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Invasive, non-indigenous corals in a tropical rocky shore environment: No evidence for generalist predation

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A B S T R A C T

The biological invasion of rocky shore communities modifies species composition and the interaction between community elements. Two species, *Tubastraea coccinea* Lesson, 1829 and *Tubastraea tagusensis* Wells, 1982 have been identified as non-indigenous and invasive to the tropical rocky shores of southeast Brazil. The aim of the current study was to investigate predator–prey interactions between a guild of native potential generalist predators and the non-indigenous corals using total exclusion and partial cages versus controls on a tropical rocky shore in the southwest Atlantic. Despite generalist predators being present in natural densities on the experimental system and substantial settlement occurring during the 2 year study (average density of *Tubastraea* spp. was 11.29 ind. 240 cm^{-2}) no significant differences were found in density or size of corals between treatments. Dominant groups in the accompanying biological community (ABC) were encrusting calcareous and turf algae, the sponge *Iotrochota* sp. and barnacles but ABC height and biomass and sediment mass did not differ between treatments. Due to transport and invasion of new communities these corals are thought to have escaped from predation despite a diverse suite of native potential generalist predators. Both corals have been shown to possess bioactive chemicals which predatory fish avoid and this would seem to be the mechanism of predator avoidance. The successful invasion by *Tubastraea* spp. in the southwest Atlantic is at least in part due to highly reduced (or nil) predation compared to the native range.

1. Introduction

In benthic marine systems community structure is determined by complex interactions between recruitment, competition, predation and disturbance (Menge and Sutherland, 1987). The biological invasion of rocky shore communities modifies species composition and the interaction between community elements. The stony coral *Tubastraea* (Scleractinia: Dendrophylliidae) is non-indigenous to the Atlantic Ocean and was probably introduced into Brazil in the late 1980s (Castro and Pires, 2001) on oil and gas platforms. Two species, *Tubastraea coccinea* Lesson, 1829 (original distribution Pacific and Indian Oceans) and *Tubastraea tagusensis* Wells, 1982 (original distribution Eastern Pacific), have been identified as non-indigenous and invasive to the rocky shores of southeast Brazil (Paula and Creed, 2004). These azooxanthellate species have established and have now invaded shallow subtidal rocky shores along 900 km of the southeast Atlantic coast in five distinct regions. *Tubastraea* spp. have been described as invasive corals which negatively impinge on endemic species (Creed, 2006; Ferreira, 2003; Paula and Creed, 2005).

Lages et al. (2011) demonstrated that the shallow tropical rocky shore communities of the southwest Atlantic are being severely modified by the range expansion of *Tubastraea* spp. as space occupying native species are being substituted by *Tubastraea* spp. There is some evidence that community change is mediated by interspecific competitive interactions between native flora and fauna and the non-indigenous corals (Creed, 2006; Lages et al., 2011). However, predation is also known to be an extremely important biotic interaction as predators can significantly influence the abundance of prey (Connell, 1961; Paine and Schindler, 2002; Peterson, 1982), as well as having a significant indirect influence on other trophic levels by top-down effects such as trophic cascade impinging on other community elements (Mumby et al., 2007; Pace et al., 1999; Pinnegar et al., 2000).

Recently Rilov (2009) reviewed predator–prey interactions of marine invaders. Of the 29 relevant studies of 21 exotic marine species he listed only two studies of predator–prey interactions where invaders were the prey on benthic hard bottoms: the invasive mussel *Brachidontes pharaonis* (Fischer P., 1870) was preferred over native food items by the whelk *Stramonita haemastoma* (Linnaeus, 1767) in the Mediterranean (Rilov et al., 2002) and predation of the invasive tunicate *Pyura praeputialis* (Heller, 1878) by native sea stars and snails fixed the lower intertidal limit of the invader in Chile (Castilla et al., 2004). Rilov (2009) did not identify a single study where a potential prey invader was not significantly predated by a native predator, a fact that may not be surprising as a 'non-interaction' may remain undetected (or unpublished).

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That is not to say that 'non-interactions' are not ecologically important, quite the contrary, one of the most common explanations for the successful establishment and invasion of non-indigenous species is the escape from natural enemies hypothesis (Lockwood et al., 2008). This is not only because non-indigenous prey species benefit from leaving their natural predators behind in the donor region but also because they gain a competitive advantage over natives which are predated as usual by native predators. Furthermore, according to optimal defense theory (Bazzaz et al., 1987) the escape from predators allows defensive energy to be reallocated to what most increases fitness (Lockwood et al., 2008). Sammarco and Coll (1992) reviewed the secondary chemistry of octocorals and found a greater abundance and diversity of secondary metabolites and their functions (including predation defense) in Pacific octocorals when compared to those in the Caribbean Sea and hypothesized that this was due to a different evolutionary contexts (reduced climate change and lower extinction levels in the Pacific).

The aim of the current study was to investigate the effects of predator–prey interactions between a guild of native potential generalist predators in the southwest Atlantic and the corals *Tubastraea coccinea* and *T. tagusensis*, non-indigenous to the southeast Atlantic and originating from the Pacific Ocean. Our study focused on the post-settlement recruitment phase when the potential influence of predators was greatest.

2. Materials and methods

2.1. Study site

The study was carried out from October 2003 to March 2005 on a tropical subtidal rocky reef in the southwest Atlantic. The study site was at Ilha dos Macacos, Ilha Grande Bay, Brazil (23° 04′ 36″ S, 44° 13′ 47″W) on a reef extending from the intertidal to a sandy plain at 4–7 m depth (Fig. 1A). Rocky reefs are typical of the region, which consists of a coastline of bays and islands, alternating rocky shores and sandy beaches. The substratum consisted of granite boulders of approximately 0.5–5 m diameter. The north-facing shore is protected from southern ocean swell and the shore in general is subjected to little wave action. Water temperature at the site varies from 17 to 28 °C, and tidal range in the region is 1.4 m. The subtidal benthic community consists of macroalgae (multi-species turf forming, crustose coralline and foliose brown algae), heterotrophic filter feeders (mainly sponges, bryozoans and ascidians) and symbiotic autotrophs (corals and zooanthid mats) which form a mosaic over the reef (Creed and De Paula, 2007).

2.2. Predation experiment

Experimental units were ceramic tiles (the unglazed side of commercially available wall tiles) measuring 15.5 × 15.5 cm, with two holes at the corners diagonally arranged for fixation. These were deployed in October 2003 onto hollow cement blocks (20 × 20 × 40 cm) which had been placed randomly along a 50 m stretch of the shore 2 years previous to the start of this study at depths of 1.0–3.0 m below mean low water spring tide. The blocks had holes drilled to allow the experimental units to be fixed with plastic cable-ties and effectively mimicked natural rocks (see Creed and De Paula, 2007). When deployed each experimental unit was subjected to one of three treatments: (1) covered by full cages (20 × 20 × 20 cm) with 2 cm mesh (full predator exclusion); (2) covered by partial cages (20 × 20 × 20 cm cage with two sides removed – partial control for cage effect); (3) uncaged (predator treatment) (Fig. 1B). One of each treatment was randomly allocated a position on each block. Twenty replicates of each treatment were deployed and experimental units were fixed vertically to reduce the variation of physical factors, such as light, sedimentation and water circulation, as recommended by Creed and De Paula (2007). The partial control always had one side and one front panel removed to allow access by both swimming and crawling predators. The cages were cleaned and/or replaced periodically so as not to accumulate fouling organisms.

After 17 months, in March 2005, the experimental units were recovered using SCUBA. At this time potential benthic predators were quantified in an area of 0.25 m^2 around and on/in each block. After recovery, the tiles were immediately photographed and placed in plastic bags and transported in seawater to the laboratory, where they were fixed in formaldehyde for subsequent analysis along with photographs. Due to some loss of experimental units $n = 16$ predator exclusion, $n = 15$ partial controls and $n = 11$ controls were recovered.

To quantify the corals, the plates were examined individually under a dissecting microscope, counted to obtain density and measured with calipers (mean of two measures: longest axis and perpendicular to longest axis) to obtain and estimate size.

As predators or treatments potentially could have indirect effects on the settlement and survival of non-indigenous corals through their influence on community development and/or sediment accumulation these were also measured. Sediment was quantified by carefully brushing the surfaces of the experimental units with a soft toothbrush and flushing off sediment with water. This was filtered through previously dried and weighed filter paper, dried in an oven (to constant final weight at 60 °C) and reweighted.

Community development was estimated by calculating the average height of the incrusting community generated from measuring

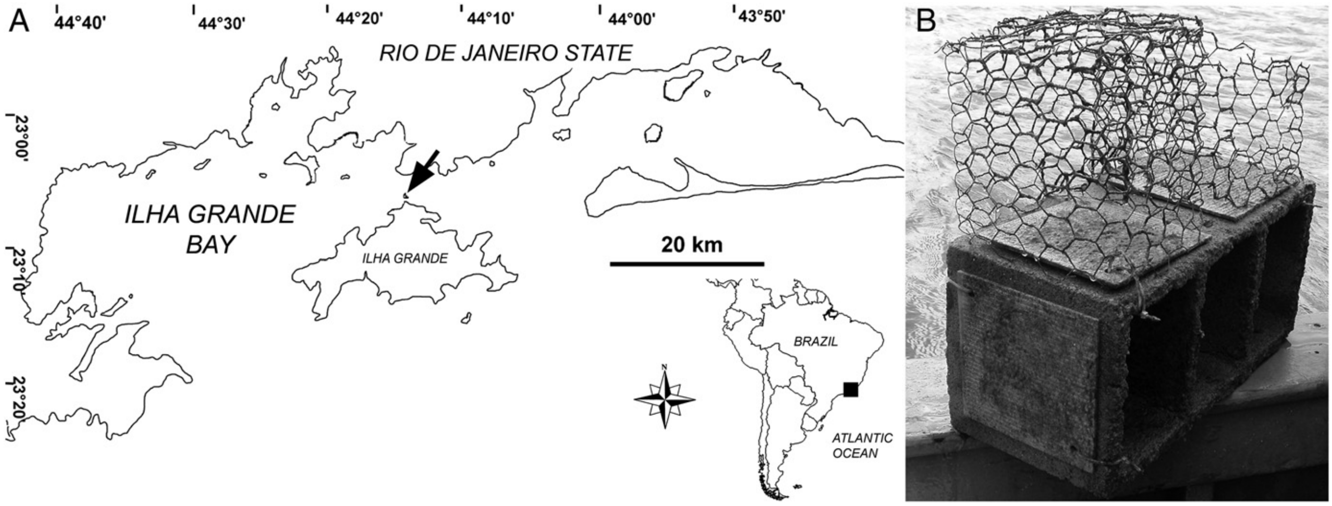

Fig. 1. (A) Location of study site at Ilha Grande, Brazil. (B) Experimental blocks, cages and units.