

Subtropical epibenthos varies with location, reef type, and grazing intensity

Kara R. Wall*, Christopher D. Stallings

College of Marine Science, University of South Florida, 140 7th Ave, St Petersburg, FL 33705, USA

ARTICLE INFO

Keywords:

West Florida Shelf
Coral
Warm temperate
Fouling
Habitat heterogeneity Settlement

ABSTRACT

Composition of marine epibenthic communities are influenced by both physical and biotic processes. For instance, the larval supply and cues that influence colonization (physical), as well as the growth and mortality of individuals (biotic), may differ across location and reef type. Determining the relative influence of these processes is important to understanding how epibenthic communities can develop in a region. Using both a partial caging experiment that controlled grazing by urchins and in situ photographic surveys of epibenthic communities, this study examined the relationship between urchin grazing and the composition of epibenthos on natural limestone and artificial reefs in the eastern Gulf of Mexico (eGOM). In the experiment, tiles that were open to urchin grazing had lower percent cover of algae (−12%) and higher cover of crustose coralline algae (CCA) (13%) than those that excluded urchins. Patterns in tile cover were likely the result of CCA either resisting grazing mortality or recolonizing exposed areas after algae were removed. Variation in colonization was observed between inshore and offshore reef groups. Urchin density was positively correlated with the structural complexity of the habitats, which was higher on artificial reefs than natural ones, a factor that potentially had important effects on several observed patterns. Results from photographic surveys indicated that natural reef communities had higher algal cover and lower cover of invertebrates (e.g., corals and hydroids) than artificial reefs. These findings were consistent with previous work conducted in both temperate and tropical ecosystems, and suggested that grazing from urchins plays an important role in shaping epibenthic community structure in the subtropical eGOM.

1. Introduction

The ecology of epibenthic communities has been a major focus of marine research for nearly 60 years (Connell, 1961; Stephenson and Searles, 1960). Much of this work has focused on understanding and disentangling the processes that influence epibenthic composition (Fraschetti et al., 2002; Hunt and Scheibling, 1997). Communities can be influenced by pre-colonization factors that dictate larval supply and settlement, such as proximity to spawning sources, reef type, chemical cues, sound, or depth (Dixson et al., 2014; Hughes et al., 1999; Pawlik, 1992; Rogers et al., 1984; Sammarco et al., 2012). After organisms colonize a reef, communities are further affected by organismal growth and mortality driven by a combination of competition and predation (Arnold et al., 2010; Bruno et al., 2008; Burkepile and Hay, 2006; Jenkins et al., 2008; Poore et al., 2012). Some factors, such as physical disturbances, extreme temperatures, and water quality can also influence communities both pre- and post-colonization (Hughes et al., 2003; Rice and Hunter, 1992; Walters and Wethey, 1996).

In both terrestrial and marine systems, mortality driven by grazing often plays an important role in organizing communities by removing

plant material, clearing space for new organisms, and increasing primary production by remineralizing nutrients to facilitate new growth (Adams Krumins et al., 2015; Box and Mumby, 2007; Paine, 1980; Ripple and Beschta, 2003; Valentine et al., 1997). When abundances of key herbivores shift, changes in grazing can dramatically alter a community (Estes et al., 2011). For example, overgrazing of temperate kelps by urchins can reduce structurally complex kelp forests to relatively flat barrens (Chapman, 1981; Estes and Duggins, 1995; Steneck et al., 2003), resulting in a reduced capacity to support kelp-associated fish and invertebrate fauna (Ebeling and Hixon, 1991; Holbrook et al., 1990; Norderhaug and Christie, 2009). Conversely, low densities of herbivorous urchins and fishes on tropical reefs can allow overgrowth by algae, which can outcompete corals (Carpenter, 1988; Chabanet et al., 1997; Lewis, 1986; Hughes, 1994; Sammarco, 1982; Tootell and Steele, 2016). The majority of marine epibenthic research has been conducted in temperate (esp. rocky intertidal) and tropical (esp. coral reef) ecosystems (Ebeling and Hixon, 1991; Poore et al., 2012). Far less efforts have been allocated to studying the role of grazing on epibenthic communities in subtropical regions.

The eastern Gulf of Mexico (eGOM) spans subtropical and warm-temperate latitudes. The region is characterized by a broad inner shelf

* Corresponding author.

E-mail address: krwall@usf.edu (K.R. Wall).

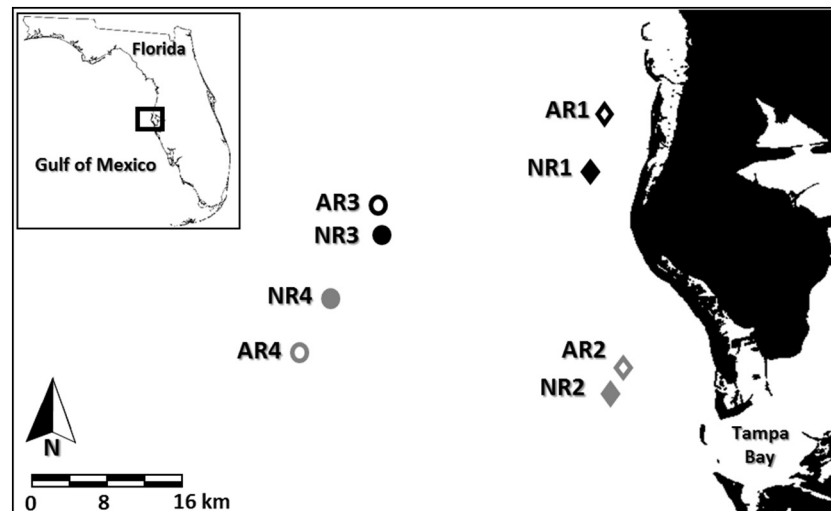


Fig. 1. Map of study locations. Natural reefs are solid symbols and artificial reefs are open symbols, while inshore sites are diamonds and offshore sites are circles.

(10–30 m depth), with heterogeneous hardbottom habitat. These reefs commonly experience annual temperature ranges from 14 °C to 33 °C and seasonal reductions in water clarity (Phillips and Springer, 1960). Due in part to the broad, shallow sloping shelf, long travel distances are commonly required for researchers to access hardbottom habitats, which are themselves not well mapped (Kington, 2013; Thompson et al., 1999). Such logistical challenges have restricted the types of field research that have been conducted in the region, thus the ecology of epibenthos in the eGOM is understudied. This paucity has left the eGOM with little baseline data of the epibenthos, which has already been problematic when attempting to assess the effects of extreme disturbances such as harmful algal blooms, oil spills, and hurricanes (Dupont et al., 2010; Murawski et al., 2016; Posey et al., 1996).

Previous descriptive work has been conducted to catalog the epibenthos of the GOM (Danek et al., 1985; Dawes and Van Breedveld, 1969; Defenbaugh, 1973; Jaap, 2015; Mahadevan et al., 1984; Phillips and Springer, 1960; Schellinger, 2013), with most attention focused on corals (Gulf of Mexico and South Atlantic Fisheries Management Council, 1982; Sammarco, 2013; Wimmons and Ab Collins, 2014), particularly in the western GOM Flower Garden Banks (Dodge and Lang, 1983; Gittings et al., 1992; Johnston et al., 2016), and on deep reefs (Cordes et al., 2008; Ross et al., 2017), with little focus on the epibenthic communities on inshore habitats (Cairns, 1977; Danek et al., 1985; Dawes and Van Breedveld, 1969; Dupont et al., 2010). Fewer experimental studies have been conducted to investigate the influence of herbivory on epibenthic communities, however, all of these were conducted on distinct habitats in the northern GOM, such as deep pinnacles and diapires (Continental Shelf Associates, 2001; Davies et al., 2013) or seagrass meadows (Valentine and Heck, 1991). No experimental studies have been conducted to investigate how grazing processes affect shallow water benthos in the eGOM. Using a field experiment and photographic surveys, this study sought to identify the factors influencing epibenthic community composition in the eGOM. Specifically, this study was designed to answer two main questions: 1) How does grazing from urchins affect the sessile epibenthic assemblages? 2) What physical and biotic factors (e.g., location, reef type, urchin density) are correlated with eGOM epibenthic cover?

2. Methods

2.1. Experimental design

2.1.1. Study area and reef complexity

Eight reefs were selected in the eGOM, on the West Florida Shelf off

the coast of Tampa Bay, Florida (Fig. 1, Supplementary Table 1). Sites consisted of both natural and artificial reefs. Natural reefs ($n = 4$) were low-relief (< 2 m), limestone ledges, while artificial reefs ($n = 4$) were high-relief structures (≥ 4 m) composed of metal and concrete materials. Offshore artificial reefs consisted of large sunken ships, and inshore artificial reefs were areas of scattered concrete and metal debris, often composed of bridge pilings, culverts, and old machinery (see Supplementary Figs. 2–5). Half of the reefs (two artificial and two natural reefs) were located inshore, in shallow water (10–15 m depth), and the other half were offshore (22–30 m depth). Comparisons between inshore and offshore reefs (here on referred to as *location*) encompassed the potential influence that both water depth and distance from shore may have had on the epibenthic communities, which were indistinguishable given the study design. Because habitat profiles differed greatly between natural and artificial reefs, complexity was measured to investigate the relationship between structural heterogeneity and urchin densities (McClanahan, 1998). Due to the low-rugosity of the study reefs, the traditional chain-and-tape method (Risk, 1972) was not deemed appropriate for measuring habitat complexity. Instead, complexity was measured as the root mean square (RMS) of depth at 0.5 m intervals along two 12.5 m long transects, for a total of 25 m sampled (Leon et al., 2015; McCormick, 1994). Transects began in the sand one meter off the edge of the reef, which ensured the survey captured the relief of each reef. The first transect was conducted parallel to the sand-reef interface on natural reefs and lengthwise on artificial reefs (e.g., bow to stern on the shipwrecks). On all reefs, the second survey was positioned perpendicular to, and began at the midpoint of, the first survey.

2.1.2. Grazing experiment

A one-year experiment was conducted to test the effects of urchin grazing across location and reef type. Grazing effects were measured by comparing assemblages on settlement tiles across experimental treatments within each site. Although the assemblages that colonized the tile surfaces may not have mimicked those that naturally settle to existing benthos, the tiles offered a standardized surface to measure urchin grazing effects. Reefs were visited approximately once every four months, which was too long to use full exclusion, as high fouling rates in the eGOM would have likely covered the cages and altered water flow (Jerabek et al., 2016). Due to this limitation, fully-enclosed exclusion cages that prohibited fish grazing could not be used, and instead, partial cages which prevented only urchin grazing were used. The effects of other grazers, such as invertebrate mesograzers and fishes may have varied across each site (Duffy and Hay, 2000; Thompson

et al., 1997), but they were assumed to be even within sites (i.e., between experimental treatments). Because tiles were placed in close proximity (< 1 m apart), it is unlikely that the effects of non-urchin grazers varied across treatments, allowing for accurate comparisons of urchin grazing across treatments within each site. This was also assumed true for other across-site differences which had potential to influence larval settlement (e.g., reef type, sedimentation rates, larval supply).

During the summer of 2015, three types of experimental modules were deployed at each reef: control (n = 3 blocks, 6 tiles), exclusion (n = 3 blocks, 6 tiles), and cage-control (n = 3 blocks, 3 tiles) (Supplementary Fig. 1). Control modules were composed of a concrete cinderblock with bolts to attach settlement tiles to the upper surface. The exclusion modules were additionally outfitted with a metal grate that extended outward from the surface of the block to prevent urchins from grazing on the tiles. The cage-control modules contained metal grating on two sides, which allowed access by urchins, while still exposing the tiles to any artifacts caused by the exclusion material. Modules were conditioned on the reef for approximately five months (summer 2015 – winter 2016) prior to the onset of the experiment (Osman and Whitlatch, 1995; Siboni et al., 2007). After the first round of tile collection, the exclusion grate material was changed from a galvanized metal to PVC coated Vexar to minimize rust. Independent tests were conducted in controlled mesocosms to confirm that the different materials were equally effective at excluding urchins. Videotaped feeding trials were conducted for 48 h, where half of the treatments were open to, and half excluded from (one metal and one Vexar) urchin grazing. Four replicate trials were conducted. In each trial urchins were documented grazing on the open tiles, but never on the exclusion tiles, despite attempts to access the tile module surface. This confirmed the efficacy of both types of exclusion grate materials.

Starting in winter 2016, terracotta tiles (15 cm × 15 cm) with a smooth upper surface and a grooved lower surface were attached horizontally to the modules (Supplementary Fig. 1). The horizontal orientation was selected as it best mimicked the flat natural reefs in the eGOM. Tiles were placed with the smooth surface facing up so colonizing organisms would have no refuge from the effects of grazing within microhabitats of the groves (Harlin and Lindbergh, 1977; Nozawa et al., 2011). During the one-year experiment, divers returned to the sites every four months to collect the tiles and replace them with clean ones, resulting in data collection spanning a total of three replicate sampling periods. When collected, each tile was labeled and returned to the surface in a solid storage container to prevent dislodging organisms. Before mounting new tiles, the surface of each module was scrubbed clean of growth. The collected tiles were kept in aerated seawater from the time they were on the boat until analysis in the lab. All tiles were analyzed within 48 h of collection to prevent death of settled organisms.

Prior to analysis, each tile was lightly dusted with a synthetic fan-paintbrush to remove overlying sediment (Kennelly, 1983). Tiles were then placed in a saltwater bath and a sampling quadrat was used to divide the tile into twenty-five 2.5 cm × 2.5 cm cells. This grid size increased the detection of small, cryptic organisms that otherwise may have been missed in a lower resolution assessment. Within each sampling grid, all organisms were identified to the lowest possible taxon and percent cover was estimated for each (Supplementary Table 2). Only sessile organisms were counted, as mobile animals had opportunity to move among tiles after collection. On the rare occasion when more than one organism occupied the same space (e.g., when a barnacle settled on top of an oyster), only the top-most organism was included in the percent cover estimate. Percent cover of top most organisms was used to estimate grazing effects because it is the epibenthic layer that is directly exposed to grazing from urchins (Poore et al., 2012; Solandt and Campbell, 2001). To avoid bias from an edge-effect, a 1.25 cm wide perimeter around the tile, and the center grid which contained the hole through which the tile was bolted, were not analyzed (Maida et al.,

1994). The composition of the tile assemblages was then calculated by summing the percent cover of each taxa across all 24 sampled grids. Due to the short deployment time, communities rarely achieved substantial vertical growth, thus percent cover, not biomass, was assumed to be an accurate measure of grazing.

2.1.3. Photo and urchin surveys

To quantify both the epibenthos and the urchin densities on each reef, SCUBA divers conducted transect surveys quarterly starting in fall 2014 and ending in spring 2016. Photo transects were selected as they allow for rapid, accurate assessments given the bottom time limitations associated with sampling on SCUBA. Using a Canon ELPH digital camera (housed in an Ikelite underwater case) attached to a 0.25 m² quadrat, photos were taken along a strip transect. Starting points were selected haphazardly and urchin abundances were recorded simultaneously along the same transect. Because the natural reefs of the eGOM have low structural complexity, communities on the reef-top often differ from those on the reef edges at the sand-reef interface (Harris, 1988). In effort to remain consistent across sampling events, transects and experimental modules were constrained to the reef edge along the sand-reef interface of natural reefs. Transects and modules on the artificial reefs were not constrained to any particular area.

Although nocturnal urchins may have sought refuge beneath reef features (Andrew and Underwood, 1989; Harvey, 1956), only urchins on the surface of the substrate were counted and identified to species level; those hiding in crevices or beneath ledges were not counted to minimize sampling bias between the two reef types. The natural ledges had deep, narrow gaps making detection of hidden urchins difficult, while urchins hidden on artificial reefs could be readily observed on the underside of reef fragments. Although this approach likely underestimated urchin populations, the inclusion of cryptic individuals would likely have inflated estimates on artificial reefs relative to natural reefs, because the fragmented nature of the reef made their detection easier. Because it is assumed that similar proportions of urchins would seek refuge across both reef types (Flukes et al., 2012), the consistent survey methods allowed for the accurate comparison of relative grazing intensity.

During each survey, 60 photos were taken at 0.5 m intervals, ensuring no overlap in photographed area. Any large portions of the reef that did not contain hardbottom (e.g., sand patches, holes) were bypassed. Best efforts were made to visit all reefs quarterly, however poor weather prevented sampling the offshore reefs in the summer of 2015, and all reefs during winter 2016. Additionally, high turbidity often limited visibility, occasionally resulting in poor quality photographs that could not be analyzed.

A subset of 30 photos were randomly selected from each sampling event (n = 1400 photos across events) for analysis with the software Coral Point Count for excel (CPCe) (Kohler and Gill, 2006). For each photo in the subset, 75 stratified random points were selected and the corresponding organism beneath each point was identified to the lowest possible taxon. It is important to note that photographic transects are limited to sampling overlying organisms, thus potentially underestimating abundance of cryptic species and overall community richness (Carleton, 1995). Prior to statistical analysis, points were removed if they were visually obscured by either mobile reef inhabitants (e.g., fishes, gastropods, urchins) or corresponded with non-hardbottom substrate (e.g., holes in a reef, sand bottom). Of the remaining points, presence of each organism was summed across all photos from the sampling event, to estimate epibenthic cover on the reefs (Supplementary Table 3).

2.2. Statistical analyses

2.2.1. Urchin populations and reef complexity

A generalized-linear, mixed-effect model (GLMM; R-package: ‘lme4’; Bates et al., 2015) with a Poisson distribution was used to test

Table 1
List of analyses for each dataset with the associated transformations and distribution types.

Dataset	Test	Full model	Transformation	Distribution
Sea urchin density	GLMM	$\mu\{\text{Taxonomic group} \mid \text{location, reef}\} = \beta_0 + \beta_1\text{location} + \beta_2\text{reef} + \beta_3\text{location:reef}$	Log(x + 1)	Poisson
Reef complexity	2-way ANOVA		Log(x + 1)	Gaussian
Reef complexity:Urchin density	LM		Urchin: SQRT; RMS: Log(x + 1)	Gaussian
Photographic surveys of epibenthos				
Total cover	LME	$\mu\{\text{Taxonomic group} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1\text{location} + \beta_2\text{reef} + \beta_3\text{urchin} + \beta_4\text{location:reef} + \beta_5\text{location:urchin} + \beta_6\text{reef:urchin} + \beta_7\text{location:reef:urchin}$	–	Gaussian
Species richness	LME		SQRT	Gaussian
Species evenness	LME		–	Gaussian
Algal cover	LME		SQRT	Gaussian
Invertebrate cover	LME		–	Gaussian
CCA cover	LME		SQRT	Gaussian
Tile assemblages from grazing experiment				
Total cover	GLMM	$\mu\{\text{Taxonomic group} \mid \text{treatment}\} = \beta_0 + \beta_1\text{treatment}$	–	Gamma
Species richness	LME		–	Gaussian
Species evenness	GLMM		–	Gamma
Algal cover	GLMM		–	Gamma
Invertebrate cover	GLMM		–	Gamma
CCA cover	GLMM		–	Gamma
Tile assemblages from exclusion tiles only				
Total cover	GLMM	$\mu\{\text{Taxonomic group} \mid \text{location, reef}\} = \beta_0 + \beta_1\text{location} + \beta_2\text{reef} + \beta_3\text{location:reef}$	–	Gamma
Species richness	LME		–	Gaussian
Species evenness	GLMM		–	Gamma
Algal cover	GLMM		–	Gamma
Invertebrate cover	GLMM		–	Gamma
CCA cover	GLMM		–	Gamma

GLMM: Generalized-linear mixed-effect model. LM: Linear regression. LME: Linear mixed-effect model. SQRT: Square-root.

whether urchin abundance differed across location (inshore and offshore) and reef type (artificial and natural). Because data were pooled across sampling events, the use of GLMMs allowed for the use of repeated measures (Zuur et al., 2009; Table 1). Additionally, these statistical approaches allow the distribution of the residuals to be defined in order to better measure treatment effects across highly variable sites. For all mixed-effects models used in this study, location and reef type were fixed effects and site was a random effect. Statistical significance for all analyses was set at $\alpha = 0.05$. Variance is reported as \pm SEM throughout.

One artificial reef (AR4) was a clear outlier, with urchin densities that were consistently two orders of magnitude higher than any other reef (See supplementary materials Table 4 and Fig. 6). All analyses were run both with and without data from AR4 to test its influence on overall results. In the majority of analyses, the presence of this outlier amplified the effect size, but did not alter tests of significance. To reduce biasing the magnitude of the results with the inclusion of this outlier, as well as to simplify reporting, only the statistics from analyses excluding AR4 are presented here.

Reef complexity data were only collected on one occasion at each site, which resulted in an over-fitted mixed effect model due to the inclusion of the random ‘site’ effect. Thus, mixed effects models were not deemed appropriate for testing relationships with reef complexity, and instead simple linear models were used to analyze the relationships with reef complexity. A linear regression was used to analyze the correlation between average urchin densities and reef complexity. Additionally, variation in complexity across location and reef type were analyzed using a two-way nonparametric ANOVA. Homogeneity was confirmed using Levene's test. For both tests, average urchin densities and complexity were log transformed to achieve normality.

2.2.2. Community analyses

For both the settlement tiles and the photographic surveys, species richness and evenness were calculated from the assemblage data, after which outliers were removed and percent cover data were condensed into four groups for analyses. Groups consisted of non-geniculate

crustose coralline algae (CCA), all other non-CCA algae (from here on referred to as *algae*), sessile invertebrates, and total cover (the combination of the three previous groups) (Supplementary Tables 2, 3). Normality was tested using Shapiro Wilk's tests and homogeneity with Levene's test. Data sets with normally distributed residuals were analyzed using linear mixed-effect models (LMEs; R-package: ‘nlme’; Pinheiro et al., 2017), and those with non-normal distributions were analyzed with a GLMM with a Gamma distribution. Gamma distribution was selected as it represented an overdispersed Poisson distribution, but allowed for the use of continuous data, such as the proportional cover calculated for tile assemblages and photo communities.

A subset of data including only the exclusion tiles were used to infer how colonization varied across reefs. While these tiles cannot be used to explicitly quantify larval supply, their young age (~four months) allowed investigation of the combined effects of larval supply and early post-colonization mortality independent of urchin grazing (from here on referred to as *colonization*). However, aspects of the sampling design limited the utility of these analyses. Because epibenthos were measured as percent cover, individual organisms could not be enumerated, and by not measuring underlying organisms, richness was potentially underestimated. Thus, it is important to note that the primary goal of these analyses was not to characterize the communities recruiting to the reefs, but instead to highlight additional potential factors influencing composition of epibenthic communities.

Canonical Analyses of Principal Coordinates (CAP) were conducted on the uncondensed, species data to examine whether assemblages differed across reefs for both the tile assemblages and the photographic surveys. Data were square-root transformed to achieve normality, and Levene's test was used to confirm homogeneity. Leave One Out Cross Validation (LOO-CV) values were calculated as a proxy of clustering strength (Anderson and Willis, 2003). Higher LOO-CV values of correct classification indicated increased distinction among assemblages. To best visualize separation among the assemblages, minimum convex polygons were drawn. Indicator species values were calculated for each taxa, and vector bi-plots were created to show which organisms most substantially influenced patterns in the CAP plots. Only taxa that

significantly influenced a group ($p \leq 0.05$) and had an index $> 25\%$ were plotted (Dufrene and Legendre, 1997).

3. Results

3.1. Grazing experiment

Tile recovery was over 75% (271 of 360 tiles; 113 control, 103 exclusion, and 55 cage-control), with tile loss apparently resulting from fishing entanglement, boat anchors, and severe weather. Across all treatments, total biotic cover averaged 68.0% (± 1.2). A total of 55 taxa were identified, of which 40 were algae, one of which was CCA, and 15 were invertebrates (Supplementary Table 2). Overall, algae were identified to a lower taxonomic level than invertebrates, which resulted in the invertebrate group appearing to have relatively lower

diversity. Average algal cover accounted for 19.3% (± 1.2) of the tile cover. The three most abundant organisms were mixed turf algae (6.0% ± 0.8), cyanobacteria (5.3% ± 0.8), and *Polysiphonia* spp. (2.5% ± 0.5). Invertebrates accounted for 30.8% (± 1.2) of total cover and the three most abundant groups were polychaetes (15.1% ± 0.9), barnacles (4.5% ± 0.6), and bryozoans (3.4% ± 0.3). CCA accounted for 17.9% (± 1.0) of the tile cover.

There were no caging artifacts detected in the comparisons between the control and cage-control tiles for either diversity indices or the cover of any taxonomic group (richness: $t = -0.49$, $p = .63$; evenness: $t = 0.51$, $p = 0.609$; total: $t = -0.70$, $p = 0.482$; algae: $t = -1.61$, $p = 0.107$; invertebrates: $t = -0.77$, $p = 0.440$; CCA: $t = 0.87$, $p = 0.385$; Supplementary Table 5). Compared to exclusion tiles, control tiles had lower richness (-1.2 species, $t = 3.51$, $p < 0.001$), lower algal cover (-12% , $t = -3.53$, $p < 0.001$), and higher CCA cover

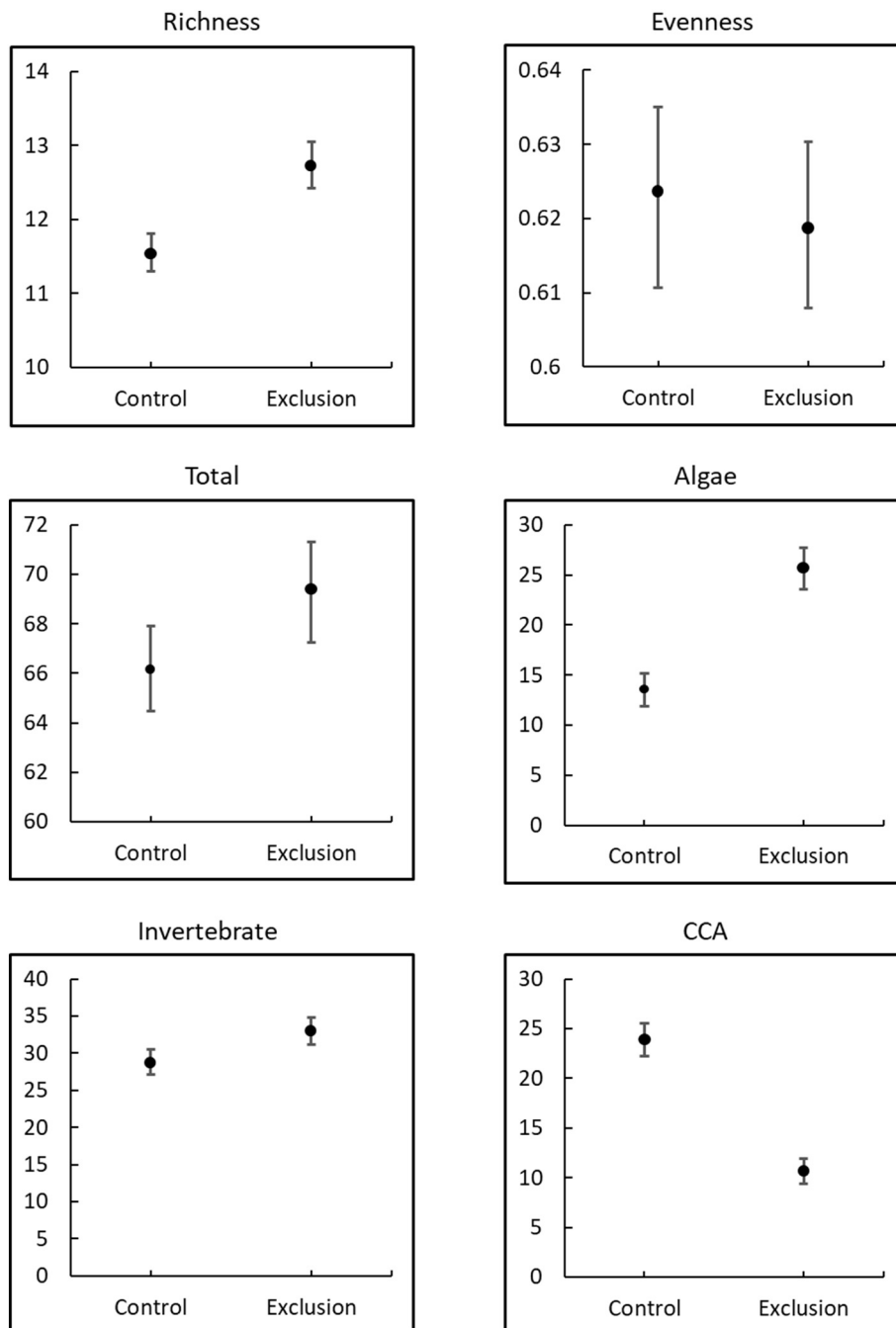


Fig. 2. Plots of means \pm SEM of diversity indices and percent cover of taxonomic groups on the settlement tiles between control and exclusion treatments.

(+13%, $t = 3.92$, $p < 0.001$; Fig. 2, Table 2). Grazing from urchins did not significantly affect total cover ($t = -1.01$, $p = 0.312$), evenness ($t = -0.23$, $p = 0.818$), or invertebrate cover ($t = -1.77$, $p = 0.077$; Fig. 2).

Focusing on data from the subset of exclusion tiles to eliminate the effects of urchin grazing (i.e., to isolate pre-colonization and early non-grazing post-colonization processes), there were no differences in any of the diversity indices or cover of taxonomic groups across reef type or location (Fig. 2; Supplementary Fig. 7, Table 6). However, assemblage composition on these tiles differed among reefs. There were two distinct groups along the first canonical axis, which was primarily indicative of location, and explained > 35% of the variation (Fig. 3). Reef type was the predictor that was most aligned with the second canonical axis, which explained 23% of the variation. Overall LOO-CV value was 71%. The two strongest indicator taxa were barnacles (IV: 86.1) and ascidians (IV: 46.8), which characterized assemblages on the inshore tiles.

3.2. Urchin surveys and reef complexity

The urchin populations on the study sites were composed of two species, *Arbacia punctulata* and *Lytechinus variegatus*. Populations were dominated by *A. punctulata*, which represented 99.5% of the individuals. There was an interaction between location and reef type on urchin density ($p < 0.001$, $Z = 4.01$; Fig. 4), driven by the high densities on the offshore artificial reef and low densities on offshore natural reefs. Urchin populations of inshore reefs were similar across both reef types. Similarly, there was an interaction between location and reef type on reef complexity ($p = 0.003$, $F_{1,3} = 118.40$). Overall, urchin densities were higher on more complex reefs ($t = 4.98$, $p = 0.004$, $R^2 = 0.83$, Fig. 4b).

3.3. Reef epibenthos

Average total cover was 59.8% (± 2.9). A total of 50 taxa were identified, including 33 algae taxa, one of which was CCA, and 17 invertebrates (Supplementary Table 3). On average, algal cover accounted for 31.1% (± 4.0) of the epibenthos. Drift algae (5.2% ± 2.5), *Caulerpa* spp. (4.6% ± 1.9), and *Botryocladia* spp. (4.2% ± 1.2), were the three most abundant algal taxa. Invertebrates accounted for 36.4% (± 3.9) of the epibenthos. The three most abundant invertebrates were hydroids (19.2% ± 3.6), sponges

(10.4% ± 1.0), and ascidians (3.7% ± 0.7). Crustose Coralline Algae accounted for 4.3% (± 0.9) of epibenthic cover.

Evenness ($p = 0.031$, $R^2 = 0.16$), total cover ($p = 0.011$, $R^2 = 0.10$), invertebrate cover ($p = 0.011$, $R^2 = 0.31$), and CCA cover ($p = 0.009$, $R^2 = 0.32$) were all positively correlated with urchin densities (Fig. 5, Table 2). Compared to natural reefs, artificial reefs had higher invertebrate cover (+15%, $t_5 = 3.09$, $p = 0.027$; Fig. 6) and marginally lower algal cover (-22%, $t_5 = -2.47$, $p = 0.057$; Fig. 6). Additionally, CCA was higher on offshore sites (+10%, $t_4 = 4.37$, $p = 0.009$; Fig. 6).

Epibenthos on the outlier reef AR4 had lower biotic cover (2.5% ± 0.70) and species richness (less than five species) than all other reefs. All sessile taxa observed on AR4 were invertebrates, dominated by the corals *Phyllangia americana* and *Cladocora arbuscula*. Non-CCA algal taxa were not observed on this reef, despite divers searching the wreck after the completion of photographic surveys.

The CAP analysis on the percent cover of the epibenthic assemblages had an overall LOO-CV value of 65% (Fig. 7). Two distinct groups formed along the first canonical axis, which represented dispersion between reef types and explained roughly 32% of the variation. Artificial reefs were characterized by hydroids (IV: 76.4) and *P. americana* (IV: 75.8). Natural reefs were characterized by red algal taxa, with the two strongest indicators being *Botryocladia* spp. (IV: 72.1) and *Gracilaria* spp. (IV: 69.9). The highest degree of overlap occurred between site NR1, and the group that consisted of the three artificial reefs (Fig. 7). Location was the predictor that was most aligned with the second canonical axis, which explained 31% of the variability.

4. Discussion

This study identified the potential for both pre- and post-colonization processes to structure the composition of epibenthos in the eastern Gulf of Mexico (eGOM). Tile assemblages differed by location, apparently due to higher colonization by estuarine invertebrates (i.e., ascidians and barnacles) on inshore sites near Tampa Bay. This pattern was consistent across reef types, and similar to trends observed in the southeastern GOM by Danek et al. (1985), where barnacles and oysters recruited in high biomass to inshore sites (~11 m depth), distinguishing inshore assemblages from those offshore (~55 m). The difference in colonization across-shelf observed in both studies suggests an influence of coastal water sources on inshore colonization, and highlights the

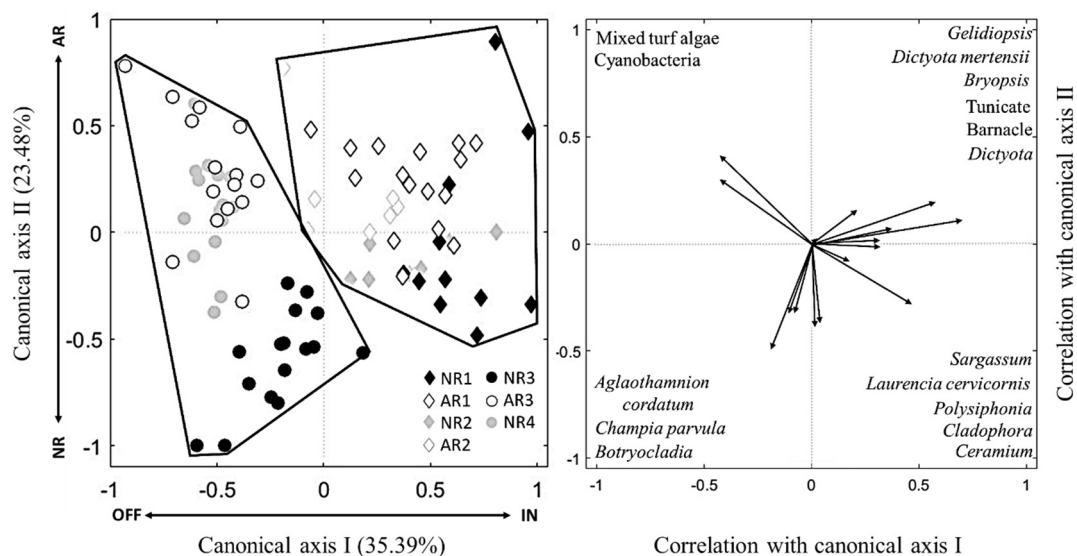


Fig. 3. CAP plot of assemblages on the exclusion tiles (natural reefs are solid symbols, artificial reefs are open, diamonds are inshore sites, and circles are offshore sites). Species vector biplot of the subset of organisms with significant species indicator values. Species are listed in corresponding, top-to-bottom order as the vectors located in their quadrant.

Table 2
Responses of taxonomic groups and diversity statistics to each factor for both the photo and the colonized assemblages. Magnitude and *p*-value are reported alongside statically significant relationships. Horizontal bars indicate no significant effect.

Percent cover	Urchins		NR:AR		IN:OFF	
	Density	Presence	Photo survey	Exclusion tile	Photo survey	Exclusion tile
	Photo survey	Grazing experiment				
Total	↑ $R^2 = 0.10$ $p = 0.010$	—	—	—	—	—
Richness	—	↓ 1.2 species $p < 0.001$	—	—	—	—
Evenness	↑ $R^2 = 0.16$ $p = 0.031$	—	—	—	—	—
Algae	—	↓ 12% $p < 0.001$	↑ 22% $p = 0.057$	—	—	—
Invertebrates	↑ $R^2 = 0.31$ $p = 0.011$	—	↓ 15% $p = 0.027$	—	—	—
CCA	↑ $R^2 = 0.32$ $p = 0.009$	↑ 13% $p < 0.001$	—	—	↓ 10% $p = 0.009$	—

potential for larval supply to structure epibenthos in the eGOM. However, because the effect of depth and distance from shore could not be distinguished, it is possible that difference in assemblages were also a result of depth effects. Differences between inshore and offshore assemblages were also observed at the site-level, however it was not clear whether these differences were due to variation in recruitment, selective settlement, or other possible post-colonization processes (e.g., nutrient availability, particulate deposition, physical disturbances from storms, grazing). For instance, assemblage differences due to mortality from overgrowth could not be measured given the sample design.

Tile assemblages differed between reef types, although the patterns were not as strong as those observed across location. Globally, epibenthos often differ between artificial and natural reefs (Burt et al., 2009; Miller, 2002; Perkol-Finkel and Benayahu, 2007; Wendt et al., 1989). Processes including larval recruitment (Caley et al., 1996; Harriott and Fisk, 1987; Jenkins, 2005), age and succession (Perkol-Finkel and Benayahu, 2005; Wendt et al., 1989), preferential grazing by faunal communities (Bohnsack and Sutherland, 1985; Osman and Whitlatch, 2004; Rilov and Benayahu, 2000), orientation of substrate features (Knott et al., 2004; Perkol-Finkel and Benayahu, 2007), substrate material (Harriott and Fisk, 1987), and variations in water movement (Eckman and Duggins, 1998; Perkol-Finkel and Benayahu, 2009; Qian et al., 2000) have all been cited as drivers of differences between reef types. Many of these effects remain unexplored here and have potential to influence the composition of tile and epibenthic assemblages. However, given the paired design of the current study, with natural and artificial reefs located adjacent to each other, larval supply and environmental conditions (e.g., temperature, salinity) were

assumed to be consistent between reef pairs. Nevertheless, differences in colonization were observed between reef types. Differences were only evident at a high taxonomic resolution, and were not apparent when the data were condensed to the three taxonomic groups (i.e., algae, invertebrates, or CCA). This suggests that species identity was important for distinguishing between reef types and that redundancy was observed at the low-taxonomic resolution. Importantly, the equal colonization observed at low-taxonomic resolution indicates that site-level differences in percent cover of three groups were likely influenced by post-colonization processes, not larval supply.

Post-colonization processes such as grazing, overgrowth and shading, and physical disturbances, can play key roles in structuring epibenthos (Connell, 1961; Horn, 1974; Hunt and Scheibling, 1997; Fraschetti et al., 2002; Lewis, 1986; Osman and Whitlatch, 2004; Quinn, 1982; Smith, 1992; Vermeij, 2006). The grazing experiment demonstrated that post-colonization grazing by urchins reduced algal cover on control tiles compared to exclusion tiles. This reduction of algal cover corresponded with increased cover of CCA, a relationship also documented in both temperate and tropical marine systems (Fairfull and Harriott, 1999; Paine, 1980; Smith et al., 2010). The increased cover of CCA on the control tiles resulted from either the structural resistance of CCA to grazing, or their colonization of the spaces cleared by urchins (Littler and Littler, 2013; O’Leary and McClanahan, 2010). CCA are pioneer species that can influence epibenthic composition by facilitating or inhibiting the colonization of other organisms (Heyward and Negri, 1999; McCoy and Kamenos, 2015; Tebben et al., 2015). Some species of CCA can benefit a community by inducing settlement of marine larvae, increasing substrate

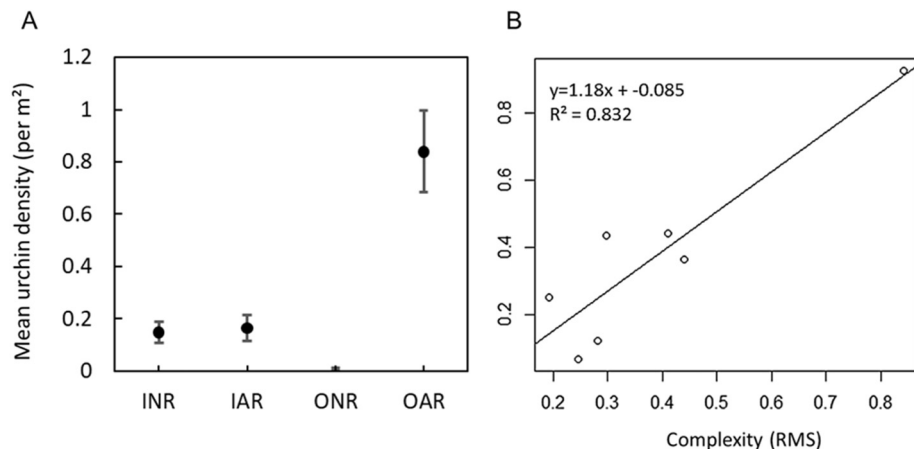


Fig. 4. (a) Log transformed mean urchin densities (\pm SEM) across reef type and location. INR: Inshore natural reefs (NR1 and NR2), IAR: Inshore artificial reefs (AR1 and AR2), ONR: Offshore natural reefs (NR3 and NR4), OAR: Offshore artificial reef (AR3). (b) Relationship between complexity (root mean square height) and urchin density.

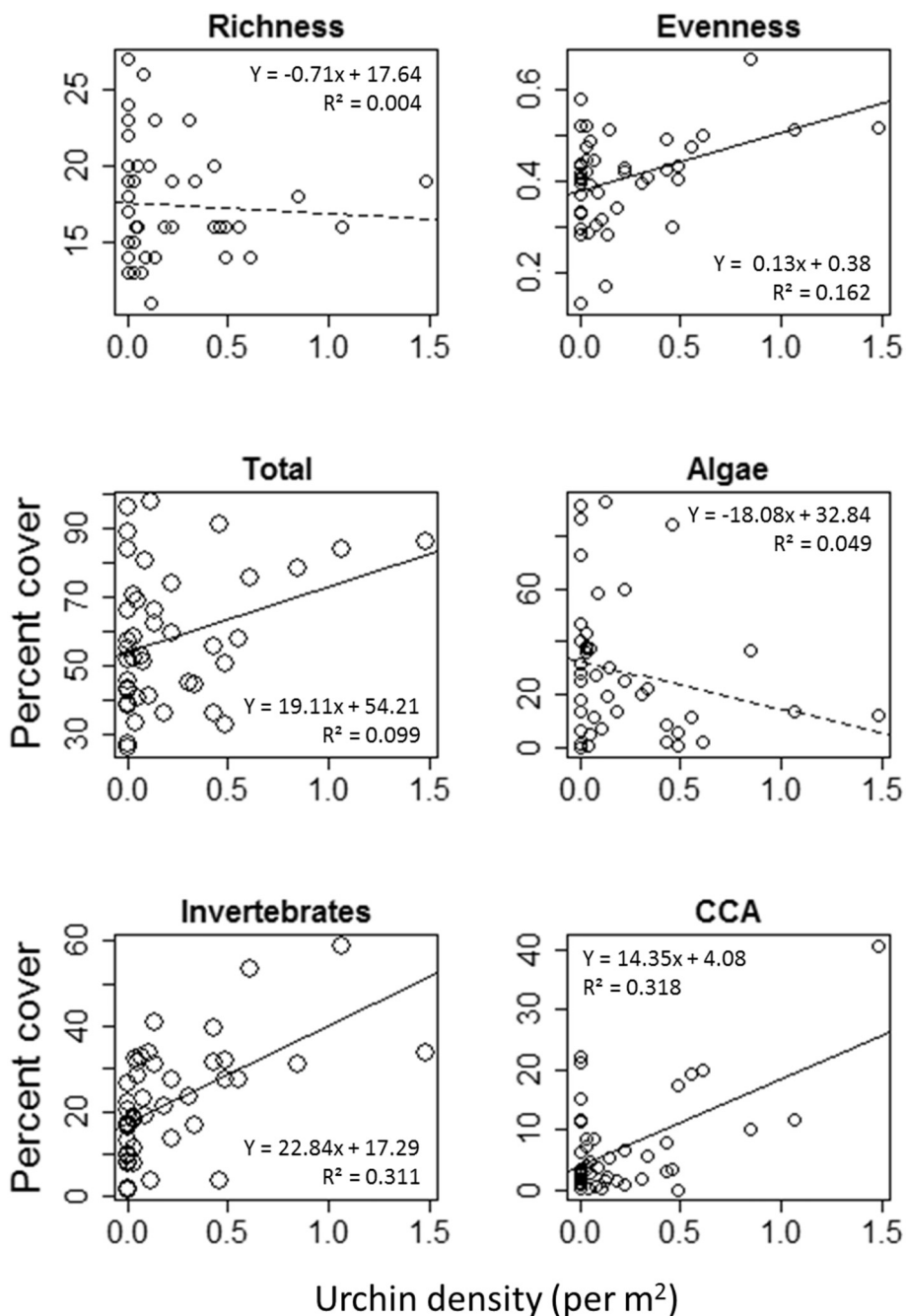


Fig. 5. Relationships between urchin densities and epibenthic cover across diversity indices and percent cover of taxonomic groups observed in the photographic surveys.

stability, and increasing available hard structure (Heyward and Negri, 1999; Littler and Littler, 2013). However, CCA can also prevent colonization through chemical deterrents or by shedding their outer layers to remove individuals that have settled to their surface (Breitburg, 1984; Bulleri et al., 2002). Given the prevalence of CCA on the settlement tiles, further research is needed to understand their role in the eGOM and how epibenthos in the region respond to changes in CCA cover.

The young age of the tile assemblages and differences in the scale of sampling methods between the experimental and observational components prevented this study from directly examining how variation in either colonization or post-colonization processes may have influenced site-level community composition of the epibenthos. Taxa that were commonly observed in the photo surveys at the site level often did not

occur on the tiles (i.e., sponges and gorgonians), possibly because these organisms are facilitated by a pre-existing community for larval settlement and survival (Connell and Slatyer, 1977; Maggi et al., 2011; Osman and Whitlatch, 1995; Rodriguez et al., 1993). Conversely most organisms on the settlement tiles were observed in situ on the sites, but many could not be detected in the photos due to their small size (i.e., filamentous algae, barnacles, and bryozoans), which is a common limitation of photographic surveys. Because of this, the composition of assemblages at the tile level could not be directly compared to benthic assemblages at the site-level, however, the experiment did identify mechanisms that could be driving community patterns.

Given the results of the grazing experiment, urchin density was expected to be correlated positively with CCA, and negatively with algal cover at the site-level. When the relationships between urchins

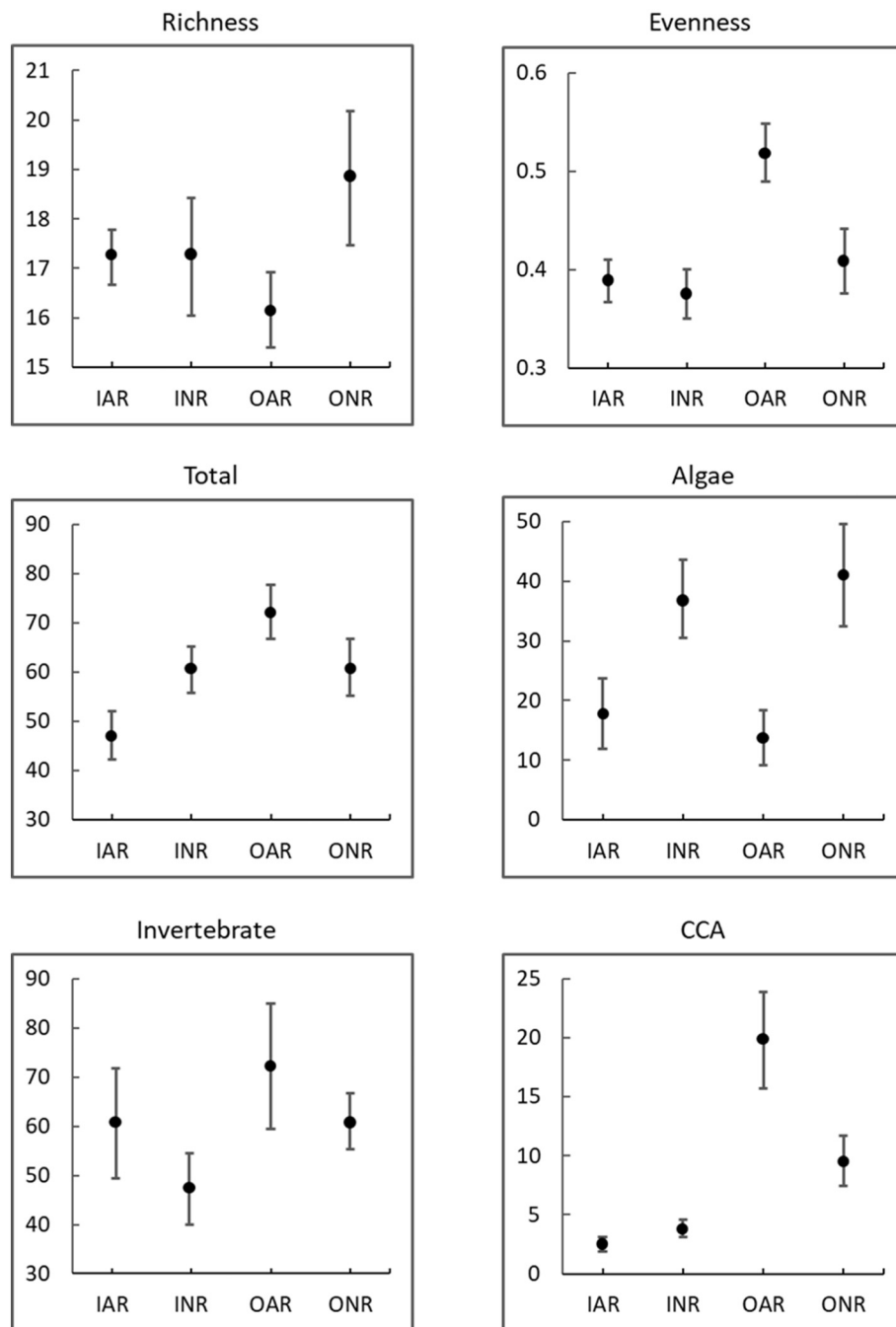


Fig. 6. Plots of means \pm SEM of diversity indices and percent cover of taxonomic groups observed in the photographic surveys across reef type and location.

and benthic cover were examined categorically by reef type, artificial reefs had higher CCA and marginally lower algal cover. The lower algal cover on artificial reefs may have been due to more intense grazing from the larger urchin populations on those sites. When data were examined across reefs, a significant and positive correlation between urchins and CCA was detected, however the negative correlation between urchins and algal cover was not statistically significant. The inability to directly correlate urchins and algal cover was possibly due to both the natural variability in algal cover and the low urchin densities recorded on the sites.

Algal cover on natural reefs in this study (mean = 32%; range = 7% to 92%), was similar to that documented in the eGOM by Dupont (2009; mean = 45%, range = 11% to 75%). In both studies, algal cover was variable through time. Large blooms (e.g., *Sporochnus pedunculatus* and *Sargassum* spp.) are natural phenomenon that have been well

documented in the GOM for nearly 50 years (Cobb and Lawrence, 2003; Dawes and Van Breedveld, 1969; Dawes and Lawrence, 1990; Dupont, 2009; Earle, 1968). Algal blooms resulted in high variability in algal cover across surveys, making it difficult to detect grazing effects. The effects of grazing were further confounded by the low urchin densities recorded in this study, particularly on natural reefs. In an attempt to minimize sampling bias between the two substrate types, divers only recorded urchins on the surface of the substrate. Thus, urchin populations were likely underestimated. However, because urchin survey methods were consistent across sites, the relative proportions of urchins should still allow for accurate comparison of grazing intensity, despite underestimating populations.

Results of this study revealed a strong positive correlation between urchin density and structural complexity, which could explain the higher urchin densities on the artificial reefs. At the site-level, natural

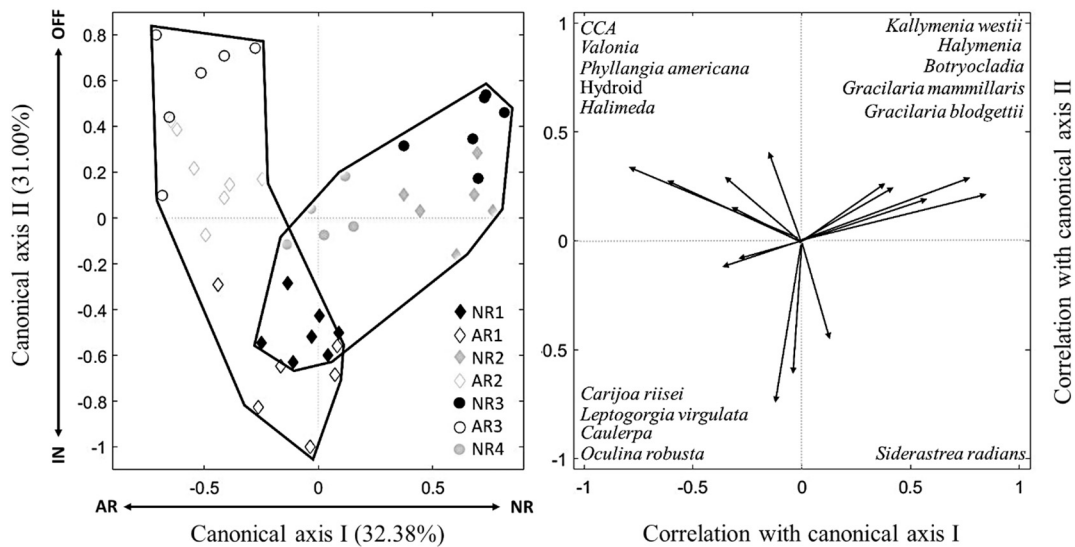


Fig. 7. CAP plot of epibenthic communities (natural reefs are solid symbols, artificial reefs are open, diamonds are inshore sites, and circles are offshore sites). Species vector biplot of the subset of organisms with significant species indicator values. Species are listed in corresponding, top-to-bottom order as the vectors located in their quadrant.

reefs were characterized primarily by algal taxa. Grazing by the dominant urchin, *A. punctulata*, may have driven some of the differences in community composition observed between reef types. The two strongest indicator species of natural reef communities were the algal genera *Gracilaria* and *Botryocladia*, both of which are preferred food sources for *A. punctulata* (Cobb and Lawrence, 2005; Hay et al., 1986). Preferential grazing from urchins likely resulted in the relatively lower abundance of these algal taxa on artificial reefs, where urchin densities were high. Community analyses also revealed a high amount of overlap between site NR1 and the artificial reefs, suggesting a greater similarity between this natural reef and the artificial ones. This finding may have been the result of increased urchin grazing on site NR1, which had densities consistent with those recorded on the inshore artificial reefs, and the highest of any natural reef in this study.

Potential effects of urchin grazing were even more pronounced on site AR4, where densities were approximately 14 times higher than those observed on the next highest reef. At their maximum, urchin densities on this reef were 29 individuals per m², similar to those reported in temperate urchin barrens (Lang and Mann, 1976; Leinaas and Christie, 1996). Epibenthos on site AR4 had lower biotic cover and lower species richness than all other sites. Without abundant epibionts, the high urchin populations on this site were possibly being sustained by the consumption of particulate organic matter deposited from the water column, diatoms, and opportunistic animal products such as fish carcasses and other urchin tests (Harvey, 1956; our personal observations). Lower epibenthic richness and cover on this site may have been a result of intense urchin grazing, lending evidence to the role they have in structuring epibenthos in the eGOM, especially when their densities are high. However, non-grazing post-colonization processes are likely the dominant factors affecting the epibenthos on reefs with low urchin densities, as was evident in the variable algal cover on the sites across seasons.

It is currently unknown what role benthic algae have in this system, although it has been suggested they are an important basal resource for faunal communities (Huelster, 2015). The high variability in algal cover noted by others in the eGOM suggest that these sites are relatively dynamic (Cobb and Lawrence, 2003; Dawes and Van Breedveld, 1969; Dawes and Lawrence, 1990; Dupont, 2009; Earle, 1968). As a subtropical system, the eGOM experiences regular disturbances from the environment in the forms of intense turbidity and deposition, temperature extremes (both hot and cold), and large amounts of sand

movement associated with extreme weather events (Brooks et al., 2003; Bullock and Smith, 1979; Dupont et al., 2010; Posey et al., 1996). Any of these disturbances can result in mortality of epibenthic organisms, resulting in changes in community composition (Dupont et al., 2010; Posey et al., 1996; Rezak et al., 1990; Thompson et al., 1999). Without an understanding of the frequency and intensity of disturbances, as well as the community responses to them, it has been difficult to assess the influence of extreme events such as red tides, hurricanes, or oil spills (Dupont et al., 2010; Engle et al., 2008; Murawski et al., 2016). Given the potential for such drastic events to structure community composition, it is important that research continues to investigate the processes influencing settlement and succession in this region.

5. Conclusions

This study presents the first investigation of grazing effects on the communities of inshore hardbottom reefs in the eGOM. Urchins potentially play an important role in structuring the epibenthos by grazing algae and small invertebrates, exposing space for colonization by new organisms. However, while the influence of grazing was apparent on newly recruited assemblages, grazing effects were less clear at the site level. Trends in lower algal cover and similarities in community composition were observed on reefs with higher urchin densities, but this study was unable to directly detect a significant correlation between urchin density and algal cover. This was likely due to a combination of the low urchin densities and high variability of algal cover documented on the sites. Epibenthic composition varied across both location and reef type, likely through a combination of factors such as grazing intensity, larval supply, and water conditions, much of which remain unexplored here. The influence of supply was apparent in the composition of the young tile communities, while grazing from urchins was likely an important source of post-colonization mortality, particularly on artificial reefs in the region. However, given the highly dynamic nature of the eGOM, it is still unclear whether the effects of grazing from sea urchins is ecologically relevant when compared to large scale disturbances and natural fluctuations in the epibenthos. By highlighting the influence of these pre- and post-colonization process this study has identified some of the mechanisms influencing epibenthos in the eGOM and highlights the need for future research in this region.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.jembe.2018.09.005>.

Funding

This work was supported by the University of South Florida's College of Marine Science, the William T. Hogarth Marine Mammal endowed fellowship, FWC Artificial Reef Program, and the Fish Florida Scholarship.

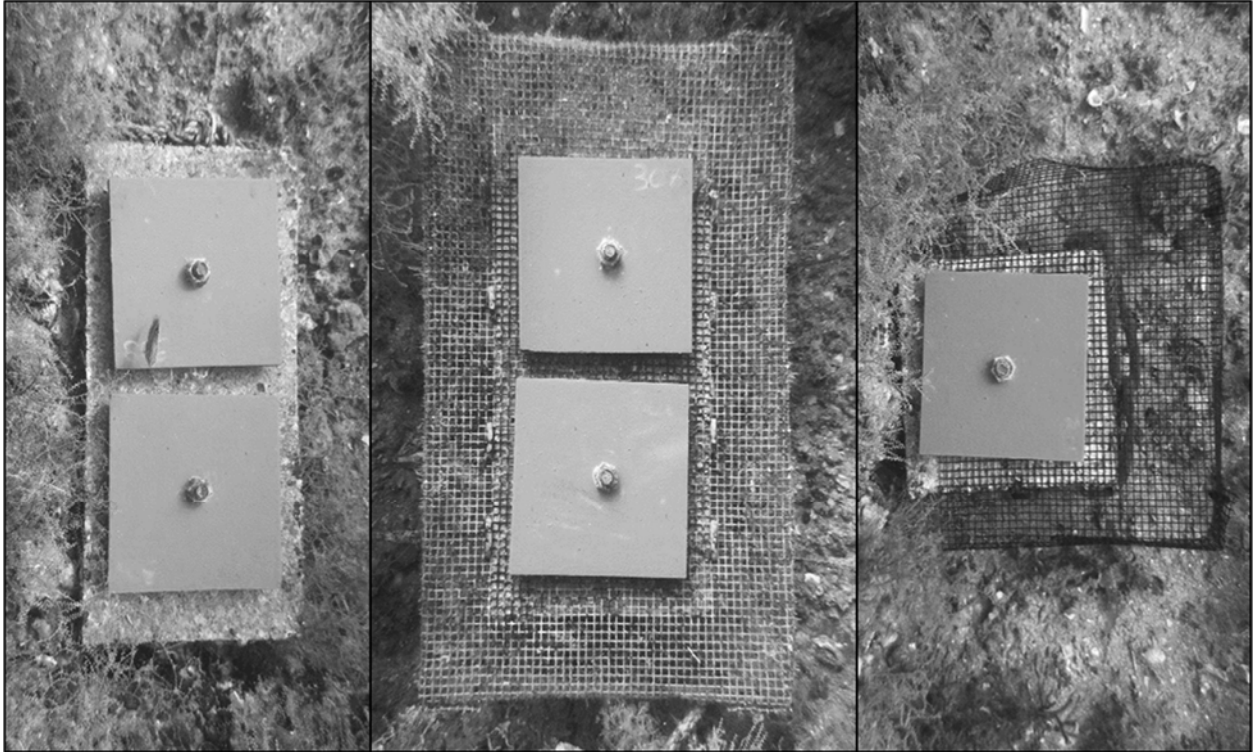
Acknowledgements

This work would not have been possible without the assistance of our dedicated volunteer divers and the support of members of the Fish Ecology Lab.

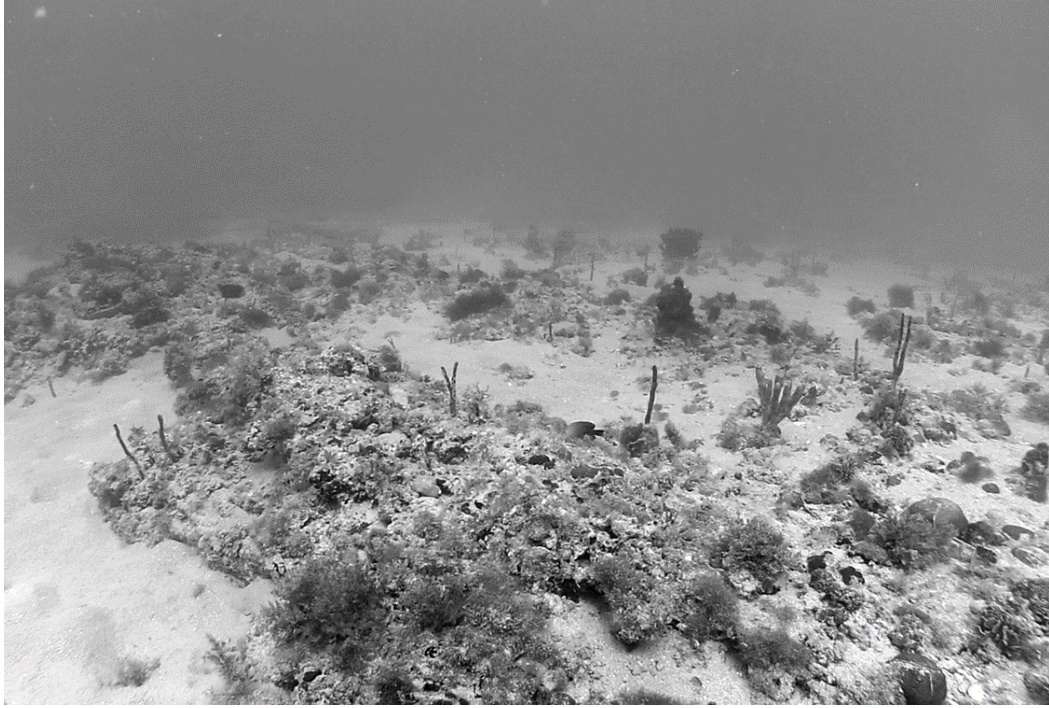
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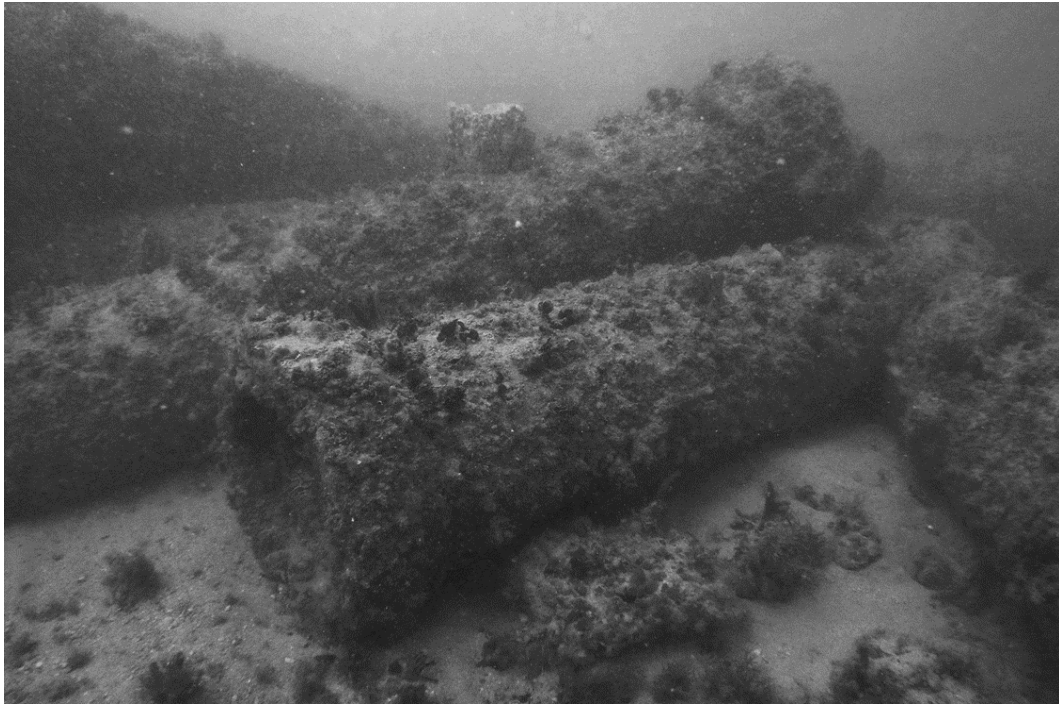
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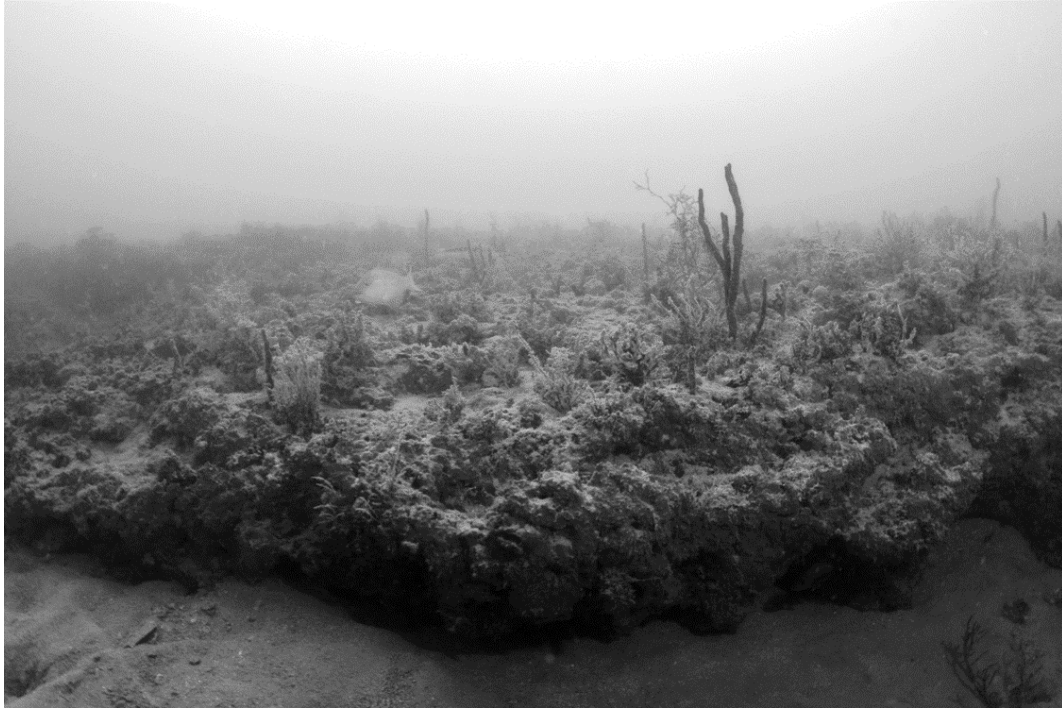
Supplementary figure 1



Supplementary Figure 2a



Supplementary Figure 2b



Supplementary Figure 3a



Supplementary Figure 3b



Supplementary Figure 4a



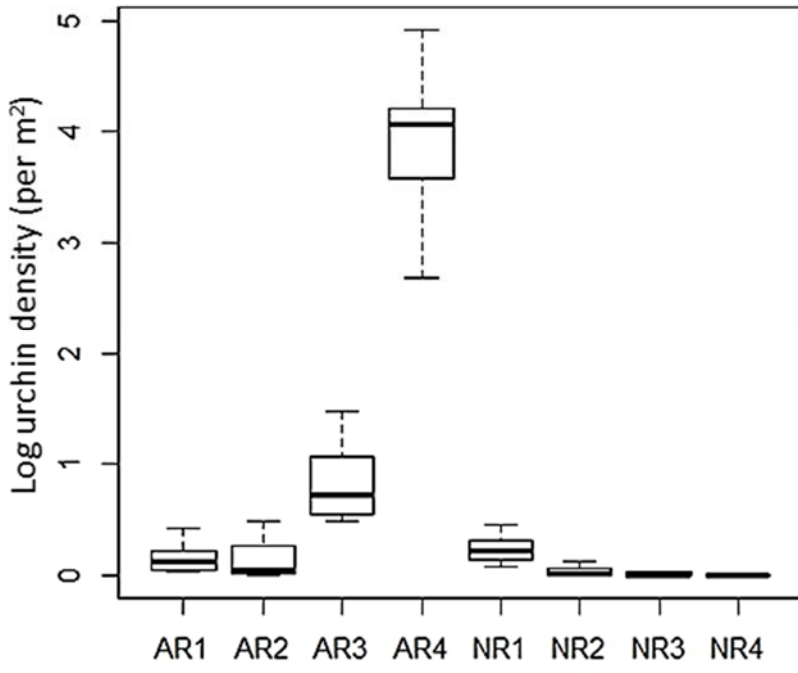
Supplementary Figure 4b



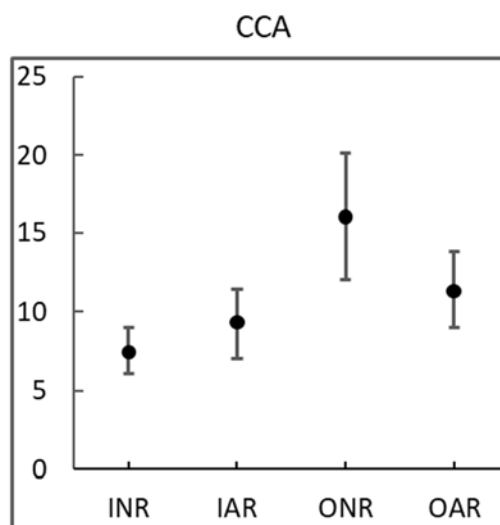
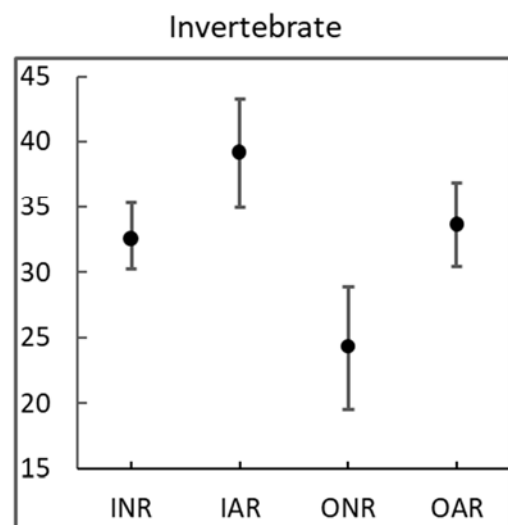
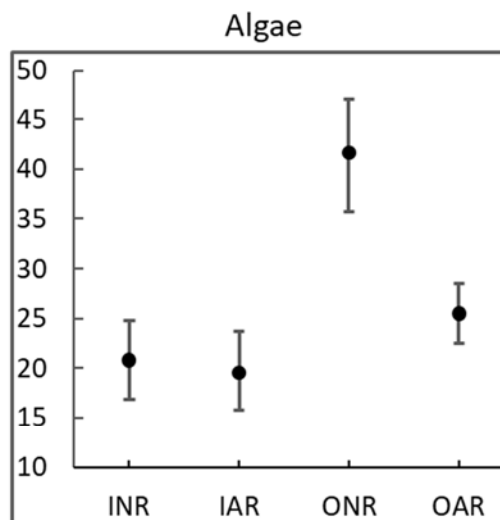
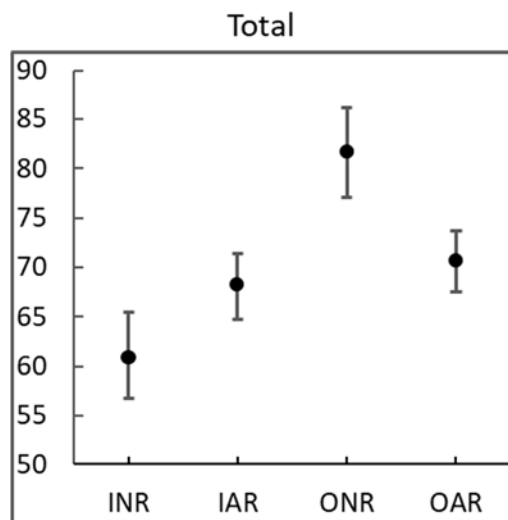
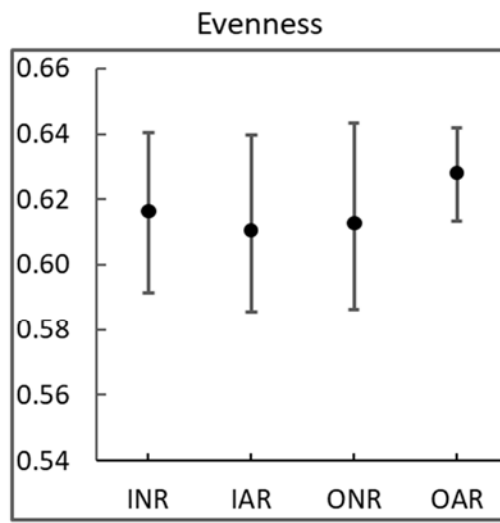
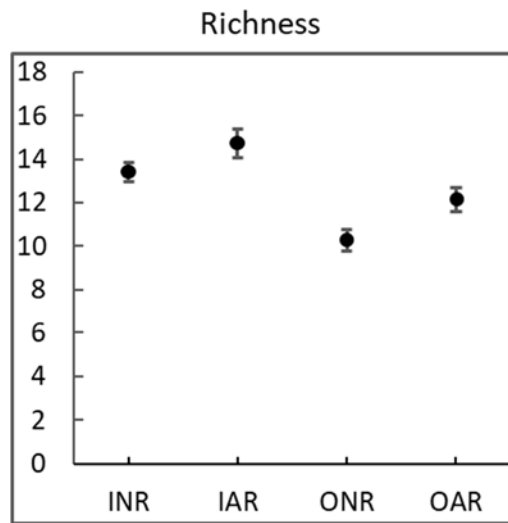
Supplementary Figure 5a



Supplementary Figure 5b



Supplementary Figure 6



Supplementary Figure 7

Supplementary Table 1

Site name	Site ID	Habitat	Depth (m)		Km from shore	Complexity (\pm SEM)	Description
21HS	NR1	Natural	13	Inshore	7.25	1.19 (\pm 0.56)	Meandering limestone reef with sloped reef ledge. ~2m of relief
Clearwater Reef	AR1	Artificial	10		6.50	1.99 (\pm 1.26)	Concrete culverts and bridge pilings deployed 1974-1999. Max relief ~4m
AC5	NR2	Natural	11		12.80	0.69 (\pm 0.31)	Limestone escarpment with patchy shallow undercuts. Relief <1m
St. Pete Beach Reef	AR2	Artificial	10		11.80	2.33 (\pm 1.30)	Steel army tanks and barge deployed in 1995. Max relief ~4m
Fisherman's Ledge	NR3	Natural	25	Offshore	41.55	0.93 (\pm 0.39)	Meandering limestone with sloped edge. Relief <1m
Pinellas II	AR3	Artificial	23		33.25	7.25 (\pm 3.56)	180 ft. steel hull ship deployed in 1982. Max relief ~11m
Caves	NR4	Natural	25		33.25	1.25 (\pm 0.68)	Limestone escarpment with ~1.5m of relief and deep undercuts
Treasure Island II	AR4	Artificial	30		47.75	8.76 (\pm 3.87)	80 ft. steel hull ship deployed in 2004. Max relief ~12m

Supplementary Table 2

Functional Group	Organism	Mean percent of total cover (\pm SEM)
Algae	Mixed turf	6.05 \pm 0.83
Algae	Cyanobacteria	5.26 \pm 0.83
Algae	<i>Polysiphonia</i> spp.	2.47 \pm 0.45
Algae	<i>Cladophora</i> spp.	1.66 \pm 0.23
Algae	<i>Ceramium</i> spp.	0.85 \pm 0.17
Algae	<i>Feldmannia indica</i>	0.76 \pm 0.22
Algae	<i>Laurencia</i> spp.	0.71 \pm 0.09
Algae	<i>Bryopsis</i> spp.	0.35 \pm 0.08
Algae	<i>Caulerpa racemosa</i>	0.24 \pm 0.14
Algae	<i>Aglaothamnion cordatum</i>	0.20 \pm 0.05
Algae	<i>Dictyota</i> spp.	0.19 \pm 0.07
Algae	<i>Dictyota mertensii</i>	0.11 \pm 0.07
Algae	<i>Chaetomorpha</i> spp.	0.08 \pm 0.02
Algae	<i>Sargassum</i> spp.	0.07 \pm 0.02
Algae	<i>Champia parvula</i>	0.05 \pm 0.03
Algae	<i>Lomentaria baileyana</i>	0.05 \pm 0.03
Algae	<i>Botryocladia occidentalis</i>	0.03 \pm 0.01
Algae	<i>Laurencia cervicornis</i>	0.03 \pm 0.01
Algae	<i>Dasya</i> spp.	0.02 \pm 0.01
Algae	<i>Caulerpa</i> spp.	0.02 \pm 0.02
Algae	<i>Rosenvingea sanctae-crucis</i>	0.02 \pm 0.02
Algae	<i>Derbesia</i> spp.	0.01 \pm 0.01
Algae	<i>Gracilaria blodgettii</i>	0.01 \pm <0.01
Algae	<i>Heterosiphonia</i> spp.	0.01 \pm 0.01
Algae	<i>Botryocladia</i> spp.	0.01 \pm <0.01
Algae	<i>Gelidiopsis</i> spp.	0.01 \pm <0.01
Algae	<i>Champia</i> spp.	0.01 \pm <0.01
Algae	<i>Cladophoropsis</i> spp.	0.01 \pm <0.01
Algae	<i>Codium</i> spp.	0.01 \pm <0.01
Algae	<i>Seriospora</i> spp.	<0.01 \pm <0.01
Algae	<i>Apoglossum</i> spp.	<0.01 \pm <0.01
Algae	<i>Enteromorpha</i> spp.	<0.01 \pm <0.01
Algae	<i>Pleonosporium</i> spp.	<0.01 \pm <0.01
Algae	<i>Branchioglossum minutum</i>	<0.01 \pm <0.01
Algae	<i>Chondria</i> spp.	<0.01 \pm <0.01
Algae	<i>Gracilaria lemaneiformis</i>	<0.01 \pm <0.01
Algae	<i>Grateloupia gibbesii</i>	<0.01 \pm <0.01

Algae	<i>Griffithsia globulifera</i>	<0.01 ±<0.01
Algae	<i>Hypnea valentiae</i>	<0.01 ±<0.01
Invertebrate	Polychaete	15.06 ±0.9
Invertebrate	Barnacle	4.53 ±0.62
Invertebrate	Bryzoan	3.36 ±0.32
Invertebrate	Hydroid	2.89 ±0.28
Invertebrate	Ascidian	2.82 ±0.73
Invertebrate	Oyster	1.68 ±0.37
Invertebrate	Jingle shell	0.20 ±0.05
Invertebrate	Stony Coral	0.10 ±0.04
Invertebrate	Unknown bivalve	0.09 ±0.02
Invertebrate	Coon oyster	0.05 ±0.02
Invertebrate	Feather duster worm	0.03 ±0.02
Invertebrate	Anemone	0.01 ±<0.01
Invertebrate	Sponge	0.01 ±<0.01
Invertebrate	Winged oyster	<0.01 ±<0.01
Invertebrate	Unknown invertebrate	<0.01 ±<0.01
CCA	Crustose coralline algae	17.94 ±1.03

Supplementary Table 3

Functional Group	Organism	Mean percent of total cover (\pm SEM)
Algae	Cyanobacteria	5.19 \pm 2.53
Algae	<i>Caulerpa</i> spp.	4.59 \pm 1.87
Algae	<i>Botryocladia</i> spp.	4.20 \pm 1.20
Algae	<i>Chondria</i> spp.	3.19 \pm 1.37
Algae	<i>Sporochnus pedunculatus</i>	2.54 \pm 1.17
Algae	<i>Amphiroa</i> spp.	1.58 \pm 0.86
Algae	<i>Gracilaria blodgettii</i>	1.47 \pm 0.42
Algae	<i>Jania</i> spp.	1.13 \pm 0.45
Algae	<i>Cladophora</i> spp.	1.06 \pm 0.54
Algae	<i>Gelidiopsis</i> spp.	0.95 \pm 0.43
Algae	<i>Sargassum</i> spp.	0.77 \pm 0.38
Algae	<i>Laurencia</i> spp.	0.66 \pm 0.20
Algae	<i>Spatoglossum schroederi</i>	0.66 \pm 0.62
Algae	<i>Halimeda</i> spp.	0.65 \pm 0.31
Algae	<i>Penicillium</i> spp.	0.55 \pm 0.24
Algae	<i>Gracilaria mammillaris</i>	0.43 \pm 0.21
Algae	<i>Halymenia</i> spp.	0.37 \pm 0.29
Algae	<i>Kallymenia westii</i>	0.34 \pm 0.30
Algae	<i>Codium</i> spp.	0.16 \pm 0.09
Algae	<i>Dictyota</i> spp.	0.14 \pm 0.07
Algae	<i>Grateloupia gibbesii</i>	0.13 \pm 0.12
Algae	<i>Ceramium</i> spp.	0.12 \pm 0.09
Algae	Unknown red algae	0.06 \pm 0.03
Algae	Unknown green algae	0.05 \pm 0.02
Algae	<i>Neogoniolithon</i> sp.	0.04 \pm 0.02
Algae	<i>Valonia</i> spp.	0.02 \pm 0.01
Algae	<i>Udotea</i> spp.	0.02 \pm 0.01
Algae	Unknown brown algae	0.01 \pm 0.01
Algae	<i>Dasya</i> spp.	0.01 \pm 0.01
Algae	<i>Padina</i> spp.	<0.01 \pm <0.01
Algae	<i>Lobophora</i> spp.	<0.01 \pm <0.01
Algae	<i>Avrainvillea</i> spp.	<0.01 \pm <0.01
Invertebrate	Hydroid	19.18 \pm 3.56
Invertebrate	Sponge	10.39 \pm 1.05
Invertebrate	Ascidian	3.67 \pm 0.72
Invertebrate	<i>Cladocora arbuscula</i>	0.69 \pm 0.08
Invertebrate	<i>Siderastrea radians</i>	0.54 \pm 0.20
Invertebrate	<i>Oculina robusta</i>	0.48 \pm 0.09
Invertebrate	<i>Phyllangia americana</i>	0.43 \pm 0.12
Invertebrate	<i>Leptogorgia virgulata</i>	0.30 \pm 0.13

Invertebrate	<i>Carijoa riisei</i>	0.27 ±0.16
Invertebrate	<i>Solenastrea hyades</i>	0.24 ±0.07
Invertebrate	<i>Siderastrea siderea</i>	0.16 ±0.07
Invertebrate	<i>Stephanocoenia intersepta</i>	0.04 ±0.02
Invertebrate	<i>Murcia</i> spp.	0.01 ±0.01
Invertebrate	<i>Meandrina meandrites</i>	0.01 ±0.01
Invertebrate	<i>Scolymia lacera</i>	0.01 ±<0.01
Invertebrate	<i>Pseudopterogorgia</i> sp.	<0.01 ±<0.01
Invertebrate	Unknown octocoral	<0.01 ±<0.01
CCA	Crustose coralline algae	4.35 ±0.92

Supplementary Table 4

Site	Min urchins	Max urchins	Mean urchins (\pm SEM)
NR1	0	8	2.69 (\pm 0.44)
AR1	0	6	1.85 (\pm 0.46)
NR2	0	2	0.22 (\pm 0.11)
AR2	0	8	1.21 (\pm 0.52)
NR3	0	1	0.16 (\pm 0.09)
AR3	1	19	8.36 (\pm 1.55)
NR4	0	1	0.04 (\pm 0.04)
AR4	27	221	112 (\pm 14)

Supplementary Table 5

	Formula	Estimate	SE	t-stat	p-value
Species Richness	Control vs Exclusion	0.18	0.05	3.51	0.001
	Control vs Cage Control	-0.03	0.06	-0.49	0.628
	Exclusion vs Cage Control	-0.21	0.06	-3.36	0.001

	Formula	Estimate	SE	t-stat	p-value
Evenness	Control vs Exclusion	-0.004	0.02	-0.23	0.818
	Control vs Cage Control	0.01	0.02	0.51	0.609
	Exclusion vs Cage Control	0.01	0.02	0.69	0.488

	Formula	Estimate	SE	t-stat	p-value
Total percent cover	Control vs Exclusion	-0.06	0.06	-1.01	0.312
	Control vs Cage Control	-0.05	0.07	-0.70	0.482
	Exclusion vs Cage Control	0.01	0.07	0.14	0.891

	Formula	Estimate	SE	t-stat	p-value
Algal percent cover	Control vs Exclusion	-2.88	0.82	-3.53	<0.001
	Control vs Cage Control	-1.64	1.01	-1.61	0.107
	Exclusion vs Cage Control	1.25	0.80	1.56	0.120

	Formula	Estimate	SE	t-stat	p-value
Invertebrate percent cover	Control vs Exclusion	-0.47	0.27	-1.77	0.077
	Control vs Cage Control	-0.26	0.33	-0.77	0.440
	Exclusion vs Cage Control	0.22	0.32	0.68	0.497

	Formula	Estimate	SE	t-stat	p-value
CCA percent cover	Control vs Exclusion	5.21	1.33	3.92	<0.001
	Control vs Cage Control	0.91	1.05	0.87	0.385
	Exclusion vs Cage Control	-4.30	1.52	-2.83	0.005

Supplementary Table 6

Model	Formula	Parameter	Estimate	SE	t-stat	p-value	AICc	Δ AICc	Weight
1	$\mu\{\text{Species richness} \mid \text{location, reef}\} = \beta_0 + \beta_1\text{location} + \beta_2\text{reef} + \beta_3\text{location:reef}$	β_0	14.72	0.96	15.34	<0.001	430.85	2.09	0.35
		β_1	-2.61	1.31	-2.00	0.140			
		β_2	-1.11	1.33	-0.84	0.4642			
		β_3	-0.73	2.04	-0.36	0.744			
2	$\mu\{\text{Species richness} \mid \text{location, reef}\} = \beta_0 + \beta_1\text{location} + \beta_2\text{reef}$	β_0	14.88	0.85	17.60	0.000	428.98	0.22	0.90
		β_1	-2.91	1.00	-2.89	0.044			
		β_2	-1.42	1.01	-1.41	0.231			
3	$\mu\{\text{Species richness} \mid \text{location, reef}\} = \beta_0 + \beta_1\text{location}$	β_0	14.16	0.75	18.89	<0.001	428.76	0.00	1.00
		β_1	-2.66	1.12	-2.38	0.060			

Model	Formula	Parameter	Estimate	SE	t-stat	p-value	AICc	Δ AICc	Weight
1	$\mu\{\text{Evenness} \mid \text{location, reef}\} = \beta_0 + \beta_1\text{location} + \beta_2\text{reef} + \beta_3\text{location:reef}$	β_0	1.63	0.07	23.84	<0.001	-124.80	3.80	0.15
		β_1	-0.04	0.09	-0.46	0.647			
		β_2	-0.01	0.09	-0.10	0.919			
		β_3	0.04	0.13	0.33	0.742			
2	$\mu\{\text{Evenness} \mid \text{location, reef}\} = \beta_0 + \beta_1\text{location} + \beta_2\text{reef}$	β_0	1.62	0.06	28.01	<0.001	-126.70	1.90	0.39
		β_1	-0.02	0.06	-0.32	0.747			
		β_2	0.01	0.06	0.18	0.858			
3	$\mu\{\text{Evenness} \mid \text{location, reef}\} = \beta_0 + \beta_2\text{reef}$	β_0	1.63	0.04	36.25	<0.001	-128.60	0.00	1.00
		β_2	-0.02	0.06	-0.38	0.706			

Model	Formula	Parameter	Estimate	SE	t-stat	p-value	AICc	Δ AICc	Weight
1	$\mu\{\text{Total percent cover} \mid \text{location, reef}\} = \beta_0 + \beta_1\text{location} + \beta_2\text{reef} + \beta_3\text{location:reef}$	β_0	0.12	0.00	24.48	<0.001	305.4	2.30	0.32
		β_1	0.00	0.01	-0.37	0.714			
		β_2	0.01	0.01	1.07	0.286			
		β_3	-0.02	0.01	-1.58	0.114			
2	$\mu\{\text{Total percent cover} \mid \text{location, reef}\} = \beta_0 + \beta_1\text{location} + \beta_2\text{reef}$	β_0	0.13	0.01	22.51	<0.001	305.1	2.00	0.37
		β_1	-0.01	0.01	-1.33	0.183			
		β_2	0.00	0.01	0.02	0.988			
3	$\mu\{\text{Total percent cover} \mid \text{location, reef}\} = \beta_0 + \beta_1\text{location}$	β_0	0.13	0.00	28.27	<0.001	303.1	0.00	1.00
		β_1	-0.01	0.01	-1.35	0.176			

Model	Formula	Parameter	Estimate	SE	t-stat	p-value	AICc	Δ AICc	Weight
1	$\mu\{\text{Algal percent cover} \mid \text{location, reef}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{location:reef}$	β_0	0.05	0.01	5.33	0.000	760.6	2.00	0.37
		β_1	-0.01	0.01	-1.01	0.312			
		β_2	0.00	0.01	-0.26	0.791			
		β_3	-0.01	0.02	-0.75	0.451			
2	$\mu\{\text{Algal percent cover} \mid \text{location, reef}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef}$	β_0	0.06	0.01	6.85	0.000	759.2	0.60	0.74
		β_1	-0.02	0.01	-2.07	0.039			
		β_2	-0.01	0.01	-1.35	0.178			
3	$\mu\{\text{Algal percent cover} \mid \text{location, reef}\} = \beta_0 + \beta_1 \text{location}$	β_0	0.05	0.01	6.98	0.000	758.6	0.00	1.00
		β_1	-0.01	0.01	-1.58	0.114			

Model	Formula	Parameter	Estimate	SE	t-stat	p-value	AICc	Δ AICc	Weight
1	$\mu\{\text{Invertebrate percent cover} \mid \text{location, reef}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{location:reef}$	β_0	0.03	0.00	7.77	0.000	772.5	1.30	0.52
		β_1	0.00	0.00	0.94	0.349			
		β_2	0.00	0.00	1.05	0.295			
		β_3	0.01	0.01	0.81	0.417			
2	$\mu\{\text{Invertebrate percent cover} \mid \text{location, reef}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef}$	β_0	0.02	0.00	8.31	<0.001	771.2	0.00	1.00
		β_1	0.01	0.00	1.67	0.094			
		β_2	0.01	0.00	1.90	0.057			
3	$\mu\{\text{Invertebrate percent cover} \mid \text{location, reef}\} = \beta_0 + \beta_2 \text{reef}$	β_0	0.03	0.00	9.73	<0.001	771.5	0.30	0.86
		β_2	0.01	0.00	1.24	0.217			

Model	Formula	Parameter	Estimate	SE	t-stat	p-value	AICc	Δ AICc	Weight
1	$\mu\{\text{CCA percent cover} \mid \text{location, reef}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{location:reef}$	β_0	0.11	0.04	2.88	0.004	550.00	3.20	0.20
		β_1	-0.02	0.04	-0.47	0.636			
		β_2	0.02	0.06	0.43	0.668			
		β_3	-0.05	0.06	-0.76	0.449			
2	$\mu\{\text{CCA percent cover} \mid \text{location, reef}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef}$	β_0	0.13	0.03	3.85	0.000	548.6	1.8	0.41
		β_1	-0.05	0.03	-1.40	0.162			
		β_2	-0.01	0.03	-0.39	0.695			
3	$\mu\{\text{CCA percent cover} \mid \text{location, reef}\} = \beta_0 + \beta_1 \text{location}$	β_0	0.12	0.03	4.37	0.000	546.8	0	1.00
		β_1	-0.04	0.03	-1.34	0.181			

Supplementary Table 7

Model	Formula	Parameter	Estimate	SE	t-stat	p-value	AICc	Δ AICc	Weight
1	$\mu\{\text{Species richness} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin} + \beta_4$ location:reef + β_5 location:urchin + β_6 reef:urchin + β_7 location:reef:urchin	β_0	1.14	0.07	16.05	0.000	-82.27	0.00	1.00
		β_1	0.08	0.04	1.96	0.145			
		β_2	0.22	0.13	1.73	0.183			
		β_3	4.64	2.04	2.27	0.030			
		β_4	-0.20	0.10	-1.91	0.152			
		β_5	-4.49	2.02	-2.22	0.034			
		β_6	-4.70	2.06	-2.28	0.029			
β_7	4.58	2.03	2.26	0.031					

Model	Formula	Parameter	Estimate	SE	t-stat	p-value	AICc	Δ AICc	Weight
1	$\mu\{\text{Evenness} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin} + \beta_4$ location:reef + β_5 location:urchin + β_6 reef:urchin + β_7 location:reef:urchin	β_0	0.37	0.09	3.97	0.000	-68.14	8.34	0.02
		β_1	0.02	0.06	0.29	0.788			
		β_2	-0.11	0.16	-0.70	0.534			
		β_3	-0.48	2.40	-0.20	0.842			
		β_4	0.09	0.12	0.69	0.538			
		β_5	0.39	2.38	0.16	0.871			
		β_6	0.76	2.43	0.31	0.756			
β_7	-0.49	2.38	-0.21	0.837					
2	$\mu\{\text{Evenness} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin} + \beta_4$ location:reef + β_5 location:urchin + β_6 reef:urchin	β_0	0.37	0.09	4.00	0.000	-70.10	6.38	0.04
		β_1	0.02	0.05	0.35	0.748			
		β_2	-0.11	0.16	-0.68	0.543			
		β_3	0.01	0.27	0.03	0.976			
		β_4	0.08	0.12	0.68	0.547			
		β_5	-0.10	0.18	-0.56	0.578			
β_6	0.26	0.25	1.05	0.302					
3	$\mu\{\text{Evenness} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin} + \beta_4$ location:reef + β_6 reef:urchin	β_0	0.37	0.09	4.07	0.000	-71.73	4.76	0.09
		β_1	0.02	0.05	0.35	0.750			
		β_2	-0.06	0.13	-0.45	0.685			
		β_3	-0.09	0.20	-0.47	0.639			
		β_4	0.04	0.10	0.43	0.694			
β_6	0.20	0.22	0.89	0.377					
4	$\mu\{\text{Evenness} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin} + \beta_6$ reef:urchin	β_0	0.35	0.08	4.57	0.000	-73.51	2.97	0.23
		β_1	0.03	0.04	0.71	0.515			
		β_2	-0.01	0.05	-0.13	0.906			
		β_3	-0.07	0.19	-0.37	0.715			
β_6	0.19	0.22	0.90	0.377					
5	$\mu\{\text{Evenness} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin}$	β_0	0.30	0.06	5.42	0.000	-74.62	1.86	0.39
		β_1	0.05	0.04	1.49	0.209			
		β_2	0.02	0.04	0.55	0.610			
		β_3	0.09	0.06	1.59	0.120			
6	$\mu\{\text{Evenness} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_3 \text{urchin}$	β_0	0.32	0.05	6.36	0.000	-76.28	0.20	0.91
		β_1	0.05	0.03	1.40	0.220			
		β_3	0.11	0.05	2.16	0.038			
7	$\mu\{\text{Evenness} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_3 \text{urchin}$	β_0	0.38	0.02	17.59	0.000	-76.48	0.00	1.00
		β_3	0.12	0.05	2.22	0.033			

Model	Formula	Parameter	Estimate	SE	t-stat	p-value	AICc	Δ AICc	Weight
1	$\mu\{\text{Total percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin} + \beta_4 \text{location:reef} + \beta_5 \text{location:urchin} + \beta_6 \text{reef:urchin} + \beta_7 \text{location:reef:urchin}$	β_0	50.93	25.22	2.02	0.052	381.56	256.58	0.00
		β_1	-2.60	21.02	-0.12	0.910			
		β_2	-6.80	31.52	-0.22	0.843			
		β_3	-39.00	59.39	-0.66	0.516			
		β_4	12.09	23.91	0.51	0.648			
		β_5	35.28	34.42	1.03	0.313			
		β_6	530.53	450.12	1.18	0.247			
2	$\mu\{\text{Total percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin} + \beta_4 \text{location:reef} + \beta_5 \text{location:urchin} + \beta_6 \text{reef:urchin}$	β_0	49.31	24.82	1.99	0.055	380.93	5.97	0.05
		β_1	-1.38	20.85	-0.07	0.952			
		β_2	-0.90	30.46	-0.03	0.978			
		β_3	-34.03	59.96	-0.57	0.574			
		β_4	7.44	23.24	0.32	0.770			
		β_5	32.31	34.74	0.93	0.359			
		β_6	44.09	47.83	0.92	0.363			
3	$\mu\{\text{Total percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin} + \beta_5 \text{location:urchin} + \beta_6 \text{reef:urchin}$	β_0	42.55	12.83	3.32	0.002	379.05	4.09	0.13
		β_1	4.55	9.34	0.49	0.651			
		β_2	-25.88	53.67	-0.48	0.633			
		β_3	8.33	9.87	0.84	0.446			
		β_5	25.87	27.98	0.92	0.362			
		β_6	39.38	45.12	0.87	0.389			
4	$\mu\{\text{Total percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin} + \beta_5 \text{location:urchin}$	β_0	43.32	12.35	3.51	0.001	377.88	2.92	0.23
		β_1	1.99	8.53	0.23	0.827			
		β_2	-3.28	46.50	-0.07	0.944			
		β_3	13.40	7.65	1.75	0.155			
		β_5	16.59	25.53	0.65	0.520			
5	$\mu\{\text{Total percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin}$	β_0	38.68	10.07	3.84	0.001	376.36	1.40	0.50
		β_1	5.24	6.93	0.76	0.491			
		β_2	12.30	7.48	1.64	0.176			
		β_3	26.04	11.05	2.36	0.024			
6	$\mu\{\text{Total percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_2 \text{reef} + \beta_3 \text{urchin}$	β_0	44.75	6.43	6.96	<0.001	374.96	0	1
		β_2	13.77	7.39	1.86	0.121			
		β_3	28.41	10.62	2.67	0.011			
7	$\mu\{\text{Total percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_3 \text{urchin}$	β_0	54.30	4.59	11.82	<0.001	375.92	0.95	0.62
		β_3	20.49	10.59	1.93	0.061			

Model	Formula	Parameter	Estimate	SE	t-stat	p-value	AICc	Δ AICc	Weight
1	$\mu\{\text{Algal percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin} + \beta_4 \text{location:reef} + \beta_5 \text{location:urchin} + \beta_6 \text{reef:urchin} + \beta_7 \text{location:reef:urchin}$	β_0	3.85	2.78	1.39	0.175	197.91	8.91	0.01
		β_1	1.10	1.70	0.65	0.562			
		β_2	1.61	4.38	0.37	0.738			
		β_3	31.40	51.29	0.61	0.545			
		β_4	-2.64	3.19	-0.83	0.468			
		β_5	-25.04	50.60	-0.49	0.624			
		β_6	-37.69	51.72	-0.73	0.472			
β_7	28.81	50.74	0.57	0.574					
2	$\mu\{\text{Algal percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin} + \beta_4 \text{location:reef} + \beta_5 \text{location:urchin} + \beta_6 \text{reef:urchin}$	β_0	4.11	2.66	1.54	0.132	196.29	7.29	0.03
		β_1	0.90	1.61	0.56	0.616			
		β_2	1.26	4.23	0.30	0.785			
		β_3	2.35	6.15	0.38	0.704			
		β_4	-2.37	3.08	-0.77	0.498			
		β_5	3.60	3.81	0.95	0.351			
β_6	-8.37	5.69	-1.47	0.151					
3	$\mu\{\text{Algal percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin} + \beta_5 \text{location:urchin} + \beta_6 \text{reef:urchin}$	β_0	5.12	2.32	2.21	0.035	194.99	5.99	0.05
		β_1	0.26	1.38	0.19	0.860			
		β_2	-1.80	1.42	-1.27	0.272			
		β_3	3.03	6.05	0.50	0.620			
		β_5	2.21	3.33	0.67	0.510			
		β_6	-7.29	5.47	-1.33	0.192			
4	$\mu\{\text{Algal percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin} + \beta_6 \text{reef:urchin}$	β_0	4.64	2.14	2.16	0.038	193.49	4.50	0.11
		β_1	0.57	1.26	0.45	0.673			
		β_2	-1.79	1.38	-1.29	0.266			
		β_3	5.51	4.58	1.20	0.238			
		β_6	-5.84	5.04	-1.16	0.255			
5	$\mu\{\text{Algal percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin}$	β_0	5.93	1.70	3.49	0.001	192.90	3.90	0.14
		β_1	-0.04	1.07	-0.04	0.973			
		β_2	-2.56	1.14	-2.26	0.087			
		β_3	0.42	1.42	0.30	0.768			
6	$\mu\{\text{Algal percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_2 \text{reef} + \beta_3 \text{urchin}$	β_0	5.87	0.67	8.80	0.000	190.90	1.90	0.39
		β_2	-2.55	1.09	-2.35	0.065			
		β_3	0.41	1.36	0.30	0.764			
7	$\mu\{\text{Algal percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_2 \text{reef}$	β_0	5.90	0.65	9.11	0.000	188.99	0.00	1.00
		β_2	-2.43	0.98	-2.47	0.057			

Model	Formula	Parameter	Estimate	SE	t-stat	p-value	AICc	Δ AICc	Weight
1	$\mu\{\text{Invertebrates percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin} + \beta_4 \text{location:reef} + \beta_5 \text{location:urchin} + \beta_6 \text{reef:urchin} + \beta_7 \text{location:reef:urchin}$	β_0	30.82	8.70	3.54	0.001	330.97	4.96	0.08
		β_1	-10.11	5.22	-1.94	0.148			
		β_2	-15.06	15.78	-0.95	0.410			
		β_3	17.39	249.45	0.07	0.945			
		β_4	18.58	12.50	1.49	0.234			
		β_5	-24.61	247.06	-0.10	0.921			
		β_6	8.08	251.86	0.03	0.975			
β_7	15.45	247.88	0.06	0.951					
2	$\mu\{\text{Invertebrates percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin} + \beta_4 \text{location:reef} + \beta_5 \text{location:urchin} + \beta_6 \text{reef:urchin}$	β_0	31.08	8.43	3.69	0.001	328.97	2.96	0.23
		β_1	-10.28	4.92	-2.09	0.128			
		β_2	-15.37	15.38	-1.00	0.391			
		β_3	1.37	27.94	0.05	0.961			
		β_4	18.79	12.14	1.55	0.219			
		β_5	-9.26	19.77	-0.47	0.643			
β_6	24.27	25.29	0.96	0.344					
3	$\mu\{\text{Invertebrates percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin} + \beta_4 \text{location:reef} + \beta_6 \text{reef:urchin}$	β_0	31.03	8.30	3.74	0.001	327.23	1.22	0.54
		β_1	-10.29	4.83	-2.13	0.123			
		β_2	-10.67	11.70	-0.91	0.429			
		β_3	-7.45	19.34	-0.39	0.703			
		β_4	15.14	9.29	1.63	0.202			
		β_6	17.73	21.47	0.83	0.415			
4	$\mu\{\text{Invertebrates percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin} + \beta_4 \text{location:reef}$	β_0	4.64	2.14	2.16	<0.001	326.01	0.00	1.00
		β_1	0.57	1.26	0.45	0.140			
		β_2	-1.79	1.38	-1.29	0.518			
		β_3	5.51	4.58	1.20	0.412			
β_4	-5.84	5.04	-1.16	0.195					
5	$\mu\{\text{Invertebrates percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin}$	β_0	19.79	5.11	3.87	0.001	327.03	1.02	0.60
		β_1	-3.97	3.31	-1.20	0.297			
		β_2	9.56	3.59	2.66	0.056			
β_3	17.23	5.75	3.00	0.005					
6	$\mu\{\text{Invertebrates percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_2 \text{reef} + \beta_3 \text{urchin}$	β_0	14.19	2.12	6.68	0.000	326.58	0.57	0.75
		β_2	10.88	3.52	3.09	0.027			
		β_3	14.71	5.51	2.67	0.011			

Model	Formula	Parameter	Estimate	SE	t-stat	p-value	AICc	Δ AICc	Weight
1	$\mu\{\text{CCA percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin} + \beta_4 \text{location:reef} + \beta_5 \text{location:urchin} + \beta_6 \text{reef:urchin} + \beta_7 \text{location:reef:urchin}$	β_0	0.48	0.85	0.56	0.578	131.06	6.08	0.05
		β_1	1.26	0.51	2.46	0.091			
		β_2	-0.79	1.54	-0.51	0.642			
		β_3	25.45	24.40	1.04	0.305			
		β_4	0.41	1.22	0.34	0.757			
		β_5	-24.80	24.17	-1.03	0.313			
		β_6	-26.67	24.64	-1.08	0.287			
β_7	26.18	24.25	1.08	0.288					
2	$\mu\{\text{CCA percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin} + \beta_4 \text{location:reef} + \beta_5 \text{location:urchin} + \beta_6 \text{reef:urchin}$	β_0	0.66	0.85	0.78	0.440	130.45	5.48	0.06
		β_1	1.09	0.50	2.20	0.115			
		β_2	-1.06	1.54	-0.69	0.541			
		β_3	-0.70	2.78	-0.25	0.804			
		β_4	0.64	1.21	0.53	0.632			
		β_5	1.22	1.96	0.62	0.538			
		β_6	-0.25	2.52	-0.10	0.921			
3	$\mu\{\text{CCA percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin} + \beta_4 \text{location:reef} + \beta_5 \text{location:urchin}$	β_0	0.71	0.72	0.99	0.331	128.47	3.49	0.17
		β_1	1.07	0.44	2.43	0.094			
		β_2	-1.13	1.32	-0.86	0.453			
		β_3	-0.75	2.70	-0.28	0.782			
		β_4	0.68	1.14	0.60	0.591			
		β_5	1.12	1.67	0.67	0.506			
4	$\mu\{\text{CCA percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin} + \beta_5 \text{location:urchin}$	β_0	0.58	0.69	0.84	0.405	126.88	1.90	0.39
		β_1	1.15	0.42	2.74	0.052			
		β_2	-0.37	0.37	-1.02	0.367			
		β_3	-1.32	2.49	-0.53	0.599			
		β_5	1.69	1.35	1.25	0.221			
5	$\mu\{\text{CCA percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_2 \text{reef} + \beta_3 \text{urchin}$	β_0	0.00	0.55	-0.01	0.996	126.52	1.54	0.46
		β_1	1.49	0.36	4.18	0.014			
		β_2	-0.26	0.39	-0.68	0.535			
		β_3	1.65	0.59	2.81	0.008			
6	$\mu\{\text{CCA percent cover} \mid \text{location, reef, urchin}\} = \beta_0 + \beta_1 \text{location} + \beta_3 \text{urchin}$	β_0	-0.17	0.52	-0.33	0.746	124.98	0.00	1.00
		β_1	1.56	0.36	4.37	0.007			
		β_3	1.43	0.52	2.76	0.009			