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Philosophical Transactions of the Royal Society B

Cyswllt i'r cyhoeddiad / Link to publication

09. Oct. 2020

Identifying multiple coral reef regimes and their drivers across the Hawaiian Archipelago

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ABSTRACT

Loss of coral reef resilience can lead to dramatic changes in benthic structure, often called regime shifts, which significantly alter ecosystem processes and functioning. In the face of global change and increasing direct human impacts, there is an urgent need to anticipate and prevent undesirable regime shifts, and conversely, to reverse shifts in already degraded reef systems. Such challenges require a better understanding of the human and natural drivers that support or undermine different reef regimes. The Hawaiian Archipelago extends across a wide gradient of natural and anthropogenic conditions and provides a unique opportunity to investigate the relationships between multiple reef regimes, their dynamics and potential drivers. We applied a combination of exploratory ordination methods and inferential statistics to one of the most comprehensive coral reef datasets available in order to detect, visualize and define potential multiple ecosystem regimes. The present study demonstrates the existence of three distinct reef regimes dominated by hard corals, turf algae, or macroalgae. Results from Boosted Regression Trees (BRT) show non-linear patterns among predictors that explain the occurrence of these regimes, and highlight herbivore biomass as the key driver in addition to effluent, latitude and depth.

Key words: boosted regression trees – coral reefs – disturbance – Hawaiʻi – multiple regimes – resilience

INTRODUCTION

The dramatic loss of live coral cover on reefs worldwide [1–3] has raised serious concerns regarding their future [4,5]. Parallel to this loss, observational [6,7,8], experimental [9,10], and modelling [11] studies suggest that many coral reefs are shifting to alternative regimes (or states) with consequences for coastal societies that depend on reef resources. While transitions from coral to macroalgae dominance are most commonly described [6,7] other degraded states, characterized by sponge, soft coral or corallimorpharian dominance, have been suggested [12].

Regime shifts in coral reefs have primarily been described in human-dominated environments [13,14] where overfishing and reduced water quality, acting in concert with climate change, have been suggested as key drivers [10,15]. Specifically, the loss of herbivores, which keep algal colonization and growth in check, has been argued to be a leading cause of regime shifts [2,7], particularly when large tracts of substratum become open for rapidly colonizing algae, e.g. following hurricanes or coral mass bleaching events [10,16,17].

Yet, recent meta-analyses of longitudinal datasets have questioned the existence (or the stability) and the generality of alternative reef regimes in coral reefs. For example, Bruno et al. [18] looked for multimodal patterns in the frequency distribution of benthic cover in 1851 reefs worldwide, and reported that most reefs were neither in a coral-dominated state (>50% coral cover) or macroalgae-dominated state (>50% macroalgal cover), challenging the assumption that coral-macroalgae shifts are a common phenomenon. Similarly, using stochastic semi-parametric modelling on reef data from the Caribbean, Kenya, and Great Barrier Reef, Żychaluk et al. [19] found no evidence of bimodality at a regional scale. However, Mumby et al. [20] argued that both studies make a number of unrealistic statistical assumptions with regards to the constancy of environmental variables, resolution of field data, and disturbance dynamics. Similarly, Hughes et al. [14] claimed that data used are often too patchy and unable to identify the complex mechanisms or processes causing long-term change. Moreover, they contested the cut-off set by Bruno et al. [18] (i.e. >50% cover) arguing that few reefs globally display such abundances of dominating benthic taxa.

Diagnosing multiple regimes from field data is problematic because coral reef may respond slowly to frequent pulse perturbations [20] that mask trends of recovery or decline. Given the critical consequences of regime shifts on ecosystem services [5,21] and their profound management implications, we need a better understanding of the processes that

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drive alternative reef regimes, and improved methods to extract evidence of their existence from field data.

Here, relying on an extensive spatial dataset gathered in the Hawaiian Archipelago across gradients of natural and anthropogenic conditions, we apply a novel approach for detecting, visualizing and defining potential multiple ecosystem regimes. We also identify the primary human and natural drivers that explain these regimes across a regional scale.

MATERIAL AND METHODS

Study area

The Hawaiian Archipelago (Hawaiʻi, USA) is one of the most isolated archipelagos in the world (figure 1). While the heavily populated Main Hawaiian Islands (MHI) are overfished [22] and subjected to a range of anthropogenic stressors [23], the North-western Hawaiian Islands (NWHI) receive minimal direct human impacts and are among the most protected coral reefs globally [24].

Organization of data

Benthic and fish data were collected in 2010 from 302 reef sites across the Hawaiian Archipelago by the Coral Reef Ecosystem Division, as part of NOAA's Pacific Reef Assessment and Monitoring Program. (For sampling methodology see the electronic supplementary material S1.)

Fish species were categorised into functional groups based on their trophic level (see the electronic supplementary material S2), and herbivores were further divided into *grazers, scrapers,* and *browsers* [25]. Grazers are fish that crop on algal turf, preventing the establishment and growth of macroalgae. Scrapers also feed on turf but they remove some component of the reef substratum, which provides bare areas for coral recruitment. Finally, browsers consistently feed on macroalgae and may play a crucial role for reversing macroalgae-dominated states [5,26]. Dietary information was collected from FishBase [27] and complemented from the literature [25] when higher-resolution data was required for herbivore classification. In cases where fish could only be identified to genus level, information on the diet of close relatives from the same genus was used. Total biomass per functional group was calculated from the biomass of individual fish obtained using the formula:

$$W = a\, TL^b$$

where W is the weight in grams, TL the total length in mm, and *a* and *b* species-specific conversion parameters extracted from FishBase [27].

In addition to benthic and fish data, a set of human-use and environmental GIS-derived variables – human population density, distance to potential impact (e.g. shore, stream), effluent discharge and stream disturbance data (composite metrics of many land cover variables) [28] – was compiled for the Main Hawaiian Islands except for Lāna'i and Ni'ihau.

(For methodology and detailed list of the variables see the electronic supplementary material S3.)

Data analyses

All statistical analyses and graphical presentations were conducted using R version 2.15.1 [29]. Specific packages used are referred to in the text or in the figure legends.

Identification of reef regimes and categorisation of sites

First, we replicated the method applied by Bruno et al. [18], to create a phase shift index (PSI) and graphically check for multimodality in the frequency distribution of benthic states. In essence, the PSI is the first component of a Principal Component Analysis (PCA) based on the cover of coral and macroalgae.

Second, a correlation-based PCA was performed using six benthic habitat variables: hard coral cover (Hcoral), macroalgae cover (MA), turf algae cover (TA), structural complexity estimate (Complexity), sand cover on the reef surface (Sand) and crustose coralline algae cover (CCA). Structural complexity was included since it is a key aspect of reef habitat quality [30], and data were standardised to account for variables measured at different scales. A hierarchical clustering of the variables was produced with the same Euclidean distance matrix as for the PCA using *pvclust* package version 1.2-2 [31], and *p*-values computed by 10 000 multi-scale bootstrap resampling [32] were assigned to each cluster to indicate how strong the cluster was supported by the data. A cluster was considered to be significant when the approximately unbiased *p*-value was above 0.95. Finally, building on the number of significant clusters obtained through the previous hierarchical analysis, a K-means partitional clustering process [33] was carried out to categorise the 302 sites with regards to their benthic habitat.

Relative influence of natural and human variables on reef regimes

To assess what key human and environmental variables were associated with different reef regimes, a Boosted Regression Trees (BRT) modelling technique [34] was performed using the *gbm* package version 2.0-8 [34] and the *gbm.step* routine described by Elith et al. [36]. For the MHI (with the exception of Lānaʻi and Niʻihau) 147 sites were modelled simultaneously against 15 predictor variables while for the NWHI, where human settings are absent, 118 sites were modelled against a set of 7 continuous and categorical predictor variables (table 1). Pairwise relationships between all variables (no Spearman rank correlation coefficient were greater than |0.75|) showed no multicollinearity. The categorisation of sites into different regimes was converted to presence-absence of each regime by survey site and analyzed using a binomial distribution. Partial dependency plots were used to visualize and interpret the relationships between each predictor variable and the regime after accounting for the average effect of all other predictor variables in the model. (For BRT methodology and details on model optimisation see the electronic supplementary material S4.)

RESULTS

Identification of reef regimes and categorisation of sites

The test for multimodality in the frequency distribution of living coral and macroalgae of the 302 Hawaiian sites (figure 2) displayed a normal distribution which is similar to the findings by Bruno et al. [18], i.e. an absence of multiple regimes. In contrast, the combination of analytical approaches used in this paper highlighted the existence of three primary regimes. The results were identical for the MHI and the NWHI and therefore, only the pattern for the archipelago as a whole is shown in figure 3.

The PCA using six benthic parameters showed a clear pattern of three distinct regimes. The first principal component axis (PC1) and the second principal component axis (PC2) accounted for 61.4 % of the total variability in the data (figure 3*a*). PC1 described a gradient from high coral cover, high CCA cover and high structural complexity (at negative PC1 scores), to high macroalgae cover, high sand cover and low complexity (at positive PC1 scores). PC2 best explained the variability of turf algae with higher turf cover at negative PC2 scores.

The hierarchical cluster analysis (figure 3*b*) confirmed the visual impression from the PCA with the benthic variables grouping into 3 significant clusters: CCA being associated with hard coral and structural complexity (*p*-value = 1), turf algae being closer to macroalgae and sand but a cluster by itself since outside of any significant cluster (*p*-value = 0.79) and macroalgae being closely associated with sand (*p*-value = 0.99).

Finally, the K-means partitional clustering differentiated the sites along these three clusters with an overrepresentation of turf algae dominated sites (figure 3*c*): 153 sites (51%) were categorised as *turf regime* (sites dominated by turf algae), 80 sites (27%) as *calcifying regime* (high structural complexity sites dominated by CCA and hard coral), and 69 sites (23%) were categorised as *macroalgal/sand regime* (low structural complexity sites dominated by macroalgae and sand). (Mapping of the categorised sites per island and average values of the benthic variables within each regime are shown in the electronic supplementary material S5.)

Relative influence of human and natural variables on reef regimes

For each region, only the four most influential predictor variables were reported and illustrated (figure 4). Preliminary threshold values below are given only in cases where the shape of the fitted function best matches the distribution of the fitted values. (See the electronic supplementary material S4 for the plots of the fitted values in relation to each predictor.)

Calcifying regime

In the MHI, a positive relationship with *scraper* biomass (22.3% relative influence) was the optimal predictor of the occurrence of structurally complex coral and CCA dominated sites (figure 4*a*). Other important predictors were negative relationships with higher *latitudes* (14.6%) and increasing *effluent* (13.1%, drop around 1.0×10^6 mgd), and a positive correlation with stream *fragmentation* (10.7%).

In the NWHI, three variables contributed most strongly to predicting *calcifying regime* occurrence (figure 4*a*): *scraper biomass* (34.1%, positively correlated), *depth* (30.5%, peaked between 12-22 meters), and *latitude* (20.7%, occurrence decreased at higher latitudes).

Turf regime

In the MHI, *grazer* biomass (18.6%) and *effluent* discharge (17.9%) were the two optimal predictors of turf algae occurrence, with positive non-linear relationships for both predictors

displaying thresholds around 10 g.m^{-2} and 1.5 x 10^6 mgd, respectively (figure 4*b*). The opposite pattern (i.e. negative correlation) was observed for stream *fragmentation* (14.5%), and *distance* to stream (12.9%).

In the NWHI, *depth* (30.3%) contributed most to explain the occurrence of turf algae with a drop near 10 m (figure 4*b*). *Grazer* biomass (19.8%) and *Latitude* (16.8%) were positively correlated, followed by a negative correlation with *scraper* biomass (11.9%).

Macroalgal/sand regime

In the MHI three key predictor variables contributed to the occurrence of macroalgae-dominated sites (figure 4*c*). Macroalgal dominance displayed negative non-linear relationships with increasing *grazer* (24%) and *browser* (15.5%) biomass. Thresholds seemed to occur around 5 g.m^{-2} and 2 g.m^{-2}, respectively. Human *population* density represented 14.8% of the relative influence and was positively correlated, whereas *scraper* biomass was negatively correlated (7.1%).

In the NWHI, herbivore biomass was again the main predictor (figure 4*c*): occurrence of *macroalgal/sand* sites decreased as the biomass of *grazers* (29%, drop at 5 g.m^{-2}), *scrapers* (22.8%, drop at 4 g.m^{-2}) and *browsers* (12.3%) increased. In addition, *latitude* (13.7%) was positively correlated.

DISCUSSION

Identifying existing regimes and understanding their drivers has great relevance for managers, policymakers and planners seeking to protect ecosystem services generated by coral reefs [5,37]. Based on a combination of exploratory and inferential statistics, this study provides a novel method to identify multiple regimes, and offers strong evidence of three distinct reef regimes occurring across the Hawaiian Archipelago – calcifying, turf algae, and macroalgal/sand regimes. It further suggests that simply testing for bimodality in the frequency distribution of present reef state [18] does not constitute a sufficient test of multiple regime existence. Our results also contribute to a deeper understanding of the relative influence of different drivers that underpin the occurrence of reef regimes, supporting the idea that they are multi-causal, driven by a combination of biotic processes, abiotic conditions and human drivers.

All three regimes occur both in the MHI and the NWHI, despite major differences in exposure to direct human impacts. This corroborates the findings of Vroom and Braun [38],who recorded high algal abundances in the NWHI and further stressed the necessity of re-evaluating the metrics used to gauge subtropical reef health. Our results also show that most reefs in this system are dominated by turf algae (51% of all sites). This raises the question whether turf-dominated reefs constitute a stable regime or an unstable transitional state that is moving towards a coral or macroalgal attractor [17]. It has been argued that turf eventually proceeds towards macroalgae dominance if herbivore density is low [39,40], but experimental studies suggest that turf can also constitute a stable regime in sediment-rich areas because herbivory of epilithic algal turfs is suppressed under sediment-laden conditions [41–43].

In this study the occurrence of all three regimes was strongly predicted, for both regions, by the biomass of herbivores, confirming the important role they play in coral reef dynamics and in mediating reef regime-shifts [2,44]. In addition, categorising herbivores into finer-scale functional groups (i.e. grazers, scrapers and browsers) allows for a better understanding of what specific ecological functions are important in supporting different regimes. The occurrence of *macroalgal/sand regimes* showed a negative non-linear relationship with the density of browsers that directly consume macroalgae, as well as with increasing biomass of grazers and scrapers that limit their growth. The *calcifying regime* was positively associated with the biomass of scrapers that provide area of clean substratum (feeding scars) for coral recruitment, whereas *turf regime* was positively correlated with grazers that prevent the transition from turf to macroalgae through top-down control. This confirms numerous studies that show how higher herbivore abundances coincide with a lower cover of macroalgae on reefs [10,11]. However, our results further suggest that an increase in herbivore biomass could lead to different regime trajectories, depending on the functional make-up of the herbivorous assemblage. Specifically, if the herbivores are predominantly grazers then the probability of turf dominance increases, while if scrapers are abundant (e.g. *Chlorurus sordidus, Chlorurus perspicillatus, Scarus rubroviolaceous*) then there is an increased chance of a reef shifting to a calcifying regime.

Human drivers also influenced the distribution of different regimes. Population density has been used as a coarse proxy for overall human influence on coral reefs [45]. However in recent studies the relationships between population density and reef states appear ambiguous [46,47]. The present study suggests that population density is a relatively poor predictor of reef regimes across the Hawaiian Archipelago, which is overwhelmed by the influence of

more refined proxies, particularly those for land-based pollution and land-use change (such as effluent discharge or stream fragmentation). In the MHI, the total amount of effluent discharged had a strong positive impact on *turf regime* while being negatively correlated with the *calcifying regime*. McClanahan et al. [48] showed that an increase in phosphorus stimulated growth of filamentous and turf algae but not the growth of macroalgae. Overall, there is ample literature about the negative effects of nutrient pollution on corals and how it can lead to excessive algae growth (45–47, but see 48), particularly in combination with loss of herbivory [53]. However, this negative impact on corals seemed countered by a positive correlation with fragmentation of streams. The rationale behind this unexpected positive effect of human-induced stream disturbance could be that higher fragmentation reduces the natural water flow, thus allowing more of the effluent to sink or to be deposited on the stream edges before reaching the reefs.

Finally, biophysical drivers also play a key role in coral reef regimes in this system. Unlike the *turf* and *macroalgal/sand regimes*, the *calcifying regime* was negatively correlated with latitude. Low temperatures have been shown to limit coral growth [54] and considering the latitudes the Hawaiian Archipelago encompasses, it is likely to have an influence on the results [55]. Depth was also an influential abiotic parameter, although mostly significant in the NWHI. This divergence in relative influence between both regions is not clear but could be the result of increased water turbidity that limits lights gradients in the MHI because of sediments. In the NWHI, we found the occurrence of calcifying regimes to peak at mid-depths, similar to results from Williams et al. [56]. However, gradients in other oceanographic variables that are known to be important in structuring benthic communities have been identified across the region [55]. For example, additional data on sedimentation [57] or wave exposure [56,58,59] will help investigators develop a better understanding of these important physical processes in influencing reef regimes.

These analyses provide a promising approach for investigating multiple ecosystem regimes and the processes underpinning them, which could help guide effective management. However, since our study does not account for historic disturbance events (e.g. hurricanes, disease outbreaks, bleaching events), it only represents a snapshot in time (year 2010). Therefore, the stability (or at least the trajectory of development) of any specific reef regime remains unknown and needs to be further explored. From a management perspective, the identification of non-linear patterns and preliminary thresholds among many predictor variables offers an interesting avenue for future studies to investigate more accurately the

location of these tipping points, in order to provide tangible management targets for both proactive avoidance of potential regime shifts and restoration of degraded reefs.

ACKNOWLEDGMENTS

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Table 1. Predictor variables used in the Boosted Regression Trees analysis. MHI, Main Hawaiian Islands; NWHI, North-western Hawaiian Islands.

	Variable	Description	Range
MHI	GrazerBiom	Grazer biomass in g.m^{-2}	0 – 28.3
	ScraperBiom	Scraper biomass in g.m^{-2}	0 – 13.9
	BrowserBiom	Browser biomass in g.m^{-2}	0 – 22
	Latitude	Latitude in decimal degrees (WGS 1984)	18.97 – 22.24
	Depth	Depth in meters	2 – 29
	DistCoast	Distance in meters from nearest shoreline to survey location	14 – 2509
	DistStream	Distance in meters from nearest stream to survey location	96 – 20130
	Effluent	The total effluent in million gallons per day (mgd) discharged within parcels that intersected with a 10km buffer from survey location	600 – 7177840
	Population	Human population density in a 10km buffer from survey location based on 2010 census data	232 – 523576
	UrbanIndex	Representation of urban disturbance standardized from 0 to 1	0 – 0.98
	PointIndex	Representation of the density of sources of point pollution standardized from 0 to 1	0 – 0.50
	FragIndex	Representation of stream fragmentation standardized from 0 to 1	0 – 0.31
	FormplIndex	Representation of lands that were formerly pineapple or sugarcane plantations standardized from 0 to 1	0 – 0.54
	DitchIndex	Representation of the relative density of ditch infrastructure standardized from 0 to 1	0 – 0.73
	AgrIndex	Representation of agricultural disturbance standardized from 0 to 1	0 – 0.65
NWHI	GrazerBiom	Grazer biomass in g.m^{-2}	0 – 29.6
	ScraperBiom	Scraper biomass in g.m^{-2}	0 – 30.8
	BrowserBiom	Browser biomass in g.m^{-2}	0 – 146.4
	LPredBiom	Large predator biomass in g.m^{-2}	0 – 2961.8
	Latitude	Latitude in decimal degrees (WGS 1984)	23.63 – 28.45
	Depth	Depth in meters	1 – 28
	ReefZone	Zones of the reef: Fore reef – Back reef – Lagoon	NA

Figure 1. Map of the study area showing the Hawaiian Archipelago and the location of the survey sites (green dots). 118 sites were surveyed in the North-western Hawaiian Islands (A, B, C, D) and 184 within the Main Hawaiian Islands (E).

Figure 2. Count histogram of the phase shift index (PSI) (Bruno et al. 2009) of 302 reef sites in the Hawaiian Archipelago.

Figure 3. *(a)* Principal Component Analysis (PCA) diagram showing the spatial variation in benthic habitat of 302 sites in the Hawaiian Archipelago along the first two principal components. Variables are plotted as vectors and dots represent sites. The smaller the angle between two variable vectors the stronger the correlation. *Hcoral*, hard coral cover; *MA*, macroalgae cover; *CCA*, crustose coralline algae cover; *TA*, turf algae cover; *Sand*, sand cover; *Complexity*, structural complexity. *(b)* Cluster dendrogram of the benthic variables from 302 sites, with *p*-values given in percentage. For a cluster with *p*-value > 95%, the hypothesis that "the cluster does not exist" is rejected with significance level 0.05. *(c)* PCA diagram with an overlaying k-means clustering of the sites. Green squares (80 sites), orange circles (153 sites) and red triangles (69 sites) represent categorisation of the sites matching the previous hierarchical grouping of the benthic variables. The ellipses encompass 80% of the dots associated to each cluster.

Figure 4. Partial dependency plots for the four most influential variables in the Boosted Regression Trees analysis of three distinct benthic regimes *(a – c)* in the MHI and the NWHI. Number of sites within each region and relative influence of each predictor are shown in parenthesis. *Photo credits: NOAA*.