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Insights on herbivory : An examination of herbivore consumption and algal production on Hawaiian coral reefs

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Insights on herbivory: An examination of herbivore consumption and algal production on Hawaiian coral reefs

A dissertation submitted in partial satisfaction of the requirements for the degree Doctor of Philosophy

in

Marine Biology

by

Emily Lindsay Allen Kelly

Committee in charge:

Professor Jennifer Smith, Chair
Professor Paul Dayton
Professor James Leichter
Professor Lisa Levin
Professor Stuart Sandin
Professor Jonathan Shurin

2015

The Dissertation of Emily Lindsay Allen Kelly is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Chair

University of California, San Diego

2015

DEDICATION

To my parents, Missy and Clinton Kelly, and my brother, Clint, who encouraged me to explore, observe, and ask questions as we adventured together as a family.

EPIGRAPH

“I love my work. I couldn’t be luckier or happier than what I’m doing now. But, say, if I could go to the beach and not have to run in and look at the algae that are growing at that particular beach, that would be nice. But I don’t do that.”

Isabella Aiona Abbott

In an interview on June 17, 2008 on how she has enjoyed her career and how her passion permeated every visit to the beach.

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I would first like to thank my advisor, Jennifer Smith, for her mentorship, guidance, and contagious love of seaweeds throughout the last seven years. Jen has always pushed me to consider the broader ecological context of my research while still being meticulous in experimental design and execution. I am indebted to Jen not only for her encouragement and wisdom, but also her enthusiasm for science, the ocean, and students and colleagues. In an early field season on Maui when many of us from the "Smith Lab in Maui Extension Office" (SLIMEO) were on island, we all loaded into our rented minivan for a tour of leeward Maui reefs, hopping in and out of the car to look at reefs we would later explore in detail. We then spent an afternoon standing in three feet of water in an old Hawaiian fishpond picking through what were then new seaweed friends. Some of these initial experiences in the field and countless since encouraged my passion for ecology and exploration and helped train my search images for tiny limu. From the intertidal in front of Hubbs Hall to the Southern Line Islands to our favorite reefs on Maui, Jen has been such a wonderful teacher and example to me of a great field ecologist. It has been such a pleasure to work with Jen, starting our Scripps years together, and I look forward to many more years of exploring ecology and looking at seaweeds under the microscope in the years to come.

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Chapter 1, in part, is currently being prepared for submission for publication of the material. Kelly, Emily L. A.; Eynaud, Yoan; Clements, Samantha; Sparks, Russell; Williams, Ivor; Smith, Jennifer E. The dissertation author was the primary investigator and author of this material.

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Chapter 4, in part, is currently being prepared for submission for publication of the material. Kelly, Emily L. A.; Sparks, Russell; Smith, Jennifer E. The dissertation author was the primary investigator and author of this material.

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ABSTRACT OF THE DISSERTATION

Insights on herbivory: An examination of herbivore consumption and algal production on Hawaiian coral reefs

by

Emily Lindsay Allen Kelly

Doctor of Philosophy in Marine Biology

University of California, San Diego, 2015

Professor Jennifer E. Smith, Chair

Herbivory is an essential component to maintaining ecosystem structure and function in both terrestrial and marine systems. Benthic fleshy algal production on coral reefs is controlled by both bottom-up influences via nutrient availability and top-down control by herbivorous fishes, urchins, and invertebrate microherbivores. Anthropogenic impacts have modified reefs around the world, shifting their composition from dominance by reef builders to increased dominance by fleshy algae and non-coral invertebrates. This dissertation is an examination of herbivory on coral reefs, exploring the contributions of individual herbivore species as well as the herbivore community as a whole to the consumption of reef algal production. I explored the functional redundancy of the diverse community of herbivorous fish at Kahekili Herbivore Fisheries Management Area (KHFMA) on West Maui, Hawaii, finding that herbivorous fish across guilds on the reef largely consume turf algae, though these turf communities may vary in composition. However, herbivorous fish are consuming different types of macroalgae, turf algae, and other substrates selectively based on benthic composition. I further developed a model for calculating benthic fleshy algal production and herbivorous fish consumption at Kahekili. Through this model, I determined benthic fleshy algal production exceeded fish community consumption by three-fold, although larger size classes of herbivores in more recent years were contributing more to the consumption budget. I then applied this model to a diverse set of reefs around Maui to determine the relative balance of algal production and fish consumption, seeing a handful of reefs with a balanced budget. I further found that consumption rates were a better predictor of benthic community structure than fish biomass. I further determined that more herbivorous fish biomass would be required to reduce algal cover on a reef than maintain low algal cover on an already high coral cover reef. Finally, I examined the relative role of the herbivorous fish community and sea urchins on reef community composition and algal biomass. I found that herbivorous fish contributed more to macroalgal removal while urchins contributed more to turf grazing and exposure of bare limestone. Herbivorous fish may be also be facilitating further urchin grazing. The results of these four chapters support the potential for herbivore management to aid in recovery of degraded reefs.

INTRODUCTION

Herbivory is an essential component to maintaining ecosystem structure and function in both terrestrial (McNaughton 1984, Borer et al. 2014) and marine (Randall 1961, Jones 1968, Carpenter 1986, Hatcher 1988) systems. Herbivore grazing keeps plant standing stock low but can also stimulate rates of productivity through regular cropping of plant biomass preventing self-shading and density dependent processes (McNaughton 1985, Williams & Carpenter 1990, Tilman et al. 1997, Van Rooij et al. 1998, Russ 2003, Kopp et al. 2010). On coral reefs, production by benthic algae (Carpenter 1986, Littler et al. 2006) and the coral holobiont (Odum & Odum 1955, Rohwer et al. 2002) combine to make one of the most productive ecosystems in the world (Westlake 1963), through rapid nutrient recycling despite having largely evolved in oligotrophic waters (Odum & Odum 1955, Johannes et al. 1972, Hatcher 1990).

Benthic algal primary production on coral reefs is controlled by both bottom-up influences via nutrient availability (Lapointe 1997, Dailer et al. 2012) as well as top-down control by herbivorous fishes, urchins, and invertebrate microherbivores (Wanders 1977, Ogden & Lobel 1978, Carpenter 1986, Van Rooij et al. 1998). Actively calcifying near-pristine tropical reefs are generally dominated by scleractinian corals and crustose coralline algae (CCA)(Sandin et al. 2008, Barott et al. 2010, but see Vroom & Braun 2010), as a result of low bottom-up influence and strong top-down control on fleshy algae (Littler & Littler 1984, Smith et al. 2010). Anthropogenic impacts, including excessive nutrient addition (Smith et al. 1981, Szmant 2002) and overfishing (Jackson 1997, Jackson et al. 2001), have modified reefs around the world, shifting their composition from dominance by reef builders to increased dominance by fleshy algae and non-coral invertebrates (Hughes 1994, Pandolfi et al. 2005, Bruno et al. 2009, Cruz et al. 2015).

This dissertation is an examination of herbivory on coral reefs, exploring the contributions of individual herbivore species as well as the herbivore community as a whole in the consumption of reef algal production. The potential of herbivore fisheries management to be used as a tool for reef restoration and/or resilience has gained growing support throughout the community of coral reef managers and scientists (Hughes et al. 2007, Rasher et al. 2013, Jackson et al. 2014). An herbivore fisheries management area geared towards herbivore protection was established in Maui, Hawaii in 2009 with the goal of increasing herbivore biomass that would theoretically consume fleshy algae and ultimately enhance the abundance of reef building species (coral and crustose coralline algae) on the benthos. Earlier that year, Belize also protected herbivores and since that time the Bay Islands of Honduras, Guatemala, and Barbuda have protected parrotfish from fishing. While we understand the importance of herbivores in reef ecosystem functioning and algal control from a coarse perspective, the importance of herbivore diversity and species-specific feeding behavior in addition to herbivore biomass must be more fully considered to understand how these communities actually affect benthic community composition and algal production. The ability of herbivores to consume benthic algae and how this translates into not just changes in biomass but changes in cover and thus community structure must be more fully explored within the context of a diverse suite of specific reef systems. The goal of this dissertation is to provide quantitative species-specific and community assessments of the role of coral reef herbivores in consuming benthic algae and thus the ability of reef herbivores to alter reef community structure.

In Chapter 1, I explored the functional redundancy of the diverse community of herbivorous fish at Kahekili Herbivore Fisheries Management Area (KHFMA) and examined their grazing preferences across herbivore guilds. I quantified species-specific preferences of herbivores in consuming different groups of reef algae and the extent of dietary overlap among them. I further placed fish bite observations within a reef context to determine how fish selected substrate type based on substrate availability. The results of this chapter show that herbivorous fish on the reef varied in both bite rate and types of substrate bitten and confirmed that fish species were selecting for different types of available algae. Despite differences in herbivore selectivity and feeding behavior, all species predominantly (73-100%) ate turf algae. However, gut content analyses revealed that different species of herbivores may even be selecting for different types of turf algal species showing a finer level of selectivity than can be observed from simple behavioral observations.

In Chapter 2 I took a functional approach towards examining the effects of the potential changes in herbivore biomass at KHFMA. I developed a model for calculating benthic fleshy algal production and herbivorous fish consumption at Kahekili utilizing parameters derived from extensive in situ experiments and observations. I used a bootstrapping approach to combine distributions of fish biomass and consumption rates to calculate total rates of consumption. These consumption rates were then compared to a bootstrapped distribution of production, derived through multiple distributions of algal growth, standing stock, and benthic percent cover data. My results showed that after five years of protection at Kahekili, herbivore consumption is still less than algal production on the reef. The results of this study highlight the increasing importance of larger herbivores, particularly of the scraper/excavator feeding guild, in consuming benthic algal production on the reef.

I applied this model to eight additional reefs around the island of Maui in Chapter 3 to quantify benthic fleshy algal production and herbivorous fish consumption through time on these reefs and to develop a better understanding of how production and consumption compare across reefs with different benthic and herbivorous fish communities. I found fish consumption rates were a better predictor for benthic community structure than was fish biomass and that net production (gross production minus herbivore consumption) was lowest at reefs with high coral cover as compared to low coral cover reefs even when those reefs had greater fish biomass. This pattern was stronger when considering benthic cover of reefs in terms of all calcifiers (coral and CCA). Examining rates of production and consumption provide a functional framework through which I estimated the consumption deficit of algal production on reefs. The results of this study suggest that the amount of herbivore biomass needed to reduce algal biomass to a point where coral cover may actually start to increase may need to be much greater on reefs that have suffered decline relative to herbivore biomass found on adjacent high coral cover reefs.

Finally, in Chapter 4 I expanded my examination of the herbivore community at Kahekli through a two-year factorial caging experiment examining the relative role of the herbivorous fish community and sea urchins (as represented by *Tripneustes gratilla*) on reef community composition and algal biomass. I found the greatest differences in benthic community composition and algal biomass were observed in experimental treatments where herbivorous fishes and fish and urchins were removed from experimental plots. I also found that open cage-control plots were most similar in cover and biomass to treatments with fish and urchins present, suggesting that both fish and urchins are important herbivores at Kahekili.

The results of this dissertation contribute to our broader understanding of the impacts of a diverse community of herbivores on coral reefs, the species-specific nature of these impacts, and the potential for using herbivores as a management strategy to aid in recovery of degraded reefs.

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CHAPTER 1:

Investigating functional redundancy versus complementarity in Hawaiian herbivorous fishes

Emily L. A. Kelly, Yoan Eynaud, Samantha Clements, Russell Sparks, Ivor Williams, Jennifer E. Smith

Abstract

The patterns of resource use of individual species provide insight into their functional roles and thus their ecological significance within a community. The functional role of herbivorous fishes on coral reefs has been defined through a variety of direct and indirect methods but from a grazing perspective little is known about the species specific preferences of herbivores on different groups of reef algae and the extent of dietary overlap across an herbivore community. We used two techniques to assess herbivore grazing at a reef on the island of Maui, Hawaiian Islands, USA. First, we tracked fish behavior in the water to record fish bite rate and type of substrate bitten. Second, we examined gut contents of a select number of herbivorous fishes to examine diet at a finer scale. Finally, we placed fish bite observations within a reef context to determine how fish selected substrate type based on substrate availability. We determined that herbivores on the reef varied in both bite rate and types of substrate bitten and that fish species were selecting for different types of available algae. Despite these differences across consumption patterns, all species predominantly (73-100%) ate turf algae. Gut content analysis suggests that herbivores may even be selectively consuming different types of turf assemblages. In situ observation combined with gut content analysis allowed us to differentiate within and between species bite rates and substrates bitten within a given reef context to provide insight into the herbivore “rain of bites” across a reefscape. These results have implications for benthic community composition and consideration of the role of multiple species within the herbivore community beyond measurements of herbivore biomass alone.

Introduction

Species with different functional roles within an ecosystem comprise a variety of guilds, in which the species of a single guild use similar resources often through similar means (Root 1967, Simberloff & Dayan 1991, Green & Bellwood 2009). While these similarities are used to identify a feeding guild, the (sometimes) diverse species within the guild may be considered to be functionally redundant, occupying the same ecological niche, or complementary, in which niches amongst species do not overlap. Theoretically, there may be a large amount of functional redundancy amongst individuals in a guild within an ecosystem but competition and/or limited availability of the resource will result in niche partitioning and an apparent functional complementarity among consumers (Hutchinson 1959, Chase & Leibold 2003). Studies across terrestrial, marine, and aquatic systems of seedling diversity in old fields (Ostfeld et al. 1997), macroalgal consumption on tropical reefs (Burkepile & Hay 2011), and insect larvae in streams (Rudolf et al. 2014) suggest that functional complementarity amongst consumers result in a wider breadth of resources being consumed and a greater efficiency in energy transfer to higher trophic levels. There is, however, still debate as to the theoretical likelihood of functional redundancy within or among ecosystems (Loreau 2004).

Ecosystems with higher species richness are more likely to capture complementary species (Loreau & Hector 2001), though the greater number of species may also suggest there be more species with overlapping functional roles (Strong 1992). Species diversity and function may therefore have implications for ecosystem resilience to both natural and anthropogenic perturbations (Strong 1992). For instance, the removal of a single species in a low diversity system with limited functional redundancy can result in a trophic cascade, as commonly observed in kelp forests where overfishing of predatory sea otters, leads to a bloom in their prey—sea urchins, causing massive loss and the denudation of kelp forests (Estes & Palmisano 1974, Estes et al. 2011). By contrast, in more complex ecosystems with higher species richness and higher functional redundancy at a given trophic level, the removal of any one species may be absorbed by other redundant species resulting in "trophic trickles" rather than cascades (Strong 1992).

On coral reefs complementarity versus redundancy within herbivorous fish communities is important for understanding how the herbivore community influences the composition, biomass and productivity of benthic algal assemblages. The complexity and high species diversity within coral reef food webs (Odum & Odum 1955, Polovina 1984) including unrelated organisms feeding on the same food source (Hay & Taylor 1985) suggest there could be high levels of functional redundancy across trophic levels within the reefscape. Grazing of algae by the herbivore guild is believed to be particularly important on coral reefs for promoting coral dominance by reducing algal standing stock and thus minimizing coral-algal competition (Ogden & Lobel 1978, McCook et al. 2001) and promoting other important reef builders such as crustose coralline algae (Smith et al. 2010). However, coral reef herbivorous fish biomass and diversity are known to be globally impacted by fishing, and particular species are more or less effected by fishing, thus there is a need to consider the role of individual species in reef dynamics (Edwards et al. 2014). Given the global decline in the abundance of reef corals and the rise in the abundance of fleshy algae (Pandolfi et al. 2005) there has been more frequent discussion of the use of herbivore restoration or enhancement as a tool for reef management (Jackson et al. 2014). In order for this approach to be effective we need a better understanding of the roles of individual herbivores, incluing the amount of redundancy versus complementarity in their consumption of benthic algal assemblages.

Benthic reef algae comprise a highly diverse and often complex group of photosynthetic organisms spanning several phyla. Those algae have evolved numerous adaptations and defenses to herbivory including physical protection of the thallus (calcium carbonate, leathery thalli, etc.), chemical defenses (secondary metabolites), cryptic growth forms, and rapid growth rates to cope with frequent grazing (Steneck & Dethier 1994, Hay et al. 1987, Williams & Carpenter 1990, respectively). Thus not all algae are equally palatable to herbivores nor are all herbivores capable of extracting nutrition from all types of algae (Choat et al. 2004). In addition, field examination of algae can be troublesome. While macroalgae are often identifiable to at least genus level, turf algae are generally too diminutive for identification by eye in the field. Turf algal assemblages can also contain hundreds of species (Adey & Steneck 1985) and be highly spatially variable even between adjacent turf-covered coral colonies (Harris et al. in review). Turf assemblages are often the most common competitors for space with corals (as reviewed in (as reviewed in McCook et al. 2001, Barott et al. 2009, Haas et al. 2010) and there is evidence that turf algae are becoming more abundant on reefs with local human impacts (Jouffray et al. 2015). Thus, there is a need to better quantify the frequency and intensity of grazing by herbivorous fishes on turf algae to provide a greater understanding of benthic community dynamics.

The functional niches of herbivorous fish may be defined based on their feeding behavior (Bruggemann et al. 1994), mouth morphology (Bellwood & Choat 1990), phylogeny (Bellwood 1994), herbivore guild (Green & Bellwood 2009), and/or assimilation rate (Ogden & Lobel 1978). While taxonomic relationships are often used to place herbivores within particular feeding guilds, predictions of feeding preferences based on phylogenetic relationships do not always hold (Choat et al. 2002). Therefore, investigation into herbivore gut contents (Choat et al. 2004) and *in situ* observational bite rate data (Hamilton et al. 2014) can provide greater insight into the nutritional ecology of fishes with regards to growth, maturation, and reproduction (Clements et al. 2009) as well as the ecological impact of fishes on the reef benthos. Field studies that investigate individual herbivore preferences for algae typically focus on grazing on macroalgae (Mantyka & Bellwood 2007, Burkepile & Hay 2008) or use grazing assays of single abundant or highly palatable macroalgal (or seagrass) species as a proxy for overall grazing rates on reefs (Hoey & Bellwood 2009, Chong-Seng et al. 2014). Fewer studies have considered bite rates on turf algae (but see Brandl & Bellwood 2014, Hamilton et al. 2014). To date comparisons among herbivores have focused on only a small subset of the herbivore community (Fox & Bellwood 2007, Mantyka & Bellwood 2007, Burkepile & Hay 2008). Here, we aim to bring together techniques for field efforts and laboratory gut content analysis to quantify species-specific preferences of the suite of herbivorous fishes within a reef community on different groups of reef algae and determine how diets may or may not overlap.

In general herbivores have been shown to prefer certain types of algae through both preference experiments in the lab and selectivity calculations in the field based on feeding rates and benthic community composition. For example, crabs in Caribbean selectively graze on two common species of fleshy macroalgae (Butler IV & Mojica

2012) while urchins in Hawaii show malleability of macroalgal preferences based on exposure or conditioning (Stimson et al. 2007). When comparing herbivore bite rates via field observation and benthic community composition, Hamilton et al. (2014) identified specific feeding preferences of herbivorous fish in the central Pacific. Placing herbivores in the context of their environment provides additional information as to how they select food based on its availability. Examining selectivity of herbivores can therefore provide insight into the future trajectory of the benthic communities that are being grazed.

In the Main Hawaiian Islands coral cover has decreased and fleshy algae have become more abundant on many reefs (Rodgers et al. 2015). While many of their counterparts in the Caribbean are typically macroalgal dominated (Roff & Mumby 2012), many reefs in the Hawaiian Islands have undergone phase shifts to both macro and turf algae; in some cases upward of 50% - 90% of the reef benthos is covered with turf algae (Jouffray et al. 2015). Herbivore populations have also declined from historic estimates as a result of fishing (Williams et al. 2008, Kittinger et al. 2011, Edwards et al. 2014). A negative relationship between algal cover and herbivore biomass has been shown for reefs in the Main Hawaiian Islands (Friedlander et al. 2007) and the Caribbean (Williams & Polunin 2001). This strong relationship implies loss of ecosystem function by the grazers on reefs that have been overfished, but we have limited data on the role of individual species of herbivores on these reefs, particularly with regards to variability in consumption of different functional groups of algae. It is therefore important to identify the feeding roles of individual herbivores to understand how species select algae from the available benthic community and how herbivore communities may directly and indirectly influence the reef benthos.

The goals of this study were to identify the individual roles of herbivorous reef fish species and to quantify the extent of functional complementarity and redundancy of herbivores on the island of Maui using several different approaches. First we used *in situ* behavioral observations to quantify the grazing intensity (bite rates) and food preferences (consumption relative to availability) of herbivores and second we examined gut contents of a subset of herbivore taxa to examine finer scale detail of the diets of these fishes. Comparing data across these two methods of inquiry and scales of observation provides insight into the functional role of herbivorous fish in the Hawaiian Islands.

Methods

This study was conducted on the leeward side of the island of Maui, Hawaiian Islands, USA. The observational component was conducted at the Kahekili Herbivore Fisheries Management Area (KHFMA), established in 2009 as a $2km^2$ no-take area for herbivorous fish and sea urchins. Destructive sampling of fish guts was conducted north of KHFMA at Kapalua Bay and south of KHFMA at Olowalu mile marker 14 (Figure 1). These additional two sites were chosen because they have similar fish and benthic communities to KHFMA and they are not no-take areas for herbivores.

Behavioral Observations

To determine the ecological impact of herbivorous fishes and their pattern of algal consumption on the reef, grazing rates for all abundant herbivorous fish species were determined using timed behavioral observations. Divers followed individuals of the families Labridae (Scarinae; parrotfish) and Acanthuridae (surgeonfish) to record bite rates and type of substrate consumed by fish during 3-5 minute timed swims. This time period allowed for multiple forays (grazing episodes) as well as other social behavior and has been successfully implemented in other studies (Bellwood & Choat 1990, Hamilton et al. 2014). If fish behavior appeared to be altered by diver presence, observation of that fish was terminated and the data excluded from analysis. Between ten and 48 observations were made for each of the 15 most common species of herbivorous fishes in Maui (determined using Hawaii Division of Aquatic Resources unpublished survey data). Observational data for other, rarer, species are included here but sample size is limited for some of those taxa. All observational data were taken between 2m and 10m depth at Kahekili Herbivore Fisheries Management Area between 2009 and 2012.

During each behavioral observation, divers recorded the herbivore species, total length (to the nearest cm), number of bites, and type of benthic substratum that was consumed per bite. Substratum type was recorded to the finest taxonomic classification possible through field identification. Macroalgae were identified to genus while turf algae, crustose coralline algae and other benthic groups were identified as functional groups. In cases where turf algae were growing as epiphytes on macroalgae, the bite was considered a bite on turf algae unless tissue from macroalgae was clearly removed. Species grazing on turf algae were recorded as grazing on “turf” despite the heterogeneous nature of the turf community because turfing algae cannot be identified at a finer scale in situ. Differentiation in these bites among turf algae was done through gut content analysis described below.

To describe the distribution of the observed bites by herbivores on different benthic taxa, the bites per minute on each benthic group for each herbivore species were averaged and data were transformed using log(x +1) to account for the large number of zeros in the dataset (Anderson et al. 2008). Bray Curtis Similarity (BCS) distances (BCS = 1 – Bray Curtis Dissimilarity distance) were then calculated for transformed data (Somerfield 2008). Non-metric multidimensional scaling (nMDS) plots were used to visualize the BCS values among the different herbivore species' bite data on different benthic categories. To account for differences among species in feeding rates, in addition to absolute bite rates, the proportion of bites for each herbivore taken on different substrate types was also calculated and averaged for each herbivore species. These data were then transformed using log(x+1) and BCS calculated for each pair. nMDS plots were used to visualize the ranked BCS among the different herbivore species' proportional bite data on different benthic categories.

To determine whether diets within herbivore species were more similar to each other than diets among species we used a single-factor permutation based multivariate analysis of variance (PERMANOVA; Anderson et al. 2008), in which fish species was the fixed factor and pseudo-F was calculated using 9999 unrestricted permutations of data. Post hoc pair-wise comparisons were used to test for significant differences in bite rates on particular algal among species. We acknowledge the possibility of a Type I Error in using multiple pair-wise comparisons, but for consistency in evaluating the evidence of differences we did not calculate an adjusted p-value (Hurlbert & Lombardi 2009, 2012).

We investigated whether diets of herbivores within feeding guild were more similar to each other than to species in other guilds. We categorized each species in this study according to feeding guild based on Green & Bellwood (2009) as follows: scraper

/ small excavator (all *Scarus* and *Chlorurus* <35cm), browser (all *Naso* and *Calatomus*), grazer / detritivore (all *Acanthurus* aside from planktivores and *Ctenochaetus*) (Table 1). We compared the mean proportion of total bites for each species on each benthic category in order to compare dietary composition as opposed to bite rate across species. These data were then transformed using log(x+1) and BCS calculated for each pair. nMDS plots were again used to visualize the ranked BCS and further overlaid with a cluster analysis of the BCS data to show similarity contours among species.

The nMDS and PERMANOVA analyses were performed using PRIMER v6.1.11 ® (Clarke & Gorley 2006) with PERMANOVA+1.0.1. add-on package (Anderson et al. 2008).

Gut Contents

To examine the fine-scale composition of herbivorous fish diets, gut contents were analyzed from six species of Acanthurids (*Acanthurus leucopareius*, *A. nigrofuscus*, *A. nigroris*, *A. olivaceus*, *A. triostegus*, and *Ctenochaetus strigosus*). Individuals of each of these species were speared by snorkelers and stored on ice immediately upon return to shore. Collected fish were dissected within two hours of being caught or frozen immediately for later dissection. Stomachs were removed, slit along the side to open, and stomach tissue and contents were stored in glass vials in 10% formalin in seawater.

In the lab, stomachs were removed from formalin and were emptied by flushing with seawater to isolate all contents into a dish. Contents in seawater were transferred into a 50 mL Falcon tube, shaken to break up clumps, and poured back into a plastic gridded petri dish where they were spread evenly. At twenty randomly chosen points on the gridded dish, contents were examined using dissecting microscope at 40x magnification. Gut contents were identified to morphological group according to functional-form groups adopted from Steneck & Dethier (1994) as follows: (1) filamentous, (2) foliose, (3) complex cylinder, (4) net-like, (5) coenocytic, (6) jointed calcareous, (7) encrusting, (8) calcified crust, and (9) thick and leathery. It was possible to identify seaweeds to this level of functional form despite their often small size or partially digested nature. Functional forms are known to reflect algal traits including the degree of grazing palatability (Padilla & Allen 2000). Cyanobacteria, detritus, sand, and invertebrates were also identified. Contents were quantified using the proportion of algal functional groups at each point to eliminate variance due to volume of gut contents per sample (Choat et al. 2002).

We examined differences within the turf algal functional group across herbivorous fish gut contents to assess whether there was evidence for selectivity at a finer scale. While turf algae are typically defined as a mixed assemblage of filamentous algae that are 2 cm or less in height (Adey & Steneck 1985), “turf” can incorporate many of the functional forms of algae described in Steneck & Dethier (1994). Here we defined turf algae functional forms in gut contents based on turf algae surveys in Hawaii (Stuercke & McDermid 2004) to include the cyanobacteria, filamentous, foliose, complex cylinder, and net-like forms.

Total gut content data and turf functional form gut content data are expressed as the mean proportion of gut contents by herbivore species with standard error. Potential differences in similarity of gut contents across herbivore species were evaluated using PERMANOVA and post hoc pair-wise comparisons were used to determine differences among species gut contents (Anderson et al. 2008) as in the analysis of observational data.

Feeding selectivity

To determine the degree to which fish bites on different benthic groups are a reflection of the availability of those groups on the benthos versus the degree to which fish preferentially selected certain species or functional groups of algae, a selectivity analysis was conducted on bite rate data following Chesson (1978, 1983). Per Chesson (1978), selectivity is defined as:

$$\hat{\alpha}_i = \frac{r_i/n_i}{\sum_{j=1}^{m} r_j/n_j}, i = 1, \dots, m$$

where α is the selectivity index between 0 and 1, r is the bite rate on a given benthic group and n is the percent cover of that benthic group on the reef. α was calculated for all algae consumed by each fish species, from 1 to m. The null selectivity (α_{null}), for the herbivore community is defined as $1/m$, where m is the total number of benthic groups available to herbivores on the reef and bitten by any of the herbivores observed. Benthic groups were assessed at the genus level for macroalgae and at the functional group level for everything else (turf algae, crustose coralline algae (CCA), cyanobacteria, coral and sand). If the calculated α equals α_{null}, then that a benthic group was bitten at a rate predicted from its availability on the reef whereas an α below α_{null} indicates the benthic group was chosen less than its availability would predict and an α above α_{null} indicates the benthic group was chosen more than its availability would predict.

Benthic cover was determined from surveys conducted twice a year (summer and winter) in both 2011 and 2012 by the Hawaii Division of Aquatic Resources and NOAA's Coral Reef Ecosystem Division at KHFMA. During each survey ~80 - 100 transects were surveyed in stratified random sampling pattern according to reef habitat types and 1 m^2 photoquadrats were taken every 1 m along 25 m belt transects. Photographs were analyzed using the image analysis program PhotoGrid 1.0 in which 15 - 100 stratified random points per photo were identified to genus level for corals and algae or functional group for turf algae, crustose coralline algae, and cyanobacteria.

Due to logistical constraints, it was not possible to instantaneously quantify benthic community composition directly at the points of substrate where herbivore were grazing at the time of each bite. Therefore, α was calculated using a resampled bootstrapped distribution of benthic cover of the habitat in which bite data were collected. This benthic distribution was then used in the calculation of α for each bite observation and the mean and standard deviation were calculated.

Results

Behavioral Observations

The overall diets of herbivorous fish based on absolute bite rate per substrate type were significantly different among species (PERMANOVA Pseudo-F = 9.162, p = 0.0001; Figure 2A and 3). However, all herbivorous fishes in this study were observed predominantly biting on turf algae. The species with the greatest bite rates on turf algae were *Acanthurus triostegus* (44.8 bites / min), *A. olivaceus* (30.0 bites / min), *A. nigrofuscus* (34.7 bites / min), *A. leucopareius* (29.8 bites / min), and *Scarus psittacus* (20.0 bites / min). In addition to bites taken on turf algae, most fish also took a small proportion of their bites on various and often different genera of macroalgae. Pair-wise comparisons show that the diets of over half of the herbivore species are between 80% and 100% similar. Despite these high levels of similarity, there are differences among several species particularly driven by *A. olivaceus* and *C. carolinus* and to a lesser extent *N. brevirostris*, *N. lituratus*, and *N. unicornis* (Figure 3A).

Non-metric Multidimensional Scaling (nMDS, 2D, stress = 0.05) using BCS distance with log(x+1) transformation (Figure 2B) shows herbivore species arranged roughly from left to right corresponding to bite rates (fastest to slowest). *Acanthurus olivaceus*, which had the second fastest bite rate of all species and took >25% bites on sand, is separated from all other species of herbivores. Those herbivores with moderate bite are still clustered in the bottom middle of the plot. Finally, herbivores with lower bite rates and the highest substrate type diversity within their bites (*Naso lituratus*, *Naso unicornis*, *Naso brevirostris*, and *Calotomus carolinus*) are all on the right-hand side of the nMDS plot.

The proportion of bites taken on all substrate types also differed among herbivorous fish species (PERMANOVA Pseudo-F = 5.392, p = 0.0001). The average relative abundance of bites on turf algae ranged from 100% to 73% across all species (Figure 2C). *Naso unicornis*, *Naso brevirostris,* and *Naso lituratus* had the greatest diversity of substrate types consumed (9, 7, and 6, respectively). *Acanthurus olivaceus* had the highest proportion of bites on something other than turf algae (sand = 27%).

Pair-wise comparisons revealed similar patterns as the bite rate and composition data, though diets of *N. brevirostris* and *A. nigrofuscus* are less similar and while *C. carolinus* and *C. strigosus* are still different, they are more similar to one another than when considering absolute bite rate data.

The nMDS plot of the diets based on BCS distance with a log(x+1) transformation of the proportion of bites (Figure 2D; 2D, stress = 0.09) data shows greater spread of species. The greater spread in these data likely reflects the similarities among the proportion of bites taken on turf by most of the herbivore species studied here. Cluster analysis of the proportional bite rate data for species organized by feeding guild showed that the browsers are most similar to one another (60% similarity) while the diets of the species in the other two guilds were less well delineated (Figure 4; see also Table 1). In this case, the diets based on proportional data for the scrapers *S. rubroviolaceus* and *C. perspicillatus* and the grazers *A. triostegus*, *A. leucopareius*, and *A. blochii* were all 80% similar while less similar to others in their guilds (60% or less).

Gut Contents

The composition of algae found in the guts of the herbivores studied here was significantly different among species (PERMANOVA Pseudo-F = 13.071, p = 0.0001; Figure 6A). When looking just at the functional forms typically found within turf algae, the composition of these forms also differed significantly among herbivore species (Figure 6B) (PERMANOVA Pseudo-F = 2.9759, p = 0.0265). Pair-wise comparisons reveal several significant differences (Figure 7). In particular, *A. olivaceus* and *C. strigosus* were both different from all other species (P(perm) < 0.05). Composition of turf algae in the guts for *A. nigrofuscus* and *A. triostegus* were also different from one another (P(perm) < 0.05). For *A. olivaceus* and *C. strigosus*, feeding observations showed high consumption on turf algae but gut contents included considerable detritus and sand that feeding fishes of those species likely combed out of turf algal assemblages they appeared to be feeding on.

Feeding selectivity

Average benthic cover between 2011-2012 across the reef at KHFMA was 34.18% (+/- 0.73) coral (*Porites lobata* = 19.05% (+/- 0.50), *Porites compressa* = 7.18% (+/- 0.33), *Montipora capitata* = 5.58% (+/- 0.25), etc.), 43.7% (+/- 0.94) turf algae, 7.70% (+/- 0.40) crustose coralline algae, and 2.63% (+/- 0.16) macroalgae (all species representing less than 1% each).

Despite the high coverage of turf on the reef, about half of the herbivore species observed biting on turf were doing so at a rate in which $\alpha_{turf} > \alpha_{null}$, indicating that these fish were disproportionately selecting turf algae (Figure 5; *Acanthurus blochii, Acanthurus leucopareius, Acanthurus nigrofuscus*, *Acanthurus triostegus, Chlorurus perspicillatus,* and *Scarus rubroviolaceus*). The scarid *C. perspicillatus* was only observed biting turf algae and nothing else ($\alpha_{turf} = 1$). This redundancy in consumption of and selection for turf algae across these herbivores is contrasted by other species that consumed turf algae as would be predicted by turf availability ($\alpha_{turf} = \alpha_{null}$; *Acanthurus olivaceus, Calotomus carolinus*, *Chlorurus spilurus*, *Ctenochaetus strigosus*, *Naso brevirostris*, *Naso lituratus, Scarus psittacus,* and *Zebrasoma flavescens*). These species were also seen biting on various species of macroalgae, coral biofilm, or sand. Because combined macroalgal cover on the reef was less than 3% of total cover, even rare bites on macroalgae genera often result in selectivity exceeding α_{null}. *N. brevirostris*, for example, consumed turf, *Melanamansia*, *Tolypiocladia*, and other macroalgae as predicted by availability and strongly selected for *Laurencia*. Some species, like *N. unicornis* strongly selected for *Turbinaria*, while avoiding turf algae ($\alpha_{turf} < \alpha_{null}$). All species were seen to select for at least one substrate type.

Discussion

Given the recognized importance of coral reef herbivorous fish for their potential to prevent or reverse coral to seaweed phase shifts (Hughes et al. 2007, Fox & Bellwood 2008, but see Cheal et al. 2010), it has become increasingly important to understand species specific diets and grazing rates. The data presented here demonstrate that herbivore species within a single reef community have different consumption patterns in terms of both bite rate and in the type of substrate bitten. While other studies have documented negative relationships between herbivore biomass and algal cover on reefs in the Caribbean and the Pacific (Williams & Polunin 2001, Friedlander et al. 2007), our work informs this relationship further in deciphering which herbivore species have the potential to impact the cover of different types of algae. While macroalgae only make up ~3% of benthic cover at Kahekili, we see functional complementarity across herbivores in macroalgal consumption. On reefs with greater abundance of macroalgal cover in the Caribbean and the Pacific (20-91%; Burkepile & Hay 2008, 2011, Rasher et al. 2013) studies have also shown functional complementarity of reef fishes in consuming macroalgae. These studies have relatively low herbivore diversity as compared to other studies in the Pacific with high herbivore diversity and low macroalgal cover that have highlighted the importance of key grazers due to their complementarity observed through grazing assays (Hoey & Bellwood 2009, Rasher et al. 2013). Studies that also incorporate turf algae in consumption patterns of fishes have shown species to exhibit moderate complementarity with regards to macroalgal grazing (Hamilton et al. 2014).

The ecological implications of macroalgal complementarity observed in this study are relevant to managing Hawaiian reefs that have undergone macroalgal phase shifts or have experienced episodic macroalgal blooms in the last several decades (Smith et al. 2002, 2005, Conklin & Smith 2005). In marine protected areas and fisheries management areas like Kahekili, these feeding behaviors provide insight into the types of algae that may be consumed further as herbivore populations recover under protected status. Understanding what types of algae herbivore species consume can also contribute to interpreting patterns of macroalgal blooms. Given the high consumption of turf relative to other algae, it is not clear that the herbivore community has the capacity to deal with invasive macroalgae blooms in the future (Smith et al. 2002). While some blooming species, such as native *Ulva lactuca* and non-native *Acanthophora spicifera*, are known to be highly preferred by herbivores (Boyer et al. 2004, Smith and Conklin, unpublished data; Kelly and Smith, unpublished data), other blooming nonnative species such as *Gracilaria salicornia*, *Hypnea musciformis*, and *Eucheuma denticulatum* are not among preferred food types (Smith and Conklin, unpublished data). Further studies in locations with high availability of these species will reveal how diet flexibility in herbivores may or may not allow the herbivore community to respond to such blooms.

While herbivore species exhibit macroalgal complementarity in this study, all herbivores predominantly ate turf algae and half of the species selected turf algae greater than expected based upon availability. This result is consistent with results from Palmyra Atoll where some herbivores clearly preferred certain species of macroalgae but selectivity analysis revealed that the majority of the herbivore community preferred turf algae (Hamilton et al. 2014). We suggest two major reasons for the predominance of bites on turf algae in this and other studies. First, turf algae are often simple filamentous and palatable fast-growing species of algae that can be readily digested as compared to more complex or defended macroalgae species. While some herbivores were observed taking bites (albeit few) on leathery species (*Turbinaria*) or chemically defended species (*Asparagopsis*) of macroalgae, selectivity identifies their preference for turf algae. Thus, the abundance of turf algae as a palatable and quickly renewable resource at Kahekili may have resulted in herbivores focusing their diets towards higher proportions of turf consumption. Second, in the absence of competition for resources, functional redundancy exists because there is no need for partitioning of resources. While there may be more feeding complementarity among grazers on reefs with higher coral cover and lower turf and macroalgal cover, this complementarity may be reduced or lost when there is an abundance of turf algae available for consumption that all but eliminates foraging time for most individuals. At Kahekili, we see some differences across grazing on macroalgal species (Figure 2B) but this is obscured by the overwhelming proportion of bites taken by all herbivores on turf algae (Figure 2A). Wellnitz & Poff (2001) note that specific ecosystem conditions cause species to behave similarly and perform the same function as other species. While species may have overlapping theoretical niches, competition and/or limited availability of a given resource results in niche partitioning and thus functional complementarity (Hutchinson 1959, Chase and Leibold 2003). However in a disturbed system such as a reef undergoing a phase-shift, the resource may be present in higher abundance and niche partitioning may dissolve. We suggest that degradation of the reef at Kahekili resulting in over 50% turf cover has inflated functional redundancy of turf algal consumption by herbivores and obscured macroalgal complementarity that may exist among species. Per optimal foraging theory (MacArthur and Pianka 1966, Emlen 1966) the search time for food would be considerably reduced on a reef where half the benthos is covered in turf algae.

The significance of high turf algal consumption in this study is important given the shifting benthic community composition documented on Hawaiian reefs. While coral to macroalgal phase shifts have been well documented in the Caribbean (Hughes 1994, Lapointe 1997), much less attention has been given to phase-shifts to turf algae dominance. Notably, turf algae are one of the most abundant benthic groups on human-impacted reefs worldwide (McCook 2001, Sandin, Sampayo, et al. 2008, Sandin, Smith, et al. 2008, Hoey & Bellwood 2009, Vermeij, Dailer, et al. 2010, Vermeij, van Moorselaar, et al. 2010). At Kahekili and adjacent reefs on Maui and the Main Hawaiian Islands in general, turf algae are the dominant component of the reef benthos (~50-90% cover with the next most abundant group being corals at ~4-30%; Jouffray et al. 2014). Turf algae are common and particularly good competitors with corals (as reviewed in McCook et al. 2001, Barott et al. 2009, Haas et al. 2010), are fast colonizers of open space on reefs after disturbance (McClanahan et al. 2001, Diaz-Pulido & McCook 2002), and are known to inhibit coral larvae settlement (Birrell et al. 2005). Thus, grazing of turf algae is essential to maintaining low standing stock biomass of turf on reefs and high functional redundancy with regards to turf algae consumption is ecologically significant for ecosystem health at reefs with high turf cover.

Importantly, it is relevant to consider functional redundancy at different levels of scale and ecological impact. While there is high redundancy of fish species in consuming turf algae as a functional group, gut contents reveal that the composition of these turf algae differ amongst herbivores examined (Figure 6B). Due to their filamentous nature and the impossibility of identification in the field, turf algae are often considered a single functional group in *in situ* analyses. Yet our results suggest that herbivorous fish species are likely discriminating among different types of turf algae on the reef and thus, finer scale consideration of turf communities would be necessary to truly evaluate functional redundancy of grazing on this group of algae. For example, we used gut contents to examine fine scale detail of the diets of *Acanthurus olivaceus* and *Ctenochaetus strigosus*, which both graze on patches of turf algae but are known to be combing and ingesting detritus, sand, and other organic matter (Choat et al. 2002). Despite what behavioral observations would suggest these fish are feeding on, their gut contents show that these fish are consuming organic material within turf assemblages while not actually removing substantial filamentous turf biomass (Figure 6A). These results corroborate work by Choat et al. (2004) in which turf-grazing Acanthurids were found to be selective and have lower bite rates than detrital Acanthurids (the analogue in this study being *A. olivaceus* and *C. strigosus*) (Figure 2A).

Categorizing herbivorous fish into functional feeding guilds of scrapers / small excavators, grazers / detritivores, and browsers (Bellwood et al. 2004, Green & Bellwood

2009, Burkepile & Hay 2010) provides a framework for understanding how herbivore populations interact with the reef benthos (Edwards et al. 2014). Based upon feeding rate and type of substrate consumed, we found all three guilds at Kahekili to be at least 40% similar to one another in grazing behavior. We further found the guild categorization for browsers to be robust at Kahekili (Figure 4). Consistent with its classification as a browser, *Naso unicornis* showed selection for both *Turbinaria* and *Laurencia* and *C. carolinus* selectively removed *Turbinaria* tissue, perhaps in pursuit of epiphytes but still contributing to ecologically relevant tissue removal of this macroalga. While *N. brevirostris* is often considered a planktivore (Choat et al. 2002), Green & Bellwood (2009) consider all *Naso* species to be within the browser guild. We saw consistent benthic grazing by *N. brevirostris* on both turf and macroalgae, though its slower bite rate compared to other species of *Naso* may partly reflect supplementary feeding in the water column by this species.

While the feeding guilds defined by Green and Bellwood (2009) were designated to reflect how herbivore species interact with the benthos, our data show that based upon what these species are eating, many of them blur the lines of functional guilds. Browsers were the most well defined group based upon their feeding habits and greater effort focused on macroalgal consumption than the other groups. However, species of scrapers / small excavators and grazers / detritivores were in some cases more similar to species in other guilds than in their own based upon what they were eating (Figure 4). This was largely driven by rapid bite rates on turf algae and an overall lower proportion of bites taken on non-turf substrate (Figure 2A and 2B). While both guilds are known to focus their diets on turf algae (Green & Bellwood 2009) their bite rates did not differentiate them particularly. However, due to differences in mouth parts and therefore feeding mechanism, the impact of these groups on the benthos may still differ.

While the majority of fish bite on turf algae in our study, the ecological impact of these bites on the reef is likely different and associated with taxonomy and morphology. The impacts of fish bites have been explored in other studies with consideration to bioerosion by both excavating and scraping parrotfish (Bellwood & Choat 1990). The ecological fate of bite scars (or lack thereof) left by herbivores also distinguishes species from one another. Grazing by some of the larger bodied scrapers such as *C. perspicillatus* results in bite scars about half of the time (Bellwood 1995, Ong & Holland 2010) where most or all of the turf biomass is removed and calcium carbonate is exposed. These bites will tend to promote CCA and coral cover by opening bare limestone substrate for new recruitment. Meanwhile, bites by other fish in which remnant turf fragments are left behind will likely not support successful CCA recruitment and could promote more rapid turf production through cropping by partial grazing as is seen in grasslands (McNaughton 1984) and reefs (Carpenter 1986). Thus, in considering the impacts of a single bite of a scraper such as *C. perspicillatus* that leaves behind a visible bite scar, and a grazer such as *Z. flavescens* that removes individual filaments with each bite leaving no visible bite scars, it is clear that the bites of these two different types of fishes have different ecological impacts. In other systems in which we see high functional redundancy amongst grazers, grazing strategies of different species results in varied ecosystem impacts (like ungulate browsers on African bush; Pringle et al. 2014). Thus, while there is a functional redundancy with regards to fish bites on turf algae, there is ecological functional complementarity with regards to the impact of different fish species' bites on the ecosystem.

Detailed analysis of feeding behavior and gut contents allows for identification of the ecological significance of specific herbivore species in a community. Namely, it identifies herbivores that could provide key roles in consumption of dominant algae on a given reef. For example, Hoey & Bellwood (2009) identified *N. unicornis* as a key herbivore in grazing macroalgae on the Great Barrier Reef where the dominant macroalga was *Sargassum*. This study utilized grazing assays of *Sargassum* and therefore may have missed key roles of other herbivores in consuming turf algae (6.6-47% benthic cover) and other macroalgae, but it highlights the goal of providing insight into key ecological players in the herbivore community. Some management areas have been established to protect parrotfish (Stockwell et al. 2009, Jackson et al. 2014) and highlight their utility in diminishing macroalgal cover on reefs. While some species of parrotfish contribute to macroalgal grazing (*C. carolinus* in this study), we would add based on our results that parrotfish will rather be essential to removing increasingly dominant turf algae, an equally important conservation goal but less frequently reported.

In our study we see rather than a single key player on the reef, a diverse assemblage of species all cropping turf algae. Yet within these herbivore species, a complementarity with regards to turf functional forms and macroalgae suggests that a diverse assemblage of herbivores may be important for maintaining low macroalgal cover and consumption of different types of turf algae. Thus, our study speaks to managing for a diverse fish assemblage (Rasher et al. 2013). The goal of the Herbivore Fisheries Management Area designated at Kahekili in this study is to increase herbivore biomass on the reef to ultimately reduce cover of problem algae and increase coral cover. While this study highlights the feeding preferences of the herbivore community, additional work into the balance of algal production on the reef and consumption of algae by herbivores is required to understand the potential future success of this management area.

Our work demonstrates that individual species within a single herbivore community have different consumption patterns on a reef and are selecting for different types of available algae. Importantly, our study incorporates an examination of grazing on turf algae, a dominant benthic group on reefs worldwide, and emphasizes the dominance of turf algae in herbivore diet. While the structure of herbivore bite patterns somewhat matched herbivore guild designation, all species took the majority of bites on turf algae. Gut content analysis provides finer-scale detail within turf algae suggesting that herbivore species may be selectively consuming different turf assemblages. In situ observation combined with lab-based gut content analysis allowed us to differentiate within and between species' bite rates and substrates bitten within a given reef context. Thus, we are able to quantify the "rain of bites" (Hamilton et al. 2014) across a reefscape, with resolution to macroalgae genera and turf algae functional form. This detailed view of the herbivore community can help inform how individual herbivores influence benthic community structure based on community algal composition. Employing similar methods across a variety of reefs with similar herbivore communities and different algal communities would provide insight into the dietary flexibility of herbivores and their capacity to consume algal blooms or contribute to algal consumption on phase-shifted reefs.

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Tables

Table 1: Species observed at Kahekili as categorized by family and feeding guild. Overall bite rate is the average bite rate of each species on all substrate types combined (+/- standard error). Total number of fish observed per species is noted. Substrate richness is the total number of substrate types each herbivore species was observed biting.

Family	Feeding guild	Species	Overall bite rate (+/- SE)	# fish observed	Substrate richness
Labridae [Scarinae]	Scraper / small excavator	*Scarus psittacus*	20.38 (+/- 1.65)	26	5
		Scarus rubroviolaceus	14.70 (+/- 1.47)	15	4
		Chlorurus perspicillatus	20.13 (+/- 4.46)	5	1
		Chlorurus spilurus	16.24 (+/- 1.65)	10	3
Acanthuridae	Browser	*Naso lituratus*	12.25 (+/- 1.15)	16	6
		Naso unicornis	9.36 (+/- 0.74)	22	8
		Naso brevirostris	6.39 (+/- 0.87)	27	7
		Calotomus carolinus	5.97 (+/- 0.80)	18	5
	Grazer / detritivore	*Acanthurus triostegus*	51.38 (+/- 5.56)	6	2
		Acanthurus olivaceus	37.33 (+/- 3.91)	27	4
		Acanthurus nigrofuscus	36.74 (+/- 1.76)	48	10
		Acanthurus leucopareius	33.93 (+/- 4.11)	11	3
		Acanthurus blochii	21.70 (+/- 5.33)	7	3
		Ctenochaetus strigosus	21.68 (+/- 1.89)	37	6
		Zebrasoma flavescens	20.18 (+/- 5.02)	13	4

Figures

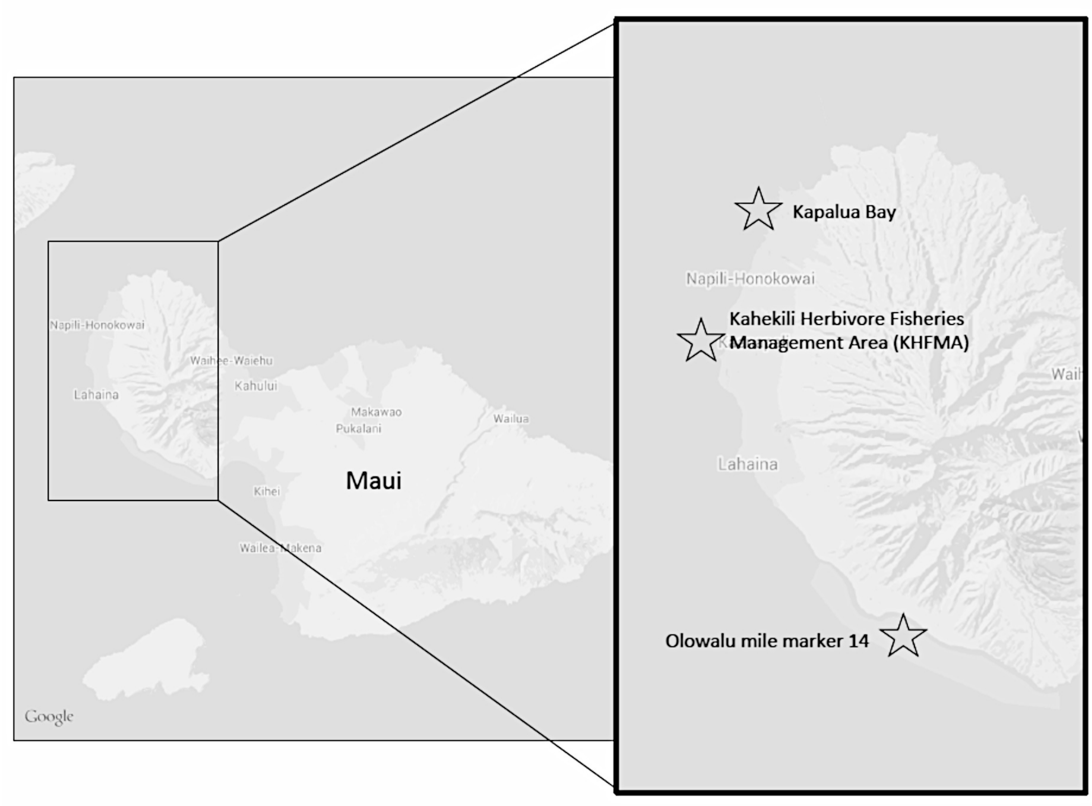


Figure 1: Observational studies were conducted at Kahekili Herbivore Fisheries Management Area (KHFMA) with gut content data from Kapalua Bay and Olowalu mile marker 14, all on West Maui, Hawaii.

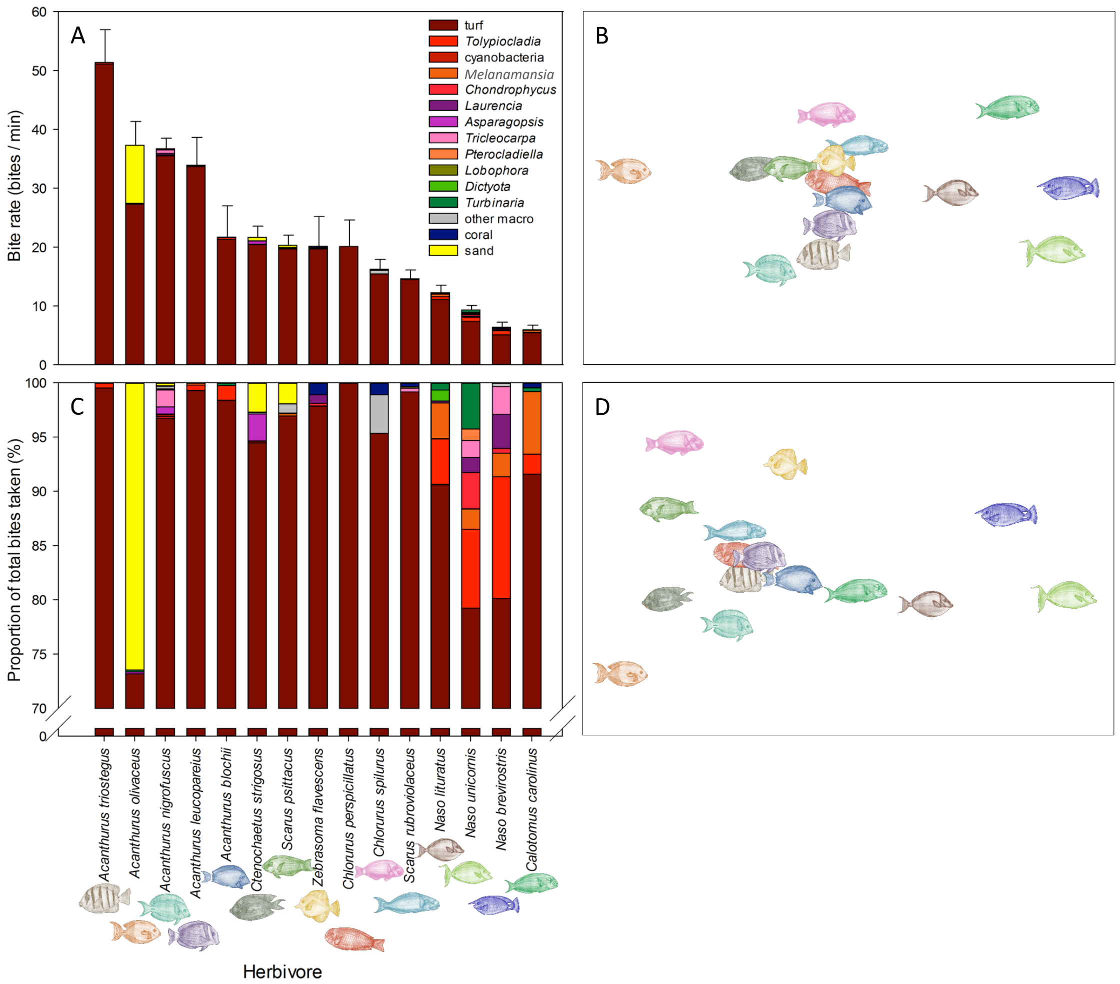
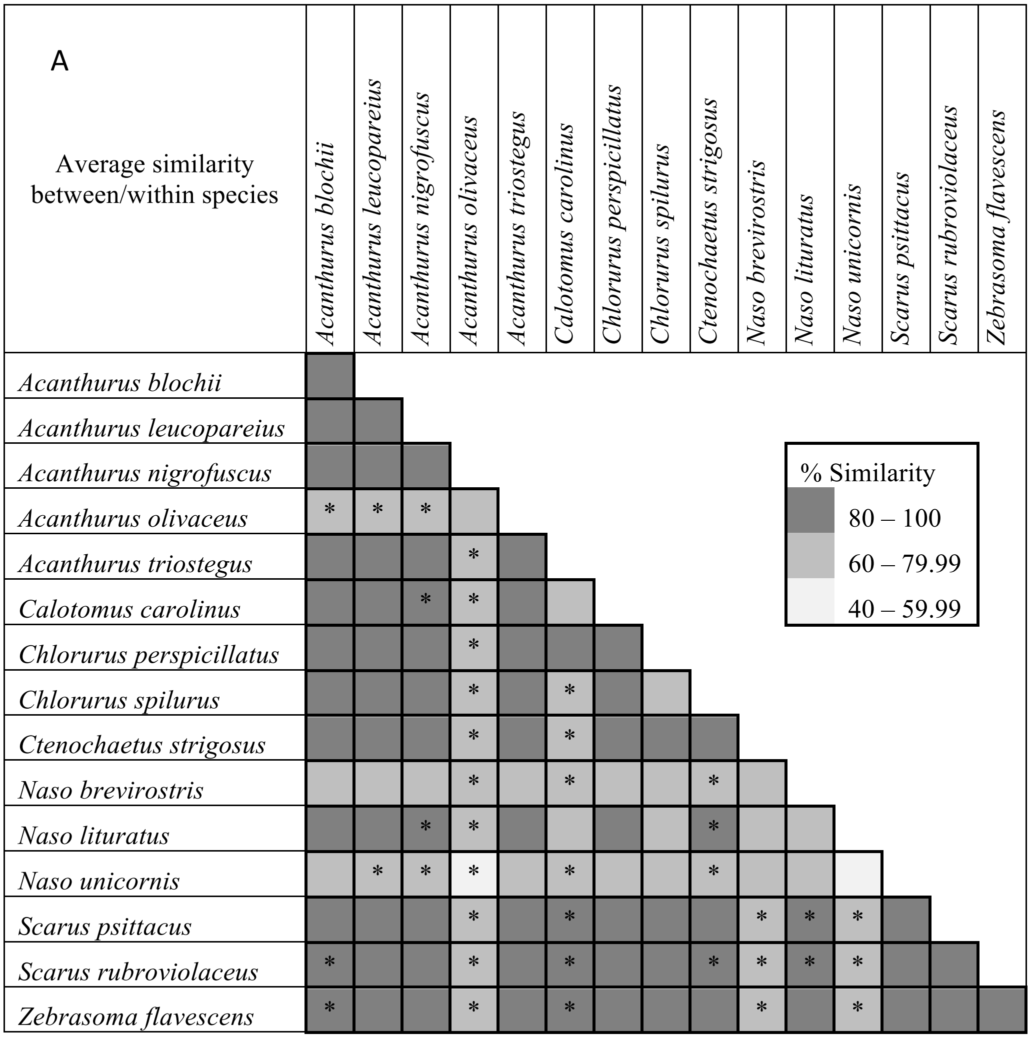


Figure 2: (A) Bite rates and substrates bitten by herbivorous fish species at Kahekili varied significantly among species. All herbivorous fish were observed biting on turf algae and many also consumed other types of macroalgae and other substrate, though the rates of consumption differed across species. (B) nMDS in which bite rates were averaged for each species and data were transformed using log (x +1). Bray Curtis Similarity (BCS) distances (BCS = 1 – Bray Curtis Dissimilarity distance) were then calculated for transformed data and plotted. Species are arranged roughly from left to right as fastest to slowest bite rates. (C) Bites on turf are over 70% of total bites for all species of herbivores on the reef, with different proportions of bites on macroalgae, sand, and other substrates thereafter. (D) nMDS of proportional bite data was created as in (B). Species are arranged roughly from left to right as those consuming mostly turf algae to those with greater richness of substrates bitten.

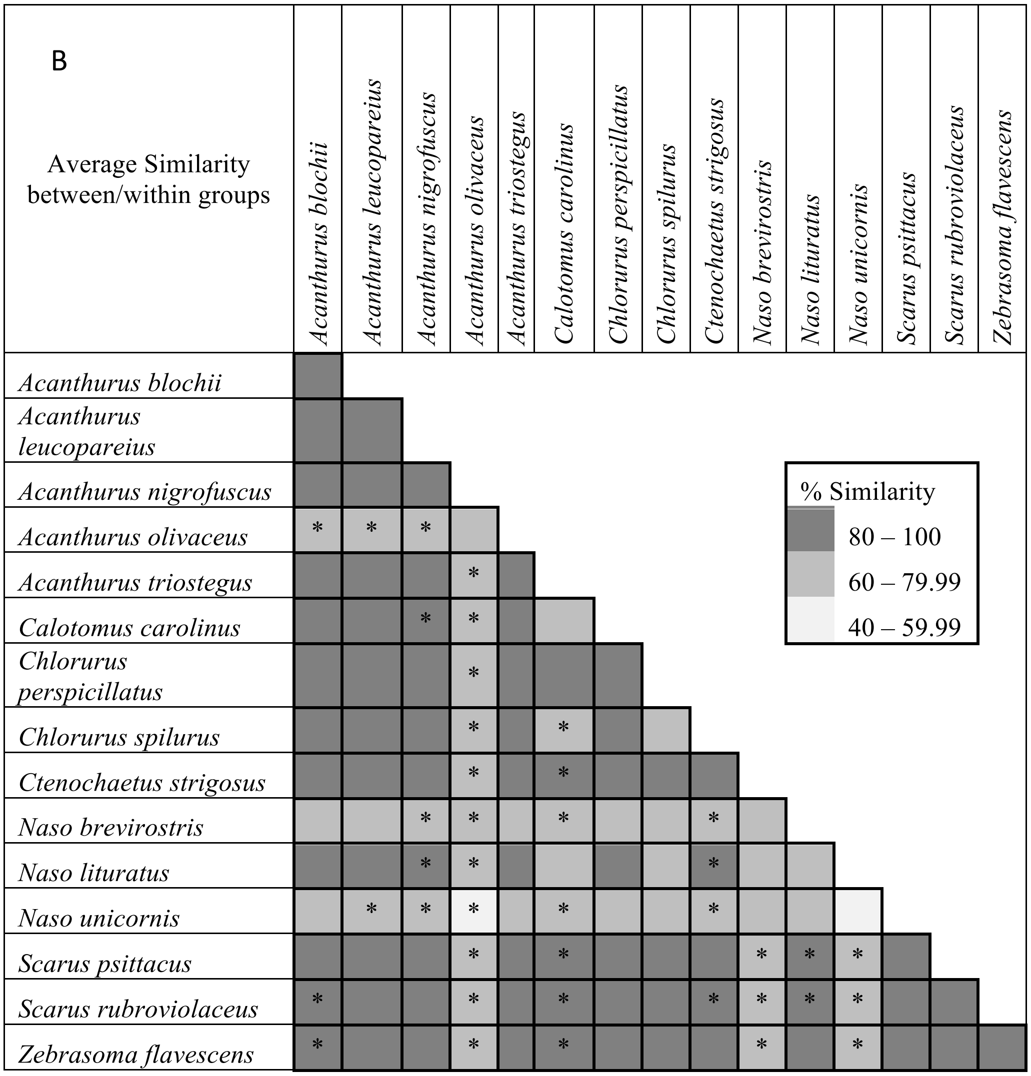


A Average similarity between/within species	*Acanthurus blochii*	*Acanthurus leucopareius*	*Acanthurus nigrofuscus*	*Acanthurus olivaceus*	*Acanthurus triostegus*	*Calotomus carolinus*	*Chlorurus perspicillatus*	*Chlorurus spilurus*	*Ctenochaetus strigosus*	*Naso brevirostris*	*Naso lituratus*	*Naso unicornis*	*Scarus psittacus*	*Scarus rubroviolaceus*	*Zebrasoma flavescens*
Acanthurus blochii	■														
Acanthurus leucopareius	■	■													
Acanthurus nigrofuscus	■	■	■												
Acanthurus olivaceus	▒ *	▒ *	▒ *	▒											
Acanthurus triostegus	■	■	■	▒ *	■										
Calotomus carolinus	■	■	■ *	▒ *	■	▒									
Chlorurus perspicillatus	■	■	■	▒ *	■	■	■								
Chlorurus spilurus	■	■	■	▒ *	■	▒ *	■	▒							
Ctenochaetus strigosus	■	■	■	▒ *	■	▒ *	■	■	■						
Naso brevirostris	▒	▒	▒	▒ *	▒	▒ *	▒	▒	▒ *	▒					
Naso lituratus	■	■	■ *	▒ *	■	▒	■	▒	■ *	▒	▒				
Naso unicornis	▒	▒ *	▒ *	░ *	▒	▒ *	▒	▒	▒ *	▒	▒	░			
Scarus psittacus	■	■	■	▒ *	■	■ *	■	■	■	▒ *	■ *	▒ *	■		
Scarus rubroviolaceus	■ *	■	■	▒ *	■	■ *	■	■	■ *	▒ *	■ *	▒ *	■	■	
Zebrasoma flavescens	■ *	■	■	▒ *	■	■ *	■	■	■	▒ *	■	▒ *	■	■	■

% Similarity

■	80 – 100
▒	60 – 79.99
░	40 – 59.99

Figure 3A: Percent similarity of bite rates and bite rate composition between and within herbivorous fish species. * indicates pair-wise comparison in which P(perm) < 0.05.



B Average Similarity between/within groups	*Acanthurus blochii*	*Acanthurus leucopareius*	*Acanthurus nigrofuscus*	*Acanthurus olivaceus*	*Acanthurus triostegus*	*Calotomus carolinus*	*Chlorurus perspicillatus*	*Chlorurus spilurus*	*Ctenochaetus strigosus*	*Naso brevirostris*	*Naso lituratus*	*Naso unicornis*	*Scarus psittacus*	*Scarus rubroviolaceus*	*Zebrasoma flavescens*
Acanthurus blochii	▓														
Acanthurus leucopareius	▓	▓													
Acanthurus nigrofuscus	▓	▓	▓												
Acanthurus olivaceus	▒ *	▒ *	▒ *	▒											
Acanthurus triostegus	▓	▓	▓	▒ *	▓										
Calotomus carolinus	▓	▓	▓ *	▒ *	▓	▒									
Chlorurus perspicillatus	▓	▓	▓	▒ *	▓	▓	▓								
Chlorurus spilurus	▓	▓	▓	▒ *	▓	▒ *	▓	▒							
Ctenochaetus strigosus	▓	▓	▓	▒ *	▓	▓ *	▓	▓	▓						
Naso brevirostris	▒	▒	▒ *	▒ *	▒	▒ *	▒	▒	▒ *	▒					
Naso lituratus	▓	▓	▓ *	▒ *	▓	▒	▓	▒	▓ *	▒	▒				
Naso unicornis	▒	▒ *	▒ *	░ *	▒	▒ *	▒	▒	▒ *	▒	▒	░			
Scarus psittacus	▓	▓	▓	▒ *	▓	▓ *	▓	▓	▓	▒ *	▓ *	▒ *	▓		
Scarus rubroviolaceus	▓ *	▓	▓	▒ *	▓	▓ *	▓	▓	▓ *	▒ *	▓ *	▒ *	▓	▓	
Zebrasoma flavescens	▓ *	▓	▓	▒ *	▓	▓ *	▓	▓	▓	▒ *	▓	▒ *	▓	▓	▓

% Similarity	
▓	80 – 100
▒	60 – 79.99
░	40 – 59.99

Figure 3B: Percent similarity of bite proportion and composition between and within herbivorous fish species. * indicates pair-wise comparison in which P(perm) < 0.05.

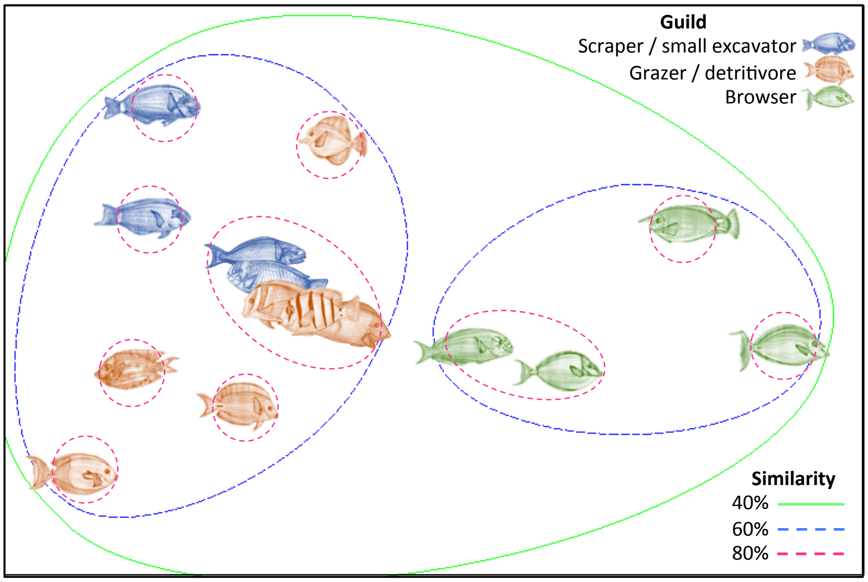


Figure 4: nMDS of averaged observed bites by herbivores within the three herbivore guilds found on Maui. Data are the average proportion of observed bites for each species and are log (x + 1) transformed. Distance is Bray Curtis Similarity. Similarity contours are the percent similarity among species using a cluster analysis overlay. While all browsers are most similar to each other, some guilds have species that are more similar in bite patterns to species in different guilds than their own.

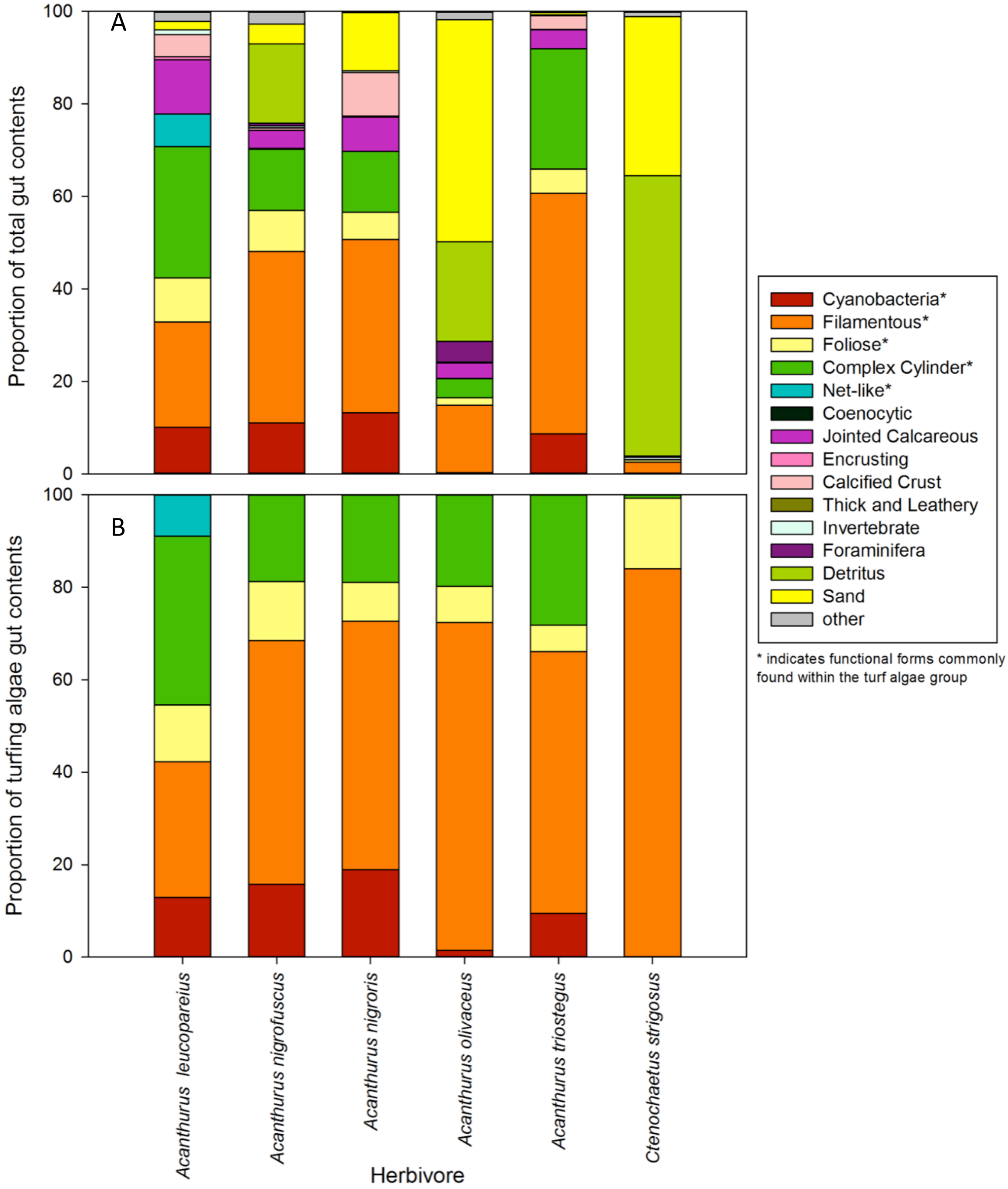
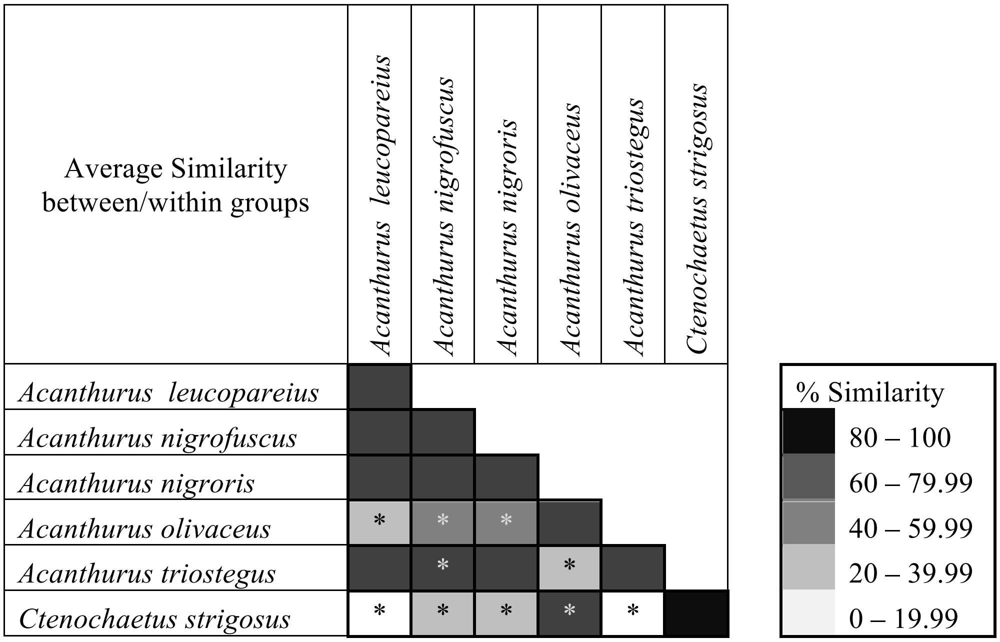


Figure 5: Results of gut content analysis showing the (A) proportion of different functional forms of algae in herbivore guts. (B) Of those functional forms that are typically found within the turf algae group (marked with *), composition of the types of turf algae that are consumed differs between herbivore species. (*A. leucopareius* n = 2, *A. nigrofuscus* n = 17, *A. nigroris* n = 2, *A. olivaceus* n = 10, *A. triostegus* n = 6, *C. strigosus* n = 6).



Average Similarity between/within groups	*Acanthurus leucopareius*	*Acanthurus nigrofuscus*	*Acanthurus nigroris*	*Acanthurus olivaceus*	*Acanthurus triostegus*	*Ctenochaetus strigosus*
Acanthurus leucopareius	▓					
Acanthurus nigrofuscus	▓	▓				
Acanthurus nigroris	▓	▓	▓			
Acanthurus olivaceus	░ *	▒ *	▒ *	▓		
Acanthurus triostegus	▓	▓ *	▓	░ *	▓	
Ctenochaetus strigosus	□ *	░ *	░ *	▓ *	□ *	■

% Similarity	
■	80 – 100
▓	60 – 79.99
▒	40 – 59.99
░	20 – 39.99
□	0 – 19.99

Figure 6: Percent similarity of gut contents between and within herbivorous fish species. * indicates pair-wise comparison in which P(perm) < 0.05.

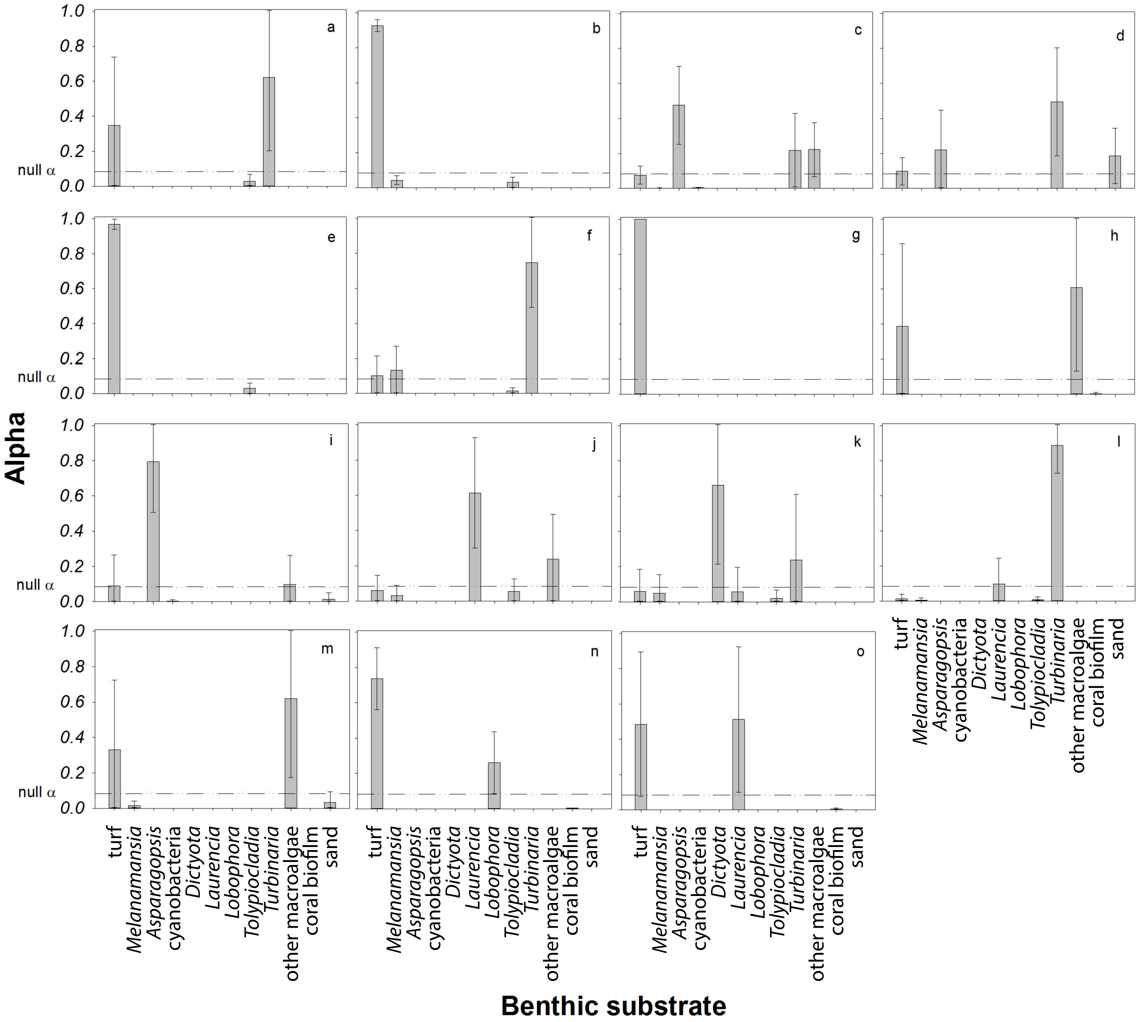


Figure 7: Selectivity of herbivores for different types of substrate indicate that most fish are choosing substrate types more than would be expected based on the availability of this substrate, as indicated by the selectivity exceeding the null selectivity ($\alpha_{null} = 1/m$). Error bars are standard deviation. Fish that only consumed turf algae (panels g, i, and o) lack error bars because all bites were taken on turf algae. (a) *Acanthurus blochii* (b) *Acanthurus leucopareius* (c) *Acanthurus nigrofuscus* (d) *Acanthurus olivaceus* (e) *Acanthurus triostegus* (f) *Calotomus carolinus* (g) *Chlorurus perspicillatus* (h) *Chlorurus spilurus* (i) *Ctenochaetus strigosus* (j) *Naso brevirostris* (k) *Naso lituratus* (l) *Naso unicornis* (m) *Scarus psittacus* (n) *Scarus rubroviolaceus* (o) *Zebrasoma flavescens*

CHAPTER 2:

A budget of herbivorous fish community consumption and algal production in an Herbivore Fisheries Management Area, Maui, Hawaii

Emily L. A. Kelly, Yoan Eynaud, Russell Sparks, Ivor D. Williams, Jennifer E. Smith

Abstract

Herbivore grazing pressure on coral reefs is considered a major driver in the maintenance of coral dominance over algae in competition for space. Numerous experimental and observational studies have shown that fleshy algal abundance is enhanced in the absence of herbivores. However few studies have attempted to quantify and compare rates of consumption by herbivores with production by the algal community. Here, we calculate a budget for herbivore consumption and algal growth on a Hawaiian coral reef by multiplying bootstrapped distributions of field-measured variables. Data were collected at Kahekili Herbivore Fisheries Management Area, established in 2009 to prohibit take of herbivorous fish and sea urchins. Daily algal production was determined through quantification of benthic community composition, standing stock of algal biomass, and growth rates of common algal components. Consumption was determined using distributions of the biomass and size class of herbivorous fish species, the consumption rates of herbivores on different species of algae, and herbivore bite sizes. Our results show that despite herbivore protection, algal production currently exceeds the grazing capacity of the herbivorous fish community by three to four times. While some of this production is consumed by urchins or converted to detritus, increased herbivore biomass will be required to effectively reduce algal abundance. Despite the gap, larger size classes of herbivores, particularly of the scraper/excavator herbivore feeding guild, are contributing more to consumption in recent years, which could have additional feedbacks that promote reef building taxa. Examining changes in herbivore grazing and algal growth budgets helps to elucidate the role of different herbivore species and guilds on benthic community composition to

ultimately determine what future changes in herbivore populations mean for the recovery of this declining coral reef, and the potential success of this type of management on other reefs around the world.

Introduction

Coral reefs are among the most productive ecosystems in the world (Westlake 1963) due to the productivity of the coral holobiont (Odum & Odum 1955, Rohwer et al. 2002) and benthic algae (Carpenter 1986, Littler et al. 2006). On reefs with high coral cover and abundant herbivores, feeding by those herbivores exerts a strong top-down control on algal communities (Carpenter 1986, Littler et al. 2006, Sandin et al. 2008, Burkepile & Hay 2009), and upwards of 100% of total daily algal production is consumed (Hatcher 1981, Carpenter 1986). This intense grazing results in low standing stock of algae on most unfished reefs (Odum & Odum 1955, Hatcher & Larkum 1983, Steneck 1988) and allows corals to maintain a competitive advantage over algae for space (as reviewed in McCook et al. 2001).

Experimental studies of herbivory have provided insight into herbivore feeding preferences (Burkepile & Hay 2011) and relative rates of consumption by various herbivores on select species of macroalgae (Fox et al. 2009, Hoey & Bellwood 2009). Observational studies of herbivores grazing in situ have added insight into herbivore preference for algae within a reef context (Bellwood 1995, Ong & Holland 2010, Brandl & Bellwood 2014, Hamilton et al. 2014). Measurements of parrotfish grazing scars used for estimation of bioerosion rates also provides a means to quantify the amount of algae removed daily by these herbivores (Bellwood 1995, Ong & Holland 2010). Most studies discuss the relative differences among herbivores without specifically quantifying algal removal by the herbivore community. Estimates of total herbivory on reefs have been based on extrapolation from detailed observations of a few abundant herbivores (Klumpp & Polunin 1990, Paddack et al. 2006), calculated through estimates of metabolic demands of fishes (Van Rooij et al. 1998), or based on consumption of algae on settlement tiles (Wanders 1976, Russ 2003).

Production on reefs was historically measured on reefs through measuring oxygen concentration differences as water flowed across the reef (Odum & Odum 1955, Kohn & Helfrich 1957), providing evidence of the high productivity of reefs relative to the open ocean, attributed to benthic algae (Kohn & Helfrich 1957). More recently, productivity has been characterized through lab measurements of oxygen production (Wanders 1976, Klumpp & Polunin 1990, Van Rooij et al. 1998) and growth of algae in the absence of herbivores (Carpenter 1986, Russ 2003, Paddack et al. 2006).

A handful of studies have examined the proportion of algal production consumed by herbivores on a variety of reef types. On high coral-cover reefs (>50%) herbivores were estimated to consume upwards of 100 percent or more of algal production (Wanders 1977, Hatcher 1981, Carpenter 1986, Van Rooij et al. 1998). On naturally algal-dominated reef flats damselfish and blennies and roving acanthurids and scarids were estimated to remove between a quarter and over double the daily production (Klumpp & Polunin 1990). Finally, on phase-shifted low coral cover reefs herbivores were estimated to consume 31-77% of algal production (Paddack et al. 2006).

Despite differences in the way in which they were derived, estimates of total production and total consumption on reefs are broadly comparable across studies.

Utilizing rates of production and consumption highlights differences in reef function between high coral-cover (>50%) and low coral-cover (<10%) reefs, and could be used to project future trajectories for such reefs. However, no study has yet examined this balance of production and consumption on a reef through time. Further, detailed estimates of experimentally derived rates are inherently variable but thus far the distributions of parameters are not fully incorporated into final estimates of production and consumption in previous studies.

This balance of production and consumption on reefs can further be considered within the context of phase shifts (Pandolfi et al. 2003, Knowlton & Jackson 2008), and the likely future trajectory of benthic composition on a reef. On a reef in which production and consumption are well-balanced, production may exceed consumption due to conversion of some algal material to detritus, material exported off the reef, and consumption by smaller herbivores. However, if production grossly exceeds consumption then it is possible for algal biomass to increase through time. Importantly, changes in algal biomass on reefs does not directly correlate to changes in algal cover on reefs as the latter depends on competition dynamics (McCook et al. 2001). Measures of production and consumption are therefore indicators of how fleshy algal standing stock on a reef may be increasing, decreasing, or remaining stable. On reefs that have undergone a phase-shift to algal dominance, this balance of production and consumption may be skewed to an extent that algal production grossly exceeds consumption. Evidence of hysteresis in many systems indicates that even when high rates of consumption are restored to an ecosystem, such rates may not be sufficient to reverse a phase shift in progress (Scheffer et al. 2001). On low coral-cover reefs (<10%), even a return of herbivore biomass to historically equivalent populations may not be enough to reverse phase shifts given the high algal standing stock now present on the reef (Paddack et al. 2006).

No-take marine protected areas (MPAs) have long been considered a viable management option for protecting marine ecosystems from decline or aiding their recovery (Bohnsack 1998, Dayton et al. 2000). MPAs have been shown to effectively increase fish biomass across trophic levels and ecosystems (Polunin & Roberts 1993, Lester et al. 2009). On coral reefs, several regional studies in the Bahamas and Philippines suggest that coral cover can increase inside MPAs (Mumby & Harborne 2010, Magdaong et al. 2014, respectively) while others in these same locations show mixed results (Russ et al. 2005, Harborne et al. 2008). A global synthesis by Selig and Bruno (2010) suggests MPAs may help prevent further coral cover loss as compared to surrounding unprotected reefs.

While there is limited demonstrated success of no-take reserves, increasing herbivore biomass to drive the reversal of phase shifts has been discussed as a management option (Green & Bellwood 2009, Rasher et al. 2013, Jackson et al. 2014) as a negative relationship between herbivore biomass and macroalgal cover has been observed across coral reefs in both the Caribbean and the Pacific (Williams & Polunin 2001, Friedlander et al. 2007, Jouffray et al. 2015). However, there have been few examples of management that has been employed to achieve such an increase (Jackson et al. 2014).

Coral cover in the Main Hawaiian Islands has declined by 5-50% at a dozen reefs over the last 20 years (Rodgers et al. 2015). Jouffray et al. (2015) assessed decline in

Hawaiian reefs and found associations between both “turf regime” and “macroalgal / sand regime” with the absence of various functional guilds of herbivore biomass. Decline in coral cover during the last 1990s and early 2000s at Kahekili reef on West Maui, Hawaii (Rodgers et al. 2015) led state managers to designate this reef an Herbivore Fisheries Management Area (HFMA). The first of its kind in Hawaii, the goal of the HFMA was to promote coral cover through increasing herbivore biomass and thus grazing pressure.

Regular monitoring of the HFMA with biannual benthic and fish surveys provides detailed tracking of the fish biomass and coral cover on the reef. By combining these data with experimental data of rates of algal production and herbivore consumption of algae, we will gain a more detailed understanding of the capacity for certain herbivore assemblages to consume different algal communities. Further, this framework will provide more predictive capacity for how altering certain components of the herbivore community will affect benthic composition over time.

The goals of this study were three-fold. First, we quantified herbivore consumption and algal production based on observational surveys and experimentally derived data. Second, we tracked these rates through time from the before the inception of an herbivore-specific fisheries management area to five years into protection in order to quantify community-level changes in algal growth and consumption with duration of protected status. And finally, through modeling production and consumption through time, we quantified the proportion of algal production consumed by the herbivore community at KHFMA to assess the capacity of herbivores to consume algal production at each time point. This study provides a functional view for understanding the amount, and type, of herbivore biomass that is necessary to reverse the declining trajectory of reef health at Kahekili, the first Herbivore Fisheries Management Area in Hawaii.

Methods

Study area and overview

All data were collected at the Kahekili Herbivore Fisheries Management Area (KHFMA) on the west side of Maui, Hawaii. Algal growth and herbivore consumption was determined through analysis of benthic community composition, standing stock of algae, growth rates of dominant algal species, abundance and biomass of herbivorous fish species, the consumption rates of herbivores on different species of algae, and the bite size of herbivores. These data were collected through a series of field and laboratory experiments as well as semiannual monitoring surveys at KHFMA.

Benthic community composition

Benthic cover was determined from surveys conducted twice a year by the NOAA Coral Reef Ecosystem Division and Hawaii Division of Aquatic Resources. These surveys were conducted across the 2 km^2 area of KHFMA, and included ~80 transects each survey. ~1m^2 photoquadrats were taken every 1m along each 25m belt transect. Photographs were analyzed using the image analysis software PhotoGrid 1.0 in which 15-100 points were superimposed on the image in a stratified random fashion and benthic cover was identified to genus level for corals and algae or functional group for turf algae, crustose coralline algae, and cyanobacteria. Benthic data were collected twice per year from 2008 – 2014.

Algal standing stock biomass

Standing stock biomass of macroalgae was collected by removing all fleshy algae inside eight 0.6m x 0.85m quadrats placed haphazardly on the reef at 5-8m depth. Algae were collected by hand using blunt metal tools and razor blades, separated by species in the lab, wet-weighed, dried in the oven at 60^{o}C for 24 hours, and dry-weighed. Prior to the removal of macroalgae, photoquadrats were taken of the area and canopy heights were measured using a ruler. Benthic cover was then related to wet-weighed and dry-weighed standing stock biomass within each quadrat.

To determine standing stock of filamentous turf algae, areas of turf covering dead massive Porites colonies were scraped off the calcium carbonate in situ and vacuumed using a marine pump. A known area of turf was scraped using a razor blade and tubing on the intake end of the pump was held adjacent to this area to capture all material removed. Tubing on the outgoing end of the pump was connected to a PVC canister capped with Nitex mesh to catch all scraped material. Samples were transferred from Nitex mesh to filter paper in the lab and then decalcified for 24 hours with 5% HCl to remove carbonate material. Samples were then filtered on preweighed Whatman Grade 1 qualitative cellulose ash free filters, dried at 60^{o}C for 24 hours, and their dry weight recorded.

Algal growth rates

To determine the growth rates of common species of macroalgae, pieces of algae from 3-5 g of a number of species collected from KHFMA were placed in small cylindrical cages constructed out of clear plastic with 1cm diameter mesh and galvanized wire frame. Algae were deployed at 10m intervals along a 150m transect at depths of 2m and 8m. The species deployed were *Acanthophora spicifera* (non-native blooming species)*, Ulva lactuca* (native blooming species)*, Amansia glomerata,* and *Turbinaria ornata* (native species). Prior to establishing cages, algal fragments were collected and placed in bags for transport to the lab. Algae were gently spun 20 times in a salad spinner, blotted with a paper towel, and weighed to obtain initial wet weight. All samples were then placed in mesh pockets and stored overnight in ambient seawater with bubblers, and returned to the reef the following morning. Cages were attached to ropes, which were staked into the limestone substrate and small floats were used to elevate samples off the benthos. After 4 to 7 days, algae were removed from cages and transported via labeled plastic baggies to the lab to obtain the final wet weight of algae. Changes in weight were compared to determine algal growth rates over the period of deployment (change in weight * initial weight^{-1} * time^{-1}).

To determine growth rates of turf algae, plots that were cleared to quantify standing stock biomass were caged with standard hardware 1-inch diameter vinyl-coated chicken wire preventing urchins with test larger than 2.54 cm and fishes greater than 5 cm from grazing inside. Turf was allowed to grow for 3-10 weeks and then resampled using the vacuum method described above, decalcified, and dried using the methods described for standing stock measurement.

Herbivore abundance and biomass

Surveys to quantify herbivorous fish abundance and biomass were conducted two survey rounds per year by the NOAA Coral Reef Ecosystem Division and Hawaii Division of Aquatic Resources. These surveys were conducted at haphazardly location sites spread across the hardbottom reef area inside the KHFMA, totaling ~80-100 transects each round. Fish densities of all observed species were estimated by visual strip transect search along each transect line. On the outward-bound leg, fish > 15cm, within a 4m-wide belt centered on the diver and within 4m of the bottom were recorded. On the return leg, fishes <15cm were recorded within a 2m-wide belt. Fish were binned into 10cm size classes (0-15cm; 16-25cm; 26-35cm; and 36-45cm). Biomass was calculated using established species-specific conversion factors taken largely from FishBase (2012).

Herbivores were categorized as grazers, scrapers, or browsers according to Green & Bellwood (2009) and (Edwards et al. 2014). Detritivores were not included in the consumption calculation as their impact in removal of algae is considered minimal (see Chapter 1; also Choat et al. 2002).

Herbivore grazing rates

Grazing rates for all abundant herbivorous fish species were determined using timed behavioral observations. Divers followed at least 10 and up to 60 individuals of all common herbivorous fish species within each of the herbivore guilds (browsers, grazers, and scrapers) to record bite rates and type of substrate consumed by fish during 3-5 minute timed swims. This time period allowed for multiple forays (grazing episodes) as well as other social behavior, and has been successfully implemented in other studies (Bellwood & Choat 1990, Hamilton et al. 2014). When fish behavior appeared to be altered by diver presence, observation of that fish was terminated and the data excluded from analysis. At least ten observations were made for each of the most common species of herbivorous fishes determined by biannual fish surveys (Hawaii Division of Aquatic Resources, unpublished data). Observational data for rare species are included here but sample size is limited for some taxa. All observational data were taken between 2m and 10m depth at Kahekili Herbivore Fisheries Management Area.

During each behavioral observation, divers recorded the herbivore species and size as total length (TL) to nearest cm, the number of bites and type of benthic substratum that was consumed per bite. Substratum type was recorded to the finest taxonomic classification possible through field identification. Macroalgae were identified to genus while turf algae, crustose coralline algae and other benthic groups were identified as functional groups. In cases where turf algae were growing as epiphytes on macroalgae, the bite was considered a bite on turf algae unless tissue from macroalgae was clearly removed. Species grazing on turf algae were recorded as grazing “turf” despite the heterogeneous nature of the turf community (Harris et al. in review) because turfing algae could not feasibly be identified in the field to a finer scale.

Herbivore bite size

Laboratory experiments were conducted to calculate the weight of algae removed per bite by representative acanthurids and scarids of varying sizes. Bite size data collection was conducted at the Maui Ocean Center using fish on display at the aquarium. *Ulva lactuca* was used in these experiments because of its low error in calculating wet weight data and its high degree of palatability. *U. lactuca* fragments were weighed initially and attached to a "fishing pole" placed in aquariums housing target fish species. A single species of fish was allowed to graze on any given piece of *U. lactuca*. The number of bites taken by a single fish on a piece of algae was recorded. After grazing, the remaining algal tissue was removed from the tank and wet-weighed as described above. Bite size per species and size class were calculated from the change in weight divided by the number of bites.

In addition to these experimental data, values extracted from the literature were also used when available for various acanthurid and scarid species. Data were either taken directly from previous studies as measurements of algal biomass removed per bite (Klumpp & Polunin 1990, Marshell & Mumby 2012) or were extrapolated from recorded values of scarid grazing scar area (Ong & Holland 2010) and combined with experimental turf standing stock biomass data in this study to determine algal biomass removed per bite per species.

Herbivore TL and bite size (BS; grams of algae removed per bite) were both log transformed and a power function was used to describe the relationship between these two factors. The relationship between herbivore size and bite size was calculated at family-level (acanthurid or scarid). Those relationships were then used to calculate bite size for each individual followed during bite observations, and bite rate data (bites taken per day) were converted into a measure of grams of algae removed per day.

Overall fish consumption

To combine the multiple sources of uncertainty that contribute to the total algal consumption estimate, we used a bootstrapping approach. For a given type of fish (e.g.

trophic group, size class), the mean algal consumption is a function of the fish biomass density sample (D: g_F m^{-2}), noted *D,* and the fish grazing capability (K: g_A g_F^{-1} day^{-1}). *K* is a function of the fish bite rates sample (R: bites day^{-1})*,* the corresponding bite size sample (S: g_A $bite^{-1}$), and the corresponding fish biomass sample (F: g_F). As explained above, the bite size sample and fish biomass sample are both calculated using the fish TL associated with the bite size sample. Thus, we can write *K* as*:*

$$K = \frac{R * S}{F}.$$

The bootstrapping procedure involved generating series of length β (=10^4) of values of D and K - randomly resampled with replacement from survey and experimental data - and respectively noted as $D^*$and K^*. Hence, the b^{th} sampled mean, a_b, can be written as:

$$a_b = \frac{1}{n}\left(\sum_{i=1}^{n} D_i^*\right) * \frac{1}{m}\left(\sum_{j=1}^{m} K_j^*\right),$$

where $b \in [1, \beta]$, *n* the length of the fish biomass density sample, *D,* and *m* the length of the fish grazing capability sample, K. By repeating this process β times, we obtained a distribution of estimated means from which a global estimated mean and 95% confidence interval were calculated. Following this procedure, we calculated mean annual fish consumption at KHFMA for each year between 2008 and 2014.

Overall algal production

We calculated overall algal production in a similar manner to consumption using a bootstrapping approach. For a given type of algae (e.g. turf or macroalgae), the overall algal growth is a function of the algal growth rate (G: g d^{-1}) and the algal benthic cover

(C: %). Because we use a bootstrapping procedure, we do not directly use our sample set, but rather a series, of length β, of randomly resampled with replacement one and respectively noted $G^*$and C^*. Hence, the b^{th} sampled mean, c_b, can be written as:

$$c_b = \frac{1}{n}\left(\sum_{i=1}^{n} G_i^*\right) * \frac{1}{m}\left(\sum_{j=1}^{m} C_j^*\right),$$

where $b \in [1,\beta]$, n the number of algal growth rate samples, and m the number of algal benthic cover samples. By repeating this process β times, we obtained a distribution of estimated means from which a global estimated mean, noted A, and its 95% confidence interval was calculated. Following this procedure, we calculated mean annual algal production at KHFMA from 2008 to 2014.

Finally, using the bootstrapped data of β samples for both consumption and production we subtracted a single element of the consumption distribution from a single element of the production distribution to create a new distribution of net production (production remaining after herbivorous fish consumption). As with the above distributions, we obtained a global estimated mean of net production from this new distribution and calculated its 95% confidence interval. Following this procedure, we calculated mean annual net production at KHFMA from 2008 to 2014.

Results

Benthic community composition

Over the course of this study (2008-2014), the reef was comprised primarily of turf algae (41.23-53.8%) and hard coral (34.03-37.28%), as well as CCA (0.33-9.24%), macroalgae (1.28-4.72%), cyanobacteria (0.01-1.39%), and other substrata including sand and other invertebrates (<10%) (Figure 2). CCA increased between 2008 and 2014 (t-test, $p<0.0001$) and turf decreased between 2008 and 2014 (t-test, $p<0.0001$). Coral cover and macroalgal cover did not change over this time period (t-test, $p=.8403$ and $p=.4672$, respectively).

Algal standing stock biomass

Assuming 100% coverage of these algal groups, macroalgal standing biomass was 51.49 g dry wt m^{-2} (SE = 17.92) and turf algal standing biomass was 78.98 g dry wt m^{-2} (SE = 11.83) (Table 1). The majority of standing biomass of macroalgae was *Melanamansia glomerata*, which accounted for 38.02 g dry wt m^{-2} (SE = 12.36) of the total macroalgal standing stock biomass.

Algal growth rates

Growth rates for turf algae and four species of macroalgae were determined at Kahekili (Figure 3). Turf algae had the fastest growth rate at 0.0708 g dry wt * g $algae^{-1}$ day^{-1} (+/- 0.0163). The growth rates of macroalgal species were as follows: *Ulva lactuca* at 0.0341 g dry wt * g $algae^{-1}$ day^{-1} (+/- 0.0051), *Acanthophora spicifera* at 0.0229 g dry wt * g $algae^{-1}$ day^{-1} (+/- 0.0099), *Melanamansia glomerata* at 0.0093 g dry wt * g $algae^{-1}$ day^{-1} (+/- 0.0021), and *Tricleocarpa fragilis* at 0.0003 g dry wt * g $algae^{-1}$ day^{-1} (+/- 0.0046).

Herbivore biomass

Overall herbivore biomass fluctuated throughout the duration of the study (Figure 4) with highest biomass in 2014 (19.67 g m^{-2} +/- 2.07 SE). Total herbivore biomass declined between 2009 (16.36 g m^{-2} +/- 2.38 SE; when the HFMA was designated) and 2010 (9.44 g m^{-2} +/- 1.10 SE). However, when considering the feeding guilds separately scraper and grazer biomass has increased from 2010 to 2014 while browser biomass, has fluctuated but remained lower than both scrapers and grazers through all years. While grazer biomass shows an increasing trend since 2010, it is proportionally composed of smaller fishes than in 2008 and 2009 (Figure 5). For scrapers the increase in biomass from 2008-2014 has been the result of more biomass in the larger size classes. Browser biomass remained low throughout the study years but with all size classes present in the last three years.

Herbivore grazing rates

Herbivore grazing rates varied across species of herbivores as well as between turf algae and macroalgae (Figure 6). Grazers had an overall higher grazing rate (with the exception of *Zebrasoma flavescens*) than scrapers, and both had higher average bite rate than all browser species. For a more detailed description of herbivore grazing rates and selectivity on benthic groups, see Chapter 1.

Herbivore bite size

Acanthurid bite size was defined (Figure 7A) as:

$$BS = 1 * 10^{-8} * (TL)^{3.446} \qquad (R^2 = 0.35603).$$

Scarid bite size was defined (Figure 7B) as:

$$BS = 5 * 10^{-10} * (TL)^{4.3744} \qquad (R^2 = 0.83078).$$

These equations defined bite size on both turf and macroalgae for these groups.

Overall algal growth and fish consumption budget

Based upon our modeled estimates, benthic algal production (turf and macroalgae) was approximately four times that of consumption by herbivorous fishes throughout the length of the study, with a trend towards declining production and increasing consumption over the last three years (Figure 8A). Production ranged from the lowest mean value of 1.93 g dry wt m^{-2} day^{-1} in 2008 to the highest mean value of 2.81 g dry wt m^{-2} day^{-1} in 2012. Consumption ranged from a low mean value of 0.24 g dry wt m^{-2} day^{-1} in 2010 to a high mean value of 0.74 g dry wt m^{-2} day^{-1} in 2014. At any given time point, the lowest amount of production consumed by the herbivore community was 9.79% in 2010 and the greatest amount of mean production consumed was 32.35 in 2014 (Table 2). Throughout the study, net production (gross production – consumption) was significantly greater than 0 (95% CI excluded 0) (Figure 8B).

Consumption rates by different size classes within each herbivore guild varied across years for both turf (Figure 9) and macroalgae (Figure 10). There was a shift in the size class distribution for the scrapers such that the upper three size classes in 2012 and 2013 were expected to have removed the most turf biomass daily (Figure 9). Mid-sized grazers were expected to have removed the most turf biomass in early years but over the last three years the smaller size classes likely removed the greatest daily biomass of turf algae. Based upon our calculations, browsers remove very little turf biomass overall. In terms of macroalgal consumption, our data suggest that browser size classes fairly evenly removed macroalgal biomass (Figure 10). Small grazers also appear important in macroalgal removal. Scrapers remove very little macroalgal biomass overall though their contribution is evenly distributed across size classes.

Discussion

Our study sought to assess the balance of algal production and herbivore consumption of production through time at an Herbivore Fisheries Management Area whose goal is to increase herbivore consumption of algae to promote coral cover. We used a novel approach to directly ask whether herbivore consumption has increased in the HFMA through time by calculating rates of production and consumption on the reef that incorporated extensive survey data and experimental results. We found that algal production exceeded herbivorous fish consumption by 3-5 times throughout the study.

Calculated annual budgets, however, reveal that this gap in production and consumption is shrinking with increasing herbivore biomass and larger size classes of herbivores, particularly of the scraper/excavator herbivore feeding guild. Further, some of the production is consumed by urchins (Ogden & Lobel 1978, and see Chapter 4), converted to detritus (Hatcher 1990), or exported off the reef (Hamner & Hauri 1981). The decline in coral cover at Kahekili and associated increase in algal cover over the last 20 years prior to HFMA designation (Rodgers et al. 2015) has resulted in high levels of production. Importantly, production is fairly stable through time, reflecting the fairly stable benthic cover data, which shows no significant change in coral cover or macroalgal cover from 2008-2014 though an increasing trend in CCA in the last several years (Figure 2).

The slight decline in turf cover and increase in CCA cover may be a result of the slight increase in consumption within the last several years, though turf still remains the most abundant of all benthic groups at KHFMA. Since production exceeds consumption throughout the study, it would be possible that turf and macroalgal biomass could be increasing over time. This biomass may not have translated into an increase in areal coverage for these algal groups as a result of competitive dynamics on the reef (McCook et al. 2001). These patterns could be due to several reasons. Its persistence may be due to increased grazing pressure, which has stimulated faster turf algal production and thus standing stock (Figure 11). Growth rate of algae can increase in response to heavy grazing (Westlake 1963) and standing stock biomass of turf algae may be greater due to a later successional stage of the turf assemblage that is more dense. These later successional turfing algae may be less palatable to herbivores and thus more persistent in the benthos. Seasonal cyanobacteria blooms over the last several years at KHFMA (see Chapter 4) may further support this idea given the often chemically defended nature of cyanobacteria. While we see evidence for increased turf growth rates, further data and analysis of the turf community is required to examine the latter.

It is also not surprising that the KHFMA has not yet achieved its goal of increasing coral cover through herbivory on the reef as the KHFMA is only five years old and it may require more years of protection to increase herbivore populations. Herbivore biomass has increased by 60% since 2009 but our model demonstrated the resulting consumption increase is not sufficient to meet production. Total herbivore biomass is still lower than reefs that have been no-take areas for decades longer than KHFMA (DAR technical report 2014). More years of fisheries management as an HFMA will also allow some of the long-lived herbivore species to reach larger size classes on the reef (Lester et al. 2009, Zgliczynski et al. in prep, but see Halpern & Warner 2002).

Both size class and herbivore guild play a role in the variation of consumption of turf and macroalgae through time. As would be expected according to their guild designations, browsers play a larger role in consumption of macroalgae than turf algae, though they remove more turf biomass than macroalgal biomass (Figures 9 and 10) as would be expected by observations of feeding (Figure 6). Contrastingly, scrapers are important turf grazers and increasingly so with larger size classes through time (Figure 9). Grazers of the two smallest size classes play important roles in both turf and macroalgal removal, likely a result of their high bite rates, which exceed those of both browsers and scrapers (Figure 6). While the two smallest grazer size classes removed the most turf biomass of any other size class of any guild each year, importantly their bites play a different ecological role on the reef than those of scrapers. While grazers are removing turf biomass from the reef, scraper bite scars open limestone available for recruitment of crustose coralline algae, a reef-building alga, and coral larvae. Thus, while this model focuses on removal of algal biomass, there are additional complex dynamics to consider in how changes on the reef may occur through increased grazing through time. (For a greater discussion of the ecological fate of a bite, see Discussion section of Chapter 1).

Placing Kahekili in a global context, both total herbivore biomass and biomass of individual herbivore guilds at KHFMA in 2014 were similar to the global mean for each of these metrics at fisheries accessible reefs (global mean = 20.5 g m^{-2}; scraper = 9.5 g m^{-2}; browser = 2.0 g m^{-2}; grazer = 17.5 g m^{-2}; Edwards et al. 2014). This level of herbivore biomass remains less than half the biomass of reefs not accessible to fishing in the Main Hawaiian Islands (~40 g m^{-2}) and the global mean of non-fisheries accessible reefs (56.4 g m^{-2}) in the same study. The Pacific remote islands and atolls (PRIAS) and additional remote cites exceed 100 g m^{-2} of herbivore biomass, though these sites are few.

Given that herbivores consumed 30% of algal production in 2014 at KHFMA, we therefore suggest that an herbivorous fish biomass must continue to increase to reduce algal biomass on the reef and ultimately reduce algal cover. While some of net production is consumed by urchins and converted to detritus, these routes likely do not account for 70% of production. Reefs in the MHI that are not accessible to fishing with 40 g m^{-2} (Edwards et al. 2014) may be reasonable near-term goals for herbivore biomass at KHFMA.

Other studies that have calculated production and consumption on reefs through a variety of methods and on a variety of reef types have seen similar results to this study in proportion to benthic cover and herbivorous fish biomass (Table 2). On reefs with less than 10% coral and high algal cover in the Florida Keys, mean production was two times production at Kahekili (1.05 vs. 0.48-0.70) (Paddack et al. 2006), which has three times the amount of coral cover and proportionally less fleshy algae. Meanwhile, herbivore fish biomass was 3 to 10 times that of Kahekili and mean consumption rates were 3 to 6 times Kahekili rates. On high coral cover reefs in the Caribbean (Wanders 1976, Carpenter 1986), production was 3 to 5 times that of Kahekili despite having a smaller proportion of the benthos being covered by algae. This result may be due to the highly productive nature of algae at these reefs in which constant grazing keeps algae in a state of high productivity (Westlake 1963).

Bite size calculations here need additional refinement but data are not currently available for bite size of size classes within individual species. Therefore, it was necessary to lump the most morphologically similar fish (ie: those from each family) together and calculate bite size accordingly. The current equations further assume that a bite on turf algae by a fish of a given size removes the same biomass as a bite from macroalgae. While these calculations are certainly estimates, they roughly follow the allometric increase in body size by length of fishes (Huxley & Tesissier 1936, Zgliczynski et al. in prep).

This study provides a functional approach to measuring the potential trajectories of reef communities based upon characteristics of the herbivore assemblage. While estimates of production and consumption have been done in the past (Table 2), this is the first study to consider rates of production on a reef through time, and thus considering the future trajectory of a reef.

The approach used here incorporates not just snap-shot survey data but measured rates of consumption and production based upon the specific composition of the benthic and herbivorous fish communities under investigation. By using these rates we may be able to begin estimating how many and what type of herbivores are needed to elicit strong top-down control on algal communities. In a time when herbivore protection is being promoted as a tool to reduce algal overgrowth of corals we need more tools to be able to predict management and set targets for the herbivore communities. These targets will be directly related to the state of a given reef community and the production of the algal community. The approach we have outlined here begins to provide such a framework to a point where modeling production and consumption on a reef provides the functional response of an ecosystem to herbivore protection and the potential impacts of future increases in herbivore abundance and biomass on the reef. The Kahekili Herbivore Fisheries Management Area and other herbivore protections that have appeared on reefs over the last five years provide a new opportunity for increasing herbivore consumption of algae on reefs to promote increases in coral cover.

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Tables

Table 1. Growth rate, standing biomass, and average percent cover of algae measured at Kahekili. Data are averages for each measurement across all years and seasons of the study (2008-2014).

**Standing biomass assumes 100% coverage of given alga in a square meter.*

Functional Group	Species	Growth rate (g dry wt m^{-2} day) (+/- SE)	Standing stock biomass* (g dry wt m^{-2}) (+/- SE)	Average percent cover (across all years)
Turf algae	mixed	0.0708 (+/- 0.0164)	78.98 (+/- 11.83)	46.9%
Macroalgae	all	--	51.49 (+/- 17.92)	4.0%
	Melanamansia glomerata	0.0093 (+/- 0.0021)	38.02 (+/- 12.36)	0.9%
	Tricleocarpa fragilis	0.0003 (+/- 0.0046)	< 0.1	< 0.1%
	Acanthophora spicifera	0.0229 (+/- 0.0099)	< 0.1	< 0.1%
	Ulva lactuca	0.0341 (+/- 0.0051)	< 0.1	< 0.1%

Table 2. Comparison across studies that have measured algal production and herbivore consumption of algae on different reef systems. For comparison to other studies, dry weight calculations in this study were converted to g C by assuming g C = 0.25 * g dry wt algae.

					Fleshy algae production			Fish consumption of fleshy algae			
study	location	protection status	reef type / depth	season	benthic % cover	mean production rate ($g C * m^{-2} * d^{-1}$)	estimated by	mean herbivorous fish biomass ($g * m^{-2}$)	mean consumption rate ($g C * m^{-2} * d^{-1}$)	estimated by	proportion of production consumed (%)
	Hawaii										
this study	ahekili, West Ma	Herbivore Fisheries Management Area	3-8m	2009 (year of designation as HFMA)	turf = 53.82%; macroalgae = 4.06%; CCA =0.33%; coral = 34.04% (Figure 3)	0.68	multiplying bootstrapped means of field-measured variables (in situ algal growth through caging experiments, standing stock biomass, and % cover) (Figure 2)	16.36	0.13	multiplying bootstrapped means of field-measured variables (herbivore bite rate, bite size, and biomass) (Figure 2)	19.31
				2014	turf = 41.23% macroalgae = 1.58%; CCA = 12.60%; coral = 36.83% (Figure 3)	0.63		19.67	0.19		29.36
	Caribbean										
Paddack et al. (2006)	Florida Keys	fish traps banned since 1981, slight commercial fishery for herbivores	averaged across all	averaged across all	turf = 28-38%; macroalage = 40-46%; CCA = 2-4%; coral = 1-6%	1.05	growth on outplanted tiles	47–121	0.34–0.76	Method 1: Detailed estimation for Sparisoma viride extrapolated to guild-wide values based upon the proportion of herbivorous fish biomass held by S. viride Method 2: Regression used in van Rooij et al. (1998)	31–77
van Rooij et al. (1998)	Bonaire	entire reef of Bonaire is a marine park, spearfishing banned since 1971, fishing on herbivores is negligible	0-3m	summer	described in Bruggeman (1994) highest proportion of living corals, including mounding and branching corals. Of seaweeds: 3.5-20.5% large turf & macroalgae 8.1-22.9% sparse turf 54.6-57.5% sparse turf on CCA 11.2-19.0% CCA	1.86	measuring changes in dissolved oxygen in incubation experiments at 1m depth on the backreef	41	1.74	herbivore biomass and trophic efficiency regression using values taken from literature	101
				winter		1.46					
Carpenter (1986)	St Croix	NA	bank barrier reef; 1.5-2m	summer	"consists largely" of Acropora palmata and where there are dead corals they are "covered with mats of small algal filaments"	1.58–2.16	growth on outplanted tiles	NR	2.5	caging experiment utilizing turf grown on outplanted tiles	97
				winter		1.98–3.11					
Wanders (1976-production; 1977-consumption)	Curaçao	NA	shallow reef 0.5-3m	averaged across all	patch reefs describes by rugosity measure cover, not % cover. "filamentous and fleshy algae constitute only an inconspicuous vegetation."	3.48	oxygen production using the light-and-dark-bottle technique	NR	not clearly defined	consumption of algae from outplanted asbestos plates	NA
Kopp et al. (2010)	Guadeloupe	half of the sites are inside an MPA	reef flat	averaged across all	NR	0.37-0.95	net algal turf production from ribbon outplanting plus herbivore grazing	NR	0.1-0.7	Method 1: proportion of organic matter in guts	27-200
			reef slope			0.35-0.50				Method 2: estimation from observed bite rates and fish size	28-140
	Great Barrier Reef										
Russ (2003)	Myrmidon	NR	reef flat	average of February and July	NR	0.2-0.5	growth on outplanted tiles	18-28	0.2-0.7	grazing on tiles as compared to fish biomass	40-100
			reef crest			0.7-1.8		30-55	0.7-2.1		38-100
			reef slope			0.2-0.3		2-8	0.2-0.4		67-100
Klumpp and Polunin (1990)	Davies	NR	reef flat	summer	15-80% CCA and turf; partitioning of these seaweeds or other cover not reported	2.51	outplanted tiles later placed in respirometer chambers (data and description of methods in Klumpp and McKinnon (1989))	not described but dominated by damselfish, blennies, 1 Acanthurid species, and 2 Scarid species	0.57–1.13	multiplying observtional data on fish bite rates, body size, and gut fullness index	winter: 42 summer: 72
				winter		1.71					
			reef slope	summer		1.72					
				winter		1.11					
Hatcher (1981)	One Tree Reef	NR	lagoon, reef crest, and reef slope; .5-10m	averaged across all	NR	0.61–0.97	growth on outplanted tiles	5–21	0.40–0.79	remote cameras taking timelapse photographs	61–290

Figures

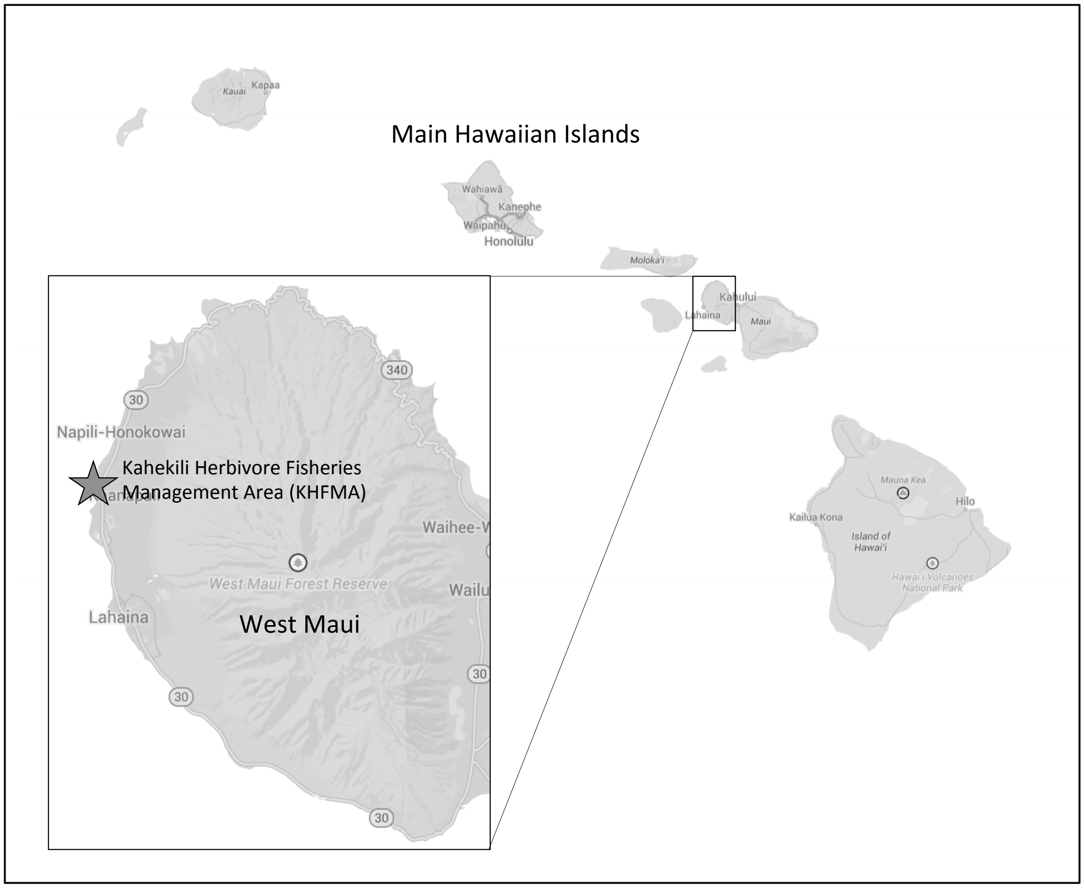

Figure 1: Location of study reef, Kahekili Herbivore Fisheries Management Area, located on West Maui in the Main Hawaiian Islands.

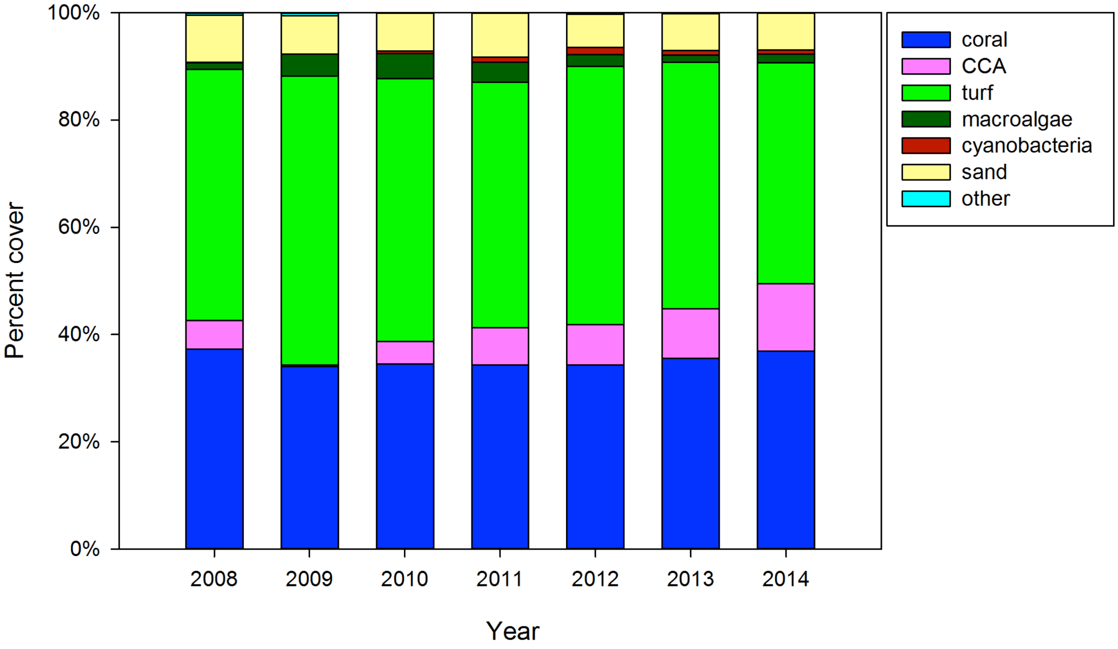

Figure 2: Benthic community composition through time across all survey years. Turf and macroalgae cover for each season and year are used in the calculation of algal production. n= 100-180 per year.

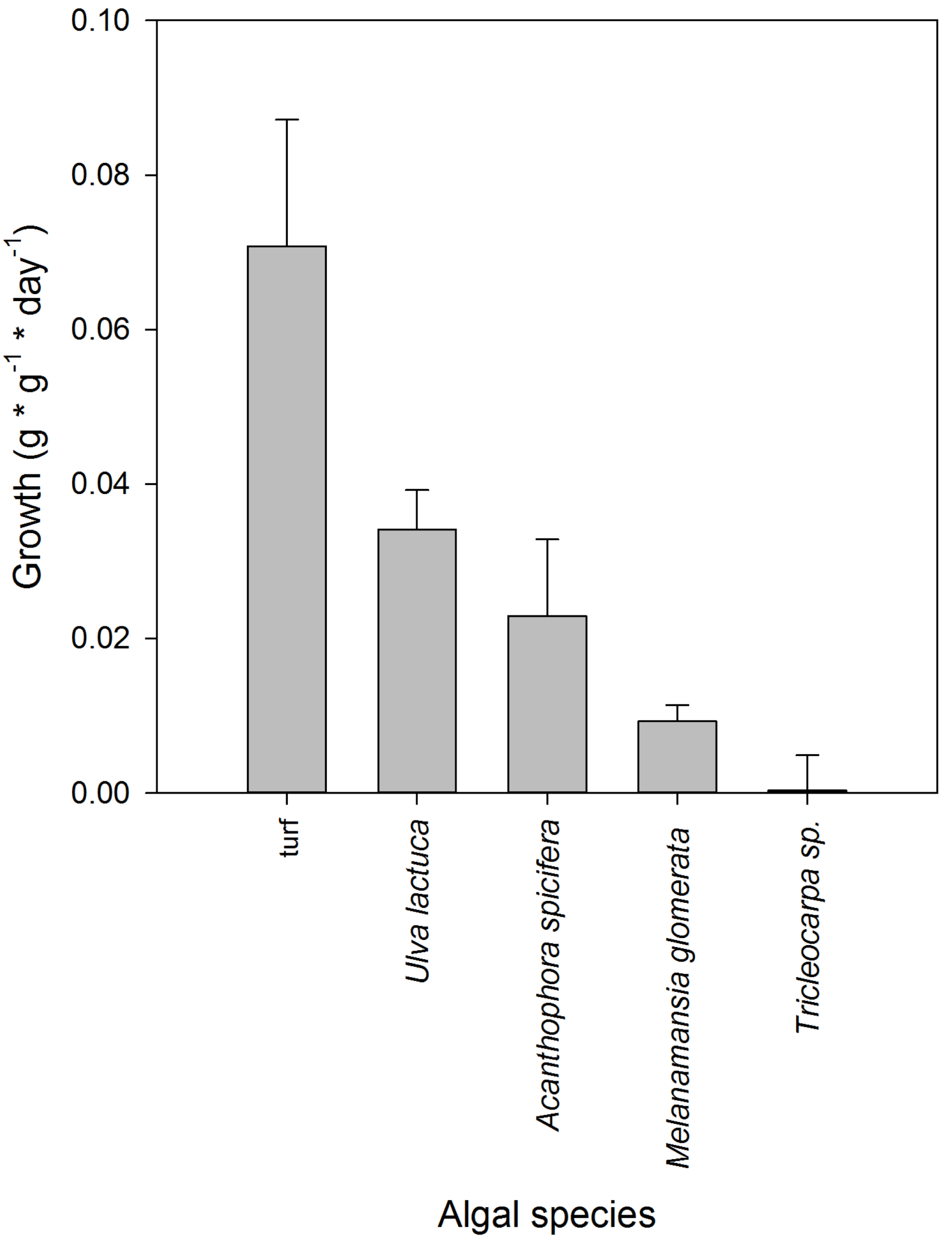

Figure 3: Growth rates of turf algae and four species of macroalgae (g dry wt * g algae^{-1} day^{-1}) at Kahekili. Bars are SE.

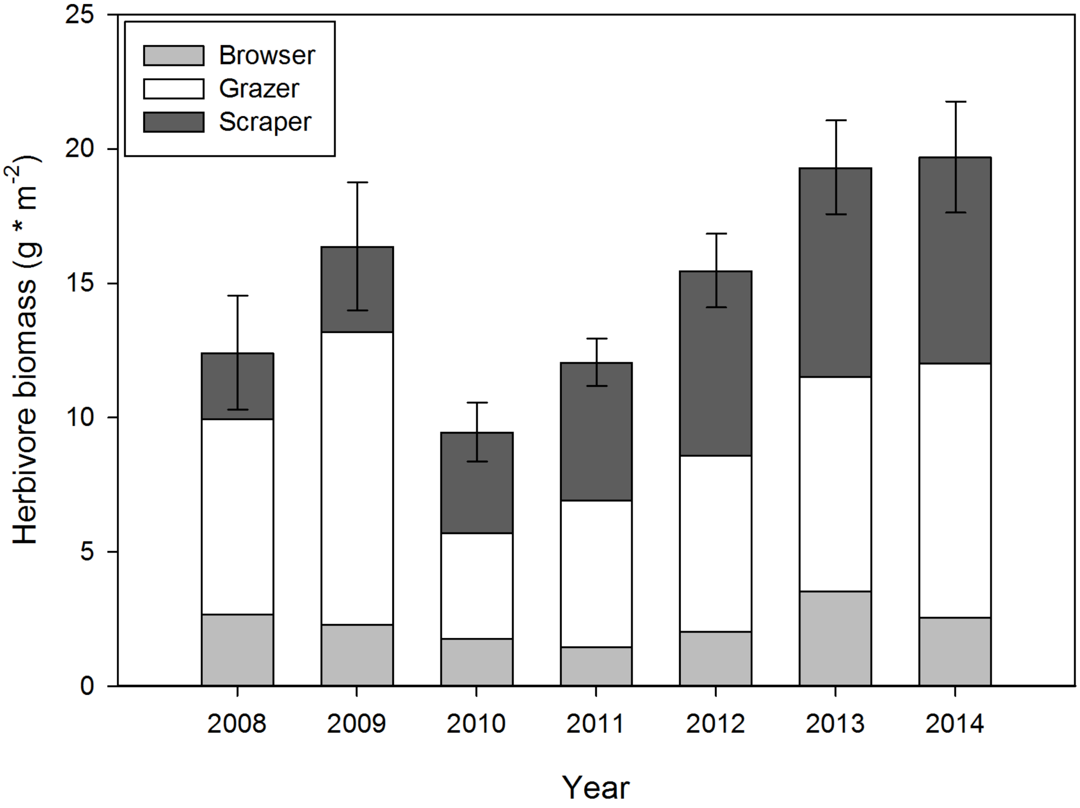

Figure 4: Fish biomass through time across all survey years. Bars are SE for total herbivore biomass. n= 100-180 per year.

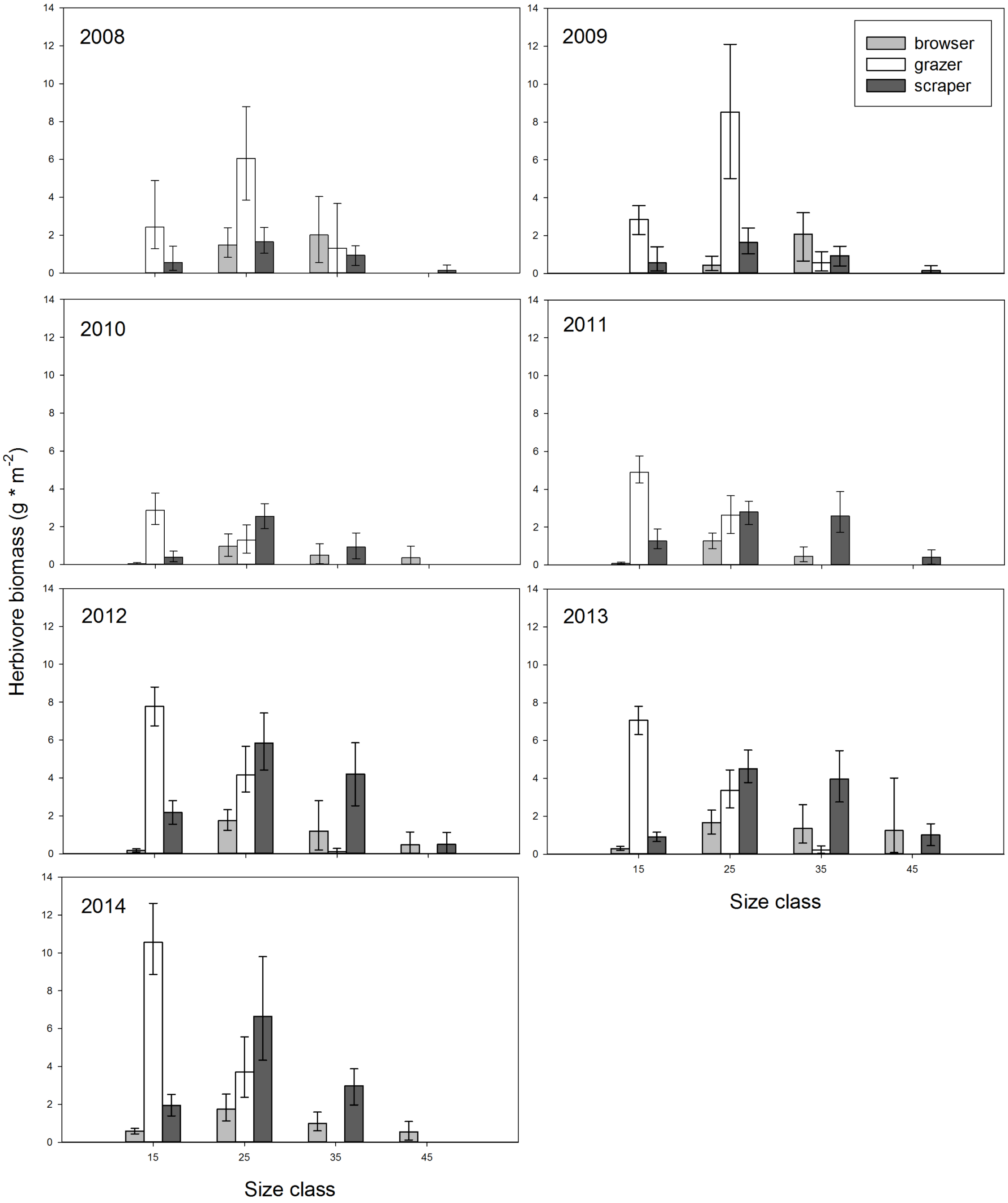

Figure 5: Herbivore biomass per year broken into guilds and size classes. Bars are 95% confidence intervals.

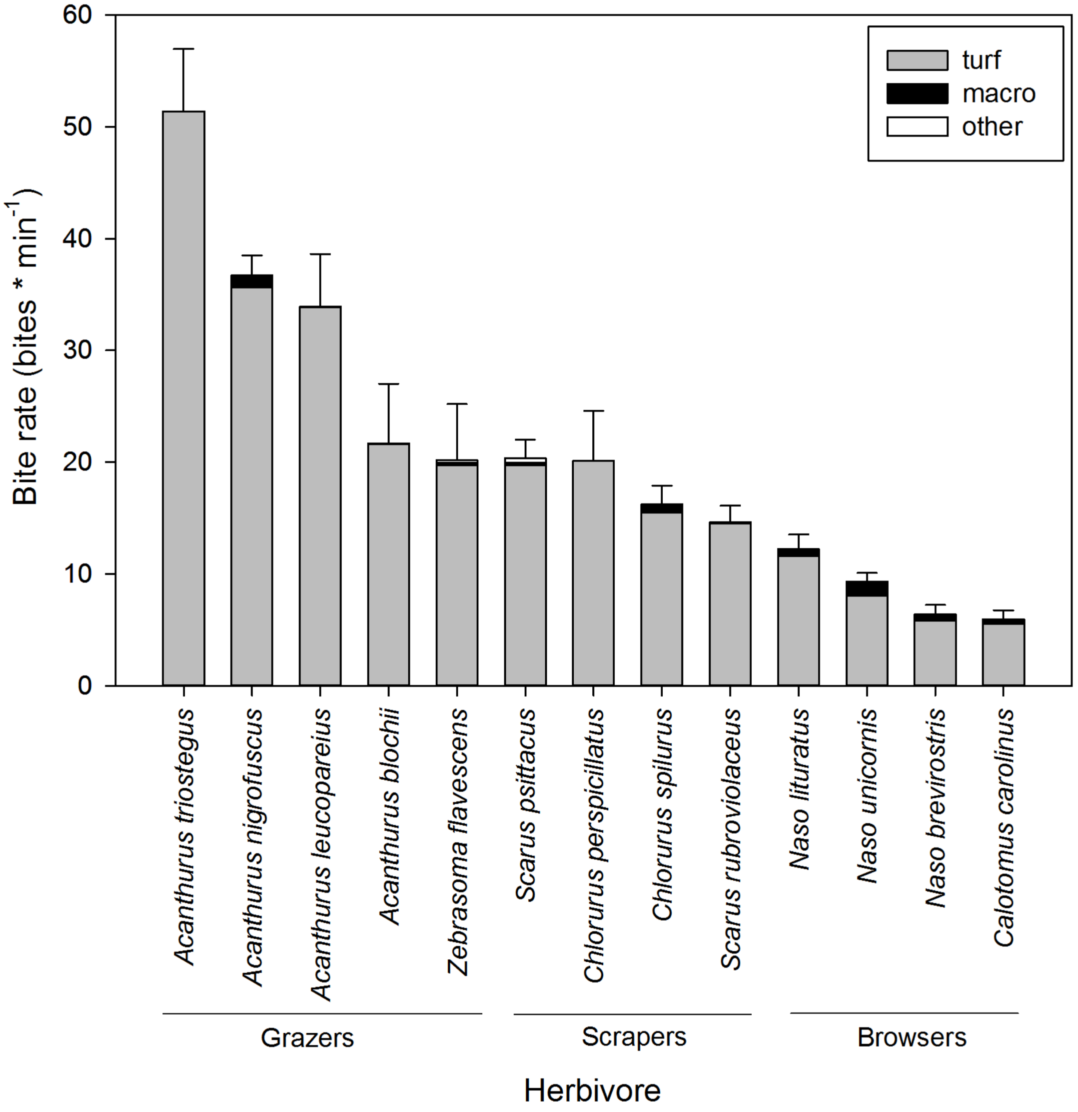

Figure 6: Herbivore species mean (+/- 1 SE) bite rates on turf algae, macroalgae, and other substrate. n = 10 - 64.

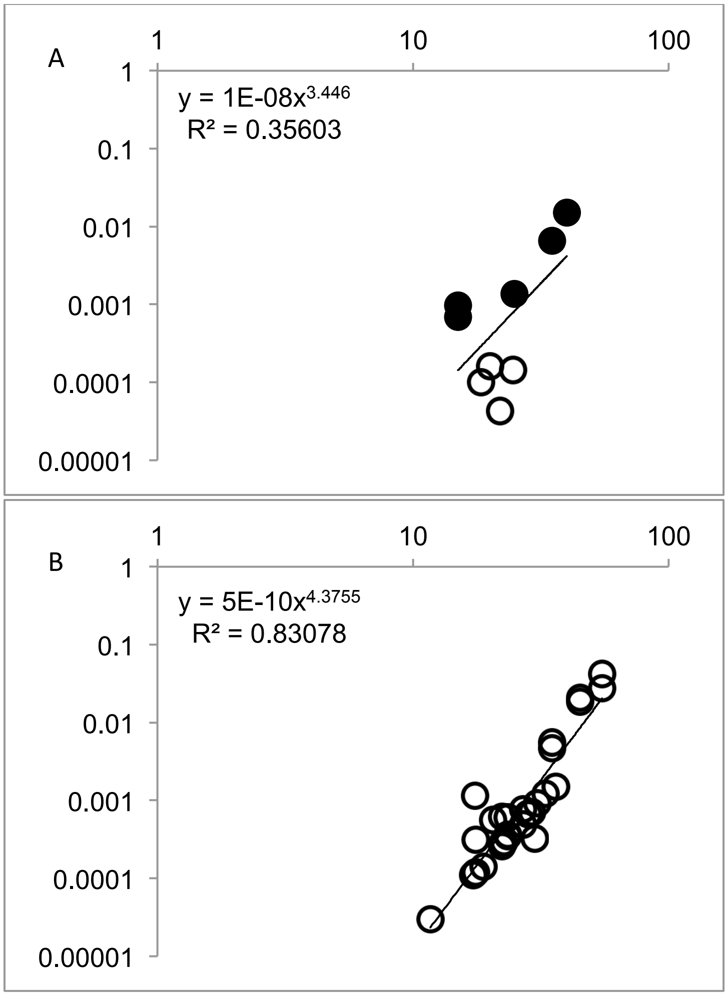

Figure 7: Herbivore bite size (g dry wt algae * bite^{-1}) derived from field experiments (solid) and literature (open) values as related to body size for both (A) Acanthurids and (B) Scarids. Data were log-log transformed and described by a power function.

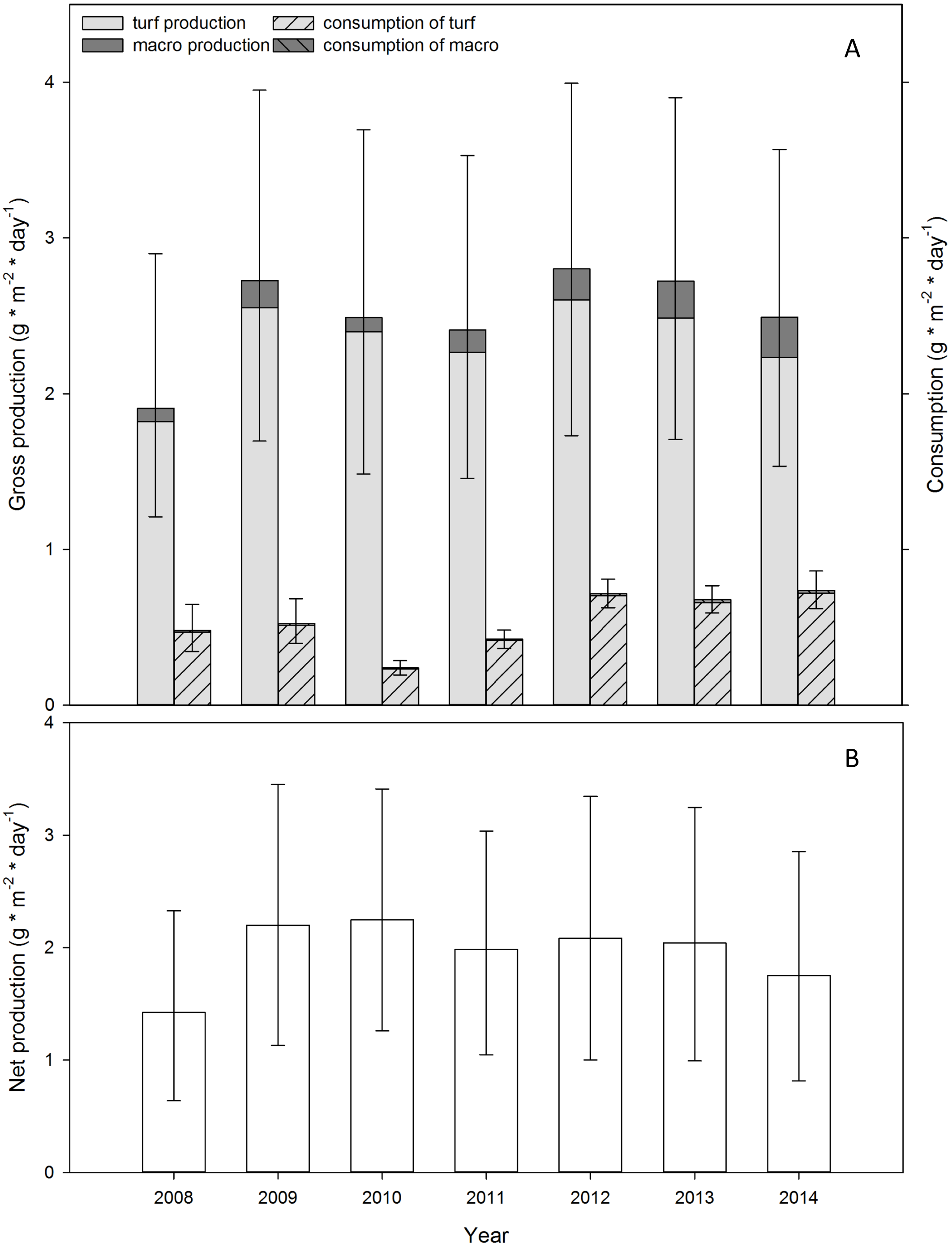

Figure 8: (A) Growth (solid bars) of macroalgae and turf algae (g m^{-2} d^{-1}) and consumption (hashed bars) of macroalgae and turf algae (g m^{-2} d^{-1}) by the herbivore community from 2008 to 2014. (B) Net production of the algal community after accounting for consumption by the herbivores. Protection of Kahekili as an Herbivore Fisheries Management Area occurred in summer 2009. Bars are 95% confidence intervals.

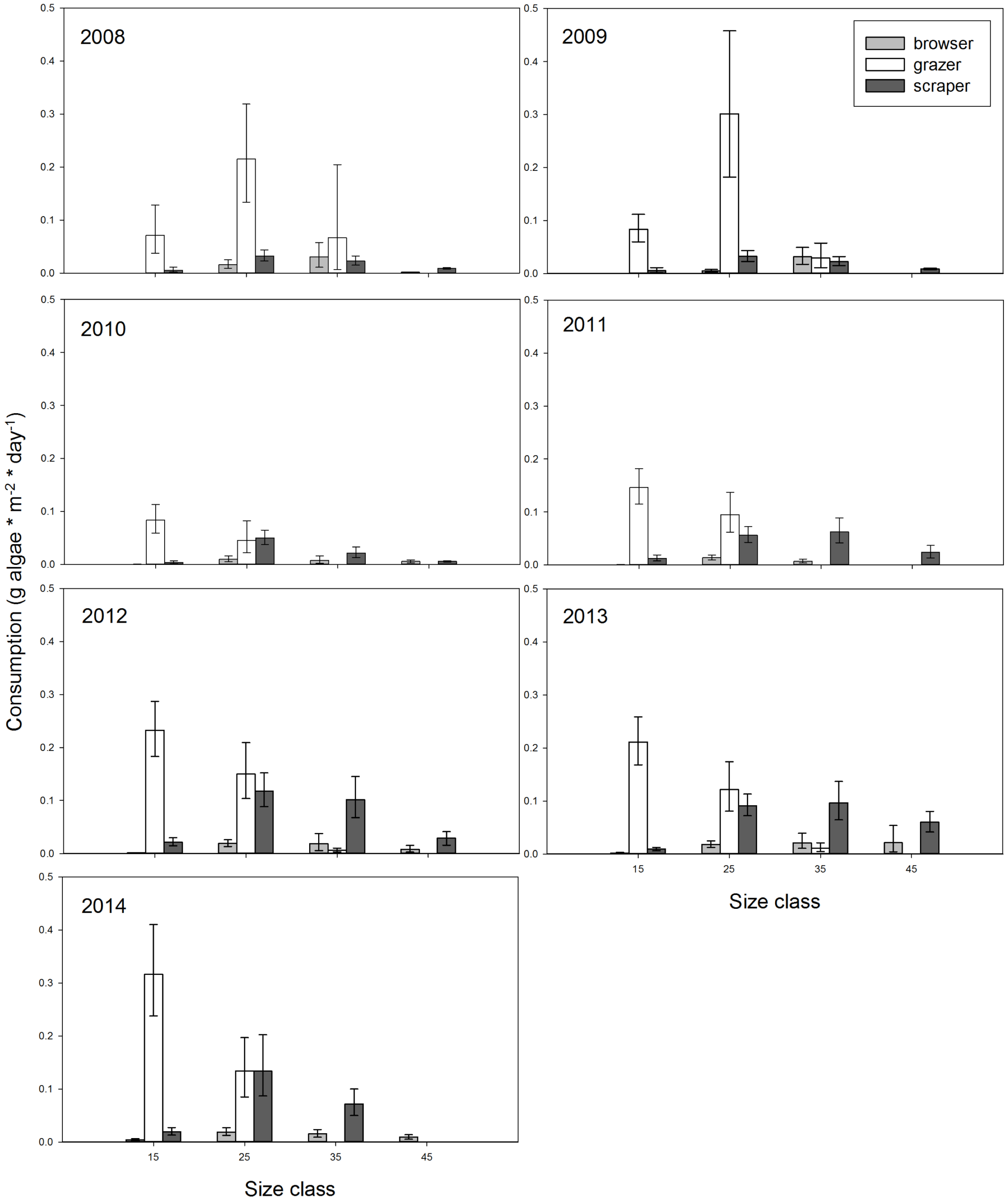

Figure 9: Herbivore consumption of turf algae from 2008-2014 by guild specific size classes based upon survey data collected each year. Bars are 95% confidence intervals.

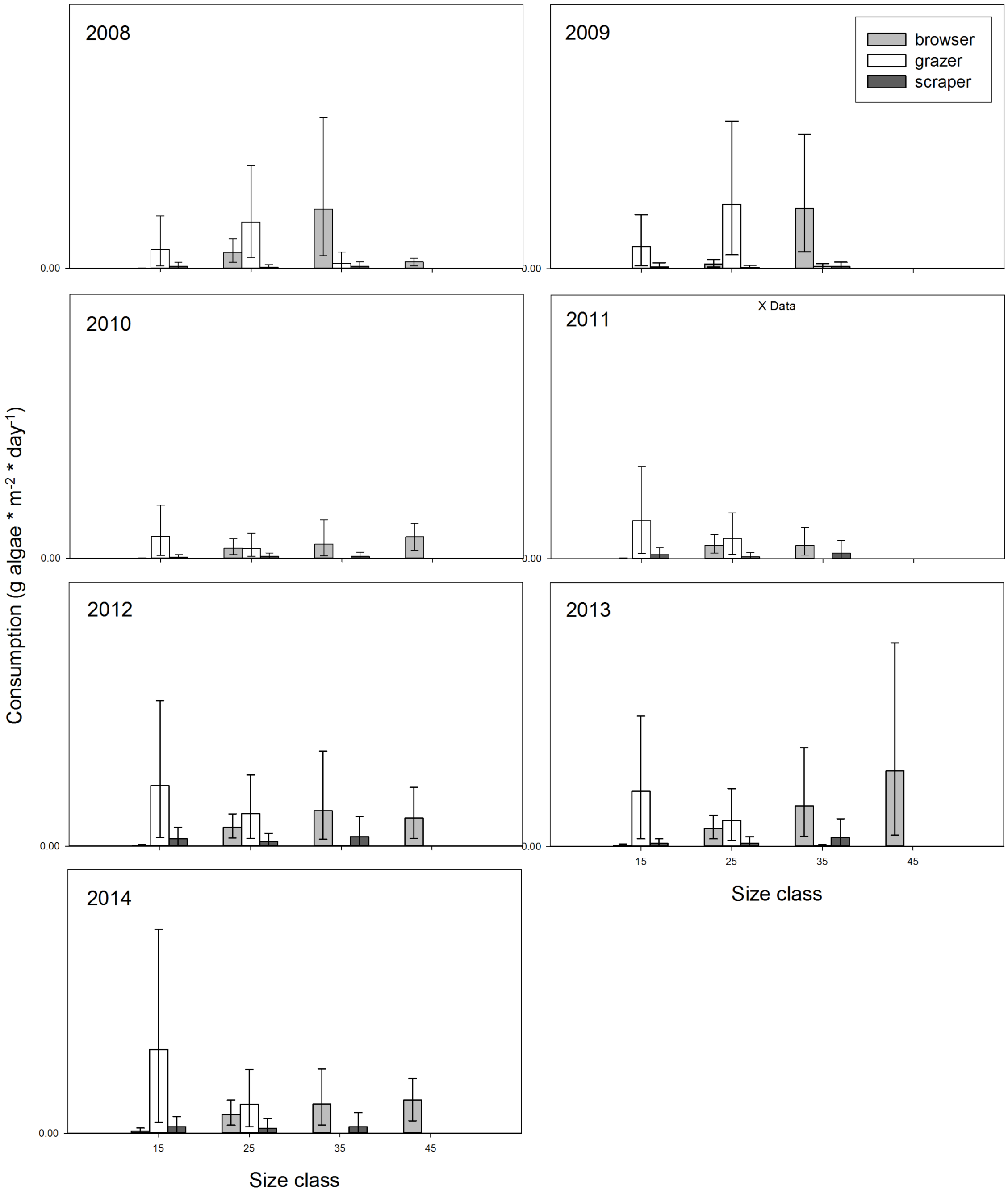

Figure 10: Herbivore consumption of macroalgae from 2008-2014 by guild specific size classes based upon survey data collected each year. Bars are 95% confidence intervals.

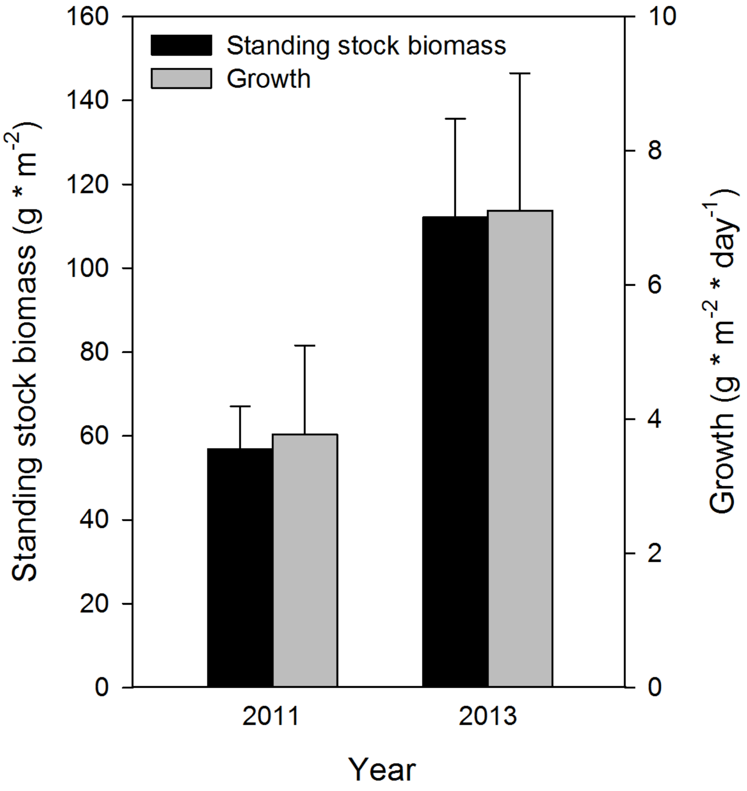

Figure 11: Turf standing stock biomass (black bars) and growth rates (gray bars) from *in situ* experiments at Kahekili in 2011 and 2013. Bars are SE. n = 24 in 2011; n = 16 in 2013.

CHAPTER 3:

Herbivore consumption and net algal production as predictors of benthic community composition and future reef trajectory on Maui, Hawaii

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Abstract

Herbivores are known for their ability to exert top-down control of algal growth on coral reefs. Their role in consuming algal production suggests that an increase in herbivore biomass on degraded reefs may result in greater consumption of algae leading to a reduction in algal cover and an increase in coral cover. However, the use of herbivores as a tool for reef restoration has not been widely used or explored. In order to know if herbivore management may be an effective means of restoring degraded, algal dominated reefs there is a need to better understand how rates of herbivore consumption and algal production compare across different benthic communities. Our study sought to estimate production and consumption at reefs around the island of Maui in order to determine how the balance of these rates at reefs varied with benthic composition and herbivorous fish biomass. We further aimed to quantify the amount of herbivore biomass that would be required to have a net negative effect on the algal community and thus may actually promote an increase in coral cover. Using parameters derived through experimentation and extensive survey data from around the island, we were able to add additional depth to reef characterization through quantifying, production, consumption, and net production. We found that net algal production was lowest at reefs with high coral cover even when fish biomass at reefs with lower coral cover was comparable or greater than on high coral cover reefs. The results of this study suggest lower herbivore biomass is required to maintain a healthy reef than to restore a degraded reef.

Introduction

Coral reefs are known for their high rates of productivity and extremely efficient nutrient cycling (Odum & Odum 1955, Johannes et al. 1972, Hamner & Hauri 1981). High rates of benthic productivity can be attributed to corals and their symbiotic zooxanthellae as well as numerous types of benthic algae (Odum & Odum 1955, Johannes et al. 1972). Despite high rates of production, historically, due to the intense grazing activity by herbivorous fishes benthic algal standing stock was generally low (Randall 1961, Wanders 1977). However, given the varying degree of fishing on most reefs around the world today there is a general understanding that the loss of herbivorous fishes corresponds to an increase in algal abundance (Jackson et al. 2001, Burkepile & Hay 2010, Smith et al. 2010). Inverse relationships between herbivore biomass and benthic macroalgal cover have been observed in studies from both the Caribbean and the Pacific highlighting these linkages (Williams et al. 2006, Friedlander et al. 2007).

Overfishing in ocean ecosystems around the world has resulted in greatly diminished fish stocks across many ecosystems (Jackson et al. 2001). Herbivorous fish on coral reefs impacted by fishing have a mean biomass 50% lower than on reefs not accessible to fishing (Edwards et al. 2014). In some cases, diminished presence of herbivores has been linked to algal overgrowth and thus the decline of coral cover on reefs (Hughes 1994). Numerous experiments focusing on experimental removal of herbivores have shown that fleshy algae are the competitive dominant in the absence of grazing (Ogden & Lobel 1978, Burkepile & Hay 2010). As a result of both observational and experimental data, herbivore restoration via increasing herbivore biomass has been suggested as a tool to reduce algal abundance and thus promote coral cover on reefs that have undergone decline (Green & Bellwood 2009, Rasher et al. 2013, Jackson et al. 2014).

By comparing herbivorous fish biomass across reefs we can gain insight into the differences in overall grazing potential of the community. However, biomass alone does not take into account different feeding behaviors including bite rate and bite size of the individual species. Further, without considering how benthic algal production varies across reefs it is not clear how many herbivores would be needed to consume a given algal community and potentially enhance coral cover at these locations. On degraded reefs in which coral cover has declined and there is greater cover of algae, a different herbivore community than previously existed will likely be needed to control algae biomass (Paddack et al. 2006). In order to begin to understand the level of herbivore biomass required to consume a given algal community, both algal production and herbivore consumption must be quantified.

To test the effects of anthropogenic influence on reefs, a long-term monitoring program of benthic community composition was established in the Main Hawaiian Islands (MHI) in the late 1990s (Brown et al. 2004). Further surveys to monitor resource fishes and aquarium fishes began in the mid 2000s. These datasets provide detailed records of benthic cover and fish biomass at reefs around the MHI. Coral cover has declined and fleshy algal cover has increased on many reefs over the last 15 years (Rodgers et al. 2015) and herbivorous fish biomass has been reduced on many reefs in the MHI (Friedlander et al. 2007). While some correlative studies utlize these parameters to characterize reef health, we seek an approach that incorporates more of the underlying ecosystem function related to reef health.

This study therefore had four goals. First, we examined change in herbivore and benthic communities at nine sites on Maui through time. Second, we examined how rates of consumption and benthic fleshy algal production changed over time based on herbivore and benthic community changes. Third, we used our estimates of consumption on these nine reefs as a predictor of benthic community composition and compared it to the approach done by others using fish biomass as a predictor of benthic community composition. And finally, we examined net production across the gradient of benthic composition and fish biomass to consider potential reef resilience to future perturbation and the amount of herbivore biomass required to push coral depauperate systems away from fleshy algal dominance.

Methods

Study area and overview

Benthic and fish data were collected at ten sites around the leeward side of Maui, Hawaii. All experimentally derived parameters were measured at the Kahekili Herbivore Fisheries Management Area (KHFMA) on West Maui. Algal growth and herbivore consumption at all locations across Maui were determined through analysis of benthic community composition, standing stock of algae, growth rates of dominant algal species, abundance and biomass of herbivorous fish species, the consumption rates of herbivores on different species of algae, and the bite size of herbivores.

Benthic community composition

Benthic cover at each of the nine reefs in this study was determined from surveys conducted annually using two approaches (Table 1). First, sites surveyed by the Hawaii Coral Reef Assessment and Monitoring Program (CRAMP) were surveyed along ten 10-m-long transects at permanently marked locations on reefs. From 1999 to 2004, video transects were recorded and analyzed for benthic cover in the laboratory. After 2004, ~1m^2 photoquadrats were taken every 1m along each transect. Photographs were analyzed using the image analysis software PhotoGrid 1.0 in which 15-100 points were superimposed on the image in a stratified random fashion. For both video and still images, benthic cover was identified to genus level for corals and algae or functional group for turf algae, crustose coralline algae (CCA), and cyanobacteria (Brown et al. 2004, Rodgers et al. 2015). Second, the West Hawaii Aquarium Project (WHAP) established four 25-m-long transects at 3-10 m depths on reefs in 2009. For both methods, ~1m^2 photoquadrats were taken every 1m along each 25m belt transect and analyzed in the same fashion as the CRAMP photoquadrats. For broader analyses, benthic organisms were later grouped according to coral, reef builders (coral and CCA), and fleshy algae (non-calcareous turf and macroalgae).

Herbivore abundance and biomass

Surveys to quantify herbivorous fish abundance and biomass were collected at each of the nine reefs in this study via two regular sampling methods by the NOAA Coral Reef Ecosystem Division and Hawaii Division of Aquatic Resources (Table 1). First, annual five-minute timed-swim surveys were conducted annually at reefs around the island. Divers swam 5 minutes (120 m) and recorded herbivores 15 cm or greater along a

5m-wide transect. Second, annual strip transect surveys were conducted at other reefs around the island. Fish densities of all observed species were estimated by visual strip transect search along each transect line. On the outward-bound leg, fish > 15cm, within a 4m-wide belt centered on the diver and within 4m of the bottom were recorded. On the return leg, fishes <15cm were recorded within a 2m-wide belt. Fish biomass for both survey methods was calculated using established species-specific conversion factors taken largely from FishBase (2012). For this study, non-juvenile fish were binned into 10 cm size classes (6-15 cm, 16-25 cm, etc). Herbivores were categorized as grazers, scrapers, or browsers according to Green & Bellwood (2009) and Edwards et al. (2014). Detritivores were not included in the consumption calculation as their impact in removal of algae is considered minimal (see Chapter 1; also Choat et al. 2002).

Production parameters

Standing biomass of algae and algal growth rates were experimentally derived at Kahekili reef by using percent cover data from the above, estimating relationships between percent cover and standing biomass and growth rates of common taxa (see Chapter 2). The data generated from Kahekili were used as estimates of these parameters across all reefs on Maui.

Consumption parameters

Grazing rates for all abundant herbivorous fish species in the grazer, scraper, and browser guilds were quantified at Kahekili reef (see Chapters 1 and 2) as well as Kapalua Bay and Olowalu (see Figure 1) for the most common herbivorous fish species around

Maui. These grazing rates were used as estimates for grazing rates across all sites in this study. Herbivore bite size was derived through laboratory experiments as well as using literature values to establish a relationship between the log of herbivore total length (TL) and log of bite size (BS; grams of algae removed per bite). See Chapter 2 for a full description of methods.

Fish consumption and benthic fleshy algal production

Consumption and production through time

To combine the multiple sources of variability that contribute to fish consumption and benthic fleshy algal production estimates, we used a bootstrapping approach to build a distribution of mean benthic algal production and mean fish consumption. We further created a bootstrapped distribution of net benthic algal production (production remaining after consumption) for each of the nine sites. See Chapter 2 for full description of the methods. In order to further assess the relative contributions of different size classes of herbivores to the total consumption budget of the herbivore community, consumption data were analyzed by feeding guild and size class.

Consumption and production as predictors of benthic composition

To determine if herbivorous fish consumption could be a better predictor of benthic community composition than herbivorous fish biomass, we calculated the correlation coefficients between these two metrics and percent fleshy algal cover and percent coral cover. Finally, we examined the distribution of reefs according to their percent cover of coral and active reef builders (coral and CCA) and total herbivorous fish biomass at each site for each year. We overlaid these points with net benthic algal production to examine patterns across the island.

Results

Benthic community composition

Across all nine sites examined in this study (Figure 1) coral cover ranged from 4.2% at Kanahena Point in 2007 to 85.5% at Molokini in 2003 (Figure 2 and A1 for sites with three or fewer years of data). Average coral cover across all sites was 37.8% (+/- SE = 7.3). Coral cover at many sites was fairly stable from 1999-2014. Exceptions included the decline in coral cover at Honolua Bay from 2000-2003, at Kanahena Point from 2004-2007, and at Kahekili from 1999-2000. From only three years of data, there are trends of decline at Keawakapu and Kapalua Bay from 2007-2013 (Figure A1). After initial decline, coral cover has increased at Kanahena Point from 2007 to 2014 though it remains one of the lowest coral cover sites in the data set (Figure 2).

CCA cover on reefs ranged from 0.0% at Honolua Bay North in 2008 to 71% at Kanahena Point in 2007. Average CCA cover across all sites was 9.2% (+/- SE = 3.6) (Figure 2). The largest increase in CCA cover was at Kanahena Point where CCA makes up to 71% of total cover despite this site having less than 10% coral cover. Across all reefs, mean cover of reef-building organisms (corals and CCA) was greatest at Keawakapu in 2011 at 92.7% (Figure A1), while it was lowest at Honolua Bay in 2008 at 8.4% (Figure 2).

At all sites, there was greater coverage of turf on reefs than of macroalgae (Figures 2 and A1). Molokini in 2011 had the lowest percent cover of fleshy algae with

6.2% cover of turf and no detectable macroalgae (Figure 2). Turf algae were most abundant at Kanahena Point in 2008 with 82.9% cover. The greatest macroalgal cover was at Kahekili in 2003 (20.9% +/- 3.0) (Figure 2). In 2003 Honolua Bay North had the greatest mean fleshy algal cover of 88.4% (Figure 2).

Herbivore biomass

Herbivorous fish biomass ranged from 0.3 g m^{-2} at Keoneoio in 2008 to 293.5 g m^{-2} at Honolua Bay in 2009 (Figure 3 and A2 for sites with three or fewer years of data). The average herbivore biomass across all sites and all years at these nine reefs in Maui was 10.4 (+/- 6.2) g m^{-2} of browsers, 13.9 (+/- 6.5) g m^{-2} grazers and 8.2 (+/- 2.2) g m^{-2} for scrapers, with an overall average total herbivore biomass of 32.6 (+/- 12.8) g m^{-2}. All sites varied by 1 – 10 fold in herbivore biomass across years (Figures 3 and A2).

The relative abundance of herbivore guild biomass differed across sites. Canoe Beach, Kahekili, and Kanahena Point had the greatest proportion of grazers (Figure A2 and 3), Honolua Bay and Kapalua Bay had the greatest proportion of browsers (Figures 3 and A2), and Keawakapu, Keoneoio, Olowalu, and Molokini had the greatest proportion of scrapers (Figures A2 and 3).

Fish consumption and benthic fleshy algal production

Consumption and production through time

Based upon our modeled estimates, benthic fleshy algal production (turf and macroalgae) ranged from the lowest mean value of 0.5 g m^{-2} day^{-1} (95% confidence interval from 0.3 to 0.7) at Keawakapu in 2011 to a the highest mean value of 5.0 g m^{-2}

day^{-1} (95% confidence interval from 3.1 to 7.2) at Kanahena Point in 2008 (Figure 4A and A3 for sites with three or fewer years of data). Herbivorous fish consumption ranged from the lowest mean value of 0.008 g m^{-2} day^{-1} (95% confidence interval from 0.003 to 0.02) at Keoneoio in 2008 (Figure A3) to the greatest mean consumption value of 4.8 g m^{-2} day^{-1} (95% confidence interval from 2.1 to 8.5) at Honolua Bay North in 2013 (Figure 4A). Net production (gross production minus herbivore consumption) ranged from -0.5 g m^{-2} day^{-1} (95% confidence interval from -4.6 to 2.8) at Honolua Bay North in 2013 to 4.8 g m^{-2} day^{-1} (95% confidence interval from 2.9 to 7.0) at Kanahena Point in 2008 (Figure 4B). Net production was not significantly different from 0 (95% confidence intervals included 0) for several years at Honolua Bay, Keawakapu, Molokini, and Kanahena Point (Figure 4B and A3).

The contribution to overall consumption by different size classes within each herbivore guild varied across years and sites for both turf and macroalgae (Figure 5). For instance, all size classes of all guilds were present at both Molokini and Olowalu, while the smaller two size class were the largest contributors to grazing at Kanahena Point, with fish of the largest size class absent (Figure 5). There was a shift in the size class distributions at Kahekili such that larger size classes contributed more to overall consumption of both turf and macroalgae after 2012 (see further details in Chapter 2).

Consumption and production as predictors of benthic composition

Herbivorous fish consumption rate was a better predictor of both percent fleshy algal cover and percent coral cover than was herbivore fish biomass (Figure 6). Increased fish consumption correlated with increase fleshy algal cover (R= 0.33, Figure

6C). The strongest correlation of these relationships was between herbivorous fish consumption and percent coral cover (R= -0.37, Figure 6D).

Looking across all reefs as a function of coral cover and fish biomass, net fleshy algal production was generally smallest at reefs with higher coral cover (>50%) even when fish biomass ranged from 10 - 45 g m^{-2} (Molokini, Kapalua Bay, Canoe Beach, Figure 7). As coral cover declined, reefs with herbivore biomass both above and below this range showed higher net productivity (Kahekili, Olowalu, Keoneoio, Kapalua Bay; Figure 7). The greatest net productivity was at Kanahena Point in 2008, which had the lowest coral cover (<10%) and lowest fish biomass (<10 g m^{-2}) of all sites and years (Figures 2, 3, and 7). Low net productivity also existed at Honolua Bay in some years in which, despite low coral cover (<10%), fish biomass was between 215 and 295 g m^{-2} (Figures 2, 3, and 7)).

Net fleshy algal productivity was almost always smallest at reefs with higher percent cover of reef builders (coral and CCA >60%) across the range of fish biomass on these reefs (Figure 8). The very high fish biomass (> 200 g m^{-2}) at Honolua Bay North was again an exception to this (Figure 8).

Discussion

Our study sought to quantify change in herbivore and benthic communities at nine sites on Maui through time and, using a novel approach we aimed to examine how herbivorous fish consumption and benthic fleshy algal production changed over this time period. Further, we sought to use this approach to further determine whether functional rates of consumption could better predict community composition on reefs than herbivorous fish biomass could and finally, we used net production across the gradient of benthic composition and fish biomass on all reefs to consider potential reef resilience to future perturbation and the amount of herbivore biomass required to push low coral cover systems towards higher coral cover. We found fairly stable benthic cover through time, with varying annual fish biomass. Benthic fleshy algal production and herbivore consumption on these reefs was similarly fairly stable. Herbivore consumption was a better predictor of benthic community composition than was herbivore biomass, although the correlations for all relationships were low ($R < 0.40$). We found that net production was lowest at reefs with high coral cover even when fish biomass was low (Figure 7). This pattern was stronger when considering all reef builders (Figure 8). The results of this study suggest that the amount of herbivore biomass needed to control fleshy algal production on a reef is context dependent.

Reefs considered in this study include some of the highest coral cover reefs on the island of Maui and a large proportion of sites that are protected from fishing (Table 1). As a result, we were able to look across a broad swath of both coral and reef builder cover as well as fish biomass on reefs. Importantly for this discussion, the protected areas were not always the sites with the highest coral cover. Honolua Bay, while protected as a no-take Marine Life Conservation District since 1978, is also downstream of now-fallow agricultural land. This reef has experienced several heavy sedimentation events in the early 2000s, likely contributing to some of the decline in coral cover at this reef (Figure 2). However, herbivore fish biomass remains high at this reef due to its no-take status. As a result, surveys at Honolua Bay North in which schools of *Acanthurus triostegus* and *A. blochii* were recorded place its fish biomass greater than 200 g m^{-2}.

Thus, Honolua Bay North had some of the lowest estimates of net fleshy algal production (Figures 4B, 6, and 7) despite some of the lowest values of coral cover (Figures 2, 6, and 7) suggesting that despite low coral cover due to sedimentation, herbivores may have strong top-down control on algae at this location.

Kanahena Point, within the no-take fisheries area of ʻĀhihi-Kīnaʻu Natural Area Reserve, also has some of the lowest coral cover in this study (<10% coral cover). A crown-of-thorns starfish outbreak in 2005 further reduced cover (Rodgers et al. 2015). Over the last ten years, however, Kanahena Point has also had some of the highest cover of reef builders out of all the nine reefs in this study and coral cover has been increasing since 2007 (Figure 2). When net fleshy algal production at this reef is viewed in terms of coral cover and fish biomass, several of the Kanahena Point time points appear to be anomalies in a cluster of points otherwise occupied by much higher net production (Figure 6). In light of the high coverage of CCA, these points fall with those of Molokini, Keawakapu, and Olowalu, all of which have higher coral cover (Figure 7). Thus, seeing very low net production in Figure 6 suggests that this reef may be recovering as a result of otherwise high herbivore biomass relative to fleshy algal cover.

Molokini, the site with highest coral cover, provides an upper bound of coral cover from which to view other reefs around the island. Molokini has very low net fleshy algal production (Figure 6) but does not have the highest grazing rates or herbivorous fish biomass (note Honolua Bay, Kapalua Bay, and Keawakapu with some points above Molokini). Importantly, other reefs with the same herbivore biomass have lower percent cover of reef building organisms (Figure 7) and hence higher fleshy algae cover and net algal production. Thus, the same herbivore population that regularly crops the algal standing biomass at Molokini is not large enough to regularly crop a larger algal standing biomass at other reefs suggesting more herbivores would be required at these other reefs to reduce net fleshy algal production.

Finally, Olowalu, a reef on West Maui that is not protected, has moderate to high coral cover with moderate to low fleshy algal relative to other Maui reefs (Figure 6). While the benthic communities at Olowalu have been fairly stable from 1999-2014 (Figure 2), moderate net fleshy algal production with moderate to low herbivore grazing rates may indicate that Olowalu is vulnerable to decline in the face of future stressors such as sedimentation events, bleaching, or continued reduction in herbivore biomass.

It is important to note that high values of net fleshy algal production did not directly translate into increased cover of fleshy algae on these reefs over time or necessarily into increased algal biomass. As such, we have not seen evidence of run-away algal communities on these reefs despite the fact that most herbivore communities are not consuming all of the algal production at these sites (Figure 2). Production that is not consumed by herbivorous fish is likely consumed by urchins (see Chapter 4), converted to detritus, or otherwise exported off the reef in addition to contributing to increased algal biomass on a given reef. However, given the higher net production we calculate on some reefs, in some cases 3-6 times the amount of algae consumed, it seems that these reefs may be less resilient to future stressors as the potential for increased algal biomass and thus potentially increases in percent cover exists.

In addition to differences in herbivore biomass across sites on Maui, reefs also had different proportions of herbivore guilds as well as different size classes of fishes (Fig 5). Large (26-35 cm and 36-45 cm) scrapers are considered to promote CCA and coral cover via their bite scars that remove fleshy algae including rhizoids and holdfasts in a given bite (Bellwood 1995, Ong & Holland 2010). Large grazers and browsers have larger bite sizes but just crop algae instead of removing all biomass and therefore do not have the same impact on the benthos. We are not able to model the impacts of large herbivore bites in our model such that we may overestimate production in some cases where large scrapers are present.

Large herbivore size classes of all guilds were present at Olowalu, Molokini, and Honolua, but only at Honolua were larger size classes consuming the greatest proportions of production (Figure 5). At both Olowalu and Molokini, smaller size classes consumed the majority of algae (Figure 5). Surprisingly, given the large proportion of CCA at Kanahena Point, there were very few large herbivores contributing to consumption (Figure 5). Rather, consumption at Kanahena Point was driven by the smallest size classes (6-15cm and 16-25cm), though herbivore biomass was above the average of all sites in this study for several survey years (Figure 3).

While herbivore biomass is a typical metric used to explore algal abundance on reefs (for example, Mumby et al. 2007), here we go a step further by examining the herbivore community more holistically in considering the assemblage as a whole with individual species bite rates, size classes, and biomass of algae removed to examine how different types of herbivore communities may relate to benthic community composition. Thus, we see herbivore rates of consumption being superior predictors of benthic community composition (Figure 6).

Coming up with an estimate of herbivore biomass that is needed on reefs to promote coral cover is context-dependent, rooted in the natural history of the reef as well as the more recent natural history of the stressors that may have contributed to a given reef's decline in coral cover. Given the net production at Molokini and Honolua Bay are similar only when Honolua Bay herbivore biomass is an order of magnitude greater than that at Molokini, our results support suggestions that herbivore biomass will need to exceed historic biomass values on reefs with high algal cover in order to promote coral cover (Scheffer et al. 2001, Paddack et al. 2006). Only with higher herbivore biomass do we then anticipate that herbivores will open space for CCA and corals, resulting in a decline in fleshy algal cover and production due to less fleshy algae present on the reef.

There are certainly limitations to our current model. For example, all of the parameter data comes from just three reefs, with the majority coming from one reef. Additional data with regards to bite rates and algal growth rates for example, at other reefs would provide a more refined approach to consumption and production at each reef and the response of its herbivorous fish community to its specific benthic community composition. Other models of herbivory have had similar limitations in experimentally derived data that has only been ground-truthed at single sites (Blackwood et al. 2012). Further detail in herbivore bite sizes and they dynamics of large scraper bites versus bites by smaller scrapers and other herbivores would provide more detail in the effects of size classes of fishes on benthic community composition on a given reef.

Despite these limitations, our approach is novel in that it provides further depth to understanding the status of a reef beyond percent cover of benthic groups and herbivore biomass by assessing the balance of production and consumption. Small net production may suggest that a reef has the potential for increased coral cover in the future while large net production may suggest that a reef is susceptible to increased fleshy algal cover especially if subject to additional future perturbations. Thus, such assessment provides a functional view of a reef's possible trajectory through using static measures of benthic community composition and fish biomass. Further, this method allows us to understand how far down "the slippery slope to slime" (Pandolfi et al. 2005) reefs may have progressed. Reefs naturally have varying coral and algal cover and herbivore populations (Sandin et al. 2008, Barott et al. 2010, Vroom & Braun 2010, Edwards et al. 2014) but estimates of net production and consumption provides a framework for understanding the shifted baseline of many reefs in which production may far exceed consumption. Therefore, our study provides a new way to understand how reefs are changing by looking not just at records of fish biomass and algal cover through time but by considering whether production and consumption are now uncoupled.

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Tables

Table 1: Overview of data used in production and consumption models.

		Benthic composition			Fish biomass		
Site name	Protected status	Years	Dataset	No. transects / yr	Years	Dataset	No. transects / yr
Canoe Beach	none	2013	WHAP	4	2009-2011, 2013-14	WHAP	4
Honolua Bay North	Marine Life Conservation District est. 1978; full no-take zone	2000-2013	CRAMP	10	2007-2014	WHAP	4
Kahekili	Herbivore Fisheries Management Area est. 2009; no-take zone for herbivorous fish and urchins	2008-2014	DAR / NOAA	100-180	2008-2014	DAR / NOAA	100-180
Kanahena Point	located inside ʻĀhihi-Kīnaʻu Natural Area Reserve est. 1973; full no-take zone	1999, 2001-2014	CRAMP	10	2007-2014	WHAP	4
Kapalua Bay	none	2007, 2011, 2013	CRAMP	4	2007-2014	WHAP	4
Keawakapu	none	2007, 2011, 2013	CRAMP	4	2007-2014	WHAP	4
Keoneoio	in Ahihi?	2007, 2011, 2013	CRAMP	4	2007-2014	WHAP	4
Molokini	Marine Life Conservation District est. 1977; full no-take zone	2000-2014	CRAMP	10	2007, 2009-2014	WHAP	4
Olowalu	none	1999-2014	CRAMP	10	2007-2014	LN	9-28

WHAP = West Hawaii Aquarium Project
CRAMP = Hawaiʻi Coral Reef Assessment and Monitoring Program
DAR / NOAA = Hawaii Division of Aquatic Rources / NOAA Coral Reef Ecosystem Division
LN = Resource fish and Lay Net survey

Figures

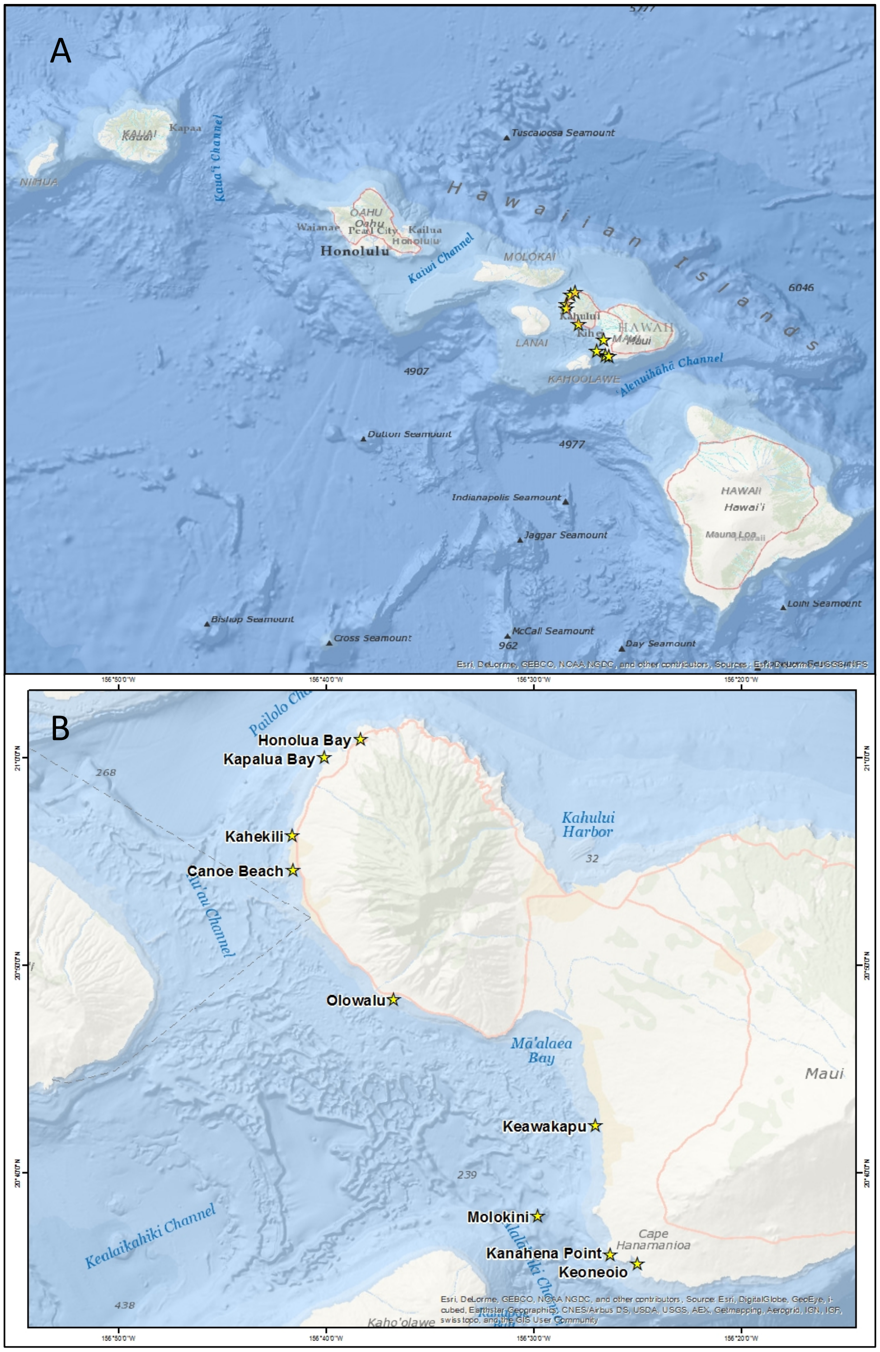

Figure 1: Map of all sites on Maui (A) within the context of the island chain and (B) within the context of leeward Maui.

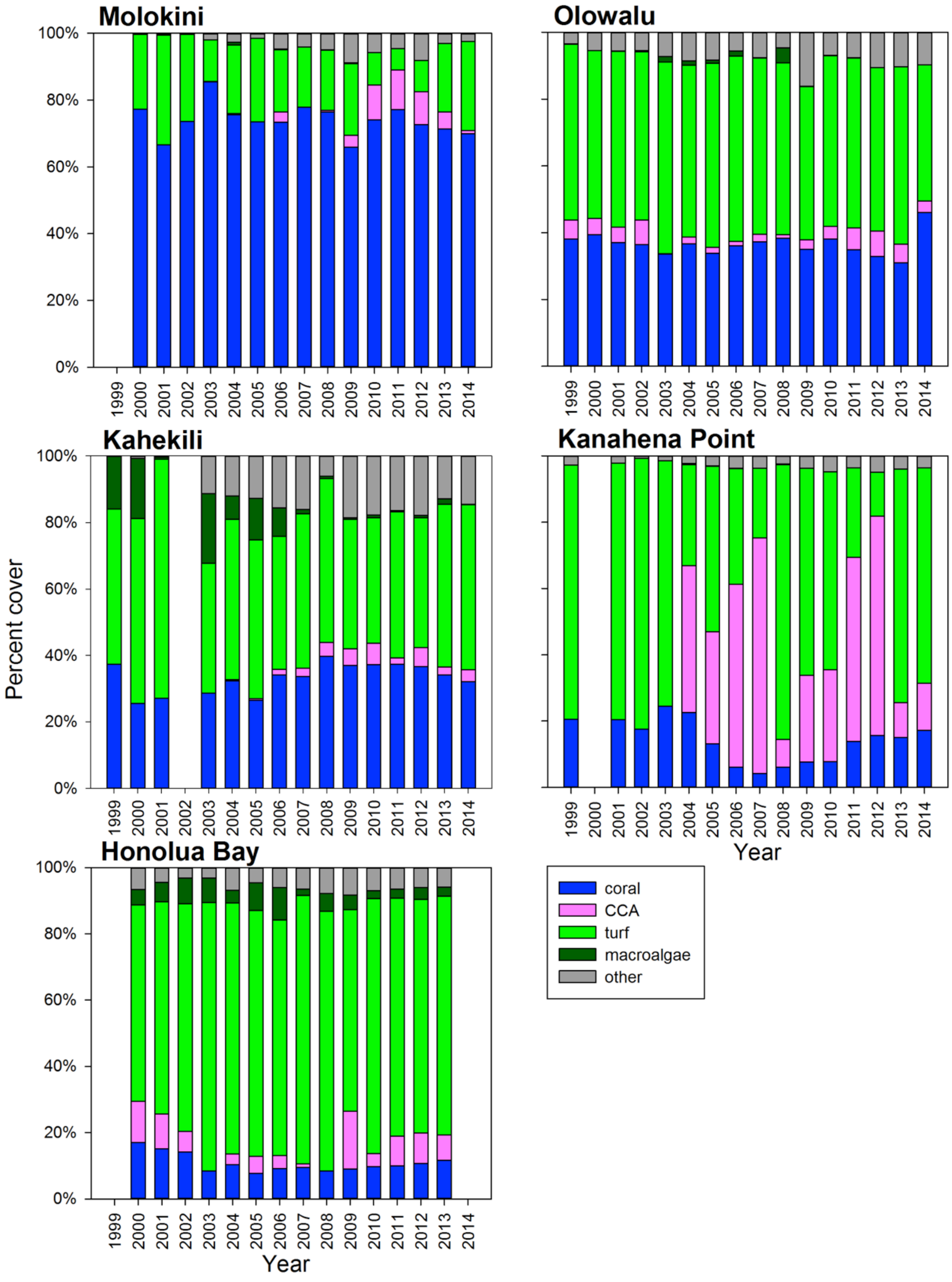

Figure 2: Benthic community composition at Molokini, Olowalu, Kahekili, Kanahena Point, and Honolua Bay.

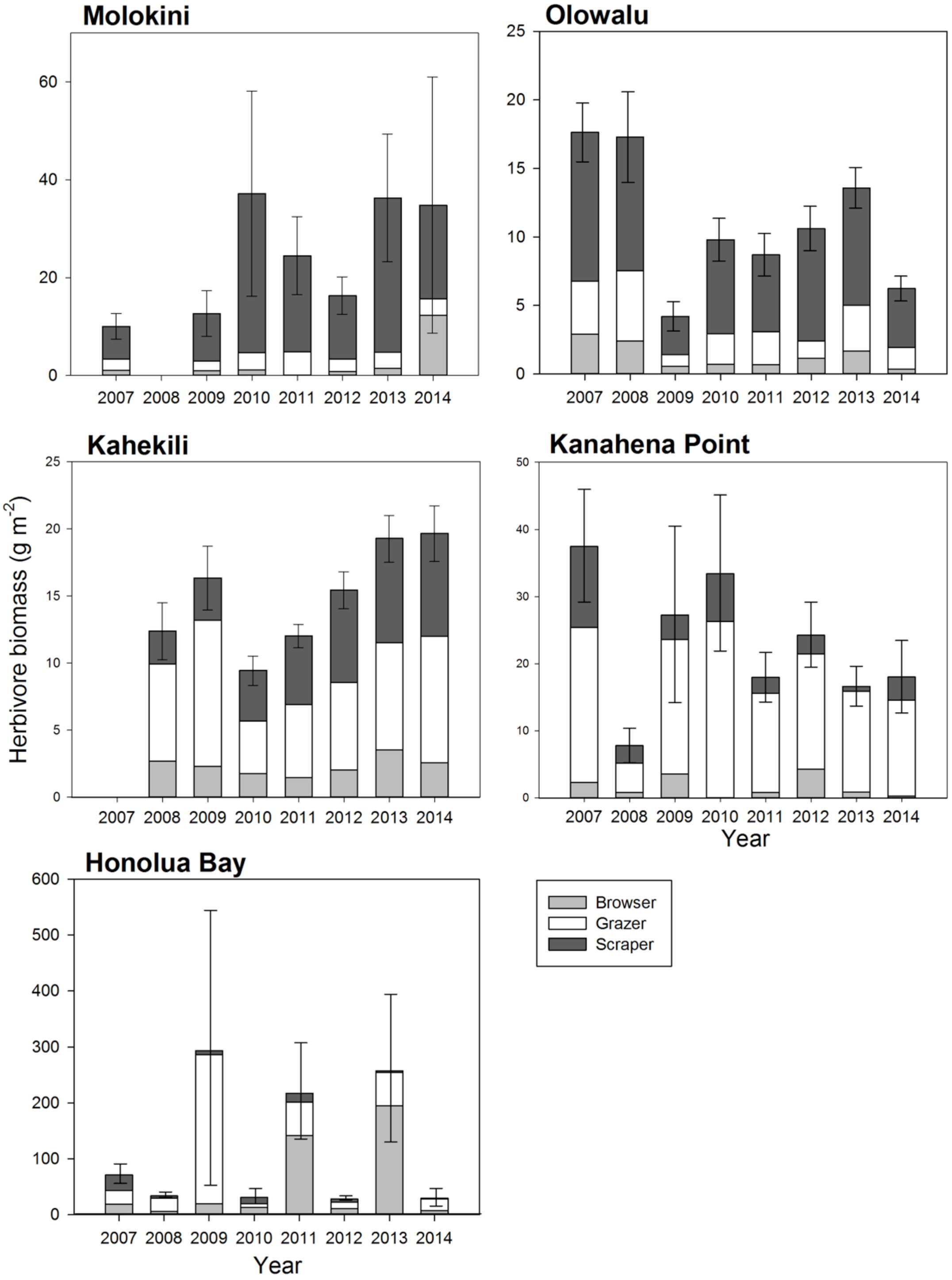

Figure 3: Herbivorous fish biomass at Molokini, Olowalu, Kahekili, Kanahena Point, and Honolua Bay. See Table 1 for N by site.

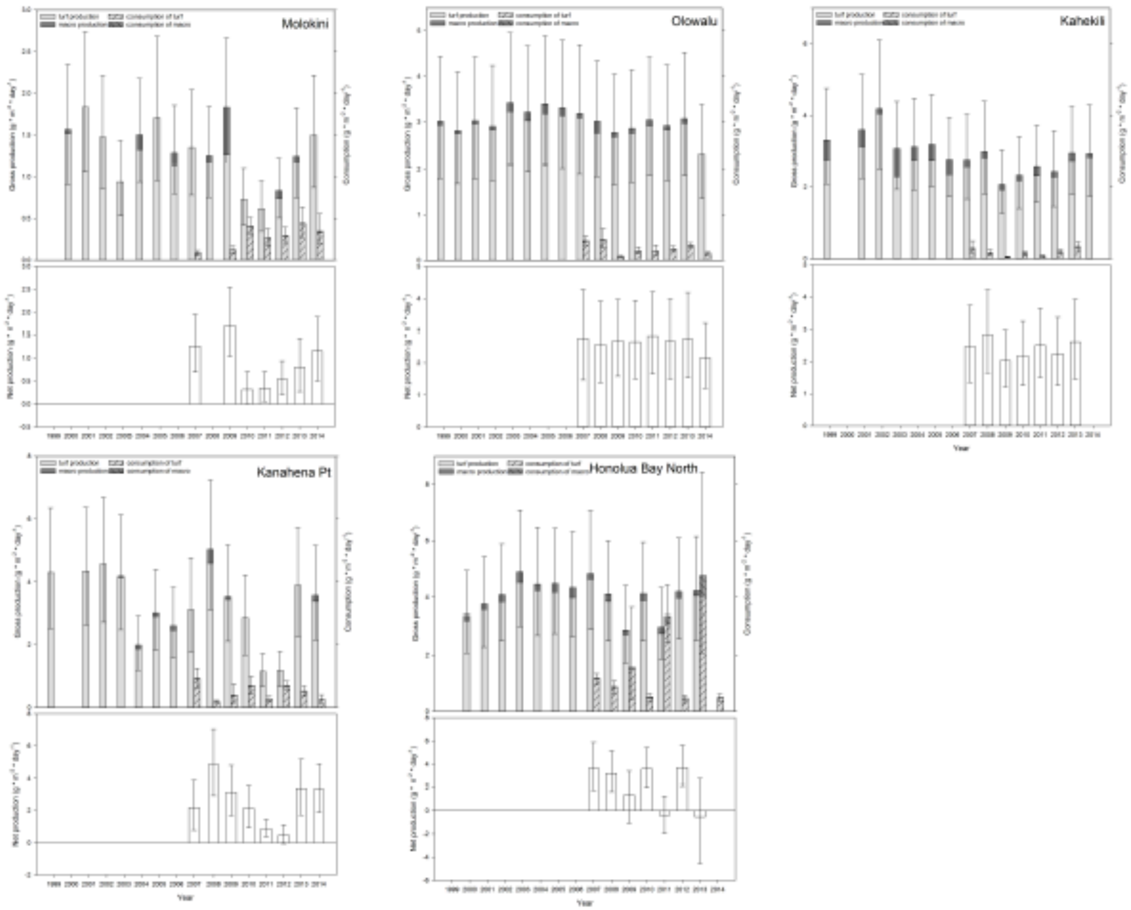

Figure 4: At Molokini, Olowalu, Kahekili, Kanahena Point, and Honolua Bay, (A) growth (solid bars) of macroalgae and turf algae (g m^{-2} d^{-1}) and consumption (hashed bars) of macroalgae and turf algae (g m^{-2} d^{-1}) by the herbivore community each year and (B) net production of the algal community after accounting for consumption by the herbivores. Bars are 95% confidence intervals.

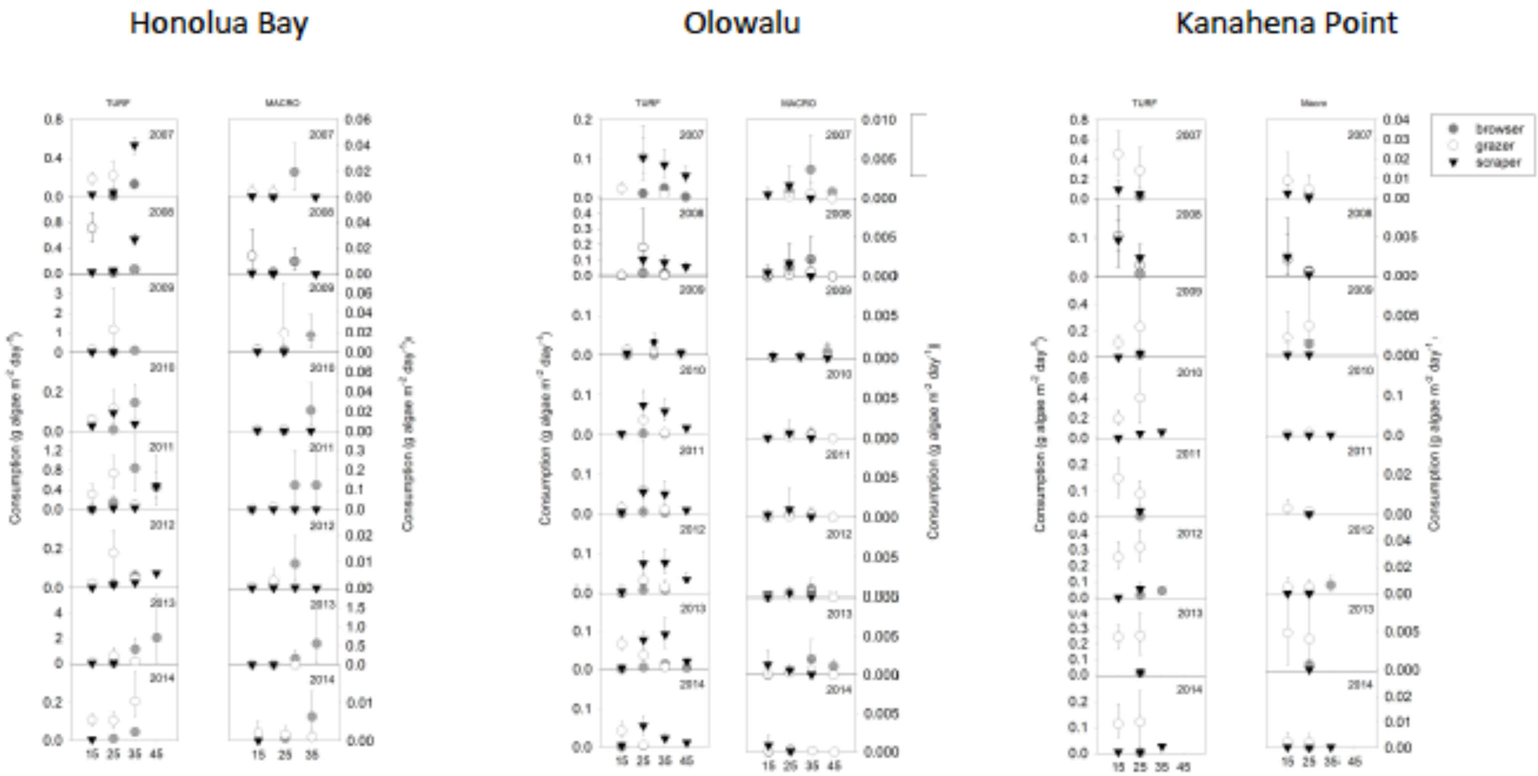

Figure 5: Herbivorous fish size class contributions to consumption at Olowalu, Kanahena Point, and Honolua Bay.

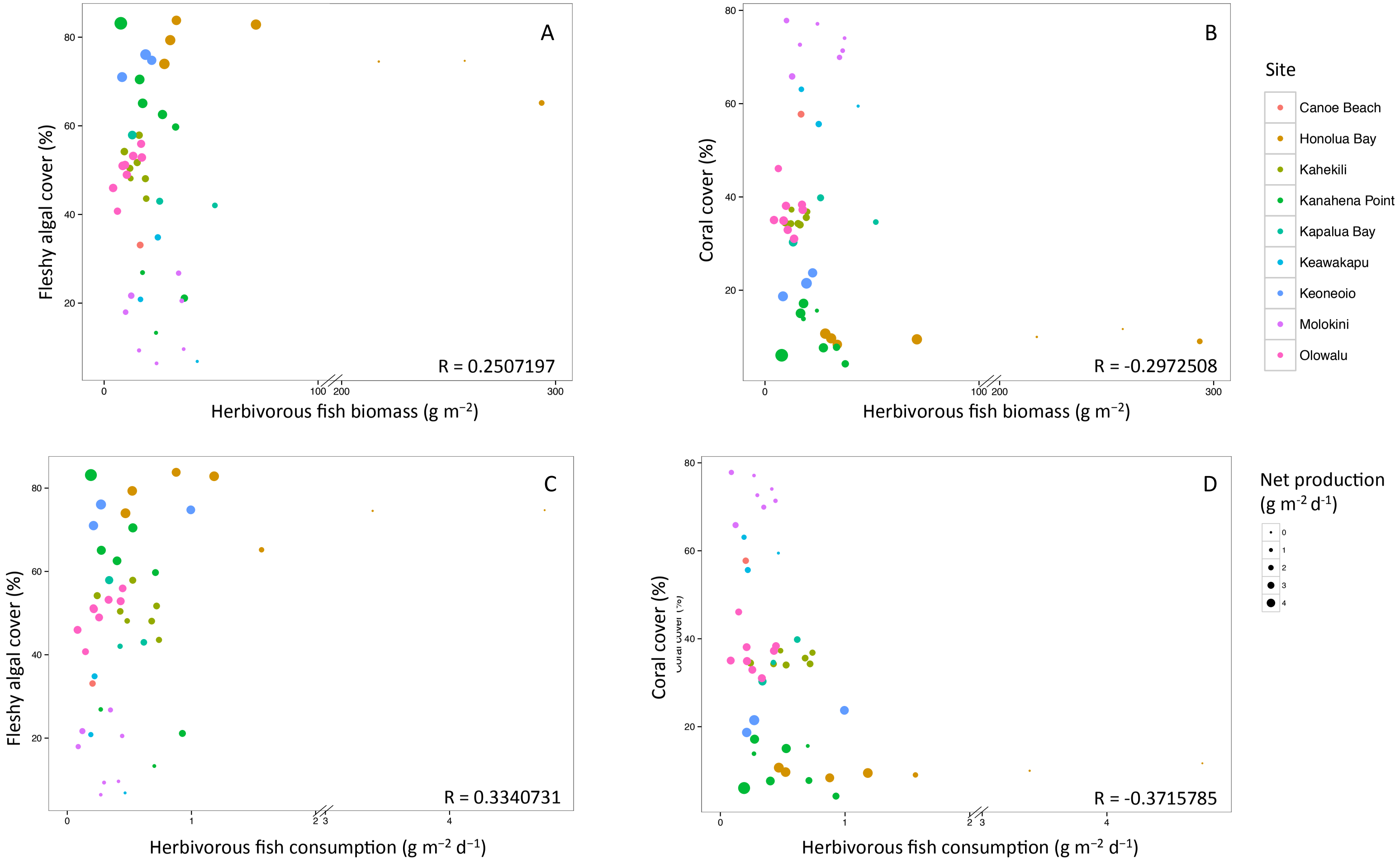

Figure 6: Comparisons of herbivorous fish biomass as a predictor of benthic community composition for both (A) percent fleshy algal cover and (B) percent coral cover with herbivorous fish consumption as a predictor of benthic community composition for both (C) percent fleshy algal cover and (B) percent coral cover. Bubble size is based on net production. All sites and years are represented on all plots.

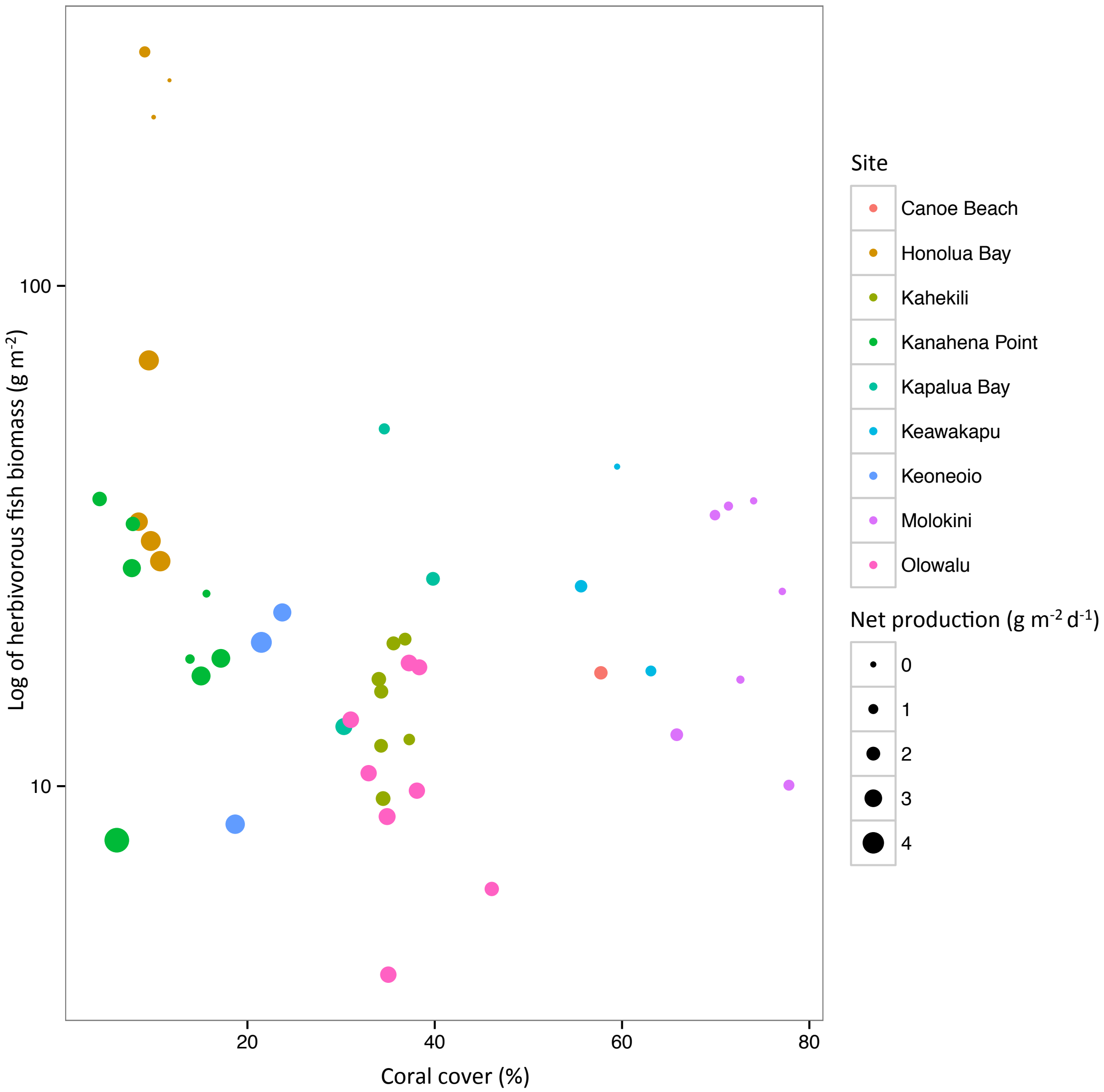

Figure 7: Comparison of net production (size of bubble) across all nine sites on Maui that vary in both percent coral cover (%, x axis) and herbivorous fish biomass (log(g m^{-2}), y axis). Net production is gross production (g algae m^{-2} day^{-1}) remaining after herbivorous fish consumption. All years of data for each site are represented. See Table 1 for full site details.

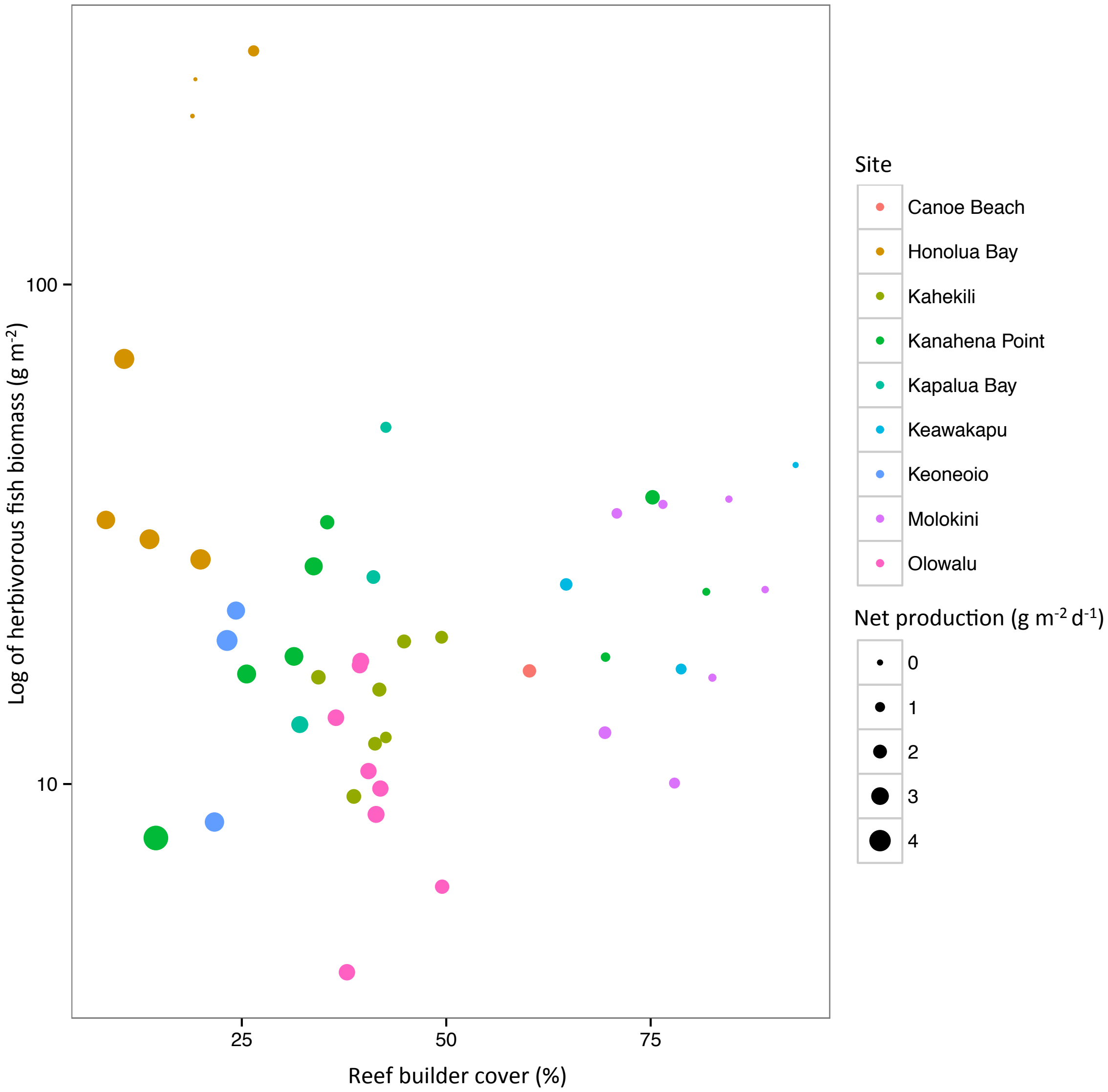

Figure 8: Comparison of net production (size of bubble) across all nine sites on Maui that vary in both percent reef builder cover (%, x axis) and herbivorous fish biomass (log(g m^{-2}), y axis). Net production is gross production (g algae m^{-2} day^{-1}) remaining after herbivorous fish consumption. All years of data for each site are represented. See Table 1 for full site details.

Appendix
Figures

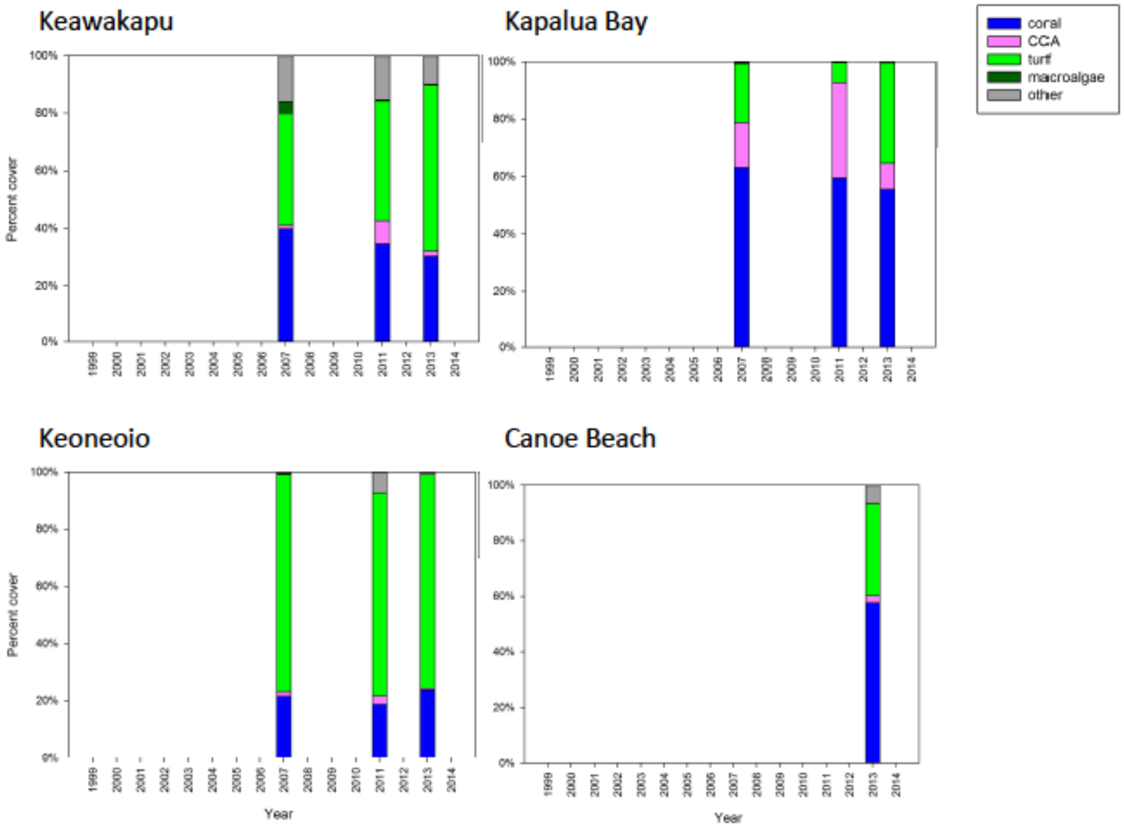

Figure A1: Benthic community composition at Keawakapu, Kapalua Bay, Keoneoio, and Canoe Beach.

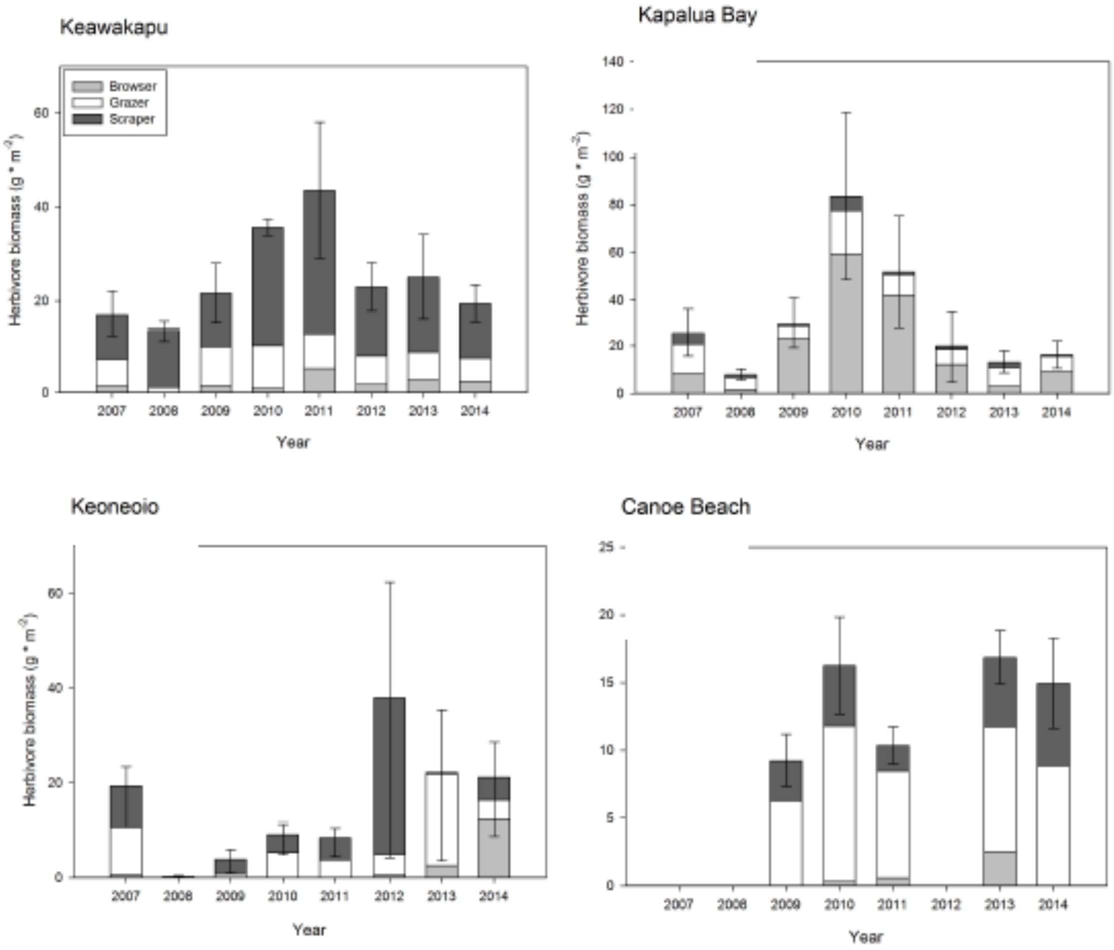

Figure A2: Fish biomass at Keawakapu, Kapalua Bay, Keoneoio, and Canoe Beach.

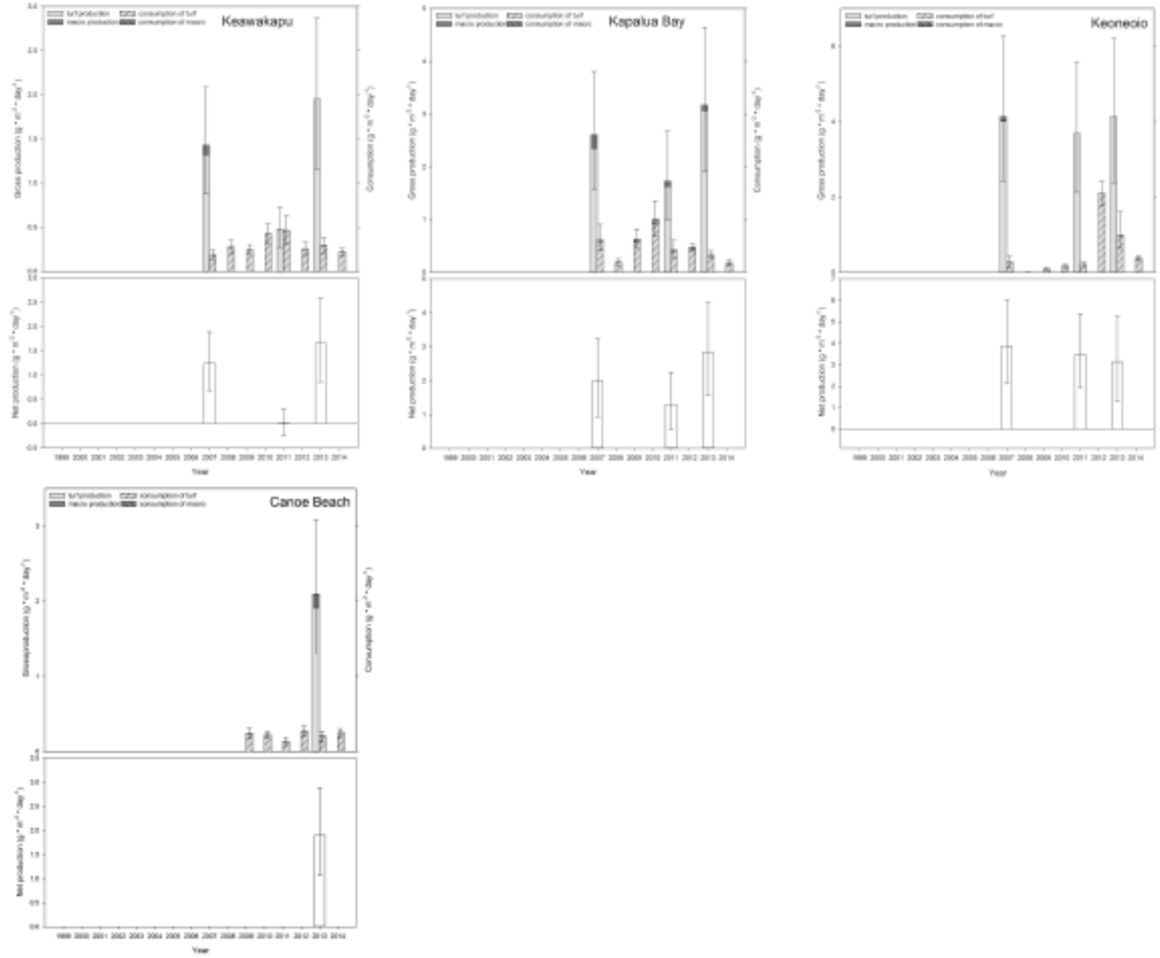

Figure A3: At Keawakapu, Kapalua Bay, Keoneoio, and Canoe Beach, (A) growth (solid bars) of macroalgae and turf algae (g m^{-2} d^{-1}) and consumption (hashed bars) of macroalgae and turf algae (g m^{-2} d^{-1}) by the herbivore community each year and (B) net production of the algal community after accounting for consumption by the herbivores. Bars are 95% confidence intervals.

CHAPTER 4:

The independent and combined effects of herbivorous fishes and urchins on benthic coral reef community composition on Maui, Hawaii

Emily L. A. Kelly, Russell Sparks, Jennifer E. Smith

Abstract

Herbivorous fishes and urchins are both considered major architects of benthic coral reef structure via grazing pressure but their impact on benthic community structure varies across reefs globally. Individually, the grazing intensity of both fishes and urchins has been examined experimentally and through correlative studies. We used a full-factorial caging approach to isolate the independent and interactive effects of fish and urchins on benthic community composition by quantifying changes in total cover, algal biomass, community structure, and diversity. We found that both urchins and fish impacted percent cover of functional groups as well as algal index of algal groups within plots but that the difference that distinguished treatments are not large. Further, both urchins and fish impacted the cover and algal index of macroalgae in plots but there was little effect of urchin removal unless fish were also removed, suggesting that fish may consume some algae that are unpalatable to urchins, which allows urchins to eat more than they would otherwise. Turf algal biomass was higher at the end of the experiment in the fish treatments, suggesting that urchins kept turf biomass lower as is shown through higher abundance of bare limestone in these treatments. Overall changes in plots were small, likely due the relatively low herbivore biomass on the reef.

Introduction

Herbivorous fish and urchins are both considered important herbivores on coral reefs, maintaining strong top-down control on algal biomass (Randall 1961, Steneck 1983, Carpenter 1986, Hughes 1994, Hughes et al. 2007, Stimson et al. 2007, Burkepile & Hay 2010). Correlative studies show that higher herbivore biomass on reefs is associated with low macroalgal cover (Williams & Polunin 2001, Friedlander et al. 2007, Sandin et al. 2008) and turf algal cover (Sandin et al. 2008, Jouffray et al. 2015). Strong top-town control through herbivory is further thought to mediate the competition between corals and algae for space on the reef (as reviewed by McCook et al. 2001).

Experimental results have shown that herbivores can consume large proportions of algal production on reefs. Estimates of rates of consumption on benthic algal production by herbivorous fishes (Wanders 1977, Hatcher & Larkum 1983, Carpenter 1986, Van Rooij et al. 1998, see also Chapter 3), urchins (Carpenter 1986), and invertebrate microherbivores (Carpenter 1986) suggest that herbivores are capable of fully grazing total daily production. Numerous exclusion experiments further highlight the importance of both fish (Hughes et al. 2007, Burkepile & Hay 2010) and urchins (Ogden et al. 1973, Hay & Taylor 1985) in preventing algal cover from overtaking other benthic taxa. Observational studies of overfishing or mass-mortality of herbivores report increases in algal cover sometimes by orders of magnitude within months of herbivore removal (Hughes 1994, Jackson et al. 2001).

While fish and urchins are both part of the herbivore community of reefs, their impact on benthic ecosystems is often considered separately. This impact is generally characterized through experimental studies of feeding preferences. Herbivorous fish have more recently been considered as members of distinct grazing guilds (Green & Bellwood 2009, Edwards et al. 2014) in which fishes consume different components of the benthic algal communities based on mouth morphology and behavior (Jones 1968, Bellwood 1995, Choat et al. 2002, Burkepile & Hay 2008, Rasher et al. 2013, Brandl & Bellwood 2014, Hamilton et al. 2014, see also Chapter 1). While urchins are considered more generalists, often grazing on the most abundant or adjacent algae (Ogden & Lobel 1978, Morrison 1988), they have also been show to have preferences (Lewis et al. in prep) or adapt their preferences based on availability (Stimson et al. 2007). Urchins are considered to be more constrained by habitat type than by food preference (Ogden & Lobel 1978). Their ranges are also constrained, as compared to herbivorous fish. This can result in regular grazing of the same area, which is thought to promote coral recruitment and growth to maturation (Sandin & McNamara 2012).

Comparisons of the impact of fish and urchins on the reef follows expectations based on their relative abundance in biomass. On reefs with high urchin biomass, experimental results of grazing by fish, urchins, and invertebrate microherbivores showed that urchin treatments were most similar to ambient benthic community composition, suggesting the dominance of this grazer at the reef (Carpenter 1986). This result has further been supported in the Caribbean (Sammarco 1980, Hughes 1994, Jackson et al. 2001) and off the coast of East Africa (McClanahan & Shafir 1990). On reefs with higher herbivorous fish biomass and low urchin biomass, fish grazing appears to be more dominant in the Caribbean (Hay 1984) and Hawaii (Randall 1961). On reefs with more equitable biomass of these two types of grazers, competition between the taxa has been suggested (Hay & Taylor 1985, McClanahan et al. 2001).

The goals of this study were to explicitly examine if and how herbivorous fishes and sea urchins independently and interactively affect benthic community composition. We address these goals by conducting a fully factorial manipulative experiment on natural reef communities on the island of Maui for 2 years. We examine the responses of several different aspects of the reef community including composition, abundance, biomass and diversity of benthic organisms.

Methods

Study area

This study was conducted on the leeward side of the island of Maui, Hawaiian Islands, USA at Kahekili Herbivore Fisheries Management Area (KHFMA) (Figure 1). Kahekili was designated as an Herbivore Fisheries Management Area in 2009, making this 2km^2 reef a no-take area for herbivorous fish and sea urchins.

Herbivore abundance and biomass

Surveys to quantify herbivorous fish abundance and biomass were collected twice a year on SCUBA by the NOAA Coral Reef Ecosystem Division and Hawaii Division of Aquatic Resources. These surveys were conducted across the 2km^2 area of KHFMA, totaling 80 transects each season. 25m transects were placed haphazardly throughout the 2km^2 KHFMA boundary between 2m and 12m depth on aggregate and spur-and-groove reef. Fish densities of all observed species were estimated by visual strip transect search along each transect line. A pair of divers swam side-by-side on each side of the line, surveying a column 2m wide. On the outward-bound leg, fish > 15cm and within 4m of the bottom were recorded. On the return leg, fishes closely associated with the bottom, juveniles, and fishes hiding in cracks and crevices were recorded. Biomass was calculated using established species-specific conversion factors from FishBase (2012) and according to Jouffray et al. (2015).

Surveys to quantify urchin abundance and biomass were also collected by the NOAA Coral Reef Ecosystem Division and Hawaii Division of Aquatic Resources. Urchins were counted along the same transects as above in a 4m swath. Urchin species and abundance were recorded within this swatch.

Herbivore exclusion

We conducted a fully factorial manipulative experiment examining the independent and interactive effects of fish and urchins on the benthic community. A total of thirty 0.25 m^2 plots were established along a transect parallel to shore on the reef at 8 m depth. Each plot was designated as one of the following treatments with six replicates of each: 1) closed cage excluding fish and urchins, 2) closed cage including 1 urchin (*Tripneustes gratilla)* only, 3) open-top cage including 1 urchin and open to fish, 4) open-top cage excluding urchins and open to fish, and 5) control quadrats marked by two stakes but open to ambient levels of urchins and fish. Cages were made of vinyl-coated chicken wire (standard harware1-inch mesh) and measured 0.5 x 0.5 x 0.5 m. Cages were secured in two corners with iron rebar. Given the volcanic nature of the island, iron was not expected to be a limiting nutrient at this site. All plots were established on areas composed of a mixed assemblage of algae and coral. Cages were scrubbed free of turf algae every 2 weeks to 1 month at which time the urchin was replaced if missing in urchin treatments (an urchin was never found to enter a treatment in which it was not intended. For a given "+ urchin" treatment, an urchin was missing on average once every 3 months).

T. gratilla is among the most dominant sea urchins in the Hawaiian Islands (Ogden et al. 1989). It was chosen as the species for the "+ urchin" treatments due to its prevalence on the reef at Kahekili (as determined by urchin surveys above) and its known generalist feeding activities on Hawaiian reefs (Stimson et al. 2007).

Response variables

Every two weeks for the first two months and every two to six months thereafter, benthic community composition was assessed in plots using a strung quadrat in which benthic group (to same level of taxonomic detail at photoquadrat analysis) was recorded below the intersection of crossed strings inside the plot. If the benthic group was an alga, height was also recorded. When multiple types of algae were growing together, both species were recorded for a given point. To track potential changes in algal biomass, an algal index (per Feingold et al. 2003) was calculated using the product of algal height and percent cover for a given benthic group. The algal index is a non-destructive sampling proxy for biomass.

At the conclusion of experimental manipulation, turf and macroalgal biomass were harvested from half of each plot. Total biomass and species diversity of algae removed were compared across treatments. The other half of each plot remained in tact to sample again two months after removal of treatment manipulation.

Data analysis

Herbivore effects on coral and algal cover

Community response

For examining change in percent cover of functional groups across treatments through time, we used a three-factor (urchins, fish, and time) permutation based multivariate analysis of variance (PERMANOVA; Anderson et al. 2008), in which pseudo-F was calculated for each of the main effects and the interaction terms using 9999 unrestricted permutations of data. Permutation tests were conducted using a Bray-Curtis similarity distance calculated from percent cover (untransformed). A two-way similarity percentage analysis (SIMPER, Anderson 2001) was conducted on the same data to determine the functional groups that defined significant groups in PERMANOVA.

Functional group response

To determine if the percent cover change of functional groups across treatments, we first calculated the change of percent cover across the course of the experiment (final minus initial) and used full-factorial ANOVA across treatments for each functional group.

Individual taxa response

To examine finer scale taxonomic percent cover change across treatments, we conducted the same analyses as for change in functional groups and used full-factorial ANOVA across treatments for individual taxa. We acknowledge the possibility of a Type I Error in using multiple pair-wise comparisons, but for consistency in evaluating the evidence of differences we did not calculate an adjusted p-value (Hurlbert & Lombardi 2009, 2012).

<u>*Herbivore effects on algal biomass*</u>

Community response

To determine if the algal community biomass, using the proxy of algal index, varied across treatments and time we used a three-factor (urchins, fish, and time) permutation based multivariate analysis of variance (PERMANOVA; Anderson et al. 2008), in which pseudo-F was calculated for each of the main effects and the interaction terms using 9999 unrestricted permutations of data. To visualize the trajectories of treatments through time we used non-metric multi-dimensional scaling (nMDS) ordination. Data were first transformed as log(x + 1) to account for the large number of zeros in algal index data and Bray Curtis similarity (BCS) measures calculated. The nMDS and PERMANOVA analyses were performed using PRIMER v6.1.11 ® (Clarke & Gorley 2006) with PERMANOVA+1.0.1. add-on package (Anderson et al. 2008).

Functional group response

To determine if the algal community biomass varied across treatments, we first calculated the change of algal index (biomass proxy) across the course of the experiment (final minus initial) and used full-factorial ANOVA across treatments. Second, we compared the biomass of macroalgae and turf algae removed from plots using full-factorial ANOVA across treatments for both groups.

Individual taxa response

We conducted the same analyses for the community functional-level data for major taxa within the plots. Again, we acknowledge the possibility of a Type I Error in using multiple pair-wise comparisons, but for consistency in evaluating the evidence of differences we did not calculate an adjusted p-value (Hurlbert & Lombardi 2009, 2012).

Herbivore effects on biodiversity

We further examined diversity change in the algal community from the beginning to the end of the experiment by treatment using the algal index as a proxy for biomass of different algal genera. We tested both the number of genera (S), the evenness of genera distribution using Shannon Weiner (H'), and the equitability of abundance of genera using Pielou's J (J') to understand how evenly genera were distributed given a maximum possible evenness if all species were equally abundant (H'max).

Re-exposure to natural herbivore populations

After 776 days in experimental treatments, all cages were removed from plots to determine how the benthic community would respond to a return of the natural herbivore community. To determine if and how benthic communities changed two months after the removal of cage treatments at the conclusion of the experimental manipulation, we used ANOVA across major benthic functional groups derived from *in-situ*-derived percent cover data.

Results

Herbivore abundance and biomass

Urchin abundance was 4.7 (+/- 0.3 SE) urchins per m^2 in 2010, 2.8 (+/- 0.1 SE) urchins per m^2 in 2011, and 2.9 (+/- 0.2 SE) urchins per m^2 in 2012 (Figure 2A).

Treatments with urchins mimicked ambient overall urchin densities at 4 urchins per m^2. Herbivorous fish biomass was 9.4 (+/- 1.1 SE) g m^{-2} in 2010, 12.0 (+/- 0.9 SE) g m^{-2} in 2011, and 15.15 (+/- 1.4 SE) g m^{-2} in 2012 (Figure 2B). Biomass consisted of three major herbivorous fish feeding guilds: scrapers, grazers, and browsers (see Chapter 1). Treatments with fish were open to the full herbivore community and fish were regularly seen grazing inside treatment plots.

Herbivore effects on coral and algal cover

Community response

When examining changes in percent cover of all functional groups over time using PERMANOVA we see significant change for all treatments and overall through time (all $p < 0.001$), though treatments did not vary differently with time (Table 1). SIMPER analysis showed that the differences between treatments were small. The differences between fish treatments were due to turf algal cover (27.88% with fish, 28.48% without fish, accounting for 24.82% of the difference in treatment), macroalgal cover (20.47% with fish, 26.06% without fish, accounting for 23.98% of the difference in treatment), and coral cover (36.65% with fish, 33.72% without fish, accounting for 22.78% of the difference). Thereafter functional groups accounted for less than 10% of cover and contributed less than 15% to the difference in treatments (Table 2). The differences between urchin treatments were also due to turf algal cover (29.34% with urchins, 27.00% without urchins accounting for 24.75% of the difference in treatment), macroalgal cover (21.01% with urchins, 25.53% without urchins, accounting for 23.47% of the difference in treatment), and coral cover (34.65% with urchins, 35.62% without urchins, accounting for 22.44% of the difference). Thereafter functional groups accounted for less than 10% of cover and contributed less than 15% to the difference in treatments. Of note is that the presence of bare limestone, while a small percentage, was present in urchin treatments only (4.28% with urchins, 0.87% without urchins, accounting for 7.31% of the difference) (Table 2).

Functional group response

The change from the beginning to the end of the experiment in macroalgal percent cover was significantly smaller when fish were present ($p < 0.0001$) and when urchins were present ($p < 0.0001$). However there was also a significant interaction between fish and urchins ($p < 0.0001$) showing that macroalgal cover was much greater when both types of herbivores were removed than when either one alone was removed. There was little effect of urchin removal unless fish were also removed (Table 3, Figure 4A).

Turf percent cover increased significantly in fish treatments ($p = 0.023$) but not in urchin treatments ($p = 0.96$). The interaction of fish*urchins was also significant ($p = 0.0069$) (Table 3, Figure 4B). The bare limestone percent cover increased significantly in both fish ($p = 0.045$) and urchin ($p < 0.0001$) treatments, but there was no effect of interaction ($p = 0.16$) (Table 3). Changes in CCA, coral, other invertebrates, cyanobacteria, and sand were not significant across treatments (Table 3, Figure 4C and D).

Open cage control plots most closely aligned with double-herbivore treatments in macroalgae and CCA cover (Figure 4A and D). Turf cover was highest in these open plots as compared to all treatments (Figure 4B) and coral cover was lowest in open plots (Figure 4C).

Individual taxa response

44 different genera of benthic organisms and nonliving substrate types were recorded during sampling (Table 4). The most abundant species of macroalgae, *Melanamansia glomerata*, showed no significant difference in percent cover change across treatment. Individual species of coral (*Porites lobata, Porites compressa, Montipora capitata*) also did not significantly change by treatment.

Herbivore effects on algal biomass

Community response

When examining all of the algal index data over time using PERMANOVA we see significant change for all treatments, the interaction of treatments, and overall through time, though treatments did not vary differently with time (Table 5). nMDS plots of the BCS values of log(x+1) transformed algal index of all algae across treatments through time showed that after one year, treatments had diverged very little from one another but rather all moved from the upper left of the plot towards the middle of the plot (Figure 7; 2D, stress = 0.17). After the full 2 years and 45 days of the experiment, however, the treatments have` diverged from one another (Figure 8; 2D, stress = 0.17).

Functional group response

The change from the beginning to the end of the experiment in the biomass proxy, algal index, for all taxa combined was significantly different for fish treatments (ANOVA, $p = 0.0377$), which showed a decrease in algal index with fish, and the interaction of fish*urchin ($p = 0.0441$), in which treatments without fish or urchins had much higher algal index than those with only one herbivore type (Table 6, Figure 5). The change in macroalgae algal index (all macroalgal taxa combined) from the beginning to the end of the experiment was significantly different for fish treatments ($p = 0.0022$), urchin treatments ($p = 0.0325$), and the interaction of fish*urchin ($p = 0.0471$) (Table 6, Figure 5). Neither all turf algae nor all cyanobacteria showed differences across treatments in the change of algal index from the beginning of the experiment to the end of the experiment ($p > 0.05$) (Table 6, Figure 5). Algal index of these functional groups in the open cage control plots most resembled the double-herbivore treatment (Figure 5).

Overall macroalgal biomass removed from plots was not significantly different across treatments (Table 7, Figure 6B; ANOVA, $p > 0.05$). Turf algal biomass removed from plots at the conclusion of the experiment was significantly different in fish treatments (Table 7, Figure 6A; ANOVA, $F= 5.64$, $p = 0.0283$), which were higher than other treatments. Total macroalgal biomass in open plots was most similar to urchins only and double-herbivore treatments (Figure 4B). Turf biomass was most similar between open plots and double-herbivore treatments and fish only treatments (Figure 4A).

Individual taxa response

The common macroalgae *Melanamansia glomerata* and *Asparagopsis taxiformis*, showed differences across treatments in the change of algal index from the beginning of the experiment to the end of the experiment ($p > 0.05$).

Chondrophycus biomass removed from plots at the conclusion of the experiment was significantly less in urchin treatments (Table 7, ANOVA, F=5.87, $p = 0.0256$).

Herbivore effects on biodiversity

Change in number of genera (S) across treatments was significantly different for fish treatments (Table 8; ANOVA, $p = 0.0112$). The number of genera of algae in a plot declined with the presence of fish. There was no significant change by treatment in evenness as measured by the Shannon Weiner index (H') but there was a significant change in Pielou's J, a measure of equitability among genera, by fish treatments (Table 8; ANOVA, $p = 0.0036$). In the presence of fish, J' increased meaning genera were more equitably abundant in plots.

Plot recovery after experimental manipulation

Two months after experimental manipulation was removed any differences that previously existed across treatments were removed and all treatments became similar to one another. Percent cover of functional groups were non-significant across treatments (Table 9, Figure 4). All algal indices - overall, macroalgae, turf, and cyanobacteria - showed no significant differences across treatments (Table 10). nMDS plots of the BCS values of log(x+1) transformed algal index of all algae across treatments through time reflects this change. Figure 8 shows that after experimental manipulation was removed, cages returned to clustering at the center of the nMDS plot.

Discussion

Our study sought to determine the individual and combined effects of fish and urchins on a reef in which both groups of herbivores have been protected. Our full-factorial experimental approach allowed us to quantify both the individual and combined effects of these herbivores on benthic community structure and composition. We found that both urchins and fish impacted percent cover of functional groups as well as algal index of algal groups within plots but that the difference that distinguished treatments are not large (Figure 2). Further, both urchins and fish impacted the cover and algal index of macroalgae in plots but there was little effect of urchin removal unless fish were also removed, suggesting that fish may consume some algae that are unpalatable to urchins, which allows urchins to eat more than they would otherwise. Turf algal biomass was higher at the end of the experiment in the fish treatments (Table 7, Figure 6A), suggesting that urchins kept turf biomass lower as is shown through higher abundance of bare limestone in these treatments (Table 3). Importantly, therefore, fish appeared to have a greater impact on reducing algal cover and biomass while urchins thinned turf alge and opened up more bare space on the reef.

A dominant paradigm in coral reef ecology and the decline of coral reefs in recent decades has been the decline in herbivores on reefs and the associated increase in macroalgal cover (Jackson et al. 2001). Over the two years of this experiment, the increase of macroalgal cover and total algal index in full exclusion cages, the moderate increase in single-herbivore treatments, and the low cover and algal index in double-herbivore cages and open plots (Figure 4A and 5) matches this expectation. The removal of biomass to expose limestone, particularly by urchins (Table 3, Figure 3), aligns with models that predict their ability to maintain algae-free space given their spatially constrained nature (Sandin & McNamara 2012). These results suggest that bare limestone present in both herbivore treatments will allow future recruitment of reef-building calcifiers (corals and CCA).

While the overall algal index and the macroalgal index both showed changes in treatments at the end of the experiment, biomass removed from these plots showed no significant differences in macroalgae (Figure 6B). This may be a result of different genera of algae contributing to overall height and cover of algae within a plot (algal index) but their sometimes-filamentous nature resulting in low overall biomass. Importantly, algal functional forms are varied (Littler & Littler 1984, Steneck & Dethier 1994) and result in different types of interactions with corals (McCook et al. 2001).

Turf algal index did not show significant change in algal index (Table 6, Figure 5) but total biomass of turf removed was significantly higher in treatments with fish (Table 7, Figure 6A). This suggests that fish grazing may be keeping turf algae at a similar cropped height to other treatments but is also contributing to a more dense assemblage, which cannot be measured using the algal index but is detectable via the measure of biomass (see Chapter 2 for further discussion of grazing stimulating greater standing stock biomass of turf). Further, the greater abundance of limestone in urchin treatments (Figure 3) supports a less dense turf assemblage in these plots.

Overall, we found less dramatic changes across treatments than anticipated based on changes seem in analogous experiments on reefs elsewhere (Randall 1965, Ogden et al. 1973, Hughes et al. 2007, Burkepile & Hay 2010, Smith et al. 2010). However, herbivore biomass at Kahekili (~10-16 g m^{-2} fish biomass, 3-5 urchins m^{-2}, Figure 2) is lower than adjacent reefs (for example, ~40 g m^{-2} fish biomass in Smith et al. 2010) in which herbivore exclusions show greater differences across treatments. Further, other studies have shown that herbivores are consuming less than half of algal production on the reef (herbivorous fish consuming 30% of production per Chapter 2). We also only used one species of urchin in this experiment. Understanding the behavior and feeding preferences of the full suite of urchins on the reef (see Lewis et al. in prep) will therefore be important to quantifying the urchin contribution to total grazing. Thus, while differences across treatments exist, the magnitude of these differences is relatively small.

In addition, as compared to experiments that use bare settlement tiles (for example, Smith et al. 2010), an ambient algal community on the reef already existed within treatments. Growth rates may therefore have been lower for the standing community as opposed to initial successional stage communities. Further, as part of this existing community there was an absence in all cages of some of the common blooming species of algae found around Maui. While the native and seasonally more abundant *Asparagopsis taxiformis* was present and bloomed only in herbivore exclusion cages (non-significant) in the second summer of the experiment, the treatments were otherwise devoid of quantifiable biomass of *Cladophora*, *Ulva*, and other species known to bloom on Maui reefs (Smith et al. 2002). Thus, more slow-growing species like *Melanamansia* were the majority of algal biomass in cages. Finally, we did not control for invertebrate microherbivores that contribute to the grazing budget within all treatments (Carpenter 1986). These microherbivores may have increased with increased algal index within plots and contributed to maintaining more modest growth of algae inside treatments. Finally, periodic cyanobacteria blooms covered algae in all treatments (Figure 5) and may have contributed to shading of macroalgae, reducing its overall growth potential across treatments.

The results of this study suggest that the fish community contributes more to reductions in macroalgal cover and may remove some species of algae not palatable or accessible to urchins while urchins are important for thinning turf density and opening up additional bare limestone on the reef. Thus, both of these grazers are important contributors to the consumption of benthic algal production on Kahekili.

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Tables

Table 1: Results of the permutation based multivariate analysis of variance (PERMANOVA, Anderson 2001) testing the effects of fish, urchin, and time on percent cover of functional groups. Permutation tests were conducted using a Bray-Curtis similarity distance calculated from percent cover (untransformed). All factors were treated as fixed effects. These results are based on 9999 permutations. All significant comparisons are shown in bold.

PERMANOVA on percent cover			
Factor	*df*	*Pseudo-F*	*P*
Fish	1	6.02	**<0.001**
Urchin	1	20.36	**<0.001**
Time	14	6.93	**<0.001**
Fish * Urchin	1	5.57	**<0.001**
Fish * Time	14	0.99	0.493
Urchin * Time	14	0.87	0.773
Fish * Urchin * Time	14	0.83	0.851

Table 2: Results of the two-way similarity percentage analysis (SIMPER, Anderson 2001) of the results of the PERMANOVA testing the differences across fish and urchin treatments. The Bray-Curtis similarity distance was calculated from functional group percent cover (untransformed). Av.Abund is the average abundance of a given functional group given the presence or absence of the herbivore treatment. Contrib% is the contribution to this functional group to the total difference between treatments. Cum Contrib% is the cumulative percentage of the difference accounted for as additional functional groups are considered.

SIMPER on percent cover				
	+ fish	- fish		
Functional group	Av.Abund	Av.Abund	Contrib%	Cum Contrib%
Turf algae	27.88	28.48	24.82	24.82
Macroalgae	20.47	26.06	23.98	48.79
Coral	36.65	33.72	22.78	71.58
Cyanobacteria	7.24	4.99	12.08	83.66
CCA	3.19	3.88	6.75	90.4
	+ urchin	- urchin		
Functional group	Av.Abund	Av.Abund	Contrib%	Cum Contrib%
Turf algae	29.34	27	24.75	24.75
Macroalgae	21.01	25.53	23.47	48.21
Coral	34.76	35.62	22.44	70.66
Cyanobacteria	5.84	6.39	11.84	82.5
Limestone	4.28	0.87	7.31	89.81
CCA	4.07	3	6.8	96.61

Table 3: Results of 2-way full-factorial analyses of variance testing the fixed effects of fish and urchin presence on the difference from the beginning of the experiment to the end of the experiment of functional group percent cover. Significant Fish * Urchin effects indicate the treatment response is not additive. All significant comparisons are shown in bold.

		Macroalgae		**Turf Algae**		**CCA**		**Coral**		**Other Invertebrates**		**Cyanobacteria**		**Sand**		**Limestone**	
Source	*df*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Fish	1	50.04	**<0.0001**	6.14	**0.023**	0.012	0.91	0.31	0.58	3.12	0.094	3.57	0.074	4.26	0.053	4.59	**0.045**
Urchin	1	32.44	**<0.0001**	0.0027	0.96	0.21	0.65	1.02	0.33	0.45	0.51	0.36	0.55	0.079	0.79	30.10	**<0.0001**
Fish * Urchin	1	18.20	**0.0004**	9.17	**0.0069**	0.0009	0.98	0.15	0.70	0.39	0.54	0.0051	0.94	0.80	0.80	24.66	0.16

Table 4: List of all algal genera identified and measured (if algae) within the strung-quadrat across the duration of the experiment. Headers indicate the functional group in which a given genera was placed in future analyses.

	Treatment				
	No herbivores	Fish	Urchin	Fish + Urchin	Open
Cyanobacteria					
cyanobacteria (general)	x	x	x	x	x
Leptolyngbya	x	x		x	x
Moorea producens	x	x	x	x	x
Symploca	x	x	x	x	x
Turf algae					
turf (general)	x	x	x	x	x
Tolypiocladia	x	x	x	x	x
Macroalgae					
Green algae					
Caulerpa	x	x	x	x	x
Chlorodesmis	x	x	x	x	x
Dictyosphaeria	x	x	x	x	x
Halimeda	x		x		x
Microdictyon		x			x
Neomeris			x		
Rhipidosiphon	x	x	x	x	x
Ventricaria	x	x	x		x
Brown algae					
Dictyota	x	x	x	x	x
Lobophora	x	x	x	x	x
Padina				x	x
Sphacelaria	x	x	x	x	x
Red algae					
Amansia	x	x	x	x	x
Asparagopsis	x	x	x	x	x
Chondrophycus	x	x	x	x	x
Dasya	x	x		x	x
Dotyella	x		x	x	x
Gelidium / Gelidiella	x	x		x	x
Gibsmithia		x	x	x	x
Jania	x	x	x	x	x
Laurencia	x	x	x	x	x
Martensia				x	
Peyssonnelia	x	x	x	x	x
Tricleocarpa			x		

Table 4 (continued): List of all algal genera identified and measured (if algae) within the strung-quadrat across the duration of the experiment. Headers indicate the functional group in which a given genera was placed in future analyses.

Golden algae					
Chrysophyte	x	x	x	x	
Crustose coralline algae					
CCA	x	x	x	x	x
Coral					
Montipora capitata	x	x	x	x	x
Montipora patula	x	x	x	x	x
Pavona varians	x	x	x	x	x
Pocillopora damicornis		x		x	x
Pocillopora meandrina	x	x	x	x	x
Porites compressa	x	x	x	x	x
Porites lobata	x	x	x	x	x
Other invertebrate					
anemone			x		
sponge	x	x	x	x	x
zooxanthid	x				
Non-living					
bare limestone	x	x	x	x	x
sand	x	x	x	x	x

Table 5: Results of the permutation based multivariate analysis of variance (PERMANOVA, Anderson 2001) testing the effects of fish, urchin, and time on benthic community composition based on the algal index of individual genera. Permutation tests were conducted using a Bray-Curtis similarity distance calculated from algal index data transformed as log(x + 1) to account for a large number of zeros. All factors were treated as fixed effects. These results are based on 9999 permutations. All significant comparisons are shown in bold.

PERMANOVA on transformed algal index			
Factor	*df*	*Pseudo-F*	*P*
Fish	1	6.02	**<0.001**
Urchin	1	20.36	**<0.001**
Time	14	6.93	**<0.001**
Fish * Urchin	1	5.57	**<0.001**
Fish * Time	14	0.99	0.493
Urchin * Time	14	0.87	0.773
Fish * Urchin * Time	14	0.83	0.851

Table 6: Results of 2-way full-factorial analyses of variance testing the fixed effects of fish and urchin presence on the overall algal index difference from the beginning of the experiment to the end of the experiment two years later (See Figure 5). Significant Fish * Urchin effects indicate the treatment response is not additive. All significant comparisons are shown in bold.

		Overall index		**Macroalgae index**		**Turf index**		**Cyanobacteria index**	
Source	*df*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Fish	1	4.95	**0.038**	12.36	**0.002**	0.55	0.465	0.79	0.384
Urchin	1	3.31	0.083	5.28	**0.033**	0.01	0.920	0.10	0.761
Fish * Urchin	1	4.61	**0.044**	4.48	**0.047**	1.40	0.251	0.07	0.983

Table 7: Results of 2-way full-factorial analyses of variance testing the fixed effects of fish and urchin presence on biomass of macroalgae and turf algae removed at the end of the experimental manipulation (see Figure 6). All genera of macroalgae were also tested for significance but only significant genera noted here. All significant comparisons are shown in bold.

		Turf biomass		**Macroalgae biomass**		***Chondrophycus* biomass**	
Source	*df*	*F*	*P*	*F*	*P*	*F*	*P*
Fish	1	5.64	**0.028**	0.08	0.779	4.17	0.055
Urchin	1	0.41	0.531	3.39	0.081	5.87	**0.026**
Fish * Urchin	1	0.002	0.969	1.00	0.330	1.78	0.197

Table 8: Results of 2-way full-factorial analyses of variance testing the fixed effects of fish and urchin presence on the change in diversity indices from the beginning of the experiment to the end of experimental manipulation. All significant comparisons are shown in bold.

		Number of genera (s)		**Shannon Weiner index H'**		**Pielou's J'**	
Source	*df*	*F*	*P*	*F*	*P*	*F*	*P*
Fish	1	7.88	**0.011**	0.0001	0.991	10.98	**0.004**
Urchin	1	0.95	0.341	0.02	0.891	0.67	0.425
Fish * Urchin	1	0.2	0.66	2.24	0.15	2.12	0.161

Table 9: Results of 2-way full-factorial analyses of variance testing the fixed effects of fish and urchin presence on percent cover of functional groups after experimental manipulation was removed (Figure 4). Comparison that were previously significant (Table 3) are highlighted in gray.

		Macroalgae cover		**Turf cover**		**Coral cover**		**CCA cover**	
Source	*df*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Fish	1	0.09	0.772	0.01	0.928	0.01	0.937	0.003	0.986
Urchin	1	0.09	0.764	4.23	0.054	2.92	0.104	0.74	0.399
Fish * Urchin	1	0.09	0.763	0.01	0.922	0.12	0.731	3.28	0.086

Table 10: Results of 2-way full-factorial analyses of variance testing the fixed effects of fish and urchin presence on algal index of major functional groups after the removal of treatment manipulations. Comparison that were previously significant (Table 3, Figure 5) are highlighted in gray.

		Overall index		**Macroalgae index**		**Turf index**		**Cyanobacteria index**	
Source	*df*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Fish	1	1.32	0.266	1.34	0.261	0.05	0.824	0.04	0.848
Urchin	1	0.29	0.595	0.65	0.429	0.20	0.662	0.40	0.535
Fish * Urchin	1	2.33	0.143	0.22	0.642	2.37	0.140	2.12	0.157

Figures

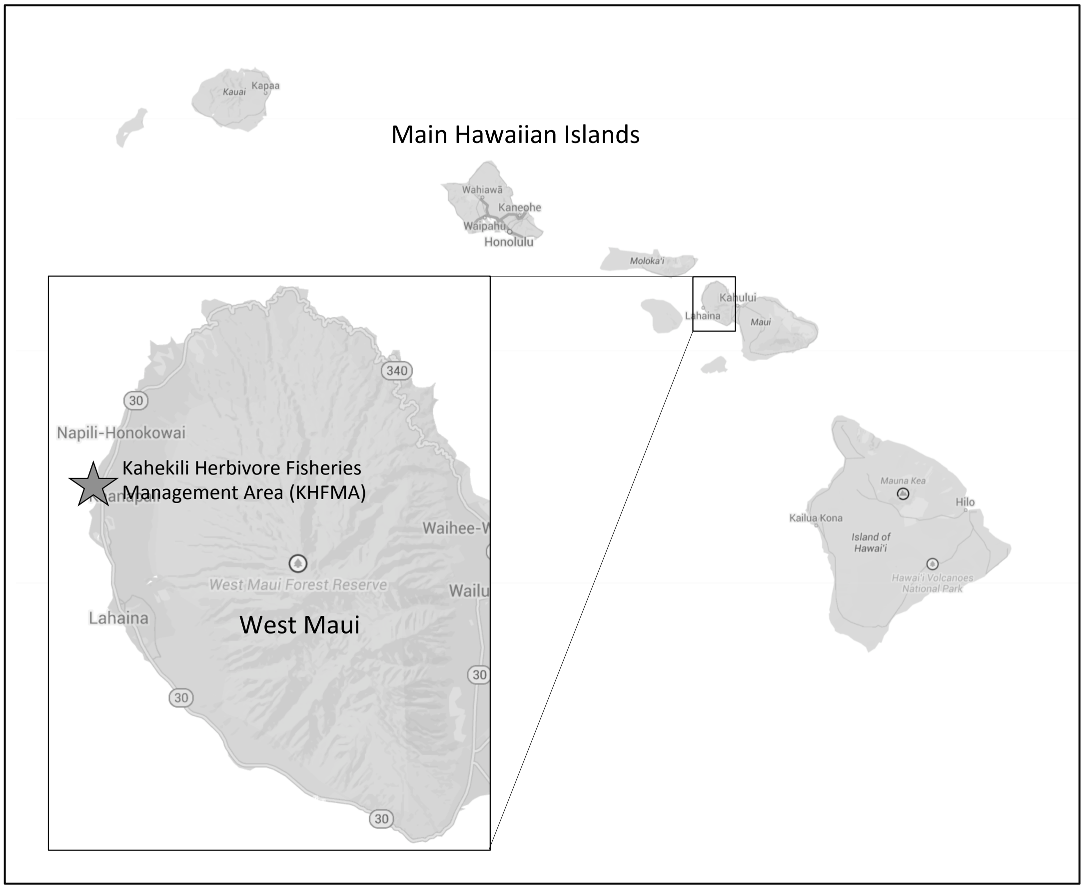

Figure 1: Location of study reef, Kahekili Herbivore Fisheries Management Area, located on West Maui in the Main Hawaiian Islands.

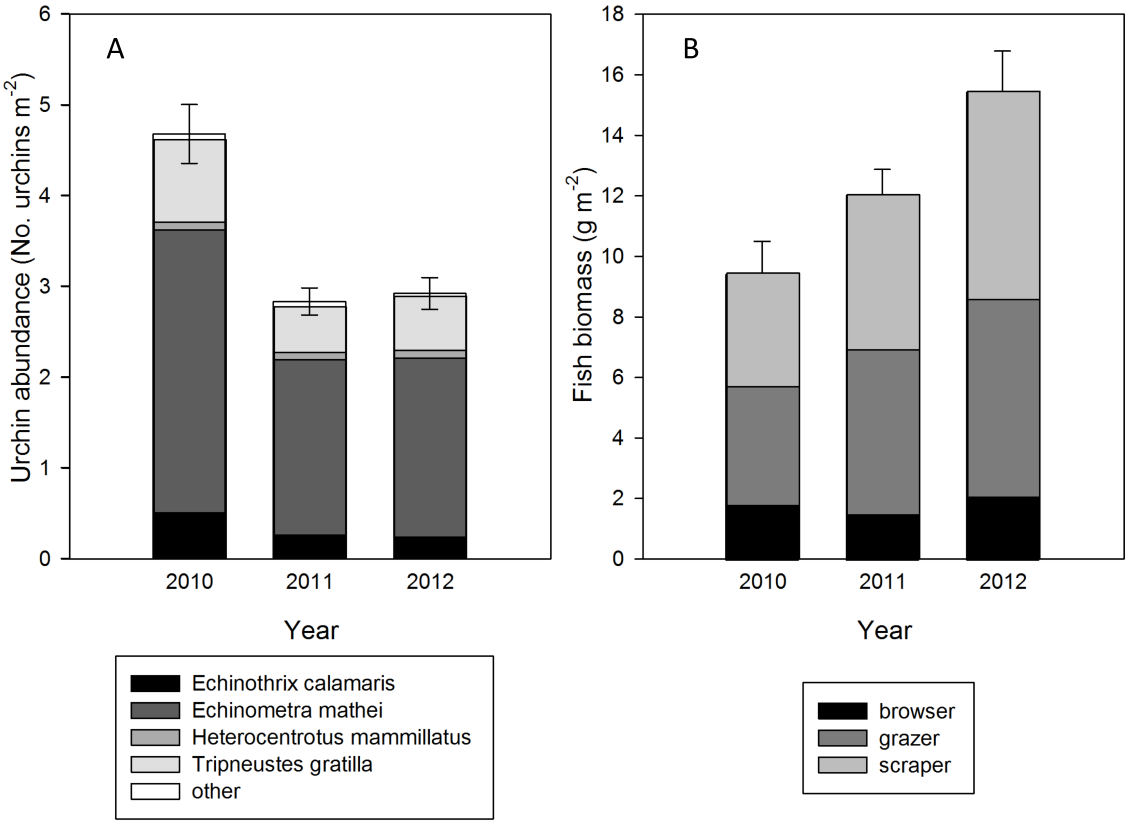

Figure 2: (A) Abundance of urchins from 2010-2012 at Kahekili. Those species in "other" have less than 0.05 urchins m^{-2} (*Actinocidaris thomasi, Chondrocidaris gigantea, Diadema paucispinum, Echinostrephus aciculatus, Echinothrix diadema, Eucidaris metularia, Echinometra oblonga*). (B) Herbivorous fish biomass by feeding guild from 2010-2012 at Kahekili. See Chapters 1, 2, and 3 for a more detailed discussion of fish herbivore guilds.

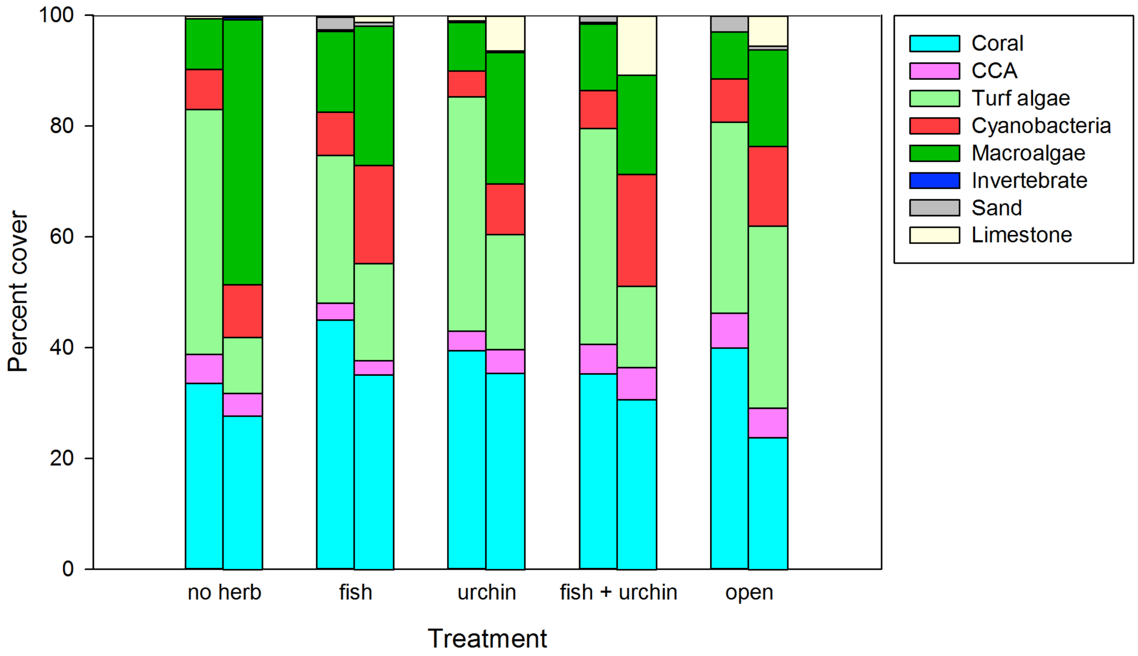

Figure 3: Percent cover of functional groups from the initial (left bars) to final (right bars) time points.

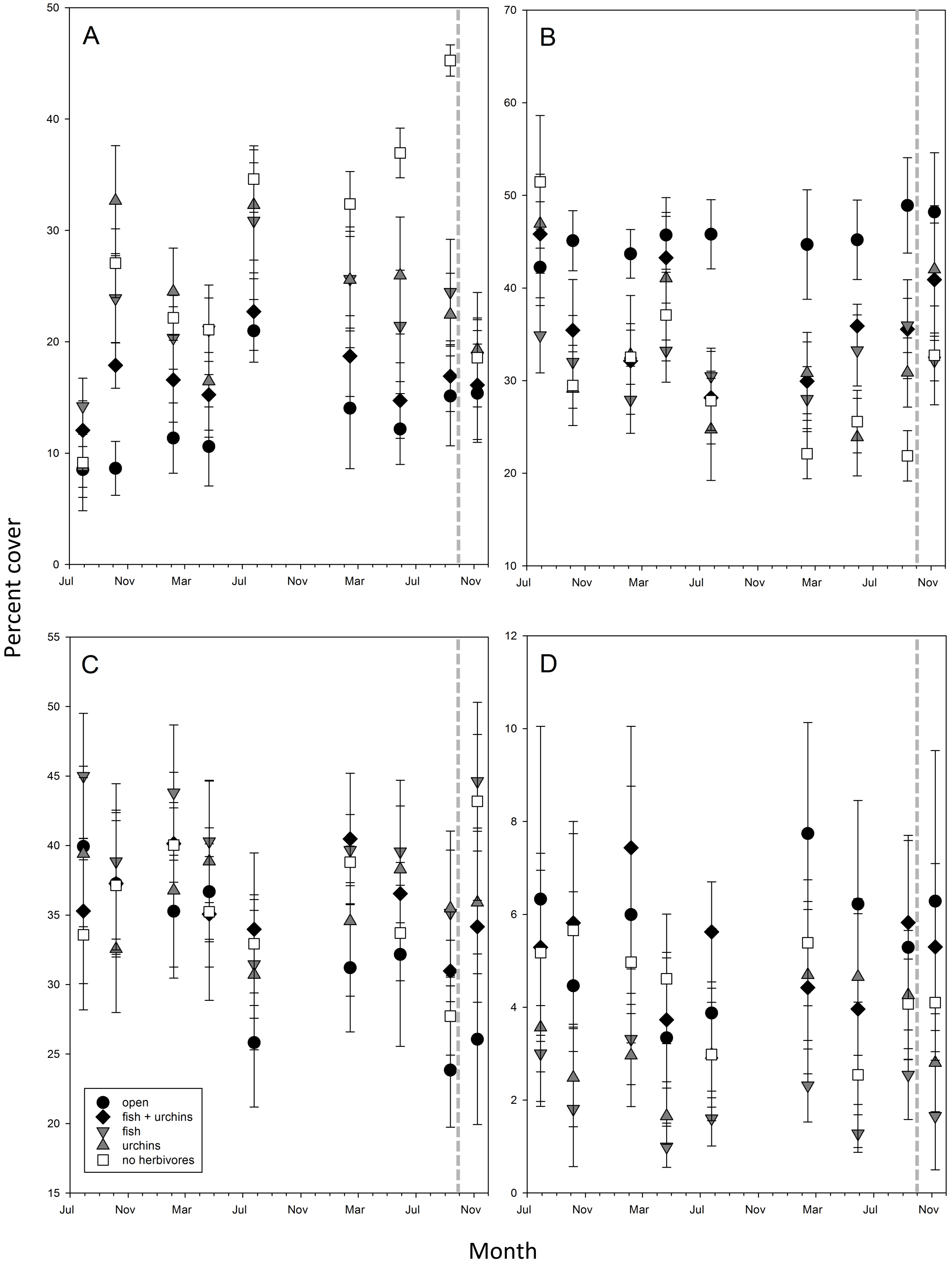

Figure 4: Percent cover through the course of the experiment of (A) macroalgae, (B) turf algae, (C) coral, and (D) CCA. Dotted line indicates when the cages were removed from treatments after 776 days. Bars are standard error.

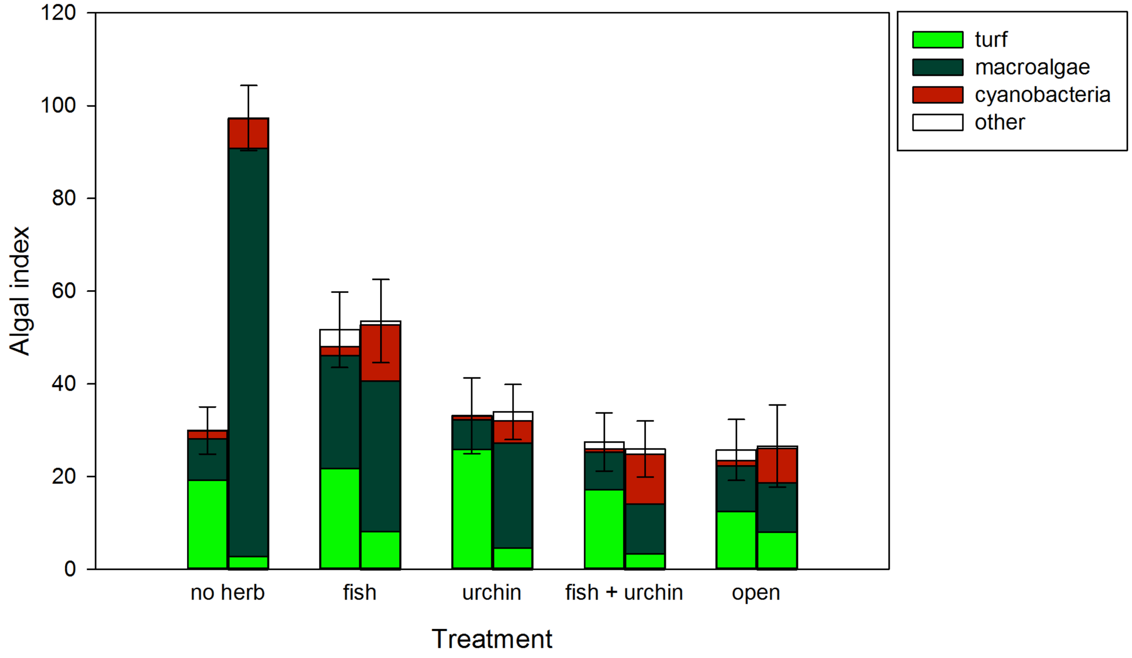

Figure 5: Change in algal index from the beginning to the end of the experiment 776 days later. Bars are standard error.

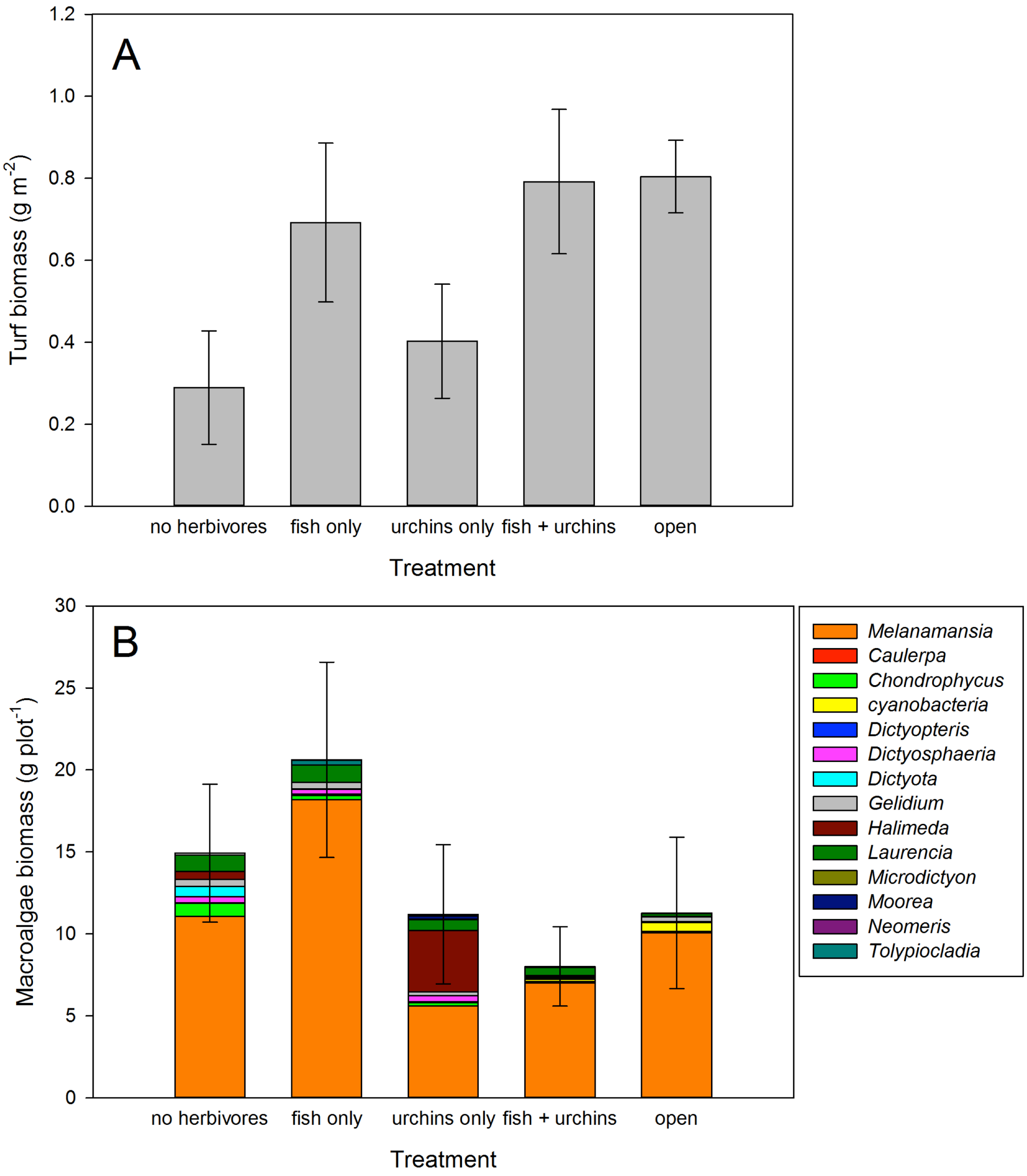

Figure 6: (A) Average dry weight (g m^{-2}) of turf algae removed at the conlcusion of the experiment. (B) Average dry weight (g plot^{-1}) by genera of macroalgae removed per plot. Bars are standard error.

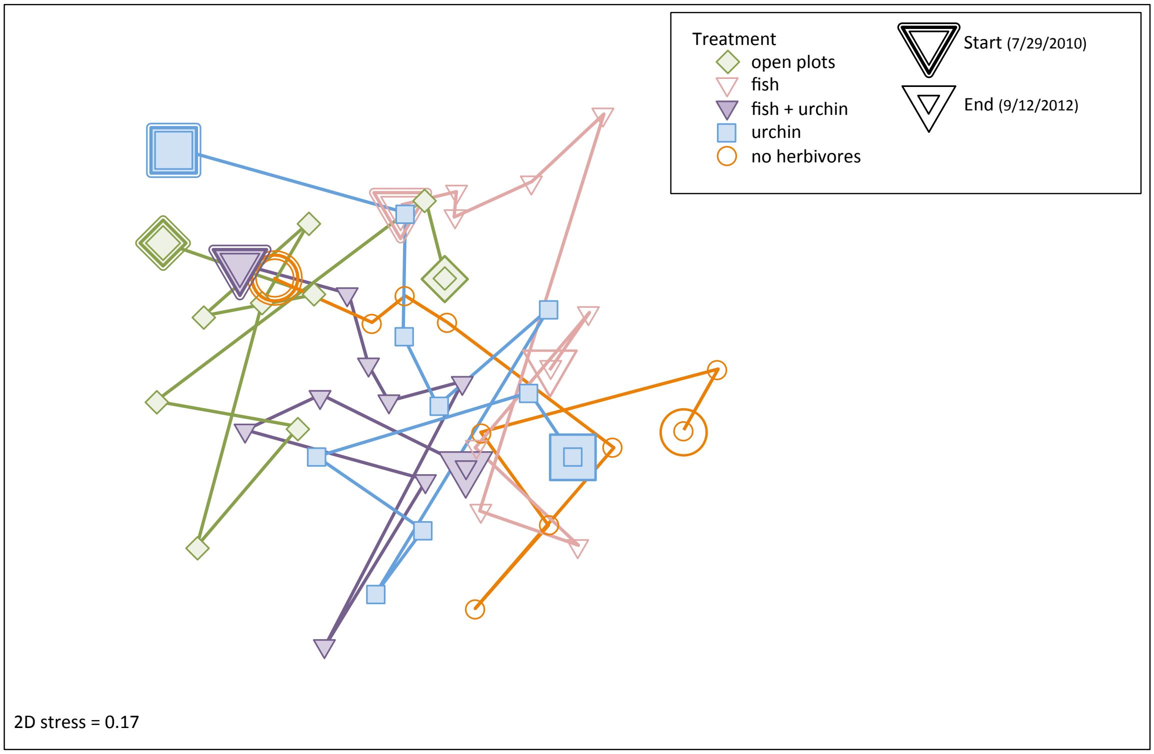

Figure 7: nMDS of herbivore treatments through the first year of the experiment. Time points are initially two weeks apart and later 1 to 3 months apart. n = 6 per treatment.

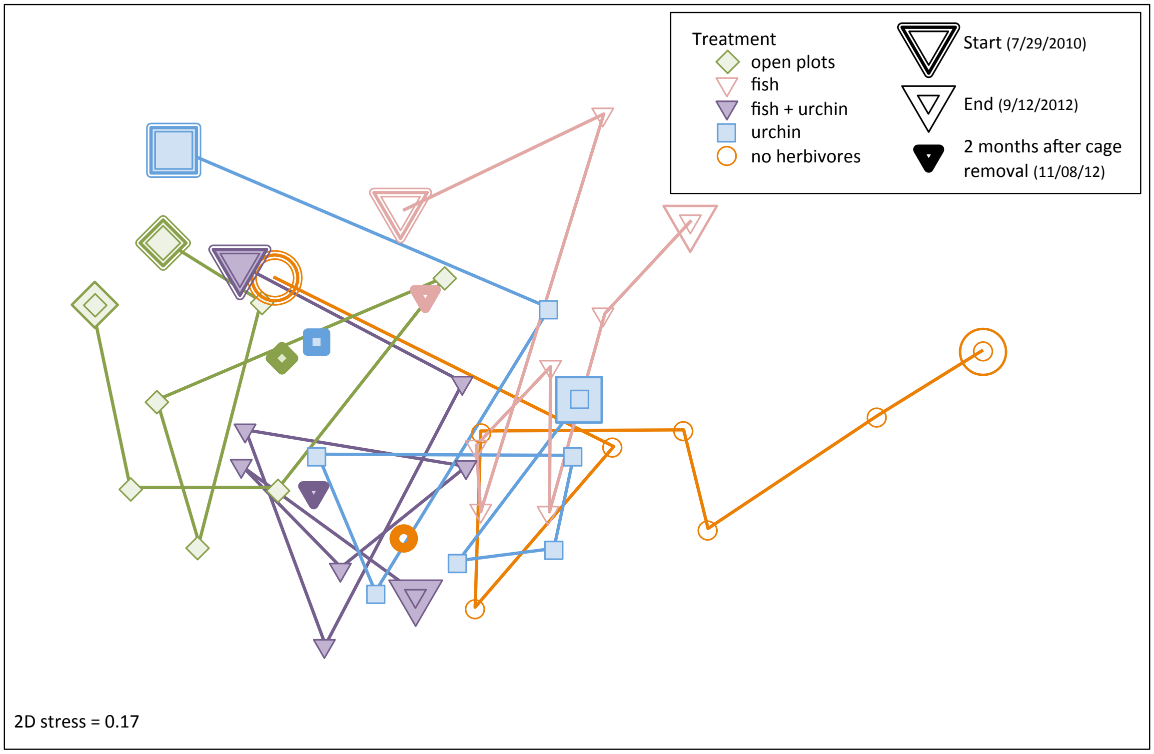

Figure 8: nMDS of herbivore treatments through the entire experiment. Time points are 2 to 3 months (maximally 6 months) apart. n = 6 per treatment.

CONCLUSION

In terrestrial ecology, the studies of herbivory often focus on overgrazing in which the loss of predators in the ecosystem has resulted in herbivore population increases and thus overgrazing on primary producer communities (Ripple & Beschta 2003, Howland et al. 2014). However, in marine ecology we often study the opposite scenario. In marine systems, fishing activity has removed large predatory fishes (Myers & Worm 2003, McClenachan 2009) and as stocks of larger species decline, progressively lower trophic level species are targeted – a phenomenon often described as “fishing down marine food webs” (Pauly et al. 1998, Steneck et al. 2002). Coral reefs that are adjacent to local human populations on average have lower fish biomass of all trophic levels (Williams et al. 2011), including herbivores (Edwards et al. 2014) and these loses are generally attributed to over exploitation. Studies of these fish-depauperate reef ecosystems in addition to numerous experimental (Randall 1961, Hughes et al. 2007, Burkepile & Hay 2008, and Chapter 4) and correlative studies (Williams & Polunin 2001, Friedlander et al. 2007) have revealed the importance of herbivores on reefs and the associated higher cover of fleshy algae that is common in their absence.

Nearly six years since the establishment of the Kahekili Herbivore Fisheries Management Area, increasing herbivore biomass on the reef and the contribution of larger bodied scrapers and browsers to the consumption budget highlight promising initial results of herbivore protection at this location. With continued increase in herbivore biomass at Kahekili, there is strong potential for future increases in coral cover as a result of fish consumption of algae. This approach to reef management is truly groundbreaking in taking scientific discussions of herbivore utility and applying them to a reef that was declining in coral cover. In addition, the HFMA designation still allows fishing for other trophic groups, providing a balance between reef management and human use.

As part of this recovery of herbivores, a diverse fish assemblage should be valued. Results presented in Chapter 1 show that fish overwhelming consume turf algae but that the communities of turf they are consuming may vary by herbivore species. In addition, the ecological impact of large parrotfish bites makes them particularly important in reef recovery as they open bare space for potential recruitment of reef builders. Further, it has been suggested that species diversity may promote ecosystem stability (Walker 1992, Hooper et al. 2005) suggesting that biogeography will play a role in predicting the stability of a given reef. Reefs in the depauperate Caribbean have seen the unfortunate consequences of the loss a single dominant herbivore and are thus now largely dominated by algae (Lessios 1988).

Another aspect of a diverse and growing fish assemblage is schooling, which was not a focus of this research but was a noted change on the reef at Kahekili after establishment of the protected area. In 2009 schools of herbivores were largely missing, save groups of a few scarids all less than 15 cm (TL). Since that time, I have seen more and larger schools of mixed acanthurids and some scarids. Schooling provides safety from territorial fishes during grazing (Robertson et al. 1976), the dynamics of how grazing changes not simply with increased herbivore biomass but with increased diverse schools of herbivores requires further exploration.

Beyond seeing the changes in fish biomass, our budgets of production and consumption at Kahekili (Chapter 2) and other reefs around Maui (Chapter 3) elucidate the shift in ecosystem function on reefs. The deficit of consumption that exists at Kahekili, Honolua Bay, Olowalu, Kapalua Bay, and others is made particularly visible through the calculation of net production. While decline of coral cover has been well documented around the island, these calculations provide a further summary of how unequal rates of production and consumption are on many of these reefs. As more reefs have been degraded or are in decline globally, this type of view highlights this mismatch in function. Such a functional assessment of grazing pressure can therefore help to fight the "shifting baselines" syndrome common on coral reefs and almost every other ecosystem impacted by humans (Knowlton & Jackson 2008, Jackson & Jacquet 2011).

The focus of this dissertation was not only on herbivorous fish but included additional investigation into the effects of urchins in Chapter 4. The manipulative factorial experiment provided insight into the low rate of herbivory given the herbivore community present at Kahekili during the experiment and the impacts of both fish and urchins on the reef community. Certainly more investigation into the impacts of the diverse community of urchins on Hawaiian reefs is necessary as well as the magnitude of the microherbivore contribution to the grazing budget.

At the outset of my dissertation research and just prior to the KHFMA designation, my goal had been to quantify the types and biomass of fish that would be required to see Kahekili increase in coral cover. What resulted from my research is not a single recipe for a healthy coral reef but rather a better picture of the impact of individual species, the deficit of consumption that exists on many reefs around Maui, and initial estimates for herbivore biomass recovery targets to effect positive changes on these reefs. Strikingly, each reef carries unique natural history of both naturally occurring benthic and fish communities as well as anthropogenic impacts of fishing, sedimentation, alteration, and continued human use. Therefore, steps towards recovery for reefs that have declined will necessarily be context dependent, even for reefs less than a mile apart.

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