UNIVERSITY OF CALIFORNIA, SAN DIEGO

Consumers on coral reefs: variation in the structure and function of herbivorous echinoid communities and their consequent effects on benthic dynamics

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

in

Oceanography

by

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2016

The Dissertation of Levi Steele Lewis is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

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DEDICATION

To my ridiculous and wonderful parents & family, my personal Wonder Woman, the warm and conscientious people of Maui Makai Watch, the dedicated brilliant minds that must and will overcome, the socially aware and responsible, the sponge-crab lovers, yellow-cake makers, tank chuckers, the gracious tigermonkacuda, the inspiring viperfish, broad spectrum antibiotics, minivans, and the legion of volunteers who gift their time and talents to the understanding and preservation of nature.

EPIGRAPH

“The ideal scientist thinks like a poet and works like a bookkeeper,”

- E.O. Wilson

"Look at me now..."

- a coral

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ACKNOWLEDGEMENTS

I would like to acknowledge Professor Jennifer Smith for her support as the chair of my committee; her guidance and support have proven invaluable. I would also like to acknowledge my thesis committee for their guidance with my education, research and critique of manuscripts. The Smith and Sandin Labs and associated volunteer researchers were critical to the completion of all research projects. The support team in Maui Hawaii, including Mark Miller, Don McLeish, Donna Brown, the Division of Aquatic Resources, Maui Ocean Center, Tom's Vans, Maui Diving Scuba Center, and the Makai Watch family provided research support and logistics in the field. The support staff at Scripps Institution of Oceanography, including the Graduate Office, Center for Marine Biodiversity and Conservation, and the Scripps Dive Program provided critical administrative, educational and research support. Many Scripps students, staff, and faculty; especially members of GDAWG, TIDES, Ball Bouncers and the Maniacs; provided critical support for mental health and social well-being. This work would not have been successful without the support of a loving and loyal network of phenomenal friends and family. All graphic art was generously provided by Adi Khen.

Chapter 2, in part is currently being prepared for submission for publication of the material. Lewis, Levi S; Price, Nicole, N.; Smith, Jennifer E. The dissertation/thesis author was the primary investigator and author of this material.

Chapter 3, in part is currently being prepared for submission for publication of the material. Lewis, Levi S; Eynaud, Yoan; Smith, Jennifer E. The dissertation/thesis author was the primary investigator and author of this material.

Chapter 4, in part, has been submitted for publication of the material as it may appear in Coral Reefs, 2016, Lewis, Levi S; Smith, Jennifer E., Springer, 2016. The dissertation/thesis author was the primary investigator and author of this paper.

Chapter 5, in part is currently being prepared for submission for publication of the material. Lewis, Levi S; Edwards, Clinton B.; Smith, Jennifer E. The dissertation/thesis author was the primary investigator and author of this material.

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ABSTRACT OF THE DISSERTATION

Consumers on coral reefs: variation in the structure and function of herbivorous echinoid communities and their consequent effects on benthic dynamics

By

Levi Steele Lewis

Doctor of Philosophy in Oceanography

University of California, San Diego, 2016

Professor Jennifer E. Smith, Chair

Herbivores facilitate the existence of coral reef ecosystems by limiting the abundance of fleshy algae. Though fishes often dominate in deeper fore-reefs, echinoids (sea urchins) often dominate herbivore communities in shallow fringing- and back-reefs. Given their strong effects on benthic dynamics in the Caribbean Sea and Indian Ocean, echinoids may drive many key biological processes on shallow coral reefs across the globe. Though described as generalists, echinoid species appear to exert unique effects on coral reef benthic communities. This dissertation examined how variation in the structure of echinoid communities drives benthic community dynamics on Hawaiian reefs. The four research projects (data chapters) used a combination of mensurative and manipulative approaches in the lab and field to address this topic and are organized into two themes: (1) spatial variation in consumer (echinoid) effects in relation to environmental conditions and (2) functional diversity among echinoid species and communities, and their consequent effects on benthic dynamics.

In sum, this dissertation demonstrates that (1) herbivory by echinoids varies greatly among sites and can be a dominant structuring force on coral reefs in Maui, HI, (2) the *in situ* effects of echinoids on coral recruitment appears to be driven by a variety of factors (e.g., echinoid community structure and sediment exposure), (3) echinoid species vary greatly (> 10-fold) in their metabolic demands, grazing rates, and diet preferences, and (4) functional diversity among species leads to significant and large differences in the effects of unique echinoid communities on benthic dynamics and coral growth. These results emphasize the importance and complexity of echinoid community demographics and consequent effects in coral reef ecosystems. Though echinoids are able and willing to consume and survive on a variety of different food items, their unique preferences and grazing behaviors can result in diverse ecological functions and effects on coral reefs. These results suggest that models of coral reef ecosystem dynamics and conservation/management efforts (particularly for shallow reefs where echinoids often dominate) likely need to account for echinoid community structure and function in order to maximize their accuracy and long-term effectiveness.

CHAPTER 1 Introduction: Herbivory, functional diversity, and the structure and function of coral reef ecosystems

Levi S. Lewis

Understanding the processes that regulate structure and function of ecosystems remains a fundamental goal of ecology. Previous work has demonstrated that both environmental conditions (Connell 1978, White 1978, Sousa 1979, Oksanen et al. 1981, Duarte 1995) and biotic interactions (Hairston et al. 1960, Paine 1966, Estes & Palmisano 1974, Tilman et al. 1997a) influence productivity across trophic levels. Bottom-up (resource-supply; e.g., nutrients) and top-down effects (e.g., herbivory and predation) both simultaneously influence ecosystems and the relative importance of these two processes appears variable and context-dependent (Oksanen et al. 1981, Burkepile & Hay 2006, Gruner et al. 2008) . In benthic marine habitats, however, top-down effects appear particularly strong (Heck & Valentine 2007) with effects often cascading across multiple trophic levels (Paine 1980).

The effects of herbivores and their predators on "foundation species" (large sessile organisms such as kelps, seagrasses, sponges, and corals whose presence transforms otherwise simple systems into more complex, productive habitats) (*sensu* P. Dayton 1972), may vary widely in marine habitats, depending strongly on the identity of dominant habitat-forming species and their associated grazers. In temperate rocky reefs, robust macroalgae (e.g., kelps) often serve as dominant habitat-forming species (Dayton et al. 1998); whereas in coral reefs and seagrass beds, fleshy algae appear to compete with habitat-forming corals and seagrasses for light, nutrients, and space (Sand-Jensen 1977, Hauxwell et al. 2001, McCook et al. 2001). In kelp forests, both macrograzers (e.g., urchins) and mesograzers (e.g., amphipods) reduce the growth and extent of habitat-forming kelps, and their predators indirectly benefit kelps (Estes & Palmisano 1974, Davenport & Anderson 2007). In contrast to kelp forests, algal grazers in coral reefs and seagrass beds are thought to facilitate the dominance of habitat-forming corals and seagrasses by limiting algal growth (van Montfrans et al. 1984, McCook et al. 2001, Williams & Heck 2001, Hughes et al. 2004, Hughes et al. 2007, Smith et al. 2010), and their loss (through fishing or predation) is thought to suppress this beneficial effect, but not always (O'Leary & McClanahan 2010, Lewis & Anderson 2012). Small crustaceans (e.g., amphipods and isopods) and gastropods appear to be the most important algal grazers in seagrass beds (Kitting et al. 1984, Orth & Vanmontfrans 1984, Jernakoff et al. 1996); whereas large fishes (e.g., parrotfishes and surgeonfishes) and echinoids appear to fill this role on coral reefs (Sammarco 1982, Carpenter 1986, Williams & Polunin 2001, Hughes et al. 2007).

Biodiversity and Ecosystem Functioning

A key biological factor in ecosystem science is biodiversity (the number and distribution of unique organisms or functional groups), which can exert strong influence on the functioning of ecosystems (Elton 1958, Stachowicz et al. 2007, Tilman et al. 2012). Ecosystem functioning might be defined or measured as production rates, standing biomass, trophic dynamics, element cycling, trophic transfer, resistance to invasion, and resource use (Stachowicz et al. 2007). Early manipulative experiments (Hooper & Vitousek 1997, Tilman et al. 1997b) explicitly explored relationships between biodiversity and production in terrestrial plant communities, and numerous similar studies in additional systems and with additional functional groups have followed (Naeem & Li 1997, Duffy et al. 2001, Covich et al. 2004). Synthetic analyses (Cardinale et al. 2006, Stachowicz et al. 2007, Cardinale et al. 2012, Hooper et al. 2012, Tilman et al. 2012, Tilman et al. 2014) have since identified consistent and strong effects of biodiversity on primary production and resource use by functional groups of organisms; however, such studies in marine subtidal ecosystems remain relatively rare (Duffy et al. 2001, Stachowicz et al. 2007, Brandt et al. 2012).

Reductions in biodiversity, therefore, can result in myriad cascading, albeit difficult to predict, ecological effects that can ultimately impact human societies (Cardinale et al. 2012). Furthermore, large, strongly-interacting species, such as keystone and dominant species that have the greatest influence on ecosystem-wide structure and function (Paine 1980, Power et al. 1996, Terborgh & Estes 2010), are often the most susceptible to defaunation and extinction (Duffy 2002, Dirzo et al. 2014). In the marine environment, anthropogenic alteration (both direct and indirect) of fish and macro-invertebrate (e.g., echinoids) communities has greatly altered benthic ecosystems across the globe (Strong 1992, Jackson et al. 2001, Byrnes et al. 2006, Steneck 2013, Steneck et al. 2013). In coral reefs, overfishing and disease have decimated consumer populations, resulting in rapid, massive, and semi-permanent transformations of coral ecosystems following disturbance (Knowlton 1992, Hughes 1994). Experimental studies of marine consumer richness have shed much light on biodiversity-trophic-guild function relationships (Duffy & Harvilicz 2001, Duffy et al. 2003, Douglass et al. 2008, O'Connor & Bruno 2009); however, fewer studies have attempted to address these questions in natural subtidal environments using manipulative experiments (Stachowicz & Whitlatch 2005, Burkepile & Hay 2008, 2010, Brandt et al. 2012). Subtidal, manipulative, field-based experiments are needed to advance our understanding of the true significance of biodiversity (and its loss) to ecosystem processes in marine ecosystems (Duffy 2002).

In coral reef ecosystems, herbivore communities serve an important function by controlling fleshy algae, thus facilitating coral survival and growth (Carpenter 1986, Hughes 1994, McClanahan 1995, Williams & Polunin 2001, Mumby et al. 2007) (Fig. 1.1). Though the importance of herbivory has been well-documented, few studies have experimentally tested the effects of herbivore diversity in these systems. For example, herbivorous fishes are often aggregated by taxonomic or course functional categories (Friedlander et al. 2003, McClanahan et al. 2007, Sandin et al. 2008, Williams et al. 2011); however, this may overlook subtle, but important, differences in feeding behaviors that result in functionally different effects (among species and communities) on benthic dynamics (Bellwood & Choat 1990, Choat et al. 2002, Burkepile & Hay 2008, Burkepile & Hay 2011).

In addition to fishes, herbivorous echinoids can also be diverse and important components of herbivore communities on certain coral reefs (McClanahan 1988, Ogden et al. 1989, Coppard & Campbell 2007, McClanahan & Muthiga 2016). Though echinoid species are often regarded as generalist consumers (Ogden & Lobel 1978a, Hay 1984, Ogden et al. 1989, Steneck 2013), they may also exhibit distinct dietary preferences and specialized behaviors (Carpenter 1981, Hay 1984, de Loma et al. 2002, Vaitilingon et al.

2003) indicative of functional diversity that could result in different (and complementary) effects on benthic coral reef communities. For example, though echinoids are generally thought to benefit reefs by controlling macroalgae and increasing resistance to algal phase-shifts (Sammarco 1982, Hughes 1994), some species appear to function primarily as reef eroders that graze live calcifiers (corals and CCA), resulting in reduced net calcification, stability, growth and resilience (Glynn et al. 1979, O'Leary & McClanahan 2010, O'Leary et al. 2013).

The long-term effects of different echinoid species (identity) or combinations of species (diversity and structure) on natural coral reef benthic communities remains unclear. Given the strong effects (positive and negative) this grazing community can exert on benthic dynamics in coral ecosystems, further exploration of this knowledge gap is warranted. Field-based manipulative studies examining variation in ecological functions among echinoid species and communities, therefore, are needed to improve our understanding of relationships between community structure and function. Results of such studies can enhance conservation and management efforts by leading to more informed and ecologically-sound decisions and strategies.

Coral Reef Ecosystems

Coral reef ecosystems thrive in shallow, warm seas with low sedimentation, low nutrients, and high consumer biomass (Birkeland 1997). Due to their great economic and ecological value (Moberg & Folke 1999), and rapid human-associated degradation (Pandolfi et al. 2003, Pandolfi et al. 2005, Bruno & Selig 2007, Sandin et al. 2008, Smith et al. 2016), the physical and biological factors that drive the development and function of coral reefs, and the consequences of local and global modification of these factors, both natural and anthropogenic, have been studied extensively (Hughes & Connell 1999). Historical ecological studies have demonstrated that natural factors (e.g., changing geomorphology, climate, predators and algae blooms) have clearly resulted in changes in coral cover prior to the rapid expansion of human populations and the industrial revolution; however, these changes were generally slow, occurring over geological time scales (e.g., thousands of years) (Pandolfi et al. 2003). In contrast, anthropogenic factors appear to have rapidly (within decades) transformed many coral reef ecosystems from calcifier-dominated to fleshy algae-dominated ecosystems (Hughes 1994, Pandolfi et al. 2005, Smith et al. 2016) resulting in the loss of reef-building capacity and the multitude of ecosystem services provided by actively accreting coral reefs (Moberg & Folke 1999, Graham 2014).

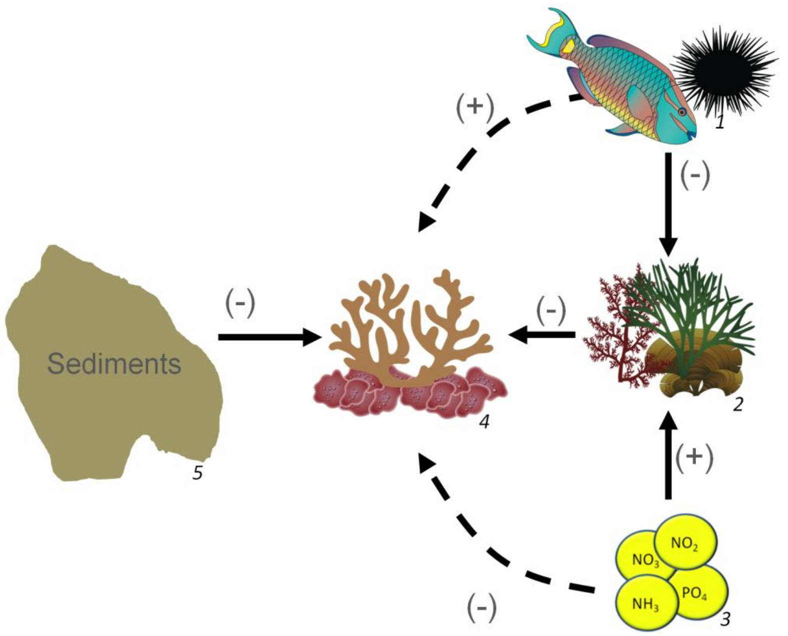

Figure 1.1. Prominent ecological dynamics of coral reef systems examined in the dissertation. Theme I of the dissertation examined how these factors vary throughout coral reefs on leeward Maui; Theme II examined the magnitude and ecological importance of functional diversity among different species of sympatric echinoid grazers. (1) Herbivore communities exert direct (solid lines), negative top-down effects on macroalgal biomass (2). Nutrients (3) exert, direct, positive bottom-up effects on macroalgal biomass. Macroalgae exert direct, negative, horizontal effects on corals (and other calcifiers, e.g., crustose coralline algae)(4) via competition for benthic space. Positive and negative indirect (dashed lines) effects of herbivores and nutrients, respectively, are exerted on corals via their strong direct effects on the abundance of algae. Sediment exposure (5) exerts direct negative effects on corals via smothering and reductions in light availability (turbidity). Images by Adi Khen.

Though the largest-scale and most rapid losses of live coral cover have been and will likely continue to be related to global factors (e.g., warming and bleaching) (Hoegh-Guldberg 1999), the inability of individual coral reefs to resist and recover from large-scale disturbances appears to be related to local human activities that disrupt important coral-facilitating ecological processes (Sandin et al. 2008, Adam et al. 2015, Smith et al. 2016) (Fig. 1.1). For example, land development, nutrient pollution, and fishing are three local human activities known to modify coastal environments and exert strong negative influence on corals (Richmond 1993, Birkeland 1997). Excessive sedimentation due to poor land use practices results in the smothering of corals and the development of stable sandy algal-dominated hardpan environments at the expense of corals (Richmond 1993, Fabricius & Wolanski 2000, Fabricius 2005, Bellwood & Fulton 2008, Erftemeijer et al. 2012). Nutrient pollution enhances the production and biomass of algae (Smith et al. 1981, Lapointe 1997, Smith et al. 2005) that kill coral through direct (McCook et al. 2001, Rasher & Hay 2010) and indirect (Smith et al. 2006) means. Overfishing, particularly of herbivores, releases fleshy algae from grazer control, also leading to increased direct and indirect mortality of corals by fleshy algae (Smith et al. 2001, Williams & Polunin 2001, Hughes et al. 2007).

Coral Reefs in the Hawaiian Islands

In the Main Hawaiian Islands, USA, multiple local stressors appear to be working in concert to degrade fringing coral reefs and limit their resistance and resilience to disturbances and global change (Pandolfi et al. 2005). Hawaii's coral reefs have long-sustained several significant, local anthropogenic stressors including (1) reductions in fish biomass due to overfishing (Friedlander & DeMartini 2002, Friedlander et al. 2007), (2) coastal inputs of nutrients from sewage and fertilizers that fuel blooms of fleshy algae (Smith et al. 1981, Smith et al. 2005, Dailer et al. 2010, Dailer et al. 2012a, Dailer et al. 2012b), and (3) increased sedimentation due to development and agriculture (Jokiel et al. 2014, Prouty et al. 2014, Stender et al. 2014). Persistent losses of live coral cover (Walsh et al. 2013) in the absence of large-scale global impacts (e.g., bleaching) previously suggested that local impacts were likely transforming Hawaii's coral reefs into stable, fleshy, non-accreting alternative states as observed in the Caribbean (Hughes 1994, Pandolfi et al. 2005). The unprecedented bleaching events that occurred throughout Hawaii in 2015-16, however, suggest that global impacts may increasingly become a primary driver of change in these systems. Observational and experimental approaches are needed to better understand the processes driving changes in patterns in Hawaii's coral reefs. Large-scale monitoring efforts have described correlations between water quality, fleshy algae, herbivores, anthropogenic pressures, erosion, and coral cover on reefs around Hawaii (Walsh et al. 2013, Silbiger et al. 2014, Jouffray et al. 2015), and have identified a variety of patterns that likely reflect spatial variation in important ecological processes.

In addition to these monitoring efforts, comparative experiments, that manipulate ecological processes in a variety of locations with unique physical and biological conditions, are needed to better understand the processes driving spatial patterns in reef condition. In contrast to most manipulative experiments that are conducted at one or a few sites, comparative experiments are conducted at many sites under a variety of environmental contexts, thus providing improved inference regarding the broader relevance of results from isolated studies (Menge 2000, Burkepile & Hay 2006, Rilov & Schiel 2006). For example, coral cover has declined precipitously over the last several decades in Maui, HI (Walsh et al. 2013), and though these reefs are believed to be highly impacted by numerous factors, local conservation efforts have largely relied on generalized ecological principles.

The need for comparative field experiments

Ecological dynamics are driven by a variety of interacting physical and biological factors, all of which demonstrate significant spatial heterogeneity. In aquatic environments, key physical factors include: the availability of inorganic macro-nutrients, water chemistry, water flow, sediment quality and fluxes, temperature, and solar radiation available for photosynthesis (PAR); whereas biological factors are widely based on the structure of the living community (density and diversity) and species interactions (e.g., consumption, competition, and facilitation) (Bertness et al. 2014). Though several studies have described important differences in ecological processes among broad ecotypes (Strong 1992, Burkepile & Hay 2006, Shurin et al. 2006), such generalizations can belie smaller-scale variation in ecological dynamics that can and should be accounted for in local management and conservation efforts. Comparative studies that (a) test for spatial variation in ecological dynamics and (b) examine potential environmental drivers of variation (Menge 2000, Burkepile & Hay 2006, Rilov & Schiel 2006), are needed to inform and enhance local conservation and management efforts. In contrast to many experiments that are conducted at one or a few sites, comparative experiments are conducted at many sites under a variety of environmental contexts, thus providing improved inference regarding the broader relevance of results from isolated studies (Menge 2000, Burkepile & Hay 2006, Rilov & Schiel 2006).

DISSERTATION RESEARCH

Herbivorous echinoids (sea urchins) are abundant consumers on shallow, nearshore coral reefs in Maui (Ebert 1971, Ogden & Lobel 1978b), and given their strong effects on benthic coral-reef dynamics in the Caribbean Sea (Sammarco 1982, Hughes et al. 1987) and Indian Ocean (McClanahan 1988, O'Leary et al. 2012), these grazers are likely to drive many key biological processes on shallow reefs across the globe. This dissertation, therefore, focused on how variation in the structure of echinoid communities drives benthic community dynamics on Hawaiian reefs. The four data chapters used a combination of mensurative and manipulative approaches to address this topic; chapters were organized into two themes: (I) spatial variation in consumer effects on benthic dynamics in relation to environmental conditions and (II) functional diversity among echinoid species and communities, and its effects on benthic dynamics.

Theme I. Spatial variation in consumer effects on benthic dynamics in relation to environmental conditions in Maui, Hawaii

In **Chapter 2**, I used a 3-year deployment (with continual maintenance) of caged and uncaged settlement tiles, combined with environmental surveys, to describe spatial variation across eight sites on Maui, Hawaii in the effects of consumers on benthic dynamics in relation to (1) their structure and biomass (2) productivity as estimated by nutrient concentrations and (3) sediment exposure as estimated by sediment accumulation rates. The goals of Chapter 2 were to elucidate spatial variation in the early succession on Maui's coral reefs, the effects of consumers throughout the system, and how variation in environmental conditions might influence the functional roles of consumers. Results of this work have direct relevance to marine spatial planning and conservation by identifying spatial variation in patterns and processes that can and should be included in conservation and management plans and activities.

Theme II. Functional diversity among echinoid species and communities, and its effects on benthic dynamics

In **Chapter 3**, I used standard metabolic assays to test and describe differences in the allometric scaling relationships of mass and metabolism for 5 common Hawaiian echinoids. Metabolic scaling of echinoids was contrasted with predictions from the Metabolic Theory of Ecology (MTE). These empirically-derived coefficients will facilitate more accurate, taxon-specific, scaling of mass and metabolism for this important trophic guild, thus enhancing our understanding of functional differences among species and improving predictions made by ecological models. In **Chapter 4**, I combined results from metabolic assays (Chapter 3) with field-based assays of grazing rates and algal preferences to test and describe taxonomic variation in total and mass-specific grazing rates, how these corresponded with metabolism and dietary preferences for six different types of algae. This chapter provided a direct test for differences in the trophic ecology of tropical echinoids on coral reefs, thus providing improved inference regarding functional redundancy and diversity within this guild. In **Chapter 5**, I used a 2-year deployment of large cages on natural mixed-aggregate coral reef communities, and manipulations of three common species of echinoids (*E. calamaris, H. mammillatus, and T. gratilla*), to examine the long-term effects of 6 different types of echinoid communities on benthic dynamics on a coral reef. This chapter provided relevance to results from Chapters 3-4 by directly testing whether functional differences among species result in unique consequences for benthic dynamics, and whether functional diversity results in synergistic, complementary effects for coral reefs. Results of this work have direct relevance to ecology and conservation by providing new insights into the existence and importance of functional diversity within a "seemingly-redundant" guild of herbivores that are known to dominate many processes in shallow coral reef ecosystems.

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CHAPTER 2 Interactions between environmental characteristics, consumer effects, and the development of benthic communities on coral reefs: a comparative experimental approach

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ABSTRACT

Many interacting biological and physical factors influence the structure and function of ecosystems; however, understanding spatial variation in the relative influence of different factors is important for understanding natural variability among systems. Using standard PVC tiles, we explored spatial variation in community development on 8 shallow coral reefs spanning 60 km of coastline in Maui, HI. Half of the 20 tiles per site were caged to examine the influence of consumers and each of the 8 sites were characterized according to 3 known local drivers of nearshore reef dynamics: sediment exposure, herbivore abundance, and nutrient availability. Spatial variation in macroalgae, total fleshy and calcified biomass, coral recruitment, and structure of sessile communities were compared among sites, between caged vs. open tiles, and in relation to site-level environmental conditions.

Environmental characteristics and communities on tiles varied significantly among sites, and among consumer treatments. Nutrient levels were within normal levels

(DIN = 0.4-1.0 µM) for coral reefs. Herbivorous fish biomass was low at all sites (1-5 g m^{-2}); however, herbivorous echinoid biomass was high (21-614 g m^{-2}) and variable among sites. Sediment accumulation rates at all sites were above thresholds of sediment stress (0.01 g cm^{-2} d^{-1}) for coral reefs, and 4 of 8 sites exceeded these by several orders of magnitude. Macroalgal biomass was higher on caged versus open tiles, yet the magnitudes of consumer effects varied among sites by over 56-fold and correlated with herbivore biomass. Consumers reduced macroalgae, increased turfs, and did not affect CCA cover on CAU surfaces; suggesting that a "sediment-suppressed herbivory" model may better predict dynamics in these reefs than a "relative dominance model." Coral recruitment varied greatly among individual tiles and sites (but not treatment), and exhibited exponential decay as a function of sediment exposure, thus supporting *a priori* sediment-stress thresholds. Overall, benthic dynamics on individual coral reefs appeared to be driven by unique ecological processes, suggesting that resource managers need to examine the specific drivers of local-regional dynamics in order to maximize the effectiveness of specific conservation efforts.

INTRODUCTION

Deterministic ecological dynamics are driven by a variety of interacting physical and biological factors. In aquatic environments, key physical factors include: the availability of inorganic macro-nutrients, water chemistry, water flow, sediment quality and fluxes, temperature, and solar radiation available for photosynthesis (PAR). Biological factors are widely based on the structure of the living community (density and diversity) and species interactions (e.g., consumption, competition, and facilitation) (Bertness et al. 2014). Though several studies have described important differences in ecological processes among broad ecotypes (Strong 1992, Burkepile & Hay 2006, Shurin et al. 2006), such generalizations can belie smaller-scale variation in ecological dynamics that can and should be accounted for in local management and conservation efforts. Comparative studies that (a) test for spatial variation in ecological dynamics and (b) examine potential environmental drivers of variation (Menge 2000, Burkepile & Hay 2006, Rilov & Schiel 2006), are needed to inform and enhance local conservation and management efforts.

Coral reef ecosystems thrive in shallow, warm seas with low sedimentation, low nutrients, and high consumer biomass (Birkeland 1997). Due to their great economic and ecological value (Moberg & Folke 1999), and rapid human-associated degradation (Pandolfi et al. 2003, Pandolfi et al. 2005, Bruno & Selig 2007, Sandin et al. 2008, Smith et al. 2016), the physical and biological factors that drive the development and function of coral reefs, and the consequences of local and global modification of these factors, both natural and anthropogenic, have been studied extensively (Hughes & Connell 1999). Historical ecological studies have demonstrated that natural factors (e.g., changing geomorphology, climate, predators and algae blooms) have clearly resulted in changes in coral cover prior to the rapid expansion of human populations and the industrial revolution; however, these changes were generally slow, occurring over geological time scales (e.g., thousands of years) (Pandolfi et al. 2003). In contrast, anthropogenic factors appear to have rapidly (within decades) transformed many coral reef ecosystems from calcifier-dominated to fleshy algae-dominated ecosystems (Hughes 1994, Pandolfi et al.

2005, Smith et al. 2016) resulting in the loss of reef-building capacity and the multitude of ecosystem services provided by actively accreting coral reefs (Moberg & Folke 1999, Graham 2014).

Though the largest-scale and most rapid losses of live coral cover have been and will likely continue to be related to global factors (e.g., warming and bleaching) (Hoegh-Guldberg 1999), the inability of individual coral reefs to resist and recover from large-scale disturbances appears to be related to local human activities that disrupt important coral-facilitating ecological processes (Sandin et al. 2008, Adam et al. 2015, Smith et al. 2016). For example, land development, nutrient pollution, and fishing are three local human activities known to modify coastal environments and exert strong negative influence on corals (Richmond 1993, Birkeland 1997). Excessive sedimentation due to poor land use practices results in the smothering of corals and the development of stable sandy algal-dominated hardpan environments at the expense of corals (Richmond 1993, Fabricius & Wolanski 2000, Fabricius 2005, Bellwood & Fulton 2008, Erftemeijer et al. 2012). Nutrient pollution enhances the production and biomass of algae (Smith et al. 1981, Lapointe 1997, Smith et al. 2005) that compete with and kill corals through direct (McCook et al. 2001, Rasher & Hay 2010, Vermeij et al. 2010) and indirect (Smith et al. 2006) means. Overfishing of herbivores releases fleshy algae from grazer control, also leading to increased direct and indirect mortality of corals via competition with fleshy algae (Smith et al. 2001, Williams & Polunin 2001, Hughes et al. 2007).

In the Main Hawaiian Islands, USA, multiple local stressors appear to be working in concert to degrade fringing coral reefs and limit their resistance and resilience to disturbances and global change (Pandolfi et al. 2005, Jouffray et al. 2015). Hawaii's coral reefs have long-sustained several significant, local anthropogenic stressors including (1) reductions in fish biomass due to overfishing (Friedlander & DeMartini 2002, Friedlander et al. 2007), (2) coastal inputs of nutrients from sewage and fertilizers that fuel blooms of fleshy algae (Smith et al. 1981, Smith et al. 2005, Dailer et al. 2010, Dailer et al. 2012a, Dailer et al. 2012b), and (3) increased sedimentation due to development and agriculture (Jokiel et al. 2014, Prouty et al. 2014, Stender et al. 2014). Persistent losses of live coral cover (Walsh et al. 2013) in the absence of large-scale global impacts (e.g., bleaching) previously suggested that local impacts were likely transforming Hawaii's coral reefs into stable, fleshy, non-accreting alternative states as observed in the Caribbean (Hughes 1994, Pandolfi et al. 2005). The unprecedented bleaching events that occurred throughout Hawaii in 2015-16, however, suggest that global impacts may increasingly become a primary driver of change in these systems. Observational and experimental approaches are needed to better understand the processes driving changes in patterns in Hawaii's coral reefs. Large-scale monitoring efforts have described correlations between water quality, fleshy algae, herbivores, anthropogenic pressures, erosion, and coral cover on reefs around Hawaii (Walsh et al. 2013, Silbiger et al. 2014, Jouffray et al. 2015), and have identified a variety of patterns that likely reflect spatial variation in important ecological processes.

In addition to these monitoring efforts, comparative experiments, that manipulate ecological processes in a variety of locations with unique physical and biological conditions, are needed to better understand the processes driving spatial patterns in reef condition. In contrast to most manipulative experiments that are conducted at one or a few sites, comparative experiments are conducted at many sites under a variety of environmental contexts, thus providing improved inference regarding the broader relevance of results from isolated studies (Menge 2000, Burkepile & Hay 2006, Rilov & Schiel 2006). For example, coral cover has declined precipitously over the last several decades in Maui, HI (Walsh et al. 2013), and though these reefs are believed to be highly impacted by numerous factors, local conservation efforts have largely relied on generalized ecological principles. Comparative experimental assessment of spatial variation in the relative influence of herbivores, nutrients and sediments could inform management about locations where enacting specific conservation efforts might be most (or least) effective.

Here, we conducted a 36-mo. (3-yr) comparative manipulative field experiment to explore spatial variation in the effects of consumers and environmental conditions on the development of benthic coral reef communities. Experiments were replicated on 8 shallow fringing coral reefs spanning a 60 km section of coastline on leeward Maui, Hawaii. At each site, we examined the influence of consumers on early community development using both open (consumer access) and caged (consumer exclusion) settlement tiles. We also quantified three environmental characteristics (sediments, nutrients, and herbivores), each known to both influence coral reef development and to be altered by human activities. After 36 months, we collected all tiles and measured (1) macroalgae, (2) total fleshy and (3) total calcified biomass; (4) coral recruitment; and (5) community structure of sessile organisms and substrates. Each metric was then compared (a) among sites, (b) among caged vs. open tiles, and (c) in relation to environmental conditions. Existing paradigms in coral reef ecology suggest that consumer exclusion should result in positive effects on fleshy macroalgae and negative effects on coral recruitment and net accretion of calcium carbonate. We predicted, however, significant site-specific variation in these (and other) predicted patterns and, furthermore, that a significant proportion of this variation could be explained by differences in environmental conditions among sites. Results from our study advance our understanding of the general strength of consumer effects on the development of benthic coral reef communities, how spatial variation in ambient environmental conditions influences these processes, and where future specific conservation and management actions in Maui would likely have the greatest positive impact for its nearshore coral reefs.

METHODS

Experimental Design

Study Region

Research was conducted on Maui, Hawaii, a high volcanic island in the central Pacific Ocean with a 2015 population of over 164,637 residents (US Census Bureau, http://www.census.gov/), and receives over 2 million visitors per year (HI Department of Business, Economic Development and Tourism, http://dbedt.hawaii.gov/). The majority of the island remains undeveloped, with most residents residing in three main coastal towns (Kahului, Kihei and Lahaina). Many of Maui’s shallow, nearshore reefs retain little coral and are dominated by fleshy turf and macroalgae (Walsh et al. 2013). The presence of numerous dead shallow carbonate reefs around the island (reported to have been lost within the past few decades), and high coral cover in certain shallow locations (e.g., Kahekili Beach Park) suggest that corals can grow and thrive in these habitats, but have been lost due to a variety of possible factors. These valuable, shallow (2-3 m depth) nearshore reefs are heavily used by tourists and impacted by coastal human activities. Despite various efforts to address anthropogenic impacts to specific coral reefs around Maui, little is known about site-specific differences in ecological dynamics and the relative importance of different stressors. For example, it is generally believed that nutrient pollution is a major concern in areas adjacent to WWRFs, sediments in areas near streams, and fishing throughout the region. Examples of continued degradation, despite strict and long-standing conservation protections (e.g., Honolua Marine Life Conservation District) (Walsh et al. 2013), demonstrate the importance of experimentally exploring local variation in key drivers of reef dynamics in order to maximize the effectiveness of specific conservation efforts (Roff & Mumby 2012).

Site Selection

Sites for settlement tile deployments (Fig. 2.1a) were selected across 60 km of Maui's leeward coastline to encompass likely gradients of natural and anthropogenic factors based on the available literature (Dailer et al. 2010, Walsh et al. 2013) and expert opinion from local researchers and resource managers. Key factors considered in site selection included: proximity to centers of human population (and waste-water treatment facilities), ambient nutrient concentrations, and accessibility from shore. We selected 8 sites to allow for effective dispersion (5-10 km) that would include sites with unique characteristics spanning the leeward side of the island. Sites were stratified across 60 km of coastline along leeward Maui and included (north-west to south-east): Kahekili

(1_KAH), Puamana (2_PUA), Olowalu (3_OLO), Ukumehame (4_UKU), Maalaea (5_MAA), Kalama (6_KAL), Keawakapu (7_KEA), and La Perouse (8_LAP). Each area was visually surveyed for nearshore reef habitats and tiles installed at 2-3 m depth among mixed reef communities that appeared representative of the site. The shortest distance to shore was measured by GPS at each site, and varied from approximately 50 m (e.g., 1_KAH) to 345 m (e.g., 4_UKU), due to variation in nearshore reef morphology (Table 2.2).

Benthic community structure was assessed using the photoquad method (Fig. 2.11). Overall, benthic communities were dominated by filamentous turf algae (61%), followed by corals (16%), and crustose coralline algae, or CCA (13%). Fleshy macroalgae were generally rare (0.1-4%) except at 5_MAA where they covered 15% of reef surface (mostly *Melanamasia sp*.). Mean coral cover ranged from approximately 4-5% at 3 sites (2_PUA, 8_LAP, and 6_KAL); 14% at 2 sites (4_UKU and 5_MAA); and 26-32% at 3 sites (3_OLO, 1_KAH, and 7_KEA). CCA cover also varied, with low values (3-5%) at 4 sites (6_KAL, 2_PUA, 3_OLO, 4_UKU), mid values at 11% at 2 sites (1_KAH and 5_MAA) and highest values at 7_KEA (22%) and 8_LAP (41%).

Calcification/Accretion Units (CAUs)

Twenty calcification/accretion units, or CAUs, (Price et al. 2012) were used to evaluate reef development and net $CaCO_3$ accretion rates at each of the eight study sites on leeward Maui (Fig. 2.1b). CAUs were constructed of a 20 cm x 0.64 cm piece of stainless steel all-thread with two settlement tiles constructed of 10 x 10 x 0.64-cm polyvinyl chloride (PVC) plastic sheets separated by a 1.3 cm nylon spacer and secured with stainless steel nuts and lock-washers. Such PVC tiles have been used successfully to study coral recruitment and benthic communities around the globe (Price 2010, Price et al. 2012) and communities on PVC tiles have been shown to be statistically indistinguishable from those on natural substrates, though appear slightly more resistant to grazing (Hixon & Brostoff 1985). Though results from different tile types may differ among studies, these units remain "effective for spatio-temporal contrasts of relative rates of recruitment when deployed in a consistent manner" (Edmunds et al. 2010). CAU tiles were installed *in situ* by hammering them approximately 6 cm into the reef and cementing the base with ZSPAR® 2-part marine epoxy. Tiles were installed in July 2011, and placed haphazardly (spaced 0.5-1 m apart) on turf-covered pavement among fringing mixed coral reef communities at 2-3 m depth.

Half (10) of all CAUs at each site were enclosed in cages that protected the tiles from consumers (herbivores and carnivores) larger than 1.25 cm in their widest dimension (Fig. 2.1c). Cages were constructed of a 12 x 12 x 20-cm stainless steel wire frame covered in clear plastic mesh (hole size, 1.25 cm). The wire frame was welded to two central stainless 2.5 cm washers at the top and bottom, through which, the all-thread was fed and secured using stainless steel nuts and lock-washers. Tiles were separated from cages (top and bottom) by 1.3 and 1.9-cm nylon spacers, respectively. All cages were thoroughly cleaned (weekly) and repaired (as necessary) during quarterly visits to the field site. Cages did not have any measurable effect on temperature or flow, thought light was reduced on average by 15% (Fig. 2.12). The mesh, however, did experience fouling in between cleaning/replacement events; therefore, it is possible that such fouling influenced development on the tiles (e.g., via light and flow reduction, and enhanced sediment & algal retention). However, given (1) the cage design and cleaning schedule, (2) the large variation among sites in macroalgal and coral recruitment onto caged tiles, (3) the long-term persistence and growth of individual corals and algal thalli in cages, and (4) the similarity in maximum values (e.g., macroalgal biomass and coral recruitment) between caged and open tiles at certain sites, we believe such artifacts were likely small relative to the influence of ecological processes.

Environmental Characteristics

The environmental conditions at each site were characterized by monitoring a suite of factors known to influence the development of benthic coral reef communities and be strongly altered by human activities: (a) herbivore biomass, (b), nutrient concentrations (NO_3+NO_2, NH_4, and PO_4), and (c) sediment exposure. Herbivores, nutrients and sediments were assessed at all 8 sites on 4, 21, and 12 separate weeks, respectively, in 2011-2013 (Table 2.3).

Herbivore biomass (HRB, fishes and echinoids)

Herbivorous fish and echinoid communities were surveyed using standard visual belt-transect methods. First, a 25 m transect was laid 5-m shoreward of the CAU array, parallel to shore. After 5 minutes, the fish observer swam the transect (transect 1, replicate 1) and recorded the identity (species), sizes (total length, cm) and density (no./m^2) of all fishes within a 4 m swath of the transect line (area = 100 m^2). The echinoid observer followed 5 m behind the fish observer, counting all large echinoids (e.g., *Echinothrix calamaris*, *E. diadema*, *Heterocentrotus mammillatus*, and *Tripneustes* *gratilla*) within a 2 m swath of the first 15 m of the transect (A = 30 m^2). After 5 min., the fish survey was repeated in the reverse direction (transect 1, replicate 2) and all small echinoids (e.g., *Echinometra matthei, E. oblonga*, and *Echinostrephus aciculata*) were counted within a 1 m swath of the original first 15 m. of the transect (A = 15 m^2). A second transect was then laid 5 m seaward of the CAU array, parallel to shore, and two additional replicate fish and echinoid transects were completed. The biomass of each fish was calculated using taxon-specific allometric length-weight functions from FishBase (www.fishbase.org) and other published sources (Friedlander et al. 2007, Sandin et al. 2008) (Table 2.4) and biomass of echinoid communities were estimated using mean taxon-specific sizes reported by a previous study in the region (Lewis and Smith *in review*, Table 2.5). Herbivore biomass (g m^{-2}) was calculated by summing the biomass of all herbivorous taxa in a given survey transect and dividing by the surveyed area.

Nutrient concentrations

Dissolved inorganic nutrient concentrations (μM) were measured in triplicate during weekly samplings at each of the 8 study sites. Three separate water samples were collected at each site using individual 60-ml plastic syringes. At the site, each syringe was rinsed three times with sample water and a final sample drawn from within 1 m of the seafloor above the tile array. Samples (45 ml) were then filtered through Whatman #2 GF/F glass fiber filters, placed into triplicate-rinsed 50-ml Falcon tubes, and stored on ice. Samples were frozen upon return to the lab and shipped on dry ice to the Marine Science Institute (MSI, UC Santa Barbara, Santa Barbara, CA) where nutrient concentrations (NO_3+NO_2, NH_4, and PO_4) were analyzed with a QuikChem 8000 Flow

Injection Analyzer by Lachat Instruments Div. (Zellweger Analytics, Inc.). Detection limits for this method were 0.1 μM for NH_3 and PO_4, and 0.2 μM for NO_3+NO_2. Water samples were collected 21 times per site during the study.

Sediment Exposure and Characteristics

Sediment accumulation rates (SAR, g $cm^{-2}d^{-1}$) (Storlazzi et al. 2011) were measured at each site using sediment traps constructed of 30 (height) x 3.8 (diameter)-cm PVC tubes (area of opening = 11.2 cm^2). We chose the SAR metric of sediment exposure over others, such as the total concentration of suspended solids (TSS) or turbidity units (e.g., NTU), because these other metrics (1) provide only instantaneous snapshots of exposure and (2) focus on fine-grained suspended sediments that influence water column properties. In contrast, SAR provides a time-integrated (6-8 days in our study) measure of exposure to heavier sediments that rapidly sink and directly smother benthic organisms, and inhibit their attachment to permanent substrates. Sediment accumulation traps were open-top, sealed-bottom, and anchored vertically by attaching them to embedded rebar posts using nylon ties. Traps were deployed 12 times during the study for approximately 1 week each. At the end of each deployment, sediments were collected and dried at 60 °C for 48 h, or until constant mass. Sediment accumulation rates were calculated as the dry mass of sediment accumulated in the tube, per area, per day. In the lab, sediment samples were homogenized and two 2-15 g subsamples (depending on the amount of material available) collected. One subsample was combusted at 500 °C for 4 hours, and the change in mass (to nearest 0.01 mg) inferred as the % organic content of the sample. The second subsample was digested with 20-40 ml of 30% peroxide solution (to remove organic material and break apart clumps), and rinsed with deionized water through stacked 300 and 63 µm sieves. The three size fractions (>300, 300-63, < 63 µm) were then dried and weighed (to 0.01 mg) to compare differences in the relative contributions of different sized grains in each sample. Organic content of sediments was analyzed for samples collected at all sites during each of 3 separate weeks (6 and 23 June, and 1 Dec) in 2012. Sediment grain size fractions were assessed for samples collected at all sites during each of 2 sampling weeks (23 June and 10 August, 2012) in 2012.

Community Development

CAU tiles were collected in July, 2014, 3 years post-deployment, and several key characteristics of the attached sessile communities (macroalgae biomass, total non-calcified and calcified biomass, coral recruitment, and community structure) were evaluated to explore spatial variation and the influence of consumers on the development of these benthic communities.

Biomass accumulation on tiles (macroalgae, total non-calcified, and total calcified)

At the end of the experiment all CAUs were recovered from the field, dismantled, and all four sides of the two tiles photographed in the lab. After photographs were taken, tiles were thoroughly rinsed in fresh water and all fleshy macroalgae (> 1cm) were removed and frozen at -20 °C. Algae were later thawed, identified (to genus or functional group, Table 2.6), secondarily rinsed in fresh water, spun and blotted, weighed (wet mass, g), then dried at 60 °C (to constant mass, usually 48 h) and re-weighed (dry mass, g). The net accumulation of biomass of calcified and non-calcified material on tiles were measured followings previous methods used for CAUs (Price et al. 2012). After thorough rinsing and removal of macroalgae and mobile fauna, CAU tiles were dried (60 °C for 48 h or constant mass) and weighed whole (W = calcium carbonate - macroalgae + tile) to the nearest 0.0001g, and subsequently decalcified in 5% hydrocholoric acid (HCl) until all calcium carbonate was removed. All remaining de-calcified material was then scraped from the tile with a razor blade and collected on an 11 cm Whatman No. 1 pre-weighed paper filter, which was then dried, reweighed and the filter mass subtracted to attain the de-calcified biomass on the CAU (dC). Total non-calcified (fleshy) mass was then calculated by adding total dry macroalgae biomass to dC. The scraped (bare) tile was then dried and weighed again (T). Calcified biomass (C) was then measured by subtracting the dry masses of fleshy material and the bare tile from that of the whole intact CAU (C = W - dC - T).

Community structure and coral recruitment

To assess differences among sites and treatments in the structure of attached sessile organisms and substrates on exposed CAU surfaces, we conducted image analysis on photos of all CAU units using the program Photogrid®. Fifty stratified random points (circles) were assigned to each image, and the substrate or organism occupying each point was identified and assigned to one of the following functional groups for analysis: inorganic (bare, frame, sand, carbonate), algae (calcified crust, fleshy crust, coralline crust, fleshy macroalgae, fleshy turf), invertebrates (coral, other calcified invertebrate, fleshy invertebrate), and other. The total number of coral recruits per CAU (area = 425 cm^2) were quantified by summing the number of individual juvenile corals visible in photographs on all four tile surfaces.

Statistical Analyses

Differences in each of the three environmental characteristics were compared among sites (k=8, fixed) by mixed-effects analysis of variance (ANOVA) with sampling week and an interaction term included as random variables. Differences in community metrics on CAU tiles were compared among sites (k=8, fixed), caging treatments (j =2, fixed), and their interaction by ANOVA. Relationships between CAU mass metrics and environmental characteristics were examined by Pearson correlation. Effect size of consumers on each metric (calculated as the log of the ratio of values on open:caged tiles, "log-response ratio") were compared using 95% confidence intervals, and relationships with environmental characteristics examined by Pearson correlation. Log response ratios provide proportional effect sizes for meaningful comparisons. For data with zero values or disordinal changes, absolute change was examined (e.g., or % cover). Assumptions of parametric statistics were evaluated using plots of distributions and residuals, and appropriate transformations of the data were employed to meet statistical assumptions when necessary (Table 2.1) (Underwood 1997). Due to zero-inflation, Poisson regression was used to compare differences in coral recruitment among sites, treatments and their interaction. All analyses above were conducted using JMP 12.0.1. Permutation-based multivariate analysis of variance (PERMANOVA) based on Bray-Curtis distances was used to test for differences in community structure on the surfaces of CAU tiles as a function of site, treatment and their interaction. Multivariate Bray-Curtis distances among individual CAUs, sites, and treatments were then visualized via a 2-dimentional projection using non-metric multidimensional scaling (nMDS) ordination. Non-parametric analyses were conducted using PrimerE v.6 (Anderson 2001).

RESULTS

Environment

Herbivore Biomass

Herbivore biomass was dominated by echinoids and varied significantly among sites (Fig. 2.2a-c, Table 2.1). Mean ± SE biomass of herbivorous fishes was low across all sites, ranging from 0.12 ± 0.01 g m^{-2} (6_KAL) to 4.4 ± 0.3 g m^{-2} (8_LAP) (Fig. 2.2a). Surgeonfishes (family Acanthuridae) were the most abundant herbivorous fishes across all sites, with brown surgeonfish (*Acanthurus nigrofuscus*), alone, contributing > 80% to total herbivorous fish biomass, followed by yellow tangs (*Zebrasoma flavescens*) and palenose parrotfish (*Scarus psittacus*) (Table 2.4). In contrast, mean ± SE biomass of herbivorous echinoids ranged from 21.7 ± 9.0 (6_KAL) to 614.9 ± 86.6 g m^{-2} (8_LAP) (Fig. 2.2b), with the rock boring *Echinometra matthaei* contributing > 85% to total herbivorous echinoid biomass, followed by the slate pencil urchin (*Heterocentrotus mammillatus*) and the blue-banded urchin (*Echinothrix diadema*) (Table 2.5). Thus total herbivore biomass (fishes + echinoids) was dominated (>99%) by echinoid biomass and ranged from 21.8 ± 9.0 g m^{-2} (6_KAL) to 619.2 ± 86.6 g m^{-2} (8_LAP), and differed significantly among sites (Fig. 2.2c, Table 2.1).

Nutrients

Nutrient concentrations were generally within normal ranges for coral reef ecosystems and varied significantly among sites (Fig. 2.2d-f, Table 2.1). Mean ± SE nitrate plus nitrite (NO_x) concentrations ranged from 0.21 ± 0.02 µM (2_PUA) to 0.68 ± 0.07 µM (7_KEA) and ammonium ranged from 0.19 ± 0.02 µM (2_PUA) to 0.37 ± 0.03 µM (5_MAA) (Fig. 2.2d-e, respectively). Ammonium and nitrate + nitrite were strongly correlated across sites, $r(6) = 0.752$, $p = 0.03$, and were thus combined into a single metric of dissolved inorganic nitrate (DIN). Mean ± SE DIN ranged from 0.40 ± 0.03 µM (2_PUA) to 1.03 ± 0.09 µM (5_MAA) and differed significantly among sites (Fig. 2.2f, Table 2.1). Mean ± SE phosphate concentrations (not shown) were all low (below or near detection limits of 0.1 µM), ranging from 0.100 ± 0.01 µM (2_PUA) to 0.139 ± 0.01 µM (1_KAH).

Sediments

Sediment exposure and characteristics varied greatly among sites (Fig. 2.2g-i, Table 2.1) and, given the arid nature of the region and minimal precipitation observed during the study period, these values reflected the resuspension and transport of existing sediment pools (versus new sediment inputs from terrestrial runoff) (Storlazzi et al. 2004). Mean ± SE organic content ranged from 3.5 ± 0.2% (7_KEA) to 10.7 ± 2.7% (5_MAA) and silt (vs. fine and course sand) content ranged from 1.6 ± 0.1% (7_KEA) to 19.9 ± 7.0% (5_MAA) (Fig. 2.2g-h). Silt and organic content were highest only at sites with lower total sediment accumulation rates, indicating that high sediment loads consisted primarily of fine- and course-grain sand. Mean ± SE total sediment accumulation rates ranged from 0.061 ± 0.019 g $cm^{-2}d^{-1}$ (5_MAA) to 2.835 ± 0.495 g $cm^{-2}d^{-1}$ (2_PUA) and varied significantly among sites (Fig. 2.2i, Table 2.1).

Community Development

Macroalgae biomass

Total macroalgae (> 1cm) biomass varied significantly among sites and caging treatment, and a significant ordinal interaction indicated that the magnitude of consumer effects varied significantly among sites (Fig. 2.3a, Table 2.1). Mean ± SE values varied from 0.007 ± 0.003 g (8_LAP) to 1.364 ± 0.349 g (5_MAA) on open tiles, and 0.132 ± 0.058 g (KAL) to 1.824 ± 0.554 g (1_KAH) when consumers were excluded (Fig. 2.3a). Macroalgal biomass was dominated by red algae (83%), followed by mixed filaments (8%), brown algae (7%), and green algae (1.5%). Red algae within the order ceramiales were most abundant (67% of all algae), with the perennial *Amansia glomerata* (47.9%%) and *Laurencia spp.* (15.49%) the two most abundant groups (Table 2.6).

Macroalgae biomass on tiles (caged and open) did not correlate significantly with ambient herbivore biomass (HRB), nutrients (DIN), or sediments (SAR) (Fig. 2.4a-c). Treatment (consumer) effect sizes on macroalgae biomass (log-response ratios between open and caged tiles) also differed significantly among sites (Fig. 2.5a), ranging from 0-5600% (mean = 400%) greater macroalgae biomass on open vs. caged tiles (though not significant at 3_OLO and 5_MAA). In contrast to raw macroalgae biomass, consumer effect size on macroalgal biomass correlated significantly with herbivore biomass ($r = -0.91$, $p = 0.0017$), but not with nutrients or sediments (Fig. 2.6a-c).

Non-calcified ("fleshy") biomass

Total non-calcified biomass on each CAU tile (total area = 425 cm^2) served as a measure of the net accumulation of non-calcified ("fleshy") biological material on CAUs over the experimental period. Non-calcified biomass varied significantly among sites and with caging treatment, and a significant ordinal interaction indicated that the magnitude of consumer effects varied significantly among sites (Fig. 2.3b, Table 2.1). Mean ± SE values varied from 2.3 ± 0.2 g (8_LAP) to 10.5 ± 0.9 g (2_PUA) on open tiles, and 1.6 ± 0.2 g (8_LAP) to 6.8 ± 0.6 g (2_PUA) g when consumers were excluded.

Non-calcified mass correlated significantly with both nutrients (DIN) and sediments (SAR), but not herbivore biomass (HRB) (Fig. 2.4d-f). Non-calcified mass decreased linearly with DIN for both open ($r = -0.815$, $p = 0.017$) and caged ($r = -0.748$, $p = 0.033$) CAU tiles. In contrast, non-calcified mass increased with SAR for open ($r = 0.860$, $p = 0.006$) and caged ($r = 0.768$, $p = 0.026$) CAUs. Magnitudes of treatment (consumer) effects differed significantly among sites, with most sites exhibiting 30-60% (mean = 38%) greater fleshy biomass on open vs. caged tiles (though not significant at 7_KEA) (Fig. 2.5b). Caging effects on non-calcified biomass did not correlate with any measured environmental parameters (Fig. 2.6d-f).

Calcified biomass

Total calcified biomass on each CAU tile (total area = 425 cm^2) was measured as an estimate of the net accretion of biogenic calcium carbonate over the experimental period. Calcified biomass varied significantly among sites and caging treatment, and a significant interaction indicated that the magnitude of consumer effects varied significantly among sites (Fig. 2.3c, Table 2.1). Differences among treatments, however, were disordinal among sites, therefore requiring further examination. Mean ± SE values varied from 20.5 ± 2.0 g (3_OLO) to 118.0 ± 16.4 g (6_KAL) on open tiles, and 23.9 ± 1.9 g (3_OLO) to 61.5 ± 9.7 g (6_KAL) when consumers were excluded.

No significant correlations between calcified biomass and ambient herbivore biomass (HRB), nutrients (DIN) or sediments (SAR) were observed (Fig. 2.4g-i). Effects of consumers on calcified biomass differed significantly among sites (Fig. 2.5c), with most sites exhibiting 30-60% greater calcified mass on open vs. caged tiles. However, tiles at 3_OLO (sig.) and 4_UKU (not sig.) exhibited the opposite trend (greater calcified biomass inside cages). Consumer effects on calcified biomass did not correlate with any measured environmental parameters (Fig. 2.6g-i). Interestingly, a factorial general linear model including site, log(calcified biomass), and their interaction, explained 79% of the variation in log(decalcified biomass), with a significant interaction term (Fig. 2.13). This indicated that at several sites, calcified organisms contributed significantly to non-calcified biomass, but that relationships also varied significantly among sites.

CAU surfaces

The composition (cover) of sessile organisms and substrates on CAU surfaces differed significantly among sites, treatments, and their interaction (Fig. 2.7, Table 2.1). Percent cover (mean ± SE) on open CAUs was dominated by fleshy filamentous turf algae (70.9 ± 5.5%) and CCA (16.3 ± 5.3%) with little to no macroalgae (0.7 ± 0.4%). Percent cover on caged CAUs differed markedly from open CAUs, with 50% less fleshy turf (33.3 ± 5.3%) than on open tiles and much higher macroalgae cover (25.3 ± 6%), similar in scale to turf. Interestingly, CCA cover (13.6 ± 2.6%) was similar on surfaces of open and caged tiles.

The magnitude of consumer effects on CAU surface communities varied significantly among sites (Fig. 2.8). Overall, cover of macroalgae was significantly reduced by consumers (25% on average); however varied from 0 (8_LAP) to 48% (2_PUA) (Fig. 2.8a). No overall effect of consumers was observed on the abundance of CCA (Fig. 2.8b). Generally, the effects of consumers on CCA cover varied among individual sites with some trending positive and some negative, though non-significant at all but 2 sites: 2_PAU (-4%) and 7_KEA (+26%). The largest effect consumers exerted on CAU surfaces was on filamentous turf algae, where 7 out of 8 sites experienced significant increases in turf cover due to consumer access (Fig. 2.8c), likely due to the reduction of macroalgal cover (Fig. 2.7).

We used non-metric multidimensional scaling ordination (Fig. 2.9) to visualize the influence of functional groups on multivariate Bray-Curtis distances (BCD) among (a) individual CAUs, (b)treatments, and (c-d) sites. Stress for this ordination was 0.11, indicating that the 2-D projection was a reasonable representation of actual distances in multidimensional space. Fleshy turf, macroalgae, and CCA contributed most to total 2-D dispersion (Fig. 2.9a). Open CAUs were generally dominated by turf algae or CCA, whereas those protected from consumers demonstrated much greater diversity of community types, many of which (though not all) exhibited elevated macroalgal cover (Fig. 2.9b).

Within-site variation for caged CAUs was large, with substantial differences in dispersion and structure both within and among sites. For example, site 1_KAH showed very high levels of macroalgal cover in 4out of 8 caged tiles, yet the other four tiles occupied nearly every other possible community state (Fig. 2.9c). In contrast, caged CAUs at site 6_KAL showed little dispersion and appeared similar to open communities. Consumers greatly reduced the diversity of community types on open tiles, with nearly all communities falling within a one-dimensional turf-CCA axis (Fig. 2.9d); however, individual CAUs within a site could be observed in either community state (e.g., at 1_KAH, 5_MAA, and 7_KEA). Consumer exclosure, therefore, caused many tiles to move along the turf-macroalgae (vs. turf-cca) axis, but also opened up the potential for many other community states; all of which appeared to be inhibited by consumers (Fig. 2.9b).

Coral Recruitment

Coral recruitment varied greatly among sites and individual CAU tiles, with many CAUs lacking any recruits (zero-inflated), and we found no evidence for an effect of herbivore exclusion (Fig. 2.10a, Table 2.1). Differences among sites, however, were significant. The median (and IQR) of coral recruits per CAU tile ranged from 0 (0) (2_PUA) to 1.5 (5.25) (3_OLO) for open tiles and 0 (0) (2_PUA and 7_KEA) to 1 (4.5) (3_OLO) when consumers were excluded (Fig. 2.10). Maximum values, however, were much more variable among sites, ranging from 1 (several sites) to 8 (5_MAA) on open tiles and 0 (7_KEA) to 9 (3_OLO) on caged tiles. Coral recruitment did not correlate with DIN or HRB, but decreased exponentially as a function of SAR (Fig. 2.10b); and though no significant effect of consumers was observed overall, the single site with the lowest SAR (5_MAA) experienced 400% greater total recruitment (summed among all

CAUs) on open vs. caged tiles (Fig. 2.10c), suggesting that the effects of consumers on coral recruits may only be detectible when stress from sediment exposure near or below threshold values (e.g., 0.01 g $cm^{-2}d^{-1}$).

DISCUSSION

Using a comparative experimental design, we demonstrated order-of-magnitude differences in environmental characteristics, ecological processes, and benthic community development on shallow coral reefs across 60 km of Maui's leeward coastline. Herbivorous fishes were relatively absent from the system, with echinoids (specifically *E. matthaei*) composing greater than 99% of total herbivore biomass. First, total herbivore biomass did not correlate with macroalgal biomass on CAUs (caged or open) across sites. However, experimental manipulation of consumer access to benthic substrates (CAU tiles) revealed strong negative effects of consumers on macroalgae biomass, and the magnitude of consumer effects varied among sites and correlated negatively (r=-0.91) with herbivore biomass. The lack of spatial correlation between herbivore biomass and macroalgal biomass on CAUs, but strong relationship with treatment effect size (from experimental manipulations), emphasizes the value of manipulative (vs. observational) studies for understanding how ecological processes shape patterns in nature. Second, in contrast to herbivores and sediments, nutrient concentrations at all sites were low and did not correlate significantly with any of the ecological processes measured other than the accumulation of total non-calcified biomass for caged and uncaged treatments (however, these may have been influenced by trapped non-calcareous sediments). Third, many (but not all) of these reefs appeared to be sediment-stressed due to the regular resuspension and deposition of existing sediment pools, and sediment stress appeared to be the strongest driver of coral recruitment in these shallow systems. Further, there is some evidence that consumers (and their community structure) may also be important for coral recruitment at sites with lower sediment stress. In sum, using standardized and repeatable experiments across 60 km of coastline on Maui's coral reefs we show considerable variation in the factors that influence community structure. Explicit consideration of spatial variation is thus needed to ensure the success of specific, local conservation actions (Roff & Mumby 2012).

Herbivore communities

The biomass of herbivorous fishes was low at all our sites, with herbivore biomass being dominated by echinoids by several orders of magnitude (Fig. 2.2c). Mean biomass of herbivorous fishes at our sites (2.2 g m^{-2}) was an order of magnitude below the global mean (20 g m^{-2}) for fisheries-accessible (vs. inaccessible or protected) coral reefs (Edwards et al. 2014), and dominated by surgeonfishes (family Acanthuridae). However our data came from shallow, nearshore coral reefs whereas other estimates are often from deeper, forereef ecosystems. Shallow coral reefs in Kenya, for example, exhibit similar values of herbivorous fish biomass on heavily fished reefs (0-2 g m^{-2}), and maximal mean values of 25 g m^{-2} at sites not impacted by fishing (Humphries et al. 2015, McClanahan & Muthiga 2016), roughly half the global mean of 40 g m^{-2} on unfished coral reefs (Edwards et al. 2014). Given previous reports of strong impacts of fishing on fish biomass throughout the Hawaiian islands, including Maui (Friedlander et al. 2007), our regular personal observations of spear-fishers in shallow waters at all study sites, and the low biomass of herbivorous fishes and high biomass of herbivorous echinoids at all sites (similar to overfished Kenyan reefs); Maui's shallow nearshore coral reefs appear to be impacted by fishing throughout the study region.

In contrast to fishes, mean echinoid biomass was high (253 g m^{-2}) at all our sites and similar to values observed on shallow reefs in Kenya, where the highest echinoid biomass (and the lowest biomass of herbivorous and predatory fishes) were observed on heavily-fished reefs (Humphries et al. 2015, McClanahan & Muthiga 2016). Similar, strongly-negative correlations of fish and echinoid (*Diadema antillarum*) biomass have also been observed in the Caribbean, where locally high echinoid:fish ratios appeared to be driven by fishing (i.e., protection from fishing), and high region-wide densities of echinoids inferred as an indicator of wide-spread and long-term fishing impacts throughout the Carribbean (Hay 1984). On Kenyan reefs, echinoid mass correlated strongly and negatively with the biomass of predatory triggerfishes (family: Balistidae) that preferentially consume echinoids (McClanahan & Shafir 1990). Furthermore, herbivorous fishes and echinoids (specifically *E. matthaei*) appeared to exert different effects on coral recruits and benthic communities, with fishes benefiting, and echinoids harming, young corals and other calcifiers such as CCA (O'Leary & McClanahan 2010, O'Leary et al. 2013). Therefore, the overfishing of predators in Kenya (and throughout the Indian Ocean) has resulted in a wide-spread trophic cascade where fishing reduces the biomass of important predators (e.g., *Balistapus undulata*, "red-line triggerfish"), resulting in a shift from herbivorous fish to echinoid (primarily *E. matthaei*) dominance that ultimate leads to the degradation of coral reef communities (McClanahan & Shafir

1990, O'Leary & McClanahan 2010, Humphries et al. 2015, McClanahan & Muthiga 2016).

Interestingly, the highest values of herbivore biomass (dominated by the echinoid *E. mattaei*) at site 8_LAP resulted in the strongest regulation of macroalgae (Fig. 2.6a), but did not correspond with increased coral recruitment (Fig. 2.10a), despite this site exhibiting relatively low sediment exposure (Fig. 2.2i). For example, we observed the highest coral recruitment at sites 3_OLO and 8_MAA (Fig. 2.10a), both of which exhibited similar sediment exposure, but had 75% lower herbivore biomass (i.e., communities less-dominated by *E. mattaei*). This pattern at 8_LAP (high herbivore biomass, low macroalgal biomass, low sediment; and yet, low coral recruitment) might be explained by the potential for *E. matthaei* to exert negative direct effects (e.g., mechanical damage) that outweigh their positive indirect effects (e.g., algal consumption) on corals and other calcifiers (Korzen et al. 2011, O'Leary et al. 2013). Whether or not variation in echinoid biomass in Maui appears to be driven by the biomass of their predators (as in Kenya), remains to be explored.

Nutrients

We conducted this study on shallow (2-3 m), nearshore (< 500 m from coast) coral reef sites where nutrient inputs were most likely to have the strongest effects. Given the strong influence nutrient enrichment can have on reef communities (Smith et al. 1981, Lapointe 1997, Fabricius et al. 2005, Smith et al. 2010) and significant evidence of anthropogenic nutrient loading into Maui's coastal waters (Dailer et al. 2010, Dailer et al. 2012a); we predicted that we would detect spatially variable but generally high levels of DIN around Maui’s reefs and that this would relate to community development on CAU tiles. In contrast, DIN concentrations were generally low (< 1 µM) and within normal ranges for unimpacted coral reefs (Lapointe 1997, Leichter et al. 2003, Knee et al. 2010). Further, DIN did not correspond with proximity to known sources of nutrient inputs or with variation in community development on CAU tiles. Based upon our limited point sample measurements, nutrient concentrations were lower than expected and appeared to have limited influence (relative to other factors) on early successional development on Maui's nearshore reefs (Szmant 2002). It is important to note, however, that we did not perform an exhaustive assessment of Maui’s nearshore nutrient dynamics.

Nutrient concentrations above reefs and macroalgae biomass on caged CAUs at sites directly adjacent to the 2 state-operated sewage injection wells (1_KAH and 6_KAL) on leeward Maui were not elevated relative to other sites (Fig. 2.2d-f, 3a). This was surprising given the high inputs (approximately 6 million gallons per day from these 2 wells, combined) of nutrient-laden groundwater that are known to elevate gross production and nitrogen content (and isotopic signatures) of fleshy macroalgae in the region and abroad (Lapointe 1997, Fabricius et al. 2005, Smith et al. 2005, Dailer et al. 2010, Dailer et al. 2012a, Dailer et al. 2012b). Though previous studies in Maui have clearly demonstrated anthropogenic nitrogen loading, biological uptake of this nitrogen, and association of algal blooms adjacent to sewage injection wells (Smith et al. 2005, Dailer et al. 2010, Dailer et al. 2012a); direct observations of elevated nutrient concentrations have occurred primarily in very shallow (<1 m) and nearshore (<50 m) reef flats and pore water extracted from sediments, whereas water column DIN concentrations over nearby coral reef communities (2-5 m) typically remained within normal levels for coral reefs (Smith et al. 2005), as observed during our study. This could be due to (a) rapid uptake of nutrients (e.g., by macro-, turf-, and micro-algae) within the reef, sand and benthic boundary layers; diffuse percolation, mixing, and dilution (Smith et al. 2005), and rapid transport away from study sites due to local oceanography (Storlazzi et al. 2006). Mean DIN concentrations on shallow coral reefs with degraded (eutrophied) water quality in the Caribbean (Lapointe 1997) and Hawaii (Smith et al. 1981) are, on average, approximately 5-fold higher (3-5 µM) than the highest mean concentrations observed in our study; and many coral reefs with stable, high coral cover exist at mean nitrate (alone) levels above 2 µM (Kleypas et al. 1999). Additional anthropogenic sources of nitrogen into leeward Maui include fertilizer and ash from agriculture (e.g. sugar cane) and large numbers of smaller injection wells and cesspools (Dailer et al. 2012a), but these did not appear to increase mean nearshore nutrient concentrations beyond normal levels at our study sites. Though non-calcified biomass correlated negatively with variation in DIN (Fig. 2.4e), we believe these results require further analysis (see below).

Though mean nutrient concentrations throughout the study region were low, it is possible that stochastic pulses of nutrient inputs (e.g., due to rain and runoff, surface wind and waves, and upwelling or internal waves) may result in rapid, short-lived, but important sources of nutrients that enhance productivity, but might have been missed by our discrete sampling schedule (Leichter et al. 2003). Each of the 21 sampling time points at each site only represented a snapshot in time that may have not reflected true fluxes of nutrients into each reef system. Supporting this notion were occasional observations of elevated nutrients (DIN = 1.5-2 µM) at sites 5_MAA, 6_KAL, and

8_LAP. Overall, however, sampling was well-stratified among seasons and mean values remained low compared to those observed in other reef systems using similar techniques.

Sediments

Sediments are major drivers of the distribution of coral reefs (Richmond 1993, Fabricius 2005, Jokiel et al. 2014); therefore, specific thresholds for sediment exposure have been suggested as strong limits to the settlement and growth of corals and other benthic organisms (Rogers 1990, Jokiel et al. 2014). All the nearshore coral reefs we studied in Maui were well above the 0.01 g cm^{-2} d^{-1} sediment accumulation rate (SAR) threshold previously established (Rogers 1990), and 4 of the sites (2_PUA, 4_UKU, 6_KAL, 7_KEA) were several orders of magnitude higher than this value (Fig. 2.2i, Fig. 2.10b-c), indicative of significant sediment-stress on Maui's shallow leeward reefs.

Similar patterns of sediment stress have been described for shallow reefs on the neighboring island of Molokai, Hawaii. These shallow reefs often experience suspended sediment concentrations (SSCs) above levels where corals can settle and grow (e.g., >10 mg l^{-1}) (Jokiel et al. 2014). Most chronic exposure of corals to sediments in this system is due to resuspension and transport of existing sediment pools which is driven largely by natural phenomena such as strong trade-winds, tides, and ocean waves; whereas terrestrial runoff from punctuated storm events is generally acute and short-lived (though can be severe) in these arid, leeward habitats (Storlazzi et al. 2004, DeMartini et al. 2013). Harmful, chronic exposure of nearshore corals to sediments by resuspension is exacerbated by coastal development that increases sediment deposition onto reefs at faster rates than sediments can be removed by natural processes (Grigg 1995, Ogston et al. 2004, Storlazzi et al. 2004, Presto et al. 2006, Storlazzi et al. 2009, Prouty et al. 2014, Stender et al. 2014).

Interestingly, the more harmful fine-grained sediments (e.g., silt) and organic content (Fig. 2.2g-h) (Storlazzi et al. 2015) made up a relatively small fraction of the sediments that we collected, and were relatively more abundant at sites where sediment accumulations rates were lower (e.g., sites 3_OLO, 5_MAA, 8_LAP). This is likely due to both (1) large movements of courser-grained sand through the system and (2) standard biases in sediment trap devices, especially on shallow reefs where water flow is rapid and turbulent (Storlazzi et al. 2011). While exposure to course sediments is best quantified using sediment traps (as used in this study) that select for rapidly sinking larger sediment grain sizes; distributions of finer suspended sediments are better-quantified via measures of suspended sediment concentrations (SSC) or their effects on light (i.e., turbidity) (Storlazzi et al. 2011, Jokiel et al. 2014). Coral recruitment, however, was often higher at sites with higher relative silt and organic content, likely because these values were negatively correlated with bulk sediment exposure. Furthermore, certain corals and coral communities have been shown to be able to adapt to turbid conditions by feeding on suspended particles (Anthony & Fabricius 2000), but are likely not as resilient to burial by large amounts of course sediments. We concluded, therefore, that the large amounts of course-grained sediments moving through our study system appeared to exert the strongest influence on coral recruitment, likely via deposition, smothering, and impaired attachment (Fig. 2.10b).

Though we only sampled sediments at each site on 12 occasions, each of these collection events were an integration of 6-8 days. Therefore, our sediment accumulation rates represent over 80 total days of sediment accumulation and were stratified among seasons, though focused in summer months. Though large variation among seasons was observed, we believe our integrated values provided excellent characterizations of relative sediment exposures at each site, including many days were anomalous or pulse events may have contributed to observed differences in mean accumulation rates.

Macroalgae biomass

The biomass of macroalgae did not vary as a function of herbivore biomass, nutrients, or sediment exposure (Fig. 2.4a-c). This was surprising given the strong effects each is known to exert on algal communities. For example, numerous studies have demonstrated strong regulation of macroalgae by herbivores, nutrients and their interaction (Sammarco 1982, Burkepile 2006, Hughes et al. 2007, Burkepile & Hay 2008, Smith et al. 2010), and sediments can limit both production and community structure of macroalgae (Eriksson & Johansson 2005). Nutrient concentrations (as measured) were low among all sites; however, variation among sites in herbivore biomass and sediment exposure were large relative to ambient ranges reported in the literature. The low biomass of macroalgae at site 6_KAL, in particular, was surprising. This site (1) existed adjacent to a sewage injection well known to discharge nutrients into the region and (2) exhibited near-zero herbivore biomass (both fishes and echinoids). Though highly sedimented, it exhibited much lower algal biomass than our even more-sedimented site 2_PUA which also exhibited 50% lower nutrient concentrations. The mechanisms maintaining algal biomass at low levels at site 6_KAL remain a mystery, though some reports suggest that coastal herbicide use could lead to impairment of production by tropical marine macrophytes (e.g., *Ulva sp.* and *Pterocladiella sp.*; both highly sensitive to commonly-used glyphosate herbicides) that are abundant on Hawaii's coral reefs (Kittle & McDermid 2016). Interestingly, removing this odd outlier (6_KAL) would result in a strong negative relationship between herbivore and macroalgal biomass across all other sites as we would predict based on the literature (Fig. 2.4a).

While there was no significant spatial correlation between herbivore and macroalgal biomass, the effect size of consumers revealed a strong, negative correlation between herbivore biomass and the difference in macroalgal biomass between caged and open treatments. Thus the magnitude of the response of macroalgae to caging was strongly correlated with herbivore biomass across our study sites. This finding suggests that experimental assessments of "algal growth potential" in the presence and absence of consumers is likely a more reliable indicator of consumer effects rather than simple observational studies examining correlations (Williams & Polunin 2001).

Though macroalgal biomass and percent cover were only examined, here, upon completion of the experiment, cover on surfaces of tiles was assessed regularly during site visits for environmental data collection and experimental maintenance throughout the 3-year experiment. Initial colonizing communities included fine algal turfs and delicate macroalgae; however, after 3 months communities appeared to stabilize and remained relatively constant, with slow successional changes throughout the remaining years of the experiment. For example, perennial macroalgae (e.g., *Amansia sp*., *Chondrocanthus sp*., *Turbinaria sp*., *Codium sp*.) appeared to stabilized and persist across seasons and years. Coral recruits were also observed on tiles within year 1, and persisted through the end of the experiment. Therefore, we believe the final data presented in this study reflect the long-term, stable successional state of benthic communities on tile surfaces, and not ephemeral communities or blooming taxa that might be aliased due to sampling dates.

Non-calcified ("fleshy") biomass

The accumulation of biomass in coral reefs is an important metric affecting reef dynamics and coral recruitment (Birkeland 1977). We predicted that if herbivore biomass and nutrients varied significantly among sites and influenced macroalgal production, that macroalgal biomass on open tiles would correlate negatively with herbivore biomass, and in exclosures, would correlate positively with nutrients. Furthermore, we predicted that total non-calcified mass would mirror macroalgal biomass and that calcified mass (e.g., CCA) would increase with herbivore biomass and nutrients, both of which stimulate the growth of CCA. Given the effects of sediments on light availability and microhabitats, we predicted that sediments would have a negative effect on all three metrics (Clausing et al. 2014). None of these correlations were significant or matched our predictions, suggesting that such relationships, though important in general, were not dominating phenomena driving the accumulation of biomass at our study sites (Fig. 2.4). Only two significant correlations were observed: non-calcified mass (both caged and uncaged) appeared to decrease with increasing nutrients and increased with increasing sediment accumulation rates (Fig. 2.4e-f).

The negative correlations between nutrients and non-calcified biomass on CAUs (both caged and open) were perplexing and counter to our hypotheses (Fig. 2.4e). Based on classic theory (Littler & Littler 2006) and empirical studies in Hawaii (Smith et al. 2010), we believed that increased nutrient concentrations would lead to greater accumulation of total non-calcified biomass (from both fleshy and de-calcified calcifying organisms such as CCA). One possible explanation for this is that DIN may increase the palatability of fleshy tissues to macro- and meso-grazers, thus leading to negative relationships between nutrients and prey biomass (Boyer et al. 2004, Chan et al. 2012). This seems unlikely, however, given that macroalgal biomass did not show a similar relationship. Increases in non-calcified material at sites with higher sediment exposure could reflect enhancement of the production of suspension-feeding invertebrates (e.g., tunicates, sponges, bryozoans) via enhanced delivery of POM. Observations of dense beds of bivalves at site 6_KAL (a sediment-stressed site) may support this theory. These results may indicate variable relationships between non-calcified vs. calcified biomass (Fig. 2.13), suggesting that variation in the composition and growth forms of calcifying communities may also determine patterns of non-calcified biomass among sites and tiles. Further exploration of the inter-tile communities on CAUs may shed additional light on variation in these bulk-biomass metrics.

However, bulk biomass accumulation estimates may have been be influenced by the analytical methods utilized. Site 2_PUA exhibited high leverage in the correlations between non-calcified biomass and environmental variables (Fig. 2.4f), exhibiting both the lowest DIN and highest SAR values. Examination of stored de-calcified samples revealed that, despite thorough rinsing, sediment may have been trapped within and beneath deep layers of algal crusts and turfs at heavily-sedimented sites. Due to the potential for deep-trapping of non-calcified sediments, it appears that the CAU decalcification method (Price et al. 2012) should include quantification of ash-free dry mass prior the calculation of non-calcified mass, especially for reefs adjacent to high islands with the potential for non-calcified inorganic inputs. As a result, we concluded that further analysis of decalcified samples (e.g., ash-free-dry mass) is needed to assess the relative importance of trapped sediments to inferences regarding non-calcified biomass values and trends. Whether or not a similar correction for calcified sediments (i.e., calcified biomass values) is feasible or needed remains unclear.

Calcified biomass

Total accretion of calcium carbonate varied significantly among sites, but not among treatments (matching the results for surface CCA cover) (Fig. 2.3c), and neither biomass nor the effects of consumers correlated with any of our measured environmental characteristics (Fig. 2.4). However, consumers clearly had strong, mostly positive, effects on calcification at many sites (23% on average, up to 92% at site 7_KEA). Consumers, therefore, exerted variable effects on calcium carbonate accretion and CCA cover on CAU tiles.

Taking the length of our experiment into account, the rate of net accretion in our system was approximately 1-3 g m^{-2} d^{-1}, similar to rates (1-5 g m^{-2} d^{-1}) on CAUs deployed on forereef communities on Central Pacific atolls (Price et al. 2012). Though CCA were important autotrophic calcifiers on exposed surfaces in both studies, surface and (especially) intra-tile spaces at several sites in our study were colonized by large, sessile, and calcified filter-feeding invertebrates (e.g., vermetid snails, oysters, pen shells, and bryozoans) that likely contributed significantly to calcified biomass. The relative contributions of different calcifiers, and the factors that influence them, remain important questions for further analysis. While it is possible that cage structures, themselves, influenced calcium carbonate accretion, we find this unlikely given (1) cages had little effect on light and flow, (2) CCA was often abundant on shaded tile surfaces and (3) cages appeared to have no effect on maximum values for macroalgae biomass and coral recruitment. Macroalgae inside of cages may have contributed to reduced calcification by via competitive (or "apparently" competitive) interactions; a hypothesis that is supported by a significant, negative correlation between log(calcified biomass) and log(macroalgal biomass) among all tiles, r(144) = -0.233, P=0.0046.

Coral Recruitment

Coral recruits were comprised of species from the genera *Porites, Pocillipora*, and *Montipora*; all of which are common on Maui and throughout Hawaii (Brown 2004, DeMartini et al. 2013, Walsh et al. 2013). Coral recruitment varied significantly among sites, ranging from 0-56 individuals m^{-2}, similar to numbers observed on tiles (e.g. approximately 40 individuals m^{-2} on average) around the island of Moorea in French Polynesia (Edmunds et al. 2010), but lower than rates previously measured on tiles in nearshore habitats around Maui (Brown 2004). Given that recruitment was only examined 3-years post-deployment in our study, and that most individuals were > 1 cm in diameter, our measurements more accurately reflected the net result of multiple seasons of recruitment and mortality on the density of juvenile corals (vs. recruitment of new settlers). Recruitment to tiles can be elevated relative to natural benthos by 4-5 fold, but our results likely reflected relative patterns in nature (Penin et al. 2010).

Overall, we observed no significant effects of consumers on recruitment (Fig. 2.10a, Table 2.1). We expected coral recruitment to be elevated on open vs. caged CAUs due to reductions in algal competitors by herbivores (Hughes et al. 2007, Mumby et al. 2007), though predictions of the indirect benefits of consumers on coral recruits can be ambivalent given their potential to exert direct negative effects via consumption and mechanical damage (Korzen et al. 2011, Penin et al. 2011, O'Leary et al. 2013). The strong non-linear negative effects of sediment exposure at our study sites, however, likely overshadowed any potential effects (positive and negative) of consumers (Fig. 2.10b) at most locations. One interesting exception occurred at site 5_MAA. At this site, sediment exposure was lowest of all sites and densities of coral recruits were 400% higher in open vs. caged plots (Fig. 2.10c). Though total macroalgae biomass did not differ among treatments at this site (Fig. 2.3a), consumers did have significant effects on algal cover on CAU surfaces (Fig. 2.7, 2.8a). Furthermore variation in consumer effects between 5_MAA and another low-sediment site (8_LAP) suggested that herbivore (i.e., echinoid) community structure may be important to coral recruitment. For example, site 5_MAA herbivore biomass was dominated by the echinoid *Tripneustes gratilla*. Though site 8_LAP had similarly low sediment exposure, and strong regulation of macroalgae by consumers, it exhibited relatively low coral recruitment and no effects of consumers (in contrast to site 5_MAA). Interestingly, the herbivore community at site 8_LAP was dominated by *E. matthaei*, a species that has been shown to exert strong negative effects on coral recruits (Korzen et al. 2011, O'Leary et al. 2013). Though the unique nature of each of these sites is somewhat anecdotal, the patterns observed match predictions that might be made given the results of previous studies in similar systems.

Relative dominance of benthic communities

The structure of benthic coral reef communities are strongly influenced by herbivory and nutrient availability. High levels of herbivory are generally expected to increase the cover of calcifiers (corals and CCA), whereas low levels of herbivory favor fleshy macroalgae and turf algae, contingent on nutrient availability (Smith et al. 2001, Littler et al. 2006, Littler & Littler 2007). Though significant coral recruitment was measured at certain sites in our study, most recruits were found in cryptic spaces, as observed elsewhere (Edmunds et al. 2010, Price 2010), and therefore contributed little to cover on CAU surfaces. Thus sessile communities on open CAUs at our sites were dominated by the abundance of turf (70%), CCA (16%) and macroalgae (0.7%) (Fig. 2.7, Fig. 2.9a); indicative of a lower-herbivore, low-nutrient system (were macroalgae are limited by nutrients, and turfs are not controlled by consumers) according the "relative dominance model," or RDM (Littler & Littler 2006); however, significant variation among individual CAUs, treatments, sites, and their interaction were observed (Table 2.1, Fig. 2.9).

In agreement with the RDM described above, herbivores decreased macroalgal cover by 25% relative to consumer exclosures, but this varied among sites from 0% (no effect, 8_LAP) to >50% (2_PUA). The lack of an effect at site 8_LAP; however, was surprising given that this site (1) had the highest herbivore biomass, (2) exhibited the strongest effect size of herbivores on macroalgal biomass, and (3) exhibited some of the highest nutrient levels among sites. These results suggested that cryptic algae (e.g. *Amansia sp.*) contributed significantly to macroalgal biomass at LAP, and that algal growth on exposed CAU surfaces was limited (in part) within consumer exclosures, possibly by smaller mesograzers. Regular observations (and removal) of small (<1 cm) echinoid (*E. matthaei*) recruits from cages at this site may support this hypothesis. The contributions of these and other cryptic invertebrates to benthic dynamics remains to be explored, but is likely underappreciated (Klumpp et al. 1988, Stachowicz & Hay 1999). Despite low levels of macroalgal cover, coral recruitment remained low at this site, possibly due to damage by *E. matthaei (O'Leary et al. 2013)*. In contrast to site 8_LAP, at site 5_MAA we observed the opposite pattern: significant effects of consumers on macroalgal cover (Fig. 2.8a), but not biomass (Fig. 2.5a). Interestingly the reduction of macroalgal cover on surfaces corresponded with a general increase in coral recruitment (Fig. 2.10a,c), suggesting that the grazing community at this site (mainly the echinoid *T. gratilla*) enhanced coral recruitment, despite its inability to limit the biomass of cryptic algae.

Crustose coralline algae (CCA) are important for coral reefs given that they can increase resilience by limiting macroalgal production (Vermeij et al. 2011), provide settlement cues for corals (Price 2010), and contribute as a "reef-builders" to net accretion and cementation of the calcareous bioherm (Smith et al. 2016). According to the relative dominance model (RDM), consumers should increase the cover of mechanically-defended (calcified) CCAs by removing fleshy turf- and macroalgal competitors (Littler & Littler 2007). In agreement with this prediction, CCA cover at site 5_MAA (though highly variable) and 7_KEA (sig.) increased by nearly 20% in the presence of consumers, suggesting that predictions based on the RDM may be relevant at these sites. However, in contrast to RDM-based predictions, consumers (in general) had no significant effects on the cover of CCA across all sites (Fig. 2.8b); instead, consumers led to approximately a 40% increase (vs. a predicted decrease) in the cover of fleshy turf algae (Fig. 2.8c). The relative dominance model assumes, however, that nutrients and herbivory are the 2 dominant drivers of ecological dynamics in a given reef system, whereas our system appeared to be strongly influenced (if not dominated) by sediment stress (Fig. 2.2i, Fig. 2.10b-c).

In sediment-stressed systems, herbivore abundance becomes decoupled from the abundance of fleshy algae due sediment-induced suppression of grazing activity (Goatley & Bellwood 2012, 2013, Gordon et al. 2016). In sediment-impacted systems, herbivores only crop exposed tips of fleshy algae that emerge from unpalatable sedimentary layers, thus leading to a cropped, highly stable, sediment-laden turf community; in the absence of herbivores, turfs and macroalgae emerge and grow above the sedimentary layers. Given our results, it appears that shallow coral reefs in Maui, in general, match the "sediment-suppressed herbivory" model better than the "relative dominance model:" herbivores are able to reduce the cover of fleshy macroalgae, but have limited impacts on the cover of sediment-laden turf communities, even at high densities and biomass.

Conservation and Management Implications

Our results have direct relevance to the conservation and management of coral reefs, both on Maui and abroad. All reefs that we examined were sediment-stressed, suggesting that measures to reduce additional sediment inputs into the system are likely of great importance. The biomass of herbivorous fishes at our sites was far lower than mean values for fisheries-accessible and inaccessible coral reefs around the globe (Edwards et al. 2014), and 90% lower than protected sites in comparable habitats in the Indian Ocean (McClanahan & Muthiga 2016). These results suggest that protection of herbivorous fishes should be a priority throughout the study region, especially given their greater benefits (vs. echinoids) to corals and other calcifiers (O'Leary et al. 2013). At site 1_KAH, existing regulations have prevented harvest of all herbivores since 2009, and though caged tiles at this site exhibited the greatest overall macroalgal biomass on tiles, consumers reduced these values by approximately 75% on open tiles. Similar patterns at sites 7_KEA and 8_LAP further demonstrated the importance of existing consumer populations (mostly echinoids) in controlling algal biomass at these sites, possibly justifying their protection.

However, not all sites exhibited greater biomass of fleshy macroalgae inside consumer exclosures. For example, site 5_MAA exhibited the third highest mean macroalgal biomass values in exclosures and the highest values for open tiles (Fig. 2.3a); therefore ambient consumers exerted no measurable effect on algal biomass (Fig. 2.4a) (though they did for percent cover of surfaces, Fig. 2.7) at this site. Furthermore, this site exhibited some of the highest coral recruitment rates on open tiles, but not caged tiles (Fig. 2.10). Given the high macroalgal production, low sediment exposure, and high recruitment potential; enhancement of herbivore populations at site 5_MAA could yield valuable long-term conservation benefits that might lead to rapid enhancement of coral settlement and growth, and thus resilience, of this shallow coral reef ecosystem.

In contrast, herbivore protection may not result in strong conservation outcomes at sites where coral recruitment appears to be limited by sediment stress (e.g., 2_PUA, 6_KAL) (Fig. 2.10b). Interestingly, coral recruitment at sites 1_KAH and 8_LAP were low despite relatively low sediment exposure and concurrent strong effects of existing consumers on macroalgal biomass; suggesting that other processes may be limiting recruitment at these sites. For example, the high use of 1_KAH by tourists and swimmers may limit coral recruitment via exposure to damaging concentrations of dissolved oxybenzone from sunscreens (Downs et al. 2016). If true, regulations limiting exposure to specific chemicals in sunscreens may be important at this (and other heavily-used) sites. At site 8_LAP, the direct negative effects (e.g., erosion and physical damage) of high densities of *E. matthaei* on coral recruits may outweigh their indirect positive effects via algal consumption (Korzen et al. 2011, O'Leary et al. 2013, McClanahan & Muthiga 2016), suggesting that protection and enhancement of (1) herbivorous fishes that have stronger net positive effects on corals (O'Leary et al. 2013), and (2) predatory fishes (e.g., Balistids), that limit *E. mathaei* populations (McClanahan & Shafir 1990), could yield significant conservation benefits at this site. While we acknowledge that many other factors not explicitly considered in this study (e.g. water temperature, carbonate chemistry, hydrodynamics and larval supply) also likely exert strong influence on benthic communities in the region; we have shown that two local properties (sediment exposure and herbivore biomass), both of which can be strongly influenced by managers and prudent policies, may explain significant quantities of variation on nearshore reefs in leeward Maui.

Conclusion

By combining surveys of environmental conditions with standardized comparative experiments, we have characterized (1) the ecological states of 8 shallow reefs systems with respect to herbivores, nutrients, sediments, and benthic communities, and (2) the ecological processes that appear to be regulating the early-successional accumulation of macroalgal biomass, juvenile corals, and sessile communities on reef surfaces across leeward Maui. We describe these reefs, generally, as low-nutrient, sediment-stressed, echinoid-dominated systems; but with significant spatial variation in the effects of consumers and sediment exposure on community development. By describing spatial variation in these ecological processes that influence community trajectories and ecological states, we can make better-informed decisions, that are both process-oriented and site-specific, that may further enhance the long-term success of specific conservation objectives.

ACKNOWLEDGEMENTS

A legion of field and laboratory assistants made this work possible: E. Kelly, C. Edwards, N. Kaplanis, L. Segui, A. Netburn, K. Nichols, J. Harris, M. Summers, M. Gleason, A. Carter, T. Pierce, M. Miller, S. Kram and G. Butler, E. Engle, M. Vanworth, E., D'Andrea, A. Khen, N. Kaplanis, T. Imam, J. Tran, M. Morgan, Y. Takeshita, T. Whitty, and A. Cannon. D. McLeish designed and constructed all consumer exclosures. The SIO Dive Program (C. McDonald and R. Walsh) and Maui Scuba Diving Snorkel Center (R. Carman) supported all diving activities, Maui Ocean Center (J. Luecke) provided wet-lab facilities, and SIO Center for Marine Biodiversity and Conservation (P. Dockry) provided much logistical support. A. Cannon, A. Khen, A. Scott, J. Shurin, L. Levin, S. Sandin and anonymous reviewers provided comments and contributions that greatly improved the manuscript. All artwork courtesy of Adi Khen. This study was a collaboration with Maui Division of Aquatic Resources (DAR; R. Sparks and D. White) under DAR permit numbers: SAP2011-90, SAP2012-68, 2013-19, and SAP2014-43. Funding came from the PADI Foundation, Edna-Bailey Sussman Foundation, Scripps Family Foundation, SciFund Challenge, NRC Ford Foundation Fellowship, and the National Science Foundation Grant No. 0903551.

Chapter 2, in part is currently being prepared for submission for publication of the material. Lewis, Levi S; Price, Nicole, N.; Smith, Jennifer E. The dissertation/thesis author was the primary investigator and author of this material.

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TABLES

Table 2.1. Results of statistical tests of environmental site characteristics and metrics of community development on CAU tiles. P-values of significant tests results are in bold.

Group	Metric	Tranform	Model						
Sites				**Factor**	**DF**	**DFDen**	**F**	**P**	**R^2adj**
	Herbivores (g m^{-2})	sqrt	Mixed Effects ANOVA	Site	7	21.00	19.65	**<0.001**	0.830
	DIN (µM)	sqrt	Mixed Effects ANOVA	Site	7	139.30	11.48	**<0.001**	0.840
	Sediments (g $cm^{-2}d^{-1}$)	log	Mixed Effects ANOVA	Site	7	70.00	44.21	**<0.001**	0.957
CAU Tiles				**Factor**	**DF**	**SS**	**F**	**P**	**R^2adj**
	Macroalgae (g)	sqrt	ANOVA (fixed)	Site	7	14.80	15.00	**<0.001**	0.505
				Cage	1	5.49	38.91	**<0.001**	
				SitexCage	7	2.54	2.57	**0.0162**	
	Accretion (g)	sqrt	ANOVA (fixed)	Site	7	310.72	34.42	**<0.001**	0.600
				Cage	1	24.06	18.66	**<0.001**	
				SitexCage	7	34.53	3.82	**<0.001**	
	FleshyTotal (g)	sqrt	ANOVA (fixed)	Site	7	27.07	43.84	**<0.001**	0.694
				Cage	1	1.21	13.69	**<0.001**	
				SitexCage	7	2.14	3.46	**<0.001**	
				Factor	**DF**	-	**Wald χ^2**	**$P > \chi 2$**	**R^2gen**
	Coral Recruits (no.)	-	GLM (Poisson, fixed)	Site	7	-	26.01	**0.001**	0.563
				Cage	1	-	0.47	0.493	
				SitexCage	7	-	8.77	0.269	
				Factor	**DF**	**SS**	**Pseudo F**	**P**	**% Var**
	Community (B-C Similarity)	-	PERMANOVA (fixed)	Site	7	41246	7.92	**<0.001**	13.4
				Cage	1	62036	83.43	**<0.001**	40.3
				SitexCage	7	19563	3.76	**<0.001**	10.7

Table 2.2. Study sites in leeward Maui. Site codes, names, latitude, longitude, and distance from shore in meters.

Code	Site	Latitude	Longitude	Distance (m)
1_KAH	Kahekili	20.93880172	-156.6932358	50
2_PUA	Puamana	20.85556448	-156.6656805	104
3_OLO	Olowalu	20.80850026	-156.6130548	180
4_UKU	Ukumehame	20.79161894	-156.5812651	345
5_MAA	Maalaea	20.79016091	-156.5093712	240
6_KAL	Kalama	20.72708918	-156.4514699	157
7_KEA	Keawakapu	20.69432072	-156.4453329	70
8_LAP	La Perouse	20.59861849	-156.420456	75

Table 2.3. Data collection for environmental characteristics. Values represent the number of time points (weeks) sampled at all 8 sites during each field visit.

Year	Months	No.weeks	Nutrients	Sediments	Herbivores
2011	Jun-Sep	12	7	3	-
	Dec	3	3	2	-
2012	Feb-Mar	3	1	0	-
	May-Aug	16	8	6	2
	Dec	3	2	1	1
2013	Mar	2	-	-	1
	total		**21**	**12**	**4**

Table 2.4. Fishes: total counts, biomass, scaling coefficients, and functional groups.

Code	Common	SSCode	Family	Genus	Species	Trophic1	Trophic2	Trophic3	LengthType	L_Cor	Mult	a	b	Count	Mass
GYME	Whitemouth moray	GYME	Muraenidae	Gymnothorax	meleagris	Pisc	Pisc	apex	TL	1.00	1.00	0.00	3.00	3	6300.0
GYFL	Yellow margin moray	GYFL	Muraenidae	Gymnothorax	flavimarginatus	Pisc	Pisc	apex	TL	1.00	1.00	0.00	3.35	1	2004.7
MUXX	Eel Unknown	MORA	Muraenidae	Muraenidae	sp	Pisc	Pisc	apex	FL	1.00	1.00	0.00	2.61	1	33.7
CEAR	Peacock Grouper (Roi)	CEAR	Serranidae	Cephalopholis	argus	APEX	Pisc	apex	FL	1.00	1.00	0.01	3.18	0	0.0
PLJO	Blueye damsel	PLJO	Pomacentridae	Plectroglyphidodon	johnstonianus	Cor	LowCarn	corallivore	TL	1.00	1.00	0.06	2.64	106	354.4
CADU	Barred Filefish	CADU	Monacanthidae	Cantherhines	dumerilii	Om	LowCarn	corallivore	TL	1.00	1.00	0.04	2.79	1	174.2
CHUN	Teardrop butterfly	CHUN	Chaetodontidae	Chaetodon	unimaculatus	Cor	LowCarn	corallivore	FL	1.00	1.00	0.05	2.83	4	122.1
CHXX	Butterflyfish unknown	BUTT	Chaetodontidae	Chaetodontidae	sp	Cor	LowCarn	corallivore	TL	1.00	1.00	0.03	2.99	3	21.8
CHOR	Ornate butterflyfish	CHOR	Chaetodontidae	Chaetodon	ornatissimus	Cor	LowCarn	corallivore	TL	1.00	1.00	0.03	2.99	1	0.8
ARME	Guinneafowl puffer	ARME	Tetraodontidae	Arothron	meleagris	Cor	LowCarn	corallivore	FL	1.00	1.00	0.41	2.70	0	0.0
CHLU	Oval butterflyfish	CHLT	Chaetodontidae	Chaetodon	lunulatus	Cor	LowCarn	corallivore	TL	1.00	1.00	0.03	2.99	0	0.0
STFA	Pacific gregory	STFA	Pomacentridae	Stegastes	fasciolatus	H	Herb	farmer	TL	1.00	1.00	0.03	2.91	301	1846.6
ACNI	Brown tang	ACNF	Acanthuridae	Acanthurus	nigrofuscus	H	Herb	herbivore	FL	0.91	0.91	0.03	3.03	1127	21599.2
ZEFL	Yellow tang	ZEFL	Acanthuridae	Zebrasoma	flavescens	H	Herb	herbivore	TL	1.00	1.00	0.01	3.16	42	1068.8
SCPS	Palenose parrotfish	SCPS	Scaridae	Scarus	psittacus	H	Herb	herbivore	FL	0.97	0.97	0.01	3.32	118	975.3
NALI	Orangespine unicornfish	NALI	Acanthuridae	Naso	lituratus	H	Herb	herbivore	FL	0.97	0.97	0.01	3.25	25	777.1
CHSP	Bullethead parrotfish	CHSO	Scaridae	Chlorurus	spiluris	H	Herb	herbivore	FL	1.00	1.00	0.02	2.97	4	623.9
CAEP	Hawaiian whitespotted toby	CAJA	Tetraodontidae	Canthigaster	jactator	H	Herb	herbivore	FL	1.00	1.00	0.04	2.82	81	436.1
ACTR	Convict tang	ACTR	Acanthuridae	Acanthurus	triostegus	H	Herb	herbivore	FL	0.87	0.87	0.08	2.57	23	212.3
SCXX	Parrotfish unknown	PARR	Scaridae	Scaridae	sp	H	Herb	herbivore	FL	0.97	0.97	0.02	2.96	20	200.0
CASA	Squaretail filefish	CASA	Monacanthidae	Cantherhines	sandwichiensis	H	Herb	herbivore	FL	1.00	1.00	0.01	3.26	13	198.4
CTST	Goldring surgeonfish	CTST	Acanthuridae	Ctenochaetus	strigosus	H	Herb	herbivore	TL	1.00	1.00	0.00	3.00	52	60.1
ACBL	Ringtail surgeon	ACBL	Acanthuridae	Acanthurus	blochii	H	Herb	herbivore	FL	0.93	0.93	0.03	3.03	8	33.7
ACLE	Whitebar surgeonfish	ACLE	Acanthuridae	Acanthurus	leucopareius	H	Herb	herbivore	TL	1.00	1.00	0.00	3.00	10	9.7
CHPE	Spectacled parrotfish	CHPE	Scaridae	Chlorurus	perspicillatus	H	Herb	herbivore	TL	1.00	1.00	0.02	3.00	1	7.0
MEVI	Pinktail durgon (trigger)	MEVI	Balistidae	Melichthys	vidua	H	Herb	herbivore	TL	1.00	1.00	0.01	3.55	0	0.0
NAUN	Bluespine unicornfish	NAUN	Acanthuridae	Naso	unicornis	H	Herb	herbivore	FL	0.96	0.96	0.02	3.04	0	0.0
THDU	Saddle wrasse	THDU	Labridae	Thalassoma	duperrey	MI	LowCarn	invertivore	FL	0.90	0.90	0.01	3.10	673	2392.0
RHRE	Reef triggerfish	RHRE	Balistidae	Rhinecanthus	rectangulus	MI	LowCarn	invertivore	TL	1.00	1.00	0.05	2.64	35	1788.1
STBA	Belted wrasse	STBA	Labridae	Stethojulis	balteata	MI	LowCarn	invertivore	TL	1.00	1.00	0.02	3.00	256	632.2
OSME	Spotted boxfish	OSME	Ostraciidae	Ostracion	meleagris	SI	LowCarn	invertivore	TL	1.00	1.00	0.11	2.55	45	532.3
PAMU	Manybar goatfish	PAMU	Mullidae	Parupeneus	multifasciatus	MI	LowCarn	invertivore	FL	0.90	0.90	0.01	3.21	33	510.0
CHLU	Racoon butterflyfish	CHLU	Chaetodontidae	Chaetodon	lunula	SI	LowCarn	invertivore	TL	1.00	1.00	0.03	2.99	8	242.4
PLIM	Brighteye damselfish	PLIM	Pomacentridae	Plectroglyphidodon	imparipennis	MI	LowCarn	invertivore	TL	1.00	1.00	0.06	2.69	60	195.1
GOVR	Bird wrasse	GOVA	Labridae	Gomphosus	varius	MI	LowCarn	invertivore	FL	1.00	1.00	0.02	2.70	42	188.5
PAFO	Blackside hawkfish	PAFO	Cirrhitidae	Paracirrhites	forsteri	Pisc	Pisc	invertivore	TL	1.00	1.00	0.02	3.13	10	165.6
ECNE	Snowflake moray	ECNE	Muraenidae	Echidna	nebulosa	MI	LowCarn	invertivore	FL	1.00	1.00	0.00	3.35	1	143.7
THPU	Surge wrasse	THPU	Labridae	Thalassoma	purpureum	MI	LowCarn	invertivore	TL	1.00	1.00	0.03	3.00	9	104.8
PUFR	Puffer (var)	PUFF	Tetraodontidae	Tetraodontidae	sp	MI	LowCarn	invertivore	FL	1.00	1.00	0.04	2.79	5	77.0
BOAL	Hawaiian Hogfish	BOBI	Labridae	Bodianus	albotaeniatus	MI	LowCarn	invertivore	TL	1.00	1.00	0.01	3.00	1	49.3
THPA	Ornate wrasse	THSP	Labridae	Thalassoma	sp	MI	LowCarn	invertivore	FL	0.90	0.90	0.01	3.10	4	35.8
CHIN	Cigar wrasse	CHIN	Labridae	Cheilio	inermis	MI	LowCarn	invertivore	FL	1.00	1.00	0.00	3.08	1	35.6
BASU	Lei trigger	SUBU	Balistidae	Sufflamen	bursa	MI	LowCarn	invertivore	TL	1.00	1.00	0.02	3.00	1	28.7
RHAC	Lagoon trigger	RHAC	Balistidae	Rhinecanthus	aculeatus	MI	LowCarn	invertivore	TL	1.00	1.00	0.05	2.64	1	22.8
PAAR	Arceye hawkfish	PAAR	Cirrhitidae	Paracirrhites	arcatus	MI	LowCarn	invertivore	TL	1.00	1.00	0.02	3.13	4	21.4
COGA	Yellowtail coris	COGA	Labridae	Coris	gaimard	MI	LowCarn	invertivore	TL	1.00	1.00	0.01	3.00	3	9.3
LAXX	Wrasse unkown	WRAS	Labridae	Labridae	sp	MI	LowCarn	invertivore	FL	0.99	0.99	0.01	3.18	10	9.1
LAPH	Cleaner wrasse	LAPH	Labridae	Labroides	phthirophagus	MI	LowCarn	invertivore	FL	1.00	1.00	0.01	3.23	9	4.7
PAXX	Goatfish unk	GOAT	Mullidae	Mullidae	sp	MI	LowCarn	invertivore	FL	0.90	0.90	0.01	3.29	1	1.9
GOAT	Unknown goatfish	GOAT	Mullidae	Mullidae	sp	MI	LowCarn	invertivore	FL	0.90	0.90	0.01	3.29	1	1.9
NOTA	Rockmover wrasse	NOTA	Labridae	Novaculichthys	taeniourus	MI	LowCarn	invertivore	TL	1.00	1.00	0.01	2.91	1	1.4
CIPI	Stocky hawkfish	CIPI	Cirrhitidae	Cirrhitus	pinnulatus	MI	LowCarn	invertivore	TL	1.00	1.00	0.02	3.00	0	0.0
MENI	Black durgon (trigger)	MENI	Balistidae	Melichthys	niger	Z	Planktivore	omnivore	TL	1.00	1.00	0.01	3.55	12	381.8
CHVR	Chromis	DAMS	Pomacentridae	Pomacentridae	sp	Om	LowCarn	omnivore	FL	0.92	0.92	0.02	3.19	256	123.7
FICO	Cornetfish	FICO	Fistulariidae	Fistularia	commersonii	Pisc	Pisc	piscivore	FL	1.00	1.00	0.00	3.05	12	1891.8
AUCH	Trumpetfish	AUCH	Aulosomidae	Aulostomus	chinensis	Pisc	Pisc	piscivore	FL	1.00	1.00	0.00	3.51	4	138.0
PACY	Blue goatfish	PACY	Mullidae	Parupeneus	cyclostomus	Pisc	Pisc	piscivore	TL	1.00	1.00	0.01	3.00	4	41.5
OXUN	Ringtail wrasse	OXUN	Labridae	Oxycheilinus	unifasciatus	Pisc	Pisc	piscivore	TL	1.00	1.00	0.02	3.00	2	9.4
ABAB	Sargeant major	ABAB	Pomacentridae	Abudefduf	abdominalis	Z	Planktivore	planktivore	FL	0.89	0.89	0.02	3.13	54	208.1
NABR	Paletail unicornfish	NABR	Acanthuridae	Naso	brevirostris	Z	Planktivore	planktivore	FL	1.00	1.00	0.01	3.24	5	123.2
DAAL	Hawaiian dascyllus	DAAL	Pomacentridae	Dascyllus	albisella	Z	Planktivore	planktivore	FL	1.00	1.00	0.05	2.91	11	6.2
STRP	Juvenile striped fish	FISH	unk	Un-id	fish	X	LowCarn	unk	FL	1.00	1.00	0.01	3.18	12	22.3
UNKN	Unknown	FISH	unk	Un-id	fish	X	LowCarn	unk	FL	1.00	1.00	0.01	3.18	12	22.3

Table 2.5. Echinoids: total counts, biomass, scaling coefficients, and functional groups.

CODE	Common Name	Family	Genus	Species	Guild	Total Count	Mass ind^{-1} (g)	Total Mass (kg)
EM	rock boring	Echinometridae	*Echinometra*	*mathaei*	RBR	5194	32.1	166.9
HM	slate pencil urchin	Echinometridae	*Heterocentrotus*	*mammillatus*	RBR	408	157.0	64.1
ED	blue banded	Diadematidae	*Echinothrix*	*diadema*	HRB	776	70.8	54.9
TG	Collector	Toxopneustidae	*Tripneustes*	*gratilla*	HRB	181	154.3	27.9
EC	black banded	Diadematidae	*Echinothrix*	*calamaris*	HRB	22	107.2	2.4
EO	black rock boring	Echinometridae	*Echinometra*	*oblonga*	RBR	32	-	-
EA	thin spine boring	Echinometridae	*Echinostrephus*	*aciculata*	RBR	13	-	-
DP	Long spined	Diadematidae	*Diadema*	*paucispinum*	HRB	0	-	-
PC	Pebble collector	Toxopneustidae	*Pseudoboletina*	*indiana*	HRB	0	-	-
CH	rough-spined pencil urchin	Cidaridae	*Chondrociaris*	*gigantea*	OMN	0	-	-
EU	pencil urchin	Cidaridae	*Eucidaris*	*sp.*	OMN	0	-	-

Table 2.6. Algae taxa and functional groups collected from CAU tiles.

Taxa	Phylum	Order	Group	Growth	Mass	Percent
Melanamansia	Rhodophyta	Ceramiales	Corticated	Foliose	58.05	47.96%
Laurencia	Rhodophyta	Ceramiales	Corticated	Terete Branching	18.75	15.49%
Lush Turf	Mixed	Mixed	Uncorticated	Filaments	9.98	8.25%
Red Corticated Other	Rhodophyta	Various	Corticated	Terete Branching	6.16	5.09%
Turbinaria	Heterokontophyta	Fucales	Leathery Corticated	Terete Branching	4.63	3.83%
Jania	Rhodophyta	Corallinales	Calcified	Terete Branching	4.53	3.74%
Peyssonelia	Rhodophyta	Peyssonneliales	Calcified	Crust	3.33	2.75%
Red Foliose Other	Rhodophyta	Various	Corticated	Foliose	3.17	2.62%
Dictyota	Heterokontophyta	Dictyotales	Corticated	Foliose	2.69	2.22%
Haloplegma	Rhodophyta	Ceramiales	Corticated	Foliose	2.52	2.09%
Acanthophora	Rhodophyta	Ceramiales	Corticated	Terete Branching	1.22	1.01%
Halichrysis	Rhodophyta	Gigartinales	Corticated	Foliose	1.15	0.95%
Cladophora	Chlorophyta	Cladophorales	Coenocytic	Terete Branching	0.93	0.77%
Padina	Heterokontophyta	Dictyotales	Corticated	Foliose	0.75	0.62%
Dasya	Rhodophyta	Ceramiales	Corticated	Terete Branching	0.70	0.58%
Neomeris	Chlorophyta	Dasycladales	Coenocytic	Terete Branching	0.59	0.49%
Botryocladia	Rhodophyta	Rhodymeniales	Corticated	Terete Branching	0.37	0.31%
Red Calcified Other	Rhodophyta	Various	Calcified	Terete Branching	0.31	0.26%
Lobophora	Heterokontophyta	Dictyotales	Corticated	Crust	0.25	0.21%
Martensia	Rhodophyta	Ceramiales	Corticated	Foliose	0.24	0.20%
Asparagopsis	Rhodophyta	Bonnemaisoniales	Corticated	Terete Branching	0.23	0.19%
Tolipiocladia	Rhodophyta	Ceramiales	Uncorticated	Filamentous	0.12	0.10%
Codium	Chlorophyta	Caulerpales	Coenocytic	Terete Branching	0.10	0.08%
Halimeda	Chlorophyta	Caulerpales	Calcified	Terete Branching	0.09	0.08%
Caulerpa	Chlorophyta	Caulerpales	Coenocytic	Terete Branching	0.07	0.06%
Ulva	Chlorophyta	Ulvales	Uncorticated	Foliose	0.05	0.04%
Hypnea	Rhodophyta	Gigartinales	Corticated	Terete Branching	0.01	0.01%
Sargassum	Heterokontophyta	Fucales	Leathery Corticated	Terete Branching	0.01	0.01%
Unknown	Unknown	Unknown	Unknown	Unknown	0.01	0.01%

FIGURES

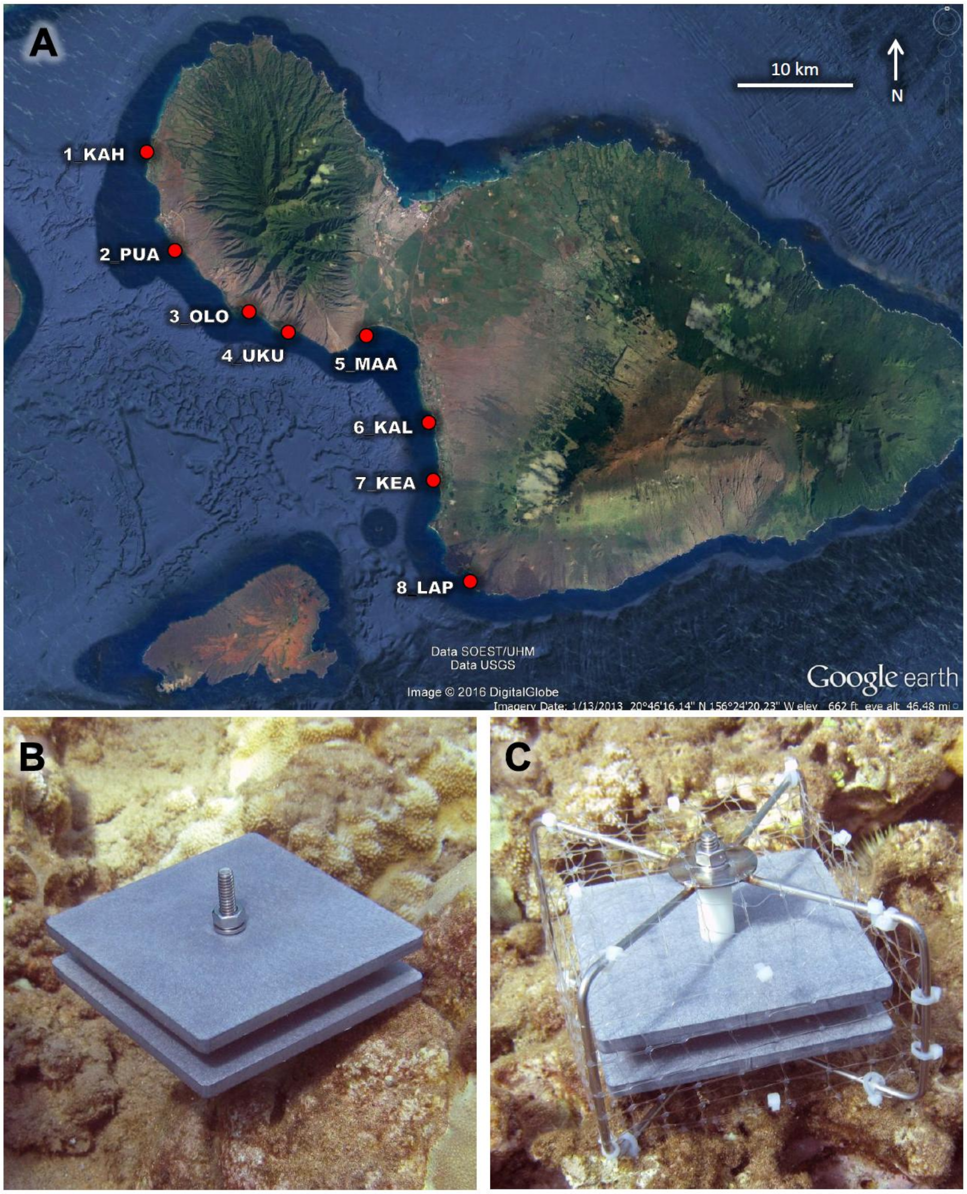

Figure 2.1. Study sites and design of settlement tiles and cages. (a) Study sites along leeward Maui, HI, and open (b) and caged (c) "calcification/accretion unit" (CAU) tiles used to examine reef development. Sites are: 1_KAH (Kahekili), 2_PUA (Puamana), 3_OLO (Olowalu), 4_UKU (Ukumehame), 5_MAA (Maaleaea), 6_KAL (Kalama), 7_KEA (Keawakapu), 8_LAP (La Perouse). See Table 2.2 for site details.

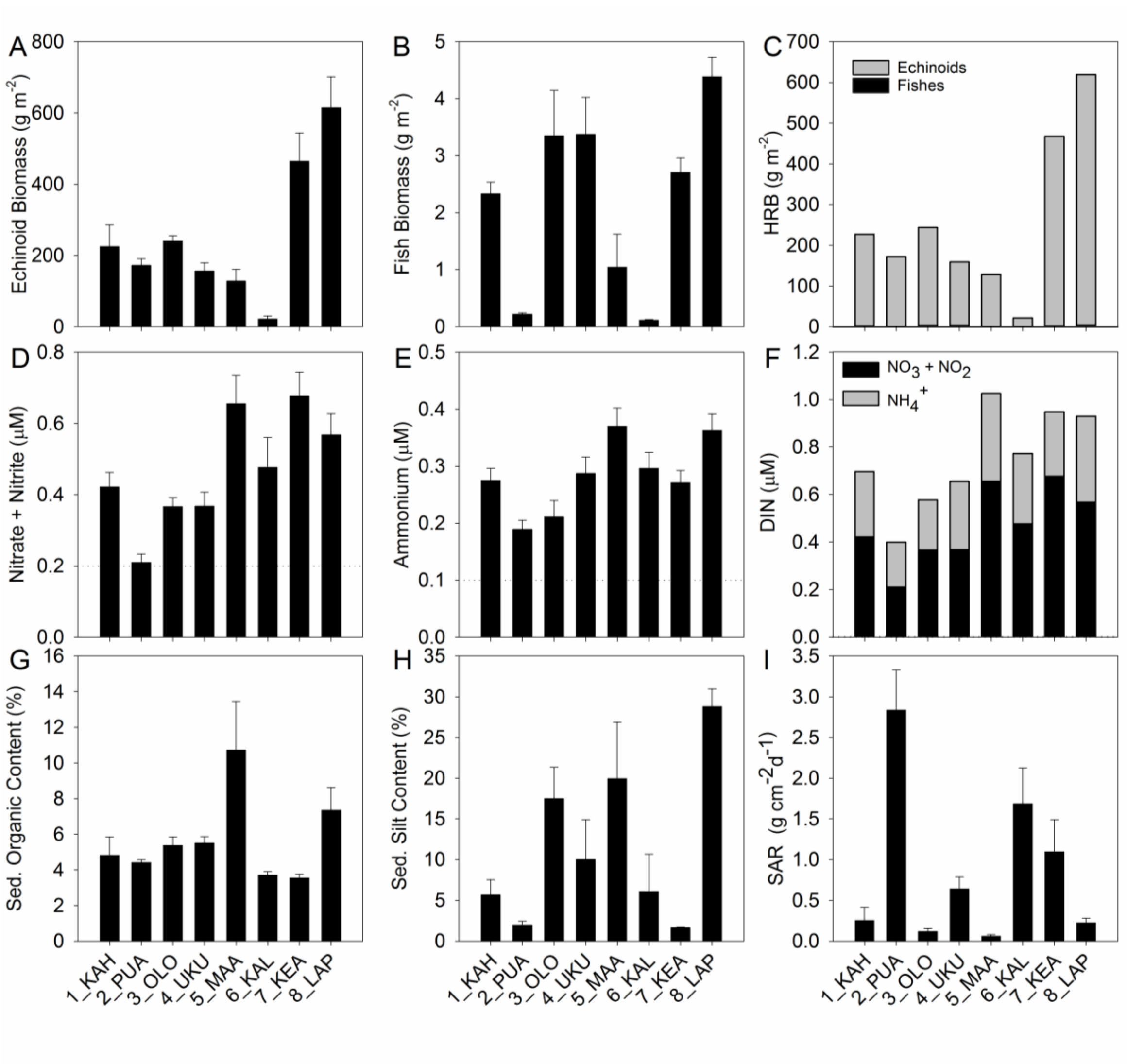

Figure 2.2. Environmental characteristics measured at each of the 8 coral reef study sites. Herbivore biomass (a-c), water column nutrients (d-f), and sediment characteristics and accumulation rates (g-i). Total values for herbivore biomass (HRB = echinoids + fishes), dissolved inorganic nutrients (DIN = nitrate + nitrite+ ammonium), and sediment accumulation rate (SAR = mass/area/time) are shown on the right (c,f,i) and were used to examine relationships between CAU metrics and environmental conditions. Mean + SE shown.

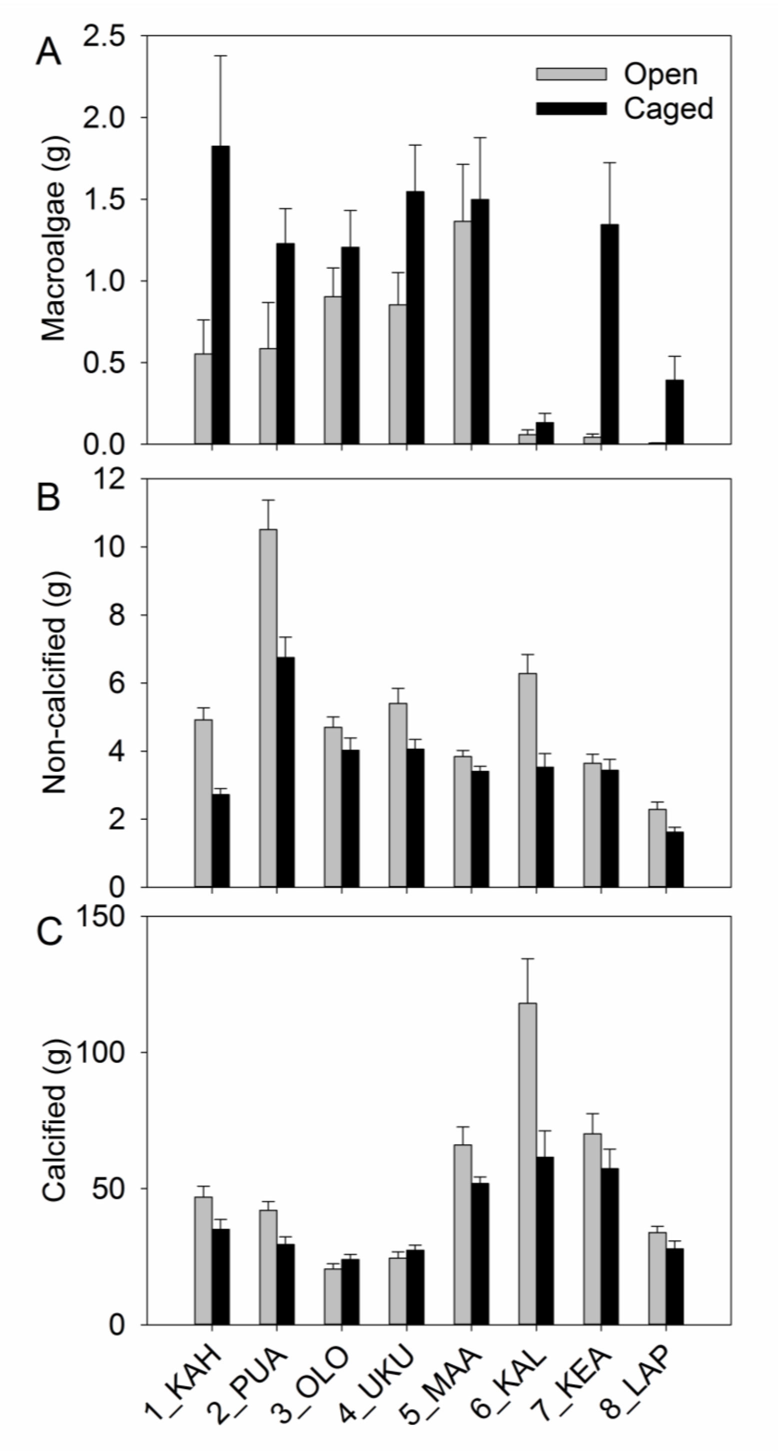

Figure 2.3. Biomass of (a) macroalgae, (b) total non-calcified and (c) calcified material on CAU tiles. CAU metrics are per 425 cm^2 (though macroalgae only grew on exposed surfaces, or 225 cm^2). Mean + SE shown.

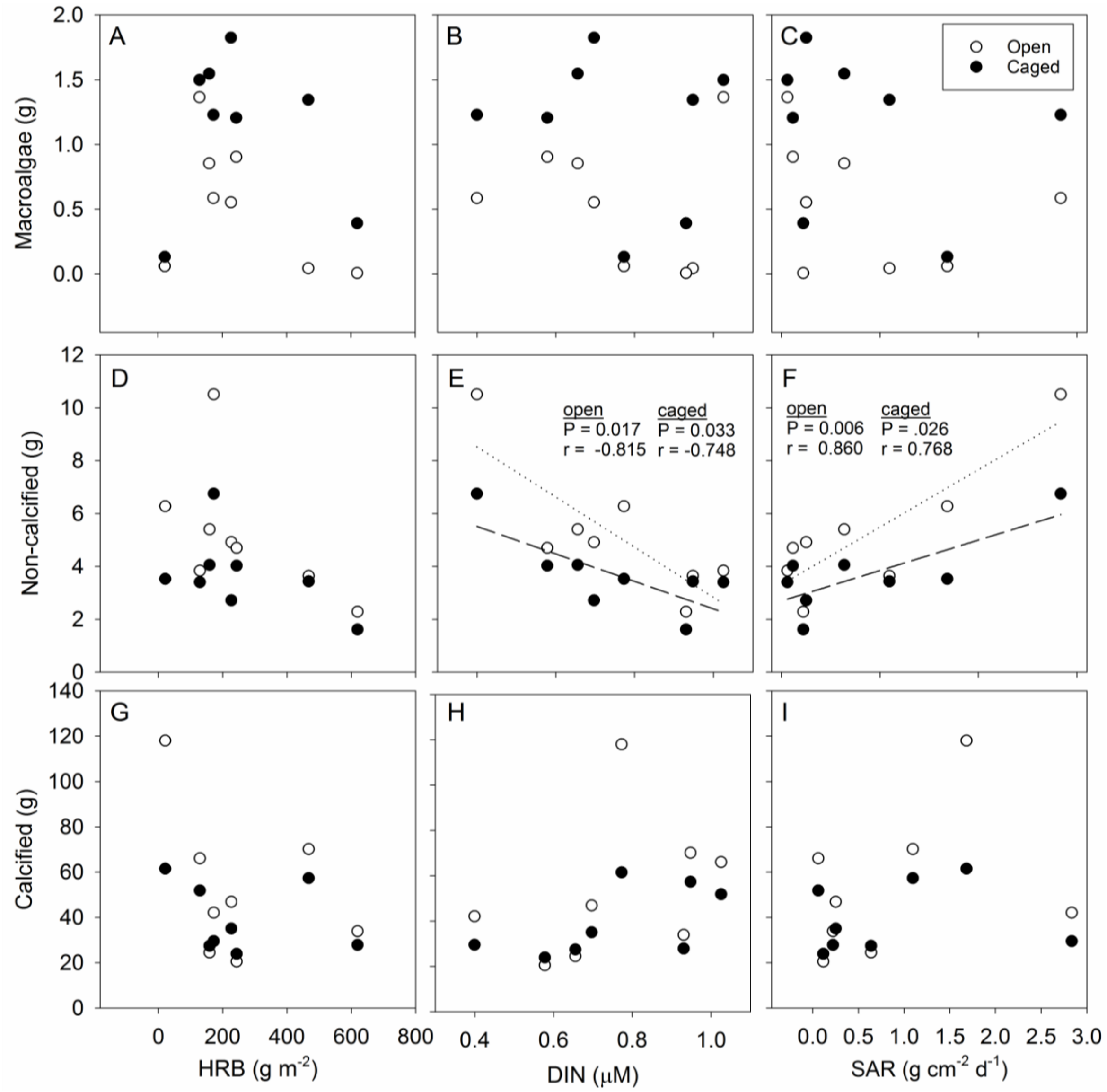

Figure 2.4. Scatterplot matrix of relationships between environmental characteristics (herbivore biomass: HRB, dissolved inorganic nutrients: DIN, and sediment accumulation rate: SAR) and dry mass of macroalgae, non-calcified and calcified material on CAU tiles. Lines of best fit for significant correlations are shown for open (dotted) and caged (dashed) CAU tiles. Total non-calcified mass correlated negatively with nutrients and positively with sediment accumulation. CAU metrics are per 425 cm^2 (though macroalgae only grew on exposed surfaces, or 225 cm^2).

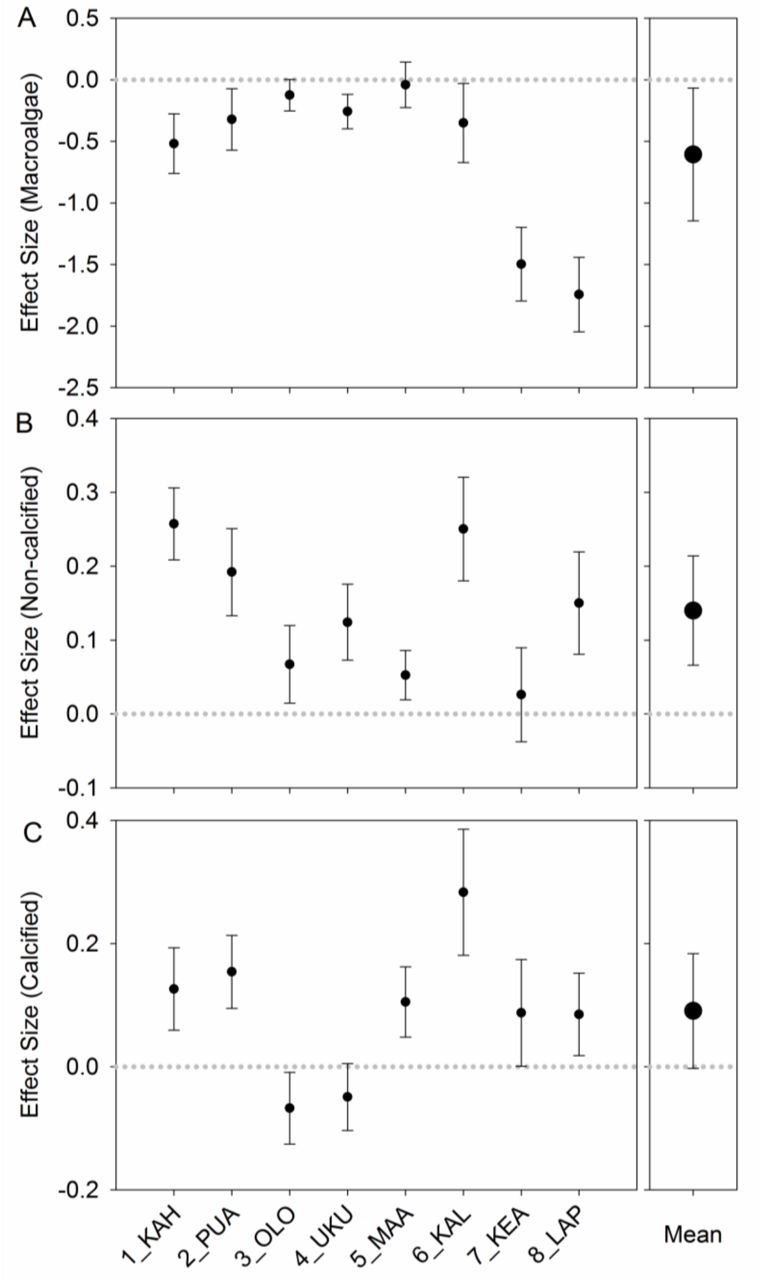

Figure 2.5. Relative magnitude of consumer effects (log response ratio of open:caged tiles) on total biomass of (a) macroalgae, (b) total non-calcified, and (c) calcified biomass on CAU tiles. Positive and negative values indicate positive and negative effects of consumers, respectively. Note that y-axes are scaled differently: biomass of macroalgae was 56-fold (5600%) greater inside cages, whereas non-calcified biomass was up to 1.6-fold (60%) greater outside cages. Mean ± 95% CI shown.

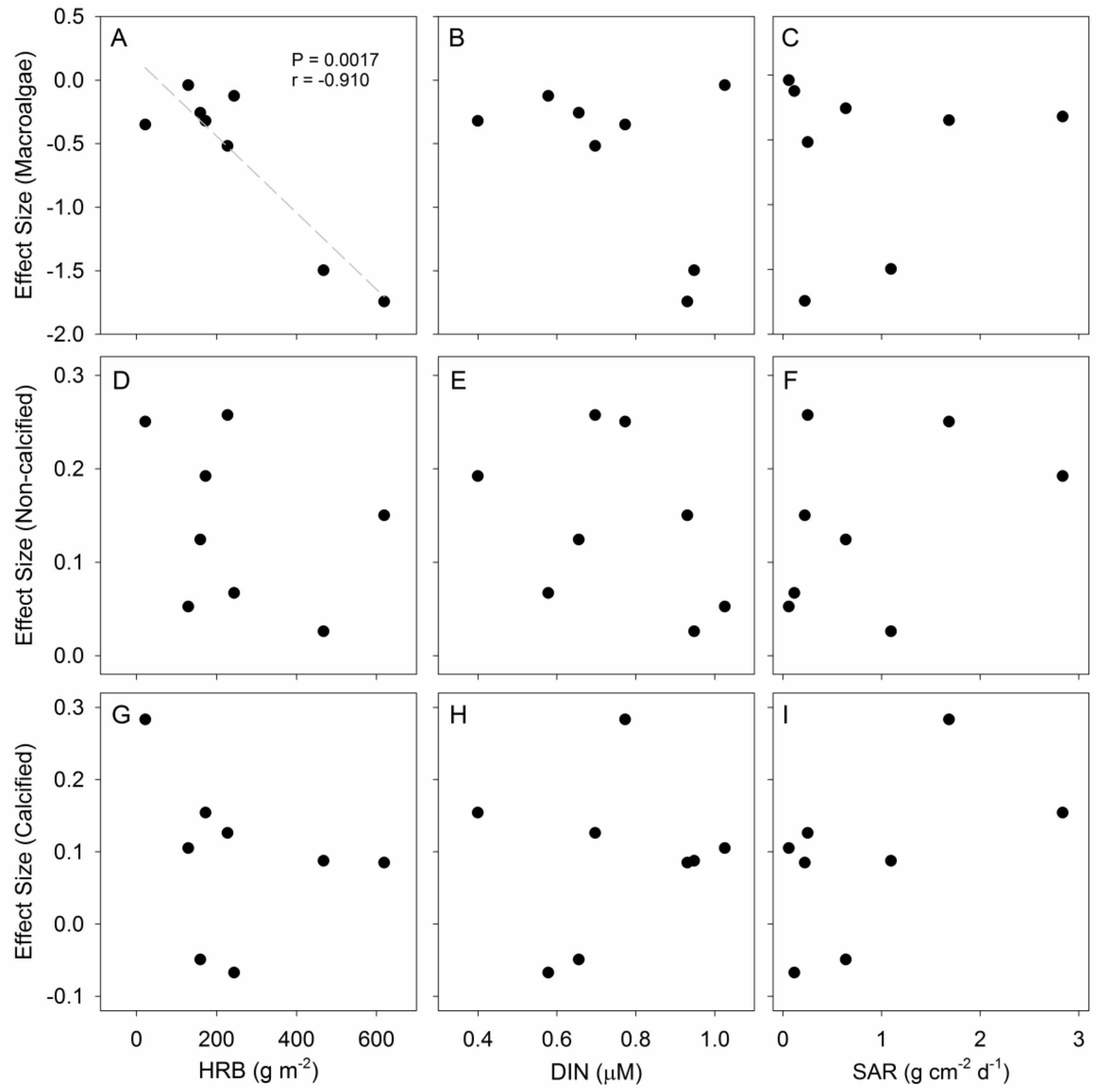

Figure 2.6. Scatterplot matrix of relationships between environmental characteristics (herbivore biomass: HRB, dissolved inorganic nutrients: DIN, and sediment accumulation rate: SAR) and the magnitude of the effects of consumers on macroalgae, non-calcified, and calcified biomass on CAU tiles. A strong correlation between herbivore biomass and their effect size on macroalgae is shown with the line of best fit; no other relationships were significant.

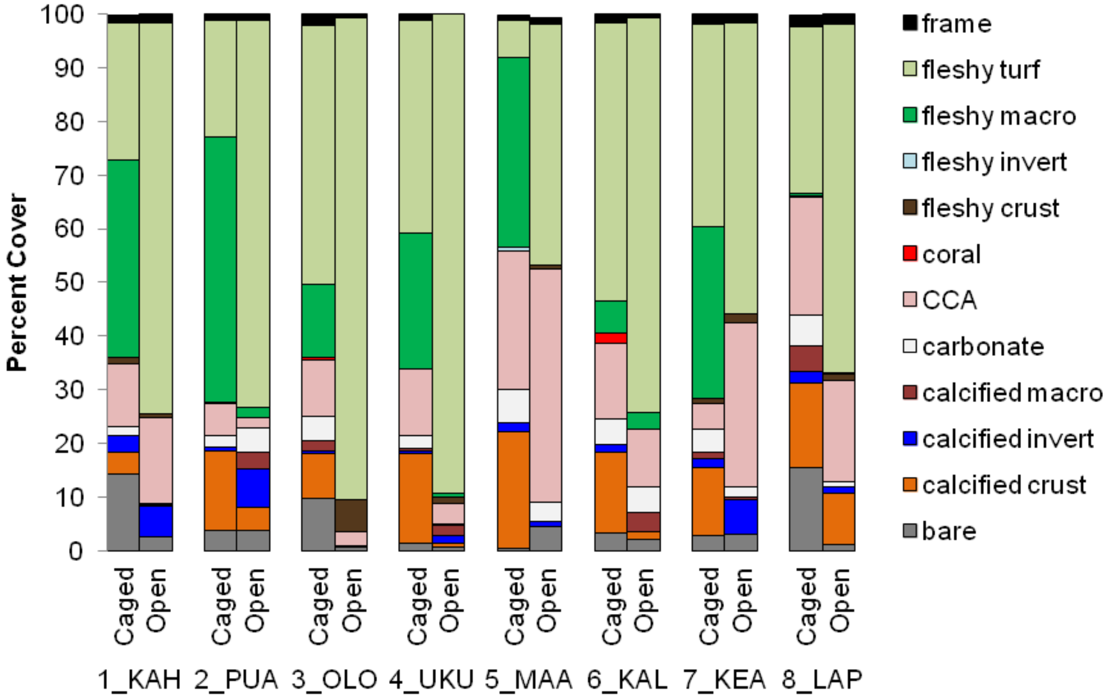

Figure 2.7. Community structure of sessile organisms and substrates on exposed surfaces of CAU tiles.

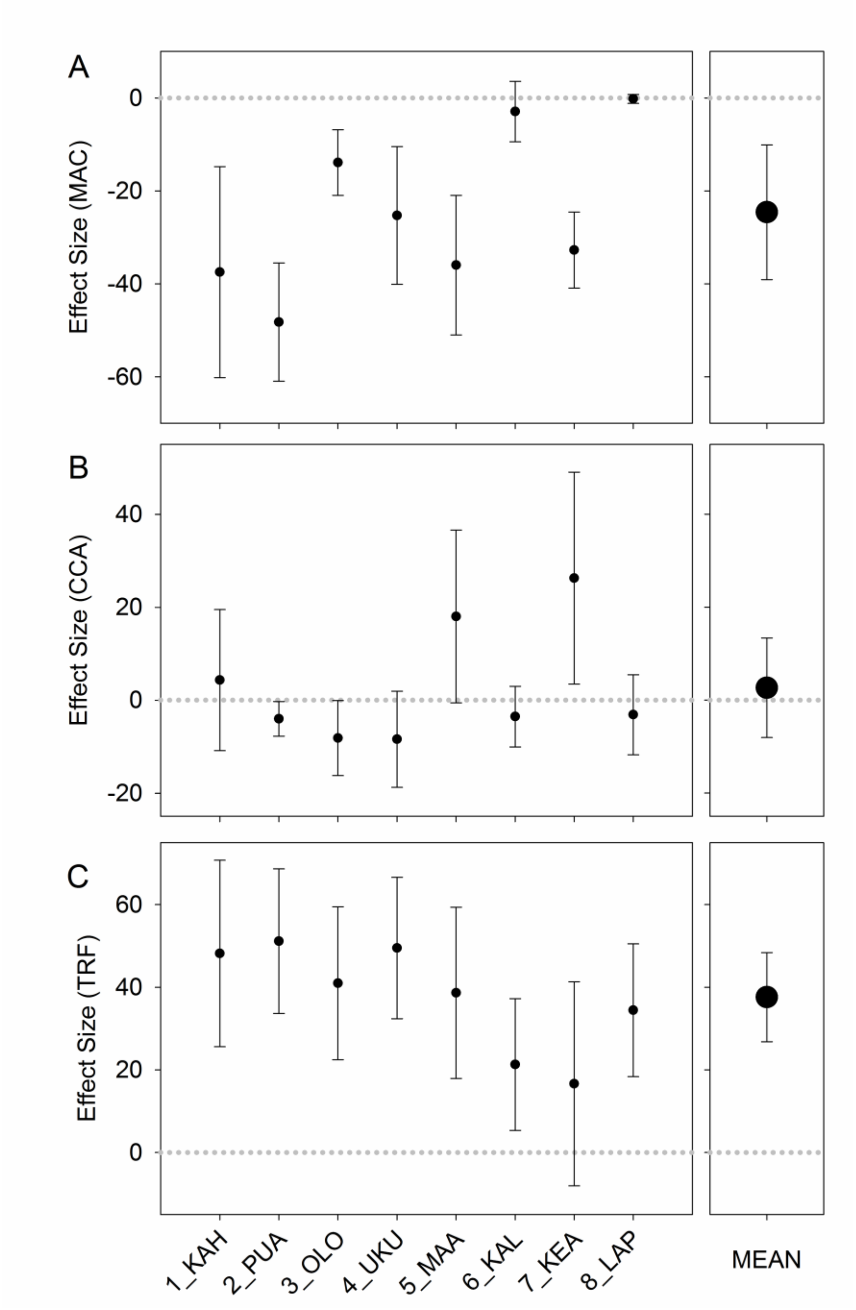

Figure 2.8. Effect size (open-cage, raw %) of consumers on the abundance (% cover) of 3 dominant benthic functional groups on CAU tiles: (A) macroalgae (MAC), (B) crustose coralline algae (CCA), and (C) mixed filamentous turf algae (TRF). Corals did not contribute significantly to percent cover on tiles. Mean ± 95% CI are shown.

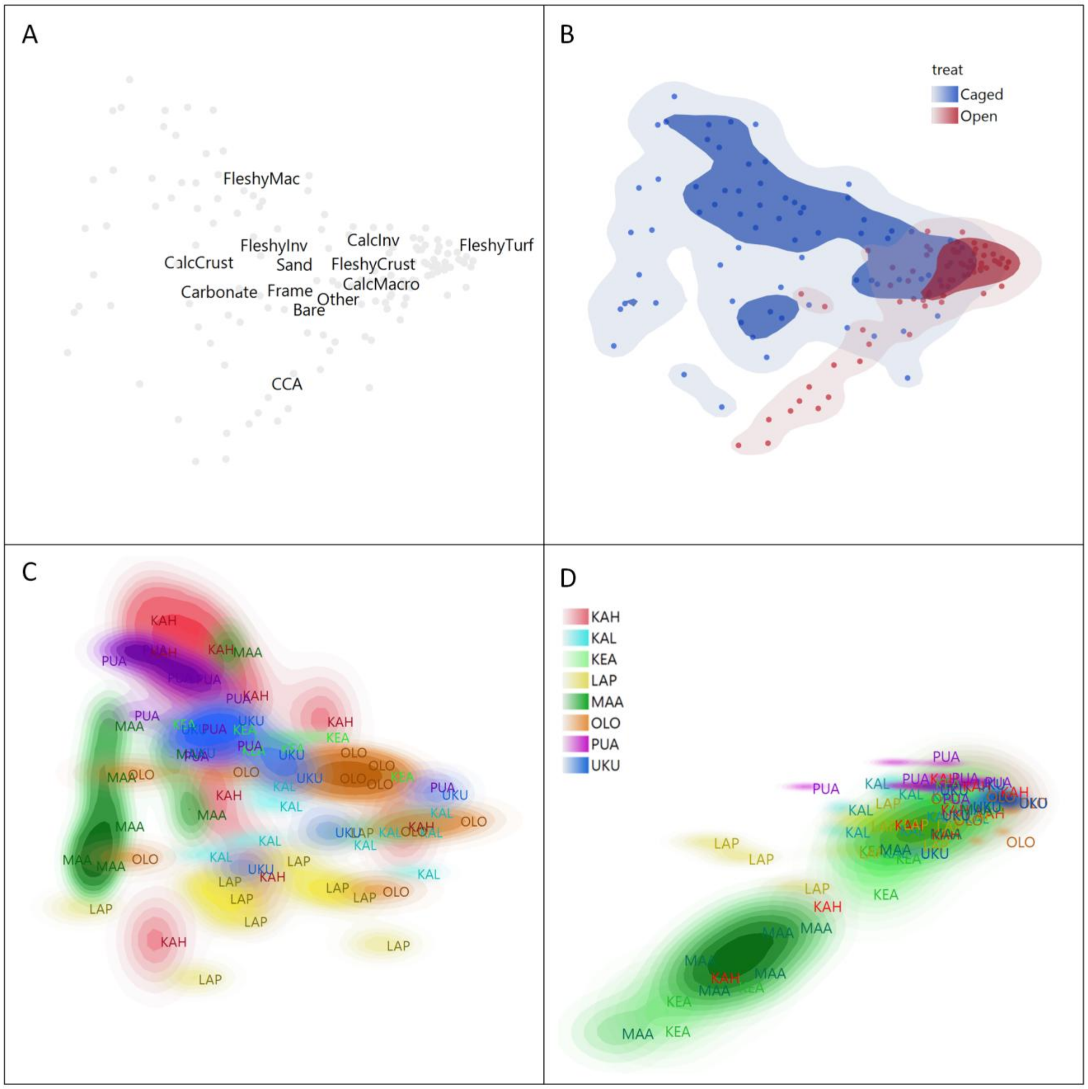

Figure 2.9. Community structure of sessile organisms on CAU surfaces: non-metric multi-dimensional scaling (nMDS) 2-dimensional projection of untransformed Bray-Curtis distances (BCD) among CAU tiles: (A) benthic functional groups contributing to distances (note: x-axis largely driven by fleshy turf algae, y-axis driven by fleshy macroalgae vs. CCA), (B) effects of consumers, and differences among sites for caged (C) and open (D) tiles. Point density contours in B (2-level) and D (10-level) are shown to highlight clustering of points in the 2-dimensional state space. Points and labels represent individual CAU tiles. Stress = 0.11.

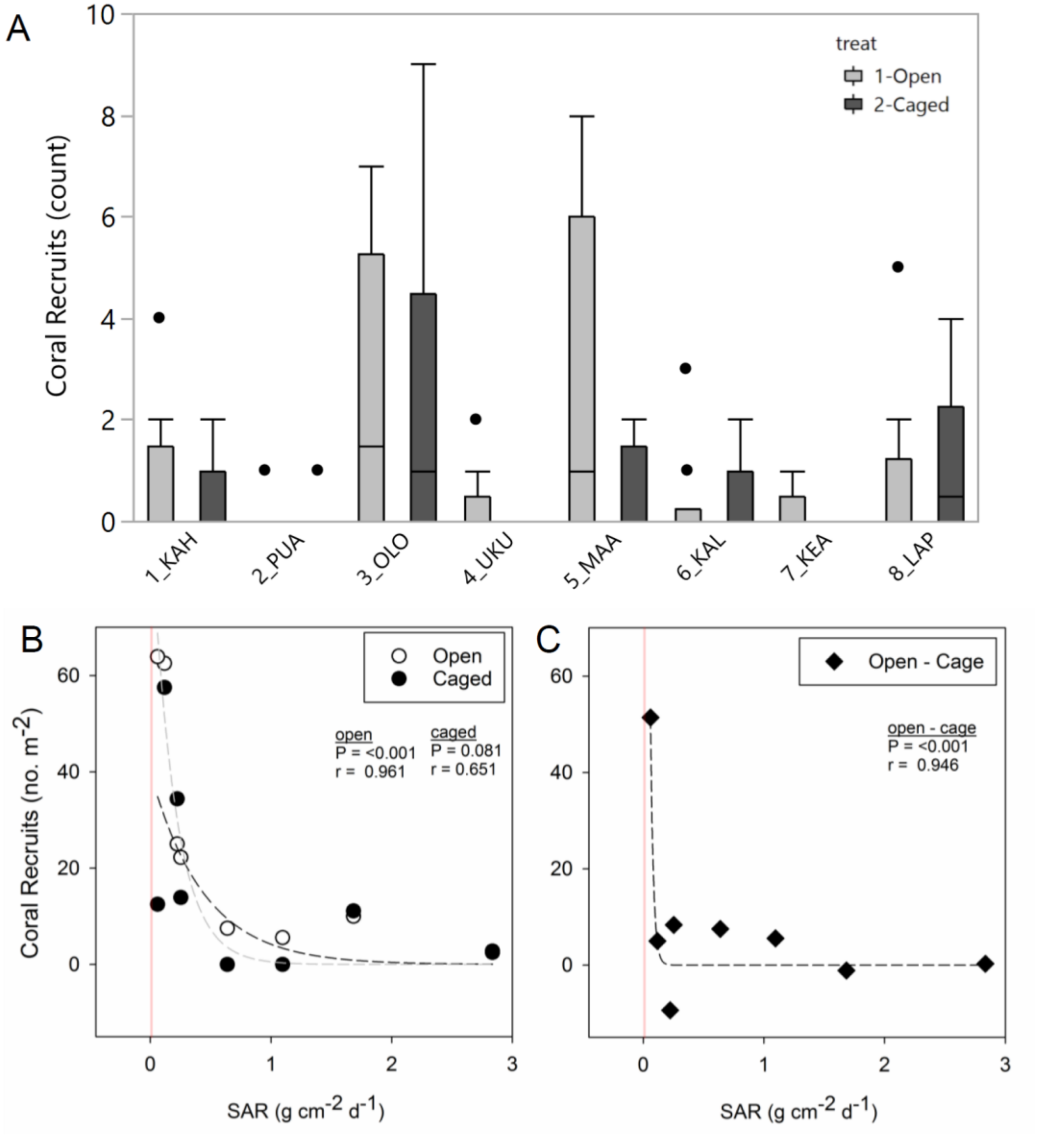

Figure 2.10. Coral recruitment among sites and in relation to sediment exposure. (A) Box plot of total number (sum) of coral recruits observed on all four sides of individual CAU tiles (per 425 cm^2) on open and caged tiles across the 8 study sites. (B) Scatterplot of mean density (scaled to per m^2) of coral recruits versus sediment accumulation rate (SAR). Dashed smoothers represent lines of best fit (exponential decay) for open (open circles, gray dashes) and caged (filled circles, black dashes) treatments. Results of non-linear correlation analyses are shown. (C) Scatter plot of the effect of consumers (open-caged) on density of coral recruits. Dashed smoother represents line of best fit (exponential decay) and results of nonlinear correlation analysis are shown. Vertical red lines in (B) and (C) represent the SAR value (0.01 g cm^{-2} d^{-1}) recommended by Rogers (1990) as a threshold for healthy ("normal") coral reefs.

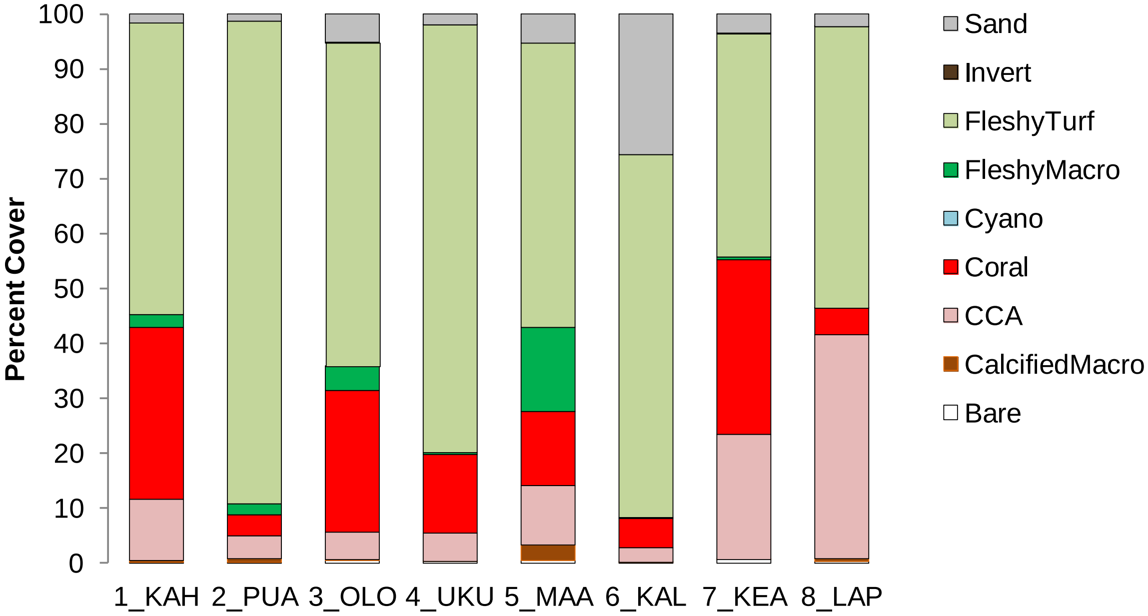

Figure 2.11. Composition of benthic communities at study sites along leeward Maui. Benthic cover was evaluated in December, 2012 by laying 2 25-m transects at each site, 10 m apart (5 m shoreward and seaward of the experimental array), and collecting benthic pictures every 2 m with a 25 cm x 25 cm photo quadrat. Percent cover of dominant functional groups was evaluated using Photogrid® software. One hundred stratified random points were assigned to each picture and the substrate or organism beneath each point was recorded.

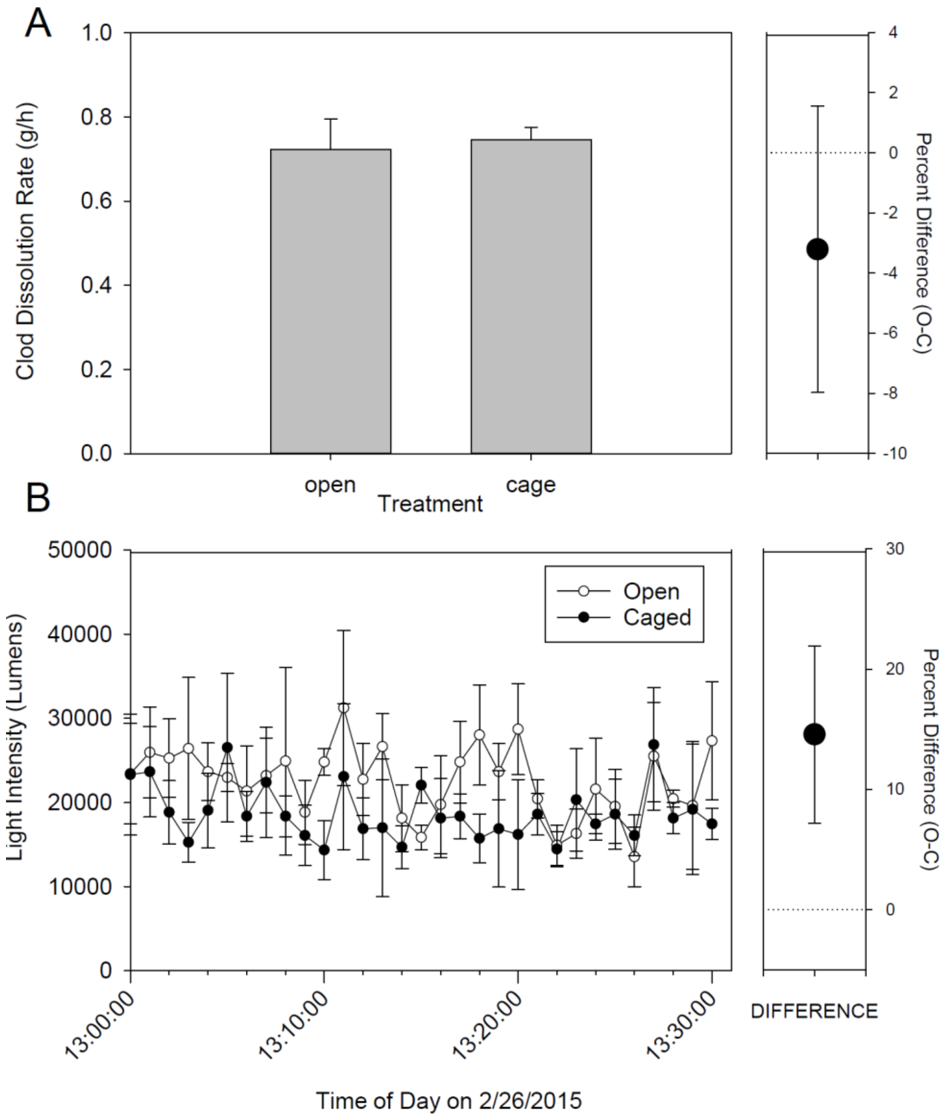

Figure 2.12. Examination of CAU tile cage artifacts. Relative effects of cages on (a) flow (22 h dissolution rate of standard gypsum plaster clod cards) and (B) light intensity during a mid-day deployment of Hobo Tidbit light loggers in February, 2015. Sample size was three replicates per treatment for both A and B.

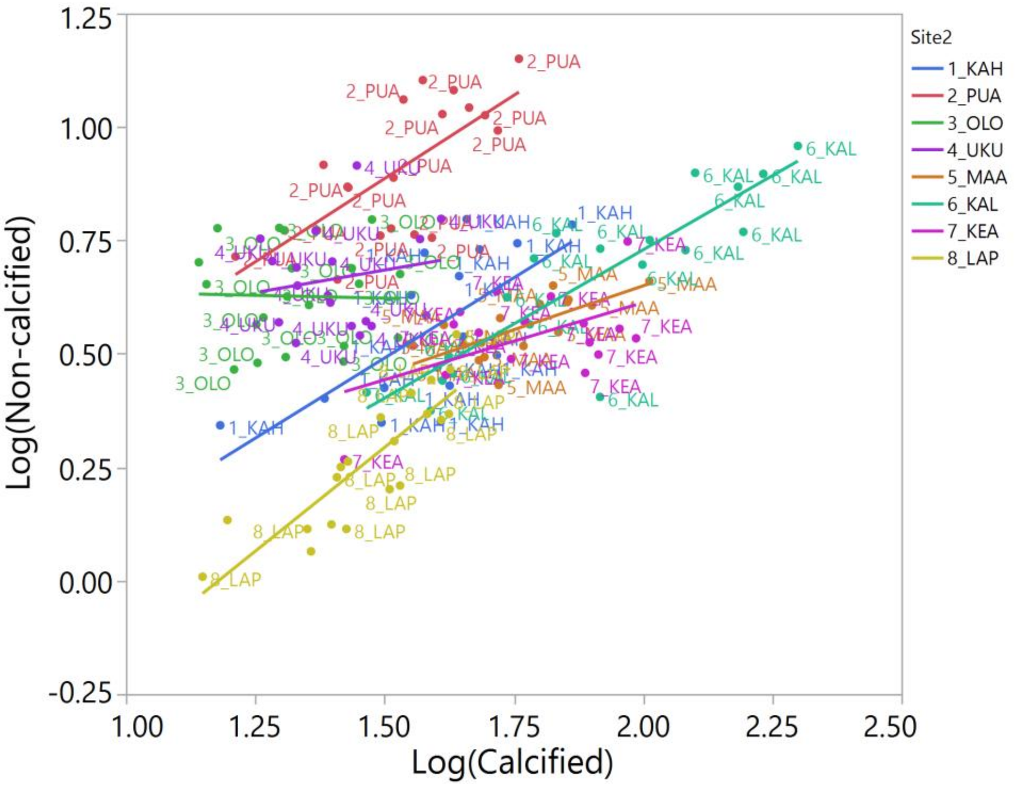

Figure 2.13. Relationships between non-calcified and calcified biomass among sites. Logged non-calcified values were modeled as functions of logged calcified values, plus site and their interaction. The overall model was highly significant ($F_{15,130} = 38.1$, $p < 0.001$) as were all factors in the model, including the interactions; thus indicating significant (generally positive) relationships that varied among sites.

CHAPTER 3 Metabolic ecology of tropical herbivorous echinoids: allometric scaling of mass and metabolism in relation to the Metabolic Theory of Ecology

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ABSTRACT

The metabolic rate of consumers is a key driver of ecosystem dynamics. In coral reefs, herbivores consume fleshy algae, and facilitate the growth of reef-building calcified organisms. While much research has focused on the functional differences in ecology among different species of herbivorous fishes, much less is known about differences among the many echinoid species found on coral reefs. Here, we conducted a standardized comparative assessment of mass and basal metabolic rates of five common species of herbivorous echinoids from three different families in the Hawaiian Islands: Diadematidae: *Echinothrix calamaris* (EC), *Echinothrix diadema* (ED); Echinometridae: *Echinometra matthaei* (EM), *Heterocentrotus mammillatus* (HM); Toxopneustidae: *Tripneustes gratilla* (TG). Using log-linear models, we examined variation in the allometric scaling of mass and metabolism in relation to the Metabolic Theory of Ecology (MTE), and explored how variation in metabolism corresponds with life-history strategies and the ecological functions of these echinoid species.

Test diameter and species identity, together, explained 98% of the variation in mass; and mass and species, combined, explained 92.4% and 87.5% of the variation in total (I) and mass-specific (B) metabolic rates, respectively. Scaling exponents did not differ among species for either mass or metabolism; however, normalizing constants did differ significantly for both metrics. Mass varied as the cube of test diameter (b = 2.914), and HM had a significantly higher mass intercept than all other species, likely due to its heavily-calcified test and spines. Total metabolic rate varied approximately as the 0.44 power of mass, much lower than that predicted by MTE (0.75), possibly due to relative increases in inorganic skeleton with size. Echinometrids (EM and HM) had significantly lower normalizing constants than other species, indicating significantly lower metabolic rates for these rock-borers. Hawaiian echinoids thus exhibited broad diversity in their mass and metabolic scaling suggesting they likely exhibit unique ecological functions in these systems. Such comparative metabolic assessments provide critical information necessary for informing theory, ecological models, and the effective management of ecosystems.

INTRODUCTION

The metabolic rates of organisms drive numerous ecological dynamics. Relative rates of production and consumption among trophic levels determine biomass accumulation, community structure, habitat complexity, and ecosystem function (Sibly et al. 2012). In coral reefs, relative rates of the production and consumption of fleshy algae, alone, can determine the state of entire communities. Coral reefs form and persist under conditions where algal consumption:production ratios are highest. When this ratio is diminished by human activities, either due to reduced consumption (e.g., via fishing) or increased production (e.g., via nutrient pollution), the system may transform into an alternative, stable state in which fleshy algae outcompete reef-building corals (Knowlton 1992). The transition to a fleshy-algal dominated system disrupts many of the key process that generate the characteristic high complexity and diversity of coral reef ecosystems; thus reefs erode into low-complexity systems with greatly diminished biodiversity and productivity (Graham 2014).

Rates of algal production and consumption are driven by numerous factors. Production is strongly influenced by the availability of limiting resources such as open space, nutrients (e.g., nitrate, phosphate, carbon, iron) and photosynthetically active radiation (PAR). Consumption is strongly influenced by herbivore community structure, biomass and metabolism. The metabolism of individual consumers is most strongly influenced by body size (mass) and temperature as described by the Metabolic Theory of Ecology (Brown et al. 2004). Though humans have modified both production (via wastewater and fertilizers) and consumption (via overfishing) on coral reefs, the removal of herbivores through fishing activities is believed to be among the most important factors favoring algal dominance at the expense of live corals (Jackson et al. 2001, Williams & Polunin 2001, Mumby 2006), and these effects may be compounded by global anthropogenic changes in temperature and chemistry (Hughes et al. 2003, Breitburg et al. 2015).

The most important grazers in coral reef ecosystems are fishes and echinoids (Carpenter 1986), and the relative importance of these two groups can vary in space and time, and can be influenced by fishing activities (Hay 1984). Though much focus has been placed on the many unique roles that different herbivorous fishes may play in coral ecosystems (Burkepile & Hay 2008, Edwards et al. 2014), much less is known about taxon-specific variation in ecological traits of diverse communities of echinoids such as those found in the tropical Pacific and Indian Oceans (McClanahan 1988, Ogden et al. 1989). In particular, little is known about how different echinoid species utilize resources, or how these species fit into metabolism-based models of coral reef ecosystem dynamics (Sibly et al. 2012, Lawrence 2013).

Here, using standard power functions, we described variation in the allometric scaling of mass and metabolic rates of five dominant echinoid species in the Hawaiian Islands. We predicted that scaling exponents would match classic theory; specifically, mass would scale as the cube (b=3) of test diameter and metabolism as the 3/4 (b=0.75) of mass as described by Kleiber's Law and MTE (Brown & Sibly 2012). We predicted significant differences among echinoid species in allometric scaling functions, with more closely related species (e.g., within a family) exhibiting similar mass and metabolic functions that correspond with phylogeny and life-history strategies. By describing and contrasting test-mass relationships, total metabolic rates (TMR, I), and mass-specific metabolic rates (MSMR, B) among several important echinoid species, we shed light on the diverse metabolic ecology within this important guild and provide estimates of key metrics necessary for parameterizing metabolic-based community and ecosystem models.

METHODS

Study Site

All field work was conducted on nearshore (5-7 m depth) fringing coral reefs on the island of Maui, Hawaii (20°56'19"N, 156°41'35"W). Reefs in the Main Hawaiian Islands (MHI) are built predominantly by scleractinian corals of the genera: *Porites, Montipora,* and *Pocillipora*. The cover of live corals around the MHI has declined rapidly over last several decades, with many reefs showing signs of rapid degradation and algal overgrowth (Pandolfi et al. 2005, Walsh et al. 2013), concurrent with historic and on-going fishing activities (Friedlander & DeMartini 2002, Friedlander et al. 2007). Marine herbivores (e.g., fishes and echinoids) are important in Hawaii given high inputs of nutrient-laden groundwater and runoff (Smith et al. 1981, Dailer et al. 2010, Dailer et al. 2012) that stimulate the growth of native and invasive algae at the expense of live corals (McCook et al. 2001, Smith et al. 2001). Rapid declines in live coral cover on Hawaii's reefs have been associated with large blooms of fleshy algae (Smith et al. 1981, Smith et al. 2005), prompting the development of herbivore-specific protected areas and even the artificial enhancement of echinoid populations for use as algal bio-control agents (Stimson et al. 2007) on Maui and Oahu.

Metabolic Assays

We measured resting oxygen consumption rates to compare differences in metabolic activity among five echinoid species: *Echinothrix calamaris* (EC), *Echinothrix diadema* (ED), *Echinometra matthaei* (EM), *Heterocentrotus mammillatus* (HM), and

Tripneustes gratilla (TG) (Fig. 31). These species represented three echinoid families: Diadematidae (EC, ED), Echinometridae (EM, HM), and Toxopneustidae (TG). Metabolic assays were conducted at the Maui Ocean Center (MOC) located in Ma’alaea, Maui. Echinoids were collected from fringing reefs in West Maui and transported (in the dark) to the MOC in a continually-aerated 142 L cooler (transport time = 30 min.). At the MOC, the cooler was immediately connected to flow-through seawater and echinoids were allowed to acclimate in the dark for 60 min. After acclimation, one individual was placed in each of three clear plastic incubation chambers containing a plastic mesh basket and 11.7 liters of fresh seawater that was stirred constantly by 2 rotating stir bars. Metabolic chambers were housed in a 142 liter cooler and bathed in ambient flow-through seawater to maintain a constant temperature of 26.2 °C (SD=0.1). All temperatures (to 0.1 °C) and dissolved oxygen concentrations (to 0.01 mg/l) were measured using a Hq40d Hach portable meter fitted with a luminescent dissolved oxygen optode and temperature probe (Hach Company, USA).

Following probe calibration (using saturated air), initial temperature and oxygen concentrations were measured in each chamber. Chambers were then sealed airtight, and the cooler closed (dark incubations). Each assay lasted 60 min., after which, temperature and oxygen concentrations were measured again without breaking the air-tight seal by placing the probe tip through a hole in the lid. Echinoids were then removed, test diameters (0.1 cm) and mass (0.1 g) measured, and then placed in a separate holding tank. Volumetric displacement of echinoids (modeled as a hemisphere), was always less than 1% of total chamber volume. Metabolic chambers were then rinsed, refilled with fresh seawater, and two additional 60 min. assays conducted (each with three additional individuals) for a total of nine individuals per species.

Each of the five echinoid species were assayed on a separate day and all were released at the site of collection the day after assays were conducted. Six 60-min. control assays were conducted daily (3 each before and after echinoid assays) to assess potential microbial contributions to oxygen consumption. Echinoid metabolic rates were corrected by subtracting the corresponding daily mean microbial (control) respiration rate from echinoid rates. Daily means of controls ranged from 0.11 to 0.53 mg O2/h (grand mean = 0.30 ± 0.035 SE). Total metabolic rate (TMR, I) was calculated by multiplying the change in oxygen concentrations by the volume of the chamber and dividing by the elapsed time (mgO_2/h). Mass-specific metabolic rate (MSMR, B) was calculated by dividing TMR by the wet mass of the corresponding individual ($mgO_2/g/h$).

Allometric Power Functions

Mass and metabolic rates were modeled using log-linear transformations of power functions. These models fit mass and metabolic data well and provide simple solutions for scaling exponents (b = slope) and normalizing constants ($a = 10^{\text{intercept}}$) (Brown et al. 2004, White et al. 2012):

$$y = ax^b \tag{1}$$

$$\log(y) = b * log(x) + \log(a) \tag{2}$$

Equation (2) was modified to fit each of the three modeled relationships below:

$$\log(M) = b * log(D) + log(a) \tag{3}$$

where D = test diameter (cm) and M = mass (g),

$$\log(I) = b * log(M) + log(a) \tag{4}$$

where I = total metabolic rate (mgO_2/h), a & b = γ and I_o in MTE, respectively), and

$$\log(B) = b * log(M) + log(a) \tag{5}$$

where B = mass-specific metabolic rate ($mgO_2/h/g$), a & b = α and B_o in MTE, respectively.

No significant differences among species in the scaling exponent (b) for any model was observed (see results, Table 3.3); therefore, log-linear slopes were considered homogeneous. Intercepts (i.e., normalizing constants), however, differed significantly among species for all models. To compare intercepts, expanded parameter estimates were examined; thus each model included an overall intercept (c) and species-specific modifier (u_i) satisfying the equation:

$$a = 10^{(u_i+c)} \tag{6}$$

Statistical Analyses

We used linear models, regression and analysis of covariance (ANCOVA), to statistically examine log-linear relationships and parameters (b = slope, a = $10^{\text{intercept}}$), and test for differences among echinoid species (White et al. 2012). Mass was modeled as a function of test diameter, oxygen consumption rates each modeled as function of echinoid mass, and species was included as a fixed effect. To assess (i.e. remove) the potential effects of the calcified skeleton and spines on body mass relationships, oxygen consumption rate was also modeled as a function of species and test volume (modeled as a sphere) (Table 3.4). Differences in model parameters were compared among species using 95% confidence intervals. Parametric assumptions were evaluated for each test using Q-Q and residual plots—any departures appeared small and these methods are robust to such departures (Underwood 1997). Statistics were conducted using JMP Pro 12.01.1 (SAS Institute Inc., Cary, NC, USA).

RESULTS

Mass vs. Test-diameter

For log-transformed models, test diameter explained 69.3 % (alone) and 98.1% (with species as a fixed factor) of the variation in echinoid mass (Table 3.1, Fig. 3.2a-b). We found no evidence for differences in the slopes (b = scaling exponent) of log-linear test-mass relationships among urchin species (Table 3.3). Echinoid mass scaled as the approximate cube (b = 2.91 ± 0.17 SE) of test diameter for all species (Table 3.3, Fig. 3.3a). Differences among species in intercepts (i.e., normalizing constants), however, were highly significant (Table 3.1). Though differences in intercepts for EC, EM, TG, and ED were small and non-significant, ED was slightly heavier (Fig. 3.3b) and HM much heavier, with greater intercepts than other species (Table 3.1, Fig. 3.3b).

Metabolism vs. Mass

For log-transformed models, mass explained 40.2 % (alone) and 92.4% (with species as a fixed factor) of the variation in echinoid total metabolic rate (I = TMR) (Table 3.1, Fig. 3.2c-d). We found no evidence for differences in the slopes (b =scaling exponent) of log-linear mass-I relationships among urchin species (Table 3.3). Echinoid TMR scaled as the approximate 2/5 exponent (b = 0.44 ± 0.14 SE) of mass for all species (Table 3.1, Fig. 3.3a), differing significantly from 3/4 (0.75) predicted by Kleiber's Law of MTE (Brown & Sibly 2012). Differences among species' intercepts (i.e., normalizing constants) were highly significant with EC>TG>ED>HM=EM (Table 3.1, Fig. 3.3b). Intercepts for EC, TG, and ED (mean $u_i = 0.22$) were all much higher than those of the echinometrids HM and EM (mean $u_i = -0.32$) (Fig. 3.3b).

For log-transformed models, mass explained 0.014 % (alone) and 87.5% (with species as a fixed factor) of the variation in echinoid mass-specific metabolic rate (B = MSMR) (Table 3.1, Fig. 3.2e-f). We found no evidence for differences in the slopes (b = scaling exponent) of log-linear mass-B relationships among urchin species (Table 3.3). Echinoid MSMR scaled as the approximate -1/2 exponent (b = -0.56 ± 0.14 SE) of mass for all species (Table 3.1), also differing significantly from the -1/4 (-0.25) predicted by MTE (Brown et al. 2004). Given that B is directly related to I (B=I/M), differences among species in intercepts (normalizing constants) were equivalent and highly significant (Table 3.1, Fig. 3.3d).

Log-linear models of metabolism as a function of modeled test volume were similar to those for mass (Table 3.4). The estimate of the slopes for TMR (b = 0.49 ± 0.14 SE) was low and similar to mass-based relationships (b = 0.44); however, did not differ significantly from MTE predictions (b = 0.75 and -0.25, respectively). Intercepts differed significantly among species and appeared similar to differences observed for mass-based models, except that HM exhibited a significantly higher metabolic rate than EM, indicating a higher metabolic rate per volume that was not observed for per mass comparisons.

DISCUSSION

Here, we described variation in the allometric scaling of mass and metabolism for five species of tropical herbivorous echinoids common to coral reefs in Hawaii and around the globe. This trophic guild plays an important role in coral reef ecosystems by consuming fleshy algae and facilitating the abundance and growth of reef-building corals and coralline algae (Sammarco 1982, Hughes 1994, Idjadi et al. 2010). Differences among species were both significant and large. HM exhibited a uniquely heavy (calcified) morphology, and EC, ED, and TG exhibited the highest metabolic rates (both individual and mass-specific), with both echinometrids (EM and HM) exhibiting the lowest. Comparing the metabolic ecology among species and communities is critical to our understanding the diversity of ecological functions within trophic guilds and ecosystems. For example, metabolic rates can inform us about biomass production, ontogenetic growth, mortality, interspecific interactions, species diversity, energy fluxes, and population and trophic dynamics (Brown et al. 2004, Sibly et al. 2012). The development and testing of this foundational theory is dependent on individual studies that examine and report metabolic rates across a variety of taxa (Gillooly et al. 2001, Seibel & Drazen 2007). Here we have described the metabolic ecology of important tropical herbivorous echinoids, thus advancing our understanding of the metabolic and trophic ecology of this guild and the coral reef ecosystems in which they thrive.

Echinoid Mass

Test diameter, alone, explained 70% of the variation in echinoid mass, and including species identity increased explanatory power to >98%. The allometric scaling exponent ($b = 2.914 \pm 0.165$ SE) for the estimation of mass from diameter did not differ among urchin species, and was similar to our prediction ($b=3$) given that volume ($\propto$ mass) is a cubic function of linear measurements (e.g., diameter). Significant variation around this expected value (95% CI = 2.58-3.24) was likely due to our limited sample sizes and size ranges of each species examined. Four of the five species exhibited similar normalization constants (a) and scaling functions, with HM being the one exception. Though HM is in the same family as EM, its large-spined morphology is similar to distantly-related "rough-spined" echinoids of the family Cidaridae. It appears that HM's unique, heavily-calcified spines greatly increased its normalization constant (i.e., relative mass). Therefore, echinoid morphology appeared to be more important for accurate mass-scaling than phylogeny.

The mass-scaling functions we developed (Table 3.2) are valuable in that they facilitate calculation of the biomass of echinoid communities from field surveys, given surveys include data on (a) echinoid identities, (2) densities, and (3) test diameters. Many long-term surveys, however, fail to include adequate data on echinoid densities, and even fewer provide estimates of echinoid test diameter (and mass). Though the importance of fish biomass (vs. density) has been identified in studies of coral reef ecology and trophic dynamics, echinoid communities are rarely described in terms of their biomass. The lack of echinoid biomass data is problematic for studies of ecosystem dynamics on coral reefs because simple estimates of density do not account for variation in population structure and biomass, both of which exert significant influence on community metabolic and grazing rates (Brown et al. 2004).

Echinoid Metabolism

Inclusion of species identity (with mass) improved our ability to explain the variation in total metabolic rates from 40% to > 92%. Thus, species identity is a critically important factor for estimating echinoid metabolism. The scaling exponent ($b=0.438$) for total metabolic rate (TMR=I) did not differ among urchin species, however it did differ significantly from our prediction ($b=0.75$) given the 3/4 scaling exponent of the MTE (Brown et al. 2004). Therefore, total metabolic rates of echinoids increased much slower (as a function of mass) than predicted by Kleiber's Law (Brown & Sibly 2012).

Similarly, the scaling exponent ($b=-0.562$) for mass-specific metabolic rate (MSMR=B) was significantly lower than our prediction ($b=-0.25$) given the -1/4 scaling exponent of the MTE (Brown et al. 2004); therefore, MSMR decreased faster with mass that predicted. The high and low scaling exponents for TMR and MSMR, respectively, indicate that metabolic rates of large echinoids were much lower than predicted by the MTE. This could be due to (a) increases in the proportion of mass composed of metabolically-inactive calcified skeleton or, (b) rapid declines in the mean metabolic activity of soft tissues as echinoids grow and age.

We did not detect significant differences among echinoid species in the scaling exponents for mass or metabolism. A shared scaling exponent may be expected given the shared phylogeny and subsequent physiological similarities among species within the guild. It is possible, however, that differences in mass or metabolic scaling do exist, but were not detectible given the replication and size ranges of each species in this study. It is also possible that other echinoid species not included in the present study (e.g. family Cidaridae) may exhibit unique scaling properties. Such variation would be interesting to test with larger sample sizes, size ranges, and numbers of species in coral reefs and across other marine ecosystems.

Given the variation in skeletal morphology (which are likely metabolically inactive), we examined echinoid metabolism as a function of modeled test volume, thus ignoring effects of heavily calcified test and spines. Scaling exponents based on mass and volume were similar for TMR, suggesting that skeleton like did not drive scaling parameters. Interestingly, HM exhibited a significantly higher intercept than EM as a function of volume (but lower as a function of mass), indicating that HM's tissues exhibit a higher metabolic rate than EM. While this may be interesting theoretically, standard methods in metabolic ecology do not include corrections for skeletal features (Sibly et al. 2012). Furthermore, the ecological and metabolic costs associated with transporting robust skeletons are important aspects of the ecology of organisms that should be included in future metabolic assessments (Costa & Shaffer 2012).

Metabolic Theory

The MTE provides standard methods for normalizing and comparing metabolic rates among species, accounting for differences in sizes of, and the temperatures at which, organisms were assayed. Here, we controlled temperature (to 26°C), and thus did not require use of the standard universal temperature dependence (UTD) model (Gillooly et al. 2001), based on the Arrhenius function ($e^{-E/kT}$) , to compare metabolic rates among echinoid species. UTD standardization, however, is necessary for comparing across studies conducted at different temperatures. Mass-correction is also necessary for comparing across studies or species using organisms of different masses. For standardized (mass-corrected) comparisons among tropical echinoids, our data suggest use of $\gamma = 0.438$ and $\alpha = -0.562$ for total (I) and mass-specific (B) echinoid metabolic rates, respectively. Though significantly different from the MTE values of 0.75 and -0.25 (for γ and α, respectively), our empirically-derived parameters likely better reflect the true mass-scaling of metabolism for these tropical echinoids (Table 3.2).

Though nearly a century of research, several seminal books, and modern syntheses all argue for a general 3/4 scaling of total metabolic rate with mass; several studies (including ours) have found evidence for scaling exponents that differ significantly from Kleiber's Law (Glazier 2005, White et al. 2012). For example, other calcified marine invertebrates (e.g. bryozoans) have been shown to exhibit nearly identical mass-scaling exponents ($\gamma = 0.47$) (White et al. 2011) to those we measured for echinoids ($\gamma = 0.44$). Metabolic rates of mammals can scale significantly lower ($\gamma = 0.67$) (White & Seymour 2003) than Kleiber's Law and scaling of γ can vary as a function of the mean mass and taxonomy (e.g., order) of the specific mammalian groups selected for analyses (Clarke et al. 2010). Furthermore, unicellular heterotrophs differ from Kleiber's Law in the opposite direction than small mammals, with linear (γ=1) scaling for protists and even superlinear (γ=2) scaling for bacteria (DeLong et al. 2010).

Though such variation in scaling exponents has caused some researchers to question the statistical validity of Keiber's Law (Heusner 1982), others have shown that such variation could potentially arise due to differences in intra- vs. interspecific scaling exponents (Feldman & McMahon 1983) and real variation among taxonomic groups, size- and age-classes, and habitats (Glazier 2005). Our low scaling exponent for echinoids included intraspecific variation in mass and, therefore, may support this hypothesis. However, mean scaling coefficients for echinoderms (on average) could support γ values of either 2/3 or 3/4 (Glazier 2005). Future studies on the mass-scaling of additional echinoid species would be valuable for exploring whether intra- and interspecific scaling exponents differ within this guild and from MTE predictions.

Conclusion

Echinoderms often exert strong top-down effects on benthic dynamics in marine ecosystems. Predation by asteroids and herbivory by echinoids are often dominant structuring forces in benthic marine ecosystems, both intertidal and subtidal, and in tropical, temperate, and polar seas (Dayton et al. 1974, Estes & Palmisano 1974, Paine 1980, Carpenter 1997, De'ath et al. 2012). Due to the strong interaction strengths imposed by these organisms, and their diversity, it is important that we examine variation in the ecological functions of coexisting taxa to elucidate strong ecological linkages that may be important for the proper understanding and management of ecosystems (Power et al. 1996). Here, we have provided new information on species-level variation in the scaling of mass and metabolism for 5 herbivorous echinoids common to coral reefs around the globe. Echinoids exhibited large differences in individual and mass-specific metabolic rates, indicative of large differences in algal consumption rates and benthic ecological interaction strengths.

Metabolic theory has contributed greatly to our understanding of how the biomass and metabolism of species and communities influence ecosystem dynamics (Sibly et al. 2012). In coral reefs, for example, metabolic rates have been used to estimate the *in situ* contributions of cryptic organisms (i.e., cryptofauna) to total grazing budgets, yielding large consumption estimates (>30% of the daily production) for this under-studied herbivore community (Klumpp et al. 1988). Furthermore, changes in metabolic rates (e.g. due to ocean warming) may result in significant, predictable changes to interaction strengths and ecosystem dynamics (Ulbricht & Pritchard 1972, Sanford 2002, Carr & Bruno 2013). Given the importance of echinoids in coral reef (among other) ecosystems and the many ecological rates that correlate strongly with biomass and metabolism, data on taxon-specific biomass and metabolism in coral reef studies remains an important gap in our understanding of community structure and function. The parameters we have provided here, combined with survey data on echinoid sizes, community structure, and density, will improve estimates of *in situ* ecological rates, interactions strengths, and will allow researchers to test and model ecological dynamics in new ways and at larger and more ecologically-relevant scales.

ACKNOWLEDGEMENTS

G. Butler and S. Kram assisted with metabolic assays in the field. The SIO Scientific Diving Program (C. McDonald and R. Walsh) and Maui Scuba Diving Snorkel Center (R. Carman) supported diving operations. Maui Ocean Center (J. Luecke) provided wet-lab facilities, and SIO Center for Marine Biodiversity and Conservation (P. Dockry) provided administrative support. R. Hechinger, L. Levin and several anonymous reviewers provided comments and contributions that greatly improved the manuscript. Artwork courtesy of Adi Khen. This study was a collaboration with the Maui Division of Aquatic Resources (R. Sparks and D. White) under DAR permit numbers: SAP2011-77, SAP2012-67, and SAP2014-42. Funding came from the PADI Foundation, Edna-Bailey Sussman Foundation, Scripps Family Foundation, SciFund Challenge, NRC Ford Foundation Fellowship, and the National Science Foundation Grant No. 0903551.

Chapter 3, in part is currently being prepared for submission for publication of the material. Lewis, Levi S; Eynaud, Yoan; Smith, Jennifer E. The dissertation/thesis author was the primary investigator and author of this material.

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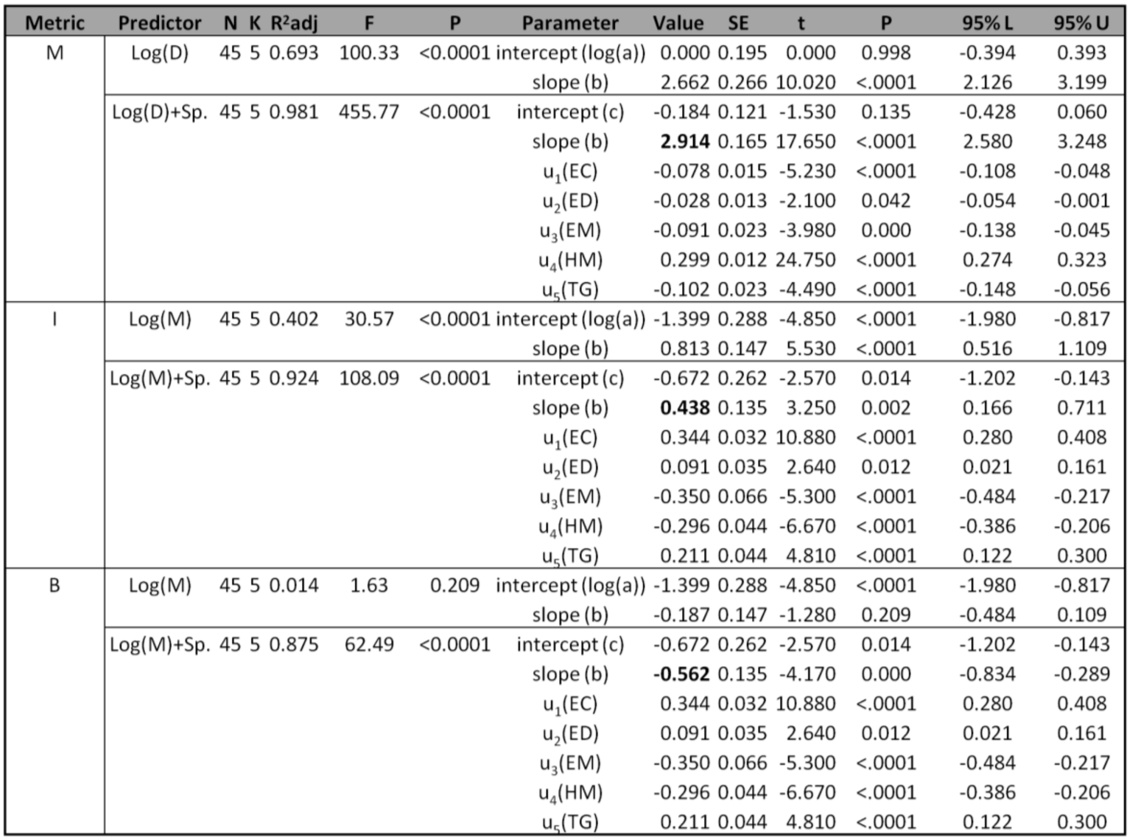
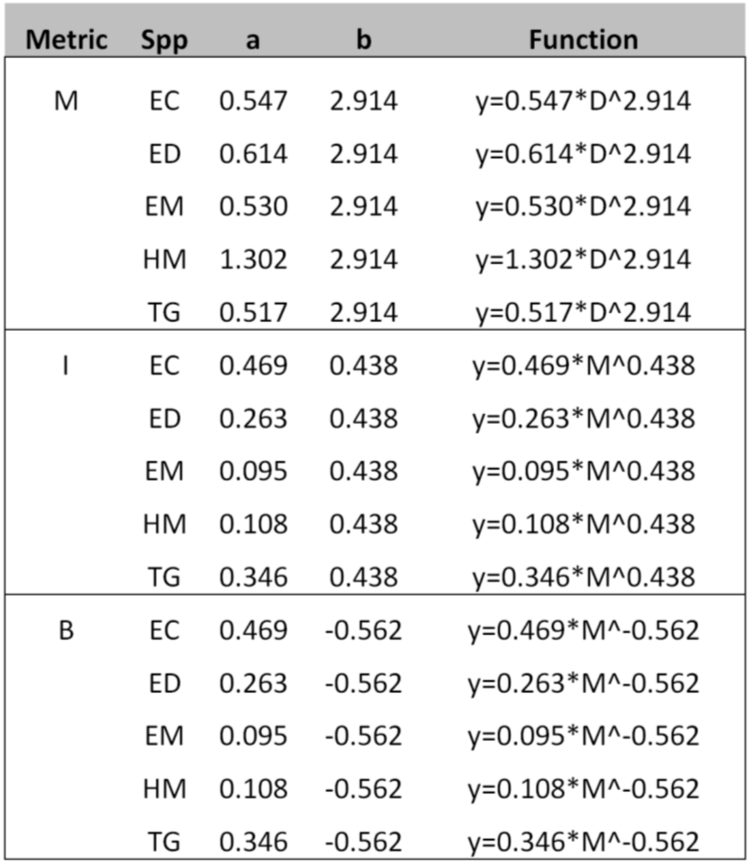
TABLES

Table 3.1. Linear regression and analysis of covariance (ANCOVA) models & coefficients (using homogeneous slopes) of $\log_{10}(x)$ transformed values. Metrics: M = mass (g), I = total metabolic rate (TMR, mg O_2/h), B = mass-specific metabolic rate (MSMR, mgO_2/h/g). Predictors: D = test diameter (cm), M = mass (g), Sp. = urchin species (EC, ED, EM, HM, TG).



Metric	Predictor	N	K	R^2adj	F	P	Parameter	Value	SE	t	P	95% L	95% U
M	Log(D)	45	5	0.693	100.33	<0.0001	intercept (log(a))	0.000	0.195	0.000	0.998	-0.394	0.393
							slope (b)	2.662	0.266	10.020	<.0001	2.126	3.199
	Log(D)+Sp.	45	5	0.981	455.77	<0.0001	intercept (c)	-0.184	0.121	-1.530	0.135	-0.428	0.060
							slope (b)	**2.914**	0.165	17.650	<.0001	2.580	3.248
							u_1(EC)	-0.078	0.015	-5.230	<.0001	-0.108	-0.048
							u_2(ED)	-0.028	0.013	-2.100	0.042	-0.054	-0.001
							u_3(EM)	-0.091	0.023	-3.980	0.000	-0.138	-0.045
							u_4(HM)	0.299	0.012	24.750	<.0001	0.274	0.323
							u_5(TG)	-0.102	0.023	-4.490	<.0001	-0.148	-0.056
I	Log(M)	45	5	0.402	30.57	<0.0001	intercept (log(a))	-1.399	0.288	-4.850	<.0001	-1.980	-0.817
							slope (b)	0.813	0.147	5.530	<.0001	0.516	1.109
	Log(M)+Sp.	45	5	0.924	108.09	<0.0001	intercept (c)	-0.672	0.262	-2.570	0.014	-1.202	-0.143
							slope (b)	**0.438**	0.135	3.250	0.002	0.166	0.711
							u_1(EC)	0.344	0.032	10.880	<.0001	0.280	0.408
							u_2(ED)	0.091	0.035	2.640	0.012	0.021	0.161
							u_3(EM)	-0.350	0.066	-5.300	<.0001	-0.484	-0.217
							u_4(HM)	-0.296	0.044	-6.670	<.0001	-0.386	-0.206
							u_5(TG)	0.211	0.044	4.810	<.0001	0.122	0.300
B	Log(M)	45	5	0.014	1.63	0.209	intercept (log(a))	-1.399	0.288	-4.850	<.0001	-1.980	-0.817
							slope (b)	-0.187	0.147	-1.280	0.209	-0.484	0.109
	Log(M)+Sp.	45	5	0.875	62.49	<0.0001	intercept (c)	-0.672	0.262	-2.570	0.014	-1.202	-0.143
							slope (b)	**-0.562**	0.135	-4.170	0.000	-0.834	-0.289
							u_1(EC)	0.344	0.032	10.880	<.0001	0.280	0.408
							u_2(ED)	0.091	0.035	2.640	0.012	0.021	0.161
							u_3(EM)	-0.350	0.066	-5.300	<.0001	-0.484	-0.217
							u_4(HM)	-0.296	0.044	-6.670	<.0001	-0.386	-0.206
							u_5(TG)	0.211	0.044	4.810	<.0001	0.122	0.300

Table 3.2. Back-transformed (anti-logged) parameters and power functions ($y=ax^b$). Predictors: D = echinoid test diameter (cm), M = echinoid mass (g). Metrics as in Table 1.



Metric	Spp	a	b	Function
M	EC	0.547	2.914	y=0.547*D^2.914
	ED	0.614	2.914	y=0.614*D^2.914
	EM	0.530	2.914	y=0.530*D^2.914
	HM	1.302	2.914	y=1.302*D^2.914
	TG	0.517	2.914	y=0.517*D^2.914
I	EC	0.469	0.438	y=0.469*M^0.438
	ED	0.263	0.438	y=0.263*M^0.438
	EM	0.095	0.438	y=0.095*M^0.438
	HM	0.108	0.438	y=0.108*M^0.438
	TG	0.346	0.438	y=0.346*M^0.438
B	EC	0.469	-0.562	y=0.469*M^-0.562
	ED	0.263	-0.562	y=0.263*M^-0.562
	EM	0.095	-0.562	y=0.095*M^-0.562
	HM	0.108	-0.562	y=0.108*M^-0.562
	TG	0.346	-0.562	y=0.346*M^-0.562

Table 3.3. Log-linear models including species x size (D = echinoid test diameter (cm), M = echinoid mass (g)) interactions. Note that P-values of all interactions terms (bold) are highly non-significant. Metrics as in Table 3.1.

Metric	Source/Factor	DF	Sum of Squares	Mean Square	F Ratio	Prob > F	R^2adj
M	Model	9	3.512	0.390	234.815	<.0001	0.979
	Error	35	0.058	0.002			
	C. Total	44	3.570				
	Species	4	0.402		60.425	<.0001	
	Log(D)	1	0.186		111.649	<.0001	
	Log(D)*Species	4	0.002		0.287	**0.8844**	
I	Model	9	5.313	0.590	57.594	<.0001	0.920
	Error	35	0.359	0.010			
	C. Total	44	5.672				
	Species	4	0.424		10.341	<.0001	
	Log(M)	1	0.057		5.571	0.024	
	Log(M)*Species	4	0.023		0.561	**0.6928**	
B	Model	9	3.082	0.342	33.405	<.0001	0.869
	Error	35	0.359	0.010			
	C. Total	44	3.440				
	Species	4	0.424		10.341	<.0001	
	Log(M)	1	0.068		6.587	0.0147	
	Log(M)*Species	4	0.023		0.561	**0.6928**	

Table 3.4. Log-linear ANCOVA models including species and volume ($V = cm^3$) as predictors of total metabolic rate (I). Scaling exponent (slope) in bold.

Metric	Predictor	N	K	R^2adj	F	P	Parameter	Value	SE	t	P	95% L	95% U
I	Log(V)+Sp.	45	5	0.928	114.50	<.0001*	intercept (c)	-0.762	0.258	-2.950	0.0053*	-1.284	-0.240
							slope (b)	**0.493**	0.135	3.650	0.0008*	0.220	0.766
							u_1(EC)	0.298	0.036	8.170	<.0001*	0.225	0.372
							u_2(ED)	0.087	0.032	2.680	0.0107*	0.021	0.152
							u_3(EM)	-0.366	0.056	-6.510	<.0001*	-0.480	-0.252
							u_4(HM)	-0.162	0.030	-5.460	<.0001*	-0.222	-0.102
							u_5(TG)	0.143	0.056	2.560	0.0145*	0.030	0.256

FIGURES

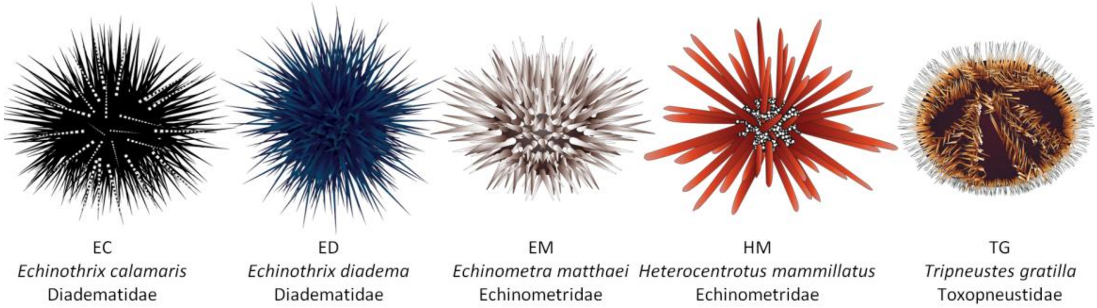


Figure 3.1. Taxonomy and morphology of 5 tropical echinoids examined in the this study.

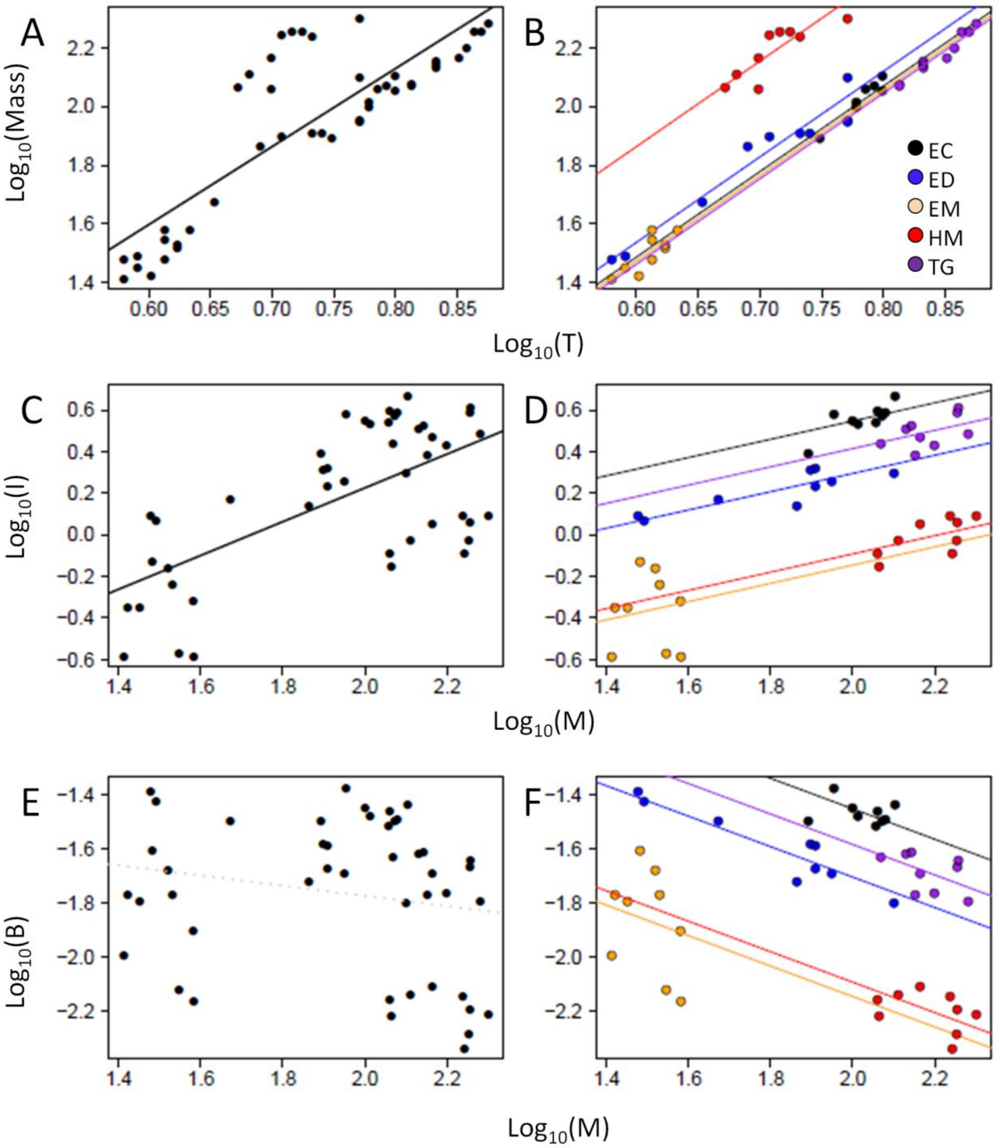


Figure 3.2. Allometric relationships of echinoid mass and metabolism for 5 tropical herbivorous echinoids. Mass (M, g) vs. test diameter (T, cm) (a-b); and individual (I, mg O$_2$ h^{-1}) (c-d) and biomass-specific (B, mg O$_2$ g^{-1} h^{-1}) (e-f) metabolic rates vs. mass. Figures on the left (a,c,e) include all individuals pooled; figures on the right (b,d,f) include species as fixed factors (slopes = homogenous). All data were Log10(x) transformed and lines represent ordinary least-square linear fits of log10(x,y) values (see Table 3.1).

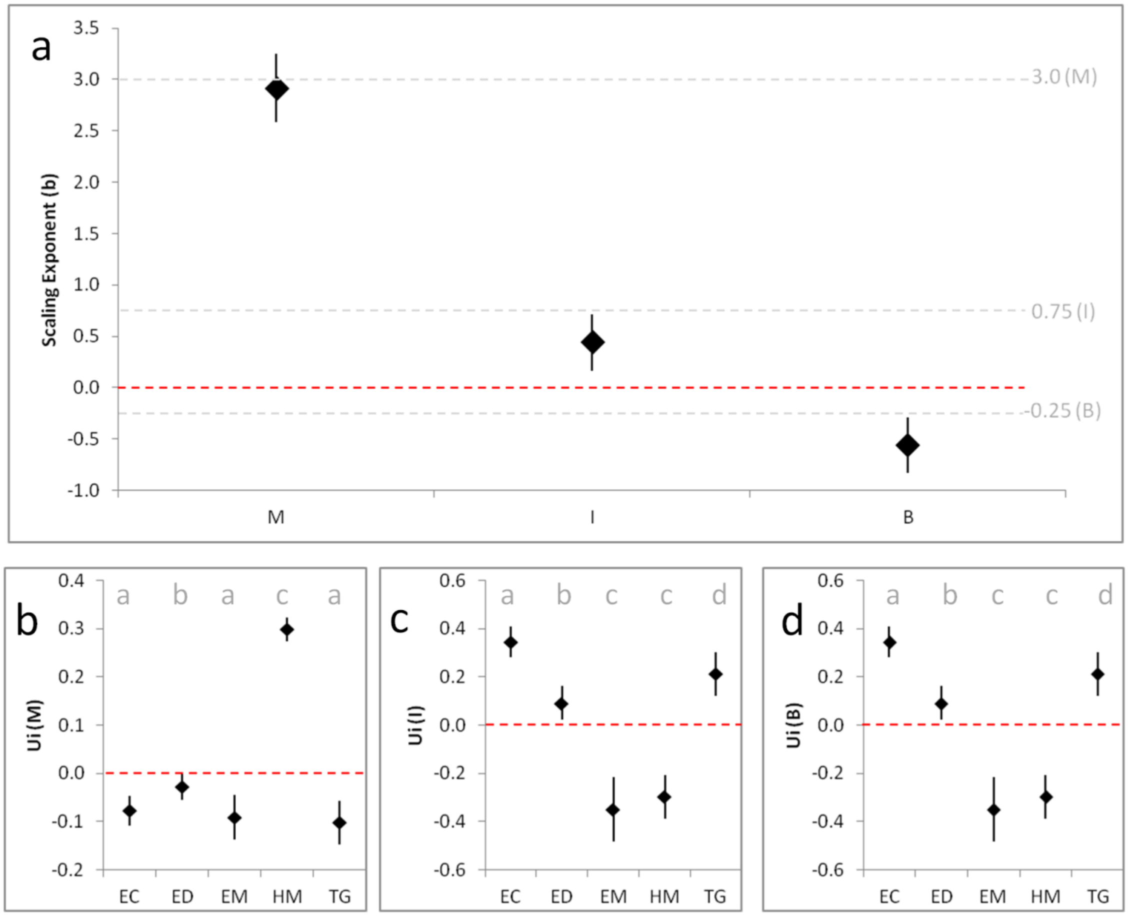


Figure 3.3. Allometric scaling coefficients for mass and metabolism of 5 tropical echinoids: (a) estimated mass-scaling exponents and predicted values (grey-dashed lines) for mass (M = 3.0), total metabolic rate (I = 0.75) and mass-specific metabolic rate (B = -0.25), and (b-d) species-specific normalizing coefficient modifiers (u_i) . Letters in (b-d) indicate groupings based on 95% confidence intervals. Mean ±95% I shown. Red-dashed lines indicate the zero line.

CHAPTER 4 Diversity in the ecological functions of sympatric herbivorous echinoids: metabolism, consumption rate, and dietary preference

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ABSTRACT

Herbivores influence the structure and function of ecosystems, especially in the marine environment where ecosystems have rapidly transformed due to the presence or absence of a single important grazer or grazing community. The importance of variation in the ecological functions of herbivores, however, remains a critical gap in our understanding of community dynamics. Tropical echinoids (sea urchins) can facilitate the growth of stony corals by consuming fleshy algal competitors, yet little is known about variation in this ecological function. We examined the functions of five sympatric herbivorous echinoids on a fringing coral reef in Maui, Hawaii. We used (1) field-based grazing assays to compare grazing rates and dietary preferences for several key algal functional groups and (2) lab-based assays to measure resting metabolic rates of each echinoid species for comparison with grazing behavior. We observed 4- to 10-fold variation among species in individual and mass-specific grazing and metabolic rates, with metabolism predicting up to 97% of the variation in grazing rate among species. Though echinoids grazed as generalists, often consuming several types of algae, species exhibited significant and unique algal preferences. Echinoids with the lowest metabolic rates exhibited the highest variation and no strong preference for any algal species; in contrast, those with the highest metabolic rates exhibited consistent preferences, suggesting a positive relationship between metabolism and preference for higher-quality foods. By combining standardized studies of grazing behavior with metabolic assays, we demonstrate significant taxon-specific variation in the grazing behavior of tropical herbivorous echinoids. Given our results, future efforts to assess the contributions of echinoid communities to benthic dynamics can and should account for variation in community structure and function.

INTRODUCTION

The ability of similar species to coexist has long fascinated ecologists (Hutchinson 1961; Connell 1978). Perhaps even more intriguing has been the importance of this diversity to the functioning of ecosystems (Elton 1958; Stachowicz et al. 2007; Tilman et al. 2012), and how species losses and invasions may affect the resilience of ecosystems to disturbance and environmental change (Williams and Smith 2007; Cardinale et al. 2012; Hooper et al. 2012; Reich et al. 2012). Relationships between biodiversity and production in terrestrial plant communities (Hooper and Vitousek 1997; Tilman et al. 1997), and similar studies in other systems (Naeem and Li 1997; Duffy et al. 2001; Covich et al. 2004), all emphasize the importance of functional diversity. Synthetic analyses have since described influences of biodiversity on biomass production, resource utilization, and stability across numerous ecosystems (Cardinale et al. 2006); though fewer studies have been conducted in subtidal marine ecosystems (Stachowicz et al. 2007). Such studies are greatly needed given that removal or loss of species or entire functional groups have greatly altered benthic marine communities across the globe (Estes and Palmisano 1974; Jackson et al. 2001).

Trophic alterations are particularly important in coral reef ecosystems, where herbivore communities control the abundance of fleshy algae and facilitate the growth of stony corals (Carpenter 1986; Hughes 1994; Smith et al. 2001; Williams and Polunin 2001; Mumby et al. 2006; Burkepile and Hay 2010). For example, changes in the functioning of herbivore communities (e.g., fishes and echinoids) due to overfishing and disease have resulted in rapid and devastating transformations of coral ecosystems in the Caribbean (Hughes 1994). Though studies of the importance of marine consumer identity and diversity are becoming increasingly common (Duffy et al. 2003; Byrnes et al. 2006; Douglass et al. 2008; O'Connor and Bruno 2009; Farlin et al. 2010; Brandt et al. 2012), the importance of herbivore identity and diversity on coral reefs have only recently been given significant attention. Though fishes on coral reefs have been grouped into specific functional groups based on differences in feeding behavior (Friedlander et al. 2003; McClanahan et al. 2007; Sandin et al. 2008; Williams et al. 2011), only recently has functional diversity within the herbivore guild been examined in observational (Cheal et al. 2010; Edwards et al. 2014) and manipulative studies (Burkepile and Hay 2008,2010,2011). Research to date indicates that it is critical to include herbivore community structure and function in ecological assessments; however, no such classification or integration has been explicitly developed for herbivorous echinoids, possibly due, in part, to a lack of information on species-specific traits (Carreiro-Silva and McClanahan 2001).

The need for experiments that examine variation in the individual and community-wide functional roles of herbivorous echinoids has long been recognized (Ogden and Lobel 1978; McClanahan 1988). Though it is generally thought that fishes are more selective than echinoids, it is clear that different taxa avoid and prefer certain types of algae and exhibit unique grazing behaviors (Lawrence 2013). Studies that have explicitly examined variation in the trophic ecology of herbivorous echinoids on coral reefs have yielded mixed results with respect to functional diversity and redundancy, and much of what we know about relative grazing preferences stems from relatively few studies that focused on laboratory-based grazing assays (Coppard and Campbell 2007; Stimson et al. 2007) or observations in the field (McClanahan 1988; Ogden et al. 1989; Furman and Heck 2009).

Though past research has demonstrated some degree of dietary preference in herbivorous echinoids, the ecological relevance of these preferences is unclear. For example, echinoid feeding behavior may be altered in laboratory settings due to starvation, preconditioning (feeding) or stress relative to field conditions (Birkeland 1989; Stimson et al. 2007). Further, studies have often examined limited numbers of echinoid species and omitted ecologically important algal functional groups. Though field observations reflect *in situ* behaviors, it is difficult to isolate preferences from variation in local availability (e.g., the most preferred items may be absent due to consumption) or to measure accurate consumption rates. Despite these limitations, some functional differences among herbivorous echinoids have been shown. For example, while some echinoids appear to benefit coral reefs by controlling macroalgae and enhancing coral growth (Hughes et al. 1987; Idjadi et al. 2010; Sandin and McNamara

2012), other species are known to function primarily as reef bioeroders, excavating carbonate and consuming calcifiers, resulting in reduced net calcification and the associated stability, growth and resilience of coral ecosystems (Glynn et al. 1979; O'Leary and McClanahan 2010).

Functional diversity among sympatric echinoids remains a gap in our understanding of benthic dynamics on coral reefs. Given their strong influence on benthic dynamics (Hughes 1994; Sandin and McNamara 2012; Steneck 2013), we need a better understanding of echinoid community structure-function relationships. We conducted field-based grazing and lab-based metabolic assays to explore variation in the functional roles among five coexisting herbivorous echinoids on a fringing coral reef in Maui, Hawaii. Grazing assays were used to test and describe differences in grazing rates and preferences on dominant algal functional groups; these data were contrasted with metabolics to evaluate species-specific functional diversity. If these echinoids exhibit diverse functions, we hypothesized that grazing rates and dietary preferences would differ significantly among species and, if differences are taxon-specific and metabolically-driven, that consumption would correlate strongly and positively with independently-measured metabolic rates. Furthermore, we predicted that species with lower metabolic rates would exhibit lower preferential consumption than those with higher metabolic rates. Our results will better inform assessments of community-wide contributions of herbivores to coral reef ecosystem dynamics.

MATERIALS AND METHODS

Study Site

Field work was conducted at 5-7 m depth on fringing coral reefs along West Maui, Hawaii (Fig. 4.1). Reefs in the Main Hawaiian Islands (MHI) are built predominantly by corals of the genera: *Porites*, *Montipora*, and *Pocillipora*. Live coral cover in the MHI has declined over the last several decades (Pandolfi et al. 2005; Walsh et al. 2013) and fish populations have been reduced by fishing activities (Friedlander and DeMartini 2002; Friedlander et al. 2007), resulting in concerns of coral to algal phase shifts as observed in the Caribbean. The loss of herbivores (e.g., fishes and echinoids) is of greatest concern given large inputs of nutrient-laden wastewater and runoff (Smith et al. 1981; Dailer et al. 2010; Dailer et al. 2012) that stimulate production of fleshy algae at the expense of corals (McCook et al. 2001; Smith et al. 2001). Declines in coral cover have been associated with algal blooms (Smith et al. 1981; Smith et al. 2005), prompting the development of herbivore-specific protected areas and the artificial enhancement of echinoid populations as algal bio-control agents (Stimson et al. 2007).

Grazing Assays

We used field-based assays to quantify grazing rates and dietary preferences of five co-existing species of herbivorous echinoids common to coral reefs in Maui, Hawaii: *Echinothrix calamaris* (EC, black banded), *Echinothrix diadema* (ED, blue banded), *Tripneustes gratilla* (TG, collector), *Heterocentrotus mammillatus* (HM, slate pencil), and *Echinometra matthaei* (EM, rock boring) (Fig. 4.2). Each species belonged to one of three echinoid families: Diadematidae (EC, ED), Echinomtridae (EM, HM) and Toxopneustidae (TG). Assays consisted of 13 replicate cages, 10 containing one echinoid each and 3 echinoid-free controls (to account for autogenic loss), installed adjacent to reefs from which echinoids were collected (Fig. 4.3a). Cages were constructed of inverted black plastic Sterilite 28 x 20 x 10 cm enclosures attached to 32 x 25 x 1.3 cm flat PVC bases; each covered with 6-mm perforations for water exchange. This design ensured all species would fit and graze comfortably (shaded) during the assay. Base corners were attached to a 50 cm long piece of 1 cm diameter rebar suspended 15 cm above pavement (Fig. 4.3b). Echinoids were presented with one sample of each algal type representing key algal functional groups (Steneck and Dethier 1994): *Ulva lactuca* (ULV, green blooming macroalga), *Turbinaria ornata* (TRB, brown perennial macroalga), *Amansia glomerata* (AMA, red perennial macroalga), *Acanthophora spicifera* (ACN, red blooming invasive macroalga), mixed CCA (CCA, perennial crustose coralline algae), and mixed turf (TRF, mixed filamentous algae) (Fig. 4.2). Algae were attached haphazardly to enclosure bases using plastic clothespins (Fig. 4.3c).

Assays were terminated after 1-4 days, depending on grazing rate, to ensure sufficient time for measurable consumption without overconsumption (minimum of 1 alga fully-grazed or 2 half-grazed). Echinoids were collected from the nearby reef and placed immediately in assay enclosures already containing algae; thus echinoids were neither starved nor conditioned. Test diameter of each individual was measured with calipers at the end of each assay (to 0.1 cm) and used to estimate biomass and mass-specific grazing rates. Two replicate assays (20 individuals and 6 controls, total) were conducted for each of the five echinoid species during May-July 2012 (EM, HM, ED) and 2014 (EC, TG), when regional temperatures were relatively constant at 26.0 (SD = 0.8) °C (NOAA CO-OPS station 1615680 http://tidesandcurrents.noaa.gov/). Control cages were randomized for each grazing assay, and contained algae without echinoids to account for ungrazed tissue loss. Increases in algal mass (due to growth or noise) were interpreted as "zero loss" for controls and "zero consumption" for echinoid treatments. All assays were conducted in 5-7 m depth adjacent to reef habitat in West Maui, HI (Fig. 4.1, Fig. 4.3a).

Algal specimens consisted of individual thalli for macroalgae and pieces of carbonate rubble with attached CCA or turf algae (Fig. 4.2). One day before each assay began, macroalgae were collected from the reef, cleaned of sediments and epiphytes, and trimmed to similar sizes (approximately 2-3 g, Fig. 4.7d). Turf and CCA were collected and a thin nylon Ziptie was used to attach samples to the assay enclosure (Fig. 4.7c). Macroalgae were spun in a salad spinner and blotted to remove excess water and weighed (to 0.001 g) before and after the grazing period. CCA and turfs were photographed before and after the grazing period; total and consumed areas (cm^2) were measured using Image J version 1.45s (National Institutes of Health, USA). Estimates of mass consumption (to 0.001 g) of CCA and turf were calculated using area-mass relationships developed in the lab (Fig. 4.7a-b). Grazing rate was calculated as the sum of all algae removed divided by the time elapsed (g/d), after being control-corrected by subtracting the mean loss observed in control cages from total loss observed in echinoid assays for each alga, divided by total assay time. Percent consumption was measured as percent mass of each alga consumed.

Echinoid biomass (g) was calculated from test diameters using taxon-specific allometric scaling relationships developed in Chapter 1 (Lewis et al., *in prep*), and mass-specific grazing rates ($mg\ g^{-1}\ d^{-1}$) were calculated by dividing grazing rates by corresponding echinoid mass. Relative preference was calculated by normalizing percent consumption for each alga as a proportion of the most consumed alga for each individual. A preference of 1 represents the most consumed (i.e., preferred) alga, 0.5 an alga consumed at half the rate of the most preferred, and 0 an avoided alga, for each echinoid assayed (e.g., Fig. 4.5b).

Metabolic Assays

Metabolic assays were conducted at the Maui Ocean Center (MOC) located in Ma'alaea, Maui. Echinoids were collected from fringing reefs in West Maui and transported (in the dark) to the MOC in a continually-aerated 142 liter cooler (transport time = 30 min.). At the MOC, the cooler was immediately connected to flow-through seawater and echinoids were allowed to acclimate in the dark for 60 min. After acclimation, one individual was placed in each of three clear plastic incubation chambers containing a plastic mesh basket and 11.7 liters of fresh seawater that was stirred constantly by 2 rotating stir bars (Fig. 4.3d-f). Metabolic chambers were housed in a 142 liter cooler and bathed in ambient flow-through seawater (Fig. 4.3e-f) to maintain a constant temperature of 26.2 (SD=0.1) °C. All temperatures (to 0.1 °C) and dissolved oxygen concentrations (to 0.01 mg/l) were measured using a Hq40d Hach portable meter fitted with a luminescent dissolved oxygen optode and temperature probe (Hach Company, USA) (Fig. 4.3d). Following probe calibration (saturated air), initial temperature and oxygen concentrations were measured in each chamber. Chambers were then sealed and the cooler closed (dark incubations).

Assays lasted 60 min., after which, temperature and oxygen concentrations were measured again through a hole in the lid. Afterward, test diameter (0.1 cm) and mass (0.1 g) were measured, and individuals placed in a holding tank. Metabolic chambers were then rinsed, refilled with fresh seawater, and two additional 60 min. assays conducted (each with three additional individuals) for a total of nine individuals per species. Volumetric displacement of echinoids (modeled as a hemisphere), was always less than 1% of total chamber volume. Each species was assayed on a separate day and all were released at the site of collection the following morning. Six 60-min. control assays were conducted daily (3 each before and after) to assess microbial oxygen consumption rates. Echinoid metabolic rates were corrected by subtracting the corresponding daily mean microbial respiration rate. Oxygen consumption rate (mg O_2/h) was calculated by multiplying the change in oxygen concentrations by the volume of the chamber and dividing by time elapsed. Mass-specific metabolic rates were calculated by dividing this value by the mass of each individual (mg O_2/g/h).

Statistical Analyses

Differences in total and mass-specific rates of grazing and oxygen consumption rates were compared among echinoid species with one-way Analysis of Variance (ANOVA). Relationships between grazing and metabolic rates were compared by linear regression. Assumptions were evaluated for each test using Q-Q and residual plots—departures from assumptions appeared small and ANOVA is robust to such departures (Underwood 1997). Differences in dietary preference profiles were visualized using non-metric multidimensional scaling (nMDS) ordination based on untransformed Bray-Curtis distances. The significance of differences in preference profiles was evaluated using permutation-based multivariate analysis of variance (PERMANOVA, species fixed, 999 permutations) and differences in multivariate dispersion evaluated using PERMDISP (Anderson 2001; Anderson and Walsh 2013). Parametric statistics were conducted using

R Studio (v. 0.95.263, RStudio, Inc.) and non-parametric analyses and ordination were conducted using PrimerE (v. 6).

RESULTS

Grazing and Metabolic Rates

Twenty grazing assays were conducted for each echinoid species except TG, where only 18 were completed. Test diameters were 4 (EM) to 7 (TG) cm and masses were 30 (EM) to 150 (HM) g total mass (Fig. 4.8a). Control algae samples demonstrated on average, zero loss of biomass for CCA and TRF, 1% loss for TRB, 10% loss of AMA and ULV, and 25% loss of ACN (Fig. 4.8c). Total and mass-specific grazing rates differed significantly among species and ranged from 0.26-4.93 g/d and 3.20-46.70 mg/g/d, respectively (Table 4.1, Fig. 4.4a-b). TG and EC exhibited similar total grazing rates that were 10-fold greater than EM & HM and 3-fold greater than ED (Fig. 4.4a). Similar patterns were observed for mass-specific grazing rates, though TG exhibited significantly lower mass-specific grazing rates than EC (Fig. 4.4b).

Nine metabolic assays were conducted for each echinoid species. Test diameters were 4 (EM) to 7 (TG) cm and masses were 30 (EM) to 160 (HM) g (Fig. 4.8b). Microbial respiration accounted for less than 0.5 mg O_2/h (Fig. S3d). Corrected total and mass-specific metabolic rates ranged from 0.46-4.67 mg O_2/h and 0.006-0.034 mg O_2/g/h, and exhibited similar patterns to respective grazing rates (Fig. 4.4c-d). All echinoids exhibited significantly different total and mass-specific metabolic rates, with EC and TG exhibiting approximately 3, 4, and 8-fold greater total metabolic rates than

ED, HM, and EM, respectively. In contrast to total rates, ED displayed significantly higher mass-specific metabolic rates than TG, and EM was 2-fold greater than HM. At the species level, total and mass-specific metabolic rates explained 94% and 81% of the variance in total and mass-specific grazing rates, respectively (Fig. 4.4e-f), confirming that the grazing rate of each echinoid species was strongly related to metabolic rate.

Percent Consumption and Preference

Mean percent consumption of algal taxa ranged from 0 to 80%, with echinoids exhibiting consistent patterns across replicate assays (Fig. 4.5a). As described by previous studies, echinoids fed as generalists, with each species consuming most algal types to at least some degree. To allow for explicit examination of algal preferences (i.e., relative consumption) we normalized percent consumption values to that of the most consumed alga by each individual (see methods). Differences in preference profiles were observed (Fig. 4.5b) and highly significant (PERMANOVA, p = 0.001, Table 4.2a-b). TG was the only echinoid to show a strong preference for the brown, leathery *Turbinaria ornata*. Both diadematids (ED and EC) exhibited similar preference profiles, consistently preferring the invasive, exotic red *Acanthophora spicifera*, followed by the native green *Ulva lactuca*. Nearly all echinoids completely avoided the calcified CCA, except for HM which showed a weak preference for CCA and filamentous turfs over all macroalgae (Fig. 4.5a-b). Both echinometrids (HM and EM) exhibited large intraspecific variability in algal preference profiles (Fig. 4.6a) and low mean preference scores for all algal types (Fig. 4.5b), indicative of limited algal selectivity. Ordinal comparisons (nMDS) of preference profiles of individuals revealed significant differences in multivariate dispersion among echinoids (Fig. 4.6a, Table 4.3). Multivariate dispersion in algal preference was 200% greater for low-metabolic (EM, HM) vs. high-metabolic (EC, ED, TG) echinoids (Fig. 4.6b), suggesting that diet specializtion was positively correlated with metabolism.

DISCUSSION

Using standardized grazing and metabolic assays, we described large differences in the ecological functions of five sympatric herbivorous echinoids on Hawaiian coral reefs. Per capita algal consumption rates varied by an order of magnitude and large differences in mass-specific rates indicated significant differences independent of size. Strong correlations between grazing and metabolic rates confirmed that differences in grazing rates were physiologically-driven. Significant differences in algal preferences indicated that species have developed unique grazing behaviors that may be complementary in nature. Those with higher metabolic rates preferred fleshier, more palatable macroalgae, indicative of a trade-off between metabolic activity and the need for higher-quality algal foods. Given our results, we suggest that future efforts to assess contributions of echinoids to benthic dynamics on coral reefs should account for variation in echinoid community structure and function.

Grazing Rates

Our in-situ grazing rates (0.26-4.93 g/d) are comparable to those estimated in previous field observations. Bronstein and Loya (2014) calculated *in situ* grazing rates of echinoids around Zanzibar, Tanzania using gut fullness and evacuation rates. They estimated total (dry) algal consumption rates of 0.13 and 3.87 g/d for EM and ED, respectively. If we assume water makes up approximately 75% of algal wet mass (Hughes et al. 1987), corresponding wet consumption rates were 0.39 and 11.61 g/d, respectively. These rates were comparable to ours, though the higher rates for ED correspond with much larger (9 cm) individuals. Estimated *in situ* grazing rates were similar in Kenya, where all three species of diadematids examined (including ED) grazed at approximately 1-2 g/d (or 3-6 g wet) and EM grazed at 0.14 g/d (or 0.42 g wet) (Carreiro-Silva and McClanahan 2001). Field observations of gut fullness at a nearby site in Maui, HI showed that HM and EM were often not actively feeding (empty stomachs), whereas EC and TG were nearly always actively grazing (Ogden et al. 1989).

In contrast, laboratory-based assays for TG, EC and ED have yielded grazing rates much higher than those *in situ*. For example, lab-assays of TG in Hawaii yielded total grazing rates 2-5 times greater than our field measurements using similar-sized (7-8 cm) individuals (Stimson et al. 2007). Lab-assays of 5 species of diadematid echinoids in Fiji (Coppard and Campbell 2007) also yielded grazing estimates 4-7 times greater than *in situ* measurements (Carreiro-Silva and McClanahan 2001). Such large discrepancies between laboratory and *in situ* measurements of grazing rates suggest potentially strong artifacts of laboratory settings.

We used a hybrid approach (*in situ* grazing assays) that minimized laboratory artifacts and still allowed for direct measurements of grazing rates and preferences. By utilizing individuals collected from nearby reefs immediately prior to the start of each assay, grazing rates and preferences were not influenced by either starving or conditioning in the lab and, therefore, were more comparable to other rates estimated *in situ*. Furthermore, given the similar grazing rates between our field-assays and *in situ* calculated estimates (using different methods), we believe our assays represent an improvement over lab-based assays and provided grazing rates more representative of echinoid behaviors in the wild.

Dietary Preference

We experimentally demonstrated unique preferences among echinoids for algae representing the most common algal functional groups (e.g., turf algae, crustose coralline algae, and perennial vs. blooming red, brown and green macroalgae). Though herbivorous echinoids are widely considered to be generalists in their feeding behaviors, numerous studies have demonstrated preferences for, and avoidances of, certain types of algae (Lawrence 2013). Though recent studies of community-wide echinoid grazing have incorporated taxon-specific estimates of total grazing rates (Bronstein and Loya 2014), such studies assume they are generalists and do not address unique grazing behaviors. Studies that have explicitly examined grazing preferences among echinoids are often limited with respect to the grazer and algal species examined, such that the ecological relevance *in situ* is difficult to infer or extrapolate. Experimental examination of differences in algal preference and avoidance among a variety of sympatric echinoid species and dominant algal functional groups, and the importance of any differences to benthic community dynamics, remain important directions for scientific inquiry.

Here, TG alone exhibited a strong preference for the brown alga *Turbinaria ornata* (Fig. 4.5b). *Turbinaria* (like other brown algae in the order Fucales) are difficult to consume and often avoided by grazers due to thick, leathery thalli, chemical defenses, and complex tissues that require specialized guts or microflora for digestion (Eppley and Lasker 1959; Clements et al. 2009; Bittick et al. 2010). These features have likely contributed to the invasion of *Turbinaria* on coral reefs throughout French Polynesia since the 1980s (Andrefouet et al. 2004; Bittick et al. 2010). Although TG is a generalist, consuming many types of algae (Stimson et al. 2007; Lawrence and Agatsuma 2013), this species appears unique in its strong preference for *Turbinaria*. Previous studies have shown TG to consume a variety of brown algae including species of *Sargassum, Padina, Dictyota* and *Turbinaria* (Lawrence and Agatsuma 2013). Though phenolic compounds in brown algae are generally thought to serve as chemical deterrents to grazers (Targett and Arnold 1998), TG appears to prefer foods with higher phenolic concentrations and without any negative effects on growth (Steinberg and van Altena 1992). The strong preference of TG for *Turbinaria* suggests this species is uniquely adapted to utilizing this type of food source and may be an important complement to echinoid communities that, otherwise, might target grazing on more palatable types of fleshy algae. Within our study area on Maui, *Turbinaria ornata* was common, but only in shallow (1-2 m) exposed areas devoid of large echinoids.

In contrast with TG, both diadematids (EC and ED) strongly preferred the two blooming and less defended macroalgae *Acanthophora* and *Ulva* over all other algal forms, including *Turbinaria*. These preferences are supported by previous laboratory grazing assays in Fiji, where 5 different species of diadematid echinoids (including EC and ED) preferred simpler algal forms (e.g., *Codium, Padina, Hydrolathrus,* and filaments), and avoided leathery browns in the order Fucales (e.g., *Sargassum* and *Turbinaria)* (Coppard and Campbell 2007). Given the high grazing rates of these species, it is possible that less-preferred algae (e.g., *Turbinaria* and *Amansia*) were consumed in our assays after most of the more palatable species were gone, such that the relative preference for blooming taxa (or avoidance of other algae) that we measured was conservative. Greater quantities of algae or shorter grazing times may have increased discrimination between algal types. Nevertheless, the low preference for *Turbinaria* by the two diadematids contrasted greatly with the strong preference for this alga exhibited by TG.

Echinometrids (EM and HM) are generally known to exhibit generalist diets and low metabolic rates (McClanahan and Muthiga 2013). In our study, HM and EM exhibited such patterns, with low grazing and metabolic rates and widely-dispersed and overlapping grazing preferences. These two species, however, appeared to differ slightly in grazing behaviors. Though HM consumed most fleshy algae, it avoided the brown alga *Turbinaria* and was the only echinoid to exhibit significant consumption of heavily-calcified CCA, which it tended to prefer more than any of the fleshy macroalgae (though not turf). These results are supported by field observations (stomach contents) that suggested HM specializes on consuming calcified algal crusts (Ogden et al. 1989). In contrast, EM avoided CCA and consumed all fleshy algae equally (including *Turbinaria).* Though EM is known to consume CCA and function as a bioeroder (McClanahan and Muthiga 2013), it appeared to prefer fleshy algae when available. This pattern may reflect this species' ability (and preference) to feed on benthic and drift algae when abundant, but also its plasticity and ability to switch between feeding behaviors (McClanahan and Muthiga 2013). We did not evaluate erosion in this study; however, the preference of HM to consume turf and CCA over macroalgae, and the deep scars it left on the underlying carbonate, suggest it is a specialized eroder. In contrast, EM's preference for fleshy algae in this study suggests bioerosion by this species may be dependent on availability (or lack thereof) of preferred food items.

Metabolism and Preference

It is well-known that the diets of herbivores are constrained by metabolic rates and that mass-specific metabolic rates (msmr) decrease predictably with size across many phyla (Brown et al. 2004). For example, the Jarman-Bell Principle (JBP)(Geist 1974) suggests that large herbivores (with low msmr) can subsist on much lower-quality foods than small (high msmr) species. In contrast, however, msmr of these echinoid species showed no significant relationship with mass overall, and the largest echinoid species exhibited both the highest (e.g., TG, EC) and lowest (e.g., HM) mean msmr values. The high-metabolic species exhibited 7-fold greater total metabolic demands than the two echinometrid species (e.g., EM, HM). In accordance with metabolic theory, large high-energy echinoid species would require large quantities of high-quality food (e.g., fleshy macroalgae), whereas smaller, low-energy species could subsist on little amounts of lesser-quality foods.

Though allometric relationships of these echinoids differed from metabolic theory, relationships between metabolism and grazing behavior appeared to be in agreement. High-energy species (EC, ED, and TG) consumed up to an order-of-magnitude more total algal biomass than low-energy species (EM and HM), and exhibited distinct preferences for larger, more palatable macroalgae (e.g., *Acanthophora*, *Ulva*, and *Turbinaria*). In previous lab-based grazing assays, growth of TG was higher when fed preferred vs. avoided algae, indicating that preferences were related to optimal growth and fitness (Stimson et al. 2007). In contrast to the high-energy species, EM and

HM exhibited little consistent preference, with HM even consuming CCA and turf algae at higher rates than fleshy macroalgae. Thus echinoids exhibited opposite biomass-msmr relationships as described for terrestrial animals, and the greater selectivity of the larger, high-energy echinoids for more palatable algae matches predictions based on classic trophic theory.

Variation in Herbivore Function

Though taxon-specific grazing behaviors likely reflect optimal behaviors during summer months in the study region, these behaviors are potentially variable in space and time. To maximize our ability to contrast grazing among species, our design controlled for season, location and predation. In the field, however, movement, reproduction and grazing behaviors of echinoids may be influenced by several factors including season, location, size, food availability, and predation (Lewis and Storey 1984; Ogden et al. 1989; Stimson et al. 2007; O'Leary and McClanahan 2010). Thus, function might vary in space or time as a function of environmental conditions (Tuya et al. 2005). Furthermore, coexistence of multiple species of herbivorous echinoids in the Hawaiian Archipelago may lead to enhanced niche partitioning according to the “diversity breeds complementarity” hypothesis (Tilman and Snell-Rood 2014). For example, on reefs with lower echinoid diversity, significantly more overlap might occur as trade-offs (e.g. metabolism, diet, habitat, behavior) are not constrained through time by competition.

Resource availability very likely influences diet overlap *in situ*. All echinoids fed on several types of algae in our assays, but also exhibited significant differences in algal preferences. On oligotrophic, highly-grazed coral reefs (where algae are scarce), it is likely that echinoids will consume any food that is available, resulting in dietary overlap.

On degraded reefs with high algal biomass, echinoids will likely consume preferred algae and exhibit unique diets. Resource-starved reefs may favor species with low metabolic demands and broad diets (e.g., EM and HM), whereas productive reefs may support species with high demands (e.g., EC, ED, and TG) (McClanahan and Muthiga 2013). Like ours, however, most studies of echinoid feeding behavior are limited in space and time and do not account for variation in food availability.

The importance of functional diversity within trophic guilds is being incorporated into studies of coral reef dynamics. Complementarity between herbivorous fishes and echinoids remains uncertain but is likely important (Ogden and Lobel 1978). Though feeding and movement patterns theoretically give these two groups different functions (Sandin and McNamara 2012), studies indicate they may be functionally redundant competitors for algal resources (Hay and Taylor 1985) or partition resources spatially (Carpenter 1986). Though some studies suggest that fishes remove more algae and cause less harm to coral recruits than echinoids (Korzen et al. 2011; O'Leary et al. 2013), others suggest that grazing by fishes also harms coral recruits (Penin et al. 2011). Functional comparisons with other herbivores such as sea turtles (Goatley et al. 2012) and highly diverse communities of meso- and micro-grazers (Klumpp et al. 1988; Stachowicz and Hay 1999; Glynn and Enochs 2011; Kramer et al. 2012) remain to be addressed. Well-designed studies that examine relative contributions and functional relationships among herbivores are needed for coral reefs; our results help to facilitate such comparisons.

Conclusion

Hawaii’s abundant and diverse echinoid communities likely exert species-specific ecological effects on coral reef community structure, and these effects may be complementary, especially on degraded reefs where algae are most abundant. Similar variation in the ecological functions among herbivorous fishes results in positive relationships between diversity, grazing intensity, and coral growth (Burkepile and Hay 2008; Rasher et al. 2013). Such experiments are needed for herbivorous echinoids, which may be the most important grazers with respect to algal consumption and coral growth in certain coral reef ecosystems (Hughes 1994; Sandin and McNamara 2012). Given that TG and EC regularly coexist, are the most voracious grazers of fleshy algae, and exhibit different algal preference profiles; management and restoration efforts in Hawaii may benefit by protecting and enhancing populations of both species. In contrast, given the low grazing rates and high contributions to erosion of echinometrids (EM, HM), coral reefs might benefit by protecting and enhancing predators (e.g., balistid fishes) that limit their populations (Birkeland 1989; O'Leary et al. 2012). Intraguild variation in the ecological functions among species and communities remains a critical gap in our understanding of ecosystem dynamics; examining these relationships will allow us to better optimize management strategies and maximize the effectiveness of future conservation efforts.

ACKNOWLEDGEMENTS

We thank those who helped with grazing assays (E. Kelly, C. Edwards, N. Kaplanis, L. Segui, A. Netburn, K. Nichols, T. Pierce, M. Miller, and G. Butler), laboratory analyses (E. Engle, M. Vanworth, E. D’Andrea, A. Khen, N. Kaplanis, and A. Cannon) and metabolic assays (G. Butler and S. Kram). The SIO Dive Program (C.

McDonald and R. Walsh) and Maui Scuba Diving Snorkel Center (R. Carman) supported diving operations, Maui Ocean Center (J. Luecke) provided wet-lab facilities, and SIO Center for Marine Biodiversity and Conservation (P. Dockry) provided administrative support. A. Cannon, A. Khen, A. Scott, J. Shurin, L. Levin, S. Sandin and anonymous reviewers provided comments and contributions that greatly improved the manuscript. Artwork courtesy of Adi Khen. This study was a collaboration with Maui Division of Aquatic Resources (DAR; R. Sparks and D. White) under DAR permit numbers: SAP2011-77, SAP2012-67, and SAP2014-42. Funding came from the PADI Foundation, Edna-Bailey Sussman Foundation, Scripps Family Foundation, SciFund Challenge, NRC Ford Foundation Fellowship, and the National Science Foundation Grant No. 0903551.

Chapter 4, in part, has been submitted for publication of the material as it may appear in Coral Reefs, 2016, Lewis, Levi S; Smith, Jennifer E., Springer, 2016. The dissertation/thesis author was the primary investigator and author of this paper.

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TABLES

Table 4.1. Results of ANOVA tests examining differences among urchin taxa in total and mass-specific grazing and metabolic rates.

Type	**Metric**	**DF**	**F**	**P**	**R^2 (adj)**
Total	Grazing Rate	4, 93	88.63	**<0.001**	0.783
	Metabolic Rate	4,40	101.09	**<0.001**	0.900
Mass-specific	Grazing Rate	4, 93	61.41	**<0.001**	0.713
	Metabolic Rate	4,40	37.84	**<0.001**	0.770

Table 4.2. Results of global PERMANOVA test examining differences in algal preference profiles among 5 urchins species and corresponding pair-wise comparisons. Bold indicates statistical significance ($P < 0.05$). Significant pair-wise comparisons for EM and HM (vs. other species) likely reflect differences in dispersion (variability) rather than a lack of overlap.

Source	**df**	**SS**	**MS**	**Pseudo-F**	**P(perm)**	**perms**
Urchin	4	35497	8874.3	7.0157	**0.001**	999
Residual	93	1.18E+05	1264.9			
Total	97	1.53E+05				

Groups	**t**	**P(perm)**	**perms**
EC,ED	1	0.400	999
EC,EM	1.7	**0.043**	999
EC,HM	2.5	**0.001**	999
EC,TG	5.1	**0.001**	999
ED,EM	1.8	**0.013**	998
ED,HM	2.8	**0.001**	999
ED,TG	4.4	**0.001**	998
EM,HM	1.6	0.052	999
EM,TG	2.6	**0.001**	999

Table 4.3. Results of global PERMDISP test examining differences in multivariate dispersion of algal preferences among 5 echinoid species, and corresponding pair-wise comparisons. Bold indicates statistical significance (P < 0.05).

Source	**df1**	**DF2**	**F**	**P(perm)**	**perms**
Urchin	4	93	39.386	**0.001**	999

Groups	**t**	**P(perm)**	**perms**
EC,ED	1.3919	0.185	999
EC,EM	8.0997	**<0.001**	999
EC,HM	7.2261	**<0.001**	999
EC,TG	0.38513	0.692	999
ED,EM	8.6591	**<0.001**	999
ED,HM	7.3858	**<0.001**	999
ED,TG	1.2268	0.212	999
EM,HM	0.44141	0.661	999
EM,TG	9.1948	**<0.001**	999
HM,TG	7.9191	**<0.001**	999

FIGURES

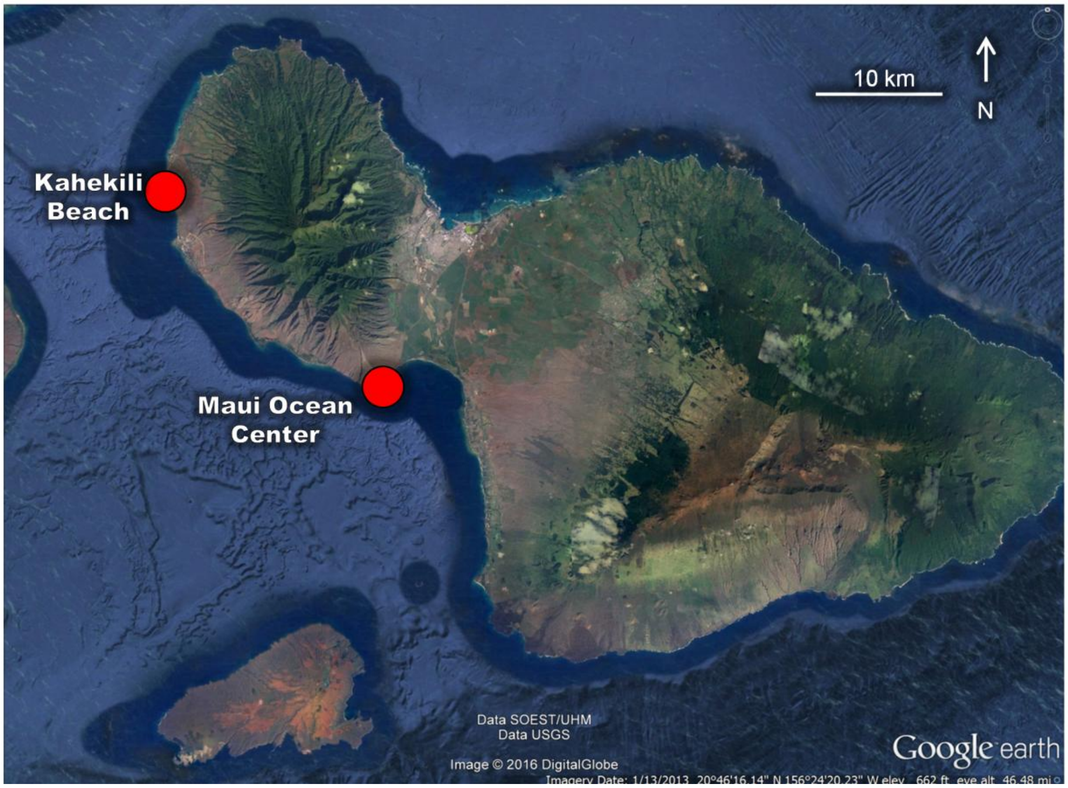

Figure 4.1. Location of echinoid collection and grazing assay site on Maui, Hawaii; and the Maui Ocean Center where metabolic analyses were conducted.

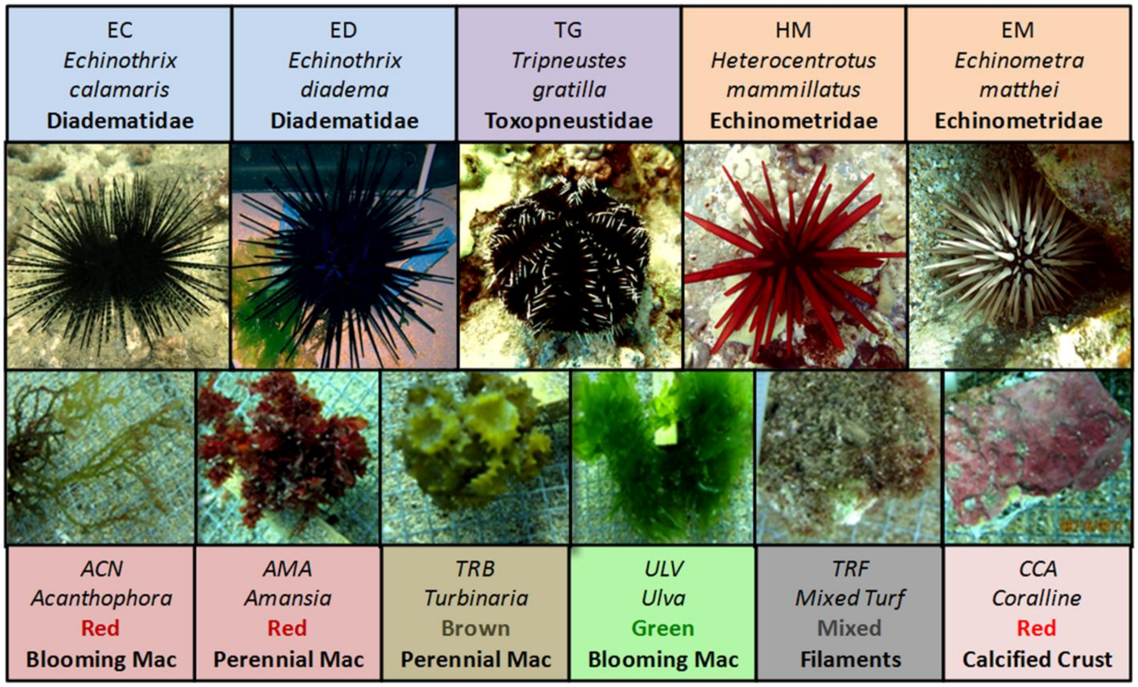

Figure 4.2. Taxonomy and mophology of echinoids (top) and algae (bottom) used in algal grazing assays.

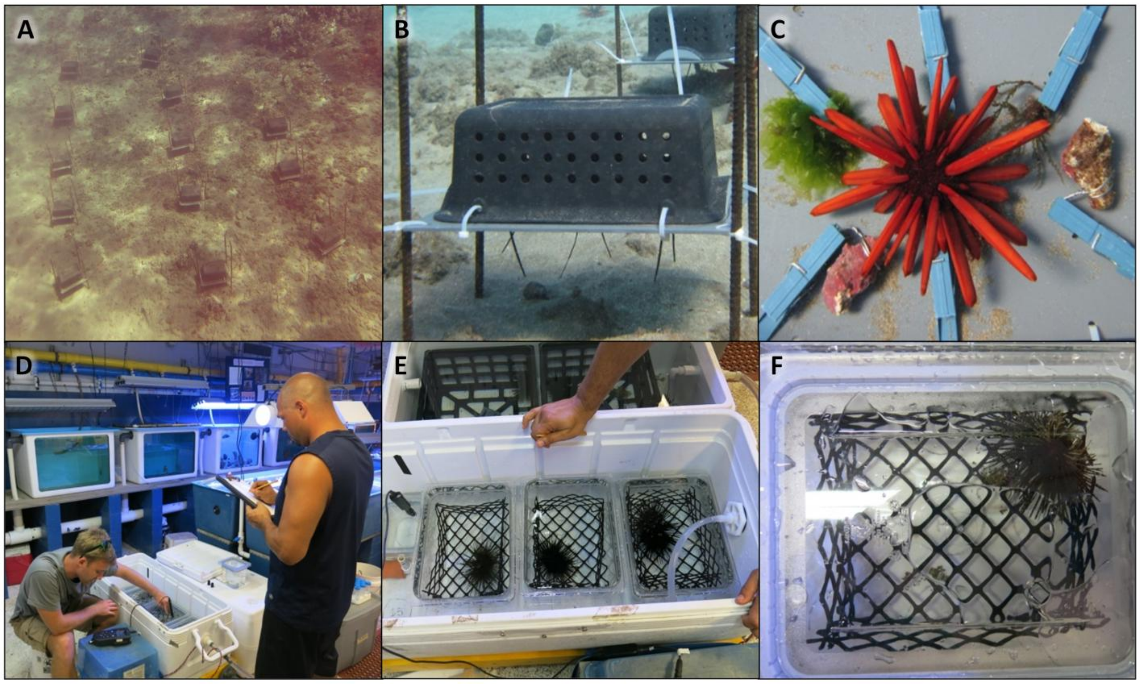

Figure 4.3. Design of field-based grazing assays (A-C) and metabolic assays (D-F).

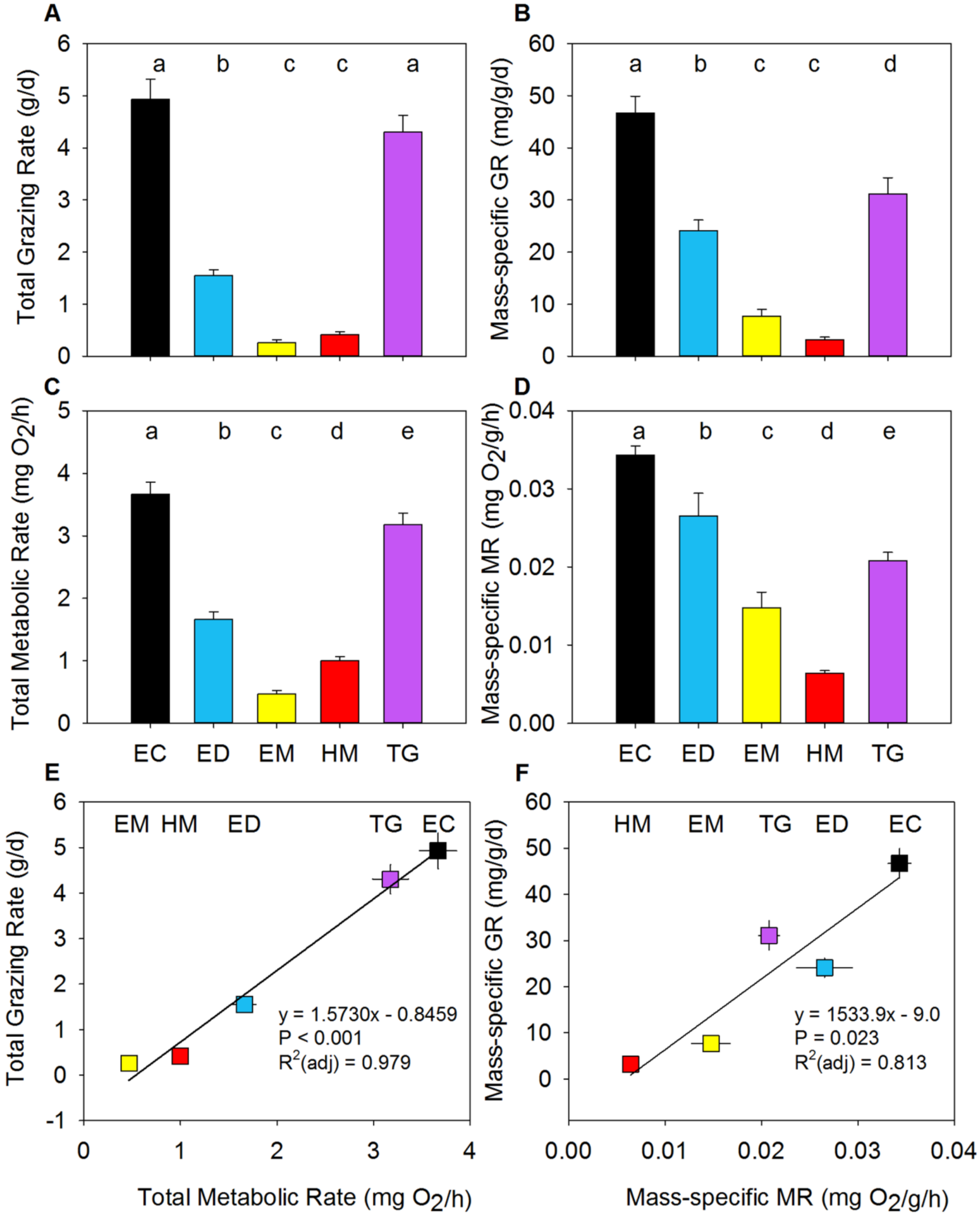

Figure 4.4. Control-corrected total and mass-specific grazing (A-B) and metabolic (C-D) rates, and relationships between total (E) and mass-specific (F) grazing vs. metabolic rates. Values are means (+SE) of 20 and 9 replicate assays for grazing and metabolism, respectively. Letters indicate groups separated by Fishers LSD test ($p < 0.05$). Urchin codes as in Fig. 4.2.

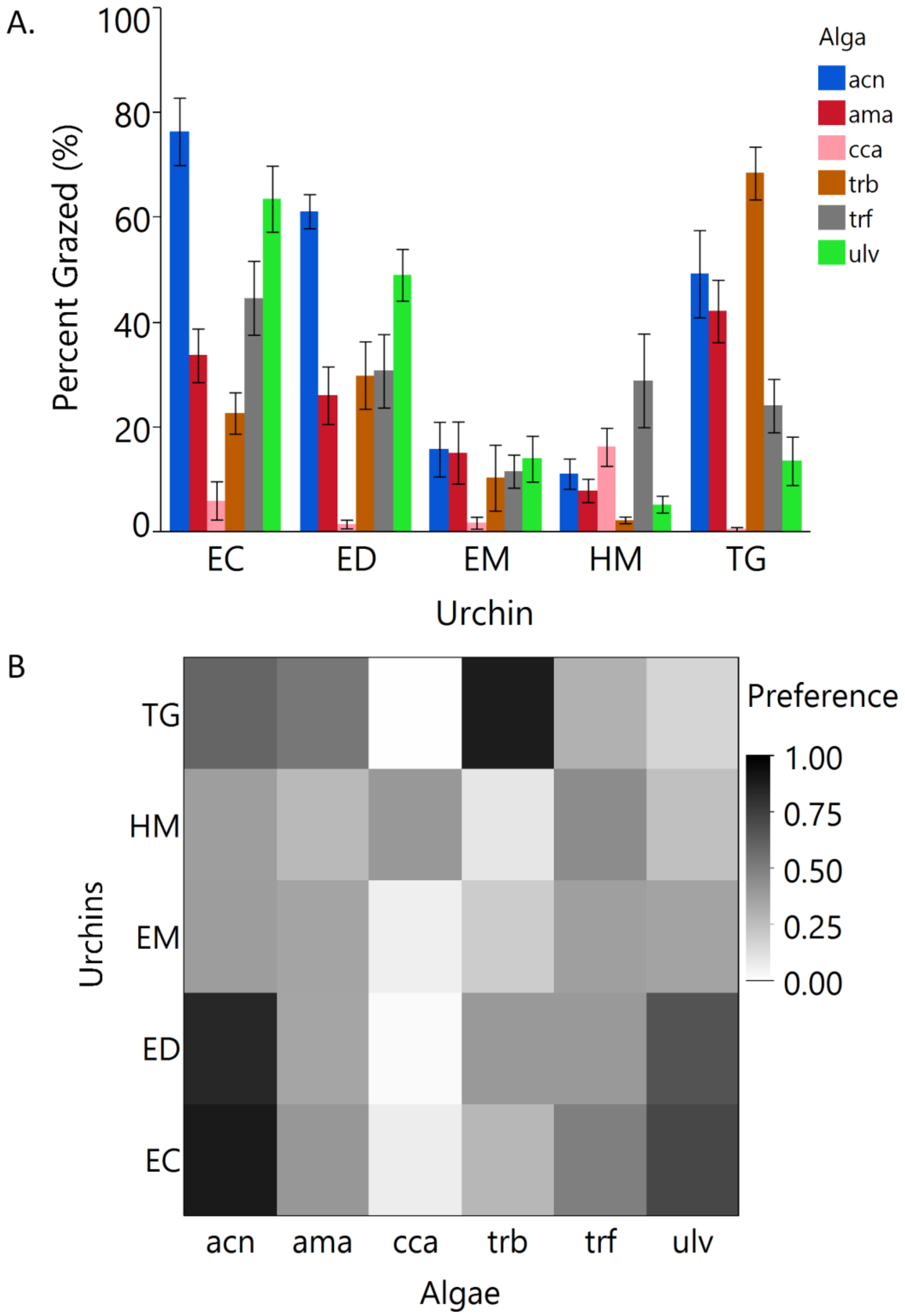

Figure 4.5. Corrected percent consumption (A) and preference (B) derived from results of field-based grazing assays. Values are means (+SE) of 20 replicate assays. Urchin and algae codes as in Fig. 4.2.

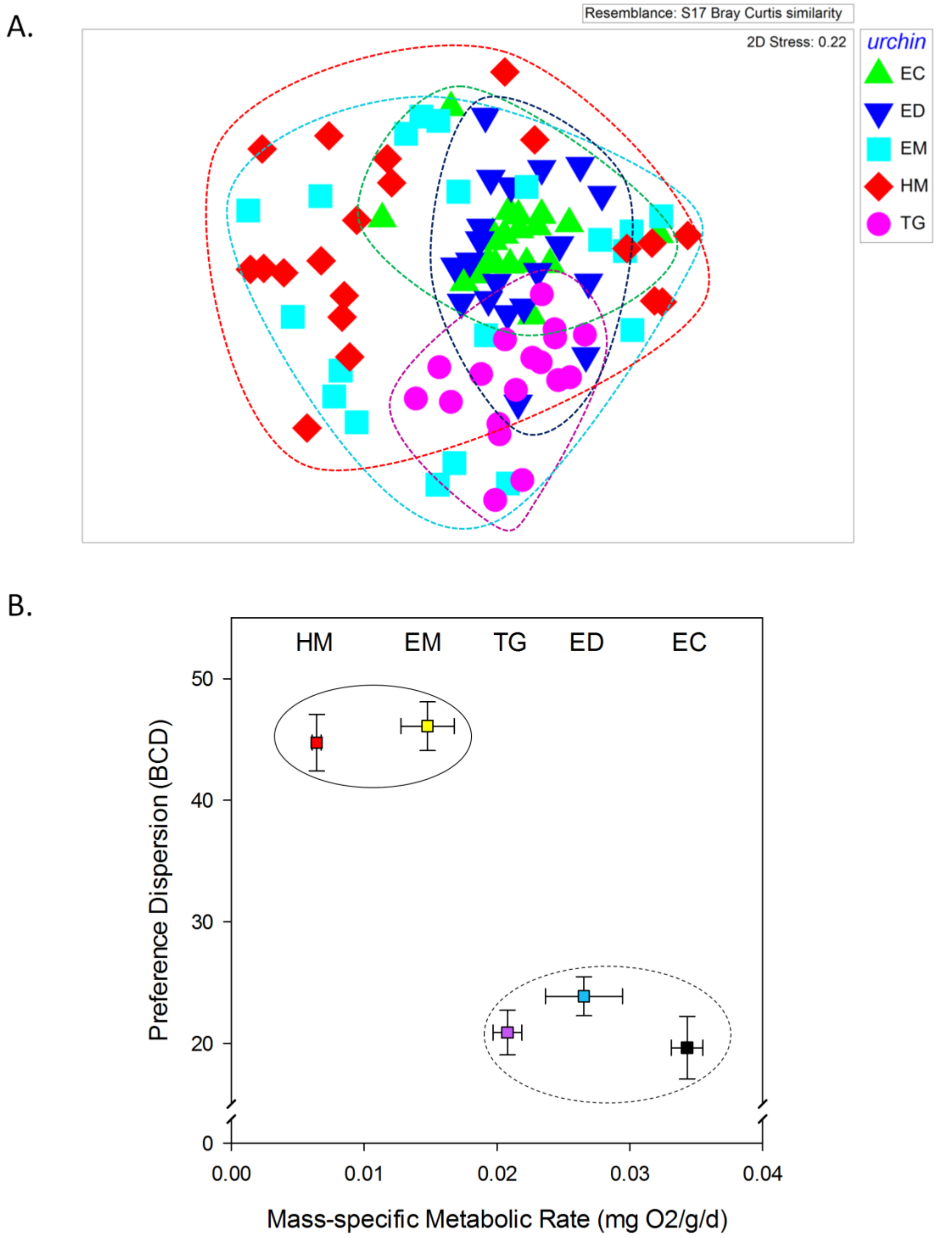

Figure 4.6. Dissimilarity in algal preference profiles and mass-specific metabolic rates: (A) nMDS biplot representing dissimilarity (Bray-Curtis distances) among points and the outer boundaries of each echinoid cluster (dashed lines) and (B) mean (+SE) Bray-Curtis distances from group centroids (preference dispersion) versus mass-specific metabolic rate (circles indicate groups with significantly different dispersion according to PERMDISP test). Echinoids and algae codes as in Fig. 4.2.

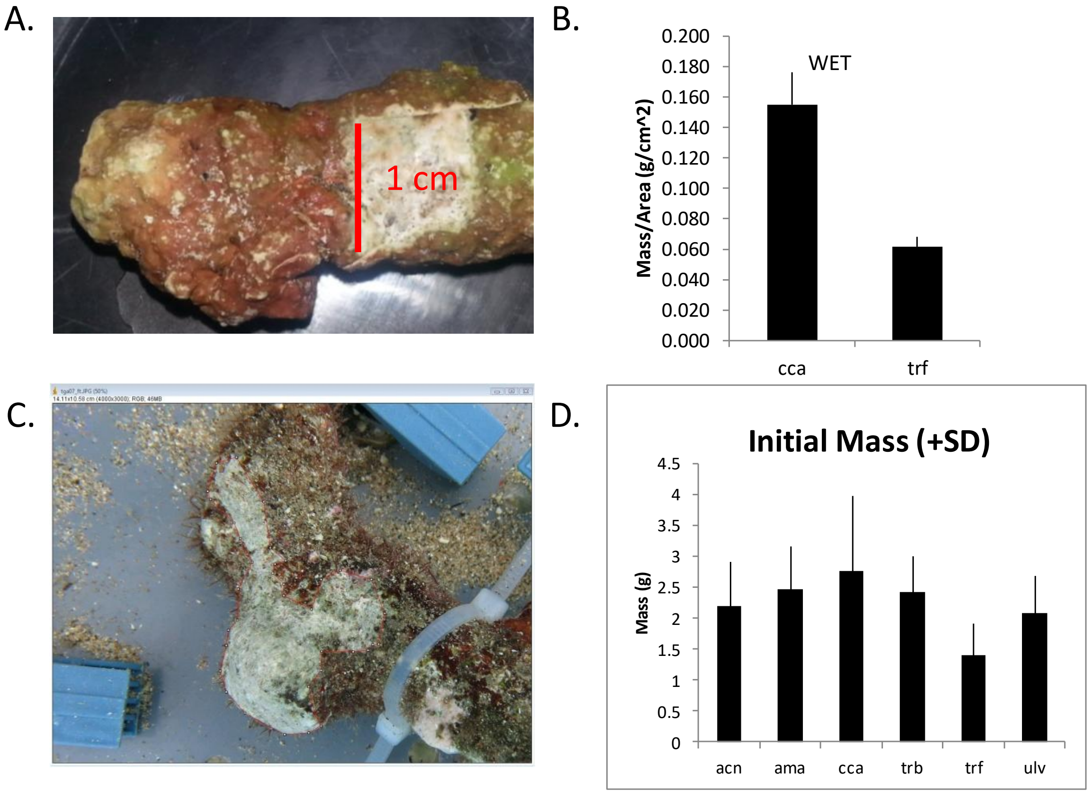

Figure 4.7. Method for estimating consumption of turf and CCA. One cm^2 sections of CCA (a) and TRF were scraped (to simulate echinoid grazing) from ungrazed control samples. The scraped material was blotted dry, weighed wet (0.001 g) and used to estimate mass:area (g/cm^2) for each alga (b). Total and grazed area (cm^2) of CCA and TRF (c) were then multiplied by respective mean mass/area values to estimate total and grazed CCA and TRF mass. Estimates of initial mass (+SD) of CCA and TRF are provided along with initial measured mass of all macroalgae (d). Mean + SE shown in (b) and (d).

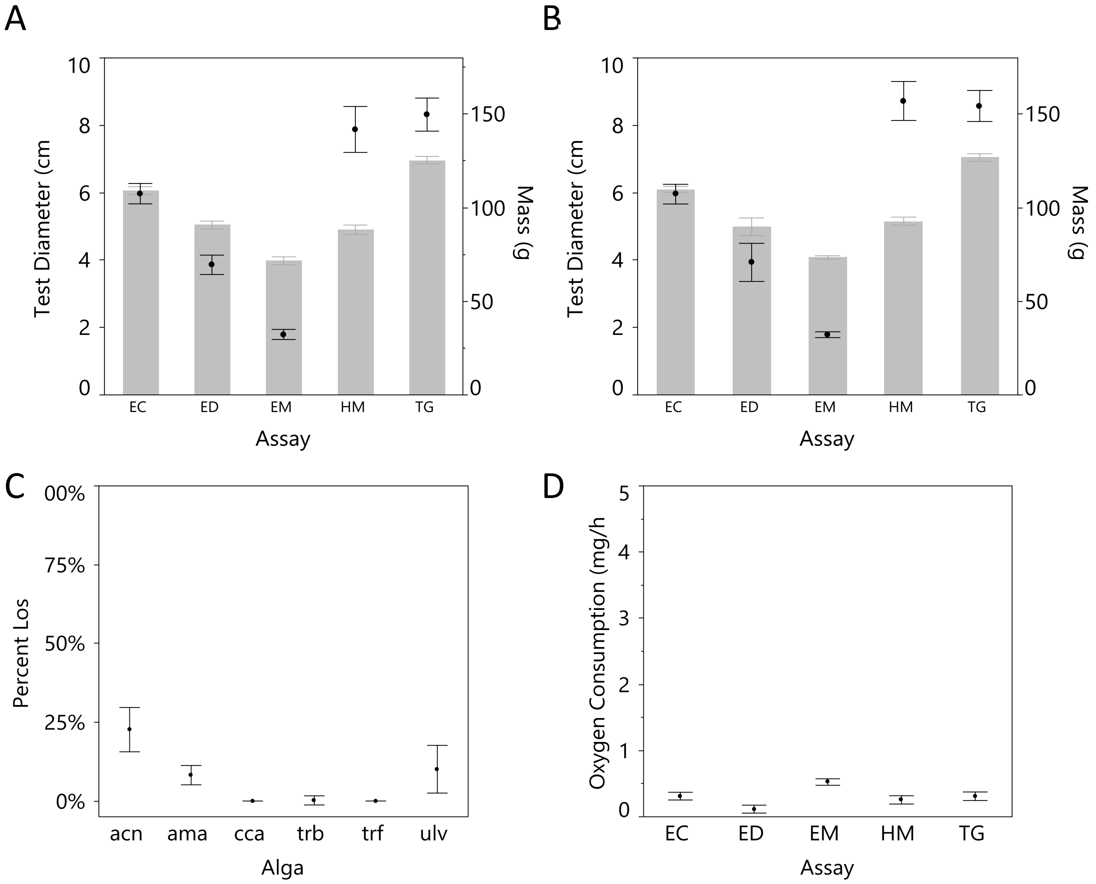

Figure 4.8. Echinoid sizes and control values for grazing and metabolic assays. Test diameter (bars) and mass (points) of echinoids used in (a) grazing and (b) metabolic assays, and control values for (c) grazing and (d) metabolic assays. Mean ± SE shown.

CHAPTER 5 Identity, diversity, and the ecological effects of herbivorous echinoid communities on a coral reef

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ABSTRACT

The structure of herbivore communities strongly influences their ecological functions across ecosystems. In coral reefs, herbivorous echinoids can regulate competitive interactions between reef building corals and fleshy algae; however, it remains unclear how community structure influences the ecological functions and effects of echinoids on benthic dynamics. We conducted a long-term (24-mo.) field-caging experiment on a natural coral reef in Maui, HI to explore functional differences among three common herbivorous echinoids: *Echinothrix calamaris* (EC), *Heterocentrotus mammillatus* (HM), and *Tripneustes gratilla* (TG). We established 8 treatments (6 with echinoids and 2 controls) to test the effects of echinoid identity (mono-sp. treatments) and diversity (multi-sp. treatments) at densities of 2 individuals m^{-2} on mixed-aggregate benthic coral reef communities. After 2 years, open (unmanipulated) plots exhibited minimal change in macroalgae and coral cover; whereas excluding consumers (greater than 3 cm) resulted in significantly higher density, diversity, cover, and biomass of macroalgae, but not significant reductions in coral cover (though the only treatment with a negative trend for coral cover). In mono-specific echinoid treatments, EC exerted the strongest, TG intermediate, and HM the weakest (e.g., no different from exclosures) effects on algal communities in experimental plots. All multi-species treatments containing EC (e.g., ECxEC, ECxHM, and ECxTG) exhibited near-elimination of all macroalgae, indicating EC as a dominant consumer. After 2 years, proportional (but not absolute) changes in coral cover (dominated by 3 genera: Montipora, Porites and Pocillipora) differed significantly among treatments, generally increasing in all echinoid treatments, but often variable and not significantly different from zero. One echinoid community (ECxTG) resulted in greater proportional coral growth than all other treatments, indicative of a synergistic relationship between these two complementary echinoid grazers that is in agreement with predictions based on their unique grazing behaviors. Our results indicate that (1) herbivore communities currently exert strong effects on macroalgal abundance and community structure on this coral reef, (2) that echinoids, when locally abundant, contribute significantly to this herbivory, (3) different echinoid species have markedly different ecological functions and effects on macroalgal communities, and (4) that certain diverse combinations of echinoid species can lead to increased growth of corals. Our results support previous empirical studies that have shown dominance of macroalgal grazing by certain species of echinoids, but also complementary effects among functionally-unique consumer that may result in the synergistic enhancement of coral growth.

INTRODUCTION

The importance of biodiversity to the functioning of ecosystems is a key focus of ecological inquiry (Elton 1958, Stachowicz et al. 2007, Tilman et al. 2012). Ecosystem functioning might be defined or measured as production rates, standing biomass, trophic dynamics, element cycling, trophic transfer, resistance to invasion, and resource use (Stachowicz et al. 2007). Seminal manipulative experiments (Hooper & Vitousek 1997, Tilman et al. 1997) explored relationships between biodiversity and production in terrestrial plant communities, and many studies across additional systems and functional groups have followed (Naeem & Li 1997, Duffy et al. 2001, Covich et al. 2004). Synthetic analyses (Cardinale et al. 2006, Stachowicz et al. 2007, Cardinale et al. 2012, Hooper et al. 2012, Tilman et al. 2012) have since identified consistent and strong effects of biodiversity on primary production and resource use by functional groups (e.g., herbivores) of organisms; however, such studies in marine subtidal ecosystems remain relatively rare (Duffy et al. 2001, Stachowicz et al. 2007, Brandt et al. 2012).

Reductions in biodiversity can result in myriad cascading, albeit difficult to predict, ecological effects that can ultimately impact human societies (Cardinale et al. 2012). Furthermore, large, strongly-interacting species, such as keystone and dominant species that have the greatest influence on ecosystem-wide structure and function (Paine 1980, Power et al. 1996, Terborgh & Estes 2010), are often the most susceptible to defaunation and extinction (Duffy 2002, Dirzo et al. 2014). In the marine environment, anthropogenic alteration (both direct and indirect) of fish and macro-invertebrate (e.g., echinoids) communities has greatly altered benthic ecosystems across the globe (Strong

1992, Jackson et al. 2001, Byrnes et al. 2006, Steneck 2013, Steneck et al. 2013). In coral reefs, overfishing and disease have decimated consumer populations, resulting in rapid, massive, and stable transformations of coral ecosystems following disturbance (Knowlton 1992, Hughes 1994). Experimental studies of marine consumer richness have shed much light on biodiversity-trophic-guild function relationships (Duffy & Harvilicz 2001, Duffy et al. 2003, Douglass et al. 2008, O'Connor & Bruno 2009); however, fewer studies have attempted to address these questions in natural subtidal environments using manipulative experiments (Stachowicz & Whitlatch 2005, Burkepile & Hay 2008, 2010, Brandt et al. 2012).

Subtidal, manipulative, field-based experiments are needed to advance our understanding of the true significance of biodiversity (and its loss) to ecosystem processes in marine ecosystems (Duffy 2002). In coral reef ecosystems, herbivore communities serve a critical function by controlling fleshy algae (that compete with corals for space), thus facilitating coral survival and growth (Carpenter 1986, Hughes 1994, McClanahan 1995, Williams & Polunin 2001, Mumby et al. 2007). Though the importance of herbivory has been well-documented, few studies have experimentally tested the effects of herbivore diversity in these systems. For example, herbivorous fishes are often aggregated by taxonomic (e.g., family) or course functional categories (Friedlander et al. 2003, McClanahan et al. 2007, Sandin et al. 2008, Williams et al. 2011); however, this may overlook subtle, but important, differences in feeding behaviors that result in functionally different effects (among species and communities) on benthic dynamics (Bellwood & Choat 1990, Choat et al. 2002, Burkepile & Hay 2008, Burkepile & Hay 2011a).

In addition to fishes, herbivorous echinoids can also be diverse and important components of herbivore communities on certain coral reefs (McClanahan 1988, Ogden et al. 1989, Coppard & Campbell 2007, McClanahan & Muthiga 2016). Though echinoid species are often regarded as generalist consumers (Ogden & Lobel 1978, Hay 1984, Ogden et al. 1989, Steneck 2013), they may also exhibit distinct dietary preferences and specialized behaviors (Carpenter 1981, Hay 1984, de Loma et al. 2002, Vaitilingon et al. 2003) indicative of functional diversity that could result in different (and complementary) effects on benthic communities. For example, though echinoids are generally thought to benefit reefs by controlling macroalgae and increasing resistance to algal phase-shifts (Sammarco 1982, Hughes 1994), some species appear to function primarily as reef eroders that graze live calcifiers (corals and CCA), resulting in reduced net calcification, stability, growth and resilience (Glynn et al. 1979, O'Leary & McClanahan 2010, O'Leary et al. 2013).

The long-term effects of different echinoid species (identity) or combinations of species (diversity and structure) on natural coral reef benthic communities, therefore, remains unclear. Exploring this lack of information is valuable given the strong effects (positive and negative) that this grazing community can have on coral ecosystems. Field-based manipulative studies examining variation in ecological functions among echinoid species and communities can improve our understanding of such structure-function relationships. Results of such studies can enhance conservation and management efforts by leading to more informed and ecologically-sound approaches.

To address these questions, we explored functional diversity among three common herbivorous echinoids on a shallow fringing coral reef in Maui, Hawaii (Fig.

1a). We used a 2-year (26-mo.) field-based manipulative experiment on natural reef isolates to examine the independent and combined effects of three common species of herbivorous echinoids (*Echinothrix calamaris, Heterocentrotus mammillatus, and Tripneustes gratilla*) on benthic coral reef communities. By comparing the relative effects of single- and multi-species treatments, we aimed to test and describe whether and how (a) individual species exhibit unique effects (functions) on coral reefs and (b) communities with different demographics (e.g., diversity and composition) result in unique community-level functions that are distinct from each other and single species treatments.

METHODS

Description of the Study Site

This study was conducted along the leeward, Kaanapali coast of Maui, HI (Fig. 5.1a), on the outer edge (7-8 m depth) of a fringing coral reef within the Kahekili Herbivore Fishery Management Area (coordinates: 20.9388, -156.6932), where the take of herbivorous fishes and echinoids has been prohibited since June 2009. This contiguous reef stretches along c.a. 1 km of coastline and extends 50-200 m offshore at depths of 2-10 m, adjacent to King Kahekili Beach. Four corals made up the majority of scleractinian cover on the reef adjacent to experimental plots: *Porites lobata*, *Montipora capitata*, *Montipora patula*, and *Pocillopora meandrina*.

Four species of herbivorous echinoid were common on the reef including: *Heterocentrotus mammillatus* (HM, slate pencil urchin), *Echinothrix calamaris* (EC, banded urchin), *Tripneustes gratilla* (TG, collector urchin), and *Echinometra matthei* (pale-spined rock-boring urchin). Mean ± SE total densities of echinoids on shallow (3 m) portions of the reef were 2.45 ± 0.31 per m^2; however, this density varied significantly by reef location and species (Lewis, unpublished data). Though *E. mathaei* was often the most abundant echinoid species on shallow reefs, its small size and boring behavior rendered it less conducive to our manipulations and its ecological function has been described in great detail in similar coral reef ecosystems (McClanahan and Muthiga 2007, O'leary and McClanahan 2010). We therefore chose to use *H. mammilatus* (HM), *E. calamaris* (EC), and *T. gratilla* (TG) in our experiment because (1) they are common components of herbivore communities on coral reefs in Hawaii and abroad, (2) are similar-sized and often found co-occurring in close proximity on Maui's coral reefs, (3) previous studies indicate significant variation in ecological traits and functions (Lewis and Smith, in review), and (4) relatively little is known about variation in their ecology on benthic coral ecosystems.

Experimental Design

We used a randomized, blocked field experiment to test the effects of echinoid species identity and diversity on oral reef benthic communities. The experiment consisted of six caged echinoid treatments to examine independent and combined effects of three echinoid species, and two controls (open plot and caged herbivore exclosure) to examine how benthic dynamics are influenced by natural and fully excluded herbivore communities (Fig. 5.1b-e, Fig. 5.2). Open plots were the only treatments exposed to herbivorous fishes greater than the mesh size. Cages were 1x1x0.5 m, constructed of 3.2

cm black plastic mesh anchored in the field by attaching each corner to a previously installed steel pin using zip ties. Cages were installed around small patch reefs on the outer edge of the reef (7-8 m depth) during June 25-July 5, 2011. On July 13-14, all invertebrates and fishes greater than the mesh size were removed from each plot, initial data and images collected, and all echinoid treatments established. Echinoids used in this study were collected from the adjacent coral reef, maximum test diameter measured with calipers and were then placed immediately in the appropriate randomly-assigned plot. Mean ± SE test diameters were 4.3 ± 0.13, 7.6 ± 0.15, and 7.7 ± 2.1 cm for HM, EC, and TG respectively (Fig. 5.6). The experimental densities (2 ind. m^{-2}) and biomass (c.a. 200-300 g m^{-2}) were within ranges commonly observed for ambient echinoid communities throughout the region (Ogden et al. 1989) (Lewis and Smith, *unpublished data*) and similar reefs abroad (McClanahan & Muthiga 2016). All plots were sampled again in August 2012 ("mid", 13-mo.) and finally in September 2013 ("final", 26-mo.).

Macroalgal Density, Diversity, and Turf Height

Algal density and height was measured at each time point. All macroalgal thalli taller than 1 cm were identified visually in the field to the lowest taxon possible (usually genus), and height measured (to nearest 0.5 cm) using a 1 m length x 3 mm diameter graduated (1 mm increments) stainless steel measuring probe. For patches of thalli greater than 5 cm in the widest dimension, multiple measurements were taken at 5 cm intervals until the entire patch had been measured. The mean height of turf algae (mixed filaments less than 1 cm) was estimated by measuring turf heights (to nearest 1 mm) at 20 haphazardly selected locations throughout each plot. Large, dense tufts of mixed filamentous algae greater than 1 cm height were measured and quantified as macroalgae. The total numbers of measurements were converted to densities (per m^2) and used to assess differences in algal density and community structure.

Macroalgal Biomass

At the end of the experiment (26 mo.), all macroalgae were removed from each cage, sorted by taxon, rinsed in fresh water, spun 10 times in a salad spinner and weighed to the nearest 0.001 g. Algae were then frozen and later dried (60 °C for 48, or until constant mass) and weighed (dry mass). Differences in the total macroalgal dry mass were compared among treatments by ANOVA and percent contributions of functional groups (calcified brown, green, and red macroalgae; cyanobacteria; fleshy brown, green and red macroalgae; fleshy green and mixed-assemblage turf) were quantified and examined.

Percent Cover and Area

For the initial and final sampling time point, a digital image (white-balanced, 12 megapixel) of each plot was collected using a Canon Powershot D10 camera attached to a large 82 x 82 cm (inner dimension) frame constructed of 1.3 cm (diameter) PVC. In the lab, images were cropped to the size of the photo frame, all substrates traced and filled in Photoshop (trace-over technique, 5 pixel borders), individual layers (by taxon) exported as .PNG files, and the number of pixels per layer quantified using R Studio statistical software. Pixel-area of each layer was then converted to cm^2 by calibrating the total inner frame pixel-area of each image to 6,724 cm^2 (82 cm x 82 cm). Percent cover was used to contrast community structure within plots using key functional groups and substrates (coral cover, cage, sand, sessile invertebrates, mixed algal turfs, cyanobacteria, CCA + carbonate), and absolute areal (cm^2) changes (final-initial) in the coverage of dominant sessile organisms (e.g., mixed turf, macroalgae, crustose coralline algae + carbonate, and corals) were then examined and compared among experimental treatments. CCA and carbonate were combined (1) due to difficulty in discrimination on images and (2) similarities as "calcified substrates" that correlate with grazing intensity and coral recruitment. Treatment effects on changes in turf cover were analyzed using sand as a covariate due to the observation that low-elevation turfs appeared to be replaced (smothered) by inundation of course-grained sediments toward the end of the experiment (Fig. 5.8).

Cage Effects

The effects of cages on light intensity (lumens), temperature (°C) and flow (clod card dissolution rate, g/d) were evaluated using standard methods (Fig. 5.7). Cages had no measurable effect on flow; however reduced temperatures of sensors by 0.3 °C and light intensity by approximately 50%. The 0.3 °C higher temperature in open plots likely reflected slight warming of the air space in the sensor due to higher light exposure, and likely does not reflect significant in-situ temperature differences (e.g., likely homogenized by flow and convection). Though shading may have reduced algal and coral growth (due to reduced radiation available for photosynthesis), it appeared that treatment effects were much stronger than cage effects. For example, dry macroalgal biomass increased dramatically inside full exclosures (greater than 200 g m^{-2}), and corals generally survived throughout the study, growing by upwards of 50% in some echinoid treatments. In contrast, algal and coral cover both remained low in open plots throughout the study. Furthermore, light is less likely to be limiting at these shallow 7-8 m depths relative to much deeper reefs (e.g., 20-30 m), where similar coral communities persist in greatly diminished light environments. Thus, we concluded that shading likely resulted in conservative rates for algal and coral growth, but that these effects were likely small compared to the strong effects of treatments within cages.

Statistical analyses

To evaluate the effectiveness of the randomization procedure at homogenizing initial community traits among treatments and blocks, initial data on algal density and turf heights were compared among sites by one-way blocked ANOVA (sites and blocks = fixed), and initial differences in community structure based on densities and percent cover were compared among treatments using one-way blocked permutational multivariate analysis of variance (PERMONAVA) (Anderson 2001) on untransformed Bray-Curtis distance matrices (9999 unconstrained permutations). Differences among treatments in final community composition (based on density and area) were then also compared among treatments by PERMANOVA. One-way blocked ANOVA based on absolute areal (cm^2) and relative (Δ, final vs. initial) changes was used to examine variation in the responses of benthic organisms to experimental treatments for total macroalgal density; turf height; percent cover of CCA + carbonate, mixed-assemblage turfs, macroalgae, and corals, and proportional changes for coral; and dry mass of macroalgae (Table 5.1). To specifically test for diversity effects (richness = 1 or 2), a nested 2-way blocked ANOVA (with treatment levels nested within levels of diversity, both as fixed factors) was used to compare changes in macroalgae and coral cover among echinoid treatments only. For significant ANOVAs, treatments were compared using Fishers LSD. Parametric statistics were conducted in JMP v. 12.0.1, and PERMANOVA in PrimerE v.6.

RESULTS

Macroalgal Density, Diversity, and Turf Height

Mean ± SE initial macroalgal density was 21.8 ± 1.4 ind m^{-2} and did not differ among treatments (Fig. 5.3, Table 5.1). Clear differences, however, were observed among treatments after year 1 (Fig. 5.3b) and these appeared to strengthen into year 2 (Fig. 5.3b, Table 5.1). Exclosure ("no urchin") plots resulted in 500% higher (91.4 ± 13.9 ind m^{-2}) algal densities than unmanipulated open plots (13.6 ind m^{-2}), indicating significant effects of ambient herbivore communities on algal densities. HMxHM treatments did not differ from exclosures, indicating that HM had limited effects on macroalgal densities (Fig. 5.3a). In contrast all treatments containing EC exhibited low algal densities (approximately 22 ind m^{-2}), similar to initial values; therefore, effects of EC-containing treatments resembled effects of herbivores in open plots. In contrast, TGxTG and TGxHM treatments exhibited intermediate effects. This indicated that enhanced herbivory with increased diversity did not occur, and that a single grazer (EC) dominated algal consumption patterns. Initial mean ± SE heights of algal turfs was 3.4 ± 0.1 mm and did not differ significantly among treatments. By the end of the experiment, turfs inside consumer exclosures increased by 2 mm, and were therefore 30-50% taller (to 5.1 ± 0.4 mm) than those in echinoid and open treatments that were either constant or declined slightly (e.g., by 1 mm) (Fig. 5.3b, Table 5.1).

Compositions (% abundance) of low-density algal communities at the beginning of the experiment were dominated by a trichomatous (filament-like) cyanobacteria (*Moorea sp.)* that created numerous small tufts throughout plots, and to a lesser degree by numerous tufts of red filamentous algae (e.g., *Tolypiocladia sp*.) (Fig. 5.3c). These tufts contributed little to total cover or biomass, but were numerically abundant on the reef. Slight initial differences among treatments and blocks (Fig. 5.3c, Table 5.1) were driven largely by random variation in the abundances of these ephemeral tufts that became less abundant at 1- and 2-year time points. Red, brown and green macroalgae became more prominent at later sampling points, and drove significant differences among treatments (Fig. 5.3c, Table 5.1). Most noteworthy, perhaps was the dominance of red macroalgae throughout all treatments (e.g., *Melanamasia sp. and Laurencia sp.)*, and the lack of brown algae (e.g., *Dictyota sp.*) in open plots, in contrast to all caged treatments which exhibited increases in brown algae, suggesting that other consumers (e.g., fishes) may selectively graze this algal group.

Macroalgal Biomass

Macroalgal biomass differed significantly among treatments at the end of the 2-yr experiment (Fig. 5.4, Table 5.1). Biomass ranged (mean ± SE) from 201.4 g m^{-2} in exclosures to only 12.25 ± 1.29 g m^{-2} in ECxHM treatments. As for algal density, HMxHM did not differ from exclosure treatments, thus indicating limited effects on both macroalgae density and biomass. Furthermore, all treatments containing EC exhibited the greatest reductions in macroalgal biomass; however, in contrast to algal densities, biomass values were significantly lower (approximately ¼) than those observed in open plots, suggesting that grazing was more intense in these treatments than in ambient conditions. Though algal densities for TGxTG were intermediate, algal biomass for TGxTG was similar to EC treatments, indicating densities were comprised of relatively smaller individual thalli in this treatment. Similarities among all EC-containing treatments confirmed results from density data, indicating that EC was a dominant consumer; however, TG appeared to be equally effective at removing algal biomass. In contrast to the diversity reflected in algal densities, algal biomass was comprised almost entirely (80-99%) of red fleshy macroalgae algae (e.g., *Melanamasia sp.*) with only trace amounts of fleshy brown macroalgae (e.g., *Dictyota*), calcified green macroalgae (*e.g., Halimeda*), and fleshy turfs (mixed) (Fig. 5.4b). Interestingly, no calcified macroalgae (e.g., *Halimeda sp.*) were observed in either controls.

Percent Cover and Change in Total Area

No differences in community structure (Bray-Curtis distances based on % cover of functional groups) were observed among treatments at the beginning of the experiment (Table 5.1); and, differences among treatments for changes in absolute coral (Fig. 5.5a) and CCA+carbonate (Fig. 5.5b) cover were non-significant at the end of the study (Table 5.1). However, changes in proportional coral cover (Fig. 5.5c), and the absolute cover of macro- (Fig. 5.5d) and turf-algae (accounting for sediment inundation, Fig. 5.8) differed significantly among treatments at the end of the experiment (Table 5.1). Proportional changes (mean ± SE) in coral cover ranged from -0.06 ± 0.08 in exclosures to 0.45 ± 0.08 in ECxTG treatments. Though exclosures exhibited the only loss in coral cover, high variability resulted in no significant differences from zero and other treatments (Fig. 5.5c). ECxTG treatments, however, exhibited significantly higher proportional coral growth than all other echinoid treatments, and higher than any individual constituent species, thus indicating significant overyielding of this specific community (Fig.5.5c). Individual coral species responded to treatments in variable and unique ways; however not all species were present in all plots, thus limiting inferences about treatment effects on individual species (Fig. 5.9).

Macroalgal cover increased from 0 (open and ECxEC) to > 2000 cm^2 (approximately 30% of the frame area) in exclosure and HMxHM treatments (Fig. 5.5d). As for density and biomass of macroalgae, HMxHM appeared to have no measurable effect on macroalgal cover relative to full exclosures. Similarly, macroalgal cover was nearly zero for all EC-containing treatments and did not differ significantly from ambient conditions, with TG-treatments intermediate. Interestingly, coral cover did not decline significantly in treatments (e.g., No Urchin and HMxHM) that resulted in large increases in macroalgal density, biomass and cover (Fig. 5.3a, 5.4a, and 5.5a,c). Adult corals, therefore, appeared to be able to effectively resist mortality and colonization by algal communities that had been released from grazer control. Nested analysis of variance, comparing diversity of 1 vs 2 echinoid species, demonstrated no significant effects of diversity *per se* on either macroalgae or proportional coral growth (Table 5.2). This was due to significant variation among individual communities within each diversity treatment (Fig. 5.5). Therefore, echinoid community structure strongly affected benthic dynamics in experimental plots, but not simply the number of echinoid species.

DISCUSSION

Here we demonstrated strong, species-specific effects of echinoid grazers on benthic communities on a coral reef. Exclusion of herbivores resulted in large increases in algal density, cover and biomass. Furthermore, consumer effects differed significantly as functions of species identity and composition. Effects of grazers on macroalgae were greatest in all treatments containing *E. calamaris* (EC), suggesting that any enhancement of grazing in more diverse echinoid communities would likely be driven by the sampling effect (dominant species), as has been observed in many consumer (vs. producer) communities (Long et al. 2007). Single-species treatments containing *H. mammillatus* (HM) were often indistinguishable from consumer exclosures, indicating that, in contrast to EC, this species exerted minimal direct effects on macroalgae; *T. gratilla* (TG) exhibited intermediate effects. In contrast to the dominant effects of EC on macroalgae, one species combination (ECxTG) resulted in 300-400% greater proportional growth of corals versus other echinoid treatments, indicative of synergistic complementary effects of these two species in sympatry.

Herbivorous echinoids, therefore, exhibited single-sp. dominance with respect to macroalgal consumption, but also, in one combination, complementarity effects with respect to the enhancement of coral growth. Species-specific differences in effects on macroalgae matched predictions based on empirically-derived metabolic and grazing rates, and unique grazing preferences, for these taxa (Lewis and Smith, *in review*). For example, HM exhibits low metabolic and grazing rates, and prefers to consume turfs and CCA over most fleshy macroalgae. Furthermore, it's smaller size, combined with lower metabolic rate, would suggest more than 90% lower per capita consumption rate for HM than EC. These unique traits of HM would explain why this species exerted little effect on macroalgal communities inside HMxHM treatments and combined echinoid treatments. Here, we controlled for density among treatments to control variation in species interactions and encounter rates; however, controlling for total biomass may yield different results with respect to the effects of HM (though still likely 8-fold lower than EC based solely on differences in mass-specific rates of metabolism).

In contrast, EC exhibits the highest metabolic demands and grazing rates, and a strong preference for fast-growing fleshy macroalgae. This likely explains the strong, dominant effects of this metabolically-active, fleshy-algal specialist in the system. TG, though also exhibiting a relatively high metabolic and grazing rate (but lower than EC), exhibited a unique dietary preference for chemically and mechanically-defended leathery brown algae over all other algal types. The high grazing rates and unique dietary preferences exhibited by EC and TG suggested their diets and grazing behaviors may be complementary in nature; synergistic enhancement of coral growth observed in this study provides additional support for this hypotheses.

Diversity, redundancy, and ecological impacts

Though echinoids are often regarded as generalist consumers (Ogden & Lobel 1978, Hay 1984, Ogden et al. 1989, Steneck 2013), our results suggest that these three species may exert unique ecological effects in coral reef systems. Other "superficially-similar" (i.e., nominally-redundant) grazers have been shown to exert markedly different impacts on marine ecosystems. For example, seemingly functionally redundant species of amphipods exhibit unique feeding behaviors and result in unique epiphytic communities on seagrasses (Duffy & Harvilicz 2001, Duffy et al. 2001, Farlin et al. 2010). Different herbivorous fishes (e.g., parrotfishes and surgeonfishes) exhibit unique feeding behaviors and complementary effects on coral reefs (Burkepile & Hay 2011b). Similarly, our data suggest that nominally-redundant echinoids on coral reefs, in fact, exhibit unique physiologies and grazing behaviors that result in diverse ecological effects on benthic communities.

We found a single species (*E. calamaris*) to provide the strongest effects on macroalgae across all echinoid treatments. These results support previous empirical and theoretical studies examining effects of biodiversity on consumer community interaction strengths. For example, a single dominant crustacean (isopod) grazers drove patterns of consumption for grazer communities in a seagrass bed (Long et al. 2007) and a single dominant echinoid species drove patterns of consumption for grazer communities in a rocky reef ecosystem in the Galapagos Islands (Brandt et al. 2012). A review of the literature suggests that enhancement of effects in more diverse consumer communities appears to often be driven by the sampling effect (chance of including a dominant consumer); in contrast to producers where complementarity and facilitation are often drivers of diversity-function relationships (Long et al. 2007, Tilman et al. 2012).

All treatments containing EC exhibited near-elimination of all macroalgae and did not differ significantly from open plots, where large herbivorous fishes and echinoids were free to graze. Thus EC, at densities of 1/m^2, appeared to exert the same influence as all echinoids and herbivorous fishes (e.g., scarids and acanthurids) in the ambient community. Though fishes and echinoids greatly reduced algae in open plots, no significant growth in coral was observed. Brown algae (e.g., *Dictyota sp.*) were often observed inside cages, but rarely in open plots, suggesting that fishes may be important in limiting the spread and growth of this alga; however, it never became dominant in any of the caged plots. Small (< 3 cm girth) scarids (*Scarus psitticus*) were regularly observed grazing inside of cages, and likely influenced turf communities somewhat, but did not appear to have strong effects on macroalgae.

Diversity, complementarity, and synergism

In contrast to macroalgae, however, we provided evidence that a single combination of grazers (*E. calamris* and *T. gratilla*) may result in overyielding with respect to proportional increases in coral cover. This unique combination of echinoids resulted in 300-400% greater mean proportional growth rates than other echinoid treatments (Fig. 5.5c). Similar synergistic effects of complementary grazers have been described in various ecosystems. In macroalgal systems, two genera of snails exert unique and complementary effects on epiphytes, thus synergistically-enhancing the growth and survival of the red macroalga *Chondrus* (Stachowicz & Whitlatch 2005). In seagrass ecosystems, complementarity among herbivorous amphipods appears to enhance consumption of microalgae in more diverse communities, leading to unique ecological states (Duffy et al. 2003). In coral reef ecosystems, surgeonfishes and parrotfishes, together limit macroalgae and enhance coral growth better than either taxon alone

(Burkepile & Hay 2008). Our results suggest, therefore, that some echinoid species exhibit similar complementarity in their ecological functions. Therefore, management efforts perhaps should aim to increase the density of both species to maximize beneficial herbivory rates to these nearshore coral reefs.

Diversity *per se*, however, did not enhance effects on macroalgae consumption or coral expansion. In contrast, a weak consumer influenced macroalgae the least, a dominant consumer influenced macroalgae greatest, and one specific combination of species led to enhanced proportional coral growth, suggesting that species identity may be more important than diversity for these echinoid communities. The actual effects of diversity (vs. community structure) may vary with the number of species included in such studies. Though our study was limited to 3 species and lacked a full 3-sp. treatment, it expanded significantly upon previous manipulative subtidal studies (Burkepile & Hay 2008, Brandt et al. 2012). The true effects of diversity, however, could change in experiments with more species (Brandt et al. 2012). Similar, but larger-scale studies with more species and treatments are needed to more definitively discriminate between effects of diversity vs. community structure (Tilman et al. 1997, Duffy 2002); however these will require extensive effort and resources, such as collaborative research networks, given the constraints of subtidal ecology.

The mechanism for the observed enhancement of proportional coral growth by ECxTG treatments remains unclear. For example, macroalgal abundance and biomass was equally low in all treatments containing EC; therefore, it is unlikely that differences in macroalgae communities drove coral responses. Several possible explanations exist. First, it is possible that ECxEC and ECxHM treatments resulted in direct consumption of corals due to the unavailability of algal food sources (Fig. 5.3a, 5.4a, 5.55d). Reports of limited direct consumption of corals by echinoids in these families are in agreement with this hypothesis. Second, it is possible that ECxTG treatments modified turf communities, thereby enhancing coral growth. For example, turfs are often the most productive, pervasive, and harmful competitors with corals (McCook et al. 2001, Jompa & McCook 2003, Vermeij et al. 2010, Wild et al. 2014, Harris et al. 2015). Though we did not evaluate differences in community structure of algal turfs, we did examine changes in turf height and cover; however, these metrics were not significantly different between ECxTG and several other echinoid treatments (Fig. 5.3c). Finally, TG was observed occasionally grazing on sides of cages and perhaps enhanced light and flow in these treatments; however, no differences in light or flow among cages with and without TG were observed. The unique, positive response of corals to ECxTG treatment appeared strong and consistent across all replicates suggesting that this combination of grazers was removing key algal competitors of corals allowing them to increase growth rates beyond that observed in other treatments. Our results suggest that these common and often abundant sea urchin grazers seem to have markedly unique roles in coral reef benthic ecology and more research is needed to understand the potential synergies among taxa.

Herbivore functional groups

Assignment of herbivorous echinoids to functional subgroups may contribute much to our understanding of the status and function of echinoid communities. For example, a trophic sub-guild classification system has been used to describe communities of tropical herbivorous fishes: large and small scrapers/excavators, grazers/detritivores, browsers, and territorial farmers (Bellwood & Choat 1990, Choat et al. 2002). Such functional classifications can improve the interpretation of survey results, thus leading to an improved understanding of the status and function of herbivore communities. A similar classification system for tropical herbivorous echinoids might also lead to improved inference regarding the status and function of tropical echinoid communities. Our data suggest that higher-order taxonomic groupings (e.g., family) may be sufficient for trophic diversity alone; however, such a classification system could account for differences in dietary preferences, movement patterns, metabolic rates, and interactions with other species and the reef matrix.

Summary

Through a 26-mo. manipulative field experiment, we were able to test and describe the effects of species identity and structure of echinoid communities on their ecological functions on a Hawaiian coral reef. We identified strong (*E. calamaris*) and weak (*H. mammillatus*) actors with respect to macroalgal consumption, and one community (ECxTG) that may enhance coral growth above other treatments. Given that the future existence of many coral reefs will likely be deermined by the effectiveness of local herbivore populations to remove algae following disturbance (e.g., bleaching and storms) (Hughes et al. 2007), it is critical that we understand and manage for those characteristics that maximize herbivore contributions to resilience (Mumby et al. 2006, Adam et al. 2011). Though it may seem conservative to maximize all aspects of herbivore communities including abundance, biomass, size, and diversity; such action should be grounded in rigorous science. For example, maximizing the abundance of

Echinometra mathaei clearly will not yield a good return on investment if the goal is maximizing net reef accretion (O'Leary & McClanahan 2010, O'Leary et al. 2013), and our results suggest the same is likely true for *H. mammillatus*. In contrast, *E. calamaris* and *T. gratilla* appear to be important and effective components of nearshore coral reef grazer communities on Hawaiian coral reefs. Given the imminence of rapid global change, we must continue to experimentally explore and identify the characteristics of herbivore communities that will yield maximum benefits toward the growth and persistence of these ecosystems.

ACKNOWLEDGEMENTS

A legion of field and laboratory assistants made this work possible: E. Kelly, C. Edwards, N. Kaplanis, L. Segui, A. Netburn, K. Nichols, J. Harris, M. Summers, M. Gleason, A. Carter, T. Pierce, M. Miller, S. Kram and G. Butler, E. Engle, M. Vanworth, E., D’Andrea, A. Khen, N. Kaplanis, T. Imam, A. Ger, J. Tran, M. Morgan, Y. Takeshita, D. McLeish, T. Whitty, and A. Cannon. The SIO Dive Program (C. McDonald and R. Walsh) and Maui Scuba Diving Snorkel Center (R. Carman) supported diving operations, Maui Ocean Center (J. Luecke) provided wet-lab facilities, and SIO Center for Marine Biodiversity and Conservation (P. Dockry) provided administrative support. A. Cannon, A. Khen, A. Scott, J. Shurin, L. Levin, S. Sandin and anonymous reviewers provided comments and contributions that greatly improved the manuscript. Artwork courtesy of Adi Khen. This study was a collaboration with Maui Division of Aquatic Resources (DAR; R. Sparks and D. White) under DAR permit numbers: SAP2011-77, SAP2012-67, and SAP2014-42. Funding came from the PADI Foundation, Edna-Bailey Sussman Foundation, Scripps Family Foundation, SciFund Challenge, NRC Ford Foundation Fellowship, and the National Science Foundation Grant No. 0903551.

Chapter 5, in part is currently being prepared for submission for publication of the material. Lewis, Levi S; Edwards, Clinton B.; Smith, Jennifer E. The dissertation/thesis author was the primary investigator and author of this material.

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TABLES

Table 5.1. Effects of experimental manipulations of echinoid communities on benthic dynamics. Results of statistical tests on differences among treatments (k=8) and blocks (j=5) in benthic community composition (initial and final communities assessed using PERMANOVA), and changes in communities (final-initial assessed by ANOVA). Proportion of explained variation (PropVar) is reported as R^2 for ANOVAs and percentage of estimated components of variation (ECV) for PERMANOVA (Anderson 2001). P-values <0.05 in bold.

Method	Organism	Comparison	Metric	Factor	DF	Test	SS	F/Pseudo-F	P	PropVar
Reef Probe	Macroalgae	Initial	Composition (%)	Treatment	7	PERMANOVA	7799	2.0053	**0.029**	**0.242**
				Block	4		5170.4	2.3265	**0.023**	**0.219**
		Final		Treatment	7	PERMANOVA	14413	3.7837	**<0.001**	**0.380**
				Block	4		3015.2	1.3852	0.195	0.112
		Initial	Density (ind. Plot^{-1})	Treatment	7	ANOVA	547.20	1.56	0.189	0.409
				Block	4		423.65	2.11	0.106	
		Δ (final-initial)		Treatment	7	ANOVA	22211.90	11.42	**<0.001**	**0.757**
				Block	4		1962.75	1.77	0.164	
	Turf	Initial	Height (mm)	Treatment	7	ANOVA	4.23	0.45	0.860	0.178
				Block	4		3.84	0.72	0.586	
		Δ (final-initial)		Treatment	7	ANOVA	51.45	3.16	**0.014**	0.459
				Block	4		3.69	0.40	0.809	
Image Analysis	ALL	Initial	Composition (%)	Treatment	7	PERMANOVA	1617.7	1.2726	0.252	0.133
				Block	4		585.46	3.224	**0.005**	**0.299**
		Final		Treatment	7	PERMANOVA	9917.6	4.7619	**<0.001**	**0.391**
				Block	4		2345.5	1.9708	**0.037**	**0.157**
	CCA + Carb.	Δ (final-initial)	Area (cm^2)	Treatment	7	ANOVA	315381.17	2.14	0.0724	0.445
				Block	4		158763.25	1.88	0.1415	
	Turf	Δ (final-initial)	Area (cm^2)	Treatment	7	GLM	18107278	8.35	**<0.001**	**0.800**
				Block	4		804640	0.65	0.6322	
				ΔSand	1		4351087	14.05	**<0.001**	
	Macroalgae	Δ (final-initial)	Area (cm^2)	Treatment	7	ANOVA	23162596	10.16	**<0.001**	**0.744**
				Block	4		3370702	2.59	0.0584	
	Corals	Δ (final-initial)	Area (cm^2)	Treatment	7	ANOVA	1181104.40	2.00	0.091	0.410
				Block	4		459124.60	1.36	0.273	
		Δ (final-initial)	Proportion	Treatment	7	ANOVA	0.76	3.29	**0.011**	**0.494**
				Block	4		0.14	1.07	0.391	
Field Collections	Macroalgae	FINAL	Macro Dry Mass (g)*	Treatment	7	ANOVA	38.19	18.00	**<0.001**	**0.821**
				Block	4		0.60	0.50	0.7379	

*log(x) transformed

Table 5.2 Results of nested ANOVAs examining differences in proportional coral growth and change in macroalgal cover as functions of echinoid species richness (diversity = 1 or 2) and community structure (treatment). P-values <0.05 in bold.

Taxon	**Source**	**DF**	**Sum of Squa**	**F Ratio**	**Prob > F**	**RSquare**
Macroalgae	Model	5	15105551	7.672	**<0.001**	0.615
	Error	24	9450876			
	C. Total	29	24556426			
	Diversity	1	1036764	2.633	0.118	
	Treat[Diversity]	4	14068786	8.932	**<0.001**	
Prop. Coral	Model	5	0.504	2.798	**0.040**	0.368
	Error	24	0.865			
	C. Total	29	1.369			
	Diversity	1	0.026	0.708	0.408	
	Treat[Diversity]	4	0.479	3.321	**0.027**	

FIGURES

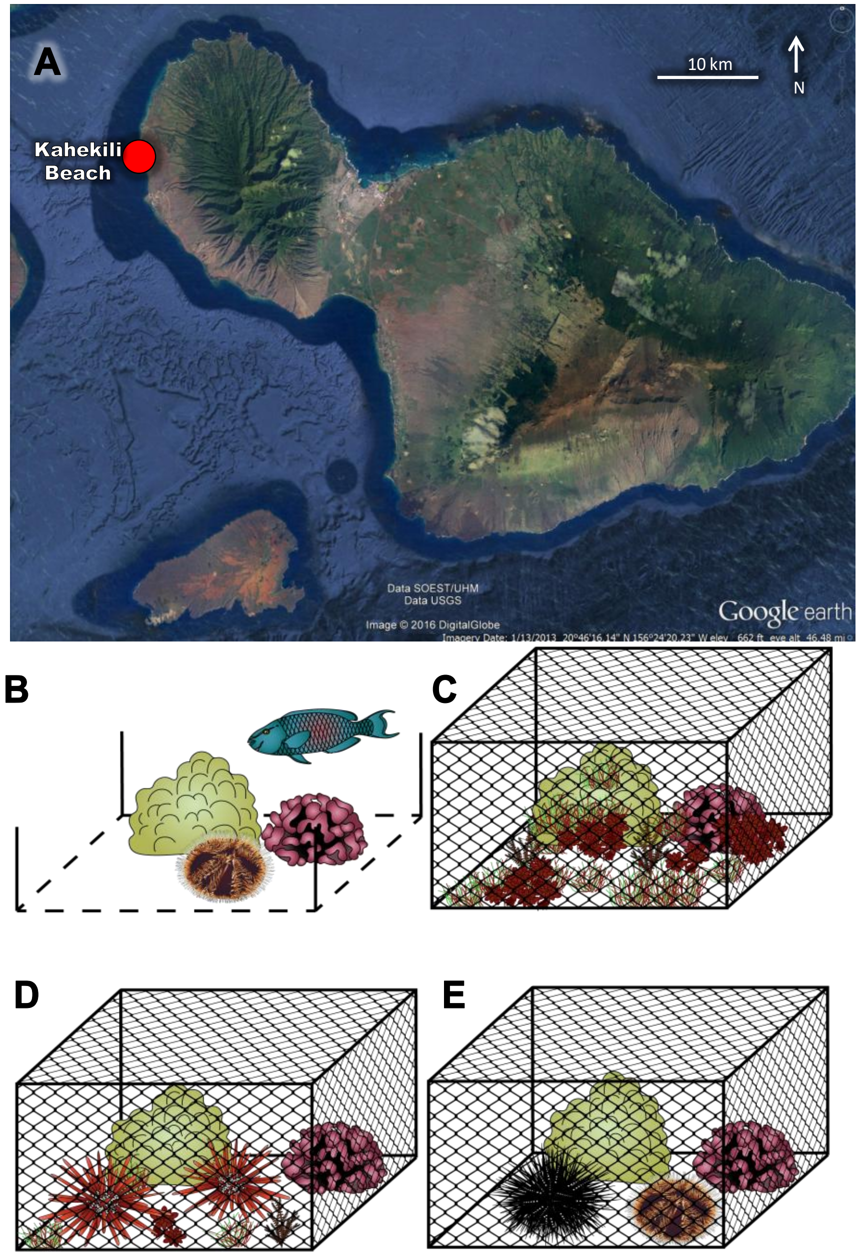

Figure 5.1. Location of study site on Maui, Hawaii (a), and examples of the four general diversity treatments: open (b), full exclosure (c), single -sp. (d), multi-sp. (e). Open plots were marked by 4 rebar and otherwise un-manipulated (open to all ambient consumers). Exclosure cages kept out all organisms greater than 3.2 cm in greatest dimension. Mono-species treatments received 2 of the same echinoid species whereas multi-species received 2 different species. All plots were 1 x 1 m and cages were 1 x 1 x 0.5 m.

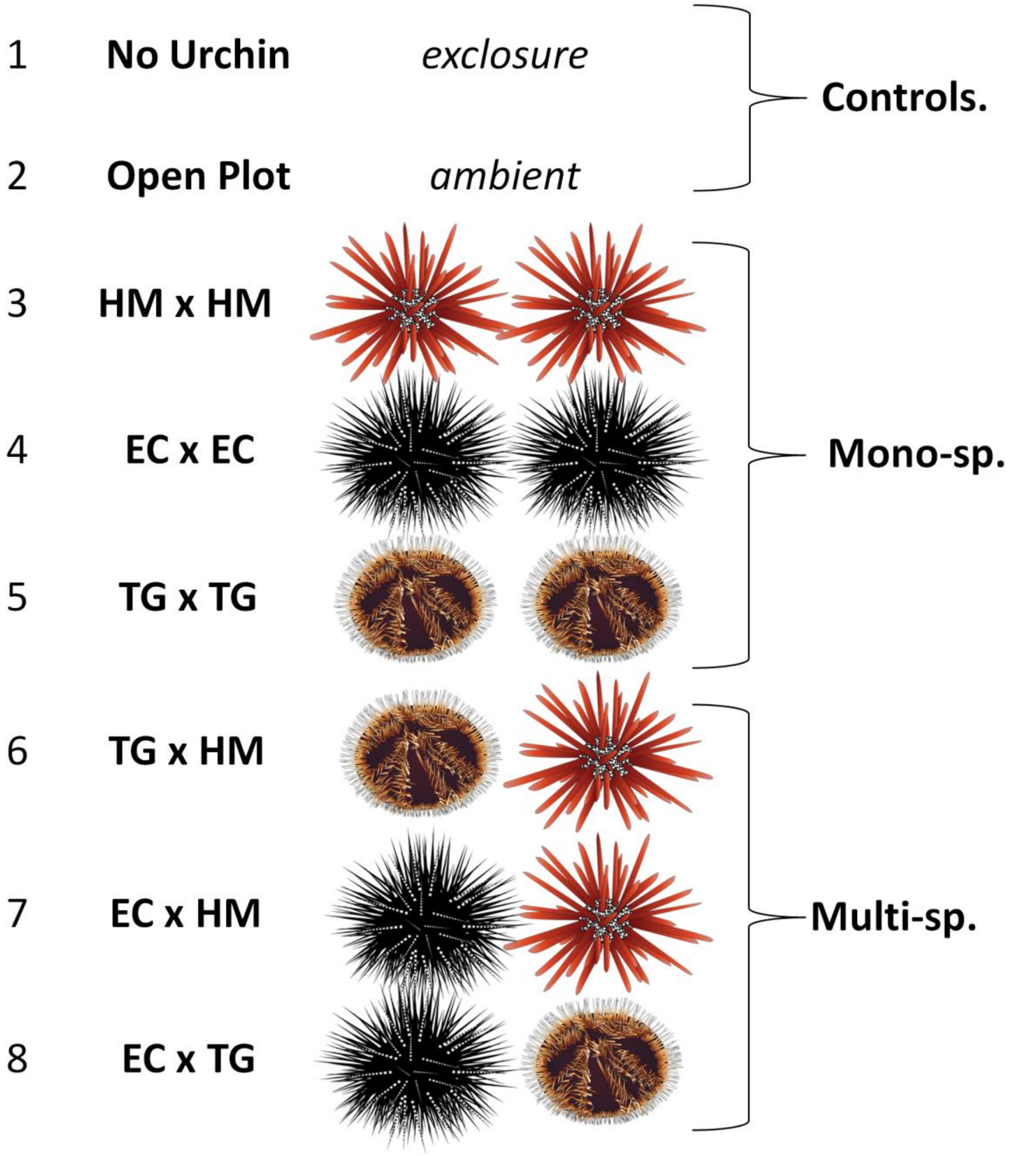

Figure 5.2. Schematic of the 8 experimental treatments established within each of the 5 spatial blocks. Echinoid species are *Tripneustes gratilla* (TG), *Echinothrix calamaris* (EC) and *Heterocentrotus mammillatus* (HM). Exclosures kept out all organisms less than 3.3 cm. Ambient plots were exposed to all grazers (fishes, turtles, and echinoids). Densities in Mono- and Multi-sp treatments were 2 ind m^{-2}.

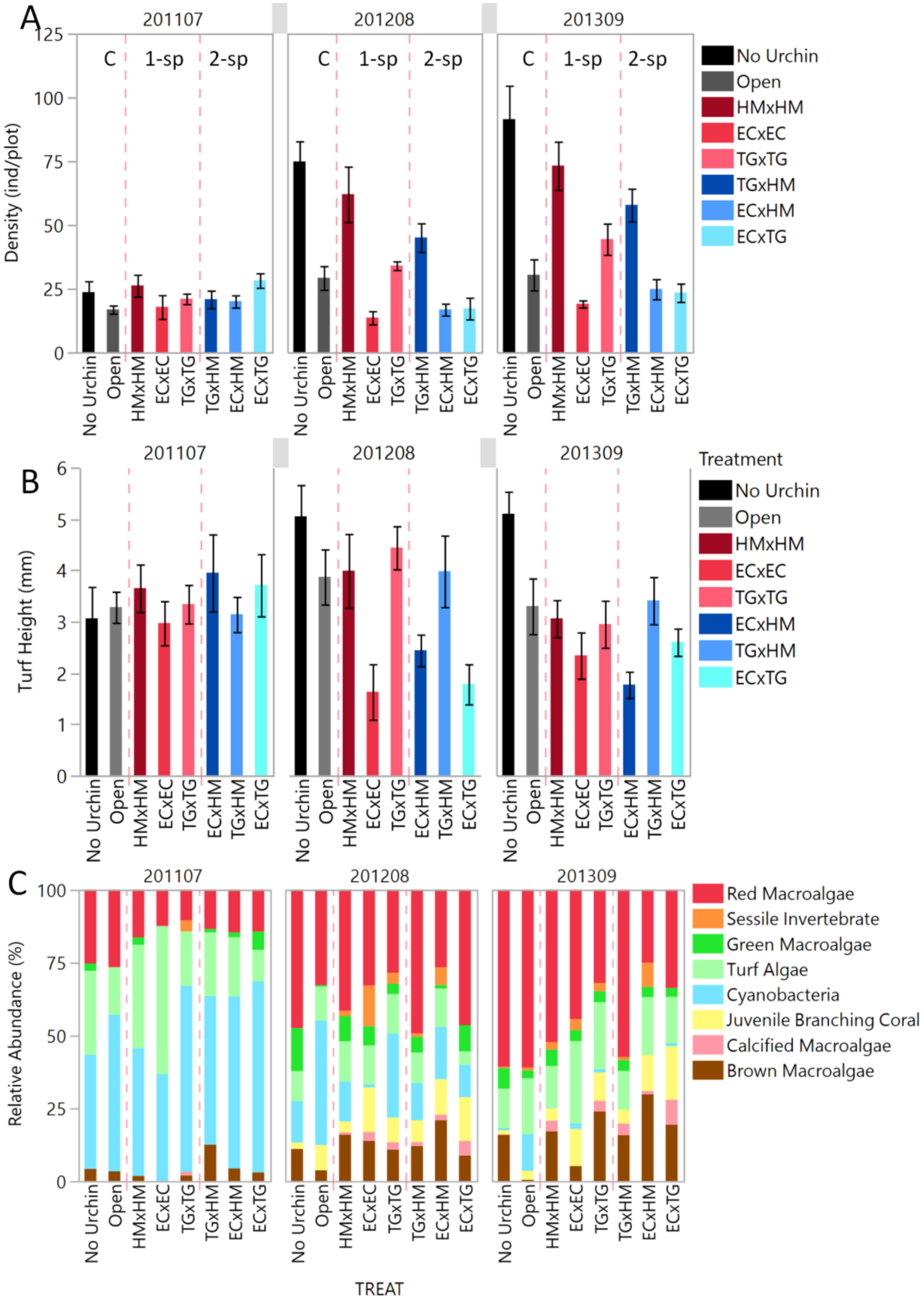

Figure 5.3. Mean (± SE) (a) densities of algal thalli, (b) turf heights, and (c) percent community composition (by density) of erect macroalgal functional groups and juvenile *P. meandrina* corals; each at initial, 1-yr and 2-yr time points (year and month provided). Control ("C"), single species treatments ("1-sp"), and multi-species treatments ("2-sp") are separated by dashed red lines. Plot size was 1 sq. m. *Note: juvenile corals were rare and not surveyed in 2011.*

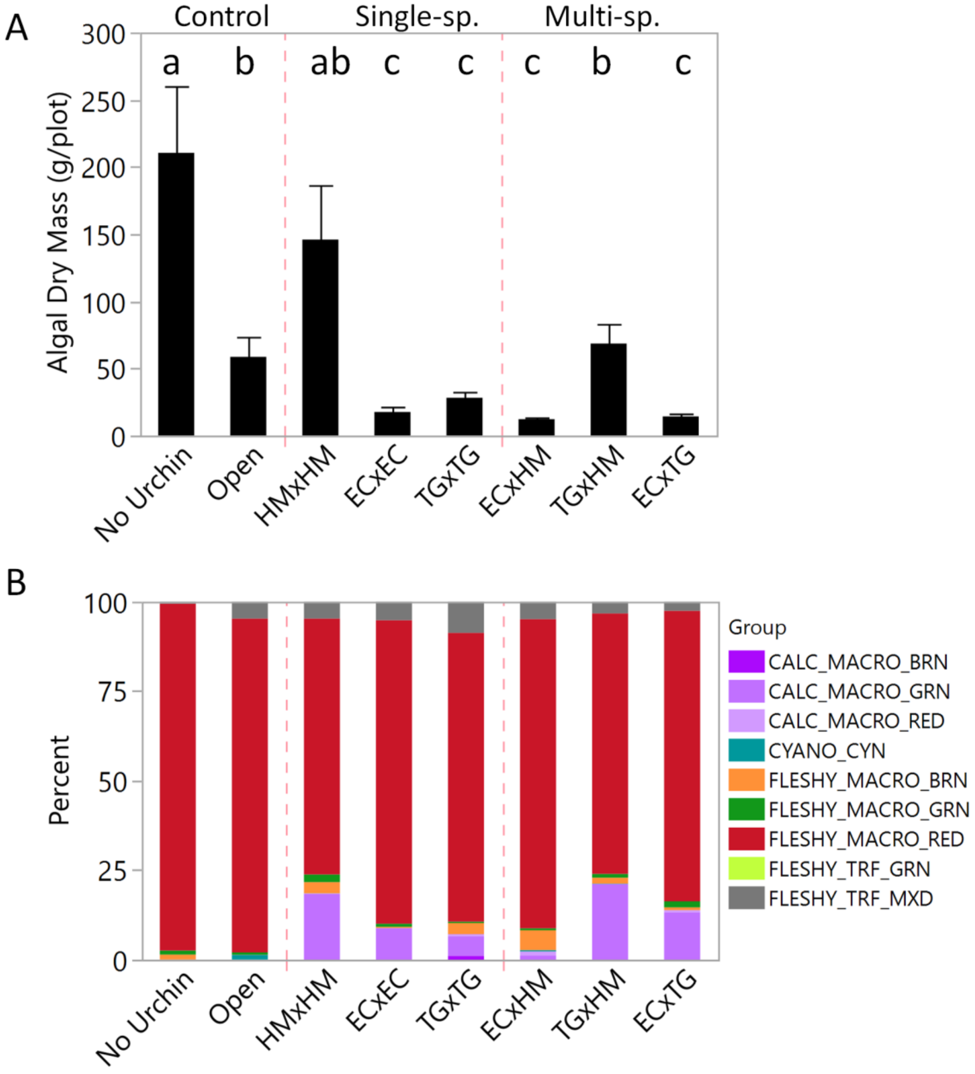

Figure 5.4. Macroalgal dry mass (a) and percent composition of biomass by functional group (b). Plot size was 1 sq. m. Values are means + SE.

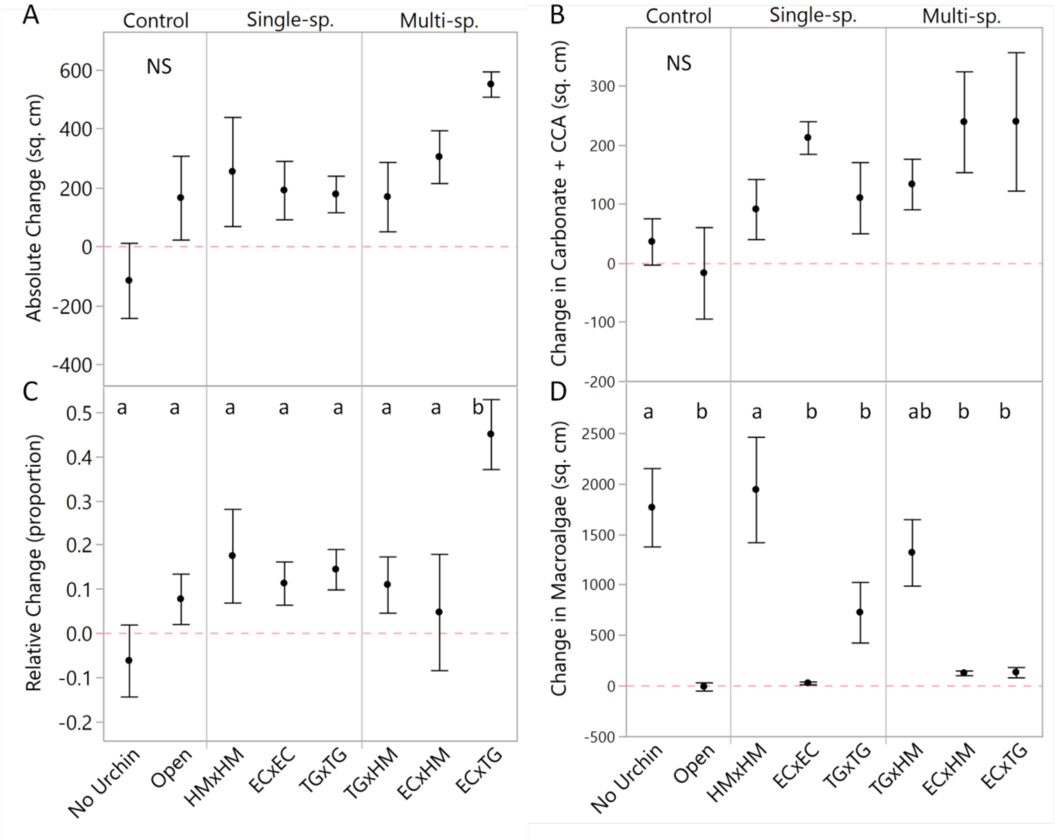

Figure 5.5. Changes in the areal cover of corals (a,c), calcified surfaces (carbonate + CCA) (b), and macroalgae (d) across treatments. All values are absolute changes (cm^2) except for (c) which is proportional. Image area was 82x82 cm (6724 sq. cm). Values are means ± SE.

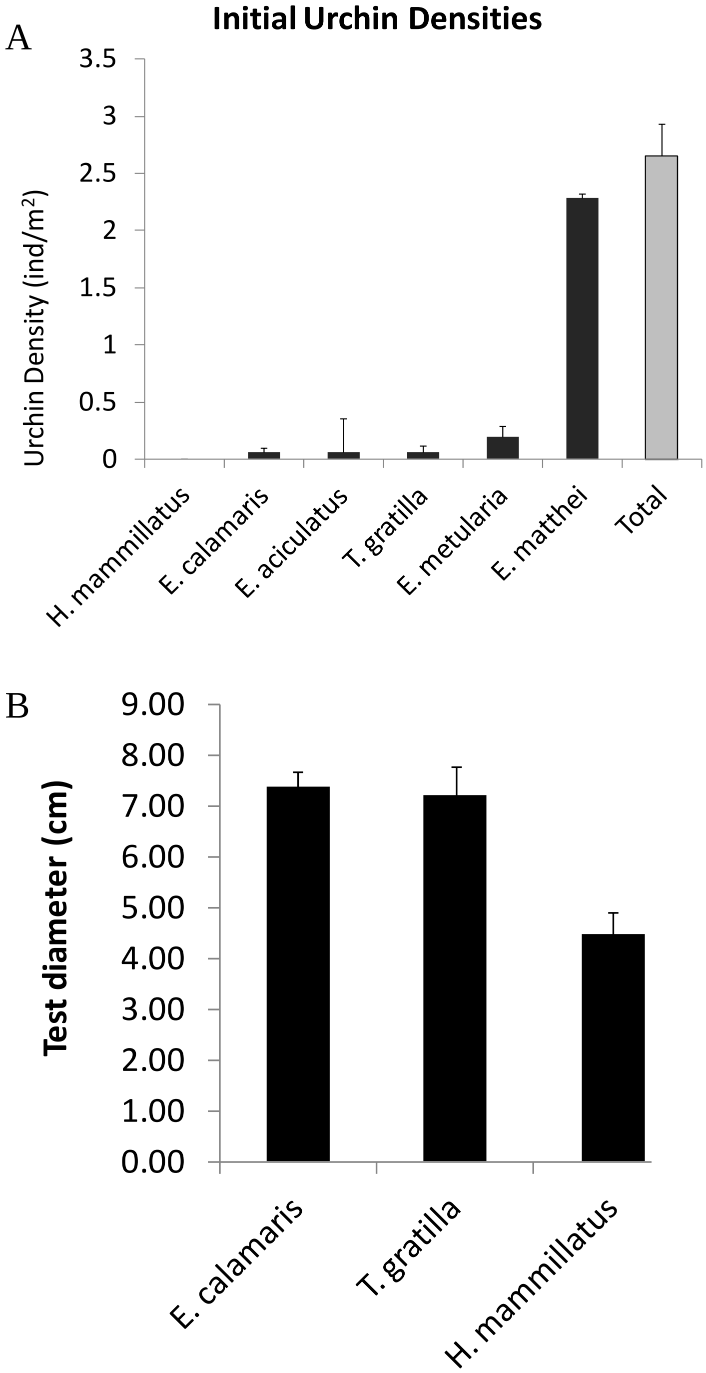

Figure 5.6. Echinoid densities on reef isolates prior to installation of experimental cages (a) and test diameters of echinoids used in experimental treatments (b). Values are means ± SE.

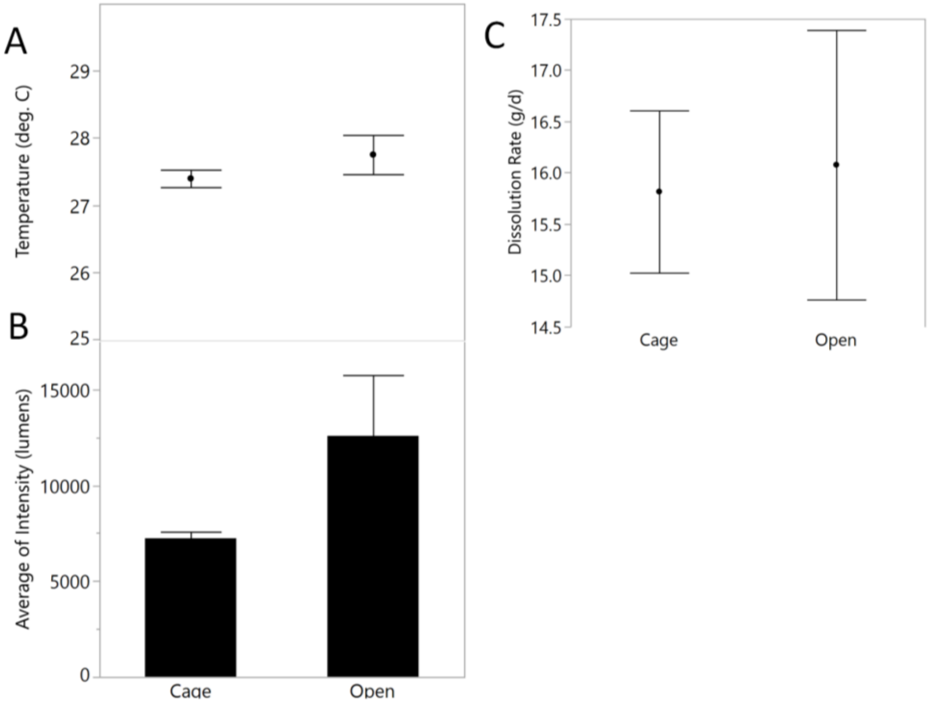

Figure 5.7. Cage effects on (a) temperature, (b) light intensity, and (c) flow by dissolution rate. (a) Cages reduced temperature slightly by 0.3 °C ($F_{1,7}$ =17.0, p = 0.005) and (b) light intensity by 50% ($F_{1,7}$ =105.2, p = <0.001). The reduction in light radiation likely accounted for the slightly cooler temperatures of sensors. No effect of cages on flow (c) were observed ($F_{1,10}$ =0.19, p = 0.671). Mean ± SE shown.

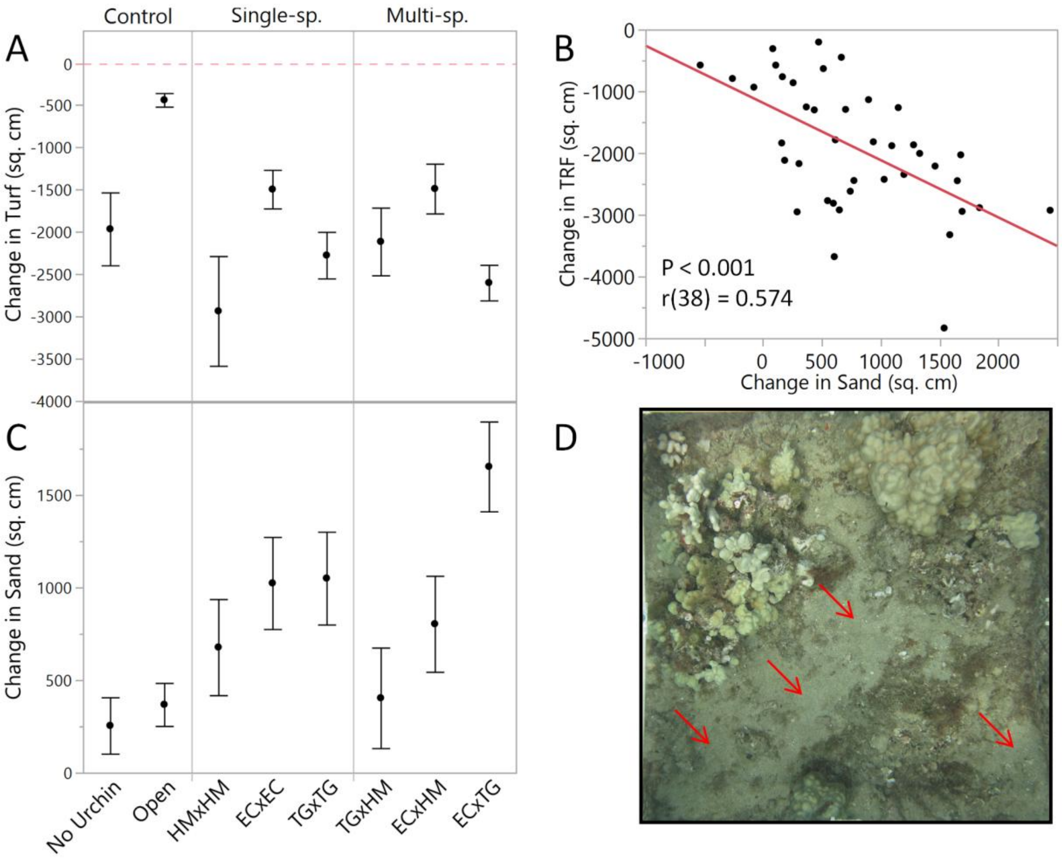

Figure 5.8. Effects of sediment inundation on cover of turf algae: (a) change in turf area, (b) correlation between changes in cover of sand and turf, (c) change in sand area, (d) image showing an example of sediment inundation (red arrows).

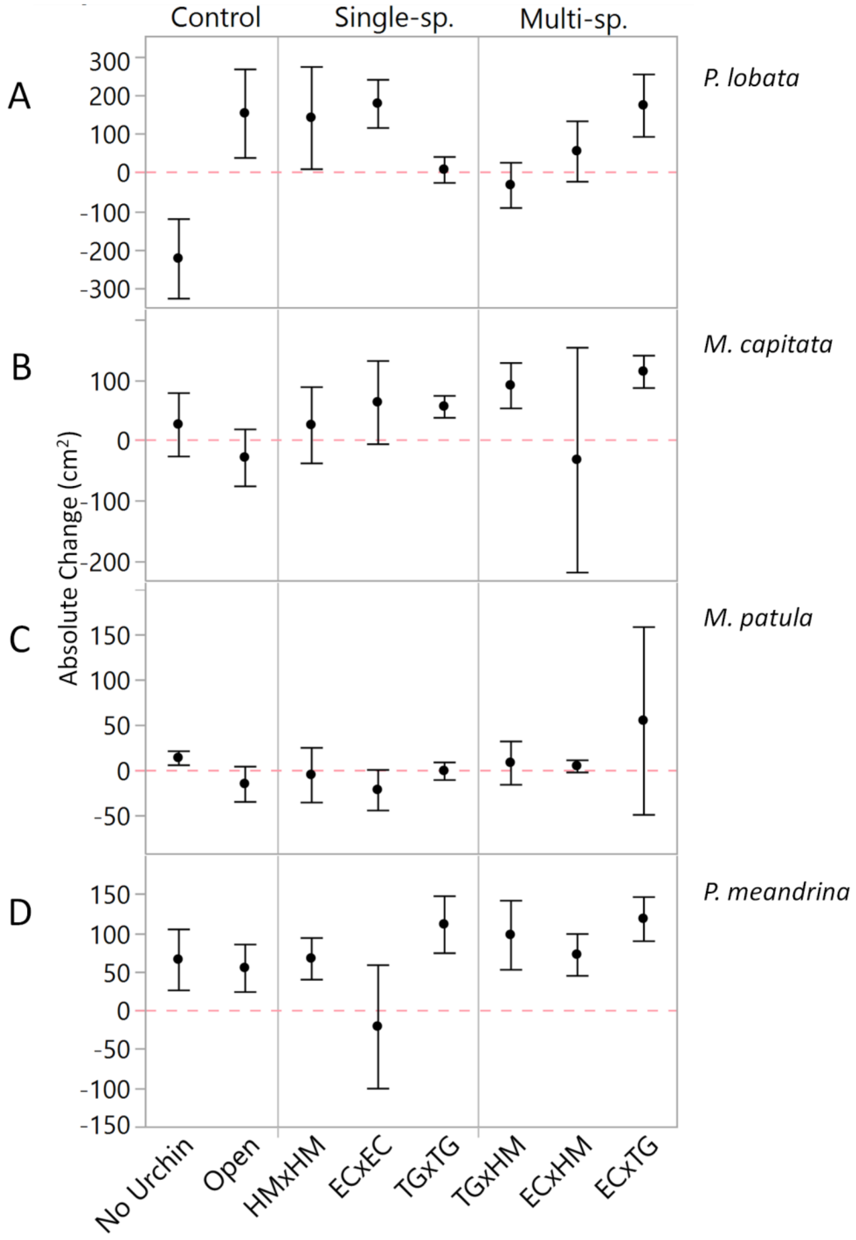

Figure 5.9. Changes (2011-2013) in the areal cover of 4 dominant coral species: (a) *Porites lobata*, (b) *Montipora capitata*, (c) *Montipora patula*, and (d) *Pocillopora meandrina* within 6 experimental echinoid treatments and 2 procedural controls. High variability limited inferences due to (1) lack of representation in all plots, (2) large individual mortality in individual plots, and (3) difficulty in identification of small individuals. Image area was 82x82 cm (6724 sq cm). Values are means ± SE.

CHAPTER 6 Conclusion: Advancing our understanding of spatial variation in consumer effects on benthic succession, interactions with the environmental setting, and the functional diversity and ecology of herbivorous echinoids on Hawaiian coral reefs

Levi S. Lewis

Herbivorous echinoids (sea urchins) are abundant consumers on shallow, nearshore coral reefs in Maui (Ebert 1971, Ogden & Lobel 1978), and given their strong effects on benthic coral-reef dynamics in the Caribbean Sea (Sammarco 1982, Hughes et al. 1987) and Indian Ocean (McClanahan 1988, O'Leary et al. 2012), these grazers are likely to drive many key biological processes on shallow reefs across the globe. This dissertation, therefore, focused on how variation in the structure of echinoid communities drives benthic community dynamics on Hawaiian reefs. The four data chapters used a combination of mensurative and manipulative approaches to address this topic; chapters were organized into two themes: (I) spatial variation in consumer effects in relation to environmental conditions and (II) functional diversity among echinoid species and communities, and its effects on benthic dynamics.

<u>THEME I</u>: *Spatial variation in consumer effects on benthic dynamics and in relation to environmental conditions.*

In **Chapter 2**, I used a 3-year deployment (with continual maintenance) of caged and uncaged settlement tiles; combined with surveys of herbivores, nutrients, and sediments; to describe significant and large spatial variation in consumer effects and their interaction with environmental conditions. Herbivore biomass was dominated by echinoids (mostly *Echinometra matthaei*, but also *Echinothrix diadema*, *Tripneustes gratilla*, and *Heterocentrotus mammillatus* at certain sites), ranging from approximately 0 to over 600 g m^{-2}, and though there was no correlation with macroalgal biomass on tiles, the effects (based on experimental manipulations) of herbivores correlated strongly with their biomass across sites. Despite strong effects on macroalgae, herbivores had no significant effect on coral recruitment, which appeared to be determined primarily by spatial variation in sediment exposure. When sediment exposure was low, however, herbivore effects appeared to be more important. Surprisingly, given much evidence for sewage discharges adjacent to several study sites, nutrients appeared to have limited influence on benthic dynamics in our study. Finally, anomalously low algal biomass and coral recruitment at otherwise "good" sites (given the values for measured variables) may indicate other limiting processes that generated additional spatial variability in benthic dynamics. A composite of major findings from **Chapter 1** are shown in Fig. 6.1.

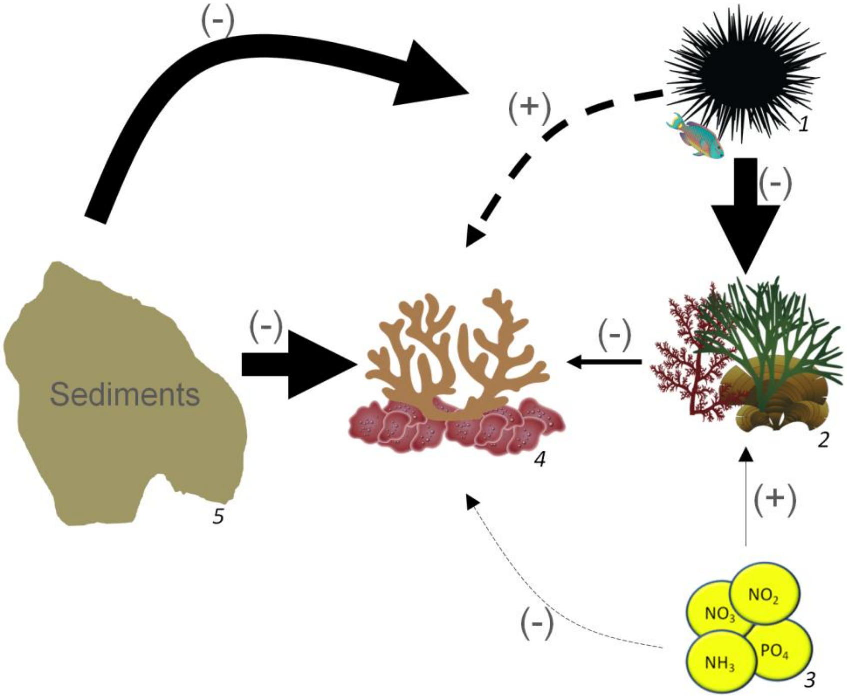

Figure 6.1. Ecological dynamics on shallow coral reefs in Maui, Hawaii. (1) Herbivore communities were dominated by echinoids (e.g., vs. fish) and exerted strong negative effects on macroalgal biomass (2). Nutrients (3) were generally low and did not correlate with any measure of community structure. Coral recruitment and cover (4) did not appear to be indirectly influenced by the strong effects of consumers on macroalgae, likely due to the strong, exponential effects of sediments (5) on coral recruitment; sediments are known to decouple the biomass of herbivores from their ability to regulate fleshy algae (e.g., sediment-laden turfs). Thus these shallow coral reefs appeared to be echinoid and sediment-dominated systems; however, significant variation existed, and results at sites with lower sediment exposures suggest that herbivore community structure, along with other environmental characteristics, may be determining benthic community structure and coral recruitment at these sites.

<u>THEME II</u>. Functional diversity among echinoid species and communities, and its effects on benthic dynamics.

In **Chapter 3,** I used standard metabolic assays to describe significant differences in the allometric scaling relationships of mass and metabolism for 5 common Hawaiian echinoids. Metabolic scaling coefficients of echinoids differed significantly from predictions based on the Metabolic Theory of Ecology. These empirically-derived coefficients, therefore, facilitate more accurate, taxon-specific, scaling of mass and metabolism for this important trophic guild. In **Chapter 4**, I combined results from metabolic assays with field-based assays of grazing rates and preferences to describe order-of magnitude variation in total and mass-specific metabolic and grazing rates, each of which were highly correlated at the species level. Thus high grazing rates corresponded with urchins that exhibited high metabolic demands (e.g., *E. calamaris, E. diadamea, and T. gratilla*). These taxa also exhibited strong preferences for robust fleshy macroalgae and limited preference dispersion (indicative of higher selectivity). Furthermore, the two species with the highest metabolic and grazing rates (*E. calamaris* and *T. gratilla*) exhibited unique preferences for different kinds of macroalgae. These 5 echinoids, therefore, exhibited unique physiology and grazing behaviors indicative of unique ecological functions.

In **Chapter 5**, I used a 2-year deployment of large cages on natural mixed-aggregate coral reef communities, and manipulations of three common species of echinoids (*E. calamaris, H. mammillatus, and T. gratilla*), to examine the long-term effects of 6 different types of echinoid communities on benthic communities on a coral reef. Responses of benthic communities within each of the 6 treatments were compared to each other, and in relation to patterns in 2 types of control plots (open-unmanipulated, and full-exclosure). Results demonstrated strong differences among species in their effects on macroalgae, with *H. mammillatus* exhibiting little effect, and *E. calamaris* exhibiting the strongest effects on macroalgae density, cover, and biomass; and these results matched predictions based on previous grazing assays. Effects appeared to be dominated by the presence of strong vs. weak interactors, indicative of a "sampling effect" according to biodiversity-ecosystem-function (BEF) theory. In contrast, one echinoid community (*E. calamaris* + *T. gratilla*) resulted in significantly enhanced proportional growth of corals, indicative of synergistic, complementary functions that may lead to transgressive enhancement of coral growth. A composite of major findings from **Chapters 3-5** are shown in Fig. 6.2.

The methods utilized in these chapters have numerous strengths and weaknesses. Chapter 2 was strong in that it included a comparative experimental design that allowed for inferences to be made about the general patterns in ecosystem dynamics island-wide and allowed for explicit contrasts between patterns and processes (e.g., grazing vs. macroalgae production). Furthermore, by comparing multiple key environmental drivers, some inference could be made regarding the roles sediments and nutrients may have in structuring these systems. This method, however, is limited by the number of sites that could reasonably be maintained and characterized, and the number of parameters that could be effectively assessed at each site. For example, while 8 sites is a great improvement on previous studies (which usually have 1-3 sites), this number of sites has little power for being able to statistically test for multiple correlations, redundancies and interactions among factors. Also, caged and open tiles were installed haphazardly and treated as independent replicates; however, pairing caged and open tiles would have greatly increased statistical power. More sites, and in particular, sites inside of reserves and in areas with abundant and healthy coral would provide further relevance and understanding about system dynamics. Last, the overwhelming influence of sediments in the nearshore environment (likely due to natural erosional processes and resuspension) overwhelmed experimental effects; repeating this experiment in deeper, lower-sediment, more rapidly accreting reefs would be greatly valuable.

Chapters 3-5 were strong by combining organismal biology with field ecology to explain variation in traits among echinoid species and testing how observed variation in traits might lead to variation in community effects on benthic dynamics as a function of community structure. The comparative standardized metabolic and field grazing rates provide some of the best comparisons of, and explanations for, variation in the feeding ecology and effects of echinoids on coral reefs. Metabolic assays may have been improved by gut evacuation; however, we aimed to incorporate digestion as a "field" (like) metabolic rate. Grazing rates in the field provided lower, but possibly more accurate grazing rates for the species studied. Increased replication, cage controls, and additional species in future experiments would strengthen the field experiment.

In sum, this dissertation demonstrates that (1) herbivory by echinoids varies greatly among sites and can be a dominant structuring force on coral reefs, (2) the *in situ* effects of echinoids on coral recruitment appears to be driven by a variety of factors (e.g., echinoid community structure and sediment exposure), (3) echinoid species vary greatly in their metabolic demands, grazing rates, and diet preferences, and (4) functional diversity among certain species of echinoids may lead to significant and large differences in the effects of unique communities on benthic dynamics and coral growth. Together, these results emphasize the importance and complexity of echinoid community demographics and consequent effects in coral reef ecosystems. Most studies of herbivore functional diversity in coral reefs have focused on fishes, often under the assumption that echinoids are generalist grazers. While it is true that echinoids are able and willing to consume and survive on a variety of different food items, this dissertation demonstrates that their unique preferences and grazing behaviors may result in diverse ecological functions on coral reefs. Therefore, conservation/management efforts and models of ecosystem dynamics for shallow coral reefs (where echinoids often dominate) should account for variation in echinoid community structure and function in order to maximize accuracy and long-term effectiveness.

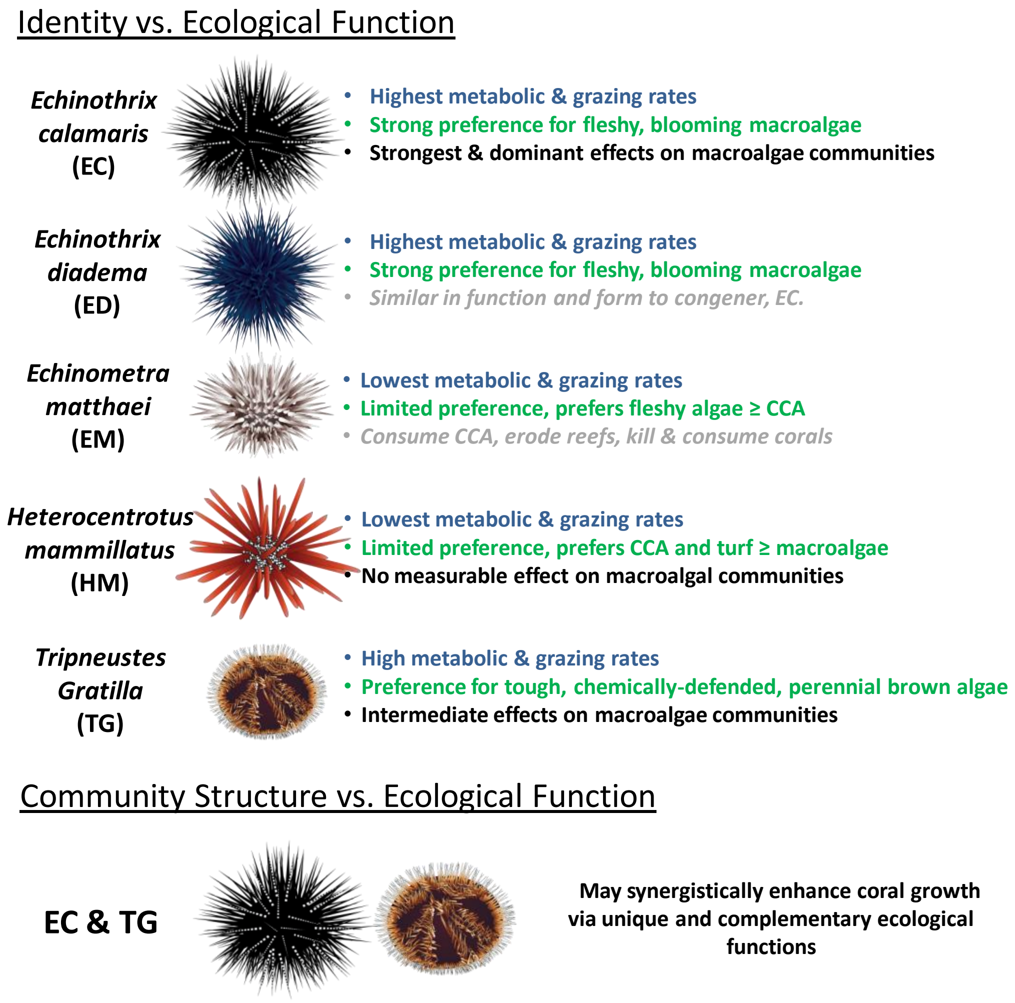

Figure 6.2. Diversity in the ecological functions of tropical herbivorous echinoids. *Echinothrix calamaris* (EC) and *Echinothrix diadema* (ED) (family: diadematidae) exhibited the highest rates of metabolism and grazing, strong preference for bloom-forming fleshy macroalgae, and the strongest effects (EC) on algal biomass on natural reefs. *Tripneustes gratilla* (TG) (family: Toxopneustidae) exhibited intermediate rates of metabolism and consumption, a uniquely high preference for chemically- and mechanically-defended leathery brown algae, and intermediate effects on benthic macroalgae. Echinoids within the family Echinometridae, *Echinometra matthaei* (EM) and *Heterocentrotus mammillatus* (HM), exhibited the lowest metabolic and grazing rates, little preference among algal types, and no measurable effect (HM) on macroalgal biomass on natural reefs. Experimental communities exhibited different effects on macroalgae driven by the dominance of strong (EC) and weak (HM) interactors ("sampling effect"). In contrast, a single combinations of species (ECxTG) resulted in enhanced proportional growth of corals, relative to all other treatments. These results suggest that the ecological functions of these two echinoids are diverse and complementary, and may enhance coral growth and the resilience of coral reefs.

Over the last 3 decades, biodiversity-ecosystem-function (BEF) theory has rapidly grown, with both theoretical and empirical studies indicating that biodiversity is one of the strongest (perhaps the strongest) drivers of ecosystem dynamics in nature (Tilman et al. 2012, O'Connor & Byrnes 2014, Tilman et al. 2014). Furthermore, losses of biodiversity (and its effects on ecosystem dynamics) has, and will likely continue to, degrade both nature and human well-being (Cardinale et al. 2012), thus providing the impetus for further research into this topic. Though the importance of diversity within herbivorous fish communities on coral reefs has been recently demonstrated (Burkepile & Hay 2008), this dissertation highlights how BEF theory pertains to a different, co-occurring group of herbivores in these systems.

Given that coral reefs are some of the most diverse habitats on the planet, taxonomic diversity within their herbivore guilds is large and varies at multiple phylogenetic levels; for example by phylum (fishes vs. echinoids), family (diadematid vs. echinometrid echinoids), genus (e.g., *Echinometra sp.* vs. *Heterocentrotus sp*., both echinometrids) and species (e.g., *E. calamaras* vs. *E. diadema*). Such depth in taxonomic diversity often results in significant niche overlap and functional redundancy that, itself, enhances long-term stability in the structure and function of a ecosystems (Naeem & Li 1997). Given that echinoids can consume and survive on a wide variety of food items, they likely function much in this regard. However, functional diversity and taxonomic diversity are not necessarily coupled, and research suggests that enhancing functional diversity within a system can have much larger effects than taxonomic diversity alone, often through the complementarity of unique functional traits (Tilman et al. 1997, Tilman et al. 2012). In our study, trophic diversity was strongest among echinoid families (differences among species and genera within families were relatively small), suggesting that feeding behavior may be homologous among family members (e.g., genera) and diverse among higher taxonomic levels. However, other dimensions of diversity (e.g., habitat) may reveal heterogeneity among genera and species. Our results emphasize the need for quantifying functional diversity (in addition to taxonomic diversity) to enhance our understanding of ecosystem dynamics and our ability to make wise decisions for the management and protection of coral reefs. Results of this dissertation advance our understanding of functional diversity within the herbivore trophic guild, its importance to benthic dynamics, and how community structure and function vary spatially on shallow coral reefs in Maui, HI.

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