

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**

Global biodiversity declines associated with anthropogenic stressors have motivated researchers to implement monitoring programs to estimate species richness for major taxonomic groups. Due to logistical challenges of species identification, there have been efforts to use biological and abiotic surrogates as indicators of species richness targets. 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. Few studies, however, have explicitly investigated surrogate effectiveness over time, and those that have are typically quite short. 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. Coral reef assessments have primarily focused on monitoring species richness of fish and hard corals due to the ecological and economical value of these taxonomic groups. The species richness of these conspicuous, well-studied taxonomic groups has been extrapolated to represent the richness of other coral reef taxa or to represent total species richness of coral reefs. However, the reliability of these extrapolations is not well-studied, and we used sponges as a case study to assess whether surrogates for fish and coral species richness can be used to predict the richness of other groups. We selected two simple biotic surrogates (total coral cover and total sponge cover) and one abiotic surrogate (reef rugosity) to predict richness of corals, fish, sponges, and richness of the three groups

pooled. To study how these surrogate-target relationships vary over time and space we used 27 years of monitoring data from eight sites around Guana Island in the British Virgin Islands. 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). To address this objective, we compared a set of simple models of each of the candidate surrogates as predictors using AICc. We found that, of our candidate surrogates, coral cover was the best surrogate for coral and sponge richness and rugosity was the best surrogate for fish richness 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. For this objective, we compared models of the best surrogate as a predictor with additional terms to account for change over the duration of the study and variation across sites using AICc. We found that coral cover was a stable surrogate for coral richness because the rankings of species richness among sites were consistent over time. The coral cover- sponge richness relationship was weak and was of limited quantitative predictive ability across both space and time. 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. The surrogate-target relationship between rugosity and richness of the three groups pooled was qualitatively stable because simple rankings of species richness among sites are expected to remain consistent over time. Notably, we found that surrogate-target relationships for coral and sponge richness changed quantitatively over the 27

years of the study. For both targets, using the initial surrogate-target relationship to extrapolate over time would have resulted in a steadily increasing underestimate of species richness. All of the surrogates tested were qualitatively stable over time in the sense that rankings of species richness among sites were consistent over nearly three decades. Our findings suggest that monitoring of cost-effective surrogates is appropriate in tracking changes in the relative species richness of coral reef communities and that priority areas selected using a one-off spatial survey are likely to retain the features that made them priority areas.

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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<sup>a</sup>; Graham E. Forrester<sup>b</sup>

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<sup>a</sup> Department of Natural Resources Science, University of Rhode Island,  
Kingston, RI 02881, USA ; [nicole-keefner@uri.edu](mailto:nicole-keefner@uri.edu)

<sup>b</sup> Department of Natural Resources Science, University of Rhode Island,  
Kingston, RI 02881, USA; [gforrester@uri.edu](mailto:gforrester@uri.edu)

## **Abstract**

Global biodiversity declines associated with anthropogenic stressors have motivated researchers to implement monitoring programs to estimate species richness for major taxonomic groups. Due to logistical challenges of species identification, there have been efforts to use biological and abiotic surrogates as indicators of species richness targets. 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. Few studies, however, have explicitly investigated surrogate effectiveness over time, and those that have are typically quite short. 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. Coral reef assessments have primarily focused on monitoring species richness of fish and hard corals due to the ecological and economical value of these taxonomic groups. The species richness of these conspicuous, well-studied taxonomic groups has been extrapolated to represent the richness of other coral reef taxa or to represent total species richness of coral reefs. However, the reliability of these extrapolations is not well-studied, and we used sponges as a case study to assess whether surrogates for fish and coral species richness can be used to predict the richness of other groups. We selected two simple biotic surrogates (total coral cover and total sponge cover) and one abiotic surrogate (reef rugosity) to predict richness of corals, fish, sponges, and richness of the three groups

pooled. To study how these surrogate-target relationships vary over time and space we used 27 years of monitoring data from eight sites around Guana Island in the British Virgin Islands. 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). To address this objective, we compared a set of simple models of each of the candidate surrogates as predictors using AICc. We found that, of our candidate surrogates, coral cover was the best surrogate for coral and sponge richness and rugosity was the best surrogate for fish richness 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. For this objective, we compared models of the best surrogate as a predictor with additional terms to account for change over the duration of the study and variation across sites using AICc. We found that coral cover was a stable surrogate for coral richness because the rankings of species richness among sites were consistent over time. The coral cover- sponge richness relationship was weak and was of limited quantitative predictive ability across both space and time. 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. The surrogate-target relationship between rugosity and richness of the three groups pooled was qualitatively stable because simple rankings of species richness among sites are expected to remain consistent over time. Notably, we found that surrogate-target relationships for coral and sponge richness changed quantitatively over the 27

years of the study. For both targets, using the initial surrogate-target relationship to extrapolate over time would have resulted in a steadily increasing underestimate of species richness. All of the surrogates tested were qualitatively stable over time in the sense that rankings of species richness among sites were consistent over nearly three decades. Our findings suggest that monitoring of cost-effective surrogates is appropriate in tracking changes in the relative species richness of coral reef communities and that priority areas selected using a one-off spatial survey are likely to retain the features that made them priority areas.

*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

“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  $\alpha$  (local) diversity, rather than differences in  $\beta$ -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,  $\theta$ , 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

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). Correlations between rugosity and different measures of fish abundance are well-established (Alvarez-Filip, Dulvy, Côté, Watkinson, & Gill, 2011), but 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). Several benthic groups (e.g. macroalgae, gorgonians, zooanthids) are routinely monitored using their total abundance, so the potential to extrapolate to predict their species richness would be of practical value. This prediction was, however, poorly-supported for sponges, because sponge abundance displayed a weak positive correlation with sponge richness, casting doubt on the widespread effectiveness of this type of higher-taxa surrogate. 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.

Although associations between coral cover and sponge richness are little-studied, negative associations between coral and sponge cover have been reported, 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.

We used sponges as a case study to test the possibility of extrapolating from well-studied taxa to other taxa. Different taxonomic groups respond differently to changes in the environment. As such, using diversity measures for one group as proxies for another group, or for total biodiversity, without evaluating this relationship 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).

The reliability of these extrapolations is not well-studied, and our results suggest that simple higher-taxa and abiotic surrogates for fish and coral species richness are unlikely to reliably predict the richness of other groups. 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). Although not our primary focus, our results also indicate that one alternative approach, the use of cross-taxa surrogates, is also unlikely to be effective because sponge richness was only weakly correlated with fish and coral richness. This finding is consistent with a recent review of biotic surrogates that found cross-taxa surrogates to be less effective than higher-taxa or subset-taxa surrogates (Mellin et al., 2011).

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

Perhaps our most important finding was that surrogate-target relationships for coral and sponge richness changed quantitatively over the 27 years of the study. For

both targets, using the initial surrogate-target relationship to extrapolate over time would have resulted in a steadily increasing underestimate of species richness. For corals, species richness in 2018 would be underestimated by more than half using the surrogate-target relationship from 1992. Underlying this change was the fact that both targets tended to increase slightly over time, whereas the surrogate steadily declined. Our study was not designed to explain why this occurred, but we suggest some alternate hypotheses. For corals, one hypothesis for increased species richness per unit coral cover over time is an increase over time in evenness of relative abundance. In other words, coral species that were initially numerically dominant have declined in abundance more severely than other species. Another, not mutually exclusive, hypothesis is an increased rate of species-colonization over time. Although beyond the scope of our study, this finding suggests that further analyses of biodiversity measures that combine species richness and relative abundance should be a priority.

Another surrogate-target relationship (rugosity-fish species richness), did not change substantially over the nearly three decades of our study. Again, we cannot explain why this relationship was temporally consistent, but suggest one hypothesis. It has been argued that reduced fish abundance in response to reductions in rugosity may show a substantial time-lag (Paddack et al., 2009). A consistent multi-year time lag displayed by many fish species could explain why the rugosity-fish richness relationship was fairly consistent over time. If correct, this hypothesis suggests that the temporal stability of resource-related surrogates, more generally, may depend on the time-span over which the target group tracks changes in the resource.

Despite quantitative changes, all of the surrogates tested were qualitatively stable over time in the sense that rankings of species richness among sites were consistent over nearly three decades. This finding has two important practical implications. First it suggests that monitoring of cost-effective surrogates is appropriate in tracking changes in the *relative* species richness of coral reef communities. Second, surrogates are widely used to identify priority conservation areas; which requires an understanding of how the size and dispersion of the areas being conserved affects the relationship between the surrogate and the target. Our results suggest that priority areas selected using a one-off spatial survey are likely to retain the features that made them priority areas.

In conclusion, we show here that 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.

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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 ( $\theta$ ). Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

<b>Model Name</b>	<b>K</b>	<b>AICc</b>	<b>Delta AICc</b>	<b>Akaike weight</b>	<b>Log-likelihood</b>	<b><math>R_N^2</math></b>
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 ( $\theta$ ). Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

<b>Model Name</b>	<b>K</b>	<b>AICc</b>	<b>Delta AICc</b>	<b>Akaike weight</b>	<b>Log-likelihood</b>	<b><math>R_N^2</math></b>
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 ( $\theta$ ). Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

<b>Model Name</b>	<b>K</b>	<b>AICc</b>	<b>Delta AICc</b>	<b>Akaike weight</b>	<b>Log-likelihood</b>	<b><math>R_N^2</math></b>
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 ( $\theta$ ). Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

<b>Model Name</b>	<b>K</b>	<b>AICc</b>	<b>Delta AICc</b>	<b>Akaike weight</b>	<b>Log-likelihood</b>	<b><math>R_N^2</math></b>
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 ( $\theta$ ). Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

<b>Model Name</b>	<b>K</b>	<b>AICc</b>	<b>Delta AICc</b>	<b>Akaike weight</b>	<b>Log-likelihood</b>	<b><math>R_N^2</math></b>
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 ( $\theta$ ). 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 ( $\theta$ ). Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

<b>Model Name</b>	<b>K</b>	<b>AICc</b>	<b>Delta AICc</b>	<b>Akaike weight</b>	<b>Log-likelihood</b>	<b><math>R_N^2</math></b>
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 ( $\theta$ ). Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

<b>Model Name</b>	<b>K</b>	<b>AICc</b>	<b>Delta AICc</b>	<b>Akaike weight</b>	<b>Log-likelihood</b>	<b><math>R_N^2</math></b>
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

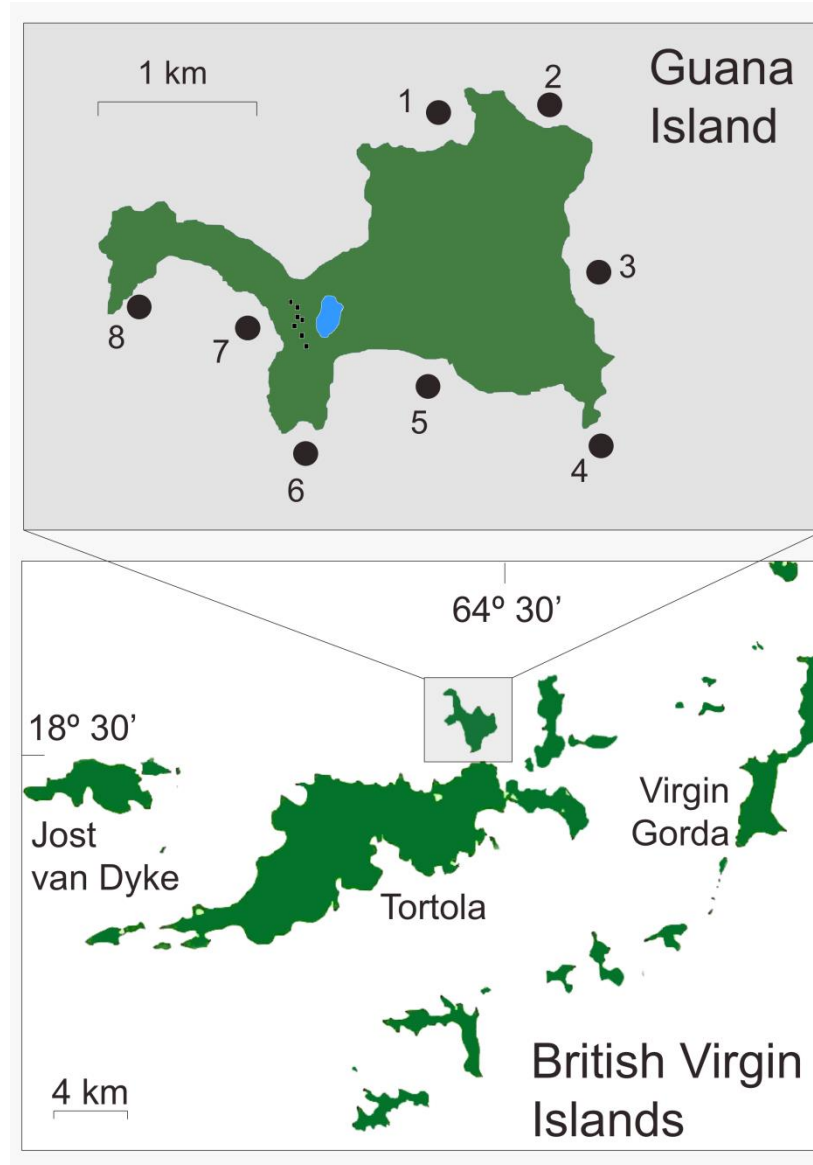


Figure 1. Top panel: a map of Guana Island, British Virgin Islands showing the eight study sites: (1) Grand Ghut, (2) Pelican Ghut, (3) Bigelow Beach, (4) Monkey Point, (5) White Bay, (6) Iguana Head, (7) Crab Cove, and (8) Long Point, also known as Muskmelon. Lower panel: the location of Guana Island within the British Virgin Islands.

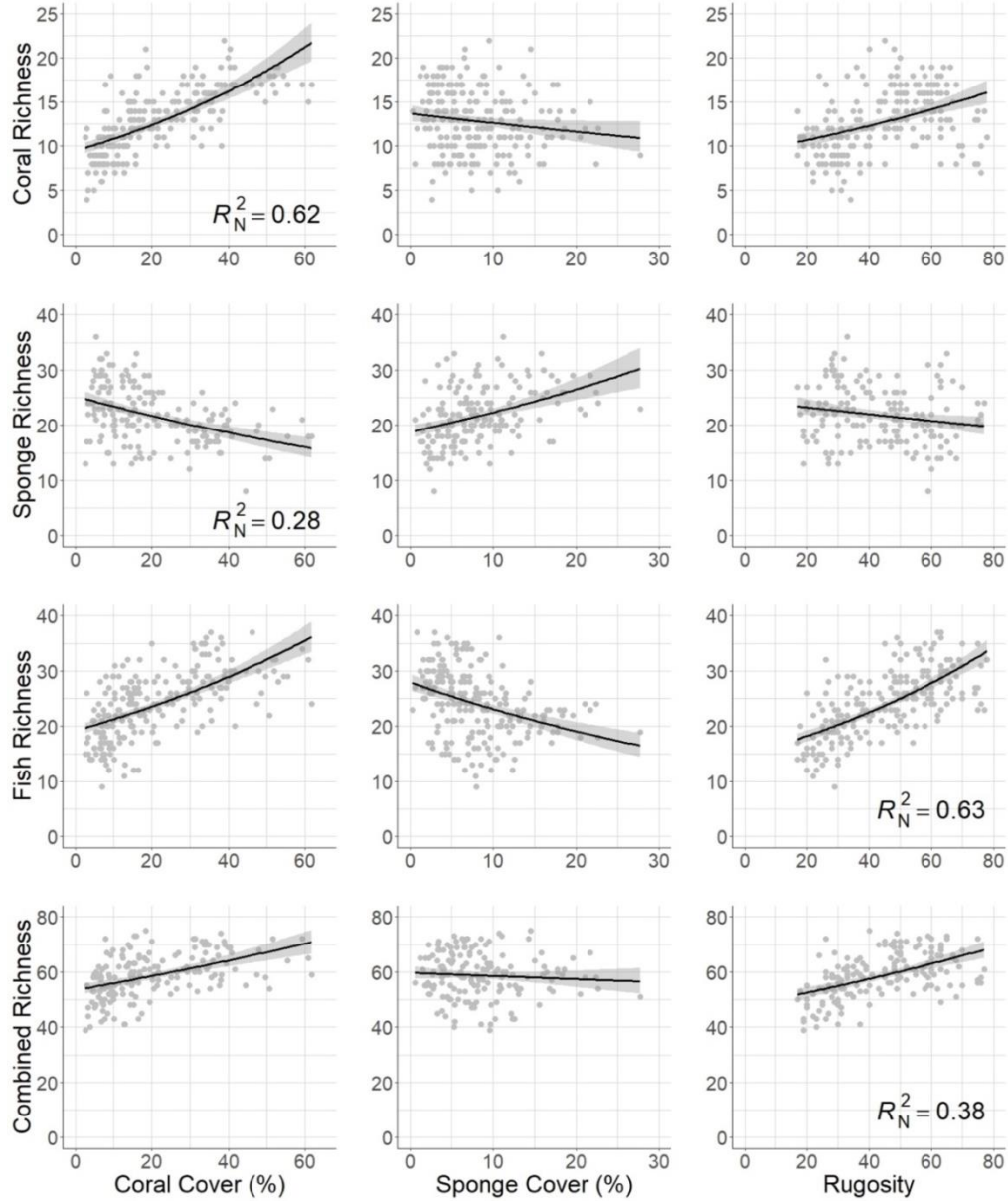


Figure 2. Potential surrogate-target relationships. Lines represent smoothed conditional means using the negative binomial distribution and the formula  $y \sim x$ , where  $y$  is a target (rows) and  $x$  is a surrogate (columns). Shaded portions represent 95% confidence intervals of fitted values. 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.



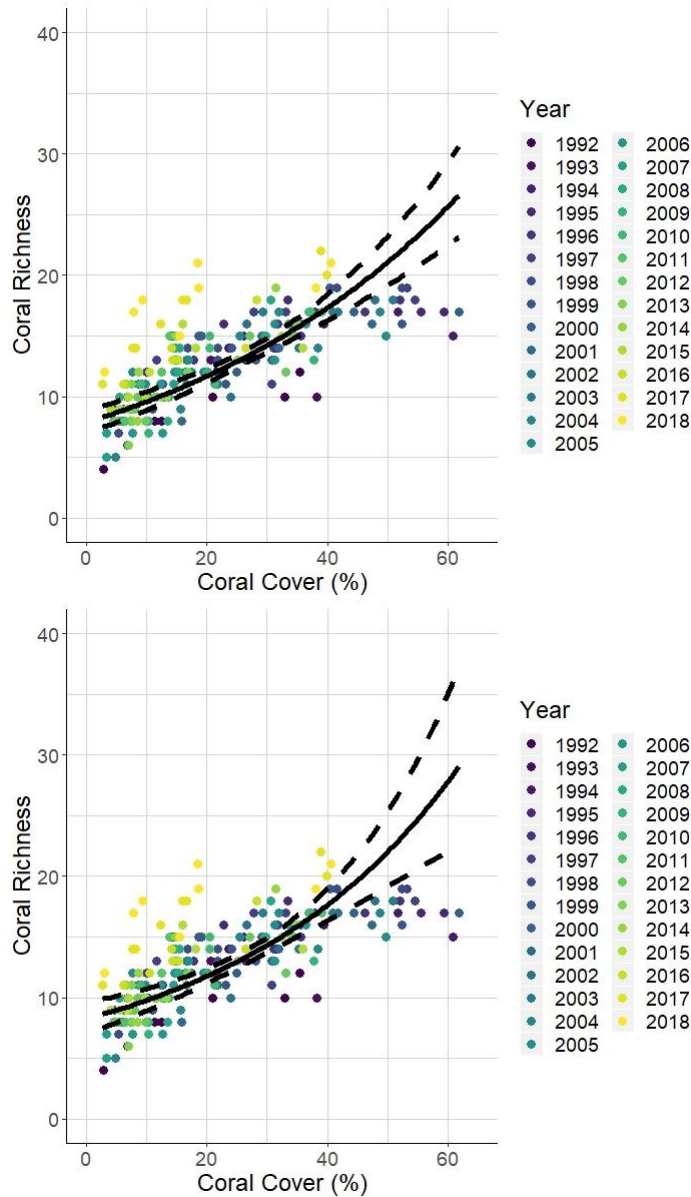


Figure 3. Competitive models for predicting coral richness included a term for year.

Solid lines represent predictions using the negative binomial distribution and the formula  $y \sim x + \text{year}$  (top panel) and  $y \sim x + \text{year} + x * \text{year}$  (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.

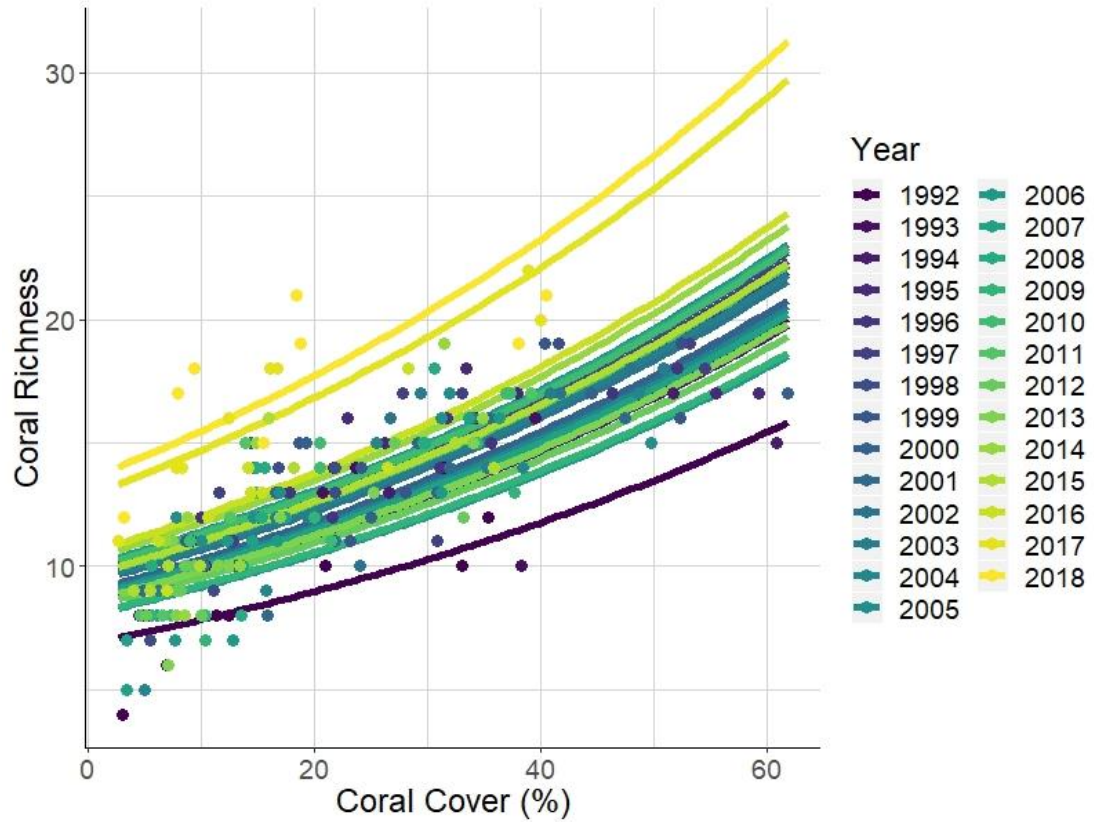


Figure 4. This figure helps to visualize changes in coral richness for a given amount of coral cover over a 27 year period. Solid lines represent predictions colored by year using the negative binomial distribution and the formula  $y \sim x + \text{year}$ , where  $y$  is coral richness,  $x$  is coral cover, and year is a categorical predictor. The formula  $y \sim x + \text{year}$ , 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.

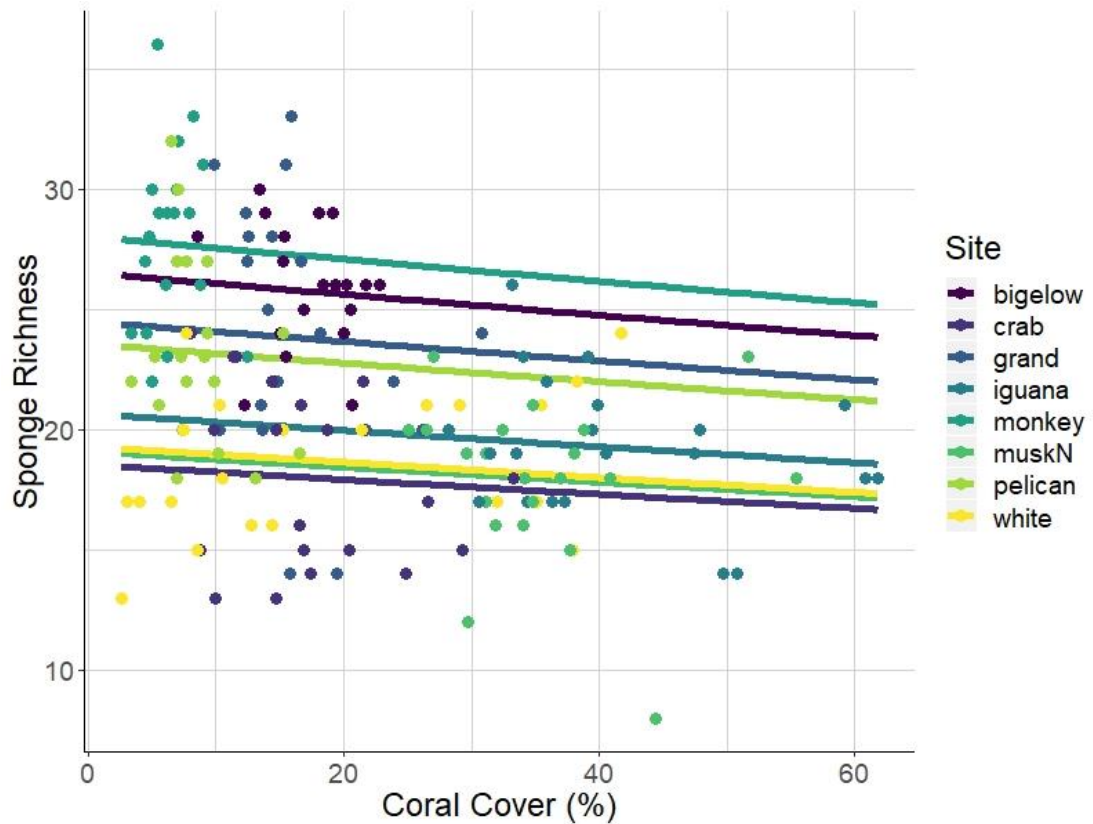


Figure 5. This figure helps to visualize large differences in sponge richness among sites for a given amount of coral cover. Solid lines represent predictions colored by site using the negative binomial distribution and the formula  $y \sim x + \text{site}$ , where  $y$  is sponge richness,  $x$  is coral cover, and site is a categorical predictor. The formula  $y \sim x + \text{year} + \text{site}$ , 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.

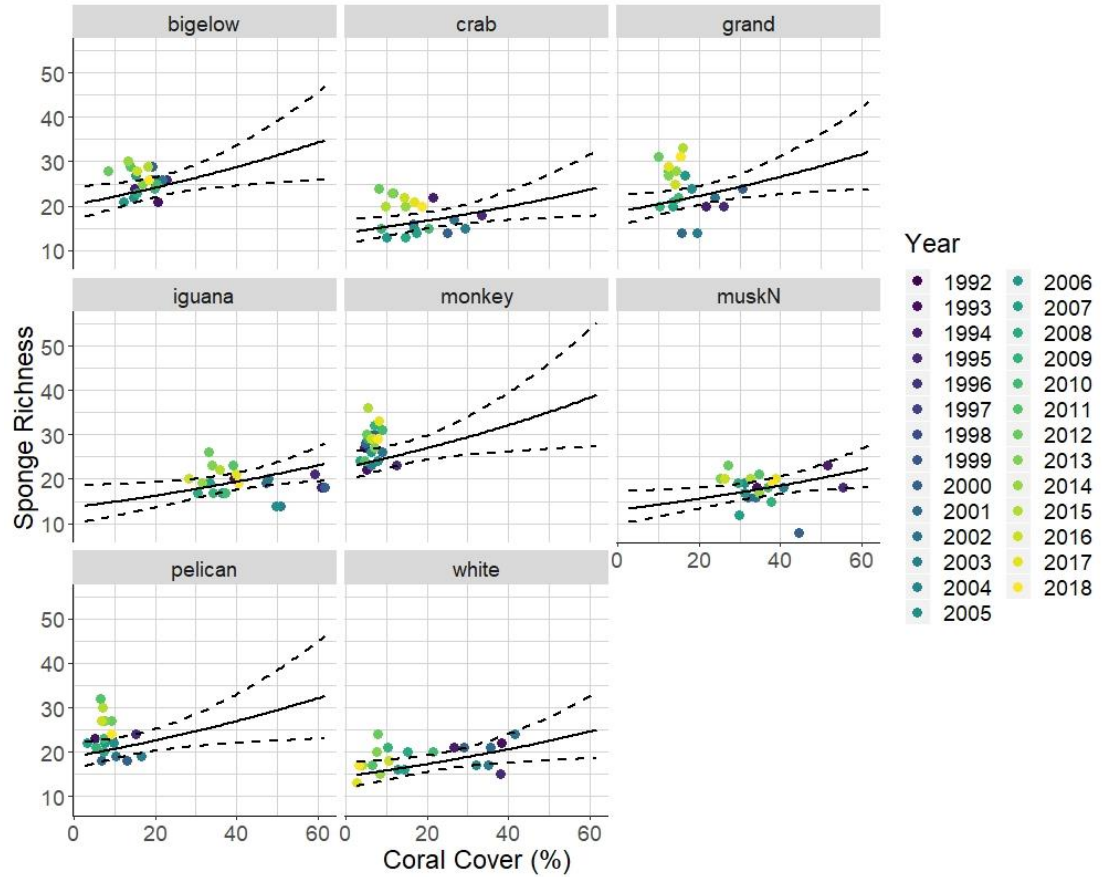


Figure 6. The most competitive model for predicting sponge richness included terms for year and site. Each panel represents one of 8 coral reefs around Guana Island, BVI. Solid lines represent predictions using the negative binomial distribution and the formula  $y \sim x + \text{year} + \text{site}$ , 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.

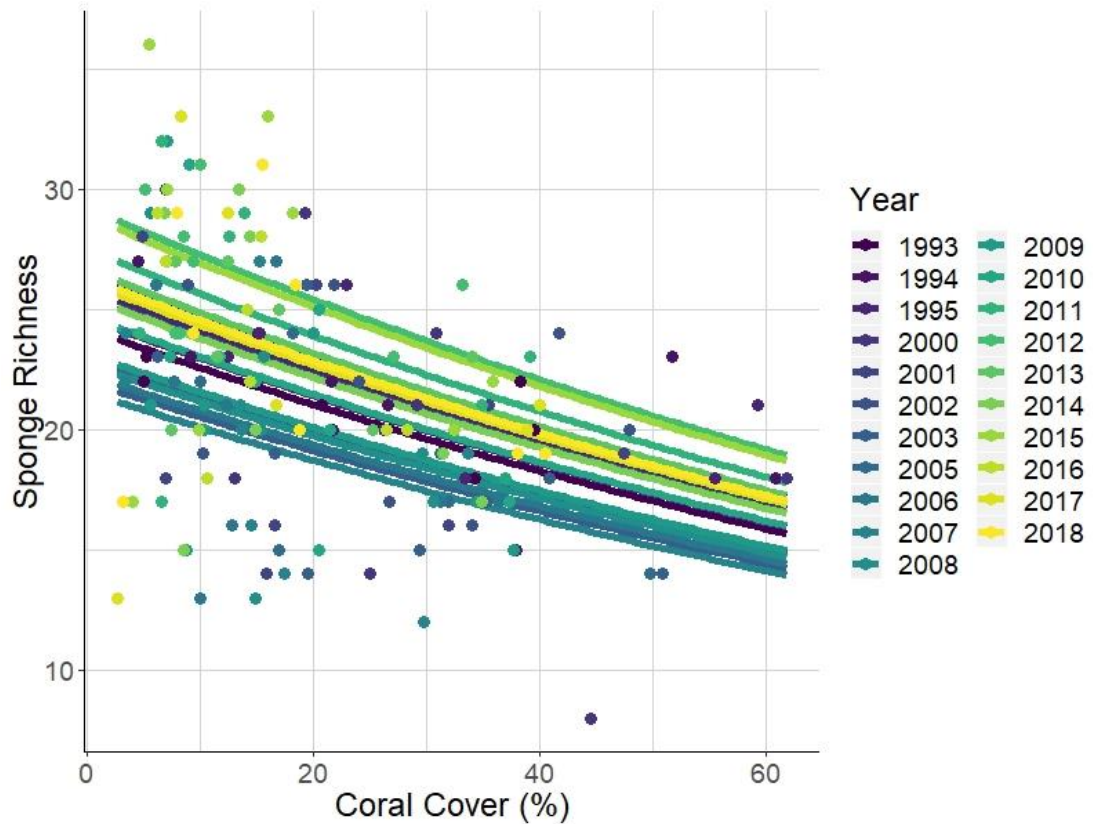


Figure 7. This figure helps to visualize changes in sponge richness for a given amount of coral cover over a 27 year period. Solid lines represent predictions colored by year using the negative binomial distribution and the formula  $y \sim x + \text{year}$ , where  $y$  is sponge richness,  $x$  is coral cover, and year is a categorical predictor. The formula  $y \sim x + \text{year} + \text{site}$ , 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.

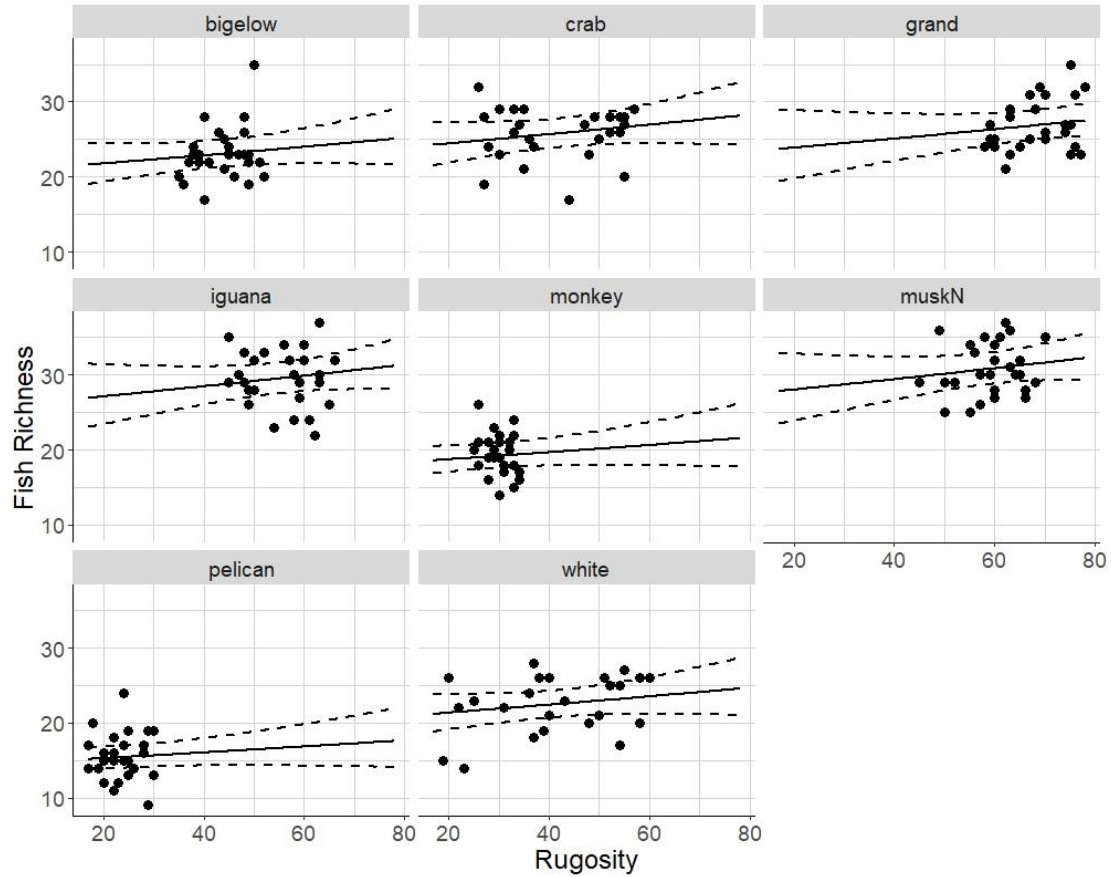


Figure 8. The most competitive model for predicting fish richness included a term for site. Each panel represents one of 8 coral reefs around Guana Island, BVI. Solid lines represent predictions using the negative binomial distribution and the formula  $y \sim x + \text{site}$ , where  $y$  is fish richness,  $x$  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.

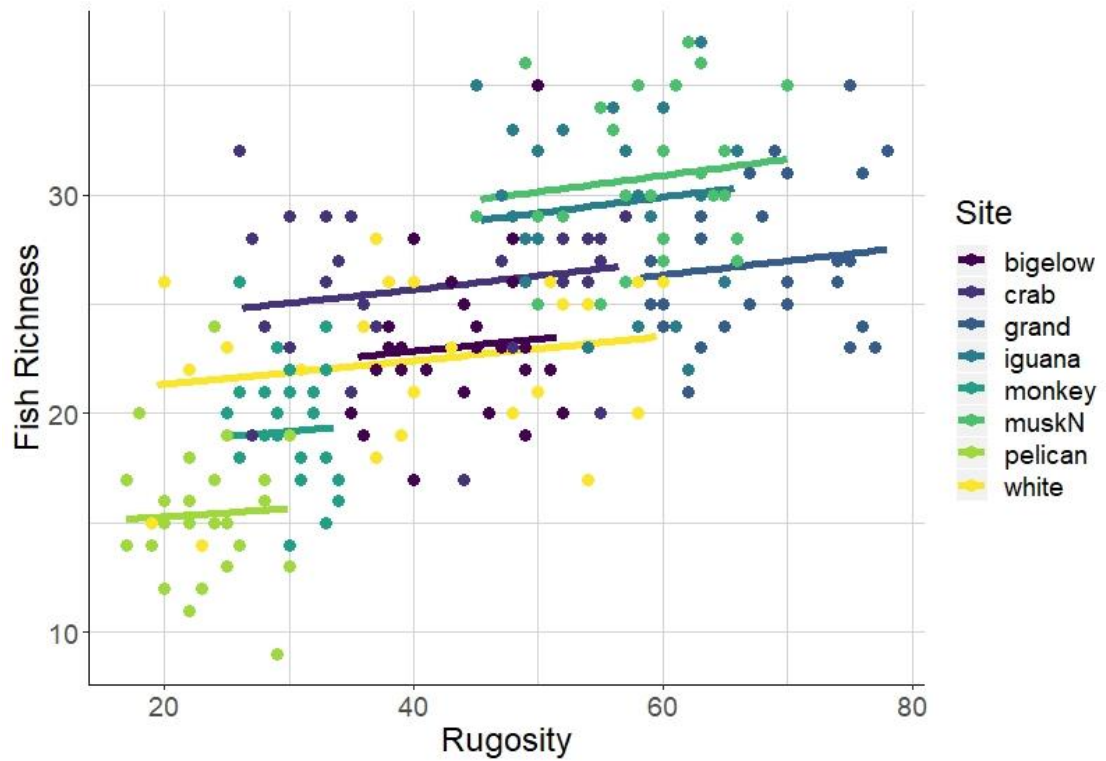


Figure 9. This figure helps to visualize differences in fish richness for a given amount of rugosity among 8 coral reefs around Guana Island, BVI. Solid lines represent predictions colored by site using the negative binomial distribution and the formula  $y \sim x + \text{site}$ , where  $y$  is fish 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  $y \sim x + \text{site}$  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.



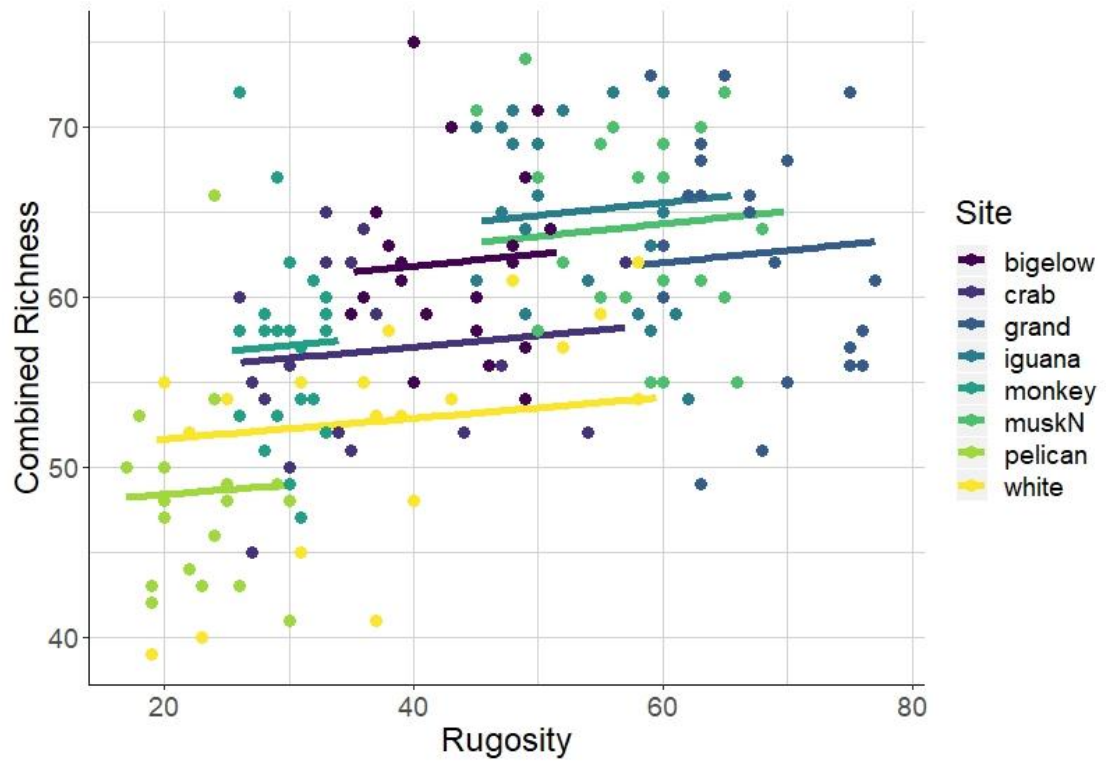


Figure 10. This figure helps to visualize differences in combined richness (the sum of coral, fish, and sponge richness) for a given amount of rugosity among 8 coral reefs around Guana Island, BVI. Solid lines represent predictions colored by site using the negative binomial distribution and the formula  $y \sim x + \text{site}$ , 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  $y \sim x + \text{year} + \text{site}$ , 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.



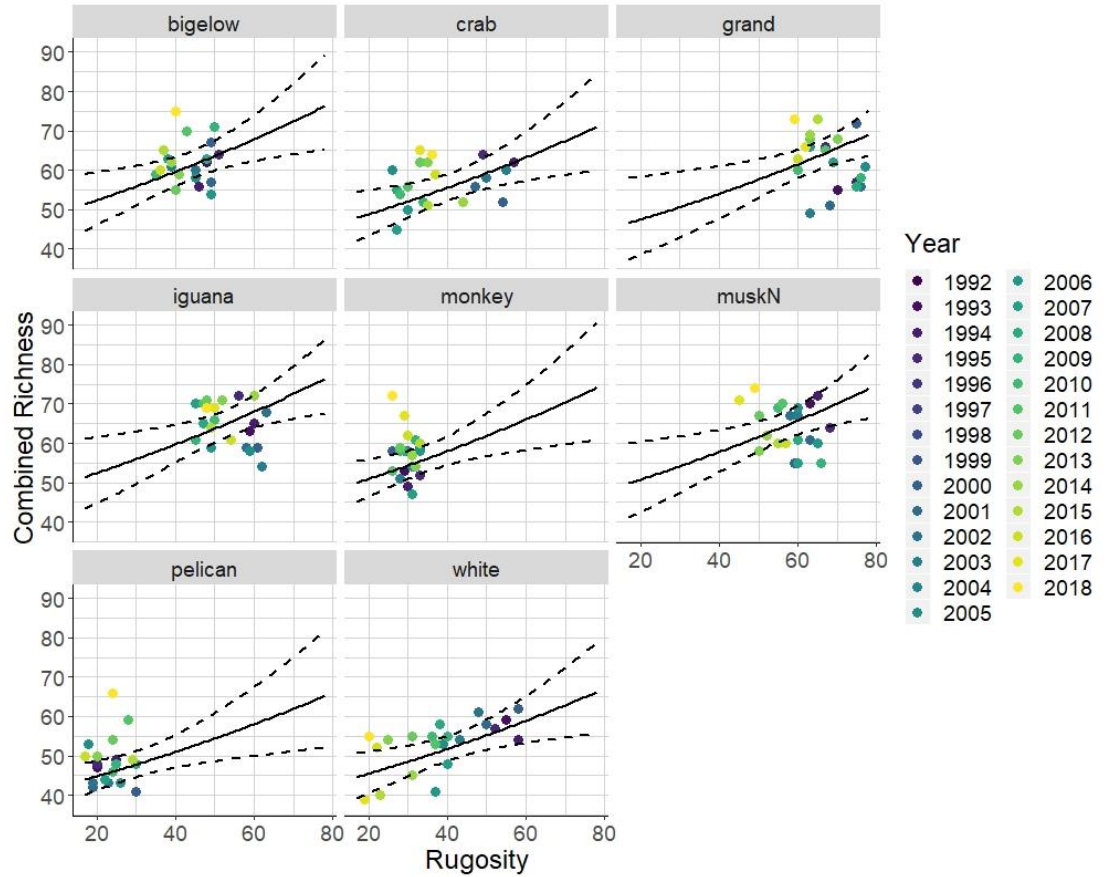


Figure 11. The most competitive model for predicting combined richness (the sum of coral, fish, and sponge richness) included terms for year and site. Each panel represents one of 8 coral reefs around Guana Island, BVI. Solid lines represent predictions using the negative binomial distribution and the formula  $y \sim x + \text{year} + \text{site}$ , 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.

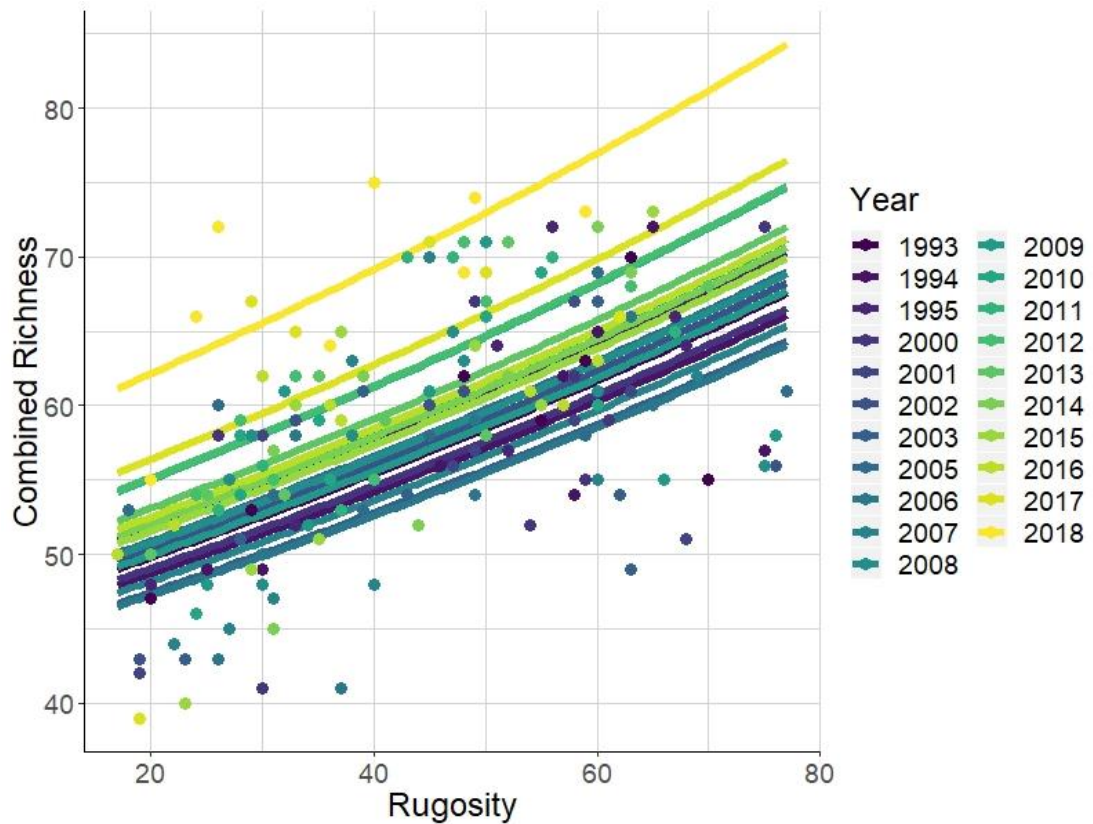


Figure 12. This figure helps to visualize changes in combined richness (the sum of coral, fish, and sponge richness) for a given amount of rugosity over a 27 year period. Solid lines represent predictions colored by year using the negative binomial distribution and the formula  $y \sim x + \text{year}$ , where  $y$  is combined richness,  $x$  is rugosity in cm, and year is a categorical predictor. The formula  $y \sim x + \text{year} + \text{site}$ , 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.
<i>Abudefduf saxatilis</i>	Sergeant major	<i>Hypoplectrus chlorurus</i>	yellowtail hamlet
<i>Acanthurus bahianus</i>	ocean surgeon	<i>Hypoplectrus guttavarius</i>	shy hamlet
<i>Acanthurus chirurgus</i>	doctorfish	<i>Hypoplectrus indigo</i>	indigo hamlet
<i>Acanthurus coeruleus</i>	blue tang	<i>Hypoplectrus nigricans</i>	black hamlet
<i>Aluterus scriptus</i>	scrawled filefish	<i>Hypoplectrus puella</i>	barred hamlet
<i>Amblycirrhitis pinos</i>	redspotted hawkfish	<i>Hypoplectrus sp.</i>	tan hamlet
<i>Anisotremus surinamensis</i>	black margate	<i>Hypoplectrus unicolor</i>	butter hamlet
<i>Anisotremus virginicus</i>	porkfish	<i>Inermia vittata</i>	boga
<i>Aulostomus maculatus</i>	trumpetfish	<i>Kyphosus sectatrix</i>	gray chub
<i>Balistes caprisicus</i>	gray triggerfish	<i>Lachnolaimus maximus</i>	hogfish
<i>Balistes vetula</i>	queen triggerfish	<i>Lactophrys bicaudalis</i>	spotted trunkfish
<i>Bodianus rufus</i>	Spanish hogfish	<i>Lactophrys quadricornis</i>	scrawled cowfish
<i>Calamus calamus</i>	saucereye porgy	<i>Lactophrys triqueter</i>	smooth trunkfish
<i>Calamus pennatula</i>	pluma porgy	<i>Lutjanus apodus</i>	schoolmaster snapper
<i>Cantherhines macrocerus</i>	whitespotted filefish	<i>Lutjanus griseus</i>	gray snapper
<i>Cantherhines pullus</i>	orangespotted filefish	<i>Lutjanus jocu</i>	dog snapper
<i>Canthigaster rostrata</i>	sharp-nose puffer fish	<i>Lutjanus mahogoni</i>	mahogany snapper
<i>Centropyge argi</i>	cherubfish	<i>Lutjanus synagris</i>	lane snapper
<i>Chaetodipterus faber</i>	Atlantic spadefish	<i>Melichthys niger</i>	black durgon
<i>Chaetodon ocellatus</i>	spotfin butterflyfish	<i>Microspathodon chrysurus</i>	yellowtail damselfish
<i>Chaetodon sedentarius</i>	reef butterflyfish	<i>Monacanthus ciliatus</i>	fringed filefish
<i>Chaetodon striatus</i>	banded butterflyfish	<i>Monacanthus tuckeri</i>	slender filefish
<i>Chaetodon capistratus</i>	four-eye butterflyfish	<i>Mulloidichthys martinicus</i>	yellow goatfish
<i>Chromis cyanea</i>	blue chromis	<i>Mycteroperca tigris</i>	tiger grouper
<i>Chromis insolata</i>	sunshinefish	<i>Mycteroperca venenosa</i>	yellowfin grouper
<i>Chromis multilineata</i>	brown chromis	<i>Nicholsina usta</i>	emerald parrotfish
<i>Clepticus parrae</i>	creole wrasse	<i>Ocyurus chrysurus</i>	yellowtail snapper
<i>Cryptotomus roseus</i>	bluelip parrotfish	<i>Odontoscion dentex</i>	reef croaker
<i>Diodon hystrix</i>	porcupinefish	<i>Pomacanthus arcuatus</i>	gray angelfish
<i>Epinephelus adscensionis</i>	rock hind	<i>Pomacanthus paru</i>	French angelfish
<i>Epinephelus guttatus</i>	red hind	<i>Pomacentrus dieneae</i>	longfin damselfish
<i>Epinephelus cruentatus</i>	graysby	<i>Pomacentrus leucostictus</i>	beaugregory
<i>Epinephelus fulva</i>	coney	<i>Pomacentrus variabilis</i>	cocoa damselfish
<i>Epinephelus striatus</i>	Nassau grouper	<i>Pomacentrus fuscus</i>	dusky damselfish
<i>Equetus acuminatus</i>	high-hat	<i>Pomacentrus partitus</i>	bicolor damselfish
<i>Equetus lanceolatus</i>	jackknife fish	<i>Pomacentrus planifrons</i>	threespot damselfish
<i>Equetus punctatus</i>	spotted drum	<i>Pseudupeneus maculatus</i>	spotted goatfish
<i>Gerres cinereus</i>	yellowfin mojarra	<i>Pterois volitans</i>	lionfish
<i>Gramma loreto</i>	fairy basslet	<i>Scarus coeruleus</i>	blue parrotfish
<i>Haemulon aurolineatum</i>	tomtate grunt	<i>Scarus croicensis</i>	striped parrotfish
<i>Haemulon carbonarium</i>	Caesar grunt	<i>Scarus guacamaia</i>	rainbow parrotfish
<i>Haemulon chrysargyreum</i>	smallmouth grunt	<i>Scarus taeniopterus</i>	princess parrotfish
<i>Haemulon flavolineatum</i>	French grunt	<i>Scarus vetula</i>	queen parrotfish
<i>Haemulon macrostomum</i>	Spanish grunt	<i>Serranus baldwini</i>	lantern bass
<i>Haemulon melanurum</i>	cottonwick grunt	<i>Serranus tabacarius</i>	tobacco fish
<i>Haemulon plumieri</i>	white grunt	<i>Serranus tigrinus</i>	harlequin bass
<i>Haemulon sciurus</i>	blue striped grunt	<i>Serranus tortugarum</i>	chalk bass
<i>Haemulon sp. unidentified</i>	unidentified grunt	<i>Sparisoma atomarium</i>	greenblotch parrotfish
<i>Haemulon striatum</i>	striped grunt	<i>Sparisoma aurofrenatum</i>	redband parrotfish
<i>Halichoeres bivittatus</i>	slippery dick	<i>Sparisoma chrysopteron</i>	redtail parrotfish
<i>Halichoeres cyanocephalus</i>	yellowcheek wrasse	<i>Sparisoma radians</i>	bucktooth parrotfish
<i>Halichoeres garnoti</i>	yellowhead wrasse	<i>Sparisoma rubripinne</i>	yellowtail parrotfish
<i>Halichoeres maculipinna</i>	clown wrasse	<i>Sparisoma viride</i>	stoplight parrotfish
<i>Halichoeres pictus</i>	rainbow wrasse	<i>Sphoeroides dorsalis</i>	marbled puffer
<i>Halichoeres poeyi</i>	blackear wrasse	<i>Sphoeroides spengleri</i>	bandtail puffer
<i>Halichoeres radiatus</i>	puddingwife	<i>Synodus intermedius</i>	sand diver
<i>Holacanthus ciliaris</i>	queen angelfish	<i>Synodus saurus</i>	bluestripe lizardfish
<i>Holacanthus tricolor</i>	rock beauty	<i>Synodus synodus</i>	red lizardfish
		<i>Thalassoma bifasciatum</i>	bluehead wrasse

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

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

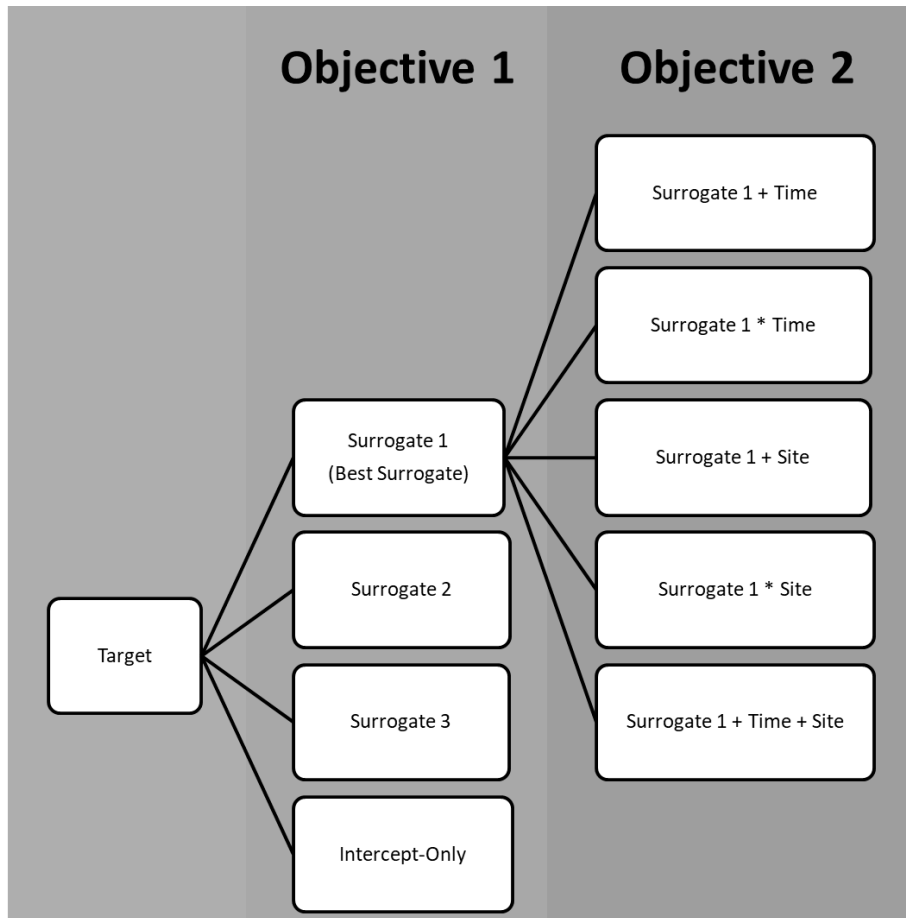


Figure A.3. Conceptual flow diagram of model sets for addressing objectives 1

(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.

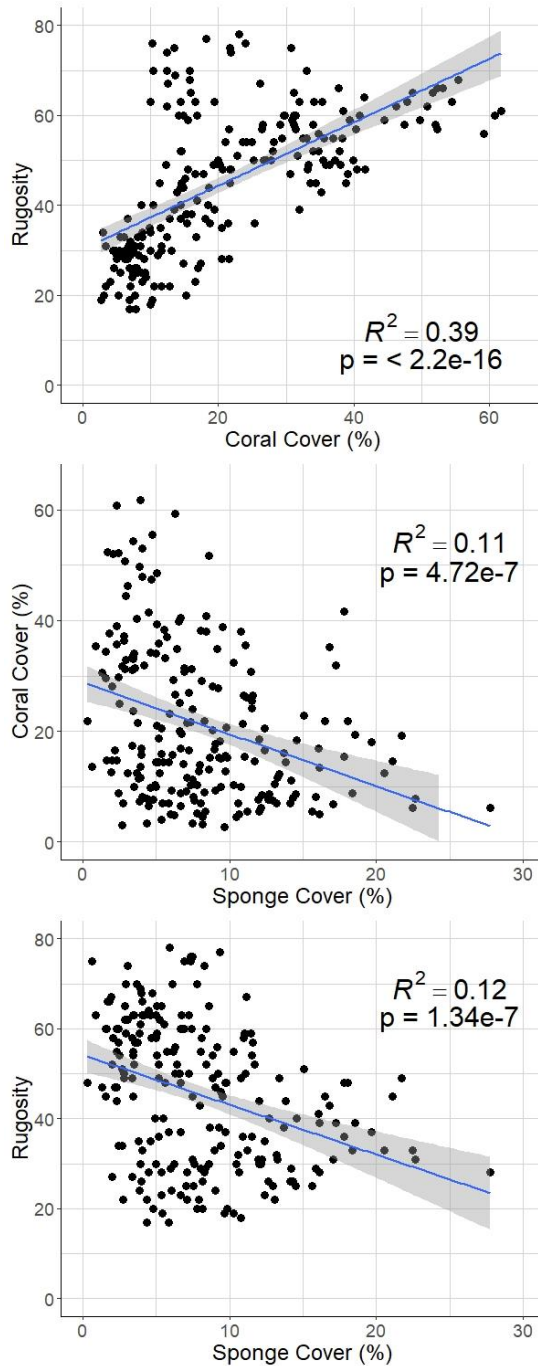


Figure A.4. Basic associations between the surrogates. Lines represent smoothed conditional means using a generalized linear model and the formula  $y \sim x$ . Shaded portions represent 95% confidence intervals of fitted values. Traditional r-squared ( $R^2$ ) and p-values are shown. Rugosity measured 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



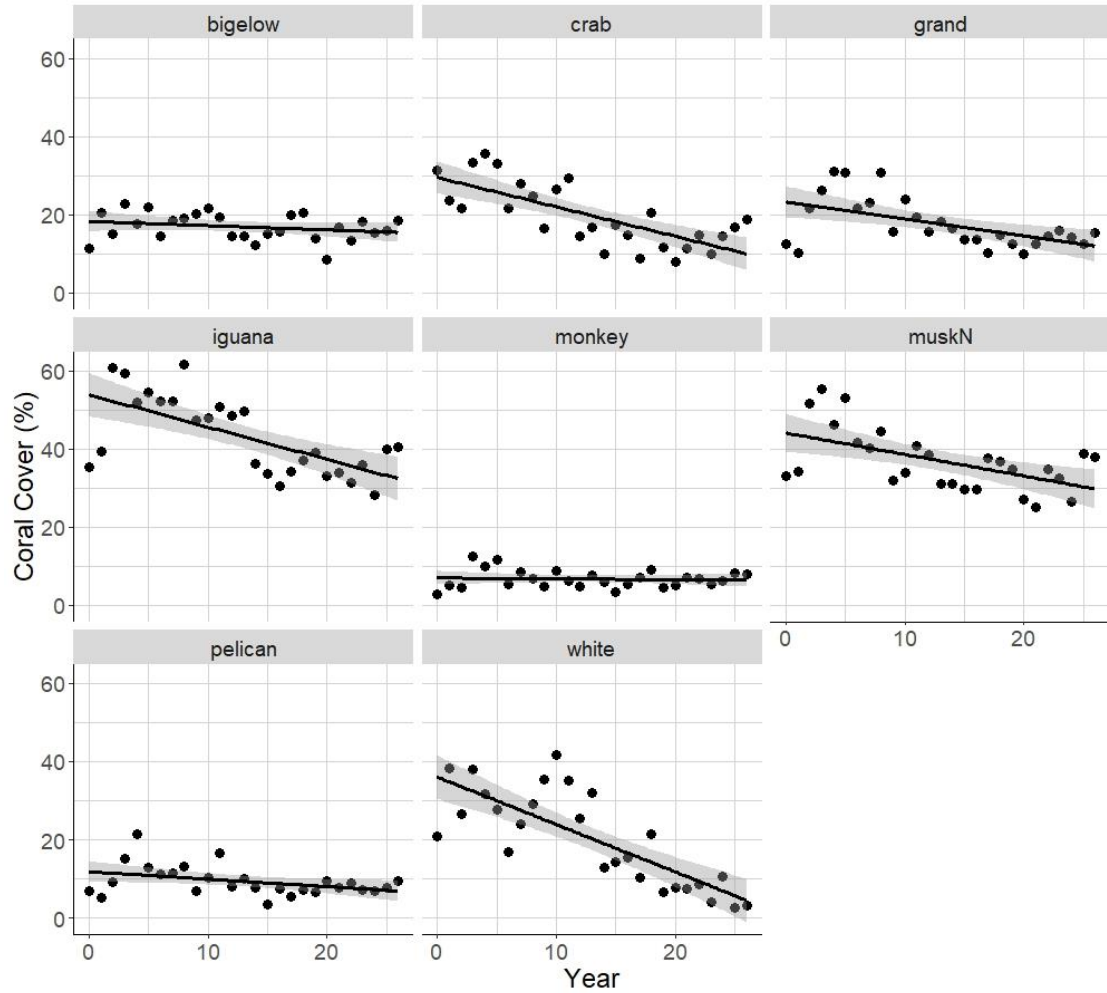


Figure A.6. Percent coral cover over the 27 year study period from 1992-2018, where year 0 is 1992. Each panel represents one of 8 coral reefs around Guana Island, BVI. Solid line represents smoothed conditional means using a generalized linear model and the formula  $y \sim x$ , where  $x$  is year as a trend. Shaded portions represent 95% confidence intervals of fitted values.

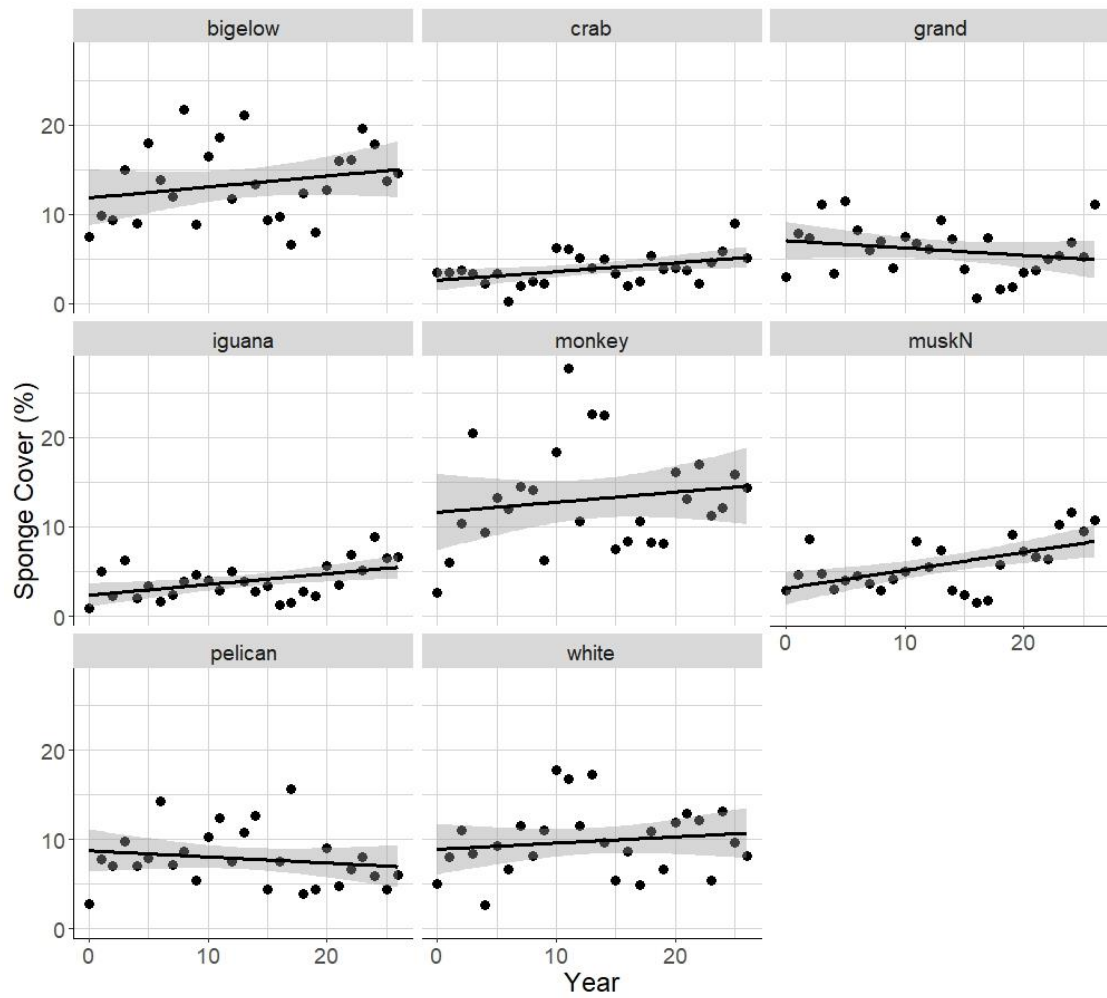


Figure A.7. Percent sponge cover over the 27 year study period from 1992-2018, where year 0 is 1992. Each panel represents one of 8 coral reefs around Guana Island, BVI. Solid line represents smoothed conditional means using a generalized linear model and the formula  $y \sim x$ , where  $x$  is year as a trend. Shaded portions represent 95% confidence intervals of fitted values.

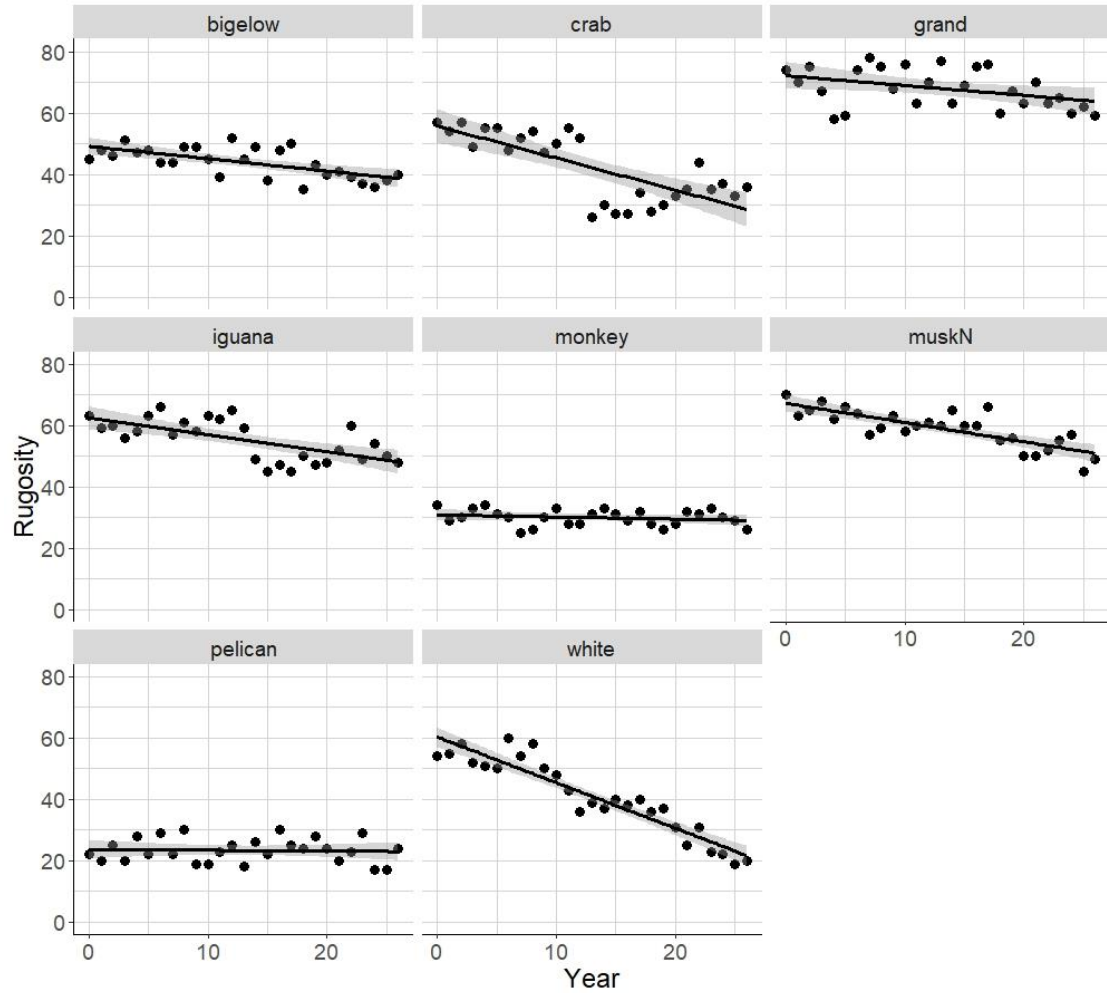


Figure A.8. Rugosity (in cm) over the 27 year study period from 1992-2018, where year 0 is 1992. Each panel represents one of 8 coral reefs around Guana Island, BVI. Solid line represents smoothed conditional means using a generalized linear model and the formula  $y \sim x$ , where  $x$  is year as a trend. Shaded portions represent 95% confidence intervals of fitted values.

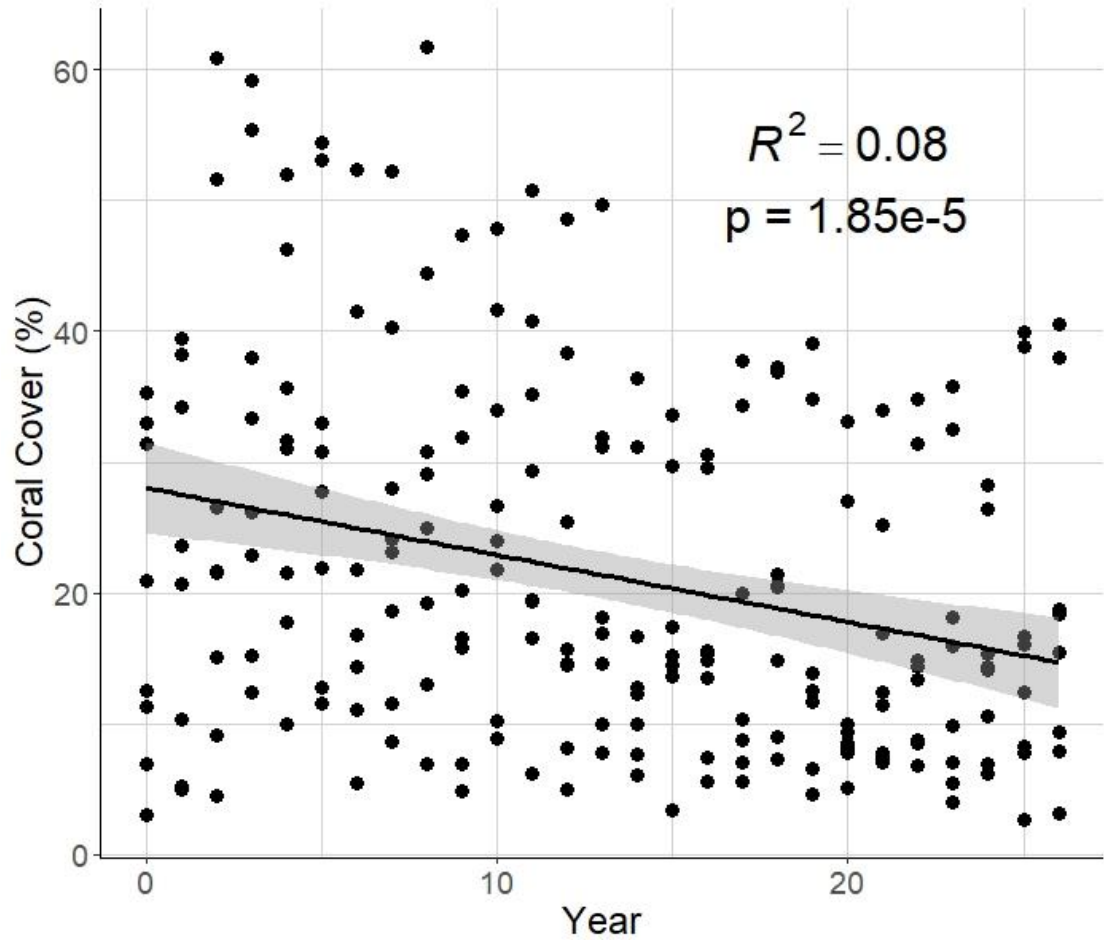


Figure A.9. Percent coral cover over the 27 year study period from 1992-2018, where year 0 is 1992. Solid line represents smoothed conditional means using a generalized linear model and the formula  $y \sim x$ , where  $x$  is year as a trend. Shaded portions represent 95% confidence intervals of fitted values. Traditional r-squared ( $R^2$ ) and p-values are shown. Data were collected from 8 coral reefs around Guana Island, BVI.

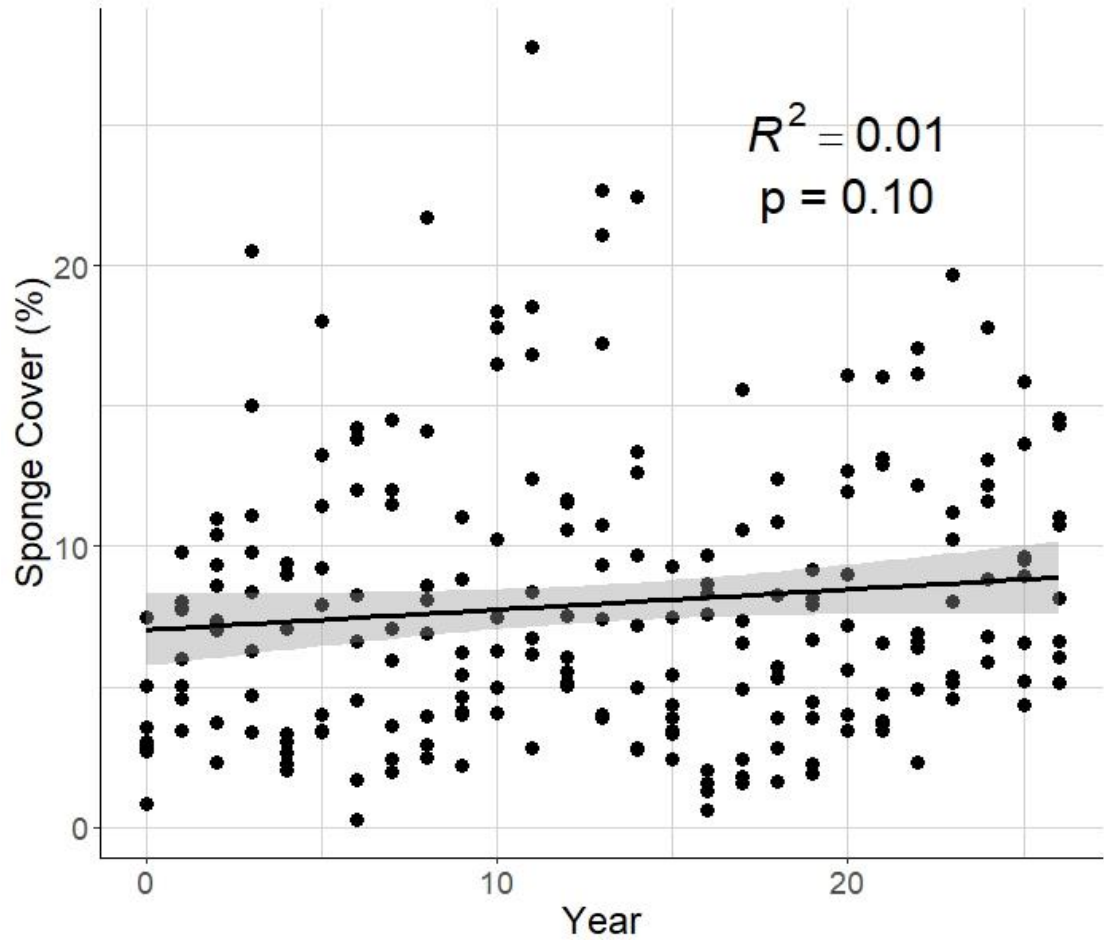


Figure A.10. Percent sponge cover over the 27 year study period from 1992-2018, where year 0 is 1992. Solid line represents smoothed conditional means using a generalized linear model and the formula  $y \sim x$ , where  $x$  is year as a trend. Shaded portions represent 95% confidence intervals of fitted values. Traditional r-squared ( $R^2$ ) and p-values are shown. Data were collected from 8 coral reefs around Guana Island, BVI.

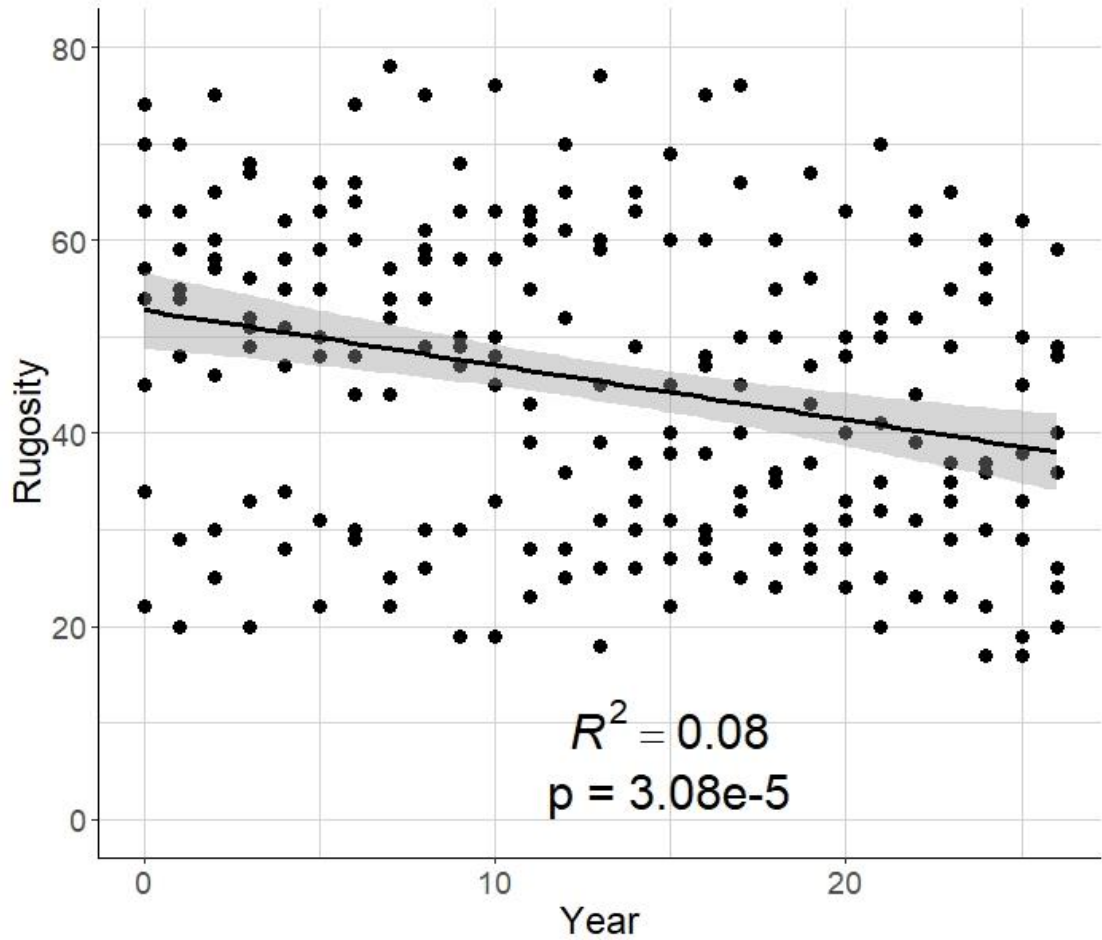


Figure A.11. Rugosity (in cm) over the 27 year study period from 1992-2018, where year 0 is 1992. Solid line represents smoothed conditional means using a generalized linear model and the formula  $y \sim x$ , where  $x$  is year as a trend. Shaded portions represent 95% confidence intervals of fitted values. Traditional r-squared ( $R^2$ ) and p-values are shown. Data were collected from 8 coral reefs around Guana Island, BVI.

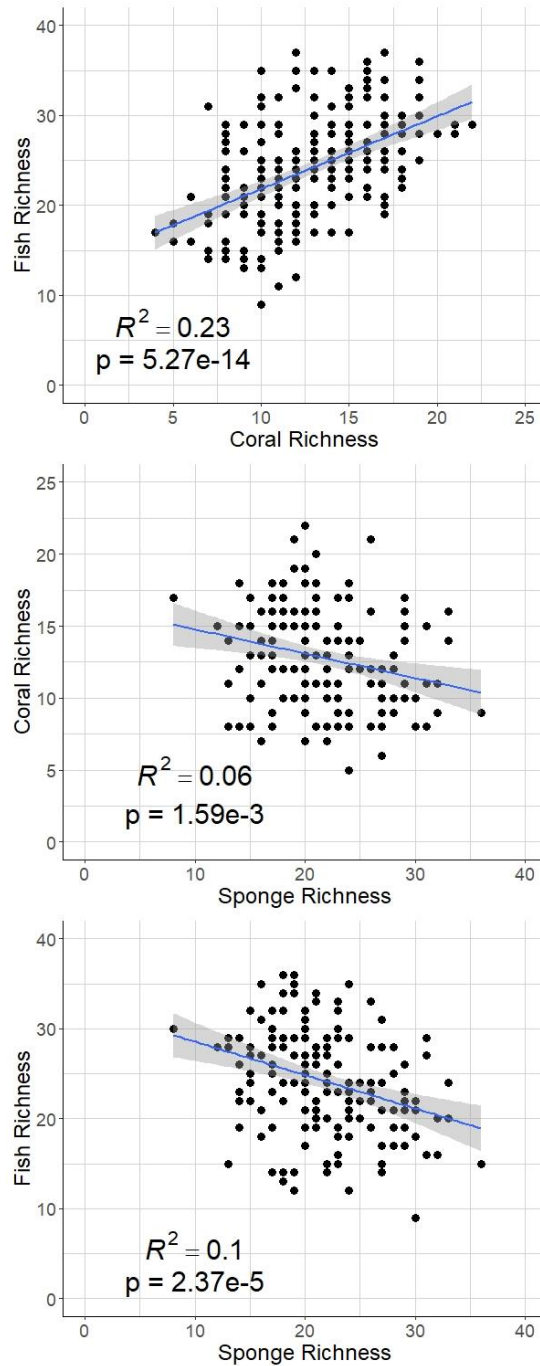


Figure A.12. Basic associations between the targets. Lines represent smoothed conditional means using a generalized linear model and the formula  $y \sim x$ . Shaded portions represent 95% confidence intervals of fitted values. Traditional r-squared ( $R^2$ ) and p-values are shown. Data were collected from 8 coral reefs around Guana Island, BVI from 1992-2018.

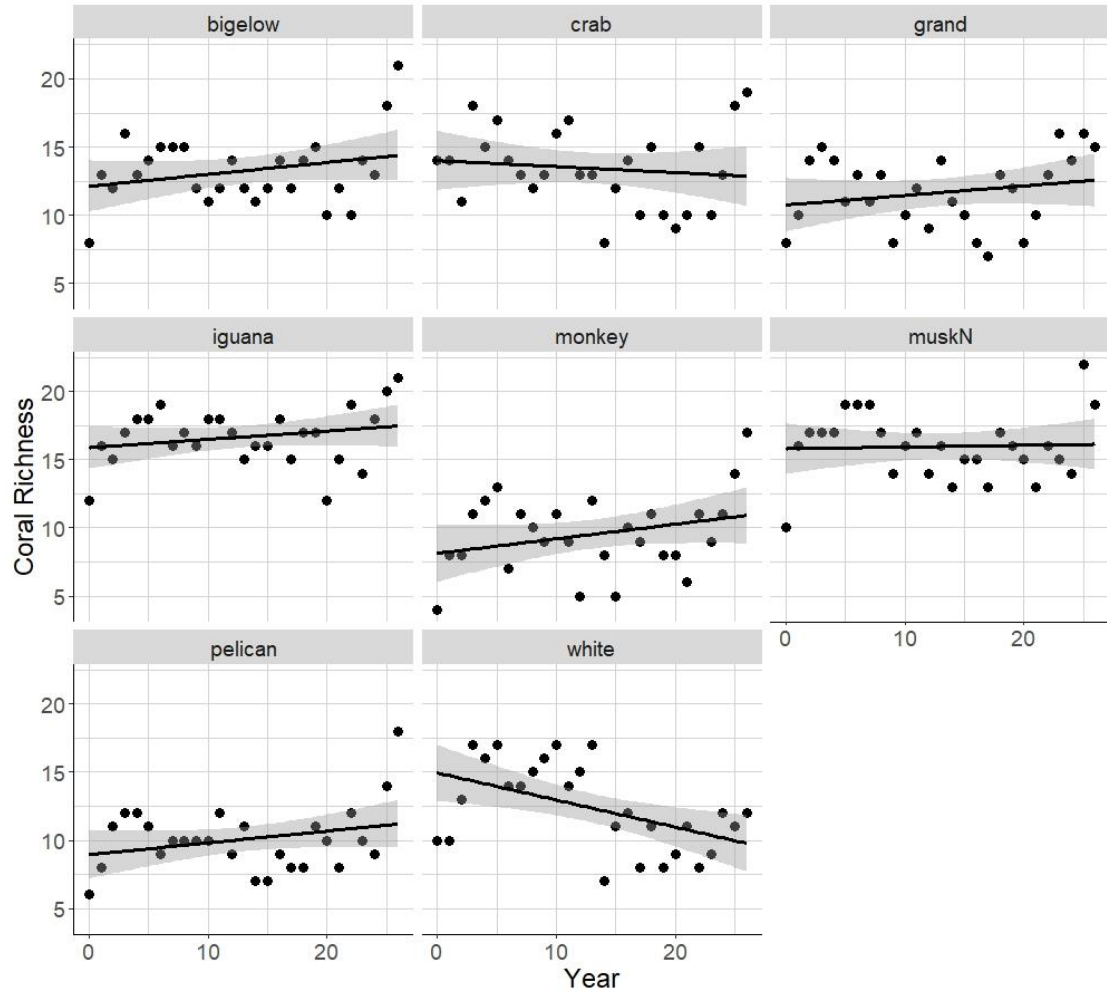


Figure A.13. Coral richness over the 27 year study period from 1992-2018, where year 0 is 1992. Each panel represents one of 8 coral reefs around Guana Island, BVI. Solid line represents smoothed conditional means using a generalized linear model and the formula  $y \sim x$ , where  $x$  is year as a trend. Shaded portions represent 95% confidence intervals of fitted values.



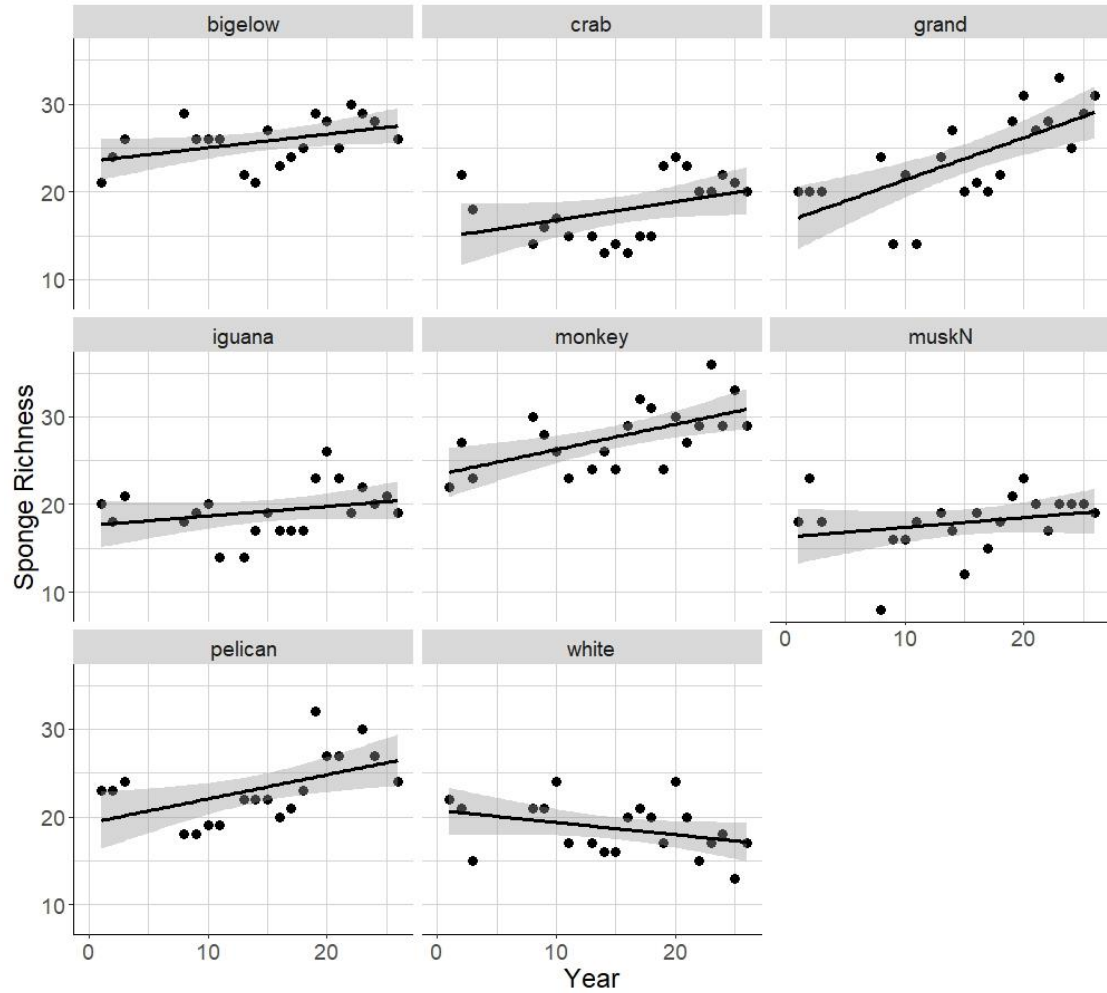


Figure A.14. Sponge richness over the 27 year study period from 1992-2018, where year 0 is 1992. Each panel represents one of 8 coral reefs around Guana Island, BVI. Solid line represents smoothed conditional means using a generalized linear model and the formula  $y \sim x$ , where  $x$  is year as a trend. Shaded portions represent 95% confidence intervals of fitted values.

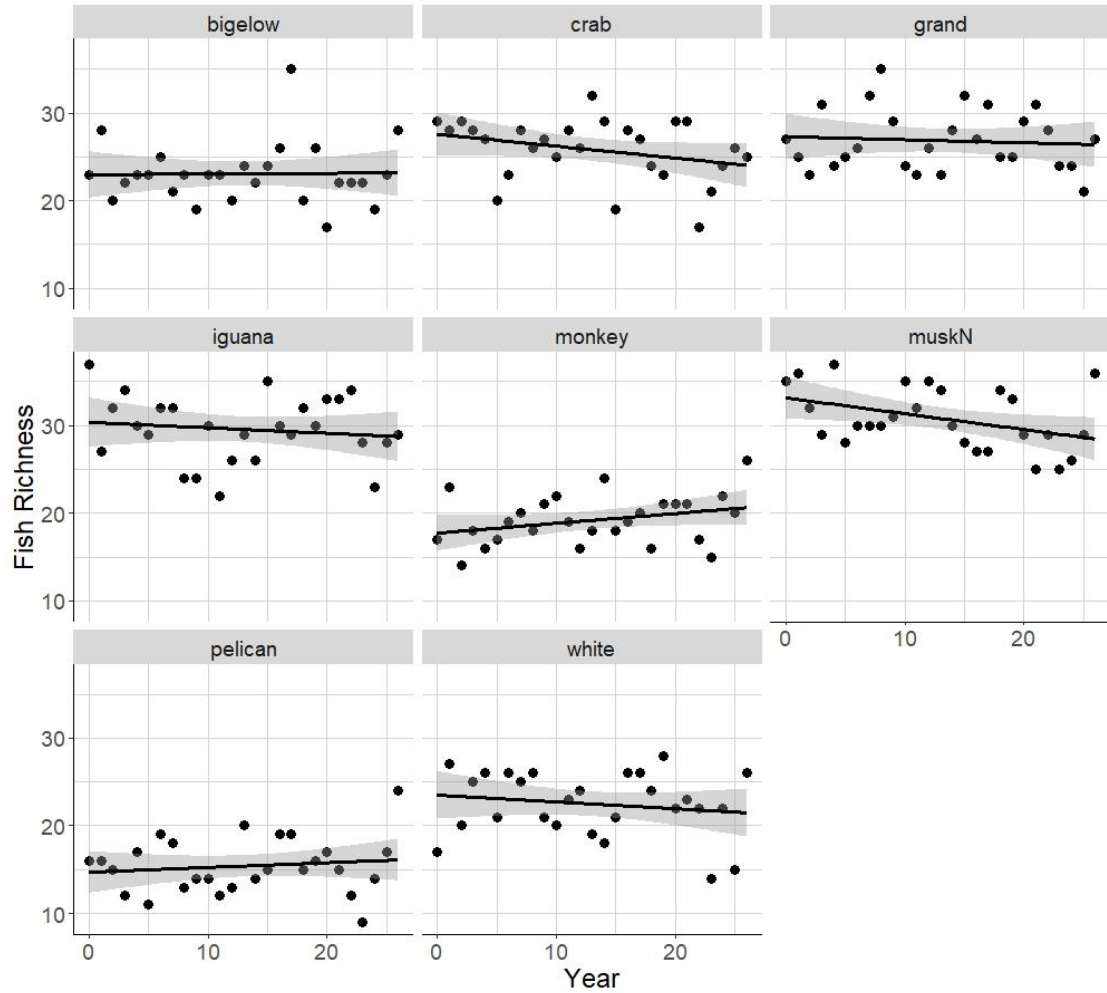


Figure A.15. Fish richness over the 27 year study period from 1992-2018, where year 0 is 1992. Each panel represents one of 8 coral reefs around Guana Island, BVI. Solid line represents smoothed conditional means using a generalized linear model and the formula  $y \sim x$ , where  $x$  is year as a trend. Shaded portions represent 95% confidence intervals of fitted values.

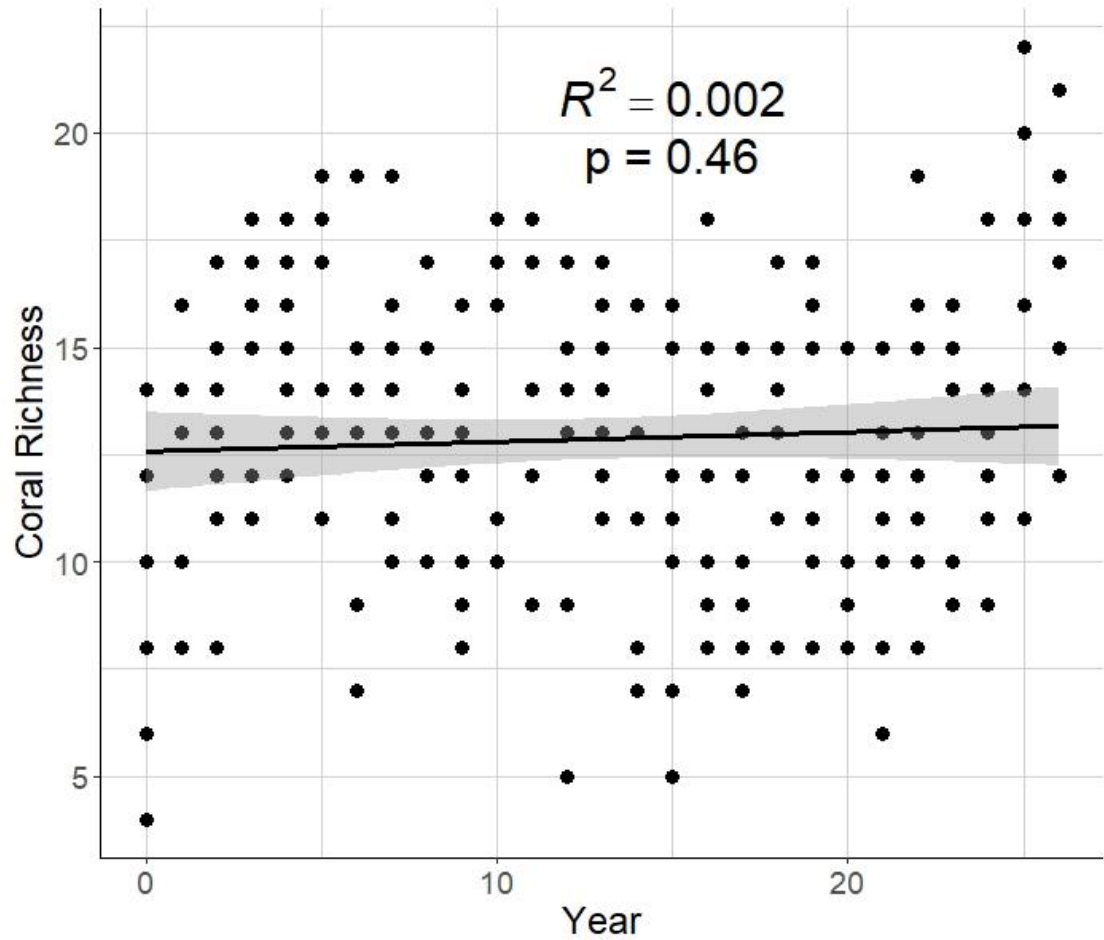


Figure A.16. Coral richness over the 27 year study period from 1992-2018, where year 0 is 1992. Solid line represents smoothed conditional means using a generalized linear model and the formula  $y \sim x$ , where  $x$  is year as a trend. Shaded portions represent 95% confidence intervals of fitted values. Traditional r-squared ( $R^2$ ) and p-values are shown. Data were collected from 8 coral reefs around Guana Island, BVI.

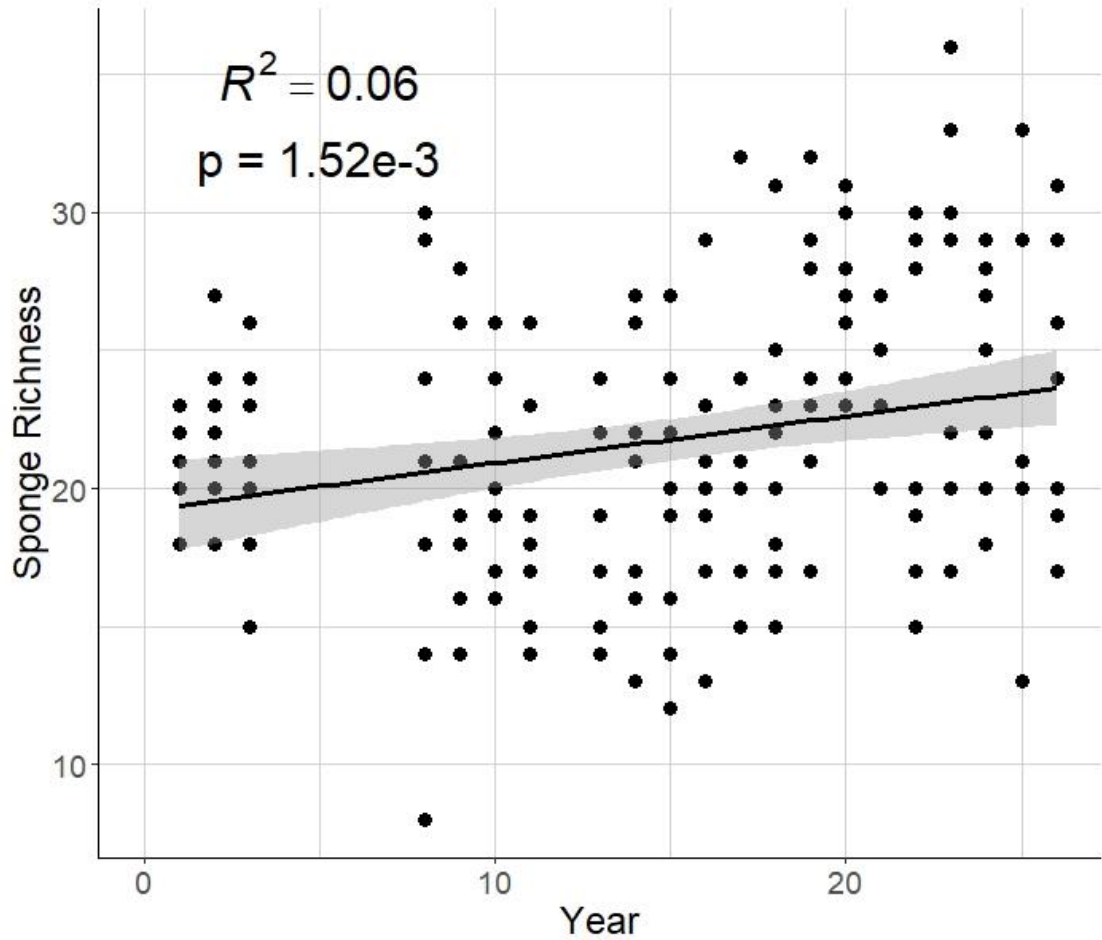


Figure A.17. Sponge richness over the 27 year study period from 1992-2018, where year 0 is 1992. Solid line represents smoothed conditional means using a generalized linear model and the formula  $y \sim x$ , where  $x$  is year as a trend. Shaded portions represent 95% confidence intervals of fitted values. Traditional r-squared ( $R^2$ ) and p-values are shown. Data were collected from 8 coral reefs around Guana Island, BVI.

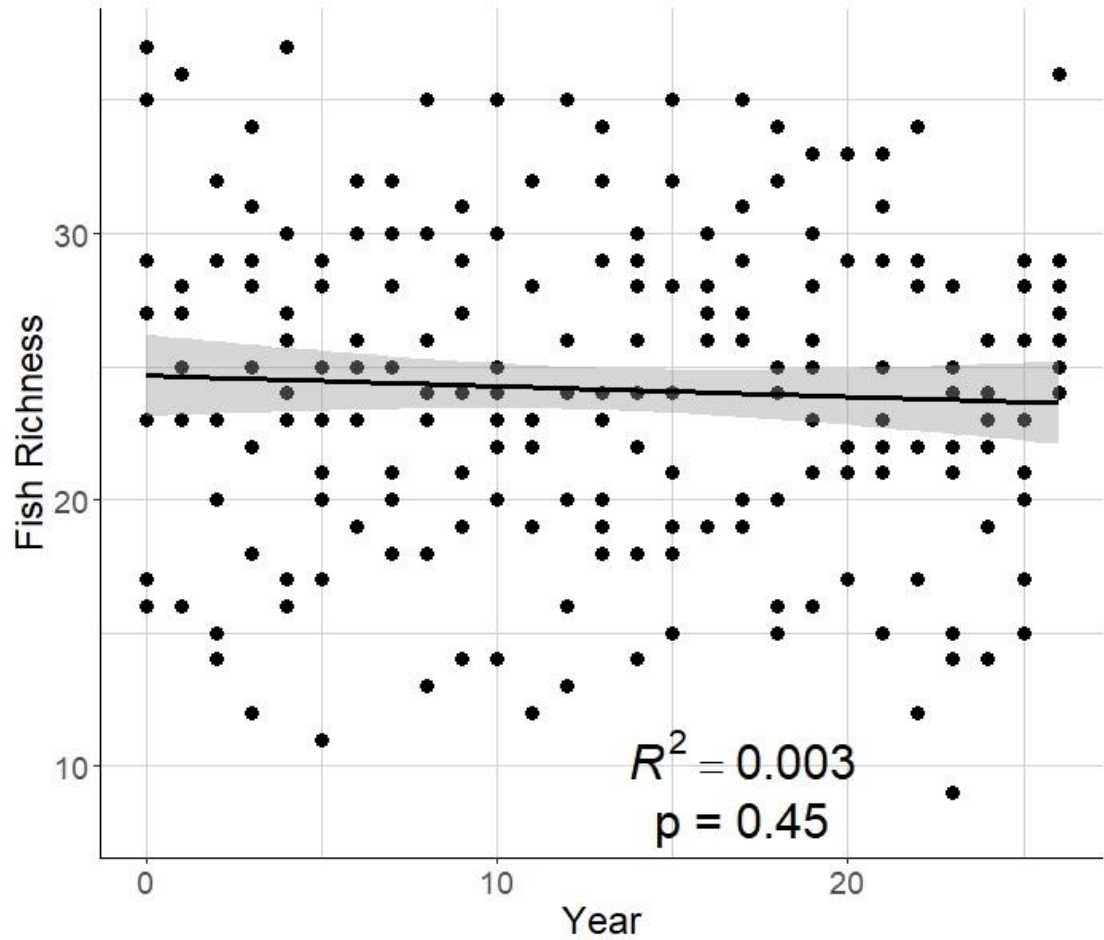


Figure A.18. Fish richness over the 27 year study period from 1992-2018, where year 0 is 1992. Solid line represents smoothed conditional means using a generalized linear model and the formula  $y \sim x$ , where  $x$  is year as a trend. Shaded portions represent 95% confidence intervals of fitted values. 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  $y \sim x + \text{year}$ , 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 ***

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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  $y \sim x + \text{year} + x * \text{year}$ , 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  $y \sim x + \text{year} + \text{site}$ , 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 ***

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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  $y \sim x + \text{site}$ , 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

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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  $y \sim x + \text{year} + \text{site}$ , 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 ***

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

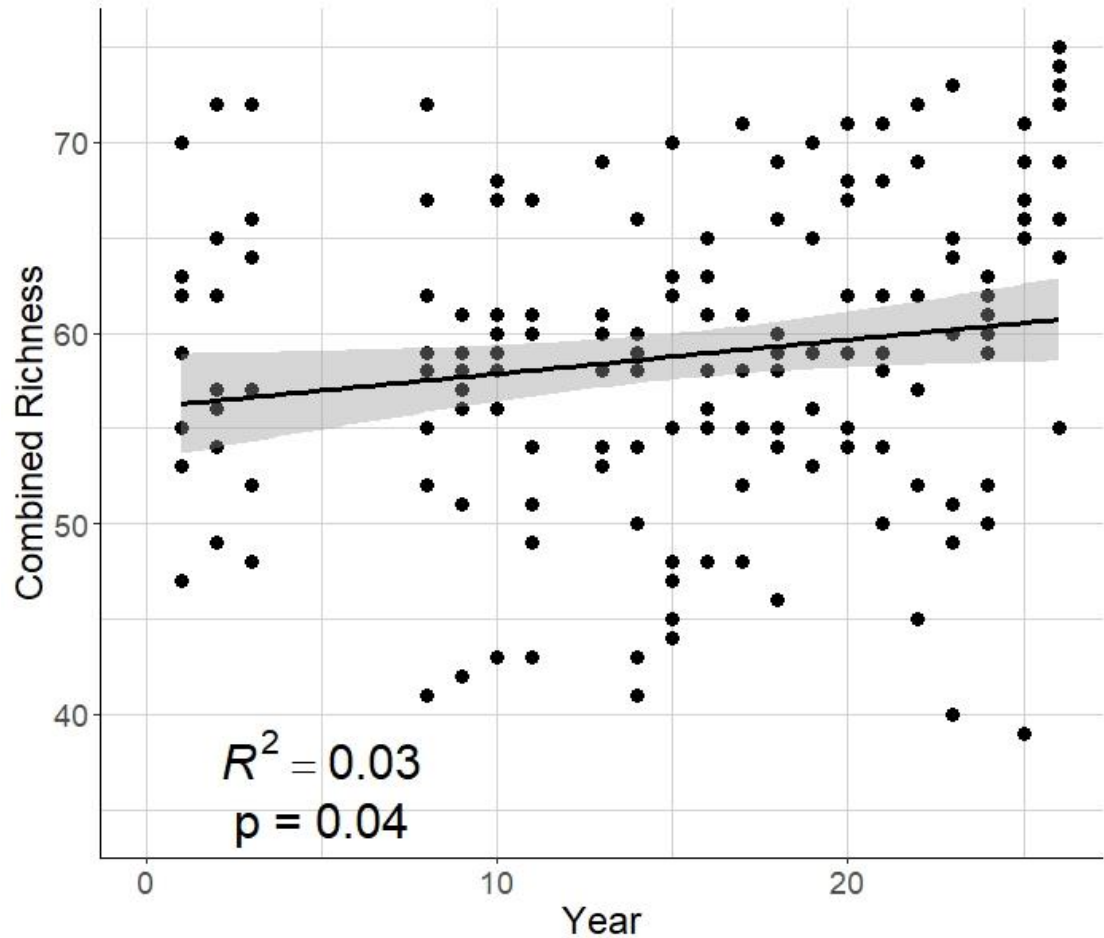


Figure A.24. Combined richness (the sum of coral, fish, and sponge richness) over the 27 year study period from 1992-2018, where year 0 is 1992. Solid line represents smoothed conditional means using a generalized linear model and the formula  $y \sim x$ , where  $x$  is year as a trend. Shaded portions 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