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Octocoral distribution is associated with substratum orientation on coral reefs in St. John, U.S. Virgin Islands

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A B S T R A C T

In marine benthic habitats, structural complexity is positively associated with diversity, and the area of hard surfaces modulates community structure. These principles are well developed on tropical coral reefs, where stony corals create complex surfaces that are favored for settlement. This study explores the relationship between substratum orientation and the distribution of arborescent octocorals on shallow reefs (< 10-m depth) in St. John, U.S. Virgin Islands. To test the hypothesis that octocorals are distributed unequally among microhabitats, their abundance on vertical, horizontal, and inclined substrata (i.e., different microhabitats) was measured. To evaluate whether octocorals were crowded in favored microhabitats, the shortest distance between pairs of octocoral was compared among microhabitats, and the consequences of microhabitat location were evaluated by measuring colony sizes for *Gorgonia ventalina*. The most common octocorals were *G. ventalina*, *Eunicea* spp., and *Antillogorgia* spp., and these taxa were distributed unequally among microhabitats, even though the microhabitats were equally abundant. Relative to a random distribution among microhabitats, more *G. ventalina* than expected was found on vertical substrata, more *Antillogorgia* spp. was found on horizontal substrata, and more *Eunicea* spp. was found on vertical substrata. On horizontal and inclined substrata, the mean distance between *G. ventalina* and the nearest octocoral was 25 ± 4 cm, but on vertical substrata, this distance was 8 ± 2 cm; most of the nearest neighbors to *G. ventalina* were *Eunicea* spp. on vertical substrata, and the mean distance between these colonies was 5 ± 1 cm (all ± SE). There was no difference in size of *G. ventalina* among microhabitats, suggesting that adult success was unrelated to microhabitat for this species. Together, these results show that most arborescent octocorals favor vertical substrata on the shallow reefs of St. John, and because of this preference, colonies are more crowded on vertical versus horizontal or sloping substrata.

1. Introduction

Variation in the structural complexity of hard surfaces is a primary cause of high biodiversity in most major biomes including tropical forests and temperate rocky shores (Loke and Todd, 2016; MacArthur and MacArthur, 1961). The mechanisms driving these relationships are not fully understood, and therefore where substratum complexity is reduced through disturbances (e.g., on coral reefs [Alvarez-Filip et al., 2009] and in mangrove forests [Valiela et al., 2001]) it is challenging to predict the effects on the populations with which these surfaces are normally associated. The importance of structural complexity is conspicuous on tropical coral reefs, where the skeletons of scleractinian corals play an important role in creating structural complexity (Vytopil and Willis, 2001), providing habitat for sessile and mobile organisms (Glynn and Enochs, 2011; Stella et al., 2010; Williams et al., 2015). Therefore, structural complexity on coral reefs is positively associated with the abundance of reef-associated organisms (Graham and Nash, 2013; Idjadi and Edmunds, 2006), in part by modulating the settlement of pelagic larvae and mediating their post-settlement survival (Bonin et al., 2009; Coker et al., 2012; Hereu et al., 2005).

In the Caribbean, evidence from shallow coral reefs suggests that octocorals have increased in abundance over the last few decades at multiple sites (Lenz et al., 2015; Ruzicka et al., 2013; Tsounis and Edmunds, 2016). If these site-scale patterns reflect regional-scale trends, then it is possible that they indicate the effects of large-scale changes in biological and environmental conditions that are favoring octocorals versus scleractinians (Edmunds and Lasker, 2016). One biological mechanism that can favor increases in organism abundance is positive density-dependent recruitment, where for example, dense populations of adults directly cause conspecific recruitment to be elevated (Courchamp et al., 1999). Although manipulative experiments are required to demonstrate cause-and-effect in density-associated phenomena (Hixon et al., 2002), examples of density-associated phenomena affecting scleractinian recruitment (sensu Vermeij and Sandin,

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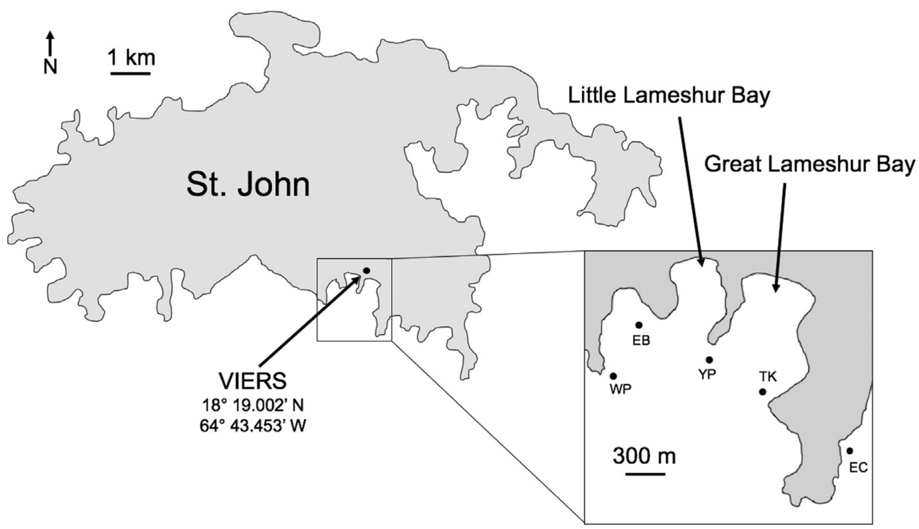

Fig. 1. Map of St. John, U.S. Virgin Islands, showing the location of the Virgin Islands Environmental Resource Station (VIERS) and the study sites along ~1 km of coastline between White Point and East Cabritte. Inset shows study sites (from L–R): White Point (WP), Europa Bay (EB), Yawzi Point (YP), Tektite reef (TK), and East Cabritte (EC).

2008) have been reported from Mo'orea, French Polynesia (Bramanti and Edmunds, 2016), and for arborescent octocorals in St. John and Puerto Rico (Privitera-Johnson et al., 2015; Yoshioka, 1996). If these patterns are caused by density-dependent recruitment, then they suggest that dense populations of octocorals would further increase in density through positive feedback of density on recruitment, at least until saturating densities of adults are achieved. However, increasing density of octocoral colonies eventually would be attenuated by crowding on the benthos, particularly if macroalgae are abundant (Bruno et al., 2009), and space is pre-empted by taxa such as scleractinians, sponges, milleporine hydrocorals, and ascidians (Colvard and Edmunds, 2011). Arborescent octocorals can escape these constraints by exploiting a tree-like morphology (Jackson, 1977) to rapidly extend upward and occupy volume in the seawater above the reef (Jackson, 1979; Sanchez et al., 2003; Yoshioka and Yoshioka, 1991).

The limited availability of space on tropical coral reefs is a classic ecological principle affecting benthic community structure (Jackson, 1977), which results in favorable microhabitats quickly being occupied by growing organisms. Upward-facing surfaces on shallow (< 10-m depth) coral reefs are preferred for settlement of photoautotrophic organisms, because they provide access to light for photosynthesis (Anthony and Hoegh-Guldberg, 2003). However, upward-facing surfaces in this habitat are quickly colonized by fast-growing algal turf (Rogers et al., 1984), particularly when herbivorous fishes are uncommon (Hoey and Bellwood, 2011). Thereafter, dense growth of algal turf can prevent other sessile taxa from settling (Kuffner et al., 2006). When space on upward-facing surfaces is fully occupied, vertically-oriented and cryptic substrata can provide alternative settlement locations (Baird and Hughes, 2000), where spatial competition typically is less intense (Doropoulos et al., 2016).

On coral reefs, variation in the intensity of inter- and intra- specific interactions among organisms on upward-facing, vertical, and cryptic substrata can modulate benthic community structure depending on the abundance of these microhabitats (Brandl et al., 2014). In shallow water (8–9-m depth) along the Pacific coast of Panama, for example, scleractinian recruits were most abundant on vertical versus horizontal surfaces, with this affect attributed to reduced spatial competition with filamentous algae on vertical surfaces (Birkeland, 1977). Likewise, on the shallow reefs of St. John, U.S. Virgin Islands, the growth of the hydrocoral *Millepora alcicornis* is affected by substratum orientation (Edmunds, 1999), with larger encrusting bases of *M. alcicornis* on vertical versus horizontal substrata, and greater densities of branches on colonies growing on horizontal versus vertical substrata (Edmunds, 1999).

The present study quantified the distribution of arborescent octocorals on shallow reefs (< 10-m depth) along the south shore of St. John, where benthic surfaces are topographically complex as a result of features created by scleractinian corals and igneous boulders (Rankin, 2002). The ecology of these reefs has been studied for decades (Edmunds, 2002, 2013; Rogers et al., 1991), and recently these studies have revealed dense octocoral communities that have increased in density over the last decade (Edmunds and Lasker, 2016; Lenz et al., 2015). Some of these reefs are dominated by dense stands of the scleractinian *Orbicella annularis*, where coral cover (mostly *O. annularis*) reaches 28% (in 2013 [Edmunds, 2015]), but many other shallow reefs in this location have much lower scleractinian cover (Edmunds, 2013). Preliminary surveys at 5–10-m depth on these reefs in July 2015 suggested that arborescent octocorals were distributed unequally between vertical and horizontal substrata, and were crowded in cracks and crevices defined on a spatial scale of 5–10 cm (see also Gambrel and Lasker, 2016).

Motivated by these observations, mensurative analyses were designed to quantify the spatial distribution of octocorals on the shallow reefs of St. John, and to evaluate the ecological consequences of their distribution. We first tested the hypothesis that octocorals exhibit a non-random spatial distribution among microhabitats differing in orientation. Assuming this hypothesis would be accepted, surveys were designed to test for two kinds of effects arising from non-random distribution. To test for crowding of octocorals in favored microhabitats, the distance between nearest neighboring octocorals was compared among microhabitats. To test for fitness-related consequences of octocoral distribution, we focused on one of the most common octocorals in the region, *Gorgonia ventalina*, and compared the size (area) of colonies among microhabitats. As the fecundity of *G. ventalina* is positively related to colony area (Page and Lasker, 2012), colony size can be used as a phenotypic measure of fitness for this species, and therefore provides insight into the fitness consequences of occupying different microhabitats.

2. Methods

2.1. Study sites and microhabitat characterization

The distribution of octocorals was evaluated in July and August 2015, and July 2016, using surveys completed on shallow fringing reefs (8–10-m depth) at White Point, Europa Bay, Yawzi Point, Tektite reef, and East Cabritte (Fig. 1). Hard substrata composed of igneous rock, dead scleractinian colonies, or crustose coralline algae were codified in a categorical scheme identifying three types of microhabitats based on the predominant orientation of their surface: vertical (~80–110°,