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Spatio-temporal variability of coral recruitment on shallow reefs in St. John, US Virgin Islands

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In this study, coral recruitment was measured on a kilometer-wide scale over two years on shallow (5–6 m depth) fringing reefs in St. John, US Virgin Islands, with the objective of determining the extent to which variation in recruitment was affected by biophysical coupling involving temperature and flow. Coral recruitment was measured using settlement tiles deployed at 10 sites along 10 km of shore. The tiles were first deployed in August 2006, and thereafter replaced every ≈6 months to sample from either August to January, or January to August over 2 years. Seawater temperature was recorded at the 10 sites using logging thermistors, and flow was quantified using drogues. Overall, corals recruited at a rate equivalent to 76 corals m^{-2} 6 $months^{-1}$, and were represented mostly by poritids (43% of recruits), agaricids (29%), faviids (17%) and siderastreids (7%). Although the density of recruits differed among sites in a pattern that varied among periods and years, there was a consistent trend for mean density to decline from ≈4 corals $tile^{-1}$ at eastern sites, to ≤1 coral $tile^{-1}$ at western sites. One aspect of seawater temperature – the daily range – differed among sites and was greater at western compared to eastern sites, and while it was related inversely to recruitment over one of the sampling periods, it was equivocal as a physical process affecting recruitment. Instead, our results are consistent with biophysical coupling involving patch depletion and downstream filtering, whereby patches of coral larvae are delivered to the south shore of St. John and depleted of larvae through settlement as the water progresses westward.

1. Introduction

For the large number of marine communities dominated by taxa releasing pelagic larvae (Cowan and Sponaugle, 2009), considerable effort has been expended to evaluate the extent to which populations are regulated by larval supply and recruitment (Gaines and Roughgarden, 1985; Morgan, 2001; Underwood and Keough, 2001). This effort emerged in the 1980s under the moniker “supply-side ecology” (Lewin, 1987), and the topic is still the subject of review (Cowan and Sponaugle, 2009; Jones et al., 2009). Over much of this period, marine populations were considered demographically “open”, with larvae coming from (and going to) a diversity of locations, and only limited reason to expect a relationship between the distribution of adults and recruits (Caley et al., 1996). Over the last 10 years, however, evidence emerged that marine populations can retain pelagic larvae and self-seed, even when the life histories of the component taxa and hydrodynamic conditions suggest that dispersal should be extensive (Cowan and Sponaugle, 2009). These findings have prompted a reappraisal of the generality of the open population model, and the new consensus suggests that marine populations are better viewed on a gradient between open and closed with regard to dispersal, recruitment, and dynamics (Cowan and Sponaugle, 2009; Jones et al., 2009).

On tropical coral reefs, the recruitment of scleractinians has been measured for decades (Lewis, 1974; Bak and Engel, 1979; Rogers et al., 1984; Connell et al., 1997; Dunstan and Johnson, 1998; Glassom et al., 2004; Adjeroud et al., 2007) with the objective of understanding the processes sustaining coral populations. Settlement tiles have been used in most of these studies – although recruits have been counted directly on natural substrata in a few cases (e.g., Piniak et al., 2005; Baird et al., 2006; Vermeij and Sandin, 2008; Roth and Knowlton, 2009) – and virtually all have revealed variation at every scale of analysis. The density of coral recruits typically differs among seasons and years (Banks and Harriott, 1996; Harriott, 1999; Dunstan and Johnson, 1998), among settlement tiles placed in a single deployment as well as among sites separated by meters, kilometers or hundreds of kilometers (Fisk and Harriott, 1990; Gleason, 1996; Dunstan and Johnson, 1998; Hughes et al. 1999, 2000; Adjeroud et al., 2007). In contrast to density, the taxonomic composition of recruiting corals is more consistent, at least based on the limited resolution (usually to family) that can be applied to small corals. For instance, coral recruits are consistently dominated by poritids, agaricids, faviids, and siderastreids in the Caribbean (Carlon, 2001; Tougas and Porter, 1992; Smith, 1997; Vermeij and Sandin, 2008), and by poritids, pocilloporids, and acroporids in the Pacific (Dunstan and Johnson, 1998; Hughes et al., 1999, 2000; Adjeroud et al., 2007; Edmunds et al., 2010). Family-

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level assemblages do, however, change throughout the year in a pattern predictable from the timing of spawning or larval release of individual taxa (Adjeroud et al., 2007).

In light of the spatio-temporal variability in coral recruitment, and uncertainty over the extent to which populations might be open or closed (Caley et al., 1996; Cowan and Sponaugle, 2009), it is not surprising that tests for association between adult corals and their early life-stages have been equivocal. Some studies have reported a significant association (Chiappone and Sullivan, 1996; Vermeij and Sandin, 2008) reminiscent of a stock-recruitment relationship (Shepherd, 1982), but others have found the distributions to be unrelated (Bak and Engel, 1979; Edmunds, 2000). These results require cautious interpretation, however, because the common use of juvenile corals as a proxy for recruits overlooks the importance of post-settlement mortality in modifying the distribution at settlement (Gosselin and Qian, 1997; Hunt and Scheibling, 1997). The importance of post-settlement events in modifying the distribution of corals has recently been underscored by Penin et al. (2010), because their results from Moorea (French Polynesia) revealed a positive association between the distribution of adult (colonies >5-cm diameter) and juvenile (colonies 1–5 cm diameter) corals, but no relationship between adults and new recruits (corals ≤3 months old); their findings implicated fish predation as a source of post-settlement mortality affecting new recruits.

The demographic role of coral recruitment in population regulation may be modified for some species where the negative demographic consequences arising from the death of large colonies can eclipse the positive effects of recruitment (Edmunds and Elahi, 2007). In this case, recruitment within the range of ecologically relevant densities was unable to halt population decline (Edmunds and Elahi, 2007), and, therefore, recruitment appeared decoupled from the population dynamics of adult corals. Despite the challenges such observations create for the task of elucidating the role of recruitment in coral populations, this undertaking remains important because sexually produced larvae remains the most common means by which coral populations are established on vacant substrata (Done et al., 1991; Dunstan and Johnson, 1998; Vermeij and Sandin, 2008). Describing spatio-temporal variation in coral recruitment, and testing for mechanisms that might drive these patterns are, therefore, important steps in understanding the distribution of corals.

The present study was motivated by the notion that there is still much to learn about coral populations from spatio-temporal variation in coral recruitment. While coral recruitment has been the topic of numerous investigations (cited above), surprisingly few have explored variation over kilometers and years, and where such variation has been addressed, mechanisms driving the patterns have often remained elusive (but see Hughes et al. 1999, 2000; Penin et al., 2010).

In the present study, shallow (5–6 m) fringing reefs along the south shore of St. John, US Virgin Islands, were used to explore the occurrence and causes of spatio-temporal variation in coral recruitment. These reefs provide a good model system in which variation in coral recruitment can be studied, because their ecology is well known, and most are located within a marine protected area (reviewed in Rogers et al. (2008)). Additionally, earlier studies of juvenile corals (≤40-mm diameter) on the same reefs suggested that corals recruited at high densities, but in a pattern that varied among sites separated on a scale of kilometers (Edmunds, 2000); preliminary analyses suggested that seawater temperature and flow differed on a comparable scale (Horst and Edmunds, in press). It was reasonable to hypothesize, therefore, that this biological process (recruitment) might be coupled with these physical phenomena (temperature and flow). Our specific goals were first, to describe spatio-temporal variability in the recruitment of scleractinian corals in St. John, and second, to explore biophysical coupling involving seawater temperature and flow as possible mechanisms to account for this variability.

2. Methods

2.1. Study sites

To test for spatio-temporal variation in coral recruitment and physical processes, 10 sites were selected along 10 km of the south shore of St. John (Fig. 1). These sites were chosen to sample across gradients in exposure to waves and thermal microenvironments, ranging from high flow with offshore temperatures (headlands and their east-facing sides) to low flow with localized warming (within semi-enclosed bays). These gradients were not quantified prior to the study, but their existence was known from years of working in this location (PJ Edmunds personal observations), and by sampling coral recruitment across them, it was possible to explore the influence of two physical processes that have strong effects on pelagic larvae. All sites were within ≈10 m of the shore on fringing reefs at 5–6 m depth, where they sampled habitats characterized by <5% cover of scleractinian corals, and ≈50% cover of macroalgae (PJ Edmunds, unpublished data from 2007).

The study began in 2006, and consisted of 4 sampling periods of ≈6 month duration: August 2006 to January 2007, January 2007 to August 2007, August 2007 to January 2008, and January 2008 to August 2008. These periods were chosen to capture seasonal variability in physical and biotic effects, although logistical constraints prevented sampling in synchrony with the astronomic seasons. The January to August sampling was characterized by low (e.g., 26.8 ± 0.1 °C, $n = 207$ d) but increasing seawater temperatures, whereas August to January was characterized by warm (e.g., 28.4 ± 0.1 °C, $n = 173$ d) but cooling temperatures (both mean ± SE based on 2008 data from 9-m depth at Yawzi Point (Fig. 1)). The northeasterly trade winds drive the prevailing waves, and therefore the south shore is protected virtually all year; occasional storms and hurricanes that pass to the south of St. John bring large waves to this shore.

2.2. Coral recruitment

Coral recruitment was measured using settlement tiles (15 × 15 × 1 cm) that were deployed in a design modified from the recommendations of Mundy (2000). The modifications affected the mode of attachment, but retained the statistical independence of each tile, the approximate horizontal deployment, and the creation of a cryptic microhabitat beneath the tile. The tiles were unglazed terracotta with a smooth top and a rough underside, and were seasoned beneath the dock in Great Lameshur Bay for ≈6 months prior to deployment. Each tile was fixed approximately horizontally to the reef using a stainless steel stud epoxied into dead coral skeletons, and was installed rough side down with a 1–2 cm gap between the tile and the reef to create a cryptic environment favored by settling coral larvae (Rogers et al., 1984; Mundy, 2000). At each site, tiles were clustered haphazardly within an area of ≈5-m radius, with individual tiles <0.5 m apart; 10 tiles site^{-1} were installed in the first year, however this number was increased to 15 tiles site^{-1} in the second year in order to increase the total number of coral recruits detected on the tiles, and increase the statistical replicates (i.e., tiles) for the site contrast.

Following the first deployment in August 2006, settlement tiles were collected and replaced at approximately 6-month intervals in January and late July/August. Freshly-collected tiles were soaked in dilute bleach to remove living tissue, and then rinsed and air dried before inspecting for coral recruits. Following scoring, the tiles were cleaned of $CaCO_3$ structures in dilute HCl and returned to beneath the dock until the next sampling. Coral recruits on the tiles consisted mostly of single corallites <2-mm diameter, and were often in the early stages of development with incompletely-formed skeletal structures. The small sizes and poorly developed skeletal features allowed recruits to be identified only to family or, when this was not possible, they were scored as “other” coral. Identification and scoring was accomplished with a dissecting microscope (40× magnification)