



Uneven abundance of the invasive sun coral over habitat patches of different orientation: An outcome of larval or later benthic processes?



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ARTICLE INFO

Article history:

Received 28 March 2013

Received in revised form 18 November 2013

Accepted 28 November 2013

Available online 28 December 2013

Keywords:

Competition

Habitat orientation

Larval behavior

Sedimentation

Settlement

Tubastraea coccinea

ABSTRACT

Larval behavior in the water column and preference among natural benthic habitats are known to determine initial spatial distribution patterns in several sessile marine invertebrates. Such larval attributes can be adaptive, promoting adult benthic distributions which maximize their fitness. Further benthic processes may, however, substantially change initial distribution of settlers. In this study, we first characterized spatial distributions of adult colonies and single-polyp recruits of the invasive azooxanthellate coral *Tubastraea coccinea* over substrates of different orientation, and evaluated their consistency at both small (several tens of meters) and intermediate (a few km) spatial scales. We then assessed, through field and laboratory experiments, larval preferences and relative settlement and recruitment rates on surfaces with different orientations to determine whether processes taking place during the larval and early post-larval stages could help explain the distribution patterns of recruits and adult colonies. Results suggest that larval passive buoyancy and active larval behavior, unrelated to light conditions, determine a clear settlement distribution pattern, in which the density of settlers is highest at undersurfaces and almost nil at upward facing horizontal substrates. Except for an almost absence of settlers, recruits and adult individuals on upward facing horizontal habitat, there is substantial mismatch between the distribution of settlers and that of recruits and adult colonies. The latter were also common in vertical substrate in the field. We speculate that coastal runoff at the study area and subsequent sedimentation may inhibit coral development on flat upward facing habitat, and that competitive interference and pre-emptive interactions with other azooxanthellate corals could constrain abundance of *T. coccinea* in underface horizontal habitat.

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1. Introduction

The native range of the sun coral *Tubastraea coccinea* Lesson comprises the Pacific and Indian Ocean (Cairns, 2000), but this species has been introduced in shallow tropical habitats at many locations worldwide (Glynn et al., 2008), including the southeastern Brazilian coast (da Silva and Barros, 2011; Ferreira, 2003; Mantelatto et al., 2011; Paula and Creed, 2005). The rapid invasion of *T. coccinea* in this region is likely due to the expansion of the oil industry and associated shipping activity (Ferreira, 2003; Paula and Creed, 2005). As many other alien sessile invertebrates and algae, *T. coccinea* has probably benefited from the provision of bare hard substrates found in pipelines and oil platforms where they establish colonies that can seed nearby natural habitat patches. Indeed, surveys and experiments conducted at Ilha Grande, RJ, Brazil, have shown that the sun coral readily settles on different man-made hard substrates (Creed and Paula, 2007; Mangelli and Creed, 2012). The new colonies can resist extreme environmental conditions (Robinson, 1985), making this species an efficient colonizer not only of artificial substrates, but also of free patches of natural

habitat. In natural substrate, colonies can attain substantial surface cover and cause important modifications in native benthic communities (Lages et al., 2011), often through establishing negative interactions with the closely-related species *Mussismilia hispida*, endemic to south-eastern Brazil (Creed, 2006).

Substrate selection by settling larvae can shape, to some extent, the spatial distribution patterns of adult benthic populations, especially over small to moderate spatial scales (Chabot and Bourget, 1988; Harrington et al., 2004; Pineda et al., 2010). For instance, larvae of several azooxanthellate coral species, including *T. coccinea*, concentrate in downward facing (negative) and vertical surfaces, or crevices, where they can find release from competition with fast-growing coral species that use symbiont microalgae and light as an energy source (Bak and Engel, 1979; Birkeland, 1977; Fenner and Banks, 2004; Ferreira, 2003; Glynn et al., 2008; Lewis, 1974; Rogers et al., 1984; Vermeij, 2005). In the case of invading species, information on larval substrate selection is particularly important to establish environmental policies to help control their spread and understand potential effects on native communities. A basic selective larval behavior is whether to settle preferentially on vertical or horizontal, upward (positive) or downward facing surfaces. Because the latter two are particularly abundant in artificial habitat, such as piers, jetties or oil platforms, selective settlement

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behavior for different orientations can increase or decrease the negative impact of such artificial structures (e.g. Glasby, 2000; Salinas-de-León et al., 2011), but it can also determine the impact on natural communities where overhangs and vertical walls are a common topographic feature. While colonization of new (artificial) habitats may strongly reflect larval preferences and settlement behavior, spatial distribution patterns of natural habitats may largely depend on biological interactions with pre-established species assemblages. In order to disentangle larval and later benthic processes it is first important to estimate larval preferences and compare results to the natural distribution of early recruits and adults in the field. As far as we are aware of, this has not been attempted in this invasive species.

In spite of being considered primitive larvae lacking specialized organs for perception of environmental change (Barnes et al., 1993; Lewis, 1974; Permata et al., 2000), coral planulae exhibit responsive behavior to different stimuli, reinforcing the idea that their distribution can be modulated by individual's own movement (Babcock and Mundy, 1996; Harrison and Wallace, 1990; Raimondi and Morse, 2000). Pressure and light are apparently key environmental factors determining larval swimming activity and substrate searching behavior, which may promote higher settlement rates at depth ranges where performance of adult coral colonies, in terms of survival and growth (Anthony and Hoegh-Guldberg, 2003; Fricke and Meischner, 1985; Wellington, 1982), are more favorable. Larvae of some species can control their position in the water column by swimming upwards when exposed to increasing pressure and moving down when exposed to decreasing pressure. This type of barotactic response is found, for instance, in the zooxanthellate coral *Porites asteroides*, which allows larvae to remain within the euphotic zone, below surface waters where temperature and UV radiation are exceedingly high (Stake and Sammarco, 2003). Light responses are probably more elaborate. Mundy and Babcock (1998) found that settlement rates over light gradients of varying intensity and spectral composition are consistent with vertical distributions of adult colonies of several zooxanthellate coral species. Interestingly, no effects of light regime on larval behavior were found for *Platygyra daedalea*, a zooxanthellate species exhibiting a broad depth range. In agreement to these findings, settlement preferences in coral species which occur at different depths, but require specific light regimes, often shift from vertical to horizontal substrates with increasing depth (Bak and Engel, 1979; Rogers et al., 1984), indicating that behavior of competent larvae change according to ambient light-conditions.

Light-mediated settlement behavior, with higher incidence of substrate search and metamorphosis under darkness, may explain spatial settlement patterns of azooxanthellate corals like *T. coccinea*. However, larval behavior and active settlement selection described so far do not fully explain why coral recruits, of a great number of zooxanthellate species restricted to shallow waters, are almost exclusively found in vertical or under-surfaces (Rogers et al., 1984). In addition, settlement rates could also reflect the relative cost-efficiency of larvae in exploring substrates of different inclination, given that energetic reserves for swimming and searching are limited (Feng et al., 2010; Harii et al., 2002). In this sense, negatively buoyant larvae would more easily exploit horizontal upward facing surfaces, while positively buoyant ones would spend less energy probing horizontal under surfaces. Such differences would result in differential settlement rates, when provided adequate substrate texture for adhesion (rugosity) and equal habitat quality for both substrate orientations.

Post-settlement sources of mortality might, however, dramatically affect distribution patterns set at time of settlement (e.g. Gosselin and Qian, 1997; Hunt and Scheibling, 1997). In corals, the negative effects of sedimentation are relatively well understood. Sediments may inhibit recruitment to adult populations as observed in *Acropora millepora* (Birrell et al., 2005), or suffocate both founder polyps and colonies in *Pocillopora damicornis* (Harriott, 1983)—both zooxanthellate corals. This source of mortality is higher at patches where filamentous algae

dominate the substratum (Linares et al., 2012; Sato, 1985), because turfs can reduce water flow in the boundary layer and thus the resuspension of sediments (Carpenter and Williams, 1993). Thus, biological interaction can alter local physical regimes which in turn can determine adult coral distribution. Other factors commonly recognized as determinants of coral recruitment are competition for space (Chadwick, 1991; Glynn, 1976; Sheppard, 1979), exogenous chemical signals (de Nys et al., 1991; Heyward and Negri, 1999; Koh and Sweatman, 2000), and disturbance by grazers (Lirman, 2001; Sammarco, 1980; Sammarco and Carleton, 1981). One of the few field experimental studies attempting to evaluate the importance of biological interactions on the sun coral distribution conducted in Brazil concluded that predation on *Tubastraea* spp. by a guild of native fish is negligible (Moreira and Creed, 2012), at least at Ilha Grande, RJ, just 140 km northeast of the study area used for field observations in this study.

Considering the natural history of the sun coral, and the scarce available information about factors that determine recruitment patterns in southeastern Brazil, we document the distribution of adult colonies and single-polyp recruits in the field, and then investigate larval settlement selectivity through field and laboratory experiments. The majority of studies on *Tubastraea* along the Brazilian coast have focused on documenting its geographic distribution, range expansions and substrate occupation over coarse spatial scales. The species was recorded on rocky shores at different sites distributed along 2000 km of the Brazilian coast, between the states of Santa Catarina and Bahia (Creed et al., 2008; Ferreira, 2003; Mantelatto et al., 2011; Paula and Creed, 2005; Sampaio et al., 2012; Silva et al., 2011). These observations were always obtained from locations within a distance of 40 km from port terminals linked to petroleum activities. Colonies of this species are frequently found on vertical, undersurfaces and crevices (Ferreira, 2003; Mantelatto et al., 2011; Sampaio et al., 2012), although at some localities this pattern is not as clear, with many colonies found on upward facing surfaces (Paula and Creed, 2005). In southeastern Brazil, colonies are usually clumped in restricted areas (Mangelli and Creed, 2012; Paula and Creed, 2005), although larvae can settle over a variety of hard substrates (Creed and Paula, 2007). Two peaks of larval release and subsequent recruitment, one in April–May and the second in September–November, have been observed at four different sites, within 3 km, in Arraial do Cabo, RJ, Brazil (Mizrahi, 2008). Beyond these general observations on recruitment we are not aware of further information on the supply-side ecology of this species in this region.

In this study, we investigate the distribution of young recruits (<2 mo old) and adult colonies of the sun coral *T. coccinea*, in a recently invaded area within the Ilhabela Archipelago (Mantelatto et al., 2011), southeastern Brazil. We then assess the combined effects of larval preference and settlement success on resultant settler density observed on substrates of different orientations, and compared these patterns with recruit and adult distribution in the field. Mismatches between the distribution of early settlers and the distribution of recruits and adults were used to advance possible processes restricting the spread of colonies in the area.

2. Materials and methods

2.1. Study site

All field work was undertaken in 2011 at Búzios Island (23 48' 11" S; 45 08' 21" W), 7.5 km east of the main São Sebastião Island, São Paulo, Brazil (Fig. 1). Distant 25 km from mainland, this is an 755 ha island inhabited by about 200 residents, whose main economic activity is fishing.

The vertical distribution of *T. coccinea* in the study area ranges from the lower limit of the intertidal zone up to a depth of 16 m. Qualitative observations in this vertical range suggest that benthic assemblages at the Búzios Island are similar to those reported at more coastal sites within the region (Eston and Bussab, 1990; Vieira et al., 2012), with

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