



Parrotfishes of the genus *Scarus* in southwestern Atlantic oceanic reef environments: occasional pulse or initial colonization?

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Abstract

Two Brazilian endemic parrotfishes of the genus *Scarus* are recorded for the first time in oceanic reef environments of the Southwestern Atlantic. A few juveniles, and initial and terminal adults of *Scarus trispinosus* were observed at Rocas Atoll and one adult was recorded at Fernando de Noronha Archipelago. Conversely, an established population of *Scarus zelindae* was found in the middle of the Vitória-Trindade Chain, at the Davis seamount. Since dispersal potential is not a limitation for the pantropical distribution of the genus *Scarus*, historical and contemporary ecologic features are possibly the main processes driving these unique records in the Southwestern Atlantic. Here, we highlight the potential ecological reasons of such intriguing biogeographic pattern.

Keywords Parrotfishes · Oceanic islands · Vitoria-Trindade seamount chain · Brazilian province · Endemism · Reef fishes

Introduction

Parrotfishes of the genus *Scarus* are key functional components of coral reefs in all tropical regions (Streelman et al. 2002; Visram et al. 2010; Choat et al. 2012; Bonaldo et al. 2014). This diverse (53 species, Parenti & Randall, 2011) and widely distributed genus has pelagic spawning, large body size and high mobility, traits known to influence successful establishment during colonization events (Luiz et al. 2012, 2013). Thus, species of

the genus *Scarus* are found both on continental shelves and in oceanic reef habitats in all tropical biogeographic regions, except for the Southwestern and Mid-Atlantic oceanic islands (Joyeux et al. 2001). This is particularly intriguing since *Scarus* species naturally occur in isolated localities in the Pacific, at Hawaii (two species) and Galapagos islands (four species) that are, respectively, 3100 and 1000 km from the coast (Reaka-Kudla et al. 1996; Ong and Holland 2010); in the Eastern Atlantic, at São Tomé and Cape Verde Archipelagos (*Scarus hoefleri* Steindachner, 1881); and in the Northwestern Atlantic, at Bermuda (six species), that are, respectively, at 250, 560 and 1049 km from the coast (Smith-Vaniz et al. 1999; Wirtz et al. 2007, 2013; Floeter et al. 2008).

Scarus trispinosus Valenciennes, 1840 and *Scarus zelindae* Moura, Figueiredo & Sazima, 2001 are the only Southwestern Atlantic *Scarus* species, both endemic to the Brazilian Province and of recent origin (~1.0 Mya, Choat et al. 2012). Despite extensive research surveys at Brazilian oceanic islands during the last 20 years (Rosa & Moura 1997; Soto 2001; Gasparini & Floeter 2001; Krajewski & Floeter 2011; Medeiros et al. 2011; Vêras and Tolotti 2011; Pinheiro et al. 2011, 2015; Pereira-Filho et al. 2011b; Simon et al.), these species have never been found in oceanic island environments. Only *Sparisoma* parrotfishes, an endemic genus of the Atlantic Ocean (Böhlke & Chaplin 1968), have been recorded in the Brazilian oceanic islands (Joyeux et al. 2001).

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The metapopulation structure of most reef fishes, including parrotfishes, is influenced by their dual life cycle, which includes a larval stage with high dispersive potential followed by recruitment and an adult stage of restricted dispersal, associated with coralline patchy habitats (Victor 1991; Leibold et al. 2004; Kritzer and Sale 2006). Processes related to pre-recruitment [e.g. dispersal limitation, such as pelagic larval duration (PLD)], post-recruitment (e.g. ontogenetic variations due to habitat suitability limitations) and adulthood life stage (e.g. chance of mating and reproductive output) are likely to determine the successful probability of reef fish establishment in a new area (Jones 1991; Leis 1991; Victor 1991), these being the most important traits explaining parrotfish distributions around tropical oceans (Choat et al. 2012). Therefore, the previous absence of *Scarus* in Southwestern Atlantic oceanic reef environments may be due to a combination of these factors. Herein we report the recent detection of these species in three oceanic reef environments of the Southwestern Atlantic and offer insights about the potential ecological reasons of such biogeographic pattern (Fig. 1).

Materials and methods

The *Scarus* occurrences were recorded during scientific diving expeditions on the Davis seamount, in the Vitória-Trindade seamount chain (VTC; February and April 2011), Fernando de Noronha Archipelago (August 2013) and Rocas Atoll (July 2014, July 2015 and January 2017; Fig. 1). Photographs of the specimens were taken using digital cameras. Most parrotfishes are protogynous hermaphrodites, normally characterized by changes in color and as sex in adults (initial and terminal phases). *Scarus zelindae* presents brown initial phase adult individuals with three to four white lateral spots and a white margin on the caudal fin, while terminal phase individuals are bluish green distally and orange basally, with a yellowish to orange distal band on the caudal fin (Moura et al. 2001). *Scarus trispinosus* presents similar initial and terminal adult phase coloration, with roughly homogeneous blue scales on flanks and bluish teeth (Moura et al. 2001). Juvenile individuals of this species also exhibit similar coloration to the adults, but with a yellowish area on the head (Moura et al. 2001). An underwater visual censuses database, consisting of belt transects in which a diver identified, counted and estimated the total length of fish species inside an area of 40 m² (Morais et al. 2017), spanning seven Brazilian coastal localities and all the four oceanic islands (Floeter and Ferreira unpubl. Data), was used to estimate the abundance of all parrotfish species (genus *Sparisoma* and *Scarus*) along the Brazilian Province (Fig. 1). A total of 1917 transects were performed in the coastal localities and 1573 in the oceanic ones, all performed in the same range-years of the new records, between 2012 and 2017, but not necessarily in the same

expeditions (Table 1). Parrotfish abundance on the Davis seamount was estimated from video recordings (Mazzei and Pinheiro unpubl. Data), and was only used to compare *Sparisoma* vs. *Scarus* abundance in that particular site. A total of 926 frames, taken every 10 s of video recording, were analyzed and the total number of parrotfishes species recorded. Therefore, the abundance estimate of *Sparisoma* and *Scarus* species along the Brazilian Province was used to identify potential processes and events related with the biogeographic pattern of parrotfish distribution in the Southwestern Atlantic. To test for differences in abundance between genera in belt transect database, we used a generalized linear mixed model with a Poisson distribution, using all individual belt transects as replicates and using locality as a random effect (Bolker et al. 2009; Zuur et al. 2009). For testing differences in abundance between genera using the video data, we employed a simple *t* test (Zar 2010).

Results and discussion

One terminal phase adult (~50 cm) of the greenback parrotfish *S. trispinosus* was recorded at a 23-m depth at Ponta da Sapata (3°52'17"S, 32°28'02"W) in Fernando de Noronha Archipelago (Fig. 2a), while 4 juveniles (~20 cm) and 5 adults, 2 initial (~35 cm) and 3 terminal phases (~50 cm), were found (from 2 to 8 m depth) at Rocas Atoll (3°51'15"S, 33°49'04"W) in July 2014, July 2015 and January 2017, respectively (Fig. 2b and c). While these sites are located on the same submarine chain 350 and 260 km, respectively, from the continental shelf (Fig. 1), they differ greatly in their geologic structure with Noronha being a rocky, volcanic island and Rocas being a biogenic, calcareous atoll. In contrast, great numbers of adults ($n = 38$), both initial ($n = 13$) and terminal phases ($n = 25$), of the Zelinda's parrotfish *S. zelindae* were found to inhabit the Davis seamount (20°34'51"S, 34°48'15"W; Fig. 2d and e), approximately 550 km from the Brazilian continental shelf, at one of the largest seamount of the VTC (Fig. 1).

Despite the presence of extensive coralline environments composed by rhodolith banks and coralline reefs over the VTC mesophotic seamount summits (Pereira-Filho et al. 2011a; Pinheiro et al. 2014, 2015), *S. zelindae* was exclusively observed over the shallower high-relief biogenic reefs of the Davis seamount (Fig. 2), at depths between 17 and 55 m. Due to limited mobility and shallow-water dependency of adult stages, it is extremely unlikely that fishes migrated to these areas swimming in open ocean or using the deep seamount summits as stepping stones. The colonization by larval dispersal from mainland remains as the most probable hypothesis for the presence of these parrotfish species in these isolated environments.



Fig. 1 Map of the Southwestern Atlantic Ocean, where the *gray line* represents the 200-m isobath. Previously, the distribution of *Scarus* species was restricted to the entire Brazilian continental margin and the main sites surveyed by our team and colleagues are indicated by *dots*.

Recent records of *Scarus* at Rocas Atoll, Fernando de Noronha Archipelago and the Davis seamount (Vitoria-Trindade Chain) are indicated by *arrows*

Sparisoma species, besides being the only parrotfishes with established populations at Brazilian islands (Table 1), are also consistently more abundant along all Brazilian coastal reefs, ranging from 3 to 20 times more abundant, and averaging about 8 times the *Scarus* abundance (Table 1; Poisson

GLMM intercept (*Scarus*) = -2.01 ± 0.56 , $Z = -3.57$, $p < 0.001$; slope (*Sparisoma*) = 2.21 ± 0.05 , $Z = 45.27$, $p < 0.0001$). On the other hand, on the Davis seamount, *S. zelindae* and *Sparisoma* species (i.e. *Sparisoma amplum* Ranzani, 1841 and *Sparisoma rocha* Pinheiro, Gasparini &

Table 1 Comparison of *Sparisoma* and *Scarus* abundance ($40\text{ m}^{-2} \pm$ standard error) on the Southwestern Atlantic reefs. The number of transects per site are given (N)

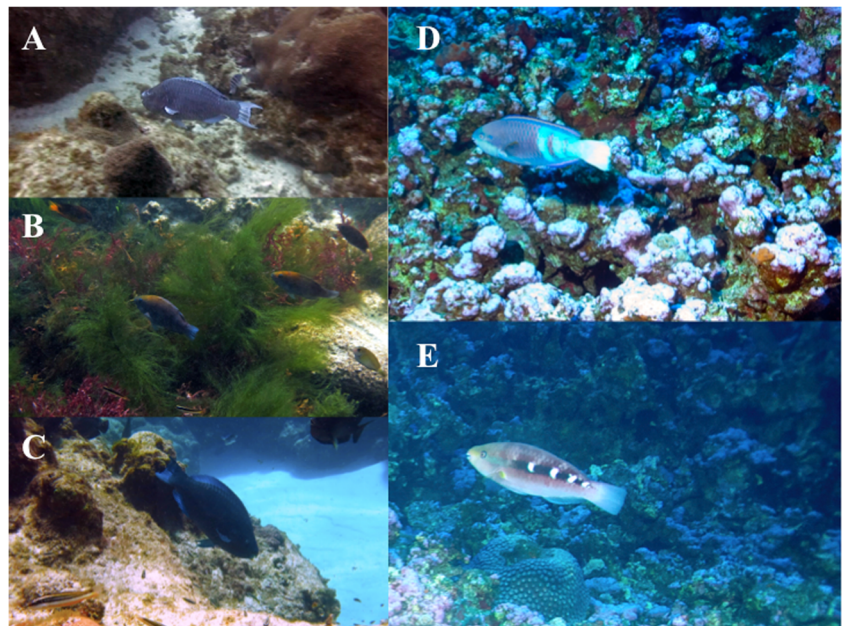
Locality	N	Reef type	Coordinates	Abundance	
				<i>Sparisoma</i> spp.	<i>Scarus</i> spp.
Manuel Luís Reefs (MA)	84	Mid-shelf	00°52'S; 44°15' W	6.92 ± 0.69	0.67 ± 0.16
Costa dos Corais (PE)	47	Inner-shelf	08°44'S; 35°04' W	4.53 ± 0.74	0.87 ± 0.30
Baia de Todos os Santos (BA)	229	Inner-shelf	13°02'S; 38°32' W	0.78 ± 0.07	0.34 ± 0.06
Abrolhos Archipelago (BA)	192	Mid-shelf	17°59'S; 38°41' W	3.08 ± 0.42	1.00 ± 0.17
Arraial do Cabo (RJ)	654	Inner-shelf	23°03'S; 42°00' W	1.41 ± 0.11	0.12 ± 0.03
Ilha Bela (SP)	106	Inner-shelf	23°56'S; 45°09' W	1.26 ± 0.29	0.23 ± 0.10
Arvoredo (SC)	605	Inner-shelf	27°17'S; 48°22' W	1.01 ± 0.10	0.05 ± 0.03
Saint Paul's Rocks (PE)	267	Oceanic	00°54'N; 29°20' W	0 ± 0 (a)	0 ± 0 (b)
Fernando de Noronha Archipelago (PE)	307	Oceanic	03°51'S; 32°25' W	3.55 ± 0.36	0 ± 0 (a)
Rocas Atoll (RN)	285	Oceanic	03°51'S; 33°48' W	2.90 ± 0.65	0 ± 0 (a)
Trindade Island (ES)	714	Oceanic	20°30'S; 29°19' W	1.00 ± 0.08	0 ± 0 (b)
Davis seamount (ES)*	926	Oceanic	20°34'S; 34°48' W	0.015 ± 0.004	0.018 ± 0.007
Mean coastal abundance				2.71 ± 0.1	0.47 ± 0.04
Mean island abundance				1.86 ± 0.15	0 ± 0

(a) presence in the site but absent from transects; (b) lack of record for the genus in the site. *Data estimated from video recordings (see methods) and is not part of the mean oceanic abundance

Sazima, 2010) have similar abundance ($t = 0.39898$, $df = 1466.1$, $p = 0.69$), with *S. zelindae* representing 55% of all parrotfishes recorded (Table 1).

Hydrodynamic flow, sedimentation rate and benthic composition are environmental factors known to affect parrotfishes' habitat and food, influencing their abundance

Fig. 2 Records of Brazilian *Scarus* at **A**) Ponta da Sapata (*S. trispinosus*; video-frame), Fernando de Noronha Archipelago, **B**) and **C**) at Farol 1 tidepool (Two juveniles and an adult of *S. trispinosus*- photos, respectively, by Luísa Queiroz and Drausio Veras), Rocas Atoll, and **D**) and **E**) at biogenic reefs of the Davis seamount (Terminal and initial-phases of *S. zelindae*; photos by R.B. Francini-Filho), Vitória-Trindade Chain



patterns, from small to large spatial scales, and for the juveniles and adults (Bonaldo et al. 2014). Most researches dealing with feeding behavior and gut analysis of parrotfishes indicate a diet based on detritus, epilithic algal communities (turf algae), macroalgae, corals and sponges (Ferreira and Gonçalves 2006; Francini-Filho et al. 2010; Bonaldo et al. 2014; Pereira et al. 2016). On the other hand, a recent review of parrotfishes' feeding biology indicated them as microphages, targeting cyanobacteria and other protein-rich autotrophic microorganisms living associated with the macro-organisms targeted (Clements et al. 2016). These food sources are not limiting factors along the Brazilian coast and oceanic islands (e.g. Krajewski and Floeter 2011; Pinheiro et al. 2011; authors observation). Moreover, *Scarus* seems to have a higher feeding rate and assimilation efficiency than Southwestern Atlantic *Sparisoma* species (e.g. Bruggemann et al. 1994). Therefore, the hypothesis of food scarcity does not appear to fully explain the absence of colonization of these oceanic islands (Joyeux et al. 2001).

Albeit exhibiting a wide range of social and mating behaviors (Streelman et al. 2002), parrotfishes' ecological and reproductive traits (e.g. social and breeding behavior) are strongly associated with habitat and do not differ consistently between parrotfish sister lineages (Choat et al. 2012). Reproductive output, due to its large dependence on body shape and size (Sadovy 1996), is expected to depend more on ontogeny than phylogeny (between lineages). Dispersal potential is not expected to differ consistently between the Southwestern Atlantic parrotfishes as both *Scarus* and *Sparisoma* have pelagic spawning and a long larval duration (Atlantic *Sparisoma* mean 50–60 days; Pacific *Scarus* 28 days; Robertson et al. 2006; Winters et al. 2010; Luiz et al. 2012, 2013). The existence of *Scarus* populations established in other oceanic islands of the Atlantic Ocean, including *S. trispinosus*' sister species *S. guacamaia* Cuvier, 1829 at Bermuda (Smith-Vaniz et al. 1999), shows that this genus is capable of reaching and surviving in isolated oceanic areas. In fact, similarly to *Sparisoma* species, both Brazilian *Scarus* are distributed along the whole Brazilian continental shelf, from Maranhão (0°52'S, 44°15'W) to Santa Catarina (27°30'S, 48°W) states. This includes mid-shelf habitats, such as Abrolhos Archipelago and Manuel Luís Reefs, which are located near large biogenic reef systems (Francini-Filho et al. 2013; Moura et al. 2016), respectively, 60 and 86 km from the shoreline. Thus, the hypothesis of limitation in reproductive output or dispersal traits is also not expected to cause the colonization and establishment constrain in the Southwestern Atlantic oceanic reef environments.

Habitat associations have a central role in explaining patterns of parrotfish distribution (Choat et al. 2012). The sister species of Brazilian *Scarus*, *Scarus guacamaia* and *S. taeniopterus* were reported to be associated with mangroves and shallow habitats as early juveniles in some parts of the

Great Caribbean (Nagelkerken et al. 2000; HT Pinheiro pers. obs.) with a dependence on coastal shallow habitats, not found or limited at oceanic islands, and also known as a limiting factor for reef fish establishment at Trindade Island (Pinheiro et al. 2015; Mazzei et al., in prep.). Habitat requirements seem a more plausible hypothesis regarding the establishment and maintenance of the Brazilian *Scarus* around oceanic islands. Moreover, environmental barriers between continental shelf and oceanic reef habitats, such as superficial currents (Brazil and North Brazil) along the outer shelf and slope, could sustain the insular isolation (Rocha 2003, Rocha et al. 2005). These superficial currents may act as ecological barriers, constraining larval flow between the continental and oceanic domains, as proposed by Pinheiro et al. (2015) for the VTC seamounts and islands reef fish assemblages.

Although there is little evidence for some ecological and connectivity limitations such as dispersal ability and niche breadth, density-dependent processes also may favor the presence of *Sparisoma* populations' over *Scarus* at Southwestern Atlantic oceanic islands. In this case, the large observed differences in abundance between the genera could simply imply a smaller frequency of mating and, therefore, a smaller amount of *Scarus* larvae reaching the oceanic reef environments from the continental shelf. It is possible that larval pulses are so scarce that they do not withstand the high mortality rates naturally associated with this fragile life phase (Leis 1991). Even when these larvae manage to get to the open ocean (Stocco and Joyeux 2015), they may not come in sufficient numbers for establishing oceanic populations within the Southwestern Atlantic.

Therefore, the juvenile and adult vagrants of *S. trispinosus* observed seem to result from a punctuated colonization event, a common outcome of the immigration-extinction dynamic process that regulates insular community richness and composition (MacArthur and Wilson 1967; Rose and Polis 2000). The isolation and area of islands affect not only the species colonization rates but also the stability of populations (Mellin et al. 2010). The ability of species to establish populations upon arrival is more important than dispersal for their maintenance (Keith et al. 2015). After the first observation of *S. trispinosus* at Rocas Atoll, its presence has been constant over the recent years of monitoring (2014–2017). Only continuous ecological monitoring will be able to answer whether *S. trispinosus* will be a recognized member of the Atoll Rocas ichthyofauna or not. Conversely, many specimens of *S. zelindae* (mainly terminal phase) were found on the Davis seamount, suggesting a possible adapted and self-sustained population on this oceanic coralline reef area.

Although Brazilian oceanic sites are partially protected as marine reserves, parrotfish populations are under intense fishing pressure in the continental coast, with abundance reduction being recorded everywhere during recent decades (Floeter et al. 2006; Bender et al. 2014). Indeed, local

fisheries, mainly by spearfishing, normally target adult *Scarus*, and they are becoming functionally extinct in many localities along the Brazilian coast, remaining abundant in few core areas (Floeter et al. 2006; Bender et al. 2014; Pereira et al. 2016). This scenario can influence density-dependent habitat selection processes, with consequences on growth, survival and reproduction (Lindberg et al. 2006), also affecting colonization and population establishment. As a consequence, *S. trispinosus* and *S. zelindae* have already been placed on the national red list as, respectively, endangered and vulnerable (MMA 2014). Thus, the established depletion along the coast gives more uncertainty on potential population growth and expansion through oceanic reef environments around the Southwestern Atlantic.

The singular biogeographic patterns found in Southwestern Atlantic oceanic reef environments are also evidence that we still know little about the dispersal and colonization processes that precede establishment (e.g. juvenile habitat requirements). Our new records represent baseline information for monitoring the establishment and persistence of parrotfishes at oceanic localities, and are fundamental for a proper assessment of the impact of the arrival of these large nominally herbivorous fishes in natural communities.

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Author contributions EFM, SRF and CELF designed the research; EFM, HTP, RAM, CELF, SRF, JCJ, DPV and LQ collected the data; EFM, HTP and RAM wrote the text and made the analysis; CELF, SRF and JCJ reviewed the text and analysis.

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