A SYNTHESIS OF CORAL REEF COMMUNITY STRUCTURE IN HAWAIʻI AND THE CARIBBEAN

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF HAWAIʻI AT MĀNOA IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN

ZOOLOGY

DECEMBER 2017

By

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ACKNOWLEDGEMENTS

I would like to thank my dissertation committee, Alan Friedlander, Jeremy Jackson, Megan Donahue, Robert Toonen, and Kirsten Oleson for the support and assistance throughout my graduate career. I have also had the wonderful support of 3 labs while pursuing my graduate education at UH, and thank everyone from the Fisheries Ecology Research Lab, the Donahue Lab, and the Oleson Lab for providing a home and foundation of support throughout my time at UH. I also thank the staff of the Biology office, the JIMAR office, the HIMB office and the Sea Grant office for their tireless work that allows our research to occur. I would especially like to thank Audrey Shintani who has stuck by me the entire time, and often went above and beyond to help me get things accomplished. My PhD was made possible by the NMFS-Sea Grant Population and Ecosystem Dynamics Fellowship, for which I am very grateful to have been selected for. I'm especially grateful to Megan Donahue and Ivor Williams for supporting my fellowship and providing mentoring throughout. My Hawai‘i research was also supported by the NOAA Coral Reef Conservation Program, the Gordon and Betty Moore Foundation, and the Hawai‘i Division of Aquatic Resources. My Caribbean research was supported by the Australian Research Council Centre of Excellence for Coral Reef Studies, International Union for the Conservation of Nature, United Nations Environmental Program, NOAA Coral Reef Conservation Program, United States Department of State, Smithsonian Tropical Research Institute, and the Summit Foundation.

My research involved large collaborations and the input and generosity of many people who provided data and scientific expertise. In the Caribbean, this includes: Robert Edward Abbott, Karl Aiken, Pedro M. Alcolado, Andrés Alegría, Jahson Alemu, Bill Alevizon, Richard

Appeldoorn, Ernesto Arias, Roy Armstrong, Althea Athurton, Andrea Atkinson, Jerry Ault, Timothy Austin, Rolf Bak, David Ballantine, Carolina Bastidas, Jim Beets, Caroline Bissada-Goode, Héctor Bonilla Reyes, Nadia Bood, Claude Bouchon, Yolande Bouchon-Navaro, Steve Box, Marilyn Brandt, Angelique Brathwaite, Thomas Bright, Graeme Browne, Dan Brumbaugh, John Bruno, Kenny Buchan, Phillippe Bush, John Bythell, Chris Caldow, Robert Carpenter, Billy Causey, Bernadette Charpentier, Ernesto Chávez, Mark Chiappone, Iliana Chollett, Randy Clark, Rodolfo Claro, Mike Colella, Sean Connolly, Jorge Cortes, Katie Cramer, Marcia Creary, Aldo Cróquer, Rachel D'Silva, Craig Dahlgren, Kalli de Meyer, Ramon de Leon, Adolphe Debrot, Denise Debrot, Ian Drysdale, Phil Dustan, Mark Eakin, Peter Edmunds, Douglas Fenner, Ana Fonseca, Kirah Forman, Graham Forrester, Alan Friedlander, Rodrigo Garza Pérez, Peter Gayle, Sarah George, Francisco X. Geraldes, David Gilliam, Brooke Gintert, Ana Giró, Steve Gittings, Anne Glasspool, Ricardo Gomez-Lozano, Shannon Gore, Benjamin Greenstein, Gabriel Grimsditch, Héctor Guzmán, Nakhle Hado, Alastair Harborne, Marah Hardt, Peter Harrison, Scott Heron, Emma Hickerson, Mark Hixon, Paul Hoetjes, Terry Hughes, Joshua Idjadi, Roberto Iglesias, Walter Jaap, Jeremy Jackson, Stephen Jameson, Chris Jeffrey, Ayana Johnson, Ross Jones, Eric Jordán Dahlgren, Mandy Karnauskus, Jake Kheel, Allison King, Lindy Knowles, Nancy Knowlton, Barbara Kojis, Karen Koltes, Patricia Kramer, Philip Kramer, Vivian Lam, Patricia Lancho, Judy Lang, Yolande Leon, Don Levitan, Max Louis, Yossi Loya, Karen Lukas, Ian Lundgren, Isaias Majil, Carrie Manfrino, Jean-Philippe Maréchal, Juan Maté, Franck Mazeas, Tim McClanahan, David McClellan, Croy McCoy, Melanie McField, Sheila McKenna, Casuarina McKinney-Lambert, Erik Meesters, Jeff Miller, Margaret Miller, Steven Miller, Jerry Mitchell, Clare Morrall, Peter Mumby, Jessie M.H. Murdoch, Thaddeus Murdoch, Ivan Nagelkerkan, Andrzej Narozanski, Raul Navas, Richard Nemeth, Gerard Nieuwland, Steve

Nimrod, Tim Noyes, Maggy Nugues, Hazel Oxenford, John Pandolfi, Eric Pante, Gustavo Paredes, Ken Pemberton, Fabián Pina Amargós, Joanna Pitt, Simon Pittman, Nicholas Polunin, Leon Pors, Pedro Portillo, Juan Posada, Martha Prada, Norman Quinn, Bernhard Riegl, Sara Rivero Calle, Rosa Rodríguez-Martínez, Alberto Rodriguez-Ramirez, Caroline Rogers, Héctor Ruiz, Benjamin Ruttenberg, Rob Ruzicka, Paul Sanchez-Navarro, Stuart Sandin, Sander Scheffers, Myra Shulman, Sven Eloy Zea Sjoberg, Struan R. Smith, Tyler Smith, Brigitte Sommer, Chris Stallings, Sascha Steiner , Bob Steneck, Robert Steneck, Wolfgang Sterrer, Richard Suckoo, Kathleen Sullivan Sealey, Gerardo Toro Farmer, Rúben Torres, Ewan Tregarot, John Tschirky, Wes Tunnell, Mark Vermeij, Estrella Villamizar, Jack Ward, Ernesto Weil, Ivor Williams, Kim Withers, Jon Witman, Nancy Woodfield Pascoe. As well as the following programs and institutions: Atlantic and Gulf Rapid Reef Assessment (AGRRA), Bahamas Reef Environment Educational Foundation (BREEF), Bermuda Zoological Society, Caribbean Adaptation to Climate Change (CPACC), Caribbean Coastal Marine Productivity Programme (CARICOMP), Caribbean Environment Programme (CEP), Corporación para el Desarrollo Sostenible del Archipiélago de San Andrés, Providencia y Santa Catalina (CORALINA), Florida Fish and Wildlife Conservation Commission (FWC), Healthy Reefs Initiative (HRI), ICRI Secretariat, Instituto de Investigaciones Marinas y Costeras (INVEMAR), IUCN Global Marine and Polar Programme (IUCN-GMPP), Mainstreaming Adaptation to Climate Change Project (MACC), National Park Service-South Florida/Caribbean Network (NPS-SFCN), NOAA Biogeography Branch, Reef Check, Stichting Nationale Parken Bonaire (STINAPA), The Khaled bin Sultan Living Oceans Foundation (LOF), and World Resource Institute (WRI). In Hawai‘i, data providers and colleagues include Ivor Williams, Eric Brown, Eric Conklin, Ku‘ulei Rodgers, Russell Sparks, Bill Walsh, Paul Murakawa, and Alan Friedlander. In addition I thank the following institutions and organizations in Hawai‘i: National Park Service, NOAA Coral Reef Ecosystem Program, Hawai‘i Division of Aquatic Resources, The Nature Conservancy, NOAA Biogeography Program, and the Hawai‘i Coral Reef Assessment and Monitoring Program. I would also like to thank my colleagues on the Ocean Tipping Points program who collaborated on Chapter 3, including: Willow Battista, Larry Crowder, Ashley Erickson, Kim Falinski, Alan Friedlander, Rod Fujita, Don Gourlie, Jamie Gove, Nick Graham, Jean-Baptiste Jouffray , Carrie Kappel, Kendra Karr, Jack Kittinger, Joey Lecky, Albert Norström, Magnus Nyström, Kirsten Oleson, Courtney Scarborough, Kim Selkoe, Lisa Wedding, Kristen Weiss, Crow White, Ivor Williams, and Gareth Williams.

I would also like to acknowledge my mentors, professors and colleagues who have helped make me into the scientist I am today, including: Ivor Williams, Ed DeMartini, Scott Hamilton, Ben Ruttenberg, Kim Selkoe, Carrie Kappel, Crow White, Lisa Wedding, Jack Kittinger, Bob Warner, Armand Kuris, Bruce Tiffney, Mark Vermeij, Sean Connolly, Katie Cramer, Kendra Karr, Brian Bowen, Anna Neuheimer, Chuck Birkeland, Jamie Gove, Mark Hixon, Orou Gaoue, Gareth Williams, Jenn Caselle, Terry Hughes, Pete Mumby, Bob Steneck, Iliana Chollett, Matt Ramsey, Eric Co, Eric Conklin, Bill Walsh, Russell Sparks , Kuulei Rogers, Darla White, Brian Neilson, Adel Heenan, Kelvin Gorospe, JB Jouffray, Albert Norstrom, Magnus Nystrom, Ashley Erickson, Kosta Stamoulis, Eva Schemmel, Stuart Sandin, Jen Smith, Nick Graham, Larry Crowder, Eric Brown, Vivian Lam, Chad Wiggens, and Jonatha Giddens.

Finally, I am forever grateful to my friends and family for their support. I am especially grateful to Joey Lecky for his love and standing by me through all of the good and bad times. I owe everything to my parents for always believing in me and supporting me no matter what.

ABSTRACT

A large focus of coral reef research to-date has been documenting the frequency, causes, and consequences of reefs shifting from dominance by corals to macroalgae, but further consideration of important components of the ecosystem, such as fishes and other benthic organisms, is needed to fully capture reef dynamics. This research investigated patterns of coral reef community composition based on both fish and benthic assemblages in Hawai‘i and the Caribbean to provide a broadened perspective on coral reef structure and indicators of change. Data were synthesized in both regions from existing sources and novel methods were developed for creating a unified database framework, which facilitated analysis of fish and benthic data from disparate sources. The status of Caribbean coral reefs varied greatly, with a 12-fold difference in biomass of fishes across 36 locations. Greater biomass and larger sizes of predators and scrapers were associated with greater coral cover and lower macroalgal cover. The state of reefs in Hawai‘i was assessed based on the composition of fish and benthic functional groups, revealing five distinct reef regimes that varied ecologically. A degraded regime with low coral and low fish biomass was identified, as well as four other novel regimes that varied significantly in their ecology, including three that were previously considered a single coral-dominated regime. Analyses of time series data reflected complex system dynamics, with multiple transitions among regimes. Finally, metrics of fish and benthic communities that relate to our understanding of resilience on coral reefs were compared between Hawai‘i and the Caribbean. Patterns of coral and macroalgal dominance, functional and response diversity, and the relationships between herbivore abundance and benthic state all varied between regions, revealing important differences in what underpins resilience in relatively species-poor geographies. This dissertation provides patterns and metrics of reefs in Hawai‘i and the Caribbean that can be used for monitoring and managing ecosystem changes on coral reefs in light of increasing human impacts and global environmental change.

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CHAPTER 1 INTRODUCTION

Beyond coral and macroalgae

A key concept foundational to this research is resilience, which can be defined and measured in different ways. Resilience can be defined as the capacity of an ecosystem to withstand disturbance without changing its overall identity in terms of structure and function (Holling 1973; Gunderson 2000; Nyström et al. 2008). This is often referred to as *ecological resilience* and includes the concept of tipping points and changes in feedbacks leading to abrupt transitions between multiple ecosystem states (Scheffer et al. 2001). Another proposed view of resilience focuses on stability, termed *engineering resilience*, which can be measured as the speed of recovery, or return to equilibrium, following a disturbance (Holling and Meffe 1996). This is in contrast to ecological resilience, where the measures are focused on movements is away from equilibrium, and can be measured as the magnitude of disturbance that can be absorbed by the system without changing its structure and function (Gunderson 2000). Debate around resilience concepts is in part a result of the difficultly of measuring resilience, since the ideas are often grounded in theory, and few empirical examples exist. Thus, differences in definitions of resilience can cause confusion over what is being measured and what the outcome will be (Brand and Jax 2007; Thrush et al. 2009). Likewise, measuring resilience will depend on the spatial and temporal context of the investigation, making generalizations difficult to achieve (Levin 2000).

This evolution of ideas regarding resilience form a theme in investigations of changes in coral reefs in response to human influences (Mumby et al. 2007; Mumby and Steneck 2008; Nyström et al. 2008; Hughes et al. 2010). Prior to large-scale human influences, coral reefs were thought to represent successional communities that reached a climax state in the absence of discrete disturbances such as hurricanes (Goreau 1959; Loya 1976; Pearson 1981; Woodley et al. 1981). More frequent disturbances were thought to lead to sub-climax communities (Connell 1978), and recovery could be prolonged depending on the successional state before the disturbance (Grigg and Maragos 1974). This view conforms to engineering resilience, where recovery was considered in terms of a return to equilibrium (Holling 1973). However, this view is limited in that it does not consider the possibility of 'ecological surprises' or rapid, non-linear shifts to alternative states captured in ecological resilience (Holling and Meffe 1996).

The concept of a single equilibrium state was challenged for coral reefs (Done 1992; Knowlton 1992; Hughes 1994), following observations such as the mass mortality of the urchin *Diadema antillarum* across the Caribbean in 1983 (Lessios et al. 1984). In Jamaica, coral cover was reduced by 92% and macroalgal cover increased by 96% following the loss of *Diadema* compounded with the occurrence of two hurricanes, providing evidence of a large scale coral reef regime shift (Hughes 1994). Evidence for regime shifts from coral to macroalgae were subsequently documented by many other coral reef researchers, forming a central area of research for several decades (McCook 1999; Nyström et al. 2000; Jackson et al. 2001, 2014; Bellwood et al. 2004; Hughes et al. 2007, 2010; Ledlie et al. 2007; Mumby et al. 2007), including documenting the negative consequences for human societies (Knowlton 2001; Cinner et al. 2009; Kittinger et al. 2012; Graham et al. 2013).

Building on the idea of alternative states, there has been increasing recognition that coral reef systems can have multiple alternative states beyond just coral or macroalgae. Norström et al. (2009) reviewed examples of regime shifts from coral to corallimorpharia, soft corals, sponges, and sea urchin barrens, suggesting that our understanding of how coral reefs respond to disturbance may be more nuanced than previously thought. Likewise, the concept of novel systems, where it may be increasingly less likely to return to historic conditions, has also been proposed for coral reefs (Graham et al. 2014).

Despite these proposals for considering alternate reef states, discussions have been largely focused around the evidence for and against the existence of coral and macroalgal stable states (Bruno et al. 2009; Mumby 2009; Dudgeon et al. 2010; Zychaluk et al. 2012; Mumby et al. 2013b). This debate is confounded by the context of the discussion, with little consensus over whether the focus is on engineering or ecological resilience. In addition, discussions are clouded by poor assumptions, such as using models uniformed by empirical data, or field data alone that come from short time series or that do not capture the full variability of the external driver (Mumby et al. 2013b). Thus, by focusing on whether coral dominated states are a stable equilibrium, key concepts of ecological resilience are ignored. Particularly, the idea that systems are “moving targets,” and states away from equilibrium are those that are subject to abrupt shifts, so measuring more than equilibrium coral cover would be needed to understand the system (Nyström et al. 2008). If the ecosystem is dynamic, then focusing on one ecological variable can also cause misinterpretation of the signs and causes of resilience. Such was the case in the Caribbean before 1984, when high coral cover was mistaken for high resilience, and declines in the overall status of the system came as a surprise following the massive die-off of *Diadema* in 1984 (Hughes et al. 2010).

In order to embrace resilience from a perspective of dynamic systems that are subject to ecological surprises we need to broaden our perspective. For coral reefs, this means moving away from the focus of coral-macroalgal phase shifts, and considering the system as a whole. For example, how does a reef with low coral and low macroalgae fit into the coral-macroalgal paradigm? Perhaps, if fishes or other components of the benthos were considered (e.g., coralline algae, sponges, etc.), then a clearer picture of the ecosystem state would be possible. In fact, in the absence of fishing, large gradients in reef fish biomass occur across uninhabited locations in the Pacific, which highlights the importance of differences in habitat and productivity across the gradient (Williams et al. 2015b). In Hawaii, distinct fish assemblages can be found in locations with different wave exposures, which also likely correlate with the structure of benthic assemblages (Friedlander et al. 2003). Therefore, there is a need to characterize coral reef communities based on more than just-coral or just-fishes and describe the dynamics of whole ecosystems in the context of resilience theory.

This dissertation addresses questions about the structure and function of coral reef ecosystems by investigating patterns in fish and benthic assemblages in both the Caribbean and Hawaii. A unifying theme throughout is moving beyond the coral-macroalgal paradigm of coral reef ecosystem structure to address multiple components of the ecosystem in a unified synthesis. This research addresses the following goals:

1) Develop comprehensive databases with a unified framework for fish and benthic communities in the Caribbean and Hawaii;
2) Quantify patterns of fish assemblage structure across the Caribbean and relate those patterns to benthic communities [Chapter 2];
3) Apply an ecosystem-based approach to quantifying and understanding coral reef regimes in Hawaii [Chapter 3]; and,
4) Compare the ecologies of Hawaiian and Caribbean coral reefs to assess how they relate to metrics of resilience [Chapter 4].

To achieve these goals at broad spatial scales across Hawaii and the Caribbean, data were synthesized from existing sources in both regions.

Synthesizing data on coral reef ecosystems from multiple sources

The need for answering ecological questions at broad scales is increasingly important in an era of global environmental change, and examples of 'big data' in ecology, where data are combined from multiple sources, are becoming increasingly prevalent (Hampton et al. 2013). With the broadening of ideas comes a growing challenge in handling complexities associated with disparate data structures, and rigorous database and statistical approaches are needed (Michener and Jones 2012; Hampton et al. 2013). One approach to scaling up ecological analyses of existing data is to synthesize primary data and apply advanced statistical approaches that build on traditional meta-analyses (Mengersen et al. 2013). Meta-analyses based on primary data are relatively rare in both ecology and evolutionary biology (Mengersen et al. 2013), and medicine (Simmonds et al. 2005), but the method holds great promise.

There have been several recent attempts to synthesize data from individual studies and long-term monitoring on coral reefs (Gardner et al. 2003; Côté et al. 2005; Bruno and Selig 2007; Paddack et al. 2009; De'ath et al. 2012; Jackson et al. 2014; MacNeil et al. 2015). However, these studies focused on either fish or coral, but not both, have largely been based on traditional meta-analysis, and suffered numerous analytical challenges. For example, systematic long-term data are only available in a few locations, and often started after changes had already occurred; so, without harnessing the full breadth of information available in the primary data, signals from early changes were missed. Likewise, relying on one or a few datasets that cover large geographies and ignoring vast amounts of individual observations limits spatial and temporal scales for inference. So, there still remains great opportunity for understanding coral reef ecology by harnessing primary data from existing sources at broad scales (Hughes et al. 2010).

A major challenge limiting the use of primary data in synthesis of coral reef status and trends is disparate and unstructured data storage that largely consists of individual researchers storing individual datasets with no central repository. Thus, data gathered from multiple sources often comes in multiple formats, raising a number of data curation challenges (Michener and Jones 2012). In addition, data from observational studies can contain a variety of sources of error (e.g., such as observer level differences and site selection bias), and the research questions and goals of the synthesis project were often different from the question the data were collected for originally. All of these factors need to be accounted for in both the database structure and statistical design.

I addressed these challenges in two ways. First, I created a database template that allows for inconsistent data structures to be formatted in a common framework while retaining important metadata that is needed for analysis. Second, I analyzed the data using hierarchical models that allowed for testing hypotheses using the primary data while accounting for variation within and among datasets.

Hierarchical models

Meta-analysis of primary data allows for flexibility in hypothesis formation since the same questions can be asked across all datasets. This can be achieved through an extension to traditional meta-analysis that relies on study means and variances (Koricheva et al. 2013), where the primary data are included in a hierarchical model (Mengersen et al. 2013). The lowest level of the model is made up of study-specific estimates, and those are combined to form a distribution of estimates around the global mean. Thus, the data are simultaneously modeled at multiple levels to achieve an analysis of the primary data that incorporates uncertainty at all levels (Figure 1.1).

For example, if the goal was to estimate a global mean from multiple datasets, the model could take the form:

$$y_i = \mu_{j[i]} + \varepsilon_i$$

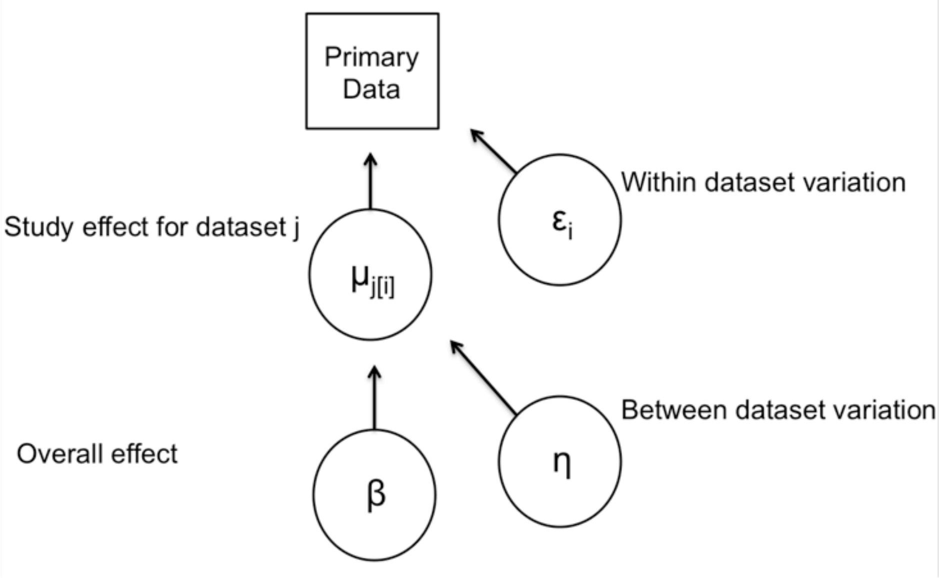
$$\mu_j = \beta + \eta$$

where i is each observation in dataset j, $\mu_{j[i]}$ is each dataset level effect, β is the global mean, and ε_i and η are error terms. This form was used throughout this dissertation through implementation as mixed-models with the *lmer* function in the package *lme4* (Pinheiro and Bates 2000; Bates et al. 2010; Skaug et al. 2013), implemented in the R environment for statistical computing version 3.3.0 (R Development Core Team (2016)). In this framework, the dataset level effect is termed a 'random effect', and models are fit using maximum likelihood, where the parameters were estimated with the likelihood of the parameters given the data $L(\mu_{j[i]}, \beta | y_i)$ (Bates et al. 2010).

Datasets

Existing data from underwater visual censuses were synthesized for both Hawaii and the Caribbean. In both regions, datasets include large-scale monitoring programs, monitoring at specific sites, and one-off surveys by individual researchers. In total, for Hawaii, the database consisted of 20,986 transects from 4,782 sites with data on fish assemblages and 11,937 transects from 3,972 sites with data on benthic cover. These data come from 20 different datasets contributed by nine different collaborators. In total, for the Caribbean, the database consisted of more than 35,000 surveys of corals, macroalgae, and reef fishes distributed among 90 reef locations in 34 countries, states, or territories. These data come from 287 different datasets contributed by 96 different collaborators. Further detail about the individual datasets and synthesis methods are included in the respective chapters where they are analyzed.

Figure 1.1 Directed acyclic graphic (DAG) of hierarchical model made up of dataset-specific estimates, combined to form a distribution of estimates around the global mean. Rectangles represent data and circles represent estimated parameters.



CHAPTER 2 Fish assemblage structure explains disparities in ecosystem state in the Caribbean

Abstract

Tight feedbacks exist between fish and benthic assemblages, and certain fishes provide critical ecosystem functions, such as removal of algae by herbivores. Previous studies have documented large scale differences in fish assemblage structure across the Caribbean, but how these patterns relate to large scale variation in benthic cover are less well understood. Therefore, we hypothesized that the biomass and size of fish functional groups across a spatial gradient in the Caribbean would be related to variation in coral and macroalgal cover. Data on fish and benthic assemblages were compiled from existing primary data sources across the Caribbean and compared to estimates of fish and benthic metrics using methods that account for data from disparate sources. Different patterns were found across fish functional groups, but in general, greater biomass and size of fishes was associated with greater coral cover and lower macroalgal cover. Predator and scraper biomass and size were particularly important indicators, as they were consistently associated with differences in benthic cover. The large spatial scale of this study provides context for finer scale observations that relate fish and benthic dynamics on reefs, and the results support previous work that suggests large predators and scraping parrotfishes are important determinants of benthic structure. The results support the use of fish functional groups as indicators of reef status, and can be used to set ecosystem-based targets for managing coral reefs broadly.

Introduction

Fishes are important determinants of coral reef benthic community structure and perform critical ecosystem functions that are believed to be essential components of coral reef resilience (Bellwood et al. 2004; Mumby and Steneck 2008; Hughes et al. 2010). Well known examples include top down controls on community composition by predators (McClanahan and Muthiga 1988; Hixon 1991), and the consumption of algae by herbivorous scrapers and grazers (Mumby et al. 2006; Burkepile and Hay 2008). The effectiveness of these different functional groups is also strongly dependent of fish size and biomass (DeMartini et al. 2008; Nash et al. 2013). For example, herbivory rates by parrotfishes are highly non-linear with body size, increasing rapidly above 15-20 cm (Bruggemann et al. 1994; Bonaldo and Bellwood 2008; Adam et al. 2015). Differences in size structure can also be a useful indicator of ecosystem status given direct and indirect size-based fishing effects (Graham et al. 2005; Vallès and Oxenford 2014; Zgliczynski and Sandin 2016). Therefore, the loss or absence of key functional groups or key size classes could help explain geographic variation in the coral and macroalgal cover throughout the Caribbean.

Several previous studies did not find a clear link between fish abundance and the benthos (Newman et al. 2006; Burkepile et al. 2013; Russ et al. 2015; Suchley et al. 2016), despite clear mechanistic links between the two. Indeed, behavioral observations and experiments have shown that the relationship between fishes and the benthos is inconsistent and complex, and involves feedbacks at different spatial and temporal scales (Mumby and Steneck 2008; Burkepile and Hay 2011; Brandl and Bellwood 2014; Chong-Seng et al. 2014; Adam et al. 2015). For example, different species may be important in different contexts, such as preventing ecosystem changes or allowing recovery of ecosystem function after a disturbance (Burkepile and Hay 2010; Chong-Seng et al. 2014). Moreover, most previous studies have been carried out over short intervals at a limited set of locations, so it is difficult to evaluate the significance of results from different studies (Levin 1992).

To address this, we compiled a synthesis database of fish and benthic underwater visual surveys from the entire Caribbean region to conduct a comprehensive analysis of fish-benthic relationships at a regional scale. Specifically, we investigated how biomass and size of fishes overall and across functional groups explained variation in coral and macroalgal cover across the Caribbean. The results strongly affirm the importance of fishes across functional groups for maintaining the balance between coral and macroalgal cover on Caribbean reefs.

Materials and methods

Data were collated from existing surveys of underwater visual censuses of fishes from several sources across the Caribbean (Table A.1). Data were transformed into a consistent format that accounts for the hierarchical structure of the data (e.g., transects within sites), and underwent quality assessments with particular documentation of methodological differences that may have an effect on estimates of fish abundance and biomass. Datasets with obvious errors, vastly different methods than the majority of other surveys, incompatible species lists, and small sample sizes were removed (full data sources are listed in Jackson et al. 2014). Because broad-scale changes in Caribbean coral reefs occurred prior to the late-1990s (Jackson et al. 2014), and because a majority of data were after this time, only data from after 1997 were included in analyses. Also, to standardize habitat to the extent possible, depths less than 20 meters were retained in the final dataset, and analyses were restricted to the *Orbicella* reef zone following published methods (Mumby and Harborne 1999; Chollett and Mumby 2012; Williams et al. 2015). All analyses were limited to one habitat, the *Orbicella* zone, because previous work has shown that functional relationships between fish and benthic communities can vary by habitat (Mumby 2014; Williams et al. 2015). Specifically, the probability that a given location was in *Orbicella* zone was calculated given a prediction from a binomial model with wave exposure as a predictor (Chollett and Mumby 2012). Wave exposure values were obtained from Chollett & Mumby (2012) at a scale of 1 km spatial resolution. This method has been shown to be relatively accurate for Belize (81%) with a 50 m spatial resolution (Chollett and Mumby 2012), and for the Caribbean basin (77%) with 1 km spatial resolution (Williams et al. 2015). To combine data at a common spatial scale, data were post-stratified into locations that were defined as a geographic cluster of survey coordinates and further defined by prevailing oceanographic conditions (windward or leeward, inshore or offshore, etc.) and political boundaries following Jackson et al. (2014) (Figure 2.1).

Datasets varied in terms of the number of species recorded during surveys, where some datasets had restricted species lists. Species lists were therefore compared across surveys and all datasets were restricted to a common species list of 105 species (Table B.1). The biomass of individual fishes was estimated using the allometric length-weight conversion: $W = a\mathrm{TL}^b$, where parameters a and b are species-specific constants, TL is total length (cm), and W is weight (g). Length-weight fitting parameters were obtained from FishBase (Froese & Pauly 2011). Extreme observations in fish counts can have high leverage on biomass estimates, so they were identified and accounted for using the following procedure. Extreme observations in fish counts were defined by calculating the upper 99.9% of all individual observations (e.g. one species, size and count on an individual transect), resulting in 51 observations out of over 0.5 million, comprised of 16 species. The distribution of individual counts in the entire database for those 16 species was then used to identify observations that fell above the 99.0% quantile of counts for each species individually. These observations were adjusted to the 99.0% quantile for analysis.

The fish assemblage was characterized into functional groups based on feeding ecology into predators, secondary consumers, and three groups of herbivores: browsers, grazers and scrapers (Table B.1). The herbivore functional groups have been suggested as important indicators of resilience on coral reefs given differences in their roles in removing, maintaining, and promoting algal assemblages (Bellwood et al. 2004; Burkepile and Hay 2008; Green and Bellwood 2009a; Heenan and Williams 2013; Rasher et al. 2013; Adam et al. 2015b). Browsers were defined as herbivores that reduce macroalgal cover by feeding directly on macroalgae and associated epiphytic material. Grazers were defined as herbivores that can prevent macroalgal growth and feed mostly on algal turfs. Scrapers were defined as herbivores that also feed on algal turfs but are also important for opening space for coral recruitment by clearing substratum.

Data on coral and macroalgal cover used the same sources as Jackson et al. (2014), and similar to the fish data, were limited to observations after 1997 and from depths less than 20 meters.

Analyses were based on a hierarchal structuring of the data and were summarized based on means of replicates within individual datasets for each location. To account for differences in sampling, methodologies, and spatial and temporal structures across the datasets, general linear mixed effects models were used to estimate means by location for each dependent variable with the *lmer* function in the R package *lme4* (Pinheiro and Bates 2000; Bates et al. 2010; Skaug et al. 2013). Dependent variables were transformed where necessary to meet assumptions of linear modeling. A random effect of dataset was included in the models to account for differences in methodologies and sampling designs across datasets. Model fits were assessed by visual inspection of residuals and restricted maximum likelihood was used to fit the models (Bolker et al. 2009). Confidence intervals were generated for estimates using the *predictInterval* function in the *merTools* package in R (Knowles and Frederickm 2016). Intervals were calculated by estimating the fitted values based on 10,000 random draws from a sampling distribution for the random and fixed effects and then defining the upper and lower 0.025% of the returned values (Gelman and Hill 2007).

Ordinary regression and generalized additive models (GAMs) were used to test for relationships between independent variables and coral and macroalgal cover, and the log ratio of coral to macroalgal cover. GAMs were fit with the *mgcv* package in R (Wood 2011). For each relationship, both models were fit and model fits were assessed by visual inspection of residuals. The assumption of constant error variance was further checked with a Breusch-Pagan test using the *ncvTest* in the package *car* in R (Fox and Weisberg 2011). In cases were error variance was not constant the response variable was square root transformed and refit. Linear and additive models were compared using Akaike Information Criterion (AIC) and Akaike weights with the *MuMIn* package in R (Bartón 2016). In cases where the relationships were significant based on $\alpha \leq 0.05$, but certain points had high leverage on the analysis based on Cook's distance > 0.05, those points were removed and the models were refit.

Patterns were further explored with multivariate techniques for testing how similarities among locations were related to coral and macroalgal cover. Data were centered, and standardized before analyses so as to be on the same scale. Redundancy analysis was used to test for multidimensional relationships between response variables and coral and macroalgal cover. Redundancy analysis is a constrained ordination method that relates linear combinations of the response variables (coral, and macroalgal cover) to explanatory variables (fish functional groups) (Legendre and Legendre 2012). Permutation tests were used to test the overall significance of the model, and of the constrained axes using the *anova.cca* function in R. All multivariate methods were conducted in the *vegan* package in R (Oksanen et al. 2015).

All analyses were conducted in the R environment for statistical computing version 3.3.0 (R Development Core Team (2016)).

Results

The final dataset consisted of 5,478 replicates of underwater visual fish censuses from 36 locations (Figure 2.1, Table C.1). Overall biomass ranged 12-fold, from 7.0 g m^{-2} (95% C.I. 6.5 -

7.5) at Jamaica North Central to 83.0 g m^{-2} (95% C.I. 78.5 - 88.4) at Jardines de la Reina in Cuba (Figure 2.2). All five of the locations with the greatest biomass were either fully or partly in no-take marine reserves (Figure 2.2). Interestingly, the location with the lowest biomass was also in a no-take marine reserve (Port Honduras Marine Reserve, Figure 2.2). The biomass of functional groups also varied greatly, especially predator biomass, which had a 68-fold range (Figure 2.2, Table E.1). All groups were positively correlated with each other (Figure H.1). In particular, the biomass of predators and secondary consumers were most closely correlated with overall biomass ($\rho = 0.84$ and 0.88, respectively) and were also well correlated with each other ($\rho = 0.82$).

The biomass of certain fish functional groups was significantly positively related to coral cover, negatively related to macroalgal cover, and positively related to the log-ratio of coral and macroalgal cover (Table 2.1, Figure 2.3). Total biomass significantly positively explained coral cover, negatively explained macroalgal cover, and positively explained the log-ratio between coral and macroalgae. Coral cover was also positively related to biomass of predators, and scrapers. Secondary consumer biomass had the strongest relationship with coral cover, and also the explained the largest variance ($R^2 = 0.28$). Macroalgal cover was negatively related to total biomass, and scraper biomass. Similarly, the log-ratio of coral and macroalgal cover was positively related to total biomass, and scraper biomass.

Mean size of the overall fish assemblage, and of certain functional groups was also positively related to coral cover, negatively related to macroalgal cover, and positively related to the log-ratio of coral and macroalgal cover (Table 2.2, Figure 2.4). Mean size of the overall fish assemblage was significantly positively related to coral cover, and the log-ratio of coral and macroalgal cover, but not to macroalgal cover. Similarly, mean size of the secondary consumers was significantly positively related to coral cover, and the log-ratio of coral and macroalgal cover, but not to macroalgal cover. Mean size of predators was negatively related to macroalgal cover, and positively related to the log-ratio of coral and macroalgal cover, but not to coral cover. Mean size of both browsers and scrapers was positively related to coral cover, and the log-ratio of coral and macroalgal cover. No significant relationships were found between the mean size of grazers and any of the benthic metrics (Table 2.2).

Redundancy analyses (RDA) revealed how all of the fish functional groups together were related to coral and macroalgal cover (Table 2.3, Figure 2.5). An RDA based on functional group biomass significantly explained 29% of the variation in coral and macroalgal cover (F = 2.89, *p* = 0.01). The first RDA axis explained 42% of variation in the fish functional group-benthic cover relationship, while the second RDA axis explained only 3% (Table 2.3, Figure 2.5A). An RDA based on mean size significantly explained 30% of the variation in coral and macroalgal cover (F = 2.68, *p* = 0.02). The first RDA again explained the most of the benthic cover-functional group relationship with 35% explained, and the second axis explained 12% (Table 2.3, Figure 2.5B). Both ordinations were similar with all fish functional groups increasing in the same direction as coral cover and in the opposite direction of macroalgal cover (Figure 2.5). Interestingly, coral and macroalgal cover were orthogonal, so they were uncorrelated. When the significance of the constrained axes (fish functional groups) was tested, predators was significant in both models ($p = 0.03$ and $p = 0.01$ for biomass and size based models, respectively), and in both cases, was strongly positively correlated with coral cover (Figure 2.5). Scraper biomass was also significant in the biomass model ($p < 0.01$) and was strongly negatively correlated with macroalgal cover and was positively correlated with coral cover, but to a lesser extent than predators (Figure 2.5A). The mean size of secondary consumers was also strongly positively correlated with coral cover ($p < 0.01$).

Discussion

This study documented large-scale variation in the state of Caribbean reefs and found important relationships between biomass and size of the fish assemblage and coral and macroalgal cover. Locations with greater overall biomass of fishes, and greater biomass and mean size of particular fish functional groups, had greater coral cover and lower macroalgal cover. Scrapers (i.e., large parrotfishes) have been previously cited for their significance in maintaining important ecosystem processes, such as coral recruitment (Williams and Polunin 2001; Bellwood et al. 2004; Mumby et al. 2006; Mumby and Steneck 2008), and both biomass and mean size of scrapers were important for explaining variation in coral and macroalgal cover (Figure 2.4, Figure 2.5). Biomass and mean size of predators were also important in explaining differences in ecosystem state. This could be related to top-down effects on community structure (Hixon 1991), and reflect important gradients in human impacts, such as fishing (Jackson et al. 2001; Friedlander and DeMartini 2002; Newman et al. 2006; Karr et al. 2015). The importance of predators and scrapers were significant when analyzed individually, and were also important in multivariate analyses of all variables together (Figure 2.5), implying these groups are particularly important indicators of differences in ecosystem state on Caribbean coral reefs.

Herbivore functional groups varied in their relationships with coral and macroalgal cover. Scraper size and biomass significantly predicted greater coral and lower macroalgal cover, which supports previous findings that parrotfishes are important for coral reef resilience (Bellwood et al. 2004; Mumby et al. 2006; Mumby and Steneck 2008). Further, these patterns support previous studies that emphasize that large scrapers, which include large *Scarus* species and *Sparisoma viride*, are particularly important for structuring benthic cover in the Caribbean (Burkepile and Hay 2010, 2011; Adam et al. 2015). Grazers (surgeonfishes) were not significant in any of the relationships examined. There are few grazing species in the Caribbean and their abundance is quite variable, which could make patterns hard to detect. While we limited our analysis to *Orbicella*/forereef habitats, it is also possible that the relationship between grazers and benthic cover is more specific. For example, a previous study conducted at a fine depth range (10-12 m) in specific habitats in the Caribbean found a strong negative relationship between grazer biomass and macroalgal cover (Williams and Polunin 2001). Also, in the Pacific, grazer biomass was better predicted by oceanographic conditions than benthic cover, further suggesting context dependence (Heenan et al. 2016). The size of browsers was positively correlated with coral cover and the ratio of coral and macroalgae, but browser biomass was not a significant predictor of benthic state. This is important because many small individuals or few large individuals could equate to the same biomass, and given the importance of size, biomass alone was a poor indicator of the ecological role of browsers on Caribbean reefs.

Predator size and biomass were also positively associated with benthic cover. In particular, mean size of predators was strongly negatively associated with macroalgal (Figure 2.4), and was the most important variable in explaining coral and macroalgal cover together (Figure 2.5). Associations between predators and benthic cover could reflect ecosystem impacts of fishing. Fishing can reduce mean size of target species that are often predators (Pauly et al. 1998), and size has been shown to be particularly useful fishing indicator on coral reefs (Zgliczynski and Sandin 2016; Robinson et al. 2017). The correlation between predators and benthic cover may also imply that top-down effects are related to ecological resilience, but the mechanisms remain enigmatic (Sandin et al. 2008; Sandin and Zgliczynski 2015). For example, increased predation could increase prey turnover rates, leading to optimized biomass production and associated differences in ecological processes that maintain coral cover (Ruttenberg et al. 2011), or greater refuge availability from increased coral cover could lead to stabilizing of predator-prey systems allowing predator biomass to be optimized (Sandin and Zgliczynski 2015).

Previous studies from the Caribbean found similar gradients in fish abundance (Newman et al. 2006; Paddack et al. 2009), but how fish functional group biomass and size relate to the benthos has not been previously explored for the entire Caribbean basin. What is clear from our analysis is that the ideal scale to study fish-benthic relationships is unknown; however, summarizing to the extent we did revealed important fish-benthic patterns that can often be characterized by noise, especially at fine scales. This matches expectations that multiple processes interact across scales on coral reefs (Mumby and Steneck 2008; Nyström et al. 2008); thus, uncovering emergent patterns may only be possible at large spatial or temporal scales (MacNeil and Connolly 2015). Future studies can build upon this idea to investigate how patterns change across multiple scales with hierarchical sampling and statistics (MacNeil et al. 2009; MacNeil and Connolly 2015). Patterns identified at large scales such as the entire Caribbean basin also provide the opportunity to discuss how regional context can determine local outcomes for conservation. However, direct comparisons of biomass to other studies should be done with caution given that a restricted species list was used in our analysis, for example sharks were not included in biomass estimates. Also, there is opportunity for confounding effects of geography and time that could affect the results in large-scale studies such as this. We found no significant correlations between fish biomass and size across latitudes and longitudes (APPENDIX I), except scraper biomass had a weak correlation with longitude, but this relationship was driven by one location. Further work is necessary to combine the results from this study with information on physical and human drivers of coral reefs to untangle these effects on the observed patterns. Also, correlations between metrics of fish and benthic assemblages do not imply causation. Some have argued that fish are drivers of the benthos and others that the benthos drives the fishes (Russ et al. 2015). Future work could inform mechanistic links between the fish functional groups and their relation to ecosystem state by combining the patterns from this study with behavior and experimental data that can be scaled up to relate biomass and size to ecosystem process and function.

The results from this study provide useful metrics for managing fish assemblages and for quantifying and monitoring coral reef status and trends. Importantly, fish functional groups have been proposed as indicators of coral reef resilience (Green and Bellwood 2009). Quantifying fish-benthic relationships based on fish functional group biomass and size was effective, and therefore has utility for use broadly in monitoring and management. For example, these variables can be used as ecosystem indicators of ecosystem state that can be used to set targets or limits for human impacts on reefs. For example, previous work has suggested that fish biomass may be a useful indicator of regime-shifts on coral reefs following reductions in biomass from fishing (McClanahan et al. 2011; Karr et al. 2015; MacNeil et al. 2015), which can be used to define a 'safe operating space' for reef fish biomass between 25-50 g m^{-2} (Norström et al. 2016). This 'safe operating space' fell within our estimates (Figure 2.3), and corresponds with a rapid increase in macroalgae below those values, suggesting that there is additional support for these indicators. Future work is needed to define 'safe operating space' for fish functional groups in the Caribbean for ecosystem-based conservation targets. In summary, greater biomass and size of fish functional groups, especially predators and scrapers, was associated with higher coral cover and lower macroalgal cover at the scale of the Caribbean.

Table 2.1 Results of linear models or general additive models (GAM) between biomass of fish functional groups and coral cover, macroalgal cover, and the log-ratio of coral and macroalgal cover. GAMs are indicated where with s(Slope), and coefficients and statistics are in labeled in parentheses for those lines where appropriate.

Dependent variable	Independent variable (Biomass g m^{-2})	Term	Beta (or EDF)	Std Err (or Ref.df)	t	*p*	F	df (n)	R^2
Coral cover	Total	Intercept	20.01	3.16	6.32	**0.00**			
		Slope	0.25	0.08	3.06	**0.00**	9.37	36	**0.21**
Coral cover	Predators	Intercept	28.26	1.61	17.54	**0.00**			
		s(Slope)	1.63	1.86		**0.01**	7.51	38	**0.27**
Coral cover	Sec. Cons.	Intercept	18.87	2.75	6.87	**0.00**			
		Slope	1.29	0.31	4.15	**0.00**	17.23	35	**0.33**
Coral cover	Grazers	Intercept	25.81	3.07	8.41	**0.00**			
		Slope	1.08	1.08	1.00	0.33	0.99	36	0.03
Coral cover	Browsers	Intercept	5.03	0.33	15.40	**0.00**			
		Slope	0.07	0.12	0.62	0.54	0.39	36	0.01
Coral cover	Scrapers	Intercept	21.40	2.82	7.58	**0.00**			
		Slope	0.88	0.34	2.61	**0.01**	6.84	35	**0.16**
Macroalgal cover	Total	Intercept	37.20	3.34	11.14	**0.00**			
		s(Slope)	1.60	1.84		**0.02**	6.11	28	**0.29**
Macroalgal cover	Predators	Intercept	6.40	0.47	13.73	**0.00**			
		Slope	-0.09	0.05	-1.86	0.07	3.44	26	0.12
Macroalgal cover	Sec. Cons.	Intercept	45.25	5.72	7.91	**0.00**			
		Slope	-0.86	0.47	-1.84	0.08	3.37	26	0.11
Macroalgal cover	Grazers	Intercept	43.78	6.50	6.74	**0.00**			
		Slope	-3.06	2.46	-1.25	0.22	1.56	26	0.06
Macroalgal cover	Browsers	Intercept	43.55	7.02	6.20	**0.00**			
		Slope	-2.69	2.49	-1.08	0.29	1.16	26	0.04
Macroalgal cover	Scrapers	Intercept	53.71	6.57	8.18	**0.00**			
		Slope	-2.42	0.80	-3.01	**0.01**	9.08	25	**0.27**
log(Coral/ Macroalgae)	Total	Intercept	-1.02	0.32	-3.20	**0.00**			
		Slope	0.02	0.01	2.99	**0.01**	8.94	25	**0.26**
log(Coral/ Macroalgae)	Predators	Intercept	-0.48	0.25	-1.92	0.07			
		Slope	0.04	0.03	1.62	0.12	2.61	25	0.09
log(Coral/ Macroalgae)	Sec. Cons.	Intercept	-0.58	0.28	-2.05	0.05			
		Slope	0.04	0.03	1.73	0.10	2.99	25	0.11
log(Coral/ Macroalgae)	Grazers	Intercept	-0.54	0.32	-1.66	0.11			
		Slope	0.15	0.12	1.25	0.22	1.57	25	0.06
log(Coral/ Macroalgae)	Browsers	Intercept	-0.60	0.33	-1.80	0.08			
		Slope	0.17	0.12	1.43	0.17	2.04	25	0.08
log(Coral/ Macroalgae)	Scrapers	Intercept	-1.06	0.28	-3.77	**0.00**			
		Slope	0.12	0.03	3.65	**0.00**	13.31	25	**0.35**

Table 2.2 Results of linear models or general additive models (GAM) between mean size of fish functional groups and coral cover, macroalgal cover, and the log-ratio of coral and macroalgal cover. GAMs are indicated where with s(Slope), and coefficients and statistics are in labeled in parentheses for those lines where appropriate.

Dependent variable	Independent variable (mean size (cm))	Term	Beta (or EDF)	Std Err (or Ref.df)	t	*p*	F	df (n)	R^2
Coral cover	Overall	Intercept	4.89	8.37	0.58	0.56			
		Slope	1.65	0.60	2.74	**0.01**	7.49	30	0.20
Coral cover	Predators	Intercept	20.51	9.46	2.17	**0.04**			
		s(Slope)	0.35	0.48	0.73	0.47	0.53	30	0.02
Coral cover	Sec. Cons.	Intercept	27.22	1.88	14.51	**0.00**			
		Slope	1.64	2.04		**0.05**	3.34	32	0.21
Coral cover	Grazers	Intercept	10.92	9.55	1.14	0.26			
		Slope	1.33	0.76	1.74	0.09	3.04	30	0.09
Coral cover	Browsers	Intercept	-1.98	10.34	-0.19	0.85			
		Slope	1.85	0.64	2.89	**0.01**	8.35	29	0.22
Coral cover	Scrapers	Intercept	5.27	7.84	0.67	0.51			
		Slope	1.59	0.55	2.88	**0.01**	8.31	30	0.22
Macroalgal cover	Overall	Intercept	54.98	20.12	2.73	**0.01**			
		s(Slope)	-1.32	1.43	-0.92	0.37	0.85	19	0.04
Macroalgal cover	Predators	Intercept	98.49	20.67	4.77	**0.00**			
		Slope	-3.37	1.10	-3.06	**0.01**	9.36	18	0.34
Macroalgal cover	Sec. Cons.	Intercept	46.38	20.77	2.23	**0.04**			
		Slope	-0.70	1.49	-0.47	0.65	0.22	19	0.01
Macroalgal cover	Grazers	Intercept	64.01	21.48	2.98	**0.01**			
		Slope	-2.12	1.65	-1.29	0.21	1.66	19	0.08
Macroalgal cover	Browsers	Intercept	60.84	24.82	2.45	**0.02**			
		Slope	-1.49	1.52	-0.98	0.34	0.96	19	0.05
Macroalgal cover	Scrapers	Intercept	55.58	18.25	3.05	**0.01**			
		Slope	-1.34	1.27	-1.06	0.30	1.11	19	0.06
log(Coral/ Macroalgae)	Overall	Intercept	-2.45	0.88	-2.80	**0.01**			
		Slope	0.17	0.06	2.66	**0.02**	7.07	19	0.27
log(Coral/ Macroalgae)	Predators	Intercept	-2.77	1.11	-2.49	**0.02**			
		Slope	0.14	0.06	2.37	**0.03**	5.60	18	0.24
log(Coral/ Macroalgae)	Sec. Cons.	Intercept	-2.27	0.92	-2.47	**0.02**			
		Slope	0.15	0.07	2.33	**0.03**	5.42	19	0.22
log(Coral/ Macroalgae)	Grazers	Intercept	-1.88	1.04	-1.80	0.09			
		Slope	0.13	0.08	1.65	0.11	2.74	19	0.13
log(Coral/ Macroalgae)	Browsers	Intercept	-2.62	1.13	-2.31	**0.03**			
		Slope	0.15	0.07	2.18	**0.04**	4.77	19	0.20
log(Coral/ Macroalgae)	Scrapers	Intercept	-2.37	0.78	-3.03	**0.01**			
		Slope	0.16	0.05	2.89	**0.01**	8.33	19	0.30

Table 2.3 Results of redundancy analysis of coral and macroalgal cover and biomass and mean size, and results of permutation tests of the model significance.

		RDA1	RDA2	PCA1	PCA2		df	Var	F	p	R^2
Biomass (g m^{-2})	Eigenvalue	0.05	0.01	0.05	0.04	Model	5	0.05	2.49	**0.02**	0.22
	Proportion explained	0.33	0.04	0.38	0.25	Residual	21	0.09			
	Cumulative proportion	0.33	0.37	0.75	1.00						
Size (cm)	Eigenvalue	0.07	0.02	0.07	0.03	Model	5	0.09	2.71	**0.02**	0.30
	Proportion explained	0.36	0.12	0.38	0.15	Residual	15	0.10			
	Cumulative proportion	0.36	0.47	0.85	1.00						

Figure 2.1 Locations with data on fish biomass and coral and macroalgal cover that were used in analyses.

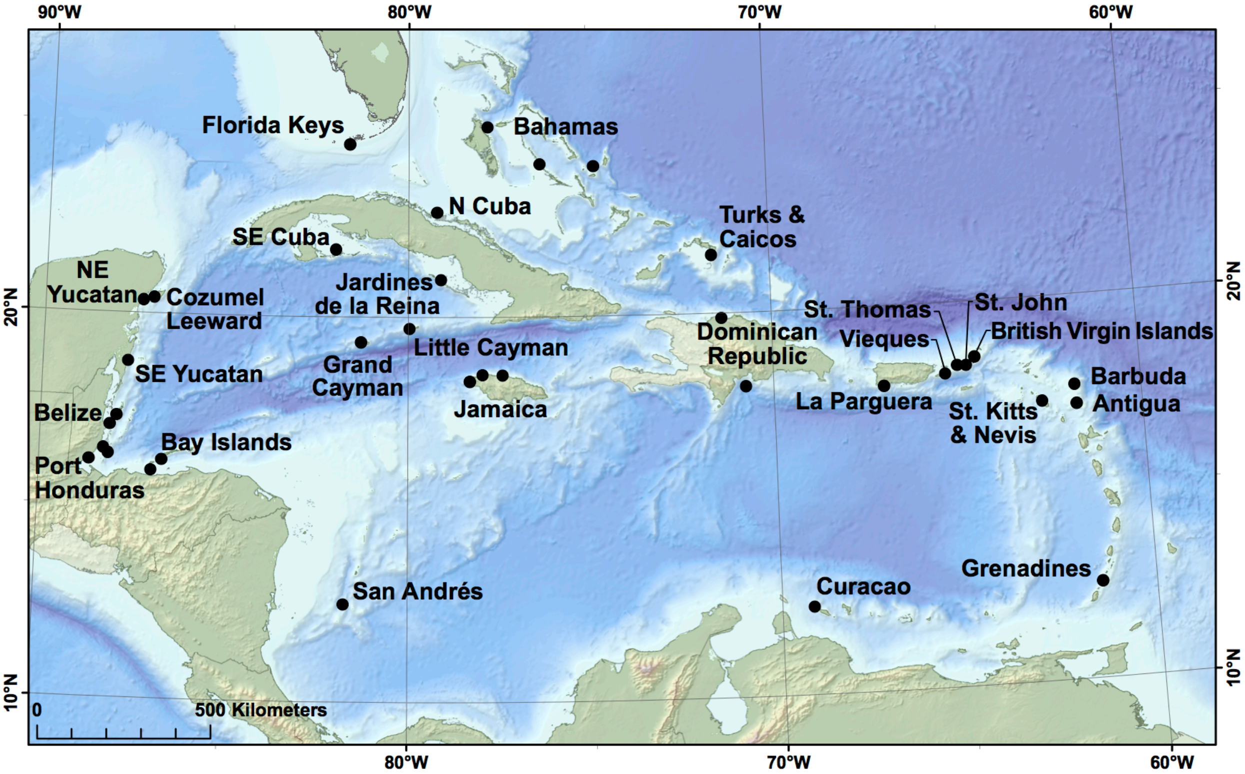


Figure 2.2 Barplot of biomass by functional group for 36 locations in the Caribbean. Locations are arranged from low to high by the summed biomass across functional groups. Black dots above bars are locations where all surveys were inside a no-take marine reserve, and white diamonds above bars are locations with a majority of surveys inside marine reserves.

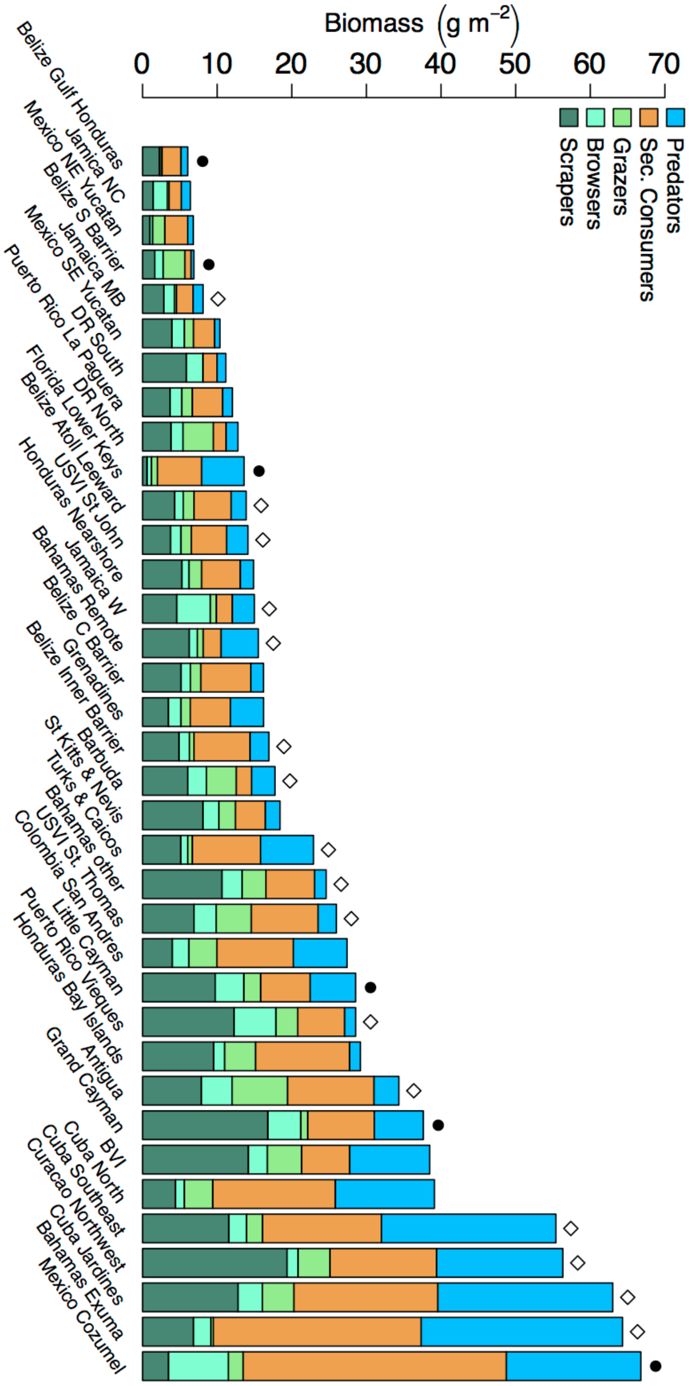


Figure 2.3 Relationships between biomass of fish functional groups and coral cover, macroalgal cover, and the log-ratio of coral and macroalgal cover. Black lines are fitted functions from either a linear or general additive model where the relationships were significant, and grey polygons are 95% confidence intervals around the fitted function. Red circles around points indicate outliers that were removed prior to fitting models.

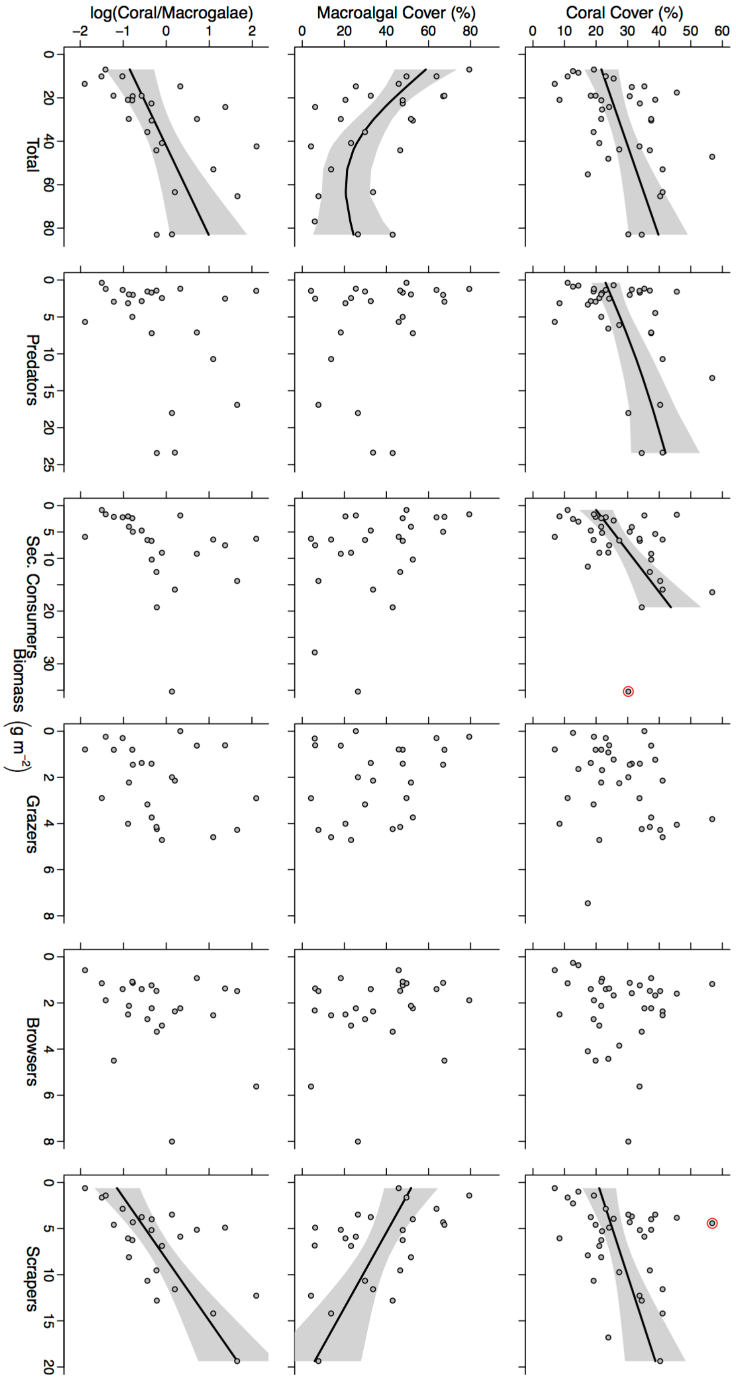


Figure 2.4 Relationships between mean size of fish functional groups and coral cover, macroalgal cover, and the log-ratio of coral and macroalgal cover. Black lines are fitted functions from either a linear or general additive model where the relationships were significant, and grey polygons are 95% confidence intervals around the fitted function. Red circles around points indicate outliers that were removed prior to fitting models.

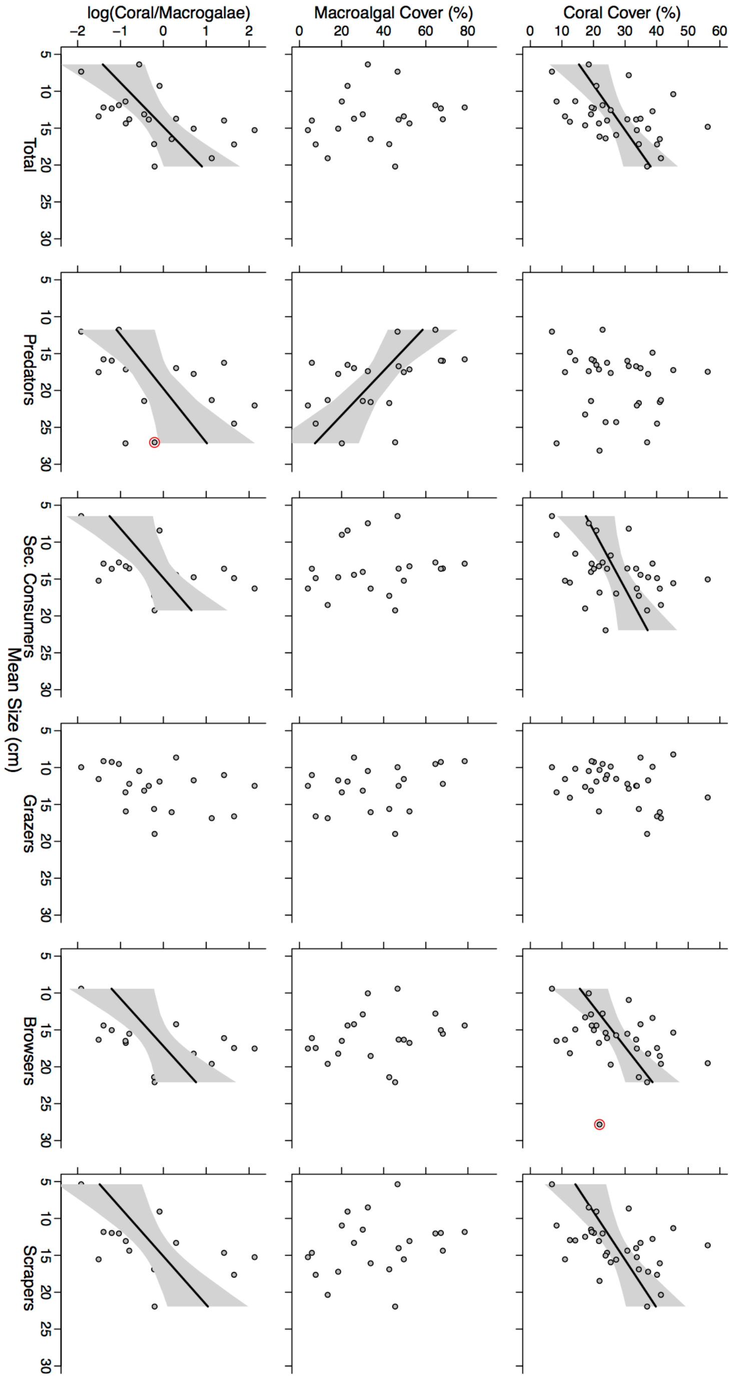
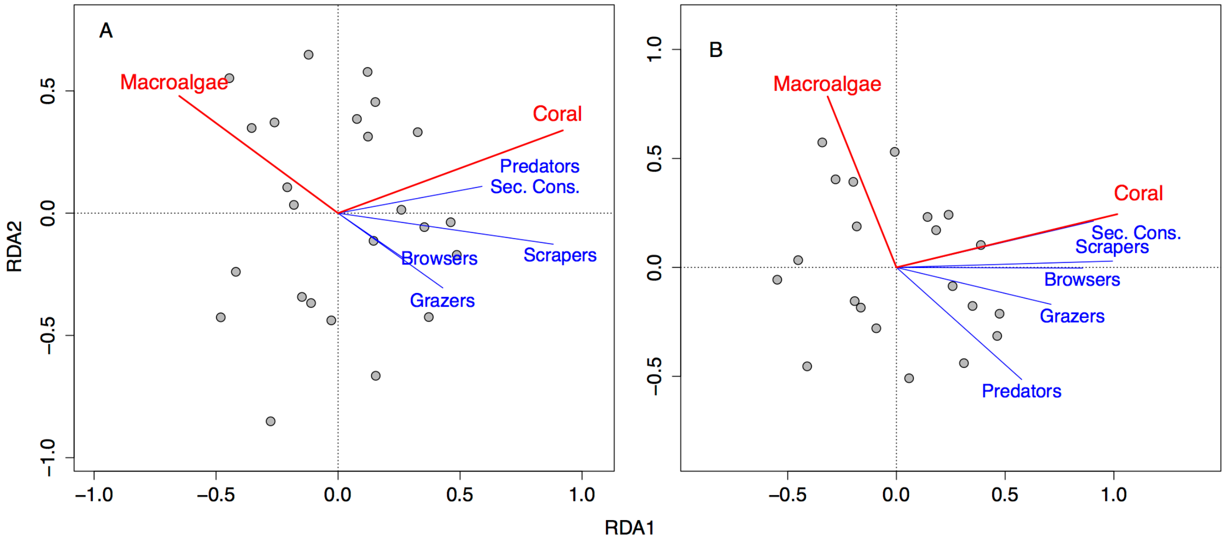


Figure 2.5 Redundancy analysis of linear combinations of the response variables (coral, macroalgal cover), plotted as blue vectors, to explanatory variables (fish functional groups), plotted as red vectors across locations (grey dots), for A) biomass, and B) mean size. Variables are perfectly correlated if the vectors are oriented in exactly the same or opposite directions, and thus uncorrelated if the difference in the angles between the two vectors is 90˚. Thus, all fish functional groups were positively correlated with coral and negatively correlated with macroalgae for both biomass and size.



CHAPTER 3 Integrating fish and benthic assemblages provides a more nuanced understanding of coral reef regimes

Abstract

Coral reefs worldwide face an uncertain future with many reefs transitioning from being dominated by hard corals to fleshy algae. This binary view of coral reefs is limited in that multiple ecological configurations, or regimes, are likely given the complexity and diversity of the ecosystem. Reef regimes are most often characterized by their benthic components; however, complex dynamics are associated with losses and gains in both fish and benthic assemblages. To capture this complexity, this study synthesized and analyzed a large database of 3,345 surveys from the Hawaiian Islands to define coral reef regimes in terms of both fish and benthic assemblages. Model-based clustering revealed five distinct regimes that varied ecologically, and showed spatial heterogeneity by island, depth and wave exposure. We identified a regime that was classified by low coral cover and low macroalgal cover but high fish biomass, as well as three other novel regimes that varied significantly in their ecology but were previously considered a single coral dominated regime. Analyses of time series data reflected complex system dynamics, with multiple transitions among regimes, and certain transitions were more common than others. By recognizing the coupling of fish and benthic assemblages, we quantified subtle but significant ecological differences among reef regimes, information that holds promise for monitoring ecosystem change and guiding ecosystem-based management of coral reefs.

Main text

Paradigms of how coral reef systems respond to disturbance have changed substantially over the past four decades, while over this same time period coral reefs globally have declined in response to increasing human impacts (Jackson et al. 2001, 2014; Pandolfi et al. 2003; Bellwood et al. 2004). Previous views that regarded reefs as robust and predictable (Goreau 1959; Loya 1976; Woodley et al. 1981) have given way to the recognition that in response to cumulative impacts coral reefs can undergo a shift from coral to macroalgal dominance (Nyström et al. 2000; Bellwood et al. 2004; Hughes et al. 2010). Although alternative benthic regime shifts have been proposed (Norström et al. 2009), coral and macroalgae are widely used as indicators of reef responses to human disturbances, but often the proximate causes of changes in these measures are variable (Gardner et al. 2003; Bruno and Selig 2007; Schutte et al. 2010; Jackson et al. 2014; Williams et al. 2015a). Detecting regime shifts can be difficult given that complex systems involve multiple feedbacks that can often go unrecognized (Levin 1998), and therefore focusing on one ecological variable, such as coral cover, can cause misinterpretation of the signs and causes of regime shifts (Hughes et al. 2010).

Thus, there is a need to gain new insights on ecological functioning of coral reefs from a broadened perspective on coral reef community structure. For example, large-scale studies across the Pacific highlight the variable cover of coral, crustose coralline algae and macroalgae regardless of human population status (Williams et al. 2015) and that inhabited and uninhabited islands are better differentiated by the cumulative cover of fleshy versus calcifying benthic organisms (Smith et al. 2016). Similarly, in Hawaii when multiple components of the benthos, such as turf and coralline algae, were considered three distinct coral reef regimes were identified (Jouffray et al. 2015). While these studies represent ways forward in defining reefs based on more than coral and macroalgae, they either excluded fishes or considered fish as drivers behind the observed benthic patterns. Defining reef regimes by both benthic and fish assemblages is a necessary next step because positive and negative feedbacks exist between fishes and the benthos that cannot be captured by the benthos alone (Mumby and Steneck 2008; Nyström et al. 2012).

The recognition that regime shifts are complex and encompass multiple components of the ecosystem has been routinely embedded in regime-shift analysis in other ecosystems, such as the open ocean (Conversi et al. 2015). Work on pelagic marine ecosystems, for example, has shown how multiple fish and plankton communities exhibit persistent jumps in time series as a response to changes in fishing pressure and other drivers (Daskalov et al. 2007). To capture the complex dynamics of coral reefs, we used a novel approach that defines regimes based on both fish and benthic variables. We used a spatially high-resolution biological dataset for coral reefs in the main Hawaiian Islands to define regimes, describe spatial and temporal variation in regimes, and describe ecological patterns across regimes. We also investigated variation within sites to explore the diversity of transitional pathways among regimes over time.

Results

Model-based cluster analysis of 10 variables, representing fish and benthic functional groups, from a total of 3,345 reef surveys across the Hawaiian archipelago (based on final model selection, Figure N.1), revealed five distinct coral reef regimes. Non-metric multidimensional scaling separated the variables in multivariate space (Figure 3.1); with the biomass of each fish functional group inversely correlated with turf and macroalgal cover (Figure 3.1C).

The five identified regimes varied significantly in the composition of the fish and benthic functional groups, reflecting differences in ecological structure and function (Table 3.1, Figure 3.2-Figure 3.3). Regime 1 was characteristic of a degraded state with overall low coral cover and low fish biomass (especially predators), and a benthos dominated by turf algae, macroalgae, and other substrate (defined as no noticeable cover of any benthic functional group examined here). Regime 2 had the highest fish biomass overall, with exceptionally high biomass of browsers, and a benthos dominated by turf algae. Coral cover in this regime was higher than in regime 1, but lower than all other regimes. Regime 3 had moderately high fish biomass across all functional groups, and high coral and turf cover and a complete absence of macroalgae. Regime 4 also had moderately high fish biomass across all functional groups, and a benthos with high coral cover and a mixture of macroalgae, turf algae, and other substrate. Regime 5 had moderate fish biomass across all functional groups, in particular lower predator biomass when compared with regimes 3 and 4, and the highest mean coral cover across all regimes, high crustose coralline algae cover and comparatively low turf algae cover. Overall, multivariate variance (dispersion) differed across regimes ($p < 0.01$), with similar variability in regimes 1 and 2. Regime 4 was the most variable, and regime 5 was the least variable (Table 3.1).

All regimes were present on all 8 islands, except for Kahoolawe, which only contained regimes 3 and 4. The majority of sites on Niihau were regime 2 (67%), and more than half of the sites on

Oahu (54%) were regime 1, and Hawaii Island was dominated by regime 5 (39%) (Figure 3.4). We also found regimes were distributed differently according to the dominant cardinal direction of the coastline (north, south, east, west). Regime 1 and 4 were predominantly distributed across east (21% and 23%, respectively), south (39% and 33%), and west (28% and 34%) shores, while regime 2, 3, and 5 were found more often on coastlines with a particular direction; regime 2 was found on north facing shores 46% of the time, and regimes 3 and 5 were both found on west facing shores 83% of the time. Further, some of the regimes correlated with depth and habitat complexity: regime 1 occurred in shallow low complexity habitat (e.g. pavement) (Tukey multiple comparison of means: $p \leq 0.02$), while regime 2 occurred in deep rugose habitat (e.g. large basalt boulders) ($p < 0.01$). There were no significant differences in depth or complexity for the other regimes.

To understand how ecological attributes varied across regimes, we investigated patterns of species composition and richness for corals and fishes. There was no significant difference in the number of coral species across regimes ($F_{4,142}=1.68$, $p=0.16$); however, the composition of the 4 most common coral species was variable. *Porites lobata*, a stress tolerant species, occurred frequently across all regimes, but often dominated in regimes 3 and 5. *Pocillopora meandrina*, a competitive species, occurred most frequently in regime 2, while *Porites compressa*, a weedy species, occurred most frequently in regimes 4 and 5, and *Montipora capitata*, also a competitively dominant species, occurred in relatively low frequencies across all regimes. Fish species richness varied across regimes ($F_{4,2798}=30.33$, $p < 0.01$), with regime 2 having a significantly greater number of species (mean 28.2 ± 0.61 S.E.; $p < 0.01$) and regime 1 having a significantly lower number compared with the other regimes (mean 17.1 m^{-2} ± 0.60 S.E.; $p < 0.01$). The composition of the fish assemblages, based on the most abundant species, was also different across regimes (PERMANOVA: $p < 0.01$). Regimes 1 and 4 had the most variable fish assemblage composition (pairwise comparisons, $p \leq 0.01$), and regime 3 had the least variable fish assemblage composition (pairwise comparisons, $p < 0.01$).

At 65 sites, data were available across at least three years between 2000 and 2012, allowing us to examine the frequency of changes among regimes at a given site over time (Figure O.1). A total of 116 regime transitions among years were observed in the dataset, and we analyzed the frequency of occurrence for a given switch for each combination of regimes (Figure 3.5). Regime 1, the degraded regime, most often remained unchanged (52%), and otherwise switched to regime 2 (29%), or to a lesser extent to regime 4 (14%) or regime 5 (5%). Regime 2 was most frequently observed remaining the same (76%), making this pattern the most frequently observed overall. Regime 3, while not well represented in the time series, never remained the same, and otherwise switched to regime 4 or regime 5. Regime 4 also frequently remained the same (44%), and otherwise switched to every other regime. Regime 5, also poorly represented in the time series, most often remained the same (50%), and rarely switched to regime 1. Overall patterns were similar when compared to calculations from the subset of sites that are from permanent monitoring sites that have at least four or six years of data, with overlapping confidence intervals in all cases (Figure O.3).

We also plotted the observations in multivariate space for 8 time series with at least four years of data spanning from 2000 to 2012 (Figure O.2). Honolua Bay, located in northwest Maui, showed a trajectory of decline in coral cover, starting in regime 5 and ending in regime 1, over the 12-year period. Two nearby bays instead remained the same regimes; Honokahua Bay remained in regime 1 across the 4 years of data, and Napili-Honokowai remained in regime 4. Kahekili, also on Maui, showed a pattern of recovery, switching to regime 1 after 2 years in regime 4 and then switching back to regime 5. Kalaupapa on the north coast of Molokai remained in regime 2, and observations were highly concordant across years. Molokini, a small islet off the south coast of Maui, remained in regime 4 across 8 years of data, but sites were not tightly clustered, revealing more variation compared to Kalaupapa. Pupukea on the north shore of Oahu also showed a pattern of recovery from regime 1 to regime 2.

Discussion

The current perceived dichotomy of reefs as being coral- or macroalgal- dominated is too simplistic (Norström et al. 2009), and we have shown that by incorporating fish and benthic functional groups multiple reef regimes may exist and follow different pathways. By taking this broadened perspective, we identified a regime that does not fit into the coral-macroalgal paradigm with low coral and macroalgal cover but high fish biomass. We also found evidence suggesting that what was previously considered one coral regime, could potentially be divided into three distinct regimes that vary in their ecological composition. Multiple transitions were identified among regimes, supporting the concept that one ecological transition from coral to macroalgae is not sufficient, and the results provide new insights into possible routes for both decline and recovery dynamics on coral reefs.

Species composition varied among regimes, with potential implications for how regimes respond to disturbance. Coral composition followed a pattern described by Jokiel (2004), where high wave energy communities are dominated by *Pocillopora meandrina* (e.g. regime 2 on north facing shores), *Porites compressa* reefs occur in calmer environments (e.g. regimes 4, 5), and *Porites lobata* reefs occur in moderate environments (e.g. regime 3). Importantly, these coral species also have different tolerances to extreme heating events both in terms of their susceptibility to bleaching mortality and their ability to recruit and regrow post-disturbance (Darling et al. 2012). Consequently, the regimes may respond differently to bleaching events, where for example, regime 2 may be particularly predisposed given dominance by *P. meandrina*, which is often one of the most susceptible species to bleaching in Hawaii (Ritson-Williams in prep). This is especially important given that in 2014 and 2015, the Hawaiian Archipelago suffered extreme coral bleaching with an estimated 20-50% coral mortality in some areas. Also, overall species richness and composition of the fish assemblage varied across regimes, indicating likely differences in their ecological resilience via response diversity and functional redundancy (Elmqvist et al. 2003; Nash et al. 2016). For example, regime 1, with low coral cover and low fish biomass, also had the lowest fish species richness. This regime could therefore represent a system with missing functional responses like grazing and browsing, with consequently a diminished ability to bounce back from disturbance. In contrast, regime 3, with high coral cover and high fish biomass, had high fish species richness and consistent fish assemblage composition, so potentially represents a system that has high resilience to disturbance.

Quantification of regimes based on multiple components of the community enabled a finer examination of reef transitions, which provide important context for understanding responses to disturbance. For example, Honolua Bay in northwest Maui has followed a classic trajectory of decline from coral to algal dominance, largely as a result of sedimentation (Dollar and Grigg 2004). However, the trajectory was not a single transition, as it began as regime 5 (high coral and high fish biomass), and transitioned to regime 4 and then regime 2 before ending in regime 1 (degraded) (Figure O.2). This multi-transitional trajectory provides an example of how the progression between regimes could be used to monitor subtle changes before a reef transitions to a degraded regime. Other time series in our dataset contradicted the expectation that degraded reefs are stable (Done 1992) by transitioning from regime 1 (low coral and fish biomass) to regimes 2, 4 and 5 (Figure 3.5). For example, Kahekili is a marine managed area where fishing of herbivores was restricted in 2009 and changes in both fish and benthic assemblages occurred following this closure (Williams et al. 2016). During this time, Kahekili transitioned from regime 4 to regime 1 and recovered to regime 5 after fish biomass increased (Figure O.2), suggesting specific harvest regulations can precipitate coral reef recovery assuming other stressors do not change. At several other sites coral reef regimes remained unchanged across time, particularly regime 2 and regime 4, bringing to question the common ecological mechanisms and management approaches that result in these patterns.

The coral-macroalgal paradigm posits that trajectories between reef regimes are the result of ecological feedbacks including herbivory, and coral recruitment mechanisms, so future work is needed to understand the feedback mechanisms that may be related to reefs that undergo multiple transitions (Mumby et al. 2007; Mumby and Steneck 2008; Nyström et al. 2008). In past studies, fishes have been considered as drivers of benthic reef regimes (Williams and Polunin 2001; Jouffray et al. 2015), but positive and negative feedbacks exist between fish and the benthos (Mumby and Steneck 2008; Nyström et al. 2012), so by considering the fish and benthos together we provide a more detailed understanding of the patterns of coral reef regimes. It is important to recognize that our identification of five regimes is context dependent, and contingent on the choice and number of variables included in the analysis (Anderson et al. 2005). Patterns of multiple transitions might also be related to the idea of slow transitions, where regime shifts to degraded states unfold slowly and can go unnoticed until it is too late (Hughes et al. 2013). We observed 3 regimes with high coral cover (3, 4 and 5), with frequent transitions among them. So, further research is needed to understand whether boundaries exist between these regimes, and if this could be informed by additional ecosystem components such as urchins or microbes.

We offer a nuanced understanding of coral reef ecosystem regimes that moves beyond the binary coral-macroalgal paradigm, and provides a new perspective for understanding and measuring reef change. Understanding the spatial distribution of the regimes and their possible transitions can also help managers understand and prioritize management actions. For example, if a management goal is to restore a location to the set of coral regimes that rely heavily on herbivory, this information could be used to inform a spatial approach that closely manages herbivore populations. Likewise, if the management goal is to maintain coral cover, it is important to consider that reefs can occur along a spectrum of coral cover, and that a low coral cover reef such as regime 2 is not necessarily a negative outcome of human pressures, but could instead can reflect natural bounds set by the surrounding abiotic environment (Williams et al. 2015a). By highlighting nuances in both the composition of regimes, and transitions among regimes, we identify new insights into the ecological complexity of coral reefs. Future work can tease apart the ecological mechanisms that underpin the different regimes, and investigate how human and natural drivers determine their structure and function.

Methods

Existing data from underwater visual surveys of fish and benthic assemblages were collated from multiple monitoring programs for the main Hawaiian Islands. Each dataset was transformed into a consistent format, and checked for errors. Data were only included in the analysis if benthic and fish surveys were co-located at a unique latitude and longitude, and were from forereef habitats, including depths 0 to 30 meters. The majority of the data (98%) were from 2000-2013. A total of 3,345 unique sites, defined as a survey location with a unique latitude and longitude, were used in the analyses. To account for spatial autocorrelation, means were taken for surveys within a defined distance of 300 meters (Appendix L), resulting in an overall sample size of 1,027. A mean was used for sites with data across multiple years. Data sources, survey methods, and other meta-data are provided in Appendix K.

To account for differences in survey method, fish data were standardized to the NOAA Biogeography Program belt transect using calibration factors (Friedlander et al. in review). Calibration factors were developed using an automated software program that utilizes general linear models and Monte Carlo simulations (Nadon 2014). Calibrations were calculated by species where possible based on the following decision rules: 1) a minimum of 10 paired observations were available within an island, 2) observations were not dominated by zeros – if they were, a delta model was run in which occurrences were modeled separately from non-occurrences, 3) residuals were normally distributed – if not data were log-transformed and the model was rerun and checked again. If a species did not pass this series of rules a calibration factor for each combination of family and trophic level (e.g. zooplanktivorous wrasses) was calculated. If a calibration factor could not be calculated at the family+trophic level, then a global calibration for the entire method was used. For all subsequent analyses, density estimates were based on calibrated densities of raw data. Benthic surveys were not calibrated as previous results found no large bias associated with percent cover among the methods used (Jokiel et al. 2005).

The biomass of individual fishes were estimated using the allometric length-weight conversion: $W=a\mathrm{TL}^b$, where parameters a and b are species-specific constants, TL is total length (cm), and W is weight (g). Length-weight fitting parameters were obtained from a comprehensive assessment of Hawaii specific parameters (Donovan et al., unpublished) and FishBase (Froese & Pauly 2011). Several fish species were removed from fish biomass calculations if aspects of their life history led to inaccurate counts with visual surveys, such as cryptic benthic species, nocturnal species, and pelagic schooling species. Likewise, manta rays were excluded, as their size is difficult to visually estimate and they have high biomass but are encountered infrequently. A procedure was developed for dealing with outliers in the fish data to account for differences that can result in exaggerated counts of schooling species. Extreme observations in the database were defined by calculating the upper 99.9% of all individual observations (e.g. one species, size and count on an individual transect), resulting in 26 observations out of over 0.5 million, comprised of 11 species. The distribution of individual counts in the entire database for those 11 species was then used to identify observations that fell above the 99.0% quantile of counts for each species individually. These observations were adjusted to the 99.0% quantile for analysis.

Fish and benthic assemblages were analyzed primarily at the level of functional groups. Benthic assemblages were broken into major functional groups including: coral, macroalgae, turf algae, crustose-coralline algae, and other substrate (e.g. sand, basalt rock, and recently dead coral). Other substrate was not broken down further due to limitations from incorporating data from different methods. The fish assemblage was characterized into three trophic groups, including herbivores, secondary consumers, and predators (Appendix M). Herbivores were further subdivided based on their feeding mode into browsers, grazers and scrapers following Edwards et al. (2014), which have been suggested as important indicators of resilience on coral reefs (Bellwood et al. 2004; Green and Bellwood 2009a; Heenan and Williams 2013). Browsers were defined as those herbivores that feed on macroalgae and associated epiphytic material and are important for reducing cover of competing macroalgae. Likewise, grazers were considered those fishes that feed largely on algal turfs, which can limit the establishment of macroalgae, and scrapers those that also feed on algal turfs but can also remove the reef substratum, opening space for coral recruitment.

The multivariate benthic and fish data were visualized with a non-metric multidimensional scaling plot using the *metaMDS* function in the *vegan* package in R (Oksanen et al. 2015). A Bray-Curtis distance matrix was created with 2 dimensions and a maximum of 50 random starts to search for a stable solution and avoid getting trapped in a local optima (Legendre and Legendre 2012). Before analysis, all data were fourth root transformed and centered to meet the assumptions of linear models and all variables were standardized to the same scale.

Regimes were identified using model-based clustering with the *mclust* package in R (Fraley et al. 2012). The cluster analysis is based on a probability model where each cluster is a mixture of multivariate normal distributions composed of the densities of each component, and each observation is assigned to a cluster based on the probability of membership given the observation. The *mclust* function uses three strategies for defining clusters: 1) initialization of the model with model-based hierarchical clustering, 2) maximum likelihood estimation with the expectation-maximization algorithm, and 3) model selection and the number of clusters that are approximated with Bayes factors and Bayesian Information Criterion (Fraley and Raftery 2002) (Appendix N). Multivariate dispersion was calculated for each regime and tested with an analysis of multivariate homogeneity of group dispersions with the *betadispr* function in the *vegan* package.

Ecological patterns across regimes were explored in multiple ways. Patterns of species richness and coral composition were examined across regimes with an Analysis of Variance, and contrasts and confidence intervals were calculated with Tukey's honest significant differences. The species composition of corals was examined by calculating the proportional cover of the four most abundant species within each regime. A trait-based approach to classifying coral species into competitive, stress-tolerant, generalist or weedy species following Darling et al. (2012), with additional species specific information on bleaching tolerance, was compared across regimes. The composition of the fish assemblage was compared across regimes with a Permutational Analysis of Variance (PERMANOVA) with the *adonis* function and an analysis of multivariate homogeneity of group dispersions with the *betadispr* in the *vegan* package in R. Only fish species that occurred in the top quantile of overall frequency of occurrence were used.

Spatial patterns across regimes were examined by comparing the proportion of each regime at each island, and by comparing the proportion of sites within a regime that was located on north, south, east, and west facing shores across islands. Additionally, depth and habitat complexity, measured as slope of slope, were calculated for each point from LiDAR derived bathymetry within a 60m radius of each survey location (Pittman et al. 2009), and were compared across regimes with an Analysis of Variance and post-hoc Tukey multiple comparisons.

Temporal transitions between regimes were assessed by predicting the regime for each year at each site individually with the function *predict.Mclust* in R. Sites were retained if there was at least a 95% probability of the regime prediction being correct, and when predictions were available for at least 3 years between 2000 and 2012. A total of 65 sites were included in the final data set, and patterns of regime transitions were compared by calculating the frequency of a given transition as a proportion of the total number of possible transitions (n=116). We tested the sensitivity of analysing data from all 65 sites compared with only analysing those with longer time series (≥ 4 or 6 years) by calculating binomial confidence intervals for each transition in each case (Figure O.3). These sites also tended to represent permanent monitoring stations, so this was also to test for the sensitivity to using observations from locations that may shift from year to year. Binomial confidence intervals were produced with the *binconf* function in the *Hmisc* package in R (Harrell 2016) using the Wilson interval.

All analyses were conducted in the R environment for statistical computing version 3.3.0 (R Development Core Team (2016)).

Table 3.1 Summary of variables used to identify regimes, including mean and standard error by regime (in parentheses), total number of sites classified into each regime, and multivariate dispersion based on an analysis of multivariate homogeneity of group dispersions. Benthic variables are % cover and fish variables are g m-2.

	REGIME (mean (SE))				
	1	2	3	4	5
Coral	5.8 (0.5)	9.8 (0.5)	26 (1.4)	23.5 (1.6)	31.1 (1)
Macroalgae	10.3 (0.9)	10.4 (0.6)	0 (0)	13 (1.5)	6.2 (0.4)
Other Substrate	13 (1)	5.4 (0.4)	5.5 (0.7)	22.6 (1.8)	9.6 (0.6)
Turf	65.6 (1.4)	64.7 (0.9)	60.3 (1.6)	31.9 (1.9)	43 (1)
Coralline Algae	3.5 (0.4)	7.2 (0.4)	6.5 (0.5)	5 (0.7)	8.1 (0.4)
Browsers	1 (0.2)	20.5 (3.4)	5.2 (1)	3.1 (0.7)	3.9 (0.3)
Grazers	5.1 (0.7)	25.4 (2.1)	16.5 (1.9)	12.2 (1.6)	11.7 (0.7)
Scrapers	1.1 (0.2)	15.1 (1.5)	11.8 (1.4)	12.6 (1.7)	10.6 (0.7)
Predators	0 (0)	9.7 (1.5)	8.7 (1.5)	8.3 (1.1)	4.1 (0.3)
Secondary Consumers	7.5 (0.5)	27 (1.8)	23.4 (1.5)	28.9 (3.8)	19.3 (0.7)
Total number of sites	205	250	158	200	214
Multivariate dispersion	1.702	1.847	1.675	2.479	1.082

Figure 3.1 Non-metric multidimensional scaling plot of all data used in analysis of reef regimes, the size of points correspond to goodness of fit to the nMDS to aid visualization (stress = 0.20), and are colored by the regime as classified by model based clustering (A), ellipses drawn around 50% of the data within each regime overlaid on points from A (B), and ellipses with vectors corresponding to variables used in the analysis (C).

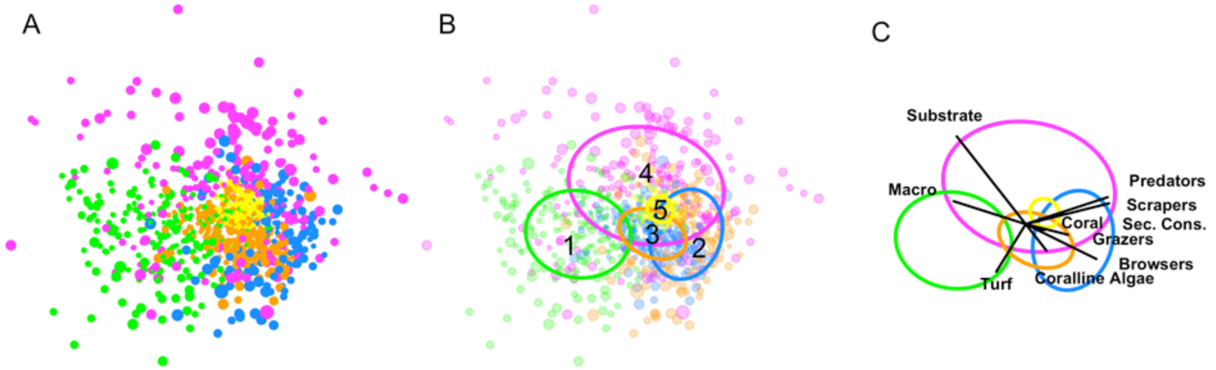


Figure 3.2 Kernel density of each fish and benthic variable for each regime with arrows corresponding to mean values for each variable for each regime. Note, x-axis transformed to same scaling as used in cluster analysis.

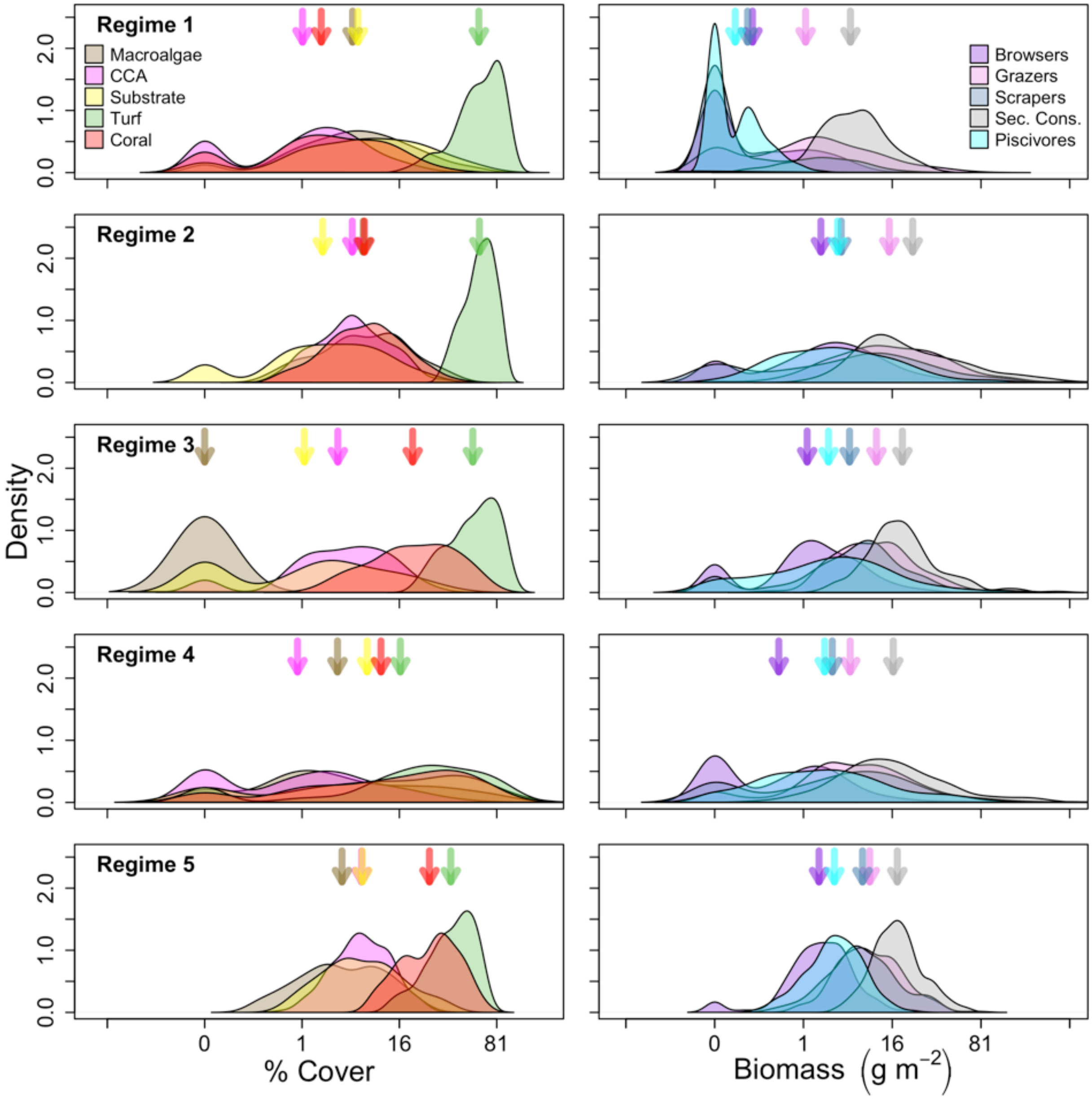


Figure 3.3 Photos representing each regime. Regime 1 has low fish biomass, low coral cover, high algal cover, and is often associated with flat bottoms. Regime 2 has moderate to high fish biomass, low to moderate coral cover, and is often associated with rugose habitats such as the boulder habitat shown. Regime 3 has high fish biomass, high coral cover, and zero macroalgal cover. Regime 4 is highly variable and has moderate to high fish biomass and moderate to high coral cover. Regime 5 is the least variable and has moderate to high fish biomass, moderate to high coral cover, and moderate algal cover. Photo credits: 1 – NOAA Coral Reef Ecosystem Program, 2 – L. Kramer/NPS, and 3-5 – Catlin Seaview.

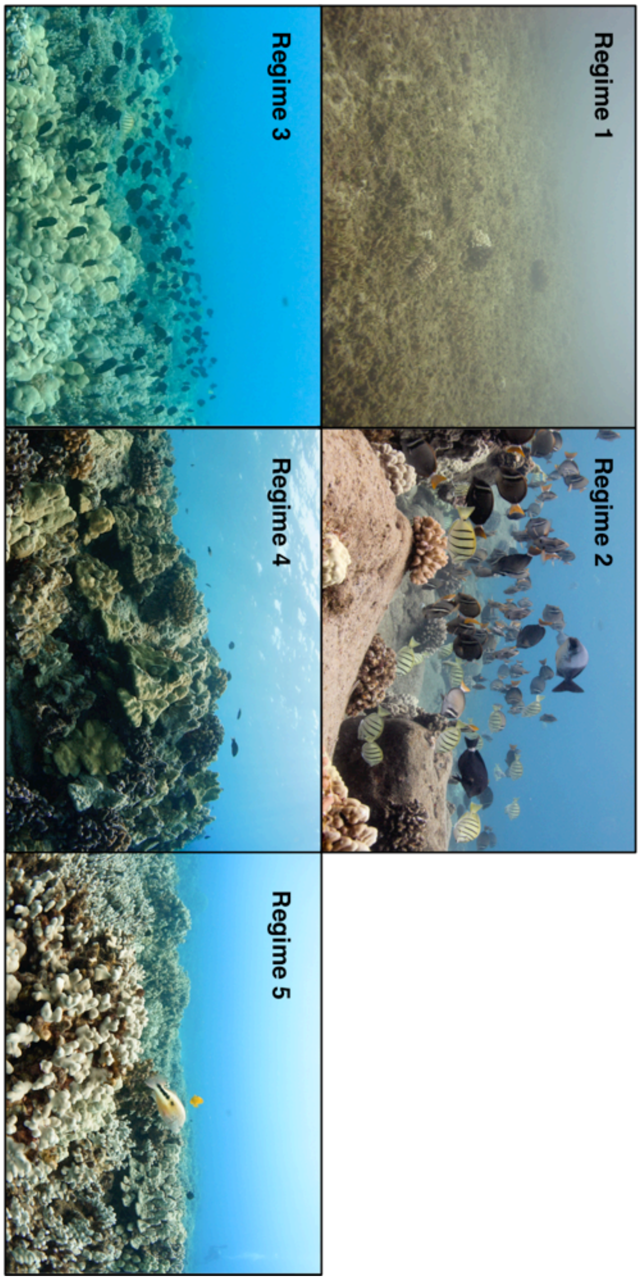


Figure 3.4 Distribution of sampling with locations colored by regime.

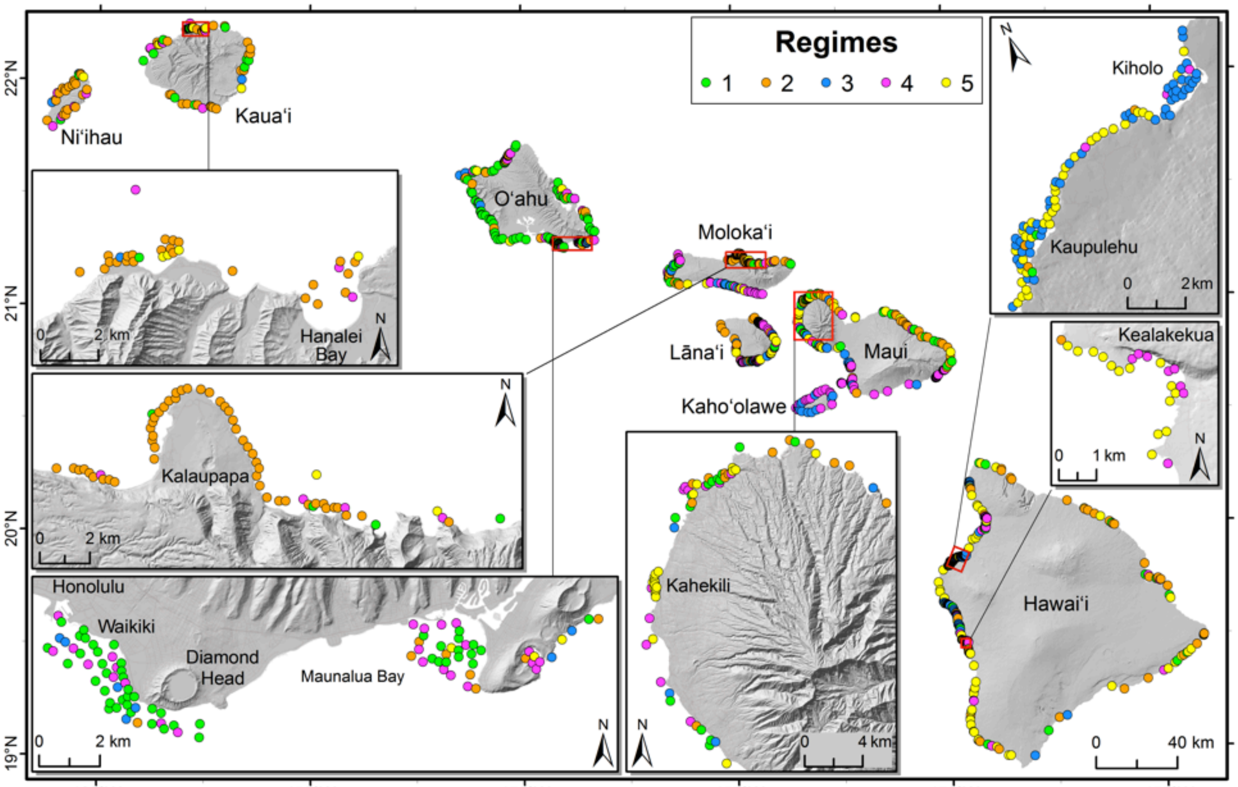
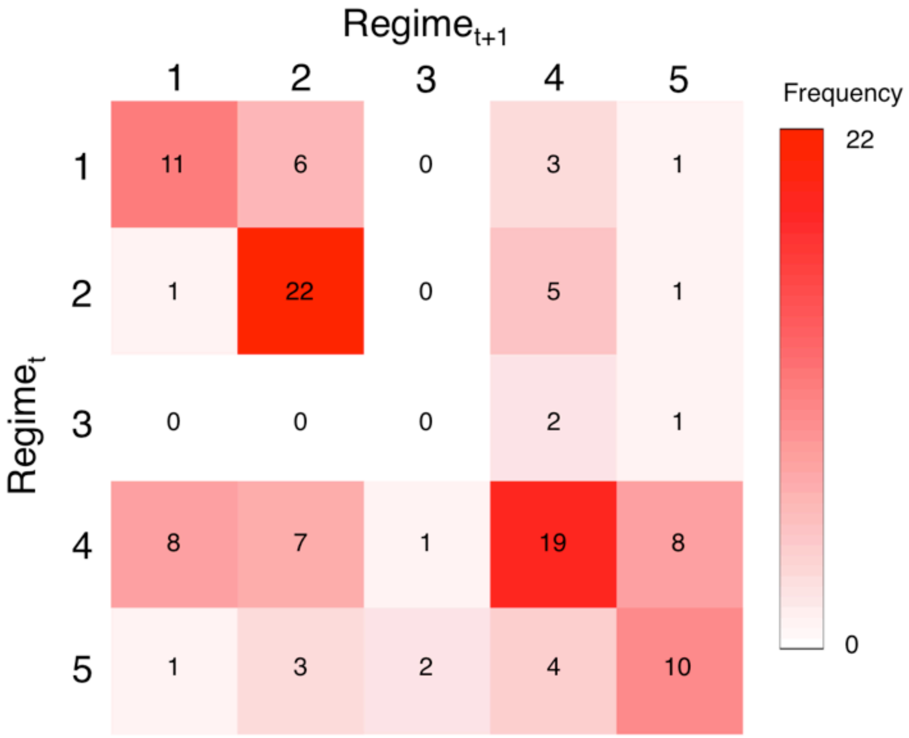


Figure 3.5 Summary of transitions between regimes with darker red corresponding to greater frequency of observation from 65 sites and 116 observed transitions. Numbers in each cell are the total number of transitions observed for that combination of regimes.



	1	2	3	4	5
1	11	6	0	3	1
2	1	22	0	5	1
3	0	0	0	2	1
4	8	7	1	19	8
5	1	3	2	4	10

CHAPTER 4 Empirical patterns underlying resilience of coral reefs in Hawaii and the Caribbean: a comparison

Abstract

Diversity of corals and fishes in Hawaii and the Caribbean represent the lower bounds of diversity on coral reefs worldwide, bringing into question the underlying mechanisms that confer resilience in both locations. Much of what we know about coral reef resilience comes from studies in the Caribbean, and resilience has been posited to be greater in the Pacific than the Caribbean. Using comprehensive syntheses of available underwater survey data from both locations, this study compared patterns in fish and benthic communities in Hawaii and the Caribbean that relate to our understanding of resilience on coral reefs. Specifically, patterns of coral and macroalgal dominance, functional and response diversity, and the relationship between herbivore abundance and benthic state were compared. This study contributes to our understanding of what ecological patterns underpin resilience in relatively species-poor geographies, and highlights patterns that are not consistent in Hawaii compared to what is known in the rest of the Pacific. Important similarities in patterns underlying hypotheses of what confers resilience on coral reefs were also identified, such as the positive relationship between parrotfish biomass and coral cover. Further, important indicators that can be used for monitoring and management included functional richness and the biomass of herbivores, which were both positively related to coral cover in both Hawaii and the Caribbean. Therefore, parrotfish and herbivore biomass, and functional richness, should be considered when designing resilience-based management strategies for coral reefs.

Introduction

Understanding the resilience of coral reef ecosystems is of great importance given the susceptibility of the system to external drivers, such as climate change and overfishing (Hughes et al. 2010). Resilience can be defined as the capacity of an ecosystem to withstand disturbance without changing its overall identity in terms of structure and function (Holling 1973; Gunderson 2000). This is often referred to as *ecological resilience* and includes the concept of tipping points, and changes in feedbacks leading to abrupt transitions between multiple ecosystem states (Scheffer et al. 2001). Coral reefs are an example of a complex system that can exhibit non-linear changes to drivers resulting in regime shifts from coral to macroalgae, and have been a focus of resilience studies for decades (Done 1992; Knowlton 1992; Hughes 1994; Bellwood et al. 2004; Nyström et al. 2008). A notable example of a loss of resilience was when sharp declines in coral cover across the Caribbean occurred after the sudden collapse of *Diadema antillarum* populations in 1983. Caribbean reefs were then left susceptible to overgrowth by algae, since herbivory by fishes had been removed by historical overfishing (Hughes 1994; Jackson et al. 2014).

A majority of studies on coral reef resilience have occurred in the Caribbean, leaving some to question the transferability of conclusions to the Pacific, where a lower proportion of macroalgal dominance has been observed (Bellwood et al. 2004; Bruno and Selig 2007; Roff and Mumby 2012). Roff and Mumby (2012) outlined a number of hypotheses to explain why resilience may vary between the Caribbean and Indo-Pacific Basins, but only a few examples of regional comparisons based on empirical data could be made. Likewise, the Indo-Pacific has a large geographic area, leaving uncertainty about how patterns might vary within the Pacific basin. For example, Hawaii is an example of why generalizing the entire Pacific basin may be difficult. Hawaii is the most isolated archipelago on earth, has high levels of endemism, and generally low species richness compared to the central and south Pacific (Randall 2007; Briggs and Bowen 2012; Kulbicki et al. 2013).

Coral reefs in Hawaii suffer from many of the same human impacts that threaten reefs worldwide (Halpern et al. 2008b), yet large gradients exist across the archipelago with relatively less impacted areas in remote locations of the main Hawaiian Islands and the Northwestern Hawaiian Islands (Friedlander & DeMartini 2002, Williams et al. 2008). Coral to macroalgal phase shifts are not unknown to Hawaii where several reefs have transitioned to an algal state in locations such as Waikiki and Maunalua Bay on Oahu and southwest Maui (Smith et al. 2002; Jokiel et al. 2004; Friedlander et al. 2007; Stimson and Conklin 2008). How coral and macroalgal cover varies across the main Hawaiian Islands, and how factors related to coral reef resilience in Hawaii compares to the hypotheses addressed by Roff & Mumby (2012) have not been well documented.

To address questions about the ecological underpinnings of coral reef resilience in Hawaii compared to the Caribbean, this study utilized data from large synthesis efforts in each region (Figure 4.1) to test 3 hypotheses outlined by Roff and Mumby (2012).

1) Phase shifts from coral to macroalgal cover will be less extreme in Hawaii compared to the Caribbean.

Evidence for regime shifts from coral to macroalgae comes from multiple geographies; however, instances in the Caribbean have been documented at twice the rate of the Indo-Pacific (Roff and Mumby 2012). Given this, the generality of regime shifts have been questioned (Aronson and Precht 2006; Bruno et al. 2009; Dudgeon et al. 2010). Several studies have documented differences in the distribution of coral and macroalgae in the Caribbean compared to the Indo-Pacific, with more severe phase shifts in the Caribbean (Connell 1997; Mumby et al. 2007; Bruno et al. 2009; Hughes et al. 2010; Roff and Mumby 2012). Despite few examples of phase shifts in Hawaii, the overall frequency of coral and macroalgal dominance across the Hawaiian archipelago is less well known than in other parts of the world (but see Jouffray et al. 2015). If processes underlying phase-shifts in the Pacific are operating in Hawaii then the expectation would be a skewed frequency towards coral in Hawaii (Roff and Mumby 2012). To test this, I compared the density of observations of coral to macroalgae from the datasets discussed in Chapters 2 and 3 (Figure 4.2).

2) Functional diversity of fishes will be positively related to coral cover in both regions.

Hawaii and the Caribbean are both underrepresented across functional groups of corals and fishes, with less species both across and within functional groups compared to the Great Barrier Reef (Figure 4.3) (Bellwood et al. 2004). This brings to question how Hawaii fits into the overall picture of coral reef resilience, and whether it is more similar to the Caribbean than the rest of the Pacific. Diversity has been cited as a critical underpinning of ecological resilience (Peterson et al. 1998), where species support critical functions and therefore more species may provide redundancy for those functions (Hooper et al. 2005). By extension, it is important to consider the diversity of responses within functional groups to variations in disturbance, since species loss is often non-random and the loss of key groups can lead to drastic ecosystem shifts (Elmqvist et al. 2003). For example, the loss of functional diversity and response diversity in corals from large-scale disturbances have been observed in the Caribbean, where White-Band Disease led to mass mortality of branching *Acorpora* species in the 1970s (Gladfelter 1982; Porter and Meier 1992; Aronson and Precht 2001; Jackson et al. 2001; Cramer and Jackson 2012). The loss of habitat formed by the two *Acropora* species marginalized the coral communities that remained, resulting in lower functional and response diversity overall (Bellwood et al. 2004; Nyström 2006).

Coral reef fishes are extremely important for reef ecosystem function and they are also very diverse, though with regional differences. For example, Caribbean reefs commonly have 10-15 herbivorous fish species and the reefs of Great Barrier Reef in Australia can have over 30 species (Bellwood et al. 2004; Bonaldo et al. 2014). The importance of fish functional diversity includes buffering impacts of global climate change with stabilizing effects on biomass (Duffy et al. 2016). Limited functional redundancy has also been cited as a critical descriptor of coral reefs, where an ecosystem process such as bioerosion can be limited to one species of parrotfish (Bellwood et al. 2003). How differences in functional diversity translate to differences in ecosystem state (e.g., coral cover) is less well understood. To test this, I compared multiple metrics of functional diversity for fishes in Hawaii and the Caribbean and related them to coral cover in each region (Table 4.1, Figure 4.4).

3) Herbivores will be more abundant in Hawaii than the Caribbean within and across functional groups and have a different functional relationship to benthic cover.

Herbivorous fishes have great potential for facilitating resilience on coral reefs as consumers of benthic algae and mediators of bioerosion (Bellwood et al. 2004, 2006; Hughes et al. 2007; Burkepile and Hay 2008; Nyström et al. 2008; Green and Bellwood 2009b; Hoey and Bellwood 2009; Cheal et al. 2013). Within the herbivore guild, three groups play complementary functional roles on reefs, the grazers, scrapers and browsers, representing the broad functional diversity of the group. Likewise, response diversity among herbivorous fishes has been shown to relate to ecosystem recovery (Graham et al. 2015; Nash et al. 2016). Both Hawaii and the Caribbean have lower species richness within and across the herbivore functional groups, and herbivores constitute different proportions of the total species pool compared to the Great Barrier Reef (Figure 4.3) (Bellwood et al. 2004; Roff and Mumby 2012). For example, the roving grazers are all surgeonfishes from the family Acanthuridae, which is represented in the Caribbean by only four species from a single genus (*Acanthurus*) compared to 13 species from two genera in Hawaii (*Acanthurus*, *Zebrasoma*). Thus, the presence of one or few species may be filling important functional roles in both regions.

Beyond the composition of the herbivore guild, it has also been proposed that the overall abundance, and therefore herbivory capacity, on reefs in the Pacific are greater than in the Caribbean (Roff and Mumby 2012; Edwards et al. 2014). Edwards et al. (2014) found that the Caribbean had low biomass of herbivores compared to anywhere on the globe, including lower mean biomass than most locations in Hawaii. The overall biomass of particular species groups is also generally thought to be lower in the Caribbean (Roff and Mumby 2012). To test this, I compared biomass by herbivore functional groups between the Caribbean and Hawaii (Figure 4.5).

Differences in the composition and abundance of herbivores among regions also brings into question whether there are differences in the relationships to benthic cover. Strong negative linear relationships between Acanthurid and Scarid biomass and macroalgal cover have been found in the Caribbean (Williams and Polunin 2001), however multiple studies in Hawaii and elsewhere in the Pacific have found no relationship or nonlinear relationships (Friedlander et al. 2007; Wismer et al. 2009; Roff and Mumby 2012; Heenan and Williams 2013; Mumby et al. 2013a; Russ et al. 2015). To test this, I compared the relationships identified in Chapter 2 with similar relationships for Hawaii (Table 4.2, Figure 4.6-Figure 4.7).

Methods

Data were collated from existing surveys of underwater visual censuses of fishes from several sources across the Caribbean (Table A.1). Data were formatted into a standardized template, and underwent quality assessments that included accounting for differences in methodologies, habitats, and outliers (see methods in Chapters 2 & 3). Data in the Caribbean were restricted to *Orbicella* reefs in depths 0 to 20 meters from 1998-2013. Similarly, Hawaii data were from forereef habitats, including depths 0 to 30 meters, and the majority of the data (98%) were from 2000-2013. In the Caribbean, data were summarized for each location (Figure 2.1). In Hawaii, data were summarized to a similar spatial extent using moku for stratification. Moku are traditional spatial boundaries that were used for customary marine management, with specific fisheries regulations in each moku (Titcomb 1972; Kirch 1989). This spatial scale was used because it provides an intermediate scale between watersheds and islands, and because it has been used previously to understand variation in fish biomass across the main Hawaiian Islands (Friedlander et al. 2016). Sites were assigned to moku using the Island Breath organization's maps (www.islandbreath.org), and attributing to the nearest moku land division (Figure 4.1). As in Chapter 2, analyses were based on a hierarchal structuring of the data and were summarized based on means of replicates within individual datasets for each location or moku. To account for differences in sampling, methodologies, and spatial and temporal structures across the datasets, general linear mixed effects models were used to estimate means by location or moku for each response variable with the *lmer* function in the R package *lme4* (Pinheiro and Bates 2000; Bates et al. 2010; Skaug et al. 2013). Response variables were transformed where necessary to meet assumptions of linear modeling. A random effect of dataset was included in the models to account for differences in methodologies and sampling designs across datasets. Model fits were assessed by visual inspection of residuals and restricted maximum likelihood was used to fit the models (Bolker et al. 2009). Confidence intervals were generated for estimates using the *predictInterval* function in the *merTools* package in R (Knowles and Frederickm 2016). Intervals were derived by estimating the fitted values based on 10,000 random draws from a sampling distribution for the random and fixed effects and then defining the upper and lower 0.05% of the returned values.

The distribution of coral and macroalgae in each region were plotted in 2 dimensions, and visualized based on the 2-dimensional kernel density of observations in R with the *heatscatter* function in the LSD package (Schwalb et al. 2015).

Functional diversity can be defined in terms of the number and types of functions that exist within a community that relate to ecosystem processes and functioning (Tilman 2001). This can be measured in multiple ways, for example, functional richness is the number of functions present in the community and is the most common metric in the literature (Hillebrand and Matthiessen 2009). Other important measures include functional evenness and distinctness that can provide insight into how function is distributed within the community. Two communities may have the same richness, but one species could dominate a particular function, and functional evenness would be low (Mouillot et al. 2005). Likewise, functional distinctness will be low if functional abundance is clustered in certain functions, but not necessarily at different abundances (Villéger et al. 2008).

I defined functional entities as the combination of trophic levels and size classes in the fish assemblage, based on the assumption that function changes with size. Nash et al. (2016) proposed this method as an approach to studying how cross-scale diversity relates to ecological resilience for coral reefs. Fish functional diversity was investigated using multiple methods based on the presence and absence of functional entities, which were defined as the combination of functional group and size class. Functional groups were defined in the same way as Chapters 2 and 3, and were based on feeding ecology into predators, secondary consumers, and three groups of herbivores: browsers, grazers and scrapers (Table B.1, Table M.1). All fish functional groups were divided into the following size classes from 0-15 cm, 15-30 cm, 30-45 cm, 45-60 cm, and greater than 60 cm, except for grazers and browsers, where all individuals greater than 45 cm were lumped with the third size bin since they did not occur frequently. This resulted in 21 functional entities with 5 groups each for predators, secondary consumers, and scrapers, and 3 groups each for browsers and grazers. Functional richness was measured as the sum of the presence of each functional group at each location or moku, and estimated with Simpon's index since it is less sensitive to rare species and sampling effects than other measures of richness (Hill 1973). Functional evenness and functional distinctness were estimated using the *dbFD* function in the *FD* package in R (Villéger et al. 2008), that account for relative abundance, following the same methods as Nash et al. (2016). Functional evenness is measured as the convex hull volume in multivariate space, and describes the distribution of biomass across functional entities. Functional distinctness was estimated by the average distance to the centroid of each entity weighted by biomass, measured with a species matrix based on Euclidean distance, and describes whether biomass is dispersed among functional entities (Anderson 2006).

Results

Distribution of coral and macroalgae

Similar to previous studies, Caribbean reefs occurred along a spectrum of macroalgal cover with generally lower coral cover. In contrast, Hawaii reefs occurred across a range of coral cover, but generally low macroalgal cover, reflected as a highly skewed 2-dimensional distribution of cover (Figure 4.2).

Fish functional diversity relationship to coral cover

In line with the prediction that larger functional diversity would be related to higher coral cover, coral cover increased with functional richness, measured as Simpson's Index, for both Hawaii (LM: $F_{1,26} = 6.49$, $p = 0.02$, $R^2 = 0.17$) and the Caribbean (LM: $F_{1,34} = 7.56$, $p = 0.01$, $R^2 = 0.16$). Interestingly, results were quite different among regions for functional evenness and functional distinctness, the latter combines richness with abundance. In Hawaii, coral cover increased with functional evenness (GAM: $p = 0.03$, $R^2 = 0.24$), and coral cover declined with functional evenness in the Caribbean (LM: $F_{1,35} = 11.2$, $p < 0.01$, $R^2 = 0.22$). So, in Hawaii, locations with high coral cover had fish abundance that was distributed evenly across functional entities. In the Caribbean, in locations where coral cover was high the abundance of fishes was high within few functional entities. Similarly, functional distinctness was negatively related to coral cover in the Caribbean (LM: $F_{1,36} = 6.1$, $p = 0.01$, $R^2 = 0.12$), and unrelated to coral cover in Hawaii (LM: $F_{1,26} = 0.01$, $p = 0.90$).

Herbivorous fish abundance and relationship to benthic cover

Hawaii had a greater mean biomass of grazers (LM: $F_{1,65} = 34.1$, $p < 0.01$), but the biomass of browsers was not significantly different (LM: $F_{1,65} = 0.14$, $p = 0.72$). Interestingly, mean biomass of scrapers was greater in the Caribbean compared to Hawaii (LM: $F_{1,65} = 6.1$, $p = 0.02$).

In both regions, there were no significant relationships between coral or macroalgal cover and grazer or browser biomass. In both regions, however, there was a significant positive relationship between scraper biomass and coral cover (Caribbean: $F_{1,35} = 6.84$, $p = 0.01$, $R^2 = 0.16$; Hawaii: $F_{1,24} = 13.1$, $p < 0.01$, $R^2 = 0.33$), and a significant negative relationship between scraper biomass and macroalgal cover (Caribbean: $F_{1,26} = 9.08$, $p = 0.01$, $R^2 = 0.27$; Hawaii: $F_{1,26} = 5.0$, $p = 0.03$, $R^2 = 0.13$).

Discussion

The skewed relationship toward coral cover, rather than macroalgal cover, was unsurprising given that many of Hawaii's reefs can be characterized as turf-dominated (Vermeij et al. 2010; Jouffray et al. 2015, Chapter 3), and that proliferations of macroalgae have been largely limited to sheltered embayments such as Kaneohe Bay (Bahr et al. 2015). Interestingly, recovery to a coral state has also occurred in Kaneohe Bay, where nutrient loading from sewage outfalls caused a decline in coral and a rise in a macroalgae (*Dictyosphaeria cavernosa*) in the 1970s, and following a diversion of the sewage offshore, macroalgal cover decreased and coral recovered to pre-sewage levels (Hunter and Evans 1995; Stimson and Conklin 2008; Bahr et al. 2015). Given the different trajectories across Hawaiʻi and the Caribbean, it is expected that factors underlying resilience in each region would be different, such as the role of fish functional diversity and the strength of herbivory (Elmqvist et al. 2003; Hughes et al. 2010; Roff and Mumby 2012).

Differences in measures of functional diversity could reflect differences in the consequences of biodiversity loss in Hawaiʻi and the Caribbean. Positive relationships between richness and coral cover in both regions mean that loss of richness could have measurable effects on ecosystem state. But, differences in the relationship between evenness and distinctness could mean that the Caribbean is more susceptible to biodiversity loss since abundance of particular functional entities were important. However, metrics that rely on abundance are more sensitive to sampling effects so these results should be interpreted with caution. Studying functional evenness implies that abundance is linked to ecosystem processes, which may not be reflective if critical functions are being filled by relatively less abundant species or functional groups. Also, trophic levels may not be appropriate classifiers of function in an ecosystem given that interactions across trophic levels can affect ecosystem processes, and therefore a finer level of classification may be necessary (Petchey and Gaston 2006). I further delineated by size, but this proxy of function assumes that those size groups provide different functions, which has not been studied rigorously for all coral reef fishes. However, this type of information is becoming better understood through experimental and observation studies of species-specific behaviors, especially for herbivores (Burkepile and Hay 2008; Rasher et al. 2011; Adam et al. 2015a).

Differences in the distribution of herbivore functional groups between Hawaiʻi and the Caribbean could be related to differences in the importance of herbivory by certain groups in each region, where for example, grazing by surgeonfishes has been posited to be much more important in the Indo-Pacific than the Caribbean (Roff and Mumby 2012). Multiple alternative hypotheses could explain why scrapers were significant and browsers and grazers were not significantly related to benthic cover. Evidence suggests that individual herbivore species may play different roles in ecosystem function (Bellwood et al. 2006; Burkepile and Hay 2008, 2010; Hoey and Bellwood 2009; Adam et al. 2015a), and therefore the functional groups as defined in this study may not be capturing how those roles translate to differences in ecosystem state. For example, ‘grazers’ is a general term which also includes species that largely eat detritus and therefore may not remove algae but rather brush it (Marshell and Mumby 2012). Further, even within functional groups, species appear to play both complementary and redundant roles depending on what species of algae they eat, how far they move, and where on a reef they actually feed (Burkepile and Hay 2008; Rasher et al. 2013; Adam et al. 2015b). Thus, the relationship between herbivore diversity and coral reef ecosystem function is likely complex and underappreciated.

The relationships identified in this study between scraper biomass and benthic cover are significant given contrasting results from previous studies (Bellwood et al. 2004; Mumby et al. 2006; Newman et al. 2006; Burkepile and Hay 2010; Burkepile et al. 2013; Bonaldo et al. 2014; Adam et al. 2015b; Russ et al. 2015; Suchley et al. 2016). A significant relationship was found in two very different biogeographic regions using large datasets that encompass the full range of variability in benthic cover and fish biomass. This is important given that a study with a smaller geographic scope may not be able to capture the full extent of variation across variables and therefore may not be able to detect the same signal. For example, a recent study evaluated how change in herbivore abundance was related to changes in macroalgal cover on the Mesoamerican reef and did not find a significant negative relationship (Suchley et al. 2016). However, the range of biomass in their study was only half of the range in biomass observed in the Caribbean dataset analyzed here. Also, the spatial scale at which the analyses were undertaken may be important and results could vary depending on what scale the individual observations were summarized. Further work is needed to understand how these relationships vary with scale, and what the implications are for our understanding of herbivore-benthic cover relationships on reefs. Finally, the relationships identified in this study are correlational, and it is not possible to make any conclusions about mechanisms. Further work is needed to scale up from behavioral studies and experiments at fine scales to link mechanism to ecosystem function at large scales.

Conclusion

This work contributes to our understanding of how ecological patterns related to coral reef resilience vary in relatively low diversity systems. By comparing metrics calculated using similar methods in Hawaii and the Caribbean, the ubiquity of lessons learned from the Caribbean for managing reefs in the Pacific could be evaluated. Hawaii and the Caribbean are very different in a number of important ways that could relate to how mechanisms of coral reef resilience may be different in each region. Hawaii is an isolated archipelago that spans over 2,400 km across tropical and subtropical latitudes and large wave events are a common element of the climatology (Gove et al. 2013). These physical features play an important role in structuring the near shore assemblages of the Hawaiian Islands (Dollar 1982; Grigg 1998; Friedlander et al. 2003). For example, naturally low coral cover reefs occur in areas of high wave exposure (Chapter 3), and this translates to differences in coral reef community structure (Friedlander et al. 2003; Franklin et al. 2013). The geologic and evolutionary history of the Hawaiian archipelago is also quite different from the Caribbean, so reef formation and origins of diversity are different in each region.

Commonalities were also identified across regions that are important for monitoring and management of coral reefs. Ecological patterns of functional richness and scraper biomass in relation to coral cover were similar, and therefore provide valuable indicators for monitoring and management. This study supports the idea that protecting parrotfish populations in both the Caribbean and Hawaii could prevent or reverse coral-macroalgal phase shifts given the strong links between scraper biomass and coral and macroalgal cover (Figure 4.6, Figure 4.7) (Bellwood et al. 2004; Hughes et al. 2010). In addition, functional richness should be considered when designing resilience-based management given the strong positive relationship to coral cover in both Hawaii and the Caribbean. Further work could tease apart how specific aspects of functional diversity translate to ecological resilience to inform this approach. This study highlighted how aspects of coral reef ecology in Hawaii and the Caribbean are both similar and different, and provides a more thorough examination of hypotheses related to coral reef resilience based on empirical data than has been possible before.

Table 4.1 Results of linear models or general additive models (GAM) between metrics of functional diversity and coral cover. GAMs are indicated where with s(Slope), and coefficients and statistics are in labeled in parentheses for those lines where appropriate.

	Independent variable	Term	Beta (or EDF)	Std Err (beta) (or Ref.df)	t	*p*	F	df (n)	R^2
Caribbean	Simpson diversity	Intercept	-27.93	20.09	-1.39	0.17			
		Slope	80.09	29.14	2.75	**0.01**	7.55	34	0.18
	Functional Evenness	Intercept	44.57	5.25	8.49	**0.00**			
		Slope	-39.20	11.71	-3.35	**0.00**	11.20	35	0.24
	Functional Distinctness	Intercept	58.78	12.47	4.71	**0.00**			
		Slope	-69.77	28.30	-2.47	**0.02**	6.08	36	0.14
Hawaii	Simpson diversity	Intercept	-12.21	9.81	-1.24	0.22			
		Slope	52.22	20.50	2.55	**0.02**	6.49	26	0.20
	Functional Evenness	Intercept	12.43	1.55	8.00	**0.00**			
		s(Slope)	1.99	2.49		**0.03**	3.93	28	0.30
	Functional Distinctness	Intercept	16.76	35.21	0.48	0.64			
		Slope	-7.90	64.16	-0.12	0.90	0.02	26	0.00

Table 4.2 Results of linear models or general additive models (GAM) between metrics of biomass of herbivore functional groups and coral and macroalgal cover. GAMs are indicated where with s(Slope), and coefficients and statistics are in labeled in parentheses for those lines where appropriate.

	Dependent variable	Independent variable	Term	Beta (or EDF)	Std Err (beta) (or Ref.df)	t	p	F	df (n)	R2
Caribbean	Coral	Grazers	Intercept	25.81	3.07	8.41	**0.00**			
			Slope	1.08	1.08	1.00	0.33	0.99	36	0.03
	Coral	Browsers	Intercept	5.03	0.33	15.40	**0.00**			
			Slope	0.07	0.12	0.62	0.54	0.39	36	0.01
	Coral	Scrapers	Intercept	21.40	2.82	7.58	**0.00**			
			Slope	0.88	0.34	2.61	**0.01**	6.84	35	0.16
Hawaii	Coral	Grazers	Intercept	15.07	3.73	4.04	**0.00**			
			Slope	-0.22	0.43	-0.51	0.62	0.26	26	0.01
	Coral	Browsers	Intercept	15.87	3.17	5.01	**0.00**			
			Slope	-1.13	1.15	-0.99	0.33	0.97	26	0.04
	Coral	Scrapers	Intercept	2.20	0.42	5.28	**0.00**			
			Slope	0.35	0.10	3.62	**0.00**	13.10	24	0.35
Caribbean	Macroalgae	Grazers	Intercept	43.78	6.50	6.74	**0.00**			
			Slope	-3.06	2.46	-1.25	0.22	1.56	26	0.06
	Macroalgae	Browsers	Intercept	43.55	7.02	6.20	**0.00**			
			Slope	-2.69	2.49	-1.08	0.29	1.16	26	0.04
	Macroalgae	Scrapers	Intercept	53.71	6.57	8.18	**0.00**			
			Slope	-2.42	0.80	-3.01	**0.01**	9.08	25	0.27
Hawaii	Macroalgae	Grazers	Intercept	9.52	1.67	5.70	**0.00**			
			Slope	-0.18	0.19	-0.95	0.35	0.89	26	0.03
	Macroalgae	Browsers	Intercept	8.61	1.46	5.92	**0.00**			
			Slope	-0.19	0.53	-0.36	0.72	0.13	26	0.01
	Macroalgae	Scrapers	Intercept	3.15	0.24	13.06	**0.00**			
			Slope	-0.10	0.04	-2.23	**0.03**	4.96	26	0.16

Figure 4.1 Distribution of sampling in Hawaii (left) and the Caribbean (right), black dots are individual replicates within each region for databases described in Chapter 2 and 3. Grey lines in Hawaiian Islands delineate moku boundaries as defined by the Island Breath organization (http://www.islandbreath.org/mokupuni/mokupuni.html).

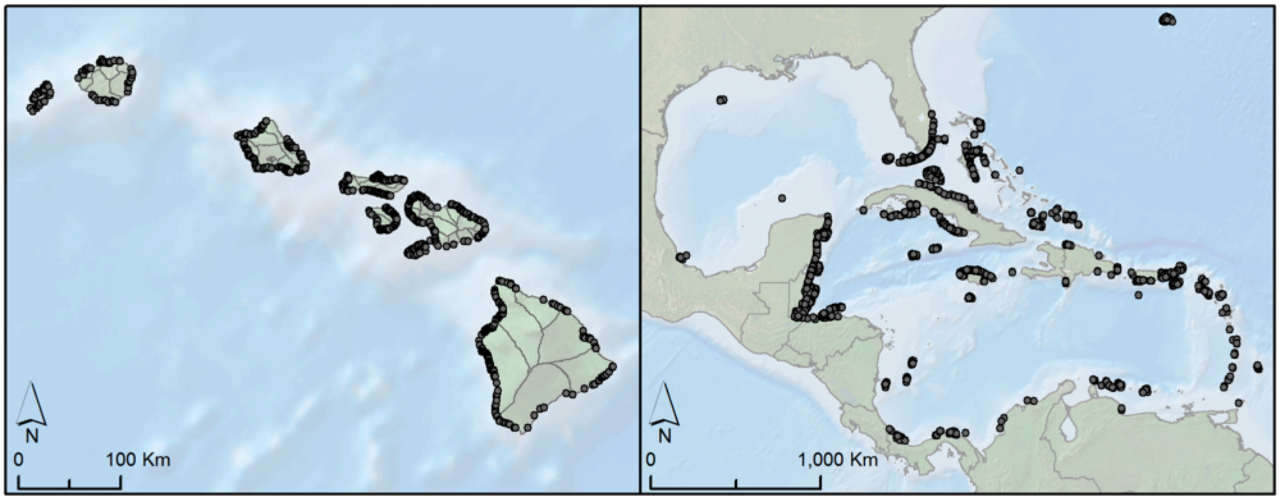


Figure 4.2 Distribution of coral and macroalgae in the Caribbean (n = 5327) and Hawaii (n = 2776). Colors correspond to the 2-dimensional kernel density of observations, with higher density in yellow-red plotted in R with the *heatscatter* function in the LSD package (Schwalb et al. 2015).

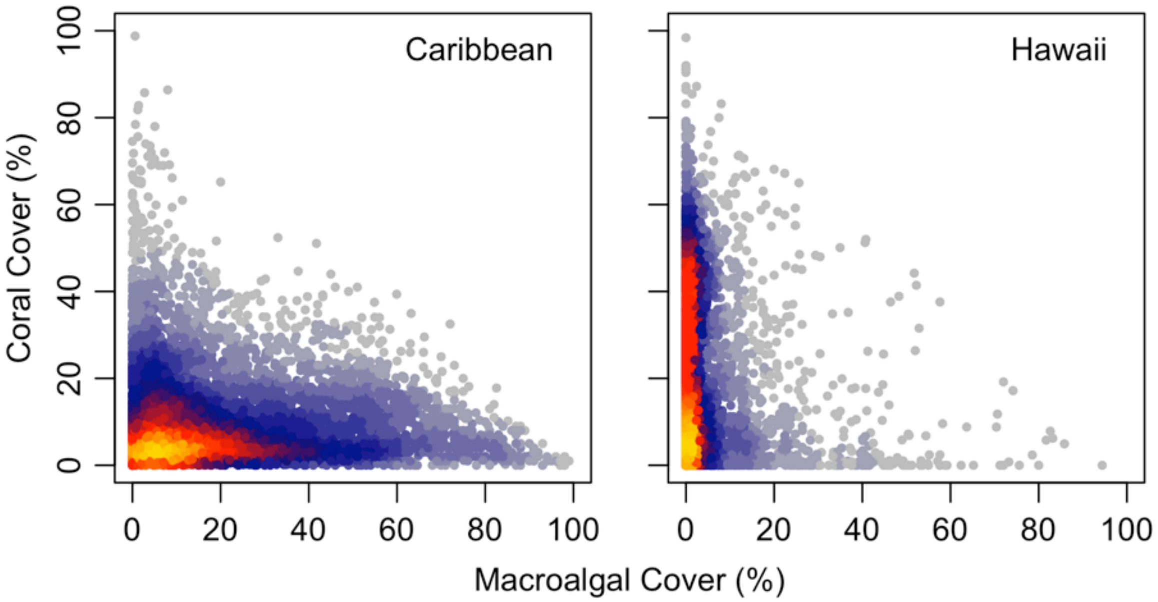


Figure 4.3 Comparison of species richness across functional groups of fishes and corals in the Great Barrier Reef (GBR), Hawaii and the Caribbean. Re-formatted from Bellwood et al. (2004) with data added for Hawaii from database described in Chapter 3.

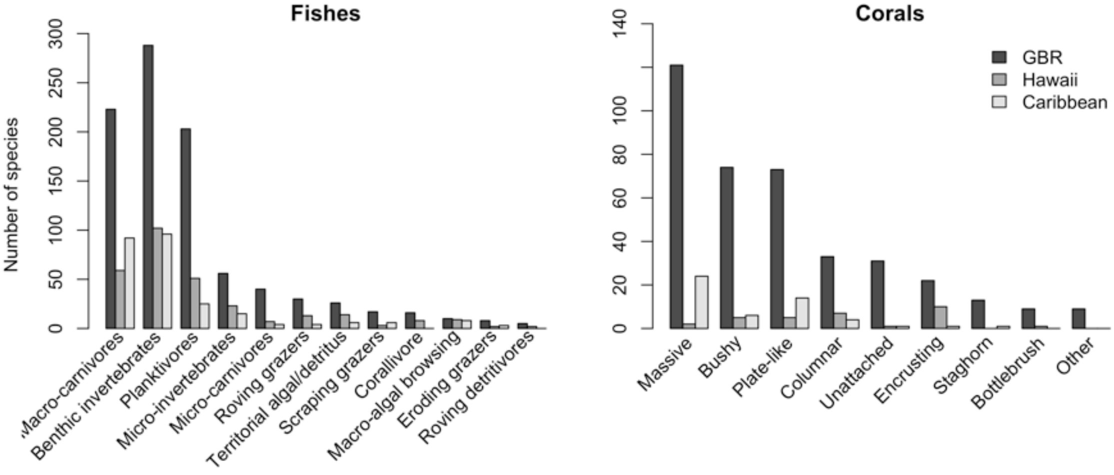


Figure 4.4 Relationships between metrics of functional diversity and coral cover in the Caribbean and Hawaii. Black lines are fitted functions from either a linear or general additive model where the relationships were significant, and grey polygons are 95% confidence intervals around the fitted function. Red circles around points indicate outliers that were removed prior to fitting models.

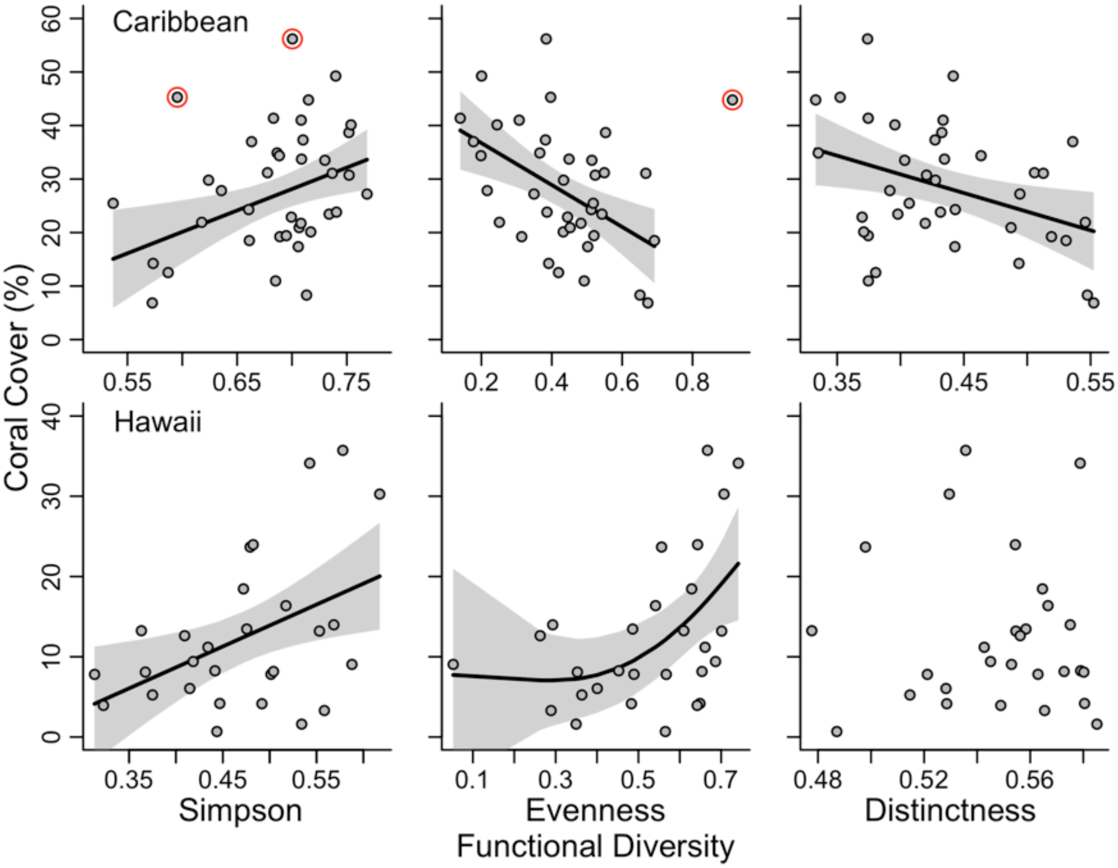


Figure 4.5 Boxplots comparing biomass by herbivore functional group between the Caribbean and Hawaii, the stars indicate significant differences between the two regions.

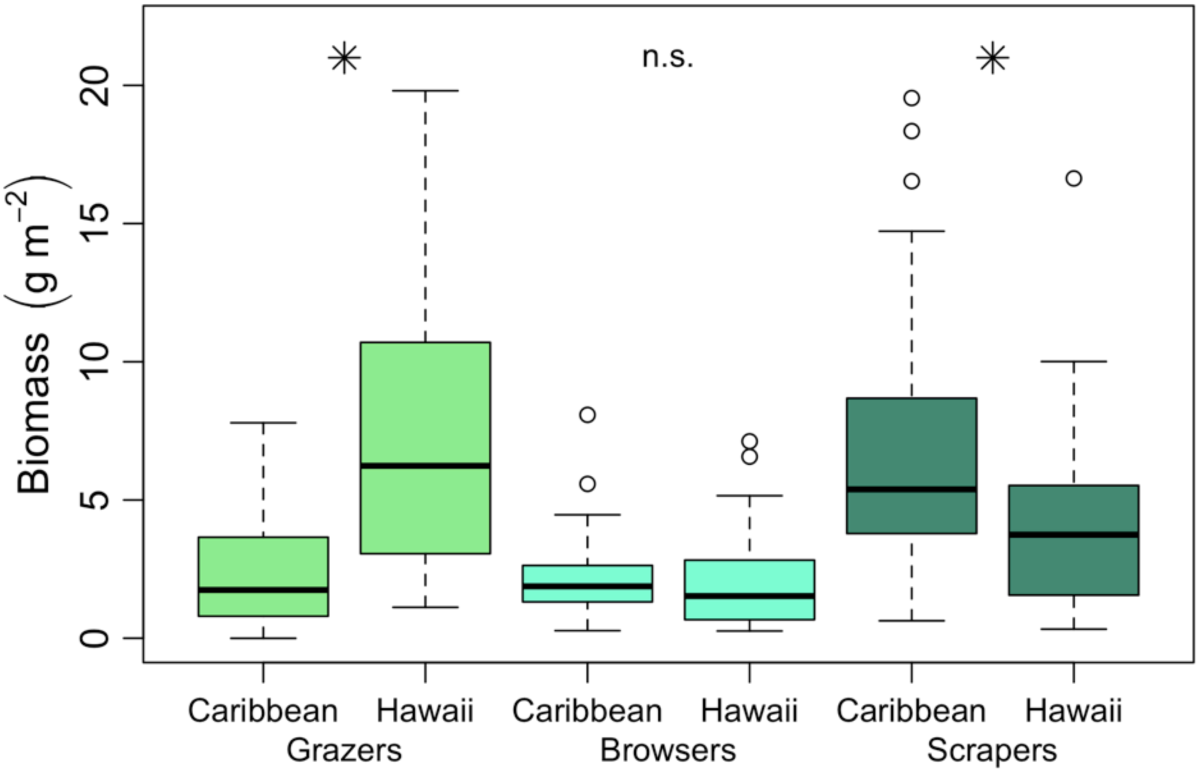


Figure 4.6 Relationships between biomass of herbivore functional groups and coral cover in the Caribbean and Hawaii (top panel re-drawn from Chapter 2). Black lines are fitted functions from either a linear or general additive model where the relationships were significant, and grey polygons are 95% confidence intervals around the fitted function. Red circles around points indicate outliers that were removed prior to fitting models.

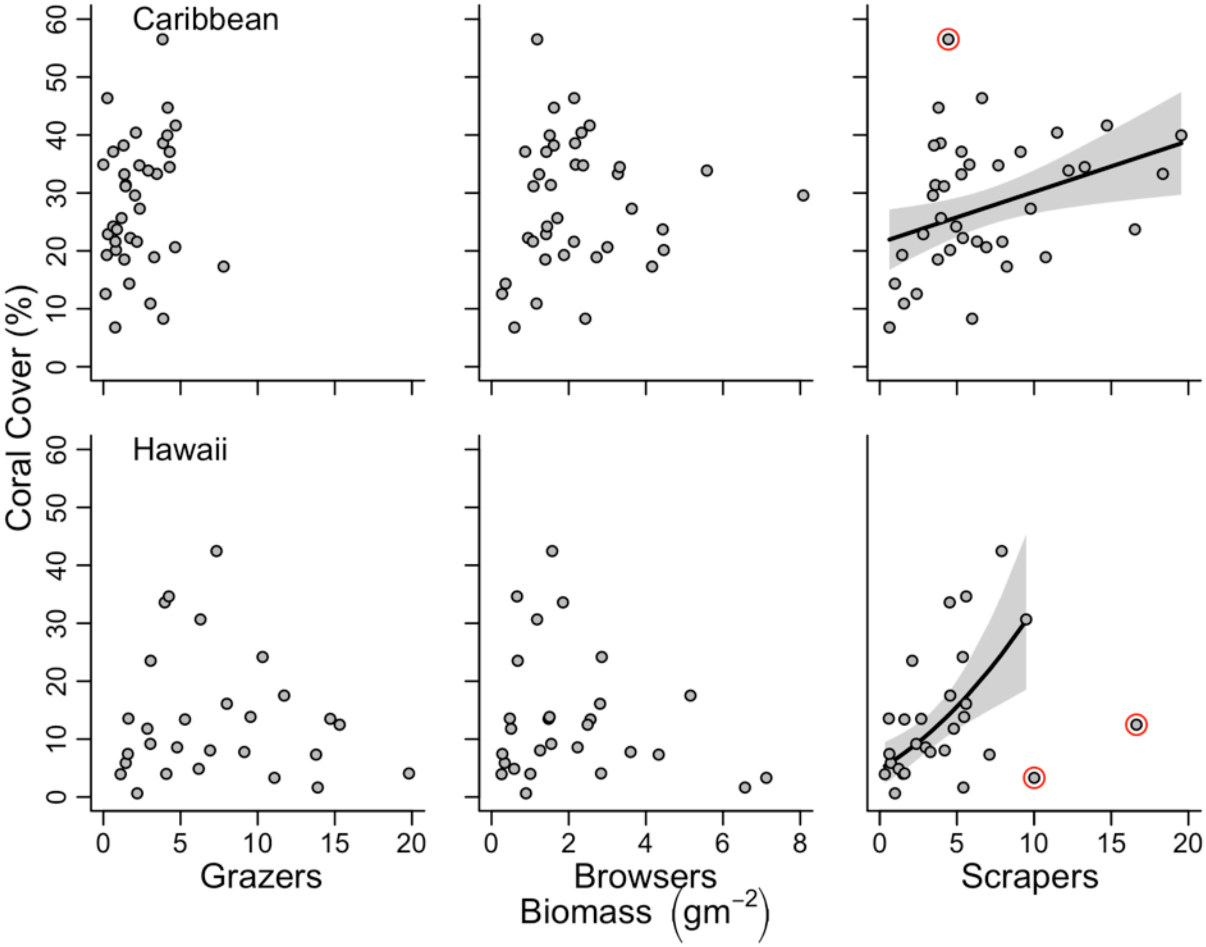
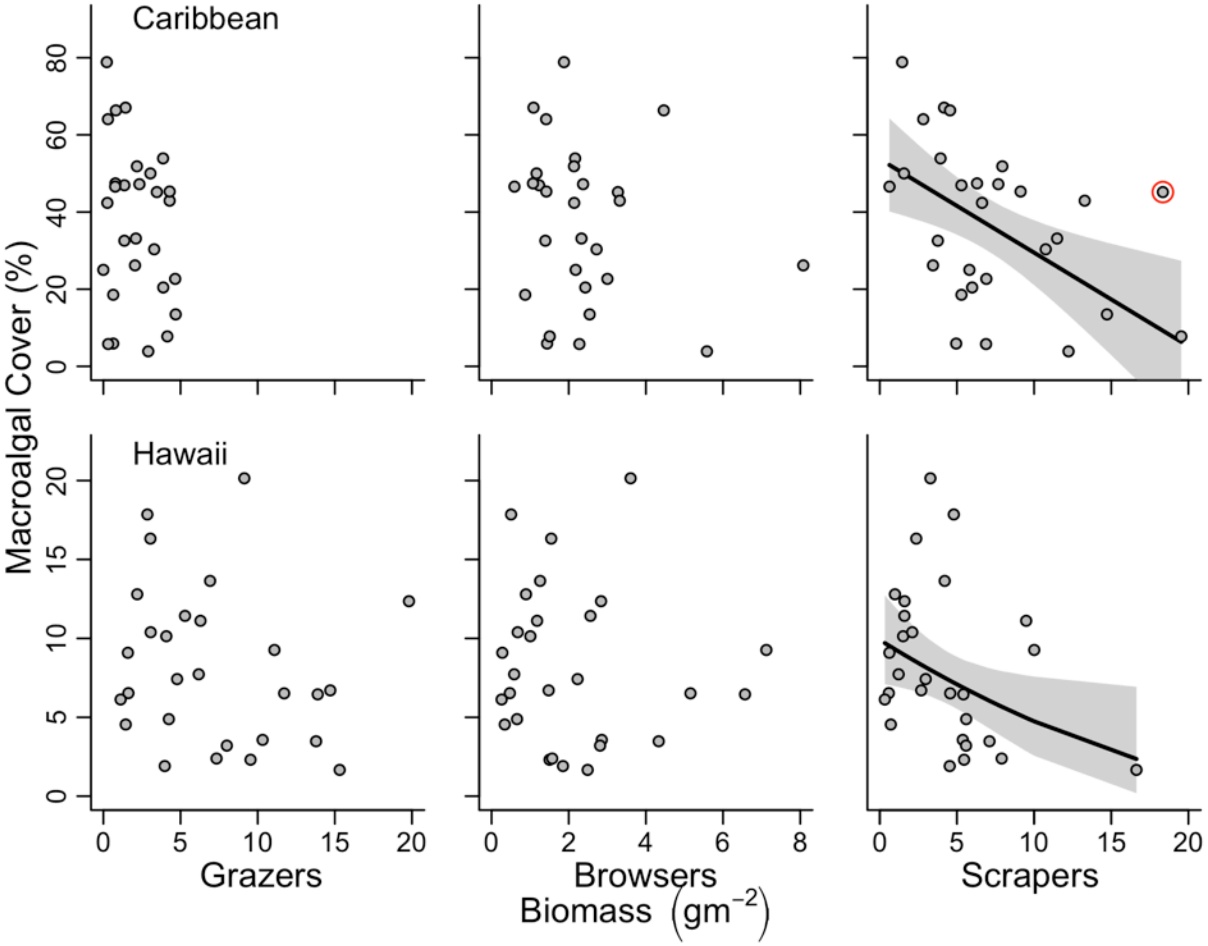


Figure 4.7 Relationships between biomass of herbivore functional groups and macroalgal cover in the Caribbean and Hawaii (top panel re-drawn from Chapter 2). Black lines are fitted functions from either a linear or general additive model where the relationships were significant, and grey polygons are 95% confidence intervals around the fitted function. Red circles around points indicate outliers that were removed prior to fitting models. Note difference in y-axis extent on top and bottom panels.



CHAPTER 5 CONCLUSION

Moving beyond simplistic dichotomies for coral reef monitoring and management

Coral reefs are among the most diverse ecosystems on earth and provide numerous benefits and services to society, including coastal protection, fisheries, medicine, tourism, and recreation (Moberg and Folke 1999). But these benefits are at risk due to increasing threats to coral reefs at local and global scales (Jackson et al. 2001; Hughes et al. 2003; Pandolfi et al. 2003; Bellwood et al. 2004). Central to mitigating threats and preserving ecosystem services is understanding how ecosystems are structured, and being able to monitor both the status of the ecosystem and the effects of management on the system. For coral reefs, past research has largely been focused on documenting regime shifts from coral to macroalgae as indicators of reef change (Hughes 1994; Mumby et al. 2007, 2013b; Bruno et al. 2009; Mumby 2009; Hughes et al. 2010; Schutte et al. 2010; Jackson et al. 2014). But, this approach ignores other important components of the ecosystem, such as fishes, and a more holistic approach is needed.

The recognition that regime shifts are complex has gained traction in other ecosystems such as the open ocean, where regime shifts have been defined as “dramatic, abrupt changes in community structure that are persistent in time, encompass multiple variables, and include key structural species” (Conversi et al. 2015). This definition emphasizes the need to include multiple components of the ecosystem when trying to understand ecosystem change, and for embracing concepts of dynamic systems that are subject to tipping points (Selkoe et al. 2015). Dynamic systems with tipping points exist because of feedbacks between components of the ecosystem, and capturing these complexities in evaluating and quantifying ecosystems is necessary (Folke 2006). Strong feedbacks exist between coral reef fishes and the benthos (Mumby and Steneck 2008). For example, declines in herbivore abundance on coral reefs could result in less bare space available for coral recruitment and therefore less coral cover over time (Bellwood et al. 2004). Thus, relying on patterns of the benthos without considering the fish assemblage limits our understanding of regime shifts on coral reefs.

This dissertation quantified fish and benthic communities together in a synthesis of community structure in the Caribbean (Chapter 2), and Hawaii (Chapter 3). Relationships were identified between multiple components of the fish community and coral and macroalgal cover in the Caribbean, which has not been done previously at such a large spatial scale. In Hawaii, I employed novel methods for quantifying reef regimes that include both fish and benthic components of the ecosystem. These regimes varied geographically, and had different relative frequencies across time. Finally, I identified common patterns in functional richness and scraper biomass with coral cover in both Hawaii and the Caribbean, which can be used as indicators of reef state given common results across such large and different biogeographic regions. Together, these results emphasize the need to consider how fish and benthic communities covary at large geographic scales to inform monitoring and management of coral reefs.

Data synthesis allowed for a new understanding of reefs

The ability to answer ecological questions at large scales was not possible until recently with the advent of ‘big data’ and ‘big science’ where large data streams are synthesized from multiple data sources (Hampton et al. 2013). As with other ecological disciplines, early studies suffered from the “quadrat” perspective, and abilities to scale up from field data were limited (Wiens 1989). Small-scale studies are also unlikely to reveal cross-scale dynamics, where processes occur within and across scales and therefore cannot be measured at one scale alone (Holling and Meffe 1996). Thus, data syntheses can provide opportunities to address questions that couldn’t be answered by one study alone, and present a new foundation for thinking about ecological questions (Peters et al. 2014). For example, studies that can analyze variation across large spatial and temporal scales are crucial for expanding the context of individual ecological studies that might be limited to sampling within a small range of environmental variables.

This dissertation was based on syntheses of primary data from two large biogeographic regions to understand patterns of coral reef fish and benthic assemblages. This approach allowed for a number of important advances that would not have been possible otherwise. In particular, the power of the method is that results from individual studies may have had contrasting results on their own, but together a synthesis emerges. Also, bringing together data from a range of locations makes it possible to assess variation along the full spectrum possible for a given variable. Both of the syntheses from this research are one of few that have used primary data to move beyond traditional meta-analysis. Additionally, no synthesis for coral reefs to date has analyzed fish and benthic data together at large geographic scales, so a comprehensive understanding of how coral reefs are structured emerged for both Hawaii and the Caribbean. Moreover, a comparison between the two regions revealed common patterns that may be emergent for coral reefs, and thus have applicability worldwide.

Summary

This dissertation investigated patterns of coral reef community composition based on both fish and benthic assemblages in the Caribbean (Chapter 2) and Hawai‘i (Chapter 3) to provide a broadened perspective of coral reef structure and indicators of change. By quantifying patterns of both fish and benthic assemblages together with large datasets at large spatial scales, new insights into how coral reefs are structured were identified. Additionally, metrics specific to hypotheses of coral reef resilience were compared across the two regions (Chapter 4). Common patterns were identified that could be emergent properties of coral reef systems given their broad applicability to two very different biogeographic regions. Finally, this dissertation relied on data synthesis that allowed for both testing the full range of variability in metrics across large geographic scales and for combining fish and benthic data at those large scales. By moving beyond quantifying the fish and benthos separately, and considering them together in a synthesis of coral reef structure, this dissertation identified important indicators of coral reefs that can be used for monitoring and management.

LITERATURE CITED

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APPENDIX A CARIBBEAN FISH DATA SOURCES

Table A.1 Data sources and metadata for fish data used in Chapter 2

Data source	**Location(s)**	**Method**	**Year(s)**	**Number replicates**	**Replicate level**
Alan Friedlander, Jim Beets, Jeff Miller, US National Park Service	St. John, USVI	Stationary count, 7.5 m radius	1998 - 2011	1008	Transects
Alan Friedlander	San Andrés, Colombia	25 x 4 m transect	2000	7	Sites
NOAA Biogeography Program	La Parguera, Puerto Rico	25 x 4 m transect	2000 - 2011	294	Transects
NOAA Biogeography Branch	USVI	25 x 4 m transect	2001 - 2011	756	Transects
USVI Coral Reef Monitoring Program	USVI	30 x 2 m transect	2003 - 2009	99	Transects
Peter Mumby, Alastair Harborne	Bahamas	30 x 2m, 30 x 4m, & 50 x 4 m transects	2002-2007	19	Sites
Marah Hardt	Cuba, Jamaica, Mexico	50 x 5 m transect	2004	84	Sites
AGRRA	Antigua, Bahamas, Belize, British Virgin Islands, Cayman Islands, Cuba, Dominican Republic, Dutch Antilles, Grenadines, Honduras, Jamaica, Mexico, Puerto Rico, St. Kitts, Turks & Caicos	30 x 2 m transect	1998 - 2011	3155	Transects
Ben Ruttenberg, Waitt Foundation	Barbuda	Stationary count, 7.5 m radius	2013	35	Sites
NOAA Southwest Fisheries Science Center	Florida Keys	Stationary count, 7.5 m radius	1998 - 2012	21	Sites
		Total	1998 - 2012	5531	

APPENDIX B CARIBBEAN FISH SPECIES

Table B.1 List of fish species included in analyses of Caribbean fishes in Chapter 2

- Predators
  - *Carangoides ruber*
  - *Cephalopholis cruentata*
  - *Cephalopholis fulva*
  - *Epinephelus itajara*
  - *Epinephelus morio*
  - *Epinephelus striatus*
  - *Lutjanus analis*
  - *Lutjanus apodus*
  - *Lutjanus cyanopterus*
  - *Lutjanus griseus*
  - *Lutjanus jocu*
  - *Lutjanus mahogoni*
  - *Lutjanus synagris*
  - *Mycteroperca acutirostris*
  - *Mycteroperca bonaci*
  - *Mycteroperca interstitialis*
  - *Mycteroperca tigris*
  - *Mycteroperca venenosa*
  - *Pterois volitans*
  - *Sphyraena barracuda*
- Browsers
  - *Kyphosus sectator*
  - *Sparisoma chrysopterum*
  - *Sparisoma radians*
  - *Sparisoma rubripinne*
- Grazers
  - *Acanthurus bahianus*
  - *Acanthurus chirurgus*
  - *Acanthurus coeruleus*
  - *Centropyge argi*
- Scrapers
  - *Scarus coelestinus*
  - *Scarus coeruleus*
  - *Scarus guacamaia*
  - *Scarus iseri*
  - *Scarus taeniopterus*
  - *Scarus vetula*
  - *Sparisoma atomarium*
  - *Sparisoma viride*
- Secondary Consumers
  - *Aluterus scriptus*
  - *Anisotremus surinamensis*
  - *Anisotremus virginicus*
  - *Balistes vetula*
  - *Bodianus rufus*
  - *Calamus bajonado*
  - *Calamus calamus*
  - *Calamus penna*
  - *Calamus pennatula*
  - *Cantherhines macrocerus*
  - *Cantherhines pullus*
  - *Canthidermis sufflamen*
  - *Chaetodon aculeatus*
  - *Chaetodon capistratus*
  - *Chaetodon ocellatus*
  - *Chaetodon sedentarius*
  - *Chaetodon striatus*
  - *Diodon holocanthus*
  - *Diodon hystrix*
  - *Epinephelus adscensionis*
  - *Epinephelus guttatus*
  - *Haemulon album*
  - *Haemulon aurolineatum*
  - *Haemulon carbonarium*
  - *Haemulon chrysargyreum*
  - *Haemulon flavolineatum*
  - *Haemulon macrostomum*
  - *Haemulon melanurum*
  - *Haemulon parra*
  - *Haemulon plumierii*
  - *Haemulon sciurus*
  - *Haemulon striatum*
  - *Halichoeres bivittatus*
  - *Halichoeres garnoti*
  - *Halichoeres radiatus*
  - *Holacanthus bermudensis*
  - *Holacanthus ciliaris*
  - *Holacanthus tricolor*
  - *Lachnolaimus maximus*
  - *Lactophrys bicaudalis*
  - *Melichthys niger*
  - *Microspathodon chrysurus*
  - *Monacanthus tuckeri*
  - *Ocyurus chrysurus*
  - *Pomacanthus arcuatus*
  - *Pomacanthus paru*
  - *Prognathodes aculeatus*
  - *Sphoeroides spengleri*
  - *Trachinotus falcatus*
  - *Xanthichthys ringens*

APPENDIX C CARIBBEAN LOCATIONS

Table C.1 Locations from Figure 2.1 and information on data available

Location	Number of datasets	Number of replicates	Size data?	Coral data?	Macroalgae data?
Antigua	1	40	Yes	Yes	No
Barbuda	1	35	Yes	Yes	Yes
Bahamas Exuma	1	6	No	No	Yes
Bahamas other	2	341	Yes	Yes	Yes
Bahamas Remote	1	7	No	Yes	Yes
Belize Atoll Leeward	1	190	Yes	Yes	Yes
Belize Central Barrier	1	188	Yes	Yes	Yes
Belize Gulf Honduras	1	87	Yes	Yes	No
Belize Inner Barrier	1	319	Yes	Yes	Yes
Belize Southern Barrier	1	20	Yes	Yes	Yes
British Virgin Islands (BVI)	1	10	Yes	Yes	Yes
Grand Cayman	1	21	Yes	Yes	No
Little Cayman	1	136	Yes	Yes	No
Colombia San Andrés	1	7	No	Yes	Yes
Cuba Jardines de la Reina	2	480	Yes	Yes	Yes
Cuba North	1	39	Yes	Yes	No
Cuba Southeast	1	294	Yes	Yes	Yes
Curacao Northwest	1	10	Yes	Yes	Yes
Dominican Republic North	1	15	Yes	Yes	No
Dominican Republic South	1	73	Yes	Yes	Yes
Florida Lower Keys	1	21	Yes	Yes	Yes
Honduras Bay Islands	1	104	Yes	Yes	Yes
Honduras Nearshore	1	99	Yes	Yes	No
Jamaica Montego Bay	2	100	Yes	Yes	Yes
Jamaica North Central	1	29	Yes	Yes	Yes
Jamaica West	1	122	Yes	Yes	Yes
Mexico Cozumel	1	29	No	Yes	Yes
Mexico NE Yucatan	1	24	Yes	Yes	No
Mexico SE Yucatan	1	3	Yes	Yes	No
Puerto Rico La Paguera	1	294	Yes	Yes	No
Puerto Rico Vieques	1	114	Yes	Yes	Yes
St Kitts & Nevis	1	147	Yes	Yes	Yes
Grenadines	1	78	Yes	Yes	No
Turks & Caicos	2	133	Yes	Yes	Yes

USVI St. John	2	1764	Yes	Yes	Yes
USVI St. Thomas	1	99	Yes	Yes	Yes
Total		**5478**			

APPENDIX D CARIBBEAN CORAL AND MACROALGAL ESTIMATES

Table D.1 Estimates of coral and macroalgal cover by location from general linear mixed effects models with a random effect of dataset, with 95% confidence intervals in brackets generated from random draws of the fixed and random effects. Cells are blank where data was not available.

Location	Coral cover (%)	Macroalgal cover (%)
Antigua	17.4 [16.5-18.4]	
Bahamas Exuma		5.9 [5.1-6.8]
Bahamas other	19.2 [18.4-20.1]	29.8 [28.1-31.8]
Bahamas Remote	21.7 [20.8-22.6]	47.7 [45.1-50.6]
Barbuda	8.4 [7.9-9]	20.5 [18.9-22.2]
Belize Atoll Leeward	30.7 [29.6-31.9]	66.9 [61.9-72]
Belize C Barrier	33.9 [32.6-35.2]	47.8 [45-50.9]
Belize Gulf Honduras	12.7 [12.1-13.3]	
Belize Inner Barrier	24.1 [23.1-25]	6.1 [5.5-6.8]
Belize S Barrier	11 [10.5-11.6]	49.5 [46.5-52.7]
BVI	41.1 [39.5-42.6]	13.7 [12.6-14.9]
Colombia San Andres	37.5 [35.9-39]	52.6 [49.6-55.5]
Cuba Jardines	34.5 [33.2-35.9]	43 [40.8-45.5]
Cuba North	56.8 [54.8-58.7]	
Cuba Southeast	41.1 [39.5-42.5]	33.6 [31.5-35.8]
Curacao Northwest	40.3 [39-41.6]	7.7 [7-8.4]
DR North	45.6 [43.7-47.6]	
DR South	35.3 [33.9-36.9]	25.4 [23.4-27.8]
Florida Lower Keys	6.9 [6.4-7.4]	45.8 [43-49]
Grand Cayman	23.9 [23-24.8]	
Grenadines	38.7 [37.1-40.3]	
Honduras Bay Islands	37 [35.6-38.6]	46.6 [43.6-49.4]
Honduras Nearshore	21.9 [20.9-22.8]	
Jamaica MB	23.1 [22.1-24]	63.8 [59.9-67.8]
Jamaica W	19.8 [18.9-20.7]	67.6 [63.2-72.1]
Jamica NC	19.3 [18.4-20.2]	79.4 [73.7-85.4]
Little Cayman	27.3 [26.1-28.5]	
Mexico Cozumel	30.2 [29-31.6]	26.5 [24.9-28.3]
Mexico NE Yucatan	14.4 [13.7-15.1]	
Mexico SE Yucatan	25.6 [24.5-26.8]	
Puerto Rico La Paguera	31.3 [30.1-32.5]	
Puerto Rico Vieques	33.8 [32.4-35.2]	4.1 [3.6-4.6]
St Kitts & Nevis	21.6 [20.6-22.7]	51.7 [48.5-54.9]
Turks & Caicos	37.4 [36-39]	18.3 [16.6-20.2]

USVI St John	18.3 [17.6-19.1]	32.5 [30.9-34.7]
USVI St. Thomas	21 [20.1-22]	23.2 [21.6-24.8]
Antigua	17.4 [16.5-18.4]	
Bahamas Exuma		5.9 [5.1-6.8]
Bahamas other	19.2 [18.4-20.1]	29.8 [28.1-31.8]

APPENDIX E CARIBBEAN BIOMASS ESTIMATES

Table E.1 Estimates of biomass by trophic levels by location from general linear mixed effects models with a random effect of dataset, with 95% confidence intervals in brackets generated from random draws of the fixed and random effects.

Location	Predators	Sec. Cons.	Grazers	Browsers	Scrapers
Antigua	3.3 [2.9-3.8]	11.6 [10.7-12.5]	7.5 [6.9-8.1]	4.1 [3.8-4.4]	7.9 [7.3-8.6]
Bahamas Exuma	27 [24.6-29.5]	27.9 [25.6-30.4]	0.3 [0.2-0.4]	2.3 [2.1-2.6]	6.8 [6.3-7.5]
Bahamas other	1.6 [1.3-1.8]	6.5 [6-7.1]	3.2 [2.9-3.4]	2.7 [2.5-3]	10.7 [9.9-11.5]
Bahamas Remote	5 [4.5-5.6]	2.4 [2.1-2.7]	0.8 [0.7-0.9]	1.1 [0.9-1.2]	6.3 [5.7-6.8]
Barbuda	3.1 [2.8-3.6]	2 [1.8-2.3]	4 [3.7-4.4]	2.5 [2.3-2.8]	6.1 [5.6-6.6]
Belize Atoll Leeward	2 [1.8-2.3]	5 [4.5-5.5]	1.5 [1.3-1.6]	1.1 [1-1.3]	4.3 [3.9-4.7]
Belize C Barrier	1.7 [1.5-2]	6.7 [6.2-7.3]	1.4 [1.3-1.6]	1.2 [1.1-1.4]	5.2 [4.8-5.6]
Belize Gulf Honduras	0.9 [0.7-1.1]	2.5 [2.3-2.8]	0.1 [0-0.2]	0.3 [0.2-0.4]	2.3 [2.1-2.5]
Belize Inner Barrier	2.5 [2.2-2.9]	7.5 [6.9-8.2]	0.6 [0.5-0.7]	1.4 [1.2-1.5]	4.9 [4.5-5.4]
Belize S Barrier	0.4 [0.3-0.5]	0.8 [0.7-1]	2.9 [2.6-3.2]	1.1 [1-1.3]	1.6 [1.4-1.8]
BVI	10.7 [9.6-12.1]	6.4 [5.9-7]	4.6 [4.2-4.9]	2.5 [2.3-2.8]	14.2 [13.1-15.3]
Colombia San Andres	7.2 [6.4-8.1]	10.2 [9.4-11.2]	3.7 [3.4-4.1]	2.2 [2-2.4]	4 [3.6-4.4]
Cuba Jardines	23.4 [21.3-25.6]	19.3 [17.9-21.1]	4.2 [3.9-4.6]	3.2 [3-3.5]	12.8 [11.8-13.8]
Cuba North	13.3 [12.2-14.5]	16.4 [15.2-17.8]	3.8 [3.5-4.1]	1.2 [1-1.3]	4.4 [4.1-4.9]
Cuba Southeast	23.4 [21.3-25.4]	15.9 [14.7-17.3]	2.1 [2-2.3]	2.4 [2.2-2.6]	11.6 [10.7-12.4]
Curacao Northwest	16.9 [15.4-18.8]	14.3 [13.3-15.6]	4.3 [3.9-4.6]	1.5 [1.3-1.7]	19.4 [18.1-21]
DR North	1.6 [1.3-1.8]	1.7 [1.5-2]	4.1 [3.7-4.4]	1.6 [1.4-1.8]	3.8 [3.5-4.2]
DR South	1.2 [1-1.4]	1.9 [1.7-2.1]	0 [-0.1-0.1]	2.2 [2-2.5]	5.9 [5.4-6.4]
Florida Lower Keys	5.7 [5-6.4]	5.9 [5.4-6.4]	0.8 [0.7-0.9]	0.6 [0.5-0.7]	0.6 [0.5-0.8]
Grand Cayman	6.6 [5.9-7.3]	8.9 [8.2-9.7]	0.9 [0.8-1]	4.4 [4.1-4.8]	16.8 [15.5-18.2]
Grenadines	4.5 [4-5]	5.4 [4.9-5.9]	1.2 [1.1-1.4]	1.7 [1.5-1.8]	3.5 [3.2-3.8]
Honduras Bay Islands	1.4 [1.2-1.7]	12.6 [11.5-13.6]	4.2 [3.8-4.5]	1.5 [1.3-1.7]	9.5 [8.8-10.3]
Honduras Nearshore	1.8 [1.5-2]	5.2 [4.7-5.7]	1.7 [1.5-1.9]	1 [0.8-1.1]	5.3 [4.9-5.7]
Jamaica MB	1.3 [1.2-1.6]	2.2 [2-2.5]	0.3 [0.2-0.4]	1.4 [1.3-1.6]	2.9 [2.6-3.2]
Jamaica W	2.9 [2.6-3.3]	2.1 [1.9-2.4]	0.8 [0.7-0.9]	4.5 [4.2-4.9]	4.6 [4.2-5]
Jamica NC	1.2 [1-1.4]	1.6 [1.4-1.9]	0.2 [0.2-0.3]	1.9 [1.7-2.1]	1.4 [1.3-1.6]
Little Cayman	6.1 [5.5-6.8]	6.6 [6.1-7.2]	2.3 [2-2.5]	3.9 [3.5-4.2]	9.7 [8.9-10.5]
Mexico Cozumel	18 [16.2-20.1]	35.3 [32.6-38.1]	2 [1.8-2.2]	8 [7.5-8.7]	3.5 [3.2-3.9]
Mexico NE Yucatan	0.8 [0.6-0.9]	3 [2.7-3.4]	1.6 [1.5-1.8]	0.4 [0.3-0.5]	1 [0.9-1.1]
Mexico SE Yucatan	0.7 [0.5-0.9]	2.8 [2.5-3.2]	1.2 [1.1-1.4]	1.7 [1.5-1.9]	3.9 [3.5-4.4]
Puerto Rico La Paguera	1.3 [1.1-1.5]	4.1 [3.7-4.5]	1.4 [1.3-1.6]	1.6 [1.4-1.7]	3.7 [3.4-4]

Puerto Rico Vieques	1.5 [1.2-1.7]	6.3 [5.8-6.8]	2.9 [2.7-3.2]	5.6 [5.2-6.1]	12.3 [11.4-13.3]
St Kitts & Nevis	1.9 [1.7-2.3]	4 [3.7-4.4]	2.2 [2-2.4]	2.1 [1.9-2.4]	8.1 [7.4-8.9]
Turks & Caicos	7.1 [6.5-7.8]	9.1 [8.4-10]	0.6 [0.5-0.7]	0.9 [0.8-1.1]	5.1 [4.7-5.5]
USVI St John	2.9 [2.5-3.2]	4.7 [4.3-5.2]	1.4 [1.2-1.5]	1.4 [1.3-1.5]	3.8 [3.5-4.1]
USVI St. Thomas	2.4 [2.1-2.8]	8.9 [8.2-9.8]	4.7 [4.3-5.1]	3 [2.7-3.3]	6.9 [6.4-7.5]
Antigua	3.3 [2.9-3.8]	11.6 [10.7-12.5]	7.5 [6.9-8.1]	4.1 [3.8-4.4]	7.9 [7.3-8.6]
Bahamas Exuma	27 [24.6-29.5]	27.9 [25.6-30.4]	0.3 [0.2-0.4]	2.3 [2.1-2.6]	6.8 [6.3-7.5]
Bahamas other	1.6 [1.3-1.8]	6.5 [6-7.1]	3.2 [2.9-3.4]	2.7 [2.5-3]	10.7 [9.9-11.5]

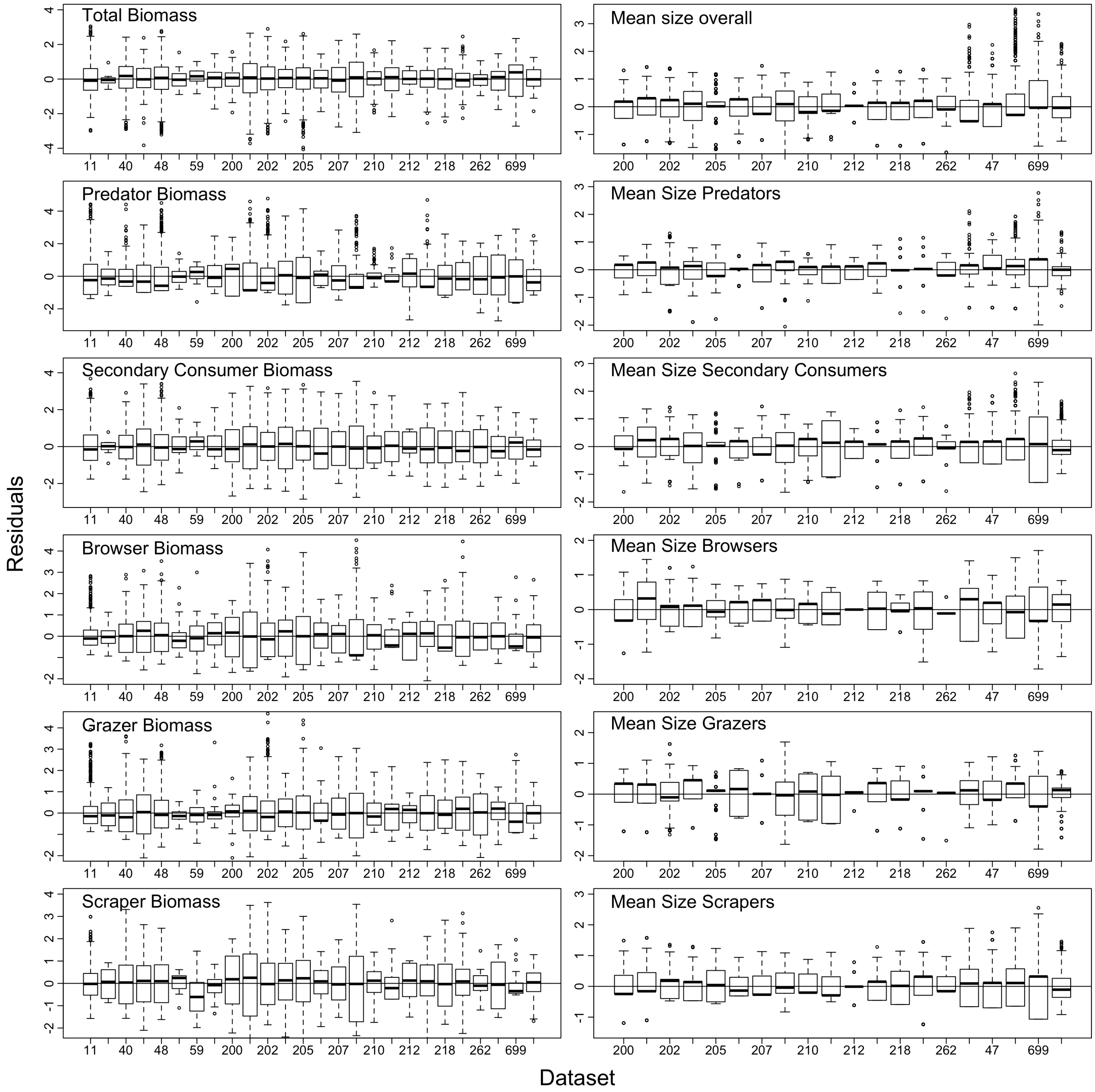
APPENDIX F CARIBBEAN SIZE ESTIMATES

Table F.1 Estimates of mean size overall and by trophic levels by location from general linear mixed effects models with a random effect of dataset, with 95% confidence intervals in brackets generated from random draws of the fixed and random effects.

Location	Overall	Predators	Sec. Cons.	Grazers	Browsers	Scrapers
Antigua	14.6 [14.1-15.1]	23.3 [22.6-24.1]	19 [18.3-19.7]	12.6 [12.2-13]	13.3 [12.8-13.9]	12.5 [12-12.9]
Bahamas other	13.1 [12.6-13.6]	21.4 [20.8-22.1]	14 [13.5-14.7]	13.1 [12.7-13.5]	12.9 [12.5-13.3]	11.5 [11.1-11.9]
Barbuda	11.4 [11-11.8]	27.2 [26.3-28]	9 [8.7-9.3]	13.4 [12.9-13.8]	16.5 [16-17.1]	11 [10.6-11.4]
Belize Atoll Leeward	13.8 [13.3-14.3]	16 [15.6-16.5]	13.6 [13-14.1]	12.2 [11.9-12.6]	15.5 [14.9-16.1]	14.4 [13.9-14.9]
Belize C Barrier	13.8 [13.4-14.3]	16.7 [16.3-17.3]	13.6 [13.1-14.1]	12.5 [12.1-13]	16.3 [15.7-16.9]	14 [13.5-14.6]
Belize Gulf Honduras	14.1 [13.6-14.6]	14.8 [14.4-15.3]	15.5 [14.9-16.1]	14.1 [13.6-14.6]	18.2 [17.4-18.9]	12.9 [12.5-13.4]
Belize Inner Barrier	14 [13.5-14.5]	16.3 [15.8-16.7]	13.6 [13.1-14.2]	11 [10.7-11.4]	16.1 [15.5-16.7]	14.7 [14.1-15.2]
Belize S Barrier	13.4 [12.9-13.9]	17.5 [16.9-18.1]	15.2 [14.7-15.8]	11.6 [11.2-12]	16.3 [15.8-17]	15.5 [14.9-16.1]
BVI	19.1 [18.4-19.8]	21.3 [20.7-22]	18.5 [17.8-19.3]	16.9 [16.3-17.4]	19.6 [18.9-20.4]	20.4 [19.6-21.1]
Cuba Jardines	17.2 [16.6-17.7]	21.7 [21.1-22.4]	17.3 [16.6-17.9]	15.6 [15.1-16.1]	21.4 [20.6-22.4]	16.9 [16.2-17.5]
Cuba North	14.8 [14.4-15.4]	17.5 [17-18]	15 [14.5-15.6]	14 [13.6-14.5]	19.5 [18.8-20.3]	13.6 [13.1-14.2]
Cuba Southeast	16.5 [15.9-17.1]	21.6 [21-22.3]	16.3 [15.7-16.9]	16 [15.5-16.6]	18.5 [17.8-19.2]	16.1 [15.5-16.7]
Curacao Northwest	17.2 [16.6-17.8]	24.5 [23.8-25.2]	14.9 [14.4-15.5]	16.6 [16.1-17.2]	17.5 [16.9-18.1]	17.6 [17-18.2]
DR North	10.4 [10.1-10.7]	17.2 [16.7-17.8]	15.6 [14.9-16.2]	8.2 [8-8.5]	15.4 [14.8-16]	11.3 [11-11.8]
DR South	13.7 [13.2-14.2]	17 [16.5-17.5]	14.4 [13.9-14.9]	8.6 [8.4-8.9]	14.2 [13.7-14.8]	13.3 [12.8-13.9]
Florida Lower Keys	7.3 [7.1-7.6]	12 [11.7-12.4]	6.5 [6.2-6.7]	10 [9.6-10.3]	9.4 [9-9.8]	5.4 [5.2-5.6]
Grand Cayman	16.4 [15.9-17]	24.3 [23.5-25]	21.9 [21.1-22.8]	11.5 [11.2-11.9]	15.4 [14.8-16]	15 [14.5-15.6]
Grenadines	12.7 [12.2-13.2]	14.9 [14.5-15.3]	12.9 [12.4-13.5]	9.9 [9.6-10.2]	13.4 [13-13.9]	12.8 [12.4-13.2]
Honduras Bay Islands	20.2 [19.5-21]	27 [26.1-27.9]	19.3 [18.5-20]	19 [18.3-19.7]	22.1 [21.3-23]	21.9 [21.1-22.7]
Honduras Nearshore	16.1 [15.5-16.7]	28.2 [27.2-29]	16.8 [16.3-17.5]	10.3 [10-10.6]	27.8 [26.9-28.9]	18.5 [17.8-19.1]
Jamaica MB	11.9 [11.5-12.3]	11.8 [11.4-12.1]	12.8 [12.3-13.3]	9.5 [9.2-9.8]	12.8 [12.3-13.3]	12 [11.6-12.5]
Jamaica W	12.3 [11.9-12.8]	16 [15.5-16.4]	13.6 [13.1-14.2]	9.2 [9-9.5]	15 [14.4-15.6]	12 [11.5-12.4]
Jamica NC	12.2 [11.8-12.6]	15.8 [15.3-16.3]	12.9 [12.4-13.4]	9.1 [8.9-9.4]	14.4 [13.9-15]	11.8 [11.4-12.3]
Little Cayman	15.9 [15.3-16.5]	24.3 [23.6-25]	17 [16.3-17.7]	11.5 [11.2-11.9]	15.7 [15.1-16.3]	15.6 [15-16.1]
Mexico NE Yucatan	11.4 [10.9-11.8]	15.9 [15.4-16.4]	11.6 [11.2-12]	10.2 [9.8-10.5]	14.9 [14.4-15.5]	13 [12.5-13.5]
Mexico SE Yucatan	12.6 [12.2-13]	17.6 [16.9-18.4]	11.8 [11.3-12.3]	9.9 [9.5-10.2]	19.7 [18.8-20.6]	15.9 [15.4-16.6]
Puerto Rico La Paguera	7.8 [7.6-8.1]	16.7 [16.2-17.3]	8.2 [7.9-8.5]	12.9 [12.4-13.3]	11 [10.6-11.4]	8.7 [8.4-9]
Puerto Rico Vieques	15.3 [14.7-15.9]	22 [21.4-22.7]	16.3 [15.7-16.9]	12.5 [12.1-12.9]	17.5 [16.9-18.2]	15.2 [14.7-15.8]
St Kitts & Nevis	14.4 [13.9-14.9]	17.1 [16.6-17.7]	13.3 [12.7-13.8]	15.9 [15.4-16.4]	16.8 [16.1-17.4]	13.1 [12.7-13.5]
Turks & Caicos	15.1 [14.5-15.6]	17.7 [17.2-18.3]	14.8 [14.2-15.4]	11.7 [11.4-12.1]	18.2 [17.5-18.9]	17.2 [16.7-17.8]
USVI St John	6.4 [6.1-6.6]	17.4 [16.9-17.9]	7.4 [7.2-7.7]	10.5 [10.2-10.8]	10 [9.7-10.4]	8.5 [8.2-8.8]
USVI St. Thomas	9.3 [8.9-9.6]	16.5 [16.1-17]	8.4 [8.1-8.7]	11.9 [11.5-12.3]	14.4 [13.9-15]	9.1 [8.8-9.4]

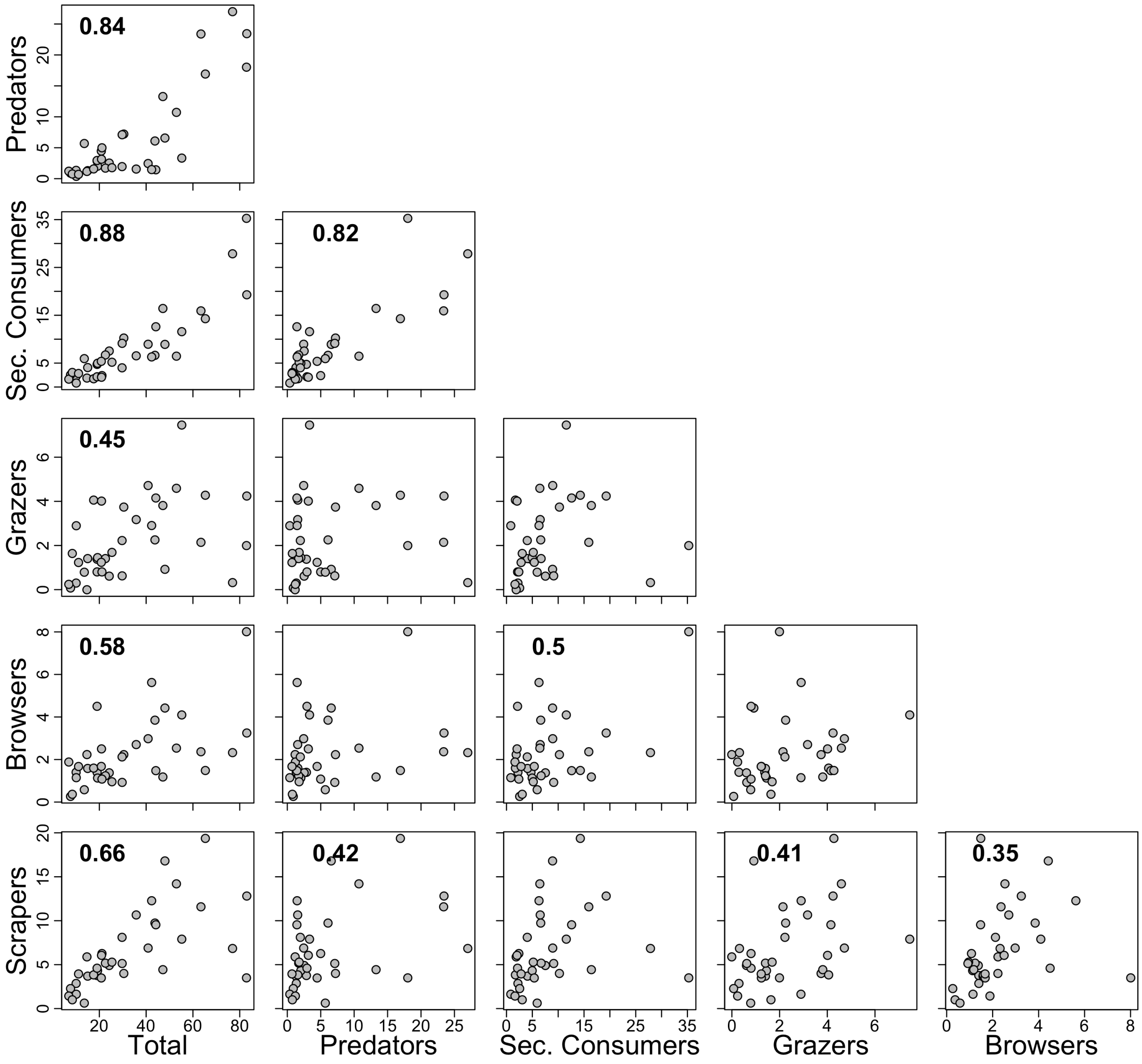
APPENDIX G RANDOM EFFECTS CARIBBEAN BIOMASS

Figure G.1 Distribution of residuals for random effect of dataset for each fish variable. Numbers along bottom are associated with DatasetID that is included in accompanying dataset.



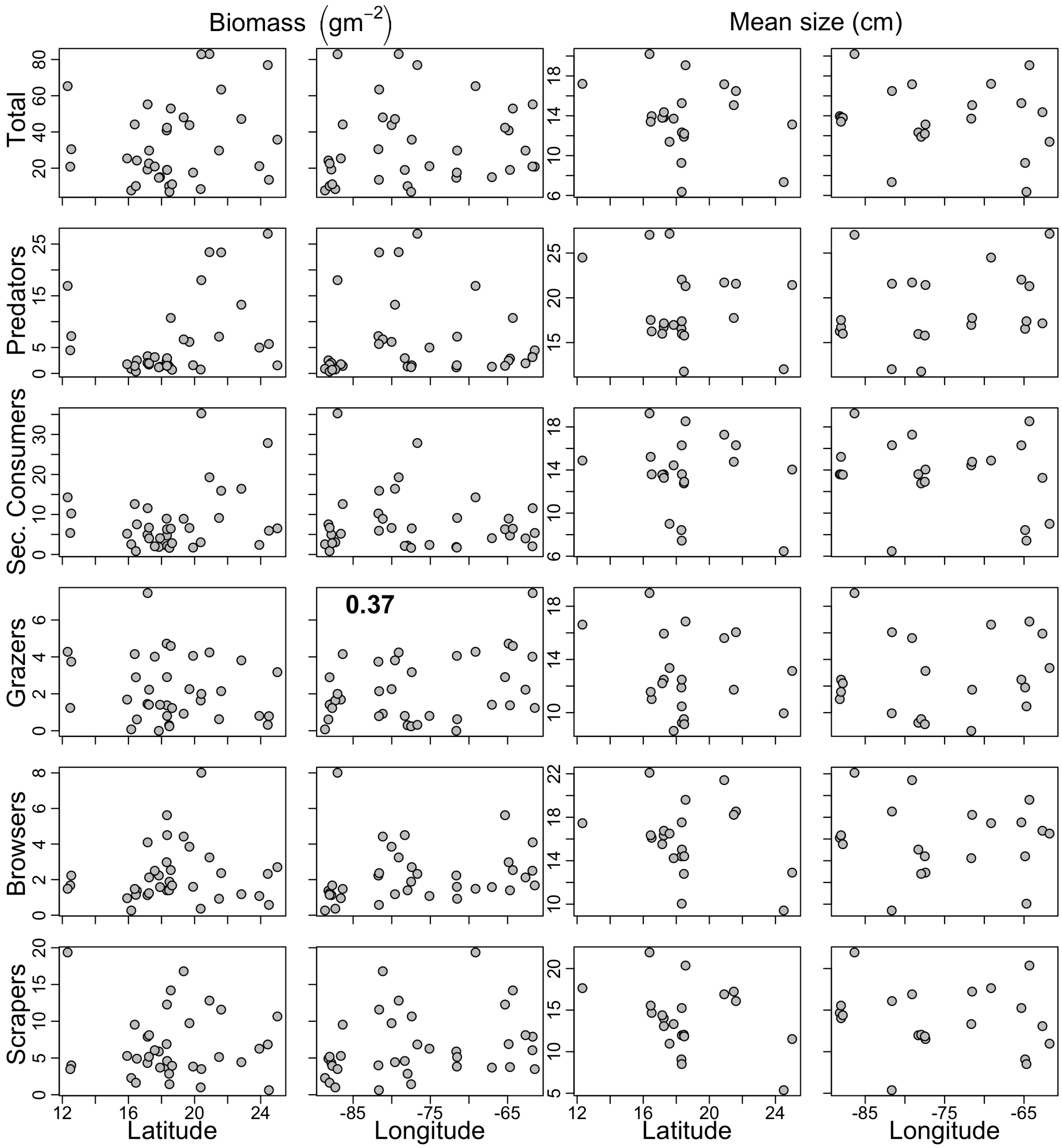
APPENDIX H CARIBBEAN BIOMASS CORRELATIONS

Figure H.1 Correlations for each combination of total and functional group biomass (g m^{-2}); bolded numbers in upper left corner are Pearson's product-moment correlations and only significant correlations are shown.



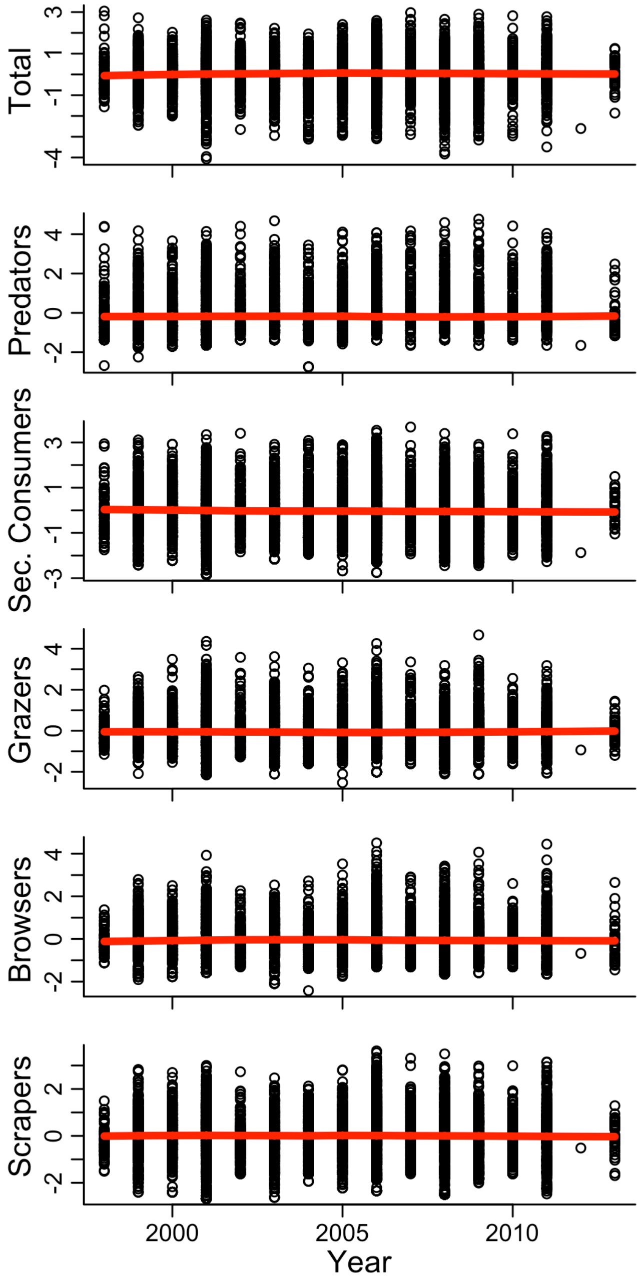
APPENDIX I CARIBBEAN LATITUDE CORRELATIONS

Figure I.1 Correlations for latitude and longitude compared to total and functional group biomass (g m^{-2}) (left) and mean size (right); bolded numbers in upper left corner are Pearson's product-moment correlations and only significant correlations are shown.



APPENDIX J CARIBBEAN RESIDUALS VERSUS TIME

Figure J.1 Residuals from general linear mixed effects models of total and functional group biomass compared with year, and lowess smoother (red line) showing no trend across time.



APPENDIX K HAWAII DATASET DETAILS

Data from multiple sources were compiled into a standardized format from large scale monitoring programs in the Main Hawaiian Islands (Table K.1).

Table K.1 Description of datasets used in analyses of reef regimes. SPC is stationary point count method, and LPI is line-point-intercept method.

Dataset	Fish method	Benthic method	N	Year range	Depth range (m)
Coral Reef Assessment and Monitoring Program - University of Hawaii					
	Belt	video	52	1999 - 2002	1.0 - 13.0
		photo-quad	46	2003 - 2012	1.0 - 13.0
NOAA Coral Reef Ecosystem Program*					
	Belt	LPI or photo-quad	117	2005 - 2008	7.5 - 17.0
	SPC	photo-quad	708	2008 - 2013	0.0 - 30.0
Division of Aquatic Resources					
	Belt	photo-quad	512	2004 - 2012	0.0 - 15.2
	WHAP Belt	photo-quad	122	2003 - 2013	1.5 - 15.0
Fisheries Ecology Research Lab - University of Hawaii					
	Belt	quadrat or photo-quad	242	1993 - 2013	0.0 - 16.7
NOAA Fish Habitat Utilization Study					
	Belt	quadrat	766	2002 - 2008	0.5 - 32.0
National Park Service					
	Belt	photo-quad	174	2004 - 2013	11.0 - 21.4
The Nature Conservancy Hawaii Marine Program					
	Belt	photo-quad	606	2009 - 2013	1.0 - 20.7
			3345	1993 - 2013	0.0 - 30.0

* Coral Reef Ecosystem Program; Pacific Islands Fisheries Science Center (2013). National Coral Reef Monitoring Program: Stratified Random surveys (StRS) of Reef Fish, including Benthic Estimate Data of the U.S. Pacific Reefs since 2007. NOAA National Centers for Environmental Information. Unpublished Dataset. https://inport.nmfs.noaa.gov/inport/item/24447

APPENDIX L HAWAII SPATIAL SCALE ANALYSIS

Before conducting analyses of reef regimes, semivariance and lacunarity analyses were used to assess the appropriate spatial scale to conduct the analysis. The goal was both to avoid violating assumptions of statistical independence, and to optimize our ability to detect patterns in community level data (Turner et al. 2001).

Semivariance

We analysed semivariance to determine the spatial scale at which spatial dependence in the raw data could be detected (Meisel and Turner 1998). In geostatisical analysis, spatial variance, which follows the theoretical form:

$$\gamma(h) = \frac{1}{2n(h)}\sum_{i=1}^{n}[x_i - z(x_i + h)]^2$$

where x_i is the value of the observed variable at observation i and $n(h)$ is the number of observations located within h distance for each other, is plotted against lag distance h to construct a spatial variogram (Dale and Fortin 2014). The empirical variogram can be constructed from the sampled data and compared to the theoretical form to estimate the distance at which spatial structure is detected. The distance where the semivariance asymptotes is referred to as the 'sill' and the corresponding value of h represents the 'practical range' where the variable of interest is no longer spatially autocorrelated (Dale and Fortin 2014).

For each variable used in the analysis, empirical semivariograms were constructed with the *variog* function in the *geoR* package in R (Diggle and Ribeiro Jr 2007) with 25 meter lag distances and a maximum distance of 1000 meters. This lag distance was chosen as the common length of the individual transects used in the analysis, and the maximum distance was used because the focus of the analysis was on observations that are close together and since spatial variance is greatest at short distances. Semivariance assumes that data are stationary, with no apparent spatial gradient, and are normally distributed. To meet this assumption of normality all variables were fourth-root transformed. Distances were calculated by converting geographic coordinates to *xy* coordinates based on an Albers Equal Area projection customized for the Hawaiian Archipelago with a central meridian of 167º and standard parallels of 26.86 minus the latitude and 20.5 minus the longitude where the latitude origin was set to 20º. Theoretical semivariograms were estimated with the *variofit* function in the *geoR* package, and assumed a spherical model with the following form:

$$\gamma(h) = 1 - 1.5\left(\frac{h}{\phi}\right) + 0.5\left(\frac{h}{\phi}\right)^3$$

where ϕ is the range parameter, and is only defined when $h > \phi$. Other bounded theoretical forms were also fit and spherical model was retained based on visual inspection of the fit. From the fitted variogram the practical range was estimated as the distance where semivariance was equal to 95% of the sill (Ribeiro Jr and Diggle 2001).

For all fish variables no levelling off of semivariance was found, and therefore no spatial dependence was observed. Benthic variables had a range of estimated spatial dependence ranging from 83 to 242 meters (Figure L.1).

Lacunarity

To further determine the appropriate spatial scale to investigate reef regimes, we also considered how the distribution of spatial patterning in the data changed with spatial scale. Lacunarity is a scale dependent estimate describing the distribution of deviation from translational invariance (Plotnick et al. 1993). In other words, it is a measure of how variable the texture of a geometric object is, and can be used to describe structure in spatial data. Lacunarity was quantified as:

$$L(s) = 1 + \frac{var(\mu(s))}{mean(\mu(s)^2)}$$

where a sequence of mean values for each variable, $\mu(s)$, was calculated for each window size s, which ranged from 25 to 2000 by 10 meter bins.

Lacunarity was plotted against distance (meters) for each variable and the distance at which the first derivative of lacunarity crossed zero was inspected. If spatial pattern is evident, we expect that lacunarity would increase before levelling off at the scale that maximizes the ratio of mean and variance. Thus, we calculated the distance at which the first derivative crossed zero. For all variables except coral cover we did not observe an initial increase in lacunarity. For coral cover, lacunarity reached an asymptote at 140 meters (Figure L.2).

Summarizing data by spatial grouping

Based on the maximum distance for which we detected spatial autocorrelation to be a concern we determined a minimum distance between transects (242 meters), and calculated means for groups of points. In ArcGIS we added the point layer to a topology with a spatial cluster tolerance of 70 meters. This uses a 70 meter by 70 meter moving window to snap point locations together, where the maximum distance a coordinate could move to the centroid of a cluster is $\sqrt{2} * 70$m. In practice, this results in varying sizes of clusters: the maximum distance between any two points in a cluster was 300 meters, and the minimum distance between any two cluster centers was 130 meters.

Figure L.1 Semivariograms for benthic variables. Open circles and black lines are empirical semivariograms at 25 meter lag distances. Red lines are theoretical semivariograms based on a spherical model, and the vertical dashed lines corresponds to the estimated practical range in meters where the semivariance is 95% of the sill.

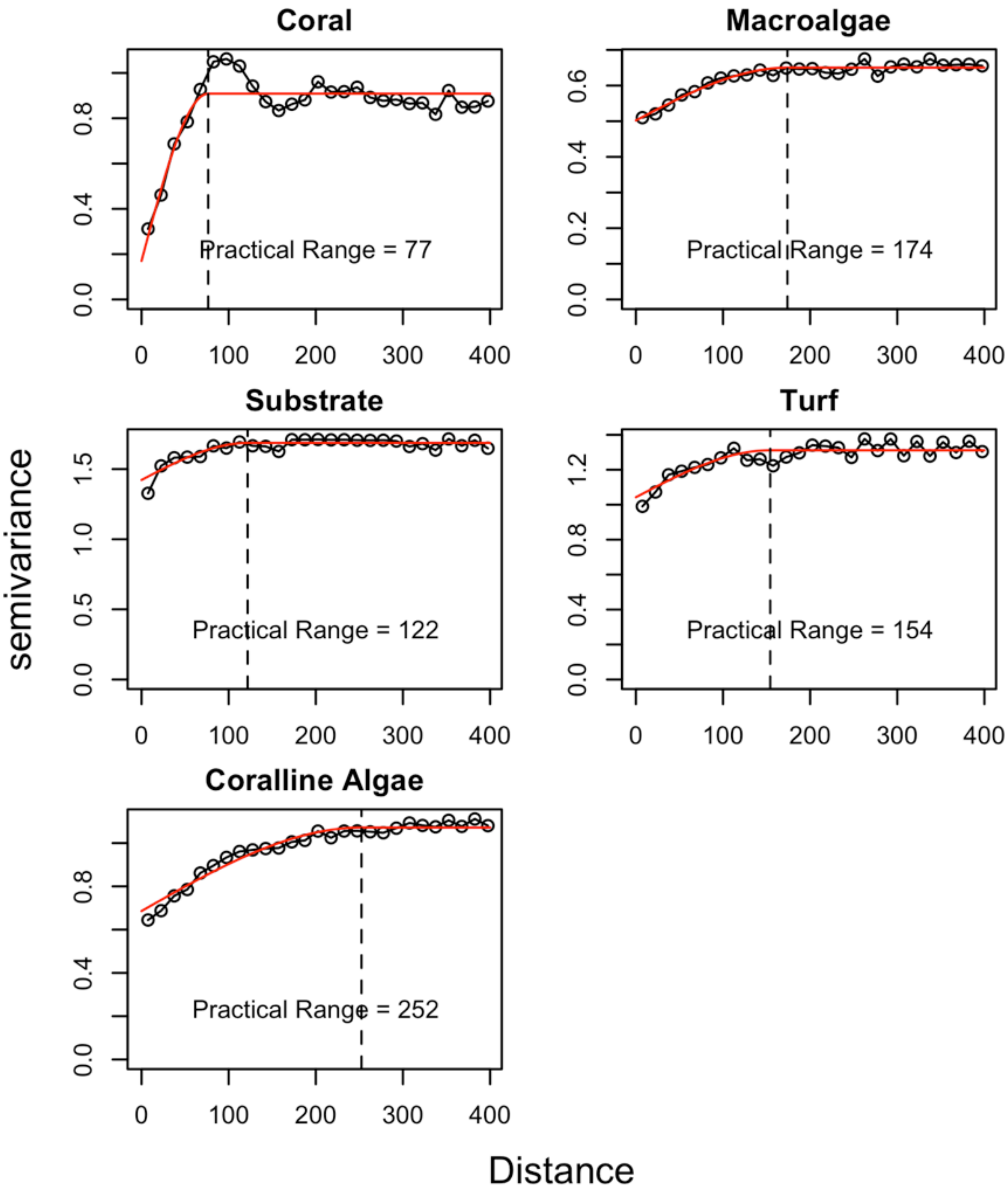
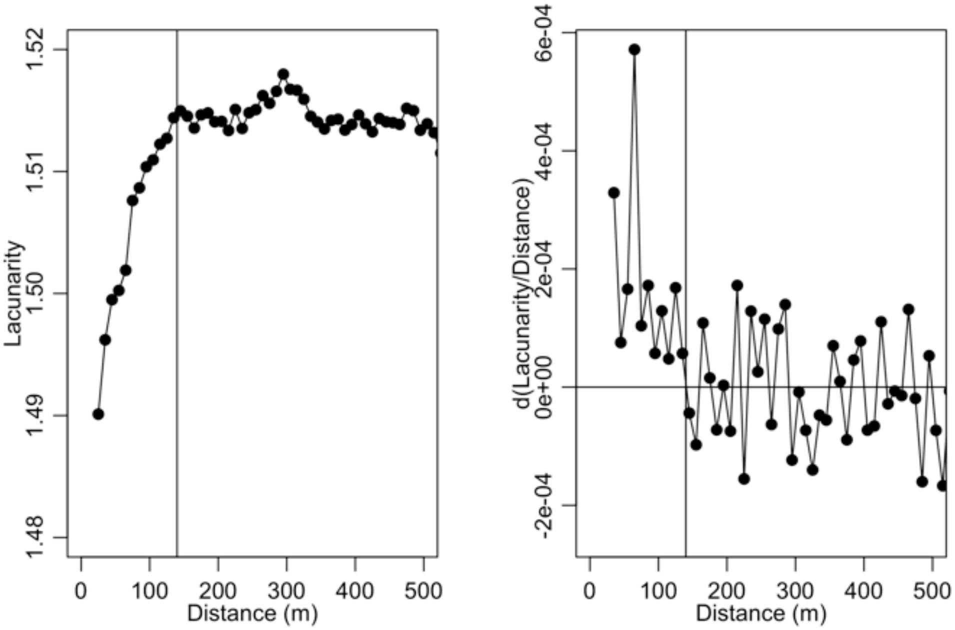


Figure L.2 Lacunarity as a function of distance (meters) (A), and first derivative of lacunarity as a function of distance (B) for coral cover.



APPENDIX M HAWAII FISH SPECIES BY FUNCTIONAL GROUP

Table M.1 Fish species used in analysis of Hawaiian reef regimes in Chapter 3

Predators

- *Antennarius commersoni*
- *Aphareus furca*
- *Aprion virescens*
- *Aulostomus chinensis*
- *Carangoides orthogrammus*
- *Caranx ignobilis*
- *Caranx lugubris*
- *Caranx melampygus*
- *Caranx sexfasciatus*
- *Carcharhinus amblyrhynchos*
- *Carcharhinus galapagensis*
- *Cephalopholis argus*
- *Epinephelus quernus*
- *Fistularia commersonii*
- *Oxycheilinus unifasciatus*
- *Pseudocaranx cheilio*
- *Saurida flamma*
- *Saurida gracilis*
- *Scomberoides lysan*
- *Seriola dumerili*
- *Seriola rivoliana*
- *Sphyraena barracuda*
- *Sphyraena helleri*
- *Synodus binotatus*
- *Synodus dermatogenys*
- *Synodus ulae*
- *Synodus variegatus*
- *Triaenodon obesus*
- *Tylosurus crocodilus*

Browsers

- *Calotomus carolinus*
- *Calotomus zonarchus*
- *Kyphosus bigibbus*
- *Kyphosus cinerascens*
- *Kyphosus hawaiiensis*
- *Kyphosus vaigiensis*
- *Naso lituratus*
- *Naso unicornis*

Grazers

- *Acanthurus achilles*
- *Acanthurus blochii*
- *Acanthurus dussumieri*
- *Acanthurus guttatus*
- *Acanthurus leucopareius*
- *Acanthurus lineatus*
- *Acanthurus maculiceps*
- *Acanthurus nigricans*
- *Acanthurus nigrofuscus*
- *Acanthurus nigroris*
- *Acanthurus olivaceus*
- *Acanthurus triostegus*
- *Acanthurus xanthopterus*
- *Zebrasoma flavescens*
- *Zebrasoma veliferum*

Scrapers

- *Chlorurus perspicillatus*
- *Chlorurus spilurus*
- *Scarus dubius*
- *Scarus psittacus*
- *Scarus rubroviolaceus*

Secondary Consumers

- *Abudefduf abdominalis*
- *Abudefduf sordidus*
- *Abudefduf vaigiensis*
- *Acanthurus thompsoni*
- *Albula glossodonta*
- *Aluterus scriptus*
- *Amblycirrhitus bimacula*
- *Anampses chrysocephalus*
- *Anampses cuvier*
- *Apogon erythrinus*
- *Apogon kallopterus*
- *Apogon maculiferus*
- *Apolemichthys arcuatus*
- *Arothron hispidus*
- *Arothron meleagris*
- *Asterropteryx semipunctatus*
- *Atherinomorus insularum*
- *Balistes polylepis*
- *Blenniella gibbifrons*
- *Bodianus albotaeniatus*
- *Bothus mancus*
- *Bothus pantherinus*
- *Brotula multibarbata*
- *Callionymus comptus*
- *Cantherhines dumerilii*
- *Cantherhines sandwichiensis*
- *Cantherhines verecundus*
- *Canthidermis maculatus*
- *Canthigaster amboinensis*
- *Canthigaster coronata*
- *Canthigaster epilampra*
- *Canthigaster jactator*
- *Canthigaster solandri*
- *Caracanthus typicus*
- *Carangoides ferdau*
- *Centropyge fisheri*
- *Centropyge flavissima*
- *Centropyge interrupta*

Centropyge loriculus
Centropyge potteri
Chaetodon auriga
Chaetodon citrinellus
Chaetodon ephippium
Chaetodon fremblii
Chaetodon kleinii
Chaetodon lineolatus
Chaetodon lunula
Chaetodon lunulatus
Chaetodon miliaris
Chaetodon multicinctus
Chaetodon ornatissimus
Chaetodon quadrimaculatus
Chaetodon reticulatus
Chaetodon tinkeri
Chaetodon trifascialis
Chaetodon unimaculatus
Cheilio inermis
Chromis acares
Chromis agilis
Chromis hanui
Chromis leucura
Chromis ovalis
Chromis vanderbilti
Chromis verater
Cirrhilabrus jordani
Cirrhitops fasciatus
Cirrhitus pinnulatus
Cirripectes obscurus
Cirripectes vanderbilti
Coris ballieui
Coris flavovittata
Coris gaimard
Coris venusta
Coryphopterus duospilus
Ctenochaetus hawaiiensis
Ctenochaetus strigosus
Cymolutes lecluse
Cymolutes praetextatus
Dascyllus albisella
Dendrochirus barberi
Diodon holocanthus
Diodon hystrix
Doryrhamphus excisus
Echeneis naucrates
Enneapterygius atriceps
Entomacrodus marmoratus
Epibulus insidiator
Eviota epiphanes
Evistias acutirostris
Exallias brevis
Foa brachygramma
Forcipiger flavissimus
Forcipiger longirostris
Genicanthus personatus
Gnathanodon speciosus
Gnatholepis anjerensis
Gnatholepis caurensis hawaiiensis
Gomphosus varius
Goniistius vittatus
Gunnellichthys curiosus
Halichoeres ornatissimus
Hemiramphus depauperatus
Hemitaurichthys polylepis
Hemitaurichthys thompsoni
Heniochus diphreutes
Heteropriacanthus cruentatus
Hippocampus fisheri
Hippocampus kuda
Iniistius aneitensis
Iniistius pavo
Iniistius umbrilatus
Istiblennius zebra
Kuhlia sandvicensis
Labroides phthirophagus
Lactoria fornasini
Lutjanus fulvus
Lutjanus kasmira
Macropharyngodon geoffroy
Malacanthus brevirostris
Melichthys niger
Melichthys vidua
Microcanthus strigatus
Monotaxis grandoculis
Mugil cephalus
Mulloidichthys flavolineatus
Mulloidichthys mimicus
Mulloidichthys pflugeri
Mulloidichthys vanicolensis

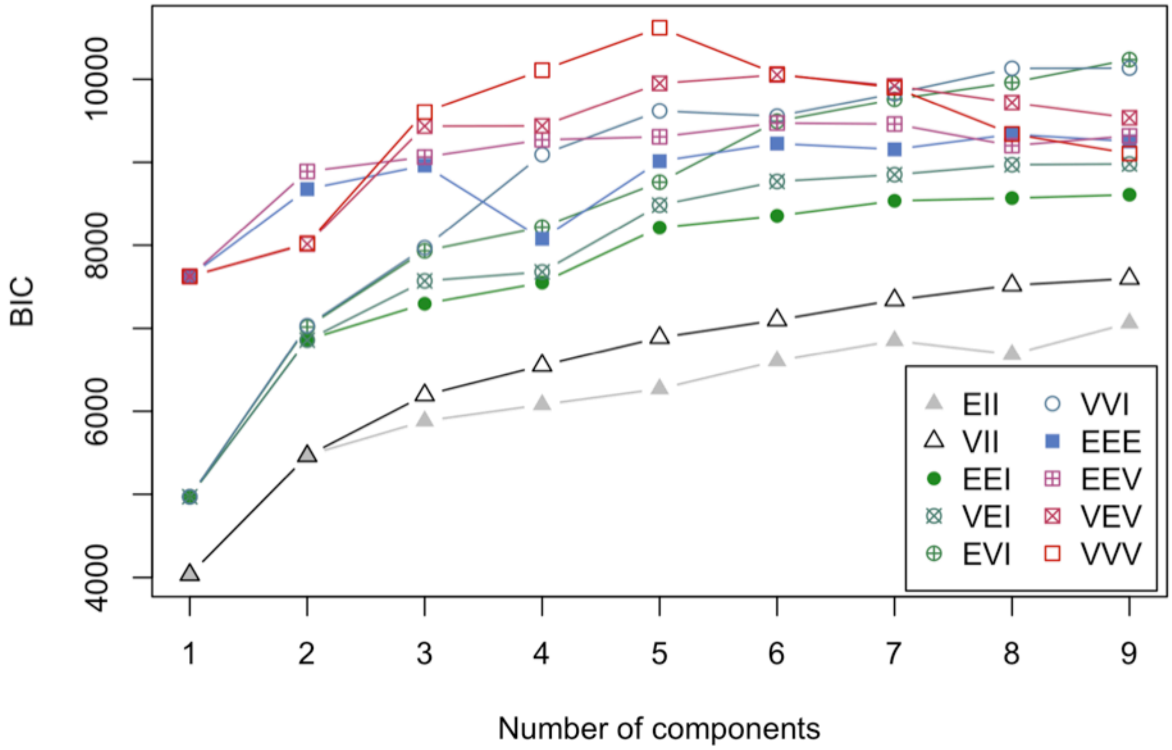
Myripristis amaena
Myripristis berndti
Myripristis chryseres
Myripristis kuntee
Myripristis vittata
Naso annulatus
Naso brevirostris
Naso caesius
Naso hexacanthus
Naso maculatus
Nemateleotris magnifica
Neomyxus leuciscus
Neoniphon aurolineatus
Neoniphon sammara
Novaculichthys taeniourus
Omobranchus rotundiceps
Oplegnathus fasciatus
Oplegnathus punctatus
Opua nephodes
Ostorhinchus maculiferus
Ostracion meleagris
Ostracion whitleyi
Oxycheilinus bimaculatus
Oxycirrhites typus
Parablennius thysanius
Paracirrhites arcatus
Paracirrhites forsteri
Parapercis schauinslandi
Parupeneus chrysonemus
Parupeneus cyclostomus
Parupeneus insularis
Parupeneus multifasciatus
Parupeneus pleurostigma
Parupeneus porphyreus
Pervagor aspricaudus
Pervagor spilosoma
Plagiotremus ewaensis
Plagiotremus goslinei
Platybelone argalus
Plectroglyphidodon imparipennis
Plectroglyphidodon johnstonianus
Pleurosicya micheli
Priacanthus meeki
Priolepis aureoviridis
Priolepis eugenius
Pristiapogon kallopterus
Pristiapogon taeniopterus
Pristilepis oligolepis
Pseudanthias bicolor
Pseudanthias hawaiiensis
Pseudanthias thompsoni
Pseudocheilinus evanidus
Pseudocheilinus octotaenia
Pseudocheilinus tetrataenia
Pseudojuloides cerasinus
Psilogobius mainlandi
Ptereleotris heteroptera
Pterois sphex
Rhinecanthus aculeatus
Rhinecanthus rectangulus
Sargocentron diadema
Sargocentron ensifer
Sargocentron punctatissimum
Sargocentron spiniferum
Sargocentron tiere
Sargocentron xantherythrum
Scorpaenodes kelloggi
Scorpaenodes parvipinnis
Scorpaenopsis brevifrons
Scorpaenopsis cacopsis
Scorpaenopsis diabolus
Sebastapistes ballieui
Sebastapistes coniorta
Stegastes marginatus
Stethojulis balteata
Sufflamen bursa
Sufflamen fraenatus
Taenianotus triacanthus
Thalassoma ballieui
Thalassoma duperrey
Thalassoma lutescens
Thalassoma purpureum
Thalassoma quinquevittatum
Thalassoma trilobatum
Trimma taylori
Upeneus arge
Wetmorella albofasciata
Xanthichthys auromarginatus
Xanthichthys mento
Zanclus cornutus

APPENDIX N MODEL-BASED CLUSTER ANALYSIS MODEL SELECTION

To identify regimes, model-based cluster analysis using the *mclust* package in R was performed (Fraley et al. 2012). Variables were modeled as Gaussian mixture models, and parameters were found with the expectation-maximization algorithm. The corresponding densities are ellipsoidal and can take different shapes based on geometric features (shape, volume and orientation), which are also parameterized in *mclust* (Figure N.1) (Fraley and Raftery 2002; Fraley et al. 2012). Model-based cluster analysis of the 10 fish and benthic variables revealed 5 distinct regimes based on a model selection of models with varying shapes, the final model was ellipsoidal, with varying volume, shape, and orientation (logL = 6450.6, n=1027, df=329, BIC=10610.7)

Figure N.1 Plot of Bayesian Information Criterion (BIC) for cluster analysis model selection based on models with equal or variable geometric features and different numbers of clusters.

The best model has the highest BIC (VVV, 5 components). Model parameterizations are: EII – equal volume, equal shape, VII – variable volume, equal shape, EEI – equal volume, equal shape, coordinate axes orientation, VEI – variable volume, equal shape, coordinate axes orientation, EVI – equal volume, variable shape, coordinate axes orientation, VVI – variable volume, variable shape, equal axes orientation, EEE – equal volume, equal shape, equal orientation, EEV – equal volume, equal shape, variable orientation, VEV – variable shape, equal volume, variable orientation, and VVV – variable volume, variable shape, variable orientation.



APPENDIX O TIME SERIES DETAILS

Temporal patterns across regimes were assessed for a total of 65 sites that were located throughout the study area (Figure O.1). These sites were located across 14 reef tracts, so some sites were spatially clustered because they occur in areas that tend to be more frequently monitored. Overall, 112 transitions were observed (Table O.1). At each site for each year the regime was predicted from the observed values of the 10 functional groups, and observations were retained for only those with at least a 95% probability of occurring in the predicted regime. We also plotted the observations in multivariate space for 8 time series with at least four years of data between 2000 and 2012 (Figure O.2).

We tested the sensitivity of analysing data from all 65 sites compared with only analysing those with longer time series (≥ 5 years) by calculating binomial confidence intervals for each transition in each case (Figure O.3). Binomial confidence intervals were produced with the *binconf* function in the *Hmisc* package in R (Harrell 2016) using the Wilson interval. Overall patterns were similar with overlapping confidence intervals in all cases.

Figure O.1 Distribution of study sites with time series data used to investigate temporal patterns across regimes.

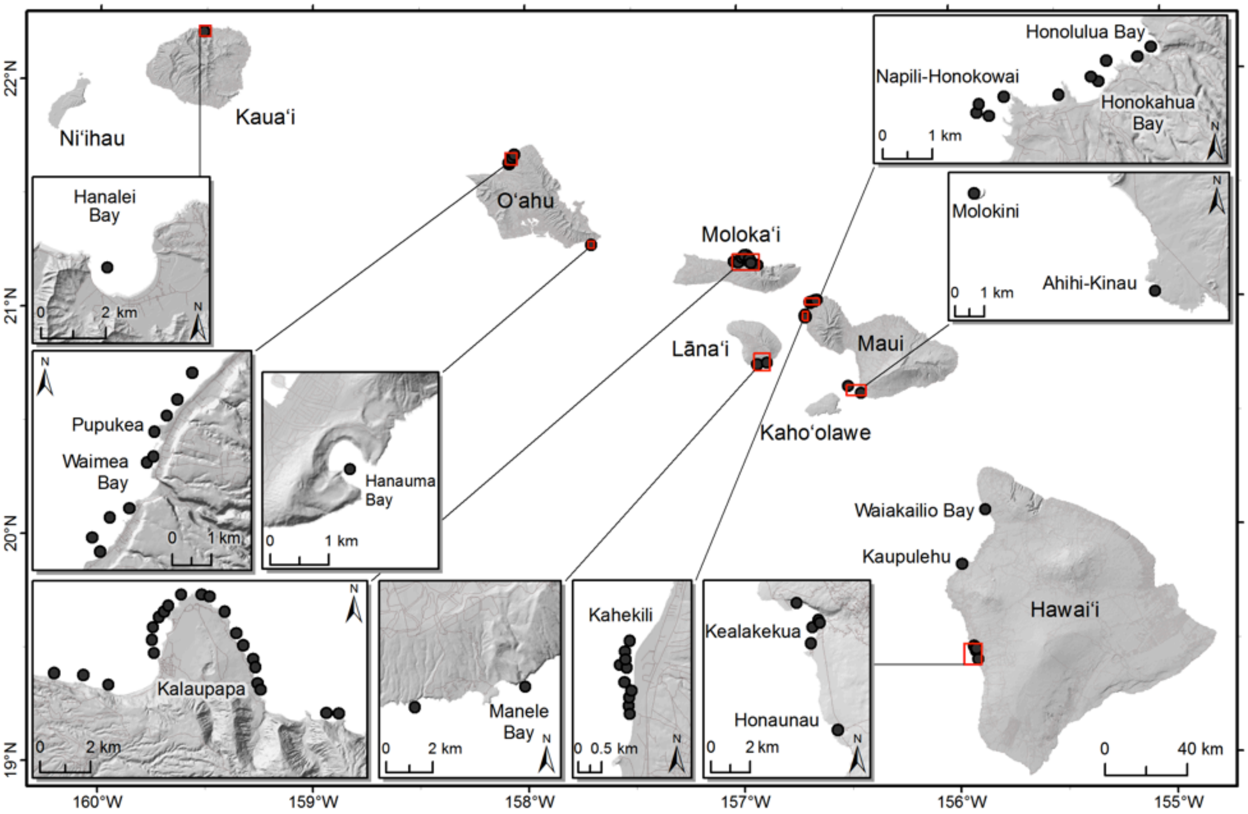


Figure O.2 Examples from sites with at least 4 years of observations plotted on top of ellipses from Figure 1, colored dots and points correspond to regime (black dots used for Regime 5), and timeline on each panel. Note that some sites do not move much (e.g. Kalaupapa), while others transition through a number of defined regimes (e.g. Kahekili).

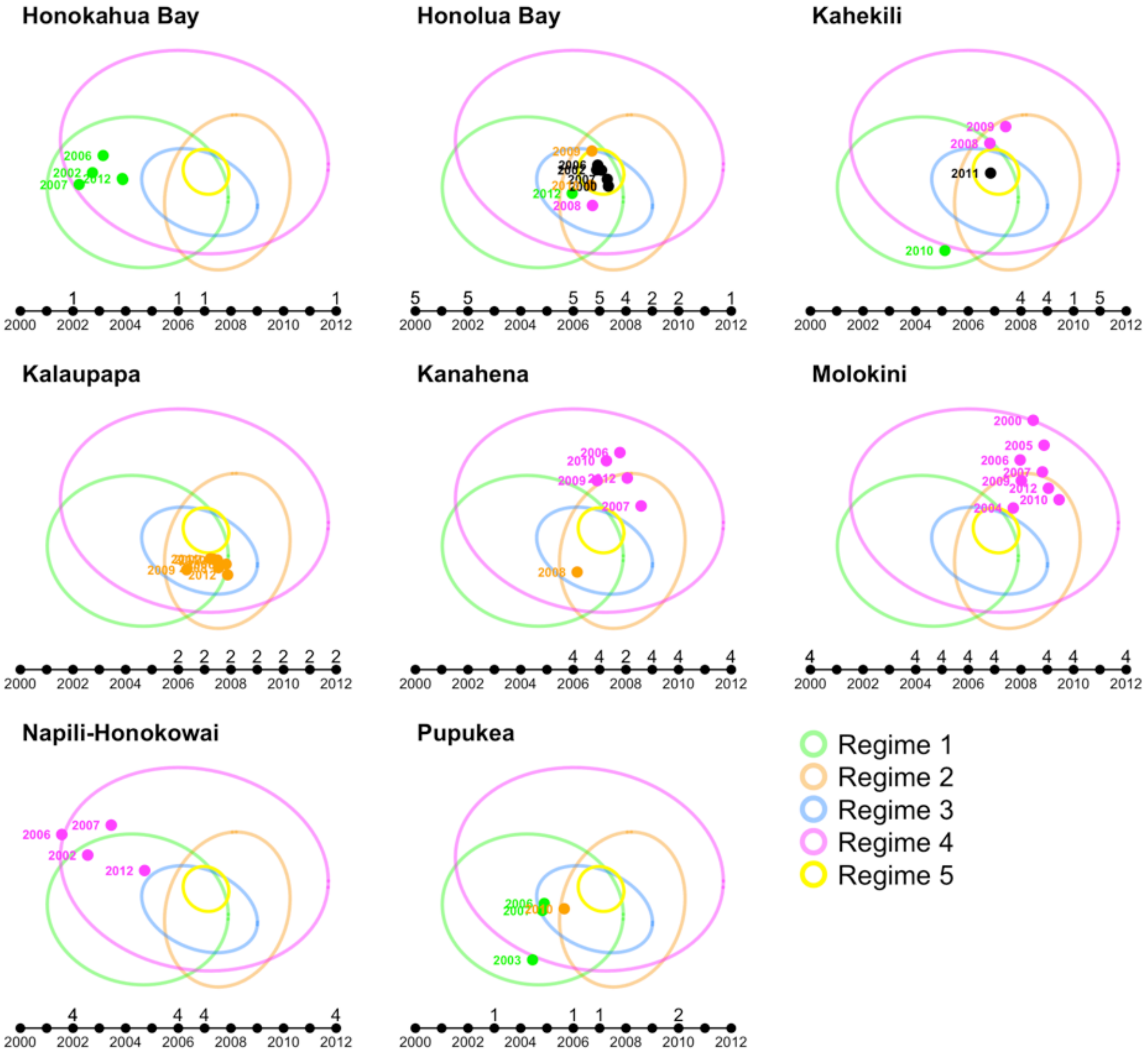


Table O.1 Predicted regime by year for 65 sites where data were available for at least three years.

								Regime						
General area	Latitude	Longitude	00	02	03	04	05	06	07	08	09	10	11	12
Honolua	21.0146	-156.6395		5				5	5	4	2			
Molokini	20.6324	-156.4970	4			4	4	4	4		4	4		4
Kalaupapa	21.1865	-157.0135						2	2	2		2	2	
Kalaupapa	21.1987	-156.9872						2	2					2
Kalaupapa	21.1939	-156.9864						2	2	2	2		2	2
Kalaupapa	21.2068	-156.9845						2	2		2		2	2
Kalaupapa	21.2087	-156.9826							2	4	1	2	2	1
Kalaupapa	21.2109	-156.9808						2	2	2	2	2		2
Kalaupapa	21.2145	-156.9681						2	2	2		2	2	2
Kalaupapa	21.2138	-156.9652						2	2	2	2	2	2	2
Kalaupapa	21.2006	-156.9552						2	2	4		2		2
Kalaupapa	21.1914	-156.9488						2	2	2	2	2		2
Kalaupapa	21.1885	-156.9478						2	2	2	2	2	2	2
Kalaupapa	21.1827	-156.9473						1	2	2	2	2	2	2
Kalaupapa	21.1718	-156.9212						2	2		4	4	2	4
Kalaupapa	21.1716	-156.9165							2	2	4	4	1	4
Kanahena	20.6014	-156.4380						4	4	2	4	4		4
Kalaupapa	21.2085	-156.9594						2	2		2	2		2
Kahekili	20.9459	-156.6953								4	4		5	5
Kahekili	20.9485	-156.6943								5	4	5	5	2
Kahekili	20.9427	-156.6945									4		5	5
Kahekili	20.9454	-156.6939								5	4		5	1
Kahekili	20.9507	-156.6932								4	4	5	5	2
Kahekili	20.9382	-156.6937								5	4	1		
Kahekili	20.9397	-156.6935									4		5	5
Kahekili	20.9409	-156.6930								1	4			1
Pupukea-Waimea	21.6468	-158.0658	4					1	2					
Kahekili	20.9470	-156.6942								4	4	1	5	
Kahekili	20.9365	-156.6934									4	5	5	
Napili	21.0031	-156.6734		4				4	4					4
Napili	21.0025	-156.6710		1				4	4			4		
Napili	21.0059	-156.6680		1				1	1					
Honokaua	21.0085	-156.6498		1				1	1					1
Honokaua	21.0123	-156.6482		1				1	1					1
Hanalei	22.2109	-159.5120	4		1	2								
Pupukea-Waimea	21.6482	-158.0643			2			5				2		
Pupukea-Waimea	21.6576	-158.0609			1			1	1					
Pupukea-Waimea	21.6613	-158.0582			1			1	1			2		
Hanauma	21.2684	-157.6938	4			4								4
Kalaupapa	21.1873	-157.0247								2		2	2	
Kalaupapa	21.1828	-157.0039									4	2		2

Kalaupapa	21.2031	-156.9868								2		2	2
Kalaupapa	21.2146	-156.9759						2	2			2	
Kalaupapa	21.1964	-156.9525					2		2		2		
Kalaupapa	21.1804	-156.9463									1	2	2
Kalaupapa	20.7342	-156.9214	3				4		4				
Manele Bay	20.7415	-156.8758					4		4				1
Napili	21.0047	-156.6729	4				4	4					
Oneloa	21.0062	-156.6575	1				1	1					
Honokaua	21.0093	-156.6512	1				1	1					
Honokaua	21.0129	-156.6421	4				4	2					
Kapulehu	19.8440	-155.9807						5				5	3
Kealakekua-Honaunau	19.4822	-155.9314			3		4	4					
Kealakekua-Honaunau	19.4634	-155.9246			4		4	5					
Kealakekua-Honaunau	19.4709	-155.9238			5		5	5					
Kealakekua-Honaunau	19.4742	-155.9208			4		4	3					
Kealakekua-Honaunau	19.4728	-155.9201			4		4	4					
Kealakekua-Honaunau	20.0810	-155.8680						5			3	5	
Kealakekua-Honaunau	19.4232	-155.9124			5		5	5					
Pupukea-Waimea	21.6295	-158.0796		1			1	1					
Pupukea-Waimea	21.6262	-158.0777		1			1	1					
Pupukea-Waimea	21.6341	-158.0751		1			1	1					
Pupukea-Waimea	21.6361	-158.0703		2			2	2					
Pupukea-Waimea	21.6539	-158.0639		4			4				2		
Pupukea-Waimea	21.6676	-158.0545		1			1	1					

Figure O.3 Comparison of binomial probabilities for each transition with 95% confidence intervals, with all 65 sites in black, 27 sites with at least 4 years of data in red, and 12 sites with at least 6 years of data in blue.