Influences of Pacific Island human communities on benthic coral reef functioning and resilience

A dissertation by

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Summary

A multitude of local and global stressors are threatening the diversity and productivity of coral reef ecosystems within the current era of the Anthropocene. Consequently, their continued provision of ecosystem services such as coastal protection, food and livelihoods is under threat. Human societies in the Pacific Island region are particularly vulnerable to these changes. While the effects of global stressors on coral reefs are relatively well understood, the role of various local human impacts and their interaction with global stressors remains under debate. This thesis aimed to improve understanding of relationships between local human impacts and benthic coral reef communities in the understudied Pacific Island region. Particularly, it addressed how various levels and types of local impacts can directly and indirectly influence benthic coral reef functioning and in turn future resilience to global stressors by using a combination of observational-, theoretical- and secondary data-based approaches. Field campaigns directly investigated the impacts of fishing and sewage pollution, and literature reviews specifically addressed regional overexploitation of key herbivorous reef fish species and increasing benthic cover of cyanobacterial mats. Additionally, a large-scale analysis of 182 reefs quantified differential benthic responses to contrasting levels of local human impact. Reefs exposed to very high levels of human impacts in terms of fishing and sewage input were found to undergo distinct benthic community shifts. Specifically, benthic cyanobacterial mats became dominant (up to 66% benthic cover), which promote strong self-reinforcing positive feedbacks that increasingly favour reef degradation. Dominance of fleshy algae and algal turfs were identified as other alternative states that Pacific Island reefs could gravitate towards. Most reefs were however existing somewhere along the ecological continuum between categorical states, appearing increasingly homogeneous in their composition. Such homogeneity makes capturing differences and trajectories within the benthos challenging. Accordingly, conventional monitoring metrics identified no differences between fished and protected reefs in Fiji, whereas newly developed indicators that capture ecosystem functioning and processes detected strong differences. Particularly, nursery quality of reef substrate (e.g. turf height, coral recruitment and succession) was improved within protected areas. A range of adaptive management tools (e.g. quota limits, seasonal closures, size limits) are proposed to maximise the ability of local management to maintain the function of herbivorous fish, which are identified as one of the most ecologically and economically important taxa in the region. Findings within this thesis also revealed that local human impacts can influence benthic assemblages even when direct effects on broad benthic groups are inconspicuous. At reefs exposed to less than 25 people km^{-2} reef, models based on spatial and physical attributes (reef depth, latitude, storm exposure) exhibited high explanatory power for benthic reef condition (59% variation explained) and coral morphological composition (67% variation explained), but as local impacts increased this power was strongly reduced (<7% variation explained). In summary, while local human impacts can directly favour alternative benthic regimes, subtler changes can be overlooked as reefs become increasingly homogeneous (e.g. favouring species tolerant of stressful conditions). These changes can profoundly alter the relationship between reefs and their physical environment, and in turn strongly compromise our ability to predict future impacts of global change. A toolbox of appropriate metrics designed to capture changes under increasing homogeneity is provided, and the importance of measuring such changes is emphasised in terms of quantifying ecosystem functionality and trajectories, and anticipating future responses of benthic assemblages.

Zusammenfassung

In der aktuellen Ära des Anthropozäns bedroht eine Vielzahl lokaler und globaler Stressfaktoren die Vielfalt und Produktivität von Korallenriffen. Folglich ist ihre Fähigkeit, kontinuierlich Ökosystemdienstleistungen wie natürlichen Küstenschutz und eine Bereitstellung von Nahrungsmittel- und Lebensunterhaltgrundlagen zu leisten, nicht garantiert, was besonders die hierfür anfälligen Küstengemeinschaften in der pazifischen Inselregion bedroht. Während die Auswirkungen der globalen Stressfaktoren auf Korallenriffe relativ gut erforscht sind, wird die Rolle der verschiedenen lokalen anthropogenen Einflüsse und ihre Interaktion mit globalen Stressfaktoren weiterhin diskutiert. Die vorliegende Arbeit zielte darauf ab, das Verständnis der Beziehungen zwischen lokalen anthropogenen Einflüssen und benthischen Korallenriffgemeinschaften in der generell wenig untersuchten pazifischen Inselregion zu verbessern. Der Fokus lag dabei insbesondere auf den Veränderungen, die verschiedene Ebenen und Arten lokaler Einflüsse direkt und indirekt auf den benthischen Teil von Korallenriffen ausüben können, und darauf, wie die zukünftige Resilienz gegenüber globalen Stressfaktoren durch eine Kombination von Beobachtungs-, statistischen und theoretischen Ansätzen abgeschätzt werden kann. In Feldstudien wurden dabei die direkten Auswirkungen von Fischerei und Abwasserverschmutzung erforscht, während Literatur-Recherchen darauf abzielten, die regionale Überfischung der wichtigsten algenfressenden Rifffischarten und das zunehmende Auftreten benthischer Cyanobakterienmatten zu untersuchen. Darüber hinaus quantifizierte eine groß angelegte Metaanalyse von 182 Korallenriffen unterschiedliche benthische Reaktionen auf lokale menschliche Einflüssen auf verschiedenen Ebenen. Korallenriffen die einem sehr hohen Maß an anthropogenen Auswirkungen in Bezug auf Fischerei und Abwasserverschmutzung ausgesetzt waren, wiesen deutliche Verschiebungen in der Zusammensetzung ihrer benthischen Gemeinschaften auf. Insbesondere benthische Cyanobakterienmatten können dabei an Dominanz gewinnen (und bis zu 66% des Benthos abdecken) und dabei selbstverstärkende kaskadenartige Prozesse in Gang setzen, die die Degradation von Korallenriffen fördern. Fleischige Makroalgen und Fadenalgen wurden als weitere alternative Zustände identifiziert, in deren Richtung sich Pazifische Korallenriffe möglicherweise bewegen. Die meisten Riffe waren jedoch entlang eines ökologischen Kontinuums von möglichen Zuständen angesiedelt, mit einer Tendenz zu zunehmender Homogenität der Korallenkomposition. Diese Homogenität stellt eine besondere Herausforderung für die Erfassung von Unterschieden und Trajektorien innerhalb der Benthosgemeinschaften dar. Dementsprechend identifizierten konventionelle Monitoring-Indikatoren keine Unterschiede zwischen befischten und geschützten Korallenriffen in Fidschi, während neu entwickelte Indikatoren, die Ökosystemprozesse erfassen, deutliche Unterschiede ergaben. Insbesondere wurde die Qualität des Riffsubstrats in Bezug auf Besiedlung durch Steinkorallen (z. B. Fadenalgenhöhe, Korallenrekrutierung und anschließendes erfolgreiches Wachstum) in Schutzgebieten verbessert. Damit lokale Managementmaßnahmen zum Positiven hin überarbeitet und die Funktion ökologisch und ökonomisch wichtiger algenfressender Fische in Zukunft erhalten werden können, wird eine Reihe von adaptiven Management-Maßnahmen (z.B. Einführung von Fangquoten, saisonale Schließungen, Größenbeschränkungen) vorgeschlagen. Die Ergebnisse dieser Arbeit zeigten auch, dass lokale menschliche Einflussfaktoren Auswirkungen auf benthische Gemeinschaften ausüben können, auch wenn die direkten Effekte oft unauffällig sind. Betrug die Dichte menschlicher Anwohner von Korallenriffen weniger als 25 Personen pro km² Riff, zeigten auf räumlichen und physikalischen Eigenschaften (Tiefe, Breitengrad, Sturmbelastung) beruhende Modelle eine hohe

Vorhersagekraft für den benthischen Riff-Zustand (59% der Datenvariation erklärt) und die morphologische Korallenzusammensetzung (67% Variation erklärt). Waren lokale Einflussfaktoren verstärkt, sank die Vorhersagekraft des Modells deutlich (<7% Variation erklärt). Zusammenfassend lässt sich sagen, dass lokale menschliche Einflüsse bestimmte alternative benthische Zustände favorisieren, während subtilere Veränderungen leicht übersehen werden könnten, da Riffe zunehmend homogener werden (z. B. durch die Bevorzugung von Arten, die eine höhere Resilienz gegenüber Stressfaktoren aufweisen). Diese Veränderungen können die Beziehung zwischen den Riffen und ihrer physischen Umgebung grundlegend verschieben und wiederum unsere Fähigkeit, die Auswirkungen des globalen Wandels vorherzusagen, stark beeinträchtigen. In dieser Arbeit wird daher eine Toolbox präsentiert, die geeignete Indikatoren enthält, um Veränderungen unter zunehmender Homogenität zu erfassen. Gleichermaßen unterstreicht sie die Wichtigkeit, solche Veränderungen in Bezug auf die Quantifizierung von Ökosystemfunktionalität und Trajektorien zu messen, damit zukünftige Reaktionen von benthische Gemeinschaften besser vorhergesagt werden können.

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Dedicated to my Grandad

and in loving memory of my Grandma

For most of history, man has had to fight nature to survive; in this century he is beginning to realise that, in order to survive, he must protect it

-- Jacques Yves Cousteau--

CHAPTER ONE

GENERAL INTRODUCTION

1.1. Coral reefs in the Anthropocene

Coral reefs, the ‘rainforests of the sea’, are among the most biodiverse and productive ecosystems on earth (Knowlton & Jackson, 2008). In turn they provide humans within critical ecosystem services in terms of food, livelihoods and coastal protection. Nowhere is this role more important than on low-lying and remote islands such as those in the Pacific, where the cultural and economic value of this ecosystem is at its highest (Foale, 2008; Pinca *et al.*, 2009; Burke *et al.*, 2011; Hoegh-Guldberg *et al.*, 2016). The continued productivity and diversity of coral reefs is however under threat within the current era of the Anthropocene where humans have become the dominant drivers behind changes in the climate and environment (Zalasiewicz *et al.*, 2010). Despite having thrived for millennia, these rapid and strong human-driven changes are seriously degrading coral reef ecosystems (Pandolfi *et al.*, 2003; Hoegh-Guldberg *et al.*, 2007). The associated loss of these systems and their ecosystem services will impact the hundreds of millions of humans living close to tropical coastlines.

As a result of climate change, reefs are being increasingly exposed to thermal stress and weather anomalies with a relentlessly narrowing window for recovery between events (Donner *et al.*, 2009; Riegl *et al.*, 2013). The 1997/1998 and 2015/2016 super El Niño events caused mass coral bleaching and extensive post-bleaching mortality in reefs worldwide, and such extreme events are predicted to become more common over the next decades (Goreau *et al.*, 2000; Cai *et al.*, 2014; Ampou *et al.*, 2017). By mid-century, the majority of reefs will experience annual bleaching under a business-as-usual scenario (RCP8.5) (van Hooidonk *et al.*, 2013; Van Hooidonk *et al.*, 2014), and even if emissions are reduced under the 2016 Paris Climate Change Conference agreement (COP21, RCP4.5), >75% of reefs are projected to experience annual severe bleaching before 2070 (van Hooidonk *et al.*, 2016). Alongside increasing thermal stress, higher intensity storms, unusual weather patterns (e.g. rainfall) and ocean acidification are among other climate change-associated (global) stressors (Pachauri *et al.*, 2014) that threaten coral reef integrity (Hoegh-Guldberg *et al.*, 2007). Not only are reefs confronted by progressively challenging climatic conditions, but increasingly human-dominated coastlines bring with them an assortment of local stressors. Most reefs are in rather close proximity to human populations, with 58% found within 30 minutes travel time from human settlements (Maire *et al.*, 2016), deeming them highly accessible and coupled to terrestrial influences. These reefs are exposed to a combination of both local and global stressors that demand high tolerance and adaptability for future growth. Unfortunately, the challenging environment that these reefs occupy is coupled with their unrivalled importance for ecosystem service provision to adjacent human communities (e.g. Costanza *et al.,* 2014).

With an estimated six million coral reef fishers (Teh *et al.*, 2013), small-scale artisanal and subsistence fisheries can have a strong (top-down) impact on reef fish communities. Globally most reefs are now overfished and projected recovery times are extensive even if fishing were stopped (35 years on average - MacNeil *et al.*, 2015). In addition to providing critical food and income sources, many targeted fish species fulfil critical ecosystem functions, such as herbivorous fish in the control of fleshy and turf algae (Green & Bellwood, 2009; Hoey & Bellwood, 2009; Bejarano *et al.*, 2013). Unsustainable harvesting of reef fish can consequently have profound effects of coral reef dynamics and processes (Bellwood *et al.*, 2004; Hughes *et al.*, 2007; Mumby *et al.*, 2007). Coral reef fisheries are indeed not limited to fish and also include organisms such as sea urchins and sea cucumbers which can be of comparative importance in terms of both economy and ecology in coastal areas (Berkes *et al.*, 2006; Mumby *et al.*, 2007; Anderson *et al.*, 2011; MacTavish *et al.*, 2012). Rapidly growing human populations along tropical coastlines are also driving strong (bottom-up) declines in coral reef water quality following factors such as increased nutrient and organic matter (OM) input (Fabricius, 2005; Burke *et al.*, 2011). Untreated sewage is one major source of nutrients and OM and is a key issue in coral reef areas (Reopanichkul *et al.*, 2009; DeGeorges *et al.*, 2010); 80–90% of discharged wastewater in the Caribbean, Southeast Asia and the Pacific region is untreated (UNEP/GPA, 2006). Even when sewage-treatment systems exist, wastewater itself must be considered an amalgamation of undesirable agents, with freshwater, (inorganic) nutrients, pathogens, suspended solids and more (Wear & Thurber, 2015) which all threaten reef integrity. As infrastructure around coastal areas develops, land-use change including agricultural and coastal development affect water quality through terrestrial run-off and riverine discharge (Hunter & Walton, 2008), which is amplified by deforestation of terrestrial and mangrove areas (Victor *et al.*, 2006).

Local anthropogenic stressors thus affect the natural balance within coral reef ecosystems, with top-down effects on critical species and overall trophic structure, and bottom-up changes of water quality both acting to shift intrinsic dynamics of benthic communities. Interactions between top-down and bottom-up drivers on benthic dynamics have been studied extensively, with outcomes such as the Relative Dominance Model (Littler *et al.*, 2006) predicting algal and coral community structure under different levels of each stressor. Nonetheless there is seemingly much more complexity behind reef responses to these stressors depending on factors such as the spatial locality and reef habitat, with for example some inshore reefs thriving in high turbidity (Morgan *et al.*, 2016). The scale of associated local anthropogenic stress also differs strongly between locations depending on factors such as development, infrastructure, reliance on marine resources, cultural beliefs and access to alternative livelihoods (e.g. Pinca *et al.*, 2009). Local population density by itself may in some instances be a poor proxy for local stress due to differences in, for example, sewage treatment, reliance on marine resources for food, the use of traditional vs. exploitative fishing techniques, environmental awareness and local management. For example, though the direct impact of humans on reef fish communities can be strong (Williams *et al.*, 2015a), additional consideration of distance to market alongside human density significantly strengthens relationships (Cinner *et al.*, 2013). The potentially less direct role of coastal human communities in the degradation of coral reef benthos is consequently still debated, with different studies concluding that increasing human density; (i) does not correlate with reef degradation (Bruno & Valdivia, 2016), (ii) directly degrades reefs (Sandin *et al.*, 2008; Smith *et al.*, 2016), or (iii) drives ecological reorganisation by selecting for more tolerant organisms (Côté & Darling, 2010). The latter hypothesis can help to explain why benthic reef structure is still strongly related to natural biophysical factors at reefs distant from humans in the US Pacific, but not at reefs close to humans (Williams *et al.*, 2015b).

The overwhelming majority of coral reefs will be exposed to annual severe bleaching even under scenario RCP4.5 where the COP21 pledges become reality (Frieler *et al.*, 2012; van Hooidonk *et al.*, 2016). Whilst reef managers and researchers cannot directly manage climate change impacts, they have the tools to target local stressors that may directly influence (i) reef condition and/or (ii) the system's response to climate change. A better understanding of these topics, particularly in understudied areas such as the Pacific Island region, is critical in allowing managers to devise effective local management plans to maximise the future persistence of this ecosystem.

1.2. Reef resilience and alternative benthic states

Ecological resilience refers to the continued gravitation towards one ecological state following disturbances, reflecting both the ecosystem's ability to resist change and its capacity to recover and return to its original state (Holling, 1973). Resilience of coral-dominated systems is considered as one that will continue to return towards a coral-dominated state following perturbations. When resilience is lost or a disturbance exceeds resilience thresholds, regime shifts can occur whereby the system is pushed into an alternative state characterised by its own set of stabilising feedbacks (Scheffer *et al.*, 2001; Mollmann *et al.*, 2014). In coral reefs, a regime shift most commonly refers to the transition from coral-dominated reefs to domination of alternative benthic organisms that are generally considered less desirable (Folke *et al.*, 2004). While the alternative benthic state classically described on reefs is one dominated by fleshy algae (Hughes, 1994), an array of organisms have now been identified to dominate alternative regimes (e.g. turf algae – Jouffray *et al.*, 2014; cyanobacteria – Albert *et al.*, 2012; soft corals, sponges – Norström *et al.*, 2009). Outside of the Caribbean, most reefs do not occupy either of the classically described regimes (e.g. dominated by either hard coral or fleshy algae), but instead sit somewhere between the two in a partially degraded and less diverse condition (Bruno *et al.*, 2009). Following disturbances, reefs may not undergo shifts to alternative organisms and instead form novel coral reef ecosystems that remain dominated by hard coral but differ profoundly in composition and function (Graham *et al.* 2014). Such functional shifts are a consequence of variable interspecies susceptibilities; for example, reefs shift away from sensitive large branching corals such as acroporids towards massive or opportunistic, weedy corals (Marshall & Baird, 2000; Van Woesik *et al.*, 2011; Riegl *et al.*, 2013).

Remote reefs are generally conceived to be able to 'bounce back' from climate change impacts (Halford & Caley, 2009; Gilmour *et al.*, 2013; Perry *et al.*, 2015), thus demonstrating greater resilience to global stressors than their more locally impacted counterparts. The conventional view is thus that resilience of coral-dominated systems can be increased by reducing controllable local impacts (Wooldridge & Done, 2009; Anthony *et al.*, 2015), However, remote and 'pristine' reefs can respond to acute global stressors as severely as reefs that are heavily impacted by local activities (Alling *et al.*, 2007; Obura & Mangubhai, 2011; Riegl *et al.*, 2013). Based on the assumption of positive co-tolerance among species to local and global stressors, an alternative hypothesis of 'resilience in a disturbed world' was proposed (Côté & Darling, 2010). Under this hypothesis, local anthropogenic activities selectively cull sensitive coral taxa (i.e. ecological reorganisation), leaving behind a more resistant system (i.e. novel coral reef ecosystem) to face global stressors. Hard evidence for co-tolerance remains low (Darling *et al.*, 2013), and the reduced diversity associated with such ecological reorganisation contradicts the ecological insurance hypothesis that states a larger species pool can display a variety of responses and fill roles once species are removed (Naeem & Li, 1997; Yachi & Loreau, 1999). However, high fish biodiversity actually correlates with higher vulnerability of community functioning to anthropogenic impacts (Mora *et al.*, 2011), dispelling the theory that species diversity itself is vital in underpinning resilience, and rather that functional diversity should be considered (Bellwood *et al.*, 2003). Functional redundancy refers to the capacity of other species to compensate for the loss of another, and response diversity refers to the range of responses from species fulfilling the same roles within the ecosystem (Lawton & Brown, 1994; Elmqvist *et al.*, 2003). High redundancy and response diversity within functional groups should improve system resilience by providing ecological insurance (Nyström, 2006; Mori *et al.*, 2013). However, managing for functional diversity to booster resilience has its own emerging challenges, with species within functional groups exhibiting contrasting responses to environmental gradients (e.g. wave exposure), and revealing further dimensions to niche partitioning beyond diet (Bejarano *et al.*, 2017). This emerging view shows a highly complex picture that requires a better understanding of the interplay of anthropogenic and environmental stressors on difference scales.

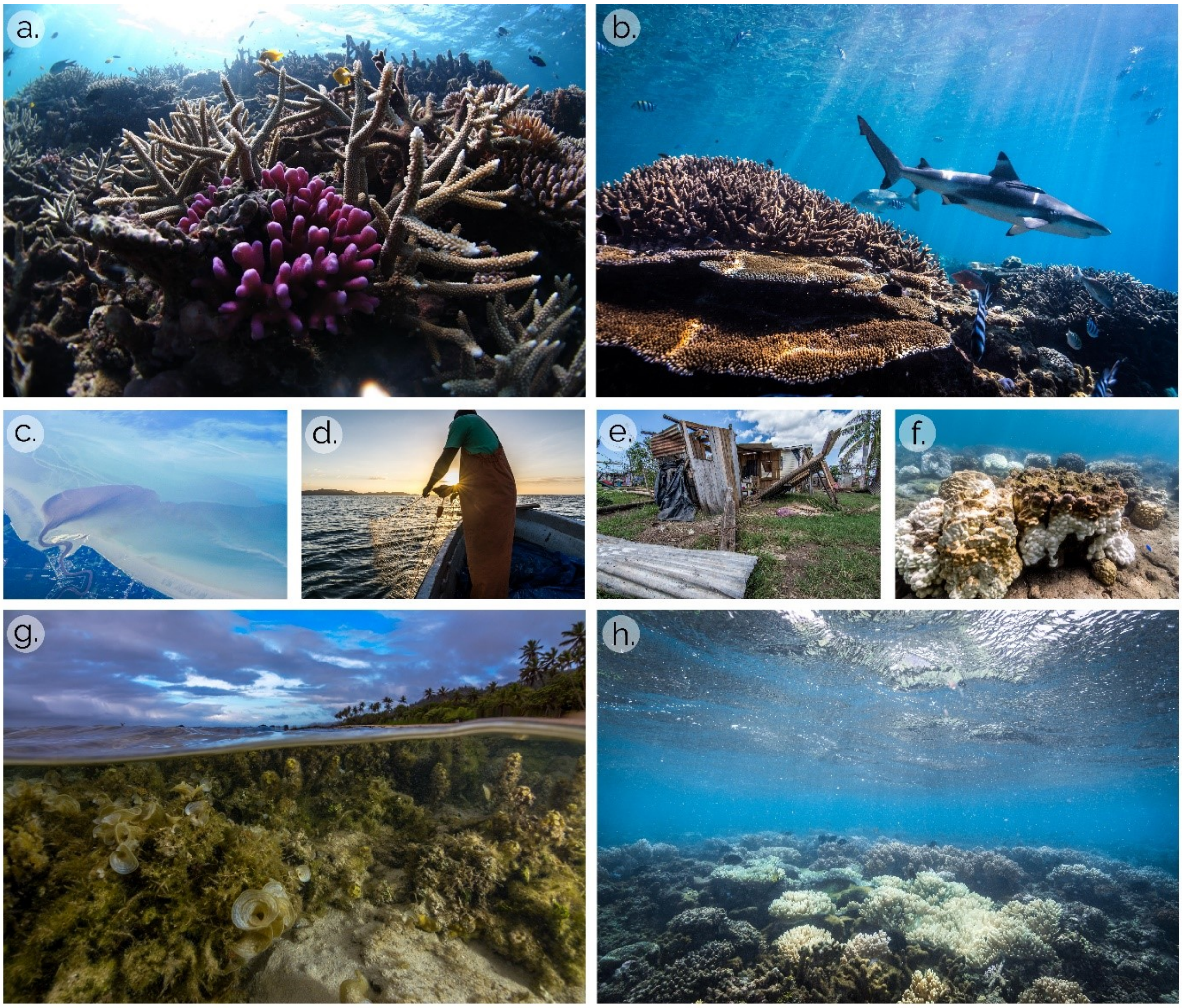

Figure 1.1: *Biodiverse and structurally complex reefs (a, b) are being threatened by a range of local and globally-derived stressors. Local stressors include declining water quality (c) and overfishing (d) which can disrupt key ecological processes. Global stressors include increasingly stressful weather events such as increasing storm intensitities (e) which can cause physical damage to hard corals and ocean warming which drives coral bleaching (f). These impacts are often leading to system regime shifts (g), with associated losses of complexity (h) and ecosystem services. Photo credits: Tom Vierus.*

Natural ecological variability on reefs at spatial scales makes it challenging to predict how combinations of stressors will interact to drive coral reef dynamics (Mora *et al.*, 2016; Harborne *et al.*, 2017). Additionally, whilst resilience is often framed in a positive light, it is important not to overlook that resilience of alternative systems is often very strong due to positive feedbacks (Nyström *et al.*, 2012). Positive feedbacks are required to drive alternative stable regimes and associated hysteretic responses (Schröder *et al.*, 2005; van de Leemput *et al.*, 2016). Where there is a high reliance on ecosystem services, ecological degradation can lead to social-ecological traps, whereby both social and ecological feedbacks mutually reinforce each other and in turn can further push a system towards an undesirable state (Cinner, 2011; Boonstra & de Boer, 2014). Reversing degradation where positive feedbacks are active requires vigorous management interventions (Nyström *et al.*, 2012), and when feedbacks are strong then environmental shocks such as storms may additionally be needed to allow the system to reset (Graham *et al.*, 2013).

1.3. Capturing resilience and ecosystem trajectories

Metrics that can be used as effective signals of resilience (or equally of vulnerability/loss of resilience) during reef monitoring are important to enable quantification of ecological status before conditions deteriorate enough that ecosystem shifts occur. Conventional coral reef monitoring focuses mainly on abundance and biomass of key organisms, providing a snapshot-in-time of the system. Such measurements provide an idea of the system's state, but give no indication of the long-term trajectory. Understanding system trajectories would allow us to determine whether the ecosystem is approaching or recovering from a critical threshold, whereas state indicators are only able to show a system's position along multiple axes (Glaser *et al.*, 2012). Regardless of the live hard coral cover, if coral recruitment has failed in recent years, or if algae have gained a competitive advantage over corals, then the system is still vulnerable to collapse (Anthony *et al.*, 2015). It is thus vital to include assessments of processes that can capture long-term ecosystem responses to stressors and indicate trajectories. A range of biological, environmental, and historical indicators have been proposed to capture system resilience (e.g. McClanahan *et al.*, 2012). Such indicators have led to novel approaches to reef monitoring, with decision-makers wanting to base management decisions on how specific reefs respond to environmental changes, as opposed to the more conventional metrics of reef state (Lam *et al.*, 2017).

As increasingly more reefs appear relatively similar and homogeneous in a semi-degraded state (e.g. Bruno *et al.*, 2009), monitoring must be able to detect subtle differences in underlying dynamics and resilience (Lam *et al.*, 2017). Since the 1970's, hard coral cover has dropped by 80 and 50% in the Caribbean and GBR, respectively (Gardner *et al.*, 2003; De'ath *et al.*, 2012). Using the Caribbean as an example, whilst surveys in the 1970's would have had strong statistical power in determining a 25% decline in hard coral cover (e.g. 55 to 41%), the ability of current surveys to detect the same relative change (e.g. 13 to 10%) is severely compromised. Coinciding with a considerable worldwide decline in coral cover, the proportion of space occupied by non-living substrate classified as dead coral, bare rock, pavement or rubble has increased significantly (e.g. Tsounis & Edmunds, 2017). Consequently, it seems intuitive that surveys should start to characterise the 'substrate condition' which realistically is seldom bare and usually covered in types of algae including coralline or algal turfs (Harris, 2015). Different colonisers of newly available substrate can act to destabilise coral reef systems and promote degradation, or support ecological processes such as coral recruitment and succession, thus facilitating reef recovery (Birrell *et al.*, 2005). Whilst algal and coral coverage provides some information, this naturally varies over spatial and temporal (e.g. seasonal blooms of algae) scales and provides only a snapshot-in-time. Additional measurements of contact points within coral-algal interactions can inform which benthic group displays dominance (Barott *et al.*, 2012). Competitive dominance of algae can indicate that algal growth is not being limited by bottom-up or top-down factors, or that coral health itself is suppressed or growth rates are low (Jompa & McCook, 2002; Vermeij *et al.*, 2010). As a result of temporal and surveyor-related discrepancies, and differential species' wariness, visual censuses for fish biomass should be supported by video observations, and measuring parameters that reflect fish function over longer scales, such as algal turf characteristics for herbivorous fish, or damselfish abundance and territoriality for predatory fish (Ceccarelli *et al.*, 2005; Vermeij *et al.*, 2015). Measurements of algal turf height and coral growth rates have been proposed as two key indicators in both identifying the stressors that have impacted a reef and in estimating the likely recovery potential (Flower *et al.*, 2017). Subtle differences that would be overlooked in conventional monitoring may be critical in determining ecosystem trajectories thus providing an essential layer of information when prioritising reefs for management, evaluating management effectiveness and understanding impacts of various stressors.

1.4. Coral reef systems in the Pacific Island region

The Pacific Island region comprises three major island groups; Melanesia, Micronesia and Polynesia. The strong socio-economic dependence of Pacific Island nations on coral reefs is crossed with a low capacity to adapt to coral reef degradation and loss, highlighting an uncertain future for coastal communities in the region (Burke *et al.*, 2011). In Melanesia, the total 'ocean asset base' (primary assets such as marine fisheries, coral reefs, mangroves and seagrass, as well as ancillary assets such as productive coastlines and carbon absorption) is estimated at $548 billion (Hoegh-Guldberg *et al.*, 2016).

Reefs in the Pacific island region are considered to naturally display stronger resilience to disturbances compared to areas such as the Caribbean, and to have so far experienced lower levels of coral reef degradation and loss (Wilkinson, 2008; Burke *et al.*, 2011). Hypothesised reasons for this greater resilience include high diversity and associated functional redundancy and response diversity in fish and benthic assemblages, superior herbivorous fish function and grazing rates (e.g. significantly higher biomass of surgeonfish) and reduced algal growth rates (Green & Bellwood, 2009; Roff & Mumby, 2012). The Indo-West Pacific region comprises 719 species of hard coral compared to only 62 in the Caribbean (Spalding *et al.*, 2001). Higher functional redundancy and response diversity within the coral community may explain why alternative benthic regimes are less commonly established following perturbations in the Pacific than the Caribbean region. Such functional diversity would rather support ecological reorganisation and the formation of novel ecosystems due to the larger number of 'winners' that could fulfil ecological niches upon loss of other species following disturbances. Despite these factors promoting ecological resilience, remote Pacific island reefs are now reflecting the globally changing environment and suffering rapid degradation (Table 1.1).

Recent changes in Pacific islands, including improved fishing techniques, access to markets, and rapidly growing populations have led to a dramatic increase in the pressure exerted on coral reef systems (Sabetian & Foale, 2006; Brewer *et al.*, 2012, 2013). For example, whilst fishers traditionally used handlines and spears (limited to daylight), a recent availability of underwater flashlights, and to a lesser extent SCUBA, throughout the region has facilitated disproportionally high catch rates (Rhodes *et al.*, 2008; Hamilton *et al.*, 2012; Lindfield *et al.*, 2014). In developing nations, fish biomass is strongly related to a U-shaped curve of socio-economic development (Cinner *et al.*, 2009), following the 'environmental Kuznets curve' hypothesis (Stern *et al.*, 1996). This hypothesis states that ecological degradation will occur as socio-economic status improves, until a point of affluence and awareness is reached and environmental quality is sought after once more. Such changes have driven some Pacific island reef fisheries close to or past collapse, with the two most depleted sites from a global data-set encompassing >800 reefs worldwide being Pacific island reefs (MacNeil *et al.*, 2015). Alongside that of reef fish, another fishery that has been massively overexploited in recent decades across the region is that of sea cucumbers which are also hypothesised to play an important role in maintaining sediment integrity in coastal systems (Wolkenhauer *et al.*, 2009; Anderson *et al.*, 2011; MacTavish *et al.*, 2012; Purcell *et al.*, 2013, 2016).

With 57% of coral reefs threatened at a medium to high level by local threats and only 44% considered healthy, Melanesian reefs are in fact no better than the global average (Table 1.1). Similarly, 35% of reefs in Melanesia are classified as threatened, and 17% identified to be at a critical stage, exceeding global averages of 20% and 15%, respectively (Chin *et al.*, 2011). Reefs within this region are significantly more degraded than those in Micronesia and Polynesia, and constitute a much larger reef area (Table 1.1). Subsistence fishing is estimated to contribute 70% of the fisheries across the region (Gillett, 2010), implying strong potential for coastal fisheries management. Customary marine tenure, high levels of local engagement in management and strong dependence on marine resources were identified as key drivers of positive anomalies ('bright spots') in reef fish community biomass (Cinner *et al.*, 2016). As the Pacific Island region is characterised by customary ownership of marine resources (Foale, 2008), strong dependence on marine resources (Burke *et al.*, 2011) and high levels of subsistence fishing (Gillett, 2010), such findings suggest well-established local coastal fisheries management could bring large ecological rewards. However, establishing and enforcing management within the region is complex with many social and governance challenges that need to be addressed and better understood.

Table 1.1. Estimated threats to coral reefs in various regions, compared with global averages. This table is adapted from Chin et al., (2011) (Table 1a), based on data from Wilkinson et al., (2008) and Burke et al., (2011).

Region	Contribution to global reef area (%)	Reefs at **Low Threat** from local threats (%)	Reefs at **Medium Threat** from local threats (%)	Reefs at **High Threat** from local threats (%)	Reefs at **Very High Threat** from local threats (%)
Australia (Pacific)	14.8	86	13	1	<1
Melanesia (inc. Papua New Guinea)	15.4	43	31	19	6
Micronesia	3.9	70	21	6	3
Polynesia (exc. Hawaii)	5.0	58	27	12	3
Hawaiian Archipelago	1.5	83	3	6	9
Pacific Island TOTAL	25.8	52	27	15	5
Global TOTAL	-----	39	34	17	10

1.5. Research gaps

When Pacific Island reefs are grouped together, the proportion of threatened and degraded reefs falls below global averages, often leading to the conclusion that coral reefs within this region are of low relative concern (Wilkinson, 2008; Burke *et al.*, 2011; Chin *et al.*, 2011). However, when these numbers are assessed specifically for different island groups, the proportion of reefs at high risk in Melanesia actually exceeds global averages (Table 1.1). Considering that Melanesia provides over 15% of the global reef area, and human communities here are vulnerable to coral reef degradation, there is an urgency for research into the local drivers of change within this relatively understudied region to inform management.

Growing coastal populations on Pacific islands suggest problems for coral reefs from increasing nutrient run-off from agricultural land-use changes and development. Low infrastructure also implies problems associated to increasing untreated sewage input, which despite being recognised as a problem for reefs for many decades (Walker & Ormond, 1982; Pastorok & Bilyard, 1985) remains massively understudied within *in situ* settings (Wear & Thurber, 2015). Small islands can offer unique systems from which to study sewage input as sewage is usually untreated and its influence can be separated from alternative sources of nutrients that are often absent (e.g. land run-off containing fertiliser from agriculture, riverine input). Particularly, it is important to understand how overharvesting of key species such as herbivorous fish and sea cucumbers work in interaction with increasing nutrient and OM input from expanding human populations in a Pacific island setting. While herbivorous fish are important for the control of reef algae, bioturbation from sea cucumbers keeps the sediment oxygenated, therefore optimising the habitat for benthic (micro-) organisms, promoting efficient nutrient recycling (MacTavish *et al.*, 2012). As such, the impact of nutrients and OM is likely to be magnified by overexploitation of key species such as herbivorous fish and sea cucumbers. Though interactions between top-down and bottom-up stressors on benthic structure and dynamics are relatively well-established in the Caribbean, relationships on Pacific reefs have been less studied and seem to show much more variability (Mumby *et al.*, 2013). Thus research gaps exist in identifying the impact of nutrient and organic matter input on Pacific Island reefs, and the associated links with local overexploitation of key species.

Pacific island reefs do not show the same propensity to switch from hard coral- to fleshy algae-dominated regimes as those in the Caribbean (Roff & Mumby, 2012). Nonetheless, emerging evidence of systems becoming increasingly dominated by filamentous algal turfs (Jouffray *et al.*, 2014; Smith *et al.*, 2016) and cyanobacterial mats (Albert *et al.*, 2012; Kelly *et al.*, 2012) suggests that Pacific island reefs may gravitate towards dominance by other alternative benthic organisms following disturbances. Another research gap is thus examining the evidence of shifts towards alternative benthic states within the region along with associated feedbacks. Feedbacks within these alternative benthic states may differ from the better understood shifts towards fleshy algae, and may have implications in falling into and escaping from potential social-ecological traps associated to the strong interactions between human populations and reefs. Such information could better inform regionally-appropriate management targeted at relevant alternative regimes.

Where distinct ecosystem shifts towards dominance of alternative benthic organisms do not occur, ecological reorganisation with the coral community whereby local stressors may select for 'winners' is likely in a functionally diverse Pacific reef setting. Understanding the impact of these novel coral systems on reef resilience and relationships with different predictors is important. In the US Pacific islands, ecological reorganisation at reefs close to people decouples the relationship between the ecosystem and biophysical drivers which remains strong at remote reefs (Williams *et al.*, 2015b). Considering the proximity of most reefs to humans (Maire *et al.*, 2016), it is important to understand not just how remote reefs differ from those close to humans, but how different scales of human disturbances drive ecological reorganisation and subsequent relationships with environmental drivers.

Finally, considering the increasingly homogeneous appearance of reefs in the Anthropocene that are existing in a partially degraded state, local stressors and also local management may drive more subtle ecosystem changes that remain undetected by conventional monitoring but still influence system functioning and resilience. To capture such subtleties, metrics that can detect changes in ecological functions and processes within the benthos (e.g. beyond cover of benthic groups and fish biomass) must be incorporated into monitoring. Without such metrics, the impact of disturbances or management on reef trajectories may be overlooked. An additional research gap is thus to explore discrepancies between conventional monitoring tools and metrics focusing on ecological functions and processes in comparing modern reefs under different conditions. If such metrics can be practically and cost-effectively integrated in ecosystem assessments, a scope exists to:

(i) support managers in deciding whether to protect areas (e.g. evaluating high vs. low-risk conservation investments)
(ii) more thoroughly evaluate management effectiveness
(iii) better understand the impact of disturbances.

1.6. Research questions

Considering these research gaps, the overarching research question for this thesis was:

What is the influence of local human populations on small Pacific Island coral reef functioning and resilience?

To address this question, three sub-questions were asked:

i. How do different dimensions of human activities (e.g. low vs. high resource exploitation) on small Pacific islands facilitate alternative regimes or ecological reorganisation within benthic coral reef communities?

ii. Where subtle changes occur within the benthos in response to human activities, which process or resilience-based metrics have the ability to capture local impacts and indicate system trajectories?

iii. How can community-based management influence benthic community responses to local human disturbances on small Pacific islands?

1.7. Approach and thesis outline

To address the key research questions, this thesis incorporated a combination of observational, statistical and theoretical approaches. Though the statistical and theoretical studies cover the three major island groups within the Pacific island region (Melanesia, Micronesia, Polynesia), the field-based research was focused within Melanesia, at Fiji and Papua New Guinea. Following this general introduction (chapter 1), the thesis comprises five research-based chapters (comprising chapters 2 through 6) in the form of full manuscripts formulated for peer-reviewed journals, and are either published, in review or in preparation. The chapters fit into three broad categories (Figure 1.2); (i) the role of island communities in driving alternative benthic regimes and novel ecosystems, (ii) capturing subtle changes within the reef benthos driven by island communities, (iii) impacts of community-based fisheries management on reef benthos. The findings of all chapters are finally summarised by a general discussion (chapter 7), and future research opportunities are discussed. Additional published work associated to this project in which I am involved as a contributing author is provided in the appendix (Appendix D), and further associated manuscripts that are in preparation are summarised (Section 1.8.2).

The thesis is structured as follows, with personal contributions of the PhD candidate outlined in Table 1.2:

Chapter 2:

LOCAL SEWAGE INPUT DRIVES BENTHIC COMMUNITY SHIFTS AT OVERFISHED REEFS

Ford AK, van Hoytema N, Moore B, Pandihau L, Wild C, Ferse SCA.

In Chapter 2, 'Local sewage input drives benthic community shifts at overfished reefs in Papua New Guinea', we carried out field research at the two small neighbouring islands Ahus and Onetah in Papua New Guinea. These two remote islands come under the same customary marine tenure system and are heavily overfished, but while Ahus is densely populated, Onetah remains uninhabited. Ahus lacks any sewage treatment, and consequently raw sewage is directly discharged onto the reef-flat. This study thus aimed to investigate the impact of untreated sewage and overfishing in driving changes within the benthic coral reef community. At sites with varying proximities to beach toilets, fore-reef herbivorous fish biomass and benthic composition were measured alongside reef-flat sedimentary oxygen consumption (SOC) incubations; high SOC reflects high organic input into coastal waters, thus serving as a potential indicator of sewage input. This chapter indicated the significant influence of sewage input from small islands in driving overfished reefs from hard coral dominance towards benthic cyanobacterial mats, which led to a subsequent review into this understudied phenomenon in Chapter 3.

This manuscript, titled 'Sedimentary oxygen consumption rates indicate that local sewage input drives distinct benthic communities at overfished reefs in Papua New Guinea' has been published in *Environmental Conservation*.

Chapter 3:

THE RISE, DRIVERS AND CONSEQUENCES OF BENTHIC CYANOBACTERIAL MATS

Ford AK, Bejarano S, Nugues MM, Visser PM, Albert S, Ferse SCA.

Chapter 3, 'The rise, drivers and consequences of benthic cyanobacterial mats', comprises a thorough literature review into emerging reports of benthic cyanobacterial mats and their associated links to reef degradation. Benthic cyanobacterial mats are an increasing threat for a number of freshwater and marine ecosystems worldwide. In coral reefs, reports from around the world indicate that their prevalence and longevity are increasing with many associated ecological and social impacts. This rise in reports combined with our own field observations (in Chapter 2) prompted us to review (i) the drivers of this phenomenon, (ii) the ecosystem feedbacks and degradation that consequently arise, and (iii) priority management strategies that can be improved by outlined research gaps.

This manuscript, titled 'Reefs under siege – the rise, putative drivers and consequences of benthic cyanobacterial mats' is in preparation.

Chapter 4:

INCREASING LOCAL HUMAN IMPACTS MODIFY ENVIRONMENT-BENTHOS RELATIONSHIPS

Ford AK, Norström A, Jouffray JB, Nugues M, Moore B, Bejarano S, Wild C, Magron F, Ferse SCA.

In Chapter 4, 'Increasing local human impacts modify environment-benthos relationships' we analyse an extensive data-set from the Pacific Island region. The data encompasses benthic and fish community data from 182 reefs close to coastal communities and spanning 63 Pacific islands. We extracted additional data on thermal stress and storm exposure from public repositories, and subsequently investigated whether different levels of local anthropogenic impacts (a) directly influence benthic regimes, and (b) shift the importance of drivers in structuring benthic assemblages. Recent work in the Pacific region indicated that reefs close to humans exhibit decoupled relationships with natural biophysical predictors compared with remote reefs. Thus our approach allowed us to develop on this work by asking how different levels of local impacts directly affect benthic communities, as well as investigating which specific predictors (e.g. biomass of herbivorous fish, reef depth, storm exposure, local human density) become most important in shaping benthic assemblages under increasing local impacts. This approach gives us insight into how reefs exposed to increasing levels of human impacts will respond to future climate change-related stressors.

This manuscript, titled 'Local human impacts influence predictability of global stressors on Pacific Island coral reef assemblages', is in preparation.

Chapter 5:

DISCREPANCIES BETWEEN DIFFERENT METRICS FOR CORAL REEF MONITORING

Ford AK, McAndrews R, Eich A, Mangubhai S, Bejarano S, Nugues MN, Moore B, Rico C, Wild C, Ferse SCA

In Chapter 5, 'Discrepancies between different metrics for coral reef monitoring', we use a combination of conventional and newly development monitoring tools to evaluate differences in reef ecosystems under local management. Considering the increasingly stressful environment for coral reefs, it is critical to define tools that enable us to evaluate their dynamics and resilience under various scenarios. In this context, surveys must go beyond conventional monitoring approaches focusing on abundance and biomass of key groups and quantify metrics that better reflect longer-term ecological functions and processes. Such a novel approach to monitoring can identify ecosystem trajectories and provide early warnings of reef degradation. We measured a suite of conventional metrics (e.g. biomass of herbivorous fish, cover of broad benthic groups) alongside complementary status and ecological function- and process-based metrics (e.g. turf height, grazing rates, coral recruitment, juvenile coral density) at locally managed and adjacent fished reefs in Fiji, where locally managed marine areas are well-established. By comparing discrepancies between the different metrics, we investigate whether conventional metrics may overlook benefits within managed reefs in terms of superior ecological functions and processes that have important implications for the ability for the system to sustain itself and recover from future perturbations.

This manuscript, titled 'Evaluation of coral reef management effectiveness using conventional versus newly developed monitoring metrics' is in revision.

Chapter 6:

BIOLOGY, ECOLOGY AND MANAGEMENT OF KEY HERBIVOROUS UNICORNFISH IN THE PACIFIC

Ford AK, Bejarano S, Marshell A, Mumby PJ

In Chapter 6, 'Biology, ecology and management of key herbivorous unicornfish in the Pacific', we evaluate the regional ecological role and fisheries status of *Naso lituratus* (orangespine unicornfish) and *Naso unicornis* (bluespine unicornfish). These species are widespread and fulfil critical ecological functions in the top-down control of coral reef macroalgae; particularly fleshy brown algae (e.g. *Sargassum* spp.) which can out-compete and smother corals. However, they are heavily targeted by nearshore fisheries, and their continued exploitation could thus have serious consequences on reef ecosystems. We summarise current management throughout the region and provide recommendations based on their biological features.

This manuscript, titled 'Linking the biology and ecology of key herbivorous unicornfish to management in the Pacific' has been published in *Aquatic Conservation: Marine and Freshwater Systems.*

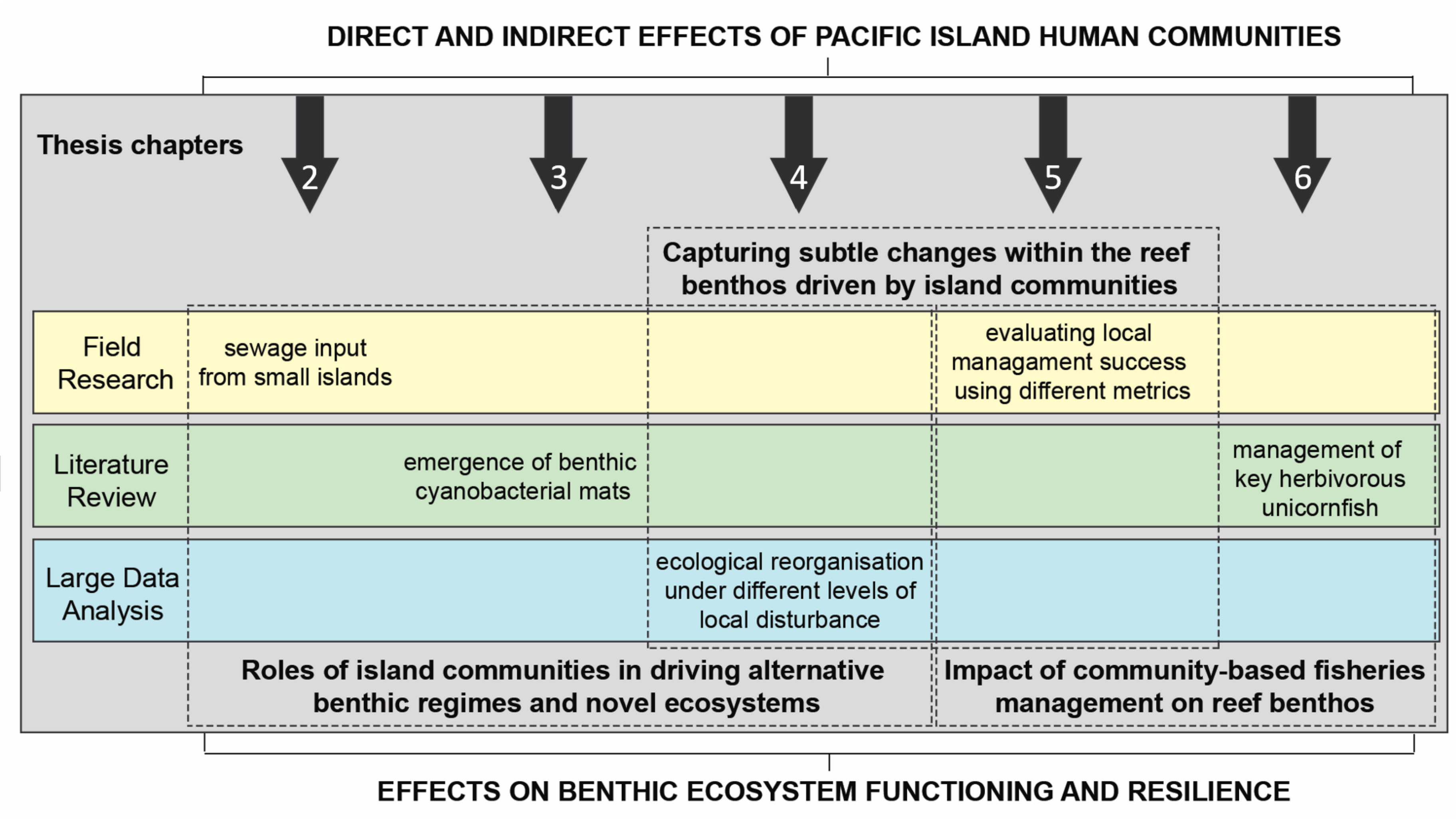

Figure 1.2. Thesis structure and approach for each of the five research-based chapters.

Table 1.2. Contributions of PhD candidate to tasks within each research-based chapter. For each chapter, each listed contributing author was involved in the development of the final manuscript following the first draft.

	Contribution of PhD candidate (%)				
Task	Ch. 2	Ch. 3	Ch. 4	Ch. 5	Ch. 6
Concept and design	50	90	75	90	50
Acquisition of data	40	-----	0	50	-----
Data analysis and interpretation	100	-----	100	90	-----
Preparation of figures and tables	100	100	100	100	100
Drafting of the manuscript	100	100	100	100	100

1.8. Additional related manuscripts

1.8.1. Published

Lee S, Ferse S, Ford AK, Wild C, Mangubhai S (2017) Effect of sea cucumber density on the health of reef-flat sediments. In: *Fiji's Sea Cucumber Fishery: Advances in Science for Improved Management* (eds. Mangubhai S, Lalavanua W, Purcell SW). pp 54-61. Wildlife Conservation Society, Suva, Fiji.

1.8.2. In preparation

Eich A, Ford AK, McAndrews RS, Nugues MM, Wild C, Ferse SCA. Epiphytes can amplify the negative effects of *Lobophora* on hard corals. In preparation for *Coral Reefs.*

Lee S, Ford AK, Wild C, Mangubhai S, Ferse SCA. Sedimentary responses to sea cucumber (*Holothuria scabra*) removal. In preparation for *Journal of Experimental Marine Biology and Ecology.*

Lee S, Ford AK, Wild C, Mangubhai S, Ferse SCA. Length-weight relationship of sea cucumber *Holothuria scabra* from Fiji. In preparation for *SPC Bêche-de-mer Information Bulletin.*

Rohe J, Schlüter A, Ford AK, Cakacaka A, Ferse SCA. Governance of coral reef social-ecological systems in the South Pacific: Between chiefs, churches, conservation and commercial industries. In preparation for *Ecology and Society*

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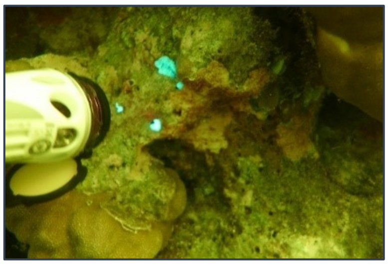
CHAPTER TWO

LOCAL SEWAGE INPUT DRIVES BENTHIC COMMUNITY SHIFTS AT OVERFISHED REEFS



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2.1. Abstract

Small island coral reef ecosystems are usually closely coupled to the activities of human inhabitants. Ahus Island (Papua New Guinea) is an isolated Pacific island with a rapidly growing population, heavy reliance on marine resources, and limited infrastructure. We hypothesised that untreated sewage was driving distinct benthic assemblages around Ahus and neighbouring uninhabited Onetah. At sites with varying proximities to beach toilets, fore-reef herbivorous fish biomass and benthic composition were measured alongside reef-flat sedimentary oxygen consumption (SOC) incubations; high SOC reflects high organic input into coastal waters, thus serving as a potential indicator of sewage input. Fish biomass was low (17.1 – 20.1 g m^{-2}), but consistent between sites. However, cyanobacteria dominated the fore-reef closest to toilets (62 ± 3 %) with highest reef-flat SOC, whereas hard corals dominated furthest away (63 ± 1 %), where SOC was lowest. To our knowledge, this is the first study that used SOC to detect local differences in sewage pollution. The results indicate that whilst (i) corals can maintain their dominance on overfished reefs, (ii) additional sewage stress may drive pronounced benthic shifts, highlighting the urgency to improve small island waste management.

2.2. Introduction

Island communities, such as those in the Pacific, have a particularly strong reliance on coral reef ecosystem services such as food, livelihoods and coastal protection. Often the high dependence on these services is coupled with a very low capacity to adapt to their loss (Burke *et al.* 2012), rendering these communities highly vulnerable to reef degradation. Modern influences and coastal population growth on Pacific islands have led to surges of non-traditional fishing methods (e.g. Hamilton *et al.*, 2012), declining water quality and land-use change (Zann, 1994), which are threatening coral reef integrity. An amalgamation of climate change and local stressors is often resulting in the replacement of hard corals by alternative benthic organisms, which frequently leads to a decline of structural complexity with associated reductions of ecosystem services (Pratchett *et al.*, 2014). Small island ecosystems are uniquely fragile to disturbance due to their close coupling with the effects of human inhabitants.

Knowing where to focus management depends on determining and extracting information on relevant key drivers of degradation at different localities. Whilst relatively simple methods for measuring herbivorous fish communities are well established, assessing nutrient and organic matter (OM) input remains challenging in areas with limited infrastructure due to difficulties regarding sample storage, processing and measurements. Studies have proposed suitable indicators of changes in water quality (Cooper et al. 2009; Fabricius *et al.*, 2012), but measurements are often static (e.g. macroalgal abundance, coral tissue thickness), and generally require laboratory facilities at some point (e.g. stable isotope analyses, exogenous sediment analyses – see Risk *et al.*, 2001). Furthermore, despite sewage-based OM input having been recognised as a key problem on reefs worldwide for many decades (e.g. Barnes, 1973), there remains a distinct lack of *in situ* studies that investigate its impacts (Wear & Thurber, 2015). Rapidly growing populations and limited infrastructure make sewage treatment a critical issue on small islands. To interpret ecosystem responses and trajectories that can provide important quantitative metrics for setting specific conservation goals, simple *in situ* indicators are required.

The current study extended existing *in situ* methods for determining local pollution by exploring the potential for sedimentary oxygen (O_2) consumption (SOC) rates to assess local anthropogenic OM input promptly in the field. In shallow-water reef environments with primary benthic cover by permeable sediments, intense benthic-pelagic coupling causes sediments to integrate OM concentration changes in the overlying water (Wild *et al.*, 2005). As key organic components of sewage are rapidly recycled in surface sediments (Wild *et al.*, 2008), elevated SOC rates should directly reflect recent sewage (OM) input. Sedimentary OM is less subject to short-term fluctuations than water column OM, implying that SOC indicates long-term processes more reliably than assessments of water parameters. If found to distinguish differences in local OM input, then SOC measurements have strong applicability to future studies in remote environments with limited infrastructure due to their simplicity and immediate results, thus offering a potential tool for island monitoring and research.

By measuring SOC alongside benthic and fish community assessments, this study aimed to investigate the roles of both overfishing and anthropogenic OM input in driving distinct benthic community assemblages of reefs fringing two small neighbouring barrier islands Ahus and Onetah in Papua New Guinea (PNG; Figure 2.1). Ahus Island is densely populated (*ca.* 700 people / ~ 2500 people km^{-2}) with a heavy dependency on marine resources; 77% of households rate fishing as primary income (Cinner, 2005) compared to the regional coastal community average of 29.5% (Pinca *et al.*, 2009). This dependency has resulted in high pressure on local reef fish populations, to such an extent that Ahus' fish biomass is now among the most degraded worldwide (MacNeil *et al.*, 2015). Additionally, Ahus lacks sewage treatment facilities, with raw sewage directly reaching the reef flat at specific points (from around ten beach toilets on the island's shoreline, located over the water at ca. 5 m from the shore), thus providing an ideal opportunity to investigate *in situ* impacts of anthropogenic OM input. Ahus' population has increased rapidly over the last decades; the local district's population grew by 36% between 2000 and 2011 (National Statistical Office, 2014), and consequently relative sewage-input and fishing pressure will have increased significantly. By contrast, Onetah (3 km east), is uninhabited, although its reefs also fall under Ahus' customary marine tenure as a fishing ground.

These study sites provided a unique opportunity to explore two islands within the same tenure system that exhibit different anthropogenic influences regarding sewage pollution. We hypothesised that (i) benthic assemblages are significantly different between Ahus and Onetah, but (ii) because of the customary marine tenure and accessibility, herbivorous fish communities are comparable. We thus further hypothesised that (iii) benthic community differences are significantly linked to proximity to beach toilets, and (iv) SOC rates will reflect higher OM degradation in closer proximity to beach toilets.

2.3. Materials and Methods

The two islands studied are located 5 km from the north coast of Manus Island, Northern PNG (Figure 2.1). Two sites were selected on the leeward side of Ahus Island (147° 6' E, 1°

56' S) directly adjacent to beach toilets ('Ahus BT'), and along the shore at 250 m from beach toilet influence ('Ahus non BT'). A third site was selected on the leeward side of uninhabited Onetah Island ('Onetah Control': 147° 8' E, 1° 57' S). Sites were consistent regarding exposure, orientation, bathymetry and distance from mainland. All fieldwork was carried out during May and June 2014.

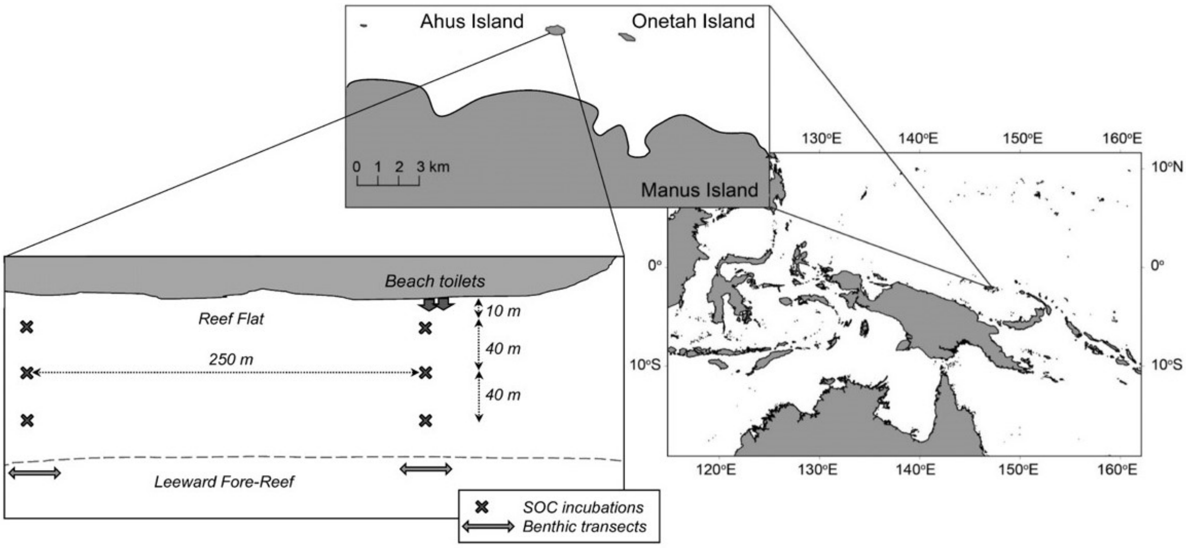

Figure 2.1. Map of study sites on the north coast of Manus Island, Papua New Guinea, including schematic diagram (bottom-left box) showing locations for sedimentary oxygen consumption incubations and fore-reef benthic transects for sites Ahus BT (right) and Ahus non BT (left).

To determine benthic community composition at the leeward fore-reef, 25 m transects (n = 3 site^{-1}) were deployed at 3 m depth parallel to and at 120–150 m distance from the shore. Cover type was recorded every 25 cm (n = 100 transect^{-1}) using the point-intercept method. Where cyanobacterial mats were observed, they were distinguished between growing over dead substrate or sand ('cyanobacteria'), and growing over live *Halimeda* spp. ('cyanobacteria on macroalgae'). Juvenile corals (< 3 cm) were counted within 0.25 m^2 quadrats (n = 10 transect^{-1}) using a GOBE Nightsea UV lamp for fluorescence detection (Piniak *et al.*, 2005). Herbivorous fish biomass was quantified using the distance sampling underwater visual census method (Labrosse *et al.*, 2002); two divers recorded abundances and fork length of all observed fish along 50 m transects (n = 6 site^{-1}) at each island's leeward fore-reef. Length and spacing of transects as well as movement patterns and extensive home ranges of some species precluded comparisons between the two Ahus sites. Data were converted to biomass using established species-specific length-weight relationships (Froese & Pauly, 2013). Herbivorous fishes were classified into four key functional groups which exhibit distinct roles of algal removal: browsers, grazers and detritivores, scrapers and small excavators, and large excavators and bioeroders (Green & Bellwood, 2009).

Due to proximity to OM input, the homogeneous shallow environment, and to document any potential changes from the shore towards the outer reef, SOC measurements were carried out on the reef flat at 10, 50 and 90 m from the shore (n = 8–10 distance^{-1} site^{-1}). Cut

50 ml syringes were used to collect 10 ml surface sediment cores (1 cm depth), which were placed into 160 ml glass vials and filled with water from the overlying water column. O_2 concentration was recorded prior to vials being sealed airtight, ensuring no air bubbles remained, and incubated *in situ* inside opaque bags for *ca.* 2 h (Onset HOBO® pendant temperature and light loggers confirmed that light was excluded), following which O_2 was re-measured. O_2 concentrations were measured using an O_2 optode sensor with a conductivity probe (MultiLine® IDS 3430, WTW GmbH, Weilheim, Germany, accuracy: ± 0.5 % of measured value) 1 cm above the sediment after the water was stirred. Temperature and salinity were monitored throughout to confirm consistency. O_2 consumption in control chambers containing only water from the overlying water column (n = 5-6 distance^{-1} site^{-1}) was averaged and subtracted from SOC rates. After accounting for incubation time, vial volume and control measurements, SOC values were calculated to $\mu g\ O_2\ cm^{-3}$ sediment h^{-1}.

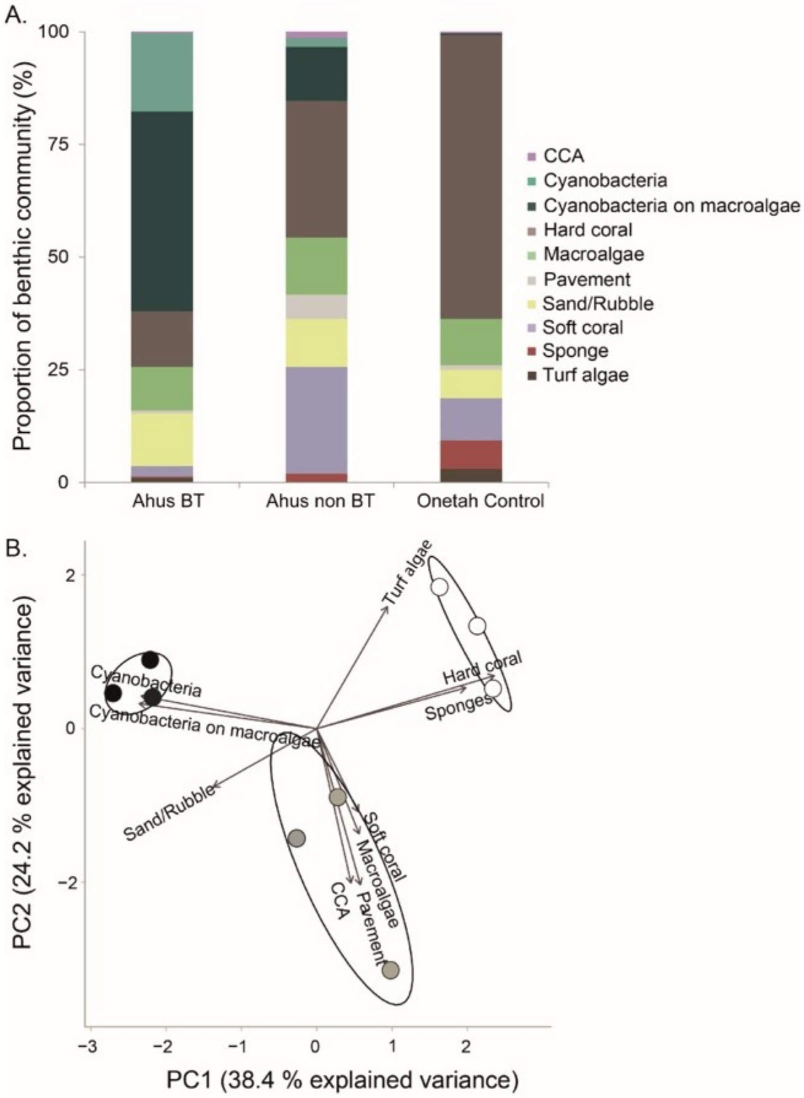

Figure 2.2. (A) Benthic community composition across the three sites. (B) Principal components analysis clusters the sites (Ahus BT = black circles, Ahus non BT = grey circles, Onetah Control = white circles) into distinct groups according to benthic composition of each transect (n=3 site^{-1}). The first (PC1) and second (PC2) principal components combined explain 62.6% of the variance.

To evaluate statistical differences between sites, benthic community transect data were entered into a principal components analysis (PCA) using the R *prcomp* (R base package version 3.1.1 - R Development Core Team 2013) and *ggbiplot* (ggplot2 package – Wickham, 2009) functions. Fish biomass data were tested by PERMANOVA using the Bray-Curtis similarity coefficient in PRIMER v.6 and PERMANOVA+ (PRIMER-E, Plymouth), with 'island' as the fixed factor, using Type 3 sums of squares and unrestricted permutation of raw data. Juvenile coral data were compared between sites by negative binomial regression using the R *MASS* package (Venables & Ripley, 2002), which amended previous overdispersion. SOC data were tested for independent and combined effects of 'site' and 'distance from shore' using two-way ANOVA hypothesis testing through the R *aov* function (R base package version 3.1.1). Lastly, dominant benthic groups of hard corals and cyanobacteria (inc. cyanobacteria on macroalgae) were compared between sites using one-way ANOVA. Shapiro-Wilk normality tests confirmed normality ($p > 0.05$) of SOC rates, hard coral and log (+1) transformed cyanobacteria data. Post-hoc Tukey HSD tests explored significant differences between groups.

2.4. Results

Benthic assemblages differed significantly between the leeward fore-reefs of all sites (Figure 2.2a). A PCA of the benthic communities emphasised these differences by distinguishing three distinct clusters according to site (Figure 2.2b), with the first two components explaining 62.6 % of the variation. The dominant benthic organisms hard coral and cyanobacteria were strongly associated to site (one-way ANOVA: hard coral – $F_{(2, 6)} = 50.03$, $p < 0.001$; cyanobacteria – $F_{(2, 6)} = 59.37$, $p < 0.001$), with hard coral decreasing and cyanobacteria increasing as sites increased in proximity to beach toilets. Directly in front of the beach toilets (Ahus BT), cyanobacteria dominated (62 ± 3%; mean ± SE), growing either on solid substrates (17 ± 2%) or on macroalgae. (44 ± 2%). Hard coral cover (12 ± 0.1 %), and juvenile coral abundances (1.3 ± 0.5 juveniles m^{-2}) were both low. Further from direct OM input (Ahus non BT), the reef was characterised by significantly lower cyanobacteria (14 ± 6%) and higher hard coral cover (30 ± 4%), though juvenile corals were still rare (1.3 ± 0.4 juveniles m^{-2}). At the furthest point from OM input

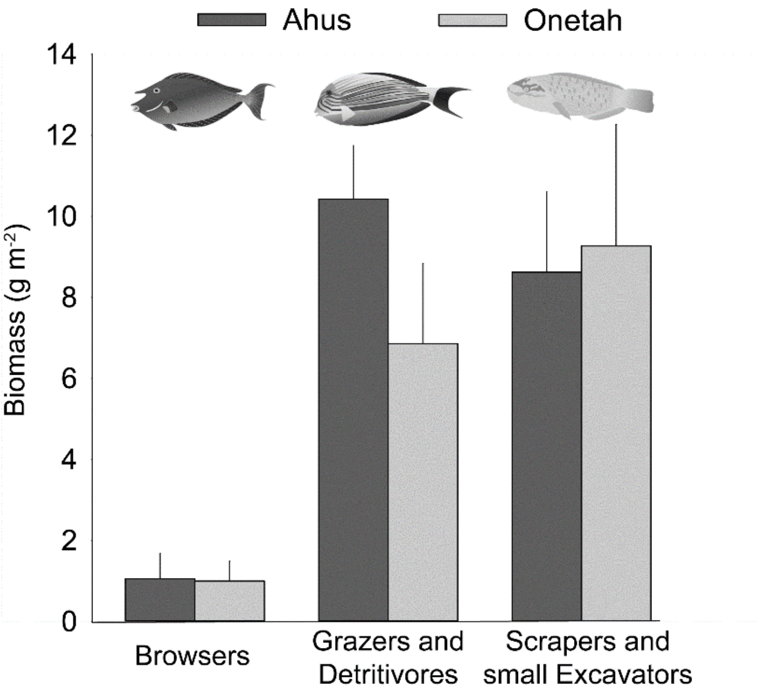

Figure 2.3. *Biomass of herbivorous fish functional groups; browsers, grazers (and detritivores), and scrapers (and small excavators), for each island. Large excavators/bioeroders were not observed, and thus are not included in the graph.*

(Onetah Control), coral cover was high (63 ± 1 %), and cyanobacteria were negligible (< 2 %), and juvenile corals (4.0 ± 0.5 juveniles m^{-2}) were significantly more abundant than at the other sites ($z = 2.3$, $p = 0.02$).

Distinct differences in benthic communities were not reflected in herbivorous fish populations; biomass was neither significantly different within functional groups nor in total between islands (PERMANOVA; $F_{(1,10)} = 0.32$, $p > 0.05$; Figure 2.3). However, SOC rates were greater at sites closer to beach toilets (two-way ANOVA; $F_{(2,77)} = 24.83$, $p < 0.001$; Figure 2.4), indicating higher OM degradation. Distance from shore did not affect SOC rates ($F_{(2,74)} = 0.04$, $p = 0.96$), and this did not vary among sites ($F_{(4,74)} = 2.30$, $p = 0.066$; Appendix A), indicating the potential of land-derived OM to affect adjacent reefs even when separated by a reef flat of at least 90 m.

2.5. Discussion

The results underline the strong potential effects of small island sewage-based OM input on the reef environment. Coral reef assemblages differed significantly between sites, with reefs closest to and furthest from the beach toilets dominated by cyanobacteria mats and hard corals, respectively. While herbivorous fish biomass was not different between the islands, SOC rates were greater at sites closer to beach toilets. As both islands show equal herbivorous fish biomass it is not possible to ascertain the specific contribution of herbivory relative to OM input on reef condition. However, the results suggest that anthropogenic OM input from sewage has a significant role in structuring benthic communities when herbivory remains consistent and low between sites.

2.5.1. Overfishing of herbivorous fish

The dependency of Ahus fishers on reef fish coupled with the rapidly growing human population promotes increasing use of non-traditional methods (e.g. night-time spearfishing) to maximise catches, thus intensifying pressure on already depleted resources. Total herbivorous fish biomass was consistently low (Onetah 17.1 ± 3.0 g m^{-2}, Ahus 20.1 ± 3.4 g m^{-2}), implying that Onetah's reefs are fished to the same extent as Ahus'. Herbivore biomass values are actually below notably overexploited Pacific Islands such as the Main Hawaiian Islands (> 30 g m^{-2} - Friedlander & DeMartini, 2002). Ahus' fish stocks are projected to require 59 years to recover if fishing were stopped (MacNeil *et al.*, 2015), and our results imply that recovery times will be similar at Onetah. Herbivorous fish communities play a central role in reef function and dynamics, and are important in maintaining reef resilience (Hughes *et al.*, 2007). Therefore, it is likely that these fished reefs are less able to resist and recover from other stressors (such as declining water quality), adding complexity to the interpretation of our findings.

2.5.2. Factors driving local benthic communities

The islands depict a common picture of overexploited fish communities and declining water quality. We suggest that the results allow for the following two interpretations: (i) even when herbivorous fish populations are heavily exploited, healthy hard coral dominated systems can be maintained when water quality is high, but (ii) under such reduced levels of herbivorous fish, OM input can have severe consequences for reef health.

Significant differences in both cyanobacteria abundance and reef flat SOC rates among sites (highest closest to beach toilets) indicate that OM input is driving cyanobacterial mat proliferation. In the Caribbean, a region also characterised by chronically low levels of herbivores (Roff & Mumby, 2012), OM degradation facilitates the release of sedimentary iron and phosphate, promoting mat development (Brocke *et al.*, 2015a). Similarly, organic carbon, phosphorous and iron input stimulated mat growth in Australia (Albert *et al.*, 2005). Once established, cyanobacterial mats release up to 79% of the total reef community dissolved organic carbon (DOC; Brocke *et al.*, 2015b), thus promoting further bacterial proliferation which can indirectly result in declining reef health through mechanisms such as increasing coral disease prevalence (Kline *et al.*, 2006). Furthermore, cyanobacteria reduce coral recruitment (Kuffner & Paul, 2004), supporting the observed juvenile coral densities, and exhibit some of the highest reef nitrogen fixation rates (Cardini *et al.*, 2014) which may further favour degradation of reef ecosystems.

2.5.3. SOC incubations as a simple and cost-effective monitoring tool

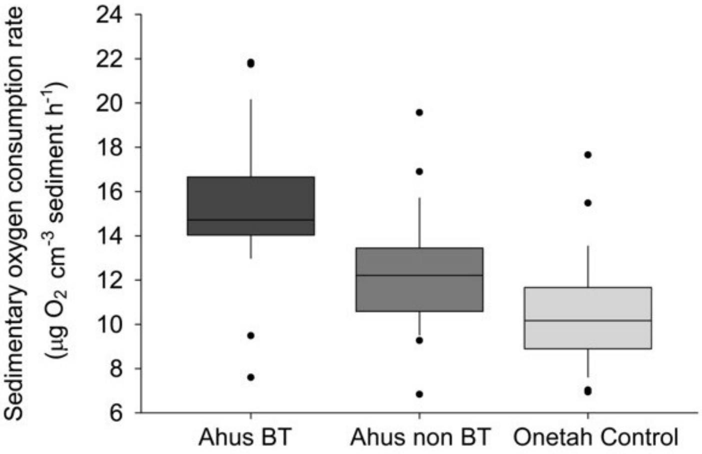

Figure 2.4*. Sedimentary oxygen consumption for each site.*

Elevated SOC rates indicate higher OM degradation at sites closer to beach toilets, demonstrating the ability of this method to identify sedimentary signals of localised sewage input on coral reef sediments. Interestingly, the lack of differences in SOC rates among different distances from shore implies that the OM homogeneously affects sediments up to at least 90 m from the source, perhaps due to tidal mixing across the reef flat (almost dry at lowest tide). Nonetheless, the capacity to distinguish significant differences at larger distance intervals (≥ 250 m) from sewage input shows the potential for rapidly comparing local pollution in situ in remote (island) situations where infrastructure and equipment are limiting. While this measurement in itself provides a useful proxy for comparing OM input at a local scale within a coastal zone, combining it with other measurements could allow for further interpretations. For example, subsequent analyses of sedimentary lipids such as coprostanol (Volkman *et al.*, 1999), stable isotopes of nitrogen, bacterial communities and/or exogenous (anthropogenically-derived) sediment contribution would allow identification of the pollution source (Risk *et al.*, 2001, 2009).

2.5.4. Ecological perspective and management implications

OM-driven proliferation of benthic cyanobacterial mats may stimulate a positively-reinforcing cycle whereby limiting nutrients become readily available (phosphate from sedimentary OM degradation, DOC and bioavailable nitrogen release from mats), and further promote reef degradation. As few organisms feed on cyanobacteria due to poor nutritional quality and chemical defences (Nagle & Paul, 1998), and mats inhibit key processes (e.g. coral recruitment - Kuffner & Paul, 2004), this cycle may become increasingly challenging to reverse. Considering that most reefs are overfished and projected recovery times are extensive (35 years on average - MacNeil *et al.*, 2015), it is critical to manage water quality to allow reefs a maximum chance of maintaining coral cover and facilitating recruitment, especially in small island environments which are particularly sensitive to anthropogenic impacts.

Management of fisheries and water quality should be accompanied by support of alternative livelihoods and food sources for island communities in a holistic management approach. A limitation of small coral islands is the scarcity of arable land (Catala, 1957) and infrastructure. One potential management tool that considers these needs and limitations is the installation of composting toilets, after due consideration of local cultural sensitivies. This could improve future food security of vulnerable communities by (i) improving production of land-based resources and (ii) promoting recovery of fish stocks by both decreasing reliance on marine resources and reducing nutrient and OM levels detrimental to reef health. Such holistic management approaches are likely to meet with more success than strict limitations on fishing effort that do not address the needs of island communities in terms of food security and livelihoods.

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CHAPTER THREE

THE RISE, DRIVERS AND CONSEQUENCES OF BENTHIC CYANOBACTERIAL MATS

This work is in preparation

Ford AK, Bejarano S, Nugues MM, Visser PM, Albert S, Ferse SCA. Reefs under siege – the rise, putative drivers, and consequences of benthic cyanobacterial mats.

Photo credits: Victor Bonito (center), Simon Albert (right)

3.1. Abstract

Benthic cyanobacteria have commonly been a small but integral component of coral reef ecosystems, fulfilling the critical function of introducing bioavailable nitrogen to an inherently oligotrophic environment. Though surveys may have previously neglected benthic cyanobacteria, or grouped them with more conspicuous benthic groups, emerging evidence indicates that they are becoming increasingly prevalent on reefs worldwide. Some species can form mats comprised by a diverse microbial consortium which allows them to exist across a wide range of environmental conditions. Once established, strong positive feedbacks (e.g. inhibition of coral recruitment, release of dissolved organic carbon) reinforce further reef degradation. This review evaluates the putative driving factors of increasing benthic cyanobacteria, and highlights previously overlooked implications of their proliferation, which extend beyond reef health and affect human health and welfare. The rise of cyanobacterial mats is particularly concerning in the face of ongoing global environmental change, including increasing sea surface temperatures, decreasing pH and declining water quality. While these environmental changes pose challenges for reef building corals, they exacerbate cyanobacterial growth rates and toxin production, placing physiologically plastic cyanobacterial mats at a considerable ecological advantage. Low palatability of cyanobacteria implies that herbivore management alone is insufficient to control the proliferation of mats, and must be accompanied by local measures to improve water quality and management of watersheds. Such efforts should focus particularly on areas where iron is at high concentrations in adjacent soil or in coastal sediment, as these may represent high-risk areas for mat development and persistence.

3.2. Introduction

Life as we know it would not exist without the earliest cyanobacteria that evolved around three billion years ago (Brocks *et al.*, 1999), introducing oxygen to the atmosphere. Marine cyanobacteria remain to this day an integral component of healthy ecosystems, offering critical functions such as nitrogen fixation and primary production (Charpy *et al.*, 2007). Such roles are particularly important within oligotrophic systems such as coral reefs, where they are also profusely embedded in algal turfs and microbial biofilms (Charpy *et al.*, 2012; Bender *et al.*, 2014; Cardini *et al.*, 2014). Some benthic cyanobacteria can form dense mats (hereon referred to as benthic cyanobacterial mats) with a diverse microbial consortium (Echenique-Subiabre *et al.* 2015). These mats usually inhabit a very small proportion of reef space (i.e. <1 %; Bednarz *et al.*, 2015), but have higher nitrogen fixation rates (8 – 110 mg nitrogen m^{-2} day^{-1}) compared to (cyano)bacteria associated with other benthic groups such as turf and fleshy algae (0.44 to 22.69 mg nitrogen m^{-2} day^{-1}) or scleractinian corals (0 - 9.75 mg nitrogen m^{-2} day^{-1}, Cardini *et al.*, 2014). While coral reef cyanobacteria are still often considered integral within the ecosystem, freshwater cyanobacteria are contrastingly notorious because of toxin production and their massive and problematic abundance following eutrophication (Bell & Codd, 1994). As emerging reports suggest the role of benthic marine cyanobacteria in coastal systems seems to be approaching that of their freshwater counterparts, the time may have come for us to approach them with more trepidation.

Recent coral reef research has primarily focused on the factors leading to shifts in the benthic community, whereby reef-building corals are replaced by alternative organisms which are generally considered less desirable. Whilst fleshy algae are most commonly recorded as dominating on shifted reefs (e.g. Hughes *et al.*, 1994), soft corals, sponges, ascidians, sea urchins, anemones, corallimorpharians (Norström *et al.*, 2009) and turf algae (Smith *et al.,* 2016) have also been implicated. We argue that benthic cyanobacterial mats should also be considered as major players on degrading reefs, where they can cover extensive areas (Figure 3.1) over relatively short timeframes (e.g. up to 30 km^2 within 2-3 months; Albert *et al.*, 2005). New genetic approaches have revealed that species richness in tropical cyanobacterial mats is very high and includes many unknown species (Echenique-Subiabre *et al.*, 2015). Tropical cyanobacteria probably also associate with several heterotrophic bacteria within mats, as shown for mats in other regions (Stal, 2012). Microbial consortia are likely to enhance production, growth and nutrient cycling over what single species or populations can achieve under similar environmental conditions, allowing mats to flourish under a wide range of conditions (Paerl *et al.*, 2000). Indeed, these mats exhibit high plasticity in their ability to modify the diversity and composition of their constituting microbial assemblages in response to environmental conditions (Echenique-Subiabre *et al.*, 2015).

So have benthic cyanobacterial mats previously been overlooked, or are they really becoming more of a problem? Increased awareness of the presence of cyanobacteria may account at least partially for the recent rise of reports (e.g. Duarte *et al.*, 2015). Previous underreporting may be a result of cyanobacteria remaining undistinguished from more conspicuous reef benthic groups such as algal turfs (Kuffner & Paul, 2001; Fong & Paul, 2011) which they often dominate (Fricke *et al.*, 2011), the organisms that they grow over (e.g. fleshy algae - Puyana & Prato, 2013), or abiotic substrate such as dead coral pavement, sand or rubble which is realistically never bare (Harris, 2015). Cyanobacterial mats can also exhibit bloom dynamics of a pulsing nature (Puyana *et al.*, 2015) that may not be prolonged or stable enough to be classified as phase-shifts, but that may catalyse lasting shifts from coral communities into alternative states. Nonetheless, there is an increasing number of reports of conspicuous cyanobacterial mats growing on tropical and sub-tropical coastlines worldwide (Table 3.1). This implies that the geographic extent and duration of cyanobacterial mats may have increased in recent years. Surveys conducted over exceptionally long temporal scales provide robust evidence that cyanobacterial mats are increasing on some southern Caribbean reefs while organisms such as scleractinian corals decline (de Bakker *et al.,* 2017). Arguably, temporary blooms of cyanobacterial mats might have been a natural phenomenon on reefs historically. However, blooms of the common mat-forming cyanobacterium *Lyngbya*, which were first restricted to the summer months, have become significantly more persistent in subtropical areas (e.g. Moreton Bay, Australia and Broward County, Florida; Albert *et al.*, 2005; Paul *et al.*, 2005).

In light of the increasing volume of reports, and the evidence for shifts towards cyanobacterial mats becoming increasingly common, the current review summarises the factors that may be facilitating this phenomenon in order to prioritise management practices. By further exploring the associated ecological and social consequences, this review aims at understanding the dynamics behind cyanobacterial mat proliferation which may shed some light on the factors influencing the probability of recovery of coral dominance vs. degradation towards alternative less desirable states. Similar to the better-studied freshwater cyanobacteria or planktonic harmful algal blooms, the occurrence of cyanobacterial mats can be strongly detrimental to both the marine ecosystem as well as to humans, and are challenging to manage. Though critical research gaps remain, this review provides tangible evidence that this emerging benthic phenomenon requires more attention from monitoring programs, researchers and managers alike.

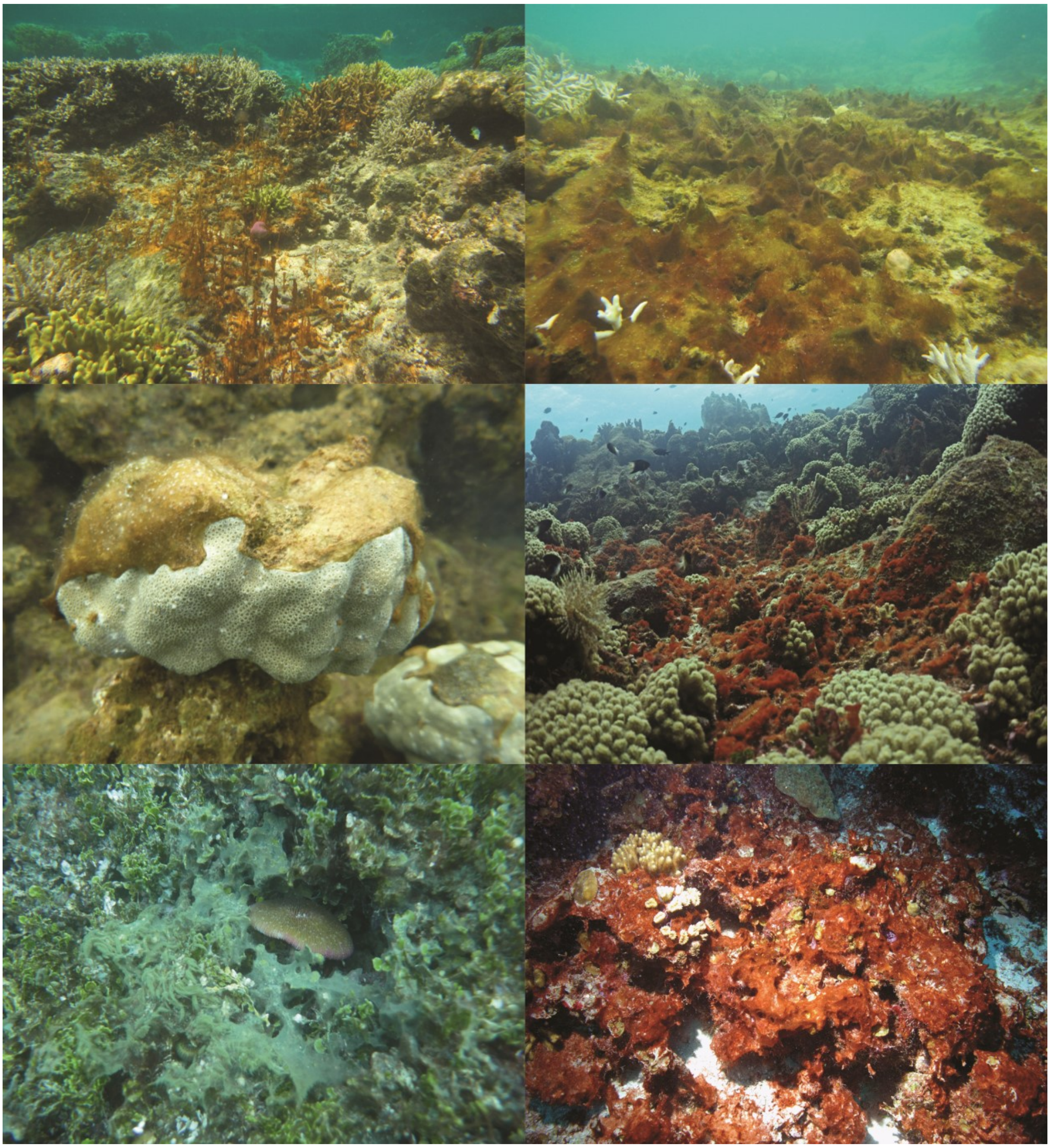

Figure 3.1. *Photographs of benthic cyanobacterial mats on coral reefs. From top-left clockwise: cyanobacterial mat at Coral Coast, Fiji (credits: Victor Bonito); cyanobacterial mat at Coral Coast, Fiji (credits: Victor Bonito); Oscillatoria-dominated mat at Curaçao (credits: Benjamin Mueller); Oscillatoria-dominated mat at Curaçao (credits: Maggy Nugues); cyanobacterial mat at Ahus Island, Papua New Guinea (credits: Amanda Ford); cyanobacteria mat at Marovo Lagoon, Solomon Islands (credits: Simon Albert).*

Table 3.1. Reports of benthic cyanobacterial mats from reefs worldwide, with genus/species identification and implicated drivers given where possible. Sections are left blank when no information is available.

Region	Location	Cyanobacterial mat extent	Species/genera encountered	Implicated drivers	Reference
Atlantic	Broward County, Florida (2002-2004)		*Lyngbya*		Paul *et al.* (2005)
Caribbean Sea	Barbados		Unknown	Domestic sewage	DeGeorges *et al.* (2010)
Caribbean Sea	Curaçao and Bonaire, Netherland Antilles	Mean cover 22.2% in 2013 (only 0.1% in 1973)	*Hydrocoleum*, *Lyngbya*, *Phormidium*, *Symploca*, *Oscillatoria*, *Tychonema*, *Schizothrix*, *Pseudanabaena, Dichothrix*	Degraded reef with low coral cover – eutrophied, high OM input	Brocke (2013); Brocke *et al.* (2015a); de Bakker *et al* (2017)
Caribbean Sea	Old Providence Island, Colombian Caribbean (2009-2010)	18 – 72%	*Okeania*, *Lyngbya*, *Symploca*, *Phormidium*, *Oscillatoria, Spirulina*	Warm waters, anthropogenic input (i.e. sewage)	Puyana *et al.* (2015)
Indian Ocean	Nosy Hara, Madagascar	Extensive mats from 3m and deeper	*Lyngbya*	Terrestrial freshwater and nutrient input	Obura (2009)

Table 3.1. cont.

Region	Location	Cyanobacterial mat extent	Species/genera encountered	Implicated drivers	Reference
Australia	Moreton Bay, Australia	Periodic dominance of shallow habitats since 1996	*Lyngbya majuscula*	High organic matter input (flooding), bioavailable phosphorous and iron, warm water, high light	Albert *et al.* (2005); Watkinson *et al.* (2005)
Pacific	Guam (1994)	Periodically dominate hundreds of meters of reef flat	*Schizothrix, Lyngbya, Hormothamnion*		Pennings *et al.* (1997); Nagle & Paul (1998)
Pacific	Manus Province, Papua New Guinea (2014)	Up to 66% at 3m depth		Untreated sewage in overfished system	Ford *et al.* (2017)
Pacific	Marovo Lagoon, Solomon Islands (2011)	Up to 100% at 6m		Eutrophication following toxic diatom and dinoflagellate bloom	Albert *et al.* (2012)
Pacific	Millennium atoll, Line Islands	Up to 71% (turf-cyanobacteria mixed assemblage)		Iron enrichment from shipwrecks	Kelly *et al.* (2012)
Pacific	Okinawa, Japan	26% *Annella reticulate* colonies affected at 20m depth	*Moorea bouillonii*		Yamashiro *et al.* (2014)
Pacific	Oundjo, New Caledonia (2004)	24% cover within lagoon			SPC unpublished data

Table 3.1. cont.

Region	Location	Cyanobacterial mat extent	Species/genera encountered	Implicated drivers	Reference
Pacific	Rose Atoll, American Samoa	Initially up to 90% cover, then remained at ~ 40% (*Jania* - cyanobacteria mixed assemblage)	*Lyngbya* and *Oscillatoria*	Ship grounding in 1995 and associated contaminant spill	Green *et al.* (1997); Schroeder *et al.* (2008)
Pacific	Sideia, Papua New Guinea (2006)	15% cover on back reef			SPC unpublished data
Pacific	Tsoilaunung, Papua New Guinea (2006)	15% on outer reef			SPC unpublished data

3.3. Putative factors promoting cyanobacterial mat proliferation

Whilst growth rates of most organisms are constrained within a given and often narrow range of conditions, cyanobacterial mats display characteristics that allow them to thrive under a multitude of environmental settings. Their physiological plasticity (Echenique-Subiabre *et al.*, 2015) provides them with a distinct advantage over most benthic organisms. Importantly, environmental changes associated with anthropogenic impacts often favour proliferation of cyanobacterial mats.

The integrity of many reefs worldwide is compromised by global environmental change, weakening reef-building organisms and generating newly available substrate easily colonisable by fast-growing cyanobacterial mats. Even on a reef where space is highly limited, cyanobacterial mats can overcome this constraint by growing directly over living organisms such as live coral and fleshy algae (Puyana & Prato, 2013; de Bakker *et al.,* 2017). Besides benefitting from newly available space and stress created by climate-change driven acute weather events (e.g. storms, thermal anomalies), cyanobacterial mats can profit directly from increased temperatures and unusual rainfall patterns (Paul, 2008; O'Neil *et al.*, 2012; IPCC, 2014). Cyanobacterium-induced coral diseases such as black band disease (BBD) become more prevalent with ocean warming (Richardson & Kuta, 2003). Increasingly acidic oceans, driven by rising atmospheric carbon dioxide, may stimulate marine cyanobacteria which have high photosynthetic demands (Levitan *et al.*, 2007). Cyanobacteria are also able to utilise bicarbonate ions as a carbon source (Badger & Price, 2003; Pearl & Paul, 2012; Visser *et al.*, 2016), and exhibit high genetic adaptability to changes in carbon availability (Sandrini *et al.*, 2016). A relative increase of *Lyngbya* within turf algal assemblages under a low pH and high temperature treatment provides further experimental evidence that future ocean acidification may favour cyanobacterial expansion (Bender *et al.*, 2014).

Exponentially growing coastal human populations in tropical regions are also having a profound effect on coastal marine environments locally, including increasing sewage input and nutrient runoff from land-use change and agricultural development (Burke *et al.*, 2012). Nitrogen-fixing cyanobacteria (e.g. *Lyngbya*) can compete for nitrogen sources while they are present, and fix it while they are limited (Paerl, 2008), implying that other nutrients are more critical for controlling their growth. Indeed, field and experimental manipulations have shown that nitrogen input does not promote cyanobacterial growth to the same extent as iron or phosphorous do (Ahern *et al.*, 2007). Consequently, changes that shift a system from phosphorous to nitrogen limitation (i.e. transitions from high to low N:P ratio) can favour cyanobacteria over other primary producers (Figure 3.2; Schindler, 1977; Kuffner & Paul, 2001).

Phosphorous can enter tropical reef systems via discharges of industrial wastewater, aquaculture, and terrestrial runoff from urbanised and agricultural land (Figure 3.2). Untreated sewage is a major issue particularly on small and remote inhabited coral reef islands (Ford *et al.*, 2017); 80 – 90 % of discharged wastewater in the Caribbean, Southeast Asia and the Pacific region is estimated to be untreated (UNEP/GPA, 2006). Alongside direct input, one pathway recognised to increase phosphorous levels is its release from surface sediments, where it otherwise remains bound with stable insoluble iron oxyhydroxides within the oxidised layer (Sundby *et al.*, 1992; Rose *et al.*, 2005). Following high organic matter (OM) input (e.g. from sewage) and/or low dissolved oxygen levels at the water-sediment interface, surface sediments become anoxic, leading to iron (III) reduction to bioavailable iron (II), and in turn releasing reactive phosphate and iron (Figure 3.2; Jensen, 1995; Brocke *et al.,* 2015a; Hanington *et al.*, 2016). A similar mechanism would apply following phytoplankton blooms (caused by eutrophication) which 'rain' OM onto the reef floor. This mechanism potentially explains a prolonged shift towards cyanobacterial mats with associated reef mortality following an extensive phytoplankton bloom (> 20 km^2) within a Solomon Islands lagoon (Albert *et al.*, 2012).

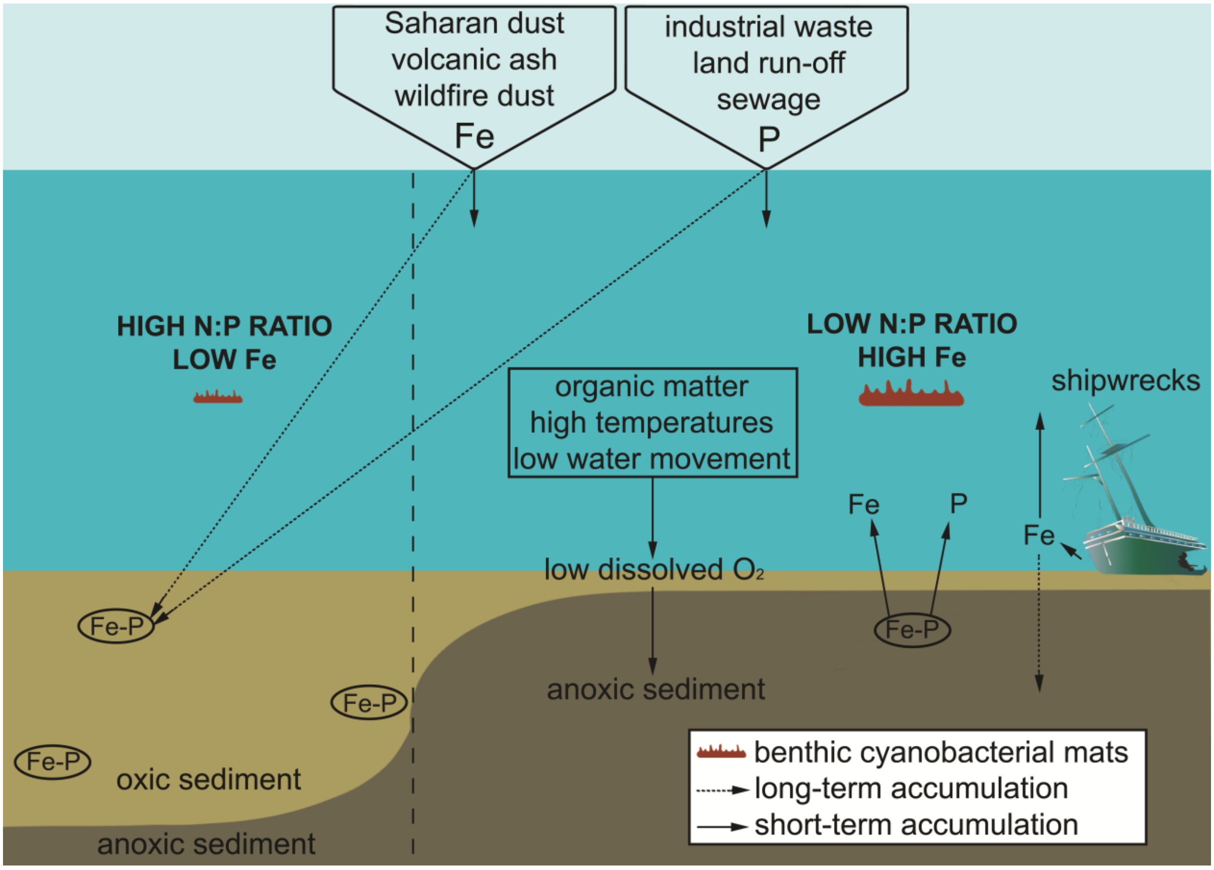

Figure 3.2. *Schematic diagram representing how sedimentary changes support the growth of benthic cyanobacterial mats, focusing on the roles of low dissolved oxygen (O_2) at the sediment-water interface leading to sediment anoxia and subsequent release of sedimentary iron (Fe) and phosphate (P). Some main external sources of Fe and P are included, with long-term accumulation within sediments and short-term accumulation in the water column differentiated.*

Alongside reactive phosphate, the associated sedimentary release of bioavailable iron (Figure 3.2) is likely important for mat development. At areas not naturally exposed to iron from Aeolian dust such as the Indo-Pacific, benthic cyanobacterial mats establish quickly following supply of iron to the water column, for instance, through shipwrecks or volcanic ash (Kelly *et al.*, 2012; Schils, 2012). Where iron is found within sediments, mat development is also stimulated by its release from anoxic sediments following flooding or phytoplankton blooms (Albert *et al.*, 2012; Hanington *et al.*, 2016). Blooms of common mat-forming *Lyngbya majuscula* (recently reclassified as *Moorea producens*; Engene *et al.*, 2012) in Moreton Bay have been attributed to increased iron availability from both catchment and marine sediment sources (Ahern *et al.*, 2005; 2007; Hanington *et al.,* 2016). As well as controlling growth, iron is critical for the nitrogenase enzyme which is responsible for nitrogen fixation (Berman-Frank *et al.*, 2001; Mills *et al.,* 2004; Ahern *et al.,* 2008). Iron concentrations differ regionally with the degree of exposure to Aeolian dust, ash from volcanic eruptions and emergent basaltic rock associated with historical volcanic activity, dust from wildfires and terrestrial run-off (Dubinsky & Stambler, 1996; Abram *et al.,* 2003; Roff & Mumby, 2012; Schils, 2012). Reefs in the central Pacific that are strongly iron-limited shift quickly from hard coral towards 'black reefs' characterised by mixed benthic assemblages of cyanobacteria, turf and fleshy algae and corallimorphs following ship groundings that introduce large amounts of iron (Kelly *et al.*, 2012). These seemingly iron-driven benthic shifts have persisted over long periods, and have had significant impacts on local fish populations (Schroeder *et al.*, 2008). Considering the rapid development of cyanobacterial mats following iron addition in areas usually limited in iron, and the capacity for iron to bind to phosphate in sediments (consequently controlling two limiting nutrients), it seems likely that iron-availability can determine the risk of an area to succumb to, or be prone to, benthic cyanobacterial mat dominance.

Top-down control of cyanobacteria is often obstructed by secondary metabolites (e.g. lyngbyatoxin-A and malyngolide) which reduce their palatability and deter grazing even in the presence of a healthy herbivore population (Thacker *et al.*, 1997; Capper et al. 2006ab, 2016). Abundance of cyanobacteria mats does not increase and can even decrease in the absence of grazers (i.e. within cages), suggesting that herbivores do not control their growth and/or that high levels of herbivory are indeed necessary for cyanobacteria to maintain dominance over fleshy algae (Wanders, 1977; Thacker *et al.,* 2001). Nonetheless, some mesograzers and a few reef fish species have been documented to graze on cyanobacterial mats directly or on foods experimentally coated in secondary metabolite extracts (see Table 3.2). The degree to which fishes feed selectively on cyanobacteria does however depend on their life stage (Paul *et al.*, 1990) and on exposure time and access to alternative food (Thacker *et al.*, 1997). Contrastingly, growth rates of cyanobacterial mats are significantly reduced in the presence of sea cucumbers both in aquaria (Uthicke, 1999; Michio *et al.*, 2003) and *in situ* (Moriaty *et al.*, 1985). Number of bacteria and concentration of photosynthetic microorganisms fell by 50 and 22%, respectively, within enclosures containing sea cucumbers when compared to controls in Madagascar (Plotieau *et al.*, 2013). This likely results from sea cucumbers feeding directly on mats (e.g. Sournia, 1976; see Table 3.2) and acting as bioturbators. Bioturbation by sea cucumbers contributes to the support of healthy sediment-associated microbial communities and the maintenance of sediment integrity (e.g. thickness of oxic sediment layers) under increasing nutrient and organic matter (OM) loads (Mactavish *et al.*, 2012). Overexploitation has depleted sea cucumber populations in several coastal areas across the Indo-Pacific (Anderson *et al.*, 2010), yet few *in situ* studies have addressed the ecological implications of this exploitation (but see Plotieau *et al.*, 2013; Lee *et al.,* 2017). This overexploitation and associated declines in sediment integrity may thus be responsible in part for increasing prevalence of cyanobacterial mats at coastal areas.

Table 3.2. Documented reports of cyanobacterial mat consumption by coral reef-associated fauna.

Group	Species	Feeding material	Type of study	Reference
Bivalve	*Tridacna maxima*	*Hydrocoleum kützing*	Tissue analysis	French Polynesia, New Caledonia, Vanuatu - Laurent *et al.*, (2008; 2012)
Crustaceans	*Cymadusa imbroglio, Menaethius monoceros, Parhyale hawaiensis*	*Lyngbya, Tolypothrix*	Laboratory	Cruz-Rivera & Paul, (2006)
Damselfish	*Pomacentrus amboinensis*	*Lyngbya*	Gut investigations	Marnane & Bellwood, (1997)
Damselfish	*Stegastes apicalis*	*Lyngbya*	Field observations	Klumpp & Polunin, (1989)
Emperorfish	*Lethrinus*	Mixed blooms - e.g. *Oscillatoria, Hydrocoleum, Anabaena*	Tissue analysis	New Caledonia - Laurent *et al.*, (2012)
Gastropods	*Haminoea cymbalum*	*Tolypothrix*	Laboratory	Cruz-Rivera & Paul (2006)
Gastropods	*Stylocheilus striatus*	*Lyngbya*	Laboratory	Cruz-Rivera & Paul (2002; 2006)
Gastropods	*Haminoea ovalis*	*Lyngbya, Tolypothrix*	Laboratory	Cruz-Rivera & Paul (2006)
Gastropods	*Trochus*	Mixed blooms - e.g. *Oscillatoria, Hydrocoleum, Anabaena*	Tissue analysis	French Polynesia, New Caledonia, Vanuatu - Laurent *et al.* (2012)
Holothurians	*Holothuria (Halodeima) atra*	*Oscillatoria limosa*	Field observations	Moorea – Sournia (1976)
Holothurians	*H. atra, Stichopus chloronotus*	Unidentified mat	Laboratory	Uthicke (1994)
Parrotfish	*Scarus schlegeli, Scarus rivulatus*	Mixed blooms - e.g. *Oscillatoria, Hydrocoleum, Anabaena*	Tissue analysis	New Caledonia - Laurent *et al.* (2012)
Parrotfish	*Chlororus sordidus, Scarus altipinnis*	Mixed blooms - e.g. *Oscillatoria, Hydrocoleum, Anabaena*	Tissue analysis	French Polynesia, Vanuatu - Laurent *et al.* (2012)

Table 3.2. cont.

Group	Species	Feeding material	Type of study	Reference
Rabbitfish	*Siganus fuscescens*	*Lyngbya* (only in absence of lyngbyatoxin-A)	Laboratory	Moreton Bay – Capper (2006b)
Rabbitfish	*Siganus argenteus* juveniles - medium (21 - 60 %) preference	*Microcoleus lyngbyaceus*	Laboratory	Guam - Paul *et al.* (1990)
Surgeonfish	*Ctenochaetus striatus*	Mixed blooms - e.g. *Oscillatoria, Hydrocoleum, Anabaena*	Tissue analysis	Vanuatu - Laurent *et al.* (2012)
Unicornfish	*Naso unicornis*	Mixed blooms - e.g. *Oscillatoria, Hydrocoleum, Anabaena*	Tissue analysis	French Polynesia, New Caledonia - Laurent *et al.* (2012)

3.4. Linking cyanobacterial mats to reef degradation

Cyanobacterial mats can be a symptom of recent reef degradation events resulting in freed space (Schroeder *et al.*, 2008), but can also push stressed systems towards alternative states (Albert *et al.,* 2012). The proliferation of cyanobacterial mats on coral reefs has serious direct and indirect effects on numerous reef organisms and ecological processes. Some mats overgrow and smother several different benthic organisms, including hard corals and fleshy algae (Ritson-Williams *et al.*, 2005; Puyana & Prato, 2013; de Bakker *et al.,* 2017). Subsequent tissue necrosis of overgrown organisms can occur as a result of oxygen deficiency, contact with allelopathic chemicals, tissue abrasion or light reduction (Puyana & Prato, 2013). Competitiveness of the cyanobacterium *Lyngbya bouillonii* against the massive coral *Porites lutea* is superior to that of fleshy algae *Dictyota dichotoma* (Titlyanov *et al.,* 2007). Other mats are specifically associated with certain organisms, where they are linked to specific infections such as black band disease (BDD) of corals (Kramarsky-Winter *et al.*, 2014). BBD is one of several diseases believed to play an important role in coral reef decline (Richardson, 2004), and is characterised by a localised mat progressing quickly over the coral's surface.

The presence of cyanobacterial mats also directly impairs coral recruitment, an ecological process essential for reef recovery and resilience to disturbances (McClanahan *et al.*, 2012). Recruitment success may be reduced by (i) coral larvae actively avoiding settling near to cyanobacteria due to negative settlement cues, or (ii) cyanobacteria actively killing newly settled corals (Kuffner *et al.*, 2006; Ritson-Williams *et al.*, 2016). *Lyngbya* have been implicated in reducing the recruitment success of both broadcast spawning and brooding corals (Kuffner & Paul, 2004; Kuffner *et al.*, 2006). Importantly, cyanobacterial mats tend to bloom at the same time of year when corals spawn, which generally occurs during the warmest months. In Fiji, for instance, both broadcast spawning and cyanobacterial blooms occur during mid-summer (Quinn and Kojis, 2008; Victor Bonito, pers. comm. 2016). At this critical time, the effects of cyanotoxins on coral recruits are strongly exacerbated by warmer temperatures (Ritson-Williams *et al.*, 2016). Large-scale inhibition of coral recruitment by cyanobacterial mats could have severe implications for the replenishment of coral populations.

Cyanobacterial mat proliferation can have direct impacts on reef fish assemblages. *Lyngbya* blooms reaching 10 to 37 % cover in Florida were associated with declines in both fish biomass and species richness (Baumberger *et al.,* 2008). A major die-off of juvenile rabbitfish *Siganus argenteus* and *Siganus spinus* was observed in Guam as reefs became dominated by a mixed-assemblage of *L. majuscula* and *Schizothrix calcicola* (Nagle, 1996; Nagle & Paul, 1998). This was also corroborated in aquaria where rabbitfish *Siganus fuscescens* chose to starve rather than to consume *L. majuscula* containing lyngbyatoxin-A (Capper *et al.*, 2006b).

The health of mature coral colonies can also be indirectly affected by the development of cyanobacterial mats which release considerable amounts of dissolved organic carbon (DOC) and bioavailable nitrogen (e.g. Cardini *et al.,* 2014; Brocke *et al.*, 2015b). Such amounts may be regarded insignificant when considering the coverage of cyanobacterial mats on healthy reefs (i.e. around 1% of the benthos, Charpy *et al.*, 2010; Bednarz *et al.*, 2015), but could be substantial when cyanobacteria bloom and predominate (i.e. over 50% of the benthos, Thacker & Paul, 2001). Both DOC and bioavailable nitrogen can shift the reef balance by favouring fast-growing primary producers (e.g. fleshy algae) over scleractinian coral. Island-wide surveys in Curaçao indicate that the abundance of benthic cyanobacterial mats was indeed negatively correlated with hard corals and positively correlated with fleshy algae (Brocke *et al.*, 2015a). At the organism-scale, increased DOC stimulates activity of coral-associated microbes within the coral mucus (Kline *et al.*, 2006; Morrow *et al.*, 2011), potentially leading to coral tissue hypoxia and subsequent mortality (Smith *et al.*, 2006). Bacteria within the coral mucus exhibiting the strongest growth responses to DOC are often pathogenic (Morrow *et al.,* 2011). Moreover, during night-time fermentation, certain cyanobacteria (e.g. *Oscillatoria*, Heyer & Krumbein, 1991) release easily degradable compounds including lactate, ethanol and acetate, which could further enhance heterotrophic metabolism and pathogenic microbes (Haas *et al.*, 2013). Similar processes are likely to apply in direct physical contacts between competing corals and benthic cyanobacteria. Coral (massive *Porites*) margins in contact with benthic cyanobacteria are characterised by a thick diffusive boundary layer and hypoxia at night, which in turn may facilitate cyanobacterial overgrowth of live corals (Jorissen *et al.*, 2016). Finally, increased levels of bioavailable nitrogen on reefs may lead to increased bleaching (susceptibility) in corals (Wiedenmann *et al.,* 2013; Rädecker *et al.*, 2015), resulting in reinforcing feedbacks and favouring reef degradation (Figure 3.3).

Cyanobacterial mats are not limited to shallow reef environments and occur at depths of up to 40 m (e.g. Curaçao – de Bakker *et al.*, 2017). Within phytoplankton communities, cyanobacteria are the group which can grow best under low light conditions (Mur *et al.*, 1999). It is thus plausible that cyanobacterial mats could perform well in mesophotic reefs, especially in comparison with other organisms such as fleshy algae. Such findings challenge the potential for the 'Deep Reef Refugia Hypothesis' (Bongaerts *et al.*, 2010), which proposes that deeper corals that are less affected by heat and light stress could restock degraded shallow areas in the future. Although vertical genetic connectivity supports this hypothesis for some coral species (Bongaerts *et al.*, 2017), if the negative effects of cyanobacterial mat proliferation extend to deeper reefs, the anticipated health of these systems may be compromised.

3.5. 'Social-ecological traps' associated with cyanobacterial mats

Benthic marine cyanobacteria may pose direct threats to human health, similar to their freshwater counterparts (e.g. Bell & Codd, 1994). Cyanobacterial blooms affecting Pacific island inshore reefs over the summer have been identified as causative agents of ciguatera-like outbreaks (Laurent *et al.*, 2008). Instead of containing the common ciguatera causative agent, (i.e. the dinoflagellate *Gambierdiscus*), these mats were dominated by *Hydrocoleum*, a common cyanobacterium within tropical mats (Abed *et al.*, 2006; Echenique-Subiabre *et al.*, 2015). *Hydrocoleum* was subsequently found to produce cyanotoxins with very similar characteristics to cigua- and paralysing toxins (Laurent *et al.*, 2008). Several fish species, some of which are prime targets of fisheries, carried the cyanotoxins, and giant clams were also intoxicated (see Méjean *et al.*, 2010, Table 3.2). A subsequent study including New Caledonia, French Polynesia and Vanuatu confirmed that the link between benthic cyanobacterial mats and ciguatera-like sickness is rather wide-spread (Laurent *et al.*, 2012). An estimated 500,000 Pacific islanders have suffered from ciguatera symptoms between 1973 and 2008, with a 60% increase from 1973-1983 and 1998-2008 (Skinner *et al.*, 2011). A human fatality has also been attributed to eating lyngbyatoxin-A-contaminated green sea turtle meat (Yasumoto, 1998). People in contact with coastal areas affected by benthic cyanobacterial blooms (e.g. bathers, fishers) have also commonly reported severe dermatitis and asthma-like symptoms during blooms of *Lyngbya* (Osborne *et al.*, 2001). These findings underline the importance of identifying management practices that can control causal organisms.

Rapidly growing coastal populations will continue to increase nutrient and OM input into coastal waters over the coming decades. In the absence of wastewater treatment and land-use management, poor water quality will likely facilitate benthic cyanobacterial blooms which may result in profuse coral mortality. Concomitant with the loss of live coral, structural complexity can be reduced, thus leading to a dangerous erosion of the capacity of reefs to protect shorelines from oceanic wave energy (Sheppard *et al.*, 2005). Flattening of coral reef architecture may also limit the availability of physical refugia for associated reef fishes and invertebrates, which could also diminish the reef's potential to sustain fisheries (Pratchett *et al.*, 2014). The accumulation of ciguatera-like toxins in fishes in connection to cyanobacterial mats may pose further limits to the utilisation of fishery resources. The potentially impaired capacity of reefs to sustain productive fisheries (Bell *et al.*, 2009) may intensify the use of fishing practices that allow for disproportionally large catches (e.g. nighttime spearfishing) and are often destructive (e.g. blast or cyanide fishing). Furthermore, as coastal communities are faced with degrading reef ecosystems and associated marine resources, they may resort more to terrestrial resources such as agriculture, leading in turn to more nutrient run-off (Figure 3.3). These practices can promote a self-reinforcing cycle that ultimately results in a social-ecological trap (Cinner, 2011) with strong positive feedbacks. Such traps have been previously identified for reefs that become heavily dominated by fleshy algae. Direct escape routes through which fleshy algal dominance can be reversed include adaptive fisheries management (Mumby *et al.*, 2006; Hughes *et al.*, 2007; Cinner, 2011). When positive feedbacks on degrading reefs are strong, 'shock' events (e.g. storms) may enable reefs with well-managed herbivore populations to reset by clearing space for coral recruits to settle and shift the system back towards a more desirable state (Graham *et al.*, 2013). However, if factors are in place to facilitate cyanobacterial mat proliferation, cyanobacteria would rapidly pre-empt bare space regardless of the presence of healthy herbivorous fish assemblages, thus truncating coral recruitment. Supporting healthy and diverse herbivorous fish assemblages through local fishing regulations may therefore be insufficient to counteract cyanobacterial proliferation. As well as by the inhibition of coral recruitment, positive feedbacks are further strengthened by increasing bioavailable nitrogen, DOC and OM, thus reinforcing reef degradation once cyanobacterial mats are established or have bloomed (Figure 3.3). Consequently, escaping a social-ecological trap whereby cyanobacterial mats have developed extensively, along with their associated ecological effects, may be very challenging. Management may thus have to go beyond a focus on herbivorous fishes and explicitly address other organisms capable of hindering cyanobacterial mat proliferation, such as sea cucumbers, as well as changing land-use practices leading to, and in turn driven by reef degradation. Managing reefs with an integrated approach to build resilience to climate change impacts (e.g. McClanahan *et al.*, 2012) may also be beneficial in promoting resilience against the initiation and establishment of cyanobacterial mats after disturbances.

3.6. Avoiding tilting reefs towards 'the slippery slope to slime'

Coral reefs and their associated ecosystem services would be better conserved if environmental conditions facilitating bloom development and longevity can be prevented. In concert with global actions, local management practices could reduce their likelihood and temporal duration in a relatively cost-effective manner. In particular, it seems critical that systems do not enter a low N:P ratio, and that iron concentrations remain negligible. Thus, where possible managers must reduce the level of phosphate and iron of terrestrial origin entering reefs which are associated to global changes in agricultural development and land-use change. This could be achieved by for example limiting the use of certain fertilizers, reducing soil erosion, and protecting mangroves. These measures can result in improved water quality and could limit nitrogen-fixing cyanobacterial growth as well as nitrogenase enzyme activity. Nutrient limitation can in turn suppress the otherwise strongly stimulating effects of increasing carbon dioxide and water temperatures on cyanobacterial growth (Visser *et al.*, 2016). The latter may thus indirectly reduce the effects of climate change that cannot be tackled at the local level.

Nutrient and OM input can trigger the release of iron and phosphate following oxygen depletion within sediments (Brocke *et al.*, 2015a; Hanington *et al.*, 2016). Targeted management of nutrient and OM input is thus particularly important in areas where iron is already present (e.g. in volcanic areas, reefs exposed to Aeolian dust, near to agricultural land). Sewage is a major source of nutrients and OM, and improved sewage treatment can reverse cyanobacterial mats to grazable algal turfs (e.g. in Barbados - DeGeorges *et al.,* 2010). Considering the nutrient-poor condition of soils on for example coral islands (Catala, 1957), composting toilets that recycle essential nutrients for use on land could yield large improvements in coastal water quality and food security for local communities. Where composting toilets are not feasible or culturally accepted, local management efforts should be dedicated to incinerating and/or physically removing waste products on small islands (Lindström, 2007).

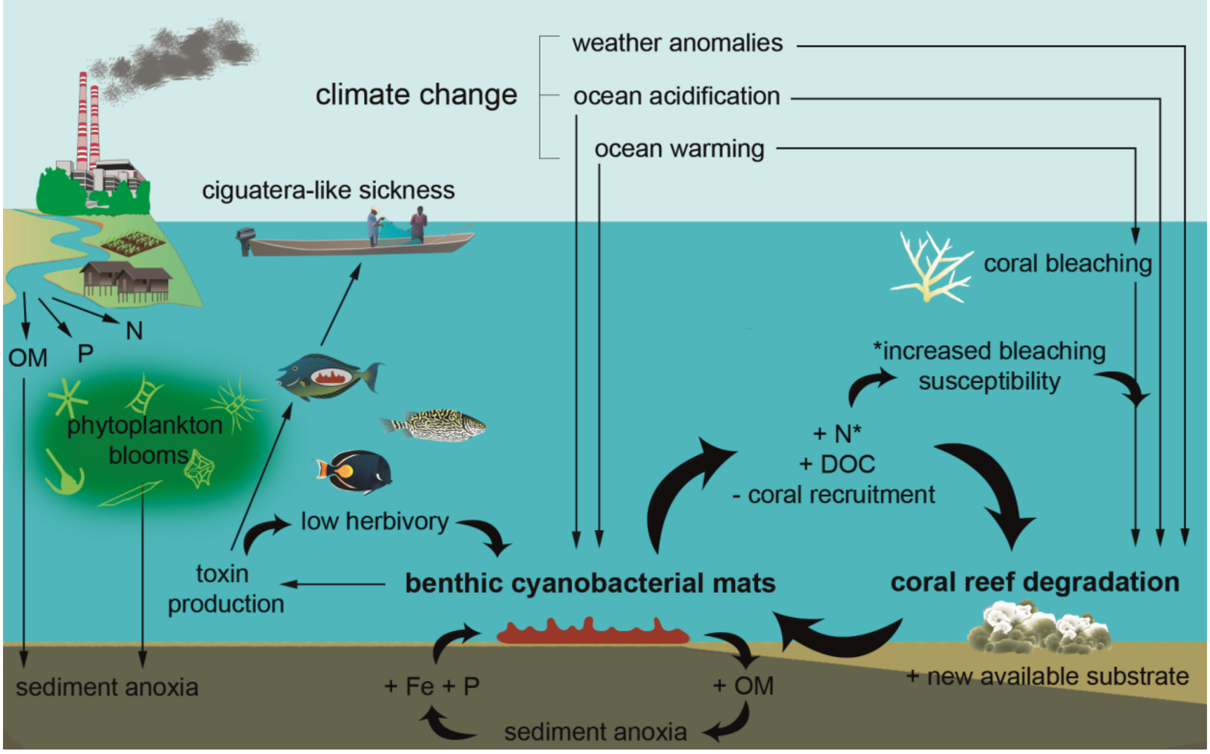

Figure 3.3. Schematic diagram showing the putative local and global drivers of benthic cyanobacterial mat growth on coral reefs, as well as the associated ecological consequences. Direct positive feedbacks that reinforce reef degradation and benthic mat growth are represented by thick curved arrows. Reef degradation will in turn drive coastal communities increasingly towards land-use changes such as agricultural development, further facilitating nutrient release and reinforcing the cycle. Abbreviations within the figure: N=nitrogen, DOC=dissolved organic carbon, Fe=iron, OM=organic matter, P=phosphate.

Sediment-feeding sea cucumbers may have a potential role in alleviating the growth of cyanobacterial mats in coastal environments. Though there is limited knowledge of the ecological implications of their removal from the ecosystem, studies suggest that this can have profound effects on sediment integrity and microbial mat formation (e.g. Uthicke, 1999). Their bioturbation activity likely moderates the development of anoxic sediment conditions that would otherwise facilitate the release of iron and phosphate. Experimental manipulations should quantify densities of sea cucumbers that are able to maintain sediment integrity and decrease formation of cyanobacterial mats. Considering that sea cucumbers are heavily exploited throughout the Indo-Pacific, a measure that could potentially safeguard their function would be the enforcement of periodic or rotational harvesting (Plagányi *et al.*, 2015). These measures may reduce the likelihood of cyanobacterial mat development in coastal areas, but managers must take into consideration alternative livelihoods for dependent fishers.

Though current knowledge implies that management of reef fish communities alone would be futile in counteracting cyanobacterial mats, *in situ* observations of fish feeding may find more novel, opportunistic species to protect in the future. Biomass of some surgeonfish and parrotfish species counterintuitively increased following the Rose Atoll oil spill and subsequent shift towards a cyanobacteria–turf algae mixed assemblage (Green *et al.*, 1997). Video observations aimed at quantifying herbivory during cyanobacterial blooms may identify opportunistic feeding on cyanobacteria by some fish species, similar to how novel species have been recorded consuming fleshy algae (Bellwood *et al.,* 2006). This knowledge could support protective measures aimed at regulating the fishery of important consumers of cyanobacteria at least where blooms are more likely (e.g. where iron levels are high) or prevalent. Herbivorous fish species may vary greatly in their sensitivity to cyanotoxins, and prior or repeated exposure may even allow for some adaptation (Thacker *et al.,* 1997; Capper *et al.*, 2006a). Trade-offs between growth and defence result in changes of anti-herbivore toxin production in fleshy algae growing in different water qualities (van Alstyne & Pelletreau, 2000). Studies into functional genes should identify whether environmental gradients also drive differences in harmful toxin production alongside the recognised changes in mat composition and diversity (Golubic *et al.*, 2010; Echenique-Subiabre *et al.*, 2015). Such patterns would suggest predictable differences in cyanobacteria palatability with water quality management or over environmental gradients. Although specific studies are currently scarce, toxin production is generally considered to increase with conditions that favour cyanobacterial growth, such as increased temperature (Kaebernick & Neilan, 2001).

Research attention should be directed to clarifying the role of cyanobacterial mats as symptoms or drivers of reef degradation. Benthic monitoring surveys need to improve their capacity to distinguish benthic cyanobacterial mats from other benthic groups. Whenever possible different cyanobacterial morphotypes should be recorded separately. This increased level of detail in benthic surveys will allow the detection of changes in benthic cyanobacterial communities. This in turn will be informative regarding their potential as a bioindicator of coral reef degradation. A study on Colombian reefs, for instance, suggested that >15% benthic cover of cyanobacteria indicates degradation (Puyana *et al.*, 2015). As overgrowth does not always lead to the death of the underlying organism, studies should identify the characteristics of coral-cyanobacteria contact. Surveys of cyanobacterial mats with a higher resolution should not be limited to shallow water, but also include mesophotic reefs (i.e. deeper than 30 m) which could play a key role in replenishing degraded shallow reefs in the future (Bongaerts *et al.*, 2010). Detailed characterisation of cyanobacterial mats is also important to predict future outbreaks of ciguatera-like sickness (Laurent *et al.*, 2008, 2012). Concurrently, to improve the understanding of the link between the sickness and cyanobacterial blooms in public health agencies, samples of mats but also from fish markets should be collected for identification and analyses to assess human pathogenicity where significant cyanobacteria cover is observed.

3.7. Concluding remarks

While an increase in awareness of the presence of cyanobacteria may account partially for the recent increase of reports, these mats appear to play an important role in the degradation of coral reefs. The proliferation and establishment of cyanobacterial mats carries important implications for ecosystem and human health. A multitude of factors are facilitating mat development and longevity, including increasing availability of space on degrading reefs and declining water quality, with areas rich in iron particularly at risk. Projected climate change conditions will favour growth of cyanobacterial mats while limiting many other benthic organisms. Systems where human populations and reefs are closely linked and that experience cyanobacterial blooms may be particularly prone to enter social-ecological traps with strong positive feedbacks. Not only can these traps threaten ecosystem services and human wellbeing, but they can be very challenging to escape from. We identify four key research areas that have been previously overlooked and present opportunities for novel future research. First, to prioritise local actions that minimise development and longevity of cyanobacterial mats, the relative contributions of different components of environmental change on cyanobacterial prevalence and toxicity require further experimental testing. Secondly, opportunistic consumption by reef fishes needs to be explored where cyanobacterial mats have bloomed, to identify species which management should target in high risk areas. Thirdly, experimental manipulations should quantify densities of sea cucumbers that can decrease the formation of cyanobacterial mats to inform managers of minimum stock sizes and maximum sustainable yields. Lastly, the relative importance of cyanobacteria as a driver or symptom of coral reef degradation needs to be better understood, which can be achieved by improved resolution of monitoring at large spatial scales and across depth gradients. Considering the serious risk that benthic cyanobacterial blooms pose directly to human health as well as the future of reefs and their associated ecosystem services, further focused research and resources for this topic are important.

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CHAPTER FOUR

INCREASING LOCAL HUMAN IMPACTS MODIFY ENVIRONMENT-BENTHOS RELATIONSHIPS

This work is in preparation

Ford AK, Norström AV, Jouffray JB, Nugues MM, Moore BR, Bejarano S, Wild C, Magron F, Ferse SCA. Local human impacts affect predictability of impacts from global environmental change on Pacific Island coral reef assemblages.

4.1. Abstract

Over half of all coral reefs are easily accessible to human populations, yet the role of increasing coastal populations on benthic reef assemblages is still debated. Do increasing local human impacts lead directly to reef degradation or ecological reorganisation? Considering this debate, we investigated the role of contrasting levels of local human impact using a spatially extensive data-set spanning 182 reefs around 63 inhabited Pacific islands. Human density was used as a proxy for local human impact level, using a threshold of 25 people km^{-2} reef, and we investigated its role in (i) driving alternative benthic states, and (ii) affecting benthic assemblage relationships to various predictors (e.g. spatial and physical attributes, local features). By addressing these questions, we examined how local human impacts may influence benthic responses to global change-related stressors. Field surveys collected data on physical parameters, benthic assemblages and fish communities, and additional data on degree heating weeks (DHW) and storm exposure were extracted from public repositories. Spatial and physical predictors had high explanatory power at reefs exposed to relatively lower human impacts, but were inadequate as human impacts increased. Conversely, different levels of local impacts did not affect the explanatory power of models based on local features. Relative importance of predictors was distinctly different according to the level of local impacts. Reef depth, latitude (collinear with DHW), scraper biomass and storm exposure were of highest importance in structuring reefs exposed to low human impacts. Contrastingly, above the threshold of 25 humans km^{-2} reef, grazer biomass and local human density emerged as the strongest predictors of benthic assemblages. These results emphasise that context-specific reef management is of paramount importance. Furthermore, whilst future impacts of global stressors on benthic assemblages and associated ecosystem service provision are predictable at reefs exposed to low human impacts, this predictability is strongly compromised as human impacts increase and in turn where human dependency on future ecosystem services is highest.

4.2. Introduction

The simultaneous occurrence of various stressors from climate change, expanding human populations and globalisation are driving significant alterations in coral reef benthic community structure and function (Hoegh-Guldberg *et al.*, 2007; Ban *et al.*, 2014). Globally, the intensity of thermal anomalies, unusual weather patterns and storms are increasing with climate change (Goreau *et al.*, 2000; Cai *et al.*, 2014; Pachauri *et al.*, 2014; Gattuso *et al.*, 2015; van Hooidonk *et al.*, 2016), and the recovery window between events is relentlessly narrowing (Donner *et al.*, 2009; Riegl *et al.*, 2013). Locally, rapidly expanding coastal communities and land-use changes are reducing water quality, whilst gear modernisation and improved market access are promoting overexploitation of reef fish (Wilkinson, 1999; Sabetian & Foale, 2006; Brewer *et al.*, 2012, 2013; De'ath *et al.*, 2012; Hamilton *et al.*, 2012; Lindfield *et al.*, 2014). Cultural change in regions such as the South Pacific is furthermore in many cases undermining effective, traditional management (Ruddle, 1993). Despite emerging complexities of the roles and interplays of various stressors, the overall response is a reduction in biodiversity and ecosystem integrity. Following perturbations systems can undergo regime shifts whereby there are long-lasting transitions in ecosystem structure and function (Holling, 1973; Mollmann *et al.*, 2014). Aside from the frequently described coral reef regime shift from hard coral to fleshy algae (e.g. Hughes 1994) there is a range of possible configurations that can occur including for instance dominance by algal turfs, cyanobacterial mats or soft corals (Norström *et al.*, 2009; Albert *et al.*, 2012; Jouffray *et al.*, 2014). However, most reefs may exist in a partially degraded state somewhere between distinct regimes (Bruno et al., 2009), perhaps undergoing ecological reorganisation within the hard coral community but not shifting into alternative organisms (Graham *et al.*, 2014). Such functional shifts are a consequence of variable interspecies susceptibilities whereby susceptible corals (e.g. acroporids) are replaced by massive or opportunistic types (Loya *et al.,* 2001; Fabricius *et al.*, 2005; Côté & Darling, 2010; Van Woesik *et al.*, 2011; Riegl *et al.*, 2013). An improved understanding of regime and functional shifts within coral reef benthic communities is critical for the future protection of these ecosystems and their associated services.

A basic principle of ecology is the ability to both predict and explain ecosystem structure given sets of predictors such as environmental and physical factors (Peters, 1991; Guisan & Zimmermann, 2000). Predicting benthic community structure can not only help predict the vulnerability to disturbances, but also the composition of associated fish communities and future provision of ecosystem services (Wilson *et al.*, 2006; Pratchett *et al.*, 2008; Bruno *et al.*, 2013). Optimising large-scale spatial predictive models is thus important for conservation and management prioritisation and planning (Guisan *et al.*, 2013; Kennedy *et al.*, 2013). However, there is complexity behind designing such models for benthic coral reef assemblages. For example, whilst models based on biophysical features such as sea surface temperature, chlorophyll content and wave energy have strong power in predicting benthic assemblages at remote reefs, this power is lost at reefs close to coastal human populations (Williams *et al.*, 2015a). Such a finding suggests that local human populations affect natural biophysical relationships within benthic coral reef communities.

It is often assumed that keeping local human impacts (e.g. fishing and nutrient input) to a minimum will support high herbivorous fish biomass, hence consistent herbivory, and avoid accelerated algal growth rates (Littler *et al.*, 2006; Mumby *et al.*, 2006; Smith *et al.*, 2010). Increasing local human population density can drive strong decreases in reef fish biomass (Williams *et al.,* 2015b), and has been found to correlate significantly with decreasing hard coral and increasing algal cover (Smith *et al.,* 2016). When direct relationships between local human populations and benthic assemblages are very weak (Bruno & Valdivia, 2016) or seemingly absent, ecological reorganisation and homogenisation within the coral community may have occurred (Côté & Darling, 2010; Riegl *et al.*, 2013; Graham *et al.*, 2014). This reorganisation can decouple natural relationships to biophysical and environmental features (Williams *et al.*, 2015a). It is important to consider that most reefs are in some way touched by humans, with human populations ever-expanding in their size and range. 58% of reefs are now within 30 minutes' travel time from human populations (Maire *et al.*, 2016). Human populations greatly range in density and reef usage (e.g. depending on marine reliance), thus exhibiting profoundly different intensities of impacts. These reefs directly in front of and used by human populations are critical for millions of humans worldwide, providing up to 98% of consumed animal protein in regions such as the Pacific Islands (Bell *et al.*, 2009). The role of human proximity as a disruptor of the biophysical-benthic structure relationship has been poorly studied. Considering that most reefs are now accessible to and influenced by local human communities at a variety of intensities, it is important to go beyond comparing how remote and 'touched' reefs differ. Thus, at reefs identified as important for human communities we must investigate the role of different intensities of local anthropogenic interference.

Here, we ask whether different levels of human impact disrupt the predictability of benthic community assemblages. To address this, we focus on 182 reefs distributed across 63 tropical Pacific islands with varying levels of anthropogenic interference. We started by identifying benthic assemblages that differ in their predominant benthic functional group(s) throughout the region. Then we categorised these reefs into low and high levels of local human impact based on relative local human density and explored any direct links between local impacts and benthic regimes. Finally, we investigated how well the spatial distribution of these assemblages is explained by different models for reefs exposed to contrasting levels of local human impacts. As explanatory models, we used various combinations of predictors (spatial and physical, local features) as well as allowing the best predictor combinations to be chosen by model selection techniques. We hypothesised that higher local human impacts (i) would not directly drive alternative benthic states, but (ii) would result in a shift in the relative importance of predictors towards those associated with local conditions. Particularly, we expected (iii) that higher local impacts would dissociate relationships between benthic assemblages and their physical environment, in turn compromising the ability to predict future outcomes of global climate change-related stressors.

4.3. Methodology

4.3.1. Site characteristics and sampling design

A total of 182 reefs across 63 locations within 17 different Pacific Island countries and territories were surveyed once between 2003-2008 (Figure 4.1), within the framework of the Pacific Regional Oceanic and Coastal Fisheries Development Programme (PROCFish/C/CoFish) under the auspices of the Pacific Community (SPC) (for sampling methodology and rationale, see Appendix Bi and Pinca *et al.*, 2009). Reef fish and benthic communities were monitored at reefs within each site, and landing surveys quantified fisheries catch. Fishing grounds for each site were delineated from information given by local fishers. Total reef area (km^2) within each site's fishing ground was then quantified from satellite images, allowing for subsequent calculation of human population (total population within villages with access to the fishing ground) and annual fisheries catch relative to reef area (i.e. local human density and relative finfish catch).

4.3.2. Field surveys

Reef fish communities were measured using the distance-sampling underwater visual census method along 50m transects (described in Labrosse *et al.*, 2002). Data on abundance and body length were recorded to species level for herbivorous fish. Counts were converted to biomass (g m^{-2}) for each species from established length-weight relationships (Kulbicki *et al.*, 2005) and averaged across transects within each reef habitat type. Benthic cover data was obtained using the medium-scale approach (described by Clua *et al.*, 2006). The method is based on a semi-quantitative description of 10 quadrats of 25 m^2 (5 x 5 m) laid down on each side of the 50 m transects used for reef fish surveys (500 m^2 per transect in total). Surveyors first recorded abiotic and live coral substrates (e.g. sand, rubble, rocky slab and boulders, and hard coral - live, bleached and long dead, with live coral divided into various morphologies e.g. branching, massive). Each component was quickly estimated using a semi-quantitative scale, estimating in units of 5% and ranging from 0 to 100%. Secondly, groups growing on the substrate (e.g. fleshy algae, cyanobacteria, turf algae, crustose coralline algae/CCA) were recorded using the same semi-quantitative scale. Joint fish-benthic transect replication varied among reefs (n = 3 to 47). Transect data were pooled for each reef habitat type within each location.

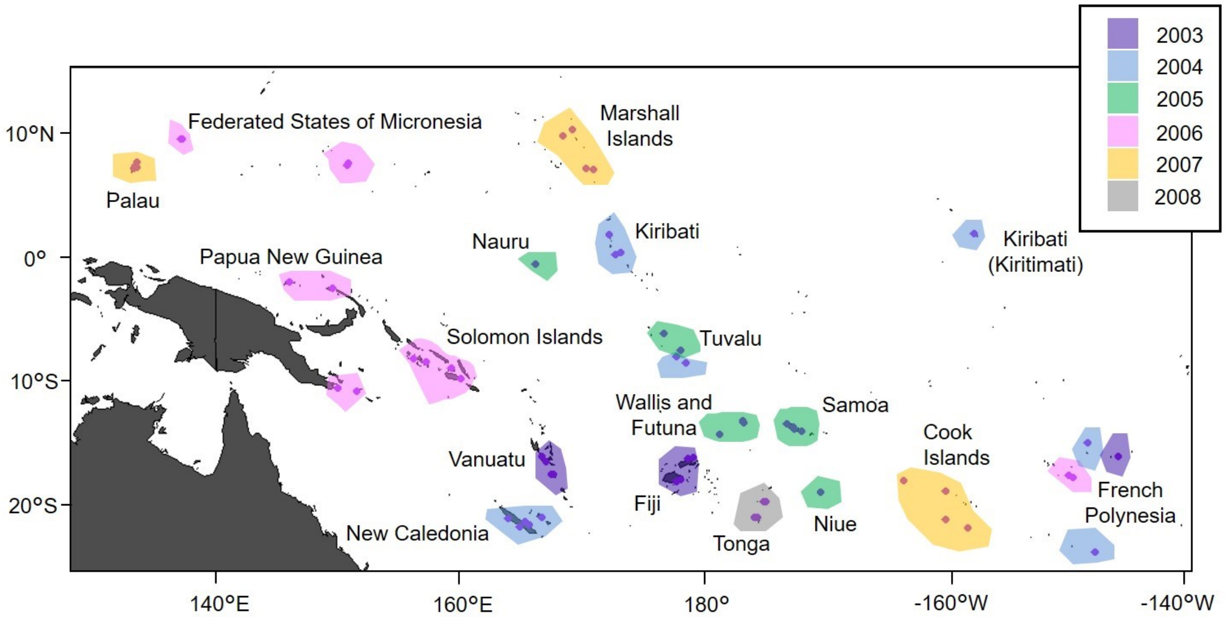


Figure 4.1. Map of 63 survey sites; temporal structure shown by colours related to survey year.

4.3.3. Intrinsic reef attributes

Dominant benthic groups (mean composition >10% of benthos) were dead coral (incorporating rubble, boulders and pavement), live hard coral, turf algae, fleshy algae and crustose coralline algae (CCA). Pairwise relationship tests (*corvif* function in R –Zuur *et al.*, 2009) between groups established no collinearity ($R^2 < 0.5$). Among-reef variation of benthic assemblages was then explored using a principal components analysis (PCA) based on Euclidean distances (built-in *prcomp* function in R - R Development Core Team 2013). A hierarchical clustering of the dominant benthic groups was produced with the same Euclidean distance matrix as for the PCA using *pvclust* package in R (Suzuki & Shimodaira, 2015). Significance values were calculated by 10,000-fold multi-scale bootstrap resampling, with independent clusters considered for significance values greater than 0.95. The first (PC1) and second (PC2) principal components of the PCA were then extracted for each site to provide one-dimensional multivariate representations of the benthic communities. Selected response parameters included arcsine transformed percentage cover of live hard coral, turf algae and fleshy algae, as well as the extracted PC1 and PC2 (Table 4.1). To explore patterns in morphological composition of the coral community, the ratio of massive to branching morphologies (i.e. higher values indicate relatively more massive corals) was used as an additional benthic response parameter.

Table 4.1. Benthic response variables and ranges throughout all reefs.

Response	Description	Range
CCA	Average benthic cover (%) of crustose coralline algae	0.0 to 43.5
dead coral	Average benthic cover (%) of dead coral; including rubble, boulders and pavement	5.5 to 61.2
fleshy algae	Average benthic cover (%) of fleshy algae	0.0 to 51.8
turf algae	Average benthic cover (%) of filamentous algal turfs	0.0 to 45.6
live hard coral	Average benthic cover (%) of live hard coral	6.1 to 65.1
pc1	Extracted first principal component from principal components analysis of key benthic groups; explaining a trend from fleshy algae and dead coral dominated reefs (negative values) to live hard coral and CCA (positive values)	-3.4 to 3.2
pc2	Extracted second principal component from principal components analysis of key benthic groups; explaining a trend from low (negative values) to high (positive values) turf algal coverage	-2.9 to 2.4
coral morphologies	Proportion of branching to massive coral morphologies within the live hard coral community; increasing values represent relatively more massive morphologies	0.0 to 70.2

4.3.4. Environmental predictors implicit for reefs

Model predictors (Table 4.2) included a variety of factors that were either collected during PROCFish surveys or extracted from public repositories. Depth was averaged over transects within each habitat at each site, and habitat represented reef habitat type (e.g. back, coastal, lagoonal, outer; Appendix Bi). Collinearity between depth and habitat precluded these predictors being used in parallel, thus depth was incorporated into models focused on outer reefs and habitat in those including different reef habitats. Due to natural latitudinal differences in reefs (Hughes *et al.*, 1999; Harriott & Banks, 2002), latitude was represented by degree distance from the equator without differentiating between north and south (0 to 23.9°). Average values for degree heating weeks (DHW - sum of previous 12 weeks that thermal stress anomalies >=1°C) at each site (n = 55; no data for some locations) were extracted from the NOAA Coral Reef Thermal Anomaly Database (CoRTAD version 4 – Casey *et al.*, 2012), at a spatial resolution of 4 km. Thermal stress anomalies refer to weekly sea surface temperature minus maximum weekly climatological sea surface temperature (Casey *et al.*, 2012). Data were averaged over the 12 years prior to each specific site's survey date, allowing all sites to encompass the strong

1998 El Niño event as well as the 2000 and 2001 bleaching events in the region (Appendix Bi), and also considering that reefs have been found to recover from acute disturbances within this timeframe (Gilmour *et al.*, 2013). Strong negative collinearity between latitude and DHW ($R^2 > -0.9$, Appendix Bii) precluded including both predictors in combination. Because of the complete data for latitude, this predictor was selected to represent both factors. Storm exposure was extracted from the NOAA IBTrACS-WMO data (Knapp et al., 2010a, 2010b) within ArcMAP 10.4 (ESRI, 2011). After projecting sites using the Behrmann projection, the number of storms (category one through five) passing within a 50 km buffer of each site was extracted. Based on the same justification as for DHW, storm exposure data were also confined to 12 years prior to the survey date for each individual location. From socioeconomic surveys, the predictor relative local human density was selected since it exhibits positive collinearity with both relative finfish catch and number of boats relative to reef area ($R^2 > 0.65$), and was thus assumed to represent relative fishing pressure as well as associated effects of human populations on coastal water quality. All herbivorous fish species encountered during visual surveys were classified into functional groups (Appendix Biii) according to Green & Bellwood (2009), enabling biomass (g m^{-2}) of grazers/detritivores, browsers, scrapers/small excavators, and large excavators/ bioeroders to be incorporated as model predictors.

Due to large variation in the scales of different terms, predictors underwent z-transformation to allow appropriate comparisons between the effect sizes (Zuur et al., 2009). Prior to modelling, pairs plots were assessed for collinearity between model terms (corvif function – Zuur *et al.,* 2009; Appendix Bii). Multi-collinearity was additionally checked using the generalised variance inflation factor (GVIF) function in R (*car* package – Fox & Weisberg, 2011) where values >3 would suggest collinearity and were not observed.

4.3.5. Defining level of human impact

We categorised reefs into those exposed to low and high local human impact according to relative local human density. Low (n = 29 outer reefs, n = 99 reefs encompassing all habitat types) and high (n = 33 outer reefs, n = 83 reefs encompassing all habitat types) local human impact was established around a threshold of 25 people km^{-2} reef. This threshold was previously identified as a breaking point within the same data-set after which phylogenetic diversity of parrotfishes was significantly reduced (D'Agata *et al.*, 2014). Relative local human density was also collinear ($R^2 = 0.7$) with relative finfish catch (tonnes reef fish km^{-2} reef $year^{-2}$). As an additional analysis allowing us to explore more specifically the impact of fisheries pressure, we categorised reefs into those exposed to low (n = 35 outer reefs, n = 107 reefs encompassing all habitat types) and high (n = 27 outer reefs, n = 75 reefs encompassing all habitat types) fishing pressure using a threshold of 5 tonnes reef fish km^{-2} reef $year^{-1}$. This value reflects a conservative estimation of maximum sustainable yield (MSY) of coral reef fisheries (Munro, 1984; Dalzell & Adams, 1996; Newton *et al.*, 2007). These two separate classifications of local impacts tested a slightly different set of reefs focused on either human densities or fishing pressure. However, because of similarities between the two factors ($R^2 = 0.8$), and difficulties determining whether low catch indicates low fishing pressure or overexploited resources, results according to relative finfish catch are confined to the appendix (Appendix Biv). All references hereafter to local human impact refer to those classified according to relative local human density.

Table 4.2. Model predictors and ranges among all reefs.

Predictor	Description	Range
browser biomass	Biomass (g m^{-2}) of browsers	0.1 to 73.2
degree heating weeks (DHW)	Measure of cumulative thermal stress – sum of previous 12 weeks where thermal stress anomaly ≥1˚C; value averaged over 12 years preceeding survey; negatively collinear (R^2 = 0.9) with latitude; only available for n=55 sites	0.6 to 3.5
depth	Average depth (m) of transects	1.25 to 10.5
excavator biomass	Biomass (g m^{-2}) of large excavators/bioeroders	0.0 to 1103.4
grazer biomass	Biomass (g m^{-2}) of grazers/detritivores	1.1 to 161.0
habitat	Reef habitat type; grouped into four geomorphological structures: sheltered coastal reef, intermediate lagoon reef (patch reef inside lagoon), back reef (inner side of outer reef) and outer reef (exposed reef)	
latitude	Degrees (˚) distance from equator, not differentiating between north and south. Negatively collinear (R^2 = 0.9) with *degree heating weeks (DHW)*	0.0 to 23.9
local human density	Number of people km^{-2} reef, positively collinear (R^2 = 0.8) with *relative finfish catch*	1.3 to 1705.0
relative finfish catch	Annual reef finfish catch (tonnes) km^{-2} reef $year^{-1}$; positively collinear (R^2 = 0.8) with *local human density*	0.1 to 78.2
scraper biomass	Biomass (g m^{-2}) of scrapers/small excavators	2.5 to 151.3
storm exposure	Total number of storms (category 1 to 5) passing within 50 km of site within previous 12 years	0 to 14

4.3.6. Model design and selection

To test which predictors show the strongest association with the various benthic response variables, a series of models were constructed (Table 4.3). Two predefined models involved (i) spatial and physical predictors (i.e. latitude, storm exposure, reef depth), and (ii) local feature predictors available from surveying each site (i.e. biomass of herbivorous fish functional groups, local human density, reef depth). Reef depth was included in both models to investigate the respective effects when accounting for this intrinsic factor which can mediate the impacts of both kinds of predictors, for example storms, temperature anomalies and fishing pressure (Tyler *et al*., 2009; Bridge *et al*., 2013). Finally, (iii) best-fit[1] models were determined from model selection techniques using the MuMIn package in R (Barton, 2016) based on AIC values corrected for finite sample sizes (AICc). From a model containing all predictors (i.e. Table 4.2) the dredge function runs all possible combinations and returns various models ranked from best to worst according to AIC. The function also returns a value between zero and one for each predictor representing its relative importance (RI; higher values represent superior relative importance) which refers to the total Akaike weight of all models containing that variable. When models included all reef habitat types, model selection was restricted to select either habitat or depth as collinearity precluded inclusion of both predictors. The best-fit model structure for each benthic response variable was retained, as well as the RI of each individual predictor.

Table 4.3. *Explanatory models with their included predictors. *Depth was included in models (i) and (ii) focusing on outer reefs only, and habitat within models (i) and (ii) encompassing all reef habitat types. Best-fit model selection for all reef habitats was restricted to select either depth or habitat.*

Model	Comments	Predictor set
(i) *Spatial and physical*	available without reef surveying	*depth*, habitat*, latitude/DHW, storm exposure*
(ii) *Local features*	available from reef surveying	*browser biomass, depth*, excavator biomass, grazer biomass, habitat*, local human density, scraper biomass*
(iii) *Best-fit*	from model selection based on Akaike Information Criterion (AIC)	selected from all possible predictors

To account for non-linear relationships between benthic assemblages and predictors, a generalised additive modelling (GAM) approach was adopted within the *mgcv* package in R (Wood, 2011). Spatial autocorrelation was checked using correlograms (*ncf* package in R – Bjornstad, 2016) for all response-model combinations, based on both response variables as well as model residuals. Spatial plots of the model residuals were also checked, with no correlations observed. All models (Table 4.3) were run separately for reefs exposed to different levels of local human impact, focused first on outer reefs (n = 62) and then for all reef habitat types (n = 182), where habitat replaced depth as a predictor in spatial and physical and local features models. To further explore differences in key predictors of benthic assemblages between reefs exposed to low and high local impacts, best-fit[1] models tailored for low impact reefs were applied to high impact reefs (best-fit[2]). To quantify the explanatory power of models, the adjusted-R^2 (adj-R^2) values were retained from each model. All data analyses were carried out in R version 3.1.1 (R Development Core Team, 2013), and graphs built using the *ggplot2* package (Wickham, 2009).

4.4. Results

4.4.1. Benthic assemblages

Benthic communities exhibited high variation among sites (Table 4.1), with live hard coral ranging from 6.1 to 65.1%, turf algae from 0 to 45.6%, and fleshy algae from 0 to 51.8%. The first principal components axis (PC1) of the principal components analysis (PCA, Figure 4.2a) differentiated reefs along a gradient from dead coral and fleshy algae at negative PC1 scores, to live hard coral and CCA at positive PC1 scores (PC1; eigenvalue 1.74, 34.9% variance explained). A gradient from low to high turf algal cover was represented across the second principal component (PC2; eigenvalue 1.14, 22.7% variance explained). Combined, PC1 and PC2 explained 57.6% of the variance in the benthic communities among all reefs. A hierarchical cluster analysis (Figure 4.2b) confirmed that benthic assemblages grouped into three separate clusters: (i) dead coral and fleshy algae (p = 1), (ii) turf algae was closer to live hard coral and CCA but represented its own (sub)cluster as separated other significant clusters (p = 0.79), and (iii) live hard coral and CCA (p = 0.98). Visual interpretations from the PCA indicate that most reefs were however positioned somewhere along an ecological continuum between distinct states.

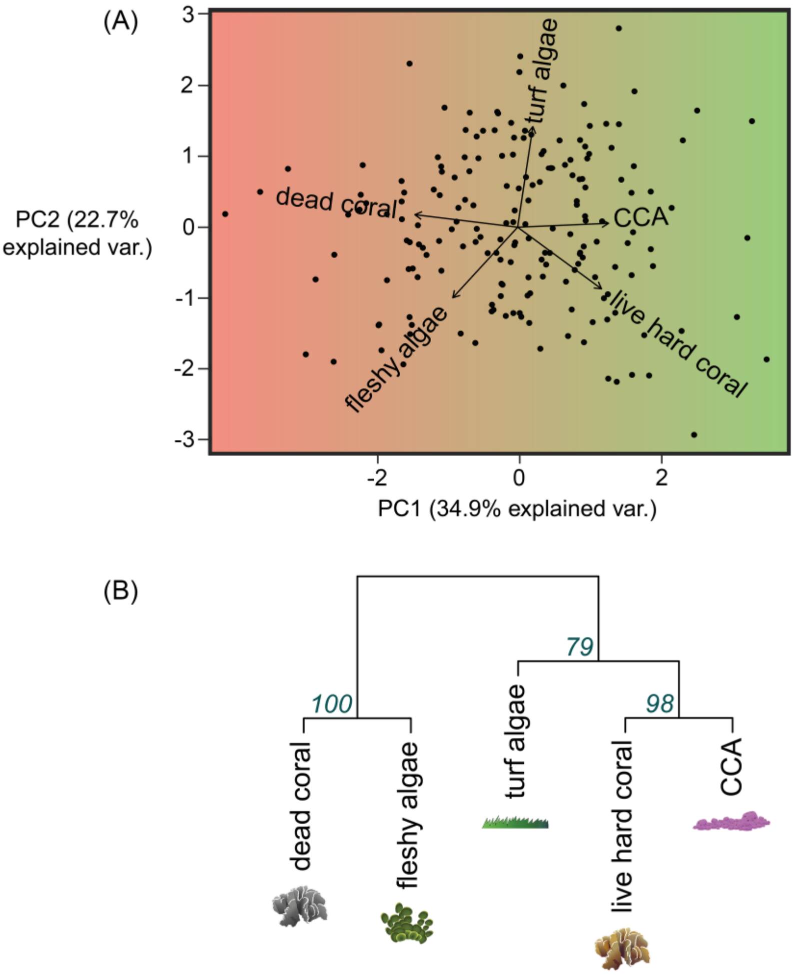


Figure 4.2. (a) Principal components analysis plot based benthic communities across all reefs, and (b) cluster dendrogram of dominant benthic groups, with significance given in percentages (significance over 95%).

At outer reefs, conspicuous influences of local human impact were restricted to benthic cover of live hard coral ($p = 0.002$), turf algae ($p = 0.002$) and subsequently in PC2 ($p < 0.001$; Figure 4.3a). More effects on broad benthic groups were observed across all reef habitats combined, with local human impacts associated to significant changes in cover of dead coral ($p = 0.04$), fleshy algae ($p = 0.04$), turf algae ($p < 0.001$; Figure 4.3a) and again PC2 ($p < 0.001$, Figure 4.3b), as well as coral morphological composition ($p = 0.02$; Figure 4.3c). However, the one-dimensional multivariate representation of benthic assemblages (PC1) remained consistent across reefs regardless of habitat type or local human impact level.

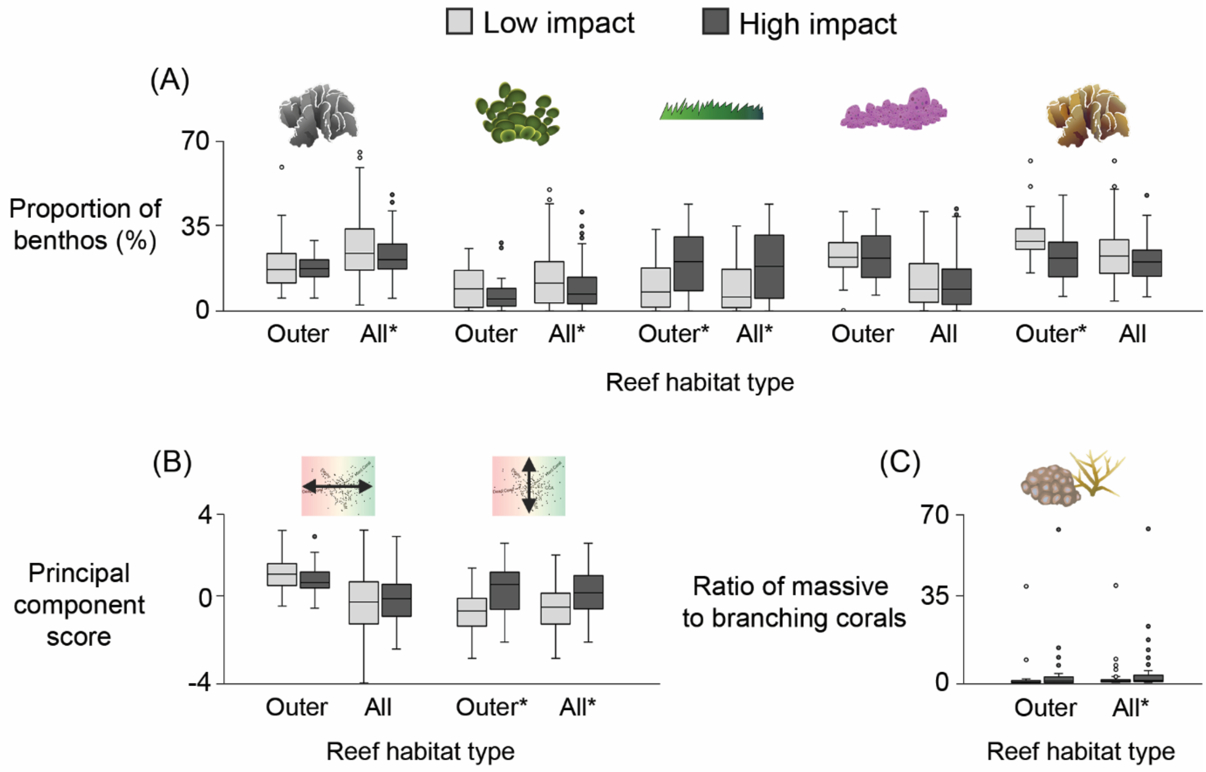


Figure 4.3. *Boxplots detailing differences in (A) benthic cover of key benthic groups (from left to right; dead coral, fleshy algae, turf algae, CCA and live hard coral), (B) the first two principal components (PC1, PC2) from the principal components analysis of dominant benthic assemblages, and (C) coral morphological ratios. For each benthic response type, data ranges are given for reefs exposed to low and high local human impact. * indicates significant differences (p < 0.05) between low and high impact sites according to two-sample equal variance t-tests.*

4.4.2. Predictive strength of models

Among the two levels of local human impact, there were significant differences in the explanatory power of each model in predicting benthic assemblages across the study locations. Though models encompassing all reef habitat types reflected patterns observed at outer reefs alone, differences between levels of local impact were consistently stronger at outer reefs.

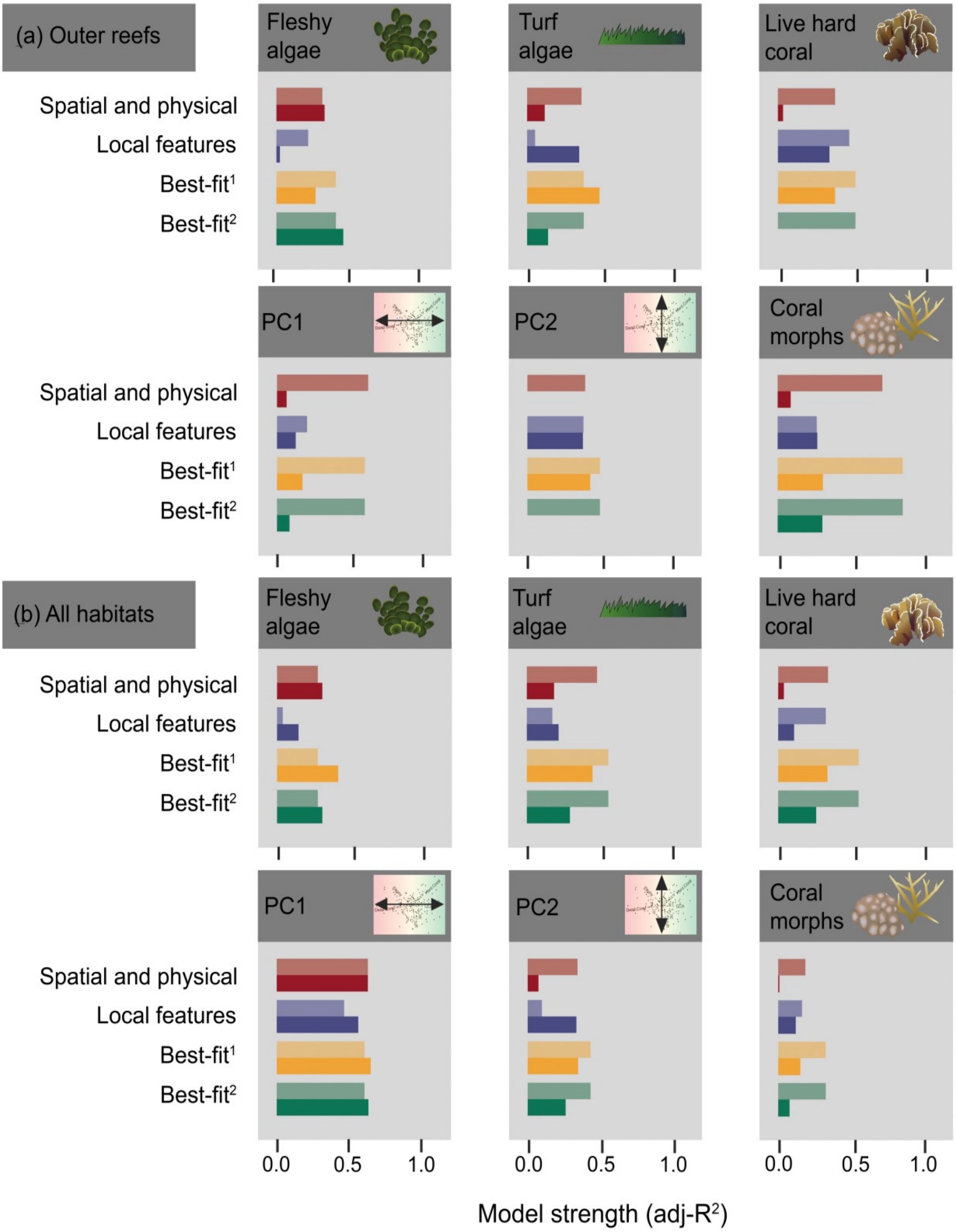


Figure 4.4. Strength of different models in predicting individual benthic responses among (a) outer reefs and (b) reefs from all habitat types. Models focused on sites of low human impact are shown by semi-transparent (upper) bars, and high human impact by solid (lower) coloured bars. For details on predictors incorporated within the spatial and physical and local features models refer to Table 4.3. See Figure 4.5A,B for predictors selected for best-fit[1] models. Best-fit[2] models incorporate best-fit[1] predictors for low impact sites, fitted anew to high impact sites.

4.4.2.1. *Spatial and physical* attributes

At outer reefs exposed to low human impacts, the spatial and physical model performed well in explaining benthic assemblage variance (Figure 4.4a). In contrast, model performance was significantly lower at reefs exposed to high human impacts (paired t-test $p = 0.01$). Particularly, when local human impacts were low, this model explained a high proportion of variance for outer reef PC1 (adj-$R^2 = 0.59$) and coral morphological composition (adj-$R^2 = 0.67$), for which models performed poorly at reefs with higher local impacts (both adj-$R^2 < 0.1$). The only benthic response variable of similar predictability between the two levels of local impacts was fleshy algae (adj-$R^2 \sim 0.3$). When applied to all reef habitats, superior predictability at lesser locally impacted reefs was reflected (paired t-test $p = 0.04$; Figure 4.4b), but to a less dramatic extent. Predictability of fleshy algal cover was again similar between the two levels of local impact (adj-$R^2 \sim 0.27$). Interestingly, the variance explained for PC1 was relatively high compared to other benthic responses, and was not different among the two levels of local human impact (adj-$R^2 = 0.59$). Even among reefs with low local impacts, the ability to predict coral morphological composition was notably compromised when considering all reef habitats (adj-$R^2 = 0.17$) rather than specifically outer reefs (adj-$R^2 = 0.67$).

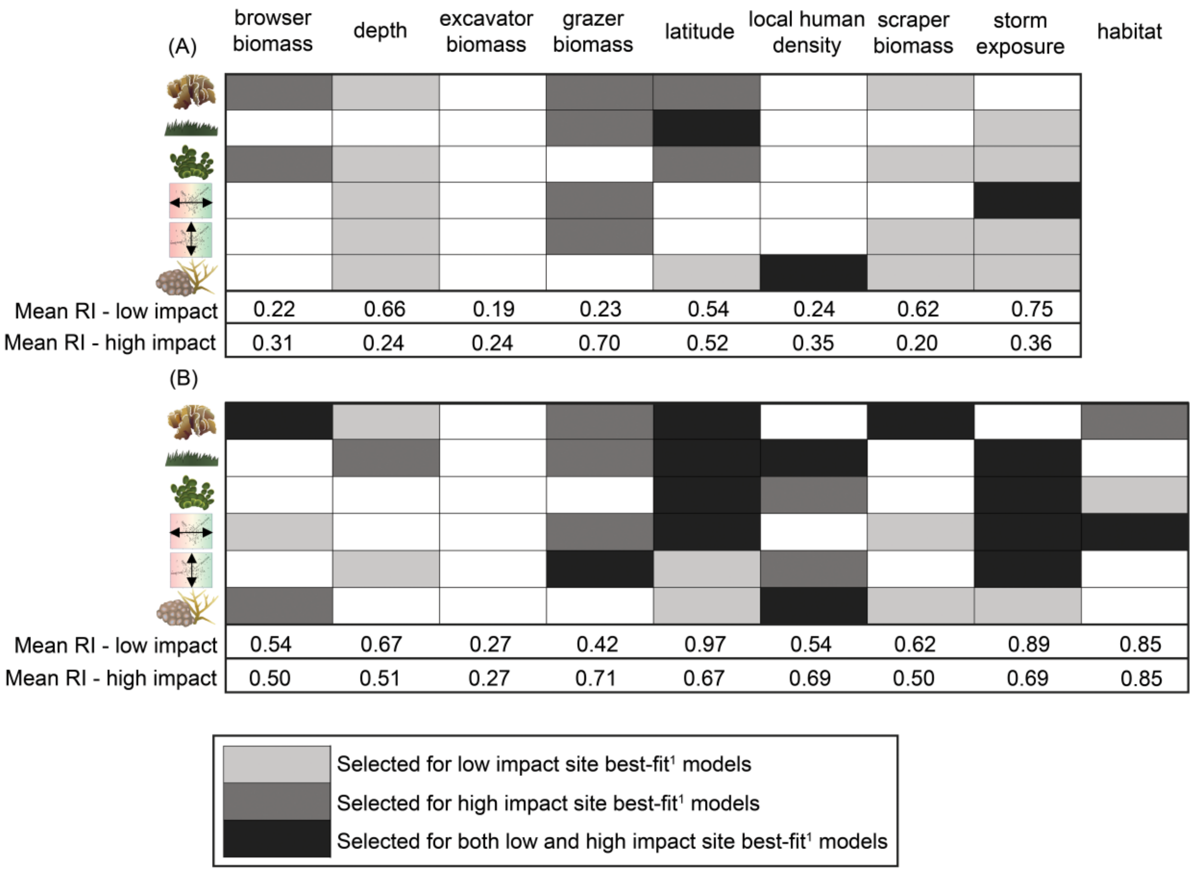
4.4.2.2. *Local features*

Under models based on local features, there were no differences between the explanatory power of models among different levels of local impacts (Figure 4.4ab). Among outer reefs with low human impacts, local features explained less variation for benthic responses then spatial and physical models (Figure 4.4a). In contrast, at more locally impacted reefs, the explanatory power of local features models was generally superior to that of spatial and physical models. PC1 and cover of live hard coral and fleshy algae remained more predictable at less rather than more locally impacted reefs. These findings were reflected when models based local feature predictors encompassed all reef habitat types (Figure 4.4b).

4.4.2.3. *Best-fit*

Model selection techniques determined strong differences in best-fit models and the relative importance of individual predictors at reefs exposed to different levels of human impacts (Figure 4.4ab; Figure 4.5ab). The best-fit^1 model tailored for outer reefs with low human impacts performed relatively well, explaining over 50% of the variation in live hard coral cover, PC1, PC2 and coral morphological ratio (Figure 4.4a). When these models tailored for reefs exposed to relatively low local impacts were fitted anew to outer reefs with high local human impacts (i.e. best-fit^2), they performed poorly (paired t-test $p = 0.01$). Contrastingly, best-fit^1 models as selected for outer reefs with high local impacts performed much better (Figure 4.4a), though with the exception of turf algal cover, explanatory power remained consistently higher at less impacted reefs. These patterns were reflected within models encompassing all reef habitat types (Figure 4.4b), where best-fit^1 models tailored to less locally impacted reefs performed poorly when fitted to reef exposed to relatively higher local impacts (best-fit^2; paired t-test $p = 0.049$). Best-fit^1 models tailored specifically for more locally impacted reefs again improved overall predictability of benthic assemblages to a similar level as those less impacted (Figure 4.4b). Despite most benthic responses remaining more predictable under best-fit^1 models at less locally impacted reefs, more variation was explained for fleshy algal cover at reefs with higher local impacts.

4.4.3. Relative importance of predictors



(A)

	browser biomass	depth	excavator biomass	grazer biomass	latitude	local human density	scraper biomass	storm exposure	habitat
	▓	░		▓	▓		░		
				▓	█			░	
	▓	░			▓		░	░	
		░		▓				█	
		░		▓			░	░	
		░			░	█	░	░	
Mean RI - low impact	0.22	0.66	0.19	0.23	0.54	0.24	0.62	0.75	
Mean RI - high impact	0.31	0.24	0.24	0.70	0.52	0.35	0.20	0.36	

(B)

	browser biomass	depth	excavator biomass	grazer biomass	latitude	local human density	scraper biomass	storm exposure	habitat
	█	░		▓	█		█		▓
		▓		▓	█	█		█	
					█	▓		█	░
	░			▓	█		░	█	█
		░		█	░	▓		█	
	▓				░	█	░	░	
Mean RI - low impact	0.54	0.67	0.27	0.42	0.97	0.54	0.62	0.89	0.85
Mean RI - high impact	0.50	0.51	0.27	0.71	0.67	0.69	0.50	0.69	0.85

░ Selected for low impact site best-fit[1] models
▓ Selected for high impact site best-fit[1] models
█ Selected for both low and high impact site best-fit[1] models

Figure 4.5. Differences in predictors selected by model selection techniques for best-fit [1] models tailored for low and high impact sites, for (A) outer reefs, and (B) reefs from all habitat types, separated for individual benthic responses (from top to bottom; live hard coral, turf algae, fleshy algae, PC1, PC2, and coral morphological composition), Mean RI refers to the average relative importance of each predictor across the six response variables.

The contrasting outcomes of low impact reef best-fit[1] models when fitted anew to high impact reefs indicated large discrepancies in the relative importance (RI) of predictors among reefs exposed to various levels of local human impact. Model selection techniques further revealed strong differences in the predictors selected for best-fit[1] models depending on the level of local human impact (Figure 4.5A,B). At outer reefs with low human impacts, reef depth, scraper biomass and storm exposure were included in best-fit[1] models for almost all individual benthic responses (Figure 4.5A) and had the highest overall relative importance (i.e. mean RI > 0.6). Contrastingly, these predictors were of low importance at reefs exposed to high local impacts (mean RI < 0.4), where biomass of grazers/detritivores emerged as the dominant predictor in terms of both inclusion in models and overall relative importance. For models comprising all reef habitat types, the predictors reef depth/habitat type, latitude and storm exposure were of highest relative importance (mean RI > 0.6) regardless of the level of local human impact (Figure 4.5B). However, whilst scraper/small excavator biomass was revealed to be another important predictor of benthic assemblages at less impacted reefs, grazer/detritivore biomass and local human density emerged as dominant predictors at more impacted reefs.

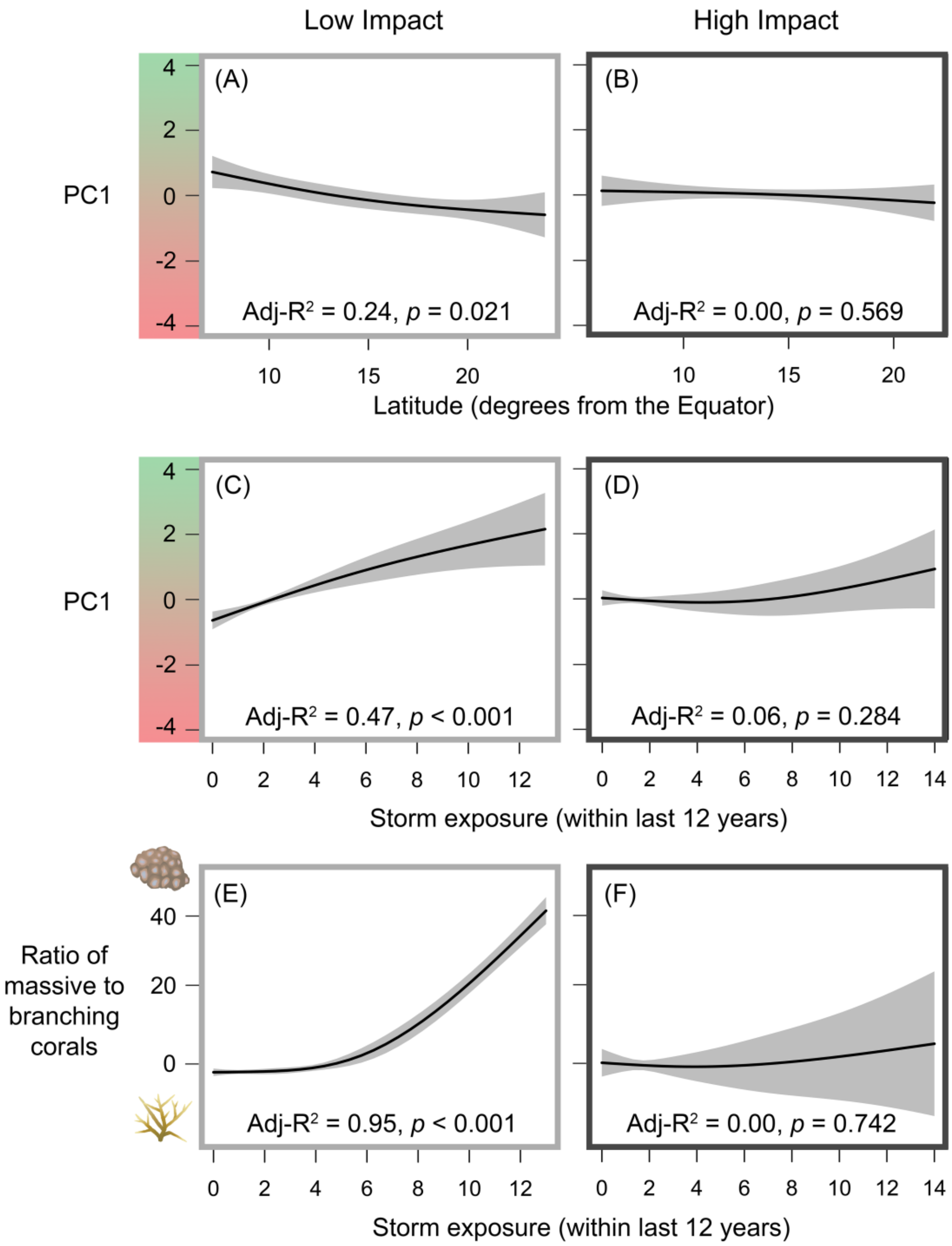


Figure 4.6. Smoother plots of normalised residuals from generalised additive models (GAMs) based on outer reefs for: the relationship between the first principal component (PC1) and latitude at (A) low and (B) high locally impacted sites, the relationship between PC1 and storm exposure at (C) low and (D) high locally impacted sites, and the ratio of massive to branching corals in relation to storm exposure at (E) low and (F) high locally impacted sites

From the best-fit[1] model selection, the spatial and physical predictors reef depth/habitat type, latitude and storm exposure emerged as generally more important in explaining benthic responses at sites exposed to low rather than high local human impacts (Figure 4.5A,B). These patterns were reiterated when plotting PC1 and coral morphological ratio as a response to latitude and storm exposure at outer reefs (Figure 4.6). Whilst PC1 was significantly related to both latitude and storm exposure at reefs exposed to relatively less local impacts (Figure 4.6A,C, there were no relationships at more locally impacted reefs (Figure 4.6B,D). Similarly, coral morphological composition was significantly related to storm exposure at reefs with reduced local impacts, with more storms favouring massive coral morphologies (Figure 4.6E), whereas no trend existed as local impacts increased (Figure 4.6F).

4.5. Discussion

Under future conditions of increasing climate-change associated stressors and local anthropogenic influence (Burke *et al.,* 2011; Pachauri *et al.,* 2014; Gattuso *et al.*, 2015), it is particularly important for researchers and planners to gauge the ability of models to predict reef assemblages. After emphasising the variation in benthic cover that exists among used Pacific Island reefs, this study revealed clear differences in both the relative importance of predictors, as well as the ability to predict benthic reef assemblages at contrasting levels of local human impacts. In particular, as local human impacts increase, the explanatory power of models based on spatial and physical attributes is strongly compromised suggesting a disassociation between the system and its physical environment. Links between these spatial and physical attributes and climate-change related factors suggest challenges in predicting future responses as local human impacts increase.

Benthic communities were not restricted to distinct regimes dominated by either hard corals or fleshy algae, supporting previous studies (Bruno *et al.*, 2009; Jouffray *et al.*, 2014; Smith *et al.*, 2016). Specifically, we show that benthic communities across these 63 Pacific islands can gravitate towards at least three benthic states: those dominated by live hard coral/CCA, turf algae and fleshy algae/dead coral. Nonetheless, most reefs exist somewhere along the ecological continuum between extreme states. Direct influences of local human impact were limited to specific benthic responses. At outer reefs, increased local human impact was associated to higher cover of turf algae and reductions in live hard coral. Across all reef habitats, increased local human impact was related to significant differences in dead coral, fleshy algae and turf algae, as well as higher proportions of massive coral morphologies. The one-dimensional multivariate representation of benthic assemblages (PC1), from reefs dominated by fleshy algae and dead coral to those characterised by calcifiers, was not affected by local human impact among outer reefs nor all reef habitat types.

Even when direct responses between local human impact and broad benthic groups were not observed, increasing local impact had a stark influence on the relative importance of drivers in determining benthic assemblages. Particularly, relationships between the benthos and spatial and physical predictors were significantly weaker at reefs exposed to higher levels of local human impacts. Reef depth/habitat type, latitude (collinear with DHW) and storm exposure appear of high relative importance in shaping benthic assemblages at reefs less impacted by humans. Both DHW and storms will be of increasing importance under climate change (Pachauri *et al.,* 2014), indicating a strong ability to predict future benthic responses to global stressors at less locally impacted Pacific island reefs. Contrastingly, the explanatory power of these predictors was strongly compromised at reefs subjected to relatively more local human impacts. Outcomes from model selection and local features models revealed that more locally impacted reefs are not per se less predictable, but that there is a distinct shift in the relative importance of predictors towards local site attributes. Furthermore, the relative importance of various functional groups of herbivorous fishes in explaining benthic assemblages differed among reefs exposed to contrasting levels of local human impacts. At more locally impacted reefs which exhibited higher coverage of algal types and dead coral, biomass of grazers/detritivores was of high importance in predicting benthic assemblages. Contrastingly at less locally-impacted reefs which were more dominated by live hard coral (at outer reefs), scrapers/small excavator biomass emerged as an important predictor. These patterns reflect recent findings from the Hawaiian Archipelago, where biomass of grazers and scrapers were the most important predictors of turf and macroalgal-, and calcified-regimes, respectively (Jouffray *et al.*, 2014).

Interesting patterns emerged when plotting individual relationships between reef condition and coral morphological composition as a function of spatial and physical attributes. At outer reefs exposed to low local human impacts, reef condition declined with increasing latitude, showing the opposite trend to that found along East Africa where coral cover increased at higher latitudes (McClanahan *et al.*, 2014). However, similar trends were found at the Hawaiian Archipelago (Jouffray *et al.,* 2014) and among a larger spatial set of US Pacific Island reefs, whereby reef builders (live hard coral and CCA) declined with increasing latitude (Smith *et al.,* 2016). This could be a result of temperature limiting coral growth at higher latitudes (e.g. Jokiel & Coles, 1977), but is surprising considering the strong negative collinearity between latitude and DHW which in turn suggests a positive trend between reef health and thermal stress. These results are in contrast to the normal detrimental effects of increased DHW on benthic health and structure (Eakin *et al.*, 2010). The trends may however may reflect that low-latitude reefs have already undergone some reshuffling or adjustment to heating and are thus less affected in recent years (Middlebrook *et al.,* 2008; Oliver & Palumbi, 2011; Castillo *et al.*, 2012), while higher latitude reefs are feeling the brunt of increasing temperatures more recently. Contrasting trends in the Pacific compared to East Africa may be in part due to a higher species pool within the Pacific from which ecological reorganisation under high temperatures is possible (Roff & Mumby, 2012). At reefs exposed to low amounts of local human impacts, reef condition also increased with storm exposure which in turn favoured relatively higher proportions of massive coral morphologies. Storms can have mixed effects, benefitting reefs by alleviating thermal stress during warmer summer months but also causing physical destruction, particularly to delicate branching coral morphologies leading to a higher proportion of massive coral morphologies (Heron *et al.*, 2005; Manzello *et al.*, 2007). Because the effects of storms are strongly dependent not only on their intensity, but also the extent of the fetch, their frequency and intrinsic reef properties such as topography (Lugo *et al.,* 2000; Heron *et al.,* 2005), this study incorporated all recorded storms (category one through five) passing within a 50km buffer of each reef. The results thus do not infer that reef condition improves with increasing storm intensity, which is projected to occur under future climate change scenarios (Pachauri *et al.*, 2014). All trends between reef condition and morphological composition with spatial and physical attributes were absent at reefs exposed to relatively higher human impacts. Differential relationships between the benthos and spatial and physical attributes may be explained by local anthropogenic stressors driving ecological reorganisation (Graham *et al.,* 2014), and reflect how natural biophysical relationships on reefs are decoupled at reefs around populated islands compared with remote reefs (Williams *et al*., 2015a). This hypothesis is supported by a direct link between increased relative cover of massive coral morphologies over branching types at high impact reefs among all reef habitat types. Perhaps in less diverse regions such as the Caribbean (Spalding *et al.,* 2001; Roff & Mumby, 2012), the limited capacity for ecological reorganisation would lead to more conspicuous negative impacts of storms (e.g. Gardner *et al*., 2005) and DHW (Eakin *et al*., 2010), even when local human impacts are low. These results suggest that the effects of storms and latitude or DHW are more predictable at reefs subject to low levels of human impacts. Increasing local human impacts thus seem to exhibit complex interactions with spatial and physical drivers and in turn global climate change-related stressors.

The strongest effects of local human influence are generally observed within models focusing specifically on outer reefs rather than models encompassing all reef habitat types. Perhaps differences would be consistently strong within all individual inshore habitats, but lower replication within each of these habitats precluded individual analyses. Naturally more variable and often challenging environments within inshore reef habitats (e.g. in terms of temperature, sediment input and light availability - Rogers, 1990; Browne *et al*., 2013; Schoepf *et al*., 2015; Morgan *et al*., 2016) may explain why the effects of local human impacts are diluted when jointly considering these habitats. Furthermore, although consistent patterns are observed regardless of how local human impact is defined (i.e. by local human density or fishing pressure), categorising by human density reveals the starkest contrasts between low and high levels of local human impact under spatial and physical predictors. These findings indicate that increasing local human population density decouples relationships between benthic reef communities and their physical and spatial environment to a larger extent than fishing pressure. These impacts are likely highly context-dependent and less easy to predict with the factors considered here, as the local feature predictors focus more towards fish. However, population density may be more tightly connected to additional impacts (e.g. sedimentation, sewage input, agriculture) than fishing pressure alone, thus more directly influencing reef benthos. Furthermore, low fishing pressure could reflect low marine reliance or previous overexploitation leading to collapsed stocks.

Local human impacts can directly drive changes in reef fish populations (Williams *et al*., 2015b; Cinner *et al.* 2016). However, the indirect or otherwise perhaps subtler direct effects of local human populations on the reef benthos may be more challenging to capture, leading some authors to conclude an absence of any effect (Bruno & Valdivia, 2016). Increasing sewage input, agricultural run-off and sedimentation are potential changes associated with increasing populations that reduce water quality and have a variety of effects on benthic communities (Fabricius, 2005; Fabricius *et al.,* 2005; Ford *et al*., 2017). Furthermore, as fishing removes functionally important fish species, important top-down control of some benthic organisms is lost (Bellwood *et al*., 2004). Thus, local human impacts may homogenise reefs by driving ecological reorganisation that favours tolerant species/organisms (Côté & Darling, 2010). Such reorganisation could explain why our candidate models varied in their predictive performance of benthic communities at these Pacific Island reefs exposed to different levels of local human impacts, and why model selection identified key differences in the relative importance of various predictors. Models based on local features revealed stronger potential to predict benthic structure at more locally impacted reefs, indicating the necessity of local information from surveys to improve model precision for reefs close to larger populations of humans.

4.6. Concluding Remarks

Even under a scenario whereby significant climate action is taken, most reefs will suffer long-term degradation by the middle of the century (Frieler *et al.*, 2012), and > 75% of reefs will experience annual severe bleaching (van Hooidonk *et al.,* 2016). Accordingly, it is urgent for spatial planners to identify those reefs with the best chance of surviving and to prioritise where to focus management efforts and resources. These results contribute to a better understanding of the interactions between local and global stressors. We quantitatively demonstrate that the ability to predict the response of benthic assemblages to global climate change-related stressors is strongly compromised under increasing local human impacts. Although direct and conspicuous effects of increasing human populations on broad benthic groups may not be observed, these results indicate that it would be dangerous to draw the conclusion that local impacts have no effect on benthic assemblages. Ecological reorganisation and homogenisation can have serious consequences on ecosystem functioning and the response to increasing global stressors, and overlooking this ecological phenomenon could thus lead to large errors in future projections. A better understanding of the complex interactions between local and global stressors is critical for designing local management approaches needed to protect reefs that can survive the increasingly challenging environment in the coming decades. The results furthermore underline that reefs in closer proximity to human populations require context-specific management approaches to maximise the future sustainability of these impacted reefs and their critical ecosystem services.

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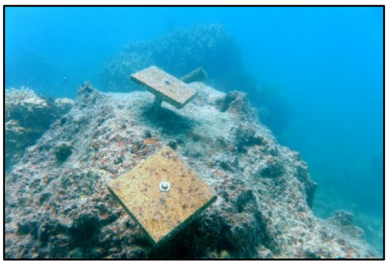
CHAPTER FIVE

DISCREPANCIES BETWEEN METRICS FOR CORAL REEF MONITORING



This work is in revision

Ford AK, Eich A, McAndrews R, Mangubhai S, Nugues MM, Bejarano S, Moore BR, Rico C, Wild C, Ferse SCA. Evaluation of coral reef management effectiveness using conventional versus newly developed monitoring metrics.

5.1. Abstract

With increasing stressors to coral reefs, it is critical to define tools to evaluate their dynamics and resilience. In this context, surveys must go beyond conventional monitoring approaches that focus on abundance and biomass of key groups and quantify metrics that better assess ecological processes and ecosystem trajectories. By measuring a variety of conventional (e.g. proportion cover of broad benthic groups, biomass of herbivorous fish) and newly developed complementary metrics based on ecological processes and functionality (e.g. turf height, coral recruitment rates, juvenile coral densities, herbivorous fish grazing rates), this study evaluated the ecosystem responses to community-based management in Fiji. The study was conducted across three paired tabu areas (periodically closed to fishing) and adjacent fished sites. Conventional metrics reflected no management effect on benthic or herbivorous fish assemblages. In contrast, complementary process and function-based metrics generally indicated positive effects of management, particularly within the benthos. Within areas closed to fishing, significant changes occurred in algal turf height (33% lower), coral recruitment rate (159% higher) and juvenile coral density (42% higher), compared to adjacent open reefs. In addition, turf height was inversely related to coral recruitment and juvenile coral density, and longer turfs (> 5 mm) were more competitive in interaction with corals. These results emphasise that conventional metrics may overlook benefits of local management to inshore reefs, and that incorporating complementary metrics such as turf height into reef survey protocols will strengthen their capacity to predict the plausible future condition of reefs and their responses to disturbances.

5.2. Introduction

The status of ecosystems over space and time has long been used as criterion for prioritisation and decision-making in conservation planning. Ecosystem assessments have focused on quantifying common status metrics such as biomass and abundance of target groups, as well as species diversity (e.g. Yoccoz *et al.*, 2001). Although such assessments offer the advantage of relying on generally fast and relatively simple estimation methods, their capacity to convey quantitative information on ecosystem function is limited (Wright et al., 2006). It is therefore urgent to identify indicators of dynamic processes to capture a further facet that may help to anticipate the likely trajectory of ecosystems over time and in response to disturbances (Glaser *et al.*, 2012). If such indicators can be practically and cost-effectively integrated into ecosystem assessments, there is scope for (i) evaluating the effectiveness of conservation tools (e.g. marine reserves) more thoroughly, (ii) better understanding the impact of disturbances, and (iii) supporting managers in decision-making (high vs. low-risk conservation investments).

Anticipating trajectories of complex and diverse ecosystems such as coral reefs is particularly challenging due to the large number of species fulfilling various functions and responding differently to a changing environment (Pandolfi, 2015). Conventional coral reef monitoring protocols focus on measuring cover of broad benthic groups, as well as fish biomass along replicate transects. Percent cover of benthic organisms fails to provide information on important ecosystem functions for a variety of reasons. First, high live coral cover is generally interpreted as a sign of ecosystem health, and the contrary is assumed of high algal cover. Healthy reefs may however display variable levels of hard coral and fleshy algal cover depending on their location (Johannes *et al.*, 1983; Kleypas *et al.*, 1999; Couce *et al.*, 2012). Just as low coral cover does not necessarily reflect unhealthy reefs, reefs dominated by live corals must not be unequivocally considered healthy and/or resilient (Mumby *et al.*, 2014; Anthony *et al.*, 2015). Second, the resolution at which benthic groups are defined differs strongly among studies. While a coarse resolution may suffice for an immediate broad diagnosis of benthic status, it may impair the detection of relationships between particular benthic attributes and fish communities or behaviours (Mumby et al., 2013). Conventional assessments cannot, for instance, provide information on the colonisation processes of free space, which has increased significantly alongside large-scale coral reef decline (e.g. Wilkinson, 2008). This space is usually recorded ambiguously as dead coral, bare rock, pavement or rubble (Harris, 2015), yet the settlement dynamics of coral larvae or algal propagules (among others) determines the success of critical reef recovery processes such as coral recruitment and succession (e.g. Birrell *et al.*, 2005). There are also limitations to how informative fish abundances are of the ecosystem functions that fishes sustain. Tidal changes, time of day, turbidity and variability among surveyors can lead to variations in the perceived fish abundance (Thompson & Mapstone, 2002; McClanahan *et al.*, 2007). Furthermore, species with crucial ecosystem functions can be wary of divers and thus not encountered in fish censuses (Kulbicki, 1998). Stationary video cameras have consequently illuminated the previously unknown, yet crucial functional roles of species that tend to be rare in visual surveys (Hoey & Bellwood, 2009; Plass-Johnson *et al.*, 2015). Conventional reef status assessments thus risk providing a superficial level of information that does not convey functionality and ecosystem robustness, and hence may not provide enough support for adaptive management decisions. Essentially, although static measures of abundance can provide an idea of the system's current state, they do not consider whether the system is most likely to improve or deteriorate over time.

The likelihood of coral reefs changing over time and in response to disturbances is a product of many factors. In an attempt to improve predictions of these complex systems, several important ecological processes have been identified and alternative monitoring tools proposed (e.g. McClanahan *et al.,* 2012). Benthic assessments are increasingly considering complementary dynamic indicators that respond quickly to changes, such as coral recruitment success, turf height and coral-algal interactions (Anthony *et al.*, 2015; Flower *et al.*, 2017). To evaluate settlement dynamics on free space, hereon referred to as biotic substrate colonisation, surveys would benefit from refining the level of detail in which different benthic categories (e.g. algal turfs, crustose coralline algae, cyanobacterial mats) are recorded. One of the fastest colonisers of available substrates are algal turfs (Diaz-Pulido & McCook, 2002), yet their cover and intrinsic properties are often neglected in surveys (Harris, 2015; Flower *et al.*, 2017). While algal turf cover itself is not so informative, it can be a strong predictor of coral recruitment and subsequent development when combined with turf height (Birrell *et al.*, 2005; Mumby *et al.*, 2013). For coral reef fish communities, efforts are increasingly invested towards monitoring key functional groups separately (Green & Bellwood, 2009) and quantifying herbivory (Fox & Bellwood, 2008; Rasher *et al.*, 2013). Spatial, temporal and surveyor-related discrepancies as well as differential species' wariness (Kulbicki, 1998) imply that visual fish biomass surveys should be supported by: (i) remote video surveys; and (ii) parameters that reflect longer-term fish functions. The latter can include algal traits and prey behaviours in response to predatory fish (e.g. Ceccarelli *et al.*, 2005; Vermeij *et al.*, 2015).

Here we evaluate the effectiveness of local management using conventional reef status metrics in combination with a set of complementary status and dynamic metrics focused on ecological processes and functionality. Conventional (e.g. percent cover of benthic groups, herbivorous fish biomass) and complementary (e.g. algal turf height, coral recruitment, juvenile coral density, herbivorous fish grazing rates) metrics were quantified in paired inshore reefs open and closed to fishing within three locally managed marine areas (LMMAs) in Fiji. We hypothesised that a substantial discrepancy would be found when interpreting the level of effectiveness from these two different types of metrics, driven primarily by the limited resolution of conventional metrics. By quantifying the nature and magnitude of this discrepancy, we provide a more nuanced approach to evaluate the success of management tools. We also evaluate the informative value of measuring turf height in an inshore Pacific island reef setting by investigating its relationship with ecological processes that are critical for system resilience.

5.3. Material and methods

5.3.1. Study area

This study focused on three inshore reef sites within traditional fishing grounds (*qoliqoli*), namely Dakuibeqa (Beqa, Rewa Province), Nasinu (Ovalau, Lomaiviti Province) and Navakavu (Suva, Rewa Province; Figure 5.1). Each *qoliqoli* contained a locally managed *tabu* area (periodically closed to fishing) that had been established for at least eight years. These locations were selected based on the premise that Fijian LMMAs represent a good example of effective community-based management (Techera, 2010; Weeks & Jupiter, 2013). All sites displayed similar characteristics regarding reef orientation (i.e. south-east facing) and topography. At paired reefs within and adjacent to each *tabu* area, surveys took place on both reef platforms (1–2 m depth) and lagoonal slopes (4–6 m depth), covering both inshore reef habitat types encompassed within all *tabu* areas. Surveys were carried out between September 2015 and February 2016.

5.3.2. Field surveys

5.3.2.1. Conventional reef status metrics

Conventional metrics into benthic and fish communities were quantified along transects at all surveys sites (Table 5.1). Benthic surveys were carried out along three 30 m transects within each of the *tabu* and open areas, and in both reef habitats, at all sites. Benthic community structure was assessed using the line-point-intercept method (English *et al.*, 1997), with benthic cover recorded at 50 cm intervals, yielding a total of 60 points per transect. Fine-scale rugosity was quantified using the chain-and-tape method (Risk, 1972) with a small link chain (5 mm). Three replicate rugosity measurements were made along each transect (averaged per transect), with each measurement covering 5 m linear distance (end value calculated to rugosity per m). Herbivorous fish biomass was quantified at all sites using underwater visual censuses (UVC) carried out along eight 30 x 5 m belt transects by a single surveyor (Dickens *et al.*, 2011). The surveyor recorded the largest and wariest species during a first pass of the transect, and more site-attached territorial species (e.g. *Stegastes* spp.) in the second pass. Individual fishes were identified to the species level and assigned to fork length size classes (i.e. 5 cm intervals) to compute taxonomic richness and biomass, respectively. Biomass values were obtained using the midpoint of the size class from established length-weight relationships (Kulbicki et al., 2005; Green & Bellwood, 2009). Taxonomic richness and biomass were also calculated per functional feeding group (i.e. browsers, grazers/detritivores, scrapers/small excavators, large excavators/bioeroders - Green & Bellwood, 2009).

5.3.2.2. Complementary indicators of ecosystem function

Complementary status and ecological function-based metrics were quantified in all survey sites along transects used for conventional metrics (Table 5.1). As proxies of the dynamics of biotic substrate colonisation, turf height and juvenile coral density were quantified (Birrell *et al.*, 2005; Flower *et al.*, 2017). Turf height was measured to the nearest mm using a plastic ruler placed perpendicular to the substrate at 30 points under each transect. We computed the turf index per site as the product of mean percent turf cover and mean canopy height (Steneck & Dethier, 1994; Mumby *et al.*, 2013). To quantify juvenile coral density, individual juvenile corals (< 3 cm in diameter) were counted within ten 0.25 m^2 quadrats per transect, using a GOBE Nightsea UV lamp to aid the detection of coral tissue fluorescence (Piniak *et al.,* 2005; Baird *et al.*, 2006). Quadrats for juvenile corals were systematically placed on substrata other than live coral tissue or sand which would typically be avoided by coral recruits. Additionally, along the first 10 m of each transect, each coral colony found (with at least 50% of its area) within a 1 m belt of the transect line was assessed for coral-algal interactions. Any type of algae in contact with the coral was identified to the functional group level, and the status of the interaction (i.e. algae winning, coral winning or neutral) was determined by any visible mortality, bleaching or overgrowth of either the coral or the algae, according to Barott *et al.* (2012).

In the most accessible area, the Navakavu *qoliqoli* (Suva), 15 recruitment tiles were installed in each reef habitat within the *tabu* and open areas. Untreated sandstone tiles (15 x 15 cm) were fixed onto dead coral using 15 cm stainless steel screws. As coral recruits preferentially settle on the undersides of surfaces, and small variations in tile angle do not affect coral recruitment patterns (Mundy, 2000), an angled 8 cm PVC pipe between the underside of the tile and the substrate ensured that tiles were suspended at an angle (~ 45 ± 20°). Consequently, sedimentation was limited and recruits were able to access both tile surfaces. Tiles were installed in mid-October 2015 and collected in mid-January 2016, thus covering the main spawning times for broadcast spawning corals (Quinn & Kojis, 2008). Upon collection, both tile surfaces were photographed, immersed in 10% household bleach for 48 h, rinsed with fresh water and dried. Individual recruits on both surfaces were counted and photographed under a stereo microscope incorporating a digital camera, followed by identification into major families (Acroporidae, Pocilloporidae and other) (Babcock *et al.*, 2003; Ferse *et al.*, 2013). Analyses into coral recruitment rates focused on the underside of the tiles where 97% of the recruits settled.

Table 5.1. Summary of the in situ conventional and complementary metrics selected for site comparisons in the current study.

Measurement	Interpretations	Reference
CONVENTIONAL METRICS		
Proportional cover of key benthic groups	State of benthic reef community according to dominance of different groups	Hughes (1994); Norström *et al.* (2009)
Herbivorous fish biomass along visual transects	High herbivorous fish biomass implies top-down control of algae; (no-take) management should increase biomass	Mumby *et al.* (2006); Hughes *et al.* (2007)
Herbivorous fish taxonomic richness on visual transects	High species diversity reflects ecological insurance; within functional groups reflects functional redundancy, and more species to replace functions if species are removed	Elmqvist *et al.* (2003); Nyström (2006)
Rugosity	A complex reef structure implies a healthier reef and a better habitat for fish; ecosystem service provision linked to rugosity	Alvarez-Filip *et al.* (2009); Graham & Nash (2013)
COMPLEMENTARY METRICS		
Turf height and index	Ability of coral recruits to settle; herbivorous grazing function; sediment input	Birrell *et al*, (2005); Goatley *et al.* (2013); Mumby *et al.* (2013); Flower *et al.* (2017)
Juvenile coral abundance	Ability of coral larvae to settle and of settlers to grow/survive; high abundance contributes to reef recovery	McClanahan *et al.* (2012)
Coral/algal interactions	Which key benthic group has a competitive advantage and to what extent; frequency and severity indicates reef trajectory	Barott *et al.* (2012); Anthony *et al.* (2015)
Coral recruitment onto tiles	Ability of coral larvae to settle and settlers to grow/survive; colonisation of open bare substrate from coral mortality or predation (e.g. bite scars); high abundance contributes to reef recovery	McClanahan *et al.* (2012)
Herbivory rates from video observations	Function and redundancy of herbivorous fish (species); top-down control of algae	Fox & Bellwood (2008); Hoey & Bellwood (2009); Plass-Johnson *et al.* (2015)

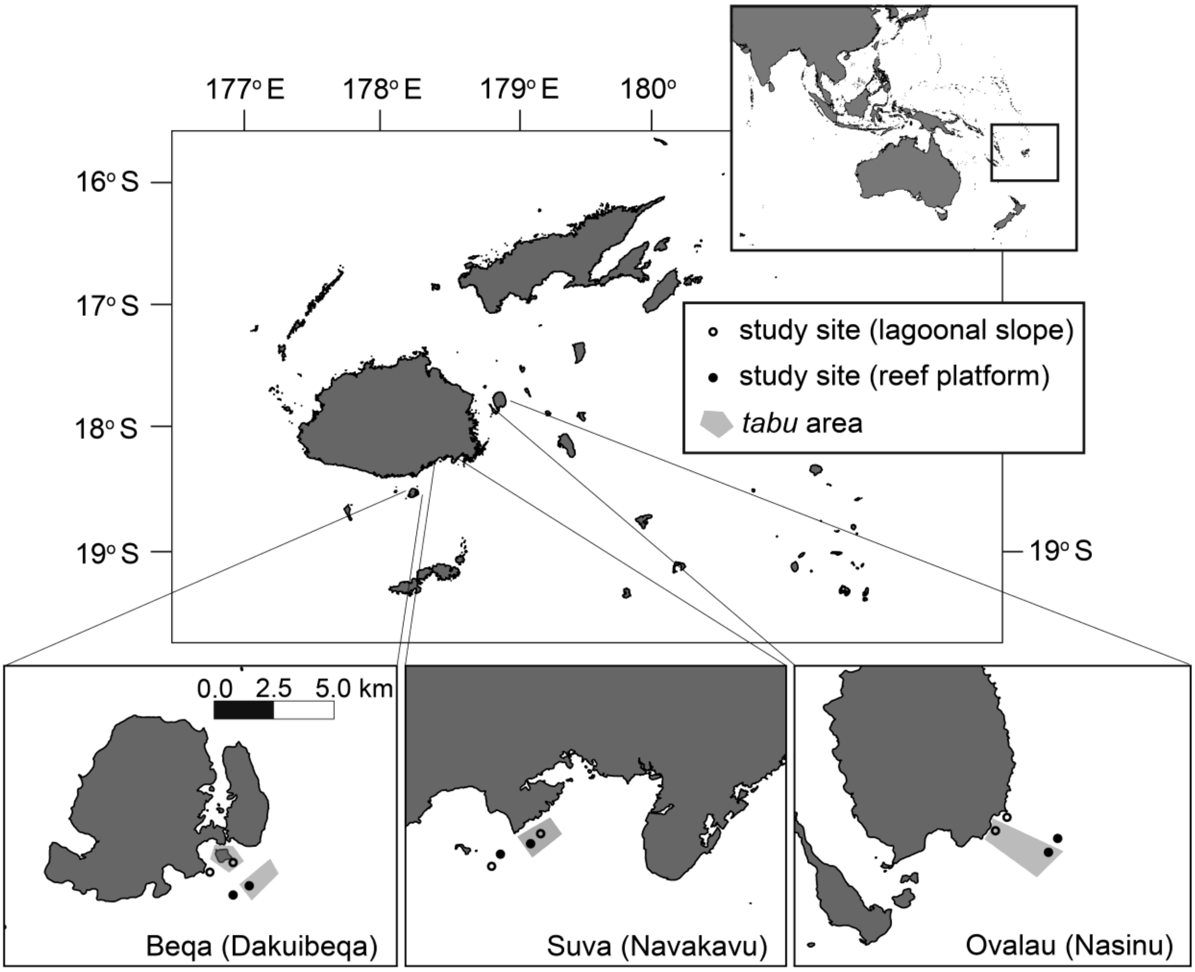


***Figure 5.1**: Map of study sites in Fiji. Scaling is consistent across maps of each study site.*

Herbivory rates were quantified through in situ GoPro video recordings. Video cameras were fixed overlooking reef substratum for *ca.* 60 min (n = 4–5 site^{-1}). A 1 m^2 quadrat was briefly placed on the benthos in front of the camera and photographed for subsequent quantification of grazable substrate (i.e. substrate other than live corals, sponges and sand). Video analysis excluded the initial 15 min to minimise any diver interference with usual fish behaviour. For the following 30 min, all nominally herbivorous fish detected within the frame were recorded to species level in order to assess taxonomic richness from video recordings. To quantify bite rates, all herbivorous fish observed feeding within the 1 m^2 quadrat frame were identified to species and the number of bites taken on the substratum were recorded. Bite rates were scaled to the amount of grazable surface available from the corresponding quadrat (bites m^{-2} grazable surface h^{-1}).

5.3.2.3. Informative value of turf height measurements

To evaluate the informative value of incorporating turf height into reef monitoring, we investigated its relationship with critical ecosystem processes that determine the continuity and renewal of coral populations after physical disturbances. To investigate the effect of turf height on coral recruitment rate, turf height was measured to the nearest mm at 3 points on each tile surface at collection. The relationship between juvenile coral density and both turf height and turf index were quantified from transect data. Effects of turf height on coral-algal interactions were evaluated by comparing the outcomes of interactions between corals and algal turfs < 5 mm and > 5 mm.

5.3.2.4. Water quality assessments

Although the close proximity of paired sites assured similar environmental conditions, water samples were collected for subsequent analyses of inorganic nutrient concentrations to confirm that observed differences between paired sites were not driven by water quality. Three water samples of 40 ml were collected from each site using syringes *ca*. 10 cm over the seabed without disturbing the sediment. Samples were immediately filtered over 0.45 µm membrane filters and transported on ice to a dry lab where they were frozen and maintained at -20˚C until nutrient analysis was conducted. Inorganic nutrient (nitrate, nitrite and phosphate) concentrations were measured at the Leibniz Centre for Tropical Marine Research (ZMT), using a SKALAR Automated Wet Chemistry Analyzer (San++).

5.3.3. Statistical analyses

The effect of local management and reef habitat on coral recruitment data (Suva only) were investigated using two-way ANOVA models (*aov* function - R base package; R Development Core Team, 2013) investigating single and interactive effects of both factors. Arcsine transformed percentage benthic cover of live hard coral, fleshy algae and algal turfs, as well as turf height, turf index, juvenile coral counts, rugosity, and log ratios (percentage winning + 1 / percentage neutral + 1) of coral-fleshy algae and coral-algal turf interaction outcomes were each individually tested for their responses to local management, reef habitat and any interactions between the two factors. Two-way ANOVA models accounted for the paired design of the study by including an error term for location to analyse within-subject (location) differences, and incorporated both management status and reef habitat as fixed interactive terms. Taxonomic richness of herbivorous fish species in total and within key functional groups was calculated per site both for data from UVC and video footage. Data were compared between *tabu* and open pairs using paired t-tests, which were also used to compare differences in the data provided by two data collection methods. Differences in biomass of herbivorous fish functional groups between *tabu* and adjacent open sites were tested by PERMANOVA (Anderson *et al*., 2008) using the PERMANOVA+ add-on in Primer v.6 (Primer-E, Plymouth, UK). PERMANOVA tests used the Bray-Curtis similarity coefficient, with type 3 sums of squares and unrestricted permutation of raw data, and incorporated the same statistical design as described for the within-subject (location) ANOVA models. To test overall differences between sites according to both conventional and complementary metrics, we used principal components analyses (PCA; built-in *prcomp* function - R Development Core Team 2013) based on Euclidean distances after removing any collinear terms ($R^2 > 0.6$). To discard that differences between paired sites were not attributable to differences in water quality, inorganic nutrient concentrations were compared between paired sites again using two-way ANOVA models incorporating location as an error term. A generalised linear regression model (glm function – R base package), incorporating a quasi-poisson distribution, evaluated the relationship between turf height and coral recruitment rate across all tiles from all sites. A changepoint analysis was run to identify any potential thresholds in mean coral recruitment rate with different turf heights (changepoint R package; Killick & Eckley, 2013). The effects of turf height and turf index on juvenile coral density were analysed using generalised linear regression models (glm function – R base package) on transect data. Finally, one-way ANOVA models investigated the effect of turf height (< 5 mm, > 5 mm) on the log ratio (percentage winning + 1 / percentage neutral + 1) of coral-algal turf interaction outcomes. Model residuals for all models were extracted and checked visually to confirm that model assumptions were not violated.

5.4. Results

Conventional reef status metrics revealed no differences in benthic or fish communities between *tabu* areas and adjacent open reefs (Table 5.2; Figure 5.2a). Benthic cover of hard coral, fleshy algae and algal turfs, as well as rugosity was consistent across *tabu* and adjacent open reefs, regardless of habitat type. Furthermore, neither biomass nor taxonomic richness of herbivorous fishes were affected by management according to UVC data (Figure 5.2a; Figure 5.3a; Table 5.2). Habitat type itself did however drive differences according to conventional metrics, with lagoonal slopes exhibiting significantly higher rugosity, benthic cover of live hard coral and herbivorous fish biomass, and lower cover of fleshy algae, in comparison to reef platforms.

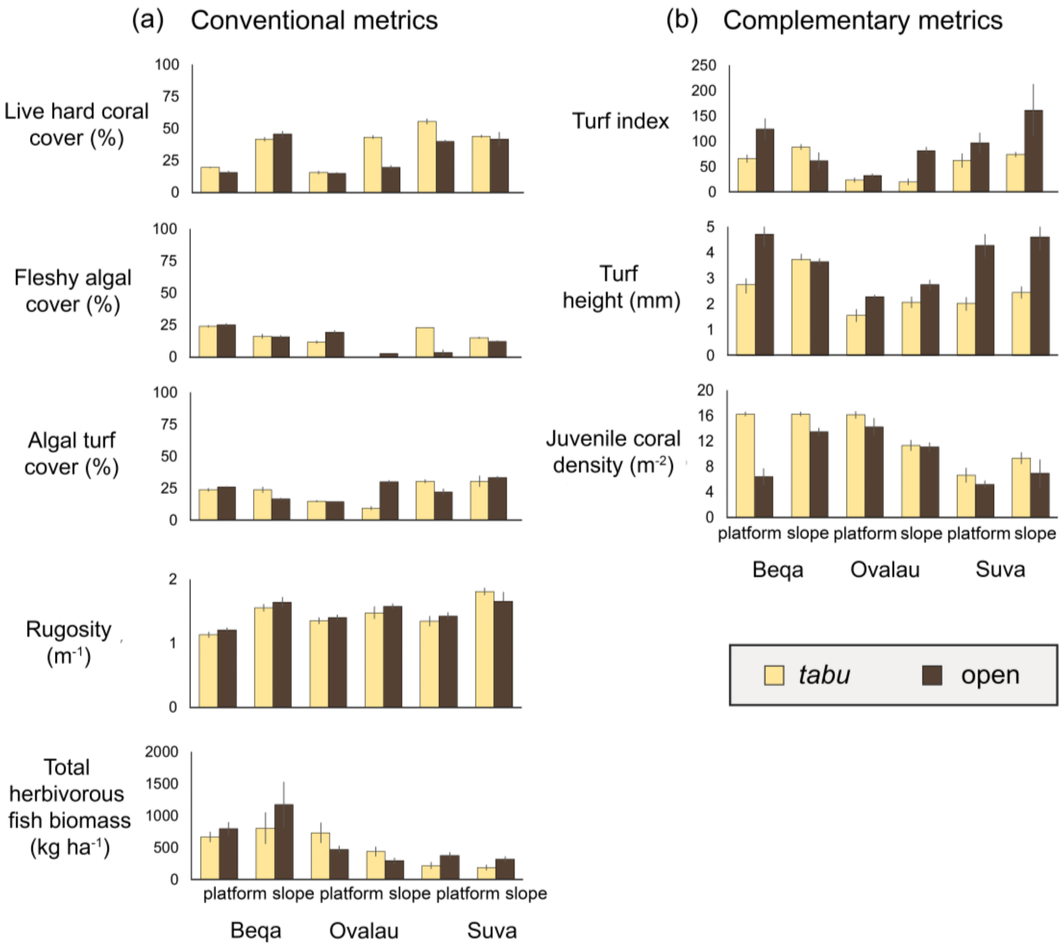


Figure 5.2: Benthic and fish community responses (mean ± SE) to local management as determined by (a) conventional and (b) complementary metrics.

Table 5.2. Results of statistical analyses comparing tabu and open reefs for conventional and complementary metrics. Superscripts refer to statistical designs used: ^{1}within-subject ANOVA, ^{2}within-subject PERMANOVA, ^{3}paired t-tests, ^{4}two-way ANOVA.

	Local management			Reef habitat			Interaction		
	F	*p*	Effect	F	*p*	Effect	F	*p*	Effect
CONVENTIONAL METRICS									
Hard coral (%)^1	$_{1,30}$ = 4.1	0.052	--------	$_{1,30}$ = 13.6	**<0.001**	PL < SL	$_{1,30}$ = 0.02	0.878	--------
Algal turfs (%)^1	$_{1,30}$ = 0.5	0.508	--------	$_{1,30}$ = 0.3	0.575	----------	$_{1,30}$ = 2.3	0.137	--------
Fleshy algae (%)^1	$_{1,30}$ = 0.1	0.767	--------	$_{1,30}$ = 10.6	**0.003**	PL > SL	$_{1,30}$ = 1.6	0.217	--------
Rugosity^1	$_{1,30}$ = 0.7	0.397	--------	$_{1,30}$ = 44.7	**<0.001**	PL < SL	$_{1,30}$ = 0.4	0.541	--------
Herbivore biomass^2	$_{1,84}$ = 2.3	0.060	--------	$_{1,84}$ = 4.1	**0.012**	PL < SL	$_{1,84}$ = 0.9	0.445	--------
Herbivorous fish taxonomic richness UVC^3		0.5	--------						
COMPLEMENTARY METRICS									
Turf height (mm)^1	$_{1,30}$ = 33.2	**<0.001**	O > T	$_{1,30}$ = 1.5	0.235	---------	$_{1,30}$ = 2.6	0.117	--------
Turf index^1	$_{1,30}$ = 8.7	**0.006**	O > T	$_{1,30}$ = 0.3	0.290	---------	$_{1,30}$ = 0.8	0.810	--------
Juvenile coral abundance^1	$_{1,30}$ = 10.5	**0.003**	O < T	$_{1,30}$ = 0.4	0.552	---------	$_{1,30}$ = 1.8	0.190	--------
Coral recruitment^4	$_{1,56}$ = 22.1	**<0.001**	O < T	$_{1,56}$ = 0.002	0.963	---------	$_{1,56}$ = 1.7	0.196	--------
Outcome coral-algal turf interactions^1	$_{1,66}$ = 6.1	**0.016**	O < T	$_{1,66}$ = 1.0	0.330	---------	$_{1,66}$ = 0.1	0.718	--------
Outcome coral-fleshy algae interactions ^{1}	$_{1,66}$ = 7.2	**0.011**	O > T	$_{1,66}$ = 22.3	**<0.001**	PL < SL	$_{1,66}$ = 1.8	0.976	--------
Herbivorous fish bite rates (m^{-2} h^{-1})^2	$_{1,44}$ = 0.2	0.752	--------	$_{1,44}$ = 0.01	**0.008**	PL > SL	$_{1,44}$ = 0.3	0.682	--------
Herbivorous fish taxonomic richness video^3		0.003	O < T						

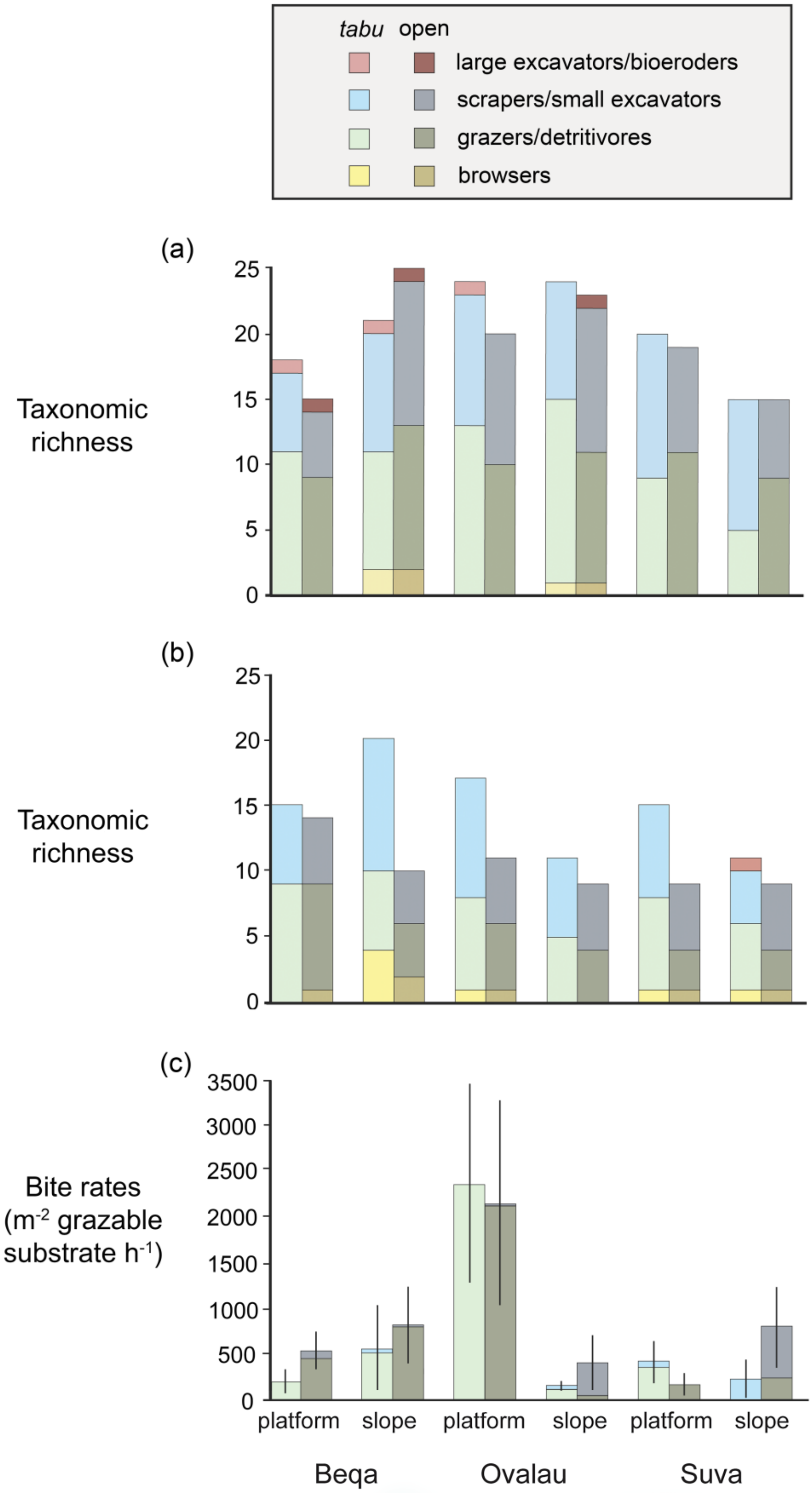


Figure 5.3: *Taxonomic richness of herbivorous fish at each reef, separated by functional group as determined by (a) UVC, and (b) from species encountered in video footage, and (c) herbivorous fish bite rates (mean ± SE) for each reef, separated by functional group.*

In contrast, complementary status and ecological function-based metrics indicated that local management was driving profound differences in biotic substrate colonisation (Figure 5.2b; Table 5.2). Mean turf height (33 ± 8% lower) and turf index (33 ± 16% lower) were significantly reduced within *tabu* areas compared to adjacent reefs open to fishing, and juvenile corals (<3 cm) were significantly more abundant (42 ± 22% higher) within *tabu* areas. The positive effect of local management on juvenile coral density was reflected by coral recruitment rates at Suva which were significantly higher within the *tabu* area (736 ± 89 recruits m^{-2}) than the adjacent open reef (284 ± 35 recruits m^{-2}; Table 5.2; Figure 5.4). The positive effect of local management was consistent across the two reef habitat types, and was reflected by the major identified families of recruits (ANOVA, Acroporidae $p = 0.016$; Pocilloporidae $p < 0.001$; Figure 5.4). In terms of coral-algal interactions, fleshy algae were more competitive against coral colonies in adjacent open areas, but in contrast algal turfs were more competitive against corals within *tabu* areas (Table 5.2; Appendix Ci).

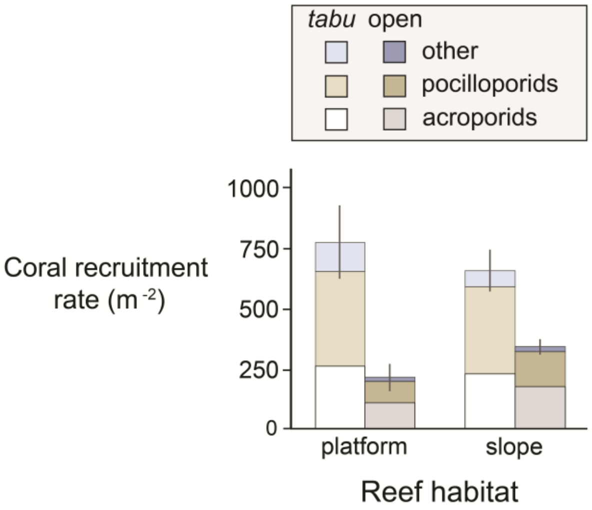


Figure 5.4: Coral recruitment rates (mean ± SE) at each study reef in Suva, with relative contributions of major families (Acroporidae, Pocilloporidae, other).

Data extracted from video footage indicated that taxonomic richness of grazers/ detritivores (paired t-test, $p = 0.007$) and in total (paired t-test, $p = 0.03$) were higher inside *tabu* areas compared with adjacent open areas (Figure 5.3b). Videos captured a higher taxonomic richness of herbivorous fish within the browser functional group than UVC (paired t-test, $p = 0.04$), but UVC found higher richness of grazers / detritivores (paired t-test $p < 0.001$) and scrapers / small excavators (paired t-test $p = 0.003$) than video footage. Bite rates of herbivorous fish showed large variation and did not differ significantly between *tabu* and adjacent open reefs within either reef habitat (Figure 5.3c; Table 5.2). Grazers / detrivitores were responsible for most bites among sites, and bite rates at the reef platform in Ovalau were significantly higher than elsewhere (PERMANOVA, $p < 0.01$; Figure 5.3c). At this site, turf height was also low (*tabu*: 1.6 ± 0.3 mm, open: 2.3 ± 0.1 mm; Figure 5.2b).

A PCA based on conventional metrics revealed similarities of open sites across the second principal component (24.9% variance explained), whereas *tabu* sites were heterogeneously dispersed around the matrix (Figure 5.5a). In contrast, when the PCA incorporated complementary status and ecological function-based metrics, a clear differentiation of local management was revealed across the first principal component (43.7% variance explained; Figure 5.5b). The PCA revealed that open reefs were associated with higher turf height and diversity of excavators as extracted from video footage. *Tabu* reefs in contrast exhibited strong positive associations with juvenile coral density, bite rates and taxonomic richness of grazers/detritivores and scrapers/small excavators as determined from video footage. Two sites behaved as anomalies and fitted into the opposing cluster: the open platform at Ovalau driven by the exceptionally high bite rates, and the *tabu* slope at Suva driven by the high number of excavators observed within video footage. Environmental data confirmed that differences between paired *tabu* and open reefs were not driven by differences in inorganic nutrient concentrations (Appendix Cii).

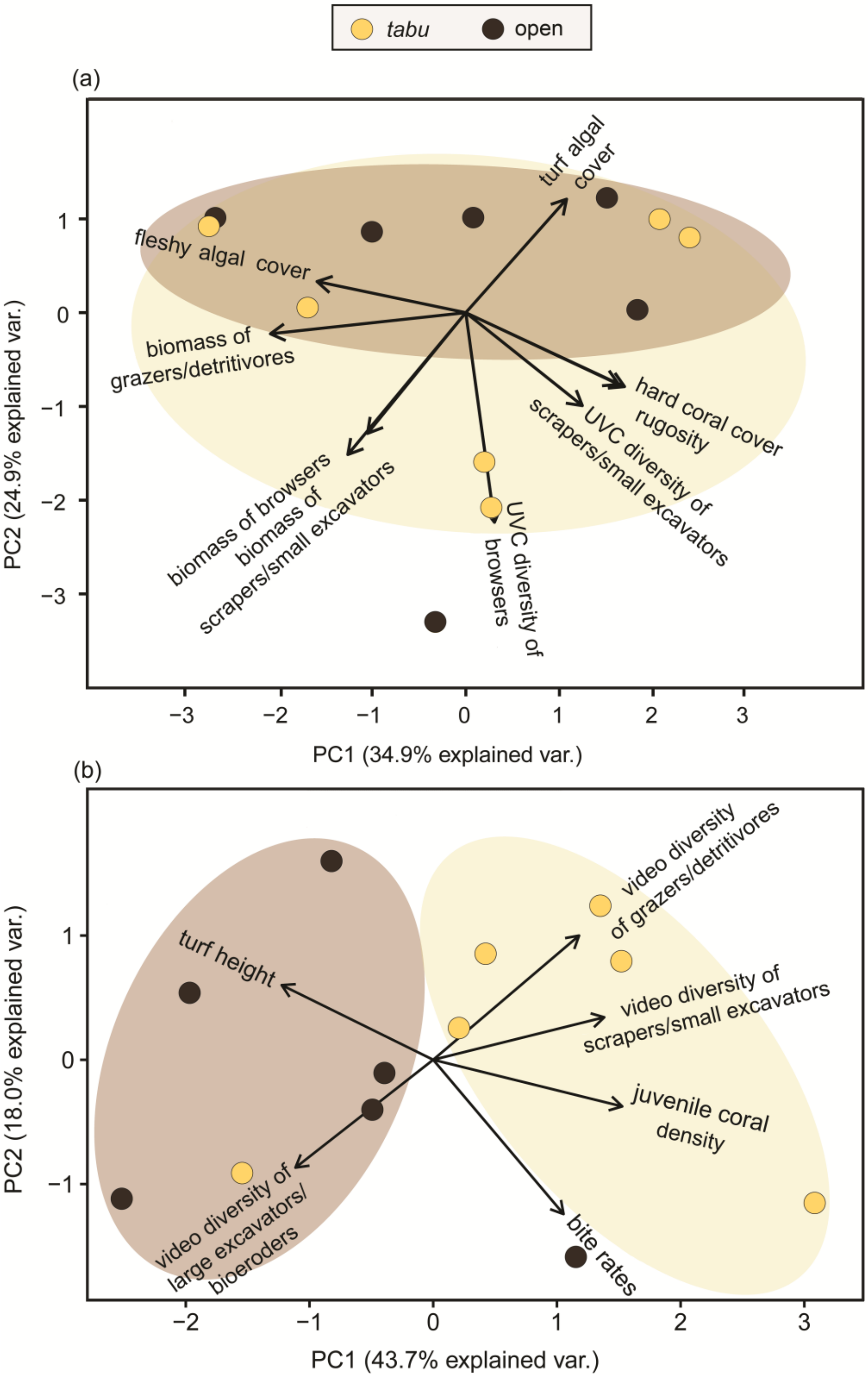


Figure 5.5: Principal components analysis based on Euclidean distances of study reefs, according to (a) conventional and (b) complementary metrics. Shaded areas represent the extent of similarities between reefs of the same management status.

As well as exhibiting significant responses to management, turf height was also itself strongly associated to other benthic processes. It was inversely related to coral recruitment rate (GLM, p = 0.028), with a threshold of 5.7 mm turf height identified after which mean recruitment rate dropped from 578 to 133 recruits m^{-2} (Figure 5.6a). Both turf height and turf index were also negatively correlated with juvenile coral density (GLM, p = 0.03; Figure 5.6b, c). In addition to being detrimental to coral recruitment and succession, algal turfs with canopy heights > 5 mm were also significantly more successful in competition with neighbouring corals compared to algal turfs < 5 mm in height (ANOVA, $F_{(1,70)}$ = 16.02, p < 0.001; Figure 5.7).

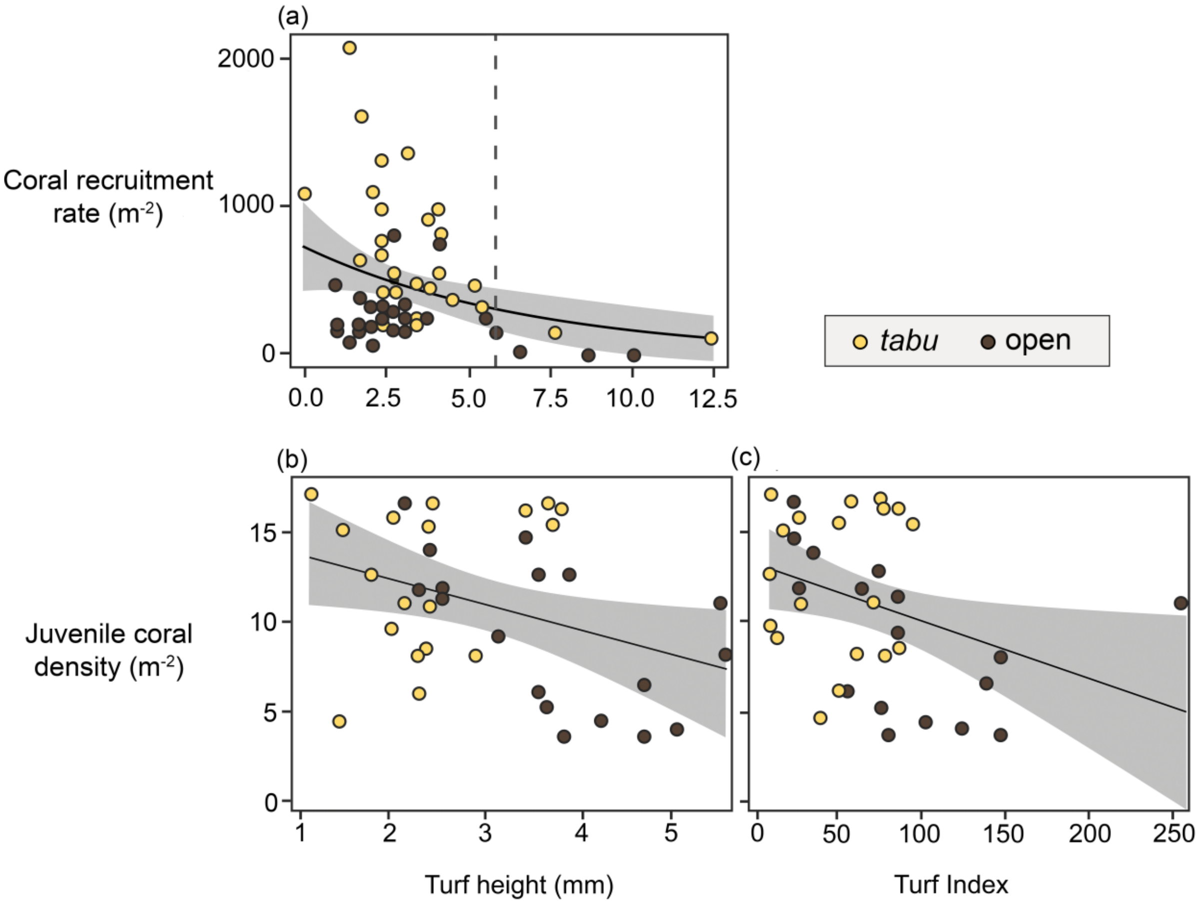


Figure 5.6: Coral recruitment rate as a function of turf height (a) according to generalised linear model output, with the dashed line indicated an identified threshold after which average recruitment significantly declines. Relationships between juvenile coral density and (b) turf height and (c) turf index.

5.5. Discussion

By measuring a variety of metrics in paired *tabu* (periodically closed to fishing) and adjacent fished areas, this study allowed us to explore the ability of different approaches to detect changes within benthic and fish communities under local coral reef management in Fiji. Results show clearly that contrasting interpretations of management effectiveness can be made depending on the metrics measured in surveys. According to conventional metrics, local management did not appear to promote more desirable benthic community attributes such as increased live hard coral cover or decreased algal biomass. Furthermore, herbivorous fish biomass and taxonomic richness from conventional visual surveys did not reflect any management effect. Nonetheless, a set of complementary status and ecological process-based metrics indicated that local management was promoting desirable ecosystem attributes in terms of securing the continuity and renewal of coral populations. Particularly, the scope of the complementary metrics to capture differences in biotic substrate colonisation allowed the detection of changes that have important implications for system resilience that would otherwise have been overlooked.

Coral recruitment rate was higher within the *tabu* area at Suva, and in turn juvenile coral density was superior among the set of *tabu* areas compared with fished reefs. Coral recruitment and successive growth are critical components of reef recovery (McClanahan *et al.,* 2012), indicating that protected areas in this study have effectively improved the resilience of the system to perturbations. Laboratory choice experiments and field observations have shown that both fish and coral larvae preferentially settle on reefs dominated by coral rather than algal communities (Lecchini *et al.*, 2013), for example at reefs that have exhibited a positive response to local management (Dixson *et al.*, 2014). Although the protected areas in this study did not exhibit conspicuous differences in broad benthic groups such as hard coral or fleshy algae, turf height and turf index were significantly reduced within *tabu* sites compared with adjacent open reefs. Coral recruitment rate indeed strongly declined with increasing turf height, with a threshold identified at *ca*. 5 mm turf height above which recruitment rates exhibited a five-fold decrease, corroborating other studies (Birrell *et al.*, 2005). Interestingly, turf height and turf index were also significantly negatively related to juvenile coral density despite turf heights consistently averaging < 5 mm, showing the opposite trend to equivalent short-cropped turfs in Micronesia (Mumby *et al.*, 2013). Algal turfs > 5 mm in height were also significantly more competitive against neighbouring corals as shown by bleached or necrotic tissue at the boundary of the interaction, despite within-site comparisons counterintuitively indicating that competitiveness of algal turfs was higher inside *tabu* areas. In contrast, fleshy algae were more competitive against corals in open areas. Under conditions where algae gain a competitive advantage against corals, the ability of coral communities to sustain dominance into the future can be compromised.

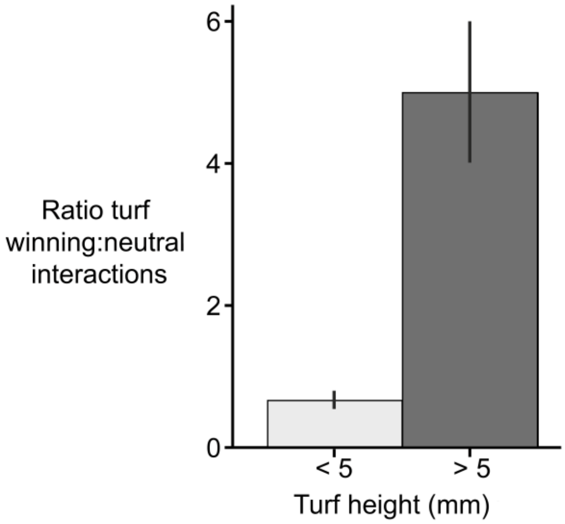


***Figure 5.7**: Ratio (mean ± SE) of winning vs. neutral interactions (algal perspective) between short (< 5 mm) and long (> 5 mm) algal turfs in interaction with neighbouring coral colonies. Larger ratios represent higher competitivity of algal turfs.*

Although benthic condition indicates that herbivorous fish function is superior inside protected areas, conventional surveys into herbivorous fish communities themselves showed no obvious benefits from local management. Neither biomass nor taxonomic richness was significantly different between *tabu* and open reefs according to UVC data. Complementary measurements of herbivorous fish bite rates also did not indicate promoted function within protected areas. Nonetheless, video footage indicated that overall taxonomic richness of herbivorous fishes was superior inside *tabu* reefs and more browsers were seen during videos than UVC, emphasising the usefulness of this surveying method. Provisional analyses of the functional space provided by herbivorous fishes also differ strongly depending on the method by which fish communities are measured (i.e. present in UVC, present in video footage or recorded grazing in video footage – Appendix Ciii). These results indicate that conflicting interpretations of herbivorous fish function and taxonomic richness can be made depending on the metrics used to measure them. Browsers such as *Naso* spp. (Acanthuridae) fulfil critical ecological roles in terms of maintaining system resilience (Hoey & Bellwood, 2009; Ford *et al*., 2016) but are particularly wary of divers and can consequently be overlooked during standard UVC (Kulbicki, 1998). Browsers were only responsible for a negligible proportion of bites, but their browsing behaviour was probably limited by the minimal presence of fleshy algal types other than encrusting *Lobophora*. Video recordings of bioassays offering alternative fleshy algal varieties may reveal further insights into the potential function of browsing fishes at these sites, indicating their ability to consume fleshy algae which can bloom following disturbances (Hoey & Bellwood, 2009; Rasher *et al*., 2013). Poaching within *tabu* areas is a problem in the region, and may explain why there are no conspicuous benefits of protection on herbivorous fish biomass in baseline surveys. Interestingly, the findings within this study are in stark contrast to a recent study from the Coral Coast in Fiji, where similar small (i.e. < 1 km^2) marine protected areas (MPAs) were found to drive significant increases in a set of conventional metrics (Bonaldo *et al.*, 2017). However, the Coral Coast MPAs had an advantage of being within close enough proximity to each other to create an MPA network which can strongly enhance beneficial effects of protection. Furthermore, the Coral Coast sites were located closer to villages on a shorter reef platform (as close as 30 m from shore) than the present study's reefs, making enforcement easier, and the Coral Coast coastline is populated by some large hotels which offer (i) alternative livelihoods to coastal communities and (ii) incentives to enforce MPAs through tourism (Ford pers. obs. 2016). Poaching within the present study's sites may primarily be focused on night time spearfishing that removes larger individuals, whilst fishers still avoid net fishing within *tabu* areas thus facilitating survival of smaller individuals. There are however many challenges associated with fish surveys, including temporal- and surveyor-related discrepancies associated with fish surveys, wariness of some key species and the potential dilution of conspicuous management effects on larger individuals caused by poaching. These challenges indicate that if surveys aim to measure system trajectories and resilience, it would strongly benefit them to incorporate complementary metrics focusing on long-term responses to fish function, such as biotic substrate colonisation.

In addition to providing information on the effect of local management on coral recruitment processes, this study provides useful information on recruitment rates during warmer months on inshore Fijian reefs, for which data is sparse. Consistent with many previous coral recruitment studies, the significant majority of recruits settled on the underside of the tiles (Harriott & Fisk, 1987; Babcock & Mundy, 1996; Doropoulos *et al*., 2014). Coral recruitment rates at Suva were relatively high, particularly within the *tabu* area (mean >700 recruits m^{-2}), compared with other studies in the region (Gleason, 1996; Quinn & Kojis, 2008) and elsewhere (e.g. Smith, 1992; Glassom *et al.*, 2004). Abundances of acroporid and pocilloporid recruits within *in situ* quadrats were similar at all sites, consistently comprising over 80% of the total coral recruit population. The high proportion of pocilloporid recruits was not reflected in adult populations at these inshore sites which were dominated by poritids and acroporids. This trend reflects a higher mortality of juvenile brooders such as pocilloporids compared with spawners such as acroporids (Doropoulos *et al.*, 2015).

Whilst strong relationships between coral reef benthos and herbivorous fish communities have been established across the Caribbean region, limited research from the Pacific region suggests that relationships are less clear (Wismer *et al.,* 2009; Mumby *et al.*, 2013). Even within the Caribbean region, studies tend to neglect shallow lagoonal habitats. Thus, this study additionally provides important information on relationships between coral reef herbivory, benthic communities and coral recruitment success in the context of inshore reefs within the Pacific Island region. Due to limited site replication and a lack of long-term data, we are hesitant to draw firm conclusions on the effectiveness of local management in Fiji. Nonetheless, we are confident from our results that local management can promote positive system trajectories and resilience dynamics within the inshore reef ecosystems. Complementary metrics related to biotic substrate colonisation suggest enhanced recovery processes and greater diversity of browsing herbivorous reef fish within managed areas. Furthermore, whilst conventional metrics were often significantly different across inshore reef habitat types, complementary metrics remained consistent, indicating their applicability to comparing different inshore reef habitats. In particular, turf height shows very strong potential as an indicator for reef trajectories and resilience, as it was significantly related to coral recruitment success, juvenile coral abundances and the outcome of coral-algae interactions. As well as suppression of herbivory by external factors such as overfishing (Mumby *et al.*, 2013; Clausing *et al.*, 2014), increased canopy height can reflect higher sediment loading and accumulation within the benthos with associated reductions of grazing (Bellwood & Fulton, 2008; Goatley *et al.*, 2013). Different characteristics of algal turfs can therefore reflect destabilised and thus degrading reef systems, or recovering reefs exhibiting healthy ecological processes. These results thus emphasise the informative value of incorporating this simple and quick measurement into future baseline surveys. Few monitoring programmes currently include this measurement or other metrics that indicate aspects of biotic substrate colonisation (Appendix Civ), demonstrating the need to re-evaluate key indicators to diagnose coral reef health and resilience (McClanahan *et al.*, 2012; Anthony *et al.*, 2015; Flower *et al.*, 2017).

5.6. Conclusions

Even under a scenario whereby climate agreements are implemented internationally, >75% of reefs will experience annual severe bleaching by 2070 (van Hooidonk *et al.*, 2016) and only 10% are projected to persist by 2100 (Frieler *et al.*, 2012). It is thus urgent that managers are able to critically scrutinise the effectiveness of different management tools as well as to prioritise areas in which to invest and focus future efforts. In data-poor regions such as many Pacific islands, long-term monitoring data from which to evaluate ecosystem trajectories may not be available. The additional inclusion of relatively simple and quick complementary status and ecological function and process-based metrics into surveys can overcome this limitation. Particularly measurements that focus on biotic substrate colonisation can be very easily incorporated and have the resolution to capture subtle but important differences between increasingly homogeneous reefs that provide a strong indication of ecosystem trajectories. Monitoring should thus focus on measurements that respond rapidly to changing conditions and that may indicate whether the system is likely to exhibit a stable temporal trajectory or to shift to alternative dominance states in response to future perturbations.

5.7. References

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CHAPTER SIX

BIOLOGY, ECOLOGY AND MANAGEMENT OF KEY HERBIVOROUS UNICORNFISH IN THE PACIFIC

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Ford AK, Bejarano S, Marshell A, Mumby PJ (2016). Linking the biology and ecology of key herbivorous unicornfish to fisheries management in the Pacific. *Aquatic Conservation: Marine and Freshwater Ecosystems*. doi: 10.1002/aqc.2623

6.1. Abstract

Naso lituratus (orangespine unicornfish) and Naso unicornis (bluespine unicornfish) are widespread species that are heavily targeted in many nearshore fisheries of Pacific Island countries. In addition to providing a critical food and income source, both species fulfil critical ecological functions in the top-down control of coral reef macroalgae; particularly fleshy brown algae (i.e Sargassum spp.) which can out-compete and smother corals. Despite heavy long-term harvesting, there are currently very limited species-specific management measures. This review assesses the biology and ecology of both species, and combines this with the current status of the fisheries in the Pacific, and proposes realistic ecosystem-based species-specific fisheries policies. Although unicornfish populations have displayed continuing resilience to heavy fishing pressure, reports of declining stocks combined with a range of life-history traits (i.e. longevity, habitat-specificity, easily-targeted aggregations), indicate that both species are vulnerable to overexploitation. Modern day common fishing practices such as SCUBA and night-time spearfishing are intensifying their exploitation. The most effective management measure would be fishing effort constraints, including banning modern and unsustainable methods. However, due to enforcement limitations in Pacific Islands, the most practical approach to management would include a combination of management tools, including periodic sales bans around identified spawning times (i.e. Hawaii; May-June), and size/catch limits. Furthermore, home range data suggest that even with limited knowledge, small MPAs (< 1 km^2) in structurally complex areas using natural boundaries should accommodate the movement patterns of both species and provide sufficient protection; although MPAs of > 10 km linear distance are recommended for N. lituratus. This comprehensive review confirms the pressing need for implementation of the aforementioned management practices to protect these species in regions where they are heavily targeted, and prevent the impairment of their critical ecological function and importance as a food and income source.

6.2. Introduction

The orangespine unicornfish, *Naso lituratus* (Forster 1801), and the bluespine unicornfish, *Naso unicornis* (Forsskål 1775), are relatively large-bodied acanthurids that are common in a variety of coral reef habitats, where they feed primarily on large fleshy macroalgae such as *Sargassum* spp. (Randall, 2001a). Both species genetically belong to the *Naso elegans* sub-clade which comprises unicornfish that are exclusively benthic foragers (Klanten *et al*., 2004). *N. lituratus* is widely distributed throughout the Pacific Ocean: from southern Japan to the Great Barrier Reef and New Caledonia, and east to the Hawaiian Islands, French Polynesia, Pitcairn Islands, and Clipperton Island (Randall, 2001). Once regarded as a wide-ranging Indo-Pacific species, morphological analyses confirmed that *N. lituratus* is replaced by *N. elegans* in most of the Indian Ocean (although these sister-species can still hybridize – see Hobbs *et al*., 2009) (Klanten *et al*., 2004). *N. unicornis* has a widespread distribution throughout the Indo-Pacific: from the Red Sea and East Africa through the Indian Ocean islands and India, east to Micronesia, Hawaii and Pitcairn Islands, French Polynesia, north to southern Japan, and south to the Great Barrier Reef and Lord Howe, Norfolk and Rapa Islands (Randall, 2001).

While the range of *N. unicornis* extends across the Indian Ocean, this review focuses specifically on the Pacific region where both species are culturally and commercially important food fishes, and are consistently among the top few species targeted by fishers (Table 6.1). Fishermen interviews in Palau highlighted the strong desirability for *N. lituratus* and *N. unicornis,* which were the most popular herbivorous fish, and became the most popular of all fish species during grouper fishery closures (Bejarano *et al,* 2013; Bejarano *et al.,* 2014). In Hawaii, *N. unicornis* has been among the top six species in the inshore fisheries for the last two decades, with harvesting continuing to increase every year (Figure 6.1), which is concerning local stakeholders (Eble *et al.,* 2009). Increased catches of these species may in part be due to shifting pressure as other more vulnerable targets have declined or succumb to more stringent management, but are also likely to be linked to ongoing fishing gear modernization. Nonetheless, the consistently dominant proportion of the catch that this species comprises indicates a high resilience to long-term fishing pressure. Yet despite this resilience, overexploitation is becoming increasingly apparent across the Pacific region (Table 6.1), particularly in Micronesia where declines of these species in the snorkelling catch have prompted fishermen to use SCUBA to access individuals at greater depths (Bejarano *et al.,* 2013; Lindfield *et al.,* 2014).

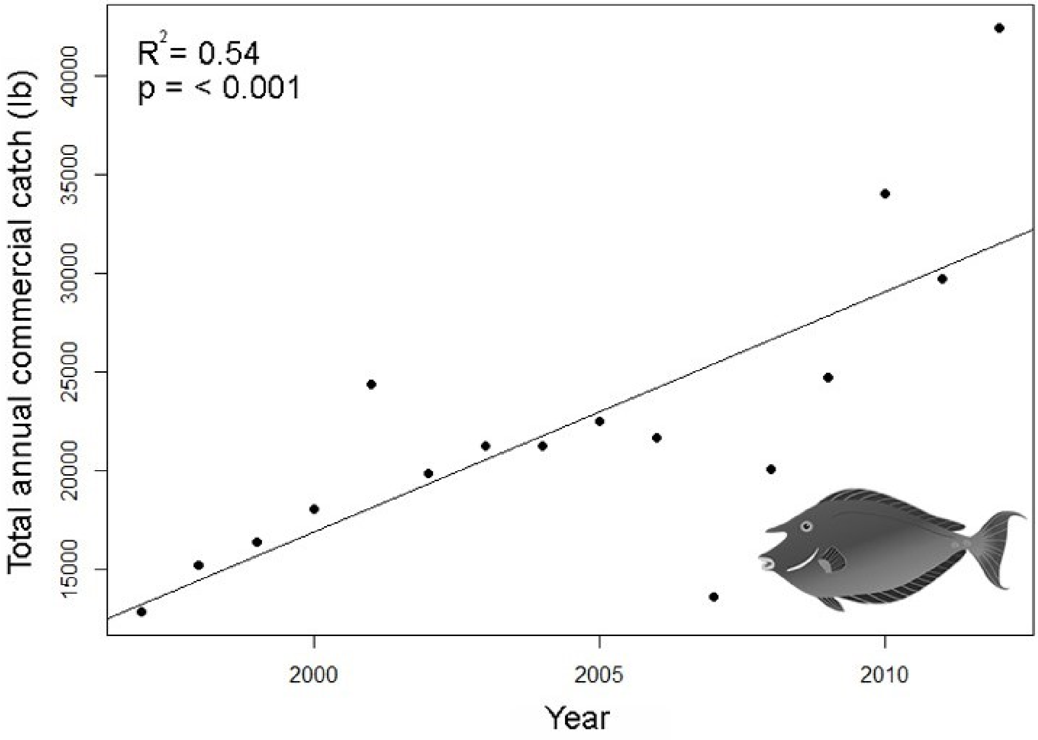

Figure 6.1. *Graph displaying increase in commercial marine fisheries landings of N. unicornis in Hawaii 1997-2012. N. unicornis has consistently been within the top 6 species in the inshore fisheries catch since 1997. Data represents landings reports from licensed fishermen, sourced from:* http://dlnr.hawaii.gov/dar/fishing/commercial-fishing/

In addition to their importance as a food and income source, these species have a key ecological function on coral reefs. The role of herbivorous fish in preventing algal phase-shifts on Indo-Pacific reefs is complex. Intense grazing upon algal turfs by key functional groups such as scrapers (e.g. *Scarus* spp.) and grazers (e.g *Acanthurus* spp.) likely plays a key role in preventing fleshy algae from emerging through the turf (Marshell & Mumby, 2012; Mumby *et al.*, 2013), though the relative role of individual species remains uncertain. However, if fleshy macroalgae do manage to escape grazing at the juvenile stage, then browsing species which feed exclusively on macroalgae are critical to reverse phase-shifts from hard coral to macroalgal domination (Green & Bellwood, 2009). Whilst other browsing species (i.e. siganids and ephippids) have been identified, *N. lituratus* and *N. unicornis* play a disproportionately important role in this group, specifically in removing established brown macroalgal varieties which are often the dominant group involved in such phase-shifts (Hoey & Bellwood, 2009b; Vergés *et al.*, 2012). As each herbivorous functional group plays a unique role in maintaining coral reef health and resilience, it is important to preserve functionally diverse communities. To achieve this, it is essential to implement management for heavily targeted species such as *N. lituratus* and *N. unicornis* with limited functional redundancy.

Although these unicornfish species are an important food and income source, and fulfil critical key ecological roles, there is a severe lack of explicit species-specific management measures (Table 6.1). A thorough evaluation of the biology, ecology and fisheries status of both species can identify which traits and factors increase their vulnerability to overexploitation, and consequently which management measures would be most effective. The information within this review aims to support the design of adequate and viable policies that promote sustainable harvesting and maintain key ecological functions.

6.3. Biology, ecology and life-history characteristics

Although population biology indicates two species with overlapping functions should be spaced in terms of resource acquisition, these two species occupy very similar niches. This overlap is permitted because of varying life-history characteristics including home range sizes, mortality and growth rates. While this section discusses these characteristics for the areas where there is available data, it is clear that there is significant spatial variation which is likely driven by latitudinal gradients and local environmental features (Trip *et al.*, 2008; DeMartini *et al.*, 2014; Taylor *et al.*, 2014b).

6.3.1. Reproduction and recruitment

N. lituratus and *N. unicornis* form aggregations of thousands of individuals in Palau (Johannes *et al.*, 1999), which local fishermen have linked to fish containing eggs (Sadovy & Colin, 2012), thus suggesting this represents spawning behaviour. Both species have spawning periods across several months and perhaps throughout the year in Micronesia (Johannes, 1981; Sadovy, 2007; Taylor *et al.*, 2014b), while *N. unicornis* spawning periodicity is highly seasonal in Hawaii, peaking in May and June (DeMartini *et al.*, 2014). This pronounced seasonality may be a result of macroalgal seasonality promoting increased mesenteric fat deposits leading to ripening of the gonads (Montgomery & Galzin, 1993). Larvae of both species have a pelagic duration of 60 - 90 days, until they reach 4 – 5 cm and actively swim towards the reef (Planes & Fauvelot, 2002; Lecchini *et al.*, 2005; Irisson & Lecchini, 2008).

6.3.2. Growth and mortality rates

Growth coefficient (K) values of <0.15, 0.15 to 0.3 and > 0.3 imply slow, medium and fast growth rates respectively (Froese *et al.*, 2000). Therefore, available data indicate that *N. unicornis* generally display slow to medium growth rates, whereas *N. lituratus* exhibits more rapid initial growth followed by an extended life span with little change in size (Figure 6.2; Table 6.2).

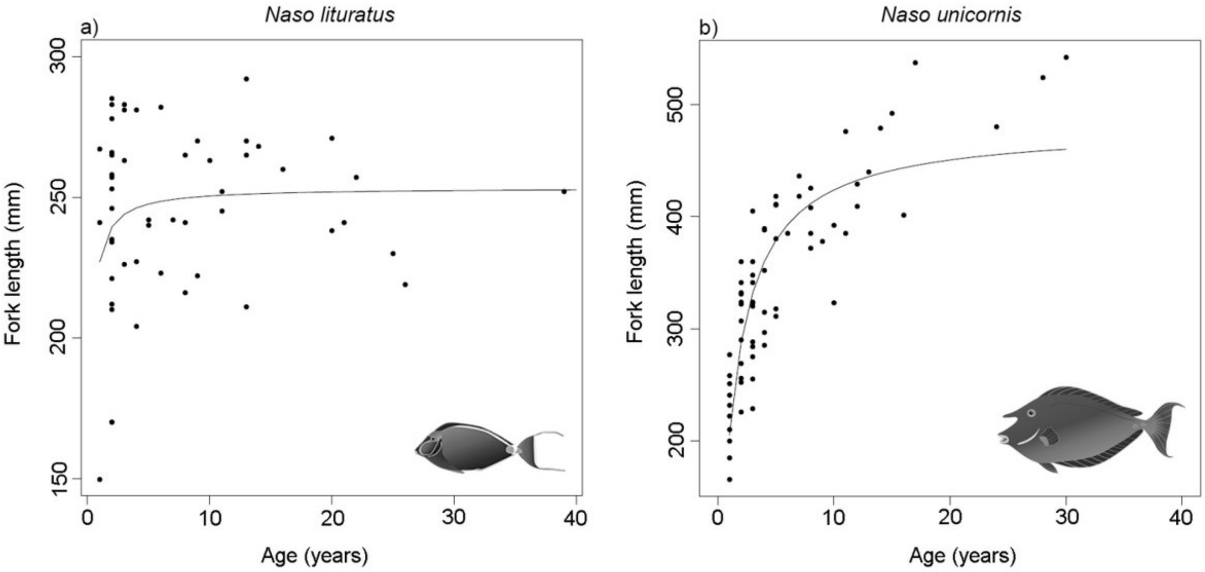

Figure 6.2. *Size-at-age data for (a) N. lituratus (n=52) and (b) N. unicornis (n=68) from the northern GBR. Length data are based on fork length (FL) (mm). Data provided by J.H. Choat.*

Mortality rates of *N. lituratus* and *N. unicornis* remain largely unknown (Table 6.2). *N. lituratus* consistently exhibits higher mortality rates than *N. unicornis* in Guam and Palau, which could be due to fast initial growth being associated with tissue damage and reduced lifespan (Mulligan & Leaman, 1992; Metcalfe & Monaghan, 2001; Lee *et al.*, 2013). Fishing (F) and natural mortality (M) rates tend to be alike for *N. lituratus,* while M is higher than F for *N. unicornis* (Table 6.2). According to Pauly (1984), fishing mortality should be around 40% of natural mortality for optimal exploitation, implying that *N. lituratus* is overexploited in Palau (Table 6.2). However, there is a severe lack of data on natural and fishing mortality from other regions and in recent years, making conclusions on the status of the fishery difficult, and which is further complicated by methodological discrepancies between studies.

6.3.3. Home ranges and movement patterns

Both *N. lituratus* and *N. unicornis* display strong site attachment, preferring structurally-complex areas which provide refuge holes (Meyer, 2003; Meyer & Holland, 2005; Marshell *et al.*, 2011). Relevant information on movements of *N. lituratus* and *N. unicornis* is only available from Guam and Hawaii, where two patterns were identified; commuting and foraying (Meyer & Holland, 2005; Marshell *et al.*, 2011). Commuters make daily crepuscular migrations over several hundred metres between night-time refuge holes and foraging areas, while forayers undertake multiple brief excursions from refuge holes to local foraging areas (10 – 40 m away). Although all home ranges were relatively small (<0.1 km^2), *N. unicornis* in Guam utilized home ranges an order of magnitude larger than in Hawaii (3.2 ha / 0.032 km^2 compared to 0.37 ha / 0.0037 km^2 average) despite both studies investigating similar fringing reef habitats. Generally home ranges correlate with body size (e.g. Welsh *et al.,* 2013), yet interestingly within these species the range of smaller *N. lituratus* (fork length: 188 – 204 mm) extended twofold further (6.8 ha / 0.068 km^2) than those of *N. unicornis* (fork length: 228 - 282 mm) in Guam. Commuters were influenced by habitat topography in both studies, using sheltered, shallow habitats for daily migrations. When presented with a system of uninterrupted barrier reefs which offer no restriction to movement through natural boundaries, unicornfish cover much larger distances (8 – 12 km in Pohnpei; unpublished data referred to in Taylor *et al.,* 2014b). Home ranges of *N. unicornis* correlate with body size, which is consistent with other acanthurids displaying ontogenetic habitat shifts, allowing larger individuals to optimize foraging once they reach a size at which they may escape predation risk (Dahlgren & Eggleston, 2000; Lecchini *et al.,* 2005; Marshell *et al.,* 2011).

6.3.4. Functional role

Both species target fleshy brown macroalgae which are consumed infrequently by other herbivore species, emphasizing the low functional redundancy of these unicornfish (Robertson & Gaines, 1986; Choat *et al.,* 2002; Choat and Robertson, 2002; Rasher *et al.,* 2013). Coral reef health is impacted by fast-growing algae that out-compete slow-growing corals when corals have been damaged by cyclones or coral bleaching (Hughes *et al.,* 2010). Algae blooms can also occur under additional conditions of eutrophication, iron enrichment, or herbivore depletion, affecting coral growth and recruitment (Mumby *et al.,* 2006; Hughes *et al.,* 2007; Steneck *et al.,* 2014). Coral recruitment can be inhibited by two major categories of algae: (1) algal turfs (Birrell *et al.,* 2005), and (2) fleshy macroalgae - particularly carpeting *Lobophora* spp., and erect *Sargassum* spp., which both reduce coral larval settlement and increase post-settlement mortality (Doropoulos *et al.,* 2014; Webster *et al.,* 2015). Coral recruitment is essential for reef recovery after disturbances, highlighting the critical need for key functional herbivores to facilitate coral settlement. Moreover, contact between adult corals and fleshy macroalgae can reduce coral growth rates and fecundity (Tanner, 1995; Foster *et al.,* 2008; Ferrari *et al.,* 2012). The impacts of algae on corals can drive a fundamental phase-shift in community structure on reefs from coral- to algal-domination (Done, 1992). While other functional groups (grazers, scrapers/small excavators, large excavators/bioeroders) are essential for controlling algal turfs, browsers such as *N. lituratus* and *N. unicornis* are responsible for removing established macroalgae (Green and Bellwood, 2009).

Sargassum spp. are one of the most common brown fleshy macroalgae on Indo-Pacific reefs, and can cover over 50% of the substrate in shallow inshore reefs (Bellwood *et al.,* 2006; Wismer *et al.,* 2009). *N. lituratus* and *N. unicornis* play a large role in controlling *Sargassum* spp. even in highly diverse fish assemblages, emphasizing the importance of looking beyond biodiversity when considering functional capacity (Hoey, 2010; Hoey & Bellwood, 2010). For example, despite accounting for only 32% of the biomass within Fijian MPAs, *N. lituratus* and *N. unicornis* were responsible for 94% of feeding on transplanted brown macroalgae (Rasher *et al.*, 2013). Correspondingly, at Lizard Island on the GBR, *N. unicornis* was responsible for 89.8% of observed bites on *Sargassum* spp., and further south at Orpheus Island, it was one of only three species (from a total of 43 herbivorous fish species present on the reef) that removed *Sargassum* spp. (Hoey & Bellwood, 2009b; Hoey, 2010). In addition to *Sargassum* spp. both species also graze on the chemically-rich brown algae *Dictyota bartayresiana*, which has been found to induce bleaching and suppress photosynthetic efficiency of *Porites* spp. (Rasher & Hay, 2010; Rasher *et al.*, 2013).

Importantly, a disparity may exist between biomass estimates and the functional impact of these species due to their recognized wariness to divers, and hence census-based assessments may have failed to capture their exact contribution to herbivory (Kulbicki, 1998). Herbivorous fish density on the GBR, for example, does not reflect browsing rates as herbivory is disproportionally driven by both unicornfish which were scarcely encountered in visual surveys (Hoey & Bellwood, 2009a,b). In video observations in the species-rich reefs of Indonesia, *N. lituratus* and *N. unicornis* accounted for up to 64 and 83% of bites on *Sargassum* spp. at different reefs, although neither species was observed in visual diver surveys (Plass-Johnson *et al.*, 2015). Such inconsistencies emphasize the difficulty in quantifying ecosystem processes using merely biomass estimates as both species may remain underrepresented. However, it is evident that there is low functional redundancy surrounding these species, and that depleted stocks could have a significant impact on benthic coral reef community structure.

6.4. Fishery (practice and status) across the Pacific

Although both species are currently found in the “Least Concern” category of the IUCN Redlist (McIlwain *et al.*, 2012a,b), a separate reclassification of the status of parrotfish and surgeonfish within the coral triangle area suggested that both *N. lituratus* and *N. unicornis* are “Near Threatened” (Comeros-Raynal *et al.*, 2012). Despite their apparent regional-scale resilience, various factors contribute to their impending vulnerability; related to life-history characteristics and the way the fishery is practised.

6.4.1. Fishing practices

Handline and spearfishing are the more traditional methods employed by fishermen in Micronesia, Melanesia and Polynesia, with night-time spearfishing being the most effective for *N. lituratus*, *N. unicornis* and other large herbivores. Relatively recent availability of underwater flashlights throughout the region has led to night-time spearfishing becoming frequently practised across the Pacific (Rhodes *et al.*, 2008; Hamilton *et al.*, 2012). Given that this modern fishing method provides easy access to inactive fish, even when they are sheltering, it facilitates disproportionally high catch rates. Night-time spearfishing is now commonly practised across most of the Pacific, despite many local fishermen being aware that this method is contributing to the decline of key species (Gillett & Moy, 2006). However, data on night-time spearfishing catches are primarily available from Micronesia, where this fishery contributes over seventy-five percent of marketed reef fish (Houk *et al.*, 2012). Guam boasts the highest catch per unit effort (CPUE) compared to Pohnpei and Palau, most likely as a consequence of the currently unrestricted SCUBA spearfishery (Bejarano *et al.*, 2013). The use of SCUBA has also become popular among spearfishers throughout the Pacific region (Gillett & Moy, 2006), enabling fishermen to exploit deeper and previously inaccessible waters (Lindfield *et al.*, 2014). SCUBA spearfishing remains legal in many parts of the Pacific, and even in areas where it is banned (e.g. Pohnpei, Palau, Fiji, Samoa – see Table 6.1), there is little catch monitoring or enforcement. In addition to gear modernizations leading to unsustainable practices, there is concern over the large proportion of immature individuals in catches. For example, across Micronesia 39-73% of *N. unicornis,* and 24-61% of *N. lituratus* individuals caught are immature (Bejarano *et al.,* 2013), and specifically in the Commonwealth of the Northern Mariana Islands (CNMI) and Guam, 90% and 75% (respectively) of harvested *N. unicornis* are immature (Houk *et al.,* 2012).

6.4.2. Vulnerable life-history characteristics

Unicornfish populations have remained relatively resilient to long-term fishing pressure in the Pacific, although both species exhibit life-history characteristics which make them vulnerable to overexploitation. Firstly, both species form large aggregations, which despite being short-lived, allow fisherman to obtain large catches at predictable times and places (Johannes, 1981; Johannes *et al.,* 1999). For example, fishers in Palau targeting *N. unicornis* aggregations can catch over 250 kg in a single trip (Sadovy de Mitcheson and Colin, 2012). Additionally, predictable spawning seasonality (e.g. in Hawaii) also restricts reproduction to a limited period annually. Secondly, unicornfish life-history characteristics such as habitat specificity, slow growth and extended longevity all increase their vulnerability to overfishing (Roberts & Hawkins, 1999); and when comparing these characteristics between the species suggest that *N. unicornis* populations are more vulnerable to overfishing than *N. lituratus* (Table 6.2). Furthermore, late maturation (particularly females) and large body size were found to be strong predictors of parrotfish vulnerabilities (Taylor *et al.,* 2014a), and *N. unicornis* displays similar values (i.e. L_{50} > 250 mm, Lmax > 400 mm fork length; see Table 6.2) to the most vulnerable species measured. Thirdly, high catches of immature individuals in the Pacific may act synergistically with high unicornfish recruitment mortality rates (Doherty *et al.,* 2004), resulting in serious consequences for natural replenishment of unicornfish populations. However, large individuals are also vulnerable to exploitation due to life-history characteristics and gear modernization. For example, as a consequence of ontogenetic habitat shifts, deeper reefs are primarily characterized by larger individuals, and thus SCUBA spearfishing is specifically exploiting the more fecund and functionally important individuals (Birkeland & Dayton, 2005; Lokrantz *et al.,* 2008). Furthermore, while smaller unicornfish are likely to find abundant suitable refugia in shallower habitats, larger individuals remain conspicuous and are more vulnerable to night-time spearfishers. Unicornfish are also more vulnerable to being caught in reefs with low topographic complexity which offer less refuge, indicating that these species are susceptible to disturbances such as storms and destructive fishing methods which destroy three-dimensional reef structure. Finally, although smaller, faster growing *N. lituratus,* have larger home ranges and higher natural mortality rates than *N. unicornis*, and should be a more sustainable fishing target, mortality data from Palau indicates that they are overexploited, while *N. unicornis* remains stable (Moore *et al.,* 2014; Table 6.2).

Table 6.1. Relative importance and awareness of overexploitation of Naso lituratus and Naso unicornis in the fisheries of some Pacific Island countries. Gaps correspond to no available information. Numbers refer to corresponding references for each locality.

Region	Relative Importance	Signs of overexploitation	Awareness among stakeholders	Laws in place	References
Melanesia (Fiji)	- Unicornfish are some of the main species targeted by spear fishers[1] - *N. unicornis* often preferred food fish[3]	- *N. lituratus* and *N. unicornis* totally absent in fished areas but comprised 32% of biomass inside 9 – 10 year old reserves (*N. lituratus*, 64 to 76 g 150 m^{-2}, *N. unicornis*, 4 to 4093 g 150 m^{-2})[5] - Observed a loss of large-bodied herbivores such as *N. unicornis* after 5 week harvest of closed area, with long-term effects[4]		- Minimum size limit 300 mm (FL) for *Naso* spp.[6] - SCUBA spearfishery banned (but low enforcement)[1]	Gillett & Moy (2006)[1]; Friedman *et al.* (2009)b[2]; Jupiter & Egli (2011)[3]; Jupiter *et al.* 2012[4]; Rasher *et al.* (2013)[5]; Fisheries Act [Cap 158] Fiji[6]
Melanesia (New Caledonia)	- *N. unicornis* dominates surgeonfish landings[1]	- Four years after reserves were created, density of *N. lituratus* > 10 times greater, *N. unicornis* density improved 3-10 times[2]			Dalzell *et al.* (1996)[1]; Wantiez *et al.*, (1997)[2]
Melanesia (PNG)	- *Naso* spp. form large proportion of surgeonfish landings[12]		- Communities identify night-time spearfishing as a major threat[3]	None	Dalzell *et al.* (1996)[1]; Friedman *et al.* (2008)[2]; Ford, pers. obs (2014)[3]

Table 6.1. cont.

Region	Relative Importance	Signs of overexploitation	Awareness among stakeholders	Laws in place	References
Melanesia (Solomon Islands)	- *Naso* spp. account for >10% of night-time spearfishery[3] - *Naso* spp. contribute significantly to combined lagoon and outer-reef catch[2]		- Communities identify night-time spearfishing as a major threat[1]	- SCUBA spearfishing banned January 2004[1]	Gillett & Moy (2006)[1]; Pinca *et al.* (2009)[2]; Hamilton *et al.* (2012)[3]
Micronesia (CNMI)		- 90% harvested *N. unicornis* immature[1]		- SCUBA spearfishery banned 2003[2]	Houk *et al.* (2012)[1]; Lindfield *et al.* (2014)[2]
Micronesia (FSM)		- 73% *N. unicornis* immature[1] - 61% *N. lituratus* immature[1]		- SCUBA spearfishing banned in Pohnpei[1] - Minimum size limit 16" (40 cm) in Pohnpei[2]	Bejarano *et al.* (2013)[1]; E. Joseph, pers. comm. (2015)[2]
Micronesia (Guam)	- Acanthurids (inc. *N. unicornis* and *N. lituratus*) account for majority of daily catch[2]	- Large proportion of *N. unicornis* catch immature (39[3]-75%[2])	- Most residents support ban of exploitative fishing methods[1]	None[4]	van Beukering *et al.* (2007)[1]; Houk *et al.* (2012)[2]; Bejarano *et al.* (2013)[3]; Lindfield *et al.* (2014)[4]

Table 6.1. *cont.*

Region	Relative Importance	Signs of overexploitation	Awareness among stakeholders	Laws in place	References
Micronesia (Guam) cont.	- *N. unicornis* highest acanthurid biomass contribution to snorkel and SCUBA spearfishery last 20 years (*N. lituratus* also one of largest contributors)[4]	- 36% *N. lituratus* immature[3] -Biomass and average length have increased in the SCUBA spearfishery over the last 20 years (probably due to more focused and deeper effort since other desirable species have declined). However, snorkel fishery mean biomass & length is in decline[4]			
Micronesia (Palau)	- *N. unicornis* the single most important commercial reef fish[2,3] - *N. lituratus* and *N. unicornis* constitute 34 and 21% acanthurid catch[4]	- 40% *N. unicornis* immature[5] - *N. unicornis* have undergone a long-term decline from the onset of the 1980s[2] - 24% *N. lituratus* immature[5]	- Fishermen have noticed serious decline[1,2]	- SCUBA spearfishing illegal[5] (but not enforced)	Johannes (1991)[1]; Kitalong & Dalzell (1994)[2]; Johannes *et al.* (1999)[3]; Friedman *et al.* (2009b)[4]; Bejarano *et al.* (2013)[5]
Polynesia (French Polynesia)	- *N. unicornis* one of the dominant species (up to 54%) in catch from all reef habitats - *N. lituratus* key part of catches (particularly in lagoon and passages).				Kronen *et al.* (2006)

Table 6.1. cont.

Region	Relative Importance	Signs of overexploitation	Awareness among stakeholders	Laws in place	References
Polynesia (Hawaii)	- *N. unicornis* consistently in top 5 species by weight in inshore fishery landings (19251 kg in 2012, 13504 kg in 2011, 15443 kg in 2010)[2]	- Declines in overall catch and size of N. unicornis[1]	- Concern over long-term sustainability due to changes in catch[1]	- Minimum size limit for Naso spp. 356 mm[1] (smaller than female L_{50})	Eble *et al.* (2009)[1]; Annual reports of Division of Aquatic Resources[2]
Polynesia (Samoa)	- Unicornfish (and specifically *N. unicornis*) are commonly caught by spearfishers			- Minimum surgeonfish size limit 200 mm (FL); SCUBA spearfishery banned	Gillett (2011)
Polynesia (Tonga)	- *N. unicornis* already commonly marketed by 1978[1] - *N. unicornis* 2nd most abundant (17%) part of SCUBA night-time spearfishing[2,3]				Uchida (1978)[1]; Gillett & Moy (2006)[2]; Gillett (2011)[3]
Polynesia (Tuvalu)	- Both *N. lituratus* and *N. unicornis* are very important in spearfishing catch[1,2,3]				Gillett & Moy (2006)[1]; Sauni *et al.* (2008)[2]; Gillett (2011)[3]

6.4.3. Status of the fishery in the Pacific

Reports from the last two decades have highlighted a growing concern over the fishing pressure exerted on *N. lituratus* and *N. unicornis* populations in Micronesia (Table 6.1). Bejarano *et al.* (2013) referred to the exploitation of *N. unicornis* as one of Micronesia's most serious fisheries management concerns, and observed that *N. lituratus* is also heavily harvested. *N. unicornis* is one of the most highly prized fish in Palau, and has been referred to as Palau's single most commercially important fish for many years despite fishermen recognising that catches were already seriously declining over two decades ago (Johannes, 1991; Johannes *et al.,* 1999). In Pohnpei, Guam and Yap, acanthurids (in particular *N. unicornis,* but also *N. lituratus*) account for the majority of the daily catch (Houk *et al.,* 2012). However, exploitation is also conspicuous beyond Micronesia (Table 6.1); for example, concerns have been raised over a recent increase in commercial fishing pressure on *N. unicornis* in Hawaii (Figure 6.1; Eble *et al.,* 2009). In addition, *N. lituratus* represents a highly valuable catch for the aquarium trade. Between 2005 - 2009 the species was worth USD$122,090 in West Hawai'i alone, with approximately 29,859 individuals caught (Walsh *et al.,* 2010). In areas where these species are most heavily targeted (i.e. Micronesia), there are currently no bag limits or closed seasons for either unicornfish species.

6.5. Improving management

N. lituratus and *N. unicornis* populations are heavily targeted by both subsistence and commercial fishing, and the aquarium trade across many regions of the Pacific. These species may have remained relatively resilient among coral reef fish due to their biology: for example, overharvested stocks are replenished by distant populations due to a long pelagic larval duration and high connectivity (Horne *et al.*, 2008, 2013; Lindfield *et al.*, 2014). However, both species are heavily exploited, of high socio-economic and ecological value, and large proportions of immature individuals are caught. Therefore, a thorough revision of species-specific management strategies is warranted. Conserving the function of browsing herbivores has become a priority as it may provide reefs with the best chance to resist and recover from increasingly erratic future disturbances (Graham *et al.*, 2013; Rasher *et al.,* 2013).

6.5.1. Gear- and effort-based restrictions

For large-scale and long-term sustainable harvesting, the foremost step would be banning the unsustainable practices of both night-time and SCUBA spearfishing in areas where they remain legal, and investing special effort into optimizing the enforcement of the bans that are already implemented. Many local stakeholders throughout the Pacific agree that both SCUBA and night-time spearfishing are unsustainable and encourage overexploitation of fish stocks (Johannes, 1991; Gillett & Moy, 2006; van Beukering *et al.,* 2007; Rhodes *et al.,* 2008; Stoffle & Allen, 2012), as well as endangering fishermen as they take increasing risks to improve their catch (e.g. SCUBA spearfishers). Potential caveats for gear- and effort- based management include the large effort required from resource and enforcement agencies to patrol over wide areas, and the associated high profitability and low investment (particularly with night-time spearfishing). Without compensation or alternative livelihoods, fishermen will be unlikely to adopt more sustainable methods that are less profitable (Cinner *et al.,* 2009). However, by conveying the importance and justification of these forms of management to local communities, and empowering and training local stakeholders, we can encourage self-regulation within communities. Furthermore, while it is challenging to prove that fish were caught using unsustainable methods compared to daytime spearfishing on snorkel, new legislation could be promoted which makes it illegal for fishermen to have SCUBA gear or underwater flashlights on the same boat or vehicle as their catch (Gillett & Moy, 2006; Lindfield *et al.,* 2014). There is some consensus that fishermen should be encouraged to move away from spearfishing entirely due to the strong association of this method with species key to maintaining coral reef health (Cinner *et al.,* 2009). Where it is feasible (at larger market areas), management could also consider incorporating licensing of fishers to restrict the number of people selling these species, and catch quotas could restrict the number of fish that individuals can catch and sell (Houk *et al.,* 2012). Restrictions could also be placed onto aquarium fishers which could be limited to specifically target abundant pelagic juveniles due to their high post-recruitment mortality (Doherty *et al.,* 2004).

6.5.2. Size limits

Management of fisheries often focuses on discouraging fishermen from removing small individuals, and thus promoting reproductive capacity of stocks. Minimum size limits have been imposed in a few countries (Table 6.1). However, not only are these limits difficult to enforce, but they may not offer adequate protection. In Hawaii, the legal minimum size limit for *N. unicornis* (356 mm) will prevent males being fished before maturity, but does not guarantee maturation of females before capture (Eble *et al.,* 2009; DeMartini *et al.,* 2014). In other areas, (e.g. Samoa) small minimum size limits correspond to all surgeonfish and are thus unlikely to protect maturation of larger species such as *N. unicornis*, though a lack of data from regions throughout the Pacific makes this difficult to ascertain. While minimum size limits promote reproductive capacity, maximum size limits can promote stock recovery by protecting the largest and thus most fecund and functionally important individuals (Froese, 2004, Birkeland & Dayton, 2005). Coral reefs harbouring high fish biomass remain functionally impaired if they are dominated by small individuals as grazing impact can be non-linearly related to body size (Mumby *et al.,* 2006; Lokrantz *et al.*, 2008). As both unicornfish species are predominantly harvested via a highly selective fishing method (i.e. spearfishing), size limits could theoretically be established. However, while the growth profile of *N. unicornis* supports the implementation of size limits (as size can be extrapolated to age and maturity), they would be futile for *N. lituratus* individuals that reach asymptotic length very early, often within two years (Taylor *et al.,* 2014b). As with gear- and effort-based restrictions, enforcing size limits is highly challenging for subsistence fishing, but has potential to be self-regulated at the local level if awareness on the importance is well conveyed. Furthermore, there is a strong potential for size limit enforcement at local fish markets by empowering and training local stakeholders.

*Table 6.2. Size, maturity, growth and mortality data from the Pacific region for N. lituratus (N. lit) and N. unicornis (N. uni). FL = fork length, TL = total length, SL = standard length. Growth (K) and mortality (N, M, F) values are shown as year^{-1}. Gaps correspond to no available information. *Data combined with Guam and Pohnpei. Numbers refer to corresponding references for each locality.*

					Mortality rates			References
Region	Species	Lmax (mm)	L50 (mm)	Growth rate (K)	Total (Z)	Natural (M)	Fishing (F)	
GBR	*N. lit*	(L∞ =) 211 TL^{2}		0.755^{2}				Choat & Axe (1996)^{1}; Choat & Robertson (2002)^{2}; Wilson (2004)^{3}
	N. uni	457 SL^{1} 494 TL^{2}		0.489^{2}	0.27^{3}			
Melanesia (New Caledonia)	*N. uni*	600 FL						Kulbicki *et al.* (2005)
Micronesia (Guam)	*N. lit*	Females 231 FL Males 251 FL	Females 145 FL Males 178 FL	0.93	0.4			Taylor *et al.* (2014b)
	N. uni	Females 520 FL Males 431 FL	Females 292 FL Males 271 FL	0.22	0.16			
Micronesia (FSM – Pohnpei)	*N. lit*	Females 250 FL Males 263 FL		1.38	0.33			Taylor *et al.* (2014b)
	N. uni	Females 494 FL Males 496 FL	Females 312 FL Males 269 FL	0.36	0.32			
Micronesia (Palau)	*N. lit*	(L∞ =) 351 FL^{1}, 423 TL^{2}	241 TL^{2*}	0.35^{1}	1.683^{1} 0.414^{3}	0.86^{1} 0.209^{3}	0.823^{1} 0.205^{3}	Kitalong & Dalzell (1994)^{1}; Bejarano *et al.* (2013)^{2}; Moore *et al.* (2014)^{3}
	N. uni	(L∞ =) 570 FL^{1}, 683 TL^{2}	371 TL^{2*}	0.14^{1}	0.683^{1} 0.161^{3}	0.413^{1} 0.130^{3}	0.27^{1} 0.031^{3}	
Polynesia (Hawaii)	*N. uni*	Females 596 FL^{2} Males 586 FL^{2}	Females 355^{2}, 378^{1} FL Males 286^{1}, 301^{2} FL	0.17^{1}				Eble *et al.* (2009)^{1}; DeMartini *et al.* (2014)^{2}

6.5.3. MPAs

While limited resources mean that fishing effort constraints are often challenging in many coral reef areas, or for all species, MPAs provide an alternative, albeit suboptimal, option under such circumstances (Brown & Mumby, 2014). Whilst site attachment, small home ranges, and a preference for structurally complex habitats increase vulnerability (Roberts & Hawkins, 1999), they also indicate that both species are ideal candidates for protection through small MPAs using natural boundaries such as sandy areas. Both species comprised 32% of the herbivorous fish biomass inside adjacent 9 – 10 year old reserves in Fiji despite being absent from adjacent fished areas (Rasher *et al.,* 2013). The increased biomass of *N. lituratus* and *N. unicornis* was considered to be primarily responsible for driving macroalgal cover from between 49 – 91% macroalgal cover (predominantly brown algae) in fished areas down to 1 – 3% inside reserves. Furthermore, biomass of *N. unicornis* improved as much as 300 times (up to 9.63 kg 500 m^{-2}) inside 8 – 11 year old small (6 – 20 ha) reserves compared to fished areas (0.03 kg 500 m^{-2}) in the central Philippines, actually showing the greatest improvement of the various species measured (Stockwell *et al.,* 2009). Correspondingly, macroalgal cover and reserve age were strongly negatively correlated. Density also improved within five year old reserves in New Caledonia for both *N. lituratus* (>10 times greater) and *N. unicornis* (3 – 10 times greater) (Wantiez *et al.,* 1997). There is therefore robust evidence that MPAs have a positive effect on both population density and individual size of these species, and consequently on the ecosystem.

Home range data indicate that MPAs can be small (< 1 km^2 - Meyer, 2003; Meyer & Holland, 2005; Marshell *et al.,* 2011), but ideally should extend 10 and 2 km linear distance (between natural boundaries in the longest dimension) for *N. lituratus* and *N. unicornis* respectively, accounting for areas extending over more than twice the home range size in all directions (Green *et al.,* 2014). Whilst strong site-attachment can reduce adult spill-over from reserves, increased juvenile recruitment to local fishing areas will still benefit local fishermen (Moffitt *et al.,* 2009; Harrison *et al.,* 2012). Designs of MPAs should restrict reserve spacing to a maximum of 15 km, and movements between critical habitats for various life history strategies should be accounted for (Green *et al.*, 2014). MPAs should also take into account that these species undergo ontogenetic habitat shifts which have implications for management on local scales, as closures focusing on specific habitats would protect particular life-stages. To allow for true replenishment of overfished populations, highly dispersive reef species such as *N. unicornis* (Horne *et al.,* 2008) would need protection using networks of MPAs at regional scales (Taylor *et al.,* 2014b).

6.5.4. Seasonal / periodic closures

Seasonal closures and sales bans around spawning periods have been implemented for other targeted reef fish, particularly serranids (Beets & Friedlander, 1998; Russell, 2001; Rhodes *et al.,* 2008). When a peak spawning season is observed, such as May - June for *N. unicornis* in Hawaii, seasonal closures and sales bans would be highly effective (DeMartini *et al.,* 2014). When spawning occurs over several months or year-round, several short-term closures over peak monthly spawning have potential (e.g. GBR grouper fishery - Sadovy de Mitcheson & Colin, 2012). For example, *N. unicornis* has been observed to synchronize spawning times with the lunar cycle year-round in Palau (Johannes, 1981), indicating that short-term closures around new and full moon could be beneficial and may also protect these species during the highest fishing pressure (at new moon, see - Rhodes *et al.,* 2008). A more recent study by Taylor *et al.* (2014b) found no relationship with the lunar cycle in other areas of Micronesia, but did identify peaks in spawning months for both species; *N. lituratus* peaked through March - November in Guam, and April in Pohnpei, while *N. unicornis* spawning was limited through May - October in Guam, and in Pohnpei reproductively active individuals were found in all months except February, October and December. These results indicate that the fisheries could benefit from periodic closures and sales bans through March – September. There is an urgent need for conclusive reproductive data from other regions within these species' ranges. To this end, local knowledge of spawning behaviour and locations can contribute substantially to research and management (Haggan *et al.,* 2007).

Though there is potential for periodic closures, as is traditional in Melanesia, managers must address the prospective functional loss in the system after harvest openings. During a five-week harvest of one MPA in Fiji, there was a significant decrease in *N. unicornis* biomass (-1303 kg ha^{-1} four weeks into harvest), and a concomitant increase in small roving grazers with reduced functional capacity (Jupiter *et al.,* 2012). These effects remained evident for one year after the area was closed to fishing again, emphasizing that a single intensive harvest can quickly undo the positive effects of long-term protection. Although managers can consider temporary closures of the fisheries immediately following a disturbance when macroalgal blooms are most likely to occur, these are unlikely to be beneficial unless pre-disturbance stock levels remain at a sufficient level for their browsing functional impact to be maintained. Managers should therefore consider also closing appropriate small areas over extended periods of time in order to act as "egg-banks", allowing the highly dispersive exported larvae to repopulate over widespread reefs.

6.5.5. Alternative species

Interviews of local fishermen in Micronesia highlighted that it would be challenging to encourage a switch from *N. unicornis* to another more sustainable target species with higher functional redundancy (Bejarano *et al.,* 2013). According to fishermen desirability, *N. lituratus* would be one of the only species that could alleviate pressure on *N. unicornis,* yet this would not provide a viable alternative due to (i) already being heavily targeted, and (ii) having correspondingly low functional redundancy. In places where protection is most difficult to enforce, catch levels of other macroalgal feeders (e.g. siganids) should not be overlooked.

6.5.6. Monitoring and research

This comprehensive review has highlighted that a severe lack of data exists, coupled with an obvious spatial disparity on key life-history characteristics which are critical for developing management tools. Mortality estimates must be conducted across more locations to enable managers to investigate trends and exploitation of populations and to define maximum sustainable yields. The apparent compensatory density dependence response of these species to harvesting requires further studies to determine maximum size limits and yields that promote optimal population growth responses. Due to demographic variability, it is essential that local data is used to develop management within each region. For example, differences in reproduction highlight that size limits must be developed specifically within each region to ensure that minimum size limits are greater than the L_{50} value of the local population.

6.6. Concluding Remarks

N. lituratus and *N. unicornis* represent two essential species in both the context of their contribution to Pacific Island fisheries, and their function as macroalgal browsers on coral reefs, for which there is very low redundancy. Although these species appear to have remained relatively resilient in many regions, the steep decline of other desirable species heralds a high risk of collapse. Of special concern is the ongoing modernization of fishing gears, which will likely continue to increase catch rates. If *N. lituratus* and *N. unicornis* stocks continue to be heavily exploited, severe economic repercussions can be expected for large human populations who rely on them as a food and income source. Serious consequences are also highly likely if their abundance is reduced far enough to impair their function, or if pathways of larval connectivity are not maintained. For more long-term sustainability, attention should be focused on implementing species-specific management strategies and promoting more sustainable targeting of fish through increasing community awareness of fishing impacts. Furthermore, when resources are available, locally sourced socio-ecological data must be used to establish appropriate local management strategies due to demographic variation of species traits as well as socio-cultural differences. Inevitable difficulties implementing and enforcing restrictions in the region indicate that ultimately a combination of different management tools and actions will be most effective.

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CHAPTER SEVEN

GENERAL DISCUSSION

The overall objective of this thesis was to fill current knowledge gaps regarding the impact of small island human populations in order to gain a better understanding of future Pacific island coral reef ecosystems under global environmental change. To achieve this, a combination of observational, theoretical and secondary data-based studies were conducted to investigate the role of local human impacts on benthic community structure and function.

The overarching question of this thesis was:

What is the influence of local human populations on small Pacific Island coral reef functioning and resilience?

To appropriately address this overarching question, it was broken down into three sub-questions:

i. How do different dimensions of human activities (e.g. low vs. high resource exploitation) on small Pacific islands facilitate alternative regimes or ecological reorganisation within benthic coral reef communities?

ii. Where subtle changes occur within the benthos in response to human activities, which process or resilience-based metrics have the ability to capture local impacts and indicate system trajectories?

iii. How can community-based management influence benthic community responses to local human disturbances on small Pacific islands?

7.1. Human activities, alternative regimes and ecological reorganisation

The studies within the current thesis emphasise the complexity of interactions between local human populations and benthic communities on Pacific Islands. Under very high levels of local human impacts, direct relationships with reef degradation could be observed. However, under increasing levels of local impacts, less conspicuous changes often occured in terms of ecological reorganisation and altered ecological processes and functions. Such changes were identified to have profound impacts on the relationship between reefs and their physical environment, and the ability of reefs to sustain themselves and recover from future perturbations.

Under an extreme scenario whereby reefs around densely populated islands are exposed to both overexploitation of reef fish stocks and untreated sewage input, they can undergo distinct shifts in dominance of benthic communities towards cyanobacterial mats (Chapter 2). Organic matter input from sewage can drive benthic cyanobacterial mat proliferation due to the release of reactive phosphate and iron following increasingly anoxic sediments (Brocke *et al.*, 2015a; Hanington *et al.*, 2016). Benthic shifts towards cyanobacterial mats are increasing around the region and the world, and may have severe implications for future coral reef functioning and ecosystem service provision (Chapter 3). Mats themselves are generally unpalatable (Capper *et al.*, 2016), inhibit coral recruitment (Kuffner & Paul, 2004; Ritson-Williams *et al*., 2016) and release bioavailable nitrogen and dissolved organic carbon (DOC), which in turn further facilitates sedimentary release of reactive phosphate and iron (Brocke *et al.,* 2015b). Increasing DOC and nitrogen levels in naturally oligotrophic waters can further promote growth of fast-growing primary producers and can increase coral disease prevalence and coral susceptibility to ocean warming (Kline *et al.,* 2006; Wooldridge & Done, 2009; Wiedenmann *et al*., 2013). Increasing nitrogen concentrations themselves could potentially induce coral bleaching and mortality (Pogoreutz, Rädecker *et al.* 2017). Once mats are established within benthic communities, conditions thus promote a self-reinforced cycle favouring continued reef degradation. This phenomenon may facilitate the development of social-ecological traps (Cinner, 2011; Boonstra & de Boer, 2014) within Pacific island systems. These traps develop when strong ecological feedbacks favouring reef degradation are amplified by associated changes in the activities of closely connected human populations. For example, faced with degraded reefs, island communities may switch to higher levels of agriculture leading to increased fertiliser run-off, and adopt increasingly destructive fishing techniques to maximise catches thus overexploiting remaining fisheries. Overexploitation of reef fish will further diminish their function in maintaining a healthy ecosystem. Future changing climatic conditions will amplify this phenomenon, with high temperatures, decreasing pH and unpredictable weather patterns (Pachauri *et al.,* 2014) favouring growth of cyanobacteria while being stressful to hard corals.

Overexploitation of other key species such as sea cucumbers (Anderson *et al*., 2011) across the Pacific Island region has likely amplified the increased prevalence and occurrence of benthic cyanobacterial mats, as suggested in previous *ex situ* studies and in temperate areas (Moriarty *et al.,* 1985; Michio *et al.,* 2003; Chapter 3). To understand the impact of sea cucumber removal on reef flat sediment, we continuously measured sedimentary parameters and processes for six months under various densities of heavily targeted sandfish *Holothuria scabra* (Appendix D; Lee *et al.,* 2017). The most severe impact of their removal occurred when 2015/2016 El Niño impacted the study site, resulting in the simultaneous occurrence of local (i.e. sea cucumber overexploitation) and global (i.e. unusually warm waters) stressors. The combination of stressors culminated in a 63% reduction in oxygen penetration depth from 32 ± 3 (mean ± SE) to 12 ± 2 mm. The observed increase in sediment anoxia may have concerning implications for the development of benthic cyanobacterial mats where sea cucumbers have been overfished in the coming years (Chapter 3). When sea cucumbers were maintained at high (300 g m^{-2}) and natural (60 g m^{-2}) densities, oxygen penetration depth remained unchanged under elevated temperatures.

Interestingly, heavily overfished reefs seem capable of maintaining hard coral dominance in the absence of additional untreated sewage input (Chapter 2). Such information is critical considering that globally 83% of reefs are already missing more than half of their expected fish biomass (MacNeil *et al*., 2015). Overexploitation of fish stocks has been amplified by increasing use of non-traditional fishing methods, most notably nighttime spearfishing within the Pacific Island region following the introduction of underwater flashlights (Gillett & Moy, 2006; Rhodes *et al.,* 2008; Hamilton *et al.,* 2012). Species such as herbivorous unicornfish *Naso lituratus* and *Naso unicornis* are particularly vulnerable to this fishing gear modernisation (Chapter 6). These browsing species are of critical importance in controlling fleshy algal communities in the region, particularly blooming varieties such as *Sargassum* spp. (Green & Bellwood, 2009; Rasher *et al.* 2013; Puk *et al.,* 2016). Often the fish species most targeted and desirable for fishers are also among the most important in ecological terms (Bejarano *et al.,* 2013). Continued heavy exploitation of such functionally important species for which there is limited functional redundancy may in turn have severe consequences for benthic coral reef assemblages in the region.

Benthic communities around Pacific islands do not show the same propensity to switch between regimes dominated by live hard coral and fleshy algae as those for example at Jamaica (Hughes, 1994; Bruno *et al.,* 2009). A large-scale analysis of Pacific Island reefs indicated that there were at least three different regimes that reefs could gravitate towards, characterised by (i) live hard coral and crustose coralline algae, (ii) turf algae, and (iii) fleshy algae and dead coral (Chapter 4). This finding was in agreement with recent analyses of reefs in the Hawaiian Archipelago and other US Pacific islands, which also identified turf algae as an alternative regime (Jouffray *et al*., 2014; Smith *et al.,* 2016).

Most reefs were however existing in a condition somewhere between categorical regimes, seemingly occupying a partially degraded state no longer dominated by live hard corals but not undergoing distinct shifts towards alternative organisms. Comparisons of reefs exposed to low and high local human impact revealed some direct relationships between the level of impact and broad benthic groups (Chapter 4). However, higher local impacts strongly influenced responses of benthic systems to physical and global change-related factors. Coral morphological composition, for example, was strongly related to storm exposure at less locally impacted reefs, with higher proportions of massive coral morphologies compared to branching growth forms following increased storm exposure. Contrastingly, relationships between coral morphological structure and storm exposure were absent at reefs exposed to higher levels of human impacts. Similarly, reef condition was strongly related to storm exposure and latitude (in turn significantly related to thermal stress) at less locally impacted reefs but not at reefs exposed to high local human impacts. These results indicate that the ability to predict the impacts of future global climate change-related stressors on benthic reef assemblages is compromised as local impacts increase. Such a trend reflects differences between remote reefs and those found close to human populations in the US Pacific islands (Williams *et al.,* 2015), and likely results from ecological reorganisation facilitating the development of novel coral ecosystems (Graham *et al.,* 2014) under increased local human impacts. However, the absence of species data within the dataset precluded analyses into taxonomic homogenisation within the coral communities. The ability to predict benthic assemblages at reefs exposed to higher levels of local impacts was not lost, as models based on local features such as herbivorous fish biomass and local human population density yielded similar explanatory power at both low and high locally impacted sites. However, the results clearly indicate that increasing local impacts drive distinct shifts in the importance of various drivers in shaping benthic assemblages.

Another key observation from Pacific Island reefs is that *Porites rus* is often the most dominant species in inshore areas (Appendix E). Although this species occurs across a large spatial scale, and is commonly reported in shallow reefs where it can form large monospecific stands (Sheppard *et al.,* 2014), its biological properties remain relatively understudied in comparison to other coral species of similar abundance. Preliminary results on skeletal micro-densities of *P. rus* collected at several sites in Fiji indicate that they were very low compared to the densities of other dominant species (1.44 ± 0.03 to 1.81 ± 0.06 g cm^{-3}; Appendix F). Not only does *P. rus* exhibit relatively high resistance to decreasing pH and low susceptibility to bleaching, but calcification rates are almost one magnitude higher at 29.3°C compared with 25.6°C (Edmunds *et al.,* 2012; Comeau *et al.,* 2013). This species is consequently at a strong advantage over many other coral genera under future oceanic climate projections regarding ocean warming and acidification (e.g.

Hoegh-Guldberg *et al.,* 2007; Pachauri *et al.,* 2014). If this tolerance comes alongside reduced tensile strength of the skeleton, this trade-off would deem reefs where it dominates more vulnerable to future increasing storm intensities (Hughes, 1987; Pachauri *et al.,* 2014).

7.2. Metrics to capture (subtle) changes among Pacific Island reefs

The ability of different monitoring approaches to detect changes within benthic and fish communities under local management was explored by measuring a variety of metrics in paired protected and adjacent fished reefs in Fiji (Chapter 5). Such a field comparison of the interpretations of different monitoring approaches was timely considering the recent attention on different metrics for diagnosing coral reef health and resilience (Flower *et al*., 2017; Lam *et al*., 2017). The results revealed that strongly contrasting interpretations of management effectiveness can be made depending on the metrics used within surveys. The implications of these findings are not limited to comparing managed and non-managed areas, but also for surveys comparing reefs pre- and post-disturbance, and when trying to identify reefs with a superior propensity to recover that could be prioritised by managers to act as future refuges. Whilst conventional metrics indicated that local management had no positive influences on either benthic or fish communities, a set of newly developed complementary status and ecological process- and function-based metrics revealed significant changes within protected areas. Particularly, the scope of the complementary metrics to capture differences in biotic substrate colonisation allowed the detection of changes that have important implications for system resilience that would otherwise have been overlooked. Reduced algal turf height and turf index (the product of benthic cover and height) were associated with higher coral recruitment rates onto tiles, successive growth and survival of juvenile corals and reduced competitiveness against neighbouring coral colonies, emphasising the informative value of incorporating simple turf algal measurements into surveys. Coral recruitment success and outcomes of coral-turf algal interactions supported previous findings of a threshold of *ca.* 5 mm turf height after which algal turfs become strongly detrimental to reef functioning (Birrell *et al.,* 2005; Harris, 2015). Reduced coral recruitment rates and increasing competitiveness of algal turfs in interaction with corals can tip the trajectory of reef benthos towards degradation, reducing future system resilience (Anthony *et al*., 2015). Quantification of biotic substrate colonisation is important considering the increase in colonisable space on degrading reefs (e.g. Edmunds & Leichter, 2016; Tsounis & Edmunds, 2017) that is quickly occupied by various benthic organisms that can determine the future trajectory of the system. Furthermore, a comparison of algal turf traits within the benthos is timely in view of the emerging evidence of algal turfs as a dominant benthic group and potential alternative regime towards which degraded reefs can gravitate (Chapter 4; Jouffray *et al.,* 2014; Smith *et al.,* 2016). Specific traits within turf assemblages may indicate whether their dominance is transitory (the system is either recovering or degrading), or permanent. Few monitoring programmes currently include metrics that indicate substrate condition and nursery quality (Appendix Civ), and these results provide further support for a re-evaluation of key indicators to diagnose coral reef health and resilience (McClanahan *et al.,* 2012; Anthony *et al.,* 2015; Flower *et al*., 2017).

Although benthic parameters (e.g. turf height, coral-fleshy algal interactions) indicate superior long-term herbivorous fish functions within protected areas in Fiji, conventional underwater visual censuses (UVC) did not identify any conspicuous benefits of local management in terms of biomass or taxonomic richness (Chapter 5). However, video footage indicated superior taxonomic richness of total herbivorous fish and specifically of browsers within protected areas. Video footage captured significantly more browsing species than UVC, emphasising the importance of unmanned video cameras to survey wary browsers such as *N. lituratus* and *N. unicornis* (Kulbicki, 1998; Chapter 6), and to avoid overlooking their disproportionately important function on reefs (Hoey & Bellwood, 2009; Plass-Johnson *et al.*, 2015). Although video footage did not find differences in bite rates of herbivorous fish between managed and open reefs (Chapter 5), offering bio-assays of fleshy algal varieties would likely yield important information on potential browsing fish function (Bellwood *et al.*, 2006; Rasher *et al.*, 2013).

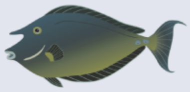
Even when direct relationships between benthic communities and local human impacts are not observed, local impacts could have driven ecological reorganisation with significant effects on future reef functioning and responses to climate change-associated disturbances (Chapter 4). Such ecological reorganisation results in reef homogenisation with associated reductions in diversity as increasing stressors favour persistence of tolerant species (Côté & Darling, 2010; Williams *et al.*, 2015). To capture such ecological reorganisation, it is important to increase the resolution of hard coral community surveys by adopting a refined functional approach. This increased resolution would increase the capacity of studies to unravel impacts of local human communities, and may minimise the number of studies concluding that humans have no direct effect on reef degradation (e.g. Bruno & Valdivia, 2016).

Another issue facing managers and researchers alike is the ability of baseline surveys to quantify water quality. In particular, there are difficulties in remote areas with limited infrastructure such as on many Pacific islands, whereby appropriate storage and processing of samples is highly challenging. Furthermore, there are challenges with reliably capturing unstable short-term fluctuations in nutrient levels in dynamic water bodies. This thesis explored simple *in situ* sedimentary parameters to provide another means to compare nutrient and organic matter input in coastal areas (Chapter 2). Shallow near-shore sediments tend to be relatively coarse and permeable, in turn allowing benthic-pelagic coupling to occur due to pore water flow enabling transport processes (Wild *et al.*, 2005). This benthic-pelagic coupling underpins many processes such as nutrient recycling and carbon turnover, and is therefore essential for ecosystem function and allowing coral reefs to thrive in the oligotrophic water (Wild *et al.*, 2008; Naumann *et al.*, 2012). By principle, sedimentary parameters are therefore effective indicators of stress exposure as changes in the overlying water will eventually be reflected in this system. Sedimentary oxygen consumption (SOC) rates reflect aerobic degradation of organic matter within sedimentary microbial communities. Furthermore, sedimentary organic matter is less subject to short-term fluctuations than water column organic matter, implying that SOC indicates long-term processes more reliably than assessments of water parameters. Following phytoplankton blooms, SOC rates increase significantly (Grenz *et al.*, 2000), coinciding with a reduction in O_2 penetration depth (Hjorth Jensen *et al.*, 1990). Therefore, both SOC rates and O_2 penetration depth seem to be effective indicators of phytoplankton blooms following flooding events. These events can also stimulate growth of benthic cyanobacterial mats (Chapter 3) with their associated negative consequences on reefs. Flooding is predicted to be a more severe problem in future climate scenarios, with projected increased episodic heavy rainfalls transporting nutrients into coastal water (Hoegh-Guldberg *et al.*, 2007; Pachauri *et al.*, 2014). Furthermore, despite reefs naturally existing in an oligotrophic state, increasing local populations with associated agricultural run-off and sewage input stimulate chronically high phytoplankton abundances. This thesis not only provides evidence of the potential for SOC measurements to indicate long-term organic matter input from sewage into coastal areas (Chapter 2), but also their ability to reflect changing sedimentary processes as result of removing bioturbators such as sea cucumbers (Appendix D). According to the findings presented within this thesis, a 'tool-box' of important metrics to include alongside conventional surveys is provided (Table 7.1).

7.3. Community-based management and local human impacts

There are a variety of local and community-based management tools that can reduce the magnitude of local human impacts on adjacent coral reefs. One principle form of local management is (temporarily) closing sections of reefs to fishing, for which Melanesia has a particularly strong cultural tradition, for example, following the death of a chief or prominent member within the community. Enforcement of these closures is challenging (Chapter 6), and poaching within *tabu* (no-take) areas is a large problem (Balawa pers. comm. 2015), potentially explaining the lack of conspicuous benefits of protection on overall fish biomass under local management in Fiji (Chapter 5). Direct benefits may also be more detectable after longer timeframes and if protected area sizes were specifically designed to encompass large home range sizes of key species with natural boundaries incorporated (e.g. sandy areas; Chapter 6). Nonetheless, left-skewed size spectra data (McAndrews unpubl. data 2015) indicate higher proportions of juvenile fishes with *tabu* areas, suggesting that they may be exhibiting some protection to smaller life-stages by for instance reducing the practice of some more obvious fishing methods (e.g. net fishing). Accordingly, video footage indicated a superior taxonomic richness of heavily targeted browsing herbivorous fish within protected areas, implying that there may be some benefit for this critical and heavily targeted functional group (Chapter 6). Furthermore, complementary metrics indicated that protected areas facilitated more desirable biotic substrate colonisation processes compared with adjacent fished areas (Chapter 5). Locally protected inshore reefs thus seem to have positive indirect benefits within the benthos that reflecting superior longer-term herbivorous fish function that (i) facilitate recovery processes such as coral recruitment and succession and (ii) would be overlooked by conventional UVC. However, if the intention of management is solely to maximise reef fish biomass, the lack of detection of conspicuous benefits observed directly within herbivorous fish communities inside protected areas indicate that it may be important for local managers to consider alternative management tools to maximise long-term sustainability of reef fisheries. There are many drivers of non-compliance with local management interventions identified in the Melanesian region, including weak enforcement whereby rule-breaking is perceived to carry a low risk, increasing incentives to break rules (e.g. improved access to markets), and a diminishing perceived legitimacy of local rules (Rohe *et al.,* in review). Alternative fisheries management tools which may receive less resistance than completely closing areas to fishing include temporary fishing restrictions (e.g. around spawning times, following a large disturbance), gear- and effort-based management and size restrictions (Chapter 6). Though these management tools all face similar challenges in enforcement, they may meet with less resistance than direct long-term closures. Customary marine tenure, high levels of local engagement in management and strong dependence on marine resources have recently been identified as key drivers of positive anomalies ('bright spots') in reef fish communities (Cinner *et al.*, 2016). Thus, there is a high potential for large ecological benefits under a scenario whereby managers strongly integrate stakeholders and fishers as allies (Ferse *et al.,* 2010), while thoroughly addressing the key regional drivers of non-compliance (Rohe *et al.,* in review).

Table 7.1. Summary of key metrics recommended to be integrated into future reef monitoring.

Metrics recommended to include in monitoring	Information provided	Method	Difficulty
Turf algal height 	Higher turf heights indicate: ↓ substrate condition and nursery quality ↓ coral recruitment ↓ juvenile corals ↑ competitiveness against neighbouring corals ↑ sediment trapping ↓ grazing rates Particularly strong implications above a threshold of *ca.* 5mm	Measure turf algal height with ruler or calliper perpendicular to the substrate	Quick and easy
Juvenile coral abundances 	High juvenile coral abundances reflect: ↑ substrate condition and nursery quality ↑ reef recovery ability	Count juvenile corals (e.g. < 3cm maximum diameter) within replicate quadrats, with assistance of blue light	Quick and easy
Remote video observations 	Capture wary fish species (particularly browsers) Quantify grazing rates on grazable surfaces Observe species grazing on bio-assays	Install remote video cameras onto reefs overlooking grazable substrate. Post-hoc observations can classify fish diversity and function	Quick and easy *in situ*, lengthy post-hoc analysis
Benthic cover of cyanobacterial mats 	Increased cover indicates: ↓ coral recruitment ↑ dissolved organic carbon ↑ bioavailable nitrogen ↓ reef health Potential ↑ in ciguatera(-like) sickness	Quantify proportion of cyanobacterial mays on benthic substrate	Requires training to identify mats, but quick and easy during surveys
Sedimentary oxygen consumption (SOC) rates 	Increased SOC rates indicate long-term organic matter input more reliably than short-term water parameters	Incubate surface sediment cores in the dark, measures oxygen prior- and post-incubation	Requires initial training and oxygen sensors, but field data is easy to collect

Considering the identified critical role of sea cucumbers in maintaining sediment integrity (Appendix D) which may in turn reduce the likelihood of cyanobacterial mat formation in coastal areas (Chapter 4), it is important that fisheries management should extend beyond reef fish and target these key organisms. Within the Pacific Island region, these organisms can be of similar economic importance as reef fish (Anderson *et al.,* 2011). Asides from fisheries management, local management should also be directed towards terrestrial sources of pollution in the form of waste(water) management and agricultural restrictions. Untreated sewage is a huge problem within the region and in many other locations in the world (UNEP/GPA, 2006). For example, more than half of surveyed island populations throughout Roviana Lagoon, Solomon Islands are currently living without access to toilets (Cakacaka unpubl. data. 2015). This thesis identifies a strong link between untreated sewage and benthic cyanobacterial mat dominance (Chapter 2, 3). After taking into account local cultural sensitivities, composting toilet installation would be one management tool whereby pollution from untreated sewage could be minimised. Compost from these toilets could also be subsequently used as a fertiliser on the often nutrient-poor soil inherent to many small islands (Catala, 1957). Composting toilets could thus not only improve adjacent water quality, but could improve crop production on islands, offering an alternative food resource to human communities. Reef fish populations could also benefit from improved benthic reef condition under improved water quality in parallel with alleviated pressure on them as a food and trade resource as islands become more productive. Considering the extensive timeframes projected for reef fish stocks to recover even under fisheries closures (e.g. 35 years on average - MacNeil *et al.,* 2015), such measures that maximise the condition of their benthic habitat as well as provide alternative livelihoods and food resources to coastal communities are urgent. Where possible managers must reduce the level of phosphate and iron of terrestrial origin entering reefs to reduce the likelihood of benthic cyanobacterial mat development which will increasingly favour reef degradation. This could be achieved by for example limiting the use of certain fertilisers within close proximity to water bodies, reducing soil erosion and protecting mangroves.

7.4. Influence of local impacts on coral reef resilience and function

The findings within this thesis indicate that increasing local impacts on Pacific islands can strongly influence benthic community composition as well as ecological functions and processes, which in turn influence future system responses to disturbances (Figure 7.1). Untreated sewage, increased agriculture and overexploitation of sea cucumbers can facilitate growth of benthic cyanobacterial mats on reefs (Chapter 2, 3). Self-reinforcing positive feedbacks associated to established mats will further favour reef degradation and erode resilience of coral-dominated systems (Chapter 3). As well as producing high amounts of DOC and bioavailable nitrogen which affect the system, toxin production and fast growth of cyanobacterial mats over bare substrate limit the ability of corals to successfully settle and grow. Coral recruitment and successive growth are critical processes in facilitating the recovery of reefs following perturbations (McClanahan *et al.,* 2012). Thus, factors that reduce coral recruitment rates and juvenile survival render reefs less resilient to an increasingly unstable future climate and associated disturbances. Resilience of subsequent degraded systems will be strong (Nyström *et al.,* 2012), making a reactive management approach highly challenging. Local stressors driving benthic cyanobacterial mat growth likely act synergistically with global stressors from climate change, amplifying the problem in the future.

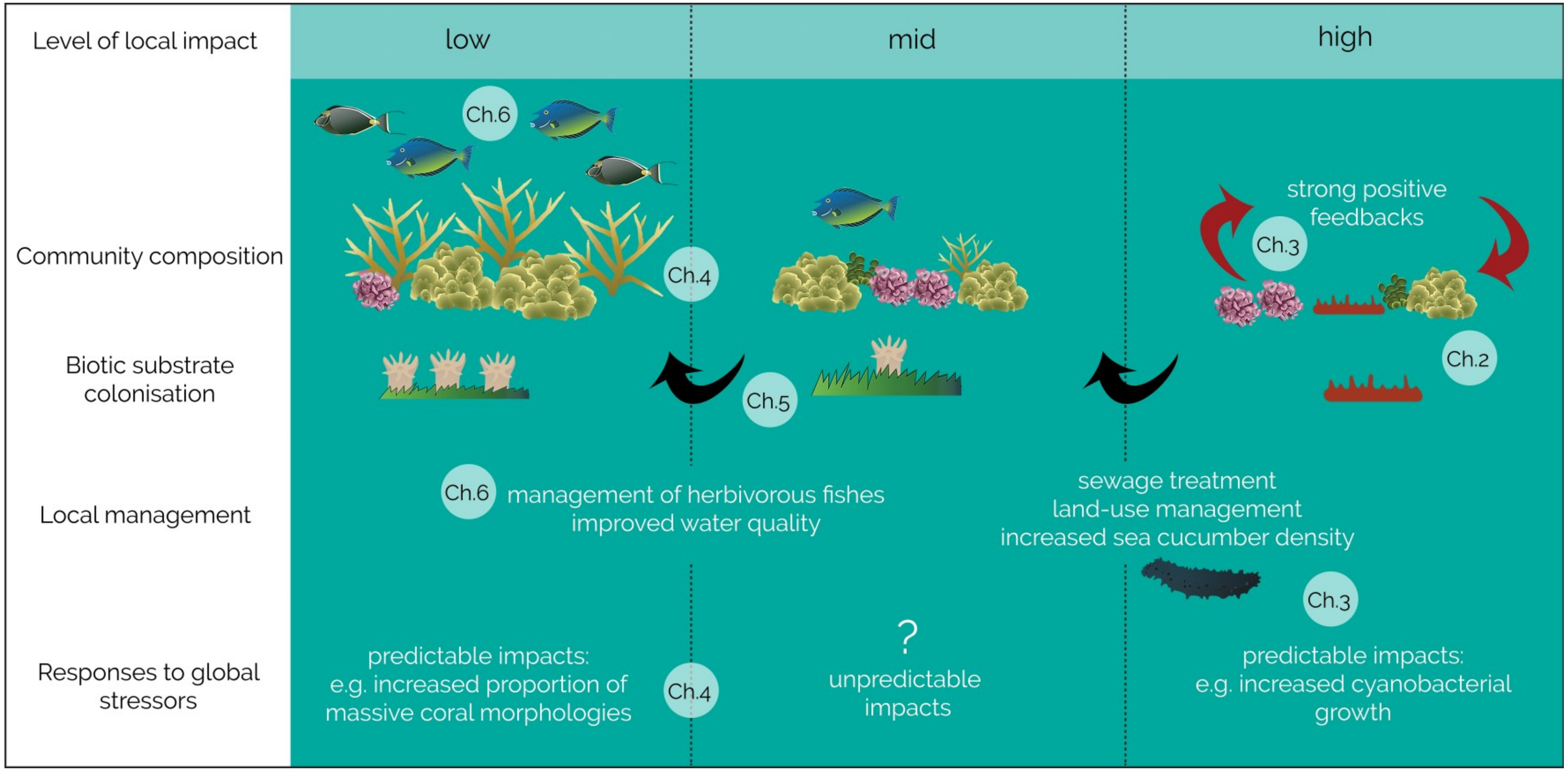


Figure 7.1. Schematic diagram of key findings within research-based chapters. A combination of research approaches across the Pacific Island region indicated that as local impacts increase, benthic communities can shift from diverse hard coral-dominated communities, to more homogeneous coral-dominated communities, and finally to communities dominated by cyanobacterial mats at the highest level of local impact (i.e. heavily overploited fish communities and high sewage input at Ahus Island). As local impacts increase, there are also changes in biotic substrate colonisation, with increasing turf height and associated reductions in coral recruitment rates and successive growth. Where benthic cyanobacterial mats become dominant, successful coral recruitment is severely compromised. Adaptive local management targeting key herbivorous reef fish, sea cucumbers, and water quality can reverse some of these degradative processes, and maximise recovery of the system. On reefs exposed to > 25 humans km^{-2} (mid-level local impact), ecological reorganisation can strongly alter future responses of the system to global change compared with those exposed to < 25 humans km^{-2} (low-level local impact).

Fishing pressure on Pacific Island reefs can indirectly lead to significant restructuring of algal turf assemblages in terms of increasing turf height (Chapter 5). This restructuring has strongly detrimental impacts on coral recruitment and successive growth, outcomes of coral-algal interactions, and in turn resilience of coral-dominated systems. Similarly, overfishing of critical herbivorous fish such as browsers can facilitate growth of blooming fleshy algal species such as *Sargassum* spp. (Chapter 6), which were found to be more competitive within fished areas in Fiji. Annual bleaching events are projected to occur within the region by *ca*. 2044 under scenario RCP 8.5 (business-as-usual; van Hooidonk *et al*., 2016; Appendix G), and by *ca*. 2060 under scenario RCP 4.5 (successful implementation of climate policies to reduce emissions). Consequently, conditions that favour growth and competitiveness of fleshy algae, unfavourable algal turf traits or benthic cyanobacterial mats will strongly compromise the future of coral-dominated systems to maintain domination during future stressful conditions. Continued overexploitation of key herbivorous fish species and sea cucumbers will thus strongly amplify the future effects of climate change-related stressors (Chapter 6, Appendix D).

Where alternative benthic organisms do not become dominant under local human impacts, ecological reorganisation and associated homogenisation within the hard coral community can also affect the ecosystem's response to global stressors from climate change (Chapter 4). Here, one of the key challenges will be predicting climate change impacts on reefs exposed to high levels of human impact where the dominant drivers of reef condition have shifted towards local features, and relationships with spatial and physical features have been disrupted (Chapter 4; Williams *et al.* 2015). As species with a high tolerance to key stressors are selected for, there may also be overlooked trade-offs whereby they are more vulnerable to other stressors. For example, thermally tolerant corals that replace susceptible species may exhibit reduced skeletal densities (Appendix E, F), deeming them more susceptible to breakage during storm surges which are also projected to increase in intensity in the future (Pachauri *et al.* 2014).

The Pacific Island region is characterised by superior taxonomic richness within fish and benthic communities (Spalding *et al.,* 2001; Roff & Mumby, 2012). Consequently, there exists a higher propensity for reef ecosystems to reorganise themselves following chronic or acute perturbations. In less diverse systems such as the Caribbean, there may be stronger signals of human impacts observed within fish and benthic assemblages. The Caribbean region is also characterised by naturally higher levels of iron, which may deem this region more likely to undergo shifts towards benthic cyanobacterial mats (Chapter 3), as observed in the Netherland Antilles (Brocke *et al.,* 2015a; de Bakker *et al.,* 2017). On the other hand, considering the very high reliance on marine resources and low capacity to adapt to coral reef degradation in the Pacific Island region (Burke *et al*., 2011), future increasing local stressors are likely to be challenging to manage compared to other regions where alternative livelihoods (e.g. within the tourism section) are easier to integrate.

7.5. Future research areas

The findings in this thesis reveal several areas for future research. The threshold by which low and high impact sites were classified within this thesis (25 people km^{-2} reef; Chapter 4) was based on a previously identified breaking point identified from this same data-set after which phylogenetic diversity of parrotfishes were significantly reduced (D'Agata *et al.,* 2014). Though this threshold revealed stark contrasts within benthic assemblages and their key drivers, future research should further identify thresholds of human density and associated factors that improve understanding and predictability of reef degradation. This would be in combination with identifying specific factors associated to human populations (e.g. sewage discharge, fishing methods) that directly drive changes within benthic communities, similar to how population density combined with distance to market significantly strengthens predictability of reef fish assemblages (Brewer *et al.,* 2012, 2013). Recently available satellite data and global datasets provide a strong basis for such studies.

Findings within this thesis identified a consistently strong SOC rate signal from a sewage-input source across distances of 90 m on a reef flat, with reductions in sewage impact already observed at 250 m distance. These results were however very small-scale (i.e. from beach toilets) on a small island, and more studies along such gradients at different scales are imperative to improve our ability to quantify bottom-up impacts on coastal systems. Future research should ultimately aim to define a mathematical function that quantifies the radius of pollution from human populations in coastal areas that is applicable for small islands. While a function appropriate at large spatial scales and for developed areas was already provided by Halpern *et al.,* (2008), its relevance at small islands and areas inhabited by subsistence communities is limited. For example, agricultural runoff is quantified from annual fertiliser usage, and point source and non-point source pollution are not captured where paved roads are absent. Impacts of sewage input and small-scale farming are thus likely overlooked despite having large impacts on adjacent reefs. To calculate a radius of impact away from such small islands, a function should incorporate factors such as human population density, presence of different forms of pollution (e.g. farming, treated vs. untreated sewage, rivers), inshore reef morphology and currents.

As ecological reorganisation becomes increasingly important on impacted reefs, it is important for research to unravel potential implications of such restructuring within the ecosystem. For example, one key observation in the Pacific Island reefs is a dominance of *Porites rus* in inshore areas (Appendix E), for which there is very limited information published. Preliminary results on skeletal densities of *P. rus* indicated that densities were very low compared to other dominant species (Appendix F). Such stress-tolerant types may be vulnerable in unseen ways if for example they have low fecundity, or they trade-off tolerance with growth rates or skeletal densities. Previous research has identified a reduction in such traits and processes in thermally-tolerant species and associated symbionts (e.g. Jones & Berkelmans, 2010) which may deem them vulnerable to alternative stressors such as increasing storm intensity which will occur in parallel to ocean warming (Pachauri *et al.,* 2014).

Considering the combined ecological and economic importance of sea cucumbers throughout the Pacific Island region, it is important that more attention is directed into this area of research. Such research should further aim to quantify the synergistic effects of sea cucumber overexploitation with global stressors such as thermal stress (and in turn their effects on sea cucumber physiology), as well as alternative local stressors such as increasing organic matter and nutrient input. Protection (and re-introduction) of these species may offer a potential tool to alleviate stress in coastal areas. By maximising oxygen penetration and consequently integrity of sediments and associated microbial communities, these organisms may have significant benefits in buffering stress from, and strengthening system resilience to, both flooding events and ocean warming. Furthermore, considering increasing reports of ciguatera(-like) sickness throughout the Pacific Island region (Skinner *et al.,* 2011) and the identification of benthic cyanobacterial mats as a causative organism (Laurent *et al.*, 2008, 2012), it is important to strengthen research links between reef degradation, benthic cyanobacterial mats, ciguatera(-like) sickness, and sea cucumbers.

7.6. Concluding remarks

In summary, this thesis provides evidence that local island populations can have a range of effects on coral reef ecosystem structure and functioning. These effects range from distinct shifts in dominance within benthic communities, to influencing the system's capacity to sustain itself and recover from perturbations, or ecological homogenisation alters the relationship between reefs and environmental attributes.

Fieldwork in Papua New Guinea indicated that whilst hard corals can continue to thrive after suffering heavy overexploitation of reef fish stocks, additional stress from local impacts such as sewage can drive profound shifts towards alternative benthic groups such as benthic cyanobacterial mats (Chapter 2). Following this, a thorough literature review of putative drivers and ecological consequences of increasing benthic cyanobacterial mats on coral reefs identified many future challenges for reef managers and coastal communities in the absence of proactive action against this emerging problem (Chapter 3). Where categorical ecological states are not observed, a large-scale regional data analysis revealed that increasing local human impacts can significantly alter the relationship between benthic assemblages and their physical environment, strongly compromising the ability to predict future responses to climate change-related stressors (Chapter 4). This analysis also revealed that most Pacific Island reefs are existing in a partially degraded state along the ecological continuum between regimes, appearing increasingly homogeneous. Considering the increasingly homogenous appearance of benthic assemblages, fieldwork in Fiji aimed to improve the ability of monitoring to detect changes in ecosystem trajectories and recovery potential (Chapter 5). A large discrepancy was identified between conventional and newly developed complementary status and ecological function- and process-based metrics. Metrics focused on biotic substrate colonisation revealed positive responses to fisheries restrictions, whereas conventional metrics lacked the resolution to identify differences between reefs. The final literature-based chapter provides a thorough review of critically important herbivorous fish within the region and identifies management challenges and priorities to maximise long-term sustainability of ecologically and economically important fisheries (Chapter 6). Additional research done alongside the key chapters of this thesis (Appendix D) quantified the ecological importance of sea cucumbers which are key alternative fisheries targets in the region.

The effects of global change with the Pacific Island region are conspicuous. While conducting the fieldwork for this thesis, the study areas were hit by both the strongest cyclone (Winston) recorded to hit land in the Southern Hemisphere, alongside the strongest El Niño (2015/2016) and the warmest year since records began. At the point of writing this thesis, we are still within the window whereby action can be taken to stabilise the climate at a level that some coral reefs can survive, with the hope that they can replenish other areas in the future. However, even under a scenario whereby climate agreements are implemented internationally, >75% of reefs will experience annual severe bleaching by 2070 (van Hooidonk *et al.,* 2016) and only 10% are projected to persist by 2100 (Frieler *et al.*, 2012). It is thus urgent that managers and stakeholders are able to critically scrutinise the effectiveness of different management tools as well as to prioritise areas in which to invest and focus future management efforts. This thesis provides some tools that maximise the ability to interpret reef trajectories and functions to support managers in reef assessments. Furthermore, it provides a better understanding of the complex interactions between local and global stressors at Pacific island reefs. Increasing local impacts strongly disrupt the relationship between reef assemblages and natural environmental features, and subsequently compromise our ability to predict how climate change-related stressors will affect benthic communities. This thesis highlights that reefs in closer proximity to inhabited islands require context-specific management approaches to maximise their future sustainability and provision of ecosystem services on which human societies so strongly rely.

7.7. References

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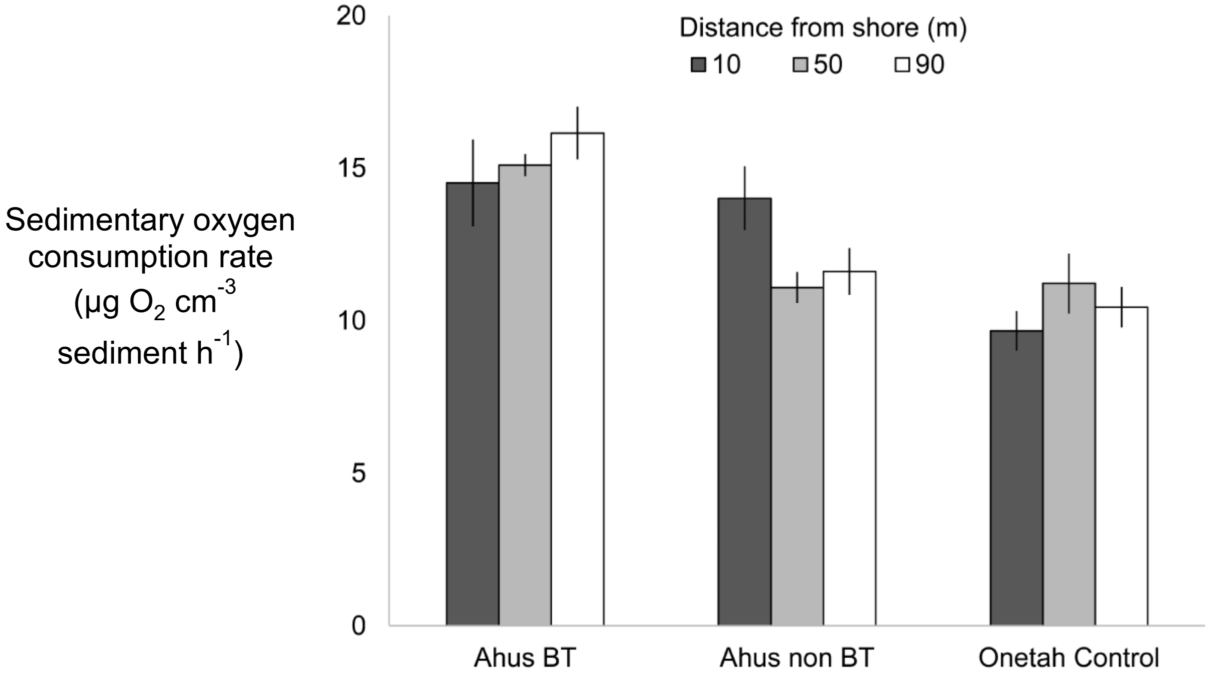
APPENDIX

Appendix A – Supplementary material from Chapter Two

Sedimentary oxygen consumption rates (mean ± SE) for each distance from shore (10, 50, 90 m) at each site.



Appendix B – Supplementary material from Chapter Four

B (i) – Site selection criteria, survey dates and history

Criteria for site selection: (i) having active reef fisheries, (ii) being representative of the country, (iii) being relatively closed systems, (iv) being appropriate in size, (v) possessing diverse habitats*, (vi) presenting no major logistical problems, (vii) having been previously investigated and (viii) presenting particular interest for the respective Fisheries Agency. For full details see Pinca et al. (2010)

*Reefs were grouped into four geomorphological structures: sheltered coastal reef (mean depth = 3 m), intermediate lagoon reef (patch reef inside lagoon: mean depth = 4 m), back reef (inner side of outer reef: mean depth = 3 m) and outer reef (exposed reef: mean depth = 7 m), with a total of 185 reefs (i.e. up to n = 4 per site depending on the reef types present).

Table containing survey dates and timelines of disturbances (up to 12 years before surveys) with associated references

Country or Territory	Surveys	History of Events	Reference
Cook Islands	Aitutaki, 02.2007 Mangaia 10.2007 Palmerston 02.2007 Raratonga 10.2007	1997: Several cyclones (including Cyclone Martin – category 3) 2000: Mass bleaching event (up to 80% Acropora bleached in Rarotonga) 2002/2003: Major cyclone 2003/2004: Major cyclone 2004/2005: Several destructive cyclones (six)	Lovell, (2001), Cumming *et al.*, (2002), Salvat, (2002), de Scally, (2008)
Fiji	Dromuna 04.2003 Lakeba 06.2003 Mali 06.2003 Muiavuso 04.2003	2000: Mass bleaching event (40-80% coral mortality) 2001: Minor bleaching 2002: Bleaching in shallow areas	Goreau *et al.*, (2000), Cumming *et al.*, (2002), Lovell *et al.*, (2004)

cont.

Country or Territory	Surveys	History of Events	Reference
French Polynesia	Fakarava 03.2004 Maatea 05-06.2006 Mataiea 09-10.2003 Raivavae 03.2002, 03.2004 Tikehau 10.2003	1994: Major bleaching but low mortality 1997: Major cyclones (including Cyclone Martin – category 3), but coral cover had almost recovered by 2003 2002: Patchy bleaching and mortality 2002: Start of COTs outbreak (at Society Archipelago and Australes) which lasted until 2010	Salvat, (2002), Vieux *et al*., (2004), Adjeroud *et al*., (2005), Trapon *et al*., (2011)
FSM	Piis-Panewu 04.2006 Riiken 04.2006 Romanum 04.2006 Yyin 05.2006	2005: Concerning levels of COTs reported from rapid assessment	George *et al*., (2008)
Kiribati	Abaiang 06.2004 Abemama 05.2004 Kiritimati 09.2004 Kuria 05.2004	2003: Fish kill in atolls of Gilbert Islands 2004: (post survey) first mass bleaching event internationally reported	Donner *et al*., (2010)
Marshall Islands	Ailuk 08.2007 Arno 09.2007 Laura 09.2007 Likiep 08.2007	2001: Bleaching mortality observed (particularly shallow Acropora) 2003: Bleaching event, high incidence of Acropora white disease 2004: Elevated COTs (>1000/km2) found in Majuro's southwestern lagoon, with high associated coral mortality	Beger *et al*., (2008)

cont.

Country or Territory	Surveys	History of Events	Reference
Marshall Islands cont.		2006: Storm caused large surf and storm surge (become Typhoon Soulik) – Acropora colonies damaged. Also bleaching event with up to 90% Acropora bleaching (20-50% mortality) in lagoons.	
Nauru	Nauru 10.2005	2000: Phosphate reserves are virtually exhausted (80% of the island's surface has been strip mined – mining started in 1908) 2002: High rainfall and some bleaching 2003: Coral bleaching and mass fish kills both linked to elevated SSTs, strong upwelling or drops in dissolved oxygen levels. 2004: Huge number of seabirds found dead without a known cause	Sulu *et al.*, (2002), Lovell *et al.*, (2004), Chin *et al.*, (2011)
New Caledonia	Luengona 06.2004 Moindou 04-09.2004 Ouasse 08.2004 Oundjo 02.2004 Thio 03.2004	1998 and 2001: Extensive coral loss due to COTs, bleaching and disease 2003: Cyclone (Erica) destroyed 10- 80% coral cover	Sulu *et al.*, (2002), Lovell *et al.*, (2004)
Niue	All Niue 05.2005	2004: Major cyclone (Cyclone Heta - category 5) caused 20-90% reefs on the western coast to be flattened, hence live coral in surveys sometimes <2%	Vieux *et al.* (2004), Kronen *et al.* (2008), Chin *et al.* (2011)

cont.

Country or Territory	Surveys	History of Events	Reference
Palau	Airai 04.2007 Koror 05.2007 Ngarchelong 04.2007 Ngatpang 04.2007	1998: Mass bleaching from El Niño reduced coral cover from 50-70% to 14-23% (exposed barrier reefs suffered more than coastal reefs). High mortality of soft corals. *Area is not exposed to cyclones and COTs outbreaks remain local events*	Golbuu, (2011)
Papua New Guinea	Andra 12.2002, 08.2006, 08.2008 Panapompom 11.2006 Sideia 10.2006 Tsoilaunung 08.2006	1996: Mass bleaching event (>50% corals at some sites) 1998: Mass bleaching from El Niño (75% Acropora affected around Kimbe Bay) 1999: Bleaching event 2000/2001: Mass bleaching event (>50% corals bleached at some sites)	Lovell, (2001), Cumming *et al.*, (2002), Foale, (2006)
Samoa	Manono-uta 06.2005 Salelavalu 08.2002 08.2005 Valioa 06.2005 Vaisala 08.2005	2004: Cyclone (Heta – category 5) damaged 13% of coral reefs	Sulu *et al.*, (2002), Lovell *et al.* (2004), Chin *et al.* (2011)
Solomon Islands	Chubikopi 12.2006 Marau 06.2006 Nggela 06.2006 Rarumana 08.2006	2000: Mass bleaching 2002: Major cyclone (Zoe – category 5)	Lovell, (2001), Cumming *et al.* (2002), Sulu *et al.* (2002)
Tonga	Ha'afutu2 09.2008 Koulo 10.2008 Lofanga 09-10.2008 Manuka 09.2008	1997: Cyclone (Hina – category 3) 1999: Cyclone (Cora – category 3) 2000: Cyclone, mass bleaching (up to 90% of Goniastrea and Platygyra colonies bleached)	Lovell, (2001), Salvat, (2002)

cont.

Country or Territory	Surveys	History of Events	Reference
Tuvalu	Funafuti 11.2004 Niutao 10-12.2004 04.2005 Nukufetau 10-11.2004 Vaitipu 03-04.2005	1997: Major cyclones (Oliwa and Keli) 2002: Mass bleaching (30-40% corals bleached)	Sulu *et al.*, (2002), Lovell *et al.*, (2004)
Vanuatu	Maskelynes 11-12.2003 Moso 07.2003 Paunagisu 07.2003 Uri-Uripiv 11-12.2003, 11.2004	2001: Bleaching event (in Moso but lack of monitoring data for other areas)	Sulu *et al.*, (2002)
Wallis and Futuna	All Futuna 11.2005 Halalo 08-09.2005 Vailala 09.2005		

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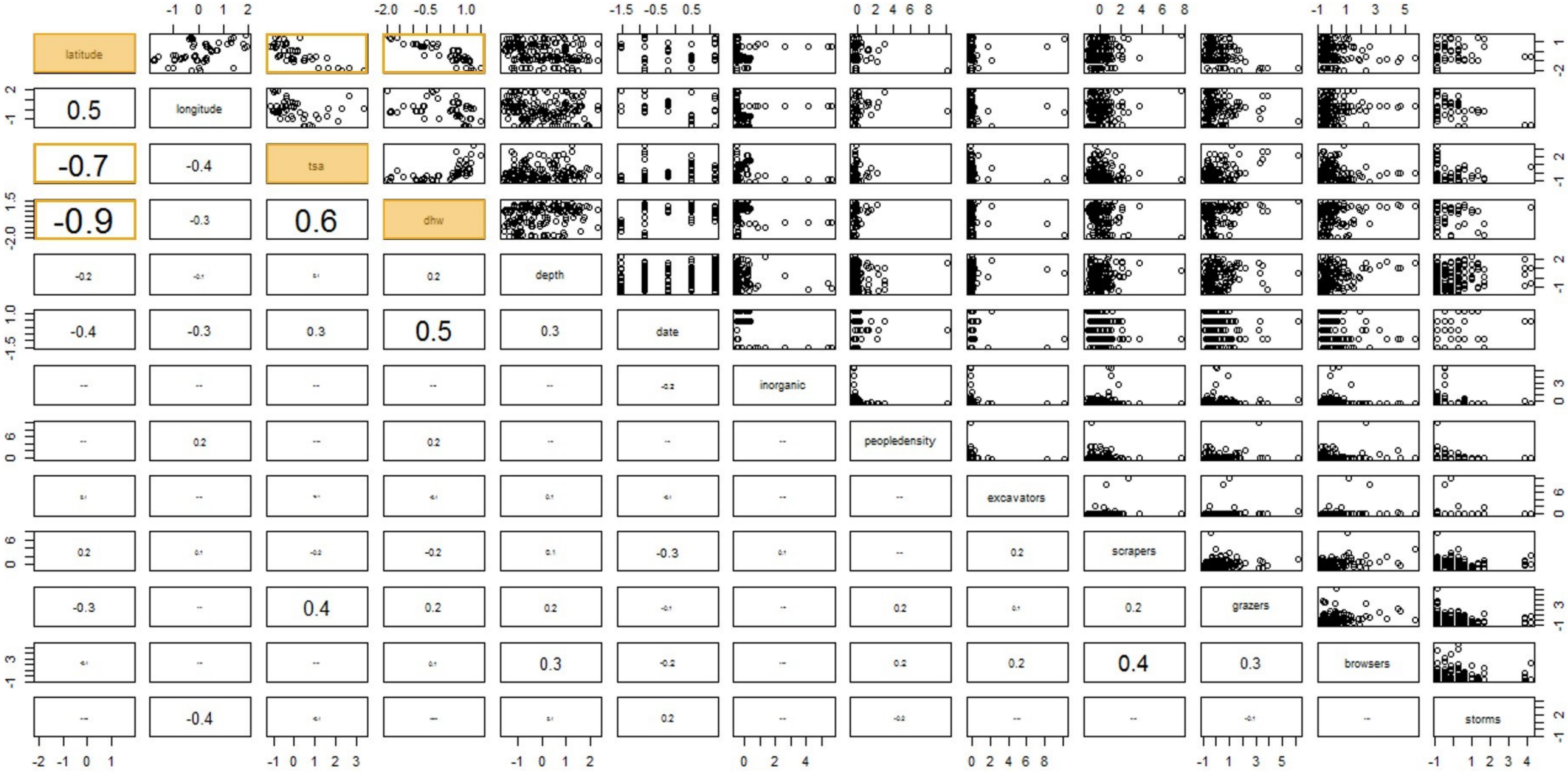
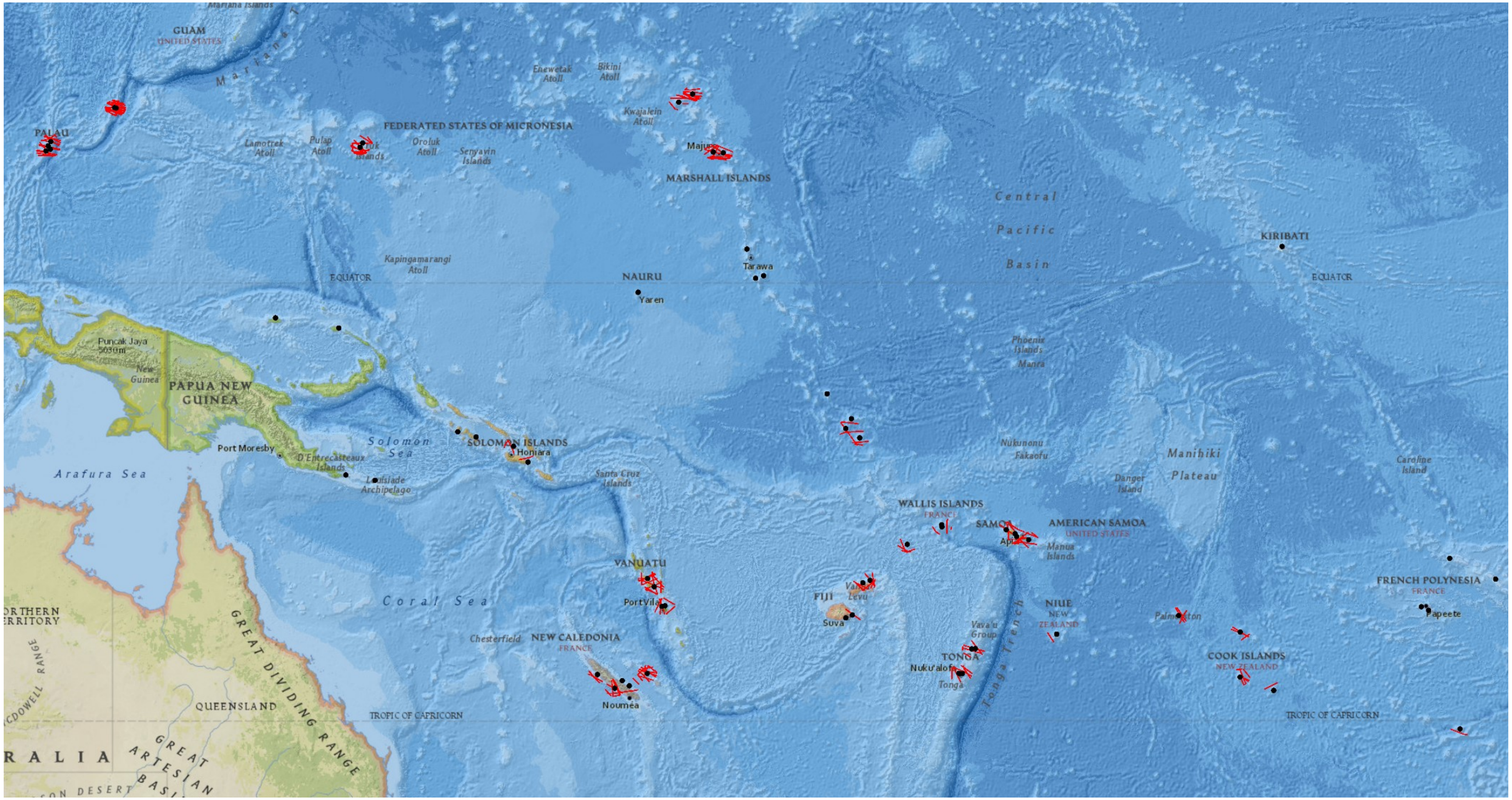
B (ii) - additional information on predictors.

Relationships between (z-transformed) predictors. TSA refers to thermal stress anomalies, DHW refers to degree heating weeks.

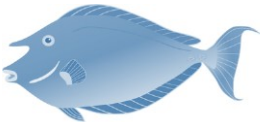
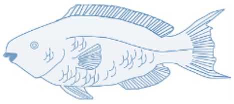


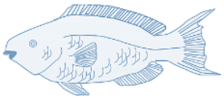
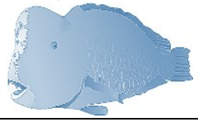
Tracks of storms (red lines) passing within 50 km buffer of study sites (black points)



B (iii) - Herbivorous fish recorded within surveys, classified into functional groups as specified in Green & Bellwood (2009).

Functional Group	Species
Grazers/detritivores 	*Acanthurus achilles* *Acanthurus auranticavus* *Acanthurus blochii* *Acanthurus dussumieri* *Acanthurus fowleri* *Acanthurus guttatus* *Acanthurus leucocheilus* *Acanthurus leucopareius* *Acanthurus lineatus* *Acanthurus maculiceps* *Acanthurus nigricans* *Acanthurus nigricauda* *Acanthurus nigrofuscus* *Acanthurus nigroris* *Acanthurus olivaceus* *Acanthurus pyroferus* *Acanthurus sp.* *Acanthurus triostegus* *Acanthurus xanthopterus* *Centropyge bicolor* *Centropyge bispinosa* *Centropyge flavissima* *Centropyge loricula* *Centropyge sp.* *Centropyge tibicen* *Centropyge vrolikii* *Siganus argenteus* *Siganus canaliculatus* *Siganus corallinus* *Siganus doliatus* *Siganus fuscescens* *Siganus guttatus* *Siganus lineatus* *Siganus puellus* *Siganus punctatissimus* *Siganus punctatus* *Siganus randalli* *Siganus* spp. *Siganus spinus*

Grazers/detritivores cont. 	*Siganus stellatus* *Siganus uspi* *Siganus vermiculatus* *Siganus vulpinus* *Zebrasoma flavescens* *Zebrasoma rostratum* *Zebrasoma scopas* *Zebrasoma* spp. *Zebrasoma veliferum*
Browsers 	*Calotomus carolinus* *Calotomus spinidens* *Leptoscarus vaigiensis* *Naso annulatus* *Naso brachycentron* *Naso brevirostris* *Naso lituratus* *Naso unicornis* *Platax orbicularis* *Platax* spp. *Platax teira*
Scrapers/small excavators 	*Chlorurus bleekeri* *Chlorurus bowersi* *Chlorurus japanensis* *Chlorurus sordidus* *Chlorurus* spp. *Hipposcarus longiceps* *Scarus altipinnis* *Scarus chameleon* *Scarus dimidiatus* *Scarus festivus* *Scarus flavipectoralis* *Scarus forsteni* *Scarus frenatus* *Scarus ghobban* *Scarus globiceps* *Scarus longipinnis* *Scarus niger* *Scarus oviceps* *Scarus prasiognathos* *Scarus psittacus* *Scarus quoyi* *Scarus rivulatus*

Scrapers/small excavators cont. 	*Scarus rubroviolaceus* *Scarus schlegeli* *Scarus* spp. *Scarus spinus* *Scarus tricolor* *Scarus xanthopleura*
Large excavators/bioeroders 	*Bolbometopon muricatum* *Chlorurus frontalis* *Chlorurus microrhinos*

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B (iv) – Explanatory power of models and relative predictor importance for reefs exposed to low (< 5 tonnes km^{-2} reef year^{-1}) and high (> 5 tonnes km^{-2} reef year^{-1}) fishing pressure.

Outcomes from models containing outer reefs in terms of adjusted-R^2, separately for reefs exposed to low and high fishing pressure. Best-fit[1] models tailored for reefs exposed to each level of fishing pressure fitted to their respective set of reefs, best-fit[2] refers to the outcome from best-fit[1] models tailored for reefs exposed to low fishing pressure fitted anew onto reefs exposed to high fishing pressure.

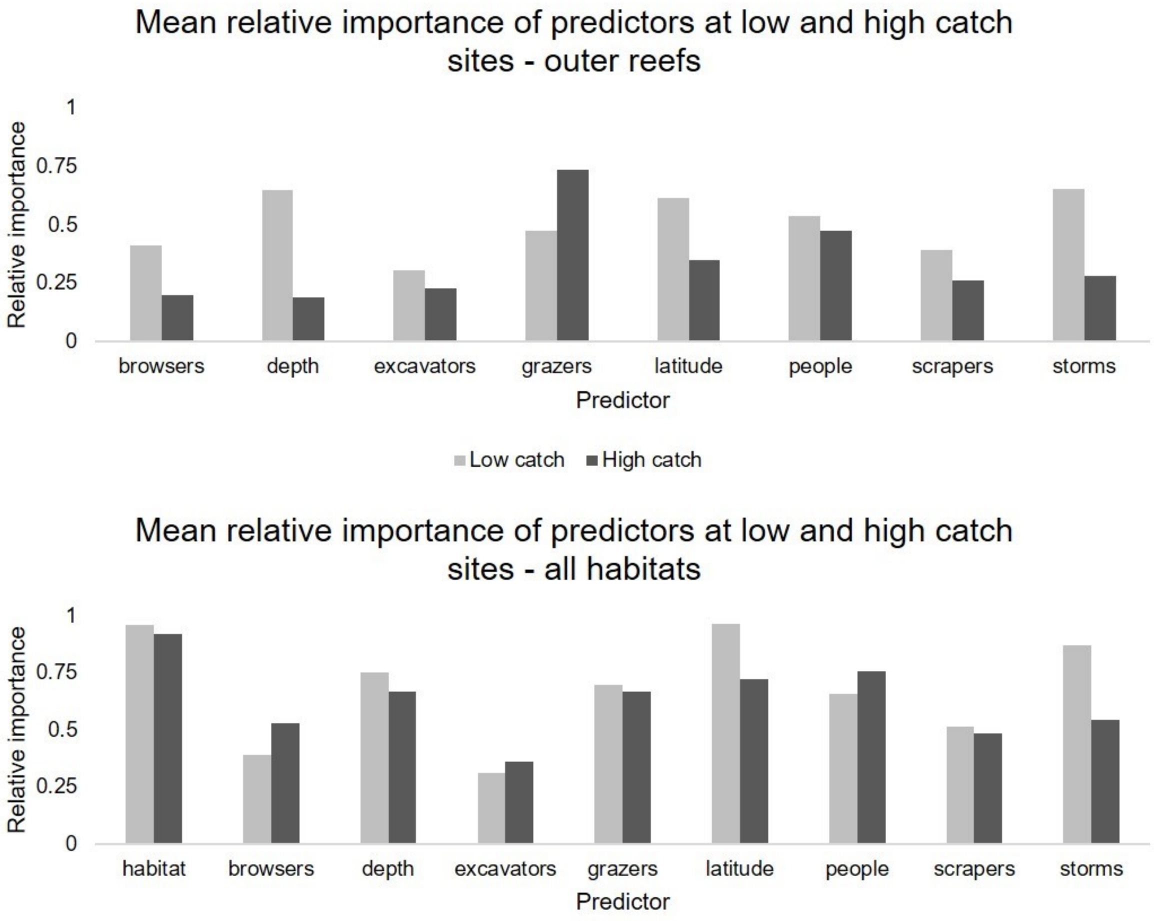
		Adjusted-R^2	
Response	Predictor set	low (n=36)	high (n=27)
Live coral	*Remote predictors*	0.28	0.00
	Local features	0.53	0.58
	Best-fit [1,2]	0.62	0.25[1], 0.47[2]
Turf algae	*Remote predictors*	0.21	0.12
	Local features	0.27	0.36
	Best-fit [1,2]	0.30	0.37[1], 0.52[2]
Fleshy algae	*Remote predictors*	0.22	0.09
	Local features	0.38	0.32
	Best-fit[1,2]	0.68	0.21[1], 0.14[2]
PC1	*Remote predictors*	0.45	0.06
	Local features	0.17	0.62
	Best-fit[1,2]	0.66	0.10[1], 0.65[2]
PC2	*Remote predictors*	0.37	0.00
	Local features	0.54	0.36
	Best-fit[1,2]	0.61	0.35[1,]0.40[2]
Coral morphological ratio	*Remote predictors*	0.55	0.05
	Local features	0.21	0.36
	Best-fit[1,2]	0.70	0.37[1], 0.40[2]
Overall	*Remote predictors*	Paired t-test **p = 0.006**	
	Local features	Paired t-test p = 0.647	
	Best-fit [1,2]	Paired t-test **p = 0.017**[1], p = 0. 184[2]	

APPENDIX B

Outcomes from models containing all reef habitats in terms of adjusted-R^2, separately for reefs exposed to low and high fishing pressure. Best-fit^1 models tailored for reefs exposed to each level of fishing pressure fitted to their respective set of reefs, best-fit^2 refers to the outcome from best-fit^1 models tailored for reefs exposed to low fishing pressure fitted anew onto reefs exposed to high fishing pressure.

		Adjusted-R^2	
Response	Predictor set	low catch (n=107)	high catch (n=75)
Live coral	*Remote predictors*	0.24	0.07
	Local features	0.26	0.24
	Best-fit ^{1,2}	0.42	0.23^1, 0.39^2
Turf algae	*Remote predictors*	0.34	0.24
	Local features	0.16	0.24
	Best-fit ^{1,2}	0.50	0.44^1, 0.43^2
Fleshy algae	*Remote predictors*	0.24	0.15
	Local features	0.02	0.17
	Best-fit ^{1,2}	0.38	0.16^1, 0.34^2
PC1	*Remote predictors*	0.53	0.55
	Local features	0.45	0.55
	Best-fit ^{1,2}	0.58	0.60^1, 0.61^2
PC2	*Remote predictors*	0.24	0.14
	Local features	0.17	0.32
	Best-fit ^{1,2}	0.44	0.41^{1,2}
Coral morphological ratio	*Remote predictors*	0.10	0.07
	Local features	0.06	0.19
	Best-fit ^{1,2}	0.29	0.21^1, 0.27^2
Overall	*Remote predictors*	Paired t-test **p = 0.033**	
	Local features	Paired t-test **p = 0.014**	
	Best-fit ^{1,2}	Paired t-test p = 0.067^1, p = 0. 093^2	

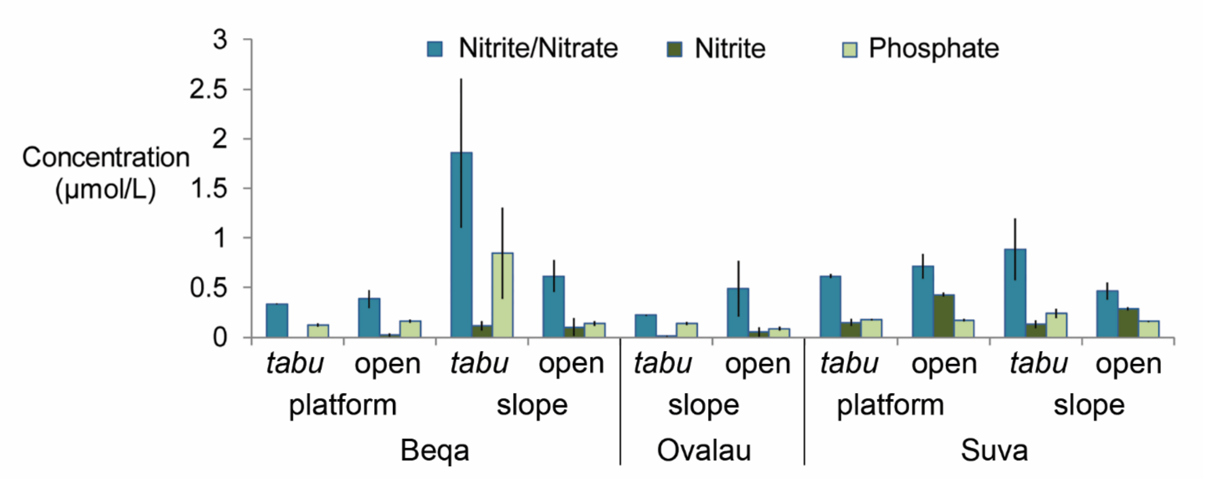
Mean relative importance of predictors at outer reefs (top) and all reef habitats (bottom), from *best-fit*[1] model selection.



Appendix C – Supplementary material from Chapter Five

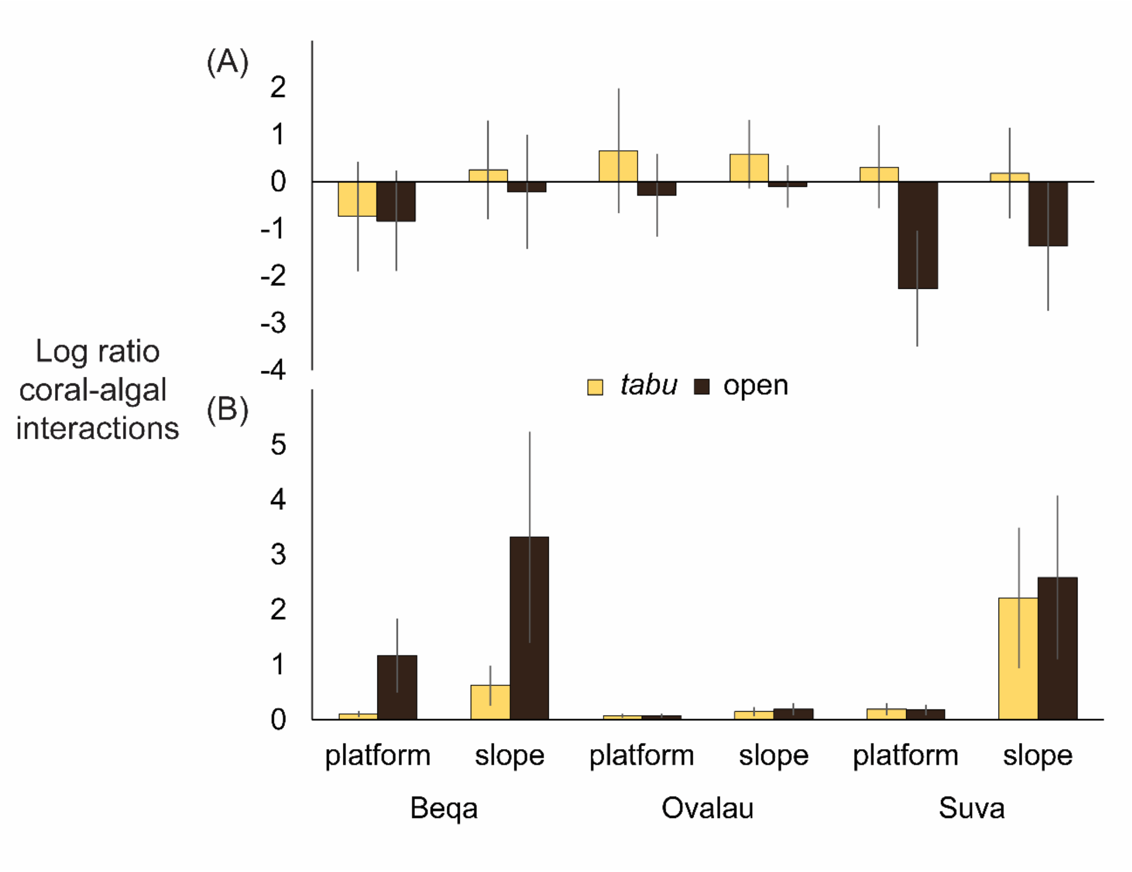
C (i) – inorganic nutrients at study sites

Concentration (mean ± SE) of nutrients (nitrite/nitrate, nitrite, phosphate) at each study site.



C (ii) - Outcomes of coral-algal interactions by site

Log ratio (mean ± SE) of outcomes for (A) coral-algal turf interactions, and (B) coral-fleshy algae interactions, with higher values reflecting more interactions being won by the algae.



C (iii) - Functional spaces of herbivorous fish communities

To further investigate how functional assemblages of herbivorous fishes differed between protected (*tabu*) and open areas, and how this was captured differently according to different methods, we calculated matrices built on various functional traits (see table for traits according to observed species): i. tooth structure (i.e. fusiform, incisiform, chaetodontiform, tricuspid), ii. consumes filamentous algae (y/n), iii. targets fleshy macroalgae (y/n), iv. clears loose sediment (y/n), vi. excavates substratum (y/n). The plots are 2D visualisations of the *dbFD* function output (computed based on 4 dimensions) from the *FD* package in R (Laliberté & Legendre, 2010; Laliberté *et al*., 2014, and constructed using the *ggplot2* (Wickham 2009) packages with *grid* (built-in R package; R Development Core Team, 2013) and *gridExtra* (Auguie, 2016) combining the plots together in a single figure. Each black dot is a unique functional entity (one or a group of species with the same functional traits coded in). Those connected by blue are scrapers and green are grazers. If they are not connected (which would be either raking *Ctenochaetus* spp. or browsing *Calotomus carolinus*) they are not part of the traditional scraper or grazer groupings.

Plots are separated according to the method by which the data were acquired:

(a) From fish assemblages observed during standard underwater visual censuses (i.e. from visual observations of a diver along 30 x 5m belt transects (n = 8 site^{-1})
(b) From fish assemblages as extracted from videos – using all herbivorous species observed within video footage during 30 min (n = 4/5 site^{-1})
(c) From fish assemblages observed feeding on grazable substrate in video footage during 30 min observations (n = 4/5 site^{-1})

The graphs consistently indicate that although you might have high species richness or diversity, many of the species observed performed the same roles as others (i.e. they were redundant according to the traits put into the R function). According to UVC data (a), functional assemblages of herbivorous fish are almost identical across fished and tabu reefs. According of fish assemblages observed within remote video footage (b), functional space can be greater within *tabu* reefs compared to adjacent fished areas, particularly at Ovalau on the reef platform, and reef slopes at Beqa and Ovalau. According to species observed feeding within video footage (c) *tabu* and open reefs are similar, though functional space within tabu reefs at Suva platform and Beqa slope exceeding their adjacent fished reefs, and in contrast Suva slope fished reefs exhibit greater functional assemblages than protected *tabu* Reefs.

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Matrix of herbivorous fish functional traits used to calculate dissimilarity scores for plotting functional niche plots.

	Species	Tooth structure[1]	Consumes filamentous algae[2]	Targets fleshy macroalgae[3]	Clears loose sediment[4]	Excavates substratum[5]
Scarinae (Labridae)	*Calotomus carolinus*[6]	Fusiform	N	Y	N	N
	Cetoscarus bicolor	Fusiform	Y	N	Y	Y
	Chlorurus bleekeri	Fusiform	Y	N	Y	Y
	Ch. microrhinos	Fusiform	Y	N	Y	Y
	Ch. sordidus	Fusiform	Y	N	Y	Y
	Hipposcarus longiceps	Fusiform	Y	N	Y	N
	Sc. altipinnis	Fusiform	Y	N	Y	N
	Sc. chameleon	Fusiform	Y	N	Y	N
	Sc. dimidiatus	Fusiform	Y	N	Y	N
	Sc. frenatus	Fusiform	Y	N	Y	N
	Sc. ghobban	Fusiform	Y	N	Y	N
	Sc. globiceps	Fusiform	Y	N	Y	N
	Sc. niger	Fusiform	Y	N	Y	N
	Sc. oviceps	Fusiform	Y	N	Y	N
	Sc. psittacus	Fusiform	Y	N	Y	N
	Sc. rivulatus	Fusiform	Y	N	Y	N
	Sc. schlegeli	Fusiform	Y	N	Y	N

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[1] Scarinae (Chen, 2002), *Zebrasoma* (Randall, 1955), *Ctenochaetus* (Purcell & Bellwood, 1993), Nasinae (Fishelson & Delarea, 2014), and Siganidae (Woodland, 1990).

[2] All scrapers and grazers following Green & Bellwood (2009), *Ctenochaetus* (Purcell & Bellwood, 1993), Nasinae (Choat *et al.*, 2002), and Siganidae (Fox & Bellwood, 2008 and R. McAndrews personal observation).

[3] Distinction between thallus and blade feeders made following Streit *et al.* (2015), *Platax* (Bellwood *et al.*, 2006).

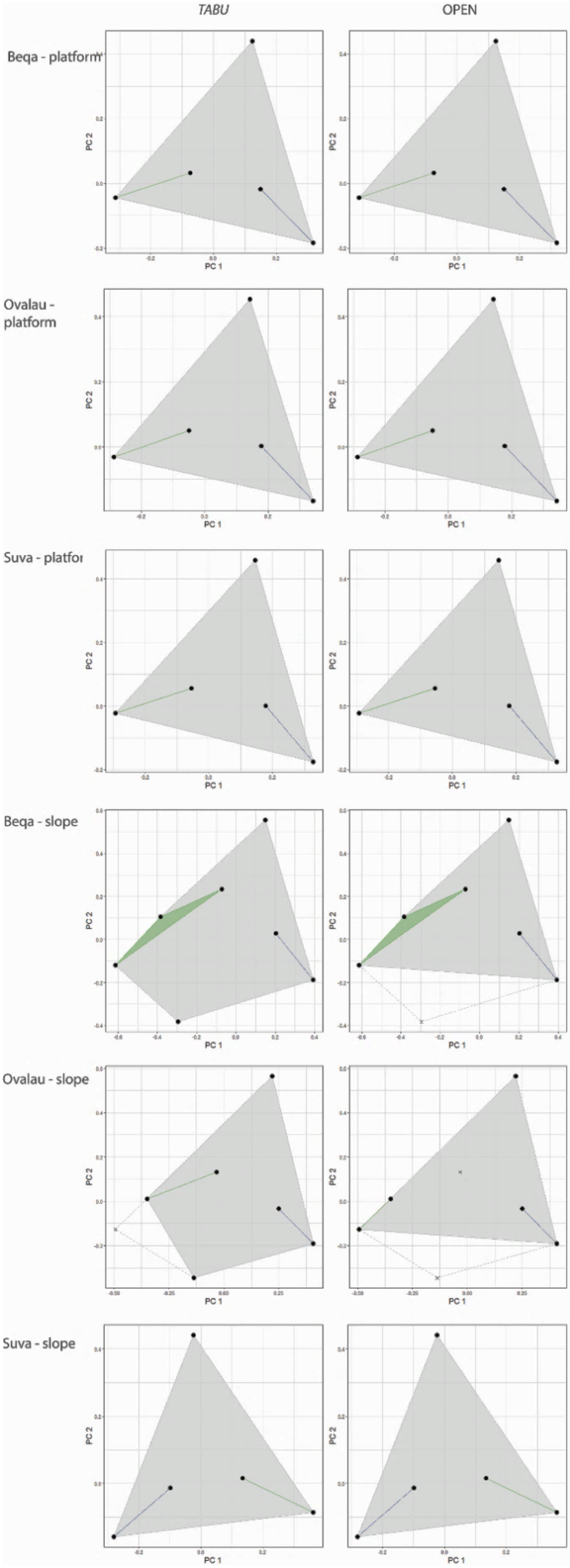
[4] All scrapers and excavators following Green & Bellwood, (2009), *Ctenochaetus*, *Acanthurus nigricauda*, and *Ac. olivaceus* following Choat *et al.,* (2002).

[5] Scrapers (included within "Ingests sediment" category) differentiated from excavators by jaw morphology and bite volume (see Bellwood, 1994)

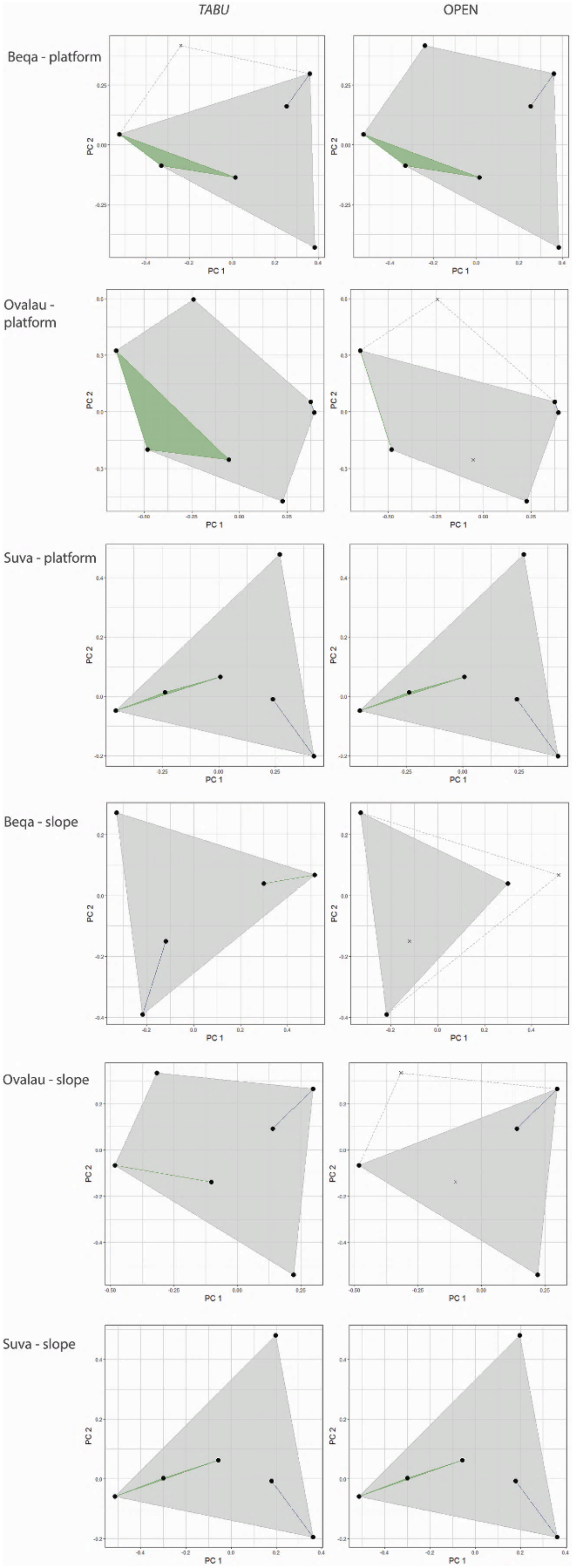
[6] Following Green & Bellwood, (2009)

Acanthuridae	*Acanthurus blochii*	Incisiform	Y	N	N	N
	Ac. lineatus	Incisiform	Y	N	N	N
	Ac. nigricauda	Incisiform	Y	N	Y	N
	Ac. nigrofuscus	Incisiform	Y	N	N	N
	Ac. olivaceus	Incisiform	Y	N	Y	N
	Ac. pyroferus	Incisiform	Y	N	N	N
	Ac. triostegus	Incisiform	Y	N	N	N
	Ac. xanthopterus	Incisiform	Y	N	N	N
	Ctenochaetus binotatus	Chaetodontiform	N	N	Y	N
	Ct. striatus	Chaetodontiform	N	N	Y	N
	Zebrasoma scopas	Incisiform	Y	N	N	N
	Ze. velifer	Incisiform	Y	N	N	N
Nasinae (Acanthuridae)	*Naso brevirostris*	Incisiform	Y	Y	N	N
	Na. lituratus	Incisiform	Y	Y	N	N
	Na. unicornis	Incisiform	Y	Y	N	N
	Na. vlamingii	Incisiform	Y	Y	N	N
Ephippidae	*Platax orbicularis*	Tricuspid	N	Y	N	N
Siganidae	*Siganus canaliculatus*	Incisiform	N	N	N	N
	Si. doliatus	Incisiform	Y	N	N	N
	Si. lineatus	Incisiform	Y	N	N	N
	Si. punctatus	Incisiform	Y	N	N	N
	Si. spinus	Incisiform	Y	N	N	N
	Si. uspi	Incisiform	Y	N	N	N
	Si. vermiculatus	Incisiform	Y	N	N	N

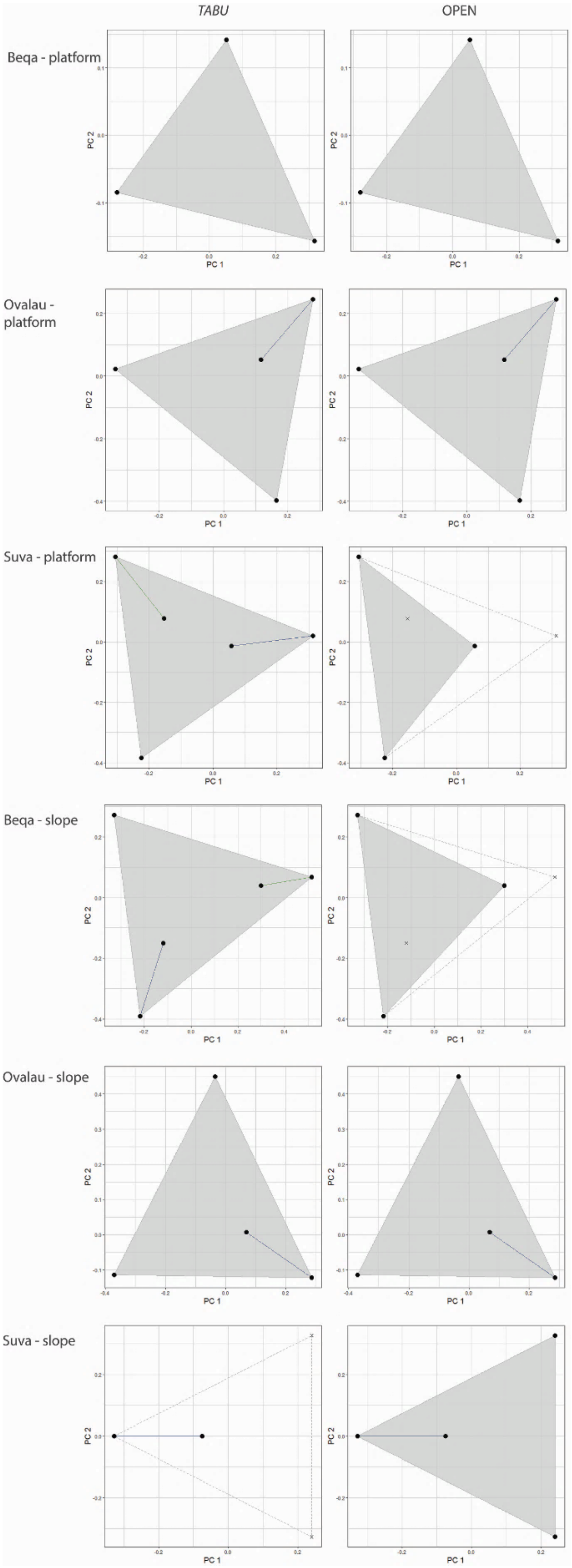
a. Functional space filled by fish observed during UVC



b. Functional space filled by fish observed during videos



c. Functional space filled by fish observed grazing during videos



C (iv) - Summary of current or recent coral reef monitoring programmes and their inclusion (or exclusion) or proposed complementary and process metrics

Monitoring protocol	Algal turf measurement	Recruitment/juvenile corals measurements	Additional notes	Reference
AGRRA Atlantic and Gulf Rapid Reef Assessment	Mean percent cover of turf algae identified.	Count 'small recruits <2cm' and 'large recruits 2-4cm' within 25 x 25cm quadrat, 80 replicates with quadrat randomly placed.	Measure prevalence and type of partial mortality, coral disease, plus bleaching signs. Categorise structural relief.	www.agrra.org
CARICOMP Caribbean Coastal Marine Productivity Program	Measure percent cover of turf algae - defined as 'may look fleshy and/or filamentous but do not rise more than one cm above the substrate'. Also record cover of non-living substrata; bare rock, bare rubble, bare boulders, recently dead coral, separately.	Not counted, stated to often fall under encrusting coral category.	Measure rugosity with chain-tape method, and check for coral diseases.	http://www.ima.gov.tt/home/images/stories/caricomp_manual_2001.pdf
Coral Reef Monitoring Protocol, National Parks Service	Measure percent cover of turf algae quantified as algae <2cm high. Most reefs fall under category 'Dead coral with algae/turf algae'.	Identify recruits <4cm	Extract turf and recruit information from videotaped frames - must be quite challenging. Monitor coral disease prevalence.	Miller *et al.*, (2007)

cont.

Monitoring protocol	Algal turf measurement	Recruitment/juvenile corals measurements	Additional notes	Reference
Coral Reef Monitoring Protocol for Assessing Marine Protected Areas	Measure percent cover of turf algae. Dead coral, rubble and rock recorded separately without acknowledging if covered in turfs.	Not measured – but census can be adapted to include recruit surveys if expert is present	Small section for notes of COTS, bleaching and disease.	Ahmadia *et al.,* (2013)
FKNMS-CRMP Florida Keys National Marine Sanctuary Coral Reef Monitoring Program	Quantify benthic cover of fine turf and thick turf	Follow juvenile survival in 16 permanent quadrats		http://floridakeys.noaa.gov/research_monitoring/zpr98.pdf
GBRMPA Great Barrier Reef Marine Park Authority		Yes – density of juveniles	Hard and soft coral cover, cover of macroalgae, density of juvenile corals, and prevalence of coral disease, crown-of -thorns starfish, Drupella, physical damage, Cliona, coral bleaching.	http://www.gbrmpa.gov.au/managing-the-reef/how-the-reefs-managed/reef-2050-marine-monitoring-program

cont.

Monitoring protocol	Algal turf measurement	Recruitment/juvenile corals measurements	Additional notes	Reference
GCRMN Global Coral Reef Monitoring Network	Proportion of algal turfs measured - use definition from English *et al.* (1997); "lush filamentous algae, often found inside damselfish territories"	Coral recruitment tiles at 5m depth at 45° angle		http://www.icriforum.org/sites/default/files/GCRMN_Ecological_monitoring.pdf
MBRS-SMP Mesoamerican Barrier Reef System Synoptic Monitoring Program	Proportion of algal turfs measured, defined as 'Densely packed algae that project less than one centimetre above the substrate they are growing on; usually filamentous'. Separately record 'bare rock' and estimate very recent, recent or older recent 'recently dead' and 'long dead' coral partially depending on algal assemblage.	Coral recruitment tiles at 2 and 10m depth for 6 months	Coralline algae not differentiated between CCA and calcareous macroalgae that doesn't extend more than 2cm from substrate. Note diseases or bleaching.	Almada-Villela *et al.,* (2003); http://www.icriforum.org/sites/default/files/GCRMN_Ecological_monitoring.pdf
NCRMN National Coral Reef Monitoring Network	Proportion of algal turfs measured and distinguished between 'Turf – no sediment', and 'Turf – with sediment', as well as substrate type.	No - individuals <4cm identified but only recorded once per transect regardless of encounters as only for species richness calculations	Surveys measure rugosity	https://coastalscience.noaa.gov/projects/detail?key=180

cont.

Monitoring protocol	Algal turf measurement	Recruitment/juvenile corals measurements	Additional notes	Reference
Pacific RAMP Pacific Reef Assessment and Monitoring Program	Proportion of algal turfs measured	Deploy Autonomous Reef Monitoring Structures (ARMS) for three years – can identify coral recruits and juveniles	Coral bleaching and disease surveys	https://pifsc-www.irc.noaa.gov/cred/survey_methods.php#arms
PROCFish	Yes – considered as epiphytes growing on any substrate, graded 1-5 depending on patchiness/thickness.	----	Rugosity determined by discrete categories	Pinca *et al.,* (2009)
Reef Check	No – record cover of 'Nutrient indicator algae', 'Recently killed coral', 'Rock' and 'Rubble'	----	Note coral damage (i.e. anchors, dynamite), and estimate percent of coral with bleaching or disease.	http://www.reefcheck.org/ecoaction/monitoring-instruction/

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Appendix D – additional publication

Lee S, Ferse S, **Ford A**, Wild C, Mangubhai S (2017) Effect of sea cucumber density on the health of reef-flat sediments. *In*: S. Mangubhai, W. Lalavanua and S.W. Purcell (eds.). Fiji's Sea Cucumber Fishery: Advances in Science for Improved Management. Wildlife Conservation Society. Report No. 01/17. Suva, Fiji. pp. 54–61.

Effect of sea cucumber density on the health of reef flat sediments

Abstract

Sea cucumbers are thought to play an important role in the recycling and remineralization of organic matter in reef sands through feeding and bioturbation. However, growing demand and high prices from Asian markets are driving the overexploitation of sea cucumbers globally, with little understanding of the consequences of local-scale removal from inshore coral reef ecosystems. Densities of Holothuria scabra were manipulated in enclosures in situ on a reef flat adjacent to Natuvu village, on the island of Vanua Levu, Fiji, between August 2015 and February 2016 to simulate an unfished and an overfished stock density. Two treatments were used: (i) high sea cucumber stocking density (350 g m^{-2}); and (ii) exclusion of sea cucumbers (0 g m^{-2}). Two controls accounted for cage effects: (i) cage controls (no cage walls); and (ii) natural density (60 g m^{-2}). Sedimentary oxygen consumption (SOC), grain size distribution, sediment porosity, and O_2 penetration depth were recorded. SOC rates were consistently lower in high density enclosures than when sea cucumbers were excluded, indicative of 'healthy' sediments. O_2 penetration depth decreased significantly when sea cucumber removal coincided with elevated sea surface temperatures which are indicative of sediment health decline. Thus the removal of sea cucumbers reduces the efficiency of reef sediment to function as a filter system to buffer organic matter pulses, and negatively affects the function and productivity of inshore reef ecosystems.

Introduction

Sediments in tropical coastal habitats are capable of trapping a substantial amount of organic matter (OM) (Wild *et al.,* 2004). Water flows are able to transport OM into and within the sediment, and small organisms living within sediments are able to efficiently degrade OM (Rush *et al.,* 2006). Because the seafloor and the overlying water are closely linked through such transport processes, changing the function of sediments can have direct negative consequences on the quality of the overlying water (Wild *et al.*, 2004). Porous sediments are thus considered as a kind of biocatalytical filter system (Rusch *et al.,* 2006).

Several factors can affect the efficiency of this filter, including temperature, water currents, the amount of organic matter entering the system, and the burrowing or burying activity of organisms digging up and turning over the sediment, referred to as bioturbation (Kristensen, 2000). Of these factors, bioturbation has the greatest effect on the efficiency of the biocatalytical filter, as it can increase the surface area of the sediment and mix the sediment (Kristensen 2000). The efficient function of this filter system is critical as it provides the marine environment with capacity to buffer pulses of OM. The ability to buffer negative effects of OM pulses becomes increasingly important as coastal ecosystems face threats from increasing nutrient and OM inputs from agriculture and sewage discharge (Barnes, 1973, Mosley & Aalbersberg, 2003).

Several species of sea cucumbers inhabit soft bottom habitats (Purcell *et al.*, 2012), interacting directly with and influencing the quality of sediments through feeding and bioturbation (Uthicke, 1999, 2001, Purcell *et al.*, 2016). The present study focused on the deposit-feeding sandfish *Holothuria scabra*, historically found in high densities on reef flats throughout the Pacific (Ward, 1972, Shelly, 1981). *H. scabra* ingests a large amount of sediment and can bury itself in soft sediments (Figure D.1) during part of the day (Mercier *et al.*, 1999; Purcell, 2004), therefore playing a key role in bioturbation. This species is also of high value in the sea cucumber trade (Pakoa *et al.*, 2013, Purcell, 2014). Our study investigated the effect of *H. scabra* on the function of the biocatalytical filter system by assessing effects on sediment composition, the depth to which oxygen (O_2) penetrated into the sediment, and sedimentary oxygen consumption (SOC), which are indicators of the decomposition of organic matter. The combination of SOC and O_2 penetration depth indicate how efficiently the sediment is functioning as a biocatalytical filter system.

Figure D.1. *Bioturbation from H. scabra burying cycle exposes anoxic sediment (black/grey) and breaks up algal mats.*

Methods

Fieldwork was conducted on an extensive reef flat in front of Natuvu village, Wailevu District East, Vanua Levu, Fiji (16°44.940'S, 179°9.280'E), between August 2015 and February 2016. The site was selected as it had been identified by the Wildlife Conservation Society as having a relatively high *H. scabra* density for the region as a result of restocking of community fish grounds in 2009 (Hair, 2012). Densities of *H. scabr*a at the study site were similar to unfished densities found in Papua New Guinea (Shelley 1981), and therefore were assumed similar to natural population densities.

Sixteen square enclosures (3 x 3 m) were constructed at the study site and stocked with two densities of *H. scabra*. Two treatments (n = 4 per treatment) were used: (i) high sea cucumber density cages (ca. 350 g m^{-2}); and (ii) cages without sea cucumbers or 'exclusion cages' (0 g m^{-2}). Two controls (n=4 per control) were established to account for cage effects; natural (*ca*. 60 g m^{-2}) and cage controls which had no walls/mesh. Natural density (*ca*. 60 g m^{-2}) was determined in a pilot study at the study site. High density (350 g m^{-2}) was based on high stocking biomass for *H. scabra* used in previous studies in natural ranching sites (Battaglene, 1999, Lavitra *et al.*, 2010).

To determine grain size distribution, sediment cores were collected to a depth of 3 cm (n=3 per enclosure) and dried in an oven at 70°C for ca. 24 hours. Dry sediment samples were weighed then transferred to a column of sieves (≥2000 µm, 1000 µm, 500 µm, 250 µm, 125 µm, <125 µm). The sieve column was shaken for seven minutes, and sediment remaining in each sieve weighed to the nearest 0.02 g. Grain size analysis, textural classifications and distribution of sediments were based on methods by Folk and Ward (1957).

Sediment porosity was determined by comparing the wet weight to dry weight of sediment cores following methods by Olson (2014). The depth to which oxygen reached (penetrated) into the sediment was measured by collecting sediment cores to a depth of 3 cm using a clear corer. The oxygen penetration depth was determined using methods adapted from Kemp et al. (2015); measured as the distance from the sediment surface to the depth at which sediment was consistently darker[1] (Figure D.2).

***Figure D.2**. Sediment corer used to quantify oxygen penetration depth. Consistently darker sediment indicates anoxic sediment, as indicated by a white arrow.*

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[1] Consistently dark sediment indicates low oxygen conditions.

Lastly, *in situ* sedimentary oxygen consumption (SOC) was measured using methods by Ford et al. (unpubl data). Sediment cores *ca.* 10 cm^3 were collected to a depth of 1 cm from enclosures and transferred immediately to glass incubation chambers (160 ml). Chambers were then filled with undisturbed water from the same location (n = 4 treatments per enclosure, n=3 controls per enclosure). Controls only contained undisturbed water from our site; this allowed us to account for microbial activity in the overlying water column. Samples were placed into opaque bags and placed in an icebox filled with water from the site to maintain temperature consistency. Approximately 30 ml of water was removed from the chamber to prevent water overflowing from the chamber during measurement. Oxygen (O_2) concentration, salinity and temperature was measured using a WTW Multi 3320™ O_2 sensor and salinity probe. Oxygen saturation was consistently at 70 – 120% at initial measurements. Water removed (*ca.* 30 ml) was replaced, and additional water (3–5 ml) collected from the site was used to top-up the incubation chamber to ensure the chamber was sealed airtight with no air bubbles. Chambers were incubated in the corresponding opaque bags, in an icebox filled with water from the site for *ca.* 1 h. Chambers were collected and O_2 concentration, salinity and temperature were re-measured. The exact durations (min) of all incubations were recorded.

Results from cage controls and natural controls, for each parameter, were compared in post-hoc tests and, if there were no significant differences between natural and cage controls, high density and exclusion treatments were compared. Data from enclosures were analysed using repeated-measures ANOVA.

Results

Cages without sea cucumbers showed no significant difference in grain size composition from September to December. However, for the same time period enclosures with high sea cucumber densities exhibited a shift towards finer grains, with an increase in particular in 125 µm grain sediments (U test, $p = 0.03$) and a significant reduction in the proportion of 1000 µm grain sediment (U test, $p = 0.03$). Due to storm surge affecting our site five days prior to January measurements, we do not consider January results to be caused by the manipulated densities of *H. scabra* in enclosures (treatment).

Sediment porosity showed a marginally significant change over time from the onset of the experiment (ANOVA, $p = 0.05$), however there were no significant differences among treatments (U test, $p > 0.05$). O_2 penetration depths were similar between high density and sea cucumber exclusion treatments in November (U test, $p\ o = 0.73$). Although O_2 penetration increased significantly in December within cages with high sea cucumber densities (U test, $p = 0.03$) (Figure D.3), there was no significant difference between high sea cucumber density cages and cages without sea cucumbers (U test, $p = 0.32$). February, however, shows a distinctly different pattern. Whilst the high-density treatments had values identical to those in November (U test, $p = 1$), oxygen penetration depth in the cages without sea cucumbers decreased significantly (U test, $p < 0.01$) by 63% from 32 mm (±3 SE) to 12 mm (±2 SE). Neither controls showed any significant differences in oxygen penetration depth over time throughout the study (U test, $p > 0.05$).

At the beginning of the study all cages had similar SOC rates (September U test, p = 0.55). Four weeks later the SOC rates increased significantly in cages with no sea cucumbers (U-test, September–October, p < 0.01) by almost two-fold from 43.0 mmol O_2 m^{-2} $day^{-}1$ (± 4.6 SE) to 75.96 (±4.7 SE) mmol O_2 m^{-2} day^{-1}. No changes occurred within the high sea cucumber density cages during the same time period (U-test, September–October, p = 0.74).

Heavy rains and flooding occurred ten days prior to November sampling (Figure D.4). Following the flooding, SOC rates increased significantly without high-density cages (U-test, October–November, *p* = 0.03). In November there were no longer significant differences among treatment cages (U-test; November; *p* = 0.25). Following further heavy rains prior to sampling in January, both treatments showed similar patterns as before (i.e. SOC rates decreased within the cages with no sea cucumbers and increased within cages with high densities of sea cucumbers), and were not significantly different from each other in January (U test, *p* = 0.99) and February (U test, *p* = 0.07).

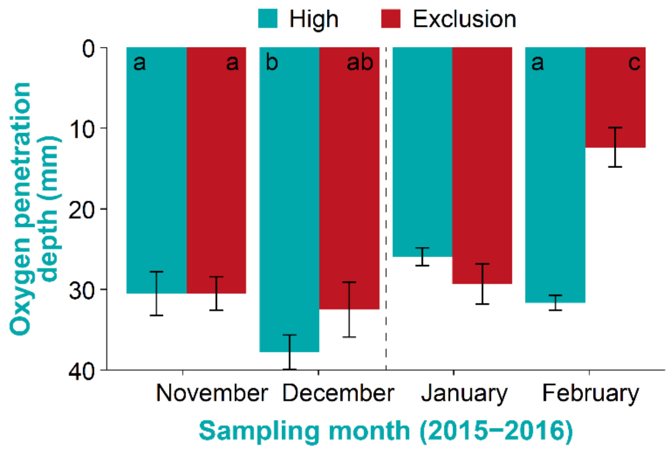

Figure D.3. Oxygen penetration depth (mm) of high density and exclusion treatments. Mean values with standard error. Vertical break indicates flooding and storm surge five days prior to January sampling. Different letters (a, b, c) indicate significant differences (p<0.05), same letters indicate no significant differences (p>0.05). January results were not considered in the analysis.

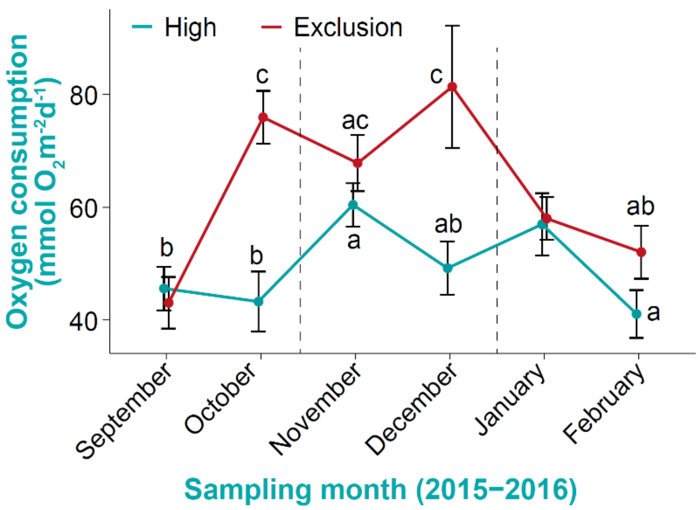

Figure D.4. Sedimentary oxygen consumption (mmol O2 m-2 day-1) of high sea cucumber density (High)and areas void of sea cucumbers (Exclusion). Mean values with standard errors. Vertical break between October and November indicates flooding 10 days prior to November sampling. Vertical break between December and January indicates flooding and storm surge 5 days prior to January sampling. Different letters (a, b, c) denote significant differences (p < 0.05), same letters (a, a/ b, b/ c, c) denote non-significant differences (p > 0.05). January results were not considered in the analysis.

Discussion

Changes to grain size composition in the presence of sea cucumbers, and the lack of any significant changes in their absence suggest that when sea cucumbers are present on inshore reef flats they play a key role in the physical reworking and change of sediment structure in marine ecosystems. Several species of sea cucumber are able to change sediment grain size through dissolution via acidity in their gut (Hammond, 1981), and potentially abrasion while sediment passes through their gut.

Generally in the presence of high densities of sea cucumbers, SOC rates exhibited a buffered response, recovering to near background levels following flooding at the study site. A similar 'buffered' response was observed in O_2 penetration depth, where the absence of sea cucumbers caused erratic changes in O_2 penetration depth.

The abrupt decrease in O_2 penetration depth from December to February coincided with increased water temperatures (26°C in December to 31°C in February) and calm weather, however O_2 penetration depth remained unaffected in areas with high densities of sea cucumbers. Warmer seawater temperatures likely caused small organisms and microbes within the sediment to consume more oxygen (Nydahl *et al.,* 2013). Relatively calm conditions for the same time period meant limited mixing of the sediment and overlying water column by wave action, normally this mixing helps to deliver oxygen into sediment and the overlying water. The buffered response of O_2 penetration depth recorded in areas with high densities of sea cucumbers suggests that during such weather conditions (warm seawater temperatures, calm seas), bioturbation by sea cucumbers may provide essential mixing, helping to deliver oxygen into the sediment.

Sea cucumbers actively feed on organic matter (OM), reducing its concentration in sediment (Uthicke & Karez, 1999, Michio *et al.*, 2003). Therefore, it is likely that there was a reduced concentration of OM in sediment where high densities of sea cucumbers were present compared to areas where sea cucumbers were excluded. The resulting high concentrations of OM in the absence of sea cucumbers likely caused an increase in the activity and abundance of small organisms (including microbes) within the sediment (MacTavish *et al.*, 2012), as they would feed on the abundant OM. Respiration of these small organisms, and their waste products, are likely to have resulted in the increased SOC rates (Kristensen, 2000).

The buffered responses of SOC and O_2 penetration depth in sediments where high densities of sea cucumbers were present are likely to have been caused by the considerable bioturbation impact *H. scabra* has on sediments (Purcell, 2004; Lee, 2016). Bioturbation increases the surface area of the sediment and helps to drive water flow into and within sediment, delivering O_2 and degradable materials. High densities of sea cucumbers likely promoted aerobic decomposition[2] of OM, which is *ca.* 10 times faster than anaerobic[3] (Kristensen *et al.*, 1995).

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[2] Aerobic decomposition – the breakdown of biodegradable material in the presence of oxygen
[3] Anaerobic decomposition – the breakdown of material in the absence of oxygen

Trends seen in SOC and O_2 penetration depth indicate that some functions of sediments, i.e. as a biocatalytical filter system, are compromised as a result of sea cucumber removal. The resistance and resilience of coastal ecosystems to local (e.g. increased nutrient or OM content) and global (e.g. increased sea surface temperatures) stressors are likely being compromised by the extensive reduction in sea cucumber stocks of inshore areas. Consequently the ecosystem functions that Pacific Island communities rely heavily on for their food and livelihoods are being undermined by the removal of sea cucumbers, leaving coastal ecosystems and the communities that rely upon them increasingly vulnerable.

Recommendations

- Moderate to high densities of sea cucumbers should be maintained on reefs through effective regulatory controls on fishing. This will allow sea cucumbers to play their role in maintaining sediment function.

- Given the current low abundances of sea cucumbers in Fiji, the proposed national sea cucumber management plan should consider a moratorium on collection and sales until stocks are able to sufficiently recover and ecosystem function is restored.

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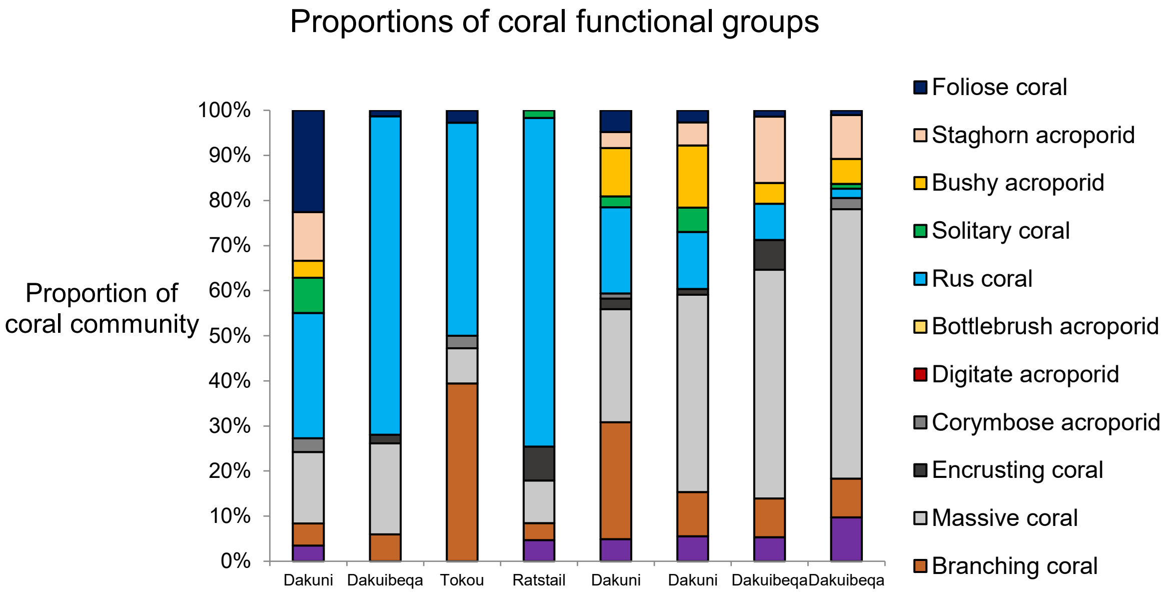
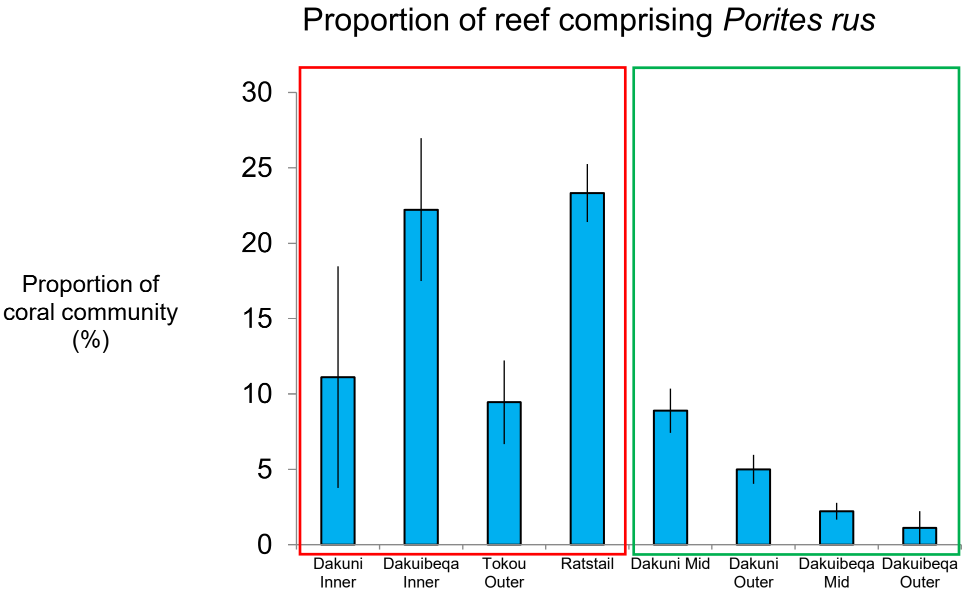
Appendix E – Coral community composition at inshore Melanesian reefs

Overall coral community composition across sites in Fiji, differentiating those directly adjacent to human communities (in red box), and further from human communities (in green box).



Specific proportions of *Porites rus* across sites directly adjacent to human communities (in red box), and further from human communities (in green box).

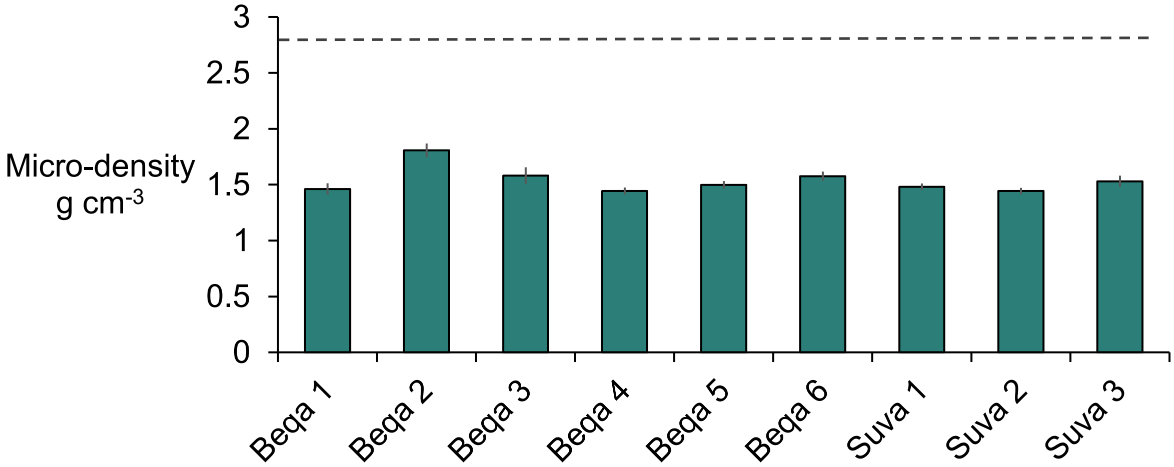


Appendix F – Skeletal densities of *Porites rus*

This study took place during August - October 2015 in Fiji near to the capital Suva, and at the island of Beqa (50 km south). Benthic surveys were performed using the line-point intercept method, identifying the cover every 50 cm along 30 m replicate transects (n=3), with corals classified to species level. Fragments of 3 – 5 cm in length were broken off from *Porites rus* colonies that exhibited a branching, or mixed branching/plating, morphology. The fragments were then placed into 10% household bleach for 48 hours, dried, and transported back to ZMT, Bremen for analysis. Micro-density was calculated using the buoyant weight technique based on Archimedes principles (Jokiel *et al.,* 1978), as in similar studies (e.g. Krief, 2010; Walsh *et al.,* 2012). After taking the weight of the fragment in water (buoyant weight, B_w), the sample is dried at 40°C for 48 hours and weighed for dry weight (D_w). Micro-density is calculated from:

$$\text{Micro-density} = D_w / (D_w - B_w) * Dens_m$$

where $Dens_m$ refers to the density of the medium (freshwater, therefore 1.00).



Skeletal micro-density from study sites in Fiji. Dashed line represents density of pure aragonite. Error bars depict standard error.

Hard coral cover was relatively consistent between all study sites, ranging from 20.56 % ± 2.42 (mean ± SE) to 46.11 % ± 2.42. However, relative proportions occupied by *P. rus* exhibited ten-fold differences, from 7.82 % ± 1.81 to 72.88 % ± 4.84, with higher values at sites with higher amounts of sedimentation and particulate organic matter (Appendix F). Skeletal micro-density ranged between 1.44 ± 0.03 and 1.81 ± 0.06 g cm^{-3}, providing very low values compared to previous measurements for other dominant corals. Coral skeletal density was previously assumed to be equal to that of pure aragonite (2.94 g cm^{-3}), but recent studies have shown this value can be as low as 2.2 g cm^{-3} for Acroporid corals, and 1.7 g cm^{-3} for massive morphotypes. Densities have also been shown to decrease with declining water quality (Mwachireya *et al.,* 2016). The results here suggest the skeletal density of inshore *P. rus* is extremely low.

References associated with study:

Jokiel PL, Maragos JE, Franzisket L (1978) Coral growth: buoyant weight technique. *In:* Stoddart DR, Johannes RE (Eds) Coral reefs: research methods. UNESCO, Paris, France. 581 pp.

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Walsh SJ, Brading P, Suggett DJ, Smith DJ (2012) Working with nature to identify coral reefs with increased environmental tolerance. In: *Proceedings of the 12th International Coral Reef Symposium, 9-13 July 2012*, Cairns, Australia.

Appendix G – Future bleaching projections

Bleaching projections extracted for REPICORE study sites in Fiji and Solomon Islands. Data was extracted in ARCMap by overlaying the site coordinates over the data layer provided by Hoiidonk *et al.* (2016), freely available at (http://coralreefwatch.noaa.gov/climate/projections/downscaled_bleaching_4km/index.php). Explanations of projected scenarios are explained below. Bleaching projections are at 4 km spatial resolution, and the onset of annual bleaching is defined as the annual exceedance of >8 DHW accumulating during any three-month period.

Country	Village	Latitude	Longitude	Projected scenario*			
				1	2	3	4
Fiji	Muaivusu	-18.1495	178.364	2062	2049	2044	2033
	Ovalau	-17.7364	178.8285	2060	2048	2044	2033
	Koro	-17.3487	179.436	2068	2059	2052	2044
	Kia	-16.2036	179.0461	2050	2041	2037	2028
Solomon Islands	Nusahope	-8.27453	157.4665	2037	2028	2032	2024
	Lokuru	-8.60436	157.359	2053	2041	2040	2032
	Munda	-8.35032	157.2429	2046	2035	2038	2029
	Raromana	-8.21262	157.0035	2053	2041	2040	2032

*Projected scenarios:

1 - Year by which bleaching will happen 10x per decade (i.e. annual bleaching), under scenario RCP4.5 which assumes emissions stabilize just after 2100 due to successful implementation of climate policies that reduce emissions.

2 - Year by which bleaching will happen 2x per decade, under scenario RCP4.5 which assumes emissions stabilize just after 2100 due to successful implementation of climate policies that reduce emissions.

3 - Year by which bleaching will happen 10x per decade (i.e. annual bleaching), under scenario RCP8.5 which assumes no climate policies are adhered to (i.e. business-as-usual)

4 - Year by which bleaching will happen 2x per decade, under scenario RCP8.5 which assumes no climate policies are adhered to (i.e. business-as-usual)

Reference

van Hooidonk R, Maynard J, Tamelander J *et al.* (2016) Local-scale projections of coral reef futures and implications of the Paris Agreement. *Scientific Reports*, **6**, doi:10.1038/srep39666.

Appendix H – Curriculum vitae of PhD candidate

Amanda K. Ford

Areas of interest: Coral reef ecology, benthic community functioning, coastal management

Publications: Three published peer-reviewed research articles, one book chapter

International experience: Work experience in the Caribbean, the Netherlands, Germany, Fiji, Papua New Guinea and Australia

Soft skills: Scientific diving, project management, team coordination, collaborations with local counterparts

Outreach: Public lectures, (integrative) teaching primary school through to postgraduates, social media

Professional Background

2013 –2017: Researcher (PhD research) at Leibniz Centre for Tropical Marine Research (ZMT) within REPICORE (Resilience of Pacific Island social-ecological systems in times of global change) project. Focus on impacts of human communities on benthic assemblages and resilience, with field campaigns to Papua New Guinea and Fiji.

2013: Marine Biology Instructor at Broadreach, Caribbean - teaching undergraduate-level courses (credits provided by University of Washington).

2012 –2013: Naturalist at Heron Island Resort, Queensland, Australia – focus on public education.

2012: Research project (MSc) at Heron Island Research Station investigating differential responses to climate change of intra-specific host and symbiont variations in *Stylophora pistillata.*

2011; Internship and research project (MSc) at CARMABI field station, Curaçao, Netherland Antilles, examining a method to detect nutrient limitation in dominant coral reef fleshy algae through nutrient induced fluorescent transients.

Educational Background

2014 - 2017: Graduate student within Bremen International Graduate School for Marine Sciences Research Theme C – Ocean and Life

2013 - 2017: PhD candidate at University of Bremen. Title: Influences of Pacific Island human comunities on benthic coral reef functioning and resilience. Advisors: Dr. Sebastian Ferse, Prof. Dr. Christian Wild, Dr. Maggy Nugues, Dr. Albert Norström

2011 – 2013: MSc Biological Sciences, track Limnology and Oceanography at the University of Amsterdam, the Netherlands. Graduated "*cum laude*" (distinction).

2007 – 2010: BSc Biological Sciences at the University of Exeter, UK. Graduated 2.1

2005 – 2007: AS & A2-level examinations at Peter Symonds College UK. A2-levels in Biology, Chemistry and Mathematics

1992 - 2005: St Swithuns School, UK

Scientific Publications

Lee S, Ferse SCA, **Ford AK**, Wild C, Mangubhai S (2017) Effect of sea cucumber density on the health of reef-flat sediments. In: *Fiji's Sea Cucumber Fishery: Advances in Science for Improved Management* (eds Mangubhai S, Lalavanua W, Purcell SW), pp 54-61. Wildlife Conservation Society, Suva, Fiji.

Ford AK, van Hoytema N, Moore B, Wild C, Ferse SCA (2017). Sedimentary oxygen consumption rates indicate that local sewage input drives benthic community shifts at overfished reefs in Papua New Guinea. *Environmental Conservation*. doi: 10.1017/S0376892917000054

Ford AK, Bejarano S, Marshell A, Mumby PJ (2016) Linking the biology and ecology of key herbivorous unicornfish to fisheries management in the Pacific. *Aquatic Conservation, Marine and Freshwater Ecosystems*. doi:10.1002/aqc.2623.

den Haan J, Huisman J, Dekker F, Jacomina L, **Ford AK**, van Ooijen J, van Duyl FC, Vermeij MJ, Visser PM (2013). Fast detection of nutrient limitation in macroalgae and seagrass with nutrient-induced fluorescence. *PloS ONE* **8**: e68834.

Conference Presentations

2016: Annual Reef Conservation UK meeting, London.

2016: 13th International Coral Reef Symposium at Honolulu, Hawai'i.

2015: Annual Conference of the Society for Tropical Ecology (Gesellschaft für Tropenökologie, GTÖ) at Zürich, Switzerland.

2015: 5th Coral Reef Ecology Symposium, Bremen, Germany.

2014: Annual Reef Conservation UK meeting, London.

Awards and Grants

2016: Best student presentation award at Annual Reef Conservation UK meeting 2016

2012: University of Amsterdam Alumni Funds - 650 EUR Travel Grant

2012: Van der Hucht De Beukelaar Stichting – 1300 EUR Research Grant

Qualifications and Skills Profile

Scientific project management
Research permit applications, project planning, building local collaborations with in-country partners, approaching and working with local communities (Melanesia), gear shipment, export permits, working and living within a team

SCUBA diving
Certified European Scientific Diver (Nov 2014 - joint instruction by Alfred-Wegener Institute and ZMT) and PADI Divemaster with >700 h experience (60% research)

Data analysis
Proficient working with large-scale (multi-national) interdisciplinary datasets using R and PRIMER (+ PERMANOVA). Confident with multivariate analyses (e.g. linear and additive mixed effect models), GIS software including QGIS and ArcMAP, and graphical software including SigmaPlot, Adobe Illustrator, Adobe Photoshop and Adobe Lightroom.

Organisation
PhD representative at Leibniz Centre for Tropical Marine Research (ZMT) 2014 –2017.

Outreach

Public (non-conference) presentations: Invited speaker at the Natural History Museum, London ('Reef Encounters'), and numerous presentations and guided tours focusing on all marine and island-associated life at Heron Island

Teaching: Experience contributing to marine biology courses at undergraduate and postgraduate level, plus integrative teaching to kids through to adults

Social media: Blogs (repicore.zmt-bremen.de; www.livingdreams.tv/whatarecoralreefs), twitter (@akford1906)

Magazine articles: SEVENSEAS (understanding the impacts of the 2015/2016 El Niño in Fiji)

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