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Density-associated recruitment in octocoral communities in St. John, US Virgin Islands

Kristin Privitera-Johnson [a], Elizabeth A. Lenz [b,c], Peter J. Edmunds [b,*]

[a] Department of Biology, California State University, 1250 Bellflower Blvd, Long Beach, CA 90840, USA
[b] Department of Biology, California State University, 18111 Nordhoff Street, Northridge, CA 91303-8303, USA
[c] Hawai'i Institute of Marine Biology, University of Hawai'i, PO Box 1346, Kāne'ohe, HI 96744, USA

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ABSTRACT

To evaluate the possibility that density-associated effects modulate octocoral abundance on a Caribbean coral reef, we tested the hypothesis that the density of octocoral recruits (colonies ≤ 4 cm tall) and adult colonies are positively associated on shallow reefs (≤14 m depth) in St. John, US Virgin Islands. Both life stages were censused for density at 8–10 sites along 7 km of shore in 2013 and 2014, and a correlative approach was used to evaluate the extent to which the densities were associated using sites as replicates. For 8 sites censused in both years, mean densities of adults (pooled among taxa) varied from 2.95 ± 1.16 colonies m^{-2} to 20.60 ± 2.62 colonies m^{-2} in 2013, and from 3.20 ± 0.75 colonies m^{-2} to 13.00 ± 1.04 colonies m^{-2} in 2014; for recruits, mean densities varied from 1.05 ± 0.34 colonies m^{-2} to 4.25 ± 0.81 colonies m^{-2} in 2013, and from 0.60 ± 0.31 colonies m^{-2} to 1.44 ± 0.40 colonies m^{-2} in 2014 (all ± SE). The most common taxa in both years among all sites were *Antillogorgia* spp., *Gorgonia* spp., and plexaurids. Density of recruits was significantly and positively correlated with population density of adult octocorals (pooled among taxa) and plexaurids in both years, and for *Gorgonia* spp. in 2013 (with a similar trend in 2014). Densities of recruits and adults of *Antillogorgia* spp. were not associated in either year. Together, these data suggest that densities of adult octocorals positively influence the density of co-occurring octocoral recruits, thereby potentially promoting population growth.

1. Introduction

Understanding the factors regulating population size is a central theme of ecology (Hixon et al., 2002; Sale and Tolimieri, 2000) that has interested scholars for centuries (Malthus, 1798). This preoccupation originates from the desire to understand why populations increase in size, remain stable, decline, or terminate with extinction (Green, 2003; Holling, 1973). For more than a century, anthropogenic disturbances have been responsible for large fluctuations in population sizes of animals and plants in every major ecosystem (Lande, 1998; Vitousek et al., 1997), and these trends underscore the contemporary importance of fundamental ecological principles involved in the regulation of population size.

Surprisingly, however, understanding of the factors regulating population size remains incomplete, particularly for sessile marine organisms in open populations (Hixon et al., 2002, 2012; Sibly and Hone, 2002). A population is considered regulated if it displays persistence, boundedness, and recovery (Hixon et al., 2012), with compensatory-density feedback (sensu Herrando-Pérez et al., 2012) serving as a regulatory mechanism. Feedback controls population size in ways that vary with the density of organisms, with classic examples provided by inter- and intra-specific resource competition (Herrando-Pérez et al., 2012). One interesting case of population size being affected by density-associated processes is provided by arborescent taxa like some plants, macroalgae, and animals (Carr, 1994; Reed and Foster, 1984), for which high population densities create a canopy that modulates conspecific recruitment beneath (Callaway, 1992). Where such organisms are photosynthetic, the attenuation of light as it passes through the canopy can play an important role in depressing conspecific recruitment below (Callaway, 1992).

Population regulation has been extensively studied on coral reefs (Hughes, 1984; Connell et al., 1997), where large changes in population sizes of key taxa can be found (Aronson and Precht, 2001; De'ath and Moran, 1998; Lessios et al., 1984). Within the last few decades, the population sizes of scleractinians and macroalgae have dramatically changed in an inverse pattern throughout the Caribbean and parts of the Indo-Pacific (Edmunds, 2013; Jackson et al., 2014; Schutte et al., 2010), and these changes are central components of the phase shifts affecting many reefs (Done, 1992; Hughes, 1994; Ostrander et al., 2000). A phase shift to macroalgal-dominance is however, only one phase into which coral reefs can transition, and in a few cases ascidians, sponges, and octocorals have become the dominant taxa on disturbed coral reefs (Loh and Pawlik, 2014; Norström et al., 2009; Ruzicka et al., 2013).

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* Corresponding author.
E-mail address: peter.edmunds@csun.edu (P.J. Edmunds).

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One change on coral reefs that has recently received attention is an increase in abundance of octocorals that has been recorded in the Florida Keys (Ruzicka et al., 2013), and in St. John, US Virgin Islands (Lenz et al., 2015). In the Florida Keys, between 1999 and 2009, the percentage cover of octocorals increased 0.97% y^{-1}, and as rapidly as 1.43% y^{-1} in shallow fore reef habitats (Ruzicka et al., 2013). Between 1992 and 2012 in St. John, densities of octocorals increased 2–5 fold at four of the six sites (they remained unchanged at the other two) (Lenz et al., 2015). Throughout the Caribbean, increased densities of octocorals creates an assemblage of taxa forming mostly arborescent colonies, which at high densities can create a canopy analogous to dense growths of trees or a kelp forest (Rossi, 2013). The formation of a flexible forest, which contrasts with the rigid forest built by scleractinians (Alvarez-Filip et al., 2011), has potentially important implications for the way in which flowing seawater and the particles it contains interacts with the benthos beneath (Denny and Gaylord, 2010; Gili and Coma, 1998).

In this study, we quantified the association between the abundance of octocoral recruits and the population density of their adults to explore the ecological implications of varying densities of octocorals that appear to be increasing in at least two locations (Lenz et al., 2015; Ruzicka et al., 2013). We tested the hypothesis that octocoral recruitment and adult population density are positively associated on shallow reefs in St. John, US Virgin Islands. Multiple sites on shallow reefs were examined in 2013 (10 sites) and 2014 (8 sites), and we used sites with different densities of adult octocorals to accomplish our goal. The outcome of an analysis of recruitment is strongly affected by the way in which recruits are defined, and here we follow Caley et al. (1996) and define a recruit as the "initial sighting of a recently settled juvenile in the adult habitat". Our preliminary surveys revealed that the smallest octocoral colonies we could detect were 1–4 cm tall, and therefore we defined recruits as colonies ≤ 4 cm tall. This definition included sufficient numbers of colonies for their densities to be normally distributed and amenable to parametric statistics, and moreover, it is similar to definitions of octocoral recruits used in previous studies (Jamison and Lasker, 2008; Lasker, 1990, 2013).

Given the lively debate associated with the role of density-associated processes in mediating population size (Caley et al., 1996; Sale and Tolimieri, 2000), it is important to note that a correlative study such as the present analysis cannot establish cause-and-effect relationships. Density-association between recruitment and population size can arise from multiple mechanisms with implications differing between open and closed populations (Sale and Tolimieri, 2000), and critically, does not necessarily correspond to density-dependent population regulation (Sale and Tolimieri, 2000). Evidence of density-association of early life stages does, however, motivate process-oriented studies to test alternative hypotheses regarding the mechanisms causing the association. While evidence of an association between recruitment and population size for octocorals is not new (Lasker, 2013; Yoshioka, 1996), the paucity of studies of such effects, as well as the shifting community ecology of Caribbean coral reefs (Jackson et al., 2014; Ruzicka et al., 2013), makes this a timely point to revisit the association and explore the role it might play in promoting increasing abundances of octocorals (Lenz et al., 2015; Ruzicka et al., 2013).

2. Methods

Field surveys in 2013 and 2014 were completed along ~7 km of the south shore of St. John to test for an association between densities of octocoral recruits and adult octocorals (Fig. 1). Coral reef community structure in this location is well known (Edmunds, 2002, 2013; Rogers et al., 2008), and in shallow water (<14 m depth) is represented by two habitats. One is dominated by *Orbicella annularis* (where coral cover was as high as 45% in 1987), and one by igneous boulders and cliffs where mean coral cover has remained <5% since 1992, and hard surfaces are dominated by macroalgae, algal turf, crustose coralline algae, bare space, and other invertebrates (Colvard and Edmunds, 2011; Idjadi and Edmunds, 2006; Edmunds, 2013). Eight sites were censused in 2013 and 2014, and are annually censused for analysis of coral reef community structure (Edmunds, 2002, 2013) that now includes octocorals (Lenz et al., 2015). In 2013, two additional sites (Booby Rock and east Cabritte) were censused to sample sites that local knowledge suggested had high densities of octocorals.

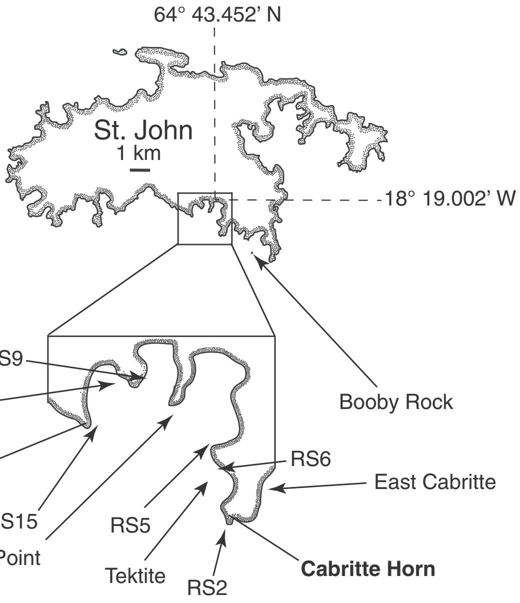

Fig. 1. Map of study sites in St. John, US Virgin Islands. Yawzi Point (Y, 9 m depth) and Tektite (T, 14 m depth) were selected in 1987, and six more sites at 7–9-m depth were selected in 1992 (RS2, RS5, RS6, RS9, RS11, RS15) (see Edmunds, 2013); these legacy sites were censused for octocorals in 2013 and 2014. In 2013, east Cabritte (EC, N18° 18.613′, W64°, 43.127′) and Booby Rock (BR, N18° 18.159′, W64° 42.598′) at 9-m depth were sampled in order to capture sites with high densities of octocorals.

Species-level resolution for octocorals often involves inspection of sclerites, which requires sampling of tissue that is not feasible at a large scale in a U.S. National Park and Biosphere Reserve. Morphological taxonomy (Sanchez and Wirshing, 2005, http://www.nova.edu/ncri/sofla_octocoral_guide/), voucher specimens, and expert identification by H.R. Lasker was used to identify octocorals, and we designed an analysis with genus- or family-level resolution. Preliminary surveys in 2012 identified 10 genera (*Antillogorgia* spp., *Briareum* spp. [erect form], *Eunicea* spp., *Gorgonia* spp., *Muricea* spp., *Muriceopsis* spp., *Plexaura* spp., *Plexaurella* spp., *Pseudoplexaura* spp., and *Pterogorgia* spp.), of which 4 (*Plexaura* spp., *Plexaurella* spp., *Pseudoplexaura* spp., and *Eunicea* spp.) were challenging to distinguish when small and were pooled and scored as plexaurids (Lenz et al., 2015). Surveys focused on taxa forming arborescent colonies that dominate octocoral communities on the shallow reefs of St. John (Lenz et al., 2015). This focus excluded *Erythropodium caribaeorum* and the encrusting form of *Briarium asbestinum*, both of which occur on shallow reefs in St. John, although only *E. caribaeorum* was common, and only then in select habitats (see Witman, 1992).

2.1. Octocoral surveys in 2013

In 2013, surveys were conducted in July and August at ten sites at 7–14 m depth (Fig. 1). Octocoral recruits were defined as colonies ≤ 4 cm tall, which includes colonies ≤ 1–2 y old assuming linear growth of ca. 2.0–4.0 cm y^{-1} (Goffredo and Lasker, 2006; Lasker et al., 2003; Yoshioka and Yoshioka, 1991), and they were counted in surveys separate from those used to census all octocorals. At two sites that have been surveyed for coral reef community structure since 1987 when they were dominated by *O. annularis* (Yawzi Point at 9 m depth and Tektite at 14 m