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A spatiotemporal analysis of coral reef regimes and fish herbivory across the Hawaiian Archipelago

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Abstract

Coral reefs can undergo shifts to alternative ecological regimes (or states) when exposed to stress. Acquiring a deeper understanding of when coral reefs become increasingly vulnerable to such shifts (i.e. regime shifts), and the stability of alternative regimes once unfolded, has important societal consequences as associated ecosystem services may change or be lost. Herbivory has been advocated as a key process that determines reef regimes. Here I show the co-occurrence of three distinct reef regimes across the Hawaiian archipelago from 2010-2015, providing empirical evidence for the existence of alternate regimes on a large spatiotemporal scale. I investigate the linkages between benthic regimes and the herbivory function, breaking down the taxonomic and functional diversity of the herbivore community through a trait-based functional space approach. This approach highlights a pattern of varying functional redundancy within herbivore communities across the regimes. A better understanding of these types of regime differences is integral for fully grasping where, when and how these shifts occur.

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Introduction

Coral reefs in the Anthropocene

Human activities exert an unprecedented influence on the biosphere and have become dominant drivers of biophysical processes at a planetary scale (Steffen et al. 2011, IPCC 2013). This has resulted in the proposition of a new geological epoch – the Anthropocene (Crutzen 2002). To understand the extent of human derived stressors and to define global boundaries above which we risk dramatically changing the stable environment provided by the Holocene, the concept of planetary boundaries and safe operating space was proposed (Rockström et al. 2009, Steffen et al. 2015). The safe operating space determines the borders within which humanity must operate to avoid changing the conditions upon which our society depends.

Safe operating spaces for coral reefs have recently been proposed for CO₂ levels (influencing temperature and ocean acidification), fishing biomass, and water quality (chlorophyll *a*) (Norström et al. 2016). The increased CO₂ levels in the Anthropocene are already putting chronic stress on reefs. Ocean acidification threatens calcifying organisms and thereby the structural complexity of hard-coral reef states (Hoegh-Guldberg et al. 2007, Wild et al. 2011). Temperature rise is affecting coral reefs both through persistently higher temperatures (chronic stress) as well as through shorter temperature anomalies (pulse stress) (Frieler et al. 2012). Last year (2015-2016) the coral reefs of the world experienced the third global mass bleaching event, following the first in 1998 and the second in 2002. These global bleaching events are a result of increased sea surface temperature anomalies, with longer periods of unusually warm water (Hughes et al. 2017). With the reoccurring pulse stressors, as well as the underlying chronic stressors, reefs are now most likely entering an era where changing community composition and species range shifts will lead to novel ecosystems (Graham et al. 2014). Similarly, increasingly frequent bleaching events might modify coral communities towards species with fast growth rates (typically branching species), that can regenerate within 10-15 years (Hughes et al. 2017). These potentially permanent changes are suggested to be a result of the higher frequency of pulse disturbances, which provide insufficient time intervals for recovery (Hughes et al. 2003). While some human-induced drivers can be managed at a local scale (e.g., fishing and water quality), others require a global approach (e.g., elevated seawater temperature and increased ocean acidification).

Regime shifts, Thresholds, Alternative states and Resilience in Coral reefs

Moving outside the safe-operating space implies an increased risk of crossing threshold values of certain drivers. Beyond these thresholds dramatic and abrupt changes in coral reef structure and function at local scales may occur, so-called regime shifts. Indeed, such shifts have been observed across a range of terrestrial and aquatic systems, such as woodlands, deserts and freshwater lakes (Scheffer et al. 2001). Coral reefs provide one of the most well studied cases in this context (Nyström et al. 2000, Nyström and Folke 2001, Hughes et al. 2003). Regime shifts are reorganisations of an ecosystem, involving key structural species, that are persistent over time (Rocha et al. 2014, Möllmann et al. 2015). On coral reefs the most recorded and investigated regime shift is that between a calcifying hard coral state and a fleshy macroalgal state (Hughes 1994, Hughes et al. 2007), although other states have been proposed (Done 1992, Norström et al. 2009, Jouffray et al. 2015). A key reason to better understand the dynamics behind regime shifts in coral reefs is due to the changes in ecosystem services they may entail for the millions of people relying on coral reefs for their well-being (Moberg and Folke 1999, Hicks et al. 2015, Elliff and Silva 2017). Calcifying coral reefs provide, among others, a source of biodiversity, seafood products, a source of revenue from tourism and coastal protection (Moberg and Folke 1999, Wild et al. 2011). Breaking waves and providing protection from erosion along the shoreline is dependent on the structural complexity provided by hard corals (Elliff and Silva 2017). The macroalgal regimes do not provide these same ecosystem services and are thus generally seen as the less preferable state. A better understanding of the interactions between the regimes and the drivers of regime shifts is therefore necessary for keeping coral reefs within the safe operating space.

The capacity of coral reefs to avoid regime shifts and return to coral dominance depends on their resilience (Nyström et al. 2000). The resilience of a system is its capacity to buffer and change in response to disturbances without losing the functions, structures and feedbacks that make up the system identity (Walker and Meyers 2004, Folke 2006). Although resilience does not protect reefs from stress and perturbations, e.g. corals will bleach if temperatures become too high, it increases the chances for reef to cope with, and reorganize after the disturbance (Nyström et al. 2000, Norström et al. 2009, Hughes et al. 2017). If resilience is eroded, new feedback processes may come into play reinforcing the degraded state. If these feedbacks are allowed to manifest at large scales, such as when many reefs in an area suffer a regime shift, reversal may be very difficult or even impossible (Nyström et al. 2012).

Coral reef resilience and herbivory

Fish herbivory is a key process that underpins the resilience of coral reefs and helps avoid the archetypical coral-to-macroalgae regime shift (Hughes 1994, Bellwood et al. 2004). Herbivores remove algae and reduce the competition for space between coral and algae, as well as opens up the substratum for new coral settlement. Their overall capacity to maintain this key function is determined by the composition of the herbivore community (Fox and Bellwood 2007), including which different species are present and at which biomass levels they exist. A relatively intact herbivore community can remove up to 90% of the net algal production (Hoey et al. 2013). There is also a balance between the level of benthic cover (coral or macro) and the levels of algal grazing required for reef recovery. An intact herbivore community in terms of species richness is therefore not enough if herbivore biomass is low and perturbations cause increases in algal growth (Hoegh-Guldberg et al. 2007). Another important aspect of the herbivorous fish community is the specific functional roles that exist. Three functional groups (grazers, browsers and scrapers) have been proposed based on fish dietary mode. Grazers target and crop algal turf, or the epilithic algal matrix, whereas browsers target and remove macroalgal stands. Scrapers also target algal turf, but are separated due to their added influence on reef erosion and their ability to open up space for coral settlement (Green and Bellwood 2009). The different functional roles are important as they have shown to have different roles in relation to regime shifts, where grazers are thought to prevent regime shifts and browsers have the ability to reverse them. Little overlap in these roles have been seen, where grazers are unable to reverse a coral-macroalgal regime shift (Bellwood et al. 2006). These functional groups are often used as a proxy to get at the herbivory function (Cheal et al. 2010, 2012, 2013). However, as herbivory is a complex function, performed by a composition of many different species, there are different approaches to understand and capture the function. Herbivory varies not only through targeting different algal types, but in rates of feeding and rates of algal depletion (Bellwood et al. 2006, Mantyka and Bellwood 2007, Cvitanovic and Bellwood 2009). Similarly, diet is not the only trait that has been seen to have influence over herbivory, a range of other traits, from size to swimming performance have been proposed (Lokrantz et al. 2008, Bejarano et al. 2017). In order to explore the influence of multiple traits the functional space method was introduced (Albouy et al. 2011). This method opens up for a wider understanding of how traits, individuals and functions interact, and has been used to tackle specific species functions (Mouillot et al. 2008, Villéger et al. 2010, Bejarano et al. 2017) as well as for exploring wider aspects of the ecosystem dynamics, such as niche and microhabitat use

(Villéger et al. 2011, Brandl and Bellwood 2014, Brandl et al. 2015). Some studies, instead of taking a single function approach, aim to assess the overall diversity of an ecosystem, using a range of traits and functions to describe the overall functional diversity within an ecosystem (Stuart-Smith et al. 2013, Mouillot et al. 2014).

Hawaiian Coral reefs

The wide geographical spread of the Hawaiian Archipelago, from tropical waters of lower latitudes to the relatively cooler waters of the higher latitudes, as well as the wide variation in anthropogenic pressure makes it a unique study site to investigate the presence of multiple reef states. In addition, long-term monitoring of Hawaiian reefs offers the rare opportunity to analyse data both over a large geographical space and across multiple years. A recent study on Hawaiian reefs has provided evidence of multiple alternate states or regimes (Jouffray et al. 2015). However, it only represented a snapshot in time (year 2010). Therefore, the knowledge gap still exists to determine the stability of these multiple alternative regimes over time. Furthermore, there is a need for investigating how fish communities, especially herbivore communities, are associated with these identified reef regimes.

This thesis aims to fill these knowledge gaps by (1) assessing the relative stability of the identified benthic regimes over several years, (2) unpacking each regime to understand the benthic and herbivorous fish community compositions, and (3) using a functional space approach to investigate the range and variance of the herbivory function within each regime.

Method

Study site, data collection and survey design

The Hawaiian Archipelago (USA) is located in the Pacific Ocean and stretches over 2500 km (Fig. 1). The Main Hawaiian Islands (MHI), are located in the south-eastern archipelago and are highly populated (Friedlander et al. 2005). The North Western Hawaiian Islands (NWHI) in contrast, are composed of islands and atolls under low anthropogenic influence (Friedlander and DeMartini 2002) which lie within the world's largest marine protected area, the Papahānaumokuākea Marine National Monument.

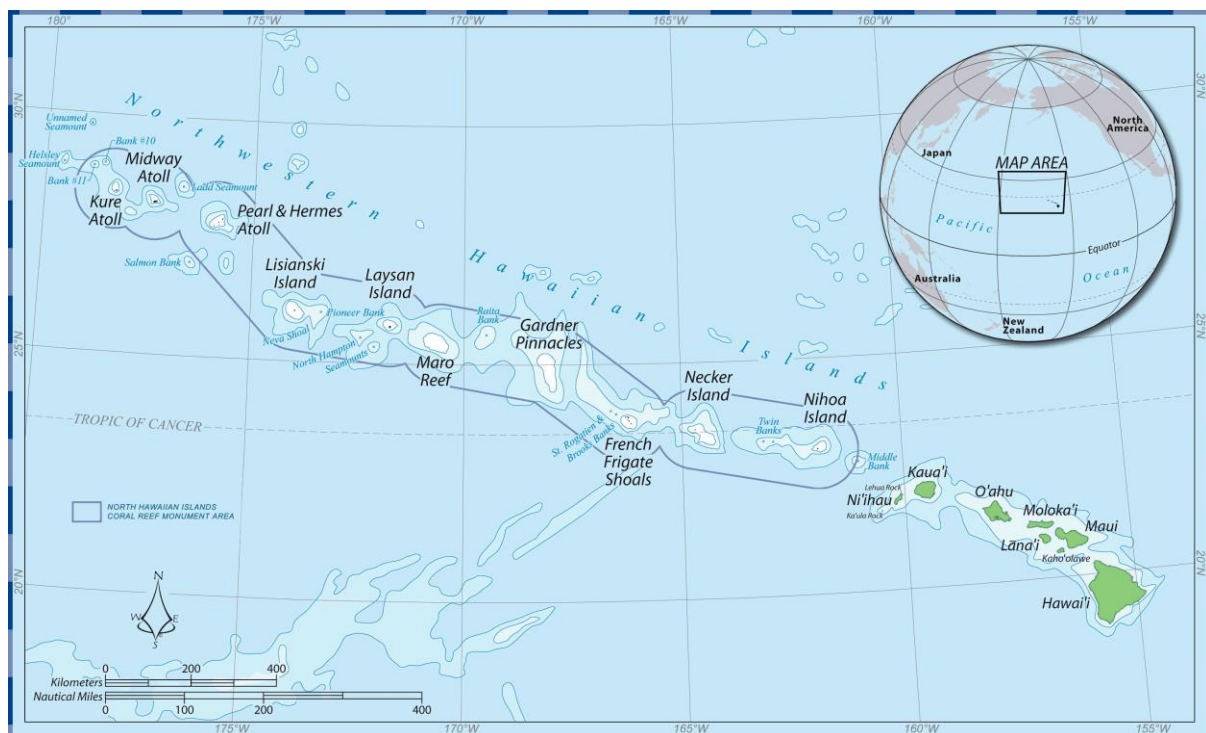


Figure 1. Map of the study area showing the Hawaiian Archipelago. Source: NOAA

Data underpinning this study is the result of the National Oceanographic and Atmospheric Administration (NOAA) monitoring activities within the Coral Reef Ecosystem Program (CREP). The dataset includes information on both benthic communities and fish assemblages from 1463 sites surveyed across both the MHI and NWHI between 2010 and 2015. The surveys follow a randomisation design, which means that site coordinates are randomly selected from bathymetry and bottom substrate maps. All sites included in the survey must have a minimum of 50% hard bottom reef habitat. If the randomisation includes a site that does not fulfil these criteria (for example a soft-bottomed, or a sandy site) it is discarded. A consequence of this

design is that a site can never be surveyed again. Hence, there exist no proper time series for a given site but rather a collection of sites surveyed across multiple years. As the analysis in this thesis is focused on the scale of the whole archipelago and there is a large number of sites within each investigated group (regime), this data series is still considered to capture temporal changes.

Not all surveyed years (2010-2015) encompassed sites from both the MHI and NWHI and therefore appropriate data subsets were selected for the different aims. To address the first aim and understand if multiple benthic regimes are present across several years, data from all years (2010-2015) was used. The inclusion of all years was due to the evidence from previous research showing that variations between the MHI and the NWHI did not influence the presence or absence of regimes (Jouffray et al. 2015). In addressing the second and third aim, data use was limited to years 2010, 2012 and 2015 as these were the only years that included data from both the MHI and the NWHI within the same calendar year (Supplementary Material 1). This data subset was selected as it is not known how benthic cover within regimes and regime herbivore communities vary across the archipelago. Surveys in these years were conducted during different times of the year: 2010 (September - November), 2012 (August - September) and 2015 (June – August) (Suppl. Material 1).

Data collection at each site is done through two stationary point counts evenly spaced along a 30 m transect. The number and size of fish species seen during the point count is noted as well as visual estimates of percentage cover of hard coral, macroalgae, turf algae, crustose coralline algae (CCA) and sand. Following the initial stationary data collection, divers will swim through the cylinder noting any additional cryptic species. For a detailed description of the survey methodology see Ayotte et al. (2011, 2015). The minimum separation between survey sites is 100 m.

All statistical analyses and graphical presentations were conducted using the R software (Versions: 3.3.1 and 3.3.2). Use of specific packages is referred to in the text.

Identifying and mapping benthic regimes

The identification of reef regimes was carried out by following the procedure described in Jouffray et al. (2015). To determine the presence or absence of multiple co-existing regimes a hierarchical clustering method was used. This method builds a hierarchy of clusters based on the distance of dissimilarity and was constructed on scaled benthic cover, using Euclidean

distance metric and Wards clustering method. P-value calculations were conducted by multiscale bootstrap resampling using 10 000 bootstrap iterations. Significant clusters are those with p-values > 0.95. Hierarchical clustering and p-value bootstrap calculations were performed using the *pvclust* package in R (Ryota 2015). K-means clustering was then used to partition the data based on the number of significant clusters.

For each island the individual study sites were plotted on satellite maps according to regime and year surveyed, to assess the geographical distribution of regimes. Mapping was conducted using the *ggplot2* and *ggmap* packages in R (Kahle and Wickham 2016).

Unpacking the Regimes: exploring benthic cover and fish community composition

To explore the benthic cover composition of each regime, the mean cover for each benthic category was calculated. This was done both to understand how much benthic cover differed between each regime and to understand the variation within a regime between years. To explore the composition of the fish community, taxonomic richness and relative biomass were calculated. One-way ANOVAs were calculated to check for statistical differences in species richness between regimes and years. To check if the data satisfied the assumptions of normality and homoscedasticity, Shapiro-Wilks test for normality and the Levene test for homoscedasticity were run. The Levene test was selected due to its suitability with non-normal data. For non-normal, homoscedastic data Tukeys HSD (Honest Significant Difference) post-hoc test was run. An ANOVA with the Welch correction was used for data that were non-normal and heteroscedastic. The Games-Howell post hoc test was similarly selected for its applicability with this type of data.

The relative percentage biomass of each dietary guild, as well as the relative percentage biomass for each individual species within a guild, was calculated. In each regime and year where a single species represented more than 50% of the biomass of that guild (scraper, grazer or browser) the species name and percentage of biomass was noted. A calculation was made to assess how many survey sites, split by regime, had at least one species within each of these three dietary guilds.

Assessing functional fish community structure

Functional categorization of herbivorous fish

To assess reef fish herbivory, two traits were selected as proxies; body size and diet. The combination of these two traits is likely to capture key aspects of the function, such as feeding niches and extent (area and volume) of function. The decision was based on available data as well as the known influence of the traits on the herbivory function. As different species of reef herbivores have been found to feed in different ways and targeting different species of algae (Bellwood and Choat 1990, Green and Bellwood 2009), diet is integral for understanding the intricacies of the herbivory function. Body size of herbivorous fishes have been seen to influence aspects of herbivory such as area (Lokrantz et al. 2008) and volume (Bonaldo and Bellwood 2008) of algal removal. Body size has also been suggested to influence foraging range, and thus the scale of the herbivore function (Nash et al. 2012, 2013, 2015). Using variation in body size has similarly been suggested for many different ecosystems as a useful proxy for understanding the scale at which a function is executed (Peterson et al. 1998). These two traits have previously been selected to encompass the functional variation within the herbivory function (Graham et al. 2015).

Diet was manually assigned in accordance to classification in Table 1. Food item data from FishBase (Froese and Pauly 2016) was used for each species, supplemented with dietary information from Kulbicki et al. (2011). Multiple sources of dietary information were used to maximise the number of species where trait data could be assigned. Rare species, usually endemic species, where no food item data could be found were excluded from the dataset. Size data was extracted from FishBase and expressed in total length (TL). Because the survey method allows only limited time for the detection of small cryptic species and therefore a higher chance of missing them, these species (e.g. from the Blennidae family) were excluded from the analysis.

Table 1. Diet Categorisation Scheme

Functional group	Diet
Browsers	Feed on macroalgae
Scrapers	Feed mainly on algal turf and remove some part of the reef substratum as they feed (includes excavating species)
Grazers	Feed on filamentous algae without scraping or excavating the reef

Functional space

The functional space is created by turning the values or categories of the selected functional traits into a distance metric. From this, a space based on the distances between points (species) can be constructed. The method is therefore used to create a single functional metric for comparing species with multiple varying traits. The full (global) functional space is created by all species present (in the case of this thesis, in all regimes). In order to build a functional space using both categorical (diet) and continuous (size) traits, the trait data was converted to a Gower's dissimilarity matrix. The functional space was created through a Principal Coordinates Analysis (PCoA) on the Gower distance matrix, using the Cailliez correction for negative eigenvalues (Laliberté and Legendre 2010). The functional space was created for the 33 herbivorous species (full list in Supp. Material 2) present in the Hawaiian archipelago for which trait data was available, using the *cluster* and *ape* packages in R. The first four axes of the functional space were selected as they explained >60% of the variance in all three investigated years (2010, 2012 and 2015). Due to the relatively small size of each site (30 m) and the small minimum separation of sites (100 m), an extrapolation of each regime herbivore community was made (Figure 2) for each year. The functional index calculations were done on these extrapolated herbivore communities.

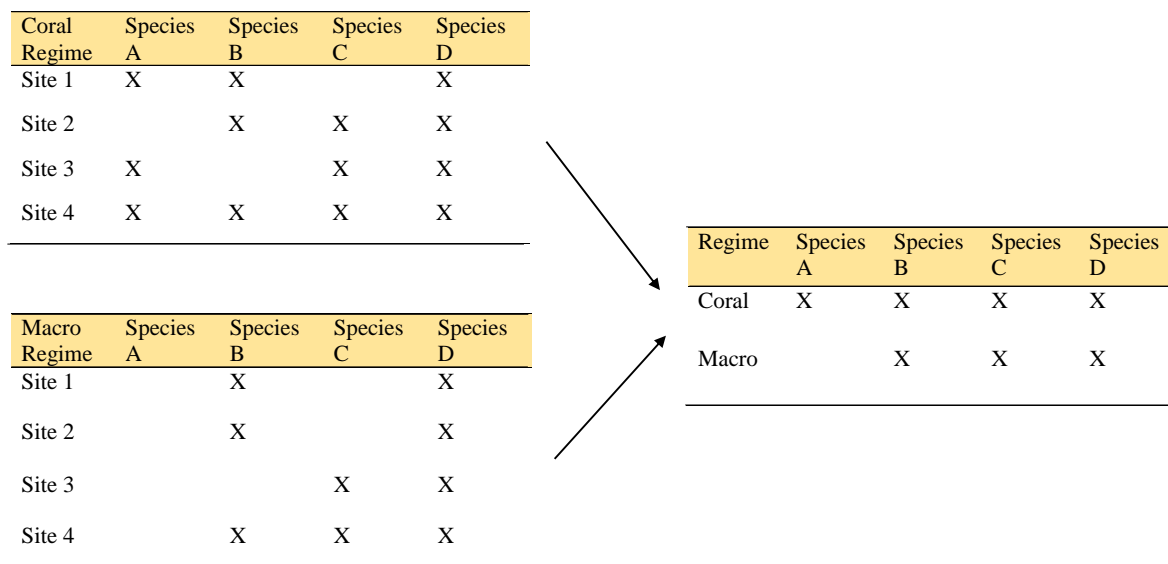


Figure 2. Conceptual diagram of method for determining the extrapolated herbivore community for each regime. All sites within a regime and year were aggregated to create an extrapolated regime herbivore community. If a species was present, at any biomass at any site within that regime (left hand table) it was included in the extrapolated community (right hand table). The biomass of each species in the extrapolated community was the mean biomass of the sites in that regime. This method was used to create regime communities for all regimes in all years. Additional information on taxonomic richness of each regime community see Supplementary Material 7.

Functional richness and functional dispersion

There exists a range of complementary functional space indices that can be used to calculate different attributes of the functional space filled by different sub-groups (here, regimes) (Mouillot et al. 2013b). Two complementary functional diversity indices were selected to analyse the herbivore fish assemblages in relation to the benthic regimes, both of which have been suggested to compare pre- and post- disturbance assemblages (Mouillot et al. 2013b). Functional Richness (Villéger et al. 2008) was selected to provide an estimate of the functional range within the herbivore community of each regime. Functional Richness (FRic) is the functional equivalent of species richness, an often-used estimate of taxonomic diversity. This index therefore indicates how functionally different the species within the regime community are. To investigate functional variance, Functional Dispersion (FDis) was calculated. The Functional Dispersion index represents the distance in functional space of each species to the abundance weighted centre of the functional space. This index gives insight into how abundance is distributed in the functional space as well as the variation in functional diversity within the community (Laliberté and Legendre 2010). Functional dispersion therefore indicates if, for example, species that are functionally similar are most abundant or if abundance is

highest at the functional extremes. By calculating both indices, information is obtained about both the range (FRic) and variance (FDis) of the fish communities within the functional space. Calculations of both functional indices were done through the multidimFD package from Villéger (Villéger 2016, 2016 version). The mean biomass per species per site for each regime was used as the abundance parameter in the functional diversity calculations.

To assess if the functional index values of the three regimes were significantly different a pairwise randomisation method was used (Villéger et al. 2010). This method was used as fish communities in the different regimes and different years have varying numbers of species with varying biomass, and the index values therefore cannot be directly compared. The randomisation method compares the observed functional index values (calculated from observed biomass) for each pairwise regime comparison with simulated functional index values (calculated from 5000 simulations). Results were considered statistically different if the observed value falls within the 95% confidence interval for the simulated values. For a more detailed description of randomisation methodology see Supplementary Material 3.

Results

Identifying and mapping benthic regimes in space and time

Hierarchical clustering revealed the presence of three regimes occurring in Hawaii from 2010-2015 (Table 2). They were significant all years apart from 2011. The three regimes were consistently (1) Hard coral and CCA regime, (2) Macroalgae and sand regime and (3) Turf algae regime. From this point on, these regimes will be referred to as the coral regime, the macro regime and the turf regime, respectively.

Table 2. Significance of the identified regimes in the Hawaiian Archipelago.

Year	Region	Regime	Percentage p-value	Significance
2010	MHI + NWHI	Coral	100	Yes
		Macro	100	Yes
		Turf	75	No
2011	NWHI	Coral	95	Yes
		Macro	89	No
		Turf	68	No
2012	MHI + NWHI	Coral	100	Yes
		Macro	98	Yes
		Turf	99	Yes
2013	MHI	Coral	100	Yes
		Macro	100	Yes
		Turf	72	No
2014	NWHI	Coral	99	Yes
		Macro	99	Yes
		Turf	98	Yes
2015	MHI + NWHI	Coral	99	Yes
		Macro	98	Yes
		Turf	87	No

As turf algae systematically clustered outside the other two significant clusters, it was considered its own regime for the K-means calculation, even in the years where it was not a significant cluster itself (2010, 2013 and 2015, Table 2).

The satellite maps where study sites and regimes have been identified can be used to visually assess the temporal stability and geographical clustering of regimes. Sites that belong to the same regime are clustered in space (Fig. 3, maps of all islands in Supplementary Material 4) and by comparing closely geographically related sites in different years (different shapes in Fig. 3) regimes can be seen to be stable over the five-year analysis period. Larger scale patterns

can also be seen, where sites of the same regime are clustered along the same coastline (Fig. 3).

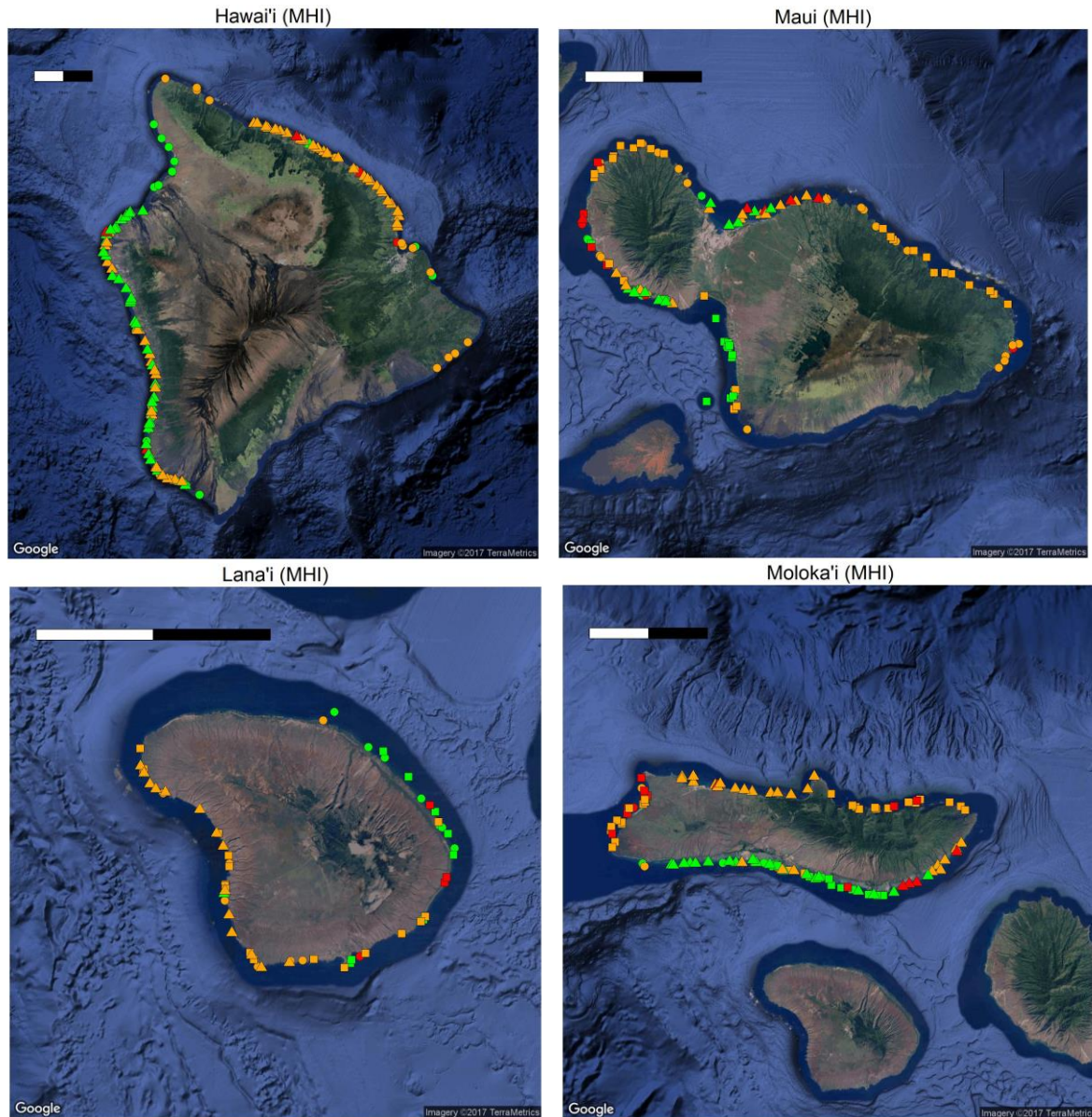


Figure 3. Examples of satellite maps, showing four islands (Hawai'i, Oahu, Lana'i and Moloka'i) in the Main Hawaiian Islands, with study sites plotted. The colour of the points indicates the prevalent regime. (Green = Coral, Orange = Turf and Red = Macroalgae). The shape of the points represents the survey year. (Circle = 2010, Square = 2012 and Triangle = 2015). The scale bar represents 20 km (10km white band and 10 km black band).

Unpacking the Regimes: exploring benthic cover and fish community composition

Benthic community

The relative coverage of different benthic categories, within the three regimes, varied across the survey years. The relative percentage of turf cover increases both within the turf regime, but also within the other regime categories between 2010-2015 (Table 3). In 2010 and 2012 the dominant benthic cover category is representative of the regime it belongs to; however, in 2015, turf cover is greater in both the coral regime (42.6% turf versus 35.4% hard coral) and the macro regime (43.6% turf versus 28.6% macroalgae). A larger difference in benthic cover was recorded between years in August (2015 – 2012 comparison) than in September (2010-2012 comparison). In the coral regime, coral cover in August ranged from a mean of 59% in 2012 to 29% in 2015. Turf cover in the coral regime differed between 23 and 27% in September and 15 and 49% in August. The full details of mean cover for each benthic cover category by month, year and regime can be found in Supplementary Material 5.

Table 3. Mean percentage cover of each benthic category within each regime cluster.

Year	Regime	Hard Coral	CCA	Macroalgae	Sand	Turf algae
2010	Coral	46.9	11.2	6.6	8.8	26.4
	Macro	6.2	3.7	44.5	17.3	28.2
	Turf	10.5	5.9	8.2	9.8	65.4
2012	Coral	55.0	8.1	7.3	8.1	21.2
	Macro	10.0	5.8	41.8	13.6	26.5
	Turf	9.7	4.9	10.4	9.4	65.1
2015	Coral	35.4	7.7	2.8	11.4	42.6
	Macro	4.7	4.2	28.6	18.5	43.6
	Turf	6.4	4.4	4.4	8.8	75.5

Herbivorous fish community

Looking at the relative biomass for all sites in each regime shows that different dietary groups are dominating the herbivore biomass in different regimes during different years (Fig. 4). The overall pattern indicates that grazers are fairly stable through the years, with higher relative biomass of grazers in the coral and turf regimes. Variation in relative biomass is instead a result of decreases or increases in the browser and scraper guilds.

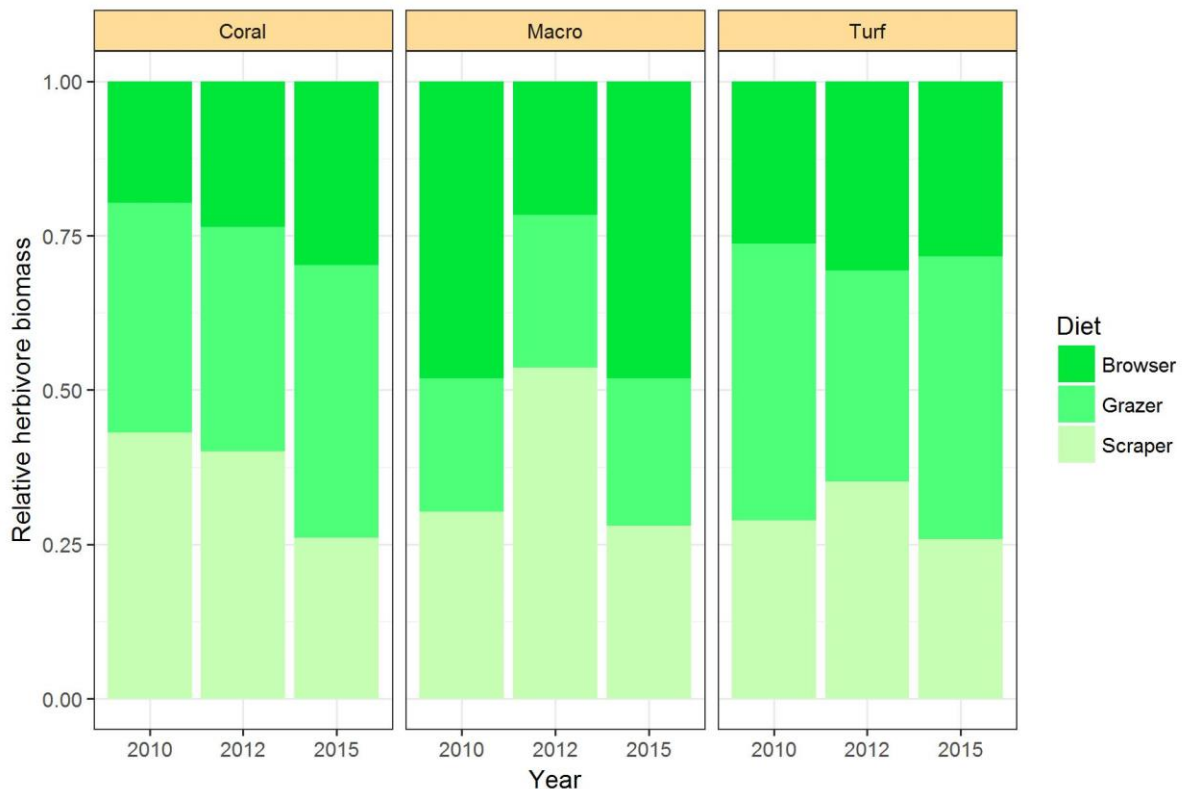


Figure 4. Relative Biomass of each diet/functional group. Breakdown of relative abundance of each species within each guild can be found in Supplementary material 6.

At a species level, fish were unevenly distributed in terms of biomass. The functional group most evenly distributed was grazers where no single species (in any regime or year) represented more than 50% of the biomass. The browser guild was on the other hand the most unevenly distributed, with single species being dominant in at least one regime every investigated year. Scraper biomass did not have a consistent pattern, where some years showed uneven biomass distribution. On three occasions, the macro regime in 2012 and 2015 and the turf regime in 2012 *Chlorurus perspicillatus* dominated the scraper biomass, occupying 50-57%. The browsers in the macro regime were dominated by *Naso unicornis* during all investigated years. *Naso unicornis* filled 94, 68 and 93% of the browser biomass in 2010, 2012 and 2015 respectively. In the coral regime, the browser functional group was also dominated by a single

species, however instead of *N. unicornis* the dominant browser was *Melichthys niger* with 52 and 53% in 2012 and 2015 respectively. In 2012, the turf regime was similarly dominated by *Naso unicornis* with 57% of the total browser biomass.

The overall taxonomic richness varied between regimes but was stable across years. The coral regimes generally had the highest mean species richness, followed by the turf regime and with the macro regime having the lowest mean species richness (Table 4). Calculations showed significant difference between taxonomic richness in all regimes in 2010 and 2012. (2010: Welch's ANOVA $F_{(2,143)} = 42.95$, $p\text{-value} < 0.001$, with $p\text{-values}$ of < 0.001 for all combinations in the post-hoc. 2012: Welch's ANOVA $F_{(2,121)} = 17.71$, $p\text{-value} < 0.001$, with $p\text{-values}$ of < 0.001 for Macro-Coral and Turf-Coral and $p < 0.05$ for Macro-Turf). In 2015, the difference in taxonomic richness was non-significant between Macro and Turf regimes, however significant for the other regime combinations. (2015: Welch's ANOVA $F_{(2,161)} = 12.44$, $p\text{-value} < 0.001$, with $p\text{-values}$ of < 0.001 for significant combinations in the post-hoc).

The temporal variation of species richness within regimes showed that in the coral regime, 2010 was significantly different from the other two years, however there was no statistical significance between 2012 and 2015 (ANOVA: $F_{(2,220)} = 10.52$, $p < 0.001$, post-hoc $p < 0.001$ for 2010-2012 and 2010-2015). In the turf regime 2012 was significantly different from the other two years. (ANOVA: $F_{(2,539)} = 10.18$, $p < 0.001$, post-hoc $p < 0.001$ for 2010-2012 and $p < 0.01$ for 2010-2015). Finally, the macro regime showed no significant difference in taxonomic richness between years.

Table 4. Mean Species Richness in each regime.

Year	Coral	Turf	Macro
2010	9.7	8.0	4.4
2012	7.8	6.1	4.6
2015	8.0	7.4	5.4

Within the coral regime, 84 – 92% of sites had at least one species present from all 3 dietary guilds, whereas this number drops to 51-66% in the turf regimes and 34 – 49% in the macro regime (Table 5).

Table 5. Percentage of sites within each regime where at least one species from each guild (Scrapers, Grazers and Browsers) were present.

Year	Coral	Turf	Macro
2010	90%	66%	36%
2012	92%	51%	34%
2015	84%	63%	49%

Functional space, functional richness and functional dispersion

Within years, certain regimes were significantly functionally different. The coral regime was functionally richer (higher FRic) in 2010 compared to the macro regime (Figure 5), whereas in 2010 the coral-turf and macro-turf comparison displayed no significant difference. In 2012, the coral regime displayed a significantly lower functional richness than both the Macro and Turf regimes. In 2015, the turf regime was significantly more diverse than both the coral and the macro regime. Every time functional richness was significantly different, it was due to the presence or absence of the same species (Fig. 5), therefore only results from 2010 are plotted. Functional dispersion only showed a significant difference in the year 2012, between the macro and turf regime, where the turf regime was more diverse. The overall pattern of functional diversity (both FRic and FDis) shows some significant difference between regimes, however without a stable temporal pattern.

Functional index calculations for temporal differences within regimes, showed that the Coral regime had a significantly higher functional richness in 2010 compared to 2012, however in all other regimes and all other years, functional richness differences were non-significant. Functional dispersion was only significantly different in the turf regimes between 2010 and 2015. The overall pattern is thus of even functional diversity within a regime across years.

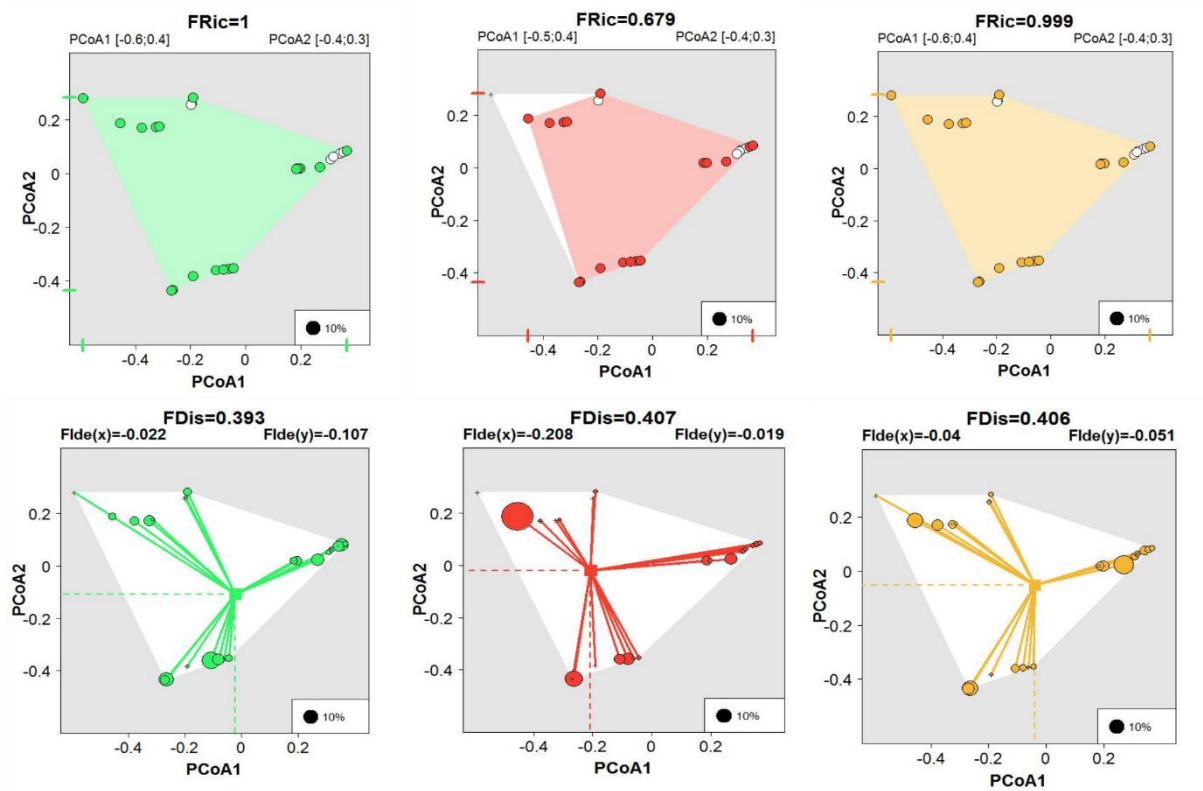


Figure 5. Differences in the functional space in 2010 between the coral regime (green), the macro regime (red) and the turf regime (orange). White space indicates the global functional space (all 33 species) and coloured space (top row) indicates the functional richness of each regime, where the number (FRic) indicates the proportion of the global space filled. Functional dispersion (bottom row) is shown through the abundance weighted center point and the distance of each species to that point. FId (Functional Identity) show the coordinates of the center point in functional space. Each point (each species) in the functional dispersion plots are weighted by relative abundance (relative to other species in regime) where size of point indicates weight. For visual convenience only the first two axes (capturing 48.6% of variance) are plotted here, plots for PCoA axes 3 and 4 are shown in Supplementary Material 7.

Discussion

In this thesis, I show a temporal stability of three reef regimes within the Hawaiian Archipelago from 2010 to 2015. Linking these regimes to their associated fish herbivore communities using functional space, I depict a variation in the herbivory function. Together these two attributes provide a unique analysis of the spatiotemporal aspects of herbivory and the persistence of coral reef regimes.

Reef regimes and their stability

Studies on alternate regimes focus primarily in defining the potential causes for regime shifts or discuss hysteresis effects inherent to the regime shift concept (Scheffer et al. 2001, Scheffer and Carpenter 2003). They are primarily based on single site investigations with long-term temporal data (Hughes 1994, Hughes et al. 2007). These types of studies have been useful in determining the existence of multiple regimes, and in highlighting the difficulties associated with reversing shifts. However, very few studies address existing alternate coral reef regimes, where long-term single site data is lacking. Recent approaches have applied powerful ordination methods to broad, spatial datasets in order to detect, visualize and define potential multiple ecosystem regimes (Jouffray et al. 2015). This study applies these methods to the same spatially extensive datasets, but across multiple years. While the results show that three regimes reoccur across years, the variation seen in benthic make-up within each regime highlights problems in how we define regime boundaries and thereby in how we identify and detect regimes. Should regime boundaries be determined by the visible make-up of the regime, such as percentage of benthic cover (Jouffray et al. 2015) or should they be determined by the feedbacks and interactions that occur on the site? Feedback processes have been brought forth as defining characteristics of the existence of alternate regimes across a range of marine systems (Nyström et al. 2012, Rocha et al. 2014, van de Leemput et al. 2016), including coral reefs (Mumby and Steneck 2008, Nyström et al. 2008). If regime boundaries are determined by visible metrics of benthic cover (Jouffray et al. 2015), and/or fish biomass (Donovan et al., in review), how does this definition account for environmental stochasticity? This study showed a variation in benthic cover between years, with a shift to more turf algae in 2015. This shift could be a result of external drivers and represent inter-annual or seasonal variation within the reef benthos. However, due to the lack of intra-annual data, it cannot be determined at which temporal scale the variations occur. External drivers that could influence benthic composition include wave and wind stress (Gove et al. 2015), eutrophication (McClanahan et al. 2002), diseases (Aronson and Precht 2001) and pulse events such as high seawater

temperature (Hughes et al. 2017). In 2014, the Hawaiian Archipelago was affected by an elevated seawater temperature event, which resulted in moderate archipelago wide coral bleaching (Ivor Williams, pers. com.). Bleaching events have been shown to trigger increases in abundance of rapidly colonizing algae that subsequently prevent coral recovery (Birrell et al. 2008). The 2014 bleaching event could therefore be a contributor to the higher turf cover in 2015. However seasonal algal blooms during the summer months do also occur in some areas of the archipelago (Ivor Williams, pers. com., Stimson et al. 1996, Vroom and Timmers 2009).

Having turf algae as a separate regime has been debated (Fung et al. 2011). One of the main problems with turf algae is the variation in specificity in its definition. Some studies use a narrow definition of turf based on the exact measured height of the algae (Bellwood and Fulton 2008, Birrell et al. 2008) whereas some apply the term more broadly to all turf-like algal growth forms (Ayotte et al. 2011). NOAA use the broader definition of turf, and thus another potential explanation for the “turf creep” could be small changes in inclusion criteria in what defines turf. Additional studies argue that turf algae, sometimes referred to as epilithic algal matrix, is a composite of algal and detrital matter where both aspects are to be considered. This approach highlights the importance of understanding sedimentation and the feedbacks between sedimentation and algal growth (Bellwood and Fulton 2008) and the influence of both on coral recruitment (Birrell et al. 2005). It also highlights the fact that many of the fish species seemingly targeting turf algae are instead targeting detrital matter (Wilson et al. 2003).

When looking at the geographic location of the regimes in this study, some interesting patterns emerge. The mapping analysis highlights the high presence of coral regimes along the leeward sides of islands such as Lana’i, Moloka’i and Maui, whereas the windwards sides are dominated by turf regimes. Studies from the wider Pacific have shown that wind stress and wave patterns alone can cause shifts from coral to turf regimes (Gove et al. 2015). The pattern seen here thus provides a baseline for further analysis into the impact of external biophysical (and anthropogenic) drivers for determining reef regimes in the Hawaiian Archipelago.

The geographic position of regime sites can also allow for insight into the buffering capacity of the herbivory function. The investigated regime herbivore communities are a composite of all the sites within that regime, and all species and thus guilds may not be present at all individual sites within that regime. The three different dietary guilds (scrapers, grazers and browsers) each signify a particular feeding niche and the presence or absence of each niche at each individual site provides an indication of the geographical redundancy within the regime.

The clear difference seen in percentage of sites where all three of these niches are filled (approx. 90% in coral, 60% in turf and 30% in macro) highlights the relative differences in the herbivore communities between regimes. The low percentage of sites within the macro regime that alone fulfil all three dietary niches suggests a higher reliance on connectivity between sites, where the function is complemented by herbivores from adjacent sites.

Functional groups as a tool to understand regimes

Benthic cover on a reef is the results of ecosystem properties and dynamics (e.g. varying fish/herbivore biomass, competition for space, disease feedback processes), and the range of external biophysical (e.g. waves, irradiance, salinity) and anthropogenic (e.g. nutrients, fishing, acidification) drivers (Norström et al. 2016). Thus, discerning the specific role of fish herbivores for benthic regimes is difficult. Using a functional approach, especially looking at dietary niches has helped our understanding of these interactions. It is known that grazers crop algal turf, preventing the establishment of larger fleshy, macroalgae (Bellwood et al. 2004). Browsing species have been found to be the only group of herbivores that target and remove macroalgal stands (Streit et al. 2015). Scrapers, as they scrape the turf algae away while feeding, open up space for coral recruitment (Bellwood and Choat 1990). To maintain a coral dominated regime, one would expect a higher presence of scrapers and grazers, whereas a higher biomass of browsers would be expected in a macro regime, due to the abundance of resources. However, as shown by the variation in relative biomass of functional groups between years, this relationship is not straightforward. It has been shown that once large macroalgal areas are established, such as a macroalgal regime, the high density algal patches (Hoey and Bellwood 2011), as well as the chemical defences of the macroalgae (Rasher et al. 2013) deters browsers from fulfilling their function.

Diversity within the functional space

Overall, all three identified regimes showed relatively even functional richness (FRic) and functional dispersion (FDis) within the functional space. This suggests that overall, the herbivore communities do not differ much in terms of function. The cases where regimes were significantly different in terms of functional richness, the difference was always attributed to a presence or absence of the largest browsing and/or grazing species (*Naso annulatus* and *Acanthurus xanthopterus*). In 2010, the coral regime herbivore assemblage contained both *N. annulatus* and *A. xanthopterus* in contrast to both the macro and turf regime, thus explaining the significant functional difference. This pattern, where the two largest herbivores have a

disproportionate impact on functional richness opens up for further investigation to how body size potentially has the ability to influence regimes and benthic cover at several scales. Other studies have looked at body size to determine functional diversity across scales and suggested approaches, such as discontinuity theory, for determining the boundaries of these functional scales (Allen et al. 2005, Nash et al. 2014, 2015). Expanding our understanding of the scale at which the herbivory function is performed, together with the understanding of how regimes are separated in space and the network that connects them, would get us one step closer to potentially predicting the spread of regime shifts both on a local and regional scale.

The uneven influence of certain species is also seen in the uneven distribution of biomass within the herbivore communities associated with each regime. The dominance by *Naso unicornis* in the browser biomass mirrors patterns found in similar, non-regime based studies (Bellwood et al. 2003, Hoey and Bellwood 2011). Here *N. unicornis* accounted for up to 94% of browser biomass. Another fish species, *M. niger*, dominated browser biomass in the coral regime. This discrepancy provides further indications of differing herbivore communities within the different regimes. It could be argued that *M. niger* due to its plasticity in diet (Kavanagh and Olney 2006) is a more competitive species in the more complex coral regime, as oppose to the lower complexity macro or turf regime, and is therefore seen in larger numbers. Speculations can be made whether the uneven biomass distributions seen is a result of the delicate interplay within the ecosystem, with species-species interaction. It is unknown whether the dominant species are abundant through outcompeting their functional peers or if the abundances of other species would be equally low in their absence.

Panel 1: Redundancy on coral reefs

The comparison in this study between how taxonomic and functional diversity varies among the regimes highlights the issue of functional redundancy within the ecosystem. Functional redundancy is “the capacity of one species to functionally compensate for the loss of another” (Nyström 2006). It describes the capacity of a system to buffer for potential disturbances. A system with high redundancy can keep all functions intact, even if some species are lost. Lately studies have highlighted the importance of differentiating between attributes of redundancy for understanding the overall vulnerability of systems (Dagata et al. 2016), showing the importance of addressing not only the number of species that perform a function but also the biomass levels at which they are present (Mouillot et al. 2013a). In this study, I provide a framework for discussing these different attributes of functional redundancy (Figure 6). Theoretical redundancy, is here defined as the numbers of species present that fulfil the same function. This is the most common attribute of functional redundancy discussed in the literature (Nyström 2006). Potential redundancy is a subset of theoretical redundancy that, encompasses also the biomass (or abundance) of the species within that functional niche. Taking biomass (or abundance) into consideration has been widely discussed, as it often reduces the expected redundancy (Mouillot et al. 2013a, Mora et al. 2016). Realised redundancy (the innermost circle in Figure 6) is the level of redundancy that exists in a system when accounting for both number of species and their biomass. I also define realised redundancy by the level of certainty of the functional execution. In this thesis, I have investigated both number of species within functional groups and the biomass levels present, I do not however know which individuals actually perform the function. I cannot therefore estimate the realised redundancy. To do so would require *in situ* observations (Bellwood et al. 2006, Hoey and Bellwood 2011). For example, Michael et al. (2013) showed in a study on the Ningaloo Reef, Western Australia, that of 31 herbivorous species present, 3 species (*Naso unicornis*, *Kyphosus vaigiensis* and *K. bigibbus*) were responsible for 85-99% of feeding, although they only represented 1-7% of biomass (cumulatively).

In the Hawaiian Archipelago, functional diversity was relatively homogenous between regimes. However, taxonomic diversity showed significant differences between regimes, with diversity being highest in the coral regime and lowest in the macro regime. This mismatch between functional and taxonomic diversity suggests that although the functional scope of the herbivore community on each regime remains intact, the redundancy differs. Sites within the macro regime had the lowest mean species richness and the herbivore function is thus filled by relatively few species, redundancy is low. The coral regime on the other hand, which has higher species richness, suggests higher functional redundancy. This redundancy, based on the comparison between functional and taxonomic diversity, indicates the level of theoretical functional redundancy on the reef. When we break this down further, consequently reducing the theoretical redundancy, the macro regime has its redundancy reduced further. Taking into account biomass, the macro regime was dominated (in terms of absolute biomass) by few species throughout all years. An uneven biomass distribution suggests that the herbivore function is not filled by all, but rather by a few species present in that regime species, indicating low potential redundancy.

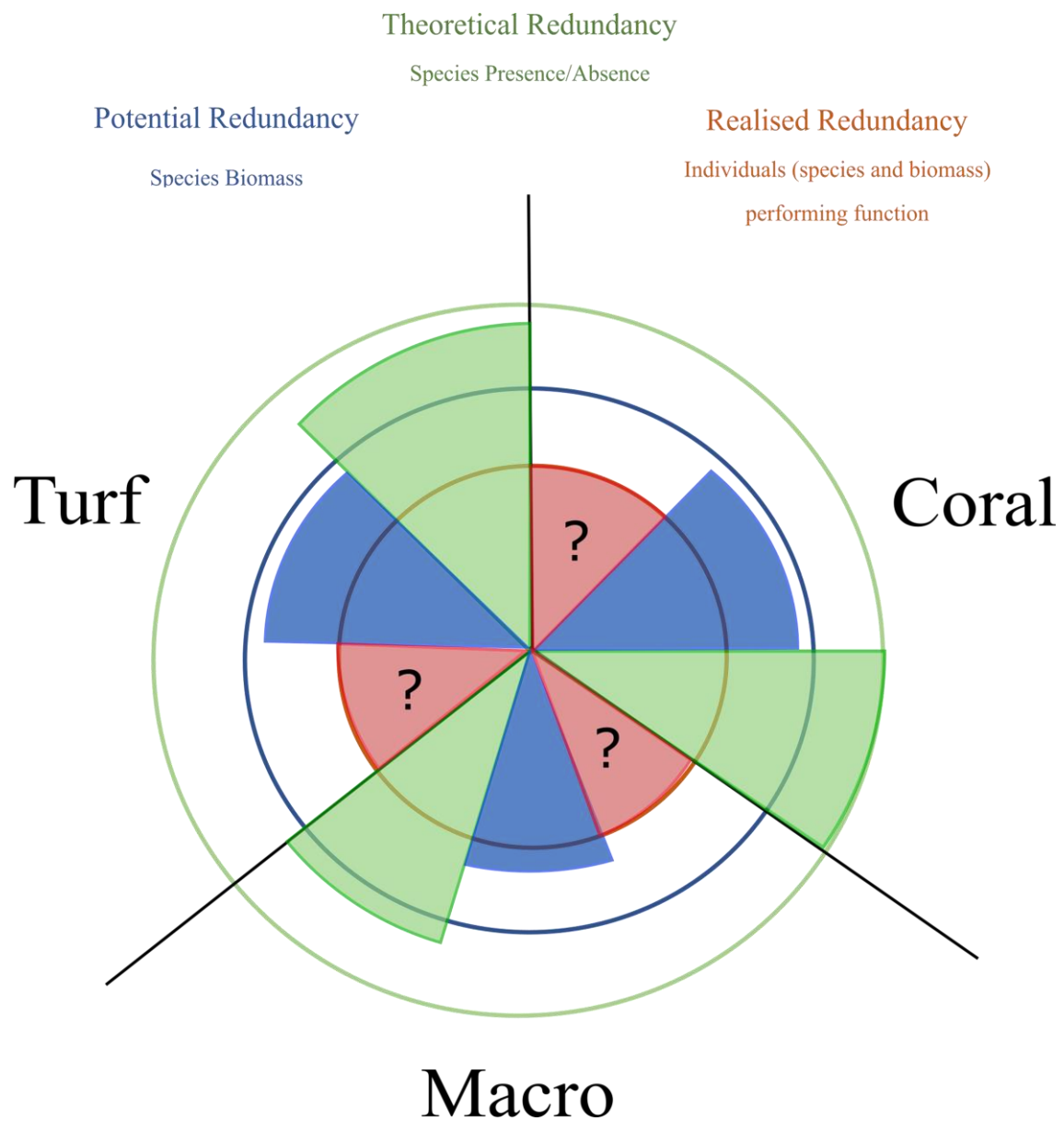


Figure 6. Framework for discussing different attributes of functional redundancy along with a conceptual use of the framework according to the Hawaiian herbivore communities analysed in this study.

The regime-concept and functional groups as tools for management

Identifying and mapping alternate regimes can be a tool for assessing the current state of the reef, gain further understanding of the influence of external drivers and adapt management methods. As inputs of nutrient, from land-based run-off has been seen to increase algal growth (Hunter and Evans 1995, McClanahan et al. 2002), being able to geographically match algal-heavy regime sites with point sources could focus management. Similarly, due to the hysteretic effects inherent to regime shifts, sites that have already shifted to a turf or macroalgal regime will require different management practises to reverse the shift than practises in place to prevent shifts in coral regimes (Scheffer et al. 2001). An important step for improved management is also to better understand the role the spatial configuration of regimes. The spatial configuration of regimes play an important role for spatial resilience (Nyström and Folke 2001) and as a warning signal for impending large-scale, cascading regime shifts (Nyström et al. 2008, Elmhirst et al. 2009).

On Hawaii, the Kahekili Herbivore Fisheries Management Area (KHFMA) on Maui, was a management tool set in place to boost herbivory, after multiple years of heavy macroalgal blooms (Cochran et al. 2014). Within the KFFMA fishing of herbivorous species is prohibited. Within the first 6 years after the KHFMA establishment, herbivore biomass had increased, resulting in changed benthic cover (Williams et al. 2016). Although both regimes and functional space approaches to management cannot address global scale challenges, such as atmospheric CO₂ concentrations, these approaches have been suggested to buy time (Edwards et al. 2011). Managing herbivore communities together with a better understanding of regime shifts, can boost the resilience of coral regimes, buying time for society to find the global scale solutions needed (Edwards et al. 2011, Frieler et al. 2012).

Conclusion

To conclude, this thesis has shown that the three regimes in Hawaii are present across a 5-year period and thus temporally stable. The regimes, although stable in presence/absence are variable in terms of benthic cover, bringing up the question of how we determine regime boundaries. I have also shown that the herbivore communities within each regime do not vary significantly in terms of diversity but rather vary in regards to redundancy, leaving the macro regime more vulnerable to disturbances. This suggests that a loss in redundancy in the herbivore community is correlated with shifts in regimes on coral reefs, either as a result or cause of a shift. Together the knowledge of existing coral reef regimes and the varying influence of herbivory on each regime can help adapt management practises to be the most effective for each case.

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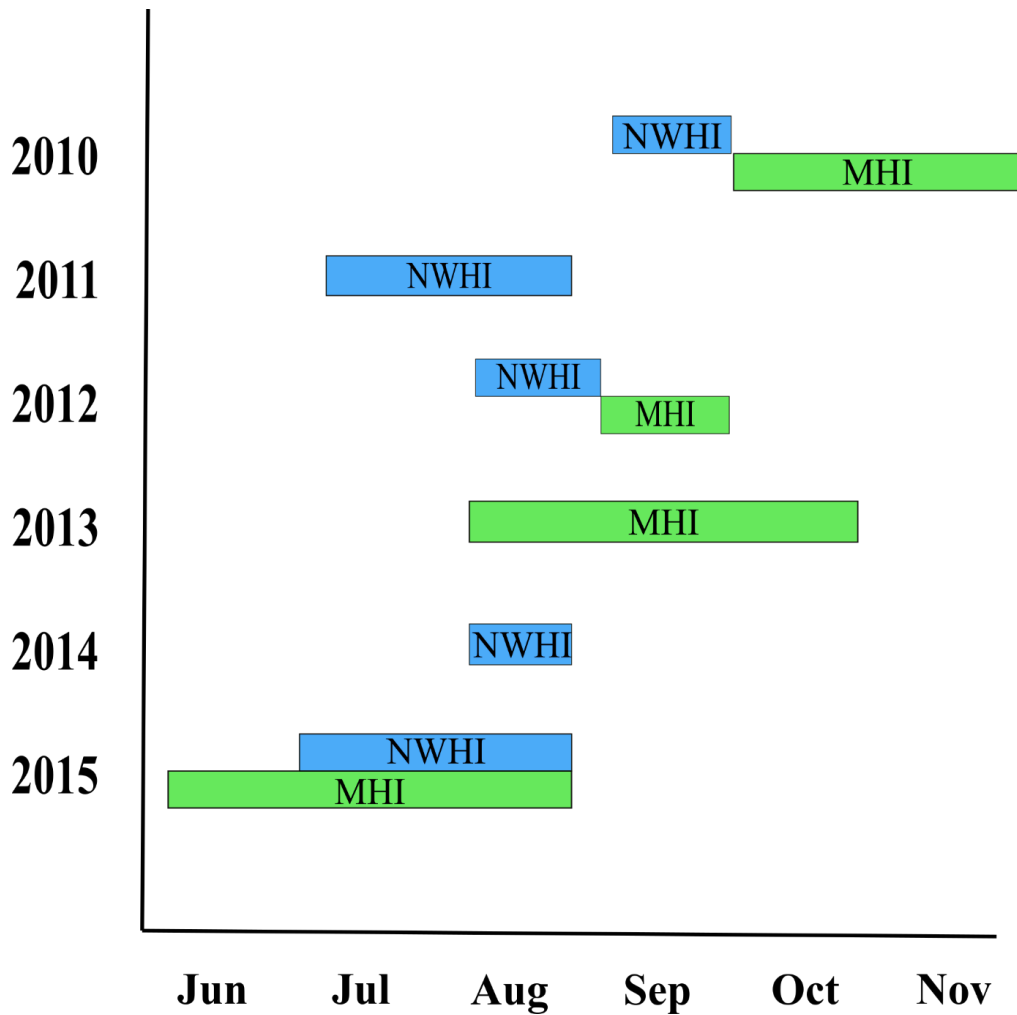
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Supplementary Material

Supplementary Material 1: Data collection timeline



Supplementary Figure 1. Time and region of data collection for each investigated year.

Supplementary Material 2: Trait Data

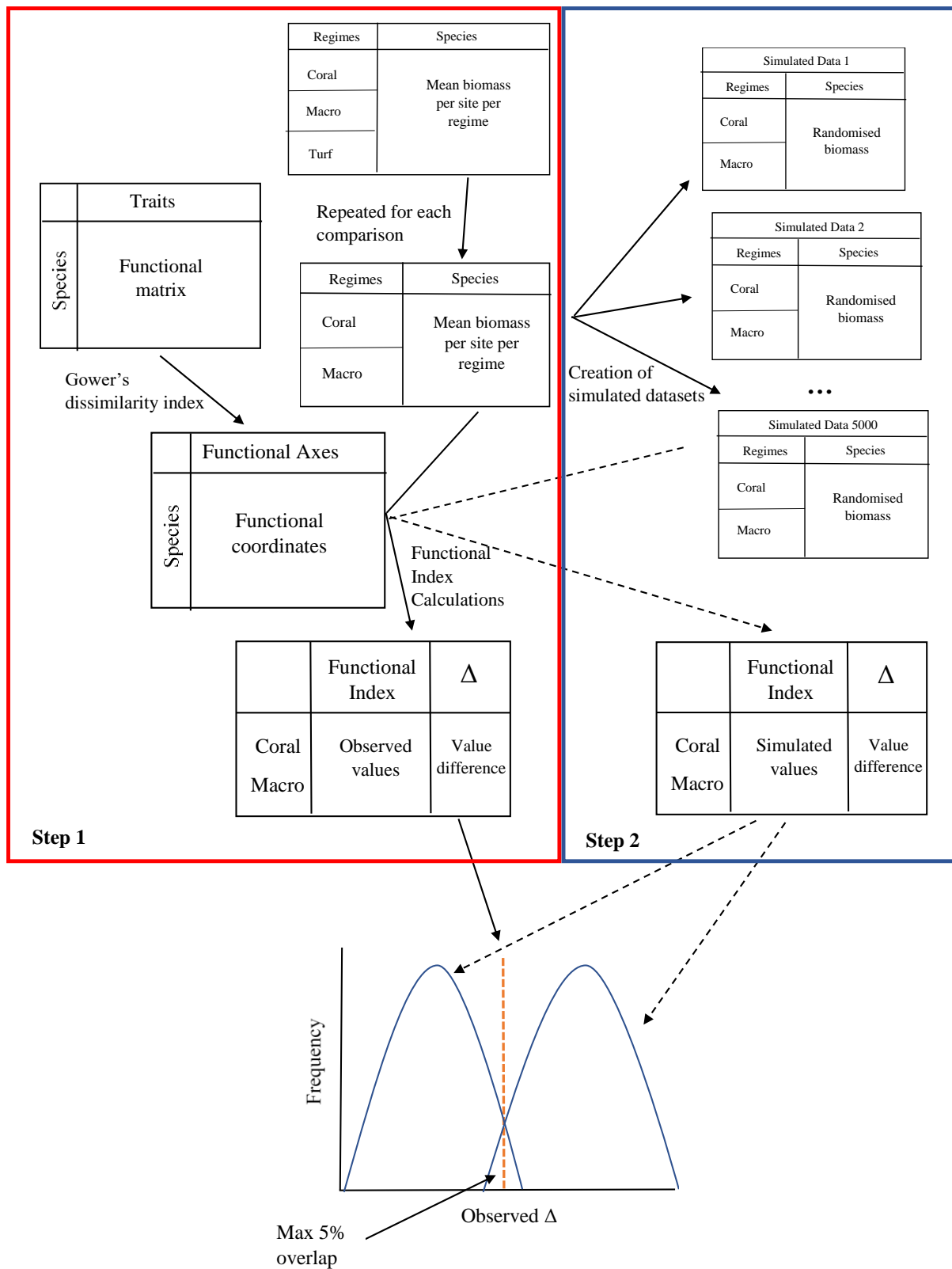
Supplementary Table 1. Full list of all herbivorous species included in analysis along with the associated trait values.

Species	Functional Guild	Size (cm)
Acanthurus achilles	Browser	24
Acanthurus leucopareius	Browser	25
Kyphosus cinerascens	Browser	50
Kyphosus hawaiiensis	Browser	41
Kyphosus sandwicensis	Browser	75
Kyphosus vaigiensis	Browser	70
Melichthys niger	Browser	50
Naso annulatus	Browser	100
Naso lituratus	Browser	60
Naso unicornis	Browser	74
Zebrasoma flavescens	Browser	20
Zebrasoma veliferum	Browser	48
Abudefduf sordidus	Grazer	24
Acanthurus blochii	Grazer	62
Acanthurus dussumieri	Grazer	54
Acanthurus guttatus	Grazer	26
Acanthurus maculiceps	Grazer	58
Acanthurus nigricans	Grazer	21
Acanthurus nigrofuscus	Grazer	21
Acanthurus nigroris	Grazer	25
Acanthurus olivaceus	Grazer	35
Acanthurus triostegus	Grazer	27
Acanthurus xanthopterus	Grazer	70
Ctenochaetus hawaiiensis	Grazer	25
Ctenochaetus strigosus	Grazer	19
Stegastes fasciolatus	Grazer	17
Calotomus carolinus	Scraper	54
Calotomus zonarchus	Scraper	33
Chlorurus perspicillatus	Scraper	69
Chlorurus sordidus	Scraper	40
Scarus dubius	Scraper	36
Scarus psittacus	Scraper	30
Scarus rubroviolaceus	Scraper	70

Supplementary Material 3: Randomisation Methodology

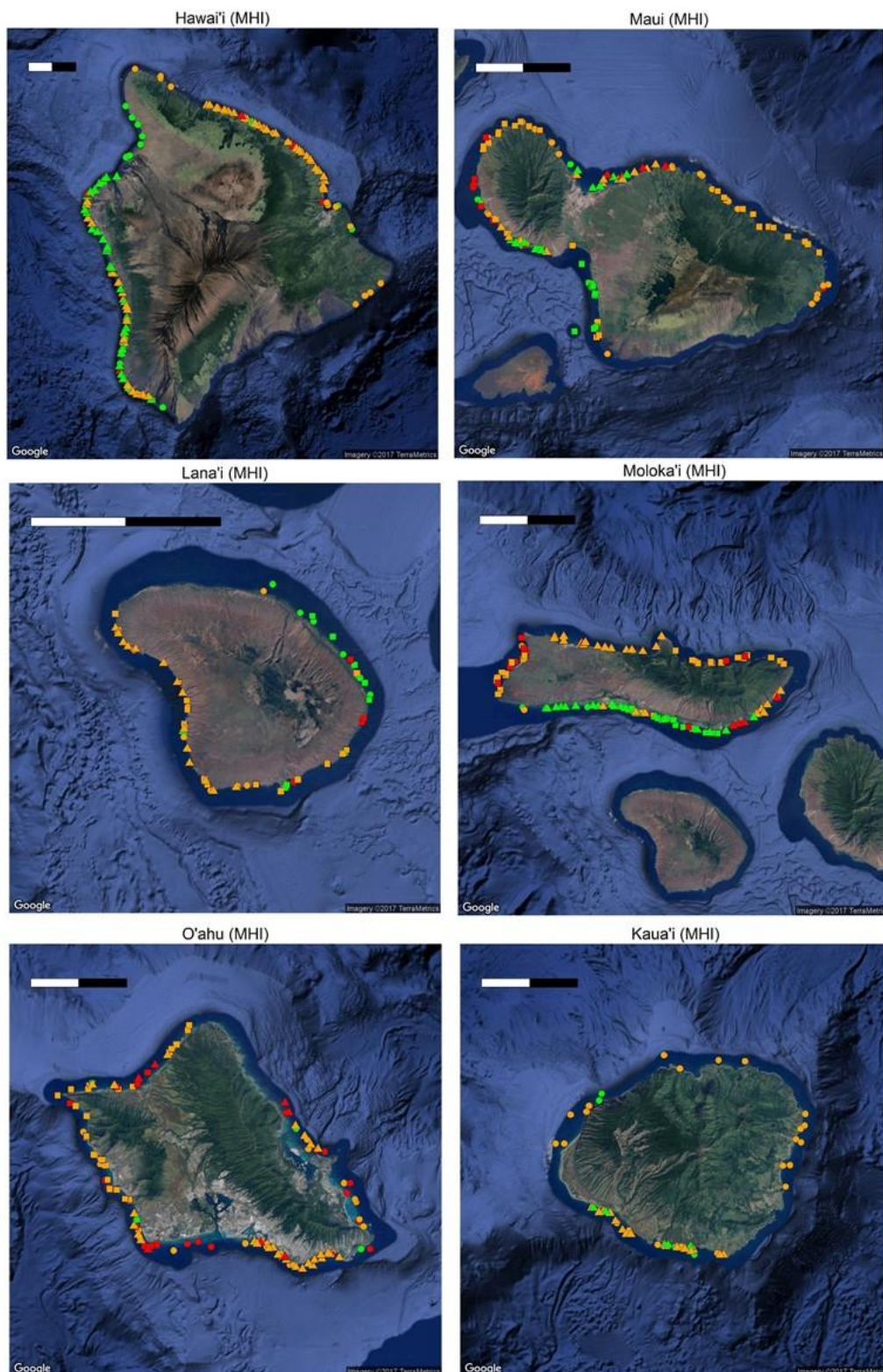
The method is comprised of two steps (Figure S2); where the first step calculates the pairwise observed index values and the second step calculates the index values based on simulated datasets. As the functional index calculations are based on relative biomass values, the observed index calculations also need to be calculated pairwise to allow for comparison with the simulated datasets. The simulated datasets are created by randomly assigning the biomass from either regime 1 or regime 2 (in the comparison) for each species present in the two regimes. 5 000 simulated datasets were created using this methodology for each of the pairwise comparisons.

The functional index values for the observed (real) data is compared between regimes and the value difference is noted. This value difference becomes the baseline from which the calculations of the simulated datasets are compared. The null hypothesis (H_0) is that there is no difference between regimes and the alternate hypothesis (H_1) is that there is a difference between regimes. If there is a significant difference between the regimes there is less than 5 % probability that the functional index value difference (ΔFD) can be obtained by random (under the biomass conditions of the two-regime comparison). Therefore, by comparing the observed ΔFD with the 5000 simulated ΔFD 's significant difference can be determined. To test for significance, the proportions of simulated ΔFD values inferior (less than) the observed ΔFD value were calculated. If this proportion is >0.975 (due to bilateral testing) then the observed change is significant. Similarly, to allow for negative ΔFD values, if the proportion of ΔFD values superior to observed is >0.975 , change is significant. The randomisation methodology was performed on each pairwise comparison (Coral-Macro, Coral-Turf, Turf-Macro) and then repeated for each investigated year.



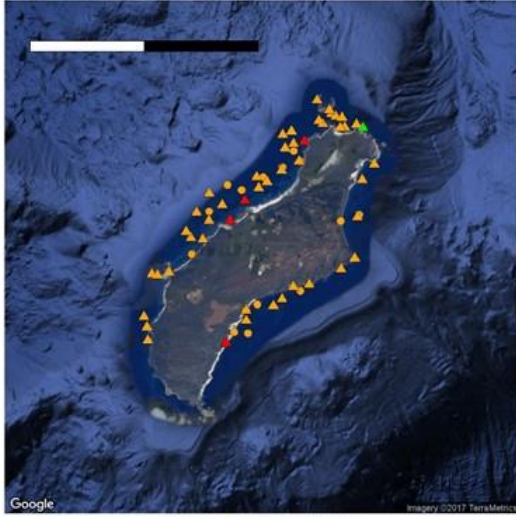
Supplementary Figure 2. Flow chart of randomisation methodology for determining significant differences in functional index values between regimes.

Supplementary Material 4: Island satellite maps

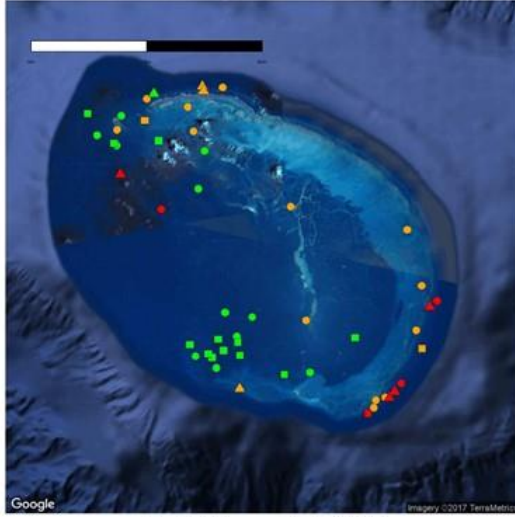


Supplementary Figure 3. Maps of all surveyed sites and islands in the Hawaiian Archipelago. The colour of the points indicates the prevalent regime. (Green = Coral, Orange = Turf and Red = Macroalgae). The shape of the points represents the survey year. (Circle = 2010, Square = 2012 and Triangle = 2015). The scale bar represents 20 km (10km white band and 10 km black band).

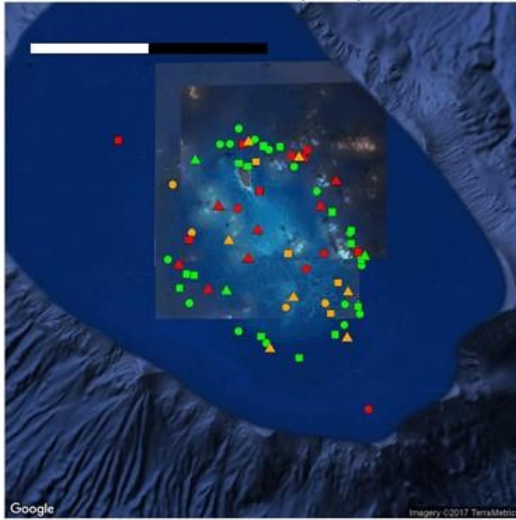
Ni'ihau (MHI)



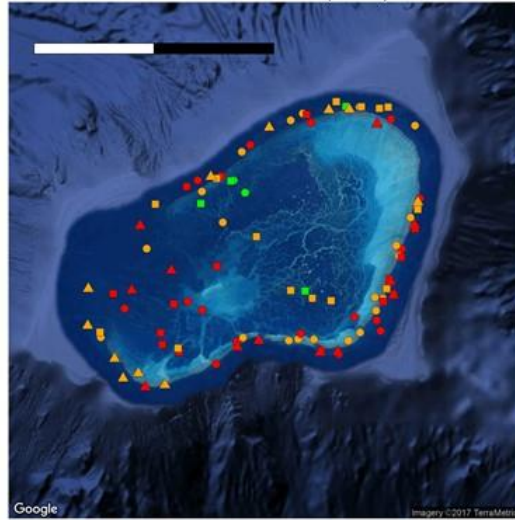
French Frigate Shoals (NWHI)



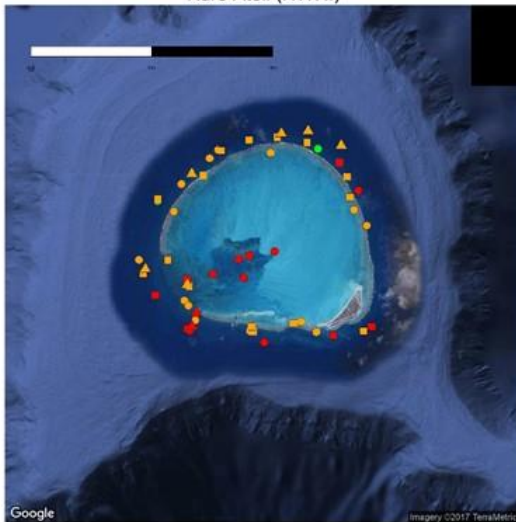
Lisianski Island (NWHI)



Pearl & Hermes Atoll (NWHI)



Kure Atoll (NWHI)

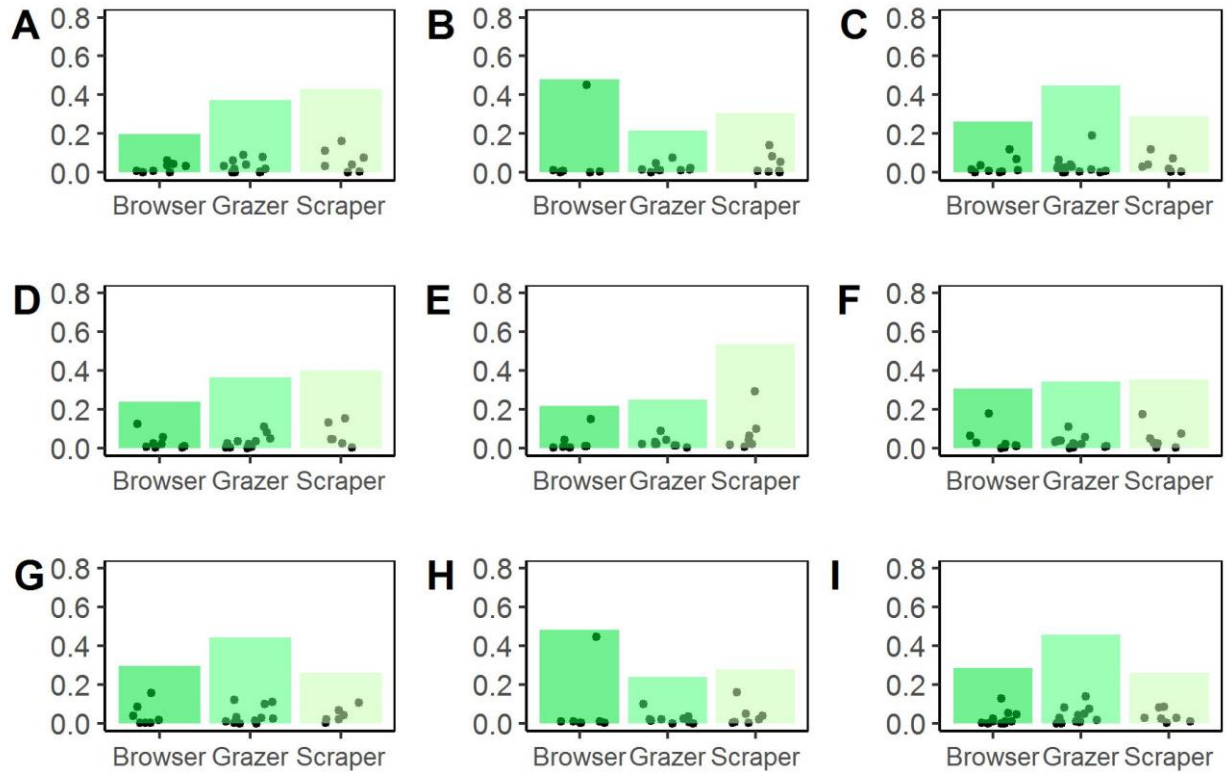


Supplementary Material 5: Mean benthic cover within regimes

Supplementary Table 2. Mean percentage cover for each benthic cover category within each month (for years and regimes).

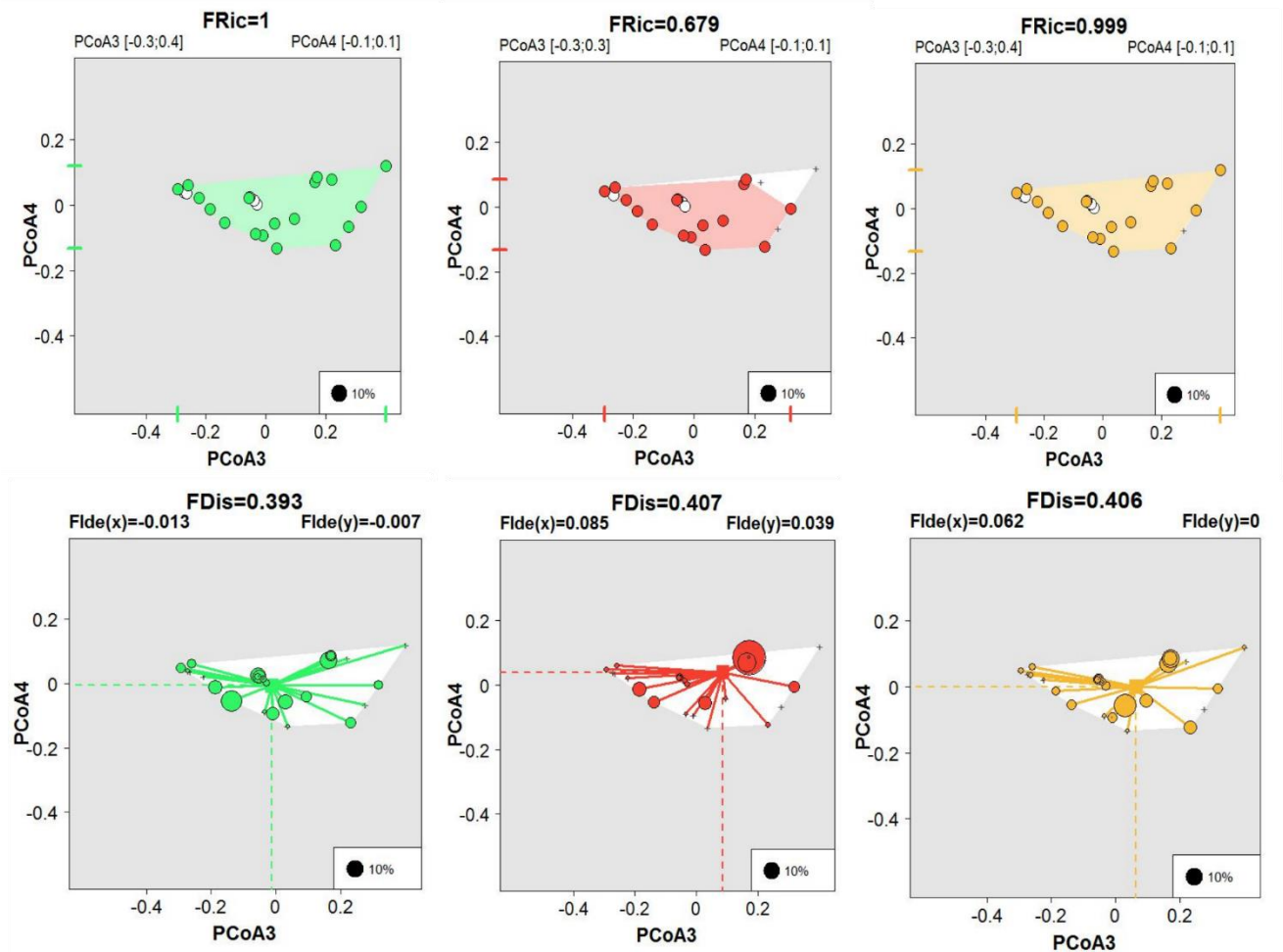
Month	Regime	Year	Hard Coral	CCA	Macroalgae	Turf Algae	Sand
6	Coral	2015	37.4	7.7	1.9	40.5	12.3
6	Macro	2015	5	3.2	28.7	43.7	18.2
6	Turf	2015	6	3.9	3	77	9.7
7	Coral	2015	29.8	7.6	0.6	48.9	13.1
7	Macro	2015	3.6	2.4	24	51.4	18.4
7	Turf	2015	9.6	3.9	4	72.4	9.4
8	Coral	2015	28.9	7.8	9.2	48.7	5.3
8	Macro	2015	4.8	5.1	29.6	42.7	18.7
8	Turf	2015	6.3	6.5	9.4	72.3	5.1
8	Coral	2012	58.8	10.6	8.3	15.1	7.2
8	Macro	2012	11.8	10.2	41.7	24	11.6
8	Turf	2012	11.6	8.6	15.2	56.1	8.3
8	Coral	2013	46	11.5	5.7	29	7.6
8	Macro	2013	6	4.2	29	40.7	19.9
8	Turf	2013	9.8	6.8	8.2	67.1	7.5
8	Coral	2014	43.8	14.4	9.6	28.3	3.7
8	Macro	2014	6.8	12.1	19.2	44.2	15.9
8	Turf	2014	3.8	5.5	8.4	75.8	6.5
9	Coral	2012	51.7	5.8	6.4	26.5	8.8
9	Macro	2012	8.2	1.5	41.9	29	15.6
9	Turf	2012	9.1	3.6	8.7	68.1	9.7
9	Coral	2010	44.7	13.7	10.9	22.7	8
9	Macro	2010	5	2.3	50.8	25.5	16.5
9	Turf	2010	9	7.2	12.8	62.1	8.5
10	Coral	2013	34	5.5	14.5	38	8
10	Macro	2013	4.8	4.9	31.8	39.5	16
10	Turf	2013	14.2	7.2	8.9	63.5	5.6
10	Coral	2010	51.6	9.2	2.9	27.8	8.6
10	Macro	2010	8.1	5.2	39	28.5	19.3
10	Turf	2010	11.4	5.5	5.5	68.6	8.7
11	Coral	2010	38.4	6.8	6.3	35.5	13.1
11	Macro	2010	6.3	6.9	31.4	37.7	17.7
11	Turf	2010	10.4	4.6	8	60.26	16.7

Supplementary Material 6: Relative fish biomass



Supplementary Figure 4. Relative biomass of each herbivorous species present in each regime and year (black dots). Green bars represent the relative biomass of that feeding guild (i.e. the sum of all species in that group). Rows represent years with A-C being 2010, D-F being 2012 and G-I being 2015. Columns represent the three identified regimes; Coral (A, D and G), Macro (B, E and H) and Turf (C, F and I).

Supplementary Material 7: Functional Space Plots



Supplementary Figure 5. PCoA 3 and PCoA 4 of functional space of 2010 Hawaiian fish community. Green represents the coral regime, red the macro and orange the turf. Top row shows functional richness, bottom row shows functional dispersion.

Supplementary Table 3. Taxonomic diversity of composite regime herbivore assemblages. Number of species upon which functional diversity indices are calculated.

Year	Coral	Macro	Turf
2010	27	22	30
2012	25	23	29
2015	26	24	32

