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Bernardi & Carlos E. L. Ferreira**

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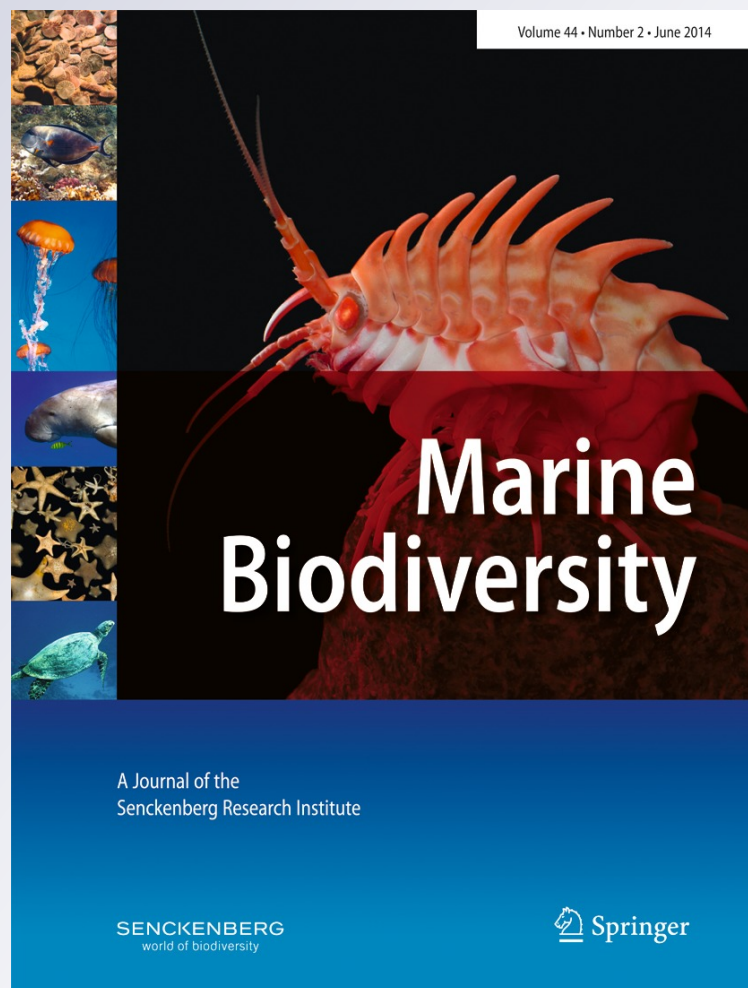
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The occurrence of *Sparisoma frondosum* (Teleostei: Labridae) in the Cape Verde Archipelago, with a summary of expatriated Brazilian endemic reef fishes

Rui Freitas · Osmar J. Luiz · Pericles N. Silva ·
Sergio R. Floeter · Giacomo Bernardi ·
Carlos E. L. Ferreira

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Abstract The occurrence of the Brazilian endemic parrotfish *Sparisoma frondosum* is confirmed for the Cape Verde Archipelago, in the Tropical Eastern Atlantic. In total, 12 species of reef fishes previously thought to be either endemic or originated in the Brazilian Province have been recently recorded as vagrants in the southern Caribbean and in West African offshore islands. We suggest that the seasonal and somewhat overlooked North Equatorial Countercurrent should receive

more attention as a potential dispersal route for marine organisms crossing the Atlantic in a west–east direction.

Keywords Dispersal · Biogeography · New record · Trans-Atlantic · North Atlantic countercurrent

Introduction

Dispersal, defined as the movement and subsequent reproduction of organisms from one area to another, is fundamental to the shaping of patterns of diversity and composition of species within communities (Vellend 2010). The movement of organisms among populations is an important process that promotes species survivorship. For example, dispersal enhances genetic connectivity, which provides a way of escaping local environmental changes and facilitates the exploitation of resource pulses (Nathan et al. 2008). Moreover, dispersal enhances the probability of geographic range expansion, eventually giving rise to sibling species if genetic isolation is maintained (Hodge et al. 2012). Although species' distribution ranges are established during a long evolutionary history and shaped by ecological and physical barriers, events of individuals dispersing out of an established distribution are not exceptional, especially in the marine realm (Gaines et al. 2009). In fact, as the configuration of oceans and continents changes through time, invasions became an expected and widespread process (Vermeij 1991, 2005).

In the Atlantic Ocean, several biogeographic provinces were defined using endemism levels of reef fish species, which are maintained by oceanographic barriers to dispersal (Floeter et al. 2008). However, those barriers are variable in their effectiveness during geologic time (Rocha 2003) and affect different subsets of species depending on their biological

R. Freitas
Departamento de Engenharias e Ciências do Mar, Universidade de Cabo Verde, CP 163 Mindelo, Cabo Verde

O. J. Luiz
Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

P. N. Silva
Instituto Nacional de Desenvolvimento das Pescas, CP 132 Mindelo, Cabo Verde

S. R. Floeter
Departamento de Ecologia e Zoologia, Universidade Federal de Santa Catarina, Florianópolis, SC 88010-970, Brazil

G. Bernardi
Department of Ecology and Evolutionary Biology, University of California, Santa Cruz, CA 95060, USA

C. E. L. Ferreira (✉)
Departamento de Biologia Marinha, Universidade Federal Fluminense, Niterói, RJ 24001-970, Brazil
e-mail: carlosferreira@id.uff.br

R. Freitas
Departamento de Ecología Y Biología Animal,
Facultad de Ciencias del Mar, Universidad de Vigo,
36310 Vigo, Pontevedra, Spain

characteristics (Luiz et al. 2012). Therefore, the biogeographic patterns in the Atlantic Ocean that we see today are the result of a dynamic process including several periods of isolation interspersed with phases of higher connectivity (Floeter et al. 2008; Rocha et al. 2008).

The Brazilian Province harbors roughly 470 species of reef fishes, from which 23 % (109 species) are endemic (Floeter et al. 2008). It encompasses all the tropical South-Western Atlantic (including its oceanic islands), being separated from the Greater Caribbean (GC) Province by the Amazon-Orinoco

Plume (AOP), a huge freshwater and sediment outflow that comes from the Amazon river into the NW South America's shore; and from the Tropical Eastern Atlantic (TEA) Province by the Mid-Atlantic barrier (MAB), the large expanse of deep ocean between the African continent and the Americas (Luiz et al. 2012).

During the last two decades, knowledge about the Brazilian endemic marine fishes has grown exponentially (e.g., Moura and Sazima 2003; Moura et al. 2001; Rocha 2004), with the realization that some common and widespread “endemics”

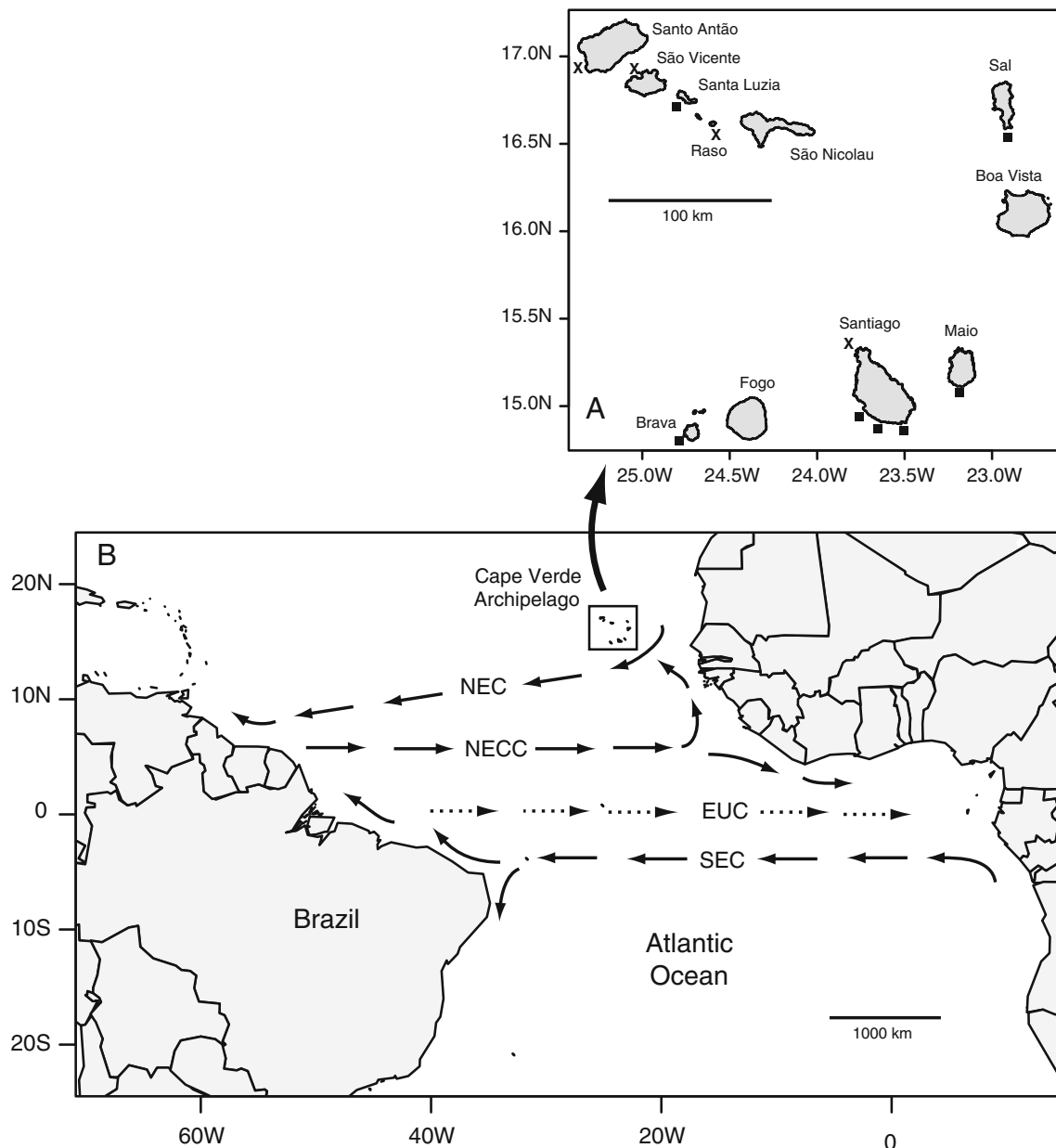


Fig. 1 **a** The occurrence of *Sparisoma frondosum* in Cape Verde Islands. × position of *S. frondosum* captures in Cape Verde (Raso islet; Tarrafal de Monte Trigo Bay, Santo Antão Is.; Ilhéu dos Pássaros, São Vicente Is. and Tarrafal area, north of Santiago Is.) and ■ other additional areas where *S. frondosum* has been reported in the Archipelago (Saragaça, São Vicente;

south of Santa Luzia, Brava and Maio Islands; Santa Maria bay, Sal Is. and Santiago Island; lighthouse Praia, Cidade Velha and Porto Mosquito), **b** Major pattern of currents and countercurrents directly related to main pathway for dispersal between the Brazilian Province and the Caribbean, and between the Western and Eastern Atlantic

have been found beyond the border of the Brazilian Province, mainly at the southern Caribbean and in the African offshore islands (Rocha 2002, 2003; Wirtz et al. 2007). Although these expatriated endemics are mostly found as vagrant waifs, monitoring their presence is important in order to understand the processes occurring at the border of species geographic ranges (Dythan 2009), i.e., the establishment and expansion of new populations and population sinks where their occurrence are dependent on a flow of individuals from distant places.

Here, the occurrence of the Agassiz's parrotfish, *Sparisoma frondosum* (Agassiz 1831), a species previously considered to be endemic to the Brazilian Province (Moura et al. 2001; Robertson et al. 2006), is reported for the first time from the Cape Verde Archipelago. In addition, we have reviewed records of expatriated Brazilian reef fish endemics and provide a summary of the species recorded and the localities in which they were found.

The parrotfishes of Cape Verde Archipelago

Located in the Tropical Eastern Atlantic Province (Briggs and Bowen 2012), the Cape Verde Archipelago is of volcanic origin and comprises 10 islands and several islets (Fig. 1a). Cape Verde's coastline totals 965 km and 5,934 km² of island shelf (depth <200 m) (Bravo de Laguna 1985; DGMP 1998). Three species of parrotfish (subfamily Scarinae) were previously known from the Cape Verde Archipelago: *Scarus hoefleri* (Steindachner 1881), *Sparisoma cretense* (Linnaeus 1758), and the recently described *Sparisoma choati* Rocha, Brito and Robertson 2012. The former two are very distinctive species while *S. choati* has been historically misidentified as *Sparisoma rubripinne* (Valenciennes 1840) in Cape Verde and in Senegal (cf. Randall 1981; Brito et al. 1999).

The probable earliest mention to *S. frondosum* in the Cape Verde Archipelago was made by Morri et al. (2000). However, they used the name *Sparisoma* cf. *strigatum* for the specimen they recorded at Sal Island, Cape Verde, as they considered it similar to *S. strigatum* (Günther 1862), which is endemic to the Central Atlantic Islands of St. Helena and Ascension. In 2008, *S. frondosum* was observed and photographed off northern Santiago Island (IP female by P. Wirtz, CCMAR, University of Algarve, personal communication) and in August 2009 off southern Brava Island (TP male by D. Cothran, Undersea Specialist at Lindblad Expeditions, personal communication). In February 2010, a female (27 cm TL) was captured by spearfishing (Fig. 2) and in April 2011 a male (32 cm TL) was caught. Both were collected off Raso islet, in the northwest of the Cape Verde Archipelago (Fig. 1a), at depths between 5 and 10 m. Muscle tissues was preserved in 96% alcohol and sent for genetic analysis to the Department of Ecology and Evolutionary Biology of the University of California at Santa Cruz, USA. Its taxonomic identity was



Fig. 2 *Sparisoma frondosum* (Agassiz 1831) specimens caught by spearfishing in 5–10 m depth, both in same area in south of Raso islet (16.61°N, 24.60°W) in Cape Verde (Eastern Atlantic). *Above* initial-phase spawned female (27 cm TL) captured on 27 February 2010; *below* terminal-phase male (32 cm TL) captured on 16 April 2011

confirmed as *S. frondosum* based on 12S rRNA and 16S rRNA sequences (GenBank accession numbers JX645341–JX645342). A second group of specimens, obtained in March and April 2010 (São Vicente and Santo Antão islands, respectively) by SCUBA at 20–30 m depth, were subjected to biometric measurements, meristic counts, and comparative morphology by J. González and the first author, according to González (1991) and González et al. (1994), and deposited in the Canary Institute of Marine Science, Canary Islands (ICCM 1029–1030). An additional specimen was captured at Tarrafal, northern Santiago Island, in the south of the Cape Verde Archipelago, preserved in formalin and deposited at the Munich Natural History Museum, Germany (ZSM 40374).

The genetic identification was supported by morphological analysis of the specimens. *S. frondosum* shows some distinctive characteristics, i.e., terminal-phase individuals lacking the crescent marking on the caudal fin margin and the turquoise area adjacent to the pectoral fin, as well as the pale-yellow area on the axial pectoral-fin, a pale spot on the upper part of the caudal peduncle in both IP and TP live individuals, and reddish dorsal, caudal, anal, and pelvic fins in IP (Moura et al. 2001).

In the Cape Verde Archipelago, small groups of 2–3 *S. frondosum* females have often been found together. All females captured to date carried mature eggs. Males were rare and moved to deeper and cooler waters when encountered. Nevertheless, 4 males accompanying harems of about 30 females were recently registered in Raso islet (T. Melo, NGO Biosfera I, Cape Verde, personal communication, November 2012) in deeper areas, during an probable reproductive season (Afonso et al. 2008). Consequently, the spearfishing of males parrotfish is facilitated in Raso islet, where little or no insular shelf is found. In recent years, the

frequency of *S. frondosum* records in the Archipelago has increased, especially in the north-western islands from Santo Antão to São Nicolau. However, underwater visual census of fishes conducted throughout the Cape Verde Islands in September 1998 (two sites per island) did not register any individual (A. Brito, University of La Laguna, personal communication). Nevertheless, it is quite common around Santiago Island and occasional at Sal Island. There is an apparent ecological partitioning between *S. frondosum* and *S. choati*. The latter is common in shallow water over rubble (down to

about 15 m depth), whereas *S. frondosum* is usually observed (together with *S. cretense*) in infra-littoral deeper water, along walls covered with the tube coral *Tubastrea* (P. Wirtz, CCMAR, University of Algarve, personal communication). Due to potential misidentifications with the recently described *S. choati*, it is not currently possible to discern whether *S. frondosum* has recently arrived at the Cape Verde Archipelago or if it is a long-term resident. Our records suggest that it may have been in Cape Verde at least since the late 1990s, perhaps longer.

Table 1 Reef fish species of putative Brazilian origin recorded outside Brazilian Province

Family/species and authority	Brazilian Province (BP) distribution Mainland/Oceanic Islands	Distribution outside BP	Reference
Congridae			
<i>Heteroconger camelopardalis</i> Lubbock 1980	Coast 03°–7°S/Fernando de Noronha	Tobago, Saba, Ascension	Robertson and Van Tassel 2012
Chaenopsidae			
<i>Emblemaria australis</i> Ramos, Rocha and Rocha 2003	Coast 03°–11°S/–	Venezuela	Robertson and Van Tassel 2012
Haemulidae			
<i>Anisotremus moricandi</i> (Ranzani 1842) ^a	Coast 02°–20°S/–	Venezuela, Curacao, Colombia, Panama, Costa Rica	Rocha 2002; Robertson and Van Tassel 2012
Labridae			
<i>Sparisoma amplum</i> (Ranzani 1841) ^b	Coast 01°–28°S/ASPSP, Fernando de Noronha, Rocas Atoll and Trindade Is.	St. Vincent	Wilk 2003
<i>Sparisoma axillare</i> (Steindachner 1878)	Coast 01°–28°S/ASPSP, Fernando de Noronha, Rocas Atoll and Trindade Is.	Venezuela	Robertson et al. 2006
<i>Sparisoma frondosum</i> (Agassiz 1831)	Coast 01°–28°S/ASPSP, Fernando de Noronha, Rocas Atoll and Trindade Is.	Cape Verde Archipelago	Present work
Pomacanthidae			
<i>Centropyge aurantonotus</i> Burgess 1974	Coast 03°–28°S/Fernando de Noronha and Trindade Is.	Barbados, Bonaire, Curacao, St. Lucia, São Tomé	Blasiola 1976; Rocha 2002; Robertson and Van Tassel 2012; Wirtz et al. 2007
Pomacentridae			
<i>Chromis jubauna</i> Moura 1995	Coast 03°–28°S/Trindade Is.	Tobago	Rocha 2003; Robertson and Van Tassel 2012
<i>Stegastes pictus</i> (Castelnau 1855)	Coast 01°–28°S/Fernando de Noronha and Trindade Is.	Antigua, Tobago	Rocha 2002; Robertson and Van Tassel 2012
Ptereleotridae			
<i>Ptereleotris randalli</i> Gasparini, Rocha and Floeter 2001	Coast 01°–24°S/–	Barbados, Bonaire, St. Vincent, Tobago	Rocha 2002; Robertson and Van Tassel 2012
Acanthuridae			
<i>Acanthurus bahianus</i> Castelnau 1855	Coast 01°–28°S/Fernando de Noronha, Rocas Atoll and Trindade Is.	Cuba	Castellanos-Gell et al. 2012
Tetraodontidae			
<i>Canthigaster figueiredoi</i> Moura and Castro 2002	Coast 01°–28°S/Fernando de Noronha, Rocas Atoll and Trindade Is.	Tobago, Venezuela	Rocha 2002; Robertson and Van Tassel 2012

^a Although *A. moricandi* meets our criteria (greater range in Brazil) to be included among the Brazilian endemics, its range in the southern Caribbean is only slightly smaller than in Brazil (2,400 vs. 2,850 km linear distance) raising uncertainty as to their province of origin

^b This occurrence is based on a single photograph of an individual with coloration that matches the diagnosis for the Brazilian form. The lack of voucher specimens and the genetic proximity between *A. amplum* with its Caribbean form *S. viride* caution that this record needs to be better substantiated

Expatriated Brazilian endemics and dispersal routes

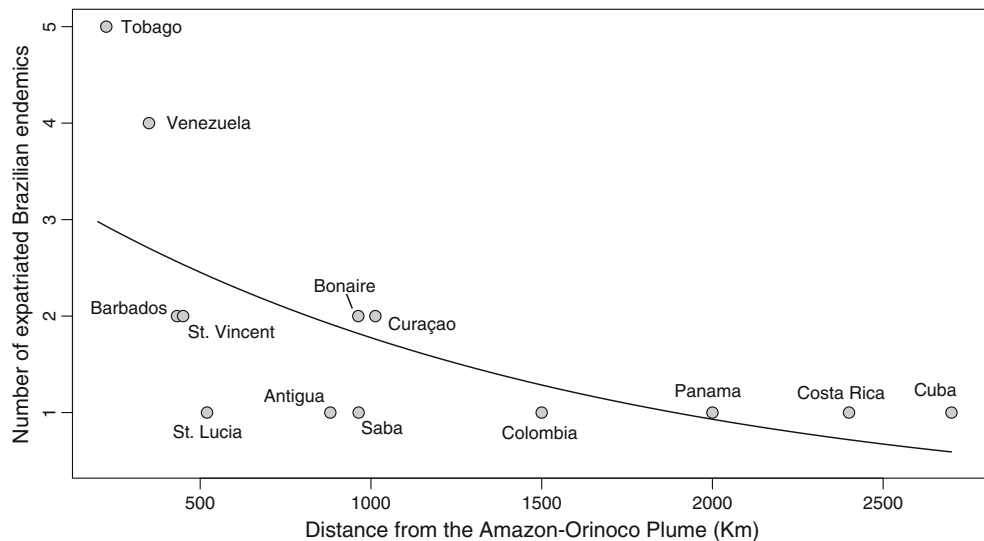
Research on Brazilian reef fishes has increased considerably during the past two decades. More detailed distribution patterns together with new species descriptions have led to a reassessment of the endemism level in the Brazilian Province (Floeter and Gasparini 2000; Moura and Sazima 2003; Floeter et al. 2001, 2008). In addition, 12 species previously considered to be endemics from Brazil have been found at the southern end of the Caribbean Province and offshore islands off the western border of the TEA (Table 1). Because these species have a broad distribution in Brazil but are recorded at only a few locations outside the Brazilian Province, it is assumed that they have recently crossed the oceanographic barriers that separate those Provinces (Joyeux et al. 2001; Rocha 2003). Moreover, the negative correlation between the number of Brazilian endemics recorded from a single southern Caribbean island and the island's distance to the border of AOP illustrates the spillover of species from Brazil into the Caribbean Province (Fig. 3).

Migration from Brazil to southern Caribbean is facilitated by the Northern Brazil Current, which flows in a general south-north direction along the Amazon area continental shelf (Rocha 2003). On the other hand, the migration of species from Brazil to the TEA is less straightforward and probably a much less common event. Paradoxically, while the bulk of trans-Atlantic shore species are considered to have migrated in a west-east direction (Vermeij and Rosenberg 1993; Floeter et al. 2008), most of the superficial currents on the tropical Atlantic flow westward from Africa to Brazil (Stramma 2001). Recent and past invasion events of reef fishes following this route have been described elsewhere (Luiz et al. 2004; Leite et al. 2009). The Equatorial Undercurrent (EUC) that flows

underneath superficial currents in the opposite direction along the Equator is considered the main mechanism of larval transport from the Caribbean and/or Brazil to TEA (Fig. 1b) (Joyeux et al. 2001; Muss et al. 2001; Wirtz 2003). However, the EUC that flows to the Gulf of Guinea is relatively deeper and colder (50–200 m, ≈ 20 °C; Muss et al. 2001) than the normal range of the majority of tropical reef species, which may restrict larval transport if the larvae have the same environmental thresholds to survival as the adults.

Nevertheless, as Scheltema (1986) pointed out, the North Equatorial Countercurrent (NECC) is also a potential conduit for eastward larval movement that has been largely overlooked by marine biogeographers. NECC is a superficial tropical current that runs from Northern South America and Southern Caribbean towards West Africa between the latitudes 3° and 10°N (Fig. 1b) (Philander 2001). Although the NECC is particularly strong between July and September, it disappears during the rest of the year (Philander 2001). Because of the NECC's high seasonality, it is often ignored in maps showing main current patterns in the Atlantic (e.g. Muss et al. 2001) and therefore may have been underestimated as a possible dispersal route (Scheltema 1986). *S. frondosum* has not been found in other regions of the TEA despite regular biological expeditions to the Gulf of Guinea (Afonso et al. 1999; Wirtz 2003; Wirtz et al. 2007). The limited occurrence of *S. frondosum* in West Africa to the Cape Verde Archipelago is better explained by transport via NECC because species transported by the EUC are expected to be found first in the Gulf of Guinea before further spread along the TEA. The MAB is one of the most potent barriers to reef fish species movement in the world (Mora et al. 2012). Luiz et al. (2012) have demonstrated that rafting in association with flotsam is an important mechanism linked to trans-Atlantic

Fig. 3 Number of species of putative Brazilian origin found in southern Caribbean localities in regards of the distance to the border of AOP barrier. The *bold line* represents fitted values estimated by a Poisson regression



movement for reef fishes. However, parrotfishes are generally not associated with rafting, suggesting that NECC indeed may have a more significant role in marine larvae migration across the Atlantic than previously thought.

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