

Fish diversity in tidepools: assembling effects of environmental heterogeneity

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Abstract Tidepools are considered ecosystems of high interchangeable fish biota. However, natural and anthropogenic actions that alter negatively marine ecosystems functioning (e.g., algal exploitation) are causing homogenization of fish biodiversity. Here, we describe the functional and taxonomic assembling of fishes in beach rocks of northeastern Brazil. Traits of fish species were retrieved from Fishbase and beta diversity was assessed by the dispersion of abundance, presence-absence and functional diversity in the multivariate space. We

explained spatial-temporal variation in: alpha diversity, taxonomic and functional community composition; as well as temporal variation in functional, beta and gamma diversities. We found an annual stability in fish diversity and composition, and that fish biota was assembled mainly per tidepools' depths. Substrate heterogeneity was correlated to depth, highlighting the role of local features as filters to organize the fish fauna vertically in tidepools, especially a cultivation of algae that influences the local assembling. We also highlight the uniqueness status of beach rocks in the Brazilian tropical region.

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Introduction

Fish community dynamics has been recently assessed through functional and beta diversities (Mouchet et al. 2010; Anderson et al. 2011; Pinheiro et al. 2013; Metcalfe et al. 2015). This is particularly interesting in tidepools, given they are established as feeding and nursery open ecosystems for producers and benthic organisms (Gibson 1972; Davis 2000; Barbier and Hacker 2011) and include protected species that require minimally invasive sampling techniques (Watson and Huntington 2016). Despite well investigated in ecological assessments, metacommunity variation and underlying environmental influences in species assembly are rarely considered (Witman et al. 2015), leading to

misinterpretations about the conservation status of the fauna in inventories of biodiversity (Vitule et al. 2016). Recent studies have indeed emphasized the need for investigations aiming to elucidate relationships between environmental variation and functional diversity (Freitas and Lotufo 2015; Witman et al. 2015); to clarify causes for spatial and seasonal turnover (Bloch and Klingbeil 2016) in rocky reefs and to identify drivers of fish diversity to the management and conservation of tidepools, under effects of global warming and biological invasions in tropical regions.

Natural disturbances, such as wave exposure and tidal elevation reveal dominance, competition, facilitation and predation amongst the main modulating interactions on fish communities in rock pools (Dethier 1984; Davis 2000) and marine “essential fish habitats” (Bizzarro et al. 2016). In other tropical rockpools, fish community mostly depends on local substrate, area, seasonality and biological interactions (Methratta 2004; Messmer et al. 2011; Chargulaf et al. 2011). While supporting conservation policies, patterns on environment-biota association highlight determinism in ecosystem services and guide managers to conciliate reef conservation with human purposes, such as recreation and tourism (Cowen 2006; Barbier and Hacker 2011), particularly in mega-diverse developing countries (Lucrezi and van der Walt 2016).

We introduced a way to match biodiversity with environmental heterogeneity in our study, emphasizing a standardized sampling and specific data analyses. To this aim, we sampled fish communities in marine ecosystems that could be used as checkpoints of aquaculture and global warming effects. Beta diversity assessments add to this task once they represent the spatial-temporal variation of the fish biota. This analysis is underused in tropical ecosystems, with biased investigations to temperate areas (Socolar et al. 2016), although designed as an alternative to explain species richness in terms of compositional variation (Whittaker 1960). Patterns in beta diversity has recently been pointed out as central to support biodiversity conservation (Heino et al. 2015; Bush et al. 2016). Understanding causes for spatial and temporal variation in beta diversity may overcome the known difficulties in represent the singularity of fish community in tidepools and beach rocks (Dethier 1984). Causes for community organization in such tropical beach rocks are even less explored despite it commonness along the Brazilian Western Atlantic (Macieira et al. 2014; Freitas and Lotufo 2015; Machado et al. 2015).

In our study, we attempt to fill these gaps in tropical tidepools at flat beach rocks, assessing causes for spatial-temporal dynamics of alpha, beta, gamma and functional fish diversities, inferring the likely effect of neutral (Rosindell et al. 2011) and niche-based processes (Levine and HilleRisLambers 2009). Through patterns in biodiversity organization, we attempted specifically to understand causes for alpha, beta and gamma taxonomic and functional diversities in typical beach rocks of northeastern Brazil. Following the classical ecological theory on community organization, we expect that environmental features of tidepools would explain taxonomic and functional diversities (Hutchinson 1959; Gibson 1972; Davis 2000; Chase 2010; Villéger et al. 2010), especially through the substrate heterogeneity per tidepool. This may be particularly relevant in our study area, the “Praia da Baleia” - hereafter called “Baleia” (Northeastern Brazil), given that the beach rocks are subject, apparently with no regulation, to widely employed algae (*Gracilaria* spp.) exploitation, that can decrease environmental heterogeneity and consequently fish diversity.

Materials and methods

Study area

The Northeastern Brazilian beach rocks are mostly sandstone shapes in carbonate flat reefs that mold tidepools. Along 570 km of coastline, tidepools with different substrates are common in the Ceará State (northeastern Brazil), including sandy, algal, rocky bottom (Godinho and Lotufo 2010; Machado et al. 2015) and soft-bottom linked to salt marshes and mangroves (Oliveira et al. 2016). The 167 species of bony fishes recorded in Ceará State corresponds to 51% of the fish fauna in northeastern Brazilian region (Freitas and Lotufo 2015). This study was held at Baleia (Ceará State – Brazil), in two beach rocks (BR’s) during low tide (varying from –0.1 m to 0.3 m), when beach strip extends along almost 0.07 km (excluding BR’s) and tidepools are mostly isolated from another (Fig. 1; Fig. SM2 - a and b; see Electronic supplementary material).

Data samplings

Fishes were sampled during daytime in 72 tidepools, monthly from August 2011 to July 2012 (see tidepool’s

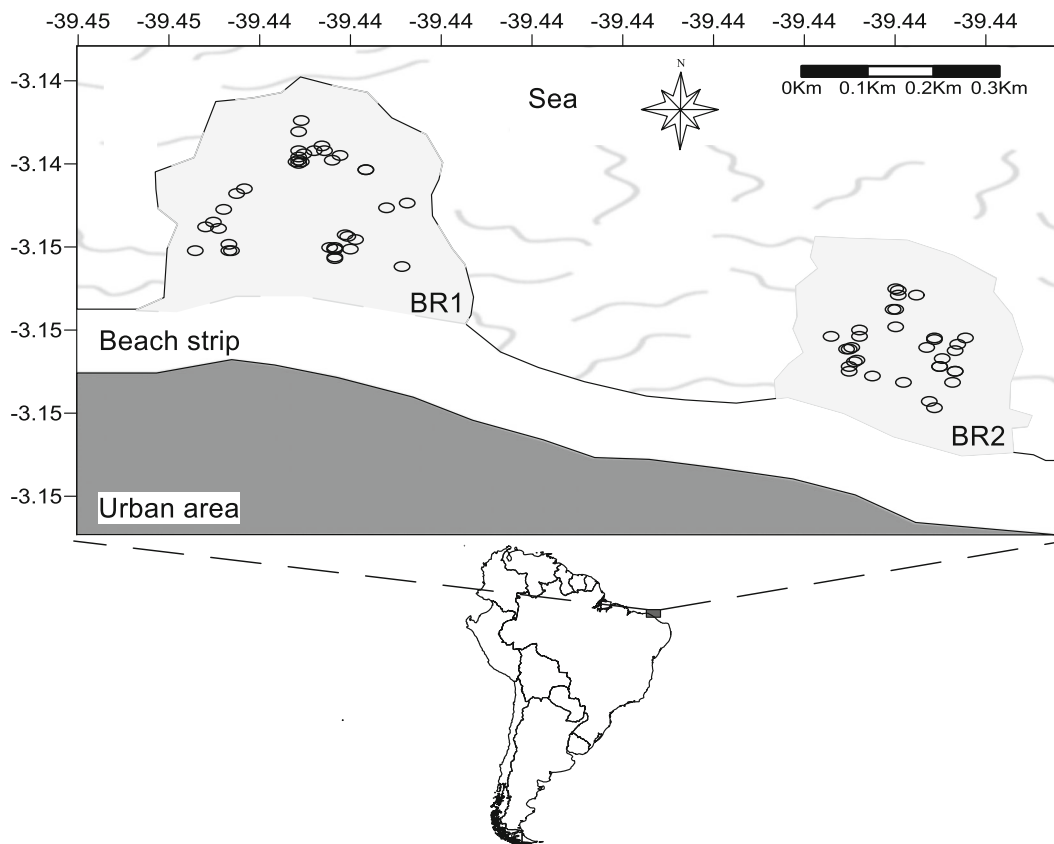


Fig. 1 Map of South America, highlighting Baleia (Northeastern Brazil) along nearly 1.2 km of coastline (sandy beach). Rounded shapes are shown the location of the 72 tidepools (not scaled, just representing their location) sampled at beach rocks BR1 and BR2,

after a strait beach strip (nearly 0.07 km) during the low tide (intertidal area). The urban area is inhabited mostly by locals that employ low-scale aquaculture and artisanal fishery

location in Fig. 1). In each sampling period, from three to six tidepools were sampled by three pre-trained researchers employing scuba snorkeling for 25 min per tidepool, based in the sufficiency observed in other scuba samplings (Christensen and Winterbottom 1981; Sabino 1999; Arakaki and Tokeshi 2006; Godinho and Lotufo 2010), therefore returning Sights-Per-Unit-Effort (Bueno et al. 2016). As any other sampling technique, Visual Census Technique (VCT) may underestimate some groups and overestimate others. However, given that our goal was not to describe the entire community, but to explain spatial and temporal variation in diversity metrics, the standard sampling described here is suitable (see also Arakaki and Tokeshi 2006; Arakaki et al. 2014; Gutterres Giordano and Neves dos Santos 2014; Pereira et al. 2014; Baker et al. 2016). Fish species were identified previously in the specialized literature and species lists (Human and

DeLoach 2002; Menezes et al. 2003; Nelson 2006; Godinho and Lotufo 2010), posteriorly registered by cameras and confirmed in electronic references (Eschmeyer and Fricke 2011; Froese and Pauly 2012). Fishes were observed during the low-tide in average depths ($1.28 \text{ m} \pm 0.57 \text{ m}$), regular temperature ($30.2 \text{ }^\circ\text{C} \pm 1.15 \text{ }^\circ\text{C}$) and volume ($4.9 \text{ m}^3 \pm 0.72 \text{ m}^3$). Considering the volumetric variation, tidepools were classified by surface area: little (until 5 m^2), medium (5 m^2 – 10 m^2) and big (higher than 10.1 m^2) and sampling was randomized monthly per researcher and tidepool width to avoid the sampler effect in species composition.

Average pool's depths were calculated after estimating depths at regular intervals in orthogonal transects at the pools, while surface area and environmental heterogeneity were assessed by scaling digital photos on specialized software. We used the average weighted substrate area of four substrata per tidepool: rocks, algae,

sand and gravel in six classes, varying from class one (NI – Non-Identified) to class five (all substrata), to create an Environmental Heterogeneity Index – EHI:

$$EHI = \frac{(\sum_{i=1}^5 a_i \times p_i)}{N + 1}$$

Therein: a_i and p_i are respectively relative percentage of substratum coverage and the weighted value of i , based on a distribution frequency of five classes in 72 tidepools and N is the number of substratum in each tidepool. The index varies from minimum (0.1) to maximum (1) heterogeneity, the last corresponding to all substrata (class five) plus NI, each having 20% of coverage. Substrate assessments were made locally in a first draft of the tidepools, then a photo was taken posteriorly to calculate the coverage area per substrate in specialized image software.

Functional traits of fish species

Functional diversity was accessed by 14 traits retrieved from rfishbase 2.0 package rewritten from Boettiger et al. (2012) at R environment (R Core Team 2015): average dorsal soft rays, average anal soft rays, aspect ratio of caudal fin, minimum depth range, maximum depth range, vulnerability to fishing, maximum length, common length, maximum weight, phylogenetic diversity, trophic level, resilience, body shape, aquarium trade. Details of how traits are estimated and what they mean are available in Fishbase (Froese and Pauly 2012). Missing data for some species were searched in counterpart's specimens from Brazilian Western Atlantic, estimated by length-weight relationships or searched in specific references (Hilomen-Garcia et al. 2003). These data are available at the Electronic supplementary material (Table SM1). We summarized functional diversity in following indexes: Functional divergence (FDiv; Villéger et al. 2008), Functional Dispersion (FDis; Laliberté and Legendre 2010) and Rao's quadratic entropy (Q; Botta-Dukát 2005) that were chosen to be three functional and non redundant indexes of diversity at community level (Mouchet et al. 2010).

In addition to explain diversity metrics, four groups were created only to describe occurrences in the beach rocks along the sample periods, adapted from Gibson and Yoshiyama (1999) and Griffiths (2003), but considering only the presence-absence criteria: “permanents” groups were observed in 11 to 13 months, “secondary

permanents” species varied from seven to 10 months, “visitors” from three to six months and “unlikely” species in one or two months. We did not use the original statuses (“opportunist”, “resident” and “visitor”) because the presence status is restricted to the occurrence of fish species monthly in a year, not in the overall life history (body size, cryptic and homing behavior) and biogeographic constraints; and because our analyses are focusing in environmental determinants over fish occupancy (Crabtree and Dean 1982). Permanence was also dissociated to resident or rare status of fish species, that depends on physiological and historical constraints (Martin 1995) not measured here.

Diversity indexes and predictors in each sampling period

Alpha, gamma and compositional (beta and functional, see below) diversities were investigated over 13 subsequent sampling periods. We used the residuals of a linear regression between number of sampled pools (npools) and diversity indexes in each month (period) as response variable, since samplings fluctuated monthly from three to six. Alpha and gamma diversities in each sampling period were respectively estimated as the mean species richness by sampled tidepools and total species richness of tidepools. Beta-diversity was estimated according to the approach proposed by Baselga (2010), in which a multiple site index of turnover (betaSIM) was generated. Functional diversity was assessed by calculating FDiv, FDis e Rao's Q, as described above.

Mean tidepools depth (MTD), area (MTA) and environmental heterogeneity (MEH) were used as predictors of diversity indexes described above. Moreover, environmental variation (EV) was estimated using the “betadisper” approach (Anderson et al. 2006), in which multivariate dispersion of environmental data (area, depth and EHI) in a certain sampling period is considered a measure of environmental variation among tidepools. We have also estimated the Sampled Geographical Extension (SGE), given that tidepools were sampled in different extents in each sampling period. SGE was estimated as the highest Euclidean distance among tidepools in a certain period. Therefore, SGE was used to control for differences in spatial extension among periods. Because MTA was correlated to SGE (r Pearson =0.81), MTA was omitted

in analyses. There was no other collinearity between predictor variables (Pearson's r always lower than 0.47).

Temporal and spatial community variation

A General Least Square (GLS) model was applied to explain among-month temporal variation in beta, gamma and functional diversity indexes described above using MTD, MTA, MEH, EV and SGE as predictors. Temporal autocorrelation patterns (Zuur et al. 2009) were controlled using “corAR1” structure, chosen as the most parsimonious (lower AIC) among all other structures in “nlme” package (Pinheiro et al. 2013).

For alpha diversity and metacommunity variation, we also explained spatial-temporal variation considering tidepools as sampling units. From the 72 tidepools (3–6 in each period), only two were coincidentally re-sampled in two periods. Therefore, we excluded repeated samplings to explain alpha and community composition (resulting in 70 communities spatially and temporally separated). We applied GLS to explain alpha using as predictors the tidepools' area (TA), depth (TD), EHI, latitude, longitude and sampling period (SP, thus representing other environmental variables temporally autocorrelated). We applied partial Redundancy Analyses (pRDA) to explain taxonomic (abundance, occurrence) and functional compositions in community-level weighted means (CWM) of trait values, using environmental and spatial predictors (Borcard and Legendre 2002). pRDA with two predictor matrices generates four components: E|S = the fraction of variation in community structure explained by environmental variables that are not spatially structured; ES = the variation in biological data explained by spatially structured environmental variables; S|E = spatial patterns in the community data that are independent of any environmental predictors included in the analysis; UN = the fraction that cannot be explained by environmental or spatial predictors (Borcard and Legendre 2002). Environmental variables were TA, TD, EHI, and SP. To explore the spatial structure of fish communities in tidepools, “Moran Eigenvector Maps” (MEM, previously the Principal Coordinates of Neighborhood Matrix – PCNM) were employed. MEM's variables were set by “pcnm” function in “vegan” package (Oksanen et al. 2015). Then, multiple scale spatial variables were created by Principal Coordinates Analysis (PCoA) and Euclidean distance was based on tidepool's geographical coordinates resulting in six eigenvectors

(PCNM1 to PCNM6), used as spatial predictors in a pRDA. We also explored further the effect of all variables by selecting the most likely environmental predictors of taxonomic and functional composition using stepwise modeling (Blanchet et al. 2008). This was done only in case of significant E|S contribution in pRDA. All analyses were carried out at R environment (R Core Team 2015).

Results

The most representative between 27 species registered on the beach rocks were *Haemulon parra*, *Sparisoma* spp., *Abudefduf saxatilis* and *Acanthurus chirurgus*, respectively with 252, 229, 129 and 95 individuals, from a total of 970 individuals (Table 1). Fish presence status is indeed described in Table 1.

Geographical extension was the only predictor of temporal variation in gamma diversity (with 6% of type I error): periods with higher geographical extensions had higher gamma diversities (Table 2). Beta diversity (betaSOR), nestedness, turnover and functional diversity indexes (FDiv, FDis and Rao's Q) were not explained by any variable.

Spatial-temporal variation in species richness is positively related to tidepool's depth and longitudinal variation; and negatively to EHI (Table 3). Other variables were related only with large type I error (> 0.10).

Spatial-temporal variation in species composition was explained by the environment variation despite spatial variables (Table 4). It is noticeable that abundances were better explained than occurrences (32% and 10% respectively). Functional composition was not explained by environmental predictors, but spatial variables explained 5% of CWM variation with a type I error of 6%.

After stepwise modeling, best variables to explain abundance composition were TD ($F = 24.93$; $P = 0.005$) and TA ($F = 7.40$; $P = 0.015$); and for occurrences was TD ($F = 8.83$; $P = 0.005$). The importance of such variables can be observed in the biplot of pRDA, considering environmental predictors (Fig. 2). The most remarkable relations in community composition were that high abundances and occurrences of *Haemulon parra*, *Sparisoma* spp., *Abudefduf saxatilis*, *Anisotremus virginicus* and *Acanthurus chirurgus* were related to high depths; and *Sparisoma* spp. were mostly observed in pools with high EHI.

Table 1 Fish species, ordered by taxa, its abundance (N) and presence status at tidepools of Baleia

Taxa	N	Presence status
Anguilliformes		
Mureanidae		
<i>Gymnothorax vicinus</i> (Castelnaud, 1855)	2	Unlikely
Beloniformes		
Belonidae		
<i>Strongylura timucu</i>	1	Unlikely
Bericiformes		
Holocentridae		
<i>Holocentrus adscensionis</i> (Osbeck, 1765)	3	Visitor
Gasterosteiformes		
Syngnathidae		
<i>Hippocampus</i> sp.	2	Unlikely
Scorpaeniformes		
Scorpaenidae		
<i>Scorpaena</i> sp.	3	Unlikely
<i>Scorpaena plumieri</i> Bloch, 1789	1	Unlikely
Perciformes		
Acanthuridae		
<i>Acanthurus bahianus</i> Castelnaud, 1855	4	Visitors
<i>Acanthurus chirurgus</i> (Bloch, 1787)	95	Permanent
<i>Acanthurus coeruleus</i> Bloch & Schneider, 1801	2	Unlikely
Gerreidae		
<i>Eucinostomus</i> sp.	14	Secondary Permanent
Gobiidae		
<i>Bathygobius</i> aff. <i>Soporator</i> (Valenciennes, 1837)	5	Visitor
<i>Coryphopterus glaucofraenum</i> Gill, 1863	2	Unlikely
Haemulidae		
<i>Anisotremus surinamensis</i> (Bloch, 1791)	23	Visitor
<i>Anisotremus virginicus</i> (Linnaeus, 1758)	54	Secondary Permanent
<i>Haemulon parra</i> (Desmarest, 1823)	252	Permanent
<i>Haemulon aurolineatum</i> Cuvier, 1830	7	Visitor
<i>Haemulon plumierii</i> (Lacepede, 1802)	1	Unlikely
Labridae		
<i>Halichoeres brasiliensis</i> (Bloch, 1791)	28	Secondary Permanent
<i>Halichoeres</i> sp.	3	Unlikely
Labrisomidae		
<i>Labrisomus nuchipinnis</i> (Quoy & Gaimard, 1824)	27	Secondary Permanent
Lutjanidae		
<i>Lutjanus</i> sp.	1	Unlikely
Pomacanthidae		
<i>Pomacanthus paru</i> (Bloch, 1787)	2	Unlikely
Pomacentridae		
<i>Abudefduf saxatilis</i> (Linnaeus, 1758)	129	Permanent
<i>Stegastes fuscus</i> (Cuvier, 1830)	2	Unlikely

Table 1 (continued)

Taxa	N	Presence status
Scaridae		
<i>Sparisoma</i> spp.	229	Permanent
Serranidae	1	Unlikely
Non Identified – NI	15	
Young NI	62	
Total	970	

Discussion

We generated strong evidence for temporal stability in gamma, beta and functional fish biodiversity in beach rocks at Brazilian tropical region. Our results are in line with previous conclusions suggesting a permanent aspect of fish assemblages in tropical beach rocks and tidepools (Carr et al. 2002; Castellanos-Galindo et al. 2005; Cunha et al. 2008; Chargulaf et al. 2011); markedly to the role of small-scale (tidepool) environmental filters, when compared to higher-scale (beach rock) filters (Mora et al. 2003; Godinho and Lotufo 2010). By considering not only temporal, but also spatial variation, we explained alpha and community composition, and highlighted the effects of depth, environmental heterogeneity and reef identity on species richness. This is the first explicit description of fish assembling in tidepools of Brazilian western Atlantic. Such patterns are in agreement with metapopulational models of target species (Shanksa and Pfisterb 2009) and occurrences of fish species spatially correlated in beach rocks (Ritter 2008), especially through the structural effect of depth and EHI over the fish assembly (Chargulaf et al. 2011; Oliveira et al. 2016). Previous studies suggest that fish distribution and biodiversity are related to substrate heterogeneity and habitat complexity in tidepools (Dethier 1984; Halpern and Floeter 2008; Mouchet et al. 2010; Messmer et al. 2011; Bloch and Klingbeil 2016; Pool et al. 2016). We showed that taxonomy and functional diversities answered positively, but differentially, to depth variation. Coexistence may be prompted by vertical segregation of species occupation in the tidepools (Barrett et al. 2015), but traits seems to be functionally redundant, considering common species (Leitão et al. 2016).

The number of species recorded during the samplings (gamma =27) is in line with surrounding beach rocks of “Iparana” (26 species; Cunha et al. 2008), “Pacheco and

Fleicheiras” (29 species; Godinho and Lotufo 2010) and in accordance to the richness and abundance of “National Park of Jericoacoara” (16 species and 733 individuals; Machado et al. 2015), all of them in Brazilian tropical region. These species are included in a recent compilation of reef fish diversity in the western Equatorial Atlantic (Freitas and Lotufo 2015). Our results reinforced the zoogeographic affinity of reef fish in such region of similar wealth conditions. Despite well known that total species richness is not a good proxy of conservation (Halpern and Floeter 2008; Vitule et al. 2016), we hypothesize a well conservational state of the fish community in the sampled beach rocks. Given its low geographical extension and the shallowness of tidepools, responses of rare species to environmental variation are less expected (see also Macieira and Joyeux 2011), when compared to the complex tropical beach rocks in volcanic regions (Bloch and Klingbeil 2016) or coral reefs (Pereira et al. 2014; Andrades et al. 2016). Contrarily to our results, fish assemblages in coralline pools can widely vary, even in tropical areas, due to recruitment. Our findings also confront perspectives in tidepools around the world that reveals seasonal patterns (Moring 1986; Jordaan et al. 2011), vertical shore distribution (Cox et al. 2011), gradients of abundance (Watson and Huntington 2016) and occurrence of specialist air-breathing fishes (Martin 1995). Such patterns occur in non-sandy ecosystems (e.g., forests of kelps) with high occupation of groups with clear seasonal dynamics (e.g., gobies).

Otherwise, the inobservance of latitudinal shore patterns support the management in the beach rocks, once breaks the conception of zonation for fish species and individual distribution across “fore reef and back reef” (Jones et al. 2002). This classification is not important for fishes in Baleia, contrarily to other regions (Gibson 1972; Cox et al. 2011), but similar to the flat reefs in Brazilian subtropical region, where fish distribution is

Table 2 Coefficient of predictor variables (β_0), Standard Error (SE), t -value and P -value of reef fish species monthly variation of gamma, beta (betaSOR, turnover and nestedness) and functional (FDiv, FDis, Rao's Q indexes) diversities in beach rocks of Baleia, along 13 months, based in a GLS model. Predictor variables: MTA – Mean tidepools area; SGE – Sample geographical extension; MTD – Mean tidepools depth; MEHI – Mean environmental heterogeneity (see [Materials and methods](#))

	β_0	SE	T	P
Gama diversity				
Intercept	0.02	0.13	0.17	0.873
MTA	-0.28	0.20	-1.35	0.214
SGE	0.41	0.19	2.18	0.061
MTD	-0.16	0.25	-0.62	0.551
MEHI	-0.02	0.23	-0.07	0.948
betaSOR				
Intercept	0.01	0.22	0.03	0.98
MTA	-0.52	0.29	-1.83	0.11
SGE	0.48	0.28	1.74	0.12
MTD	-0.48	0.36	-1.33	0.22
MEHI	-0.04	0.33	-0.11	0.91
Turnover				
Intercept	0.001	0.31	-0.01	0.99
MTA	-0.39	0.31	-1.29	0.23
SGE	0.29	0.31	0.92	0.38
MTD	-0.53	0.39	-1.36	0.21
MEHI	-0.07	0.36	-0.20	0.85
Nestedness				
Intercept	-0.01	0.35	-0.02	0.98
MTA	-0.32	0.33	-0.99	0.35
SGE	0.42	0.34	1.26	0.24
MTD	-0.29	0.42	-0.68	0.52
MEHI	0.42	0.39	1.07	0.32
FDiv				
Intercept	0.001	0.01	0.001	0.997
MTA	0.001	0.01	-0.24	0.813
SGE	-0.01	0.01	-0.73	0.485
MTD	0.001	0.02	-0.26	0.802
MEHI	-0.01	0.02	-0.39	0.710
FDis				
Intercept	0.001	0.01	-0.09	0.934
MTA	0.001	0.02	0.05	0.965
SGE	0.001	0.02	-0.24	0.819
MTD	-0.01	0.03	-0.55	0.598
MEHI	-0.03	0.02	-1.27	0.240
Rao's Q				
Intercept	-0.01	0.03	-0.22	0.834
MTA	0.06	0.04	1.56	0.157

Table 2 (continued)

	β_0	SE	T	P
SGE	-0.01	0.04	-0.17	0.872
MTD	-0.02	0.05	-0.32	0.757
MEHI	0.05	0.04	1.23	0.252

independent of reef pools' isolation from the sea (Macieira and Joyeux 2011). On the other hand, distance among tidepools mattered, considering a wider scale of (gamma) diversity. It means the future investigations should be aware about the degree in which pools are exposed. Indeed, longitudinal variations of diversity occurred due increasing distances among tidepools in the two neighbor beach rocks (BR1 and BR2 in Fig. 1), therefore highlighting the uniqueness status of tidepools while promoting biodiversity in beach rocks (Gibson 1972; Sale 1980; Macieira and Joyeux 2011). It was suggested previously in the region (Godinho and Lotufo 2010), as well as that dominant status of the species registered by us, considered “suprabenthic individuals of great mobility” (Cunha et al. 2008). They are common and functionally redundant in tropical areas (Halpern and Floeter 2008; Godinho and Lotufo 2010), in which congeners of *A. saxatilis* coexists with another dominant species, partitioning resources over increasing depths. The monthly sampling designed here is considered of high temporal resolution to tidepool fishes (Machado et al. 2015). Patterns of permanent species (present in most samples) are those clearest in dbRDA results, indicating that Permanents are those mostly related to the predictors used.

Table 3 Coefficients (B), Standard Error (SE), t -value and P -value of variables to explain fish species richness in tidepools of Baleia, in accordance to a GLS model. EHI = Environmental Heterogeneity Index (see [Materials and methods](#)). Tidepools' Area (TA), depth (TD), EHI and sampling period (SP)

Pool's Predictor	B	SE	T	P
Intercept	4.14	0.35	11.87	<0.001
TA	-0.18	0.18	-0.98	0.329
TD	1.58	0.26	6.08	<0.001
EHI	-0.43	0.22	-1.98	0.052
Latitude	0.43	0.42	1.02	0.312
Longitude	0.74	0.41	1.81	0.075
SP	-0.33	0.21	-1.59	0.118

Table 4 Variation partitioning results for environmental and spatial contributions (%) for taxonomic (abundances and occurrences) and functional compositions of tidepool fish assemblages.E|S = pure environmental effect; S|E = pure spatial effect; ES = joint contribution of environmental and spatial variables; UN = unexplained. Adjusted R^2 and P values are shown

	Abundance		Occurrence		Functional	
	AdjR ² (%)	<i>P</i>	AdjR ² (%)	<i>P</i>	AdjR ² (%)	<i>P</i>
E S	31.8	0.001	9.7	0.001	< 0.1	0.686
S E	< 0.1	0.527	1.1	0.200	4.6	0.061
ES	< 0.1	-	< 0.1	-	< 0.1	-
UN	68.2	-	89.1	-	95.4	-

The nursery status of tidepools was represented through the abundance of juveniles (yni, 6% of the total abundance) that accounted to the uniqueness status of tidepools as ecosystems. Juveniles could not be identified to the lower taxonomic level due to limitations of VCT. Even so, species richness of juveniles is also related to increasing depth and EHI (see Fig. 2). We suggest that, depending on the goal, ecological assessments for other species can be successfully done by registering patterns of juveniles with VCT (Rangel et al. 2007). Such methodology is widely employed in freshwater and marine ecosystems, with low impact compared to manipulative sample methods (Sale 1980; Christensen and Winterbottom 1981; Sabino 1999; Cunha et al. 2008; Godinho and Lotufo 2010; Bueno et al. 2016; Ferreira et al. 2015), particularly in clean waters that facilitate visual records (Baker et al. 2016). If well employed, VCT has been proved to be as effective as caught methods (Arakaki and Tokeshi 2006; Arakaki et al. 2014; Baker et al. 2016). Such non-invasive methodology facilitates long-term monitoring with short-term sampling that can be coupled with cameras to access the behavioral ecology of the fish fauna (Watson and Huntington 2016). Indeed, Gutterres Giordano and Neves dos Santos (2014) comparing visual censuses of a cryptic species (*Scartella cristata*) concluded that sampling by scuba dive or free dive did not influence fish abundance assessments in rocky reefs, suggesting the potential of the human eye to differentiate among environment and cryptic organism underwater. For instance, a recent visual censusing from 2007 to 2012 in Japan was dominated by Gobiidae (25 species) and Blenniidae (14 species), families commonly containing cryptic species (Arakaki et al. 2014). Even so, we cannot deny the obvious limitations on visual counts and detection of cryptic species (Bozec et al. 2011),

including the small and cryptic species of Blenniidae and Gobiidae families. However, even investigations using invasive methods nearby our study area found only two species of Gobiidae: Machado et al. (2015): *B. saporator* and *B. geminatus*. Also, Oliveira et al. (2016) found only one blenny species (*Omobranchus punctatus*) that was introduced from the Indo-Pacific. In accordance with our results, Godinho and Lotufo (2010) using visual census found only one goby: *B. saporator* and no Blenniids. Apart from the possible bias, we reinforce that given the goal was to reveal likely determinants of diversity (and not to make a full inventory of fauna), the standard VCT was suitable. Non-invasive methodologies have clear implications for monitoring juveniles of threatened species, such as Mero (*Epinephelus itajara*) and doctorfish (*A. chirurgus*) (Shulman 1985). The former occurred from Florida to southern Brazil and seems to be recovering recently in Atlantic west (Bueno et al. 2016), with recent registers in reef pools of northern Brazil (Lobato et al. 2016).

We can never discard that variation due to recruitment may occur in the sampled beach rocks, by us using another sampling design: samplings considering the reproductive periods instead of monthly variations have detected fish variation due to recruitment (Adjeroud et al. 2015) and homing behavior (White and Brown 2013). Nevertheless, we successfully identified ecological mechanisms responsible for explaining local assembly, that is central in tidepools (Kolasa et al. 2012; Mittelbach and Schemske 2015), particularly in Brazilian tropical region, given the imminent threat of the arrival and spread of non-native species. The introduced fish *Omobranchus punctatus* is already considered as a resident species in tidepools of “National Park of Jericoacoara” (Machado et al. 2015) near to our study area, and lionfish (*Pterois volitans*) was recently

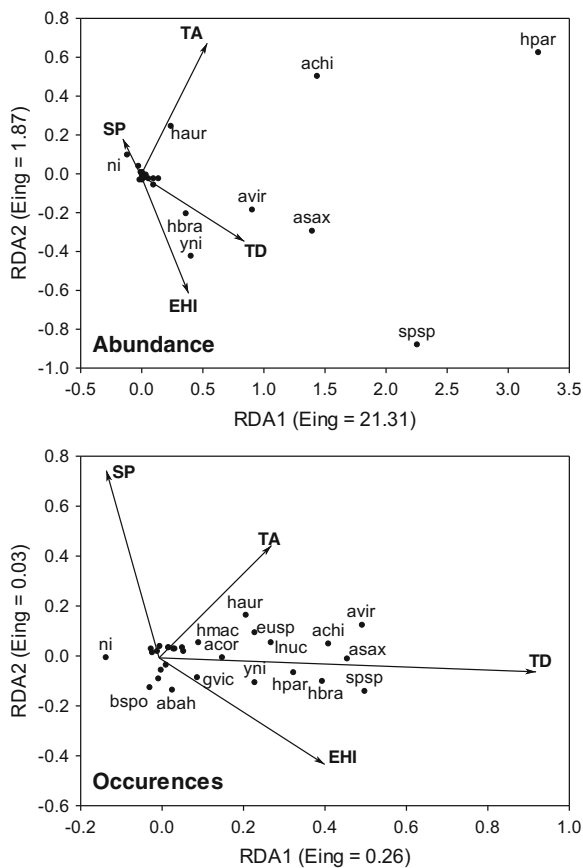


Fig. 2 Environmental variation in a pRDA in tidepools of Bahia. Tidepools' area (TA), depth (TD), Environmental Heterogeneity Index (EHI) and sampling period (SP) are represented. Species: *Abudefduf saxatilis* (asax), *Acanthurus chirurgus* (achi), *Acanthurus coeruleus* (acor), *Anisotremus surinamensis* (asur), *Anisotremus virginicus* (avir), *Bathygobius* aff. *Soporator* (bspo), *Euclinostomus* sp. (eusp), *Gymnothorax vicinus* (gvic), *Haemulon aurolineatum* (haur), *Haemulon parra* (hpar), *Halichoeres brasiliensis* (hbra), *Halichoeres* sp. (hmac), *Labrisomus nuchipinnis* (Inuc), Non-Identified (ni), *Scorpaena* sp. (scsp), *Sparisoma* spp. (spsp), young-non-identified (yni)

recorded in Brazilian coasts (Ferreira et al. 2015). There is a great concern in the spread of lionfish in Atlantic coast line during the next years, particularly given climate changes (Grieve et al. 2016) and because this species grow faster in the invaded habitat than in their native range (Pusack et al. 2016).

In conclusion, we did emphasize that fish biodiversity is linked to the uniqueness status of tidepools as ecosystems, since community variation is described by ubiquitous visitor species assembling in tidepool's depth. The temporal stability of taxonomic (gamma and beta) and functional fish diversities, which resulted in low predictive power of this facets of biodiversity,

also highlights tidepool's local features as a proxy of local community filters. Effects of the aquaculture over fish biodiversity generated evidences to an increasing fish species richness, although with redundant functional diversity. Such macroalgae cultivation should be monitored in future investigations. A ubiquitous occupation of this algae may either cause fish assemblage homogenization (e.g. *Gracilaria* spp. decreasing substrate heterogeneity), or differentiation (e.g. *Gracilaria* spp. increasing vertical complexity); given that increasing depths may promote coexistence but not functional diversity. In a similar vein, functional segregation was used to evaluate human disturbance effects (Villéger et al. 2010). However, a complete understanding of fish coexistence is only reached considering life history and key fish interactions that indeed influence taxonomic, functional and trophic organization (Leitão et al. 2016; Pool et al. 2016). Algae has been removed by locals, at least during the past 40 years, and exploitation is species-specific orientated since 2005, when propagules of *Gracilaria* spp. were first used by a local cooperative to be cultivated in long-line aquaculture. Understanding the relationship among fish diversity and local extensive algal production is central to orientate management policies to this and other human activities and prevent future homogenizing effects in beach rocks.

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