Herbivorous coral reef fish responses to local and global stressors

by

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BSc, Dalhousie University, 2017

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Abstract

Given the current state of the climate and continuing local human impacts to coral reefs, conservation of these ecosystems requires active management efforts to arrest further deterioration. Some current management strategies focus on regulating local impacts such that reefs are provided the best chance at resisting further degradation from global, climate change-induced disturbances. One such strategy is to manage local herbivore populations. Herbivorous coral reef fish are considered natural drivers of reef recovery due to their prevention of algal overgrowth on coral and of further degradation of the reef to an undesirable state dominated by macroalgae. While the numerical response of herbivorous fish to disturbance is commonly investigated, the response of their key function to large-scale, global disturbance is still not well understood. In this thesis, I attempt to take a functional approach to describe herbivory on Kiritimati (Christmas Island), the largest coral atoll, located in the equatorial Pacific Ocean. First, I describe species-specific herbivory using three metrics: (i) bite rates; (ii) grazing impacts; and (iii) selectivity, to explore how these metrics vary with herbivore identity, individual size and life phase, and to determine if they are influenced by local gradients of human disturbance and whether or not they respond to a pulse heat stress and coral bleaching disturbance that resulted from the 2015–2016 El Niño. I found that herbivore functional groups and species exhibit distinct herbivory, driven, in part, by differences in fish size. Disturbance at a local level does not appear to have a significant influence on species-specific herbivory, but I detected an increase in bite rates and grazing impacts in response to a global heat stress event. These findings have implications for how herbivores respond to different levels of disturbance. I then scale up species-specific grazing impacts using site-averaged species' densities to explore how the herbivore assemblage grazing function responds to disturbance. Further, I summed average species' impacts at each site by functional group and detected distinct grazing impacts among groups and an increase following a global heat stress event. These findings suggest that the herbivory function of the assemblage is relatively robust to withstanding disturbance. Given that global scale disturbances of reef ecosystems are projected to become more frequent in the future, it is imperative to understand how this function will be influenced by disturbance at different scales. Taken together, the results in this thesis provide insight into the differing impacts of local and global scale disturbances on the herbivory function and suggest a somewhat promising outcome for the potential recovery of reefs following future disturbance.

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Dedication

Dedicated to the memory of the RMS Titanic –

whose stories served as early inspiration for my fascination

with the ocean and the power it holds

Chapter 1 – Introduction

Coral reefs are unique ecosystems that typically occupy nutrient-poor tropical waters, but are able to harbour high biological productivity and support high biodiversity, allowing them to provide key services to a multitude of species that rely on them (Hoegh-Guldberg 1999; Moberg and Folke 1999; Coker et al. 2014). Despite occupying less than 0.1% of the ocean floor, coral reefs are home to thousands of marine creatures, harbouring at minimum one quarter of marine species worldwide, and serving as essential habitats, migratory refuges, and feeding havens for resident and far-ranging marine species alike (Coker et al. 2014; Fisher et al. 2015). Humans also benefit from coral reefs, as they serve as the backbone of many tropical coastal communities, supporting populations by providing food, income and coastal protection (Hoegh-Guldberg et al. 2017).

Coral reefs are, however, threatened by human activities, from localized impacts such as overexploitation and pollution, to global impacts of climate change (Hughes et al. 2010; Hoegh-Guldberg et al. 2017; Hughes et al. 2017a). Global climate change is increasing the frequency of severe disturbances, like pulse heat stress events, which trigger mass coral bleaching, to the extent that many reefs will not have time to recover to mature coral assemblages before the next event occurs (Osborne et al. 2018; Hughes et al. 2018a). A lack of coral recovery may initiate ecosystem degradation (Knowlton 2004; Hughes et al. 2007; Holbrook et al. 2016). In fact, climate-induced impacts are degrading the health of these ecosystems such that the distribution of reef states is moving towards increasing emergence of more ‘mediocre’ or ‘poor’ coral reefs (Mumby 2017). The loss of healthy and functioning coral reefs will have dramatic consequences for biological diversity (Pratchett et al. 2011; 2014), land protection (Quataert et al. 2015), and local economies (Moberg and Folke 1999).

Degradation of coral communities can cascade to other components of the food web, including reef fishes, which rely on having adequate live coral cover for food, habitat, and protection (Coker et al. 2014; Ruppert et al. 2018). Complex coral habitats support a higher number of fish species and groups performing distinct functions compared to low-complexity, macroalgal habitats (Chong-Seng et al. 2012, 2014; Robinson et al. 2019b). Thus, some of the major consequences of ecosystem disturbance and degradation for reef fish assemblages are a loss of diversity (Cheal et al. 2010) and homogenization of assemblage structure (Richardson et al. 2018). Of particular concern is what a decline in abundance and diversity of coral reef fishes could mean for the eventual loss of certain ecosystem functions (Pratchett et al. 2011).

With this thesis, I attempt to enhance our understanding of the impacts of anthropogenic-induced disturbances on the feeding responses of herbivorous coral reef fish and the implications for ecosystem functioning. First, I explore the literature on coral reef herbivory, what is known about its response to disturbance and how to quantify this ecological function.

1.1 Coral reef herbivory

Coral reefs generally support a diverse assemblage of fishes performing distinct ecological functions, of which reef herbivores are one component. Herbivorous coral reef fishes are the most abundant and widespread marine herbivores on tropical reefs, and have evolved a diverse array of highly specialized jaw structures and unique stomach morphologies that allow them to efficiently consume algae (Choat 1991; Bellwood 2003). Two of the main coral reef herbivore families in the Indo-Pacific are the surgeonfish (family Acanthuridae) and the parrotfish (family Scaridae).

Early on, when scientists began evaluating the role of herbivores on reefs, it was fairly simple to quantify patterns of abundance and diversity, but it remained a challenge for early ecologists to come up with a standard method for measuring herbivory (Steneck 1983). Now, there is a large body of work dedicated to observing and evaluating the role of herbivores, and a few methods are employed to quantify herbivory. Techniques employed fall under two broad categories: experimental manipulation or observational measurements. In the former, herbivore exclusion cages can be used to assess herbivore ability to consume algal production, by comparing algal abundance, cover, or biomass between treatments with and without herbivores to determine the effect that the presence (or absence) of herbivores has on algal levels (e.g. Bellwood et al. 2006; Hughes et al. 2007; Burkepile and Hay 2008; Smith et al. 2010; Suchley and Alvarez-Filip 2017). Another method is to conduct a macroalgal assay experiment to determine the ability of herbivorous fish to remove algal biomass from a certain part of the reef (e.g. Mumby et al. 2006; Hoey and Bellwood 2009; Longo et al. 2015; Plass-Johnson et al. 2015). In this case, comparing algal mass from the onset to the end of the experiment determines how much was removed, which is assumed to be due to herbivore consumption. Observational measurements to evaluate herbivory require records of foraging activity and involve documenting the species, size and life phase of individual feeding fish and timing the number of bites taken from a certain substrate. These can be conducted underwater by divers (e.g. Bruggemann et al. 1994a; Fox and Bellwood 2007; Hoey and Bellwood 2008; Hoey et al. 2016a; Hamilton et al. 2014; Kelly et al. 2017) or analysed from videos of feeding behaviour (e.g. Bruggemann et al. 1994b; Fox and Bellwood 2008; Hoey and Bellwood 2009; Longo et al. 2015; Marshell and Mumby 2015). Whether conducted *in situ* or from video analysis, observations of fish foraging and bite rate data can yield realistic estimates of herbivore impact (Fox and Bellwood 2008).

Some general patterns about the natural variation in herbivory have emerged from these studies which allow us to understand important species and site-specific factors that can influence herbivory. For example, surgeonfish (family Acanthuridae) exhibit higher grazing rates compared to parrotfish species (family Scaridae) (e.g. Kelly et al. 2016). Coral reef herbivores are often further divided into finer functional groups, to acknowledge that species have different methods for exploiting algal resources and as such, perform distinct functions (Green and Bellwood 2009; Bonaldo et al. 2014; Puk et al. 2016): (i) *grazers*, consume algal turfs (e.g. most surgeonfishes: Marshell and Mumby 2015); (ii) *scrapers*, scrape algal material from coral structures (e.g. the *Scarus* genus of parrotfish: Adam et al. 2018); (iii) *excavators,* take deeper bites of coral skeletons (e.g. *Chlorurus* genus of parrotfish: Bellwood 1995 and *Bolbometopon muricatum:* McCauley et al. 2014), and (iv) *browsers,* consume larger, fleshy macroalgal fronds (e.g. *Naso* genus of surgeonfish: Chong-Seng et al. 2014; Streit et al. 2015, and *Sparisoma* and *Calotomus* genus of parrotfish: Bonaldo et al. 2014). We now recognize the importance of species identity in influencing the herbivore function, as species exhibit varied grazing rates (Fox and Bellwood 2007; Burkepile and Hay 2010; Adam et al. 2018; Lefcheck et al. 2019). Investigating herbivory at a species-level is critically important for gaining a more comprehensive understanding of the unique functional roles carried out by one or a few species (Hoey et al. 2013; Tebbett et al. 2017a). For example, studies have revealed disproportionate importance of some species, with certain functions solely carried out by one or two key species [e.g. browsing by a batfish species (Bellwood et al. 2006), bioeroding by humphead parrotfish (Bellwood et al. 2003; McCauley et al. 2014)]. Body size or life phase of individual species is also a factor that can influence herbivory. For example, smaller fish and juvenile life phases generally have higher bite rates than larger, more mature life phases (Bruggemann et al. 1994b;

Bonaldo et al. 2006), which tend to exhibit greater herbivore impacts due to their larger size (Bonaldo and Bellwood 2008; Ong and Holland 2010).

Herbivory is also related to site-specific factors and influenced by abiotic conditions. Studies have documented variable grazing amongst habitats, with some documenting higher grazing in more exposed, predator-dominated habitats (Hamilton et al. 2014), while others have observed lower grazing rates in open versus sheltered lagoon habitats (Longo et al. 2015). Generally, the habitats with higher productivity support higher grazing intensity (Marshell and Mumby 2015; Carlson et al. 2017). Across larger spatial scales, higher grazing has been observed in inner or mid-shelf reefs (Hoey and Bellwood 2008; Marshell and Mumby 2015) compared to offshore areas (Cvitanovic and Bellwood 2009). Herbivory also appears to differ between broader regions (Hoey et al. 2016a), generally declining as you move from warm tropical regions into more southern sub-tropical areas (Longo et al. 2014); these differences are attributed to differences in environmental factors. Finally, there is also natural variation in herbivory according to season. Warmer summer seasons generally see an increase in the levels of herbivory (Bellwood 1995).

Herbivorous fish can play a key role in coral reef dynamics by exerting top-down control on algae, limiting its proliferation and allowing corals to establish or maintain their dominance (Mumby et al. 2006; Burkepile and Hay 2008, 2010; Steneck et al. 2014; Fong et al. 2016). The role of herbivory in influencing the competitive interaction between corals and algae, is thought to be key to allowing reefs to recover to coral-dominated states following major disturbance events (Hughes et al. 2007; Rasher et al. 2013; Adam et al. 2015; Holbrook et al. 2016). Their role as top-down regulators of algae is thought to be so key that some management strategies, including the establishment of Marine Protected Areas (MPAs), are often touted as a solution for enhancing reef resilience due to the cascading benefits that herbivore protection might have on coral recruitment (Hughes et al. 2007; Steneck et al. 2014) or adult coral colony growth (Mumby and Harborne 2010). This reef management solution, however, is not universally accepted, as some studies highlight that there may be no benefit of herbivore protection on coral recovery (reviewed by Bruno et al. 2019).

In 2015–2016, a pulse heat stress event associated with an extreme El Niño triggered the worst global coral bleaching event to date (Claar et al. 2018; Eakin et al. 2019), resulting in severe bleaching and subsequent coral mortality in all tropical oceans (Hughes et al. 2018a). A disturbance event such as this can result in a fundamental change in the benthic coral assemblage (Hughes et al. 2018b), potentially allowing for opportunistic algal species to colonize and take over, ultimately driving an ecosystem shift to algal dominance (termed a phase or regime shift). Recent work with long-term coral reef datasets indicates that repetitive bleaching events are driving fundamental shifts in fish communities as well, such that even if species richness returns after a bleaching event, species compositions are not recovering to their pre-bleaching configurations (Bellwood et al. 2012; Robinson et al. 2019b). Quantifying how disturbances alter herbivore populations and their herbivory is therefore important for understanding how the function they carry out for the ecosystem may in turn help drive subsequent reef recovery (Done 1992; Hughes 1994; Bellwood et al. 2004).

1.2 Herbivorous reef fish responses to disturbance

Previous studies indicate that herbivorous coral reef fish responses to disturbances can be highly variable (Hoey et al. 2016b), with moderate to high response diversity within this functional group compared to other reef fish functional groups (Pratchett et al. 2011; 2014). For example, most of the early studies published following significant coral bleaching events quantified changes in herbivorous fish abundance, density or biomass: some of these documented herbivore increases (likely due to increased algae following the event), while others found no change or even declines (see Appendix A1). The true effect of a disturbance on the fish assemblage is highly context-dependent and can be difficult to extract since there appear to be no consistent trends, especially for herbivorous fish, either within or between species, or even between the same species in different regions (Pratchett et al. 2018).

In most studies, the biomass of herbivore species or functional groups has been used as a proxy for the function of herbivory, rather than directly quantifying how disturbance influences the herbivory function (Graham et al. 2015). While some suggest presence in a fish survey can be a reason enough to assume occurrence of fish feeding (Streit et al. 2019), this metric overlooks the influence that individual behaviour has in determining function. The few studies that have quantified how herbivory responds to disturbance either (i) employed experimental techniques to artificially enhance algal availability or manipulate benthic cover and then measured changes in herbivore grazing, or (ii) compared grazing patterns between protected and unprotected areas to infer how herbivory differs on reefs in different states. Some have examined the response to disturbances other than coral bleaching, such as fishing, localized impacts or wave exposure (Appendix A1). Direct estimates of the impacts of natural pulse disturbances, and especially the most recent global heat stress event, on the direct, quantitative response of herbivory are rare.

The behavioural responses of fish to disturbance events like coral bleaching are also not frequently studied (Pratchett et al. 2018). It is only more recently that studies have begun investigating the behavioural effect of coral bleaching on coral reef fishes (e.g. Keith et al. 2018, who examined aggressive butterflyfish behaviour). Taking a behavioural approach can provide a better understanding of how fish performance might be disrupted by climate change and whether or not this translates to a loss of a coral reef function (e.g. herbivory). Since loss of function is a grave consequence of disturbance that further degrades the health of the reef ecosystem, taking such an approach might help identify mechanisms that underpin the structure and dynamics of ecological communities in a transforming world.

1.3 Quantifying the herbivory function

One of the challenges in determining the role that herbivores can have on reef recovery is deciding how to scale up individual herbivore behavioural feeding responses to a broader assemblage level. Quantifying the herbivory function at a larger scale is necessary for making any general conclusions about how it responds to significant disturbances. A recent synthesis of herbivore browsing studies suggested that herbivore diversity rather than biomass was a better predictor of macroalgal browsing rates (Topor et al. 2019), with potential implications for reef studies that commonly use biomass as a proxy for function.

In light of this, other approaches are being taken to quantify how fish function varies at a community level without solely relying on fish biomass (see Appendix A2). One method is to take a functional diversity approach to quantify functional structure concomitantly with taxonomic structure (i.e. species richness of an assemblage). Generally, this method involves describing a matrix of functional traits for species of interest and then coupling it with a matrix of species abundances to define specific functional metrics that are independent of species richness, in order to make unbiased comparisons between communities. It uses a combination of multivariate and linear regression analyses to test hypotheses about how these vary spatially or temporally (Appendix A2). The main conclusions from studies implementing such an approach are (a) that changes in taxonomic structure are generally distinct from the variation in functional structure of the community, and (b) that one consequence of significant disturbance is an apparent decline in specialized coral reef functions (Appendix A2). One issue with this approach, however, is that it still mainly relies on the change in species abundance when discussing functional changes in the assemblage and does not directly examine a change in behaviour.

Other approaches to quantifying changes in herbivore function do take herbivore behaviours into account (Appendix A3). Probably the most common method of quantifying assemblage-level herbivory is to couple behavioural observations of fish feeding, with estimates of fish abundance (or density). The body of work that defines key functional roles of herbivores has largely focused on a few easy-to-follow (or measure) species. For example, a lot of the early work on herbivore functional roles references studies of the stoplight parrotfish (*Sparisoma viride*)*,* and some foundational papers that defined certain biological relationships between fish body size and food intake for parrotfish (e.g. Bruggemann et al. 1994a,b; van Rooij et al. 1998). This led to the inclusion of a mass-standardized estimate of feeding rates due to the influence that fish size could have on a species' feeding impact and by extension its function in the community (Bellwood et al. 2006). Fish size is also important as it relates to gape size (Dunic and Baum 2017) and thus larger fish tend to have larger bites and greater impacts on the benthic substrate (Mumby 2006; Bonaldo and Bellwood 2008). To reflect this, some estimates of herbivory include bite volumes taken from bite scar measurements, although most seem to be estimates gleaned from the literature (Bellwood et al. 2003). Since some fish, like surgeonfish, do not leave noticeable bite scars, this could preclude the inclusion of bite size in a quantification of herbivore function for an assemblage of fish that contains herbivores besides parrotfish.

Most of the work on herbivore functional roles at larger scales agrees that herbivore identity is key to defining ecological impacts, as different species can be dominant drivers of impacts across a wide spatial scale (e.g. Ruttenberg et al. 2019). Quantifying the functional roles of herbivores at the assemblage-level thus requires some estimate of (i) species-specific bite rates, to indicate feeding behaviour, (ii) fish sizes, to represent per-capita impacts, and (iii) abundance or density, to estimate the overall species impact. Rather than quantifying responses to disturbance, most studies that have quantified fish functional roles focus on biological comparisons amongst species, habitats, seasons, and spatial scales or quantify the drivers of herbivory (Appendix A3). Due to a paucity of studies that examine the behavioural responses of herbivorous fish to disturbance, and coral bleaching in particular (Pratchett et al. 2018), we have yet to gain a comprehensive understanding of how the herbivore function is altered by significant disturbance.

Regardless of the specific approach taken to quantifying herbivory, there is a need for a more functional, behavioural and 'impact-focussed' assessment rather than a simple 'numerical' approach to examining the herbivore community and its change over spatial or temporal scales. Indeed, coral reef scientists are calling for more functional approaches when examining ecosystem impacts of disturbance (Bellwood et al. 2019b). It is this approach that I have taken to investigate the herbivore response to disturbance on Kiritimati Island.

1.4 Thesis Research

This thesis attempts to enhance our understanding of the impacts of anthropogenic-induced disturbances on herbivory rates and their implications for ecosystem functioning. Specifically, I examine the effects of a severe heat stress event and local human disturbance on (1) species-specific herbivore responses and (2) assemblage-level herbivory. I utilize data that were collected from shallow forereefs of Kiritimati (Republic of Kiribati), a coral atoll in the central equatorial Pacific Ocean, which was devastated by the 2015–2016 El Niño that caused mass coral bleaching worldwide (Claar et al. 2018). Given the intensity of the heat stress, and the resulting decline in coral cover observed around the island, I predicted that we would detect a behavioural response in the herbivorous reef fish community, although it would likely vary depending on the functional group examined. I also predicted that the extent of this response might be influenced by the intensity of local human disturbance experienced at sites around the island.

In Chapter 2, I attempt to quantify herbivory at a species level. Using herbivore feeding observations and benthic community composition from before (1 year prior), during, and after (1 year following) severe heat stress, I calculate three metrics to represent herbivore responses: (i) bite rates, taken directly from observations of herbivores feeding over a timed observation period; (ii) grazing impact, calculated from bite rates and the individual's bite size; (iii) an index for selectivity, as an indication of an individual's feeding preference. Using generalized linear modelling, I examine what effects functional group (and species), size, life phase, global heat stress and local human disturbance have on herbivore response metrics. This chapter provides insight about the ecologically relevant variation in herbivory and the behavioural response of this function to local and global stressors. I show that herbivore functional groups had varied responses, but the degree to which they varied depends on the functional group and the metric examined. Notably, we found that high bite rates do not necessarily translate to a high grazing impact, thus bite size somewhat modulates our understanding of herbivory. Bite rates and grazing impacts increased during global heat stress but were unaffected by local human disturbance. Conversely, herbivore selectivity for algal turf substrates was unaffected by global heat stress but did vary with local human disturbance. These results provide evidence of a short-term positive impact of severe heat stress on herbivory and highlight the opposing effects that local and global stressors can exert on ecosystem functions.

In Chapter 3, I attempt to scale up our measure of grazing impact to examine the effects of disturbance on an assemblage-level estimate of herbivory. Using bite observations and fish survey data collected before (2 years prior) and after (1 and 2 years following) the severe heat stress and significant coral bleaching event, I multiply average estimates of species-specific grazing impacts on turf substrates by average site-level density to calculate a metric for average species impact. I take a multivariate approach to observe spatial and temporal variation in average species impacts. I also apply a generalized linear mixed model to the summed species impacts for each functional group in order to examine the effects of functional group, global heat stress and local human disturbance on the assemblage-level grazing impact function. I show that the overall grazing function of herbivory is influenced by the functional group identity and increases after a significant heat stress event but is fairly robust to human disturbance. These findings are reassuring considering the influence that herbivores can have in driving coral reef dynamics following severe disturbance events.

In sum, the results of this thesis enhance our understanding of the behavioural response of coral reef herbivores to an extreme thermal stress event, within the context of local disturbance. In the face of accelerating climate change and human intervention, it is critical that we quantitatively examine the interacting effects that multiple stressors can have on ecosystem functions. If coral reef management is seeking to preserve the healthy functioning of these systems, it is critical to understand how key functional groups will respond and what capacity they have to carry out their functions despite repetitive disturbance to the ecosystem. Our findings add to the limited but growing, body of coral reef literature concerning the behavioural response of critical functions to severe thermal stress and support the assertion that herbivores are key players to protect in our effort to preserve the health of these increasingly threatened ecosystems.

Chapter 2 – Species-specific herbivory increases with global heat stress

Will be submitted as a report to Oecologia

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2.1 Abstract

Anthropogenic stressors are subjecting coral reefs to increasingly severe disturbances. Herbivores are considered essential for maintaining resilience to such disturbances due to their role in mediating coral-algal competition. Thus, understanding how anthropogenic stressors at local and global scales affect herbivore feeding is key to understanding the functional role of these organisms in driving ecosystem dynamics. In this study, we investigated the feeding response of four herbivore functional groups to disturbance on Kiritimati Island, by coupling *in situ* feeding observations of surgeonfish (grazers) and parrotfish (scrapers, excavators, browsers) with benthic surveys from shallow forereef sites along a local gradient of human disturbance. Sampling was done at three time points (2013, 2015, 2017) over five years, spanning a significant coral bleaching and mortality event, driven by the heat stress induced by the 2015–2016 El Niño. We estimated bite rates (bites min^{-1}), grazing impact (bite $s^{-1} \times$ gape area (mm^2)) and selectivity (Manly's α) to examine how herbivory varies across functional groups and between species, within the context of local and global disturbance. Although grazers had the highest bite rates, grazing impact, which accounts for bite size, was highest in scrapers; the functionally distinct browser *Calotomus carolinus* had the lowest bite rates and grazing impacts. Bite rates and grazing impacts increased significantly whilst subjected to heat stress, but neither was influenced by local human disturbance. In contrast, selectivity was impacted by local disturbance but not heat stress, with higher selectivity for turf at very high disturbance sites. Our results likely reflect a short-term herbivore response to a significant heat stress event, which was universal along a gradient of local disturbance. We highlight the importance of taking a behavioural approach to quantifying functional responses of coral reef herbivores to disturbance.

2.2 Introduction

Human disturbance affects coral reefs on multiple scales, from local stressors such as overexploitation and pollution (Wilson et al. 2010b) to global stressors like climate change (Hughes et al. 2017b). In particular, recent episodes of unprecedented ocean warming have triggered mass coral bleaching and mortality worldwide (Hughes et al. 2017a) even at highly isolated reefs (Hughes et al. 2018a). Such heat stress can shift coral community composition and lead to coral reproductive failure (Hughes et al. 2018b, 2019), while the resulting loss of coral habitat complexity leads to a reduction and homogenization of fish diversity (Cheal et al. 2010; Chong-Seng et al. 2012; Richardson et al. 2018). Local disturbances, such as fishing pressure more directly impact the fish community by altering size spectra (Wilson et al. 2010b) and reducing fish biomass (Edwards et al. 2014). Reductions in herbivorous fish biomass can be particularly concerning, as herbivores act as top-down regulators of algae competitors and can enhance coral settlement, growth and survival (Mumby et al. 2006; Burkepile and Hay 2008, 2010). This herbivory function is thought to be key for enabling reef recovery to a coral-dominated state following major disturbances (Hughes et al. 2007; Adam et al. 2015; Holbrook et al. 2016).

Responses of herbivorous fishes to bleaching disturbances are, however, variable (Hoey et al. 2016b); herbivores show moderate to high response diversity compared to other reef fish functional groups (Pratchett et al. 2011, 2014), leading to uncertainty as to what role they play as a group for coral reef resilience (Bruno et al. 2019). For example, some studies have documented positive responses of herbivores following disturbance (e.g. Graham et al. 2007; Gilmour et al. 2013; Han et al. 2016), but others have observed no change (e.g. Glynn et al. 2014) or even declines (e.g. Halford et al. 2004; Stuart-Smith et al. 2018). The different ways that herbivore functional groups (commonly divided into grazers, scrapers, excavators and browsers: Green and Bellwood 2009; Bonaldo et al. 2014) exploit their algal resources can contribute to this response diversity. The herbivore function may also be influenced in turn by factors such as species identity (Fox and Bellwood 2007; Burkepile and Hay 2010; Lefcheck et al. 2019), individual behaviour (Tebbett et al. 2017a), life phase (Bruggemann et al. 1994a), and body size (Bonaldo and Bellwood 2008; Ong and Holland 2010). For instance, larger-bodied species generally have greater herbivore impacts (Bonaldo and Bellwood 2008; Ong and Holland 2010). Species-specific traits can also contribute to response diversity and are therefore important considerations for quantifying the functional roles of herbivores (Cvitanovic and Bellwood 2009; Chong-Seng et al. 2014; Adam et al. 2018) and understanding any stabilizing effects of functional redundancy (Mouillot et al. 2014; Mora et al. 2016), since some key functions are limited to one or a few species (e.g. Bellwood et al. 2006; Hoey et al. 2013; Tebbett et al. 2017a).

Most studies of herbivory on reefs post-disturbance have quantified changes in herbivorous fish abundance, density, or biomass as a proxy for herbivore function (reviewed by Graham et al. 2015), but do not directly quantify ecosystem functions as they relate to ecological processes or their response to changes in global ecosystems (Mouillot et al. 2013; Bellwood et al. 2019b). Using a numerical proxy to quantify herbivory could obscure the influence of behaviour on herbivore function and the capacity of herbivores to deliver ecosystem services and drive reef resilience. Some studies have explicitly examined herbivore foraging activity (Bruggemann et al. 1994a, 1994b) and attempted to quantify functional roles (e.g. Mumby 2006; Hoey et al. 2016a; Suchley and Alvarez-Filip 2017), but few of these studies quantified herbivory with the objective of investigating its response to disturbance. Instead, previous research has primarily focussed on biological comparisons amongst species (e.g. Bellwood and Choat 1990; Choat and Clements

1993; Polunin et al. 1995; Alwany et al. 2009), habitats (e.g. Hoey and Bellwood 2008; Hamilton et al. 2014; Longo et al. 2015), seasons (Bellwood 1995), or spatial scales (Carlson et al. 2017). The few studies to quantify herbivore responses to disturbance have done so either experimentally (e.g. Bellwood et al. 2006; Holbrook et al. 2016; Kuempel and Altieri 2017) or by comparing sites at varied levels of degradation (e.g. Mumby 2006; Chong-Seng et al. 2014; Ferguson et al. 2017) with fewer examining the joint effects of local and global disturbances from temporally separated natural observations of the herbivore community.

Herbivory needs to be investigated directly, using species-specific measures like bite rates, if we are to understand how herbivore functional groups respond to disturbances on different scales and influence coral reef resilience (Adam et al. 2015; Plass-Johnson et al. 2015). Measures of herbivory will also have to incorporate two critical aspects of herbivore function: gape size and selectivity. Few studies use fish gape size directly when measuring herbivory, and in doing so, overlook the distinction between fish taking many small bites versus few large bites, instead opting to standardize bite rates by body mass (e.g. Bellwood et al. 2006; Hoey and Bellwood 2009; Longo et al. 2015, but see Fox and Bellwood 2007; Kelly et al. 2017; Suchley and Alvarez-Filip 2017). The particular substrates that are targeted also affect herbivore function (Clements et al. 2016). Herbivores generally target turf algae (Ledlie et al. 2007; Ong and Holland 2010; Marshell and Mumby 2015), however some parrotfish species exhibit varied diet preferences, targeting macroalgae (Mantyka and Bellwood 2007; Hamilton et al. 2014), coral (Burkepile et al. 2019), and microscopic organisms within these substrates (Clements et al. 2016). Thus, both individual size and selectivity can modulate the functional response to disturbance, requiring their integration into functional measures in studies of the impact of disturbances on herbivory.

Here, we aim to examine ecologically relevant variation in herbivory and understand the influence of local and global stressors on this coral reef function. To do so, we assessed herbivory for the major species of herbivorous fishes in each of four functional groups (grazers, browsers, scrapers, and excavators) on Kiritimati (Republic of Kiribati; central equatorial Pacific), at sites spanning the atoll's gradient of local disturbance (Fig. 2.1; Walsh 2011; Watson et al. 2016) and over the course of the 2015–2016 El Niño warming event (Claar et al. 2019). During this El Niño, Kiritimati experienced temperature anomalies exceeding 1°C above the island's historical maximum monthly temperature for nine months (Claar et al. 2019). We quantified herbivory in three ways: (i) bite rates, (ii) 'grazing impact' (i.e. bite rate × gape area), to account for differences in bite size amongst individual fishes and species, and (iii) substrate selectivity. First, we were interested in examining variation in herbivore metrics in relation to herbivore identity and size. We hypothesized that each of these metrics would vary significantly across herbivore functional groups and species and that we would detect an influence of individual size: we expected that grazers, which feed primarily on turf algae, would have the highest bite rates, but not necessarily the highest grazing impact because of their small gape sizes; we expected large parrotfish functional groups with their larger gapes to have higher grazing impacts. We also expected that most species would selectively feed on turf. Second, we aimed to understand the influence of local and global stressors on species-specific herbivory. We further hypothesized that although local and global stressors would not influence the fundamental feeding ecology of reef herbivores (and hence bite rates or grazing impact), that these factors might influence selectivity for different substrates, due to differences in the availability of preferred substrates across the local disturbance gradient and over the course of the heat stress event.

2.3 Methods

2.3.1 Study site and overview

We surveyed the herbivorous fish and benthic substrate communities at 21 shallow forereef sites (10–12m depth) before (2013), during (2015), and after (2017) the 2015–2016 El Niño event on Kiritimati (Christmas Island, Republic of Kiribati; 01°52'N 157°24'W). The largest coral atoll by land mass, Kiritimati is part of the Northern Line Islands in the central equatorial Pacific Ocean (Fig. 2.1). The 2015–2016 El Niño caused mass coral bleaching and mortality on Kiritimati's reefs (Claar and Baum 2019; Claar et al. 2019; Magel et al. 2019). Kiritimati is home to ~6,500 human inhabitants (Kiribati National Statistics Office 2016) who rely on the reef as a source of food and livelihood (Watson et al. 2016). Due to the greater population density on the northwestern side of the island (Watson et al. 2016), there is a spatial gradient of local human disturbance that affects the surrounding reefs. Survey sites have previously been assigned to one of four human disturbance levels (very low, low, medium, and very high), by combining spatial data on fishing intensity (Watson et al. 2016) and human population density (Claar et al. in revision; Magel et al. 2019; Magel et al. in revision) (Fig. 2.1).

2.3.2 Data collection and treatment

Herbivore feeding observations

Feeding observations were recorded for surgeonfish and parrotfish species, as these are the most common herbivorous fish families on Kiritimati. At each site, a trained scientific diver located a 'focal' herbivorous fish and followed it for between two to six minutes (mean 4.09 min +/- 0.02 SE) at a distance of at least two metres, so as not to disturb feeding behaviour (Table B1). For each observation, the diver recorded the species, life phase (Juvenile [J], Intermediate [IP] or Terminal Phase [TP] of parrotfish), size (total length) of the individual, the number of bites taken during the timed interval classified by food substrate type, and the time and length (in seconds) of the observation. Observations were conducted during daylight hours (overall range: 07:42 – 17:43 hrs; range of 95% of observations: 07:58 – 16:45 hrs) to minimize diurnal differences in feeding behaviour and were discontinued if the fish showed a marked response to the diver's presence. Food substrates were categorized as turf algae, encrusting coralline algae (CCA), coral, or macroalgae identified to genus (i.e. *Halimeda*, *Caulerpa*, *Dictyosphaeria, Galaxaura, Lobophora* and *Mesopora*). We summed bites across macroalgal genera into a single 'Macroalgae' category, because all macroalgae were eaten only infrequently. We categorized the observed herbivore species into functional groups following Yeager et al. (2017): (i) *grazers*, which consume algal turfs (e.g. surgeonfishes); (ii) *scrapers*, which scrape algal material from coral structures (e.g. the *Scarus* genus of parrotfish); (iii) *browsers,* which consume larger, fleshy macroalgal fronds (e.g. the *Calotomus* genus of parrotfish) and (iv) *excavators,* which take deeper bites of coral skeletons (e.g. the *Chlorurus* genus of parrotfish).

Benthic cover

We quantified benthic community composition at each site along two 25 m transects (separated by 10 m) that spanned the 10–12 m isobath. Between 12–15 quadrats (1 m^2) were randomly placed on either side of each transect, with their placement determined by a random number generator, and the reef substrate within each quadrat was photographed. We later identified the benthic substrate under 100 randomly placed points on each quadrat image using the open source program CoralNet (coralnet.ucsd.edu). Benthic categories were defined as: 'CCA', 'Coral', 'Substrate Consolidated Hard Rock (SCRO)', 'Rubble', 'Sand', 'Sediment', 'Macroalgae' (summed cover of macroalgal genera: *Caulerpa*, *Dictyosphaeria*, *Halimeda*, *Lobophora*, *Peyssonnelia*, and *Padina*) and 'Turf' (summed cover of what was categorized as 'thin turf algae covering a hard surface', thicker 'algal turf mats', and 'cyanobacteria'). We calculated the percent cover of each benthic category as the average of all quadrats at each site for each year.

2.3.3 Data analysis

Functional group- and species-specific bite rates and grazing impacts

We first assessed if bite rates (number of bites per individual fish) varied by herbivore functional group, fish size, global heat stress or local human disturbance, by fitting a generalized linear mixed model (GLMM) with a negative binomial error distribution and a 'log' link function, to accommodate the overdispersion in the data, using the *glmmADMB* package (Fournier et al. 2012; Skaug et al. 2016). We included functional group (grazer, scraper, browser, excavator), heat stress period (as year; 2013 = before, 2015 = during, 2017 = after), disturbance level (very low, low, medium, very high), body size (continuous), and time of day (continuous) as fixed effects; species and site were random effects, and the length of the observation period (as a logarithm) was used as an offset. Prior to analysis, we centered and standardized the continuous input variables. Second, to examine species-specific differences, we modelled bite rates for each functional group individually, using the same model structure and variables as for the model above, but including species as a fixed effect for the two functional groups comprised of multiple species (grazers = 5 species, scrapers = 6). We also included life phase (juvenile, intermediate, terminal) as a fixed effect for the three parrotfish functional groups.

Next, we constructed a similar set of models as above, but with 'grazing impact' (bites per second × gape area) as the response variable. Since grazing impact is a non-negative continuous number, we fit models with a gamma distribution and a 'log' link using the *lme4* package (Bates et al. 2015). Grazing impact was occasionally zero, which cannot be handled by a gamma distribution; for these we added a small number to the response (0.25; approximately ½ of the smallest non-zero value). We estimated the gape area for each observed herbivore using published regression equations relating gape size (gape width and gape height in mm) to fish body size (Dunic and Baum 2017). Species-specific equations were available for five of our herbivore species (*Acanthurus nigricans*, *A. olivaceus, Chlorurus sordidus, Scarus frenatus, S. rubroviolaceus*). For the remaining species, we used the average gape size ~ body size relationship of its congeners, except for *Calotomus carolinus*, for which we used the gape regressions for *S. frenatus,* which were the closest available estimates (Table B2). Gape area was estimated for each individual assuming gape area was approximately circular ($A = \pi r^2$, i.e. gape area was the product of $\pi \times$ ½ gape height $\times$ ½ gape width), which introduced a quadratic nonlinearity in the relationship between gape size and body size. We considered the same fixed parameters in this set of models as in the bite rate models, but also included a polynomial (degree 3) term for the body size covariate to account for the nonlinearities introduced by the gape size ~ body size regressions and the log-link of the model.

Size analysis

Prior to fitting our models above, we conducted a regression analysis for the bite rate and grazing impact responses separately with our size covariate alone to investigate its influence (Figures B1–B2). Based on these analyses, we determined there was a significant linear relationship between size and overall bite rate, so we included a linear term for the size covariate in our bite rate models. A linear term for size in a gamma model of grazing impact, however, did not predict impacts well at high sizes, because of the non-linearity introduced in the relationship between gape size and body size, so we tried fitting a quadratic and a cubic polynomial term for size. This is similar to what Lokrantz et al. (2008) found with their regression between body size and area scraped, to which they fit a power function. From exploratory analysis of the residual and model prediction plots, we determined a polynomial (degree 3) term for the body size covariate was the best fit for the overall grazing impact response. To be confident about our inclusion of the size covariate, we fit both bite rate and grazing impact models without size to assess its influence.

Selectivity

To assess herbivore feeding preferences, we calculated an index of selectivity for each substratum α_i (turf, CCA, coral or macroalgae), similar to Hamilton et al. (2014), using Manly's α selectivity index, derived from Chesson (1983):

$$\alpha_i = \frac{r_i/n_i}{\sum_{i=1}^{m} r_i/n_i} \;,\; i = 1 \dots m$$

Here, for each observed individual, the index of selectivity for each substratum (α_i) is calculated as the proportion of bites on the substratum (r_i) divided by the relative cover of that substratum (n_i) as measured from the benthic community survey data from the same site and year and then scaled by the sum of this ratio for all (m=4) substrate types. We removed observations (n=31) where zero total bites were observed, as these do not provide any selectivity information.

We modelled turf selectivity only, because this substrate accounted for the vast majority of bites in feeding observations (97% of Acanthuridae bites and 87% of Scaridae bites). We fit two sets of generalized linear mixed models (overall and for individual functional groups), each with the same covariates as in the bite rate model above (excluding time of day and size). Because the selectivity response is bounded by 0 and 1, we fit models with a beta error distribution and a 'logit' link function, using the *glmmTMB* package (Magnusson et al. 2017), adding or subtracting a small value (0.0000001) from the zeros and ones in the turf selectivity values before fitting the models (Smithson and Verkuilen 2006).

For each set of models, we used likelihood ratio tests (LRT) to test hypotheses about the influence of functional groups (and species), size (and life phase), the global heat stress event, and the local human disturbance gradient on the variation in herbivory response metrics. If a predictor had a significant effect, we then conducted post-hoc multiple comparisons using pairwise Tukey tests to determine which differences between the levels of the predictor were significant. The p-values were adjusted for multiple comparisons using the single-step method of the *glht* function in the *multcomp* package (Hothorn et al. 2008).

All analyses were conducted using R version 3.3.3 (R Core Team 2017).

2.4 Results

In total, we observed the feeding activity of 1,984 individual herbivorous fishes from 21 different species [10 surgeonfish (family Acanthuridae) and 11 parrotfish (family Scaridae)]. We limited analyses to the 13 most commonly observed species ($n \geq 25$ observations each; n=1,942 observations total (97.8% of all observations); Tables 2.1–2.2); these species accounted for ~84% of total herbivore biomass recorded in fish census surveys across years on Kiritimati.

2.4.1 Bite rates

Bite rates varied substantially, from an average high of 51.53 bites min^{-1} (± 4.15 SE) by the grazer *Acanthurus nigricauda* to an average low of 6.70 bites min^{-1} (± 0.49 SE) by the browser *C. carolinus* (Fig. 2.2a; Table B3). This difference was mirrored across species, with all surgeonfishes (i.e. grazers; except for *A. lineatus*) having higher bite rates than parrotfishes (Fig. 2.2a; Table B3).

Similarly, in the overall model, bite rates were significantly higher in grazers and significantly lower in browsers, compared to other functional groups (Fig. 2.3; LRT = 28.2, df = 3, $p<0.001$; Table B4). Within functional groups (Table B5), bite rates varied significantly amongst grazer (LRT = 10.1, df = 4, $p<0.05$) and amongst scraper (LRT = 53.7, df = 5, $p<0.001$) species. For grazers, differences were driven primarily by the low bite rates of *A. lineatus* relative to the other species (Fig. 2a), although only the difference between *A. lineatus* and *A. nigricans* was statistically significant, likely because of the low sample size of the two other species (Table B6). *Acanthurus nigricauda* and *A. olivaceus* were found only at a few sites of higher disturbance, and the model did not predict these species' high bite rates well from their lower sample size, especially once accounting for other factors. For scrapers, *S. rubroviolaceus* and *S. ghobban* had significantly lower bite rates relative to the other species (Table B6).

Across all species, bite rates decreased significantly with body size (LRT = 53, df = 1, $p<0.001$; Table B4). This result was driven by a significant decline in bite rate with body size for scrapers (LRT = 12.7, df = 1, $p<0.001$), which was reflected in scraper life phase: intermediate and terminal phase scrapers had marginally lower bite rates than juvenile scrapers, although the overall effect of life phase on scraper bite rates was non-significant (Table B5). In contrast, surgeonfish grazers exhibited a significant positive relationship between body size and bite rate (LRT = 20.9, df = 1, $p<0.001$); body size and life phase were non-significant for excavators and browsers (Table B5). Generally, removing size from our bite rate models did not change the overall significance of our effects. When the size covariate was removed from functional group models, however, phase had a significant effect for scrapers and excavators (Table B7).

Bite rates increased significantly when herbivores were subjected to heat stress (in 2015), but declined significantly (relative to 2015), one year after heat stress had subsided (LRT = 47.2, df = 2, p<0.001; Fig. 2.3; Table B4). This pattern was driven primarily by the grazers and scrapers, both of which exhibited significantly higher bite rates under heat stress (grazers: LRT = 17.8, df = 2, p<0.001; scrapers: LRT = 19.7, df = 2, p<0.001; Fig. 2.4; Table B6). Local disturbance had no effect on overall bite rates (Fig. 2.3; Table B4), and results for all functional group models were non-significant (Fig. 2.4; Table B5). Models that were fit without size were robust to these effects of disturbance on bite rates (Table B7).

2.4.2 Grazing impact

In contrast to bite rates, parrotfishes in the scraper functional group had the highest estimated grazing impacts (Fig. 2.2b). In the overall model, however, accounting for size and multiple comparisons, the only statistically significant difference in grazing impact across functional groups was a lower impact of browsers (LRT = 14.8, df = 3, p<0.01; Table B8). Grazing impact also differed significantly by species within the grazer (LRT = 14.5, df = 4, p<0.01) and scraper (LRT = 36.2, df = 5, p<0.001) functional groups (Table B9). For grazers, differences were driven primarily by the lower grazing impact of *A. nigricans* relative to the other species (Figure 2.2b), however, by accounting for size, it offset any differences between species such that the only difference that remained statistically significant was between *A. nigricans* and *A. lineatus* (Table B10). For scrapers, differences were mainly driven by a lower impact of *S. psittacus* and a higher impact of *S. rubroviolaceus* relative to the other species (Figure 2.2b; Table B11), but when accounting for size, this reversed pairwise differences such that *S. ghobban* showed a lower impact given its size and *S. tricolor* had a higher impact for a given size relative to the other parrotfish species (Table B10).

Grazing impact increased significantly with body size overall (LRT = 1427.1, df = 3, p<0.001; Table B8) and within each functional group (grazers: LRT = 357. 8, df = 3, p <0.001;

scrapers: LRT = 386.3, df = 3, p <0.001; browsers: LRT = 20.2, df = 3, p < 0.001; excavators: LRT = 256.8, df = 3, p <0.001), but did not vary with life phase for the parrotfish functional groups (Table B9). We found that life phase was a significant predictor of parrotfish grazing impact if the size covariate was removed (Table B11).

Overall, grazing impact was significantly higher in 2015 during the global heat stress event, but had significantly declined one year after heat stress had subsided (LRT = 33.4, df = 2, p<0.001; Fig. 2.3; Table B8). Again, this pattern was driven primarily by the grazers and the scrapers which both had significantly higher grazing impact in 2015 (grazers: LRT = 18.4, df = 2, p<0.001; scrapers: LRT = 12.6, df = 2, p<0.01; Fig. 2.4; Table B10). Local disturbance had no effect on overall grazing impact (Fig. 2.3; Table B8) or that of individual functional groups (Fig. 2.4; Table B9). Grazing impact results overall, without size, were robust to these effects of disturbance, except that differences between years were instead driven by scrapers and excavators (Table B11).

2.4.3 Selectivity

Most species showed the highest selectivity for turf algae (Fig. 2.2c; Table B12). However, turf selectivity still varied across functional groups (LRT = 19.1, df = 3, p<0.001), being significantly higher for grazers (except when compared to the excavators) and significantly lower for the browser (Fig. 2.3; Table B13). Selectivity did not vary amongst grazer species, but did amongst scrapers (LRT = 25.5, df = 5, p<0.001; Table B14): turf selectivity was significantly higher in *S. globiceps* compared to other scraper species, and that of *S. rubroviolaceus* was significantly higher than *S. ghobban* (Table B15). Parrotfish life phase affected turf selectivity only for excavators, with terminal phase individuals selecting for turf significantly more than other life phases (LRT = 12.3, df = 3, p<0.05; Table B15).

Overall, turf selectivity was not significantly affected by heat stress (LRT = 5.08, df = 2, p=0.079), except for in the excavators (LRT = 7.40, df = 2, p<0.05), which showed a slight decline in turf selectivity in 2015, followed by a significant increase in 2017 after the heat stress subsided (Table B15). Conversely, turf selectivity did vary significantly with human disturbance (LRT = 18.0, df = 4, p<0.001), with higher selectivity exhibited at sites with very high human disturbance and significantly lower selectivity at very low compared to low disturbance levels (Fig. 2.5a; Table B13). The browsers (LRT = 15.7, df = 3, p<0.01), excavators (LRT = 10.9, df = 4, p<0.05), and scrapers (LRT = 19.4, df = 4, p<0.001) all responded to very high disturbance in this way (Table B15); however the grazer species showed no significant differences across disturbance levels (LRT = 1.59, df = 4, p = 0.662; Table B14). There were some other differences across functional groups in their selectivity response to local disturbance. Turf selectivity was second highest at very low disturbance for both scrapers and browsers (Figure 2.5b). In fact, turf selectivity at these sites was significantly different from low and medium sites in scrapers and from medium sites in browsers (Table B15). In contrast, for excavators, turf selectivity was second highest at medium disturbance (Figure 2.5b), which significantly differed from low disturbance levels (Table B15). In general, turf selectivity was low at low disturbance sites for all functional groups (Figure 2.5b).

2.5 Discussion

Our results revealed substantial variation in bite rates, grazing impact and selectivity, but the degree to which these differ depends on the functional group and herbivory metric examined. We found that grazers had the highest bite rates and the highest selectivity for turf, but not necessarily the highest grazing impact, while our browser exhibited the slowest rates, the lowest grazing impact, and lower selectivity for turf. Within a multi-species functional group, we also detected significant differences between species, although responses were more variable between species within the scraper functional group than between pairs of grazer species. These results highlight the importance of species identity in quantifying herbivory (Adam et al. 2018; Ruttenberg et al. 2019).

We were also interested in examining the influence of fish size on herbivory. In accordance with other studies, we detected a significant relationship between bite rates and fish size (Bruggemann et al. 1994a; van Rooij et al. 1998), but again, the influence of body size differed depending on the functional group examined. Scrapers reduced their bite rates at larger sizes, while grazers showed increased rates with increasing fish size, and the relationship was unimportant for browsers and excavators. When we considered how body size relates to grazing impact, we found a significant positive linear relationship with fish size for all functional groups. This suggests that, despite varied influence of body size on species bite rates in different functional groups, an individual's grazing impact will be higher for the larger fish in all functional groups. This corroborates other studies which report larger herbivore impacts for larger-sized fish (Mumby 2006; Bonaldo and Bellwood 2008). Taken together, our results suggest these herbivores do exhibit different feeding behaviours, with a significant influence of size, and thus are likely playing different functional roles in the ecosystem.

We included 'grazing impact' to determine whether bite size modulates our understanding of the herbivore response at a species-level. This is somewhat similar to efforts carried out by others to calculate a metric for herbivore grazing pressure, although these commonly use grazing rates standardized by body mass rather than bite size (e.g. Bellwood et al. 2006; Hoey and Bellwood 2009; Longo et al. 2015; Lefcheck et al. 2019). Grazing impact was less variable across functional groups than bite rates, reflecting the modulating effect of gape size and suggesting that bite rates do not necessarily reflect an individual's herbivory impact. Grazers, as hypothesized, focussed their feeding on turf substrates, and thus had the highest bite rates; however, as they are smaller fish taking smaller bites, this did not translate to the highest grazing impact. In fact, when we account for fish size in our model, we detected no differences amongst grazer, scraper and excavator grazing impacts, only browsers showed significantly lower grazing impact. This counters our predictions that the larger parrotfish functional groups might exhibit greater impacts, as we expected that scraper impact would be significantly higher than the grazers. Other studies incorporating size into a metric for herbivory use biomass due to this influence of fish size on feeding rates (Bruggemann et al. 1994a,b; Hoey and Bellwood 2008; Lokrantz et al. 2008) and often find that larger-bodied fish exhibit greater impacts (Bonaldo and Bellwood 2008). These are often comparing within a single parrotfish species (e.g. *Scarus rivulatus*: Bonaldo and Bellwood 2008; *Bolbometopon muricatum*: McCauley et al. 2014) or consider a few parrotfishes (e.g. Lokrantz et al. 2008; Ong and Holland 2010), Here, we explicitly compare across functional groups (i.e. grazing surgeonfish vs. parrotfish) using individual bite size to guide our understanding of herbivore impact. We suggest that faster rates of small bites from grazers may be functionally similar to slower rates of larger bites from the scrapers and excavators. Our distinction between bite rates and grazing impact caution against using one metric alone to assess species-specific herbivory, as it may not reflect true differences between herbivores.

Our study also contributes insight to the discussion about functional redundancy in the herbivore community (see Burkepile and Hay 2011; Rasher et al. 2013; Streit et al. 2015; Kelly et al. 2016; Nash et al. 2016b). When bite rates alone are considered, our herbivore functional groups exhibit distinct differences and might be considered less redundant, but when grazing impacts are also considered, our results suggest some complementarity between functional groups. Surgeonfish grazers are thought to perform complementary functions to some parrotfish scrapers (Marshell and Mumby 2015; Kelly et al. 2016), but it is surprising that excavators also exhibit similar grazing impacts. When selectivity is also considered, however, the excavator functional group did exhibit varied responses, and thus is distinguished from the other functional groups. Notably, our browser (*Calotomus carolinus*) showed significantly distinct bite rates, grazing impact and selectivity compared to the other herbivore functional groups. In fact, *C. carolinus* was the only species that was frequently observed taking bites out of macroalgal fronds, suggesting there may be limited redundancy on Kiritimati's reefs with respect to the browsing function. This runs counter to previous reports of functional overlap between some herbivore species (Rasher et al. 2013; Brandl and Bellwood 2014); however, it corroborates a study of Hawaiian herbivores which found that browsers separated more distinctly from other functional groups when selectivity was taken into account (Kelly et al. 2016). There could be important ramifications for Kiritimati's reefs if this species is lost, as there would be few replacements to carry out the important macroalgal browsing function. That being said, we also found that *C. carolinus'* herbivore responses were relatively unaffected by either local human disturbance or severe thermal stress, suggesting that this function may be robust to both local and global disturbances.

Grazing impact and bite rates increased during the heat stress, contrary to our predictions that reef fish would not alter their feeding behaviours in response to such a stressor. The response was functional-group-specific, driven by significant changes in scraper and grazer functional groups. We detected no change in selectivity over time, which suggests that the response was not likely due to a change in what substrates the herbivores were feeding on. A number of studies investigating fish responses to heat stress and coral bleaching disturbance have documented how herbivores respond numerically, with most detecting an increase in herbivore density or biomass (Garpe et al. 2006; Adam et al. 2011; Gilmour et al. 2013), and some noting a greater effect of coral bleaching on smaller bodied individuals (Graham et al. 2007; Ledlie et al. 2007; Nash et al. 2016b). Studies that consider how herbivory rates are affected by disturbance generally consider sites at the same time points with differing benthic composition, or experimentally manipulate algal levels to compare how herbivory rates vary with altered substrate availability. Grazing rates did not differ between experimental treatments in one study (Williams et al. 2001), but most find that different compositions of fish are feeding in areas with different benthic composition (Bellwood et al. 2003; Bellwood et al. 2006; Chong-Seng et al. 2012; Plass-Johnson et al. 2015). We know generally that herbivore rates are determined by species identity (e.g. Adam et al. 2018), can vary over the course of the day (Bruggemann et al. 1994a; Polunin et al. 1995; Afeworki et al. 2013), and are influenced by fish size (Bonaldo et al. 2006; Lokrantz et al. 2008; Afeworki et al. 2013), but few explicitly consider a large-scale heat stress disturbance event as a driver of herbivory rates. Recently, a study of fish behaviour reported no change in overall bite rates following the 2015–2016 El Niño, which counters what we found here, although that study documented butterflyfish behaviour and not herbivorous fish (Keith et al. 2018). Since few studies directly quantifying herbivory have explicitly considered temporal variation (but see Lefèvre and Bellwood 2011), our results present a unique perspective on the response of herbivory to an extreme heat stress event. Given that we detected a reduction in bite rates and grazing impact once heat stress had subsided, it suggests that the response is short-lived, and may not necessarily reflect a sustained alteration of herbivore feeding behaviour.

One potential explanation for the detected increase in bite rates is the influence of the external environment. In 2015, Kiritimati experienced temperatures that were 1–2°C above its historical monthly maximum, with similar temperature increases regardless of position around the atoll (Claar et al. 2019). Metabolic theory suggests that metabolic rates of organisms scale with body size and temperature (Brown and Sibly 2012), with temperature increasing metabolism (Brown et al. 2004), up to an organism's thermal optimum, at which point processes like protein denaturation can reverse that relationship (Barneche et al. 2014). Since herbivorous fish are tropical ectotherms, their metabolic rates are mediated by the external environment, such that an increase in temperature would trigger increased metabolic demand (Brown et al. 2012). Indeed, across environments, it has been shown that metabolic rates are faster at warmer temperatures (Gillooly et al. 2001). In response to this increased metabolic demand, individuals exposed to warmer temperatures will likely respond by increasing consumption rates (Brown et al. 2012). Studies of marine systems have shown increased consumption at higher temperatures for herbivorous urchins (Carr and Bruno 2013) and an overall increase in total respiration of reef fish communities in response to increases in temperature (Barneche et al. 2014). Indeed, temperature is an important driver of many biological rates and for reef fish in particular it has also been shown to influence growth, which declines with increasing temperature (Munday et al. 2008b), and can modify reproductive success. For example, larval development of fish may be increased at warmer temperatures, but temperature may influence timing of reproduction to reduce success rates overall (Munday et al. 2008a). Our results could therefore reflect the influence of temperature on metabolic rate—herbivores may have increased their bite rates when temperatures were higher than normal in an attempt to meet increased energy demands through heightened resource consumption. Local human disturbance did not change the behavioural ecology of their feeding as temperature increases were similar across sites at all disturbance levels. This aligns with the results of other studies suggesting that temperature increases the grazing rates of certain species (Floeter et al. 2005; Smith 2008; Afeworki et al. 2013), and that some herbivores have higher feeding rates during the warmer summer months (Bellwood 1995; Lefèvre and Bellwood 2011). We did not find increased feeding rates during heat stress for all functional groups (e.g. browsers and excavators exhibited no change); however, the positive relationship between feeding and temperatures may not necessarily be universal among herbivores. For example, some Hawaiian parrotfish that experience seasonal temperature fluctuations of 2°C exhibit no change in feeding activity, or even show an increase during the cooler months (Ong and Holland 2010). Indeed there is evidence for species and even individual variation in responses to temperatures (Afeworki et al. 2013; Bruno et al. 2015). Our results highlight species variability in feeding responses to global heat stress, and caution against lumping herbivores into a single group when attempting to disentangle impacts of anthropogenic disturbance on the fish community.

The increased bite rates and grazing impact observed here suggest a behavioural response of the herbivorous fish on Kiritimati to El Niño-induced heat stress, which may have important implications for algal control following coral bleaching events. Many studies have documented changes in herbivore biomass following coral bleaching, with a general consensus that bleaching can positively affect herbivore abundance, and—by extension—the function of herbivory (e.g. reviews by Pratchett et al. 2008, 2011, 2014; Graham et al. 2015; Hoey et al. 2016b). As far as we are aware, our study is one of the first to document a direct positive response of species herbivory to a severe disturbance event. As of yet, we have not documented a clearly defined phase shift (as per Done 1992; Knowlton 2004) to algal dominance on Kiritimati, such that the detected increase in herbivory during the heat stress may have had some role in limiting algal proliferation. Although the increased feeding rates reported here were observed prior to the start of mass coral mortality, they likely continued throughout the heat stress event and may therefore have helped to limit algal proliferation following the onset of coral bleaching. Interestingly, the excavator *C. sordidus*—which did not exhibit a change in bite rates over time—showed increased turf selectivity following the extreme thermal stress event, which might have also helped to limit some turf algae. We do not suggest, however, that this function is solely carried out by this one species; rather, it is likely to be the result of a combination of herbivores working together (Rasher et al. 2013), and could be helped by diminutive species that are not normally observed (except see Kuempel and Altieri 2017). Alternatively, it could be a combination of physical factors and herbivory that is limiting algae following coral loss (Plass-Johnson et al. 2015; Heenan et al. 2016; Kumagai et al. 2018).

In contrast to the significant changes in herbivory that we observed through time, we found that local human disturbance did not influence herbivore bite rates or grazing impacts. These results contrast other studies that have found differing herbivore bite rates and feeding pressure across spatial scales (Hamilton et al. 2014; Longo et al. 2014) and differing rates between sites with varying levels of herbivore protection (Nash et al. 2016a). However, they are in line with others that did not report spatial differences (Cvitanovic and Bellwood 2009; Ferguson et al. 2017). The local disturbance gradient did have a limited effect on selectivity, in support of our predictions. Selectivity for turf was greater at higher levels of human disturbance (Fig. 2.5a), possibly because the substrate cover at the very high disturbance sites mostly consists of sediment or sand, so herbivores at these sites must concentrate their feeding on turf where it is available. Thus, while the rate of herbivory appears to remain constant across the gradient, we did detect some effect of local human disturbance on herbivore selectivity.

The fact that herbivore bite rates and grazing impact were affected by the heat stress event but were not significantly influenced by levels of local human disturbance suggests that these stressors are not impacting herbivores in the same way. The differential effect of these stressors is encouraging, as it could help to maintain the resilience of this ecosystem in the face of extreme climate-induced disturbance despite the co-occurring chronic local disturbance (Mora et al. 2016). However, this ability hinges on the health of the herbivore community, in terms of having both an abundant and diverse group of herbivores. Although herbivorous fish are not the main fisheries target on Kiritimati, they are still caught for consumption. If a combination of herbivore overfishing and increasing stress from climate change work together to harm this community in the future, we might see a loss of resilience and a phase shift to algal dominance if the reduced number of herbivore consumers are no longer able to control algal abundance (Mumby et al. 2006; Holbrook et al. 2016). We also found that herbivorous parrotfish species were more variable in their herbivory responses compared to surgeonfish species. The varied responses between herbivores in terms of bite rates, grazing impacts and selectivity highlight the importance of maintaining a diverse herbivore community; this is also an important consideration for management strategies that seek to protect herbivores and, ultimately, drive coral reef recovery (Mumby 2017).

Our functional group models for excavators and browsers are somewhat limited by only having one species representative, however since we were also interested in characterizing species-specific herbivory, we thought it fair to include them. Since the species in each of these models are the most abundantly observed for these functional groups, they were the best candidates to represent the group. An increased number of herbivore observations for other species belonging to these functional groups (e.g. *Chlorurus sp.* for excavators and *Naso sp.* for browsers) would increase the generality of the model results to apply to the rest of the functional group. This might be especially true for the browsers, for which we observed distinct responses, in order to identify whether the results observed represent a unique herbivory response of *C. carolinus* or whether they also apply to other browsers more generally.

With this study, we have taken the first step to quantifying herbivory at a species-level for four key herbivore functional groups on Kiritimati and we examine the influence of herbivore identity, size, and local and global stressors on the herbivore function. We have not yet attempted to scale herbivory estimates in order to make spatial or temporal comparisons at the community level, however we expect that herbivory might differ across a spatial gradient and over time if site-level density is also taken into account (Ruttenberg et al. 2019). Taken together, our results support the body of work on coral reef fish that indicate it is not advisable to consider herbivores as one functional entity, but rather as a guild made up of distinct species performing many functional roles (Adam et al. 2018). We maintain that our understanding of herbivory is context-dependent and size- and species-specific quantification is necessary, especially when quantifying functional roles to inform management strategies that seek to enhance reef resilience.

Table 2.1 Number of feeding observations for each herbivore species in each year, classified by family (Acanthuridae = surgeonfishes; Scaridae = parrotfishes) and functional group (FG). Bolded species are the 13 most commonly observed (n≥ 25 feeding observations) which were retained in the functional group analysis. Within each functional group, species are listed in descending order by their total number of observations.

FG	Family	Species	2013	2015	2017	Total
Browser	Scaridae	***Calotomus carolinus***	**15**	**1**	**70**	**86**
Excavator	Scaridae	***Chlorurus sordidus***	**211**	**75**	**144**	**430**
		C. microrhinos	0	0	1	1
Grazer	Acanthuridae	***Acanthurus nigricans***	**173**	**158**	**126**	**457**
		A. olivaceus	**5**	**32**	**15**	**52**
		A. lineatus	**19**	**8**	**10**	**37**
		A. nigricauda	**5**	**31**	**1**	**37**
		A. achilles	**23**	**3**	**5**	**31**
		A. triostegus	8	10	0	18
		A. nigrofuscus	4	1	0	5
		A. leucocheilus	1	0	1	2
		A. nigroris	1	0	0	1
		A. xanthopterus	0	1	0	1
Scraper	Scaridae	***Scarus frenatus***	**161**	**40**	**117**	**318**
		S. rubroviolaceus	**66**	**30**	**124**	**220**
		S. tricolor	**68**	**10**	**40**	**118**
		S. ghobban	**34**	**20**	**33**	**87**
		S. psittacus	**11**	**6**	**27**	**44**
		S. globiceps	**10**	**11**	**4**	**25**
		S. oviceps	1	0	12	13
		S. forsteni	1	0	0	1
		Total	817	437	730	1984

Table 2.2 Feeding observations for the 13 most commonly observed herbivore species (n≥ 25 observations) included in our functional group (FG) analysis at each disturbance level over three survey years. Within each functional group, species are listed in descending order by their total number of observations.

FG	Family	Species	Year	Very Low	Low	Medium	Very high	Total
Browser	Scaridae	*Calotomus carolinus*	2013	1	2	9	3	15
			2015	0	0	1	0	1
			2017	10	4	45	11	70
Excavator	Scaridae	*Chlorurus sordidus*	2013	44	68	83	16	211
			2015	13	10	46	6	75
			2017	59	26	56	3	144
Grazer	Acanthuridae	*Acanthurus nigricans*	2013	6	45	110	12	173
			2015	36	15	73	34	158
			2017	40	23	53	10	126
		A. olivaceus	2013	0	0	2	3	5
			2015	0	0	0	32	32
			2017	0	0	0	15	15
		A. lineatus	2013	10	6	3	0	19
			2015	0	4	4	0	8
			2017	0	10	0	0	10
		A. nigricauda	2013	0	0	4	1	5
			2015	0	0	3	28	31
			2017	0	0	1	0	1
		A. achilles	2013	1	0	11	11	23
			2015	0	1	2	0	3
			2017	0	0	5	0	5
Scraper	Scaridae	*Scarus frenatus*	2013	22	38	93	8	161
			2015	9	2	29	0	40
			2017	36	23	58	0	117
		S. rubroviolaceus	2013	5	12	30	19	66
			2015	1	1	17	11	30
			2017	28	29	49	18	124
		S. tricolor	2013	4	17	19	28	68
			2015	0	0	0	10	10
			2017	7	11	7	15	40
		S. psittacus	2013	1	0	4	6	11
			2015	0	0	0	6	6
			2017	2	0	10	15	27
		S. ghobban	2013	0	2	19	13	34
			2015	0	0	3	17	20
			2017	3	0	10	20	33
		S. globiceps	2013	5	4	1	0	10
			2015	5	0	1	5	11
			2017	3	1	0	0	4
		Total		351	354	861	376	1942

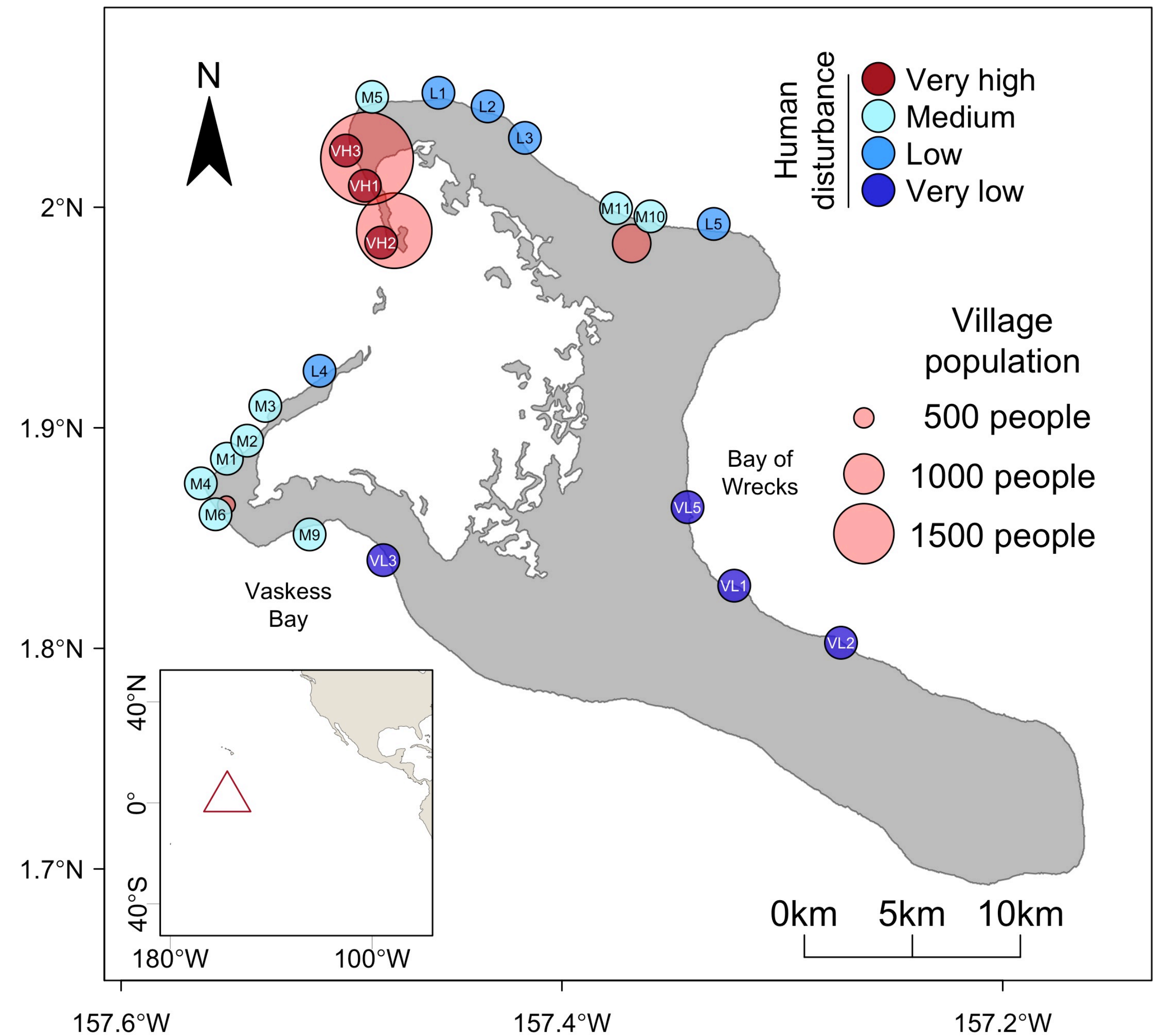

Figure 2.1 Map of twenty-one forereef study sites and villages on Kiritimati (Christmas Island), Republic of Kiribati. Sites are coloured based on levels of local human disturbance, and villages (red circles) are scaled to the human population. Inset indicates the island's location (triangle) in the equatorial Pacific Ocean.

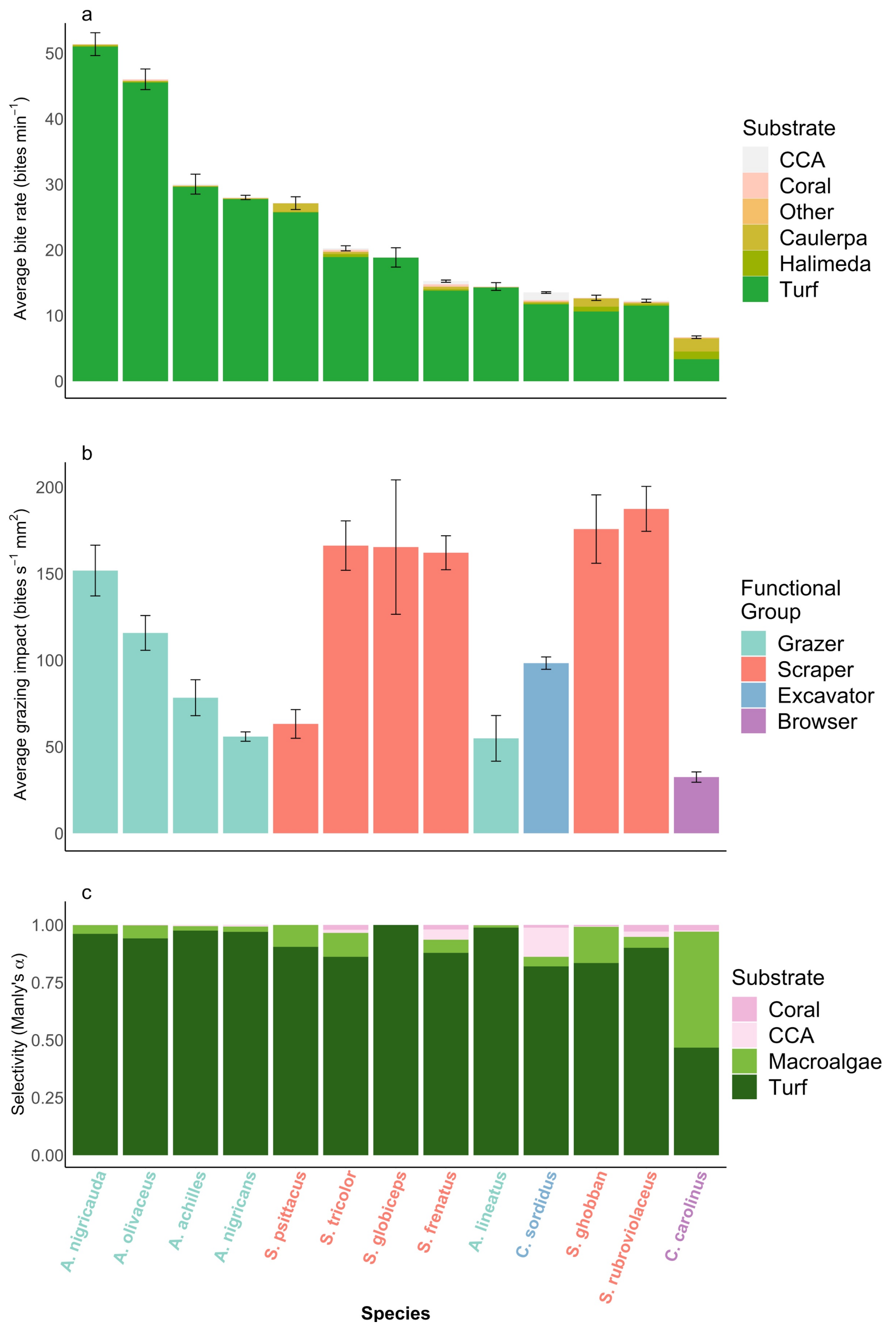

Figure 2.2 Herbivory: (a) bite rate (±SE); (b) grazing impact (±SE) (bite rate × gape area); (c) selectivity, derived from in situ feeding observations of herbivorous (surgeonfish and parrotfish) reef fishes, averaged over three years (2013, 2015, 2017) for the 13 most commonly observed species on Kiritimati. Species are ordered from highest to lowest bite rate, with the species' text colour denoting functional group, following colour coding in panel (b). CCA= crustose coralline algae.

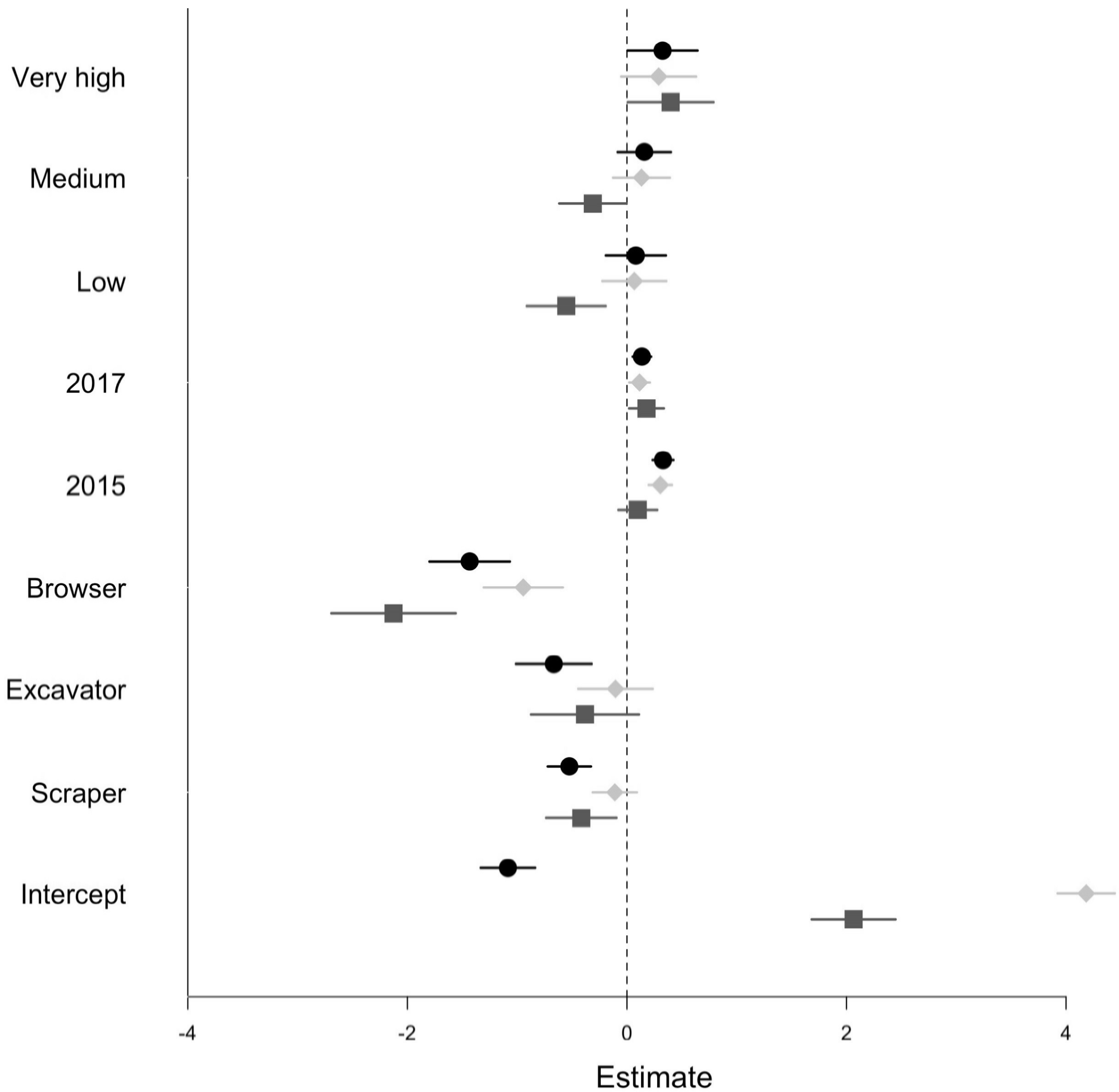

Figure 2.3 Effect size estimates and 95% confidence intervals for predictor coefficients: Local Disturbance (Very high, Medium, Low relative to Very low); Year (2017, 2015 relative to 2013); Functional Group (Scraper, Excavator, Browser relative to Grazer) from generalized linear mixed models of overall herbivore: (●) bite rates, (◇) grazing impact and (■) selectivity responses.

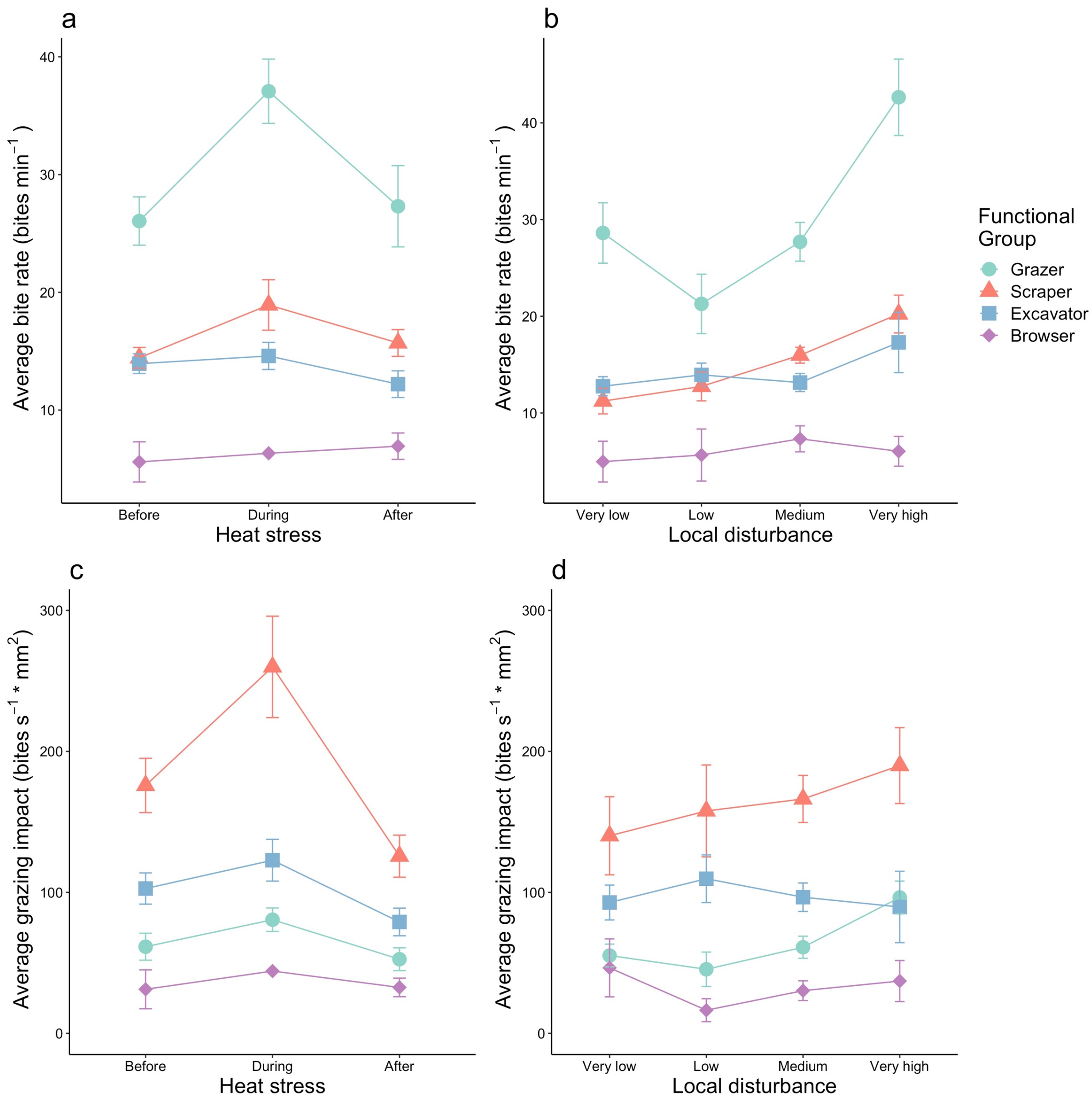

Figure 2.4 Herbivorous fish functional group mean and 95% confidence intervals of (a, b) bite rates and (c, d) grazing impacts to (a, c) heat stress and (b, d) local human disturbance.

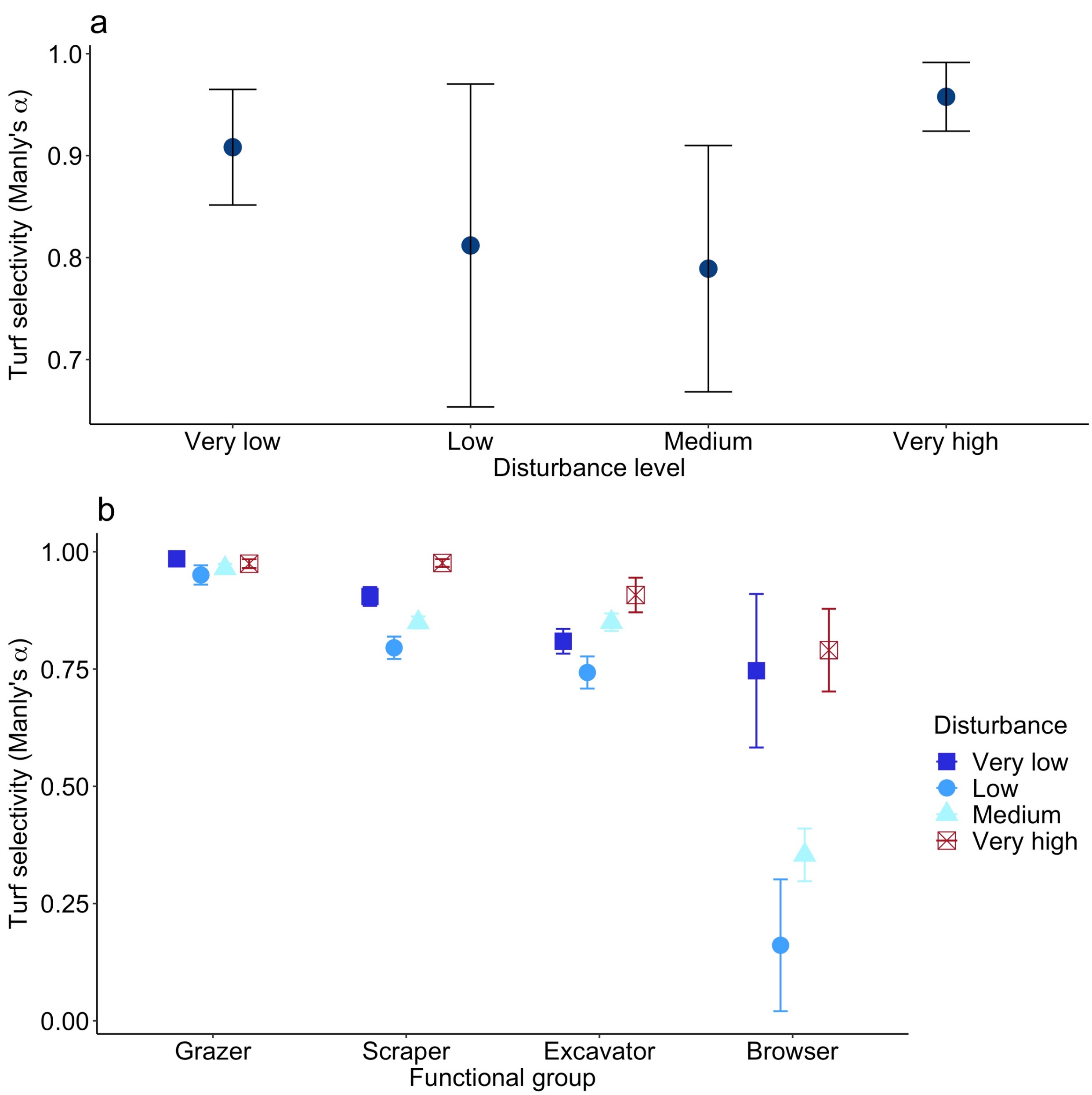

Figure 2.5 Mean and 95% confidence intervals of estimated herbivore selectivity for turf substrates: (a) averaged across all observed species for each disturbance level; (b) by functional group for each disturbance level.

Chapter 3 – Herbivore assemblage grazing impact is robust to a significant coral bleaching event

3.1 Abstract

The prevalence of marine heatwaves and their implications for ecosystem functioning has renewed interest in understanding the response of ecological functions to global ecosystem disturbance. The 2015–2016 El Niño elevated ocean temperatures over a prolonged period causing mass coral bleaching worldwide. Here, we aimed to assess the ecosystem role of herbivorous coral reef fishes [surgeonfish (family Acanthuridae) and parrotfish (family Scaridae)] in terms of turf algae removal, to understand how the grazing function of this assemblage is affected by chronic local disturbance and a global pulse heat stress event. To determine grazing function, we quantified a metric for average species impact, measured in bites per year, by integrating species' and size-specific estimates of herbivore grazing, derived from fish bite rate observations, with underwater visual census (UVC) data of species' abundances at sites spanning a gradient of chronic local disturbance (from very low to very high) on Kiritimati (Christmas Island; central equatorial Pacific). Both data types were recorded prior to (2013) and after (2017 and 2018) the El Niño heat stress event. Multivariate redundancy analysis, constrained by the levels of local disturbance and a factor for 'Before' or 'After' the El Niño, showed that herbivore species exerted similar impacts at sites around the island, despite being subject to varying levels of local disturbance. Species' impacts at sites exposed to very high human disturbance, however, were more distinct and driven by few species. Further, we summed average species' impacts at each site by functional group and utilized generalized linear modelling to determine the influence of herbivore identity, local disturbance and global heat stress on assemblage-level grazing impact. Herbivore assemblage grazing impact was distinct among the different functional groups and increased after the El Niño, implying that the grazing

function of the assemblage was not compromised by a global heat stress event. Our results suggest that the ecosystem role of herbivorous fish, in terms of their grazing function, is fairly robust to disturbance, which is an encouraging prospect for future recovery given anticipated increase in anthropogenic disturbance to coral reef ecosystems.

3.2 Introduction

Marine heatwaves and severe disturbance events are becoming more prevalent, with significant consequences for ecological structure and functioning of marine ecosystems (Smale et al. 2019). Given worldwide decline in coral reef cover (Bruno and Selig 2007), shifts in coral reef assemblages (Hughes et al. 2018b), and the increasing occurrence of severe coral bleaching events (Hughes et al. 2018a), there is continued interest in understanding the response of these ecosystems to large-scale disturbance. There is also growing recognition that we need to better understand the response of certain ecological functions to ecosystem disturbance and how it might modulate the capacity of certain organisms to deliver ecosystem services (Bellwood et al. 2019b). This becomes especially pertinent if the ultimate goal is management of reef functions for conferring resilience to devastating disturbance events (Bellwood et al. 2004; Bellwood et al. 2019a; Williams et al. 2019).

The management of coral reef herbivores is one approach proposed for conferring reef resilience and recovery from severe disturbance events. This is often achieved through the establishment of Marine Protected Areas (MPAs) and designating areas as off-limits to fishing or extraction (e.g. Edgar et al. 2014). The idea behind establishing MPAs for achieving reef resilience (a.k.a the 'managed resilience hypothesis') is that it acts through a cascading pathway from grazing herbivores to the benthic coral community (e.g. see Bruno et al. 2019). In essence, the absence of fishing benefits the large herbivorous fish, which can then consume the algae, to open up space and facilitate new coral recruitment, eventually enabling re-establishment and growth of adult coral colonies. Some go further to suggest the restocking of herbivore populations as a mechanism of algal control (Abelson et al. 2016). While some studies have demonstrated the benefit of herbivores on coral recruitment and cover (Mumby et al. 2006; Steneck et al. 2014; Suchley and Alvarez-Filip 2017; Steneck et al. 2018), others believe that establishing MPAs does not necessarily result in improved coral resilience or protection of the ecosystem against environmental stressors (Hilborn 2015; Bruno et al. 2019). Regardless, these management approaches indicate the influence of herbivores for driving coral reef ecosystem dynamics.

In order to understand the role herbivores play in mediating reef dynamics, it is necessary to quantify their functional impact, and a lot of effort has gone into understanding ecosystem functions of herbivorous fish (reviewed by Bonaldo et al. 2014; Puk et al. 2016). In this chapter, we define 'herbivore function' in terms of their feeding impact, and we consider the overall impact of a species to be the result of its per-capita effects as well as its density in the community.

Three main feeding functions attributed to parrotfish herbivores are scraping (i.e. removing algal turfs from hard substrates), browsing (i.e. targeting larger, fleshy macroalgal fronds) and excavating (i.e. taking deeper bites of coral substrates, encompassing another key parrotfish function of bioerosion) (Green and Bellwood 2009). These functional roles are distributed between genera within the parrotfish family, for example, *Scarus* species function as scrapers (Adam et al. 2018), while browsing is mainly carried out by *Sparisoma* species in the Caribbean and *Calotomus* species in the Indo-Pacific (Bonaldo et al. 2014). Larger species in the *Chlorurus* genus function as excavators (e.g. Bellwood 1995), but some of the larger species in other genera (e.g. *Sparisoma viride*) are also attributed with this function (Bruggemann et al. 1994a, 1994b). One species, the humphead parrotfish (*Bolbometopon muricatum*), is a particularly large and influential excavator when present in some locations, but can be largely absent from others due to overfishing (Bellwood et al. 2003). Herbivorous surgeonfish (family Acanthuridae) are considered complementary to parrotfish in reef ecosystems because they also carry out important grazing functions (i.e. removing algal turfs: Marshell and Mumby 2015).

One challenge in determining the role of herbivores as drivers of reef resilience is how to scale individual herbivore feeding responses to an assemblage-level estimate of ecosystem function. Such a step is necessary to make conclusions about how their capacity to deliver the ecosystem service of algal control may be altered by significant disturbances. Biomass of functional groups is often used as a proxy for function when investigating fish assemblage response to disturbance (e.g. reviewed by Pratchett et al. 2014; Graham et al. 2015). This allows the use of fish survey data to determine how fish abundance changes with a significant disturbance event and is usually based on the assumption that presence in surveys equates to function. This has been found to be a fair assumption in some cases of remote fish surveys which indicated that herbivore presence in a video was usually associated with an observation of the fish feeding (Fox and Bellwood 2008; Streit et al. 2019). However, some caution using biomass alone to quantify ecosystem processes as species that are responsible for a particular ecosystem function may be missed by conventional survey methods (Ford et al. 2016). As an example, some species not usually counted by fish surveys, have been captured on video as the sole species carrying out a particular function in certain reef habitats (e.g. rabbitfishes in Fox and Bellwood 2008; Ford et al. 2016; *Naso* sp in Plass-Johnson et al. 2015).

In light of this, approaches to quantify ecological functioning in response to disturbances do not typically rely solely on changes in fish biomass. One such method is to take a 'functional diversity' approach to examine changes in functional assemblage structure concurrent with changes in taxonomic structure (e.g. Villéger et al. 2008; Villéger et al. 2010; Mouillot et al. 2013; Mouillot et al. 2014; Boersma et al. 2016; Bierwagen et al. 2018). Results of this approach indicate that change in taxonomic structure is distinct from the variation in functional structure of the assemblage and suggest there are diverse responses by fish functional groups to significant disturbance events (Bierwagen et al. 2018; Richardson et al. 2018; Stuart-Smith et al. 2018; McClure et al. 2019). In particular, coral bleaching disturbances will impact fish assemblages by driving a loss of species that carry out specialized functions as the assemblage shifts to be dominated by more generalist species (Richardson et al. 2018; Stuart-Smith et al. 2018; McClure et al. 2019). The consequent loss of certain functions can further degrade the overall health of the ecosystem (Pratchett et al. 2011). Importantly, functional diversity studies indicate that even highly diverse systems, which seem to exhibit high redundancy for some ecological functions, are still vulnerable to species loss and loss of function (Mouillot et al. 2014). One issue with the functional diversity approach, however, is that it still mainly relies on the change in relative species abundance when discussing changes in functional structure and does not directly examine responses in behaviour.

Other approaches to quantify herbivore function do account for feeding behaviours, the most common is to take a direct approach by observing individual foraging behaviour and then multiplying it by species' densities from fish surveys (e.g. Fox and Bellwood 2007; Hoey et al. 2016; Ruttenberg et al. 2019; Robinson et al. 2019a). The body of work that defines key functional roles of herbivores has largely focused on a few key species. A lot of the early work on herbivore functional roles references studies of the stoplight parrotfish, *Sparisoma viride,* and some foundational papers that defined certain biological relationships between fish body size and food intake (Bruggemann et al. 1994a, 1994b; van Rooij et al. 1998). For example, when defining the functional role of the herbivore guild, some use the estimates of one species and scale up to a guild-wide estimate assuming the relationships are conserved phylogenetically (e.g. Paddack et al. 2006). But, studies have also shown that the ecological impact of herbivores is significantly different between species and even between fish of different sizes or life phases (Mumby 2006; Fox and Bellwood 2007; Bonaldo and Bellwood 2008). Most agree that herbivore identity is key in defining ecological impacts, as different species can be dominant drivers of impacts in different reef habitats (Ruttenberg et al. 2019). Fish size is also important as it relates to gape size (Dunic and Baum 2017) and thus larger fish tend to have larger bites and greater impacts on the benthic substrate (Mumby 2006). Some studies take size into account by standardizing bite rates by fish biomass (e.g. Bellwood et al. 2006) and others include bite volumes taken from bite scar measurements, usually gleaned from the literature (Bellwood et al. 2003). Since some fish, like surgeonfish, do not leave noticeable bite scars, this could preclude the inclusion of bite size in a quantification of herbivore impact. But there is still a case for taking a species and size-specific approach when calculating an estimate of ecosystem function for the herbivore assemblage.

Quantifying the functional roles of herbivores at an assemblage-level thus requires some estimate of (i) species-specific bite rates, to indicate feeding behaviour, (ii) gape sizes, to represent size-specific per-capita impacts, and (iii) abundance or density, to estimate overall species impact. Rather than quantifying responses to disturbance, most studies that have quantified fish functional roles using this approach focussed on biological comparisons amongst species (e.g. Bellwood and Choat 1990; Choat and Clements 1993; Polunin et al. 1995; Alwany et al. 2009; Hoey and Bellwood 2009; Ong and Holland 2010; Streit et al. 2015; Tebbett et al. 2017a; Adam et al. 2018), or habitats (Fox and Bellwood 2007; Hoey and Bellwood 2008, Cvitanovic and Bellwood 2009; Rasher et al. 2013; Hamilton et al. 2014; Longo et al. 2015; Marshell and Mumby 2015; Ferguson et al. 2017; Kelly et al. 2017). From these studies, we have come to understand that different functional groups, species within a functional group, and even individuals of different sizes within species exhibit varied feeding behaviours, with different consequences for the functional roles they carry out. The composition of species at particular sites across a spatial gradient can also determine ecosystem function in a given habitat, as some have shown certain functions such as bioerosion or macroalgal browsing to be carried out by one species alone (e.g. Alwany et al. 2009; Hoey et al. 2009; Lefèvre and Bellwood 2011). Others consider the drivers of assemblage-level herbivory, indicating the influence of biomass and species diversity on herbivore assemblage function, but also highlighting the role that benthic processes such as turf height or substrate availability can have on the grazing function (Lefcheck et al. 2019; Robinson et al. 2019a). Due to a paucity of studies that examine the behavioural responses of herbivorous fish to ecosystem-wide disturbance (Pratchett et al. 2018), we have yet to gain a comprehensive understanding of how key herbivore feeding functions are altered over time by significant disturbance events, especially events of extreme thermal stress which are now a predominant threat to coral reef ecosystem health.

In this study, we examine the ecosystem function of herbivores within the context of local and global (i.e. heat stress) disturbance. We integrate visual census surveys of coral reef fish assemblages of Kiritimati (Christmas Island, Republic of Kiribati; 01°52’N 157°24’W) with size- and species-specific estimates of grazing impact to quantify the per-capita impacts of surgeonfish and parrotfish herbivores in terms of their turf removal function (hereby referred to as ‘average species impact’). We use these per-capita impacts to examine spatiotemporal variation in herbivore function across a gradient of local human disturbance and over time. Further, we use our quantification of the per-capita grazing impact function (i.e. average species impact) to examine how the summed impacts of the herbivore assemblage varies i) across functional groups, ii) along a local gradient of human disturbance and iii) between years that span a significant coral bleaching and mortality event, driven by the 2015–2016 El Niño thermal stress event. We hypothesize that we will detect spatiotemporal variation in per-capita grazing impacts as a result of species occupying different densities in different sites across a spatial gradient. Further, we hypothesize the summed impacts to be significantly variable between functional groups, due to differences in per-capita species impacts combined with varied densities. Finally, we expect the overall herbivore assemblage function will be influenced by anthropogenic disturbances.

3.3 Methods

3.3.1 Study site

We surveyed the herbivorous fish assemblage [surgeonfish (family Acanthuridae) and parrotfish (family Scaridae)] of Kiritimati (Christmas Island, Republic of Kiribati; 01°52’N 157°24’W) at 23 shallow forereef sites (10–12 m depth) over a six year period that included time points before (2013) and after (2017 and 2018) the 2015–2016 El Niño global heat stress event that caused mass coral mortality. Kiritimati is the world’s largest coral atoll by land mass, located within the Pacific Ocean’s Northern Line Islands. The island’s 6,500 inhabitants (Kiribati National Statistics Office 2016) aggregate on its northwestern side creating a spatial gradient of local human disturbance on the surrounding reefs. Survey sites have been assigned to one of five human disturbance levels (very low, low, medium, high, very high), by combining spatial data on fishing intensity (Watson et al. 2016) and human population density (Claar et al. in revision; Magel et al. 2019; Magel et al. in revision) (Fig. 3.1).

3.3.2 Data collection

Herbivore behavioural observations

Feeding observations were recorded for surgeonfish and parrotfish species as these are the most common herbivorous fish families on Kiritimati. At each site, a trained scientific diver located a 'focal' herbivorous fish and followed it at a distance of at least two metres so as not to disturb feeding behaviour. Divers recorded the species, life phase (Juvenile [J], Intermediate [IP] or Terminal Phase [TP] of parrotfish), size estimate (total length), and the number of bites taken out of each major food substrate type over a timed interval that ranged from two to six minutes (mean 4.03 min ± 0.02 SE). Observations were discontinued if the fish showed a marked response to the diver's presence. Food substrates were categorized as turf algae, encrusting coralline algae (CCA), coral, or macroalgae identified to genus (i.e. *Halimeda*, *Caulerpa*, *Dictyosphaeria, Galaxaura, Lobophora* and *Mesopora*). Herbivores were categorized into four functional groups: grazers, scrapers, excavators, and browsers (Yeager et al. 2017).

Herbivore surveys

Standard underwater visual census (UVC) surveys were used to quantify the abundance of herbivores in the fish community on Kiritimati. The UVC surveys were conducted using standard belt transect methods following Sandin et al. (2008) to generate site-level estimates of herbivore density (Table C1). At each site, a pair of scientific divers swimming in tandem along the belt transect recorded fish size (total length), abundance and species identification. Three 25 m transects, each separated by 10 m were laid along a 10–12 m isobath. For each transect, fishes

≥ 20 cm total length were counted in an 8 m wide strip, followed by fishes < 20 cm total length counted in a 4 m wide strip while divers swam in the reverse direction.

Fish dives were carried out during daylight hours between 07:23 – 17:43 hrs for herbivore observations and 07:35 – 18:04 hrs for fish surveys. All scientific divers were experienced in species identification and practiced in estimating fish lengths to the nearest cm.

3.3.3 Data processing

Calculating herbivore impact

Our dataset for average species impact included 18 species from 23 sites totalling 258 observations over three sampling years (Table 3.1; Table C1). We focus on turf substrates as it was the primary benthic substrate targeted by these species (97% of Acanthuridae bites, 85% of Scaridae bites). The species grazing impact was calculated by multiplying individual turf bite rates by size-specific gape area and taking the average over all individuals of a species observed at a site in a given year (**Equation 1**). We used published regression equations (Dunic and Baum 2017) relating gape area (gape width and gape height in mm, converted to m^2 for analysis) to fish body size for five of our herbivore species (*Acanthurus nigricans*, *A. olivaceus, Chlorurus sordidus, Scarus frenatus, and S. rubroviolaceus*). For the remaining species, we used average gape size ~ body size regressions of its congeners except for *Calotomus carolinus,* for which we used the gape regressions of *S. frenatus,* as it was our closest species estimate in the Scaridae family (Table B2). We converted species impact to units of m^2 per day, assuming a 10-hour feeding day (similar to Bonaldo and Bellwood 2008; Hamilton et al. 2014).

Equation 1 : $Sp.Impact = mean[\frac{\#\ bites\ on\ turf}{day} \times\ gape\ area\ (m^2)]$

We calculated the per-capita average species impact by multiplying the average species grazing impact (i.e. *Sp. Impact* from Equation 1) by the average species density per site in a given year (**Equation 2**). Site and year specific mean densities per m^2 were calculated by standardizing the species count per site per year by area surveyed and averaging observer replicates for each species. A yearly impact was found by multiplying the estimate by 365.

Equation 2: $Average\ Species\ Impact = Sp.Impact\ \left(\frac{bites \cdot m^2}{day}\right) \times\ Mean\ Sp.\ Density\ \left(\frac{\#\ fish}{m^2}\right) \times \frac{365\ days}{1\ year}$

We ended up with a metric of the per-capita average species impact in bites per year. To account for errors in our estimate, we estimated the standard deviation and variance of each measurement mean in the calculation (e.g. average species grazing impact, average site-level density; similar to Ruttenberg et al. 2019). Since the per-capita average species impact was a result of a multiplication of two estimated measurements, we calculated the compound error associated with this estimate as follows (similar to Bellwood 1995; Hoey and Bellwood 2008; Hoey et al. 2016):

$$Error = |Average\ Species\ Impact\ Estimate| \cdot \sqrt{\left(\frac{\delta\ Sp.\ Impact}{Sp.\ Impact}\right)^2 + \left(\frac{\delta\ Sp.Density}{Sp.Density}\right)^2}$$

With the uncertainty in the species grazing impact and species density estimates (δ) represented as the standard deviation of the means.

3.3.4 Data visualization

To visualize the ecosystem function of herbivory, we present the community impact values (i.e. a matrix of site-year combinations by average species' impacts) with a constrained redundancy analysis (RDA). It is essentially an extension of a principle components analysis (PCA) that explicitly models response variables as a function of explanatory variables, which is appropriate for relating multiple species with multiple explanatory variables (Zuur et al. 2007). Mathematically, performing an RDA extends multiple linear regression by allowing for the regression of multiple response variables on multiple explanatory variables and then subjects the generated matrix of fitted response values from those regressions to PCA (Legendre and Legendre 2012). Generally, it is used to extract and summarise the variation in a set of response variables (in our case average species impact values) that might be explained by a set of explanatory (or constraining) variables (Buttigieg and Ramette 2014).

First, we use the multivariate RDA analysis to visualize how the per-capita average species' impacts vary across sites that span our local disturbance gradient and over a time span associated with the 2015–2016 El Niño heat stress event. This constrained ordination allows us to visualize which species are associated with different levels of our constraints. It also affords us the ability to determine how much of the variation in herbivore impact values is explained by our constraining variables. Then, we summed the per-capita average species' impacts at each site by functional group and applied a univariate approach to model assemblage-level grazing impact as a function of herbivore identity (functional group), local disturbance and the El Niño factor for the global heat stress event to determine their influence on the overall grazing impact function.

3.3.5 Data analysis

Multivariate analysis

Our multivariate assessment consisted of fitting a constrained ordination model using the *rda* function in the *vegan* package (Oksanen et al. 2017) with standardized average species' impacts as the response, constrained by local human disturbance and a factor identifying the timing of the El Niño heat stress disturbance [Before (2013) and After (2017, 2018)]. Prior to analysis and plotting, we used the *decostand* function in the *vegan* package (Oksanen et al. 2017) to standardize average species impact values by scaling to zero mean and unit variance. We chose to standardize our response since it was not raw count data and such a step is an acceptable alternative for performing data transformations (Legendre and Legendre 2012). We present the redundancy statistic from the output of our multivariate RDA model which is analogous to the R^2 of multiple regression (Legendre and Legendre 2012). To assess the significance of our overall RDA model and of our constraining explanatory variables on average species' impacts, we conducted anova-like permutation tests with 9999 permutations using the *anova.cca* function in *vegan* (Oksanen et al. 2017). We also conducted a variance partitioning analysis to determine the amount of variation in the community that was explained by each of our constraining variables, using *varpart* from the *vegan* package (Oksanen et al. 2017).

Univariate analysis

To assess whether the herbivore assemblage-level grazing impact varies by functional group, across a gradient of local disturbance, or over time following a significant global heat stress event, we modelled average species impact summed by functional group at each site in each year as a response with a gamma distributed (link = "log") generalized linear mixed model using *glmer* (Bates et al. 2015). We included predictors for herbivore functional group (grazer, scraper, excavator, and browser), local disturbance level (very low, low, medium, high and very high), and a factor for the timing of the El Niño heat stress (Before or After) as fixed effects with site as a random effect. We accounted for the error associated with the estimates of grazing impact by including the compound error term as a weight in our model. Specifying analysis weights acknowledges that these are 'known' values that vary from observation to observation, and by including the weight term in our model, the parameter estimates are divided by these values for each observation (Bates et al. 2015). We conducted likelihood-ratio tests (LRT) to determine the significance of our fixed factor predictors on the herbivore assemblage-level grazing impact. If there was a significant effect detected, we conducted post-hoc pairwise Tukey tests to compare levels. The p-values were adjusted for multiple comparisons using the single-step method employed by the *glht* function in the *multcomp* package (Hothorn et al. 2008).

Analyses were conducted in R version 3.3.3 (R Core Team 2017).

3.4 Results

3.4.1 Multivariate analysis

The RDA produces an ordination plot to help visually summarise patterns of variation in our per-capita average species impact response which can be explained by our disturbance explanatory variables. The distances between the observations (site and year combinations) can be interpreted as an approximation of their distance in multivariate space, such that points that ordinate closer together are expected to have similar variable (per-capita average species impact) values (Zuur et al. 2007). The RDA of the community described a significant solution for herbivore species' impacts (pseudo-F = 1.58 df = 5, $p < 0.05$), as determined by permutation test on the overall significance of the canonical relationship. Our constraining variables for local human disturbance and the El Niño heat stress, together, explained ~17% of the variation in the standardized herbivore community impact, however once adjusted for sample size and the number of explanatory variables, it accounted for ~6% (Table C2). Local human disturbance accounted for 13.7% (Adjusted redundancy statistic = 5%) of the variation in the community, while the El Niño accounted for 3.7% of that variation (Adjusted redundancy statistic = 1.5%), however our variance partitioning analysis and permutation tests suggest these constraining variables were not a significant to explain the variation on their own (Table C2). The first two canonical axes (RDA1 and RDA2) accounted for 12% of the total variance of the ordination (Table C3) and 69% of the constrained variance (Table C4).

The local disturbance gradient is contributing to the variation in the first RDA axis and the timing associated with the El Niño is contributing to the second (Fig. 3.2). The average scores for sites at very high disturbance levels were higher than other disturbance levels, and the centroid score for this level separated out from others along RDA1 (Fig. 3.2a; Fig. 3.3a). The variation created across disturbance levels is due, in part, to the association of *Acanthurus olivaceus* and *Scarus tricolor* with very high disturbance sites (Fig. 3.2b). The average scores for sites after the El Niño were higher than scores for sites before, and the centroid scores for this factor separated out along RDA2 (Fig. 3.2a; Fig. 3.3b). *Acanthurus nigrofuscus, A. nigricauda,* and *S. rubroviolaceus* grouped together and were associated with the centroid score for 'Before'. Similarly, *S. forsteni, S. globiceps, S. psittacus,* and *A. leucocheilus* showed similar impacts associated with the centroid score for 'After' the El Niño. Notably, the species score for *Calotomus carolinus* did not ordinate closely to other species (Fig. 3.2b).

3.4.2 Univariate analysis

We found that assemblage-level grazing impact varied significantly amongst functional groups (LRT = 561.72, df = 3, p <0.001; Fig. 3.4; Table C5). Scrapers had the highest impact, followed by grazers then excavators, and browsers had the lowest grazing impact (Fig. 3.5a; Table C5). Although grazing impact tended to be higher at sites with very high local disturbance, the high variability in estimates at these sites, meant that this difference was not statistically significant (LRT = 3.67, df = 4, p = 0.45; Fig. 3.5c). The model indicated a significantly higher grazing impact of herbivores after the El Niño (LRT= 70.30, df = 1, $p < 0.001$; Fig. 3.5b; Table C5).

3.5 Discussion

Our multivariate assessment revealed limited variation in average species' impacts with respect to disturbance. A greater proportion of the variation across sites was explained by the local human disturbance gradient than the time period associated with an extreme thermal stress event and global coral bleaching disturbance, however these factors alone were not strong explanatory variables for the variation. When we summed herbivore species' impacts at each site by functional group, we found functional groups exhibited significantly variable grazing impacts, which were similar across the local disturbance gradient, but increased following the global heat stress event.

Per-capita effects

Anthropogenic differences

Over our spatial gradient of local human disturbance, most sites appeared together in the ordination, but we did observe greater species' impacts at very high disturbance levels, driven mainly by *Acanthurus olivaceus* and *Scarus tricolor*. This is in line with our hypothesis that per-capita species impacts across a spatiotemporal gradient will be driven by different species occupying different densities in different sites This separation of herbivore impacts at very high disturbance is also in accordance with other studies that have documented spatial differences in herbivore ecological processes (e.g. Longo et al. 2014; Ruttenberg et al. 2019). It was surprising to find, however, that herbivore impacts were higher where human disturbance was also highest. One might expect that herbivores would fare better where proximity to human populations and fishing pressure were reduced such that herbivory would be higher in areas of low human presence (Robinson et al. 2019a), but we found the opposite. We did find, however, that there were a greater number of species contributing per-capita impact values at the lower disturbance levels. What this suggest is that two species, *A. olivaceus* and *S. tricolor,* were able to maintain high levels of impact, despite being in highly disturbed areas, such that the herbivory function was being disproportionately carried out by a few locally abundant species where disturbance was very high. In less disturbed sites, the herbivory function was spread between a greater number of species. Other studies of herbivore functional roles also tend to find that functions are driven by different species compositions in different areas (e.g. Rasher et al. 2013; Longo et al. 2015; Carlson et al. 2017). Some also document disproportionate feeding pressure to fish biomass for some acanthurid species (Longo et al. 2015), similar to what we saw for the surgeonfish *A. olivaceus*. *Acanthurus olivaceus* appears to exhibit distinct feeding behaviours compared to other species (Kelly et al. 2016) and in our case, it seems to be an important herbivore at very highly disturbed sites. Our results highlight the importance of species identity and diversity of the herbivore assemblage in examining function (similar to Nash et al. 2016a; Topor et al. 2019).

Species differences

Our constrained redundancy analysis also revealed that herbivore functional groups did not separate out in multivariate space, but rather we observed species from different functional groups that appeared more closely clustered, and sometimes further away from other species in the same functional group. This is seen, for example, with two species classified as grazers, *A. nigricauda* and *A. nigrofuscus*, which grouped with a scraper *Scarus rubroviolaceus*. One exception was *Calotomus carolinus,* our browser, whose species score did not appear in close proximity to many of the others. This last finding is similar to the results of a multivariate analysis of herbivore functional roles in Hawaii, which looked at clustering of herbivores by bite rates, and found that *C. carolinus* and other browsing *Naso* species clustered separately from grazing and scraping species (Kelly et al. 2016). It should be noted that in our analysis of herbivore grazing function, we only quantified herbivore impacts on turf substrates and did not quantify other functional roles such as macroalgal browsing or coral bioerosion, which are known to be important functions carried out by herbivorous fish (e.g. McCauley et al. 2014; Streit et al. 2015; Adam et al. 2018; Ruttenberg et al. 2019). Our multivariate assessment suggests that in terms of removing turf algae, most of the herbivore species on Kiritimati perform this function to a similar extent, except for *C. carolinus,* which is likely focussed more on browsing larger macroalgae than grazing turf (Bonaldo et al. 2014). Indeed, surgeonfish and parrotfish are thought to be complementary in their algal grazing function (Kelly et al. 2016), and our results suggest there is species and even functional group overlap in the Kiritimati herbivore assemblage with respect to their average species' impacts.

Assemblage-level effects

Species differences

When we summed the average species' impacts at each site, we found that herbivore functional groups were significantly distinct in terms of their overall grazing impacts. This likely occurred, as hypothesized, because we have a different number of herbivore species representative of each functional group and thus different densities. Indeed, impacts are higher for the scrapers and grazers compared to excavators and browsers, which each only have one species representative. Despite this disparity, however, differences in grazing impact were least pronounced between grazer and excavator functional groups. This finding could highlight the importance that one species, the excavator *Chlorurus sordidus* in this case, can have on herbivore grazing function, as it appears to be functionally similar to the multi-species grazer functional group. Another study has previously shown the impact that one species can have on herbivore function, with the bioerosion function being dictated by the presence of the humphead parrotfish (*Bolbometopon muricatum*); this function was virtually absent in sites where *B. muricatum* was absent due to high fishing pressure (Bellwood et al. 2003). Because of the significant distinction in grazing impact that we found between functional groups, our results corroborate with the body of work on herbivory that suggests taking a functional group approach when quantifying ecological processes (e.g. Adam et al. 2015, 2018; Robinson et al. 2019a).

Anthropogenic differences

We found no significant effect of the human disturbance gradient on assemblage-level grazing impact. This suggests to us that the herbivore function, when assessed at an assemblage-level, is robust to local disturbance driven by human pressure. It seems that different densities of species feeding in different sites sum to a similar impact.

We did detect, however, a significant influence of the El Niño disturbance on herbivore assemblage grazing impact. Studies examining the numerical response of herbivores to disturbance generally recognize a benefit to herbivores, especially from bleaching disturbances, by documenting increased herbivore abundance and biomass in years following a significant coral bleaching event (e.g. Adam et al. 2011; Gilmour et al. 2013; Han et al. 2016; Holbrook et al. 2016). When taken as a proxy for function, the increased biomass suggests an increased ability to carry out the herbivory function, which might lead to enhancing reef resilience from such disturbance events (Holbrook et al. 2016). Our direct quantification of the herbivore grazing function reveals that assemblage-level herbivory also increased after a severe thermal stress-induced coral bleaching event, which suggests that herbivores are able to continue to carry out their critical function, despite the ecosystem undergoing significant disturbance. Also, we have not yet documented a complete regime shift to an ecosystem state dominated by macroalgae (as per Knowlton 2004) at our sites, which might imply that the increase in herbivore grazing might have contributed to limiting algal growth. As time goes on, however, and as the reef structural complexity responds to increased disturbances (Magel et al. 2019), we may see a shift in the delivery of key reef functions. Indeed, other functions, like bioerosion for example, may take on disproportionately important roles in influencing reef dynamics, especially if the reef continues to be degraded by climate change stressors (Arias-Godínez et al. 2019).

It should be noted that while we found that our constrained ordination was a significant solution for the variation in species' impacts in the herbivore assemblage, local disturbance and El Niño heat stress did not contribute to the majority of the variation. There was still 80% of the variation unaccounted for, which could be driven by other unassessed factors, such as reef characteristics (e.g. level of sedimentation: Bellwood and Fulton 2008; Tebbett et al. 2017b), algal productivity (e.g. Fox and Bellwood 2007), resource availability (e.g. Carlson et al. 2017), competition between herbivores or with other coral reef fish (e.g. Davis et al. 2017), or other physical and environmental factors like wave exposure (e.g. Bejarano et al. 2017).

In summary, we took a species and size-specific approach to quantify the turf removal function (average species impact) of the herbivore assemblage of Kiritimati. We highlight that a diverse group of herbivores is necessary to maintain this function across the island, which has important implications for herbivore management. That said, we also found that this key grazing function is fairly robust to disturbance, which is encouraging given projected increases in marine heatwaves (Smale et al. 2019), severe coral bleaching events and diminishing return times for ecosystems to recover from such disturbances (Hughes et al. 2018a).

Table 3.1 Number of instances that species had herbivore feeding observations and density estimates from the same site in each year to calculate a metric for average species impact. Species are classified by functional group (FG) and arranged within each group in descending order by the total number of estimates.

FG	Family	Species	2013	2017	2018	Total
Browser	Scaridae	*Calotomus carolinus*	2	9	9	20
Excavator	Scaridae	*Chlorurus sordidus*	15	13	11	39
Grazer	Acanthuridae	*Acanthurus nigricans*	15	13	12	40
		A. olivaceus	2	2	2	6
		A. lineatus	2	1	2	5
		A. nigricauda	3	1	1	5
		A. achilles	4	0	0	4
		A. nigrofuscus	2	0	0	2
		A. triostegus	2	0	0	2
		A. leucocheilus	0	1	0	1
Scraper	Scaridae	*Scarus frenatus*	16	11	9	36
		S. rubroviolaceus	12	14	9	35
		S. tricolor	11	8	3	22
		S. psittacus	3	5	11	19
		S. ghobban	5	4	2	11
		S. oviceps	0	4	1	5
		S. globiceps	1	0	3	4
		S. forsteni	0	0	2	2
		Total	95	86	77	258

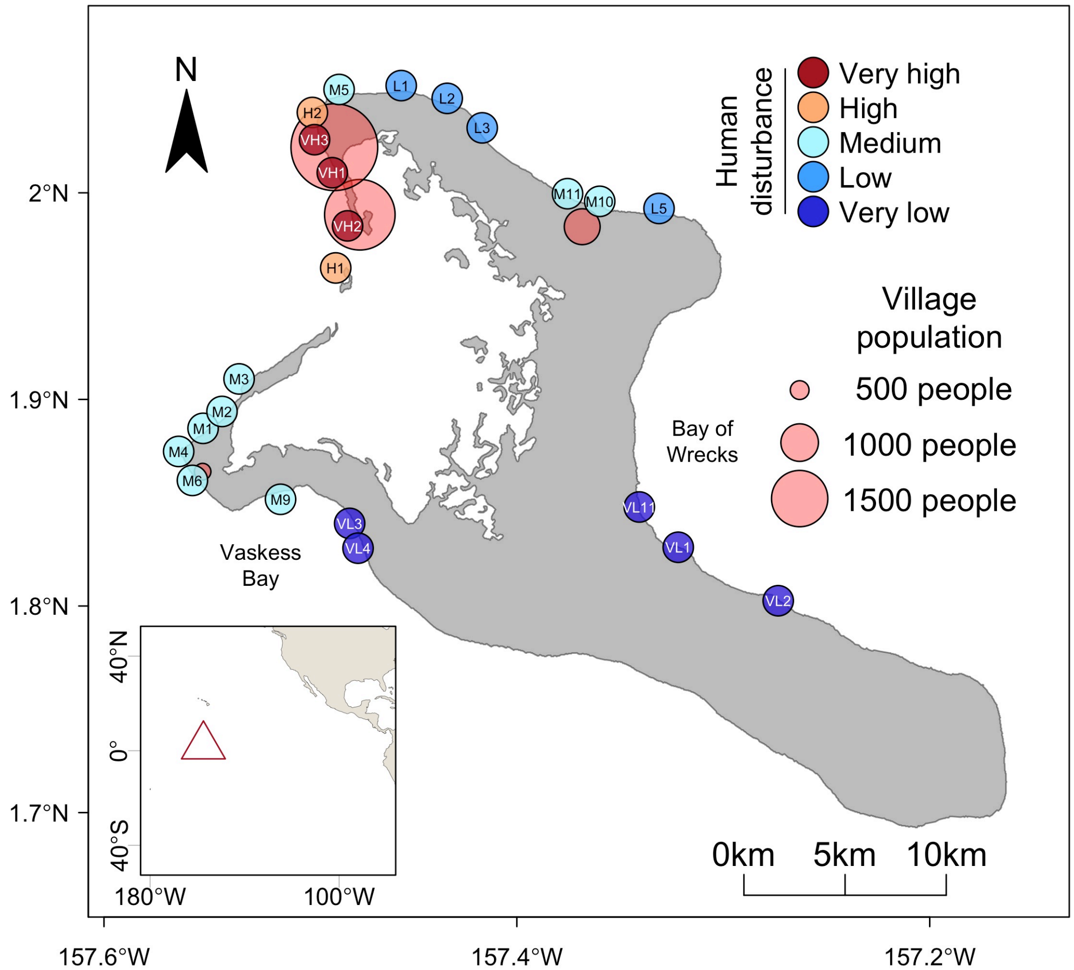

Figure 3.1 Map of twenty-three forereef study sites and villages on Kiritimati (Christmas Island), Republic of Kiribati. Sites are coloured based on levels of local human disturbance, and villages (red circles) are scaled to the human population. Inset indicates the island's location (triangle) in the equatorial Pacific Ocean.

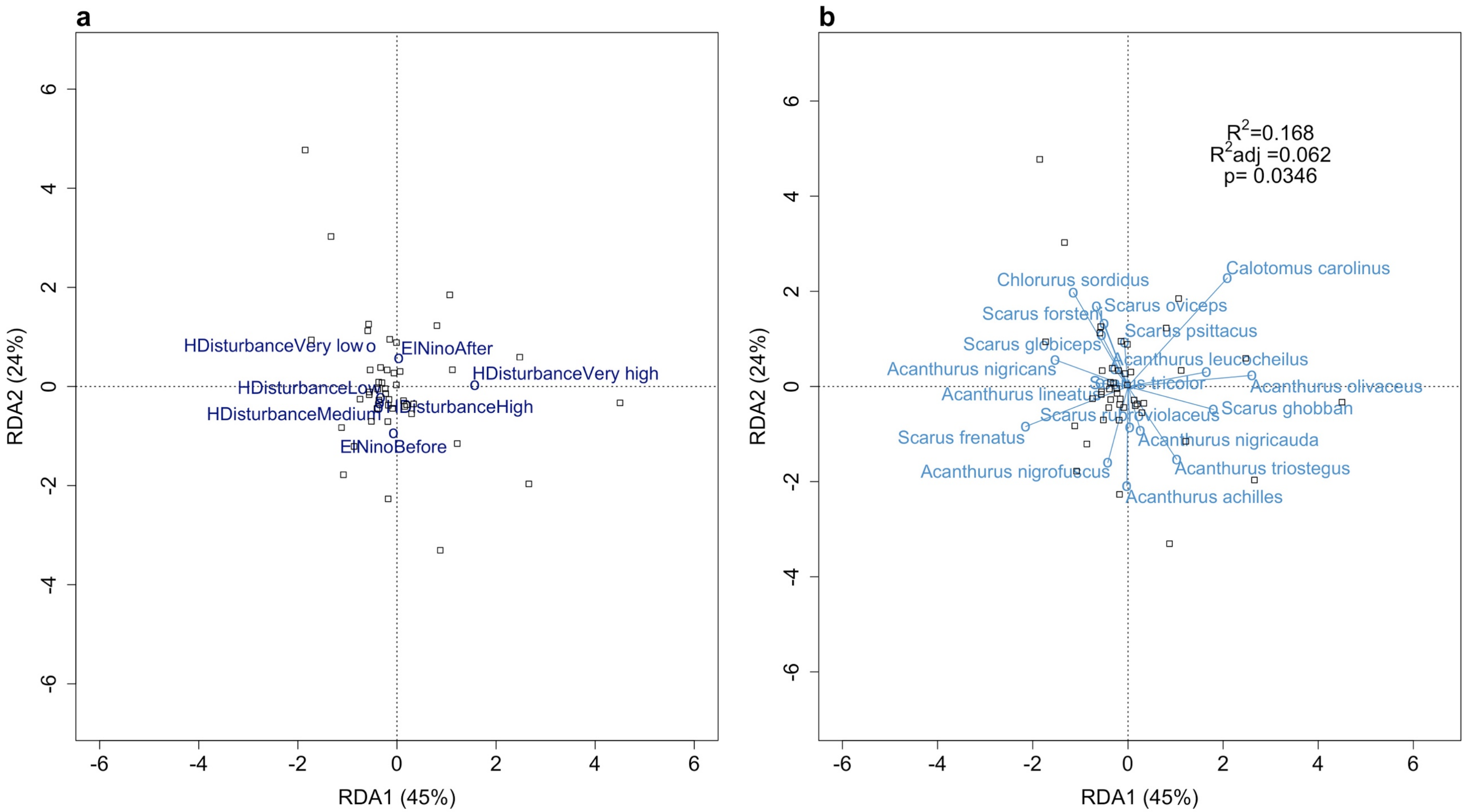

Figure 3.2 Redundancy analysis of the herbivore community impact constrained by local human disturbance and global heat stress. (a) Triplot displaying site scores (open squares) and text labels to indicate centroid scores (open circles) of the constraining variable factor levels. (b) Biplot for the species (open circles) and site scores (open squares). The R^2, R^2 adj and the p-value for the significance of the overall fit of the constrained ordination are displayed in the top right-hand corner of panel (b). Axis labels include the cumulative proportion of constrained variance.

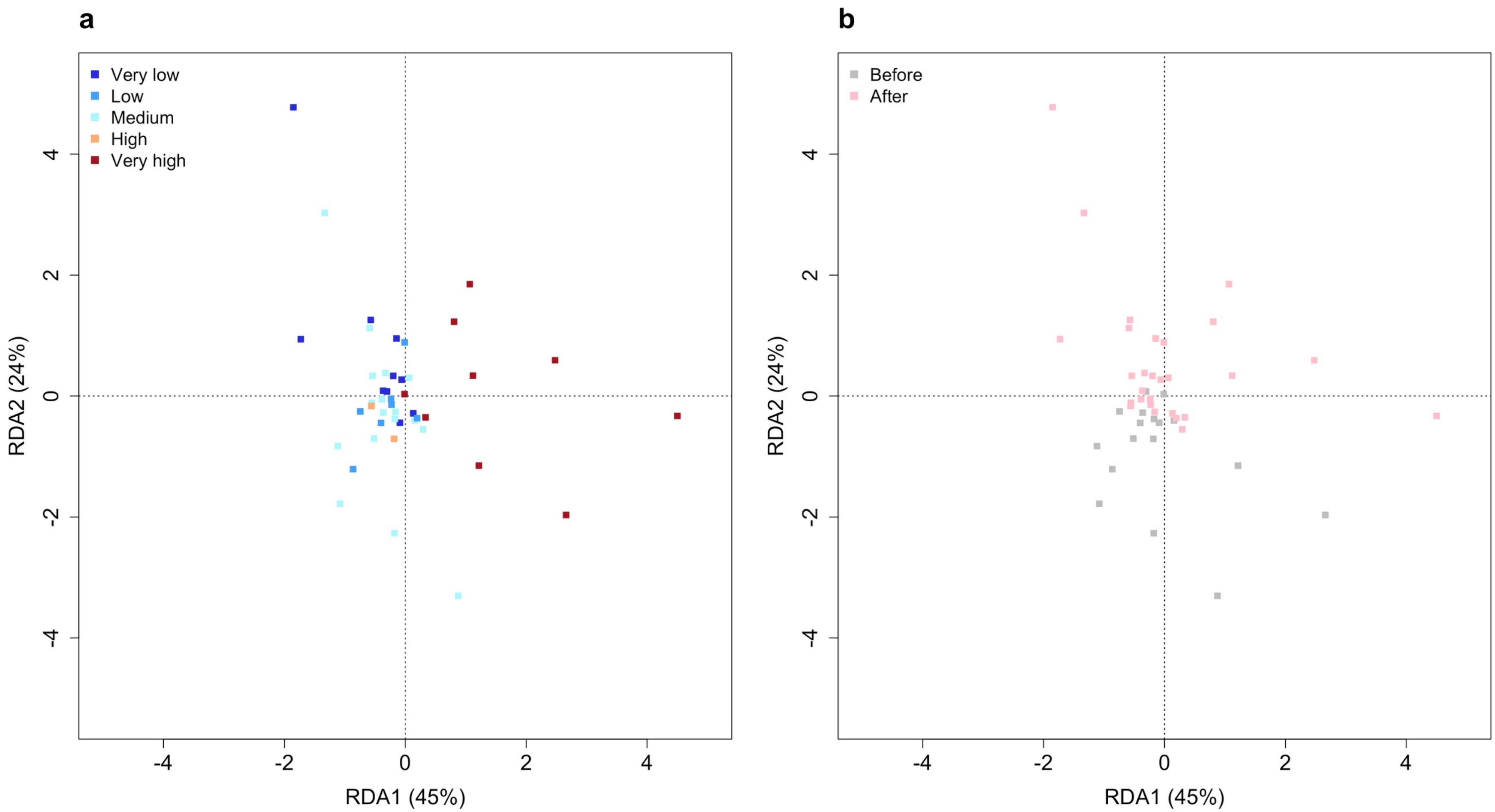

Figure 3.3 Redundancy analysis of the herbivore community impact constrained by local human disturbance and heat stress. (a) Biplot displaying site scores coloured by the human disturbance levels. (b) Biplot displaying site scores coloured by time period associated with the El Niño. Axis labels include the cumulative proportion of constrained variance.

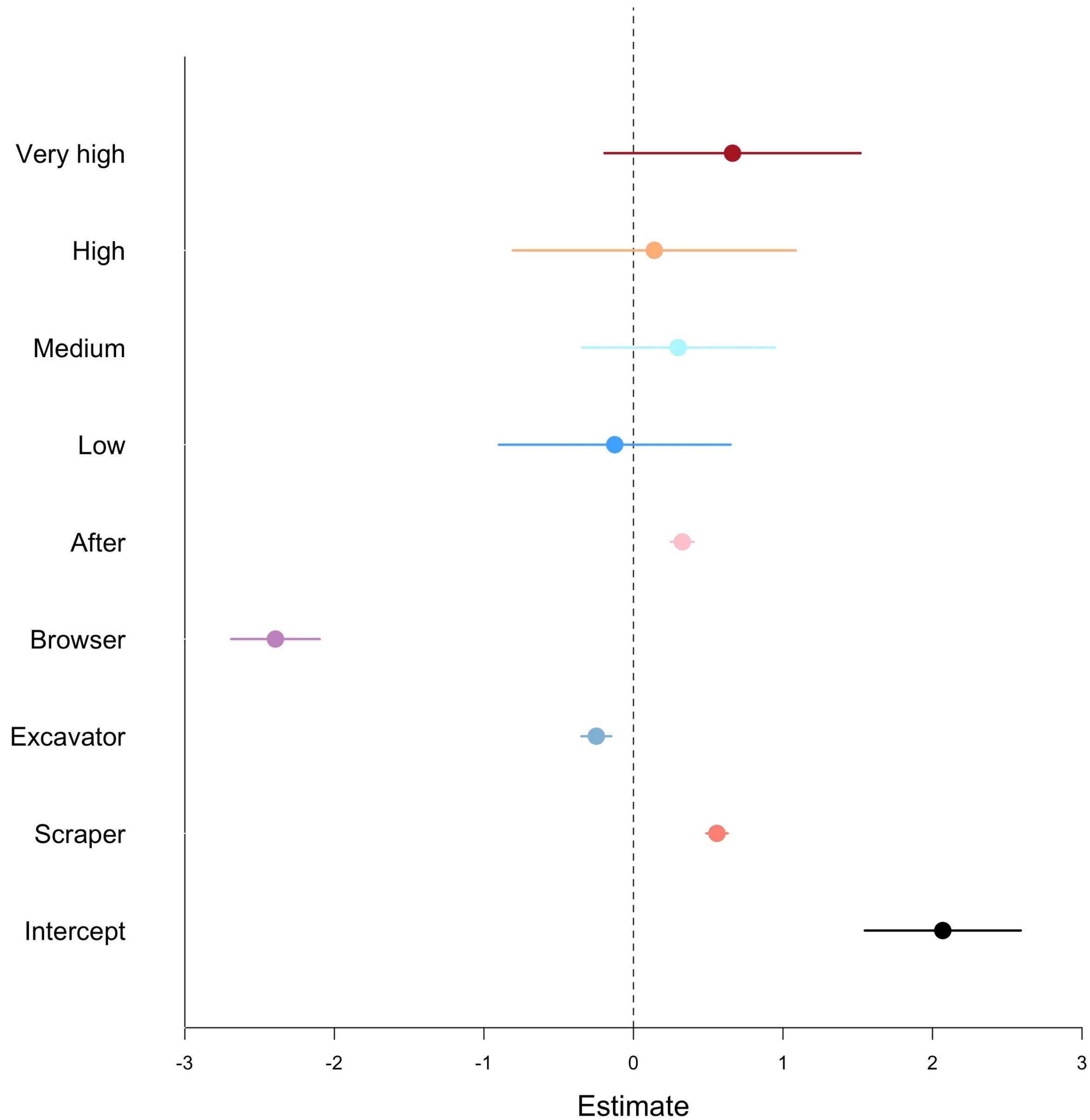

Figure 3.4 Effect size estimates and 95% confidence intervals for fixed predictor coefficients: Local disturbance (Very high, High, Medium, Low relative to Very low); El Niño (After relative to Before); Functional group (Browser, Excavator, Scraper relative to Grazer) from generalized linear mixed model of assemblage-level grazing impact.

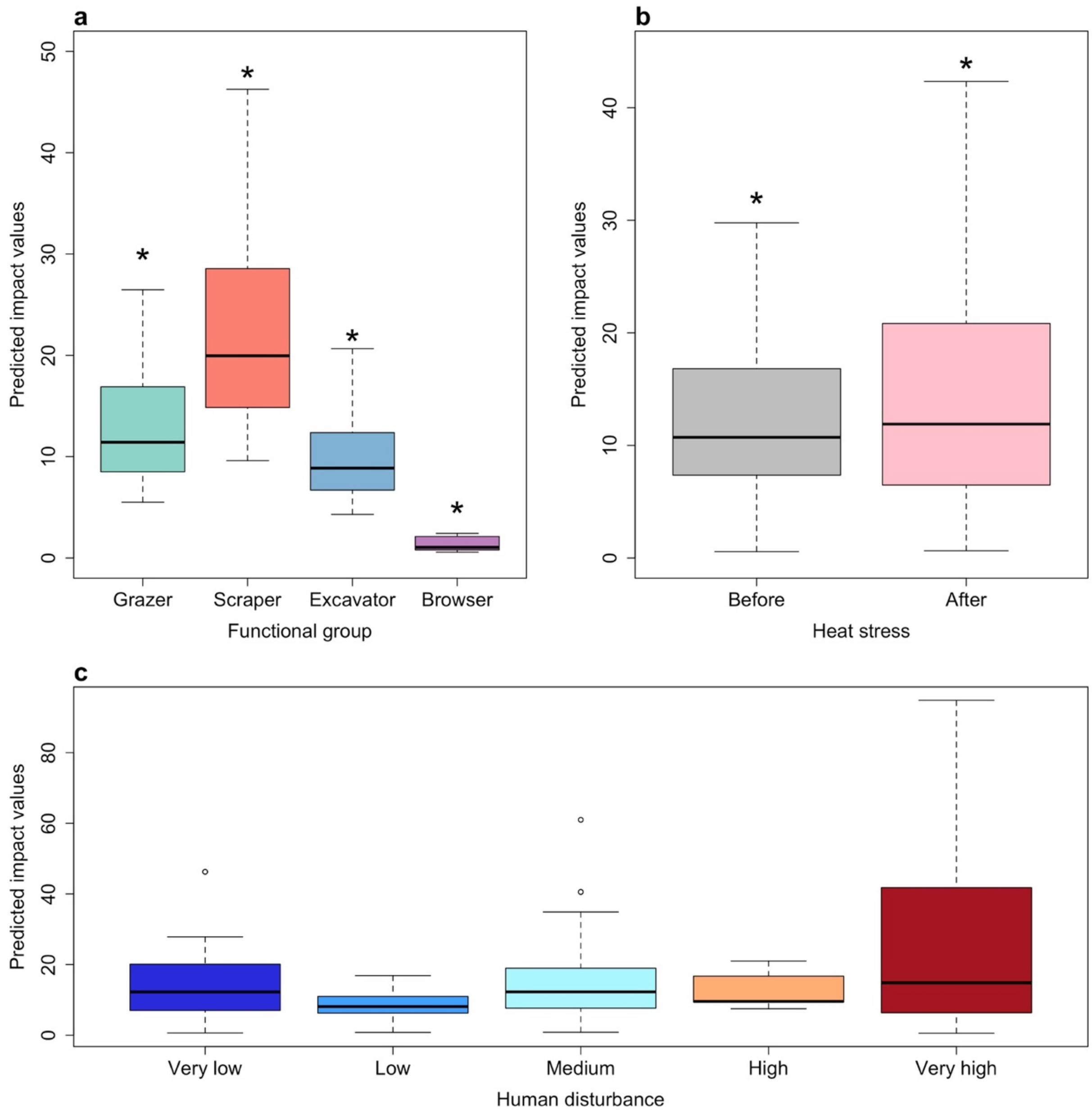

Figure 3.5 Boxplot of model predictions of grazing impacts at each level of the fixed effect predictors included in our generalized linear model of assemblage-level grazing impact: (a) model predictions of grazing impact by functional group, (b) time period associated with the global El Niño heat stress disturbance, and (c) local disturbance level. Asterisk indicates significant (by Tukey test) differences between levels of the fixed predictors. Horizontal lines indicate the median, the upper and lower limits of boxes indicate the interquartile range. Outliers are removed from panel (a) (3 Grazer, 3 Scraper, 2 Excavator, 1 Browser) and panel (b) (4 Before, 3 After) to enable a better view of patterns.

Chapter 4 – Conclusion

If unabated, anthropogenic climate change will continue to subject coral reefs to severe episodes of thermal stress (Smale et al. 2019), leaving less time in between events to allow full recovery of these ecosystems (Hughes et al. 2018a). Episodes of mass coral bleaching have become more frequent, with some regions experiencing back to back years with significant bleaching episodes (Hughes et al. 2017). A few decades ago, when episodes of global mass coral bleaching were still relatively rare, coral reef ecologists began to recognize the potential that herbivorous fish could have as drivers of reef recovery (Bellwood et al. 2004). Following this, many studies began investigating the effects of coral bleaching on reef assemblages, with particular focus on how the herbivores responded (e.g. Graham et al. 2007; Bellwood et al. 2012; Gilmour et al. 2013). These studies made use of data that had been collected from quantitative surveys of fish abundance and used herbivore biomass as a proxy for their ecological function (Graham et al. 2015). Dividing the assemblage into functional groups allowed for general conclusions about how these groups and by extension how certain ecological functions would be impacted by severe disturbance (Cheal et al. 2010; Bellwood et al. 2012; Glynn et al. 2014; Mangubhai et al. 2014). While this body of work made use of quantitative data collected before and after significant disturbances, in order to investigate changes in fish functional structure, it lacked the finer resolution to investigate how individual feeding activity changed. While some argue that presence in a fish survey might be reason enough to assume occurrence of fish feeding (Streit et al. 2019), it overlooks the influence that individual behaviour has in determining function.

Other studies have looked at a finer spatial scale to quantify fish function, and herbivory in particular. Using behavioural feeding observations as the basis for quantifying function, these studies tended to make species or spatial comparisons (Bellwood et al. 2003, 2006; Fox and Bellwood 2007; Alwany et al. 2009; Hoey et al. 2016a), but lacked the temporal resolution to be able to compare function across a coral bleaching event (but see Keith et al. 2018). Even fewer studies investigated the interplay between local anthropogenic disturbance and global heat stress, especially in how it influenced herbivore function. So, despite the important ecological role herbivores play in ecosystem dynamics, and the influence they might have as a mechanism for driving coral reef recovery, the consequences of disturbance on their ability to carry out their ecological function was still not well understood.

Given increased occurrence of climate change-mediated disturbances, coral reef researchers are building datasets to include behavioural data from before and after significant coral bleaching episodes to be able to investigate questions about how disturbance events influence behaviour and by extension how certain functions are affected (e.g. Keith et al. 2018; Zambre and Arthur 2018). It is this approach that I have taken in trying to untangle the effects that local and global scale disturbance can have on the herbivorous fish assemblage by utilizing behavioural and quantitative herbivore data collected from coral reefs around Kiritimati (Republic of Kiribati) from time points visited before and after the reef had suffered from extreme thermal stress and a severe coral bleaching episode induced by the 2015–2016 El Niño pulse heat stress.

In Chapter 2, I employed functional group and species-specific approaches to investigate how herbivory metrics (bite rates, grazing impact, substrate selectivity) vary with herbivore identity, individual size, and life phase, and if herbivory is influenced by local human disturbance or by heat stress. This approach allowed me to investigate ecologically relevant variation in herbivory metrics, especially as it pertained to differences amongst functional groups, and how individual size influences our interpretation of function. I found that size does modulate our understanding of herbivory, for example, a high bite rate does not necessarily equate to a high grazing impact. In particular, there were opposite responses amongst grazer and scraper functional group bite rates in relation to fish size: scrapers slowed their bite rates at larger sizes while grazers increased rates with increasing fish size. Despite this difference with bite rates, we noted that individual grazing impacts increased with fish size for all functional groups. Herbivore functional groups exhibited varied bite rates, but differences between herbivores were not as pronounced if accounting for size when considering grazing impacts. Grazers, scrapers and excavators did not exhibit significant differences in grazing impact. This suggests that despite differences in body size between different herbivore functional groups, there is some complementarity in their grazing impact. Notably, our browser was more distinct, suggesting limited functional redundancy for the browsing function. We did not detect differences in bite rates or grazing impacts across our gradient of local human disturbance, but we did document a significant increase when heat stress was high on Kiritimati. These returned to normal after heat stress had subsided, signifying a short-term response in species-specific herbivory to a global heat stress event. Selectivity, on the other hand, showed the opposite response, with no significant change over time detected, but exhibited variation across the local human disturbance gradient. Taken together, these results provide insight into how species-specific herbivory responds to disturbance and highlight the opposing effects that local and global stressors can exert on ecosystem functions.

In Chapter 3, I scaled up our measure of grazing impact to investigate spatiotemporal patterns of the herbivore assemblage-level impact on turf substrates. Since overall herbivore impact is influenced by fish behaviour, but also by the abundance of fish performing those behaviours, I match our estimate of species-specific grazing impact with estimates of site-averaged species density. I found that the variation in herbivore impacts constrained by human disturbance and the timing of the El Niño was significant, but these factors together only explained 17% of the variation in community herbivory. Sites subject to very high disturbance were distinguished from the others by having only a few locally abundant feeding herbivores, while the other disturbance levels had a larger number of species contributing to herbivore species impact. When we summed the impact at each site by herbivore functional group, we found that functional groups did exhibit significantly different grazing impacts, and these were higher after the El Niño pulse heat stress event but did not vary across the local disturbance gradient. It would seem as though the assemblage-level grazing function is fairly robust to disturbance, which is encouraging, given the anticipated increase in anthropogenic disturbances.

A key goal for management is to conserve the proper functioning and promote the delivery of ecological services provided by the coral reef (Ladd et al. 2018; Bellwood et al. 2019a; Williams et al. 2019). In a broad sense, the state of the reef is driven by a dynamic balance between pairs of ecological processes such as calcium carbonate production and bioerosion, primary production and herbivory, secondary production and predation, and nutrient uptake and release (Brandl et al. 2019). Having an adequate definition of ecosystem functioning is a top priority for reef managers, but characterizing reef functions and the role of biodiversity in influencing ecological processes has not been previously approached in a systematic and quantitative way (Bellwood et al. 2019b; Brandl et al. 2019). With this thesis, I attempted to understand the role of herbivore functional group diversity in shaping the species-specific and overall herbivore grazing function, while accounting for local and global stressors on the community. I demonstrated that a diverse herbivore assemblage is necessary for carrying out herbivory, but the overall function is fairly robust to disturbance, which is reassuring for the fate of this ecological process in an ever-changing world. However, the theory that herbivores are necessary drivers of reef recovery is coming into question now, because of the overriding impact from climate change-driven stressors on coral reefs (Bruno et al. 2019). Since the effects of climate change are extensive, it seems that the consequences of global change might obscure the finer scale influences of other important reef-shaping processes.

Given that episodes of extreme heat stress and coral bleaching are projected to become more frequent (Hughes et al. 2018a), predicting the consequences of repeated heat stress on the physiological heat tolerance of coral reef herbivores, is something that is not yet well understood. The positive relationship between temperature and metabolism is pretty well established (Gillooly et al. 2001; Brown et al. 2004, 2012), but what remains to be seen is how the elevated temperatures from climate-induced heat stress may influence the metabolic ecology of species in the long-term (Wilson et al. 2010a). There is some suggestion that warming climates will have a deleterious effect on the performance of individuals leading to metabolic meltdown, especially if heightened metabolic demand at higher temperatures is not met with increased availability of food resources (Huey and Kingsolver 2019). What needs to be investigated now, is if or how climate change might modify physiological responses of reef organisms in such a way that the dynamics established in interspecies relationships (such as the interaction between corals, algae and herbivores) will shift as a result (e.g. Matis et al. 2018; Bellwood et al. 2019b). For example, even if herbivory could be maintained, a recovery to full coral cover may never manifest, if the physiological tolerance of corals cannot sustain elevated temperatures caused by climate change (e.g. Eakin et al. 2019), or if conditions shift to favour algal growth such that macroalgae take the competitive edge over corals (Brown et al. 2019) and their rampant growth overwhelms any suppression herbivores might be able to provide (Holbrook et al. 2016).

Additionally, the effects of heat stress, coral bleaching and ocean acidification are increasing the incidence of coral disease and erosion of the reef structure, which has further negative impacts for corals that then extends to the broader community through loss of habitat structure (Eakin et al. 2019). Thus, protecting herbivore populations might be one strategy to allow coral reefs a better chance at recovery from significant disturbance (Williams et al. 2019), but perhaps the approach that might offer a better guarantee in terms of recovery outcome and return of these ecosystems to their former glory, is to limit the emission of fossil fuels into the atmosphere and target the root cause of the degradation by addressing global climate change (Skirving et al. 2019).

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Appendices

Appendix A - Literature review of coral reef fish herbivory

Appendix A1 Herbivore responses to disturbance. Studies investigating the impacts of disturbance events on the herbivore fish community. Studies are grouped by responses measured and arranged chronologically by year published then alphabetically within a year. COT is for the Crown-of-Thorns seastar; CPUE is catch per unit effort; GBR is the Great Barrier Reef.

Response	Authors/Year	Disturbance	Fish studied	Response detected
Abundance/ Density/ Biomass Responses	Halford et al. 2004	*Natural* disturbance (likely a storm)	Acanthuridae, Chaetodontidae, Labridae, Pomacentridae, Scaridae	11/19 Families declined in abundance after impact. Acanthuridae not affected, Scaridae more affected.
	Garpe et al. 2006	Coral bleaching (1998 El Niño)	Whole fish assemblage – including roving herbivores (Acanthuridae, Scaridae)	Roving herbivores increased initially following bleaching – then declined with coral erosion.
	Graham et al. 2007	Coral bleaching (1998 El Niño)	Fish functional groups: herbivores, corallivores, planktivores, piscivores, mixed diet feeders	Small herbivores declined; larger size classes increased.
	Ledlie et al. 2007	Coral bleaching (1998 El Niño)	*Chlorurus sordidus* and *C. strogylocephalus* (bioeroders), *Scarus niger* and *S. rubroviolaceus* (scrapers), *Acanthurus triostegus* and *A. leucosternon* (grazers)	No consistent trend (either increase or decrease) in abundance or biomass of herbivores. Smaller individuals were more affected.
	Pratchett et al. 2008	Mass coral bleaching (Review)	Fish assemblage	45/116 fish species exhibited a *change* (ranging from extinction to increase). Roving herbivores exhibit increases in abundance.
	Cheal et al. 2010	Coral bleaching and cyclone disturbance	Herbivore assemblage: scrapers, grazers, detritivores, browsers	Diversity/abundance lower at reefs in macroalgal transition phase. Parrotfish show no relationship to macroalgal cover.
	Adam et al. 2011	COT outbreak	Herbivorous fish and urchins	Herbivorous fish doubled in density, tripled in total biomass. Assemblage became increasingly dominated by parrotfish (accounting for ~50% of biomass).
	Bellwood et al. 2012	Coral bleaching (1998 El Niño)	Cryptobenthic fish	Assemblage shifted after bleaching – relative abundance of functional groups changed.
	Gilmour et al. 2013	Coral bleaching (1998 El Niño)	Herbivorous fish assemblage	Increase in herbivore density detected several years after bleaching.
	Glynn et al. 2014	Coral bleaching (1983 & 1998 El Niño)	Fish assemblage	Reef fish density remained stable – herbivores had no pattern with increasing coral cover.
	Mangubhai et al. 2014	Coral bleaching (2002–2003 El Niño)	Fish assemblage	Average Acanthuridae and Scaridae abundance did not change across sites between pre- and post-bleaching years.

Appendix A1 Herbivore responses to disturbance (cont'd)

Response	Authors/Year	Disturbance	Fish studied	Response detected
	Han et al. 2016	Pulse perturbations: COT outbreak and then cyclone	Herbivore assemblage: browsers, detritivores, excavators, farmers, grazer/detritivores, scrapers	Island-wide biomass of scrapers and excavators increased three-fold. Assemblage shifted to increased representation of scrapers/excavators.
	Holbrook et al. 2016	COT outbreak then cyclone	Acanthuridae and Scaridae	Herbivorous fish biomass on fore-reef more than doubled island-wide.
	Nash et al. 2016b	Coral bleaching (1998 El Niño)	Fish assemblage	Small fish more negatively affected by bleaching – increase in larger individuals.
	Hoey et al. 2016b	Climate-driven coral loss (Review)	Fish assemblage	Increase in herbivore biomass generally documented with decline of coral cover (but they note it is variable).
	Ruppert et al. 2018	Human activities – compare top-down effects to bottom-up (i.e. humans altering benthic community)	Fish assemblage	Human activities directly impact top-level carnivores, but herbivores and lower level carnivores are more impacted by the habitat changes that humans cause (i.e. indirect impact of humans).
	Steneck et al. 2018	Fishing (comparing islands with fishing bans to those where fishing is unconstrained)	Vagile species of fish assemblage considered. Surgeonfish, parrotfish and urchin (*D. antillarum*) herbivores quantified.	No-take reserves had higher biomass for predatory and herbivorous fish – less variation explained by fishing pressure variable for surgeonfish compared to groupers or snappers. Turf canopy height was lower in reserves and there was a weak negative impact of turf canopy height and macroalgal cover on juvenile coral density, but a positive effect of parrotfish biomass on juvenile coral density.
Diversity/ Abundance/ CPUE	Arias-Godínez et al. 2019	Habitat degradation (i.e. decline in coral cover)	Fish assemblage	Found evidence of an assemblage change due to a change in structural complexity of the benthic community (i.e. decline in coral cover and increase in *Caulerpa* algae): decline in fish diversity (Shannon-diversity index), abundance and CPUE. Fish community was more homogenous in degraded habitats (in the time period after degradation). Noted a reduction in functional redundancy with bioerosion becoming 'favoured' over other functional roles (predation).
Abundance/ Biomass/ Functional metrics	Stuart-Smith et al. 2018	Coral bleaching (2015–2016 El Niño)	Fish assemblage	Abundance and biomass of scraping herbivores declined on Northern GBR reefs, while excavators increased. Herbivore biomass increased on southern reefs where functional richness also increased. Excavators were more abundant on southern reefs in Coral Sea.

Appendix A1 Herbivore responses to disturbance (cont'd)

Response	Authors/Year	Disturbance	Fish studied	Response detected
	McClure et al. 2019	Two Category 4 cyclones and one bleaching event	Herbivore fish assemblage: croppers, detrital feeders, browsers, excavators, scrapers	Saw distinct assemblage structure before and after disturbance: assemblage more distinct across the shelf after the disturbance. Documented a decline in species richness at all shelf positions. Saw increases in croppers and detrital feeders, but declines in excavators, browsers and scrapers after the disturbance. Also saw that the numbers of characteristic species declined to 1 or 2 sp. for each shelf position. Documented changes in taxonomic and trait characteristics, notably they document an increase in trait specialization and originality of herbivore assemblages at inner reefs, but it was the opposite for mid-shelf reefs and no change at outer reefs.
Taxonomic/ functional metrics	Bierwagen et al. 2018	Hurricane disturbance	Fish assemblage and benthic community assemblage	Total fish density showed no significant differences between pre- and post-disturbance time points. Functional groups had variable responses – some showed no pattern of response to disturbance (piscivores) while some declined (corallivores, grazers, detritivores, macro-invertivores) after the disturbance.
	Richardson et al. 2018	Coral bleaching (2015–2016 El Niño)	Fish assemblage	Little change in taxonomic or functional richness across habitats. Functional originality of assemblages increased.
Grazing response	Williams et al. 2001	Experimental manipulation of coral cover	Scarids and Acanthurids - sufficient data for *Acanthurus bahianus, Scarus isertii, Sparisoma aurofrenatum;* also pooled by family	Scaridae species and family data showed no difference in grazing rates or grazing pressure between experimental treatments. *A. bahianus* increased grazing rates in plots with increased coral cover.
	Mumby et al. 2006	Fishing (from caged experiments)	*Scarus sp.* and *Sparisoma sp.*	Grazing intensity of parrotfish is higher inside a marine reserve than outside.
	Bellwood et al. 2006	Caging experiment to simulate overfishing of herbivores	*Platax pinnatus*	One species of batfish was responsible for reversing a phase shift.
	Ledlie et al. 2007	Coral bleaching (1998 El Niño)	*Chlorurus sordidus* and *C. strogylocephalus* (bioeroders), *Scarus niger* and *S. rubroviolaceus* (scrapers), *Acanthurus triostegus* and *A. leucosternon* (grazers)	No differences among study sites in the proportion of bites on different substrates.

Appendix A1 Herbivore responses to disturbance (cont'd)

Response	Authors/Year	Disturbance	Fish studied	Response detected
	Bellwood and Fulton 2008	Sediment loading of environment	Acanthuridae, Pomacentridae, Kyphosidae, Labridae, Siganidae	Herbivore feeding rates increased (~3.8x) with removal of sediment, and that resulted in a decline in algal turf height. There were more fish observed feeding in sediment removal plots (20 vs. 12 sp.). Sediment can affect herbivore feeding behaviour.
	Chong-Seng et al. 2014	Coral bleaching (1998 El Niño) and comparing herbivory on coral-dominated vs. algal-dominated reefs	Herbivore assemblage	Assemblage of fishes feeding on macroalgal assays in coral dominated versus algal-dominated reefs differed. *S. puelloides* fed on algae in coral-dominated reef areas while *N. elegans* accounted for the majority of bites on macroalgal-dominated reefs.
	Plass-Johnson et al. 2015	Localized impacts (coastal development, eutrophication, fishing etc.)	Herbivores feeding on algal assays (identified by video) at different sites along a gradient of human disturbance.	The function of herbivory is influenced by localized disturbance. On reefs that are heavily impacted, herbivory is maintained by a few key species (*Siganus sp.)* versus reefs further offshore (less impacted) which have more species feeding on and more bites taken from algae (i.e. *Naso sp.* and *B. muricatum* feed more than *Siganus sp.*).
	Holbrook et al. 2016	Caged treatments (to mimic fishing or disturbance) to estimate relationship between herbivory and macroalgae.	Scaridae, Acanthuridae	Found a non-linear relationship between herbivory and macroalgae. Low levels of herbivory were able to suppress macroalgal growth. Found no relationship at landscape level between herbivore biomass and cover of macroalgae.
	Bejarano et al. 2017	Wave exposure	Parrotfish, surgeonfish and rabbitfish	Different functional groups had different feeding performances predicted from their different functional traits and responses to wave exposure – this disturbance can act as an environmental filter on feeding behaviour.

Appendix A2 Herbivore functional structure. Studies that investigate spatial or temporal variation in herbivore assemblage functional structure and ecological roles. Studies are in chronological order and organized alphabetically within a year. LM is linear model; GLM is generalized linear model.

Authors/ Year	Location	Approach to quantifying herbivore assemblage	Data presented	Aim of study	Findings
Hoey and Bellwood 2008	Lizard Island, Great Barrier Reef	Quantify herbivore community functional roles	Metrics calculated for functional roles that represent grazing, coral predation, sediment reworking and bioerosion – products of feeding rates, bite sizes and fish densities	Characterize the community of parrotfishes between inner, mid and outer reef, testing the hypothesis that fish communities vary along a spatial gradient.	Variation in functional roles show a cross-shelf pattern. Inner shelf reefs had high density, low biomass of parrotfish, but high grazing and sediment reworking. Outer shelf had high biomass but low density and high coral predation and erosion.
Villéger et al. 2008*	-	Trait-based approach to quantify functional diversity indices of community.	1) Functional richness; 2) Functional evenness; 3) Functional divergence	To provide the reader with a practical framework for calculating and analyzing the three presented indices of functional diversity.	Need a matrix of values for selected functional traits for species (generally these are standardized continuous variables) that you convert to a distance matrix. Also need a matrix of relative abundance of the species in the community. Indices are designed to be independent of species richness to allow for comparison of communities with different species richness without bias. Suggests multivariate techniques for visualization and ANOVA-like tests for testing differences in the indices.
Villéger et al. 2010	Terminos Lagoon, Gulf of Mexico	Trait-based approach to quantify functional diversity of tropical fish community.	1) Functional richness; 2) Functional evenness; 3) Functional divergence; 4) Functional specialization	To contrast how tropical fish populations compare at two different time points (sampled 18 years apart) with an environmental shift documented (decline in habitat quality/habitat degradation).	Species richness increased between the two periods and biomass declined, causing a modification in community structure, but it did not necessarily translate to a similar change in functional composition. Functional richness increased and evenness was high overall, but saw different responses in different habitat zones. A decline in functional divergence was observed, despite increased richness and seemed to be explained by a decline in functional specialization (generalist species replaced the specialized species).

Appendix A2 Herbivore functional structure (cont'd)

Authors/ Year	**Location**	**Approach to quantifying herbivore assemblage**	**Data presented**	**Aim of study**	**Findings**
Mouillot et al. 2013+	-	Trait-based approach to assess community change following disturbance.	Quantitative complementary indices to describe functional community structure: Functional identity, Functional richness, Functional evenness, Functional divergence, Functional dispersion, Functional entropy, Functional specialization, Functional originality.	Review paper that aims to 1) explain theoretical expectations of 3 types of disturbance on functional structure of community; 2) compare expected trends of taxonomic vs. trait-based indices of community structure along disturbance gradients; 3) review quantitative tools to assess changes in community structure after disturbance and methods to test them.	Need to characterize the functional strategy of each species with relevant combination of functional traits, present it in multidimensional space along axes that represent raw functional traits or synthetic traits (e.g. PCA). Also need to describe the distribution of species in the community and abundances of those species. Statistical tests include assessing differences in values compared to null model, estimating diversity components across space or time and using null models to assess significance of dissimilarity values along disturbance gradients.
Brandl & Bellwood 2014	Great Barrier Reef	Trait-based approach using bites, substrate bitten, extent of penetration into substrate of the Acanthuridae, Labridae and Siganidae families of herbivores.	Quantify the functional niche volume and overlap.	Compare niche volumes based on feeding microhabitats.	Functional niche volumes varied – high degree of complementarity among herbivorous fishes was found with no two species having >50% overlap.
Mouillot et al. 2014+	-	Trait-based approach to quantify functional diversity of tropical fish assemblages.	Identified functional entities (FE) based on unique combinations of 6 categorical functional traits. Assessed level of 1) Functional diversity; 2) Functional redundancy; 3) Functional vulnerability	Global study to investigate how species are distributed among functional groups and to what extent there is functional redundancy and vulnerability in fish faunas of tropical reefs.	The more species rich fauna had more species packed in functional space (higher functional redundancy). Coined the term "functional over redundancy" to describe overrepresentation of some FEs in terms of species richness. Results highlight that even in high diversity systems, the high probability of functional redundancy does not protect against species loss because species pack disproportionately into a few FEs instead of spreading evenly. They also note a bias in vulnerability distribution, with larger-bodied more vulnerable than smaller-bodied fishes.

Appendix A2 Herbivore functional structure (cont'd)

Authors/ Year	**Location**	**Approach to quantifying herbivore assemblage**	**Data presented**	**Aim of study**	**Findings**
Steneck et al. 2014	Glover's Reef, Carrie Bow Cay - Belize Barrier Reef	Attempt to scale up herbivory to ecosystem effect.	Grazing rates, size and density of bite marks, algal abundance, coral recruitment, total grazing intensity (using bite rates and census data). Grazing intensity of reefs with depleted herbivores was the total multiplied by the bite rate in caged treatments / control treatments for all size classes and scaled to longer term (6 months).	Experimental study to look at the effect of parrotfish deterrents around coral settlement tiles to see how parrotfish influence algal cover and phase shifts and what effect that might have on coral recruitment.	Deterring the parrotfish from feeding on the tiles can cause microphase-shifts in algal abundance. Found that total parrotfish grazing intensity declined by 52% in treatments where they deterred parrotfish. Thus, evidence of indirect control from herbivory (algal control) on coral recruitment.
Maire et al. 2015*	-	Trait-based approach to quantify the functional space and functional diversity pattern of an assemblage.	1) Functional richness; 2) Functional entropy	Simulation study to determine how changing species richness, number of traits and type of traits used to describe assemblages can affect the identity and quality of functional space and how that in turn affects the functional diversity pattern seen in local assemblages.	Simulations showed that the type of representation (dendrogram vs. multidimensional space) and the types of traits selected to describe species are the main determinants of the quality of functional spaces. The quality of functional space decreased with increasing species richness, while number of traits only marginally influenced the quality. Categorical traits decrease the quality of the functional space. The quality of functional space for regional species pools affects assessment of functional diversity in local assemblages and can bias estimations of ecological processes that structured these assemblages.

Appendix A2 Herbivore functional structure (cont'd)

Authors/ Year	Location	Approach to quantifying herbivore assemblage	Data presented	Aim of study	Findings
Boersma et al. 2016*	French Joe Canyon (case study)	Trait-based approach to quantify functional diversity in order to detect community assembly patterns.	1) Functional richness; 2) Functional dispersion; 3) Functional distance.	Methods paper to provide a general framework for selecting quantitative functional diversity methods to test hypotheses that address a broad array of ecological questions. Presented with the idea of 'before/after' disturbance comparison of communities and provides an example with a case study.	Need a combination of metrics to support a hypothesis. Metrics should be used in combination with abundance of individuals to enable quantitative tests of how functional trait differences between disturbed and undisturbed communities differ (e.g. use Welch's T-test to determine differences before vs. after disturbance). Functional diversity indices are derived from dissimilarity matrices in trait compositions between replicate communities.
Nash et al. 2016b	Seychelles	Abundance and composition of the fish community taken as their function.	Spatial cross-scale comparison of sites. PCA to look at variation in benthic community composition. Functional dispersion and functional evenness quantified.	Empirical assessment of cross-scale redundancy within important functional groups to test whether it is an indicator of response diversity on reefs through a climate-induced disturbance.	After temperature induced disturbance the loss of small herbivores was compensated by increase in large herbivores (high response diversity drove overall increase in herbivore biomass at recovering sites). No effect of fishing on redundancy metrics.
Bierwagen et al. 2018	Central Great Barrier Reef	Quantify taxonomic and functional structure of benthic and fish community.	Fish assigned to functional groups and Bray-Curtis dissimilarity matrices were compared for benthic assemblage and fish groups.	Assess the reef variability and community structure over time to see if certain functional groups contribute to the variability and whether an observed change in functional structure after a disturbance is an indicator of reef vulnerability or reassembly.	Did detect functional group assemblage variation over time – planktivores and corallivores increased post disturbance. The differences in fish assemblage structure among reefs and through time was a result of different variation in the proportion of individual functional groups. They did detect variability in reef community structures across the shelf. The 'reassembly' after the disturbance was not uniform for fish functional groups.

Appendix A2 Herbivore functional structure (cont'd)

Authors/ Year	Location	Approach to quantifying herbivore assemblage	Data presented	Aim of study	Findings
Maire et al. 2018	1894 Indo-Pacific reefs	Quantify taxonomic and trait-based functional assemblage of coral reefs	Taxonomic: size, abundance, biomass, coral cover. Traits: size, mobility, period of activity, schooling, vertical position in water column, diet. Calculated Functional richness	Take a 'community-wide scan' of entire fish community to detect potential links of the community with ecosystem function and services at a large scale.	Individual key species, but also the accumulation of key species, was linked to high levels of ecosystem services. Herbivorous fish were identified as key species for predicting fish biomass and live coral cover of the reef. The community-wide scan approach identifies the key species that are linked to the delivery of key services. In their case the fish biomass and live coral cover were proxies of coral reef services because they support food security, shoreline protection and recreational value.
Richardson et al. 2018	Lizard Island, Great Barrier Reef	Trait-based approach to quantify functional diversity of fish community.	1) Functional richness; 2) Functional dispersion; 3) Functional originality – assessed variation in structure of fish assemblages using community-weighted means of assemblages before, during and after bleaching with linear mixed effect models.	To assess the susceptibility of different species configurations to coral bleaching. Trait-based approach to compare taxonomic and functional structure of reef assemblages among coral reef habitats at three time points.	Documented changes in taxonomic and functional characteristics in response to bleaching event, but the nature of the changes varied among habitats. Evidence of response diversity in corals and reef fishes. They document an increase in similarity in taxonomic and functional diversity of fish assemblages across distinct habitat types (i.e. evidence of biotic homogenization). Functional richness was largely unchanged, but functional originality increased – may be indication of a loss of functional redundancy. After bleaching they documented a significant directional shift towards small-bodied, habitat generalist, algae-farming species.

Appendix A2 Herbivore functional structure (cont'd)

Authors/ Year	Location	Approach to quantifying herbivore assemblage	Data presented	Aim of study	Findings
Stuart-Smith et al. 2018	Great Barrier Reef and western Coral Sea	Quantify taxonomic and functional structure of fish community.	1) Benthic cover; 2) Abundance/biomass of coral reef fish; 3) Functional richness of community	Regional-wide approach to investigating the changes that occurred following the 2016 El Niño event, studying 186 reefs in the Great Barrier Reef region and western Coral Sea.	Documented declines in coral cover for most reefs that experienced warm temperatures; noted increase in herbivore abundance on some reefs, but not consistently on all reefs that experienced bleaching. Structure of reef communities in the southern part of the range became more similar to those in the north. Functional richness increased on southern reefs where biomass of herbivores (fish and urchins) increased.
McClure et al. 2019	Turtle Island Group, Northern Great Barrier Reef	Quantify taxonomic and functional composition of herbivorous fish assemblage.	Taxonomic: species richness, abundance, biomass, etc. Traits: diet, maximum body size, social grouping, position in water column, mobility between reefs and time of activity. Calculated 3 complementary indices of trait diversity: 1) Trait richness; 2) Trait specialization; 3) Trait originality	Examine the cross-shelf variation in herbivore fish assemblages and whether there is a differential response to a disturbance event.	Assemblage structure was distinct among shelf positions both before and after a disturbance event. The assemblage became more distinct among shelf positions after a disturbance, but more variable within a shelf such that the disturbance increased cross-shelf differences in the assemblage in multivariate space. They detected changes in taxonomic and trait characteristics in response to disturbance, but the nature of the changes varied with the metric and shelf position. Trait richness and taxonomic diversity declined with disturbance. Trait originality and specialization did not vary with shelf position. On inner reefs they increased, whereas specialization declined on mid-shelf reefs and there was no change in either on outer reefs.

Appendix A2 Herbivore functional structure (cont'd)

Authors/ Year	**Location**	**Approach to quantifying herbivore assemblage**	**Data presented**	**Aim of study**	**Findings**
Ruttenberg et al. 2019	Florida Keys, Caribbean	Quantify ecological processes of parrotfish herbivores.	1) Algal consumption; 2) Areal grazing; 3) Bioerosion	Explore how the species identity of herbivorous parrotfish controls ecological processes among habitats and across multiple spatial scales	Found significant differences in parrotfish assemblages and the important ecological processes they perform among habitats and over multiple spatial scales. Ecological processes were driven by species density, but biomass was less important for predicting ecological processes, thus community composition is more important for estimating herbivory.
Streit et al. 2019	Lizard Island, Great Barrier Reef	Map spatial extent of feeding for each herbivore functional group at each site (using kernel densities).	1) Maximum utilized area; 2) Core usage area; 3) Feedable area	To measure the overlap of feeding functional groups in order to determine the spatial complementarity and spatial redundancy. LMs to assess whether sizes of areas, movement extent, core feeding areas etc. differed with functional group or amongst sites. GLMs to assess measures of feeding overlap and to compare to null hypotheses of 1) random feeding 2) feeding when present 3) stable area sizes.	Fish feeding occurred 51% of time and fish movement occurred 67% of time, thus fish presence is a fairly reasonable proxy for fish feeding across temporal scales. Documented poor spatial overlap of core feeding areas when functional groups feed next to each other, indicating that the delivery of ecosystem functions is patchy across the reef. Thus, even with a diverse assemblage, the comprehensive delivery of function is effectively reduced since they feed in small, non-overlapping, high intensity feeding areas.

*Indicates studies that describe the methodology rather than apply the approach to a certain location.
[+]Indicates global scale or review studies that are not associated with one particular study site/location.

Appendix A3 Herbivores grazing rate quantification and studies. Studies that use feeding observations or bite rates to investigate herbivory, arranged chronologically by year and alphabetically within a year. EAM is for epiphytic algal matrix; GBR is Great Barrier Reef; IP and TP are Intermediate and Terminal Phase of parrotfish.

Authors/ Year	**Location**	**Metrics measured**	**Herbivore(s) studied**	**Goal of quantifying herbivory**	**Findings**
Bellwood and Choat 1990	GBR	Feeding rate, feeding foray, bite rate, bite speed	*Scarus frenatus, S. sordidus*	Morphological and behavioural comparison of feeding between two parrotfish functional groups (scrapers and excavators).	Scrapers have less powerful, but take more numerous bites per minute in intensive feeding bouts; excavators have more powerful, but take fewer, larger bites and have slower feeding rates.
Choat and Clements 1993	GBR	Number and size of feeding forays, bite speed, bite form, bite location	*Scarine* parrotfishes (*S. frenatus, S. schlegeli, S. sordidus*)	Measure morphological feeding metrics as a basis for comparison about different parrotfish functional groups.	Most scarids feed on EAM. Excavators have lower (but variable) bite rates; take fewer bites per foray compared to the rapid feeding rate of scrapers.
Bruggemann et al. 1994a	Caribbean	Food intake per bite, foraging effort, daily algal intake	*Sparisoma viride*	Quantitative description of food intake and energy assimilation of this parrotfish species.	Feeding rates affected by time of day, fish size, life phase and substrate type. Higher rates mid-day then it drops off. Feeding is inversely related to fork length. IP have highest rates. Food intake per bite is affected by substrate.
Bruggemann et al. 1994b	Caribbean	Foray size (# of successive bites in a foray), size of feeding scar	*Sparisoma viride*	Quantitative description of foraging by this parrotfish species.	Foray size is an indication of food preference – longer forays are taken on substrates that enable higher yields per bite. Size of scars are linearly related to fish length.
Bellwood 1995	GBR	Bite rates, bite location, defecation location, bite area/volume	*Chlorurus gibbus, C. sordidus*	Provide basic information about the temporal feeding patterns; to compare species erosion rates and seasonal effects.	First study to provide quantitative estimate of bioerosion by parrotfishes. Found variation in bioerosion even within excavating functional group. Bites were concentrated on convex surfaces. Found little seasonal variation.
Polunin et al. 1995	Moorea	Bite rates, defecation rates, gut fullness	*Acanthurus nigrofuscus Ctenochaetus striatus, Scarus sordidus, Stegastes nigricans, Zebrasoma scopas*	Compare foraging and food processing patterns among 5 of the most common herbivorous species on this reef.	Bite rates peaked in the afternoon, with most species showing a steady increase during the day. Differences in bite rates best explained by species factor. Ranked the species based on variables assessed: *Z. scopas*, *St. nigricans* had lowest rank, followed by *C. striatus*, *S. sordidus* and then *A. nigrofuscus.*

Appendix A3 Herbivore grazing rate quantification and studies (cont'd)

Authors/ Year	**Location**	**Metrics measured**	**Herbivore(s) studied**	**Goal of quantifying herbivory**	**Findings**
Williams et al. 2001	Belize	Abundance, grazing pressure (bites/min/plot) × abundance, benthic cover and algal abundance	Acanthurids and scarids	Experimental study to test alternative hypothesis to why there is increased algal abundance even in absence of eutrophication, overfishing, mass mortality of sea urchins: rise may be a side effect of loss of coral cover and overwhelming of herbivory.	No variation in scarid grazing rates and pressure among treatments, but did see variation in acanthurids (assumed in response to improved grazing conditions). Increasing coral cover had a proportional effect on decline in macroalgal cover which suggests support for an upper threshold of substratum that can be controlled by grazing of herbivorous fish.
Bellwood et al. 2003	GBR/Indo-Pacific	Bite rates, bite scar volumes, fish abundance, and selectivity	*Chlorurus sp.*, *Scarus sp.* and *Bolbometopon muricatum*	Calculate bioerosion (carbonate removal) of important bioeroders. Use densities to determine how human activities influence this ecosystem process across a biogeographical region (44 sites in the Indo-Pacific).	On low-no impact reefs (GBR) bioerosion is carried out by two species only (*C. microrhinos* and *B. muricatum*). Bioerosion was almost completely absent from sites where human impact is higher. There is a tight correlation between human impact and bioerosion regardless of geographical location.
Bellwood et al. 2006	GBR	Number and bite location, bite rate standardized by biomass, algal area, volume mass, fish densities	Roving herbivore assemblage	Experimental study to determine how herbivore exclusion affects herbivory.	One species of batfish, *Platax pinnatus,* is solely responsible for reversing a phase shift. It was previously thought to be an invertebrate feeder.

Appendix A3 Herbivore grazing rate quantification and studies (cont'd)

Authors/ Year	Location	Metrics measured	Herbivore(s) studied	Goal of quantifying herbivory	Findings
Bonaldo et al. 2006	Fernando de Noronha, Brazil	Snorkel observations of feeding bouts, availability of food substrate, fish distribution	*Sparisoma amplum, Sp. axillare, Sp. frondosum*	Address 6 questions about foraging behavior of 3 *Sparisoma* parrotfish: 1) Any food selection by the adult phases of 3 sp.? 2) If yes, does it differ between IP and TP of same species and amongst the 3 sp.? 3) Do feeding rates differ throughout the day? 4) Is there a difference between feeding rates of IP and TP of same sp.? 5) Do the 3 sp. have different feeding microhabitats on the reef? 6) Do the 3 sp. and phases forage solitarily or in groups?	1) and 2): species differed in food selection, but the phases of each species did not. 3) and 4): feeding rates differed for the different species, IP individuals had higher feeding rates than TP. All showed similar patterns in diel feeding frequencies. 5): *Sp. amplum* and *Sp. axillare* were more abundant during the afternoon, *Sp. frondosum* more abundant during the morning. *Sp. amplum* and *Sp. frondosum* were more abundant on rocky shore, while *Sp. axillare* were more abundant on the interface. 6) *Sp. axillare* most frequently found foraging in groups of the three species but most foraged solitarily. Found that only IP would forage in groups.
Mumby 2006	Caribbean	Grazing intensity (bite rate scaled by fork length and bite size) summed for all species, size categories and life phases	Scaridae	Model Scaridae grazing to calculate the net impact of grazers on the algal community and the impact of depleting total biomass of fish on grazing.	Parrotfish can maintain 30% of reef in grazed state. Depleting parrotfish grazing can lead to an algal-dominated state.
Paddack et al. 2006	Florida Keys	Algal consumption (bite rates scaled by biomass)	Acanthuridae, Scaridae, Pomacentridae	Quantify the algal consumption rate of herbivores.	Herbivores are consuming enough of the new algal production to sufficiently limit its proliferation.
Fox and Bellwood 2007	GBR	Daily disturbance impact, total impact of species	Roving herbivore assemblage	Quantify herbivory across a reef depth gradient.	Species differed in abundance across zones, biomass varied, and the feeding rates varied widely among species.

Appendix A3 Herbivore grazing rate quantification and studies (cont'd)

Authors/ Year	**Location**	**Metrics measured**	**Herbivore(s) studied**	**Goal of quantifying herbivory**	**Findings**
Ledlie et al. 2007	GBR	Coral structural community, fish abundance, feeding habits, diet composition, electivity	Herbivore assemblage	Analyze the change in coral reef community structure and how it changes the fish assemblage (community and feeding habits)	Noted a decline in coral cover, no change in numerical abundance or biomass of grazers, scrapers, bioeroders, but change in size structure observed. Species differed in feeding rates, but sites did not differ. Electivity indices showed most species consumed epilithic algae and avoided other substrata.
Mantyka and Bellwood 2007	GBR	Selectivity (total bites on each macroalgal species), first bites, time for macroalgae to be reduced	*Chlorurus microrhinos*, *Hipposcarus longiceps*, *Pomacanthus sexstriatus, Scarus rivulatus*, *Siganus canaliculatus*, *Si. doliatus*	Experimental manipulation to examine the feeding selectivity of herbivorous fish in order to make species comparisons.	*Siganus sp.* (rabbitfish) were highly selective on *Sargassum* (i.e. limited functional redundancy for these species) and parrotfish were more selective on calcified *Halimeda* (i.e. feeding complementarity exhibited with rabbitfish). The different selectivity is thought to be due to differences in feeding apparatus. The omnivorous *P. sexstriatus* were the least selective.
Bellwood and Fulton 2008	GBR	Visual surveys of herbivores and detritivores, sediment removal and video analysis of feeding rates, algal turf height	Acanthuridae, Kyphosidae, Labridae, Pomacentridae, Siganidae	Experimentally evaluate the effect of natural sediment loads on rates of herbivory in an intact coral reef ecosystem.	Herbivore feeding rates increased (~3.8x) with removal of sediment, and that resulted in a decline in algal turf height. There were more fish observed feeding in sediment removal plots (20 vs. 12 species). Sediment can affect herbivore feeding behaviour.
Bonaldo and Bellwood 2008	GBR	Feeding rates and grazing impact (bites day^{-1} × bite size / body mass of size class)	*Scarus rivulatus*	Quantify size-dependent variation in species functional role.	No variation in feeding rates of different size classes. Grazing impact, however, did increase with fish size. Size classes showed same pattern in their substratum selection.
Burkepile and Hay 2008	Florida Keys	Species abundance, species composition, bite rates	*Acanthurus bahianus, Sparisoma aurofrenatum*	Test the role of a particular herbivore species (or herbivore diversity) on driving community patterns.	Herbivore richness controls macroalgal community and has a positive effect on coral survivorship and growth. Mixed-species treatments better than single-species. Species richness can play a role in affecting the health of coral reefs through complementary resource use.
Hoey and Bellwood 2008	GBR	Bite rates, bite scar dimensions, bite area, feeding day length	Labridae (parrotfish)	Quantify functional role of parrotfish and compare along a cross-shelf gradient.	Grazing decreased from inner to outer shelf reefs.

Appendix A3 Herbivore grazing rate quantification and studies (cont'd)

Authors/ Year	**Location**	**Metrics measured**	**Herbivore(s) studied**	**Goal of quantifying herbivory**	**Findings**
Lokrantz et al. 2008	Tanzania	Bite rates, bite scar dimensions, fish abundance	*Scarus niger, Chlorurus sordidus, and C. strongylocephalus*	Examine the relationship between body size and 'scraping performance' for three parrotfish species.	Bite rates were not correlated to body size for *S. niger, C. strongylocephalus,* but were negatively related to body size for *C. sordidus.* The area scraped over time (incorporating bite rates and bite scars) increased with body size for all three species, with the relationship best described using a power function.
Alwany et al. 2009	Red Sea	Abundance, bite rates	*Cetoscarus bicolor, Chlorurus gibbus, C. sordidus, Scarus ferrugineus, S. frenatus, S. ghobban, S. niger*	Quantify scarid bioerosion on Red Sea reefs through examination of feeding activity and abundance.	Species showed consistent patterns in daily feeding (rates peaked in the afternoon). Two groups emerged for high vs. low bioerosion rates. *Chlorurus sordidus* and *S. ghobban* are main contributors to overall erosion rates in Red Sea. No difference in bioerosion rates were detected between sites.
Cvitanovic and Bellwood 2009	GBR	Algal assays and video cameras to count herbivore bites	Acanthuridae, Ephippidae, Kyphosidae, Siganidae	Quantify the variation in herbivory within local bays.	No difference in herbivory between bays but found variation within a bay.
Hoey and Bellwood 2009	GBR	Mass standardized bite impact and grazing preference index	Acanthuridae, Ephippidae, Kyphosidae, Labridae, Pomacanthidae, Siganidae.	Algal assay and video analysis to quantify herbivore feeding assemblage to make spatial and species comparisons.	A single species – *Naso unicornis* – was removing *Sargassum.*
Ong and Holland 2010	Hawaii	Bite rates, time of first bite, depth, fraction of bites resulting in scars	*Chlorurus perspicillatus, Scarus rubroviolaceus*	Quantify bioerosion to compare scraper (*S. rubroviolaceus*) vs. excavator (*C. perpicillatus*) species and quantify factors affecting bioerosion rates.	Species showed similar daily feeding patterns, and both selected for crustose algae. Bite volumes and erosion rates did not differ between species but increased with increasing size of species.
Goatley and Bellwood 2010	GBR	Feeding rates, bite size, pellets, gut contents	*Ctenochaetus striatus*	Quantify amount and direction of sediment transported by this species to make comparisons between habitats.	Sweeping detritus feeder with feeding rates that did not decline nearing the end of the day, but rather stopped abruptly. It removes about 35% of sediment to deeper waters.

Appendix A3 Herbivore grazing rate quantification and studies (cont'd)

Authors/ Year	Location	Metrics measured	Herbivore(s) studied	Goal of quantifying herbivory	Findings
Burkepile and Hay 2011	Florida Keys	Feeding rates, fish richness, benthic cover	Herbivore assemblage with removal of *Acanthurus bahianus, Sparisoma aurofrenatum*	Caging experiment to test the notion of complementarity versus redundancy, using feeding rates from videos and fish richness as an indication of function.	They detected complex patterns of feeding complementarity and redundancy – herbivores divided into two broad groups: 1) *A. bahianus, S. iseri, S. taeniopterus;* and 2) *A. coeruleus, Sp. aurofrenatum, Sp. chrysopterum, Sp. viride,* and large *Scarus sp.* were similar.
Lefèvre and Bellwood 2011	GBR	Feeding intensity measured monthly using *Sargassum* assays and remote videos to quantify bite rates and identify the herbivores responsible for removal of macroalgae	Herbivore assemblage from videos with focus on three dominant species: *K. vaigiensis, N. unicornis, S. rivulatus*	Understand the temporal variability in the nature of algal-herbivore interaction.	Removal rates were significantly higher in the summer months, and ~ 4 times lower in winter months. No apparent temporal trend in distribution and total biomass of herbivorous fishes over the 12 months. The pattern was more than simply a change in feeding activity of a single species, but rather it also incorporated changes in which species were responsible for removal of *Sargassum.* Forty-three species were recorded, but only 3 played a significant role in removal: *K. vaigiensis, N. unicornis, S. rivulatus.* In the summer, removal was due to *K. vaigiensis* and hardly any bites were taken in winter months (although it was present in videos). In winter months, there was an increase in *S. rivulatus* bites which were largely reduced in summer months. Temporal variability in herbivore functional roles suggests functional redundancy on reefs is less than previously assumed because feeding activities are spatially and temporally constrained.
Afeworki et al. 2013	Red Sea	Bite rates (bites/min), defecation rates (defecation/min), and yield per bite (mass ingested bite)	*Scarus ferrugineus* (3 life phases: IP – 20-25 cm; TP – 30-35 cm; Territorial(T) TP – 30-35)	Determine the factors that impact feeding intensity in order to better predict response of grazers to changing conditions.	Bite rates increased over the day, peaking in the afternoon. IP bite rates increased linearly with seawater temperature while TP bite rates had quadratic relationship with water temperature, maximized at 32 degrees. Yield per bite in IP and TP did not differ with time of year. Total daily bites were highest in IP throughout the year and lowest in TTP. Intake and defecation rates peaked from April to July. The quadratic temperature response of TP suggests large individuals may be close to upper thermal limit implying temperature rises are likely to negatively affect large-bodied parrotfishes.

Appendix A3 Herbivore grazing rate quantification and studies (cont'd)

Authors/ Year	**Location**	**Metrics measured**	**Herbivore(s) studied**	**Goal of quantifying herbivory**	**Findings**
Rasher et al. 2013	Fiji	Videos of bites on algal transplants	Herbivore assemblage	Compare herbivore diversity and quantify herbivory between no-take marine reserves and adjacent fished areas to assess functional redundancy vs. complementarity of herbivorous fish.	Of the herbivorous fish species, only four (*Naso lituratus, N. unicornis, Chlorurus sordidus, Scarus argenteus)* were noted feeding on macroalgae (accounted for 97% of algal bites) with little overlap between which algal species were consumed. Found negative relationship between herbivore diversity and macroalgal abundance, suggesting support for the idea that high herbivore diversity is necessary to effectively control algae.
Chong-Seng et al. 2014	Seychelles	Mass of algae, number of bites, length of fish, abundance of herbivores	Herbivore assemblage detected in videos	Conduct macroalgal assays on reefs in different conditions to determine whether the herbivore function differs.	Assemblage of fish feeding on assays had distinct nMDS patterns. Different species accounted for the majority of bites depending on whether it was a coral-dominated or algal-dominated reef. *Naso sp*. were more important on algal-dominated reefs. Different abundance of species also found in the different reef conditions.
Hamilton et al. 2014	Palmyra	Bite rates, selectivity, foraging impact	Scaridae and Acanthuridae	Quantify herbivory between two reef habitats.	Higher bite rates in predator exposed reef crest habitats. Acanthuridae and Scaridae had different feeding preferences.
Longo et al. 2014	Brazil	Feeding pressure, fish composition, evenness of feeding pressure, fish abundance, and biomass	Roving herbivores and territorial herbivores	Make large-scale comparisons between 3 reefs that span 10-degree latitudinal gradient to determine if feeding pressure varies across spatial scales and to identify the species that perform higher feeding pressure than predicted by abundance.	Noted a decline in feeding pressure from north to south driven by a decline in roving herbivores. Feeding pressure was skewed to a few strong scraping species; composition of species and functional groups performing feeding pressure significantly varied among the studied sites. Feeding pressure was not correlated to abundance of species or functional groups, but it was correlated with biomass. Two functional groups represented higher feeding pressure than predicted by biomass: scrapers at northernmost sites and fine browsers (acanthurid species).
McCauley et al. 2014	Palmyra and Tabueran	Bite rates, amount of material removed annually, resource selection ratios	*Bolbometopon muricatum*	Examine behaviour and feeding ecology of the largest parrotfish and its effects on coral reef diversity/dynamics.	Average bite rate is 3.3 bites/min. Average adult consumes ~4480 kg of material each year. It shows a preference for pocilloporid corals.

Appendix A3 Herbivore grazing rate quantification and studies (cont'd)

Authors/ Year	**Location**	**Metrics measured**	**Herbivore(s) studied**	**Goal of quantifying herbivory**	**Findings**
Longo et al. 2015	Rocas Atoll	Mass-standardized bite impact, algal assays, stomach analysis, selectivity	Fish assemblage and *Acanthurus sp.* diet analysis	Quantify herbivory between open and closed pools.	Herbivorous fishes (*Acanthurus sp.*) were dominant in closed pools where non-calcified algal turfs were more dominant that calcareous algae (as in open pools). Bite rates of acanthurids were lower in open pools.
Marshell and Mumby 2015	GBR	Grazing intensity, grazing impact from tile deployment and video analysis	Acanthuridae, Siganidae, Scaridae	Quantify grazing across a depth and exposure gradient to investigate the role of grazer/detritivore surgeonfish species in maintaining algal turf biomass on coral reefs.	Grazing intensity was greatest where productivity was highest. No differences in bite rates between depths. Grazing was unrelated to standing EAM crop.
Plass-Johnson et al. 2015	Spermonde Archipelago, Indonesia	Algal transplants, fish abundance, macroalgal removal and feeding rates	Herbivore assemblage	Experimental test of herbivory (bioassays of *Sargassum*) to quantify removal of algae by herbivorous fishes along a gradient of impact. Spatial comparison of herbivory along the onshore-offshore gradient from heavily populated to less populated in order to determine the importance of the function on impacted reefs.	On degraded reefs herbivory is maintained by a few key species. Patterns of algal removal and feeding were variable among sites. Herbivore diversity and biomass increased with distance from shore – only a few species noted feeding at all sites, thus only a few robust in maintaining their function under changing environmental conditions.

Appendix A3 Herbivore grazing rate quantification and studies (cont'd)

Authors/ Year	**Location**	**Metrics measured**	**Herbivore(s) studied**	**Goal of quantifying herbivory**	**Findings**
Streit et al. 2015	GBR	Video analysis of feeding behaviour: bites/foray, bites/s, social grouping, presence of headflick during bite, part of algae bitten. Morphological analyses: gape size, jaw-lever ratio, AM-muscle mass, tooth shape	*Kyphosus vaigiensis, Naso unicornis, Siganus canaliculatus, Si. doliatus*	Macroalgal assay and video analysis to quantify how behavioural and morphological traits may influence removal of macroalgal material.	Species were distinguished mainly by the algal material they targeted with *K. vaigiensis* and *N. unicornis* targeting entire thallus versus *Siganus* species avoiding the stalks and only biting leaves. This led to further categorization of herbivore browsers as 'entire-thallus biters' or 'leaf-biters'.
Hoey et al. 2016a	Arabian reefs	Abundance and composition of fish, feeding rates, functional roles	Labridae	Quantify functional role of parrotfish to compare across regions.	Regional variation in parrotfish functions: differences observed between Red Sea, Arabian Sea and Arabian Gulf assemblages are attributed to differing environmental conditions.
Kelly et al. 2016	Hawaii	Bite rates (per substrate type), selectivity	Acanthuridae, Labridae	Determine ecological impact of herbivores and their consumption patterns.	All species predominantly fed on turf; 80-100% similarity in foraging behaviour for bite rates; more variation in foraging behaviour for proportion of bites.
Nash et al. 2016a	Philippines	Foraging mobility, grazing rate	*Scarus niger, Chlorurus bleekeri*	Determine which drivers (benthic community, management status, competitor or predator biomass, size, focal sp.) are the main influences on foraging and grazing rate.	Management status and species were best predictors in grazing rate model. Grazing rates were higher in no-take areas than fished areas.
Carlson et al. 2017	Palmyra	Selectivity, spatial distribution of bite scars	*Chlorurus microrhinos*	Quantify fine-scale spatial patterns of herbivory.	*C. microrhinos* feeding behaviour is related to resource availability. Foraging more focussed where resources are more abundant.

Appendix A3 Herbivore grazing rate quantification and studies (cont'd)

Authors/ Year	Location	Metrics measured	Herbivore(s) studied	Goal of quantifying herbivory	Findings
Davis et al. 2017	Palmyra and Mo'orea	Space use (50 and 90% kernel utilizations), bite rates, fish densities, inter- and intra-specific interactions	*Chlorurus spilurus*	Examine the influence of bottom up (resource abundance and quality), horizontal (competition) and top-down (predation risk) factors on herbivorous foraging behaviours (space use and bite rates)	Feeding rates are influenced by direct interference competition and chronic predation risk, as bite rates were explained by herbivore and piscivore biomass. Space use is primarily related to exploitative competition with surrounding herbivore community, as territory size and core use are best explained by herbivore biomass. Competitive chases occurred between territorial surgeonfishes (*A. nigricans, A. lineatus*), damselfish and larger TP *C. spilurus.* Reactions to predators were rare.
Ferguson et al. 2017	West Coast Australia	Fish abundance, videos of bites on algal assays.	Girrellidae, Kyphosidae	Quantify abundance, grazing rates, and feeding pathways on reefs inside vs. outside marine reserves.	Marine reserves have no effect on size or abundance of non-targeted herbivores. Rates are consistent across zones and due to site-specific factors rather than effects of protection.
Kelly et al. 2017	Hawaii	Bite rates, fish biomass, algal assays for algal growth rate	Grazers, scrapers and browsers	Quantify herbivore consumption to compare with algal production between protected vs. non-protected sites.	Herbivore consumption is lower than algal production, but in the first 5 years of management there is a diminishing margin between them.
Kuempel and Altieri 2017	Panama	Benthic % cover, algal assay for algal mass, herbivore exclusion for effect of herbivore presence on algal cover, herbivore rates	Herbivorous fish and urchin assemblage	Experimental manipulation to look at the relationship of algal cover, coral cover and herbivore composition, biomass and presence.	Diminutive species of herbivores (*Echinometra viridis* urchin and juvenile *Scarus iseri*) play an important role by exerting sufficient grazing function to pre-empt macroalgal dominance following mass coral mortality. Herbivore presence affected algal biomass, and there was less algae in cages that excluded large, but not small herbivores. Rates of herbivory differed by site, fleshy macroalgae was lower at sites where there was significant herbivore intensity.
Suchley and Alvarez-Filip 2017	Caribbean	Bite rates	Acanthuridae, Scaridae	Herbivore exclusion to quantify the role of herbivory in influencing coral calcification.	Herbivore exclusion had a significant effect on macroalgal cover and coral growth. Herbivory can facilitate coral calcification.
Tebbett et al. 2017a	GBR	Video of bites on experimental rocks	*Acanthurus nigrofuscus, Ctenochaetus striatus*	Clarify functional roles of two herbivores.	*C. striatus* does not play a functional role in removing algal turfs as the (visually similar) *A. nigrofuscus* does.

Appendix A3 Herbivore grazing rate quantification and studies (cont'd)

Authors/ Year	Location	Metrics measured	Herbivore(s) studied	Goal of quantifying herbivory	Findings
Adam et al. 2018	Caribbean	Bite rates, food items targeted, foray size	9 species of *Scarus* and *Sparisoma*	Comparative analysis of foraging behaviour to determine if parrotfish are one functional group or if species have distinct foraging ecology.	On broad scale, parrotfish genera have different functional roles (*Sparisoma* vs. *Scarus*): *Sparisoma* consume macroalgae and *Scarus* feed on turf. They target different types of turf assemblages, but also found that even within a genus species exhibit distinct foraging ecology.
Steneck et al. 2018	Caribbean	Benthic: abundance of juvenile corals, canopy height of non-encrusting algae, % cover and algal volume, rugosity. Fish: size, density, biomass of important reef species. Quantified grazing pressure from bite rates per species and body size divided by grazeable area (reef complexity index and proportional cover of grazeable substrates).	*Scarus iseri, S. taeniopterus*, *S. vetula, Sparisoma aurofrenatum*, *Sp. chrysopterum* and *Sp. viride*.	Determine the reserve effects on herbivore grazing pressure, algae and juvenile coral – as a test of the 'managed resilience hypothesis' and the cascading effect of management (through fishing restriction) on the base of the ecosystem.	No take reserves had increased herbivore biomass, reduced algal cover and height, and increased abundance of juvenile corals, illustrating the value of managing fish stocks to maintain herbivory. They also noted that loss of coral resulted in algal colonization and reduced the per-area bite rate of local grazers to effectively reduce herbivory (i.e. changes in herbivory are less appreciated if only examining changes in distribution, abundance and biomass).
Eurich et al. 2018	Kimbe Bay, Papua New Guinea	Bite rates (as indication of herbivore foraging pattern), aggressive interactions with damselfish, max N of species in videos, benthic cover	Acanthuridae, Scaridae, Siganidae (roving herbivores); *Pomacentrus adelus* (territorial damselfish)	Examine the effect of territorial damselfish behaviour and how it influences herbivorous fish foraging activities (through experimental removal of *P. adelus*)	Damselfish do not exert a strong influence on roving herbivore foraging behaviour. No significant difference in foraging activity for surgeonfish (Acanthuridae), parrotfish (Scaridae) or rabbitfish (Siganidae) between treatments. No difference in herbivore relative abundance following removal of *P. adelus.*

Appendix A3 Herbivore grazing rate quantification and studies (cont'd)

Authors/ Year	Location	Metrics measured	Herbivore(s) studied	Goal of quantifying herbivory	Findings
Eggertsen et al. 2019	Mafia Island, Tanzania	Fish and benthic community composition, algal assays to monitor feeding, bite scar dimensions	Acanthuridae, Labridae, Siganidae	Quantify the distribution and foraging patterns of herbivore and detritivore communities across multiple habitats (coral reefs, macroalgal beds and seagrass meadows) and the extent to which patterns are driven by bottom-up processes (to identify habitat variables that are important in structuring reef communities).	The three habitat types had distinct assemblages of species, with different abundances and species compositions. The densities of the functional groups were driven, to a certain extent, by bottom-up processes. Habitat variables that explained fish abundance (such as food resources targeted) differed between habitat types. Fish were observed feeding most in coral reef habitat; scars were higher in number and size in coral reef sites.
Lefcheck et al. 2019	Caribbean	Videos of bite rates, visual transects for benthic assessment, turf algal canopy height, density of juvenile corals, urchin density	Herbivore assemblage: *Acanthurus bahianus, A. coeruleus, Scarus iseri, S. taeniopterus, S. vetula, Sparisoma aurofrenatum, Sp. chrysopterum, Sp. rubripinne, Sp. viride*	1) Evaluate the relationship between herbivore diversity and the process of herbivory. 2) Determine which species contribute to herbivory on the reef. 3) Assess cascading consequences of herbivory and determine whether or not top-down biodiversity effects observed in nature are associated with ecosystem structure.	1) Mass-standardized bite rates (their metric of herbivory) are significantly associated with fish community biomass, alpha diversity and beta diversity, but not coral cover, turf abundance or sea urchin abundance. 2) Four herbivore species independently affect herbivore rates (*A. bahianus, A. coeruleus, S. iseri, Sp. aurofrenatum*). 3) Turf algal canopy height was negatively correlated with mean grazing rate, which in turn was negatively associated with density of juveniles, thus there is some evidence of a cascading effect of herbivory.

Appendix A3 Herbivore grazing rate quantification and studies (cont'd)

Authors/ Year	**Location**	**Metrics measured**	**Herbivore(s) studied**	**Goal of quantifying herbivory**	**Findings**
Robinson et al. 2019a	72 Indo-Pacific reefs (Seychelles, Maldives, Chagos Archipelago and GBR)	*In situ* observations of bite rates from Red Sea, Indonesia, and GBR, bite scar dimensions (from following individual biting parrotfish), fish biomass from UVC	Croppers (Acanthuridae and Siganidae); Scrapers (tribe Scarinae)	Integrate feeding observations with biomass data from UVC to calculate the grazing potential of 'croppers' and 'scrapers' in order to 1) examine how fishing pressure and benthic composition influences grazing rates of these two major feeding groups; 2) examine how grazing rates are controlled by both biomass and size structure of grazing assemblages.	1) Cropper potential grazing function is influenced by benthic, 'bottom-up' processes (structural complexity, macroalgal cover, substrate availability for turf); their function is relatively unaffected by fishing. Scraper function on the other hand, is more influenced by fishing (lower where human population and fishing is higher) and less affected by bottom-up processes (except structural complexity is still a significant influence). 2) Fishing and benthic processes influence herbivore functioning through their effect on biomass. For a given level of biomass, assemblages that constitute a majority of smaller-bodied fish have higher grazing rates. Biomass is linked to grazing function, such that protecting fish biomass will help ensure herbivory processes remain intact on degraded coral reefs.
Ruttenberg et al. 2019	Caribbean	Bite rates, bite area, bite volume, fish densities	*Scarus coelestinus*, *S. coeruleus*, *S. guacamaia*, *S. iseri*, *S. taeniopterus*, *S. vetula*, *Sparisoma aurofrenatum*, *Sp. chrysopterum,* *Sp. rubripinne*, *Sp. viride*	Explore how species identity controls ecological processes among habitats and across multiple spatial scales.	Community composition was more important than biomass for estimating herbivory. Ecological processes of herbivory (i.e. macroalgal consumption, areal grazing, scraping, and bioerosion) was driven by species density and identity. Found evidence of 'zonation' with different functional groups dominating in different habitats. Biomass was not as important for estimating herbivory.

Appendix B - Supplemental tables and figures for Chapter 2

Table B1 Number of herbivore feeding observations made by each scientific diver in each year, ordered from greatest to least.

Observer	2013	2015	2017	Total
SD	-	208	319	527
SC	191	229	-	420
TAP	-	-	411	411
JKB	215	-	-	215
TB	199	-	-	199
JLG	151	-	-	151
MW	61	-	-	61
Total	817	437	730	1984

Table B2 Species-specific regression equations used for calculating individual gape heights and gape widths used in the grazing impact models. Estimated gape area was calculated (to approximate the area of a circle) as π × ½ gape height × ½ gape width. Species are arranged alphabetically within functional groups (FG; B=browser, E=excavator, G=grazer, S=scraper).

FG	Family	Species	Gape height	Gape width	Source
B	Scaridae	*Calotomus carolinus*	1.4 x – 1.9	1.3 x – 1.8	Regression equations of *S. frenatus*
E	Scaridae	*Chlorurus sordidus*	1.2 x – 1.4	1.2 x – 1.6	Dunic & Baum (2017)[1]
G	Acanthuridae	*Acanthurus achilles, A. leucocheilus, A. lineatus, A. nigricauda, A. nigrofuscus, A. nigroris, A. triostegus, A. xanthopterus*	1.35 x – 1.8	1.15 x – 1.6	Average of *A. nigricans* and *A. olivaceus*
		A. nigricans	1.4 x – 1.9	1.1 x – 1.5	Dunic & Baum (2017)
		A. olivaceus	1.3 x – 1.7	1.2 x – 1.7	Dunic & Baum (2017)
S	Scaridae	*Scarus frenatus*	1.4 x – 1.9	1.3 x – 1.8	Dunic & Baum (2017)
		S. forsteni, S. ghobban, S. globiceps, S. oviceps, S. psittacus, S. tricolor	1.4 x – 1.9	1.25 x – 1.7	Average of *S. frenatus* and *S. rubroviolaceus*
		S. rubroviolaceus	1.4 x – 1.9	1.2 x – 1.6	Dunic & Baum (2017)

[1] Dunic JC, Baum JK (2017) Size structuring and allometric scaling relationships in coral reef fishes. J Anim Ecol 86:577-589.

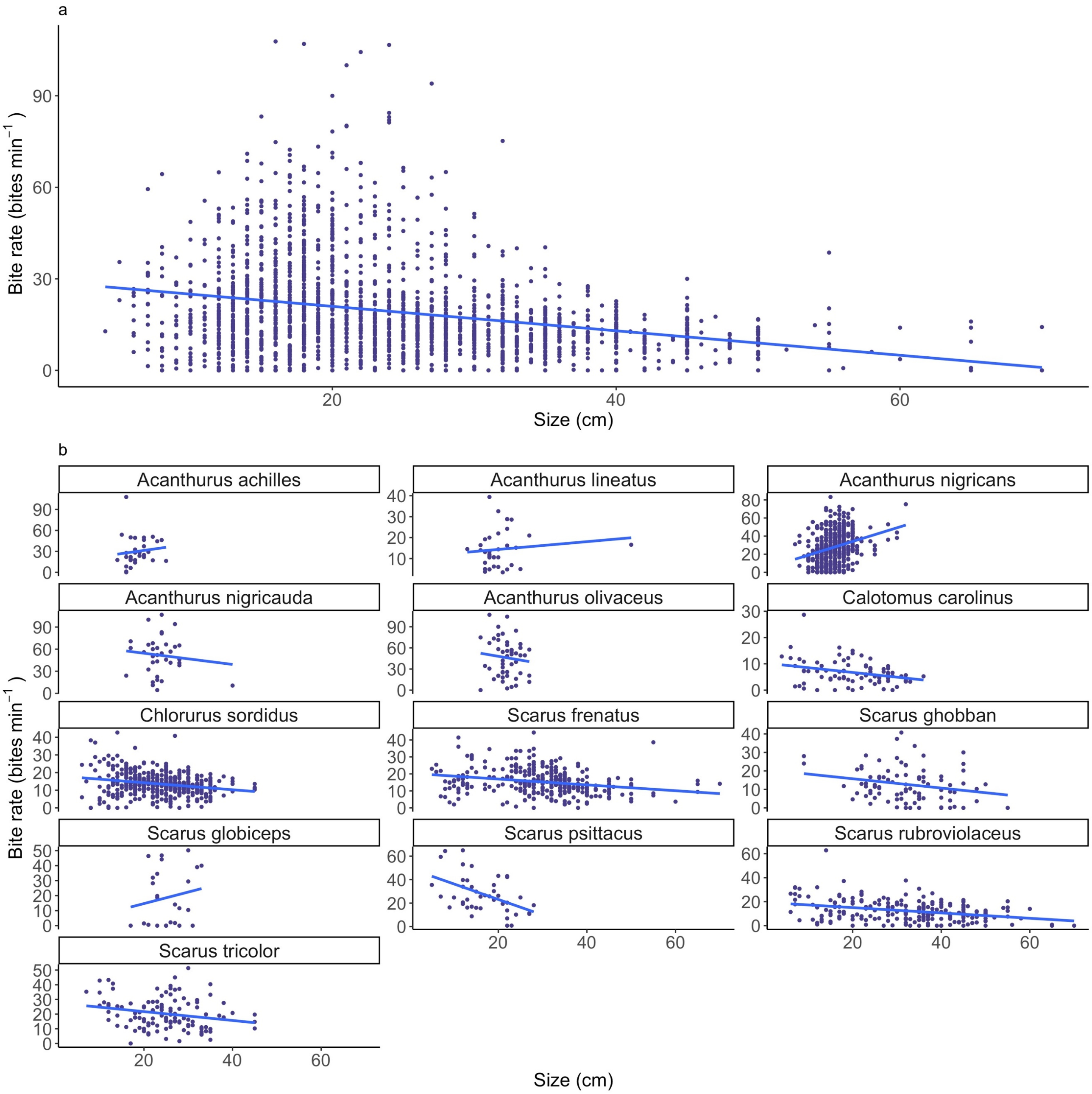

Figure B1 Bite rate by size for (a) all herbivores and (b) the 13 most commonly observed species on Kiritimati.

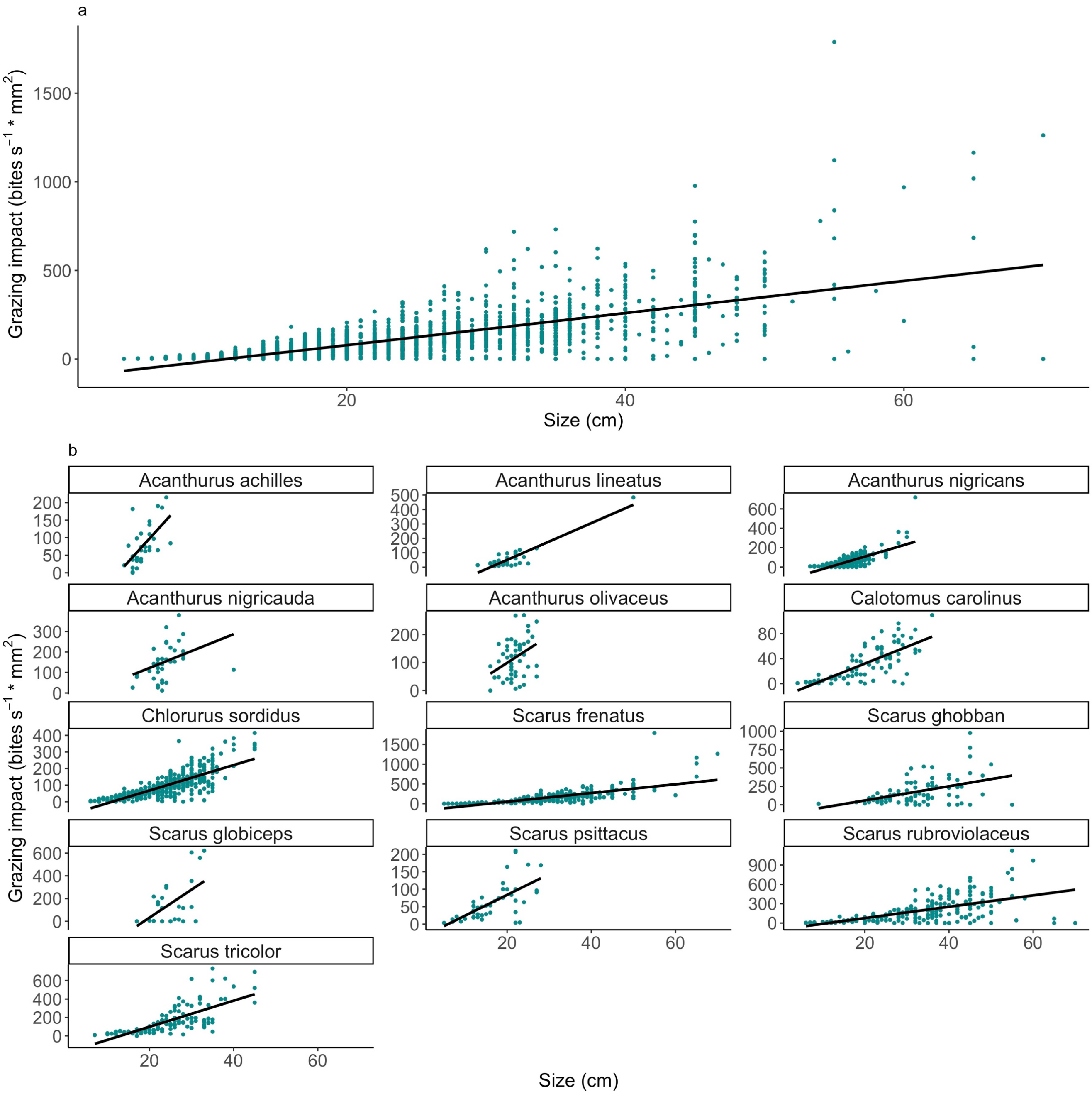

Figure B2 Grazing impact by size for (a) all herbivores and (b) the 13 most commonly observed species on Kiritimati.

Table B3 Overall mean (± SE) and substrate-specific mean bite rates (bites min^{-1}) for each surgeonfish (family Acanthuridae) and parrotfish (family Scaridae) species, averaged across sites and years. FG is functional group (B=browser, E=excavator, G=grazer, S=scraper), and N is the number of observations used to calculate bite rate. Substrates are ordered left to right from most to least bitten on average. The bottom row indicates the mean (± SE) substrate-specific bite rates averaged across species.

FG	Species	N	Overall rate	Turf	Caulerpa	CCA	Halimeda	Coral	Lobophora	Galaxaura	Mesopora
B	*Calotomus carolinus*	86	6.7 ± 0.49	3.6 ± 0.51	2.36 ± 0.37	0.02 ± 0.02	1.26 ± 0.19	0.04 ± 0.02	0.15 ± 0.1	0 ± 0	0 ± 0
E	*Chlorurus sordidus*	430	13.47 ± 0.3	12.72 ± 0.37	0.2 ± 0.05	1.11 ± 0.12	0.22 ± 0.03	0.21 ± 0.03	0.04 ± 0.04	0 ± 0	0 ± 0
G	*Acanthurus nigricauda*	37	51.53 ± 4.15	51.56 ± 4.4	0.13 ± 0.12	0 ± 0	0.15 ± 0.13	0.05 ± 0.04	0 ± 0	0 ± 0	0 ± 0
	A. olivaceus	52	46.02 ± 3.68	46.95 ± 4.15	0.14 ± 0.14	0 ± 0	0.17 ± 0.12	0.25 ± 0.25	0 ± 0	0 ± 0	0 ± 0
	A. achilles	31	30.04 ± 3.57	32.67 ± 4.66	0.1 ± 0.08	0.14 ± 0.1	0.05 ± 0.03	0.04 ± 0.03	0 ± 0	0 ± 0	0 ± 0
	A. nigricans	457	28.01 ± 0.78	29.09 ± 0.9	0.06 ± 0.01	0.03 ± 0.01	0.05 ± 0.01	0.05 ± 0.01	0 ± 0	0.02 ± 0.01	0 ± 0
	A. lineatus	37	14.43 ± 1.44	16.96 ± 1.99	0.02 ± 0.02	0.01 ± 0.01	0.03 ± 0.02	0.1 ± 0.06	0 ± 0	0 ± 0	0 ± 0
S	*Scarus psittacus*	44	27.73 ± 2.34	29.43 ± 2.98	1.37 ± 0.51	0 ± 0	0.11 ± 0.05	0 ± 0	0 ± 0	0.01 ± 0.01	0 ± 0
	S. tricolor	118	20.25 ± 0.95	19.46 ± 1.17	0.32 ± 0.09	0.16 ± 0.07	0.39 ± 0.09	0.27 ± 0.07	0 ± 0	0 ± 0	0.01 ± 0.01
	S. globiceps	25	18.87 ± 3.63	21.02 ± 4.13	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
	S. frenatus	318	15.24 ± 0.41	15.86 ± 0.53	0.44 ± 0.07	0.47 ± 0.1	0.23 ± 0.03	0.36 ± 0.05	0 ± 0	0 ± 0	0 ± 0
	S. ghobban	87	12.7 ± 0.96	11.02 ± 1.01	1.36 ± 0.33	0.02 ± 0.01	0.69 ± 0.23	0.07 ± 0.04	0 ± 0	0 ± 0	0 ± 0
	S. rubroviolaceus	220	12.26 ± 0.58	12.31 ± 0.64	0.28 ± 0.06	0.13 ± 0.04	0.26 ± 0.07	0.15 ± 0.03	0.01 ± 0.01	0 ± 0	0 ± 0
	Total	1942	**Substrate average**	19.51 ± 0.39	0.39 ± 0.03	0.36 ± 0.03	0.25 ± 0.02	0.16 ± 0.01	0.02 ± 0.01	0.01 ± 0	0 ± 0

Table B4 a) Overall herbivore bite rate model results for the fixed effect parameters and b) pairwise comparisons between significant (by likelihood ratio tests) categorical predictors. Bold indicates significant values [pr(>|z|)], at α = 0.05, and asterisks indicate levels of significance (* p < 0.05, ** p < 0.01, *** p < 0.001).

		a) Bite rate model summary			
Fixed effects	Factor levels	Estimate	Standard Error	z-value	p-value
Intercept	-	**-1.0842**	**0.1242**	**-8.73**	**<2e-16*** **
Time of Day	-	**0.1636**	**0.0170**	**9.62**	**<2e-16*** **
Size (cm)	-	**-0.1378**	**0.0188**	**-7.35**	**2.0e-13*** **
Functional Group	**Scraper**	**-0.5246**	**0.0987**	**-5.32**	**1.1e-07*** **
(baseline: Grazer)	**Excavator**	**-0.6662**	**0.1725**	**-3.86**	**0.00011*** **
	Browser	**-1.4327**	**0.1834**	**-7.81**	**5.6e-15*** **
Year (baseline:	**2015**	**0.3286**	**0.0479**	**6.87**	**6.6e-12*** **
2013)	**2017**	**0.1364**	**0.0425**	**3.21**	**0.00133** **
Disturbance	Low	0.0814	0.1370	0.59	0.55225
(baseline: Very low)	Medium	0.1580	0.1215	1.30	0.19330
	Very high	**0.3244**	**0.1596**	**2.03**	**0.04207***
		b) Pairwise comparisons			
Linear Hypotheses		Estimate	Standard Error	z-value	Pr(>|z|)
Scraper – Grazer = 0		**-0.53368**	**0.09677**	**-5.515**	**<0.001*** **
Excavator – Grazer = 0		**-0.67603**	**0.17024**	**-3.971**	**<0.001*** **
Browser – Grazer= 0		**-1.43674**	**0.18089**	**-7.943**	**<0.001*** **
Excavator – Scraper = 0		-0.14235	0.23570	-0.604	0.90939
Browser – Scraper = 0		**-0.90306**	**0.20447**	**-4.417**	**<0.001*** **
Browser – Excavator = 0		**-0.76071**	**0.24316**	**-3.128**	**0.00773** **
2015 – 2013 = 0		**0.32549**	**0.04770**	**6.824**	**<0.001*** **
2017 – 2013 = 0		**0.12811**	**0.04226**	**3.031**	**0.00683** **
2017 – 2015 = 0		**-0.19738**	**0.06002**	**-3.289**	**0.00307** **

Table B5 Functional group bite rate model results for the fixed effect parameters for a) grazers, b) scrapers, c) the browser (*Calotomus carolinus*) and d) the excavator (*Chlorurus sordidus*). Bold indicates significant values [pr(>|z|)], at α = 0.05; asterisks indicate levels of significance (* p < 0.05, ** p < 0.01, *** p < 0.001). IP = Intermediate Phase, TP = Terminal Phase.

Fixed effects	Factor levels	a) Grazer			
		Estimate	Standard Error	z-value	p-value
Intercept	-	**-0.92624**	**0.13847**	**-6.69**	**2.2e-11*** **
Time of Day	-	**0.23841**	**0.03296**	**7.23**	**4.7e-13*** **
Size (cm)	-	**0.17328**	**0.03836**	**4.52**	**6.3e-06*** **
Species (baseline: *Acanthurus nigricans*)	*A. olivaceus*	-0.02310	0.17130	-0.13	0.8927
	A. lineatus	**-0.48920**	**0.15333**	**-3.19**	**0.0014** **
	A. nigricauda	0.03513	0.16554	0.21	0.8319
	A. achilles	-0.00569	0.14681	-0.04	0.9691
Year (baseline: 2013)	**2015**	**0.38682**	**0.09393**	**4.12**	**3.8e-05*** **
	2017	**0.23635**	**0.09762**	**2.42**	**0.0155***
Disturbance (baseline: Very low)	Low	-0.07456	0.16992	-0.44	0.6608
	Medium	-0.04324	0.14490	-0.30	0.7654
	Very high	0.14583	0.19345	0.75	0.4509

Fixed effects	Factor levels	b) Scraper			
		Estimate	Standard Error	z-value	p-value
Intercept	-	**-1.5446**	**0.1589**	**-9.72**	**<2e-16*** **
Time of Day	-	**0.1516**	**0.0262**	**5.78**	**7.4e-09*** **
Size (cm)	-	**-0.1222**	**0.0339**	**-3.60**	**0.00031*** **
Species (baseline: *Scarus frenatus*)	***S. rubroviolaceus***	**-0.2838**	**0.0599**	**-4.74**	**2.2e-06*** **
	S. tricolor	0.0503	0.0766	0.66	0.51118
	S. ghobban	**-0.4980**	**0.0863**	**-5.77**	**8.0e-09*** **
	S. psittacus	0.1321	0.1176	1.12	0.26112
	S. globiceps	0.1344	0.1461	0.92	0.35755
Phase (baseline: Juvenile)	IP	-0.0894	0.0910	-0.98	0.32574
	TP	**-0.2437**	**0.1111**	**-2.19**	**0.02822***
Year (baseline: 2013)	**2015**	**0.3270**	**0.0742**	**4.40**	**1.1e-05*** **
	2017	0.1061	0.0586	1.81	0.07031
Disturbance (baseline: Very low)	Low	0.1060	0.1760	0.60	0.54714
	Medium	**0.3093**	**0.1555**	**1.99**	**0.04666***
	Very high	**0.4267**	**0.2000**	**2.13**	**0.03293***

Table B5 (cont'd)

Fixed effects	Factor levels	c) Browser			
		Estimate	Standard Error	z-value	p-value
Intercept	-	**-2.7134**	**0.4322**	**-6.28**	**3.4e-10*** **
Time of Day	-	0.0679	0.0891	0.76	0.45
Size (cm)	-	-0.1988	0.1648	-1.21	0.23
Phase (baseline:	IP	0.2570	0.3510	0.73	0.46
Juvenile)	TP	0.0284	0.4592	0.06	0.95
Year (baseline:	2015	0.3826	0.7813	0.49	0.62
2013)	2017	0.2516	0.2417	1.04	0.30
Disturbance	Low	-0.1215	0.4123	-0.29	0.77
(baseline: Very low)	Medium	0.2292	0.2608	0.88	0.38
	Very high	0.0617	0.3156	0.20	0.85
Fixed effects	Factor levels	d) Excavator			
		Estimate	Standard Error	z-value	p-value
Intercept	-	**-1.49802**	**0.14877**	**-10.07**	**<2e-16*** **
Time of Day	-	**0.12472**	**0.02589**	**4.82**	**1.5e-06*** **
Size (cm)	-	-0.03693	0.03783	-0.98	0.329
Phase (baseline:	IP	0.03309	0.12225	0.27	0.787
Juvenile)	TP	-0.19034	0.15137	-1.26	0.209
Year (baseline:	**2015**	**0.14703**	**0.07314**	**2.01**	**0.044***
2013)	2017	-0.03152	0.06177	-0.51	0.610
Disturbance	Low	0.04618	0.10103	0.46	0.648
(baseline: Very low)	Medium	-0.00498	0.08804	-0.06	0.955
	Very high	0.26046	0.14885	1.75	0.080

Table B6 Results of pairwise comparisons between significant (by likelihood ratio tests) categorical predictors for the a) grazer, and b) scraper bite rate models. Bolded values indicate significant pairwise differences [pr(>|z|)], at α = 0.05 and asterisks indicate levels of significance (* p < 0.05, ** p < 0.01, *** p < 0.001).

Linear Hypotheses	a) Grazer			
	Estimate	Standard Error	z-value	Pr(>|z|)
A. olivaceus – *A. nigricans* = 0	-0.023098	0.171300	-0.135	0.9999
***A. lineatus* – *A. nigricans* = 0**	**-0.489199**	**0.153330**	**-3.190**	**0.0113***
A. nigricauda – *A. nigricans* = 0	0.035131	0.165540	0.212	0.9995
A. achilles – *A. nigricans* = 0	-0.005694	0.146810	-0.039	1.0000
A. lineatus – *A. olivaceus* = 0	-0.466101	0.242856	-1.919	0.2856
A. nigricauda – *A. olivaceus* = 0	0.058229	0.189336	-0.308	0.9978
A. achilles – *A. olivaceus* = 0	0.017404	0.209908	0.083	1.0000
A. nigricauda – *A. lineatus* = 0	0.524330	0.234489	2.236	0.1521
A. achilles – *A. lineatus* = 0	0.483505	0.212334	2.277	0.1396
A. achilles – *A. nigricauda* = 0	-0.040825	0.205439	-0.199	0.9996
2015 – 2013 = 0	**0.38682**	**0.09393**	**4.118**	**<0.001*** **
2017 – 2013 = 0	**0.23635**	**0.09762**	**2.421**	**0.0398***
2017 – 2015 = 0	-0.15047	0.12085	-1.245	0.4211

Linear Hypotheses	b) Scraper			
	Estimate	Standard Error	z-value	Pr(>|z|)
***S. rubroviolaceus* – *S. frenatus* = 0**	**-0.283782**	**0.059904**	**-4.737**	**<0.001*** **
S. tricolor – *S. frenatus* = 0	0.050303	0.076565	0.657	0.98376
***S. ghobban* – *S. frenatus* = 0**	**-0.497958**	**0.086315**	**-5.769**	**<0.001*** **
S. psittacus – *S. frenatus* = 0	0.132119	0.117570	1.124	0.85317
S. globiceps – *S. frenatus* = 0	0.134445	0.146130	0.920	0.93157
***S. tricolor* – *S. rubroviolaceus* = 0**	**0.334085**	**0.097502**	**3.426**	**0.00697** **
S. ghobban – *S. rubroviolaceus* = 0	-0.214177	0.104923	-2.041	0.28908
***S. psittacus* – *S. rubroviolaceus* = 0**	**0.415901**	**0.132797**	**3.132**	**0.01872***
S. globiceps – *S. rubroviolaceus* = 0	0.418227	0.159630	2.620	0.08083
***S. ghobban* – *S. tricolor* = 0**	**-0.548261**	**0.097552**	**-5.620**	**<0.001*** **
S. psittacus – *S. tricolor* = 0	0.081816	0.117003	0.699	0.97857
S. globiceps – *S. tricolor* = 0	0.084143	0.157500	0.534	0.99369
***S. psittacus* – *S. ghobban* = 0**	**0.630078**	**0.109441**	**5.757**	**<0.001*** **
***S. globiceps* – *S. ghobban* = 0**	**0.632404**	**0.161968**	**3.904**	**0.00120** **
S. globiceps – *S. psittacus*= 0	0.002326	0.179772	0.013	1.00000
2015 – 2013 = 0	**0.32701**	**0.07424**	**4.405**	**<0.001*** **
2017 – 2013 = 0	0.10611	0.05862	1.810	0.1532
2017 – 2015 = 0	-0.22091	0.09866	-2.239	0.0589

Table B7 Results of likelihood ratio tests for our categorical predictors included in models (without size) of herbivore bite rates overall and each functional group (FG). Bolded values indicate significant pairwise differences [pr(>|z|)], at α = 0.05 and asterisks indicate levels of significance (* p < 0.05, ** p < 0.01, *** p < 0.001).

Response	Model	Predictor	DF	Deviance	Pr(>Chi)		Significant pairwise
Bite Rates	Overall	**FG**	**3**	**27**	**5.89e-06**	***	Grazer > All FG; Browser < Scraper
		Year	**2**	**40.2**	**1.87e-09**	***	2015 > 2013; 2017 > 2013
		Disturbance	3	4.6	0.2035		
	Grazer	Species	4	8.26	0.08251		
		Year	**2**	**14.66**	**0.0006556**	***	2015 > 2013; 2017 > 2013
		Disturbance	3	1.64	0.6504		
	Scraper	**Species**	**5**	**84.88**	**<2.2e-16**	***	*S. ghobban* and *S. rubroviolaceus* < all other species except each other
		Phase	**3**	**41.38**	**5.43e-09**	***	IP and TP > J
		Year	**2**	**16.92**	**0.002118**	***	2015 > 2013
		Disturbance	3	6.06	0.1087		
	Browser	Phase	3	4.658	0.1986		
		Year	2	1.454	0.4834		
		Disturbance	3	2.144	0.5431		
	Excavator	**Phase**	**3**	**32.36**	**4.39e-07**	***	Pairwise differences are not significant
		Year	2	5.8	0.05502		
		Disturbance	3	4.16	0.2447		

Table B8 a) Overall herbivore grazing impact model results for the fixed effect parameters and b) pairwise comparisons between significant (by likelihood ratio tests) categorical predictors. Bold indicates significant values [pr(>|z|)], at α = 0.05, and asterisks indicate levels of significance (* p < 0.05, ** p < 0.01, *** p < 0.001).

Fixed effects	Factor levels	a) Grazing impact model summary			
		Estimate	Standard Error	z-value	p-value
Intercept	-	**4.18400**	**0.13050**	**32.062**	**<2e-16*****
Time of Day	-	**0.16173**	**0.01892**	**8.549**	**<2e-16*****
Size (polynomial)	1st order	**41.97292**	**0.93763**	**44.765**	**<2e-16*****
	2nd order	**-13.01431**	**0.81062**	**-16.055**	**<2e-16*****
	3rd order	**6.32038**	**0.85281**	**7.411**	**1.25e-13*****
Functional Group	Scraper	-0.11015	0.10043	-1.097	0.2728
(baseline: Grazer)	Excavator	-0.10462	0.16972	-0.616	0.5376
	Browser	**-0.94418**	**0.18027**	**-5.238**	**1.63e-07*****
Year (baseline: 2013)	2015	**0.30415**	**0.05304**	**5.734**	**9.82e-09*****
	2017	**0.11488**	**0.04706**	**2.441**	**0.0146***
Disturbance (baseline:	Low	0.06701	0.14578	0.460	0.6458
Very low)	Medium	0.13238	0.12942	1.023	0.3064
	Very high	0.28881	0.17066	1.692	0.0906
Linear Hypotheses		**b) Pairwise comparisons**			
		Estimate	Standard Error	z-value	Pr(>|z|)
Scraper – Grazer = 0		-0.110146	0.100434	-1.097	0.678
Excavator – Grazer = 0		-0.104623	0.169720	-0.616	0.923
Browser – Grazer= 0		**-0.944185**	**0.180273**	**-5.238**	**<0.001*****
Excavator – Scraper = 0		0.005523	0.166054	0.033	1.000
Browser – Scraper = 0		**-0.834039**	**0.175659**	**-4.748**	**<0.001*****
Browser – Excavator = 0		**-0.839562**	**0.223035**	**-3.764**	**<0.001*****
2015 – 2013 = 0		**0.30415**	**0.05304**	**5.734**	**<0.001*****
2017 – 2013 = 0		**0.11488**	**0.04706**	**2.441**	**0.0387***
2017 – 2015 = 0		**-0.18927**	**0.05155**	**-3.672**	**<0.001*****

Table B9 Functional group grazing impact model results for the fixed effect parameters for a) grazers, b) scrapers, c) the browser (*Calotomus carolinus*) and d) the excavator (*Chlorurus sordidus*). Bold indicates significant values [pr(>|z|)], at α = 0.05, and asterisks indicate levels of significance (* p < 0.05, ** p < 0.01, *** p < 0.001). IP = Intermediate Phase, TP = Terminal Phase.

		a) Grazer			
Fixed effects	Factor levels	Estimate	Standard Error	z-value	p-value
Intercept	-	**3.79023**	**0.15423**	**24.575**	**<2e-16*******
Time of Day	-	**0.24154**	**0.03387**	**7.132**	**9.86e-13*******
Size (polynomial)	**1st order**	**18.55216**	**0.90118**	**20.587**	**<2e-16*******
	2nd order	**-5.38991**	**0.71612**	**-7.527**	**5.21e-14*******
	3rd order	**1.61757**	**0.73938**	**2.188**	**0.02869***
Species (baseline:	***A. olivaceus***	**-0.41977**	**0.18081**	**-2.322**	**0.02026***
Acanthurus	***A. lineatus***	**-0.47195**	**0.15616**	**-3.022**	**0.00251****
nigricans)	***A. nigricauda***	**-0.37590**	**0.17632**	**-2.132**	**0.03302***
	A. achilles	-0.01802	0.15086	-0.119	0.90492
Year (baseline:	**2015**	**0.40804**	**0.09615**	**4.244**	**2.20e-05*******
2013)	**2017**	**0.24545**	**0.10100**	**2.430**	**0.01510***
Disturbance	Low	-0.02643	0.19700	-0.134	0.89329
(baseline: Very	Medium	-0.03026	0.16792	-0.180	0.85701
low)	Very high	0.14772	0.22698	0.651	0.51516

		b) Scraper			
Fixed effects	Factor levels	Estimate	Standard Error	z-value	p-value
Intercept	-	**4.366460**	**0.207812**	**21.012**	**<2e-16*******
Time of Day	-	**0.153536**	**0.031990**	**4.800**	**1.59e-06*******
Size (polynomial)	**1st order**	**29.375688**	**1.293925**	**22.703**	**<2e-16*******
	2nd order	**-8.946772**	**1.143116**	**-7.827**	**5.01e-15*******
	3rd order	**3.400508**	1.046242	**3.250**	**0.001153****
Species (baseline:	*S. rubroviolaceus*	-0.033643	0.074667	-0.451	0.652297
Scarus frenatus)	***S. tricolor***	**0.359164**	**0.094859**	**3.786**	**0.000153*******
	S. ghobban	**-0.279081**	**0.106077**	**-2.631**	**0.008515****
	S. psittacus	**0.366352**	**0.148070**	**2.474**	**0.013354***
	S. globiceps	**0.421706**	**0.181649**	**2.322**	**0.020258***
Phase (baseline:	IP	0.003844	0.164540	0.023	0.981360
Juvenile)	TP	-0.141404	0.175791	-0.804	0.421175
Year (baseline:	**2015**	**0.320663**	**0.091468**	**3.506**	**0.000455*******
2013)	2017	0.087469	0.071922	1.216	0.223921
Disturbance	Low	0.074529	0.190975	0.390	0.696349
(baseline: Very	Medium	0.290247	0.168562	1.722	0.085087
low)	Very high	0.403161	0.216509	1.862	0.062589

Table B9 (cont'd)

Fixed effects	Factor levels	c) Browser			
		Estimate	Standard Error	z-value	p-value
Intercept	-	**2.60856**	**0.63018**	**4.139**	**3.48e-05*** **
Time of Day	-	0.06907	0.10232	0.675	0.4996
Size (polynomial)	**1st order**	**9.48035**	**2.02144**	**4.690**	**2.73e-06*** **
	2nd order	-2.40896	1.27471	-1.890	0.0588
	3rd order	0.57436	0.84436	0.680	0.4964
Phase (baseline:	IP	0.27208	0.57061	0.477	0.6335
Juvenile)	TP	0.02712	0.64462	0.042	0.9664
Year (baseline: 2013)	2015	0.37899	0.85750	0.442	0.6585
	2017	0.23979	0.26769	0.896	0.3704
Disturbance (baseline:	Low	-0.12477	0.46141	-0.270	0.7868
Very low)	Medium	0.22623	0.30291	0.747	0.4552
	Very high	0.06435	0.36378	0.177	0.8596

Fixed effects	Factor levels	d) Excavator			
		Estimate	Standard Error	z-value	p-value
Intercept	-	**4.26241**	**0.18437**	**23.119**	**<2e-16*** **
Time of Day	-	**0.12535**	**0.02940**	**4.263**	**2.01e-05*** **
Size (polynomial)	**1st order**	**16.50263**	**0.90895**	**18.156**	**<2e-16*** **
	2nd order	**-3.11313**	**0.61023**	**-5.102**	**3.37e-07*** **
	3rd order	1.12024	0.64246	1.744	0.0812
Phase (baseline:	IP	0.13091	0.15891	0.824	0.4101
Juvenile)	TP	-0.08970	0.18143	-0.494	0.6210
Year (baseline: 2013)	2015	0.15744	0.08568	1.838	0.0661
	2017	-0.03032	0.07156	-0.424	0.6717
Disturbance (baseline:	Low	0.04098	0.12896	0.318	0.7507
Very low)	Medium	-0.01209	0.11305	-0.107	0.9148
	Very high	0.26618	0.18576	1.433	0.1519

Table B10 Results of pairwise comparisons between significant (by likelihood ratio tests) categorical predictors for the a) grazer, and b) scraper grazing impact models. Bolded values indicate a significant pairwise difference [pr(>|z|)], at α = 0.05 and asterisks indicate levels of significance (* p < 0.05, ** p < 0.01, *** p < 0.001).

Linear Hypotheses	a) Grazer			
	Estimate	Standard Error	z-value	Pr(>|z|)
A. olivaceus – *A. nigricans* = 0	-0.41977	0.18081	-2.322	0.1304
***A. lineatus* – *A. nigricans* = 0**	**-0.47195**	**0.15616**	**-3.022**	**0.0198***
A. nigricauda – *A. nigricans* = 0	-0.37590	0.17632	-2.132	0.1963
A. achilles – *A. nigricans* = 0	-0.01802	0.15086	-0.119	1.0000
A. lineatus – *A. olivaceus* = 0	-0.05219	0.22895	-0.228	0.9994
A. nigricauda – *A. olivaceus* = 0	0.04387	0.16111	0.272	0.9987
A. achilles – *A. olivaceus* = 0	0.40175	0.20220	1.987	0.2599
A. nigricauda – *A. lineatus* = 0	0.09606	0.22395	0.429	0.9924
A. achilles – *A. lineatus* = 0	0.45393	0.19761	2.297	0.1379
A. achilles – *A. nigricauda* = 0	0.35788	0.20182	1.773	0.3744
2015 – 2013 = 0	**0.40804**	**0.09615**	**4.244**	**<1e-04*** **
2017 – 2013 = 0	**0.24545**	**0.10100**	**2.430**	**0.0396***
2017 – 2015 = 0	-0.16259	0.08368	-1.943	0.1258
Linear Hypotheses	b) Scraper			
	Estimate	Standard Error	z-value	Pr(>|z|)
S. rubroviolaceus – *S. frenatus* = 0	-0.033643	0.074667	-0.451	0.99735
***S. tricolor* – *S. frenatus* = 0**	**0.359164**	**0.094859**	**3.786**	**0.00179*** *
S. ghobban – *S. frenatus* = 0	-0.279081	0.106077	-2.631	0.08044
S. psittacus – *S. frenatus* = 0	0.366352	0.148070	2.474	0.11873
S. globiceps – *S. frenatus* = 0	0.421706	0.181649	2.322	0.16877
***S. tricolor* – *S. rubroviolaceus* = 0**	**0.392807**	**0.103126**	**3.809**	**0.00162*** *
S. ghobban – *S. rubroviolaceus* = 0	-0.245438	0.105208	-2.333	0.16453
S. psittacus – *S. rubroviolaceus* = 0	0.399995	0.152108	2.630	0.08073
S. globiceps – *S. rubroviolaceus* = 0	0.455349	0.191457	2.378	0.14876
***S. ghobban* – *S. tricolor* = 0**	**-0.638245**	**0.118921**	**-5.367**	**<0.001*** **
S. psittacus – *S. tricolor* = 0	0.007188	0.148438	0.048	1.00000
S. globiceps – *S. tricolor* = 0	0.062542	0.188741	0.331	0.99940
***S. psittacus* – *S. ghobban* = 0**	**0.645433**	**0.163293**	**3.953**	**0.00103*** *
***S. globiceps* – *S. ghobban* = 0**	**0.700787**	**0.198513**	**3.530**	**0.00501*** *
S. globiceps – *S. psittacus* = 0	0.055354	0.214655	0.258	0.99982
2015 – 2013 = 0	**0.32066**	**0.09147**	**3.506**	**0.00134*** *
2017 – 2013 = 0	0.08747	0.07192	1.216	0.44061
2017 – 2015 = 0	**-0.23319**	**0.09283**	**-2.512**	**0.03144***

Table B11 Results of likelihood ratio tests for our categorical predictors included in models (without size) of herbivore grazing impact overall and each functional group. Bolded values indicate significant pairwise differences [pr(>|z|)], at α = 0.05 and asterisks indicate levels of significance (* p < 0.05, ** p < 0.01, *** p < 0.001).

Response	Model	Predictor	DF	Deviance	Pr(>Chi)		Significant pairwise
Grazing Impact	Overall	**FG**	**3**	**15.85**	**0.001218**	**	Scraper > Grazer and Browser
		Year	**2**	**46.68**	**1.63e-11**	***	2015 > 2013; 2015 > 2017
		Disturbance	3	0.586	0.8996		
	Grazer	**Species**	**4**	**18.57**	**0.0009554**	***	*A. nigricauda* > *A. nigricans*
		Year	2	5.251	0.0724		
		Disturbance	3	2.434	0.4874		
	Scraper	**Species**	**5**	**35.54**	**1.17e-06**	***	*S. psittacus* < all other species except *S. globiceps*; *S. rubroviolaceus* > *S. psittacus* and *S. globiceps*
		Phase	**3**	**235.9**	**<2.2e-16**	***	TP > IP > J
		Year	**2**	**26.74**	**1.56e-06**	***	2015 > 2013; 2015 > 2017
		Disturbance	3	1.621	0.6548		
	Browser	**Phase**	**3**	**51.56**	**3.73e-11**	***	IP and TP > J
		Year	2	0.056	0.9725		
		Disturbance	3	4.264	2.34e-01		
	Excavator	**Phase**	**3**	**164.8**	**<2.2e-16**	***	TP > IP > J
		Year	**2**	**15.67**	**3.96e-04**	***	2015 > 2013; 2015 > 2017
		Disturbance	3	1.222	0.7476		

Table B12 Average (± SE) substrate-specific selectivity (Manly's α) observed for surgeonfish (family Acanthuridae) and parrotfish (family Scaridae) species from three years of recorded feeding observations and benthic cover. FG is the functional group; N is the number of observations used to average selectivity values. Substrates are ordered left to right by preference.

FG	Species	Year	N	Turf	Macroalgae	CCA	Coral
Grazer	*Acanthurus achilles*	2013	21	0.972 ± 0.01	0.022 ± 0.01	0.006 ± 0	0 ± 0
		2015	3	1 ± 0	0 ± 0	0 ± 0	0 ± 0
	Acanthurus lineatus	2013	19	0.984 ± 0.01	0.014 ± 0.01	0.001 ± 0	0.001 ± 0
		2015	7	1 ± 0	0 ± 0	0 ± 0	0 ± 0
	Acanthurus nigricans	2013	147	0.977 ± 0.01	0.018 ± 0.01	0.002 ± 0	0.002 ± 0
		2015	132	0.971 ± 0.01	0.014 ± 0.01	0.014 ± 0.01	0 ± 0
		2017	86	0.956 ± 0.02	0.043 ± 0.02	0.002 ± 0	0 ± 0
	Acanthurus nigricauda	2013	5	0.799 ± 0.2	0.201 ± 0.2	0 ± 0	0 ± 0
		2015	27	0.992 ± 0.01	0.007 ± 0.01	0 ± 0	0.001 ± 0
	Acanthurus olivaceus	2013	4	0.84 ± 0.16	0.14 ± 0.14	0 ± 0	0.02 ± 0.02
		2015	28	0.933 ± 0.03	0.067 ± 0.03	0 ± 0	0 ± 0
		2017	11	1 ± 0	0 ± 0	0 ± 0	0 ± 0
Scraper	*Scarus frenatus*	2013	146	0.874 ± 0.02	0.079 ± 0.01	0.035 ± 0.01	0.013 ± 0
		2015	38	0.852 ± 0.04	0.008 ± 0.01	0.103 ± 0.04	0.038 ± 0.01
		2017	90	0.897 ± 0.02	0.044 ± 0.01	0.036 ± 0.01	0.022 ± 0.01
	Scarus ghobban	2013	28	0.774 ± 0.05	0.222 ± 0.05	0.002 ± 0	0.002 ± 0
		2015	16	0.936 ± 0.04	0.034 ± 0.03	0.011 ± 0.01	0.019 ± 0.01
		2017	31	0.837 ± 0.05	0.163 ± 0.05	0 ± 0	0 ± 0
	Scarus globiceps	2013	7	1 ± 0	0 ± 0	0 ± 0	0 ± 0
		2015	8	1 ± 0	0 ± 0	0 ± 0	0 ± 0
	Scarus psittacus	2013	10	0.951 ± 0.04	0.049 ± 0.04	0 ± 0	0 ± 0
		2015	4	1 ± 0	0 ± 0	0 ± 0	0 ± 0
		2017	23	0.868 ± 0.05	0.132 ± 0.05	0 ± 0	0 ± 0
	Scarus rubroviolaceus	2013	61	0.955 ± 0.01	0.032 ± 0.01	0.01 ± 0.01	0.003 ± 0
		2015	30	0.859 ± 0.05	0.024 ± 0.02	0.076 ± 0.04	0.041 ± 0.02
		2017	89	0.878 ± 0.02	0.066 ± 0.02	0.015 ± 0.01	0.041 ± 0.02
	Scarus tricolor	2013	62	0.85 ± 0.03	0.129 ± 0.03	0.01 ± 0.01	0.011 ± 0
		2015	10	0.916 ± 0.08	0 ± 0	0 ± 0	0.084 ± 0.08
		2017	32	0.868 ± 0.04	0.088 ± 0.03	0.024 ± 0.02	0.021 ± 0.01
Excavator	*Chlorurus sordidus*	2013	191	0.861 ± 0.02	0.036 ± 0.01	0.098 ± 0.01	0.006 ± 0
		2015	72	0.707 ± 0.04	0.027 ± 0.02	0.254 ± 0.04	0.011 ± 0
		2017	109	0.824 ± 0.03	0.062 ± 0.01	0.094 ± 0.02	0.021 ± 0.01
Browser	*Calotomus carolinus*	2013	13	0.42 ± 0.12	0.58 ± 0.12	0 ± 0	0 ± 0
		2015	1	0.522 ± 0	0 ± 0	0.345 ± 0	0.133 ± 0
		2017	52	0.478 ± 0.06	0.495 ± 0.06	0 ± 0	0.027 ± 0.02

Table B13 a) Overall herbivore turf selectivity (Manly's α) model results for the fixed effect parameters and b) pairwise comparisons between significant (by likelihood ratio tests) categorical predictors. Bold indicates significant values [pr(>|z|)], at α = 0.05 and asterisks indicate levels of significance (* p < 0.05, ** p < 0.01, *** p < 0.001).

Fixed effects	Factor levels	a) Selectivity model summary			
		Estimate	Standard Error	z-value	p-value
Intercept	-	**2.06479**	**0.19111**	**10.804**	**<2e-16*** **
Functional Group (baseline: Grazer)	**Scraper**	**-0.41575**	**0.16035**	**-2.593**	**0.00952** **
	Excavator	-0.38213	0.24610	-1.553	0.12048
	Browser	**-2.12627**	**0.28338**	**-7.503**	**6.22e-14*** **
Year (baseline: 2013)	2015	0.09892	0.08858	1.117	0.26408
	2017	**0.17798**	**0.07939**	**2.242**	**0.02497***
Disturbance (baseline: Very low)	**Low**	**-0.55291**	**0.17977**	**-3.076**	**0.00210** **
	Medium	**-0.31087**	**0.15287**	**-2.034**	**0.04199***
	Very high	**0.39806**	**0.19553**	**2.036**	**0.04177***

Linear Hypotheses	b) Pairwise comparisons			
	Estimate	Standard Error	z-value	Pr(>|z|)
Scraper – Grazer = 0	**-0.41575**	**0.16035**	**-2.593**	**0.044***
Excavator – Grazer = 0	-0.38213	0.24610	-1.553	0.392
Browser – Grazer = 0	**-2.12627**	**0.28338**	**-7.503**	**<0.001*** **
Excavator – Scraper = 0	0.03363	0.23217	0.145	0.999
Browser – Scraper = 0	**-1.71051**	**0.27113**	**-6.309**	**<0.001*** **
Browser – Excavator = 0	**-1.74414**	**0.32875**	**-5.305**	**<0.001*** **
Low – Very low = 0	**-0.5529**	**0.1798**	**-3.076**	**0.0109***
Medium – Very low = 0	-0.3109	0.1529	-2.034	0.1723
Very high – Very low = 0	0.3981	0.1955	2.036	0.1715
Medium – Low = 0	0.2420	0.1491	1.623	0.3606
Very high – Low = 0	**0.9510**	**0.1939**	**4.905**	**<0.001*** **
Very high – Medium = 0	**0.7089**	**0.1682**	**4.215**	**<0.001*** **

Table B14 Functional group selectivity model results for the fixed effect parameters for a) grazers, b) scrapers, c) the browser (*Calotomus carolinus*) and d) the excavator (*Chlorurus sordidus*). Bold indicates significant values [pr(>|z|)], at α = 0.05, and asterisks indicate levels of significance (* p < 0.05, ** p < 0.01, *** p < 0.001). IP = Intermediate Phase, TP = Terminal Phase.

Fixed effects	Factor levels	a) Grazer			
		Estimate	Standard Error	z-value	p-value
Intercept	-	**2.22318**	**0.18355**	**12.112**	**<2e-16*** **
Species (baseline: *Acanthurus nigricans*)	*A. olivaceus*	-0.09092	0.21884	-0.415	0.6778
	A. lineatus	-0.05033	0.23221	-0.217	0.8284
	A. nigricauda	-0.13376	0.23250	-0.575	0.5651
	A. achilles	0.01767	0.24104	0.073	0.9416
Year (baseline: 2013)	2015	0.23419	0.12211	1.918	0.0551
	2017	0.15670	0.14579	1.075	0.2824
Disturbance (baseline: Very low)	Low	-0.13220	0.18782	-0.704	0.4815
	Medium	-0.13206	0.15326	-0.862	0.3889
	Very high	0.03012	0.19422	0.155	0.8767

Fixed effects	Factor levels	b) Scraper			
		Estimate	Standard Error	z-value	p-value
Intercept	-	**2.46192**	**0.25695**	**9.581**	**<2e-16*** **
Species (baseline: *Scarus frenatus*)	*S. rubroviolaceus*	0.07689	0.11368	0.676	0.498833
	S. tricolor	-0.26250	0.15009	-1.749	0.080307
	S. ghobban	**-0.54019**	**0.17181**	**-3.144**	**0.001666** **
	S. psittacus	-0.39998	0.21669	-1.846	0.064912
	S. globiceps	**0.79100**	**0.30472**	**2.596**	**0.009436** **
Phase (baseline: Juvenile)	**IP**	**-0.33116**	**0.16596**	**-1.995**	**0.046002***
	TP	-0.28789	0.17118	-1.682	0.092603
Year (baseline: 2013)	2015	0.04284	0.13574	0.316	0.752285
	2017	0.16872	0.11019	1.531	0.125725
Disturbance (baseline: Very low)	**Low**	**-0.86475**	**0.25991**	**-3.327**	**0.000877*** **
	Medium	**-0.62104**	**0.21228**	**-2.926**	**0.003439** **
	Very high	**0.52522**	**0.25845**	**2.032**	**0.042131***

Fixed effects	Factor levels	c) Browser			
		Estimate	Standard Error	z-value	p-value
Intercept	-	**2.0138**	**0.8657**	**2.326**	**0.02000***
Phase (baseline: Juvenile)	**IP**	**-0.9535**	**0.4793**	**-1.990**	**0.04665***
	TP	**-1.1081**	**0.5062**	**-2.189**	**0.02857***
Year (baseline: 2013)	2015	1.1285	1.5885	0.710	0.47744
	2017	0.0614	0.4863	0.126	0.89953
Disturbance (baseline: Very low)	**Low**	**-2.0753**	**0.9808**	**-2.116**	**0.03435***
	Medium	**-2.0015**	**0.6345**	**-3.155**	**0.00161** **
	Very high	0.1426	0.6750	0.211	0.83266

Table B14 (cont'd)

Fixed effects	Factor levels	d) Excavator			
		Estimate	Standard Error	z-value	p-value
Intercept	**-**	**0.96160**	**0.36108**	**2.663**	**0.00774****
Phase (baseline:	IP	0.53686	0.31994	1.678	0.09334
Juvenile)	**TP**	**0.86680**	**0.32155**	**2.696**	**0.00702****
Year (baseline: 2013)	**2015**	**-0.42488**	**0.18596**	**-2.285**	**0.02233***
	2017	0.08809	0.15986	0.551	0.58160
Disturbance (baseline:	**Low**	**-0.62357**	**0.27342**	**-2.281**	**0.02257***
Very low)	Medium	0.11439	0.22712	0.504	0.61449
	Very high	0.61689	0.35516	1.737	0.08240

Table B15 Results of pairwise comparisons between significant (by likelihood ratio tests) categorical predictors for the a) scraper, b) browser and c) excavator selectivity models. Bolded values indicate a significant pairwise difference [pr(>|z|)], at α = 0.05 and asterisks indicate levels of significance (* p < 0.05, ** p < 0.01, *** p < 0.001).

Linear Hypotheses	a) Scraper			
	Estimate	Standard Error	z-value	Pr(>|z|)
S. rubroviolaceus – *S. frenatus* = 0	0.07689	0.11368	0.676	0.98251
S. tricolor – *S. frenatus* = 0	-0.26520	0.15009	-1.749	0.47211
***S. ghobban* – *S. frenatus* = 0**	**-0.54019**	**0.17181**	**-3.144**	**0.01819***
S. psittacus – *S. frenatus* = 0	-0.39998	0.21669	-1.846	0.40937
S. globiceps – *S. frenatus* = 0	0.79100	0.30472	2.596	0.08733
S. tricolor – *S. rubroviolaceus* = 0	-0.33939	0.14915	-2.275	0.18542
***S. ghobban* – *S. rubroviolaceus* = 0**	**-0.61708**	**0.16610**	**-3.715**	**0.00248****
S. psittacus – *S. rubroviolaceus* = 0	-0.47687	0.21645	-2.203	0.21567
S. globiceps – *S. rubroviolaceus* = 0	0.71412	0.30982	2.305	0.17399
S. ghobban – *S. tricolor* = 0	-0.27769	0.17769	-1.563	0.59770
S. psittacus – *S. tricolor* = 0	-0.13748	0.22074	-0.623	0.98794
***S. globiceps* – *S. tricolor* = 0**	**1.05350**	**0.31988**	**3.293**	**0.01117***
S. psittacus – *S. ghobban* = 0	0.14021	0.23258	0.603	0.98961
***S. globiceps* – *S. ghobban* = 0**	**1.33119**	**0.33338**	**3.993**	**<0.001*****
***S. globiceps* – *S. psittacus* = 0**	**1.19099**	**0.35895**	**3.318**	**0.01014***
Low – Very low = 0	**-0.8648**	**0.2599**	**-3.327**	**0.00484****
Medium – Very low = 0	**-0.6210**	**0.2123**	**-2.926**	**0.01817***
Very high – Very low = 0	0.5252	0.2584	2.032	0.17344
Medium – Low = 0	0.2437	0.2176	1.120	0.67331
Very high – Low = 0	**1.3900**	**0.2633**	**5.279**	**<0.001*****
Very high – Medium = 0	**1.1463**	**0.2226**	**5.151**	**<0.001*****

Table B15 (cont'd)

Linear Hypotheses	b) Browser			
	Estimate	Standard Error	z-value	Pr(>|z|)
Low – Very low = 0	-2.07529	0.98078	-2.116	0.1387
Medium – Very low = 0	**-2.00155**	**0.63447**	**-3.155**	**0.0081****
Very high – Very low = 0	0.14261	0.67497	0.211	0.9964
Medium – Low = 0	0.07374	0.79057	0.093	0.9997
Very high – Low = 0	**2.21791**	**0.85322**	**2.599**	**0.0424***
Very high – Medium = 0	**2.14417**	**0.47894**	**4.477**	**<0.001*****
Linear Hypotheses	c) Excavator			
	Estimate	Standard Error	z-value	Pr(>|z|)
IP– J = 0	0.5369	0.3199	1.678	0.3031
TP – J = 0	**0.8668**	**0.3215**	**2.696**	**0.0294***
TP – IP = 0	**0.3299**	**0.1292**	**2.554**	**0.0438***
2015 – 2013 = 0	-0.42488	0.18596	-2.285	0.0575
2017 – 2013 = 0	0.08809	0.15986	0.551	0.8453
2017 – 2015 = 0	**0.51297**	**0.19095**	**2.686**	**0.0199***
Low – Very low = 0	-0.6236	0.2734	-2.281	0.09822
Medium – Very low = 0	0.1144	0.2271	0.504	0.95668
Very high – Very low = 0	0.6169	0.3552	1.737	0.29552
Medium – Low = 0	**0.7380**	**0.2340**	**3.153**	**0.00849****
Very high – Low = 0	**1.2405**	**0.3696**	**3.356**	**0.00387****
Very high – Medium = 0	0.5025	0.3389	1.483	0.43794

Appendix C - Supplemental tables for Chapter 3

Table C1 Number of site-averaged density estimates from underwater visual census surveys of herbivore species for which we had feeding observations. Number in brackets indicates instances at each site that had matching species' feeding observations and density estimates in each year in order to calculate a metric for average species impact. See the list of species in Table 3.1.

Site	2013	2017	2018	Total
VL1	6(5)	10(5)	5(4)	21(14)
VL2	5(3)	9(6)	8(0)	22(9)
VL3	0	10(6)	13(9)	23(15)
VL4	0	10(6)	7(5)	17(11)
VL11	0	6(3)	0	6(3)
L1	6(5)	12(6)	9(7)	27(18)
L2	0	3(3)	8(7)	11(10)
L3	10(6)	8	0	18(6)
L5	5(5)	10	0	15(5)
M1	10(4)	11(7)	9(7)	30(18)
M2	11(7)	12(7)	13(9)	36(23)
M3	7(7)	12(6)	8(7)	27(20)
M4	9(8)	9	0	18(8)
M5	7(6)	13(10)	7(5)	27(21)
M6	5(4)	6	0	11(4)
M9	0	8(4)	0	8(4)
M10	10(5)	8	0	18(5)
M11	6(4)	9	0	15(4)
H1	0	11(4)	10	21(4)
H2	9(5)	10	0	19(5)
VH1	10(6)	8(3)	2(2)	20(11)
VH2	9(8)	8(5)	11(9)	28(22)
VH3	12(7)	10(5)	8(6)	30(18)
Total	137(95)	213(86)	118(77)	468(258)

Table C2 Redundancy statistics (R^2, adjusted R^2) and anova-like permutation test output (n permutations = 9999) a) for overall RDA under reduced model; b**)** by terms (constraining variables). Bold number indicates significant values [pr(>|F)], at $\alpha = 0.05$, and asterisk indicates level of significance (* $p < 0.05$).

a) Overall model		R^2	Adj. R^2	df	Pseudo-F	Pr(>F)
		0.1682	**0.0615**	**5**	**1.5772**	**0.0346***
b) Constraining variables	Levels	R^2	Adj. R^2	df	Pseudo-F	Pr(>F)
El Niño	Before After	0.03718	0.01479	1	1.4762	0.818
Local human disturbance	Very low Low Medium High Very high	0.13671	0.05038	4	1.5357	0.066

Table C3 Eigenvalues for the constrained (RDA1–5) and unconstrained (PC1–18) axes and their contribution to the variance in the RDA model of herbivore community impact.

	RDA1	RDA2	RDA3	RDA4	RDA5	PC1	PC2	PC3	PC4	PC5	PC6	PC7	PC8	PC9	PC10	PC11	PC12	PC13	PC14	PC15	PC16	PC17	PC18
Eigenvalue	1.37	0.74	0.65	0.17	0.10	2.98	2.43	1.91	1.76	1.14	1.00	0.77	0.68	0.58	0.50	0.42	0.28	0.16	0.11	0.10	0.07	0.05	0.02
Proportion Explained	0.08	0.04	0.03	0.01	0.01	0.17	0.13	0.11	0.10	0.06	0.05	0.04	0.04	0.03	0.03	0.02	0.02	0.01	0.01	0.01	0.00	0.00	0.00
Cumulative Proportion	0.08	0.12	0.15	0.16	0.17	0.34	0.47	0.58	0.68	0.74	0.79	0.83	0.87	0.90	0.93	0.95	0.97	0.98	0.99	0.99	1.00	1.00	1.00

Table C4 Accumulated constrained eigenvalues and the importance of each canonical axis component to the constrained variation in herbivore community impact.

	RDA1	RDA2	RDA3	RDA4	RDA5
Eigenvalue	1.367	0.739	0.651	0.171	0.099
Proportion Explained	0.452	0.244	0.215	0.057	0.033
Cumulative Proportion	0.452	0.696	0.911	0.967	1.000

Table C5 a) Model results for fixed effect parameters in model of herbivore assemblage-level grazing impact. b) Results of pairwise comparisons between levels of significant (by likelihood ratio test) categorical predictors in the grazing impact model. Bold numbers indicate significant values [pr(>|z|)], at α = 0.05, and asterisks indicate levels of significance (* p < 0.05, ** p < 0.01, *** p < 0.001).

Fixed Effect	Factor Level	a) Summed grazing impact model results			
		Estimate	Standard Error	z-value	Pr(>|z|)
Intercept	-	2.06872	0.26080	7.932	**2.15e-15*** **
Functional Group	**Scraper**	**0.55818**	**0.03572**	**15.628**	**<2e-16*** **
	Excavator	**-0.24826**	**0.04999**	**-4.966**	**6.82e-07*** **
	Browser	**-2.39450**	**0.14798**	**-16.181**	**< 2e-16 *** **
El Niño (baseline: Before)	**After**	**0.32664**	**0.03788**	**8.623**	**<2e-16*** **
Human disturbance (baseline: Very low)	Low	-0.12518	0.38757	-0.323	0.747
	Medium	0.29874	0.32260	0.926	0.354
	High	0.13946	0.47292	0.295	0.768
	Very high	0.66264	0.42820	1.548	0.122
Linear Hypotheses		b) Pairwise comparisons			
		Estimate	Standard Error	z-value	Pr(>|z|)
Scraper – Grazer = 0		**0.55818**	**0.03572**	**15.628**	**<1e-07*** **
Excavator – Grazer = 0		**-0.24826**	**0.04999**	**-4.966**	**2.49e-06*** **
Browser – Grazer = 0		**-2.39450**	**0.14798**	**-16.181**	**< 1e-07*** **
Excavator – Scraper = 0		**-0.80644**	**0.04282**	**-18.833**	**< 1e-07*** **
Browser – Scraper = 0		**-2.95268**	**0.14590**	**-20.237**	**< 1e-07*** **
Browser – Excavator = 0		**-2.14624**	**0.14803**	**-14.498**	**< 1e-07*** **
After – Before = 0		**0.32664**	**0.03788**	**8.623**	**< 2e-16*** **