TEMPORAL EFFECTIVENESS OF BIODIVERSITY SURROGATES IN CORAL

REEFS IN THE BRITISH VIRGIN ISLANDS

BY

NICOLE B. KEEFNER

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NICOLE B. KEEFNER

APPROVED:

THESIS COMMITTEE:

MAJOR PROFESSOR: GRAHAM FORRESTER

CO-MAJOR PROFESSOR: BRIAN GERBER

GAVINO PUGGIONI

CARLOS PRADA

DEAN OF THE GRADUATE SCHOOL: NASSER ZAWIA

UNIVERSITY OF RHODE ISLAND

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ABSTRACT

Taxonomic diversity on coral reefs has declined due to anthropogenic stressors. These declines have motivated monitoring programs to estimate species richness for major taxonomic groups: fish and corals. Due to logistical challenges of species identification, there have been efforts attempting to estimate species richness on reefs using landscape features as surrogates, simple indicators that provide an estimate of a target component of biodiversity, often referred to more simply as a target. Many of these efforts are limited in spatial or temporal scope, focus on rugosity and coral cover as predictors, and use coral and fish richnesses as proxies for total species richness. Here we examine how top surrogate-target relationships vary over 27 years and across 8 study sites. We also examine whether frequently measured landscape features of reefs can serve as reliable surrogates for sponge richness. Finally, this study is one of the first to investigate the ability of sponge cover to predict richness of dominant taxonomic groups on coral reefs. This study provides additional support to the idea that surrogate-target relationships should be assessed over space and time because it can provide insight into these relationships and how the ecosystem changes. We also show that including sponges in monitoring studies may provide a broader understanding of how biodiversity is changing on reefs.

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DEDICATION

This thesis is dedicated to my loving mother, Teresa M. Keefner, my support in all things that led me to complete this work and the woman who taught me to persist through even the most inconceivable challenges.

PREFACE

The following thesis has been submitted in manuscript format following the

formatting guidelines of the *Journal for Nature Conservation*.

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CHAPTER 1

Temporal effectiveness of biodiversity surrogates in coral reefs in the British Virgin

Islands

Authors

Nicole B. Keefner[a]; Graham E. Forrester[b]

[a] Department of Natural Resources Science, University of Rhode Island, Kingston, RI 02881, USA ; nicole-keefner@uri.edu

[b] Department of Natural Resources Science, University of Rhode Island, Kingston, RI 02881, USA; gforrester@uri.edu

Abstract

Taxonomic diversity on coral reefs has declined due to anthropogenic stressors. These declines have motivated monitoring programs to estimate species richness for major taxonomic groups such as fish and corals. Due to logistical challenges of species identification, there have been efforts to estimate species richness on reefs using landscape features as surrogates, simple indicators that provide an estimate of a target component of biodiversity, often referred to as a target. Many of these efforts are limited in spatial or temporal scope, focus on rugosity and coral cover as predictors, and use coral and fish richnesses as proxies for total species richness. Here we examine how surrogate-target relationships vary over 27 years and across 8 study sites. We also examine whether frequently measured landscape features of reefs can serve as reliable surrogates for sponge richness. Finally, this study is one of the first to investigate the ability of sponge cover to predict richness of dominant taxonomic groups on coral reefs. This study provides additional support to the idea that surrogate-target relationships should be assessed over space and time because it can provide insight into these relationships and how the ecosystem changes. We also show that including sponges in monitoring studies may provide a broader understanding of how biodiversity is changing on reefs.

Keywords: biodiversity surrogate, British Virgin Islands, Caribbean, coral diversity, fish diversity, sponge diversity.

Introduction

        Biodiversity declines associated with increasing levels of anthropogenic impact are of great concern because they reflect loss of species, disruption of community dynamics and diminished ecosystem function (Dobson et al., 2006; Duffy, 2009; Ehrlich & Wilson, 1991; Naeem, Thompson, Lawler, Lawton, & Woodfin, 1994; Staudinger et al., 2013; Stork, 2010). Documenting these declines is based on tracking different aspects of biodiversity (i.e. landscape, ecosystem, taxonomic, and genetic) over time and space (Duelli & Obrist, 2003; Noss, 1990). Taxonomic diversity, particularly species richness (a count of species in a defined area), is the most commonly studied component of biodiversity in ecological and conservation-related field research because it offers a simple, intuitive measure of biodiversity that can be readily compared across similar environments (Blake & Loiselle, 2000; Rahbek & Graves, 2001).

        Monitoring species richness requires substantial effort and taxonomic expertise (Derraik et al., 2002; Hirst, 2008; Sebek et al., 2012). Even for taxonomic groups that can be completely inventoried in principle, monitoring strategies that could detect all species in a given habitat are often prohibitively expensive and time-consuming (Kati et al., 2004). Because a complete inventory of species present in an area is unattainable in many ecosystems, particularly in high diversity systems, surrogates are often used instead. Surrogates are simple indicators that provide an estimate of a target component of biodiversity, often referred to more simply as a target (Noss, 1990).

        Several types of biological and abiotic surrogate have been developed as indicators of species richness targets. Biological surrogates can be classified as

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"higher-taxa surrogates", when a high-level taxon is used as a surrogate for the species richness of taxa at lower taxonomic levels, "cross-taxa surrogates", when species richness of one taxon is used as a surrogate for species richness of another taxon at the same taxonomic level, or "subset-taxa surrogates" when one taxon acts as a surrogate for a larger target group of which it is a part (Mellin et al., 2011). Abiotic surrogates include variables related to resource use (e.g. light, nutrients), variables influencing physiological tolerances (e.g. temperature), and variables indirectly related to either of these (e.g. depth, latitude; McArthur et al., 2010).

An effective surrogate has two essential features: first, it takes less time, money, and experience to measure than the target and second, it maintains a consistently strong correlation with the target over space and time (Colwell & Coddington, 1994; Magierowski & Johnson, 2006; Moreno, Rojas, Pineda, & Escobar, 2007). Several studies have evaluated how effectively surrogates predict patterns of species richness across sites (Anderson, Diebel, Blom, & Landers, 2005; Darling et al., 2017; Eglington, Noble, & Fuller, 2012; Smale, 2010). The frequency of studies analyzing the spatial predictability of surrogates may reflect their widespread use to identify priority conservation areas; this task requires an understanding of how the size and dispersion of the areas being conserved affects the relationship between the surrogate and the target (Margules, Pressey, & Williams, 2002; Padoa-Schioppa, Baietto, Massa, & Bottoni, 2006; T. J. Ward, Vanderklift, Nicholls, & Kenchington, 1999). Few studies, however, have explicitly investigated surrogate effectiveness over time, and those that have are typically quite short (e.g., 13 months and 1 year; Magierowski & Johnson, 2006; Rubal, Veiga, Vieira, & Sousa-Pinto, 2011). Although

not well-studied, several authors have argued that an effective surrogate must maintain a stable relationship with the target over time, in other words any environmental changes that influence the target must have a qualitatively similar influence on the surrogate (Bevilacqua, Mistri, Terlizzi, & Munari, 2018; Lewandowski, Noss, & Parsons, 2010; Mellin et al., 2011).

Our main aim was thus to study how surrogate-target relationships vary in space and time, with a particular emphasis on multi-decadal temporal changes. We used coral reefs as a study system because they support high biodiversity and have been strongly affected globally over the past several decades by natural and anthropogenic stressors, including storms, ocean acidification, persistent high temperatures, coastal development, and overfishing (Comeau, Lantz, Edmunds, & Carpenter, 2016; Hughes, 1994; Hughes et al., 2017).

As is true for most ecosystems, the monitoring of species richness on coral reefs has been biased towards a few taxonomic groups. Fishes and hard corals (Scleractinia) dominate assessments of biodiversity on coral reefs, which is understandable because these groups are of functional importance ecologically (Bellwood, Hughes, Folke, & Nyström, 2004) and economically important to humans (Gill, Schuhmann, & Oxenford, 2015; Jennings & Polunin, 1996). Concerns regarding declines in the total abundance of corals and fish have motivated research documenting the species richness of these groups in order to better understand patterns and causes of decline (Mouillot et al., 2014; Pratchett, Hoey, Wilson, Messmer, & Graham, 2011). However, recent studies, particularly those using environmental DNA (eDNA; Deiner et al., 2017), have highlighted the presence of many other taxa on

coral reefs that are typically small or cryptic, whose presence has not been well-documented, but comprise a large fraction of overall species richness (Pearman et al., 2018; Stat et al., 2017).

Because corals and fish are such conspicuous, well-studied taxonomic groups, they have been used as cross-taxa surrogates (their species richness is extrapolated to represent the richness of other coral reef taxa) or subset-taxa surrogates (their richness is extrapolated to represent total species richness) (Graham et al., 2006). The reliability of these extrapolations is not well-studied, and we used sponges as a case study in order to assess whether surrogates for fish and coral species richness can be used to predict the richness of other groups. We selected sponges because they represent a common benthic group that is of functional importance (Bell, 2008), yet relatively few studies have investigated temporal patterns in their abundance or species richness (Berman et al., 2013; Wulff, 2006).

Researchers have used a variety of criteria when selecting surrogates (Noss, 1990). We selected two simple biotic surrogates (total coral cover and total sponge cover) and one abiotic surrogate (reef rugosity) for largely practical reasons. Total coral cover (the proportion of reef surface covered by live Scleractinian coral) is the simplest potential higher-taxa surrogate for coral species richness and is arguably the most widely-monitored variable in this ecosystem (Alvarez-Filip, Dulvy, Gill, Côté, & Watkinson, 2009; Gardner, Côté, Gill, Grant, & Watkinson, 2003; Jackson, Donovan, Cramer, & Lam, 2014). Reef rugosity (a simple measure of surface roughness) has also been monitored routinely by coral reef biologists, and is expected to be a good resource-related abiotic surrogate for fish species richness because the habitat

requirements of many fishes include structural reef features. Higher rugosity should thus provide structure that may be utilized by a greater number of fish species (Darling et al., 2017; Graham et al., 2006; Gratwicke & Speight, 2005; Newman et al., 2015). Rugosity is also potentially a better surrogate for fish species richness than live coral cover because, even though corals create reef structure, many fishes utilize structural features even when the coral is dead (Wilson, Graham, Pratchett, Jones, & Polunin, 2006). Although less-widely monitored than coral cover or rugosity, we also selected sponge cover (the proportion of reef surface covered by live sponges) as the simplest potential higher-taxa surrogate for sponge species richness.

Our goal was to understand whether monitoring of cost-effective surrogates is appropriate in tracking changes in the species richness of coral reef communities. We specifically tested how surrogate-target relationships vary over time and space using 27 years of monitoring data from eight sites around Guana Island in the British Virgin Islands (Forrester et al., 2015). Our first objective was to determine which of three candidate surrogates (coral cover, sponge cover, rugosity) was most strongly correlated with each of four separate targets (species richness of corals, fishes, sponges, and richness of the three groups pooled). Our second objective was to determine if the relationships between the surrogate and corresponding target remain consistent among sites and, most importantly, are stable over time.

Material and Methods

Field study design

We used data collected as part of an ongoing monitoring program at eight sites around Guana Island in the British Virgin Islands (Forrester et al., 2015; Fig. 1). All sites were similar in covering 0.6-1.0 hectares of sloping fringing coral reef adjacent to the island at a depth of 9-10 m. Sites varied in exposure to prevailing weather; sites on the windward north side of the island are more exposed to prevailing winds and swell than those on the southern leeward side (Fig. 1). Although distributed across a gradient of prevailing wave exposure, the sites were similar enough in other respects that they represent broadly similar habitats. In other words, we assume that spatio-temporal shifts in species richness primarily reflect changes in α (local) diversity, rather than differences in β-diversity (between habitats; Whittaker, 1960). Corals, fishes, and reef rugosity were sampled annually between June and August from 1992-2018. Logistical constraints meant that sponges were not sampled in all years (no counts in 1992, 1996-1999, 2004, 1993 at Crab Cove, 2014 at Pelican Ghut, and 2017 at Bigelow Beach and Pelican Ghut). All surveys were performed using 30-m transects, placed at haphazardly selected locations within each site. The number of transects sampled per site varied among years (n = 3-22). However, because species richness estimates are dependent on sampling effort, we opted to standardize to three transects per site per year. The three transects for analysis were selected at random.

Survey methods

Corals (Scleractinia), sponges (Porifera), fishes (Actinopterygii), and rugosity were sampled using well-established visual survey methods. Because identifying taxa

to species is not always possible or practical in field surveys, corals, sponges, and fish were identified to the lowest taxonomic group possible (Tables A.1-A.2). All fish were identified to species, while corals and sponges were sometimes identified as multi-species recognizable taxonomic units (D. F. Ward & Stanley, 2004), or RTU's, for the following reasons: (1) taxonomists either split or grouped taxa during the 27 years of the study, or (2) several species are visually indistinguishable in the field. In all cases, the lowest resolution RTU was used and, for simplicity, RTU's are referred to as "species" hereafter. Surveys were conducted with the approval of the BVI Department of Conservation and Fisheries, and fish counts were approved by the URI Institutional Animal Care and Use Committee (protocol AN13-04-016).

Fishes were counted within a belt transect 30 m long x 1.5 m wide, and a T-shaped bar was used to determine the transect width as the diver swam along a 30-m transect tape. Like all visual surveys, the underwater fish counts were limited to species that are amenable to detection using this method; that is, day-active species that are relatively site-attached and reliably visible to divers (Willis, 2001). Nocturnal species, highly mobile groups such as mackerels (Scombridae) and jacks (Carangidae) that are transient visitors to the sites, and small cryptic groups like gobies (Gobiidae) and blennies (Blennioidei) that often hide in crevices were not surveyed. Newly recruited juvenile fishes (< 1 month on the reef) were also excluded because their abundance is affected by lunar cycles, which complicates the detection of long-term trends (Robertson, 1992). Because fish were the only mobile organisms surveyed, the fish survey was conducted first for each transect in order to reduce any bias caused by divers disturbing the fish (Emslie, Cheal, MacNeil, Miller, & Sweatman, 2018).

Corals were surveyed using a linear point-intercept method, wherein a diver swam along the 30-m transect tape and identified the taxon under the tape at 0.25 m intervals (n = 120 points per transect; Canfield, 1941). All corals were identified to species, whereas other taxa encountered were classified into broader groupings (all sponges were counted as one group). The point-intercept data was thus used to estimate coral species richness as well as the total cover (%) of corals and total cover (%) of sponges (Almada-Villela, Sale, Gold-Bouchot, & Kjerfve, 2003). Because sponge cover was lower than coral cover, we used a different method to estimate sponge richness designed to sample a greater number of sponge colonies along each transect tape. Sponge species richness was, therefore, estimated using a line-intercept method, in which any sponge that intercepted the tape was recorded and identified to species.

Reef rugosity was measured as a proxy for three-dimensional structural complexity using the consecutive height difference method (McCormick, 1994), where a diver recorded the difference between the height of the transect tape and the substrate at 1 m intervals along the first 10 m of each transect. Rugosity (in cm) was calculated as the square root of the sum of the squared differences between successive height measurements. A rugosity value of 0 is flat and vertical complexity increases as the rugosity value increases.

To minimize bias introduced by using multiple observers, fish counts and sponge counts were each made by a single expert observer (Bernard, Götz, Kerwath, & Wilke, 2013; Thompson & Mapstone, 1997). Both observers, however, compared their counts to those of another fish and sponge expert respectively. These two

observers independently surveyed the same transects as the authors for one year, and their species identifications were consistent with the authors' (data not shown). Coral data were collected by three observers, but new observers' species identifications and counts were calibrated with those of another observer during a training period of at least 15 dives before their data were incorporated into the study.

Statistical Analysis

We used sites as replicates because they represent spatial units large enough to be analogous to areas monitored to assess local conservation and management actions. For surrogates (coral cover, sponge cover, and rugosity), replicates were thus means for the 3 randomly-selected transects per site per year. To estimate species richness, we pooled the 3 randomly-selected transects for each year and site and calculated the total number of species observed. Richness was calculated separately for each of the three focal taxonomic groups (fish, corals, and sponges), and combined species richness was thus only calculated for sites and years for which richness of all three taxonomic groups was available.

Species richness is a count variable that takes non-negative integer values and is prone to overdispersion. We therefore modeled species richness using negative binomial regression with the 'MASS' package in version 3. 5. 3 of the R statistical programming language (R Core Team, 2019; Venables & Ripley, 2002). All models include the parameter, theta (θ), which accounts for overdispersion. Graphical assessment revealed no patterns in the Pearson residuals or deviance residuals for any of the models included in the analysis, indicating the data conformed to the assumptions of the negative binomial models.

Before modeling surrogate-target relationships, we first examined simple correlations between the surrogates (between coral cover, sponge cover, and rugosity) because correlations, or lack thereof, among the targets might help explain differing spatio-temporal relationships between the surrogates and targets. We also examined simple correlations between the targets because fish and coral richness have been used as cross-taxa surrogates in the past (their species richness extrapolated to represent the richness of other coral reef taxa). We thus assessed whether fish and coral richness were intercorrelated and, more importantly, whether they were correlated to sponge richness.

Objective 1:

To determine which of the candidate surrogates was the best predictor of each target, we created a set of simple models using each of the candidate surrogates as predictors (Fig. A. 3). To select the best model, we then compared these single-surrogate models using Akaike Information Criterion corrected for small sample sizes (AICc; Burnham & Anderson, 2002). Lower ("better") AICc values reflect both model simplicity (fewer parameters) and goodness of fit relative to other candidate models. Following established convention, models differing in AICc values by < 2 were judged to be of similar quality (Burnham & Anderson, 2002). Pseudo-r-squared values were also used for model interpretation by providing an additional measure of goodness-of-fit. Pseudo-r-squared values were used in place of traditional r-squared values because the negative binomial distribution uses a log-link function, for which there is no goodness-of-fit measure directly equivalent to traditional r-squared. We used Nagelkerke's pseudo-r-squared (R_N^2) instead of other pseudo-r-squared metrics

because it scales like traditional r-squared (ranges from 0-1) and is used to evaluate the improvement from a null to a fitted model. Only the best surrogate identified for each target using this model-selection procedure was used for subsequent modeling.

Objective 2:

To determine if relationships between the best surrogate and the target remain consistent over space and time, we added additional terms to the surrogate-only model to account for change over the duration of the study and variation across sites (Fig. A.3). The variable "site" was a categorical predictor with 8 levels (the 8 locations around Guana Island). Temporal trends were modeled using "year" as a discrete linear variable (years 0-27). For each of the targets (dependent variables), AICc was used to compare surrogate-only models to a set of additional candidate models. Additional models included a term for year, site, or terms for both year and site. We also included a model with two interaction terms (surrogate x year and surrogate x site). The interactive models allowed us to test whether the slope of the surrogate-target relationship changed over time or across sites. We did not consider more complex models with higher-order interaction terms because, if more complex models were supported, their interpretation would be sufficiently complicated to undermine the value of the surrogate. We used the same model selection procedure for objective 1, using AICc values to select the best model from each candidate set and Nagelkerke's pseudo-r-squared value (R_N^2) as an intuitive index of model fit.

Results

Associations between surrogates

Rugosity and coral cover were positively correlated, whereas sponge cover displayed a weaker and negative correlation to both coral cover and rugosity (Fig. A.4). All three candidate surrogates displayed substantial differences among sites and changes over time (summarized in Table A.5 and Fig. A.6-8). The positive and negative correlations between the surrogates appear, however, to reflect the fact that coral cover and rugosity both generally declined over the 27 years of the study, whereas sponge cover showed a slight, but not significant, increase over time (Fig. A.9-11).

Associations between targets

We recorded 117 fish species, 30 coral species, and 58 sponge species for a total of 205 species across all 27 years for all 8 sites around Guana Island. Fish richness and coral richness were positively correlated, whereas sponge richness displayed a weaker and negative correlation to both fish and coral richness (Fig. A.12). Like the surrogates, the three targets displayed substantial differences among sites and changes over time (summarized in Table A.5 and Fig. A.13-15). Sponge richness, however, displayed a different general trend over the 27 years of the study than that observed for fish and coral richness. Sponge richness showed a slight, but significant general increase over time, whereas there was no detectable trend in fish or coral richness (Fig. A.16-18). Coral and fish richness are thus potential cross-taxa surrogates for one another because their richness covaried, but the potential for either to function as cross-taxa surrogate for sponge richness appears limited.

Objective 1: Identify the best surrogate for each target

Coral cover and rugosity were both positively correlated with coral richness, but the correlation was stronger for coral cover and so it was the best of the candidate surrogates for coral richness (Table 1; Fig. 2). Sponge cover showed a weak positive association with sponge richness, and there was a weak negative association between coral cover and sponge richness. Coral cover, however, was a slightly better predictor of sponge richness than sponge cover and so, although none of the surrogates were highly correlated with the target, coral cover was the best of the candidate surrogates (Table 2; Fig. 2). Fish species richness was positively correlated with both coral cover and rugosity, but rugosity was the better predictor of fish richness and so was the best surrogate for fish richness (Table 3; Fig. 2). Rugosity was also the best surrogate for combined richness (Table 4; Fig. 2).

Objective 2: Test how surrogate-target relationships vary in time and space

Coral Cover - Coral Richness:

Further modeling of the coral cover versus coral richness relationship indicated that this surrogate-target relationship was not stable over the duration of the study. The model with coral cover and year was the best of the candidate models (Table 5 and Tables A.19-20) and all models with any AICc weight included the variable year (Table 5). There were thus changes in coral richness over time that were not explained by the surrogate alone. Underlying this temporal instability is the fact that mean coral richness showed a slightly increasing trend over the study period (Fig. A.16), whereas coral cover steadily declined (Fig. A.9). As a result, the elevation of the relationship between coral cover and coral richness changed over time (Table 5, Fig. 3). To

visualize this finding, we plotted year as a categorical factor (Fig. 4), which illustrates how coral species richness increased over time for a given amount of coral cover. For example, a reef with 20 percent coral cover in 1992 was predicted to have about 9 coral species, whereas in 2018 it was predicted to have about 17 coral species (Fig. 4). Notably, however, the relationship between coral cover and coral richness is always positive. In qualitative terms, the surrogate is thus stable in the sense that rankings of species richness among sites were consistent over time.

Coral Cover - Sponge Richness:

Coral cover was the best surrogate for sponge richness, but sponge richness was not well-predicted by any of our candidate surrogates (Fig. 2). There was thus considerable unexplained variation in sponge richness, some of which was associated with differences among sites (Fig. 5) and with change over time (Table 6, Fig. 4, and Table A.21). Underlying the temporal shift in the surrogate-target relationship was slight, but steady, increase in mean sponge richness over the study period, whereas coral cover steadily declined throughout (Fig. A.9 and Fig. A.17). As a result, the elevation of the relationship between coral cover and sponge richness changed over time (Table 6, Fig. 6). To illustrate this change, we again plotted year as a categorical factor (Fig. 7) to visualize how sponge species richness increased over time for a given amount of coral cover. A reef with 20 percent coral cover, for example, would be predicted to have 3-4 more sponge species towards the end of the study interval than earlier in the study (Fig. 7). The relationship between sponge cover and coral richness was, however, always negative. The surrogate-target relationship is thus qualitatively stable in the sense that a ranking of sites by relative species richness should remain

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consistent over time. Overall, the surrogate-target relationship for sponge richness was weak and was of limited quantitative predictive ability across both space and time.

Rugosity - Fish Richness:

Comparing the candidate models for fish richness revealed the best model to be one including terms for rugosity and site, and both candidate models with any AICc weight included the variable site (Table 7 and Table A.22). There was thus little evidence for systematic temporal change in the surrogate-target relationship over the study-period, but there were marked differences among sites in the elevation of the surrogate-target relationship (Fig.8-9). In other words, at any given rugosity value, predicted fish richness might differ among sites by as much as 12-13 species (Fig. 9). In summary, rugosity was a relatively poor spatial surrogate for fish richness but, at any given site, temporal changes in the rugosity-fish richness relationship were comparatively minor.

Rugosity - Combined Richness:

The best model for combined richness included terms for rugosity, year, and site (Table 8 and Table A.23), indicating variation in combined richness across sites and years not explained by rugosity. Similar to the rugosity-fish richness relationship, there were marked differences among sites in the elevation of the relationship between rugosity and combined richness (Fig. 10). The specific sites with high and low combined richness were, however, not the same as those with highest and lowest fish richness (Fig. 10). The temporal shift in the surrogate-target relationship arose because mean combined richness increased slightly, but steadily, over the study period, whereas rugosity steadily declined (Fig. A.11 and Fig. A.25). As a result, the elevation

of the relationship between rugosity and combined richness changed over time (Table 8 and Fig. 11). Consequently, a reef with any given level of rugosity was predicted to have higher combined richness towards the ends of the study period than at its beginning (Fig. 12). This temporal trend was, however, not expected to qualitatively change the surrogate-target relationship because the relationship between rugosity and combined richness was always positive. The surrogate-target relationship is thus qualitatively stable in the sense that simple rankings of species richness among sites are expected to remain consistent over time (Fig. 12).

Discussion

Objective 1: Identifying effective surrogates for each target

  We were able to identify simple and reasonably effective surrogates for coral and fish species richness. For fish species-richness, the resource-related surrogate rugosity was the best surrogate. This finding supports the hypothesis that abiotic surrogates can be effective when there is a clear conceptual link between the surrogate and target. As summarized in the introduction, this conceptual link is based on the assumption that the habitat requirements of many reef-associated fishes include structural reef features, and rugosity is thus a simple index of fish habitat (Darling et al., 2017; Graham et al., 2006; Gratwicke & Speight, 2005; Newman et al., 2015). Although correlations between rugosity and different measures of fish abundance are well-established (Alvarez-Filip, Dulvy, Côté, Watkinson, & Gill, 2011), ours is one of few studies demonstrating an association between rugosity and fish species richness (Darling et al., 2017; Graham et al., 2006; Gratwicke & Speight, 2005; Newman et al., 2015). Although reductions in coral cover have been correlated with declines in fish richness in the Pacific (Pratchett, Hoey, Wilson, Messmer, & Graham, 2011), coral cover was a less-effective surrogate than rugosity at our sites. One hypothesis for this possible regional difference is that the Caribbean has a longer history of human impact than other regions supporting coral reefs, so the present-day fish fauna is dominated by habitat generalists and has few species that depend directly on corals for resources.

  A simple higher-taxa surrogate (coral cover) was effective for coral species richness. The use of higher taxa surrogates, though not always explicitly justified, is based on the straightforward expectation that more individuals at a higher taxonomic

level means more taxa at a lower level (e.g. more corals means more coral species). Perhaps surprisingly, this prediction was poorly-supported for sponges, because sponge abundance displayed a weak positive correlation with sponge richness. Instead, the best surrogate for sponge richness was coral cover. This, relatively poor, cross-taxa surrogate was based on the weak negative correlation between coral cover and sponge richness.

Negative associations between sponge and coral abundance have been reported in the literature, based on the potential for competition for space between sponges and corals. Competition over space has been shown to be related to chemical inhibition, or allelopathy, in interspecific relationships between sponges and corals. Allelopathic sponges, may reduce coral cover at local scales (Pawlik, Steindler, Henkel, Beer, & Ilan, 2007). Other studies have shown that unpalatable sponges, those that use chemicals to deter predation by fish, are also allelopathic toward corals and are relatively common on Caribbean coral reefs (Loh, McMurray, Henkel, Vicente, & Pawlik, 2015). Despite some potential benefits sponges can have on coral structures and reef nutrient cycles, even palatable sponges can outcompete corals for space by overgrowing coral structures (Loh & Pawlik, 2014; Stella, Pratchett, Hutchings, & Jones, 2011). Over time, the abundance of these palatable sponges has increased with the reduced abundance of spongivorous fish due to overfishing (Loh & Pawlik, 2014; Powell et al., 2014). Despite this potential for negative sponge-coral interactions, the association between coral cover and sponge richness was weak.

Extrapolating among target groups

We used sponges as a case study to test the possibility of extrapolating from well-studied taxa to other taxa.

New limitations section

We suggest that the use of RTU's, although it affects estimates of absolute species richness, should not alter the outcome of the analysis.

Assessing surrogate effectiveness over space and time

Local richness can vary for a variety of reasons, including: dispersal limitation, changes in environmental or landscape features, and competition over space.

Dispersal ability of reef species may be able to explain spatial variations in richness. It has been established that there is high variability in the distances traveled and dispersal mechanisms employed by different coral reef species (Jones et al., 2009). These differences in dispersal ability relate to genetic connectivity and, as a result, the biodiversity of reefs (Almany et al., 2009).

Changes in environmental or landscape features like those investigated in our study, such as rugosity and coral cover, may also be used to predict richness of taxonomic groups on coral reefs. Other studies have found that reduced coral richness resulted in a reduction of rugosity which, in turn, led to a decrease in fish abundance (Alvarez-Filip et al., 2011). Although we did not include fish abundance as a target in our results, we did observe a reduction in the number of fish species and overall species present at lower levels of rugosity. We also found rugosity to be negatively associated with coral richness; however, we found coral cover to be a better surrogate of coral richness. The relationship between coral richness and coral cover varied over time; one explanation being, the increase in coral species richness for a given amount

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of coral cover over time is due to an increase in evenness over time. In other words, the abundance of the most dominant species is reduced over time. The study mentioned above found the variance in rugosity observed at higher levels of coral cover was the result of dominance by a particular genus of coral; some dominant corals were more structurally complex than other dominant corals (Alvarez-Filip et al., 2011). Spatial differences in rugosity governed patterns in fish richness and combined richness, and combined richness also increased over time. White Bay and Crab Cove had high variability in rugosity over time compared to other sites, suggesting there might be some factor affecting rugosity at these two sites leading to subsequent fluctuations in fish richness and combined richness.

Competition over space has been shown to be related to chemical inhibition, or allelopathy, in interspecific relationships between sponges and corals. These relationships may explain why coral cover was the best candidate surrogate for sponge richness and also why sponge cover and sponge richness are negatively correlated with coral cover and coral richness respectively. Allelopathic sponges, may reduce coral cover at local scales (Pawlik et al., 2007). Other studies have shown that unpalatable sponges, those that use chemicals to deter predation by fish, are also allelopathic toward corals and are relatively common on Caribbean coral reefs (Loh et al., 2015). Despite some potential benefits sponges can have on coral structures and reef nutrient cycles, even palatable sponges can outcompete corals for space by overgrowing coral structures (Loh & Pawlik, 2014; Stella et al., 2011). Over time, the abundance of these palatable sponges has increased with the reduced abundance of spongivorous fish due to overfishing (Loh & Pawlik, 2014; Powell et al., 2014).

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Species richness can vary across spatial and temporal scales for many reasons, some of which are described here. As such, studies proposing surrogates to predict species richness and other diversity measures should explicitly address the spatial and temporal limitations of using the candidate surrogates, especially when planning large-scale or long-term studies.

Value of sponge monitoring

Different taxonomic groups respond differently to changes in the environment. As such, using diversity measures for one group as proxies for total biodiversity without evaluating this relationship (taxonomic surrogacy) can lead to false conclusions regarding taxonomic groups not directly measured. For example, windward reefs had higher coral and fish diversity than leeward reefs, but the latter supported higher sponge diversity (Acosta, Barnes, & McClatchey, 2015). Had this environmental gradient been extrapolated to diversity of taxonomic groups other than fish and corals, it may have been used to make management decisions that would negatively affect sponge diversity. Similarly, we found that sponges do not conform to the same patterns (over space, time, or with landscape features) as corals and fish. The traditional measures of coral cover and rugosity might be good predictors of coral richness and fish richness respectively, but caution should be exercised when making extrapolations to total reef diversity as richness of some groups, here we looked at sponge richness, is not strongly correlated with these variables. In addition, we found that sponge cover does not follow the same patterns as coral cover or rugosity over time or across sites. Perhaps sponges are not the only taxonomic group of organisms on coral reefs that are difficult to predict with coral cover or rugosity; there are many

coral-associated invertebrates that may provide insight into coral reef diversity (Stella et al., 2011) and it is unlikely that all of these taxonomic groups will be adequately predicted by rugosity or coral cover alone.

Because sponge richness and sponge cover follow different patterns than other variables in this study, comparing patterns in sponges to other taxonomic groups and landscape features can provide a fuller picture of reef biodiversity. It has already been suggested that "non-umbrella" species can provide insight into overall site biodiversity at local scales in terrestrial ecosystems (Gerlach, Samways, & Pryke, 2013). As we show here, understudied taxonomic groups may not share surrogates with well-studied groups and the direction of the relationships may even be contradictory; something that has also been demonstrated in similar studies conducted in tropical forests (Lam et al., 2014). Therefore, diversity of these understudied taxonomic groups should be measured directly until a reliable surrogate can be identified. If not, studies that comment on species diversity should be transparent about which taxonomic groups they include in their estimates.

In conclusion, we show here that the commonly measured surrogates, rugosity and percent coral cover, can be reliable predictors of fish richness and coral richness respectively. However, we suggest that future reef biodiversity studies incorporate sponge-related measures to get a broader interpretation of reef biodiversity as they reveal different patterns than other measures. Reef biodiversity studies that do not incorporate sponge-related measures should be explicit about the taxonomic groups included in the analyses and exercise caution when estimating total reef biodiversity.

Acknowledgements

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Tables

Table 1. AICc table of models with coral richness as the response variable (target) and

the candidate surrogates as predictors. The intercept model represents the null

with no surrogates. K is the number of parameters in the model, AICc is the

Akaike Information Criterion corrected for small sample sizes, Delta AICc is the

difference in AICc values between a given model and the model with the lowest

AICc, Akaike weight is the likelihood of a model relative to the other models in

the set, log-likelihood is the negative log-likelihood of a given model, and R_N^2 is

Nagelkerke's pseudo-r-squared. All models use the negative binomial distribution

and include the parameter, theta (θ). Data were collected from 8 coral reefs

around Guana Island, BVI from 1992-2018.

Model Name	K	AICc	Delta AICc	Akaike weight	Log-likelihood	R_N^2
coralcover	3	1058.2	0.0	1.00	-526.1	0.62
rugosity	3	1131.2	73.0	0.00	-562.5	0.23
spongecover	3	1161.1	102.8	0.00	-577.5	0.03
intercept	2	1163.5	105.3	0.00	-579.7	NA

Table 2. AICc table of models with sponge richness as the response variable (target)

and the candidate surrogates as predictors. The intercept model represents the

null with no surrogates. K is the number of parameters in the model, AICc is the

Akaike Information Criterion corrected for small sample sizes, Delta AICc is the

difference in AICc values between a given model and the model with the lowest

AICc, Akaike weight is the likelihood of a model relative to the other models in

the set, log-likelihood is the negative log-likelihood of a given model, and R_N^2 is

Nagelkerke's pseudo-r-squared. All models use the negative binomial distribution

and include the parameter, theta (θ). Data were collected from 8 coral reefs

around Guana Island, BVI from 1992-2018.

Model Name	K	AICc	Delta AICc	Akaike weight	Log-likelihood	R_N^2
coralcover	3	967.5	0.0	0.96	-480.7	0.28
spongecover	3	973.9	6.4	0.04	-483.9	0.24
rugosity	3	995.4	27.9	0.00	-494.6	0.05
intercept	2	999.0	31.5	0.00	-497.5	NA

Table 3. AICc table of models with fish richness as the response variable (target) and

the candidate surrogates as predictors. The intercept model represents the null

with no surrogates. K is the number of parameters in the model, AICc is the

Akaike Information Criterion corrected for small sample sizes, Delta AICc is the

difference in AICc values between a given model and the model with the lowest

AICc, Akaike weight is the likelihood of a model relative to the other models in

the set, log-likelihood is the negative log-likelihood of a given model, and R_N^2 is

Nagelkerke's pseudo-r-squared. All models use the negative binomial distribution

and include the parameter, theta (θ). Data were collected from 8 coral reefs

around Guana Island, BVI from 1992-2018.

Model Name	K	AICc	Delta AICc	Akaike weight	Log-likelihood	R_N^2
rugosity	3	1266.3	0.0	1.00	-630.1	0.63
coralcover	3	1295.4	29.2	0.00	-644.7	0.53
spongecover	3	1359.7	93.4	0.00	-676.8	0.21
intercept	2	1389.9	123.6	0.00	-692.9	NA

Table 4. AICc table of models with combined richness (the sum of coral, fish, and

sponge richness) as the response variable (target) and the candidate surrogates as

predictors. The intercept model represents the null with no surrogates. K is the

number of parameters in the model, AICc is the Akaike Information Criterion

corrected for small sample sizes, Delta AICc is the difference in AICc values

between a given model and the model with the lowest AICc, Akaike weight is the

likelihood of a model relative to the other models in the set, log-likelihood is the

negative log-likelihood of a given model, and R_N^2 is Nagelkerke's pseudo-r-

squared. All models use the negative binomial distribution and include the

parameter, theta (θ). Data were collected from 8 coral reefs around Guana Island,

BVI from 1992-2018.

Model Name	K	AICc	Delta AICc	Akaike weight	Log-likelihood	R_N^2
rugosity	3	1106.8	0.0	0.99	-550.3	0.38
coralcover	3	1116.3	9.6	0.01	-555.1	0.32
intercept	2	1152.6	45.9	0.00	-574.3	NA
spongecover	3	1153.8	47.1	0.00	-573.8	0.01

Table 5. AICc table of models with coral richness as the response variable (target) and

  percent coral cover as the best candidate surrogate. K is the number of parameters

  in the model, AICc is the Akaike Information Criterion corrected for small

  sample sizes, Delta AICc is the difference in AICc values between a given model

  and the model with the lowest AICc, Akaike weight is the likelihood of a model

  relative to the other models in the set, log-likelihood is the negative log-

  likelihood of a given model, and R_N^2 is Nagelkerke's pseudo-r-squared. All

  models use the negative binomial distribution and include the parameter, theta

  (θ). Data were collected from 8 coral reefs around Guana Island, BVI from 1992-

  2018.

Model Name	K	AICc	Delta AICc	Akaike weight	Log-likelihood	R_N^2
coralcover + year	4	1044.2	0.0	0.58	-518.0	0.69
coralcover + year + year*coralcover	5	1045.6	1.4	0.29	-517.7	0.69
coralcover + year + site	11	1047.2	2.9	0.13	-511.9	0.74
coralcover	3	1058.2	14.0	0.00	-526.1	0.62
coralcover + site	10	1062.5	18.3	0.00	-520.7	0.67
coralcover + site + site*coralcover	17	1064.2	19.9	0.00	-513.5	0.72

Table 6. AICc table of models with sponge richness as the response variable (target) and percent coral cover as the best candidate surrogate. K is the number of parameters in the model, AICc is the Akaike Information Criterion corrected for small sample sizes, Delta AICc is the difference in AICc values between a given model and the model with the lowest AICc, Akaike weight is the likelihood of a model relative to the other models in the set, log-likelihood is the negative log-likelihood of a given model, and R_N^2 is Nagelkerke's pseudo-r-squared. All models use the negative binomial distribution and include the parameter, theta (θ). Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

Model Name	K	AICc	Delta AICc	Akaike weight	Log-likelihood	R_N^2
coralcover + year + site	11	909.3	0.0	1.00	-442.8	0.71
coralcover + site	10	922.3	12.9	0.00	-450.4	0.64
coralcover + site + site*coralcover	17	933.8	24.5	0.00	-447.8	0.67
coralcover + year	4	966.3	56.9	0.00	-479.0	0.31
coralcover + year + year*coralcover	5	966.6	57.3	0.00	-478.1	0.32
coralcover	3	967.5	58.2	0.00	-480.7	0.28

Table 7. AICc table of models with fish richness as the response variable (target) and

rugosity (in cm) as the best candidate surrogate. K is the number of parameters in

the model, AICc is the Akaike Information Criterion corrected for small sample

sizes, Delta AICc is the difference in AICc values between a given model and the

model with the lowest AICc, Akaike weight is the likelihood of a model relative

to the other models in the set, log-likelihood is the negative log-likelihood of a

given model, and R_N^2 is Nagelkerke's pseudo-r-squared. All models use the

negative binomial distribution and include the parameter, theta (θ). Data were

collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

Model Name	K	AICc	Delta AICc	Akaike weight	Log-likelihood	R_N^2
rugosity + site	10	1203.8	0.0	0.75	-591.4	0.82
rugosity + year + site	11	1206.0	2.2	0.25	-591.4	0.82
rugosity + site + site*rugosity	17	1217.0	13.2	0.00	-590.0	0.83
rugosity + year + year*rugosity	5	1260.9	57.1	0.00	-625.3	0.65
rugosity + year	4	1261.6	57.8	0.00	-626.7	0.65
rugosity	3	1266.3	62.4	0.00	-630.1	0.63

Table 8. AICc table of models with combined richness (the sum of coral, fish, and
sponge richness) as the response variable (target) and rugosity (in cm) as the best
candidate surrogate. K is the number of parameters in the model, AICc is the
Akaike Information Criterion corrected for small sample sizes, Delta AICc is the
difference in AICc values between a given model and the model with the lowest
AICc, Akaike weight is the likelihood of a model relative to the other models in
the set, log-likelihood is the negative log-likelihood of a given model, and R_N^2 is
Nagelkerke's pseudo-r-squared. All models use the negative binomial distribution
and include the parameter, theta (θ). Data were collected from 8 coral reefs
around Guana Island, BVI from 1992-2018.

Model Name	K	AICc	Delta AICc	Akaike weight	Log-likelihood	R_N^2
rugosity + year + site	11	1079.7	0.0	0.96	-528.0	0.65
rugosity + site	10	1086.5	6.8	0.03	-532.5	0.60
rugosity + year	4	1092.8	13.1	0.00	-542.3	0.49
rugosity + site + site*rugosity	17	1093.2	13.5	0.00	-527.5	0.65
rugosity + year + year*rugosity	5	1094.8	15.1	0.00	-542.2	0.49
rugosity	3	1106.8	27.0	0.00	-550.3	0.38

Figures
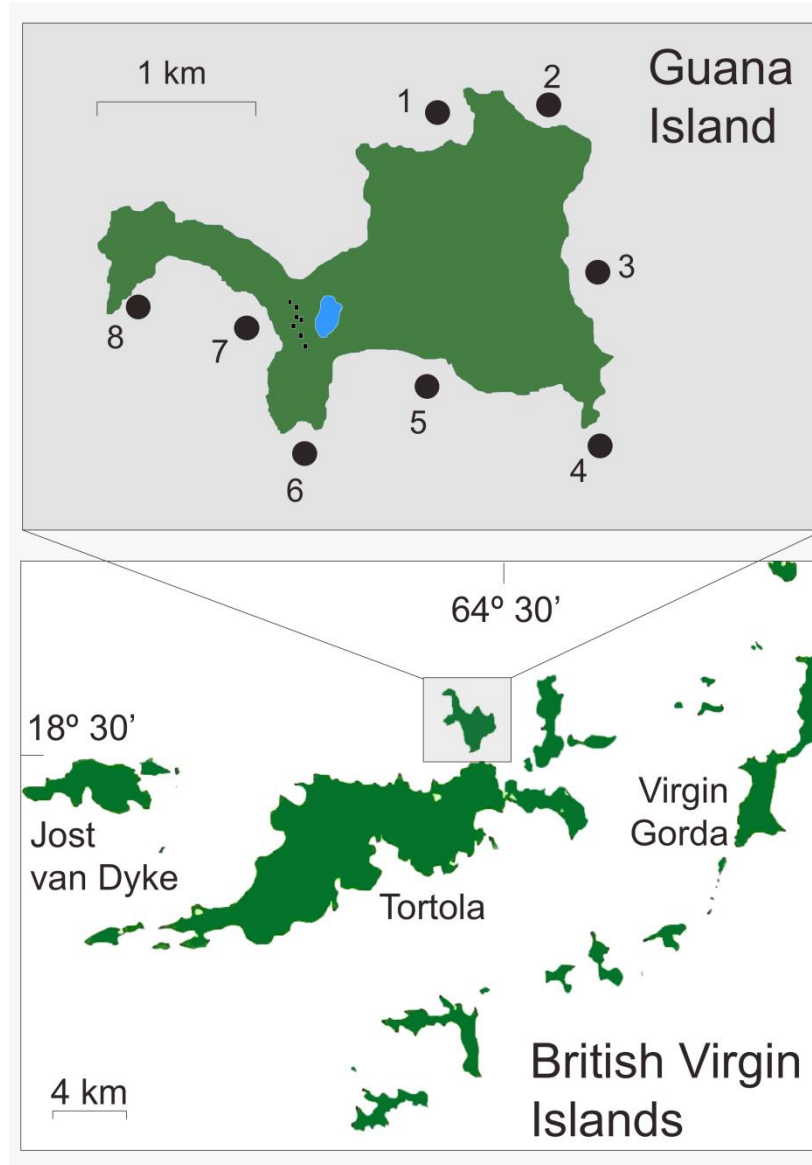
Figure 1. Top panel: a map of Guana Island, British Virgin Islands showing the eight

study sites: (1) Grand Ghut, (2) Pelican Ghut, (3) Bigelow Beach, (4) Monkey

Point, (5) White Bay, (6) Iguana Head, (7) Crab Cove, and (8) Long Point, also

known as Muskmelon. Lower panel: the location of Guana Island within the

British Virgin Islands.
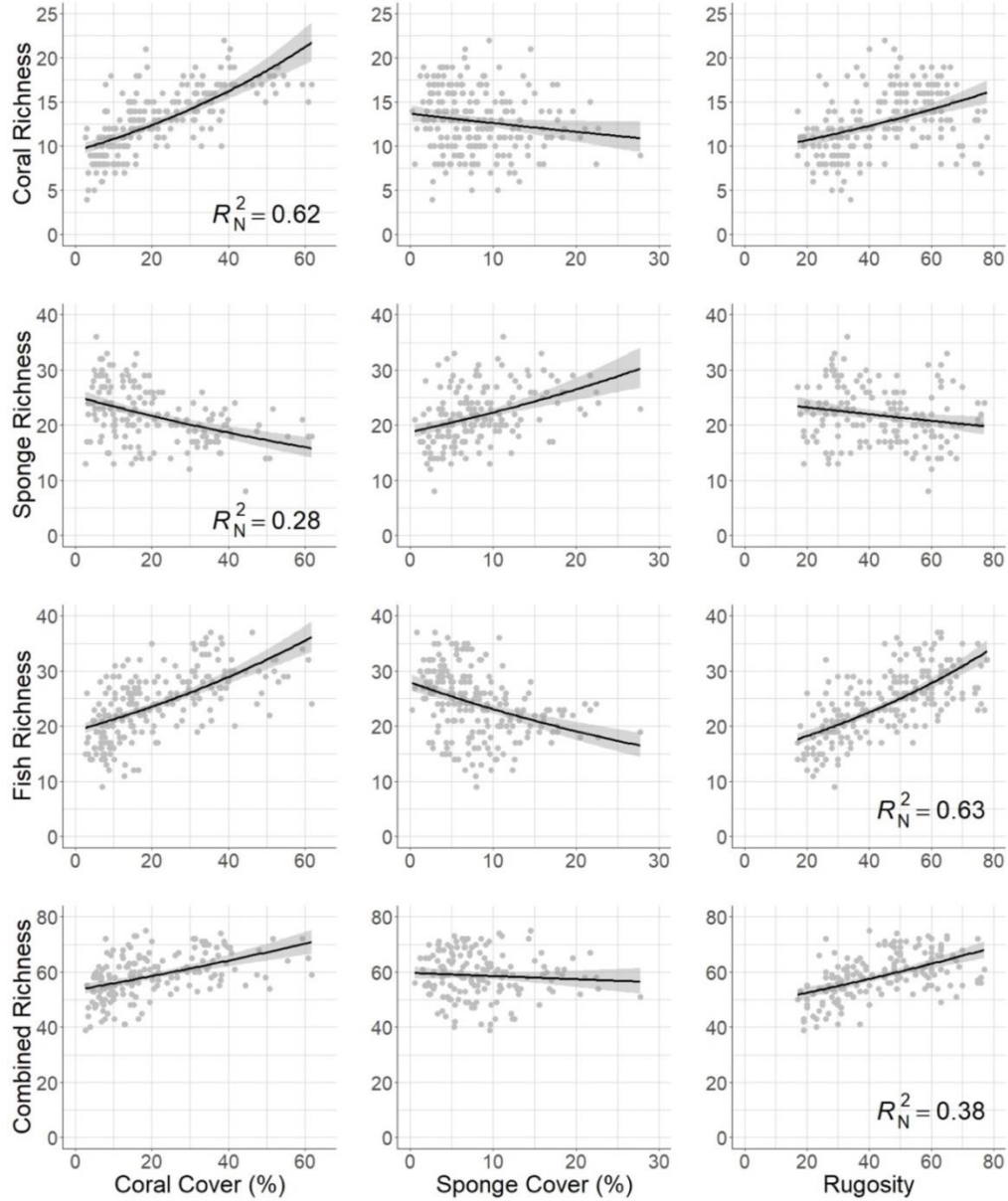
Figure 2. Potential surrogate-target relationships. Lines represent smoothed

conditional means using the negative binomial distribution and the formula y ~ x,

where y is a target (rows) and x is a surrogate (columns). Shaded portions

represent 95% confidence intervals of fitted values. Nagelkerke's pseudo-r-

squared values (R_N^2) are shown for the best surrogate for each target. Rugosity

measured in centimeters. Data were collected from 8 coral reefs around Guana

Island, BVI from 1992-2018.
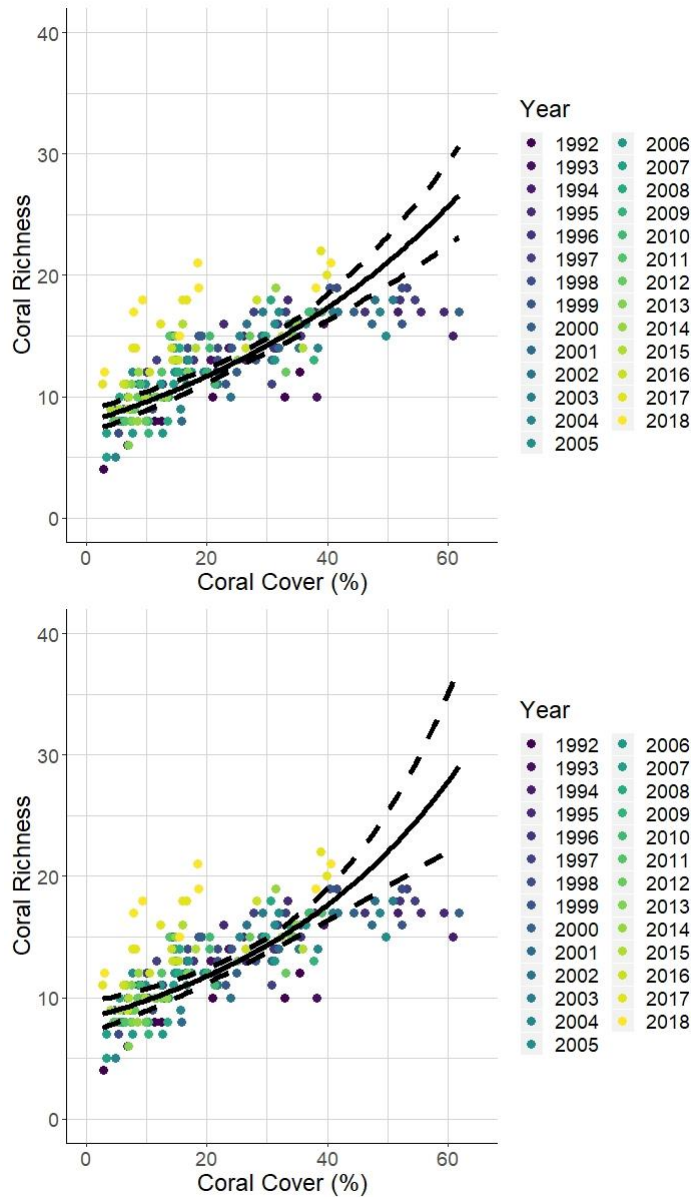
Figure 3. Competitive models for predicting coral richness included a term for year.

Solid lines represent predictions using the negative binomial distribution and the

formula y ~ x + year (top panel) and y ~ x + year + x * year (bottom panel),

where y coral richness, x is coral cover, and year is a trend. Dashed lines

represent 95% confidence intervals of fitted values. Points represent observed

values colored by year. Data were collected from 8 coral reefs around Guana

Island, BVI from 1992-2018.

Figure 4. This figure helps to visualize changes in coral richness for a given amount of

coral cover over a 27 year period. Solid lines represent predictions colored by

year using the negative binomial distribution and the formula y ~ x + year, where

y is coral richness, x is coral cover, and year is a categorical predictor. The

formula y ~ x + year, with year as a trend, was the most competitive model to

predict coral richness. Confidence intervals are not shown. Points represent

observed values colored by year. Data were collected from 8 coral reefs around

Guana Island, BVI from 1992-2018.
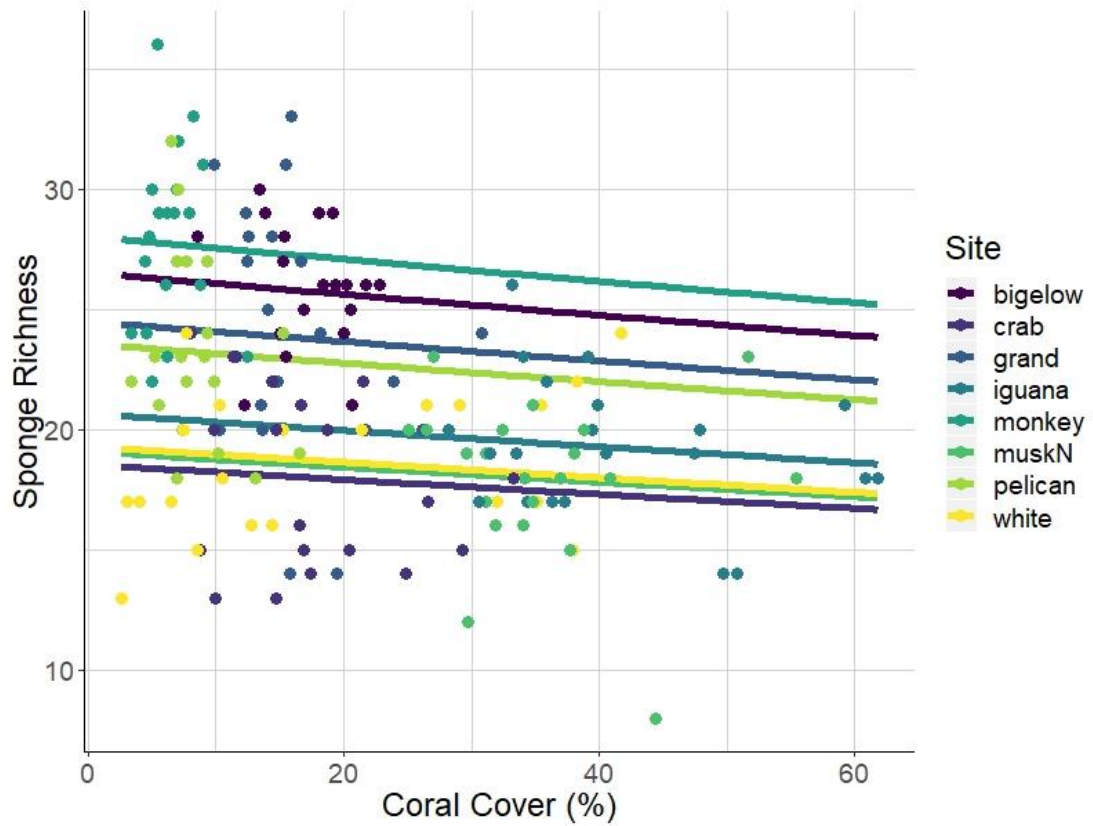
Figure 5. This figure helps to visualize large differences in sponge richness among

sites for a given amount of coral cover. Solid lines represent predictions colored

by site using the negative binomial distribution and the formula y ~ x + site,

where y is sponge richness, x is coral cover, and site is a categorical predictor.

The formula y ~ x + year + site, with year as a trend, was the most competitive

model to predict sponge richness. Confidence intervals are not shown. Points

represent observed values colored by year. Data were collected from 1992-2018

at 8 coral reefs around Guana Island, BVI.
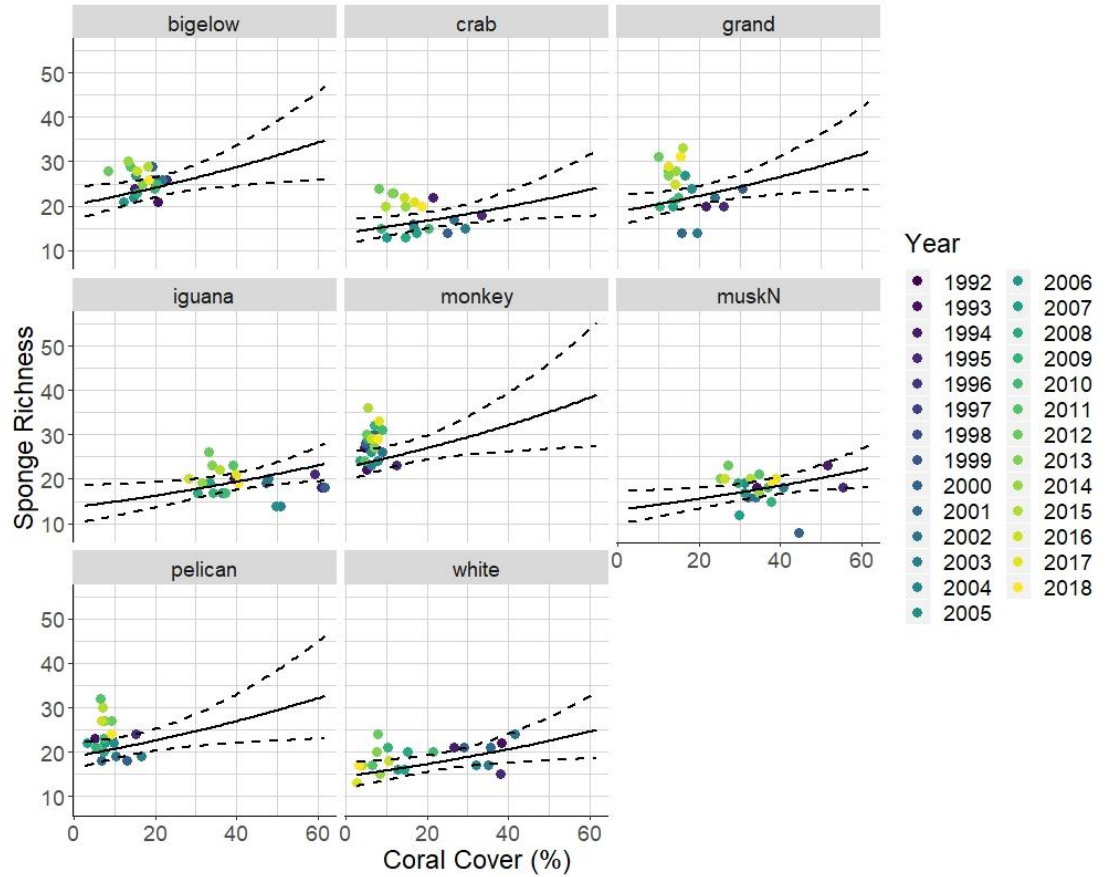
Figure 6. The most competitive model for predicting sponge richness included terms

for year and site. Each panel represents one of 8 coral reefs around Guana Island,

BVI. Solid lines represent predictions using the negative binomial distribution

and the formula y ~ x + year + site, where y is sponge richness, x is coral cover,

year is a trend, and site is a categorical predictor. Dashed lines represent 95%

confidence intervals of fitted values. Points represent observed values colored by

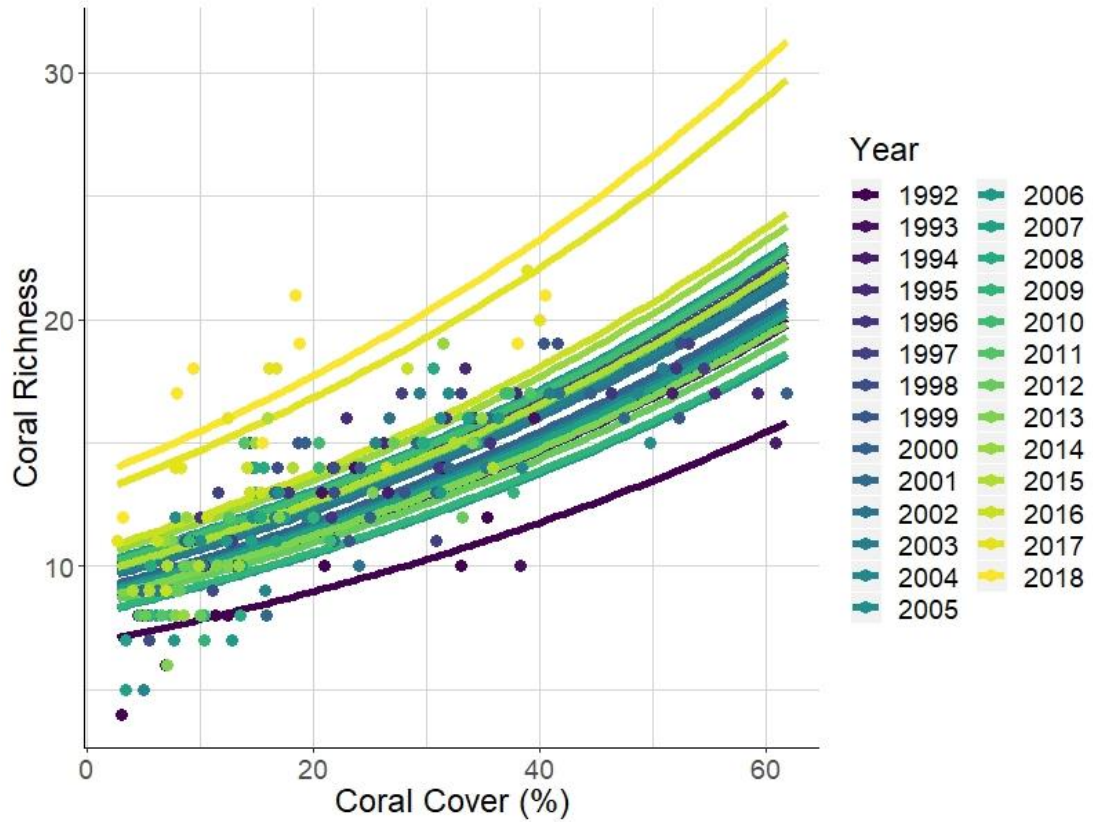year. Data were collected from 1992-2018.

Figure 7. This figure helps to visualize changes in sponge richness for a given amount of coral cover over a 27 year period. Solid lines represent predictions colored by year using the negative binomial distribution and the formula y ~ x + year, where y is sponge richness, x is coral cover, and year is a categorical predictor. The formula y ~ x + year + site, with year as a trend, was the most competitive model to predict sponge richness. Confidence intervals are not shown. Points represent observed values colored by year. Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.
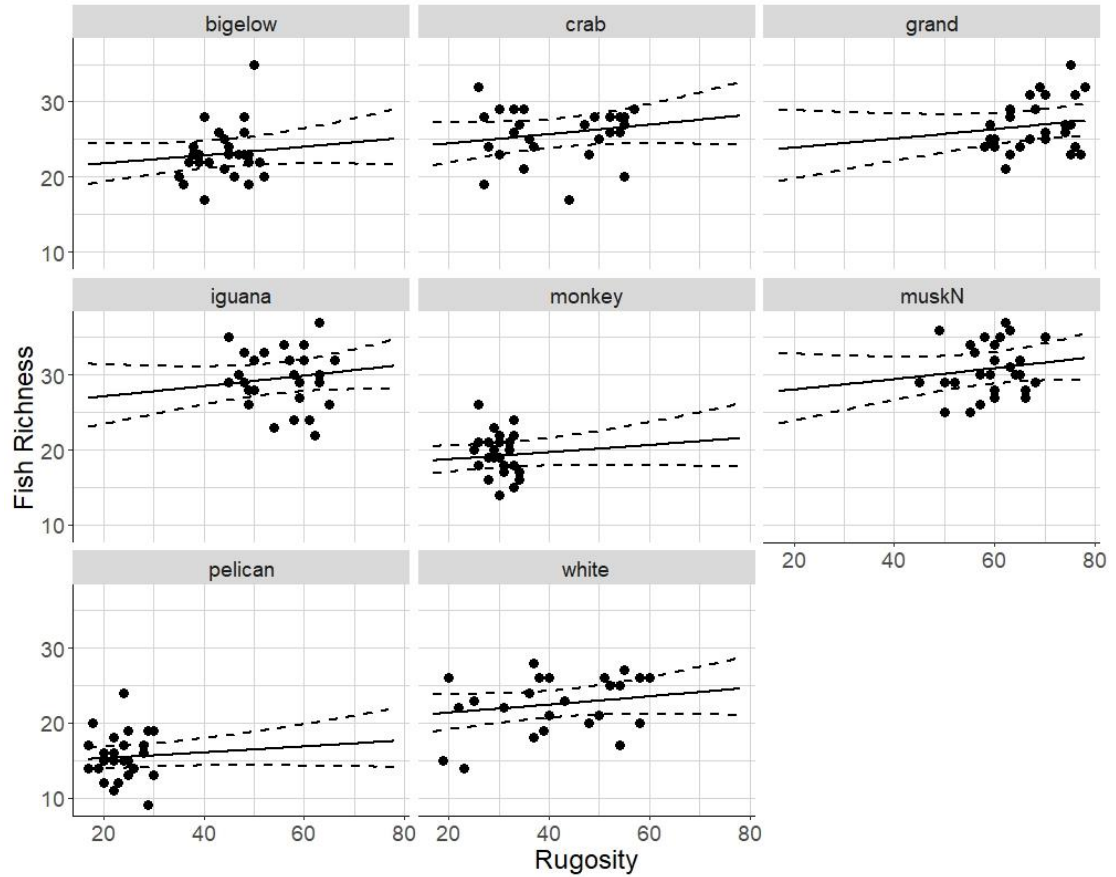
Figure 8. The most competitive model for predicting fish richness included a term for

site. Each panel represents one of 8 coral reefs around Guana Island, BVI. Solid

lines represent predictions using the negative binomial distribution and the

formula y ~ x + site, where y is fish richness, x is rugosity in cm, and site is a

categorical predictor. Dashed lines represent 95% confidence intervals of fitted

values. Points represent observed values. Data were collected from 1992-2018.

Figure 9. This figure helps to visualize differences in fish richness for a given amount

of rugosity among 8 coral reefs around Guana Island, BVI. Solid lines represent

predictions colored by site using the negative binomial distribution and the

formula y ~ x + site, where y is fish richness, x is rugosity in cm, and site is a

categorical predictor. Lines are truncated to correspond with the observed ranges

of rugosity for each site. The formula y ~ x + site was the most competitive

model to predict fish richness. Confidence intervals are not shown. Points

represent observed values colored by year. Data were collected from 1992-2018.
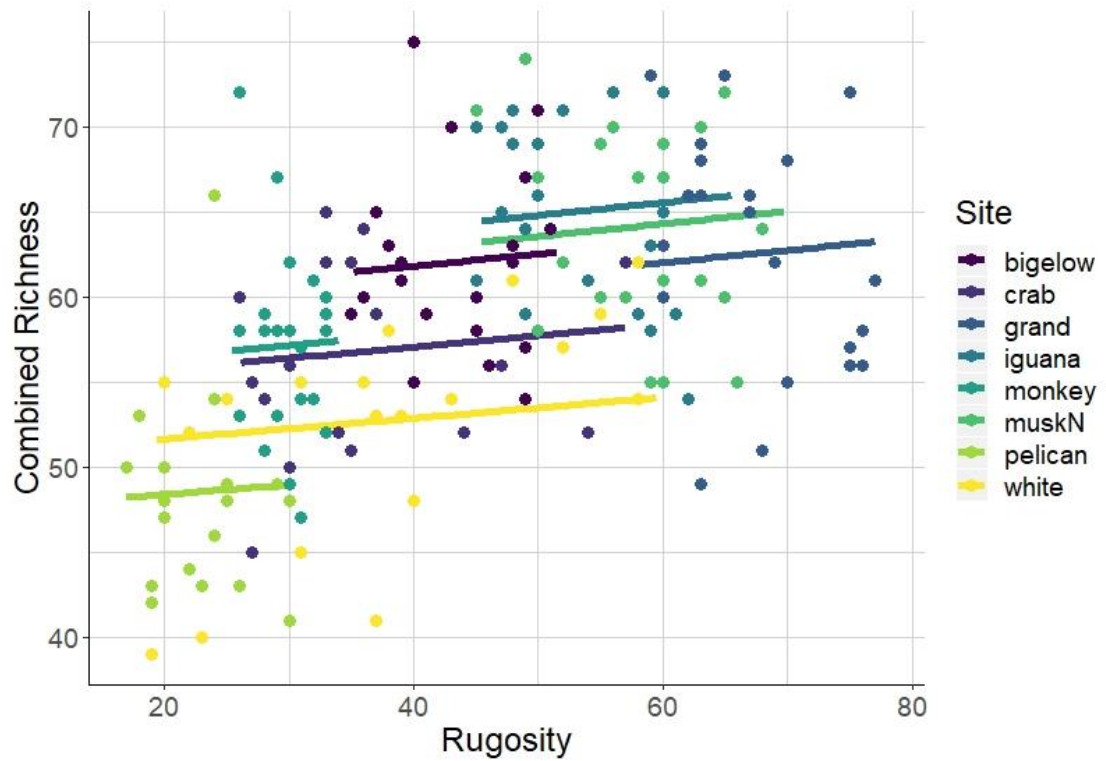
Figure 10. This figure helps to visualize differences in combined richness (the sum of

coral, fish, and sponge richness) for a given amount of rugosity among 8 coral

reefs around Guana Island, BVI. Solid lines represent predictions colored by site

using the negative binomial distribution and the formula y ~ x + site, where y is

combined richness, x is rugosity in cm, and site is a categorical predictor. Lines

are truncated to correspond with the observed ranges of rugosity for each site.

The formula y ~ x + year + site, with year as a trend, was the most competitive

model to predict combined richness. Confidence intervals are not shown. Points

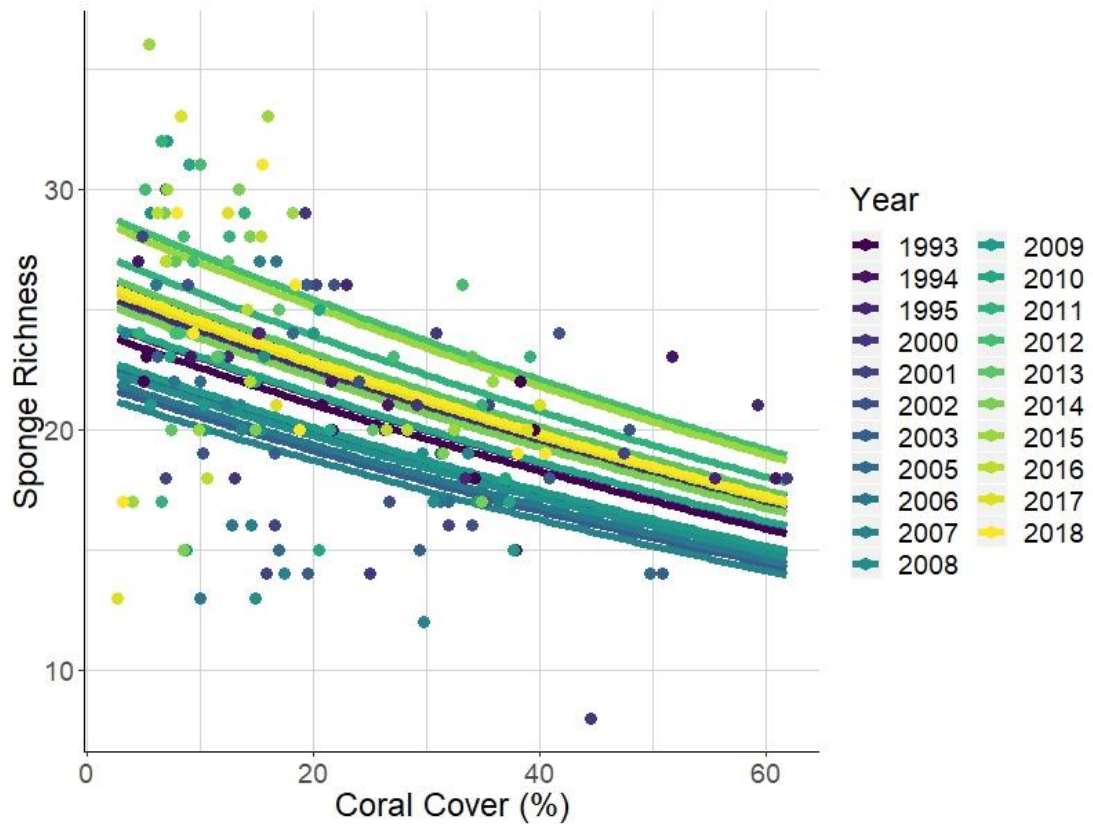represent observed values colored by year. Data were collected from 1992-2018.
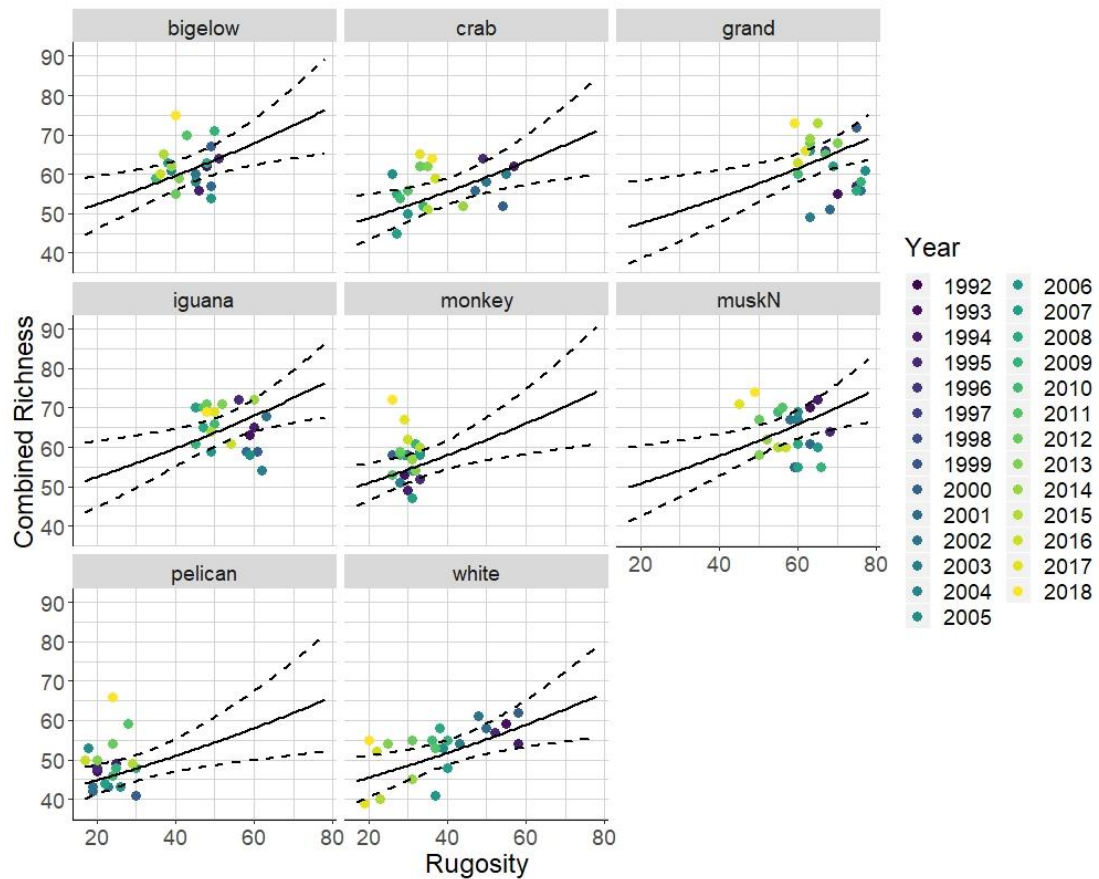
Figure 11. The most competitive model for predicting combined richness (the sum of

coral, fish, and sponge richness) included terms for year and site. Each panel

represents one of 8 coral reefs around Guana Island, BVI. Solid lines represent

predictions using the negative binomial distribution and the formula y ~ x + year

+ site, where y is combined richness, x is rugosity in cm, year is a trend, and site

is a categorical predictor. Dashed lines represent 95% confidence intervals of

fitted values. Points represent observed values colored by year. Data were

collected from 1992-2018.
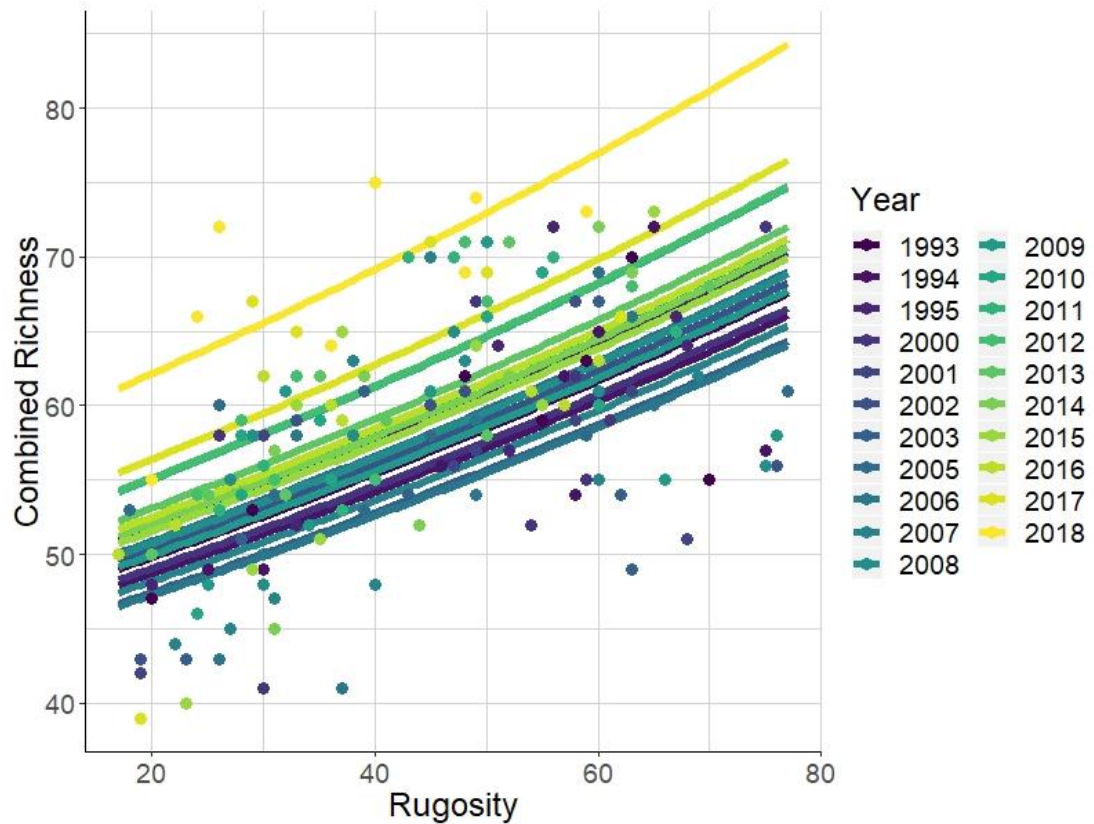
Figure 12. This figure helps to visualize changes in combined richness (the sum of
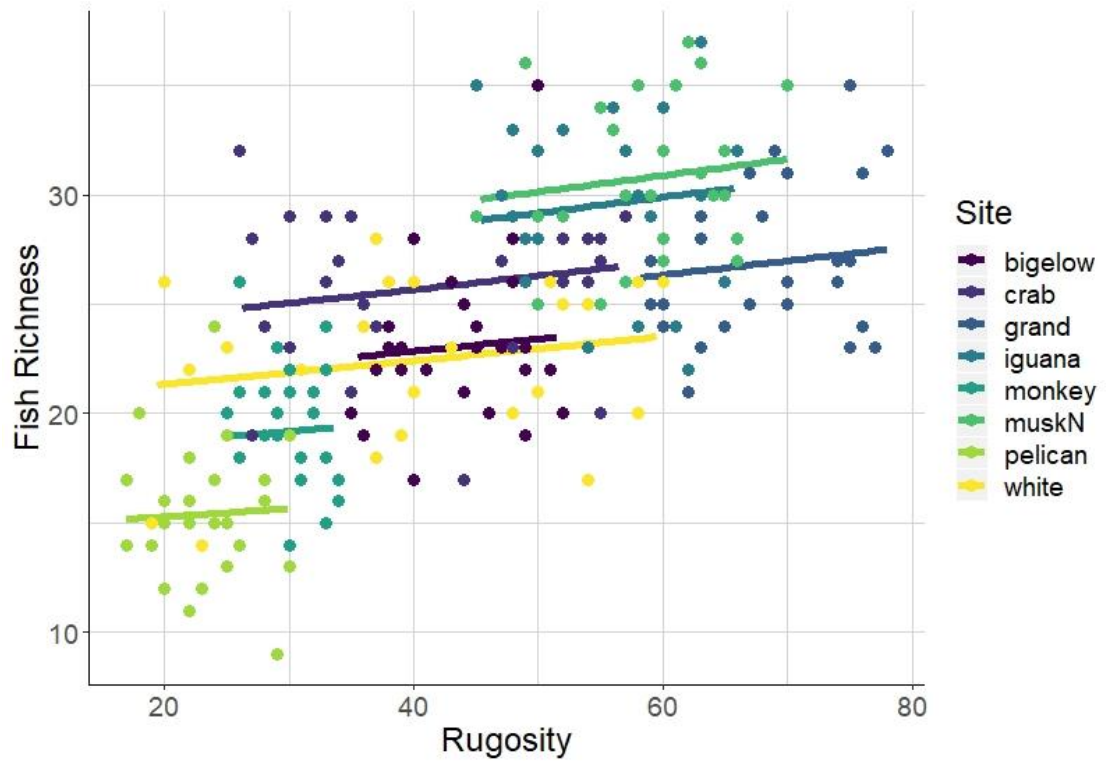coral, fish, and sponge richness) for a given amount of rugosity over a 27 year
period. Solid lines represent predictions colored by year using the negative
binomial distribution and the formula y ~ x + year, where y is combined richness,
x is rugosity in cm, and year is a categorical predictor. The formula y ~ x + year
+ site, with year as a trend, was the most competitive model to predict combined
richness. Confidence intervals are not shown. Points represent observed values
colored by year. Data were collected from 8 coral reefs around Guana Island,
BVI from 1992-2018.

Appendices

Table A.1. Fish species included in richness calculations.

Fish species	Fish common name	Fish species cont.	Fish common name cont.
Abudefduf saxatilis	Sergeant major	*Hypoplectrus chlorurus*	yellowtail hamlet
Acanthurus bahianus	ocean surgeon	*Hypoplectrus guttavarius*	shy hamlet
Acanthurus chirurgus	doctorfish	*Hypoplectrus indigo*	indigo hamlet
Acanthurus coeruleus	blue tang	*Hypoplectrus nigricans*	black hamlet
Aluterus scriptus	scrawled filefish	*Hypoplectrus puella*	barred hamlet
Amblycirrhitus pinos	redspotted hawkfish	*Hypoplectrus sp.*	tan hamlet
Anisotremus surinamensis	black margate	*Hypoplectrus unicolor*	butter hamlet
Anisotremus virginicus	porkfish	*Inermia vittata*	boga
Aulostomus maculatus	trumpetfish	*Kyphosus sectatrix*	gray chub
Balistes capriscus	gray triggerfish	*Lachnolaimus maximus*	hogfish
Balistes vetula	queen triggerfish	*Lactophrys bicaudalis*	spotted trunkfish
Bodianus rufus	Spanish hogfish	*Lactophrys quadricornis*	scrawled cowfish
Calamus calamus	saucereye porgy	*Lactophrys triqueter*	smooth trunkfish
Calamus pennatula	pluma porgy	*Lutjanus apodus*	schoolmaster snapper
Cantherhines macrocerus	whitespotted filefish	*Lutjanus griseus*	gray snapper
Cantherhines pullus	orangespotted filefish	*Lutjanus jocu*	dog snapper
Canthigaster rostrata	sharp-nose puffer fish	*Lutjanus mahogoni*	mahogany snapper
Centropyge argi	cherubfish	*Lutjanus synagris*	lane snapper
Chaetodipterus faber	Atlantic spadefish	*Melichthys niger*	black durgon
Chaetodon ocellatus	spotfin butterflyfish	*Microspathodon chrysurus*	yellowtail damselfish
Chaetodon sedentarius	reef butterflyfish	*Monacanthus ciliatus*	fringed filefish
Chaetodon striatus	banded butterflyfish	*Monacanthus tuckeri*	slender filefish
Chaetodon capistratus	foureye butterflyfish	*Mulloidichthys martinicus*	yellow goatfish
Chromis cyanea	blue chromis	*Mycteroperca tigris*	tiger grouper
Chromis insolata	sunshinefish	*Mycteroperca venenosa*	yellowfin grouper
Chromis multilineata	brown chromis	*Nicholsina usta*	emerald parrotfish
Clepticus parrae	creole wrasse	*Ocyurus chrysurus*	yellowtail snapper
Cryptotomus roseus	bluelip parrotfish	*Odontoscion dentex*	reef croaker
Diodon hystrix	porcupinefish	*Pomacanthus arcuatus*	gray angelfish
Epinephelus adscensionis	rock hind	*Pomacanthus paru*	French angelfish
Epinephelus guttatus	red hind	*Pomacentrus diencaeus*	longfin damselfish
Epinephelus cruentatus	graysby	*Pomacentrus leucostictus*	beaugregory
Epinephelus fulva	coney	*Pomacentrus variabilis*	cocoa damselfish
Epinephelus striatus	Nassau grouper	*Pomacentrus fuscus*	dusky damselfish
Equetus acuminatus	high-hat	*Pomacentrus partitus*	bicolor damselfish
Equetus lanceolatus	jacknife fish	*Pomacentrus planifrons*	threespot damselfish
Equetus punctatus	spotted drum	*Pseudupeneus maculatus*	spotted goatfish
Gerres cinereus	yellowfin mojarra	*Pterois volitans*	lionfish
Gramma loreto	fairy basslet	*Scarus coeruleus*	blue parrotfish
Haemulon aurolineatum	tomtate grunt	*Scarus croicensis*	striped parrotfish
Haemulon carbonarium	Caesar grunt	*Scarus guacamaia*	rainbow parrotfish
Haemulon chrysargyreum	smallmouth grunt	*Scarus taeniopterus*	princess parrotfish
Haemulon flavolineatum	French grunt	*Scarus vetula*	queen parrotfish
Haemulon macrostomum	Spanish grunt	*Serranus baldwini*	lantern bass
Haemulon melanurum	cottonwick grunt	*Serranus tabacarius*	tobacco fish
Haemulon plumierii	white grunt	*Serranus tigrinus*	harlequin bass
Haemulon sciurus	blue striped grunt	*Serranus tortugarum*	chalk bass
Haemulon sp. unidentified	unidentified grunt	*Sparisoma atomarium*	greenblotch parrotfish
Haemulon striatum	striped grunt	*Sparisoma aurofrenatum*	redband parrotfish
Halichoeres bivittatus	slippery dick	*Sparisoma chrysopterum*	redtail parrotfish
Halichoeres cyanocephalus	yellowcheek wrasse	*Sparisoma radians*	bucktooth parrotfish
Halichoeres garnoti	yellowhead wrasse	*Sparisoma rubripinne*	yellowtail parrotfish
Halichoeres maculipinna	clown wrasse	*Sparisoma viride*	stoplight parrotfish
Halichoeres pictus	rainbow wrasse	*Sphoeroides dorsalis*	marbled puffer
Halichoeres poeyi	blackear wrasse	*Sphoeroides spengleri*	bandtail puffer
Halichoeres radiatus	puddingwife	*Synodus intermedius*	sand diver
Holacanthus ciliaris	queen angelfish	*Synodus saurus*	bluestripe lizardfish
Holacanthus tricolor	rock beauty	*Synodus synodus*	red lizardfish
		Thalassoma bifasciatum	bluehead wrasse

Table A.2. Benthic species included in richness calculations. * indicates recognizable
taxonomic unit.

Coral species	Sponge species
Acropora cervicornis	**Agelas citrina*, *Agelas clathrodes*, or *Clathria faviformis*
Acropora palmata	*Agelas conifera*
Agaricia agaricites	**Agelas* spp.
*Agaricia spp. (mostly *Agaricia humilis* and *Agaricia lamarcki*)	**Aiolochroia crassa* and *Verongula rigida*
	Amphimedon compressa
Cladocora arbuscula	**Amphimedon* sp. (maybe *Amphimedon complanata*)
Colpophyllia natans	*Amphimedon viridis*
Dendrogyra cylindrus	**Aplysina fistularis*, *Aplysina fulva*, and *Aplysina insularis*
Diploria labyrinthiformis	*Aplysina cauliformis*
*Diploria strigosa and *Diploria clivosa*	**Aplysina lacunosa*, *Suberea* sp., and *Verongula reiswigi*
Dichocoenia stokesi	**Artemisina melana* or *Iotrochota arenosa*
Eusmilia fastigiata	*Black, spiny, purple exudate, but not slimy
Favia fragum	*Breadcrumb (*Calyx podatypa*, *Svenzea cristinae*, or *Svenzea zeai*)
Helioceris cucullata	
Isophyllia sinuosa	*Callyspongia fallax*
Manicina areolata	*Like *Callyspongia fallax* but soft with pinched tube ends
Montastraea cavernosa	*Callyspongia plicifera*
*Madracis mirabilis and *Madracis decactis*	*Callyspongia vaginalis*
Meandrina meandrites	*Cervicornia cuspidifera*
*Montastraea annularis, M. franksi, M. faveolata (genus name now Orbicella)	*Chondrilla caribensis*
	Cinachyrella kuekenthali
Mussa angulosa	*Clathria venosa*
*Mycetophyllia ferox, Mycetophyllia lamarckiana	*Clathria virgultosa*
*Oculina spp.	*Cliona delitrix*
Porites astreoides	*Cliona laticavicola*
Porites colonensis	*Cliona varians*
Porites furcata	**Cribochalina vasculum* and *Petrosia pellasarca*
Porites porites	*Desmapsamma anchorata*
*Scolymia spp.	*Dictyonella funicularis*
*Siderastrea siderea and *Siderastrea radians*	*Dragmacidon reticulatum*
Solenastrea bournoni	*Dysidea janiae*
Stephanocoenia intersepta	**Dysidea* sp. (maybe etheria)
	Ectyoplasia ferox
	Halisarca caerulea
	*Higginsia coralloides (may include *Ptilocaulis walpersii*)
	*Hyrtios sp. or *Spheciospongia vesparium*
	Iotrochota birotulata
	*Iotrochota sp.
	Ircinia campana
	Ircinia felix
	Ircinia strobilina
	*Maybe "Ircinia smooth" or Spongia
	Monanchora arbuscula
	Mycale laevis
	Mycale laxissima
	Neofibularia nolitangere
	*Neopetrosia proxima (may include *Xestospongia subtriangularis*)
	*Niphates erecta (may include *Niphates amorpha*)
	*Niphates sp. or *Lissodendoryx* sp.?
	*Orange encrusting
	Pandaros acanthifolium
	*Plakortis sp.
	*Red Encrusting
	Scopalina ruetzleri
	*Spirastrella coccinea and *Spirastrella hartmani*
	Spongosorites coralliphaga
	Tectitethya crypta
	*Unidentified
	Xestospongia muta
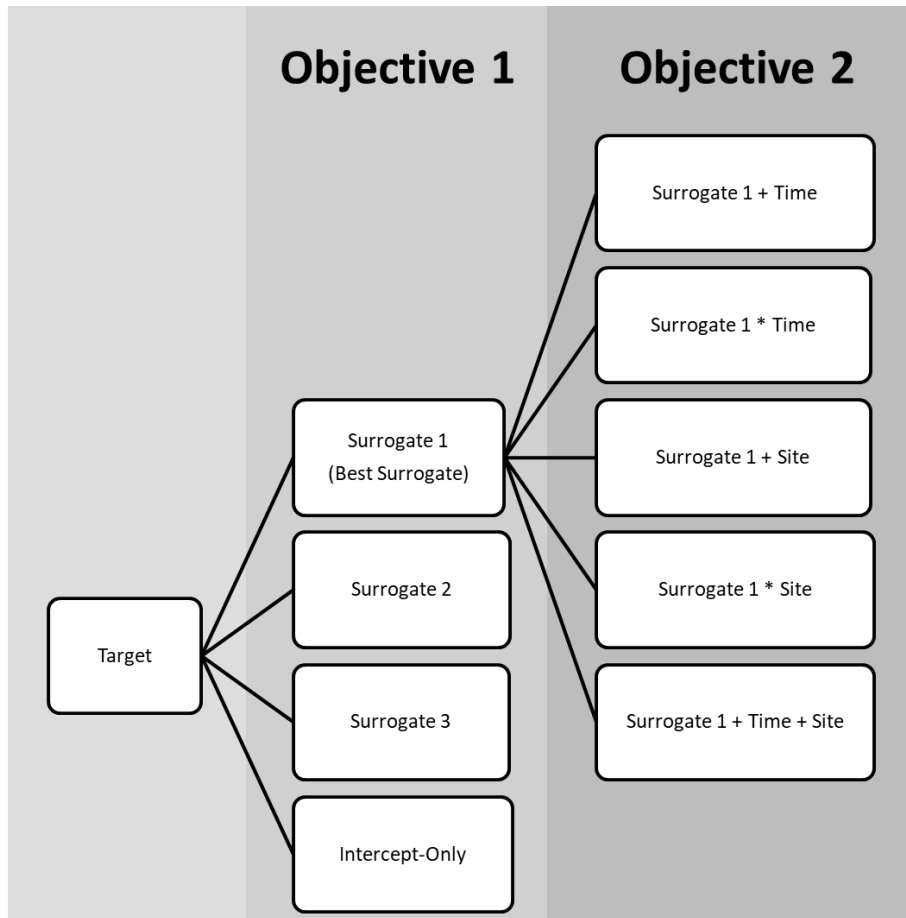
Figure A.3. Conceptual flow diagram of model sets for addressing objectives 1

(identify the best candidate surrogate for each target) and 2 (evaluate the best

surrogate-target relationship for consistency among sites and over time). Target

represents one of four target components of biodiversity: coral richness, sponge

richness, fish richness or combined richness (the sum of coral, fish, and sponge

richness). Surrogate 1 represents the most competitive of three surrogates

(percent coral cover, percent sponge cover, and rugosity) when compared to an

intercept-only model and models of the other surrogates. Time represents the

variable "year", which is a temporal trend. Site is a categorical predictor with 8

levels (the 8 locations around Guana Island, BVI). "+" represents an additive

effect and "*" represents an interaction.

Figure A.4. Basic associations between the surrogates. Lines represent smoothed

conditional means using a generalized linear model and the formula y ~ x.

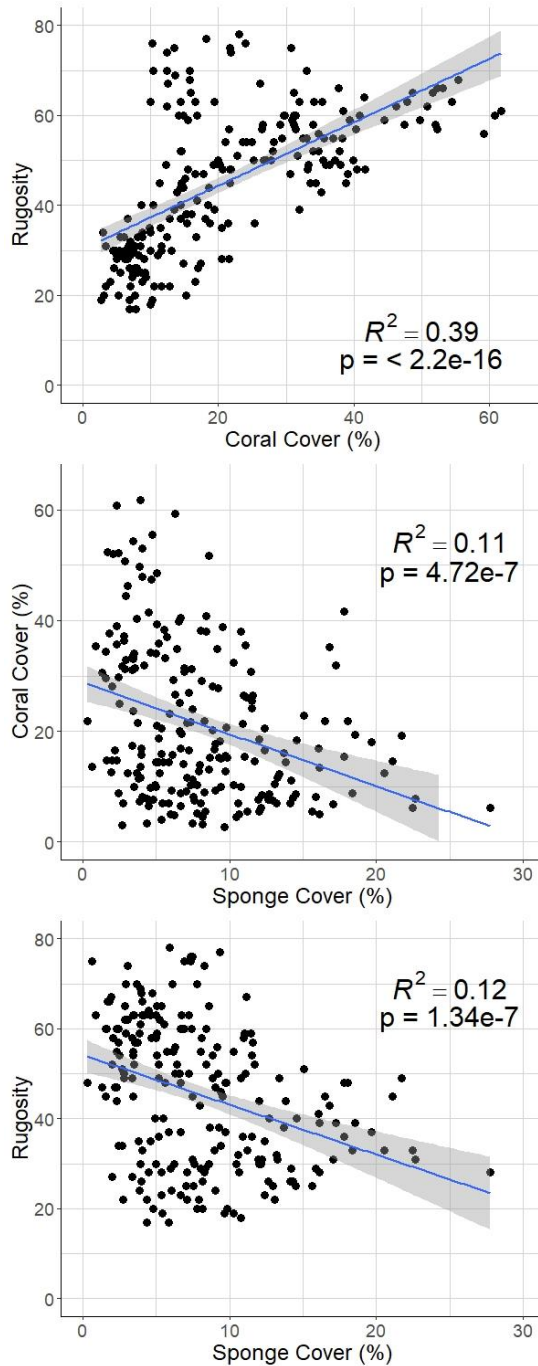Shaded portions represent 95% confidence intervals of fitted values. Traditional

r-squared (R^2) and p-values are shown. Rugosity measured in centimeters. Data

were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

Table A.5. Summary statistics of 3 randomly selected transects for each site and year

combination. n represents sample size as the number of site and year

combinations (lower for sponge richness, which was not recorded for every site

and year, and for combined richness, as the sum of coral, fish, and sponge

richness). Targets are cumulative in that richness is not averaged across 3

transects, but accounts for all species within the respective taxon found on all 3

transects. Surrogates are means of the 3 randomly selected transects per site per

year. Data were collected from 8 coral reefs around Guana Island, BVI from

1992-2018.

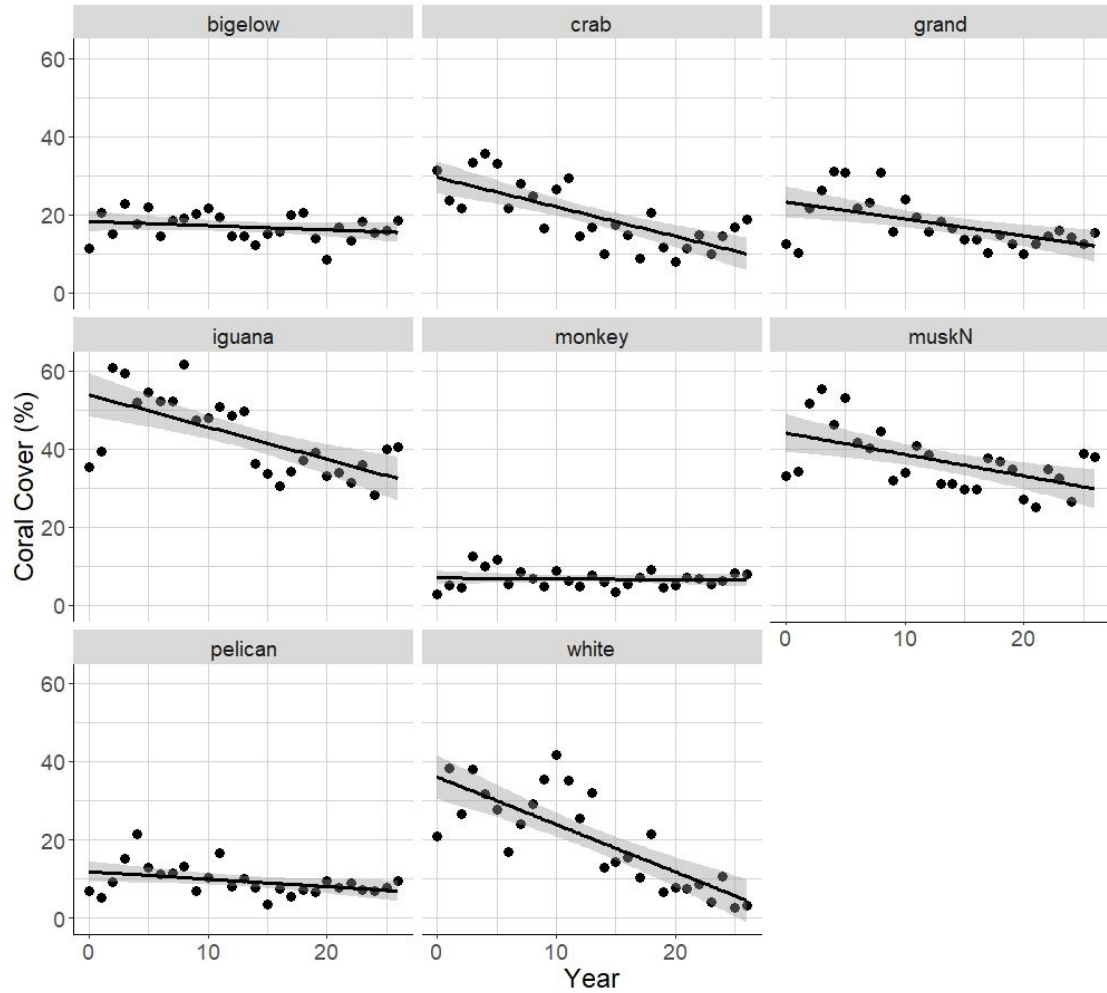| Variable	Mean	Standard Deviation	Minimum	Maximum	n
Targets					
Coral richness	13	4	4	22	216
Sponge richness	22	5	8	36	164
Fish richness	24	6	9	37	216
Combined richness	59	8	39	75	164
Surrogates					
Coral cover (%)	21.36	13.95	2.68	61.75	216
Sponge cover (%)	7.96	4.98	0.28	27.77	216
Rugosity (cm)	45	16	17	78	216

Figure A.6. Percent coral cover over the 27 year study period from 1992-2018, where

year 0 is 1992. Each panel represents one of 8 coral reefs around Guana Island,

BVI. Solid line represents smoothed conditional means using a generalized linear

model and the formula y ~ x, where x is year as a trend. Shaded portions

represent 95% confidence intervals of fitted values.
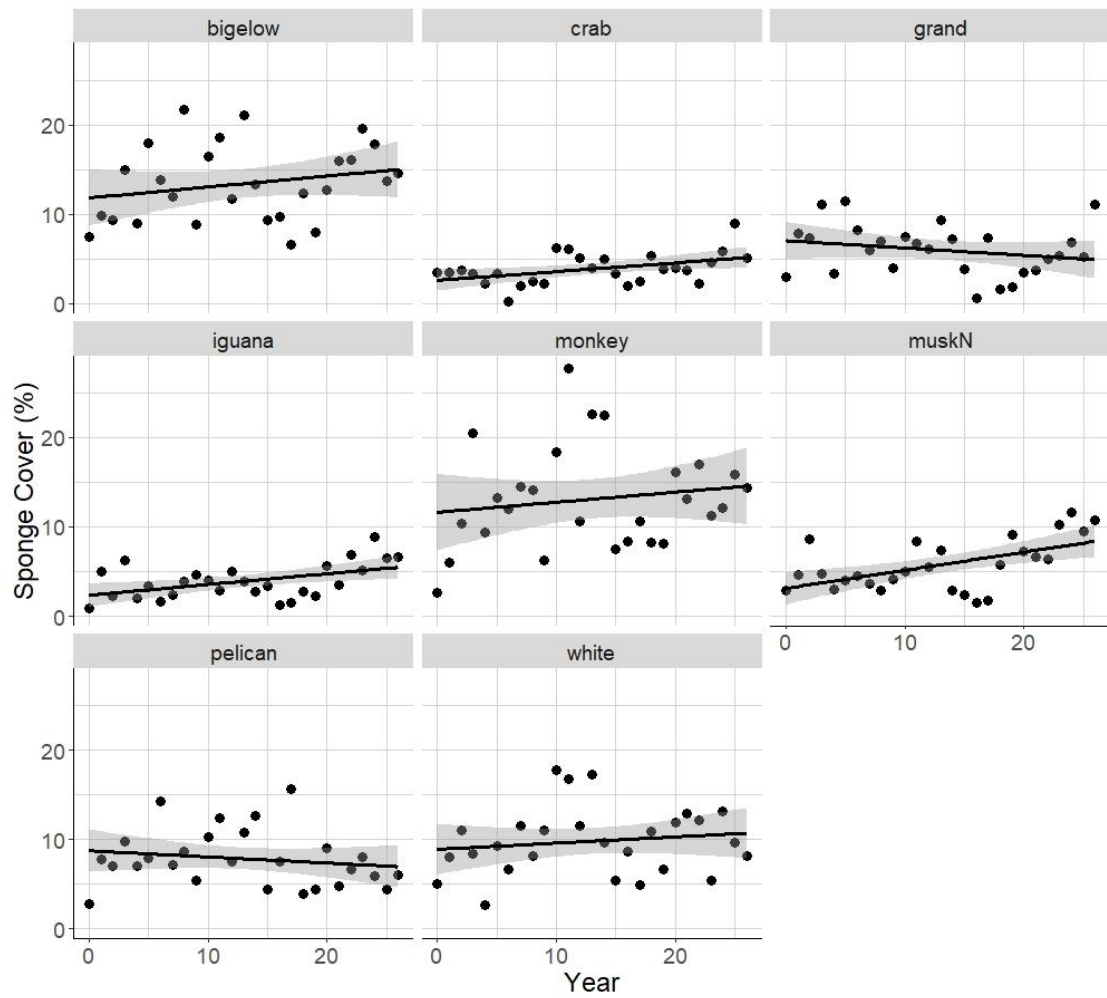
Figure A.7. Percent sponge cover over the 27 year study period from 1992-2018,

where year 0 is 1992. Each panel represents one of 8 coral reefs around Guana

Island, BVI. Solid line represents smoothed conditional means using a

generalized linear model and the formula y ~ x, where x is year as a trend.

Shaded portions represent 95% confidence intervals of fitted values.
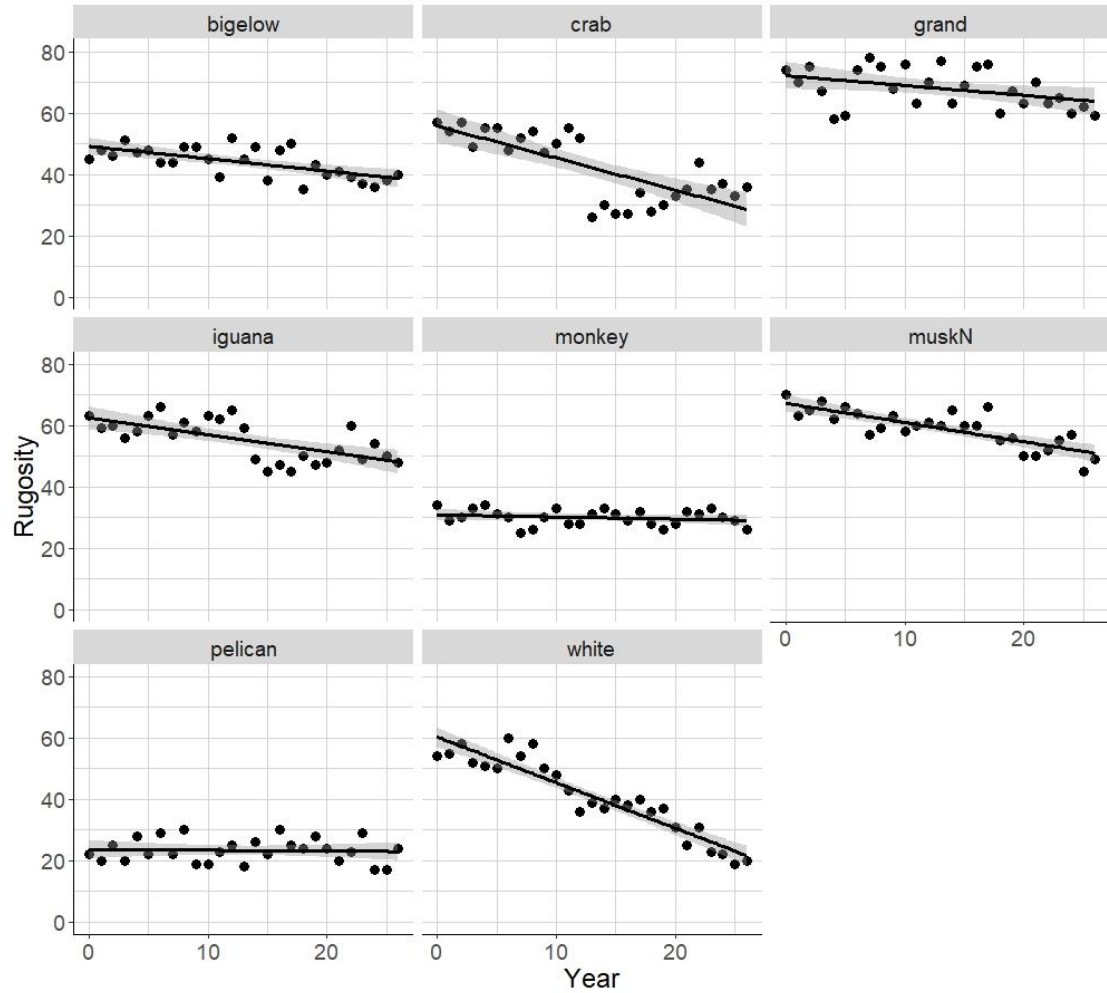
Figure A.8. Rugosity (in cm) over the 27 year study period from 1992-2018, where

    year 0 is 1992. Each panel represents one of 8 coral reefs around Guana Island,

    BVI. Solid line represents smoothed conditional means using a generalized linear

    model and the formula y ~ x, where x is year as a trend. Shaded portions

    represent 95% confidence intervals of fitted values.

Figure A.9. Percent coral cover over the 27 year study period from 1992-2018, where

year 0 is 1992. Solid line represents smoothed conditional means using a

generalized linear model and the formula y ~ x, where x is year as a trend.

Shaded portions represent 95% confidence intervals of fitted values. Traditional

r-squared (R^2) and p-values are shown. Data were collected from 8 coral reefs

around Guana Island, BVI.

Figure A.10. Percent sponge cover over the 27 year study period from 1992-2018,

where year 0 is 1992. Solid line represents smoothed conditional means using a

generalized linear model and the formula y ~ x, where x is year as a trend.

Shaded portions represent 95% confidence intervals of fitted values. Traditional

r-squared (R^2) and p-values are shown. Data were collected from 8 coral reefs

around Guana Island, BVI.

Figure A.11. Rugosity (in cm) over the 27 year study period from 1992-2018, where

year 0 is 1992. Solid line represents smoothed conditional means using a

generalized linear model and the formula y ~ x, where x is year as a trend.

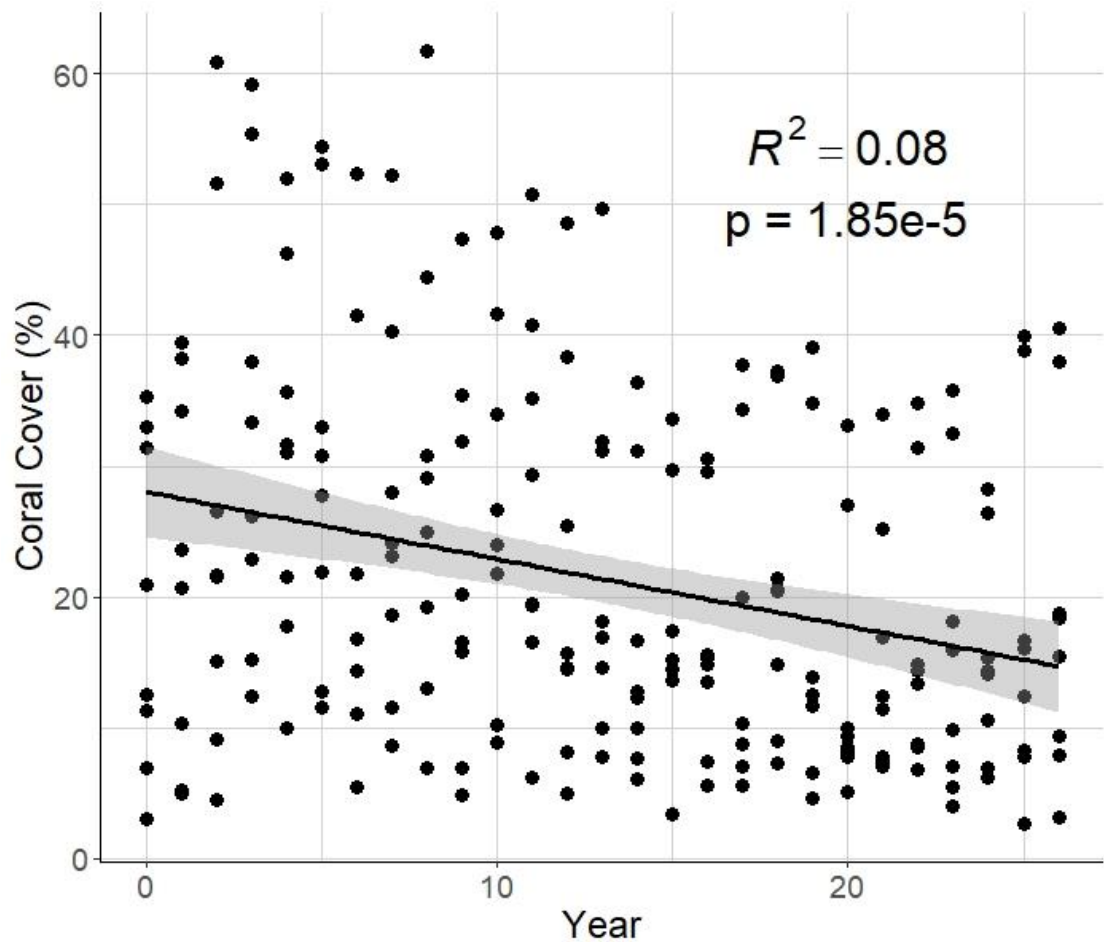Shaded portions represent 95% confidence intervals of fitted values. Traditional

r-squared (R^2) and p-values are shown. Data were collected from 8 coral reefs

around Guana Island, BVI.
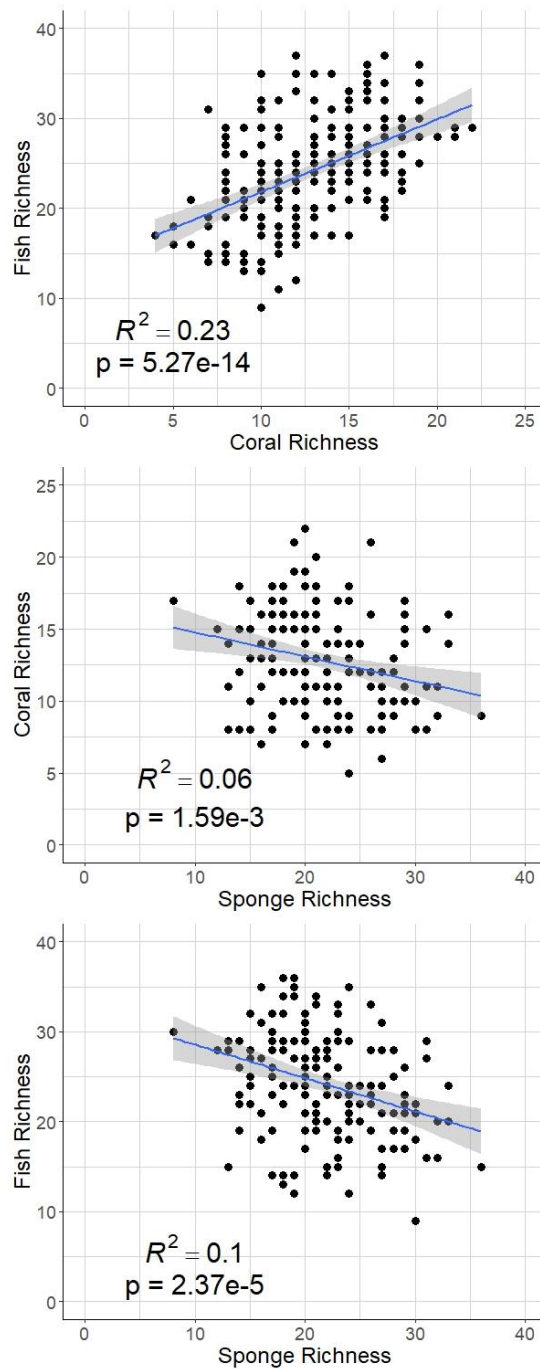
Figure A.12. Basic associations between the targets. Lines represent smoothed

conditional means using a generalized linear model and the formula y ~ x.

Shaded portions represent 95% confidence intervals of fitted values. Traditional

r-squared (R^2) and p-values are shown. Data were collected from 8 coral reefs
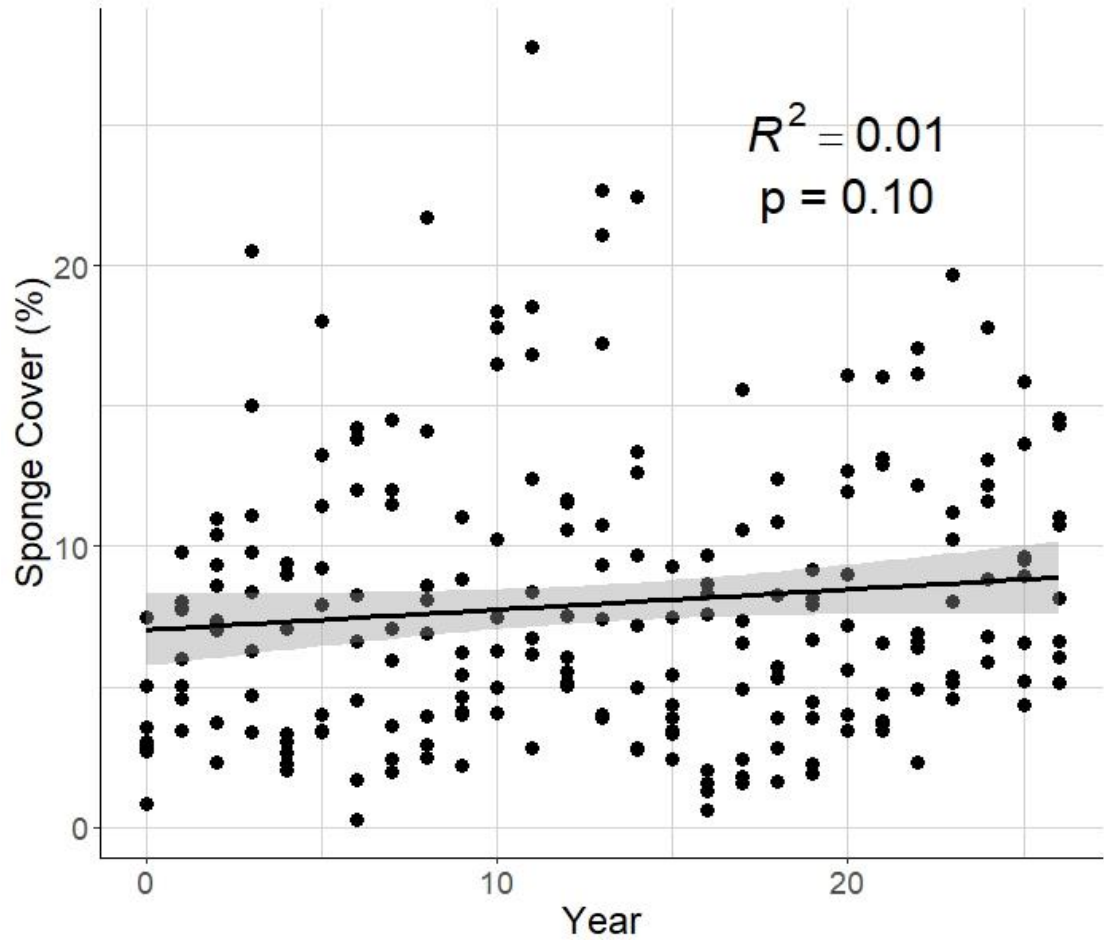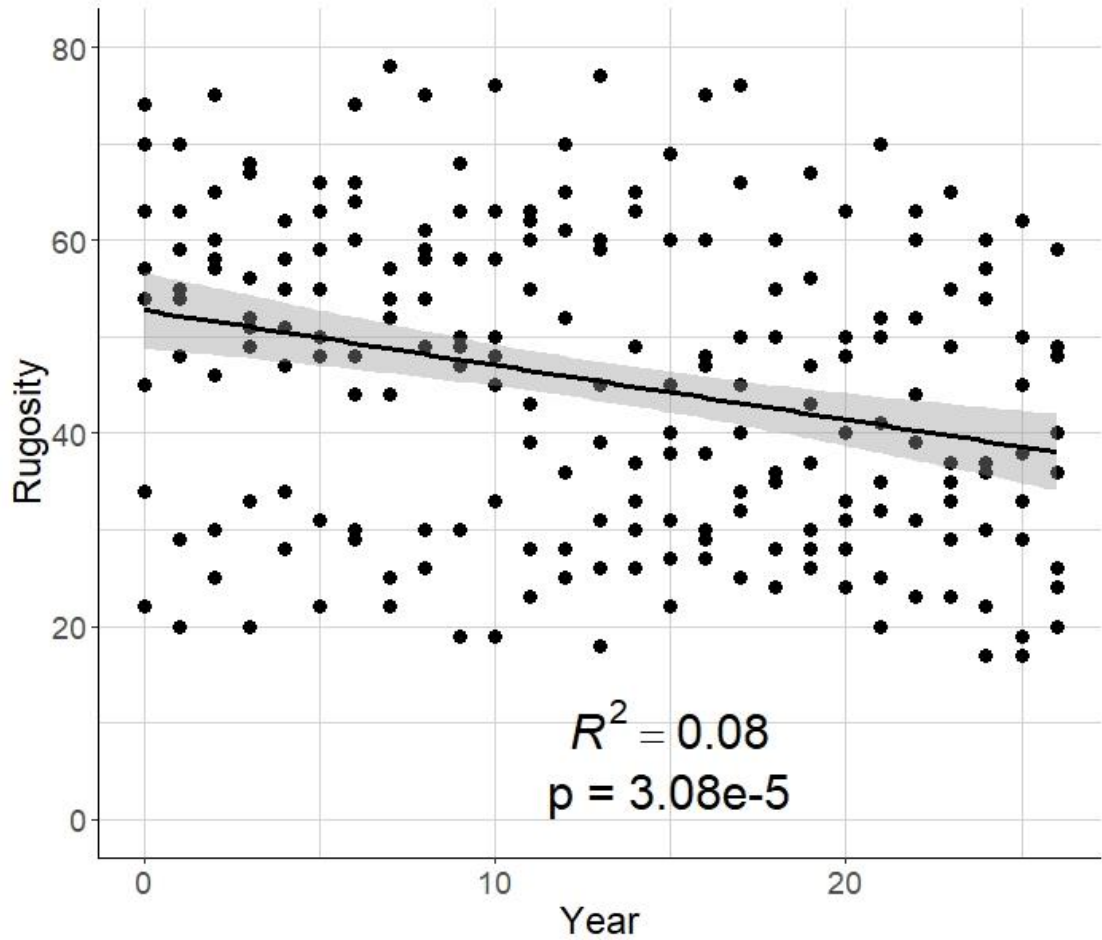
around Guana Island, BVI from 1992-2018.

Figure A.13. Coral richness over the 27 year study period from 1992-2018, where year

0 is 1992. Each panel represents one of 8 coral reefs around Guana Island, BVI.

Solid line represents smoothed conditional means using a generalized linear

model and the formula y ~ x, where x is year as a trend. Shaded portions

represent 95% confidence intervals of fitted values.

Figure A.14. Sponge richness over the 27 year study period from 1992-2018, where

year 0 is 1992. Each panel represents one of 8 coral reefs around Guana Island,

BVI. Solid line represents smoothed conditional means using a generalized linear

model and the formula y ~ x, where x is year as a trend. Shaded portions
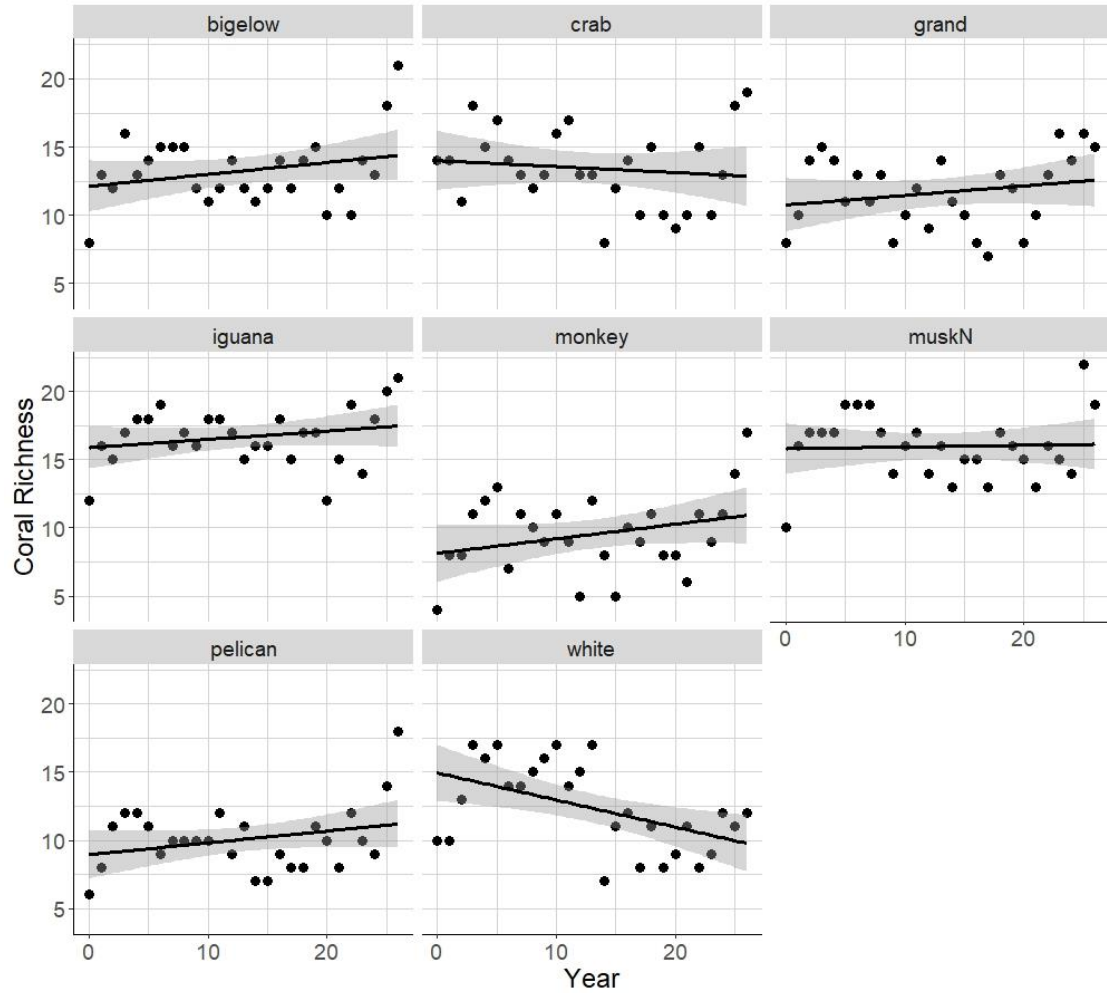
represent 95% confidence intervals of fitted values.
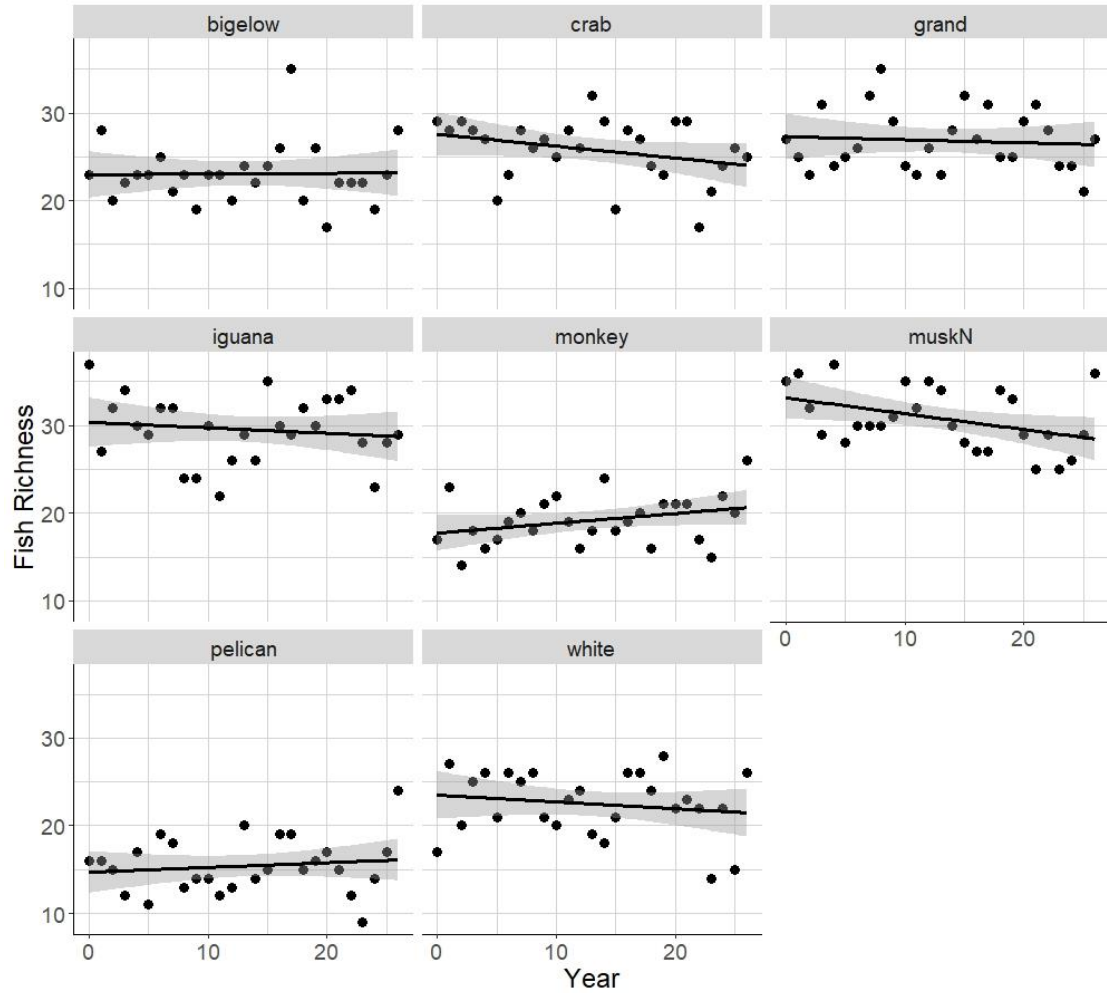
Figure A.15. Fish richness over the 27 year study period from 1992-2018, where year

0 is 1992. Each panel represents one of 8 coral reefs around Guana Island, BVI.

Solid line represents smoothed conditional means using a generalized linear

model and the formula y ~ x, where x is year as a trend. Shaded portions

represent 95% confidence intervals of fitted values.

Figure A.16. Coral richness over the 27 year study period from 1992-2018, where year

0 is 1992. Solid line represents smoothed conditional means using a generalized

linear model and the formula y ~ x, where x is year as a trend. Shaded portions

represent 95% confidence intervals of fitted values. Traditional r-squared (R^2)

and p-values are shown. Data were collected from 8 coral reefs around Guana

Island, BVI.
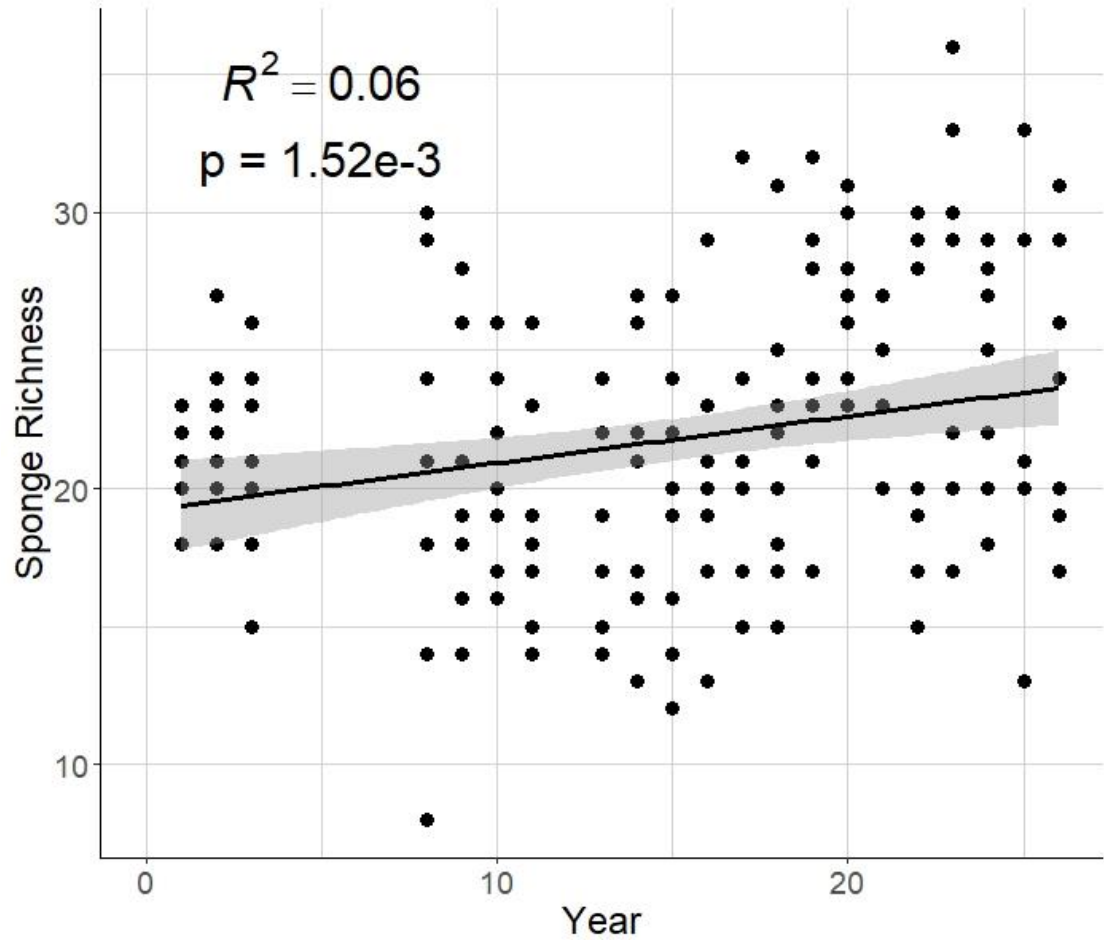
Figure A.17. Sponge richness over the 27 year study period from 1992-2018, where

year 0 is 1992. Solid line represents smoothed conditional means using a

generalized linear model and the formula y ~ x, where x is year as a trend.

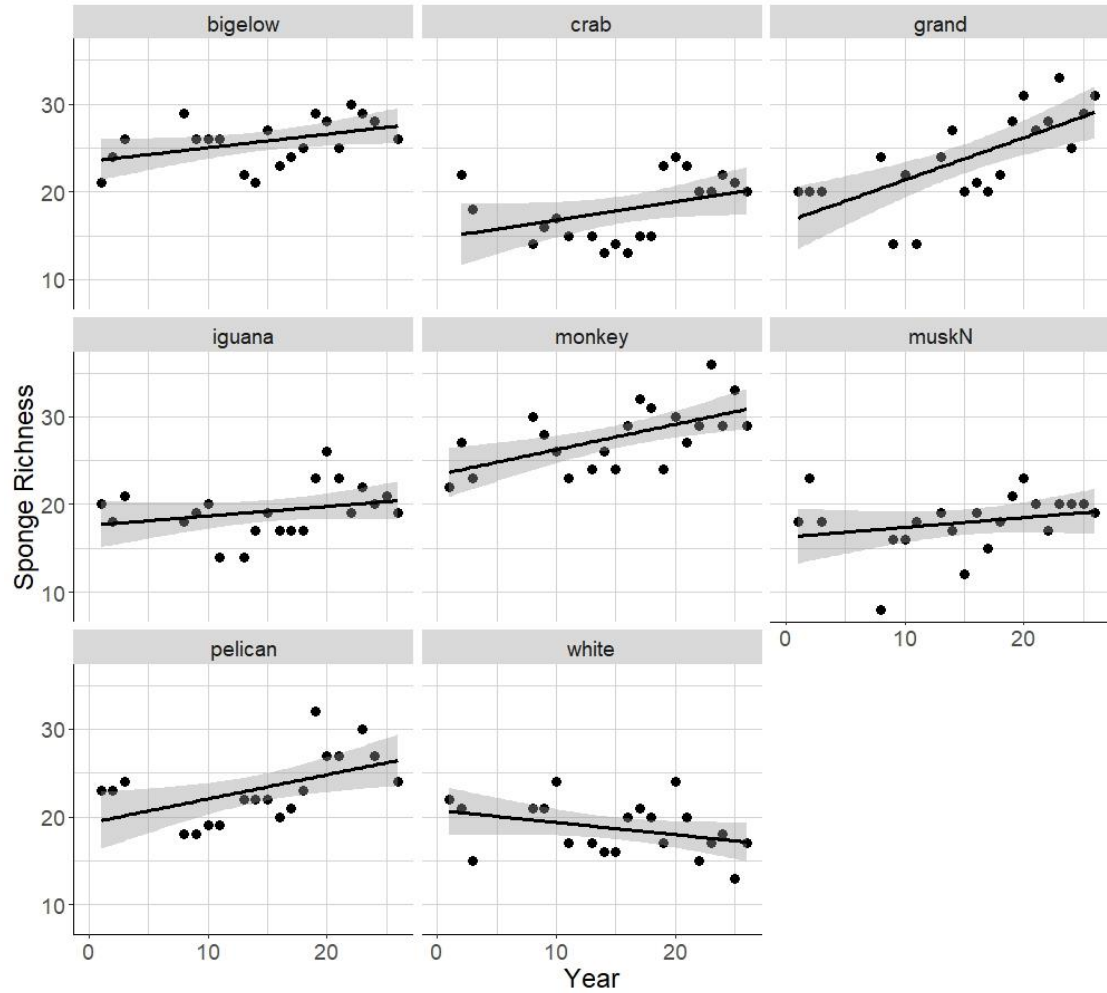Shaded portions represent 95% confidence intervals of fitted values. Traditional

r-squared (R^2) and p-values are shown. Data were collected from 8 coral reefs

around Guana Island, BVI.
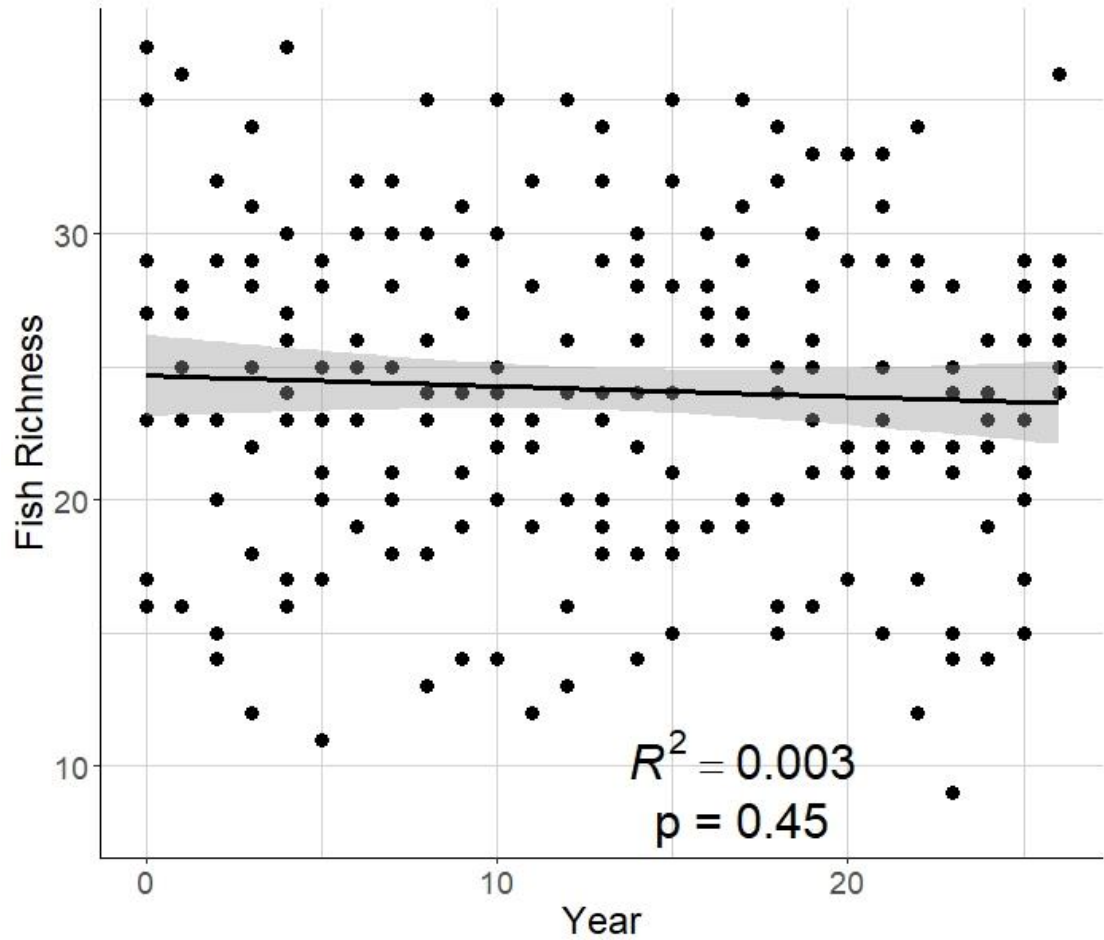
Figure A.18. Fish richness over the 27 year study period from 1992-2018, where year

0 is 1992. Solid line represents smoothed conditional means using a generalized

linear model and the formula y ~ x, where x is year as a trend. Shaded portions
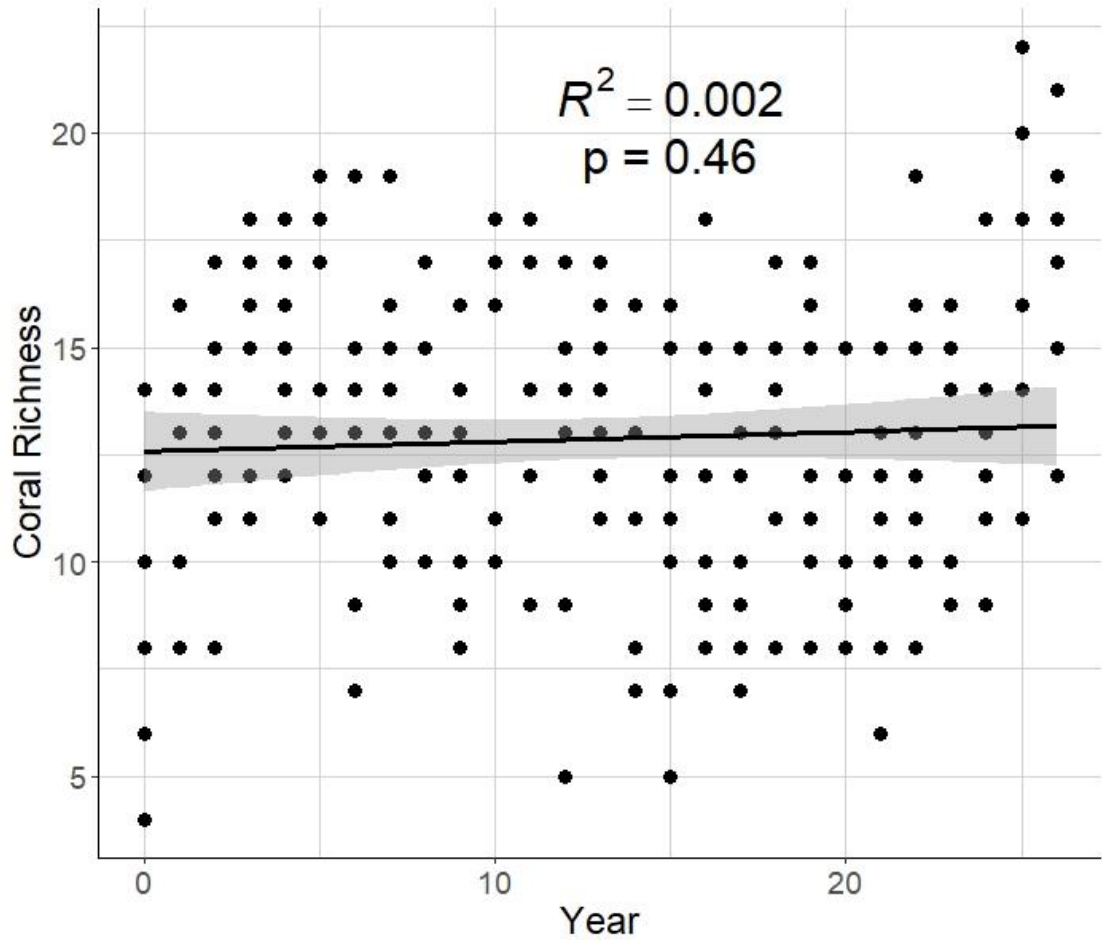
represent 95% confidence intervals of fitted values. Traditional r-squared (R^2)

and p-values are shown. Data were collected from 8 coral reefs around Guana

Island, BVI.

Table A.19. Model output for the most competitive model for predicting coral richness

including a term for year. Estimates calculated using the negative binomial

distribution and the formula y ~ x + year, where y coral richness, x is coral cover,

and year is a trend. Data were collected from 8 coral reefs around Guana Island,

BVI from 1992-2018.

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	2.0751	0.0571	36.350	< 2e-16 ***
Percent_Coral_Cover	0.0152	0.0013	11.275	< 2e-16 ***
Year	0.0103	0.0026	4.012	6.03e-05 ***

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table A.20. Model output for the most competitive model for predicting coral richness

including terms for year and the interaction between coral cover and year.

Estimates calculated using the negative binomial distribution and the formula y ~

x + year + x * year, where y coral richness, x is coral cover, and year is a trend.

Data were collected from 8 coral reefs around Guana Island, BVI from 1992-

2018.

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	2.1163	0.0757	27.950	< 2e-16 ***
Percent_Coral_Cover	0.0136	0.0024	5.763	8.25e-09 ***
Year	0.0070	0.0048	1.478	0.139
Percent_Coral_Cover:Year	0.0001	0.0002	0.823	0.411

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table A.21. Model output for the most competitive model for predicting sponge

richness including terms for year and site. Estimates calculated using the negative

binomial distribution and the formula y ~ x + year + site, where y is sponge

richness, x is coral cover, year is a trend, and site is a categorical predictor. Data

were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	3.0204	0.0901	33.511	< 2e-16 ***
Percent_Coral_Cover	0.0041	0.0029	1.443	0.148955
Year	0.0106	0.0027	3.885	0.000102 ***
Sitecrab	-0.3709	0.0688	-5.392	6.95e-08 ***
Sitegrand	-0.0802	0.0628	-1.276	0.201957
Siteiguana	-0.3964	0.0964	-4.110	3.96e-05 ***
Sitemonkey	0.1110	0.0671	1.655	0.097956 .
SitemuskN	-0.4417	0.0862	-5.124	2.99e-07 ***
Sitepelican	-0.0650	0.0694	-0.937	0.348668
Sitewhite	-0.3335	0.0673	-4.957	7.16e-07 ***

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table A.22. Model output for the most competitive model for predicting fish richness including terms for site. Estimates calculated using the negative binomial distribution and the formula y ~ x + site, where y is fish richness, x is rugosity in cm, and site is a categorical predictor. Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	3.0322	0.0908	33.394	< 2e-16 ***
Rugosity	0.0024	0.0019	1.309	0.190702
Sitecrab	0.1161	0.0552	2.103	0.035468 *
Sitegrand	0.0932	0.0706	1.321	0.186509
Siteiguana	0.2199	0.0575	3.822	0.000132 ***
Sitemonkey	-0.1508	0.0648	-2.325	0.020081 *
SitemuskN	0.2524	0.0600	4.206	2.60e-05 ***
Sitepelican	-0.3540	0.0739	-4.790	1.67e-06 ***
Sitewhite	-0.0193	0.0572	-0.337	0.736017

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

Table A.23. Model output for the most competitive model for predicting combined

richness (the sum of coral, fish, and sponge richness) including terms for year and

site. Estimates calculated using the negative binomial distribution and the

formula y ~ x + year + site, where y is combined richness, x is rugosity in cm,

year is a trend, and site is a categorical predictor. Data were collected from 8

coral reefs around Guana Island, BVI from 1992-2018.

Coefficients:

	Estimate	Std. Error	z value	Pr(>|z|)
(Intercept)	3.8663	0.0991	39.023	< 2e-16 ***
Rugosity	0.0043	0.0018	2.383	0.017150 *
Year	0.0052	0.0017	3.002	0.002678 **
Sitecrab	-0.0706	0.0418	-1.690	0.090956 .
Sitegrand	-0.0986	0.0594	-1.659	0.097162 .
Siteiguana	0.0016	0.0434	0.037	0.970659
Sitemonkey	-0.0275	0.0469	-0.587	0.556993
SitemuskN	-0.0314	0.0474	-0.661	0.508411
Sitepelican	-0.1573	0.0565	-2.783	0.005388 **
Sitewhite	-0.1422	0.0423	-3.366	0.000764 ***

Significance codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
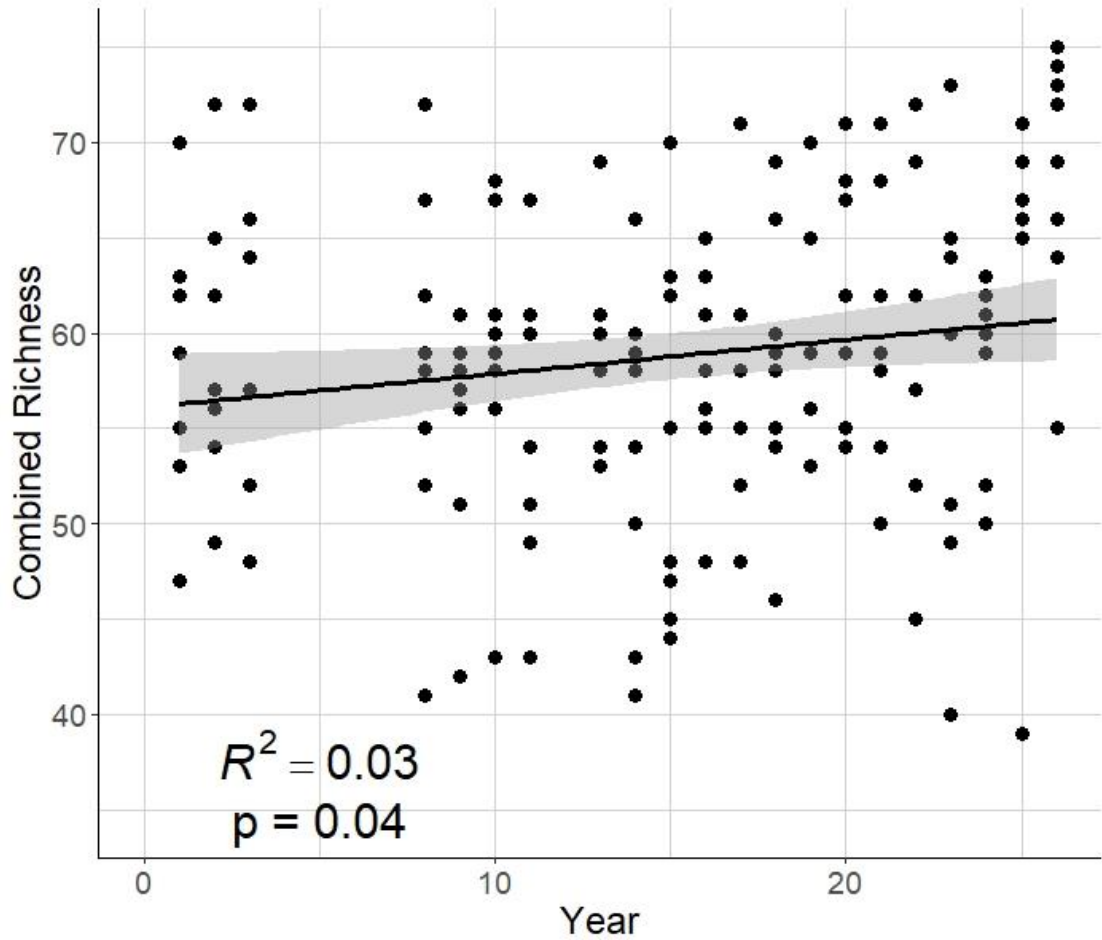
$$R^2 = 0.03$$
$$p = 0.04$$

Figure A.24. Combined richness (the sum of coral, fish, and sponge richness) over the

27 year study period from 1992-2018, where year 0 is 1992. Solid line represents

smoothed conditional means using a generalized linear model and the formula y

~ x, where x is year as a trend. Shaded portions represent 95% confidence

intervals of fitted values. Traditional r-squared (R^2) and p-values are shown. Data

were collected from 8 coral reefs around Guana Island, BVI