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Colonization of coral rubble by motile cryptic animals: Differences between contiguous versus raised substrates from the bottom

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ABSTRACT

Recent studies have demonstrated that interstices of coral rubble harbor rich and diverse assemblages of motile cryptic animals. Habitats of coral rubble are prone to frequent physical disturbances, so colonization is an important process to maintain the assemblages of these cryptic animals. In order to examine the pattern of colonization, field experiments were carried out using mesh traps with defaunated coral rubble: one treatment placed on the bottom and the other raised 15 cm above the bottom (throughout as "raised") to restrict colonizers to only organisms that are able to invade via the water column. Results of nMDS and PERMANOVA showed significant differences between the assemblages of the bottom and raised treatments. Species-specific variations in the rate of colonization, which were estimated by fitting the von Bertalanffy equation, contributed to the variations in the cryptic assemblages. Generally, decapods and gastropods colonized via the benthic pathway with colonizing individuals moving on the surface of the bottom substrate, while copepods and non-shelled gammarids colonized via the planktonic pathway. Variations in cryptic assemblages in coral rubble microhabitats may be partly due to differences in contributions via the two colonization pathways.

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1. Introduction

Colonization is an important component of population and community ecology. Under frequent disturbances of local habitat patches, persistence of local populations and maintenance of community composition depend on the ability of component species to recolonize areas (Leibold et al., 2004; Sousa, 1984). Coral lagoons are composed of habitat patches of coral microatolls, seagrass beds, and bottoms of sand and coral rubble. Within these habitats, the coral rubble habitat is intrinsically associated with habitat disturbances because coral rubble is formed by destruction and fragmentation of hermatypic corals, which is accumulated and re-worked by regular currents and waves in addition to episodic typhoons and seasonal storms (Harmelin-Vivien, 1994; Kobluk and Lysenko, 1993). Therefore, the mechanism of colonization of new or disturbed coral rubble habitats is a crucial process to understand the dynamics of populations and communities in coral reef ecosystems and to develop methods to maintain this diverse but highly cryptic part of the coral ecosystem.

The high diversity and productivity of coral reefs is accounted for not only by corals, algae, and fishes, but also cryptic animals that inhabit interstices of dead corals and coral rubble (Enochs, 2012; Enochs and Manzello, 2012; Gischler, 1997; Kramer et al., 2014; Peyrot-Clausade, 1980; Plaisance et al., 2009; Takada et al., 2008). Recent studies have revealed that colonization of motile cryptic animals into coral rubble or dead coral frameworks take less than a few weeks (Enochs et al., 2011; Takada et al., 2007; Valles et al., 2006). Rapid colonization of motile animals is partly due to the active migration of individuals from surrounding undisturbed habitats, whereas recruitment from planktonic larvae and subsequent growth is necessary for sessile animals to develop assemblages.

Experimental deployments of coral rubble or dead coral frameworks have been developed as field methods to demonstrate possible effects of local environmental conditions on motile cryptic assemblages (Enochs et al., 2011; Peyrot-Clausade, 1980; Takada et al., 2008, 2012, 2014). However, little is known about the process of colonization. Peyrot-Clausade (1980) briefly described a colonization pattern of cryptic animals on fragments of branched corals (*Acropora* sp.) enclosed in a mesh bag; that is during the first 2 weeks small crustaceans (amphipods, isopods, and tanaids) colonized, then followed by larger animals (especially galatheid anomurans) within 2 to 5 weeks. However, Takada et al. (2007) demonstrated evidence of more rapid colonization of cryptic motile animals using mesh traps with defaunated coral rubble

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for 1-week to 8-week periods. Results of Takada et al. (2007) showed that some of the colonization occurred within the first 1 week and a cryptic assemblage was established within a 2–4 week period. For this rapid colonization, individuals of cryptic animals are thought to follow either a planktonic pathway through the water column or a benthic pathway migrating along the bottom substrate. Colonization via the benthic pathway may not be effective for isolated coral rubble habitats: for example, coral rubble on the upper part of a dead coral head of tabular or branching coral which is raised from the bottom substrate by a coral stalk. On the other hand, similar chance of colonization via the planktonic pathway may be expected when the coral rubble habitats are equally exposed to the water column. Thus, comparison between traps placed on the bottom of coral rubble habitat and experimentally raised traps would give us insights into the relative contributions and importance of these two colonization pathways for the establishment of the motile cryptic assemblage in coral rubble habitats.

In this study, effects of the vertical position for the colonization of cryptic motile animals were investigated using coral rubble traps with two vertical positions: one was directly placed on the bottom substrate, the other raised above the bottom in order to limit colonizers to only those capable of swimming or drifting in the water column. Short-term colonization patterns of the cryptic assemblages were examined by a time-series sampling of coral rubble traps deployed in a shallow coral lagoon. Three main questions were addressed in this study: (1) Does the vertical position of coral rubble habitats affect the assemblage of cryptic motile animals? (2) Does the vertical position affect short-term colonization patterns of the cryptic motile animals? (3) Are there any differences in the short-term colonization patterns among different taxonomical groups?

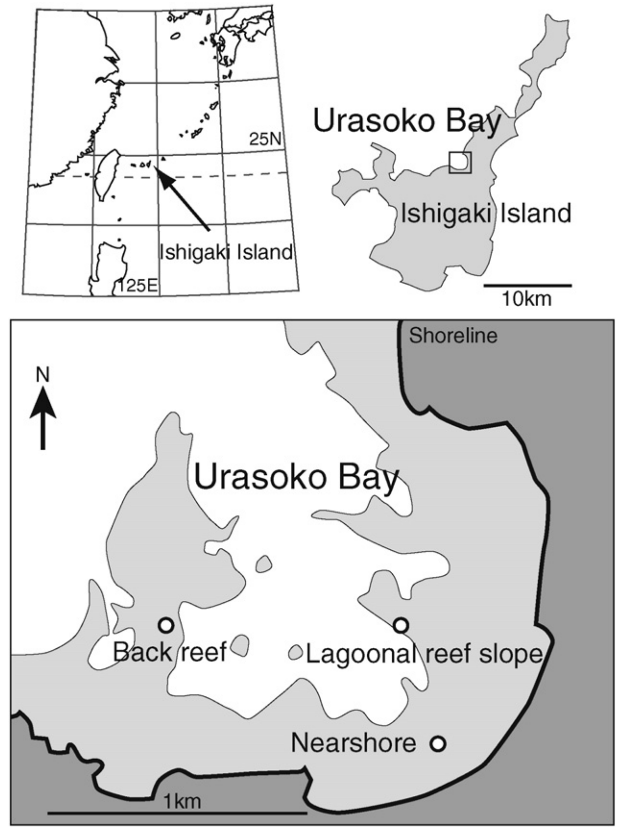

Fig. 1. Three study sites (Back reef, Nearshore, and Lagoonal reef slope) in Urasoko Bay, northern side of Ishigaki Island, southern Japan. Thin line shows approximate 5-m depth contour.

2. Materials and methods

2.1. Study sites and traps with coral rubble

This study was carried out in a coastal lagoon of Urasoko Bay (124°13′E, 24°27′N; Fig. 1) on the northern side of Ishigaki Island, Japan. The mean tidal range there is 1.7 m during spring tides. Seawater temperature ranges from 21 to 30 °C (Fujioka, 1999; Takada et al., 2005), and salinity ranges from 32 to 35 psu (Takada et al., 2005). Three study sites were selected (Fig. 1) for the two sets of experiments: the first experiment was carried out at back reef (1.5 m below the mean low water of spring tides) and nearshore (1.0 m), and the second experiment was carried out at lagoonal reef slope (1.5 m). At the back reef, the bottom substrate consisted of coral rubble produced from adjacent patches of branching corals (mainly *Acropora* spp.). At the lagoonal reef slope and the nearshore sites, the bottom was mainly sand and coral rubble among microatolls of *Porites* spp. Coral cover of the three sites were less than 5% but higher coral covers were recorded adjacent to the study sites in Urasoko Bay (Fujioka et al., 2006).

In order to enable quantitative sampling of motile animals living in the interstices of coral rubble, we used mesh trays (21.5 × 17.5 × 6.0 cm, mesh diameter = 6 mm) filled with coral rubble (Takada et al., 2007). The coral rubble was formed of fragments of dead branching corals (mainly *Acropora* spp.) of 3–15 cm lengths and 0.5–1.5 cm diameters. The coral rubble was dried and exposed to the sunlight for 2 weeks to remove organisms. Each mesh tray contained 1.0 kg (dry weight) of the coral rubble.

Two types of trap were used to examine the effects of position on the colonization of cryptic motile animals: one set on the bottom and the other raised 15 cm above the bottom. Each raised trap was set on a rack of stainless steel frame fixed onto the bottom using stakes (Fig. 2). The bottom traps were placed on the coral rubble substrate directly. Natural projections within the coral rubble of the substrate underneath the traps were used to anchor the traps to the bottom.

Fig. 2. Underwater photograph showing a raised trap with coral rubble at the lagoonal reef slope.

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