Functional structure of herbivorous fish communities in the Wakatobi National Park, Southeast Sulawesi

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Abstract

Marine fish play important functional roles on coral reef systems in regulating ecosystem resilience. Herbivores are key indicators of a reefs resilience to disturbances in particular to regime shifts to algae dominated states. The importance of understanding the functional role of key taxa in maintaining coral reef biodiversity and resilience is now more important than ever as acute and long-term environmental change threatens these systems further. We aimed to understand the spatio-temporal variation among herbivore functional roles and how these were partitioned across species. We quantified the functional role of herbivores by excluding grazing activity on the reef. Algal communities responded with a significant increase in benthic cover (+47.47%) over the 12 month exclusion period. We further identified herbivore abundance and biomass and how this was partitioned across reefs zones and how benthic composition drove variation in the Wakatobi National Park, Indonesia. Herbivore abundance and biomass decrease within the reef from the flat to the slope, this was consistent from 2013 to 2017; however overall abundance and biomass increased over time. Herbivore functional roles were found to be distributed across 64 species. Abundance and biomass of herbivores and secondary functional groups (SFG), decrease with increased algal cover across all grazing guilds, this was best predicted by the fish abundance of guilds and particularly the SFG's nested within herbivores. SFG's revealed that Acanthuridae spp. were the most abundant and contributed to the fish most biomass within herbivore communities and Signanidae spp. with greater individual mean biomass. *Ctenochaetus striatus* was responsible for driving community differences. These taxa are key in maintaining reef resilience through high functional grazing, and vital for increased conservation and monitoring efforts against direct pressures to mitigate effects of further environmental change.

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Abbreviations

AIC – Akaike Information Criterion

ANOSIM - Analysis of similarities

B3 – Buoy 3

CCA – crustose coralline algae

CPCe - Coral Point Count with Excel extensions

DSLR – Digital single lens reflex

EAC – Epilithic algae community

EAM – Epilithic algae matrix

ENSO – El Niño and the Southern Oscillation

GBR- Great Barrier Reef

K1 – Kaledupa (site)

KDS – Kaledupa Double Spur

nMDS - non-metric multidimensional scaling

Opwall – Operation Wallacea

PK – Pak Kasims

PVC – Polyvinyl chloride

R1 – Ridge 1

S1 – Sampela

SE – Standard Error

SFG – Secondary functional groups

SIMPER - Similarity of Percentages

SL – Standard length

SVS – Stereo video system

TL – Total length

WNP – Wakatobi National Park

Introduction

Coral reef ecosystems are among the most diverse, productive and complex found in the world (Bellwood and Hughes, 2001; Mumby and Steneck, 2008; Harborne *et al.*, 2017). They are of high importance to the marine environment and to the livelihoods of millions of people (Martin *et al.*, 2017a; Ruppert *et al.*, 2018). Human populations utilise tropical coral reefs as a source of food (Martin *et al.*, 2017a), and economic resources obtained from direct extraction of raw materials (Harborne *et al.*, 2017) as well as through revenue generated through local and international tourism (Moritz *et al.*, 2017; Spalding *et al.*, 2017) and fisheries. However, coral reef ecosystems are facing threats on both local and global scales. The type of disturbances a reef is faced with varies with location (Wilson *et al.*, 2006; Ruppert *et al.*, 2018). In the U.S. and Australia, the aesthetic value of the reef is of high importance and face threat the of storm damage and loss of biodiversity through bleaching events (Descombes *et al.*, 2015) degrading the aesthetic appeal and value. Whereas reefs located in more developing countries are most often exploited for fisheries or otherwise impacted through coastal development (Smith *et al.*, 2016; Ruppert *et al.*, 2018).

In communities where over-fishing has been taking place for generations, what is now found is that communities are “fishing down the food chain” (Ruppert *et al.*, 2018). This is where previously targeted species which were usually top-predators are lost or rare (Dulvy *et al.*, 2004; Martin *et al.*, 2017a), and the target species for local fisheries tend to be that of mesopredators and herbivores in particular parrotfish and surgeonfish (Hughes *et al.*, 2010; Martin *et al.*, 2017a). In addition, highly destructive fishing methods such as blast fishing have caused major loss of structural complexity and consequently associated biodiversity (Hoey and Bellwood, 2011; Harborne *et al.*, 2017). Human populations that are in close proximity to reefs have also caused changes to water quality either directly through nutrification (e.g. sewage input) or indirectly through coastal modification (e.g. removal of mangrove forest) and / or land management (changes to adjacent terrestrial vegetation (e.g. conversion of forest in to Palm Oil plantations) leading to high turbidity and sedimentation (Ruppert *et al.*, 2018). Consequences of these disturbances to the ecosystem include top-down (predation risk/removal), bottom-up (resource quality and availability) and horizontal effects (changes in competition amongst present communities) (Davis *et al.*, 2017; Ruppert *et al.*, 2018).

In addition to local disturbances, global disturbances such as increased severity and frequency of extreme climate events (e.g. higher precipitation, storm bursts; Wasko and Sharma, 2015; Hay *et al.*, 2016), chronic and acute increases in sea temperatures, ecological disruptions such as stimulation of corallivorous crown of thorn starfish outbreaks (Wilson *et al.*, 2006) and increased incidents of coral diseases, have been on the rise in recent years. These multi-stressors have resulted in an increased risk of coral loss, reduction in habitat complexity and loss of ecological resilience reducing the system’s ability to recover from increasing severity and frequency of disturbances events (Hughes *et al.*, 2013).

We have a combination of factors that operate both globally and locally that serve to modify habitat structure and/or community structure with consequences for biodiversity and ecosystem service provision. However in the coral triangle, the most biodiverse marine system on the planet, we are yet to observe the ecological collapse of the system which has been highly apparent in other areas of the world that have lower regional biodiversity. Understanding the role high biodiversity therefore plays, and potential ecological tipping points are key to successful management.

As well as supporting huge biological wealth, coral reefs also provide services and goods critical to millions of people in coastal communities (Hughes *et al.*, 2017; Ruppert *et al.*, 2018). Coastal protection (Hoegh-Guldberg *et al.*, 2007), water purification, recreation and tourism and the provision of animal protein source are a few examples of the key services and goods provided by coral reefs and their connecting ecosystems of seagrass beds and mangrove forests. These services are provided as a result of the ecological characteristics of the ecosystem, for example, where coral reef absorbs high energy storms and dissipate before it is able to damage vulnerable shoreline habitats these habitats then providing further services, for example, water filtering, further shoreline protection and food production.

Understanding our collective current knowledge of functional roles, redundancy and complementarity in biodiversity hotspots from a methodological, ecological and conservation standpoint, will allow us to disentangle the key mechanisms that underpin the ability of natural ecosystems to withstand disturbances and recover from impacts related to events such as those driven by ENSO events. The ability of the ecosystem to tolerate and rapidly recover from major disturbances is key to the long-term ecological viability and status of coral reefs.

Regime shifts and the resilience of coral reefs

Anthropogenic disturbances coupled with natural local and widespread global disturbances are increasing the vulnerability of reefs and reducing their natural resilience (e.g. bleaching events, over-exploitation for resources, and, nutrification leads to greater vulnerability to disease). In particular studies on reduced resilience in coral reef ecosystems, have been focused on regime shifts which have been widely documented (Hughes, 1994; Bellwood *et al.*, 2004, 2006a; Mumby and Steneck, 2008; Dudgeon *et al.*, 2010; Hughes *et al.*, 2010). Regime shifts are often found to be shifts from coral-dominated states to macro-algae or fleshy-algae dominated states (Hughes *et al.*, 2010; Smith *et al.*, 2016), with a few studies investigating potential shifts to sponge-dominated states (Bell *et al.*, 2013).

The resilience of an ecosystem refers to the ability of a system to recover from disturbances and maintain ecological structure, function, goods, services and feedbacks (Mumby *et al.*, 2007; Cheal *et al.*, 2013; Maynard *et al.*, 2015). Feedback mechanisms of a reef are the drivers in which determine the dynamics of a coral reef.

These feedbacks can be positive or negative, where strong negative feedbacks can lead to regime shifts after major disturbances (Mumby and Steneck, 2008).

Regime shifts are characterised by major changes in ecosystems from one state to another (Hempson *et al.*, 2017), they could occur after disturbances to a reef, causing an imbalance within the ecosystem thereby tipping the system over the critical threshold towards an undesired state (Bellwood *et al.*, 2004; Hoegh-Guldberg *et al.*, 2007; Mumby and Steneck, 2008). The energy required to exceed this tipping point or threshold can happen very rapidly (Holbrook *et al.*, 2016) and the energy required to reverse such shift is significant. Regime shifts on coral reefs tend to occur when corals are outcompeted by other competitive benthic organisms, namely algae (Peterson *et al.*, 1998; Dudgeon *et al.*, 2010).

Coral reefs are complex ecosystems which are driven by multifaceted interactions that involve biotic and abiotic drivers (Nash *et al.*, 2016). Many coral reef managers, scientists and researchers are looking towards management to ensure that the reefs are maintained or restored to a healthy reef state which provides the many functions and services to those that depend on them. The increased need for management action has driven for resilience studies which have been focusing on ways to actively manage and anticipate these disturbances and pressures (Hughes *et al.*, 2007b; Bellwood *et al.*, 2012; Rogers *et al.*, 2015). Resilience studies increased significantly in the early 2000s after the global bleaching event of 1998.

Scientists are labelling our epoch the Anthropocene (Crutzen, 2000; Smith and Zeder, 2013; Lewis and Maslin, 2015) and many coral reef studies are now focused on ecosystem responses in the Anthropocene where local and global disturbances are occurring in higher intensity and frequency (Maynard *et al.*, 2017; Hughes *et al.*, 2018). In particular as the occurrence of disturbance events increase, many will coincide with one another and be enough to push a reef system to a new ecological state – e.g. regime shift.

Herbivores as a functional group

Species can be divided into groups that share similar behaviours or into biotic groups defined by their trophic level (Naeem, 1998). Traditionally researchers have divided fish groups into broad guild classifications, whereby the species occupy the same trophic level (Blondel, 2003) e.g. predators, herbivores and primary producers. As studies have evolved these groups have been sub-dived further into more specific and descriptive guilds, for example, apex predators and meso-predators, planktivores, herbivores, and detritivores, and benthic primary producers. However, we can divide these groups of species further when we consider the specific role a species performs within the ecosystem leading to more functional classification and groupings (Blondel, 2003).

As we look into functional roles that are found on the reefs, studies in the recent decade have identified and focused efforts on a particular role; herbivory (Bellwood *et al.*, 2004; Burkepile and Hay, 2010; Pratchett *et al.*, 2011; Fox and Bellwood, 2013; Adam *et al.*, 2015). When we refer to the functional role of a species we are specifically focused on their actions which result in an important process e.g. grazing or predation. Herbivores are key drivers and indicators used in resilience studies due to the key functional roles they play within a coral reef setting (Harborne *et al.*, 2017). They play an important role in regulating community dynamics and maintaining community stability, and prevent large-scale changes in community structure through regime shifts, (Edwards *et al.*, 2014; Adam *et al.*, 2015). Herbivore activity may result in reduced macro-algae competition thereby facilitating the formation of more structurally complex reef growth, or herbivores may operate on smaller scales by removing micro-algae which may otherwise limit coral recruitment (Burkepile and Hay, 2010; Johansson *et al.*, 2013; Kelly *et al.*, 2016). In this sense herbivore activity will increase the resilience of coral reefs to environmental a change (Hughes *et al.*, 2007a; Adam *et al.*, 2015) by maintaining the stabilising processes of the ecosystem (Allgeier *et al.*, 2017).

Herbivore classification over the past two decades have been further divided into secondary functional groups (Table 1) defined by their feeding behaviour (Pet-Soede *et al.*, 2001; Green and Bellwood, 2009; Obura and Grimsditch, 2009; Pratchett *et al.*, 2011; Pinheiro *et al.*, 2013; Boaden *et al.*, 2015; Osuka *et al.*, 2016). Classifications of the secondary functional groups have varied between studies, for example, *Acanthurus nigrofuscus* has been classified as a Grazer/Detritivore, grazer and turf algal cropper by Green & Bellwood (2009), Osuka *et al.,* (2016) and Pratchett *et al.,* (2011) respectively. This could be due to the variation of feeding behaviours across large spatial scales, the treatments in which they were studied, and/or variation in standing biodiversity, therefore, competition and, highlights the importance of biological interactions.

These groupings have been established to clarify the specific roles that herbivores provide within coral reef ecosystems and key species identified for use of monitoring resilience of reefs (Green and Bellwood, 2009). The role of cryptic species is often overlooked and underestimated due to the difficulty to assess them in their natural environment, for example, Blennidae species are considered important herbivores but are widely excluded from monitoring assessments (Green and Bellwood, 2009).

Investigating the mechanisms and processes in which herbivorous fish are able to partition resources and niches allows us to understand how species grouped into the same functional group are able to co-exist (Fox and Bellwood, 2013) and the level of complementarity that may be present in terms of overall functionality. Further understanding of the finer details in which they do this will allow us to understand how plastic these species may be due to changes in the environment and community composition present in the reef

Table 1. Summary of herbivores and secondary functional groups including roving detritivore adapted from (Green and Bellwood, 2009; Pratchett *et al*., 2011; Osuka *et al*., 2016)

Herbivores	**Genus**	**Species**	**Functional Group**
Parrotfishes	*Hipposcarus* spp.		Scrapers/Small Excavators
	Scarus spp.		Scrapers/Small Excavators
		Bolbometopon muricatum	Scrapers/Small Excavators (<35cm SL)
			Large excavators/bioeroders (>35cm SL)
		Cetoscarus bicolor	Scrapers/Small Excavators (<35cm SL)
			Large excavators/bioeroders (>35cm SL)
	Chlorurus *spp.*		Scrapers/Small Excavators (<35cm SL)
			Large excavators/bioeroders (>35cm SL)
	Calotomus spp.		Browsers
	Leptoscarus spp.		Browsers
Rabbitfishes	Siganidae		Grazers/detritivores
		Siganus canaliculatus	Browsers
Surgeonfish	*Zebrasoma* spp. (all)		Grazers/detritivores
	Acanthurus spp.		Grazers/detritivores
		Acanthurus nigrofuscus	Grazers/detritivores
	Ctenochaetus spp.		Roving detritivore
Unicornfishes	*Naso* spp.		Browsers
Angelfish (small)	*Centropyge* (all)		Grazers
Damselfish	*Pomacentrus* spp.		Omnivores
		Pomacentrus adelus	Territorial farmer
	Chrysiptera spp.		Omnivores
	Dischistodus spp.		Omnivores
	Hemiglyphidodon spp.		Omnivores
	Plectroglyphidodon spp.		Omnivores

	Stegastes spp.		Territorial farmers
Batfishes	Ephippidae		Browsers
Rudderfish	Kyphosidae		Browsers

The functional role of herbivory

Assessing the functional role of herbivores can be done through underwater observations in the field (Brandl and Bellwood, 2014). Observational bias can occur due to the effects of the observer on test species. Any behavioural response will depend also on the environmental setting. A standardised methodology should be adapted to overcome these factors (Villéger *et al.*, 2017). However, diver error or variation should be taken into account when analysing the data, unless methods such as video recordings are done in which more time can be taken to identify, behaviours, and feeing patterns. Other methods which have been used to assess herbivores have used stomach content (Dulčič, 1995; Longo *et al.*, 2015; Heenan *et al.*, 2016), metagenomics (Ngugi *et al.*, 2017) and manipulative experiments, such as in-situ herbivore exclusion experiments (Lirman, 2001; Thacker *et al.*, 2001; Hughes *et al.*, 2007a; Ceccarelli *et al.*, 2011; Afeworki *et al.*, 2013).

Heenan & Williams, (2013), found that biomass of specific functional groups was much more representative of function than abundance and species richness. Villéger *et al.*, (2017) also recommend the use of biomass over length measurements as it is more related to metabolism and trophic status and allows for inter-specific comparisons.

Assessing the consumption rate of herbivores is done through observations by recording the bites taken per unit time, with a record of the prey item (algae, coral) and sometimes the target substrate (rubble, rock, dead coral) from which it fed upon. Alternatively, feeding assays have been deployed with known amounts of algae and seagrass and the removal of biomass per unit time is assessed (Mantyka and Bellwood, 2007; Fox and Bellwood, 2008b; Gil *et al.*, 2017; Li *et al.*, 2017). These behavioural observations can then be related to morpho-anatomical traits to profile feeding acquisition. For example the relative size, shape, form and/or position of the body parts involved in each step of the food acquisition process (e.g., detection, capture and digestion (Villéger *et al.*, 2017).

Herbivore exclusion and manipulation experiments have been used to assess the function of grazing, by assessing the ability of algae stands becoming dominant in reference to potential regime shifts through prohibiting grazing activity. Additionally, once algae have become dominant within the exclusion zone, assessing the community that is responsible for grazing the dominant macro-algae stands allows us to understand species function in potentially reversing regime shifts (Hughes *et al.*, 2007a). Studies have also used exclusion experiments to understand roles of particular groups or species in top-down processes, food selectively (Longo *et al.*, 2015), and algae palatability (Littler *et al.*, 2006).

Secondary functional groups have allowed researchers to define the functional roles of herbivores in more detail and accuracy. A study by Fox & Bellwood (2013), found a unique function of herbivorous rabbitfishes through niche partitioning of microhabitats. Rabbitfish first thought to be comparable in function to Surgeonfishes, in the functional role of grazers of algal and detrital components of the epilithic algae matrix (EAM). Rabbitfish have been found to utilise crevice microhabitats to forage among the EAM, and therefore are termed “crevice-browser”. The ability to feed in crevice habits through subtle differences in morphology could play an important functional role against algae impacts in coral reefs and drive partitioning that in highly diverse communities represent complementarity.

Brandl and Bellwood, (2014), continued to investigate microhabitats, behavioural observations and trait-based functions to differentiate niche or resource partitioning in herbivores. Here they presented a high level of functional complementarity comparing surgeonfish, parrotfish and rabbitfish. Their results revealed that surgeonfish and parrotfish fall into one broad group which has small niche volumes and high levels of complementarity, feeding on open and exposed reefs or sandy substrata. The second group largely comprising rabbitfish, revealed larger niches volumes, more overlap in functions and thus less complementarity due to high levels of variation among individuals. They emphasise the importance of assessing variation among individuals across multiples axes, as this will provide more representative knowledge of the mechanisms in which function is partitioned within an ecosystem.

A study by Adam *et al.*, (2015) on Caribbean parrotfish supported the previous studies and found that species in the genus *Scarus* targeted filamentous and endolithic algae whereas *Sparisoma* targeted macro-algae. Additionally, that species prefer different habitats and feeding on different substrata when feeding on similar algae types. Again this study highlighted the need to consider multiple factors of functional traits in order to determine species' niches and their functional role.

Using gut contents on six species of surgeonfish in Hawaii, Kelly *et al.*, (2016) showed that all six species appeared to feed on similar turf algae, however, gut content analysis showed the algae species they consumed were significantly different between herbivore species. This demonstrates that redundancy may be observed to be high when using observational *in situ* methods, but reveal complementarity when using more resolute methods and techniques of analysis. This highlights the importance of considering function at different scales, as niche or resource partitioning may not be captured by just observational methods alone. However, by complementing observational methods, with morphological studies, we can further understand and attribute variation in feeding strategy and therefore function.

Redundancy decreases and important information is discovered when considering multiple factors (i.e. diet, feeding behaviour, habitat and gut content). This could reveal that many species that have been previously considered redundant or functionally weak, may actually be providing important functions to the ecosystem. Behavioural and monitoring of herbivorous fish assemblages have been a key indicator in the resilience of reefs, this is low cost and can be done on a relatively regular basis. With monitoring programmes across global coral reefs, functional groups can indicate much more into the functional roles taking place upon a reef.

Secondary Functional Groups

Secondary functional group provides unique functional roles within grazing activity, as their classification has been defined through their feeding behaviour, e.g. how they remove algae from the reef, target different algae species for consumption and the scale in which they feed across the reef (Pet-Soede *et al.*, 2001; Green and Bellwood, 2009; Obura *et al.*, 2011; Pratchett *et al.*, 2011; Pinheiro *et al.*, 2013; Boaden *et al.*, 2015; Osuka *et al.*, 2016).

Benthic Feeders & Territorial damsels

Species of damselfish fall into the functional group of Benthic Feeders and Territorial Damsels. They provide localised and highly specialised functional roles to the reef, and are drivers in benthic structure and have additionally been found to indirectly influence the grazing behaviour of larger roving herbivore species through altering the EAM (Eurich *et al.*, 2018).

Species of Damselfish are highly abundant and though are relatively small compared to other herbivores species, play important roles on the reef. Across studies the two groups can be considered interchangeable as they both display varying levels of territorial and farming behaviours, however, territorial damselfish in this study refers to species that are considered “farmers” such as *Stegastes nigricans,* as these species have been found to alter the benthic structure within their territories (Hata and Kato, 2002; Ceccarelli, 2007) to a much greater extent than the benthic feeder species.

Benthic Feeders are highly associated with the reef and feed mainly on benthic algae and form small aggregations, whereas Territorial Damsels are highly aggressive and farm algae (Eurich *et al.*, 2018). Territorial Damsels, shape benthic community structure through allowing more “favourable” algae assemblages to establish within territories by restricting access from grazing fish and invertebrates (Hata and Ceccarelli, 2016). The functional role of the Benthic Feeders and Territorial Damsels are tightly associated to small-scale areas of the reef, therefore the role in grazing is localised to small patchy ranges across the reef (Frédérich *et al.*, 2009; Gajdzik *et al.*, 2016).

Benthic Feeders and Territorial Damsels were classified as species purely within the Pomacentridae family. Damselfish have previously been excluded from general herbivory studies due to their small size, however there are many studies which specialise on this family and focus on their farming behaviour and aggression in relation to herbivory and the role they play in driving benthic structure (Jones *et al.*, 2006; Hata *et al.*, 2010; Hoey and Bellwood, 2010; Peyton *et al.*, 2014; Eurich *et al.*, 2018).

Browsers

Browsers are often associated with grazing on patches of macro-algae and seagrasses (Hughes *et al.*, 2007a; Obura and Grimsditch, 2008; Green and Bellwood, 2009), and have been found to operate over mid-scale areas whilst foraging (Nash *et al.*, 2013).

Browsers are considered important in potentially reversing regime shifts through the consumption of dominant macro-algae stands (Hughes *et al.*, 2007a). However, studies have demonstrated that browsers also target the EAM as a consequence of limited algae cover, revealing that browsers exhibit plastic feed behaviour as a response to resource availability (Bellwood *et al.*, 2006b; Nash *et al.*, 2013).

Scraper/Small excavators

These species operate on a large foraging scale (Nash *et al.*, 2013) having been observed to roam large distances in search for suitable foraging areas. This group provides an important function in controlling algae through the complete removal of all algae type through scraping and excavating bites (Steneck and Dethier, 1994). Through removal and/or clearing of hard substratum and therefore the EAM and micro-organisms, the reef is cleared which facilitates settlement of new benthic organisms including hard corals by reducing the intensity and frequency of competition (Harborne and Mumby, 2018).

Scrapers/Small Excavators are species that are found within the Scaridae family (Parrotfish) and are distinguished from large excavators by being <35cm total length (Green and Bellwood, 2009). This secondary functional group is responsible for grazing activity of the reef by consuming the EAM on/in hard substratum (Harborne and Mumby, 2018) such are rock, dead coral and hard coral through scraping the surface area and top layer of the hard substratum itself (Green and Bellwood, 2009; Obura and Grimsditch, 2009). However, scraping and excavating provides clear distinctions between forging behaviour, with scraping removing the surface layer resulting in scaring marks and excavating removes chunks of hard substratum (Johansson *et al.*, 2012; Tebbett *et al.*, 2017a; Harborne and Mumby, 2018).

Grazer/Detritivores

This secondary functional group has been defined as species that primarily graze on the EAM (Green and Bellwood, 2009), however within this group there is much variation present within the modes of foraging including pure grazers, that feed on epilithic algal turfs, Grazer/Detritivores that feed upon the EAM (a combination of epilithic algal turf, sediment and some animal material) and detritivores. In this instance, grazers and Grazer/Detritivores were combined as many of these are schooling species and can consume a significant amount of algae (Green and Bellwood, 2009). Detritivore species have been combined into this group due to their nature of feeding on the EAM and their role in the mechanical removal of algae and/or detrital material (Pratchett *et al.*, 2011).

Functional roles across fish communities (e.g. consider different feeding guilds) and functional groups within guilds, are extremely important reef components and increasing our understanding of how changes to the functional role species play under different environmental settings, is key to conservation and active management activities. Next, we will look at how the benthic community is driven by the behaviour of herbivores and the dynamics and interactions that influence structure and composition, of both communities (herbivores and benthos).

Benthic Community Composition

Coral reef ecosystems that are more structurally complex provide habitats for food, reproduction and other resources for many inhabitants on the reef. This influences the biodiversity and therefore the ecosystem productivity and functioning and more species are able to co-exist and utilise similar resources across different scales (González-Rivero *et al.*, 2017). Habitat composition has been found to be an important factor in the structure of fish assemblages on coral reef systems (Osuka *et al.*, 2016).

On the other hand, herbivores have been identified to play an important role in controlling algae growth in coral reefs (Vroom *et al.*, 2006). In order to assess the effectiveness of herbivore functional roles, we must recognise how the benthic community is changing and affected by herbivory. This allows us to measure the rate of change or recovery from disturbances and regime shifts, in relation to less disturbed and desired reef states.

Measurements are often taken using observations *in situ*, and percentage cover of benthic communities is calculated. Studies have found that a diverse herbivore community maintains ecosystem functioning as herbivores target and feed on different types of algae which has complementary impacts on the benthic community (Adam *et al.*, 2015). Much like fish, algae have been divided into functional groups, such as microalgae, filamentous within the turf algae group, foliose, leathery, calcareous articulated within macro-algae and crustose algae (Diaz-Pulido & McCook, 2008). Dividing algae into functional groups facilitates a better understanding of how algae are distributed and will respond to control mechanisms (grazing), disturbances and environmental change (Diaz-Pulido & McCook, 2008).

In 2006, Littler *et al.*, carried out a manipulation experiment to assess the role of bottom-up (nutrient input) and top-down controls (herbivory) on benthic algal communities. Their results showed that high levels of herbivory alone do not prevent the growth of fleshy algae when nutrient levels are increased. However, low nutrient levels and high herbivory levels combined practically eliminates all forms of fleshy micro and macro-algae. When herbivory reduces fleshy algae biomass this allows for reef-building and coralline algae to expand.

However, algae have evolved to vary in space and time, by growing seasonally, on shallow reef flats or unstructured sand plains where herbivores were rare due to physical stress or the risk of predation. For example, on coral reefs, *Halimeda* species is commonly found to grow at the base of branching corals, where few herbivores are able to access, in addition to being calcified which deters herbivory (Castro-Sanguino *et al.*, 2016).

In response to algae adaptations, fish with robust mouth parts took advantage of the morphological and structural defences that algae evolved; with *Acanthuridae* spp. processing algae in acidic thin-walled stomachs, *Ctenochaetus* spp. selectively removing particles within the EAM and parrotfishes excavating whole pieces of rock for epilithic and endolithic algae (Steneck *et al.*, 2017). This study also shows how the morphological differences in teeth shapes and form allow herbivores to partition resource uptake along the EAM.

When investigating the interaction of herbivores and algae, we need to understand the productivity of algae (e.g. its growth rates). A study by Kelly *et al.*, (2017) investigated algal production and compared the consumption rates by herbivores. The study was conducted in a managed area where taking herbivorous fish and urchins were prohibited and was established in 2009. The findings show that algae productions exceeded grazing capacity from the beginning of the study in 2009 (consumption 20.8% of production), however in 2014 at the end of the study consumptions began to exceed production of algae (consumption 67.0% of production) due to increased consumption rates by larger sized herbivores e.g. *Scaridae* spp. as a result of increased biomass.

The study by Kelly *et al.*, (2017) highlights, the need to understand the long-term dynamics by assessing algal biomass, changes in biomass (i.e. productivity and growth) combined with grazing activity and how grazing activity responds to variable algal biomass – i.e. the dynamics of the interaction between algal and their grazers, in order to effectively monitor reefs for potential regime shifts.

Herbivore exclusion experiments have been conducted to assess the rate of recovery of reefs from a coral to macro-algae dominated reef after major coral mortality (Hughes *et al.*, 2007a). The long-term caging experiment by Hughes *et al.*, (2007b) following the 1998 bleaching event was conducted over a 3 year period. They showed that areas which excluded herbivores had an explosion of macro-algae, in contrast to controls where algae abundance was low. In control areas, coral cover doubled due to recruitment, where macro-algae suppressed recruitment and survival of corals.

The epilithic algae matrix is significantly important in the function of grazing by herbivores as it is the primary grazing surface for many reef fish and is ubiquitous in coral reefs (Wilson *et al.*, 2003). Originally coined the epilithic algal community (EAC), which was understood to be low turfs or mats of small algae (Hatcher and Larkum, 1983). However, research has shown that this is a much more complex structure and includes detritus, bacteria, fungi, microbes and micro-algae (Wilson and Bellwood,

1997) and then was re-named the epilithic algae matrix with filamentous algae making up the majority of material (Wilson *et al.*, 2003). Research which has incorporated the EAM as a food/nutritional resource has demonstrated that fish classified as herbivores can derive nutrition from the detritus rather than the algae itself (Wilson *et al.*, 2003; Ferreira and Gonçalves, 2006; Marshell and Mumby, 2012; Tebbett *et al.*, 2017b). Understanding that the EAM is a complex structure with multiple food groups highlights the difficulties in disentangling functional roles of herbivores that feed upon this resource (Cvitanovic *et al.*, 2007)

It is clear that herbivore community composition and biodiversity are key to maintaining a healthy functional reef. However, our knowledge of interactions between algae and grazers are limited to few studies that have managed to combine, historical community and benthic data in relation to functional partitioning and herbivore exclusion experiments. There are severe gaps in our knowledge on the interactions between different species (how functional herbivory is partitioned) that exist in high biodiversity environments and in particular what consequences of the loss of species is in such environments. As species loss and reduction in overall biomass is now the norm in most reef systems, a key question to address is; what is the functional role of grazing in high biodiverse regions; and how the functional roles of herbivory are divided across the reef landscape and overtime.

Conclusion

Investigating how functional roles are partitioned across guilds, groups and species can offer important information about the ecological processes that herbivores provide in terms of reef resilience. Few studies have actively revealed the finer scale variations between herbivore species functioning and potential levels of redundancy and complementarity.

Further investigation and yearly comparisons can reveal how herbivore abundance and biomass is changing over time. Additionally, how the herbivore community assemblage changes over time and how similar/dissimilar these communities are, will allow us to reveal potential shifts in functional roles. By identifying the key differences between herbivore species abundance, biomass, community assemblage and critically the functional roles, will provide critical information to enhance management of herbivores and coral reefs ecosystems and improve the resilience to highly diverse reefs, which face increasing pressure to disturbances as we enter the Anthropocene.

The overarching aims of this study were to investigate the spatial and temporal variation in abundance and biomass of the herbivore community and understand how functional roles dominant herbivores play in sculpturing reef benthic community structure and to understand whether these roles are partitioned across different fish guilds and secondary functional groups. In addition, how benthic composition can actually drive variation in herbivore abundance and biomass. Finally, evaluating the similarity of fish guild communities' structure across reef zones and years and how this may explain variance in fish communities. Furthermore, quantifying the functional role of grazing activity provided by herbivores through assessing the response of algae cover due to the exclusion of grazing activity by herbivorous fish. Finally

The key objectives were (1) determine the natural benthic community composition and quantify how algae responds to the exclusion of herbivory by herbivorous fish, (2) determine change in fish density, biomass and mean biomass across grazing functional groups and benthic percentage cover between 2013, 2015 and 2017, (3), determine grazing functional group community similarity between 2013, 2015, and 2017, (4) determine if there is a relationship between benthic communities and changes in the herbivore community (abundance and biomass) and (5) determine change in relative density, biomass and mean biomass of secondary functional groups.

H.1) Percentage cover of algae will dominate over other benthic organisms when grazing activity by herbivorous fish is removed.

H.2) An increase in the percentage cover of algae will decrease the abundance and biomass (g) of herbivores.

H.3) An increase in the percentage cover of algae will decrease the abundance and biomass (g) in secondary functional group

Materials & Methods

Study site

The study sites were located in the reefs of Hoga and Kaledupa Island found in the Wakatobi National Park (WNP) in southeast Sulawesi, Indonesia. The WNP was designated in 1996 and covers 1.39 million hectares (Exton *et al.*, 2019), within the national park, the nearshore fisheries are a combination of subsistence and commercially driven operations, which can range from small motorised boats, fish fences and diving compressors used with spear gun fishing (Exton *et al.*, 2010). Six reefs were studied and are a part of a long-term monitoring programme that began in 2002. The six sites are Buoy 3 (B3), Pak Kasims (PK), Ridge 1 (R1), Sampela (S1), Kaledupa 1 (K1) and Kaledupa Double Spur (KDS). B3, PK and R1 are located on the reefs of Hoga Island and S1, K1 and KDS are located on the reefs of Kaledupa Island (Figure 1). The study sites are all located in the channel between Hoga and Kaledupa Islands and form fringing reefs on both islands, with Sampela being the only site found within a lagoon.

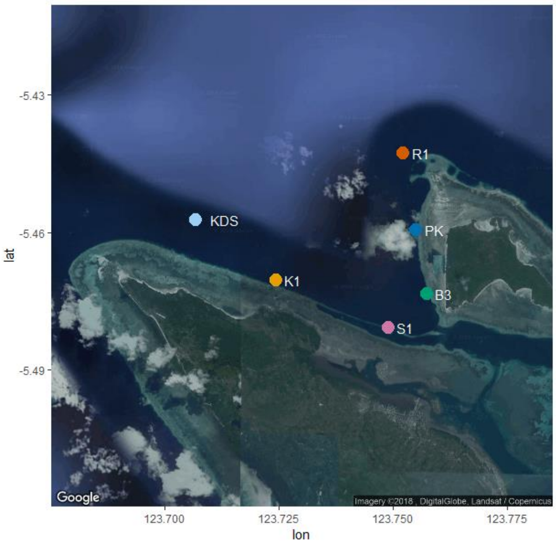
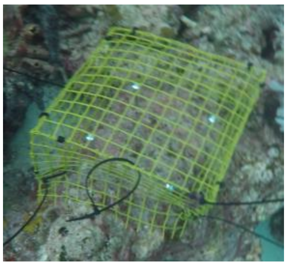
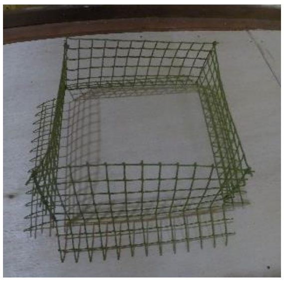
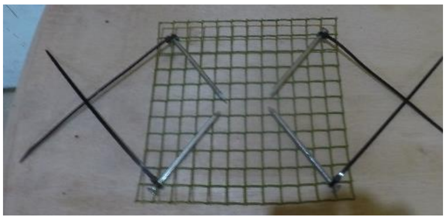


Figure 1. Study sitemap of Hoga and Kaledupa Islands, located in the Wakatobi National Park in Southeast Sulawesi, Indonesia. Sites - Buoy 3 (B3), Pak Kasims (PK), Ridge 1 (R1), Sampela (S1), Kaledupa 1 (K1) and Kaledupa Double Spur (KDS).

Herbivore Exclusion Experiment

To investigate the functional role fish exhibit in coral reef ecosystems through grazing activity on the sessile benthic community, a herbivore exclusion experiment was designed. Cages of 25 x 25 x 10 cm were created from green garden PVC mesh; mesh size 19mm. These cages were constructed for fully caged treatments, and to control for the effects of the cage three control treatments were deployed; control were marked areas of the reef, top were caged areas with open sides and side were caged areas with an open top (Table 2). All treatments were deployed at the Hoga Home Reef (Figure 2), cages were attached to bare patches of reef mainly on rock. The reef substratum was not scraped clean to allow for the natural biofilm to remain, this was to simulate a more natural disturbance effect (Bozec *et al.*, 2018).

Table 2. Exclusion experiment treatments deployed in June 2017 until June 2017, depicting fully caged treatments (full), open top treatments (side), open side treatments (top) and completely open treatments (control).

Treatment	Cage dimensions (cm)	Number deployed	Picture
Full	25 x 25 x 25 x 10	13	
Side	25 x 10 open cube	5	
Top	25 x 25 flat lid attached large nails approx. 5 cm above the reef	5	
Control	15 x 15 area marked using nails	5	

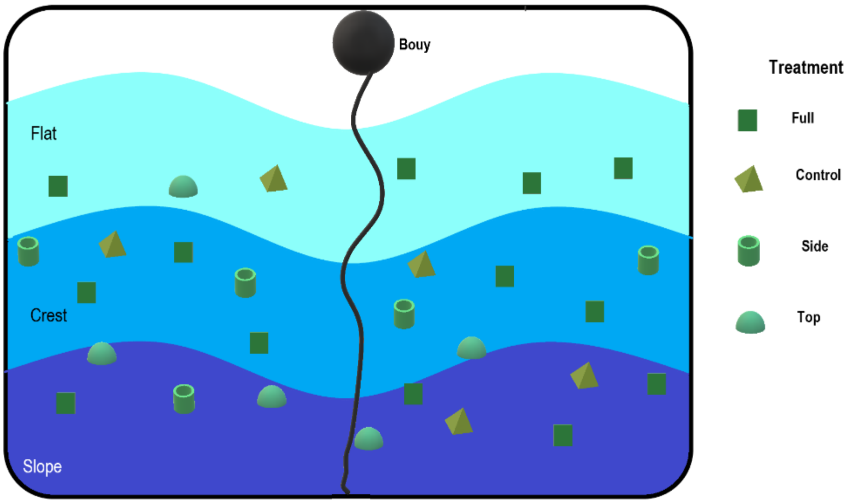


Figure 2. Experimental design schematic for herbivore exclusion experiment deployed at Pak Kasims from June 2017 to June 2018. Squares, fully caged treatments, pyramid, control treatment, tube, side cage control treatment and dome top cage control treatment, across reef flat, crest and slope.

The experiment was set up on the Hoga home reef during June and July 2017. Images of the caged area of reef were taken at the time of deployment, and a 15 cm x 15 cm quadrat was laid in the exclusion test area to give a scale of the area; images were taken using a GoPro Hero4. Additional images were then taken in April 2018 and June 2018, images were used to extract percentage benthic cover of the reef substratum (Appendix II). Deployment of cages and images were all taken by myself, with deployment facilitated by my supervisor Prof. Dave Smith.

For the duration of deployment, the cages were regularly cleaned using brushes to ensure that organisms did not over-grow the cage and affect the water flow and light reaching the benthos. The cleaning and maintenance of the cages were maintained by myself during the months of June to August 2017, and from March to April 2018. Out of these periods the cage maintenance was carried out by the dive manager based on Hoga Island.

Data Collection

Historical data of the fish and benthic community was obtained from the long-term monitoring program that is conducted every year around Hoga Island. Data is collected by a dedicated science team alongside dissertation research students and volunteer research assistants. The collected data is then processed on site by the team and assistants, data is validated using video and imagery. This dataset was kindly provided by Prof. Dave Smith and Operation Wallacea.

Long-term monitoring data

Data were collected at six sites, each site was surveyed at the reef flat, crest and slope, at each zone three transects were recorded, with only Ridge 1 not having a reef flat to record. Surveys were conducted along a 50 m transect, with a total of 9 transects recorded per site (N.B. Ridge 1 total of 6 transects recorded), resulting in a total of 51 transects being recorded for both fish and benthic data each year. The reef crest is identified as the area in which the reef starts to drop off (3-8m) , often towards the reef slope which is the area of the reef with the steepest gradient also known as the wall (8-15m), with the reef flat being behind the crest extending towards the shore (0-3m).

While surveys have been conducted since 2002 – due to a change in methods from 2012 only data since then is included in the current study. Data was collected from June to August in the years 2013, 2015 and 2017. Data from 2013, 2015 and 2017 were selected for this study, as these years represent pre-disturbance (2013), to the El Niño of 2015, causing a major global bleaching event that extended into 2016 and post-disturbance (2017). As bleaching was not observed in the WNP, these years were retained as indicators of major global disturbances. To gain an insight into the natural benthic community at Pak Kasims, benthic data from 2018 was also included as a comparison for the herbivore exclusion experiment.

Fish and Benthic Surveys

Fish monitoring was recorded using a stereo-video system (SVS) along a 50m transect. The SVS (Figure 3) recorded using two Canon DLSR cameras during the years 2013 and 2015, this was then changed to using GoPro action cameras in 2017. The two cameras are calibrated to record overlapping footage along the same transect to allow for size measurements of individual fish. Video footage is then imported and analysed using the software Eventmeasure (SeaGIS Pty Ltd, http://www.seagis.com.au/); to ensure measurements are accurate a calibration video is recorded and uploaded into the software; fish species, abundance and length are recorded.

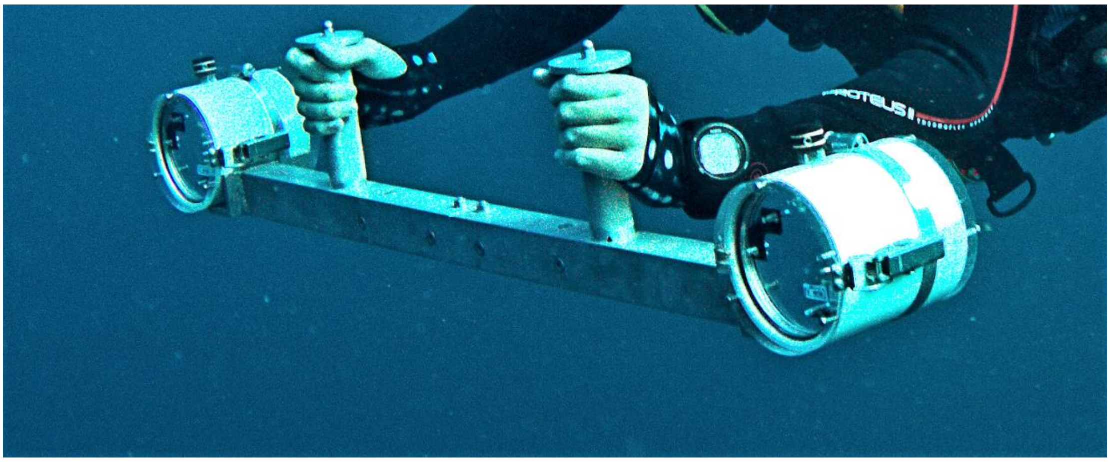


Figure 3. Image of the stereo-video system used for fish monitoring surveys in Hoga, using GoPro Hero5 cameras. Photo courtesy of Kuyer Fazekas 2018.

Benthic coverage monitoring was surveyed by video recording along the 50m transects approximately 30 to 50 cm above the transect line using action cameras (GoPro like). Data is then analysed from the video footage using the point-intercept method and benthic type is recorded every 25cm, resulting in 201 data points being logged along one 50m transect.

Data Analysis

Herbivore Exclusion Experiment

Quadrat images taken during the herbivore exclusion experiment were processed using Coral Point Count with Excel extensions (CPCe) software (Kohler and Gill, 2006). Area measurements were recorded for each benthic type found within the 15 cm^2 quadrats. These were then exported into excel and calculated for percentage cover.

Fish and Benthic data

Biomass of fish was calculated from the recorded total length using the length-weight allometric equations (Bohnsack and Harper, 1988).

(1) $W = a\mathrm{TL}^b$

Where W is weight in grams, TL is the total length in cm and a and b constants were obtained for each species from FishBase (Froese and Pauly, 2018) where possible. Species that did not have a, b values, biomass was calculated using constant values of trophically and morphologically similar species.

All species were maintained in the analysis that had a record of abundance. Individuals that could not be identified down to species were removed from further analysis (2653 individuals removed across all years). In 2017, one individual was removed from the dataset as it was profoundly skewing the biomass data, this individual was a dogtooth tuna (*Gymnosarda unicolor*), with a calculated biomass of 2486.57 g. As we are mainly interested in the interactions of herbivores, the removal of the data point will not affect the overall community analysis. Table 4 shows the summary of fish recorded during the long-term monitoring programmes in 2013, 2015 and 2017 that have been included for analyses in this study. Appendix III displays all recorded fish species and families.

Table 3. Summary of total fish recorded during the long-term monitoring programme across 2013, 2015 and 2017; the total number of individuals, the total number of species and the total number of families.

	2013	2015	2017	All years
Number of individuals (12,750 m^{-2})	7276	9974	14249	31499
Number of species (12,750 m^{-2})	190	187	291	375
Number of families (12,750 m^{-2})	29	31	35	36

Transect replication was pooled and all sites were pooled by reef zone; i.e. B3, P.K., R1, S1, K1 and KDS at the crest were pooled for further community analysis within each year. This was done for both the fish monitoring data and the benthic data.

Fish guilds were assigned to each species based on literature and Fishbase; guilds represented were carnivores, facultative corallivores (Fac corallivores), herbivores, invertivores, obligate corallivores (Ob corallivores), omnivores, piscivores and planktivores (Frédérich *et al.*, 2008; Green and Bellwood, 2009; Obura and Grimsditch, 2009; Froese and Pauly, 2018). Fish species that were classified as herbivores, were further divided into secondary functional groups and were summarised across reef zone and years. Secondary functional groups have been classified through the variation in foraging strategy and resource use that has been adapted from studies by Frédérich *et al.*, 2009; Obura and Grimsditch, 2009; Hoey and Bellwood, 2010. The secondary functional groups (Appendix III) that are included in this study are (1) Benthic Feeders, these species are found within the Pomacentridae family and usually found close to reef bottoms and solitary (Frédérich *et al.*, 2009), (2) Browsers, these species feed on consistently macro-algae (Green and Bellwood, 2009; Obura and Grimsditch, 2009), (3) Grazer/Detritivores, are species that feed intensely on epilithic algal turfs and/or a combination of epilithic algal turf, sediment and animal material (Green and Bellwood, 2009; Obura and Grimsditch, 2009), (4) Scrapers/Small Excavators, these species are found within the Scaridae family and feed on epilithic algal turf and remove sediment and other material including coral polyps by scraping reef substratum (Green and Bellwood, 2009; Obura and

Grimsditch, 2009), (5) Territorial Damsel, these species are found within the Pomacentridae family, and are highly Territorial Damselfish that can also be considered algae farmers often excluding other herbivorous fish from algae patches in the reef (Hoey and Bellwood, 2010).

Benthic types of “water” and “unknown” were removed from analyses. These are redundant for further analysis and are due to sampling and data processing variance by multiple teams over the years of the long-term monitoring project. Dead coral with algae was grouped into algae, and dead coral with corallites visible was grouped into dead coral.

Statistical Analysis

All statistical analyses were computed using the free software R version 3.4.4 (R core team, 2018) and RStudio version 1.1.442 (RStudio Team, 2016).

Herbivore Exclusion Experiment

Percentage benthic cover was recorded from the day of deployment (0 months), 1 month, 9 months and 12 months. Algae cover was tested for change over time and between treatments and for any interaction effects using an unbalanced Two-way ANOVA, additionally, reef zone was incorporated as a random effect. The interaction between time and treatment was not found to be significant, therefore and further tests were conducted to test for differences between treatments and time. The random effect of reef zone was found to be minimal and therefore excluded from the final Two-way ANOVA.

Fish and Benthic data

In order to gain an insight into how the fish community composition of herbivores may have changed spatiotemporally, data was analysed across the reef zone and across years. Fish monitoring data for the years 2013, 2015 and 2017 was summarised across years and reef zones to calculate fish density (no. /m^2), biomass (g/m^2) and mean biomass. Benthic data for the same years was summarised for overall benthic composition, where percentage cover for each benthic type was calculated.

Community analyses

To investigate how the total fish community composition changed across reef zones and across years, non-metric multidimensional scaling (nMDS) plots were created in the “vegan” v.2.4-6 package (Oksanen *et al.*, 2018). Data was square–root transformed to reduce the range found within the data and then subject to Wisconsin double standardization, these standardisations methods improve the quality of ordination (Oksanen *et al.*, 2015). The total fish community nMDS plots were based on Bray-Curtis dissimilarity using the “metaMDS” function. In order to visualise any trends across reef zones, convex hulls were drawn over each zone using the “chull” function in R. This was repeated for the fish communities of herbivores, and secondary functional groups.

ANOSIM analyses were conducted in order to understand the dissimilarities within secondary functional group communities across reef zone and years. Species-level abundance assemblages was used for the analyses. Further testing was conducted using SIMPER analyses to disentangle the species that were most influential in community differences. ANOSIM and SIMPER analyses were conducted using the “vegan” v.2.4-6 package (Oksanen *et al.*, 2018) in R.

Data modelling

General linear models were used to assess the relationship of fish abundance and biomass to benthic communities. The regression family was negative binomial as the data showed over-dispersion in the count data. Models were created for herbivore and secondary functional groups communities based on absolute abundance and biomass. Benthic types that were included in the analyses were sand, soft coral, hard coral, sponge, algae, rock and rubble. All other benthic types were excluded due to large amounts of missing data points. All models were calculated in R using the “MASS” v. 7.3-49 package (Ripley, 2011), using the function “glm.nb”. Tests for multicollinearity among benthic predictors were conducted prior to analysis using the “pairs” function in R. Akaike Information Criterion (AIC) was used to evaluate the candidate models

Results

Herbivore exclusion benthic community response

Over the years 2013, 2015, 2017 and 2018 combined, the benthic community at Pak Kasims at the reef flat was predominately covered by rock (28.27%), followed by sand (18.18%), hard coral (15.32%), soft coral (14.99%), rubble (13.03%), silt (6.10%) and algae contributing a proportion of 2.16% of the benthic cover. Hard coral dominates over other benthic types at the reef crest with 25.11% cover, followed by rock (23.24%), soft coral (23.16%), rubble (13.99%), algae (5.66%) and sand (3.79%). At the reef slope, rock (19.02%) and soft coral (18.72%) dominate, followed closely by rubble (18.13%) and hard coral (17.66%). Sponge (8.98%), sand (8.43%) and algae (6.60%) contribute the lower proportions of the benthic community at the reef slope with the remaining benthic types contributing less than 1.3% each (Figure 4A).

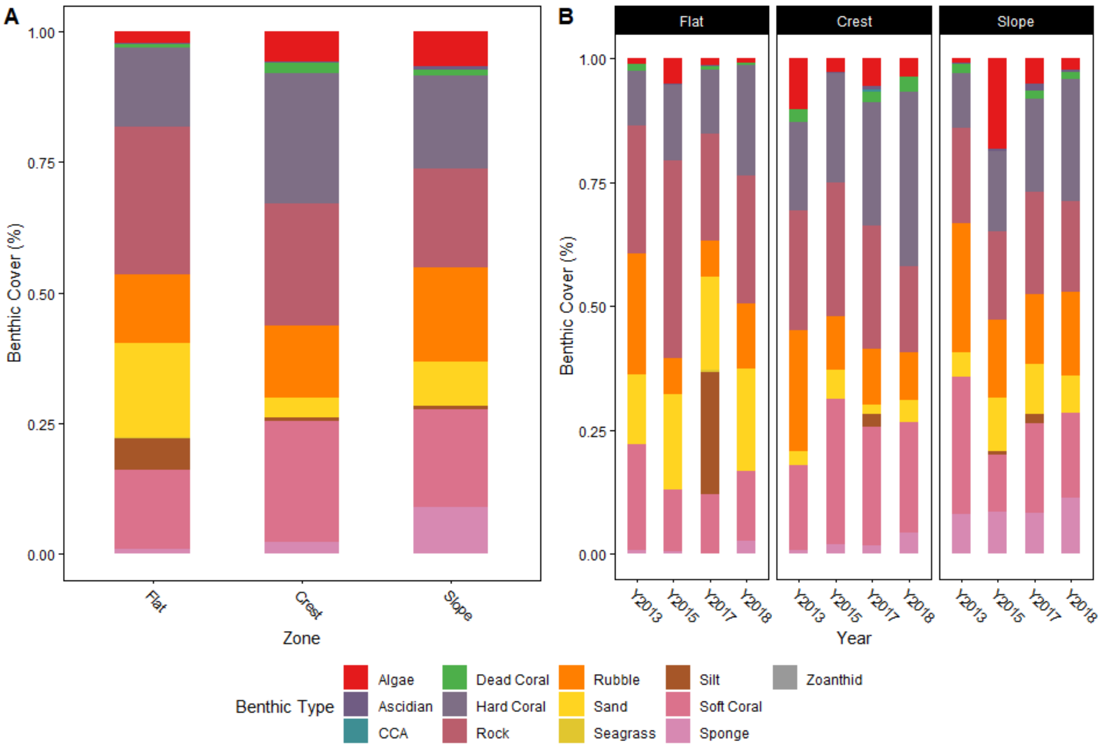


Figure 4. Benthic percentage cover (%) at Pak Kasims, (A) between reef zones (flat, crest and slope), across all years (B) between reef zones (flat, crest and slope) and years (2013, 2015, 2017 and 2018).

Algae percentage cover was lowest at the flat increasing to the crest and slope (Figure 4A). Through the years the reef flat at Pak Kasims had very low percentage cover of algae, yet there was an increase in the year 2015 from 1.16% in 2013 to 5.14% which decreased to 1.33% in 2017 and 1% in 2018. At the reef crest, the highest percentage of algae was recorded in 2013 (10.39%), decreasing in 2015 (2.82%) and rising slightly in 2017 (5.68%) and decreasing once again in 2018 (3.82%). The reef slope in 2013 recorded 1.01% of algae and increased drastically to 18.31% in 2015 to decrease to 5.15% and 2.39% in 2017 and 2018 respectively (Figure 4B).

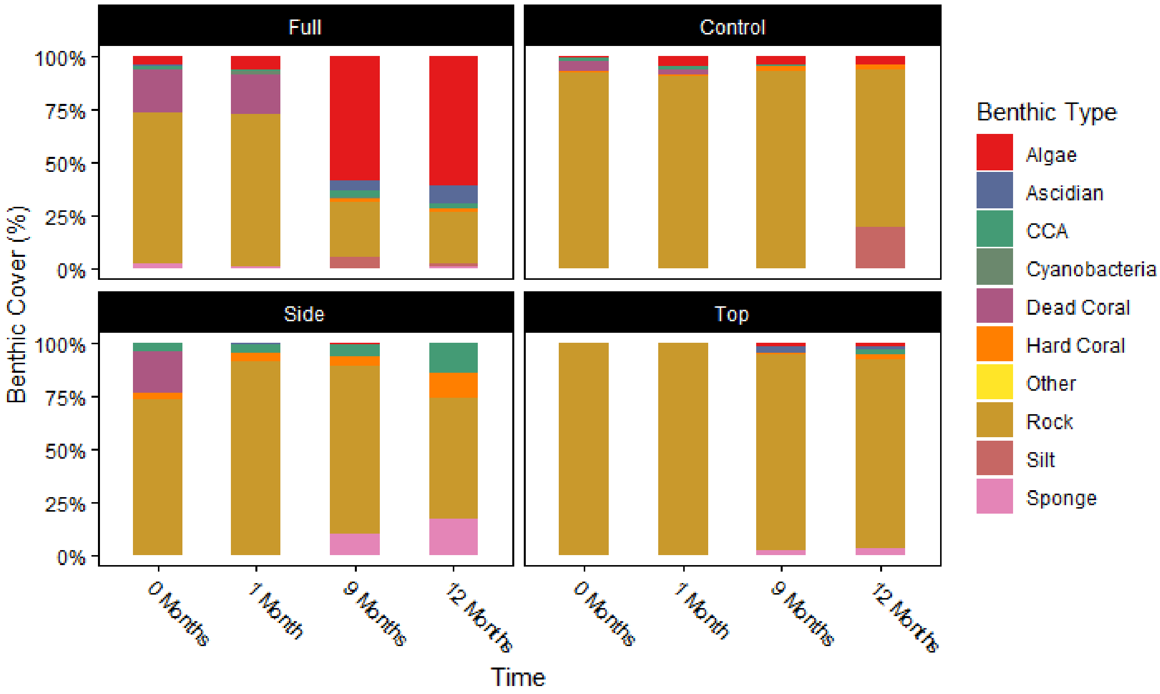


Figure 5. Benthic Cover (%) of benthic reef organisms in the exclusion experiment, for the full, control, side and top treatments over time

0 months in the herbivore exclusion experiment displays the baseline of the benthic percentage cover in each treatment (Figure 5). In the fully caged treatment (full), benthic composition changed over time with algae recorded at 0 months at 3.90 % increasing to 6.51%, 58.46% (1 month and 9 months respectively) and at 12 months to 60.56%. In the control treatment fluctuations of algae cover was recorded at 0 months 1.04%, to 4.69%, 3.89% and 4.33 % at 1 month, 9 months and 12 months

respectively. In the side treatment algae cover was only recorded for 1 month (0.46%) and 9 months (0.85%). Algae was recorded only after 9 months (1.26%) and 12 months (1.98%) in top treatments (Figure 6).

There were highly significant differences between treatments of algae cover ($F_{3, 40}$ = 16.611, P = <0.001); posthoc Tukey testing revealed that control (P = <0.001), side (P = <0.001) and top treatments (P = <0.001) were significantly different to the full treatment of the experiment, additionally side versus control treatments displayed significant differences (P = <0.05). Algae cover was found to have significant differences over time ($F_{3, 40}$ = 4.377, P = <0.01); posthoc Tukey testing revealed that differences were found from the start (0 months) and after 9 months (P = <0.01) and 12 months (P = <0.01).

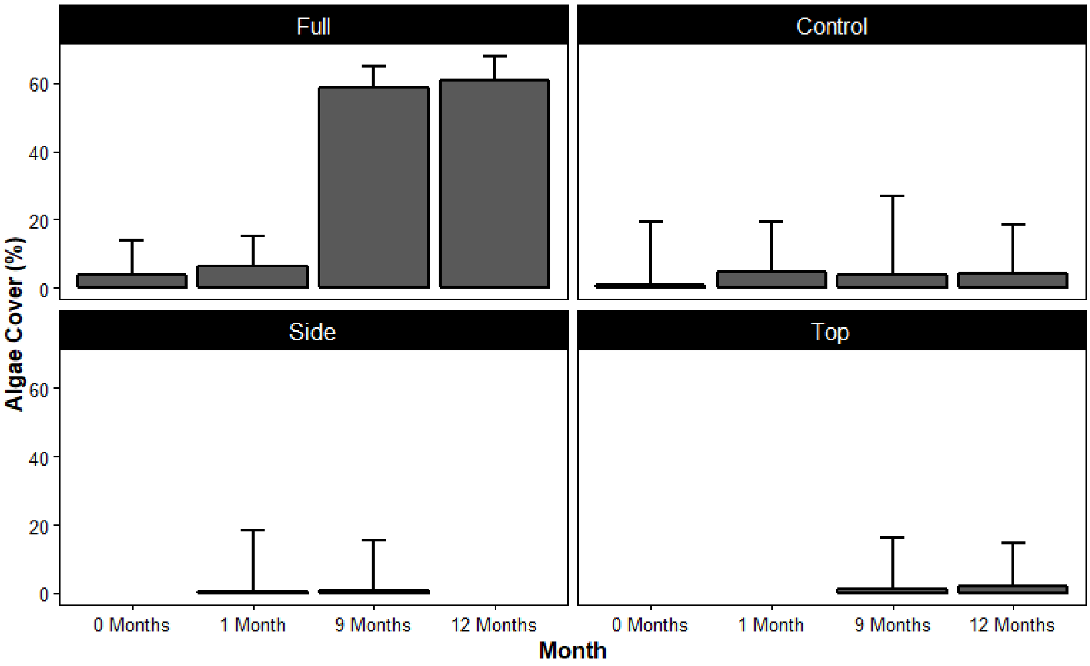


Figure 6. Benthic cover (%±SE) of algae in the exclusion experiment, for the full, control, side and top treatments over time.

Benthic composition

Over all years, the benthic community in the Wakatobi at the reef flat was predominately covered by rubble (25.85%), followed by rock (23.79%), sand (13.51%), soft coral (13.51%), hard coral (12.39%) and algae contributing 3.50%. At the crest, rock dominates with 25.04% followed by rubble (19.82%), soft coral (18.99%), hard coral (18.34%), with algae contributing to 4.82% benthic cover. Hard coral dominates the reef slope with 19.57% of benthic cover, followed by soft coral (15.89%), rock (15.80%), and rubble (15.28%), with algae contribution to 8.27% (Appendix III).

Percentage cover of algae tends to increase from the reef flat to the reef slope, this is true for years 2013 and 2017. However, in 2015 the reef flat had a slightly higher cover of algae at the reef flat (5.80%) than the reef crest (5.63%) with the highest cover between years at the reef slope with 11.13% algae cover (Appendix III).

Herbivorous fish assemblages

Herbivore density and biomass was found to generally decrease from the reef flat towards the reef slope. However, biomass between the reef flat and crest were found to have less variation and was more evident in the years 2013 and 2015 (Figure 7B). In 2017 overall herbivore density and biomass were recorded at greater values than 2013 and 2015. Mean biomass (g/m^2) within years had little variation across reef zones (Figure 8), with maximum variation recorded ~0.05 (g/m^2) from the reef crest to slope in 2017.

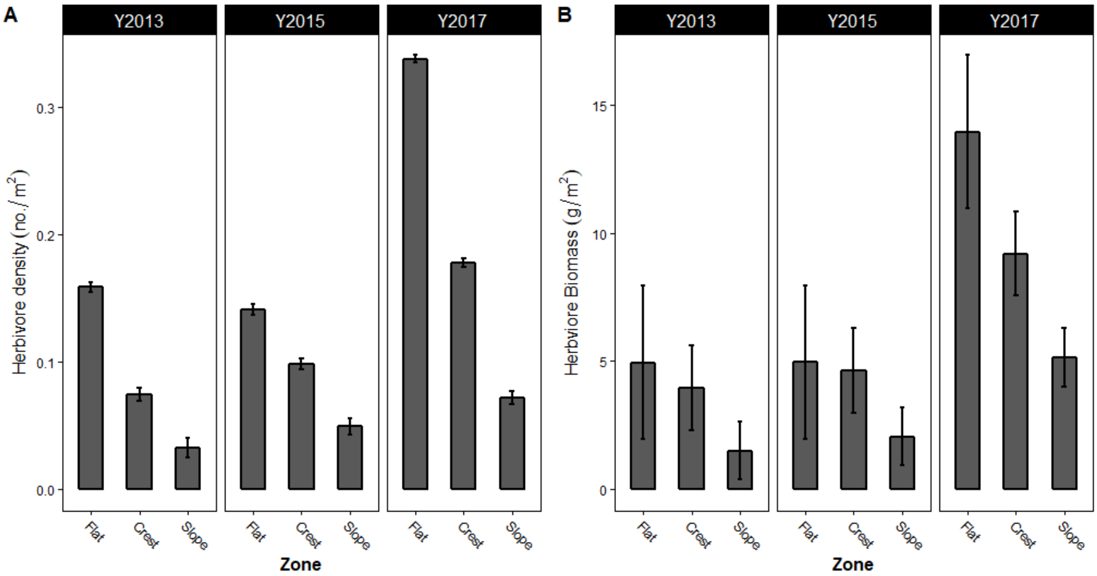


Figure 7. Herbivore (A) density (no. /m^2 ± SE) and biomass (g/m^2±SE) across reef zones (flat, crest and slope) and years (2013, 2015 and 2017).

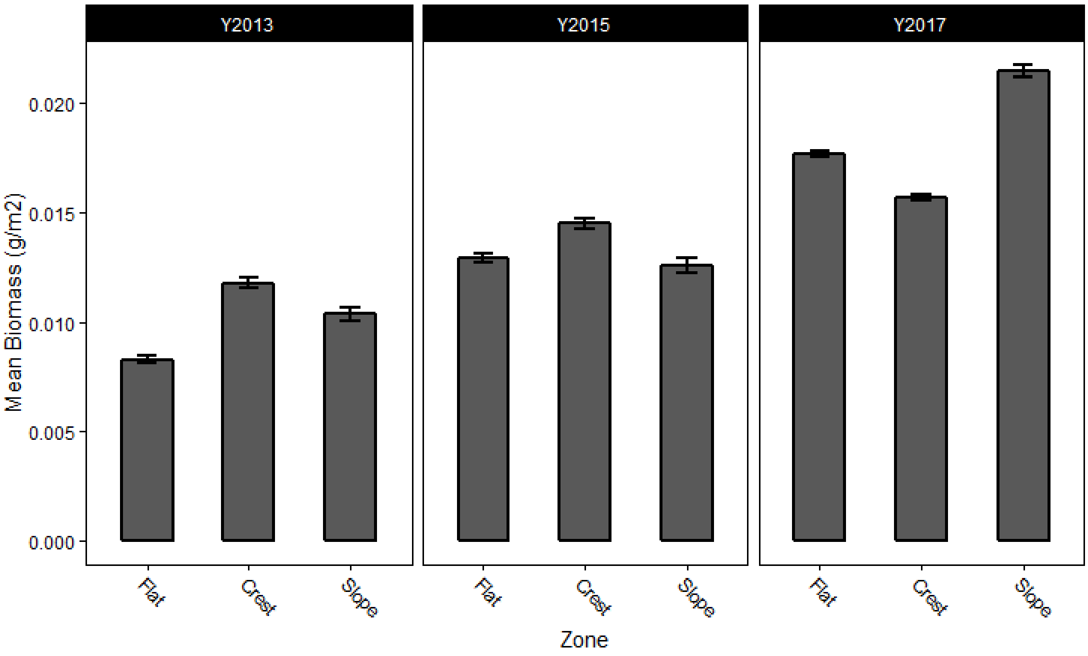


Figure 8. Herbivore mean biomass (g/m^2 ± SE) across reef zones (flat, crest and slope) and years (2013, 2015 and 2017).

Secondary Functional Groups

Herbivore species were further defined into secondary functional groups, Table 4 summaries the number of individuals recorded within each group across 2013, 2015, 2017 and across all years.

Table 4. Summary of total number of individuals recorded within each secondary functional groups found within the herbivore guild, in the years 2013, 2015, 2017 and all years combined.

Secondary	2013	2015	2017	All years
Benthic Feeders (12,750 m^{-2})	211	113	788	1112
Browsers (12,750 m^{-2})	6	3	17	26
Grazers/detritivores (12,750 m^{-2})	653	948	1145	2746
Scrapers/Small Excavators (12,750 m^{-2})	199	159	416	774
Territorial Damsel (12,750 m^{-2})	8	20	24	52

Grazer/Detritivores have the greatest overall density and biomass when pooled reef zones and years 0.658 ± 7.248E^{-}05 (no. /m^2) and 30.890 ± 5.002E^{-}05 (g /m^2) respectively. Benthic Feeders are the second most abundant group with a recorded density of 0.277 ± 1.190E^{-}04 (no. /m^2), followed by Scrapers/Small Excavators (0.188 ± 5.735E^{-}05 no. /m^2) with very few Territorial Damsels (0.013 ± 2.384E^{-}05 no. /m^2) and browsers (0.006 ± 1.665E^{-}05 no. /m^2). Scrapers/Small Excavators followed Grazer/Detritivores, in recorded biomass (18.040 ± 6.188E^{-}03 g /m^2), browsers (0.832 ± 3.330E^{-}03 g /m^2), Benthic Feeders (0.351 ± 1.991E^{-}04 g /m^2) and Territorial Damsels (0.230 ± 4.172E^{-}04 g /m^2). Across reef zones, secondary functional group density tended to decrease from the reef flat to the reef slope and increased over time (Figure 9). Biomass in secondary functional groups, in particular with Grazer/detritivores and Scrapers/Small excavators decreased from the reef flat to the reef slope, however, this between the reef flat and crest biomass recorded similar values. All other secondary functional groups had very low recorded biomass (Figure 10).

Overall, mean biomass when pooled across reef zones and years was recorded to be highest in Browsers (0.291 ± 8.280E^{-}05 g/m^2). Scrapers/small excavators followed (0.221 ± 3.050E^{-}05 g/m^2), and Grazer/detritivores (0.120 ± 2.322E^{-}05 g/m^2). As expected Territorial Damsels (0.035 ± 2.148E^{-}05 g/m^2) and Benthic Feeders (0.007 ±

1.172E^{-}05 g/m^{2}) recorded the lowest mean biomass. Mean biomass of secondary functional groups' remained relatively consistent across reef zones and years. However, in 2015 at the reef crest, Browsers was recorded with the greatest mean biomass (Figure 11).

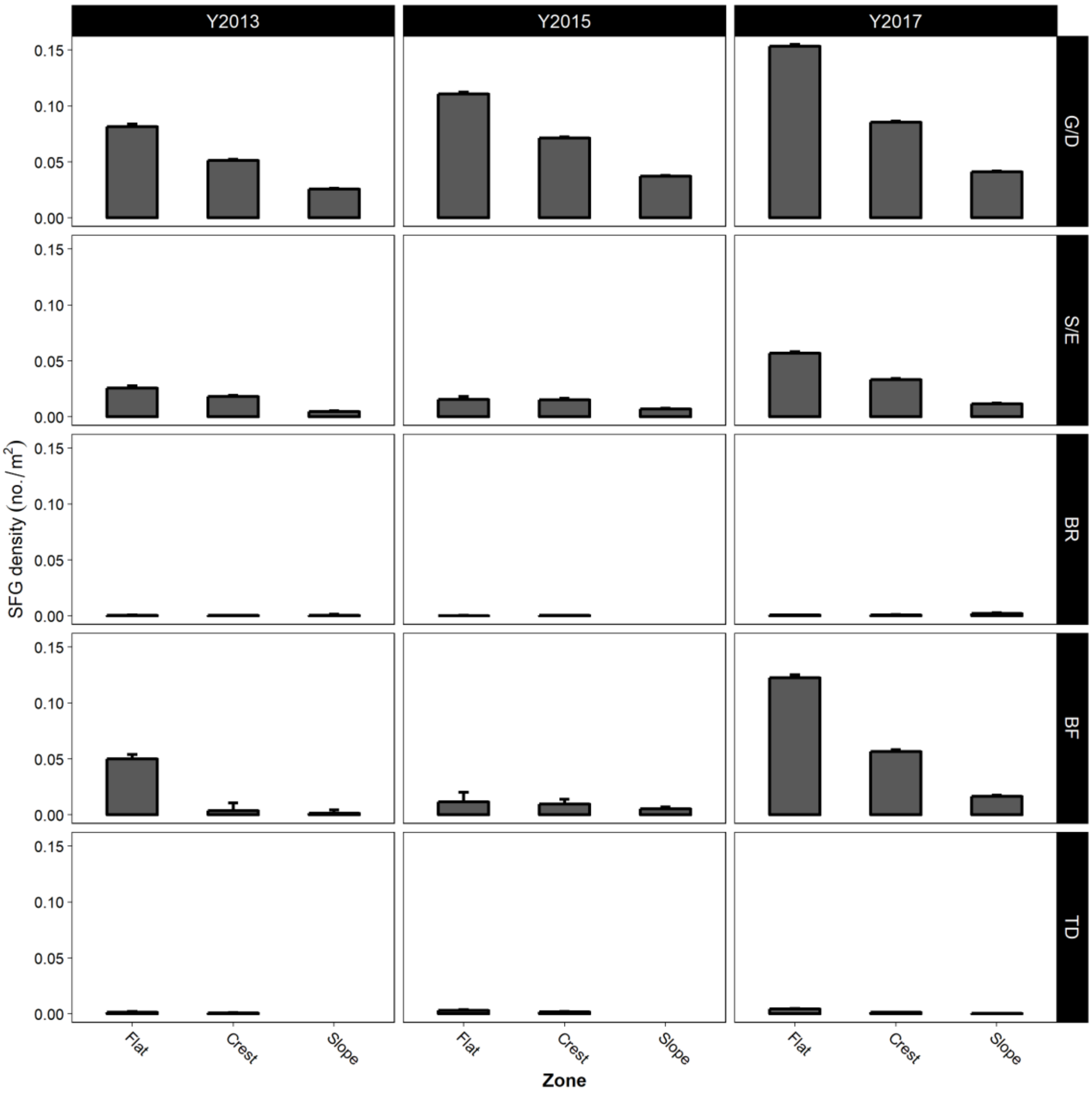


Figure 9. Secondary functional group density (no. /m^2±SE) across reef zones (flat, crest and slope) and years (2013, 2015 and 2017). G/D = Grazer/detritivores, S/E = Scrapers/Small excavators, BR = Browsers, BF = Benthic Feeders and TD = Territorial Damsels.

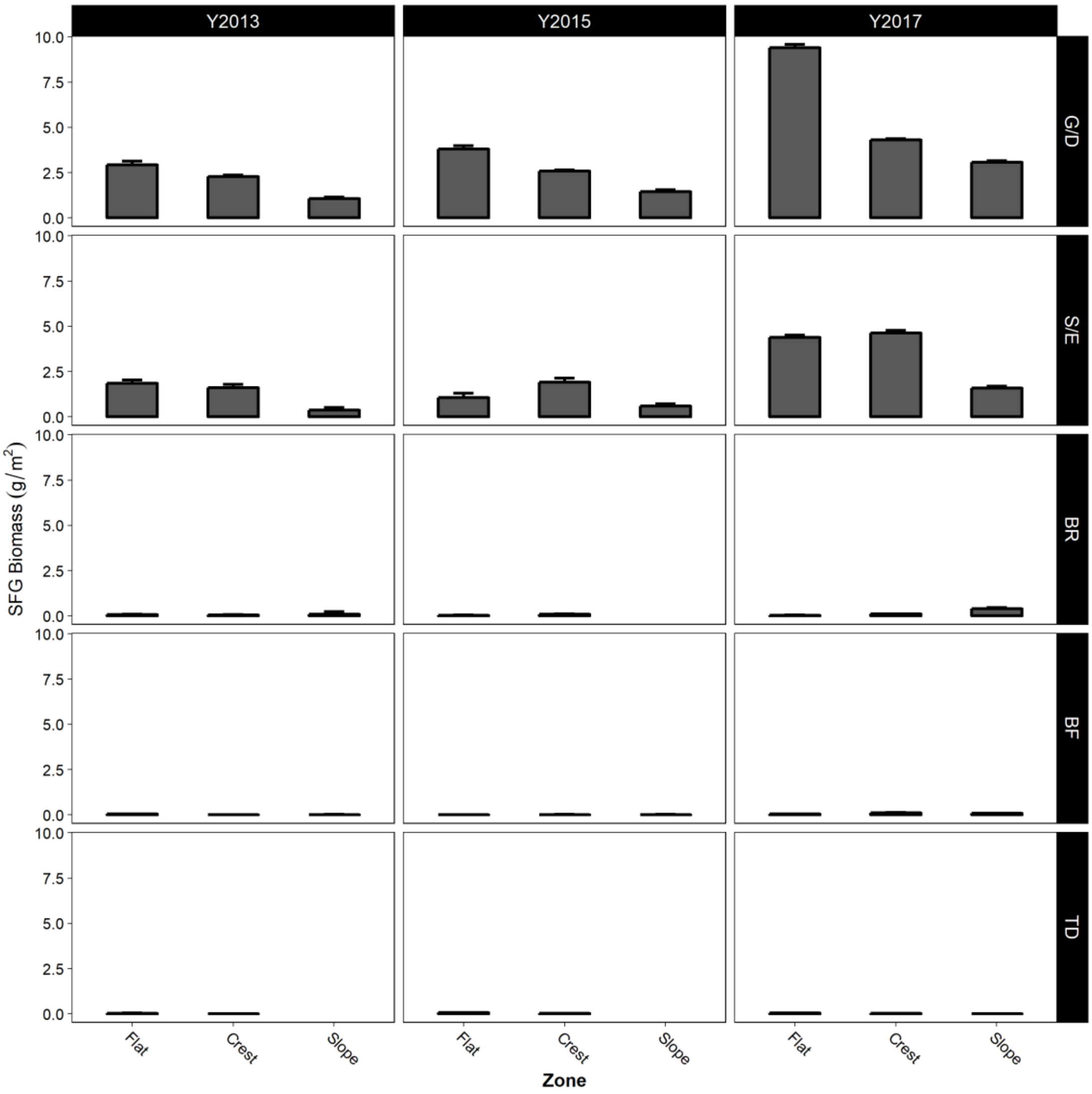


Figure 10. Secondary functional group biomass (g/m^2±SE) across reef zones (flat, crest and slope) and years (2013, 2015 and 2017). G/D = Grazer/detritivores, S/E = Scrapers/Small excavators, BR = Browsers, BF = Benthic Feeders and TD = Territorial Damsels.

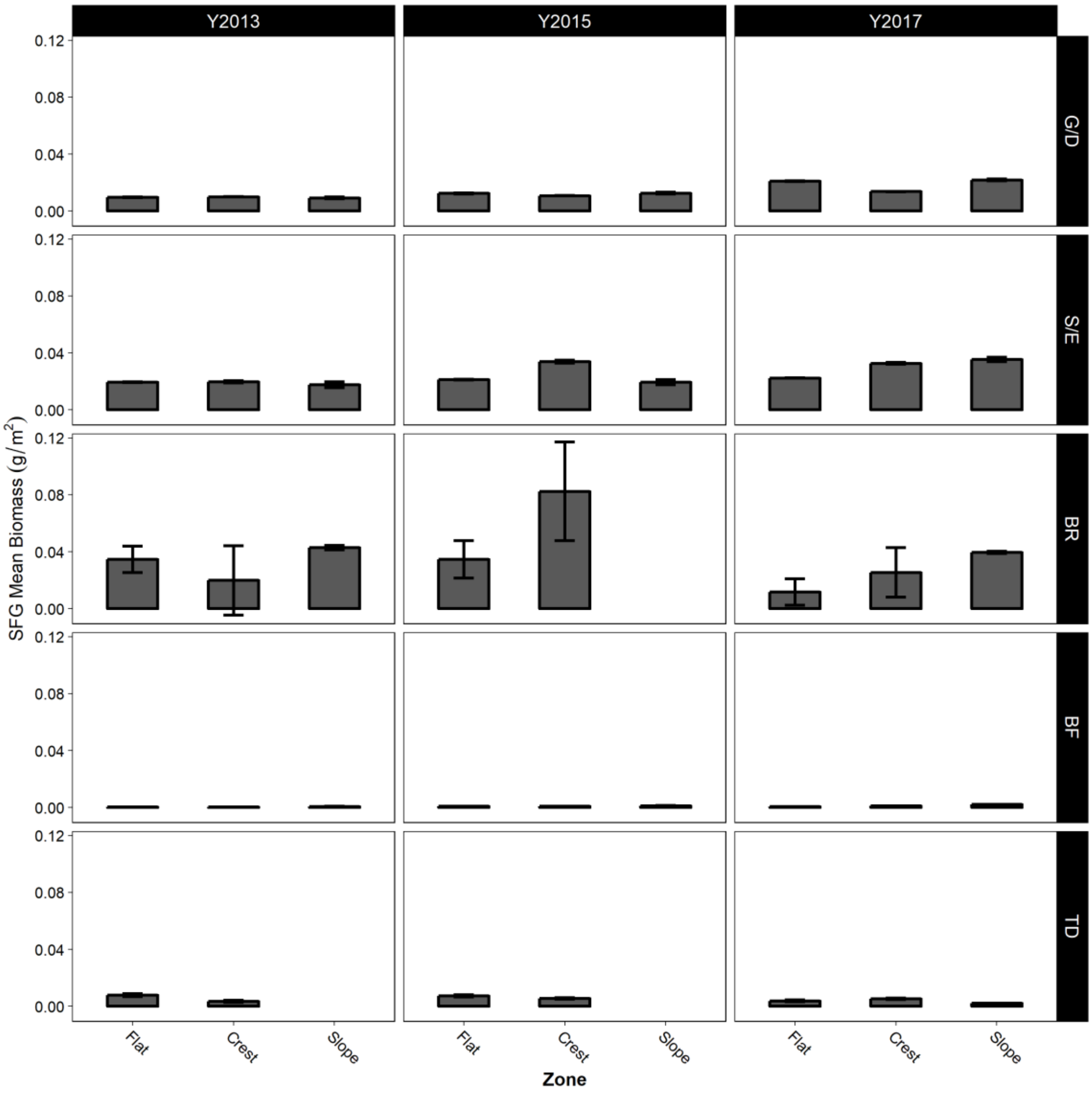


Figure 11. Secondary functional group mean biomass (g/ m^2 ±SE) across reef zones (flat, crest and slope) and years (2013, 2015 and 2017). G/D = Grazer/detritivores, S/E = Scrapers/Small excavators, BR = Browsers, BF = Benthic Feeders and TD = Territorial Damsels.

Benthic drivers of herbivore abundance and biomass

Overall, models which used fish abundance were favoured in model selection, with AIC scores much lower than models created using fish biomass (Appendix V).

Herbivore abundance model revealed that five out of seven of the modelled benthic coefficients had positive effects on herbivore (Figure 12A). Sand had a positive relationship with herbivore abundance and was highly significant among the computed benthic types abundance (P = <0.01; pseudo R^2 = 0.38; y = 0.20). However, sponge had a significant negative relationship (P = <0.05; pseudo R^2 = 0.38; y = – 0.34) on herbivore abundance and algae modelled to have a slightly larger, significant negative relationship (P = <0.05; pseudo R^2 = 0.38; y = – 0.35).

Benthic Feeders' abundance model revealed that four out of seven of the modelled benthic coefficients had positive effects on Benthic Feeders' abundance (Fig. 32A). Sponge (P = <0.01; pseudo R^2 = 0.61; y = – 0.87) and algae (P = <0.05; pseudo R^2 = 0.61; y = – 0.59) both had significant negative relationships; with sand (P = <0.05; pseudo R^2 = 0.61; y = 0.29) having a positive significant relationship with benthic feeder abundance.

Grazer/Detritivore abundance model showed that two out of seven of the modelled benthic coefficients had a negative relationships with Grazer/Detritivore abundance (Fig. 18B). Sand (P = <0.01; pseudo R^2 = 0.28; y = 0.20) soft coral (P = <0.01; pseudo R^2 = 0.28; y = 0.20) and rubble (P = <0.01; pseudo R^2 = 0.28; y = 0.15) had highly significant positive relationships with Grazer/Detritivore abundance. Algae revealed a comparatively weaker negative relationship towards abundance (P = 0.29; pseudo R^2 = 0.28; y = 2.22 - 0.13).

Scrapers/Small Excavators' abundance model revealed that four out of the seven modelled benthic coefficients had a negative relationship Scrapers/Small Excavators' abundance (Figure 12D). Soft coral (P = <0.05; pseudo R^2 = 0.28; y = 0.28) was the only significant coefficient and had a positive relationship with abundance; algae revealed a negative and near significant relationship with abundance ($P = 0.05$; pseudo $R^2 = 0.28$; $y = - 0.41$).

Modelled benthic variables had variation across secondary functional groups, with only sponge and algae showing a consistent negative relationship across groups. Sand and rubble had consistent positive relationships across groups (Appendix V).

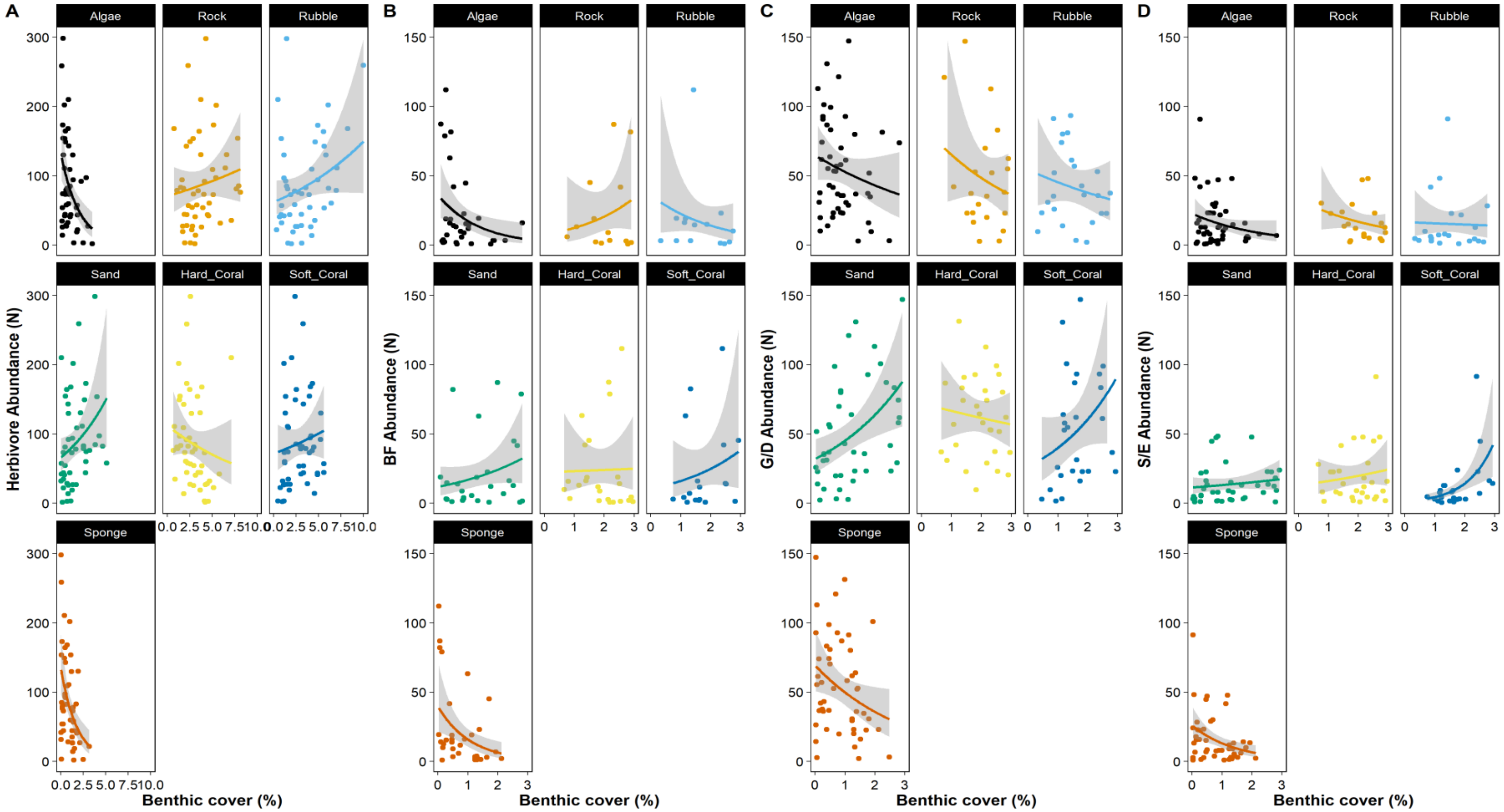


Figure 12. Scatterplots of benthic percentage cover (%) and (A) herbivore abundance (N), Secondary functional groups; (B) Benthic Feeders abundance (N), (C) Grazer/detritivore abundance (N) and, (D) Scraper/small excavator abundance. Lines = fitted negative binomial regression value ± SE. Note varying scale on the x-axis

Community analyses

The sub-communities of total fish in 2017 was found to be more dissimilar than the communities of 2013 and 2015; with these sub-communities were closer in similarity Figure 13A). Across reef zones, slope communities were more dissimilar compared to the reef crest and flat. Herbivores communities in 2013 and 2015 again were found to be more similar to each other than in 2017. Over the reef zones, communities were not dissimilar with the slope overlapping both the reef flat and crest (Figure 13B). Secondary functional group communities revealed that slope communities were more dissimilar to those found at the reef flat and crest. Across the years, in 2015 the reef slope community was found to highly dissimilar to the slope communities of 2013 and 2017 (Figure 13C).

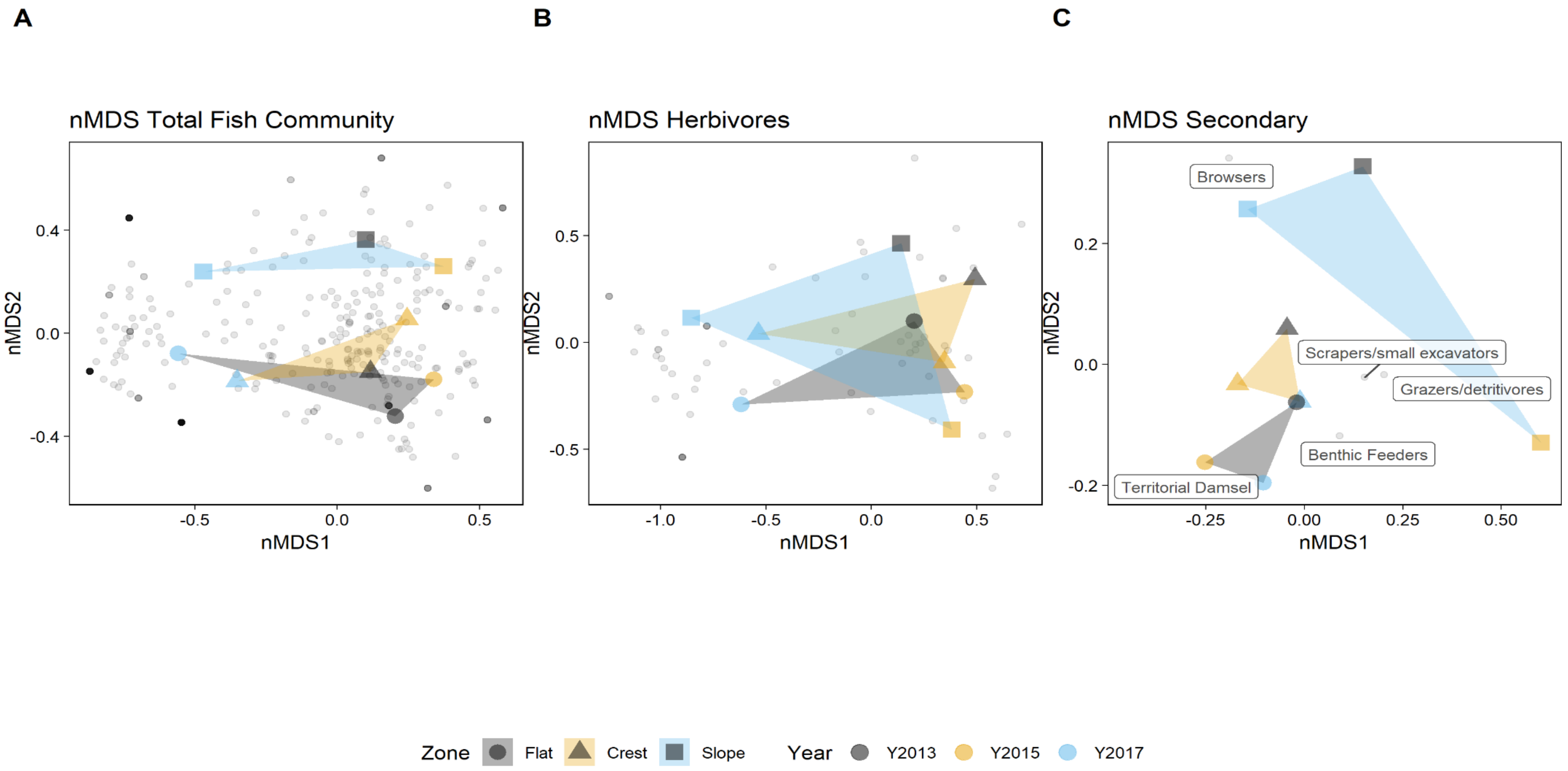


Figure 13. nMDS plots of (A) total fish community (stress = 0.13), (B) herbivores (stress = 0.06) and (C) secondary functional groups (stress = 0.06) across reef zones (flat, crest and slope) and years (2013, 2015 and 2017). Note varying scales on x and y axes.

Secondary functional group partitioning

In order to disentangle and partition the functional roles of herbivores and the secondary functional groups, we examined the community structure of each group and the contributing fish families and species. Recorded individuals within the secondary functional groups were made up of 64 species that fall into 6 fish families; Acanthuridae, Ephippidae, Pomacanthidae, Pomacentridae, Scaridae and Siganidae. Pomacentridae, were the sole families for Benthic Feeders and Territorial Damsels, with Scaridae the only family in Scrapers/Small Excavators. Browsers were formed of Acanthuridae and Ephippidae, where Grazer/Detritivores were formed of Acanthuridae, Pomacanthidae and Siganidae.

Table 5 displays the number of species represented under each secondary functional group. “Overall” within each year represents the number of distinct species recorded within each secondary functional group. Grazers/detritivores, were the group found with the most number of distinct species across all years, followed by scrapers/small excavators. Benthic feeders and Territorial damsels were represented by a low number of species across the years. Browsers had only one distinct species recorded in 2013 and 2015, jumping to four in 2017.

Table 5. Summary of total number of species recorded within each secondary functional groups found within the herbivore guild, in the years 2013, 2015, 2017 and across reef zones. Overall, represents the number of unique species recorded within each group in each year.

Secondary Functional Group	2013				2015				2017			
	Flat	Crest	Slope	Overall	Flat	Crest	Slope	Overall	Flat	Crest	Slope	Overall
Benthic Feeders	2	3	2	3	1	1	1	1	6	4	3	6
Browsers	1	1	1	1	1	1	0	1	2	3	2	4
Grazers/detritivores	11	10	10	15	9	10	12	13	18	20	18	26
Scrapers/small excavators	10	7	6	11	8	7	6	10	15	14	12	18
Territorial Damsel	1	1	0	1	2	1	0	2	3	3	1	4

Species abundance across zones (ANOSIM: R = 0.523, P = <0.05) were more explanatory for community dissimilarity than year (ANOSIM: R = 0.276, P = 0.06). SIMPER analyses revealed the most influential species of dissimilarity across reef zone groups (Table 6). Species found to contribute most to abundance assemblage dissimilarity were found with the secondary functional groups of Grazer/detritivores, Benthic feeders and, Scrapers/small excavators. Territorial damsels and Browsers were found to contribute minimally to abundance assemblage dissimilarities across reef zone. *Ctenochaetus striatus* was found to be the most influential species across all reef zone dissimilarities.

Table 6. SIMPER analyses summary of the cumulative contribution of most influential species between reef zones. Species listed contribute to up to 72% of community dissimilarities.

Reef Zone	Secondary Functional Group	Family	Species	% Cumulative contribution
Crest_Flat	Grazer/detritivores	Acanthuridae	*Ctenochaetus striatus*	17.16
	Benthic Feeders	Pomacentridae	*Chrysiptera springeri*	32.66
	Benthic Feeders	Pomacentridae	*Chrysiptera cyanea*	44.66
	Benthic Feeders	Pomacentridae	*Chrysiptera glauca*	53.66
	Grazer/detritivores	Acanthuridae	*Ctenochaetus binotatus*	57.89
	Benthic Feeders	Pomacentridae	*Chrysiptera rex*	61.96
	Grazer/detritivores	Acanthuridae	*Zebrasoma scopas*	65.64
	Scrapers/small excavators	Scaridae	*Chlorurus sordidus*	69.16
	Benthic Feeders	Pomacentridae	*Chrysiptera parasema*	72.14
Crest_Slope	Grazer/detritivores	Acanthuridae	*Ctenochaetus striatus*	24.60
	Benthic Feeders	Pomacentridae	*Chrysiptera glauca*	37.48
	Grazer/detritivores	Acanthuridae	*Zebrasoma scopas*	46.02
	Scrapers/small excavators	Scaridae	*Chlorurus sordidus*	53.40
	Scrapers/small excavators	Scaridae	*Chlorurus bleekeri*	58.11
	Benthic Feeders	Pomacentridae	*Chrysiptera rex*	62.56
	Benthic Feeders	Pomacentridae	*Chrysiptera springeri*	66.40
	Grazer/detritivores	Acanthuridae	*Ctenochaetus binotatus*	69.34
	Scrapers/small excavators	Scaridae	*Scarus psittacus*	71.07
Flat_Slope	Grazer/detritivores	Acanthuridae	*Ctenochaetus striatus*	30.81
	Benthic Feeders	Pomacentridae	*Chrysiptera springeri*	42.63
	Benthic Feeders	Pomacentridae	*Chrysiptera cyanea*	53.34
	Scrapers/small excavators	Scaridae	*Chlorurus sordidus*	59.31
	Grazer/detritivores	Acanthuridae	*Zebrasoma scopas*	64.88
	Benthic Feeders	Pomacentridae	*Chrysiptera rex*	68.41
	Benthic Feeders	Pomacentridae	*Chrysiptera glauca*	71.49

Pooled across reef zones and years, overall secondary functional groups density and biomass was dominated by one species; *Ctenochaetus striatus* found within the Grazer/Detritivore group (Appendix VI). *Ctenochaetus striatus* was the most abundant (N=1624), with a density of 0.0425 ± 5.60E^{-}05 (no. /m^{2}). This was followed by *Chrysiptera springeri* (0.0317 ± 6.82E^{-}04 no. /m^{2}), *Chrysiptera glauca* (0.0199 ± 4.10E^{-}04 no. /m^{2}), and, *Chrysiptera cyanea* (0.0114 ± 3.66E^{-}04 no. /m^{2}) species all within the Benthic Feeders secondary functional group.

Biomass was found to also be highest in *Ctenochaetus striatus* 0.467 ± 1.88E^{-}03 (no. /m^{2}). This was followed closely by *Siganus lineatus* (0.455 no. /m^{2}), two species of scraper/small excavators were recorded with the next highest biomass; *Scarus psittacus* (0.198 ± 2.89E^{-}03 no. /m^{2}) and *Chlorurus sordidus* (0.195 ± 2.21E^{-}03 no. /m^{2}).

The top six species with the highest mean biomass differ from the highest density and highest biomass species. Noticeably Siganus spp. are present among the species with the highest mean biomass within Grazer/Detritivores, but have very low density. Browsers have a markedly large mean biomass, however, contribute very low proportions of density and biomass. Table 7 summaries the top six species with the highest mean biomass among Grazer/Detritivores and Scrapers/Small Excavators.

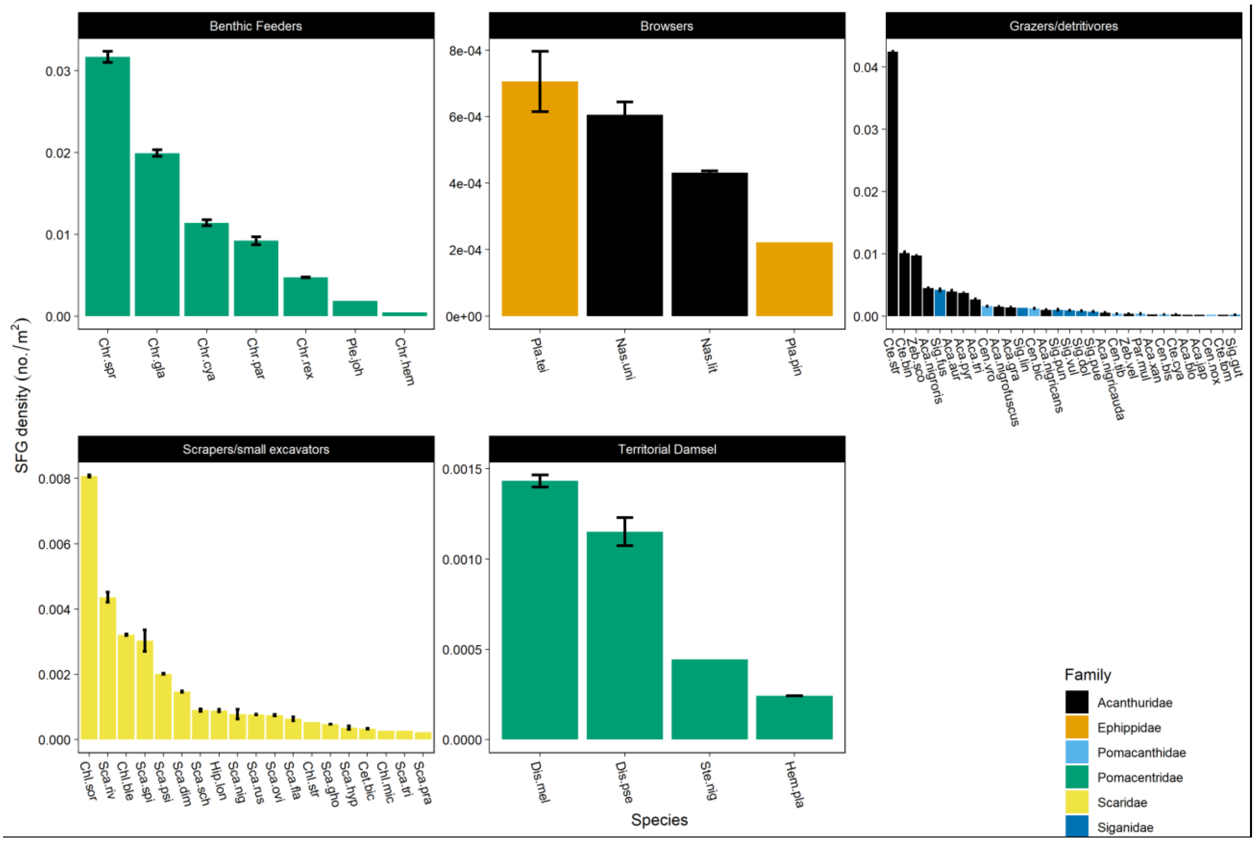


Figure 14. Species density (no. /m^2 ± SE) within herbivore secondary functional groups, grouped by family. Note varying scale on the y- axes.

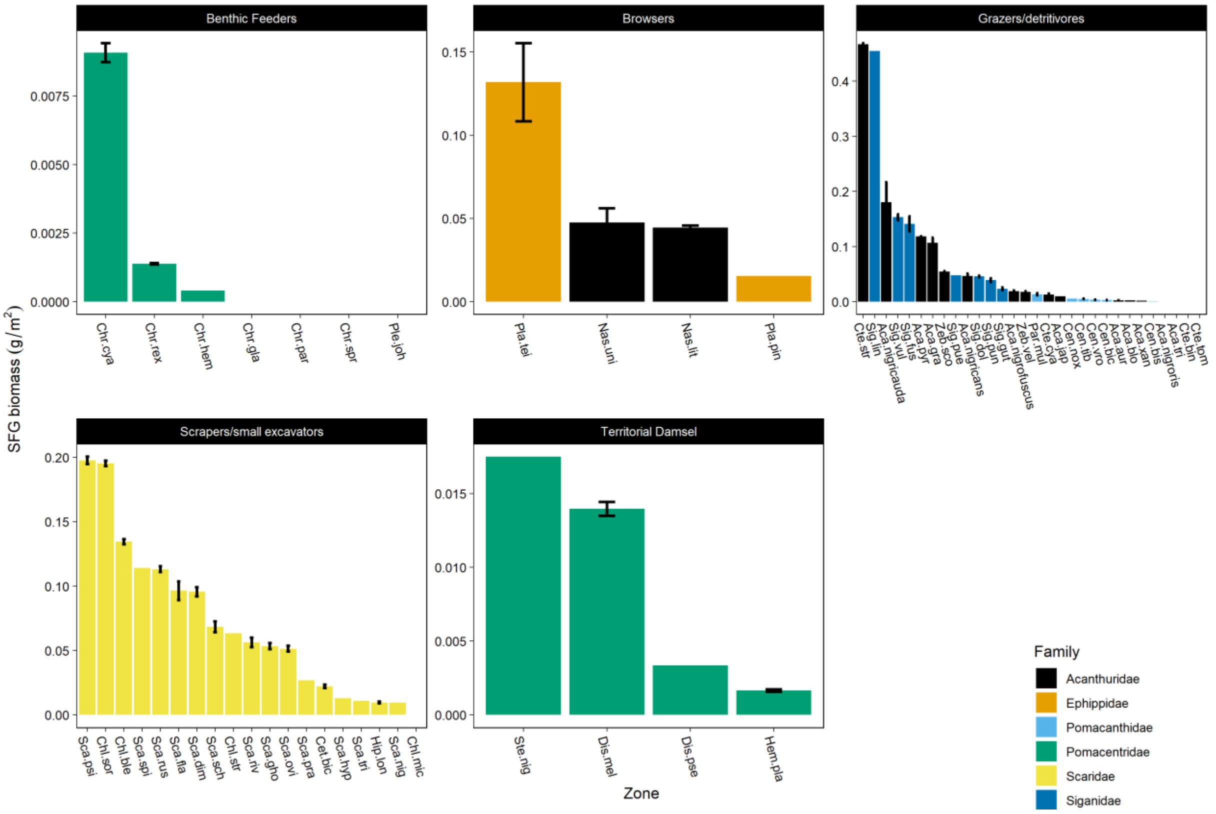


Figure 15. Biomass (g/ m^2 ±SE) of species with herbivore secondary functional groups, grouped by family. Note varying scale on the y- axes.

Table 7. Summary of the top six species with the highest mean biomass and standard error within secondary functional groups of Grazer/Detritivores, Scrapers/Small Excavators and all species within browsers.

		Mean biomass (g)	Standard Error
Grazer/Detritivores	*Siganus lineatus*	341.12	95.64
	Acanthurus nigricauda	327.83	208.30
	Siganus vulpinus	268.47	27.57
	Acanthurus auranticavus	195.43	10.95
	Siganus puellus	146.81	72.25
	Acanthurus grammoptilus	106.75	19.42
Scrapers/Small Excavators	*Chlorurus bleekeri*	168.25	21.29
	Scarus oviceps	157.15	26.52
	Scarus flavipectoralis	151.18	37.36
	Scarus russelii	150.42	25.39
	Scarus schlegeli	142.72	15.96
	Scarus ghobban	141.26	48.49
Browsers	*Platax teira*	210.07	30.76
	Naso lituratus	125.44	31.68
	Naso unicornis	78.51	21.66
	Platax pinnatus	69.59	-

Discussion

The functional role of herbivory

Herbivore functional role was investigated through a herbivore exclusion experiment and revealed that the grazing fish community controlled algae through top-down processes (Littler *et al.*, 2006; Burkepile and Hay, 2008; Smith *et al.*, 2010; Kelly *et al.*, 2017). The removal of grazing by herbivorous fish saw a significant increase in algae cover (Jessen *et al.*, 2012), with macro-algae becoming the dominant benthic type recorded within the fully caged treatments similar to experiments conducted in the Caribbean and Great Barrier Reef (Burkepile and Hay, 2006; Hughes *et al.*, 2007a).

Herbivore exclusion experiments have been widely used to investigate the functional role of grazing activity and the response of algae on coral reefs. Hughes *et al.*, (2007b) excluded areas of 100m$_{-}^{2}$ on the lee side of a fringing reef on the Great Barrier Reef for 30 months and found that tall 3m *Sargassum* stands dominated the exclusion zone up to 91% cover. Doropoulos *et al.*, (2017) excluded herbivory on 500 cm$_{-}^{2}$ of the reef using recruitment tiles and found over 17.5 months of exclusion, algae-dominated in reefs with high wave exposure. Though the scale of this experiment was limited to relatively small patches of reef, the findings were still similar to those of large-scaled and longer-term experimental periods (Burkepile and Hay, 2006; Hughes *et al.*, 2007a; Holbrook *et al.*, 2016; Doropoulos *et al.*, 2017).

The succession of the benthos that follows a disturbance has proven that macro-algae can outcompete hard coral (Fox and Bellwood, 2008a). Though algae was found to be the dominant benthic type in fully caged treatments after 12 months, I also found an increase in ascidians and CCA. In side treatments, where the cage would exclude grazing activity to the reef from possible herbivorous invertebrates that move laterally along the reef, I found an increase in CCA, sponge and hard coral. Suggesting that algal herbivory comes from directly above the substratum and that herbivores that access the reef laterally are responsible for controlling CCA, sponge and hard coral growth. This shows that utilising different orientations to the access the reef for grazing activity by herbivorous fish and invertebrates' can influence the benthic structure through different feeding strategies (Fox and Bellwood, 2013), and is evident that herbivorous grazing from fish directly above the substratum is controlling algal biomass.

The composition of the algae that responded to herbivore exclusion is additionally important, as many algae have defences against herbivory, e.g. *Halimeda* is a calcifying alga which is suspected to deter herbivore grazing (Castro-Sanguino *et al.*, 2016). Thus, the timescales of macro-algae development are important to regard when looking at long-term changes. There was evidence of seasonal patterns and/or successional mechanisms among the algae communities. The dominant algae type varied across the exclusion period, I observed that in one cage areas covered by largely by *Halimeda* at 9 months was overgrown with filamentous algae by 12 months, this could be due to changes in seasonal productivity of alga (Duran *et al.*, 2016).

This experiment did not remove all herbivory from the exclusion areas e.g. small fish and invertebrate grazers such as crustaceans and urchins smaller than 19mm would be able to access the algae. This highlights the functional roles of the grazing fish community and their dietary demands, in controlling dominant of macro-algae stands. It could be that only large fish have foraging efforts high enough to limit algal growth. In the Wakatobi reefs, there is no evidence of regime shifts from desirable coral dominated to degraded and less desirable algae-dominated states. This is likely due to the diversity, abundance and functional role of grazers, found in this region.

Benthic community drivers of herbivore abundance and biomass

In complex systems, fish community structure and natural benthic habitats are factors in the underpinning mechanistic processes of herbivore and algae dynamics (Loffler *et al.*, 2015; Gil and Hein, 2017), in that, variation in fish assemblages will respond to benthic community assemblages and vice versa.

Natural stands of algae cover in the Wakatobi has been recorded at very low levels across the reef zones, however, there was an increase of algae cover recorded in 2015. It has been observed that the bleaching event that was a consequence of the El Niño, did not affect the reefs in the Wakatobi to the extent that was found in the GBR (Rodgers *et al.*, 2017). In the Wakatobi, the biomass and abundance of herbivores increase when algae cover decreases, similar to a study that investigated the spatial patterns of macro-algae consumption found that areas of low cover and biomass of macro-algae and the presence of unpalatable species had greater herbivore biomass (Vergés *et al.*, 2011).

Algae cover had significant negative relationships with abundance and biomass across herbivores, which is supported by similar studies in the GBR (Wismer *et al.*, 2009). Models using herbivore abundance were better explained by benthic types over biomass.

Algae showed to have negative effects on herbivore biomass and abundance though considered to be their main food resource where you may expect an increase in biomass and abundance due to increased resources. A caveat of the benthic surveys is the species and composition of algae assemblages were not recorded in this study. This could indicate that the recorded algae in the Wakatobi are that of mainly unpalatable macro-algae such as *Halimeda* spp., *Turbinaria* spp. and *Amphiroa* spp. Studies of macro-algae have demonstrated that natural stands of macro-algae are relatively unpalatable; and herbivore exclusion experiments shifted the composition of algae towards relatively palatable macro-algae (Thacker *et al.*, 2001). In contrast, in my exclusion experiment, I observed that the composition of algae ranged between palatable fleshy macro-algae (*Dictoya* spp.) and filamentous algae to less palatable species (*Halimeda* spp., *Turbinaria* spp. and *Amphiroa* spp.).

Within the benthic community, the models revealed that sand was the main driver in the variation of herbivore abundance with a positive relationship. As herbivores are traditionally associated with algae, many studies have revealed that taxonomy and guild classification alone poorly predict the complex interactions between herbivores and algae (Burkepile and Hay, 2011; Bellwood *et al.*, 2019).

Models for the secondary functional groups revealed that benthic drivers varied across benthic feeders, grazer/detritivores and scrapers/small excavators. Sponge was found to increase benthic feeder abundance, this could be due to the more plastic qualities of damselfish feeding behaviour, or even for habitat availability or refuge. Additionally, sand was also found to increase abundance and whereas algae decreased abundance.

Grazer/detritivores were driven by sand, soft coral and rubble. This combination of benthic drivers is likely due to the species found with this secondary functional group. Sand in this instance represents the sediment on the benthos which contains not only sand but detrital material, microbes and other organic material which provides a resource of nutrition (Goatley *et al.*, 2016). Additionally, this would suggest that there is a major misrepresentation of available food resources for this functional guild. Moreover, many studies focus on the dynamics of the EAM and found that some Grazer/Detritivore species target the detritus as it much more nutritionally valuable compared to algae (Tebbett *et al.*, 2017c). This could indicate that this guild has plastic feeding characteristics and increase the likelihood of species ability to move from one resource to another. Species within this group have been found to remove particulate matter and be influenced by sediment dynamics such as *Ctenochaetus* spp. (Tebbett *et al.*, 2017c, 2018). Additionally, rubble can be indirectly associated with the resource availability of the epilithic algae matrix, which many species found within this group feed upon (Hoey *et al.*, 2013). Rubble provides a hard substrate which enables the EAM to develop and has been found to be highly with detritivorous species (Osuka *et al.*, 2016). Kuo *et al.*, (2015) found a group of *Signaus fuscescens* feeding on algae overgrowing soft corals and consequently feeding into the tissue of *Sarcophyton.*

Scrapers/small excavator models revealed that soft coral drove the most variation in abundance. Studies have found that parrotfish density is driven by benthic communities, however in contrast to our findings. Russ *et al.*, (2015) found that increased dead substrata such as dead coral, rubble and, rock alongside decreased hard coral cover increased parrotfish density. They also found soft coral to affect density however across their study sites these effects were both positive and negative. This could indicate that the combination of the whole benthic community assemblage is important to variation in abundance of scraper/small excavators in the Wakatobi.

Community Partitioning

Across the total fish community, distinctions across the reef zone and years were revealed. With communities at the reef slope being more dissimilar to those at the reef flat and crest. Communities that took into account species within the herbivore guild did not reveal variation across the reef zones. However, when divided into secondary functional groups, clear distinctions across the reef zones were found, with browsers being found at the reef slope. Additionally, the community at the reef slope in 2015 was dissimilar to those in 2013 and 2017, due to the presence of fewer browsers. Between reef zones, community dissimilarity was best explained across all reefs zone by *Ctenochaetus striatus*. Reef zones dissimilarity have been observed among herbivore functional groups, with grazer/detritivores and scraper/small excavators present more from the reef crest to slope. Damsel benthic feeders being found on the reef flat to crest. From the flat to crest dissimilarities were of a mix of Benthic feeders, Grazer/detritivores and scraper/small excavators.

These reef associations could be a combination of benthic composition and topography found in the Wakatobi. With the reef flats being composed more of hard coral patches and hard substrata from which territorial damsels can farm and harvest algae in addition to providing refuge to benthic feeders. Grazer/detritivores and scraper/small excavators ranged across all reef zones, however, favoured exposed sandy and rubble patches from feed upon. These areas are highly available in the Wakatobi due to the history of destructive blast fishing (Exton *et al.*, 2010). Browsers found in low numbers across few species were mainly found upon the reef slope, due to the elusive nature of *Naso* spp. (Mumby *et al.*, 2013) and *Platax* spp. favouring deeper waters.

Functional roles and partitioning within secondary functional groups

Benthic Feeders were found at greater densities than territorial damsels, this could be due to the limited number of desirable habitats in which territorial damselfish settle and farm (Hata and Ceccarelli, 2016). They both contributed to very low proportions of biomass to the total herbivore community. This could be an indication of a low level of functionality, however, if we consider the scale of their grazing activity, and unique feeding behaviours it may suggest that they have low redundancy within each group.

Browsers were found to have a very low density and biomass among the herbivore community (Nash *et al.*, 2013; Martin *et al.*, 2017b), however, they do have comparatively large mean biomass among the secondary functional groups. Browsers were represented by few species (*Platax teira, Naso lituratus, Naso unicornis* and *Platax pinnatus*), the low richness within the group could indicate a low level of functional redundancy within the Browsers (Nash *et al.*, 2013).

Macro-algae and seagrass were recorded at very low levels across all years and zones. This could indicate that the abundance and biomass of Browsers on the reefs of the Wakatobi, is at a level where macro-algae stands are maintained to desirable levels. Therefore to control macro-algae in coral dominated reefs, requires a low level of functional algae browsing.

Personal observations of the Wakatobi reefs through remote video footage have revealed that grazing activity by browsers can remove up 100% of algae cover a 225 cm^2 area of palatable macro-algae (*Dictoya* spp.) over a 3 hour period, providing macro-algae removal potential of up to $18m^2$ of macro-algae within a 24 hour period. The low abundance and biomass of browsers recorded in the Wakatobi could be attributed to the underwater visual census using the SVS methodology, as similar studies have found that browsers e.g. *Naso* species are particularly wary of divers (Mumby *et al.*, 2013; Ford *et al.*, 2018) and could be misrepresented in these studies.

Overall, Browsers provide a critical functional role in the reef by controlling established macro-algae stands. However, as they are represented by few species, have larger mean biomass, low redundancy and operate on mid-scale movements within the reef, they could be highly vulnerable to disturbances, and their loss could result in ecologically significant impacts (Nash *et al.*, 2013).

Scrapers/Small Excavators had relatively low density but similar to that of Benthic feeders in 2013 and 2015, however, had lower densities comparably in 2017. In contract, the biomass of this group was highest after the Grazer/detritivores. In the GBR parrotfish were considered to be habitat generalists with biomass being influenced weakly by benthic types (Gust, 2002), this is in agreement with the regression analyses where biomass models were much weaker than that for abundance, and biomass was variable across sites ranging 0.04 g to 1072.22 g across all years.

Grazer/Detritivores were the most abundant of all and had the greatest biomass across secondary functional groups. This group was also the most species-rich with 30 species recorded across 3 families.

On the Wakatobi reefs the majority of functional grazing activity is provided by the Grazer/detritivores and in particular, species of the Acanthuridae family. Highly abundant *Ctenochaetus striatus* and *C. binotatus* have been found to be predominantly detritivorous and uptake sediment and animal material from the EAM, with specialised teeth and remove little algae from the reef (Steneck *et al.*, 2017), however studies have found small amounts of algae in their digestive tract (Choat *et al.*, 2002). *C. striatus* has been found to be one of the most abundant species recorded, not only in my study but across studies throughout the species range (Tebbett *et al.*, 2018). A recent study aimed to clarify the role of *C. striatus* and found that this species uses a “dustpan and brush” mechanism to facilitate feeding upon particulate material in algae turfs (Tebbett *et al.*, 2018). Additionally, *C. striatus* is a highly selective feeder and overall did not reduce mature algae turf stands, however, small amounts of filamentous algae were found in their digestive tracts (Tebbett *et al.*, 2017b).

Zebrasoma scopas, Acanthurus pyroferus, Acanthurus auranticavus, and *Acanthurus nigroris* were among the top six species for density after *C. striatus* and *C. binotatus. Siganus lineatus, Acanthurus nigricauda, Siganus vulpinus, Signaus fuscescens,* and *Acanthurus pyroferus* were among the top six species for biomass after *C. striatus* within Grazer/Detritivores and are largely herbivorous, feeding upon the EAM.

Z. scopas has been identified as a true grazer and algal browser and crops turfing algae from the EAM, studies on stomach content have found that this species crops down stands of red thallate algae and have been found to be selective towards green and red turfing algae (Choat *et al.*, 2004; Cheal *et al.*, 2012). *A. pyroferus* has been classed as an algal browser that specifically crops turf and/or macro-algae, ingesting little of the other components that make up the EAM (Cheal *et al.*, 2012). *A. auranticavus* and *A. nigroris* are found to be Grazer/Detritivores and feed upon the EAM, ingesting not only algal turf but additionally sediment, detritus, microalgae and most likely macro-algae before they become established (Cheal *et al.*, 2012). The variation in target algae species for consumption reveals that functional grazing is partitioned across very fine scales and that levels of redundancy are potentially extremely low within this group, even though it is the most species-rich and abundant group where we would expect high levels of redundancy.

Species in the Siganidae family were found to have density but relatively high biomass in the Grazer/Detritivore group, and had larger mean biomass among other Acanthuridae spp. *Siganus lineatus* is an algal browsers species that form schools rather than pairs (as is common in other species such as *Siganus vulpinus* and *Siganus puellus;* see Green and Bellwood, 2009; Cheal *et al.*, 2010, 2012). These species are not highly represented across the reefs of the Wakatobi, but *Siganus fuscescens* was the most abundant and *Siganus lineatus* recorded the highest biomass among the *Siganus* species.

Studies have found that *Siganus* species have little overlap in foraging areas due to their specialisation of feeding in crevices (Fox and Bellwood, 2013). Understanding that this species can provide a unique function on the reefs, allows us to predict the ecological significance that the decline of this group may entail. Low functional redundancy is evident among these species and consequently, their ecological value is increased, therefore the management of this group should be enforced to ensure regime shifts are prevented (Cheal *et al.*, 2012), from algae growing in crevices require specialist foragers to control them.

Historically the level of algae recorded in the Wakatobi has been relatively low, this could be due to the fact that macro-algae is very patchy. Therefore detection of algae along transects is low, but the algae records do not encompass the EAM, where algae stands are low/small (Wilson *et al.*, 2003) and very therefore difficult to detect visually (but numerous). Studies that have quantified the EAM have used recruitment tiles or settlement blocks, that have been then processed in the lab for dry weights of the EAM

(Scott and Russ, 1987; Marshell and Mumby, 2015). Other methods used to quantify the EAM have been to record turf algae <10mm as the EAM. The EAM is a critical resource on the reef and is ubiquitous across the system (Wilson *et al.*, 2003; Kramer *et al.*, 2012), but clearly, the EAM is underrepresented in this study. We should consider that the EAM is present over most hard substratum and could identify proxies of benthic types to represent this, for example using rock, rubble and dead coral cover could reveal a larger resource for Grazer/Detritivores in the reef system.

Functional redundancy and complementarity

Among the secondary functional groups recorded in this study, it is clear that the functional roles of the Grazer/Detritivores are a major component of the Wakatobi reefs. However, it is evident that the roles across and within groups are highly variable and groups that are represented by a few species have low levels of redundancy. Browsers, Benthic Feeders, Territorial Damsels show low levels of redundancy within their groups due to the low density and biomass spread across a few species. This highlights their importance as few species would be able to replicate the function they provide to the reef. Additionally, Benthic Feeders and Territorial Damsels, serve to increase herbivore biomass across the reef ensuring that this guild is highly represented.

Grazer/Detritivores and Scraper/Small Excavators present higher levels of functional redundancy, however, within both of these groups, the abundance and biomass are skewed towards few species. This suggests that few species play major roles and the remaining species have minor roles in the grazing activity or are highly specialised (Tebbett *et al.*, 2018), for example, *Siganus* species. Species considered to play minor roles are not unimportant and may become the new drivers of function should conditions change (Nyström, 2006).

The herbivore functional guild in the Wakatobi is highly diverse and represented by a considerably higher number of species compared to the composition found bioregions (Bellwood *et al.*, 2019). It raises the question of how these particular species co-exist as seemingly they are in competition for similar and limited food resources. The role of complementarity within these functional guilds and groups have arisen through the specialisation of particular species, i.e. differences in grazing behaviour and morphological and physiological traits may have driven complementary (Burkepile and Hay, 2011) and suggests there may be little functional redundancy though there is high diversity.

In the Caribbean there is evidence that Parrotfish display very little aggression among species and that the overlap of habitat is very small, suggesting very low levels of redundancy (Harborne and Mumby, 2018). We should consider that highly specialised roles such as bio-eroding parrotfish, would be limited in redundancy as these are the primary group which carries out this function through grazing activity and could not necessarily be replaced by species from other secondary functional groups (Green and Bellwood, 2009). Therefore low levels of redundancy mean that functional diversity is highly vulnerable to loss of species and could have significant ecological impacts (Mouillot *et al.*, 2014).

Functional grazing roles are not limited to the functional guild of herbivores, but most likely spread across omnivores and facultative corallivores which provide additional functionality and as such increases functional grazing activity on the reef. For example, from personal observations of remote video footage of triggerfish (*Melichthys vidua*) have been observed to graze and consume turf and macro-algae stands and can provide important controls to algae dominance within the reef on top of herbivores, additionally, *Balistapus undulates* removed significant stands of algae in search of prey. Therefore, we can consider functional grazing activity to follow a gradient within the reef. Loss of species and functions, therefore may not be compensated by similarly grouped species but by more versatile foragers such as species within the omnivore and facultative corallivore guilds.

Due abundances and number of species of herbivorous spanning the functional groups recorded in my study, it is clear that the Wakatobi is resilient towards regime shifts despite the continued removal of herbivore biomass through local fishing efforts. In order to maintain high reef resilience, we need to retain the functional characteristics of grazing fish (Cheal *et al.*, 2013). Additionally, we must consider the complex interactions between fish and benthic community structure; that in order to simply ensure all functional characteristics in herbivorous communities are retained is to maintain the diversity of the entire functional guild (Burkepile and Hay, 2011; Cheal *et al.*, 2012, 2013; Harborne and Mumby, 2018).

Conclusion

This study highlights the importance of the functional roles that grazing fish species provide to coral reef ecosystems in controlling algae through top-down processes. The diversity and composition of grazers found among functional guilds and secondary functional groups are important in regulating the benthic structure.

The emphasis on secondary functional groups reveals the Wakatobi reefs have high resilience to regime shifts, due to high levels of preventative grazing activity provided by the Grazer/Detritivore secondary functional group which controls algae stands before they become established and threaten to outcompete hard corals. Of particular significance is the diversity among herbivores and the functional roles are represented by 64 species, much higher than bioregions which suffer major bleaching events and consequently regime shifts.

However, it is critical to preserve the diversity and abundance of herbivores and grazing fish in coral reef ecosystems and ensure that more directed conservation and monitoring efforts are in place for these groups. I conclude that Acanthuridae and

Siganidae species within the Grazer/Detritivores should be focused on conservation and monitoring efforts. In particular *Ctenochaetus striatus*, *Ctenochaetus binotatus, Zebrasoma scopas, Acanthurus pyroferus, Acanthurus auranticavus, Acanthurus nigroris, Acanthurus nigricauda, Siganus lineatus*, *Siganus vulpinus*, and *Siganus fuscescens.* These species provide the critical roles of preventative functional grazing activity within the reef and are under increasing pressure as herbivore are targeted in local fisheries. It is important to monitor these key species overtime to ensure that the loss of preventative grazing control is not lost and therefore resilience to regime shifts is maintained. It is recommended that fishing efforts should be limited on these key species and further research should focus on the minimum biomass and density required to maintain high reef resilience for future management purposes.

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Appendices

I. Herbivore exclusion experiment

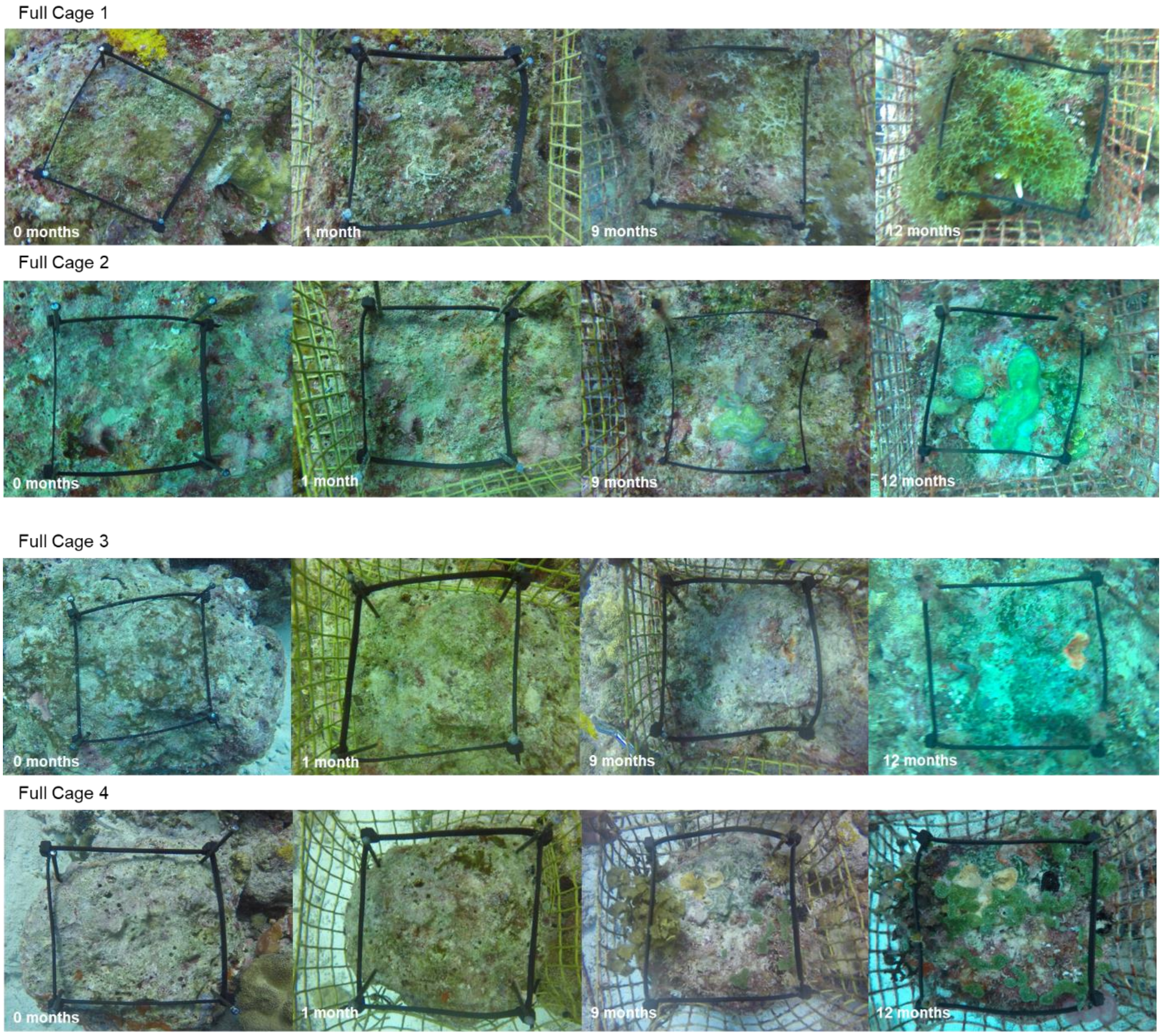
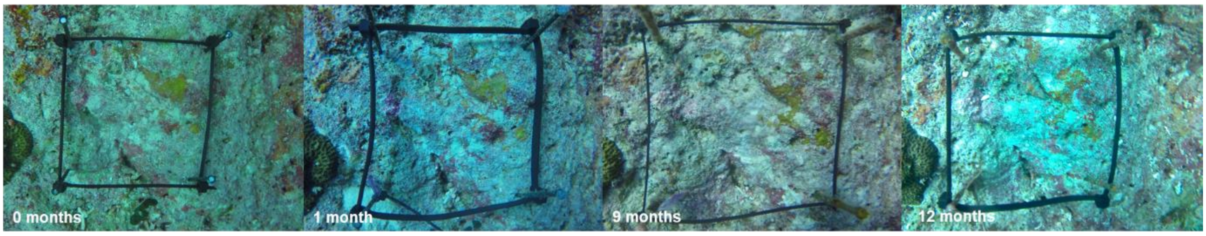


Figure 16. Time series images of herbivore exclusion experiment fully caged treatments.

Control Cage 1



Control Cage 2

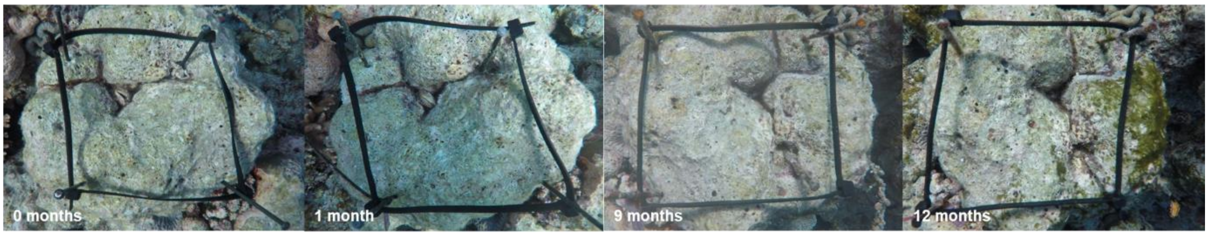
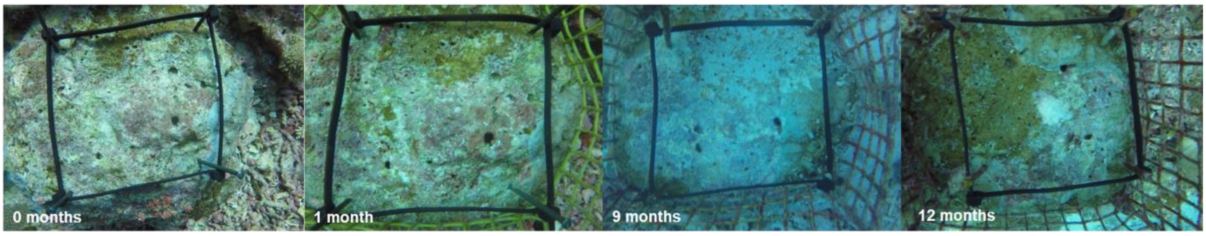


Figure 17. Time series images of herbivore exclusion experiment control treatments.

Side Cage 1



Side Cage 2

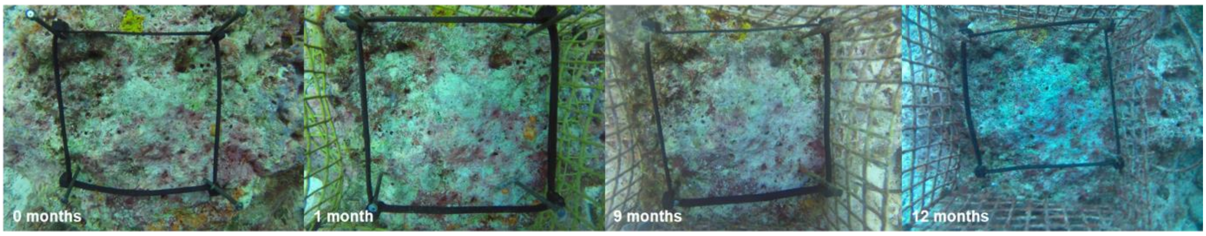
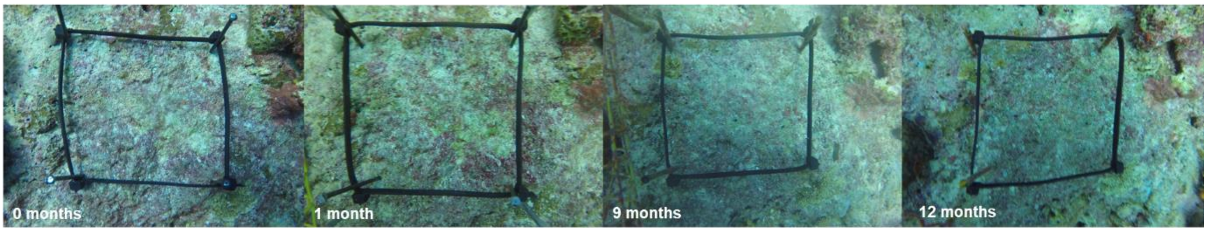


Figure 18. Time series images of herbivore exclusion experiment side treatments.

Top Cage 1



Top Cage 2

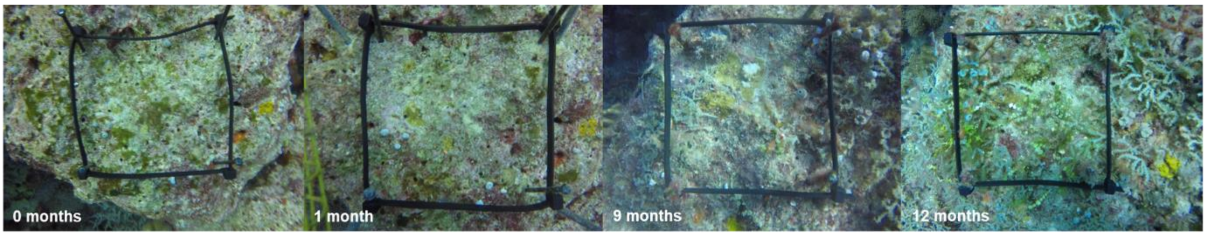


Figure 19. Time series images of herbivore exclusion experiment top treatments.

II. Summary of fish community

Table 8. Summary of all fish recorded in surveys conducted in 2013, 2015 and 2017, classified into secondary functional groups.

Secondary Functional Group	Family	Species	Common Name
Benthic Feeders	Pomacentridae	*Chrysiptera cyanea*	Sapphire devil
	Pomacentridae	*Chrysiptera glauca*	Grey demoiselle
	Pomacentridae	*Chrysiptera hemicyanea*	Azure demoiselle
	Pomacentridae	*Chrysiptera parasema*	Goldtail demoiselle
	Pomacentridae	*Chrysiptera rex*	King demoiselle
	Pomacentridae	*Chrysiptera springeri*	Springer's demoiselle
	Pomacentridae	*Plectroglyphidodon johnstonianus*	Johnston Island damsel
Browsers	Acanthuridae	*Naso lituratus*	Orangespine unicornfish
	Acanthuridae	*Naso unicornis*	Bluespine unicornfish
	Ephippidae	*Platax pinnatus*	Dusky batfish/ Pinnate spadefish
	Ephippidae	*Platax teira*	Longfin batfish
Grazers/detritivores	Acanthuridae	*Acanthurus auranticavus*	Orange-socket surgeonfish
	Acanthuridae	*Acanthurus blochii*	Ringtail surgeonfish
	Acanthuridae	*Acanthurus grammoptilus*	Finelined surgeonfish
	Acanthuridae	*Acanthurus japonicus*	Japan surgeonfish
	Acanthuridae	*Acanthurus nigricans*	Whitecheek surgeonfish
	Acanthuridae	*Acanthurus nigricauda*	Black streak / Black barred surgeonfish
	Acanthuridae	*Acanthurus nigrofuscus*	Brown surgeonfish
	Acanthuridae	*Acanthurus nigroris*	Bluelined surgeonfish
	Acanthuridae	*Acanthurus pyroferus*	Chocolate/Mimic surgeonfish
	Acanthuridae	*Acanthurus tristis*	Indian Ocean Mimic surgeonfish
	Acanthuridae	*Acanthurus xanthopterus*	Yellowfin surgeonfish
	Acanthuridae	*Ctenochaetus binotatus*	Twospot surgeonfish
	Acanthuridae	*Ctenochaetus cyanocheilus*	Short-tail bristle-tooth
	Acanthuridae	*Ctenochaetus striatus*	Striated/Bristletooth surgeonfish
	Acanthuridae	*Ctenochaetus tominiensis*	Tomini surgeonfish
	Acanthuridae	*Zebrasoma scopas*	Twotone tang
	Acanthuridae	*Zebrasoma veliferum*	Sailfin tang
	Pomacanthidae	*Centropyge bicolor*	Bicolor angelfish
	Pomacanthidae	*Centropyge bispinosus*	Coral beauty
	Pomacanthidae	*Centropyge nox*	Midnight angelfish
	Pomacanthidae	*Centropyge tibicen*	Keyhole angelfish
	Pomacanthidae	*Centropyge vroliki*	Pearlscale angelfish
	Pomacanthidae	*Paracentropyge multifasciata*	Barred angelfish
	Siganidae	*Siganus doliatus*	Barred spinefoot
	Siganidae	*Siganus fuscescens*	Mottled spinefoot
	Siganidae	*Siganus guttatus*	Orange-spotted spinefoot
	Siganidae	*Siganus lineatus*	Golden-lined spinefoot
	Siganidae	*Siganus puellus*	Masked spinefoot
	Siganidae	*Siganus punctatissimus*	Peppered spinefoot

	Siganidae	*Siganus vulpinus*	Foxface rabbitfish
Scrapers/Small Excavators	Scaridae	*Cetoscarus bicolor*	Bicolour parrotfish
	Scaridae	*Chlorurus bleekeri*	Bleeker's parrotfish
	Scaridae	*Chlorurus microrhinos*	Blunt-head parrotfish
	Scaridae	*Chlorurus sordidus*	Bullethead parrotfish
	Scaridae	*Chlorurus strongylocephalus*	Roundhead parrotfish
	Scaridae	*Hipposcarus longiceps*	Pacific longnose parrotfish
	Scaridae	*Scarus dimidiatus*	Yellowbarred parrotfish
	Scaridae	*Scarus flavipectoralis*	Yellowfin parrotfish
	Scaridae	*Scarus ghobban*	Blue-barred parrotfish
	Scaridae	*Scarus hypselopterus*	Yellow-tail parrotfish
	Scaridae	*Scarus niger*	Dusky parrotfish
	Scaridae	*Scarus oviceps*	Dark capped parrotfish
	Scaridae	*Scarus prasiognathos*	Greenthroat parrotfish
	Scaridae	*Scarus psittacus*	Palenose parrotfish
	Scaridae	*Scarus rivulatus*	Rivulated parrotfish
	Scaridae	*Scarus russelii*	Eclipse parrotfish
	Scaridae	*Scarus schlegeli*	Yellowband parrotfish
	Scaridae	*Scarus spinus*	Greensnout parrotfish
	Scaridae	*Scarus tricolor*	Tricolour parrotfish
Territorial Damsel	Pomacentridae	*Dischistodus melanotus*	Black-vent damsel
	Pomacentridae	*Dischistodus pseudochrysopoecilus*	Monarch damsel
	Pomacentridae	*Hemiglyphidodon plagiometopon*	Lagoon damselfish
	Pomacentridae	*Stegastes nigricans*	Dusky farmerfish

Table 9. Summary of all fish recorded in surveys conducted in 2013, 2015 and 2017.

Guild	Family	Species	2013	2015	2017
Carnivore	Anthinae	*Pseudanthias dispar*	0	0	118
	Anthinae	*Pseudanthias evansi*	0	0	704
	Anthinae	*Pseudanthias huchtii*	75	134	28
	Anthinae	*Pseudanthias hypselosoma*	0	0	1
	Anthinae	*Pseudanthias pleurotaenia*	14	103	59
	Anthinae	*Pseudanthias squamipinnis*	0	0	1
	Anthinae	*Pseudanthias tuka*	0	2	0
	Aulostomidae	*Aulostomus chinensis*	5	2	1
	Balistidae	*Sufflamen chrysopterum*	7	0	37
	Balistidae	*Sufflamen chrysopterus*	0	2	0
	Carangidae	*Carangoides plagiotaenia*	0	1	0
	Carangidae	*Caranx melampygus*	3	0	7
	Fistulariidae	*Fistularia commersonii*	0	0	1
	Fistulariidae	*Fistularia commersonii*	1	0	3
	Haemulidae	*Pentapodus trivittatus*	0	0	1
	Haemulidae	*Plectorhinchus vittatus*	1	2	9
	Holocentridae	*Neoniphon sammara*	19	6	8
	Holocentridae	*Priacanthus hamrur*	3	0	0
	Labridae	*Cheilinus trilobatus*	19	1	0
	Labridae	*Cheilinus undulatus*	0	0	1
	Labridae	*Cheilio inermis*	0	2	0
	Labridae	*Epibulus insidiator*	4	0	0
	Labridae	*Gomphosus varius*	2	12	5
	Labridae	*Hologymnosus doliatus*	4	0	0
	Labridae	*Oxycheilinus celebicus*	0	0	1
	Labridae	*Oxycheilinus digramma*	3	0	0
	Labridae	*Oxycheilinus unifasciatus*	1	0	0
	Latidae	*Psammoperca waigiensis*	0	0	1
	Lethrinidae	*Gnathodentex aureolineatus*	15	2	1
	Lethrinidae	*Lethrinus erthropterus*	0	0	3
	Lethrinidae	*Lethrinus erythracanthus*	0	0	8
	Lethrinidae	*Lethrinus harak*	1	0	3
	Lethrinidae	*Lethrinus microdon*	0	0	1
	Lethrinidae	*Lethrinus olivaceus*	0	0	1
	Lethrinidae	*Lethrinus ornatus*	0	0	2
	Lutjanidae	*Lutjanus biguttatus*	3	0	4
	Lutjanidae	*Lutjanus bohar*	0	1	4
	Lutjanidae	*Lutjanus decussatus*	1	2	19
	Lutjanidae	*Lutjanus ehrenbergii*	4	3	157
	Lutjanidae	*Lutjanus fulviflamma*	1	0	0
	Lutjanidae	*Lutjanus fulvus*	0	0	8
	Lutjanidae	*Lutjanus monostigma*	0	0	1

	Lutjanidae	*Lutjanus semicinctus*	0	0	3
	Lutjanidae	*Macolor macularis*	0	9	0
	Lutjanidae	*Macolor niger*	0	1	0
	Mullidae	*Mulloidichthys flavolineatus*	48	0	14
	Mullidae	*Mulloidichthys vanicolensis*	0	0	70
	Mullidae	*Parupeneus trifasciatus*	0	1	0
	Mullidae	*Parupeneus barberinus*	9	13	5
	Mullidae	*Parupeneus bifasciatus*	0	0	5
	Mullidae	*Parupeneus trifasciatus*	1	0	0
	Nemipteridae	*Scolopsis bilineata*	21	30	41
	Nemipteridae	*Scolopsis ciliata*	0	8	2
	Nemipteridae	*Scolopsis lineatus*	69	16	93
	Nemipteridae	*Scolopsis margaritifera*	4	5	6
	Nemipteridae	*Scolopsis temporalis*	2	2	13
	Nemipteridae	*Scolopsis trilineata*	0	4	5
	Plotosidae	*Plotosus lineatus*	0	0	1
	Pomacentridae	*Plectroglyphidodon lacrymatus*	26	0	0
	Pseudochromidae	*Labracinus cyclopthalmus*	0	0	1
	Scombridae	*Grammatorcynus bilineatus*	7	0	5
	Scorpaenidae	*Pterois antennata*	1	0	0
	Scorpaenidae	*Pterois volitans*	1	0	2
	Serranidae	*Cephalopholis argus*	4	0	17
	Serranidae	*Cephalopholis formosa*	0	0	1
	Serranidae	*Cephalopholis urodeta*	10	8	10
	Serranidae	*Epinephelus bontoides*	0	0	1
	Serranidae	*Epinephelus chlorostigma*	0	0	1
	Serranidae	*Epinephelus fasciatus*	0	3	0
	Serranidae	*Epinephelus merra*	10	10	5
	Serranidae	*Epinephelus spilotoceps*	0	0	1
	Serranidae	*Epinephelus tauvina*	1	0	2
	Serranidae	*Plectropomus laevis*	0	1	0
	Serranidae	*Variola louti*	0	0	1
Fac Coralivore	Chaetodontidae	*Chaetodon adiergastos*	2	2	0
	Chaetodontidae	*Chaetodon auriga*	1	3	5
	Chaetodontidae	*Chaetodon bennetti*	0	0	1
	Chaetodontidae	*Chaetodon citrinellus*	0	2	0
	Chaetodontidae	*Chaetodon ephippium*	0	3	4
	Chaetodontidae	*Chaetodon falcula*	0	0	1
	Chaetodontidae	*Chaetodon kleinii*	49	68	47
	Chaetodontidae	*Chaetodon lineolatus*	13	0	5
	Chaetodontidae	*Chaetodon lunula*	16	3	0
	Chaetodontidae	*Chaetodon lunulatus*	5	18	37
	Chaetodontidae	*Chaetodon oxycephalus*	1	0	0
	Chaetodontidae	*Chaetodon punctatofasciatus*	2	4	4
	Chaetodontidae	*Chaetodon rafflesi*	4	1	5

	Chaetodontidae	*Chaetodon semeion*	2	0	0
	Chaetodontidae	*Chaetodon speculum*	1	0	0
	Chaetodontidae	*Chaetodon trifascialis*	1	0	1
	Chaetodontidae	*Chaetodon ulietensis*	4	5	11
	Chaetodontidae	*Chaetodon unimaculatus*	3	8	13
	Chaetodontidae	*Chaetodon vagabundus*	10	14	14
	Chaetodontidae	*Heniochus acuminatus*	1	0	0
	Chaetodontidae	*Heniochus chrysostomus*	7	4	10
	Chaetodontidae	*Heniochus varius*	25	8	7
Herbivore	Acanthuridae	*Acanthurus auranticavus*	1	0	67
	Acanthuridae	*Acanthurus blochii*	0	0	1
	Acanthuridae	*Acanthurus grammoptilus*	0	3	27
	Acanthuridae	*Acanthurus japonicus*	0	0	1
	Acanthuridae	*Acanthurus nigricans*	4	0	5
	Acanthuridae	*Acanthurus nigricauda*	0	0	7
	Acanthuridae	*Acanthurus nigrofuscus*	0	8	30
	Acanthuridae	*Acanthurus nigroris*	0	0	57
	Acanthuridae	*Acanthurus pyroferus*	46	60	36
	Acanthuridae	*Acanthurus tristis*	0	0	34
	Acanthuridae	*Acanthurus xanthopterus*	0	0	1
	Acanthuridae	*Ctenochaetus binotatus*	0	0	129
	Acanthuridae	*Ctenochaetus cyanocheilus*	0	0	3
	Acanthuridae	*Ctenochaetus striatus*	477	624	523
	Acanthuridae	*Ctenochaetus tominiensis*	0	0	1
	Acanthuridae	*Naso lituratus*	6	3	2
	Acanthuridae	*Naso unicornis*	0	0	5
	Acanthuridae	*Zebrasoma scopas*	73	149	149
	Acanthuridae	*Zebrasoma veliferum*	4	1	3
	Ephippidae	*Platax pinnatus*	0	0	1
	Ephippidae	*Platax teira*	0	0	9
	Pomacanthidae	*Centropyge bicolor*	8	17	22
	Pomacanthidae	*Centropyge bispinosus*	0	2	0
	Pomacanthidae	*Centropyge nox*	1	0	0
	Pomacanthidae	*Centropyge tibicen*	2	2	2
	Pomacanthidae	*Centropyge vroliki*	6	28	5
	Pomacanthidae	*Paracentropyge multifasciata*	3	0	0
	Pomacentridae	*Chrysiptera cyanea*	186	0	2
	Pomacentridae	*Chrysiptera glauca*	0	0	254
	Pomacentridae	*Chrysiptera hemicyanea*	2	0	0
	Pomacentridae	*Chrysiptera parasema*	0	0	76
	Pomacentridae	*Chrysiptera rex*	23	113	45
	Pomacentridae	*Chrysiptera springeri*	0	0	404
	Pomacentridae	*Dischistodus melanotus*	8	19	2
	Pomacentridae	*Dischistodus pseudochrysopoecilus*	0	1	18
	Pomacentridae	*Hemiglyphidodon plagiometopon*	0	0	2

	Pomacentridae	*Plectroglyphidodon johnstonianus*	0	0	7
	Pomacentridae	*Stegastes nigricans*	0	0	2
	Scaridae	*Cetoscarus bicolor*	1	4	2
	Scaridae	*Chlorurus bleekeri*	31	38	54
	Scaridae	*Chlorurus microrhinos*	0	1	0
	Scaridae	*Chlorurus sordidus*	108	63	138
	Scaridae	*Chlorurus strongylocephalus*	0	0	2
	Scaridae	*Hipposcarus longiceps*	1	3	14
	Scaridae	*Scarus dimidiatus*	20	13	10
	Scaridae	*Scarus flavipectoralis*	1	0	10
	Scaridae	*Scarus ghobban*	0	0	6
	Scaridae	*Scarus hypselopterus*	0	0	3
	Scaridae	*Scarus niger*	0	1	6
	Scaridae	*Scarus oviceps*	4	0	15
	Scaridae	*Scarus prasiognathos*	0	0	1
	Scaridae	*Scarus psittacus*	17	29	31
	Scaridae	*Scarus rivulatus*	2	0	70
	Scaridae	*Scarus russelii*	11	6	9
	Scaridae	*Scarus schlegeli*	3	1	19
	Scaridae	*Scarus spinus*	0	0	25
	Scaridae	*Scarus tricolor*	0	0	1
	Siganidae	*Siganus doliatus*	4	2	15
	Siganidae	*Siganus fuscescens*	0	38	0
	Siganidae	*Siganus guttatus*	1	0	1
	Siganidae	*Siganus lineatus*	0	0	6
	Siganidae	*Siganus puellus*	0	0	9
	Siganidae	*Siganus punctatissimus*	15	0	2
	Siganidae	*Siganus vulpinus*	8	14	9
Invertivore	Apogonidae	*Ostorhinchus aureus*	1	0	0
	Balistidae	*Balistoides conspicillum*	0	0	1
	Blenniidae	*Meiacanthus grammistes*	0	3	0
	Blenniidae	*Meiacanthus vicinus*	0	0	42
	Chaetodontidae	*Forcipiger flavissimus*	7	13	18
	Chaetodontidae	*Forcipiger longirostris*	87	51	81
	Chaetodontidae	*Heniochus monoceros*	1	0	2
	Chaetodontidae	*Heniochus singularius*	0	0	2
	Dasyatidae	*Taeniura lymma*	0	0	1
	Haemulidae	*Diagramma melanacrum*	0	0	1
	Haemulidae	*Plectorhinchus lessonii*	0	0	2
	Haemulidae	*Plectorhinchus lineatus*	45	1	7
	Labridae	*Anampses caeruleopunctatus*	0	0	5
	Labridae	*Anampses geographicus*	0	0	9
	Labridae	*Anampses melanurus*	1	1	0
	Labridae	*Anampses meleagrides*	6	0	9
	Labridae	*Anampses twisti*	8	3	0

	Labridae	*Bodianus axillaris*	0	2	1
	Labridae	*Bodianus mesothorax*	1	5	2
	Labridae	*Cheilinus chlorourus*	0	11	1
	Labridae	*Cheilinus fasciatus*	6	12	6
	Labridae	*Cheilio inermis*	1	0	0
	Labridae	*Choerodon anchorago*	0	12	1
	Labridae	*Cirrhilabrus solorensis*	102	0	9
	Labridae	*Coris gaimard*	6	5	3
	Labridae	*Diproctacanthus xanthurus*	0	0	19
	Labridae	*Halichoeres chrysus*	0	2	2
	Labridae	*Halichoeres hortulanus*	12	23	9
	Labridae	*Halichoeres leucurus*	0	0	1
	Labridae	*Halichoeres nigrescens*	0	0	3
	Labridae	*Halichoeres podostigma*	0	0	2
	Labridae	*Halichoeres prosopeion*	6	18	8
	Labridae	*Halichoeres richmondi*	0	0	1
	Labridae	*Halichoeres scapularis*	0	0	20
	Labridae	*Halichoeres trimaculatus*	1	0	0
	Labridae	*Hemigymnus fasciatus*	3	5	9
	Labridae	*Hemigymnus melapterus*	0	6	17
	Labridae	*Labriodes bicolor*	0	0	3
	Labridae	*Labroides bicolor*	8	4	0
	Labridae	*Labroides dimidiatus*	17	14	31
	Labridae	*Labroides pectoralis*	3	7	0
	Labridae	*Labropsis xanthonota*	1	0	0
	Labridae	*Novaculichthys taeniourus*	1	1	1
	Labridae	*Thalassoma hardwicke*	20	25	52
	Labridae	*Thalassoma lunare*	56	46	110
	Labridae	*Thalassoma lutescens*	1	0	0
	Lethrinidae	*Monotaxis grandoculis*	4	0	4
	Lethrinidae	*Monotaxis granducolis*	0	0	1
	Lethrinidae	*Monotaxis heterodon*	0	0	4
	Monacanthidae	*Amanses scopas*	1	1	2
	Monacanthidae	*Cantherhines pardalis*	2	0	0
	Mullidae	*Parupeneus ciliatus*	1	1	1
	Mullidae	*Parupeneus crassilabris*	4	0	2
	Mullidae	*Parupeneus indicus*	0	0	1
	Mullidae	*Parupeneus macronemua*	0	0	3
	Mullidae	*Parupeneus multifasciatus*	5	7	22
	Nemipteridae	*Scolopsis affinis*	2	0	26
	Pomacanthidae	*Pomacanthus imperator*	2	0	4
	Pomacanthidae	*Pomacanthus navarchus*	1	2	1
	Pomacanthidae	*Pomacanthus xanthometopon*	0	4	0
	Pomacentridae	*Neoglyphidodon crossi*	0	0	5
	Pseudochromidae	*Manonichthys splendens*	1	0	1

	Pseudochromidae	*Pictichromis paccagnellae*	12	33	1
Ob Coralivore	Chaetodontidae	*Chaetodon baronessa*	10	5	6
	Chaetodontidae	*Chaetodon melannotus*	2	16	15
	Chaetodontidae	*Chaetodon meyeri*	1	2	2
	Chaetodontidae	*Chaetodon ocellicaudus*	2	1	0
	Chaetodontidae	*Chaetodon ornatissimus*	0	1	0
Omnivore	Acanthuridae	*Naso vlamingii*	337	0	140
	Apogonidae	*Ostorhinchus nigrofasciatus*	0	2	0
	Balistidae	*Balistapus undulatus*	9	24	15
	Balistidae	*Balistoides viridescens*	0	0	1
	Balistidae	*Melichthys niger*	210	29	25
	Balistidae	*Melichthys vidua*	100	61	25
	Balistidae	*Odonus niger*	434	178	421
	Balistidae	*Rhinecanthus aculeatus*	0	1	2
	Balistidae	*Rhinecanthus verrucosus*	0	0	1
	Balistidae	*Sufflamen bursa*	3	4	4
	Blenniidae	*Aspidontus taeniatus*	0	1	7
	Labridae	*Coris aygula*	0	0	1
	Labridae	*Coris batuensis*	0	0	4
	Labridae	*Oxycheilinus digramma*	0	10	0
	Labridae	*Pseudodax moluccanus*	2	4	0
	Lethrinidae	*Monotaxis grandoculis*	0	8	0
	Lutjanidae	*Lutjanus semicinctus*	1	0	0
	Monacanthidae	*Cantherhines dumerilii*	0	0	3
	Monacanthidae	*Cantherhines fronticinctus*	0	2	0
	Monacanthidae	*Pervagor nigrolineatus*	0	0	1
	Ostraciidae	*Ostracion cubicus*	3	0	1
	Ostraciidae	*Ostracion meleagris*	0	0	1
	Ostraciidae	*Ostracion solorensis*	0	1	0
	Pholidichthyidae	*Pholidichthys leucotaenia*	0	539	0
	Pomacanthidae	*Apolemichthys trimaculatus*	0	0	1
	Pomacanthidae	*Chaetodontoplus mesoleucus*	1	0	1
	Pomacanthidae	*Neoglyphidodon melas*	1	0	0
	Pomacanthidae	*Pomacanthus sexstriatus*	0	2	7
	Pomacanthidae	*Pomacanthus xanthometopon*	2	0	0
	Pomacanthidae	*Pygoplites diacanthus*	7	13	16
	Pomacentridae	*Abudefduf sexfasciatus*	0	0	14
	Pomacentridae	*Abudefduf vaigiensis*	15	29	13
	Pomacentridae	*Acanthochromis polyacanthus*	0	0	5
	Pomacentridae	*Amblyglyphidodon aureus*	137	4	30
	Pomacentridae	*Amblyglyphidodon curacao*	327	474	830
	Pomacentridae	*Amblyglyphidodon leucogaster*	434	359	461
	Pomacentridae	*Amblyglyphidodon ternatensis*	6	0	2
	Pomacentridae	*Amphiprion clarkii*	33	13	11
	Pomacentridae	*Amphirion melanopus*	0	0	1

	Pomacentridae	*Amphirion ocellaris*	2	0	2
	Pomacentridae	*Amphirion polymnus*	0	2	0
	Pomacentridae	*Chrysiptera rollandi*	0	14	1
	Pomacentridae	*Chrysiptera unimaculata*	0	0	3
	Pomacentridae	*Dascyllus aruanus*	0	54	0
	Pomacentridae	*Neoglyphidodon melas*	505	71	71
	Pomacentridae	*Neoglyphidodon nigroris*	442	491	547
	Pomacentridae	*Neoglyphidodon oxyodon*	2	19	2
	Pomacentridae	*Neopomacentrus azysron*	0	0	9
	Pomacentridae	*Neopomacentrus violascens*	0	7	4
	Pomacentridae	*Plectroglyphidodon lacrymatus*	71	0	9
	Pomacentridae	*Pomacentrus adelus*	0	0	1
	Pomacentridae	*Pomacentrus alexanderae*	30	60	20
	Pomacentridae	*Pomacentrus amboinensis*	8	1	8
	Pomacentridae	*Pomacentrus armillatus*	25	0	0
	Pomacentridae	*Pomacentrus auriventris*	143	0	0
	Pomacentridae	*Pomacentrus bankanensis*	0	3	1
	Pomacentridae	*Pomacentrus brachialis*	51	729	309
	Pomacentridae	*Pomacentrus burroughi*	0	146	8
	Pomacentridae	*Pomacentrus chrysurus*	1	0	23
	Pomacentridae	*Pomacentrus coelestis*	1	0	407
	Pomacentridae	*Pomacentrus lepidogenys*	105	87	20
	Pomacentridae	*Pomacentrus littoralis*	0	0	10
	Pomacentridae	*Pomacentrus moluccensis*	6	685	406
	Pomacentridae	*Pomacentrus nigromanus*	1	2	15
	Pomacentridae	*Pomacentrus nigromarginatus*	0	3	6
	Pomacentridae	*Pomacentrus pavo*	0	0	1
	Pomacentridae	*Pomacentrus philippinus*	5	2	6
	Pomacentridae	*Pomacentrus reidi*	71	130	7
	Pomacentridae	*Pomacentrus simsiang*	0	1	0
	Pomacentridae	*Pomacentrus smithi*	0	0	2
	Pomacentridae	*Pomacentrus wardi*	0	0	795
	Tetradontidae	*Arothron hispidus*	0	2	0
	Tetradontidae	*Arothron nigropunctatus*	0	4	0
	Tetradontidae	*Canthigaster solandri*	0	1	0
	Tetradontidae	*Canthigaster valentini*	0	6	0
	Tetraodontidae	*Arothron caeruleopunctatus*	1	0	0
	Tetraodontidae	*Arothron hispidus*	0	0	1
	Tetraodontidae	*Arothron manilensis*	0	0	1
	Tetraodontidae	*Arothron nigropunctatus*	1	0	3
	Tetraodontidae	*Canthigaster bennetti*	1	0	0
	Tetraodontidae	*Canthigaster papua*	0	0	1
	Tetraodontidae	*Canthigaster solandri*	1	0	0
	Zanclidae	*Zanclus cornutus*	28	45	83
Piscivore	Holocentridae	*Sargocentron caudimaculatum*	4	5	7

	Serranidae	*Plectropomus areolatus*	0	0	3
	Serranidae	*Plectropomus laevis*	1	0	0
	Synodontidae	*Synodus binotatus*	0	0	1
	Synodontidae	*Synodus variegatus*	0	1	1
Planktivore	Acanthuridae	*Acanthurus mata*	0	0	2
	Acanthuridae	*Acanthurus thompsoni*	309	404	242
	Acanthuridae	*Naso caeruleacauda*	2	24	8
	Acanthuridae	*Naso caesius*	13	2	132
	Acanthuridae	*Naso hexacanthus*	0	24	0
	Acanthuridae	*Naso vlamingii*	0	104	0
	Caesionidae	*Caesio caerulaurea*	0	1	10
	Caesionidae	*Caesio cuning*	45	40	17
	Caesionidae	*Caesio lunaris*	0	200	23
	Caesionidae	*Caesio teres*	0	1	18
	Caesionidae	*Caesio xanthonota*	1	0	0
	Caesionidae	*Pterocaesio diagramma*	0	0	1
	Caesionidae	*Pterocaesio pisang*	0	0	46
	Caesionidae	*Pterocaesio randalli*	0	197	1
	Caesionidae	*Pterocaesio tile*	99	13	660
	Caesionidae	*Pterocaesio trilineata*	0	0	246
	Chaetodontidae	*Hemitaurichthys polylepis*	92	275	122
	Chaetodontidae	*Heniochus acuminatus*	0	2	2
	Cirrhitidae	*Paracirrhites forsteri*	2	2	2
	Holocentridae	*Myripristis adusta*	0	0	3
	Holocentridae	*Myripristis berndti*	0	0	1
	Holocentridae	*Myripristis kuntee*	0	0	4
	Holocentridae	*Myripristis murdjan*	0	3	1
	Holocentridae	*Myripristis violacea*	0	2	10
	Labridae	*Cirrhilabrus cyanopleura*	34	0	0
	Labridae	*Pseudocoris yamashiroi*	1	0	0
	Labridae	*Thalassoma amblycephalum*	0	244	0
	Lutjanidae	*Macolor macularis*	7	0	35
	Monacanthidae	*Paraluteres prionurus*	0	0	1
	Nemipteridae	*Dascyllus melanurus*	0	0	1
	Pomacentridae	*Acanthochromis polycanthus*	0	7	0
	Pomacentridae	*Chromis agilis*	0	0	42
	Pomacentridae	*Chromis alpha*	0	0	125
	Pomacentridae	*Chromis amboinensis*	245	301	42
	Pomacentridae	*Chromis analis*	231	195	334
	Pomacentridae	*Chromis atripectoralis*	2	0	3
	Pomacentridae	*Chromis atripes*	0	0	3
	Pomacentridae	*Chromis caudalis*	0	29	35
	Pomacentridae	*Chromis fumea*	0	0	108
	Pomacentridae	*Chromis lepidolepis*	5	20	21
	Pomacentridae	*Chromis lineata*	0	0	1

	Pomacentridae	*Chromis margaritifer*	47	76	50
	Pomacentridae	*Chromis opercularis*	0	0	2
	Pomacentridae	*Chromis retrofasciata*	3	6	0
	Pomacentridae	*Chromis ternatensis*	49	260	783
	Pomacentridae	*Chromis viridis*	0	88	418
	Pomacentridae	*Chromis weberi*	110	29	248
	Pomacentridae	*Chromis xanthochira*	0	0	5
	Pomacentridae	*Chromis xanthura*	156	56	264
	Pomacentridae	*Chrysiptera talboti*	0	19	0
	Pomacentridae	*Dascyllus melanurus*	0	0	89
	Pomacentridae	*Dascyllus reticulatus*	98	489	514
	Pomacentridae	*Dascyllus trimaculatus*	82	57	86
	Pomacentridae	*Neoglyphidodon thoracotaeniatus*	0	1	0
	Pomacentridae	*Pomacentrus auriventris*	0	345	0
	Ptereleotridae	*Nemateleotris magnifica*	0	3	0
	Ptereleotridae	*Ptereleotris evides*	0	9	0
	Tripterygiidae	*Helcogramma striatum*	0	2	0

III. Benthic Background

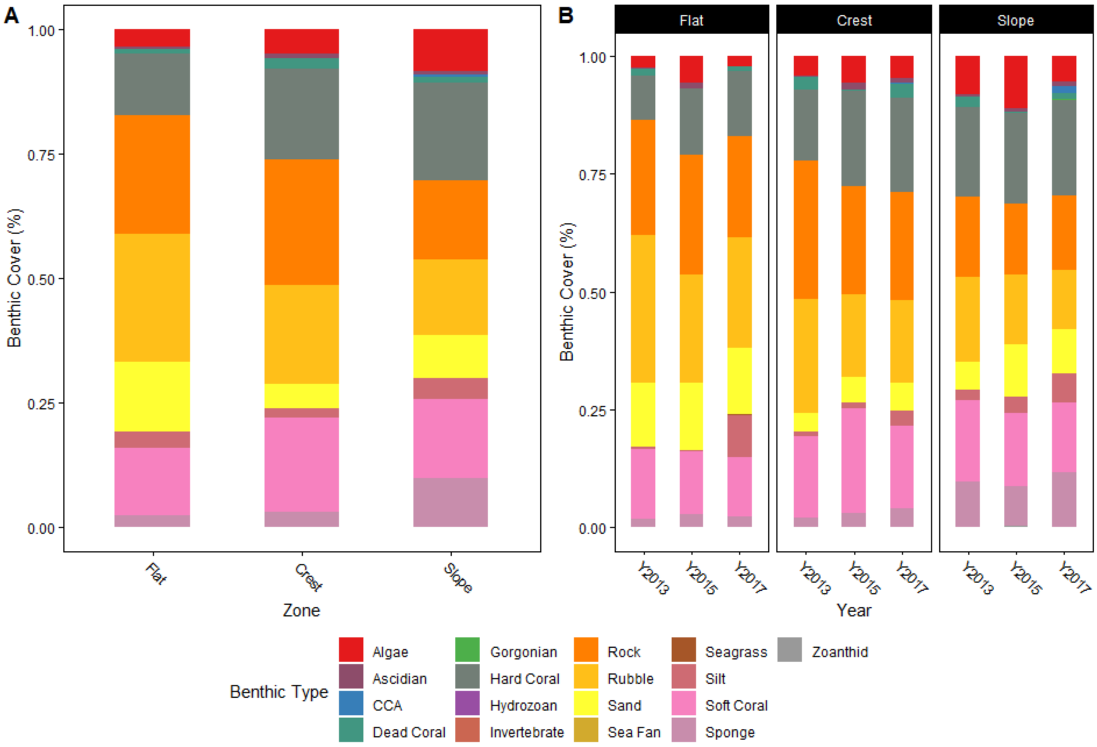


Figure 20. Benthic percentage cover (%) in the Wakatobi, (A) between reef zones (flat, crest and slope), across all years (B) between reef zones (flat, crest and slope) and years (2013, 2015 and 2017).

IV. Regression multicollinearity

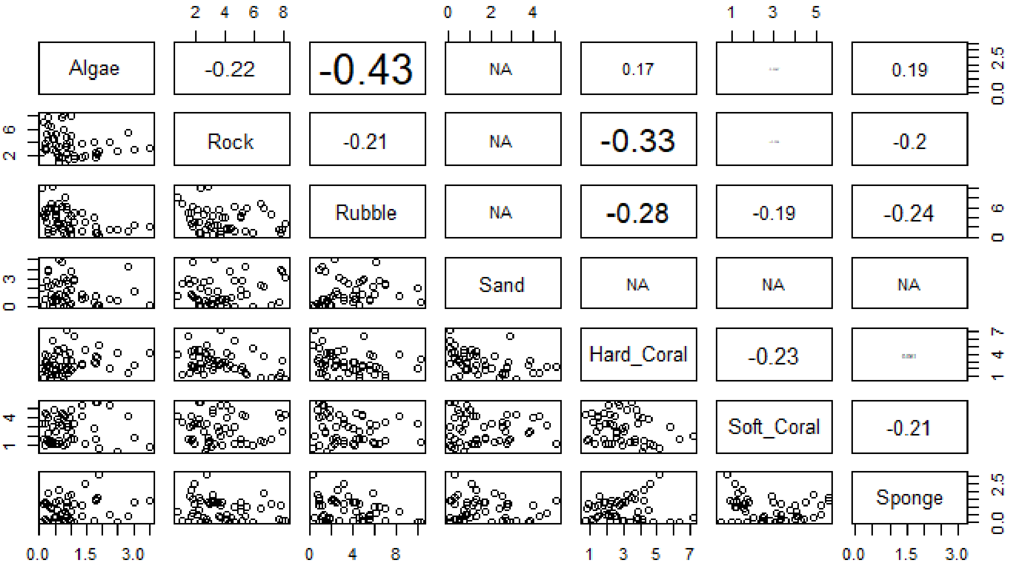


Figure 21. Summary of correlation matrix of benthic types used in generalised linear mixed effect models.

V. Benthic type regression analyses

Table 10. Negative binomial regressions on Herbivores and secondary functional groups; Benthic Feeders, Grazer/Detritivores and Scrapers/Small Excavator communities regressed on benthic types, sand, soft coral, hard coral, sponge, algae, rock and rubble. Pseudo R^2 = Pearson's.

		Herbivore					**Benthic Feeders**					**Grazer/Detritivores**					**Scrapers/Small Excavators**				
Model	Variable	Co-efficients	Std. Error	Z	P		Co-efficients	Std. Error	Z	*P*		Co-efficients	Std. Error	Z	*P*		Co-efficients	Std. Error	Z	*P*	
Abun-dance	Intercept	3.10673	0.90013	3.451	0.000558	***	3.933095	1.617588	2.431	0.01504	*	2.2194	0.7947	2.793	0.00523	**	2.52383	1.21748	2.073	0.0382	*
	Sand	0.20426	0.07661	2.666	0.007667	**	0.294977	0.147542	1.999	0.04558	*	0.19528	0.06737	2.899	0.00375	**	0.18034	0.09875	1.826	0.0678	·
	Soft Coral	0.18373	0.07733	2.376	0.017506	*	-0.200044	0.169488	-1.18	0.23789		0.19834	0.06858	2.892	0.00383	**	0.27814	0.10923	2.546	0.0109	*
	Hard Coral	0.14895	0.09002	1.655	0.097972	·	0.239986	0.151972	1.579	0.1143		0.03134	0.07958	0.394	0.6937		-0.05203	0.11851	-0.439	0.6606	
	Sponge	-0.33789	0.15022	-2.249	0.024495	*	-0.873339	0.297309	-2.937	0.00331	**	-0.13488	0.13411	-1.006	0.31453		-0.38229	0.22243	-1.719	0.0857	·
	Algae	-0.35085	0.14244	-2.463	0.013772	*	-0.587034	0.27884	-2.105	0.03527	*	-0.13425	0.12611	-1.065	0.28708		-0.41369	0.21454	-1.928	0.0538	·
	Rock	0.06724	0.06341	1.06	0.288946		-0.099758	0.10549	-0.946	0.34432		0.10613	0.05573	1.904	0.05686	·	-0.08004	0.08272	-0.968	0.3332	
	Rubble	0.10498	0.05583	1.88	0.060054	·	0.004981	0.098745	0.05	0.95977		0.14898	0.04917	3.03	0.00245	**	0.02627	0.07352	0.357	0.7208	
	AIC score	536.81					306.99					477.68					354.18				
	Pseudo R^2	0.38					0.61					0.28					0.28				
	Log Likelihood	-518.815					-288.99					-459.675					-336.178				
	SSE	0.516					0.252					0.728					0.401				
Biomass	Intercept	6.98211	1.06178	6.576	4.84E-11	***	4.05118	1.87435	2.161	0.03067	*	5.8973	0.98512	5.986	2.15E-09	***	7.21925	1.31412	5.494	3.94E-08	***
	Sand	0.14282	0.09063	1.576	0.115		0.05719	0.17309	0.33	0.74111		0.20791	0.08408	2.473	0.0134	*	-0.0234	0.10825	-0.216	0.8289	
	Soft Coral	0.20913	0.09084	2.302	0.0213	*	0.31781	0.21382	1.486	0.13718		0.15023	0.08429	1.782	0.0747	·	0.29253	0.11964	2.445	0.0145	*
	Hard Coral	0.13981	0.10633	1.315	0.1885		0.26456	0.175	1.512	0.13058		0.16832	0.09865	1.706	0.0879	·	0.1273	0.13082	0.973	0.3305	
	Sponge	-0.0231	0.17499	-0.132	0.895		-0.2829	0.34405	-0.822	0.41092		0.06445	0.16237	0.397	0.6914		-0.37773	0.23365	-1.617	0.106	
	Algae	-0.37419	0.16521	-2.265	0.0235	*	-0.3931	0.31802	-1.236	0.21644		-0.244	0.15329	-1.592	0.1114		-0.46926	0.23241	-2.019	0.0435	*

Rock	0.03867	0.07492	0.516	0.6058		-0.3586	0.12143	-2.953	0.00314	**	0.09017	0.06951	1.297	0.1946		-0.05621	0.08986	-0.626	0.5316
Rubble	0.07935	0.06607	1.201	0.2298		-0.09677	0.11384	-0.85	0.39527		0.12429	0.0613	2.028	0.0426	*	-0.03188	0.08076	-0.395	0.693
AIC score	933.14					317.49					878.76					760.01			
Pseudo R^2	0.17					0.21					0.21					0.24			
Log Likelihood	-915.135					-299.491					-860.765					-742.006			
SSE	0.325					0.183					0.382					0.247			

VI. Secondary Functional Group Partitioning

Table 11. Summary of species abundance (N), total biomass (g), biomass (g / m2 ± SE), density (no. / m2 ± SE), and species code recorded within each secondary functional group, pooled across reef zones and years. Note SE is provided when enough data was available, missing values for biomass, due to lack of length records.

Secondary	Family	Species	Abundance	Total Biomass (g)	Biomass (g / m2 ± SE)			Density (no. / m2 ± SE)			Species Code
Benthic Feeders	Pomacentridae	*Chrysiptera cyanea*	188	149.839	9.08E-03	±	3.45E-04	1.14E-02	±	3.66E-04	Chr.cya
		Chrysiptera glauca	254				3.44E-04	1.99E-02	±	4.10E-04	Chr.gla
		Chrysiptera hemicyanea	2	1.793	3.99E-04			4.44E-04			Chr.hem
		Chrysiptera parasema	76					9.21E-03	±	4.92E-04	Chr.par
		Chrysiptera rex	181	52.722	1.38E-03	±	2.78E-05	4.73E-03	±	3.30E-05	Chr.rex
		Chrysiptera springeri	404					3.17E-02	±	6.82E-04	Chr.spr
		Plectroglyphidodon johnstonianus	7					1.87E-03			Ple.joh
Browsers	Acanthuridae	*Naso lituratus*	11	1133.184	4.44E-02	±	1.18E-03	4.31E-04	±	4.83E-06	Nas.lit
		Naso unicornis	5	392.558	4.76E-02	±	8.37E-03	6.06E-04	±	3.83E-05	Nas.uni
	Ephippidae	*Platax teira*	9	1680.551	1.32E-01	±	2.34E-02	7.06E-04	±	9.06E-05	Pla.tei
		Platax pinnatus	1	69.590	1.55E-02			2.22E-04			Pla.pin
Grazers/detritivores	Acanthuridae	*Acanthurus auranticavus*	68	42.024	2.44E-03	±	4.65E-05	3.94E-03	±	2.07E-04	Aca.aur
		Acanthurus blochii	1	8.955	1.99E-03			2.22E-04			Aca.blo
		Acanthurus grammoptilus	30	2315.478	1.06E-01	±	9.47E-03	1.38E-03	±	5.41E-05	Aca.gra
		Acanthurus japonicus	1	43.962	9.77E-03			2.22E-04			Aca.jap
		Acanthurus nigricans	9	420.247	4.67E-02	±	3.90E-03	1.00E-03	±	2.62E-05	Aca.nigricans
		Acanthurus nigricauda	7	2294.829	1.80E-01	±	3.66E-02	5.49E-04	±	6.85E-05	Aca.nigricauda
		Acanthurus nigrofuscus	38	483.457	1.90E-02	±	1.17E-03	1.49E-03	±	5.54E-05	Aca.nigrofuscus
		Acanthurus nigroris	57					4.47E-03	±	6.49E-05	Aca.nigroris
		Acanthurus pyroferus	142	4512.310	1.18E-01	±	5.46E-04	3.71E-03	±	1.18E-05	Aca.pyr

		Acanthurus tristis	34			2.67E-03 ± 1.02E-04	Aca.tri
		Acanthurus xanthopterus	1	5.452	1.45E-03	2.67E-04	Aca.xan
		Ctenochaetus binotatus	129			1.01E-02 ± 2.25E-04	Cte.bin
		Ctenochaetus cyanocheilus	3	161.423	1.27E-02 ± 2.15E-03	2.35E-04	Cte.cya
		Ctenochaetus striatus	1624	17858.092	4.67E-01 ± 1.88E-03	4.25E-02 ± 5.60E-05	Cte.str
		Ctenochaetus tominiensis	1			2.22E-04	Cte.tom
		Zebrasoma scopas	371	2088.206	5.46E-02 ± 5.89E-04	9.70E-03 ± 3.27E-05	Zeb.sco
		Zebrasoma veliferum	8	381.687	1.75E-02 ± 1.06E-03	3.68E-04 ± 1.45E-05	Zeb.vel
	Pomacanthidae	*Centropyge bicolor*	47	98.745	2.58E-03 ± 6.87E-05	1.23E-03 ± 1.28E-05	Cen.bic
		Centropyge bispinosus	2	4.064	4.93E-04	2.42E-04	Cen.bis
		Centropyge nox	1	23.014	5.11E-03	2.22E-04	Cen.nox
		Centropyge tibicen	6	74.895	4.76E-03 ± 3.39E-04	3.81E-04 ± 1.50E-05	Cen.tib
		Centropyge vroliki	39	79.622	3.22E-03 ± 2.96E-04	1.58E-03 ± 2.94E-05	Cen.vro
		Paracentropyge multifasciata	3	111.677	1.35E-02 ± 1.85E-03	3.64E-04 ± 4.95E-05	Par.mul
	Siganidae	*Siganus fuscescens*	38	1268.536	1.41E-01 ± 1.35E-02	4.22E-03 ± 1.53E-04	Sig.fus
		Siganus doliatus	21	1164.043	4.56E-02 ± 1.69E-03	8.24E-04 ± 3.62E-05	Sig.dol
		Siganus guttatus	2	208.143	2.31E-02 ± 2.34E-03	2.22E-04	Sig.gut
		Siganus lineatus	6	2046.727	4.55E-01	1.33E-03	Sig.lin
		Siganus puellus	9	605.323	4.75E-02	7.06E-04 ± 2.61E-05	Sig.pue
		Siganus punctatissimus	17	669.203	3.88E-02 ± 3.15E-03	9.86E-04 ± 8.23E-05	Sig.pun
		Siganus vulpinus	31	5163.243	1.53E-01 ± 5.37E-03	9.19E-04 ± 1.83E-05	Sig.vul
Scrapers/small excavators	Scaridae	*Cetoscarus bicolor*	7	466.819	2.22E-02 ± 1.32E-03	3.33E-04 ± 9.86E-06	Cet.bic
		Chlorurus bleekeri	123	5146.566	1.35E-01 ± 1.95E-03	3.22E-03 ± 2.21E-05	Chl.ble
		Chlorurus microrhinos	1			2.67E-04	Chl.mic
		Chlorurus sordidus	309	7469.767	1.95E-01 ± 2.21E-03	8.08E-03 ± 3.35E-05	Chl.sor
		Chlorurus strongylocephalus	2	237.780	6.34E-02	5.33E-04	Chl.str
		Hipposcarus longiceps	18	195.651	9.66E-03 ± 7.59E-04	8.89E-04 ± 3.74E-05	Hip.lon

		Scarus dimidiatus	43	2796.658	9.56E-02	±	3.60E-03	1.47E-03	±	2.12E-05	Sca.dim
		Scarus flavipectoralis	11	1662.955	9.64E-02	±	7.14E-03	6.38E-04	±	6.12E-05	Sca.fla
		Scarus ghobban	6	682.110	5.35E-02	±	2.41E-03	4.71E-04			Sca.gho
		Scarus hypselopterus	3	107.632	1.30E-02			3.64E-04	±	4.95E-05	Sca.hyp
		Scarus niger	7	86.502	9.61E-03			7.78E-04	±	1.48E-04	Sca.nig
		Scarus oviceps	19	1310.121	5.14E-02	±	2.25E-03	7.45E-04	±	2.16E-05	Sca.ovi
		Scarus prasiognathos	1	121.469	2.70E-02			2.22E-04			Sca.pra
		Scarus psittacus	77	7562.332	1.98E-01	±	2.89E-03	2.01E-03	±	1.61E-05	Sca.psi
		Scarus rivulatus	72	929.096	5.63E-02	±	3.59E-03	4.36E-03	±	1.51E-04	Sca.riv
		Scarus russelii	26	3816.831	1.13E-01	±	2.24E-03	7.70E-04	±	1.06E-05	Sca.rus
		Scarus schlegeli	23	1743.288	6.84E-02	±	4.20E-03	9.02E-04	±	3.29E-05	Sca.sch
		Scarus spinus	25	942.255	1.14E-01			3.03E-03	±	3.26E-04	Sca.spi
		Scarus tricolor	1	41.176	1.10E-02			2.67E-04			Sca.tri
Territorial Damsel	Pomacentridae	*Dischistodus melanotus*	29	282.561	1.40E-02	±	4.68E-04	1.43E-03	±	3.39E-05	Dis.mel
		Dischistodus pseudochrysopoecilus	19	55.257	3.35E-03			1.15E-03	±	7.73E-05	Dis.pse
		Hemiglyphidodon plagiometopon	2	13.597	1.65E-03	±	7.25E-05	2.42E-04			Hem.pla
		Stegastes nigricans	2	78.742	1.75E-02			4.44E-04			Ste.nig