Spatial variability of coral reef communities: implications for conservation of benthic and herbivorous fish communities across Hawaii

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Abstract

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Over the last two decades there has been a proliferation of reports documenting the decline of coral reef systems across the globe (Gardner et al. 2003, Bellwood et al. 2004, Cote et al. 2005, Bruno and Selig 2007). In response, multiple studies have attempted to establish conservation baselines for benthic and fish communities using observations from remote, uninhabited coral reefs (Sandin et al. 2008, Edwards et al. 2011, Williams et al. 2011, Smith et al. 2016). These efforts have highlighted drastic differences in the composition and abundance of benthic and fish communities between remote and populated coral reefs. However, previous studies have focused on island- and archipelago-wide comparisons of reef communities that mask finer-scale spatial variability of coral reef communities within remote, unpopulated reef systems.

The focus of my thesis was to describe the spatial variability of benthic and herbivorous fish communities across populated and unpopulated islands in the Hawaiian Archipelago and to examine how such variability affects views about coral reef conservation. I chose to focus on benthic and herbivorous fish communities because: (1) the decline of coral reefs is often associated with persistent shifts in benthic composition from abundant reef building organisms (coral and crustose coralline algae) to abundant fleshy algae (Done 1992, Hughes 1994) and (2)

the prevailing view is that herbivorous fishes are the main driver of benthic community composition and thus overfishing of herbivorous fishes contributes to benthic community shifts (Hughes 1994, Bellwood et al. 2004, Mumby et al. 2006, Adam et al. 2015). Furthermore, this topic is highly relevant in Hawaii where herbivore fishing bans are being considered and implemented to conserve and promote healthy benthic habitats.

The first chapter of my thesis addressed the view that herbivorous fish are main drivers of benthic community composition in the remote Northwestern Hawaiian Islands (NWHI). I described three benthic community types (*reef builder*, *mixed-turf*, and *Microdictyon*) whose occurrences varied across forereefs in the NWHI. Using these community groups, I found herbivorous fish biomass to be associated with benthic composition which is consistent with prevailing views about the importance of these consumers to benthic community structure. However, herbivorous fish-benthic community relationships varied across islands and patterns suggested that environmental factors may have stronger influences on benthic community composition across some parts of the NWHI.

The second chapter of my thesis examined environmental influences on four measures of herbivorous fish community biomass (total, scraper, grazer, and browser) across the Hawaiian Archipelago and their effects on estimates of unfished biomass ($B_{unfished}$) and depletion in the Main Hawaiian Islands (MHI). I found environmental factors were strongly associated with herbivorous fish biomass in Hawaii and accounting for environmental differences across islands in the archipelago resulted in variable estimates of unfished biomass. Failure to account for environmental influences on unfished biomass resulted in different conclusions about herbivore depletion in the MHI. Overall, depletion estimates which controlled for environmental differences indicated that biomasses of the four herbivorous fish categories across much of the

MHI are near or above 0.5 $B_{unfished}$. However, scraper and browser biomass on Oahu, the island with the highest human population density, were near or below 15% of $B_{unfished-local}$, highlighting the potential importance of spatial and functional group variability when assessing fishing effects on coral reefs.

Together the results of this thesis advance knowledge of natural variability of benthic and herbivorous fish communities across the Hawaiian Archipelago. These results highlight the importance of controlling for environmental variability when assessing anthropogenic influences on coral reef communities. These findings will be useful for resource manages in Hawaii who are developing conservation plans to promote coral reef resilience. Additionally, the approaches outlined in this thesis can be applied to other reef systems to examine the broader relevance of spatial variability in benthic and fish communities to the identification of conservation targets in coral reefs.

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Chapter 1: Ecological and environmental associations of benthic communities across the remote Northwestern Hawaiian Islands

INTRODUCTION

Coral reef benthic communities are influenced by both ecological and environmental factors (Hughes & Connell 1999, Littler et al. 2006). For example, top-down control of algae by grazing herbivorous fishes is important for maintaining conditions that support abundant calcifying organisms (Lewis 1986, Paddack et al. 2006, Hughes et al. 2007a, Mumby 2009). Separately, environmental factors such as water temperature, nutrients, and wave energy have been associated with differences in algae and coral abundance (Jokiel 1977, Dollar 1982, Grigg 1983, Grigg 1998, Leicter et al. 1998, Franklin et al. 2013). On top of these natural influences, humans have altered top-down and bottom-up controls of reef benthos through the exploitation of herbivorous fishes and eutrophication (Lapointe 1997, Lapointe et al. 2004a, Mumby et al. 2006a, Mumby et al. 2012). These human influences have been linked to shifts in benthic community structure from abundant reef building organisms (hard coral and crustose coralline algae) to abundant fleshy algae and are a major threat to coral reefs across the globe (Done 1992, Hughes 1994, Hughes et al. 2010).

In response to increasing reports of benthic community shifts and coral reef degradation in general (Hughes et al. 2010, Gardner et al. 2003, Bruno et al. 2007), a growing number of studies have attempted to examine the relative influences of top-down and bottom-up factors on benthic reef communities (Littler et al. 2006, Mork et al. 2009, Burkepile & Hays 2009, Smith et al. 2010). Investigations have mostly relied upon experimental manipulations of herbivorous fish abundance and nutrient levels (Littler et al. 2006, Mork et al. 2009, Burkepile & Hays 2009, Smith et al. 2010). These studies suggest that while both factors influence the composition of benthic communities, grazing by herbivorous fishes has a stronger effect on the types and abundance of benthic organisms. Though it is unlikely that experimental manipulations can replicate the variability of coral reef systems (Cheal et al. 2010, Russ et al. 2015), the view that herbivorous fishes are main drivers of benthic community structure is further supported by observational studies demonstrating negative associations between herbivorous fish and macroalgae abundance (Williams & Polunin 2001, Newman et al. 2006, Friedlander et al. 2007) as well as theoretical models (Mumby 2006, Blackwood et al. 2012). However, observations of abundant fleshy algae at remote reefs where fishing and other anthropogenic influences are minimal (Williams & Pollunin 2001, Vroom & Richards 2010, Hoey et al 2011) indicate that there are likely multiple controls on benthic reef organisms.

The potential for concurrent and/or interactive effects between top-down and bottom-up control of benthic reef assemblages is highly relevant to conservation efforts to prevent shifts in benthic community composition (Adam et al. 2015, Roff et al. 2015, Russ et al. 2015). A primary goal of many such efforts has been to preserve and enhance herbivorous fish populations to increase the resilience of benthic communities to phase-shifts (Hughes et al. 2010, Mumby et al. 2007, Mumby & Steneck 2008). This goal assumes two things: (1) low abundances of herbivorous fishes are the result of overfishing, and (2) the abundances of herbivorous fishes control the abundance of algae on coral reefs and therefore more abundant herbivorous fishes lowers the probability of coral-algal community shifts. However, under certain environmental conditions high algal productivities may overwhelm the ability of herbivorous fish to keep algae in a cropped state, even when herbivorous fish abundance is high (Williams et al. 2001). Consequently, a better understanding of the factors that control benthic composition can help guide efforts to conserve the structure and function of benthic coral reef communities.

A growing number of studies have suggested that spatial patterns of benthic community composition at remote, uninhabited reef systems could serve as relevant baselines for conservation efforts in populated reef systems (Bruno et al. 2014, Smith et al. 2016). The remote Northwestern Hawaiian Islands (NWHI) are an interesting setting for exploring potential interactions between environmental and ecological associations with benthic communities because the region contains both abundant algae and calcifying (coral & CCA) communities (Vroom & Braun 2010). Recently, an analysis of benthic communities across the NWHI found herbivorous fishes to be a key driver of calcifying, turf, and macroalgal abundance (Jouffray et al. 2015). In addition to herbivorous fishes, Jouffray et al. (2015) found environmental factors such as latitude and depth also influenced benthic community composition. However, their analysis did not investigate whether the influence of herbivorous fishes on benthic communities varied spatially due to differences in latitude and/or depth.

Here I expand on the study by Jouffray et al. (2015) to explore the additive and/or interactive influences of herbivorous fishes and environmental factors on benthic communities across the NWHI. I use an extensive spatial dataset of benthic and herbivorous fish community data with environmental covariates to describe ecological and environmental associations of benthic communities across the remote NWHI. In order to examine these relationships, I first describe the major benthic communities and their occurrence across the NWHI. My community analysis differs from Jouffray et al. (2015) in that I identify benthic communities using a mix of functional group and finer resolution data (genera level for coral and macroalgae). This finer resolution data allowed me to identify benthic communities which did not align with functional group classifications (see Appendix B). I then use these community classifications to investigate two general hypotheses about the spatial variability of benthic communities in the NWHI: (H1 –

additive effects) herbivorous fishes are primary drivers of benthic composition, but there influence on benthic community composition varies with environmental conditions, and (H2 – interactive effects) both herbivorous fishes and environmental factors influence benthic communities and their interactions result in environmental factors being the primary driver of benthic community composition under certain conditions.

METHODS

Study area and survey design

The NWHI are a remote group of sub-tropical reefs, pinnacles, and atolls stretching 2,030 km northwest of the Main Hawaiian Islands. Reef sizes vary across the NWHI and the northern atolls are exposed to much colder water compared to the southern atolls (~ 4°C gradient in lower climatological mean sea-surface; Table 1). Fishing has been prohibited in the NWHI since its designation as a marine sanctuary in 2000 and fishing for herbivorous fishes before then was likely minimal due to the geographic isolation of the region (Kittinger et al. 2011). Therefore, variable fish biomass should reflect natural variability rather than influences from human exploitation.

This study focused on describing benthic communities on forereefs of the seven largest islands in the NWHI. Sites were selected according to a stratified random sample design where the survey domain was defined as depths shallower than 33 m containing hard bottom habitat at each reef. The survey domain was stratified by island (7 islands) and depth (three strata: shallow 0-6m, moderate 7-18m, and deep 9-30m). A geographic information system was used to delineate the survey domain, strata boundaries, and sample units (100 x 100 m cells) and facilitated random selection of sites. Further details on sample design and geospatial data are provided in Ault and Smith (2007), while sample design and effort statistics are provided in Table 1.1.

Data collection and handling

Benthic cover data were collected at a total of 240 sites between 2007 and 2011 (Appendix A, Figure 1A). At each site, proportional cover of benthic community classes was estimated using one of two methods. The line-point-intercept (LPI) method was used to estimate benthic cover at 67 sites between 2007 and 2009 (Vroom & Braun 2010); benthic taxa were recorded every 20cm along each of two 25m transects at each site. In 2010 and 2011, benthic photographs (BP) were taken at 173 sites and later analyzed to estimate benthic cover. Photos were taken every 2m along two 30m transects at each site (30 photos/site) with a Cannon camera attached to a 1 meter monopod. The monopod ensured a fixed height above the seafloor and resulted in a consistent image area of roughly 0.15 m^2 (.45 m by .34 m). Benthic photos were analyzed in Coral Point Count with Microsoft Excel extensions (Kohler and Gill 2006). Photo analysis involved randomly projecting 15 points onto a 5 by 3 grid overlaid on each photo (total of 225 points per transect). Taxonomic resolution varied by benthic groups and method but was always aggregated at the genus-level for corals and two macroalgae (*Halimeda* and *Microdictyon)* and functional group-level for all other fleshy algae, crustose coralline algae (CCA), and turf algae (Table 1.2). A comparison of benthic cover estimates across 63 sites where both LPI and BP data were collected indicated these methods provided similar estimates of benthic cover (differences in benthic cover estimates rarely exceeded 15%). I calculated benthic cover by pooling transect data at each site and summing the number of points in each benthic class divided by the total number of points at that site. Prior to pooling data, I removed unconsolidated substrate (sand and rubble) data points to standardize percent cover estimates by available hard bottom substrate.

Identifying benthic communities

I used multivariate cluster analysis to describe the structure of benthic communities across the NWHI. Because multivariate classifications of ecological communities have uncertainty, I used a “fuzzy” clustering approach (Salski 2007). The FANNY cluster algorithm (Kaufman and Rousseeuw 1990) allows sites to belong to more than one group via membership weights which sum to 1. FANNY is a fuzzy application of k-means partitioning and, therefore, requires an *a priori* structure or number of groups to be specified. I examined the structure of benthic communities in the NWHI based on the *a priori* assumption that between two and seven community groups existed across the NWHI. I used average silhouette scores to identify the number of communities best supported by the data (Rousseeuw 1987).

Prior to cluster analysis, benthic classes which occurred in less than 15% of sites were removed (5 of 13 classes, max site-level percent cover never greater than 2.3%). The resulting matrix of percent cover for all 240 sites was then converted to Bray-Curtis similarities without transformation. Following cluster analysis, sites were classified based on the cluster group with the largest fuzzy membership weight for each site. The benthic classes best characterized by each community were identified via Indicator Species Analysis (ISA), a technique that combines relative abundance and frequency of occurrence data to assess association across any categorical classification of samples (Dufrene & Legendre 1997). In ISA, group associations range from 0 to 100 and are greatest when a species (or benthic class) is only observed in a particular group and not found at any remaining sites. Inter-relationships among benthic community groups were visually assessed by superimposing cluster results on a non-metric multi-dimensional scaling

(NMDS) ordination and by plotting distributions of benthic cover for benthic indicator classes associated with each community group. Distinct benthic communities were expected to show clear separation in the MDS ordination and to have minimal overlap between proportional cover ranges of indicator classes across community types.

Spatial patterns of benthic communities

I estimated the occurrence of each benthic community type across the NWHI and at each island using principles of complex survey designs (Cochran 1977). The goal was to explicitly estimate how much hard-bottom habitat at each island, and across the NWHI, was occupied by each benthic community type. Spatial weights were calculated as the proportions of hard-bottom habitat at each island and in each depth strata relative to the total area of the survey domain (Table 1.1). These weights were then used to calculate island and region-wide means and variances according to the methods outlined in (Cochran 1977). Briefly, community occurrence means and variances were calculated for each strata (island x depth = 21 strata) and then island-wide and NWHI-wide occurrences were obtained by summing the respective strata estimates at each spatial-level.

Ecological and environmental predictor variables

I examined a range of ecological and environmental covariates known to influence benthic reef communities, including herbivorous fish biomass, depth, sea-surface temperature, and unique islands (Table 1.3). Total herbivorous fish biomass at each site was used to represent top-down control on benthic communities. Although recent studies have shown fine-scale associations between three major herbivore functional groups (browsers, grazers, and scrapers) which share similar feeding habits and individual components of benthic communities, such as CCA, fleshy macroalgae, and turf algae cover (Burkepile & Hay 2011, Heenan & Williams

2013), preliminary analyses indicated that total biomass was the best predictor of benthic communities in the NWHI. Data on herbivorous fish biomass at each site were provided by NOAA’s Coral Reef Ecosystem Division and Papahānaumokuākea Marine Monument. Data collection and biomass calculations are described in Williams et al. (2011). The logarithm of herbivore biomass was used to reduce the influence of extreme biomass values.

Potential bottom-up control of benthic community composition was represented by two environmental covariates (depth & water temperature) and a nominal variable reflecting unmeasured environmental variation (Island). Depth has been linked to a variety of environmental factors that can influence benthic communities from wave energy to light attenuation (Dollar 1982, Williams et al. 2014). Because water temperatures vary throughout the year, I used average sea-surface temperatures calculated during the coldest month of each year from 1985-2009 (SSTL, taken from Gove et al. 2015) to reflect the thermal gradient across the NWHI. SSTL is highly correlated with latitude (r = 0.99), which was used in the Jouffray et al. (2015) analysis. Additionally, I included the nominal variable “island” to reflect environmental variability that may differ between- and within- islands but was not captured by the aforementioned variables.

Analysis of ecological and environmental associations with benthic communities

I determined whether community groups identified from multivariate cluster analysis were predictable based on two general hypotheses about additive effects of ecological and environmental factors (H1) and interactions between ecological and environmental factors (H2, Table 1.4). The first hypothesis (H1) represented strong top-down control of benthic communities but allowed the response of benthic communities to vary dependent upon environment conditions. Models representing H1 included both ecological and environmental covariates (Table 1.4, models 1-7). Spatial patterns of benthic community occurrence across islands and depth categories indicated potential interactions (Appendix D: Figure 1D). Therefore, an island x depth interaction was included. Because combinations of environmental factors may influence benthic community structure in the NWHI and these relationships may vary spatially, two-way combinations and interactions were examined. The nominal variable island and island averaged SSTL were not included in the same model because these terms were redundant. The second hypothesis (H2) represented the additive and interactive effects of ecological and environmental factors on benthic communities. Models in these groups (Table 1.4, Models 8-22) were simply all the models from H1 with the addition of interactions between herbivore biomass and either SSTL or Island, depth, and/or combinations of the two. Collinearity between herbivore biomass and environmental factors was not problematic (highest r = -.47, herbivore-depth). Three-way interactions were not investigated because they were biologically uninterpretable and all terms were modeled as fixed-effects.

I used multinomial logistic regression to examine support for the 22 candidate models representing my two hypotheses about benthic community associations with environmental and ecological factors (Table 1.4). The multinomial distribution is a generalization of the binomial distribution for categorical variables with more than two response types. Therefore, multinomial regression was used to model the probability that each site belonged to each of the three benthic community groups (*see Results)* given a set of predictor variables. Support for each hypothesis was assessed using model weights calculated from Akaike's Information Criterion corrected for small sample sizes (AICc, Burnham and Anderson 2002). Predicted probabilities for community group occurrence were used to present model results because interpretation of model coefficients (log-odds) from multinomial regression are difficult to understand when there is no clear “reference” group. Goodness of fit was assessed both visually and using a multinomial corrected chi-square test (Fagerland et al. 2008). All analyses were conducted using R version 3.0.3 (R Development Core Team 2015).

RESULTS

Identifying benthic communities

According to fuzzy cluster analysis, the structure of benthic communities across the NWHI was best described by three community groups (avg. silhouette width = 0.57). The first community was characterized by higher abundances of *Montiporid* and *Poritid* corals as well as two calcified algae classes: CCA and *Halimeda* (Appendix B: Table B1). The second community group was characterized by higher abundances of turf algae, fleshy algae, and *Pocilloporid* coral (Appendix B: Table B1). The third community was characterized by a single algae class: *Microdictyon* (Appendix B: Table B1). Each of the three community groups was given a name based on characteristics of respective assemblages to enable more intuitive references compared to arbitrary numeric titles. Community group 1 was comprised mostly of calcifying organisms, and thus the title “reef builder” provided a unifying theme for summarizing its four characteristic benthic classes. (Note that *Pocilloporid* corals are not primary contributors to the reef framework in Hawaii (Engels et al. 2004)). Community groups 2 and 3 were named *mixed-turf and Microdictyon*, respectively.

The three benthic community groups were highly distinguishable in both univariate and multivariate space (Figure 1.1). Fuzzy membership weights indicated that 82 sites (34% of total) had less than two-thirds support for any one community. Mapping cluster results from the remaining 158 sites (see Appendix C for explanation) onto an nMDS ordination of all 240 sites showed the three community groups occupied distinct regions of ordination space (Figure 1.1).

Distributions of benthic cover summed across indicator classes for each of the three community groups (highlighted in color) indicated minimal overlap when compared to distributions for the other two community types (Figure 1.1). Importantly, indicator classes constituted a median of 60% benthic cover for the community type for which they were named after; thus, these benthic classes made up a substantial portion of the benthos at most sites in each of the three community groups. The clear separation between community groups in both multivariate and univariate space suggest these community types are distinct across the NWHI.

Spatial patterns of benthic communities

Spatial variability in the occurrence of the three benthic community types among islands and depths was striking, ranging from as little as <1% occurrence to >90% occurrence (Figure 1.2). Mean *reef builder* community occurrence was 47.2% (95% CI: ± 5.2) across forereef habitat in the NWHI. The *reef builder* community constituted the majority of forereef habitat at both Maro and Lisianski (87.7 and 83.8%, respectively) and more than half of the forereef at French Frigate Shoals (Figure 1.2). No sites at Midway or Kure Atoll were classified as reef builders. The *mixed-turf* community was estimated to occur at 28.9% ± 5.0% (mean ± 95% CI) of the forereef in the NWHI and was most common at Midway (mean occurrence = 88.9%, 95% CI: ± 12.7, Figure 1.2). The *Microdictyon* community type was estimated to occur at 23.9% ± 3.8% (mean ± 95% CI) of the forereef in the NWHI and occurred at 85.1% ± 11.1 % (mean ± 95% CI) of the reef at Laysan Island (Figure 1.2). The *Microdictyon* community was also abundant at Pearl & Hermes and Kure Atoll where it covered 36.0% and 34.7% of the benthos, respectively. Patterns of benthic community occurrence also varied by depth with the *mixed-turf* community being most common at shallow depths (mean: 67.2%, 95% CI: ± 10.3), *reef builder* at moderate depths (mean: 60.8%, 95% CI: ± 7.5), and *Microdictyon* at deeper depths (mean: 58.5%, 95% CI: ± 8.6; Figure 1.2).

Ecological and environmental associations with benthic communities

Model selection strongly supported interactions between herbivorous fish biomass and environmental factors (H2), with more limited support for additive effects (H1; Table 1.5). The top model (M20) received over 70% of the AICc weight and included the nominal variable *island*, the sum of *herbivorous fish biomass*, *depth*, as well as interactions between *island* & *depth* and *depth* & *herbivorous fish biomass* (Table 1.5) and correctly predicted benthic community groups for 203 (85%) of the 240 sites. Model predictions superimposed on plots of observed herbivore biomass versus fuzzy membership weights for each community type and island demonstrated adequate agreement (Figures 1.3 & 1.4) as did the multinomial corrected goodness of fit test (χ^2 =6.15 , d.f. = 12, p=0.90).

Predictions of benthic community group occurrence varied by island, herbivore biomass levels, and depth. In general, the probability of *reef builder* and *mixed-turf* community occurrences increased with increasing herbivorous fish biomass, while *Microdictyon* community occurrence decreased (Figure 1.3). The two northern atolls, however, did not have any sites classified as *reef builder* community (Figure 1.3). It is worth noting the different shapes of occurrence response curves between islands, especially the relatively high *reef builder*/low *Microdictyon* probabilities at French Frigate Shoals, Maro, and Lisianski at low herbivore biomass levels, compared to Laysan and Pearl & Hermes which exhibited more gradual increases in *reef builder* occurrence and decreases in *Microdictyon* occurrence with increasing herbivore biomass. Predictions of *mixed-turf* community occurrence were highest at shallow depths while the *Microdictyon* community generally increased with depth (Figures 1.3 & 1.4).

DISCUSSION

Herbivorous fishes are widely viewed as the main driver of benthic community composition on coral reefs (Hughes 1994, Bellwood et al. 2004, Mumby et al. 2006, Adam et al. 2015). This view was recently supported in the NWHI where benthic community groups were strongly associated with herbivore biomass in addition to latitude and depth (Jouffray et al. 2015). I found the occurrences of three benthic community groups (*reef builder*, *mixed-turf*, and *Microdictyon*) in the NWHI to be associated with herbivore biomass, depth, and island-specific differences. While these results are broadly similar to Jouffray et al. (2015), my analysis resulted in a more detailed description of how these benthic community associations vary spatially. These results suggest environmental factors may have a stronger influence on benthic community composition than previously thought, which raises questions about the relative role of herbivorous fishes as a driver of benthic community structure across the NWHI.

Strong top-down control of benthic communities on coral reefs is expected to produce positive associations between herbivorous fishes and reef building organisms (Mumby et al. 2012). However, in this study increasing herbivore biomass in the NWHI did not always translate to high probabilities for *reef builder* community occurrence. At the two northern-most atolls (Midway & Kure), which had some of the highest observations of herbivorous fish biomass, no sites were classified as *reef builders*. Additionally, low levels of herbivorous fish biomass did not always translate to low probabilities for *reef builder* community occurrence. There are at least three, non-mutually exclusive, potential explanations for these patterns: (1) nutrient dynamics dominate those caused by fish herbivory, (2) non-fish herbivores contribute significantly to benthic community composition, and (3) wave energy dominates the effects of fish herbivory on benthic community composition.

The lack of association between reef builder community occurrence and herbivore biomass has been hypothesized to occur when environmental conditions favor high algal productivities that can overwhelm the ability of herbivorous fishes to maintain algae in a cropped state and thus promote reef building organisms (Williams et al 2001). High algal and herbivorous fish abundances have been reported in sub-tropical reef systems where cooler water temperatures, often associated with higher nutrient levels, could explain this pattern (Hoey et al 2011). Thus, cooler water temperatures at the two northern atolls could be driving the higher algal abundances at Midway and Kure even though herbivore biomasses at these reefs were the highest in the NWHI. However, in my analysis the interaction between SSTL and herbivore biomass was not included in the top model for predicting benthic community occurrence. In addition, the relatively low probability of *reef builder* community at Laysan is not consistent with SSTL being the sole driver of because Lisianski, which is north of Laysan and is exposed to colder SSTL, and had the highest *reef builder* occurrence in the NWHI. Thus, further study is needed to clarify the interplay between nutrient dynamics and fish herbivory in effecting patterns of benthic community composition.

A second explanation for why associations between herbivorous fishes and reef building organisms in the NWHI did not mirror those from previous studies in other regions could be that non-fish herbivores contribute significantly to benthic community composition. I found high probabilities for *reef builder* community occurrence at relatively low herbivore biomass levels at Lisianski, French Frigate Shoals, and Maro. This observation does not necessarily equate to herbivory not influencing benthic communities at these reefs. Rather it could suggest fish herbivore biomass is not a good proxy for herbivory at Lisianski, French Frigate Shoals, and Maro. Fish are not the only consumers of algal biomass as micro- and macro-invertebrate have been shown to be important regulators of algae (Hughes 1994, Carpenter 1986). Information on non-fish herbivores was not unavailable for this study and the influence of grazing by non-fish herbivores on algal communities in the NWHI is largely unknown and therefore, could be a topic for future research.

A third explanation for why associations between herbivorous fishes and reef building organisms in the NWHI did not mirror those from previous studies in other regions could be the importance of wave energy on the presence of calcified organisms. In Hawaii, wave energy has been shown to control the distribution and composition of coral communities with the highest coral abundances being located in areas of low wave energy (Dollar 1982, Grigg 1983, Grigg 1998, Franklin et al. 2013). The three reefs with the highest occurrences of *reef builder* communities across the NWHI (Lisianski, French Frigate Shoals, and Maro) are all considered open atolls, reefs that have unique geomorphological characteristics compared to the other atolls in the NWHI (Rooney et al. 2008). The complex geomorphology of open atolls alters incoming wave energy and creates wave environments more similar to protected lagoons (Rooney et al. 2008). Therefore, the lower wave energies at these reefs could favor coral growth and explain the abundance of reef builders in the absence of high herbivorous fish biomass. While high resolution, spatial wave energy data were not available for the NWHI at the time of writing, future availability should help explain the distribution of benthic communities.

Though less widely discussed in the coral reef literature, a distinct possibility is that benthic community composition determines the biomass of herbivorous fishes, rather than the other way around. Support for this idea in the NWHI comes from patterns of benthic community predictions at low herbivore biomass levels. Community occurrence probabilities changed the most when herbivore biomass levels were below 10 g m^{-2}. This type of response at low herbivore et al. 2015) and suggests one of two things: either very low herbivorous fish biomass levels are required to influence the composition of benthic communities at these locations, or these patterns reflect habitat driving the abundance of herbivorous fishes. Sharp declines in occurrence probabilities of the *Microdictyon* community at low herbivore biomass are unlikely to be the result of grazing by herbivores because *Microdictyon* is largely unpalatable (Lapointe et al. 2004b). Rather the high occurrence of *Microdictyon*, especially at deep depths has been linked to high nutrient availability associated with upwelling and internal tides (Leichter et al. 1998, Vroom & Braun 2010).

This study clarifies descriptions of benthic communities in the NWHI (see Appendix B) and highlights spatial variability in the associations between benthic community composition and ecological and environmental factors. The correlative nature of this observational study prevented assigning causation to benthic community associations, yet several lines of evidence suggest the importance of environmental factors over top-down control of benthic communities across the NWHI. The results of this study add to calls for a re-examination of top-down control of benthic community composition in marine reef communities (Russ et al. 2015), and imply that such studies should be done carefully in order to account for environmental influences on the structure of coral reef communities.

Table 1.1. Summary of stratified random survey design. Depth strata at each island were: shallow (S), moderate (M), and deep (D). Sample units are the total number 100m x 100m units used in probability sampling by island and depth strata. Spatial weights were calculated as the proportion of sample units in each depth strata by island and across the NWHI survey domain. Sites correspond to the number of surveys at each island-depth strata.

		Sample Design			
Island	**Depth strata**	**Sample units**	**Island weight**	**NWHI weight**	**Sites**
FFS		**10666**		**0.29**	**39**
	S	926	0.08	0.03	2
	M	7959	0.75	0.22	25
	D	1781	0.17	0.05	12
MAR		**5577**		**0.15**	**38**
	S	721	0.13	0.02	18
	M	4337	0.78	0.12	12
	D	519	0.09	0.01	8
LAY		**5484**		**0.15**	**27**
	S	84	0.02	0.00	2
	M	723	0.13	0.02	9
	D	4677	0.85	0.13	16
LIS		**5590**		**0.15**	**43**
	S	880	0.16	0.02	8
	M	3356	0.60	0.09	21
	D	1354	0.24	0.04	14
PHR		**4659**		**0.13**	**41**
	S	599	0.13	0.02	10
	M	2797	0.60	0.078	19
	D	1263	0.27	0.04	12
MID		**2787**		**0.08**	**27**
	S	584	0.21	0.02	8
	M	1474	0.53	0.04	10
	D	729	0.26	0.02	9
KUR		**1670**		**0.05**	**25**
	S	208	0.13	0.01	5
	M	1142	0.68	0.03	12
	D	320	0.19	0.01	8
Total		**36433**			**240**

Table 1.2. List of benthic classes.

Functional group	Benthic classes
Hard coral	Acropora (ACRO)
	Fungia (FUNG)
	Leptastrea (LEPT)
	Massive Porites (MPOR)
	Montipora (MOSP)
	Pavona (PAVO)
	Pocillopora (POCS)
	Pssamacora (PSSA)
Macroalgae	Halimeda (HASP)
	Microdictyon (MICRO)
	Fleshy (FLESH)
Turf Algae	Turf Algae (TALG)
Crustose Coralline Algae	Crustose Coralline Algae (CCA)

Table 1.3. List of predictor variables, descriptions, data ranges, and sources.

Variable	Description	Range	Source
Herb	Biomass (g/m^2) of herbivorous fishes (by site)	0 – 314	Survey data, CRED
Depth	Maximum depth in meters at survey sites (by site)	3 – 30	Survey data, CRED
SSTL	Lower climatological mean of sea surface temperature (°C), i.e. the average of mean temperature in the coldest month of each year between 1985 and 2009 (by island)	18.9 – 22.8	Gove et al. (2013)
Island	Nominal factor	7 levels	

Table 1.4. Candidate list of models and terms for testing hypotheses about the control of benthic communities across the NWHI. The multinomial response for all models was the probability of each benthic community group.

Model	Hypothesis	Model terms
1	H1: top-down + bottom-up control	SSTL + Herb
2		Depth + Herb
3		Island + Herb
4		SSTL + Depth + Herb
5		Island + Depth + Herb
6		SSTL + Depth + SSTL:Depth + Herb
7		Island + Depth + Island:Depth + Herb
8	H2: top-down x bottom-up control	SSTL + Herb + SSTL:Herb
9		Depth + Herb + Depth:Herb
10		Island + Herb + Isl:Herb
11		SSTL + Depth + Herb + SSTL:Herb
12		SSTL + Depth + Herb + Depth:Herb
13		SSTL + Depth + Herb + SSTL:Herb + Depth:Herb
14		SSTL + Depth + Herb + SSTL:Depth + SSTL:Herb
15		SSTL + Depth + Herb + SSTL:Depth + Depth:Herb
16		SSTL + Depth + Herb + SSTL:Depth + SSTL:Herb + Depth:Herb
17		Island + Depth + Herb + Island:Herb
18		Island + Depth + Herb + Depth:Herb
19		Island + Depth + Herb + Island:Herb + Depth:Herb
20		Island + Depth + Herb + Island:Depth + Island :Herb
21		Island + Depth + Herb + Island:Depth + Depth:Herb
22		Island + Depth + Herb + Island:Depth + Island:Herb + Depth:Herb

Table 1.5. Multinomial model selection results. All models with AICc weights > 0.05 are shown. Model equations are given in Table 1.4.

Model	Hypothesis	ΔAICc	Weight
20	H2: top-down x bottom-up control	0.0	0.72
7	H1: top-down + bottom-up control	3.6	0.28

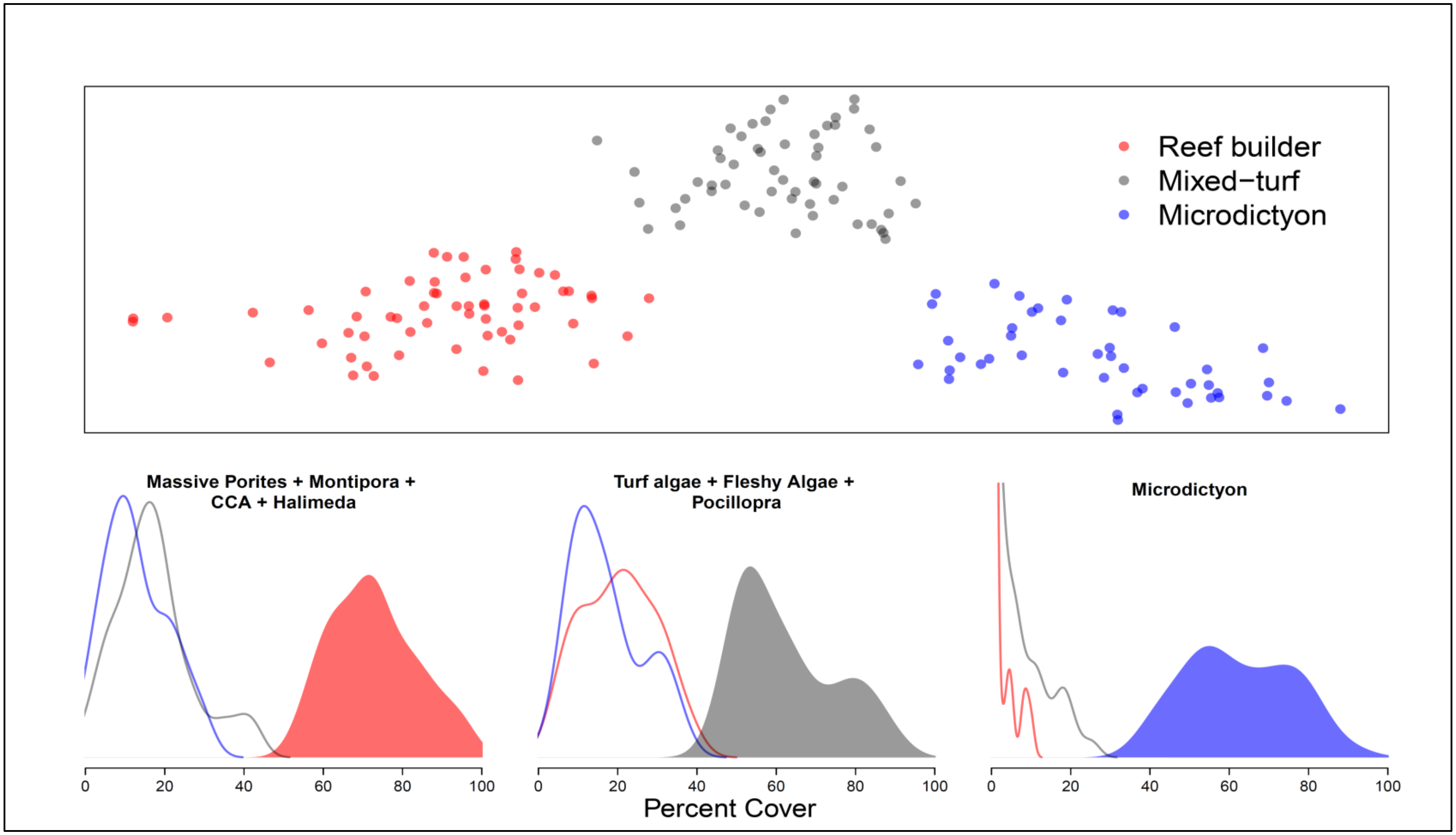

Figure 1.1. (top) nMDS ordination of 240 benthic sites (2D stress = 0.16). Symbol colors indicate community groups identified by fuzzy cluster analysis: reef builder (red), mixed turf (grey), *Microdictyon* (blue). Sites which did not show strong support for a single community group (membership weights < 0.66) were omitted. (bottom) Distributions of benthic cover values summed across indicator classes associated with each of the three benthic communities. Distribution colors correspond to the same community groups shown in the nMDS plot above. The filled-in distribution corresponds to the community associated with the indicator classes in the title of each plot (left: reef builder, middle: mixed-turf, right: Microdictyon) and is meant to highlight differences in benthic cover ranges compared to the other two community groups.

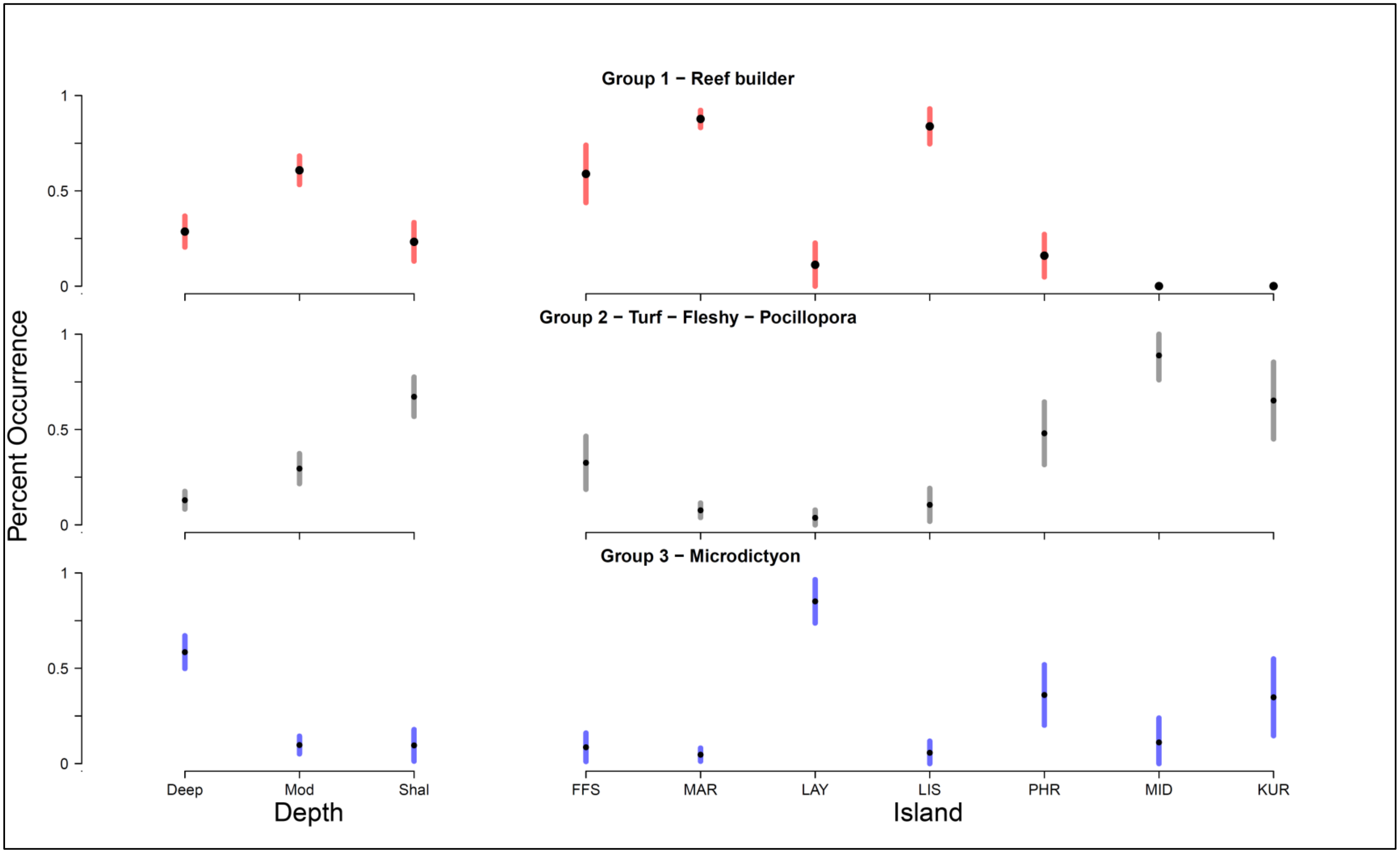

Figure 1.2. Spatially weighted occurrence estimates and 95th percentile confidence intervals for *reef builde*r (top) *mixed-turf* (middle) and *Microdictyon* communities (bottom) across the three depth strata (left) and each island (right). Islands are arranged south to north, from left to right.

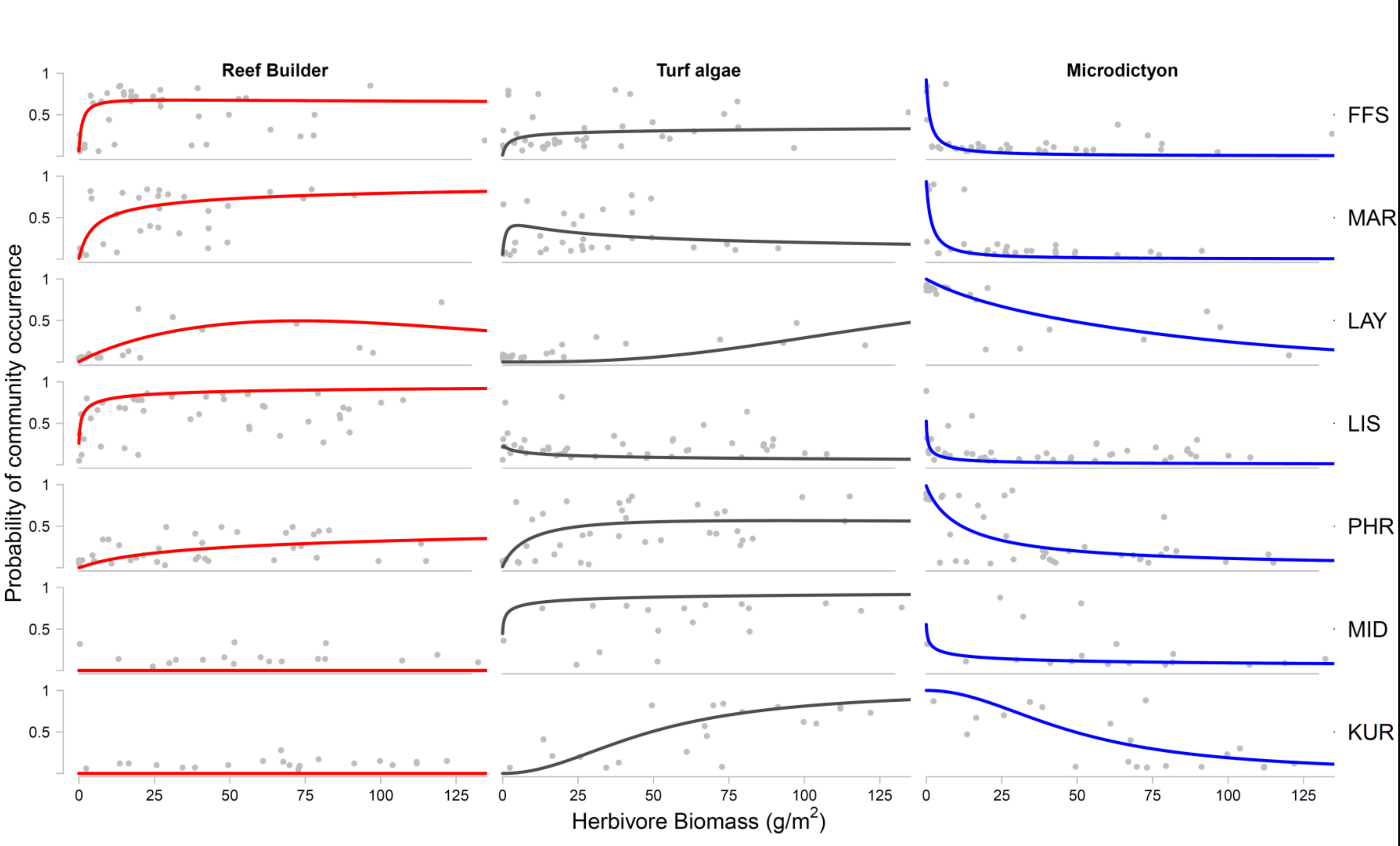

Figure 1.3. Predicted occurrence probabilities for *reef builder* (left), *mixed-turf* (middle), and *Microdictyon* communities (right) based on herbivore biomass at each island (rows). Data points reflect membership weights from fuzzy cluster analysis at each site.

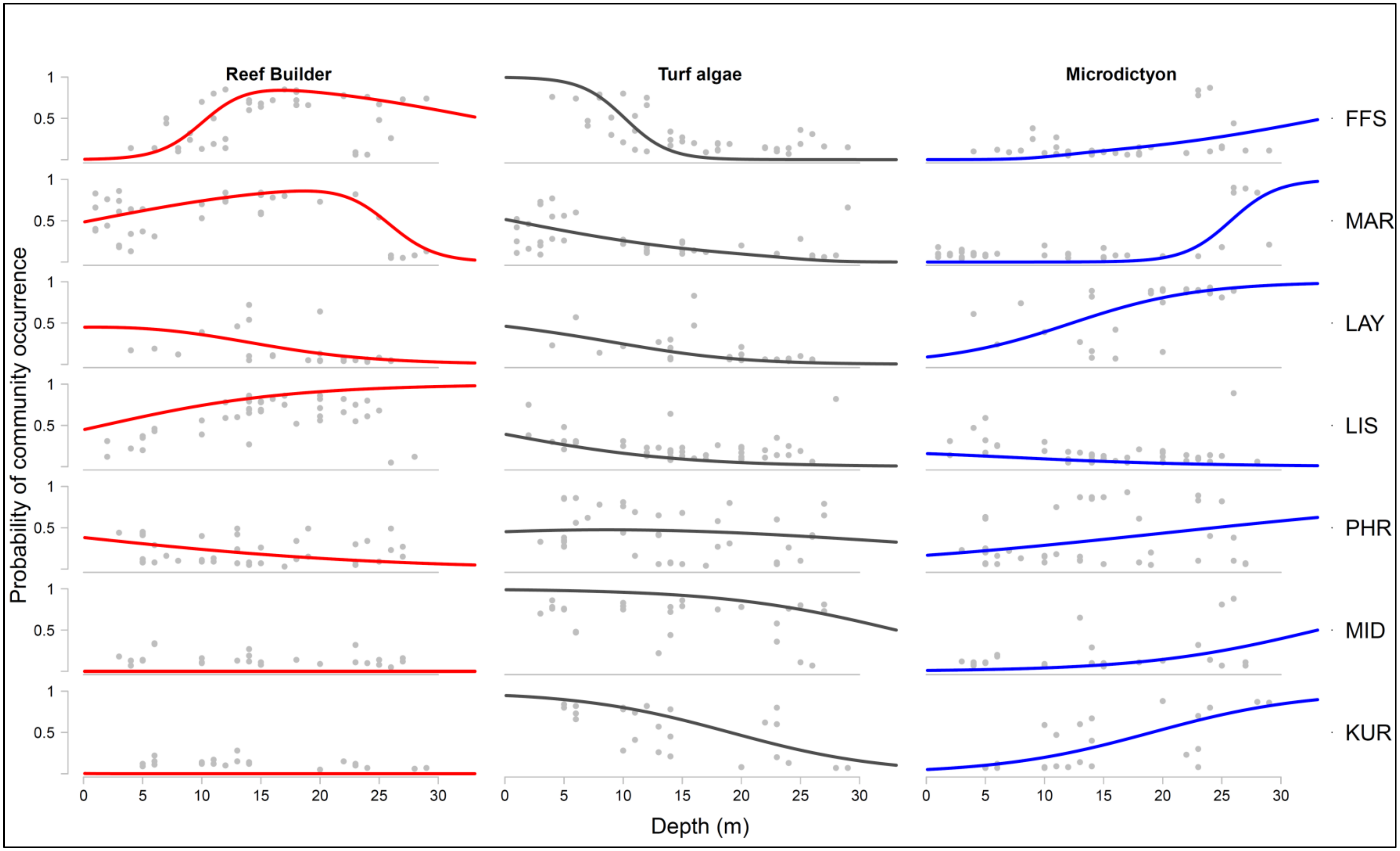

Figure 1.4. Predicted occurrence probabilities for *reef builder* (left), *mixed-turf* (middle), and *Microdictyon* communities (right) based on depth at each island (row

Chapter 2: Fishing and environmental influences on herbivorous fish biomass across the Hawaiian Archipelago

INTRODUCTION

Estimating unfished biomass ($B_{unfished}$) is a key component for assessing fisheries depletion, the difference between current and unfished biomass levels (Hilborn & Walters 1992, Quinn & Deriso 1999). While there is strong evidence that environmental forcing can influence fish biomass in addition to fishing (Williams et al. 2015), the incorporation of environmental variability into estimates of unfished reference points and assessments of fisheries depletion have been limited (Haltuch et al. 2009, King et al. 2015). When studies have controlled for environmental influences on fish biomass, there were marked improvements in estimates of unfished biomass (Williams et al. 2015) and detectability of fishing effects (Hamilton et al. 2010, Caselle at al. 2015). Thus, properly accounting for environmental variability may increase the accuracy of assessing fisheries resources.

Failure to integrate environmental influences into evaluations of depletion status is especially common in data poor systems such as coral reefs. The paucity of long term catch and biomass data in coral reef fisheries has limited the application of traditional stock-assessment methods for estimating unfished reference points (Zeller et al. 2014). Instead, first-order approximations of $B_{unfished}$ are typically generated from current biomass estimates at unfished locations such as remote, unpopulated areas or long established marine protected areas where the effects of fishing are minimal (Williams et al. 2001, Edwards et al. 2013, McClanahan et al. 2007, but see Ault et al. 2008, Nadon et al. 2015 for alternatives using length-based methods). Consequently, past studies of fishing effects on coral reef fishes have generally had two key ingredients for depletion estimates: (i) current estimates of herbivore biomass in populated, fished areas, and (ii) current estimates of herbivore biomass in unpopulated areas or regions where fishing is prohibited. However, biomass at unfished locations may not be a reasonable proxy for unfished biomass at locations where fishing is currently nonzero, especially if environmental conditions vary between fished and unfished areas (Hamilton et al. 2010, Caselle at al. 2015). Thus, a third key ingredient for estimating depletion of fish biomass when implicit space-for-time substitutions are used to approximate $B_{unfished}$ is a proper accounting of environmental factors that might differ between fished and unfished locations.

In this study I describe spatial patterns of herbivorous fish biomass across fished and unfished regions of the Hawaiian Archipelago to evaluate whether accounting for environmental variability between these regions alters estimates of unfished biomass and fisheries depletion. I focus on herbivorous fishes because of their importance in maintaining the function and resilience of coral reef benthic communities (Mumby et al. 2007, Hughes et al. 2010). These consumers graze turf and macroalgae, groups that compete with coral for space (Lewis 1986, Paddack et al. 2006, Hughes et al. 2007a, Mumby 2009). When abundances of herbivorous fishes are reduced, algae are released from grazing which can lead to shifts in benthic community composition from abundant corals to abundant macroalgae (McClanahan 1997, Burkepile et al. 2008, Hughes et al. 2007b). Consequently, overfishing of herbivorous fishes has been identified as a driver of increases in macroalgae and coral reef degradation (Burkepile & Hay 2009, Hughes et al. 2010, Jouffray et al. 2015). In the Hawaiian Archipelago, substantial declines of herbivorous fish biomass have been reported along gradients of human population density (Williams et al. 2008) and biomass levels in fished locations have been estimated to be less than 35% of biomass at unfished locations (Williams et al. 2011). These differences in fish biomass, however, did not account for spatial variability in environmental factors known to influence fish biomass in Hawaii such as habitat complexity, depth, and benthic composition (Friedlander & Parrish 1998, Friedlander et al. 2003, Friedlander et al. 2007). Instead, biomass differences were solely attributed to the presence of humans. Here, I re-assess differences in herbivorous fish biomass between fished and unfished regions of the Hawaiian Archipelago with a novel data set and analytical approach to answer two questions: (1) how do environmental factors influence herbivorous fish biomass across the HA? and (2) how does incorporating spatial variability of environmental conditions affect estimates of $B_{unfished}$ and depletion in the MHI?

METHODS

Study region

The Hawaiian Archipelago is comprised of 18 islands and atolls which span 2600 km in the central Pacific Ocean. The archipelago is broadly divided into the inhabited Main Hawaiian Islands (MHI) and the sparsely habited Northwestern Hawaiian Islands (NWHI). The MHI have variable human populations ranging from the lightly populated island of Niihau (170 persons) to the heavily populated island of Oahu (953,207 persons, Table 2.1). Human populations in the NWHI are limited to small groups of workers at French Frigate Shoals and Midway Atoll and seasonal field camps at other reefs. Despite the geographic isolation of the NWHI, anthropogenic influences are present (Selkoe et al. 2008). However, the magnitude of human influence in the NWHI is much less compared to the populated MHI. Over the past century, fishing effort in the NWHI, especially for reef fish, has been relatively low (Kittinger et al. 2011) and fishing has been prohibited in the region since 2000. In contrast, fisheries in the MHI have been exploited since AD 1250 with increasing pressure commensurate with a growing population during the last century (Kittinger et al. 2011).

Sampling framework and fish survey method

This study focused on forereef habitat at the seven largest islands in the MHI and NWHI (Table 2.1). Between 2010 and 2013, fish and benthic surveys were conducted at 517 forereef sites with data being collected between August and November of each year (Appendix A: Figure A1). Survey sites were randomly selected from shallower than 30 meter, hard bottom habitat at each reef. At each site, divers surveyed fishes using a modified stationary point count (SPC) method (Williams et al. 2011). For the SPC, two divers conducted simultaneous counts in adjacent 15 m diameter cylinders extending from the substrate to the limits of vertical visibility. Each SPC consisted of two components: a 5-minute species enumeration period in which divers recorded all fish species present in or moving through their cylinder, followed by a tallying portion, in which divers systematically recorded the number and size (total length to nearest cm) of all fishes of each taxon on their list.

Response variables and biomass calculations

Site-level estimates of fish biomass per unit area were used as the core response variables in this study. Because feeding preferences of herbivorous reef fishes are diverse and functional differences have been linked to different aspects of benthic community composition in the HA (Jouffray et al. 2015), I examined spatial biomass patterns of three main herbivore feeding guilds (scrapers, grazers, and browsers) in addition to the aggregate sum of herbivore biomass (Appendix G: Table G1). Scrapers included parrotfish in the *Scarus* and *Chlorurus* genera that feed on the surface of reef substrates providing areas clear of algae important for coral and crustose coralline algae settlement (Mumby 2006b). Grazers limit the establishment of macroalgae by intensely feeding on algal turfs and included surgeonfish species from the

Acanthurus, *Ctenochaetus*, and *Zebrasoma* genera (Marshell & Mumby 2015. Browsers feed directly on macroalgae and included surgeonfish from *Naso* genus and parrotfish from the *Calotomus* genus (Hoey & Bellwood 2010). Additionally, the three functional groups vary broadly in their susceptibility to fishing as scrapers and browsers tend to be larger and have lower natural mortality rates compared to grazers, while scrapers are one of the most targeted reef fish in Hawaii (Friedlander & Parrish 1997, Choat & Robertson 2002, Froese & Pauly 2010). Therefore, by analyzing herbivore functional group data separately and in summation, I was able to investigate whether depletion varied within herbivorous fish communities in the MHI.

Mass of individual fishes was calculated using length to weight conversion parameters taken from published and web-based sources (Froese & Pauly 2010, Kulbicki et al 2005). Because SPC replicates at each site were not independent and varied (either 2 or 4 reps/site), biomasses were summed by species for each SPC replicate and averaged by site. Site-level species biomasses were then pooled into the four response variables (total herbivore, scrapers, grazers, and browsers biomass), based on feeding information taken from FishBase (Froese & Pauly 2010, appendix).

Predictor variables – site scale

I considered three site-level predictor variables (depth, habitat complexity, and benthic composition; Table 2.1) known to influence reef fish abundance (Friedlander & Parrish 1998, Friedlander et al 2003). Information on each predictor was collected by divers during each fish survey. Depth (DEPTH) was recorded in situ directly from pressure gauges. Habitat complexity (COMP) was measured in two ways: In 2010 and 2011, divers estimated complexity on a 5-point scale (1 = very low, to 5 = very high). In 2012 and 2013, divers estimated the maximum vertical relief within their cylinder and the proportion of their cylinder in different relief bins (<0.2 m; 0.2–0.5 m; 0.5–1.0 m; 1.0–1.5 m; >1.5 m from substrate) which were used to generate a mean vertical relief value for each cylinder. Because habitat complexity was estimated using two different methods, I used a data calibration from Williams et al. (2015) to generate an estimate of mean vertical relief at each site surveyed in 2010 and 2011 (Williams et al. 2015).

To determine benthic composition, divers took photographs at 1 m intervals along the diameter of each SPC cylinder. Benthic photographs were taken with a Cannon camera attached to a 1 meter monopod to ensure a fixed height above the seafloor (image area: roughly 0.15 m^2; .45 m by .34 m). Photos were later analyzed to estimate benthic cover by randomly projecting 15 points onto a 5 by 3 grid overlaid on each photo (450 points/site) and identifying the benthos under each point. Taxonomic resolution of benthic organisms varied, but produced estimates of the proportion of non-calcified substrate at each site (turf algae and non-calcified fleshy macroalgae). I used the proportion of non-calcified substrate at each site as a simple proxy for food availability (FOOD) where high values of non-calcified substrate represented more grazeable substrate.

Predictor variables – island scale

The island-scale predictor variables I considered included both anthropogenic (fishing pressure) and environmental (sea-surface temperature) factors known to influence reef fish abundance (Table 2.1; Williams et al. 2008, Floeter et al. 2005). Information on fishing pressure in the MHI is not available. Instead, human population density scaled by reef area (HUM) was used as a proxy for fishing pressure (Williams et al. 2008, Table 2.1). Human population data came from the 2010 US census (www.census.gov/2010census). Following Gove et al. (2015), I quantified temperature using the lower climatological mean sea-surface temperature (SSTL) at each island. Water temperatures vary seasonally, therefore, SSTL is a good representation of the absolute thermal gradient across the HA. These estimates were calculated from remotely-sensed data collected between 1985 and 2009 (Gove et al 2015).

Data analysis

Data analysis proceeded in two phases. In the first phase, I described associations of fishing and local environmental factors with herbivorous fish biomass. I generated hypotheses for explaining spatial patterns of herbivorous fish biomass from site- and island-scale predictor variables and evaluated the support for each hypothesis using generalized linear models (GLMs). In the second phase, I used model predictions of fish biomass from phase 1 to estimate unfished biomass ($B_{\text{unfished-local}}$) at each island. This approach is similar to Williams et al. (2015) but I used site-level fish biomass as a response variable rather than islands-averages of biomass. Therefore, predictions of $B_{\text{unfished-local}}$ accounted for both site-and island-scale variability in environmental factors. Additionally, I estimated unfished biomass from fish biomass observations across the NWHI ($B_{\text{unfished-regional}}$), which is identical to previous studies which utilized space-for-time substitutions to estimate unfished biomass (Williams et al. 2011, Edwards et al. 2014). This allowed me to compare how depletion estimates vary when unfished biomass reference points account for environmental differences ($B_{\text{unfished-local}}$) and do not ($B_{\text{unfished-regional}}$).

Hypotheses for spatial patterns of herbivore biomass

I generated eleven hypotheses (candidate models) for assessing spatial patterns of herbivorous fish biomass from site- and island-scale predictor variables (Table 2.2). All hypotheses included human population density and habitat complexity because both fishing and habitat have been shown to influence fish biomass across a wide range of studies (fishing: Newman et al. 2006, Sandin et al. 2008, Williams et al. 2011; habitat: (Hixon & Brostoff 1985, Hixon & Beets 1989, Hixon & Beets 1993, Friedlander & Parrish 1998). I included a habitat complexity and food availability interaction based on evidence that both habitat complexity and food availability can influence herbivorous fish biomass (Mumby et al. 2013) and the potential for herbivore biomass to respond differently to high complexity habitat with high proportions of un-calcified substrate (lots of food & good habitat) compared to low complexity habitat with low proportions of un-calcified substrate (little food & poor habitat). I did not include a fishing and depth interaction (potential for depth refuge from fishing; Tyler et al. 2009, Lindfield et al. 2014) or a fishing and habitat complexity interaction (potential for fishing effects to differ between habitat complexities). While ecologically plausible, exploratory analysis did not indicate that these interactions were present. I limited models to 5 terms and included all combinations of depth, SSTL, food availability, and the habitat complexity & food availability interaction to prevent overfitting the data (11 candidate models; Table 2.2).

Environmental and human associations with herbivore biomass

I used mixed-effects GLMs to evaluate support for 11 candidate models of potential influences on site-level herbivorous fish biomass. Human population density, depth, SSTL, and food availability were included as fixed-effects and the nominal variable island was included as a random-effect to account for the non-independence of sites within each island (Table 2.2). Exploratory analysis of biomass data indicated scraper and browser categories had an abundance of zeroes (25.5% and 35.4%, respectively). To accommodate this statistical issue, I used a 2-stage modeling approach for scraper and browser response variables (Figure 2.1). In the first stage, I modeled occurrence (presences/absence) using a binomial distribution with the probability of fish occurrence linked to predictor variables via a logit function. Because SSTL and the habitat & food availability interaction were not expected to influence the occurrence of scraper or browser biomass, I examined a different set of candidate models for explaining the presence of scrapers and browsers (Appendix F). Fish biomass conditional on presence was then modeled in the second stage. Because fish biomass data were positively skewed, I used the Gamma distribution with a log link for conditional biomass models. Predicted biomasses for scraper and browser categories were then calculated as the product of occurrence probabilities and predicted conditional biomasses. Herbivores and grazers were present at all sites and, therefore, only the conditional abundance model (stage-2) was used to predict biomass for these categories. Prior to analyses, human population density was square root transformed, the proportion of un-calcified substrate was logit transformed, and collinearity among predictor variables was examined using Pearson correlations and variance inflation factors (VIF). Collinearity was not problematic as the two highest correlation coefficients were between human population density and SSTL ($r = .58$), and structural complexity and calcified substrate ($r = .38$), and the highest VIF for any of the model combinations examined was low (max = 1.24).

I evaluated the relative levels of support for each hypothesis using Akaike Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson 2002). I calculated an AICc-based relative-importance weight (w_i) that indicated the level of support for each model, given the other models considered and the data (Burnham and Anderson 2002). I interpreted models with > 5% of the model-based support from w_i results as “top models” which were supported by the data (Burnham & Anderson 2002). Model assumptions were validated through visual inspection of residuals and a crude goodness- of-fit test (see Appendix E).

To describe the strength of associations between fish biomass and predictor variables from “top models,” I plotted model-averaged predictions weighted according to Akaike model weights (w_i). For each variable of interest, I predicted fish biomass across the range of that variable's minimum and maximum value, while setting all other predictor variables to their means. Because I was interested in describing the influence of environmental factors on fish biomass without the confounding influence of fishing, human population density was set to 0 for all predictions.

All models were fit in R (R Development Core Team 2015) using the lme4 package (Bates et al. 2015).

Estimates of unfished biomass and herbivore depletion

I estimated unfished biomass for each of the four herbivorous fish biomass categories using two methods. To account for within- and across- island differences in environmental factors and their influence on unfished biomass, I predicted $B_{unfished\text{-}local}$ at each island and across the MHI. For each island, $B_{unfished\text{-}local}$ was calculated from model-weighted predictions of herbivorous fish biomass. First, I predicted fish biomass at each site based on site-specific environmental covariates and human population density set to 0. Next, I averaged site-level biomass predictions by island (and MHI) to incorporate local variability of environmental conditions into predictions of $B_{unfished\text{-}local}$. Similar to previous studies which did not account for environmental influences on estimates of unfished biomass, I used mean observed biomasses across the unfished NWHI as an alternative reference point to unfished biomass ($B_{unfished\text{-}regional}$). Because fishing is prohibited in the NWHI, estimates of $B_{unfished}$ should closely match observed biomass levels. Therefore, I examined how well island predictions of ($B_{unfished\text{-}local}$) and estimates of ($B_{unfished\text{-}regional}$) matched mean observed biomass at each island in the NWHI as a coarse approximation of model fit (see Appendix E).

I defined depletion as the ratio between observed fish biomass at fished locations to unfished biomass (B_{fished} : $B_{unfished}$). I calculated depletion at each island as well as the MHI using both $B_{unfished\text{-}local}$ ($Depletion_{unfished\text{-}local}$) and $B_{unfished\text{-}regional}$ ($Depletion_{unfished\text{-}regional}$) as reference points for unfished biomass. Uncertainties in observed mean biomasses, $B_{unfished\text{-}local}$, and depletion were estimated with nonparametric bootstrapping. Data were resampled with replacement 10,000 times. For each bootstrapped sample, mean biomass was recalculated for each island and the NWHI region ($B_{unfished\text{-}regional}$), weighted model averages were used to predict $B_{unfished\text{-}local}$, and depletion was calculated for each island (and MHI) using both $B_{unfished\text{-}local}$ and $B_{unfished\text{-}regional}$. Uncertainties were then calculated for observed biomasses, $B_{unfished\text{-}regional}$, and both local and regional depletion using bias-corrected 90th percentile confidence intervals.

To examine potential differences in herbivore depletion estimates when environmental influences on unfished biomass were ($B_{unfished\text{-}local}$) and were not accounted for ($B_{unfished\text{-}regional}$), I used the following test statistic:

$$(1) \quad Depletion_{diff} = \frac{Depletion_{unfished-local} - Depletion_{unfished-regional}}{Depletion_{unfished-local}}$$

where $Depletion_{diff}$ is the relative difference between depletion estimates which used $B_{unfished\text{-}local}$ ($Depletion_{unfished\text{-}local}$) and depletion estimates which used $B_{unfished\text{-}regional}$ ($Depletion_{unfished\text{-}regional}$) as references for unfished biomass. A test statistic of zero indicates no difference in depletion estimates between the two measures of unfished biomass. Positive test statistics indicate underestimation of depletion by $B_{unfished\text{-}regional}$; while negative test statistics indicate overestimation of depletion by $B_{unfished\text{-}regional}$. This test statistic was calculated for each of the four herbivorous fish categories during each bootstrapped sample and significant differences were determined to exist when confidence intervals did not overlap 0.

RESULTS

Hypotheses for spatial patterns of herbivore biomass

Model selection results for total herbivore biomass strongly favored the fishing and habitat-food availability interaction model (M5, Table 2.3). While there was support for the addition of depth (M10) and temperature (M9) terms (Table 2.3), it was limited and these variables had minimal influences on biomass predictions (predicted biomass difference between min and max values of respective variables < 10%). Model selection results for grazer biomass strongly favored the fishing, temperature, and habitat-food availability interaction model (M9, Table 2.3).

Predictions of scraper and browser biomass incorporated results from both occurrence and conditional biomass models. Scraper occurrence was strongly associated with habitat complexity with limited support for depth and/or human influences (Appendix F: Table F1 & Figure F1). Model selection results for conditional scraper biomass strongly favored the fishing, habitat, depth, and food availability model (M8, Table 2.3). Predictions of browser biomass incorporated results from both occurrence and conditional biomass models. Browser occurrence was not strongly associated with any of the predictor variable (deviance explained only 4.8% for the top model). Therefore, I assumed browser presence was the same across all sites and used the null estimate of browser presence (64.6%) as the browser occurrence probability. Model selection results for conditional browser biomass showed similar levels of support for the habitat, depth, food availability, and fishing model (M8) and the fishing and habitat-food availability interaction model (M5, Table 2.3), however the interaction was weak.

Environmental and human associations with herbivore biomass

Overall, environmental factors strongly influenced predictions of herbivorous fish biomass in addition to human population density (Figure 2.2). Habitat complexity and food availability were important for all four response variables (total, scraper, browser, grazer biomass; Figures 2.2 & 2.3). Biomass of herbivorous fishes and the occurrence of scrapers demonstrated strong positive associations with complexity (Figure 2 & Appendix F: Figure F1). Predictions of herbivorous fish biomass increased more than 4-fold across the range of complexity values (Figure 2.2). However, there was support for an interaction between complexity and food availability for total herbivore and grazer response variables (Table 2.3). Predictions of herbivore and grazer biomass were low when both food availability and habitat complexity were low, but were disproportionately high when food availability and complexity were high (Figure 2.3). Browser biomass had the strongest positive association with food availability (>14 fold increase; Figure 2.2). Depth was only found to be important for the scraper and browser categories, but there responses varied (scraper biomass positively associated, browser biomass negatively associated with depth; Figure 2.2). Grazer biomass was the only response variable associated with temperature, with biomass expected to double across the SSTL gradient (Figure 2.2). All four response variables had negative associations with humans (Figure 2.2). The association with human influence was greatest for scraper biomass, which was expected to be reduced to 10.8% of its maximum when human population density was 0, and weakest for grazer biomass, which was only expected to be reduced to 51.7% of its maximum when fishing was absent (Figure 2.2).

Estimates of unfished biomass and herbivore depletion

Predictions of unfished biomass that accounted for environmental influences on biomasses of herbivorous fish categories ($B_{\text{unfished-local}}$) illustrated considerable variability across islands in the Hawaiian Archipelago compared to estimates of $B_{\text{unfished-regional}}$ which ignored differences in environmental conditions (Figure 2.4). Predictions of $B_{\text{unfished-local}}$ varied among herbivorous fish categories and across islands (Figure 2.4). Overall, predictions of $B_{\text{unfished-local}}$ for all herbivorous fishes varied by a factor of two and were highest at Midway (mean=24.9 g m^{-2}, 90% prediction interval: 18.7-31.2) and lowest at Oahu (mean=12.1 g m^{-2}, 90% prediction interval: 7.8-16.4). Predictions of $B_{unfished-local}$ for scrapers also varied by a factor of almost two and were highest at Lisianski (mean=9.5 g m^{-2}, 90% prediction interval: 7.1-11.9) and lowest at Oahu (mean=5.0 g m^{-2}, 90% prediction interval: 3.9-6.1). Predictions of $B_{unfished-local}$ for grazers varied by a factor of almost three and were highest at Hawaii (mean=12.0 g m^{-2}, 90% prediction interval: 7.8-16.1) and lowest at Kure (mean=4.2 g m^{-2}, 90% prediction interval: 1.9-6.4). Predictions of $B_{unfished-local}$ for browsers were the lowest of all herbivorous fish categories. Browser predictions of $B_{unfished-local}$ varied by a factor of four and were highest at Midway (mean=6.2 g m^{-2}, 90% prediction interval: 4.6-7.8) and lowest at LIS (mean=1.1 g m^{-2}, 90% prediction interval: 0.2-2.1). Mean observed biomasses across the NWHI ($B_{unfished-regional}$) for each of the four herbivorous fish categories are presented in Figure 4. Estimates of $B_{unfished-regional}$ were generally higher than $B_{unfished-island}$ predictions for the scraper category, lower for grazers, and variable for browser and total herbivore categories (Figure 2.4).

Conclusions about herbivore depletion in the MHI varied based on which unfished biomass reference point ($B_{unfished-local}$ or $B_{unfished-regional}$) was used. Estimates of depletion based on $B_{unfished-regional}$, tended to overestimate scraper depletion by up to 42% (Oahu 90% CI: 33.0-49.5) and underestimate grazer depletion (Figure 2.5). Depletion patterns for herbivore and browser biomass were less consistent across islands (Figure 2.5). Comparisons of mean observed biomasses at islands in the NWHI with predictions of $B_{unfished-local}$ and estimates of $B_{unfished-regional}$ indicated that predictions of $B_{unfished-local}$ were generally closer to mean observed biomass at each island in the NWHI compared to $B_{unfished-regional}$ (Figure 2.4 & Appendix E); therefore, depletion estimated based on $B_{unfished\text{-}local}$, were used to describe depletion patterns of herbivorous fish biomass in the MHI.

Overall, scraper biomass was the most depleted and grazer biomass the least depleted in the MHI (Figure 2.6), however, spatial depletion patterns varied greatly. Scraper biomass depletion was highest on Oahu (mean=11.4%, 90% CI: 6.8-17.1) and was estimated to be greater than 50% at Kauai, Hawaii, and Maui (Figure 2.6). Yet, scraper biomass at the least populated island in the MHI, Niihau, was estimated to be 86.6% of $B_{unfished\text{-}local}$ (90% CI: 65.6%-108.1%). Grazer depletion was highest on Oahu, but was only estimated to be at 59.4% of $B_{unfished\text{-}local}$ (90% CI: 47.6-70.3) while grazer biomass at Molokai was estimated at 93.5% of $B_{unfished\text{-}local}$ (90% CI: 76.6%-112.6%).

DISCUSSION

Over the last decade, a growing number of studies have estimated differences in reef fish biomass between fished and unfished areas (Williams et al. 2011, Edwards et al. 2014, Karr et al. 2015). However, only recently have studies begun to account for environmental influences on unfished biomass reference points (Williams et al. 2015). The main findings of this study show that (1) site-level variability of environmental conditions, as well as human population density, are strongly associated with herbivorous fish biomass in the Hawaiian archipelago, (2) local environmental factors affect island-scale predictions of unfished biomass, (3) ignoring the influence of local environmental factors on herbivorous fishes can result in both over- and under-estimation of biomass depletion, and (4) overall, herbivorous fish biomass across the MHI is above 50% of $B_{unfished\text{-}local}$, however, localized depletion varies both spatially (by island) and by herbivore functional groups. In sum, these results suggests that failure to account for environmental influences on fish biomass results in strikingly different conclusions about herbivore depletion in coral reef fish communities.

Clearly, humans alter fish communities on coral reefs (Newman et al. 2006, Newton et al. 2007, Williams et al. 2011), yet local environmental influences can play an equivalent or greater role in determining fish biomass. In the Main Hawaiian Islands, when local environmental factors were ignored, depletion of herbivorous fish biomass was exaggerated in some cases and underestimated in others. For scrapers, which are highly prized fisheries targets and perform the key ecological function of creating new calcified substrate on the reef benthos while foraging (Bellwood et al. 2012), biomass depletion was exaggerated by up to 45% when environmental factors were ignored. The exaggeration of scraper biomass depletion based on $B_{\text{unfished-regional}}$ was partially related to the failure to account for differences in habitat complexity between the unfished NWHI and the fished MHI. Habitat complexity had a strong positive association with scraper presence and conditional biomass and because complexity was generally higher in the NWHI compared to the MHI, predictions of $B_{\text{unfished-local}}$ for scrapers in the MHI tended to be lower than $B_{\text{unfished-regional}}$.

In contrast to predictions of unfished scraper biomass, predictions of $B_{\text{unfished-local}}$ for grazer biomasses in the MHI were almost always higher than $B_{\text{unfished-regional}}$. Therefore, when $B_{\text{unfished-regional}}$ was used to estimate grazer depletion, depletion was not only underestimated, but observed biomass levels in the MHI were often higher than $B_{\text{unfished-regional}}$. The idea that biomass of lower-trophic level species can exceed unexploited levels is consistent with the idea of prey-release associated with trophic cascades (Boaden & Kingsford 2015). Expectations of prey release in fished areas could influence depletion estimates and should be accounted for. However, during exploratory data analysis, a relationship between grazer biomass and piscivorous fishes across the NWHI was not evident. Furthermore, a trophic release due to reduction in predation in the MHI is unlikely for grazers because all fishes in this functional group are targets of either subsistence or aquarium fishing in Hawaii (Friedlander & Parrish 1997, Williams et al. 2008). An alternative explanation for the expected increase in grazer biomass in the MHI is that environmental conditions in this region can support more grazer biomass than the NWHI. Lower climatological mean sea-surface temperatures were 5°C warmer at the southernmost island of Hawaii compared to the northernmost island, Kure Atoll and grazer biomass in this study had a strong positive association with sea-surface temperatures. For example, biomasses of the yellow tang (*Zebrasoma flavescens*) were generally higher in the warmer MHI and large *Acanthurids* (*A. blochii, A. dussumieri, A. maculiceps, A. olivaceus, A.xanthopterus*) were relatively uncommon at the three northern atolls which are exposed to the coldest water temperatures in the Hawaiian Archipelago (almost a 2°C drop in SSTL compared to the closest island: Lisianski). While previous work has shown colder sea-surface temperatures can limit the abundance of herbivorous fishes possibly due to decreased feeding and metabolic efficiencies (Floeter et al. 2005), it is also possible that the thermal SST gradient in the Hawaiian Archipelago is explaining variability in grazer biomass related to other oceanographic processes. For example, ocean currents and eddies in the southern islands of the MHI contribute to local retention of fish larvae in these regions (Christie et al. 2010). Thus, more work is needed to evaluate mechanistic explanations for elevated expectations of grazer biomass in the MHI. Regardless of the mechanism, after controlling for the predicted increase in grazer biomass in the MHI, grazer biomass was expected to be less than unfished levels ($B_{unfished\text{-}local}$), which is consistent with the idea that exploitation rather than prey release is influencing grazer biomass in the MHI.

Given the strong environmental associations of herbivorous fish community biomass in the Hawaiian Archipelago, depletion estimates that account for spatial differences in unfished biomass provide a better representation of fishing effects on herbivorous fish biomass in the MHI. Biomasses of the four herbivorous fish categories across much of the MHI were near or above 0.5 $B_{\text{unfished-local}}$, a common reference point for fisheries sustainability based on single-species surplus-production models (Hilborn 2010). These results suggest that herbivorous fish in Hawaii may not be as depleted as previously believed (Williams et al. 2011, Edwards et al. 2013) which is consistent with a recent stock assessment of Hawaii reef fish (Nadon et al. 2015). Many areas in the MHI are relatively far from human population centers and inaccessible to fishermen without boats (Williams et al. 2008). These factors may contribute to the relatively low depletion levels of herbivorous fish communities across much of the MHI and should translate to these reef areas having higher resilience to shifts in benthic communities (Mumby et al. 2007, Hughes et al. 2007). This is not true, however, on the island of Oahu where the combination of the high human population density and low predictions of unfished biomass led to the highest depletion estimates for herbivore biomass in the MHI.

It is worth noting that anthropogenic activities can affect reef fishes directly through exploitation and indirectly through habitat degradation. Oahu, the island with the highest human population density in the MHI, also had the least complex habitat of any island in this study (Appendix G: Figure G1). High human population densities have been linked to increased sedimentation and eutrophication which can degrade coral reef habitat (Edinger et al. 1998). In the Caribbean, human presence has been associated with the loss of physical reef structure, which can further exacerbate the effects of fishing (Alvarez-Filip et al. 2009). A valid concern, therefore, is that human population density could confound fishing and habitat degradation influences on fish biomass. Habitat complexity, however, was not correlated with human population density in the Hawaiian Archipelago. Instead, the lower mean habitat complexities on Oahu and Kauai seem related to island geomorphology and exposure to large wave events (Grigg 1997, Franklin et al. 2013). Furthermore, patterns of reef fish decline associated with human population density previously reported in Hawaii are not consistent with habitat degradation being a causative factor (Williams et al. 2008). Therefore, associations of herbivorous fish biomasses with human population densities in the MHI are probably more strongly related to the influence of fishing as opposed to habitat degradation.

This study highlighted the importance of accounting for environmental variability when describing spatial differences in fish biomass related to the exploitation of herbivorous fishes in the MHI. Spatial patterns of herbivorous fish biomass across the remote and unfished NWHI add to an emerging recognition that substantial differences in fish biomass can exist, even when fishing is absent (Williams et al. 2015). Furthermore, this study illustrated the importance of site-level spatial variability in habitat complexity, depth, and benthic composition for explaining spatial patterns of herbivorous fish biomass in addition to island-scale variability of oceanographic conditions. This work also contributed more broadly to efforts focused on assessing ecosystem effects of fishing on coral reefs. Recent investigations have shown it is possible to maintain important measures of coral reef ecosystem structure and function when fish biomass is maintained above 0.5 B_{unfished} (McClanahan et al. 2011, Karr et al. 2015). A key assumption of those studies was that gradients of fish biomass broadly reflect difference in fishing pressures. In other words, those studies assumed that fish biomass is a metric that is insensitive to factors other than fishing. This study and others (Valles et al. 2015) have shown that fish biomass is sensitive to environmental variability and should be controlled for when assessing fishing effects on coral reef fish. Therefore, it remains unclear how sustainable fishing reference points, such as 0.5 $B_{unfished}$, relate to key aspects of ecosystem structure and function on coral reefs. Moving forward, the depletion patterns of herbivorous fishes in the MHI described in this study could be used to generate hypotheses about ecosystem responses to fishing that can be tested with data.

Table 2.1. Study locations, number of surveys per island, and predictor variables. HUM – human population density; COMP – structural complexity; FOOD – proportion of un-calcified substrate; DEPTH – depth (m); SSTL – lower climatological sea-surface temperature (°C).

Region	Island	Forereef Area (HA)	# of surveys	**HUM**	**COMP**	**FOOD**	**DEPTH**	**SSTL**
MHI	Hawaii (HAW)	16,840	96	10.99	0.64	0.30	13.5	24.12
	Maui (MAI)	11,122	56	12.99	0.60	0.22	12.2	23.85
	Lanai (LAN)	3,004	35	1.03	0.55	0.20	10.7	24.10
	Molokai (MOL)	12,730	40	0.58	0.51	0.24	12.0	23.89
	Oahu (OAH)	25,119	44	37.95	0.33	0.15	12.9	23.87
	Niihau (NII)	9,266	37	0.02	0.46	0.06	14.1	23.65
	Kauai (KAU)	18,127	45	3.62	0.40	0.12	13.3	23.56
NWHI	French Frigate (FFS)	8,873	26	0	0.53	0.50	14.7	22.78
	Maro Reef (MAR)	25,607	21	0	0.62	0.57	12.6	21.73
	Laysan (LAY)	3,400	20	0	0.42	0.21	17.7	21.53
	Lisianski (LIS)	30,955	33	0	0.89	0.64	14.6	21.33
	Pearl & Hermes (PHR)	8,498	31	0	0.71	0.32	13.0	19.69
	Midway (MID)	3,294	17	0	0.65	0.18	15.1	19.31
	Kure (KUR)	2,438	16	0	0.70	0.27	13.7	18.98

Forereef area of <30m hard-bottom habitat per island comes from NOAA GIS maps used for survey design, and collated from a range of internal and external sources. Values of predictor variables represent island-means with the exception of HUM. Human population data per island comes from the 2010 US census (http://www.census.gov/2010census/). COMP was visually-estimated by divers during fish surveys. FOOD was estimated from benthic photos taken at each site. Max DEPTH was recorded at each site. SSTL were obtained Gove et al. (2013) and represent long-term (1985-2009) averages of oceanic surface waters surrounding islands.

Table 2.2. List of 10 candidate sets of fixed-effects used to quantify patterns of fish biomass. All models included a random ISLAND term to account for non-independence of sites within islands.

Model	Inferred Process	Fixed-effect terms	K
M1	Habitat and fishing	COMP + HUM	2
M2	Habitat, temperature, and fishing	COMP + SSTL + HUM	3
M3	Habitat, depth, and fishing	COMP + DEPTH + HUM	3
M4	Habitat, food availability, and fishing	COMP + FOOD + HUM	3
M5	Habitat, food availability, and fishing (interaction)	COMP + FOOD + COMP:FOOD + HUM	4
M6	Habitat, temperature, depth, and fishing	COMP + SSTL + DEPTH + HUM	4
M7	Habitat, temperature , food availability, and fishing	COMP + SSTL + FOOD + HUM	4
M8	Habitat, depth, food availability, and fishing	COMP + DEPTH + FOOD + HUM	4
M9	Habitat, temperature, food availability, and fishing (interaction)	COMP + SSTL + FOOD + COMP:FOOD + HUM	5
M10	Habitat, depth, food availability, and fishing (interaction)	COMP + DEPTH + FOOD + COMP:FOOD + HUM	5
M11	Habitat, temperature, depth, food availability, and fishing	COMP + SSTL + DEPTH + FOOD + HUM	5

Fixed-effect terms: HUM – human population density; COMP – structural complexity; FOOD – proportion of calcified substrate; DEPTH – depth (m); SSTL – lower climatological sea-surface temperature (°C).
K: number of fixed-effect parameters

Table 2.3. Model Selection results for conditional biomass of the four herbivore categories. All models with AICc weights > 0.05 are shown.

	Fixed-effect terms						Model Support	
Model	COMP	SST	DEPTH	FOOD	COMP:SUB	HUM	ΔAICc	w_i
Herbivores								
M5	X			X	X	X	0.0	0.52
M10	X		X	X	X	X	1.2	0.27
M9	X	X		X	X	X	2.1	0.19
Scrapers								
M8	X		X	X		X	0.0	0.80
M4	X			X		X	4.1	0.11
M3	X		X			X	4.4	0.09
Grazers								
M9	X	X		X	X	X	0.0	0.77
M5	X			X	X	X	3.6	0.12
M2	X	X				X	5.5	0.05
Browsers								
M8	X		X	X		X	0.0	0.49
M5	X			X	X	X	0.3	0.42

Details on predictor variables are given in Table 1: HUM – human population density; COMP – habitat complexity; FOOD – proportion of calcified substrate; DEPTH – depth (m); SSTL – lower climatological sea-surface temperature (°C). Details on models are given in Table 2.

w_i: AICc relative-importance weight

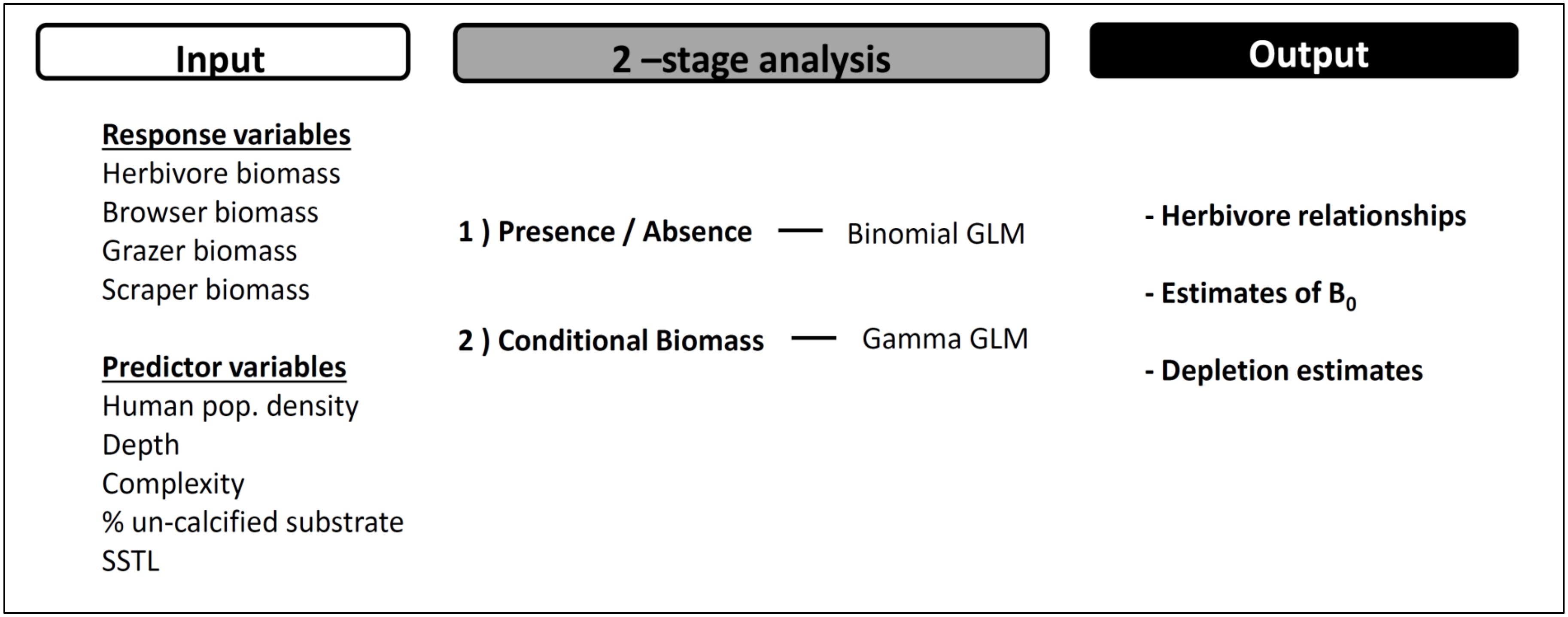

Figure 2.1. Conceptual diagram of data analysis.

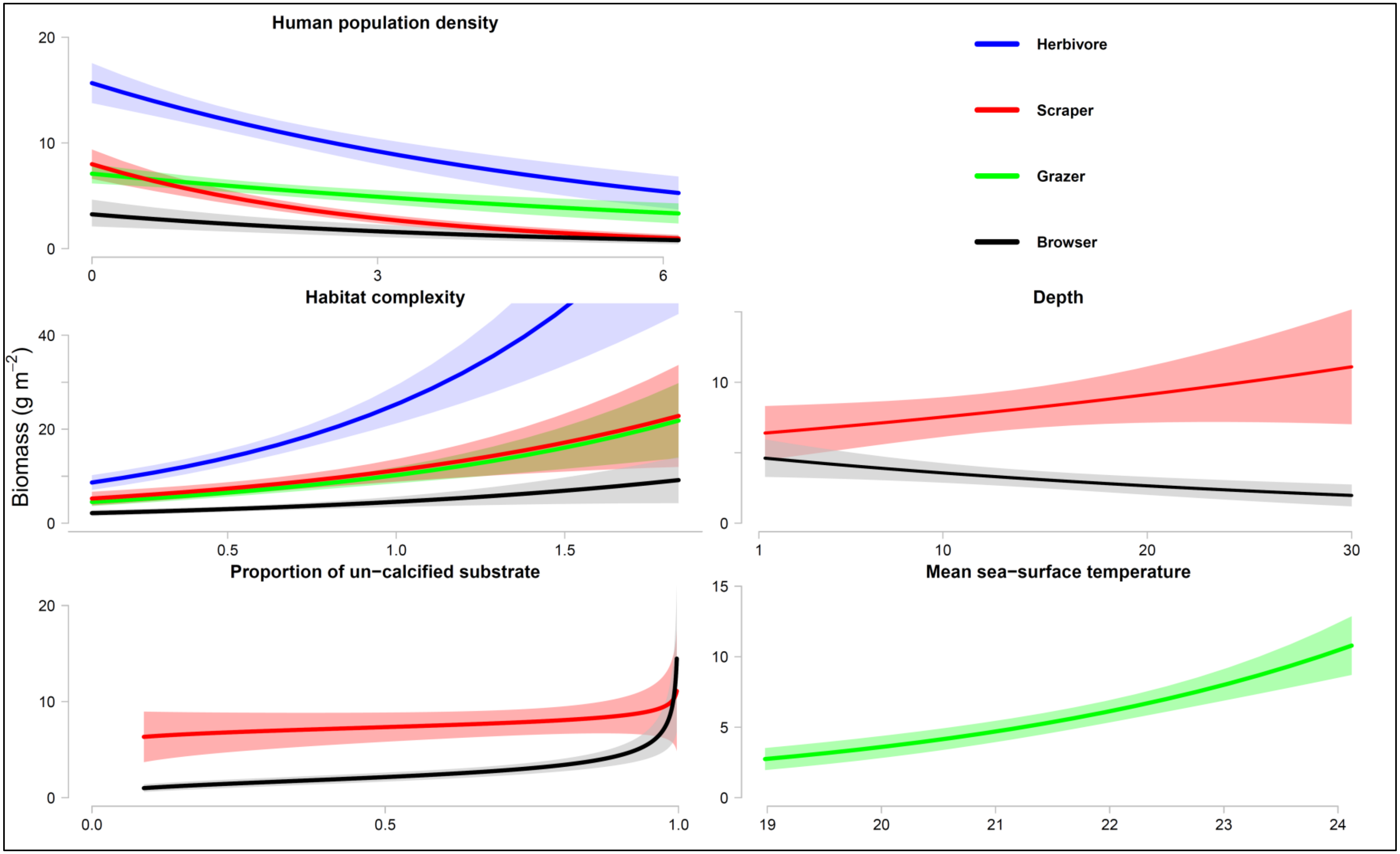

Figure 2.2. Predicted biomass relationships of all four herbivore categories (colored lines) across the five fixed-effect variables. Shaded regions reflect 95% confidence intervals. Only meaningful relationships are shown. For predictions, data values were held at variable means for variables other than the predictor, which was set to values equally spaced between the min and max across the HA.

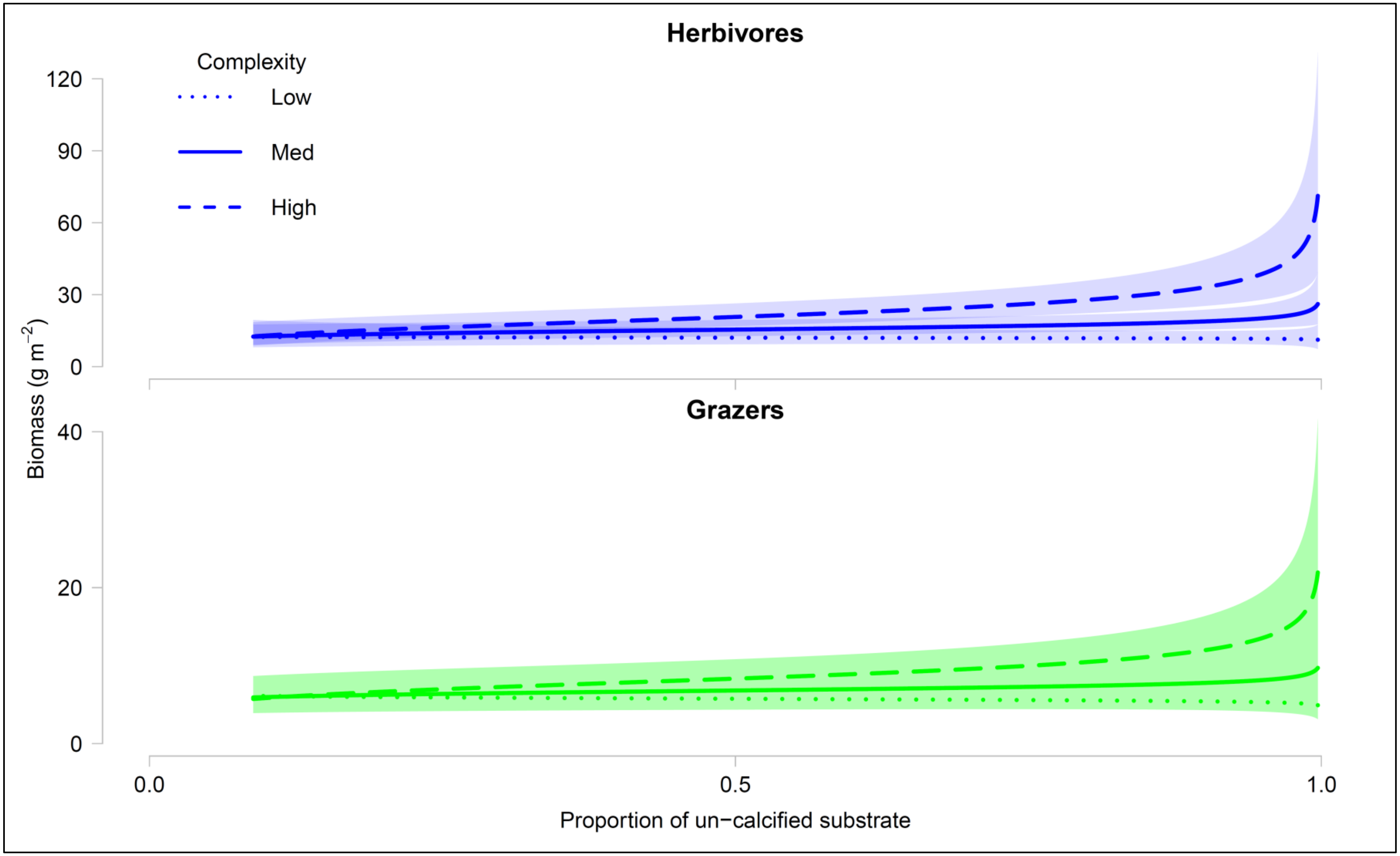

Figure 2.3. Predicted biomass relationships for herbivores and grazers (colored lines) based on the habitat complexity x food availability interaction. Lines represent three levels of habitat complexity (low, medium, and high). Shaded regions reflect 95% confidence intervals.

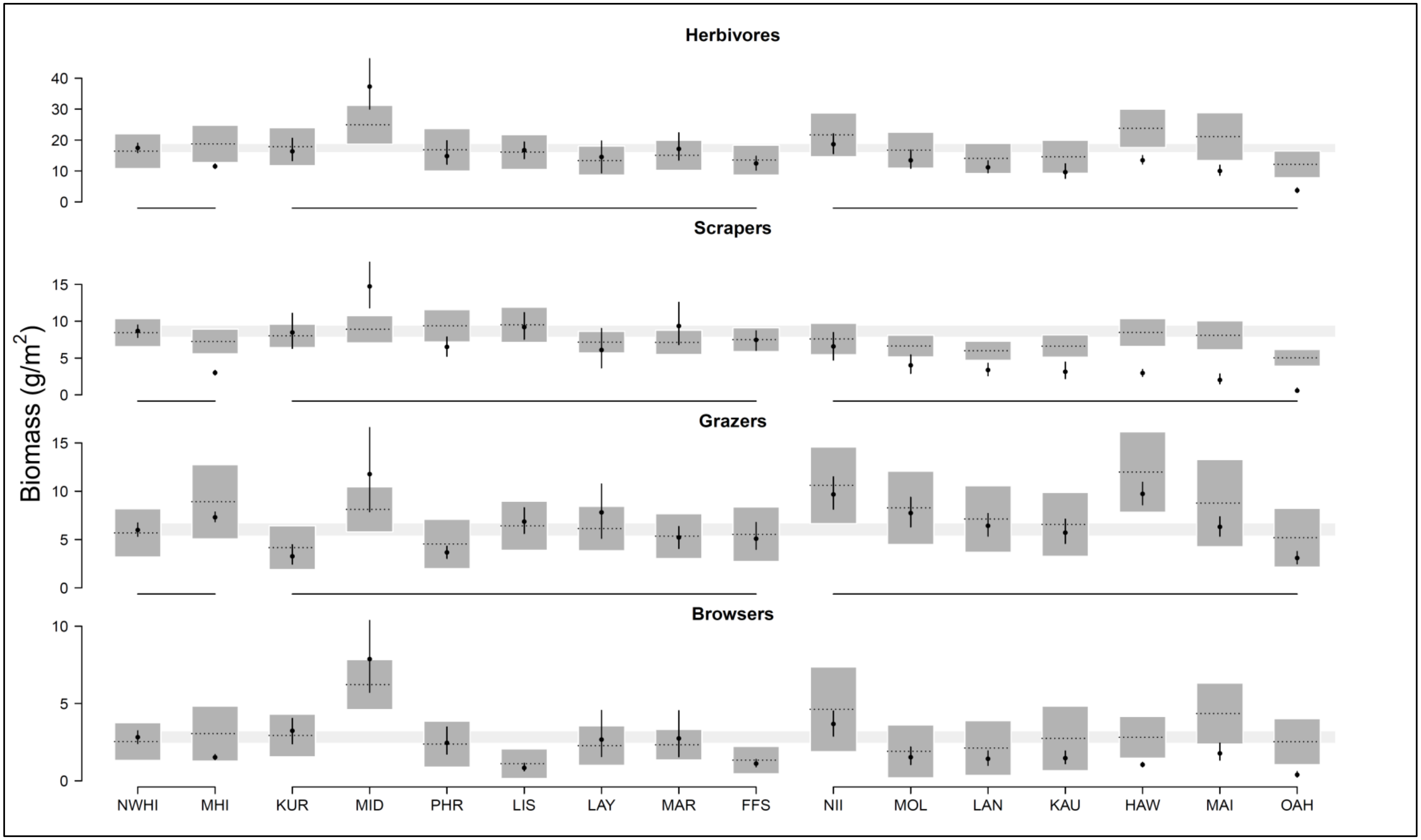

Figure 2.4. Variability in unfished biomass estimates and observed mean biomass in the Hawaiian Archipelago for the four herbivore categories. Dots and line segments represent observed mean biomass and 95% confidence intervals for each region (MHI & NWHI, left) and island (right). Observed biomass in the NWHI was used as an estimate of unfished biomass ($B_{\text{unfished-regional}}$) and is highlighted by the light grey rectangle. Dotted lines represent predictions of $B_{\text{unfished-local}}$ and dark grey rectangles represent 95% prediction intervals. Islands in the NWHI are sorted from north to south; MHI are sorted from low to high human population density.

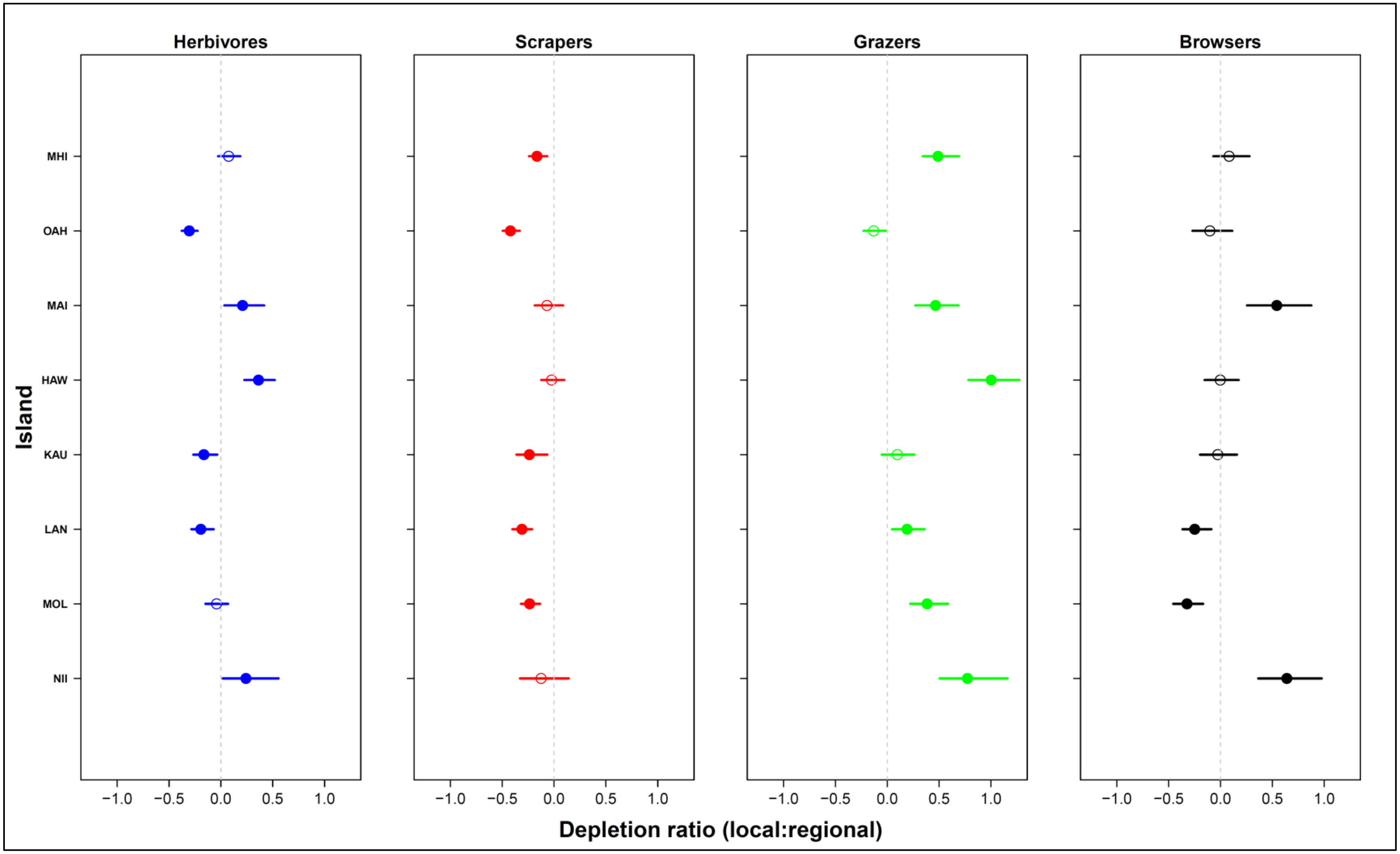

Figure 2.5. Relative differences between Depletion$_{\text{unfished-local}}$ and Depletion$_{\text{unfished-regional}}$. The dotted grey vertical line represents no difference between depletion estimates. Negative values indicate an overestimation of depletion by Depletion$_{\text{unfished-regional}}$, while positive values indicate underestimation. Depletion estimates presented for each island in the MHI (rows) and the four herbivorous fish categories (columns). Segments are 95% confidence intervals.

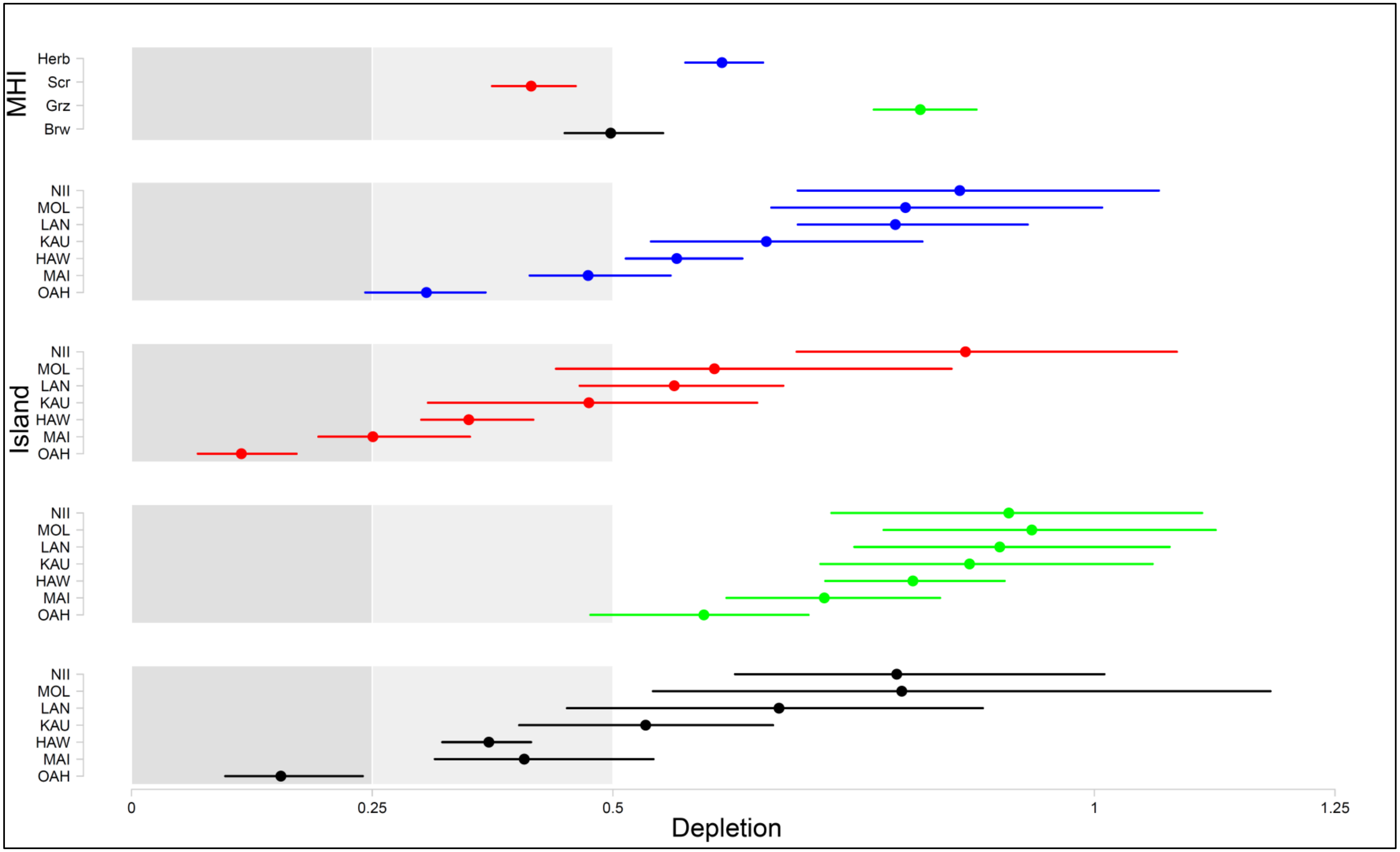

Figure 2.6. Depletion estimates (dots) and 95% confidence intervals (segments) based on $B_{\text{unfished-local}}$ for the four herbivore categories in the MHI by region (top) and by island (bottom). Colors correspond to herbivorous fish categories (blue – herbivores, red – scrapers, green – grazers, black - browsers). Islands are sorted from lowest to highest population density.

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Appendix A: Locations of surveys in the MHI and NWHI.

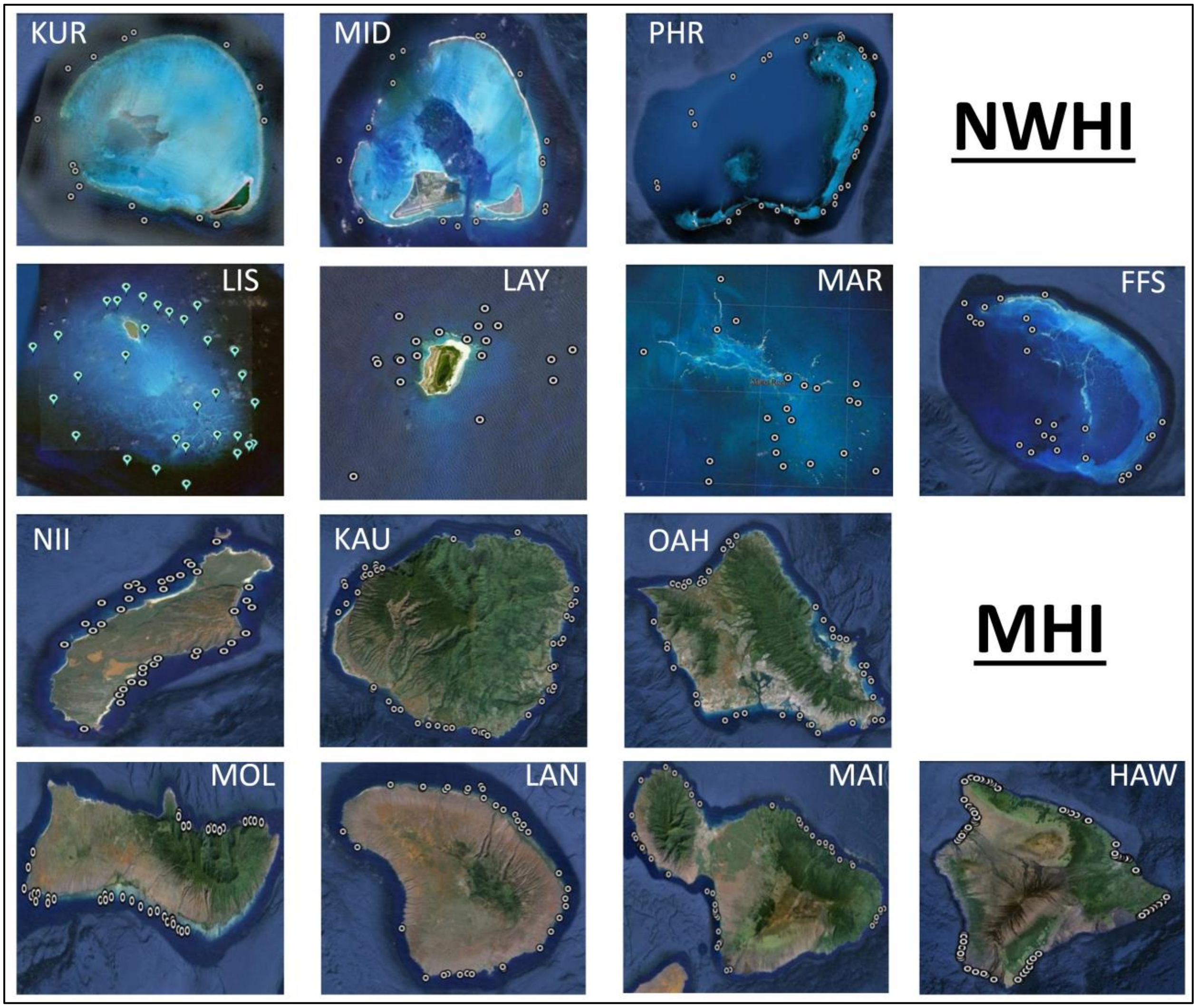


Figure A1. Locations of 517 surveys in the MHI and NWHI.

Appendix B: Chapter 1 supplement - Do benthic communities align with benthic functional groups?

The composition of benthic coral reef communities has most often been examined using functional group (hard coral, macroalgae, turf algae) data (Bruno et al. 2009, Zychaluk et al. 2012, Jouffray et al. 2015). Functional group data are easy to measure and widely available. However, the aggregated qualities of functional data may be too simple for describing communities in a complex system such as a coral reef. Functional groups are comprised of multiple species/genera/morphologies with varying life histories and environmental preferences. The use of aggregated data to describe benthic community structure assumes all members of an aggregated group respond to environmental/ecological change in the same manner. This assumption is not consistent with ecological succession and disturbance theories which predict species will not respond to changes equally (Grigg & Maragos 1974, Connell 1997, Hughes & Connell 1999). The coarse resolution of functional group data, therefore, may not accurately describe communities where members of different functional groups co-occur.

To examine whether benthic communities in the NWHI (a) aligned with benthic functional groups or (b) contained members of multiple functional groups, I compared characteristics of communities identified using coarse functional group data and finer resolution data which included a mix of coral and algal genera and functional group data (Table B1). The same multivariate cluster analysis was performed on each data resolution.

Cluster analysis of both coarser- and finer- resolution data revealed benthic community structure in the NWHI was best described by three community types. While the three community types identified by each data resolution were similar, subtle differences existed due to the co-occurrence of macroalgae and hard corals in the reef builder and mixed turf (Table B1).Of the 240 sites, 39 (16.3%) were classified differently (Figure B1).

To examine whether differences in community classifications based on benthic data resolution influence overall patterns of community occurrence across the NWHI, I used the following test statistic:

(B1) $$\frac{O_c - O_f}{O_f}$$

Where O_c is the occurrence of communities identified from coarser resolution data and O_f is the occurrence of communities identified from finer resolution data. A test statistic of zero indicates no difference in community occurrence estimates between the two data resolutions. Positive test statistics indicate occurrence of communities determined from coarser data were estimated to be greater than occurrence of communities determined from finer resolution data; while negative test statistics indicate the opposite. To evaluate the significance of the test statistic, I used a randomization approach. First, sites were randomly selected with replacement from each island-depth category to ensure the integrity of the sample design was preserved. Next, community classifications at each site determined from cluster analyses of the two data resolutions were used to estimate spatially weighted, mean occurrence at each island and across the NWHI region. The test statistic was then calculated for each island and region. Uncertainty was calculated using bias-corrected 90% confidence intervals. Significant differences were determined to exist when confidence intervals did not overlap 0.

There were no significant differences between the occurrence of benthic communities identified by coarser and finer resolution functional data at the scale of the NWHI region (Figure B2). At the island-scale, however, there were significant differences in community occurrence at all islands except for FFS (Figure B2). Significant differences were associated with islands that had relatively higher abundances of *Halimeda* (MAR, LIS, PHR), *Pocillopora* (KUR), and fleshy algae (MID) compared to other islands (Figure B3).

Table B1. Significant associations between benthic classes and cluster groups from Indicator Species Analysis for both coarser (left) and finer resolution benthic data. Coral classes are highlighted in blue, macroalgae in green.

Coarser resolution Functional group data

Cluster group	Benthic Class	Indicator value
1 - Coral + CCA	Hard coral	0.84
	CCA	0.71
2 -Turf	Turf algae	0.76
3 - Macroalgae	Macroalgae	0.79

Finer resolution functional group data

Cluster group	Benthic Class	Indicator value
1 - Reef builder	*Montipora* sp	0.83
	Massive *Porites* sp	0.81
	CCA	0.74
	Halimeda sp	0.74
2 -Mixed turf	Turf algae	0.76
	Fleshy algae	0.71
	Pocillopora sp	0.64
3 - *Microdictyon*	*Microdictyon* sp	0.93

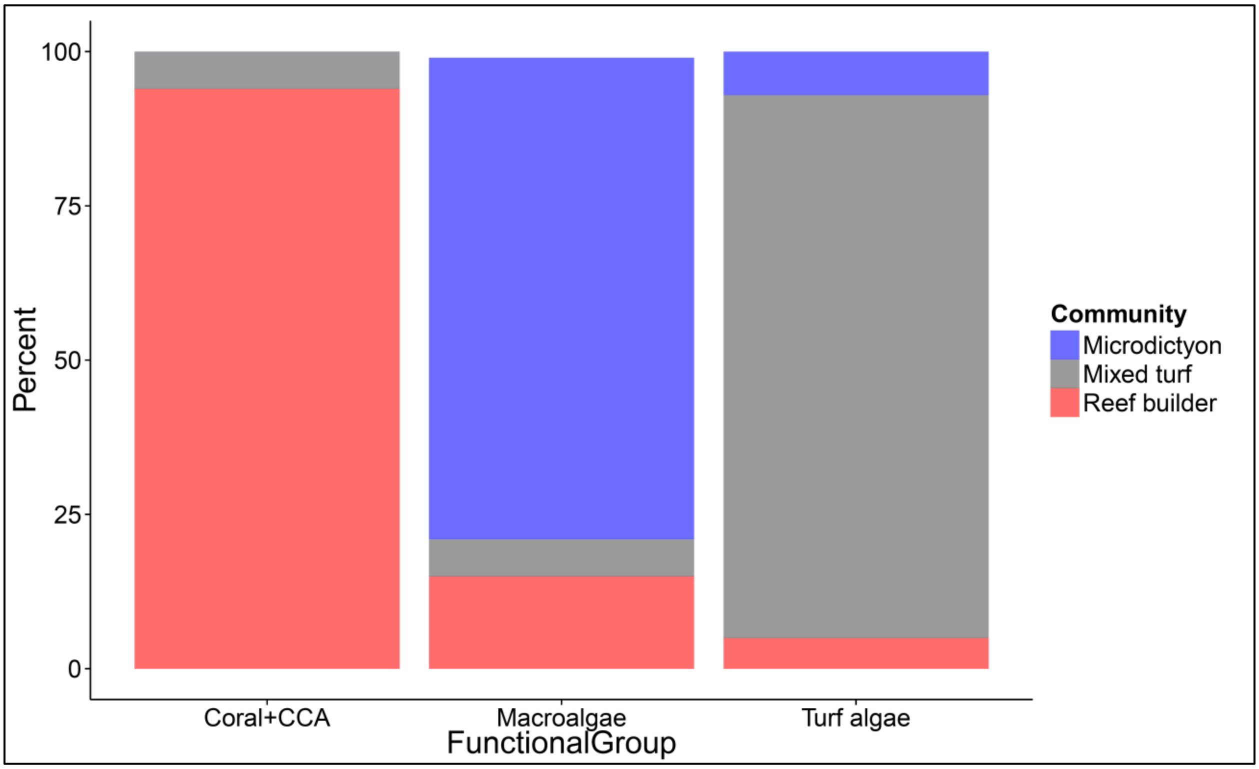


Figure B1. Comparison of the classification of 240 sites into benthic communities based on coarser functional group data (x-axis) and finer resolution functional group data (colored rectangles). Mixed-turf (gray), Microdictyon (blue), and Reef builder (red) communities largely corresponded with community results from functional group data, with the exception of a small percentage of sites that were classified outside of their functional group.

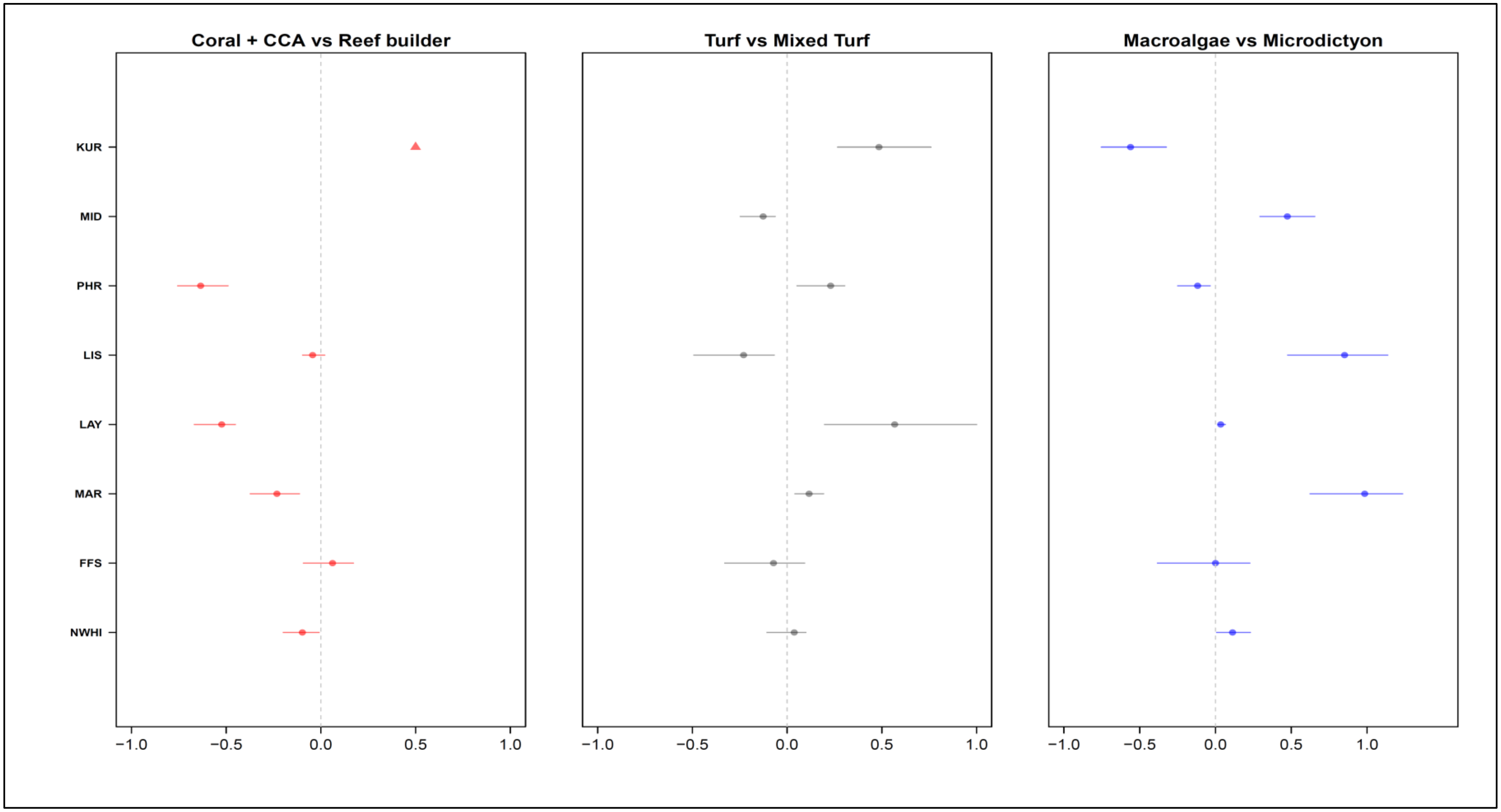


Figure B2. Differences in community occurrence estimated from coarser and finer resolution functional data for each community pairing (columns) and for each island and the NWHI region (y-axis). The dotted grey vertical line represents no difference between community occurrence estimates. Positive values indicate community occurrence based on coarser resolution data were greater than community occurrence estimated from finer resolution data. Colors represent the three community type comparisons: coral+CCA versus reef builder (red), turf versus mixed-turf (grey), and macroalgae versus *Microdictyon* (blue). Horizontal bars indicate 95% confidence intervals.

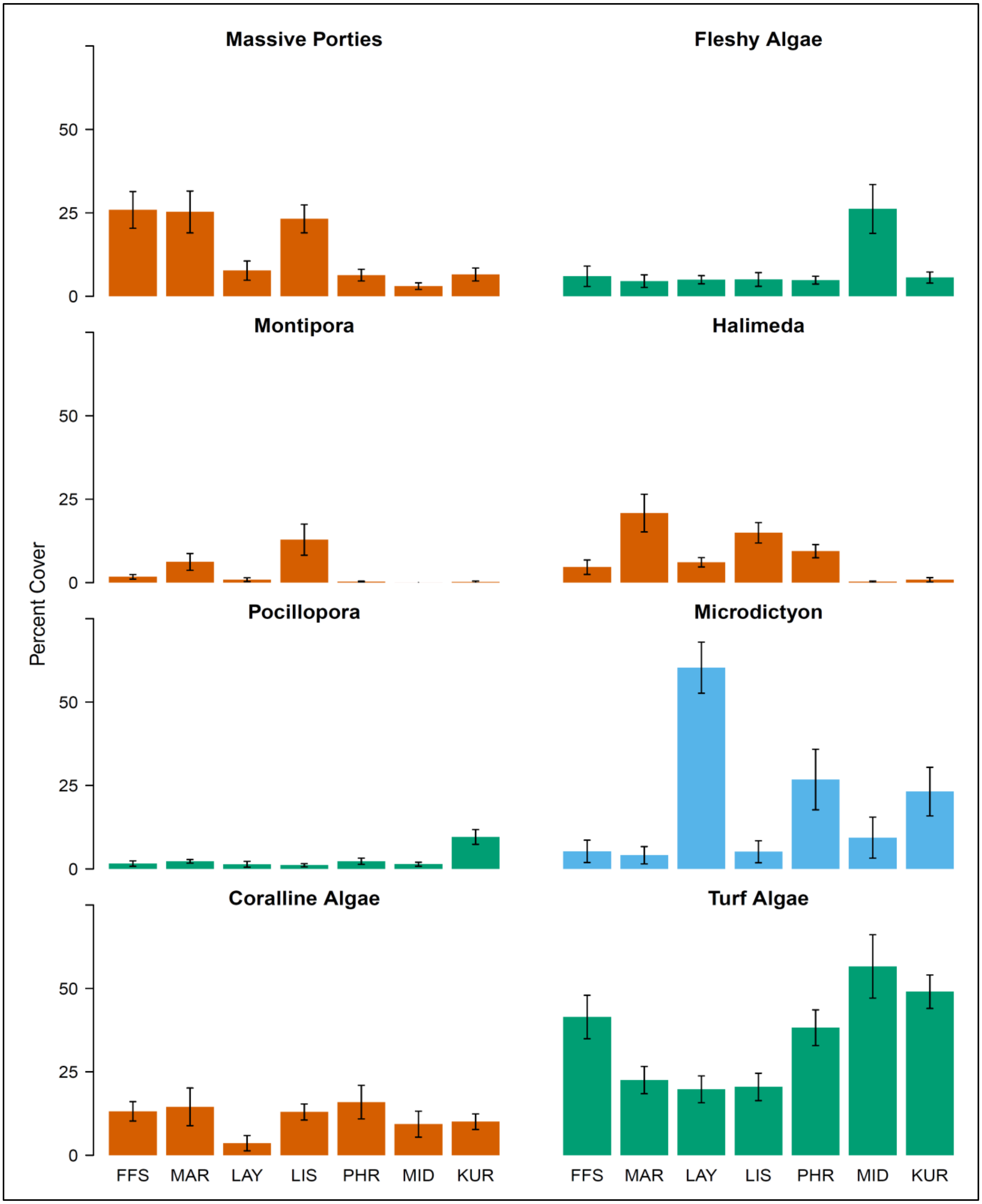


Figure B3. Mean percent cover of higher resolution function group categories by island. Error bars represent 95% confidence intervals. Islands are arranged from south to north (left-right). Colors reflect benthic categories associated with the reef builder (red), *Microdictyon* (blue), and mixed-turf (grey) communities.

Appendix C: Chapter 1 supplement - fuzzy cluster analysis

Mapping fuzzy cluster results onto an nMDS ordination showed community groups occupied three distinct regions of ordination space, though communities were not well separated (Figure C1, bottom row). A lack of separation in ordination space is to be expected when communities vary along a continuum and sampling is random as opposed to purposeful selection of sites in different habitats. Sites with fuzzy membership weights that never exceeded two-thirds for any community group were flagged as "community transition" sites. Transition sites were located along community group boundaries in the nMDS ordination and masking their presence improved the separation between community types. Examination of the distributions of benthic cover sums of indicator classes associated with each community type also illustrated better separation between community types (Figure C1, top row). Therefore, community characteristics of non-transition sites were deemed a better representation of the three benthic community types identified in the NWHI.

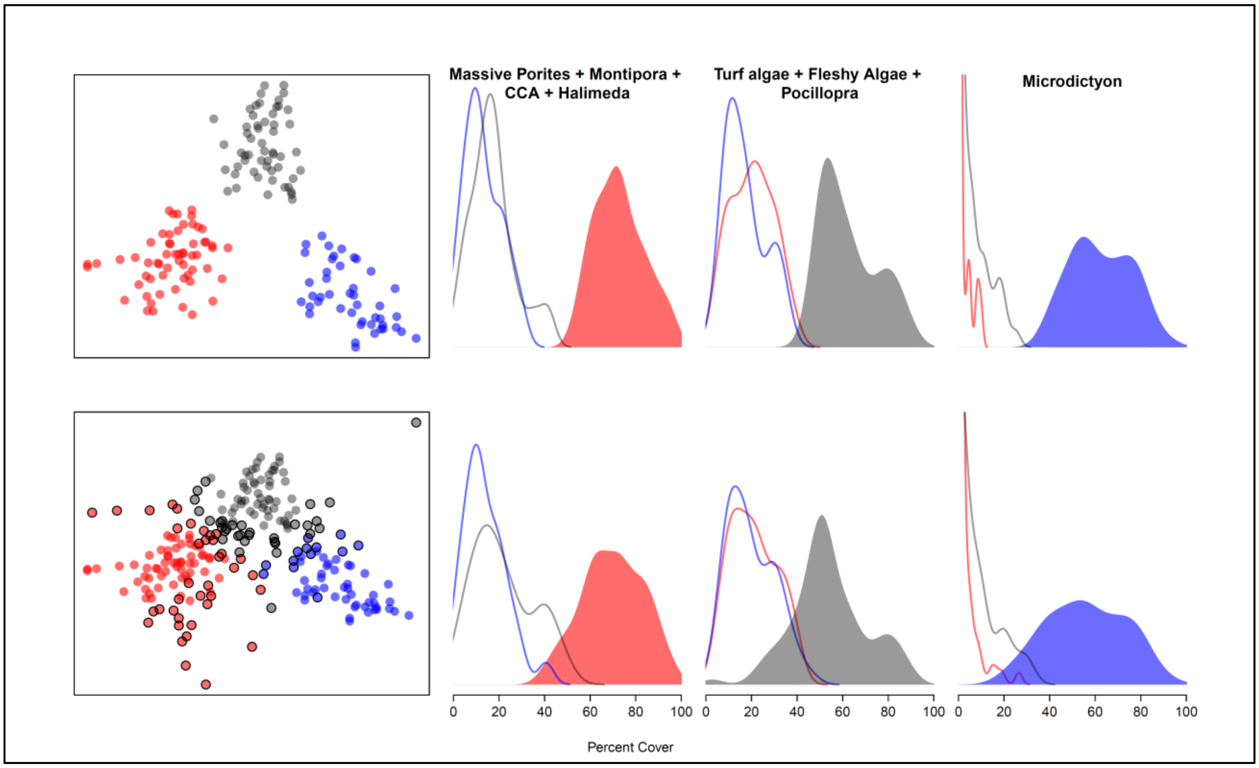


Figure C1. (left) Plot of nMDS ordination for 240 benthic sites (2D stress = 0.16) with sites flagged for having less than 2/3rds membership weight (transition sites) for any one group masked (top left) and same plot showing the locations of transition sites which are outlined in black (bottom left). Symbol colors indicate community groups: reef builder (red), mixed turf (grey), *Microdictyon* (blue). (right) Distributions of benthic cover values summed for indicator classes (labeled in the title above each plot) for each of community group (depicted by colored density curve lines) with (bottom right) and without transition sites (top right). The community group associated with the indicator classes in each graph is emphasized by shading the full distribution compared to individual density curves. Bottom row includes all transition sites, top row excludes transition sites.

Appendix D: Chapter 1 supplemental figures

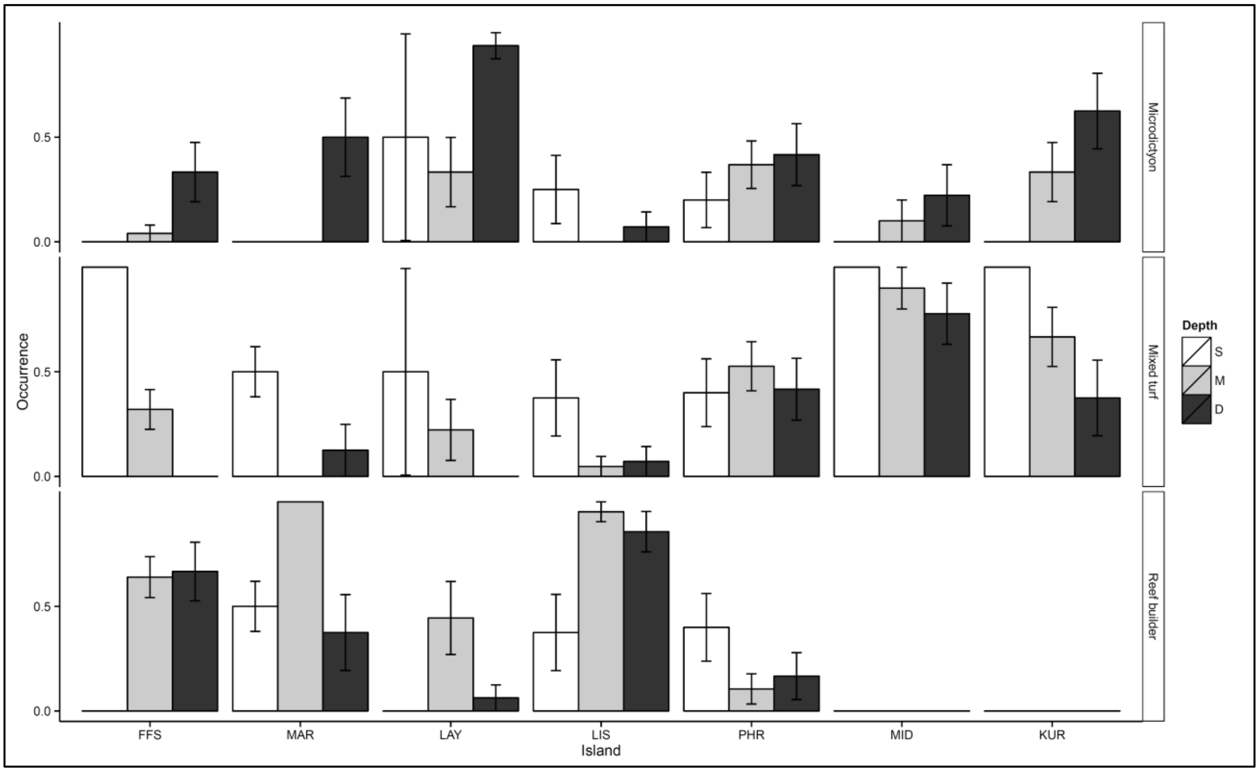


Figure D1. Spatial patterns of benthic community occurrence by island (x-axis) and depth categories (vertical bars) in the NWHI. Top row: Microdictyon, Middle row: Mixed-turf, Bottom row: Reef builder.

Appendix E: Chapter 2 supplement – Modified goodness-of-fit test for estimates of $B_{unfished}$

In theory, modeled predictions of $B_{unfished}$ for islands in the NWHI should closely match observed biomass levels because fishing is prohibited in the NWHI. Therefore, I calculated standardized differences between mean observed fish biomass at each island in the NWHI and expectations of $B_{unfished}$ as a crude measure of model fit. I used the following equation:

$$\text{(E1)} \quad \text{model fit}_j = \sum_{ij} \frac{\left(observed_{ij} - expected_{ij}\right)^2}{expected_{ij}}$$

where $observed_{ij}$ was mean biomass for herbivorous fish group *j* at island *i* in the NWHI and $expected_{ij}$ was the estimate of $B_{unfished}$ for herbivorous fish group *j* at island *i*. Model fit was calculated using estimates of $B_{unfished}$ that did and did not account for environmental differences ($B_{unfished\text{-}local}$ and $B_{unfished\text{-}regional}$, respectively). Smaller model fit values represent better agreement between observed and expected biomass levels.

Table E1. Standardized differences between mean observed biomass at islands in the unfished NWHI and the two measures of unfished biomass ($B_{unfished\text{-}local}$ & $B_{unfished\text{-}regional}$) used to approximate $B_{unfished}$. Results are presented for each herbivorous fish category (columns) and island (rows). Smaller values represent better agreement between observed and expected biomass levels and are highlighted in grey.

Island	Herbivores		Scrapers		Grazers		Browsers	
	$B_{unfished\text{-}local}$	$B_{unfished\text{-}regional}$	$B_{unfished\text{-}local}$	$B_{unfished\text{-}regional}$	$B_{unfished\text{-}local}$	$B_{unfished\text{-}regional}$	$B_{unfished\text{-}local}$	$B_{unfished\text{-}regional}$
FFS	0.09	1.43	0.00	0.17	0.04	0.13	0.04	1.03
MAR	0.28	0.01	0.70	0.05	0.00	0.10	0.07	0.00
LAY	0.10	0.49	0.16	0.77	0.46	0.56	0.07	0.01
LIS	0.02	0.03	0.01	0.03	0.03	0.13	0.07	1.40
PHR	0.25	0.40	0.88	0.54	0.17	0.90	0.00	0.05
MID	6.11	22.54	3.80	4.21	1.64	5.59	0.44	9.06
KUR	0.13	0.07	0.03	0.01	0.19	1.23	0.03	0.06
Total	6.98	24.97	5.57	5.79	2.53	8.64	0.72	11.60

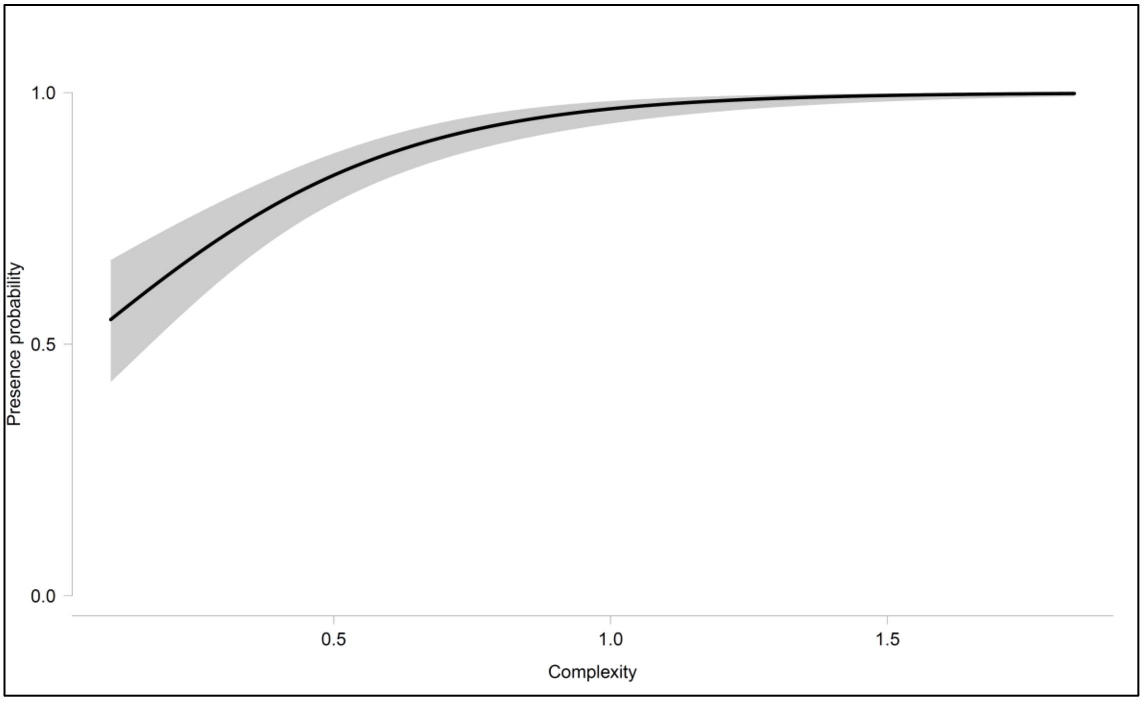
Appendix F: Chapter 2 supplement – Scraper and browser occurrence models

I examined a different set of explanatory models for explaining scraper and browser occurrences. I did not expect sea-surface temperature to affect scraper or browser occurrence so I did not include this covariate. Additionally, there was no evidence to suggest that human population density strongly affected scraper or browser presence. Therefore, HUM was not included in all models. In total, I examined all 15 combinations of HUM, COMP, SUB, and DEPTH ranging from models with only one term to four. Model selection results for scraper presence and its relationship with habitat complexity are presented below. None of the predictor variables were strongly associated with browser presence, therefore it was assumed to be the same across all sites (null model).

Table D1. Model Selection results for scraper presence. All models with AICc weights > 0.05 are shown. Details on predictor variables are given in Table 1: HUM – human population density; COMP – habitat complexity; DEPTH – depth.

Model Terms			Model Support	
Hum	Comp	Depth	ΔAICc	Weight
	X	X	0.00	0.45
	X		0.25	0.24
X	X	X	1.61	0.20
X	X		1.66	0.11

Figure D1. Relationship between the probability of scraper presence and habitat complexity. Shaded areas are 95th confidence intervals.



Appendix G: Chapter 2 supplemental tables and figures

Table G1. List of herbivorous fish species by functional group.

Fish Category	Species name	Common name	Max. size (cm)
Scrapers	Chlorurus perspicillatus	Spectacled parrotfish	62
	Chlorurus sordidus	Daisy parrotfish	40
	Scarus dubius	Regal parrot	38
	Scarus psittacus	Common parrotfish	33
	Scarus rubroviolaceus	Ember parrotfish	70
Grazers	Acanthurus achilles	Achilles tang	25
	Acanthurus blochii	Ringtail surgeonfish	43
	Acanthurus dussumieri	Eyestripe surgeonfish	56
	Acanthurus guttatus	Whitespot surgeonfish	29
	Acanthurus leucopareius	Whitebar surgeonfish	25
	Acanthurus lineatus	Lined surgeonfish	38
	Acanthurus maculiceps	White-speckled surgeonfish	41
	Acanthurus nigricans	Whitecheek surgeonfish	23
	Acanthurus nigroris	Brown surgeonfish	21
	Acanthurus nigrofuscus	Bluelined surgeonfish	21
	Acanthurus olivaceus	Orangesot surgeonfish	40
	Acanthurus triostegus	Convict tang	27
	Acanthurus xanthopterus	Yellowfin tang	65
	Ctenochaetus hawaiiensis	Chevron tang	28
	Ctenochaetus strigosus	Spotted surgeonfish	24
	Zebrasoma flavescens	Yellow tang	20
	Zebrasoma veliferum	Sailfin tang	40
Browsers	Calotomus carolinus	Carolines parrotfish	54
	Calotomus zonarchus	Yellowbar parrot	30
	Naso lituratus	Orangespine unicornfish	46
	Naso unicornis	Bluespine unicornfish	70

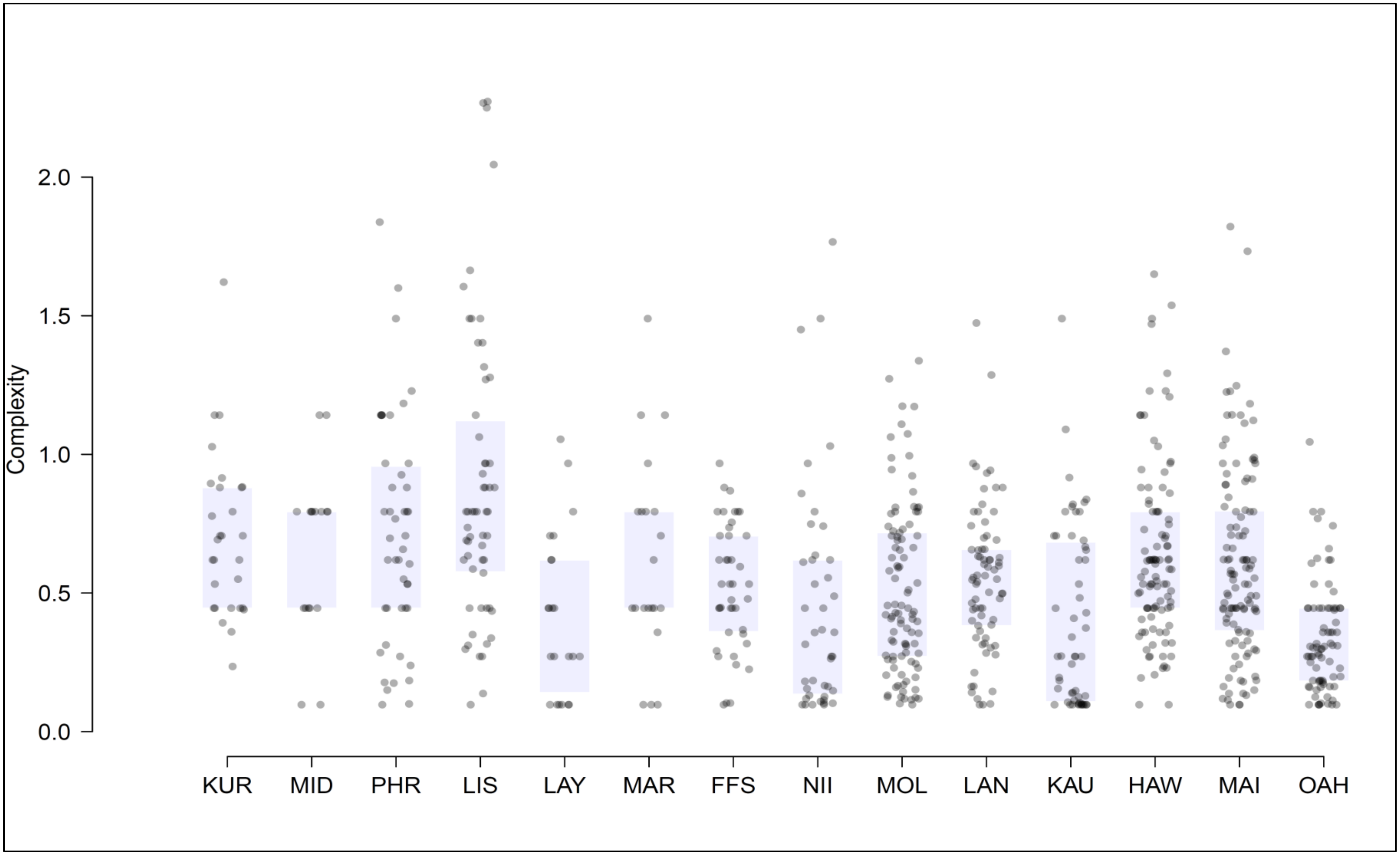


Figure G1. Distribution of habitat complexity values at each island. Grey bars reflect the 25th and 75th quantile ranges of values.