

Empirical and mechanistic  
approaches to understanding and  
projecting change in coastal  
marine communities

by

*Daniel Bayley*

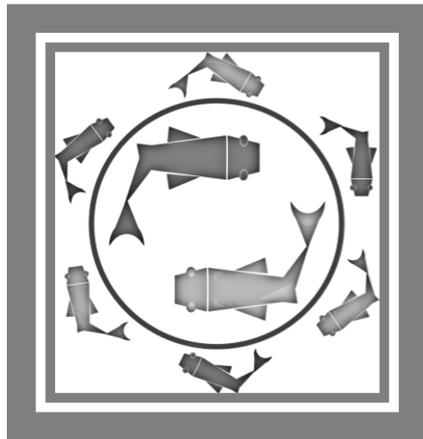
*A thesis submitted for the Degree:*

*Doctor of Philosophy*

*in Marine Ecology*









## Declaration of originality

I, Daniel Bayley confirm that the work presented in this thesis is my own. Where information has been derived from other sources, I confirm that this has been indicated in the thesis.

Signature

Date

The following chapters have been published / submitted, with collaboration from other authors:

**Chapter 1** - Part of this chapter is published in the book '*World Seas: An Environmental Evaluation*' with Dr Andy Mogg as co-author. I wrote the majority of the published text and reviewed the remaining final section.

**Chapter 2** - This chapter is submitted to *PeerJ* as an original research paper, co-authored with Dr Andy Mogg, Prof Heather Koldewey, and Prof Andy Purvis. I was responsible for all aspects of the design, data collection, analysis and writing of the paper. The other three authors provided some initial data processing (through the NERC data facility) as well as comments on study design, manuscript structure and clarity.

**Chapter 3** - This chapter is submitted to *Aquatic Conservation: Marine & Freshwater science* as an original research paper, co-authored with Dr Andy Mogg, Prof Andy Purvis and Prof Heather Koldewey. I was responsible for all aspects of the design, data collection (aside from in situ fish abundance counts, conducted by my assistant), analysis and writing of the paper. The other three authors provided some initial data processing (through the NERC data facility) as well as comments on study design, manuscript structure and clarity.

The following chapters used some external raw data, not collected within this PhD period:

**Chapter 4** – Long term raw benthic and fishery data was used with permission from collaborators at ZSL / Project Seahorse. I was responsible for all other aspects of the design, analysis and writing of this chapter.

**Chapter 5 & 6** – Data for level of wave exposure around the Chagos archipelago was used with permission from collaborators at Exeter University. Coral cover raw data within the Chagos archipelago for 2015 was used with permission from collaborators at Bangor University. I was responsible for all other aspects of the design, data collection, analysis and writing of these chapters. A small part of the imagery outputs and methods from chapter 6 is also published in the *Atoll Research Bulletin* as an original research paper, led by Prof. Charles Sheppard.

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## **Impact statement**

My work aimed to apply new imaging technologies to the monitoring of coral reefs allowing researchers to assess the impact of disturbance events and to monitor the rate of subsequent recovery. Technology for creating 3D underwater landscapes has been available for a number of years through methods such as multibeam echosounding and LiDAR, however these methods have been prohibitively expensive and impractical across small-scale shallow sites (which are typically of interest in assessments of reef health and disturbance impacts and for coastal communities). The method trailed in this study is successful in achieving a cheap, rapid and accurate alternative which could be invaluable for use in monitoring projects worldwide, giving a permanent interactive record of the reef-scape for future re-analysis and comparison, as well as material for outreach and engagement.

The project in a wider sense will feed into the growing body of evidence documenting the effectiveness of MPAs and their benefits for maintaining healthy reefs. It further aims to feed into larger bodies of work to investigate the impacts of climate specifically, which can feed into policy guidance, and to investigate whether changes in structure, richness and compositional change are consistent across biogeographic realms and along gradients of local human pressure.



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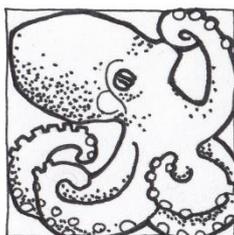
## **Abstract of PhD**

This work details the effects of disturbance events on tropical coral reefs and highlights emerging techniques for improved monitoring and assessment of benthic change. The first chapter is in the form of a literature review, which aims to give a broad introduction to reef ecology, the impacts experienced by this system, and the methods used to monitor and assess change. The second chapter highlights a recently developed photogrammetric methodology which can be used to assess change in the marine environment. The methodology is then assessed for accuracy and comparability to standard benthic monitoring techniques.

The proceeding four chapters aim to address a number of ecological and management questions relating to reef community ecology, focussing on physical structure and demonstrating the utility of 'Structure from Motion' (SfM) photogrammetry as a monitoring and assessment tool. Chapters three and four more specifically use community managed small-scale Marine Protected Areas (MPAs) in the Philippines as a case study applying SfM, and assess the effectiveness of these MPAs. These chapters further highlight how physical changes can affect the function of the reefs and their associated fisheries. Chapters five and six then investigate how extreme climatic events can affect the structure and growth of reefs in the Indian Ocean, away from the array of confounding anthropogenic factors seen in the Philippines.

The final section looks to bring together these chapters to discuss the benefits of new technology, and the future of reefs under a changing climate.





## *Chapter 1: Introduction to tropical coral reefs and modern benthic analysis*

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Part of this chapter has been adapted for the following publication:

- Bayley DTI, Mogg AOM. (2018). *New advances in benthic monitoring technology and methodology*. In: Sheppard CRC, editor. *World Seas: An Environmental Evaluation*, Elsevier Inc.

### **Background**

Our planet and the diversity of life which inhabits it, is changing at an unprecedented rate (Ceballos *et al.*, 2015; IPCC, 2018). Anthropogenic activities have progressively altered global environmental processes and have systematically degraded ecosystem biodiversity and function, leaving behind little remaining true ‘wilderness’ that is unmodified by human activity (Dornelas *et al.*, 2014; Tittensor *et al.*, 2014; Johnson *et al.*, 2017; Watson *et al.*, 2018). Humans have impacted the Earth to such a degree in fact that many observers have concluded that we have now entered a new geological epoch termed the ‘Anthropocene’ (Corlett, 2015).

High levels of biodiversity are essential for the continued functioning of global ecological processes, and for the continued supply of a range of services which humans rely upon for their well-being (Cardinale *et al.*, 2006; Isbell *et al.*, 2017). However, the species and habitats

which constitute this diversity of life are currently in a phase of accelerating global decline (Pimm *et al.*, 2014; Tittensor *et al.*, 2014), risking the loss of essential ecosystem functions and their array of associated societal benefits, in spite of the growing evidence for the high value of biodiversity both to humans and to ecosystem stability (Costanza *et al.*, 1997; Cardinale *et al.*, 2012; Naeem *et al.*, 2012). The degradation of ecological systems also presents risks for the future prosperity of society through overshooting Earth's key biophysical limits, known as 'planetary boundaries' (Steffen *et al.*, 2015). This conceptual framework assesses the risks that human-induced perturbations will destabilise key Earth-system processes at planetary scales, resulting in the loss of ecosystem functional integrity and threatening the 'safe operating space' in which humans can continue to thrive.

The world's oceans and their biomes have been heavily impacted through time by human pressures, primarily through increases in global levels of pollution, over-extraction of resources, and rapidly changing environmental conditions such as climate (Halpern *et al.*, 2015; Maxwell *et al.*, 2016; Harvey *et al.*, 2018). The cumulative effect of these multiple pressures has led to concern that key marine processes have been degraded to such a degree that we are now approaching the boundary thresholds for many marine systems (Hoegh-Guldberg, 2014; Nash *et al.*, 2017).

## **Pressures on tropical reef ecosystems**

Tropical coral reefs are at particular risk from human pressures, having both a global distribution (ranging latitudinally from approximately 30°N to 30°S), and typically being distributed close to shore in shallow waters (Muir *et al.*, 2015). Globally, 58% of coral reefs

are located less than 30 minutes from a human settlement, and 25% of reefs are located less than four hours from the nearest major market (Maire *et al.*, 2016). On a local and regional scale, over-intensive fishing, pollution, land-use change (leading to eutrophication and sediment loading), and coastal development are the primary causes of coral ecosystem degradation (Mora, 2008; Hoegh-Guldberg, 2014; Jones *et al.*, 2018). Consequently, proximity to dense human population is often used as an indicator of a range of these pressures in large scale marine studies, and therefore as a predictor of reef health generally (Sanderson *et al.*, 2002; Williams *et al.*, 2011; Cinner *et al.*, 2013; Williams *et al.*, 2015a; Smith *et al.*, 2016).

Rapid anthropogenic land-use alterations from natural vegetation such as primary or secondary forest to urban or cropland areas, is the most significantly driver for increased flow of nutrients, sediment and pollution into the world's oceans through coastal and riverine run-off at a global scale (Vitousek *et al.*, 1997; Syvitski, 2005). The rate of global forest loss is most severe in the tropics, and is still accelerating year on year (Hansen *et al.*, 2013). Therefore, some of the largest increases in the flow of land-based sediments to the oceans are seen in tropical developing countries such as Indonesia where catchment reservoirs are not present and land-use alteration is extensive (Syvitski, 2005; Hansen *et al.*, 2013).

The flow of sediment and nutrient-rich run-off into the sea significantly affects coastal coral reef communities at both a regional and local scale (Edinger *et al.*, 1998; Koop *et al.*, 2001; Halpern *et al.*, 2008; Kroon *et al.*, 2012; Risk, 2014; Fredston-Hermann *et al.*, 2016; Brown *et al.*, 2017b). Impacts include smothering and resource competition (Fabricius, 2005; Erftemeijer *et al.*, 2012; Brown and Hamilton, 2018) as well as damaging levels of hypoxia and algal blooms (Grall and Chauvaud, 2002; Gray *et al.*, 2002). Chronically elevated turbidity and nutrient

levels also cause alterations in benthic community structure (Mallela *et al.*, 2004; Fabricius, 2005; De'ath *et al.*, 2010; Wenger *et al.*, 2016; Brown *et al.*, 2017b), and reductions in coral survival (Côté *et al.*, 2016), compositional turnover (Brown and Hamilton, 2018), and associated fish diversity (Fabricius *et al.*, 2005; Brown *et al.*, 2017a). More recently, in addition to the coastal pollution impacts from run-off of agricultural fertilisers, sediments, heavy metals, and sewage, the influx of general litter such as plastics has rapidly increased (Eriksen *et al.*, 2014; Lavers and Bond, 2017), leading to damage and infection in exposed ecological communities (Shahidul Islam and Tanaka, 2004; Riegl *et al.*, 2009; Lamb *et al.*, 2018)..

Alongside the damage caused regionally to benthic communities, associated demersal and pelagic fish communities are also in widespread decline .The continued over-exploitation of fish stocks has caused steep declines in apex species (Baum *et al.*, 2003; Myers and Worm, 2003; Roff *et al.*, 2018) and community-wide declines and collapses in the abundance and size-structure of global fisheries (Pauly, 1998; Jackson *et al.*, 2001; Knowlton and Jackson, 2008; Butchart *et al.*, 2010; Estes *et al.*, 2011; MacNeil *et al.*, 2015; Pauly and Zeller, 2016). The pervasiveness of human pressure on marine ecosystems globally has led to the rapid loss of remaining locations which can be considered 'pristine' or 'wilderness areas', where human impacts are negligible (Graham and McClanahan, 2013; Graham *et al.*, 2017, 2018; Barlow *et al.*, 2018; Jones *et al.*, 2018). This bombardment by a host of pressures is leading to the loss of function and increased difficulty in our ability to predict and mitigate the combined range of pressures simultaneously (Hughes *et al.*, 2013; Steffen *et al.*, 2015; Cinner *et al.*, 2016; D'Agata *et al.*, 2016).

Aside from the more typically regional- and local-scale human pressures, global-scale pressures to reefs come primarily from climatic change, which has resulted in increased water temperature, water acidity and storm occurrence, each of which incur large detrimental impacts regardless of the reef's remoteness (Madin and Connolly, 2006; Pandolfi *et al.*, 2011; Emanuel, 2013). The negative effects on the biodiversity and structure of marine systems from temperature increases have been particularly pronounced following the major El Niño Southern Oscillation (ENSO) episodes of 1982-83 and 1997-1998 (Glynn, 1993), due to the wide-spread and severe incidences of heat-induced bleaching and mortality of corals which these and other smaller episodes caused (Gardner, 2003; Bruno and Selig, 2007; Butchart *et al.*, 2010). Most recently, reefs have experienced a further global bleaching episode across the period 2015-16 (Figure 1), the third global bleaching on record, which caused high levels of mortality across shallow tropical reefs globally (Hughes *et al.*, 2017, 2018a).

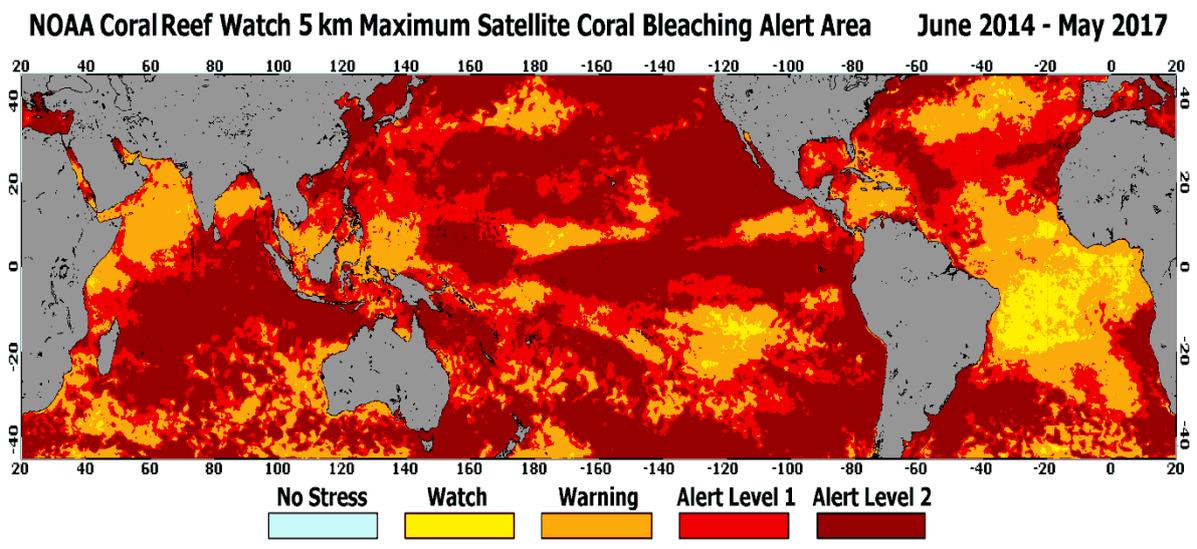


Figure 1. Extent of predicted bleaching and mortality for reefs globally from NOAA Coral Reef Watch's satellite monitoring programme (<https://coralreefwatch.noaa.gov>). The map shows areas that experienced the high heat stress that can cause coral bleaching, from June 1, 2014 to May 31, 2017, at 5

km resolution. Categories range from no heat stress, to sustained water temperatures above the mean temperature of the climatologically warmest month at the location (Alert level 2 predicts widespread and severe bleaching and mortality following 8 continuous 'degree heating weeks' (Liu *et al.*, 2014).

'Bleaching' is a physiological stress response in which corals expel the symbiotic zooxanthellae living within their tissues, leaving only a transparent layer covering the white skeleton beneath (Figure 2). This response most typically occurs due to prolonged elevated heat anomalies outside of their acclimatised temperature range, which causes the symbiotic algae to deteriorate and start producing toxic levels of oxygen. The coral's response is to digest and expel the algae to reduce oxidative stress damage, which in turn stops the supply of sugars and amino acids to the coral from the symbiotic relationship, commonly resulting in coral mortality (Baker *et al.*, 2008; Fujise *et al.*, 2014).



Figure 2. A 'bleached' coral. The image shows the appearance of an *Acropora cerealis* colony following prolonged high temperatures, leaving the white underlying skeleton visible after symbiotic zooxanthellae is expelled.

Instances of intense regional and global bleaching are now accelerating in frequency, allowing less time for regeneration in interim years (Heron *et al.*, 2016; van Hooidonk *et al.*, 2016; Hughes *et al.*, 2018a). Additionally, the Intergovernmental Panel on Climate Change (IPCC) estimates that more than 90 % of the energy accumulated between 1971 and 2010 has been stored in the oceans, with recent estimates showing that globally the ocean has warmed within the upper 75 m of depth by 0.11°C per decade since 1971. Sea surface temperatures are predicted to rise (primarily in the tropics and Northern sub-tropical regions) by between 0.6 – 2.0°C by the end of the century, with lesser heat increases also affecting deep ocean waters down to 2000 m, which will exacerbate this issue still further (IPCC, 2013).

### ***Future changes***

Projections indicate that the continued cumulative influence of these multiple global pressures, will cause major changes to marine habitat structure and extent (Hoegh-Guldberg and Bruno, 2010; Gattuso *et al.*, 2015; IPCC, 2018), and cause climate-induced latitudinal range shifts in both pelagic and demersal species into the future (Pereira *et al.*, 2010). Recent predictions further suggest that current pressures will lead to the potential loss of coral reefs systems as we currently know them, moving towards a more simplified and depauperate ecosystem state (Pandolfi *et al.*, 2011; Hoegh-Guldberg, 2014; van Hooidonk *et al.*, 2016; IPCC, 2018). Some of these predicted effects are indeed already being realised with many reefs now in a state of rapid net erosion (Newman *et al.*, 2015; Januchowski-Hartley *et al.*, 2017; Perry and Morgan, 2017), persistent assemblage phase-shifts observed across multiple reef sites (Hughes *et al.*, 2010), and broad declines in marine-ecosystem functioning and ocean productivity, and altered species distributions and food-web dynamics (Bellwood *et*

*al.*, 2004; Hughes *et al.*, 2007; Rosenzweig *et al.*, 2008; Hoegh-Guldberg and Bruno, 2010; Pecl *et al.*, 2017).

On a number of reefs, primarily within the Caribbean, the interaction of chronic anthropogenic pressures with acute heating episodes, have led to a community 'phase shift' or change in stable state from hard coral dominance to fleshy brown and green macro-algae dominance (Done, 1992; McManus and Polsenberg, 2004; Hughes *et al.*, 2007, 2010; Roff and Mumby, 2012). Whilst there are various views on whether the combined pressures leading to such a change are synergistic, antagonistic or additive (Darling *et al.*, 2010; Bozec and Mumby, 2014), the result is a distinct reduction in both the level of biodiversity and the functionality associated with the reef system affected (McManus and Polsenberg, 2004; Hughes *et al.*, 2007). The phase shift is often temporary, however some reefs, such as those around Jamaica, have demonstrated a sustained, perhaps permanent, alteration to an algal-dominated state (Norström *et al.*, 2009), even after the removal of long-term pressures such as fishing (Done, 1992; Scheffer *et al.*, 2001; Gardner, 2003; Hughes *et al.*, 2003; Bates *et al.*, 2013).

A similar but less widely observed phenomenon is that of 'Tropicalization' whereby previously kelp-dominated temperate or sub-tropical systems shift to a coral-dominated system, following a sustained increase in temperature associated with shifts in poleward-flowing boundary currents. Such temperature changes facilitate tropical species' range expansion and alter local systems through changing the levels of herbivory and competition (Vergés *et al.*, 2014; Takao *et al.*, 2015).

The loss and decline of marine biodiversity it seems will not just damage ecosystem services and livelihoods, but will importantly also lower the ability of systems to withstand further

impacts. (Worm *et al.*, 2006). In parallel to this, the increased frequency of disturbance events such as high temperatures and sustained poor water quality are making it far harder for systems to recover in between impacts (Ainsworth *et al.*, 2016; Wenger *et al.*, 2016; Hughes *et al.*, 2018a), making the future highly uncertain for reefs, and certainly less than rosy (Harborne *et al.*, 2017).

Periods of large decline and even extinctions of corals have however occurred before, i.e. in the Paleogene, Neogene and current Quaternary period, with these declines correlated with episodes of significant environmental perturbation, such as changes in global temperature and episodes of widespread high turbidity (Johnson *et al.*, 1995; Klaus *et al.*, 2008). Reconstructions of coral palaeo-physiology and reef accretion in the recent geological past show that a hiatus in growth of corals occurred for around 2,500 years, approximately 4,100 years ago. This halting of growth appears to be associated with biotic and climatic threshold factors, with cooler temperatures and high precipitation causing abrupt 'reef shut-down' (Toth *et al.*, 2015). Such abrupt change could therefore feasibly occur in current corals if the climate (or other environmental variables), continue to alter.

It is unclear how present-day corals will deal with the current bombardment of new pressures brought on by human influence. Life-history traits that previously helped corals to survive regional change and allow certain taxa to selectively persist, are now potentially less useful under the novel regime of anthropogenic pressures, resulting in reefs with less resilient species, and an uncertain future (Johnson *et al.*, 1995).

## Reef function and resilience

One of the greatest remaining areas of uncertainty regarding why reefs are in such dramatic decline, is in finding consensus on how local and global disturbance factors interact to impact the ecosystem (McClanahan *et al.*, 2006; Darling *et al.*, 2010; Kennedy *et al.*, 2013). While a number of studies still look to single factors (Aronson and Precht, 2006), more recently the idea that communities subject to chronic local impacts will have reduced resilience to acute global impacts is becoming more popular (Roberts *et al.*, 1995; Jennings and Kaiser, 1998; Knowlton and Jackson, 2008; Mumby *et al.*, 2014; Standish *et al.*, 2014).

'Ecological Resilience' describes the ability of an ecosystem to recover from both natural and anthropogenic impacts, or '*the capacity of a system to absorb disturbance and reorganise while undergoing change so as to still retain essentially the same function, structure, identity and feedbacks.*' (Walker *et al.*, 2004). Quantitative indicators or measurable aspects of the level of resilience in marine communities are generally attributable to: the structure and level of functional group abundance and species diversity found within the reef, i.e. specific organism 'resistance', community redundancy and re-growth along with localised meta-population dynamics; and the level of connectivity with other reefs, which allow influx of new colonising species through dispersal of larvae to the disturbed reef area and subsequent recruitment (Nyström *et al.*, 2000).

Community dynamics and connectivity alone do not however give the full picture, and recent research indicates further mechanisms are involved in reef resilience, such as structural complexity and level of herbivory from reef-associated organisms (Graham *et al.*, 2015). Improving our understanding therefore of why a community is resilient in both biodiversity and structure, why it breaks down due to intense pressure, or how it re-builds

following disturbance, will be necessary for any effective and sustainable management to occur (Bellwood *et al.*, 2004; Hughes *et al.*, 2005; Dornelas *et al.*, 2014).

Anthropogenic impacts can affect both the complexity and number of interactions within a system, through alteration of the ecosystem itself, or the environment surrounding it, resulting in degraded processes and function (Tilman, 2000). Functional change to marine systems occur at both local and global scales and can be extremely rapid (Symstad *et al.*, 2003; Worm *et al.*, 2006; Kennedy *et al.*, 2013). This emerging field of functional trait ecology, identifying the diversity and range of phenotypic components an organism or habitat exhibits which influence ecosystem processes, is increasingly being employed to help understand systems (Lavorel *et al.*, 1997; Grime, 2006; Violle *et al.*, 2007; Suding *et al.*, 2008; Reiss *et al.*, 2009; Schleuter *et al.*, 2010; Gardner *et al.*, 2014). Understanding and assessing ecosystem traits for marine benthos (and coral reefs specifically) still remains a largely understudied area of research (Naeem, 2006; Bremner, 2008). More recent work to improve our knowledge and understanding of how traits can be applied to marine ecological management is proving useful for increasing our mechanistic understanding of change (Darling *et al.*, 2012, 2017; Mouillot *et al.*, 2013; Stuart-Smith *et al.*, 2013; McClanahan *et al.*, 2014; Madin *et al.*, 2016b). However, the work investigating marine environment-trait relationships is generally conducted at relatively small spatial scales and is often primarily descriptive (Bremner *et al.*, 2006; Rachello-Dolmen and Cleary, 2007; Darling *et al.*, 2010; Törnroos and Bonsdorff, 2012; Mouillot *et al.*, 2013).

## Ecosystem management & Marine Protected Areas

In recent years, national and regional scale networks of Marine Protected Areas (MPAs) with highly specific management objectives, such as those designated in the UK and Australia, have been developed as an effective means to broadly protect a range of marine species and habitats (Tundi Agardy, 1994; McClanahan *et al.*, 2006; Spalding *et al.*, 2013). There has also been a growing push for the creation of ever larger MPAs (Singleton and Roberts, 2014) in order to adequately protect highly-mobile pelagic species and whole ecosystem integrity (Figure 3), as well as to meet international Aichi and UN Sustainable Development Goal targets to effectively protect at least 10 % of coastal and marine areas, and the biodiversity they contain (Thomas *et al.*, 2014).

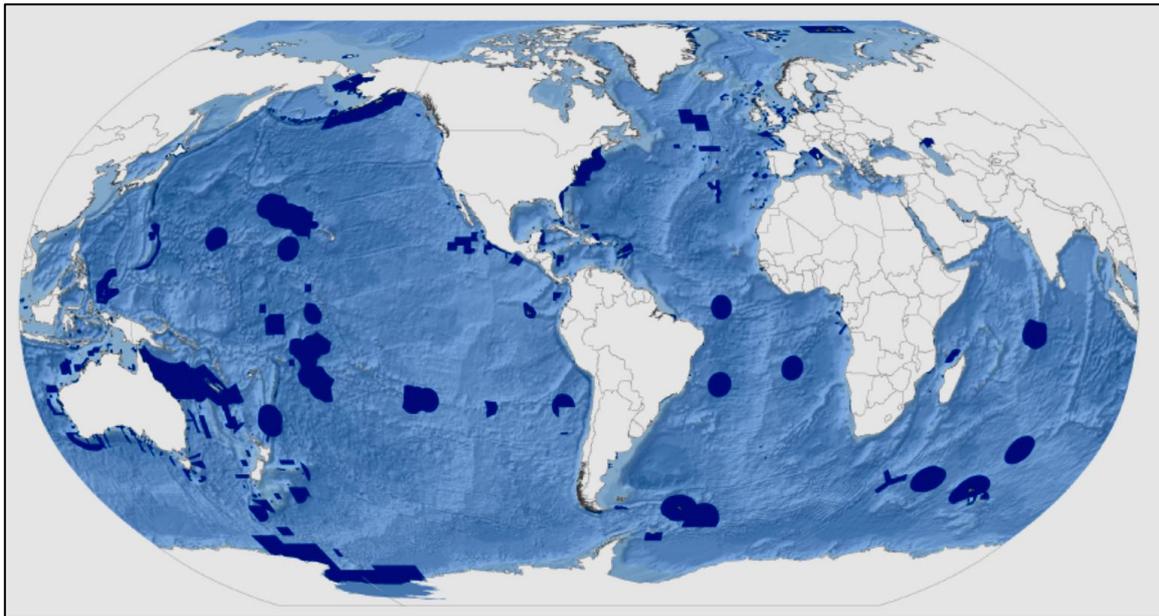


Figure 3. Global MPA location and coverage as of July 2018. Protected areas cover a total of 7.27% of global waters, with 2.25% protected in exclusive 'no-take' zones. Source UNEP-WCMC (<https://protectedplanet.net/marine>)

Whilst MPAs have been contentious historically due to lack of evidence proving efficacy, along with mismanagement or lack of enforcement often creating ‘paper parks’ (Agardy *et al.*, 2011; Gill *et al.*, 2017), they are now seen to be essential tools to protect marine ecosystems and their associated services, providing that parallel measures such as effective fisheries management and social-economic initiatives to incentivise compliance and alternative livelihoods and are run in conjunction (Kaiser, 2005; Edgar *et al.*, 2014; Ahmadi *et al.*, 2015; Gill *et al.*, 2017). Further commonalities of adequate size, number, length of establishment, adequate connectivity, and isolation have shown to consistently produce conservation gains and increased ecosystem resilience from their use (Edgar *et al.*, 2014; Cinner *et al.*, 2016; Mellin *et al.*, 2016; Lam *et al.*, 2017; Giakoumi *et al.*, 2018; Jones *et al.*, 2018).

Despite the wide array of benefits of MPAs for management of marine communities, climate change impacts still occur in even the remotest regions, with very strong management in place (Roberts *et al.*, 2017; Bruno *et al.*, 2018; Jones *et al.*, 2018). Therefore management now needs to be considered in the context of increasing resilience wherever possible through multiple conservation and design avenues, both to limit the cumulative impacts on a system and increase likely conservation wins (Maina *et al.*, 2008, 2015; Kachelriess *et al.*, 2014; Cinner *et al.*, 2016; Camp *et al.*, 2018; Ford *et al.*, 2018).

## **Measuring change: Modern monitoring methods**

In order to assess the state of present conditions and monitor changes within the marine environment, whether it is for assessing the impact of disturbance events or judging the effectiveness of a management intervention, researchers need to be able to measure

characteristics of the underwater environment through time or across space (Dornelas *et al.*, 2014; Edgar *et al.*, 2016; Cardinale *et al.*, 2018). In marine science, the ability to record change is notoriously difficult, as John Shepherd phrased it: '*Managing fisheries is hard: it's like managing a forest, in which the trees are invisible and keep moving around*'. The limitations on viewing organisms and physical features underwater has therefore forced researchers to use methods which are often more simplified than the terrestrial counterparts.

Traditional methods for the collection of biological monitoring parameters in coastal or shallow marine benthic environments have not changed drastically since surveys began, and primarily focus on either sediment grabs / dredges or rapid visual assessments of parameters such as percentage habitat cover or abundance, using variations on the application of transects or quadrats to sample them. Alongside these biological parameters, corresponding recordings of physical parameters (such as temperature or physical structure) are recorded, typically using analogue measures (Rogers *et al.*, 1994; English *et al.*, 1997; Davies *et al.*, 2001; Wilkinson *et al.*, 2003; Hill and Wilkinson, 2004; Bergman *et al.*, 2009; Wilson and Green, 2009). While such survey methods have proved relatively effective and useful for a number of applications, they tend to be limited in their scale, are often non-repeatable or qualitative, and can therefore also be prone to observer-bias (Edgar *et al.*, 2004; Wilson *et al.*, 2007a).

Rapid recent developments in technology (particularly the decrease in component size and increase in battery life), as well as the shifting of monitoring priorities (for instance toward a greater focus on assessment of ecosystem function), have led to marked changes in the way that the marine benthos is routinely monitored (Strong *et al.*, 2015; Danovaro *et al.*, 2016; Mumby, 2017). Furthermore, in recent years there has been a strong push to scale-up the

traditional range of assessment methods in order to more appropriately track changes and manage ecosystems in a world that is experiencing rapid large-scale disturbance (Tittensor *et al.*, 2014). This ‘scaling-up’ includes greater collaboration and up-take of consistent systematic global and regional assessments rather than various ad-hoc surveys, and includes the previously under-used concept of ‘citizen science’ (Silvertown, 2009; Cigliano *et al.*, 2015; Edgar *et al.*, 2016).

Crucially, modern methods also aim to apply better use of statistical and computing tools to ‘big data’, and ensure the use of reliable ecological indicators which can be incorporated into policy guidance and broad-scale threat mitigation (Edgar *et al.*, 2016; La Salle *et al.*, 2016).

### ***Remote sensing***

Perhaps the greatest jump in our ability to conduct effective marine monitoring has come through the development of ‘remote-sensing’ technology, which is increasingly becoming integral to ecosystem management and conservation both on land and in the sea (Mumby, 2000; Kachelriess *et al.*, 2014; Rose *et al.*, 2015; Hedley *et al.*, 2016). The term includes a range of techniques from both aircraft and satellite platforms, and broadly includes the use of laser (LiDAR), photo imagery, hyperspectral and multispectral radiometry, and radar (i.e. altimetric gravity) technologies to map large areas of the sea surface and floor (Mumby *et al.*, 2004; Goetz *et al.*, 2008; Strong and Elliott, 2017; Purkis, 2018). These methods can be applied to a host of different applications in benthic monitoring, including the semi- automated classification of habitat types (Saul and Purkis, 2015), the large-scale mapping of deep sea bathymetry (Sandwell *et al.*, 2014), or the estimation of shallow water habitat complexity (Zawada and Brock, 2009) to name just a few.

In order to measure across very large scales in high detail, remote sensing with bio-optical validation, is increasingly being used alongside traditional field measurements to enable more economical and effective large scale evaluation of water quality (Harvey *et al.*, 2015; Hedley *et al.*, 2016; Valente *et al.*, 2016). Coastal and marine pollution for instance comes in a range of forms, from both land and sea-based sources. Coastal pollution monitoring is therefore intrinsically linked to management and monitoring of terrestrial activities, and therefore requires monitoring not only of the marine systems, but of whole catchments (Bartley *et al.*, 2014; Fredston-Hermann *et al.*, 2016). In a similar vein, important ecological metrics such as productivity can also now be measured across a range of scales using remote optical /radiometry methods (Hochberg and Atkinson, 2008; Hedley *et al.*, 2016), allowing far more frequent and widespread assessment of these factors to take place.

Alongside environmental factors, the close monitoring of a range of socio-economic factors that interact with marine systems has been gradually recognised as being essential for effective ecosystem management (Cinner *et al.*, 2009; Allen *et al.*, 2011; Cumming and Allen, 2017; Gill *et al.*, 2017). These factors such as nearby population size, level of protection and compliance, tourism, level of fishery landings, access to markets etc., are all strongly linked to the present health of a system (Cinner *et al.*, 2016), and can fortunately now all be fairly easily recorded from remote sensed data (Hamel and Andréfouët, 2010; Kachelriess *et al.*, 2014; Rose *et al.*, 2015; Levin and Phinn, 2016). While factors such as accurate monitoring of fishing effort and landings is still notoriously difficult to accurately estimate, particularly in remote regions (Agnew *et al.*, 2009; Pauly and Zeller, 2016), the collaborative use of big data, alongside innovative use of a range of satellite data sources with machine learning is slowly

bridging that gap (Mills *et al.*, 2007; Arias and Pressey, 2016; De Souza *et al.*, 2016; Pauly and Zeller, 2016).

### *Acoustic - based methods*

The use of active sounding systems (Sonar) for the characterisation of seafloor bathymetry and topography, has been commonplace for the last three decades, primarily in the form of multibeam-echosounder, sidescan (single-beam) systems, or Acoustic Ground Discrimination Systems (Kenny *et al.*, 2003; White *et al.*, 2003). These technologies can measure the size of objects to the metre resolution level, along with their depth (bathymetry) and hardness through transmitting and receiving sound pulses, which are then re-interpreted into a digital scene (Brown and Blondel, 2009).

Sonar technologies have proven integral to broad-scale mapping and monitoring of marine ecosystems across the world (Brown *et al.*, 2011), and the subsequent integration of object-based image analysis techniques has made this mapping method both rapid and accurate (Lucieer, 2008). The downside to these particular methods is that they are limited to a fairly coarse resolution of roughly 1 metre or larger; they are often limited in their depth range (i.e. excluded from very shallow or very deep habitats); they require high levels of training to operate effectively, and most importantly; such systems are often prohibitively expensive for many organisations and researchers. This has led to the development of a number of more recent technologies (such as digital stereo-photogrammetry), which can record benthic topography at very high detail on a small scale, and which are typically far cheaper to deploy.

While 'active' acoustics have been extremely useful for characterising physical parameters, 'passive' acoustics techniques are very effective at describing a range of biological

parameters. As knowledge continues to increase on the role that 'bioacoustics' play in the ecology of marine ecosystems, monitoring methods have also evolved to accommodate this field (Montgomery & Radford 2017). Anthropogenic noise is a strong driver of both larval recruitment (Simpson, 2005) and survivorship (Simpson *et al.*, 2016) of reef fish, as well as contribute to behavioural change in a range of marine taxa (Williams *et al.*, 2015c). Subsequently, acoustic monitoring of soundscapes has begun to be incorporated into management and monitoring programmes due to its importance in driving ecological processes as well as for its facility as a proxy for biological health, even in remote locations. Measurable proxies include species occurrence, abundance and time-specific level of activity of a location (Lammers *et al.*, 2008; Munger *et al.*, 2012), or estimation of the level of human disturbance, for instance through engine noise and blast fishing monitoring (Woodman *et al.*, 2004; Gervaise *et al.*, 2007). Furthermore, physical data such as the noise generated from earthquakes, waves or rainfall can also be collected (Ryan *et al.*, 2016).

Similar techniques such as acoustic 'telemetry' can be used to assess the movement and interactions of many mobile species that interact with the benthos, even in deep waters (Hussey *et al.*, 2015). The knowledge of how organisms interact through space and time can be essential for effective management, and when used in conjunction with in-situ 'biologgers' (Rutz and Hays, 2009) this data can give a detailed picture of animals' behaviour, physiology, distribution and environment, and therefore gives a clearer view of an ecosystem's overall structure, function and health.

### ***Optics - based methods***

Despite the difficulties involved in collecting light-based imagery underwater (such as high pressures, corrosion risk, the need for specialist lighting etc.), in-situ optical methods have

always been a mainstay of environmental monitoring both on land and in the sea. However, while camera imagery has been possible underwater for over a century, it is primarily the last few decades (Figure 4), which have seen an explosion in technological developments enabling increasingly complex and novel optical techniques to be applied to marine monitoring assessments (Kocak *et al.*, 2008; Bicknell *et al.*, 2016).

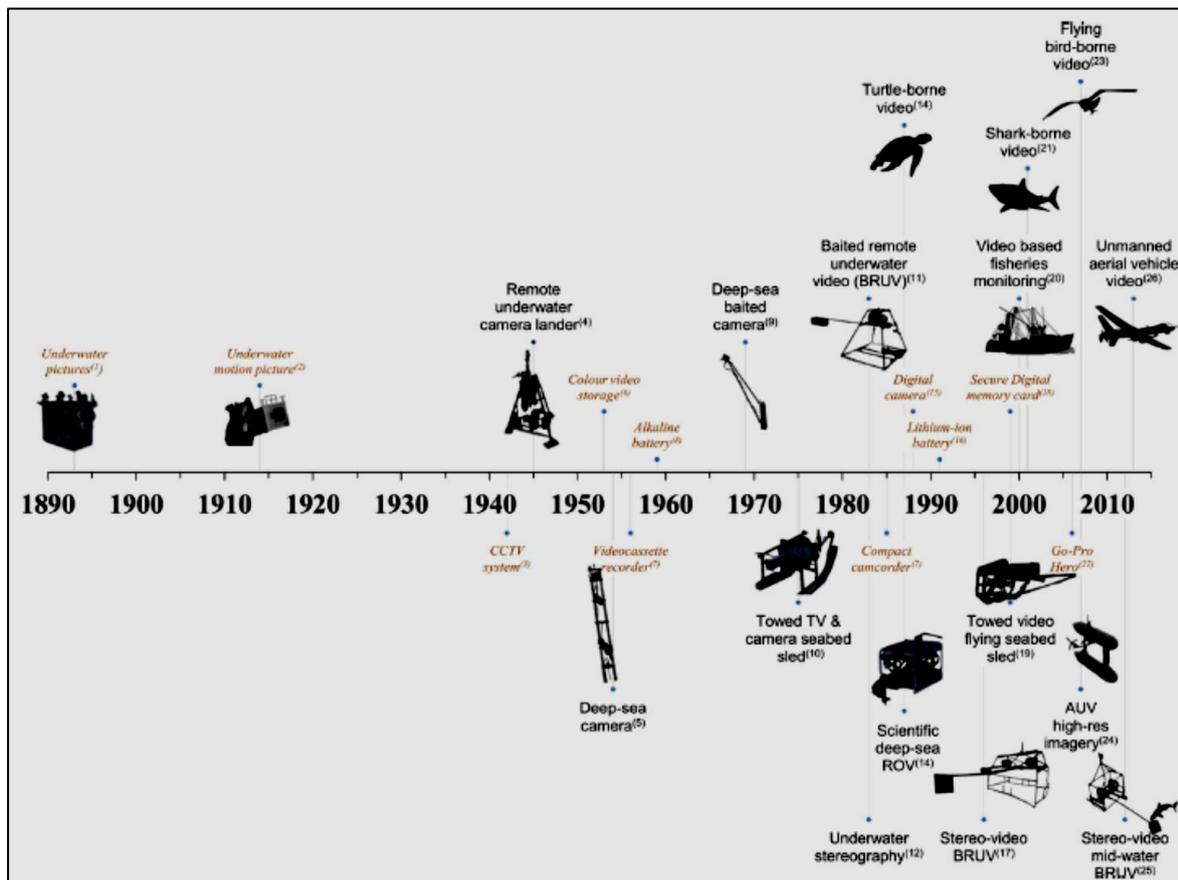


Figure 4. Timeline illustrating the development of camera imaging techniques used for monitoring of marine biodiversity. Sourced from Bicknell *et al.* (2016).

There are multiple benefits of optical techniques for monitoring benthic communities above methods such as grab sampling or acoustic techniques. Firstly they are largely non-destructive (Beisiegel *et al.*, 2017) allowing the community to be observed complete in its environment. Secondly, most optical techniques can be used remotely - be it on a towed

camera system (Jones *et al.*, 2009; Sheehan *et al.*, 2010) or whilst left stationary and in-situ for prolonged periods of time using baited cameras or time-lapse methods (Bailey *et al.*, 2007; Watson *et al.*, 2010). These remote in-situ techniques allow benthos and associated communities to be viewed at great depths and in a natural (undisturbed) setting. Thirdly, optical imaging can be used to observe changes in benthos across a range of scales in high resolution, from the microscopic scale using novel in situ microscopy (Mullen *et al.*, 2016) and hyperspectral imaging techniques (Chennu *et al.*, 2013), right up to the macroecological scale using manned or unmanned aerial based imaging to measure broad-scale health and abundance (Hughes *et al.*, 2017; Colefax *et al.*, 2018). Lidar has also become far more common, allowing benthic physical structure to be observed over large areas without ever entering the water (Brock and Purkis, 2009; Costa *et al.*, 2009; Zawada and Brock, 2009). The use of Automated Underwater Vehicles (AUVs) and Remote Operated Vehicles (ROVs) further enable the investigation of geological or biological formations on the seafloor in extreme / in accessible conditions (i.e. under polar ice sheets or around deep sea hydrothermal vents), or simply over great distances in high resolution (Wynn *et al.*, 2014).

Over recent years underwater camera technology has rapidly increased in terms of build-quality, resolution, and cost-effectiveness allowing even amateur divers and tourists to collect ultra-high definition imagery with ease. Alongside these developments, computer memory, processor speeds and battery life have also increased, allowing underwater imagery to be processed and analysed in far more complex ways than has been historically possible. In response to the large increase in quantity of high definition imagery from benthic monitoring, new approaches to analysis using 'machine learning' techniques have been developing fast to allow large quantities of data to be processed and annotated

efficiently with limited or even no human supervision (Kotta *et al.*, 2013; Steinberg *et al.*, 2015; Gauci *et al.*, 2016; Mahmood *et al.*, 2016; Manderson *et al.*, 2017; Matabos *et al.*, 2017). Such techniques have been shown to be highly accurate at classifying cover of broad substrate types as well as being able to identify coral genera (Marcos *et al.*, 2005; Beijbom *et al.*, 2015; Manderson *et al.*, 2017). Further improvements are also currently developing through the incorporation of novel imaging methods such as wide band fluorescence (Beijbom *et al.*, 2016) and hyperspectral imaging (Chennu *et al.*, 2017), allowing scientists soon to be able to rapidly characterise benthic community structures across ecologically relevant scales and time.

## **Structure from Motion stereo-photogrammetry**

The joint increases in computing power and camera resolution described above have allowed for a potential 'step-change' in benthic survey and monitoring through the application of 'Structure from Motion multiview stereo-photogrammetry', or 'SfM' (Turner *et al.*, 2012; Westoby *et al.*, 2012; McCarthy and Benjamin, 2014; Burns *et al.*, 2015). SfM allows the production of scaled, three dimensional, digital models from a series of overlapping images (Figure 5), whilst also automatically resolving the effects of underwater refraction.

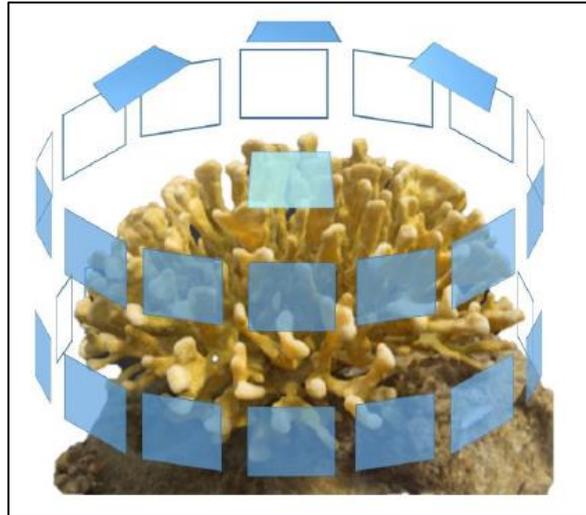


Figure 5. An illustration of how SfM reef models are created, using multiple overlapping images (blue squares) taken of the object of interest, creating a scaled model with ortho-rectified imagery re-draped over the surface.

These models allow scientists to examine a range of different properties of the benthic community, such as surface area, volume and structural complexity, as well as facilitate objective analysis of any changes in these metrics through time (Ferrari *et al.*, 2017). It further allows for accurate assessment of benthic composition, size-frequency structure, and spatial distribution of sessile individuals over ecologically meaningful scales, such as a reef-scape, through the creation of high definition ortho-rectified image mosaics (Edwards *et al.*, 2017).

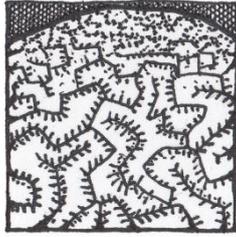
While stereo-photogrammetry technology has been used extensively in aerial survey and terrestrial cultural heritage for a number of years (Remondino and El-Hakim, 2006; Verhoeven, 2011; Doneus *et al.*, 2013), and is increasingly being employed to rapidly and cost-effectively assess difficult to reach marine areas and map island extent and canopy structure through the use of 'Unmanned Aerial Vehicle' (drone) SfM (Mlambo *et al.*, 2017; Joyce *et al.*, 2018), it is still relatively novel within an underwater survey setting. Nevertheless, underwater SfM is rapidly gaining popularity and has already been applied to

a variety of environments, using both diver-operated cameras and Remote Operated Vehicles, and from shallow coral reefs (Burns *et al.*, 2015) to hydrothermal vents (Teague *et al.*, 2017) and deep sea canyons (Robert *et al.*, 2017).

One of the prime drivers in the development of underwater photogrammetry has been the quantitative investigation of coral reefs, due to their ecological interest and societal value. Tropical coral reefs are thankfully well suited to photogrammetric analyses owing to their hard structures, preference for clear waters and general shallow depth range, allowing relatively easily accessible survey locations. The first notable example of the use of diver-based digital SfM to generate seafloor bathymetry and structural complexity came from Hu *et al.* (2012), who showed good agreement between in situ measurements and the digital model. Following this initial jump to marine systems, multiple studies have looked to develop the applications of this technology within shallow benthic settings and quantify the associated errors (Burns *et al.*, 2015; Figueira *et al.*, 2015; Lavy *et al.*, 2015; Burns *et al.*, 2016b; Ferrari *et al.*, 2016b; Bryson *et al.*, 2017; Ferrari *et al.*, 2017; González-Rivero *et al.*, 2017). Further studies have demonstrated the effectiveness and accessibility of such diver-based techniques using low cost hardware and software (Raoult *et al.*, 2016; Young *et al.*, 2017), showing that the technology can easily be implemented in existing monitoring programmes at a minimal cost.

In the following chapter I aim to look at underwater SfM in greater detail and investigate its use and application within the monitoring of tropical coral reef environments. I also aim to highlight a number of ways in which surface morphological data can be analysed in order to assess a range of structural characteristics of a reef, with the goal of facilitating greater insight into reef ecological processes and interactions.





## *Chapter 2: Capturing complexity - Quantifying structure in new ways*

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The manuscript presented in this chapter is submitted for publication as:

- *Bayley, D.T.I., Mogg, A., Koldewey, H. & Purvis, A. (2019). Capturing complexity: Field-testing the use of 'structure from motion' derived digital models to replicate standard measures of reef physical structure. PeerJ. 7:e6540.*

### **Abstract**

Reef structural complexity provides important refuge habitat for a range of marine organisms, and is a useful indicator of the health and resilience of reefs as a whole. Marine scientists have recently begun to use 'Structure from Motion' (SfM) photogrammetry to accurately and repeatably capture the 3D structure of physical objects underwater, including reefs. There has however been limited research on the comparability of this new method with existing analogue methods already used widely for measuring and monitoring 3D structure, such as 'tape and chain rugosity' and graded visual assessments. My findings show rugosity can be reliably converted over a standard 10-metre reef section (SfM rugosity =  $1.348 \times \text{chain rugosity} - 0.359$ ,  $r^2 = 0.82$ ; and Chain rugosity =  $0.606 \times \text{virtual rugosity} + 0.465$ ) for rugosity values up to 2.0, however SfM rugosity values above this become increasingly divergent from traditional tape and chain measurements. Additionally I found SfM rugosity correlates well with visual assessment grades over a 10 x 10 metre area (SfM rugosity =  $0.1461 \times \text{visual grade} + 1.117$ ;  $r^2 = 0.83$ ). The SfM method is shown to be affordable and non-destructive whilst also allowing the data collected to be archival, less biased by the observer, and broader in its scope of applications than standard methods. This work allows researchers to easily transition from analogue techniques to digital and improve the value of structural data collected for monitoring and assessment work.

## Introduction

The physical structure of coral reef habitats is a strong determinant of the abundance and diversity of many reef-associated organisms (Graham and Nash, 2013; Darling *et al.*, 2017). Morphologically complex coral structures also indicate a reef's current health and its likelihood of rebounding from disturbance events such as heat-induced bleaching (Alvarez-Filip *et al.*, 2009; Graham *et al.*, 2015). Changes to reef structure can be ecologically relevant at a range of scales according to the reef-associated organism's body size; therefore, even centimetre-level changes in habitat can be important to reef community structure on a local scale (Nash *et al.*, 2013).

Despite the importance of reef structural complexity and its incorporation into many standard reef-monitoring protocols (Bayley and Mogg, 2019), quantification and monitoring of structural changes through time has remained relatively simplistic. Typical monitoring budgets tend to be restrictive, so coarse visual or analogue methods that combine practicability with low cost – such as 'tape-and-chain rugosity' (Risk, 1972), broad qualitative visual estimation (Wilson *et al.*, 2007a) or depth measures (Dustan *et al.*, 2013) – are most commonly used. Structural assessments conducted using such methods tend, however, to be limited in scale due to SCUBA time restraints as they rely on researchers being in the water and are time-consuming to complete (Knudby and LeDrew, 2007; Harborne *et al.*, 2012).

Standard analogue techniques have proven useful for broadly describing reef structure for ecological analysis (Alvarez-Filip *et al.*, 2009; Graham and Nash, 2013; Graham *et al.*, 2015), but are criticised for being highly variable in their results due to recorder bias (Wilson *et al.*, 2007b), and for often giving high variability from even small changes in measure placement.

Furthermore, standard topographic measures such as ‘rugosity’ usually produce only one unbounded linear metric at a single coarse (centimetre) resolution, limiting the usefulness of such measures for describing complex differences in the physical form of individual underwater structures or reefs. The use of just one simplistic and poorly-repeatable metric is likely therefore to also limit our ability to relate reef structure to reef fish population sizes and community structure (Knudby and LeDrew, 2007; Nash *et al.*, 2013; Young *et al.*, 2017).

Recent advances in digital technologies and computing power are providing new, data-dense and quantitative virtual techniques to measure the 3D structure of objects underwater. The use of Lidar, Sonar, and satellite-based technologies to assess benthic structure and bathymetry is now commonplace (Brown *et al.*, 2011), and has revolutionised the measurement of benthic topography, revealing new patterns and interactions in spatial ecology (Brock and Purkis, 2009; Costa *et al.*, 2009; Purkis, 2018). However, such methods are extremely costly to deploy, require specialist training to operate and are restricted by water depth. Furthermore they can only detect features greater than roughly one metre in size (Kenny *et al.*, 2003; Costa *et al.*, 2009).

Land-based methodologies for accurate, cost-effective 3D measurement have been advancing rapidly and are now being adapted for use in aquatic environments. One such approach that has been gaining popularity is ‘Structure From Motion’ (SfM) photogrammetry (Westoby *et al.*, 2012), which creates scaled 3D digitally-derived surface model renderings of objects in fine detail from multiple overlapping photographic or video images and reference markers. The imagery needed for such models can be collected using a single standard underwater camera, with no need for an expensive rig. Once the virtual reef

surface has been created and calibrated using open-source or specialist software, detailed morphometric surface analyses can be undertaken on the object of interest.

Several studies have recently detailed the application of the SfM technique to underwater marine environments, showing the technique to be useful for quantifying structure across scales from colony to reef-scape (Burns *et al.*, 2015; Leon *et al.*, 2015; Ferrari *et al.*, 2016b; Teague and Scott, 2017; Young *et al.*, 2017). SfM has also been shown to be fast, accurate and repeatable (Burns *et al.*, 2015; Figueira *et al.*, 2015; Lavy *et al.*, 2015; Storlazzi *et al.*, 2016; Bryson *et al.*, 2017). However, there has been limited research into whether this new method of assessment can provide measurements that are directly transferable from current standard monitoring protocols, meaning it is not yet clear whether ongoing surveys can transition to this new technique without risking the loss of comparability with older survey data.

Here, I aim to empirically compare standard structural survey methods for coral reefs with SfM photogrammetry and to test whether the resulting data can be inter-calibrated. I do this by comparing the SfM technique to the two most widely used standard methods of structure assessment: 'tape and chain rugosity' and graded visual assessment. I use a much larger set of validation transects than existing method comparisons, increasing our certainty in the accuracy of this new method (Ferrari *et al.*, 2016b; Young *et al.*, 2017), and I do so over a range of reef morphology types, at the most widely applied scale of 10 metres, to allow specific limitations within typical habitats to be usefully highlighted. I finally discuss additional outputs possible through SfM and the technique's costs and benefits, in order to facilitate uptake of this new methodology. I argue that SfM increases versatility, repeatability, and archival value of reef benthic surveys.

## Materials and Methods

### *Data collection*

Surveys were carried out at six locations in the same reef complex within the Danajon Bank double barrier reef, north of Bohol, Philippines (10°10'56.7"N, 124°04'55.0"E). Surveys were conducted at depths of 5 to 8 metres in the daytime during November 2016, with horizontal visibility ranging from > 10 to 5 m.

Reef structure was recorded within varying visual grades of reef rugosity over a square 10 x 10 m (100 m<sup>2</sup>) reef area following the method described by Polunin & Roberts (1993), with grades ranging from 0 to 4, corresponding to: 0 = no vertical relief; 1 = low and sparse relief; 2 = low but widespread relief; 3 = moderately complex; 4 = very complex with numerous caves and fissures. For each survey area the dominant broad substrate type (i.e. > 40 % cover of sand / rubble / hard coral growth form / soft coral / algae) was also recorded visually (English *et al.*, 1997).

Inside each 100 m<sup>2</sup> area, Rugosity Index (RI) was calculated for 8 – 10 parallel transects using the widely-used 'tape and chain' method (English *et al.*, 1997). A 10-metre brass chain with 1-cm links was moulded to the hard substratum in order to measure the topographic (surface) distance. The direct horizontal distance between the start and end of the chain was then recorded, giving linear distance (Figure 6). Rugosity Index (RI) is then calculated as *Surface distance (SD) / linear distance (LD)*

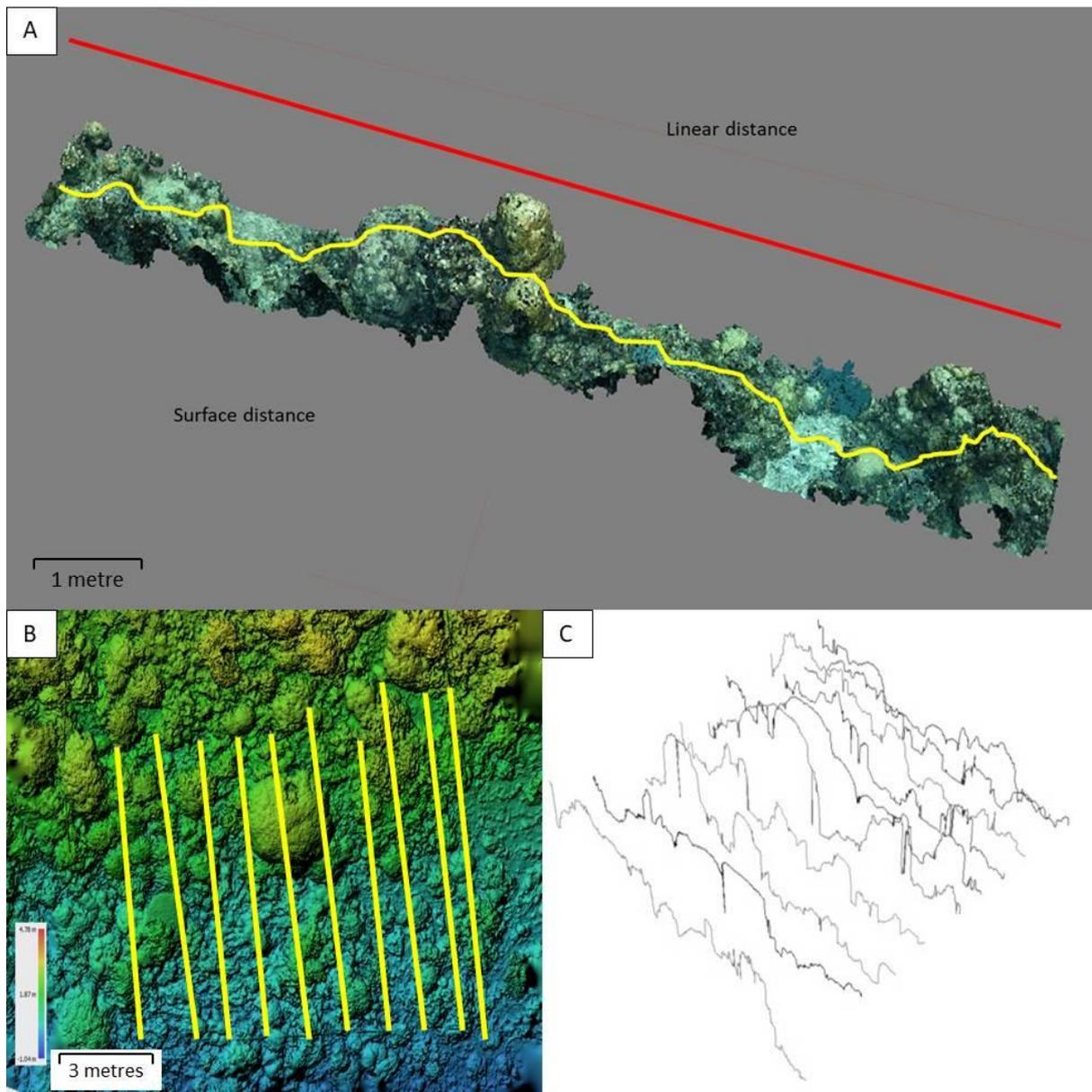


Figure 6. A) Visualisation of linear and surface distance measurements across a typical 10 x 1 metre cross-section of reef; B) A DEM of a medium rugosity mixed growth form Philippine reef, illustrating the layout of a ~100 m<sup>2</sup> benthic quadrat (scale and depth shown); and C) Ten digital rugosity transects, each with a 10 m Surface length.

After each chain was laid, a weighted reflective marker of known dimensions (147 x 50 mm) was placed at the start and end of the chain and left in place while the chains were removed. This process resulted in a set of 20 fixed start and end markers in each quadrat, indicating LD for each transect (Figure 6).

Following the in situ RI measurement, each whole quadrat was imaged across its full area in a lawnmower pattern from a distance of ~2 metres above the substrate (dependent on visibility), following Burns *et al.* (2015), to collect multiple overlapping images of the reef, using a Nikon D750 DSLR camera with a wide-angle fixed 20 mm Nikor lens and dome port. The same camera was used for all imaging, to capture high detail (6016 x 4016 px) images to prevent any potential variation between resulting models from differing camera or lens types (Lavy et al. 2015). The footprint of a typical photo in this study was approximately 2.5 m x 1.75 m, (though this area can increase and decrease as the camera orientation shifts). Linear overlap of each photograph's footprint varied in line with substrate complexity, but ranged from 75 % to 95 % across this study. Sidelap (lateral overlap) ranged from 75%, up to 90%. Overlaps were calculated post hoc by placing markers in the middle of images and measuring the linear and lateral distances between image sets.

Once images were collected, a digital surface model (DSM) of the area photographed was created using Agisoft Photoscan Professional software (Agisoft LLC, 2017). Each ~100m<sup>2</sup> model was based on the alignment of approximately 600 – 1000 overlapping digital photographs, dependent upon light levels and structure of the benthic topography (alignment settings = High accuracy, generic pre-selection of images, 40,000 key-point limit, 10,000 tie-point limit). This process typically gave a dense XYZ point-cloud of around 4,000 matched points per m<sup>2</sup>. The dense point-cloud was then converted into a Delaunay Triangulated Irregular Network (TIN) wireframe mesh, with high accuracy alignment, aggressive depth filtering and standard interpolation settings applied. Finally, using tiled imagery overlaid onto the filled reef mesh, ten of the in-situ reflective markers' lengths were used to calibrate each model to these known distances (147 mm) in xyz space, giving overall

averaged scaling accuracies of < 5 mm (Figure 7). Approximate depth (Z dimension) of the first marker in each quadrat was measured using a Suunto Gekko dive computer, and the models were orientated to a level XY plane using an in-situ spirit-level.

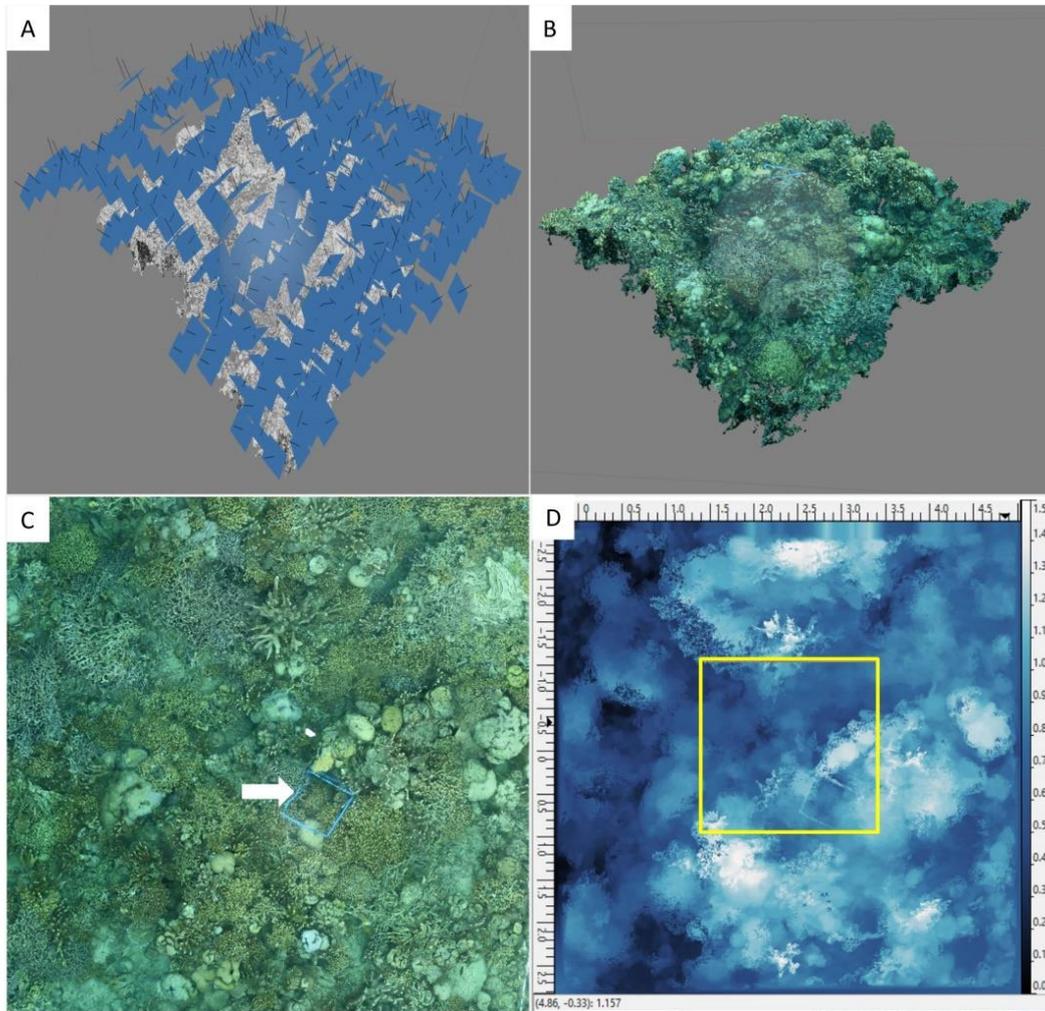


Figure 7. Typical SfM process and 3D outputs from a site in Batasan, Philippines, illustrating (A) the initial dense point-cloud, with individual camera locations shown; (B) TIN mesh with draped colour imagery; (C) a high definition ortho-rectified image mosaic of a 5 x 5 metre reef area, with in-situ blue quadrat (0.5 x 0.5 m) shown centre with white arrow; and (D) a calibrated XYZ point-cloud with a virtual 2 x 2 metre quadrat illustrated in the centre.

The xyz pointclouds of each rendered reefscape were exported from Photoscan and analysed for Rugosity Index metrics within Gwyddion software (Nečas and Klapetek, 2012),

using the surface roughness analysis tool, following rasterization (1 cm pixel resolution, with averaged linear point interpolation, with mirrored exterior), and surface distance measurement with zero cut-off. Surface points were averaged across 10 pixels to account for any fine-scale deviation of the in situ chain from the perfectly straight virtual transect line used in the analysis(Figure 8).

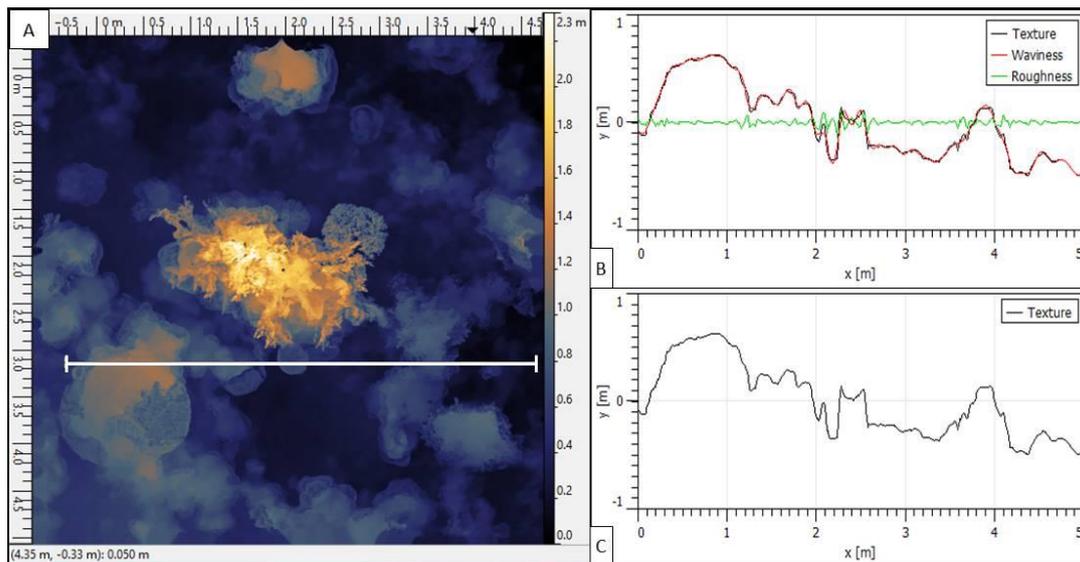


Figure 8. A 25 m<sup>2</sup> reef area displayed within 'Gwyddion' software, with A) XYZ pointcloud shown in false colour, with a white 5 m 'virtual transect' length selected; B) 'Roughness', 'waviness' (at 0.2 m sampling frequency cut-off) and 'texture' of the virtual transect surface; and C) Overall texture of the transect – equivalent to rugosity 'surface distance' at 1 cm resolution.

### *Data Analysis*

Linear regression was used to relate the matched linear distances and RI values (n=58) from in situ and virtual transects. If both methods give very similar RI estimates, the regression between them is expected to have an intercept of 0 and a slope of 1; Student's t-tests were used to assess whether the data fitted this expectation. I also used linear regression to relate the in situ and virtual measures of RI to visual reef estimation techniques (Polunin and Roberts, 1993) on a five point scale (0-4). Analysis of covariance was used to test whether the

relationships between virtual and in situ RI varied among dominant substrate types. I explored log-transformation of RI estimates because, by inspection, variances were higher at higher values of RI; but transformation did not fully remedy this and made very little difference to goodness-of-fit, so I report the results from the untransformed data. All analyses were carried out using the `lm` function in R, version 3.4.1 (R Core Team, 2016).

## Results

### *Tape & Chain method*

In situ (chain-measured) and virtual (SfM-derived) values of linear distance were practically identical ( $R^2 = 0.9994$ , mean difference = 0.002, SD = 0.02 m; all mean differences are reported as virtual - in situ measurement), as expected. Comparison of surface distance between the same points for the in situ chain-measured distance of 10 metres and the virtually measured distance gave good agreement within simple substrates i.e. rubble fields (Mean difference = 0.01, SD= 0.29 m), foliose dominated reefs (Mean difference = 0.17, SD= 0.44 m), and mixed table / massive corals on sand (Mean difference = 0.12, SD= 0.33 m). There was, however, less agreement between the methods within more complex habitats, with higher variance and with virtual distances tending to be larger than in situ measurements (Figure 9) i.e. dense branching *Acropora* thickets (Mean difference = 1.41, SD= 0.74 m), and mixed corymbose and massive growth form communities (Mean difference = 1.39, SD= 0.59 m).

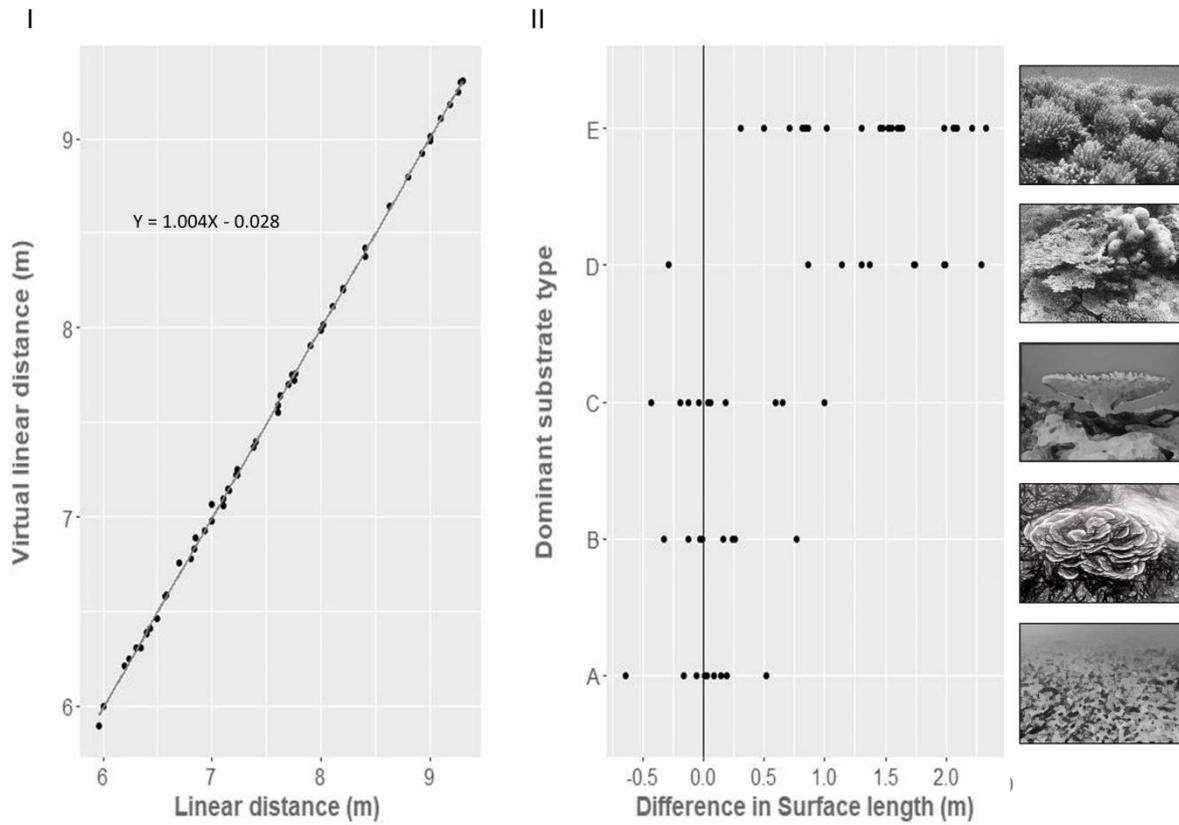


Figure 9. Showing I) in-situ tape measured linear horizontal distance against virtually measured linear horizontal distance, and II) the difference between in-situ chain measured surface distance (10 m) and virtually measured surface distance, within five broad substrate types (A= Flattened rubble, B= Foliose growth forms, C= Table and massive growth forms on sand, D= Sparse branching and massive growth forms, E= Dense branching and massive growth forms).

Virtual RI was well-predicted by in situ SfM RI in the regression ( $R^2 = 0.82$ ; Figure 10).

However, the intercept differed significantly from zero (estimate = -0.359,  $t = -3.095$ , 56 d.f.,  $p = 0.003$ ) and the slope differed significantly from 1 (estimate = 1.348,  $t = 15.78$ , 56 d.f.,  $p < 0.001$ ), because values for virtual RI gradually become greater for every corresponding value of in-situ RI as surfaces become more complex. The regression equations for converting between in situ and virtual estimates of RI are:

$$\text{Virtual RI} = 1.348 \times (\text{in situ chain RI}) - 0.359$$

$$\text{In situ chain RI} = 0.606 \times (\text{virtual RI}) + 0.465$$

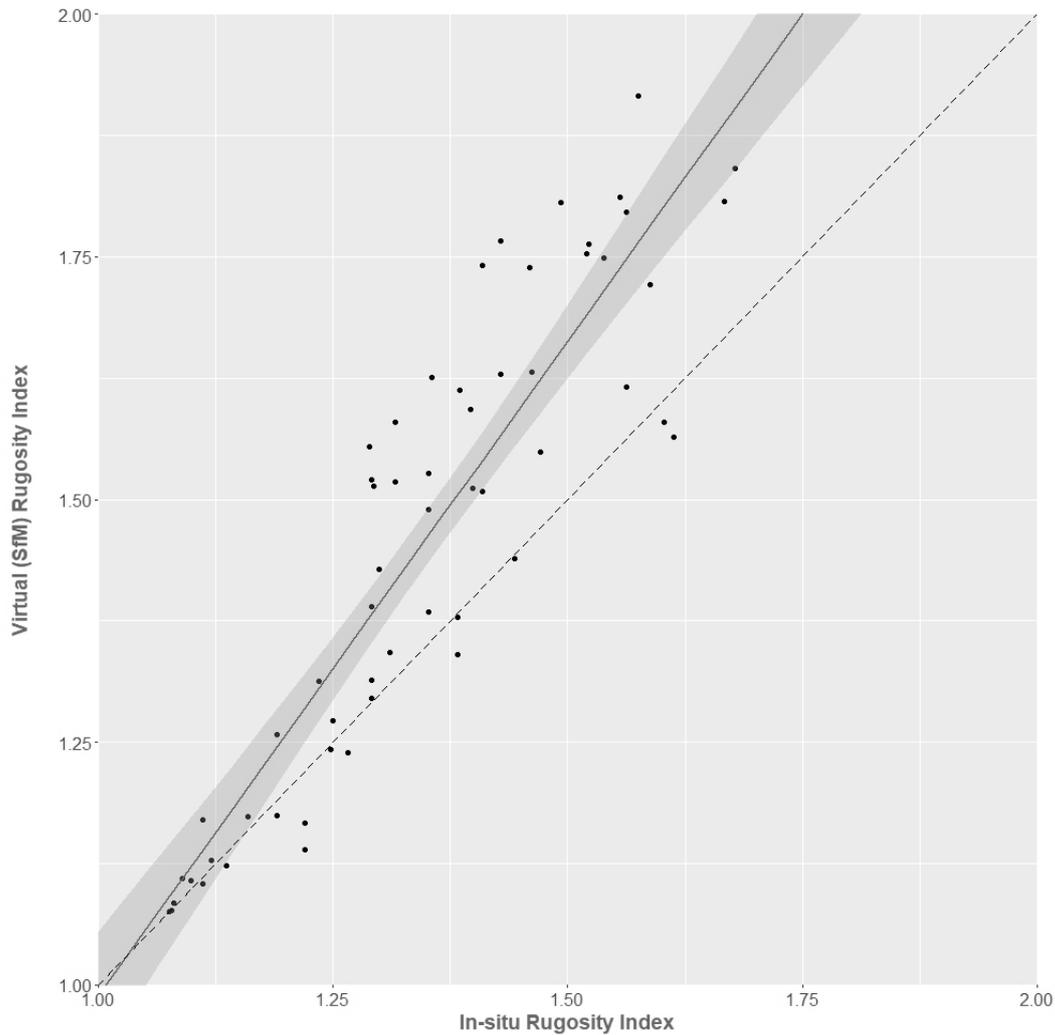


Figure 10. In situ chain-measured Rugosity Index against virtually-measured Rugosity Index, showing the linear relationship between the measures (95% Confidence Intervals). A dashed reference line (slope=1, intercept=0) is shown for reference.

Inclusion of dominant substrate type as a factor increased the predictive ability of the regression (ANCOVA;  $F_{6,51} = 104.6$ ,  $p < 0.001$ ,  $R^2 = 0.92$ ), demonstrating that the level of substrate complexity affects the accuracy of the RI comparisons.

### *Visual estimation method*

In situ and SfM-based methods both fit broadly to the visual assessment method proposed by Polunin & Roberts (1993) (Figure 11). However, the fit was markedly better for the virtual method ( $R^2 = 83.1\%$ ,  $F_{1,56} = 274.7$ ,  $p < 0.0001$ ) than for the in-situ chain method ( $R^2 = 66.3\%$ ,  $F_{1,56} = 110.4$ ,  $p < 0.0001$ ). The regression equations for converting between virtual or in-situ estimates of RI and visual estimates are:

$$\text{Virtual Rugosity Index} = 0.1461 \times \text{visual grade} + 1.117$$

$$\text{In-situ Rugosity Index} = 0.087 \times \text{visual grade} + 1.144$$

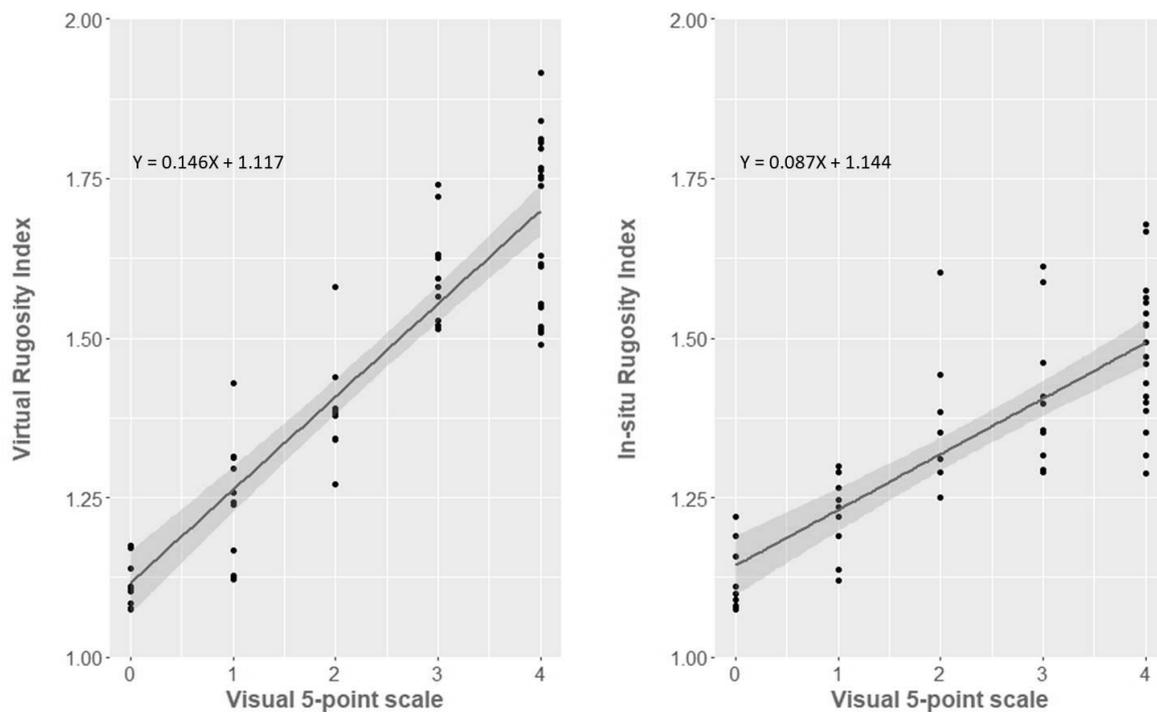


Figure 11. Comparison between (Polunin & Roberts, 1993) visual method of 'rugosity' assessment and the 'tape and chain' / SfM methods. 95% Confidence Intervals shown.

## Discussion

### *Rugosity assessment*

Surface distances, and hence estimates of Rugosity Index (RI), produced by Structure from Motion (SfM) photogrammetry over coral reefs correlated strongly with those from in-situ tape and chain measurement, but SfM values were larger and more variable than tape and chain estimates in more structurally complex reefscapes. There are three likely reasons for the disparity in estimates of surface distance (and therefore RI). Firstly, the models created through SfM become increasingly likely to produce areas of misaligned points as the complexity of the surface of interest increases, even with aggressive filtering of anomalous points from the dense point-cloud. These misaligned points lead to the need for greater post-processing cleaning for highly complex objects, or an expectation of some limited complexity overestimation.

The second reason for increased complexity values from the SfM derived method is because soft organisms, such as soft corals, extended polyp tentacles of hard coral, algae, worm feeding appendages and crinoids, all have structure which would not be recorded by the tape and chain method (Ferrari, 2017), but they will be recorded by SfM as long as these organisms are stationary during imaging. Relatively still water conditions are therefore needed for accurate assessment of soft structures such as these.

Finally, it is likely that the virtual surface created through SfM more accurately reflects the real structural complexity than in situ methods because an in-situ chain will typically fall off of finely branching structures and tend towards the lowest stable points of the reef through gravity.

This makes measurement of slender, overhanging or highly complex objects difficult and likely to be under-estimated in terms of their rugosity, even if additional time is spent moulding the chain to complex / overhanging surfaces. The SfM technique shares this limitation of typically not being able to fully capture overhanging surfaces, however incorporating an increased numbers of oblique angle or upward facing photos where possible (with appropriate lighting) will minimize this limitation and can allow vertical structures to fully overhanging cave systems to be imaged using SfM (Hernández *et al.*, 2016; Robert *et al.*, 2017; De Waele *et al.*, 2018).

One shared limitation between the tape and chain and SfM methods for measurement of RI is an inability to fully assess structures such as densely branching growth forms and tightly packed overhanging structures such as terraced table corals. While SfM can capture more of this structure through oblique angled photography and good lighting, it is still limited by what can be seen, so obscured areas within a coral matrix for instance will still not be quantified (Lavy *et al.*, 2015). Likewise, good underwater visual conditions are essential for adequate model creation as turbid, low light environments will produce lower quality outputs (Bryson *et al.*, 2017).

### ***Visual complexity assessment***

In a similar fashion to the comparison with tape and chain rugosity, SfM Rugosity Index correlated very well to visual estimates of structural complexity. The SfM method furthermore improves our ability to compare visual complexity to Rugosity Index values, with the visual estimates of structural complexity explaining 23% more of the variance from correlation to virtual (SfM) RI than from correlation to the in situ (tape and chain) RI. This indicates that SfM better matches how the eye naturally assesses complexity of structures.

The reduced coefficient of determination using the chain method was primarily driven by the lack of differentiation in rugosity indices within higher complexity sites (2 – 4 on the visual scale) and the wider variance of rugosity values at each grade. While no other studies that I know of directly compare SfM Rugosity Index to visual assessments of structure, my results do match well with the study by Wilson, Graham & Polunin (2007), which found visual estimates of reef topography were significantly correlated with tape and chain estimated rugosity.

This analysis furthermore illustrates the pitfalls of taking single measures of Rugosity Index, as relatively high variance of RI values are observed at each visual grade for both in situ and virtual techniques. This shows the need for multiple replicates of linear RI to be taken at each site whichever method is applied, in order to give a reliable approximation of overall structure.

### *Costs, benefits & limitations*

The concept of 'photogrammetry' has been around as long as photography, but it is only within roughly the last five years that we have reached a point where advances in both digital camera technology and digital processing power have made the SfM technique economically viable and time-effective. The development of fast digital photogrammetry algorithms and the now widespread use of low-cost underwater action cameras such as GoPro™ opens up a plethora of opportunities in the marine world for recreating virtual benthic formations such as reefs, and enables us to analyse them in an efficient, objective and cost-effective way. These measures allow us to move from the simplistic chain or visual methods to objective and quantitative morphometric analyses of volume, surfaces, traits, and spatial distribution of individual colonies, which can be analysed at the scale of interest

to the study. Work has indeed already begun to scale-up this method and integrate the use of this technology with drones to allow much greater area coverage with reduced risks and costs (Chirayath and Earle, 2016), which is likely to revolutionise shallow reef monitoring work.

Table 1 details the costs and benefits of each method discussed in this work, in terms of field and processing time, scope of analyses possible, and reproducibility of the analyses. The comparisons are not comprehensive but give a broad view of the most widely used methods contrasted against Structure from Motion using single or cluster-based processing. In this sense, a ‘cluster’ is a network of two or more computers acting as linked servers (nodes), essentially allowing greater processing power by combining the resources of each computer.

Table 1. Cost-benefits of four reef structure assessment techniques for analysing an area of ~100 m<sup>2</sup> (using Structure from Motion (SfM) or visual techniques), or for ten (10 m) in situ transects using the ‘tape and chain’ rugosity technique. SfM processing time based on ~ 400 images within Agisoft Photoscan run with a 32GB RAM, Intel Core i7 processor, and NVIDIA GeForce GTX 960 graphical processor. The cluster used three nodes, each with the above specifications.

Technique	Field time	Processing time	Repeatable	Other analyses possible?	Remote assessment possible?
Tape and chain	< 1hr	None	No	No	No
Visual	< 5 mins	None	No	No	Yes
SfM	< 1hr	~ 1 day	Yes	Yes	Yes
SfM – cluster computing	< 1hr	< 1hr	Yes	Yes	Yes

Whilst the time costs of initial data collection are comparable for each methodology, the initial processing time of SfM is the primary limiting factor currently, and is explicitly dependent upon the computer processing power available to the researcher. As processing

time is reduced, through cluster-based processing, (or through likely future accelerated processing speeds as computing power advances), the range of added benefits from the SfM method become apparent.

Agisoft Photoscan is the software currently most commonly used for this type of 3D model generation of reefs, due to its easy interface, range of capabilities, relative low cost, and facility to integrate with workstreams such as Python. However, there are a range of other brands available such as Pix4D, Bundler and Autodesk, with differing specialities but broadly similar capabilities. Post processing measurements can also be completed with a number of different software packages, dependent on the specified objective. Some frequently used packages are ArcGIS '3D analyst', Rhino, and the open-sourced Meshlab and R. I chose to use Gwyddion due to its versatility of functions, easy interface and because it is also open-source with good documentation. While Gwyddion was originally designed for electron microscope surface metrology, the techniques needed to analyse a reef surface are nevertheless the same.

There are of course still limitations to the SfM technique within a marine setting. For effective models to be created, the images collected need to be clear and sharp, and this can be a challenge in low-light / turbid / high energy environments. Steady camera work with adequate water clarity and good lighting is therefore essential. One of the benefits of SfM however is its ability to generate image mosaics far larger than those captured by an individual image. This means that, whilst it is possible to model objects of great size, it is also possible to model objects in very poor visibility, given sufficient image overlap. The relationship between the distance of the camera from the object and the resulting photographic footprint is a linear one, meaning that the footprint will be twice the size at

twice the distance. In turn, this means that a survey conducted in poor conditions (e.g. 0.5 m effective visibility) will require 4 times the number of images to cover just the same photographic width as a single image from a survey conducted at 2 m effective visibility. This resulting increase in photographic number has a knock-on effect on the computing power and resources need to model a single area, possibly rendering such an effort impractical in poor conditions with current general/mid-level computing systems. Conversely in good visibility conditions, the photographer must make a decision between coverage and detail, as image resolution will be lost the further the camera moves from the substrate (Hitchin *et al.*, 2015).

Linked with the issue of adequate visibility is the need to bear in mind obscurement of objects, particularly in dense coral thickets, or from overlapping table growth forms (Goatley and Bellwood, 2011; Figueira *et al.*, 2015). I was able to minimise the error associated with such habitats in this study by increasing the number of images taken in more complex habitats, by incorporating oblique angle photos (whilst ensuring to minimize large blue-water sections in the images), and by maintaining good lighting (Burns *et al.*, 2015; Hitchin *et al.*, 2015; Pizarro *et al.*, 2017). Despite these considerations, some sections of reef, such as areas of dense coral matrix and highly branching variable height sections where oblique images are restricted, will always have some level of obscurement that will introduce gaps to the model. While these gaps are interpolated in the model building process, they will be of course only be statistical estimations and this uncertainty must be considered and minimised whenever using this technique.

Following on from these stated limitations, this study investigates tropical coral reef habitats only, and not rocky or temperate biogenic reefs. While it is unlikely that any significant

differences in the conversion between in situ and virtual measures of structure will occur in these differing habitats given the technique's accuracy (Figueira *et al.*, 2015; Bryson *et al.*, 2017; Raoult *et al.*, 2017), this has not been explicitly tested here. I would therefore recommend future research across these different habitats and conditions, including further investigations into the effects of scale (i.e. colony to reefscape), and fractal dimension / resolution of measurement.

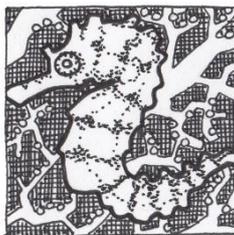
Despite these current limitations, my study demonstrates that the SfM technique can be used to easily transition from analogue to digital structural assessment, allowing continued long-term coral reef structure monitoring. Furthermore, the increased range of analyses available from the creation of virtual reefscales is likely to lead to a clearer understanding of the ecological processes related to reef physical structure.

## **Conclusions**

The SfM technique shows great promise for future survey efforts due to its ease of use across multiple depths, scales, and reef types as well as its non-destructive nature. The outputs from a single survey can be used in a number of different analyses, for instance digital transects can easily be applied to currently laborious field methodologies such as estimation of carbonate budgets (Perry *et al.*, 2012), increasing the speed, scale and accuracy of assessments. Additionally, the ability to measure not just hard corals but other often neglected aspects of the reef which provide important structure, such as soft corals or macro-algae, may help give insight into associated community dynamics.

Perhaps most importantly however, the SfM method is quantitative, less biased by the recorder, and is replicable. The technique therefore allows detailed spatially explicit observation of community change through time rather than typical purely qualitative descriptions (Ferrari *et al.*, 2016a). Our ability to visualise and store the reef models will therefore allow verifiable and archival observations, an ability increasingly sought after within the concept of reproducible science (Munafò *et al.*, 2017).





## *Chapter 3: Evaluating the efficacy of small-scale MPAs: A case study applying emerging monitoring technology*

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### **Abstract**

Marine Protected Areas (MPAs) are widely used as a management tool to conserve species and ecosystems at risk from human impact. Coastal managers often focus MPA designation on biogenic reef environments due to their ecosystem service value and sensitivity to damage. However, difficulties in enforcement and a lack of capacity to adequately monitor MPAs often make it hard for managers to assess the effectiveness of MPAs, particularly in under-resourced, low-income countries, leaving these reefs at high risk of degradation.

In this chapter I analyse reef community data collected at three long-term managed reserves within the heavily populated Western Visayas region of the central Philippines in order to assess the state of reef and fish community structure inside and outside of small-scale locally managed MPAs. I show that community-run MPAs can be effective even when small (10-20 ha). Mean fish biomass, fish diversity, richness, and size were all significantly increased within present-day protected sites. No significant structural differences were observed inside and outside of MPA areas, however average reef rugosity, height, and roughness were significantly higher in unfished reefs compared to blast-fished reefs. Reef substrate complexity, composition, and level of management, were further shown to structure fish community assemblages, with the link between reef structure and fish richness/abundance disrupted outside of MPAs. SfM photogrammetry allowed a greater range of quantitative reef morpho-metrics to be assessed than traditional survey methods, and can additionally be archived, increasing reproducibility and data value for managers wishing to monitor and quantify reef health through time.

## Introduction

In response to rapid anthropogenic changes in global levels of land-based pollution, over-extraction of resources, and changing environmental conditions (Halpern *et al.*, 2015; Maxwell *et al.*, 2016), marine protected areas (MPAs) are increasingly being used as a management mechanism to conserve individual species or entire systems at risk (Pimm *et al.*, 2001; Lester *et al.*, 2009; Roberts *et al.*, 2017). Globally agreed targets now aim for at least 10% of the oceans to be protected through well-enforced MPAs by 2020 (Thomas *et al.*, 2014), and still more may be needed for effective protection (Sciberras *et al.*, 2013; O'Leary *et al.*, 2016). MPAs are commonly used by tropical coastal managers to protect coral reefs from disturbances such as fishing (McClanahan *et al.*, 2006; Tamayo *et al.*, 2018) in order to preserve the ecosystem services that reefs provide through food and tourism and maintain this important habitat's associated species (Paulay, 1997; Cole *et al.*, 2008).

MPAs can be highly effective in reef environments if designed and managed correctly (Lester *et al.*, 2009; Roberts *et al.*, 2017); however, there are still frequent disagreements over the extent of MPAs' socio-economic benefits, their optimal size, number and location (Kaiser, 2005; Edgar *et al.*, 2014; Singleton and Roberts, 2014; Hargreaves-Allen *et al.*, 2017), and even whether apparent biotic benefits arise from changed animal behaviour rather than true diversity change (Langebrake *et al.*, 2012; Januchowski-Hartley *et al.*, 2015). Alongside these concerns, uncertainty remains over the timescales over which managers can see tangible results and the best ways in which to objectively measure and record change (McClanahan *et al.*, 2006; Hudson *et al.*, 2014; Mouillot *et al.*, 2016). Discussions commonly focus on whether a more integrated 'holistic' approach to management is needed, and whether management is currently enforced sufficiently to prevent these areas simply being

'paper parks', existing only on maps (Mora *et al.*, 2006; Riegl *et al.*, 2009; Agardy *et al.*, 2011; Gill *et al.*, 2017). Underlying many of these discussions is the frequent inability of managers to quantitatively capture objective measures of a reef's current or historic state, particularly in low-income countries whose limited resources and high dependence on reef services therefore place their reefs at high risk of degradation (Marinesque *et al.*, 2012; Gill *et al.*, 2017).

I present a case study comparing surveys of reef structure and fish communities inside and outside a set of small, locally managed MPAs within the Visayas region of the central Philippines. In this region in the heart of the 'Coral triangle', reefs are an essential component to local people's livelihoods, but are also subject to a range of chronic and acute pressures, in the form of overfishing, destructive fishing techniques such as 'blast fishing', and earthquake / storm damage (Samoilys *et al.*, 2007; Magdaong *et al.*, 2014; Selgrath *et al.*, 2017). Blast fishing in particular is known to be extremely damaging to coral reefs and leads to long-term effects on benthic community dynamics (Fox and Caldwell, 2006). Despite the practice being both dangerous and illegal, the short-term economic gains have led to its use being widespread in the Philippines since the 1930s, resulting in extensive damage to the benthos and fisheries in this region (Alcala and Russ, 2002).

The resilience of reefs to degradation and community phase shifts following disturbance is bolstered by a number of key ecosystem attributes, which include structural complexity, depth, high densities of both juvenile corals and herbivorous fishes, and low nutrient loads (Graham *et al.*, 2015). High structural complexity in particular seems to be integral to a number of ecological functions and services (Graham and Nash, 2013; Perry *et al.*, 2018): complex reefs provide food and habitat for many species, resulting in higher fish density

and biomass (Graham and Nash, 2013), shape fish community structure (Darling *et al.*, 2017), and influence predator-prey behavioural dynamics (González-Rivero *et al.*, 2017).

While the physical 3D complexity of a reef is often highlighted as being important to its functioning, it is typically either measured inadequately (due to time and technology constraints) or even overlooked in health assessments. Linear surface 'rugosity' (*sensu* Luckhurst and Luckhurst 1978) is the most commonly used measurement, but is inherently sensitive to subjective choices of placement, is non-repeatable, and can be highly variable in the scale of assessment, replication and accuracy. Other more qualitative visual assessments (reviewed in Wilson *et al.*, 2007) avoid some of these problems but are still subjective and often cannot be directly re-assessed or validated for that point in time as they are conducted *in situ*.

Recent advances in technology and computing power have allowed the development of new techniques for more detailed and objective recording of reef morphometrics (Bayley and Mogg, 2019). 'Structure from Motion' stereo-photogrammetry (SfM) – allows detailed scaled 3D digital models of the reef to be created over large areas (from above or below water), using multiple overlapping imagery (Westoby *et al.*, 2012; Burns *et al.*, 2015). This technique has been shown to be both accurate and repeatable at a range of scales underwater and is therefore rapidly gaining popularity as a reef survey tool (Figueira *et al.*, 2015; Lavy *et al.*, 2015; Ferrari *et al.*, 2016b; Gutierrez-Heredia *et al.*, 2016; Bryson *et al.*, 2017; Raoult *et al.*, 2017; House *et al.*, 2018). Alongside the utility to create 3D models, SfM further allows users to create large-scale ortho-rectified photo-mosaics in high definition, enabling both spatial and compositional analysis of coral communities (Edwards *et al.*, 2017).

Here I aim to combine SfM with standard benthic and demersal fish monitoring surveys in order to document the current state of the coral reef and reef-associated fish within the three Philippine case study sites. I furthermore test whether local management has resulted in benthic and fish community difference inside and outside of these MPAs. Finally, I use this localised case study to explore how the emerging SfM method can usefully be applied to measure the effects of disturbance and management on reefs more generally, and how it might best be integrated into existing monitoring programmes similar to here within the Philippines.

## **Materials and Methods**

### *Location*

Surveys were carried out in November 2016 at four locations along the western extent of the Danajon Bank reef system, north of Bohol, Philippines (Figure 1). The double barrier reef system covers a total area of 271.7 km<sup>2</sup> and encompasses three major provinces of the Philippines (Cebu, Bohol and Leyte). Reefs were assessed inside and outside of three community-managed MPAs (Batasan, Bilang-bilangan and Pandanon) and at an unmanaged control site within the same inner barrier reef flat system (Canlangi).

### *Level of impact /compliance*

The sites range in their age and size, but are all small in area (~16 - 33 ha). MPA distances to the shore of Bohol are between 6 and 9 km and general reef conditions are comparable across sites. Major reef pressures from blast fishing and recent (2013) earthquake damage

varied from low to high across the three MPA sites, although all have high community engagement and have been locally managed for close to two decades (Table 2).

Table 2. Characteristics of the three Marine Protected Areas (MPAs) along the Danajon Bank reef system, including measures of management and compliance based on (Alcala *et al.*, 2008; Yasué *et al.*, 2012). The Coastal Conservation & Education Foundation (CCEF) management scoring system ranges from 0 (lowest) to 40 (highest). \*Refer to (White *et al.*, 2006) for further details of score calculation and grading.

MPA name	Year est.	Total size (ha)	CCEF score (0-40)*	CCEF description*	Blasting	Earthquake
<b>Bilang - Bilangan</b>	1999	15.5	39	'Enforced' and good management	None	No
<b>Batasan</b>	1999	21	38	'Institutionalized' and excellent management	Low	Yes
<b>Pandanon</b>	2002	33.1	34	'Enforced' and good management	High	No

In 2011, the Philippines changed their system for rating the effectiveness of MPAs to the 'Management Effectiveness Assessment Tool' (MEAT), and in 2015 all three sites scored 49-50 (of a maximum 84 points), inferring 'very good management' (Cabral *et al.*, 2014); however, the previous Coastal Conservation & Education Foundation (CCEF) system was used in this study for consistency over a longer period of assessment. CCEF scores can range in value from 0 to 40 (based on periodic assessments of enforcement, monitoring, local community participation, planning and economic viability of the MPA (White *et al.*, 2006).

Unprotected areas across the region are subject to fishing pressure from multiple gear types (including 'blast fishing; fish corrals; gleaning; hook-and-line; nets; poison fishing; skin diving; and traps'), which target a mixed-species fishery, primarily exploited for local subsistence use (Selgrath *et al.*, 2017).

#### Bilang-Bilangan (Low impact area)

This site has had ongoing MPA management since 1999, with biannual (wet and dry season) or annual benthic and demersal community monitoring since 2001 and periodic CCEF management assessments.. The management score is currently very high (Table 2), but was at an initial value of 22 following the first CCEF assessment in 2006 (White *et al.*, 2006). There was only minor recorded damage to these reefs following the 2013 earthquake aside from some island subsidence, and no blast fishing was observed during survey or within discussion with local managers.

#### Batasan (Moderate impact area)

This site has had ongoing management protecting the MPA since 1999, with biannual or annual monitoring benthic and demersal community monitoring since 2001, and periodic CCEF management assessments.. The management score has been consistently high due to good enforcement and compliance (Table 2), noting however that the last CCEF management assessment was in 2010. Heavy damage was experienced in this area following the 7.2-magnitude earthquake that hit central Bohol in late 2013, with large fissures and cracks forming. From discussions with local fisherman and from observation whilst surveying, there are also currently low levels of blast fishing occurring in the area.

#### Pandanon (High impact area)

This site has had ongoing management protecting the MPA since 2002 with biannual benthic and demersal community monitoring and periodic CCEF management assessments. However, the site was severely damaged by blast fishing previous to management implementation, with many sites already predominantly rubble. Current MPA enforcement is classed as 'good' (Table 2), but was historically poorer with an initial score of 25 in 2006

under the CCEF scoring system. Reefs in the surrounding area are however very poorly managed and still heavily impacted by blast fishing and occasional cyanide fishing. During survey, regular blast fishing activity was observed in the local vicinity (blasts heard roughly every 30 minutes), with typical activity anecdotally more frequent and more localized from discussions with barangay fishermen.. The extent of any earthquake damage is unknown due to the site already being in a state of extensive damage, but no fissures or obvious earthquake signs were observed from monitoring reports and the site is further from the epicentre than the other two sites.

#### Canlangi (Control site / unmanaged area)

This area lies within the same reef type and impact area as the three MPA study sites, but has no management in place currently or historically. This region experiences a range of fishing types, and visual evidence of low-level blast fishing and net fishing was seen across the area surveyed.

#### ***Data collection and processing***

Thirty-five survey stations were analysed across the four site locations for their benthic physical and community structure and associated fish community structure (Figure 12). Ten replicate surveys were conducted for each MPA site (five inside managed areas and five in close proximity outside the managed areas), with a further five surveys conducted in a comparable but unprotected control site in the same reef system. All reef surveys were structured in a stratified random design, and were conducted in the daytime during November 2016 at depths of 5 to 8 metres. Visibility ranged from clear (>10 m) to moderately turbid (>5 m), with a minimum survey cut-off of 5 m horizontal visibility to ensure accurate fish assessments and benthic photography.

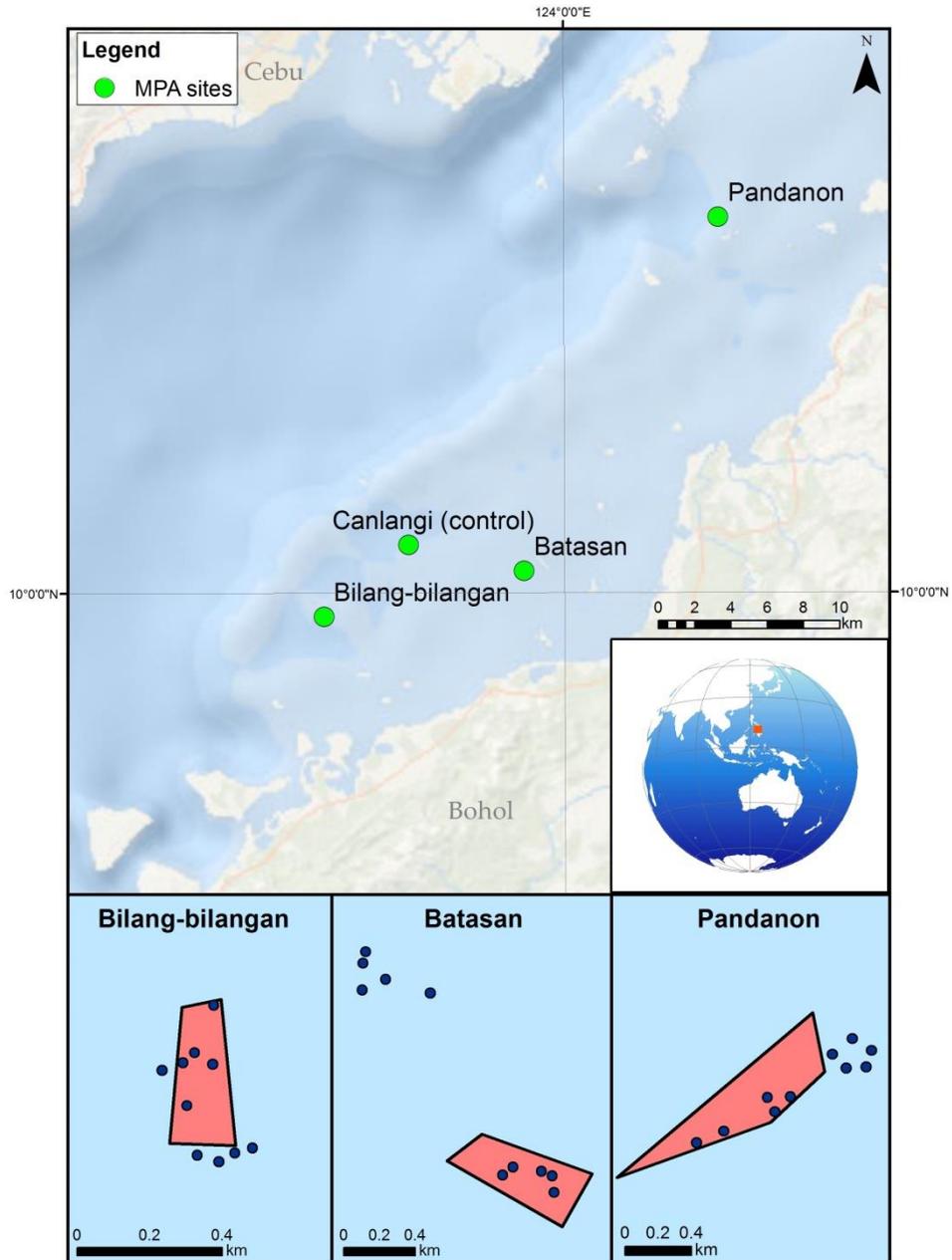


Figure 12. Location of the three MPA boundaries and individual site stations (shown with points) surveyed in 2016 within the Danajon Bank reef system, Philippines. The control site (Canlangi) is also marked.

### Benthic community analysis

Using the location of the fish observer as a central point, benthic surveys were conducted after each fish census to digitise a planar area of reef totalling >25 m<sup>2</sup>. Following (Burns *et al.*,

2015), each whole quadrat was imaged across its full area in a boustrophodonic pattern at ~ 1-2 metres above the substrate (dependent on visibility). A single diver used a Nikon D750 DSLR camera (with a wide-angle fixed lens and dome port) for all imaging, to capture high detail (6016 x 4016 px) images and prevent any potential variation between resulting models caused by use of differing camera or lens types (as highlighted in Lavy et al. 2015). A digital surface model of the area photographed was then created using 'Photoscan Professional' software (Agisoft LLC, 2017). Each individual model used between 300 - 400 overlapping digital photographs, depending on the ambient light levels and benthic topography. Following calibration to multiple in-situ marker points of known dimensions in xyz space, the reefscape point clouds were clipped and aligned to a 5 x 5 metre square area, and exported for analysis of multiple structural complexity metrics within Gwyddion freeware (Nečas and Klapetek, 2012), following a process of rasterization with linear interpolation (Appendix 1).

Surface models (PLY format) of all reefs used in this analysis are freely available from an online repository: ([http://morphosource.org/Detail/ProjectDetail/Show/project\\_id/437](http://morphosource.org/Detail/ProjectDetail/Show/project_id/437)).

### 3D structural metrics

Nine reef surface sub-samples were taken across five (5 x 5 m) reef digital models, with each sub-sample covering a planar area of 1 m<sup>2</sup>, and a gap of 1 metre between each sample, giving a total of 45 replicates per management type (IN / OUT of MPA) per site. I assessed four metrics of 3D structure, which were: '3D rugosity', defined as 3D surface area / 3D projected area (of 1 m<sup>2</sup>); 'height difference', defined as the difference between the maximum and minimum vertical 'Z' dimension depth values of each 1 m<sup>2</sup> surface; 'RMS variation', defined as the Root Mean Squared variation of the total 1 m<sup>2</sup> area Z height irregularities

from a central plane across the surface; and 'kurtosis' / 'skew', the positive or negative 'spikiness' or bend of the 1 m<sup>2</sup> surface, computed from 4th central moment of data values across the surface. Further detail on each metric recorded is available from Gwyddion (Klapetek *et al.*, 2016)

Broad substrate cover metrics

Broad substrate type has been shown to strongly influence associated fish community structure (Richardson *et al.*, 2017a). I used SfM to produce high definition scaled planar ortho-mosaic photo images of each site's 25 m<sup>2</sup> sample area from the 2016 benthic surveys. I then assessed the stitched image for percentage cover of eight broad substrate classes (live coral, dead coral / rock, soft coral, sponge, turf algae, urchin, rubble and sand). I further subdivided live corals into seven distinct growth-forms (branching / corymbose, encrusting, foliose, massive, mushroom, sub-massive / columnar and tabular).

#### Fish community analysis

A timed fish count was conducted at each survey station by a local trained field assistant following the method of Nash *et al.* (2013), with all non-transient, non-cryptic diurnally-active fish recorded to species level within a 5 m radius of the diver, who conducted all survey assessments. Fish were identified sequentially within fish families, starting with the larger more mobile species and ending with the lower mobility families within each observational patch area. Standard length of each fish was estimated visually by the observer following in-water training using known object lengths. The same diver surveyed each patch immediately on arrival to the reef and for 10 minutes in total to ensure consistency of survey effort. Each survey patch was a minimum of 15 metres distance from

any other surveyed patch to prevent any potential repetitive counts of individuals (Wilson *et al.*, 2007a).

Fish biomass was calculated for each (size-grouped) species following the standard Weight - Length relationship (Froese, 2006), where  $W = a L^b$ , with the values of constants  $a$  and  $b$  based on species-specific calculations obtained from 'Fishbase' (Froese *et al.*, 2014; Froese and Pauly, 2018). Biomass was further classed into target and non-target species. Target families include: Acanthuridae, Caesionidae, Haemulidae, Labridae, Lethrinidae, Lutjanidae, Mullidae, Nemipteridae, Pomacanthidae, Scaridae, Serranidae and Siganidae. Diversity metrics were calculated for each species assemblage using the R package 'vegan' (Oksanen *et al.*, 2017), with resulting richness values rarefied using the `rarefy()` function.

#### Fish traits

Traits linked with each reef-associated fish species were extracted from Fishbase using the R package 'Rfishbase' (Boettiger *et al.*, 2012). Fish 'Feeding type' was split into six categories (substrate browsers, aquatic plant grazers, macrofauna predators, parasite cleaner, selective planktivores, and variable feeders). 'Resilience to fishing' was split into four categories (High, Medium, Low, Very low), and is based on multiple life-history parameters including, intrinsic population growth rate, von Bertalanfy growth co-efficients, fecundity, age at maturity and longevity, for all matching species. The 'low' and 'very low' categories were pooled due to limited occurrence of the 'very low' resilience fish. For more detail on how each resilience category was defined please refer to (Musick, 1999; Supplementary material)

#### Baseline reference data

Baseline data for benthic substrate composition (Pandanon,  $n = 6$ ; Batasan,  $n = 6$ ; Bilang-bilangan,  $n = 7$ ), and family level fish community composition (Pandanon,  $n = 10$ ; Batasan,  $n$

= 11; Bilang-bilangan, n = 12) were assessed in 1999 (the year of site designations) for each MPA site. Surveys were conducted at comparable depths of 4-10 metres using in situ visual techniques. Substrate cover metrics were assessed using replicated haphazardly placed 50 m 'Line Intercept Transects' inside and outside of each MPA. Broad substrate types and coral growth forms were categorised in the same way as the 2016 survey methodology with eight broad substrate classes and seven coral growth sub-categories. Family-level fish abundance data was collected along ~15 minute (50 x 5 m) belt transects, with fish sampling locations matched with the benthic substrate surveys. For further survey details please refer to Samoily et al. (2007).

### ***Statistical Analysis***

Each structural metric and transect-pooled measures of fish biomass, size (standard length) and diversity were compared for differences among sites and between management type (inside or outside of MPA) using two-way crossed ANOVAs (with MPA management type as a two-level fixed factor, i.e., protected and unprotected, and sites as a three-level fixed factor (Control site excluded). Post-hoc Tukey's HSD tests were applied, following tests for normality and homogeneity of variance (using Shapiro-Wilk and Levene's tests respectively). Reef 3D Kurtosis and fish biomass were both log transformed for normality before analysis.

Permutational multivariate analysis of variance (PERMANOVA) was performed over 9999 permutations on a square root-transformed Bray-Curtis dissimilarity matrix (with an added dummy variable to account for zero values) using the R 'vegan' package functions `adonis()` and `vegdist()` (Oksanen *et al.*, 2017), to assess for differences in community composition between sites and MPA treatments, respectively (Clarke *et al.*, 2006b; Anderson and Walsh,

2013). This mild transformation was chosen in order to down-weight highly abundant dominant species, and reduce noise, allowing community differences amongst both rare and common species to be detected (Clarke *et al.*, 2006a). A similarity percentage analysis (SIMPER) was also applied in *vegan* to identify species contributing the most to the level of dissimilarity between locations.

Distance-based Redundancy analysis (Legendre and Andersson, 1999) was applied to the fish Bray-Curtis dissimilarity matrix, using the *capscale* () function within the R 'vegan' package, to investigate any associations between site fish community assemblages and structural or substrate variables. PERMutational ANOVA tests for significance were based on best-fit environmental data with management factor (whether Inside / Outside MPA) partialled out to test the underlying association between fish and benthos.

Linear regressions between reef rugosity and fish richness, abundance, diversity and evenness were conducted using the R function *lm* (), and subsequently tested for differences in 2016 inside and outside of protection (two level factor) using ANCOVA. Differences in baseline live coral cover and fish abundance inside and outside of the MPAs and at a control site were tested using two-way ANOVA, without an interaction effect due to unbalanced sample sizes. Fish data was square-root transformed to meet the assumptions of normality. ANCOVA was used to investigate the interacting effect of protection on live coral through time. No tests were applied to test changes in fish communities through time due to non-comparable sampling strategies.

All analyses were carried out using R: version 3.4.1 (R Core Team, 2016).

## Results

### *Benthos*

#### Baseline coral cover (1999)

Two-way crossed ANOVA showed no significant difference in coral cover inside MPAs compared to outside for any site ( $F_{1,15} = 0.126$ ,  $p = 0.728$ ), but a significant difference in cover was seen between sites ( $F_{2,15} = 12.279$ ,  $p < 0.001$ ) due to significantly decreased cover in Pandanon ( $p < 0.001$ ) relative to Bilang-bilangan, following Tukey post-hoc tests.

#### Benthic broad substrate cover

Reefs within the Bilang-bilangan MPA (low impact area) have the highest mean live coral cover of all sites at  $80 \% \pm 6$  (SE), and cover is predominantly composed of structurally complex branching or corymbose growth forms ( $58 \% \pm 9$ ), massive growth forms ( $16 \% \pm 3$ ), and very little rubble ( $9 \% \pm 4$ ) (Figure 13). Live coral cover is significantly lower on reef outside of protection at  $53\% \pm 3$  (SE), and is largely a monocrop of stands of branching *Acropora* spp. ( $51 \% \pm 4$ ), much of which is damaged, leading to relatively high levels of rubble ( $43 \% \pm 4$ ).

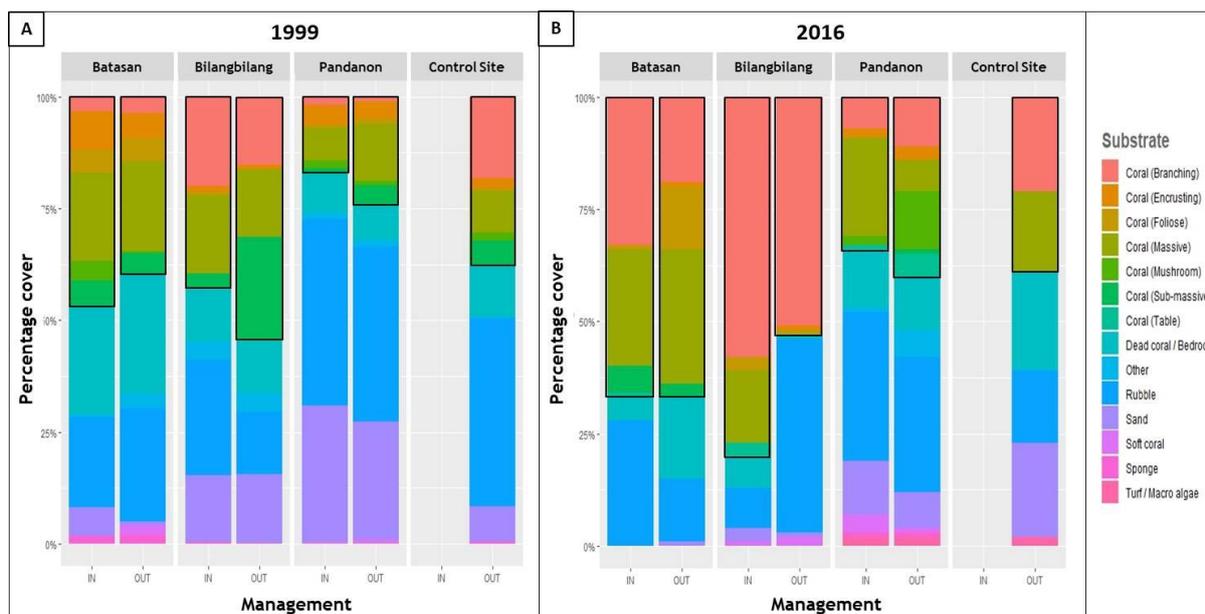


Figure 13. Average percentage cover of broad substrate classes found inside and outside of MPAs within the Danajon Bank, Philippines during A) 1999 and B) 2016. Live coral is highlighted with a black border line and is further split into 7 major coral growth forms.

High overall live coral cover is seen within the Batasan MPA (moderate impact area), with a mean of  $67\% \pm 10$  (SE), primarily composed of branching / corymbose ( $33\% \pm 10$ ) and massive growth forms ( $26\% \pm 7$ ). There is however high variation among samples, due to damage of the dominant branching forms, with rubble coverage reaching  $28\% \pm 8$ . Although overall live coral cover outside the MPA is also  $67\% \pm 6$  (SE), mean dead coral cover is three times higher at  $18\% \pm 4$ , with high rubble  $14\% \pm 2$ . Overall live cover is largely driven by mono-crops of fast-growing and structurally complex foliose *Montipora*  $14\% \pm 10$  and branching *Acropora*  $19\% \pm 6$ , similar to the situation observed around Bilang-bilangan.

The lowest overall live coral cover is seen in the Pandanon MPA (high impact area), with a mean of  $34\% \pm 8$  (SE), primarily composed of massive colonies  $22\% \pm 8$  with the remaining substrate dominated by fine loose rubble  $33\% \pm 10$  as well as dead standing coral  $13\% \pm 5$  and gravelly sand  $12\% \pm 8$ . This area is also the only site with turf macro-algae observed ( $2\%$ ).

$\pm 4$  both inside and outside of the MPA) and *Diadema* urchin presence ( $1\% \pm 1$  and  $6\% \pm 3$  inside and outside of the MPA respectively). Outside of the MPA live coral is at  $40\% \pm 6$ , composed of a varied mix of growth forms, but dominated by mushrooms ( $13\% \pm 7$ ), branching ( $11\% \pm 3$ ), and massive ( $7\% \pm 3$ ) forms.

Although cover of live coral is higher outside of the Pandanon MPA, this difference is driven largely by the inundation of high densities of free-living *Fungia* in a number of samples, living on top of underlying highly mobile rubble (Appendix 2). The mushroom coral aggregations were of mixed species from the family Fungiidae and were observed in multiple locations at peak densities of  $\sim 250$  individuals  $m^{-2}$ , compared to average surrounding densities of 1-4 individuals  $m^{-2}$ . The communities consisted primarily of species from the genera *Fungia*, *Herpolitha* and *Ctenactis* living on top of a mobile coral rubble matrix. When this is accounted for, hermatypic live coral cover falls from 40% to 27% outside of protection.

Comparable ratios of substrate cover are seen in the control site of Canlangi to Pandanon, with low overall coral cover of  $39\% \pm 4$  (SE), with only massive and branching growth forms, and high quantities of rubble ( $16\% \pm 5$ ), coarse sand ( $21\% \pm 7$ ), dead coral ( $22\% \pm 4$ ), and turf algae ( $2\% \pm 2$ ) (Supplementary material).

ANCOVA found level of MPA protection to be a significant predictor for percentage cover of live coral over time in the sampled sites ( $F_{5,42} = 3.282$ ,  $p = 0.0137$ ,  $Adj R^2 = 0.195$ ). Protected sites saw the only significant slopes through time ( $t=3.166$ ,  $p= 0.0029$ ), with average cover increasing by  $1.75\% \pm 0.55$  per year over the sample period, and with no significant effects observed for sites outside of protection or at the control site.

### Benthic 3D physical structure

Two-way crossed ANOVA showed significantly different reef 3D rugosity ratios between sites ( $F_{2,24} = 44.507$ ,  $p < 0.001$ ; Figure 14), due to lower rugosity in Pandanon ( $p_{\text{adj}} < 0.001$ ). There was no overall significant difference in reefs inside MPAs compared to outside ( $F_{1,24} = 2.502$ ,  $p = 0.127$ ), however there was an interaction effect ( $F_{2,24} = 4.071$ ,  $p = 0.030$ ), due to lower rugosity inside Batasan MPA compared to outside ( $p_{\text{adj}} = 0.036$ ).

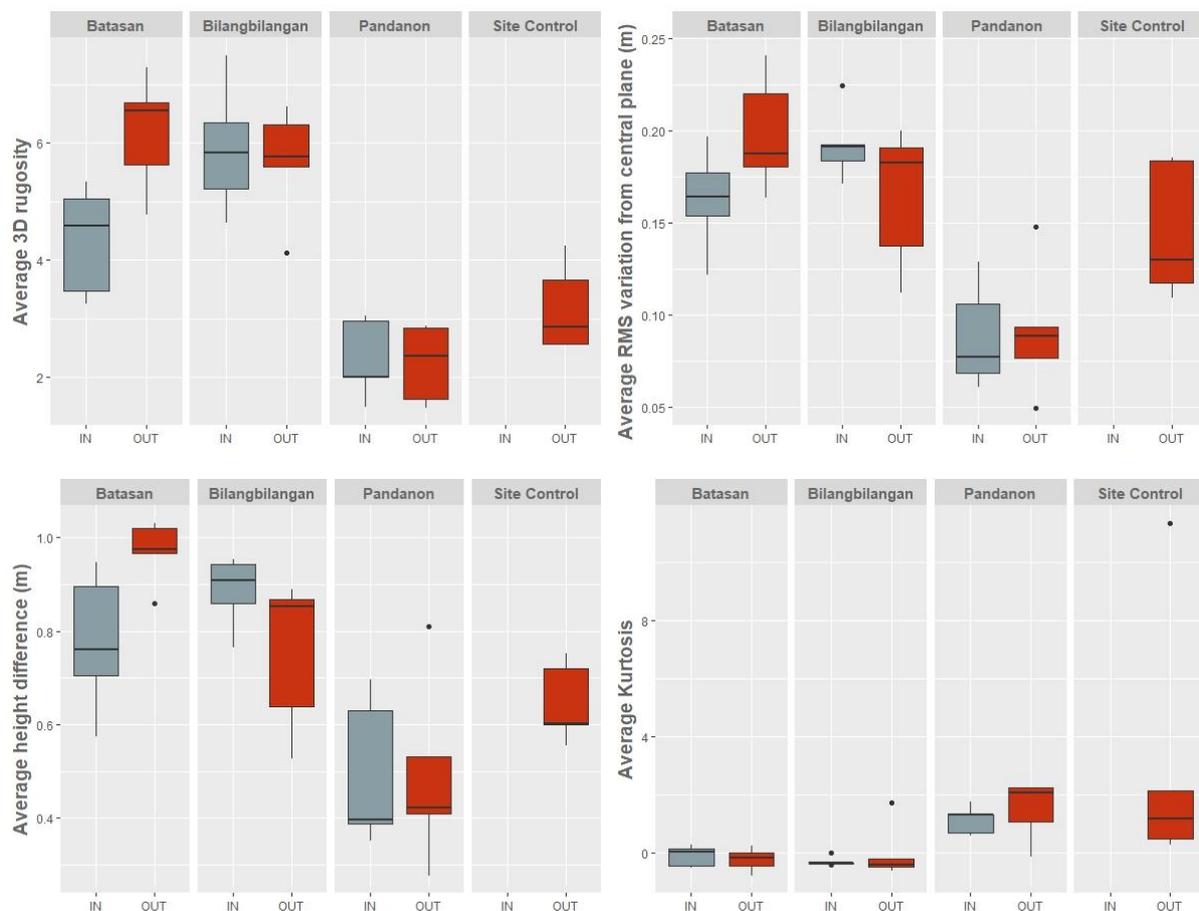


Figure 14. Boxplots of 3D structural metrics (rugosity, RMS point variation, surface kurtosis, and surface height difference) of reefs found inside and outside of MPAs within the Danajon Bank, Philippines. Values for each metric were obtained from averaging across nine sub-samples for each site replicate. Boxplots illustrate the median values, inter-quartile range (filled boxes) and outlier values for each site.

Reef height (max-min) variation was significantly different between sites ( $F_{2,24} = 20.712$ ,  $p < 0.001$ ) due to lower reef height in Pandanon ( $p_{\text{adj}} < 0.001$ ). There was no overall significant difference in reefs inside MPAs compared to outside ( $F_{1,24} = 0.146$ ,  $p = 0.705$ ), however there was a marginal interaction effect ( $F_{2,24} = 3.216$ ,  $p = 0.058$ ), due to lower height inside Batasan MPA compared to outside ( $p_{\text{adj}} = 0.047$ ).

Reef 'spikiness' / roughness (RMS variation from a central plane) was significantly different between sites ( $F_{2,24} = 28.366$ ,  $p < 0.001$ ) due to flatter reefs in Pandanon ( $p_{\text{adj}} < 0.001$ ). There was no overall significant difference in reef spikiness inside MPAs compared to outside ( $F_{1,24} = 0.101$ ,  $p = 0.753$ ), however there was a marginal interaction effect ( $F_{2,24} = 2.699$ ,  $p = 0.088$ ), due to flatter reef inside Batasan MPA compared to outside ( $p_{\text{adj}} = 0.024$ ).

Reef kurtosis (sharpness/ spikiness of the surface) was significantly different between sites ( $F_{2,24} = 13.433$ ,  $p = 0.002$ ) due to sharper peaks in Pandanon relative to Batasan ( $p_{\text{adj}} = 0.002$ ) and Bilang-bilangan relative to Batasan ( $p_{\text{adj}} = 0.037$ ). There was no overall significant difference in reef kurtosis inside MPAs compared to outside ( $F_{1,24} = 2.010$ ,  $p = 0.190$ ), or any significant interaction effect ( $F_{2,24} = 0.256$ ,  $p = 0.625$ ).

### *Fish community metrics*

#### Baseline fisheries data (1999)

Two-way crossed ANOVA showed no significant difference in fish abundance inside MPAs compared to outside ( $F_{1,29} = 0.322$ ,  $p = 0.575$ ), but a significant difference in abundance was seen between sites ( $F_{2,29} = 6.689$ ,  $p = 0.004$ ) due to significantly increased abundance in Bilang-bilangan relative to Batasan, ( $p = 0.005$ ) and to Pandanon ( $p = 0.046$ ) following Tukey post-hoc tests.

Present fisheries data (2016)

Two-way crossed ANOVA showed significantly higher Shannon-Weiner diversity of fish species inside MPAs than outside ( $F_{1,24} = 37.37$ ,  $p < 0.001$ ; Figure 15), but there was no significant difference in diversity between sites ( $F_{2,24} = 0.996$ ,  $p = 0.384$ ), and no interaction effect ( $F_{2,24} = 0.681$ ,  $p = 0.516$ ).

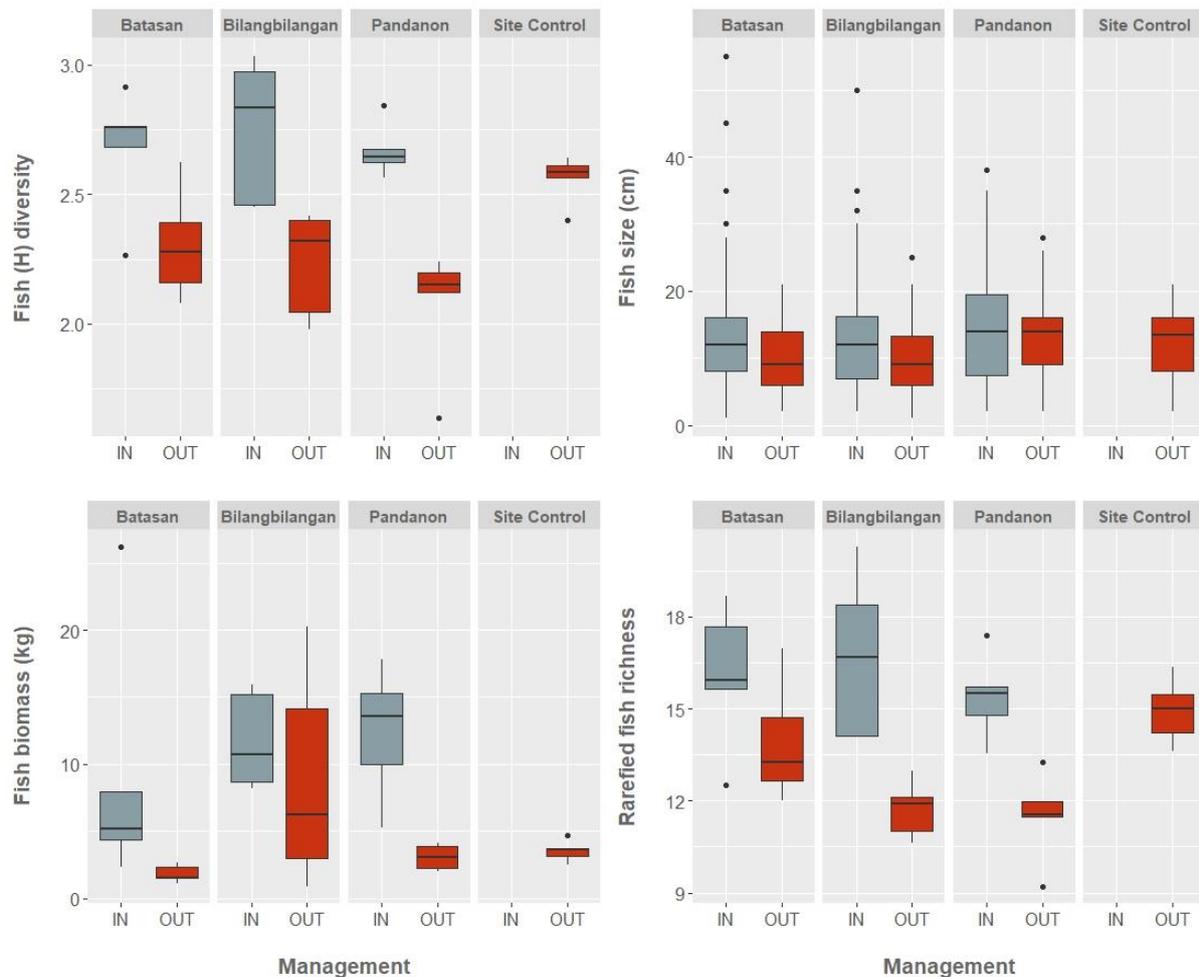


Figure 15. Boxplots of fish Shannon-Weiner diversity index, size (standard body length), biomass (kg), and rarefied richness, split between locations inside and outside of management within the Danajon Bank. Boxplots illustrate the median value, inter-quartile range (filled boxes) and outlier values for each site. Control site also shown.

There was significantly higher fish size inside MPAs than outside ( $F_{1,24} = 21.862$ ,  $p < 0.001$ ), and significant differences between sites ( $F_{2,24} = 5.368$ ,  $p = 0.012$ ), caused by marginally

higher fish size in Pandanon relative to Batasan ( $p_{\text{adj}} = 0.086$ ), and no interaction effect ( $F_{2,24} = 0.669$ ,  $p = 0.521$ ).

There was significantly higher fish biomass density inside MPAs than outside ( $F_{1,24} = 19.905$ ,  $p < 0.001$ ). Total biomass density inside = 424.48 tonnes  $\text{km}^{-2}$  (of which target species = 295.63 tonnes  $\text{km}^{-2}$ ), while total biomass density outside = 174.87 tonnes  $\text{km}^{-2}$  (of which target species = 114.98 tonnes  $\text{km}^{-2}$ ). There were furthermore significant differences between sites ( $F_{2,24} = 3.834$ ,  $p = 0.036$ ), caused by the lower biomass in Batasan relative to Bilang-bilangan ( $p_{\text{adj}} < 0.001$ ), but no interaction effect ( $F_{2,24} = 0.634$ ,  $p = 0.539$ ). There was significantly higher rarefied fish richness inside MPAs than outside ( $F_{1,24} = 28.082$ ,  $p < 0.001$ ), but there was no significant difference in richness between sites ( $F_{2,24} = 1.693$ ,  $p = 0.205$ ), and no interaction effect ( $F_{2,24} = 1.397$ ,  $p = 0.267$ ). Finally, there were no differences in evenness at a management level ( $F_{1,24} = 2.546$ ,  $p = 0.124$ ), site level ( $F_{2,24} = 0.687$ ,  $p = 0.513$ ), or through interaction effect ( $F_{2,24} = 0.959$ ,  $p = 0.398$ ).

PERMANOVA showed fish communities to be significantly different between sites (pseudo- $F_{3,28} = 6.193$ ,  $p = 0.001$ ), and between management type (pseudo- $F_{3,28} = 3.326$ ,  $p = 0.001$ ), explaining 32.9 % and 17.6 % of community dissimilarity respectively. Dendrogram cluster analysis further showed that Batasan and Bilang-bilangan (both inside and outside of protection) were clustered (at the 3<sup>rd</sup> branch level), as was Pandanon (outside of the MPA) with the unprotected control site, and with a final distinct community inside the Pandanon MPA (Figure 16). At the 5<sup>th</sup> branching level of clusters, Pandanon (inside), the site control, and Bilang-bilangan all further separate to form additional distinct cluster groups.

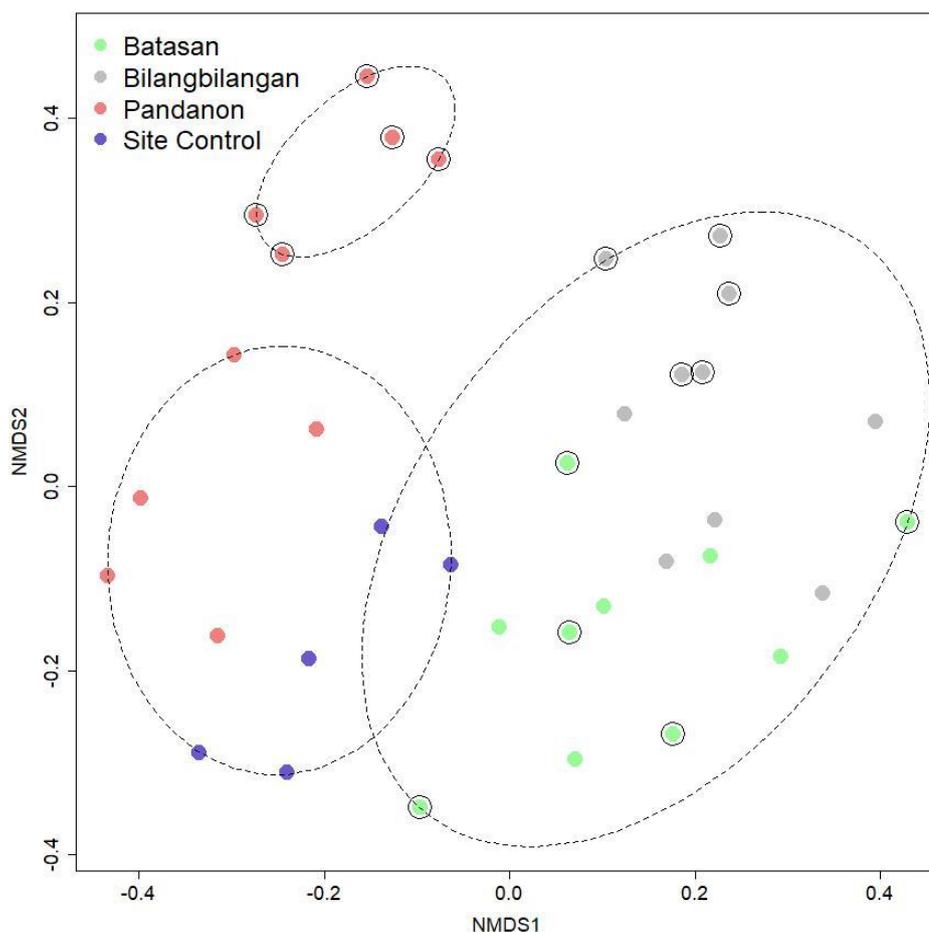


Figure 16. NMDS plot of fish community dissimilarities within the Danajon Bank, Philippines, with site and management type as factors. Sites inside MPA management illustrated with black circles, 3rd group level similarity cluster convex hulls shown with dashed line. 2D Stress = 0.20

SIMPER analysis showed that over half of the dissimilarity between protected and unprotected sites related to differences in relative abundances of species from the Pomacentridae family, with species from Scaridae and Labridae representing the next most important families for driving community differences (Figure 17). On a site level, the outside of Pandanon saw the most notably loss in family diversity, with the Acanthuridae and Pomacanthidae, (both common inside the MPA), entirely lost outside, and being replaced by proportionally higher abundances of families such as Labridae and Siganidae.

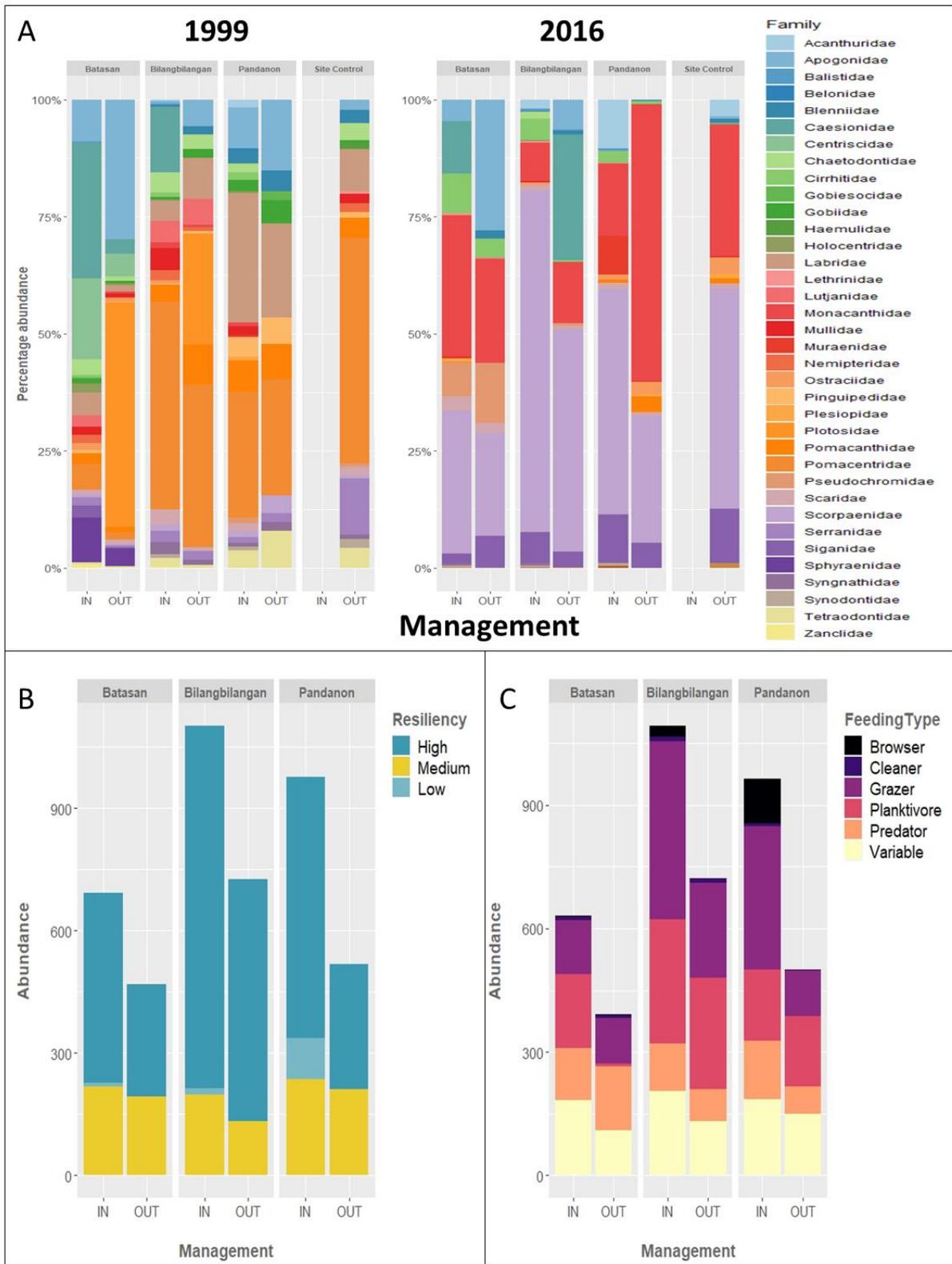


Figure 17. Relative percentage abundances of: A) fish families during 1999 and 2016; B) 2016 fish resiliency, and; C) 2016 feeding guilds at each of the three sites along the Danajon Bank, inside and outside of MPA management.

In terms of generalised family-level feeding guilds, sites show a reduction of guilds outside of the MPAs from six to four types, (losing substrate browsers and parasite cleaners), and showing reductions in macrofauna predators, plant grazers and planktivores (Figure 17).

Communities outside of MPAs only had species which are classed as medium-highly resilient, i.e. fish with high fecundity / rapid growth etc. (Froese and Pauly, 2018), whereas communities inside of MPAs contained high-very low resilience fish species. Low/very low resilience species at this location included: *Ctenochaetus striatus*, *Naso unicornis*, *Scarus altipinnis*, *Coris aygula*, *Plectorhinchus chaetodonoides*, and *Cheilinus undulatus*, which all have a minimum population doubling time of 4.5 - 14 years (Froese and Pauly, 2018). These slow-growing species, which are particularly vulnerable to over-extraction, were found to *only* occur inside MPAs (Figure 17).

### ***Fish-reef associations***

Distance-based redundancy analyses were conducted to investigate the associations between fish community assemblages (based on Bray-Curtis dissimilarity) and the benthos. Analyses were split into A) fish assemblages against benthic 3D structure metrics, and B) fish assemblages against cover of broad reef substrate class, with the effect of the MPA management variable removed (partialled out) from the analysis. The 3D structural complexity metrics (rugosity ratio, kurtosis, skew, RMS variation and Z height difference) together explained 19.5 % of the fish variation between sites (Figure 18), however rugosity ratio was the only significant structural metric (Capscale permutation tests:  $p = 0.005$ ), explaining 10.1 % of the fish assemblage variation. Bilang-bilangan's reef fish assemblage is structured by relatively higher rugosity, increased relative height and greater surface

roughness, whereas Pandanon and Canlangi's reef fish assemblages are structured by higher kurtosis and skew, but strongly reduced rugosity and roughness.

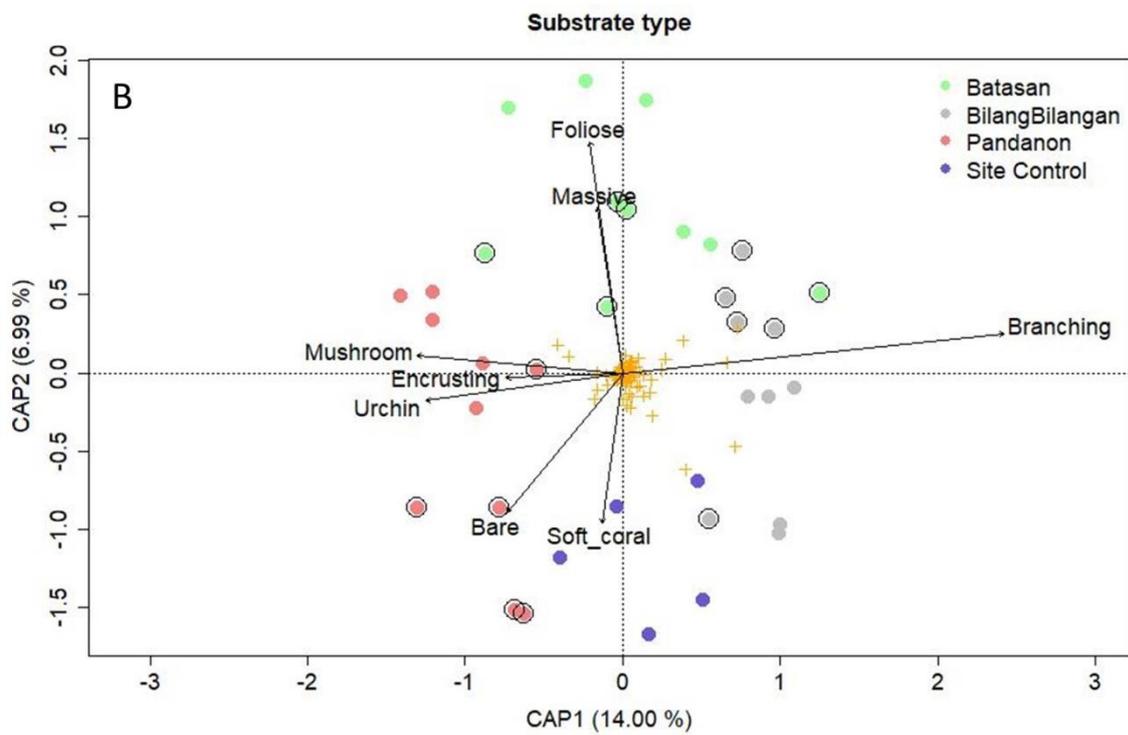
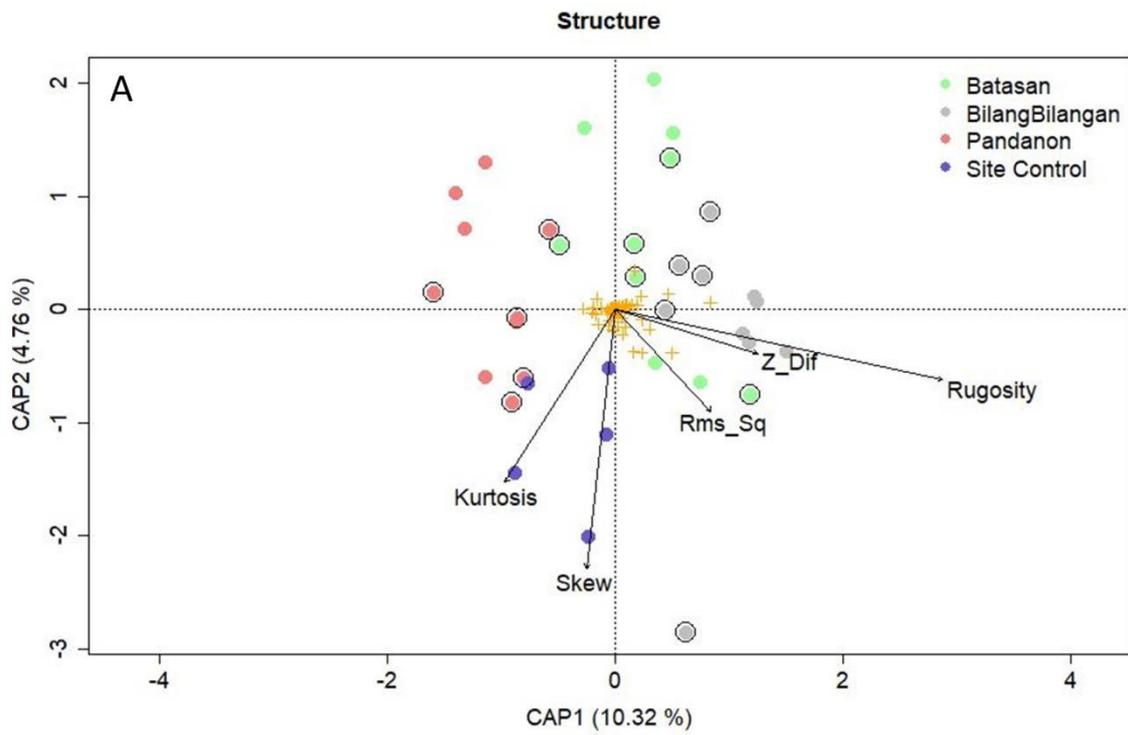


Figure 18. Distance-based redundancy analysis of fish community structure relative to A) benthic structural metrics ('Rms\_Sq' = Root Mean Square surface roughness; 'Z\_Dif' = Height difference) and B) broad substrate type and coral growth forms for all sites. Relative positioning of coloured circles shows levels of community similarity for each site, with arrows showing direction and strength of each abiotic factor in explaining fish community structure. Orange crosses symbolise species' importance, and the sites within MPA protection are illustrated with black outer rings.

Benthic substrate types and coral growth form sub-categories collectively explained 38.4 % of fish variation (Figure 18). Branching coral, table coral and bare/dead coral were the only substrate types causing significant variation in fish communities (Capscale permutation tests:  $p = 0.005$ ,  $p = 0.025$  and  $p = 0.015$ , respectively), together explaining 21.2 % of the fish variation. Bilang-bilangan and Batasan's fish assemblages are structured by benthos with higher levels of branching, foliose and massive corals, whereas Pandanon's fish assemblages are structured by higher levels of encrusting, mushroom and table corals, and greater turf and urchin abundance. Canlangi's fish assemblages are structured by substrates with higher soft coral cover.

Linear regressions showed a significant positive relationship between 3D rugosity ratio and fish richness ( $F_{1,13} = 5.96$ ,  $p = 0.030$ ) for areas sampled inside MPAs, with rugosity explaining 31.4 % of the variation in fish richness (Figure 19). However rugosity was not significantly related to fish richness for samples outside of MPAs ( $F_{1,13} = 0.61$ ,  $p = 0.449$ ), and explained only 4.5 % of the variance. A similar pattern emerged for the relationship between rugosity and abundance, which was significant inside ( $F_{1,13} = 3.62$ ,  $p = 0.079$ ), but not outside of MPAs ( $F_{1,13} = 1.59$ ,  $p = 0.230$ ), and rugosity explained 21.8 % of the variation in fish abundance inside MPAs. Values of fish richness, abundance and diversity were all typically higher inside MPAs.

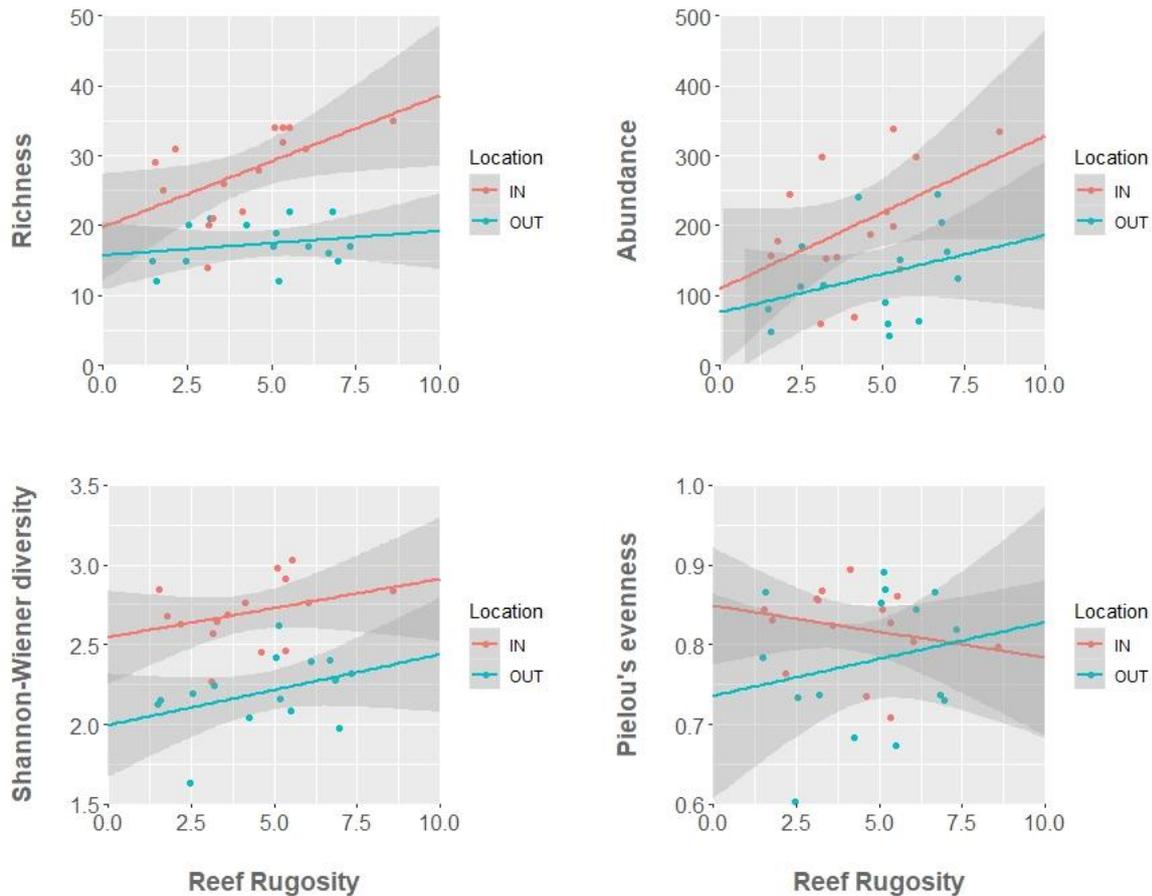


Figure 19. linear models of the relationship between rugosity and fish richness, abundance, diversity (Shannon-Weiner), and evenness, inside and outside of 3 MPAs in the Danajon bank, Philippines. Standard error confidence boundaries shown.

There was no significant relationship inside or outside of MPAs between rugosity and Shannon-Weiner diversity ( $F_{1,13} = 1.53$ ,  $p = 0.239$ ;  $F_{1,13} = 2.25$ ,  $p = 0.158$ ), Simpson's Index ( $F_{1,13} = 0.43$ ,  $p = 0.525$ ;  $F_{1,13} = 0.95$ ,  $p = 0.348$ ) or evenness ( $F_{1,13} = 0.78$ ,  $p = 0.393$ ;  $F_{1,13} = 0.61$ ,  $p = 0.449$ ). Analysis of Covariance showed significant variation inside and outside of MPAs in the relationship between rugosity and fish richness ( $F_{1,27} = 40.79$ ,  $p < 0.001$ ), Shannon-Weiner diversity ( $F_{1,27} = 44.87$ ,  $p < 0.001$ ), and abundance ( $F_{1,27} = 9.44$ ,  $p = 0.0048$ ), but not evenness ( $F_{1,27} = 2.59$ ,  $p = 0.119$ ).

## Discussion

This study found higher biomass, richness, diversity and size of fish inside protected areas compared with outside, despite their relatively small size (16-34 ha), consistent with other studies, both globally and in this region (Edgar *et al.*, 2014; Russ *et al.*, 2015; da Silva *et al.*, 2015; Turnbull *et al.*, 2018). In broad terms the long-term management of the three small scale study sites is therefore seen to be working for fish communities. The effect of protection was most markedly seen in Batasan with roughly four times greater total biomass inside the MPA than outside. Alongside the greater fish diversity and biomass in managed areas, fish community composition was also significantly different, with highly reef-dependent fish families such as the damselfish (pomacentridae) being lost from areas where structure was reduced. The key drivers of these differences in community assemblages were seen to be the MPA management, level of reef rugosity, and the relative proportion of coral growth forms.

The presence of high structural complexity is an essential metric for predicting the recovery outcome of a disturbed reef system, and influences the diversity and productivity of associated organisms (Graham *et al.*, 2015). In this study I found that structural complexity explains a significant amount of the variation in fish community structure and is positively correlated to fish abundance and richness (most strongly within protected reef sites). Historic methods of structural complexity assessment which typically record only a single dimensionless aspect of the reef's morphology (with low accuracy, precision and repeatability) therefore need to be improved upon if we are to fully capture important structural changes.

The 'Structure from Motion' photogrammetric method applied within this case study was found to be a useful technique for the rapid quantification of multiple aspects of structure, and for producing large-scale ortho-rectified HD images of the reef. Both such outputs are very valuable for detailed monitoring and assessment of a reef's status, and help to give consistency and transparency to monitoring programmes, since data can directly compared and re-analysed ex-situ. The range of morphometric outputs which one is able to relatively simply extract from the technique enables researchers to improve their ability to quantitatively describe the physical characteristics of a reef environment through time. These metrics are also produced in an archivable format, allowing for greater insight (either now or retrospectively) into the state of the reefs, the reasons for any changes which have occurred, and the appropriate management measures from which they may benefit. SfM is furthermore non-destructive, and aside from the cost of the underwater camera and a medium performance computer, is in most parts free to use, i.e. relatively affordable in terms of software use, even for low-budget monitoring programmes (Bayley *et al.*, 2019).

There are however important limitations to the application of this technique for appropriate monitoring and assessment. Firstly it is necessary to have relatively clear water, appropriate lighting and preferably slack / still waters in order to produce models which are clear and have full coverage. In the case of strong swell or currents it can be physically exhausting for the diver to image large areas, and such conditions can cause excessive motion of semi-mobile substrate (for example soft corals or algae) making it extremely difficult to create useful models over a large area with this technique. Similarly, highly turbid waters become difficult to adequately image as the distance from the reef to the lens has to be reduced (and therefore image number must increase to allow sufficient image overlap), losing light to the

lens and resulting in overly dark / flat / blurred images which typically create low-quality models (Ferrari *et al.*, 2016b; Raoult *et al.*, 2016). Linked with all these factors is the need for a good basic understanding of underwater photography, as while action cameras such as GoPros are affordable and easy to operate, the 'SLR' or even 'compact' style cameras (which will typically produce higher resolution results), are initially harder to master. This initial learning curve may potentially be a limiting factor in the uptake of this method if appropriate training is not available.

A further consideration is the site topography itself, with the technique best suited to level reef flats and light slopes, with low to moderate surface relief. As the slope incline increases to a 90° wall or overhang, the technique (while still possible) becomes logistically more difficult at large scales (> 10 m) using diver-operated systems. This is due to the multiple successive changes in depth needed over a steep slope in order to produce a zig-zagged 'lawn-mower' overlapping grid pattern. Reefs which are extremely complex, containing dense branching coral thickets, highly overlapping table corals, or multiple tall bombies etc., are also problematic, often causing the model to produce multiple areas of 'occlusion'. Occlusion occurs when aspects of the reef scene are obscured and it becomes impracticable to image the surface adequately, resulting in empty / un-modelled sections of the 3D model. This can lead to over-estimation of volume from interpolated occluded sections of the reef surface, particularly with table growth forms, or underestimation of complexity / roughness with branching/corymbose growth forms (Lavy *et al.*, 2015; Raoult *et al.*, 2017; Bayley *et al.*, 2019).

A final technical consideration is the quality of the camera itself and the resolution of the images which are used to create the model. Digital resolution is the most basic limiter to the

detail and accuracy with which models can be created. However, the benefits of using higher resolution imagery need to be balanced with the corresponding increases in processing time and computing requirements to create a model. Coupled with these considerations is the need to think carefully about the scale and fractal dimension at which any post-processing surface structure analysis is conducted, as this will strongly affect the outputs.

There is clearly still further research needed on how each of these described factors affects the accuracy and comparability of model outputs. However, the requirement of having adequate computer resources, and the associated software training needed to process and analyse models, is likely to be the main initial hurdle for wider uptake of this technology, particularly in low income areas. This issue is nevertheless likely to be short-lived, due to the rapid development of computing power and the expansion of cloud-processing solutions.

Ultimately the choice of whether to employ this method will depend on the nature of the reef assessment work which is being carried out. Visual methods are rapid, cheap and require minimal training, but are limited in their outputs and lack quantitative detail, whereas acoustic methods such as multibeam echosounding can cover large areas, but can be prohibitively expensive, are difficult to operate, and lack fine-scale detail (Bayley and Mogg, 2019). SfM is therefore perhaps best suited for small or medium-scale reef sites where there is a need to improve fine-detail quantitative reef structure data (greater than a basic visual assessment), particularly for lower-income countries due to the relatively low costs (Bayley *et al.*, 2019). But despite this technique being relatively straightforward to instigate, for any new technology to be successfully adopted and usefully applied by local managers with limited resources, some initial training in survey technique, processing and model

analysis would be required, along with standardised protocols of how to apply this method over various habitat types and scales (Bergman *et al.*, 2009; Carboni *et al.*, 2016).

### ***Ecological effects of management***

The reduction in the number and range of families and feeding guilds observed outside of the MPAs would appear to be driven by fishing exploitation, but given that many of the fish species are not typically directly exploited for food, these differences could also potentially be driven by the loss of a range of invertebrate food sources which normally live in healthy reef structures (Pratchett *et al.*, 2011). The loss of live coral as a food source for obligate corallivores in the heavily blast-damaged sites could also potentially be driving the associated declines in fish abundance and diversity. These differences in fish community assemblage structures have led to three broad groups appearing: firstly the Batasan and Bilang-bilangan sites show a great deal of overlap in communities, even outside of protection; then the communities of the control site and Pandanon (outside of protection) are shown to be grouping together; and finally a transitional group in the protected Pandanon area, somewhere in-between the two is shown. Alongside the changes in abundance it is also apparent that the composition of fish species has shifted for all sites since their creation 17 years ago. Despite having baseline data for these sites, it is important to be careful interpreting or extrapolating the observed effects of these reserves since natural (non-management) site effects on abundance and community structure may be confounding the recovery outcomes (Osenberg *et al.*, 2011). This is especially important given the relatively low number of sites included in this case study.

The greatest differences between benthic communities were seen between sites, rather than relating to the reef's position inside or outside of an MPA. The structural differences between sites appear to have been caused by the heavy blasting around the Pandanon site, where reefs were an average of 3 times less rugose, and had on average half the height of other reefs (with some samples outside the MPA, reduced to solely fine loose rubble and a rugosity value close to 1). My observations fit well with other studies, where reefs similar to Pandanon (which have historically experienced widespread extensive blasting), tend to be unable to recover over long periods due to the unconsolidated rubble killing any newly settled coral recruits through current or wave-induced movement (Fox and Caldwell, 2006; Raymundo *et al.*, 2007). Furthermore, Fox and Caldwell (2006) showed smaller scale or low frequency damage from blasting caused only localized short-term damage to the reef, with many reefs recovering to comparable pre-damage states within five years. This compares well to the the Bilang-bilangan and Batasan sites here, where blasting has either been discontinued or happens only at low frequency, and no significant differences were seen in structure inside and outside of the MPAs or between the two sites.

The reefs inside the Batasan MPA were observed to be impacted by the local earthquake in 2013, with the physical collapse of many coral stands, a loss of live coral cover, and multiple 1-5 metre fissures forming. The corresponding collapse of the MPA guardhouse is also likely to have led to a reduction of enforcement effectiveness, particularly given that blast fishing activity was known to occur here historically. It should further be noted that increased coral head removal was observed, for use in rebuilding or elevating local island structures following earthquake-induced land subsidence and sea-level rise. Island adaptation to

subsidence-induced flooding through elevation of flooring is known to also occur at Bilang-bilangan (Jamero *et al.*, 2017), but was not directly observed here.

Across the impacted site of Pandanon, where reefs are now typically flattened rubble fields with very low coral diversity and structure, I observed an unusual proliferation of free-living mushroom coral species, which now form the dominant component of the reef ecosystem. One previous study (Hoeksema, 2012) suggests that dynamite blasts may in fact cause little damage to free-living mushroom corals, and instead may confer high population densities, due to mushroom coral's ability to regenerate from fragmentation and move freely to re-populate damaged areas and take advantage of the increased light availability. The loss of structural complexity more generally outside of the MPA due to very heavy blast activity, may also be limiting future recruit settlement through the loss of the structure-generated turbulence needed to deliver larvae to the substrate (Hata *et al.*, 2017), and through the loss of sensory cues such as noise, normally generated from healthy reefs (Simpson, 2005).

### ***Study limitations***

The lack of any statistically significant physical structural differences inside and outside of the MPA boundaries in this study (aside from the earthquake damage in Batasan) was unexpected, and is likely due to two main factors. Firstly, the study is not starting from a pristine baseline scenario for any of the MPAs, and is instead comparing recovery rates from an initially degraded state both inside and outside of MPAs over 17 years. Secondly, I do not have explicit data for level or type of fishing effort at each site. From what is known, much of the fishing pressure in this region is net-, line- or spear-fishing and is therefore typically not directly affecting the substrate. Besides these factors, the significant differences in reef

structure between Pandanon and the other sites (within environments which are otherwise comparable) strongly indicates that blast fishing is not only highly destructive, but has consequences for the structure of the reef and fish assemblages which can be discerned even decades following impact.

In addition to the above points, we need to consider an important limitation of the benthic survey method, in regard to the fact that both reef kurtosis and roughness (RMS variation) metrics recorded using SfM will likely follow a bell-shaped distribution as disturbance (such as blasting) increases. I.e. at low disturbance we would expect a healthy reef to have a relatively even surface over a coarse scale. However, as holes appear in the reef from blasting damage, the 3D surface layer will be recorded as having higher kurtosis as it becomes more uneven and fractured. Finally, after heavy disturbance such as sustained blasting, the reef will eventually become flattened again as the coral collapses down, resulting in lower kurtosis (toward a zero value) and lower surface variation / roughness. This means that very healthy and very damaged reefs could in theory have similar metrics, so it is essential that for these two metrics (and related measures such as surface skew or fractal dimension), that 3D measures are considered collectively in context with one-another, and that optimally the metrics are monitored through time. This will allow a correct and more nuanced assessment of the current comparative state of the reef along with an indication of the trajectory in which the reef is heading.

The effects of different disturbance types on surface metrics will need further research, however if these factors are appropriately accounted for it may potentially be ultimately be possible to make predictions as to the type of pressure affecting the system just using a suite of measured surface metrics, i.e. high sediment loads would likely be indicated by reduced

kurtosis, reduced roughness, and retained height, while heavy blasting would be indicated by increased kurtosis, reduced roughness, and reduced height.

### ***Management implications***

Improved enforcement and compliance through education and engagement around the damaging effects of illegal blast fishing must be the first priority for future effective management of the benthic communities across this area, but it is also recommended that following successful cessation of blast fishing, some method of rubble stabilization be implemented at the Pandanon site (Raymundo *et al.*, 2007). Stabilization is likely to enhance recovery of this reef, which is currently in a highly degraded state even inside some parts of the MPA, by allowing new coral recruits to establish and re-form a permanent reef.

While it is apparent that capacity shortfalls, inappropriate targets and poor monitoring tools are hindering the effective use of MPAs in many countries (Ahmadia *et al.*, 2015; Gill *et al.*, 2017; Parsons *et al.*, 2017), MPA management is still typically shown to be a valuable cost-effective tool for producing multiple biological benefits for marine systems across scales (Lester *et al.*, 2009; Roberts *et al.*, 2017), a finding supported by this study. The ability to effectively manage and build reef resources is an important tool within a wider integrated social-ecological system approach. However, such management must be applied in conjunction with the improvement of linked socio-economic factors such as human welfare, institutional capacity, and alternative employment opportunities, if it is to be successful long-term and continue to benefit the surrounding communities (Cinner *et al.*, 2009).

Well maintained reefs and their associated fisheries are integral to the livelihood, shoreline stability and food security of many coastal communities, particularly in lower income countries such as the Philippines (Barbier *et al.*, 2011; Spalding *et al.*, 2017; Cabral and Geronimo, 2018). Ongoing work to form a Philippine country-wide network of MPAs and to adequately monitor their individual management performances (Maypa *et al.*, 2012; Cabral *et al.*, 2014; Horigue *et al.*, 2014; Anticamara and Go, 2016), is therefore extremely important for the proper protection of the reefs and fisheries of this archipelago, which continues to experience a range of pressures as the human population grows (Muallil *et al.*, 2014a; Selgrath *et al.*, 2017). Incorporating new and easy to instigate methods such as SfM photogrammetry could help to feed into this existing monitoring work, particularly as accurately assessing reef structural complexity has been shown to be one of the hardest MPA management effectiveness indicators to assess using traditional methods (Tupper *et al.*, 2015).

As the concept of Ecosystem Based Management (EBM) becomes commonplace in marine systems (Curtin and Prellezo, 2010), a shift towards the application of adaptive management is recognised as playing an important role in both the design and appraisal of marine reserves (Grafton and Kompas, 2005). In order to for this type of management to be effective however, continuous monitoring is necessary of multiple components of the ecosystem so that site specific management objectives can be constantly updated according to changing needs, cumulative pressure effects, or dynamic environmental variables (Curtin and Prellezo, 2010; Long *et al.*, 2015). Given the speed in which large areas of reef can be assessed for both reef structural complexity and broad substrate cover metrics using this technique, it will likely be a useful and efficient tool for the rapid quantitative data acquisition needed to

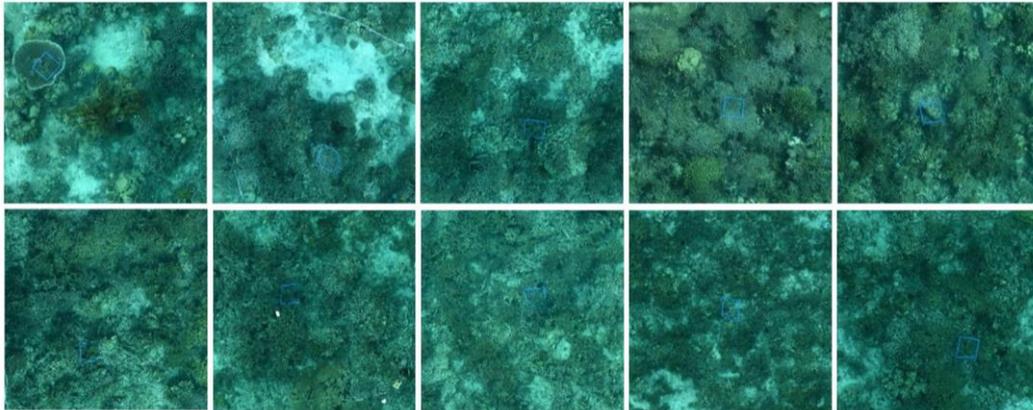
inform such adaptive management (Bayley *et al.*, 2019). Furthermore the ortho-mosaic outputs can be used as an effective visualisation and engagement tool for stakeholder discussions and decision making, which are integral aspects of the EBM process (Grafton and Kompas, 2005; Long *et al.*, 2015).

## Conclusions

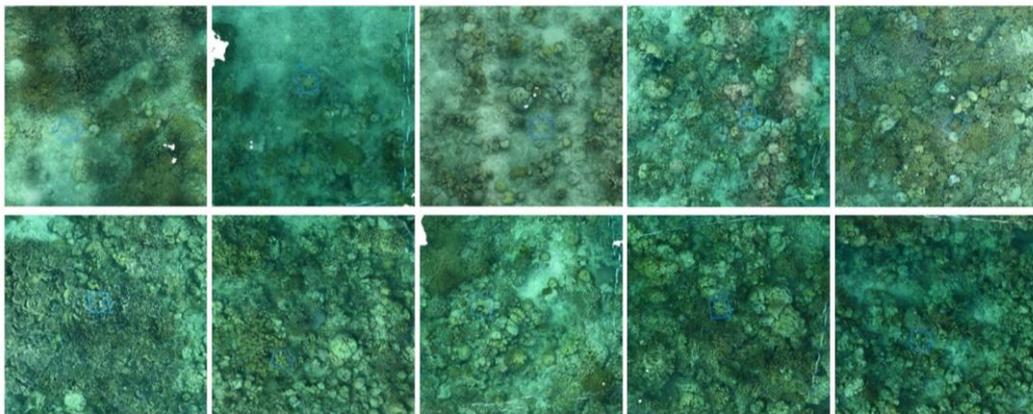
This analysis indicates that the community-led MPAs of this region are being relatively successful at restoring and protecting fish biodiversity on a small scale. There is still cause for concern however regarding the continued use of blast fishing, and potential infractions of the reefs in Pandanon. Maintaining and building on the current level of community engagement and management for this MPA network would seem critical for the continued health of these reefs into the future (Maliao *et al.*, 2009; Hind *et al.*, 2010; Karr *et al.*, 2017). More broadly, there is a need for better management of the reefs and fisheries outside of the MPAs, in order to stop continued reef degradation across the region. Roughly two-thirds of the Philippines' reefs are currently rated as having a high or very high local threat of damage from human impacts, and the country as a whole is in the highest category of 'dependence on reef resources', and 'vulnerability to degradation' globally (Burke *et al.*, 2012). Without committed action to limit regional impacts alongside local management, only limited successes can ever be expected to be achieved.

# Appendices

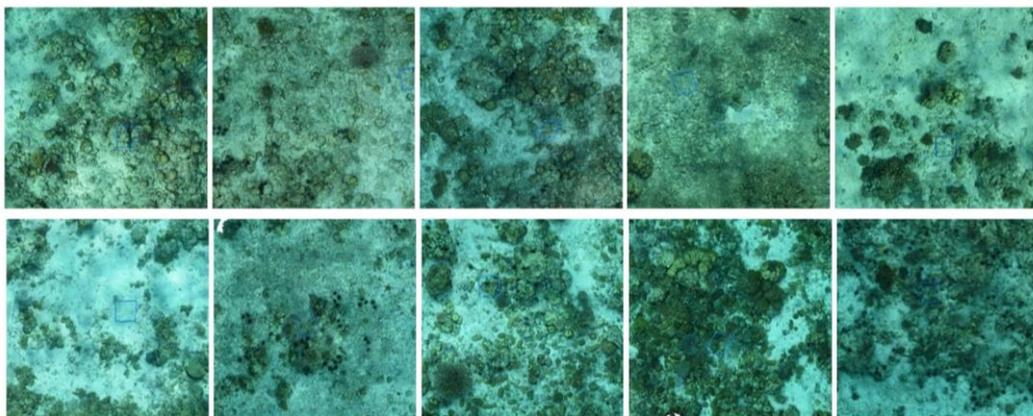
## BILANG-BILANGAN (LOW IMPACT)



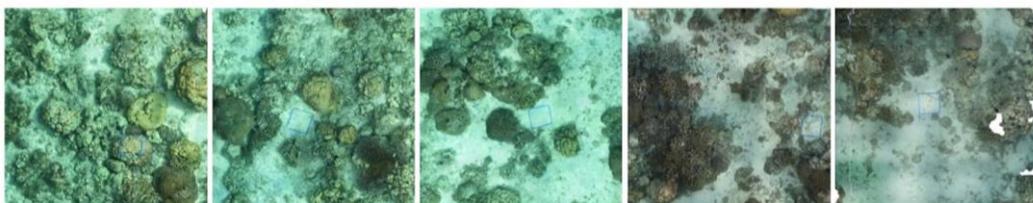
## BATASAN (MODERATE IMPACT)



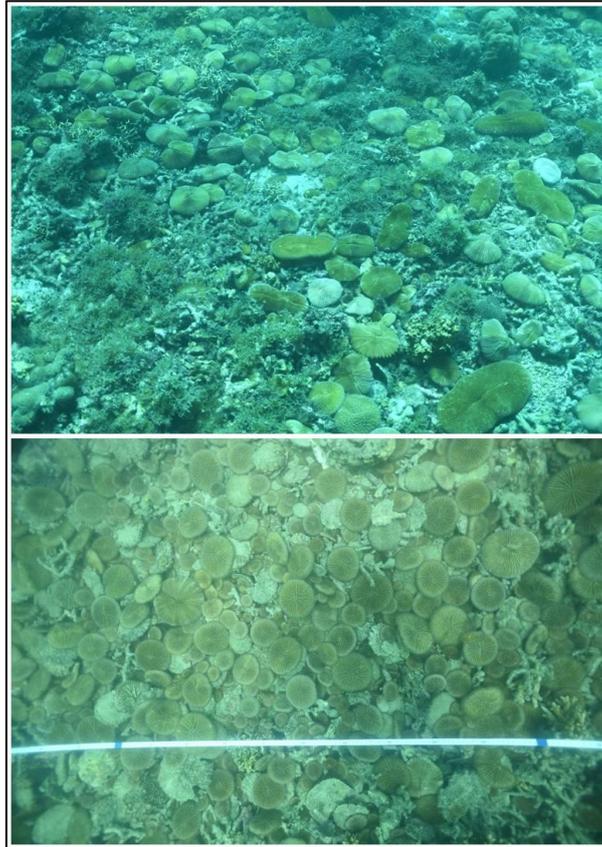
## PANDANON (HIGH IMPACT)



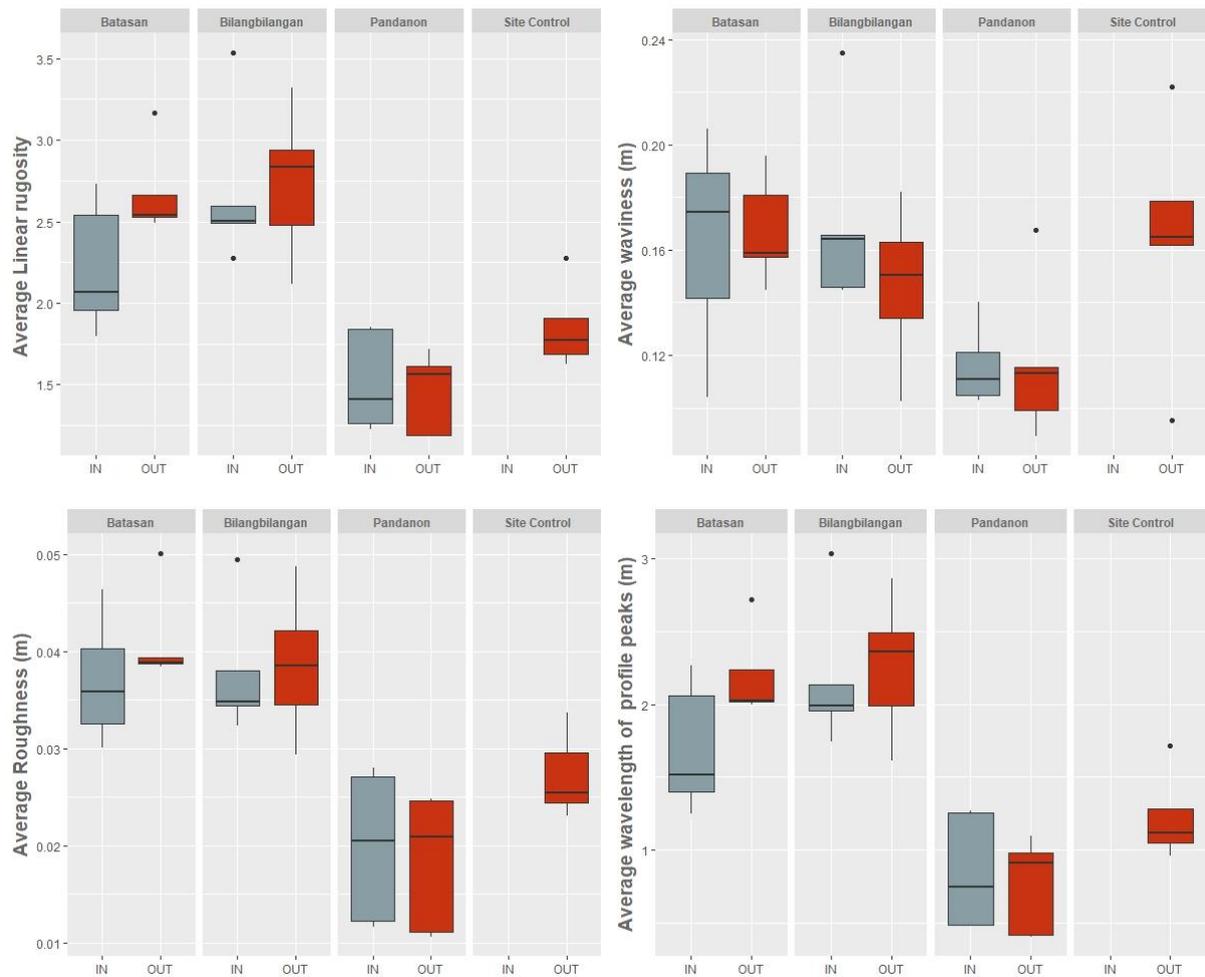
## CANLANGI (CONTROL)



Appendix 1. Ortho-rectified photo mosaics of each site (top row of each site is inside MPA, bottom row outside MPA). Sites ordered in relation to expected MPA performance level, with Bilang-bilangan (high) to Pandanon (low). Each image represents an area of 25m<sup>2</sup> planar area of reef. Blue quadrat indicates 0.5 x 0.5 m in area.

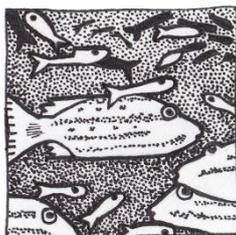


Appendix 2. Images of the proliferation of mushroom corals at high densities, interspersed with algae and loose rubble in Pandanon. Blue tape markers show 1 metre.



Appendix 3. Additional linear 3D metrics of reef structure including linear rugosity ratio, waviness, roughness, and wavelength, each measured in metres. Values for reefs found inside and outside of MPAs within the Danajon Bank, Philippines.





## *Chapter 4: Temporal community dynamics of reefs inside and outside of community managed MPAs*

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### **Abstract**

Tropical coral reefs are subject to multiple chronic and acute pressures from both natural and anthropogenic drivers. The combination of these pressures have led to widespread declines in reef cover and fish abundance in these areas and a push towards the increased use of marine management tools such as Marine Protected Areas (MPAs). While MPAs have proven effective if well-designed and enforced, there are limited long-term studies investigating community changes inside and outside of small-scale MPAs.

This study finds that the small-scale community managed MPAs located along the Danajon Bank of the Philippines have had some success in reducing the rate of decline of fish biomass through time, and preserving key trophic groups and larger-bodied fish within protected reefs. However, fish inside of protection are still declining in many individual MPAs and across the system in general, and surprisingly, benthic cover appear to be unchanged by placement of MPAs, despite continued sporadic use of dynamite fishing in this region. The continued decline of both large and small-bodied fish across the region, points to a combination of both size-selective fishing pressure causing significant changes in fish trophic structure, and lingering effects of the 1998 bleaching event on these reef communities. These shifts in community structure both inside and outside of MPAs could lead to future reductions in fishery productivity and stability, and will be further exacerbated if wider fishery regulation is not instated in this region.

## Introduction

Marine ecosystems provide a wide range of ecologically, economically and socially valuable resources to people, through services such as tourism, commercial food supply, recreation and cultural heritage (Beaumont *et al.*, 2007; Barbier *et al.*, 2011; Hoegh-Guldberg *et al.*, 2015). As a consequence of the sea's high cultural and economic value, human populations in coastal regions are typically very large, with approximately 41% of the world's global population and roughly 60% of the world's 'megacities' found within 50 km of the coast (Martínez *et al.*, 2007). The consequent combination of high population densities, easy access to fish markets, and coastal urban development typically leads to intense pressure on the surrounding marine ecosystems, reducing associated biodiversity and productivity, and limiting the ecosystem's ability to provide functional services (Worm *et al.*, 2006; Cinner *et al.*, 2013).

Total global fish harvest (from fish, crustacean and mollusc fisheries) rose from 65 million tonnes in 1970 to 125 million tonnes in 1999 (FAO, 2016). By 2030, annual global fish consumption is predicted to rise to 150-160 million tonnes, and over three billion people are projected to rely on fisheries and aquaculture for food and livelihoods worldwide (FAO, 2016). In low-income countries the majority of these coastal-based livelihoods are focussed on products from coral reef environments, which are home to roughly a quarter of all fish species caught in tropical regions (Wells and Ravilious, 2006). These fisheries are exploited primarily for local consumption, trade, or for export to aquaria, and account for roughly \$80 billion in revenues annually from fisheries export alone - more than any other agricultural commodity (Wells and Ravilious, 2006; FAO, 2016). The common mixture of chronic

overfishing, pollution, and acute regional impacts (such as from coral bleaching), typically cause long-term alterations in reef community composition and reductions in the overall abundance and function of both reef fisheries and benthic systems (Jackson *et al.*, 2001; Knowlton and Jackson, 2008; Hughes *et al.*, 2018b).

Alongside the reductions in total abundance of fish, the size-selective nature of fishing, which often targets adult life stages and larger-bodied species, can cause pronounced changes in predator-prey dynamics (Bascompte *et al.*, 2005; Robinson *et al.*, 2017b). Such changes are capable of destabilising trophic cascades, and causing a resultant shift in size-spectra (i.e. the distribution of community-wide body sizes) towards a dominance of smaller fish with r-selected life-history traits (Jennings and Blanchard, 2004; Robinson *et al.*, 2017b). Concomitant reductions in functionally important reef-associated groups such as the herbivorous scrapers, grazers and browsers, which help to prevent post-environmental disturbance algal phase shifts and promote resilience, can cause further indirect damage to the benthos (Hughes *et al.*, 2007; Graham *et al.*, 2013, 2017; Hempson *et al.*, 2018).

Direct damage to reef structure can occur through coastal development, destructive fishing practices such as dynamite / blast-fishing, or through natural disturbances such as typhoons (Fabricius, 2005; Fox and Caldwell, 2006; Bozec *et al.*, 2015; Portugal *et al.*, 2016; Wenger *et al.*, 2016). Physical damage typically results in the loss of functionally important reef characteristics, such as the ability to provide 3D habitat structure, and can lead to a reduced range of growth forms (Alvarez-Filip *et al.*, 2009; Graham and Nash, 2013; Denis *et al.*, 2017). Direct damage can furthermore lead to a reduction in overall carbonate accretion rate i.e. growth potential (Januchowski-Hartley *et al.*, 2017; Perry *et al.*, 2018), and the loss of economic value from tourism (Spalding *et al.*, 2017).

Management of reef systems through Marine Protected Areas (MPAs) and fishing gear / quota restrictions allows benthic organisms and fisheries to avoid direct damage, to recover from previous disturbance, and to re-populate surrounding areas (Lester *et al.*, 2009; Koldewey *et al.*, 2010; Harrison *et al.*, 2012; Cabral *et al.*, 2016), as well as potentially attenuating environmental pressures including heat anomalies (Roberts *et al.*, 2017). However, the time needed to recover from a degraded state can be highly variable (Russ and Alcala, 2004; Fox and Caldwell, 2006; McClanahan, 2014; MacNeil *et al.*, 2015; McClanahan *et al.*, 2016), and the benefits gained are tightly linked to the level of protection, compliance and enforcement (Ahmadia *et al.*, 2015; Gill *et al.*, 2017). Additionally, the benefits of MPAs are generally seen to increase more rapidly if they are 'no-take' (i.e. no extractive activity allowed), older than 10 years, larger than 100 km<sup>2</sup> and isolated in some way (Edgar *et al.*, 2014).

While there has been a global push in recent years towards increasing the coverage of very large MPAs (Singleton and Roberts, 2014), small-scale MPAs are also seen to have benefits if designed and managed well (Lester *et al.*, 2009). In the Philippines, which is a global centre of marine biodiversity (Carpenter and Springer, 2005), only 2.7 – 3.4 % of coral reefs are protected, and these have a median size of only 0.15 km<sup>2</sup> (Weeks *et al.*, 2010). Additionally, 95% of these protected reefs are community-managed (i.e. designated under local or municipal level ordinances) and are therefore typically without government funding (Weeks *et al.*, 2010). Despite the small area of reef protected, country-wide coral cover increased overall between 1981 and 2010 (Magdaong *et al.*, 2014). Conversely, most small scale fisheries are declining, and labelled as unsustainable (Muallil *et al.*, 2014a, 2014b). These changes in Philippine reef communities take place in the context of intense localised fishing,

pollution and development pressures (Burke *et al.*, 2012; Selgrath *et al.*, 2017), alongside a range of large-scale environmental impacts, including coral bleaching in 1997-1998 and 2010 (Magdaong *et al.*, 2014), and sporadic typhoon, tsunami and earthquake damage (Shimozono *et al.*, 2015; Anticamara and Go, 2017; Jamero *et al.*, 2017).

Chapter 3 showed that small scale MPAs in the Bohol region of the Philippines exhibited differences in fish community assemblage when comparing between inside and outside of enforced MPAs, and that the effects of blast fishing on reef benthic structure and composition can linger many years following impact. However, given the different techniques used between the baseline monitoring assessments and recent assessments (and an undocumented 17-year intervening time period), it is difficult to assess recovery or decline rates accurately for these reef communities or to identify reef community 'winners and losers' within this system. To address this knowledge gap, I use long-term monitoring data, which was collected with a consistent annual monitoring protocol. The ecological time-series begins in 1999 and ends in 2011, with MPAs ranging in age from 7-15 years by the end of the time-series. This study is therefore set in the context of a recovering, post-disturbance community, following the 1998 major coral bleaching, which caused widespread coral mortality and the loss of fish habitat across the Philippines.

In this chapter I aim to describe the rate and direction of change in both coral cover and family-level fish abundance, size and trophic group over more than a decade within this reef system, following major community disruption. I furthermore investigate whether the presence of local MPA management has altered the rate at which communities have declined or recovered, and whether factors, including fish commercial value, feeding type, habitat preference or coral growth form, have affected their success.

## Materials and methods

### *Location*

The Danajon Bank reef system is located within the central Visayas region of the Philippines and covers a total area of 271.7 Km<sup>2</sup> encompassing the Cebu, Bohol and Leyte provinces (Figure 20).

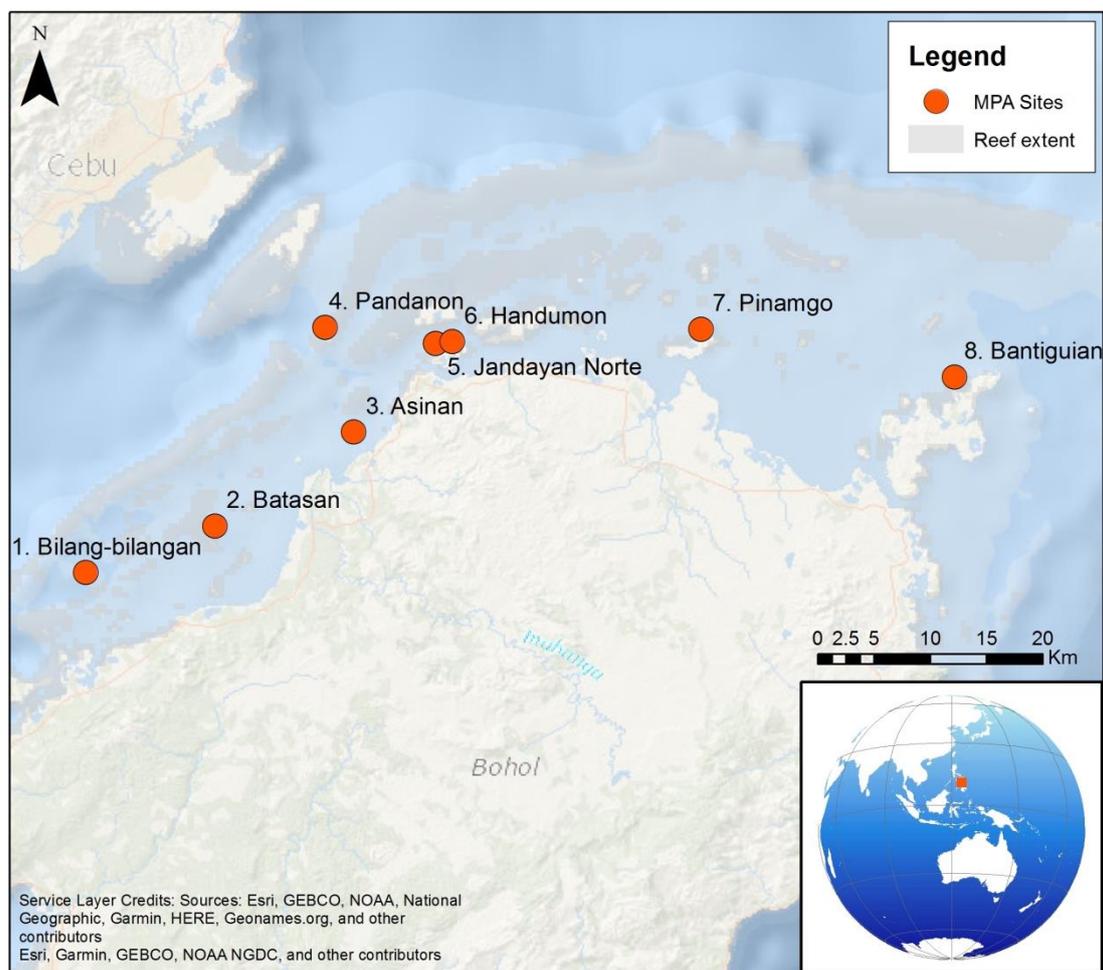


Figure 20. The location of the eight Marine Protected Area (MPA) sites along the Danajon Bank reef system within the Philippines. The islands of Cebu and Bohol are shown for context, with the limits of Cebu City shown in beige.

### *Site information*

Assessments were conducted inside and outside of eight community-led Marine Protected Areas (MPAs), within five municipalities of Bohol (Table 3). The sites range in their age and level of enforcement, but are all typically small (ranging between 10 and 50 ha), with the oldest site being designated in 1995 (however the earliest baseline data begins in 1999).

Table 3. Characteristics of the eight Marine Protected Areas (MPAs) along the Danajon Bank reef system, including measures of management and compliance based on (Alcala *et al.*, 2008; Yasué *et al.*, 2012). \* The Coastal Conservation & Education Foundation (CCEF) management scoring system ranges from 0 (lowest) to 40 (highest). Refer to (White *et al.*, 2006) for further details of score calculation and grading.

<b>Name of Marine Reserve</b>	<b>Municipality</b>	<b>Total Area (ha.)</b>	<b>Year Est.</b>	<b>CCEF score (0-40)*</b>
1. Bilangbilangan Fish Sanctuary	Tubigon	10.5	1999	39
2. Batasan Marine Sanctuary	Tubigon	21	1999	38
3. Asinan Fish Sanctuary	Buenavista	50	2000	40
4. Pandanon Fish Refuge & Sanctuary	Getafe	20	2002	34
5. Jandayan Norte Fish Refuge & Sanctuary	Getafe	24.9	2002	33
6. Libaong (Handumon) Marine Sanctuary	Getafe	50	1995	38
7. Pinamgo Fish Sanctuary	Bien Unido	37.8	2000	37
8. Bantiguian Saguise Marine Sanctuary	Carlos P. Garcia	10.6	2004	38

In 2015 the Philippines changed their system for rating the effectiveness of MPAs to the 'Management Effectiveness Assessment Tool' (MEAT scores available at: <https://database.mpasupportnetwork.org>), however, I use the previous Coastal Conservation & Education Foundation (CCEF) system here for consistency over a longer period of assessment relevant to this study timeline (with scores ranging from 0-40). These

sites are all considered 'well enforced' according to this system, with scores ranging from 33-40, and were chosen as they held complete information on the level and duration of MPA management, have complete and consistently recorded replicate datasets using a standardised protocol (Samoilys *et al.*, 2007), and are spread across the whole Danajon Bank region of Bohol.

### ***Pressures***

Unprotected areas across this region are subject to fishing pressure from multiple gear types (including 'blast fishing; fish corrals; gleaning; hook-and-line; nets; poison fishing; skin diving; and traps'), which target a mixed-species fishery, primarily for local subsistence use (Selgrath *et al.*, 2017). Alongside localised fishing pressures, there is extensive pollution, sedimentation and coastal development (primarily from the population hub of Cebu ~20 km to the North West of northern Bohol), alongside a range of global threats from occasional bleaching episodes and sporadic typhoon damage. The largest major bleaching event was in 1998 associated with the global El Nino – induced global bleaching (Goreau *et al.*, 2000).

### ***Survey transects***

Biannual surveys were conducted along the Danajon Bank in the dry (March-May) and wet season (September-December) from 2000 to 2011 for eight sites. Samoilys *et al.* (2007) showed wet and dry season surveys in this region do not contribute significantly to fish variation among sites, therefore data were pooled by year for all fish and benthos surveys to increase within-replicate sample sizes. All surveys were conducted on reef flats at depths of 4 - 10 m, along 50 m randomly placed fixed transects in a hierarchical nested design, assessing benthic composition, and family-level fish abundance and total length simultaneously (Table 4).

Table 4. Total number of site-level benthic and fish surveys from 2000 to 2011, inside and outside of all eight Marine Protected Areas (MPAs). All years surveyed except for 2007 (all sites), 2008 (sites 3, 7 and 8), and 2009 (sites 1,2,4 and 5).

	Site 1		Site 2		Site 3		Site 4		Site 5		Site 6		Site 7		Site 8	
<b>Survey years</b>	2000 - 2011		2000 - 2011		2000 - 2011		2000 - 2011		2003 - 2011		2000 - 2011		2002 - 2011		2004 - 2011	
<b>MPA</b>	In	Out														
<b>Benthic</b>	51	34	36	36	34	17	34	17	24	23	37	39	26	24	20	20
<b>Fish</b>	63	41	45	46	42	22	40	20	28	28	44	44	30	29	24	24

The composition of benthic substrate cover was assessed using Line-Intercept Transects (English *et al.*, 1997), with two transect replicates per site, per management type (inside or outside the MPA), per season (wet or dry), per survey year. Broad substrate groups were recorded, including seven coral growth morphologies (branching, encrusting, foliose, massive, mushroom, sub-massive and tabular).

Fish abundance was assessed within belt surveys (again with two survey belt replicates per site, per management type (inside or outside the MPA), per season (wet or dry), per survey year), recording the abundance and size of all diurnally active non-cryptic reef-associated fish families within a 5x5 m window. Size estimation and family ID was conducted in-situ visually by trained observers. Fish length estimates were validated against bars of known length in-situ during training, and then periodically through field surveys. Carangidae (jacks/trevallies) were excluded from the analysis of biomass across time as large mobile piscivores such as these are often strongly over-estimated in these sorts of localised visual censuses, and typically over-inflate and skew results (Williams *et al.*, 2015b; Robinson *et al.*, 2017b).

Following surveys, all observed families were classified into groups (Appendix 4) according to their broad commercial food and aquaria trade value (low, medium or high), feeding type (corallivore, detritivore, herbivore, invertivore, piscivore, planktivore, scavenger or spongivore), and their degree of reef-association (low, medium or high) using data from Fishbase (Froese and Pauly, 2018) and related literature (Samoilys *et al.*, 2007; McClanahan, 2014).

Fish biomass estimates were calculated for each family using the standard Weight - Length relationship (Froese, 2006), where  $W = a L^b$ , with the values of constants  $a$  and  $b$  based on species-specific calculations obtained from Fishbase (Froese *et al.*, 2014; Froese and Pauly, 2018) using the Rfishbase() web-interface package in R. Given that the fisheries data were collected at the Family taxonomic level, I pooled size-based growth values for all species known to occur in this region (Bayley *et al.*, 2018), and then used the mean values for the family averaged groups.

### ***Analysis***

A mixed effects linear regression, fit by restricted maximum likelihood, was used to assess the significance of MPA management and length of enforcement in explaining variations in total fish biomass. 'MPA management' (In / Out) and 'length of enforcement' (years) were set as fixed factors and 'MPA site' (n=8) was set as a random effect with random slope and intercept included (following log likelihood ratio test assessment). A log transformation was applied to biomass to achieve a normal distribution of model residuals, and the plotted residuals were checked for homoscedasticity prior to using the results of the model. Following the overall analysis, the data were then split into eight trophic groups, with

individual models run for each group (with site remaining as a random factor with random slopes). The trophic groups were corallivores, detritivores, herbivores, invertivores, piscivores, planktivores, scavengers, and spongivores. Dominant trophic feeding strategy was chosen for each fish family if multiple strategies existed across species or life-stage.

Further mixed effects linear regressions were used to assess the significance of MPA management and length of enforcement in explaining variations in live coral cover through time. 'MPA management' and 'length of enforcement' were again set as fixed factors and 'MPA site' (n=8) was set as a random effect with random slope and intercept included (following log likelihood ratio test assessment). A square root transformation was applied to percentage cover values to achieve a normal distribution of model residuals, and the plotted residuals were checked for homoscedasticity prior to utilising the results of the model. While the error distribution of percentage cover data is technically binomial in nature, in practice the range of cover values did not exceed 0.2-0.8, residuals fitted a normal Gaussian distribution, and model predictions were bounded within the expected 0-100 range, so a simpler linear model was chosen over a generalised linear model. Site level differences were investigated using the function `Lmlist()`, dividing the pooled data into eight groups, based on the random factor of site.

The linear mixed effects models were generated using the `lmer()` function in the R package `lme4`. Significance (p) values for the selected models were calculated using Kenward-Roger standard errors and degrees of freedom. Confidence intervals are calculated at the 95 % level.

To test for overall changes in size spectra through level of management and time, linear regressions were calculated for (log transformed) fish density (250 m<sup>-2</sup>) inside and outside

protected sites, for the period 2000 to 2011. Data were pooled across eight sites and all families, and these dates were used in order to cover the largest time span where all sites were monitored consistently with adequate sample replication. Fish counts were separated into 10 cm (total length) size bins, analysing each separately. The 40 cm+ size class includes all size classes 40 – 100 cm, due to limited abundances within these classes. The linear regressions were conducted using the R function `lm()`. Differences in fish total length frequency distributions between MPA management (In/Out) were tested for the eight pooled sites at 0, 5 and 10 years since MPA designation using the permutational 'sm.density.compare' function in the R package 'sm' (Bowman and Azzalini, 2018).

### Community analysis

To test for differences in coral trait composition between sites (n=8), MPA management (n=2) and years since designation (n=16), I used permutational multivariate analysis of variance (PERMANOVA) over 9999 permutations on a log-transformed Bray-Curtis dissimilarity matrix using the R 'vegan' package functions `adonis()` and `vegdist()` (Oksanen *et al.*, 2017). Principal co-ordinate analysis was then conducted on benthic community structure and coral growth morphology including years since designation, for all sites, with MPA management type and site name as factors.

Forest plots were used to show effect sizes for differences in fish community through time and between management. Plots were based on natural log transformed response ratios (LnRR) of fish family mean total abundances, pooled for all MPAs (n=8). The LnRR is a robust measure of relative differences within a community and can be widely compared with larger meta-analyses (Goldberg *et al.*, 1999; Cote *et al.*, 2001). Samples inside and

outside of protection were analysed separately, with zero and single individual counts removed. I further analysed the responses to protection for the year 2011 alone, following 10-15 years of enforcement. Forest plots were created using the `escalc ()` function within the R Metafor package.

All analyses were carried out using R: version 3.4.1 (R Core Team, 2016).

## Results

### *Effect of enforcement and time on reefs*

#### Coral cover through time

Linear mixed effects models showed no significant individual or interaction effects between live coral cover, management and length of time since designation for pooled sites. (Table 5).

Table 5. Outputs of linear mixed effects model of the effect of time (years since designation) and management (In / Out of a Marine Protected Area (MPA) on square-root transformed) coral cover. \*\*\*  $p < 0.001$ ; \*\*  $p < 0.01$ ; \*  $p < 0.05$ .

	Model estimate	t value	95% CI range
(Intercept)	5.23 ***	10.28	[4.23, 6.22]
Years	-0.04	-0.83	[-0.12, 0.05]
MPA (OUT)	-0.10	-0.41	[-0.55, 0.36]
Years: MPA (OUT)	-0.01	-0.30	[-0.12, -0.04]
N (Transects)	472		
N (Sites)	8		
R <sup>2</sup> (fixed effects)	0.01		
R <sup>2</sup> (total)	0.46		

The majority of the variance (45% of the 46% explained) within the model was explained by site-level variation, but while there is an indication of declining cover from negative slopes for each management type, no significant trends were seen across the Danajon bank during the observation period (Figure 21).

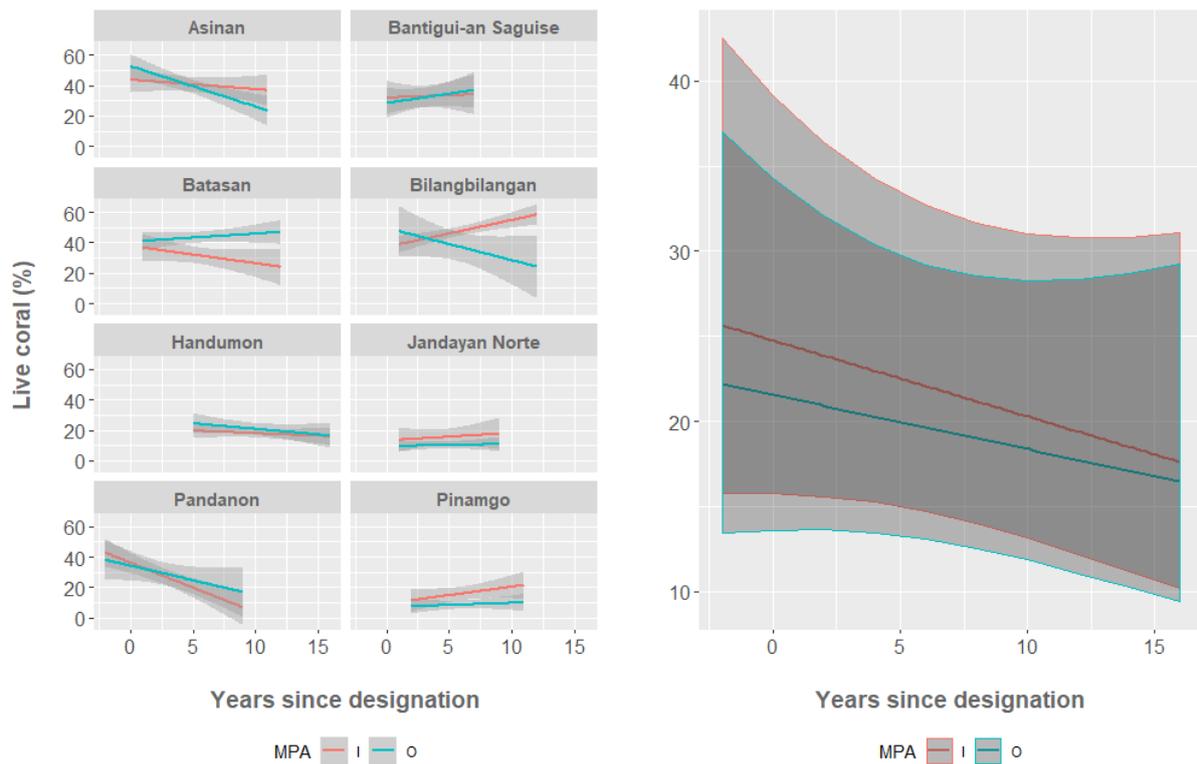


Figure 21. Percentage live coral cover recorded inside (I) and outside (O) of Marine Protected Area (MPA) management within the Danajon bank, Philippines. Linear models plotted with annual time since designation, for each site (left), and linear mixed effect model outputs from all sites (right). 95% CI of models shown in grey.

On a site level, only at Bilangbilangan and Pandaon changed significantly through time (Appendix 5). Within Bilangbilangan the management type caused significant differences in cover through time (estimate = - 0.262, SE = 0.091,  $t_{1,440} = -2.895$ ,  $p = 0.004$ ), with cover outside MPAs declining, and cover inside MPAs increasing (estimate = 0.134, SE = 0.057,  $t_{1,440} = 2.350$ ,  $p = 0.019$ ). For Pandanon a significant negative effect was observed inside MPAs (estimate = - 0.336, SE = 0.070,  $t_{1,440} = - 4.803$ ,  $p < 0.001$ ), while the slope outside the MPA was slightly (and non-significantly) less negative (estimate for difference = 0.141, SE = 0.121,  $t_{1,440} = - 1.160$ ,  $p = 0.247$ ).

### *Benthic community composition*

Separation of benthic groups into eight substrate classes allowed dissimilarities in community composition to be explored through time and between site and management factors (Appendix 6). Principal Component Analysis showed sample stations were clustered by site, showing distinct local variation in substrate composition, but showed no strong differences between management type (inside or outside) for any site (PCA1 = 32.17%, PCA2 = 18.20%).

PerMANOVA showed no interaction effect between time and management level ( $F_{18, 143} = 0.409$ ,  $p = 1$ ,  $R^2 = 0.054$ ) for the substrate groups and no effect of management ( $F_{1, 143} = 1.301$ ,  $p = 0.223$ ,  $R^2 = 0.010$ ). However, there was a weak interaction effect between time and site ( $F_{46, 143} = 1.795$ ,  $p = 0.75$ ,  $R^2 = 0.182$ ), with both time ( $F_{18, 143} = 1.524$ ,  $p = 0.001$ ,  $R^2 = 0.095$ ) and site ( $F_{7, 143} = 19.658$ ,  $p < 0.001$ ,  $R^2 = 0.475$ ) signalling a shift in community similarity towards sites with greater proportions of rubble, dead coral, sponge, and sand.

A further PCA focussing on the coral growth morphological difference alone showed that the sample station coral growth forms were again clustered by site (PCA1 = 23.87%, PCA2 = 16.03%), but PerMANOVA showed no interaction effect between time and management level ( $F_{18, 143} = 0.553$ ,  $p = 0.998$ ,  $R^2 = 0.074$ ) for the coral trait composition, and no interaction effect between time and site ( $F_{46, 143} = 1.059$ ,  $p = 0.324$ ,  $R^2 = 0.195$ ). However, there was a strong effect of site ( $F_{7, 143} = 16.027$ ,  $p < 0.001$ ,  $R^2 = 0.424$ ) causing differences in coral community traits, and also a smaller effect of management type within each site ( $F_{8, 143} = 3.052$ ,  $p < 0.001$ ,  $R^2 = 0.092$ ).

## *Effect of enforcement and time on fisheries*

### Biomass

Fish biomass did not change significantly over time inside the MPAs and did not differ significantly between inside and outside at the time the MPAs were established. However, fish biomass did decrease significantly over time outside the MPAs (Table 6).

Table 6. Outputs of Linear mixed effects model of the effect of time, in Years Since Designation (YSD) and management (In / Out of an MPA) on the log-transformed total fish biomass (g) per 250 m<sup>2</sup> transect. \*\*\* p < 0.001; \*\* p < 0.01; \* p < 0.05.

	<b>Model estimate</b>	<b>t value</b>	<b>95% CI range</b>
<b>(Intercept)</b>	8.95 ***	28.86	[8.34, 9.56]
<b>YSD</b>	-0.03	-0.72	[-0.10, 0.05]
<b>MPA (OUT)</b>	-0.18	-1.35	[-0.45, 0.08]
<b>YSD: MPA (OUT)</b>	-0.08 ***	-4.17	[-0.12, -0.04]
<b>N (Observations)</b>	570		
<b>N (Sites)</b>	8		
<b>R<sup>2</sup> (fixed effects)</b>	0.11		
<b>R<sup>2</sup> (total)</b>	0.55		

The majority of the variance (44% of the 55% explained) within the mixed-effects model was among-site variation, indicating an array of responses to protection, but an overall trend towards losses outside of MPAs. The Danajon bank region-wide change in biomass outside of MPAs equates to a loss of ~802.9 g fish biomass per transect, or ~ 3.2 g m<sup>-2</sup> year<sup>-1</sup> over the time period 2000-2011 (Figure 22).

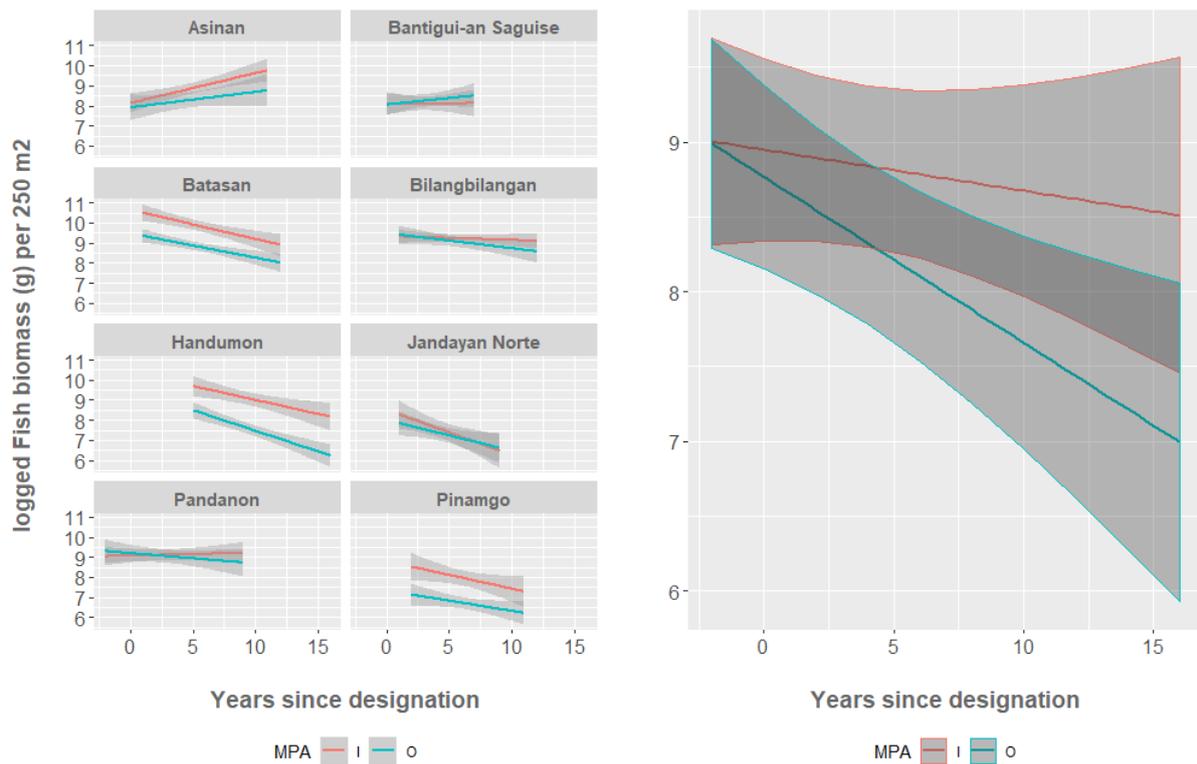


Figure 22. Logged fish biomass ( $\text{g m}^{-2} \text{ year}^{-1}$ ) recorded inside (I) and outside (O) of Marine Protected Area (MPA) protection within the Danajon bank, Philippines. Linear models plotted with biannual time since designation, for each site (left), and for pooled sites (right). 95 % CI of models shown in grey.

On a site level Asinan saw increases in fish biomass through time both inside and outside of MPAs, while Batasan, Handumon, Jandayan Norte and Pinamgo all saw significant declines inside and outside of MPAs (although Batasan's decline was slightly faster inside). Bantigui-an-Saguisse, Bilang-bilangan and Pandanon saw no change through (Appendix 8).

## *Fish community changes through time*

### Size distribution

The size spectra of fish found throughout the Danajon bank has shifted towards proportionally higher abundance of smaller-bodied (~ 5-10 cm) fish through time, in unprotected reef areas (Appendix 7). Inside MPAs the size spectra is more evenly spread with the majority of fish in the range of 5-25 cm long. In the first year of designation size spectra densities were not significantly different inside and outside of MPAs ( $p = 0.32$ ), but became significantly right skewed outside of MPAs in year 5 ( $p < 0.001$ ), and year 10 ( $p < 0.001$ ). Following separation of fish abundance density data into five binned size-classes, no size categories inside MPAs except the 20-30 cm class showed significant decline (Figure 23).

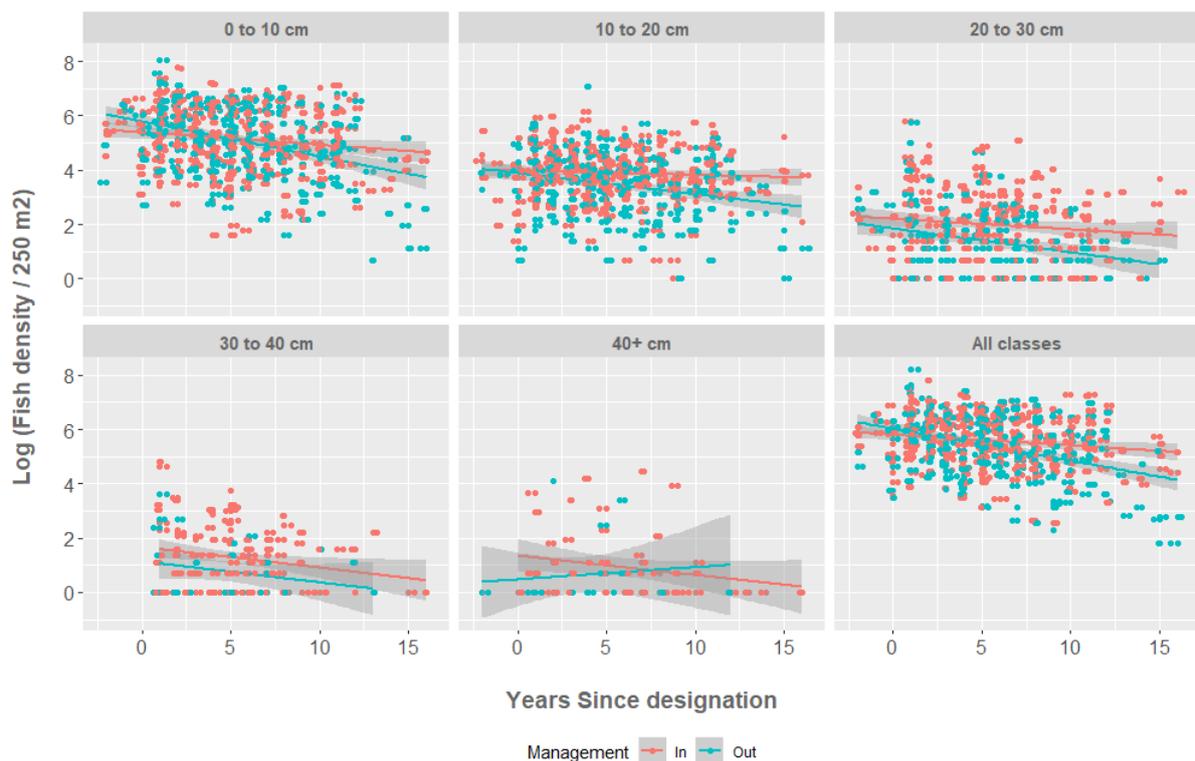


Figure 23. Linear regressions for (logged) fish count density ( $m^{-2}$ ) inside and outside sites, for the period 2000 to 2011, within eight small-scale Philippine MPAs. Fish separated into five 10 cm (total length) size bins, and pooled for all size classes. The 40 cm+ size class includes all size classes 40 – 100 cm. Note data points  $< 0$  represent pre-designation monitoring.

However, outside of protection, the rate of change in density through time was shown to differ significantly within the 0-10 cm, 10-20 cm, and 20-30 cm size classes, with the greatest rate of decline seen in the 20-30 cm size class fish outside of protection (Appendix 9). Significantly reduced initial density was observed in the 20-30 and 30-40 cm size classes outside of protection, and significantly elevated density found outside in the 0-10 cm size class.

#### Relative fish abundances

The relative mean abundances of the small-bodied and highly reef-associated Apogonidae, Blennidae, Centriscidae, Gobiidae, Monacanthidae, Plotosidae, Pinguipedidae, Syngnathidae and Tetradontidae decreased significantly both inside and outside of protection across the Danajon bank through the period 2000 to 2011 (Figure 24).

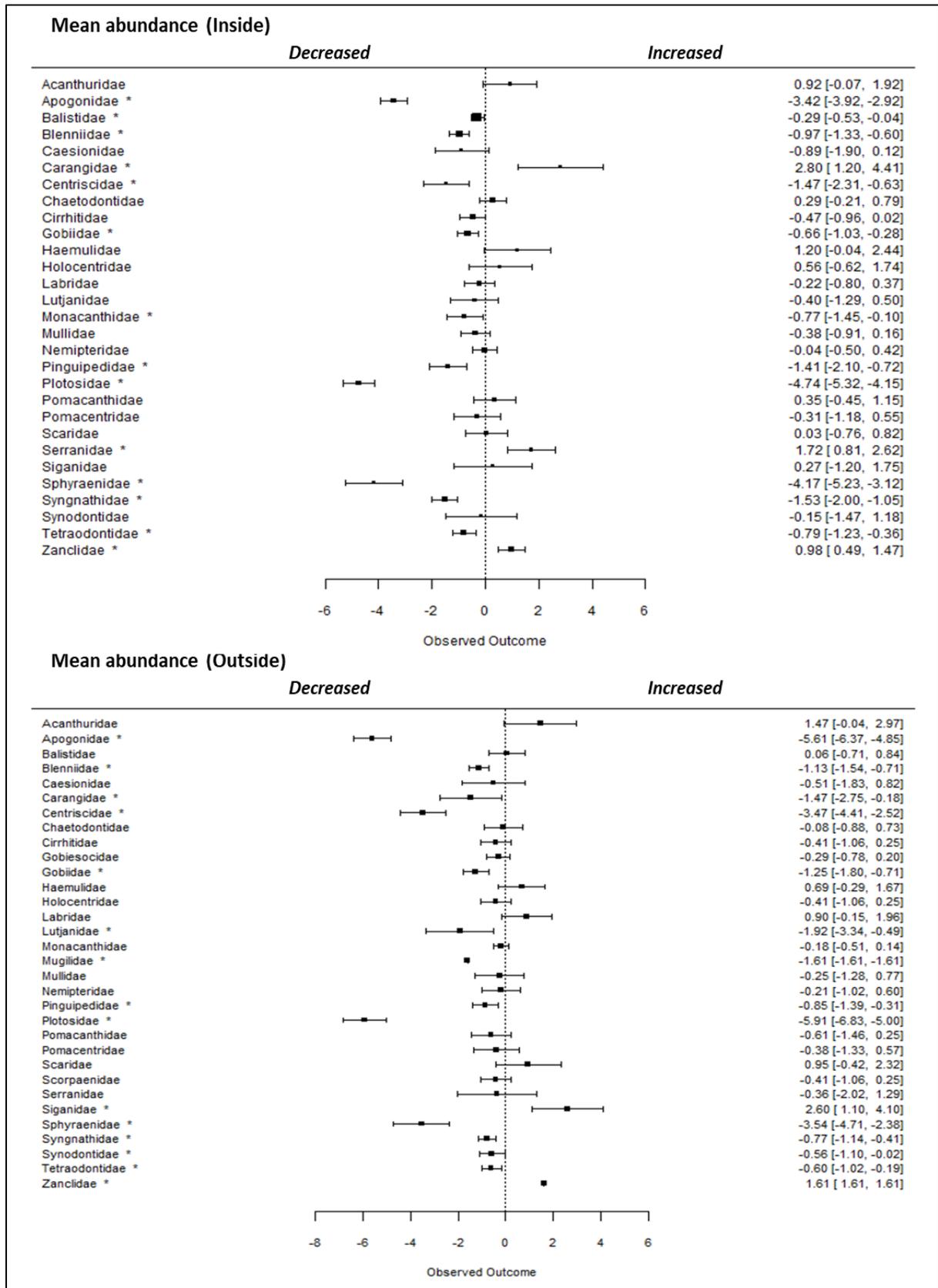


Figure 24. Forest plots of the natural log transformed response ratio (lnRR) of fish Family mean abundances from eight Philippine Marine Protected Areas (MPAs), between the period 2000 to 2011

(inside and outside of MPAs shown in top and bottom plot respectively). Effect size from zero illustrated with squares, with lines illustrating 95% CI and significance indicated with (\*). Mean and CI values also printed right.

The larger-bodied Balistidae and Sphyraenidae also significantly decreased inside protected areas, while the commercially valuable Carangidae, and Serranidae were seen to significantly increase, along with marginally significant increases in Acanthuridae and Haemulidae, which are also commonly targeted.

Outside of protection, along with the reductions of the small-bodied / low trophic level fish, significant decreases were seen in the high commercially valued Carangidae, Lutjanidae, Mugilidae, and Sphyraenidae, as well as losses in the common bycatch fish the Synodontidae, and significant increases in the Signanidae foodfish and Zanclidae, with marginally significant increases in the Acanthuridae.

In 2011 alone, (after protection of 8-15 years across sites), significant differences are seen inside versus outside of MPAs in Chaetodontidae, Haemulidae, Holocentridae, and Serranidae, which were all more abundant inside managed areas (Figure 25). All these families are large-bodied commercial valuable food fish, or in the case of the Chaetodontidae are valuable for the aquaria trade and sensitive to disturbance, being typically corallivores (Appendix 4). The only Family with significantly higher abundance outside of MPAs was Zanclidae.

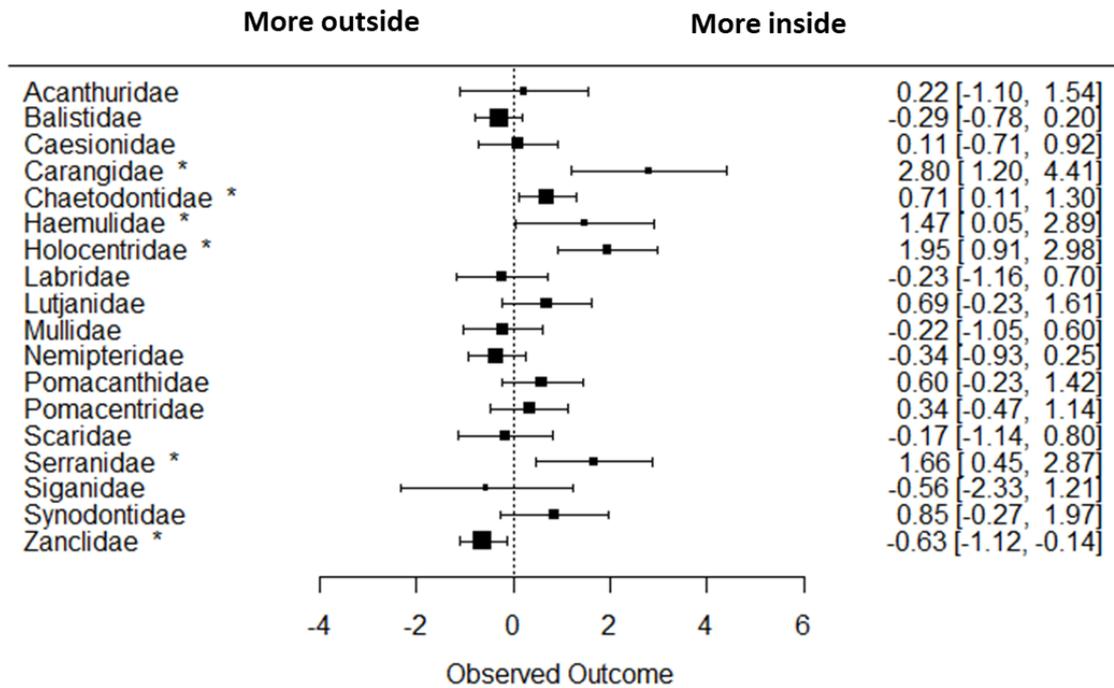


Figure 25. Forest plots of the natural log transformed response ratio of fish Family mean abundances inside and outside of eight Philippine Marine Protected Areas (MPAs), in 2011. Effect size from zero illustrated with squares, with lines illustrating 95% CI and significance indicated with (\*). Mean and CI values also printed right.

### Fish trophic composition

Following separation of the fish family biomass into trophic groups, declines through time were seen both inside and outside of MPAs for the piscivores, scavengers and invertivores (Figure 26).

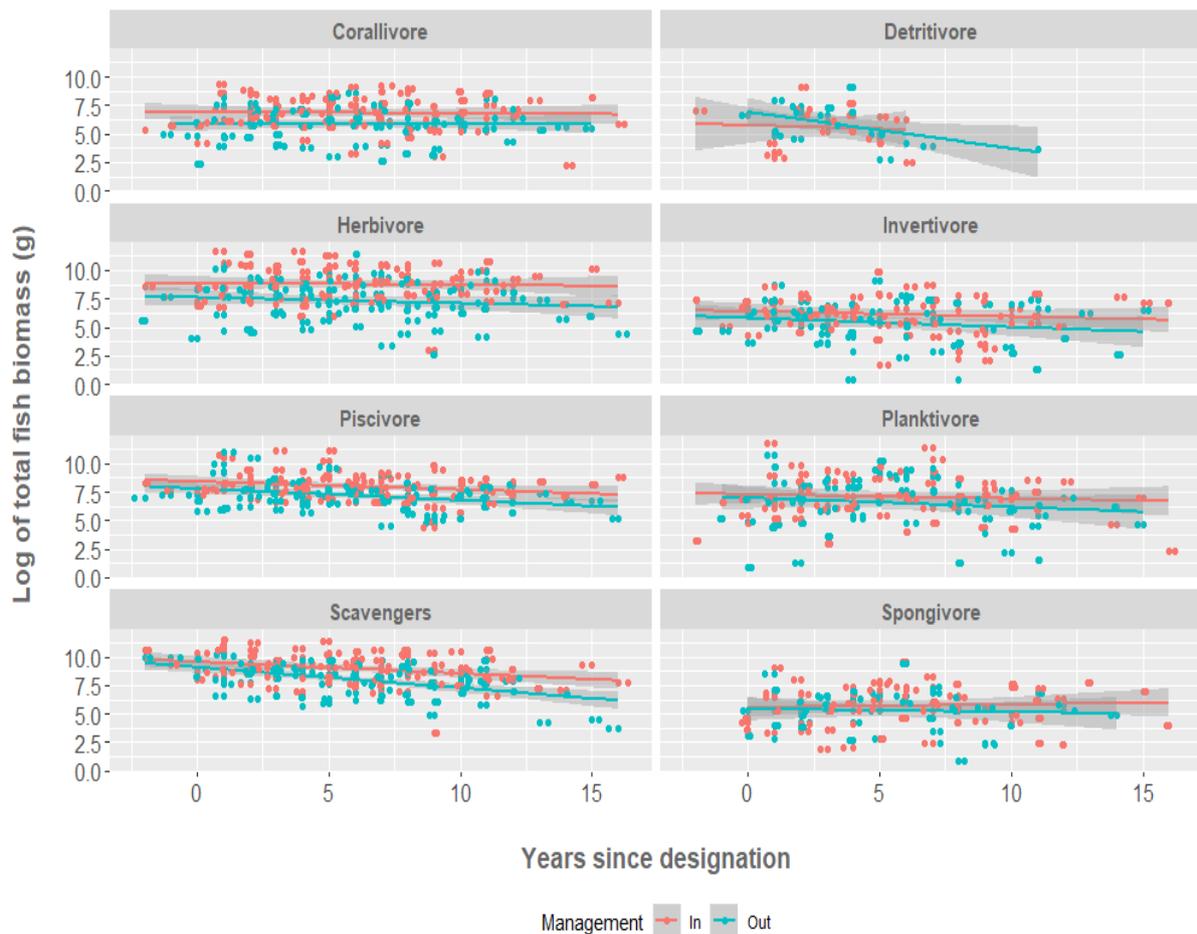


Figure 26. Log-transformed fish biomass (g / 250 m<sup>2</sup>) inside and outside of Marine Protected Areas (MPAs) through time, for eight Family-level trophic groups in the Danjon bank. Data pooled across all eight MPA locations and SE shown.

Declines in fish biomass through time were most pronounced in the scavengers (i.e. the Haemulidae (grunts), Labridae (wrasse) and Mullidae (goatfish)), with significant declines both inside and outside of MPA protection, but with steeper declines outside and significantly lower initial biomass (Appendix 10). The Piscivores (i.e. the Carangidae (jacks), Lethrinidae (emperors), Serranidae (groupers) *etc.*) similarly showed significant declines both inside and outside of protection, with reduced initial biomass outside, but no difference observed in the rate of decline between management. Invertivores (i.e. the Gobiidae (gobies), Balistidae (triggerfish), and Monacanthidae (filefish) *etc.*) again saw significant declines

inside and outside, but no significant difference between management types. All other groups saw no significant decline through time following MPA designation, however the corallivores and herbivores had significantly reduced biomass outside of protection.

## Discussion

Overall fish biomass and abundance declined significantly in unprotected areas across the Danajon bank region over the 12 year study period. This decline was most pronounced for larger fish (20 cm +), most likely due to their higher value as food fish in the region. This suggestion is supported by analysis of which families have seen the greatest declines, which are largely high- to medium-value food fish, such as the jacks, snapper, mullet and barracuda, all targeted heavily by local fisheries. Concurrent increases in Serranidae (grouper), Haemulidae (grunts), Holcentridae (soldierfish) and Pomacanthidae (angelfish) were seen inside protected sites, indicating that the MPA sites are being effective to some degree in protecting exploited fisheries. While all size groups were seen to be declining (with larger bodied fish (20-30 cm) outside of protection declining fastest of all size groups), the community overall shifted towards a greater proportional dominance of small-bodied fish, which indicates focussed removal of more valuable adult fish and potentially a result of shifting tropho-dynamics due to reduced predation from the large piscivore / scavenger fish throughout the reef (Wilson *et al.*, 2008; Ritchie and Johnson, 2009; Mumby *et al.*, 2012).

Chaetodontidae (butterflyfish), which are highly reef-associated small-bodied obligate corallivores, and therefore typical indicators of healthy reefs (Hodgson, 1999), were consistently more abundant within protected sites than outside. However, while the proportion of smaller fish within the community as a whole increased through time, significant reductions were seen both inside and outside of sites for a number of specific small-bodied, highly reef-associated family groups, including the Apogonidae (cardinalfish), Syngnathidae (pipefish), Blennidae (blennies) and Centriscidae (shrimpfish), with small (0-10 cm) body size fish declining faster outside of management.

As most of these fish families are not typically targeted for the aquarium trade, their decrease suggests that the benthos was seeing a loss in coral cover, or more specifically losing the coral diversity and structure, within which these groups live and feed (Syms and Jones, 2000; Darling *et al.*, 2017; Richardson *et al.*, 2018). There was however no evidence of significant declines in live coral cover over this period, or any significant shift in the composition of the major substrate categories within each site, even outside of protection. A weak shift towards communities with less branching, table, foliose and mushroom growth forms was observed but was again not significantly different between management types for each site or through time.

Given that no overall changes were observed in benthic form, cover or composition through time, and differences were instead largely due to site level heterogeneity, with indicators of coral health such as the butterflyfish remained stable, the fishing in this localised region would appear to typically not be directly damaging to the benthos unless intensive blast-fishing is employed (Selgrath, Gergel & Vincent 2017; Chapter 3). However, it is also noted here that the lack of any significant change in benthic composition could be in part due to the survey method missing species-level changes, as only broad substrate types and growth forms were recorded (Bertrand *et al.*, 2006; Murphy and Jenkins, 2010). If one is to assume the lack of benthic community change is correct, it would seem reasonable to conclude that the size-selective reduction in fish populations is then largely due to focussed fishing pressure of medium to large-bodied commercially valuable fisheries, rather than any significant overall declines in benthic habitat availability (Pauly, 1998; Robinson *et al.*, 2017b; Cinner *et al.*, 2018b). The losses in small-bodied fish could then be due to a trophic cascade effect of the loss of large piscivores and scavengers (Casey *et al.*, 2017; Robinson *et al.*, 2017b)

creating a meso-predator release and greater predation of low trophic groups (Ritchie and Johnson, 2009; Hempson *et al.*, 2018).

However, the loss of a range of some smaller-bodied fish families both inside and outside of MPAs, could also potentially demonstrate a lag effect of the 1998 global bleaching episode, which saw Philippines-wide reductions in coral cover, including around Bohol (Magdaong *et al.*, 2014), and subsequent loss of habitat and food before focussed monitoring began for this study (Wilson *et al.*, 2006; Robinson *et al.*, 2018). This explanation matches well to modelled predictions of fish biomass loss following habitat degradation (Rogers *et al.*, 2018a, 2018b), and to a similar study in the Seychelles, where post-bleaching reductions in structural complexity and habitat availability led to reductions in small and large fish in the region, regardless of MPA protection, for many years after the disturbance (Graham *et al.*, 2007).

Post-disturbance regime / phase shifts have been well documented in many reef systems following the 1998 global bleaching event, which saw many reefs move from a coral-dominated system to an algae-dominated system as the effects of wide-spread heat-induced coral mortality, high localised nutrient loads and reduced herbivorous fish abundance from over-fishing, interacted to inhibit coral recovery (Hughes *et al.*, 2007; Graham *et al.*, 2015; Hughes *et al.*, 2018b). The subsequent effects on associated fish community trophic structure are however less well studied, but are likely to be widespread given the heavy reliance of many fish on reefs for food and shelter (Wilson *et al.*, 2006; Pratchett *et al.*, 2011; Robinson *et al.*, 2018). While no significant increase in algae has been observed in this system following the major bleaching event, the alteration in relative biomass across trophic levels is similar to those seen in other reefs recovering from combined bleaching and local pressures, with

relatively elevated biomass at low trophic levels, and reduced biomass at mid to top trophic levels (Graham *et al.*, 2017; Hempson *et al.*, 2018). The observed state of the reef communities would therefore seem to be indicative of a community both still in recovery from global environmental pressures (i.e. heat-induced mortality), and under sustained localised fishing pressures, but not regime-shifted.

Changes through time to coral cover on a site by site level were only significant in Bilang-bilangan (seeing a significant increase inside), and Pandanon (seeing a significant decrease inside), which matches well to my earlier studies which found Bilang-bilangan to be relatively well managed whereas Pandanon was seen to have regular blast-fishing occurring, even inside the MPA limits earlier in the site's reserve history, causing loss of structure and difficulty recovering (Chapter 3).

Trends in fish biomass were much more consistently negative within sites across the region than trends in substrate, with the only site seeing an increase in biomass being Asinan. Significant reductions were seen across all other sites except Bantigui an-Saguise and Bilang-bilangan, with the strongest declines in the central sites of Jandayan Norte, Handumon, and Pinango. Given that the CCEF management effectiveness scores around all sites were high, the increased rate of decline in biomass occurring around the central sites of the municipality of Getafe relative to other sites is likely due to their close proximity to the population hub of Cebu city and its ports, which is the second most populous area of the Philippines. This reduction in over fish stocks (both inside and outside of sites) matches well with larger studies showing that as population size and accessibility to reefs, termed 'gravity' of human impacts, increases (Cinner *et al.*, 2018b), the biomass of fish seen in these areas - even inside MPAs - will typically be lower (Cinner *et al.*, 2016; Heenan *et al.*, 2016).

Robinson *et al.* (2017) found that the size structure of fish communities was a reliable indicator for level of exploitation, with the slope relating fish size-spectra index to human population size steepening as proximity to market increased (i.e. relative reductions are observed in biomass of large fish, and increases are observed in small fish). While the usefulness of size-based fishery indicators is still understudied (Nash and Graham, 2016), the results of my research indicate that this fishery is likely being most impacted by selective fishing pressure through time, but that the use of MPAs as a management tool is slowing this effect overall. Despite this, the current extent of overall biomass reduction and continued decline in large fish seen throughout the Danajon bank is likely to increasingly hinder these fisheries' future sustainability through reduced numbers of large fecund female fish, which are able to re-populate exploited reefs (Pauly *et al.*, 2002; Hixon *et al.*, 2014).

## **Conclusions**

This study has shown that this reef system is under a range of intense localised pressures, from high levels of fishing and close proximity to dense human populations, which are leading to sustained declines in fish populations. This area is furthermore still recovering from large-scale disturbance events including coral bleaching and frequent typhoons which have long-term effects on both the benthos and associated fish populations. Despite these impacts, small-scale MPAs that are well enforced appear to reduce the rate at which fisheries are declining across a range of fish sizes and life-history characteristics, protecting a range of exploited family groups. While some individual sites are faring better than others, the higher rates of decline in MPAs in close proximity to population hubs indicate that larger MPAs or broader fisheries management in areas close to populated areas, would be highly beneficial. Finally, given that many of the sites have declining fish biomass even inside the

MPA limits, which may be a result of edge effects from their small size, lack of connectivity, or an inadequate patch size to viably maintain the community (Joint Nature Conservation Committee, 2010; Edgar *et al.*, 2014; Roberts *et al.*, 2017), an increase in the number of these small sites or an enlargement of their size may help slow the overall decline of fish populations in this region by better protecting the more mobile and highly exploited large adult fish.

At the other end of the conservation spectrum to these small locally-managed reserves, 'Very Large Marine Reserves' (VLMRs), designed to reduce the slow declines from edge effects and unviable patch sizes, have seen some success in both enhancing connectivity and protecting highly-mobile species such as sharks and turtles (Singleton and Roberts, 2014). However, these areas can nonetheless still be impacted by large-scale environmental disturbances (Halpern *et al.*, 2015; Jones *et al.*, 2018). In the next chapter I investigate the effect of such environmental disturbance on a remote reef system within one of the world's largest MPAs, the 'British Indian Ocean Territory Marine Protected Area', to disentangle the effects of human and environmental pressures on reef benthic physical structure.

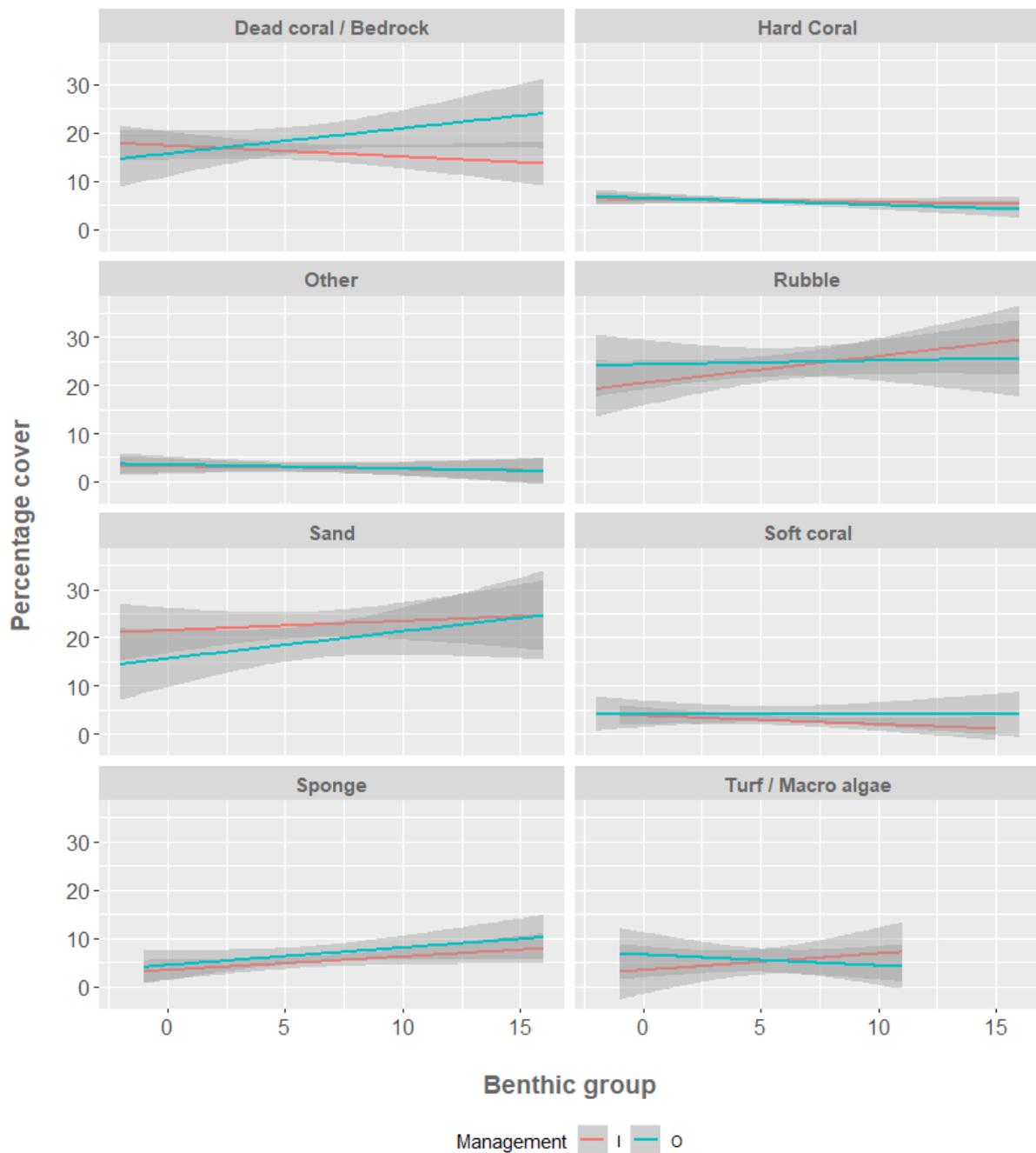
## Appendices

Appendix 4. Broad classification of fish families by commercial value for food, whether generally valued for the aquaria trade, their typical trophic group, and level of reef association. Categories based on (Samoilys *et al.*, 2007; McClanahan, 2014; Froese and Pauly, 2018).

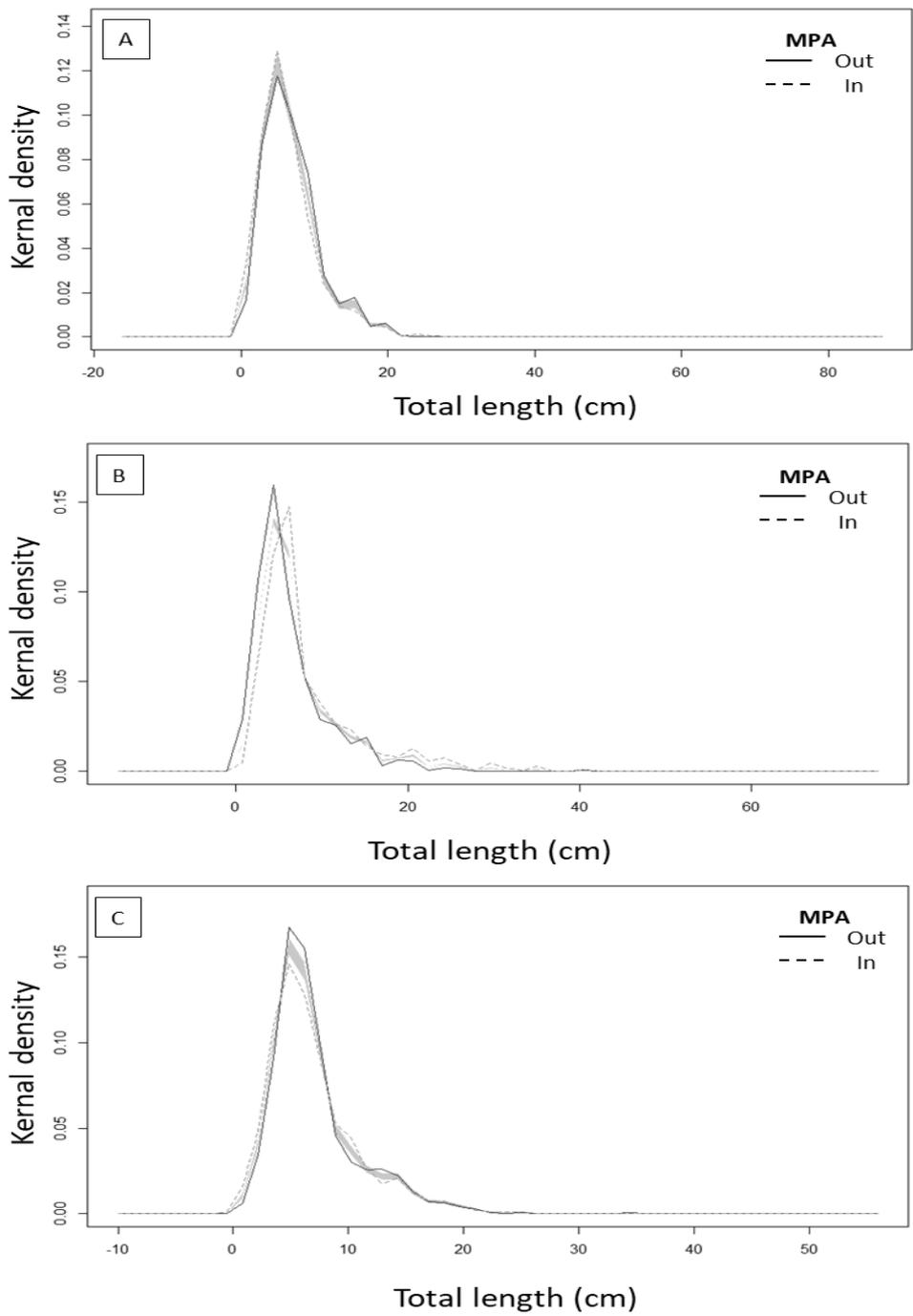
Family	Commercial food value	Aquaria species	Primary typical feeding trait	Reef-association
<b>Acanthuridae (Surgeonfish)</b>	Medium	Yes	Herbivore	Medium
<b>Apogonidae (Cardinalfish)</b>	Low	Yes	Planktivore	High
<b>Balistidae (Triggerfish)</b>	Medium	No	Invertivore	Medium
<b>Blenniidae (Blennies)</b>	Low	No	Herbivore	High
<b>Caesionidae (Fusiliers)</b>	Low	No	Planktivore	Medium
<b>Carangidae (Jacks)</b>	High	No	Piscivore	Low
<b>Centriscidae (Shrimpfish)</b>	Low	Yes	Planktivore	Medium
<b>Chaetodontidae (Butterflyfish)</b>	Low	Yes	Corallivore	High
<b>Cirrhitidae (Hawkfish)</b>	Low	No	Invertivore	High
<b>Gerreidae (Silver biddies)</b>	Low	No	Invertivore	High
<b>Gobiesocidae (Clingfish)</b>	Low	No	Invertivore	High
<b>Gobiidae (Gobies)</b>	Low	No	Invertivore	High
<b>Haemulidae (Sweetlips/grunts)</b>	High	Yes	Scavengers	Medium
<b>Holocentridae (Soldierfish)</b>	Medium	No	Invertivore	Medium
<b>Labridae (Wrasses)</b>	Medium	No	Scavengers	Medium
<b>Lethrinidae (Emperors)</b>	High	No	Piscivore	Medium
<b>Lutjanidae (Snappers)</b>	High	No	Piscivore	Medium
<b>Monacanthidae (Filefish)</b>	Low	Yes	Invertivore	Medium
<b>Mugilidae (Mullet)</b>	Medium	No	Detritivore	Medium
<b>Mullidae (Goatfish)</b>	Medium	No	Scavengers	Medium
<b>Nemipteridae (Breems)</b>	High	No	Piscivore	Medium
<b>Pinguipedidae (Sandperch)</b>	Low	No	Piscivore	Medium
<b>Plotosidae (Eeltail Catfish)</b>	Low	Yes	Detritivore	Medium
<b>Pomacanthidae (Angelfish)</b>	Medium	Yes	Spongivore	Medium
<b>Pomacentridae (Damsel fish)</b>	Low	Yes	Herbivore	High
<b>Scaridae (Parrotfish)</b>	Medium	No	Herbivore	Medium
<b>Scorpaenidae (Scorpionfish)</b>	Low	Yes	Piscivore	High
<b>Serranidae (grouper)</b>	High	No	Piscivore	Medium
<b>Siganidae (Rabbitfish)</b>	Medium	No	herbivore	Medium
<b>Sphyrnidae (Barracudas)</b>	High	No	Piscivore	Low
<b>Syngnathidae (Pipefish)</b>	Low	Yes	Planktivore	High
<b>Synodontidae (Lizardfish)</b>	Low	No	Piscivore	High
<b>Tetraodontidae (Pufferfish)</b>	Low	Yes	Piscivore	High
<b>Zanclidae (Moorish Idol)</b>	Low	No	Spongivore	Medium

Appendix 5. Model estimates from a linear mixed effects model of the effects of time (years) and management (in / out of eight Marine Protected Area sites within the Danajon Bank) on (square-root transformed) coral cover, separated to illustrate site-level random effects within the model. \*\*\* p < 0.001; \*\* p < 0.01; \* p < 0.05

Site	Parameter	Intercept (Inside)	Year	Management	Year x Management
<b>Asinan</b>	Estimate	6.50	-0.04	0.76	-0.17
	t value	<b>16.16 ***</b>	-0.65	1.10	-1.43
<b>Bantigui-an Saguise</b>	Estimate	5.57	0.00	-0.48	0.13
	t value	<b>12.17 ***</b>	0.01	-0.75	0.79
<b>Batasan</b>	Estimate	6.04	-0.11	0.31	0.15
	t value	<b>14.16 ***</b>	-1.72	0.51	1.61
<b>Bilangbilangan</b>	Estimate	6.03	0.13	0.30	-0.26
	t value	<b>15.94 ***</b>	<b>2.35 *</b>	0.51	<b>-2.90 **</b>
<b>Handumon</b>	Estimate	4.71	-0.06	0.47	-0.02
	t value	<b>7.01 ***</b>	-0.93	0.51	-0.19
<b>Jandayan Norte</b>	Estimate	3.40	0.06	-0.35	-0.05
	t value	<b>6.73 ***</b>	0.62	-0.48	-0.36
<b>Pandanon</b>	Estimate	5.82	-0.34	-0.16	0.14
	t value	<b>19.46 ***</b>	<b>-4.80 ***</b>	-0.30	1.16
<b>Pinamgo</b>	Estimate	3.07	0.12	-0.51	-0.09
	t value	<b>5.13 ***</b>	1.31	-0.58	-0.69



Appendix 6. Linear model outputs for percentage cover change since Marine Protected Area (MPA) designation for surveys within eight sites, both inside (I) and outside (O) of MPA protection, within the Danajon Bank, Philippines. Outputs grouped by benthic type with SE shown in grey.



Appendix 7. Fish total length kernel distributions for all fish species surveyed inside and outside of eight Marine Protected Areas (MPAs) along the Danajon Bank, Philippines during 1999 – 2011. Years since designation shown A) 0 years, B) 5 years, and c) 10 years. The grey-shaded area indicates one standard error either side of the null model of no difference in length distribution based on protection.

Appendix 8. Model estimates from a linear mixed effects model of log-transformed fish biomass against the interacting effects of Years Since Designation (YSD) and whether in / out of Marine Protected Area (MPA). Table separated to individual sites to illustrate site-level random effects within the model. \*\*\*  $p < 0.001$ ; \*\*  $p < 0.01$ ; \*  $p < 0.05$

Site	Parameters	Intercept (Inside)	YSD	Management	YSD x Management
<b>Asinan</b>	Estimate	8.14	0.15	-0.23	-0.07
	t value	<b>34.96 ***</b>	<b>3.73 ***</b>	-0.59	-1.06
<b>Bantigui-an Saguise</b>	Estimate	8.11	0.00	-0.05	0.06
	t value	<b>28.38 ***</b>	0.02	-0.13	0.59
<b>Batasan</b>	Estimate	10.64	-0.15	-1.18	0.03
	t value	<b>44.79 ***</b>	<b>-3.95 ***</b>	<b>-3.53 ***</b>	0.48
<b>Bilangbilangan</b>	Estimate	9.34	-0.02	0.14	-0.06
	t value	<b>42.89 ***</b>	-0.61	0.41	-1.08
<b>Handumon</b>	Estimate	10.38	-0.14	-0.87	-0.07
	t value	<b>28.19 ***</b>	<b>-3.78 ***</b>	-1.68	-1.27
<b>Jandayan Norte</b>	Estimate	8.50	-0.23	-0.51	0.07
	t value	<b>26.52 ***</b>	<b>-3.65 ***</b>	-1.13	0.83
<b>Pandanon</b>	Estimate	9.08	0.01	0.12	-0.07
	t value	<b>51.44 ***</b>	0.36	0.38	-0.96
<b>Pinamgo</b>	Estimate	8.79	-0.14	-1.47	0.04
	t value	<b>23.01 ***</b>	<b>-2.43 *</b>	<b>-2.63 **</b>	0.44

Appendix 9. Linear mixed effects model estimates of fish density, investigating the interacting effects of Management – whether in / out of Marine Protected Areas (MPAs), and Years Since Designation (YSD) for all eight sites in the Danajon Bank. Analyses separated into five (10 cm) Total Length size class bins. Site is a random factor.

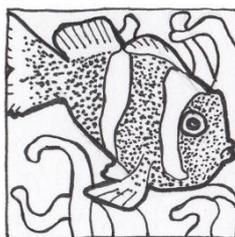
<b>0 - &lt;10 cm</b>	<b>Estimate</b>	<b>t value</b>	<b>95% Confidence interval</b>	<b>R<sup>2</sup> (fixed)</b>	<b>R<sup>2</sup> (total)</b>
(Intercept)	5.22 ***	19.64, p = 0.00	[4.70, 5.74]	0.05	0.63
YSD	-0.03	-0.87, p = 0.20	[-0.10, 0.04]		
Management(Out)	0.47 ***	3.89, p = 0.00	[0.23, 0.70]		
YSD:Management(Out)	-0.07 ***	-4.16, p = 0.00	[-0.11, -0.04]		
N (transects)	570.00				
<b>≥10 - &lt; 20 cm</b>					
(Intercept)	3.87 ***	20.01, p = 0.00	[3.49 - 4.25]	0.04	0.37
YSD	-0.01	-0.16, p = 0.44	[-0.07, 0.06]		
Management(Out)	-0.07	-0.47, p = 0.32	[-0.34, 0.21]		
YSD:Management(Out)	-0.05 **	-2.61, p = 0.00	[-0.09, -0.01]		
N (transects)	569.00				
<b>≥ 20 - &lt; 30 cm</b>					
(Intercept)	2.23 ***	6.78, p = 0.00	[1.59, 2.88]	0.13	0.36
YSD	-0.08 *	-2.46, p = 0.02	[-0.14, -0.02]		
Management(Out)	-0.37 *	-1.85, p = 0.03	[-0.75, 0.02]		
YSD:Management(Out)	-0.05 *	-1.76, p = 0.04	[-0.12, 0.01]		
N (transects)	395.00				
<b>≥ 30 - &lt; 40 cm</b>					
(Intercept)	1.49 ***	4.79, p = 0.00	[0.92, 2.06]	0.07	0.20
YSD	-0.08	-1.65, p = 0.09	[-0.14, -0.01]		
Management(Out)	-0.71 *	-1.79, p = 0.04	[-1.47, 0.06]		
YSD:Management(Out)	0.03	0.51, p = 0.31	[-0.09, 0.16]		
N (transects)	155.00				
<b>≥ 40 cm</b>					
(Intercept)	1.16 *	2.52, p = 0.02	[0.37, 1.95]	0.03	0.12
YSD	-0.03	-0.40, p = 0.36	[-0.16, 0.09]		
Management(Out)	-0.77	-1.40, p = 0.08	[-1.81, 0.27]		
YSD:Management(Out)	0.10	0.93, p = 0.18	[-0.10, 0.29]		
N (transects)	72.00				

Appendix 10. Linear mixed effects model outputs for each of eight fish trophic groups in the Danajon bank, investigating the interacting effects of Management – whether in / out of Marine Protected Areas (MPAs), and Years Since Designation (YSD). Data pooled across eight MPAs monitored between 2000 and 2011.

Parameters	Estimate	t value	95% Confidence interval	R <sup>2</sup> (fixed)	R <sup>2</sup> (total)
<b>Corallivore</b>					
(Intercept)	7.17 ***	16.66, p = 0.00	[6.33, 8.01]	0.12	0.44
YSD	-0.06	-1.16, p = 0.14	[-0.15, 0.04]		
Management (Out)	-1.16 ***	-3.30, p = 0.00	[-1.85, -0.47]		
YSD: Management (Out)	0.02	0.40, p = 0.34	[-0.08, 0.12]		
N (Transects)	164.00				
<b>Detritivore</b>					
(Intercept)	5.74 ***	7.81, p = 0.00	[4.41, 7.07]	0.11	0.11
YSD	-0.06	-0.30, p = 0.39	[-0.44, 0.31]		
Management (Out)	1.18	1.05, p = 0.15	[-0.71, 3.07]		
YSD: Management (Out)	-0.26	-0.83, p = 0.21	[-0.74, 0.23]		
N (Transects)	37.00				
<b>Herbivore</b>					
(Intercept)	9.13 ***	15.35, p = 0.00	[7.97, 10.30]	0.17	0.71
YSD	-0.07	-1.26, p = 0.12	[-0.17, 0.04]		
Management (Out)	-1.25 ***	-4.20, p = 0.00	[-1.83, -0.66]		
YSD: Management (Out)	-0.04	-0.87, p = 0.19	[-0.12, 0.04]		
N (Transects)	174.00				
<b>Invertivore</b>					
(Intercept)	7.22 ***	12.85, p = 0.00	[6.12, 8.32]	0.24	0.64
YSD	-0.24 *	-2.75, p = 0.01	[-0.41, -0.07]		
Management (Out)	-0.51	-1.24, p = 0.11	[-1.32, 0.30]		
YSD: Management (Out)	-0.07	-1.05, p = 0.15	[-0.19, 0.06]		
N (Transects)	132.00				
<b>Piscivore</b>					
(Intercept)	9.04 ***	21.34, p = 0.00	[8.21, 9.87]	0.30	0.66
YSD	-0.18 **	-4.07, p = 0.00	[-0.26, -0.09]		
Management (Out)	-0.64 **	-2.52, p = 0.01	[-1.14, -0.14]		
YSD: Management (Out)	-0.03	-0.83, p = 0.20	[-0.10, 0.04]		
N (Transects)	172.00				
<b>Planktivore</b>					
(Intercept)	7.90 ***	9.72, p = 0.00	[6.32, 9.48]	0.09	0.46
YSD	-0.13	-1.66, p = 0.06	[-0.28, 0.01]		
Management (Out)	-0.41	-0.80, p = 0.21	[-1.39, 0.58]		
YSD: Management (Out)	-0.05	-0.61, p = 0.27	[-0.19, 0.10]		
N (Transects)	134.00				

<b>Scavengers</b>					
(Intercept)	9.61 ***	18.68, p = 0.00	[8.60, 10.62]	0.22	0.71
YSD	-0.10 *	-2.19, p = 0.03	[-0.20, -0.01]		
Management (Out)	-0.46 *	-1.93, p = 0.03	[-0.94, -0.01]		
YSD: Management (Out)	-0.08 **	-2.40, p = 0.01	[-0.15, -0.01]		
N (Transects)	174.00				
<b>Spongivore</b>					
(Intercept)	5.22 ***	7.71, p = 0.00	[3.91, 6.54]	0.04	0.37
YSD	0.04	0.61, p = 0.28	[-0.08, 0.16]		
Management (Out)	-0.23	-0.40, p = 0.34	[-1.31, 0.85]		
YSD: Management (Out)	-0.08	-0.88, p = 0.19	[-0.23, 0.08]		
N (Transects)	110.00				





## *Chapter 5: Climate-driven declines in the physical structure of Indian Ocean coral reefs*

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### **Abstract**

Following the global bleaching episode of 2014 – 2017, reefs around the world have experienced widespread coral mortality and corresponding changes to the abundance and diversity of reef benthic and demersal species assemblages. Coral mortality is typically followed by rapid erosion of the physical 3D structure of colonies, which results in a flattening and simplification of the reef as whole, and ultimately a loss of both food and habitat for reef-associated fish. The remote, protected nature of the Chagos Archipelago in the centre of the Indian Ocean allows observation of the direct effects of climate-induced disturbance without the confounding pressures of nearby human populations.

In this study, I use an emerging monitoring technology, termed ‘Structure from Motion’ photogrammetry to assess the changes in 3D structure within the Chagos Archipelago. Surface complexity and reef height significantly declined while skew significantly increased within medium and highly exposed reefs from 2015 – 2018. Low exposure sites, including lagoon areas saw no significant change in structure through the period. Seaward reefs were affected by loss of structure down to 15 m, with significant losses occurring in depths of 5-10 m. The composition of the reef communities preceding heat stress was a strong indicator of the rate of subsequent decline. Reefs dominated by ‘competitive’ / ‘Complex’ clade species such as *Acropora Cytherea* and *A. Clathrata* were most vulnerable to heat-induced mortality, and the loss of their typically branching or tabular structure leading to the fastest declines in 3D complexity. Lagoon communities, dominated by species with stress-tolerant / ‘Robust’ clade traits, and a higher proportion of heterotrophs with massive / sub-massive morphologies fared best of all, appearing resilient to the heat stress despite the extended period of disturbance. Post-bleaching recruitment and re-growth has been observed within

the archipelago, but has not yet led to significantly increased 3D structure. Despite the remote and protected nature of these reefs, the significant declines in reef structure, following mortality initiated directly by a climatic heat anomaly, show that even in the absence of direct human pressures, reefs are no more resistant than elsewhere to climate change, and this pressure alone is capable of rapidly restructuring benthic communities.

## Introduction

The world's marine systems are undergoing a rapid period of change, brought about by a range of anthropogenic impacts which are fundamentally altering their ability to function, and are leading them – and the people who depend on them – toward an increasingly uncertain future (Harborne *et al.*, 2017; Nash *et al.*, 2017). Of the multiple impacts to which marine systems are subjected, increasing global temperatures and changing patterns of weather are of primary concern, particularly for highly sensitive ecosystems such as coral reefs (Graham *et al.*, 2006; Hoegh-Guldberg and Bruno, 2010; Hughes *et al.*, 2018b). The increasing frequency of coral bleaching events globally and the trends of future climate scenarios threatens the long-term sustainability of shallow tropical reef systems (Ainsworth *et al.*, 2016; van Hooidonk *et al.*, 2016; IPCC, 2018) and are likely to significantly alter reef benthic community assemblage structures (Darling *et al.*, 2013; Hughes *et al.*, 2018b), and the structure of associated fish communities (Richardson *et al.*, 2018).

The capacity for coral reefs to withstand potential regime shifts (from a coral to algal-dominated system) following climate-driven disturbance is attributed to a number of physical and ecological factors (McManus and Polsenberg, 2004; Hughes *et al.*, 2007, 2013). Reefs which are located at greater depth and which have high structural complexity, high density of juvenile corals, high abundances of herbivorous fishes and low nutrient loads, are more likely to survive than others (Graham *et al.*, 2015). High structural complexity in particular has been shown to be a key predictor for post-disturbance ecosystem trajectory, and has also been shown more widely to be integral to a number of ecological processes

associated with reefs, and the services that they provide (Graham and Nash, 2013; Richardson *et al.*, 2017b; Harris *et al.*, 2018; Rogers *et al.*, 2018b).

Loss of coral reef structural architecture can occur regionally through disease outbreaks and climate-induced mortality, or on a more localised scale through storm damage, destructive fishing or coastal development (Fabricius 2005; Fox & Caldwell 2006; Wilson *et al.* 2006; Alvarez-Filip *et al.* 2009; Chapter 3). The cumulative effect of these pressures has resulted in a generalised 'flattening' and simplification of reef structure, which is occurring over ecologically important scales (Alvarez-Filip *et al.*, 2009; Hoegh-Guldberg and Bruno, 2010). Coupled with the observed increase in direct physical disturbance to reefs is a reduced physiological capacity for subsequent regrowth as corals begin to reach environmental thresholds of thermal tolerance, acidity, carbonate-ion concentrations and aragonite saturation levels (Silverman *et al.*, 2009; Wild *et al.*, 2011; Descombes *et al.*, 2015; Hoegh-Guldberg *et al.*, 2017). However, the observed losses of structural complexity are typically non-linear and the confounding nature of multiple interacting pressures make it difficult to isolate the individual effects of each pressure (Alvarez-Filip *et al.*, 2009).

The British Indian Ocean Territory (BIOT), also known as the Chagos Archipelago, provides a rare opportunity to study the effect of climate-induced bleaching events in isolation from most other pressures, as it contains vast intact marine ecosystems, the majority of which have had no human habitation for the last 45 years (Sheppard *et al.*, 2012; Samoilyis *et al.*, 2018). The archipelago is situated on the Chagos-Laccadive ridge ~ 500 km south of the southern tip of the Maldives Archipelago, in the centre of the Indian Ocean. The archipelago comprises 58 small islands with fringing reefs, as well as a number of submerged atolls and slopes, with the central 'Great Chagos Bank' constituting the largest living coral atoll in the

world (Sheppard *et al.*, 2002). These reefs sit within a 'no-take' marine protected area (MPA), which was established in 2010 and covers the total Exclusive Economic Zone of 640,000 m<sup>2</sup> (Sheppard *et al.*, 2012). A UK-US naval base is located on Diego Garcia atoll in the south, and is the only inhabited island within the territory, accounting for approximately 1 % of the total area.

The BIOT MPA is an excellent reference site for the Indian Ocean despite the historic effects of over 200 years of human presence in these remote areas on the terrestrial ecology (Stoddart and Taylor, 1971), reefs (Hamylton and East, 2012; Graham *et al.*, 2018) and fisheries (Price and Harris, 2009; Ferretti *et al.*, 2018) of the archipelago. The level of current legislative protection, presence of the military base, low human population, and inherently remote nature of the islands make this one of the most 'pristine' and remote areas of reef in the world, away from the array of anthropogenic pressures normally experienced by reefs (Guitart *et al.*, 2007; Graham and McClanahan, 2013; Robinson *et al.*, 2017a; Jones *et al.*, 2018). This makes BIOT a useful location for answering questions about how ecosystems are changing due to climate-induced environmental disturbances.

During the period spanning 2014 – 2017, reefs across the world were exposed to an intense and prolonged period of elevated ambient water temperature triggered by an El-Niño Southern Oscillation (Eakin *et al.*, 2017), which caused widespread heat stress-induced coral bleaching and mortality (Hughes *et al.*, 2018a). The reefs of the Chagos Archipelago were no exception, with the sea-surface temperature (SST) anomaly period (between April 2015 – June 2016) resulting in extensive loss of live coral cover, particularly in shallow waters (<15 m), and with reefs across this region moving towards net negative carbonate budgets i.e. seeing many reefs shift to an erosional phase (Perry and Morgan, 2017; Sheppard *et al.*,

2017). Perry & Morgan (2017) recorded losses to the gross rugosity of reefs at 8 – 10 m across this region in the period immediately following the bleaching episode, however no published studies have quantified the extent of erosion or recovery over the two subsequent years within the Chagos Archipelago, or investigated the relationship between bleaching disturbance and 3D structure across depths.

The SfM approach allows us to assess larger scale rates of change than is typically possible using standard transect based measures, and can deliver detailed morphometric data on spatial patterns of substrate breakdown. In this study, I aim to quantify the extent to which a severe climate-driven heat anomaly has resulted in habitat-scale shifts in reef structural complexity, and test whether the rate of change is affected by wave-exposure regimes. I furthermore investigate which physical and biological components of the benthos contributed to spatial differences in the rate and extent of post-disturbance structural degradation in order to test whether individual species or traits have led to more severe / rapid structural declines..

## Materials and Methods

### *Data collection and experimental design*

Benthic surveys were conducted at 21 GPS and rebar marked sites across the British Indian Ocean Territory in April 2015, immediately preceding bleaching, and matched with comparable surveys at the exact same sites in April 2018, 18 months after the end of the extended bleaching episode. Sites were chosen to represent a range of exposure conditions in each region, with multiple replicates allowing statistical comparison across the archipelago (low exposure, n = 6; medium exposure, n = 10; high exposure, n = 5). In the intervening years of 2016 and 2017, a sub-section of sites (n=5 and n=15 respectively) were visited annually in April to examine the progression of physical change through time, focussing on just the sites in the northern atolls of the archipelago to increase statistical power.

Sites were grouped spatially into clusters separated by at least the typical maximum larval dispersal distance of corals (~25 – 50 km), based on estimates from multiple studies within the Indian Ocean (Underwood *et al.* 2013; Markey *et al.* 2016). This grouping resulted in three atoll regions across the archipelago: 1) Peros Banhos, 2) Salomon and Blenheim atoll, and 3) Western Great Chagos Bank (Figure 27; Appendix 11).

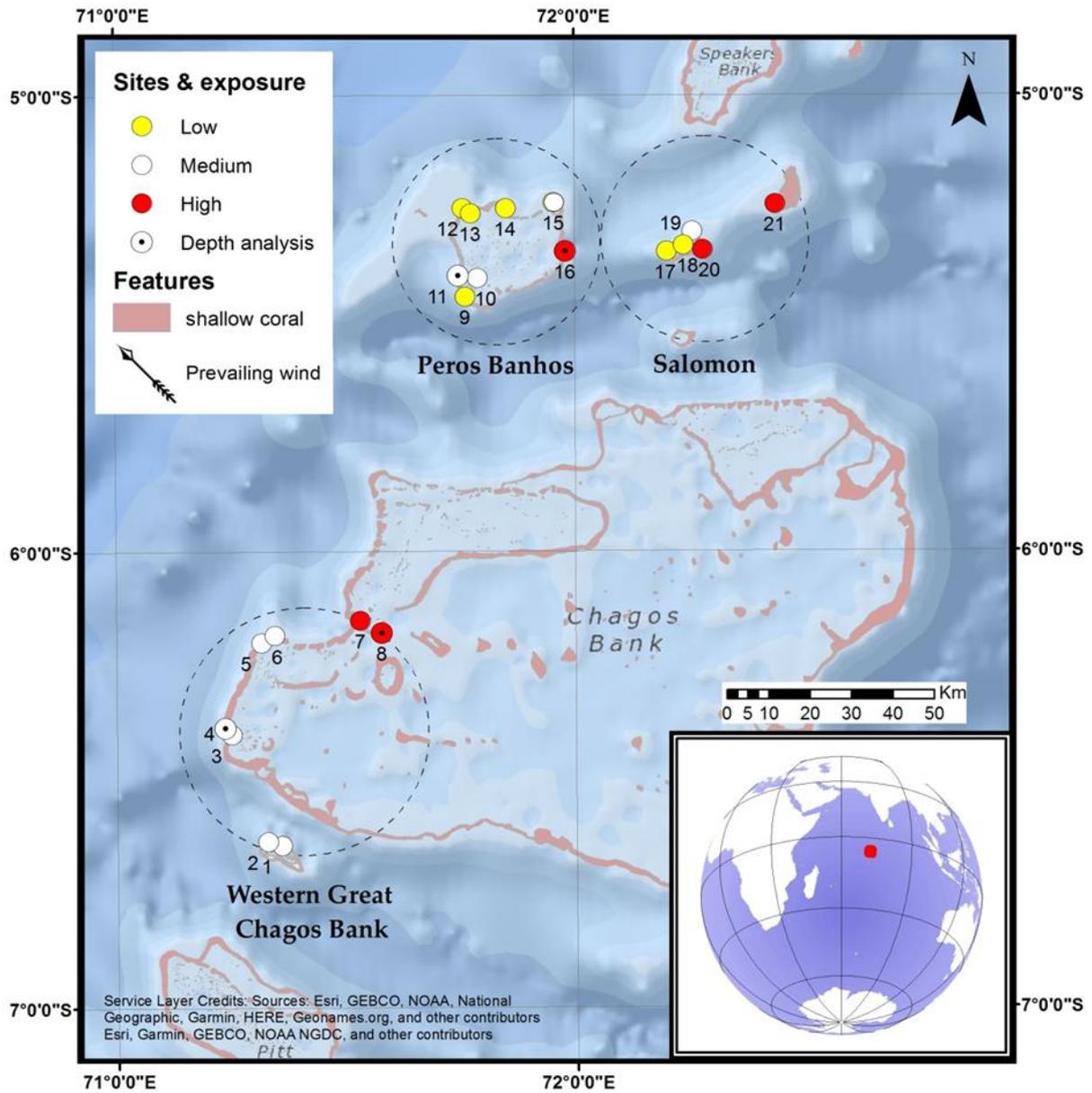


Figure 27. Site locations for surveys conducted within the Chagos Archipelago in April 2015 and 2018 (pre and post bleaching impact). Atoll groups based on 50 km centroid buffer (sites 1-8 = Western Great Chagos Bank group; sites 9-16 = Peros Banhos group; sites 17-21 = Salomon group). Low, medium and highly exposed sites illustrated with yellow, white and red circles respectively. Sites with additional depth analysis are shown with a central point.

In a subset of four sites across the archipelago (Location 4, 8, 11, and 16; Figure 27), video footage was recorded along three separate five-metre depth bands (20 – 15 m, 15 – 10 m and 10 – 5 m) in April 2015 and April 2018. These sites represent one sheltered and one exposed seaward site within each of two regions, the southern ‘Western Great Chagos Bank region’ and the northern ‘Peros Banhos atoll region’ (Figure 27).

### ***Imagery specification and analysis***

The 2015 analyses used video imagery captured using a Sony HDRCX550 digital camera (Sony Corporation, Tokyo, Japan) in a Light and Motion Bluefin housing with Fathom 90 wide angle port and red filter (Light & Motion Industries, California, USA) at 25 fps. Imagery was taken at ~1-2 m from the substrate, with reef-level scaling ascertained using camera-attached laser markers spaced 10 cm apart. Adobe Photoshop software was used to extract 2-minute sections of continuous footage from the middle of each of the three depth zones at each site. The footage was then converted into individual photo frames at a rate of 3 frames per second, following image de-interlacing. The resulting ~360 images per section were then stitched together using ‘structure from motion’ photogrammetric algorithms within ‘Agisoft Photoscan Professional’ software (Westoby *et al.*, 2012; Agisoft LLC, 2017), resulting in a dense xyz surface point cloud reconstruction of the reef. Each point cloud equated to a roughly 20 x 1 m reef area coverage once scaled (accuracy < 5 mm, calibrated from 3 scaling reference points).

The 2016, 2017 and 2018 analyses used camera imagery captured using a Nikon D750 DSLR camera (with 20 mm wide angle fixed lens and dome port) under ambient lighting at ~1-2 m from the substrate with in-situ reference scales positioned across the survey area. Surveys covered a planar area of approximately 200 m<sup>2</sup> consisting of ~1000 images per site. Images

were stitched together as above, with the resulting dense xyz pointcloud (accurate to < 5 mm) clipped to 20 x 2 m and exported to Gwyddion (Figure 28).

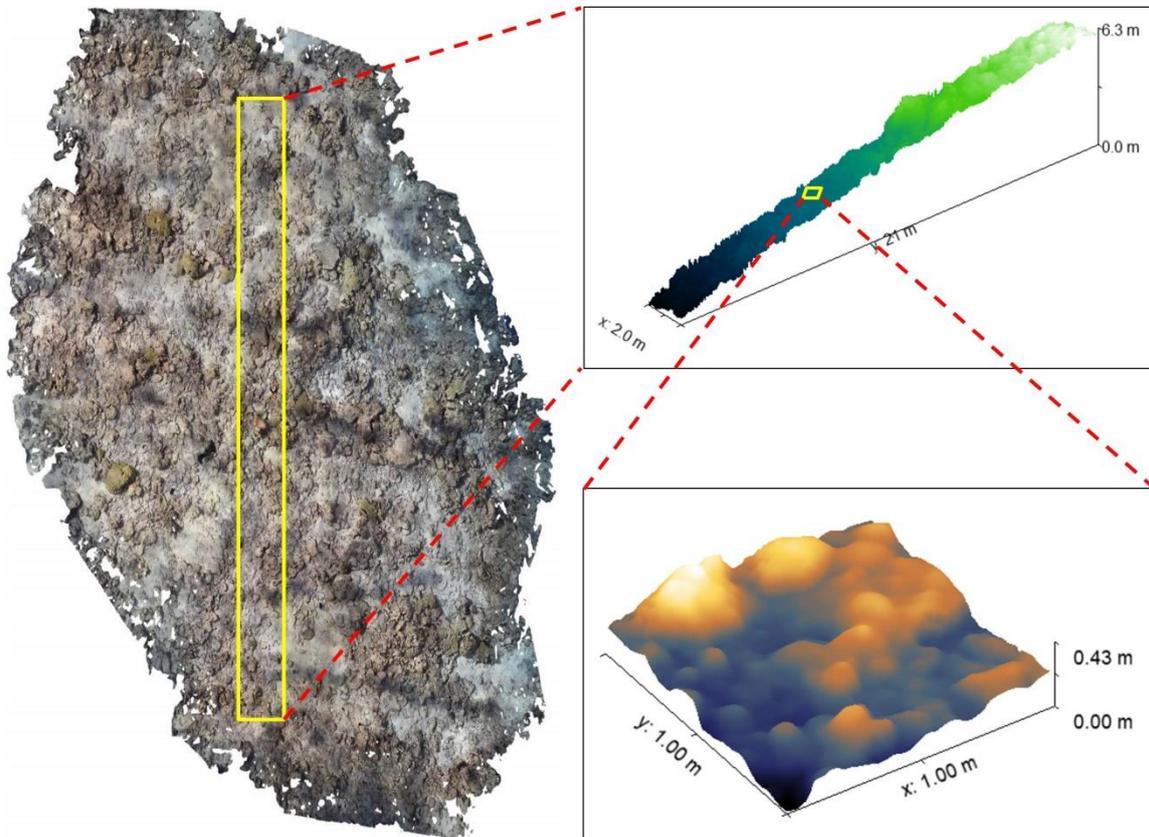


Figure 28. The process of surface extraction from a large 600 m<sup>2</sup> Structure from Motion (SfM) derived model. Virtual transects of ~ 20 x 2 m were extracted from scaled site models, and then sub-sampled using 1 m<sup>2</sup> cropped reef sections at 1 cm resolution. Transect and sub-sample (shown right) displayed in false colour to show topographic height.

For each year surveyed at each site, ten (1 x 1 m) virtual surface section replicates were then clipped from the site's point cloud. and the structural complexity and surface texture metrics extracted at a resolution of 1 cm per pixel (1 cm<sup>3</sup> per voxel) using the freeware 'Gwyddion' (Nečas and Klapetek, 2012). The xyz point-cloud rasterization process was based on averaged point interpolation with a mirrored exterior.

I chose to investigate changes in four specific reef structural metrics for this study: 1) 3D rugosity ratio i.e., total projected planar area / total surface area, 2) root mean square (RMS) variation from the 3D plane, 3) difference between z-plane maximum and minimum heights, and 4) fractal dimension through 'cube-counting' (Figure 29). The 'cube-counting' method for estimation of Fractal Dimension, also known as the Kolmogorov Dimension, gives a measure of volumetric complexity across varying scales of observation. The output values for each analysed surface are based on the following steps: *'a cubic lattice with lattice constant  $l$  is superimposed on the z-expanded surface. Initially  $l$  is set at  $X/2$  (where  $X$  is length of edge of the surface), resulting in a lattice of  $2 \times 2 \times 2 = 8$  cubes. Then  $N(l)$  is the number of all cubes that contain at least one pixel of the image. The lattice constant  $l$  is then reduced stepwise by factor of 2 and the process repeated until  $l$  equals to the distance between two adjacent pixels'* (Klapetek et al., 2016). These four metrics were chosen based on a subset of measurements used in standard surface metrology analysis (Jiang and Whitehouse, 2012) and which have been shown to give useful ecological insights from similar studies (Burns et al., 2016b; Young et al., 2017).

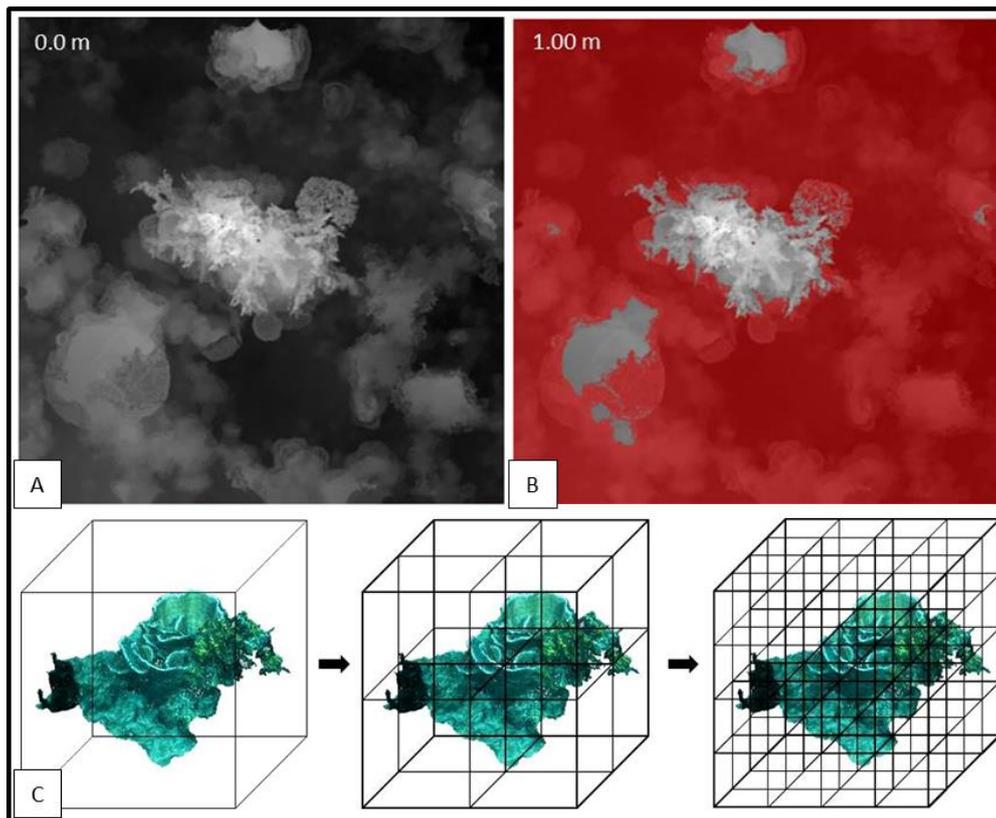


Figure 29. Visualisations of surface measurement concepts: A) An XYZ point cloud of a reef coloured to show a height scale from the lowest points (black) to the highest points (white); B) The same XYZ point cloud as 'A', with the volume of the virtual space filled to a height of 1.00 m from the lowest point (in red); C) Fractal dimension analysis through cube counting of a reef space. The number of squares filled at each progressive scale level is an indication of 'fractal self-similarity' / complexity.

## *Environmental factors*

### Heat stress

Heat stress data (Figure 30) were collected for each site using Coral Reef Watch remote-sensed data (NOAA, 2018) at 5 km resolution in NetCDF4 format, converted to raster layers within ArcGIS in order to extract point values for the years 2014, 2015, 2016 and 2017 to assess likely coral mortality in the year preceding each survey. I chose the preceding year because the process of post-disturbance coral collapse and loss of structure from biological and physical erosion (Perry *et al.*, 2012) can take from months to years to occur (Nyström *et*

*al.*, 2000). These data were utilised as composite annual (January - December) maximum Degree Heating Week (DHW) values from daily sea surface temperature satellite recordings.

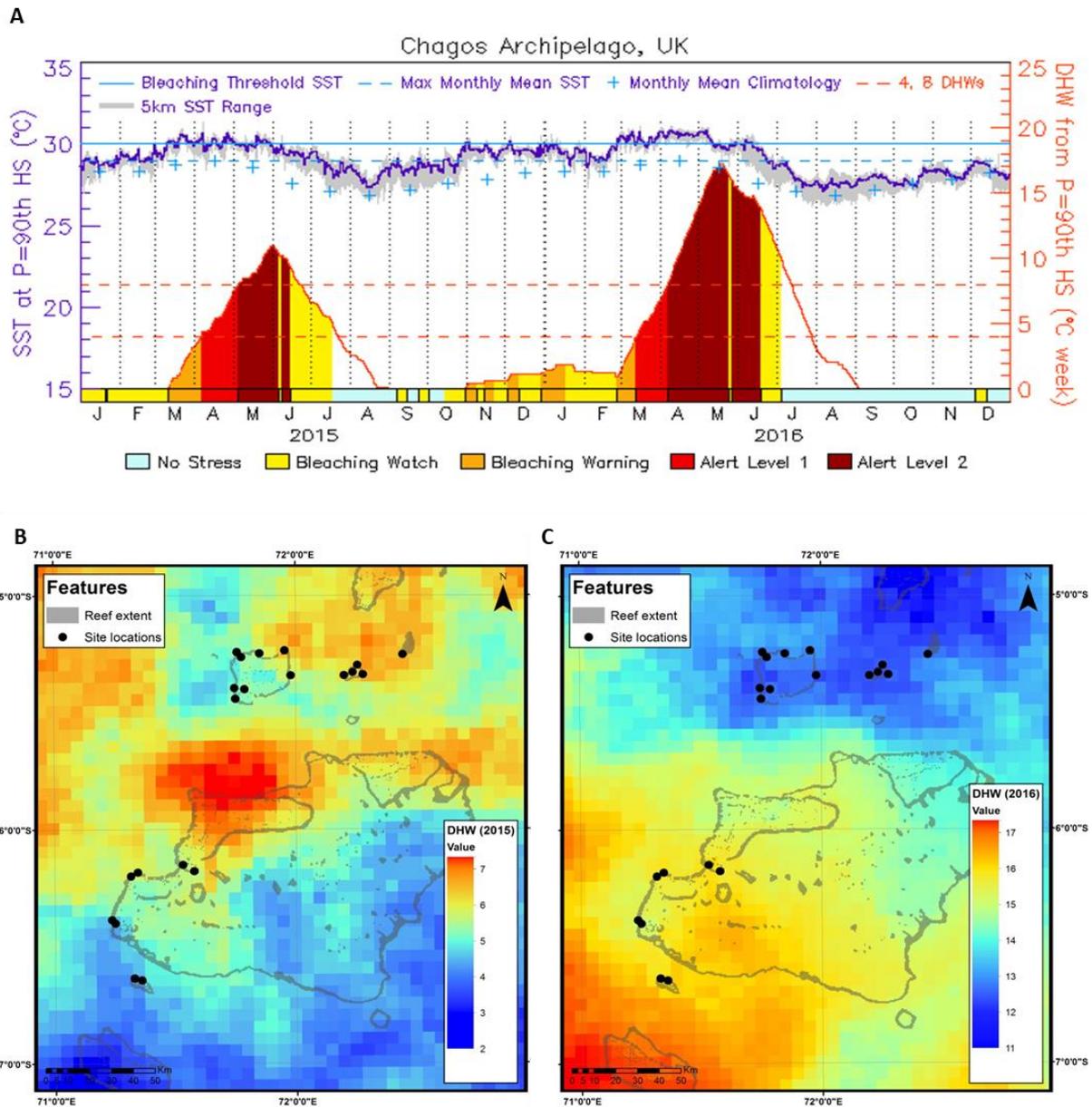


Figure 30. Bleaching stress in relation to A) Total Degree heating weeks (DHW) and sea surface temperature (SST) within the entire Chagos archipelago region through the years 2015 and 2016, with mortality threat rated on a scale from 'No stress' to 'Alert level 2' - indicating > 8 DHW and likely widespread bleaching and mortality; B) Annual maximum DHW during 2015 at 5 km spatial resolution; and C) Annual maximum DHW during 2016 at 5 km spatial resolution. All data Sourced from NOAA Coral Reef Watch (2018).

DHW are calculated based on the level of accumulated heat stress within a 5 km pixel over a 12 week moving window of time, with the total value being a mean of the cumulative daily hotspots (an increase of 1°C above maximum monthly mean ambient sea surface temperature) over this extended period. Bleaching and some mortality is expected after 4 DHWs, with widespread mortality expected after 8 DHWs (Liu *et al.*, 2014). While there is a wide range of bleaching and mortality susceptibility between coral taxa, (Swain *et al.*, 2016), the likelihood of any surviving stressed corals recovering *Symbiodinium* algal symbionts after 16 – 24 weeks of continued heat stress is very limited and will likely result in the death of the whole colony (Diaz-Pulido and McCook, 2002).

#### Wave Exposure

Aside from the bio-erosional effects of fish and invertebrates, the predominant physical drivers of erosion of reef structure following bleaching mortality in this area are storm damage and broad level of wave exposure (Dollar, 1982; Nyström *et al.*, 2000; Perry *et al.*, 2012). Sites were therefore chosen to cover a range of wave exposures, categorising sites into 'Low' (<500 J m<sup>-3</sup>), 'Medium' (500 - 1000 J m<sup>-3</sup>), or 'High' (>1000 J m<sup>-3</sup>) energy regimes using data derived from spatially explicit estimations of wave exposure modelled as a function of wind speed and direction, and fetch length, using methods described in Perry *et al.* (2015). The division of sites into three bins follows natural breaks in the data, and recognises the distinctness of enclosed lagoon or lagoon-like conditions.

#### Community composition

For each site in 2015, 20 individual frame grabs were taken from video footage along each of three depth bands (10-15, 15-20 & 20-25 m). Frames were chosen at random, but any blurred, empty or distant (farther than 2 metres from substrate) images were discarded and replaced

with the nearest clear frame. Individual frames were analysed for species composition and cover using (NCRI) Coral Point Count with Excel extensions software. Fifteen stratified random points were used per frame, in a random stratified 5 x 3 point grid arrangement. Benthic forms were identified to the lowest (i.e. most precise) taxonomic level possible from the digitised video footage, used in parallel with a collection of photographic still images taken during the same surveys, following Turner & Klaus (2005).

### ***Statistical analysis***

Linear mixed-effects regressions, fitted by restricted maximum likelihood in the lme4 R package (Bates *et al.*, 2012), were used to model variations in 3D structure (including surface complexity, skew, RMS variation and vertical height) through time. 'Exposure' (High / Medium / Low) and 'length of time' (years) were set as interacting fixed factors, along with additive effects of DHW of initial bleaching impact (2015), and DHW of secondary bleaching impact (2016). 'Site' (n=20) was set as a random effect with random slope and intercept, nested within 'atoll region' (n=3) following log likelihood ratio test assessment (Zuur *et al.*, 2009). A log<sub>10</sub> transformation was applied to all surface metrics (except fractal dimension, which needed no transformation) to achieve a normal distribution of model residuals, and the plotted residuals were checked for homoscedasticity prior to using the results of the model. Significance (p) values for the selected models were calculated using Kenward-Roger standard errors and degrees of freedom. Confidence intervals were calculated at the 95 % level using the package Jtools (Long, 2018).

Two-way ANOVAs were used to test for differences in five structural metrics (3D rugosity, Z height variation, roughness, skew and fractal dimension) between depth (3 levels) and

bleaching impact (2 levels), with Tukey post-hoc tests. Each analysis was tested for homogeneity of variance and normality using Levene's and Shapiro-Wilk testing.

Permutational multivariate analysis of variance (PERMANOVA) was performed over 9999 permutations on a square root-transformed Bray-Curtis dissimilarity matrix of hard and soft coral species (surveyed using video recordings in 2015, pre-bleaching) using the R 'vegan' package functions `adonis()` and `vegdist()` (Oksanen *et al.*, 2017). Rate of change in structural rugosity over 3 years following initial bleaching in 2015, estimated for each site by linear regression on log<sub>10</sub>-transformed rugosity data, was grouped into four bins (of 0.1 rugosity ratio per year, ranging from + 0.1 to – 0.3) and used as the grouping factor.

Redundancy analysis was further conducted on the benthic community structure for all sites (Legendre and Andersson, 1999), with the same grouping factor to ordinate the community variation. Finally, a SIMPER analysis (Oksanen *et al.*, 2017) was conducted to ascertain the species contributing most to community dissimilarity in the sites which had the greatest and least declines in structure. The species within each community were matched to life-history traits extracted from Coraltraits.org (Madin *et al.*, 2016a), giving a classification of either 'competitive' (i.e. *'large, branching and plating species that grow quickly, occur at shallow depths and reproduce by broadcast spawning'*), 'weedy' (i.e. *'opportunistic colonisers...which can reproduce by brooding and have smaller colony sizes'*), 'stress-tolerant' (i.e. *'slow-growing species that reproduce by broadcast spawning and have primarily domed morphologies, large corallites and high fecundity'*), or 'generalist' (i.e. *'domed and plating colonies...with moderate growth rates and can reach large colony sizes'*), based on a range of underlying individual species traits from Darling *et al.* (2012).

All analyses were carried out using R: version 3.4.1 (R Core Team, 2016).

## Results

### *Level of heat exposure*

All sites experienced two successive heat stress episodes, resulting in high likelihood of widespread mortality in 2015, with a subsequent more extreme heating event in 2016, causing further mortality of any remaining shallow reef. Heat stress did not reach levels expected to result in bleaching events in either 2014 or 2017 (Figure 31).

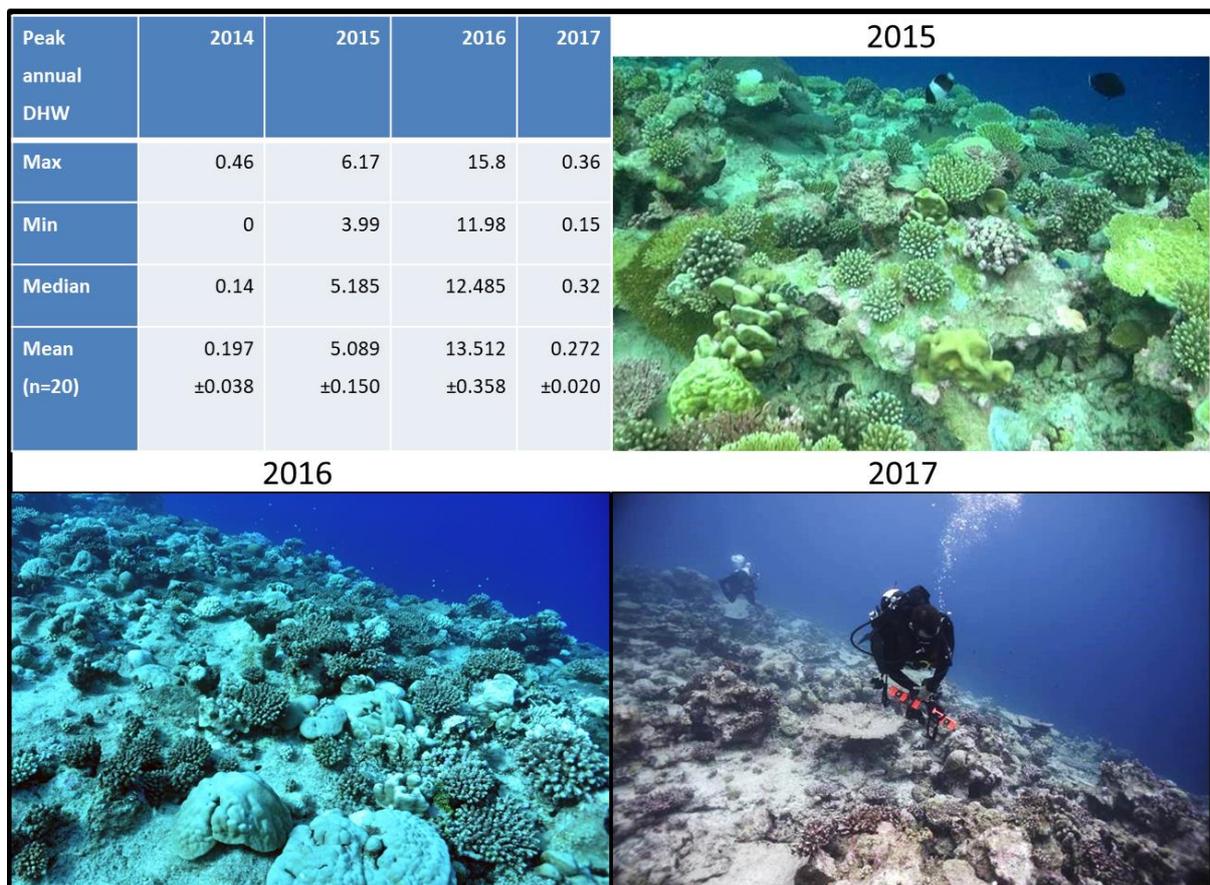


Figure 31. Maximum, minimum, median and mean ( $\pm$ SE) peak annual DHW, for all sites across the years 2014-2017 within the Chagos archipelago (top left). Images showing change in seaward coral reefs from April 2015 to April 2017, covering the period before, during and after bleaching at the same location in South Brothers (site 8), Great Chagos Bank, BIOT.

## 1 *Metrics of complexity*

2 Model selection of random effects through likelihood ratio testing found neither initial coral  
3 cover or peak DHW of the preceding year significantly improved the prediction of surface  
4 complexity within this model ( $\chi^2$  (1) = 1.9817, p=0.1592;  $\chi^2$  (1) = 1.3722, p=0.2414  
5 respectively); however, sites (nested within atoll) had a significant interaction effect ( $\chi^2$  (4) =  
6 10.751, p=0.0295) and were therefore retained with random slopes and intercepts within  
7 each model.

8 3D rugosity (i.e. surface area) of medium and high exposure shallow reefs significantly  
9 declined over the three years following the initial heating anomaly, at a negative rate of -  
10 0.172 and 0.153 yr<sup>-1</sup> respectively (Table 7;Figure 32 ). Initial 3D rugosity was greatest for  
11 medium exposure reefs at 2.138 (declining to 1.622), followed by the high exposure reefs at  
12 1.905 (declining to 1.445). No significant decline was seen in low-exposure sites, which  
13 instead saw a non-significant increase of 0.049 yr<sup>-1</sup> from 2.042 to 2.188. Furthermore, there  
14 was no significant difference in initial 3D rugosity across exposure types, despite a  
15 difference of 0.28 between low and high exposure sites. A value of 1 would be equivalent to  
16 a flat surface and a value of  $\geq 2$  a complex reef with numerous caves / fissures (Bayley *et al.*,  
17 2019).

18 Surface skew (i.e. the proportion of isolated surface peaks) of low exposure reefs increased  
19 significantly (estimate = 0.09, t = 1.96, p < 0.1) for high and medium exposure reefs at a  
20 positive rate of 0.093 and 0.064 yr<sup>-1</sup> respectively (Table 7). Low exposure reefs were  
21 significantly different to other sites (estimate = -0.02, t = -2.01, p < 0.05), instead non-  
22 significantly reducing skew at a rate of -0.024 yr<sup>-1</sup>. Initial skew was significantly different for  
23 all exposure types and was greatest in low exposure reefs (0.562 reducing to 0.490), followed

24 by medium exposure (0.468 increasing to 0.661) and high exposure modelled reefs (0.324  
25 increasing to 0.603).

26 Vertical Z-axis height variation in medium and high exposure reefs has not significantly  
27 declined (estimate = -0.02,  $t = -1.21$ ,  $p > 0.1$ ) over the three years (-2.6 cm yr<sup>-1</sup> and 2.2 cm yr<sup>-1</sup>  
28 respectively) following the initial heating anomaly (Table 7). Low exposure reefs were  
29 significantly different (estimate = -0.04,  $t = 2.36$ ,  $p < 0.05$ ), with a height gain through time  
30 from 0.631 to 0.832 at 6.7 cm yr<sup>-1</sup>. There was no significant variation in initial reef height  
31 variation with all reefs starting with a height variation of between 0.51 and 0.63 m per m<sup>2</sup>  
32 sample.

33 The fractal dimension (a measure of complexity through self-similarity across scales)  
34 declined significantly (estimate = -0.01,  $t = -2.06$ ,  $p < 0.1$ ) across all exposure types, decreasing  
35 at 0.09 yr<sup>-1</sup> for both high and low exposure, and at 0.04 yr<sup>-1</sup> for medium exposure reefs (Table  
36 7). Initial fractal dimension did not differ significantly for exposure types, ranging from  
37 2.171 to 2.166.

38

39 Table 7. Linear mixed effect model outputs for (logged) 3D rugosity, (logged) surface skew, (logged) height variation (Z), and fractal dimension over four  
 40 years across the British Indian Ocean Territory, following bleaching disturbance in 2015/2016. Year and wave exposure (3 levels) are fixed factors, with sites  
 41 nested within atolls as a random factor. N (overall) = 520 for 3D rugosity, surface skew and height variation; N (overall) = 550 for fractal dimension. N (Site:  
 42 Atoll) = 21, N (atoll) = 3 for all metrics. P-value significance shown in regard to high exposure sites (\*\*\*)  $\leq 0.001$ , \*\*  $\leq 0.01$ , \*  $\leq 0.05$ , †  $\leq 0.1$ ).

Parameters	(log) 3D Rugosity			(log) Surface Skew			(log) Height variation			Fractal dimension		
	Estimate	t value	CI	Estimate	t value	CI	Estimate	t value	CI	Estimate	t value	CI
Intercept (High)	0.28 ***	7.95	[0.21, 0.35]	-0.49 **	-4.47	[-0.71, -0.28]	-0.29 ***	-6.76	[-0.38, -0.21]	2.17 ***	274.4	[2.15, 2.18]
Year (High)	-0.04 *	-2.44	[-0.07, -0.01]	0.09†	1.96	[0.00, 0.18]	-0.02	-1.21	[-0.06, 0.01]	-0.009†	-2.06	[-0.02, 0.00]
Exposure (Medium)	0.05	1.28	[-0.03, 0.12]	0.16†	1.58	[-0.04, 0.36]	0.07	1.32	[-0.03, 0.17]	0.001	0.07	[-0.02, 0.02]
Exposure (Low)	0.03	0.81	[-0.05, 0.12]	0.24 *	2.12	[0.02, 0.47]	0.09	1.49	[-0.03, 0.21]	-0.004	-0.48	[-0.02, 0.01]
Year: Exposure (Medium)	0	0.14	[-0.03, 0.03]	-0.04	-0.81	[-0.13, 0.06]	0	-0.14	[-0.05, 0.04]	0	0.04	[-0.01, 0.01]
Year: Exposure (Low)	0.05 *	2.61	[0.01, 0.08]	-0.11 *	-2.01	[-0.22, -0.00]	0.06 *	2.36	[0.01, 0.11]	0.005	0.97	[-0.01, 0.02]
R <sup>2</sup> fixed	0.15			0.04			0.19			0.05		
R <sup>2</sup> total	0.34			0.09			0.48			0.23		

43

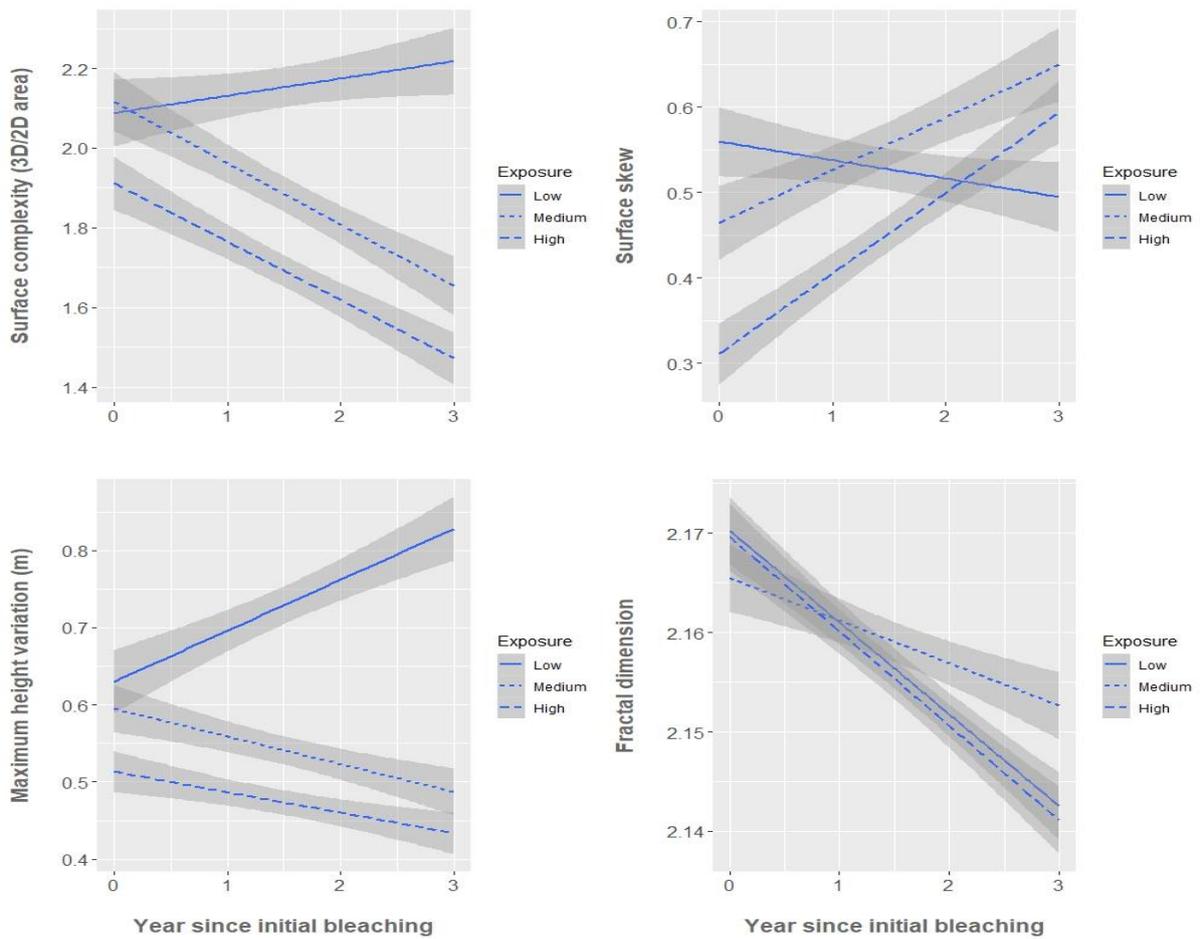


Figure 32. Modelled variation in surface complexity (3D surface area / 2D planar area), surface skew, maximum Z-dimension vertical height variation, and fractal dimension for reefs within the British Indian Ocean Territory following heat stress induced mortality in 2015 and 2016. Models split by level of wave exposure, with 95% predicted confidence Intervals Shown.

### *Structure across the archipelago by exposure and location*

I examined the changes at each site applying the most commonly used metric i.e., rugosity ratio, (which also saw the biggest responses in this study). Site-level changes in reef rugosity ratio from 2015 to 2018 were predominately negative, with sites 3, 5, 6, 7, 10, 11, 13, 16, and 21 all significantly declining. Sites 1, 2, 14, 19, and 21 all had non-significant negative slopes, and sites 9, 17 and 18 had non-significant increases (Appendix 12; Figure 33).

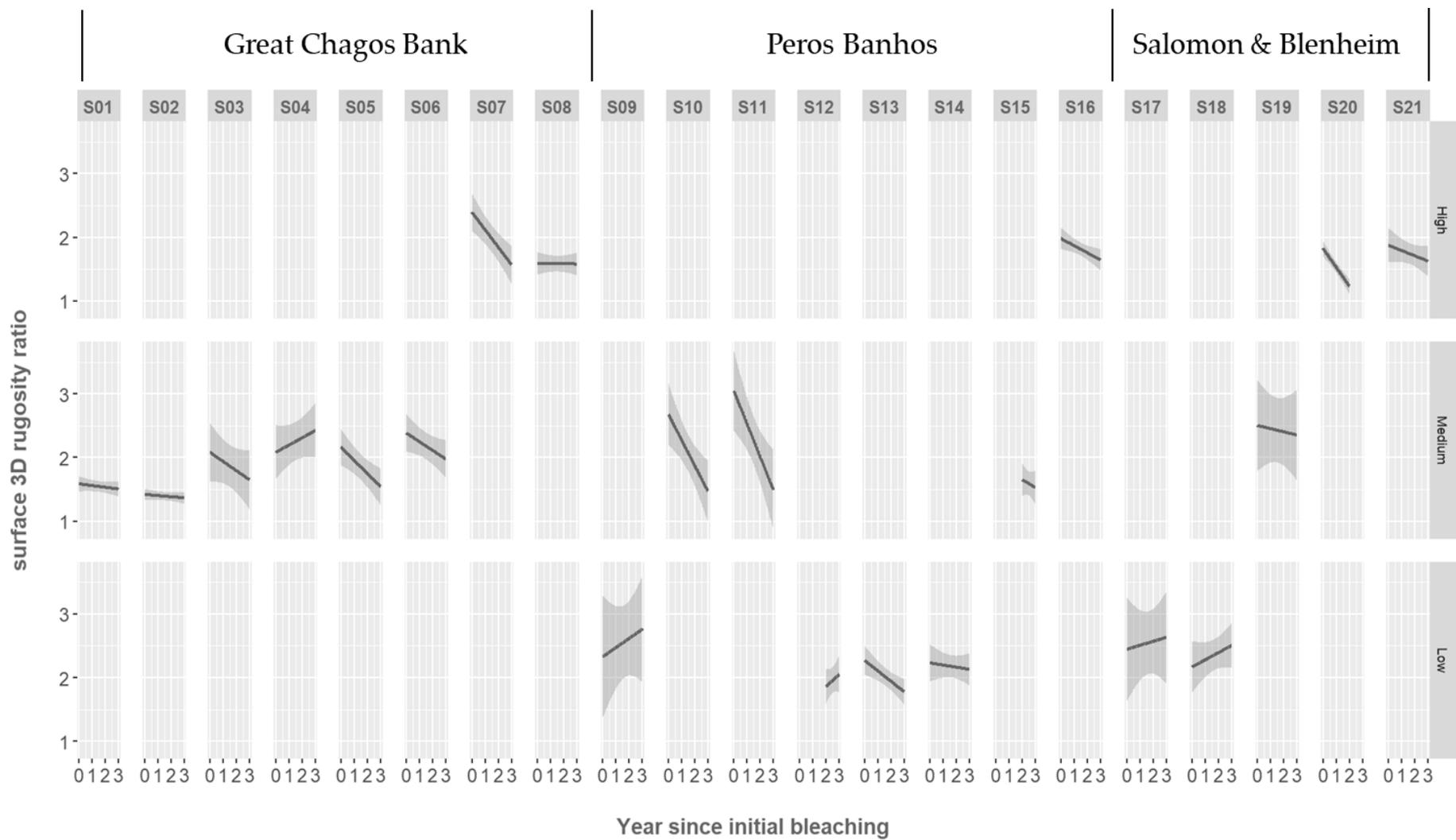


Figure 33. Linear models showing site-level changes in 3D rugosity metrics over the 3 years following initial bleaching in the Chagos Archipelago (BIOT). The 21 sites (labelled as per Figure 1) are grouped by atoll region, and level of wave exposure. 95 % Confidence interval shown in grey bands.

The greatest rate of decline was seen in the Peros Banhos sites which had medium wave energy exposure regimes. High energy wave exposure sites already had reduced relative structure, but consistently declined further from 2015 – 2018. Low energy exposure sites (i.e. lagoonal and highly sheltered sites), experienced no change in the Peros Banhos atoll region and marginal increase in the Salomon atoll region (Figure 34).

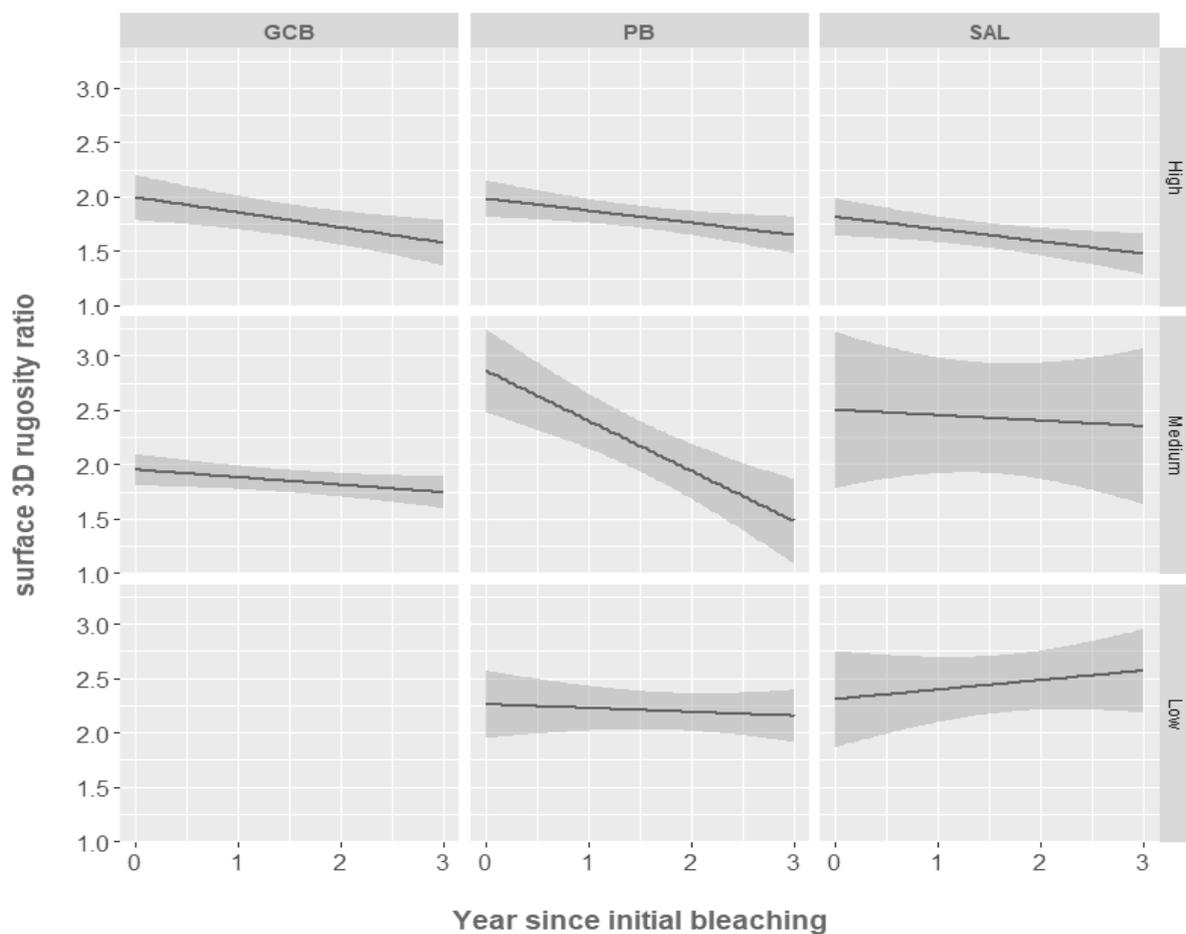


Figure 34. Linear models of the relationship between 3D rugosity ratio and time, separated by atoll and level of exposure within the Chagos Archipelago (BIOT). Sample number = 570, 95 % Confidence interval shown in grey bands.

### *Structure before and after bleaching by depth*

There were significant differences in 3D rugosity, Z height, and surface roughness across depth bands, driven by the reduced structure at 5 – 10 m compared to the 15 – 20 m depth bands in each case (Tukey post-hoc tests;  $p = 0.007$ ,  $p < 0.001$  and  $p < 0.001$  respectively), as well as between the 10 – 15 and 15 – 20 m depth bands in terms of roughness. Fractal dimension and rugosity were significantly reduced following bleaching, with fractal dimension showing an interaction effect between depth and impact in the 5 – 10 m depth band ( $p = 0.011$ ). No significant differences were seen for measures of skew (Table 8; Figure 35).

Table 8. ANOVA results of five measures of structural complexity for before –after bleaching impact (2015 – 2018) and for depth effects (5-20 m). Significance levels: '\*\*\*\*' = 0.001 '\*\*\*' = 0.01 '\*\*' = 0.05 '.' = 0.1.

Parameters	Df	Sum sq	Mean sq	F value	Pr(>F)	
<b><i>Rugosity ratio</i></b>						
Before-After	1	0.159	0.159	6.823	0.012	*
Depth	2	0.244	0.122	5.214	0.009	**
Before-After: Depth	2	0.109	0.054	2.324	0.108	
Residuals	54	1.261	0.023			
<b><i>Z Height</i></b>						
Before-After	1	0.017	0.017	0.871	0.355	
Depth	2	0.404	0.202	10.089	0.000	***
Before-After: Depth	2	0.052	0.026	1.305	0.280	
Residuals	54	1.081	0.020			
<b><i>Roughness</i></b>						
Before-After	1	0.004	0.004	2.128	0.150	
Depth	2	0.036	0.018	10.421	0.000	***
Before-After: Depth	2	0.002	0.001	0.474	0.625	
Residuals	54	0.094	0.002			
<b><i>Fractal (cube counting)</i></b>						
Before-After	1	0.036	0.036	8.722	0.005	**
Depth	2	0.004	0.002	0.536	0.588	
Before-After: Depth	2	0.026	0.013	3.160	0.050	*
Residuals	54	0.225	0.004			
<b><i>Skew</i></b>						
Before-After	1	19.5	19.495	2.102	0.153	
Depth	2	12.8	6.423	0.693	0.505	
Before-After: Depth	2	14.2	7.115	0.767	0.469	
Residuals	54	500.7	9.272			

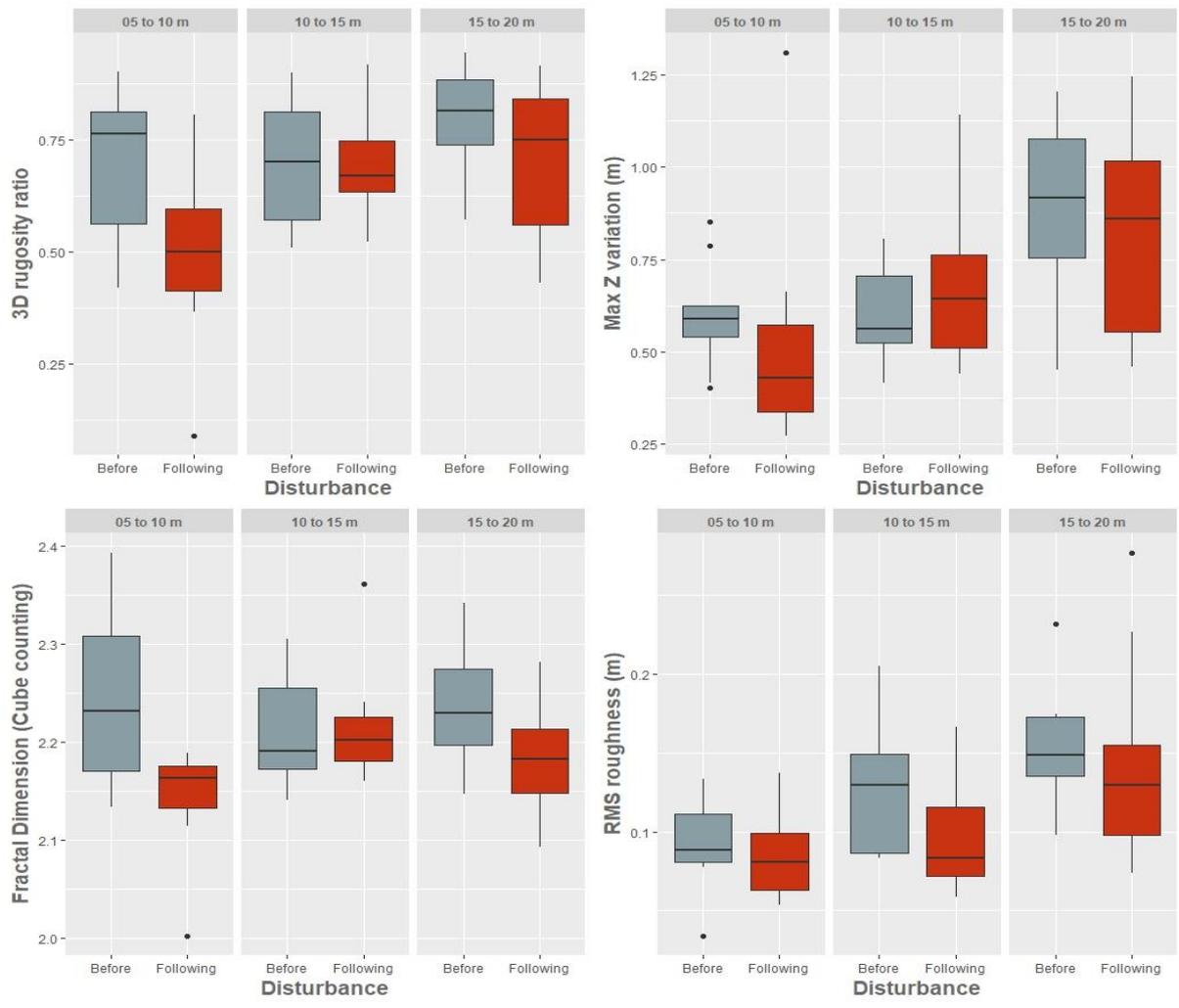


Figure 35. Boxplots of changes in 3D rugosity, max Z height variation, fractal dimension and RMS of roughness of reefs in the Chagos archipelago before (grey) and after (red) bleaching (between 2015 - 2018), across three (5 m) depth bands. Median, upper and lower quartiles of data point and outliers shown.

## Community composition

PERMANOVA following species redundancy analysis of 2015 video survey data found initial benthic species composition in 2015 was significantly associated with the rate of subsequent structural rugosity decline at each site ( $F_{3,19} = 1.673$ ,  $p = 0.021$ ), explaining 23.9% of the variation in the communities relative to the factor of rugosity ratio change (Figure 36).

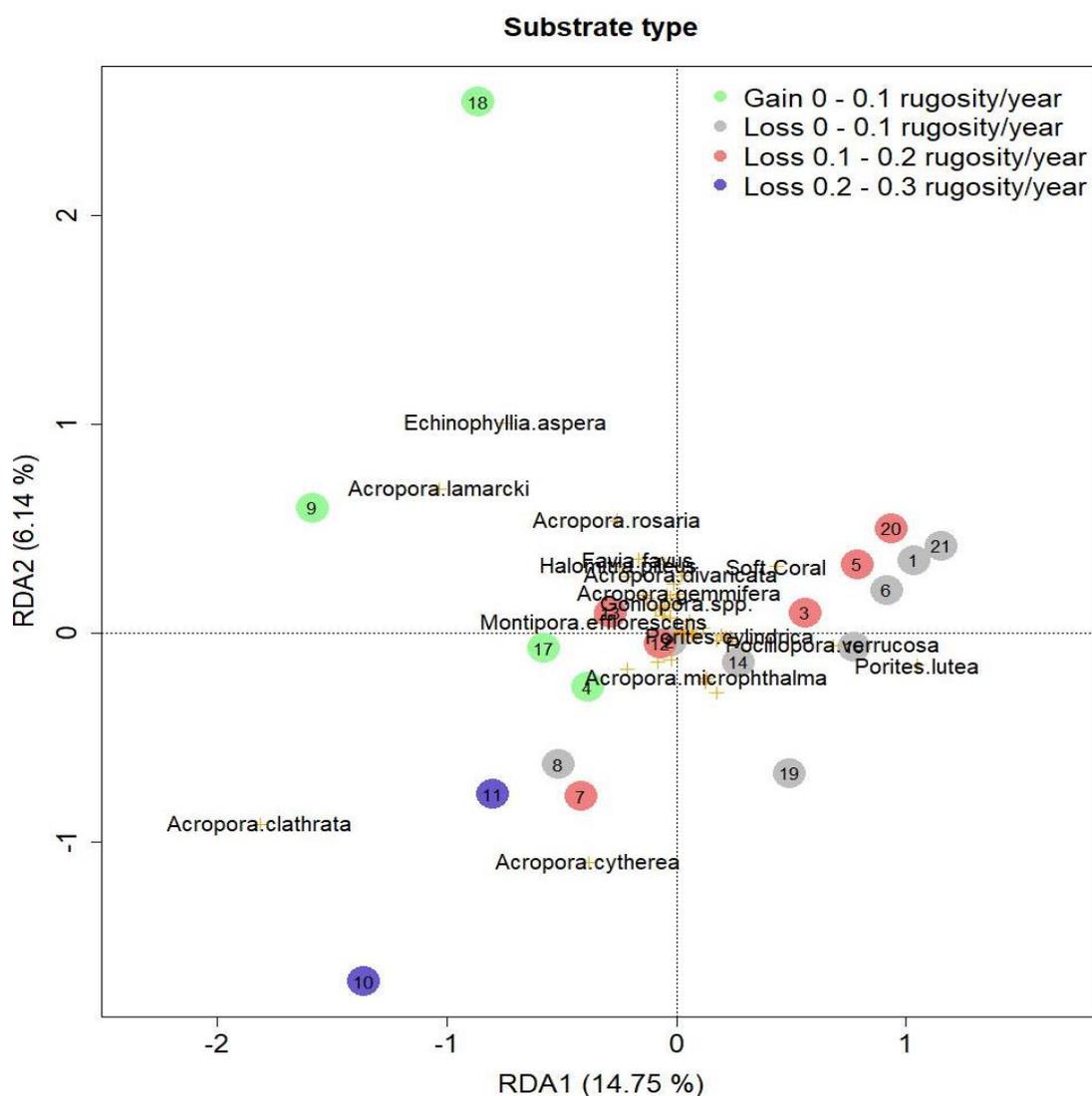


Figure 36. Redundancy analysis for coral communities in the Chagos archipelago, restricted by community correlation to extent of change in structural rugosity ( $m^{-2} year^{-1}$ ) split into four categories, measured over a 3 year period following bleaching. Sites numbered as per Fig 1, and species contributing up to 75 % of the community differences between rugosity change in sites are labelled (orange crosses indicate remaining species).

Further SIMPER analysis of which species are driving the site differences ordinated in Figure 36 show that communities which had the greatest losses in structure (3D rugosity change of  $-0.2$  to  $-0.3$   $\text{yr}^{-1}$ ) had relatively higher initial abundance of the table Acropora (*A. clathrata* & *A. cytherea*), and arborescent / branching Acropora (*A. microphthalma* & *A. plantaginea*) and *Porites solida*. Communities which had no net losses or slight gains in structure (i.e. 3D rugosity change of  $0$  to  $-0.1$   $\text{yr}^{-1}$ ) had relatively higher abundance of the Acropora (*A. lamarcki* & *A. rosaria*), the massive *Porites lutea* and *Favia favus*, and plating *Echinophyllia aspera*. The sites seeing gains (3D rugosity change of  $0$  to  $0.1$   $\text{yr}^{-1}$ ) were all lagoonal, with typically higher relative proportions of the columnar *Lobophyllia hemprichii*, large domed mushrooms *Halomitra pileus*, plating *Montipora efflorescens*, soft corals, and the sub-massive heterotrophs *Goniopora.spp* (Figure 37).

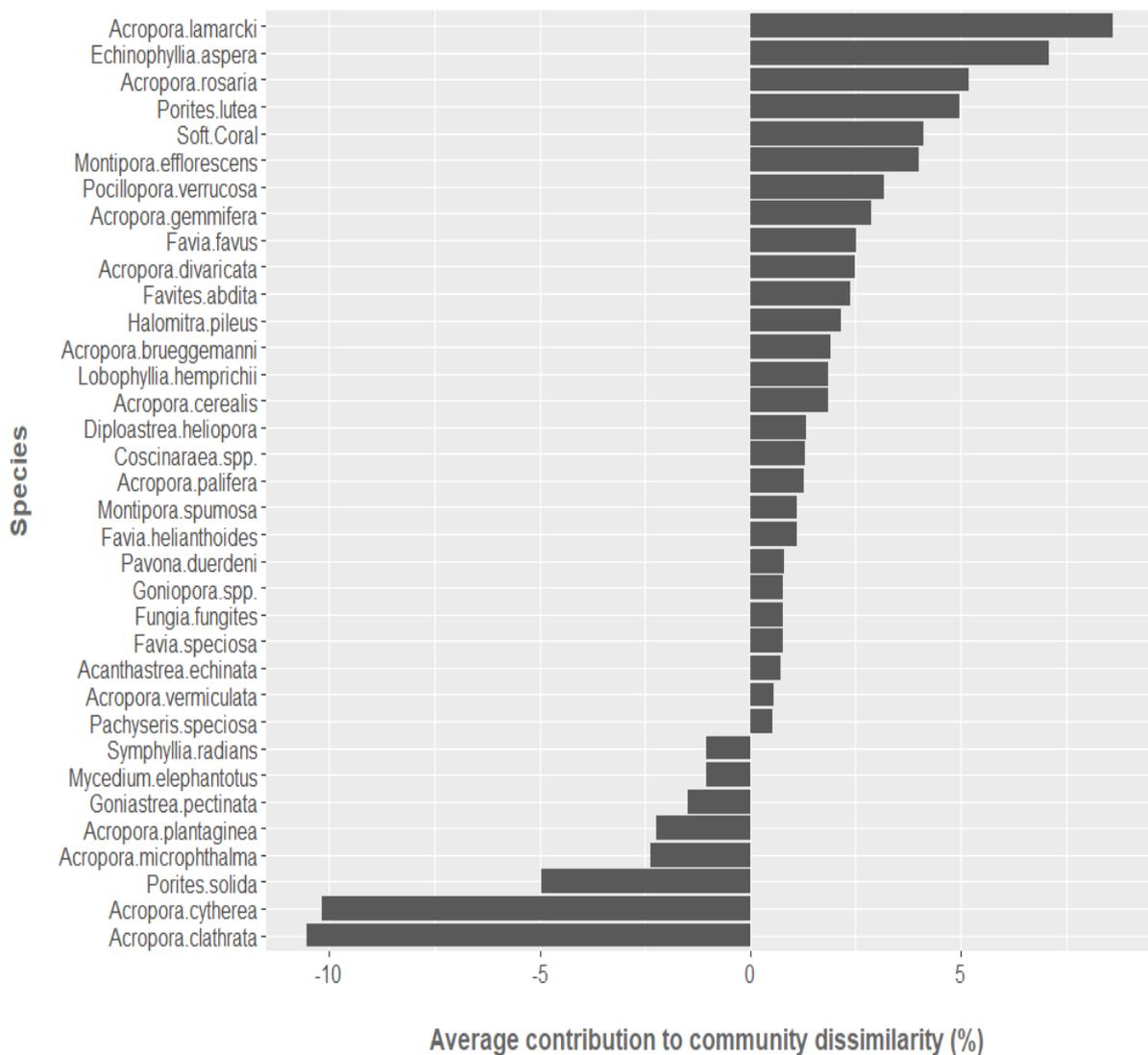
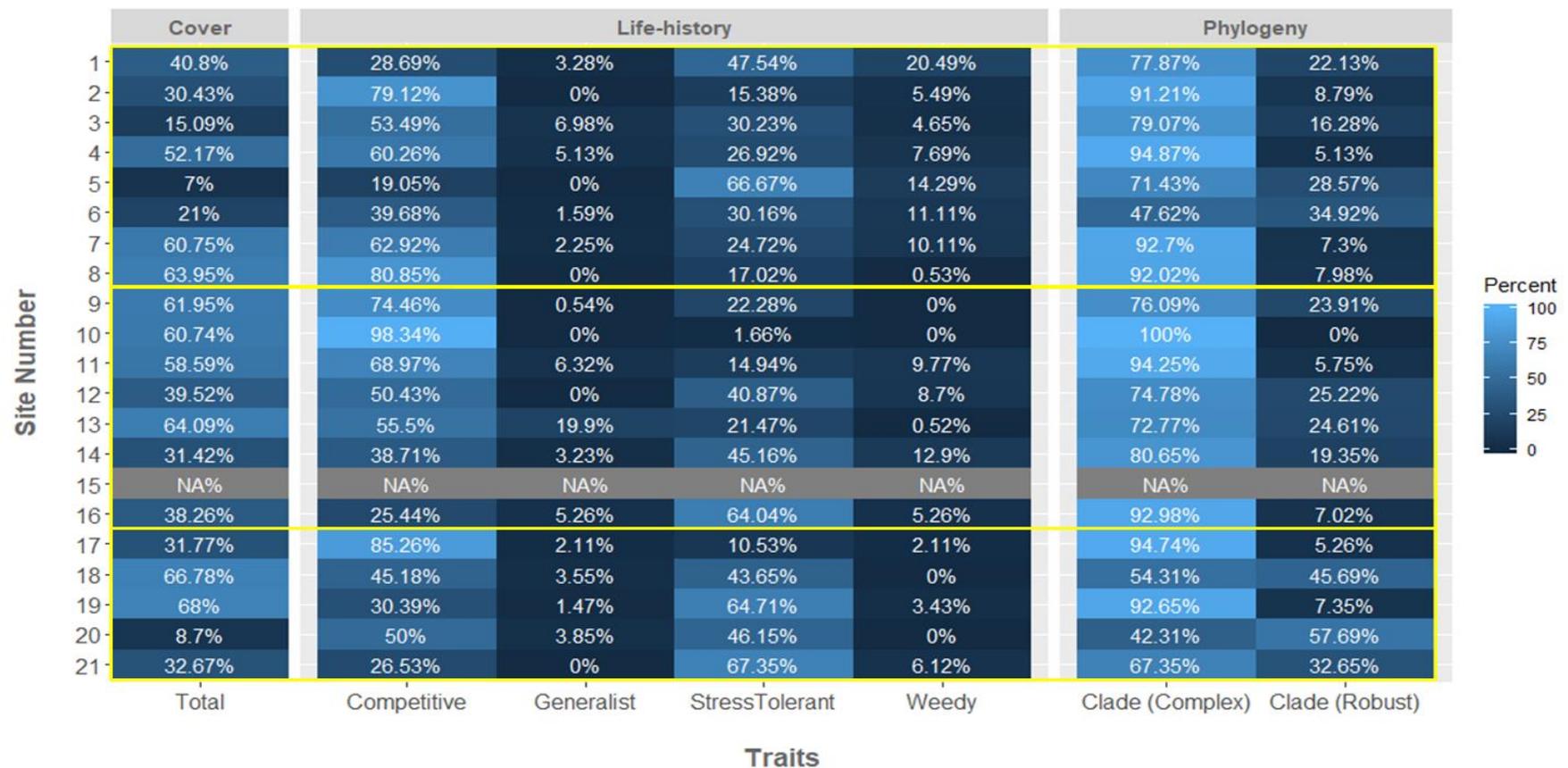


Figure 37. The percentage contribution to dissimilarity between sites in the Chagos archipelago which had the highest losses to structural rugosity following bleaching (left) and the sites which had no losses / marginal gains (right).

Linking species to their life-history trait characteristics shows a predominance of species from the ‘complex’ clade across the archipelago, and either ‘competitive’ or ‘stress-tolerant’ traits being dominant within site-level coral communities. Most sites have a spread of individuals from a number of trait groupings; however, site 8, 10 and 17 see  $\geq 80\%$  of their species all within the typically heat-sensitive ‘competitive’ group. Total percentage cover for all sites has a mean value of  $42.7 \pm 4.74$ ; however, sites 3, 5 and 20 had lower than 20% initial

live coral cover, indicating already degraded reefs which are approaching the potential threshold of 10 % cover where reefs are likely to have shifted to a net erosional state (Table 9; Appendix 13).

Table 9. Data for 20 sites surveyed within BIOT in 2015 pre-bleaching, numbered as per Figure 1 and grouped by atoll (yellow lines). Initial mean percentage cover of live coral for each site in 2015 shown left. Relative proportions of life-history trait groups within the reef benthic community in 2015 shown centre (groups = Competitive, Generalist, Stress-tolerant and Weedy), and phylogenetic clade (Complex vs. Robust) shown left based on species & genus level data from coraltraits.org (Madin *et al.*, 2016a). Percentages coloured and labelled for clarity. Data unavailable for site 15 - 'Yeye' as the site was not surveyed in 2015.



## Discussion

The reefs of the Chagos archipelago experienced widespread declines in multiple aspects of structural complexity down to ~15 m depth following the bleaching episode of 2015-2016, due to extensive post-bleaching mortality (Head *et al. (in Press)*; Sheppard *et al.* 2017). The level of wave exposure was an important factor governing the rate of change in structure, but surprisingly, the number of Degree Heating Weeks (DHW) experienced by each site did not cause significant differences in the rates of decline. This lack of difference in structural decline according to DHW was potentially due to relatively low spatial variation of the thermal anomalies, with the 4 – 6 DHWs experienced by all sites in the initial bleaching period consistently causing mean losses of almost half of live coral cover in shallow seaward waters to around 15 m in the Northern BIOT atolls (Head *et al. (in Press)*). The far more severe subsequent bleaching, ranging from 12 – 16 DHW across sites, reduced the remaining live coral cover still further, again fairly evenly across sites, reducing average live cover over the whole back-to-back bleaching period from ~ 40 – 50% pre-bleaching to ~ 5% post-bleaching (Sheppard *et al.*, 2017). An alternative explanation for the lack of significant correlation could however be attributed to the coarseness of satellite-derived sea temperature data compared to *in situ* temperature recordings. This can result in the assignment of the same temperature value to sites less than 5 km apart even if they have different temperatures at a finer scale, which can lead to regression dilution (i.e. a reduced ability to distinguish significant effects within a model).

Given this level of thermal stress across the archipelagos, the lack of change or even marginal increase in structural metrics within lagoon and highly sheltered sites was an interesting finding. Low energy sites were significantly different from the high and medium

energy sites in terms of changes in rugosity (i.e. surface area), surface skew, and reef height. These differences have been previously observed within BIOT, when lagoons showed higher coral cover and survivorship following the major bleaching episode in 1998 (Sheppard *et al.*, 2002, 2012).

Three major factors could be contributing to the observed differences between protected and exposed sites. First, lagoon and sheltered seaward sites are inherently protected from the heavy physical erosional forces experienced by the seaward sites, which are buffeted by prevailing winds, strong currents, and storm damage (Kjerfve, 1986; Scoffin, 1993). Therefore, while some protected sites may have experienced high levels of post-bleaching mortality, the skeletal remains will be more likely to remain intact and retain their structure, having only to withstand biological erosion. The retention of structure facilitates settlement and regrowth of recruits on the stable and complex structures (Mallela *et al.*, 2004; Hata *et al.*, 2017; Holbrook *et al.*, 2018; Viehman *et al.*, 2018). In addition to the retention of suitable immobile complex habitat for successful coral recruitment, the confined oceanographic circulation cells which can exist within fully enclosed reefs are likely to promote greater local re-settlement post-disturbance (Hench *et al.*, 2008).

The second potential reason for the differences found between reef types is that the corals within the confined calm waters of enclosed lagoon areas typically experience relatively stable elevated temperatures due to the lack of currents and fetch (Kjerfve, 1986; Sheppard, 1999; Sheppard *et al.*, 2017), and can become conditioned / acclimatised to be more tolerant of this heat (West and Salm, 2003; Grimsditch and Salm, 2006; Palumbi *et al.*, 2014).

The third reason for the difference may be attributed to the differing benthic community composition in typical seaward and lagoon sites. This analysis showed that the sites

experiencing the greatest losses were dominated by fast-growing competitive colonisers such as the acroporids which typically take on a branching or tabular form but have low heat resistance (Hoey *et al.*, 2016). The lagoon sites were however dominated by stress-tolerant and generalist species, such as *Echniophyllia apsera*, *Favia favus* and *Lobophyllia hemprichii*, which typically have a very stable massive or sub-massive morphology. Alongside this dominance of species that are more robust to heat anomalies and subsequent physical damage, the lagoons also typically held higher abundances of species with fully heterotrophic or alternate heterotrophic - autotrophic feeding strategies such as *Goniopora spp.*, meaning that even if in a bleached state, these corals could utilise an alternate energy source during acute heat stress episodes. This alternate feeding strategy has been observed more widely to increase survivorship during bleaching events, accelerate recovery post-bleaching and facilitate calcification (Grottoli *et al.*, 2006; Fox *et al.*, 2018).

Furthermore, lagoon-type areas show not only a higher proportion of heterotrophic feeding strategies but also an increased proportion of corals from the 'robust' clade rather than the 'complex' clade (Romano and Palumbi, 1996). While there has been some debate over the distinction between the physiological differences between these two lineages (Okubo, 2016), species in the 'robust' clade are broadly considered to be typified by relatively solid structures with heavier skeletal calcification densities, have growth forms with greater tissue depth, and usually grow by intra-tentacular budding. By contrast, the 'complex' taxa are more lightly calcified with greater porosity, have architecturally complex growth forms with shallow tissue depth, and the majority grow by extra-tentacular budding (Romano and Palumbi, 1996). These physiological characteristics typically leave the 'complex' clade taxa more vulnerable to heat-stress (Loya *et al.*, 2001; Wooldridge, 2014). Given this increased

typical susceptibility to bleaching, the predominance of this clade across the archipelago (with the majority of sites containing coral compositions with greater than 70 % 'complex' corals), fits well with widespread level of post-heat anomaly mortality and loss of structure. Similarly the increased relative proportions of the 'robust' clade in lagoon sites, such as site 18 'Sam's knoll', which was the only site which saw a marginal increase in structure, is indicative that this distinction may be an important driver of post disturbance community trajectory.

The steepest declines in structure were observed at sites 10 'Bernard's knoll' and 20 'Takamaka', both in the Northern extent of the archipelago. While Bernard's knoll is located in a semi-enclosed 'lagoon' site of the Northern Peros Banhos atoll, it is still exposed to medium (500 – 1000 Jm<sup>-3</sup>) levels of wave energy due to extended breaks in the atoll rim allowing the flow of water and generation of wave fetch across this area. The shallow section of this site pre-bleaching was composed of 98 % tabular *Acropora clathrata* and *A. cytherea*, both from the 'complex' clade, which rapidly colonised the site following the 1998 beaching episode (Figure 38). These species are excellent structure forming colonisers, but are highly sensitive to heat stress and grow physically unstable top-heavy structures, easily toppled by storms or heavy wave-action (Scoffin, 1993; Madin and Connolly, 2006; Hoey *et al.*, 2016). This resulted in an almost complete site-level extirpation of these species during the recent bleaching and rapid collapse of their associated structure.

Within Takamaka, a highly exposed seaward slope location dominated by soft coral species (*Sinularia* spp., *Sarcophyton* spp. *Alcyonacea* spp. and *Xenia*. spp), and only ~ 9 % hard coral structure, half of the coral species exhibited 'competitive' / non- stress-tolerant traits. Following bleaching, soft corals, which constituted ~15 – 20% of the benthic cover and which

despite being soft-bodied are important structure-forming species (Ferrari, 2017), suffered a complete die-off. Unlike the hard corals which leave hard calcium carbonate skeletal remains, the soft corals leave no trace of their presence behind aside from minute spicules. This resulted in an essentially flat bedrock surface remaining following bleaching in these soft coral dominated sites, as was also observed during the 1998 bleaching episode (Sheppard *et al.*, 2002).

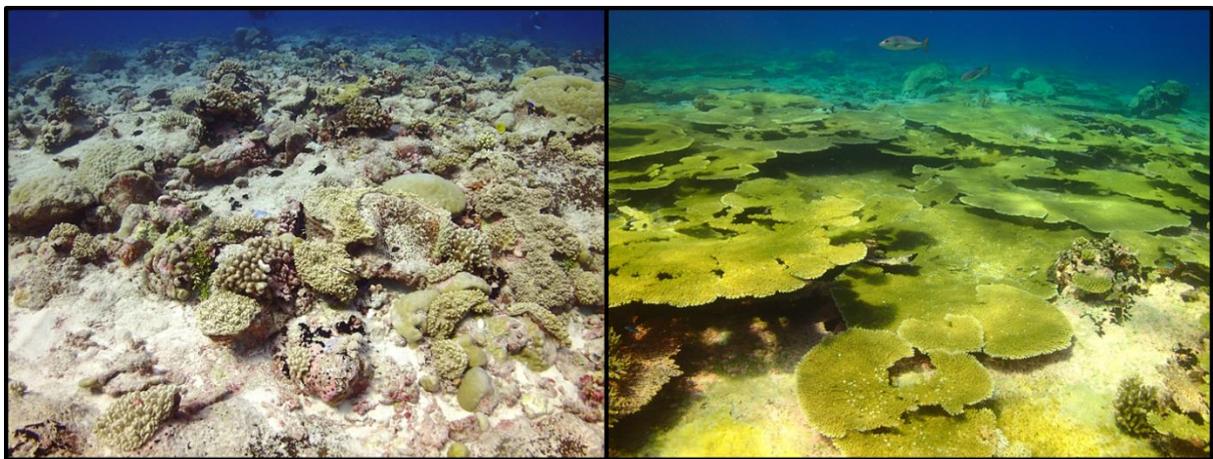


Figure 38. Site 20 'Takamaka' (left) and site 10 'Bernard's knoll' (right) in 2015 just before extensive bleaching across the reefs of the Chagos archipelago. Site 20 dominated by *Sinularia* spp., *Lobophyton* spp and *Xenia* spp. soft corals and *Porites lutea*. Site 10 dominated by *Acropora cytherea* and *Acropora clathrata*. Images courtesy of Bangor University.

The weak observed decline in fractal dimension across the reefs was surprising given the extent of mortality and cover loss across sites, and the rate of change in all other metrics. One explanation is that rubble and damaged substrate can still produce high fractal dimension outputs due to their randomly arranged and jagged nature (Imre and Bogaert, 2004; Bayley, 2009; Reichert *et al.*, 2017), meaning that healthy complex sites and heavily damaged sites with high levels of remaining rubble, could potentially have similar fractal

dimension measurements. Secondly the scale at which this study was conducted (1 cm resolution) will limit the extent to which fractal complexity can be effectively measured, limiting the differences to coarse / gross scale changes.

While overall the reefs of BIOT saw extensive losses in structure, there were signs of recent recovery and some regrowth in 2017 and 2018, with a range of coral recruits and juveniles being observed in relatively high densities in many sites (Sheppard *et al.*, 2017). Given the size of a number of these juveniles (> 18 cm high in some cases), they are likely several years old now and have remarkably withstood the heat anomalies. A number of remnant patches were observed where a single or small group of polyps survived the bleaching period and are now rapidly re-growing over the dead colony surface, potentially facilitated by low levels of observed algal growth in the area, which in more nutrient-rich and over-fished regions has been shown to inhibit coral recovery (Hughes *et al.*, 2007).

The Chagos Archipelago was noted for its increased rate of recovery relative to other regions of the Indian Ocean following the major bleaching of 1998 (Sheppard *et al.*, 2012), and indications are that a similar recovery may now be underway again, likely facilitated through reseeded from deeper cooler water refuges (Riegl and Piller, 2003; Van Oppen *et al.*, 2011) and from areas protected by cold water upwellings / bores (Sheppard, 2009; Wall *et al.*, 2015). However, the recruitment from deep water refuges is limited by the number of taxa which can live at increased depths (Bongaerts *et al.*, 2017), and new recruits are currently generally settling on areas of unconsolidated rubble and unstable structures, meaning that any recovery will initially be slow and will result in communities likely to be quite different from those which occurred there before (McClanahan and Muthiga, 2014).

## *Limitations*

While the purpose of this study was to apply new monitoring technology to directly observe the changes in 3D physical structure following large-scale heat-induced coral mortality, the lack of data on abundance of key bioeroders such as reef fish and urchins limits our ability to fully explain the mechanisms causing such changes. Future work in this area would include these biological metrics in order to improve our ability to predict conservation outcomes for different reef community scenarios. However, although these data were collected by the broader team in this study, they will not become available for use in such collaboration until they have been published in their own right, which means this is outside the scope of this thesis.

A second limitation was the limited number of sites and replicates given the large scale of the total site area and the exclusion of the southern Diego Garcia sites, which would have provided an interesting further atoll group with different heat anomaly records, and likely different coral and fish communities. The Diego Garcia sites (and additional replicate sites in each atoll group) will be part of future work in this region, however no scaled video data were available for these sites pre-bleaching, and the Diego Garcia atoll sites were only accessible in 2018 (Appendix 14). However, preliminary observations in 2018 saw many sections of healthy surviving reef around the Diego Garcia atoll, suggesting that reefs around this atoll exhibited increased survivorship relative to the more northern atolls, potentially due to differing environmental conditions, demanding future investigation.

Finally, this study opportunistically used historic video data to assess pre-bleaching physical 3D structure. Using recent technological advances I was able to extract information additional to the data for which the video was originally surveyed. While I was able to

successfully extract structural metrics from this video data, it was of lower resolution and quality than the imagery collected later in the study expressly for this work. This meant I was restricted in which sites I could assess and by the detail at which I could assess structure. I therefore limited the resolution to 1 cm and the area to 20 m<sup>2</sup> per transect to make studies consistent between years, whereas if this restriction did not exist the resolution could have been increased to ~ 2 mm (based on maximum SfM model scaling accuracy) over areas up to 600 m<sup>2</sup>, and would have had a greater number of sites, potentially making any structural changes easier to detect. It is important to note here also that the varying approaches of video and photo-based SfM do not give significantly different results as long as a high video frame rate is used (Raoult *et al.*, 2017; Young *et al.*, 2017). This was further demonstrated here with the mixed effect model interaction terms showing that temporal differences are not just caused by methodological differences.

## Conclusions

The shallow reefs (between 5 and 15 m) of the northern and central atolls of the Chagos archipelago have experienced widespread damage to their physical structure following prolonged high temperatures, rapidly losing surface area, height, and complexity across medium and highly exposed locations. The low exposure areas, most notably the true enclosed / 'choked' lagoons (Kjerfve, 1986), largely escaped this damage, with this resilience appearing to be driven to some degree by their distinct community composition and varying environmental micro-habitats relative to the seaward reefs (Sheppard *et al.*, 2002; Hoogenboom *et al.*, 2017). Despite observations of good coral recruitment and re-growth from these new arrivals and surviving remnants (Sheppard *et al.*, 2017), the overall trend in structural metrics is still negative, two years following the end of the heating anomaly. The loss of structure and live coral already experienced in the archipelago, coupled with the resulting instability of the substrate following erosional collapse, will inhibit re-growth and successful recruitment for a number of years, regardless of any further bleaching (Hata *et al.*, 2017; Roth *et al.*, 2018; Viehman *et al.*, 2018). Furthermore, the marine communities which rely on this complex reef structure for food, habitat and shelter will have already been severely affected by these losses (Darling *et al.*, 2017; Richardson *et al.*, 2018; Rogers *et al.*, 2018a), leaving the reefs of the Chagos Archipelago with an uncertain future.

In the next Chapter I take a closer look at the current net rate of carbonate production balanced against the losses via erosional forces. This metric, quantifying the balance of coral growth and decline is termed the 'carbonate budget' and is an indicator of whether the reef's physical integrity and function as a habitat will be maintained (Mace *et al.*, 2014), or if they will instead eventually disappear.

## Appendices

Appendix 11. Level of modelled wave exposure (Joules m<sup>-2</sup>) and degree heating weeks (DHW) between 2014-2017 for all sites investigated within the Chagos archipelago, BIOT. Sites grouped by atoll region.

Number ID	Site	Wave (Jm <sup>2</sup> )	DHW 2014	DHW 2015	DHW 2016	DHW 2017
1	Egmont Mid	856	0.14	3.99	15.8	0.34
2	Egmont North	639	0.14	3.99	15.8	0.34
3	Danger East	584	0	4.11	14.78	0.15
4	Danger West	804	0	4.11	14.78	0.15
5	Eagle West	728	0	5.46	15.48	0.3
6	Eagle East	762	0	5.34	15.4	0.15
7	Middle Brother	1186	0	5.27	15.67	0.15
8	South Brother	1210	0	5.23	15.41	0.3
9	Ile Coin	199	0.14	4.85	12.3	0.33
10	Bernard's Knoll	523	0.14	4.99	12.37	0.32
11	Ile Poule	805	0.14	4.67	12.09	0.32
12	Ile Diamont West	488	0.44	4.77	12.44	0.16
13	Ile Diamont East	395	0.43	4.94	12.53	0.16
14	Moresby	149	0.44	5.14	12.54	0.16
15	Yeye	876	0.44	5.96	12.53	0.32
16	Petite Coquillage	1398	0.3	5.32	11.98	0.34
17	Ile Anglaise South	498	0.29	5.69	12.07	0.36
18	Sam's Knoll	64	0.29	5.85	12.07	0.35
19	IleDuPasse	667	0.29	5.84	12.16	0.35
20	Takamaka	1697	0.29	6.17	12.23	0.34
21	Blenheim South	620	0.46	6.05	12.33	0.36

Appendix 12. Linear model outputs for site-level changes in reef rugosity ratio over the three years following initial bleaching (April 2015 – 2018) across the Chagos archipelago.

Site	Parameter	Estimate	Std. Error	t value	Pr (> t )	F statistic	d.f.	R <sup>2</sup>																																																																																																																																																																																																																																																								
<b>Bernard's Knoll</b>	(Intercept)	0.409	0.038	10.830	0.000	17.810	1,38	0.301																																																																																																																																																																																																																																																								
	Year*	-0.085	0.020	-4.220	0.000				<b>Blenheim South</b>	(Intercept)	0.270	0.030	9.106	0.000	3.080	1,28	0.067	Year	-0.025	0.014	-1.755	0.090	<b>Danger East</b>	(Intercept)	0.315	0.040	7.865	0.000	5.706	1,18	0.199	Year*	-0.045	0.019	-2.389	0.028	<b>Danger West</b>	(Intercept)	0.303	0.038	7.873	0.000	1.508	1,18	0.026	Year	0.022	0.018	1.228	0.235	<b>Eagle East</b>	(Intercept)	0.369	0.024	15.360	0.000	5.116	1,18	0.036	Year*	-0.026	0.011	-2.262	0.036	<b>Eagle West</b>	(Intercept)	0.325	0.029	11.023	0.000	11.930	1,18	0.365	Year*	-0.048	0.014	-3.455	0.003	<b>Egmont Mid</b>	(Intercept)	0.196	0.016	12.511	0.000	0.771	1,18	-0.012	Year	-0.006	0.007	-0.878	0.391	<b>Egmont North</b>	(Intercept)	0.150	0.013	11.922	0.000	0.975	1,18	-0.001	Year	-0.006	0.006	-0.987	0.337	<b>Ile Anglaise Sth</b>	(Intercept)	0.348	0.058	6.047	0.000	0.121	1,28	-0.031	Year	0.010	0.028	0.348	0.730	<b>Ile Coin</b>	(Intercept)	0.338	0.055	6.098	0.000	0.411	1,28	-0.021	Year	0.017	0.027	0.641	0.526	<b>Ile Diamont East</b>	(Intercept)	0.349	0.025	14.192	0.000	8.541	1,28	0.206	Year*	-0.035	0.012	-2.922	0.007	<b>Ile Poule</b>	(Intercept)	0.418	0.040	10.414	0.000	10.060	1,38	0.189	Year*	-0.068	0.021	-3.172	0.003	<b>Middle Brother</b>	(Intercept)	0.370	0.027	13.464	0.000	21.340	1,18	0.517	Year*	-0.060	0.013	-4.619	0.000	<b>Moresby</b>	(Intercept)	0.338	0.027	12.616	0.000	0.181	1,28	-0.029	Year	-0.005	0.013	-0.426	0.674	<b>Petite Coquillage</b>	(Intercept)	0.291	0.019	15.108	0.000	6.330	1,38	0.016	Year*	-0.026	0.010	-2.516	0.016	<b>Ile Du Passe</b>	(Intercept)	0.364	0.055	6.603	0.000	0.093	1,18	-0.050	Year	-0.008	0.026	-0.305	0.764	<b>Sam's Knoll</b>	(Intercept)	0.329	0.034	9.779	0.000	1.232	1,28	0.008	Year	0.018	0.016	1.110	0.276	<b>South Brother</b>	(Intercept)	0.198	0.022	9.171	0.000	0.032	1,18	-0.054	Year	-0.002	0.010	-0.179	0.860	<b>Takamaka</b>	(Intercept)	0.258	0.013	19.666	0.000	81.750	1,18	0.810	Year*
<b>Blenheim South</b>	(Intercept)	0.270	0.030	9.106	0.000	3.080	1,28	0.067																																																																																																																																																																																																																																																								
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<b>Danger East</b>	(Intercept)	0.315	0.040	7.865	0.000	5.706	1,18	0.199																																																																																																																																																																																																																																																								
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	Year	0.022	0.018	1.228	0.235				<b>Eagle East</b>	(Intercept)	0.369	0.024	15.360	0.000	5.116	1,18	0.036	Year*	-0.026	0.011	-2.262	0.036	<b>Eagle West</b>	(Intercept)	0.325	0.029	11.023	0.000	11.930	1,18	0.365	Year*	-0.048	0.014	-3.455	0.003	<b>Egmont Mid</b>	(Intercept)	0.196	0.016	12.511	0.000	0.771	1,18	-0.012	Year	-0.006	0.007	-0.878	0.391	<b>Egmont North</b>	(Intercept)	0.150	0.013	11.922	0.000	0.975	1,18	-0.001	Year	-0.006	0.006	-0.987	0.337	<b>Ile Anglaise Sth</b>	(Intercept)	0.348	0.058	6.047	0.000	0.121	1,28	-0.031	Year	0.010	0.028	0.348	0.730	<b>Ile Coin</b>	(Intercept)	0.338	0.055	6.098	0.000	0.411	1,28	-0.021	Year	0.017	0.027	0.641	0.526	<b>Ile Diamont East</b>	(Intercept)	0.349	0.025	14.192	0.000	8.541	1,28	0.206	Year*	-0.035	0.012	-2.922	0.007	<b>Ile Poule</b>	(Intercept)	0.418	0.040	10.414	0.000	10.060	1,38	0.189	Year*	-0.068	0.021	-3.172	0.003	<b>Middle Brother</b>	(Intercept)	0.370	0.027	13.464	0.000	21.340	1,18	0.517	Year*	-0.060	0.013	-4.619	0.000	<b>Moresby</b>	(Intercept)	0.338	0.027	12.616	0.000	0.181	1,28	-0.029	Year	-0.005	0.013	-0.426	0.674	<b>Petite Coquillage</b>	(Intercept)	0.291	0.019	15.108	0.000	6.330	1,38	0.016	Year*	-0.026	0.010	-2.516	0.016	<b>Ile Du Passe</b>	(Intercept)	0.364	0.055	6.603	0.000	0.093	1,18	-0.050	Year	-0.008	0.026	-0.305	0.764	<b>Sam's Knoll</b>	(Intercept)	0.329	0.034	9.779	0.000	1.232	1,28	0.008	Year	0.018	0.016	1.110	0.276	<b>South Brother</b>	(Intercept)	0.198	0.022	9.171	0.000	0.032	1,18	-0.054	Year	-0.002	0.010	-0.179	0.860	<b>Takamaka</b>	(Intercept)	0.258	0.013	19.666	0.000	81.750	1,18	0.810	Year*	-0.084	0.009	-9.042	0.000																																						
<b>Eagle East</b>	(Intercept)	0.369	0.024	15.360	0.000	5.116	1,18	0.036																																																																																																																																																																																																																																																								
	Year*	-0.026	0.011	-2.262	0.036				<b>Eagle West</b>	(Intercept)	0.325	0.029	11.023	0.000	11.930	1,18	0.365	Year*	-0.048	0.014	-3.455	0.003	<b>Egmont Mid</b>	(Intercept)	0.196	0.016	12.511	0.000	0.771	1,18	-0.012	Year	-0.006	0.007	-0.878	0.391	<b>Egmont North</b>	(Intercept)	0.150	0.013	11.922	0.000	0.975	1,18	-0.001	Year	-0.006	0.006	-0.987	0.337	<b>Ile Anglaise Sth</b>	(Intercept)	0.348	0.058	6.047	0.000	0.121	1,28	-0.031	Year	0.010	0.028	0.348	0.730	<b>Ile Coin</b>	(Intercept)	0.338	0.055	6.098	0.000	0.411	1,28	-0.021	Year	0.017	0.027	0.641	0.526	<b>Ile Diamont East</b>	(Intercept)	0.349	0.025	14.192	0.000	8.541	1,28	0.206	Year*	-0.035	0.012	-2.922	0.007	<b>Ile Poule</b>	(Intercept)	0.418	0.040	10.414	0.000	10.060	1,38	0.189	Year*	-0.068	0.021	-3.172	0.003	<b>Middle Brother</b>	(Intercept)	0.370	0.027	13.464	0.000	21.340	1,18	0.517	Year*	-0.060	0.013	-4.619	0.000	<b>Moresby</b>	(Intercept)	0.338	0.027	12.616	0.000	0.181	1,28	-0.029	Year	-0.005	0.013	-0.426	0.674	<b>Petite Coquillage</b>	(Intercept)	0.291	0.019	15.108	0.000	6.330	1,38	0.016	Year*	-0.026	0.010	-2.516	0.016	<b>Ile Du Passe</b>	(Intercept)	0.364	0.055	6.603	0.000	0.093	1,18	-0.050	Year	-0.008	0.026	-0.305	0.764	<b>Sam's Knoll</b>	(Intercept)	0.329	0.034	9.779	0.000	1.232	1,28	0.008	Year	0.018	0.016	1.110	0.276	<b>South Brother</b>	(Intercept)	0.198	0.022	9.171	0.000	0.032	1,18	-0.054	Year	-0.002	0.010	-0.179	0.860	<b>Takamaka</b>	(Intercept)	0.258	0.013	19.666	0.000	81.750	1,18	0.810	Year*	-0.084	0.009	-9.042	0.000																																																				
<b>Eagle West</b>	(Intercept)	0.325	0.029	11.023	0.000	11.930	1,18	0.365																																																																																																																																																																																																																																																								
	Year*	-0.048	0.014	-3.455	0.003				<b>Egmont Mid</b>	(Intercept)	0.196	0.016	12.511	0.000	0.771	1,18	-0.012	Year	-0.006	0.007	-0.878	0.391	<b>Egmont North</b>	(Intercept)	0.150	0.013	11.922	0.000	0.975	1,18	-0.001	Year	-0.006	0.006	-0.987	0.337	<b>Ile Anglaise Sth</b>	(Intercept)	0.348	0.058	6.047	0.000	0.121	1,28	-0.031	Year	0.010	0.028	0.348	0.730	<b>Ile Coin</b>	(Intercept)	0.338	0.055	6.098	0.000	0.411	1,28	-0.021	Year	0.017	0.027	0.641	0.526	<b>Ile Diamont East</b>	(Intercept)	0.349	0.025	14.192	0.000	8.541	1,28	0.206	Year*	-0.035	0.012	-2.922	0.007	<b>Ile Poule</b>	(Intercept)	0.418	0.040	10.414	0.000	10.060	1,38	0.189	Year*	-0.068	0.021	-3.172	0.003	<b>Middle Brother</b>	(Intercept)	0.370	0.027	13.464	0.000	21.340	1,18	0.517	Year*	-0.060	0.013	-4.619	0.000	<b>Moresby</b>	(Intercept)	0.338	0.027	12.616	0.000	0.181	1,28	-0.029	Year	-0.005	0.013	-0.426	0.674	<b>Petite Coquillage</b>	(Intercept)	0.291	0.019	15.108	0.000	6.330	1,38	0.016	Year*	-0.026	0.010	-2.516	0.016	<b>Ile Du Passe</b>	(Intercept)	0.364	0.055	6.603	0.000	0.093	1,18	-0.050	Year	-0.008	0.026	-0.305	0.764	<b>Sam's Knoll</b>	(Intercept)	0.329	0.034	9.779	0.000	1.232	1,28	0.008	Year	0.018	0.016	1.110	0.276	<b>South Brother</b>	(Intercept)	0.198	0.022	9.171	0.000	0.032	1,18	-0.054	Year	-0.002	0.010	-0.179	0.860	<b>Takamaka</b>	(Intercept)	0.258	0.013	19.666	0.000	81.750	1,18	0.810	Year*	-0.084	0.009	-9.042	0.000																																																																		
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	Year*	-0.060	0.013	-4.619	0.000				<b>Moresby</b>	(Intercept)	0.338	0.027	12.616	0.000	0.181	1,28	-0.029	Year	-0.005	0.013	-0.426	0.674	<b>Petite Coquillage</b>	(Intercept)	0.291	0.019	15.108	0.000	6.330	1,38	0.016	Year*	-0.026	0.010	-2.516	0.016	<b>Ile Du Passe</b>	(Intercept)	0.364	0.055	6.603	0.000	0.093	1,18	-0.050	Year	-0.008	0.026	-0.305	0.764	<b>Sam's Knoll</b>	(Intercept)	0.329	0.034	9.779	0.000	1.232	1,28	0.008	Year	0.018	0.016	1.110	0.276	<b>South Brother</b>	(Intercept)	0.198	0.022	9.171	0.000	0.032	1,18	-0.054	Year	-0.002	0.010	-0.179	0.860	<b>Takamaka</b>	(Intercept)	0.258	0.013	19.666	0.000	81.750	1,18	0.810	Year*	-0.084	0.009	-9.042	0.000																																																																																																																																																																				
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Appendix 13. Species level trait data for scleractinian corals surveyed within the Chagos during 2015.

Traits based on information from the coraltraits.org database.

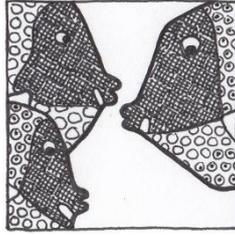
Species	Major clade	Family (molecules)	Family (morphology)	L-H Trait group
<i>Acanthastrea echinata</i>	Robust	Lobophyllidae	Mussidae	stress-tolerant
<i>Acropora brueggemanni</i>	Complex	Acroporidae	Acroporidae	competitive
<i>Acropora cerealis</i>	Complex	Acroporidae	Acroporidae	competitive
<i>Acropora clathrata</i>	Complex	Acroporidae	Acroporidae	competitive
<i>Acropora cytherea</i>	Complex	Acroporidae	Acroporidae	competitive
<i>Acropora divaricata</i>	Complex	Acroporidae	Acroporidae	competitive
<i>Acropora formosa</i>	Complex	Acroporidae	Acroporidae	competitive
<i>Acropora gemmifera</i>	Complex	Acroporidae	Acroporidae	competitive
<i>Acropora lamarcki</i>	Complex	Acroporidae	Acroporidae	competitive
<i>Acropora microphthalma</i>	Complex	Acroporidae	Acroporidae	competitive
<i>Acropora palifera</i>	Complex	Acroporidae	Acroporidae	competitive
<i>Acropora plantaginea</i>	Complex	Acroporidae	Acroporidae	competitive
<i>Acropora rosaria</i>	Complex	Acroporidae	Acroporidae	competitive
<i>Acropora vermiculata</i>	Complex	Acroporidae	Acroporidae	competitive
<i>Astreopora suggesta</i>	Complex	Acroporidae	Acroporidae	stress-tolerant
<i>Coscinaraea spp.</i>	Robust	Coscinaraeidae	Siderastreidae	NA
<i>Diploastrea heliopora</i>	Robust	Diploastraeidae	Faviidae	stress-tolerant
<i>Echinophyllia aspera</i>	Robust	Lobophyllidae	Pectiniidae	stress-tolerant
<i>Echinopora lamellosa</i>	Robust	Merulinidae	Faviidae	generalist
<i>Favia fava</i>	Robust	Merulinidae	Faviidae	stress-tolerant
<i>Favia helianthoides</i>	Robust	Merulinidae	Faviidae	stress-tolerant
<i>Favia maritima</i>	Robust	Merulinidae	Faviidae	stress-tolerant
<i>Favia speciosa</i>	Robust	Merulinidae	Faviidae	stress-tolerant
<i>Favites abdita</i>	Robust	Merulinidae	Faviidae	stress-tolerant
<i>Favites halicora</i>	Robust	Merulinidae	Faviidae	stress-tolerant
<i>Fungia fungites</i>	Robust	Fungiidae	Fungiidae	stress-tolerant
<i>Galaxea fascicularis</i>	Complex	Euphylliidae	Oculinidae	stress-tolerant
<i>Goniastrea pectinata</i>	Robust	Merulinidae	Faviidae	stress-tolerant
<i>Goniastrea peresi</i>	Robust	Merulinidae	Faviidae	stress-tolerant
<i>Goniopora spp.</i>	Complex	Poritidae	Poritidae	stress-tolerant
<i>Halomitra pileus</i>	Robust	Fungiidae	Fungiidae	NA
<i>Heliopora coerulea</i>	NA	NA	NA	NA
<i>Leptoseris incrustans</i>	Complex	Agariciidae	Agariciidae	NA
<i>Lobophyllia hemprichii</i>	Robust	Lobophyllidae	Mussidae	stress-tolerant
<i>Montipora efflorescens</i>	Complex	Acroporidae	Acroporidae	generalist
<i>Montipora floweri</i>	Complex	Acroporidae	Acroporidae	generalist
<i>Montipora spumosa</i>	Complex	Acroporidae	Acroporidae	generalist
<i>Mycedium elephantotus</i>	Robust	Merulinidae	Pectiniidae	generalist
<i>Pachyseris rugosa</i>	Complex	Pachyseridae	Agariciidae	generalist

<b><i>Pachyseris speciosa</i></b>	Complex	Pachyseridae	Agariciidae	generalist
<b><i>Pavona duerdeni</i></b>	Complex	Agariciidae	Agariciidae	stress-tolerant
<b><i>Pavona venosa</i></b>	Complex	Agariciidae	Agariciidae	stress-tolerant
<b><i>Platygyra lamellina</i></b>	Robust	Merulinidae	Faviidae	stress-tolerant
<b><i>Platygyra sinensis</i></b>	Robust	Merulinidae	Faviidae	stress-tolerant
<b><i>Plerogyra sinuosa</i></b>	Robust	Plesiastreidae	Euphyllidae	stress-tolerant
<b><i>Pocillopora damicornis</i></b>	Robust	Pocilloporidae	Pocilloporidae	weedy
<b><i>Pocillopora eydouxi</i></b>	Robust	Pocilloporidae	Pocilloporidae	competitive
<b><i>Pocillopora verrucosa</i></b>	Robust	Pocilloporidae	Pocilloporidae	competitive
<b><i>Porites cylindrica</i></b>	Complex	Poritidae	Poritidae	weedy
<b><i>Porites lutea</i></b>	Complex	Poritidae	Poritidae	stress-tolerant
<b><i>Porites solida</i></b>	Complex	Poritidae	Poritidae	weedy
<b><i>Stylophora pistillata</i></b>	Robust	Pocilloporidae	Pocilloporidae	weedy
<b><i>Symphyllia radians</i></b>	Robust	Lobophyllidae	Mussidae	stress-tolerant
<b><i>Symphyllia recta</i></b>	Robust	Lobophyllidae	Mussidae	stress-tolerant

Appendix 14. Full list of sites visited across the Chagos archipelago in each year 2016 – 2018 where SfM was conducted, with broad atoll region, gross ecology, and survey type conducted shown. Values represent square metres of SfM surveys for the large quadrat arrangement. Surveys conducted in a transect arrangements were all four sets of 20 x 2 m surveys. All surveys conducted at ~ 10 m depth.

Site	Atoll	Location	2018	2017	2016
Canon Point	Diego Garcia	Seaward	400	-	-
Middle Island	Diego Garcia	Seaward	200	-	-
Horsborough Point	Diego Garcia	Seaward	400	-	-
Barton Point	Diego Garcia	Seaward	200	-	-
Ile Coin	Peros Banhos	Lagoon	200	100	-
Ile Poule	Peros Banhos	Seaward	400	200	Transects
Bernard Knoll	Peros Banhos	Lagoon	400	200	Transects
Ile Fouquet	Peros Banhos	Seaward	-	200	Transects
Ile Diamont	Peros Banhos	Seaward	200	200	-
Ile Diamont	Peros Banhos	Lagoon	200	200	200
Moresby	Peros Banhos	Seaward	200	200	Transects
Ile de la Passe	Peros Banhos	Seaward	200	200	-
Petit Coquillage	Peros Banhos	Seaward	400	100	200
Yeye	Peros Banhos	Seaward	200	200	-
Ile Anglaise South	Salomon	Seaward	200	200	-
Ile du passe	Salomon	Seaward	200	200	-
Takamaka	Salomon	Seaward	-	200	-
Ile Anglaise Mid	Salomon	Seaward	-	-	Transects
Court's Knoll	Salomon	Lagoon	200	-	Transects
Sam's knoll	Salomon	Lagoon	200	200	Transects
Ile Jacobin	Salomon	Seaward	-	-	Transects
Ile Fouquet	Salomon	Seaward	-	-	Transects
Blenheim South	Blenheim	Seaward	300	200	-
Blenheim East	Blenheim	Seaward	-	200	-
Nelson Island	Great Chagos Bank	Seaward	200	-	-
Middle Brother	Great Chagos Bank	Seaward	100	-	-
South Brother	Great Chagos Bank	Seaward	100	-	Transects
North Brother	Great Chagos Bank	Seaward	100	-	-
Eagle Seaward	Great Chagos Bank	Seaward	300	-	-
Eagle Lagoon	Great Chagos Bank	Lagoon	200	-	-
Danger	Great Chagos Bank	Seaward	200	-	-
Danger lagoon	Great Chagos Bank	Lagoon	100	-	-
Egmont Mid	Great Chagos Bank	Seaward	100	-	Transects
Egmont North	Great Chagos Bank	Seaward	200	-	-
Egmont South	Great Chagos Bank	Seaward	-	-	Transects





## *Chapter 6: Post-bleaching growth and erosion rates of central Indian Ocean coral communities*

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Initial outputs of this chapter have been adapted for the following publications:

- Sheppard C, Sheppard A, Mogg AOM, Bayley DTI, Dempsey AC, Roche R, Turner, J., & Purkis, S. (2017) *Coral Bleaching & Mortality in the Chagos Archipelago*. *Atoll Res. Bull.*, 1-26.

### **Abstract**

The mounting pressures now facing tropical coral reefs, such as regular bleaching events and increasingly acidified waters, are making it difficult for reefs to maintain their structure and growth against the constant biological and physical erosional forces of the ocean. Net carbonate production is an indicator of biome-level change on a reef, giving an overall measure of whether the system is growing or eroding (i.e. a measure of health) over a broad scale. This study finds the majority of the sites surveyed within the northern reefs of the Chagos Archipelago are currently in a state of net erosional loss of carbonate structure (mean 'G' (carbonate budget value) =  $-4.62 \pm 1.04 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ yr}^{-1}$  around Peros Banhos atoll), two years following the end of a global bleaching episode, which caused widespread heat-induced coral mortality. Despite the overall loss in reef carbonate budget, lagoons have remained net positive (model estimate =  $+2.03 \text{ G}$ ,  $t = 1.05$ ,  $p = 0.31$ ), while seaward reef budget estimates from mixed-effects model range from  $-5.03 \text{ G}$  ( $t = -2.69$ ,  $p < 0.03$ ) to  $-5.88 \text{ G}$  ( $t = -2.49$ ,  $p < 0.03$ ) across low – high wave exposure regimes. Carbonate levels for seaward reefs are now well below the amount of  $\geq 1 \text{ kg m}^{-2} \text{ yr}^{-1}$  net budget proposed as a boundary threshold for maintenance of this biome (Mace *et al.*, 2014), meaning that the extent and functionality of this system is being rapidly lost. Good levels of recruitment and re-growth of surviving corals were observed on seaward slopes, with initial estimates showing individuals of *Acropora cytherea* and *Porites lutea* to be growing at the high end of published regional growth rates for these species. This study further demonstrates the utility of emerging monitoring tools in estimating carbonate budgets, with the results from 'Structure from Motion' photogrammetry comparable to established methods, yet requiring less specialist species knowledge and less in-field time in order to assess large areas of reef.

## Introduction

By 2100, sea levels are projected to rise by 0.26 - 0.77 metres relative to 1986-2005 due to climate change, even within the lowest temperature increase scenario of 1.5°C (IPCC, 2018). Sea level increases of this scale are likely to lead to flooding / inundation, damage to infrastructure and loss of shoreline for many low-lying coastal regions and islands (van Woesik *et al.*, 2015; IPCC, 2018). In addition, ocean acidification and both the frequency and magnitude of mass coral bleaching and major storms is also rising (Pandolfi *et al.*, 2011; Emanuel, 2013; Heron *et al.*, 2016; Hughes *et al.*, 2018a). These mounting pressures are leading to the global loss of coral reef cover and complexity, which plays an important role in reducing coastal wave energy and maintaining island sediment stability (Ferrario *et al.*, 2014; Quataert *et al.*, 2015; Harris *et al.*, 2018). The ability of reefs to maintain their overall growth in line with these rapid environmental changes is far from certain, but will be highly unlikely under the highest projected warming scenarios of 8.5°C, and very challenging even under the lowest scenario (Gattuso *et al.*, 2015; IPCC, 2018; Perry *et al.*, 2018).

The balance between the rate of reef accretion through calcification and the rate of loss through bio-physical erosion and dissolution gives a measure of the net rate of biologically driven carbonate production through time, and therefore a measure of overall reef growth or decline (Januchowski-Hartley *et al.*, 2017). Accretion and erosion potential are controlled by a number of biotic and abiotic factors that can have effects over a range of time scales (Nyström *et al.*, 2000; Kennedy *et al.*, 2013). Abiotic factors include temperature, pH, water chemistry and physical disturbance from storms and wave action (Dollar, 1982; Nyström *et al.*, 2000; Silverman *et al.*, 2009; Koweek *et al.*, 2015; Ainsworth *et al.*, 2016). Biotic factors include variables such as the abundance and species type of calcifying benthic organisms

like corals, or the rate of grazing and endolithic bio-erosion, such as from parrotfish and boring sponges, respectively (Koweek *et al.*, 2015; Perry *et al.*, 2015).

Overall erosion rates can change through time if variables such as fishing effort increase in an area because bio-eroders such as parrotfish are progressively lost, leading to reduced bio-erosion and reduced lithification from their sand waste (Perry *et al.*, 2015; Cramer *et al.*, 2017). Similarly, if the extent and richness of species of calcifying organisms such as corals is reduced following a disturbance event, overall calcification will also reduce (Alvarez-Filip *et al.*, 2009; Perry *et al.*, 2013; Januchowski-Hartley *et al.*, 2017; Perry and Morgan, 2017).

The importance of net carbonate production as a suitable indicator of biome-level change of a reef, signifies both the integrity and functioning of this system over a broad scale (Kennedy *et al.*, 2013; Mace *et al.*, 2014; Perry *et al.*, 2018). A number of techniques have therefore been developed to assess rates of reef calcification, such as instantaneous Eulerian or Lagrangian chemistry-based estimates of net community calcification (Koweek *et al.*, 2015), and the 'ReefBudget' census-based budgetary approach (Perry *et al.*, 2012).

The ReefBudget technique applies averaged coral growth and density values to species or growth forms surveyed within a particular biogeographic region to attain spatial estimates of annual coral community carbonate production for a reef. This estimate of growth is then balanced against estimated cumulative erosion from parrotfish and bio-eroding urchins, based on the abundance and size of those fish species and their bite rates (Perry *et al.*, 2012).

One issue with this technique is that estimates of coral species-level growth and rates of species-level bio-erosion can vary substantially over a bio-geographic region (Perry *et al.*, 2012; van Woesik *et al.*, 2015; Yarlett *et al.*, 2018). Therefore under-studied taxa or remote and

under-studied areas of the world that are lacking in data, have greater uncertainty within their budgetary estimates. Furthermore, changes in abiotic environmental conditions such as increases in pH through time will change the rates of accretion or dissolution (e.g. the process of calcification uses a greater amount of energy as waters become more acidic), and production estimates can become inaccurate (Pandolfi *et al.*, 2011; Roik *et al.*, 2018). However, a greater issue with this technique is that it relies heavily on surveys of bio-eroder abundances taken at a single point in time, and is therefore just a snapshot which may not be representative of the site more generally. Parrotfish are key bio-eroders on reefs (Perry *et al.*, 2015; Yarlett *et al.*, 2018), but have home ranges which can be many thousands of square metres (Welsh and Bellwood, 2012), and their movement is typically patchy, focussing on different reef areas at different hours of the day or seasons of the year (Davis *et al.*, 2017). While much of this uncertainty is recorded as part of the ReefBudget method, it leaves a great range of possible error within assessments and subsequent predictions.

Over recent years there have been rapid advances in the development and use of emerging technologies such as photogrammetry and LiDAR to quantify the physical structure of underwater environments (Bayley and Mogg, 2018; Hamylton *et al.*, 2017; Chapter 1). ‘Structure from Motion’ (SfM) photogrammetry in particular now allows us to quantitatively assess the morphological properties of objects to a high accuracy, and therefore to assess the changes in physical characteristics, such as surface area or volume of reefs through time (Burns *et al.* 2015; Figueira *et al.* 2015; Ferrari *et al.* 2017; Chapter 2).

In 2015 and 2016, reefs across the globe experienced widespread mortality following bleaching from two extended periods of anomalously elevated sea temperature in rapid succession (Hughes *et al.*, 2017; Chapter 1). The heating periods caused the carbonate

budgets of Maldivian shallow fore-reefs to shift from being strongly net positive (mean 5.92 kg CaCO<sub>3</sub> m<sup>-2</sup> yr<sup>-1</sup>) to being strongly net negative (mean -2.96 kg CaCO<sub>3</sub> m<sup>-2</sup> yr<sup>-1</sup>) over the eight months following the extended bleaching (Perry and Morgan, 2017).

In this study I use SfM to assess annual growth and erosion rates of reefs in the neighbouring Northern atolls of the Chagos archipelago between 2017 and 2018 following bleaching-induced mortality (Sheppard *et al.* 2017; Chapter 5). I use volume change measurements to calculate estimates of net carbonate budget rates within varying wave exposure environments in order to test for generalised differences in rates and direction of change. I further aim to demonstrate the novel use of SfM as a comparable alternative method for rapid estimation of net carbonate production that integrates gains and losses between successive survey dates, eliminating some of the assumptions (and associated uncertainty) inherent in other currently used assessment methodologies.

## Methods

### *Location and design*

Twelve sites were assessed within the shallow (~10 m) reef flats of the Northern extent of the British Indian Ocean Territory during April 2017 and 2018, one and two years following a large-scale bleaching episode which occurred across the Indian Ocean (Figure 39). Sites were located across three atolls within close proximity to one-another (~50 - 100 km), across varying levels of exposure. Level of exposure was split into four categories of sheltered lagoon ( $\leq 500 \text{ J m}^{-3}$ , n=3), and low ( $\leq 500 \text{ J m}^{-3}$ , n=3), medium ( $> 500 - \leq 1000 \text{ J m}^{-3}$ , n=4), and highly exposed seaward reefs ( $> 1000 \text{ J m}^{-3}$ , n=2). Categories were based on modelled

exposure levels for the Chagos Archipelago from Perry *et al.* (2015b), with the division of sites into 500 J m<sup>-3</sup> bins following natural breaks in the data, while recognises the distinctness of enclosed lagoon or lagoon-like conditions. The wave exposure modelling method is further described in Chapter 5. Three – six 10 m<sup>2</sup> blocked samples were taken at each site, with three samples measured per site block.

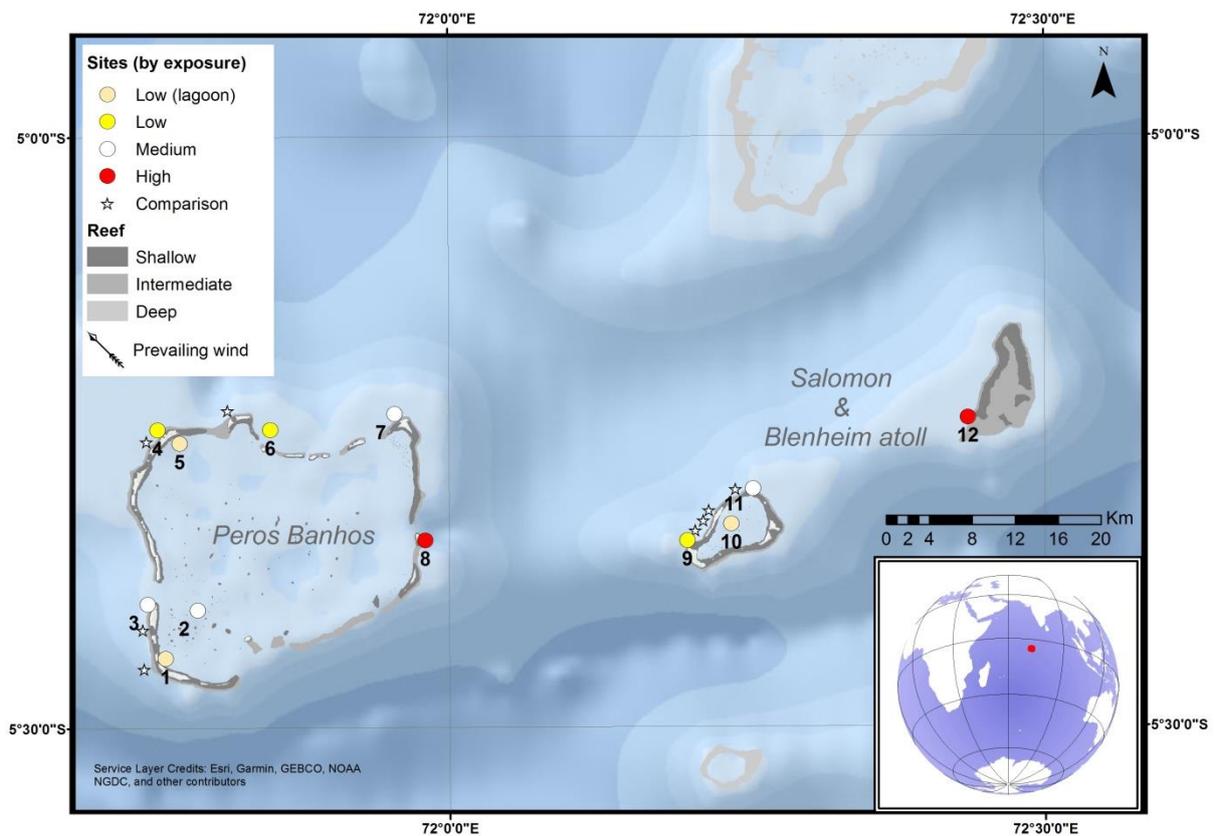


Figure 39. Locations of each of the twelve sites surveyed in the British Indian Ocean Territory during April 2017 & 2018. Broad remote-sensed reef categories (shallow – deep) (Andréfouët *et al.*, 2006), site wave exposure categories (lagoon & low – high exposure seaward sites) and prevailing wind direction (Perry *et al.*, 2016) shown. Site 1 = Ile du Coin, 2 = Bernard’s knoll, 3 = Ile Poule, 4 = Ile Diamont (West), 5 = Ile Diamont (East), 6 = Ile Moresby, 7 = Ile Yeye, 8 = Petit Coquillage, 9 = Ile Anglaise South, 10 = Sam’s knoll, 11 = Ile du Passe, 12 = Blenheim atoll. Site locations from the comparison study by Lange & Perry (2018) shown with stars.

In 2017 and 2018, a planar area of between 100 – 400 m<sup>2</sup> was surveyed at each of the twelve Northern atoll sites. Permanent GPS marked rebar metal stakes were placed in each site, along with eight smaller metal markers at cardinal points surrounding the central rebar in order to allow exact overlap of the survey areas for each year. Reefs were surveyed at approximately 2 m above the substrate using a Nikon D750 DSLR camera, with a 20 mm wide-angle fixed lens and dome port under ambient lighting conditions. Each site had multiple reference markers (0.5 m x 0.5 m quadrats) placed across the survey area in order to calibrate scale, along with a tripod-mounted spirit level and compass at known depth in order to calibrate xyz-axis dimensions.

The captured images (~ 700 HD overlapping images per site) were then processed as in previous chapters using 'Structure from Motion' photogrammetric algorithms within Agisoft Photoscan (Agisoft LLC, 2017) to produce twelve paired sets of high definition xyz point-clouds, detailing the reef surface for each year at each site. Each model was based on high-accuracy optimised alignment settings, with generic preselection, 40,000 key points, and had dense cloud quality set to high with aggressive depth filtering. The resulting dense point-clouds typically had > 17 million modelled vertices. Post-processing included removal of any anomalous 'floating' points missed in the filtering process. Models were then orientated to the compass and spirit-level, and calibrated to a scaling accuracy of < 5 mm (Figure 40; Appendix 15-13).

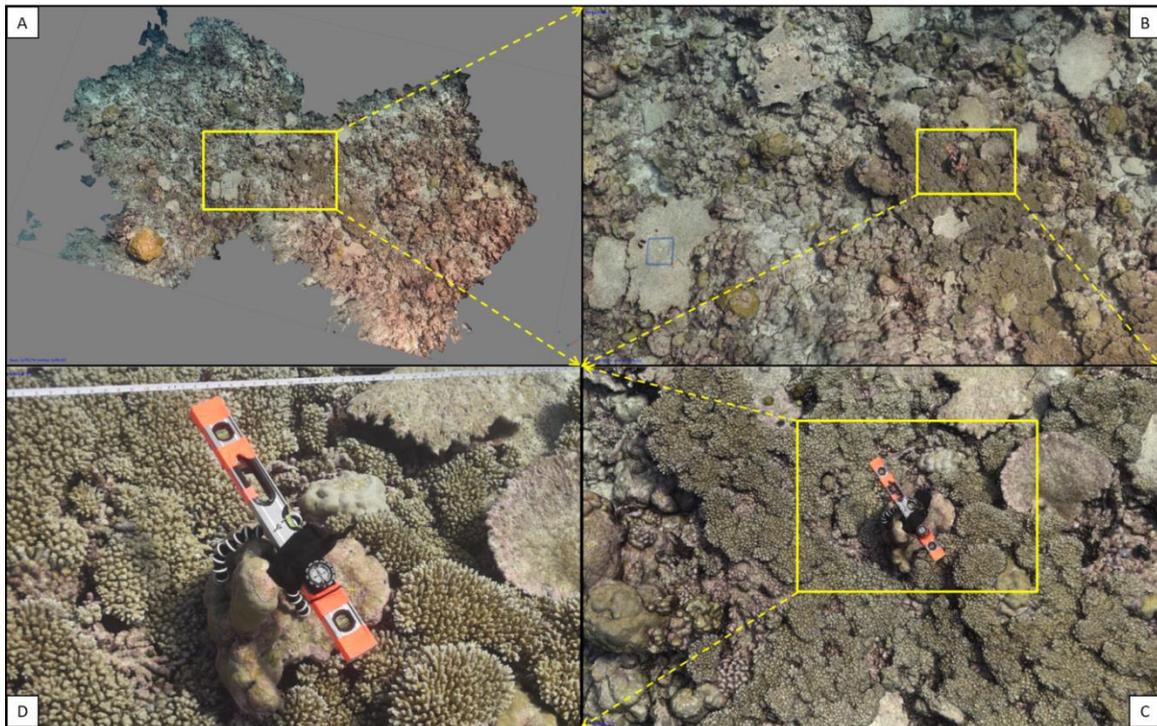


Figure 40. Visualisation of a typical model created during the photogrammetry process, showing detail across scales ranging from  $\sim 500 \text{ m}^2$  (A) to  $\sim 1 \text{ m}^2$  (D) for a section of reef in Ile Diamont, BIOT, surveyed during 2018. Spirit level used for calibration shown (D) and blue reference quadrat seen in situ (B). Models calibrated to  $< 5 \text{ mm}$ .

### *Overlay of models*

Following point-cloud creation and calibration for the years 2017 and 2018, each site was split into two blocks (separated by roughly 10 m). The two corresponding point-cloud layers for each block at each site were cropped to broadly overlapping  $50 \text{ m}^2$  sections and exported as dense point-clouds to the open-source software ‘CloudCompare’ (Girardeau-Montaut, 2018) for direct point-cloud to point-cloud surface comparison.

The two 2017 and 2018 point-cloud layers for each block were initially roughly aligned using the ‘Equivalent point pairing’ tool, based on matching at least four separate points between each cloud layer to give broad overlap (Figure 41). Following this step, fine-scale final

alignment was achieved using the 'Iterative Closest Point' tool, based on 5000 random samples per model ( $1.0e^{-5}$  Root Mean Square averaged difference over the sample area). Scale adjustment was enabled, based on the 2017 reef as the reference layer, giving typical surface matching of  $> 96\%$ . Once the two clouds were fully aligned, I cropped the data into three  $\sim 10\text{ m}^2$  sample strips per block, with  $\sim 3\text{ m}$  spacing between strips (giving three to six reef sample strip replicates per site). The average point-point Z plane (height) difference between 2017 and 2018 models was calculated for each sample strip (with empty cell interpolation selected, and modelled at a resolution of  $5\text{ mm}$ ) to ascertain the '2.5D' volume change ( $\text{m}^3$ ) over the whole cloud surface area ( $\text{m}^2$ ). 2017 was used as the reference data layer in all models.

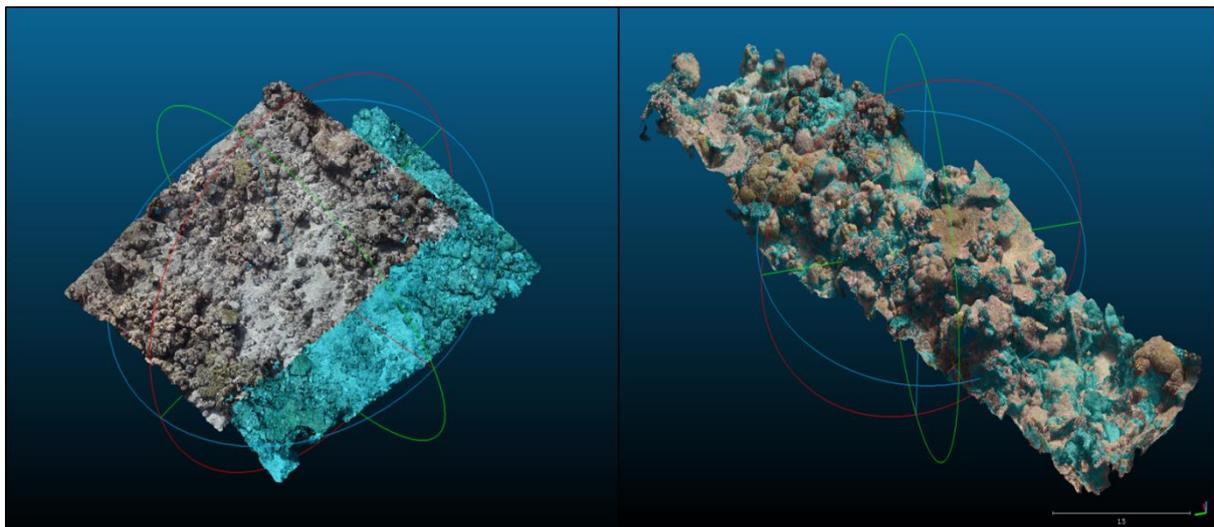


Figure 41. Illustrating the process of aligning two dense point-cloud sections from SfM outputs of repeat annual surveys along the Chagos archipelago reef during 2017 and 2018 (left), and a fully aligned (composite point-cloud)  $10\text{ m}^2$  clipped section (right).

### *Carbonate budget calculation*

The approximate net balance (G) of carbonate (CaCO<sub>3</sub>) accretion versus erosion was calculated by multiplying the net annual volume change of the reef between the two years against the averaged Indo-Pacific regional measurements of coral skeletal density (g cm<sup>-3</sup>) (Figure 42). I used averaged species and growth form-specific estimations from a range of published assessments collated for species within the Indo-Pacific region for use with the 'ReefBudget' method (Perry *et al.*, 2012). These density values from the literature were based on a mix of Alizarin red stain / Archimedes bath / X-radiography assessment methods (

Table 10).

Table 10. Average skeletal density of coral growth forms from published studies within the Indo-Pacific marine region. Data is from the 'ReefBudget' methods database (Perry *et al.*, 2012). Values are coral growth-form averages from multiple species and multiple published studies, listed within the ReefBudget database.

<b>Coral Growth form</b>	<b>Mean skeletal density (g cm<sup>-3</sup>)</b>	<b>SD</b>
Branching	1.413	0.095
Encrusting (under review)	Unavailable	-
Foliose / frondose	1.271	0.44
Massive	1.457	0.208
Mushroom (under review)	Unavailable	-
Plating	1.271	0.44
Sub-massive	1.395	0.035
<b>ALL</b>	<b>1.361</b>	<b>0.227</b>

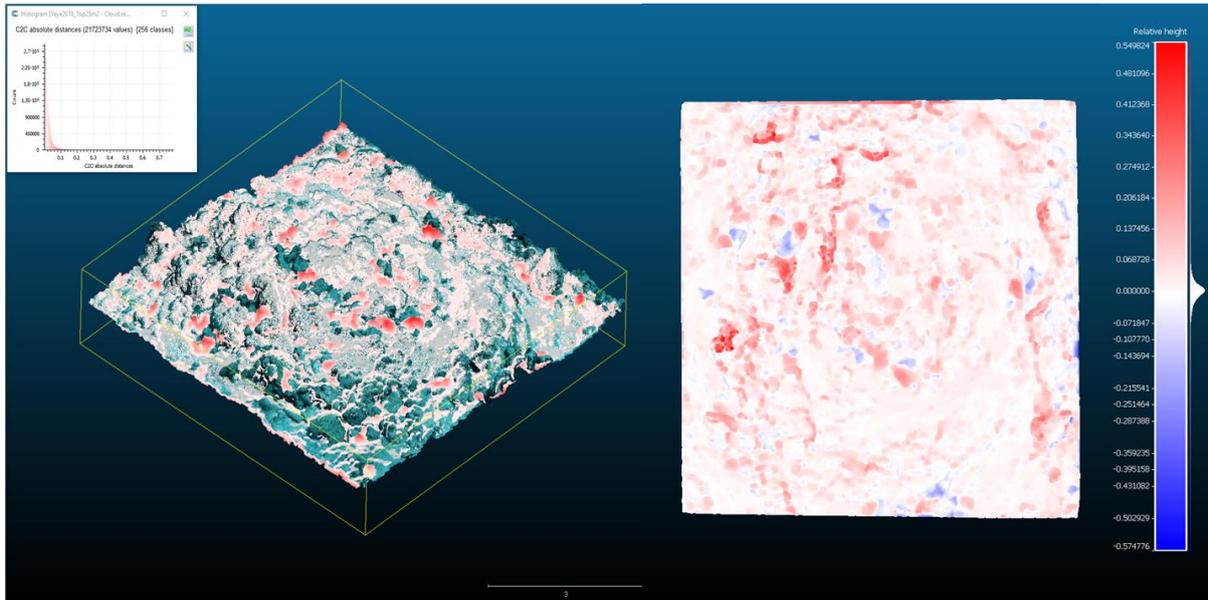


Figure 42. Visualisation of annual volumetric change across a 7 x 7 m reef patch from overlay of two dense point-clouds, collected through Structure from Motion (SfM) photogrammetry in 2017 and 2018 within the Chagos archipelago. 3D reef model from an oblique view shown left with volume change colouration overlaid, and the same reef section in planar view shown right, with average height difference between point-cloud layers coloured red (+) and blue (-). Image colour legend set to saturation at 0.01 m changes. Distribution of cloud-cloud changes also shown.

To compare the values found in this study with estimates in this same region using the currently widely used Carbonate 'Reefbudget' method, I used estimates of gross carbonate production for six sites in the Northern atolls of BIOT (four sites around the leeward side of Peros Banhos, and four around the leeward side of Salomon & Blenheim - although only the two matching locations at sites 9 & 11 are used in the comparison study), which were assessed in 2018 (Lange & Perry, In review). Within the 'ReefBudget' methodology, Carbonate production rates are calculated using '*colony level morphology and basic geometric relationships, together with coral growth rates and density measures averaged from published studies in the Indo-Pacific. These are converted to linear relationships of the form  $y = mx + b$  to account for colony size.*' (Perry *et al.*, 2016). These gross production estimates were balanced against atoll

level measurements of the average recorded overall bio-erosion from 'micro' (endolithic) and 'macro' (clionaid sponge, polychaetes, bivalves etc.) bio-eroders, urchins and parrotfish assessed in 2015 (Perry *et al.*, 2016) as local erosion estimates were unavailable for 2018. Given that the 2015 erosion rates were based on parrotfish erosion pre-bleaching, and that bio-erosion rates increased by an average of 236 % (from 1.754 G to 4.15 G) in the neighbouring archipelago of the Maldives following the same bleaching event (Perry and Morgan, 2017), I assumed two scenarios:

**Scenario 1:** Unchanged bio-erosion rates. For Peros Banhos the median rate of bio-erosion reported by Perry *et al.* for sheltered sites was  $-3 \text{ kg m}^{-2} \text{ yr}^{-1}$  with a range of  $-1.5$  to  $-7.5 \text{ kg m}^{-2} \text{ yr}^{-1}$  across the atoll, while Salomon atoll had a median value of  $-3.5 \text{ kg m}^{-2} \text{ yr}^{-1}$  with a range of  $-1.5$  to  $-5 \text{ kg m}^{-2} \text{ yr}^{-1}$  across the atoll.

**Scenario 2:** Bio-erosion rate increases within the Chagos Archipelago in line with the Maldives. For Peros Banhos the rate of bio-erosion for sheltered sites would be  $-7.1 \text{ kg m}^{-2} \text{ yr}^{-1}$  with a range of  $-5.9$  to  $-10.6 \text{ kg m}^{-2} \text{ yr}^{-1}$  across the atoll, while Salomon atoll had a median value of  $-8.3 \text{ kg m}^{-2} \text{ yr}^{-1}$  with a range of  $-4.7$  to  $-11.8 \text{ kg m}^{-2} \text{ yr}^{-1}$  across the atoll.

### *Colony level growth*

Preliminary analysis was conducted on two commonly found and structurally important coral species within the Chagos Archipelago, the massive / sub-massive *Porites lutea* and the tabular *Acropora cytherea*. The *Porites* colonies are typically more heat-resistant than the *Acropora* (Hoey *et al.* 2016; Chapter 5), and *Porites* survivorship in the Chagos archipelago was relatively high following bleaching compared to the *Acropora* colonies which were largely lost in 2016 (Sheppard *et al.*, 2017). This growth analysis looked at lateral extension for the small juvenile *Acropora* recruits, and overall growth and volume for the larger adult *Porites*. Extension rates for *Acropora* colonies were calculated based on the mean of the maximum X and Y plane distances for each colony in planar view, with a sample of (n = 8) colonies in 2017 and (n = 16) colonies in 2018 (2017 colonies inclusive). Growth of *Porites* coral was based on the calculation of dense cloud surface averaged relative point-to-point distances between 2017 and 2018 SfM surfaces, based on a 5 mm scaling resolution, using the 'CloudCompare' cloud-distance tool (Figure 43).

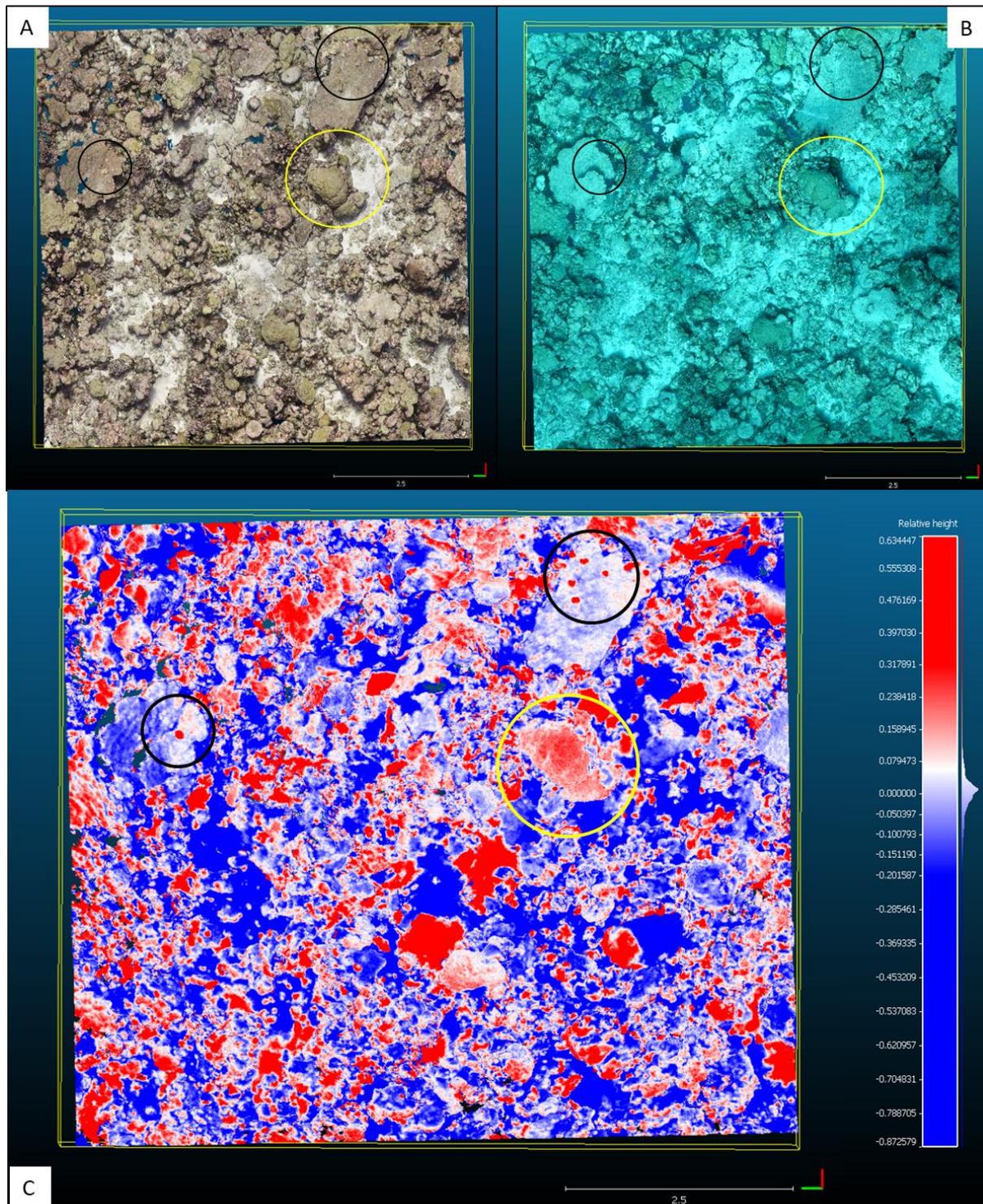


Figure 43. A ~ 50 m<sup>2</sup> scaled reef section from the Northern atolls of the Chagos archipelago, showing A) 2018, B) 2017, and C) the resulting average height difference between the years (red = increase in relative height, blue = decrease in relative height (m)). Black rings indicate sections with growing juveniles *Acropora* spp seen and the yellow ring indicates a large growing *Porites lutea* colony. Colours set to saturation at 0.15 m.

### ***Statistical analysis***

ANOVA with Tukey post-hoc testing was conducted to test whether volume change differed significantly among sites (n = 12) and exposure types (n= 4) as factors. Tests were performed separately for losses and gains of volume. ANOVA tests were further performed to compare carbonate budget estimates from this study and estimates based on the ReefBudget method (n=6 for both studies) under comparable typical exposure regimes (of < 1000 Jm<sup>-3</sup>). Each analysis was tested for homogeneity of variance and normality using Levene's and Shapiro-Wilk testing.

Linear mixed-effects regressions, fitted by restricted maximum likelihood in the lme4 R package (Bates *et al.*, 2012), were used to model variations in net Carbonate production (G) across four exposure categories (High / Medium / Low / Low - lagoon). 'Site' (n=12) was set as a random effect, nested within 'atoll region' (n=2) following log likelihood ratio test assessment (Zuur *et al.*, 2009). The plotted residuals were checked for homoscedasticity and normality prior to using the results of the model. Significance (p) values for the selected models were calculated using Kenward-Roger standard errors and degrees of freedom. Confidence intervals are calculated at the 95 % level using the package jtools (Long, 2018).

All analyses were carried out using R: version 3.4.1 (R Core Team, 2016).

## Results

### *Volume change*

There were significant differences in the amount of volume gain between sites (ANOVA,  $F_{8, 54} = 3.498$ ,  $p = 0.003$ ), and between exposure types (ANOVA,  $F_{3, 54} = 4.863$ ,  $p = 0.004$ ; Figure 44). Volume gains were significantly higher in lagoon sites relative to sites in medium and high exposure environments (Tukey tests:  $p < 0.001$  and  $p = 0.040$  respectively). Low exposure sites were not significantly different to lagoon sites (Tukey test:  $p = 0.187$ ) but had significantly greater gains than medium exposure sites (Tukey test:  $p = 0.029$ ). On a site level there were significant differences between site 4 (Ile Diamont (west)), which had the lowest gains in volume, and site 1 (Ile du Coin) and site 9 (Ile Anglaise South), which saw the greatest gains (Tukey tests:  $p = 0.029$  and  $p = 0.046$  respectively). There were however, no significant differences in the amount of volume lost between sites (ANOVA,  $F_{8, 54} = 1.501$ ,  $p = 0.179$ ), and between exposure types (ANOVA,  $F_{3, 54} = 0.149$ ,  $p = 0.179$ ).

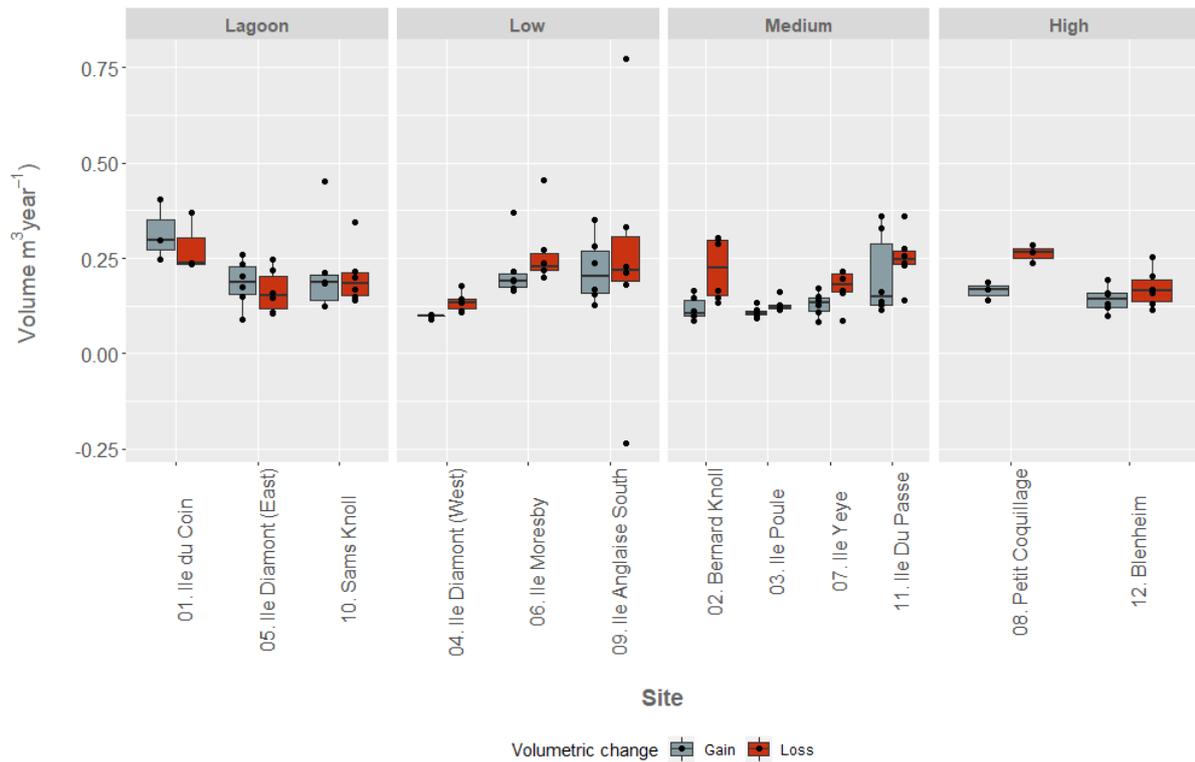


Figure 44. Figure shows site-level gains and losses in volume (m<sup>3</sup> year<sup>-1</sup>) between 2017 and 2018 for twelve sites within the Chagos archipelago. Boxplots show median line and interquartile range, with data points overlaid. Grey show relative gains, red shows relative loss.

### *Carbonate production*

Mean net G for Peros Banhos was  $-4.62 \pm 1.04$  (SE), and mean net G for Salomon was  $-3.71 \pm 2.74$  (SE) across all sites. The three true lagoon sites were the only sites to see a positive net G (Figure 45).

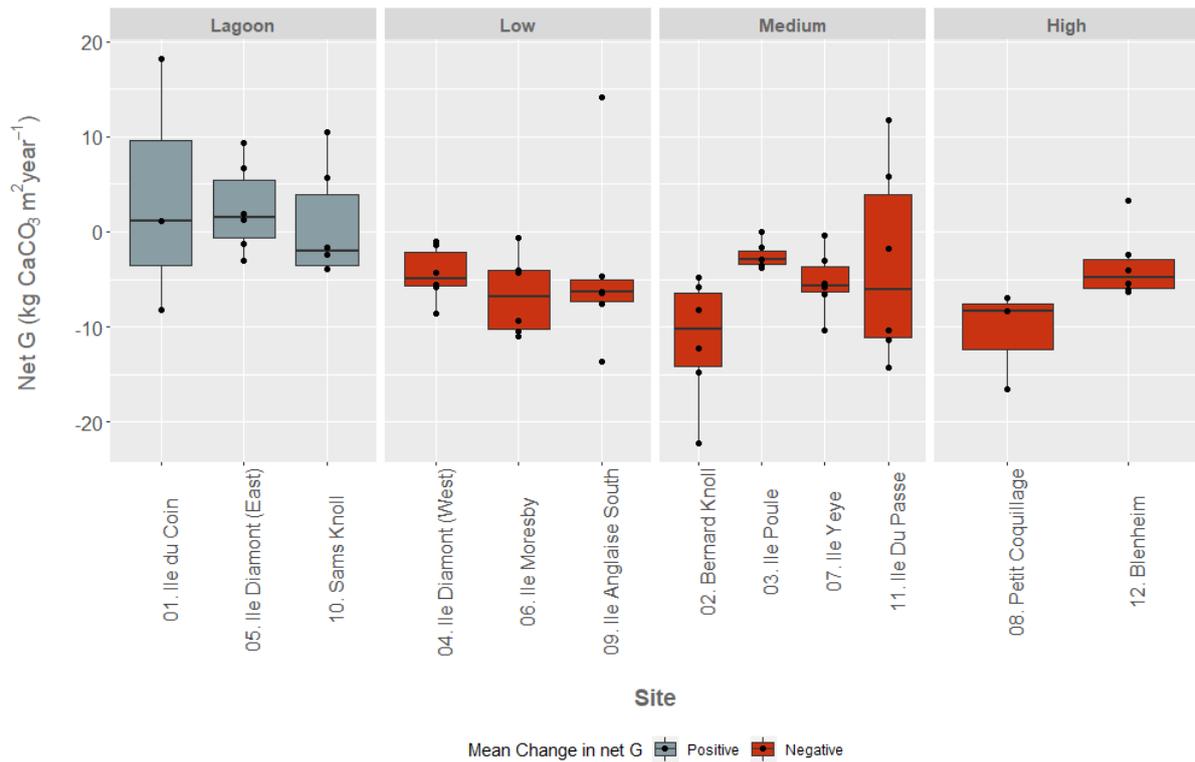


Figure 45. Net G (kg CaCO<sub>3</sub> m<sup>2</sup> year<sup>-1</sup>) for all sites surveyed around Peros Banhos atoll, Salomon atoll and Blenheim reef during over a one year period (April 2017 – April 2018), within BIOT. Sites separated by level of wave exposure (lagoon and seaward reefs differentiated), with sites showing mean positive G coloured red. Boxplots indicate median, IQR and 1.5 × IQR, with data points overlaid.

Mixed-effects model estimates of net carbonate budget pooled for all sites within the northern Chagos Archipelago and with level of wave exposure as a factor, found lagoons to have a (non-significant) net positive value of 2.03 G (CI = -1.66, 5.90; Table 11). However there were significantly lower net carbonate values on low – high exposure seaward slopes (G = -5.03, CI = -12.34 to -1.97; and G = -5.88, CI = -14.51 to -2.29 respectively), indicating broad-scale loss of carbonate structure.

Table 11. Estimates from mixed effects models of net carbonate budget (kg CaCO<sub>3</sub> m<sup>-2</sup> yr<sup>-1</sup>) for twelve sites in the Chagos Archipelago, with the fixed factor of Exposure level (4 groups), and random nested effects of atoll, site, and site block.

Parameter	Estimate	t value	Confidence Interval
Intercept (Lagoon)	2.03	1.045, p = 0.31	[-1.66, 5.90]
Exposure (Low)	-7.06 *	-2.686, p = 0.015	[-12.34, -1.97]
Exposure (Medium)	-7.64 *	-3.086, p = 0.006	[-13.57, -3.20]
Exposure (High)	-7.91 *	-2.493, p = 0.023	[-14.51, -2.29]
N	66		
N (Block: Site: Atoll)	20		
N (Site : Atoll)	12		
N (Atoll)	2		
R <sup>2</sup> (fixed)	0.25		
R <sup>2</sup> (total)	0.33		

### *Comparison to 'ReefBudget' method*

Using all six comparison sites, the three scenarios were found to be significantly different ( $F_{2,15} = 21.26$ ,  $p < 0.001$ ), due to significantly less negative values of net carbonate budget in scenario 1 compared with both this study ( $p < 0.001$ ) and Scenario 2 ( $p < 0.001$ ), but not between this study and Scenario 2 ( $p = 0.608$ )(Figure 46). Further direct comparison of Peros Banhos atoll with scenario 2 ( $n = 4$ ), again found no significant difference between studies ( $F_{1,6} = 5.849$ ,  $p = 0.052$ ) despite the slightly less negative values in Scenario 2 overall.

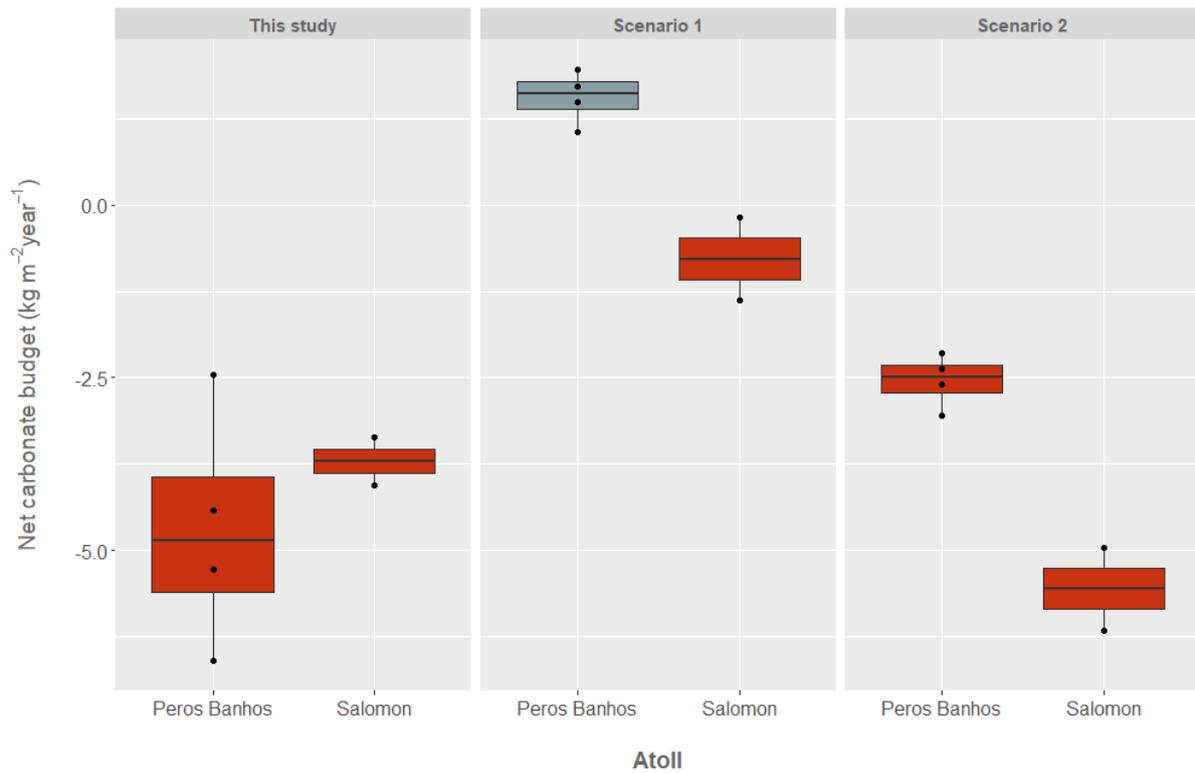


Figure 46. Comparison of the SfM – based methodology for post-bleaching carbonate budget determination described in this study, compared with estimates derived from the ‘ReefBudget’ method (Perry *et al.*, 2012) for the same atolls in the northern extent of the Chagos Archipelago. Reef sites used for this comparison are all from moderately exposed seaward reefs. Scenario 1 includes Carbonate production values from 2018 surveys and bio-erosion estimates (from fish survey) for 2015. Scenario 2 instead uses bio-erosional estimates based on percentage increase in parrotfish herbivory following the same bleaching event in the neighbouring atolls of the Maldives. Boxplots show median value and interquartile range with datapoints overlaid (red = mean negative budget, grey = mean positive budget).

## ***Recruitment and colony growth***

### ***Acropora cytherea***

Initial analysis of juvenile *Acropora cytherea* coral colonies from the slopes of the northern Salomon atoll (Figure 47) found two cohorts of recruitment to be evident. The first set of recruits are likely to have settled following the March 2016 spawning event and had a mean diameter of 3.36 cm (SE = 0.188) in 2017, growing to a diameter of 15.31 cm (SE = 1.023) in 2018, while the second cohort (which were not present in April 2017 surveys), had a mean diameter in 2018 of 6.83 cm (SE = 0.569). This gives an approximate lateral growth rate of 3.36 cm for juveniles in 2017, and a range of 11.95 cm and 6.83 cm (for the recruits of 2016 and 2017 respectively). Average values from published literature within the ReefBudget database (Perry *et al.*, 2012) give a mean value of 10.8 cm yr<sup>-1</sup> with a range of 6.5-13 cm in the neighbouring Maldives.

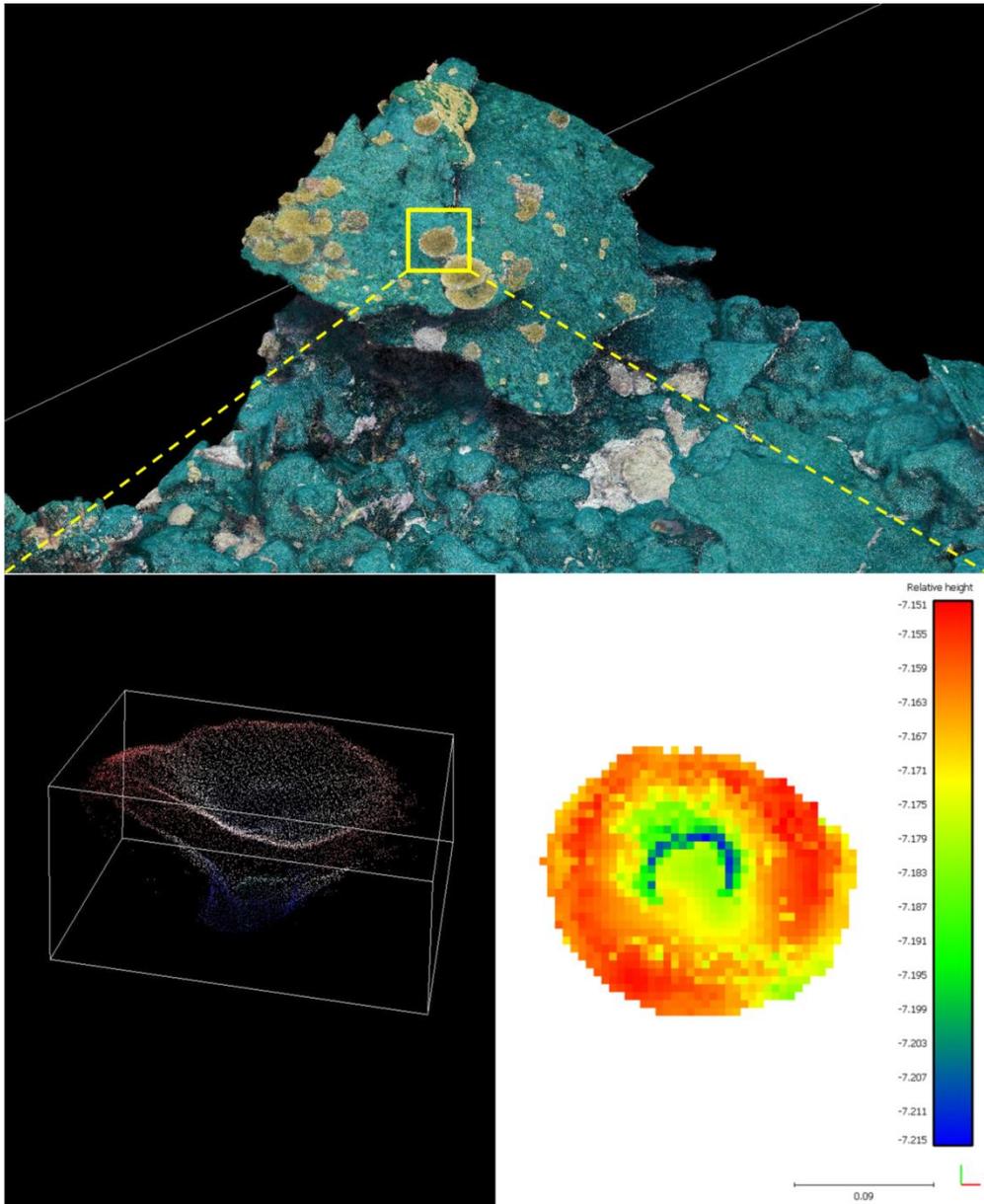


Figure 47. Analysis of individual coral recruits is shown based on *Acropora cytherea* colonies from Ile Anglaise in the northern atolls of the Chagos Archipelago (shown in situ top). Bottom left shows a cropped dense point-cloud of an individual of ~ 18 cm diameter and 0.02 m<sup>3</sup> (2.5D) volume, viewed at an oblique angle. Bottom right image shows the same colony in planar view and illustrates relative Z plane growth (coloured blue to red, for low to high growth from a constant plane).

Porites lutea

Initial analysis for growth of *Porites lutea* colonies between 2017 to 2018 (Figure 48) found 95 % of 0.2 million cloud-to-cloud point's relative distances over the 1 year period (i.e. annual growth) to be  $\leq 1.30$  cm and an increase in volume from 4.002 to 4.125 m<sup>3</sup>. Average values from published literature within the ReefBudget database (Perry *et al.*, 2012) give a mean value of 1.21 cm yr<sup>-1</sup> (SE = 0.026) to a maximum of 3.59 cm in the neighbouring Maldives.

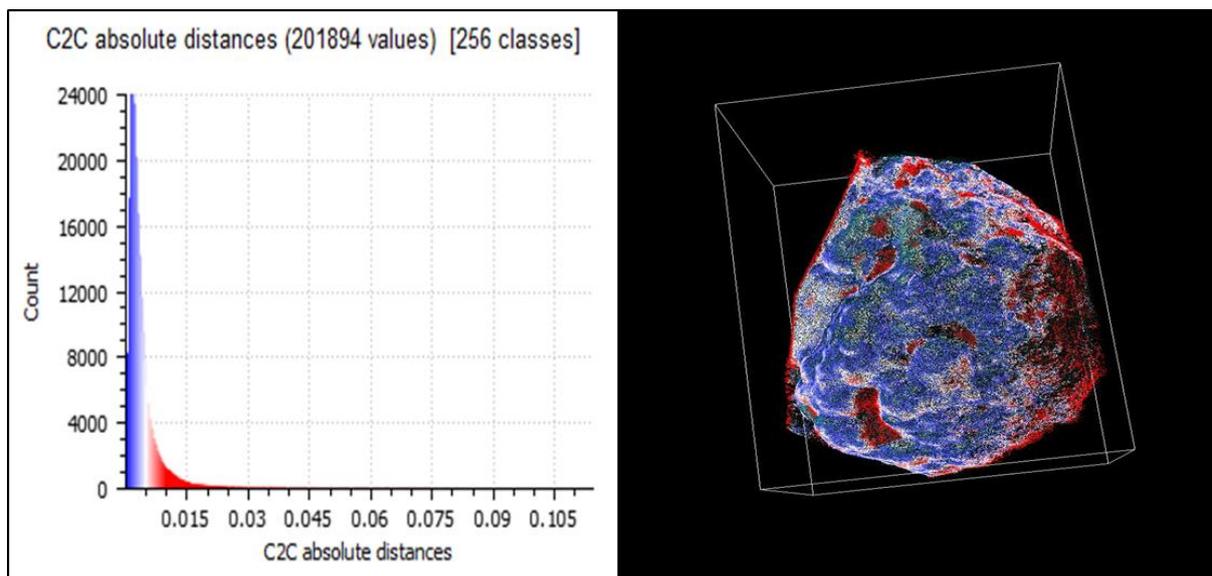


Figure 48. Growth in XYZ averaged planes for a *Porites lutea* coral colony of  $\sim 4$  m<sup>3</sup> volume covering a planar area of  $\sim 0.4$  m<sup>2</sup> in the northern atolls of the Chagos Archipelago. Distribution of > 0.2 million Cloud – Cloud (C2C) point distances (shown left) for a colony (shown right) surface measured in 2018 and 2017. Distances displayed in metres, and coloured nearest (blue), mid-length (white), to farthest (red).

## Discussion

This study has shown that seaward reef sites in the northern Chagos Archipelago are currently in a heavily net erosional phase across all levels of wave exposure. Fully enclosed 'choked' lagoon reefs (Kjerfve, 1986) are however still in net positive growth following the elevated high sea temperatures of 2015 – 2016 which caused widespread coral mortality (Sheppard *et al.*, 2017). The retained growth of the calmer lagoon areas matches well to the findings of Chapter 5 where metrics of structural complexity were only retained within the low exposure reefs. In a similar fashion to the maintenance of complexity, the continued growth in lagoons following the major bleaching is likely due to the combination of 1) increased heat-stress resilience and survival in lagoon-adapted species (Hoey *et al.*, 2016; Madin *et al.*, 2016b; Hoogenboom *et al.*, 2017); and 2) reduced wave and current action within the enclosed lagoons, resulting in reduced physical erosion and storm damage (Dollar, 1982; Kjerfve, 1986; Scoffin, 1993; Burns *et al.*, 2016b).

The post-bleaching net carbonate budget estimates from this study (Table 11) were very similar to those found in the neighbouring reefs of the Maldives, where Morgan and Perry (2017) observed a shift from strongly net positive budget reefs in 2016 (mean  $5.92 \pm 2.2$  G, range: 3.6 to 8.6 G) to strongly net negative budget reefs post-bleaching (mean  $-2.96 \pm 1.06$  G, range:  $-1.9$  to  $-4.7$  G). The range of observations within this study fit within the range of budget values observed in the broader Western Indian Ocean and Central Indian Ocean regions from a global study of carbonate budget values by Perry *et al.* (2018), which indicated that reefs will be unlikely to maintain enough growth to track sea-level rise under increasingly high temperatures.

A post-bleaching study of the Maldives in 2016 by Perry and Morgan (2017), found that the increase in post-bleaching parrotfish abundance (alongside coral loss), was driving the net negative balance in carbonate. They hypothesised that this reflected higher bio-erosion from higher exploitation of newly-available filamentous algae overgrowing the now-dead coral substrate. While observations of limited increases in *Halimeda* spp. and filamentous algae were observed in some sites in the Chagos Archipelago post-bleaching, the very limited nutrient flow to these remote uninhabited islands – aside from bird guano inputs (Graham *et al.*, 2018) – mean that this increased herbivory effect may be less pronounced than observed within Maldivian reefs.

Site- and exposure-level differences were driven primarily from increased relative rates of overall growth in the lagoons rather than differences in the rate of volume loss, as all sites lost broadly the same volume of reef through the year irrespective of exposure. This could imply that similar bio-erosion rates are occurring across sites and that storm damage resulted in similar losses through the northern archipelago. Additionally, these site-level differences in growth suggest that survivorship of corals rather than inherent protection from erosion is the most important factor governing maintenance of carbonate structure. To test this further, future analysis of the size-class distribution of site-level volume losses relative to their level of exposure, would provide insight into whether particular site locations saw rapid removal of whole large coral-heads from storm surge, or whether the losses were from smaller fragmentation of delicate coral branches and scraping action of bio-eroders such as the parrotfish.

### *Methodological comparison*

The new methodology for estimation of carbonate budgets described in this study produced values that were broadly comparable to expected values produced from the well-established ReefBudget method (Perry *et al.*, 2012) (Figure 46). The methods will of course need further direct comparison and calibration to evaluate the accuracy and exact causes of any differences over the same reef patch. However, existing studies measuring coral growth on a smaller, individual coral colony, scale have both high accuracy and resolution (Ferrari *et al.*, 2017; Raoult *et al.*, 2017), but with notable reduced precision in more morphologically complex structures such as the corymbose growth-form corals (Figueira *et al.*, 2015). Given the apparent high accuracy of this method, the ability to incorporate carbonate budget assessment within SfM surveys of reefs could further add to the usefulness and time-saving benefits of SfM photogrammetry used as a benthic monitoring tool. Furthermore, the SfM method requires little to no knowledge of local species identification compared to the ReefBudget method, which instead requires knowledge of fish, coral and urchin species. The ease of measurement using the SfM method could then help increase the number and extent of surveys that are possible, improving our knowledge of the spatial and temporal dynamics of carbonate change, whilst also improving repeatability (Burns *et al.*, 2016a; Ferrari *et al.*, 2016b, 2017; Young *et al.*, 2017).

The current final annual carbonate budgets for the Chagos Archipelago through the ReefBudget method are not yet available, but the ReefBudget estimations used in the study comparison here are found to be slightly less negative than those derived through the SfM method. One factor that may be driving the differences in carbonate budget estimates between assessments is that the skeletal densities used in this study have been generalised.

In future studies, greater certainty in the assessment's overall carbonate budget could be attained through applying species-level density values and growth rates to percentage cover estimates of each species (and growth form) within the survey section. A second driver for the observed differences would likely be from the inclusion of precise spatial losses or gains of volume within this study (i.e. if a boulder were to roll into or out of the survey area over the course of the year, this change would be calculated as volume change). In the ReefBudget method on the other hand, estimates are all based on instantaneous assessments of whatever is found along the survey transects at the time of survey only and therefore volume changes will likely differ. However it should be noted that this second driver is more likely to cause noise between estimates rather than a strong bias, unless the sites are on steep slopes.

A notable limitation of the SfM-based carbonate growth estimation method trialled here is through the apparent reduced accuracy of estimates attained from sites which are dominated by large tabular growth forms (such as site 2 – Bernard Knolls). Within such sites, the SfM technique will tend to incorrectly fill the space under or within overlaps of table surfaces, which are in reality just obscured from vision (Goatley and Bellwood, 2011; Bryson *et al.*, 2017). While the effect was not a major issue within this particular study as only site 2 (Bernard Knolls) had a reef dominated with these growth forms, the effects of shadowing and obscurement need to be considered and minimised to as large an extent as possible while conducting SfM photogrammetry. The described survey method deliberately tries to limit these effects through good lighting, high image overlap, and multiple oblique images as well as planar view images, but it is impossible to prevent obscurement (occlusion) completely.

This same occlusion effect will also occur on a smaller scale if the reef has densely branching or corymbose coral morphologies present as areas of space deeper within a colony or reef matrix will be difficult or impossible to see just using a camera. These areas hidden from view will therefore be interpreted as solid volume, with only the top visible surface structure being fully captured. This will typically lead to over-estimation of volume and under-estimation of structural complexity. In addition this method will not pick up the amount of internal bio-erosion that has occurred in a reef (i.e. from reef-boring organisms such as sponges), and instead assumes a consistent skeletal density, based on growth-form averaged values. This assumption will lead to a degree of uncertainty in the final calculation of carbonate present in an area (based on volume change). To improve this uncertainty, assessments of volume could be further sub-divided by growth form or even species to allow more precise carbonate calculations. Similarly, location assessments of internal bio-erosion could be conducted using micro-CT scans of site colonies, allowing average skeletal densities for the site in question to be adjusted accordingly.

A further limitation of this method relates to sites which have undergone very extensive changes and which are therefore much more difficult to accurately align, even over a large area. For the models to accurately align, multiple distinct features of the surface need to remain stationary through the survey period to give fixed matched reference points of change. In sites which have highly complex habitat structures and which have undergone storm damage or rapid die-off, the matching process becomes far more difficult. In this study a number of the pegs and markers used to identify the site were lost between survey years, and while it was still possible to match sites based on the remaining primary rebar markers and bedrock features, an improvement – which was not possible for this study due

to BIOT Authority restrictions – would be to cement in place 3 - 4 large concrete marker blocks across each site (in a random / non-linear pattern). These more noticeable and immovable markers would speed up the model overlay stage and potentially improve accuracy further.

Despite the limitations stated, the broadly comparable reef level estimates of carbonate budget, the high accuracy of model alignments (> 96 %) during the overlay of surface models, and the detailed scaling accuracy of < 5 mm resolution gives promise for this method's usefulness. Adding to the confidence in the accuracy of the SfM technique, are the colony-level growth rates ascertained from *Porites lutea* and *Acropora cytherea* colonies. The growth rates of these commonly found species, which take massive and tabular growth forms respectively, were again comparable to existing published estimates of species growth rates in the neighbouring Maldives, derived from well-established methods including X-radiography of growth rings (Perry *et al.*, 2012). Furthermore, while the limited sample size of the colony-level growth estimates limits the inferences we can make, the differing rates of growth for the two cohort years of recruits potential shows a slowed / inhibited growth following the bleaching stress period (Leder *et al.*, 1991; Manzello, 2010).

### ***Future prospects***

The successful recruitment of corals in both 2016 and 2017 seen in this study and by Sheppard *et al.*, (2017), coupled with the apparent rapid subsequent re-growth seen in this study, give some promise for the future recovery of the reefs of the Chagos Archipelago (Figure 49). While there is still a great deal of recovery needed, reflected by the currently erosional phase of the reefs, the region has previously recovered rapidly from similar

disturbance events, such as following the 1998 El Nino heating episode of 1998 (Sheppard *et al.*, 2002). However it is worth considering that factors such as sea level rise are also already affecting the islands in this region and these low-lying areas may soon be unable to track future changes (Sheppard *et al.*, 2012; Perry *et al.*, 2018).



Figure 49. Coral recruits (primarily *Acropora*) rapidly settling and re-growing over a dead table coral in the Chagos Archipelago following widespread heat-induced mortality. Image also shows a large *Porites lutea* colony which survived the bleaching (left), collapsed rubble matrix (background) and a roundhead parrotfish (*Chlorurus strongycephalus*) seen back centre.

Whether the reefs and islands will continue to sustain themselves in the face of reduced calcification and growth in increasingly warm and acidified waters (Manzello, 2010; Pandolfi *et al.*, 2011; Gattuso *et al.*, 2015), rising sea-levels (IPCC, 2018; Perry *et al.*, 2018) and increased storm and bleaching prevalence in the coming years (Emanuel, 2013; Heron *et al.*, 2016; Hughes *et al.*, 2018a) remains to be seen.

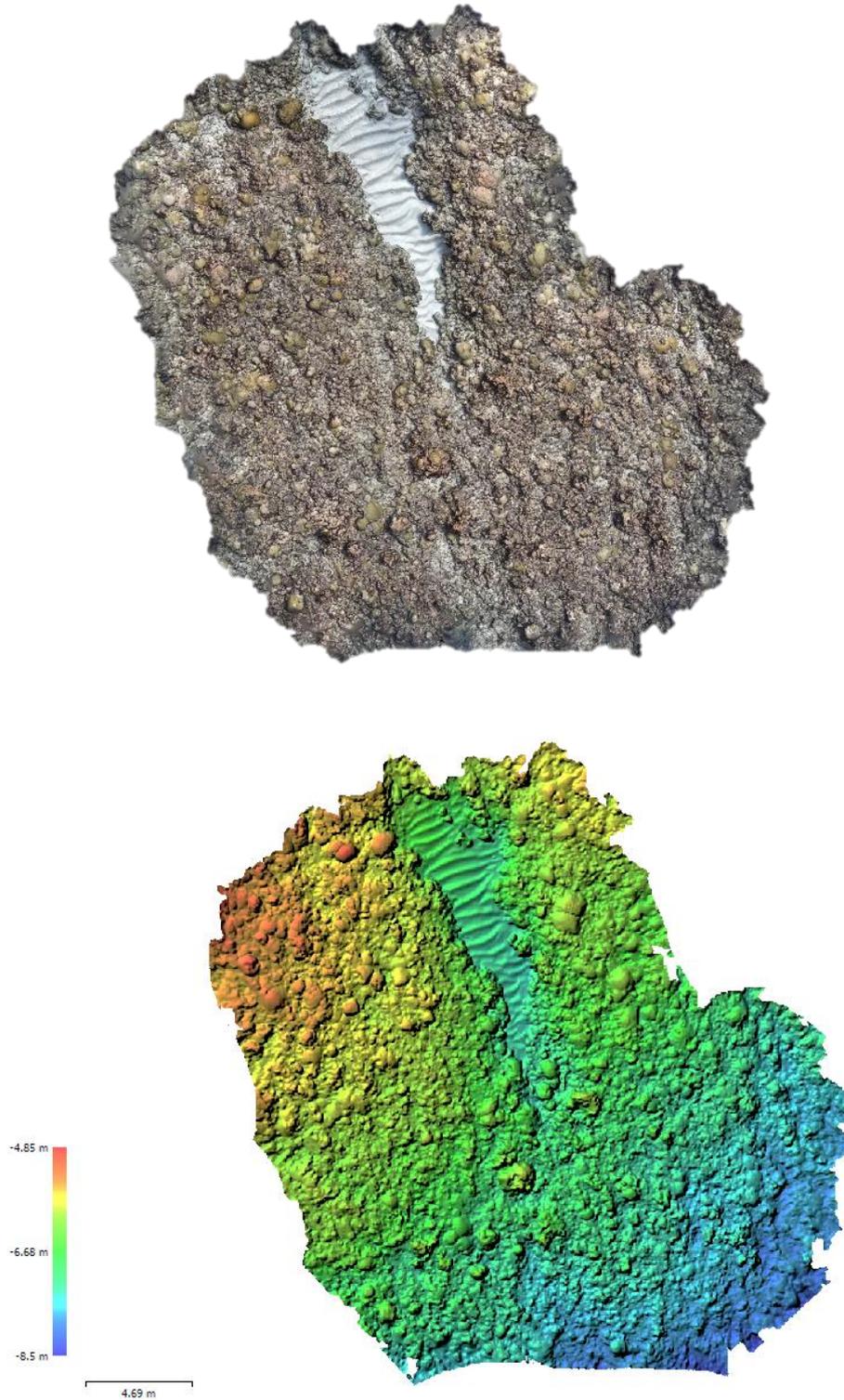
## Conclusions

The current net loss of carbonate structure in the shallow seaward reefs which dominate this system (Table 11) is well below the amount of  $\geq 1 \text{ kg m}^{-2} \text{ y}^{-1}$  positive net budget proposed as a boundary threshold for stable continued function and integrity of this biome (Mace *et al.*, 2014). This threshold is incorporated within the 'planetary boundary' conceptual framework, which defines a science-based analysis of the risk that human perturbations will lead to de-stabilized systems on a planetary scale (Steffen *et al.*, 2015), giving cause for concern over the future of this remote reef system.

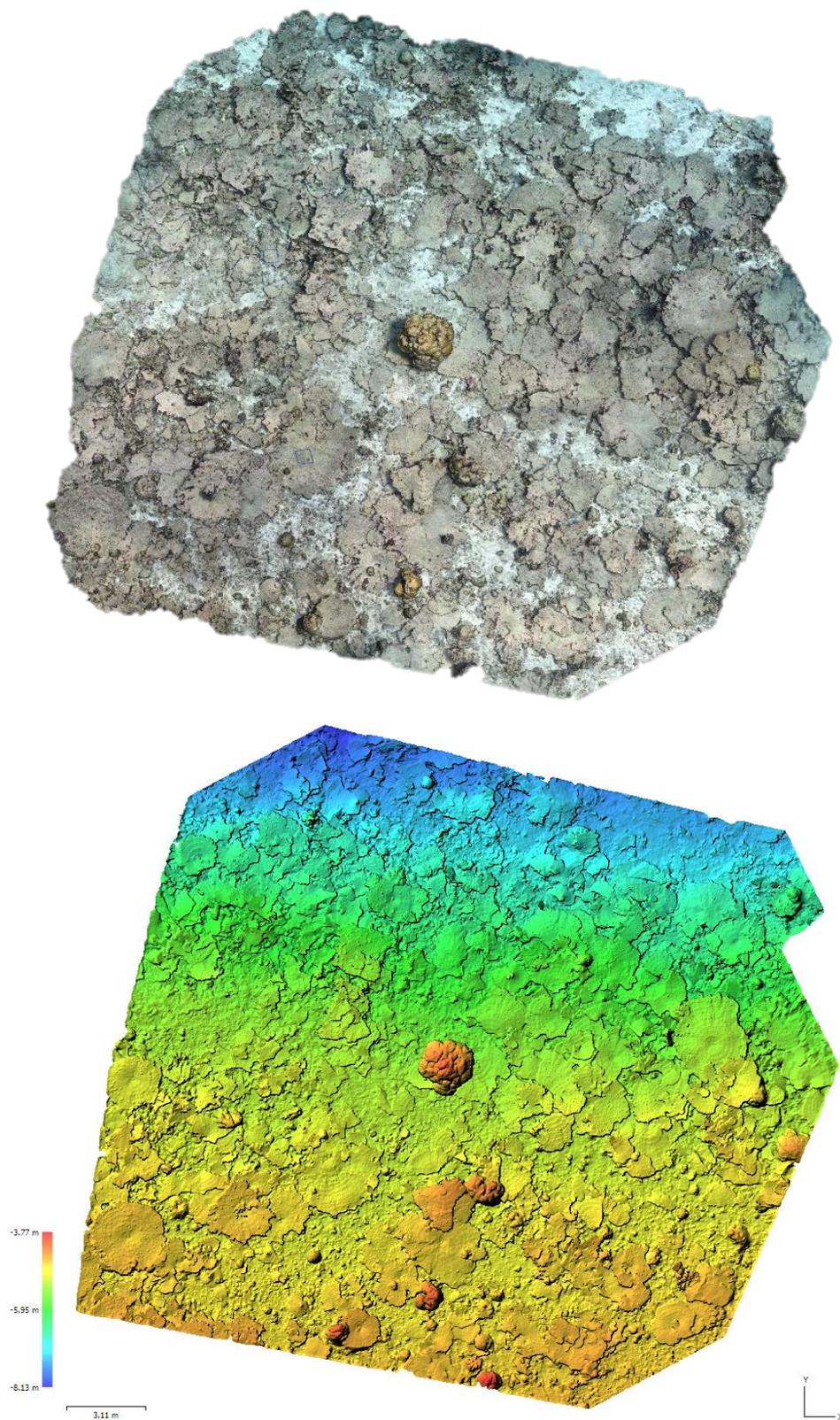
Considering that the reefs of BIOT can be regarded as a reference or 'control site' to some extent for the reefs of the wider Indian Ocean, the significant loss of reef physical structure following bleaching in this location, which is removed from the typical wide range of anthropogenic factors which inhibit reef growth and recovery, the rate of reef loss is extremely worrying. It is therefore essential that for reefs in the wider Indian Ocean region as well as these remote sites, communities build adaptive capacity (Cinner *et al.*, 2018a) and mitigate current reef pressures through evidence-based, long-term management of marine ecosystems and surrounding land catchments, i.e. reduction / prevention of over-fishing and pollution (Bartley *et al.*, 2014; Sale *et al.*, 2014; Trathan *et al.*, 2015; Cinner *et al.*, 2016; Nash *et al.*, 2016; Weijerman *et al.*, 2018). It is furthermore essential that reefs systems are adequately protected and managed before threshold boundaries are crossed and essential ecosystems services are lost (Knowlton, 1992; Hughes *et al.*, 2013, 2018b; Mumby *et al.*, 2014; Harborne *et al.*, 2017), and this is likely only possible if greenhouse gas emissions are limited in line with the most conservative current scenarios (IPCC, 2018).

# Appendices

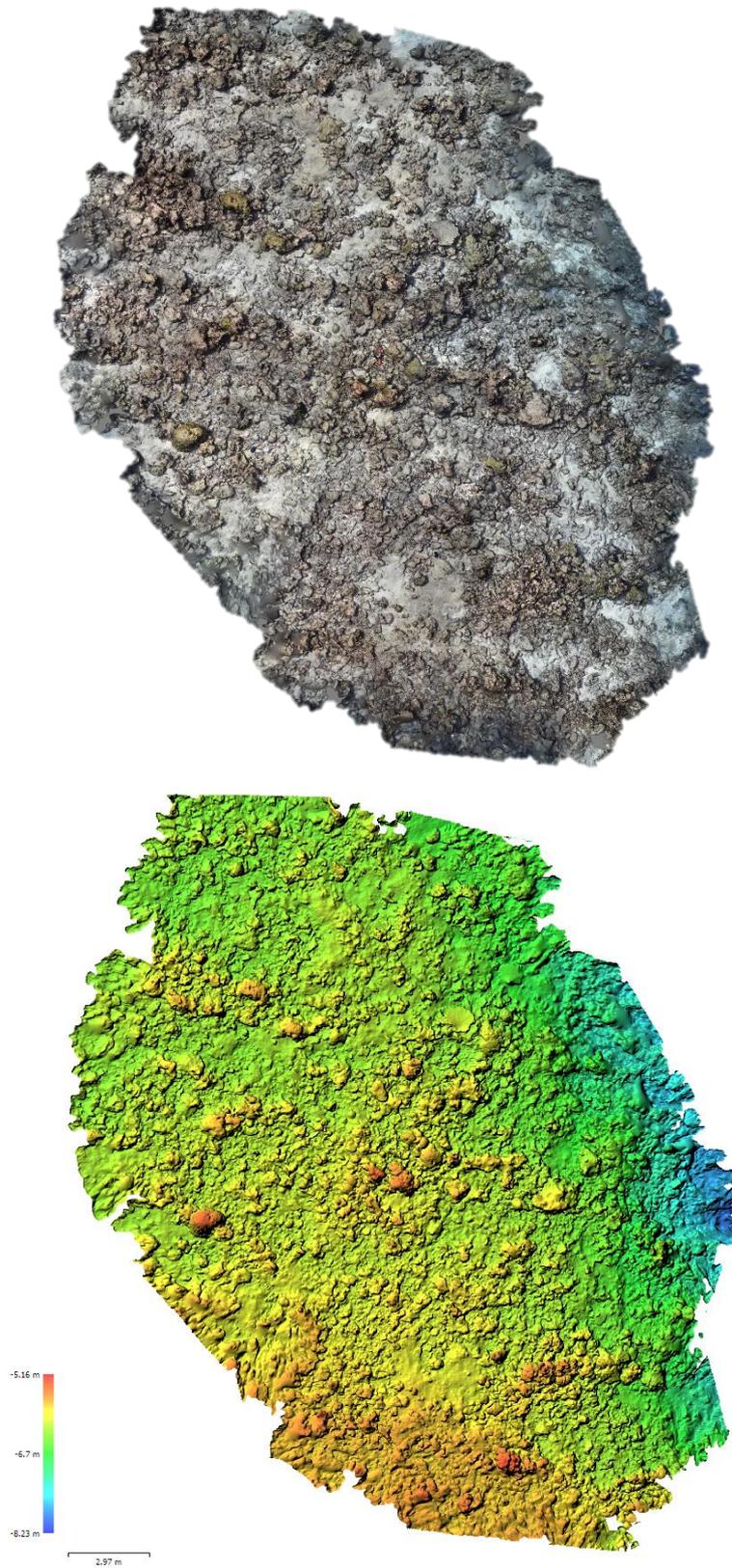
Appendix 15. Blenheim atoll, BIOT 2018 (highly exposed site). Ortho-mosaic (top) and DEM (bottom) shown.



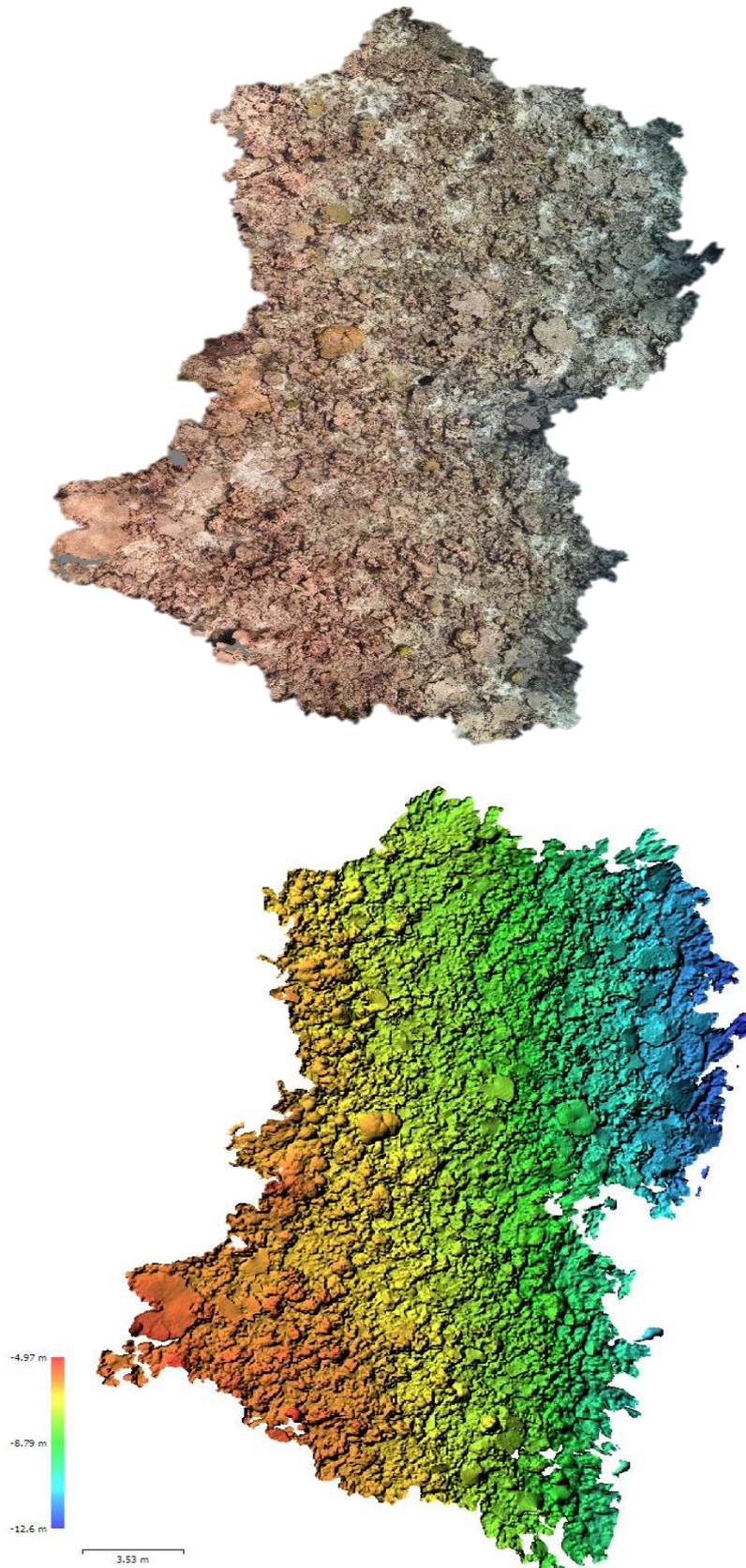
Appendix 16. Bernard knolls, BIOT 2018 (Medium exposure / lagoon site). Ortho-mosaic (top) and DEM (bottom) shown.



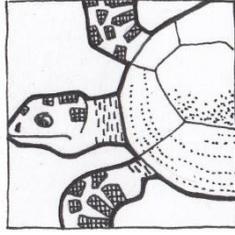
Appendix 17. Ile Yeye, BIOT 2018 (Medium exposure site). Ortho-mosaic (top) and DEM (bottom) shown.



Appendix 18. Ile Moresby, BIOT 2018 (Low exposure site). Ortho-mosaic (top) and DEM (bottom) shown.







## *Chapter 7: Summary conclusions*

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### **Contribution to knowledge**

This first section of the thesis investigated the use of 'Structure from Motion' (SfM) photogrammetry as a coral reef research tool. The very recent development of this technology in an underwater setting means that limited analysis has been conducted to assess its usefulness for measuring reef structure. There has also been limited in-depth comparison of this method to existing benthic monitoring tools. My work found the technique to produce results that were can be integrated within existing monitoring and assessment programmes as well as converted to allow consistent long-term analyses to be conducted. In addition, the new technique allows a number of gains to be made from its use. First and foremost the range and detail of analyses possible is vastly increased, allowing researchers to accurately measure multiple properties of structures in 3D, assess ortho-rectified, scaled HD images of whole reef-scapes down to individual corallites, and map objects at an affordable cost. The benefits of this technology are also through its reproducibility and the ability to use the outputs as both an archival resource and outreach tool.

In the subsequent two chapters I used a collection of small-scale locally managed Marine Protected Areas (MPAs), located in the heart of the 'coral triangle' biodiversity hotspot, as a case study to demonstrate the integration of SfM into assessments. I further used these locations to look in greater depth at spatial and temporal changes in the community structure of the reef fish and benthos, with a view to assess whether management measures are being effective. Overall I found that despite the small size of the MPAs there was typically larger fish with higher overall biomass and diversity inside of enforced areas. Reef benthos was found to generally be stable unless the practice of blast-fishing was still currently taking place, or had extensively damaged the structure historically. Despite the apparent successes of these MPAs, I found an overall decline in fish biomass and size through time in this region, even within MPAs (although the effect was less pronounced). This indicates that the region is likely still recovering from the effects of the mass bleaching in 1998, which caused widespread coral mortality, subsequent alterations in fish community structure, and loss of fish biomass. In addition the proportionally higher loss of the larger fish across all sites indicates that size-selective fishing is causing significant changes in fish abundance and trophic structure. Wider management and potentially an increase in the size and number of MPAs is recommended to prevent the continued decline of fish stocks and productivity in this region into the future, which are integral to people's livelihoods.

The two final chapters move the location of focus to the British Indian Ocean Territory MPA in the centre of the Indian Ocean. The reefs of the Chagos Archipelago within this MPA are some of the most remote and un-impacted in the world, considered a 'wilderness' area away from the majority of human pressures. This remote location allows the effects of climate change to be investigated without confounding anthropogenic factors. I applied SfM to

investigate changes in physical structure following another mass bleaching, this time from 2015 – 2016, where an El Niño-induced heating event caused widespread coral mortality globally. I found that multiple measures of reef structural complexity had declined over the three years of study across the shallow reefs of the archipelago and that overall the reefs have shifted to a net erosional phase. The greatest declines in structure and carbonate were seen within the medium to highly exposed seaward reefs. However, low-exposure areas, and particularly the true enclosed lagoons, remained structurally complex and net-producers of carbonate, demonstrating some degree of resilience to the abnormally high water temperatures. This resilience was linked to the initial community structure of the corals, and potentially to an adapted resistance to the higher temperatures typically experience in still water lagoon environments. Furthermore the physical protection afforded by enclosed lagoons and sheltered lee-ward reefs is likely to have at least limited the physical erosion experience by these corals, producing better retention of structure for re-settlement post-disturbance.

## **Study limitations**

Structure from Motion was found to be useful for rapidly mapping reefs and collecting information on structure, even from historic video footage, not originally captured for this purpose. The technique was also adapted to allow measures of carbonate loss and gain to be collected through time, which are comparable to established survey methods. Further research is however needed to fully validate both the accuracy of the complexity assessment method and the carbonate budget method. Primarily this further work needs to quantify the

extent to which volume and structural information is lost through occlusion across habitat types and at higher levels of reef complexity (such as highly branching coral thickets or tabular growth-form dominated sites. While the initial work shown here indicates that this technique could prove a valuable time-effective addition to standard monitoring protocols, it is essential that any new monitoring method can incorporate historic data sets (to see temporal trends), and that specific limitations are known and mitigated.

As this technology is still only recently developed and has only been used in a handful of studies so far, there is a clear need for future standardization of image collection method and processing techniques, and ultimately for the creation of protocols for both data collection and storage. Such protocols will ensure consistently high standards of measurement and allow researchers to pool data resources collaboratively for larger studies.

Three further current limitations which may hamper the uptake of this method are: 1) the initial cost involved in purchasing camera and computing equipment of sufficient quality to create good models; 2) the processing time and computing power needed for large / detailed models; and 3) a need for skills training in this new monitoring method. The rapid development of computing hardware and software are likely to result in the first two points becoming far less important obstacles, with high specification cameras such as the GoPro now available for a few hundred pounds and requiring limited training. However, one of the benefits of the SfM technology is also that it only requires a normal underwater camera and a high power computer (both of which are typically a standard part of a survey teams' toolkit. Therefore, aside from the software needed, these limitations may not infer a too heavy additional cost for lower income projects / regions). Furthermore, the increasing accessibility of the internet and development of 5G technology will likely allow even

relatively remote locations to soon be able to upload data to cloud-based / cluster processors, minimizing the processing time necessary locally, and allowing larger areas of reef to be surveyed through increased memory and processing capacity.

Once computing power has developed sufficiently to allow processing times to be reduced, (and the associated computing costs lowered), the methodology can be begin to be scaled across areas of far greater size than the ~ 400 m<sup>2</sup> limit at which this study has worked. As we are restricted to only medium-scale discrete patches of reefs, we are potentially missing changes occurring elsewhere, or changes which are occurring over larger spatial scales (Aston *et al.*, 2019). If we are able to increase spatial coverage of data recorded at this high resolution, likely through the use of Autonomous Underwater Vehicles and Unmanned Aerial Vehicles (drones), we may be able to start seeing such patterns. This will in turn allow deeper insight into coral reef ecology (including how associated organisms such as sharks use this space), while also allowing more effective monitoring to be conducted (Lea *et al.*, 2016; Fukunaga *et al.*, 2019).

## **Future directions**

The rapid development of applied scalable technologies and increases in computing power are allowing researchers to gain greater resolution, accuracy and repeatability within surveys than has ever been possible before. The combination of in situ and remote sensing methodologies further allows for greater holistic understanding of ecosystem change, which in turn facilitates rapid assessment of marine impacts and their remediation, as well as improving management efficiency. With this range of novel methods now available, greater synergistic and standardized approaches to their application will be required, along with

thought as to how to appropriately analyse this “big data”, and the array of new metrics available. As technology and computing power continues to increase, so in turn will the scale, detail, and spatial spread of this information. Ultimately, these approaches will allow marine scientists to accurately profile and monitor habitats that have previously defied full in-depth quantification and to gain far greater understandings of ecosystem processes.

As with any ecological survey work, our understanding of the mechanisms and extent of change within an area is limited by the amount of data that we are able to collect and analyse. In this study, I was limited by the amount of time available to assess the extent of changes in the Chagos Archipelago. Initial indications of regrowth are apparent and it will be interesting to continue to track the changes to structure as the reef recovers and to attempt to link this to fish community structure trajectories. Similarly, while the Philippines study used a relatively long-term dataset, the community was still undergoing change and showed a clear need to introduce wider management. It will be important to continue to track these changes and feed these results into focused management interventions when required.

While this body of work has only touched on one new technological advance, this particular technology has shown results which are readily usable within existing protocols, and allows greater detail and reproducibility than has been available from existing methods. The scope of outputs from SfM techniques has however not been fully explored. The integration of this technique with machine-learning techniques (King *et al.*, 2018; Villon *et al.*, 2018) to investigate spatial size-frequency distribution (Edwards *et al.*, 2017), automated identification of benthic structure (Beijbom *et al.*, 2015; Manderson *et al.*, 2017), and fine-scale measurement of individual colony growth (Ferrari *et al.*, 2017) across whole reefs, will allow

a new level of insight into fine scale ecological community dynamics. It will also allow a far more mechanistic understanding of ecosystem processes, improving our ability to predict future changes. During this work I also trialed the integration of fluorescent photogrammetry to allow automated identification of living coral (Zweifler *et al.*, 2017) and detection of individual polyps, typically an extremely time consuming and skilled task (Figure 50).

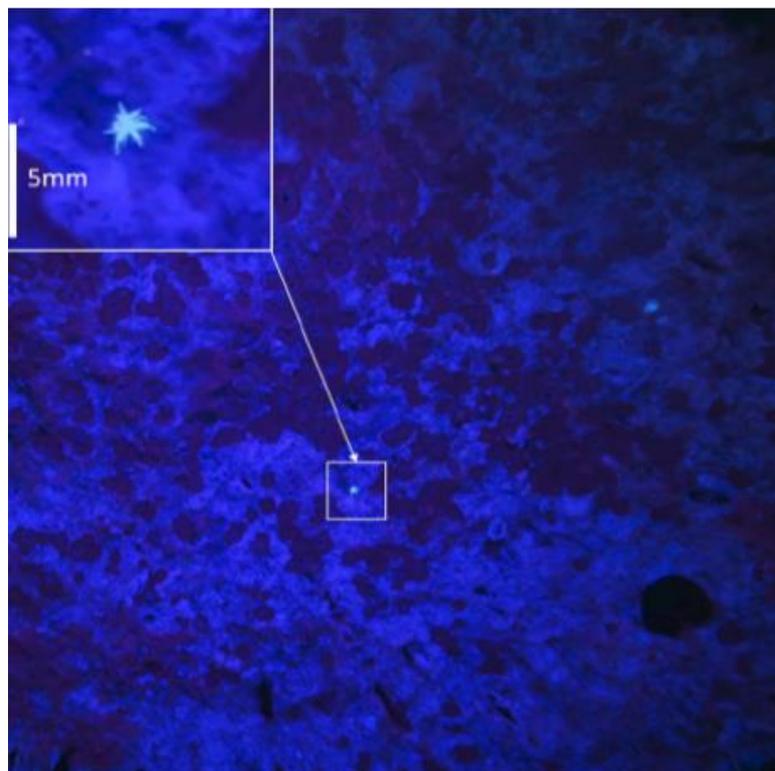


Figure 50. Blue light fluorescence 3D photogrammetric image of  $\sim 0.001 \text{ m}^2$  of reef, at 10 m depth. The image shows a single newly-recruited polyp on to the reef at Peros Banhos lagoon, within the British Indian Ocean Territory

Most recently, the development of a process termed 'fluid lensing' alongside drone-based photogrammetry now enables surveyors to see through wave turbulence and create accurate ortho-mosaic maps and 3D reconstructions of shallow marine benthos over large areas from outside of the water (Chirayath and Earle, 2016). While the future of reef systems is in many respects uncertain and in ever greater need of scaled conservation management, the rapidity of scientific advances and scope of observation now possible, means the future of marine research is an exciting one.



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