Spatial distribution of nominally herbivorous fishes across environmental gradients on Brazilian rocky reefs

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Assemblages of roving herbivores were consistently different between eastern, warmer, sheltered sites and western, colder, more wave-exposed sites. At eastern sites, detritivorous-herbivorous species dominated while omnivores had the highest biomass and were dominant at western sites. Macroalgivores did not show any trends related to location. These distributional patterns, at relatively small spatial scales of a few kilometres, mirror large-scale latitudinal patterns observed for the studied species along the entire Brazilian coast, where cold water associated species are abundant on south-eastern rocky reefs (analogous to the western sites of this study), and tropical species are dominant on north-eastern coral reefs (analogous to the eastern sites). Species-level analyses demonstrated that depth was an important factor correlated with biomasses of *Diplodus argenteus*, *Sparisoma axillare* and *Sparisoma tuiupiranga*, probably due to resource availability and interspecific competition. Herbivorous fish assemblages in the study area have been historically affected by fishing, and combined with the variation in assemblage structure, this is likely to have important, spatially variable effects on the dynamics of benthic communities.

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Key words: browser; scraper; south-western Atlantic; trophic guild; upwelling; wave exposure.

INTRODUCTION

Roving herbivores are among the most conspicuous elements of the fish fauna in reef environments (Choat, 1991), influencing the distribution (Williams & Polunin, 2001), diversity (Hixon & Brostoff, 2010) and biomass of algae (Hay, 1981). Most tropical species typically feed on the epilithic algal matrix (Bellwood *et al.*, 2004), and are responsible for maintaining algae at an early successional stage with high rates of primary production (Carpenter, 1986; Polunin & Klumpp, 1989), indirectly favouring the maintenance of greater diversity in benthic communities (Hughes *et al.*, 2007a). On coral reefs, the role of herbivores in maintaining coral-dominated states has been

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intensely studied, and is recognized as a key top–down process to be protected or re-established to maintain and increase reef resilience (Hughes *et al.*, 2007*b*; Mumby *et al.*, 2007; Cheal *et al.*, 2010). Subtropical reefs constitute important and fragile transition habitats that are complex systems where biogeographical overlap of taxa is shaped by mixed environmental conditions (Beger *et al.*, 2013). In subtropical rocky systems, however, the functional importance of herbivores remains uncertain. Herbivorous fishes show a generally lower taxonomic diversity towards higher latitudes (Choat, 1991; Floeter *et al.*, 2005), implying different assemblages of herbivores that have distinct diets, feeding behaviour and food processing modes (Bellwood & Choat, 1990; Choat *et al.*, 2002, 2004, Clements *et al.*, 2009). Furthermore, subtropical reef systems tend to have higher cover of algae and lower biomass of herbivorous groups when compared with tropical reefs (Vroom & Braun, 2010; Hoey *et al.*, 2011). Such differences are crucial for understanding differences in ecological functioning between tropical and subtropical reefs.

The main components of the Atlantic fish community, that are nominally herbivorous (*i.e.* species of reef fishes that consume a wide range of dietary items including detrital aggregates, turf and macroscopic algae and macrozooplankton), include members of the families Acanthuridae, Labridae (tribe Scarini) and Kyphosidae (Ferreira *et al.*, 2004). Within this biogeographic region, Brazilian reefs support three species of surgeonfish (from the genus *Acanthurus* Forsskål 1775; Rocha *et al.*, 2002), 10 parrotfish species (from the genera *Cryptotomus* Cope 1871, *Nicholsina* Fowler 1915, *Scarus* Fowler 1915 and *Sparisoma* Swainson 1839; Moura *et al.*, 2001) and four species of *Kyphosus* Lacépède 1801 (Knudsen & Clements, 2013). Ecological studies involving roving herbivores along the Brazilian coast encompass topics from latitudinal variation (Floeter *et al.*, 2005), community structure and diet (Ferreira & Gonçalves, 2006) and resource partitioning (Dias *et al.*, 2001; Bonaldo *et al.*, 2006; Francini-Filho *et al.*, 2010). There is a gap in literature, however, concerning the distribution patterns of herbivores, and how these patterns are related to physical factors across environmental gradients in reef systems in the South Atlantic Ocean.

Reef fishes are closely associated with consolidated reef areas, and variations in populations are often related to abiotic habitat characteristics (Benfield *et al.*, 2008). For example, aspects such as structural complexity have positive correlations with the diversity, richness and abundance of reef fishes (Brokovich *et al.*, 2006; Dominici-Arosemena & Wolff, 2006; Graham & Nash, 2013), while depth and degree of wave exposure have negative correlations with these assemblage metrics (Ferreira *et al.*, 2001; Lecchini *et al.*, 2003; Nemeth & Appeldoorn, 2009), although some herbivorous fishes have been observed to be associated with higher wave exposure (Taylor & Schiel, 2010). Also, associations between herbivore biomass and macroalgal cover have been investigated, but with divergent conclusions. Herbivore biomass may either be negatively correlated (Williams & Polunin, 2001; Hoey & Bellwood, 2011) or unrelated (Carassou *et al.*, 2013) to macroalgal abundance. Understanding how environmental gradients affect the abundance patterns of herbivore species is the first step to recognition of the drivers of ecological processes, such as herbivory and bioerosion, at a range of spatial scales in order to aid the management of reef areas (Mumby *et al.*, 2006).

In this study, the relationship between variations in roving herbivorous assemblages along depth gradients on Brazilian rocky reefs was examined. Also, sites were surveyed across relatively small spatial scales that represent considerable variations in

wave exposure and temperature. In order to ensure that patchy and potentially rare roving herbivores (Welsh & Bellwood, 2011) were adequately surveyed, long-timed visual censuses were conducted. By linking the assemblage composition of herbivorous fishes to abiotic gradients, new insights into the ecology of these functionally distinct species, and highlights to the spatial variation in their functional roles are discussed.

MATERIALS AND METHODS

The studied sites were located inside the Marine Extractive Reserve of Arraial do Cabo (22° 57′ S; 41° 01′ W), which consists of a protected area where only traditional fishermen are allowed to exploit natural resources. Despite some fishing restrictions and quotas, there are no effective no-take areas or control of fishing activities, and all sorts of fishing gears are used, from nets to spearfishing (Bender *et al.*, 2014). The Arraial do Cabo region consists of an isthmus and two islands dominated by rocky shores (Fig. 1). Upwelling events in the region are triggered by a combination of prevailing winds and coastal morphology, which leads to two major distinct habitat conditions: the western side of the isthmus that is affected directly by cold, upwelling waters (mean temperature <18° C), and the eastern side with comparative higher mean water temperatures (averaging 22° C) [Valentin, 1984; see Appendix SI (Supporting Information)]. The west side of the isthmus is also characterized by higher chronic wave exposure and deeper habitats (see Appendix SI, Supporting Information), conferring warm-temperate characteristics on this location. Sites located to the east of the isthmus are less influenced by upwelling waters and show subtropical–tropical characteristics in their benthic composition (see Appendix SI, Supporting Information).

Nominally herbivorous fishes were classified into functional groups based on trophic categories and diet (Ferreira *et al.*, 2004; Ferreira & Gonçalves, 2006; Halpern & Floeter, 2008; Longo *et al.*, 2014), nutritional ecology (Clements *et al.*, 2009) and complemented by extensive field observations, either on a family or genus level according to the available information. Fishes' feeding mode and food processing are closely linked to their trophic role, consequently influencing how the consumed material will be transferred through the trophic chain (Clements *et al.*, 2009; Raubenheimer *et al.*, 2009; Karasov *et al.*, 2011). The proposed classification here is an attempt to combine both nutritional and functional approaches, once they cannot be ecologically disentangled. Consequently, nominally herbivorous fishes were divided into two major functional groups: detritivore-herbivores and macroalgivores. The first group included two acanthurids [ocean surgeonfish *Acanthurus bahianus* Castelnau 1855 and doctorfish *Acanthurus chirurgus* (Bloch 1787)] and six scarini labrids [the parrotfishes *Sparisoma amplum* (Ranzani 1841), *Sparisoma axillare* (Steindachner 1878), *Sparisoma frondosum* (Agassiz 1831), bucktooth parrotfish *Sparisoma radians* (Valenciennes 1840), *Sparisoma tuiupiranga* Gasparini, Joyeux & Floeter 2003 and *Scarus zelindae* Moura, Figueiredo & Sazima 2001]. These fishes are of tropical origin (Bernardi *et al.*, 2000; Streelman *et al.*, 2002), encompass both scraper and excavator feeding modes (Bellwood & Choat, 1990; Choat *et al.*, 2002), and do not present any characteristics of a fermenting-like species [*e.g.* acid stomach, long gut or a hindgut fermentation chamber: Lobel (1981); Horn (1989)]. In the Brazilian province, these species have similar proportions of plant material and detritus in their diets (Ferreira & Gonçalves, 2006), and thus represent detritivorous-herbivorous species. Macroalgivores consistently feed on macroalgae by selecting and cropping individual algal components without removing the reef substratum or large amounts of detritus (Choat *et al.*, 2002, 2004). As strict algal feeders, ingesting macroalgae almost exclusively, these species rely on endosymbiotic bacteria to ferment the highly complex algal carbohydrates they ingest (Clements & Choat, 1995). Here, macroalgivores comprised an acanthurid species (blue tang surgeonfish *Acanthurus coeruleus* Bloch & Schneider 1801), and a group of kyphosid species [brown chub *Kyphosus bigibbus* Lacépède 1801, Bermuda sea chub *Kyphosus sectatrix* (L. 1758) and the brassy chub *Kyphosus vaigiensis* (Quoy & Gaimardi 1825)]. Kyphosid species were grouped at genus level due to difficulties in identification during censuses. In addition, an omnivorous sparid species [South American silver porgy *Diplodus argenteus* (Valenciennes 1830)] was included as a third functional group within the analyses. Despite omnivores showing a high plasticity in diet
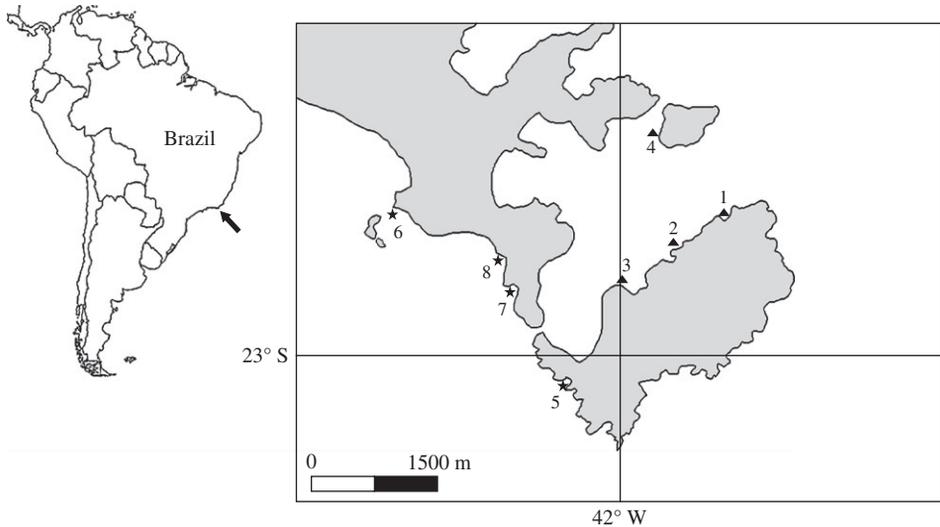
Fig. 1. Map of the Arraial do Cabo region (Rio de Janeiro, Brazil) indicating sampled sites (▲, east; ★, west). The maximum depth of each area is shown in parentheses after the site name: 1, Anequim (10 m); 2, Abobrinha (8 m); 3, Maramutá (6 m); 4, Ilha dos Porcos (15 m); 5, Ingleses (25 m); 6, Franceses (6 m); 7, Sometudo (15 m); 8, Sonar (7 m). Sites 5–8 are influenced by cold upwelling water.

by definition, algal material was found to be a representative item in the diet of species from the genus *Diplodus* Rafinesque 1810 in the Mediterranean Sea and Atlantic Ocean (Stoner & Livingston, 1984; Sala & Ballesteros, 1997). Similarly, *D. argenteus* was included here as a functional herbivore based on the high proportion of algal material commonly observed in the gut content of this species in southern Brazil (Dubiaski-Silva & Masunari, 2004), and at the study region, where red and green filamentous and corticated algae comprised >40% of *D. argenteus* gut contents (T. C. Mendes, K. D. Clements & C. E. L. Ferreira, unpubl. data).

Roving herbivorous fishes were counted using timed-transects (10 min duration, 4 m width) and categorized into total length (L_T) classes: 10–20, 21–30, 31–40, 41–50 and >51 cm (maximum size observed was 60 cm). Divers used an underwater propeller (Sea Scooter SeaDoo VS Supercharger; www.seacooterexpress.com) in order to keep a reasonably constant speed (*c.* 5 km h^{-1}) during the transect surveys and diminish the odds of double counting the same specimens due to the high mobility of fishes. Large, timed-transects are the most appropriate methods for large species, such as herbivorous fishes (Hill & Wilkinson, 2004; Green & Bellwood, 2009), which usually show clumped distributions and can be rare (Choat & Pears, 2003). Despite the possible noise generated by the propeller, which could scare some species, such behaviour was not observed for target species within transects. If any individuals were scared out of the sampling area, this could not be estimated and is considered an artefact of the technique that is highly unlikely to be systematically biased across the censuses. Transect distances were not equal because of differences in environmental conditions (*e.g.* currents) and fish abundances that could reduce the length of an individual transect due to small delays caused by the annotation involved in recording species. All transects were geo-referenced at the beginning and the end, and the transect length was estimated based on the distance between those points following the coastal contour. The timed-transect surveys were conducted between March and June 2013 at eight sites (Fig. 1). For areas with maximum depths <10 m, only two strata were surveyed with each interval corresponding to half of the maximum local depth (*i.e.* shallow and mid-depth). For sites >10 m in maximum depth, the depth strata were: shallow (1–5 m), mid-depth (6–9 m) and deep (10–15 m). At least six timed-transects were surveyed in each depth stratum at each site. As the total length of transects differ, for each transect, the density of fishes was obtained by

dividing the abundance of fishes by the transect area, then standardizing it to number of fishes $100\,m^{-2}$.

The biomass of each species was calculated by applying abundance data to L_T–mass relationships available in the literature (Froese & Pauly, 2014). When no species-specific information was available, the conversion values were based on congeneric species. The conversion to biomass values was done by multiplying fish abundances in each L_T class by the biomass corresponding to the mid-point of the L_T class. For the analyses, the biomass of all size categories was summed to generate total fish biomass for each species.

DATA ANALYSIS

The east and west sides of the isthmus represent significant differences in two major abiotic factors, with frequent cold water from upwelling and high wave exposure to the west, and warmer, calmer waters to the east. For example, wave exposure analysis (see Appendix SI, Supporting Information) indicated that western sites are up to 120 times more influenced by wave surge than eastern sites. Consequently, large-scale temperature and exposure gradients, both of which can have important influences on reef-fish communities, co-vary within the study area and their relative importance cannot be distinguished. Therefore, the combined influence of these natural gradients was represented in the analyses as a categorical variable named location. Therefore, any significant influences of this location variable are subsequently interpreted as being caused by changes in temperature or wave exposure or both factors acting together.

Given the multivariate data of herbivore species abundances, a multivariate analysis (de-trended correspondence analysis, DCA) was applied to visualize differences in the composition of herbivorous assemblages among depth strata and between locations. Also, a permutational multivariate analysis of variance (PERMANOVA) was used to evaluate the significance of factors (location and strata) on the biomass of herbivorous. In the PERMANOVA, the factor site was included as random (as surveys at multiple depth were conducted at each site) and other factors as fixed categorical (location and strata). The SIMPER routine was applied to investigate the dissimilarity among factors and the relative contribution of each species to total dissimilarity. The similarity of assemblages among sites and between locations was further illustrated with a cluster analysis using group average similarity based on the Bray–Curtis distance. In addition to these multivariate analyses, the biomass of each fish species was tested using linear mixed-effect models (LMM) designed similarly to the PERMANOVA of fixed and random factors (*i.e.* site as random, and location and strata as fixed). Univariate data analysis was done using the R software (R Development Core Team; www.r-project.org) and the package nlme (Pinheiro *et al.*, 2013*b*). The model selection was based on best-fit with stepwise selection and AIC (Burnham & Anderson, 2002) using the drop1 function (MASS library; Venables & Ripley, 2002). Significant interactions among factors were analysed for each pair of interacting factors using the function interaction.plot (package *stats*, R Development Core Team) based on best-fit models.

RESULTS

A total of 130 timed-transects were performed at the eight sites, with a median length of $209\cdot0\,m$ ($Q_1 = 177\cdot2$, $Q_3 = 218\cdot3$, minimum $= 133\cdot0$, maximum $= 352\cdot0$). The $\log_{10}$-transformed mean length of transects did not vary significantly according to depth stratum (ANOVA, $F_{2,124} = 0\cdot49$, $P > 0\cdot05$), location (ANOVA, $F_{1,124} = 1\cdot97$, $P > 0\cdot05$) or the interaction of these factors (ANOVA, $F_{2,124} = 0\cdot48$, $P > 0\cdot05$). A total of 21 235 fishes were found in the $113\cdot54\,km^2$ of total area covered by the timed-transects. The overall dominant species in terms of abundance were *D. argenteus* (76·2% of total), followed by *A. chirurgus* (10%), *A. bahianus* (5·1%) and *Kyphosus* spp. (3·7%). More than 54% of all individuals were within the first size category ($10 \leq L_T \leq 20\,cm$) and 41·3% were in the second size category ($21 \leq L_T \leq 30\,cm$)
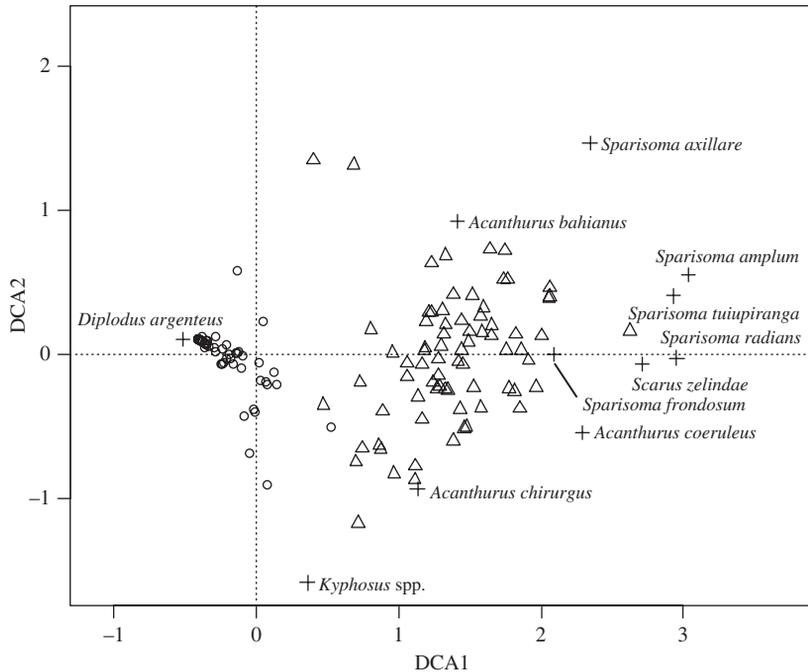
FIG. 2. De-trended correspondence analysis (DCA) of density of nominally herbivorous fishes on rocky reefs of Arraial do Cabo, Brazil. ○, sites to the west; △, sites to the east; +, species.

(Appendix SI, Supporting Information). Only 12 fishes (0·056% of the total) found in transects were $L_T \geq 40$ cm (*S. axillare*, $n = 8$; *S. zelindae*, $n = 1$, *S. frondosum*, $n = 1$; *Kyphosus* spp., $n = 2$). The species *S. tuiupiranga* and *S. radians* were represented only by specimens in the first size class because the maximum size of these species seldom exceeds 20 cm.

Differences in assemblage composition were observed in the DCA diagram (Fig. 2), where samples from western and eastern locations were distributed into two groups along the *x*-axis. The factor location was a significant factor accounting for the differences in roving herbivore biomasses in the PERMANOVA (Table I). In the DCA diagram, *D. argenteus* is positioned close to samples from the western region, *Kyphosus* spp. at an intermediate position and all other species are scattered around samples from eastern sites, indicating a gradient in species contribution leading to a differentiation of locations. In fact, most species were more abundant at the eastern location with some of them (namely *S. axillare*, *S. tuiupiranga*, *S. zelindae*, *S. amplum* and *S. radians*) occurring exclusively at those sites. Assemblages of western sites were more homogeneous in composition (SIMPER, average similarity = 71·8%) than eastern sites (58·9%). More than 50% of total dissimilarity between locations observed in the SIMPER analysis was attributed to *D. argenteus* (19·7%), *A. bahianus* (12·3%), *Kyphosus* spp. (11·8%) and *A. chirurgus* (9·8%), with *D. argenteus* being more abundant at western sites and the other species more abundant at eastern sites. All four species were found at all sites and in all depth strata, and the remaining species were restricted to eastern sites or were rare at western sites (Fig. 3). The species *S. radians* and *S. amplum*

TABLE I. Summary results for permutational multivariate analysis of variance (PERMANOVA) (fixed variables only) for the biomass of roving herbivore fish species on rocky reefs in Arraial do Cabo, Brazil

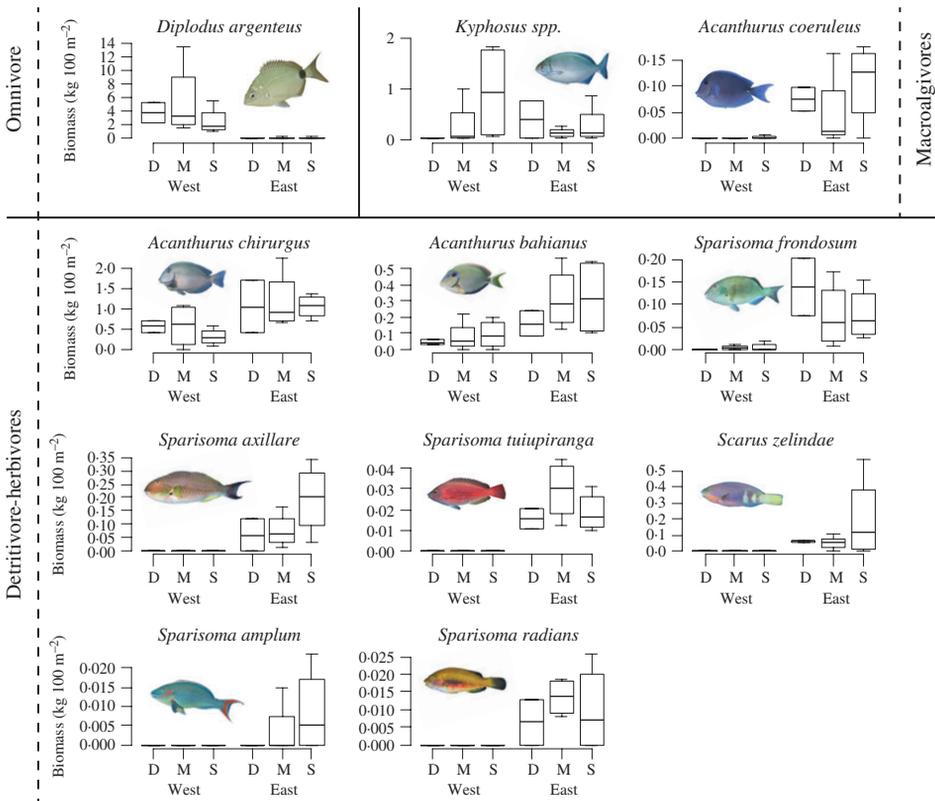| Source	d.f.	SS	MS	Pseudo-F	P (perm)	Unique perms	Pair-wise test
Location	1	55 735	55 735	11·74	0·001	4981	East $\neq$ West
Strata	2	2007·5	1003·8	1·13	>0·05	4989	$t = 3·4, P < 0·001$
Location × strata	2	1638·5	819·6	1·24	>0·05	4976	
Residual	110	64 700	588·2				
Total	129	152 000					

FIG. 3. Biomass of nominally herbivore species according to depth strata (D, deep; M, mid-depth; S, shallow) and location (west and east). Box-plot represents the median, Q_1, Q_3, minimum and maximum values.

were found in <5% of transects and showed a relatively low total abundance ($n = 15$ and $n = 6$); therefore, they were not included in further analyses.

In general, species showed higher mean biomasses at shallow depths. *Sparisoma tuiupiranga*, *S. radians* and *D. argenteus* were more abundant at intermediate depths, and *S. frondosum* was more abundant in the deep stratum (Fig. 3). Only *D. argenteus* and *Kyphosus* spp. had higher biomasses on the western side of the isthmus

(Fig. 3). Differences in the composition of assemblages were reflected in significant species-level differences between locations as shown in the LMMs. *Acanthurus bahianus* and *A. chirurgus* showed significantly higher biomasses at eastern sites (Table II). *Diplodus argenteus* had a significantly lower biomass at the eastern location, and a significant interaction between location and the mid-depth stratum (Table II), which reflects the dominance of this species at western sites, especially in the mid-depth stratum (Appendix SI, Supporting Information). Significant differences were found for *S. axillare* and *S. tuiupiranga* across depth strata, with higher biomass associated with shallow and mid-depth strata, respectively (Table III). The biomass of *A. coeruleus*, *Kyphosus* spp., *S. frondosum* and *S. zelindae* did not show significant correlations with any of the factors tested.

When species were grouped into functional categories, omnivores were dominant at western sites in terms of biomass, and detritivore-herbivores were the most characteristic group at eastern sites (Fig. 4), which is reflected by the significant influence of location for these groups in the LMMs (Table IV). Macroalgivores were observed to have similar biomasses in both locations, and did not show significant differences across depth strata or locations (Table IV). Multivariate differences in mean biomasses of trophic groups were only found between western and eastern sites (pseudo-$F = 20\cdot4$, $P < 0\cdot001$), whereas depth strata (pseudo-$F = 2\cdot2$, $P > 0\cdot05$) and interaction of factors (pseudo-$F = 1\cdot4$, $P > 0\cdot05$) were not significant. As in the analysis of species composition, the random factor site was also significant for inter-site variation (pseudo-$F = 5\cdot8$, $P < 0\cdot01$). Although site-level differences in fish assemblages were not a focus of this study, some patterns among sites are shown in Fig. 5, although the herbivore assemblages within locations are relatively homogeneous. Dissimilarities of 80·2% were found between locations for multivariate analyses of functional groups, with omnivores contributing 64·3% of total dissimilarity, followed by detritivore-herbivores (24·4%) and macroalgivores (11·3%).

In summary, there was a clear differentiation in the assemblages of roving herbivores between eastern and western sites, reflected in the grouping of sites within locations (Fig. 5). Sites to the west of the isthmus had a higher contribution of omnivores while eastern sites showed a dominance of detritivorous-herbivorous species. Furthermore, the sites on the west side of the isthmus had a high proportional contribution to the total biomass of herbivorous species found in the studied region (Fig. 5), mainly associated with the abundance of a single omnivorous species (*D. argenteus*).

DISCUSSION

In this study, the distributional patterns of herbivorous fish assemblages vary among the studied sites within a few kilometres, similar to the described latitudinal variations in species distribution along the Brazilian coast (Ferreira *et al.*, 2004; Floeter *et al.*, 2005). These gradients result mainly from a combination of exposure and temperature extremes, the latter probably being more likely to influence fishes' distribution according to species temperature affinities and evolutionary origin. The main implication of this strong segregation of herbivorous assemblages is the potential variation in ecological functions exerted by species at each location.

The location factor combines multiple environmental drivers, with western sites exhibiting lower mean annual water temperature, higher wave exposure and deeper

TABLE II. Summary results for analysis of best-fitted predictive linear mixed-effect models for biomasses of roving herbivore fish species on rocky reefs in Arraial do Cabo, Brazil. Values are coefficients (s.e.) and t-values [d.f.]. Only significant terms are shown in the table, except for those present in significant interactions. For categorical terms (location and depth), significance is relative to the western location and deepest stratum, respectively

	Diplodus argenteus		t-Value	Kyphosus spp.	t-Value	Acanthurus chirurgus	t-Value	Acanthurus bahianus	t-Value
Intercept	2223·4*	(1039·8)	2·09 [118]	371·3* (158·6)	2·34 [122]	467 (179)	1·81 [122]	84·1 (65·2)	1·12 [122]
L-eastern	−2218·6	(1462·8)	−1·47 [6]	—	—	582* (249)	2·54 [6]	220·8* (89·1)	2·46 [6]
S-mid-depth	3625·5***	(148·1)	3·24 [118]	—	—	—	—	—	—
S-shallow	91·9	(151·2)	0·15 [118]	—	—	—	—	—	—
L-eastern × S-mid-depth	−3540·1***	(204·5)	−2·46 [118]	—	—	—	—	—	—
L-eastern × S-shallow	3·9	(203·1)	0·16 [118]	—	—	—	—	—	—

L, location; S, strata. ***$P < 0.001$; **$P < 0.01$; *$P < 0.05$; −, non-significant.

TABLE III. Summary results for analysis of best-fitted predictive linear mixed-effect models for biomasses of roving herbivore fish species on eastern rocky reefs from Arraial do Cabo, Brazil. Values are coefficients (S.E.) and *t*-values [d.f.]. Only significant terms are shown in the table, except for those present in significant interactions. For categorical terms (location and depth), significance is relative to the western location and deepest stratum, respectively

	Spa fro	t-Value	Spa axi	t-Value	Aca coe	t-Value	Spa tui	t-Value	Sca zel	t-Value
Intercept	79·2*** (21·5)	2·31 [68]	43·1 (54·7)	0·69 [68]	75·3*** (20·9)	3·07 [70]	21·8* (6·3)	3·1 [68]	114·0 (59·4)	1·91 [70]
L-eastern	na	na	na	na	na	na	na	na	na	na
S-mid-depth	–	–	40·0 (53·3)	0·76 [68]	–	–	15·3* (7·3)	–	–	–
S-shallow	–	–	159·6** (51·7)	3·06 [68]	–	–	5·6 (7·2)	–	–	–
L-eastern×S-mid-depth	na	na	–	–	na	na	–	–	na	na
L-eastern×S-shallow	na	na	–	–	na	na	–	–	na	na

L, location; S, strata. ***P <0·001; **P <0·01; *P <0·05; –, non-significant; na, not applicable; Spa fro, Sparisoma frondosum; Spa axi, Sparisoma axillare; Aca coe, Acanthurus coeruleus; Spa tui, Sparisoma tuiupiranga; Sca zel, Scarus zelindae.
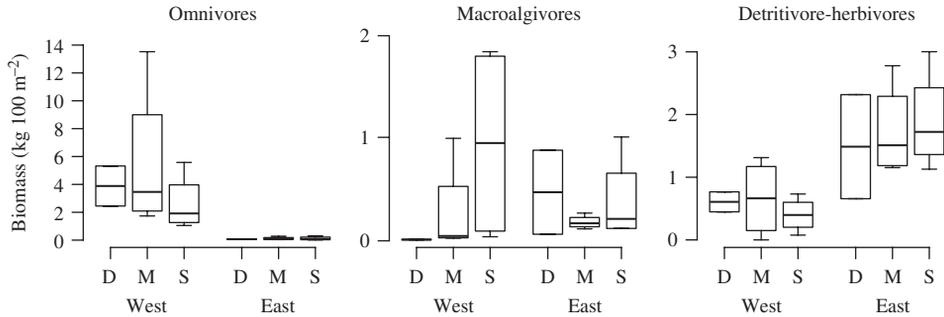
FIG. 4. Biomass of nominally herbivorous trophic groups in rocky shores of Arraial do Cabo (Brazil) according to depth strata (D, deep; M, mid-depth; S, shallow) and location (west and east). Box-plot represents the median, Q_1, Q_3, minimum and maximum values.

waters. In contrast, the sites on the eastern side of the isthmus have calmer, shallower and warmer waters. Wave exposure normally acts in conjunction with depth, creating variation in wave-induced turbulent fluxes (Ortega-Borges *et al.*, 2009). Wave energy decreases approximately in a logarithmic proportion with increasing depth (Pond & Pickard, 1983), which means that the shallow stratum is much more affected by wave surge, limiting the distribution of species according to their swimming ability (Friedlander & Parrish, 1998; Bellwood *et al.*, 2002; Wainwright *et al.*, 2002; Fulton & Bellwood, 2004; Fulton *et al.*, 2005; Johansen *et al.*, 2007). Due to their high mobility, however, roving species are able to avoid areas with excessively high wave action by moving to deeper or more sheltered waters. In contrast, when fishes are exposed to large upwelling events, the geography of the area is likely to preclude their access to warmer, non-upwelling eastern areas. Consequently, fishes at western sites can rarely avoid the effects of lower temperatures and, therefore, it is suggested that temperature may be the most important abiotic gradient within the study area. As shown in Appendix SI (Supporting Information), the sampling effort was concentrated during the season with less upwelling occurrence. Therefore, the present results can be considered conservative: it is possible that the significant differences in fish assemblages between the east and west side of the isthmus may be even more dramatic during upwelling events.

Arraial do Cabo constitutes a warm-temperate enclave of Brazilian rocky reefs due to the frequent local upwelling events on only one side of the isthmus (Valentin, 1984). This situation makes the region a natural laboratory to study the effect of temperature on different processes (Mendes *et al.*, 2009), and also provides opportunities to use data on temperature effects on species with wide distributions in the western Atlantic to explain the patterns observed in the region. Temperature may limit the distribution of a number of species and processes, but the mechanisms by which it occurs remain controversial. While Floeter *et al.* (2005) proposed the existence of a physiological constraint on the digestive process of herbivorous fishes associated with cold water, recent studies highlighted the weakness of their argument and suggested the existence of ecological and phylogenetic constraints to explain the absence of nominally herbivorous fishes in cold water (Clements *et al.*, 2009; Trip *et al.*, 2014). For example, some macroalgivores have demographic traits contrary to a nutritional constraint hypothesis [*e.g.* reproduction and growth of Odacini; Trip *et al.* (2014)]. Furthermore, acanthurids

TABLE IV. Summary results for analysis of best-fitted predictive linear mixed-effect models for biomass of trophic groups in rocky shores of Arraial do Cabo, Brazil. Values are coefficients (S.E.) and *t*-values [d.f.]. Only significant interactions are shown in the table. For categorical terms (location and depth), significance is relative to the western location and deepest stratum, respectively

	Omnivores	*t*-Value	Macroalgivores	*t*-Value	Detritivore-herbivores	*t*-Value
Intercept	3371·9*** (1405·9)	2·39 [122]	412·0* (168·4)	2·44 [122]	585·8* (294·1)	1·99 [122]
L-eastern	−3984·0** (1671·2)	−2·38 [6]	—	—	1194·5* (398·6)	2·99 [6]
S-mid-depth	—	—	—	—	—	—
S-shallow	—	—	—	—	—	—

L, location; S, strata. ***P < 0·001; **P < 0·01; *P < 0·05; −, non-significant.
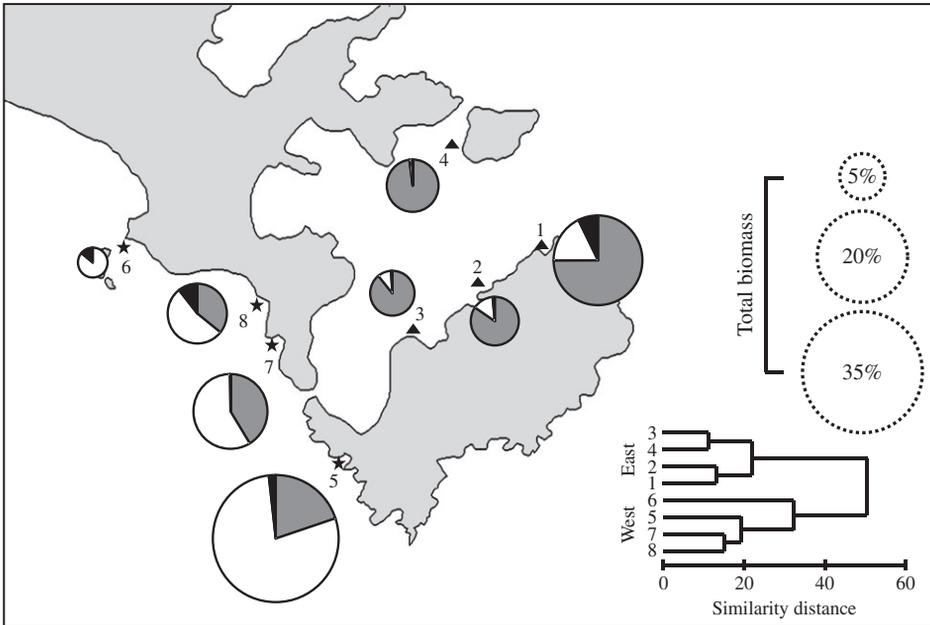
Fig. 5. Relative contribution (SIMPER) of trophic groups to similarities among sites (dendrogram), and the relative total biomass of each site. Circle areas are proportional to the relative contribution of each site to total biomass for the entire study. In the circles, detritivore-herbivores (■), omnivores (white area) and macroalgivores (■) are indicated. Sampled sites are east (▲) and west (★).

(except for *A. coeruleus*) and parrotfishes, including those from the genus *Sparisoma* and *Scarus*, ingest high quantities of detritus (Ferreira & Gonçalves, 2006) and rely on a protein-rich diet instead of digesting algae to meet their nutritional demands like macroalgivorous species (Choat *et al.*, 2004; Crossman *et al.*, 2005).

Contrasts among the assemblages of herbivores observed in this study are similar to the described latitudinal variations in species distributions along the Brazilian coast (Ferreira *et al.*, 2004; Floeter *et al.*, 2005). On the Brazilian coast, fishes with tropical origins from the genera *Sparisoma*, *Scarus* and *Acanthurus* (Bernardi *et al.*, 2000; Streelman *et al.*, 2002) decrease in abundance towards higher latitudes (Ferreira *et al.*, 2004). Only *Kyphosus* spp. and *D. argenteus*, both of subtropical or temperate origin (Summerer *et al.*, 2001; Knudsen & Clements, 2013), have been observed to increase in abundance in southern Brazil (Ferreira *et al.*, 2004; Floeter *et al.*, 2007). Indeed, the latter has been reported as expanding its distributional range into Argentinean waters (Galván *et al.*, 2009). This study is consistent with the wider latitudinal distribution limits, as *D. argenteus* and *Kyphosus* spp. were present at eastern sites, but were dominant at colder sites directly influenced by upwelling. *Acanthurus chirurgus* and *A. bahianus* were also found in both locations, but had lower biomasses at colder western sites. The southernmost point of the distribution of these acanthurid species represents annual mean temperatures of 20° C (Floeter *et al.*, 2005), which indicates that these species exhibit tolerances to subtropical temperatures, but are not as well adapted as co-occurring species such as *Kyphosus* spp. or *D. argenteus*.

Kyphosus species were associated with sites with high wave exposure in previous studies conducted on Brazilian rocky reefs, mainly due to their good swimming ability and the presence of their main food resources (high density of seaweeds) at these sites (Ferreira *et al.*, 2001; Floeter *et al.*, 2007; Pinheiro *et al*, 2013*a*). In this study, however, this species showed a wide distribution across all gradients explored, and thus no significant association with tested factors was detected. Despite being of temperate affinities (Knudsen & Clements, 2013), kyphosids are abundant all along the Brazilian coast and oceanic islands (Ferreira *et al.*, 2004; Pinheiro *et al.*, 2013*a*).

Depth was significant only at the species level, indicating that this factor was not important to the entire assemblage, but had a significant influence on particular species. Higher values of biomass associated with shallow waters are commonly described in the literature for roving herbivore species, mostly attributed to higher temperatures and lower predation risk at these depths (Ferreira & Gonçalves, 2006; Fox & Bellwood, 2007; Brokovich *et al.*, 2010). Depth is also intrinsically influential over light intensity, sedimentation and wave-surge variation (Garrabou *et al.*, 2002), which in turn directly affects algal and herbivore distribution patterns (Hay *et al.*, 1983; Russ, 2003). In the studied region, only *S. tuiupiranga*, *S. axillare* and *D. argenteus* showed some influence of depth on their distribution. The first two species occurred exclusively at eastern sites, where the territorial dusky damselfish *Stegastes fuscus* (Cuvier 1830) attains high densities in shallow areas (Ferreira *et al.*, 1998), which could force this small-sized parrotfish to the deep strata in order avoid the aggressive behaviour of damselfishes. *Diplodus argenteus* showed significantly higher biomass at mid-depth stratum, which may suggest that the effect of higher wave surge at the shallow strata could lead to this species spending more time in deeper habitats.

FUNCTIONAL ROLE AND CONSERVATION

The patterns observed in the study area suggest a strong spatial segregation among roving herbivore functional groups on either side of the isthmus, but a high overlap within these locations and across depth gradients. The relative contribution of functional herbivore groups in each location is clearly skewed towards omnivore dominance on the western side of the isthmus, and detritivore-herbivore dominance on the eastern side of the isthmus. Macroalgivore biomass was not significantly associated with location.

Considering the eastern sites, the higher diversity of species within the same trophic group can potentially lead to a high functional redundancy or more diverse benthic feeding strategies. Studies assessing the diet of the genera *Acanthurus*, *Sparisoma* and *Scarus* in Brazilian reef environments indicate that there is a significant overlap in the items consumed by species from these genera (Ferreira & Gonçalves, 2006; Francini-Filho *et al.*, 2010). Considering that, it is possible that within the detritivore-herbivore group differences could exist in the nutritional targets and food processing modes, varying among families and influencing functional overlap as suggested by Mendes *et al.* (2015). To date, however, there is no detailed analysis of the diet and nutritional ecology of these species to make conclusive inferences about their diets. Consequently, further refinements of the species grouping will be important to understand the implications of herbivores on the structure of benthic communities by different species. Additionally, there is also a need for a better understanding of what the drivers of food selection are for the omnivorous *D. argenteus,* as well as its

effects on algal cover. Considering that the amount of algae ingested can increase with fish size (Dubiaski-Silva & Masunari, 2004), this species may be an important grazer at some sites.

It was clear that there is a lack of large-sized individuals among roving herbivore populations in Arraial do Cabo, particularly for the parrotfishes that represent the majority of the detritivore-herbivores. Most parrotfishes can attain large sizes and represent a fishing target in many tropical and subtropical reefs (Comeros-Raynal *et al.*, 2012; Rasher *et al.*, 2013). On many Brazilian reefs, they have become a fisheries target in the past 20 years, as populations of top predators collapsed and spearfishers started to recognize them as an alternative target (Floeter *et al.*, 2006; Francini-Filho *et al.*, 2010; Bender *et al.*, 2014). Fishery activities in Arraial do Cabo region are historically important, and spear guns were introduced as a common fishing technique in the past 40 years (Bender *et al.*, 2014). Unfortunately, despite being permitted in some areas, there is poor enforcement of regulations by local authorities (*e.g.* minimum size of capture and species restrictions). Apart from *S. tuiupiranga* and *S. radians*, all other parrotfish species recorded in this study attain maximum sizes of at least 50–60 cm L_T (Francini-Filho *et al.*, 2010; Froese & Pauly, 2014), but fishes in this size category were very rare within the study area. Parrotfishes are known for being sequential hermaphrodites and terminal males are normally the largest individuals (Bonaldo *et al.*, 2006). Under scenarios with limited abundance of large individuals, reproductive output can be reduced (Hawkins & Roberts, 2004; Birkeland & Dayton, 2005). Indeed, one Brazilian endemic parrotfish species (*Scarus trispinosus* Valenciennes 1840) has recently been considered ecologically extinct in the Arraial do Cabo region as an effect of overfishing by spearfishing activity (Bender *et al.*, 2014). Although *S. trispinosus* once reached densities of up to 9·7 individuals 160 m^{-2} (Ferreira *et al.*, 2001), not a single individual was detected during the present sampling.

This study is the first to describe distributional patterns of herbivore assemblages across an environmental gradient in the south-eastern Atlantic Ocean, matching patterns found on a larger scale and probably related to temperature. The present results suggest the importance of additional studies on the nutritional ecology of species to disentangle the different effects of low temperatures on detritus feeding among parrotfishes and surgeonfishes, and to understand the use of high quantities of algae by omnivorous species at both high and low temperatures. Perhaps more importantly, there is a clear need to create conservation plans for the herbivore assemblages in the study area. Herbivorous fishes can exert an important influence on benthic communities in different ecosystems and habitats, and their functional role on subtropical reefs in Arraial do Cabo and on the south-eastern Brazilian coast is currently poorly understood. This study suggests, however, that the key ecological process of grazing varies significantly with abiotic gradients within the region, and this must be incorporated into conservation initiatives. As most individuals recorded were small relative to the maximum size attained by the species, exploitation is probably having important consequences for both the fishes and possible trophic cascades to benthic assemblages. Management approaches considering the interaction between spatially variable fish assemblages and fishing pressure are going to be critical for maintaining pivotal ecological functions locally, increasing habitat health, and helping to sustain goods and services provided by these reef areas.

Supporting Information

Supporting Information may be found in the online version of this paper:

Appendix SI. Additional information on the local temperature variation, benthic cover, species' size and density for the rocky reefs of Arraial do Cabo (Brazil) region.

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