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Trophic relationships in tidepool fish assemblages of the tropical Southwestern Atlantic

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Abstract

Trophic studies are fundamental to understanding the dynamics of assemblages and functional roles of species within ecosystems, contributing to the identification of factors responsible for the organization and structure of communities. This study aimed to analyse the trophic organization of tidepool fish assemblages in the tropical Southwestern Atlantic, based on the underlying idea that food resources are not limiting and that trophic guild formation is not driven by food competition. Diets were based on feeding index values of food categories for 12 representative species collected in six tidepools (20°49′ S, 40°36′ W) at quarterly intervals (2005 to 2007). The main food categories were small crustaceans, polychaetes and macroalgae. Multivariate techniques evidenced two multispecific trophic guilds: small-prey carnivores, including *Bathygobius soporator*, *Bathygobius geminatus*, *Malacoctenus delalandii* and *Halichoeres poeyi*, and herbivores, including *Sparisoma axillare* and *Acanthurus bahianus*. Other species presented significantly different diets and were classified into the following guilds: omnivores feeding on filamentous algae and copepods (*Abudefduf saxatilis*); large-prey carnivores (*Labrisomus nuchipinnis*); omnivores feeding on polychaetes and filamentous algae (*Stegastes fuscus*); and polychaete feeders (*Ahlia egmontis*). *Gymnothorax funebris* and *Gymnothorax moringa* were classified as carcinophagores and piscivores, respectively. Trophic organization appears related to species convergence toward the use of abundant food resources, driven by a combination of factors allowing some resource partitioning through inter-specific differences in consumer size, microhabitat, behavior, and trophic specialization.

KEYWORDS
Brazil, diet, feeding ecology, guilds, inter-tidal, reef fishes

1 | INTRODUCTION

The inter-tidal zone displays an enormous abundance and diversity of organisms despite being the marine ecosystem with the largest and fastest variation in environmental conditions (Little & Kitching, 1996). Its ecological importance is relevant considering the role it plays as feeding, breeding and nursery grounds for many organisms, especially for fishes and crustaceans (Gibson & Yoshiyama, 1999; Horn, Martin, & Chotkowski, 1999; Oliveira et al., 2016). Tropical ecosystems exhibit a wide range of inter-tidal habitats, including both unconsolidated substrates such as mudflats and sandy beaches (Andrades et al., 2014; Oliveira et al., 2016) and hard bottoms as such rocky shores and reef flats (Machado et al., 2015; Macieira & Joyeux, 2011; Macieira et al., 2015). One of the most striking features of the inter-tidal zone is when water is trapped in cavities and depressions on the substratum during low tide forming tidepools

(Horn et al., 1999). These pools provide refuge against desiccation for organisms that can withstand drastic changes in water characteristics (Gibson, 1986; Zander et al., 1999), especially temperature, salinity and dissolved oxygen. Mostly, these changes are caused by the inter-play between tidepool position (e.g. height and isolation), morphology (e.g. volume, surface area, depth and rugosity), substrate composition and physicochemical conditions (Macieira & Joyeux, 2011; Oliveira et al., 2016). However, factors influencing the organization and structure of tidepool communities remain understudied (Machado et al., 2015; Norton & Cook, 1999) and considerably less understood than those of communities exposed to the atmosphere at low tide (Zander et al., 1999).

Tidepool fishes present distinct adaptations to inhabit these harsh environments, being classified as residents, which are species that are highly adapted to spending their entire life in pools, opportunists, which spend only part of their life (usually juveniles) in pools, or transients, which generally do not have adaptations for inter-tidal life and only occasionally enter pools (Griffiths, 2003; Macieira & Joyeux, 2011). There is a growing understanding that residents, opportunists and transient species form the coastal trophic web and act as important energy conductors within pools and between these and adjacent habitats (Castellanos-Galindo & Giraldo, 2008; Horn et al., 1999). However, algae and invertebrates have traditionally received more attention, possibly because they are abundant and easily studied, whereas the ichthyofauna has often been neglected, possibly due to its small size and apparent rarity (Horn et al., 1999; Zander et al., 1999).

The Brazilian coastline presents several types of rocky shores (granite, gneiss, basalt) and reef flats (laterite, sandstone, carbonate). However, despite the country's extensive coastline and high environmental heterogeneity, studies on tidepool fish communities are relatively scarce (e.g. Almeida, 1973; Almeida, 1983; Barreiros, Bertoncini, Machado, Hostim-Silva, & Santos, 2004; Cunha, Monteiro-Neto, & Nottinghan, 2007; Macieira & Joyeux, 2011; Machado et al., 2015; Macieira et al., 2015; Oliveira et al., 2016; Rosa et al., 1997), with a single unpublished work focusing on trophic ecology (Zamprogno, 1989). The identification of trophic guilds is fundamental to understanding the dynamics of fish assemblages, the functional role of species in the ecosystem and the factors responsible for organization and structure of communities (Castellanos-Galindo & Giraldo, 2008; Muñoz & Ojeda, 1997). Competition, resource partitioning (Castellanos-Galindo & Giraldo, 2008; Grossman, 1986) and predation (Macieira & Joyeux, 2011; Rojas & Ojeda, 2010) are probably the most relevant of these factors (Loreau, 2009). However, environmental complexity may promote the co-existence of potentially competing species, providing shelters against predators or increasing the variety of available habitats (Rojas & Ojeda, 2010), although the mechanisms involved and its relative importance in shaping inter-tidal fish communities are only beginning to be discerned (Faria & Almada, 2001; Macieira & Joyeux, 2011).

Moreover, studies on diet and trophic ecology of tropical inter-tidal fishes (Castellanos-Galindo & Giraldo, 2008; Kotrschal & Thomson, 1986; Zamprogno, 1989) are incipient when compared to tropical subtidal fishes (Dubiaski-Silva & Masunari, 2008; Ferreira & Gonçalves, 2006; Ferreira, Floeter, Gasparini, Ferreira, & Joyeux, 2004; Ferreira, Gonçalves, Coutinho, & Peret, 1998; Randall, 1967) or temperate inter-tidal fishes (Grossman, 1986; Hielscher, Malzahn, Diekmann, & Aberle, 2015; Muñoz & Ojeda, 1997, 1998, 2000; Velasco et al., 2010). The inter-tidal reef of Castelhanos beach, in the tropical Southwestern Atlantic, has a carbonate substrate and undergoes complete submersion at high tide (Macieira & Joyeux, 2011). These characteristics allow a high abundance and diversity of pool organisms that are supported by high structural complexity, tide-driven resource renewal and physiological stress softening. Therefore, based on the underlying idea that food resources are not limiting and that trophic guild formation is not driven by food competition, the present study aimed at (i) describing the diet of the main species of Castelhanos tidepool fish assemblages, (ii) identifying the trophic guilds of these species and (iii) investigating the relationships between the environmental conditions of tidepools and guild organization.

2 | MATERIAL AND METHODS

2.1 | Study area

The research was conducted on a flat carbonate reef located at Castelhanos beach (20°49′ S, 40°36′ W), state of Espírito Santo, Southeastern Brazil (Figure 1). This reef is composed of encrusting coralline algae and stony coral skeletons with sparse lateritic (ferruginous) rocks. During high tide, the reef is completely submerged. Tidepools formed at low tide are structurally more complex than pools in crystalline rocky shores. The bottom substrate of these tidepools often consists of sand and gravel and the almost vertical walls are normally irregular, covered by turf algae, soft macroalgae, crustose coralline algae, encrusting soft coral and stony corals (for details, see Macieira & Joyeux, 2011).

2.2 | Sampling and morphological characterization of tidepools

Six isolated tidepools (without connectivity to the sea or other pools during the ebb tide) were selected: two located near the sand beach (pools 1 and 2), two in an intermediary position (pools 3 and 4) and two closer to the water edge (pools 5 and 6). Quarterly samplings (*n* = 8) were carried out always in these same six tidepools, during the morning of two consecutive days between August 2005 and June 2007. On the first day of each sampling water temperature, salinity, macroalgae cover (only for pool walls and consolidated bottom areas) and bottom composition were measured. Surface area, depth and bottom rugosity of the tidepools were characterized only once. During the second day, the ichthyofauna was collected using hand nets after the application of clove oil anesthetic solution in each tidepool (e.g. Castellanos-Galindo & Giraldo, 2008; Griffiths, 2003). Due to seasonal variation in beach profile, pool 1 was covered by sand

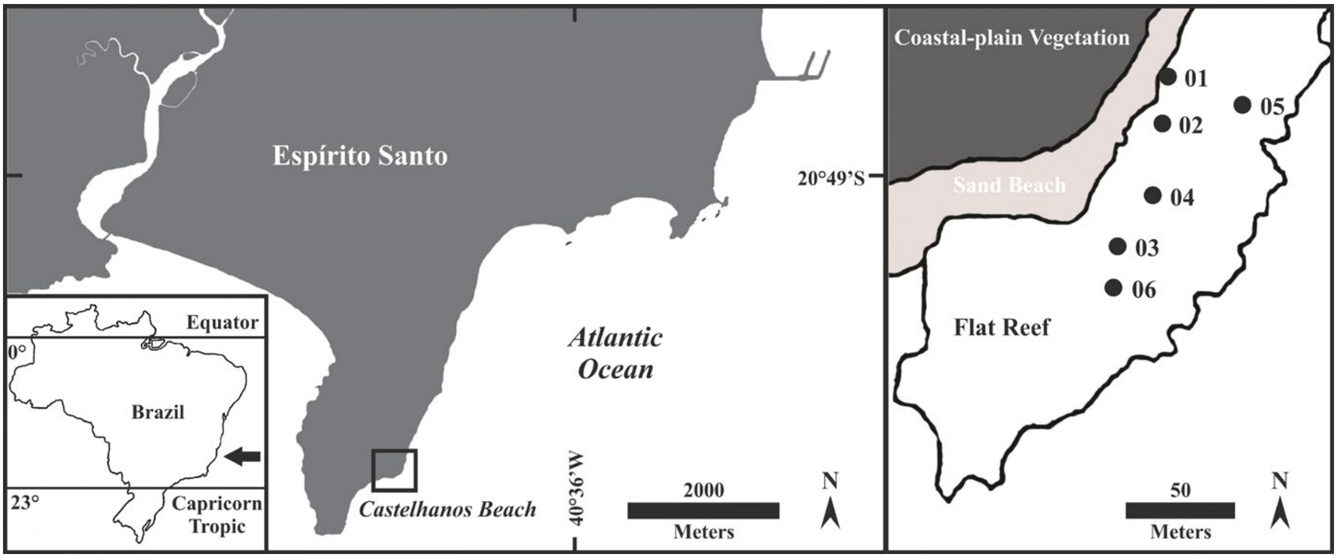

FIGURE 1 Location of Castelhanos beach on the coast of Espírito Santo, Brazil, is shown on the map on the left. Spatial distribution of tidepools on the reef flat is shown on the map on the right (extracted with permission from Macieira & Joyeux, 2011)

during the August 2006 sampling. Fishes collected were later fixed in 10% formalin (for details, see Macieira & Joyeux, 2011; Table 1).

2.3 | Sample processing and selection of species for trophic analyses

Fishes were identified to species level, measured (total length; TL) to the nearest mm and weighed (individual total wet weight) with 0.01 g precision. Based on the 2 years of data (n = 47 samples), the index of relative importance (IRI) of each species [equation (1); modified from Pinkas et al., 1971] was calculated:

$$\mathrm{IRI} = (\%\mathrm{N} + \%\mathrm{M}) * \%\mathrm{F}$$

where %N, %M and %F respectively are, for each species, the numerical (number of individuals of the species *versus* total number of fishes, in %), gravimetric (species weight *versus* total fish weight, in %) and occurrence (number of positive samples *versus* total number of samples, in %) frequencies (Hyslop, 1980). The IRI is appropriate to weight and rank fish species within the community according to both their abundance and their biomass. Weighting and ranking allow a straightforward and unbiased selection of the most important species to be included in further analyses. The IRIs computed for each species of the community were summed up and the species that cumulatively totaled 90% were selected for the trophic analyses (Table 2).

Stomach contents of 588 specimens belonging to 11 species were analysed; whenever possible, each species was sub-sampled accordingly to length with two small, two median and two large specimens selected from each season and tidepool. Three size classes of equal amplitude were determined for each species according to the variation in TL of the individuals collected. Only individuals collected in the first year of sampling were used due to the seasonal variation in the beach profile. The digestive tracts were sectioned in the portion of esophagus and anus. Each stomach was separated from the remaining digestive tract and the contents transferred to a Petri dish. For species that do not have a defined stomach [i.e. *Halichoeres poeyi* (Steindachner, 1867) and *Sparisoma axillare* (Steindachner, 1878)], the same procedure was performed using the initial third of the digestive tract. Screening of food items was done under a binocular dissecting microscope. Broad taxonomic identification was based on specific literature (Joly, 1967; Ribeiro-Costa & Rocha, 2002; Ruppert & Barnes, 1996; Schultz, 1969) and the precise identification of the most frequent items was realized with the aid of experts. Due to their small mass, food items were grouped into food categories, which were weighted (total wet weight with precision of ± 0.0001 g) by tidepool and season. The mass of nematodes (µg) was estimated utilizing equation (2) (modified from Andrassy, 1956):

$$\mathrm{Nematod_{mass}} = \left(\mathrm{TL} * \mathrm{W}^2\right) / 1{,}600{,}000$$

were TL is the total length (µm) and W the greatest width (µm).

All data (n = 446) for *Labrisomus nuchipinnis* (Quoy & Gaimard, 1824) were provided by P. S. Jesus Jr from an unpublished diet study. Specimens had been caught for Macieira and Joyeux (2011)'s study during their sampling. Due to the way diet items were grouped to compute the mass of food categories (i.e. by season and size class), it was not possible to select the specimens of the first year.

2.4 | Data analysis

Diets were described through the feeding index (FI) [equation (3); modified from Kawakami & Vazzoler, 1980], an index based on the frequency of occurrence (%F) and gravimetric frequency (%M) of food categories. According to Kawakami and Vazzoler (1980), FI

TABLE 1 Morphometric characteristics, substrate composition, macroalgae cover and physicochemical parameters of tidepools from Castelhanos beach, tropical Southwestern Atlantic (extracted with permission from Macieira & Joyeux, 2011). Tidepools were characterized once for depth, surface area, volume and rugosity, and every 3 months between August 2005 and June 2007 for substrate, cover, and physicochemical parameters ($n = 8$ for all pools except pool 1 where $n = 7$)

	Morphometric characteristics				Substrate			Cover	Physicochemical parameters	
Pool	Depth (max.) (cm)	Area (m^2)	Vol. (m^3)	Rug.	Sand (%)	Gravel (%)	Rock (%)	Algae (%)	Temperature*(°C)	Salinity*
1	8.30 (20.5)	6.35	0.53	1.11	30	10	60	20	26.1 (22.5–35.0)	28.1 (17.0–35.8)
2	22.2 (36.3)	10.15	2.24	1.19	80	10	10	40	24.4 (21.5–29.6)	34.3 (32.0–38.0)
3	17.4 (25.5)	1.36	0.24	1.26	30	60	10	40	24.8 (22.0–30.1)	34.3 (31.4–37.0)
4	28.2 (49.0)	7.88	2.22	1.30	40	20	40	70	24.2 (21.8–29.7)	34.5 (32.0–37.0)
5	23.8 (46.0)	16.12	3.81	1.20	10	10	80	30	24.7 (22.2–28.0)	34.8 (31.3–39.0)
6	25.6 (51.0)	6.52	1.67	1.27	20	50	30	40	24.5 (22.2–24.9)	34.7 (31.0–38.0)

*Mean (range: minimum–maximum).
Depth (max) = mean depth (and maximum depth); area = surface area; vol. = volume; rug. = rugosity.

enables a more accurate distinction of the importance of each food category than the use of single frequencies.

$$\mathrm{FI} = \frac{(\%\mathrm{F} \times \%\,\mathrm{M})}{\sum(\%\mathrm{F} \times \%\,\mathrm{M})}$$

The trophic guilds were identified through a hierarchical agglomerative cluster analysis conducted in BOOTCLUS (McKenna, 2003) on the FI data matrix, using the Bray–Curtis similarity coefficient and the unweighted pair-group method using arithmetic averages linkage method. Cluster significance ($\alpha = 0.05$) at different similarity levels within each of the resulting branches of the dendrogram was verified through bootstrapping after 1000 pseudo-replications (Castellanos-Galindo & Giraldo, 2008). A non-metric multidimensional scaling (nMDS) analysis was also performed on the similarity matrix. *Gymnothorax funebris* Ranzani, 1839 and *Gymnothorax moringa* (Cuvier, 1829) showed either empty stomachs or stomach contents in an advanced stage of digestion and were excluded from the cluster and nMDS analyses. The trophic guilds to which these species belong were identified based on our data and literature source (Randall, 1967). Relationships between spatial distribution of trophic guilds and environmental characteristics of tidepools were explored through a canonical correlation analysis (CCA; Ter Braak, 1986) in MVSP v. 3.12 using the standardized environmental data and the average number of individuals of each trophic guild by tidepool in the 2 years of sampling. The eigenvalues and eigenvectors for canonical axes and the whole model are presented in Supporting Information (Table S1).

3 | RESULTS

A total of 1034 fishes belonging to seven families and 12 species were trophically analysed, being eight permanent residents and four opportunist species (Table 2). Smaller-sized species were *Abudefduf saxatilis* (Linnaeus, 1758), *Bathygobius geminatus* Tornabene, Baldwin & Pezold, 2010, *Bathygobius soporator* (Valenciennes, 1837), *Malacoctenus delalandii* (Valenciennes, 1836), *Sparisoma axillare* and *Stegastes fuscus* (Cuvier, 1830) (mean TL < 50 mm). *Acanthurus bahianus* Castelnau, 1855, *Ahlia egmontis* (Jordan, 1884), *Gymnothorax funebris*, *Halichoeres poeyi* and *Labrisomus nuchipinnis* presented an intermediate size (50 < mean TL < 150 mm), while *Gymnothorax moringa* was the largest species (mean TL > 150 mm).

The range of resources used by the whole fish assemblage comprises 29 distinct food categories (Table 3). No food category was used by all species. Filamentous algae (FI = 0.43), mainly from the genus *Ulva* (but previously classified as *Enteromorpha*), and copepods (FI = 0.38) were the most important food categories of the opportunist species *Ab. saxatilis*. The diet of another opportunist, *Ac. bahianus*, was dominated by cylindrical (FI = 0.57), especially *Hypnea* sp., filamentous (FI = 0.23) and foliaceous algae (e.g. *Ulva* sp.; FI = 0.20), with sporadic occurrences of polychaetes, insect larvae and copepods. The permanent residents and congeners *B. geminatus* and *B. soporator* showed very similar diets, preying mainly upon copepods (FI = 0.40 and 0.33, respectively), polychaetes (FI = 0.28 and 0.13) and amphipods (FI = 0.13 and 0.32).

TABLE 2 Taxonomic list of species (family order follows Nelson et al., 2016), figures' abbreviations of the species' names, residency status (according to Macieira & Joyeux, 2011), number of individuals, percentage of the index of relative importance (IRI) and mean (±*SD*) and range (minimum–maximum) of total length of the individuals utilized for stomach content analysis

Family and species	Figures' abbreviation	Residency status	*n*	%IRI	Total length (mm) Mean ± *SD*	Total length (mm) Range
Muraenidae						
Gymnothorax funebris Ranzani, 1839	*Gym fun*	PR	21	4	92 ± 37	49–187
Gymnothorax moringa (Cuvier, 1829)	*Gym mor*	PR	21	8	331 ± 143	130–641
Ophichthidae						
Ahlia egmontis (Jordan, 1884)	*Ahl egm*	PR	47	2	143 ± 38	67–226
Pomacentridae						
Abudefduf saxatilis (Linnaeus, 1758)	*Abu sax*	O	59	3	29 ± 13	15–70
Stegastes fuscus (Cuvier, 1830)	*Ste fus*	PR	55	4	47 ± 21	13–94
Labridae						
Halichoeres poeyi (Steindachner, 1867)	*Hal poe*	O	68	5	58 ± 19	19–127
Sparisoma axillare (Steindachner, 1878)	*Spa axi*	O	73	4	38 ± 15	17–100
Labrisomidae						
Labrisomus nuchipinnis (Quoy & Gaimard, 1824)	*Lab nuc*	PR	446	33	71 ± 28	25–137
Malacoctenus delalandii (Valenciennes, 1836)	*Mal del*	PR	59	2	38 ± 8	21–53
Gobiidae						
Bathygobius geminatus Tornabene, Baldwin & Pezold, 2010	*Bat gem*	PR	109	18	32 ± 12	12–60
Bathygobius soporator (Valenciennes, 1837)	*Bat sop*	PR	45	3	44 ± 21	14–81
Acanthuridae						
Acanthurus bahianus Castelnau, 1855	*Aca bah*	O	31	4	64 ± 20	36–117

PR = permanent resident; O = opportunist; T = transient.

Copepods (FI = 0.60 and 0.61) and amphipods (FI = 0.23 and 0.20) were also the main food categories of the opportunist *H. poeyi* and the permanent resident *M. delalandii*, respectively. The permanent resident *L. nuchipinnis* preyed mainly on amphipods (FI = 0.35) and brachyuran crabs (FI = 0.24). The diet of the opportunist *Sp. axillare* was composed essentially by cylindrical algae (e.g. *Hypnea* sp.; FI = 0.54), filamentous algae (mainly *Ulva*) and copepods (FI = 0.19 for both).

Based on the dietary data, three significantly distinct species groups and two isolated species were evidenced by the cluster analysis (Figure 2). However, the group composed by *St. fuscus* and *Ah. egmontis* was not considered a guild because diet similarity between the two was low. *Ahlia egmontis* almost exclusively fed on polychaetes (FI = 0.99), while these only represented about 50% (FI = 0.48) of *St. fuscus*'s diet, which included such other items as filamentous algae (FI = 0.22) and copepods (FI = 0.16). The nMDS results (Figure 3) corroborated this segregation. Therefore, there were two multispecific trophic guilds: (A) the small-prey carnivorous guild, formed by *B. soporator*, *B. geminatus*, *M. delalandii* and *H. poeyi*; and (B) the herbivorous guild that included *Sp. axillare* and *Ac. bahianus*. All other species presented significantly different diets and were classified as: filamentous algae and copepods omnivorous guild (*Ab. saxatilis*); large-prey carnivorous guild (*L. nuchipinnis*); polychaetes and filamentous algae omnivorous guild (*St. fuscus*); and polychaete feeders guild (*Ah. egmontis*). According to Randall (1967) and our own few data, *G. funebris* and *G. moringa* were classified as carcinophagores (only crustaceans fragments, possibly from shrimp, were found) and piscivores (only isolated bones and scales were found), respectively.

The CCA showed that tidepools presented different morphometric characteristics but similar physicochemical conditions, except for pool 1 (Figure 4). Ordination axis 1 opposed temperature to size (i.e. depth, volume and area), structural complexity (i.e. rugosity and algal cover) and salinity, while axis 2 opposed pools with substrate dominated by sand to those dominated by rock. The polychaete feeders guild (*Ah. egmontis*) did not show a clear relationship with environmental variables. The small-prey carnivorous (A) and the carcinophagores guild (*G. funebris*) presented a moderate relationship with high temperature, low salinity, shallow and low complexity pools (pool 1; lower right quadrant in Figure 4). The filamentous algae and copepods omnivorous guild (*Ab. saxatilis*) was associated with large and sandy pools (pool 2; upper right quadrant in Figure 4) and pool 1. The large-prey carnivorous (*L. nuchipinnis*), the herbivorous (B) and the piscivorous guild (*G.

TABLE 3 Diet composition (feeding index, FI) of the tidepool fish species from Castelhanos beach, tropical Southwestern Atlantic. *n* = number of stomachs analysed. Food categories are in phylogenetic order and the main ones (FI values ≥ 0.19) for each species are in bold. The fish species are following the cluster results and the Guilds A and B are as in the Figures 2 and 3

	Guild A								Guild B	
	Bathygobius geminatus	*Bathygobius soporator*	*Malacoctenus delalandii*	*Halichoeres poeyi*	*Abudefduf saxatilis*	*Labrisomus nuchipinnis*	*Stegastes fuscus*	*Ahlia egmontis*	*Sparisoma axillare*	*Acanthurus bahianus*
Food category	*n* = 100	*n* = 39	*n* = 49	*n* = 56	*n* = 59	*n* = 446	*n* = 55	*n* = 21	*n* = 71	*n* = 31
Cylindrical algae	0	0	0	0.03	0.02	0.02	0.07	0	**0.54**	**0.57**
Filamentous algae	0.05	0.16	<0.01	<0.01	**0.43**	0.02	**0.22**	0	**0.19**	**0.23**
Foliaceous algae	<0.01	<0.01	<0.01	<0.01	0.02	0.02	0.04	0	0.07	**0.20**
Nematodes	<0.01	0	0	0	<0.01	0	<0.01	0	0	0
Polyplacophorans	0	0	<0.01	0	0	<0.01	0	0	0	0
Gastropods	0	0	0	0	0	0.03	0	0	0	0
Polychaetes	**0.28**	0.13	0.04	0.03	<0.01	0.01	**0.48**	**0.99**	0	<0.01
Arachnids (Acarines)	<0.01	<0.01	<0.01	0	<0.01	0	0	0	0	0
Pycnogonids	<0.01	0	0	<0.01	0	0	0	0	0	0
Megalopa larvae	<0.01	<0.01	0	0	0	0	0	0	0	0
Nauplius larvae	0	0	0	0	<0.01	0	0	0	0	0
Zoea larvae	0	0	<0.01	0	0	0	0	0	0	0
Cladocerans (daphnids)	0	<0.01	0	0	0	0	0	0	0	0
Barnacle larvae	<0.01	0	0	0	<0.01	0	<0.01	0	0	0
Ostracods	0.05	0.03	0.03	<0.01	0	<0.01	0	0	0	0
Copepods	**0.40**	**0.33**	**0.61**	**0.60**	**0.38**	0.02	0.16	0	**0.19**	<0.01
Penaeoidea (Shrimps)	<0.01	0	0	0	0	0.04	0	<0.01	0	0
Anomuran crabs	0	0	0	0	0	0.11	0	0	0	0
Brachyuran crabs	0	<0.01	0	0	0	**0.24**	0	0	0	0
Cumaceans	<0.01	<0.01	0	0	0	0	0	0	0	0
Tanaids	0.03	<0.01	0.03	<0.01	0	0	0	0	0	0
Isopods	0.04	<0.01	<0.01	0.05	0.10	0.03	<0.01	0	0	0
Amphipods	0.13	**0.32**	**0.20**	**0.23**	0.02	**0.35**	<0.01	0	<0.01	0
Pterygotean insects	0	0	0	0	<0.01	0	0	0	0	0
Chironomid larvae	0.01	<0.01	0.07	0.03	<0.01	0	0.01	0	<0.01	<0.01
Sipunculans	<0.01	0	0	0	0	<0.01	<0.01	0	0	0
Fish eggs	0	0	0	0	0	<0.01	0	0	0	0
Fish scales	<0.01	<0.01	<0.01	0	0.01	0.12	<0.01	0	0.01	0
Teleostei	0	<0.01	0	<0.01	0	0.02	0	0	0	0

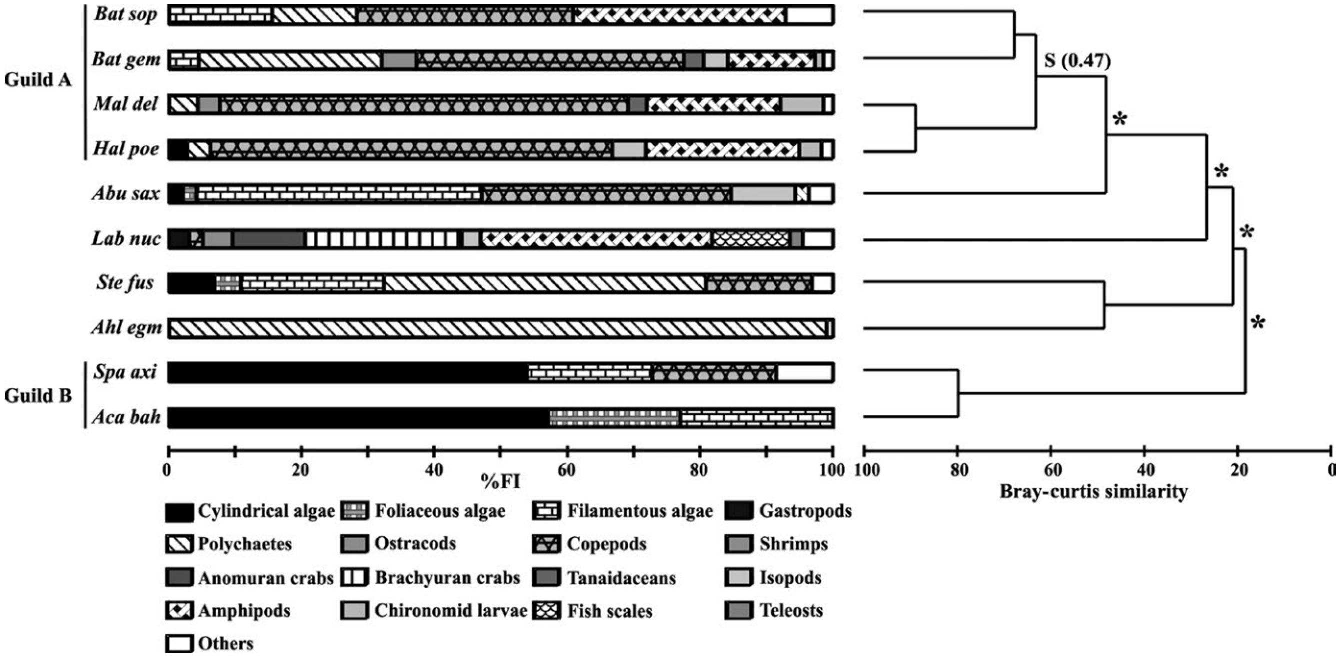

FIGURE 2 Diet composition [% feeding index (%FI)] and dendrogram built with BOOTCLUS (McKenna, 2003) using Bray–Curtis similarity and the unweighted pair-group method using arithmetic averages linkage method. Trophic guild formation for each of the linkages and significance levels after the bootstrapping routine are shown. * indicate significant differences of the linkage fusing the two assemblages (α ≤ 0.05). S indicates a linkage where the probability value is near the significance level. Guild A: small-prey carnivores; guild B: herbivores. Single species guilds: *Abu sax* = omnivores feeding on filamentous algae and copepods; *Lab nuc* = large-prey carnivores; *Ste fus* = omnivores feeding on polychaetes and filamentous algae; *Ahl egm* = polychaete feeders

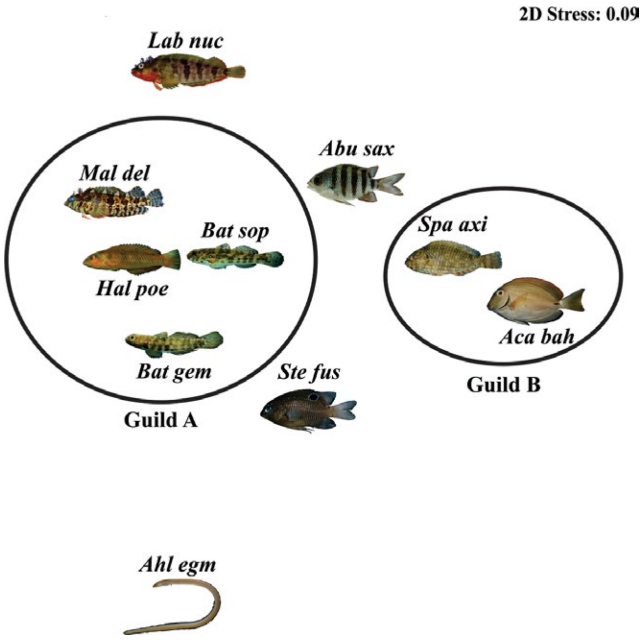

FIGURE 3 Trophic guilds of the tidepool fish assemblage formed by the non-metric multidimensional scaling analysis. Species coordinates are located at the center of the abbreviations' names. The fish pictures are not to scale. Guild A: small-prey carnivores; guild B: herbivores. Single species guild: *Abu sax* = omnivores feeding on filamentous algae and copepods; *Lab nuc* = large-prey carnivores; *Ste fus* = omnivores feeding on polychaetes and filamentous algae; *Ahl egm* = polychaete feeders

moringa) presented a good relationship with deep and structurally more complex pools (pools 4 and 6; upper left quadrant in Figure 4), while the polychaetes and filamentous algae omnivorous guild (*St. fuscus*) was associated with large pools and dominated by rocks (pool 5; lower left quadrant in Figure 4).

4 | DISCUSSION

Among habitats of the inter-tidal zone (including sandy beaches, mud flats, mangroves), rocky shores present the greatest diversity of potential prey for fishes (Norton & Cook, 1999). In fact, the rockpool fish assemblage of Castelhanos beach consumed a wide variety of food items, including nektonic (e.g. fishes), planktonic (e.g. crustacean larvae and daphnids) and benthic (e.g. crustaceans and polychaetes) organisms. As for other tidepool fish assemblages, crustaceans, particularly copepods and amphipods, and polychaetes were the main food resources (Castellanos-Galindo & Giraldo, 2008; Muñoz & Ojeda, 1997, 1998; Velasco et al., 2010). Together they represented more than half (55%) of all that was consumed, confirming that carnivory is the most important feeding strategy in these habitats (Castellanos-Galindo & Giraldo, 2008). In fact, crustaceans are the predominant preys of fishes in both temperate (Grossman, 1986; Muñoz & Ojeda, 1997, 1998; Velasco et al., 2010) and tropical rocky inter-tidal pools (Castellanos-Galindo & Giraldo, 2008; Zamprogno, 1989). Macroalgae are also important food sources (25%), demonstrating that omnivory and herbivory are important in

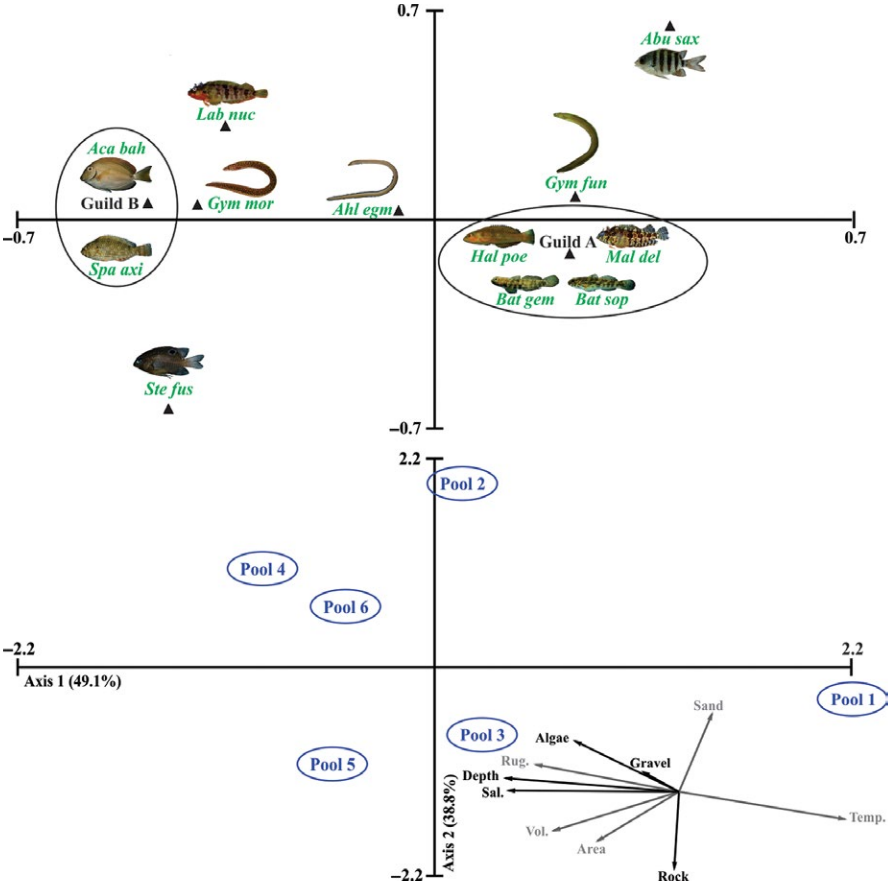

FIGURE 4 Graphic representation of the two first axes of the canonical correlation analysis, presenting the trophic guilds in their environmental settings (vectors) in tidepools. Gray vectors indicate the variables ignored in the analysis due to multicollinearity. Correlation between trophic guilds and environmental variables is shown after the axis name. Guild A: small-prey carnivores; guild B: herbivores. Single-species guilds: *Abu sax* = omnivores feeding on filamentous algae and copepods; *Lab nuc* = large-prey carnivores; *Ste fus* = omnivores feeding on polychaetes and filamentous algae; *Ahl egm* = polychaete feeders; *Gym fun* = carcinophagores; *Gym mor* = piscivores. Area = surface area; Depth = average depth; Rug. = rugosity; Sal. = salinity; Temp. = temperature; Vol. = volume

the assemblage. The absence of exclusively planktivorous species [e.g. *Chromis multilineata* (Guichenot, 1853) and *Thalassoma noronhanum* (Boulenger, 1890)] is characteristic of rocky inter-tidal fish communities (Gibson & Yoshiyama, 1999) although planktivory is a common foraging strategy of subtidal fish communities (Norton & Cook, 1999). Probably, planktivores (e.g. atherinopsids and clupeids) are migrants that follow the tide in and out over the reefshore and do not remain in pools at low tide. Therefore, Castelhanos beach's inter-tidal fish assemblage integrates the local benthic trophic web, with macroalgae, microphytobenthos and detritus as the most likely primary sources of carbon (e.g. Soares et al., 2008), and the food resources are primarily autochthonous (Norton & Cook, 1999) except, probably, insects and daphnids.

For a long time the formation of guilds was thought to be entirely associated with inter-specific competitive processes (Castellanos-Galindo & Giraldo, 2008). In this sense, competition occurs when a species exerts a negative effect on another, consuming or controlling access to limited resources (Keddy, 2001). In nature, however, a population of a species is affected by populations of different species that share the same resources (e.g. Grossman, 1986). Therefore, guild formation would be a way to reduce this diffuse competition, i.e. reducing the cumulative negative effect of several competing populations (Pianka, 1974, 1980). In the present study, it is not possible to state if the availability of food resources is limited, as no survey on the abundance of these resources has been carried out. However, rocky inter-tidal is an extremely productive environment, especially in tropical regions where diversity and abundance are high (Fernández, Holl, & Kimberlin, 2007) for both primary producers (algae and plants) and consumers (mainly invertebrates) (Little & Kitching, 1996; Norton & Cook, 1999). The fact that only three groups of organisms (i.e. small crustaceans, polychaetes, and algae) comprise the trophic base of this tidepool fish assemblage suggests that they are abundant enough to be shared by several species and that, therefore, food is not a limiting resource. Then, the formation of trophic guilds would not be related to inter- or intra-specific food competition but to species convergence in the use of abundant food resources (e.g. Castellanos-Galindo & Giraldo, 2008). Convergence is made possible by a combination of factors allowing some resource partitioning through inter-specific differences in consumer size (e.g. small-prey and large-prey carnivorous guilds), microhabitat and behavior (omnivorous guilds), and trophic specialization (polychaete feeders and herbivorous guilds).

In this sense, the small-prey carnivorous guild results from the convergence toward copepod and amphipod use by fish species of different ecological requirements (i.e. the permanent residents *Bathygobius geminatus*, *Bathygobius soporator* and *Malacoctenus delalandii* and the opportunist *Halichoeres poeyi*). Although showing distinct spatial distribution patterns, driven by different physico-chemical and ecological factors (Macieira & Joyeux, 2011), the similarity in mean size (Table 2) probably allowed these microcarnivorous species to share superabundant food resources (e.g. Castellanos-Galindo & Giraldo, 2008), such as copepods and amphipods (Norton

& Cook, 1999). In contrast, the isolation of *Labrisomus nuchipinnis* into the large-prey carnivorous guild probably results from its larger size relative to small-prey carnivores (Table 2), an expected size segregation (e.g. Grossman, 1986; Muñoz & Ojeda, 1998; Castellanos-Galindo & Giraldo, 2008). Furthermore, this cryptobenthic species was closely associated with pools of high algal cover providing for its needs for camouflage (Sazima, 1986), protection and ambush (Kotrschal & Thomson, 1986) of amphipods and crabs typical of inter-tidal algal communities (Carpenter, 2007; Stillman, 2007).

Inter-specific size and microhabitat differences also occur between the moray eels *Gymnothorax funebris* (carcinophagores) and *Gymnothorax moringa* (piscivores). The former was mostly found as small recruits (Table 2) in high physicochemical variability pools (e.g. pool 1; Figure 4), probably selected for protection (Rojas & Ojeda, 2010). The latter was most often caught at a higher ontogenetic stage in larger and structurally more complex pools (e.g. pools 4 and 6; Figure 4) probably used for night-foraging or day-resting. The emptiness of the digestive tracts of these two congeneric species implies either occasional or sunset/nocturnal feeding (authors' personal observations). The carnivore specialist *Ahlia egmontis* was associated with gravel bottoms (e.g. pools 3 and 6; Figure 4; Zamprogno, 1989), microhabitat from which it can extract its prey, almost exclusively made up of mobile and burrowing polychaetes.

As in other environments (Dubiaski-Silva & Masunari, 2008; Randall, 1967), the omnivorous *Abudefduf saxatilis* presented one of the most diverse diets, albeit well balanced between animal and vegetal items (e.g. Zamprogno, 1989). In contrast to the algae-rich diet reported for reef environments (e.g. Randall, 1967; Ferreira et al., 1998), *Stegastes fuscus*'s diet was dominated by animal items (e.g. Zamprogno, 1989), which counterposes its usual adult classification as a territorial herbivore (Ferreira et al., 2004). These omnivorous species also showed inter-specific differences in size (Table 2), behavior and microhabitat in tidepools (e.g. Zamprogno, 1989). While *Ab. saxatilis* usually formed small schools in pools with large open areas (e.g. pool 2), *St. fuscus* established their territories in large pools presenting consolidated substrate in sunlit areas (e.g. pool 5), for the maintenance of their "gardens" (Macieira & Joyeux, 2011; Zamprogno, 1989). Rojas and Ojeda (2010) demonstrated that small fishes prefer pools of low structural complexity where there are fewer ambush areas for predators. Moreover, schools provide some advantages to fishes like access to a greater variety of food resources, areas of foraging and protection against potential predators (Pereira et al., 2012).

Two roving herbivores (*Acanthurus bahianus* and *Sparisoma axillare*; Ferreira et al., 2004; Ferreira & Gonçalves, 2006) formed the herbivorous guild. *Acanthurus bahianus* presented a diet practically restricted to algae, ingesting possibly unintentionally less than 1% of other organisms, while *Sp. axillare* presented a slightly more diversified diet, consisting approximately of 80% algae, as well as small crustaceans, fish scales and chironomid larvae. These diet differences are probably related to distinct feeding modes, given that as an adult the former species is classified as a scraper herbivore and the second as an excavator/scraper herbivore (Ferreira & Gonçalves, 2006). Furthermore, as juveniles in tidepools, *Ac. bahianus* probably exhibits a browser herbivore feeding mode, like its congener species *Acanthurus chirurgus* (Bloch, 1787) (Zamprogno, 1989). However, both *Ac. bahianus* and *Sp. axillare* were more associated with deep and structurally complex pools (e.g. pools 4 and 6), due to the need for a large area and adequate substrate for foraging (Lawson et al., 1999).

Another herbivorous species, present but unstudied due to its rarity in our samples, is *Ac. chirurgus*, which is classified as a browser herbivore in the inter-tidal environment (Zamprogno, 1989). In shallow reef environments, herbivorous reef fishes are important members of the community, influencing the distribution not only of algae but also indirectly of corals (Ferreira & Gonçalves, 2006; Floeter, Behrens, Ferreira, Paddack, & Horn, 2005). Contrarily, in the tidepools of Castelhanos beach herbivores represent a small part of the fish assemblage, representing only 5% of the species and contributing 10% in abundance and 13% in biomass (see Macieira & Joyeux, 2011). This is a peculiar feature of inter-tidal fish communities (Horn & Ojeda, 1999), probably associated with the capacity of species to withstand the extreme conditions of this environment and to be able to use it as a nursery or feeding area. Another important factor for this pattern is the food ontogeny of some species (e.g. *Stegastes* spp.), which are omnivorous when juveniles in pools (Zamprogno, 1989) and become herbivorous when adults in outer reefs (Ferreira et al., 1998, 2004; Randall, 1967).

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At Castelhanos inter-tidal reef, the trophic structure of assemblages is built upon convergence toward food items partitioned within feeding guilds by inter-specific differences in consumer size, microhabitat, behavior and trophic specialization. However, ontogenetic changes in diet, such as in omnivorous species shifting to herbivory in adulthood, also lead to changes in trophic guilds throughout life (Muñoz & Ojeda, 1998, 2000) and induce temporal variations at both guild and community structure levels (Wilson & Sheaves, 2001). In this respect, stable isotope and fatty acid analyses are promising approaches to characterize complex trophic interactions and define trophic niches (Hielscher et al., 2015) through the integration of spatial and temporal information of the trophic relationships within communities (Nagata et al., 2015).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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