

FISHING FOR RESILIENCE: HERBIVORE AND ALGAL DYNAMICS ON CORAL REEFS IN KENYA

Thesis submitted in partial fulfillment
of the requirements for the degree of

Doctor of Philosophy

at

Rhodes University

By

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December 2013

ABSTRACT

Herbivory is a key process that mediates the abundance of primary producers and community composition in both terrestrial and aquatic ecosystems. On tropical coral reefs, changes in herbivory are often related to phase shifts between coral-dominance and dominance by seaweeds, or foliose macroalgae. Resilience or capacity to resist and reverse such phase shifts is, therefore, viewed as a critical function on coral reefs. This thesis used grazer exclusion and assay experiments at six sites within three different fisheries management regimes in Kenya to identify the impacts of herbivores (sea urchins and fishes) on algal dynamics in the context of coral reef resilience. First, I examined the grazing rates necessary to prevent phase shifts by quantifying consumption and algal production. Here, I found that, over a 390-day experiment, at least 50% of algal production must be consumed to avoid accumulation of algal biomass. Using video observations, I also showed that scraping parrotfishes remove more algae (per unit of fish biomass) than previously assumed, and that sea urchins, if released from predation, have similar impacts to fishes. Then I focused on algal succession, and found that sea urchins and fishes have different effects that are mediated by their abundances and species composition. Where sea urchins were less abundant and parrotfishes absent (e.g. young fisheries closures), progression of algae from turfs to early and then late successional macroalgae occurred rapidly and within 100 days. I then turned my focus to the removal of already established macroalgae (grown for > 1 yr in the absence of herbivores) and showed that sea urchins and browsing fishes were able to remove significant amounts of macroalgae where either herbivore was abundant. However, using multiple-choice selectivity assays and *in situ* video recordings, I

found that browsing fishes fed very selectively with low overlap in diet among species, leading to low functional redundancy within a high diversity system. Finally, using long-term survey data (from 28 sites) to build a 43-year chronosequence, I showed that it is possible that the effects of herbivory will not be constant across transitions from open fishing to fishery closures through non-linear grazing intensity. Therefore, increases in herbivory within fisheries closures may not be immediate and may allow a window of opportunity for algae to go from turf to unpalatable macroalgae until scraping and browsing fishes fully recover from fishing (~ 20 years). The findings in this thesis are novel and raise concern over the potential implications of the slow recovery of parrotfishes or, given lower than expected functional redundancy in grazing effects, the absence of even one browsing fish species in fisheries closures. Overall, this thesis highlights the importance of herbivore community dynamics in mediating interactions among algae, and provides new insights for conservation and management actions that attempt to bolster the resilience of coral reefs.



ACKNOWLEDGEMENTS

I will start by dedicating this thesis to Gunner, my furry companion. Gunner, I know you are a dog and cannot read this, and that I should buy you better food, but you waited for me back home while I was in Africa - you provided me continuity throughout this process and I am grateful for your childlike soul. Now that writing this thesis is finished, I promise to not be as boring of an owner.

A lot of folks deserve a big “thank you” for helping me in various ways to get to this point in the process, but I will begin with my thesis advisor. Christopher McQuaid, thank you for not hating me after Americanizing your name and my ~~ehronie~~ occasional truancy while living and doing field work in east Africa. You have been a supportive mentor by allowing me freedom to pursue my interests while holding me to a higher standard of writing and grammar (even in emails). The balance you strike between family, work, and play is inspiring. I am also incredibly indebted to Tim McClanahan who unknowingly took me under his wing in Kenya for the better part of three years. Tim, you taught me how to count fish and fundamentally changed my opinion on what constitutes an adequate research budget. Your perfectly organized data sets (yeah right!) helped me learn how to write code and also how to look beyond immediate patterns in ecology. Most importantly, you inspired me to be curious. I am also grateful for Nyawira Muthiga who served as a calming and maternal figure for me during my time in Kenya, and also allowed me to live on the office porch! Tim and Nya, some of your data contribute to part of this thesis, and for this I am grateful (and the organizations that fund your work).

The majority of my time over the last four years has been spent in and around Mombasa, Kenya. Numerous people made this experience valuable in diverse ways. I especially want to thank the Wildlife Conservation Society's Coral Reef Conservation Project staff, which accepted me like one of their own and tolerated my constant butchering of the Swahili language. Special thanks go to Carol Abunge, Joshua Kinyili, Pascal Thoya, and Jimmy Dena, whose infectious laugh and kind soul will forever be etched into my memory. Also, I am grateful for James Mariara who taught me the importance of remaining active throughout life and that field research equipment has an eternal life span (if you have a needle, thread, and some rubber). I also thank my two best friends and field assistants in Kenya, Collins Katana and Macdonald Muramba, for always having my back. I will never forget you and could not have done this work without your help. I feel very lucky to have spent time with such humble people. Emily Darling, thanks for being there when I needed it, keeping me sane, and laughing at my impersonations of Tim (which I'm pretty good at, by the way). And to Isaac Mutinda, thank you for helping me with all things automobile and for bailing me out of some volatile situations. Lastly, to all the others that helped me in Kenya with one thing or another: Rodgers Charo, Christina Hicks, Nick Graham, Josh Cinner, Aaron MacNeil, Jennifer O'Leary, Sander and Sarah den Haring, and the Kanamai fishermen among others. I also thank the Kenya Marine and Fisheries Research Institute, especially Jacqueline Uku and Jared Bosire, for facilitating the acquisition of permits to conduct research in Kenya and in the National Marine Parks from the Kenya Office for Science and Technology and the Kenya Wildlife Service.

An amazing community of family and friends were peripheral to my research, but central to all else. To my family in South Africa, Dave and Joeleen Beyers, thank you for taking care of me. Dave, thank you for not kicking my ass or throwing me out of the house after thinking Jo picked up a homeless man on the side of the street! Also, thank you for putting new meaning to 'night swimming'. Jo, thanks for keeping the fridge (and bar) full, treating me like your younger brother, buying me water bottles when I didn't need them, and constantly worrying about my wellbeing. Dave Hasek, thanks for teaching me how to surf and taking me to get annihilated by waves at Port Alfred, over and over again. Our many trips to J-bay and Mozambique were educational in so many ways. And to Alexis and Meyrick Bowker, thank you for being awesome people and sharing your home and farm with me. Bringing it closer to home, Wayne Dengler, I am forever grateful to you and Beth for taking care of Gunner while I was on another continent. You both did an incredible service and I will never be able to fully convey my gratitude to you – thank you for not expunging him for his hatred of cats. Thanks also to Laura Frey for checking on Gunner and sending me updates and photos. To Meg Baldwin, thank you for making this last year so fulfilling on a personal level and enduring my complaints about this thesis. All my friends that I have not mentioned here by name, you know who you are, and thank you for everything. And finally, to my family, who have always been supportive of my endeavors even though they do not really understand what I do. I appreciate your unconditional love.

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CHAPTER 1

GENERAL INTRODUCTION

1.1 Drivers of change on coral reefs

Coral reefs are among the most productive and biodiverse ecosystems in the world (Odum and Odum 1955, Connell 1978). Over 100 countries have coastlines with coral reefs and tens of millions of people depend on them for food and livelihood through the services they provide (Moberg and Folke 1999). These services can include coastal protection, fisheries, recreational activities, tourism, building materials, or even new biochemical compounds (Salvat 1992, Moberg and Folke 1999). Coral reefs also provide aesthetic benefits and contribute to the social fabric and cultural welfare of people (Wilkinson 1996, Bene 2009). Unfortunately, coral reefs are in global decline from climate change, ocean acidification, overexploitation, and pollution among other human pressures (Bruno and Selig 2007, Hoegh-Guldberg et al. 2007). Estimates vary on the rate of coral decline or change in community structure of reefs and few effective mitigation tools have been identified. This may be a result of the difficulty in discriminating among various drivers of change or determining cumulative or synergistic impacts of multiple stressors (Darling and Côté 2008, Darling et al. 2010, Hoegh-Guldberg and Bruno 2010). For instance, climate-related disturbances like coral bleaching events may interact with fishing to affect community dynamics of organisms (Darling et al. 2010).

Drivers of change on coral reefs can be pulse events that can cause substantial immediate damage, or chronic disturbances that operate over variable spatial and

temporal scales. For example, climate change impacts such as rising sea surface temperatures and increasing ocean acidification are chronic global drivers that can influence ecological processes in complex ways (Cooper et al. 2012). Alternatively, human impacts such as overfishing are chronic regional drivers that can mediate the abundance of functionally important organisms on a reef (Graham et al. 2011) and may be responsible for much of the historical deterioration of coral reefs (Jackson et al. 2001). At a local-scale, little can be done to mitigate global impacts, however, it has been argued that managing local drivers of change may strengthen the ability of a reef to cope with climate change in the medium-term future (Bellwood et al. 2004, Hughes et al. 2010, Cinner et al. 2013). Consequently, there is a need to better understand effects of local disturbances in conjunction with global increases in carbon emissions (Pandolfi et al. 2003, Gylfason 2006).

Overfishing is a critical local scale driver of deterioration of coral reefs, affecting key ecosystem processes and feedback mechanisms, changing species abundances, composition, and overall fish demographics (Jackson et al. 2001, McClanahan et al. 2008a, Graham et al. 2011). Exploitation may also have wider ecosystem consequences with diverse and surprising outcomes (Sala et al. 1998, Dulvy et al. 2004, Mumby et al. 2006). For instance, there is evidence for sea urchin and starfish-mediated trophic cascades on coral reefs where predator removal results in elevated abundances of these species, which in turn influences the base of the food web (Pace et al. 1999, O’Leary and McClanahan 2010). Restricting fishing can lead to a recovery of fish stocks and associated ecosystem function, but this response may be non-linear (McClanahan et al. 2007a) and responses can occur beyond the threshold at which the original changes occurred (known as “hysteresis effect”;

Hughes et al. 2003, 2010). Additionally, it is unlikely that restricting fishing will fully reinstate the original assemblage structure and subsequent ecosystem functioning that would be expected on reefs in a “pristine” state (Knowlton and Jackson 2008, Sandin et al. 2008). The time required for the recovery of coral reef ecosystems to either an ecological equilibrium or hypothetical historical condition is not well understood and estimates vary greatly (Halpern and Warner 2002, Micheli et al. 2004, Russ and Alcala 2004, McClanahan et al. 2007a, Aburto-Oropeza et al. 2011).

1.2 Resilience of coral reefs and phase shifts

The resilience of a system can be defined as its ability to absorb recurrent disturbances or shocks and respond to change without losing its basic structure and function (Holling 1973, Scheffer et al. 2001). Two key components of resilience are resistance and recovery. Resistance is the ability of an ecological community to absorb a disturbance without suffering major changes in its composition or functioning, and recovery is the ability of a community to recover from a disturbance and return to its original condition (Pimm 1984, West and Salm 2003). Where resistance has been weakened, a phase shift can occur, involving a change to an alternative state of the community, dominated by a different suite of organisms (Scheffer et al. 2001). For coral reefs, this may mean a shift from coral- to seaweed-dominance (macroalgae) that is often assumed to be mediated by grazing intensity, herbivore functional redundancy, feeding selectivity, or a combination of these factors (Roff and Mumby 2012). Such alternate states may be considered undesirable because they often compromise ecosystem functioning and provide fewer services, but this is not always true (e.g. McClanahan et al. 2008b, Hicks et al.

2009). Nevertheless, the exact ways in which herbivores interact to affect the ability of a reef to resist and reverse macroalgal phase shifts remain poorly understood.

Alternative phases or degraded states can be resilient to change, with their reversal and stability dependent on contrasting sets of feedbacks that reinforce and maintain them (Lebel et al. 2006, Mumby and Steneck 2008, Hughes et al. 2010). For example, macroalgae that become established may prevent successful coral recruitment and outcompete corals by shading and overgrowing juveniles, or chemically inhibiting coral growth (Kuffner et al. 2006, Rasher and Hay 2010). Conversely, destabilizing feedbacks can weaken the macroalgal state if conditions benefit the recruitment of herbivore species that feed on mature macroalgae (e.g. by increasing functional redundancy; Hoey and Bellwood 2011), or complementary feeding occurs (Burkepile and Hay 2008, Rasher et al. 2013). The interplay between the relative strengths of feedbacks that stabilize or destabilize alternate benthic states will determine how easily macroalgal phase shifts may be reversed. Only in relatively small-scale localized instances has the reversal of phase shifts proved possible (Bellwood et al. 2006, Carpenter and Edmunds 2006, Stockwell et al. 2009, Smith et al. 2010), thereby justifying a need to examine mechanisms and the efficacy of management solutions aimed at increasing the probability of reversal of macroalgal phase shifts at ecologically-relevant scales (Graham et al. 2013).

Evidence from the literature has been somewhat equivocal in determining whether the frequency of phase shifts is increasing over short time scales (10 years or less; Bruno et al. 2009). However, there is mounting evidence that resilience has increasingly been eroded to the point where many reefs are unable to recover after

disturbances that they have historically (i.e. on geologic time scales) been able to withstand (Pandolfi et al. 2003, Pandolfi and Jackson 2006). These discrepancies highlight the differences that exist between temporal and spatial scales in reef resilience and the difficulty in preventing or reversing phase shifts.

Diversity in the functional roles of herbivores, which depend on their feeding morphology and behavior, is critical for reef resilience because different groups are responsible for creating a community with complementary effects that can both resist and reverse macroalgal phase shifts on coral reefs (Mantyka and Bellwood 2007, Burkepile and Hay 2008, Hoey and Bellwood 2009). For example, parrotfishes (family Scaridae) are functionally classified as scrapers and use their teeth to scrape the surface of the substratum, removing algal turf and portions of calcium carbonate along with macroalgal propagules (Bonaldo and Bellwood 2009). These fishes are viewed as particularly important on coral reefs because of their ability to promote coral accretion (by freeing suitable recruitment space) and structural complexity, with cascading effects on associated organisms (Mumby et al. 2006, 2007, O'Leary et al. 2013). Grazer fishes, such as surgeonfishes (family Acanthuridae), use a suction-like method for removing algal turf and detritus. Scrapers and grazers may complement one another in preventing macroalgae from establishing, and thus preventing the development of phase shifts (Cheal et al. 2010). In contrast, browsing fishes (family Acanthuridae, Scaridae, Siganidae) primarily consume mature macroalgae and therefore play a critical role in the reversal of phase shifts (Hoey and Bellwood 2009). Sea urchins are different from fishes in that they may consume both algal turf and macroalgae and thus contribute to both the prevention and reversal of phase shifts (Ogden and Lobel 1978). However, sea urchins also

bioerode the substratum and prevent the settlement of coral larvae, potentially compromising reef sustainability (O’Leary and McClanahan 2010).

1.3 Managing reef futures

Fisheries closures, or no-take marine reserves, are a common spatial management tool often intended to increase biodiversity and produce a facsimile of historical conditions and ecosystem function (Knowlton and Jackson 2008). In recent years, fisheries closures have received considerable attention as a means to increase the resilience of coral reefs to climate change (Hughes et al. 2003, 2005, Cinner et al. 2013). In the context of macroalgal phase shifts, this may require the recovery of parrotfish biomass (Mumby et al. 2006) and the enhancement of key grazing processes such as complementary feeding through functional redundancy (i.e. more than one species performing a function; Burkepile and Hay 2008). A good example of how low functional redundancy can be detrimental to reef resilience, and where fisheries closures could possibly have prevented detrimental damage to reefs, is in the mass die-off of sea urchins (*Diadema* sp) in the Caribbean in the early 1980s (Hughes 1994). There, where fishing was allowed, sea urchins had replaced fishes as the dominant herbivore on reefs. After the disease-mediated mass mortality of sea urchins, macroalgae were released from top-down pressure, which led to unprecedented macroalgal blooms that persist today throughout many of the fished reefs in the Caribbean (Hughes et al. 2010). Using fisheries closures to increase herbivorous fish diversity and biomass on these reefs may help to build functional redundancy in herbivory and contribute toward a more stable future for Caribbean coral reefs.

A number of countries are attempting more inclusive and participatory approaches to fisheries management (i.e. co-management or community-based management) that allow resource users greater participation in developing and enforcing fisheries rules (Pomeroy et al. 2001, Granek and Brown 2005, Gelcich et al. 2010). This type of bottom-up management may in fact be more effective than top-down management of fisheries in some places and result in increased harvests and less conflict (Gelcich et al. 2010). In fact, co-management in the Solomon Islands has formed the basis for arrangements of protected areas, resulting in a doubling of parrotfish biomass (Aswani and Sebetian 2010). Community-based collaborative management arrangements used in conjunction with fisheries closures in Kenya showed improvements in resilience of coral reef fisheries to climate change (Cinner et al. 2013). Collaborative management is becoming increasingly common in nations with coral reefs and its success hinges on strong leadership within communities as well as social capital and incentives (Cinner et al. 2012). A critical question for the ecology and resilience of these reefs is whether or not community-managed closures respond to protection in ways similar to larger government-managed closures and wilderness areas (Graham and McClanahan 2013).

Co-managed or not, fisheries closures may be effective management tools in some areas, while other areas may need additional strategies to bolster reef resilience. Herbivorous fishes are particularly vulnerable to fishing in some locations (Graham et al. 2007), and the groups of species harvested depend on the type of fishing gear used (Cinner et al. 2009). For example, up to 50% of the catch targeted by fishers in Papua New Guinea using spear guns are species that either prevent or reverse macroalgal phase shifts through herbivory (Cinner et al. 2009). By understanding the

socioeconomic and ecological dynamics of local fisheries (Daw et al. 2011), as well as the functional roles of herbivores (Burkepile and Hay 2008), management of reefs may aim to limit the harvest of functionally important species while maintaining profitability (Cinner et al. 2009). This could include restrictions on the type of gear used or even modifications to existing gear types (e.g. escape gaps in fish traps; Mbaru and McClanahan 2013). Such management strategies may be necessary for increasing reef resilience especially in areas where herbivorous fish populations have already been decimated or fisheries closures are not socially acceptable (Cinner 2007).

1.4 Study need and aims

Impacts of human stressors on coral reefs and the ecological mechanisms that may mediate these impacts remain poorly understood and are among the greatest uncertainties for predictions of future change. It is often assumed that overfishing on coral reefs decreases resilience or the ability of a reef to prevent or reverse macroalgal phase shifts (e.g. Mumby et al. 2007, Hughes et al. 2010). Therefore, many management strategies are intended to reinstate or strengthen proper ecosystem functioning via increased grazing (Bellwood et al. 2004, Hughes et al. 2007). Such management strategies, however, assume overfished reefs are compromised and provide inferior services. This hinges on non-fisheries species (i.e. sea urchins) being unable to fill comparable niches when released from predation and competitive interactions with fishes. Thus, an important goal of coral reef ecology and conservation should be to provide a better understanding of how fishing and recovery processes interact to affect herbivores and bolster or erode reef

resilience, especially on reefs where multiple types of herbivores may co-occur (Bellwood et al. 2004, Hughes et al. 2007).

The literature is replete with studies examining the effects of herbivory on coral reefs, and as such, it has long been known that herbivores control benthic conditions and mediate reef resilience in these ecosystems. However, few researchers have examined how such effects vary along a gradient of herbivore abundance and composition produced by different fisheries management approaches. This thesis explores how different herbivore communities affect algal dynamics, and thus resilience, on coral reefs in Kenya. To do this, I utilize study sites under different management regimes to reflect a gradient in herbivore abundance and composition. I then use a variety of experiments and survey techniques across sites to examine the two key components of resilience, which are resistance to, and recovery from, macroalgal phase shifts (Hughes et al. 2010). This structures the 4 main chapters of this thesis, where Chapters 2 and 3 are focused on resistance, and Chapter 4 on the reversal of macroalgal phase shifts. Chapter 5 brings together these two concepts of resilience with a larger data set to examine correlations over decadal time scales. Specifically, I use Chapter 2 to examine the thresholds of herbivory needed to prevent algal biomass accumulation by quantifying consumption and production on reefs. In Chapter 3, I focus on how different herbivore assemblages affect algal succession and development of fleshy macroalgae from turf algae. For Chapter 4, I identify feeding preferences of macroalgal browsing fishes and the relationship between herbivore diversity and functional redundancy in the context of removing already established macroalgae, or reversing macroalgal phase shifts. I then apply these results to long-term survey data in Chapter 5 to build a 43-year

chronosequence and evaluate the direct and indirect effects of fisheries closures. Each of these 4 main chapters represents a novel contribution to the larger narrative of coral reef resilience. Finally I use the general discussion, or Chapter 6, to summarize all findings and place them in the context of other studies.

1.5 Study region and sites

There are important regional-scale differences in how fishing and herbivores may influence algal dynamics and key processes on coral reefs (Roff and Mumby 2012). For instance, biogeographic differences exist between and among coral reef communities in the Caribbean and Indo-Pacific regions in terms of species richness, faunal composition, trophic structure and grazing pressure, the life-histories and reproductive traits of key species, as well as habitat connectivity (Vermeij 1978, Birkeland 1988, Richmond and Hunter 1990). There are also geographic differences in local fishing practices and management techniques, as well as susceptibility to macroalgal phase shifts and climate-induced changes such as coral bleaching and ocean acidification (McClanahan et al. 2004, 2007b, Cinner and Aswani 2007, Hoegh-Guldberg et al. 2007, Bruno et al. 2009, Roff and Mumby 2012). These differences have made clear that the present ecological state and impacts of stressors on reefs in different regions originate from their individual characteristics and historical setting (Roff and Mumby 2012). Such differences should be considered, and appropriate caution taken, when attempting to extrapolate results from individual studies/areas.

In Kenya, reefs are severely affected by fishing. Here, fishing is intense, mainly conducted at an artisanal level, largely non-selective, and dictates the distribution

and abundance of herbivores more than bottom-up environmental conditions (McClanahan and Arthur 2001, McClanahan et al. 2007a). With the removal of fish, sea urchins have few predators and can reach densities of over 140 individuals per square meter (McClanahan and Shafir 1990, McClanahan 2000). In contrast, at fisheries closures, total fish biomass may reach over 1200 kg per hectare and sea urchin abundance may be less than one individual per square meter (McClanahan and Shafir 1990).

A fringing reef runs parallel to Kenya's coastline, which experiences predictable seasonality. The northeast monsoon season occurs from September to March and is characterized by drier weather and moderate rainfall, river discharge, and wind energy, while solar insolation and air temperatures are high (McClanahan 1988). The southeast monsoon season occurs from April to August and is characterized by thick cloud cover, heavy rains, strong winds, large waves and fast currents (McClanahan 1988).

Data in Chapters 2, 3, and 4 were primarily collected from six sites representing three fisheries management treatments along a ~150 km stretch of Kenyan coast: two heavily fished open access reefs, two younger and smaller community-managed fisheries closures, and two older and larger government closures (Fig. 1.1). Sites representing these treatments are interspersed. The community closures, Kuruwitu (-3.4799°, 39.9501°) and Mradi (-3.9417°, 39.7823°), are managed by local fishers and have received protection from fishing since 2005 and 2010, respectively. Both of these closures are approximately 0.3-0.4 km² in size. The government closures, Mombasa (-3.9912°, 39.7511°) and Malindi (-3.2634°, 40.1501°), have received

protection from fishing since 1991 and 1968, respectively; Mombasa is approximately 6 km² in size, whereas Malindi is 10 km². The Kenya Wildlife Service manages these government closures. The official start of active management of fisheries closures is difficult to estimate with accuracy in this study region. There are legal dates with a time period when fishing was prohibited, but this time can vary slightly among sites. Nonetheless, compliance to restrictions in both community- and government-managed fisheries closure sites in this study is high (pers obs). Fishing at Kanamai (-3.9061°, 39.7965°) and Ras Iwatine (-4.0212°, 39.7334°) is intense and highly unselective with a variety of gear types being used (e.g. spear guns, nets, traps), and beach seines are not used at Ras Iwatine. Sites include coral and algae-dominated areas in back-reef lagoons that are protected from strong waves and approximately 1.5 m deep at low tide.

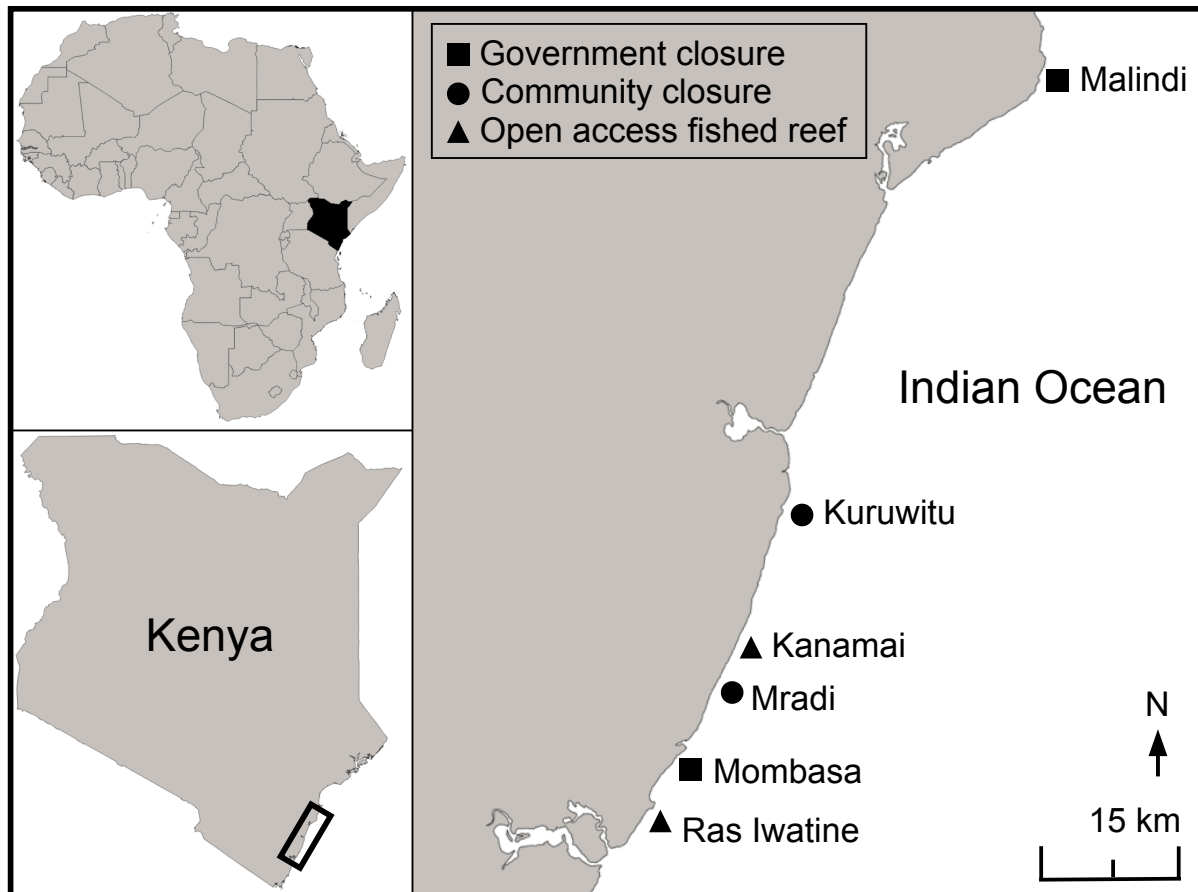


Fig. 1.1. Study sites located along the coast of east Africa in Kenya. Shapes indicate fisheries management type: government closures are managed by the Kenya Wildlife Service, community closures are managed by local fishers, and open access reefs are heavily fished year-round.

CHAPTER 2

QUANTIFYING ALGAL PRODUCTIVITY-CONSUMPTION RATES NEEDED TO PREVENT PHASE SHIFTS ON CORAL REEFS IN KENYA

2.1 Introduction

Many coral reef ecosystems are in rapid decline and experiencing shifts from coral- to macroalgal-dominance as a result of the interaction between anthropogenic and climate-induced stressors (Jackson et al. 2001, Bellwood et al. 2004, Baker et al. 2008, Hughes et al. 2010). Top-down consumption is argued to be more important for preventing the proliferation of fleshy macroalgae than bottom-up factors that may increase algal growth rates (Burkepile and Hay 2006, Heck and Valentine 2007). Thus, the ability of reefs to maintain coral-dominance hinges on the ability of grazers to remove algae, redistributing photosynthetically fixed energy across multiple trophic levels (McManus and Polsenberg 2004). Consequently, fisheries management and herbivore exploitation can have substantial impacts on ecosystem structure and function by transforming food web diversity and stability, and thus the flow of energy, either allowing algal biomass to accumulate at the primary production level or inhibiting accumulation (Littler and Littler 1984, McClanahan 1995, McManus et al. 2000, Mumby 2006). As such, the ability to identify critical grazing thresholds where algal consumption exceeds production is necessary to inform management decisions aimed at resisting undesirable shifts in benthic composition.

Parrotfishes (family Labridae, subfamily Scarinae) are viewed as particularly important grazers on coral reefs because of their ability to promote coral accretion

(by freeing suitable recruitment space) and structural complexity, with cascading effects on associated organisms (Mumby et al. 2006, 2007, O'Leary et al. 2013). In many coral reef fisheries, however, parrotfishes make up a large component of the catch (Munro 1983, McClanahan and Mangi 2001, Hawkins and Roberts 2003), which results in declining abundance and biomass as well as demographic changes, with reductions in mean body size (Russ 1991, Shin et al. 2005). These changes have consequences for the sustainability of parrotfish populations as well as ecosystem functioning through potentially non-linear effects (Lokrantz et al. 2008). For instance, reefs with a high biomass of parrotfishes may still be functionally impaired if dominated by small-sized individuals (< 15 cm) and the capacity to remove algae may be lower than expected considering their biomass (Mumby 2006, Lokrantz et al. 2008). Given these ecosystem-level consequences, the recovery dynamics of parrotfish are especially critical, leading to efforts to reduce or restrict their harvesting in some areas (e.g. Belize).

Foraging by herbivores can be challenging to quantify in a natural setting because of their mobility, feeding mode, and the difficulty of making direct observations of multiple species simultaneously. Previous studies have quantified consumption rates of one or a few species of fish and generally found that total food intake, or grazing impact, increases linearly with fish weight (Klumpp and Polunin 1989, Montgomery et al. 1989, Bruggemann et al. 1994a, 1994b, 1994c, van Rooij et al. 1998). Collating these results, van Rooij and colleagues (1998) derived an equation to estimate consumption by all herbivorous fishes on a reef, regardless of species or functional group. However, spatial and temporal variation exists among herbivorous fish species and functional groups in their grazing rates, which may be a function of

behavior as well as factors such as the influence of temperature on grazer metabolic requirements, algal nutritional quality, and algal productivity (Carpenter 1988, Targett and Targett 1990, Ferreira et al. 1998, Russ 2003, Bonaldo et al. 2006, Smith 2008, Afeworki et al. 2011, 2013). Consequently, there is a need to observe and quantify algal consumption rates by multiple species in a field setting to determine if previous estimates are widely applicable.

Evidence from the Caribbean suggests that even robust herbivorous fish populations may only be able to consume 30-40% of algal production (Williams et al. 2001, Mumby et al. 2007), whereas other studies suggest grazers and scrapers are able to remove up to, and greater than, 100% of the daily production of turf algae (Carpenter 1986, van Rooij et al. 1998, Paddock et al. 2006). Additionally, sea urchins are estimated to graze as much as 40% of the substratum and models assume fish and sea urchins can graze the same areas (Mumby 2006). Here, my objective is to test these grazing and energy hypotheses of grazers and scrapers using an algal growth experiment and underwater video cameras on coral reefs with different herbivore assemblages in Kenya. Specifically, I compare observed algal (turf) consumption rates against algal production rates and biomass accumulation on experimental substrata to determine what proportion of production fishes and sea urchins can consume. By using video cameras to observe grazing, I am able to compare whether published rates of algal intake (based on biomass; van Rooij et al. 1998) are widely applicable and appropriate for this study system. The fringing coral reefs of Kenya provide an ideal system to test these hypotheses because they represent a gradient in herbivore assemblages mediated by fisheries management regime.

2.2 Materials and methods

2.2.1 Study sites

See Chapter 1 for site descriptions and locations (Fig. 1.1).

2.2.2 Herbivore surveys

Sea urchins were identified to the species-level and counted in 10 m², haphazardly placed plots (n = 9-18 site⁻¹). Wet weight was estimated by multiplying average numbers of individuals by average wet weights per species using values from McClanahan and Shafir (1990). Herbivorous fishes were counted and identified to species and size (total length, TL) estimated to the nearest 5 cm by underwater visual census (via snorkel) using 2-4 haphazardly placed replicate belt transects (belt transect = 5 x 100 m) per site. Parrotfishes under 10 cm TL were grouped together as “juveniles” due to the difficulty of identifying them to species level in the field. Transects were conducted during neap tides when the water was between ~1 and 4 m deep, in the same areas as benthic transects to control for habitat effects, and during the calm, northeast monsoon season (Aug – Dec). Small and cryptic taxa such as blennies, tobies, and gobies were recorded but probably underestimated (Ackerman et al. 2004). Mass was determined by converting fish counts to biomass using published length-weight relationships (Letourneur et al. 1998, Froese and Pauly 2006; Appendix 2.1.1). Herbivorous fishes were assigned to functional groups (scrapers, grazers, browsers) based on published information on diets (Froese and Pauly 2006, Green et al. 2009). Grazers and detritivores were combined into one functional group (herein referred to as “grazers”) because they have been shown to have similar influences on algae (Marshall and Mumby 2012). There were no

excavating fishes (parrotfishes > 45 cm) at these reefs and therefore all parrotfishes were considered scrapers.

In this chapter, biomass units for fish are expressed as g m^{-2} and not kg ha^{-1} (as in subsequent chapters) to be consistent with similar studies on grazing rates of algae (e.g. Bruggemann et al. 1994a, van Rooij et al. 1998, Paddock et al. 2006). Also, sea urchin abundance (ind m^{-2}) is used in this chapter as opposed to biomass to facilitate consumption rate calculations and only scraper and grazer fishes are reported here because browser fishes do not readily forage on algal turf (Rasher et al. 2013), which is the focus of this particular study.

To evaluate differences in herbivore abundances among site and management type, I used separate one-way analyses of variance (ANOVA) on log-transformed sea urchin abundance and fish biomass data, followed by individual contrasts using Tukey tests. Data were log-transformed to improve spread and satisfy assumptions of normality. Model diagnostics were performed visually using frequency histograms, funnel and quantile-quantile (Q-Q) plots, and the final models met the assumptions of normality and homogeneity of residuals.

2.2.3 Algal production and biomass accumulation

Experimental substrata (algal growth plates) were made from ~2.5 cm cross-sections of dead massive *Porites* coral (mean plate size \pm SE was $184 \pm 11 \text{ cm}^2$; $n = 288$ plates; Appendix 2.1.2). Plates had flat surfaces but irregularly shaped edges. Holes were drilled in individual plates allowing them to be attached to plastic cage flooring. Plates were deployed in sets of 4 attached at least 5 cm apart to the same piece of

flooring to form a single replicate. Three experimental treatments were created to allow access to the plates by different groups of herbivores: (1) cage treatments, which represented a control (for site-specific, bottom-up differences in environmental variables), or herbivore exclusion preventing animals > 2.5 mm minimum dimension (defined as “large herbivores”), (2) fence treatments that allowed herbivory only by fishes, and (3) open treatments that allowed herbivory by both fishes and sea urchins (Appendix 2.1.3). Cages and fences were made from plastic mesh material (2.5 x 2.5 cm square holes) and attached to bare substratum using u-bolts. Cages were approximately 1 x 1 x 0.5 m (L x W x H) in size. Previous work has found that cages similar to these had no significant effect on algal standing crop or species composition other than the effect of excluding grazers (Scott and Russ 1987). At each reef site, treatments were deployed in four blocks, each including one replicate from each cage, fence, and open treatment (Fig. 2.1). Blocks were placed > 20 m apart from one another, and treatments within blocks were < 3 m apart. Areas for deployment were typical of the larger reef areas and away from damselfish territories.

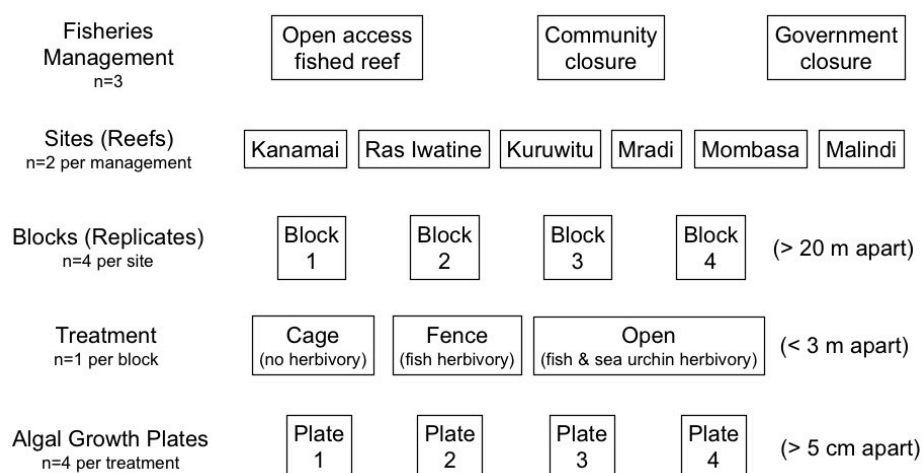


Fig. 2.1. Schematic of experimental design with replicate numbers.

The experiment began during the northeast monsoon season between September and October 2011. This is a time when bare substratum is most likely to occur because it is just after the seasonal peak in wave energy and most likely to resemble the natural seasonal process of succession (McClanahan 1988, 1997).

Algal production rate (expressed per unit area; $\text{g algae m}^{-2} \text{ day}^{-1}$) was estimated as (dry) algal biomass accumulation in the absence of large herbivores per unit time (Russ 2003); I scraped a 5 x 5 cm area on each plate at cage treatments 30 days after initial deployment. I also performed scrapings at regular time intervals (samples were taken a total of 6 times over the ~390 day duration of the experiment) to quantify algal biomass accumulation (g algae m^{-2}) on the plates through time. I sampled areas that seemed typical of the whole plate and it was not possible to determine the area of the plate that was previously scraped. All algal samples were immediately placed on ice and returned to the laboratory where wet weight was initially recorded. Samples were then dried at 60°C to a constant weight and ground in a Wiley mill and weighed (dry calcified weight). To remove calcium carbonate and determine dry algal weight (or weight of organic matter), I placed the samples in 10% acetic acid for 24 h (stirring regularly), vacuum-filtered them onto Whatman ashless filters, rinsed them with deionized water, and dried them at 60°C to a constant weight (herein referred to as “algae”). All weights were measured to the nearest 0.001 g. Samples were processed in this manner to have comparable units to similar studies (e.g. Bruggemann et al. 1994a, 1994b, van Rooij et al. 1998, Russ 2003, Paddock et al. 2006, Marshall and Mumby 2012), where units represent grams of dry organic material, or algae.

This experimental design involved sacrificial pseudoreplication (Hurlbert 1984), and average values of algal production rate and biomass accumulation for the four plates within a treatment replicate were subsequently used in all calculations and models. I used one-way ANOVAs to test for an effect of fisheries management on algal production rate. Site was included as a nested effect within fisheries management and treatment was not included in these models because only plates from the cage treatments were sampled to determine algal production rate. Using a two-way ANOVA, I tested for effects of fisheries management (with site as a nested factor) and treatment (with block as a nested factor) and their interaction, on the accumulation of algal biomass on the experimental substrata at the final sampling event (~day 390). I followed this with one-way ANOVAs at each site to determine if algal biomass accumulation was different by treatment at the final sampling event. Model diagnostics were performed as described for herbivore surveys to meet assumptions of normality and homogeneity of residuals, and site was treated as a nested variable within management.

2.2.4 Herbivore grazing intensity

To calculate algal turf consumption rate by fishes, I used stationary underwater video cameras (GoPro). Cameras were deployed at each site and positioned 1-2 m from a haphazardly selected open treatment. Filming commenced and continued without disturbance for ~4 h, and between 15 and 20 repetitions were conducted at each site using different replicates (15-20 reps x 4 h = 60-80 h footage site⁻¹). All video footage was viewed and the number of bites taken on the experimental plates by each fish species and the sizes (TL) of these fish were recorded and standardized to bites taken per hour (Appendix 2.1.4). Estimates of fish size were calibrated by placing an

object of known length in front of the treatment at the beginning of each video, and sizes were converted to biomass using length-weight regression equations (Appendix 2.1.1). Bite rate data were combined with published algal yield per bite (g algae bite⁻¹) regression equations (as a function of fish biomass) from Bruggemann et al. (1994a) for parrotfishes (Labridae), and Marshall and Mumby (2012) for surgeonfishes (Acanthuridae; Table 2.1a). I derived equations for algal yield per bite from Marshall and Mumby (2012) indirectly by considering fish length and the mean values of biomass removed in their “sparse” and “dense” algal turf experiments. Examples of this footage can be viewed at <http://vimeo.com/austinhumphries/grazer> (password: grazer) and <http://vimeo.com/austinhumphries/scraper> (password: scraper).

To calculate the grazing rate of sea urchins, I combined abundance data from visual surveys with published grazing rate values for each species (Table 2.1b). For sea urchin species where data were unavailable, I estimated grazing rate by scaling values to body size from taxonomically similar species. Since *Tripneustes gratilla* and *Toxopneustes pileolus* are known to feed primarily on seagrasses (Herring 1972, James 2000), I did not include them in grazing estimates of algal turf. I realize this method requires extrapolation of “general” grazing rates by sea urchins to grazing on the plates, and (unlike the fish) cannot allow for aggregation/attraction/avoidance effects. However, because of the diel feeding patterns of sea urchins (Nelson and Vance 1979) and their mobility, it was not possible to estimate time spent on plates from video observations. I feel this method accurately quantifies sea urchin grazing because species-specific values were derived from studies conducted on these exact reefs with rigorous methods

(stomach content analysis) and large sample sizes (McClanahan and Kurtis 1991, Carreiro-Silva and McClanahan 2001).

To determine if observed grazing rates from video observations differed among fisheries management, I used separate one-way ANOVAs for each functional group (i.e. scraper, grazer, sea urchin) followed by individual contrasts using Tukey tests. Model diagnostics were performed as described for herbivore surveys to meet assumptions of normality and homogeneity of residuals, and data were square-root transformed to down weigh abundant groups and satisfy model assumptions. I used linear regression (with 95% confidence intervals) to examine the relationship between functional group (fish) biomass of scrapers and grazers and observed algal consumption rates from video observations. For comparison and visual purposes, I also modeled the regression equation provided by van Rooij and colleagues (1998) using a dashed line.

Table 2.1. Equations used to estimate (a) herbivorous fish and (b) sea urchin algal consumption. Number of bites and fish wet weight (g; FWW) from video observations were used as the variables for fish consumption (g algae bite^{-1}) and sea urchin abundance (ind m^{-2}) was used as the variable for sea urchin consumption ($\text{g algae m}^{-2} \text{ind}^{-1} \text{day}^{-1}$). Asterisks indicate that the equation was derived indirectly (see text for explanation).

(a) Fish (g algae bite^{-1})		
Species	Consumption	Source
<i>Acanthurus</i> sp.	$0.217 * 10^{-6} * \text{FWW}$	Marshall and Mumby 2012*
<i>Ctenochaetus</i> sp.	$0.481 * 10^{-6} * \text{FWW}$	Marshall and Mumby 2012*
<i>Chlorurus/Scarus</i> sp.	$2.324 * 10^{-6} * \text{FWW}$	Bruggemann et al. 1994a
(b) Sea urchins ($\text{g algae m}^{-2} \text{ind}^{-1} \text{day}^{-1}$)		
Species	Consumption	Source
<i>Diadema savignyi</i>	$0.40 * \text{ind}$	Carreiro-Silva and McClanahan 2001
<i>Diadema setosum</i>	$1.11 * \text{ind}$	Carreiro-Silva and McClanahan 2001
<i>Echinothrix calamaris</i>	$2.19 * \text{ind}$	Carreiro-Silva and McClanahan 2001*
<i>Echinothrix diadema</i>	$2.19 * \text{ind}$	Carreiro-Silva and McClanahan 2001
<i>Echinometra mathaei</i>	$0.14 * \text{ind}$	McClanahan and Kurtis 1991
<i>Echinostrephus molaris</i>	$0.01 * \text{ind}$	McClanahan and Kurtis 1991*
<i>Stomopneustes variolaris</i>	$0.29 * \text{ind}$	Herring 1972, McClanahan and Kurtis 1991*

I estimated grazing strength on algal biomass accumulation using the natural log-response ratio (LRR; Osenberg et al. 1997) to allow comparisons and control for differences in algal biomass of the cage (control) treatments. LRRs are a commonly used effect metric because they are amenable to biological interpretation and are also proportionally symmetrical and have a sampling distribution that approximates normality (Hedges et al. 1999). These were calculated as

$$LRR = \ln\left(\frac{B_C}{B_O}\right)$$

where B_C is algal biomass at the cage treatment and B_O is algal biomass at the open treatment. Higher LRR values indicate a greater reduction of algal biomass by herbivores at the open treatments as compared to cage treatments with no herbivory. I formally tested these results using a one-way ANOVA on data from the final sampling period, followed by individual contrasts using Tukey tests.

2.2.5 Proportion of algal production consumed

The proportion of algal production consumed by herbivores was obtained by dividing the consumption rate estimate from the video recordings with the experimentally derived estimates of algal production (i.e. the expected percentage of algal production consumed using video observations only). A second measure of the proportion of algal production consumed was derived directly from the experimental substrata by calculating the percentages consumed by fishes (C_F) and sea urchins (C_{SU}) at each sampling event using the equations

$$C_F = \left(1 - \left[\frac{B_F}{B_C} \right] \right) * 100$$

and

$$C_{SU} = \left(\left[1 - \left\{ \frac{B_O}{B_C} \right\} \right] * 100 \right) - C_F$$

where B_C is algal biomass at the cage treatment, B_F is algal biomass at the fence treatment, and B_O is algal biomass at the open treatment (i.e. the observed percentage of algal production consumed). The total percentage consumed by both fishes and sea urchins was calculated by summing C_F and C_{SU} . All data analyses were performed using the program “R” (v. 2.15.1; R Development Core Team 2013).

2.3 Results

2.3.1 Herbivore surveys

The open access fished reefs, Kanamai and Ras Iwatine, had the lowest biomass of herbivorous fishes of any other site or management type ($p < 0.05$), and neither site had biomass values of more than 1.11 g m^{-2} (Table 2.2a). Between these two sites, there were only 6 species of herbivorous fishes present. Sea urchins were most abundant at Kanamai, with 14.57 ind m^{-2} , and Ras Iwatine had significantly fewer ($p < 0.05$), but these were made up of the large species *Echinothrix diadema* (Table 2.2b). The community closures, Kuruwitu and Mradi, had significantly more fish biomass than the open access reefs (16 and 19 g m^{-2} , respectively; $p < 0.01$), mostly comprising grazers. *Ctenochaetus striatus* and *Acanthurus nigrofuscus* were the

most abundant grazers, while only one species of scraper was present (*Chlorurus sordidus*) at the community closures. Sea urchins at Kuruwitu and Mradi had abundances of between 2 and 3.4 ind m⁻², which was not significantly different from Ras Iwatine or Mombasa ($p > 0.05$). Differences in fish biomass between these government closures and community closures were greatest for the scraper functional group. Malindi had 7 species of scraping parrotfishes present and the most abundant species were *Chlorurus sordidus* and *Scarus ghobban*. Sea urchin abundance at Mombasa was lower than at open access and community closure sites, and was 1 ind m⁻². On the other hand, Malindi had significantly fewer sea urchins than any other site ($p < 0.01$). Browser fishes were not reported here and in subsequent analyses because they do not significantly contribute to consumption of algal turf (Mantyka and Bellwood 2007, Rasher et al. 2013), which is to say, they do not function to prevent algal biomass accumulation, which is the focus of this study.

2.3.2 Algal production and biomass accumulation

Algal production rates were similar among all three management types ($p > 0.05$; Fig. 2.2). At the open access fished reefs, Kanamai and Ras Iwatine, mean algal production rates were 2.00 (± 0.64) and 2.44 (± 0.51) g algae m⁻² day⁻¹, respectively. The community closures, Kuruwitu and Mradi, had mean algal production rates of 2.35 (± 0.65) and 2.23 (± 0.47) g algae m⁻² day⁻¹, respectively; the government closure sites, Mombasa and Malindi, had 2.09 (± 0.44) and 1.64 (± 0.13) g algae m⁻² day⁻¹, respectively. The overall mean algal production rate for all six sites was 2.13 g algae m⁻² day⁻¹. From the initial 288 plates, some were not recovered: Kanamai = 2 open, 1 fence, 4 cage; Ras Iwatine = 4 open, 3 fence, 2 cage; Kuruwitu = 0 open, 0

fence, 4 cage; Mradi = 2 open, 0 fence, 0 cage; Mombasa = 4 open, 4 fence, 4 cage; Malindi = 0 open, 0 fence, 4 cage.

Table 2.2. Mean (a) herbivorous fish biomass (g m^{-2} ; \pm SE) and (b) sea urchin abundance (individuals m^{-2} ; \pm SE) at each study site by fisheries management type. Grazers and detritivores were grouped together because their influence on algae may be similar (Marshall and Mumby 2012).

a) Fish Family	Species	Open access			Community closure			Government closure	
		Functional group	Kanamai	Ras Iwatine	Kuruwitu	Mradi	Mombasa	Malindi	
Acanthuridae	<i>Ctenochaetus striatus</i>	Grazer	0 (0)	0.37 (0.01)	8.91 (0.85)	10.52 (0.26)	3.98 (0.45)	12.32 (0.98)	
	<i>Acanthurus nigrofuscus</i>	Grazer	0 (0)	0.09 (0.09)	0 (0)	6.77 (0.41)	3.88 (3.88)	5.61 (2.28)	
	<i>Zebrasoma scopas</i>	Grazer	0 (0)	0 (0)	0 (0)	0.15 (0.15)	5.64 (2.11)	2.69 (1.74)	
	<i>Acanthurus triostegus</i>	Grazer	0.09 (0.09)	0 (0)	5.73 (0.21)	0 (0)	0 (0)	0 (0)	
	<i>Zebrasoma veliferum</i>	Grazer	0 (0)	0 (0)	0 (0)	0 (0)	0.55 (0.55)	0 (0)	
	<i>Acanthurus leucosternon</i>	Grazer	0 (0)	0 (0)	0 (0)	0.71 (0.71)	0.91 (0.2)	5.53 (1.59)	
	<i>Ctenochaetus strigosus</i>	Grazer	0 (0)	0 (0)	0 (0)	0.2 (0.2)	0 (0)	0 (0)	
	<i>Acanthurus nigricauda</i>	Grazer	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.73 (0.26)	
	<i>Acanthurus dussumieri</i>	Grazer	0 (0)	0 (0)	0 (0)	0 (0)	0.55 (0.55)	0.97 (0.02)	
		<i>Chlorurus sordidus</i>	Scraper	0 (0)	0 (0)	1.35 (1.35)	0.21 (0.21)	9.51 (2.55)	2.97 (0.26)
Labridae	<i>Scarus ghobban</i>	Scraper	0 (0)	0.35 (0.21)	0 (0)	0 (0)	0 (0)	2.92 (1.12)	
	<i>Scarus frenatus</i>	Scraper	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0.9 (0.9)	
	<i>Scarus psittacus</i>	Scraper	0 (0)	0.28 (0.28)	0 (0)	0 (0)	0 (0)	1.26 (0.36)	
	<i>Scarus niger</i>	Scraper	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1.66 (0.76)	
	<i>Scarus rubroviolaceus</i>	Scraper	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2.21 (1.4)	
	<i>Hipposcarus harid</i>	Scraper	0 (0)	0 (0)	0 (0)	0 (0)	1.51 (1.51)	0 (0)	
	Juvenile sp (< 10cm)	Scraper	0.37 (0.33)	0.02 (0.01)	0.14 (0.1)	0.16 (0.05)	0.2 (0.09)	0.08 (0.05)	
Pomacanthidae	<i>Centropyge multispinis</i>	Grazer	0 (0)	0 (0)	0 (0)	0.49 (0.14)	0.63 (0.32)	0.74 (0.19)	
Total			0.46 (0.42)	1.11 (0.58)	16.13 (2.47)	19.19 (0.2)	27.36 (4.47)	40.57 (2.36)	
b) Sea urchins									
Family	Species	Open access			Community closure			Government closure	
		Functional group	Kanamai	Ras Iwatine	Kuruwitu	Mradi	Mombasa	Malindi	
Diadematidae	<i>Diadema savignyi</i>	Grazer/Scraper	0.45 (0.27)	0.67 (0.03)	0.43 (0.03)	0.52 (0.04)	0.02 (0.01)	0.02 (0.01)	
	<i>Diadema setosum</i>	Grazer/Scraper	0.36 (0.25)	0.29 (0.21)	0.54 (0.11)	0.12 (0.03)	0 (0)	0.01 (0.01)	
	<i>Echinothrix calamaris</i>	Grazer/Scraper	0 (0)	0 (0)	0 (0)	0.04 (0.01)	0.01 (0)	0 (0)	
	<i>Echinothrix diadema</i>	Grazer/Scraper	0.03 (0.01)	0.85 (0.26)	0.01 (0.01)	0.31 (0.06)	0.28 (0.01)	0.01 (0.01)	
Echinometridae	<i>Echinometra mathaei</i>	Grazer/Scraper	13.73 (3.38)	0.21 (0.01)	2.33 (1.44)	1.07 (0.27)	0.45 (0.13)	0.01 (0.01)	
	<i>Echinostrephus molaris</i>	Grazer/Scraper	0 (0)	0.12 (0)	0 (0)	0.01 (0.01)	0.24 (0.07)	0.07 (0.04)	
Stomopneustidae	<i>Stomopneustes variolaris</i>	Grazer/Scraper	0 (0)	0.01 (0)	0 (0)	0 (0)	0 (0)	0 (0)	
Total			14.57 (3.01)	2.15 (0.45)	3.32 (1.39)	2.07 (0.18)	1.01 (0.32)	0.11 (0.02)	

ANOVA results testing algal biomass accumulation on the experimental substrata at the final sampling event revealed a significant interaction term ($p < 0.001$), indicating there were significant changes in algal biomass among treatments depending on the management regime (Appendix 2.1.5). Algal biomass immediately increased at the cage treatments (no herbivory) at all six sites, then leveled off after 100 days at around $\sim 150 \text{ g algae m}^{-2}$ for the remainder of the experiment (Fig. 2.3). An exception was Ras Iwatine where algal biomass rose more slowly at first, but continued to increase until the end of the experiment. The open access reefs, Kanamai and Ras Iwatine, showed significant decreases in algal biomass at the open treatments with fish and sea urchin herbivory ($p < 0.01$), but not the fence treatments where only fishes could access the plates ($p > 0.76$). At the community closures, Kuruwitu and Mradi, the fence and open treatments were not significantly different from the cage treatments ($p > 0.25$), and all were greater than $80 \text{ g algae m}^{-2}$ at the conclusion of the experiment. The open and fence treatments at the government closure sites, Mombasa and Malindi, both had significantly lower values than the cage treatments ($p < 0.01$), and never reached above $35 \text{ g algae m}^{-2}$ throughout the experimental period. Also, the fence and open treatments were not significantly different from one another, indicating that fishes were responsible for the majority of algal biomass reduction.

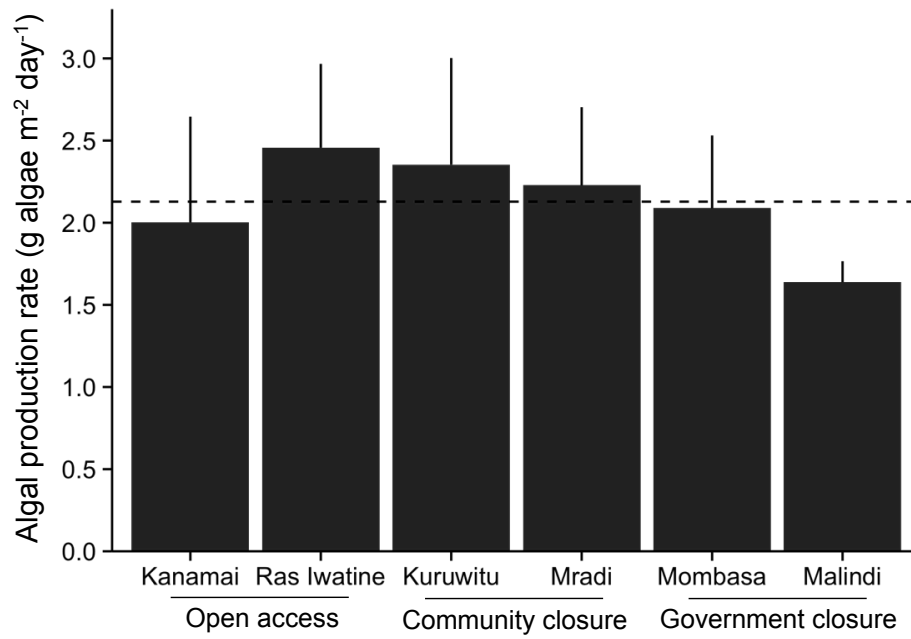


Fig. 2.2. Mean (+ SE) algal production rate (g algae m⁻² day⁻¹) on experimental substrata at each study site. Dashed horizontal line indicates overall mean of all sites.

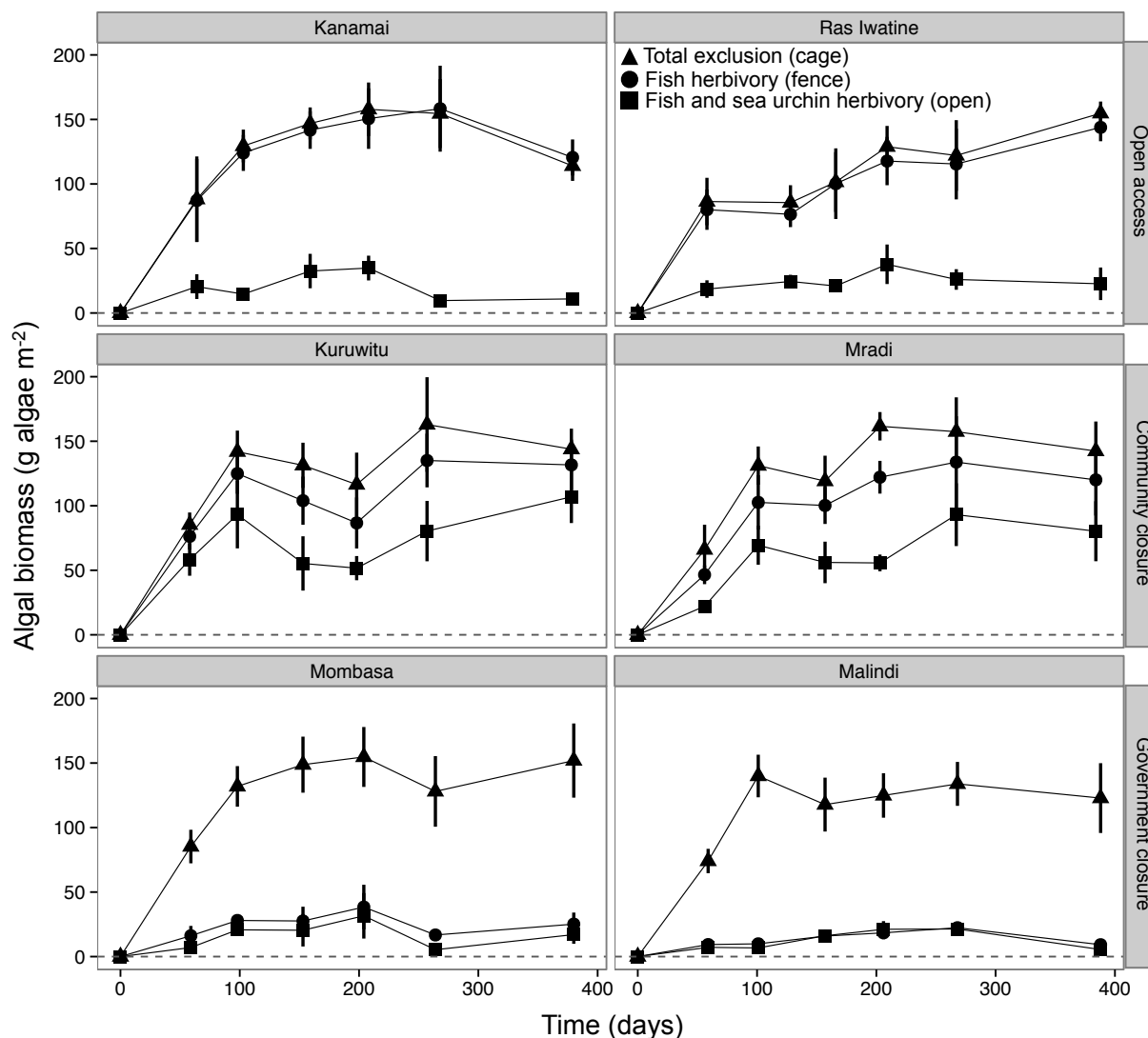


Fig. 2.3. Time series of the mean (\pm SE) algal biomass accumulation (g algae m^{-2}) at the six study sites by fisheries management type. Shapes indicate treatment.

2.3.3 Herbivore grazing intensity

Video observations revealed total consumption rates (all herbivores) were greatest at open access and government closures sites, but did not differ significantly among management types ($p = 0.23$; Fig. 2.4a). Consumption rates differed significantly for sea urchins ($p < 0.01$) and were greatest at the open access reefs, Kanamai and Ras Iwatine, with values of $2.58 (\pm 0.11)$ and $2.49 (\pm 0.79) \text{ g algae m}^{-2} \text{ day}^{-1}$, respectively (Fig. 2.4b). These rates were significantly greater ($p < 0.05$) than both

government closure sites, Mombasa and Malindi, where consumption rates were $0.78 (\pm 0.06)$ and $0.03 (\pm 0.02)$ g algae $m^{-2} day^{-1}$, respectively. The community closures, Kuruwitu and Mradi, had intermediate sea urchin consumption rates of $1.13 (\pm 0.11)$ and $1.27 (\pm 0.15)$ g algae $m^{-2} day^{-1}$, respectively. Scraper consumption rates varied significantly by site ($p < 0.01$), and were highest in the government closures, where rates were greater than 1.43 g algae $m^{-2} day^{-1}$. Grazer consumption rates also varied significantly by site ($p = 0.01$), and were greatest in the government closure sites. Grazers had greater consumption rates than scrapers in the community closure sites, but the opposite was true in the government closures. For both scrapers and grazers, consumption rates at community closures were greater (> 0.15 g algae $m^{-2} day^{-1}$) than for the open access reefs, though the difference was not significant (grazer: $p = 0.788$; scraper: $p = 0.899$).

On open access reefs, the majority of grazing was due to small grazers (< 15 cm), and juvenile scrapers < 10 cm (Fig. 2.5). There were only 3 size classes represented for grazers and scrapers at these sites, with no grazing by fishes greater than 20 cm. A similar trend was apparent in the community closures, however, scrapers and especially grazers greater than 15 cm also contributed to the overall consumption; four size classes of grazers and scrapers were observed feeding on the experimental plates at the community closures. Most of the grazing at these sites was by *Ctenochaetus striatus* and juvenile parrotfishes (Appendix 2.1.6). At the government closure sites, consumption by grazers was more evenly distributed (5 size classes represented) with the greatest contribution coming from fishes 18 cm in length, followed closely by the 13 and 23 cm size classes. At these sites, there was a total of 7 size classes that contributed to herbivory by scrapers, with a relatively even

distribution of importance, but the greatest contribution coming from individuals of 20-25 cm. A majority of the grazing done by scrapers at the government closures was due to *Chlorurus sordidus*, followed by *Scarus ghobban* and *S. rubroviolaceus*, and for grazers *Ctenochaetus striatus* and *Acanthurus leucosternon* had the greatest grazing impact.

Plotting the relationship between grazer and scraper biomass (g m^{-2} ; x) and algal consumption rate ($\text{g algae m}^{-2} \text{ day}^{-1}$; y) from video observations and calculations yielded strong positive relationships with high predictive power (grazer: $y = 0.0249x$, $R^2 = 0.81$, $n = 20$, $df = 19$, $F\text{-value} = 68.71$, $p < 0.001$; scraper: $y = 0.1197x$, $R^2 = 0.89$, $n = 15$, $df = 14$, $F\text{-value} = 108.3$, $p < 0.001$; Fig. 2.6).

LRRs indicated grazing strength on algal biomass was significantly greater at open access and government closure sites than community closures ($p < 0.001$; Fig. 2.7). Grazing at the open access sites came primarily from sea urchins, whereas grazing and scraping herbivorous fishes were responsible at the government closure sites (Fig. 2.4b and Appendix 2.1.7).

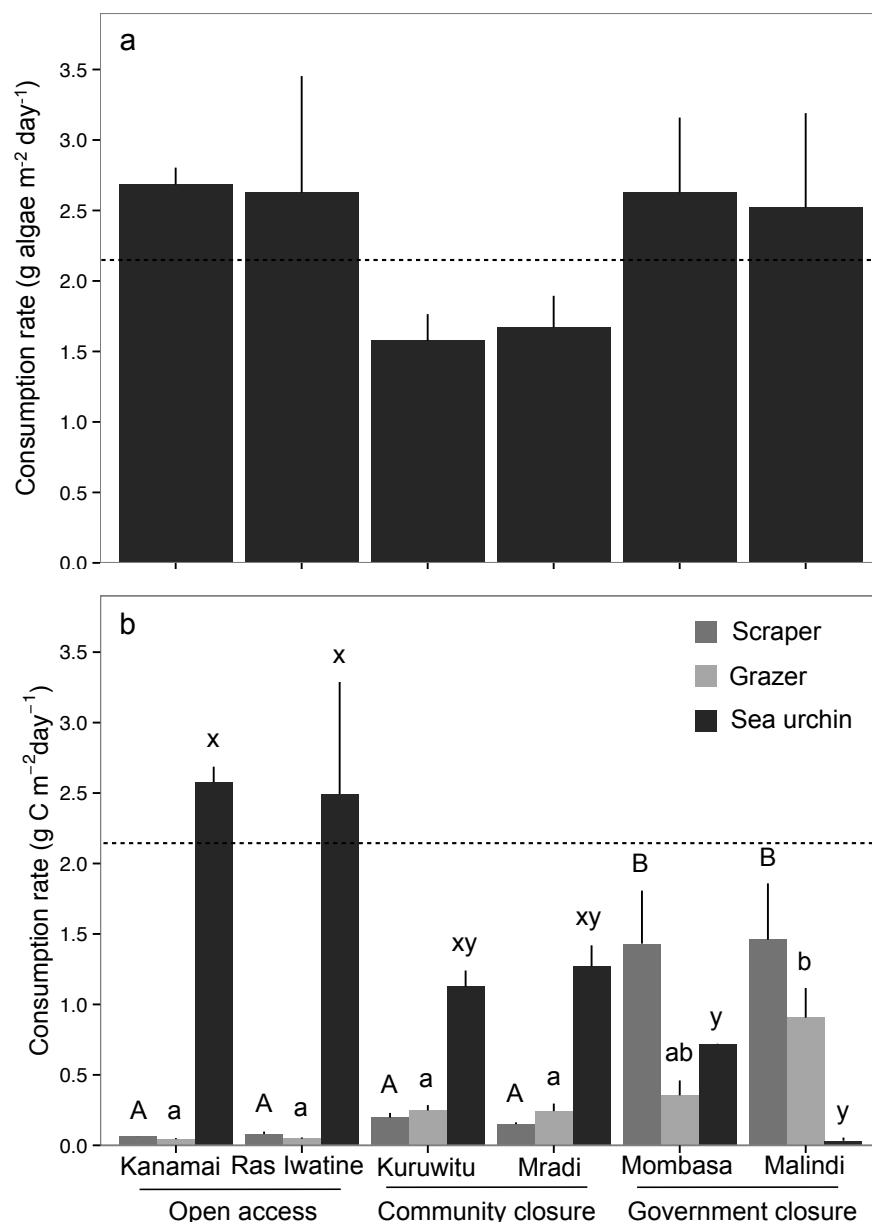


Fig. 2.4. Mean (+ SE) algal consumption rate ($\text{g algae m}^{-2} \text{ day}^{-1}$) of (a) all herbivores and (b) functional groups. Fish consumption calculated from bite counts of video observations combined with equations by Bruggemann et al. (1994a; scrapers) and Marshall and Mumby (2012; grazers) for algal consumption (g algae bite^{-1}). Sea urchin consumption calculated from abundance data combined with species-level consumption rates per individual by Carreiro-Silva and McClanahan (2001) and McClanahan and Kurtis (1991). Letters indicate homogeneous subgroups ($p < 0.05$) in (b), and the dashed line is for visual purposes and indicates the mean algal production rate, which is $2.13 \text{ g algae m}^{-2} \text{ day}^{-1}$.

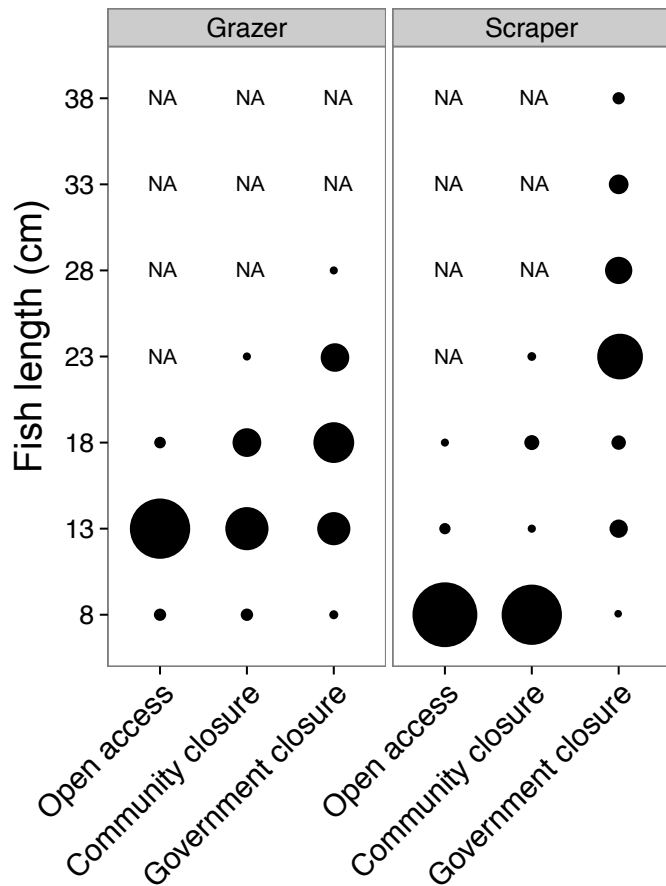


Fig. 2.5. Importance of fish length (cm) for algal consumption ($\text{g algae m}^{-2} \text{ day}^{-1}$) of grazers and scrapers at reefs with different fisheries management types ($n = 2$ sites mgmt^{-1}). Circle size indicates relative importance for a particular size class; larger circles represent more influential size classes than smaller circles, and “NA” represents not applicable, or no influence.

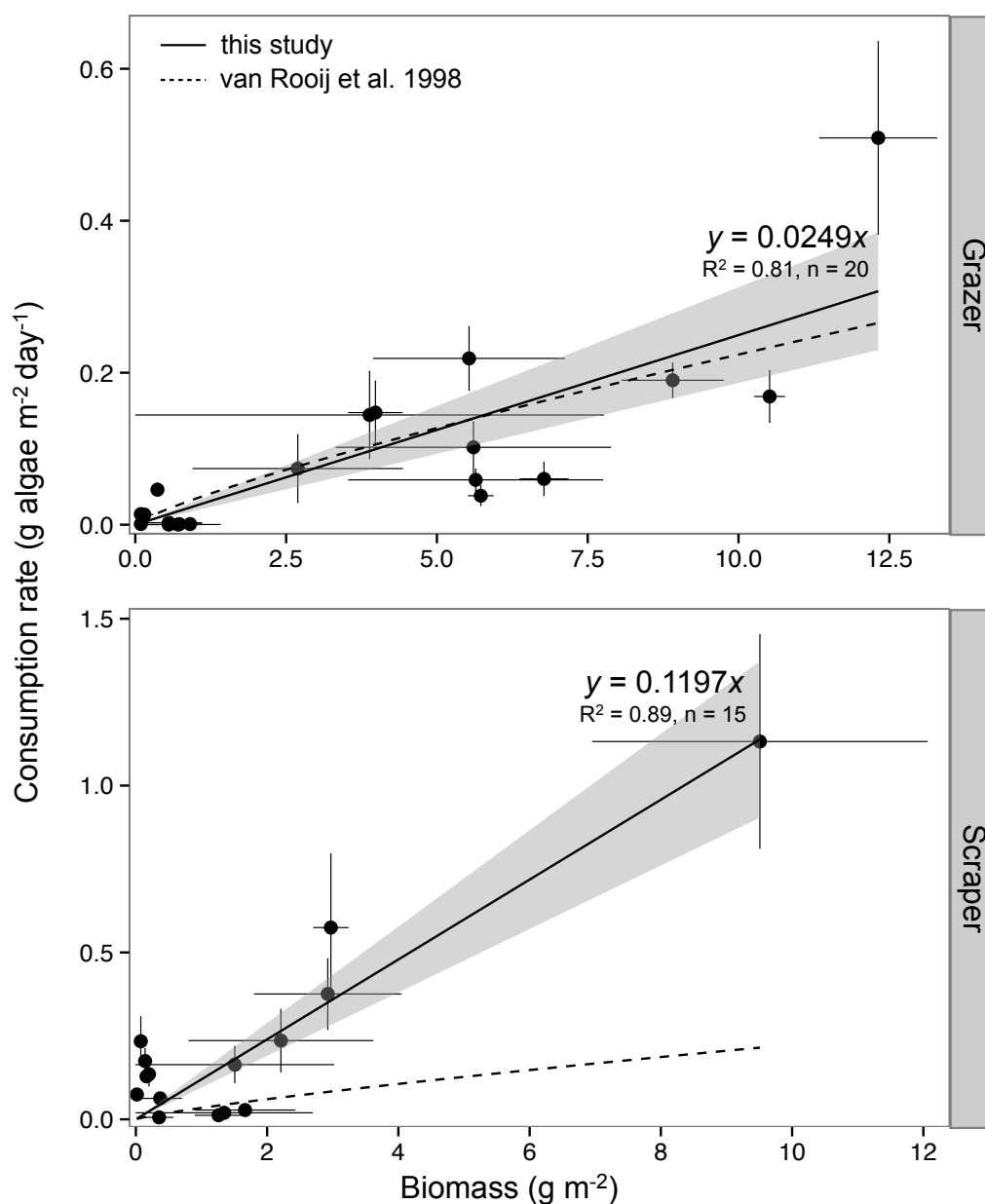


Fig. 2.6. Relationship between mean (\pm SE) fish biomass (g m^{-2}) and algal consumption rate ($\text{g algae m}^{-2} \text{ day}^{-1}$) for grazing and scraping herbivorous fishes (solid line). Shaded bands represent 95% confidence intervals for the linear model. For comparison, the regression equation provided by van Rooij and colleagues (1998) is also shown (dashed line). Data points represent species-level site data on algal consumption from video observations ($n = 60\text{-}80 \text{ h footage site}^{-1}$).

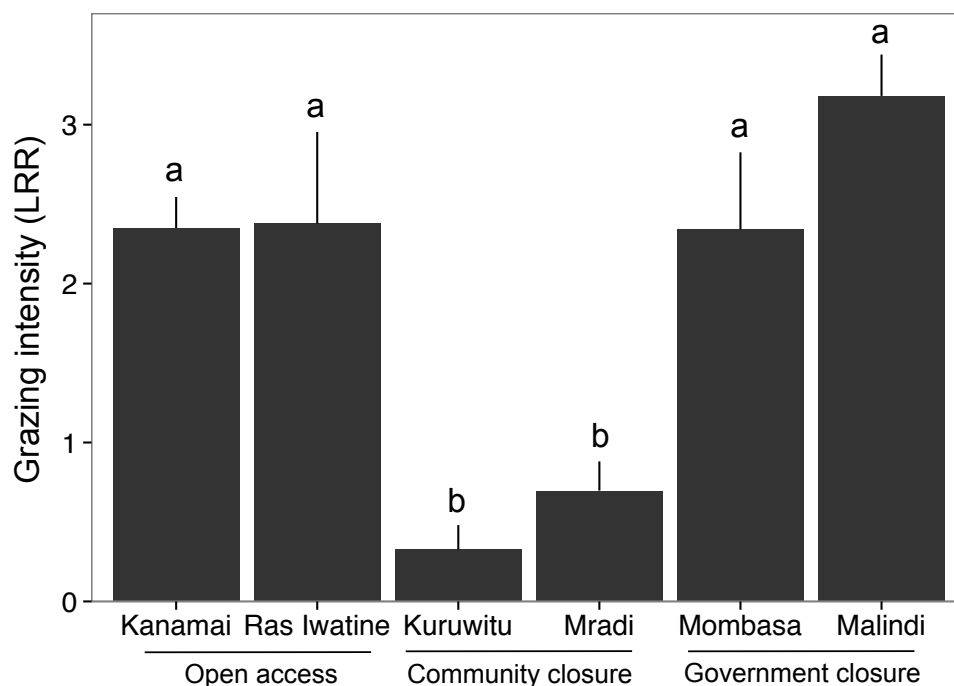


Fig. 2.7. Mean (+ SE) natural log-response ratio (LRR) of grazing strength, or algal biomass removed (g algae m^{-2}), in open treatments as compared to cage treatments at the final sampling period for each study site. Higher LRR values indicate greater grazing strength, or that more algal biomass was removed by herbivores (fishes and sea urchins), than lower LRR values. Letters indicate homogeneous subgroups ($p < 0.05$).

2.3.4 Proportion of algal production consumed

Estimates of the proportion of algal production consumed produced slightly different values between methods of calculation (Table 2.3). Calculations of fish consumption rates from the video footage combined with sea urchin abundance (“video”) were all greater than estimates derived from the experimental plates (“plates”). Furthermore, video estimates of consumption exceeded 100% of calculated algal production rates at the open access and government closure sites, indicating a surplus of grazing; estimates from the experimental plates were approximately 60-70% less than those from the video observations at all sites and no site displayed over 90% of algal production consumed (Appendix 2.1.7). This is partly because it is impossible to have greater than 100% grazing experimentally on the plates. Regardless of method,

the lowest proportion of algal production consumed was always at the community closure sites, Kuruwitu and Mradi. With values of 80.27 and 106.92 g algae m⁻², algal biomass at the final sampling event was between 4 and 20 times greater at the community closure sites than the open access and government closure sites, where it was always below 23 g algae m⁻², and only 5.46 g algae m⁻² at Malindi.

Table 2.3. Mean algal biomass accumulation (g algae m⁻²) and proportion of algal production consumed (%) from video observations (“video”) and the experimental plates (“plates”). Estimates for algal biomass accumulation were obtained experimentally from plates at the final sampling event at the open treatments. Values for “video” were estimated by the ratio of algal production rate (obtained experimentally; g algae m⁻² day⁻¹) and algal consumption rates calculated from video observations. Values for “plates” were estimated from the proportion of algal production consumed on the experimental plates at the final sampling event.

Management	Site	Biomass accumulation (g algae m ⁻²)	Plates (% consumed)	Video (% consumed)
Open access	Kanamai	10.92	81	134
	Ras Iwatine	22.63	76	107
Community closure	Kuruwitu	106.92	40	67
	Mradi	80.27	49	75
Government closure	Mombasa	17.05	85	126
	Malindi	5.46	88	154

2.4 Discussion

The algal standing crop that was maintained under each fisheries management regime in this study suggests that herbivores must consume at least 50% of algal production to prevent significant biomass accumulation. Herbivores were able to consume as much as 88% of algal production where herbivory was greatest. I found the impact of larger (> 20 cm), non-juvenile scrapers (i.e. parrotfishes) to be particularly important in preventing algal biomass accumulation at reefs where fishing was prohibited, and these reefs were largely devoid of sea urchins. For these

fishes, the rate of algal removal per unit biomass was higher than expected and previously reported in other regions (Bruggemann et al. 1994, van Rooij et al. 1998, Paddack et al. 2006). In contrast, grazer fishes had consumption rates and grazing impacts (per unit biomass) similar to those reported from other regions and studies (van Rooij et al. 1998). Also, herbivory in this study system may come from sea urchins or fishes, but I found little evidence supporting the idea that these groups can co-occur and graze the same area effectively and prevent algal biomass accumulation. These findings provide useful insights into the differential grazing pressures of herbivores and allow a greater understanding of their impacts on preventing algal accumulation and the preemption of phase shifts.

Herbivorous fishes are assumed to be inferior competitors with sea urchins, simply filling an available niche when intense fishing pressure reduces the abundance of their competitors (Hay 1984). In other words, fishing mediates competitive interactions between sea urchins and herbivorous fishes on coral reefs and may prevent them from co-occurring on reefs (McClanahan and Shafir 1990). This was true except at reefs where fishing had only recently been eliminated (< 10 years). Here, sea urchins and fishes did co-occur at intermediate levels but were ineffective at preventing algal biomass accumulation. Herbivory was less than 50% of algal production, which suggests this mixed community does not have complementary feeding preferences or that there are simply not enough individuals of either herbivore group to significantly alter algal accumulation. However, the fact that these community closures have low existing macroalgal cover and high coral cover suggests that, although grazing pressure is low, it is currently sufficient to limit the spread and proliferation of macroalgae at the scale of the entire reef. In contrast,

where fishing had been prohibited for more than 10 years, few sea urchins were present and scraping parrotfishes alone were able to graze as much as 70% of the daily algal production. Where fishing occurred, sea urchins were also very effective at preventing algal biomass accumulation, grazing more than 75% of daily algal production. Both of these observations were greater than estimates based on models from other regions (i.e. Caribbean; Williams et al. 2001, Mumby 2006).

It has been suggested that there is a threshold of the total reef area that herbivores can maintain in a turf state, and that if this threshold is not reached, algae will dominate with potentially negative reef-scale consequences (Williams et al. 2001, Mumby 2006). While I measured algal biomass accumulation on experimental substrata and not at the scale of the entire reef, my results do suggest that this threshold exists somewhere around 50% of daily algal production at these particular reefs in Kenya. If herbivores remove a lower proportion of algal production, algae are not effectively distributed through the food web and may proliferate on the benthos. This threshold of herbivory, however, is not expected to be static and may differ by region or vary with time. For example, any factor that increases algal growth or colonization rates, such as a rise in nutrient levels and/or the amount of substratum available for algal colonization (e.g. death of live corals due to temperature-induced bleaching) may shift thresholds. At some point, the ability of herbivorous fishes and sea urchins to prevent algal accumulation will be overwhelmed (Edwards et al. 2011). Furthermore, spatial differences in the intensity of grazing will dictate whether herbivores can reach this threshold. For instance, herbivore communities may aggregate in areas and increase their foraging rates in response to increases in algal production and water temperature (Horn and Gibson 1990, Ferreira et al. 1998, Russ

2003), creating ungrazed patches. Understanding these fluctuations and responses is critical for reef management in the face of climate change, but parsing out the various mechanisms has proven difficult. Nonetheless, over the 390-day period of this experiment, results were relatively steady after the initial ~100 days, and no major disturbances significantly influenced grazing thresholds or the intensity of grazing.

Exploitation of fishes has the ability to reduce grazing intensity and ecosystem functioning on reefs drastically if other species cannot replace them (Bellwood et al. 2004). Here, sea urchins were able to replace fishes effectively and remove algae at fished reefs. This transition, however, was not linear and grazing intensity decreased below algal production at reefs in small ($< 1 \text{ km}^2$), young (< 10 years) fisheries closures. Consequently, the recovery dynamics of fishes that are associated with the interaction of the age and size of fisheries closures may be especially important in achieving a grazing rate sufficient to prevent algal accumulation (Claudet et al. 2008). Results here and in other studies indicate this is especially critical for scraping parrotfishes greater than 20 cm in length, which may require more than 10 years to recover after protection and have a disproportionate grazing impact on reefs (McClanahan et al. 2007a, Lokrantz et al. 2008).

Algal production rates in the absence of large herbivores in this study provide the first estimates for reefs in Kenya and are comparable but slightly higher than values from studies in other regions (Wanders 1976, Carpenter 1986, van Rooij et al. 1998, Klumpp and McKinnon 1989, Russ 2003, Paddock et al. 2006). This is surprising because reefs in the Caribbean have been shown to have higher algal growth rates

than those in the Indo-Pacific (Roff and Mumby 2012). My results may be partly explained by the shallower depths in this study (< 1.5 m at low tide) where light intensity and temperature are the greatest, both of which can increase algal productivity (Hatcher and Larkum 1983, Klumpp and McKinnon 1989). Variability in these factors, as well as the biogeography of species of algae (i.e. different species have different growth rates) and other factors that moderate algal productivity such as water motion, nutrient availability, and sedimentation, may also contribute to the observed differences. My data, however, suggest nutrient enrichment does not have a significant effect in this area because the algal production rates measured were only slightly greater than those from other studies (e.g. Bruggemann et al. 1994a, van Rooij et al. 1998, Paddack et al. 2006). Furthermore, nutrient enrichment has been shown to be low on the reefs in this particular study area (McClanahan 1997)

This study provides detailed information on simultaneous intake rates of algal turf by multiple fish species. Previous studies have typically quantified the intake rate of one or a few species of fishes and extrapolated this to produce guild-wide estimates (e.g. van Rooij et al. 1998, Paddack et al. 2006). My estimates of fish consumption rates per unit biomass, which were derived from video observations and published algal yield per bite data, were greater than expected in comparison to other studies, especially for scrapers (Bruggemann et al. 1994a, van Rooij et al. 1998, Paddack et al. 2006); scraper consumption rates were as much as 5 times greater in this study than would be expected based on the equation of van Rooij and colleagues (1998), which may not be surprising given that van Rooij and colleagues use only a limited number of fish species. In contrast, the intake rates I observed for grazers are in line with other estimates (e.g. Chartok 1983, Montgomery et al. 1989). It is unclear why I

observed such high intake rates for scrapers, but I feel these estimates are potentially more representative because of the species-specific resolution in the data and the non-intrusive sampling technique (small video cameras), which minimized observer effects on fish behavior. However, I do acknowledge differences in methods of calculation among studies and the limitations of these comparisons. For instance, daily consumption, as measured by algal intake per bite in this study, is dependent on algal standing crop (Bruggemann et al. 1994), which I did not take into account. An other potential source of error may include methodological differences in determining algal (ash-free) dry weight (e.g. combustion versus decalcification). While the estimated intake rates are likely valid for the present methods and reefs in Kenya, these discrepancies should be noted and considered when extrapolating results.

If I estimated fish consumption at our study sites using the equation and energy assumptions provided by van Rooij and colleagues (i.e. Fig 1; 1998), none of the fish communities would be expected to prevent algal biomass accumulation. This obviously was not the case, as results from the government closure sites indicated that fish there were capable of consuming the majority (> 80%) of algal production. A potential source of variation between studies is the use of experimental substrata to quantify algal consumption. Fish may have been attracted to this introduced material that was initially clean of any algae. Different magnitudes and directions of experimental artifacts such as this may influence the interpretation and comparison of field experiments (Peterson and Black 1994), however, the experimental substrata used for this experiment was a natural substance and not foreign (e.g. limestone tiles; Russ 2003, Paddock et al. 2006). Another potential caveat to consider with this

study is the overestimation of grazing strength (algal consumption versus production) from video observations as compared to the experimental algal growth plates. This suggests that while the use of underwater video cameras may provide valuable insights into species-specific grazing patterns, it may also inflate actual grazing impacts by assuming intake rates can be greater than production rates. The challenge estimating these processes and comparing them should not be underestimated.

The correlation between the occurrence of species and species biomass in visual surveys and grazing intensity was high in this study. For example, most of the grazing came from juvenile parrotfishes and *Ctenochaetus striatus* at the community closure sites, which would be expected as these fishes had the greatest biomass. At Mombasa, *Chlorurus sordidus* dominated the biomass for scraping parrotfishes and also had the greatest consumption rate, whereas at Malindi, scraper and grazer biomass and consumption was distributed more equally among species. I was unable to determine this relationship for sea urchins because of their feeding mode and diel foraging patterns (Nelson and Vance 1979). These results suggest that visual survey techniques were relatively good at predicting grazing intensity on these reefs and there was no significant source of variation, such as diel migrations from pelagic habitats (Robblee and Zieman 1984, Mora and Sale 2002).

Reductions in herbivory, through removal of sea urchin grazing in the treatments, resulted in a rapid accumulation of algal biomass over the first 100 days of this experiment. After this time, standing crop was relatively constant, suggesting that algae in these treatments were not able to increase standing stocks further. This

may have been a result of algae reaching maturity or self-shading, where an increase in algal biomass may actually limit production and prevent further biomass accumulation (Hatcher and Larkum 1983). This seems to represent an upper limit to the biomass that can be attained by algal turfs and macroalgal species in this system, which is 7-25 times greater than where grazing pressure is high. This is consistent with other studies that displayed a significant effect of grazing on algal community biomass, with biomass quickly reaching a plateau in the absence of herbivores (e.g. Sammarco et al. 1974, Adey et al. 1977, Connor and Adey 1977, Carpenter 1986). Similar patterns have also been demonstrated at a regional scale in the Caribbean since the mass mortality of *Diadema antillarum* (Carpenter 1988, Schutte et al. 2010).

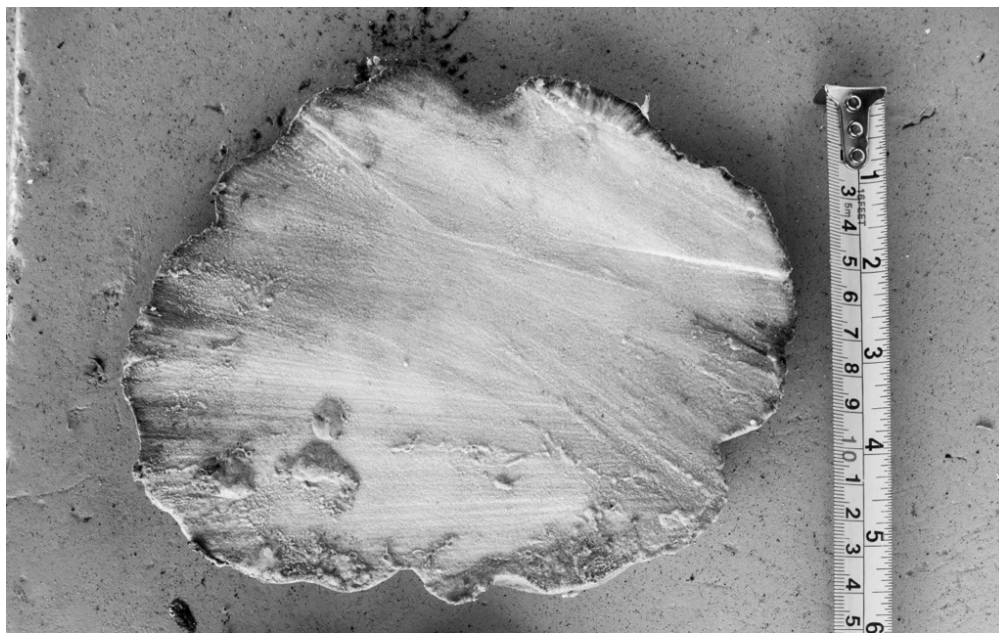
High grazing pressure is especially important for reef resilience by preventing algal accumulation and phase shifts to macroalgal-dominance (Hughes et al. 2007). Herbivores will only be able to perform this function on a reef once they exceed a grazing threshold, and the results presented here suggest consumption needs to be at or greater than 50% of algal production to prevent accumulation. Algal consumption on both heavily fished and older fisheries closures was high, though due to different taxa, and a majority of the algal production was consumed (> 75%). Certain herbivores may be particularly important in achieving consumption rates greater than 50%, and in this study, parrotfishes had a greater impact than expected and previously reported. Consequently, reefs protected from fishing devoid of larger-bodied scraping fishes may have grazing intensities below the threshold required to prevent algal accumulation. However, these reefs may only need more time to recover and allow competitive interactions to run their course.

Appendix 2.1

Appendix 2.1.1. Length-weight relationships and relevant source used to estimate fish biomass (g) using the equation: $a \times TL^b$ where a and b are constants and total length (cm) is derived from underwater visual census. Functional groupings are based on published diet information following methods by Green et al. (2009).

Family	Species	Functional group	a	b	Source
Acanthuridae	<i>Acanthurus dussumieri</i>	Grazer	0.0554	2.7990	Letourneur et al. 1998
Acanthuridae	<i>Acanthurus leucosternon</i>	Grazer	0.0169	2.9605	Froese and Pauly 2006
Acanthuridae	<i>Acanthurus nigricauda</i>	Grazer	0.0261	3.0240	Letourneur et al. 1998
Acanthuridae	<i>Acanthurus nigrofuscus</i>	Grazer	0.0301	2.9670	Letourneur et al. 1998
Acanthuridae	<i>Acanthurus triostegus</i>	Grazer	0.1317	2.3920	Letourneur et al. 1998
Acanthuridae	<i>Ctenochaetus striatus</i>	Grazer	0.0254	3.0270	Letourneur et al. 1998
Acanthuridae	<i>Ctenochaetus strigosus</i>	Grazer	0.0042	3.1263	Froese and Pauly 2006
Acanthuridae	<i>Naso annulatus</i>	Browser	0.0309	2.9100	Froese and Pauly 2006
Acanthuridae	<i>Naso elegans</i>	Browser	0.0309	2.9100	Froese and Pauly 2006
Acanthuridae	<i>Naso unicornis</i>	Browser	0.0216	2.9880	Letourneur et al. 1998
Acanthuridae	<i>Zebrasoma scopas</i>	Grazer	0.0400	2.8670	Letourneur et al. 1998
Acanthuridae	<i>Zebrasoma veliferum</i>	Grazer	0.0339	2.8550	Letourneur et al. 1998
Ephippidae	<i>Platax teira</i>	Browser	0.0952	2.7694	Froese and Pauly 2006
Kyphosidae	<i>Kyphosus vaigiensis</i>	Browser	0.0219	2.9878	Froese and Pauly 2006
Pomacanthidae	<i>Centropyge multispinis</i>	Grazer	0.0319	2.9206	Froese and Pauly 2006
Labridae	<i>Calotomus carolinus</i>	Browser	0.0122	3.1670	Froese and Pauly 2006
Labridae	<i>Hipposcarus harid</i>	Scraper	0.0203	3.0000	Froese and Pauly 2006
Labridae	<i>Leptoscarus vaigiensis</i>	Browser	0.0173	2.9650	Letourneur et al. 1998
Labridae	<i>Scarus frenatus</i>	Scraper	0.0320	3.0600	Froese and Pauly 2006
Labridae	<i>Scarus ghobban</i>	Scraper	0.0169	3.0490	Letourneur et al. 1998
Labridae	<i>Scarus niger</i>	Scraper	0.0142	3.1400	Letourneur et al. 1998
Labridae	<i>Scarus psittacus</i>	Scraper	0.0222	2.9820	Letourneur et al. 1998
Labridae	<i>Scarus rubroviolaceus</i>	Scraper	0.0136	3.1090	Froese and Pauly 2006
Labridae	<i>Chlorurus sordidus</i>	Scraper	0.0200	3.0400	Froese and Pauly 2006
Labridae	Juvenile sp (< 10cm)	Scraper	0.0210	3.0322	Froese and Pauly 2006
Siganidae	<i>Siganus argenteus</i>	Browser	0.0131	3.0880	Letourneur et al. 1998
Siganidae	<i>Siganus sutor</i>	Browser	0.0597	2.7550	Froese and Pauly 2006

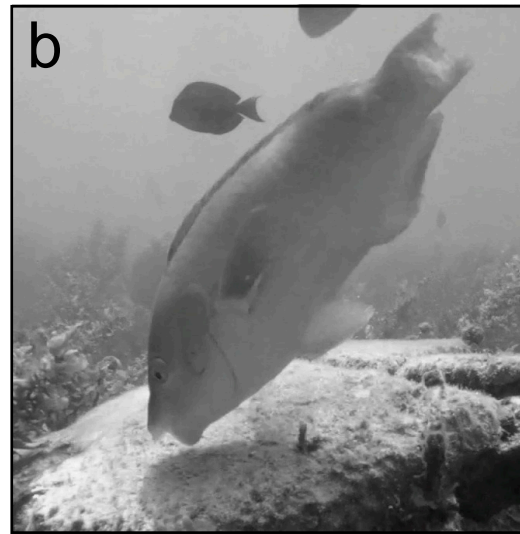
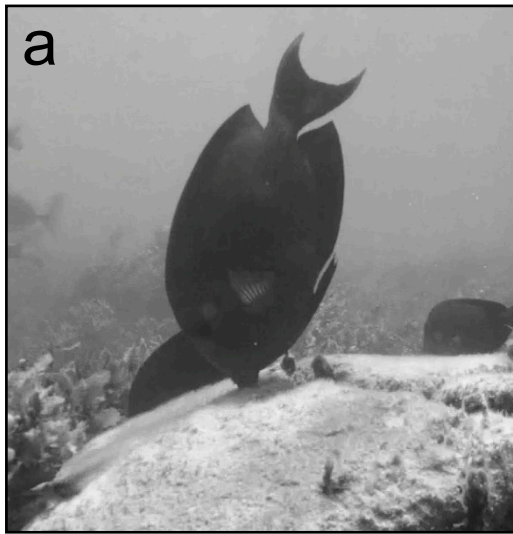
Appendix 2.1.2. Photograph of experimental plate used as an algal growth substratum, which is a cross-section of massive *Porites* coral head.



Appendix 2.1.3. Photo of a (a) fence and (b) cage treatment with experimental plates at deployment.



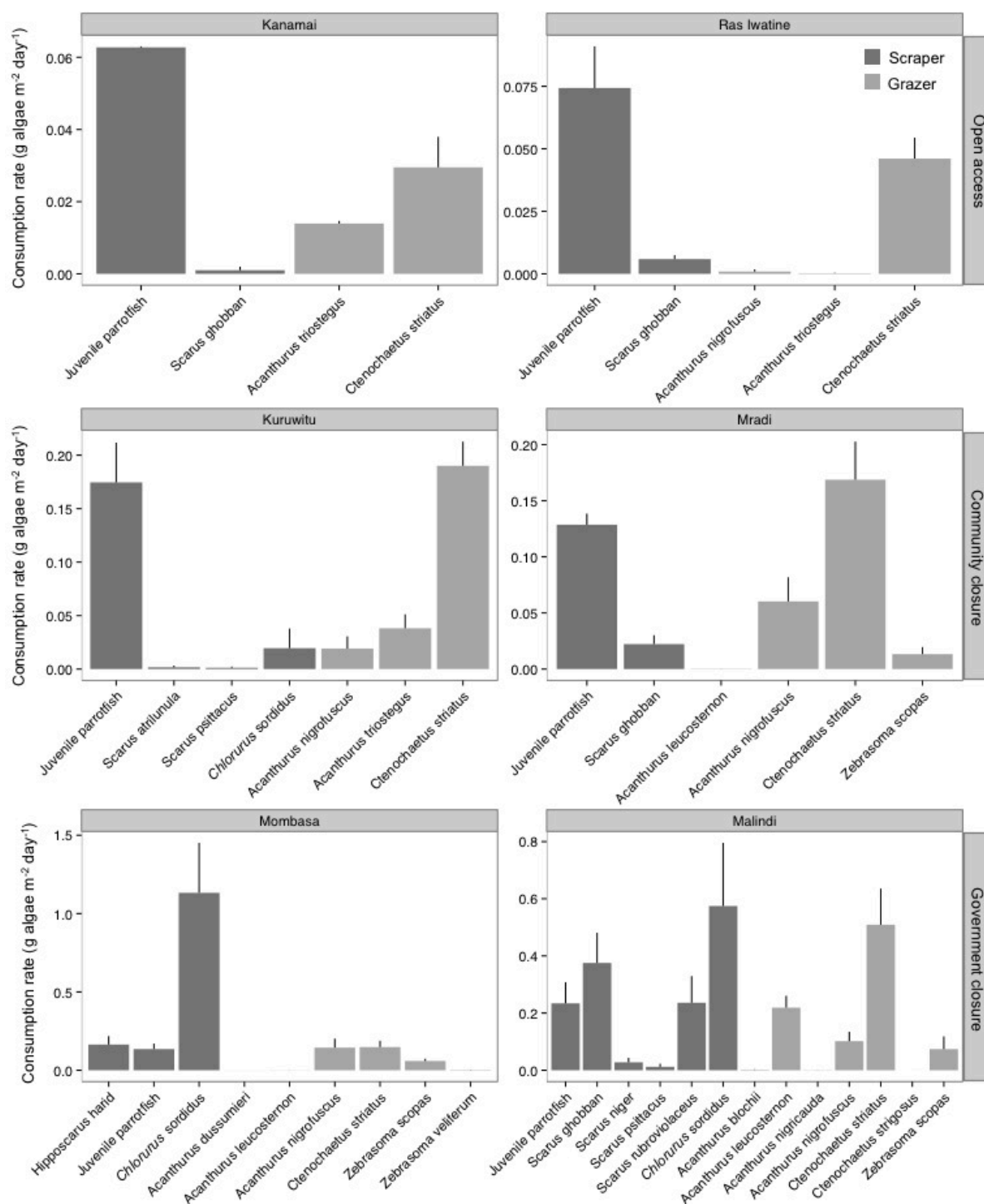
Appendix 2.1.4. Photo of a (a) grazing surgeonfish and (b) scraping parrotfish foraging on experimental substrata.



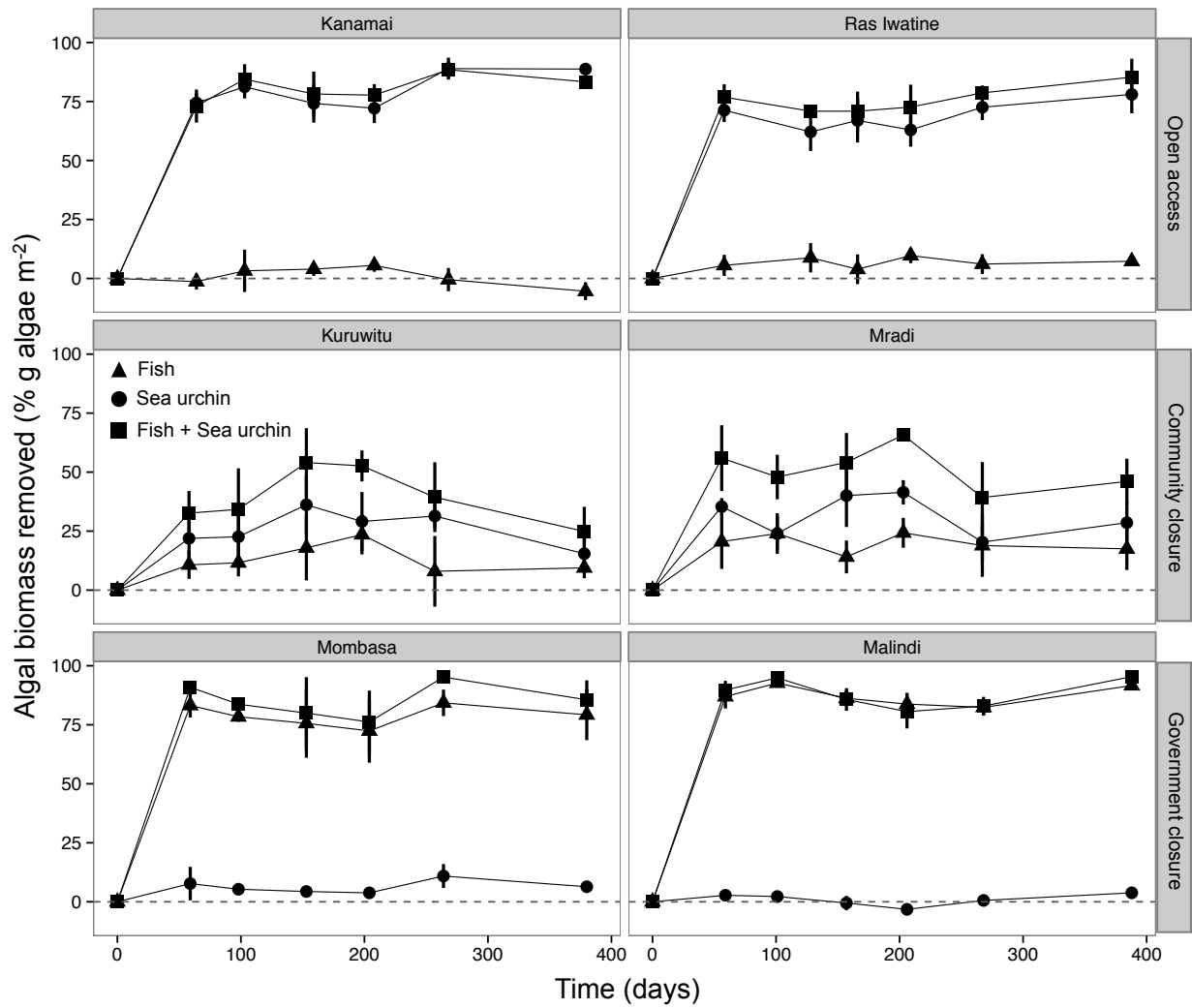
Appendix 2.1.5. Results from two-way ANOVA used to evaluate the effects of fisheries management type (open access fished reefs, community closures, government closures) and treatment (cage, fence, open) on algal biomass accumulation (g algae m^{-2}) on the experimental plates. Data used in the model were from the final sampling event (\sim day 390). *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

	df	F-value	p-value
(Intercept)	1	587.46	***
Management	2	22.47	***
Treatment	2	72.46	***
Management x Treatment	4	13.01	***

Appendix 2.1.6. Mean (+ SE) algal consumption rate (g algae m⁻² day⁻¹) of fish species at study sites by fisheries management type. Values calculated from bite counts of video observations combined with equations of algal consumption (g algae bite⁻¹; Bruggemann et al. 1994a, Marshall and Mumby 2012). Shades of bars indicate functional groups. Notice different scales on y-axes.



Appendix 2.1.7. Time series of the mean (\pm SE) algal biomass removed (% g algae m^{-2}) at the six study sites by fisheries management type. Shapes indicate herbivore type.



CHAPTER 3

DIFFERENTIAL IMPACTS OF CORAL REEF HERBIVORES ON ALGAL SUCCESSION IN KENYA

3.1 Introduction

In both terrestrial and aquatic systems, herbivory is a key top-down process that mediates the abundance of primary producers and community composition (Jones 1992, Schmitz et al. 2000, Scheffer et al. 2001, Mumby et al. 2006). On tropical coral reefs, macroalgae compete with corals for space, nutrients, and light, and herbivores influence interactions between these two primary space occupiers (Hay 1997, McCook et al. 2001). A critical factor governing coral reef growth and sustainability is the maintenance of suitable recruitment space for coral larvae, which is often achieved through high herbivore abundance and low abundance of fleshy macroalgae (Mumby 2006). However, herbivore communities are increasingly being affected by overfishing, potentially undermining the ability of reefs to resist a phase shift to dominance by macroalgae (Hughes 1994, McClanahan et al. 2011a) and recover from disturbances (Nugues and Bak 2006, Hughes et al. 2007). Here, transitions to macroalgae generally progress from filamentous turf algae and crustose coralline algae (CCA) to corticated and fleshy macroalgae, then to leathery and coarsely branched macroalgae or calcified algae that are unpalatable to most herbivores (Hixon and Brostoff 1996, McClanahan 2000, Diaz-Pulido et al. 2007). Thus, it is important to identify how different herbivores influence algal composition and succession on coral reefs, and what this means in the context of preventing

shifts to macroalgal-dominance (Hughes 1994, McClanahan et al. 2001, Hoey and Bellwood 2009).

The functional roles herbivores play on coral reefs may reflect their mobility (Sandin and McNamara 2012), feeding preferences (Mantyka and Bellwood 2007), life-history characteristics (Russ and Alcala 1998), or resistance and recovery responses to disturbances like fishing and coral bleaching (McClanahan et al. 2007a, Graham et al. 2011, McClanahan and Humphries 2012). These traits ultimately affect competition, size, and predation risk, all of which are important factors that influence not only the functional role of a herbivore in an ecosystem, but also the foraging distribution of animals (Werner and Anholt 1993, Dulvy et al. 2004). In Kenya, scrapers and grazers/detritivores are fishes that may play similar roles in contributing to coral reef resilience by preventing the establishment of macroalgae and providing areas of clean substratum for coral recruitment (Cheal et al. 2010). Their activities can also facilitate the establishment of crustose coralline algae (CCA), which are important for reef growth (Steneck 1983, McClanahan 1997, O'Leary and McClanahan 2010). Scrapers feed primarily on epilithic algal turf while closely cropping or scraping the reef surface (Bellwood and Choat 1990). Grazers feed on a similar diet to scrapers, and detritivores on a combination of turf, sediment, and plankton; however, grazers and detritivores can have similar impacts on algal dynamics (Marshall and Mumby 2012).

Fishes represent one group of herbivores on coral reefs in Kenya, however, sea urchins are key grazers in many benthic ecosystems and have the ability to dictate benthic composition and maintain algal turfs (McClanahan 1997). As spatially

constrained organisms with different feeding properties, the patterns in algal and coral composition that sea urchins are able to mediate may be different from those maintained by fish (O’Leary and McClanahan 2010, O’Leary et al. 2012). Fish are vagile consumers and more wide-ranging than sea urchins, with relatively large home ranges (75-300 m² in the Caribbean; Mumby and Wabnitz 2002), whereas an individual sea urchin may only forage within an area of just 1 m² on coral reefs (Carpenter 1984). Fish may be selective foragers in these larger areas and select algae based on properties of palatability (Burkepile and Hay 2008), while sea urchins are less selective and select algae primarily on the basis of accessibility (Ogden and Lobel 1978, Sandin and McNamara 2012). This can create a dynamic mosaic of intensely grazed and ungrazed areas on a reef that reflects patchiness in sea urchin abundance. These differences suggest that herbivorous fishes and sea urchins will have quite different effects on ecosystem functioning and community structure of algae on coral reefs.

In Kenya, all herbivorous fish species are heavily and indiscriminately exploited and sea urchins are not (McClanahan et al. 2008). Here, fisheries closures represent a management tool intended to prevent overfishing, which will create reefs with variable herbivore abundances and species assemblages (McClanahan et al. 2007a). In this study, I use the rapidly emerging establishment of community-managed fisheries closures together with older government closures and fished reefs as a “natural experiment” to examine the differential influence of herbivore assemblages on algal succession. To do this, I use survey techniques coupled with regular estimates of algal abundance (percentage cover) on experimental substrata over a ~390 day period. Here, I test two hypotheses: (1) that sea urchins and fishes

affect algal abundance and succession differently, and (2) that algal succession will trace similar paths across fisheries management regimes because herbivorous fishes will replace sea urchins as fishing is eliminated on reefs.

3.2 Materials and methods

3.2.1 Study sites

See Chapter 1 for site descriptions and locations (Fig. 1.1).

3.2.2 Existing herbivore and benthic community composition

Herbivorous and non-herbivorous fishes and sea urchins were identified and their abundance (ind m⁻²) and biomass (kg ha⁻¹) calculated as described in Chapter 2 (section 2.2.2).

Benthic cover was surveyed using 9 haphazardly placed 10 m line-intercept transects. The distances covered by major benthic components (hard coral, turf algae, CCA, and erect macroalgae) underlying each transect line were measured to the nearest centimeter. Macroalgae were further identified to the genus level and percentage cover was calculated as the sum of the lengths divided by the total transect length. Transects were conducted during neap tides when the water was between ~1 and 4 m deep, in the same areas as fish and sea urchin transects to control for habitat effects, and during the calm, northeast monsoon season (Aug – Dec).

3.2.3 Algal dynamics and succession on experimental substrata

Experimental substrata, treatments, and design were as described in Chapter 2 (section 2.2.3, Fig. 2.1).

The algal communities growing on the plates were described by taking digital photographs (Canon G10 at 12 megapixel resolution) at each site every 6-8 weeks; samples were taken a total of 7 times over the ~390 day duration of the experiment. Photographs were processed and percent compositions of algal turf, macroalgae, calcareous algae, and CCA were determined using a stratified random point-intercept method ($n = 50$ points plate⁻¹) with digital photography software (Adobe Photoshop). Macroalgae were further identified to the genus level as *Dictyota*, *Padina*, *Sargassum*, *Turbinaria*, *Hypnea*, and *Cystoseira*, or placed in an “other” category. The approach involved sacrificial pseudoreplication, and average values of algal cover for the four plates within a replicate were subsequently used in the analyses.

3.2.4 Statistical analyses

I used separate one-way ANOVAs to test for an effect of fisheries management (fished reefs, community closures, government closures), with site as a nested effect, on: total fish biomass, herbivorous fish biomass, sea urchin biomass, herbivorous fish functional group biomass (scrapers, browsers, grazers), and benthic abundance (coral, turf, CCA, macroalgae). Using separate two-way ANOVAs, I tested for an effect of fisheries management and treatment (cage, fence, open), and their interaction, on the percentage cover of algal groups on the experimental substrata. Algal groups tested were: algal turf, upright macroalgae (all macroalgal

genera combined), *CCA*, *Dictyota*, *Padina*, *Sargassum*, *Turbinaria*, *Hypnea*, and *Cystoseira*. The 'other' macroalgal category was excluded from analyses because it accounted for < 3% of overall abundance. Data used in these models were from the last sampling event (~day 390). Site was nested within fisheries management for all models, and where necessary, data were log-transformed to improve the spread of the data and to meet model assumptions of normality and homoscedasticity. Model diagnostics were performed visually using frequency histograms, funnel plots and quantile-quantile (Q-Q) plots, and the final models met the assumptions of normality and homogeneity of residuals. All significant models were followed by individual contrasts using Tukey tests to identify pairwise differences.

I estimated grazing strength on upright macroalgae using the natural log-response ratio (LRR; Osenberg et al. 1997). Here, LRRs were calculated as

$$LRR = \ln\left(\frac{A_C}{A_T}\right)$$

where A_C is the abundance (% cover) in the cage treatment and A_T is the abundance (% cover) in either the fence or open treatment. Positive LRR values indicate a reduction of macroalgal abundance by consumption, while negative LRR values indicate that grazers promoted the abundance of macroalgae through fertilization or competition-type effects. Zero values indicate no difference in macroalgal abundance from control (cage) treatments, or no grazing or fertilization effect. I then used one-way ANOVAs of the LRR values to determine if there was a significant grazing or

fertilization effect among fisheries management type at the fence and open treatments at the final sampling event.

To determine how treatment and fisheries management affected algal community structure through time, I used a multivariate randomization procedure to create a matrix of Bray-Curtis similarity measures (for the final sampling event as well as one in the middle of the experiment; ~180 and 390 days). I analyzed these distance matrices using permutational analysis of variance (PERMANOVA; $n = 999$ permutations) and used non-metric multidimensional scaling (MDS) ordination to visualize similarities in algal community structure. I then used correlation-based principal components analysis (PCA) on Euclidean distances with data from the open treatments at the final sampling event. Multivariate homogeneity of the treatments was confirmed using Levene's test for equality of variances (Levene 1960). All data analyses were performed using the program "R" (v. 2.15.1; R Development Core Team 2013).

3.3 Results

3.3.1 Existing herbivore and benthic community composition

There was strong similarity between the paired sites within management types and significant differences among management types in the composition of herbivore communities ($p < 0.001$; Fig. 3.1 and 3.2). The fished reefs, Kanamai and Ras Iwatine, had low abundances of fish, total fish biomass being only 70.6 and 96.5 kg ha⁻¹, respectively. For Kanamai, herbivores comprised 4.6 kg ha⁻¹, or 7.8% of total fish biomass, for Ras Iwatine they contributed 13 kg ha⁻¹, or 13.4%. Herbivorous fish were small at these sites, mostly under 15 cm with only a few exceptions (Fig. 3.3).

Sea urchins were abundant at these two sites with a mean biomass of 6095 kg ha⁻¹ and 4401 kg ha⁻¹ at Kanamai and Ras Iwatine respectively. At Kanamai, most urchins were *Echinometra mathaei* (4530 kg ha⁻¹), whereas at Ras Iwatine most were *Echinothrix diadema* (2956 kg ha⁻¹).

The community closures, Kuruwitu and Mradi, had greater fish biomass but fewer urchins than the fished reefs (Fig. 3.1 and 3.2). Kuruwitu had a total fish biomass of 364 kg ha⁻¹ and a sea urchin biomass of 2591 kg ha⁻¹, whereas Mradi had 440 kg ha⁻¹ of fish and 2664 kg ha⁻¹ sea urchin biomass. At Kuruwitu, herbivores accounted for 49% of the total fish biomass, or 178 kg ha⁻¹. The majority of these herbivores were grazers and detritivores, with less than 10% being browsers or scrapers. Furthermore, herbivorous fishes were typically small and less than 20 cm except for a few larger grazers (Fig. 3.3). Sea urchins at Kuruwitu were mostly either *Diadema* spp. or *E. mathaei*. Mradi had 209 kg ha⁻¹ of herbivorous fishes, forming 47% of its total fish biomass. Much like Kuruwitu, the majority of the herbivorous fishes at Mradi were grazers and detritivores, with less than 5% being browsers or scrapers. The sea urchin community at Mradi consisted of mostly *E. diadema* (1272 kg ha⁻¹).

Mombasa and Malindi, the government closures, had the highest fish biomass and lowest sea urchin biomass (Fig. 3.1 and 3.2). Mombasa had a mean fish biomass of 954 kg ha⁻¹, with 460 kg ha⁻¹ of that being herbivores, or 48%. Herbivorous fishes at Mombasa were dominated by browsers (187 kg ha⁻¹), followed by grazers and detritivores (161 kg ha⁻¹), and scrapers (112 kg ha⁻¹). Malindi had the highest fish biomass of all sites with 1165 kg ha⁻¹, of which 578 kg ha⁻¹, or almost 50% were herbivores. Herbivorous fish functional groups were somewhat evenly distributed at

Malindi, with biomass of groups ranging between 120 and 172 kg ha⁻¹. Fish were large at these sites and most of the scraper biomass came from the 31-40 cm size class (Fig. 3.3). Grazers and browsers were mostly in the 26-35 cm size class. The sea urchin community at Mombasa comprised mostly *E. diadema* and had an overall biomass of 1411 kg ha⁻¹. With a total biomass of 60 kg ha⁻¹, Malindi had the fewest sea urchins of any site.

Existing benthic cover varied among sites and fisheries management, with the highest hard coral and lowest macroalgal cover at Mradi and Kanamai (hard coral: 46 and 34.8%, macroalgae: 8.5 and 0.9%, respectively; Table 3.1). Ras Iwatine had the lowest hard coral abundance with 7.1%, and Mombasa had the highest macroalgal abundance with 25.7%. CCA was highest at Malindi with 20.4% cover. Algal turf abundance was highest at the open access reefs, Kanamai and Ras Iwatine, with greater than 42% cover. Macroalgal genera varied by site and management; *Sargassum* was most abundant at Mombasa (23.2%) and *Turbinaria* was most abundant at Malindi (9%). Other macroalgal genera were never greater than 5% at sites.

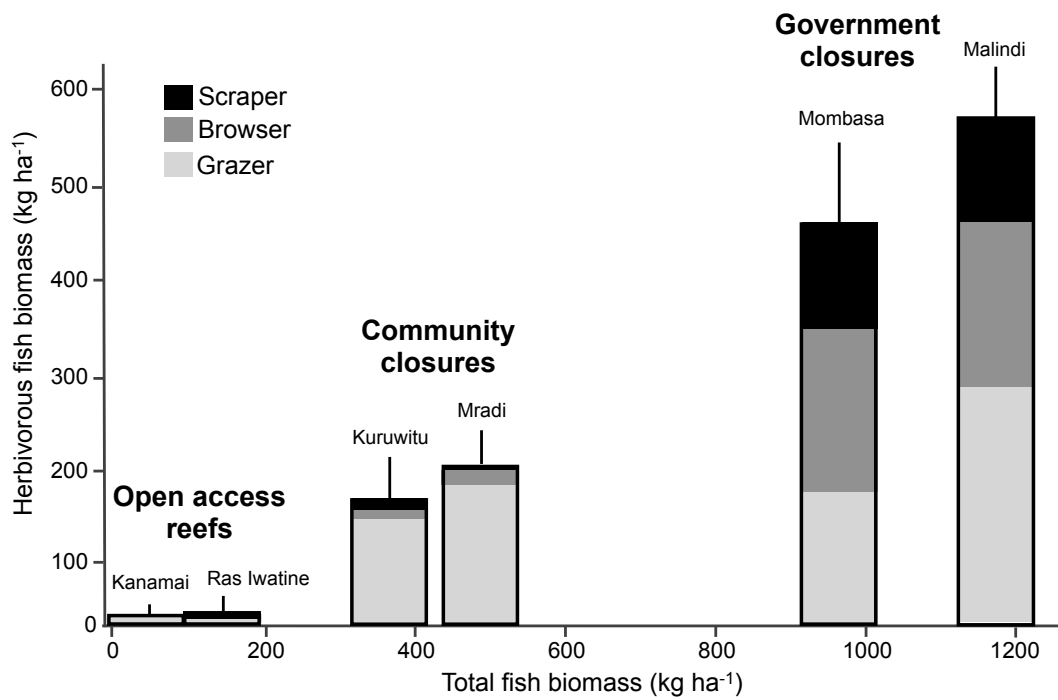


Fig. 3.1. Mean (+ SE) herbivorous fish and total fish biomass (kg ha⁻¹) at the six study sites. Colors of bars indicate functional group. Site names and fisheries management type are indicated above bars.

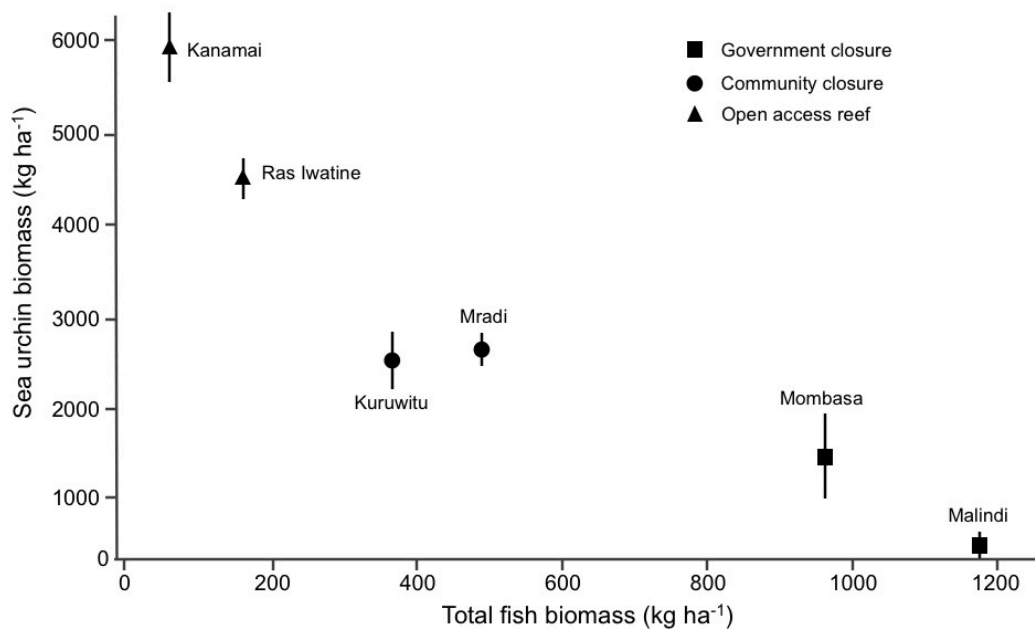


Fig. 3.2. Mean (\pm SE) sea urchin and total fish biomass (kg ha⁻¹) at the six study sites. Shapes indicate fisheries management type and names of sites are indicated next to data points.

Model results indicated significant differences among all fisheries management types for all fish and herbivorous fish biomass ($p < 0.01$ in all cases; Table 3.2). Although sea urchins generally decreased in biomass as fish increased, the difference in urchin biomass among management types was only statistically significant when comparing fished reefs to government closures ($p = 0.021$). Scraper and browser fish biomass were significantly greater at government closures ($p < 0.001$), but there was no difference between open access reefs and community closures ($p = 0.955$ for scrapers, and $p = 0.809$ for browsers). Grazer fish biomass was significantly higher at government closures when compared to fished reefs ($p < 0.001$), but not community closures ($p = 0.266$); however, community closures had more grazer and detritivore biomass than fished reefs ($p = 0.001$). Fisheries management was a poor predictor ($p > 0.05$) for most benthic categories, with the exception of algal turf where fished sites were greater than both types of closures, and CCA where government closures were greater than other management types (Appendix 3.1.1). Macroalgae genera did not differ by management type except for *Turbinaria* where it was greater at government closures.

Table 3.1. Mean abundance (% cover; \pm SE) of the major substratum categories and macroalgae genera at each of the six study sites by fisheries management type.

Major substratum	Open access		Community closure		Government closure	
	Kanamai	Ras Iwatine	Kuruwitu	Mradi	Mombasa	Malindi
Hard coral	34.77 (6.79)	7.1 (4.56)	26.17 (8.38)	46.01 (13.12)	20.23 (10.08)	27.17 (14.77)
Algal turf	42.6 (9.48)	42.8 (12.77)	37.33 (13)	21.05 (16.59)	33.18 (12.6)	24.86 (15.49)
Macroalgae	0.93 (2.01)	13.88 (11.62)	12.44 (7.82)	8.5 (6.27)	25.73 (7.95)	9.3 (6.34)
CCA	1.77 (2.06)	8.56 (2.61)	3.18 (2.47)	10.21 (5.35)	13.16 (6.17)	20.44 (7.94)

Macroalgae genera	Open access		Community closure		Government closure	
	Kanamai	Ras Iwatine	Kuruwitu	Mradi	Mombasa	Malindi
<i>Cystoseira</i>	0 (0)	0 (0)	1.57 (1.24)	0.25 (0.25)	0 (0)	0 (0)
<i>Dictyota</i>	0.03 (0.05)	1.25 (1.4)	0.75 (0.54)	1.21 (0.02)	0.45 (0.35)	0.09 (0.13)
<i>Hypnea</i>	0.04 (0.06)	1.35 (0.54)	0.41 (0.37)	3.62 (2.53)	0 (0)	0.1 (0)
<i>Padina</i>	0.25 (0.16)	3.63 (0.37)	1 (0.81)	1.24 (0.2)	0.03 (0.04)	0 (0)
<i>Sargassum</i>	0.07 (0.1)	7.11 (1.37)	4.93 (1.37)	0.67 (0.67)	23.17 (2.66)	0 (0)
<i>Turbinaria</i>	0.5 (0.53)	0.52 (0.37)	1 (0.11)	0.83 (0.83)	1.95 (0.03)	9.04 (2.24)

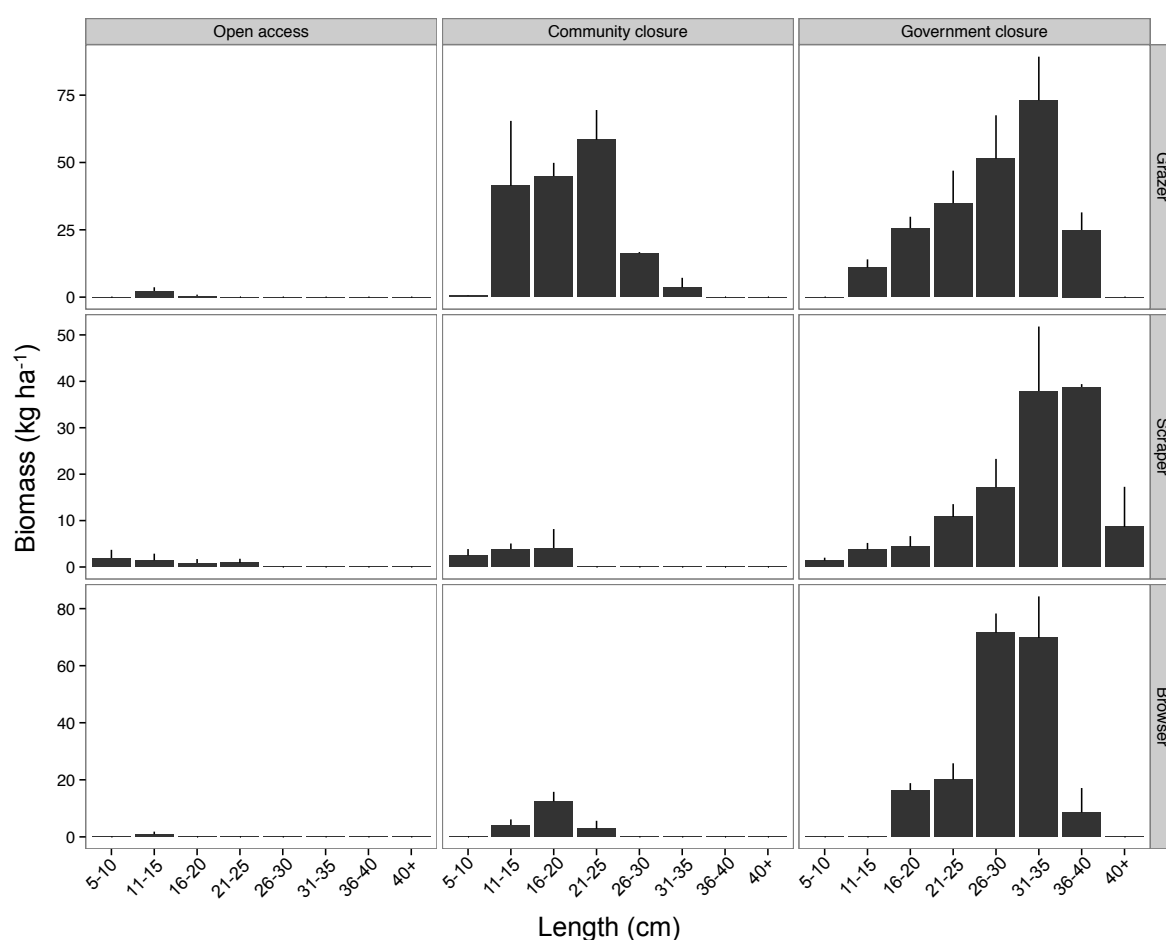


Fig. 3.3. Mean (+ SE) biomass (kg ha^{-1}) for each size-class (total length; cm) of herbivorous fishes (by functional group) at each fisheries management regime.

Table 3.2. Pairwise comparisons of herbivore communities by fisheries management type from ANOVAs of biomass (kg ha^{-1}) data. Sea urchin data were log-transformed to meet assumptions of normality and homoscedasticity. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

All fish	Estimate	Z-value	p-value	Herbivorous fish	Estimate	Z-value	p-value
Fished - Government	-976.00	-12.87	***	Fished - Government	-508.76	-14.83	***
Community - Government	-657.28	-8.67	***	Community - Government	-324.34	-9.45	***
Community - Fished	318.72	4.20	**	Community - Fished	184.42	5.38	***
Sea urchin	Estimate	Z-value	p-value	Browser	Estimate	Z-value	p-value
Fished - Government	2.93	3.46	*	Fished - Government	-183.65	-6.38	***
Community - Government	2.26	2.47	0.088	Community - Government	-165.58	-5.75	***
Community - Fished	-0.67	-0.73	0.751	Community - Fished	18.07	0.63	0.809
Grazer	Estimate	Z-value	p-value	Scraper	Estimate	Z-value	p-value
Fished - Government	-214.10	-6.91	***	Fished - Government	-111.01	-7.71	***
Community - Government	-51.93	-1.68	0.266	Community - Government	-106.83	-7.42	***
Community - Fished	162.17	5.23	***	Community - Fished	4.18	0.29	0.955

3.3.2 Algal dynamics and succession on experimental substrata

Percentage cover and LRRs of total upright macroalgae showed distinct trends through time among treatments and fisheries management (Fig. 3.4), however, responses of individual macroalgal genera were less clear through time (Fig. 3.5). CCA (open treatments only) was significantly greater at the government closures than other management types ($p < 0.001$), and increased through time to reach an overall percentage cover greater than 20% (Appendix 3.1.2). From the initial 288 plates, some were not recovered: Kanamai = 2 open, 1 fence, 4 cage; Ras Iwatine = 4 open, 3 fence, 2 cage; Kuruwitu = 0 open, 0 fence, 4 cage; Mradi = 2 open, 0 fence, 0 cage; Mombasa = 4 open, 4 fence, 4 cage; Malindi = 0 open, 0 fence, 4 cage.

MANOVAs revealed a significant interaction term for 6 of the 9 algal groups, indicating that significant effects ($p < 0.05$) of treatment type on the abundance of algal groups depends on the fisheries management regime (Appendix 3.1.3). This trend was true for all groups except *Turbinaria*, *Hypnea*, and *Padina*.

At the fished reefs, succession of macroalgal genera in the cage and fence treatments mostly began with *Padina* and *Hypnea* dominating the assemblage, but later transitioned into a more mixed assemblage with increasing cover of *Sargassum* as the experiment progressed (Fig. 3.5). Total upright macroalgae in the cage and fence treatments reached and remained around or above 40% after ~100 days (Fig. 3.4a). The open treatment at these sites developed very little macroalgal cover through time, remaining consistently at or below ~10%. There were slight fluctuations in percentage cover in the cage and fence treatments around ~210 days,

when the stronger winds and currents of the southeast monsoon season may have caused a reduction in the already established macroalgal community. The ANOVA by treatment for percentage cover of total upright macroalgae was significant ($p < 0.01$), and pairwise comparisons indicated that the fence and cage treatments at the open access reefs were not significantly different from one another ($p = 0.894$), however, open treatments were significantly lower than both fence and cage treatments ($p < 0.001$; Appendix 3.1.4). The ANOVAs of LRRs corroborated these findings with a significant grazing effect on total upright macroalgae at the open treatment ($p < 0.001$), but not the fence treatment at the fished reefs ($p = 0.443$; Fig. 3.4b).

Padina and *Hypnea*, with *Sargassum* and *Cystoseira* dominated succession of macroalgal genera for all treatments at the community closures and increased through time (Fig. 3.5). Total upright macroalgae at all treatments traced similar successional trajectories; there was an immediate increase in total upright macroalgae at all treatments that reached the highest levels around day ~150, and then again at the end of the experiment at ~50% cover (Fig. 3.4a). Similarly to the open access reefs, there was a slight decrease in percentage cover between ~200 and ~300 days, most likely due to seasonal monsoon effects. The ANOVA by treatment for percentage cover of total upright macroalgae was not significant ($p = 0.532$) and LRRs corroborated this, with no significant grazing or fertilization effect (open: $p = 0.577$; fence: $p = 0.247$; Fig. 3.4b).

At the government closure sites, succession of macroalgal genera in cage treatments began mostly with *Padina*, *Cystoseira*, and *Hypnea*, then transitioned into

a mixed assemblage with *Sargassum* becoming dominant and *Turbinaria* present (Fig. 3.5). Total upright macroalgae in the cage treatments increased and was at or above ~40% cover after ~150 days (Fig. 3.4a). Total upright macroalgae in the fence and open treatments remained low for the duration of the experiment and percentage cover never exceeded ~10%. The ANOVA by treatment for percentage cover of total upright macroalgae was significant ($p < 0.001$), and pairwise comparisons indicated a significant difference between both the open and fence treatments with the cage treatment ($p < 0.001$); however, fence and open treatments were not significantly different from one another ($p = 0.997$; Appendix 3.1.4). The ANOVAs of LRRs corroborated these findings and indicated a significant grazing effect of total upright macroalgae in both fence ($p < 0.001$) and open treatments ($p < 0.001$; Fig. 3.4b).

Results from the MDS showed that algal community structure in the cage treatment had a high variance and sites failed to cluster by fisheries management in axis space at either ~180 or ~390 days (Appendix 3.1.5). Model results indicated poor explanatory power of these plots, and the results were not significant (~180 days: $R^2 = 0.123$, $p = 0.205$; ~390 days: $R^2 = 0.120$; $p = 0.203$). For the fence treatment, there was a differentiation between the government closure sites and the community closures and fished reefs at both ~180 and ~390 days. This was driven by the presence of turf algae at government closures and macroalgae at community closures and fished reefs. These plots explained > 40% of the variation in the models and, although explanatory power was low, both were significant (~180 days: $R^2 = 0.407$, $p < 0.001$; ~390 days: $R^2 = 0.464$, $p < 0.001$). The open treatment showed the clearest effect of management type. Government closures and fished

reefs tended to cluster together, being characterized by algal turf and, in the case of government closures CCA, whereas community closures being distinctly different, with a high abundance of macroalgae at both ~180 and ~390 days. Model results indicated stronger explanatory power for these plots, with > 50% of the variance explained by the model (~180 days: $R^2 = 0.562$, $p < 0.001$; ~390 days: $R^2 = 0.498$, $p < 0.001$). Stress values for all plots were below 0.16.

The first principal components axis (PC1) of the PCA differentiated fisheries management by herbivore group with fishes (scrapers, browsers, grazers) at negative PC1 scores and sea urchins at positive PC1 scores (Fig. 3.6). The second principal components axis (PC2) differentiated fisheries management along a gradient from algal communities with turf and CCA at negative PC2 scores, to those with macroalgae at positive PC2 scores. PCA results show overlap and suggest fisheries management mediated algal assemblages through herbivore composition: turf algae were representative of fished reefs because of sea urchins, turf algae and CCA were representative of government closures because of scrapers (and browsers), and macroalgae dominated in community closures because of intermediate levels of sea urchins and the presence of very few scrapers and browsers (only grazer fishes).

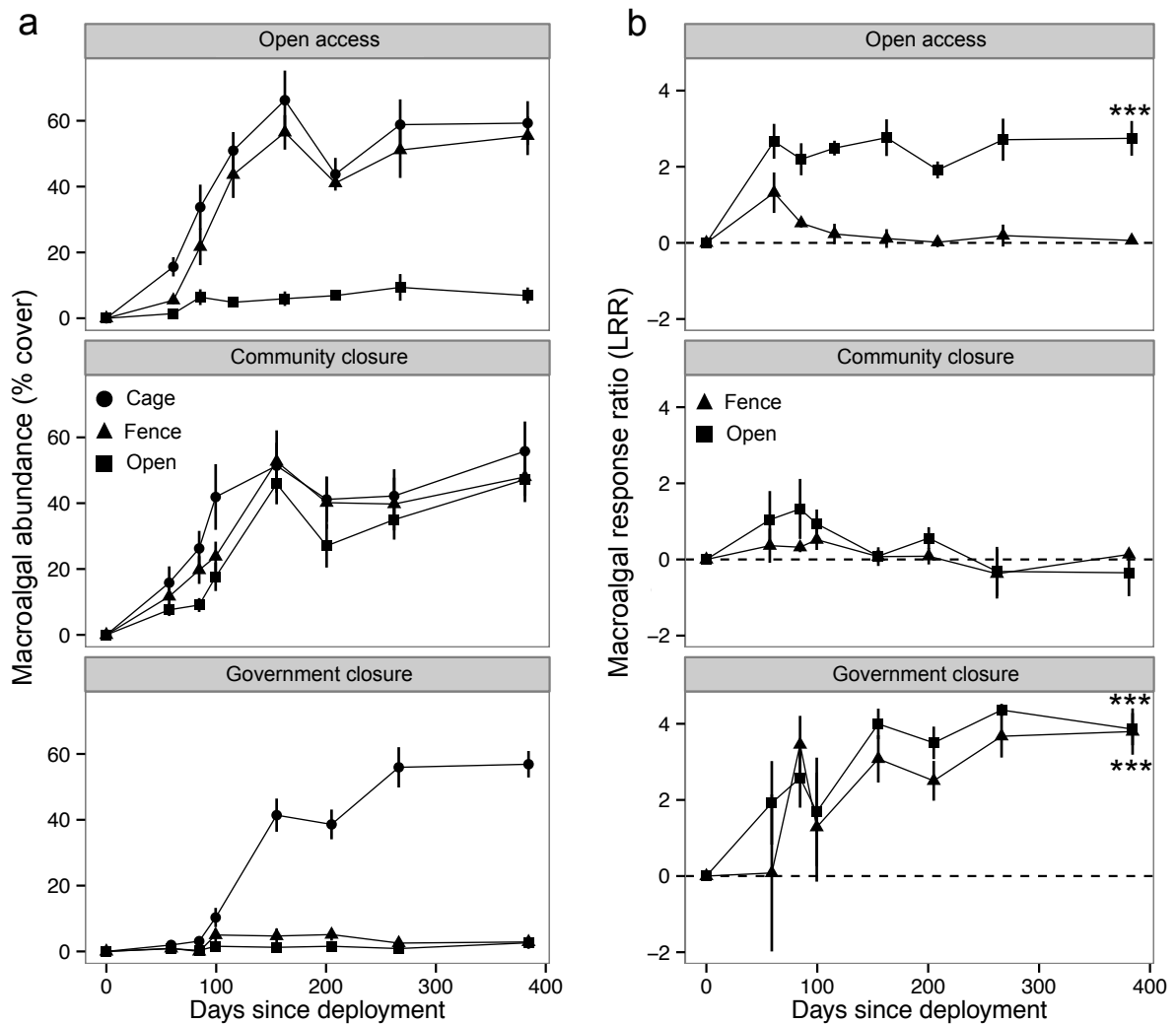


Fig. 3.4. Time series of the mean (\pm SE) (a) abundance of macroalgae (% cover), and (b) natural log-response ratio (LRR) on the experimental plates over ~390 days by fisheries management type. Shapes indicate treatment type. Positive values of LRR indicate reduction of macroalgal abundance by consumption, negative values of LRR indicate that grazers promote the abundance of macroalgae through fertilization, and zero values indicate no difference in macroalgal abundance from control (cage) treatments. Statistics in (b) are from ANOVAs of the final sampling event. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

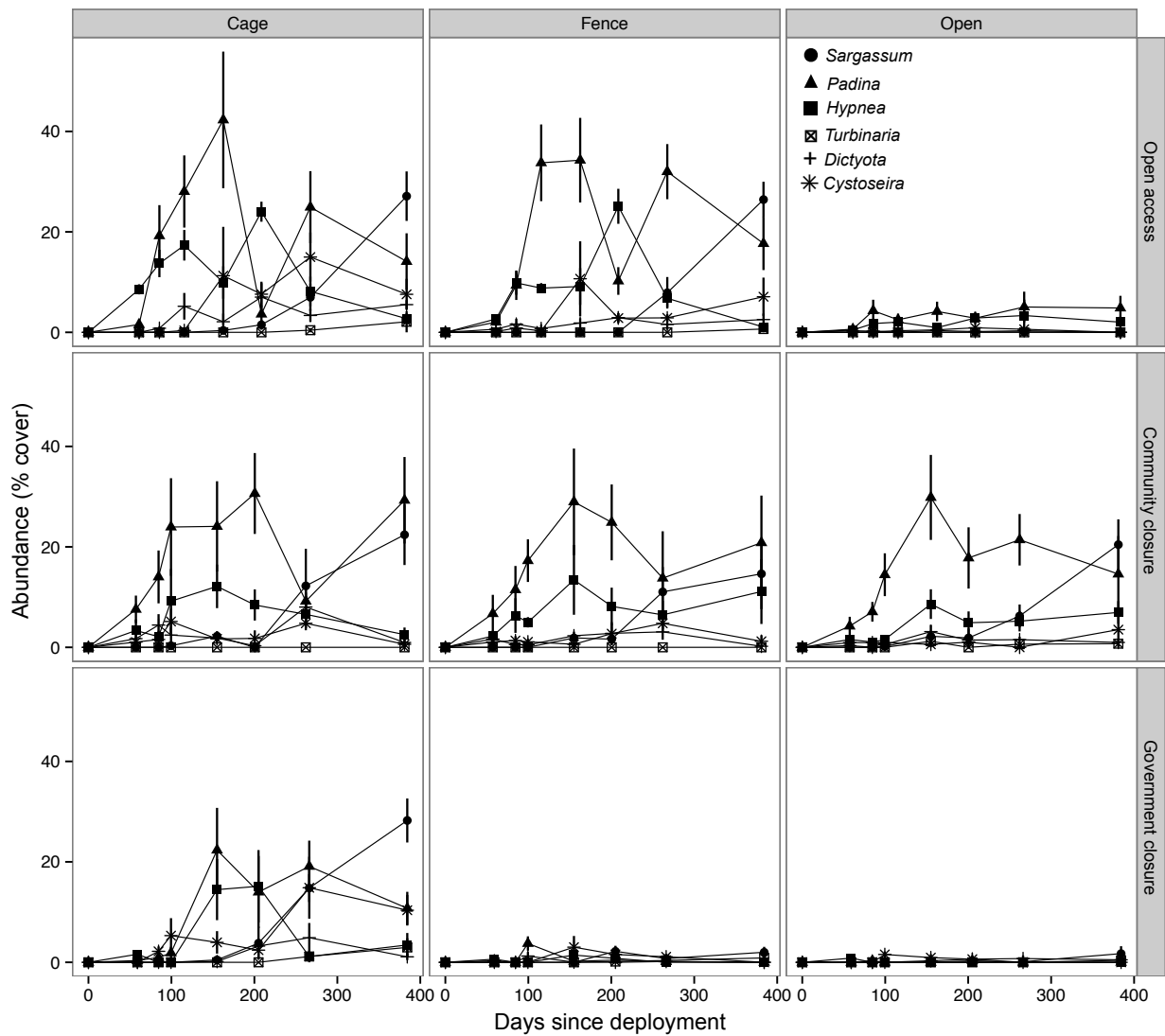
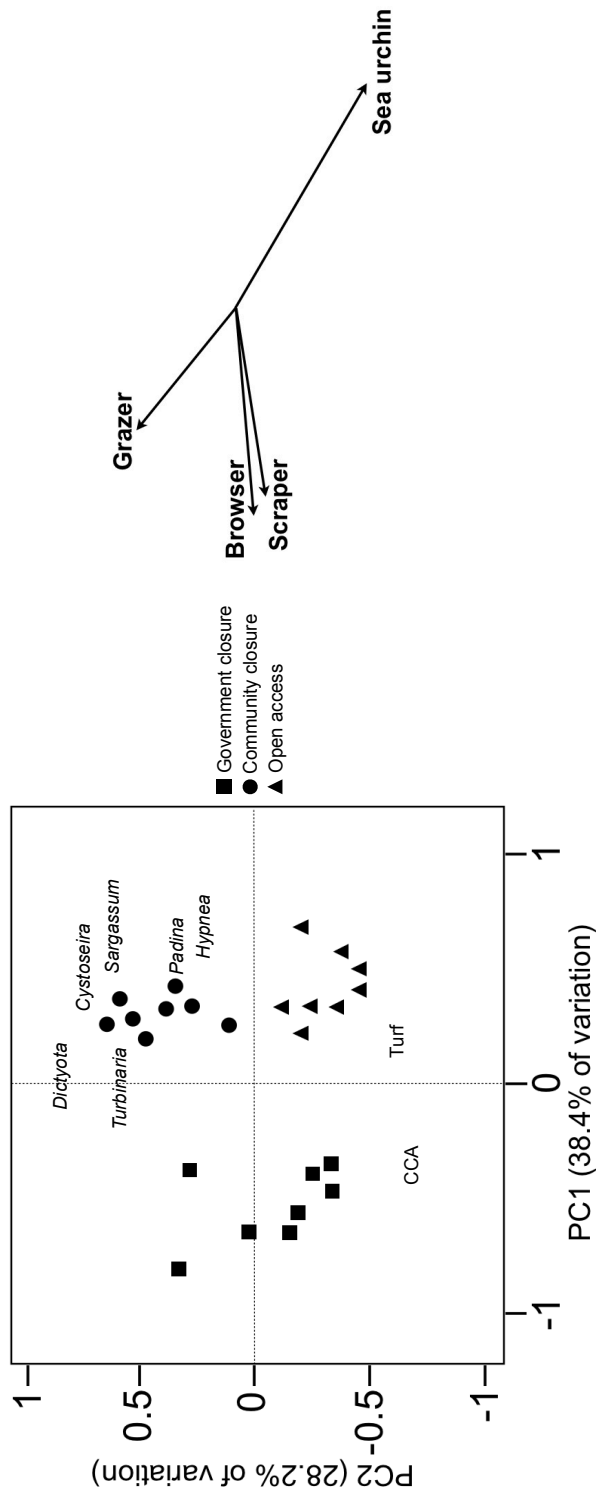


Fig. 3.5. Time series of mean abundance (% cover; \pm SE) of macroalgal genera by treatment and fisheries management type on the experimental plates at the six study sites over ~390 days. Shapes indicate macroalgal genera. If the total percentage cover is < 100, remaining algae is turf.

Fig. 3.6. The spatial variation in algal composition on experimental plates and relative contribution of herbivores using principal components analysis (PCA) on Euclidean distances. Data points represent open treatments (herbivory by urchins and fishes) after ~390 days since deployment, and different shapes represent fisheries management type. Points that are closer together in ordination space are more similar in terms of algal community, and individual algae were overlaid to visualize dominant assemblages.



3.4 Discussion

Patterns of algal succession on the experimental substrata followed different trajectories in the presence and absence of herbivores, and according to management type. Specifically, the results were linked to the grazer assemblages found at the sites under different management regimes: larger scraping (and browsing) fishes were associated with algal turfs and CCA at the older and larger government closures, and sea urchins co-occurred with turfs at open access fished reefs. The younger community-managed fisheries closures had intermediate levels of sea urchins and mostly grazer fishes, which allowed algae to quickly transition from turf into assemblages dominated by fleshy macroalgae. Here, macroalgae that became established early primarily consisted of *Hypnea* and *Padina*, followed by a late stage dominated by *Sargassum* and some *Turbinaria*. These particular reefs may represent a transitional system of herbivore dominance that exists prior to the full recovery of fish biomass and larger-bodied scrapers in no-take fisheries closures. These results provide further support for other studies that have identified differential grazing effects between sea urchins and fishes (Ogden and Lobel 1978, McClanahan 1997, O'Leary and McClanahan 2010). This study also highlights the importance of herbivore species composition, biomass, and size-class distribution in preventing algal turf from transitioning to early and then late successional macroalgae species that may be detrimental to coral growth (Rasher and Hay 2010). Furthermore, creating a complementary grazing guild that is able to prevent macroalgae proliferation (Burkepile and Hay 2010) may not be achieved immediately after establishment of fisheries closures.

In the absence of sea urchin and fish grazing, as well as in treatments with low levels of grazing, algal succession over the ~390 days generally progressed from turf to an early dominance by blades and finely branched brown and red algae, including *Padina* and *Hypnea*. Following these macroalgae were coarsely branched and leathery macroalgae, such as *Sargassum* and *Turbinaria*. This trend is mediated by competitive interactions and life-history characteristics of algae that reflect a species' growth, reproduction, and survival rate (Grime 1977, Huston and Smith 1987, Duffy and Hay 1990). The results here agree with theory and findings from similar experiments in other regions (e.g. Carpenter 1986, Hixon and Brostoff 1996, Ceccarelli et al. 2011), indicating that early successional algae invest energy in continuous rapid growth, and invade newly opened space first rather than costly structural and chemical defenses that may mean slower rates of establishment (Duffy and Hay 1990). A concern for reefs containing a high abundance of these late successional species is that stabilizing feedbacks will strengthen the macroalgae state because they are unpalatable by the majority of herbivores (Hay 1991). This may prevent successful coral recruitment (Kuffner et al. 2006) and compromise reef growth and sustainability (McCook et al. 2001). Preventing algal shifts to dominance by unpalatable macroalgae in this experiment was ultimately dependent on the ability of sea urchins or large-bodied groups of fishes (i.e. scrapers) to maintain a surface of cropped or calcified algae.

Few studies have examined algal succession under differing levels of herbivore composition and abundance created by management, but studies do exist in the absence of herbivory. In this study, colonization by macroalgae was rapid in all treatments where grazing was absent and reached levels of ~55% cover within 100

days. These rates were similar to, or slightly greater than, previous experiments at Australian (Great Barrier Reef) and Hawaiian reefs (Hatcher and Larkum 1983, Scott and Russ 1987, Hixon and Brostoff 1996, Smith et al. 2010), but ~20% lower than at Caribbean reefs (Carpenter 1986, Morrison 1988, Sotka and Hay 2009, Ferrari et al. 2012). The number of macroalgal genera also remained relatively high in this experiment at ungrazed treatments even at the end of the sampling period as compared to other studies. Differences among regions and reefs most likely occur because of biogeographic differences in algal species composition, or differential rates of algal recruitment mediated by surrounding conditions, propagule dispersal, and herbivore community composition (Stiger and Payri 1999, Vermeij et al. 2013). Differences in physical forces such as waves and tides may also contribute to the heterogeneity between regions, as these factors can sometimes have a stronger effect than herbivory on algal communities (Gaylord et al. 2002, Lefèvre and Bellwood 2010, Ferrari et al. 2012). Therefore, the specific herbivory levels needed to prevent shifts to macroalgal dominance may be region- or site-specific, and dependent on local physical and spatial factors (Lefèvre and Bellwood 2010, Roff and Mumby 2012).

While the mechanisms by which fishing structures communities may differ among harvesting methods, regions, or ecosystems, understanding the recovery patterns of herbivores can help with conservation and harvest models aimed at increasing reef resilience to phase shifts (Halpern and Warner 2002, Gaylord et al. 2005). At the reefs in this study area, herbivore composition is primarily a function of fishing intensity. For instance, at heavily fished reefs, sea urchins have few predators and biomass can exceed 4000 kg ha^{-1} (McClanahan 1997). This is mediated by the

removal of large invertebrate-feeding fish species, like the triggerfish *Balistapus undulatus* (McClanahan 2000). When fishing is reduced or eliminated, fish biomass may exceed 1200 kg ha⁻¹ and sea urchins can drop to < 60 kg ha⁻¹ (McClanahan 1997). At these two extremes of fisheries management and herbivore dominance, I found herbivory to be high on the experimental substrata, which were dominated by algal turf (and CCA at the older government closures). I did, however, find community closures that were relatively young (< 10 years since protection) and small (< 0.5 km²) had herbivore communities somewhere between the extremes with a mixture of sea urchins and fishes. The slow recovery of herbivorous fish biomass, and in particular scraping parrotfishes, in these younger closures led to herbivory levels that were insufficient to prevent macroalgae from establishing and overtaking algal turf, eventually ending in greater than 50% cover. This does not necessarily mean community closures are ineffective management tools and may never have the grazing potential to prevent macroalgal dominance, but they may need more time to develop to be efficient conservation strategies in this area.

If results from these experiments can be scaled up to real world patterns, then *in situ* algal abundance should be low at the fished sites and within the government closures (due to high sea urchin and fish grazing, respectively), and should be high within the community closures. Fleshy macroalgae, however, developed on experimental substrata at sites where they were uncommon on existing substratum (Kuruwitu, Mradi), and *vice versa* (Mombasa). Mradi had only 8.5% macroalgae cover at the site but macroalgae quickly established on the experimental plates and moved into a late-successional assemblage consisting of larger, canopy-forming species such as *Sargassum* by the end of the experiment. This discrepancy may be

a result of the extremely high coral cover at Mradi (it is more than double that of most of the other study sites) and indicate the site is nearing a threshold where any increase in substratum availability has the potential to enter a macroalgae-dominated state (Steneck and Dethier 1994, Williams et al. 2001). At Mombasa, experimental plates developed very little macroalgae throughout the experiment, which is in contrast to existing conditions where there was 25% macroalgal cover, consisting primarily of *Sargassum*. Such discrepancies could be a result of previous events at the site where macroalgae were released from grazing pressure and able to develop into a late successional stage consisting of species resistant to herbivory (e.g. 1998 mass coral-bleaching event; McClanahan et al. 2001). Both of these examples stress the importance of the interaction between the histories of sites and existing herbivore assemblages, and how the timing of disturbances may be especially important in determining benthic conditions (Graham et al. 2013).

Grazing by sea urchins in this study prevented the development of fleshy macroalgae, however, sea urchins can have reef erosion rates greater than herbivory rates (Carreiro-Silva and McClanahan 2001) and prevent the establishment of CCA (O'Leary and McClanahan 2010). This can result in the loss of key services such as the creation of new reef material through calcification, stabilization of reefs through the binding of coral rubble, and a reduction in chemical cues important for coral recruitment (Bak 1976, Morse and Morse 1996, O'Leary et al. 2012). In this study, fishing on open access reefs may have increased the ability of reefs to resist the establishment and proliferation of macroalgae, however, trade-offs with increased rates of bioerosion should also be considered in the context of reef sustainability and growth.

The diversity of species present and the potential for a disease outbreak should also be considered at the fished reefs in this study. For instance, the major *Diadema* mortality experienced in the Caribbean in 1983 (Lessios et al. 1984) led to a 95% increase in algal abundance and 60% reduction in coral cover on Jamaican reefs (Hughes et al. 1985). Similar to reefs in this study, the fished reefs in Jamaica had relatively low levels of existing herbivorous fish biomass (Hughes et al. 1985). However, a fundamental difference between the fished reefs of the Caribbean and Kenya is the high number of sea urchin species present in Kenya, where there are nine species of herbivorous sea urchins. This provides a greater degree of redundancy within the sea urchin guild in Kenya, and may therefore buffer against a species- or genus-specific disease outbreak at fished reefs. For example, if the competitive dominant species, *Echinometra mathaei*, experienced mass mortality, subordinate species (e.g. *Diadema savignyi*, *D. setosum*, *Echinothrix diadema*) would be expected to be released from competition because the distributions of sea urchin species are dictated by trade-offs associated with resource utilization and predator susceptibility (Connell 1978, McClanahan 1998).

The establishment of fisheries closures with no additional management action (e.g. gear restrictions) may be insufficient to facilitate the recovery of herbivore populations in some areas, and fishing intensity around closures is likely to be a major factor in the success of closures (Côté et al. 2001, Lester et al. 2009, McClanahan et al. 2009, Pollnac et al. 2010, Daw et al. 2011). Large herbivores have been shown to have slow recovery times from fishing (Abesamis and Russ 2005, McClanahan et al. 2007a), and these fish are particularly important for

herbivory on a reef (Lokrantz et al. 2008). For example, parrotfishes (family Scaridae) greater than 20 cm take more than 20 years to recover (McClanahan et al. 2007a) and have a disproportionate impact on algal grazing (Lokrantz et al. 2008). Thus, it is not possible to infer the full benefits of community closures from this study since both study sites are less than 10 years old and parrotfish populations have not fully recovered. One solution to prevent macroalgal phase shifts here could be to complement fisheries closures with alternative management strategies (e.g. gear restrictions), especially when the herbivorous fish communities have already been decimated. For example, removal of certain types of nets (i.e. beach seine) may aid in fish recovery by allowing juveniles and adults time to disperse and shorten the period required for fish to return to reefs in surrounding fisheries closures (Öhman et al. 1998). The herbivore community would then only be able to maintain a macroalgal-free reef once it is beyond a grazing threshold, and this threshold will vary amongst locations (Williams and Polunin 2001, Mumby et al. 2007).

The recovery of herbivores in fisheries closures may have lasting effects on coral reef functioning and resilience by influencing algal succession and the pre-emption of space (McClanahan et al. 2011b, Hoey and Bellwood 2011). Here, the data show that large-bodied parrotfishes are vital in preventing dominance by unpalatable macroalgae where fishing is prohibited (i.e. fisheries closures and not fished reefs). However, if a reef has only large scraping herbivores and no sea urchins or small grazing fishes, macroalgae may still become established (Cheal et al. 2010). Consequently, each herbivore has an important role on the reef that contributes to complementary grazing and the prevention of macroalgal phase shifts (Burkepile and Hay 2008, 2010, 2011); while large bodied scraping herbivores are important

(Mumby 2006), so are small ones and other functional groups, such as grazers and sea urchins (Ogden and Lobel 1978, McClanahan and Shafir 1990, Ceccarelli et al. 2011). At reefs where smaller grazers and sea urchins are dominant, such as the community closures in this study, additional management strategies (e.g. gear restrictions) may be necessary to prevent a transition from turf to early then late successional macroalgae that are better defended against herbivory and erode reef resilience.

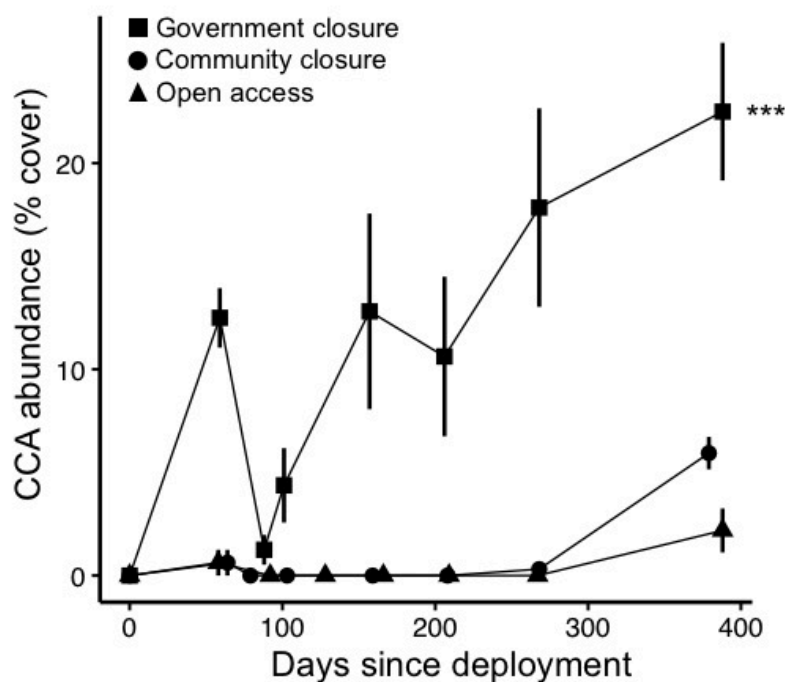
Appendix 3.1

Appendix 3.1.1. Results from ANOVAs used to evaluate the effect of fisheries management type (open access fished reef, community closure, government closure) on the existing abundance of major substratum groups and macroalgae genera. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, and df for all categories is 2.

Major substratum	F-value	p-value
Hard coral	1.64	0.247
Algal turf	7.55	*
Macroalgae	1.51	0.272
CCA	6.22	*

Macroalgae genera	F-value	p-value
<i>Cystoseira</i>	2.90	0.107
<i>Dictyota</i>	1.85	0.212
<i>Hypnea</i>	1.62	0.248
<i>Padina</i>	2.53	0.135
<i>Sargassum</i>	1.23	0.337
<i>Turbinaria</i>	4.90	*

Appendix 3.1.2. Time series of mean abundance (% cover; \pm SE) of crustose coralline algae (CCA) on the experimental plates over ~390 days. Shapes indicate fisheries management type. Data are from open treatments only and statistics are from ANOVA at the final sampling event. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.



Appendix 3.1.3. Results from MANOVAs used to evaluate the effects of fisheries management type (open access fished reef, community closure, government closure) and treatment (cage, fence, open) on algal abundance (% cover) of major groups (algal turf, upright macroalgae, CCA) and individual macroalgae (*Hypnea*, *Dictyota*, *Padina*, *Sargassum*, *Turbinaria*, *Cystoseira*) on the experimental plates. Data used in the models was from the final sampling event (~day 390). *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

Algal turf				Upright macroalgae				CCA			
	df	F-value	p-value		df	F-value	p-value		df	F-value	p-value
(Intercept)	1	1029.02	***	(Intercept)	1	413.67	***	(Intercept)	1	23.21	***
Management	2	14.11	***	Management	2	26.70	***	Management	2	11.72	***
Treatment	2	27.20	***	Treatment	2	39.15	***	Treatment	2	5.22	**
Management x Treatment	4	9.51	***	Management x Treatment	4	12.54	***	Management x Treatment	4	2.57	*

<i>Hypnea</i>				<i>Dictyota</i>				<i>Padina</i>			
	df	F-value	p-value		df	F-value	p-value		df	F-value	p-value
(Intercept)	1	15.69	***	(Intercept)	1	40.11	***	(Intercept)	1	42.65	***
Management	2	4.88	**	Management	2	11.43	***	Management	2	8.17	**
Treatment	2	0.21	0.810	Treatment	2	8.84	***	Treatment	2	3.19	*
Management x Treatment	4	1.79	0.142	Management x Treatment	4	6.18	***	Management x Treatment	4	0.58	0.681

<i>Sargassum</i>				<i>Turbinaria</i>				<i>Cystoseira</i>			
	df	F-value	p-value		df	F-value	p-value		df	F-value	p-value
(Intercept)	1	120.13	***	(Intercept)	1	6.67	*	(Intercept)	1	20.56	***
Management	2	4.22	**	Management	2	0.95	0.392	Management	2	1.50	0.230
Treatment	2	14.69	***	Treatment	2	1.68	0.195	Treatment	2	4.30	*
Management x Treatment	4	6.06	***	Management x Treatment	4	0.84	0.504	Management x Treatment	4	3.78	**

Appendix 3.1.4. Pairwise comparisons between treatments by fisheries management type of macroalgal abundance (% cover) on the experimental plates at the final sampling event.

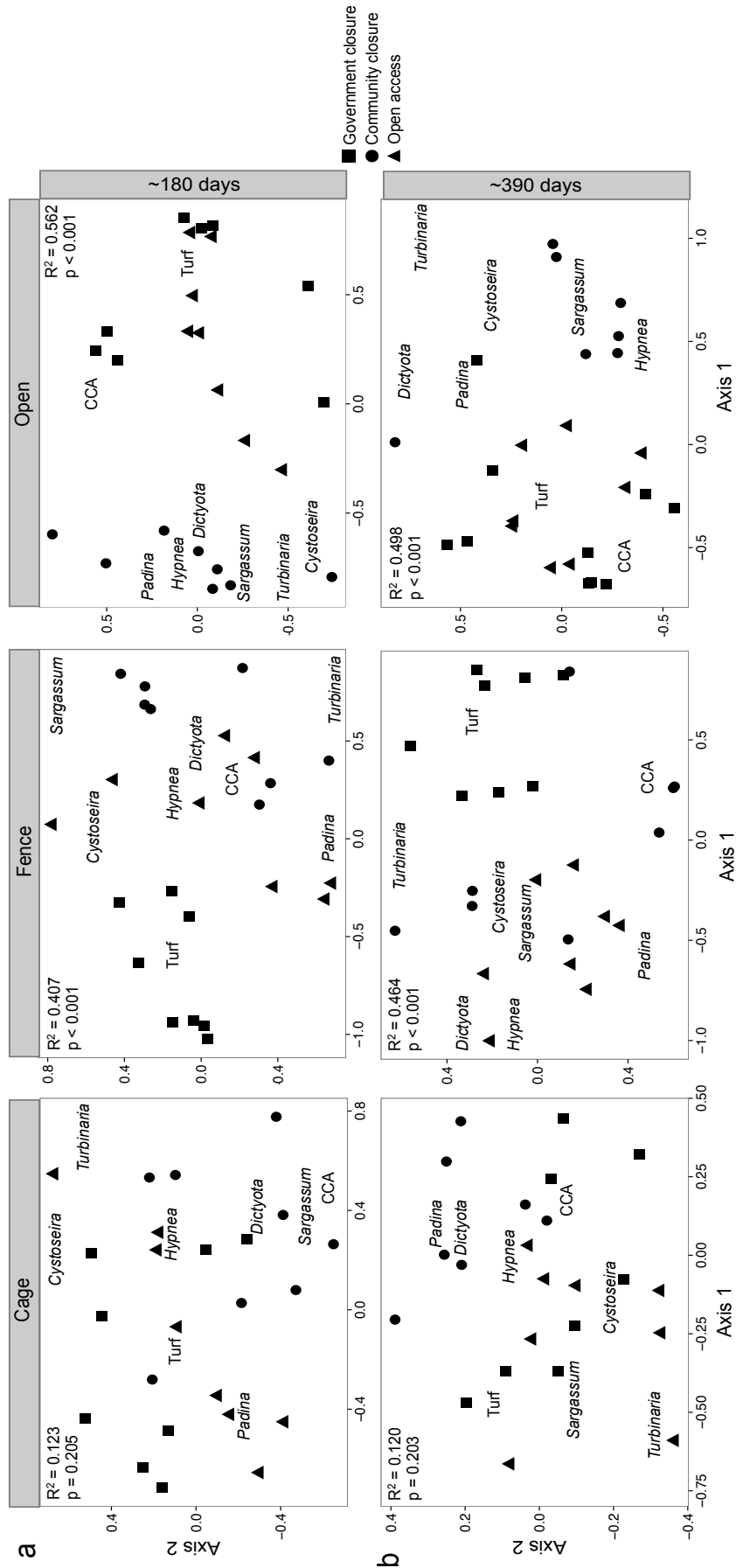
*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

Open access	Estimate	Z-value	p-value
Fence - Cage	-2.81	-0.45	0.894
Open - Cage	-54.35	-8.74	***
Open - Fence	-51.54	-8.28	***

Community closure	Estimate	Z-value	p-value
Fence - Cage	-11.18	-1.35	0.370
Open - Cage	-10.68	-1.28	0.404
Open - Fence	0.51	0.06	0.998

Government closure	Estimate	Z-value	p-value
Fence - Cage	-53.35	-14.40	***
Open - Cage	-53.59	-15.39	***
Open - Fence	-0.24	-0.07	0.997

Appendix 3.1.5. Non-metric multidimensional scaling (MDS) describing the similarity of the algal communities by treatment. Data are for (a) ~180 days and (b) ~390 days since deployment. Different shapes represent different fisheries management. Associated R² and p-values from PERMANOVAs are displayed in the upper corner of each plot. Points that are closer together in ordination space are more similar in terms of algal community composition and individual algae are overlaid to visualize dominant species. Stress for all plots was < 0.16.



CHAPTER 4

KEY CORAL REEF HERBIVORES MEDIATE MACROALGAL PERSISTENCE IN KENYAN FISHERIES CLOSURES

4.1 Introduction

Although there has been protracted debate concerning the relationship between ecosystem diversity and stability (see McCann 2000), it is believed that the functioning, stability, and productivity of ecosystems are frequently linked to biodiversity (Worm et al. 2006, Thibaut and Connolly 2013). Consequently, in theory, a greater diversity of herbivores should suppress algal overgrowth of corals on tropical coral reefs more effectively because higher species diversity increases the probability that key herbivores will be present (Bellwood et al. 2006) and that any given alga will be edible by at least one consumer (Duffy 2002). Thus, diversity combined with differential selectivity can, in principle, produce additive and complementary effects (Burkepile and Hay 2008). Present understanding of herbivore-algal relationships on coral reefs comes, however, primarily from considering herbivores collectively as members of groups described as guilds or functional groups (e.g. sea urchins, grazers, browsers, scrapers), and less is known about how the feeding preferences of individual species, or within-group dominance and diversity, influence ecosystem functioning. These findings have implications for management decisions that reflect foci on species, functional groups, or overall herbivore diversity.

On many coral reefs, multiple stressors have eroded resilience such that fleshy macroalgae have replaced reef-building corals (Gardner et al. 2003, Bruno et al. 2009). Once macroalgae dominate, it may be difficult to reverse the reef to coral-dominance because macroalgae can be unpalatable to a majority of herbivores (McClanahan et al. 1999, 2001, 2002). This creates a negative feedback that further limits coral recovery and reinforces macroalgal dominance (Mumby and Steneck 2008) with the potential to suppress the recovery of herbivores themselves (McClanahan et al. 2001, 2011c). Thus, compensatory dynamics between groups of herbivores can contribute to the stability and maintenance of macroalgae on coral reefs (Thibaut et al. 2012). There is evidence, however, that reefs can recover to a coral-dominated state in the absence of other forms of disturbances when macroalgal grazers are abundant (Grottoli et al. 2006, Smith et al. 2010), or potentially in response to pulse disturbances (Graham et al. 2013). However, differences in the effects of feeding between, and even within, groups of herbivores are still poorly understood, especially on reefs where multiple grazers co-occur.

A critical gap in understanding coral reef resilience is knowledge of the relationship between herbivore species diversity and functional redundancy (Bellwood et al. 2003, McClanahan et al. 2012, Roff and Mumby 2012). The loss of an herbivore on coral reefs can act as a release mechanism for certain macroalgae where functional redundancy is low, or where species forage selectively and exhibit markedly different feeding strategies (Bellwood et al. 2003, Hoey and Bellwood 2009). On coral reefs in east Africa, sea urchins and browsing fishes dominate as a function of fishing pressure, creating two groups of macroalgal consumers and associated life history and foraging behaviors (McClanahan et al. 1994, Sandin and McNamara 2012). Sea

urchins are spatially constrained herbivores that consume algal turfs and macroalgae and select food based mostly on abundance and habitat rather than palatability or nutritional value (Ogden and Lobel 1978). In contrast, herbivorous fishes are vagile and can therefore search and exhibit greater feeding selectivity in their diet (Mantyka and Bellwood 2007, Burkepile and Hay 2008, Rasher et al. 2013). Both types of herbivores influence coral settlement and recruitment, and therefore have consequences for reef sustainability (O’Leary and McClanahan 2010, O’Leary et al. 2013). As a result, the resilience of a reef and persistence of macroalgae following a phase shift may depend on the types of herbivore present and the intensity, complementarity and functional redundancy of their feeding habitats (Micheli and Halpern 2005).

Levels of redundancy among coral reef fishes may be lower than expected even in areas with high diversity (Bellwood et al. 2003) and can change ontogenetically within species (Plass-Johnson et al. 2013). Here, I tested the hypothesis that species diversity has a positive relationship with functional redundancy (Petchey and Gaston 2002) for macroalgal browsers on coral reefs, and ask what this means for macroalgal persistence and the reversal of phase shifts. To do this, I investigated how herbivore diversity and identity influence consumption and persistence of macroalgae on the fringing coral reefs of Kenya. Using a variety of experiments, I examined: (a) the consumption and feeding selectivity of browsing herbivorous fishes, (b) the efficacy of browsing fishes and sea urchins in removing previously established macroalgae, and (c) whether a relationship exists between herbivore diversity and macroalgal diversity and abundance on these reefs. To achieve these objectives, I used selectivity assays and underwater video cameras in a no-take

marine reserve, as well as experimental algal growth plates and visual surveys across reefs that represent a gradient in herbivore assemblages.

4.2 Materials and methods

4.2.1 Macroalgal grazing selectivity of herbivorous fishes

To determine grazing selectivity and the susceptibility of macroalgae to herbivorous fish, I collected six common macroalgal genera from fished reefs and deployed them in a deeper channel (~4 m) within a no-take fisheries closure (Katana; -3.94166°, 39.7823°) with underwater digital video cameras, and quantified loss of mass relative to caged controls over a 24 h period. Macroalgae selected for the experiment were: *Sargassum*, *Dictyota*, *Hypnea*, *Padina*, *Cystosieria*, and *Turbinaria*. These six macroalgal genera were chosen because they are among the most commonly found macroalgae on reefs along the coast of Kenya (Table 2.1), encompass a wide range of morphological and functional forms, and represent the Rhodophyta and Phaeophyta taxonomic divisions. I did not use specific macroalgal species in this experiment because species-level identification can be difficult in the field, especially within the rhodophytes, and algal taxonomy in Kenya and the Indo-Pacific is not well resolved. Individual algae were chosen and care taken to ensure that the same species was used within each genera, as well as to reflect common sizes of each genus found on Kenyan reefs. Furthermore, algae were visually inspected to roughly standardize size among individuals within genera. Excess water was removed from each alga using a salad spinner (10 revolutions) and the plant was then weighed in the field to the nearest 0.01g. Initial masses of macroalgal genera were (g; mean \pm SE): *Sargassum* (1.79 \pm 0.08), *Dictyota* (0.89 \pm 0.07), *Hypnea* (0.90 \pm 0.07), *Padina* (0.95 \pm 0.05), *Cystoseira* (1.17 \pm 0.08), and *Turbinaria* (1.28 \pm 0.07). Algae were

then transported in plastic self-sealed bags and one thallus of each of the six macroalgal genera was attached in random order approximately 10 cm apart from one another on an 80 cm section of nylon rope. Each alga was held in place using clothespins attached to the rope and weighed down using 200g weights. Paired treatment (exposed to herbivores) and control (caged) ropes were assembled in the same manner ($n = 5$). Cages for control lines were made from plastic mesh material (2.5 x 2.5 cm square holes) and placed over assays to prevent browsing from all large-bodied herbivores (Scott and Russ 1987).

Each experimental trial began by placing paired treatment and control ropes along the reef in areas dominated by coral and accessible to herbivores during both low (~1 m depth) and high (~4 m depth) tidal periods. Paired treatment and control ropes were attached to dead coral fragments within 1 m of one another, and deployed on the substratum at 10-15 m intervals. Assays were deployed at calm periods between 0800 – 1000 h during neap tidal cycles. The experiment was not run during spring tidal cycles because of the strong currents associated with the ~4 m tidal range in Kenya. Assays were collected after 24 h and weighed as for initial mass. Mass consumed, M_c , by herbivores was calculated as

$$M_c = \left[T_i * \left(\frac{C_f}{C_i} \right) \right] - T_f$$

where T_i and T_f were the initial and final masses (g; respectively) of a treatment alga exposed to herbivores, and C_i and C_f were the initial and final masses (g), respectively, of its paired control. Percentage consumed was calculated to allow

comparisons among macroalgal genera. Thirteen trials were performed during three separate neap tidal cycles in the calm, northeast monsoon season (August and September) in 2012, each with five paired treatment and control assay lines that were haphazardly moved along the reef prior to each trial.

Herbivore feeding preferences and their rate of grazing on macroalgae may depend on the identity and quantity of other available resources. Therefore, when multiple macroalgae (i.e. treatments) are simultaneously offered to herbivores in multiple-choice feeding assays, they may not be independent and therefore violate the assumptions of ANOVA procedures (Roa 1992, Lockwood 1998). Alternative approaches are available to address this issue, such as the rank-based Friedman's test, or Lockwood's (1998) modification of the multivariate Hotelling's T² test (Roa 1992, Lockwood 1998). Data from my selectivity assays could not be transformed to meet multivariate assumptions; therefore I analyzed them with Friedman's test (Roa 1992, Lockwood 1998). Significant differences were further evaluated using Friedman's post-hoc multiple comparison tests.

Stationary underwater video cameras (GoPro; n = 2-3) were used during each trial to identify herbivores feeding on the macroalgal assays. Cameras were deployed at the onset of each trial (0800 – 1000 h) and positioned 1-2 m from a haphazardly selected treatment rope. After deployment, filming continued without disturbance for ~4 h per trial. In total, 30 treatment assays were filmed (~128 h) over the 13 trials. All video footage was viewed and the number of bites taken on the experimental assays by each species of fish was counted and scaled (bites h⁻¹). An example of this footage can be viewed at <http://vimeo.com/austinhumphries/selectivity> (password:

selectivity). Videoed feeding assays ($n = 2-3$) were conducted on different treatment ropes concurrently within a trial, and therefore may not be independent, so I averaged results for each fish species within a trial as one replicate ($n = 13$ replicates). Feeding rates could not be transformed to meet assumptions of ANOVA because of the high frequency of zeros, so I conducted rank-based Friedman's tests for each of the six dominant browsing herbivores (Roa 1992, Lockwood 1998). These six herbivore species accounted for $> 95\%$ of all recorded bites on macroalgae. Significant differences were further evaluated using Friedman's post-hoc multiple comparison tests.

I surveyed existing herbivore assemblages at Katana, the no-take fisheries closure, using methods described in Chapter 2 (section 2.2.2).

4.2.2 Efficacy of macroalgal browsers

See Chapter 1 for site descriptions and locations (Fig. 1.1).

To assess the efficacy of herbivores in browsing previously established macroalgae, I allowed algae to grow on experimental algal growth plates for over one year (~390 days) before allowing access by herbivores. This amount of time was chosen to allow macroalgae the opportunity to fully develop into a late stage of succession and mimic substratum that had gone from being dominated by algal turfs and coral, to one of dominance by large macroalgae. Cages were made from plastic mesh material (2.5 x 2.5 cm square holes) and attached to bare substratum using u-bolts. Cages were approximately 1 x 1 x 0.5 m (L x W x H) in size. Previous work found that cages similar to these had no significant effect of on algal standing crop or

species composition other than the effect of excluding grazers (Scott and Russ 1987). Plates were made from ~2.5 cm cross-sections of dead massive *Porites* coral (mean plate size [\pm SE] was $177 \pm 15 \text{ cm}^2$, $n=96$ plates) and had flat surfaces but irregularly shaped edges (Appendix 2.1.2). Holes were drilled in individual plates and attached to plastic cage flooring at least 5 cm apart in sets of 4 plates per block. Blocks ($n = 4 \text{ site}^{-1}$) were placed > 20 m apart from one another (Fig. 2.1).

After cages were removed, all experimental plates were left *in situ* and exposed to grazers for ~90 days. Description of the algal community growing on the plates was achieved by taking digital photographs every ~14 days and as described in Chapter 3 (section 3.2.3).

I evaluated differences in abundance (percentage cover) of algal groups from the first to the last sampling event using separate one-way ANOVAs for each site. Total upright macroalgae (all fleshy algae combined) was analyzed, as well as individual genera. Data were log-transformed when necessary to improve spread, achieve normality, and alleviate heterogeneity of variance among the data. Model diagnostics were performed as described above and an autocorrelation residual structure (AR-1) was used to account for non-independence (Zuur et al. 2009).

To determine how the algal community structure changed through time on the experimental plates, I performed multivariate analyses. The macroalgal abundance data were used to create a matrix of Bray-Curtis similarity measures for the initial and final sampling events at each site. This matrix was then analyzed using permutational analysis of variance (PERMANOVA) with fisheries management as a

fixed effect and site nested within management type. PERMANOVA analyzes distance measures in a linear model with categorical variables to test for significance of factors ($n = 999$ permutations). I then used non-metric multidimensional scaling (MDS) ordination to visualize similarities in algal community structure across sites and over time. Ordination showed the presence of contrasting algal communities between the government closure sites, Mombasa and Malindi, at the final sampling event. Therefore, to investigate key fish species mediating these differences, I ran a similarity of percentages (SIMPER) analysis using a subset of the fish species matrix (only browsers). All multivariate analyses were done with the R package “vegan” (v. 2.0-8; Oksanen et al. 2013).

4.2.3 Herbivore diversity and macroalgal persistence

Herbivorous fishes, sea urchins, and benthic conditions for all sites were visually surveyed following methods in Chapter 2 (section 2.2.2). Along with abundance and biomass calculations, I also determined the average diversity of macroalgal and herbivore species at each site by calculating their Shannon’s H in each transect.

To evaluate differences in macroalgal-browsing herbivores among sites, I used separate one-way ANOVAs on sea urchin and browser fish biomass, as well as total herbivore diversity (Shannon’s H). Sea urchin data were log-transformed and significant ANOVAs were followed by individual contrasts using Tukey tests to compare sites. Model diagnostics were performed as described above. I also used linear regressions to determine whether herbivore diversity (sea urchins and fishes combined) could be used as a predictor of existing macroalgal abundance and diversity, as well as to examine the relationship between macroalgal abundance and

diversity. All data analyses were performed using the program “R” (v. 2.15.1; R Development Core Team 2013).

4.3 Results

4.3.1 Macroalgal grazing selectivity of herbivorous fishes

Mean overall herbivorous fish abundance at Katana was 95.5 ind 500m⁻², and individual species ranged from 0.3 to 17.5 ind per 500m⁻² (Table 4.1). Mean overall biomass of herbivorous fishes was 460.8 kg ha⁻¹, and individual species ranged from 0.1 to 81.9 kg ha⁻¹. Browser species that feed primarily on macroalgae accounted for 32% of the overall herbivorous fish biomass, with 147.9 kg ha⁻¹, and 41.3 ind 500m⁻².

Consumption rates of transplanted macroalgae by fishes were variable, with a significant effect of algal genera ($p < 0.001$; Fig. 4.1). Although homogeneous groups formed a continuum, it is clear that *Padina* was consumed at higher rates than other macroalgae (51.7% 24h⁻¹), and *Cystoseira* (which was not significantly lower than *Padina*), *Hypnea*, and *Sargassum* were consumed at intermediate rates, of between 21 and 39% 24h⁻¹. *Dictyota* and *Turbinaria* were little consumed (10.5% and 7.1% 24h⁻¹, respectively).

I quantified a total of 1,472 fish bites on the six genera of macroalgae in the selectivity assays. There were generally very clear algal preferences among fishes, many preferring *Padina*, *Cystoseira*, or *Hypnea*. The parrotfishes *Calotomus carolinus* and *Leptoscarus vaigiensis* fed exclusively on *Padina*, whereas the unicornfish *Naso unicornis* fed exclusively on *Sargassum* ($p < 0.001$, Fig. 4.2). Both species of rabbitfishes, *Siganus sutor* and *S. argenteus*, fed mostly on *Cystoseira*,

with some feeding on *Hypnea* ($p < 0.05$). The surgeonfish *Ctenochaetus striatus* bit *Cystoseira* and *Hypnea* mostly, but also some *Dictyota* and *Padina* ($p = 0.05$), however, videos revealed that consumption of macroalgae by this fish was rare, as they were observed spitting out the material from these bites.

Table 4.1. Mean (\pm SE) herbivorous fish abundance (ind 500m⁻²) and biomass (kg ha⁻¹) at Katana, the experimental selectivity assay study site, which is a no-take fisheries closure.

Family	Species	Function	Abundance	Biomass
Acanthuridae	<i>Acanthurus dussumieri</i>	Grazer	6.8 (0.3)	51.9 (4.5)
Acanthuridae	<i>Acanthurus leucosternon</i>	Grazer	0.5 (0.5)	0.2 (0.2)
Acanthuridae	<i>Acanthurus nigricauda</i>	Grazer	2.3 (1.3)	7.9 (1.5)
Acanthuridae	<i>Acanthurus nigrofuscus</i>	Grazer	9.3 (1.8)	81.9 (15.7)
Acanthuridae	<i>Acanthurus tennentii</i>	Grazer	1.8 (0.8)	9.2 (2.2)
Acanthuridae	<i>Acanthurus triostegus</i>	Grazer	3.3 (0.8)	8 (1.8)
Acanthuridae	<i>Acanthurus xanthopterus</i>	Grazer	0.8 (0.3)	4.8 (2.8)
Acanthuridae	<i>Ctenochaetus striatus</i>	Grazer	17.5 (0)	60.3 (3.6)
Acanthuridae	<i>Ctenochaetus strigosus</i>	Grazer	0.3 (0.3)	0.1 (0.1)
Acanthuridae	<i>Naso annulatus</i>	Browser	8.3 (2.8)	19.8 (0.3)
Acanthuridae	<i>Naso brevirostris</i>	Browser	3 (0.5)	7 (3)
Acanthuridae	<i>Naso unicornis</i>	Browser	4.3 (1.8)	19.3 (6.4)
Acanthuridae	<i>Zebrasoma scopas</i>	Grazer	2 (0)	2.2 (0)
Ephippidae	<i>Platax teira</i>	Browser	1 (0.5)	3.4 (1.7)
Kyphosidae	<i>Kyphosus vaigiensis</i>	Browser	2 (0.5)	11.1 (2.9)
Pomacanthidae	<i>Centropyge multispinis</i>	Grazer	0.3 (0.3)	3.3 (3.3)
Labridae	<i>Calotomus carolinus</i>	Browser	8.3 (0.8)	42.2 (4.2)
Labridae	<i>Cetoscarus bicolor</i>	Scraper	0.5 (0)	1.6 (0)
Labridae	<i>Leptoscarus vaigiensis</i>	Browser	4 (1)	14.8 (3.7)
Labridae	<i>Scarus frenatus</i>	Scraper	1 (0.5)	10.6 (4.6)
Labridae	<i>Scarus ghobban</i>	Scraper	5.8 (0.8)	52.1 (2.3)
Labridae	<i>Scarus psittacus</i>	Scraper	0.3 (0.3)	1.1 (1.1)
Labridae	<i>Chlorurus sordidus</i>	Scraper	2.5 (0.5)	17.8 (3.6)
Siganidae	<i>Siganus sutor</i>	Browser	10.5 (1.5)	30.2 (4.8)

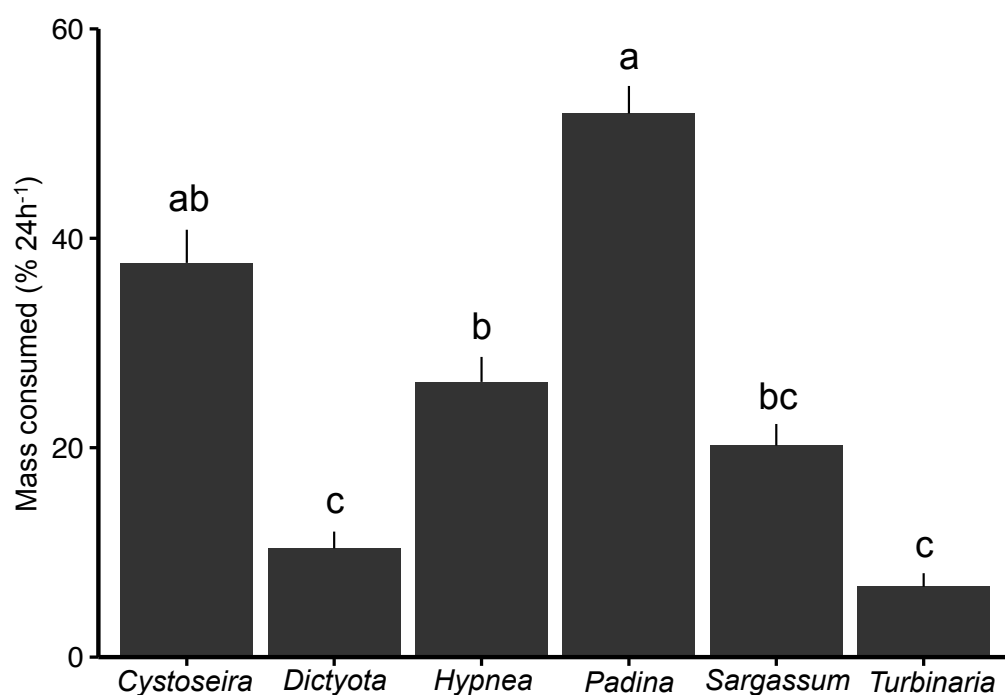


Fig. 4.1. Mass of macroalgae removed (% 24h⁻¹; mean + SE) by herbivorous fishes from experimental selectivity assays. Data were evaluated using Friedman's test and letters indicate homogeneous subgroups. n = 13.

4.3.2 Efficacy of macroalgal browsers

The abundance and species composition of macroalgae growing on the experimental algal growth plates differed strongly among management types. Herbivores caused significant decreases in overall macroalgal cover from first to last measurements at open access sites, Kanamai ($p < 0.01$) and Ras Iwatine ($p < 0.001$), and the government closures, Mombasa ($p < 0.05$) and Malindi ($p < 0.01$), but not the community closures, Kuruwitu ($p = 0.73$) and Mradi ($p = 0.52$; Fig. 4.3). Total macroalgal cover was reduced from initial levels of between 50 and 70%, to ~15% or lower at the two open access reefs and one government closure site, Malindi, though the effect was weaker (cover > 25% after 90 days) at the other government closure site, Mombasa. Macroalgal cover at the community closure sites

remained relatively constant throughout the experiment, ranging from approximately 50 to 70%.

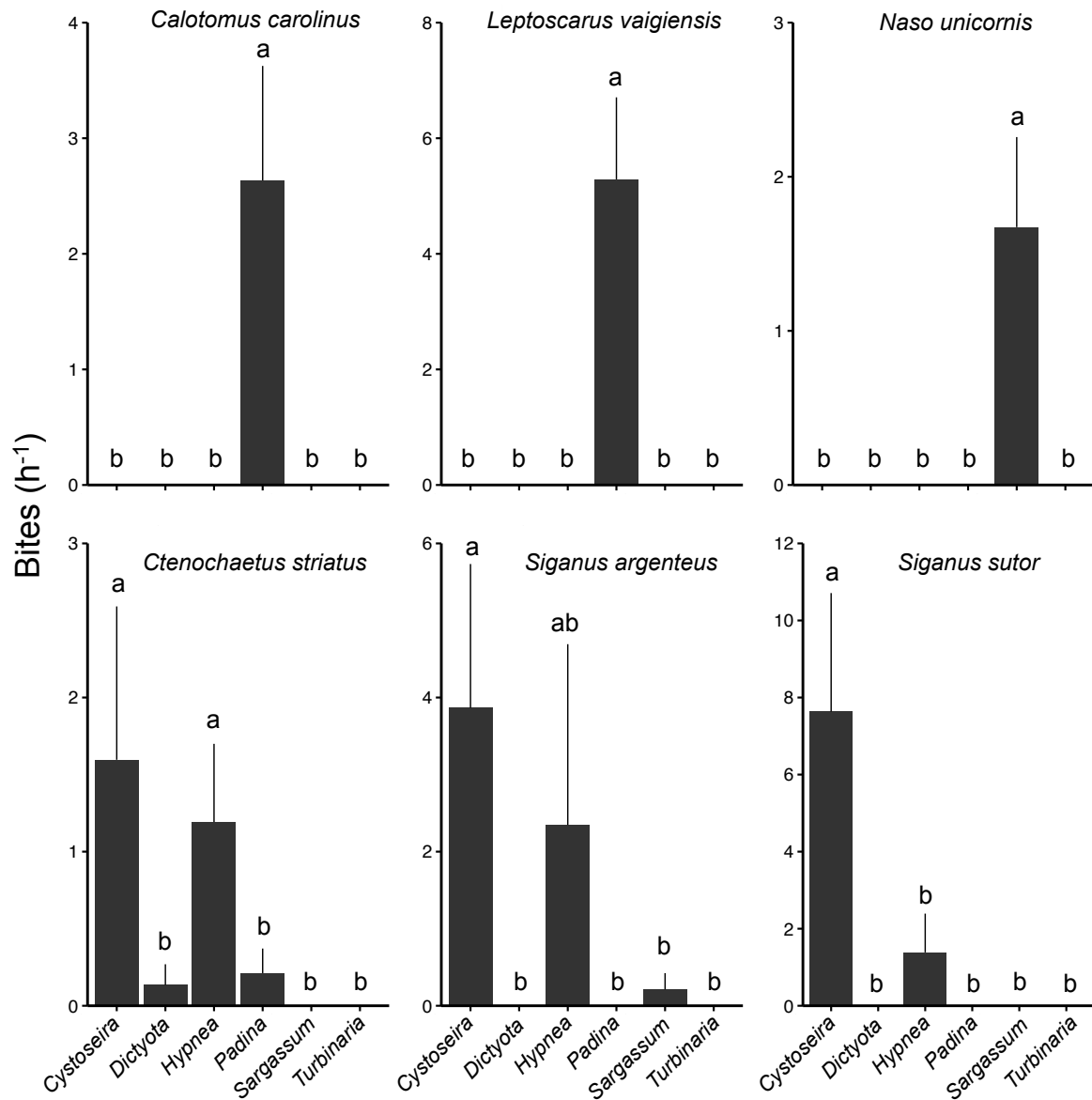


Fig. 4.2. Mean bite rate per hour (+ SE) of fish on experimental selectivity assays of macroalgae. Data for each consumer were analyzed separately using Friedman's test and letters indicate homogeneous subgroups. Note different y-axis scales. n = 13.

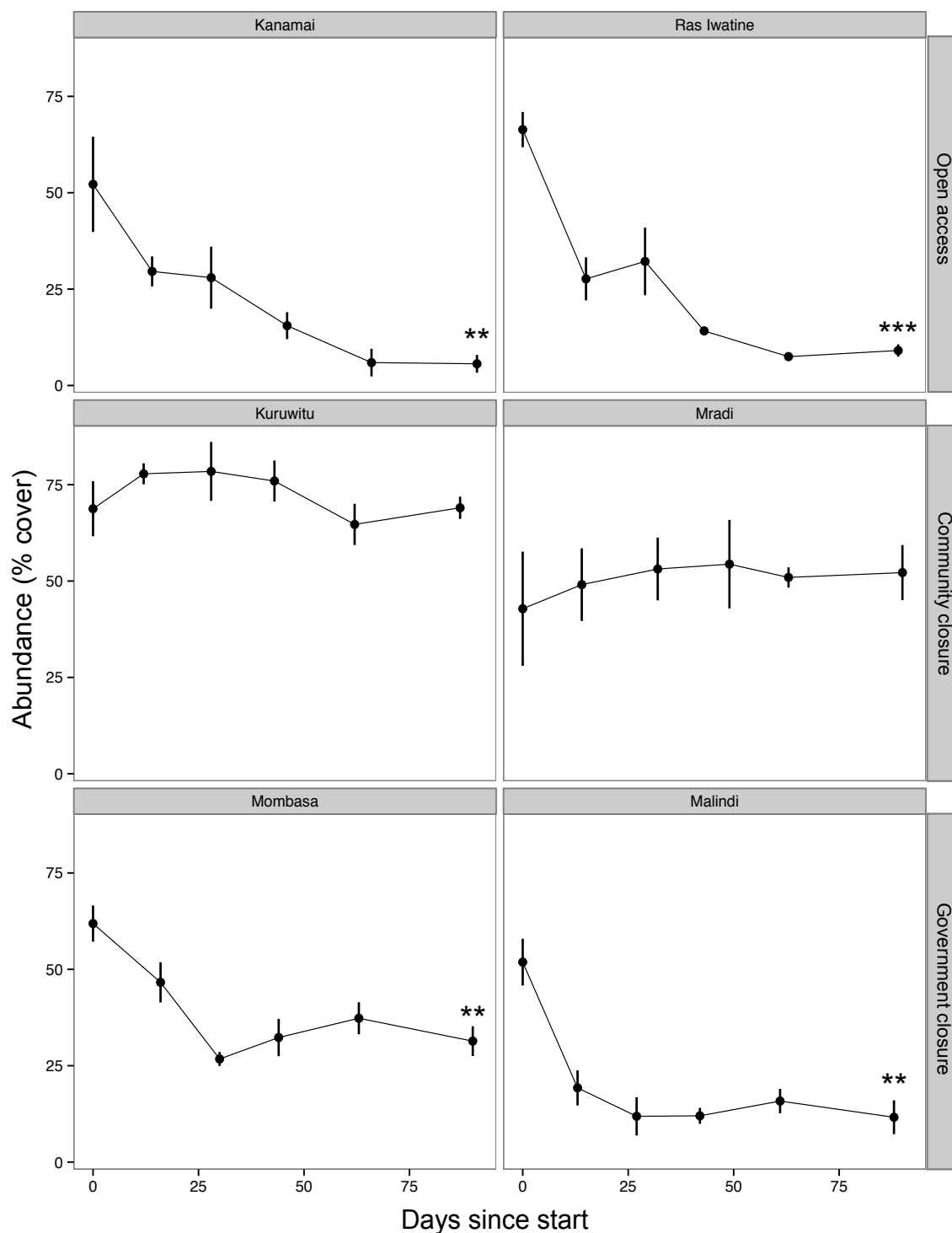


Fig. 4.3. Time series of the mean abundance (% cover; \pm SE) of all macroalgae on the experimental substrata at the six study sites by fisheries management type over a ~90 day period. Algae were allowed to grow on plates with no herbivory (in cages) for over one year before starting the experiment. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

Consumption of specific macroalgal genera on the plates also differed significantly among fisheries management treatments (Fig. 4.4 and Table 4.2). Consumers at the open access sites reduced cover of *Dictyota* and *Sargassum* ($p < 0.05$), and all other macroalgal genera were consumed except *Turbinaria* and *Hypnea* at Kanamai.

Herbivores at the community closures had little effect on macroalgal cover, with the exception of *Padina* at Kuruwitu, which decreased significantly ($p = 0.001$). In contrast, *Sargassum* cover increased significantly at Kuruwitu ($p = 0.002$), whereas other macroalgal genera either increased or decreased only slightly. All macroalgal genera were consumed and their abundances reduced at the government closures except *Sargassum* at Mombasa and *Turbinaria* at Malindi, both of which increased in cover.

Algal community composition at both community closures and one government closure site, Mombasa, converged, resulting in similar algal communities at the final sampling event (~ day 90), even though they had different communities at day 0 (Fig. 4.5). The successional trajectories of these three sites were also much shorter than the fished sites and the other government closure site, Malindi, indicating algal assemblages did not change considerably through time. Mombasa experienced a significant change in algal community structure, but the resulting assemblage consisted primarily of *Sargassum*. SIMPER analysis indicated that unicornfishes, *Naso elegans* and *N. unicornis*, as well as the sea chub, *Kyphosus vaigiensis*, contributed most to dissimilarities between the browser fish community assemblages at the two government closures (Table 4.3).

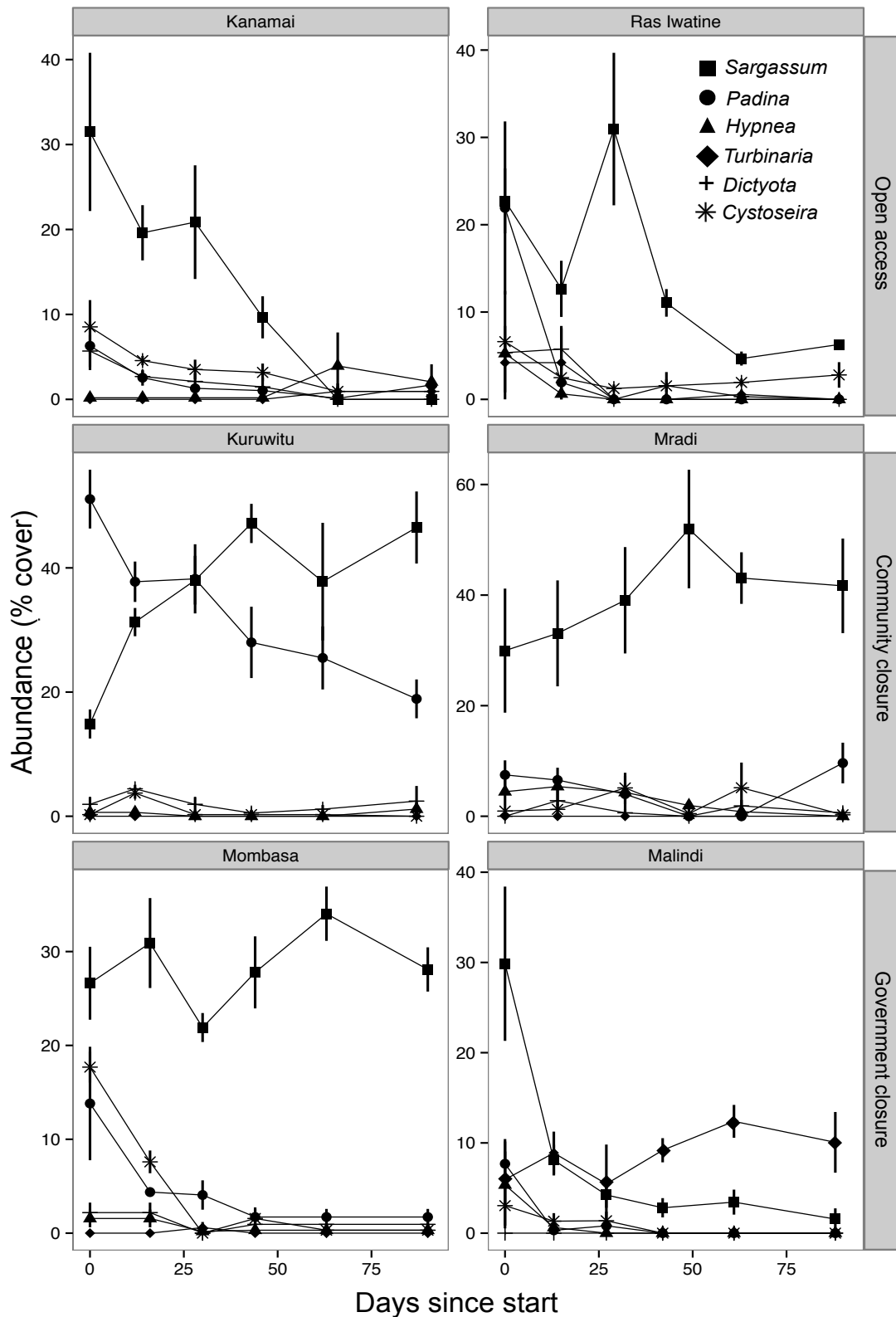


Fig. 4.4. Time series of the mean percentage cover (\pm SE) of individual macroalgal genera on the experimental coral plates at the six study sites by fisheries management type over a ~90 day period. Shapes indicate macroalgal genera. Algae were allowed to grow on plates with no herbivory (in cages) for over one year before starting the experiment. Notice different y-axis scales.

Table 4.2. Results of ANOVAs used to evaluate the effect of time (days since deployment) on percentage cover of individual macroalgal genera on experimental plates at each study site. An overall increase in abundance is indicated by a '+' symbol and a decrease by a '-' symbol. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.

	Open access		Community closure		Government closure					
	Kanamai		Kuruwitu		Mombasa		Malindi			
	F-value	p-value + / -	F-value	p-value + / -	F-value	p-value + / -	F-value	p-value + / -		
<i>Dictyota</i>	8.98	*	0.04	0.855	1.00	0.356	1.04	0.346	NA	NA
<i>Hypnea</i>	0.82	0.400	0.16	0.700	3.04	0.132	1.60	0.253	1.23	0.310
<i>Padina</i>	2.34	0.177	32.14	***	0.22	0.652	3.93	0.095	7.86	*
<i>Sargassum</i>	11.43	*	25.58	**	0.69	0.438	0.11	0.757	10.75	**
<i>Turbinaria</i>	1.00	0.356	NA	NA	NA	NA	NA	NA	NA	0.403
<i>Cystoseira</i>	5.60	0.056	1.00	0.356	0.48	0.516	107.14	***	1.90	0.217

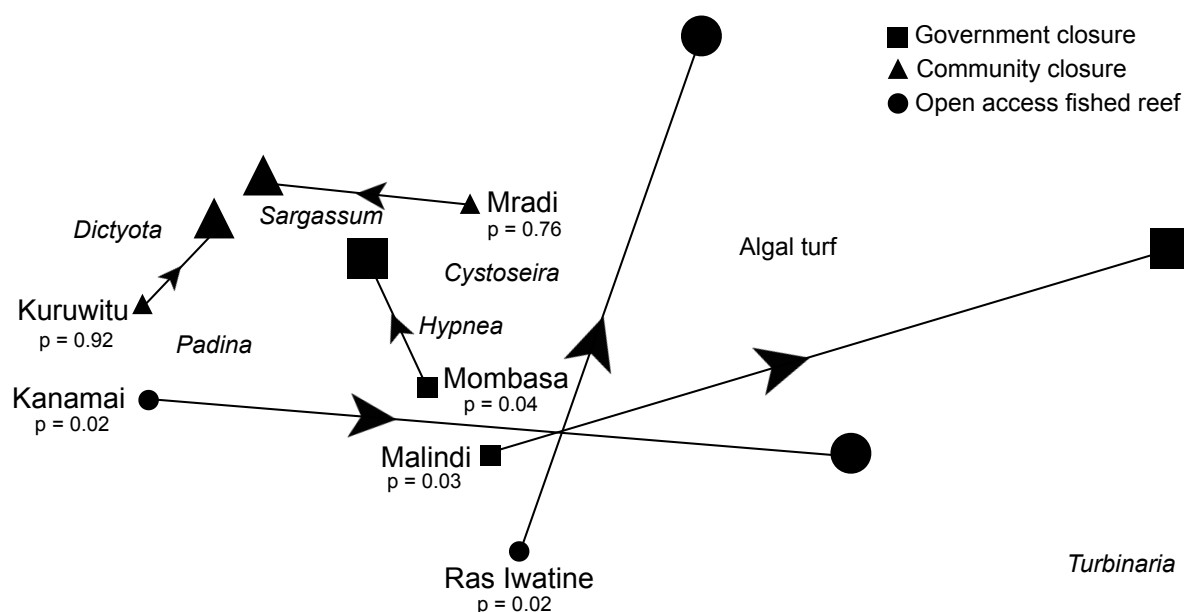


Fig. 4.5. Non-metric multidimensional scaling analysis (MDS) of successional trajectories showing how the similarity of algal communities changed on the experimental plates from when the cages were removed to the final sampling event (~90 days) at the six study sites. Shapes represent fisheries management type. Points that are closer together in ordination space are more similar in terms of algal community composition, and individual algae are overlaid to visualize dominant assemblages. The points adjacent to site labels indicate the initial algal community present on the experimental plates (day 0), and the enlarged data points indicate the algal community present at the final sampling event (day 90). Arrowheads on lines indicate direction of successional change and are scaled to the magnitude of change in the algal community. Distance matrices were analyzed separately for each site using permutational analysis of variance (PERMANOVA; $n = 999$ permutations). Stress = 0.11.

Table 4.3. Results from similarity of percentages analysis (SIMPER) of browser fish taxa biomass (kg ha^{-1}) contributing to the dissimilarity (%) between the two government closure sites, Mombasa and Malindi. Cutoff for low contributions was 70%.

Family	Species	Dissimilarity
Acanthuridae	<i>Naso elegans</i>	18.9
	<i>Naso unicornis</i>	17.5
Kyphosidae	<i>Kyphosus vaigiensis</i>	16.1
Siganidae	<i>Siganus argenteus</i>	13.9
	<i>Siganus sutor</i>	11.8
	Total	78.2

4.3.3 Herbivore diversity and macroalgal persistence

Browser fish and sea urchin assemblages differed among sites and fisheries management (Table 4.4). Sea urchins at the two open access fished reefs were abundant, with a mean biomass of 4401 - 6095 kg ha⁻¹, and species diversity was relatively low (1.12 and 1.07). These reefs had very few fish, and total fish biomass was between 71 - 97 kg ha⁻¹ (Fig. 2.2), with *Siganus sutor* at Ras Iwatine being the only species of fish browser present at either site. The community closures had greater browser fish biomass but fewer urchins than the open access fished reefs; Kuruwitu had a total fish biomass of 364 kg ha⁻¹ and a sea urchin biomass of 2591 kg ha⁻¹, whereas Mradi had 440 kg ha⁻¹ of fish and 2664 kg ha⁻¹ of sea urchin biomass. Herbivores accounted for 47 to 49% of the total fish biomass, however, less than 5% (22 kg ha⁻¹) of total fish biomass at either site consisted of browsers. Sea urchin diversity was high at these two sites (1.37 and 1.42) and only 2 fish browser species were present at Kuruwitu, whereas Mradi had a more diverse assemblage, with 5 species. The two government closure sites had the highest fish biomass and diversity, and lowest sea urchin biomass and diversity. The sea urchin community at Mombasa consisted of mostly *Echinothrix diadema* and Malindi had the fewest sea urchins of any site, with less than 61 kg ha⁻¹. Mombasa had a mean fish biomass of 954 kg ha⁻¹, with 460 kg ha⁻¹, and 48% of that was herbivores. Browsers dominated the herbivorous fish guild at Mombasa (187 kg ha⁻¹); *Calotomus carolinus* was the most abundant browser at Mombasa. Malindi had the highest fish biomass of all sites with 1165 kg ha⁻¹, of which almost 50% were herbivores. Browsers represented 180 kg ha⁻¹ at Malindi and consisted of 8 species, which was the most speciose of any site.

Table 4.4. Mean biomass (kg ha⁻¹; ± SE) of (a) browser fish and (b) sea urchin species at each experimental plate study site.

a) Fish Family	Species	Open access			Community closure			Government closure		
		Kanamai	Ras Iwatine	Mradi	Kuruwitu	Mradi	Mombasa	Malindi		
Acanthuridae	<i>Naso annulatus</i>	0 (0)	0 (0)	2.5 (2.5)	0 (0)	2.5 (2.5)	3.5 (3.5)	22.5 (10.2)		
	<i>Naso elegans</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	15.8 (2.8)		
	<i>Naso unicornis</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	10.5 (6.8)		
Labridae	<i>Calotomus carolinus</i>	0 (0)	0 (0)	5.6 (1.4)	0 (0)	5.6 (1.4)	92.2 (46.9)	46.4 (10.2)		
	<i>Leptoscarus vaigiensis</i>	0 (0)	0 (0)	3.5 (3.5)	7.8 (0.8)	3.5 (3.5)	24.9 (9.9)	26.1 (10)		
Siganidae	<i>Siganus sutor</i>	0 (0)	1.8 (1.8)	2.8 (0.9)	8.7 (5)	2.8 (0.9)	0 (0)	24 (24)		
	<i>Siganus argenteus</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	61.2 (26.9)	15 (15)		
Ephippidae	<i>Platax teira</i>	0 (0)	0 (0)	2.1 (2.1)	0 (0)	2.1 (2.1)	1.1 (1.1)	0 (0)		
Kyphosidae	<i>Kyphosus vaigiensis</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	9.7 (3.4)		
Total		0 (0)	1.8 (1.8)	21.5 (2.6)	16.5 (5.8)	21.5 (2.6)	189.2 (84.5)	177.4 (7.7)		
b) Sea urchins Family	Species	Open access			Community closure			Government closure		
		Kanamai	Ras Iwatine	Mradi	Kuruwitu	Mradi	Mombasa	Malindi		
Diadematidae	<i>Diadema savignyi</i>	562.5 (340.3)	841.2 (33.8)	645.8 (48.6)	534.7 (34.7)	645.8 (48.6)	20.8 (6.9)	20.8 (6.9)		
	<i>Diadema setosum</i>	541.7 (375)	441.2 (307.8)	179.2 (37.5)	816.7 (166.7)	179.2 (37.5)	0 (0)	16.7 (16.7)		
	<i>Echinothrix calamaris</i>	0 (0)	0 (0)	154.2 (38.6)	0 (0)	154.2 (38.6)	38.6 (0)	0 (0)		
	<i>Echinothrix diadema</i>	115.7 (38.6)	2956.3 (912.8)	1079.6 (192.8)	38.6 (38.6)	1079.6 (192.8)	983.2 (19.3)	19.3 (19.3)		
Echinometridae	<i>Echinometra mathaei</i>	4530.2 (1116.5)	68.2 (2.2)	352.9 (88.9)	768.2 (474.8)	352.9 (88.9)	148.5 (42.2)	1.8 (1.8)		
	<i>Echinostrephus molaris</i>	0 (0)	2.9 (0.1)	0.2 (0.2)	0 (0)	0.2 (0.2)	6 (1.8)	1.8 (1)		
Stomopneustidae	<i>Stomopneustes variolaris</i>	0 (0)	11.7 (3.3)	6.3 (6.3)	4.2 (4.2)	6.3 (6.3)	8.3 (8.3)	0 (0)		
Toxopneustidae	<i>Tripneustes gratilla</i>	345.2 (151.4)	79.8 (5)	51.5 (27.2)	417.8 (6.1)	51.5 (27.2)	163.5 (151.4)	0 (0)		
	<i>Toxopneustes pileolus</i>	0 (0)	0 (0)	2.8 (2.8)	11.1 (11.1)	2.8 (2.8)	11.1 (0)	0 (0)		
Total		6095.2 (591.2)	4401.1 (1187.5)	2472.4 (192)	2591.2 (402.8)	2472.4 (192)	1380 (160.8)	60.4 (29.9)		

Existing benthic cover differed among sites and fisheries management types, with the highest hard coral and lowest macroalgal cover at Mradi and Kanamai (hard coral: 46 and 34.8%, macroalgae: 8.5 and 0.9%, respectively; Table 2.1). Ras Iwatine had the lowest hard coral abundance with 7.1%, and Mombasa had the highest macroalgal abundance with 25.7%. Crustose coralline algae (CCA) was highest at Malindi with 20.4% cover. Algal turf abundance was highest at the open access reefs, Kanamai and Ras Iwatine, with greater than 42% cover.

Herbivore (fishes and sea urchins combined) diversity in the field was generally lower at fished reefs versus unfished reefs, and greatest in the old and larger government managed closures ($p < 0.001$; Appendix 4.1.1). Macroalgal diversity displayed a non-significant, negative relationship with macroalgal abundance ($R^2 = 0.10$, $p = 0.31$), as did herbivore diversity and macroalgal diversity ($R^2 = 0.33$, $p = 0.06$; Fig. 4.6). In contrast, herbivore diversity displayed a non-significant, positive relationship with macroalgal abundance across the six study sites ($R^2 = 0.22$, $p = 0.12$).

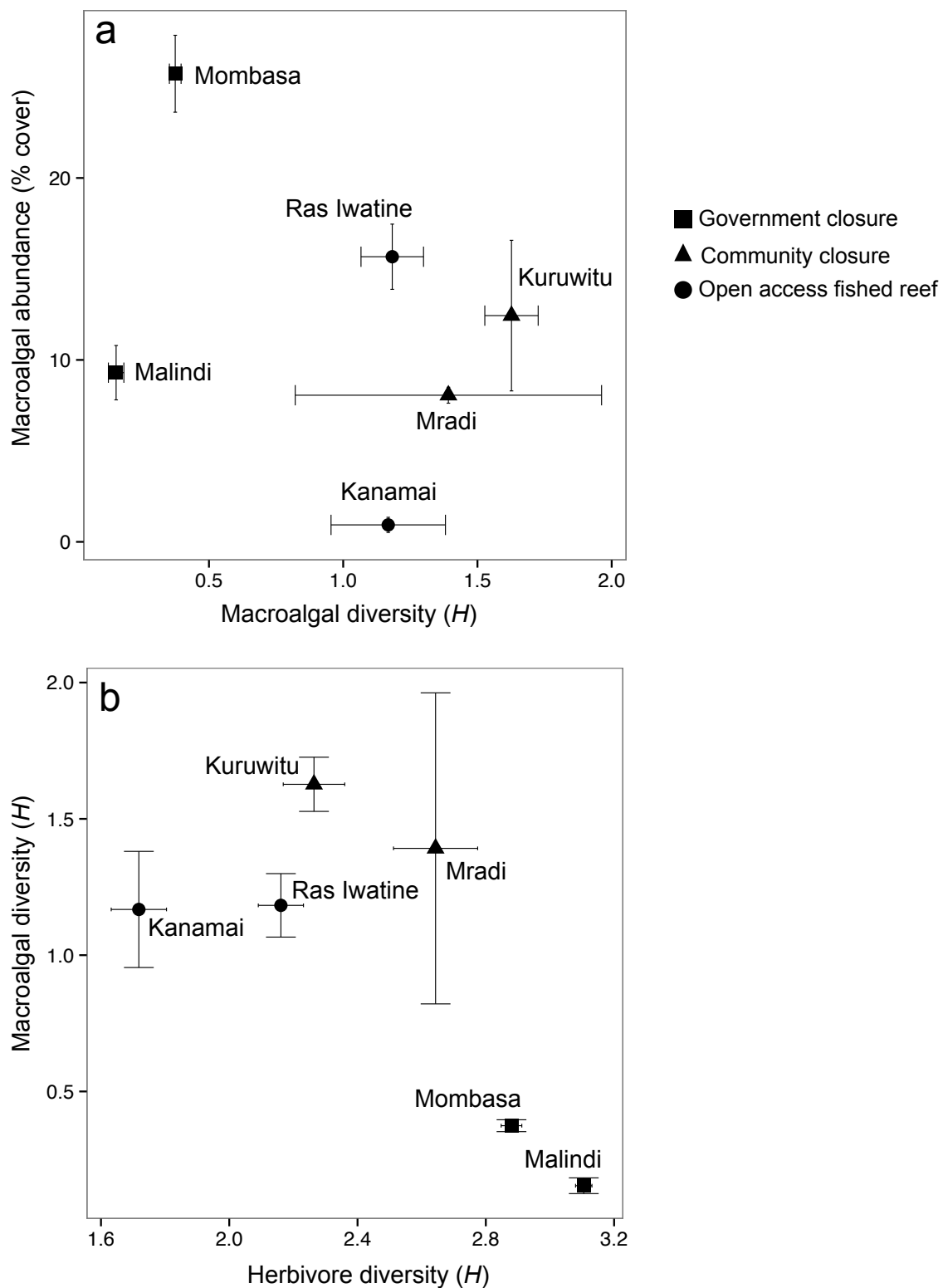


Fig. 4.6. Relationship between mean existing (a) macroalgal diversity (Shannon's H ; \pm SE) and abundance (% cover; \pm SE), (b) herbivore and macroalgal diversity (Shannon's H ; \pm SE), and (c) herbivore diversity (Shannon's H ; \pm SE) and macroalgal abundance (% cover; \pm SE) at each of the six study sites. Shapes represent fisheries management type at each site.

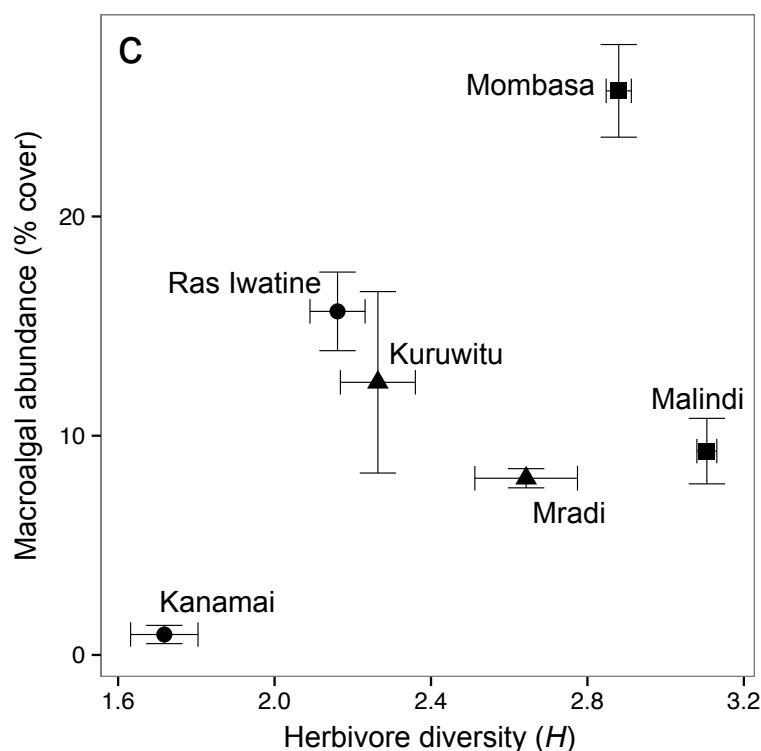


Fig. 4.6 (cont). Relationship between mean existing (a) macroalgal diversity (Shannon's H ; \pm SE) and abundance (% cover; \pm SE), (b) herbivore and macroalgal diversity (Shannon's H ; \pm SE), and (c) herbivore diversity (Shannon's H ; \pm SE) and macroalgal abundance (% cover; \pm SE) at each of the six study sites. Shapes represent fisheries management type at each site.

4.4 Discussion

4.4.1 Macroalgal grazing selectivity of herbivorous fishes

When I transplanted macroalgae from the fished reef to the fisheries closure, very few were rapidly consumed and fish fed selectively and in a complementary way to one another so that different species focused on different algae. The brown alga *Padina* was the only genus consumed and reduced by more than 50%, while *Dictyota* and *Turbinaria* were grazed very little. Videos indicated that species-specificity of feeding was strong on macroalgae because only a quarter of the species within the herbivorous fish assemblage consumed any macroalgae at all (6 of 24 species). Three of these fish species displayed a high degree of feeding

selectivity: the unicornfish *Naso unicornis* (family Acanthuridae) fed exclusively on *Sargassum*, while the parrotfishes *Calotomus carolinus* and *Leptoscarus vaigiensis* (family Labridae) fed exclusively on *Padina*. The rabbitfishes *Siganus sutor* and *S. argenteus* (family Siganidae) fed less selectively and consumed mostly *Cystoseira*, but also some *Hypnea*. While the complementary feeding observed in this experiment may increase reef resilience by maximizing macroalgal removal (Burkepile and Hay 2008), the limited overlap in diet reduces functional redundancy, which could be detrimental to ecosystem functioning if even a single species is removed (Bellwood et al. 2003, Micheli and Halpern 2005, Hoey and Bellwood 2009).

Most feeding studies on tropical coral reefs have argued that maintaining herbivore species richness is critical for preserving reefs because complementary feeding produces positive, indirect effects on corals (Mantyka and Bellwood 2007, Burkepile and Hay 2008, Rasher et al. 2013). My results corroborate these findings, but also show how only a few species that represent a small portion of the herbivorous fish community account for almost all of the feeding on the transplanted macroalgae. For instance, *Naso unicornis* was responsible for 100% of the browsing on *Sargassum*, but only represented 4% of the herbivorous fish species richness and biomass. Similarly, the parrotfishes *Calotomus carolinus* and *Leptoscarus vaigiensis* represented 12% of the herbivorous fish biomass and species richness, but accounted for 96% of *Padina* consumption. These species of herbivorous fishes have a disproportionate impact on macroalgal browsing, which suggests that species-specific management may be necessary to ensure maintenance of ecosystem function in this system.

Diet partitioning and selectivity among parrotfishes (family Labridae) in this experiment differed from other studies, which may be a function of the species found on these and other reefs, and their respective feeding modes (Choat et al. 2002). The parrotfishes observed by Mantyka and Bellwood (2007) on the Great Barrier Reef (GBR) in Australia, and Rasher et al. (2013) in Fiji, were of the genera *Hipposcarus*, *Chlorurus*, and *Scarus*, and fed on different species of macroalgae with variable degrees of selectivity. On the GBR, they fed on the calcareous alga, *Halimeda* (Mantyka and Bellwood 2007), and in Fiji, on the red algae *Galaxaura* and *Amphiroa*, as well as algal turf (Rasher et al. 2013). These parrotfishes, however, are primarily regarded as grazers of algal turf, but under experimental conditions, may also feed on macroalgae (Fox and Bellwood 2007). They have jaw morphologies that allow them to scrape the substratum and even take deeper excavating bites from hard surfaces (Bellwood and Choat 1990). In contrast, the parrotfishes I observed feeding on macroalgae were of the genera *Calotomus* and *Leptoscarus*, and are not known to feed on algal turf (Bellwood 1994), have teeth that allow clipping of algae (Nakamura et al. 2003, Cvitanovic and Bellwood 2009), and are from the *Sparisomatinae* evolutionary lineage. I observed these species feeding exclusively on the brown algae *Padina*.

Manipulative studies are used to elucidate cause and effect in natural communities but it is difficult to avoid experimental artifacts completely. I used underwater digital video cameras to record foraging of macroalgae at transplanted assays. Cameras have been shown to have a negative effect on algal biomass removed, with consumption decreased by as much as 20% (Michael et al. 2013). It is possible this influenced results in the mass removed from transplanted macroalgal assays,

however, the size of my cameras (8 x 6 x 4 cm) was very small compared to those used in previous studies (Mantyka and Bellwood 2007, Fox and Bellwood 2008, Vergés et al. 2012, Michael et al. 2013). If anything, the presence of paired control assay lines with cages was a more likely artifact of this assay experiment. Species-specific avoidance behavior may exist even in no-take fisheries closures (pers obs) because fishing is intense in Kenya, and the use of traps is common (McClanahan and Mangi 2004). This could be one explanation for why I did not record species such as the sea chub *Kyphosus vaigiensis* feeding on the assays when similar experiments have indicated they are prevalent foragers of *Sargassum* (Vergés et al. 2012, Michael et al. 2013). However, this is also unlikely because *K. vaigiensis* often feeds on drift algae midway in the water column (Littler et al. 1983).

4.4.2 Efficacy of macroalgal browsers

There were marked differences in herbivore composition among the six study sites and three fisheries management types. The resulting interplay of the various herbivore guilds led to different responses of macroalgae on the experimental algal growth plates. For example, the cover of fleshy algae on the plates remained constant from initial levels (between 50 and 70% cover) throughout the experiment at community closures, with *Sargassum* largely dominating these assemblages. This result was driven by the almost complete absence of browsing fishes and a lower abundance and impact of the diverse sea urchin community. At open access fished reefs, high abundances of sea urchins ($> 4400 \text{ kg ha}^{-1}$) quickly led to the suppression of all types of macroalgae to levels below ~10% cover, even though sea urchin diversity was low. Browsing fishes had similar effects on macroalgae at the government closure sites where most types of fleshy algae were significantly

reduced. One exception was at Mombasa where *Sargassum* remained prevalent throughout the experiment (~30% cover) even though browser diversity was high; *Sargassum* was not consumed due to the absence of a few key herbivore species, primarily unicornfishes *Naso unicornis* and *N. elegans*, and perhaps the sea chub *Kyphosus vaigiensis*. Additionally, *Turbinaria* increased slightly throughout the experiment at Malindi, suggesting that it is well defended against all browsers in this system.

Macroalgae are common on reefs following disturbances and herbivore removal (Hughes et al. 2007, McClanahan et al. 2011c), and sea urchins and fishes may differentially impact these algae (Ogden and Lobel 1978, Sandin and McNamara 2012). I found complementary feeding and species-specificity of feeding to be high among the herbivorous fish community in the transplanted assays, but I found the opposite in feeding patterns within the sea urchin community in this experiment. At the open access reefs where fish were absent and sea urchins were abundant, macroalgae were consumed non-selectively and reduced significantly despite low diversity and differences in sea urchin species assemblages between the sites (*Echinometra mathaei* was the dominant sea urchin species at Kanamai, and *Echinothrix diadema* at Ras Iwatine). All types of brown algae were consumed by sea urchins even though the phlorotannins found in brown algae have been shown to deter feeding by some invertebrates (Steinberg 1988). While differential tolerances to chemical and structural defenses may be common among herbivorous fishes and lead to greater feeding selectivity on coral reefs, sea urchins appear to be less affected and as a result are highly unselective foragers where biomass may be

more important than species diversity (Ogden and Lobel 1978, Hay and Kappel 1994, Hay 1997, Clements et al. 2009).

Chemical and structural defenses of macroalgae interact to dictate feeding preferences of grazers (Hay 1986, 1997, Choat et al. 2002, 2004, Rasher et al. 2013), and may change through time in response to herbivory or as the algae mature (Hay 1981). I excluded herbivores and allowed macroalgae to mature for over one year on the experimental plates (using exclusion cages) before allowing access to consumers. Here, *Padina* was rapidly consumed by fishes where *Calotomus carolinus* and *Leptoscarus vaigiensis* were present (at the government closures), which was likely due to *Padina* changing its growth form in the absence of herbivory to a rapidly growing upright blade (Lewis 1986). This form is very susceptible to fish grazing as compared to the prostrate, thin-branching form that is found where herbivory is high (Lewis 1986). I also selected mature specimens of macroalgae in the transplanted assay experiment from areas on fished reefs with no herbivory (no sea urchins or fishes; shallow intertidal pools), which may also explain why *Padina* was rapidly consumed during those trials. In contrast, *Turbinaria* and *Dictyota* were rarely consumed by fishes as both are known to produce chemical compounds (e.g. pachydictyol-A) that act as feeding deterrents regardless of growth form or maturity (Hay 1996, Targett and Arnold 1998).

4.4.3 Herbivore diversity and macroalgal persistence

Results from these experiments led me to predict that not just herbivore diversity *per se* predicts existing macroalgal assemblages at these reefs, but that species identity is also critical, especially where sea urchins are less abundant (e.g. old and larger

marine reserves). Corroborating this hypothesis, I found contrasting and weak, marginally non-significant associations among herbivore diversity and macroalgal diversity and abundance at sites, as well as between macroalgal abundance and diversity. The negative relationship between herbivore and macroalgal diversity is consistent with theory and other empirical studies (Duffy 2002, Burkepile and Hay 2008, Rasher et al. 2013), but in this case it had low predictive power ($R^2 = 0.33$). While the relationship between herbivore diversity and macroalgal cover was non-significant ($p = 0.12$), there was a trend of increasing cover as herbivore diversity increased, which is contradictory to findings from similar studies (Cheal et al. 2010, Rasher et al. 2013). This suggests that, while herbivore diversity in this system may reduce the overall number of algal species on reefs, it may not necessarily reduce overall abundance of macroalgae. This likely reflects species-specific differences in foraging (i.e. feeding selectivity and complementarity) and suggests that even diverse assemblages may still lack key browser species (Bellwood et al. 2003). Therefore, managing strictly for herbivore diversity may not be appropriate on reefs where sea urchins and herbivorous fishes co-occur.

Fisheries closures, or no-take marine reserves, are a common management tool often intended to increase reef resiliency and restore stability and reef structure and function (Hughes et al. 2007, Selig and Bruno 2010, Thibault et al. 2012). The relationships between herbivore diversity and macroalgae I describe here provide an example of why some protected reefs may not be able to recover to coral-dominance following phase shifts to macroalgal-dominance. For instance, Mombasa has a high diversity of herbivores, comprising mostly fishes, but lacks key unicornfishes (*Naso* sp.), which are particularly important for the removal of *Sargassum*. Therefore, other

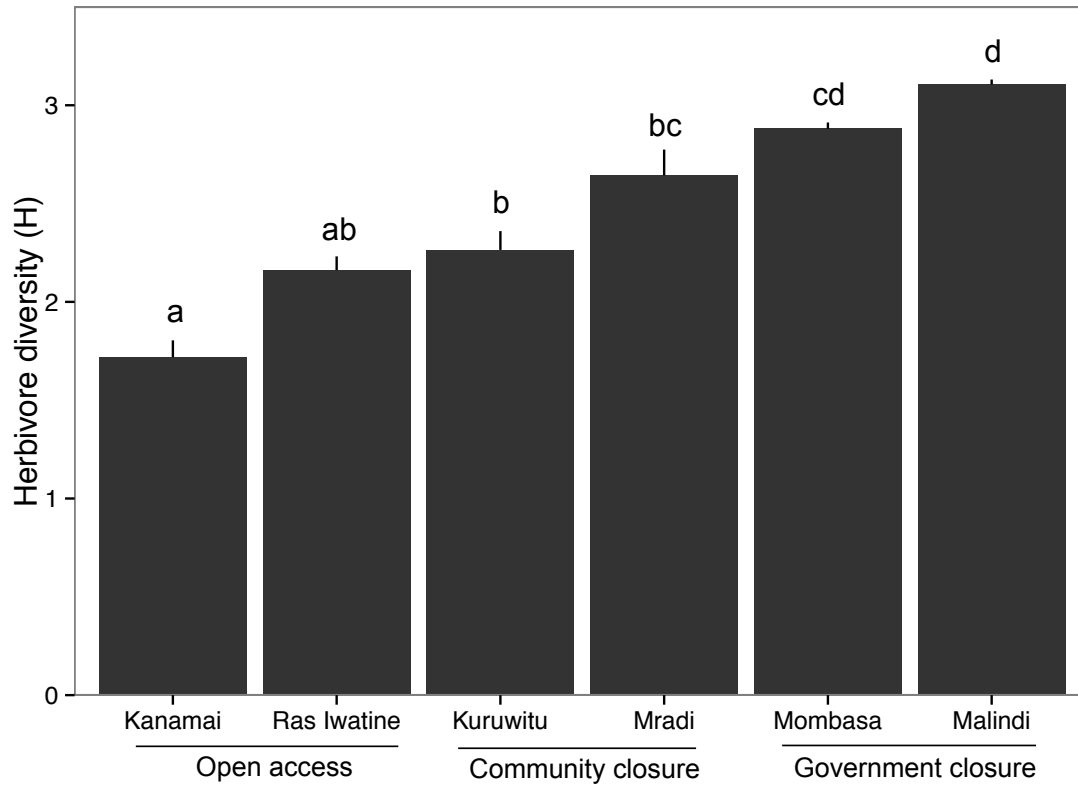
species of macroalgae are reduced while *Sargassum* remains prevalent (~23% cover). On the other hand, Malindi has a lower diversity of fishes but includes a portfolio of key species that feed in a complementary fashion to one another, reducing both the diversity and abundance of macroalgae.

4.4.4 Conclusions

Ecosystem function is often associated with biodiversity, and herbivores that are able to consume macroalgae are critical in performing key ecological process and facilitating the recovery of reef-building corals where macroalgae have become dominant (Bellwood et al. 2006, Cheal et al. 2010). These findings indicate that the removal of macroalgae is not strictly dependent upon herbivore abundance and diversity *per se*, but that herbivore identity is particularly important because of complementary feeding, especially where sea urchins are absent (i.e. no-take marine reserves). This demonstrates the importance of feeding selectivity and complementarity to critical ecosystem processes of herbivory on coral reefs, but also highlights the potential for low functional redundancy even in old and larger fisheries closures where species diversity is high (Bellwood et al. 2003). Therefore, consequences from the failed recovery of one or a few key herbivore species may be crucial for the proliferation of macroalgae and reversal of macroalgal phase shifts, thus leading to compromised ecosystem functioning in fisheries closures.

Appendix 4.1

Appendix 4.1.1. Mean herbivore diversity (Shannon's H ; + SE) at each study site by fisheries management type. Letters indicate homogeneous subgroups ($p < 0.05$).



CHAPTER 5

DIRECT AND INDIRECT EFFECTS OF CORAL REEF FISHERIES CLOSURES IN KENYA: DECADAL TRENDS IN HERBIVORES AND ALGAE

5.1 Introduction

Disturbance and recovery processes structure ecological communities through direct and indirect species interactions (Connell 1978, Tilman 1980, Rogers 1993). Fishing represents a type of disturbance (Pauly et al. 1998) and is one that can indirectly influence reef structure and processes through cascading effects (Roberts 1995, Jennings and Kaiser 1998, O'Leary and McClanahan 2010). On coral reefs, herbivory is a process that is critical in determining the magnitude of such indirect effects because it mediates primary producer assemblages (Lubchenco and Gaines 1981, Olf and Ritchie 1998). Here, herbivory is considered especially critical because the overgrowth of algal turf into fleshy macroalgae can outcompete corals and trigger a macroalgal phase shift (Scheffer et al. 2001, Hughes et al. 2010). Fisheries closures are becoming a common management tool intended to facilitate the recovery of species assemblages and ecosystem processes such as herbivory following disturbances (Russ and Alcala 2004). However, critical questions persist in coral reefs and other high-diversity ecosystems relating to the recovery trajectories of organisms and how they influence direct and indirect effects.

Conditions on coral reefs that maintain a high abundance of algal turf are generally considered favorable for coral recruitment, reef growth, and ecological functioning (Mumby et al. 2007). Algal turf species are highly productive (Odum and Odum

1955) and have opportunistic life-history characteristics, including the ability to maintain high surface area to volume ratios (Rosenberg and Ramus 1984). However, where top-down grazing pressure remains low, algal turfs may be replaced by fleshy macroalgae, precipitating a macroalgal phase shift (Sammarco et al. 1974, Lubchenco and Gaines 1981, Carpenter 1986, Done 1992, McCook 1999, Hughes et al. 2007, Ceccarelli et al. 2011). Here, establishment and succession of macroalgae may follow distinct stages that reflect life histories and structural, chemical, and nutritional characteristics. For example, there may be early dominance by fast-growing simple filamentous and blade genera (e.g. *Hypnea*, *Padina*), followed by a late stage dominated by coarsely branched and leathery genera better defended against herbivory (e.g. *Sargassum*, *Turbinaria*; Hixon and Brostoff 1986, Hay et al. 1987, Duffy and Hay 1990). Therefore, it is important to examine under what conditions, how quickly, and in what ways algae may transition into and out of less desirable, foliose forms.

Switches in the dominance of the grazer guild from sea urchins to fishes, and within groups of fishes, can greatly influence the ecology of coral reefs because of differences in mobility and feeding characteristics (Ogden and Lobel 1978, Hay and Taylor 1985, Morrison 1988, McClanahan 1992, Sandin and McNamara 2012, O'Leary et al. 2013). For example, fishes that consume algal turfs and also scrape the substratum, such as parrotfishes (family Labridae), are viewed as especially critical in preventing the settlement and establishment of macroalgae (Williams and Polunin 2001, Williams et al. 2001). Conversely, a different functional group of herbivorous fishes, browsers, is responsible for removing mature macroalgae (Mantyka and Bellwood 2007, Hoey and Bellwood 2011, Rasher et al. 2013). Sea

urchins, on the other hand, may consume both algal turfs and macroalgae less discriminately because their selection of food is based less on palatability or nutritional value (Ogden and Lobel 1978). The transfer of grazing from one group of herbivores to another is also important because certain functional groups may be more vulnerable to fishing and their recovery patterns may differ (McClanahan et al. 2007a, Graham et al. 2011). Consequently, where fishing is prohibited, the type and intensity of herbivory may change through time as reefs recover fish biomass.

Because disturbances and ecological processes vary over considerable spatial and temporal scales in an ecosystem, there is a need to collect and analyze data at multiple scales (Kelly and Harwell 1990). Long-term empirical data can be sparse and studies are often based on meta-analyses that combine disparate sites and ecosystems (Halpern and Warner 2002, Micheli et al. 2004, Claudet et al. 2008, Lester et al. 2009) or include only a limited number of site-specific studies (Russ and Alcala 2004). Using alternate methods may be necessary in order to examine long-term (decadal-scale) trends relevant to management and conservation objectives. This study utilizes a chronosequence to examine the time course and temporal variation of direct and indirect effects of protection in Kenyan coral reef fisheries closures, with a focus on herbivores and algae. These no-take marine protected areas represent among the oldest fully protected fisheries closures in the Indian Ocean (McClanahan et al. 2009), and using a space-for-time substitution, they create a 43-year chronosequence from the initial protected areas closures in 1968. Here, I specifically asked how long it takes for direct and indirect effects to be detected for herbivores and algae at unfished reefs, how stable such effects are through time, and whether levels of variation differ among fished areas through time.

5.2 Materials and methods

5.2.1 Study sites

Data were collected between 1992 and 2012 at 28 unique sites (11 no-take closures and 17 open-access fished reefs) along the Kenyan coast (Fig. 5.1 and Table 5.1). Unfished closure sites were located within five enforced government-managed no-take Marine National Parks (Malindi, one site; Watamu, one site; Mombasa, two sites; Kisite, two sites; Lamu, three sites) and two sites were enforced community-managed no-take closures (Kuruwitu and Mradi). Year of closure varies from 1968 to 2010. Fished sites were interspersed along the coast and are heavily exploited throughout the year (McClanahan et al. 2005, McClanahan et al. 2008a).

The closure sizes varied from 0.29 to 250 km² (Kuruwitu and Mradi, 0.29 km²; Mombasa, 6 km²; Malindi and Watamu, 10 km²; Kisite 28 km² and Kiunga 250 km², but the actual area occupied by coral reef in Kisite and Kiunga is < 10 km²). Previous analyses of the ecological effects of closure size have found that it is not important relative to socioeconomic variables in the surrounding areas and, therefore, not evaluated here (Daw et al. 2011).

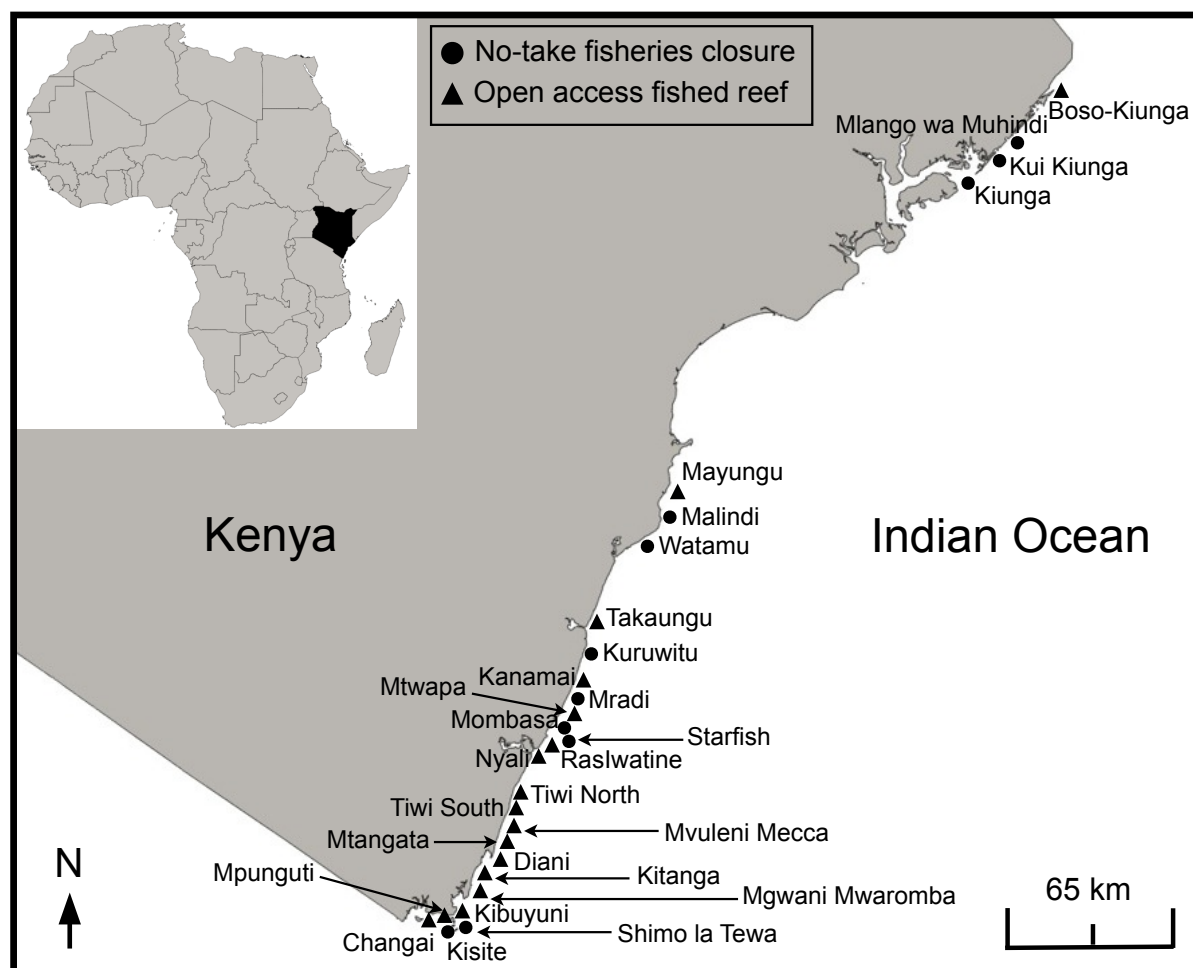


Fig. 5.1. Map of the coastline of Kenya and study sites. Shapes indicate fisheries management type.

All sites were in shallow (2 to 5 m) and calm back-reef lagoons typical of Kenya's fringing reef system where the main substratum is living corals, coral rubble, sand and seagrass, and habitat complexity is similar among fished and unfished closures (McClanahan and Graham 2005). Common anthropogenic stressors, such as sedimentation and eutrophication, are limited at these sites due to strong currents and tidal flushing (McClanahan and Obura 1997, Obura 2001). The 28 sites do vary in reef height and water retention during low tides, which can affect water flow, temperature variability, and subsequently algal dynamics; however, there are no

systematic differences in these features between fished and unfished reefs

(McClanahan and Maina 2003, McClanahan et al. 2009).

Table 5.1. Study sites, fisheries management regime, and year of closure enforcement. Also presented is the number of years each site was sampled from 1992 to 2012, along with the total number of fish, sea urchin, and benthic transects.

Reef	Management	Year of closure	Years sampled	Fish transects	Sea urchin transects	Benthic transects
Boso-Kiunga	Open access	NA	1	2	9	6
Changai	Open access	NA	1	2	9	9
Diani	Open access	NA	5	19	90	91
Kanamai	Open access	NA	5	17	81	79
Kibuyuni	Open access	NA	1	2	9	9
Kisite	Closure	1973	4	12	72	70
Kitanga	Open access	NA	1	2	9	6
Kiunga	Closure	2002	1	2	9	6
Kui Kiunga	Closure	1979	1	2	9	6
Kuruwitu	Closure	2005	7	24	142	122
Malindi	Closure	1979	6	21	126	98
Mayungu	Open access	NA	1	2	9	9
Mgwani Mwaromba	Open access	NA	1	2	9	15
Mlango wa Muhindi	Closure	1979	1	2	9	6
Mombasa	Closure	1991	7	30	144	132
Mpunguti	Open access	NA	1	4	18	12
Mradi	Closure	2010	2	4	16	18
Mtangata	Open access	NA	1	2	18	9
Mtwapa	Open access	NA	1	2	9	9
Mvuleni Mecca	Open access	NA	1	2	9	9
Nyali	Open access	NA	2	6	36	36
Raslwatine	Open access	NA	4	12	36	27
Shimo la Tewa	Closure	1979	1	1	9	9
Starfish	Closure	1991	1	2	9	9
Takaungu	Open access	NA	1	2	9	4
Tiwi North	Open access	NA	1	4	9	9
Tiwi South	Open access	NA	1	2	9	9
Watamu	Closure	1972	5	16	54	54

5.2.2 Field methods

At each site, fish and sea urchin biomass and abundance and benthic cover were quantified and sampled concurrently. All sites were surveyed 1 to 7 times over the 20-year time period by either Tim McClanahan (n = 49) or myself (n = 16) for a total

of 65 site by year replicates. To determine if observer bias affected results, I compared data at a subset of reefs where both Tim and I simultaneously performed surveys ($n = 10$) and no significant differences were found ($p > 0.05$). The number of transects per reef varied but were sampled in the same locations each year during the northeast monsoon season (Aug – Dec; Table 5.1). All field collection methods are as described in Chapter 2 (section 2.2.2) and Chapter 3 (section 3.2.2). I realize there may be some seasonality in the data (e.g. macroalgae), however, it was not possible to capture this given the nature of data collection methods.

5.2.3 Data analyses

Among-reef variation in herbivore assemblages was first assessed using correlation-based principal components analysis (PCA) on Euclidean distances of biomass data. Data were log-transformed to improve the spread. Pairwise relationships between all variables within the herbivore biomass matrix showed no collinearity ($r < 0.6$; Zuur et al. 2007). Chronosequences were then established by assigning each sampling year to a year since fishing closure (McClanahan and Humphries 2012); the areas closed to fishing were assigned to a year since fishing closure that was calculated by subtracting the sampling year from the year it was closed from fishing. For example, Kuruwitu in year 2007 is given a value of 2 for years since closure since it was closed to fishing in 2005. Similarly, Mombasa in year 1993 is given a value of 2 for years since closure since it was closed to fishing in 1991. The reefs open to fishing were pooled and assigned a value of 0 for years since closure.

The relationship between years since fisheries closure and biomass values for each herbivore functional group (i.e. scraper, browser, grazer, sea urchin) was examined

using generalized additive mixed models (GAMM). GAMMs incorporate the possibility of non-linear relationships between the response and predictive variables while also allowing for nested data structures and temporal and spatial correlation between observations (Zuur et al. 2009). I included reef in each GAMM as a nested effect variable within sites using maximum likelihood estimation (REML) with the `gamm` function of the 'mgcv' package in R (Wood 2013). The plotted residuals from fitting GAMMs to the data showed a clear violation of the independence assumption, and therefore, I extended the model to include a residual structure to account for temporal autocorrelation (AR-1; Zuur et al. 2007, 2009). Model diagnostics were performed visually using frequency histograms, funnel and quantile-quantile (Q-Q) plots, and the final models met the assumptions of normality and homogeneity of residuals. I also fitted GAMMs in the same way to the abundance of all major benthic groups (hard coral, CCA, algal turf, macroalgae) to test for a significant effect of time since fisheries closure. In a previous study of the same sites, there was no evidence for spatial autocorrelation of benthic cover across sites or an initial bias in the selection of un-fished reefs (Darling et al. 2013).

Algal turf consumption rates ($\text{g algae m}^{-2} \text{ day}^{-1}$) for each site were calculated by using species-specific grazing rates for sea urchins (McClanahan and Kurtis 1991, Carreiro-Silva and McClanahan 2001) and functional group-specific grazing rates for herbivorous fishes (Chapter 2, section 2.2.4). These rates were used to calculate mean values (\pm SE) for each year since closure. Mean algal production rate ($2.13 \text{ g algae m}^{-2} \text{ day}^{-1}$; Fig. 2.1), was also presented to visualize where a grazing surplus or deficit occurs in the chronosequence. Browsers were given a value of zero for algal

turf consumption because they feed primarily on fleshy macroalgae (Mantyka and Bellwood 2007, Rasher et al. 2013).

To examine the relative abundance of algal turf versus fleshy macroalgae on reefs, I used the natural log-response ratio (LRR; Osenberg et al. 1997). LRRs were calculated as

$$LRR = \ln\left(\frac{A_T}{A_M}\right)$$

where A_T is the abundance (% cover) of algal turf and A_M is the abundance (% cover) of macroalgae. Positive LRR values indicate a greater amount of algal turf as compared to macroalgae and negative LRR values indicate a greater amount of macroalgae as compared to algal turf.

I classified the most commonly recorded macroalgal genera at each reef (> 5% of total macroalgal abundance) into two groups representing different stages in succession using the functional-form model as described by Steneck and Dethier (1994): early succession = blade/filamentous genera; late succession = leathery/coarsely branched genera (Littler 1980, Hay 1981, Steneck and Watling 1982, Littler et al. 1983, Hixon and Brostoff 1996). Using a functional group approach according to features such as body plan, behavior, or life-history strategy allows for making community-level comparisons more broadly in space and time (Steneck and Dethier 1994). *Padina*, *Hypnea*, and *Dictyota* comprise the majority of genera in the early successional group with blade and filamentous morphologies (Hixon and Brostoff 1996). *Sargassum* and *Turbinaria* were the most common genera in the late successional group with tough leathery and coarsely branched

morphologies (Hixon and Brostoff 1996). Abundance data (% cover) were used to calculate mean values (\pm SE) for each year since closure and at fished reefs.

The chronosequence method relies on the assumption of site similarity such that all sites are similar to one another in their development (i.e. they have traced similar histories; Johnson and Miyanishi 2008). To address this assumption and test whether these fished reefs were changing in similar ways through the entire 20-year data set, I fitted generalized linear mixed models (GLMM) to all response variables by year: coral/CCA/turf/macroalgae abundance, herbivorous fish (by functional group) and sea urchin biomass, consumption rate, natural log-response ratio of algal turf abundance to macroalgae abundance, and abundance of early and late successional macroalgae species. I included reef in each GLMM as a nested effect variable using REML with the `lmer` function of the 'lme4' package in R (Bates et al. 2008) and I also extended the model to include a residual structure to account for temporal autocorrelation by site (AR-1; Zuur et al. 2007, 2009). Coral, CCA, algal turf, and macroalgae abundance data were log transformed to improve the spread of the data and meet model assumptions (Zuur et al. 2009). Model diagnostics were performed visually as described above and the final models met the assumptions of normality and homogeneity of residuals. All data analyses were performed using the program "R" (v. 2.15.1; R Development Core Team 2013).

5.3 Results

Herbivore assemblages were variable among the 65 site by year replicates and the first principal components axis (PC1) of the PCA differentiated replicates along a gradient from high sea urchin biomass at negative scores, to high herbivorous fish biomass at positive scores (Fig. 5.2). A separation from grazer-dominated

herbivorous fish assemblages to more mixed assemblages dominated by browsers and scrapers was represented by the second principal components axis (PC2). The combination of these axes represents the succession from fished reefs to reefs in early recovery (1-20 years since closure) and late recovery (21-43 years since closure) stages.

Herbivorous fishes responded to protection in different ways but years since closure was a significant and strong predictor for all functional groups (Fig. 5.3 and Table 5.2). Browsers at the fished reefs (year 0) had a mean biomass of only 4.7 kg ha^{-1} , which increased to a peak around year 20, followed by a slight decrease all the way to the end of the chronosequence; browser biomass, as compared to grazer and scraper biomass, remained relatively low throughout the time series and model predictions never reached above 100 kg ha^{-1} (Fig. 5.3c). Grazers increased linearly as a function of time since fisheries closure, beginning with a mean biomass of 19.7 kg ha^{-1} and ending with model predictions greater than 300 kg ha^{-1} (Fig. 5.3a). Scraper biomass immediately increased from 4.9 kg ha^{-1} with the cessation of fishing until it peaked around year 20 with a biomass of approximately 200 kg ha^{-1} (Fig. 5.3b). From this point to the end of the time series, scraper biomass leveled and even decreased slightly, finishing with approximately 150 kg ha^{-1} . Models had high predictive power for herbivorous fish recovery, especially for grazers and scrapers where the models explained more than 65% of the variance. Sea urchin biomass was greatest at year 0 of the chronosequence, or at fished reefs, where the mean was 4424 kg ha^{-1} (Fig. 5.4). Biomass immediately decreased with the establishment of fisheries closures and began to level between years 20 and 25 of the time series, where biomass was less than 25% of that at fished reefs.

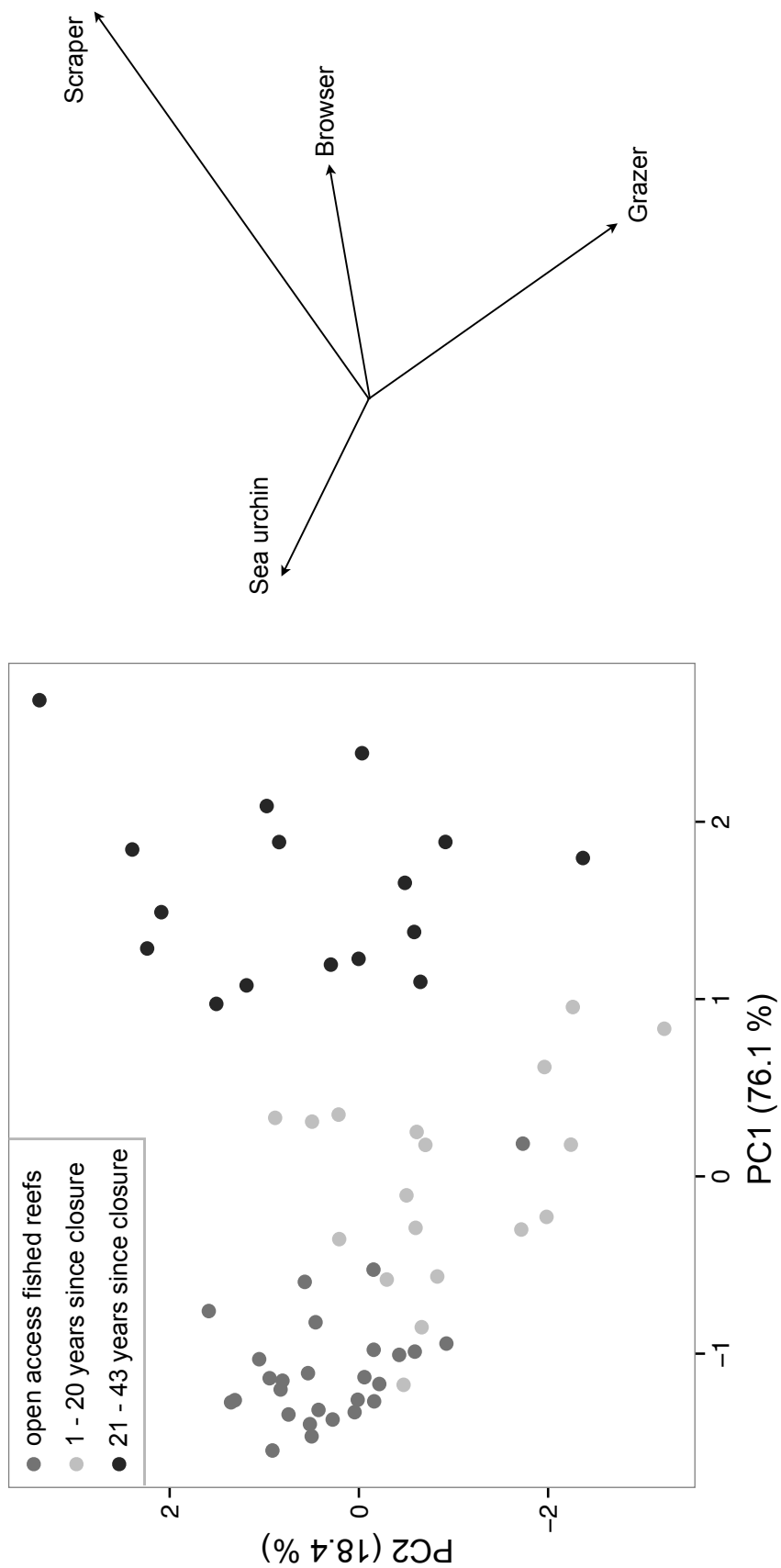


Fig. 5.2. The spatial variation in herbivore community composition at all site by year replicates ($n = 65$) and relative contribution of herbivores using principal components analysis (PCA) on Euclidean distances. Color of data points group reefs by time since fisheries closure, with early and late successional stages separated at year 20. Points that are closer together in ordination space are more similar in terms of herbivore community composition.

Algal turf and macroalgal abundance were variable and generally mirrored one another with opposite trends through time (Fig. 5.5a and 5.5c). Algal turf generally remained between 30 and 40% cover and increased slightly by the end of the chronosequence. Macroalgae increased initially but then decreased and ended below 10% in the older closures. Abundance of CCA showed a significant positive and non-stabilizing trend with time since closure, and represented greater than 18% of the substratum for the final 10 years (Fig. 5.5b). Hard coral abundance, on the other hand, was highly variable and did not change significantly as a function of years since closure, remaining around 30% (Fig. 5.5d).

The algal turf consumption rate of herbivores varied as a function of years since closure and fell below the grazing threshold, or rate of algal production, of $2.13 \text{ g algae m}^{-2} \text{ day}^{-1}$ immediately following the establishment of fisheries closures (Fig. 5.6a). Consumption remained below this threshold, with the exception of years 15 and 16, until year 20 and reached as low as $1.3 \text{ g algae m}^{-2} \text{ day}^{-1}$. The greatest rates of algal turf consumption occurred in the later stages of fish recovery where values reached as high as $5.0 \text{ g algae m}^{-2} \text{ day}^{-1}$.

The LRR values of algal turf abundance to macroalgal abundance showed a generally decreasing trend from fished reefs at year 0 to closures at year 15, where macroalgae were more abundant than turf (negative LRR values; Fig. 5.6b). LRRs from year 16 to 20 remained low and around zero, indicating an almost equal abundance of turf to macroalgae, until they increased and remained above 1.5 for

the duration of the chronosequence. The greatest LRR, or abundance of algal turf compared to macroalgae, was in year 28 when it was 4.3.

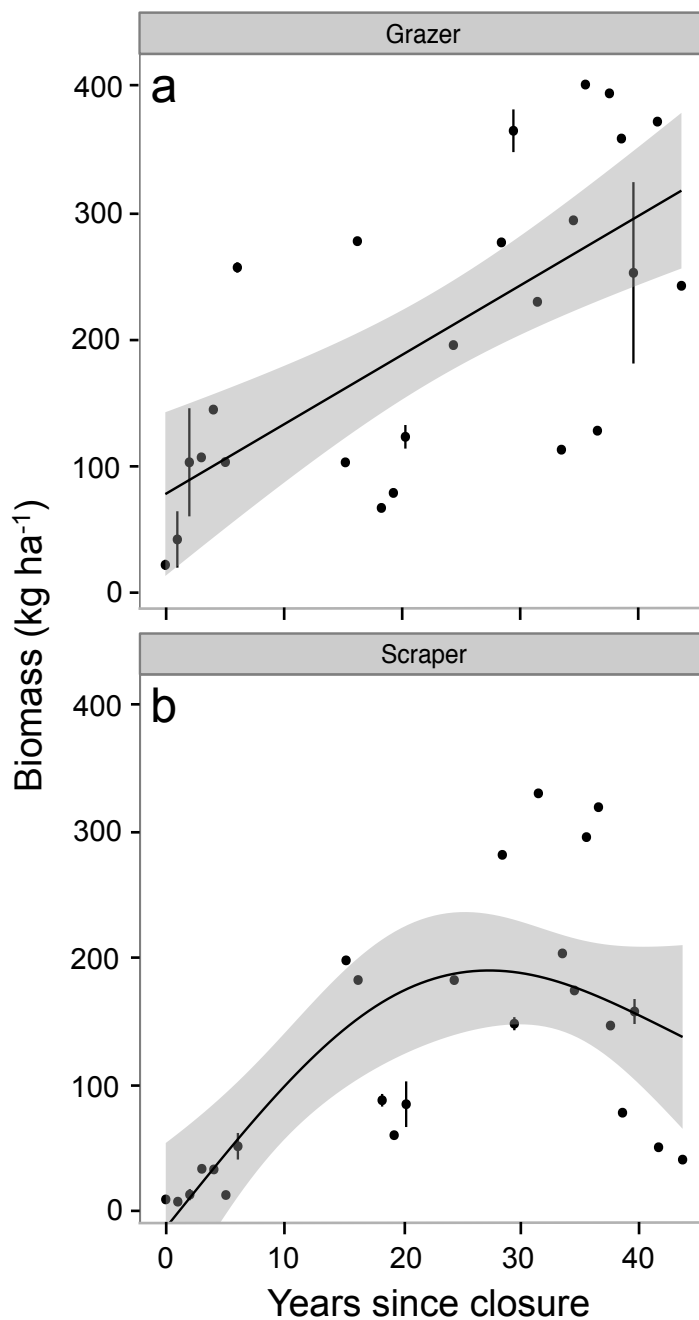


Fig. 5.3. Mean (\pm SE) fish biomass (kg ha^{-1}) of (a) grazers, (b) scrapers, and (c) browsers in Kenyan fisheries closures as a function of the number of years since protection (closure; year 0). Solid lines represent results from generalized additive mixed models (GAMM) and the shaded bands are the 95% confidence intervals.

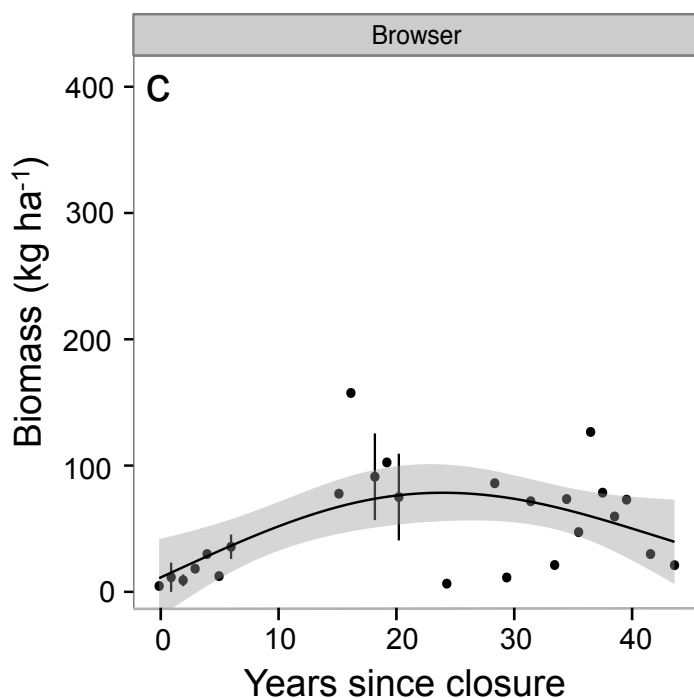


Fig. 5.3 (cont.). Mean (\pm SE) fish biomass (kg ha^{-1}) of (a) grazers, (b) scrapers, and (c) browsers in Kenyan fisheries closures as a function of the number of years since protection (closure; year 0). Solid lines represent results from generalized additive mixed models (GAMM) and the shaded bands are the 95% confidence intervals.

Table 5.2. Results of generalized additive mixed models (GAMM) used to model (a) herbivore biomass (kg ha^{-1}) and (b) substratum variables (abundance; % cover) in relation to the number of years since protection (closure). Estimated degrees of freedom (df) are for the smooth term (years since closure; 1 = linear). *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, and "NS" is not significant or $p > 0.05$.

(a) Herbivore	df	F-value	p-value	R ²
Browser	1.82	13.48	***	0.483
Grazer	1.00	38.48	***	0.652
Scraper	2.25	39.55	***	0.683
Sea urchin	1.38	26.94	**	0.486
(b) Substratum	df	F-value	p-value	R ²
Macroalgae	1.61	0.06	NS	0.028
CCA	1.02	28.26	***	0.571
Algal turf	1.21	1.01	NS	0.052
Hard coral	1.09	1.17	NS	0.171

Blade and filamentous macroalgae (early successional genera) were less abundant than leathery and coarsely branched macroalgae (late successional genera) at

fished reefs, or year 0 in the chronosequence (Fig. 5.6c). Both types of macroalgae remained between 2 and 6% until year 5 where leathery and coarsely branched macroalgae increased drastically and reached levels as high as 25% (year 19). After year 20, leathery and coarsely branched macroalgae decreased and never reached levels above 12% for the remainder of the time series. After year 6, blade and filamentous macroalgae was never the most abundant type of macroalgae on the reef (except for year 38) and was always less than 5%.

For all dependent variables analyzed in this study, variance was low among the fished sites by year and none changed significantly through time (Table 5.3). This indicates sites were changing in similar ways through time and there was low between-site variability.

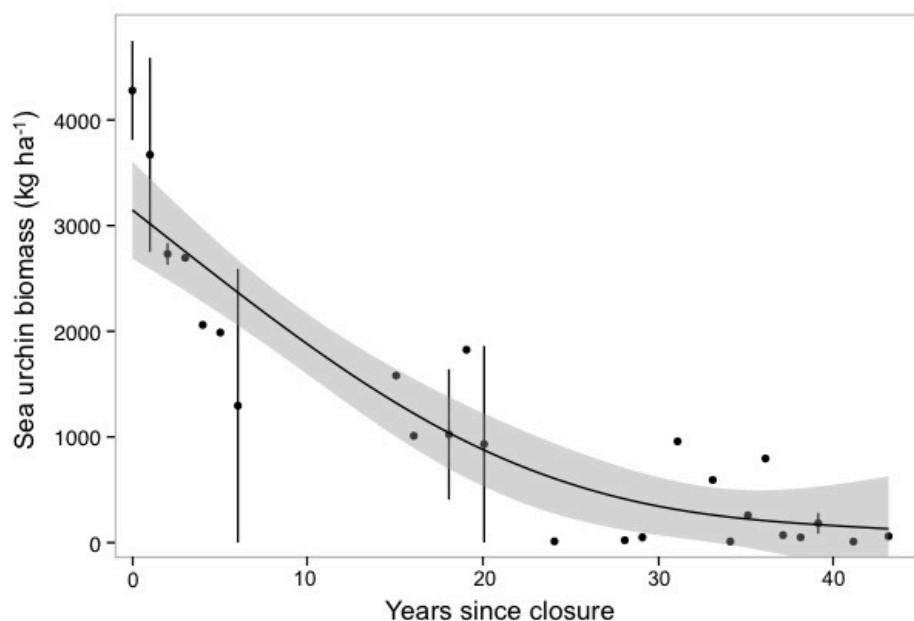
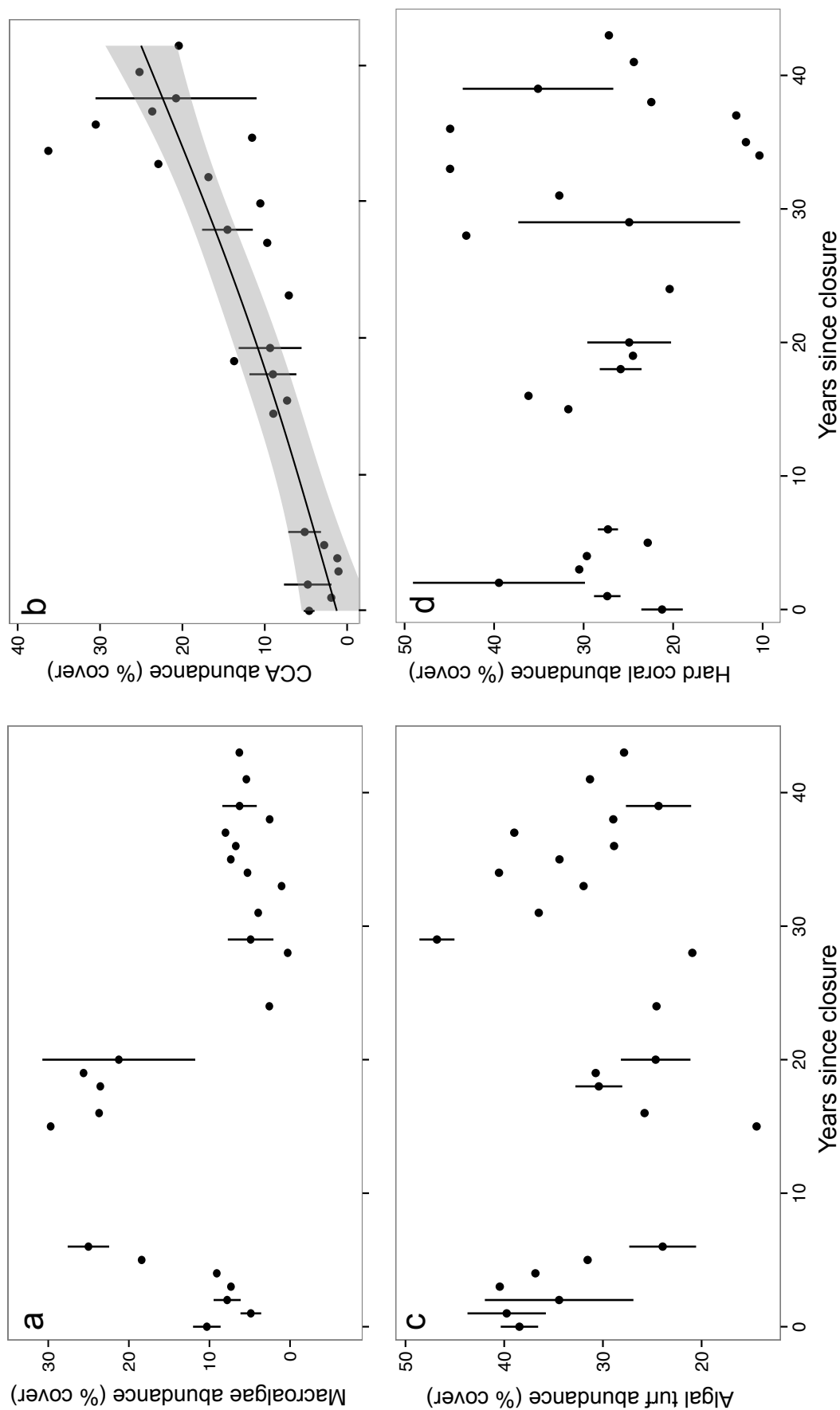


Fig. 5.4. Mean (\pm SE) sea urchin biomass (kg ha^{-1}) in Kenyan fisheries closures as a function of the number of years since protection (closure; year 0). Solid line represents result from generalized additive mixed model (GAMM) and the shaded area is the 95% confidence interval.

Fig. 5.5. Mean abundance (\pm SE) of (a) macroalgae, (b) CCA, (c) algal turf, and (d) hard coral in Kenyan fisheries closures as a function of the number of years since protection (closure; year 0). Solid lines represent results from generalized additive mixed models (GAMM) and the shaded bands are the 95% confidence intervals.



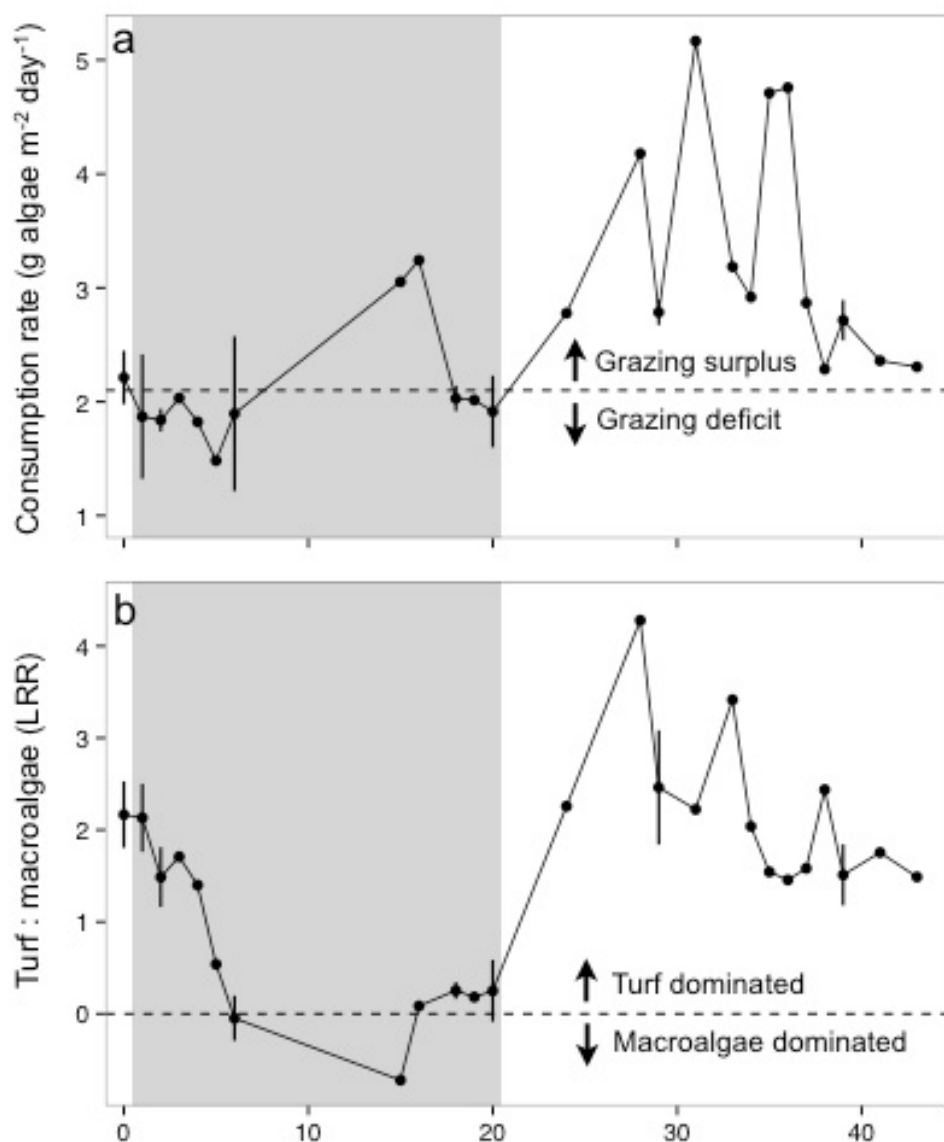


Fig. 5.6. Mean (\pm SE) (a) algal turf consumption rate (g algae m⁻² day⁻¹), (b) natural log-response ratio (LRR) of algal turf to macroalgal abundance, (c) and macroalgal abundance (% cover) in Kenyan fisheries closures as a function of the number of years since protection (closure; year 0). The dashed line in (a) represents the mean algal production rate (g algal m⁻² day⁻¹; Fig. 3.1), such that values above it represent a grazing surplus and values below it represent a grazing deficit. The dashed line in (b) represents where algal turf and macroalgal abundance are equal and values above it represent more algal turf than macroalgae and *vice versa*. Color of data points in (c) represent early (blade/filamentous) or late (leathery/coarsely branched) successional macroalgal genera.

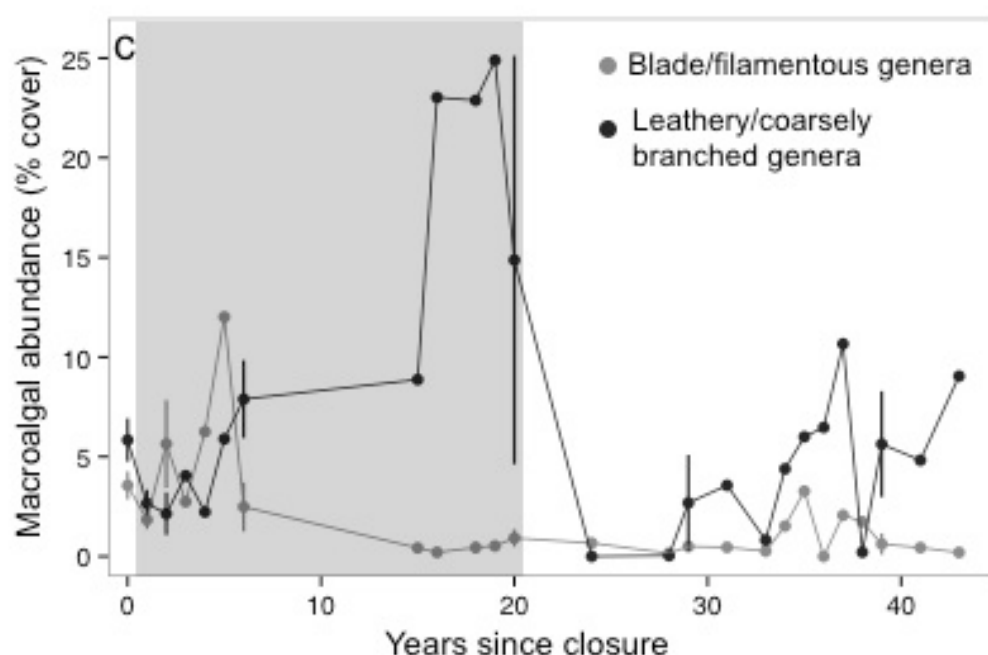


Fig. 5.6 (cont.). Mean (\pm SE) (a) algal turf consumption rate ($\text{g algae m}^{-2} \text{day}^{-1}$), (b) natural log-response ratio (LRR) of algal turf to macroalgal abundance, (c) and macroalgal abundance (% cover) in Kenyan fisheries closures as a function of the number of years since protection (closure; year 0). The dashed line in (a) represents the mean algal production rate ($\text{g algal m}^{-2} \text{day}^{-1}$; Fig. 3.1), such that values above it represent a grazing surplus and values below it represent a grazing deficit. The dashed line in (b) represents where algal turf and macroalgal abundance are equal and values above it represent more algal turf than macroalgae and *vice versa*. Color of data points in (c) represent early (blade/filamentous) or late (leathery/coarsely branched) successional macroalgal genera.

Table 5.3. Results from generalized linear mixed models (GLMM) of all response variables at fished reefs in this study ($n = 31$ site by year replicates) testing for an effect of calendar year (with reef as a nested variable) over the 20-year data set.

Response variable	F-value	p-value
Hard coral abundance (% cover)	0.38	0.855
CCA abundance (% cover)	1.21	0.335
Algal turf abundance (% cover)	2.40	0.106
Macroalgae abundance (% cover)	1.31	0.298
Scraper biomass (kg ha^{-1})	0.64	0.675
Browser biomass (kg ha^{-1})	1.71	0.174
Grazer biomass (kg ha^{-1})	1.65	0.190
Sea urchin biomass (kg ha^{-1})	1.02	0.431
Algal consumption rate ($\text{g algae m}^{-2} \text{d}^{-1}$)	0.32	0.896
Algal turf : macroalgae (LRR)	1.06	0.409
Blade/filamentous macroalgae (% cover)	0.63	0.679
Leathery/coarsely branched macroalgae (% cover)	1.45	0.247

5.4 Discussion

Herbivores and algae immediately responded to protection from fishing in this study, and some organisms stabilized after a period of time whereas others did not.

Differential rates in the decline of sea urchins and recovery of herbivorous fish groups influenced grazing intensity, and thus, the abundance and community composition of algae. At fished reefs, however, changes were not detected through time, suggesting these reefs are relatively stable and are tracing similar histories.

The results here support the findings of other studies on the efficacy of no-take marine reserves in the recovery of herbivorous fishes (Halpern 2003, McClanahan et al. 2007a, Claudet et al. 2008, Molloy et al. 2009), but also demonstrate the value of time series data in providing a longer-term view of temporal dynamics and what this means for indirect effects to the substratum.

Direct effects of reserve establishment on all herbivores were rapid, but different functional groups responded to protection differently. For example, grazers increased linearly through time and showed no evidence of stabilizing even after 43 years of protection. Scrapers and browsers, however, recovered midway through the time series, between 20 and 25 years since closure, then remained relatively stable. Sea urchins immediately declined with protection and this decline continued until approximately year 20 after which abundance remained stable and low. In general, these differences in recovery represent three stages of reef succession: (1) fished reefs; (2) young closures recovering from fishing and between 1 and 20 years old; and (3) older closures, 21 to 43 years old. Fished reefs were characterized by dominance of sea urchins, which then transitioned at the onset of marine reserve establishment into a mixed herbivore assemblage with the emergence of

herbivorous fishes. In these young closures, herbivorous fish assemblages contained grazers with the gradual appearance of browsing and scraping fishes and a decline in sea urchins. Reefs then progressed into a later stage of succession where herbivore assemblages were void of sea urchins and browsers and scrapers had fully recovered. These older closures contained a portfolio of herbivorous fishes that may serve complementary functions in the grazing of algae (Burkepile and Hay 2008), which is considered important for reef resilience (Hughes et al. 2010).

Variations in algal grazing intensity may come from fluctuations in overall herbivore biomass, changes in grazer composition, or a combination of both (Morrison 1988, Mumby 2006). Results from this study showed that sea urchins at fished reefs were able to maintain high algal consumption rates that were above the grazing threshold where consumption exceeds algal production. Here, there was relatively low variation in sea urchin biomass, and consequently algal grazing intensity, through time. Once fishing was restricted at reefs, the initial stages of change in types of grazers caused grazing to drop below the rate of algal production. Consumption rates remained below algal production between years 1 and 20, with the exception of a sharp rise in year 15 and 16 due to high year-to-year variance in scraper biomass. This period, which is the early or initial stage of recovery from fishing, was the only time where there was a grazing deficit in the entire 43-year time series. Once reefs entered a late stage of recovery after ~20 years of protection and scrapers had fully recovered, there was always a grazing surplus. This suggests that herbivory may not be constant across transitions from fishing to closures, and the recovery of the full suite of herbivorous fishes, particularly scrapers, is critical in maintaining a grazing surplus. Consequently, calls for protected areas to demonstrate immediate increases

in herbivory may not be applicable to all coral reef regions (Bellwood et al. 2004, Hughes et al. 2010). Note, however, the patterns in grazing intensity found here may not occur in coral reef regions and habitats where non-fisheries grazers, such as sea urchins, are not abundant (Lessios 1988, McClanahan et al. 1994).

Algal turf is expected to be abundant and macroalgae to decline as grazing intensity and fisheries species increase with age since closure (Williams and Polunin 2001, Babcock et al. 2010). This assumption, however, hinges on the abundance of unfished herbivores, which for this system maintained grazing rates above algal production rates. The response ratios on fished reefs reflected this grazing surplus, as there was a high ratio of algal turf to macroalgae. These ratios began to gradually decrease after closure establishment, which probably reflects responses to grazing intensity. Ratios eventually reached a point where they were either negative (macroalgae were more abundant than turf) or hovered around zero (equal abundance of macroalgae and turf) in the early stages of reef recovery (1-20 years since closure), and did not recover to pre-protection levels until 20+ years after closure. These findings not only indicate that algal turf and macroalgal abundance may respond to fisheries protection in non-linear ways, but that a tight coupling exists between the direct and indirect effects of protection through time. This is important for reserve stakeholders because it suggests that if herbivores recruit to marine reserves and grazing intensity is sufficient, algae will respond quickly and in predictable ways. Such indirect effects may not respond as rapidly to environmental disturbances such as coral bleaching (Graham et al. 2007).

Macroalgal genera that dominated in fished reefs and old closures were those that are typically more resistant to consumption than those genera found in the young closures. As fished reefs were closed and marine reserves established, the abundance of blade and filamentous genera (e.g. *Padina*, *Hypnea*) increased and was often greater than the abundance of coarsely branched and leathery genera (e.g. *Sargassum*, *Turbinaria*). These changes likely reflect the interaction between variations in browsing intensity and the different life-history characteristics of macroalgae because certain species have quicker generation times, but are more susceptible to herbivory (Duffy and Hay 1990). For example, Littler and Littler (1980) suggested that late successional macroalgae tend to be less nutritious, tougher, and more toxic because of a suite of physical and biological selective pressures. In contrast, Poore and colleagues (2012) showed that leathery macrophytes and foliose algae might in fact be the most susceptible to grazing in some scenarios (e.g. temperate reefs). Deciphering the importance of covariation of deterrent traits and other life-history characteristics is difficult and in need of further investigation. However, as soon as browsing fishes fully recovered around year 20 in the time series, the abundance of late successional macroalgae decreased immediately. This suggests macroalgal composition is highly dependent on the recovery of browsers and the specific feeding preferences within this group that may complement one another (Rasher et al. 2013). As more browsers recovered on these reefs, the likelihood of macroalgae being resistant to all species diminished (Lewis 1985, Mantyka and Bellwood 2007).

Indirect effects of protection on the abundance of calcifying substrata were variable in this study. Time since fisheries closure had a weak effect on hard coral cover, as

there were no consistent changes in abundance through the time series. This result supports other studies that indicate coral cover is largely resilient to the effects of fishing (Selig and Bruno 2010, Zychaluk et al. 2012), but it may also mask differential responses of specific coral taxa to protection that change community composition (Darling et al. 2010, 2013). In contrast to coral, CCA cover increased steadily through time as closures matured and showed no evidence of stabilizing by the end of the 43-year time series. This trend has been reported previously and most likely reflects differences in the feeding mode between sea urchins and fishes, where sea urchins bioerode the substratum and limit the establishment of CCA where they are abundant (O'Leary and McClanahan 2010). Perhaps a less obvious conclusion from this finding is that herbivorous fishes may not limit CCA and other factors (e.g. sedimentary environment) contribute to its continual increase as fish biomass stabilizes (Fabricius and De'ath 2001).

A warming event (El Niño Southern Oscillation, ENSO) occurred in 1997-1998 that caused large declines in coral cover (McClanahan 2008). This likely contributed to some of the coral and algal variability observed here, but smaller changes occurred in abundance and taxonomic composition of algae in the fisheries closures than fished reefs (McClanahan 2008). This is surprising given the fact that coral mortality was greater in fisheries closures from more temperature-sensitive taxa (Darling et al. 2013), which increased the available substratum for colonization. Also, the effect of the ENSO on CCA was found to be lower than the magnitude of the effect of sea urchin grazing at fished sites (O'Leary and McClanahan 2010).

The space-for-time substitution method employed here to create a 43-year chronosequence assumes that variance among sites is not significant through time (Stevens and Walker 1970). Model results indicated the data satisfy this assumption for all 12 dependent variables ($n = 29$ site by year replicates) and that sites are tracing similar histories through time (Johnson and Miyanishi 2008). This is likely a result of site selection where all are similarly located in a back-reef lagoon setting along a uniform fringing reef system. All areas except marine reserves, where fishing is prohibited and strongly enforced, are fished intensely and non-discriminately throughout the year (McClanahan et al. 2008a). Consequently, sites represent small differences in spatial heterogeneity and share similar types of disturbances that are relatively uniform (aside from fisheries effects) even though there may be small to moderate differences in temperature variability and water quality (McClanahan et al. 2009, Carreiro-Silva and McClanahan 2012). Similar non-significant differences in the overall fish community were found by McClanahan and Humphries (2012) over 18 years at fished reefs, which supports the assertion of low variability and similar habitat and environmental conditions through time among sites in this system.

Age since closure is expected to directly and indirectly impact species and ecosystem functioning in marine reserves (Babcock et al. 2010). Here, I found evidence for immediate impacts of protection on herbivores and algae. Different responses to protection among herbivore functional groups mediated algal abundance and species composition through fluctuations in grazing intensity and browsing selectivity. These results suggest that the transfer of grazing from non-fisheries (e.g. sea urchins) to fisheries species with reserve establishment may not be a linear process and have cascading consequences for the substratum; reefs in

early stages of recovery (< 20 years since closure) may be more vulnerable to changes in algal composition from turf to macroalgae and represent a transitional community as reefs go from being dominated by sea urchins to fishes. Only once scrapers and browsers have fully recovered will protected reefs go back to being dominated by algal turfs and early successional macroalgae. In addition to eliminating fishing, additional management strategies may be necessary to facilitate the recovery of herbivorous fish populations in some locales, especially where fishing intensity is high and scraping parrotfish populations have been diminished.

CHAPTER 6

GENERAL DISCUSSION

6.1 Patterns and processes

The roles of individual species and of functional groups are central processes in the structuring of ecological systems (Walker 1992). Using coral reefs as a study system, the aim of this thesis was to examine the effects of grazing by herbivores in regulating algal dynamics, and thus reef resilience. The nested design employed here was novel in using different types and ages of fisheries management, which provided a means of assessing the impacts of various combinations of herbivores. The results expand on the work of others that have described the importance of herbivores for critical ecosystem processes on coral reefs (e.g. Ogden and Lobel 1978, Carpenter 1986, Hixon and Brostoff 1996, Mumby 2006, Burkepile and Hay 2008, Hoey and Bellwood 2009, Cheal et al. 2010, Roff and Mumby 2012, Rasher et al. 2013). However, important additional patterns and trends emerged that further our understanding of the mechanisms affected by different herbivores. The emergence of these trends suggests that, while a functional-group approach can be useful for understanding patterns in algal dynamics and ecosystem functioning on coral reefs (Heenan and Williams 2013), it may be necessary to identify the critical role of particular herbivore species or sizes of individuals (Bellwood et al. 2003). The patterns seen throughout these studies serve to emphasize the importance of complementary roles of organisms in resilience theory and fisheries management analyses.

6.2 Resistance to phase shifts

One aspect of resilience is the ability to absorb disturbances or shocks and prevent a shift to an alternative state (Holling 1973). For coral reef ecosystems, this often means preventing a shift to macroalgal-dominance by maintaining low algal biomass with levels of herbivore consumption that are greater than algal production. The herbivore community would only be able to maintain a macroalgal-free reef once it is beyond this grazing threshold, which for Kenyan reefs is 50-70% of algal production, but this threshold will vary amongst locations (Williams and Polunin 2001, Mumby et al. 2007). In early studies, Carpenter (1986) and others (e.g. Bruggemann et al. 1994a, van Rooij et al. 1998) demonstrated that the amount of algae removed was highly dependent on herbivore biomass and less on the species or type of herbivore. Expanding on these findings, this thesis provides strong evidence that scraping parrotfishes may remove more algae (per unit of fish biomass) than previously assumed, and that sea urchins, if released from predation, may similarly prevent algal biomass accumulation (Chapter 2). Overall, these consumption rates demonstrate the potential of both fishes and sea urchins to limit the accumulation of algal biomass on reefs in Kenya with contrasting management regimes (open access fished reefs and fisheries closures). These findings are novel and provide the mechanistic basis through which thresholds are determined and the conditions under which algal biomass may accumulate and persist.

Not only is preventing the accumulation of algal biomass critical to resisting macroalgal phase shifts, but so are the successional patterns and trajectories of algal species. Building on a growing body of literature from the Caribbean and Indo-Pacific that has shown that herbivores influence algal composition and succession

(e.g. Hatcher and Larkum 1983, Scott and Russ 1987, Hixon and Brostoff 1996, Thacker et al. 2001, Ceccarelli et al. 2011), this thesis consolidates the view that sea urchins and fishes have differential effects on algae that are mediated by species abundance and identity. Studies conducted in the Caribbean and Indo-Pacific have reported that scraping parrotfishes may have a disproportionately high impact on algal dynamics and their recovery in fisheries closures is critical for reef resilience (Hay 1981, Carpenter 1986, Lewis 1986, Hixon and Brostoff 1996, Steneck 1997, Williams and Polunin 2000, Williams et al. 2001, Mumby et al. 2006, Nyström 2006, Burkepile and Hay 2008, Bonaldo and Bellwood 2008, Lokrantz et al. 2008, Mumby 2009; but see Cheal et al. 2010). However, the limited spatial extent of some of these studies and high variance in local herbivore assemblage structure raises questions as to the generality of their results. Examining these patterns across broader spatial scales and fisheries management regimes, this thesis extends the findings of these previous studies, and demonstrates the potential for transitional herbivore communities where parrotfishes have not yet fully recovered from fishing. Here, reefs with both sea urchins and fishes allowed rapid succession of algae from turf to early and then late successional macroalgae (Chapter 3). This highlights the possibility for inefficient transfer of grazing from sea urchins to fishes on coral reefs initially recovering from fishing, as well as the importance of parrotfish recovery dynamics on the ability of a reef to resist phase shifts.

6.3 Reversal of phase shifts

Theory suggests that a greater diversity of consumers will effectively consume prey (e.g. macroalgae) by making it unlikely an individual will be defended against all potential consumers (Cardinale et al. 2006, Duffy 2002). However, the vast majority

of studies have been conducted within relatively simple systems with a limited subset of algae or grazers (e.g. Naeem et al. 1994, Tilman et al. 2001).

Consequently, the degree to which this occurs in ecosystems with high biodiversity such as coral reefs is poorly understood. Here, I tested this hypothesis in the context of the consumption of multiple types of macroalgae and found that browsing fishes fed very selectively with low diet overlap among species (Chapter 4). This led to low functional redundancy within a highly diverse browser community. Consequently, the potential consequences for the loss or absence of even one browser species may be critical for its preferred food and the persistence of macroalgae. This finding expands on the work by Bellwood and colleagues (2003) on the Great Barrier Reef by providing an example with browsing instead of scraping fishes.

The effective removal of established macroalgae is achieved only by sea urchins and a subset of fish species (browsing fishes; Mantyka and Bellwood 2007, Cvitanovic and Bellwood 2009, Michael et al. 2013, Rasher et al. 2013) and the reversibility of macroalgal phase shifts has proved to be possible, but typically only in relatively small-scale localized instances (e.g. Bellwood et al. 2006, Carpenter and Edmunds 2006, Stockwell et al. 2009, Smith et al. 2010). This thesis used multiple sites across a broad spatial scale and contributed to the literature by showing the potential of sea urchins and/or fishes to remove established macroalgae where either group is abundant (Chapter 4). In contrast to fishes, sea urchins are highly unselective foragers and their effects were determined more by biomass than species identity or diversity. The dependence on a few key fish species (i.e. *Naso unicornis*, *N. lituratus*) in limiting *Sargassum* abundance even in highly diverse and abundant herbivore assemblages was striking. While previous studies have reported

the removal of *Sargassum* to be dominated by a single or limited number of species, there has been marked variation in the identity of the species (Mantyka and Bellwood 2007, Hoey and Bellwood 2009, Rasher et al. 2013). This thesis highlights an apparent lack of functional equivalents within the fish guild performing key macroalgal browsing functions on coral reefs in Kenya, which should be of concern for managers tasked to increase the resilience of reefs.

6.4 Effects of fisheries closures

Fisheries closures have been advocated as a spatial management tool to hedge risks of overexploitation and environmental stochasticity by increasing resilience (McLeod et al. 2008). Studies across numerous coral reef regions call for protected areas to increase resilience through increasing herbivory (e.g. Bellwood et al. 2004, Hughes et al. 2010). Collectively, the results of this thesis expand on these suggestions by showing it is also possible herbivory will not be constant across transitions from fishing to closures, and increases in herbivory from fisheries closures may not be immediate (Chapter 5). Such trends may allow succession from algal turf to unpalatable macroalgae until scraping and browsing fishes have fully recovered from exploitation (~ 20 years or 300-600 kg ha⁻¹ of total fish biomass in this thesis). This has the potential to increase the vulnerability of newly protected reefs by facilitating competitive interactions between corals and macroalgae. However, temporary reductions in grazing intensity may not occur in all coral reef regions and habitats, particularly where non-fisheries grazers, such as sea urchins, are not abundant (Lessios 1988, McClanahan et al. 1994).

A number of countries, including Kenya, have attempted more inclusive and participatory approaches to fisheries management that allow resource users greater participation in developing and enforcing fisheries rules (Pomeroy et al. 2001, Granek and Brown 2005, Gelcich et al. 2010). This has led to the development of several no-take community closures managed by local fishers. A critical question for the ecology of these reefs is whether these community-managed closures respond to protection in ways similar to larger government-managed closures and wilderness areas (Graham and McClanahan 2013). Results from this thesis support the growing evidence that not all closures have the same effects (Roberts et al. 2001, Halpern and Warner 2002, Gell and Roberts 2003, Graham et al. 2008, Lester et al. 2009, Babcock et al. 2010) and because closure age interacts with fishing and fish life histories (McClanahan and Humphries 2012), findings are not always transferrable. If community closures continue to be established in Kenya without other types of management, including gear restrictions and species-specific harvest bans, the results presented in this thesis suggest reefs may initially be vulnerable to ecological shifts from coral- to macroalgal-dominance due to slow recovery of larger-bodied scraping parrotfishes and macroalgal-removing browsers.

6.5 Conclusions

Overall, this thesis has provided direct evidence for the potential importance of different groups and species of herbivores on coral reefs for overall functioning and reef resilience. While a suite of physical and biological factors may also influence patterns of algal dynamics on coral reefs, the findings provide evidence of strong top-down control by both sea urchins and herbivorous fishes of algal composition, succession, and consumption. Although the ability of a reef to resist macroalgal

phase shifts appears to depend on certain assemblages of species or functional groups (i.e. sea urchins or large-bodied parrotfishes), the reliance on individual species removing established macroalgae was surprising and highlights an inconsistency between diversity and ecological function. The failed recovery of a single group of herbivores, or the loss of a single species, may severely erode ecological function and subsequently the capacity of reefs to resist or reverse macroalgal phase shifts. Given that human impacts on coral reef ecosystems are increasing as a consequence of climate change, overexploitation, habitat loss, pollution, and invasive species (Chapin et al. 2000, IPCC 2007, Newton et al. 2007, Halpern et al. 2008), the capacity to resist and reverse macroalgal phase shifts is increasingly recognized as key processes for reef sustainability. Ultimately, the removal of algae is dependent on a limited group of species, and these should be considered as especially critical to the health of coral reefs.

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