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ORIGINAL PAPER

Reef fish associations with sea urchins in an Atlantic oceanic island

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Abstract Many reef fish are known to be associated with particular microhabitats that provide food and refuge, such as branching corals, gorgonians, macroalgal beds and sea urchins. We investigate the association of reef fishes with the long-spined sea urchin *Diadema antillarum* in shallow reefs of Trindade Island, southeastern Brazil. A total of 1283 fish individuals from seven families and nine species were associated with 495 sea urchins. Sea urchins provide important shelter especially for juveniles of the Noronha wrasse, *Thalassoma noronhanum*. Larger fishes were found at higher densities associated to sea urchins with larger spines. At reefs lacking structurally complex organisms, such as branching corals, sea urchins can be an important refuge for juveniles or small-bodied reef fish species, influencing their distribution and acting as ecosystem engineers.

Communicated by O. Aksel Bergstad

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Introduction

Habitat structure and complexity are known to influence reef fish abundance and diversity at various spatial scales from micro to mega habitats (Roberts and Ormond 1987; Ferreira et al. 2001; Rogers et al. 2014). In reef environments, many fish species are known to be associated with particular habitats, mostly due to optimal refuge against predators and availability of food (Dahlgren and Eggleston 2000). Many organisms are known to modify the environment or create microhabitats, being described as ecosystem engineers (Jones et al. 1994). Several species of small sized or juvenile reef fish can be associated with microhabitats provided by complex biogenic sessile structures such as branching corals (Pereira and Munday 2016), macroalgae (Chaves et al. 2013), gorgonians (Goh et al. 1999) and mobile organisms such as sea urchins, cucumbers and crinoids (Karplus 2014).

The fish-sea urchin association has long been reported, especially for the cardinalfishes (Apogonidae) and clingfishes (Gobiesocidae) families with sea urchins from the family Diadematidae (Randall et al. 1964; Karplus 2014). The structural complexity generated by sea urchin spines harbors a diversity of small fish that can be closely associated, favoring the development of juvenile stages or even a whole life stage as an obligatory association (Randall et al. 1964; Sakashita 1992). For some fish species, sea urchins may influence the density of their commensals in the reef by providing refuges against predators. For instance, Hartney and Grorud (2002) found a close association among the crowned sea urchin, *Centrostephanus coronatus,* and the blue-banded goby *Lythrypnus dalli.* Results showed that the crowned sea urchin has an influence on the abundance, recruitment, migration rates and survival of this small fish. However, only a small fraction of associated fish is permanent and obligatory (Karplus 2014). Most of the fish and sea urchin associations are facultative and

commensal (Moore and Auster 2009). Fish from the Gobioesocidae and Gobbidae families are also described as ectoparasitic, in which the associated fish feed on the tube feet or pedicelaria of their hosts (Dix 1969; Karplus 2014).

In some reefs, sea urchins occur at higher abundances, providing an increase in the reef complexity and, consequently, microhabitats for the marine biota. This may have positive effects for reef fish by providing them habitat structure, otherwise at some tropical reefs, sea urchins can largely increase bioerosion (McClanahan and Kurtis 1991) and erode reef structural complexity (Graham and Nash 2012). However, in the southwestern Atlantic reefs, such associations between reef fish and sea urchins remain poorly described (Dalbern and Floeter 2012).

The sea urchin *Diadema antillarum* was once abundant in Atlantic tropical reefs and referred to as a keystone species up until the 1980s, when an event of mass mortality led to significant depletion (Lessios et al. 2001). Here, we describe the association among the long-spined sea urchin *Diadema antillarum* and reef fishes at Trindade Island, an oceanic island located in the southwestern Atlantic. At Trindade Island, in the shallow reefs, this is the most abundant sea urchin, and is usually found forming densely packed groups of dozens of individuals (Cordeiro et al. unpubl.). Individuals of *D. antillarum* are commonly found in caves, overhangs, and crevices that provide protection against predators and are more abundant in zones protected from strong waves (Alvarado 2008). The aim of this study was to describe which fish species are associated with *D. antillarum* and verify whether density and body size of associated fish vary according to the size of sea urchin spines. In addition, we determined if density of fishes associated with sea urchins was correlated to those not associated with urchins, for instance, fish moving across the reef or fish associated with other structures.

Methods

Study area

Trindade Island, along with the Martin Vaz Archipelago, comprises the most isolated island complex of the Brazilian coast, and is located 1160 km off the coast with a terrestrial area of 9.2 km² (Gasparini and Floeter 2001). Compared to the Brazilian coast, the remote location makes Trindade Island home to impoverished fish (Floeter et al. 2008; Pinheiro et al. 2011) and benthos assemblages (Pereira-Filho et al. 2011).

Along the Brazilian coast, *D. antillarum* is more abundant in the tropical northeastern region (Attrill and Kelmo 2007), and rare in the subtropical reefs along the south and southeastern coastline (Cordeiro et al. 2014). In the shallow reefs (5-12m depth) of Trindade Island, *D. antillarum* is the dominant species among the five sea urchin species found locally [38% of total abundance of sea urchins and 0.01–1.5. ind.m⁻² at five

sites around the island (Cordeiro et al. unpubl.)], and is the only species with long spines that hosts different fish species.

Data collection

Data were collected from August to September 2014 at three shallow sites (3–10 m depth) in the north of Trindade Island: Cabritas, Calheta and Ponta Norte. Observations were conducted in rocky reefs through 26 roving scuba diving counts, in which two observers searched for the specimens. To avoid sampling the same sea urchin twice, observers roved parallel to the reef in the same direction. When a sea urchin was found, the observer slowly approached to verify the presence of any associated fish, and when found, the abundance and body size of the fish species was described (total length – TL). Fish were identified using checklists from Trindade Island (Gasparini and Floeter 2001; Pinheiro et al. 2015). The size of the sea urchin spines was visually estimated based on the length of the largest primary spines and grouped into three categories: short (≤5 cm), medium (6–15 cm) and long (>15 cm). Additionally, observers described the behavior of the fish associated with sea urchins and recorded their spatial distribution among the urchin's spines.

In order to assess reef fish abundance, an underwater visual census were performed using belt transects (20x2m) at all the sampled sites (Cabritas, *n* = 11, Orelhas, *n* = 10, and Ponta Norte, *n* = 15). Sampling units were distributed randomly along rocky reef areas, and all fish observed within transects were counted and measured.

Data analysis

Differences between body size and density of the most abundant fish species (species of which >15 individuals were recorded) associated with sea urchins were compared using a non-parametric ANOVA (Kruskal-Wallis test), since the response distribution was non-normal and data was nonparametric. A post-hoc analysis using the Dunn's test was performed to verify differences among categories of sea urchin spine size. Composition of fish assemblages and mean fish density amongst sites were tested using a PERMANOVA (9999 permutations, package *vegan*, function *adonis*) and ANOVA, respectively. A Pearson correlation was used to verify whether overall abundance of the non-associated fish with sea urchins was correlated with abundance of fish associated with the urchin *D. antillarum*. Analyses were conducted using the R software (R Core Team 2016).

Results

A total of 1283 fish from seven families and nine species were recorded in association with 495 individuals of *D. antillarum*

with short ($n = 98$), medium ($n = 196$) and long ($n = 201$) spine sizes. Individuals of *D. antillarum* with long and medium spines have higher densities of commensal fishes than short-spined sea urchins (Kruskal-Wallis test, H = 117.1, $p < 0.001$; Dunn's test: long = medium > short). Seventy-three percent of sea urchins with short spines hosted no commensal fishes, while 83% of sea urchins with medium spines and 89% with long spines had fishes associated with them. The most frequent species found among *D. antillarum* spines were *Thalassoma noronhanum*, occurring with 81% of sea urchins sampled at a mean density of 2.11 (±0.17 SE) individuals per sea urchin. The second most abundant species was *Malacoctenus brunoi*, found in 12% of sea urchins surveyed at a mean density of 0.32 (±0.04) (Table 1). Higher densities of *T. noronhanum* were detected in long-spined urchins (H = 6.9, $p = 0.03$; post-hoc test: long = medium > short; Fig. 1a, b), while densities of *M. brunoi* were similar regardless of spine size. Higher densities of *Chromis multilineata* and *Apogon americanus* were also observed in sea urchins with larger spines, although non-significant (Fig. 1c, d). Fish body size increased proportionally along different size categories of sea urchin spines for *T. noronhanum* (H = 23.9, $p < 0.001$), and *M. brunoi* (H = 22.4, $p < 0.001$) (Fig. 2a, b). *Chromis multilineata* and *A. americanus* were not found associated with small sea urchins, and their body sizes were similar to individuals found associated with medium and long spines sizes (Fig. 2c, d). *Amblycirrhitus pinos* and *Coryphopterus thrix* were only associated with sea urchins with long spines. Four fish species associated with sea urchins were recorded only during the juvenile stage, and the other five only as adults (Table 1).

The assemblage composition (PERMANOVA, $F_{3,44} = 1.22$, $p = 0.19$) and mean fish abundance (ANOVA, $F_{3,41} = 2.68$, $p = 0.06$) were similar among sampled sites. Differences in the density of *T. noronhanum* among sites were correlated with lower abundance of individuals associated with sea urchin spines (Pearson, $r = 0.74$, $p < 0.02$) at Cabrita. For other species, the correlation was not significant or could not be tested due to a low number of individuals. Therefore, results should be interpreted carefully because they represent cryptic behavior and incidence is underestimated when sampling by visual census methods.

Fish species were observed inhabiting different areas of the sea urchin's spines. *Thalassoma noronhanum* and *M. brunoi* generally inhabited the tips of the spines, while *A. americanus* and *C. multilineata* were more associated with the base, near the test (Fig. 3). Individuals of *Ophioblennius trinitatis* were found only as a single individual in contact with the bottom and were rarely seen in the presence of another fish species. The behaviors of the most abundant species (>15 individuals observed) are described in Table 2.

Discussion

Our results suggest that at Trindade Island, *Diadema antillarum* function as an alternative refuge for reef fish, especially for juveniles of *T. noronhanum*. By offering shelter, they are a significant determinant of reef fish abundance at local scales (Graham and Nash 2012), the habitat structure provided by sea urchins may reduce the effects of predation. Trindade Island lacks branching corals or other structural complexity builders. Branching corals and macroalgal beds are known to provide microhabitats that shelter juveniles of several fish species (Chaves et al. 2013; Coni et al. 2013; Leal et al. 2013). Thus, because of the abundance of *D. antillarum* and the refuge provided by its spines, we suggest that this species has the same functional significance as branching corals and other biogenic structures found in coastal areas,

Table 1 Reef fish species recorded in association with sea urchins in the Trindade Island, Brazil

Family	Species	No. of individuals	Life stage	Fish density (mean ± SE)	Body size (mean ± SE)
Labrisomidae	*Thalassoma noronhanum*	1043	J	2.11 ± 0.17	3.9 ± 0.06
Labrisomidae	*Malacoctenus brunoi*	157	A	0.32 ± 0.04	5.2 ± 0.08
Pomacentridae	*Chromis multilineata*	40	J	0.08 ± 0.03	4.9 ± 0.24
Apogonidae	*Apogon americanus*	15	J	0.03 ± 0.01	4.1 ± 0.12
Pomacentridae	*Stegastes fuscus*	10	J	0.02 ± 0.006	4.6 ± 0.27
Blennidae	*Ophioblennius trinitatis*	7	A	0.01 ± 0.005	4.1 ± 0.26
Gobiidae	*Elacatinus pridisi*	7	A	0.01 ± 0.007	4.7 ± 0.47
Cirrhitidae	*Amblycirrhitus pinos*	3	A	0.006 ± 0.003	6.6 ± 0.33
Gobiidae	*Coryphopterus thrix*	1	A	0.002 ± 0.002	4 ± 0
	Total	1283			

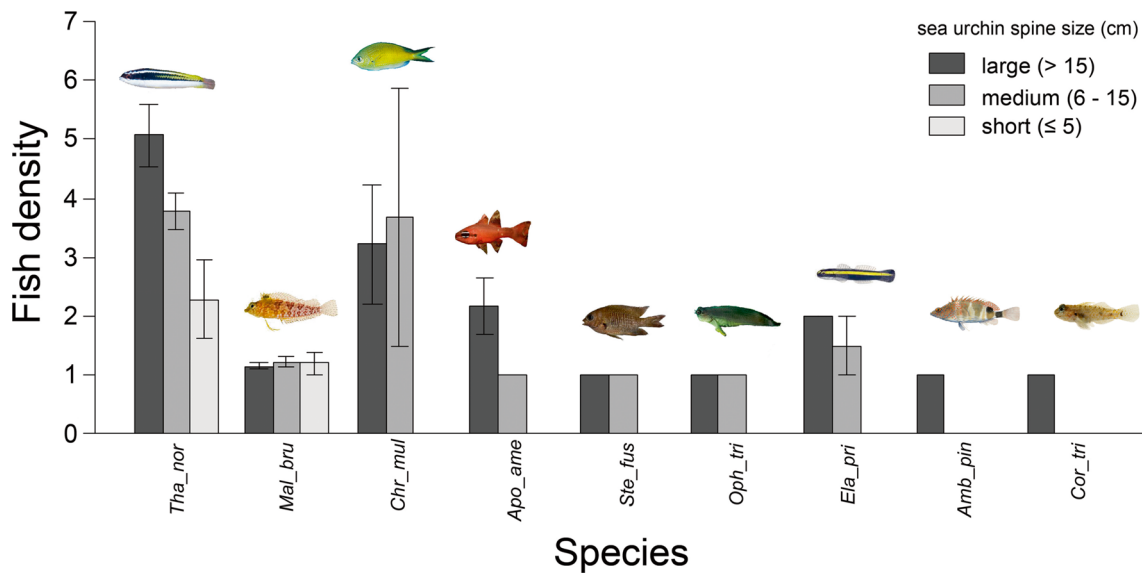Life stage: J) juvenile and A) adult.

Fig. 1 Mean density of reef fishes associated with sea urchins according to the spine size. The deviations are standard errors. Species names: *Thalassoma noronhanum* (*Tha_nor*); *Malacoctenus brunoi* (*Mal_bru*); *Chromis multilineata* (*Chr_mul*); *Apogon americanus* (*Apo_ame*); *Stegastes fuscus* (*Ste_fus*); *Ophioblennius trinitatis* (*Oph_tri*); *Elacatinus pridisi* (*Ela_pri*); *Amblycirrhitus pinos* (*Amb_pin*); and *Coryphopterus thrix* (*Cor_*tri)

functioning as ecosystem engineers for some species and providing a microhabitat for small fish that are associated with parts of the reef of lower structural complexity.

The wrasse *T. noronhanum* was the most predominant species associated with the sea urchins. The species was found in shoals of 5–15 individuals swimming near sea urchins and seeking refuge amongst them when approached by the observer. Such behavior clearly indicates the close association between these two animals. This is possibly a causal commensal relationship since fish benefit from shelter against predators,

whereas for sea urchins such association is likely to be neutral (not detrimental). However, sea urchins can benefit from this association, since fish may use the urchin's ectoparasites as a food resource (Karplus 2014).

To the best of our knowledge, this is the first time that the associations between sea urchins and fish are reported for the nine observed fish species (see Table 1). Our observations comprise ~14% of the 61 species described as associated with 16 species of sea urchins (Karplus 2014). Including data from this study, fishes described as associated with sea urchins

Fig. 2 Body size (measured as total length) of the most abundant fishes associated with *D. antillarum* according spines size. (**a**) *Thalassoma noronhanum*; (**b**) *Malacoctenus brunoi*; (**c**) *Chromis multilineata* and (**d**) *Apogon americanus*. The deviations are standard errors
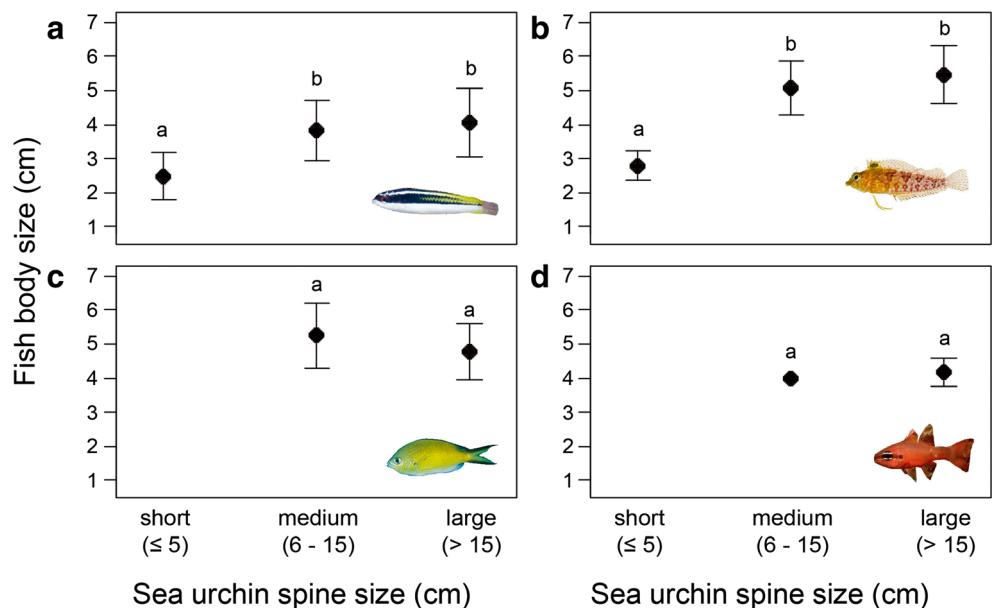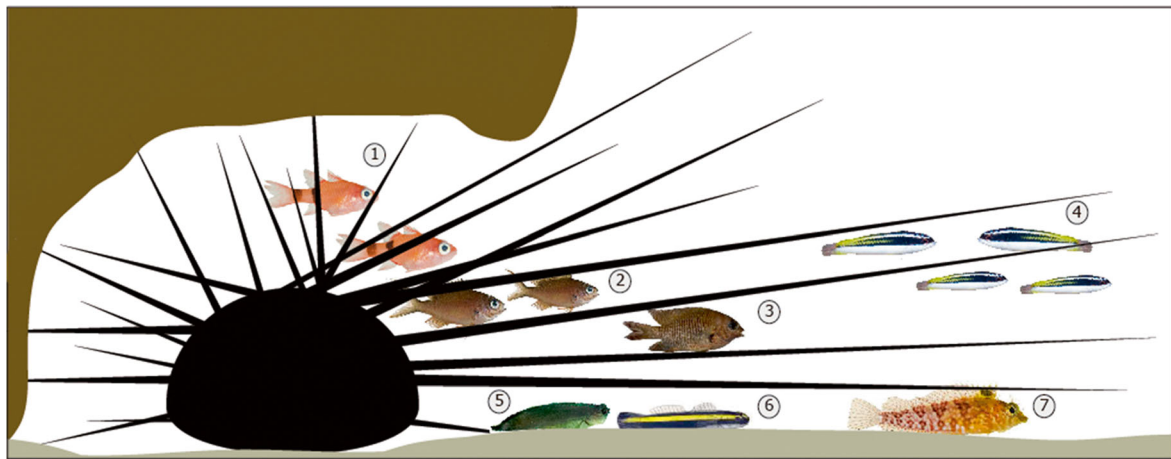
Fig. 3 Representative sketch of a sea urchin indicating the spatial distribution of the associated fish species observed. 1) *Apogon americanus*; 2) *Chromis multilineata*; 3) *Stegastes fuscus*; 4) *Thalassoma noronhanum*; 5) *Ophioblennius trinitatis*; 6) *Elacatinus pridisi*; and 7) *Malacoctenus brunoi*

represent 15 families, but associations are most frequent in Apogonidae (29 species), Gobioesocidae (12 species) and Gobiidae (10 species). Regarding the genera *Diadema* and *Echinothrix*, they were the urchins most commonly having fish associates, and the most important species was *D. antillarum* (Karplus 2014). Sixteen fish species were associated with that species, and 12 with *D. setosum*. These urchin species are long-spined and are generally preferred by organisms seeking shelter, because they provide structurally complex microhabitats used as refuge against predators (Graham and Nash 2012).

Fish species described as associated with sea urchins in this study comprise ~6% of the teleost fish species known to inhabit Trindade Island (Pinheiro et al. 2015). However, it is important to highlight that we found fewer than ten individuals of *O. trinitatis*, *E. pridisi*, *A. pinos* and *C. thrix* associated with sea urchins. Although observed associations are likely to be opportunistic, the presence of adults and juveniles of some species in the spines suggests that either sea urchins are an optimal shelter, or that space limitation mediates ontogenetic spatial segregation for these species. In the first case, urchins are good shelter providers for the adult and juvenile species observed among sea urchin spines. To them, the urchins serve as a microhabitat. In the latter, the juvenile species observed may probably be taking advantage of this association until they attain a large enough size to escape predation (Scharf et al. 2000). Also, some species of the Indo-Pacific ocean, such as *Siphamia tubifer* also present daily site fidelity and might return to the same sea urchin after being displaced two kilometers away (Gould et al. 2014). In this study, we verified for a specific sea urchin the same number of *A. americanus* specimens during three consecutive days. This suggests shelter fidelity during non-active periods, since this species is nocturnal.

Table 2 Behavior of reef fishes associated with sea urchins in Trindade Island, Brazil

Species	Behavior
Thalassoma noronhanum	Sighted in small shoals in the reef (5–15 individuals). Take shelter randomly in the closest sea urchin when the diver presence was detected. Remain at the final portion of spines and leaves the sea urchin when the threat ceases
Malacoctenus brunoi	Found in contact with the substrate at the final portion of long spines, mainly in medium and large sea urchins
Chromis multilineata	Inhabit medium and large sea urchins on dark crevices, distant from the final portion of the spines, near the carapace. Small shoals (2–5 individuals)
Apogon americanus	Inhabit medium and large sea urchins on deep and dark crevices
Stegastes fuscus	Inhabit medium and large sea urchins on dark crevices
Ophioblennius trinitatis	Found solitary, with no other species. Associated with the bottom, near the sea urchin carapace. Hides away near the sea urchin carapace in the presence of threats
Elacatinus pridisi	Associated with the substrate, in pairs on the sea urchins in shallow and less shaded crevices

Individuals of *D. antilarum* with larger spines were more densely populated by commensal fish. Similarly, by providing better refuge, sea urchins with medium and long spines were preferred by larger individuals. Longer spines are described to play a major role in sea urchin attractiveness (Hartney and Grorud 2002). They form a network of interstices within which the fish found a more effective shelter than that of short-spined urchins (Karplus 2014). Longer spines hosted more species, but fish were spatially distributed along zones of the spines. Despite the high number of fish of different species associated with some long-spined sea urchins, we did not observe agonistic behavior among them, as has been observed for fish in branching corals (Leal et al. 2013). The distribution of species along spines could be associated with species behavior or guild (see Bellwood et al. 2006). For instance, the invertebrate feeders *T. noronhanum* and *M. brunoi* occupied the tips of spines and the planktivore *C. multilineata* was observed close to the base of spines. Sea urchins might also serve as a feeding station where some species can lie down and wait for prey. Invertivorous species inhabit the tips of spines, from where they can make short excursions on the surrounding substrate to search for food. Nevertheless, it is possible that our results were underestimated because some sea urchins were sheltered in deeper crevices, out of the observer's view. The number of fish species associated might be underestimated because some species can only be detected by displacing the sea urchin (Patzner 1999).

The color patterns of fish associated with sea urchins does not follow the longitudinal striped dark pattern (see Fig. 3), common among fish who seek shelter in sea urchins (Karplus 2014). This color pattern was intended to assist in the fish's camouflage (Lachner 1955). This suggests that species found at Trindade Island have a more distant association than other species do to such as clingfishes and cardinalfishes.

By providing a structurally complex microhabitat in the impoverished reefs of Trindade Island, *D. antillarum* is an important refuge to juveniles of one of the most abundant fish species *T. noronhanum*, and other small reef-associated fish species. The limitation of natural complexity providers such as corals and other reef builder organisms at Trindade Island may enhance other types of intra- and interspecific interactions. However, in order to confirm this hypothesis, future experimental work with mimics of structures provided by reef builder organisms will provide a greater understanding on this spatial limitation puzzle. This study adds to the body of knowledge that structurally complex benthic organisms provide microhabitats that are an important habitat for small-bodied reef fishes, possibly acting as ecosystem engineers.

References

Alvarado JJ (2008) Seasonal occurrence and aggregation behavior of the Sea Urchin *Astropyga pulvinata* (Echinodermata: Echinoidea) in Bahía Culebra, Costa Rica. Pac Sci 62:579–592

Attrill MJ, Kelmo F (2007) Opportunistic responses of *Diadema antillarum* (Echinodermata: Echinoidea) populations following the 1997–98 El Niño event in Bahia, Brazil. Estuar Coast Shelf Sci 73:243–248

Bellwood DR, Wainwright PC, Fulton CJ, Hoey AS (2006) Functional versatility supports coral reef biodiversity. P Roy Soc B-Biol Sci 273:101–107. doi:10.1098/rspb.2005.3276

Chaves L, Pereira PHC, Feitosa JLL (2013) Coral reef fish association with macroalgal beds on a tropical reef system in North-eastern Brazil. Mar Freshw Res 64:1101–1111. doi:10.1071/MF13054

Coni EOC, Ferreira CM, Moura RL, Meirelles PM, Kaufman L, Francini-Filho RB (2013) An evaluation of the use of branching fire-corals (*Millepora* spp.) as refuge by reef fish in the Abrolhos Bank, eastern Brazil. Environ Biol Fish 96:45–55. doi:10.1007/s10641-012-0021-6

Cordeiro CAMM, Harbone AR, Ferreira CEL (2014) Patterns of distribution and composition of sea urchin assemblages on Brazilian subtropical rocky reefs. Mar Biol 161:2221–2232. doi:10.1007/s00227-014-2500-0

Core Team R (2016) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Dahlgren CP, Eggleston KL (2000) Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. Ecology 81:2227–2240

Dix TG (1969) Association between the echinoid *Evechinus chloroticus* (Val.) and the clingfish *Dellichthys morelandi* Briggs. Pac Sci 23:332–336

Dalben A, Floeter SR (2012) Cryptobenthic reef fishes: depth distribution and correlations with habitat complexity and sea urchins. J Fish Biol 80(4):852–865. doi:10.1111/j.1095-8649.2012.03231.x

Ferreira CEL, Gonçalves JEA, Coutinho R (2001) Community structure of fishes and habitat complexity on a tropical rocky shore. Environ Biol Fish 61:353–369. doi:10.1023/A:1011609617330

Floeter SR, Rocha LA, Robertson DR, Joyeux JC, Smith-Vaniz WP, Edwards AJ, Barreiros JP, Ferreira CEL, Gasparini JL, Brito A, Falcón JM, Bowen BW, Bernardi G (2008) Atlantic reef fish biogeography and evolution. J Biogeogr 35:22–47. doi:10.1111/j.1365-2699.2007.01790.x

Gasparini JLR, Floeter SR (2001) The shore fishes of trindade island, western south Atlantic. J Nat Hist 35:1639–1656. doi:10.1080/0022293013170922379

Goh NKC, Peter KLN, Chou LM (1999) Notes on the shallow water gorgonian-associated fauna on coral reefs of Singapore. Bull Mar Sci 65:269–282

Gould AL, Harii S, Dunlap PV (2014) Host preference, site fidelity, and homing behavior of the symbiotically luminous cardinalfish, *Siphamia tubifer* (Perciformes: Apogonidae). Mar Biol 161:2897–2907. doi:10.1007/s00227-014-2554-z

Graham NAJ, Nash KL (2012) The importance of structural complexity in coral reef ecosystems. Coral Reefs 32:315–326. doi:10.1007/s00338-012-0984-y

Hartney KB, Grorud KA (2002) The effect of sea urchins as biogenic structures on the local abundance of a temperate reef fish. Oecologia 131:506–513. doi:10.1007/s00442-002-0908-6

Jones CG, Lawton JH, Shachak M (1994) Organisms as ecosystem engineers. Oikos 69:373–386

Karplus I (2014) The associations between fishes and echinoderms. In: Karplus I (ed) Symbiosis in fishes: the biology of interspecific partnerships, first edition. Wiley, New Jersey, p 460p

Lachner EA (1955) Inquilinism and a new record for *Paramia bipunctata*, a cardinal fish from the Red Sea. Copeia 1955:53–54

Leal ICS, Pereira PHC, De Araujo ME (2013) Coral reef fish association and behaviour on the fire coral *Millepora* spp. in north-east Brazil. J Mar Biol Assoc UK 93:1703–1711. doi:10.1017/S0025315413000234

Lessios HA, Garrido MJ, Kessing BD (2001) Demographic history of *Diadema antillarum*, a keystone herbivore on Caribbean reefs. Proc R Soc Lond B 268:1–7. doi:10.1098/rspb.2001.1806

McClanahan TR, Kurtis JD (1991) Population regulation of the rock-boring sea urchin *Echinometra mathaei* (de Blainville). J Exp Mar Biol Ecol 147:121–146. doi:10.1016/0022-0981(91)90041-T

Moore JA, Auster PJ (2009) Commensalism between juvenile cusk eels and pancake urchins on western North Atlantic seamounts. B Peabody Mus Nat Hi 50:381–386. doi:10.3374/014.050.0205

Patzner RA (1999) Sea urchins as a hiding-place for juvenile benthic teleosts (Gobiidae and Gobiesocidae) in the Mediterranean Sea. Cybium 23:93–97

Pereira PHC, Munday PL (2016) Coral colony size and structure as determinants of habitat use and fitness of coral-dwelling fishes. Mar Ecol Prog Ser 553:163–172. doi:10.3354/meps11745

Pereira-Filho GH, Amado-Filho GM, Guimarães SMPB, Moura RL, Sumida PYG, Abrantes DP, Bahia RG, Guth AZ, Jorge RR, Francini-Filho RB (2011) Reef fish and benthic assemblages of the Trindade and Martin Vaz island group, southwestern Atlantic. Braz J Oceanogr 59:201–212. doi:10.1590/S1679-87592011000300001

Pinheiro HT, Ferreira CEL, Joyeux J-C, Santos RG, Horta PA (2011) Reef fish structure and distribution in a south-western Atlantic Ocean tropical island. J Fish Biol 79:1984–2006. doi:10.1111/j.1095-8649.2011.03138.x

Pinheiro HT, Mazzei EF, Moura RLM, Amado-Filho GM, Carvalho-Filho A, Braga AC, Costa PAS, Ferreira BP, Ferreira CEL, Floeter SR, Francini-Filho RB, Gasparini JL, Macieira RM, Martins AS, Olavo G, Pimentel CR, Rocha LA, Sazima I, Simon T, Teixeira JB, Xavier LB, Joyeux J-C (2015) Fish biodiversity of the Vitória-Trindade Seamount Chain, southwestern Atlantic: an updated database. PLoS One 10, e0118180. doi:10.1371/journal.pone.0118180

Randall JE, Schroeder R, Starck W (1964) Notes on the biology of the echinoid *Diadema antillarum*. Caribb J Sci 4:421–433

Roberts CM, Ormond RF (1987) Habitat complexity and coral reef fish diversity and abundance on Red Sea fringing reefs. Mar Ecol Prog Ser 41:1–8

Rogers A, Blanchard JL, Mumby PJ (2014) Vulnerability of coral reef fisheries to a loss of structural complexity. Curr Biol 24:1000–1005. doi:10.1016/j.cub.2014.03.026

Sakashita H (1992) Sexual dimorphism and food habits of the clingfish, *Diademichthys lineatus*, and its dependence on host sea urchin. Environ Biol Fish 34:95–10. doi:10.1007/BF00004787

Scharf FS, Juanes F, Rountree RA (2000) Predator size - prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. Mar Ecol Prog Ser 208:229–248