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Refuges modulate coral recruitment in the Caribbean and the Pacific

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A B S T R A C T

The recruitment of scleractinian corals to settlement tiles is widely used to infer relative rates of recruitment to natural reef surfaces. On tiles fixed approximately horizontally, the majority of corals settle to lower surfaces, and it is assumed that this distribution reflects the benefits of avoiding algal competition, grazers, and sedimentation on upper surfaces. Using settlement tiles with and without refuges (shallow depressions, 2–10 mm in width and depth), we tested the hypothesis that coral recruits are not found on the upper surfaces of smooth settlement tiles because these surfaces lack refuges suitable for small colonies. Tiles were deployed for 4 to 14 months over 2 years in near-horizontal orientations on shallow reefs (~5-m depth) of one Caribbean and six Pacific islands, and following collection, tiles were inspected for coral recruits. In eight of nine deployments and in both regions, densities of recruits in upward-facing refuges were indistinguishable from densities on lower surfaces, or were several-fold higher in upward-facing refuges. In the ninth deployment (lasting 14 months in the Caribbean) refuges were occluded by sediment and calcareous algae, and on these tiles densities of coral recruits were higher on the lower surface. Together, these results expand from a local-scale (Nozawa, 2008) to a global-scale the conclusion that the highest area-normalized density of coral recruits occurs in upward-facing refuges. An important implication of this finding is that coral recruitment on upward-facing natural reef surfaces will be increased by refuges that can be occupied by small corals.

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1. Introduction

The rate at which scleractinian corals recruit to tropical reefs is a critical aspect of their community ecology (Connell et al., 1997). Measuring coral recruitment therefore has long been an important objective of coral reef ecologists (Glassom et al., 2004; Mundy, 2000), although the means to achieve this goal have remained imperfect. Ideally, coral recruits are defined as individuals that can be detected when they enter the population at 1–2 mm diameter (Caley et al., 1996), and they should be censused on natural reef surfaces to obtain an ecologically relevant measurement of recruitment. Such a census rarely is obtained however, because small corals are difficult to detect, particularly on topographically complex coral reefs. There are exceptions to this generalization, for instance where coral recruits are found on flat surfaces (Vermeij and Sandin, 2008), and fluorescence becomes a tractable means by which they can be visualized (Baird et al., 2006; Piniak et al., 2005; Roth and Knowlton, 2009; Schmidt-Roach et al., 2008), but most research on this topic has relied for more than a century on settlement tiles to estimate what settles on natural surfaces (Mundy, 2000; Vaughan, 1912).

Settlement tiles consist of plates engineered from terracotta, plastic, marble, coral, or some other surface, and they are fixed to the reef in a variety of configurations (Harriott and Fisk, 1988; Mundy, 2000). A common configuration is horizontal and adjacent to reef surfaces with a cryptic habitat beneath (Mundy, 2000), but tiles have also been deployed on racks above the benthos (e.g., Smith, 1997; Tougas and Porter, 2002). Larvae contact settlement tiles during their substrate selection phase (Raimondi and Morse, 2000), and if appropriate cues are present (Harrington et al., 2004; Morse et al., 1994; Negri et al., 2001), they settle and metamorphose. While settlement tiles have been criticized due to the statistical implications of their deployment arrays (Mundy, 2000), and the extent to which they provide a meaningful evaluation of recruitment on natural surfaces (Harriott and Fisk, 1988), when deployed in a consistent manner, the results are effective in describing relative differences among times or sites (Glassom et al., 2004; Hughes et al., 1999, 2002).

One striking feature of the recruitment of corals to settlement tiles is that virtually all recruits are found on the lower surface of tiles oriented horizontally (Birkeland et al., 1981; Rogers et al., 1984; Tomascik, 1991). The cryptic location of coral recruits on the underside of tiles typically is explained as settlement choice beneficial to the avoidance of grazers and competition with macroalgae (Birkeland et al., 1981), as well as sediment accumulation (Harriott and Fisk, 1988; Rogers et al. 1984), and presumably these recruits extend out of their cryptic microhabitats to the

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open reef as they grow. However, the ecological relevance of the settlement of corals on lower surfaces of tiles has been questioned on the basis that upper surfaces of most settlement tiles lack rugosity on a scale that can provide refuge to small corals, and therefore are unfavorable settlement locations (Brock, 1979; Nozawa et al., 2011; Penin et al., 2010). When coral larvae are exposed to upward-facing rugose surfaces, they settle in large numbers, at least in experiments conducted at the Hawaii Institute of Marine Biology (Brock, 1979) and in the Rotterdam Zoo (Petersen et al., 2005), on textured tiles at 24-m depth on the Flower Gardens Banks, Gulf of Mexico (Davies et al., 2013), and on tiles augmented with numerous holes and placed at 5-m depth off Shikoku Island, Japan (Nozawa et al., 2011). Within such holes, coral recruits survive better than on adjacent smooth surfaces, presumably through avoidance of grazers (Nozawa, 2008). The detection of a positive relationship between cm-scale reef rugosity and coral recruitment on the Great Barrier Reef (Carleton and Sammarco, 1987) suggests that refuges also enhance coral recruitment on natural reef surfaces. This study describes the most extensive test to date of the possibility that refuges on upward-facing reef surfaces are a limiting resource affecting the distribution of coral recruits.

In the present study, settlement tiles with and without refuges on their upper surfaces were deployed on reefs in the Pacific and the Caribbean, and were fixed near-horizontally to surfaces at ~5-m depth. Tiles were deployed around 3 islands off Taiwan, 3 islands off the Philippines, and 1 island in the Caribbean, and were sampled after 4–14 months of immersion for the presence of coral recruits; 2 islands were sampled in each of 2 years. Through a comparison of recruitment among upper smooth surfaces, upper rugose surfaces (i.e., in refuges), and lower cryptic surfaces, we tested the hypothesis that coral recruitment is low on upward-facing smooth surfaces due to a lack of refuges in which small corals can shelter. By performing similar experiments in both the Caribbean and the Pacific, we tested for generality of our previous work in which we found coral recruitment in Japan to be augmented on upward-facing surfaces by the provision of refuges (Nozawa, 2008; Nozawa et al., 2011).

2. Materials and methods

2.1. St. John

Settlement tiles with and without refuges were made from unglazed terracotta tiles (15 × 15 × 1 cm) augmented where necessary with acrylic tiles into which, holes were drilled to create refuges. Acrylic tiles were used because of the ease with which large numbers of holes can be drilled in them to make refuges, although we recognize this mismatch of materials (acrylic on top, terracotta below) creates the potential for tile material to confound the interpretation of the settlement pattern of coral recruits. We suspect this effect was small because the 12 months deployments ensured tile surfaces were heavily fouled by crustose coralline algae by the time they were collected, and it was mostly on these surfaces that coral recruits were found, even if they were in refuges. Settlement tiles were secured to shallow (5-m depth) fringing reefs using a single stainless steel stud for each tile. Studs were epoxied into non-living reef rock in clusters of 15 at five sites (each <500 m apart) between Cabritte Horn and White Point (N 18°18′ 53″, W 46°43′35″, Fig. 1) (see Green and Edmunds, 2011). In this design, each tile was independent and served as a statistical replicate, and for the present analysis the results were pooled among sites to provide ~75 terracotta tiles sampling^{-1}.

Terracotta tiles were seasoned for ~12 months under the dock in Great Lameshur Bay prior to deployment, and were secured horizontally with the smooth surface upward and the lightly roughened surface downward. A spacer was inserted to create a ~1 cm high habitat beneath the tile that is favored for coral settlement (Birkeland et al., 1981; Carleton and Sammarco, 1987). To create refuges on the upper surface, most of the terracotta tiles were augmented with 15 × 15 × 0.6 cm acrylic sheets that either had refuges or were smooth (controls). Acrylic sheets were seasoned for ~14 days before deployment, with the assumption that the ~12 month deployments would minimize any effects of the acrylic fabrication on larval settlement. Refuges were created by drilling the surface of the acrylic tiles with 64 (Year 1) or 255 (Year II) 5-mm diameter holes with a depth of 5 mm (cf Nozawa, 2012). As our objective was to explore the absence of refuges on the upper surface of tiles as a means to explain why corals settle predominantly on lower surfaces, acrylic sheets with refuges were added to the upper surface of the terracotta tiles with the holes facing up. Five refuge tiles and five controls tiles (smooth acrylic sheet) were added at four of the St. John sites. Together, this sampling scheme provided 75 terracotta tiles y^{-1} whose lower surfaces were inspected for recruits, 20 acrylic tiles y^{-1} with refuges that were inspected for recruits, and 20 smooth acrylic tiles y^{-1} whose smooth upper surfaces were inspected for recruits.

Tiles were deployed in August 2010 and recovered in June 2011 (~10 months, Year I), and then replaced until August 2012 (~14 months, Year II). Tiles were retrieved, cleaned of tissue in dilute bleach, dried, and scored for coral recruits using a dissecting microscope (40× magnification). Coral recruits were separated into the families Acroporidae, Poritidae, Siderastreidae, Faviidae, and Agariciidae, and "others".

2.2. Taiwan

Settlement plates with and without refuges were constructed from unglazed terracotta tiles (10 × 10 × 1 cm) having a grooved lower surface (14 grooves; 5 mm wide, 100 mm long, and 2 mm deep) and a plain upper surface. Tiles were assembled in pairs, with the two smooth surfaces facing outward to create a "no refuge" treatment, and with the two grooved surfaces facing outward to create the refuge treatment (cf Nozawa, 2012). In 2010, settlement tiles were deployed at 5-m

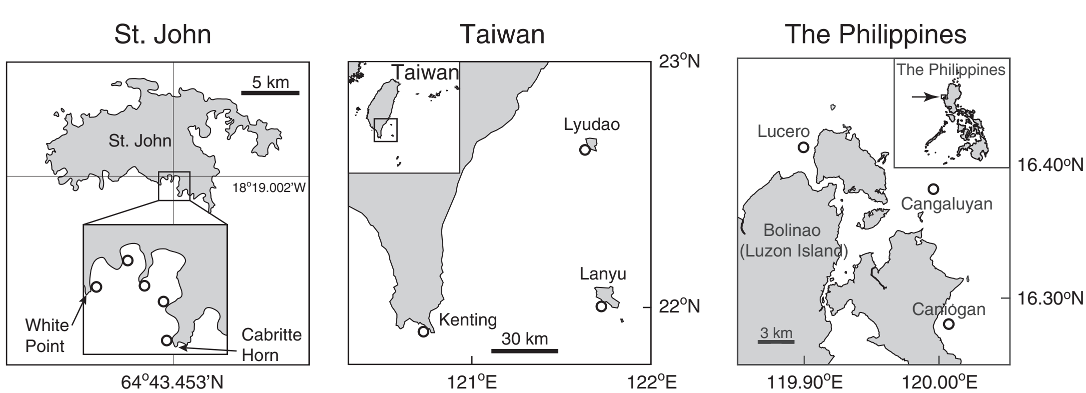

Fig. 1. Maps showing location of tile deployment sites (circles) in St. John, US Virgin Islands, Taiwan (3 islands), and the Philippines (3 islands). Settlement tiles were deployed at 5-m depth and were attached independently to the reef in near-horizontal orientations (±45° from horizontal).

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