reef degradation from a coral- to macroalgal-dominated state due to loss of resilience (shown in red), catalysing a shift in reef state (represented by grey circles) to alternative, degraded states dominated by non-reef building organisms. Adapted from McDonald et al., 2016 and Mumby & Steneck, 2011.*

1.2.2 Origins in the Caribbean

Undoubtedly the most influential case study was the dramatic shift from coral- to macroalgal-dominated reefs in Discovery Bay, Jamaica in the 1980s, which has been widely cited and is now synonymous with the ‘phase shift’ phenomenon (Hughes, 1994). The abrupt shift in community composition was triggered in 1983 by the disease-induced mass mortality of the urchin *Diadema antillarum*. At the time, *D. antillarum* was responsible for most of the grazing pressure exerted on macroalgal communities. Chronic over-exploitation of herbivorous fish throughout the 1950s and 1960s effectively diminished the resilience of the system (Hughes, 1994). In 1980, Hurricane Allen caused widespread coral mortality throughout the Caribbean, after which some coral recovery did occur due to the presence of urchins keeping macroalgal cover at bay. The lack of resilience was fully realised in 1983 when reduced urchin populations and existing low levels of herbivorous fish triggered macroalgal proliferation and concurrent coral decline. In this example, a lack of herbivory was the key driver for the persistent shift in community composition. This is often identified as the greatest contributing factor to dramatic shifts on Caribbean reefs, since widespread historical overfishing reduced the ecological resilience of many reefs in this region (Jouffray et al., 2015). Additional contributing factors have been suggested, however, including fast macroalgal growth rates, high algal recruitment, and iron-enrichment of algal growth (Roff & Mumby, 2012). Compounded by coral disease outbreaks and reduced structural complexity, the loss of resilience from Caribbean reef ecosystems facilitated localised stressors to further trigger dramatic shifts to degraded macroalgal-dominated reef states, with severely reduced coral populations (Cramer, Jackson, et al., 2020; Cramer, O'Dea, et al., 2020; Gardner, 2003).

Other examples of shifts from coral- to macroalgal-dominated ecosystems in the Caribbean include the lionfish invasion to mesophotic depths in the Bahamas, triggering *Lobophora* spp. overgrowth (Lesser & Slattery, 2011; Slattery & Lesser, 2014); tourist infrastructure development triggering macroalgal proliferation and coral decline in Mexico (Martinez-Rendis et al., 2016); and a phase shift from coral- to macroalgal-dominance occurring throughout 1996 to 2000 in the Florida Keys National Marine Sanctuary (Maliao et al., 2008). The seminal work on reef community shifts documenting sharp declines in coral communities and parallel expansion of fleshy macroalgae guided future research, emphasising the coral-macroalgal shift and the influence of herbivory. As research has expanded to regions other than the Caribbean, it has become apparent that the drivers of persistent ecosystem change and mechanisms for loss of resilience are not uniform and are often region-specific. For example, reef community shifts documented in the Seychelles were triggered by the 1998 global mass bleaching event (Ledlie et al., 2007), recovery from which was dependent on the role of key fish species (Graham et al., 2015). In Palau, it was the 2012 cyclone that triggered a shift to *Lobophora* spp. dominated communities in areas of high wave exposure, facilitated by an initial bloom of *Liagora* spp., with herbivory not purported to directly contribute to this shift (Mumby et al., 2016; Roff, Chollett, et al., 2015; Roff, Doropoulos, et al., 2015). Other benthic organisms such as sponges and corallimorphs are now known to be just as pervasive as macroalgae in their capacity to dramatically alter reef communities (Norström et al., 2009). Even supposedly resilient reef regions, such as offshore areas of the GBR and regions within the Central Pacific, are at risk of persistent shifts in reef community composition due to shock events such as shipwrecks (Hatcher, 1984; Kelly et al., 2012). Importantly, the mechanisms for such change are an artefact of historical impacts, closely tied to socioeconomic and cultural parameters (e.g., fishing practices, tourism, infrastructure development), exemplified by the Caribbean example of historical over-fishing of herbivores.

1.2.3 How does this relate to ecosystem change on inshore GBR reefs?

There is some evidence that the observed trends of inshore reef community change on the GBR align with the 'phase shift' phenomenon, namely persistent coral decline paired with prolific macroalgal overgrowth on some inshore reefs (Ceccarelli et al., 2020; Cheal et al., 2010; Done, 1992; McCook, 1999; Thompson et al., 2021). The causal mechanisms are complex but appear to be related to poor water quality (i.e., increased nutrient levels, sedimentation, and turbidity) compromising coral recovery following acute disturbances such as cyclones, mass bleaching and predator outbreaks (Ceccarelli et al., 2020; Roff et al., 2013). The suspected drivers of benthic community change on inshore GBR reefs are seemingly distinct from the decline in herbivory responsible for many Caribbean case studies, since herbivore populations have not been historically over-exploited on the GBR (Abdo et al., 2021). For example, a recent meta-analysis of inshore GBR reefs highlighted that herbivorous fish density was not as influential as expected in driving changes in community structure (Ceccarelli et al., 2020). Evidence suggests that water quality is more influential on coral recovery rates compared to herbivory, though these relationships are poorly understood due to the historical emphasis on herbivory as a key driver, derived from Caribbean based case studies (MacNeil et al., 2019). Further studies at the local scale to delineate mechanistic drivers of persistent community change on inshore GBR reefs (for example, Bellwood et al., 2006; Ceccarelli et al., 2020; Hoey & Bellwood, 2011; Lam et al., 2018) is, therefore, necessary to manage these valuable ecosystems into the future.

1.3 Managing the Great Barrier Reef: localised restoration strategies

Management of reefs within the GBR is guided by action plans involving partnerships between government, Traditional Owners, local community members and other stakeholders (GBRMPA, 2019). The Reef 2050 Long Term Sustainability Plan (Reef 2050 Plan), released in 2015 and updated in 2018, is the current management framework synthesising action plans for the GBR (Commonwealth of Australia, 2018). The Reef 2050 Plan shifts the focus from traditional management to increase actions to improve reef resilience, such as changing land use practices to improve water quality, increasing CoTS control and implementing techniques to actively restore coral populations. Notwithstanding the underlying priority of reducing greenhouse gas emissions, locally focused management efforts are paramount to improving reef health (Boström-Einarsson et al., 2020; Ceccarelli et al., 2020; Williamson et al., 2019). The revised Reef 2050 Plan includes a new priority to ‘undertake localised restoration activities’ (Commonwealth of Australia, 2018). Developing active intervention methods that are ecologically effective and financially viable have been identified as an urgent research challenge (Anthony et al., 2020). These objectives, however, have been difficult to achieve due to barriers associated with coral restoration effectiveness and scale (Bellwood, Pratchett, et al., 2019; Boström-Einarsson et al., 2020; Hughes et al., 2017). The urgency of addressing such challenges is reflected in recent Australian government investment aimed specifically at accelerating progress towards meeting the targets outlined in the revised Reef 2050 Plan (Department of Climate Change, Energy, the Environment and Water, 2022).

A review by Boström-Einarsson et al. (2020) highlighted a diversity of techniques and technologies that are being developed to facilitate coral recovery and rehabilitate coral reef ecosystems. Techniques such as coral gardening, larval enhancement, substratum stabilisation or enhancement, among others, are gaining traction. However, rigorous monitoring of such techniques as well as a consensus on what metrics to consider when assessing effectiveness are still lacking (Boström-Einarsson et al., 2020). Physical removal of macroalgae is a form of substratum enhancement, which has been proposed as a localised intervention approach to aid coral recovery for inshore reefs overgrown by fleshy macroalgae through clearing space for coral juveniles to settle and reducing competition with adult coral colonies (Ceccarelli et al., 2018; Mastroianni, 2019; Neilson et al., 2018). Modelling studies indicate the theoretical success of removing herbivory-resistant mature macroalgal stands on coral reefs (Briggs et al., 2018), however, the empirical scientific basis asserting the efficacy of macroalgal removal and the impacts on inshore reef ecology is limited.

Some experimental trials of macroalgal removal have shown positive impacts on coral reef habitats at local scales. For example, removal of macroalgae from experimental plots around Heron Island (southern GBR) led to increased growth and fecundity of *Acropora* spp. (Tanner, 1995). Removal of the dominant native macroalgae *Sargassum* spp. from Kenyan reefs led to an increase in the calcified algae *Halimeda* spp., and resulted in taxa-specific increases in herbivory, facilitating low re-growth of fleshy macroalgae (McClanahan et al., 2002; McClanahan et al., 1999). In Hawaii, removal of invasive macroalgal species supplemented with urchin biocontrol has been effective in shifting the reef community towards assemblages more conducive to coral recovery (Conklin & Smith, 2005; Hancock et al., 2017; Kittinger et al., 2016; Neilson et al., 2018). More recently, removal of *Turbinaria* spp. from French Polynesian reefs was shown to increase coral recruitment but only when holdfasts were removed (Bulleri et al., 2018). Similarly, benefits to coral recruitment were demonstrated following removal of canopy-forming macroalgae (predominantly *Sargassum* spp.) from an inshore GBR reef (Smith et al., 2021). In contrast, experimental macroalgal reduction in Belize resulted in rapid algal regrowth and negligible coral recovery despite increased herbivore populations (McClanahan et al., 2001). The effectiveness of macroalgal removal may, therefore, be dependent on supplementary efforts including herbivore enhancement and fisheries management, as well as how and when the macroalgal removal effort is implemented (Ceccarelli et al., 2018). Furthermore, environmental factors such as water flow may be potentially more influential in governing coral health compared to macroalgal cover. (McClanahan et al., 2001; McClanahan et al., 2000, 2011). For example, McClanahan et al. (2011) found that bleaching and mortality of *Porites asteroides* were higher in unfished reef areas cleared of macroalgae compared with control areas. They attributed this to low water flow due to the positive relationship found between water flow and *P. asteroides* growth rate (McClanahan et al., 2011). On the GBR, reef fisheries are relatively well managed and it is apparent that macroalgal increases are not attributable to reduced herbivore populations (GBRMPA, 2019). Therefore, the increasing dominance of native macroalgal species on some reefs (e.g., Magnetic Island, Keppel Island) warrants investigation of the region-specific drivers of macroalgal population dynamics (Ceccarelli et al., 2018, 2020). Macroalgal removal experiments present an opportunity to improve understanding of altered ecosystem structure and function, and how active intervention efforts could be implemented to manage inshore reefs (Ceccarelli et al., 2018; Hughes et al., 2017).

1.4 Local stressors impacting inshore reefs of the GBR

Inshore reefs of the GBR region warrant attention due to tight coupling with anthropogenic pressures resultant from their proximity to the coastline and the value they provide to coastal community economies (McCook, 1999). In contrast to their offshore counterparts, inshore reefs are characterised by naturally higher turbidity due to terrestrial runoff and higher nutrient concentrations due to their proximity to coastal development and agricultural runoff (De’ath & Fabricius, 2010; McCook, 1999; Thompson et al., 2021). These differences underpin the variability in species composition between inshore and offshore reefs within the GBR, with inshore reefs generally characterised by more abundant macroalgal communities, lower fish abundance, and less diverse coral communities adapted to high levels of turbidity and nutrients (Boström-Einarsson et al., 2020; De’ath & Fabricius, 2010; McCook, 1999; Sofonia & Anthony, 2008). Some of these features, such as high macroalgal abundance, can also be representative of reef degradation. However, for many inshore reefs that have persisted through time as functional ecosystems, these features may also be characteristics of communities well-adapted to local environmental conditions. Evidence suggests turbid shallow inshore reefs have the capacity to accommodate rich and diverse coral reef assemblages, highlighting the importance of distinguishing between localised adaptation and degradation (Fabricius, 2005; Fulton et al., 2019; Hughes et al., 2007; Schaffelke et al., 2017). Physical and biological variability (e.g., wave exposure, rugosity, species interactions) occurs not only across reef regions but between and within individual reefs. As a result, localised knowledge is needed to understand complex reef dynamics and local drivers of ecosystem change on a per-reef basis. Long-term assessments, however, have suggested that some inshore and offshore reefs of the GBR are experiencing parallel trends of coral decline and community shifts to low complexity coral communities, though the underlying causal mechanisms are distinct (Fine et al., 2019).

1.4.1 Water quality: a major local stressor for inshore reefs

Water quality is a strong predictor of coral reef health on the GBR, driving variation in species distribution and diversity (De'ath & Fabricius, 2010; Fabricius, 2005). Poor water quality is the major local stressor for inshore GBR reefs, due to their proximity to anthropogenic inputs of pollutants, and is driven primarily by agricultural industries as well as urban and industrial development (Ceccarelli et al., 2020; De'ath et al., 2012; GBRMPA, 2019; Roff et al., 2013; Schaffelke et al., 2005; Thompson et al., 2021). Water quality parameters that can detrimentally affect reef ecosystems include elevated levels of dissolved inorganic nutrients, particulate matter and organic aggregates; increased herbicides, pesticides, and heavy metals; as well as debris such as plastics (Fabricius, 2005; Schaffelke et al., 2005, 2017; Waterhouse et al., 2021). Of these components, nutrient and sediment loads are thought to be the major stressors for inshore reefs due to their impact on benthic communities (Schaffelke et al., 2017). There is substantial variation in nutrient and sediment loading of inshore reef waters dependent on local catchment attributes such as land use, soil type, slope angle, vegetation cover, distance to major river outlets, rainfall, and hydrodynamics (Schaffelke et al., 2005). These factors affect nutrient and sediment concentrations at localised scales and fluctuate spatially and temporally in response to episodic disturbance (De'ath & Fabricius, 2010; Schaffelke et al., 2005). For example, inshore chlorophyll *a* [Chl *a*] concentrations (indicative of nitrogen [N] and phosphorous [P] loads) vary considerably, with concentrations two to three times greater in the central and southern GBR regions relative to the northern region, attributed to variation in agricultural activity (Haynes et al., 2007). Furthermore, during flood events in the summer wet season (November - April), nutrient and sediment levels can be 10 to 400 times higher compared to the dry season (Devlin et al., 2001; Schaffelke et al., 2005). Flood events therefore become the major mechanism for nutrient and suspended sediment delivery to coastal GBR waters (Furnas, 2003; Schaffelke et al., 2005; Waterhouse et al., 2021). In addition, global climate change is increasing the frequency and severity of flood events, further exacerbating water quality stressors (Haynes et al., 2007; Schaffelke et al., 2017). Current estimates of fine sediment delivery to the GBR lagoon are on average five times greater than prior to European colonisation in the mid-1800s (Furnas, 2003; GBRMPA, 2019).

Poor water quality resulting from terrestrial runoff affects inshore reef communities in various ways including reducing coral reproduction, recruitment, and calcification rates (Fabricius, 2005; Uthicke et al., 2014). Water quality is also linked with increasing primary production, causing micro- and macro-algal blooms (Schaffelke et al., 2005; Waterhouse et al., 2021). These changes impact species interactions such as competition, predation, and herbivory. The risks of poor water quality to inshore reef ecology remain prevalent, with severe consequences for coral recovery and ecosystem-wide resilience (GBRMPA 2019; Gruber et al., 2019; MacNeil et al., 2019). Strong evidence exists linking high macroalgal cover and poor water quality on GBR reefs, highlighting the role of water quality in potentially driving persistent shifts from coral- to macroalgal-dominated communities (De'ath & Fabricius, 2010; Schaffelke et al., 2005). As such, current management priorities focus on improving land-based catchment activities to mitigate water quality issues on inshore reefs.

1.4.1.1 Increased nutrient loads: impact on inshore reef communities

Elevated nutrients, primarily N and P, have varied impacts on inshore reef communities. In particular, it is thought that dissolved inorganic N presents the greatest threat to GBR ecosystem change, due to its accessibility for uptake by primary producers such as phytoplankton, macroalgae, and microalgal coral symbionts (Schaffelke et al., 2017). Increased nutrient uptake by these organisms leads to increased photosynthesis, boosting growth and reproduction (Schaffelke et al., 2017). Key demographic processes of reproduction, recruitment, and growth of reef organisms are, therefore, affected by increased nutrients, and concurrently, species interactions through symbiosis, predation, and herbivory are also altered (Fabricius, 2005).

For hard corals, the effects of N and P are often adverse (Schaffelke et al., 2017). Coral reproduction and recruitment are sensitive to elevated nutrient concentrations, causing detrimental effects on early life stages (Bassim & Sammarco, 2003; Fabricius, 2005; Gil, 2013; Haynes et al., 2007; Ward & Harrison, 1997). At increased levels of dissolved inorganic nutrients, the widespread coral genus *Acropora* suffers reductions in fecundity, egg size, fertilisation rate of eggs, and embryo development (Fabricius, 2005; Humanes et al., 2017), though little is known about the specific causal mechanisms. Furthermore, vulnerability of corals to disease and thermal stress is heightened when exposed to increased nutrients (e.g., *Diploria strigosa* larval development and mortality significantly reduced (Bassim & Sammarco, 2003)), which can occur as a result of flood events (Haapkylä et al., 2011). For example, microbial activity is enhanced by high levels of dissolved organic carbon which can promote coral disease (Gruber et al., 2019). Interactions between corals and other reef organisms, such as through trophic links including predation, are also affected by high nutrient concentrations. Specifically, nutrient increases have been linked to CoTS outbreaks, which are a serious threat to coral populations (Brodie et al., 2005; Brodie et al., 2017; Fabricius et al., 2010; Pratchett et al., 2017). Despite increased susceptibility to disease and predator outbreaks, coral communities exposed to poor water quality have been found to be more resistant to bleaching relative to corals on reefs further offshore (MacNeil et al., 2019). This community level resistance has been attributed to a coral community composed of species more tolerant to acute and chronic disturbance. However, the rate of post-disturbance coral recovery observed on poor water quality reefs has been low, despite apparent localised acclimation (MacNeil et al., 2019). The effect of poor water quality on coral recovery, therefore, reduces overall reef resilience but is likely to be highly site-specific (GBRMPA, 2019; MacNeil et al., 2019).

In contrast to the effects of nutrients on coral, nutrient enrichment generally tends to favour marine algae. For micro- and macro- algae, elevated nutrient levels lead to increases in primary production and consequent increases in growth, which can alter the structure of inshore reefs due to the canopy- and habitat-forming nature of many fleshy macroalgal species (Fabricius, 2005; Schaffelke et al., 2005, 2017; Thompson et al., 2019). Macroalgal populations have been found to increase along water quality gradients with higher algal abundance correlating with higher levels of dissolved nutrients (De'ath & Fabricius, 2010; Fabricius & De'ath, 2004). Despite high productivity and growth, many macroalgal species are N- or P-limited (Fabricius & De'ath, 2004; McCook, 1999). On inshore reefs, the fleshy, canopy-forming *Sargassum* spp. is naturally widespread and has a seasonal growth pattern with high abundances observed in the summer and senescence in the winter (Martin-Smith, 1993; Schaffelke et al., 2005). During flood events, when nutrients are in excess, *Sargassum* spp. have the capacity to store surplus nutrients to sustain prolonged periods of increased productivity (Schaffelke et al., 2005). The impact of nutrients on macroalgal growth and health is complex, due to species-specific responses. Slow-growing macroalgal species such as *Chlorodesmis fastigiata* and *Turbinaria ornata* are not nutrient limited and are therefore more likely to be regulated by grazing (Schaffelke et al., 2005). Co-regulation of macroalgal populations via nutrient availability and herbivory makes it difficult to determine causal relationships between nutrients and macroalgae in complex reef ecosystems (Diaz-Pulido & McCook, 2003; Fabricius, 2005; Smith et al., 2010). Some evidence suggests herbivory may be a stronger driver of macroalgal population dynamics compared with nutrients, however the relative importance of bottom-up versus top-down processes is likely to be taxa-specific (Diaz-Pulido & McCook, 2003). In contrast, observations of increased growth of inshore macroalgal populations under excess nutrient conditions even when herbivory is high suggests that water quality may be a more influential regulating factor on these reefs (Fabricius, 2005).

Due to their high nutrient demand and capacity to access nutrients in different forms, many macroalgal species are likely to thrive in areas exposed to high levels of terrestrial runoff; conditions which are typical of inshore reefs (De'ath & Fabricius, 2010; Schaffelke et al., 2005). Since corals demonstrate largely negative responses to increased nutrients and are in direct competition with macroalgae for light, space, and food, inshore reefs are at greater risk of coral decline and concurrent macroalgal growth compared to offshore reefs (Haynes et al., 2007). This emphasises the necessity to closely monitor and manage inshore reef communities alongside water quality management.

1.4.1.2 Increased sediment loads: impact on inshore reef communities

High levels of suspended sediment are also typical of inshore GBR reefs and are generally derived from land-based runoff. High sediment loads lead to increased turbidity and sedimentation due to deposition of heavier particles on benthic organisms (GBRMPA, 2019). The combined impacts of turbidity and sedimentation are among the greatest stressors to inshore reefs, causing shading, smothering, and burial of benthic organisms (Schaffelke et al., 2005). Fine sediments (<63 μm) are of the greatest concern, as they can remain suspended in the water column for extended periods, prolonging the impact of turbidity-induced light reduction (Brodie et al., 2017; GBRMPA, 2019; Schaffelke et al., 2017). While many naturally turbid inshore reefs are home to healthy coral populations, events increasing sedimentation may be detrimental (Castro et al., 2012). Sediment overload can compromise the competitive advantage of corals against other benthic organisms (including macroalgae), hampering recovery of reef assemblages following disturbances (Crabbe & Smith, 2005; Evans et al., 2020; Fabricius & De'ath, 2004; Junjie et al., 2014). High sediment stress may, therefore, drive shifts to less diverse but well-adapted coral assemblages as well as increasing macroalgal populations, thus altering reef ecosystem structure and function (Fabricius, 2011; Haynes et al., 2007; Schaffelke et al., 2017; Sofonia & Anthony, 2008).

Sediment deposition on benthic reef organisms can have both positive (e.g., heterotrophy (Anthony & Fabricius, 2000; Rosenfeld et al., 1999)) and negative effects (e.g., smothering (Fabricius & Wolanski, 2000; Jones et al., 2019)). However, the physiological response is dependent on species-specific capacity to acclimate to sediment loading and low light (Junjie et al., 2014; Sofonia & Anthony, 2008). This discrepancy in response drives species distribution along turbidity and depositional gradients (Junjie et al., 2014). The predominant effect of increased turbidity on most primary producing benthic organisms is reduced light availability for photosynthesis (Waterhouse et al., 2017b). This causes a reduction in productivity and growth of primary producers including microalgal coral symbionts (Schaffelke et al., 2017). During periods of thermal stress, moderate turbidity-induced light reductions may actually be beneficial to corals, minimising the chance of bleaching (Anthony et al., 2007; Fisher et al., 2019; Sully & van Woesik, 2020). When aggregated, suspended sediment and organic matter form heavier flocs ('marine snow'), which, upon deposition, can cause stress to benthic organisms (Fabricius & Wolanski, 2000). While often detrimental to corals, flocs can incur a positive effect on nutrient-limited macroalgae, which are capable of extracting nutrients from ‘marine snow’ deposits. This may explain the capacity of some fleshy macroalgal species, such as *Sargassum* spp., to flourish in turbid and high deposition environments where nutrients are limited (Schaffelke et al., 2005).

Deposition of sediment on coral colonies can cause physical stress via abrasion, smothering, and burial, all of which can increase mortality at high sedimentation rates (Fabricius, 2005; Junjie et al., 2014; Schaffelke et al., 2005; Tuttle & Donahue, 2020). Early life stages are most at risk of mortality, but high sediment loads on adult colonies can lead to reduced reproductive capacity (R. Jones et al., 2015; Schaffelke et al., 2017; Waterhouse et al., 2017b). Sediment deposition can also preclude the growth of crustose coralline algae [CCA], which is widely considered an essential cue for settlement of many coral species (Junjie et al., 2014). Moreover, corals that are able to successfully recruit are at risk of burial during juvenile phases (Babcock & Smith, 2000; Duckworth et al., 2017; Fabricius, 2011; Haynes et al., 2007). Sediment deposition within algal turf environments can further limit coral recruitment (Birrell et al., 2005; Haynes et al., 2007). The epilithic algal matrix, which encompasses algal and non-algal constituents of the turf environment, readily traps sediments more so than bare rock or other surfaces (Tebbett, Goatley, et al., 2018). Positive feedback loops, owing to lack of herbivory on sediment-laden turfs and thus turf growth, can lead to long, unpalatable, sediment-laden turfs, which can further suppress herbivory, promote pathogen proliferation, and cause hypoxia and infection of coral tissue (Tebbett, Goatley, et al., 2018; Tebbett & Bellwood, 2019, 2020). Each of these processes thus impairs coral reproduction, settlement, and recruitment (Birrell et al., 2005; Evans et al., 2020; Speare et al., 2019). The mechanisms for which deposited sediments may negatively affect coral life history processes are varied, including increased expenditure of energy in removing sediment particles leading to less energy available to invest in reproductive output; binding of sediment particles with egg-sperm bundles preventing bundle break-up and consequently less successful fertilisation; and preference of coral larvae to not settle on sediment-laden surfaces (Jones et al., 2015; Ricardo et al., 2017). Furthermore, Birrell et al. (2005) found that settlement of *Acropora millepora* was significantly reduced in the presence of algal turfs and sediment, however the effect of the algal turf varied depending on the assemblage. The effect of increased sediment loads on inshore waters does not always negatively impact coral communities. Some species of corals such as *Turbinaria mesenteria* and *Acropora valida* have been found to thrive in high sediment environments with no adverse effect on physiology, demonstrating the importance of understanding species-specific tolerances to increased sediment loads (Anthony, 2006).

The impact of sediment stress on reef ecosystems varies with the level of anthropogenic activity, hydrodynamic regime, terrestrial runoff, and tolerances of benthic organisms. For example, localised acclimation of certain coral taxa to turbid and high sedimentation environments has been observed on some inshore GBR reefs (Anthony, 2006; Schaffelke et al., 2017). To appropriately manage inshore reefs into the future, improved site-specific understanding of reef community response to elevated sediment levels is required along with an improved understanding of species-specific adaptation capacity (Castro et al., 2012; Fabricius, 2005).

1.4.2 Water quality and other environmental stressors: synergistic effects

The impacts of poor water quality on reef communities are complex, and are exacerbated by global environmental change (Schaffelke et al., 2017). The predicted increase in frequency and intensity of severe cyclones and subsequent flooding due to climate change, will exert further water quality stress on inshore reef communities (Haynes et al., 2007). The outcome is likely to involve increased coral mortality, particularly during periods of thermal stress.

A recent meta-analysis of inshore GBR reef monitoring data indicated synergistic effects of local (e.g., water quality) and global (e.g., increasing sea surface temperature) stressors, resulting in site-specific responses to environmental change (Ceccarelli et al., 2020). This study highlighted water quality as a stronger predictor of macroalgal cover compared to coral cover, indicating that monitoring macroalgal communities alongside water quality parameters may be essential to understanding benthic community response to changes in local environmental conditions (Ceccarelli et al., 2020). Variation in sediment load may also interact with thermal stress to cause synergistic or antagonistic impacts. A recent analysis of global bleaching, temperature, and turbidity data found that corals in turbid environments are less vulnerable to thermal bleaching events, indicating moderate levels of turbidity may act as a buffer for thermal stress (Sully & van Woesik, 2020). Similarly, laboratory analyses of *Acropora intermedia* collected from an inshore GBR reef found a high sediment environment led to reduced mortality under high temperature and light stress (Anthony et al., 2007). Dredging-induced turbidity may have a similar effect. A study conducted on northern Western Australian inshore reefs found that high levels of sedimentation generated during a capital dredging campaign interacted synergistically with thermal stress producing increased bleaching-induced coral mortality (Fisher et al., 2019). However, an antagonistic effect resulted with low dredging-generated sediment loads. Specifically, bleaching-related mortality was reduced due to low light conditions resulting from dredging-related turbidity. Nutrient loads, turbidity, and sedimentation may, therefore, have the capacity to lessen the net impact of pressures such as high sea surface temperatures, though management of multiple synergistic stressors is complex, and mitigation of all stressors is still the best practice for maintaining reef function.

1.5 Patterns of inshore reef community change on the GBR

Poor water quality can create unsuitable conditions for coral recovery following a coral mortality event by allowing opportunistic macroalgal colonisation and proliferation (Ceccarelli et al., 2020; Fabricius & De'ath, 2004; Lam et al., 2018; Vieira, 2020). It is, therefore, likely that increased nutrient availability, turbidity, and sediment deposition have contributed somewhat to the shift observed from coral- to macroalgal- dominance on some inshore GBR reefs over recent decades (Ceccarelli et al., 2020; Thompson et al., 2021). Some studies point to this issue of unsuitable conditions for coral recovery following a coral mortality event (e.g., thermal bleaching, storm) leading to a coral-macroalgal shift. For example, a shift to macroalgal dominance was observed on the reefs of North Keppel Island following a bleaching event in 2006, where coral cover declined from 46% to 10%, with macroalgal cover increasing rapidly and persisting at high levels (60%) after three years (Diaz-Pulido et al., 2009). Similarly, monitoring of Havannah Island from 1997 to 2007 indicated a possible shift from coral dominance to overgrowth by *Lobophora variegata,* a common inshore macroalgal species (Cheal et al., 2010). Monitoring between 1999 and 2017 observed significant declines in coral cover on four inshore regions of the GBR (Magnetic, Keppel, Palm, and Whitsunday Island reefs), with Magnetic and Keppel island reefs showing evidence for a persistent shift from coral to macroalgal dominance (Ceccarelli et al., 2020). Each of these examples provide evidence of persistent shifts from coral- to macroalgal-dominance occurring on the GBR.

Declining coral cover has broad demographic effects that impact coral reproduction, larval supply, and recruitment. These impacts are highlighted by an 89% decline in GBR-wide coral recruitment in 2018 relative to pre-2016 (GBRMPA, 2019; Thompson et al., 2021), and are exacerbated by prolific macroalgal growth, competing aggressively with corals for space, light, and nutrition. Coral-algal interactions are complex and species-specific, affecting reef health in a variety of ways depending on local environmental parameters such as temperature, light, nutrient availability, hydrodynamics, and substrata (Jompa & McCook, 2003; Vieira, 2020). On healthy inshore reefs, macroalgae perform essential ecosystem functions, providing habitat, food, and reef framework consolidation (Diaz-Pulido & McCook, 2008; Fulton et al., 2019; Schaffelke et al., 2005). Macroalgal canopies, such as those formed by *Sargassum* spp., can have positive effects on coral colonies through shading, hence reducing the incidence of bleaching-induced mortality, and providing protection from predation by CoTS and parrotfish (McCook, 1999). However, increased growth and abundance of macroalgae beyond what is considered healthy for inshore reefs can have negative effects. Prolific macroalgal growth limits coral larval settlement and recruitment by space exclusion and allelopathy; reduces coral development by direct competition, excessive shading and abrasion; and resists herbivory once mature (Birrell et al., 2008; Clements et al., 2018; Hoey & Bellwood, 2011; Johns et al., 2018; van Woesik et al., 2018). These effects are known to retard coral recovery following disturbances such as mass bleaching, with low macroalgal cover linked to greater coral recovery on some inshore reefs (Evans et al., 2020). Ecological homogenisation can occur when degraded reefs with low-complexity, macroalgal-dominated habitats exhibit generalist communities with low diversity in favour of highly diverse communities with more specialised species (Chong-Seng et al., 2012). This effectively results in simpler ecosystems lacking important functional groups, exhibiting reduced functionality and less economic potential (Chong-Seng et al., 2012). Macroalgal-dominated reefs may, however, be able to provide unique ecosystem goods and services, distinct from coral-dominated reefs (Fulton et al., 2019). As inshore GBR reefs continue to change in structure and function, detailed localised knowledge of coral-algal interactions and the role of regional water quality stress will be required to appropriately manage these vulnerable yet valuable ecosystems under increasing anthropogenic pressure (Fulton et al., 2019; Hughes et al., 2017).

1.5.1 Case study of a coral-macroalgal shift: Magnetic Island, inshore GBR

Magnetic Island (Yunbenun, 19°9'S, 146°50'E), the study site for this thesis, is located eight kilometres offshore from Townsville in the central region of the GBR and is typical of many inshore continental islands in this region. Surrounded by fringing reefs, it is one of the most well studied islands within the GBR (Brown, 1972; Mapstone et al., 1992; Morrissey, 1980). Its fringing reefs have been impacted by a suite of acute and chronic disturbances including poor water quality (Ceccarelli et al., 2020; Williamson et al., 2019), high sedimentation and turbidity (Benson et al., 1994; Brown, 1972; Umar et al., 1998), periodic bleaching (Jones et al., 1997; Williamson et al., 2019), cyclones (Bainbridge et al., 2012; Williamson et al., 2019), and disease events (Haapkylä et al., 2013); making it an ideal site to illustrate inshore reef ecosystem change. In particular, Magnetic Island is exposed to terrestrial runoff from the Burdekin region, a major catchment dominated by sugarcane farming. Riverine outflow from the Burdekin River is the dominant source of sediment and nutrient input to the GBR lagoon (GBRMPA, 2019; Schaffelke et al., 2017).

There is extensive information for the reefs surrounding Magnetic Island (Brown, 1972; Mapstone et al., 1992; Morrissey, 1980) as a result of regular surveys being conducted over the past three decades. In particular, long-term regular monitoring has been associated with development of the large international port in Townsville, as well as development of marina infrastructure on Magnetic Island. The evidence from repeat monitoring over several decades indicates a persistent shift from coral to macroalgal dominance has occurred on reefs surrounding Magnetic Island (Ceccarelli et al., 2020; Lam et al., 2018; Thompson et al., 2019, 2021; Williamson et al., 2019). However, these records do not pre-date anthropogenic impact and, therefore, a true historical baseline is missing, which makes estimating the full extent of change difficult. Earlier records can give some indication of a historical baseline. For example, Brown (1972) detailed coral communities throughout the 1960s, noting 'Nelly, Geoffrey, Arthur and Florence Bay reefs were well developed with extensive coral colonies'. Rigorous monitoring of these reefs in the years following was in response to the noticeable impact of turbidity and sedimentation from dredge spoil dumping in adjacent waters, purported to be responsible for the decline of the eastern fringing coral communities (Brown, 1972). A thorough impact assessment conducted two decades later documented variation in coral and macroalgal cover (Mapstone et al., 1992). This assessment showed that while healthy coral colonies were noted in the eastern-facing bays, high macroalgal cover was emerging on some reefs, demonstrating the continued risk of anthropogenically derived sediment stress to coral communities (Mapstone et al., 1992). Since the first quantitative assessments of Magnetic Island fringing reef communities in the 1980s, regular documentation of macroalgal and coral cover has occurred, with the emergent pattern indicating a shift away from high coral cover towards macroalgal proliferation (Thompson et al., 2021). This was thought to be triggered initially by dredging-related sedimentation and has been sustained due to multiple factors likely related to chronic poor water quality (Ceccarelli et al., 2020; Williamson et al., 2019). Extensive investment to improve land management practices and reduce sediment and nutrient input to the GBR lagoon are being implemented as part of the Reef 2050 Water Quality Improvement Plan [WQIP] (State of Queensland, 2018). However, the decadal scale lag between load reduction and environmental effect means water quality stressors remain prevalent for Magnetic Island reefs (State of Queensland, 2018). As anthropogenic pressures increase, it is likely that nutrient and sediment inputs from the Burdekin catchment region as well as expanding dredging activities associated with the maintenance and expansion of the Port of Townsville, will continue to exert chronic stress on Magnetic Island reefs into the future, further compromising coral recovery (Williamson et al., 2019).

1.6 Macroalgal removal as a localised inshore reef restoration strategy

In line with changes to the Reef 2050 plan, which highlighted the need to develop active local intervention strategies to help reefs recover and regain resilience, new methods are rapidly being explored to increase coral resilience (Anthony et al., 2020; Commonwealth of Australia, 2018). One proposed strategy to mitigate macroalgal proliferation and restore inshore GBR reef resilience is to manually remove macroalgae, thus reducing a biological barrier to coral recovery (McDonald et al., 2016; see Figure 1.3 for a conceptual representation). Macroalgal removal may be effective in assisting coral re-establishment as an alternative, or in addition to, protection of herbivorous fish in areas where fish populations are targeted or mature macroalgal stands demonstrate resistance to herbivory (Briggs et al., 2018; Hoey & Bellwood, 2011). A review on global macroalgal removal efforts was conducted in 2018, suggesting best practice approaches and potential for coral recovery (Ceccarelli et al., 2018). Ceccarelli et al. (2018) reported a scarcity of robust literature documenting the effectiveness of macroalgal removal as a method to support coral recovery. This highlights the importance of macroalgal removal experiments aimed at improving knowledge of the associated ecological impacts on inshore reef ecology (Birrell et al., 2008; Brown et al., 2017; Ceccarelli et al., 2018). Improved understanding of how key ecological processes are impacted by macroalgal removal on inshore reefs will help determine how it may complement other localised recovery strategies such as coral larval enhancement, herbivory enhancement and improved water quality (Duarte et al., 2020).

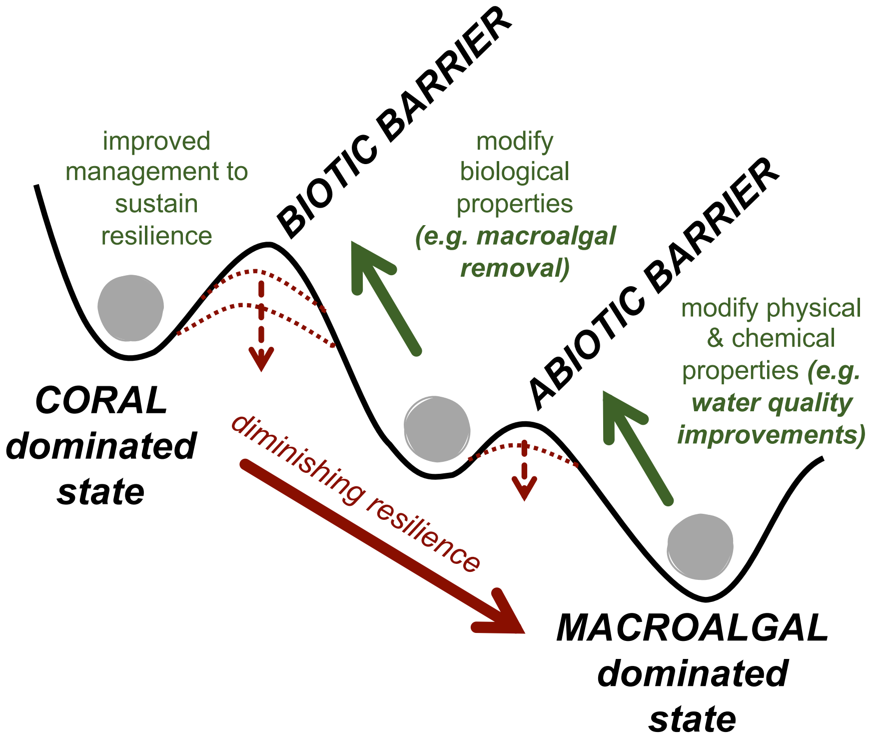


Figure 1.3 *A conceptual representation of reef degradation from a coral- to macroalgal-dominated state due to a loss of resilience (shown in red), catalysing a shift in reef state (represented by grey circles) to alternative, degraded states dominated by non-reef building organisms. The measures required to regain resilience are shown in green. Alteration of the physical and chemical environment, such as improving water quality, is required to remove*

abiotic barriers to coral recovery. Following this, biotic barriers to recovery must be mitigated and macroalgal removal may be an effective way to achieve this on inshore GBR reefs. Adapted from McDonald et al., 2016 and Mumby & Steneck, 2011.

Considering the current state of knowledge, this thesis synthesises research conducted to assess the ecological impact of macroalgal removal on the fringing reefs of Magnetic Island, an inshore reef of the GBR. A preliminary study was conducted from October 2018 through to July 2019 (Mastroianni, 2019), upon which this project builds to assess the ecological effect of macroalgal removal. This thesis extended the scope of the preliminary study, further developing the scientific basis underlying macroalgal removal in the recovery of inshore reef communities. This thesis provides valuable insight into the ecological relationships occurring on degraded inshore reefs dominated by canopy-forming macroalgae and helps to inform localised restoration practices. The overarching goal of this thesis is to improve understanding of the wider ecosystem impacts following macroalgal removal and assess the potential for macroalgal removal to improve ecosystem conditions for recovery of inshore reefs of the GBR, which are increasingly impacted by anthropogenic stressors. To achieve this, two main research areas were addressed:

1.6.1 Thesis Aim 1: Assess the impact of macroalgal removal on benthic community composition.

Monitoring and reporting programs such as the AIMS Marine Monitoring Program (Thompson et al., 2021) and the Reef 2050 Integrated Monitoring and Reporting Program [RIMReP] (GBRMPA & Queensland Government, 2018; Williamson et al., 2019) capture the long-term trends of coral reef communities and ecosystem health along the GBR. While highly informative, these monitoring programs focus on measures of coral and algae cover alone. There is a requirement for more comprehensive quantitative data on reef assemblages that distinguishes between different algal forms (Birrell et al., 2008; Diaz-Pulido & McCook, 2008; GBRMPA, 2019). Specifically, the taxonomic resolution of existing data is relatively low or inconsistent, with few studies focusing on fine-scale, comprehensive benthic community composition analysis (Diaz-Pulido & McCook, 2008). Incorporating higher taxonomic resolution of macroalgae into assessments of coral reef recovery potential, rather than documenting percent cover alone, is crucial in delineating nuanced processes of ecosystem change. Critical effects of macroalgae on coral demography are often taxa specific, such that different species of algae have markedly different effects on corals (Birrell et al., 2008; Jompa & McCook, 2003). This highlights the importance of incorporating the taxonomic and functional classification of algae into an assessment of impact to corals and reef ecosystem functioning (Birrell et al., 2008; Cannon et al., 2019; Evensen et al., 2019; Jompa & McCook, 2003; McCook et al., 2001; Vieira, 2020). Additionally, removing one particular genus of macroalgae is likely to impact community dynamics such that newly available space may be colonised by other fast-growing macroalgal species or organisms such as sponges or soft corals, as opposed to scleractinian corals. This underscores the value of documenting the succession of benthic communities following the removal of macroalgae and thereby accurately assessing the impact to coral reef communities (González-Rivero et al., 2011; Norström et al., 2009).

To capture the ecological dynamics associated with macroalgal removal at Magnetic Island, this thesis investigated benthic community composition changes through time in response to macroalgal removal. It was expected that benthic communities would undergo considerable alteration following the removal of fleshy macroalgae. It is likely that fast-growing algal species, such as turfing and encrusting forms, would colonise newly available space more quickly than corals due to their reproductive strategies and rapid growth, demonstrating the importance of algal taxonomic identification during the initial phases of ecological succession. Experimental macroalgal removal ultimately provides valuable insights into inshore coral reef community composition dynamics. Along with high taxonomic resolution benthic community data incorporating spatiotemporal variation, achieving this aim provides nuanced understanding of the ecological impacts of macroalgal removal. This information is essential for future reef management as coral reefs globally continue to change in structure, function, and value (Fulton et al., 2019; Graham et al., 2020; Hughes et al., 2017).

1.6.2 Thesis Aim 2: Assess the impact of macroalgal removal on inshore reef sedimentation and algal turfs.

The impact of macroalgal removal on sedimentation of inshore reefs has been relatively unexplored. Sediment deposition on inshore coral reefs has been recognised as a contributing factor to coral reef degradation, directly affecting coral recruitment, survival, and growth (Babcock & Smith, 2000; Bainbridge et al., 2012; Brown, 1972; Fabricius, 2005). Whilst the impacts of water quality and turbidity on corals are relatively well-studied, less is known regarding the relationships between macroalgae, sediment deposition, and benthic processes in coral reef ecosystems (Bégin et al., 2016; Latrille et al., 2019; Tebbett & Bellwood, 2019). Altered sedimentation dynamics owing to macroalgal removal are likely to affect environmental conditions conducive to coral settlement, survival, and growth (Birrell et al., 2008). For example, coral recruitment is severely impacted by sediment-trapping macroalgae (Fabricius, 2005), suggesting the potential for macroalgal removal to be effective in catalysing coral recovery. Alternatively, removing canopy-forming algae may lead to deposition of sediment directly onto corals or bare substrata, thus smothering or rendering the substrate not conducive to settlement or coral growth.

Delineating the impact of macroalgal removal and sedimentation on corals is, therefore, key to assessing the potential for coral recovery and re-establishment at Magnetic Island. This is particularly pertinent considering the planned expansion of the shipping channel that services the Port of Townsville and runs adjacent to the proposed study sites on Magnetic Island. The Port of Townsville has planned to commenced capital dredging-related activities in 2022 to widen the Platypus Channel and Sea Channel, with plans of dredging 3.9 million cubic metres over 3.5 years (Port of Townsville Limited, 2017). This is likely to contribute additional sedimentation to the fringing reefs of Magnetic Island, compounding existing anthropogenic stressors. This aspect of the thesis will, therefore, provide a baseline for the impacts of macroalgal removal on sedimentation prior to capital dredging activities. Substantial coral declines due to dredging-related sedimentation were documented at Magnetic Island almost half a century ago (Brown, 1972). The detrimental impacts of coral smothering and disease associated with dredge spoil are well documented (Erftemeijer et al., 2012; Jones et al., 2019; Pollock et al., 2014), demonstrating the necessity to incorporate sedimentation analysis for assessing the impact of macroalgal removal and long-term restoration efforts on coral recovery (Brown, 1972). It was expected that physically removing macroalgae would noticeably impact net sediment deposition, affecting coral smothering and, therefore, potential for coral recovery, as well as algal turf height, which is inversely related to coral recruitment (Ford et al., 2018).

Chapter 2: Removal of canopy-forming macroalgae on an inshore reef leads to increased coral cover

2.1 Introduction

Monitoring of coral reef benthic communities is integral to understanding ecosystem change through time, enabling assessments of ecosystem health (Ceccarelli et al., 2020; Souter et al., 2021b; Thompson et al., 2022). Recent global reef assessments have reported persistent declines in scleractinian coral cover and simultaneous increases in macroalgal cover (Souter et al., 2021a). Macroalgae compete directly with corals for space and light (reviewed in Birrell et al., 2008). On healthy reefs and at relatively low abundance, macroalgae fulfil important roles such as primary production (Hatcher, 1988; Schaffelke & Klumpp, 1997), food and habitat provision (Diaz-Pulido & McCook, 2008; Fulton et al., 2019), reef framework consolidation (Diaz-Pulido & McCook, 2008), and have been shown to protect juvenile corals from bleaching due to their shading effect (Jompa & McCook, 1998). However, proliferation of macroalgae can detrimentally increase shading of corals (Hauri et al., 2010), decrease available space for coral larval settlement and recruitment (Birrell et al., 2008), increase juvenile coral mortality (Box & Mumby, 2007), and affect the surrounding water chemistry via allelopathic chemical release (Birrell et al., 2008; Bonaldo & Hay, 2014).

The causes of macroalgal proliferation are complex, yet factors such as increased nutrient loads (De'ath & Fabricius, 2010; Fabricius, 2005), reduced grazing intensity (Smith et al., 2010), and reduced competitive pressure from corals attributable to mortality events (Cheal et al., 2010) are likely contributors. Furthermore, following a disturbance to a reef ecosystem (e.g., bleaching, storm event), initial colonising species are generally fast-growing, with slower-growing species taking longer to establish (Connell & Slatyer, 1977). On a typically healthy coral reef, fast growing algal turfs, crustose coralline algae, and fleshy macroalgae generally colonise an area first, and hard corals and other secondary colonisers then compete with these organisms to become established, facilitated by top-down processes such as herbivory (Doropoulos et al., 2017). If conditions are not conducive to coral recovery, however, then initial colonisers such as macroalgae can proliferate and dominate the ecosystem, outcompeting and precluding establishment of secondary colonisers such as hard corals (Doropoulos et al., 2017; Fukunaga et al., 2022; Hughes et al., 2007). In addition, feedback mechanisms can perpetuate high levels of macroalgae, preventing the recovery of corals and leading to a loss of reef resilience (Birrell et al., 2008; Fulton et al., 2019; Johns et al., 2018). Combining such feedback mechanisms with the competitive superiority of macroalgae on degraded reefs can lead to shifts in the dominant reef species away from corals and toward macroalgae.

Incidences of coral-algal shifts have been documented globally (see **General Introduction**), including on inshore reefs of the GBR (Cheal et al., 2010). Inshore regions of the GBR are exposed to elevated nutrient and sediment inputs resulting from erosion following land clearing, riverine runoff linked to agricultural development, port-associated dredging, and other coastal development activities (Bainbridge et al., 2012; De'ath & Fabricius, 2010; GBRMPA, 2019; Waterhouse et al., 2017b; Williamson et al., 2019). Despite inshore reefs on the GBR exhibiting naturally higher levels of macroalgae relative to their offshore counterparts (Ceccarelli et al., 2018; Diaz-Pulido & McCook, 2008; Fabricius, 2005), some inshore reefs have undergone substantial proliferation of macroalgae alongside declines in hard coral cover over the last two decades (Ceccarelli et al., 2020; De'ath et al., 2012; De'ath & Fabricius, 2010; Thompson et al., 2021). Shifts towards macroalgal dominance are expected to become more pervasive in response to increasing anthropogenic pressure, thus threatening the resilience of coral reefs (Graham et al., 2015).

Manual removal of macroalgae has been proposed as a localised intervention technique to create space for coral recovery and alleviate competitive pressure imposed by dense macroalgal stands (Ceccarelli et al., 2018; Mastroianni, 2019; Neilson et al., 2018). Adverse effects on coral growth due to competition with macroalgae have been found to be density-dependent (Clements et al., 2018; van Woesik et al., 2018). Manually reducing the density of macroalgae on degraded reefs may, therefore, be an effective, low-cost strategy to reduce a biotic barrier to coral recovery (Ceccarelli et al., 2018). Furthermore, manual removal of macroalgae has been found to allow increased settlement of coral juveniles (Smith et al., 2022), though the effects of removal on broader reef dynamics and coral health have yet to be tested. This strategy may be especially effective on reefs where methods to alleviate abiotic barriers to coral recovery are already being implemented, such as water quality improvement (State of Queensland, 2018), which is known to affect macroalgal growth (De'ath & Fabricius, 2010). The small-scale nature of macroalgal removal on inshore reefs lends itself well to citizen science engagement, highlighting other socio-economic benefits of macroalgal removal (Kittinger et al., 2016; Theobald et al., 2015).

On the GBR, rigorous investigation into the effects of macroalgal removal on degraded inshore reefs is only in its infancy (Ceccarelli et al., 2018). Recent experiments suggest macroalgal removal can have a positive impact on coral larval settlement and recruitment (Smith et al., 2021), as well as benefits to post-bleaching coral recovery (Smith et al., 2022), yet the broader, longer-term ecological effects are yet to be assessed. To fill this knowledge gap, macroalgal removal experiments were conducted on a degraded inshore coral reef of the GBR and changes in benthic community composition documented over multiple years.

Benthic cover of reef organisms, predominantly corals and macroalgae, is a key metric used to assess reef condition and quantify changes in reef communities (Thompson et al., 2021), and, therefore, a necessary index required to understand the potential of macroalgal removal as an effective reef restoration strategy. It was hypothesised that regular removal of macroalgae, particularly fleshy, canopy-forming macroalgae, would lead to increased coral cover, reduced macroalgal regrowth, and substantially different benthic community composition. It was expected though, that sustained increases in coral cover would take longer to detect relative to the likely more immediate impact on macroalgal re-growth due to the different growth rates of corals and macroalgae.

2.2 Methods

2.2.1 Study site and macroalgal removal experimental design

This study was conducted on the fringing coral reefs of Arthur Bay (19.1291°S, 146.8776°E) and Florence Bay (19.1220°S, 146.8805°E) on the eastern coast of Magnetic Island. Magnetic Island is located in the central inshore region of the GBR, 8 kms offshore from Townsville in northern Queensland, Australia (Figure 2.1). Twelve 25 m^2 (5 x 5 m) experimental plots were established in each bay, approximately 2 to 5 m deep, haphazardly placed after conducting visual surveys to ensure topographical consistency and representation of the wider reef ecosystem. Within each bay, six plots acted as controls (referred to herein as ‘control plots’) while the remaining six treatment plots were periodically cleared of predominantly fleshy macroalgae (referred to herein as ‘removal plots’) (Figure 2.1). Macroalgae were manually removed from removal plots in October 2018, July and October 2019, July and October 2020, and April, July, and October 2021. The October removal events were timed prior to mass coral spawning each year. Removal events were conducted on snorkel and SCUBA with the assistance of citizen science volunteers from Earthwatch Institute.

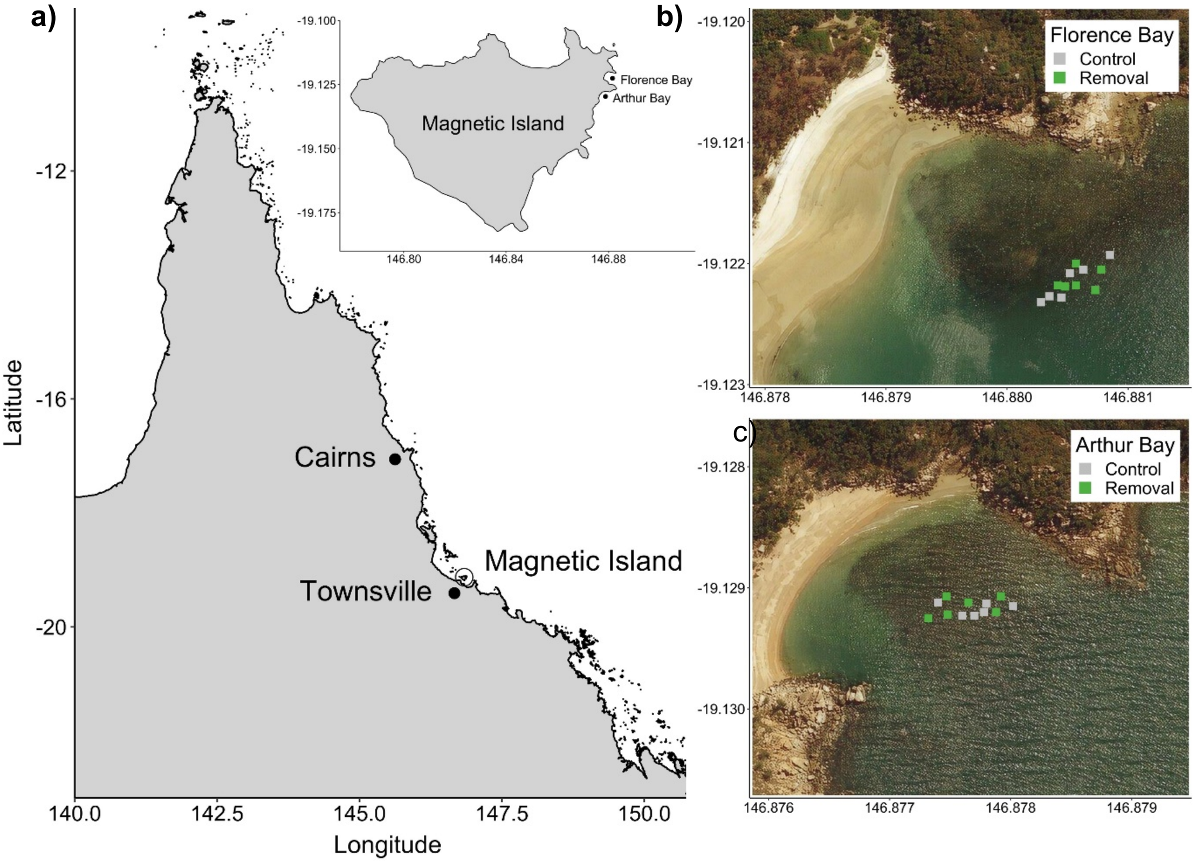


***Figure 2.1** Location of study sites in **(a)** Queensland, Australia; and maps of **(b)** Florence Bay and (**c**) Arthur Bay showing experimental plot arrangement. In each bay, six 25 m^2 control plots (grey squares), and six 25 m^2 removal plots (green squares) were periodically cleared of macroalgae (predominantly* Sargassum *spp.). Plots were approximately 2 to 5 m deep. Note plot icons are not to scale*

2.2.2 Collection of benthic community composition data

To document changes in benthic community composition, photographic surveys were conducted before (pre-removal surveys) and one to seven days after (post-removal surveys) each removal event. In addition, surveys were undertaken during summer when *Sargassum* spp. are at their peak abundance (Vuki & Price, 1994) to capture seasonal variation. A 25 m^2 grid was laid out using transect tapes across each plot, and digital photographs were captured of each 1 m^2 square, totalling 25 photos per plot. Photographs were edited using Lightroom (Adobe Systems, 2019) to enhance image quality prior to analysis. Point count software CPCe v4.1 (Kohler & Gill, 2006) was then used to collect percent cover data from the photos by overlaying 30 random points on each image and identifying the underlying benthic organism to genus level where possible, and abiotic substrata identified as dead coral, rubble, or sand. Percent cover for each plot was then averaged across all 25 photos for statistical analysis. Upon inspection of edited photographs, the October 2019 pre-removal and post-removal surveys were excluded from the analysis due to low visibility and subsequent poor image quality.

2.2.3 Statistical analysis

Percent cover of all macroalgal genera combined (including crustose coralline algae (CCA) and algal turfs) and percent cover of all hard coral genera combined, were modelled as a function of treatment (macroalgal removal) and survey timepoint using Bayesian generalised linear mixed effects models [BGLMMs]. In both the macroalgal and hard coral models, treatment and timepoint were fitted as interacting population effects and plot number was treated as a varying effect to account for the lack of spatial independence. Both models used a Beta distribution with a logit link, and weakly informative priors were used (see Supplementary Table 2 for prior details and chain specifications). A total of 20,000 Markov-chain Monte Carlo [MCMC] sampling iterations across three chains with a warmup of 10,000 and thinned to every fifth observation were performed. For both macroalgal and coral models, all diagnostics (trace plots, autocorrelation plots, r-hat (potential scale reduction factor) plots, posterior predictive checks, effective sample sizes, residual plots) suggested model assumptions were met, chains were well mixed and converged on a stable posterior (all r-hat values <1.05; Supplementary Figure 1). Model validation did not reveal any patterns in the residuals. Bayesian models were run using the brms package (Bürkner, 2017) in the statistical and graphical software R (R Core Team, 2021).

Patterns in composition of macroalgal and coral communities across treatments and timepoints were visualised using ordination plots generated using a non-metric multidimensional scaling (NMDS) based on a Bray-Curtis matrix of Hellinger transformed percent cover data, separately for macroalgal and coral communities. Prior to scaling and standardisation, taxa observed in less than 10% of surveys were removed. This totalled 35 rare taxa, which if included in the analysis, would have added noise rather than information to the statistical result and were not the focus of this analysis. Statistical differences in both the macroalgal and coral community composition between control and removal plots, as well as survey timepoint, and the interaction between these factors, were assessed using a permutational multivariate analysis of variance using the function ‘adonis’ with 999 permutations and blocked by plot. Analysis of multivariate homogeneity of group dispersions was performed using the ‘betadisper’ function to test the assumption of homogeneity of dispersion. Multivariate analyses were performed using the vegan package (Oksanen et al., 2020) in the statistical and graphical software R (R Core Team, 2021).

To further supplement the NMDS ordination plots, Shannon's diversity index, richness, and evenness were calculated for both macroalgal and coral communities. These metrics were calculated after rare taxa were removed. The effect of treatment and timepoint on each of the diversity metrics was determined using generalised linear mixed effects models (GLMMs). For Shannon's diversity, a Gamma distribution with a log link, for richness a Poisson distribution with a log link, and for evenness a Beta distribution with a logit link were used. Treatment and timepoint were incorporated into all models as interacting fixed effects with bay fitted as an additive fixed effect and plot number fitted as a random factor to account for the dependency structure of the hierarchical blocking design. Model selection was informed using second-order Akaike Information Criterion (AICc), and the most parsimonious model was selected for each of the diversity metrics (see Supplementary Table 6 for model details). Model fits and assumptions were assessed via simulated residual plots, which were satisfactory in all cases. All models were fit using the glmmTMB package (Brooks et al., 2017) in the statistical and graphical software R (R Core Team, 2021). Significant differences among levels in the fixed factors as estimated by the models (estimated marginal means) were distinguished via post-hoc tests using the Tukey *p*-value adjustment method.

2.3 Results

2.3.1 Observed benthic community composition

Across all time points, the benthic communities within all experimental plots (both control and removal) consisted predominantly of canopy-forming macroalgae and encrusting and plating corals. The most common macroalgal genera observed throughout the entire study were *Sargassum* (35.69 ± 1.47%), *Lobophora* (8.23 ± 0.59%), *Dictyota* (6.33 ± 0.54%), and *Padina* (1.13 ± 0.10%); values represent the highest mean for each genus ± SE percent cover averaged across all plots in both bays and the entire study period. Less common genera included the calcified red algae *Amphiroa* and *Galaxaura*, as well as the ephemeral brown alga *Colpomenia*, the frondose brown alga *Spatoglossum,* and the red alga *Hypnea*, with other genera contributing, on average, less than 0.1% cover. Turfing algae averaged 5.95 ± 0.35% across all plots for the entire study period, with crustose coralline algae appearing considerably less (0.45 ± 0.08%). Encrusting and plating *Montipora* (15.87 ± 0.51%), branching *Acropora* (2.62 ± 0.17%), and mounding *Porites* (0.18 ± 0.02%) were the most common hard coral genera with other hard coral genera such as encrusting *Astreopora*, foliose *Turbinaria*, massive *Favites,* and *Lobophyllia* each contributing less than 0.1% cover on average. The encrusting soft coral *Briareum* was the most common soft coral genus (0.33 ± 0.06%). Reef substrate consisted primarily of rubble (15.03 ± 0.60%), which on average represented almost four times higher coverage of the benthos than sand (4.31 ± 0.29%). The full list of genera and categories identified are listed in Supplementary Table 1. Benthic cover of different macroalgal and coral genera through time in control and removal plots are shown in Supplementary Figure 2 and Supplementary Figure 3.

2.3.2 Macroalgal removal events

Over the eight removal events from October 2018 through October 2021, 23.22 ± 1.91 (mean ± SE) kg of wet biomass per 25 m^2 plot were removed, with a total of 2,090 kg of macroalgae removed over the entire study period (see Supplementary Figure 1 or more details).

Photo-quadrat surveys conducted immediately following each macroalgal removal event showed that with each removal event, average percent cover of macroalgae was approximately halved (52.50 ± 3.01 (mean ± SE) % reduction, Figure 2.2a). The removed macroalgae consisted predominantly of *Sargassum* spp. but also other commonly occurring genera including *Lobophora, Dictyota*, *Padina,* and *Colpomenia*. Complete removal (100% reduction in percent cover) of macroalgae was not feasible due to the difficulty in removing both non-canopy-forming genera (e.g., *Lobophora* spp., turf-forming species) and holdfasts of canopy-forming genera (e.g., *Sargassum* spp.), as well as time limitations in the field. Post-removal surveys also showed that with each removal event, hard coral cover increased by 51.42 ± 15.91% on average, though this was not a true increase attributable to growth, but an artefact of removing the macroalgal canopy, which had previously obscured the benthos below (Smith, Boström-Einarsson, et al., 2022) (Figure 2.2b). This value can, therefore, be used to provide an estimate of the extent of coral increase observed in removal plots that can be attributed to obscuration by the macroalgal canopy versus coral recovery, and is informative for estimating coral cover in control plots below the canopy.

2.3.3 Modelled patterns in macroalgal cover

The modelled relationship representing macroalgal percent cover (sum of all macroalgal genera percent cover) as a function of treatment and survey timepoint was strong. When accounting for both the population (treatment, timepoint) and varying (plot number) effects, 90% of the variation in macroalgal percent cover could be explained (conditional r^2 = 0.90). Furthermore, there was evidence for an interaction between treatment and survey timepoint, suggesting that the effect of macroalgal removal was dependent on the survey timepoint (Supplementary Table 3). In October 2018 when the study commenced, estimated average macroalgal cover was similar in both the control and removal plots with 87.04% (80.63, 92.74) (mean % (lower and upper limits of 95% credibility interval)) in control plots, and 81.35% (72.90, 88.86) in removal plots (Figure 2.2a). At the end of the study in October 2021, average macroalgal cover had decreased to 37.84% (28.58, 47.79) pre-removal and 19.34% (12.85, 25.98) post-removal in removal plots; in contrast to control plots with 83.39% (77.56, 89.05) macroalgal cover.

Calculated Bayesian probabilities emphasise the effect of macroalgal removal through time. Macroalgal cover in October 2021 (pre-removal, end of study period) was less than half of October 2018 levels (pre-removal, start of study period) in removal plots with 73% certainty, yet 0% certainty for the same change in control plots. At the start of the study in October 2018, the probability of there being less than 50% cover of macroalgae in both control and removal plots was 0%. By October 2021, that probability remained at 0% for control plots but had risen to 99% for removal plots. Interestingly, in October 2020 (after two years of removal events), there was only a 4.0% chance that macroalgal cover had declined to less than 50% in the removal plots, with 0% chance in the control plots (see Supplementary Table 4 for a full summary of Bayesian probabilities).

There was a clear seasonal pattern in macroalgal percent cover, reflecting winter senescence of canopy-forming species such as *Sargassum* spp. (Vuki & Price, 1994), which dominated the trend in macroalgal percent cover. Across the entire study period, macroalgal cover in control plots in winter (July surveys), was on average 16.78 ± 1.74 (mean ± SE) % lower than in spring (October surveys) and this difference was consistent year to year (Figure 2.2a). A similar pattern occurred in the removal plots, with macroalgal cover in winter on average 38.25 ± 8.55% lower than in spring, however this difference was not consistent through time (Figure 2.2a). In 2018/2019, macroalgal cover in removal plots was 59.08 ± 12.71% lower in winter than in spring; in 2020 this difference declined to 33.34 ± 14.69%, and in 2021 winter cover of macroalgae was only 22.33 ± 2.73% lower than spring cover.

2.3.4 Modelled patterns in coral cover

Population and varying effects explained 95% of the variability (conditional $r^2 = 0.95$) in coral cover (sum of all coral genera percent cover) when modelled as a function of treatment and survey. In October 2018, there was no difference in estimated average coral cover between control plots (7.47% (5.21, 10.02) (mean % (lower and upper limits of 95% credibility interval)) and removal plots (5.65% (3.80, 8.43); Figure 2.2b). Coral cover increased with greater than 99% certainty from October 2018 (pre-removal) to October 2021 (pre-removal) in both control and removal plots. For example, the estimated average coral cover increased in control plots in October 2021 to 10.39% (7.28, 13.22), approximately a 40% increase between October 2018 and October 2021. Coral cover in removal plots increased substantially more though, rising by more than 510% to reach 35.09% (28.17, 42.11) cover in October 2021 (pre-removal), driven largely by the fast-growing genera

Acropora. Coral cover post-removal in October 2021 was 39.42% (32.01, 46.47) in removal plots.

Considering that on average, approximately 50% of the benthos is obscured by the macroalgal canopy, if there was no effect of macroalgal removal on coral cover attributable to a true increase in coral recovery, it could be expected that coral cover in control plots in October 2021 would be observed as 19.71% (i.e., half of the post-removal coral cover observed in removal plots in October 2021 (39.42%)). However, coral cover in control plots in October 2021 was only 10.39%, just over half of what would be expected if the increase in coral cover in removal plots was solely attributable to the obscuration effect of the macroalgal canopy. This indicates that the strong evidence found in this study for an effect of macroalgal removal on coral cover is representative of a true increase in coral recovery, and not just due to a methodological artefact. Furthermore, Bayesian probability calculations indicated that there was a 100% likelihood that coral cover more than doubled between October 2018 and October 2021 in removal plots, yet only 29% likelihood in control plots, suggesting that coral cover increased more in reef areas that had been cleared of macroalgae (see Supplementary Table 4 for a full summary of Bayesian probabilities).

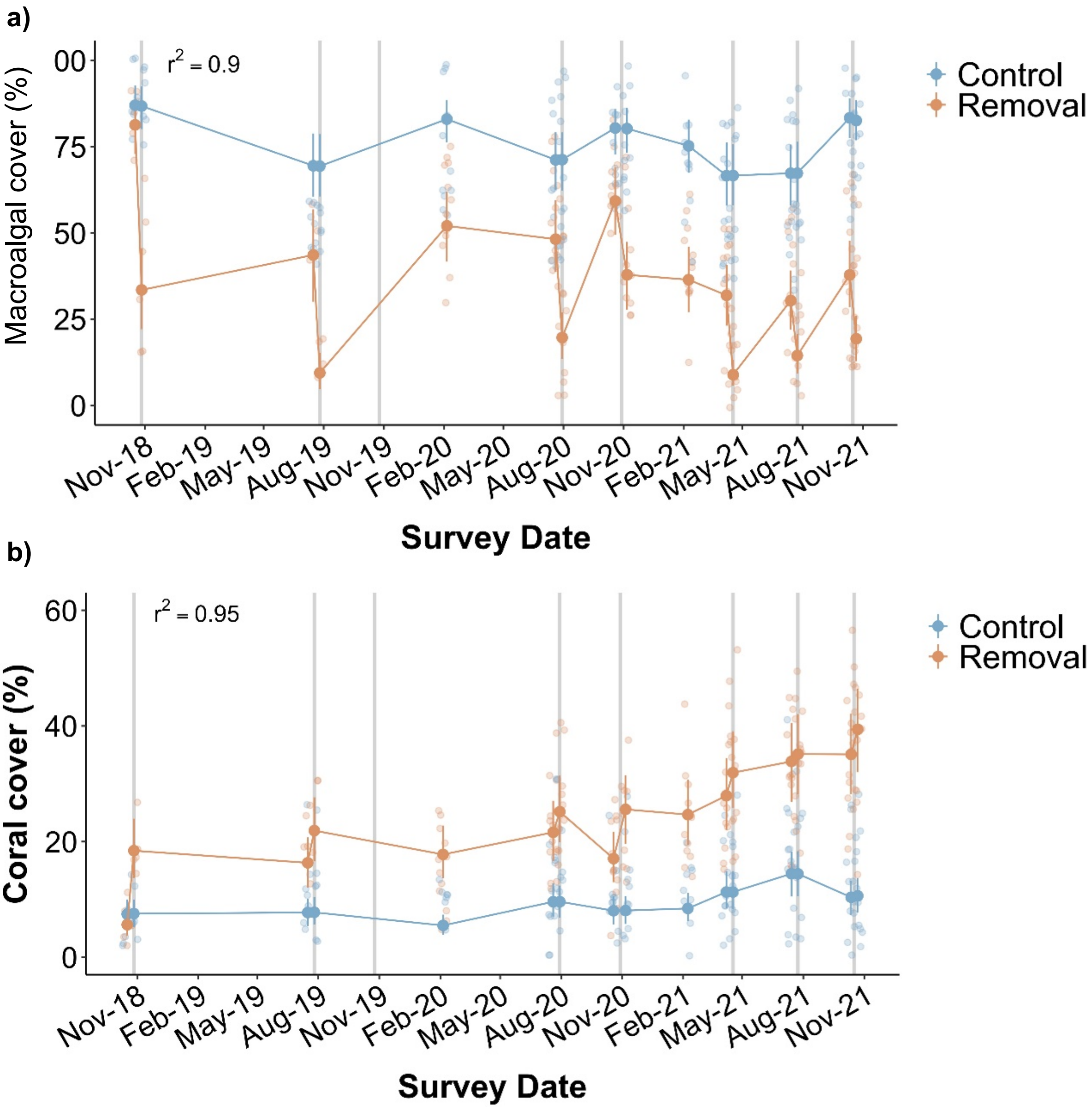
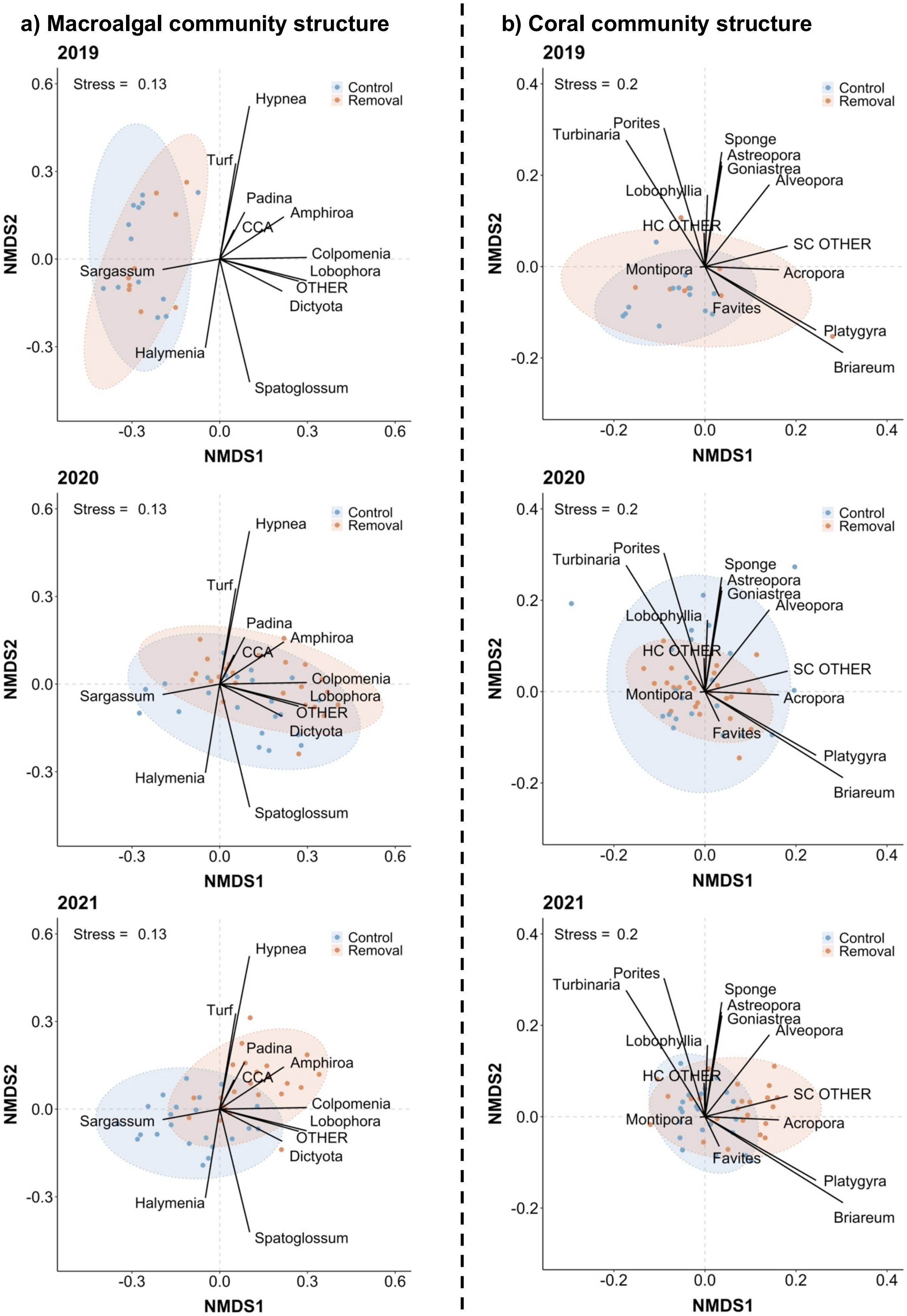


Figure 2.2 *Percent cover of* ***(a)*** *macroalgae and* ***(b)*** *scleractinian corals within experimental plots in two bays (Arthur Bay, Florence Bay) of Magnetic Island, Australia. Solid, coloured points represent mean predicted fits of Bayesian generalised linear mixed effects models (Beta distribution with logit link, conditional pseudo-r^2 =* ***(a)*** *0.90,* ***(b)*** *0.95), with predictions for control plots shown in blue and removal plots shown in orange. The respective coloured vertical lines represent 95% credibility intervals. Partialised observations (sum of fitted values and residuals) are shown as faint-coloured points. Vertical grey lines indicate when macroalgae were cleared from removal plots. Note that macroalgae were removed in October 2019, however photo-quadrat surveys from this timepoint were not used in statistical analyses due to low visibility and subsequent poor image quality*

2.3.5 Patterns in the composition of macroalgal and coral communities

Ordination plots generated by NMDS applied to percent cover of 10 macroalgal genera as well as algal turfs and crustose coralline algae, illustrated differences between control and removal plots through time (Figure 2.3a). Treatment was found to have a significant effect on macroalgal assemblages (Treatment - $F_{1,113} = 29$, $r^2 = 0.08$, $p < .01$; Supplementary Table 5), and tests for homogeneity of multivariate dispersion ('betadisper') identified no significant dispersion among control and removal plots (betadisper: $F = 0.002$, $p = .96$). This effect can be visualised on the ordination plots, with *Sargassum,* appearing to contribute most to the community differences observed between control and removal plots (Figure 2.3a). Timepoint was also found to have a significant effect on macroalgal assemblages, as well as the interaction between treatment and timepoint (adonis: Timepoint - $F_{5,113} = 29$, $r^2 = 0.41$, $p < .01$; Treatment*Timepoint - $F_{5,113} = 2.8$, $r^2 = 0.04$, $p < .01$; Supplementary Table 5). The significance of these effects may be driven by different within-group variation (dispersion), however, as opposed to true differences in community composition, due to significant dispersion among timepoints (betadisper: $F = 5.9$, $p < .01$).



a) Macroalgal community structure

b) Coral community structure

***Figure 2.3** Non-metric multidimensional scaling (NMDS) ordination of N = 114 sampling units based on Bray-Curtis dissimilarity indices of Hellinger transformed percent cover data in 2019, 2020, and 2021 of **(a)** n = 12 macroalgal genera and **(b)** n= 14 non-macroalgal genera (including hard coral, soft coral, sponges) around Magnetic Island, Australia. Coloured points represent location of each survey in multivariate space with control plot surveys shown in blue, and removal plot surveys shown in orange. 95% confidence ellipses are shown for treatment groupings in each year. Black lines represent **(a)** macroalgal genera **(b)** non-macroalgal genera.*

Diversity metrics for the macroalgal assemblages further support patterns visualised in the NMDS plots (see Supplementary Table 6a and Supplementary Figure 5a). Shannon's diversity index and evenness were both affected by macroalgal removal (Supplementary Table 6a); however, richness was relatively consistent for both control and removal plots throughout the study period with the total number of macroalgal genera unaffected by removal of the macroalgal canopy (*t* = -0.53, *df* = 113, *p* = .60; Supplementary Table 6a). In 2018 and 2019, the macroalgal communities across both control and removal plot communities were dominated by *Sargassum* and had comparably low diversity (October 2018: *t* = -0.47, *df* = 12, *p* = 1; July 2019: *t* = -1.4, *df* = 112, *p* = 1; Supplementary Figure 5a). Similarly, there was no difference in evenness of the macroalgal communities between control and removal plots at the beginning of the study (October 2018: *t* = 0.36, *df* = 12, *p* = 1; July 2019: *t* = -1.5, *df* = 112, *p* = 1; Supplementary Figure 5a). The ordination plots indicate that by 2020, the macroalgal communities had shifted slightly in both control and removal plots, but the modelled diversity metrics showed no effect. There was no difference between control and removal plots in diversity (July 2020: *t* = -0.22, *df* = 112, *p* = 1; October 2020: *t* = -2.6, *df* = 112, *p* = 0.43), nor evenness (July 2020: *t* = 0.39, *df* = 112, *p* = 1; October 2020: *t* = -2.3, *df* = 112, *p* = 0.86; Supplementary Figure 5a). By 2021, the macroalgal community in the removal plots was noticeably different to the control plots (Figure 2.3a), and this change was supported by the modelled diversity metrics. In July and October 2021, diversity of removal plots (July 2021: 1.46 ± 0.12 (estimated marginal mean ± SE), October 2021: 1.48 ± 0.12) was significantly greater than in control plots (July 2021: 0.91 ± 0.08, October 2021: 0.72 ± 0.06) (July 2021: *t* = -3.9, *df* = 12, *p* < .05; October 2021: *t* = -5.9, *df* = 112, *p* < .05, Supplementary Figure 5a). Furthermore, the cover of macroalgae in removal plots was more evenly distributed across genera, with significantly greater evenness in removal plots (July 2021: 0.73 ± 0.029; October 2021: 0.70 ± 0.030) relative to control plots (July 2021: 0.49 ± 0.035; October 2021: 0.38 ± 0.034) (July 2021: *t* = -5.2, *df* = 112, *p* < .05; October 2021: *t* = -6.6, *df* = 112, *p* < .05; Supplementary Figure 5a).

NMDS ordination plots applied to percent cover of 14 non-macroalgal groups (11 scleractinian coral genera, two soft coral groups, one group for sponges), illustrated differences between control and removal plots through time (Figure 2.3b). The temporal patterns shown in the ordination plots were supported by permutational multivariate analysis of variance tests, with significant variability in coral community structure through time seemingly driven by changes in *Acropora* (Figure 2.3b; adonis: $F_{5,113} = 4.1$, $r^2 = 0.15$, $p < .01$; Supplementary Table 5). The difference between coral communities in control and removal plots was, however, not statistically significant (adonis: $F_{1,113} = 2.5$, $r^2 = 0.02$, $p = .058$; Supplementary Table 5). Importantly though, coral community composition was significantly influenced by the interaction between treatment and timepoint (adonis: $F_{5,113} = 1.3$, $r^2 = 0.05$, $p < .05$; Supplementary Table 5). This represents a significant change in the difference between control and removal plot coral community composition through time. This was not supported, however, by the diversity metrics modelled for coral communities. Macroalgal removal had no effect on the diversity ($t = -2.3$, $df = 110$, $p = .02$), richness ($t = -1.9$, $df = 113$, $p = .07$), nor evenness ($t = 0.32$, $df = 110$, $p = .75$; Supplementary Table 6b; Supplementary Figure 5b) of hard coral communities. Tests for homogeneity of multivariate dispersion (betadisper) identified no significant dispersion for coral communities among control and removal plots (betadisper: $F = 0.02$, $p = .89$), nor among timepoints (betadisper: $F = 1.3$, $p = .29$).

2.4 Discussion

Percent cover of benthic organisms is a key metric used to quantify reef condition and monitor changes through time and space. This study showed strong evidence that removing macroalgae from experimental plots on a degraded inshore reef led to increased coral cover and concurrent steep declines in macroalgal re-growth. The impact of macroalgal removal was particularly promising for live hard coral cover, with the three-year intervention producing a 5-fold increase, reaching 35.09% coral cover at the end of the study in October 2021 in removal plots (pre-removal), and 39.42% post-removal. This is higher than both the average trend reported in the latest Annual Report for Inshore Coral Reef Monitoring 2019-20 (approximately 30% in 2020) (Thompson et al., 2021) for the Burdekin region, which includes Magnetic Island, and the live hard coral cover reported for Magnetic Island reefs in 2019 (30%) by Williamson et al. (2019). This suggests that consistently removing macroalgae from an inshore reef can enhance natural increases in coral cover within only three years.

Over the three years of this study, macroalgal cover in removal plots was reduced to less than 40% of starting levels, falling to 37.84% cover by the end of the study. This is in stark contrast to macroalgal cover in control plots, which remained at greater than 80% cover throughout the entire study period. The persistence of dense macroalgal stands, specifically *Sargassum* spp., on Magnetic Island reefs is highlighted in the latest Annual Report for Inshore Coral Reef Monitoring 2019-20 (Thompson et al., 2021), and is strongly correlated with Chl *a* levels, indicative of nutrient availability (Ceccarelli et al., 2020; Williamson et al., 2019). This indicates that nutrient availability remains high on Magnetic Island reefs, potentially favouring macroalgal dominance and limiting the capacity for corals to compete against macroalgae (Birrell et al., 2008). Removing the dense macroalgal canopy may, therefore, reduce this competitive pressure under chronic nutrient loads, allowing corals to increase in benthic cover. However, the average macroalgal cover in removal plots at the end of the study (37.84%) was still higher than a proposed threshold of 20% macroalgal cover for negative coral-algal relationships on inshore reefs of the GBR (Ceccarelli et al., 2020). After each removal event in 2020, however, macroalgal cover was reduced to less than 20%, so these brief periods of low macroalgal cover prior to regrowth may provide beneficial conditions for coral recovery. The reefs studied here may, therefore, require continued removal of macroalgae until macroalgae no longer functionally dominate the system.

Interestingly, there was evidence for an increase in coral cover in the control plots over the three-year study period, however, this increase was less than half that experienced in the removal plots. This could be the result of several factors. Firstly, it may be attributable to the short-term, GBR-wide recovery occurring as reported in the most recent Annual Report for Inshore Coral Reef Monitoring 2019-20 (Thompson et al., 2021), as well as the most recent Reef Snapshot (GBRMPA et al., 2022). The Thompson et al. (2021) report described increases in coral cover and low mortality in the Burdekin region following the 2020 bleaching event. The report also indicated that inshore reef coral communities are continuing to recover, despite increasing macroalgal cover, from the last low point for reef condition coinciding with Cyclone Yasi in 2011. The observations documented in the report are reflected in this study, indicating that reef communities at Magnetic Island are capable of recovery. In more general terms, the GBR overall has been experiencing a recovery period in recent years due to the lack of major CoTS outbreaks and few impacts from severe cyclones (last major cyclone in 2017), so it is likely that removing macroalgae has supported this recovery.

A second possible contributor to the overall increase in coral cover in both control and removal plots could be related to the findings of the latest Annual Report for Inshore Water Quality Monitoring on the GBR (Waterhouse et al., 2021). Despite the long-term water quality trend still declining for the inshore waters in the Burdekin region, a short-term improvement from 2018-19 to 2019-20 was observed (Waterhouse et al., 2021). This is likely due to below average rainfall and river discharge in the 2019-20 season compared to the major flood event that occurred in February 2019 (Thompson et al., 2021; Waterhouse et al., 2021). This short-term improvement to water quality may have contributed to relatively good recovery following the 2020 bleaching event, despite a high incidence of bleaching at Magnetic Island (Thompson et al., 2021), and thus an overall increase in coral cover observed in this study. Longer term studies examining water quality and benthic condition changes will help to understand the potential for increased coral recovery under macroalgal removal intervention regimes.

A third factor influencing overall coral cover is the scale at which this study was conducted. The control and removal plots were positioned in a cluster within each bay. Taking away macroalgal biomass from the removal plots could have positive implications for the adjacent areas of the inshore reef where control plots were located. Potential mechanisms for this could include changes to water chemistry via reduced allelopathic chemical release by macroalgae (Birrell et al., 2008; Bonaldo & Hay, 2014). These potential effects may have contributed to the increase in coral cover in the control plots as well as the removal plots despite no physical intervention occurring in the control plots.

The composition of benthic communities at Magnetic Island documented in this study is consistent with what has been reported in the literature and also that of other GBR inshore reef communities (Ceccarelli et al., 2020; Thompson et al., 2021; Williamson et al., 2019). The manual removal of macroalgae at regular intervals over three years in this study resulted in significant changes to the benthic community. The macroalgal community composition in removal plots changed over time in response to the removal effort, with the dominance of *Sargassum* spp. in removal plots at the start of the study being significantly reduced by the end of the study. Rather than the macroalgal community being dominated by *Sargassum* spp., the removal plots showed greater diversity of other algal genera including the corticated red algae *Hypnea*, the upright calcareous red algae *Amphiroa,* the common brown algae *Padina,* the ephemeral brown algae *Colpomenia,* and the mat-forming brown algae *Lobophora,* amongst others. These changes in macroalgal community composition are likely to have varying effects on reef ecology and would be worthy of further investigation. For example, calcareous algae contribute to reef accretion and production of marine sediments, so increased prevalence of these algae in response to removal of fleshy canopy-forming brown algae is likely to have positive effects on coral reefs (Diaz-Pulido et al., 2007). On the other hand, there may be the potential for different non-canopy forming algae to dominate in the absence of canopy-forming algae such as *Sargassum* spp.*,* which may pose varying levels of risk since different algal species are known to vary in their effects on coral (Jompa & McCook, 2003). For example, *Lobophora* spp. are known to inhibit coral settlement and recruitment via waterborne compounds (Box & Mumby, 2007; Evensen et al., 2019; Johns et al., 2018). An increase in *Lobophora* spp. prevalence in the absence of *Sargassum* spp. may, therefore, result in negative effects on corals, prohibiting any potential benefits of canopy removal. Conversely, Jompa & McCook (2003) found that *Hypnea pannosa,* which is often found growing amongst branching corals, has no effect on the tissue of the branching coral *Porites cylindrica.* Thus, increased prevalence of *Hypnea* spp. may pose little or no threat to coral reef communities, as opposed to the known negative effects of dense *Sargassum* spp. canopies on corals (Leong et al., 2018).

The change in composition of coral communities was less prominent, likely attributable to the slower growth rate of corals compared to macroalgae. Whilst the coral community in removal plots did not differ in diversity to the coral community in control plots, they did display higher proportions of coral genera with massive growth forms including *Astreopora, Alveopora, Lobophyllia, and Favites*. In contrast, the control plot communities consisted primarily of only a few, common coral genera, including plating *Montipora,* branching *Acropora,* and mounding *Porites*. These findings suggest that manually reducing macroalgal cover on inshore reefs is unlikely to lead to changes in coral community composition and diversity within a three-year period. Whilst the diversity of the coral communities in the removal plots did not increase through time, there was no observed decline in diversity. This can be viewed as a positive result because a loss of coral biodiversity can instigate negative feedback loops that suppress reef resilience (Clements & Hay, 2019). It is challenging, however, to delineate whether the increased relative abundance of massive genera represents a true change in the coral community in response to macroalgal removal, or whether it is representative of increased visibility of small or cryptic corals. For example, the increases in massive corals observed in this study may be an artefact of the obscuring effect of the macroalgal canopy making it more difficult to see smaller, less common corals on the benthos. If this study was to be conducted again, it would be valuable to record *in situ* percent cover estimates of benthic organisms, as well as derive percent cover estimates of the canopy from planar photo-quadrats. This would provide a more detailed assessment of the benthic community beneath the macroalgal canopy.

Despite the difficulty in observing small and cryptic coral genera due to the obscuration effect of the macroalgal canopy, it is likely that a considerable proportion of the coral cover increases observed in this study were attributable to true increases in coral cover and not only an artefact of the methodology. Factoring in approximately 50% obscuration (this value was derived from the average difference in coral cover between pre- and post-removal surveys which can be attributed to increased detectability of the benthos) by the macroalgal canopy, theoretically it could be expected that coral cover in control plots would be 19.71% (post-removal coral cover in removal plots was 39.42% in October 2021) by the end of the study if the removal effort had no true impact on coral recovery. However, coral cover in control plots in October 2021 remained low at 10.39% cover. Thus, the increases in coral cover observed in the removal plots can be attributed to true increases in coral recovery on top of the obscuration effect of removing the macroalgal canopy. These findings suggest that with regular intervention, reef communities at Magnetic Island, and likely other inshore reefs on the GBR, are capable of a community shift towards less dominance of canopy-forming macroalgae allowing for a more diverse macroalgal community, and increased dominance of hard corals.

It is important to note that the effect of macroalgal removal in this study was not realised immediately. After two years of removal, the effect in terms of percent cover and community composition was minimal, with little evidence for substantial changes between control and removal plots (Supplementary Table 4), though after three years, the effect was clear. In removal plots, macroalgal cover remained low, sustaining a reduction by more than 50%, and coral cover had significantly increased by more than 510%. Furthermore, the trends of decreasing macroalgae cover and increasing coral cover are yet to plateau, suggesting the potential for further benefits with continued, long-term removal efforts. These findings suggest removal efforts need to occur regularly and over a period greater than two years to ensure sustained reduction in macroalgae. Sporadic removal events are unlikely to achieve beneficial outcomes in terms of reducing macroalgal levels nor providing benefit to corals.

Seasonal variation in macroalgal cover, which was dominated by *Sargassum* spp., was observed in both control and removal plots, reflecting the known growth dynamics of canopy-forming macroalgae on inshore reefs (Ceccarelli et al., 2018; Lefèvre & Bellwood, 2010; Martin-Smith, 1993; Schaffelke & Klumpp, 1997; Vuki & Price, 1994). Low macroalgal cover in winter across both control and removal plots (July surveys) represents senescence of canopy-forming macroalgal species, leading to a decline in biomass (Martin-Smith, 1993). The increase in macroalgal cover between winter and spring (October surveys) represents the main growth period for canopy-forming macroalgae. Since this pattern was observed in both control and removal plots, it is unlikely that the act of removing macroalgae would substantially influence the seasonal growth dynamics. The seasonal difference did become less prominent in removal plots through time, thus, in the long-term, regular macroalgal removal may lead to a loss of seasonality in canopy-forming macroalgal assemblages, which may have flow-on effects for non-canopy-forming species or ephemeral genera such as *Colpomenia* and *Dictyota*. Alternatively, the reduction in seasonal differences in macroalgal cover may be due to fewer reproductive adult thalli as a result of macroalgal removal, or reduced regrowth of senesced thalli.

The findings from this study indicate regular macroalgal removal efforts performed over a period greater than two years may be effective in reducing macroalgal cover and curbing re-growth, as well as increasing coral cover. If the patterns observed in this study persist in response to continued removal events (even if only reducing macroalgal percent cover by half), the trajectory of the reef community at Magnetic Island has the potential to breach a theoretical biotic barrier to coral recovery, following a path more conducive to re-establishment of the coral-dominated state. Macroalgal removal trials in other areas are required, though, to investigate how various environmental drivers of reef change on different reefs may influence the impact of macroalgal removal on coral recovery. Longer-term studies will help to determine the persistence of the patterns observed in this study to better understand the potential for macroalgal removal to be used as a restoration technique.

Chapter 3: Inshore reef sediment dynamics and turf height unaffected by canopy-forming macroalgae

3.1 Introduction

Reefs globally are subjected to increasing stress from climate change and other anthropogenic influences (Harborne et al., 2017), which has, on average, led to substantial and persistent losses of live coral cover within the last two decades (Souter et al., 2021b). In addition to climatic changes, land-based sediment runoff poses an additional localised threat to reef ecosystems (Bainbridge et al., 2018; Waterhouse et al., 2017a), and is a focus of reef management agencies (Eberhard et al., 2017). The interactions governing sedimentation on coral reefs are complex but are often related to terrestrial influences, local hydrodynamics, and the propensity for algal turfs to trap sediments (Tebbett, Goatley, et al., 2018; Tebbett & Bellwood, 2020). Algal turfs readily trap suspended organic and inorganic sediments (when aggregated this is referred to as the epilithic algal matrix [EAM]) and the build-up of turfs and sediments can alter reef functions, including the settlement of corals (Birrell et al., 2005; Speare et al., 2019) through to trophic dynamics (Tebbett, Bellwood, et al., 2018; Tebbett, Goatley, et al., 2020). Understanding the multiple pathways whereby sediments, algal turfs, and other reef components (e.g. corals, macroalgae) interact is of increasing importance on degraded reefs (Tebbett & Bellwood, 2019).

Inshore coral reefs of the GBR are exposed to waters rich in sediment and dissolved organic matter relative to reefs further offshore (Waterhouse et al., 2021). This is due to erosion following land clearing, nutrient-rich riverine runoff linked to agricultural development, port-associated dredging, and other coastal development activities (Bainbridge et al., 2012; De’ath & Fabricius, 2010; GBRMPA, 2019; Waterhouse et al., 2017b; Williamson et al., 2019). High levels of sediments and nutrients can favour macroalgal growth over corals (Birrell et al., 2008; Sura et al., 2021), with feedback mechanisms leading to shifts in reef communities characterised by fleshy, canopy-forming macroalgae (Johns et al., 2018; Nugues & Roberts, 2003). Such community shifts are generally accepted as strong indicators of coral reef degradation (Birrell et al., 2008; Diaz-Pulido & McCook, 2008; Done, 1992; Williamson et al., 2019). At some sites on the GBR, substantial declines in hard coral cover and concurrent increases of macroalgae have been reported over the last two decades (Ceccarelli et al., 2020; De’ath et al., 2012; De’ath & Fabricius, 2010; Thompson et al., 2021). However, the influence of macroalgal canopies on sedimentation regimes, particularly on inshore reefs subjected to high sediment inputs, remains to be investigated.

Macroalgae directly interact and compete, through a variety of mechanisms depending on the macroalgal taxa (Jompa & McCook, 2003), with other benthic organisms, including corals and turf algae, for space and light (reviewed in Birrell et al., 2008). For example, proliferation of macroalgae can reduce coral growth rates via abrasion (River & Edmunds, 2001), increase shading of corals and decrease available space for coral larvae settlement and recruitment (Birrell et al., 2008), as well as affect the surrounding water chemistry via allelopathic chemical release (Bonaldo & Hay, 2014). In addition to the biological effects on other reef organisms, benthic macroalgae can alter abiotic conditions by reducing turbulence, consequently trapping sediment, and enhancing deposition of sediment on the benthos (Birrell et al., 2008). Such increased sedimentation has variable flow-on effects on benthic reef taxa. For example, increased sediment deposition directly reduces coral reproduction, recruitment, survival, and growth (Babcock & Smith, 2000; Bainbridge et al., 2012; Brown, 1972; Fabricius, 2005; Rogers, 1990; Weber et al., 2012). The severity of the effect varies since the capacity of corals to actively remove sediment is dependent on sediment characteristics such as particle composition and size (Weber et al., 2006).

Algal turfs are also affected by sediment deposition on coral reefs. Short (< 5 mm), productive algal turfs [SPATs] are major contributors to primary productivity on healthy reefs (Carpenter, 1985; Goatley et al., 2016; Hatcher, 1988; Latrille et al., 2019). Sediment deposition can reduce productivity (Tebbett & Bellwood, 2020), resulting in long (> 5 mm), sediment-laden algal turfs [LSATs] (Goatley et al., 2016; Gordon et al., 2016; Purcell, 2000; Tebbett & Bellwood, 2019). LSATs are unpalatable to herbivores relative to SPATs (Goatley & Bellwood, 2013) and can further facilitate deposition of benthic sediments (Goatley et al., 2016), perpetuating a degraded algal turf environment with flow-on negative effects to other benthic organisms such as corals (e.g. pathogen proliferation causing hypoxia and infection of coral tissue) (Birrell et al., 2005; Speare et al., 2019; Tebbett, Bellwood, et al., 2018; Tebbett & Bellwood, 2019, 2020). Reduced sediment deposition on reef substrata could be achieved via changes to the macroalgal canopy (i.e., removal), due to its role as a physical barrier to water flow. In turn, a reduced macroalgal canopy and subsequent changes to sediment dynamics could, potentially reduce sediment deposition, increase incident light, enhance productivity, and attract herbivores, creating conditions in favour of SPATs. Alternately, removal of the macroalgal canopy could eliminate deposition surfaces in the water column (i.e., macroalgal fronds), thereby enhancing deposition on the benthos and within the EAM.

While net sedimentation is an important metric in understanding the interactions between reef community constituents, the responses of coral and other reef benthic taxa to sedimentation can further be influenced by sediment characteristics such as particle size, organic content, duration and frequency of exposure (reviewed in Tuttle & Donahue (2020)). Fine sediment derived from agricultural runoff is recognised as one the main water quality pollutants threatening inshore areas of the GBR as it travels furthest into the marine system relative to larger size fractions that settle out close to shore (Bainbridge et al., 2018; Bartley et al., 2017). Fine sediments can also aggregate with organic material making it more difficult for corals to remove relative to larger grain sizes (Bainbridge et al., 2018; Fabricius & Wolanski, 2000; Flores et al., 2012). Furthermore, fine, organically-rich sediment particles can alter the water column both physically (reduce light attenuation) and chemically (reduce pH), and are more easily resuspended from the benthos relative to coarser, inorganic sediments (Bainbridge et al., 2018). It was expected that the composition of deposited sediments would differ based on the depositional environment, for example, corals may accumulate a greater proportion of fine, organic sediment relative to algal turfs which may accumulate a greater proportion of coarse particles, and that the presence of a macroalgal canopy would affect these patterns. Quantifying sediment deposition and composition in areas with and without a macroalgal canopy will, therefore, provide valuable information about how sediment characteristics may be influenced by canopy-forming macroalgae, and in turn could affect other reef organisms.

Understanding the multifaceted relationships between macroalgae, algal turfs, and sedimentation is critical to predict the flow-on effects to other reef benthic taxa, particularly corals (both juvenile and adult life-stages). This chapter investigates how removing macroalgae from degraded fringing reefs on the inshore GBR impacts sediment deposition and algal turf communities. Manual removal of fleshy macroalgae, such as *Sargassum* spp., from degraded reefs with low coral cover and high macroalgal cover theoretically removes a biological barrier to coral recovery (Birrell et al., 2008; Smith et al., 2021). The technique, however, could introduce changes to sediment dynamics (e.g., increased sediment deposition) and downstream turf processes (e.g., increased turf height and sediment accumulation in EAM), which could undermine the potential for benefits on inshore reefs exposed to high sediment inputs. Any long-term benefits to coral recovery resulting from increased benthic space and reduced coral-algal competition created by macroalgal removal, could therefore be dependent on the sedimentation regime and EAM characteristics that influence coral recruitment, growth, and health (Birrell et al., 2005). Improved understanding of the relationships between macroalgae, algal turfs and sedimentation is not only integral to understanding inshore reefs, but necessary for developing effective management strategies to assist coral recovery on degraded inshore reefs (Bellwood, Pratchett, et al., 2019; Tebbett, Streit, et al., 2020).

3.2 Methods

3.2.1 Study site and macroalgal removal experimental design

The study site and macroalgal removal regime is described in Chapter 2 (see **section 2.2.1** for details).

3.2.2 Sediment deposition and organic fraction

Net sediment deposition was measured using SedPods and TurfPods, which are concrete-filled sections of PVC pipe with either a rough concrete surface or artificial turf surface, respectively (see Field et al., 2013; Latrille et al., 2019 for full description). These devices are a well-established proxy for accurate and cost-effective measurement of net sediment deposition in comparison to traditional methods such as sediment traps (Field et al., 2013; Latrille et al., 2019). SedPods and TurfPods allow for resuspension of material, which is not possible in sediment traps, and therefore provide a more ecologically representative estimate of what a coral or algal turf surface would experience naturally (Field et al., 2013; Latrille et al., 2019). SedPods were constructed using short sections (9 cm diameter, 7 cm high) of PVC pipe filled with concrete to act as a proxy coral surface. TurfPods were similarly constructed, with a layer of artificial turf 3 mm to 5 mm high (‘Astroturf’) affixed to the concrete to act as a proxy for algal turfs. Three ‘Pods’ of each type were deployed in every plot over a 1-week period at each sampling timepoint and distributed haphazardly throughout each plot to account for substrate variation. Pods were affixed to the benthos using a star picket hammered into the substrate, with a PVC ring to hold the pod in place. The baseline deployment occurred in May 2020 prior to macroalgal removal in July 2020. Further deployments occurred in August 2020 and November 2020, following removal events in July 2020 and October 2020, respectively. A final deployment occurred in February 2021 prior to the April 2021 removal event, to capture wet season dynamics. Pods were capped upon collection to ensure all deposited sediment was retained, then sealed in plastic bags while underwater, then stored at 4°C until processed.

Upon returning to the laboratory, sediment samples were prepared by carefully removing each pod from its bag and rinsing the collected sediment into a bucket with copious (>750 ml) reverse osmosis water to remove salts. Samples were settled out for >24 hours to allow sediment to fully settle, after which the supernatant was siphoned off and samples topped up to approximately 500 ml with reverse osmosis water to further remove salts. Samples were then wet sieved through a 1.4 mm stainless steel mesh, retaining all material less than 1.4 mm. Across all samples there was negligible grain size sediment particles greater than 1.4 mm. Each sample was brought up to 900 ml with filtered fresh water, and a subsample of known volume (200 ml for SedPods, 20 ml for TurfPods) processed via vacuum filtration using a pre-weighed 42 mm glass microfibre filter (Whatman, United States of America) and dried at 105°C for 24 hours according to the American Public Health Association [APHA] Standard Method 2540D to yield total dry mass, with at least 10% of all samples analysed in triplicate (American Public Health Association, 2018). Sediment deposition rate (mg cm^{-2} d^{-1}) for both SedPods and TurfPods was calculated as follows:

$$Deposition\ rate\ (mg\ cm^{-2}\ d^{-1})\ = \frac{\left[\frac{900ml \times dry\ mass\ in\ subsample\ (mg)}{subsample\ volume\ (ml)}\right] / \left[pod\ surface\ area\ (63.6\ cm^{2})\right]}{number\ of\ days\ deployed\ (d)}$$

The filter was then combusted at 550°C for 1 hour in a Carbolite muffle furnace according to APHA Standard Method 2540E and reweighed to yield the mass of the non-volatile solid component (American Public Health Association, 2018). The weight lost upon ignition denoted the volatile solid component in the deposited sediment, approximating the proportion of organic material in the sample.

3.2.3 Grain size analysis

To determine if the composition of sediments varied between control and removal plots, the distribution of grain sizes was assessed. The three replicate samples for each pod type in each plot were merged (see Supplemetary) and treated with the common dispersal agent Calgon (5% sodium hexametaphosphate solution). The merged sample was then sonicated for 10 minutes immediately prior to analysis to separate flocculated particles and analysed via laser diffraction using a Malvern Mastersizer 3000 particle size analyser (refractive index: 1.52, samples ultrasonically dispersed at 15% power for 30 seconds prior to measurement) to yield grain size distribution for each sample. The average of the three measurements calculated by the Mastersizer was used for analysis.

3.2.4 Assessment of algal turfs within experimental plots

Algal turf height was measured to quantify the sediment trapping potential and productivity of the EAM. This is a cost-effective, non-destructive way to quantify the EAM such that algal turf height paired with sediment deposition can serve as a predictor for benthic productivity and suitability of the substrate for coral settlement and recruitment (Ford et al., 2018; Tebbett & Bellwood, 2019). Using plastic Vernier calipers, algal turf height was recorded at 10 haphazardly selected locations within three 1 m^2 quadrats within each 25 m^2 experimental plot. Algal turf surveys were conducted in May, July and November 2020 and February, April, and July 2021.

3.2.5 Physical environmental parameters

Two temperature loggers (HOBO MX2202) were installed in each bay for the duration of the study. Publicly available water temperature data for Magnetic Island collected by loggers installed by the Australian Institute of Marine Science were also used to supplement water temperature data throughout the study period. Two current meters (Marotte HS-1) were deployed in each bay for the duration of each pod deployment period to measure current speed and direction and assess hydrodynamic variation across sites.

3.2.6 Statistical analysis

Following inspection of raw data, outliers due to measurement error in each of the datasets were removed prior to statistical analysis (see Supplementary Table 7). Variation in sediment deposition rate, organic content of sediment, and algal turf height, was investigated using generalised linear mixed effects models (GLMMS). For sediment deposition rate and algal turf height, a Gamma distribution and log link were used, and organic content was modelled using a Beta distribution with logit link, following exploratory analysis of data distributions. Net sediment deposition rate was analysed separately for SedPods and TurfPods because the scale of sedimentation differed by an order of magnitude between the two pod types. For each pod type, sediment deposition rate was compared between control and removal plots, across deployment dates, and between bays (Arthur Bay and Florence Bay). For the analysis of organic content, the proportion of organic material in the deposited sediment was compared between control and removal plots, pod types, deployments, and bays. The substrate type on which each pod was placed was incorporated into the sediment deposition rate and organic content models as an additive fixed factor to account for substrate variation within plots. Algal turf height was compared between control and removal plots, survey timepoints, and bays.

A suite of models was defined for both SedPod deposition and TurfPod deposition incorporating macroalgal removal treatment, bay, deployment number, and substrate type as fixed effects. For organic content, pod type was also used as a fixed effect. For algal turf height, the predictor variables treatment, bay, and survey timepoint were fitted as fixed effects. In all models, plot number was fitted as a random factor. For SedPod and TurfPod sediment deposition and organic content, pod number was fitted as a random factor nested within the plot to account for the dependency structure of the hierarchical blocking design. Similarly, for algal turf height, quadrat number was fitted as a random factor nested within the plot.

Model selection was informed using second-order Akaike Information Criterion (AICc), and the most parsimonious model was selected for each dataset (see Supplementary Table 9 for model details). Model fits and assumptions were assessed via simulated residual plots, which were satisfactory in all cases. All models were fit using the glmmTMB package (Brooks et al., 2017) in the statistical and graphical software R (R Core Team, 2021). Significant differences among levels in the fixed factors as estimated by the models (estimated marginal means) were distinguished via post-hoc tests using the Tukey *p*-value adjustment method.

Grain size distribution data obtained from Mastersizer measurements were aggregated into nine grain size classes according to the Wentworth grain size intervals across the range 0.01 – 3500 µm (clay: < 3.9 µm, fine silt: 3.9 - 15.6 µm, coarse silt: 15.6 – 63 µm, very fine sand: 63 – 125 µm, fine sand: 125 – 250 µm, medium sand: 250 – 500 µm, coarse sand: 500 – 1000 µm, very coarse sand: 1000 – 2000 µm, gravel: > 2,000 µm (gravel sized particles were absent due to sieving but some flocculation of sediment particles occurred in some samples prior to particle size analysis leading to occasional occurrences of particles greater than 2,000 µm) (Wentworth, 1922). Out of a total of 564 observations, 105 outliers (18.6%) were removed prior to analysis due to measurement error. The outlying observations displayed distinctly different percent volume distributions, often with a single large peak indicative of a processing artefact and thus not reflective of the sediment sample. Problems like these are not uncommon when measuring particle size via laser diffraction and can lead to misrepresentation of the true particle size, which is why the results were rigorously scrutinised and inaccurate measurements rejected prior to analysis (Sabin, 2011).

Patterns in grain size distribution were visualised using a non-metric multidimensional scaling (NMDS) based on a Euclidean distance matrix of fourth-root scaled and Wisconsin double standardised volume density data, separately for SedPods and TurfPods. Differences between control and removal plots, deployments, and bays, were assessed using a permutational multivariate analysis of variance using the function ‘adonis’. Treatment, bay, and deployment were treated as fixed factors while plot number was treated as a random factor. Pair-wise tests were performed following the permutational multivariate analysis of variance to determine where differences occurred between the factors of interest. Analysis of multivariate homogeneity of group dispersions was performed using the ‘betadisper’ function to test the assumption of homogeneity of dispersion. Multivariate analysis was performed using the vegan package (Oksanen et al., 2020) in the statistical and graphical software R (R Core Team, 2021).

3.3 Results

3.3.1 Removal of macroalgae

See **section 2.3.3** for details on macroalgal biomass removed during the removal events.

3.3.2 Sediment deposition

Net sediment deposition on SedPods (proxy coral surface) ranged between 0.019 mg cm^{-2} d^{-1} and 0.75 mg cm^{-2} d^{-1} (Figure 3.1). TurfPods (proxy algal turf surface) accumulated more sediment, ranging between 0.37 mg cm^{-2} d^{-1} and 57.18 mg cm^{-2} d^{-1}. Overall, the removal of macroalgae had no significant effect on net sediment deposition rate on the SedPods, nor on the TurfPods. However, there was evidence for some interactions between treatment, bay, and deployment (Supplementary Table 9). Net sediment deposition on the SedPods in Arthur Bay was consistently lower in control plots (0.17 ± 0.02 (estimated marginal mean ± SE) mg cm^{-2} d^{-1}) relative to removal plots (0.27 ± 0.03 mg cm^{-2} d^{-1}), though this difference was only statistically significant in May 2020 when deposition in control plots (0.10 ± 0.02 mg cm^{-2} d^{-1}) was 54 ± 11% less than deposition in removal plots (0.23 ± 0.04 mg cm^{-2} d^{-1}) (t = -3.4, df = 269, p < .05; Figure 3.1a). In Florence Bay, a significant difference in net sedimentation between control and removal plots was only observed during the November 2020 deployment (control plots: 0.16 ± 0.03 mg cm^{-2} d^{-1}, removal plots: 0.36 ± 0.07 mg cm^{-2} d^{-1}, t = -3.3, df = 269, p < .05; Figure 3.1a). TurfPods experienced a similar pattern, with a lower rate of sediment deposition in control plots relative to removal plots, however this difference was not statistically significant (Supplementary Table 9; Figure 3.1b). The modelled relationship representing net sediment deposition as a function of treatment, bay, deployment, and substrate was stronger for TurfPods compared to SedPods, with approximately 81% and 57%, respectively, of the variation in net deposition rate explained by both the fixed and random effects (conditional pseudo-r^2: TurfPods = 0.81, SedPods: 0.57, Supplementary Table 9).

For both SedPods and TurfPods, there was, on average, no difference in net sediment deposition between bays. However, TurfPods had consistently greater deposition in Florence Bay compared to Arthur Bay for all deployments except May 2020 (May 2020: t = -3.2, df = 272, p = .063; August 2020: t = -5.5, November 2020: t = -3.6, February 2021: t = -5.5, df = 272, p < .05; Figure 3.1b). Interestingly, for the SedPods, the May 2020 deployment was the only time when location had a significant effect on deposition (t = -5.1, df = 269, p < .05; Figure 3.1a), with Florence Bay experiencing higher deposition compared to Arthur Bay in that timepoint.

Data collected from the current meters showed low current speeds across both bays and all deployments ranging from 1.0 cm s^{-1} to 17 cm s^{-1}. Across all deployments, net current speed in Arthur Bay (4.0 ± 0.38 cm s^{-1}) was lower than in Florence Bay (7.0 ± 0.74 cm s^{-1}; Figure 3.1). Averaged across both bays, net current speed was consistently low across the four deployments: May 2020: 6.3 ± 0.99 cm s^{-1}, August 202: 6.0 ± 1.0 cm s^{-1}, November 2020: 5.4 ± 0.92 cm s^{-1}, February 2021: 5.0 ± 0.78 cm s^{-1}).

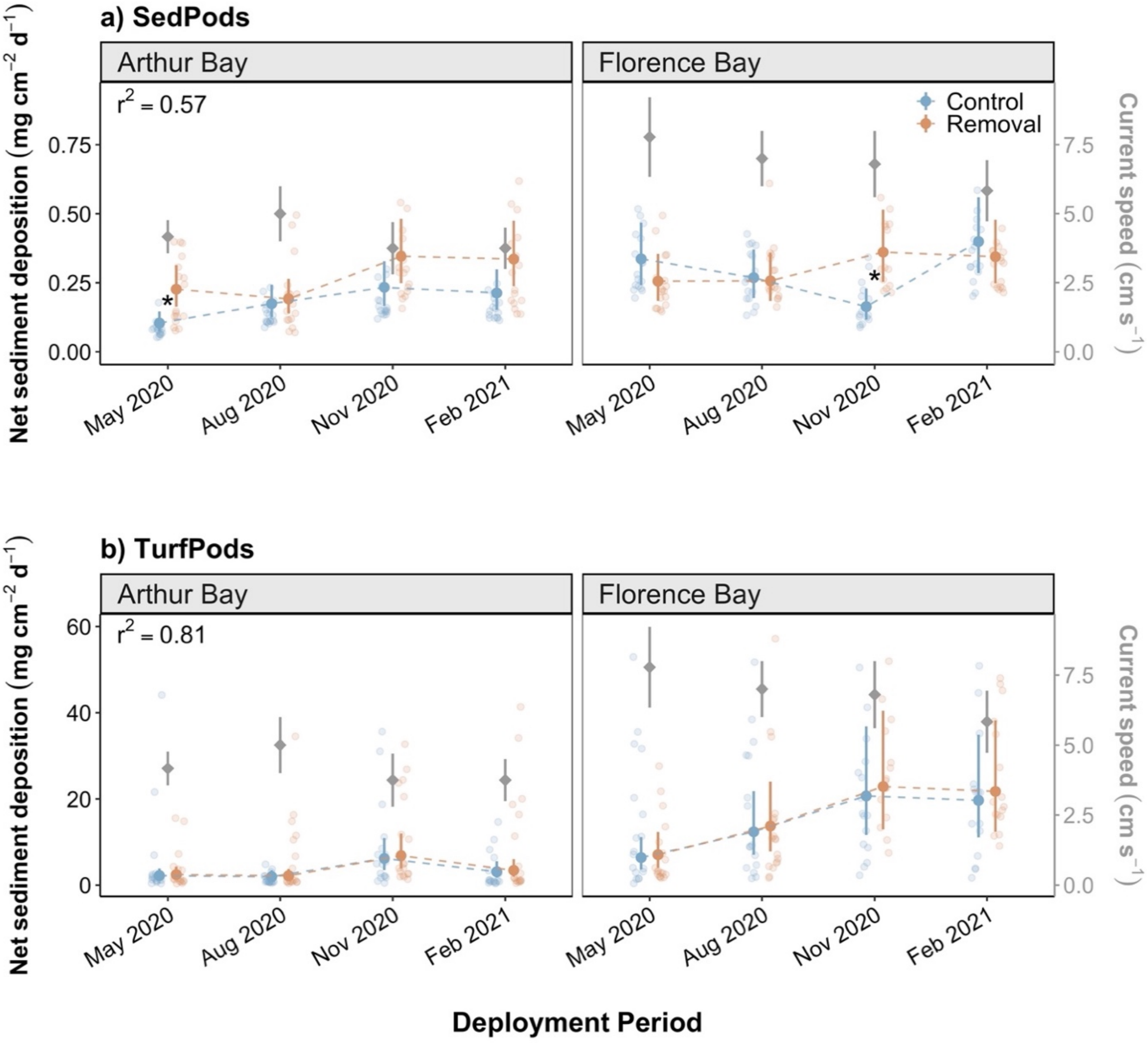


***Figure 3.1** Net sediment deposition rate (mg cm^{-2} d^{-1}) on **(a)** ‘SedPods’, a proxy hard coral surface, and **(b)** ‘TurfPods’, a proxy algal turf surface, for four pod deployment periods throughout 2020 - 2021 in two bays of Magnetic Island, Australia. Coloured points are mean predicted fits of generalised linear mixed effects models (Gamma distribution with log link), with predictions for control plots shown in blue and removal plots shown in orange. Coloured vertical lines represent 95% confidence intervals. Partialised observations (sum of fitted values and residuals) are shown as faint-coloured points. Asterisks represent statistically significant differences in net sediment deposition between control and removal plots. Grey*

points and vertical lines represent average current speed (cm s^{-1}) and standard error, respectively

3.3.3 Organic content

Overall, the proportion of organic material in the deposited sediment in removal plots was statistically no different to that of control plots (t = -0.53, df = 551, p = 1). The sediment deposited on both SedPods and TurfPods contained between 2.51% and 31.82% organic material, with SedPods containing on average 13.47 ± 0.33% (estimated marginal mean ± SE) organics and TurfPods 9.07 ± 0.32% organics. There were consistently higher proportions of organic material in the SedPod sediments relative to the TurfPod sediments, however the statistical significance of this difference varied depending on both location and time of deployment (Figure 3.2; Supplementary Table 8). Fixed and random effects explained 70% of the variability (conditional pseudo-r^2 = 0.70) in organic proportion when modelled as a function of pod type, treatment, bay, and deployment (Supplementary Table 9).

Spatial variation was evident, with consistently greater proportions of organic material in sediments from Arthur Bay relative to Florence Bay (Figure 3.2; Supplementary Table 8). This difference, however, was statistically significant for the August 2020 (t = 5.6, df = 551, p < .05) and February 2021 deployments only (t = 4.2, df = 551, p < .05). The proportion of organic material in deposited sediment also varied temporally (Figure 3.2). In particular, the proportion of organics at the end of the study (February 2021) was significantly lower relative to the start of the study (May 2020) (Arthur Bay SedPods: t = 3.6, Arthur Bay TurfPods: t = 4.1, Florence Bay SedPods: t = 5.5, Florence Bay TurfPods: t = 5.2; df = 551, p < .05).

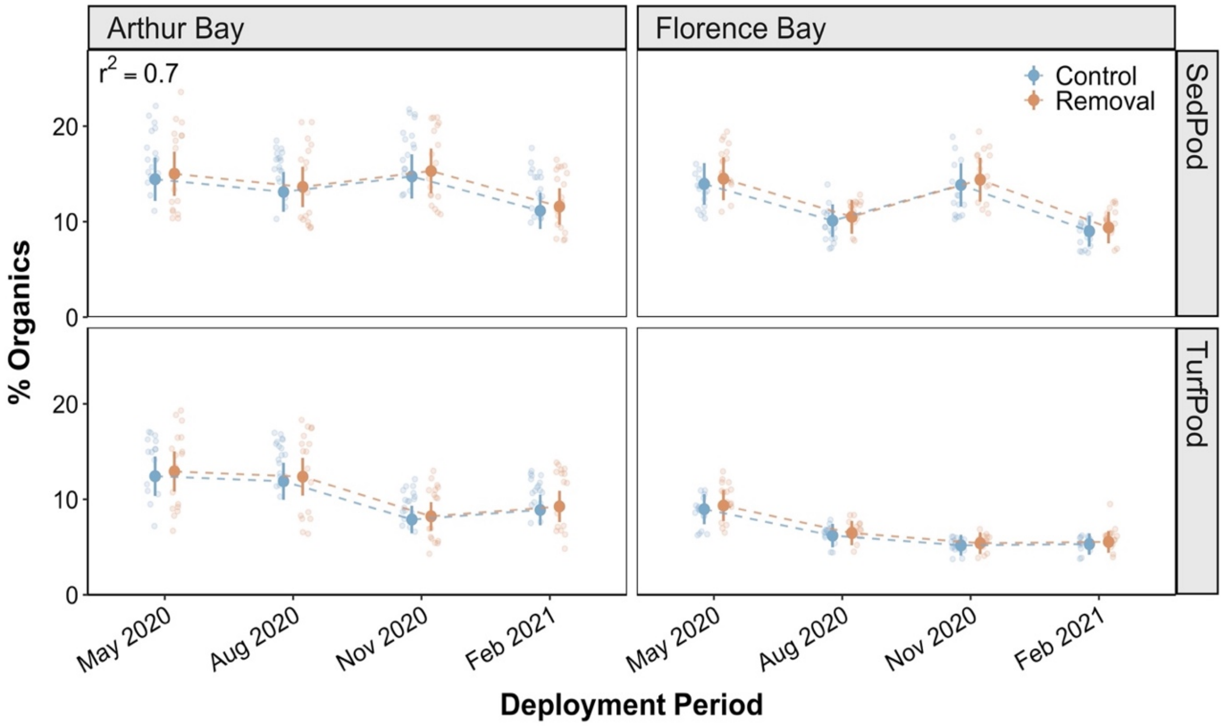


Figure 3.2 *Percentage of organic matter in deposited sediment samples on 'SedPods', a proxy hard coral surface, and 'TurfPods', a proxy algal turf surface, for four pod deployment periods throughout 2020 to 2021 in two bays of Magnetic Island, Australia. Coloured points are mean predicted fits of a generalised linear mixed effects model (Beta distribution with logit link – conditional pseudo-r^2 = 0.70), with predictions for control plots shown in blue and removal plots shown in orange. Solid vertical lines represent 95% confidence intervals. Partialised observations (sum of fitted values and residuals) are shown as faint-coloured points*

3.3.4 Grain size distribution

The ordination plots showed no major distinction in grain size distribution between control and removal plots for both the SedPods and TurfPods (adonis: SedPods - $F_{1,73}$ = 1.45, r^2 = 0.02, p = .138, TurfPods - $F_{1,78}$ = 0.29, r^2 = 0.00, p = .57; Supplementary Table 10; Figure 3.4). There was no difference in grain size distribution between bays for the SedPods (adonis: $F_{1,73}$ = 2.5, r^2 = 0.03, p = .083; Supplementary Table 10), however, a significant difference in grain size between bays was detected for the TurfPods (adonis: $F_{1,78}$ = 35, r^2 = 0.27, $p < .05$; Figure 3.4; Supplementary Table 10). This may be due to significantly different dispersion between bays, as opposed to a true difference in grain size distribution (betadisper: Bay - F = 6.6, $p < .05$).

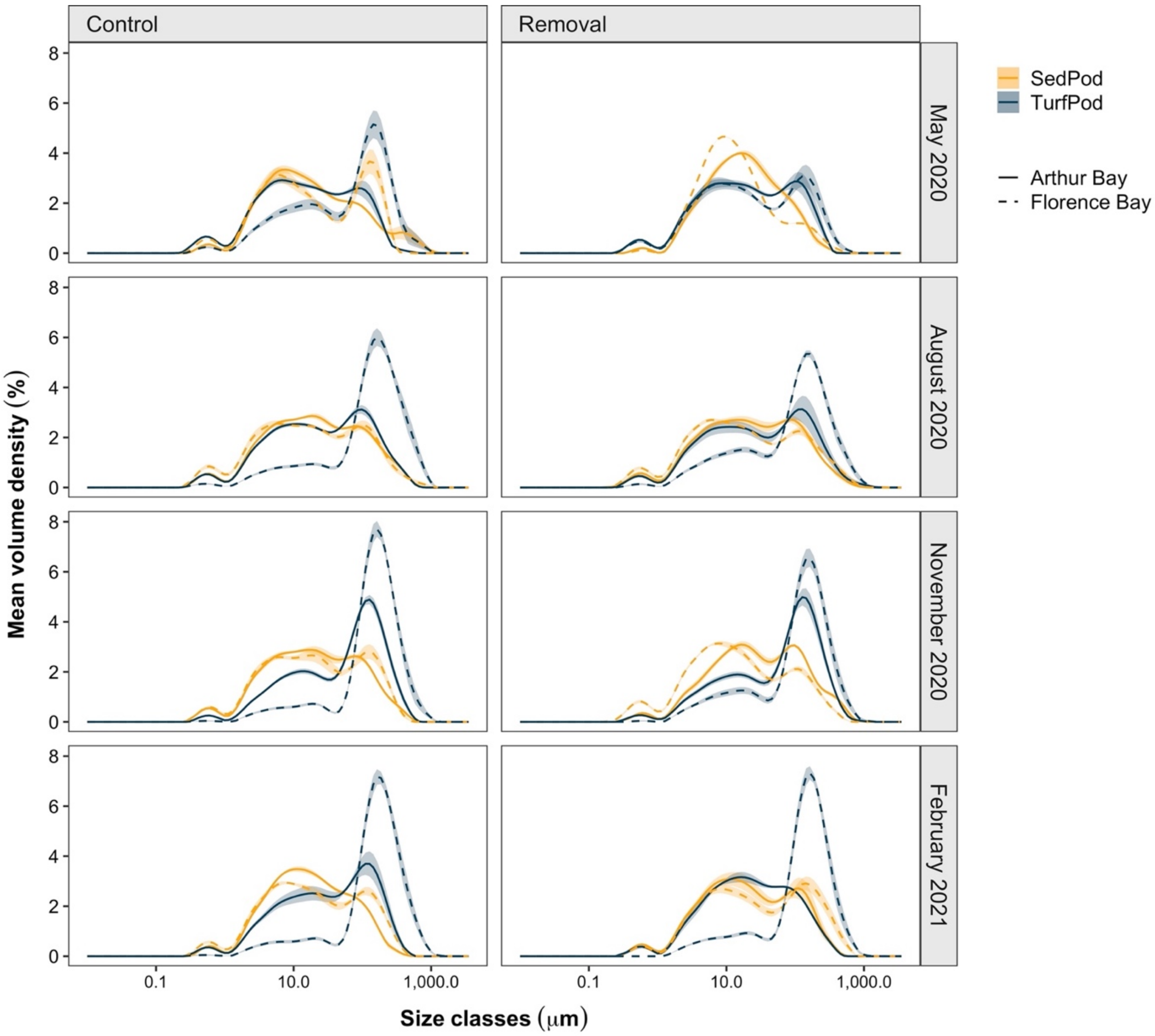
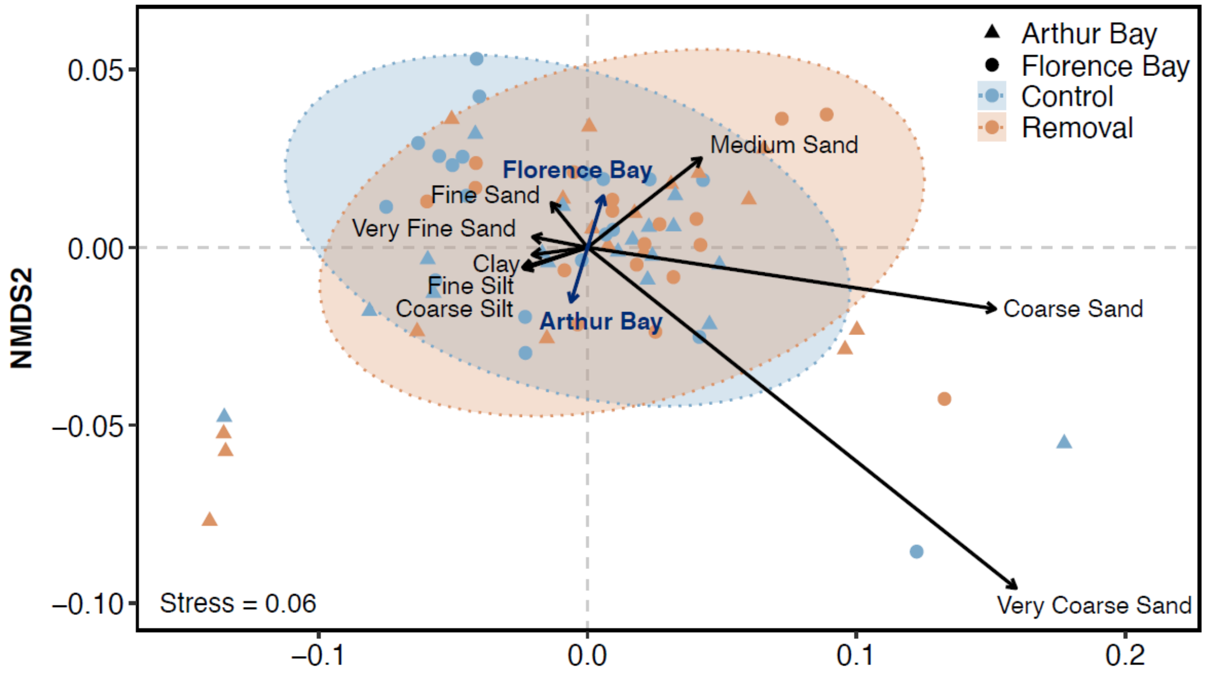


Figure 3.3 *Average grain size distribution represented as percent volume density (% distribution by volume) for deposited sediment samples on 'SedPods' (yellow lines), a proxy hard coral surface, and 'TurfPods' (blue lines), a proxy algal turf surface, for four pod deployment periods throughout 2020 - 2021 in two bays of Magnetic Island, Australia (Arthur Bay (solid lines) and Florence Bay (dashed lines)). Coloured ribbons surrounding each line represent standard errors*

The greatest variation in grain size distribution was seen when comparing the deposition surfaces. Sediment deposited on TurfPods had a higher proportion of coarser sediments and more variable grain size distributions relative to sediments collected on SedPods (Figure 3.3). The mean particle diameters at the 90th percentile (D90) for TurfPod sediments reflected this pattern, ranging from 118 µm to 433 µm, which were on average larger than those for SedPod sediments, which ranged from 95 µm to 240 µm

(Supplementary Table 8). Furthermore, fine sediments (<20 μm) were more prevalent in the deposited samples from SedPods (52 ± 0.6% (mean ± SE)) relative to the TurfPods (31 ± 1.1%) (Supplementary Table 8). For both pod types, the larger grain size classes (very coarse sand (1000 – 2000 μm) and gravel (>2000 μm)) were present in only a few samples due to flocculation of particles after sieving (Figure 3.4).

a) SedPods



b) TurfPods

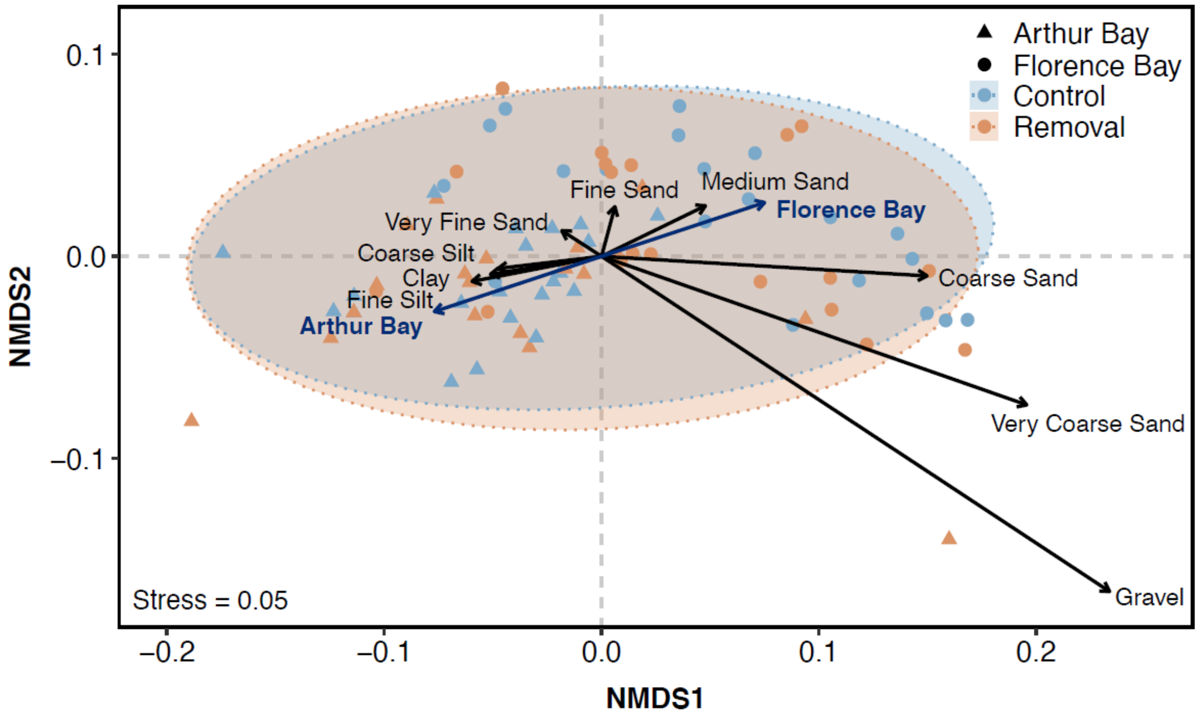


***Figure 3.4** Non-metric multidimensional scaling (nMDS) ordination of sampling units based on Euclidean distances of fourth-root scaled and Wisconsin double standardised volume densities of p = 9 grain size classes in a total of **(a)** n = 74, **(b)** n = 79 sampling units around Magnetic Island, Australia. Symbols show the bay from which the sediment sample was collected (Arthur Bay shown as triangles, Florence Bay shown as circles), and colours show the treatment (control plots shown in blue, removal plots shown in orange). Black arrows represent grain size classes. Dark blue arrows represent environmental factors of interest projected onto the ordination plot*

3.3.5 Algal turf height

Algal turf height ranged from 1 mm to 19 mm during the study period, and the modelled relationship connecting treatment, bay, and timepoint to algal turf height was relatively weak (conditional pseudo-r^2 = 0.30; Figure 3.5; Supplementary Table 9). Macroalgal removal had largely no effect on algal turf height, with the only statistically significant difference identified in the November 2020 survey in Florence Bay, where control plot turfs (6.13 ± 0.26 mm (estimated marginal mean ± SE)) were 42% taller than removal plot turfs (4.45 ± 0.19 mm) (t = 5.4, df = 4271, p < .05; Supplementary Table 9). Similarly, there was no difference in turf height between bays. Temporal variation in turf height was the most prominent trend, where turfs were significantly taller at the start of the study period (May 2020, control plots: 8.54 ± 0.28 mm, removal plots: 9.13 ± 0.31 mm) relative to the end of the study (July 2021: control plots: 4.19 ± 0.14 mm, removal plots: 4.46 ± 0.15 mm) (Arthur Bay: control plots: t = 13, removal plots: t = 13; Florence Bay: control plots: t = 6.6, removal plots: t = 13; df = 4271, p < .05), however, there was no significant interaction between treatment and timepoint, indicating that the observed temporal trend did not differ between control and removal plots (Figure 3.5; Supplementary Table 9). Temperature data showed seasonal fluctuations ranging from 21°C to 31°C throughout the study period, however, there was no distinct pattern observed between temperature and turf height (Figure 3.5).

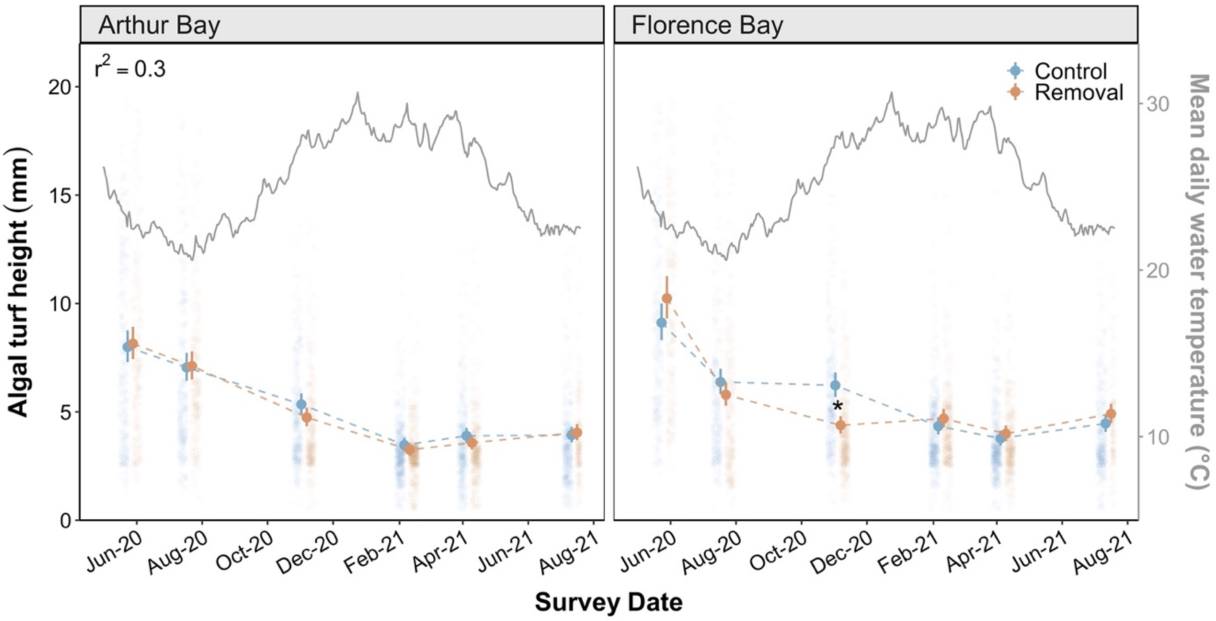


Figure 3.5 *Height of algal turfs in two bays of Magnetic Island, Australia, across six survey timepoints throughout 2020 - 2021. Solid coloured points are mean predicted fits of a generalised linear mixed effects model (Gamma distribution with log link – conditional pseudo-r^2 = 0.3), with predictions for control plots shown in blue and removal plots shown in orange. Solid vertical lines represent 95% confidence intervals. Partialised observations (sum of fitted values and residuals) are shown as faint-coloured points. Asterisks represent statistically significant differences in algal turf height between control and removal plots. Average daily water temperature is shown as a solid grey line to provide environmental context*

3.4 Discussion

In this study, removing the macroalgal canopy, predominantly *Sargassum* spp., from inshore reefs had no statistically significant impact on the rate of sedimentation nor the composition of deposited sediments within experimental plots. Despite this, consistently less deposition was observed in control plots relative to removal plots in Arthur Bay. This result points to the hypothesis that removing macroalgae may allow sediments to settle out of suspension onto the benthos rather than being accumulated on the macroalgal canopy. However, physical parameters such as wind, rain, and currents are likely to influence sediment dynamics to a greater extent and at larger spatial scales, than biological factors such as macroalgal canopies.

Hydrodynamics are the major force governing sediment deposition and resuspension, giving rise to variability in geomorphology and hydrodynamic regimes across different reefs (Purcell, 2000; Schlaefer et al., 2021). Both spatial and temporal variation in sediment deposition were observed in this study despite no difference between control and removal plots. Canopy-forming macroalgae can influence fine-scale water dynamics (Birrell et al., 2008), but the larger-scale hydrodynamic parameters of current, wind, and rainfall at a site, are likely to have a greater effect on water flow and, subsequently, the physical load of deposited sediment. The results observed here suggest that the current speed and direction changing through time and space, may be driving sediment deposition more so than changes in the macroalgal canopy. Physical data collected during this study supports this theory with lower current speeds broadly corresponding with greater sediment deposition and vice versa.

The impact of deposited sediment on benthic organisms is influenced not only by the physical load of sedimentation but also by the amount of associated organic material and the grain size distribution (Weber et al., 2006). Organic and nutrient-related parameters of sediment are more strongly related to stress levels of benthic organisms, such as corals, compared with physical parameters (Weber et al., 2006). In this study, the composition of the sediments was consistent across experimental plots irrespective of macroalgal removal. Inshore coral reefs such as those surrounding Magnetic Island, are at a heightened risk of exposure to organically enriched sediments derived from terrestrial runoff relative to reefs further offshore (Furnas, 2003; Weber et al., 2012; Wolanski et al., 2005). Organic sediment aggregates can be detrimental to corals and algal turfs, due to stimulation of microbial processes causing tissue degradation and increasing disease transmission and prevalence (Bainbridge et al., 2018; Jones et al., 2019; Studivan et al., 2022; Weber et al., 2012). Removing macroalgae at these sites on Magnetic Island did not appear to expose corals to increased organic aggregates and associated microbial stress. Sediment-related stressors are, therefore, unlikely to be exacerbated by removal activities at the scale investigated in this study.

The grain size distribution of deposited sediment was also not influenced by macroalgal removal. Sediment grain size and propensity to aggregate with organic material can synergistically affect benthic marine organisms due to the formation of marine snow, which has been found to cause mortality to corals (Bainbridge et al., 2018; Fabricius & Wolanski, 2000). Fine grain size classes less than 63 μm (clay and silt) are considered more detrimental to corals than larger grain size classes (sand and gravel) because they are more difficult for corals to remove from their oral cavity (Bainbridge et al., 2018; Bainbridge et al., 2012; Jones et al., 2019; Weber et al., 2006). Moreover, finer grain sizes readily aggregate with organic material, giving rise to microbial proliferation which can result in coral tissue necrosis (Weber et al., 2012). Accumulation of fine organic sediment aggregates in algal turfs can also elicit conditions detrimental to coral settlement and recruitment (Speare et al., 2019), reduce benthic productivity (Clausing et al., 2014; Tebbett & Bellwood, 2020), and detrimentally affect detritivore feeding behaviour (Tebbett et al., 2017). Material reaching the GBR lagoon via flood plumes is primarily constituted of terrigenous particles less than 20 µm, and this finer grain size fraction is arguably the most relevant size class for inshore GBR corals (Bainbridge et al., 2018; Bartley et al., 2017). On average, between a third to a half of the sediment content analysed in this study was less than 20 µm, highlighting that the reefs of Magnetic Island are subjected to fine grain sizes. However, at the scale investigated in this study, macroalgal removal did not increase the risk of fine sediment accumulation and associated organic aggregation on corals and algal turfs.

Thresholds of sediment deposition as low as 1 mg cm^{-2} d^{-1} for coral larvae and 4.9 mg cm^{-2} d^{-1} for coral adults have been reported as detrimental to coral health (Tuttle & Donahue, 2020). Specific to inshore GBR corals, a study by Fabricius et al. (2003) found that coral juveniles were able to survive sedimentation up to 14 mg cm^{-2}, however, similar loads enriched with organic material resulted in increased mortality. This variability in susceptibility of corals to sedimentation depending on life stage as well as sediment composition emphasises the need for site-specific understanding of sedimentation thresholds to assist reef and catchment management. On the reefs surrounding Magnetic Island, high sedimentation and turbidity is derived from terrestrial runoff from the Burdekin River (Doropoulos et al., 2022; GBRMPA, 2019; Humanes et al., 2017; Ricardo et al., 2017, 2021; Schaffelke et al., 2017), and to a lesser extent dredging activities (which leads to sediment resuspension) associated with the Port of Townsville (Benson et al., 1994; Brown, 1972; McCook et al., 2015; Umar et al., 1998). The net level of sedimentation on corals estimated in this study via the use of SedPods (0.02 – 0.75 mg cm^{-2} d^{-1}) was below any proposed limit for detrimental impacts to corals. However, no major acute disturbances (e.g., floods) occurred during the study period, which are the primary mechanism of sediment delivery to inshore reefs (Furnas, 2003; Schaffelke et al., 2005; Waterhouse et al., 2017b). Furthermore, field logistics necessitated deployment of Pods in calm (i.e., low wind) weather windows, which may have distinctly different dynamics compared to times of stronger winds. Investigation of sedimentation of corals during flood events when terrigenous sediments are delivered to the reef system, as well as during periods of high winds and dredging activities, are required to determine the level of sedimentation stress experienced by corals at Magnetic Island.

Sediment deposition thresholds have also been suggested for algal turfs, with loads higher than 10 mg cm^{-2}(sampled from natural turfs) thought to elicit declines in algal turf productivity and particulate nutritional value (Tebbett & Bellwood, 2020). Much of the sediment deposited on coral reefs is bound in algal turfs, which can reduce water flow in the boundary layer up to 15-fold relative to free-stream flow, causing sediment to settle out of suspension (Birrell et al., 2008; Carpenter & Williams, 1993). The difference in deposition between EAM colonised surfaces and surfaces not colonised by EAM (e.g., coral surfaces) was demonstrated in this study, whereby the artificial turf layer accumulated 20-fold higher levels of deposited sediment. Additionally, sedimentation on TurfPods (0.37 – 57.18 mg cm^{-2} d^{-1}) was more variable relative to the SedPods, and at the upper end considerably greater than the proposed 10 mg cm^{-2} threshold. Sedimentation stress may, therefore, be a more concerning factor for algal turfs and EAM productivity on Magnetic Island reefs.

Turf algae is a strong indicator of benthic productivity, with a height threshold of 5 mm proposed, beyond which the EAM develops into LSATs (Goatley et al., 2016; Gordon et al., 2016; Purcell, 2000; Tebbett & Bellwood, 2019) and becomes potentially unsuitable for coral settlement and recruitment with subsequent declines in productivity (Ford et al., 2018; Tebbett & Bellwood, 2020). Algal turf height averaged approximately 5 mm in this study, which is around this critical threshold and consistent with the high, though also highly variable, sediment deposition rates measured on the proxy algal turf surface. High deposition on the TurfPods coincided with the surveys that recorded relatively short algal turf height (less than 5 mm), which is not consistent with relationships previously reported between turf height and sediment deposition (Gordon et al., 2016; Purcell, 2000; Tebbett & Bellwood, 2020). However, there may be a disconnect in the timing of sedimentation and turf growth. Furthermore, the declining temporal trend observed in turf height may have been driven by other factors not measured in this study, such as herbivory. The effects of sediment deposition and herbivory have been shown to interact to affect algal turfs, with herbivore presence mediating negative effects of sedimentation (Clausing et al., 2014; Tebbett, Bellwood, et al., 2018). An increase in herbivory throughout the study period could, therefore, explain the decrease in turf height through time, however this is speculative as fish populations were not assessed in this study.

Macroalgal removal led to little observed change in turf height throughout this study. This could suggest removal of the macroalgal canopy is unlikely to drive unwanted increases in algal turf height and associated detrimental bottom-up effects on key reef ecosystem processes such as benthic productivity, and coral settlement and recruitment (Tebbett, Goatley, et al., 2018; Tebbett & Bellwood, 2020). The weak statistical relationship between macroalgal removal and turf height does, however, indicate there may be a more complex suite of factors driving turf height dynamics. Other EAM characteristics, such as algal turf cover and community composition, or associated microbial communities should be investigated, to assess their influence on the suitability of the EAM for coral settlement and recruitment, as well as benthic productivity (Birrell et al., 2005; Cetz-Navarro et al., 2015). Grazing patterns are also known to affect algal turfs and sediment composition. Documenting the herbivorous fish communities in conjunction with metrics quantified in this study may help to understand the relationship between macroalgae, turf algae, and sedimentation (Birrell et al., 2008; Bonaldo & Bellwood, 2011; Clausing et al., 2014; Tebbett & Bellwood, 2019).

The order of magnitude difference between deposition of sediment on the proxy coral surface and the proxy algal turf surface is consistent with previous studies utilising these instruments (Latrille et al., 2019). These findings reflect the difference in boundary layer complexity, emphasising the variation in sedimentation experienced by different benthic organisms on coral reefs (Birrell et al., 2008; Latrille et al., 2019). Despite less net sediment deposition occurring on the SedPods, the sediment deposited contained on average approximately 50% higher proportion of organic material and approximately 65% higher proportion of fine grain size classes (less than 20 μm) relative to TurfPod sediments. This is consistent with a previous study comparing SedPods and TurfPods, as well as other sediment trapping devices (Latrille et al., 2019). This is likely due to the differences between the deposition surfaces; with the propensity of the flat SedPod surface to develop a biofilm and accumulate fine organic sediment aggregates, in contrast to the artificial turf layer capable of trapping more coarse, inorganic particles. Less sediment deposition on the proxy coral surface, yet a higher organic proportion and finer grain sizes relative to the proxy turf surface, may indicate that the impact of deposited sediment is disproportionate to the physical load. Furthermore, spatiotemporal variation in net sediment deposition, organic content, and grain size distribution was more pronounced for TurfPods relative to SedPods. This suggests sedimentation of algal turfs may be more variable through space and time compared with hard corals. Measuring a range of sediment characteristics across varying temporal and spatial scales is therefore essential to accurately quantify the impact on benthic organisms. Thus, sedimentation of the proxy algal turf surface may be a more relevant measure for coral recruits and juveniles on inshore reefs, whereas sedimentation of the proxy coral surface may be more relevant to coral growth and health during later life stages. Furthermore, the use of SedPods may serve as a proxy for measuring sediment deposition on CCA; an important settlement cue for coral larvae (Jorissen et al., 2021; Tebben et al., 2015). This could be more relevant for measuring impacts of sedimentation on early life stage corals on offshore reefs where CCA is more abundant (Dean et al., 2015).

It is important to interpret these results in the context of the temporal and spatial scales at which this study was conducted. Coral reef sedimentation is known to vary substantially over small temporal scales due to tide and wind interactions (Schlaefer et al., 2021; Whinney et al., 2017). Data collection in this study was conducted during calm weather conditions within short deployment periods, thus, under high winds and strong currents, different sediment dynamics would likely be observed. Studies that occur during both low and high wind conditions, as well as on a longer-term scale than investigated here, are required to further understand the variability in coral reef sediment dynamics and the relationship with macroalgae. This is particularly pertinent for inshore reefs, which are exposed to a relatively high proportion of fine grained, organic sediment (as observed in this study), which is more easily suspended by wind and currents (Bainbridge et al., 2018; Bartley et al., 2017; Fabricius & Wolanski, 2000). From a spatial perspective, the plots (25 m^2) used in this study may be too small to influence sediment dynamics relevant to the broader hydrodynamic patterns occurring at larger spatial scales. At a bay-wide scale, however, hydrodynamic patterns may be influenced to a greater extent by macroalgal removal having flow-on effects for sedimentation and algal turfs. Furthermore, edge effects may have contributed to this lack of resolution. Removing macroalgae from larger areas i.e., an order of magnitude greater, may be required to avoid edge effects and enable delineation of the biological and physical parameters influencing sediment dynamics on inshore reefs.

Results of this study provide insights into the impact of macroalgal removal on sedimentation dynamics and algal turf height on inshore coral reefs experiencing high sediment input. Overall, this study suggests the relationship between sedimentation, algal turfs, and macroalgae on Magnetic Island reef communities, and likely other inshore GBR reefs, is complex and dynamic. For example, sedimentation stressors may act synergistically with other factors such as temperature and light (Anthony et al., 2007), which in isolation may not lead to the same responses. Despite the complexity of the relationships investigated in this study, it was clear that removing the macroalgal canopy on a small scale had minimal effect on sediment deposition and composition, as well as algal turfs. Thus, sediment-related stressors for corals and algal turfs are unlikely to be worsened nor alleviated following macroalgal removal.

Chapter 4: General discussion

4.1 Thesis contribution & key findings

The condition of many inshore reefs of the GBR is continuing to decline due to multiple local and global stressors, as substantiated by the declining coral index reported in the latest Annual Report for Inshore Coral Reef Monitoring 2019-20 (Thompson et al., 2021). The common signs of inshore reef degradation are prolific macroalgal growth (predominantly canopy-forming species such as *Sargassum* spp.), low coral cover, and reduced benthic community diversity (Birrell et al., 2008; Diaz-Pulido & McCook, 2008; Done, 1992; Williamson et al., 2019). The drivers of macroalgal overgrowth and inshore reef degradation in some regions of the GBR are multifactorial and have occurred over decades. Unfortunately, in recent years there have been signs of accelerating macroalgal overgrowth and coral loss (Ceccarelli et al., 2020; De'ath et al., 2012; De'ath & Fabricius, 2010; Thompson et al., 2021).

There is substantial momentum behind improving management of inshore GBR reefs to facilitate recovery and prevent further degradation (Boström-Einarsson et al., 2020; State of Queensland, 2018; Williamson et al., 2019). Yet, major contributing factors to coral reef degradation, such as climate change, which is linked to increasing severity and frequency of extreme weather events, cannot be mitigated at a local scale. Management to reduce chronic stressors locally is more feasible and could have a positive effect on reef recovery and resilience on a local scale. On inshore reefs overgrown by fleshy macroalgae, corals are often outcompeted and persistent feedback loops can prevent them from re-establishing (Birrell et al., 2008; Fulton et al., 2019; Johns et al., 2018). To assist recovery on such reefs, physical removal of macroalgae to reduce algal biomass, theoretically reduces competitive pressure against corals, allowing them to grow uninhibited. As detailed in **Chapter 1**, macroalgal removal experiments have shown positive effects on reef recovery, including increased coral recruitment (Briggs et al., 2018; Smith et al., 2021), though a comprehensive understanding of the positive and negative effects are not fully established (Ceccarelli et al., 2018).

In **Chapter 2**, the impact of macroalgal removal on inshore coral reef communities was investigated. Monitoring the benthic cover of corals and macroalgae over the three-year study period gave a clear picture of the effect of regular macroalgal removal events, resulting in a substantial increase in coral cover and sustained reduction in macroalgal cover. The strong evidence for increased hard coral cover in removal plots and simultaneous increase, albeit smaller, in control plots is a positive indicator that a singular change to inshore reef structure has the potential to promote coral reef recovery on inshore GBR reefs.

Furthermore, removing macroalgae at regular intervals throughout the study period resulted in substantial change to the composition of the benthic community within removal plots. The macroalgal community in removal plots increased in diversity and evenness through time in response to macroalgal removal. Importantly, after three years of repeated macroalgal removal events, the removal plots were no longer dominated by canopy-forming *Sargassum* species. These findings bode well for pursuing macroalgal removal as a strategy to assist localised coral recovery on degraded inshore reefs.

In **Chapter 3**, the unique relationships between the macroalgal canopy, algal turf environment, and sedimentation were thoroughly investigated, elucidating the complexity of these relationships. Interestingly, removing the macroalgal canopy was found to have negligible effect overall on sedimentation of algal turfs and hard corals. Specifically, the quantity of sediment deposited on the proxy coral surfaces (SedPods) and proxy turf surfaces (TurfPods), was no different in removal plots compared with control plots following macroalgal removal. The composition of deposited sediment in terms of organic content and grain size distribution was also not significantly different between control and removal plots for both proxy surfaces. However, slightly higher proportions of organic material were consistently found in the removal plots. Despite there being no effect of macroalgal removal on sediment characteristics, the deposition surface significantly affected sediment load and composition. The proxy algal turf surface (TurfPods) collected higher amounts of coarse sediment and more variable grain sizes, whereas the proxy hard coral surface (SedPods) collected low quantities of very fine, organically rich sediment. Algal turf height was not affected by removal of macroalgae, and it is likely that factors other than those measured in this study are what is driving algal turf dynamics on inshore reefs. Sedimentation stressors, which are key contributing factors to change on inshore reefs, are, therefore, unlikely to be worsened nor alleviated upon removal of the macroalgal canopy. Nevertheless, coral sedimentation dynamics are complex, and this study was conducted at a relatively small scale (experimental plot size 25 m^2) with short deployments (~1 week) of sediment accumulation devices. How dynamics differ across larger spatial scales and variable temporal conditions (i.e., high wind resuspension events) should be investigated to further explore these questions.

4.2 Conservation and management implications: feasibility of macroalgal removal as a localised inshore reef restoration technique

Inshore reefs of the GBR are subject to a unique set of environmental and anthropogenic pressures (outlined in **Chapter 1**) distinguishing them from their offshore counterparts. Consequently, management of inshore reef ecosystems must address local conditions and stressors to be effective. With increasingly more emphasis on researching and implementing active coral reef restoration strategies for the GBR, there is an urgent need to improve knowledge across the board regarding potential restoration activities (Boström-Einarsson et al., 2020; Suggett & van Oppen, 2022).

Poor water quality has likely contributed to inshore reef degradation by creating unsuitable conditions for coral recovery post-disturbance, resulting in coral decline and simultaneous macroalgal proliferation (Ceccarelli et al., 2020). Improvements to water quality within the GBR lagoon are dependent on improvements to land and catchment management, which are being implemented via the Reef 2050 WQIP (State of Queensland, 2018). However, the long timeframe between changes on land and detectable improvements in water quality in the GBR lagoon, means interventions in the interim are required to assist coral recovery until water quality has measurably improved. Particularly for inshore reefs, which experience localised water quality stress to a greater extent relative to their offshore counterparts, it is vital to intervene in the short-term to assist coral recovery in the longer-term. Active interventions such as macroalgal removal, as investigated throughout this thesis, may therefore help to delay further reef degradation, and assist in localised reef recovery, alongside water quality improvements.

Removal of macroalgae is emerging as a promising technique to boost coral settlement and recruitment (Smith et al., 2021). However, it is important to assess other ecological processes which may be affected by the removal of a macroalgal canopy, including those studied here. Rigorous assessment of the impact of proposed reef restoration techniques is essential to optimise coral reef management and ensure appropriate prioritisation of interventions. The findings of this thesis suggest that macroalgal removal could be a successful restoration strategy to assist coral recovery at a local scale. There is strong evidence provided to suggest that coral recovery, in terms of live hard coral cover, is substantially greater in reef areas cleared of macroalgae. Thus, regular macroalgal removal efforts on a local scale, have the potential to rapidly improve coral recovery on degraded inshore reefs. If patterns observed in this thesis persist in response to continued macroalgal removal events, inshore reef communities at Magnetic Island, and likely other inshore reefs of the GBR, have the potential to overcome a biotic barrier to coral recovery (see Figure 4.1 for conceptual representation). The result is a path more conducive to re-establishment of the coral-dominated state. However, the extent of these benefits, are dependent on mitigation of abiotic barriers to coral recovery, which is critical for inshore reefs on the GBR exposed to high sediment inputs. Removal of the macroalgal canopy (*Sargassum* spp.) was found to have no impact on the amount and composition of deposited sediments, as well as no significant effect on algal turf height. This suggests macroalgal removal as a small-scale restoration technique is unlikely to affect sediment dynamics and turf environments.

Sediment-related stressors for corals and algal turfs are unlikely to be worsened nor alleviated following the removal of the macroalgal canopy. Consequently, the benefits observed during this study, such as increased coral cover, are likely to be even further enhanced with improvements to water quality and reductions in sedimentation stress.

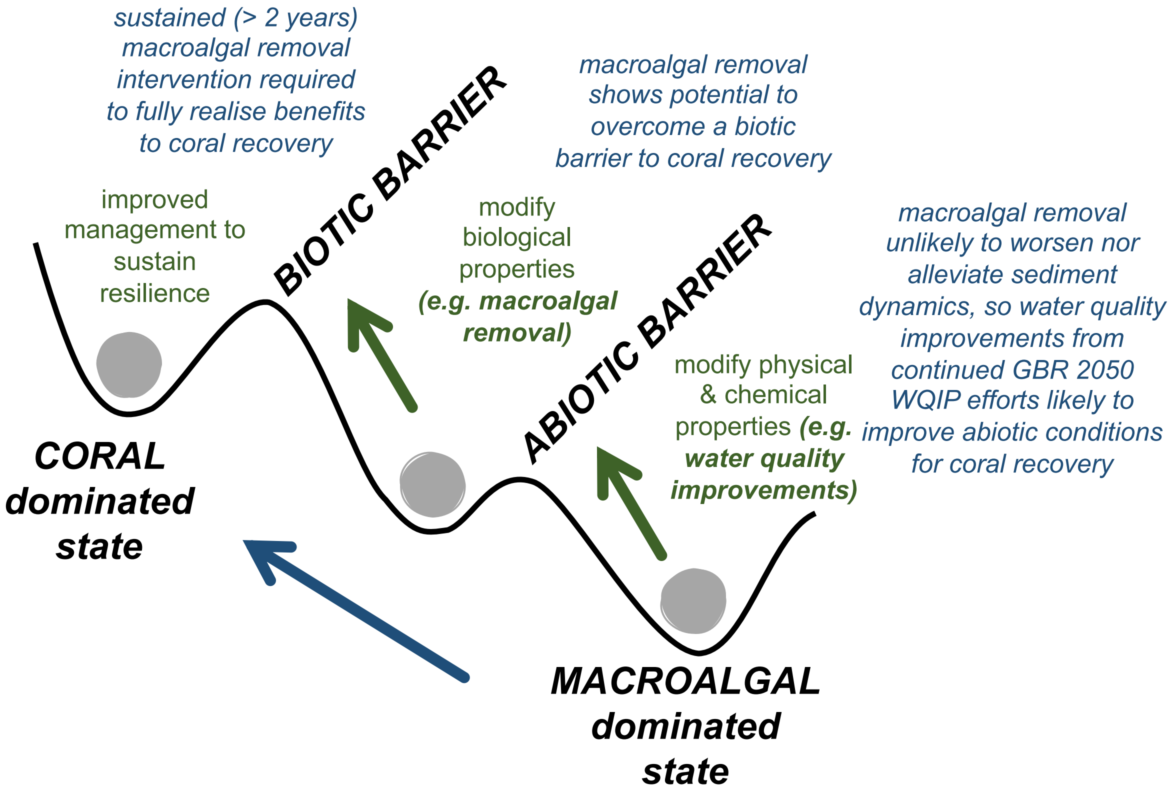


Figure 4.1 *A conceptual representation of the measures required to shift from a macroalgal-dominated state to a coral-dominated state. Blue text summarises how this thesis contributes to broader knowledge of the impact of macroalgal removal on degraded reefs, assisting management decisions to improve coral recovery on inshore reefs of the GBR. Adapted from McDonald et al., 2016 and Mumby & Steneck, 2011*

The results from this current study are promising, considering inshore reefs are likely to continue to experience water quality stress until improvements to land management are realised as sustained sediment and nutrient load reductions in the GBR lagoon. The absence of sustained improvements to inshore reef water quality on the GBR (Gruber et al., 2020; Waterhouse et al., 2021) is likely due to the complexity of relationships between terrestrial runoff and water quality paired with a lag in response time. Fortunately, current management plans (Reef 2050 WQIP 2017-2022 (State of Queensland, 2018)) and the recent federal government Reef Protection Package investment (Department of Climate Change, Energy, the Environment and Water, 2022) are working to improve water quality on the GBR. There is evidence emerging for this with the latest Inshore Coral Reef Monitoring Report for 2019-

2020 showing increases in the short-term water quality index, despite the long-term trend still in decline (State of Queensland, 2018). If the year-on-year trends for inshore water quality continue to improve, macroalgal removal does have the potential to assist coral recovery on degraded inshore reefs, without leading to any adverse effects on sedimentation of benthic organisms.

However, even with management plans in place to improve water quality, climate change will continue to compound localised stressors via increased frequency and severity of acute disturbances such as floods, which are the primary mechanism for sediment delivery to GBR waters (Haynes et al., 2007; Schaffelke et al., 2017; Waterhouse et al., 2017a), and thermal bleaching events. For example, Magnetic Island reefs were subject to thermal bleaching in 2016 (Thompson et al., 2017), 2017 (Thompson et al., 2018), 2020 (Thompson et al., 2021), and most recently in February 2022 (GBRMPA et al., 2022; Slezak, 2022). Promisingly, macroalgal removal has been shown to improve coral recovery following a bleaching event (Smith et al., 2022). Thus, macroalgal removal can help to support reef resilience whilst efforts to significantly reduce greenhouse gas emissions to curb climate warming and continued improvements to water quality are implemented. This combination of actions is required to effectively catalyse coral recovery and long-term re-establishment on degraded inshore GBR reefs.

4.3 Future directions

This thesis provides a solid basis for continuing macroalgal removal experiments and for understanding where future efforts should be focused. The findings distilled from this work are promising for applying macroalgal removal as a strategy to assist localised coral recovery on degraded inshore reefs of the GBR. However, more research is required to better understand the impacts at larger scales and the influences of other ecological processes.

4.3.1 Scaling up for inshore reef restoration: complementary methods and broader ecological impacts

There is often an incongruity between the temporal scale of experimental studies and that of natural disturbance cycles on the GBR, which can affect the conclusions drawn from short-term research (Boström-Einarsson et al., 2020). Continuing macroalgal removal experiments beyond the timeframe of this study will help to understand the longer-term impacts of regular macroalgal removal on inshore reefs. Furthermore, conducting macroalgal removal experiments during periods of bleaching, cyclones, and floods will give a more well-rounded view on the impact of macroalgal removal on reef dynamics and elucidate any potential synergistic or antagonistic effects on reef condition (Fong et al., 2018). Recent work at Magnetic Island (Smith et al., 2022) surveying reefs at these study sites during the 2020 bleaching event observed no additive bleaching impact from removal of macroalgae. Furthermore, recovery of bleached corals was faster in plots where macroalgae were removed indicating that localised removal of the macroalgal canopy did not increase bleaching stress (Smith et al., 2022). Though, avoiding macroalgal removal events during periods that approach summer thermal maxima may allow corals some protection from bleaching through canopy effects reducing light stress. Longer term studies to assess the persistence of improved reef communities under macroalgal removal regimes will also help to optimise this technique for restoration purposes.

Technologies to assist in macroalgal removal may help to increase capacity for removal on a larger scale. For example, a macroalgal removal experiment in Kāneʻohe Bay, Hawaii, achieved 85% reduction in invasive macroalgae following the use of an underwater vacuum to assist in macroalgal removal (Neilson et al., 2018). Urchin biocontrol was also implemented to assist with maintenance of low macroalgal levels. Even though this case study was based in Hawaii, there are still relevant implications for inshore reef management on the GBR. Enhancing manual macroalgal removal with herbivore biocontrol, for example, may assist with maintaining low macroalgal levels between removal events Ceccarelli et al., 2018). This could reduce the number of removal events required to achieve the same benefit within a given period, accelerating the realised impact of macroalgal removal. This could be particularly effective since positive effects of macroalgal removal in this study were not realised until after two years of consistent removal. Considering the urgency required for intervention techniques to assist coral recovery on the GBR, it would be worthwhile investigating complementary methods, such as increasing herbivores beyond natural levels, to rapidly upscale and accelerate the onset of benefits of macroalgal removal. Further research into the potential for herbivory to supplement manual macroalgal removal events on inshore GBR reefs is required.

The relationships between herbivorous fish, corals, and macroalgae have been highlighted as requiring further attention on inshore GBR reefs (Ceccarelli et al., 2020). Improved localised understanding of the role fish communities have on inshore reef coral-algal dynamics will greatly assist in determining the potential for macroalgal removal programs to not only enhance coral recovery, but also increase fish abundance and diversity, particularly herbivore populations. Historically, many coral-algal shifts around the world have been implicated with reductions in herbivory (Hughes et al., 2007; Ledlie et al., 2007; McManus & Polsenberg, 2004). Herbivorous fish populations are relatively healthy on inshore GBR reefs, due to historically well-regulated fishing and low demand for herbivorous fish in the Australian market (Abdo et al., 2021). It is, therefore, unlikely that herbivory is the key driver of coral-algal shifts on inshore GBR reefs (Thompson et al., 2021). However, herbivorous fish play important roles in shaping coral and algal communities on inshore reefs and can contribute to negative feedback loops that reinforce macroalgal dominance. For example, Hoey & Bellwood (2011) found that grazing and browsing fishes exercised a preference for reef areas with low macroalgal cover, actively avoiding areas with high densities of *Sargassum* spp. On *Sargassum* spp. dominated reefs, the farming damselfish *Stegastes apicalis* precludes fleshy macroalgal growth, and coral cover can be quite high in areas where these damselfish inhabit (Ceccarelli et al., 2011). However, they have been found to deter other grazing fish (Ceccarelli, 2007), which may hinder natural herbivory control of fleshy macroalgal canopies. Furthermore, sedimentation can also deter grazers (Bellwood & Fulton, 2008; Goatley et al., 2016), further contributing to macroalgal dominance on inshore reefs exposed to high sediment input. Improved understanding of how macroalgal removal affects the role of herbivorous fish in shaping coral-algal dynamics on inshore reefs would help to understand the implications for localised reef restoration in a broader ecological context.

4.3.2 Effect of macroalgal removal on the role of chemical and microbial processes associated with coral-algal dynamics on inshore reefs

This thesis has largely focused on the physical and biological effects of macroalgal removal on inshore reefs. Specifically, how macroalgal removal influences the composition of benthic communities, the amount and composition of sediments deposited on the benthos, and the physical characteristics of algal turfs. However, the effect of macroalgal removal on chemical and microbial process remains to be investigated. Benthic microbial communities are important primary producers, contributing to chemical processes in coral reef ecosystems (Haas et al., 2013).

The release of chemical compounds from macroalgae can affect microbial communities associated with corals (Barott & Rohwer, 2012; Rasher et al., 2011). This allelopathic process can promote opportunistic pathogens and negatively impact coral fitness, with flow-on effects to overall reef ecosystem structure and functioning (Barott & Rohwer, 2012). Furthermore, high macroalgal biomass can expediate increases in microbial growth, which may contribute to reinforcing macroalgal dominance on degraded inshore reefs (Ceccarelli et al., 2018; Haas et al., 2013). Thus, it is not simply the physical effects of macroalgal canopies that preclude corals from recovering and re-establishing on degraded inshore reefs. For example, a macroalgal removal study in French Polynesia found that increased coral recruitment was only observed when the *Turbinaria* spp. canopy, holdfasts, and macroalgal understorey were all removed (Bulleri et al., 2018). This extent of macroalgal removal was necessary to cause the required change to microbial community composition that would allow improved conditions for coral settlement and recruitment (Bulleri et al., 2018). Investigating the impact of macroalgal removal on microbial community composition and allelopathic chemical release may help to determine effects on coral health and fitness, rather than just coral cover and community composition as examined in this thesis.

Additionally, chemical and microbial process associated with coral reef communities are often the first to change following disturbance, so could become an important metric for measuring the impact of interventions (Barott & Rohwer, 2012). Understanding how manual reductions in macroalgal biomass on inshore coral reefs affects allelopathic mechanisms, could help to understand the micro-scale effects of macroalgal removal on overall reef health. This will help to optimise macroalgal removal regimes for reef restoration applications.

4.3.3 Macroalgal removal and citizen science potential for localised reef restoration

Macroalgal removal is a relatively simple, hands-on task that lends itself well to citizen science engagement. The manual removal of macroalgae in this study was conducted with the assistance of citizen science volunteers from Earthwatch Institute Australia through the ‘Recovery of the Great Barrier Reef’ program (Earthwatch Institute Australia, n.d.). Whilst not discussed in this thesis, the benefits and limitations of engaging citizen scientists in reef restoration research is worthy of further investigation. Citizen science engagement has been shown to benefit coral restoration programs, with direct benefits further enhanced by educational opportunities (Hesley et al., 2017). Furthermore, citizen science programs can help fund and provide valuable resources for restoration activities, allowing programs to be scaled up temporally and spatially beyond the limits enabled by traditional funding and resourcing avenues (Theobald et al., 2015). There is considerable potential for citizen science programs to assist in scaling up macroalgal removal into a feasible active intervention.

4.4 Concluding remarks

This study provides the first rigorous assessment on the impact of macroalgal removal on inshore reef communities of the GBR. Specifically, the complex relationships between macroalgae, algal turfs, sedimentation, and corals were diligently investigated in this thesis. Repeated macroalgal removal events were undertaken over the duration of the project, contributing to refining methods aimed at assisting inshore coral reef recovery on the GBR, and to understand more about the dynamics of inshore reefs dominated by macroalgae. The effect of removing canopy-forming macroalgae from degraded inshore reefs on the GBR was positive in terms of live hard coral cover, and negligible in terms of sediment and algal turf dynamics. Regular removal of macroalgae from an inshore reef of the GBR over a three-year period resulted in higher coral cover and sustained reductions in macroalgae. Consequently, this thesis contributes to establishing a scientifically rigorous basis from which to implement macroalgal removal as a localised restoration strategy. This may lead to improved benthic conditions for coral recovery on inshore reefs of the GBR and analogous reefs globally.

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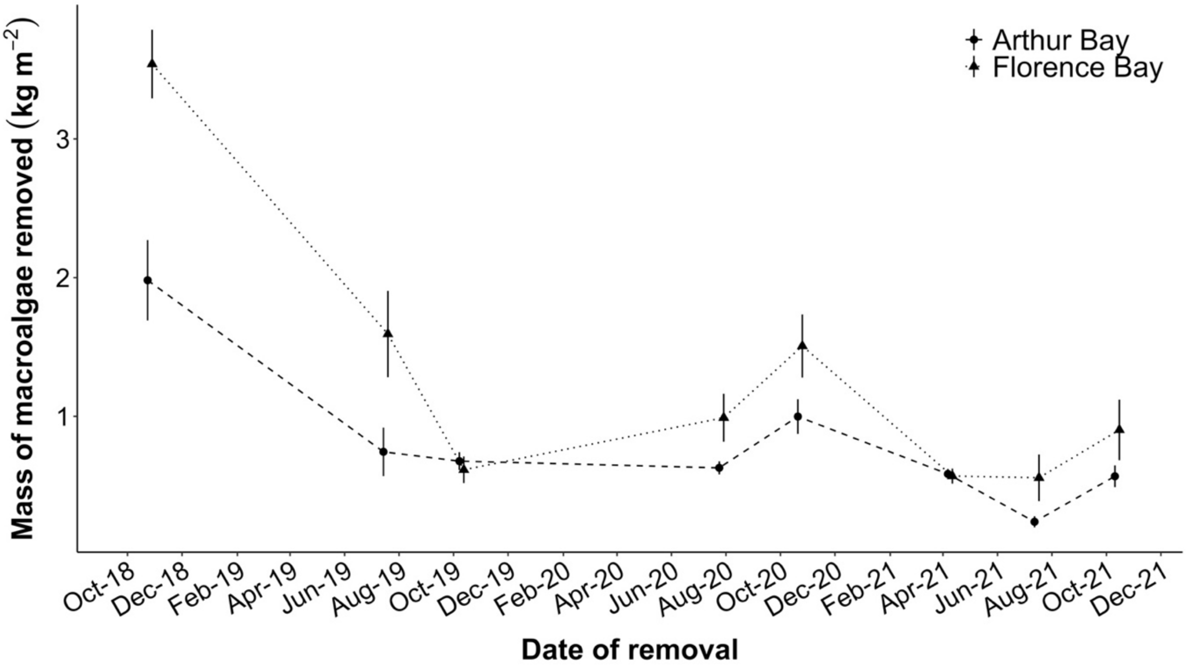
Appendices

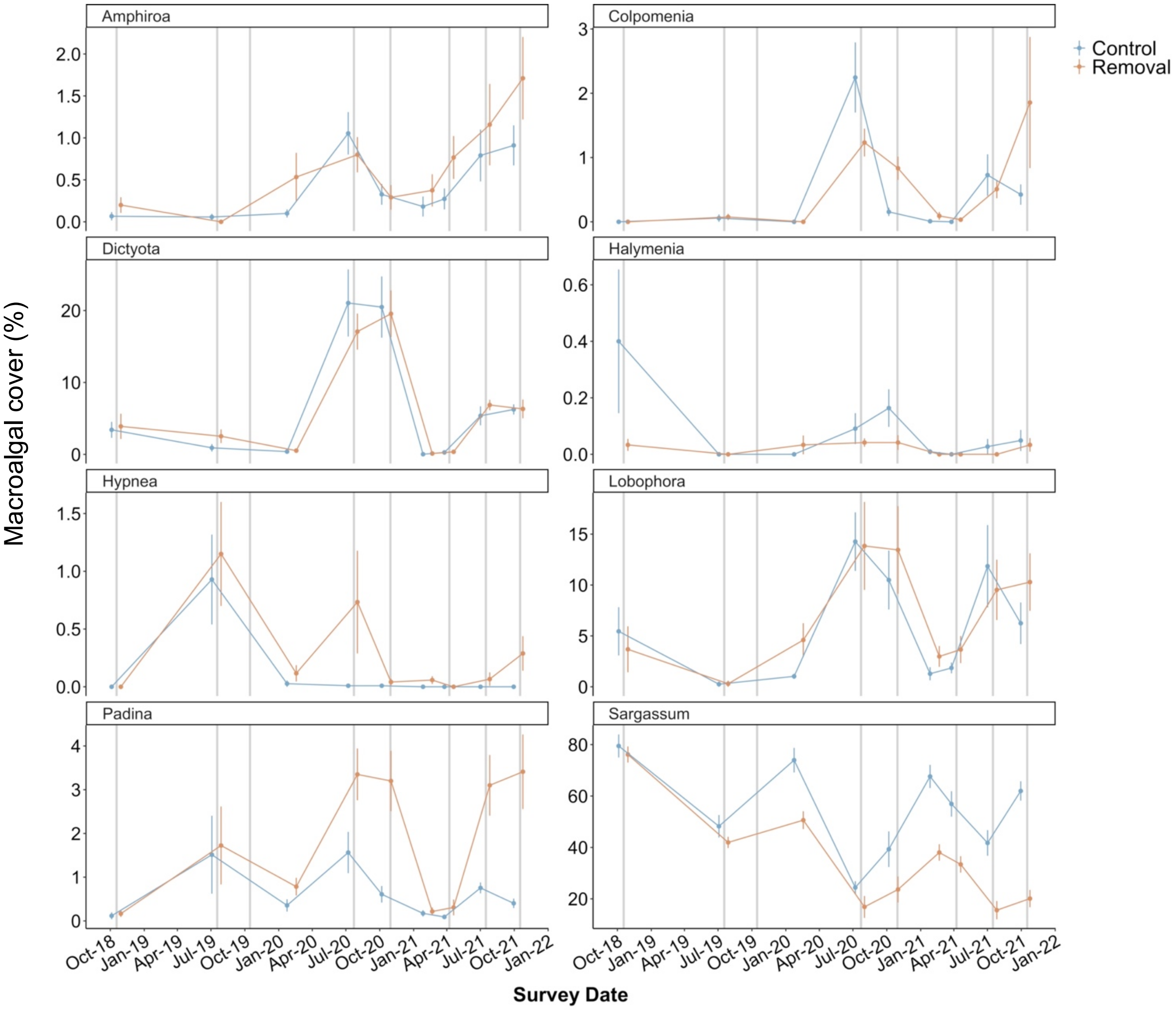
6.1 Appendix A. Supplementary materials for Chapter 2



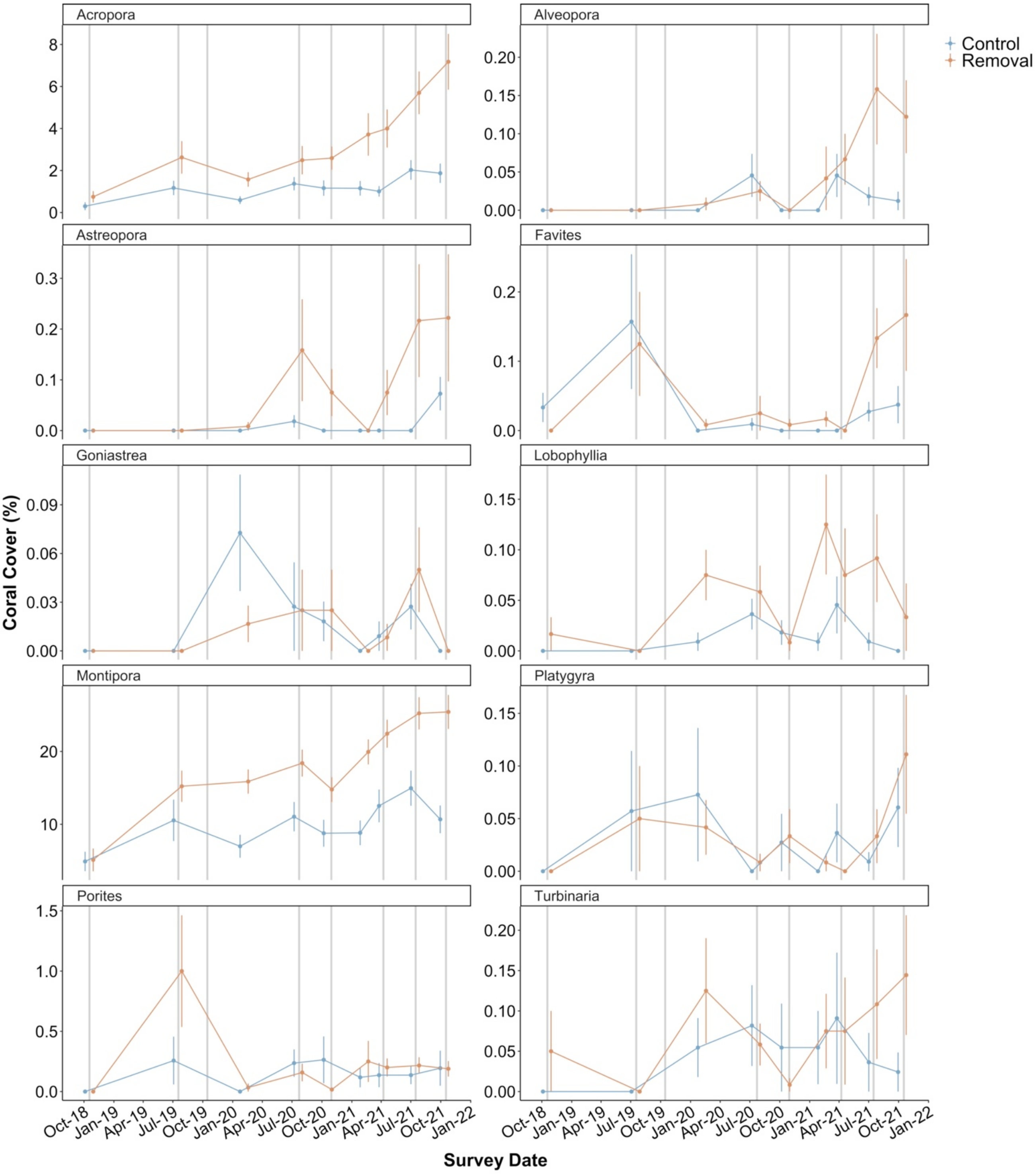
Supplementary Figure 1. *Biomass (kg m^{-2}) of macroalgae removed from removal plots (n = 6 plots per bay, each 25 m^2) in two bays of Magnetic Island, Australia, during each removal event from October 2018 to October 2021. Solid points represent mean mass removed with circles representing Arthur Bay and triangles representing Florence Bay; vertical lines represent standard error*

Supplementary Table 1. *Percent cover, shown as mean and standard error, of benthic organisms observed within 24 experimental plots (each 25 m^2) in two bays of Magnetic Island, Australia, averaged across a three-year period (2018 – 2021). Genera are ordered from most common (highest mean percent cover averaged across all plots and entire study period) to least common (lowest mean percent cover) within each functional group. The category labelled 'OTHER' within each functional group was used when visibility was poor and genus level identification was not possible. Genera observed in less than 10% of photo-quadrat surveys were excluded from analyses and are not listed here*

Functional group	**Genus / category**	**Percent cover**	
		Mean	**± SE**
Hard Coral	*Montipora*	15.87	0.51
	Acropora	2.62	0.17
	Porites	0.18	0.02
	Astreopora	0.07	0.01
	Turbinaria	0.07	0.01
	Favites	0.05	0.01
	Alveopora / Goniopora	0.04	0.01
	Lobophyllia	0.04	0.01
	OTHER hard coral	0.04	0.01
	Platygyra	0.04	0.01
	Goniastrea	0.02	0.00
Macroalgae	*Sargassum*	35.69	1.47
	Lobophora	8.23	0.59
	Dictyota	6.33	0.54
	Padina	1.13	0.10
	OTHER macroalgae	0.76	0.14
	Amphiroa	0.71	0.07
	Colpomenia	0.47	0.06
	Spatoglossum	0.21	0.05
	Hypnea	0.12	0.03
	Halymenia	0.05	0.01
Turf	Algal turfs	5.95	0.35
CCA	Crustose coralline algae	0.45	0.08
Soft Coral	*Briareum*	0.33	0.06
	OTHER soft coral	0.11	0.04
Sponges	Sponge	0.40	0.03
Coral Health	Dead coral	0.17	0.03
	Bleached coral	0.09	0.03
Substrate	Rubble	15.03	0.60
	Sand	4.31	0.29
Unknown	Unknown or blurry	0.65	0.23



Supplementary Figure 2. *Percent cover of different macroalgal genera within experimental plots in two bays of Magnetic Island, Australia. Solid, coloured points represent the mean percent cover averaged across all control plots (blue) and removal plots (orange) with vertical lines representing the associated standard error. Vertical grey lines indicate when macroalgae was cleared from removal plots. Only pre-removal survey timepoints are shown here for simplicity*

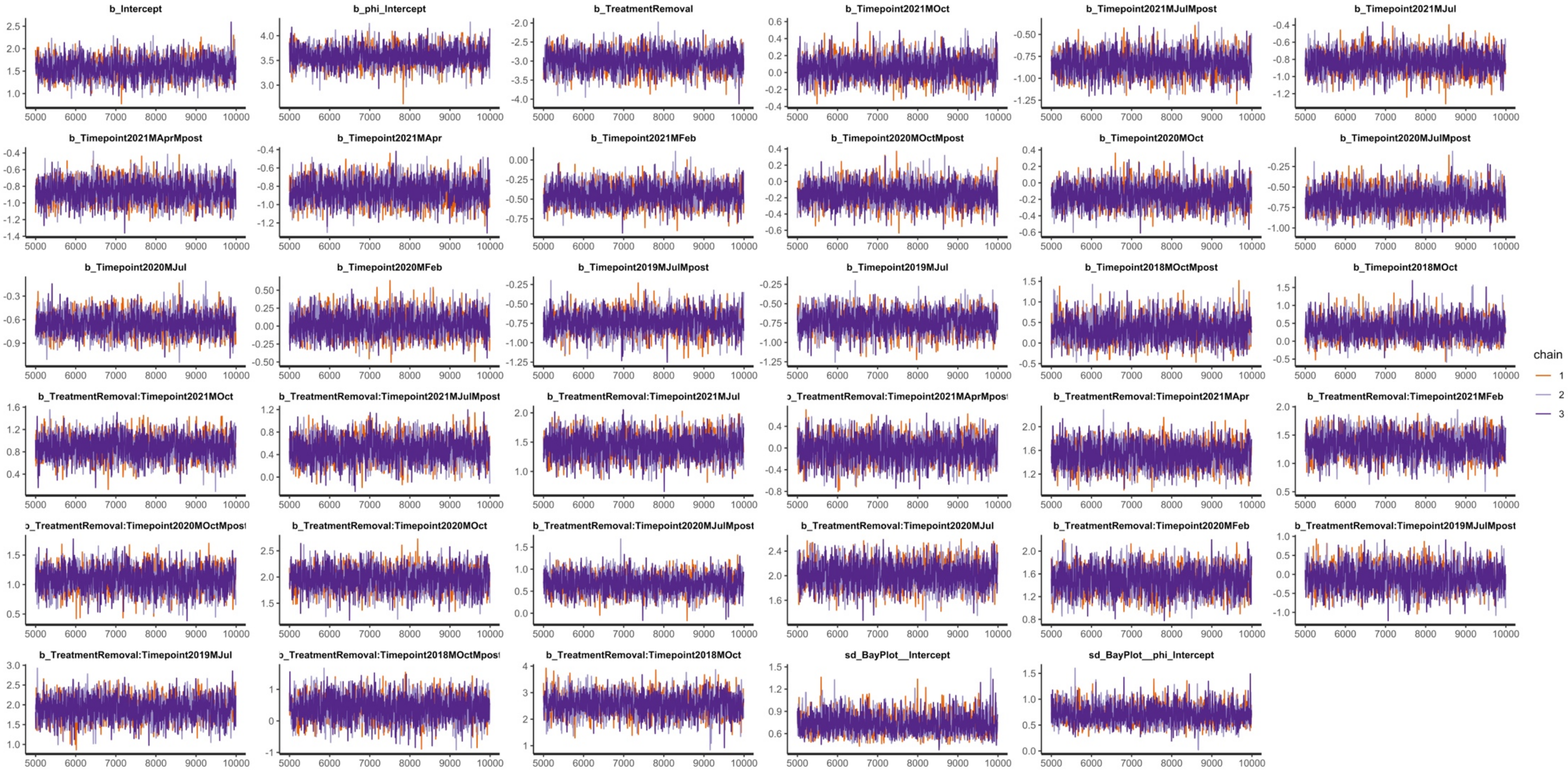


Supplementary Figure 3. *Percent cover of different hard coral genera within experimental plots in two bays of Magnetic Island, Australia. Solid, coloured points represent the mean percent cover averaged across all control plots (blue) and removal plots (orange) with vertical lines representing the associated standard error. Vertical grey lines indicate when macroalgae was cleared from removal plots. Only pre-removal survey timepoints are shown here for simplicity*

Supplementary Table 2. Bayesian generalised linear mixed effects model specifications detailing prior values (adjusted scale) and chain characteristics for models used to investigate the relationships through time between benthic cover and macroalgal removal (treatment) in two bays of Magnetic Island, Australia, throughout 2018 to 2021

Response variable	Total observations	Distribution	Prior Information	Iterations	Thinning	Chains	Warm-up
Macroalgal cover (fraction) MA ~ Treatment * Timepoint + (1 | BayPlot) phi ~ (1 | BayPlot)	322	Beta (logit link)	Intercept (normal(0.7, 2)) Variance (normal(0, 2)) Phi (cauchy(0, 5)) Phi intercept (normal(0, 5)) Phi variance (cauchy(0, 5))	10000	5	3	5000
Coral cover (fraction) HC ~ Treatment * Timepoint + (1 | BayPlot) phi ~ (1 | BayPlot)	322	Beta (logit link)	Intercept (normal(-2, 1)) Variance (normal(0, 1)) Phi (cauchy(0, 5)) Phi intercept (normal(0, 5)) Phi variance (cauchy(0, 5))	10000	5	3	5000

(a)


b_Intercept
b_phi_Intercept
b_TreatmentRemoval
b_Timepoint2021MOct
b_Timepoint2021MJulMpost
b_Timepoint2021MJul
b_Timepoint2021MAprMpost
b_Timepoint2021MApr
b_Timepoint2021MFeb
b_Timepoint2020MOctMpost
b_Timepoint2020MOct
b_Timepoint2020MJulMpost
b_Timepoint2020MJul
b_Timepoint2020MFeb
b_Timepoint2019MJulMpost
b_Timepoint2019MJul
b_Timepoint2018MOctMpost
b_Timepoint2018MOct
b_TreatmentRemoval:Timepoint2021MOct
b_TreatmentRemoval:Timepoint2021MJulMpost
b_TreatmentRemoval:Timepoint2021MJul
_TreatmentRemoval:Timepoint2021MAprMpost
b_TreatmentRemoval:Timepoint2021MApr
b_TreatmentRemoval:Timepoint2021MFeb
_TreatmentRemoval:Timepoint2020MOctMpost
b_TreatmentRemoval:Timepoint2020MOct
b_TreatmentRemoval:Timepoint2020MJulMpost
b_TreatmentRemoval:Timepoint2020MJul
b_TreatmentRemoval:Timepoint2020MFeb
b_TreatmentRemoval:Timepoint2019MJulMpost
b_TreatmentRemoval:Timepoint2019MJul
_TreatmentRemoval:Timepoint2018MOctMpost
b_TreatmentRemoval:Timepoint2018MOct
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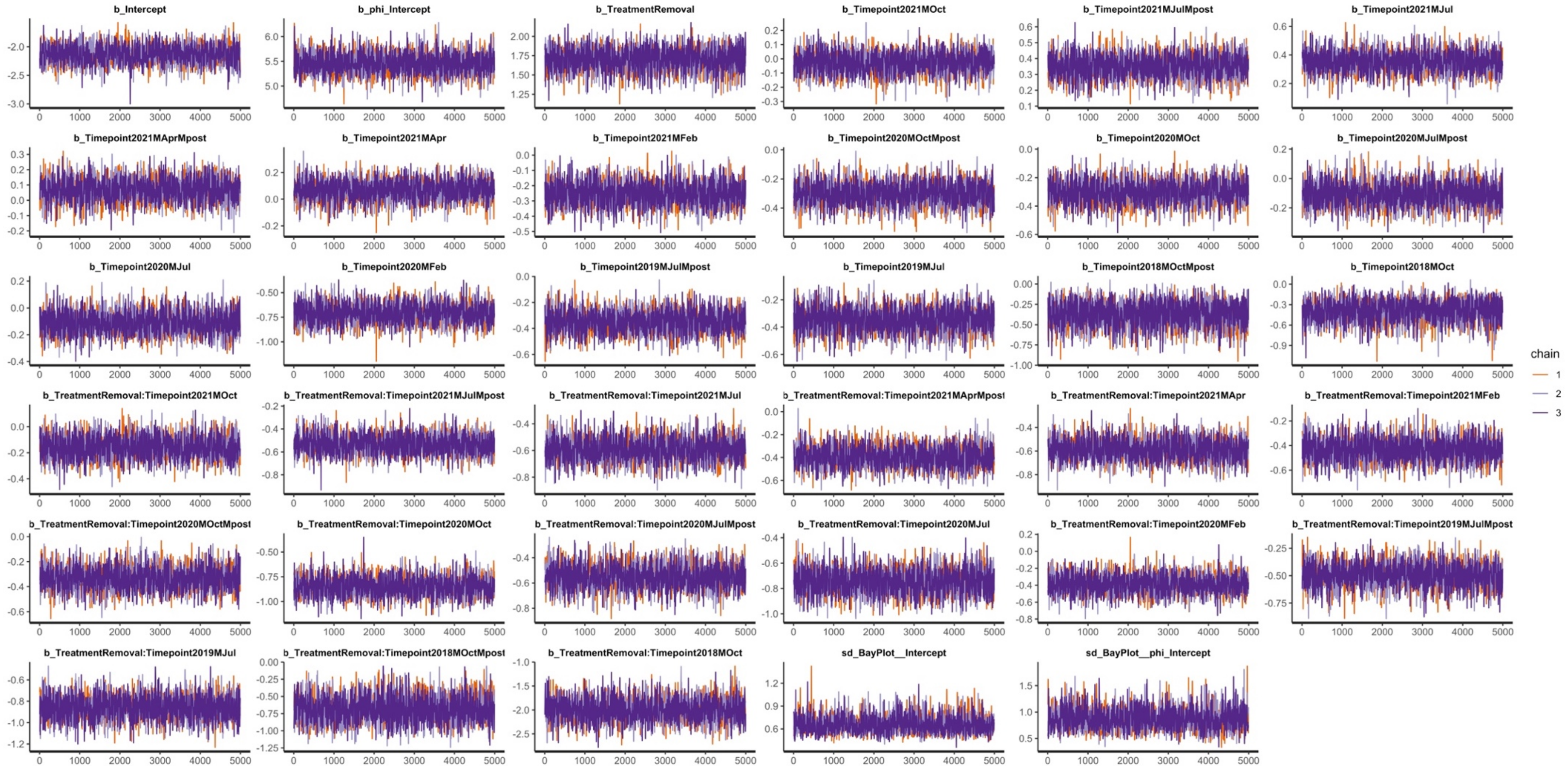
5000
6000
7000
8000
9000
10000
chain
1
2
3

(b)



Supplementary Figure 4. *Trace plots indicating level of chain mixing for Bayesian generalised linear mixed effects models for **(a)** macroalgal percent cover and **(b)** coral percent cover*

Supplementary Table 3. Summary table for Bayesian generalised linear mixed effects model used to investigate the relationship through time between **(a)** macroalgal cover, **(b)** coral cover and macroalgal removal (treatment) in two bays of Magnetic Island, Australia, throughout 2018 to 2021. Values are on the link scale; hence, 95% credibility intervals (CI) show an effect of the associated term when the interval does not include zero

(a)

Response variable	Distribution	Term	Estimate	Error	95 % CI		Rhat	Bulk ESS	Tail ESS
					lower	upper			
Macroalgal cover (fraction)	Beta (logit link)	Intercept	1.57	0.21	1.16	1.99	1	2230	2754
		phi_Intercept	3.58	0.18	3.23	3.95	1	2905	2554
		TreatmentRemoval	-3	0.26	-3.52	-2.48	1	2233	2847
		Timepoint2021Oct	0.06	0.13	-0.19	0.32	1	2732	2587
		Timepoint2021JulMpost	-0.83	0.12	-1.08	-0.59	1	2416	2577
		Timepoint2021Jul	-0.84	0.12	-1.08	-0.59	1	2693	2604
		Timepoint2021AprMpost	-0.86	0.13	-1.12	-0.62	1	2417	2899
		Timepoint2021Apr	-0.86	0.12	-1.1	-0.61	1	2686	2751
		Timepoint2021Feb	-0.45	0.13	-0.69	-0.19	1	2512	2949
		Timepoint2020OctMpost	-0.15	0.13	-0.4	0.1	1	2619	2940
		Timepoint2020Oct	-0.15	0.13	-0.4	0.11	1	2544	2797
		Timepoint2020JulMpost	-0.65	0.13	-0.91	-0.37	1	2782	2846
		Timepoint2020Jul	-0.65	0.13	-0.9	-0.38	1	2464	2474
		Timepoint2020Feb	0.03	0.16	-0.28	0.35	1	2629	2829
		Timepoint2019JulMpost	-0.74	0.14	-1.02	-0.47	1	2708	2662
		Timepoint2019Jul	-0.73	0.14	-1.01	-0.47	1	2534	2571
		Timepoint2018OctMpost	0.32	0.28	-0.19	0.94	1	2514	2843
		Timepoint2018Oct	0.35	0.29	-0.18	0.94	1	2662	2815
		TreatmentRemoval:Timepoint2021Oct	0.88	0.2	0.48	1.27	1	2642	2721
		TreatmentRemoval:Timepoint2021Julpost	0.49	0.21	0.07	0.91	1	2696	2535
		TreatmentRemoval:Timepoint2021Jul	1.44	0.2	1.05	1.83	1	2808	2603
		TreatmentRemoval:Timepoint2021Aprpos	-0.03	0.23	-0.49	0.41	1	2640	2998
		TreatmentRemoval:Timepoint2021Apr	1.53	0.2	1.14	1.92	1	2551	2734
		TreatmentRemoval:Timepoint2021Feb	1.32	0.21	0.91	1.73	1	2492	2790
		TreatmentRemoval:Timepoint2020Octpos	1.09	0.2	0.69	1.46	1	2522	2983
		TreatmentRemoval:Timepoint2020Oct	1.96	0.21	1.53	2.36	1	2681	2945
		TreatmentRemoval:Timepoint2020Julpost	0.67	0.22	0.24	1.09	1	2418	2813
		TreatmentRemoval:Timepoint2020Jul	2.02	0.2	1.61	2.41	1	2639	2767
		TreatmentRemoval:Timepoint2020Feb	1.49	0.22	1.05	1.9	1	2493	2758
		TreatmentRemoval:Timepoint2019Julpost	-0.09	0.31	-0.71	0.54	1	2652	2884
		TreatmentRemoval:Timepoint2019Jul	1.9	0.28	1.35	2.45	1	2604	2621
		TreatmentRemoval:Timepoint2018Octpos	0.42	0.38	-0.34	1.16	1	2653	2793
		TreatmentRemoval:Timepoint2018Oct	2.56	0.39	1.76	3.32	1	2453	2648

(b)

Response variable	Distribution	Term	Estimate	Error	95 % CI		Rhat	Bulk ESS	Tail ESS
					lower	upper			
Coral cover (fraction)	Beta (logit link)	Intercept	-2.13	0.16	-2.45	-1.82	1	2146	2182
		phi_Intercept	5.45	0.21	5.06	5.87	1	2827	2372
		TreatmentRemoval	1.7	0.15	1.39	1.97	1	2622	2865
		Timepoint2021Oct	-0.03	0.07	-0.17	0.11	1	2535	2687
		Timepoint2021Julpost	0.35	0.07	0.21	0.49	1	2620	2778
		Timepoint2021Jul	0.35	0.07	0.21	0.5	1	2582	2512
		Timepoint2021Aprpost	0.07	0.07	-0.08	0.22	1	2615	3119
		Timepoint2021Apr	0.07	0.07	-0.08	0.21	1	2366	2986
		Timepoint2021Feb	-0.25	0.08	-0.4	-0.1	1	2678	2654
		Timepoint2020Octpost	-0.3	0.08	-0.45	-0.15	1	2688	2867
		Timepoint2020Oct	-0.31	0.08	-0.46	-0.15	1	2466	2757
		Timepoint2020Julpost	-0.11	0.08	-0.27	0.05	1	2530	2732
		Timepoint2020Jul	-0.11	0.08	-0.27	0.06	1	2566	2890
		Timepoint2020Feb	-0.71	0.1	-0.91	-0.52	1	2524	2790
		Timepoint2019Julpost	-0.35	0.09	-0.51	-0.18	1	2682	2644
		Timepoint2019Jul	-0.35	0.09	-0.52	-0.18	1	2795	2843
		Timepoint2018Octpost	-0.37	0.15	-0.69	-0.1	1	2653	2721
		Timepoint2018Oct	-0.39	0.16	-0.73	-0.12	1	2763	2803
		TreatmentRemoval:Timepoint2021Oct	-0.16	0.09	-0.33	0.01	1	2517	2909
		TreatmentRemoval:Timepoint2021Julpost	-0.53	0.09	-0.69	-0.36	1	2458	2855
		TreatmentRemoval:Timepoint2021Jul	-0.59	0.08	-0.76	-0.42	1	2623	2580
		TreatmentRemoval:Timepoint2021Aprpost	-0.39	0.09	-0.57	-0.21	1	2407	2777
		TreatmentRemoval:Timepoint2021Apr	-0.58	0.09	-0.76	-0.41	1	2309	2793
		TreatmentRemoval:Timepoint2021Feb	-0.43	0.09	-0.61	-0.25	1	2757	2833
		TreatmentRemoval:Timepoint2020Octpost	-0.33	0.09	-0.51	-0.15	1	2702	2947
		TreatmentRemoval:Timepoint2020Oct	-0.84	0.1	-1.03	-0.65	1	2453	2817
		TreatmentRemoval:Timepoint2020Julpost	-0.55	0.09	-0.74	-0.36	1	2326	2695
		TreatmentRemoval:Timepoint2020Jul	-0.75	0.1	-0.94	-0.56	1	2606	2902
		TreatmentRemoval:Timepoint2020Feb	-0.38	0.11	-0.6	-0.17	1	2461	2623
		TreatmentRemoval:Timepoint2019Julpost	-0.49	0.11	-0.71	-0.29	1	2517	2766
		TreatmentRemoval:Timepoint2019Jul	-0.86	0.11	-1.08	-0.65	1	2881	2909
		TreatmentRemoval:Timepoint2018Octpost	-0.69	0.19	-1.04	-0.3	1	2708	2813
		TreatmentRemoval:Timepoint2018Oct	-1.99	0.24	-2.45	-1.52	1	2641	2810

Supplementary Table 4. *Bayesian probabilities for a range of percent cover values for both macroalgae and corals at selected timepoints throughout the study period in control plots (C) and removal plots (R) located in two bays of Magnetic Island, Australia, i.e., the probability that there was less than 70% macroalgal cover in control plots in July 2021 is 0.72. Light grey shading indicates probability greater than 0.5, and dark grey shading indicates probability of 1*

Bayesian probabilities		October 2018		July 2019		July 2020		October 2020		July 2021		October 2021	
		C	R	C	R	C	R	C	R	C	R	C	R
Macroalgal cover	< 30 %	0.00	0.00	0.00	0.02	0.00	0.00	0.00	0.00	0.00	0.46	0.00	0.05
	< 50 %	0.00	0.00	0.00	0.82	0.00	0.63	0.00	0.04	0.00	1.00	0.00	0.99
	< 60 %	0.00	0.00	0.03	0.99	0.00	0.99	0.00	0.55	0.05	1.00	0.00	1.00
	< 70 %	0.00	0.01	0.54	1.00	0.39	1.00	0.00	0.99	0.72	1.00	0.00	1.00
	< 80 %	0.02	0.38	0.99	1.00	0.98	1.00	0.45	1.00	1.00	1.00	0.13	1.00
Coral cover	> 50 %	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	> 40 %	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.05	0.00	0.09
	> 30 %	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.89	0.00	0.93
	> 20 %	0.00	0.00	0.00	0.06	0.00	0.75	0.00	0.11	0.01	1.00	0.00	1.00
	> 10 %	0.03	0.00	0.04	1.00	0.39	1.00	0.07	1.00	0.99	1.00	0.61	1.00

Supplementary Table 5. *Results from a three-factor permutational multivariate analysis of variance of* ***(a)*** *macroalgal and* ***(b)*** *coral community composition surveyed throughout 2018 to 2021 in two bays of Magnetic Island, Australia. Asterisks indicate significance at $p < .05$*

a) Macroalgal community composition

Community composition ~ Timepoint * Treatment + Bay, strata: BayPlot

Factor	df	Sum of Squares	Mean Squares	*F* - value	*r*2	*p* - value
Timepoint	5	2.98	0.60	28.88	0.41	<0.01 *
Treatment	1	0.60	0.60	28.91	0.08	<0.01 *
Bay	1	1.31	1.31	63.48	0.18	<0.01 *
Timepoint:Treatment	5	0.29	0.06	2.79	0.04	<0.01 *
Residuals	101	2.08	0.02		0.29	
Total	113	7.25			1.00	

b) Hard coral community composition

Community composition ~ Timepoint * Treatment + Bay, strata: BayPlot

Factor	df	Sum of Squares	Mean Squares	*F* - value	*r*2	*p* - value
Timepoint	5	0.58	0.12	4.07	0.15	<0.01 *
Treatment	1	0.07	0.07	2.50	0.02	0.058
Bay	1	0.22	0.22	7.89	0.06	<0.01 *
Timepoint:Treatment	5	0.19	0.04	1.31	0.05	<0.05 *
Residuals	101	2.87	0.03		0.73	
Total	113	3.93			1.00	

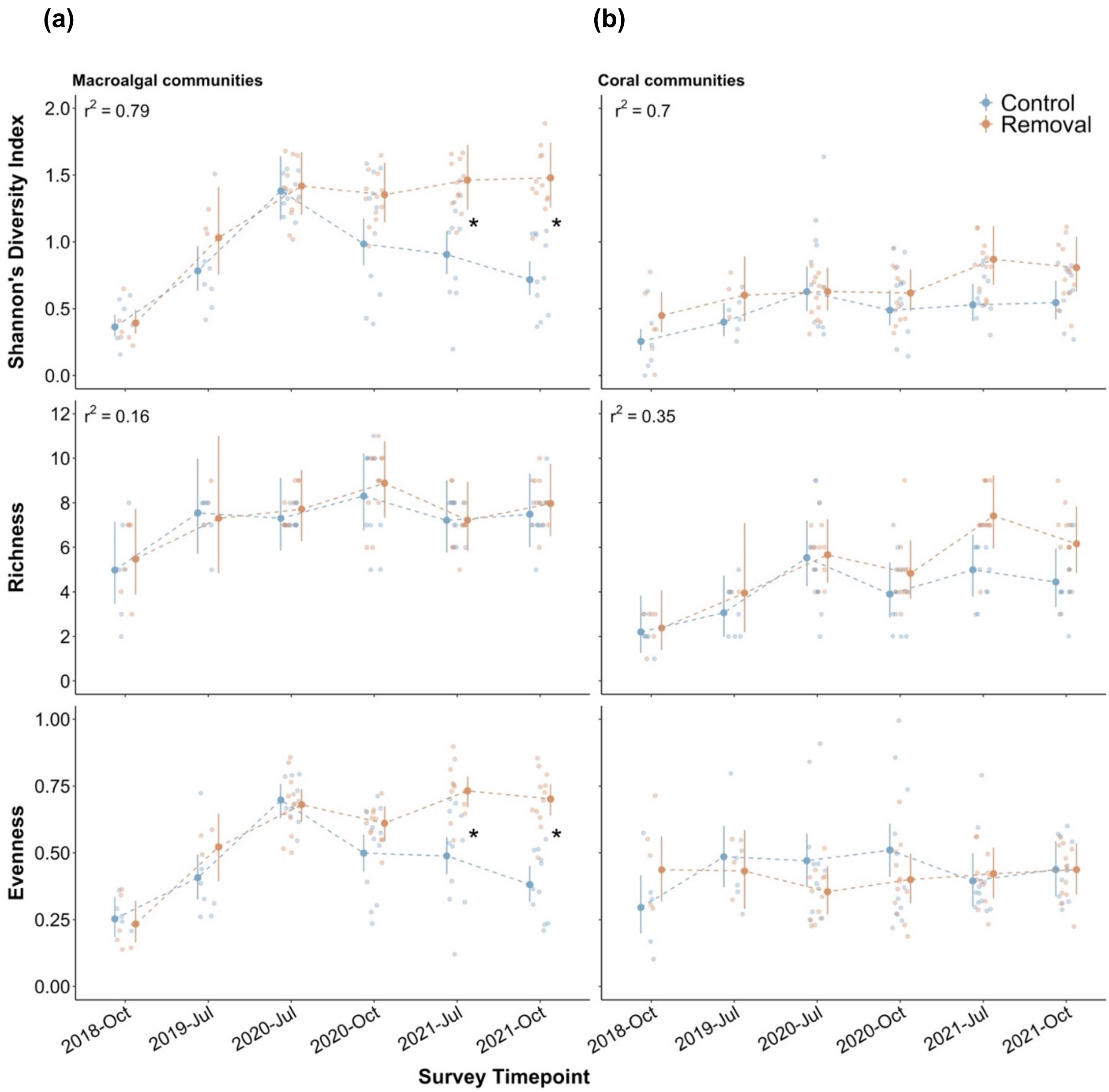
Supplementary Table 6. *Summary of generalised linear mixed effects model results used to examine patterns in Shannon's diversity index, richness, and evenness of* ***(a)*** *macroalgal communities and* ***(b)*** *coral communities throughout 2018 to 2021, in two bays of Magnetic Island, Australia*

(a)

Response variable	**Distribution**	**Conditional r^2**	**Term**	**Estimate**	**SE**	**z-value**	**p-value**
Macroalgal communities							
Diversity ~ Treatment * Timepoint + Bay + (1 | BayPlot)							
Shannon's diversity index	Gamma (log link)	0.79	(Intercept)	-0.849	0.118	-7.188	< 0.01
			TreatmentRemoval	0.076	0.162	0.465	0.642
			Timepoint2019-Jul	0.765	0.148	5.178	< 0.01
			Timepoint2020-Jul	1.333	0.133	10.055	< 0.01
			Timepoint2020-Oct	0.994	0.131	7.615	< 0.01
			Timepoint2021-Jul	0.910	0.131	6.969	< 0.01
			Timepoint2021-Oct	0.677	0.131	5.189	< 0.01
			BayFlorence Bay	-0.321	0.076	-4.236	< 0.01
			TreatmentRemoval:Timepoint2019-Jul	0.200	0.240	0.832	0.406
			TreatmentRemoval:Timepoint2020-Jul	-0.049	0.190	-0.261	0.794
			TreatmentRemoval:Timepoint2020-Oct	0.242	0.186	1.300	0.194
			TreatmentRemoval:Timepoint2021-Jul	0.404	0.186	2.171	< 0.05
			TreatmentRemoval:Timepoint2021-Oct	0.648	0.186	3.478	< 0.01
Richness ~ Treatment * Timepoint + Bay + (1 | BayPlot)							
Richness	Poisson (log link)	0.16	(Intercept)	1.697	0.185	9.157	< 0.01
			TreatmentRemoval	0.095	0.252	0.378	0.706
			Timepoint2019-Jul	0.416	0.231	1.806	0.071
			Timepoint2020-Jul	0.383	0.214	1.789	0.074
			Timepoint2020-Oct	0.512	0.211	2.431	0.015
			Timepoint2021-Jul	0.370	0.214	1.727	0.084
			Timepoint2021-Oct	0.408	0.213	1.911	0.056
			BayFlorence Bay	-0.183	0.070	-2.622	0.009
			TreatmentRemoval:Timepoint2019-Jul	-0.129	0.357	-0.362	0.717
			TreatmentRemoval:Timepoint2020-Jul	-0.040	0.295	-0.136	0.892
			TreatmentRemoval:Timepoint2020-Oct	-0.029	0.290	-0.099	0.921
			TreatmentRemoval:Timepoint2021-Jul	-0.094	0.296	-0.318	0.751
			TreatmentRemoval:Timepoint2021-Oct	-0.033	0.294	-0.112	0.910
Evenness ~ Treatment * Timepoint + Bay + (1 | BayPlot)							
Evenness	Beta (logit link)	NA	(Intercept)	-0.870	0.212	-4.097	< 0.01
			TreatmentRemoval	-0.105	0.295	-0.358	0.720
			Timepoint2019-Jul	0.706	0.260	2.712	< 0.01
			Timepoint2020-Jul	1.919	0.244	7.855	< 0.01
			Timepoint2020-Oct	1.079	0.233	4.635	< 0.01
			Timepoint2021-Jul	1.037	0.232	4.463	< 0.01
			Timepoint2021-Oct	0.598	0.235	2.548	< 0.05
			BayFlorence Bay	-0.427	0.132	-3.238	< 0.01
			TreatmentRemoval:Timepoint2019-Jul	0.570	0.422	1.350	0.177
			TreatmentRemoval:Timepoint2020-Jul	0.025	0.347	0.071	0.943
			TreatmentRemoval:Timepoint2020-Oct	0.559	0.337	1.656	0.098
			TreatmentRemoval:Timepoint2021-Jul	1.156	0.341	3.389	< 0.01
			TreatmentRemoval:Timepoint2021-Oct	1.444	0.340	4.245	< 0.01

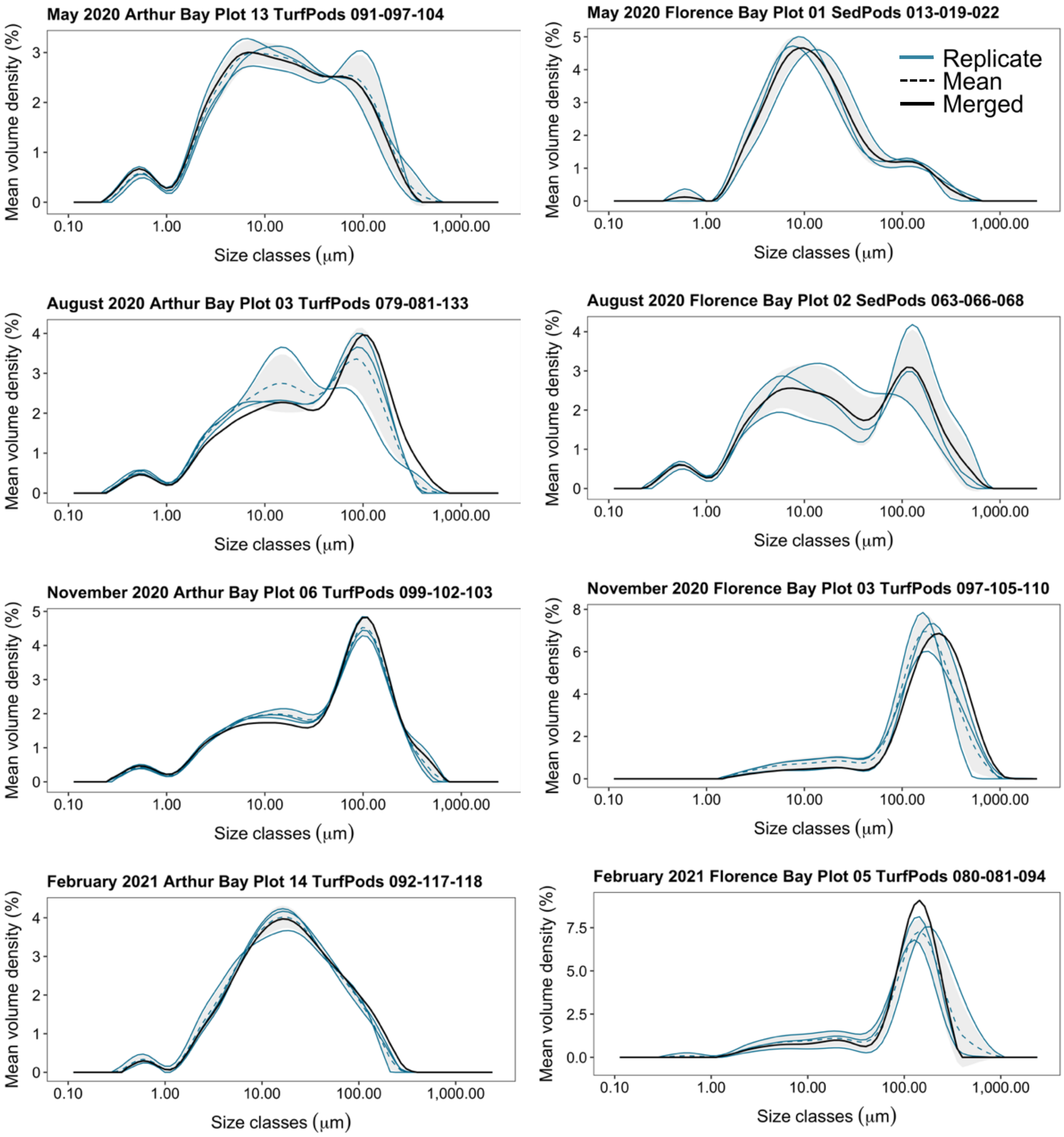
(b)

Response variable	Distribution	Conditional r^2	Term	Estimate	SE	z-value	p-value
Coral communities							
Diversity ~ Treatment * Timepoint + Bay + (1 | BayPlot)							
Shannon's diversity index	Gamma (log link)	0.70	(Intercept)	-1.366	0.157	-8.695	< 0.01
			TreatmentRemoval	0.563	0.221	2.548	< 0.05
			Timepoint2019-Jul	0.449	0.187	2.408	< 0.05
			Timepoint2020-Jul	0.899	0.165	5.440	< 0.01
			Timepoint2020-Oct	0.650	0.166	3.917	< 0.01
			Timepoint2021-Jul	0.728	0.164	4.450	< 0.01
			Timepoint2021-Oct	0.759	0.165	4.606	< 0.01
			TreatmentRemoval:Timepoint2019-Jul	-0.156	0.294	-0.530	0.596
			TreatmentRemoval:Timepoint2020-Jul	-0.562	0.231	-2.431	< 0.05
			TreatmentRemoval:Timepoint2020-Oct	-0.329	0.230	-1.430	0.153
			TreatmentRemoval:Timepoint2021-Jul	-0.065	0.229	-0.285	0.776
			TreatmentRemoval:Timepoint2021-Oct	-0.171	0.230	-0.741	0.459
Richness ~ Treatment * Timepoint + Bay + (1 | BayPlot)							
Richness	Poisson (log link)	0.35	(Intercept)	0.788	0.281	2.804	< 0.01
			TreatmentRemoval	0.079	0.390	0.202	0.840
			Timepoint2019-Jul	0.332	0.357	0.929	0.353
			Timepoint2020-Jul	0.923	0.309	2.985	< 0.01
			Timepoint2020-Oct	0.573	0.320	1.790	0.073
			Timepoint2021-Jul	0.819	0.312	2.625	< 0.01
			Timepoint2021-Oct	0.704	0.316	2.230	< 0.05
			TreatmentRemoval:Timepoint2019-Jul	0.175	0.535	0.327	0.744
			TreatmentRemoval:Timepoint2020-Jul	-0.056	0.428	-0.130	0.897
			TreatmentRemoval:Timepoint2020-Oct	0.135	0.439	0.308	0.759
			TreatmentRemoval:Timepoint2021-Jul	0.317	0.427	0.744	0.457
			TreatmentRemoval:Timepoint2021-Oct	0.248	0.432	0.575	0.566
Evenness ~ Treatment * Timepoint + Bay + (1 | BayPlot)							
Evenness	Beta (logit link)	NA	(Intercept)	-0.654	0.295	-2.213	< 0.05
			TreatmentRemoval	0.614	0.344	1.788	0.074
			Timepoint2019-Jul	0.810	0.314	2.578	< 0.05
			Timepoint2020-Jul	0.750	0.285	2.637	0.008
			Timepoint2020-Oct	0.910	0.280	3.249	< 0.01
			Timepoint2021-Jul	0.442	0.289	1.528	0.126
			Timepoint2021-Oct	0.619	0.291	2.126	< 0.05
			BayFlorence Bay	-0.432	0.247	-1.747	0.081
			TreatmentRemoval:Timepoint2019-Jul	-0.829	0.469	-1.770	0.077
			TreatmentRemoval:Timepoint2020-Jul	-1.094	0.375	-2.916	< 0.01
			TreatmentRemoval:Timepoint2020-Oct	-1.061	0.371	-2.860	< 0.01
			TreatmentRemoval:Timepoint2021-Jul	-0.504	0.378	-1.332	0.183
			TreatmentRemoval:Timepoint2021-Oct	-0.616	0.379	-1.624	0.104



Supplementary Figure 5. *Diversity metrics for **(a)** macroalgal and **(b)** coral communities from 2018 to 2021 in two bays of Magnetic Island, Australia. Coloured points are mean predicted fits of generalised linear mixed effects models (conditional r^2 shown in top left corner of each panel, except for evenness where r^2 values are not applicable), with predictions for control plots shown in blue and removal plots shown in orange. Solid vertical lines represent 95% confidence intervals. Partialised observations (sum of fitted values and residuals) are shown as faint-coloured points. Asterisks represent statistically significant differences between control and removal plots.*

6.2 Appendix B. Supplementary materials for Chapter 3



Supplementary Figure 6. *Grain size distribution represented as percent volume density (percent distribution by volume) for 8 representative groups of 3 sediment samples each. Samples were analysed separately then merged to demonstrate consistency of replicates and justify merging of replicates within a plot. Blue lines represent each replicate, dashed blue line represents the mean of the 3 replicates surrounded by a grey standard error ribbon, and solid black line represents grain size distribution of the merged sample (equal volumes of replicates mixed thoroughly prior to processing)*

Supplementary Table 7. Details of data used to define generalised linear mixed effects models investigating the impact of macroalgal removal on sediment deposition rate, organic content of deposited sediment, and algal turf height

Model	**Response variable &** ***appropriate distribution***		**Number of observa-tions**	**Number of outliers removed**	**Data type**	**Predictor variables**	**Data type**		**Relationship between predictor variables**
1	Net sediment deposition rate (mg cm^{-2} d^{-1}) *Gamma*	SedPods	281	17	Continuous numerical	Treatment	Categorical	Nominal	interacting fixed effects
						Bay		Nominal	
						Deployment		Ordinal	
						Substrate type		Nominal	additive fixed effect
2		TurfPods	282	7	Continuous numerical	Treatment	Categorical	Nominal	additive fixed effect
						Bay		Nominal	interacting fixed effects
						Deployment		Ordinal	
						Substrate type		Nominal	additive fixed effect
3	Organic content of deposited sediment (proportion) *Beta*		563	9	Continuous numerical	Pod type	Categorical	Nominal	interacting fixed effects
						Bay		Nominal	
						Deployment		Ordinal	
						Treatment		Nominal	additive fixed effect
4	Algal turf height (mm) *Gamma*		4320	46	Continuous numerical	Treatment	Categorical	Nominal	interacting fixed effects
						Bay		Nominal	
						Survey timepoint		Ordinal	

Supplementary Table 8. *Results for sediment samples collected from SedPods and TurfPods deployed across 24 plots each 25 m^2 (12 control plots (C), 12 macroalgal removal plots (R)) during four deployment periods from 2020 to 2021 in two bays of Magnetic Island, Australia (Arthur Bay (A) and Florence Bay (F)). Grain-size distribution results are given by the D-values (D10, D50, D90), which represent the median particle diameter, in µm (i.e., D50 = 50% by volume of the particles is smaller than this diameter), and the particle diameter at the 10th and 90th percentiles. The percentage of sediment grains <20 µm is shown to indicate the fraction of fine sediment that is most ecologically relevant (Bainbridge et al., 2018). All data are means, averaged across all plots and pods for each grouping shown, with standard error in brackets*

Pod Type	**Deploy-ment**	**Site**	**Treat-ment**	**Deposition** mg cm-2 d-1	± SE	**% Organic**	± SE	**Grain size (µm)**						**% Fine** (<20µm)	± SE
								D10	± SE	**D50**	± SE	**D90**	± SE		
SedPod	May-20	A	C	0.13	± (0.05)	20.79	± (4.07)	3.28	± (0.20)	20.71	± (3.78)	197.75	± (45.35)	56	± (2.68)
			R	0.24	± (0.05)	17.66	± (2.64)	4.29	± (0.31)	18.87	± (1.35)	95.55	± (7.53)	54	± (2.22)
		F	C	0.36	± (0.06)	12.60	± (0.75)	2.65	± (0.06)	24.44	± (4.12)	153.26	± (14.33)	54	± (3.83)
			R	0.26	± (0.04)	17.24	± (1.65)	3.68	± (0.00)	12.91	± (0.05)	95.42	± (0.96)	67	± (0.13)
	Aug-20	A	C	0.14	± (0.02)	15.50	± (0.93)	2.84	± (0.15)	20.96	± (0.99)	172.60	± (3.82)	50	± (1.11)
			R	0.21	± (0.05)	13.66	± (1.33)	2.98	± (0.35)	22.39	± (1.51)	175.42	± (8.45)	49	± (1.65)
		F	C	0.35	± (0.07)	9.33	± (0.94)	2.22	± (0.24)	20.54	± (2.53)	163.70	± (11.75)	54	± (2.64)
			R	0.28	± (0.04)	11.06	± (0.92)	2.14	± (0.16)	19.63	± (1.67)	219.54	± (22.96)	54	± (1.64)
	Nov-20	A	C	0.18	± (0.02)	17.29	± (1.59)	3.00	± (0.26)	19.89	± (1.11)	147.80	± (3.57)	51	± (1.40)
			R	0.30	± (0.03)	15.86	± (0.93)	4.58	± (0.43)	28.41	± (1.63)	211.28	± (8.20)	43	± (1.64)
		F	C	0.26	± (0.07)	15.79	± (2.42)	2.70	± (0.15)	22.15	± (2.13)	167.45	± (10.43)	51	± (1.58)
			R	0.45	± (0.08)	15.24	± (1.28)	2.08	± (0.15)	13.54	± (0.32)	147.06	± (5.43)	60	± (0.28)
	Feb-21	A	C	0.17	± (0.02)	13.96	± (1.10)	3.23	± (0.12)	16.94	± (0.46)	108.14	± (2.05)	56	± (0.63)
			R	0.34	± (0.06)	11.69	± (1.00)	3.14	± (0.13)	25.97	± (4.90)	148.62	± (16.69)	51	± (2.90)
		F	C	0.44	± (0.07)	8.10	± (0.61)	2.83	± (0.19)	18.82	± (1.36)	160.20	± (5.88)	53	± (1.58)
			R	0.31	± (0.03)	10.12	± (0.66)	3.45	± (0.12)	45.45	± (8.94)	240.27	± (24.90)	46	± (2.54)

TurfPod	May-20	A	C	5.45 ± (2.71)	19.03 ± (4.00)	2.42 ± (0.10)	19.35 ± (2.55)	117.85 ± (7.07)	55 ± (2.23)
			R	3.56 ± (1.08)	15.01 ± (2.27)	3.02 ± (0.22)	28.25 ± (4.91)	132.99 ± (14.14)	51 ± (3.27)
		F	C	13.65 ± (3.56)	8.69 ± (1.28)	5.64 ± (0.66)	90.22 ± (13.08)	289.25 ± (35.79)	30 ± (3.08)
			R	7.40 ± (1.85)	10.03 ± (1.00)	3.36 ± (0.39)	35.76 ± (10.15)	192.22 ± (19.67)	49 ± (4.41)
	Aug-20	A	C	1.47 ± (0.29)	14.77 ± (1.05)	2.97 ± (0.09)	28.61 ± (2.17)	184.00 ± (5.07)	46 ± (1.38)
			R	6.03 ± (2.09)	12.24 ± (1.41)	6.54 ± (2.06)	47.06 ± (14.93)	205.27 ± (29.99)	44 ± (4.62)
		F	C	16.89 ± (3.83)	6.13 ± (0.75)	13.06 ± (1.75)	165.11 ± (10.87)	433.11 ± (31.86)	15 ± (1.16)
			R	14.11 ± (3.40)	8.69 ± (2.18)	8.97 ± (1.16)	121.17 ± (9.89)	377.11 ± (28.11)	22 ± (1.74)
	Nov-20	A	C	8.44 ± (2.38)	8.93 ± (0.90)	5.25 ± (0.22)	73.21 ± (6.44)	236.28 ± (11.06)	31 ± (1.30)
			R	10.25 ± (2.46)	8.62 ± (0.98)	6.05 ± (0.78)	77.88 ± (9.28)	250.89 ± (10.52)	30 ± (2.34)
		F	C	26.68 ± (5.62)	5.09 ± (0.40)	31.61 ± (4.69)	169.93 ± (8.06)	389.73 ± (30.01)	10 ± (1.05)
			R	32.31 ± (5.33)	4.77 ± (0.21)	12.54 ± (1.73)	139.30 ± (11.80)	342.00 ± (24.55)	18 ± (1.91)
	Feb-21	A	C	3.25 ± (0.96)	10.51 ± (0.96)	4.06 ± (0.22)	50.03 ± (9.07)	179.00 ± (17.74)	40 ± (3.30)
			R	8.87 ± (2.94)	10.07 ± (1.29)	3.80 ± (0.50)	22.47 ± (1.43)	144.67 ± (6.69)	48 ± (1.62)
		F	C	23.71 ± (5.20)	5.77 ± (0.72)	36.72 ± (6.81)	181.20 ± (9.53)	424.27 ± (30.16)	11 ± (1.32)
			R	29.14 ± (4.21)	5.63 ± (1.30)	25.22 ± (5.94)	161.94 ± (9.11)	361.33 ± (25.31)	12 ± (0.99)

Supplementary Table 9. *Summary of generalised linear mixed effects model results used to examine patterns in deposition and organic content of sediments deposited on SedPods and TurfPods deployed from 2020 to 2021, as well as patterns in algal turf height surveyed from 2020 to 2021 in two bays of Magnetic Island, Australia*

Response variable	**Model used**	**Conditional r^2**	**Predictors**	**Estimate**	**SE**	***z* - value**	***p* - value**	**95% CI**	
				(fractional scale)				**lower**	**upper**
SEDPODS	DEPOSITION ~ TREATMENT * DEPLOYMENT * BAY + SUBSTRATE + (1 | PLOT) + (1 | PLOT:PODNUMBER)								
Net sediment deposition rate	GLMM - Gamma (log link)	0.57	(Intercept)	0.090	0.016	-13.229	< 0.001	0.063	0.129
			TREATMENTRemoval	2.178	0.496	3.414	< 0.001	1.393	3.404
			DEPLOYMENT2	1.677	0.305	2.839	0.005	1.174	2.396
			DEPLOYMENT3	2.243	0.414	4.379	< 0.001	1.562	3.220
			DEPLOYMENT4	2.049	0.372	3.949	< 0.001	1.435	2.925
			BAYFlorence Bay	3.235	0.739	5.141	< 0.001	2.068	5.061
			SUBSTRATEMACROALGAE	0.810	0.096	-1.781	0.075	0.642	1.021
			SUBSTRATERUBBLE	1.104	0.135	0.806	0.420	0.868	1.403
			SUBSTRATESAND	1.830	0.333	3.322	< 0.001	1.281	2.614
			SUBSTRATETURF	1.242	0.287	0.939	0.348	0.790	1.953
			TREATMENTRemoval:DEPLOYMENT2	0.504	0.130	-2.647	0.008	0.304	0.837
			TREATMENTRemoval:DEPLOYMENT3	0.681	0.178	-1.470	0.142	0.408	1.137
			TREATMENTRemoval:DEPLOYMENT4	0.724	0.190	-1.234	0.217	0.433	1.209
			TREATMENTRemoval:BAYFlorence Bay	0.349	0.112	-3.266	0.001	0.186	0.656
			DEPLOYMENT2:BAYFlorence Bay	0.476	0.121	-2.918	0.004	0.289	0.784
			DEPLOYMENT3:BAYFlorence Bay	0.217	0.057	-5.846	< 0.001	0.130	0.362
			DEPLOYMENT4:BAYFlorence Bay	0.579	0.150	-2.102	0.036	0.348	0.964
			TREATMENTRemoval:DEPLOYMENT2:BAYFlorence Bay	2.498	0.916	2.496	0.013	1.217	5.126
			TREATMENTRemoval:DEPLOYMENT3:BAYFlorence Bay	4.265	1.598	3.871	< 0.001	2.046	8.888
			TREATMENTRemoval:DEPLOYMENT4:BAYFlorence Bay	1.568	0.590	1.195	0.232	0.750	3.278
TURFPODS	DEPOSITION ~ TREATMENT + DEPLOYMENT * BAY + SUBSTRATE + (1 | PLOT) + (1 | PLOT:PODNUMBER)								
Net sediment deposition rate	GLMM - Gamma (log link)	0.81	(Intercept)	2.221	0.648	2.735	0.006	1.254	3.935
			DEPLOYMENT2	0.889	0.158	-0.665	0.506	0.627	1.259
			DEPLOYMENT3	2.801	0.502	5.752	< 0.001	1.972	3.979
			DEPLOYMENT4	1.407	0.256	1.874	0.061	0.985	2.010
			BAYFlorence Bay	2.892	0.965	3.183	0.001	1.504	5.560
			TREATMENTRemoval	1.105	0.327	0.338	0.735	0.619	1.974
			SUBSTRATEMACROALGAE	0.770	0.108	-1.862	0.063	0.585	1.014
			SUBSTRATERUBBLE	0.906	0.147	-0.609	0.543	0.658	1.246
			SUBSTRATESAND	2.182	0.436	3.902	< 0.001	1.474	3.228
			SUBSTRATETURF	0.643	0.177	-1.607	0.108	0.376	1.102
			DEPLOYMENT2:BAYFlorence Bay	2.181	0.555	3.066	0.002	1.325	3.592
			DEPLOYMENT3:BAYFlorence Bay	1.156	0.296	0.565	0.572	0.700	1.908
			DEPLOYMENT4:BAYFlorence Bay	2.187	0.560	3.054	0.002	1.323	3.613

ORGANICS	ORGANIC PROPORTION ~ POD * DEPLOYMENT * BAY + TREATMENT + SUBSTRATE + (1 | PLOT) + (1 | PLOT:PODNUMBER)								
Proportion organic	GLMM - Beta (logit link)	0.70	(Intercept)	0.181	0.018	-17.527	< 0.001	0.150	0.219
			PODTurfPod	0.840	0.071	-2.053	0.040	0.711	0.992
			DEPLOYMENT2	0.894	0.072	-1.388	0.165	0.764	1.047
			DEPLOYMENT3	1.023	0.081	0.291	0.771	0.876	1.196
			DEPLOYMENT4	0.742	0.062	-3.577	< 0.001	0.630	0.874
			BAYFlorence Bay	0.960	0.109	-0.358	0.721	0.769	1.199
			TREATMENTRemoval	1.046	0.089	0.527	0.598	0.885	1.235
			SUBSTRATEMACROALGAE	1.091	0.055	1.726	0.084	0.988	1.205
			SUBSTRATERUBBLE	0.900	0.051	-1.848	0.065	0.805	1.006
			SUBSTRATESAND	0.678	0.056	-4.735	< 0.001	0.578	0.796
			SUBSTRATETURF	1.058	0.110	0.542	0.588	0.863	1.298
			PODTurfPod:DEPLOYMENT2	1.064	0.125	0.532	0.595	0.846	1.340
			PODTurfPod:DEPLOYMENT3	0.590	0.073	-4.278	< 0.001	0.463	0.751
			PODTurfPod:DEPLOYMENT4	0.926	0.114	-0.623	0.533	0.728	1.179
			PODTurfPod:BAYFlorence Bay	0.723	0.089	-2.627	0.009	0.568	0.921
			DEPLOYMENT2:BAYFlorence Bay	0.774	0.092	-2.152	0.031	0.613	0.977
			DEPLOYMENT3:BAYFlorence Bay	0.969	0.113	-0.270	0.787	0.771	1.218
			DEPLOYMENT4:BAYFlorence Bay	0.823	0.100	-1.608	0.108	0.648	1.044
			PODTurfPod:DEPLOYMENT2:BAYFlorence Bay	0.911	0.165	-0.517	0.605	0.638	1.299
			PODTurfPod:DEPLOYMENT3:BAYFlorence Bay	0.948	0.175	-0.289	0.773	0.661	1.361
			PODTurfPod:DEPLOYMENT4:BAYFlorence Bay	1.007	0.187	0.037	0.970	0.700	1.448
ALGAL TURFS	TURF HEIGHT ~ TREATMENT * BAY * TIMEPOINT + (1|PLOT) + (1 | PLOT:QUADRAT)								
Height of algal turf	GLMM - Gamma (log link)	0.30	(Intercept)	7.994	0.373	44.521	< 0.001	7.295	8.760
			TREATMENTRemoval	1.019	0.067	0.287	0.774	0.896	1.160
			BAYFlorence Bay	1.140	0.076	1.978	0.048	1.001	1.299
			TIMEPOINTJul 2020	0.882	0.047	-2.345	0.019	0.794	0.980
			TIMEPOINTNov 2020	0.669	0.036	-7.500	< 0.001	0.602	0.743
			TIMEPOINTFeb 2021	0.434	0.023	-15.560	< 0.001	0.391	0.482
			TIMEPOINTApr 2021	0.487	0.026	-13.462	< 0.001	0.439	0.541
			TIMEPOINTJul 2021	0.492	0.026	-13.239	< 0.001	0.443	0.547
			TREATMENTRemoval:BAYFlorence Bay	1.102	0.104	1.032	0.302	0.916	1.327
			TREATMENTRemoval:TIMEPOINTJul 2020	0.990	0.075	-0.130	0.897	0.854	1.149
			TREATMENTRemoval:TIMEPOINTNov 2020	0.870	0.066	-1.836	0.066	0.750	1.009
			TREATMENTRemoval:TIMEPOINTFeb 2021	0.919	0.070	-1.112	0.266	0.793	1.066
			TREATMENTRemoval:TIMEPOINTApr 2021	0.901	0.068	-1.379	0.168	0.777	1.045
			TREATMENTRemoval:TIMEPOINTJul 2021	1.009	0.076	0.120	0.905	0.870	1.170
			BAYFlorence Bay:TIMEPOINTJul 2020	0.794	0.060	-3.035	0.002	0.684	0.921
			BAYFlorence Bay:TIMEPOINTNov 2020	1.021	0.078	0.273	0.785	0.880	1.185
			BAYFlorence Bay:TIMEPOINTFeb 2021	1.096	0.083	1.207	0.227	0.944	1.272
			BAYFlorence Bay:TIMEPOINTApr 2021	0.851	0.065	-2.131	0.033	0.733	0.987
			BAYFlorence Bay:TIMEPOINTJul 2021	0.995	0.076	-0.060	0.952	0.858	1.155
			TREATMENTRemoval:BAYFlorence Bay:TIMEPOINTJul 2020	0.816	0.088	-1.882	0.060	0.660	1.008
			TREATMENTRemoval:BAYFlorence Bay:TIMEPOINTNov 2020	0.720	0.078	-3.040	0.002	0.583	0.890
			TREATMENTRemoval:BAYFlorence Bay:TIMEPOINTFeb 2021	1.047	0.113	0.422	0.673	0.847	1.293
			TREATMENTRemoval:BAYFlorence Bay:TIMEPOINTApr 2021	1.044	0.113	0.401	0.688	0.845	1.290
			TREATMENTRemoval:BAYFlorence Bay:TIMEPOINTJul 2021	0.970	0.105	-0.282	0.778	0.785	1.199

***Supplementary Table 10.** Results from a three-factor permutational multivariate analysis of variance of grain size distributions of sediment samples deposited on **(a)** SedPods and **(b)** TurfPods deployed from 2020 to 2021 in two bays of Magnetic Island, Australia. Asterisks indicate significance at p < .05*

a) SedPods

Grain Size Distribution ~ TREATMENT + SITE + DEPLOYMENT, strata: PLOT

Factor	**df**	**Sum of Squares**	**Mean Squares**	***F* - value**	**r2**	***p* - value**
Treatment	1	0.01	0.01	1.45	0.02	0.138
Site	1	0.01	0.01	2.46	0.03	0.083
Deployment	3	0.06	0.02	3.51	0.13	<0.05 *
Residuals	68	0.36	0.01		0.82	
Total	73	0.43			1.00	

b) TurfPods

Grain Size Distribution ~ TREATMENT + SITE + DEPLOYMENT, strata: PLOT

Factor	**df**	**Sum of Squares**	**Mean Squares**	***F* - value**	**r2**	***p* - value**
Treatment	1	0.00	0.00	0.29	0.00	0.571
Site	1	0.21	0.21	35.06	0.27	<0.05 *
Deployment	3	0.14	0.05	7.49	0.17	<0.05 *
Residuals	73	0.45	0.01		0.56	
Total	78	0.80			1.00	