

Effects of the sand tilefish *Malacanthus plumieri* on the structure and dynamics of a rhodolith bed in the Fernando de Noronha Archipelago, tropical West Atlantic

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ABSTRACT: Rhodoliths are free-living calcareous nodules composed of non-geniculate coralline Rhodophyta algae. One potential rhodolith bioturbator is the sand tilefish *Malacanthus plumieri*, which builds mounds with these nodules over sand bottoms. Here, we tested (1) whether mounds act as a different habitat within a rhodolith bed, supporting specific associated assemblages, and (2) the potential role of *M. plumieri* as a bioturbation agent on rhodolith beds. We used multiple techniques (benthic and fish assemblage assessments, and videos with marked rhodoliths to assess fish behavior) to compare fish-built mounds with non-mounded control areas. *M. plumieri* was not observed removing rhodoliths from mounds; however, it spent 15% of its time rearranging mounds or adding new rhodoliths to the mound. A higher fish richness was recorded on mounds (mean = $9.4 \pm \text{SE } 1.7$) compared with the non-mounded control areas ($5.5 \pm \text{SE } 2.7$) ($t = -2.2$; $p < 0.05$). The benthic assemblages also differed between the mounds and the control areas (PERMANOVA, Pseudo- $F = 11.8$ and $p < 0.01$). The categories that contributed most to dissimilarity between mounds and non-mounded control areas (SIMPER) were crustose coralline algae free of epiphytes and sand (15.5%), *Dictyota jamaicensis* (9.8%), *Dictyota pulchella* (9.4%), sand (9.3%) and *Dictyopteris justii* (8.2%). Because of their contribution to seascape heterogeneity, we suggest that the presence of *M. plumieri* mounds is an important variable in predicting diversity in rhodolith beds.

KEY WORDS: Rhodophyta · Dispersion · Benthic assemblages · Reef fish assemblages · Oceanic island · Seascape · Rhodolith · Ecological engineers

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INTRODUCTION

The presence of some organisms modifies abiotic conditions, altering the variety of ecological niches available and consequently, facilitating or inhibiting

the occurrence of other species (Jones et al. 1994, Donadi et al. 2015). Due to the importance of such organisms in modulating the environment and in redistributing resources, Jones et al. (1994) proposed the term 'ecosystem engineers'. At the spatial scale

within habitats, ecosystem engineers cause shifts in the community composition, resulting in changes in species richness and abundance (Crooks 2002). However, at the landscape level, ecosystem engineers can increase habitat heterogeneity and enhance local biodiversity (Jones et al. 1997, Wright et al. 2002, Erwin 2005).

Rhodoliths are free-living calcareous nodules that are composed primarily (>50%) of non-geniculate coralline algae (Rhodophyta: Corallinales and Sporolithales) (Foster 2001). At the local scale, they provide a hard 3-dimensional substrate that creates conditions for a wide diversity of microorganisms, invertebrates, algae and fish (Foster et al. 1997, Steller et al. 2003, Cavalcanti et al. 2014). Rhodoliths normally occur at high densities and over large areas (10s to 1000s of km²), forming extensive beds. This ecosystem is among the 'Big Four' benthic communities dominated by marine macrophytes, ranking with kelp forests, seagrass meadows and coralline reefs (Foster 2001, Foster et al. 2013). While rhodoliths themselves are ecosystem engineers, there are other organisms which also play engineering roles in rhodolith beds, including invertebrates and fish (James 2000, Pereira-Filho et al. 2011), thus forming ecosystem engineer networks.

Water motion has been considered an important factor that determines rhodolith bed occurrence and distribution (Hinojosa-Arango et al. 2009). Periodic rotation of nodules is essential to allow light to reach all sides of them and also to avoid their burial and fouling (Steneck 1986, Marrack 1999). However, excessively strong water motion can break thalli and prevent rhodolith formation and growth, whereas weak water motion can cause stabilization and the growth of reef buffer organisms, resulting in algal framework reefs (e.g. Pereira-Filho et al. 2015), or burial by sediments, leading to death (Villas-Bôas et al. 2014). Water motion drives the structure of rhodolith beds, influencing their area, bed margins and the density of nodules (Bosence 1985, Scoffin et al. 1985, Marrack 1999). For example, dissipation of water motion energy with depth produces burial and discontinuities in beds (Steller 1993). Nodules in the middle of the bed and in deep margins experience less water motion than those in shallow portions of the bed (Marrack 1999). However, bio-induced movements may enhance the dynamics and play a role in the maintenance of rhodolith beds and their boundaries, especially in the middle and deep margins (Prager & Ginsburg 1989, Marrack 1999).

Prager & Ginsburg (1989) described 2 main types of movements that can occur in rhodoliths: (1) physical

transport during surge events or hurricane-strength storms and (2) bio-induced repositioning due to biotic activities, such as movement by the red heart urchin *Meoma ventricosa* (Prager & Ginsburg 1989), the sea urchin *Toxopneustes roseus* (James 2000), or the sand tilefish *Malacanthus plumieri* (Pereira-Filho et al. 2011, Amado-Filho et al. 2012a). The latter is found from southern Brazil to North Carolina, USA (Clark et al. 1998) and is known to build mounds composed of coral gravels, shells of mollusks, stones and rhodoliths (e.g. Büttner 1996, Pereira-Filho et al. 2011, Pereira-Filho et al. 2015). By undulating its body, this fish first forms a depression in the sand to find a hard substrate. It then continues to dig by performing undulating movements and pushing its snout against the substrate, taking out small substrate fragments and dropping them at the top of the burrow. Furthermore, it searches for available substrate fragments in the surrounding area and collects them to build a mound on its burrow (Büttner 1996).

The function of the mounds for *M. plumieri* is controversial. Different hypotheses have been proposed, for example that the mounds provide an orientation reference during foraging (Botero & Gutierrez 1980), a refuge from predation (Baird 1988, Baird & Liley 1989), or a nutritional source (Büttner 1996), and/or are important for social organization (Clark et al. 1998). The sand tilefish lives in groups and maintains harems, where male territories encompass more than one female territory (Clark et al. 1998, Baird 1988).

Along the Brazilian coast, the distribution of *M. plumieri* largely overlaps with the occurrence of rhodolith beds (Clark et al. 1998, Foster 2001), and the majority of its mounds are constructed from rhodoliths (e.g. Pereira-Filho et al. 2011, Amado-Filho et al. 2012a). Once they are built, mounds are easily distinguished within the rhodolith bed, and appear to locally change environmental factors (e.g. water movement and retention of sediments) by increasing the structural complexity of the bottom (e.g. Büttner 1996, Amado-Filho et al. 2012a, Pereira-Filho et al. 2015); thus, similar to rhodolith-forming algae, *M. plumieri* can also be considered an ecosystem engineer.

Albeit still poorly documented, networks of ecosystem engineers seem to be ubiquitous in several ecosystems (Donadi et al. 2015). Therefore, in order to further develop this promising concept, it is crucial to identify additional cases and their respective players and net effects on the seascape (Donadi et al. 2015). Here, we tested (1) whether the mounds built by *M. plumieri* act as different microhabitats within a rhodolith bed and support particular benthic and fish

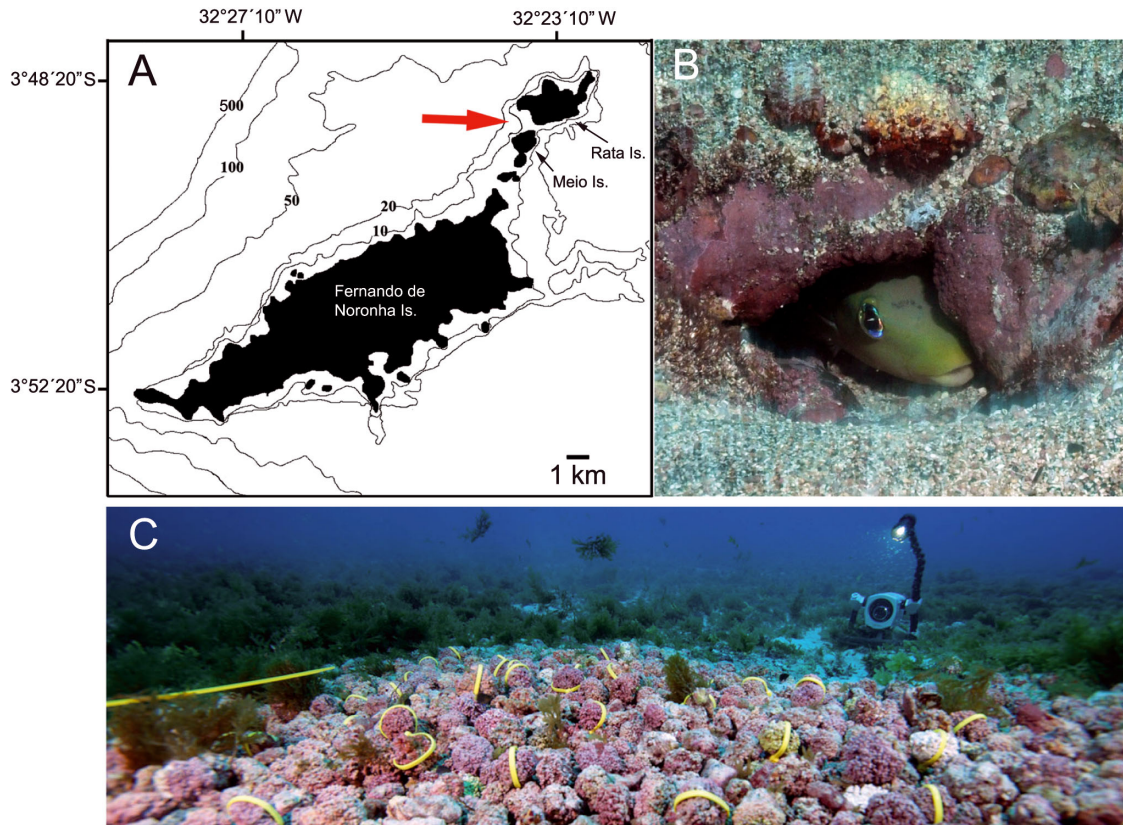


Fig. 1. Study area and field procedure. (A) Map of Fernando de Noronha Archipelago, Southwest Atlantic. Red arrow indicates the experimental site in the Ressureta area. Isobaths are shown in meters. (B) An adult sand tilefish *Malacanthus plumieri* inside its burrow just below the rhodolith mounds. (C) A rhodolith mound built by *M. plumieri* with many marked rhodoliths (yellow tie wraps) and a video recorder camera to capture images. Photos: G.H.P.-F (B) and Z.M. (C)

assemblages, and (2) the potential role of *M. plumieri* as an agent of bioturbation on rhodolith beds. The data highlight the importance of *M. plumieri* for rhodolith bed dynamics, especially in sites where water motion is too slow to move them.

MATERIALS AND METHODS

The Fernando de Noronha Archipelago (FNA) is located at 3° 50' S and 32° 25' W, 345 km from the northeastern Brazilian mainland. Since 1988, most of the FNA has been included in a National Marine Park (fully protected from fishing) that covers an area of 112.7 km². Flat areas of the insular shelf are covered by rhodolith beds at depths between 10 and 100 m (Amado-Filho et al. 2012a). Our experiments were performed in the Ressureta channel (10–15 m depth), between the islands of Meio and Rata (Fig. 1A). The study was chosen based on the presence of an extensive rhodolith bed and high density of *Malacanthus plumieri* mounds (Amado-Filho et al.

2012a). Sampling was performed in July 2012 using SCUBA.

To evaluate whether the benthic and fish assemblages differed between inhabited mounds and the non-mounded typical rhodolith habitats, we used photoquadrats and stationary visual census techniques (cf. Francini-Filho et al. 2013 and Minte-Vera et al. 2008, respectively). We considered inhabited mounds to be those where we observed the burrow just below the mounds to have been used by *M. plumieri* (Fig. 1B). Non-mounded control areas were considered to be those covered by rhodoliths at least 8 m distant from the closest mound.

Fifteen photoquadrats were obtained just above haphazardly selected mounds (i.e. one photoquadrat per mound), and 15 were randomly obtained for non-mounded control areas. According to Amado-Filho et al. (2012a), the diameter of *M. plumieri* mounds ranges between 1.8 and 2.2 m in the FNA. For benthic organisms that are sessile and are not much larger than a rhodolith (~5 cm in diameter), we considered 0.7 m² quadrat samples to be representative

of benthic assemblages. We used the Coral Point Count software (CPCe) (Kohler & Gill 2006) to analyze the images; 225 points were randomly generated per quadrat (cf. Pereira-Filho et al. 2011). Organisms immediately below each point were identified to the most precise taxonomic level possible. Quantitative analyses were performed, considering the following major benthic categories: live crustose coralline algae forming rhodoliths (CCA), sand, fleshy macroalgae (e.g. Order Dicyotales), bryozoans, sponges, coenocytic algae (e.g. *Caulerpa* spp.) and scleractinian corals (i.e. *Siderastrea stellata*). We also used photoquadrats to measure the density of rhodoliths, which was multiplied by 1.43 in order to present values as rhod. m⁻².

The same mounds and sites in non-mounded control areas were sampled for fish assemblage data. We used a stationary visual census technique (cf. Minte-Vera et al. 2008) with samples positioned at the same locations for which photoquadrats were obtained. Because fishes are mobile organisms, we considered that a distance of ~1 m from mound boundaries still affects fish assemblages. Each sample started with an identification period of 5 min, in which all species within a cylinder of 4 m diameter and 1 m height (defined by a meter tape) were identified and listed. After this period, quantitative data were recorded separately for all identified species, resulting in values of ind. 12 m⁻³ (approximately the volume of the cylinder). Each individual was visually categorized into one of 2 size categories according to their total length (TL): 0–2 cm (i.e. recruit or 'young-of-year'), and >2 cm (i.e. all settled fish) (see Carr & Syms 2006). Fish assemblages were sampled between 10:00 and 12:00 h for 3 successive days (July 2012), totaling 10 censuses per day (5 on mounds and 5 in non-mounded control areas). We marked the sampled sites to avoid repeated samples.

For both fish and benthic assemblages, mounds and non-mounded areas were compared using a permutational multivariate analysis of variance (PERMANOVA). The influence of relatively rare and abundant taxa was minimized by fourth-root transformation for both benthic cover data and fish density (Quinn & Keough 2001). The experimental design considered only habitat type (mound vs. non-mounded control areas) to be a fixed factor. Thereafter, the data were graphically summarized using a non-metric multidimensional scaling technique (nMDS) based on the Bray-Curtis similarity index (Clarke & Warwick 1994). When differences between groups were observed, we used a similarity analysis (SIMPER) to obtain a better description of the most

contributive species of each group. After log(x+1) transformation, we also used the univariate *t*-test to determine the differences in fish size classes for each species between the mounds and the non-mounded control areas. To evaluate the relative influence of the benthic cover on the fish assemblages between the mounds and non-mounded control areas, we used a canonical correspondence analysis (Ter Braak 1996). A forward selection procedure was applied, and only the independent variables that contributed to an increase in the explanatory power of the model, defined by a Monte Carlo permutation test (999 permutations), were included in the final model. Multivariate statistical analyses were performed using the packages Primer v. 6.1.13 with Permanova v. 1.0.3 extension and Canoco v. 4.5, and the software Statistica v.12 was used for univariate analysis.

To test whether *M. plumieri* transports rhodoliths from mounds to other regions we sampled 3 nearly equidistant mounds (~15 m distance apart), each inhabited by adults (35–45 cm total length, TL). In each mound, 50 randomly selected rhodoliths were marked using plastic tie wraps of the same color (red, yellow, or green), to enable their identification at each mound. The behavior of *M. plumieri* at each experimental mound was studied by fixing a high-resolution video camera (Sony full HD XR550V, 1920 × 1080 resolution) at a distance of ~0.6 m and recording 100 continuous minutes per mound (totaling 300 min) (Fig. 1C). All records were taken between 10:00 and 14:00 h. The frequency and duration of each event of rhodolith relocation were recorded, as was the number of new rhodoliths added, as well as the transport of fleshy macroalgae. These data are given as percentages of the total video duration.

Experimental mounds were revisited 1, 5 and 10 d after the rhodoliths were marked, to verify whether marked rhodoliths had been removed from the mounds. During each survey, we counted the number of marked rhodoliths in each mound and carefully searched for marked rhodoliths in a 50 m radius around each mound.

RESULTS

Influence of *Malacanthus plumieri* on benthic cover

In both the non-mounded control areas and the *M. plumieri* mounds, rhodoliths covered 100% of the bottom. However, the densities in mounds (851.7 ± 55.7 rhod. m⁻²) were higher than in non-mounded control areas (194.1 ± 31.0 rhod. m⁻²) ($t = -10.3$, $p <$

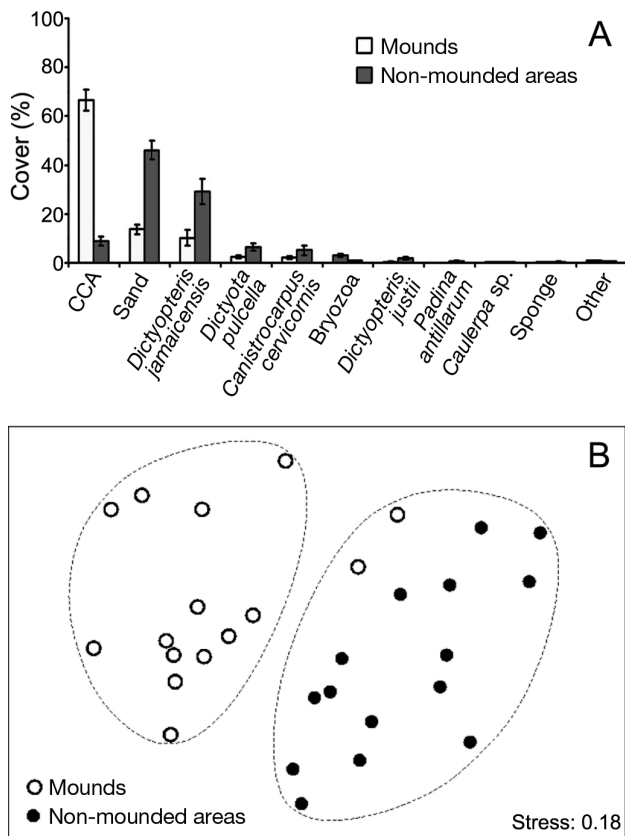


Fig. 2. Structure of the benthic assemblage on both *Malacanthus plumieri* mounds and adjacent rhodolith beds. (A) Mean and standard error of coverage by benthic taxa. (B) MDS based on the Bray-Curtis similarity index. Dotted lines correspond to the 70% similarity level. CCA = crustose coralline algae. Species names refer to macroalgal taxa

0.001). Three major benthic categories dominated (>70%) both sample sites: CCA, sand, and fleshy macroalgae of the order Dictyotales (*Dictyopteris jamaicensis*, *Dictyota pulchella*, *Dictyopteris justii* and *Canistrocarpus cervicornis*). Samples from mounds were mainly composed of CCA, those from non-mounded areas of fleshy macroalgae and sand (Fig. 2A).

Two-dimensional nMDS ordination showed a clear separation of benthic assemblages (similarity level of 70%) between the mounds and the non-mounded control areas (Fig. 2B). The differences between these groups were corroborated by the PERMANOVA results (Pseudo- $F = 11.8$, $p < 0.01$). The mean dissimilarity between groups was 32.9% (SIMPER), and the categories that contributed most to dissimilarity (>50%) were: CCA (15.5%), *D. jamaicensis* (9.8%), *D. pulchella* (9.4%), sand (9.3%) and *D. justii* (8.2%). Mounds and non-mounded control area groups exhibited, within mean similarity, values

higher than 75%. The categories that contributed most (>50%) for non-mounded areas were sand (26.6%), *D. jamaicensis* (20.5%), CCA (14.9%) and *C. cervicornis* (12.4%), whereas in the mounds, the most characteristic groups were CCA (30.6%), sand (18.5%), and *D. jamaicensis* (14.7%). These data indicate that the benthic community associated with the rhodolith bed from the studied site is dominated by fleshy algae (order Dictyotales), with a larger amount of sediment being trapped by them. On the other hand, the benthic community associated with *M. plumieri* mounds is depauperate with higher values of rhodolith-forming CCA without epiphytes and a lower amount of sediment trapping.

Influence of *Malacanthus plumieri* on reef fish assemblages

We observed a total of 33 reef fish species associated with the mound and non-mounded areas combined (Table 1). The species richness was higher over *M. plumieri* mounds (9.4 ± 1.7) (mean \pm SE) than in non-mounded control areas (5.5 ± 0.7) ($t = -2.2$; $p < 0.05$). Ten species were observed exclusively on *M. plumieri* mounds (*Lutjanus jocu*, *Malacoctenus* aff. *triangulatus*, *Doratonotus megalepis*, *Dasyatis americana*, *Haemulon parra*, *Halichoeres poeyi*, *Abudefduf saxatilis*, *Sphyraena barracuda*, *Centropyge aurantonotus*, and *Stegastes rocasensis*), whereas 6 species were recorded only at the non-mounded areas (*Opistognathus aurifrons*, *Xyrichtys splendens*, *Melichthys niger*, *Acanthurus coeruleus*, *Sparisoma amplum* and *Acanthostracion polygonius*) (Table 1).

No differences in total fish densities were observed between the mounds and non-mounded control areas ($t = -2.0$ and $p > 0.05$), with mean values ranging from 11.5 ± 1.9 to 18 ± 2.5 ind. 12 m^{-3} (mean \pm SE), respectively. *Stegastes pictus* was observed in both the non-mounded areas and the *M. plumieri* mounds. This fish species was by far the most abundant one on mounds (6.8 ± 2.0 ind. 12 m^{-3}), followed by *Thalassoma noronhanum* (2.4 ± 0.8 ind. 12 m^{-3}), *M. aff. triangulatus* (0.9 ± 0.2 ind. 12 m^{-3}), *Halichoeres dimidiatus* (0.8 ± 0.3 ind. 12 m^{-3}), *Halichoeres radiatus* (0.8 ± 0.4 ind. 12 m^{-3}) and *Sparisoma radians* (0.7 ± 0.4 ind. 12 m^{-3}). Conversely, the fish assemblages from non-mounded control areas did not contain any evident dominant species (Fig. 3A).

Unlike the benthic assemblages, the 2-dimensional nMDS ordination based on fish abundances did not show a clear difference between the mounds and the non-mounded areas (Fig. 3B). However, differences

Table 1. Presence (+) and absence (-) of fish species observed on both *Malacanthus plumieri* mounds and non-mounded areas and their respective trophic categories (based on Ferreira et al. 2004). CAR: carnivore, MIF: mobile invertebrate feeder, OMN: omnivore, PIS: piscivore, PLA: planktivore, RH: roving herbivore, SIF: sessile invertebrate feeder, TH: territorial herbivore

| Trophic category | Species | Mounds | Non-mounded areas |
|------------------|---------------------------------------|--------|-------------------|
| CAR | <i>Caranx crysos</i> | + | + |
| CAR | <i>Cephalopholis fulva</i> | + | + |
| CAR | <i>Lutjanus jocu</i> | + | - |
| CAR | <i>Malacanthus plumieri</i> | + | + |
| CAR | <i>Opistognathus aurifrons</i> | - | + |
| MIF | <i>Dasyatis americana</i> | + | - |
| MIF | <i>Doratonotus megalepis</i> | + | - |
| MIF | <i>Haemulon parra</i> | + | - |
| MIF | <i>Halichoeres dimidiatus</i> | + | + |
| MIF | <i>Halichoeres poeyi</i> | + | - |
| MIF | <i>Halichoeres radiatus</i> | + | + |
| MIF | <i>Malacoctenus aff. triangulatus</i> | + | - |
| MIF | <i>Mulloidichthys martinicus</i> | + | + |
| MIF | <i>Pseudupneus maculatus</i> | + | + |
| MIF | <i>Xyrichtys splendens</i> | - | + |
| OMN | <i>Abudefduf saxatilis</i> | + | - |
| OMN | <i>Coryphopterus glaucofraenum</i> | + | + |
| OMN | <i>Gnatholepis thompsoni</i> | + | + |
| OMN | <i>Melichthys niger</i> | - | + |
| PIS | <i>Carangoides bartholomaei</i> | + | + |
| PIS | <i>Sphyrnaena barracuda</i> | + | - |
| PLA | <i>Thalassoma noronhaum</i> | + | + |
| RH | <i>Acanthurus coeruleus</i> | - | + |
| RH | <i>Achanturus chirurgus</i> | + | + |
| RH | <i>Cryptotomus roseus</i> | + | + |
| RH | <i>Sparisoma amplum</i> | - | + |
| RH | <i>Sparisoma axillare</i> | + | + |
| RH | <i>Sparisoma frondosum</i> | + | + |
| RH | <i>Sparisoma radians</i> | + | + |
| SIF | <i>Acanthostracion polygonius</i> | - | + |
| TH | <i>Centropyge aurantonotus</i> | + | - |
| TH | <i>Stegastes pictus</i> | + | + |
| TH | <i>Stegastes rocasensis</i> | + | - |
| | Total taxa | 27 | 23 |
| | Exclusive taxa | 10 | 6 |
| | Shared taxa | | 17 |

were detected by PERMANOVA (Pseudo- $F = 4.8$ and $p < 0.01$). The mean similarities within the groups were 36.7 and 19.2% for the mounds and non-mounded control areas, respectively (SIMPER), although the mean dissimilarity between them remained high (81.6%). The fishes that contributed the most (>50%) to the dissimilarity between the mounds and non-mounded areas were *S. pictus* (16.1%), *T. noronhanum* (8.8%), *Cryptotomus roseus* (6.3%), *H. dimidiatus* (5.8%), *M. aff. triangulatus* (5.6%), *S. radians* (5.2%) and *Sparisoma axillare* (4.4%). How-

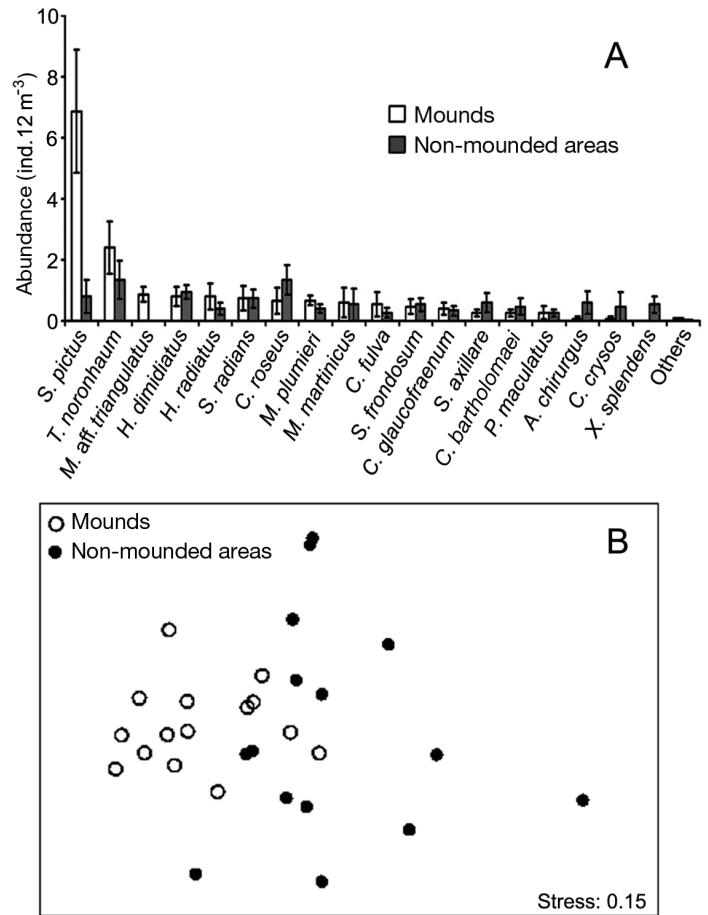


Fig. 3. Structure of fish assemblages by habitats: *Malacanthus plumieri* mounds and non-mounded control areas (see Table 1 for genera). (A) Mean and standard error of the fish abundances. Fish assemblages were sampled in a cylinder with a base of 4 m diameter and a height of 1 m (i.e. a cylinder with a volume of approximately 12 m³). (B) MDS based on the Bray-Curtis index

ever, differences in abundance were observed only for *S. pictus* ($t = -4.9$ and $p < 0.001$) (Fig. 3A).

We observed no differences in the size of fishes between the mounds and non-mounded control areas, except for *S. pictus* in which we observed higher values of both size classes on the *M. plumieri* mounds ($t = -3.3$, $p < 0.01$ and $t = -2.7$, $p < 0.01$ for 0–2 and >2 size classes, respectively).

Relationship between benthic and reef fish assemblages

The first 2 axes of the canonical correspondence analysis explained 77.8% of the relationship between the benthic cover and the structure of the fish assemblages. Crustose coralline algae alone, which

had a higher coverage on the mounds (Fig. 2A), explained most of the variation in the structure of the reef fish assemblages (Monte Carlo Permutation test, F -value = 2.23 and p -value estimate = 0.001).

***Malacanthus plumieri* and rhodolith movement**

M. plumieri spent $15 \pm 3\%$ (mean \pm SE) of the sampled time moving rhodoliths: $10 \pm 2\%$ rearranging the mounds and $5 \pm 1\%$ adding new rhodoliths and attaching macroalgae to the mounds. The addition of new rhodoliths occurred throughout the study period, but no rhodoliths were recorded being removed by *M. plumieri* from the mounds in the same period (see edited video in the Supplement at www.int-res.com/articles/suppl/m541p065_supp/).

The various footages also allowed us to record the yellow goatfish *Mulloidichthys martinicus* (Actinopterygii: Mullidae) moving rhodoliths. Groups of 10 to 15 individuals of this mobile invertebrate feeder invaded and turned rhodoliths over from the *M. plumieri* mounds while searching for invertebrates (see video in the Supplement). This behavior occurred during 3% of the recording time, always while *M. plumieri* left the mounds (usually for 1–3 min). In all cases, groups of *M. martinicus* left the mounds immediately after an agonistic behavior by *M. plumieri*. We did not observe marked rhodoliths outside their original mounds at 1, 5, or 10 d after the initiation of the experiment.

DISCUSSION

Our data indicate that *Malacanthus plumieri* changes the structure and dynamics of the rhodolith bed and their associated reef fish assemblages. Benthic assemblages associated with non-mounded rhodolith areas are characterized by a high coverage of sand, CCA, *Dictyopteris jamaicensis* and *Canistrocarpus cervicornis*, whereas those from the sand tilefish mounds were less diverse, exhibiting higher cover of CCA and lower cover of the other benthic groups. The sand tilefish spent approximately 10% of the observed time rearranging rhodoliths on their mounds. However, not one rhodolith was observed being removed from mounds, in keeping with its high density (i.e. rhod. m^{-2}) on mounds compared to non-mounded areas. Büttner (1996) demonstrated that the removal of *M. plumieri* in both artificial and natural mounds resulted in sand coverage in just a few days. Buried mounds were less complex and

attracted fewer fish (Büttner 1996). In fact, our analysis indicated that CCA (i.e. rhodoliths free of epiphytes and sand) was the most important benthic coverage in predicting the fish-associated assemblage (Monte Carlo permutation).

The greater abundance of *Stegastes pictus* on the mounds was the major difference between the reef fish assemblages of mounds vs. non-mounded areas (Fig. 3A). This small territorial herbivorous fish seems to depend on the availability of local refuges (Feitosa et al. 2012, Peyton et al. 2014), using the many crevices of the mounds as shelter. This association between *M. plumieri* and *S. pictus* might be important for both species, since we did not record any agonistic behavior between them and also because *Stegastes* spp. are known to farm their territories (Ferreira et al. 1998), contributing to the cleaning of the mound. Associations involving pomacentrids and *M. plumieri* mounds has been previously reported by Büttner (1996), who also described the mounds as nursery habitats for juveniles of some carnivorous fishes. *M. plumieri* bioturbation might also contribute to soft-bottom communities by oxygenating sediments, as described by Volkenborn et al. (2007) for the lugworm *Arenicola marina* (Polychaeta). The epi-endo-engineering exclusion hypothesis states that where epibenthic structures generated by autogenic ecosystem engineering cover most of the sediment surface, endobenthic ecosystem engineering is excluded (Bouma et al. 2009). Thus, epibenthic and endobenthic diversity are each facilitated at the expense of the other, thereby decreasing total diversity. However, *M. plumieri* appears to act at the same time as both an epi- (by building mounds) and an endobenthic (by burrowing soft bottom) allogenic ecosystem engineer, increasing the general local biodiversity. In addition, its continuous rearrangement of rhodoliths may improve the CCA growth conditions (i.e. removal of sediments and epiphytes, and nodule turning), representing a feedback relationship between endo- and epi-benthic engineers.

The coexistence of rhodoliths and *M. plumieri* can affect the habitat and communities in different ways. For example, fish assemblages associated with *M. plumieri* mounds present higher richness and abundance than those recorded in the non-mounded areas, while macroalgal communities respond negatively to the effects of the coexistence of these ecosystem engineers. Indeed, the co-occurrence of multiple ecosystem engineers can have a positive, negative or neutral effect on biodiversity and heterogeneity of a seascape (Jones et al. 1997). These species can form nested communities that increase the

diversity and abundance of organisms and can create mosaics of patches dominated by antagonistic ecosystem engineers that promote distinction between communities (Angelini et al. 2011, Eklöf et al. 2011). In addition, Büttner (1996) observed that after any damage, the sand tilefish could completely reconstruct its mound, moving more than 2000 separate pieces within a 4-week period. Therefore, the process of rhodolith grouping and scattering by *M. plumieri* and by environmental factors appears to be an important means by which rhodolith beds could change the seascape (i.e. allogenic engineer role) over soft bottoms.

Thus, *M. plumieri* mounds associated with rhodolith beds appear to contribute to the biodiversity on a wide spatial scale range. Over large spatial scales (>100 m), the rhodolith beds encompass a greater diversity compared with other less complex habitats, such as soft bottoms (Steller & Foster 1995). On an intermediate (~50 m) scale, mounds constitute patches within a homogeneous seascape, thus increasing the spatial heterogeneity of the entire set of rhodolith beds. At smaller scales (<0.5 m), the rhodolith's structure provides a 3-dimensional substrate and traps sediment, thus forming different microhabitats for a wide diversity of invertebrates and associated algae and fishes (Foster et al. 1997, Steller et al. 2003, Foster et al. 2013). Our findings corroborate these patterns and show how mounds built by *M. plumieri* change habitat provision for fish, macroinvertebrates, and macroalgae, and influence diversity patterns.

The rhodolith beds in Brazil are among the most extensive in the world, occurring over continental and oceanic insular shelves and over seamounts (Pereira-Filho et al. 2011, Amado-Filho et al. 2012a,b, Pereira-Filho et al. 2012). However, our knowledge of the biodiversity associated with the southwestern Atlantic rhodolith beds is still insufficient to classify areas related with higher biodiversity (Amado-Filho & Pereira-Filho 2012, Foster et al. 2013). The magnitude of the ecosystem services provided by the rhodolith beds is still unknown (e.g. Amado-Filho & Pereira-Filho 2012, Cavalcanti et al. 2014). In contrast, investments to discover and explore new oil areas, as well as carbonate mining activities, are increasing at much faster rates than the initiatives to understand and manage marine biodiversity, especially in the southwestern Atlantic Ocean (Moura et al. 2013). Because of its contribution to seascape heterogeneity, we suggest that the presence of *M. plumieri* mounds is an important variable in predicting diversity in rhodolith beds. Additional studies are necessary to further clarify the role of this fish as an

endobenthic ecosystem engineer, and especially to improve the understanding of its relationship with local biodiversity on different spatial and time scales. Finally, we provided an emblematic and ubiquitous case of an ecosystem engineering network in coastal and marine ecosystems.

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LITERATURE CITED

- Amado-Filho GM, Pereira-Filho GH (2012) Rhodolith beds in Brazil: a new potential habitat for marine bioprospection. *Rev Bras Farmacogn (Braz J Pharmacog)* 22:782–788
- Amado-Filho GM, Pereira-Filho GH, Bahia RG, Abrantes DP, Veras PC, Matheus Z (2012a) Occurrence and distribution of rhodolith beds on the Fernando de Noronha Archipelago of Brazil. *Aquat Bot* 101:41–45
- Amado-Filho GM, Moura RL, Bastos AC, Salgado LT and others (2012b) Rhodolith beds are major CaCO₃ bio-factories in the tropical South West Atlantic. *PLoS ONE* 7: e35171
- Angelini C, Altieri AH, Silliman BR, Bertness MD (2011) Interactions among foundation species and their consequences for community organization, biodiversity, and conservation. *Bioscience* 61:782–789
- Baird TA (1988) Female and male territoriality and mating system of the sand tilefish, *Malacanthus plumieri*. *Environ Biol Fishes* 22:101–116
- Baird TA, Liley NR (1989) The evolutionary significance of harem polygyny in the sand tilefish, *Malacanthus plumieri*: resource or female defence? *Anim Behav* 38: 817–829
- Bosence D (1985) The morphology and ecology of a mound-building coralline alga (*Neogoniolithon strictum*) from the Florida Keys. *Palaeontology* 28:189–206
- Botero JGG, Gutierrez G (1980) Establecimiento y desarrollo de la comunidad ictica en un arrecife artificial construido con llantas de desecho. *Bol Mus Mar* 10:63–81
- Bouma TJ, Olenin S, Reise K, Ysebaert T (2009) Ecosystem engineering and biodiversity in coastal sediments: posing hypotheses. *Helgol Mar Res* 63:95–106
- Büttner H (1996) Rubble mounds of sand tilefish *Malacanthus plumieri* (Bloch, 1787) and associated fishes in Colombia. *Bull Mar Sci* 58:248–260
- Carr M, Syms C (2006) Recruitment. In: Allen LG, Pondella DJ, Horn MH (eds) *The ecology of marine fishes: California and adjacent waters*. University of California Press, Berkeley, CA, p 411–427
- Cavalcanti GS, Gregoracci GB, Santos EO, Silveira CB and others (2014) Physiologic and metagenomic attributes of the rhodoliths forming the largest CaCO₃ bed in the South Atlantic Ocean. *ISME J* 8:52–62

- Clark E, Pohle JF, Halstead B (1998) Ecology and behavior of tilefishes, *Hoplostethus starcki*, *H. fronticinctus* and related species (Malacanthidae): non-mound and mound builders. *Environ Biol Fishes* 52:395–417
- Clarke KR, Warwick RM (1994) Chance in marine communities: an approach to statistical analysis and interpretation. Nat Environ Res Councl UK, Swindon
- Crooks JA (2002) Characterizing ecosystem-level consequences of biological invasions: the role of ecosystem engineers. *Oikos* 97:153–166
- Donadi S, Tjisse H, Theunis P, Els Z and others (2015) Multi-scale habitat modification by coexisting ecosystem engineers drives spatial separation of macrobenthic functional groups. *Oikos* 124:1502–1510
- Eklöf JS, Heide T, Donadi S, Zee EM, O'Hara R, Eriksson BK (2011) Habitat-mediated facilitation and counteracting ecosystem engineering interactively influence ecosystem responses to disturbance. *PLoS ONE* 6:e23229
- Erwin DH (2005) Seeds of diversity. *Science* 308:1752–1753
- Feitosa CV, Chaves LCT, Ferreira BP, De Araújo ME (2012) Recreational fish feeding inside Brazilian MPAs: impacts on reef fish community structure. *J Mar Biol Assoc UK* 92:1525–1533
- Ferreira CEL, Gonçalves JEA, Coutinho R, Peret AC (1998) Herbivory by the dusky damselfish *Stegastes fuscus* (Cuvier, 1830) in a tropical rocky shore: effects on the benthic community. *J Exp Mar Biol Ecol* 229:241–264
- Ferreira CEL, Floeter SR, Gasparini JL, Ferreira BP, Joyeux JC (2004) Trophic structure patterns of Brazilian reef fishes: a latitudinal comparison. *J Biogeogr* 31:1093–1106
- Foster MS (2001) Rhodoliths: between rocks and soft places. *J Phycol* 37:659–667
- Foster MS, Riosmena-Rodríguez R, Steller DL, Woelkerling WJ (1997) Living rhodolith beds in the Gulf of California and their implications for paleoenvironmental interpretation. In: Johnson ME, Ledesma-Vazquez J (eds) Pliocene carbonates and related facies flanking the Gulf of California, Baja California, Mexico. *Geol Soc Am Spec Issue no. 318*, Boulder, CO
- Foster MS, Amado-Filho GM, Kamenos NA, Riosmena-Rodríguez R, Steller DL (2013) Rhodoliths and rhodolith beds. *Smithson Contrib Mar Sci* 39:143–155
- Francini-Filho RB, Coni EOC, Meirelles PM, Amado-Filho GM and others (2013) Dynamics of coral reef benthic assemblages of the Abrolhos Bank, eastern Brazil: inferences on natural and anthropogenic drivers. *PLoS ONE* 8:e54260
- Hinojosa-Arango G, Maggs CA, Johnson MP (2009) Like a rolling stone: the mobility of mærl (Corallinaceae) and the neutrality of the associated assemblages. *Ecology* 90:517–528
- James DW (2000) Diet, movement, and covering behavior of the sea urchin *Toxopneustes roseus* in rhodolith beds in the Gulf of California, Mexico. *Mar Biol* 137:913–923
- Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. *Oikos* 69:373–386
- Jones CG, Lawton JH, Shachak M (1997) Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78:1946–1957
- Kohler KE, Gill SM (2006) Coral Point Count with Excel extensions (CPCe): a visual basic program for the determination of coral and substrate coverage using random point count methodology. *Comput Geosci* 32:1259–1269
- Marrack E (1999) The relationship between water motion and living rhodolith beds in the southwestern Gulf of California, Mexico. *Palaios* 14:159–171
- Minte-Vera CV, Moura RL, Francini-Filho RB (2008) Nested sampling: an improved visual-census technique for studying reef fish assemblages. *Mar Ecol Prog Ser* 367:283–293
- Moura RL, Secchin NA, Amado-Filho GM, Francini-Filho RB and others (2013) Spatial patterns of benthic megahabitats and conservation planning in the Abrolhos Bank. *Cont Shelf Res* 70:109–117
- Pereira-Filho GH, Amado-Filho GM, Guimarães SMPB, Moura RL and others (2011) Reef fish and benthic assemblages of the Trindade and Martin Vaz island group, southwestern Atlantic. *Braz J Oceanogr* 59:201–212
- Pereira-Filho GH, Amado-Filho GM, Moura RL, Bastos AC and others (2012) Extensive rhodolith beds cover the summits of Southwestern Atlantic Ocean seamounts. *J Coast Res* 28:261–269
- Pereira-Filho GH, Francini-Filho RB, Pierozzi-Jr I, Pinheiro HT and others (2015) Sponges and fish facilitate succession from rhodolith beds to reefs. *Bull Mar Sci* 91:45–46
- Peyton KA, Valentino LM, Maruska KP (2014) Dual roles of an algal farming damselfish as a cultivator and opportunistic browser of an invasive seaweed. *PLoS ONE* 9:e109007
- Prager EJ, Ginsburg RN (1989) Carbonate nodule growth on Florida's outer shelf and its implications for fossil interpretations. *Palaios* 4:310–317
- Quinn GP, Keough MJ (2001) Experimental design and data analysis for biologists. Cambridge University Press, Cambridge
- Scoffin TP, Stoddart DR, Tudhope AW, Woodroff C (1985) Rhodoliths and coralloliths of Muri Lagoon, Rarotonga, Cook Islands. *Coral Reefs* 4:71–80
- Steller DL (1993) Ecological studies of rhodoliths in Bahia Concepcion, Baja California Sur, Mexico. MS thesis, California State University, Moss Land Mar Lab
- Steller DL, Foster MS (1995) Environmental factors influencing distribution and morphology of rhodolith in Bahia Concepcion, B.C.S., Mexico. *J Exp Mar Biol Ecol* 194:201–212
- Steller DL, Riosmena-Rodríguez R, Foster MS, Roberts CA (2003) Rhodolith bed diversity in the Gulf of California: the importance of rhodolith structure and consequences of disturbance. *Aquat Conserv: Mar Freshw Ecosyst* 13:S5–S20
- Steneck RS (1986) The ecology of coralline algal crusts: convergent patterns and adaptive strategies. *Annu Rev Ecol Syst* 17:273–303
- Ter Braak CJF (1996) Unimodal methods to relate species to environment. Centre for Biometry Wageningen (DLO Agricultural Mathematics Group), Wageningen
- Villas-Bôas AB, Tâmega FTS, Andrade M, Coutinho R, Figueiredo MAO (2014) Experimental effects of sediment burial and light attenuation on two coralline algae of a deep water rhodolith bed in Rio de Janeiro, Brazil. *Cryptogam Algal* 35:67–76
- Volkenborn N, Hedtkamm SIC, Beusenkom JEE, Reise K (2007) Effects of bioturbation and bioirrigation by lugworms (*Arenicola marina*) on physical and chemical sediment properties and implications for intertidal habitat succession. *Estuar Coast Shelf Sci* 74:331–343
- Wright JP, Jones CG, Flecker AS (2002) An ecosystem engineer, the beaver, increases species richness at the landscape scale. *Oecologia* 132:96–101