Coral identity and structural complexity drive habitat associations and demographic processes for an increasingly important Caribbean herbivore

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ABSTRACT: Habitat complexity plays a vital role in shaping ecological communities, but many coral reef ecosystems are shifting to alternative states with altered community compositions and reduced complexity. Sea urchins are common inhabitants of reefs, and their importance for controlling the distribution and abundance of algae in marine ecosystems is well understood. Less understood is the role of habitat complexity and species identity of foundational species in dictating the abundance of reef herbivores. We explored how the structural complexity and identity of 3 corals commonly observed on contemporary Caribbean reefs mediate the abundance, behavior, and demographic characteristics of an increasingly important herbivore, the sea urchin *Echinometra viridis*. Tethered urchins survived better on the more structurally complex coral *Agaricia tenuifolia* and hydrocoral *Millepora alcicornis* than on less complex branching *Porites* species. However, natural densities of urchins on these corals did not follow the same pattern, suggesting that coral identity, independent of complexity, also contributes to habitat associations. In habitat choice experiments, urchins preferred the structurally complex coral *A. tenuifolia* only when waterborne cues of predators were introduced. Despite minimal differences in the standing stock of algae associated with the different corals, urchins inhabiting *Porites* colonies had a marginally higher reproductive condition than those collected from the other corals, suggesting a fitness trade-off to inhabiting the riskier coral. Understanding the drivers of herbivore habitat associations is vital for predicting the persistence of coral-dominated reefs due to feedbacks between changing coral reef communities (both species identity and habitat complexity) and shifts to algal dominance.

KEY WORDS: Habitat complexity · Foundation species · Predation risk · Gonadosomatic index · *Agaricia tenuifolia* · *Echinometra viridis* · *Millepora alcicornis* · *Porites*

INTRODUCTION

The degree of architectural complexity offered by foundation species or abiotic habitat mediates ecological processes at the population and community levels. Species diversity, abundance, recruitment, predation, and reproduction can all be affected by habitat complexity (Huffaker 1958, MacArthur & MacArthur 1961, Gaines & Roughgarden 1987, Beukers & Jones 1998, Barone & Frank 2003, Grabowski 2004), and complexity can have particularly strong impacts on predator-prey interactions (Heck & Crow-

der 1991). Prey are generally found in higher abundance in more structurally complex habitats because such habitats offer increased refuge or food resources (Bell & Westoby 1986, Olabarria et al. 2002, Gratwicke & Speight 2005, Webley et al. 2009). However, habitat associations can change in light of predation risk, food availability, life stage, physiological condition, and the interaction of these factors (Jordan et al. 1997, Dahlgren & Eggleston 2000, Alonzo 2002, Tait & Hovel 2012, Harrington & Hovel 2015). Generally, whether habitat association patterns result from reduced predation mortality in complex habitats, active habitat selection, or nonrandom association (for instance, an interaction of the above factors) can be difficult to discern (Olabarria et al. 2002, Underwood et al. 2004).

Despite the benefits of residing in complex habitats, there can also be costs that result in trade-offs. For example, sheltering in refuges from predators can result in reductions in foraging that subsequently reduce growth and fecundity (Lima & Dill 1990, Orrock et al. 2013). Given these fitness costs, predation risk must be substantial for selection to favor sheltering behavior (Levitan & Genovese 1989). The type of refuge available can determine the strength of these trade-offs because total and partial refuges differ in the degree of protection and resources they provide, which in turn alters the costs and benefits of refuge use (Orrock et al. 2013). Because the degree of habitat complexity has these direct and indirect effects on ecological processes, the anthropogenic impacts that reduce the complexity of biogenic habitats likely has cascading effects on species interactions and ecosystem functioning (Ellison et al. 2005, Alvarez-Filip et al. 2009, Waycott et al. 2009). A comparative approach of examining patterns of prey association with foundation species that vary in structural complexity can offer mechanistic insights to better understand the role of trade-offs that will determine the response of ecological communities to changes in foundation species habitats.

The complex architecture created by reef-building corals provides the foundation for one of the most diverse ecosystems on Earth (Knowlton et al. 2010). However, coral cover has declined globally (Gardner et al. 2003, Bruno & Selig 2007), and Caribbean reefs in particular are rapidly changing, undergoing a phase shift to algal domination (Dudgeon et al. 2010) and/or transitioning to a flattened coral community with reduced rugosity (Alvarez-Filip et al. 2009, 2011). The importance of reefscape-scale rugosity for fish biomass and diversity is widely recognized (Graham & Nash 2013, Pratchett et al. 2014),

but an understanding of complexity at different spatial scales is required in order to fully understand the effects of architectural elements on biotic processes (Tokeshi & Arakaki 2012). Small-bodied, coral-associated fish are strongly affected by habitat structure, as decreasing colony-scale complexity leads to enhanced predation risk, reduced abundance, lower growth rate, and lower diversity (Beukers & Jones 1998, Nemeth 1998, Holbrook et al. 2003, Pereira & Munday 2016). The effects of habitat structure on coral reef-associated invertebrates have received less attention, and the studies that have examined coral-invertebrate relationships generally measure patterns of community-level diversity and abundance (Idjadi & Edmunds 2006, Nelson et al. 2016). The relative paucity of mechanistic studies of species-specific interactions between invertebrates and contemporary reef-building corals is surprising given the importance of invertebrates as grazers on coral reefs (Edmunds & Carpenter 2001, Aronson et al. 2004, Kuempel & Altieri 2017) and in transferring energy from primary producers to higher trophic levels (Glynn & Enochs 2011, Kramer et al. 2015). However, elucidating the species-specific roles of foundation species that differ in habitat traits is important because colony-scale complexity is likely to decrease as coral communities affected by anthropogenic change move away from large, high-rugosity reef-building corals to species with hardier life histories and high turnover rates, which are generally smaller and contribute less to reefscape-scale complexity (Alvarez-Filip et al. 2011, Darling et al. 2012).

The loss of the sea urchin *Diadema antillarum* following a region-wide population collapse revealed the importance of grazers for maintaining the health of Caribbean coral reefs (Lessios 2016). However, other urchin species, namely *Echinometra viridis*, appear to be filling important functional roles, including grazing (Sangil & Guzman 2016a, Kuempel & Altieri 2017) and bioerosion (Griffin et al. 2003, Brown-Saracino et al. 2007), on many reefs in the western Caribbean. *E. viridis* can also facilitate recruitment of both scleractinian corals (Sammarco 1982) and other urchin species (Lessios 1995). Additional work suggests that abundances of *E. viridis* on reefs is dependent on the availability of complex coral structure (Nelson et al. 2016). Given the ability of sea urchins to control the abundance of primary producers at large spatial scales, and thereby determine habitat structure, in multiple marine environments (Ogden et al. 1973, Harrold & Pearse 1987, Valentine & Heck 1991), it is imperative to understand the potential feedbacks

between urchins and the foundation species upon which contemporary coral reef communities are built. Here, we explored 4 potential mechanisms contributing to the habitat association patterns of *E. viridis* on coral reefs in Caribbean Panama: (1) predation mortality, in which we predicted that more structurally complex corals would provide greater refuge from predation; (2) algal presence and community composition, whereby differences in the algal community associated with each coral species may provide insight on urchin habitat associations; (3) habitat preference, in which we predicted that urchins would prefer to inhabit more structurally complex corals over less complex corals due to increased provision of predation refugia; and (4) habitat-specific reproductive condition, in which we predicted that reproductive status of urchins would be inversely related to coral structural complexity due to refuge-induced trade-offs.

MATERIALS AND METHODS

Study site and focal species

Our study took place in the lagoon surrounding the Bocas del Toro archipelago on the Caribbean coast of Panama, with field and lab work based at the Smithsonian Tropical Research Institute (STRI) Bocas Research Station. The Bocas del Toro archipelago contains numerous islands and mangrove islets (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m577p033_supp.pdf) which are typically surrounded by shallow fringing reefs made up of 3 habitat forming coral species with different branching or plate-like morphologies. These include finger coral *Porites* spp., branching fire hydrocoral *Millepora alcicornis*, and thin leaf lettuce coral *Agaricia tenuifolia* (Fig. 1; see the Supplement). These 3 corals occur in both small patches interspersed among one another (cm to m diameter patch scale) and in larger mono-specific stands (10s of m diameter patch scale). This coral assemblage is typical for shallow reefs in the western Caribbean following the disease-induced die off of acroporid corals, which have been replaced by short-lived, rapidly growing weedy corals such as *Agaricia* and *Porites* species (Sammarco 1982, Guzman 2003, Aronson et al. 2005, Green et al. 2008, Alvarez-Filip et al. 2011). We examined how the reef urchin *Echinometra viridis*, a highly abundant herbivore in this system, interacts with these corals. *E. viridis*, a small-bodied herbivore (<50 mm test diameter), has

been the dominant urchin species on the lagoonal reefs of Bocas del Toro for millennia (Aronson et al. 2004, 2005, Cramer et al. 2017) and can now be observed on all types of benthic substrates, including live corals, coral rubble, woody debris, and sand. We used the Caribbean spiny lobster *Panulirus argus* as a predator in our experiments because of its generalist diet, including sea urchins (Segura-García et al. 2016), and because it is observed on the reefs of Bocas del Toro, while large predatory finfish are virtually absent (Cramer 2013, Seemann et al. 2014).

Coral complexity

At 6 shallow, fringing reefs located within the Bocas del Toro archipelago (STRI Bay East, STRI Bay West, San Cristobal North, San Cristobal Middle, San Cristobal South, and Isla Popa; Fig. S1), we used transect surveys to characterize the structural complexity of habitat provided by the 3 focal corals. On each survey, we haphazardly placed a 50 m transect at 1 to 2 m depth running parallel to shore. Every 5 m along this transect, we located the nearest coral colony of each species, haphazardly placed a 0.25 × 0.25 m quadrat over the colony, and took a picture of the quadrat. From these photographs, we used the image analysis program ImageJ (Schneider et al. 2012) to measure the 2-dimensional size of a randomly selected crevice from each colony, then calculated the mean and frequency distribution of crevice size openings for each coral species (see the Supplement for detailed methodology). We fitted lognormal distributions to the crevice opening size-frequency data for each coral species, and calculated the median, skewness, and coefficient of variation of these distributions. We compared distributions of crevice sizes to each other with a series of 2-sample Kolmogorov-Smirnov tests. We also statistically compared ln-transformed mean crevice size among corals with a linear mixed model with coral as a fixed factor and site as a random effect. For this and other linear models, we visually inspected residuals to assess normality and tested for homoscedasticity using Levene's test, transforming data if required to meet statistical assumptions. All statistical analyses were conducted in R v. 3.1.2 (R Development Core Team 2014), and mixed effects models were constructed using the package *nlme* (Pinheiro 2016).

For half of the coral colonies photographed for crevice size, we also measured colony rugosity using the chain-line method. At these colonies, we laid a
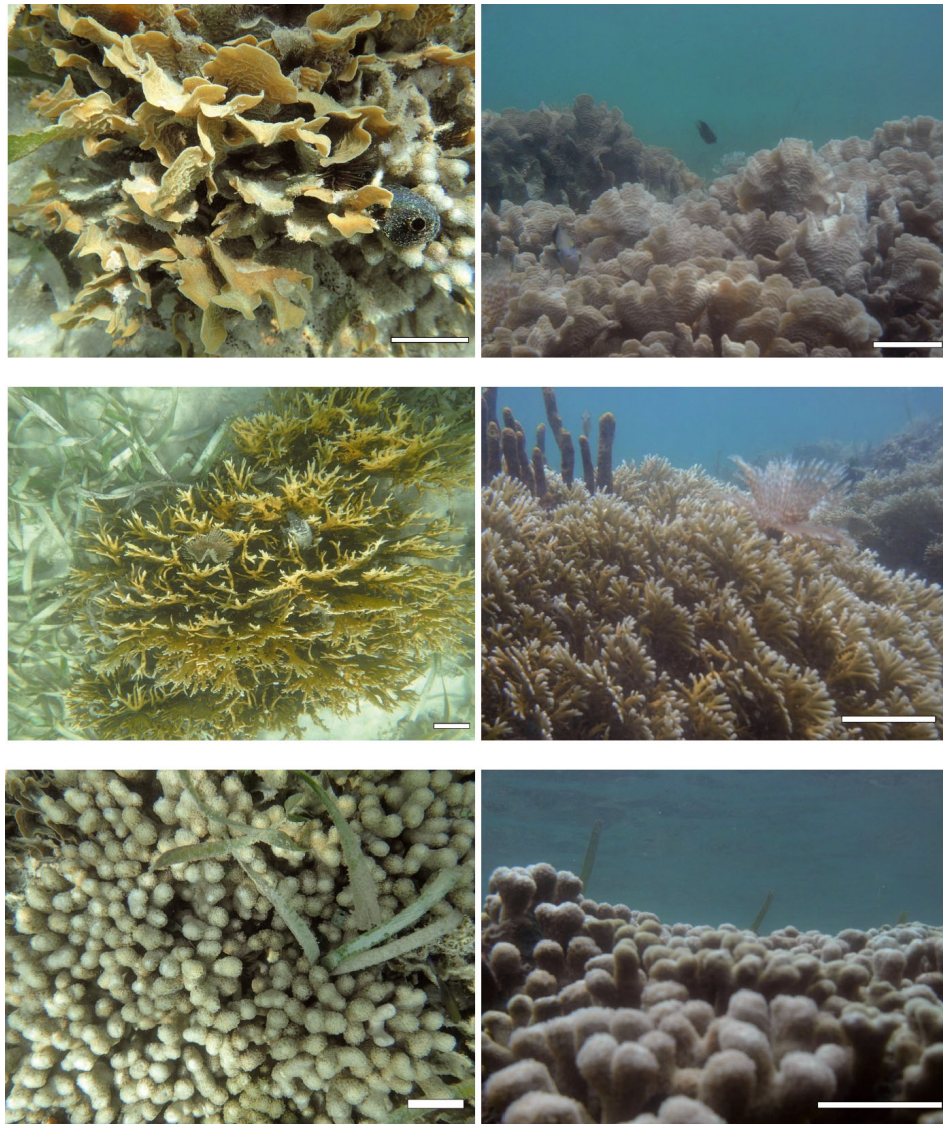
Fig. 1. Three corals commonly found on fringing reefs of Bocas del Toro, on the Caribbean coast of Panama. Rows show each coral species from above (left) and horizontally across the surface of the colony (right); white scale bar = 5 cm. Top: Thin leaf lettuce coral *Agaricia tenuifolia.* Middle: Branching fire hydrocoral *Millepora alcicornis.* Bottom: Branching finger coral *Porites* spp.

150 cm long chain with 0.5 cm links perpendicular to the branches and into each interstitial space along the surface of the colony (Fig. S2 in the Supplement). The 0.5 cm chain links were small enough to provide a measure of coral colony rugosity at the approximate scale experienced by our focal urchin species. The length of chain required to cover the surface of the coral was divided by the linear distance across the same path traced by the chain to calculate a dimensionless index of rugosity for each coral colony. We analyzed ln-transformed rugosity using a linear mixed model with coral as a fixed factor and site as a random effect.

Urchin density and sheltering behavior

We used quadrat surveys to quantify the density of urchins and the proportion of exposed urchins on each coral species at the same 6 fringing reefs surveyed for coral complexity as described above. We swam a 50 m transect parallel to shore at 1 to 2 m depth (different transect than described above), and at 10 m intervals along the transect, we identified the nearest coral colony of each of the 3 species and haphazardly placed a 0.5 × 0.5 m quadrat over each colony. We counted all visible urchins within each quadrat and recorded the number of those which

were deemed 'exposed'. For these surveys, we define exposed as being observed in a location open to a predator on at least 3 sides (including within a crevice large enough to admit a predator). To ensure consistency in evaluating exposure, one researcher (R. Dunn) made all counts of the number of exposed urchins. If the surveyed coral colony was smaller than the area of the quadrat, we scaled urchin densities according to the portion of the quadrat covered by the coral. Proportion of urchins exposed was calculated as the number observed in an exposed position divided by the total count within that quadrat. We analyzed both of these response variables with linear mixed models including coral species as a fixed factor and site as a random effect.

Urchin predation mortality

We used tethering to compare relative predation mortality of urchins inhabiting each of the 3 coral species. We deployed tethered *E. viridis* on reefs at 3 sites: STRI Bay, San Cristobal North, and San Cristobal South (Fig. S1). Tethering methodology followed the procedure commonly used for studies of urchin predation (Boada et al. 2015); briefly, we threaded monofilament line from the oral to the aboral surface of each urchin, tied the line in a loop, and kept tethered urchins in the lab for the following 24 h to allow recovery and screening of injured urchins prior to experimental deployment. We collected urchins for tethering and preference experiments (see below) from rubble, sand, or woody debris to avoid a bias due to urchins being predisposed to one focal coral habitat.

We conducted 8 tethering trials at STRI Bay and 3 trials each at San Cristobal North and San Cristobal South. During each trial, we placed 4 tethered urchins on a single coral colony of each species. Each each urchin had a 30 cm leash giving an area of mobility of 0.28 m^2. Within a trial, the 3 experimental coral colonies were at least 5 m apart, and subsequent trials at each site were at least 50 m apart. We recorded the test diameter (TD) for all urchins in order to monitor size-based mortality (20.4 ± 0.5, mean ± 1 standard error, TD in mm), then deployed tethers between 15:00 h and 18:00 h and checked them every 24 h for the following 5 d. We also deployed caged, tethered urchins (n = 48 urchins) to verify that any mortality observed during trials was not due to tethering artefacts, and we found that caged urchins experienced 100% survival over 5 to 7 d. Urchins for which the outcome was unclear for

any reason, such as a broken tether, were removed from the analysis, leaving 155 of the 168 original deployed urchins (n = 52 on *Millepora*, 51 on *Porites*, and 52 on *Agaricia*). We analyzed tethering data with a linear mixed effects model comparing relative survival of urchins tethered on the 3 coral species, pooling data across sites and trials and accounting for the repeated measurements on the same urchins by treating coral colony as a random effect. The response variable in the model was the logit transformed daily mean proportional survival of the 4 urchins on each coral colony. We used the logit transformation because it is appropriate for non-binomial proportion data, and we added a small correction (0.05) to both the numerator and denominator of the logit function for 0 and 1 values to prevent undefined (i.e. $-\infty$) transformed data (Warton & Hui 2011). To test for an effect of urchin size on survival, we conducted a second analysis in which we modeled survival probabilities based on urchin TD using logistic regression. We conducted separate regressions for each coral species using survival data at the end of the 5 d exposure period.

Algal community

We used the photographs described above to also assess the presence and community composition of algae on each of the coral species across all 6 reef sites. Each image sampled 0.0625 m^2 of the benthos (n = 10 images per coral species at each of 6 sites), for which we visually determined whether any of 5 common primary producers (*Dictyota* spp., *Gracilaria* spp., *Halimeda opuntia*, *Thalassia testudinum*, and turfing algae spp.) were present. This included algae that were adjacent but not necessarily in contact with the coral colony, if the photographed colony was smaller than the full quadrat. If any of the 5 primary producers were present, that image received a score of 1, while it was scored as 0 if no algae was present. Each of the 5 taxa were then individually scored as either present (1) or absent (0) to characterize algal community composition. Using these data, we conducted 2 analyses to determine the interactions between coral species and the standing stock of primary producers observed on each. First, we conducted a χ^2 test to determine whether the 3 coral species differed in the number of photographs with algae present versus absent. Second, we tested for differences in algal community composition on each coral species using non-metric multi-dimensional scaling (nMDS) followed by permutational multivari-

ate analysis of variance (PERMANOVA) with coral species and reef site as factors, as well as the interaction of species and site. Both nMDS and PERMANOVA were conducted using Raup-Crick dissimilarity for presence/absence data with the *vegan* package v.2.2-1 in R (Oksanen et al. 2017).

Urchin habitat preference

To test if a behavioral habitat preference contributes to the urchin habitat associations we observed, we conducted assays in the laboratory to determine the preferred coral habitat of *E. viridis.* Quantifying habitat preference requires that individuals are tested under both choice and no-choice conditions to show that they have made an active selection rather than simply exhibited a nonrandom association, and we followed a prescribed method for quantifying habitat preference (Olabarria et al. 2002, Underwood et al. 2004). In our preference assays, experimental tanks contained 3 coral fragments (~12 × 8 × 8 cm) which had been cleaned of all algae and other organisms that could drive a habitat preference and were arranged in a triangle in the center of the tank (Fig. S3 in the Supplement). There were 4 habitat treatments: 'choice', which included a single fragment of each of the 3 corals (*A. tenuifolia*, *M. alcicornis*, and *Porites* spp.), and 3 different 'no-choice' treatments which included 3 fragments of the same coral species. We had 24 total tanks divided into 4 blocks, and all 6 tanks in a block were filled with seawater coming from the same head tank using seawater drawn from STRI Bay. Within each block, there were 3 replicate tanks of the choice treatment, and 1 replicate for each of the 3 no-choice treatments. At the start of each trial, we placed a single *E. viridis* on a pre-assigned coral fragment in each tank, with an urchin starting on one of the 3 species in each of the choice tanks and starting at the fragment in the same position in the corresponding no-choice tank within each block (see Fig. S3 for schematic of experimental layout). Urchins were introduced to tanks at 17:00 h, and we recorded the position of each urchin after 5 h and after 16 h. At these checks, we recorded which coral fragment the urchin was inhabiting, or if it was located elsewhere in the tank not on any coral. We repeated the assays, and between each, we drained and re-filled all 24 tanks and haphazardly re-organized the locations of coral fragments across blocks and the location of treatments across tanks within blocks. We used new urchins for each assay.

Using this set-up, we ran 3 types of habitat preference assays testing: (1) whether urchins had an inherent preference for one of the coral species in the absence of epiphytic algae (seawater-only control; 6 trials × 4 replicates per treatment combination, n = 24); (2) if urchin habitat preference changed when algae was available *ad libitum* (4 trials, n = 16); and (3) if the preference changed in the presence of waterborne cues coming from a predator (4 trials, n = 16). For assays with algae available *ad libitum*, we threaded blades of *Dictyota* spp. through the interstices of all coral fragments to eliminate differences in algal availability and replaced algae as necessary to maintain treatments. We observed urchins grazing, but algae on a single coral fragment were never completely consumed over the course of one assay. Predator cues were introduced by holding a single Caribbean spiny lobster *Panulirus argus* in each of the 4 head tanks used to fill the experimental tanks. Lobsters were fed 2 *E. viridis* at 17:00 h daily during each assay and had been fed reef urchins *ad libitum* prior to experimental use. After assays that included lobster cues, we scrubbed and rinsed all tanks to remove any potential residual predator odors.

Following the methods of Olabarria et al. (2002) and Underwood et al. (2004), we tested specific *a priori* hypotheses to determine if *E. viridis* exhibited a preference for any of the 3 coral species under each set of environmental conditions. We analyzed 2 response variables from each type of assay, both of which tested the *a priori* null hypothesis of no difference between the choice and no-choice treatments for a particular coral species. First, we used Fisher's Exact tests to compare the number of urchins at the end of each trial (i.e. 16 h after urchins were placed in tanks) that were observed on the coral fragment on which they were initially placed. Second, to test for an effect of urchin size on the likelihood of remaining on the initial coral fragment, we used a logistic regression of urchin location at 2 time points during the course of the trial. The response variable at each time point was 1 if the urchin was observed on the original coral fragment or 0 if the urchin was observed anywhere else within the tank. We used generalized estimating equations (GEE; Zeger et al. 1988) to estimate the marginal (population-level) log-odds of an urchin remaining on the coral fragment on which they were initially placed. Each GEE model used a binomial response, logit link and exchangeable correlation structure, and models included factors of tank type (choice/no choice) and observation time, urchin size as a covariate, and urchin ID to designate the measurement unit within the repeated

measures framework. Urchin ID was a number given to each urchin for use as an identifier within the model, but we used new urchins in each assay. We back calculated odds-ratio estimates and their associated 95% confidence intervals (CI) using the robust standard errors computed by the *gee* package in R (Carey 2015).

Urchin gonadosomatic index

To explore the hypothesis that reproductive condition of *E. viridis* varies across coral habitats, we measured the gonad condition of urchins inhabiting each coral species. On each of 2 sampling trips to each of the 6 study sites described above, we swam a 20 m transect at 1 to 2 m depth, haphazardly collecting one urchin from the nearest coral colony of each species every 5 m for a total of 4 urchins from each coral species per site and per trip. Urchins were returned to the laboratory and processed within 8 h of collection by quantifying their test diameter and wet weight and then dissecting them to remove their gonads, which were then weighed separately. We

calculated the gonadosomatic index, GSI, as: (gonad mass / total mass) × 100. Some urchins had no gonads present and were excluded from the analysis, and at one site, we encountered few *Agaricia* on either transect, so only one urchin was collected from *Agaricia* colonies at this site. In total, we calculated the GSI for 39 urchins collected from *Agaricia* colonies and for 47 urchins each from *Porites* and *Millepora*. To compare GSI of urchins collected from different corals, we used a linear mixed model with coral species as a fixed factor, site as a random effect, urchin test diameter as a covariate, and the interaction of coral species and urchin test diameter.

RESULTS

Coral complexity

Colony rugosity was highest for *Millepora*, intermediate for *Agaricia*, and lowest for *Porites* (Coral factor, $F_{2,82} = 47.25$, p < 0.0001; Fig. 2A). Crevice opening size followed a similar pattern; *Millepora* colonies had the largest crevice openings, *Porites* the

Fig. 2. Coral geometry characterization based on (A) colony-scale rugosity, (B) mean crevice size, and (C) frequency distributions of crevice opening sizes. Colony-scale rugosity of each coral species was measured using the chain-line method (n = 30 replicate measurements per coral species). Mean and frequency distributions of crevice sizes were calculated from measurements of 1 randomly selected crevice in each of 60 replicate images per coral species. For all panels, we used ln-transformed data for statistical analyses but plot untransformed data for ease of interpretation. In (A) and (B), error bars are +1 standard error (SE) and lowercase letters denote statistical groupings based on linear mixed models and Tukey's post-hoc means comparisons of ln-transformed data (α = 0.05). In (C), crevice opening size-frequency distributions with 2.0 cm² bins are overlaid with their accompanying probability density kernels. Black and grey vertical lines represent mean and median crevice sizes, respectively. Estimates of skewness and the coefficient of variation from the lognormal distribution fits are: −0.374 and 35.16 for *Agaricia*, 0.14 and 43.57 for *Millepora*, and 0.817 and 35.87 for *Porites*
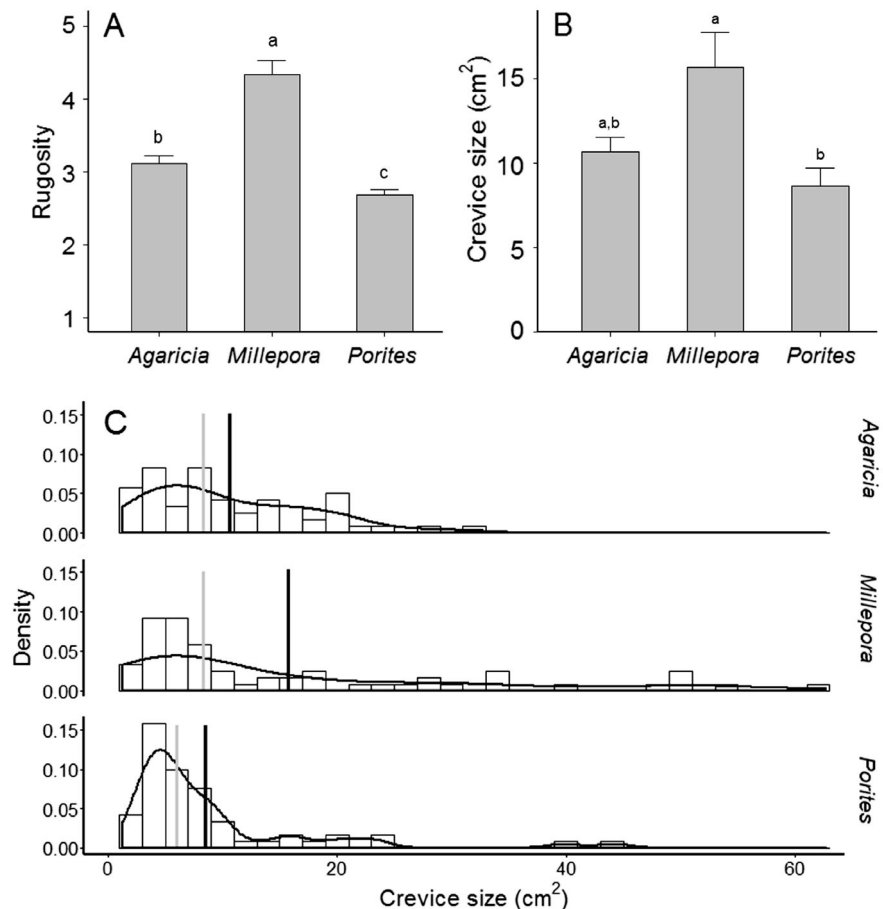
smallest openings, and *Agaricia* was intermediate but statistically indistinguishable from the other two (Coral factor $F_{2,172}$ = 3.6, p = 0.029; Fig. 2B). Crevice size distributions differed significantly between *Agaricia* and *Porites* (K-S test, *D* = 0.267, p = 0.028; Fig. 2C). Comparisons of crevice size distributions between *Agaricia* and *Millepora* and between *Porites* and *Millepora* appeared qualitatively different (Fig. 2C) and were marginally different statistically (K-S tests: *D* = 0.22, p = 0.11 and *D* = 0.23, p = 0.076, respectively). Values of the median, skewness, and coefficient of variation for each distribution provide more detailed insight on the differences between coral species (Fig. 2C). Specifically, the median value of the *Porites* crevice distribution was smaller than those of *Millepora* or *Agaricia* because of the high frequency of small crevices, the *Agaricia* distribution was the only negatively skewed distribution due to the lack of a large right tail (i.e. no extremely large crevices), and the coefficient of variation was highest for *Millepora* because these colonies had both many small and many very large (>25 cm^2) crevices (Fig. 2C). We propose the following qualitative ranking of overall habitat complexity relative to how the environment is experienced by a sea urchin: *Millepora* ≈ *Agaricia* >> *Porites*. This is because of the high rugosity and large crevices for *Millepora,* medium rugosity and a high frequency of appropriate sized crevices for *Agaricia*, and the fact that *Porites* had the lowest rugosity and a high frequency of crevices below the size at which urchins could inhabit them.

Urchin density and sheltering behavior

Colonies of *Agaricia* had the highest densities of urchins, *Millepora* had the lowest densities, and *Porites* had intermediate but indistinguishable densities from the other two (Coral factor $F_{2,82}$ = 3.67, p = 0.029; Fig. 3A). More than 35% of urchins were exposed on colonies of *Agaricia* and *Porites*, while a significantly lower proportion of urchins were exposed on *Millepora* (Coral factor $F_{2,68}$ = 7.16, p = 0.001; Fig. 3B).

Urchin predation mortality

Few tethered *Echinometra viridis* were consumed on *Millepora* and *Agaricia* colonies, whereas urchin survival on *Porites* colonies was significantly lower (Coral factor $F_{2,36}$ = 5.91, p = 0.006), with almost no difference in survival between urchins on *Agaricia*
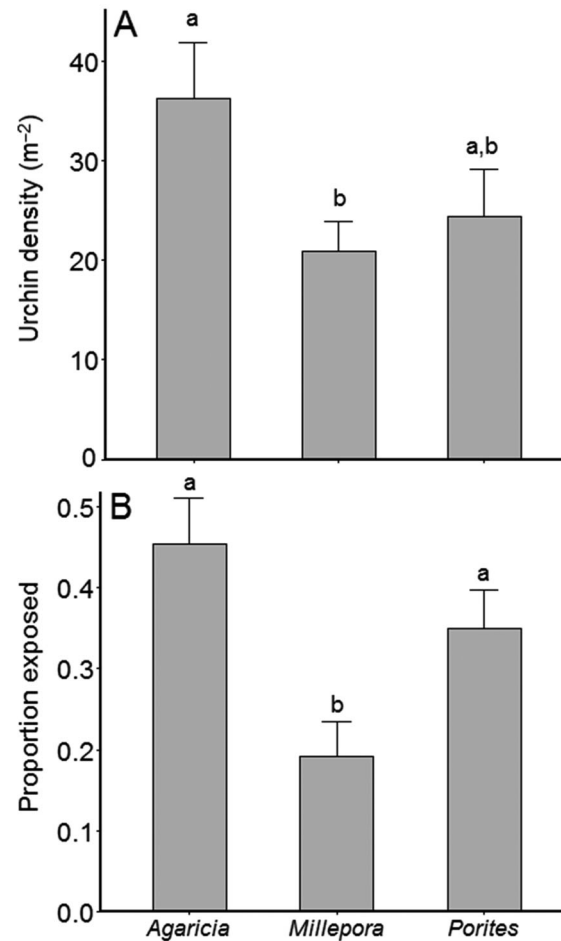

Fig. 3. *Echinometra viridis* (A) density and (B) proportion exposed on coral colonies of each type, calculated from 30 replicate quadrats per coral species. Lowercase letters denote statistical groupings based on a linear mixed model and Tukey's post-hoc means comparisons (α = 0.05). Error bars are +1 SE

and *Millepora* beyond Day 2 and the proportion of urchins surviving on *Porites* diverging 3 d after deployment to reefs (Fig. 4). Surprisingly, urchin size was not a significant predictor of urchin survival probability on any of the 3 coral species after 5 d of exposure on reefs (p > 0.45 for urchin test diameter predictor in logistic regression models for all corals; see Fig. S4 in the Supplement).

Algal community

Overall, we did not observe strong differences in algal presence or community composition between the 3 coral species. The number of images with algae present (80%, 70%, and 80% for *Agaricia*, *Millepora,* and *Porites*, respectively) did not differ by coral spe-
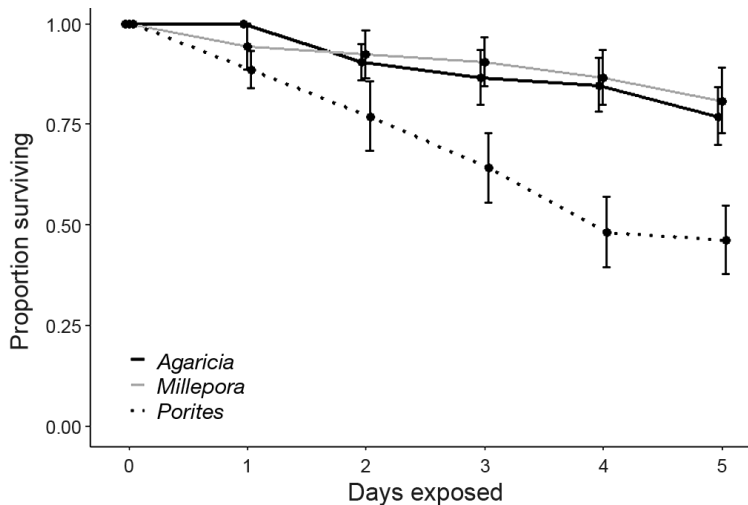
Fig. 4. Proportion of tethered *Echinometra viridis* surviving on colonies of each coral species over 5 d deployments to reefs based on linear mixed effects model of logit transformed proportions. Tukey's post-hoc means comparisons ($\alpha = 0.05$) showed lower urchin survival on *Porites* than on the other 2 corals. Points represent mean survival across all deployments for each coral species, and error bars are ± 1 SE. We used the logit transformation for statistical analysis but present untransformed data for ease of interpretation

cies ($\chi^2 = 2.236$, p = 0.3269), and there was a strong interaction between coral species and reef site for the algal community analysis (PERMANOVA Pseudo-$F_{10,116} = 2.683$, p < 0.001). The nMDS ordination showed overlap between the algal communities on colonies of *Millepora* and *Porites*, while colonies of *Agaricia* clustered separately, but with slight overlap (Fig. 5). When grouping by site, reefs at San Cristobal Middle clustered independently, corresponding to high abundance of *Dictyota*, while 3 other sites (STRI Bay East, STRI Bay West, San Cristobal South) had high abundance of *Thalassia testudinum* (Fig. S5 in the Supplement). Separate PERMANOVAs for each site revealed that when the algal community differed among corals (Popa, San Cristobal North and San Cristobal South; all PERMANOVA p < 0.02), *Agaricia* generally clustered separately and was associated with turfing algae (Fig. S6 in the Supplement).

Urchin habitat preference

During assays in both the seawater-only control and with algae available *ad libitum*, *E. viridis* did not exhibit a habitat preference when allowed to choose among coral species overnight (Table 1). However, when predator cues were added to the seawater entering experimental tanks, urchins preferred to inhabit *Agaricia* over the other coral species (Table 1).

The same pattern emerged when accounting for the repeated measurements taken on each urchin: *E. viridis* demonstrated a preference to inhabit *Agaricia* when predator cues were added, but did not exhibit a habitat preference in control assays or assays with algae available (Table 2). The GEE also demonstrated that urchin test diameter was a strong predictor of staying or leaving the original coral fragment (Table 2). Specifically, larger urchins were generally less likely to be found on their original coral fragment regardless of coral species under all 3 environmental conditions (95 % CI for this factor was < 1.0 in 8 out of 9 cases; Table 2).

Urchin gonadosomatic index

Mean values of urchin gonadosomatic index were marginally different between coral species (Coral factor $F_{2,124} = 2.54$, p = 0.083) with urchins collected from *Porites* having a higher GSI than urchins from other coral species (Fig. 6). Urchin TD was a significant covariate ($F_{1,124} = 9.49$, p = 0.002), and urchin TD did not interact with coral species (Coral × TD, p = 0.68).
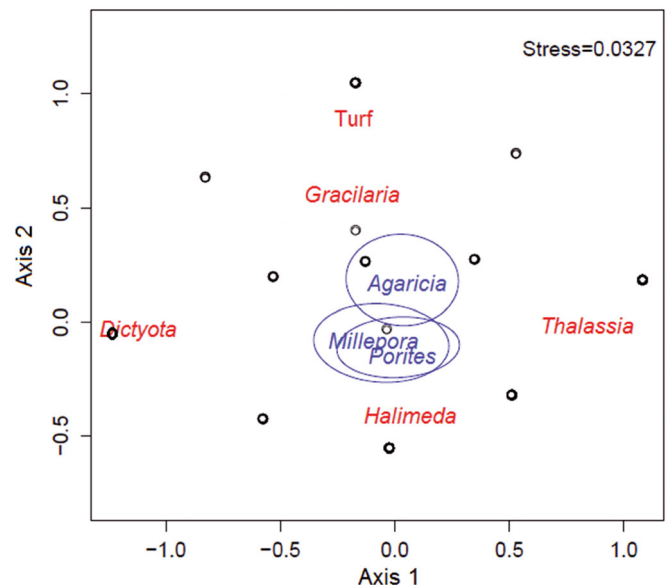

Fig. 5. nMDS ordination ($k = 2$) of the algal communities observed in images of each coral species. Points represent each original algal community sample based on presence/absence data (identical communities are over-plotted); red letters show the location of each algal community member, and blue ovals show 95 % confidence ellipses for each coral species

Table 1. Results of laboratory-based habitat preference assays. We compared the number of urchins observed on the initial coral fragment where they were placed at the beginning of each trial, testing specific *a priori* hypotheses regarding choice and no-choice (NC) tanks for a given coral species to determine if urchins exhibit a preference. We show only the percentage of urchins that stayed on the initial fragment in each trial (the percentage that left the fragment = 100 − %Stay). Results of Fisher's Exact test for each set of experiments are in parentheses, and bold values indicate significant results (α = 0.05) for that set of assays

| | Seawater control (n = 24) | | | Predator cue (n = 16) | | | Algae available (n = 16) | | |
| | %Stay | | p | %Stay | | p | %Stay | | p |
	Choice	NC		Choice	NC		Choice	NC	
Agaricia	37.5	54.2	0.385	**75**	**18.7**	**0.003**	31.3	43.7	0.716
Millepora	29.2	25	0.999	18.7	12.5	0.999	12.5	12.5	0.999
Porites	29.2	41.7	0.547	18.7	0	0.226	6.3	25	0.332

Table 2. Results of generalized estimating equations comparing the log-odds of an urchin being observed on the same coral fragment on which it was originally placed, while accounting for the repeated measurements taken for each urchin. We used separate models that included factors of Habitat Status (Choice or No Choice), Urchin test diameter (TD) and Hour (repeated measurement) for each coral species within each of the 3 types of assays. Marginal coefficient estimates and 95% confidence intervals (CI) have been converted to odds-ratios to aid in interpretability. **Bold** values indicate that the 95% CI does not include 1.0 for a given predictor

| | Seawater control | | Predator cue | | Algae available | |
	Estimate	95%CI	Estimate	95%CI	Estimate	95%CI
Agaricia						
Intercept	4397.562		2115.253		13.040	
Status: No Choice	2.486	0.542, 11.402	**0.204**	**0.057, 0.728**	2.506	0.540, 11.636
TD	**0.637**	**0.503, 0.807**	**0.730**	**0.625, 0.851**	**0.819**	**0.709, 0.946**
Hour	0.913	0.839, 0.993	0.925	0.820, 1.043	1.017	0.961, 1.075
Porites						
Intercept	54.183		44.526		181.370	
Status: No Choice	1.169	0.361, 3.778	0.469	0.100, 2.196	2.437	0.518, 11.449
TD	**0.797**	**0.691, 0.919**	0.830	0.647, 1.063	**0.740**	**0.611, 0.898**
Hour	0.968	0.917, 1.022	0.870	0.804, 0.942	0.859	0.781, 0.931
Millepora						
Intercept	9.189		7.861		6.280	
Status: No Choice	0.592	0.195, 1.794	0.818	0.161, 4.161	0.463	0.078, 2.758
TD	**0.883**	**0.801, 0.974**	**0.837**	**0.716, 0.979**	**0.856**	**0.743, 0.986**
Hour	0.971	0.916, 1.028	0.977	0.887, 1.078	0.947	0.847, 1.060
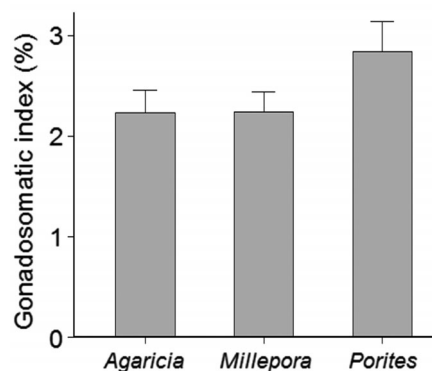
Fig. 6. Gonadosomatic index (GSI) of *Echinometra viridis* collected from each coral species. Error bars are +1 SE. The overall effect of the Coral factor was marginally significant (p = 0.083), so we did not conduct post-hoc means comparisons

DISCUSSION

Our study demonstrates that while coral structural complexity mediates predation mortality of the reef urchin *Echinometra viridis*, top-down factors alone are insufficient to fully explain the patterns of abundance observed in the field. The species identity of the coral habitat also plays an important role in determining spatial urchin distributions, through both a behavioral preference and potentially via a coral-specific trade-off in reproductive condition. Urchin grazing is critical for maintaining coral dominance and preventing a phase shift to algae (Mumby et al. 2007, Kuempel & Altieri 2017), and emerging evidence suggests that *Echinometra viridis* historically

has been, and continues to be, a dominant grazing force on some Caribbean reefs (Aronson et al. 2004, 2005, Sangil & Guzman 2016a, Kuempel & Altieri 2017) and is itself dependent on the habitat provided by corals (Nelson et al. 2016). Therefore, the relationship between provision of refuge habitats by reef-building corals and grazing by urchins, which promotes coral dominance, could be destabilized if extrinsic factors reduce the structural complexity of reefs.

Complexity-mediated habitat associations

We did not test the effects of habitat complexity per se; rather, we measured the architecture of 3 different foundational species and evaluated the relationship between each species and our focal herbivore in light of these characterizations. Nevertheless, 3 lines of evidence demonstrate that higher complexity habitats reduce predation risk and contribute to the distribution of urchins we observed. First, urchins survived at higher rates on more architecturally complex corals. Colony-scale rugosity and crevice size interact to drive the strength of predation risk experienced by urchins, and the coral *Agaricia tenuifolia* maximizes both architectural aspects, with small crevices and relatively high rugosity. This coral species had the highest densities of urchins and had higher relative urchin survival than a less rugose species. Second, despite the clear difference in survival of tethered urchins between *Porites* and the other 2 coral species, it was only when waterborne predatory cues were introduced during preference assays that urchins preferred to inhabit 1 of the 2 'safer' corals, *Agaricia*. Thus, the presence of a predator appears to drive the preference for *Agaricia*, likely also contributing to the densities we observed in the field. Finally, the higher-than-expected densities of urchins observed on the least complex and most risky coral, *Porites,* may stem from the fact that urchins collected from this species had marginally higher gonadosomatic index (GSI) values than those from *Millepora* or *Agaricia*, suggesting that there may be a fitness incentive to inhabiting a low rugosity, high risk coral. This finding agrees with evidence from freshwater ecosystems documenting reduced prey fecundity in habitats with predation refugia (Orrock et al. 2013). However, an unknown aspect of our GSI samples is the habitat history of the urchins; while we collected them from a particular coral species, we have no information on the length of time they had inhabited that coral colony prior to collection.

Colonies of *Millepora* had equally low densities of urchins as colonies of *Porites* despite having higher survivorship of tethered urchins. This pattern can be attributed to the species identity of the habitat through reduced recruitment, reduced food availability, or increased emigration, all in response to the stinging nematocysts found on branches of *Millepora* (Lewis 2006), among other potential mechanisms. Thus, our study highlights the need to mechanistically explore multiple potential drivers of habitat associations, because while habitat complexity limits predation mortality for *E. viridis*, other species-specific factors also play a role in determining habitat associations for this species.

Alternative explanations for urchin habitat associations

We found strong differences in urchin susceptibility to predation among the coral species, and this pattern aligned with our measurements of coral rugosity. Nevertheless, alternate hypotheses also could contribute to the patterns of urchin mortality we observed. For instance, potential differences in the spatial distribution of the 3 coral species on the seascape could have driven urchin susceptibility to predation. We do not believe this to be the case because these corals were intermixed within a relatively narrow depth range (1 to 3 m) at all of our study reefs, and we did not observe spatial differences in predator abundance at this scale (unpubl. data). Second, the stinging cells on live branches of *Millepora* could reduce predation rates independent of structural complexity if predators are less likely to forage in this habitat and the prey can withstand the stinging themselves. Again, we do not believe this is the main driver of the differences we observed because predatory fish will reside and actively feed within colonies of live *M. alcicornis* (Coni et al. 2013), and the main predatory species in our system, decapod crabs and lobsters, have a hard exoskeleton that makes them well adapted to dealing with the nematocysts of *Millepora* (Castro et al. 2006). Thus, coral species identity alone is unlikely to be the explanation for the relative mortality rates we documented. Finally, we observed contrasting evidence for the hypothesis that differences in the standing stock of algae on the 3 corals altered urchin habitat associations. While we did not find differences in the likelihood of algal presence between the coral species, and coral-specific differences in algal community composition were not universal, at sites where the algal community dif-

fered among corals, colonies of *Agaricia* clustered more closely to turfing algae than did the other corals. Although *E. viridis* are generalist herbivores, they have been shown to preferentially consume turfing algae over fleshy and calcareous algae (Sangil & Guzman 2016a), and this preference may have contributed to the habitat associations we documented in which urchins were highly abundant on *Agaricia* despite being observed in vulnerable positions at a higher proportion (Fig. 3). Thus, the relative importance of algae in affecting predation rates and driving habitat associations for coral-associated herbivores remains equivocal and merits additional experimental work because in some cases resource availability can interact with the threat of predation to drive animal behavior, including habitat use (Lima & Dill 1990, Heithaus & Dill 2002).

Top-down and bottom-up control on fringing coral reefs

The main predators of echinometrid urchins on coral reefs are triggerfish and large wrasses (McClanahan 1999, 2000, Young & Bellwood 2012). Neither of these fish families are common on the reefs of Bocas del Toro (Seemann et al. 2014), yet on urchins tethered on *Porites* colonies, we regularly found remnants of urchin tests or whole tests with the Aristotle's lantern and all soft tissues removed (Fig. S7 in the Supplement), indicative of predation mortality. We suggest that cryptic species such as clinging crabs *Mithrax* spp., toadfish (Family: Batrachoididae), and reef-dwelling spiny lobsters *Panulirus argus* and *P. guttatus* likely act as predators of reef urchins in this system. We observed one predation event in progress, when a clinging crab was seen consuming a tethered urchin on a *Millepora* colony. We also regularly observed toadfish living in crevices on fringing reefs and in adjacent seagrass beds, and the toadfish *Amphichthys cryptocentrus* is known to consume *E. viridis* on reefs of Caribbean Panama (Robertson 1987). On patch reefs in the Florida Keys, the spiny lobster *P. guttatus* provides strong top-down control on invertebrates, including a congeneric urchin, *E. lucunter* (Butler IV & Kintzing 2016). Panulirid lobsters in Bocas del Toro are smaller and not as abundant as in other parts of the Caribbean (Guzman & Tewfik 2004), but we observed lobsters on reefs throughout the archipelago, and there is a sufficient population to support a fishery on the reefs in our study area. Additional work is needed on the interaction between predator identity and habitat complexity on coral reefs because the role of cryptic predators in shaping community structure remains poorly understood (but see Goatley et al. 2017), and habitat architecture likely affects various predators differently (Beukers & Jones 1998, Nemeth 1998).

While we observed strong differences in sea urchin survival on alternative coral habitats, the relative importance of top-down and bottom-up control on echinometrid urchins, and the consequent effects on coral reef communities, appear to be context-dependent. For instance, a trophic cascade induced by triggerfish predation on *E. mathaei* is an important predictor of calcifier cover on reefs in the western Indian Ocean (McClanahan & Muthiga 2016), and on patch reefs within an offshore atoll in Belize, urchins tethered in areas with higher reefscape-scale rugosity suffered lower relative mortality than those deployed to low complexity patches (McClanahan 1999). Importantly, these study sites often had established populations of large predatory fish, unlike many Caribbean reefs (Stallings 2009), and in some instances, predators induced strong cryptic behavior by *E. viridis* (McClanahan 1999), unlike on the reefs we studied. Conversely, on reefs just off of mainland Belize, predatory fish abundance and urchin abundance were uncorrelated, algal cover was generally low, and urchins had little organic material in their gut (Brown-Saracino et al. 2007). Rather than top-down control, Brown-Saracino et al. (2007) suggest that *E. viridis* competes with herbivorous parrotfish and is controlled from the bottom-up through food limitation. In such cases, the importance of habitat complexity is likely difficult to detect. When predators are abundant, small-bodied herbivores are likely to persist within crevices (McClanahan 1999), as long as the structural complexity of the coral habitat is sufficient to provide refuge, as we demonstrate here for *E. viridis*, and as Nelson et al. (2016) showed for the complete invertebrate community found on *Agaricia* colonies.

As the community composition of foundational corals shifts, a habitat-specific understanding of herbivore population dynamics, as undertaken here, will allow for management aimed at increasing reef resilience through enhanced herbivory potential. This is particularly important for species such as *E. viridis* because there is strong evidence that this herbivore can regulate algal cover and mediate coral persistence and diversity on Caribbean reefs. Field surveys detected a negative relationship between *E. viridis* density and algal cover and revealed that its presence strongly contributes to algal community structure (Sangil & Guzman 2016a,b). Recent experi-

mental evidence demonstrated that a community of small-bodied herbivores, dominated by *E. viridis*, is sufficient to prevent phase shifts from coral to algae at large spatial scales following mass coral mortality events (Kuempel & Altieri 2017). Thus, knowing what coral assemblage characteristics determine the abundance of *E. viridis* will allow us to predict which areas are more or less resistant to undergoing a coral-algal phase shift. While McClanahan (1999) proposed that *E. viridis* does not have a strong impact on algal cover because it relies on cryptic behavior and subsists on drift algae, we suggest that *E. viridis* can be an abundant and important grazer on contemporary Caribbean reefs as long as sufficient structurally complex coral habitat (e.g. *Agaricia* spp.) remains available.

CONCLUSION

While the importance of coral reefscape rugosity to ecosystem services and functioning is clear (Graham & Nash 2013, Pratchett et al. 2014), we provide evidence that both species identity and colony-scale rugosity can affect habitat associations for an increasingly important herbivore on Caribbean reefs. The reduced mortality suffered by *Echinometra viridis* on structurally complex corals likely contributes to the persistence of coral-dominated reefs through positive feedbacks between refuge provision and grazing that prevents algal dominance. Given the inability of herbivorous fish to control macroalgal cover on some Caribbean reefs (Burkepile et al. 2013, Loh et al. 2015, Suchley et al. 2016) and the lack of widespread recovery of *Diadema antillarum* (Lessios 2016), there is a growing dependence on other herbivores to reduce algal cover on many reefs (Kuempel & Altieri 2017). Therefore, an improved understanding of the feedbacks between habitat complexity and herbivory, which underlie the resilience of contemporary Caribbean reefs, will aid in our ability to predict the response of reefs to anthropogenic threats.

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