Inferring labrid functional roles through morphological and ecological traits

G. C. Cardozo-Ferreira[1,*], R. M. Macieira[1,2], R. B. Francini-Filho[3], J. C. Joyeux[1]

[1]Laboratório de Ictiologia, Departamento de Oceanografia e Ecologia, Universidade Federal do Espírito Santo, Vitória ES, Brazil
[2]Laboratório de Ecologia Marinha, Complexo Biopráticas, Universidade Vila Velha, Vila Velha ES, Brazil
[3]Departamento de Engenharia e Meio Ambiente, Universidade Federal da Paraíba, Rio Tinto PB, Brazil

ABSTRACT: The functional approach, using morphology and/or ecological traits, allows grouping of species that play similar roles in an ecosystem. Although species may have unique functions, some may overlap in key morphological traits, leading to similar functions (i.e. functional redundancy). To understand the functional roles of southwestern Atlantic labrids, we analyzed 21 species, focusing on morphological characteristics linked to habitat use, feeding habits and swimming ability, and further taking ontogeny into account by analyzing 3 size categories (small, medium and large) that vary in life history aspects. A comprehensive functional analysis using 11 functional traits defined according to 12 morphological measurements was performed to generate a consensus tree that segregated species into 9 functional groups. Body elongation was the most important characteristic separating parrotfishes from wrasses. Small size class was separated from medium and large size class wrasses and parrotfishes through eye size and eye positioning, respectively. *Thalassoma noronhanum* was grouped with invertivorous species, despite its classification as a planktivore in previous studies. This species, together with *Xyrichtys splendens* and *Scarus zelindae*, showed no size-related shifts in functional role with increasing size. Although recognized as members of different trophic guilds, different size classes of different labrid species may play similar functional roles. This suggests the need for taking size and species identity into account when measuring functional diversity and redundancy in reef ecosystems, key features for maintaining the health and robustness (i.e. resistance/resilience) of reef systems.

KEY WORDS: Functional morphology · Atlantic labrids · Wrasses · Parrotfishes · Ontogeny

INTRODUCTION

Labridae (including wrasses, parrotfishes and odacines) is one of the most representative families in terms of species richness on reef systems. Its 637 recognized species are morphologically highly diverse and harbor a great variety of shapes, behaviors and ecological characteristics (Walker & Westneat 2002, Kuiter 2010). Parrotfishes and odacids (tribes Scarini and Odacini, respectively) were previously classified in families separate from Labridae, but recent comprehensive phylogenetic studies have now included all of them within Labridae (Clements et al. 2004, Westneat & Alfaro 2005, Baliga & Law 2016). In the southwestern Atlantic (SWA), 26 labrid species

(distributed among 11 genera) are recognized, 12 of which are endemic to the Brazilian Province (composed of the Brazilian coast and oceanic islands; Floeter et al. 2008). Morphological diversity might be a result of the evolutionary history of different lineages or the emergence of morphological novelties inside a clade (Wainwright 2007). Labridae lineages provide many examples of morphological characteristics leading to diversification (see Alfaro et al. 2005), as exemplified by clades dominated by herbivores, in particular scrapers/bioeroders (e.g. *Scarus* and *Sparisoma*), carnivores (e.g. *Doratonotus*), planktivores (e.g. *Clepticus*) and predators of benthic invertebrates (e.g. *Bodianus*, *Halichoeres* and *Xyrichtys*).

The evolution of many traits closely linked to feeding habits and swimming ability is detectable in Labridae phylogeny (Choat 1991, Streelman et al. 2002, Westneat & Alfaro 2005). Studies on functional ecology have pointed to fin shape and size, as well as body shape, as being highly influential in fish swimming ability and habitat use (Bellwood & Wainwright 2001, Fulton & Bellwood 2002, Wainwright & Bellwood 2002, Albouy et al. 2011). In addition, feeding ecology is mainly influenced by mouth gape (i.e. depth and width) and orientation (i.e. inferior or superior), as well as dentition arrangement and type (i.e. coalesced, caniniform or incisiform) (Gatz 1979, Clifton & Motta 1998, Albouy et al. 2011). Body shape and size may influence the preference for diurnal microhabitats and sleeping sites. Wrasses (elongated and relatively small) tend to hide in crevices or bury themselves within the sandy bottom (Potts 1973, Nishi 1989), while parrotfishes (taller and more robust) often lie on the bottom of the reef. Although each species (and ontogenetic stages) may have unique functions in the environment, different species may have overlapping traits and play similar ecological roles (Halpern & Floeter 2008), thus being pooled into the same functional groups. The more species within each functional group, the higher the functional redundancy. For instance, if 2 coexisting species perform the same function, the absence of one species will not cause the loss of that function in the ecosystem (Bellwood et al. 2004, Halpern & Floeter 2008). Therefore, increased functional redundancy is expected to result in a more stable ecosystem (Guillemot et al. 2011).

Functional roles, resource use and performance may be quantified by measuring ecologically relevant functional traits of species (Bellwood & Choat 1990, Bellwood et al. 2002). Community-level studies on reef fish have been conducted, aimed at distinguishing species' functional roles (Ferreira et al. 2004, Halpern & Floeter 2008). However, the within-family functional ecology remains poorly explored for reef fishes, possibly because great morphological similarities would lead to functional overlap. Nonetheless, detailed studies on functional traits/roles would provide evidence for coexistence rules, trophic interactions and redundancy within families, as well as different impacts of species on the ecosystem (Dumay et al. 2004). Understanding the functional roles of fish species in reef ecosystem health is important for conservation issues, since ecosystem equilibrium depends, partially, on well-preserved functions and species redundancy within functional groups (Bellwood et al. 2004).

Here, we evaluated the functional differentiation among 21 SWA labrid species based on morphological traits and their correlation with habitat use (e.g. eye position, linked to the vertical position in the water column), feeding habits (e.g. oral width and gape surface, related to prey size) and swimming ability (e.g. caudal peduncle throttling, related to caudal propulsion efficiency). Conversely, we inferred how much these different and phylogenetically related species are similar based on morphology and performance profiles, and how this affects different functional roles. In addition, we included a size-class variation by considering intra- and interspecific changes among small, medium and large size classes, which could represent different ontogenetic stages.

MATERIALS AND METHODS

Data collection

Morphometric measurements were performed on 158 specimens of 21 labrid species from 9 genera available in major ichthyological collections for Brazilian reef fishes (CIUFES, MZUSP, and ZUEC-PIS; collection acronyms follow Sabaj-Pérez 2014). Changes in form due to preservation processes are stronger for smaller individuals (i.e. shrinking) than larger ones (Parker 1963, Fox 1996, Fey & Hare 2005). Deformation is highest in the first 3 d of preservation and reduces to less than 0.1% after 90 d (Fey & Hare 2005). All our specimens were fixed and stored using the same method (10% formalin to 70% ethanol) for at least 90 d of preservation, thus minimizing the variation and increasing homogeneity within samples. Five species found in the Brazilian Province (Floeter et al. 2008) were not included here due to their rarity, lack of ontogenetic stages or non-availability in ichthyological collections: *Bodianus insularis* Gomon & Lubbock 1980, *Halichoeres radiatus* (Linnaeus 1758), *Halichoeres sazimai* Luiz, Ferreira & Rocha 2009, *Lachnolaimus maximus* (Walbaum 1792) and *Nicholsina usta* (Valenciennes 1840). Size-class classification of species was based on body size using the maximum standard length (SL_{max}) according to available literature, except in cases when this value was less than our own data (Table 1). Small sized fishes (S) were represented by individuals with $SL < \frac{1}{3}$ of SL_{max}, medium-size (M) were between $\frac{1}{3}$ and $\frac{2}{3}$ of SL_{max}, and large-sized fishes (L) showed $SL > \frac{2}{3}$ of SL_{max} (Nagelkerken & van der Velde 2002).

Table 1. Size limits (mm) between small and medium (S/M) and medium and large (M/L) size classes of 21 southwestern Atlantic labrid species. The maximum standard length (SL_{max}) reached by the species and its reference are shown; n: number of individuals in each size class. Trophic guilds are based on Randall (1967), Westneat (1995) and Ferreira et al. (2004): MIF: mobile invertebrate feeders; PLK: planktivores; MCAR: micro-carnivores; HERB: herbivores

Species	Size limits (mm)			n S, M, L	Reference for SL_{max}	Trophic guild
	S/M	M/L	SL_{max}			
Bodianus pulchellus (Poey, 1860)	77	154	232	3, 3, 3	Gomon (2006)	MIF
Bodianus rufus (Linnaeus, 1758)	126	252	378	3, 3, 3	Present study	MIF
Clepticus brasiliensis Heiser, Moura & Robertson, 2000[a]	82	165	248	2, 3, 3	Heiser et al. (2000)	PLK
Cryptotomus roseus Cope, 1871	43	88	130	1, 1, 3	Robins & Ray (1986)	HERB
Doratonotus megalepis Günther, 1862	30	60	100	3, 3, 1	Kuiter (2010)	MCAR
Halichoeres brasiliensis (Bloch, 1791)[a]	131	262	395	3, 3, 3	Rocha & Rosa (2001)	MIF
Halichoeres dimidiatus (Agassiz, 1831)[a]	90	180	270	3, 3, 3	Present study	MIF
Halichoeres penrosei Starks, 1913[ab]	40	80	119	3, 3, 3	Present study	MIF
Halichoeres poeyi (Steindachner, 1867)	61	123	183	3, 3, 3	Present study	MIF
Halichoeres rubrovirens Rocha, Pinheiro & Gasparini, 2010 [ab]	77	154	231	1, 1, 3	Rocha et al. (2010)	MIF
Scarus trispinosus Valenciennes, 1840[ab]	200	400	600	1, 1, 3	Moura et al. (2001)	HERB
Scarus zelindae Moura, Figueiredo & Sazima, 2001[ab]	110	220	332	3, 1, 2	Moura et al. (2001)	HERB
Sparisoma amplum (Ranzani, 1841)[a]	130	260	390	3, 3, 3	Moura et al. (2001)	HERB
Sparisoma axillare (Steindachner, 1878)[ab]	145	290	436	3, 2, 3	Present study	HERB
Sparisoma frondosum (Agassiz, 1831)[ab]	115	230	345	3, 1, 2	Moura et al. (2001)	HERB
Sparisoma radians (Valenciennes, 1840)[a]	66	132	200	1, 2, 1	Kuiter (2010)	HERB
Sparisoma rocha Pinheiro, Gasparini & Sazima, 2010[ab]	101	202	305	3, 3, 3	Present study	HERB
Sparisoma tuiupiranga Gasparini, Joyeux & Floeter, 2003[a]	51	104	154	3, 2, 3	Gasparini et al. (2003)	HERB
Thalassoma noronhanum (Boulenger, 1890)[a]	42	85	128	3, 3, 3	Present study	PLK
Xyrichtys novacula (Linnaeus, 1758)	100	200	300	2, 3, 0	Quignard (1966)	MIF
Xyrichtys splendens Castelnau, 1855	46	93	140	1, 3, 3	Kuiter (2010)	MIF

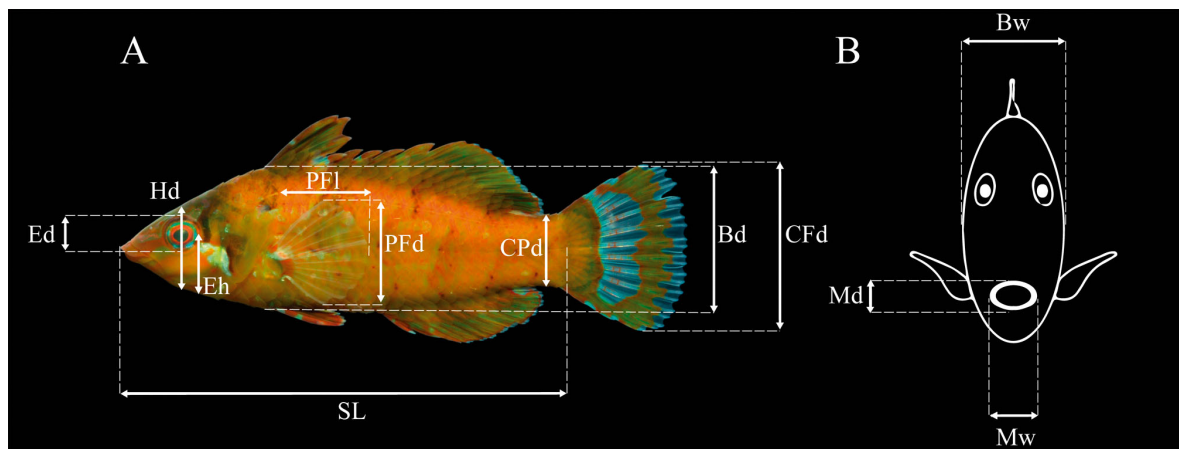[a]Brazilian Province endemic species; [b]Red listed species (MMA 2014)

Fig. 1. Morphometric measurements performed on each specimen. The species model is *Doratonotus megalepis* Günther 1862. (A) Side view; (B) front view. SL: standard length; Ed: eye diameter; Eh: eye height; Hd: head depth; PFl: pectoral fin length; PFd: pectoral fin depth; CPd: caudal peduncle depth; Bd: body depth; CFd: caudal fin depth; Bw: body width; Md: mouth depth; Mw: mouth width

Morphometric measurements and functional traits

A total of 12 morphological measurements (Fig. 1) obtained by using an analogical caliper rule with 0.05 mm precision were used to calculate 11 functional traits (Table 2) (based on Gatz 1979, Fulton et al. 2001, Dumay et al. 2004, Albouy et al. 2011, Claverie & Wainwright 2014).

Two coded variables were added in the analysis considering that (1) herbivorous, carnivorous and planktivorous exert a distinct function (Wikramanayake 1990, Winemiller 1991) and (2) the maximum size of each species/size class is correlated with their functional roles (Bonaldo & Bellwood 2008, Francini-Filho et al. 2008). Species were classified according to their number of teeth and dentition type (DT) (see

Table 2. Functional traits derived from 12 morphometric measurements, with abbreviations (see Fig. 1), formula, ecological meaning and references for selected traits. na: not applicable

Functional trait	Abbreviation	Formula	Ecological meaning
Oral gape surface	Osf	$(Mw \times Md)/(Bw \times Bd)$	Nature/size of captured items (Albouy et al. 2011)
Oral width	Orw	Mw/SL	Size of captured items (Gatz 1979)
Eye size	Edst	Ed/Hd	Prey detection (Albouy et al. 2011)
Eye position	Eps	Eh/Hd	Vertical position in the water column (Gatz 1979)
Body transversal shape	Bsh	Bd/Bw	Vertical position in the water column/hydrodynamism (Gatz 1979)
Pectoral fin shape	PFsh	PFl/PFd	Pectoral fin use for maneuverability (Dumay et al. 2004)
Pectoral fin relative area	PFra	$(PFl \times PFd)/(SL \times Bd)$	Swimming/hydrodynamism (Fulton et al. 2001)
Caudal peduncle throttling	CPt	CFd/CPd	Caudal propulsion efficiency through reduction of drag (Albouy et al. 2011)
Body elongation index	BEi	SL/Bd	Elongated bodies allow swimming closer to substratum (Claverie & Wainwright 2014)
Dentition type	DT	na	Nature of feeding habits (Pouilly et al. 2003)
Size class limit	SClim	na	Size limit between small, medium and large

Pouilly et al. 2003) as follows: (1) species with few (<50), caniniform or conical teeth (associated with biting or cutting food items); and (2) species with many (>50) filiform teeth (associated with scraping or excavating). The second coded variable was the size limit between size classes and the maximum size (see Table 1). For instance, *Bodianus pulchellus* has a SL_{max} of 232 mm; thus, the top limit for the small class (following Nagelkerken & van der Velde 2002, as cited above) is 77 mm, and for the medium class is 154 mm. Therefore, size was coded 77, 154 or 232 depending upon the size class to which the specimen belonged. These limit values were inserted to each size class of each species as a coded variable prior to standardization.

Resource use was classified by assigning species to the trophic categories mobile invertebrate feeders (MIF), planktivores (PLK), micro-carnivores (MCAR) and herbivores (HERB) (see Table 1; Randall 1967, Westneat 1995, Ferreira et al. 2004, Ferreira & Gonçalves 2006).

Statistical analyses

To group species according to morphological similarity and to differentiate the function of each group in the environment, we ran a sequence of 3 analyses. Clustering was performed through a consensus tree using 2 distances (Gower's and Euclidean) and 5 grouping methods (Ward, Single, Complete, unweighted pair group method with arithmetic mean [UPGMA] and weighted pair group method with averaging [WPGMA]) based on functional traits. All variables were centered and reduced (mean = 3; SD = 1) prior to analysis. A similarity profile routine (SIMPROF)

was applied ($\alpha = 0.05$; 9999 permutations) on the groups produced in the consensus tree. SIMPROF uses the final cluster, searching for the best arrangement of branches, calculating between every pair of samples (here, species and respective size class) (Clarke et al. 2008). SIMPROF shows which groups are significantly different from each other by assigning different colors to them. The analysis was performed using the Generalized Functional Diversity Index (GFD) with source codes provided by Mouchet et al. (2008) and using the 'clustsig' package (Whitaker & Christman 2014) implemented in R (R Core Team 2017). To elucidate which variables (traits) drove the differentiation between functional groups, discriminant analyses were run for each dichotomy (see Table 3) and for each group in comparison to all the other species groups (see Table 3). A stepwise method with a maximum number of 22 steps, maximum partial F to enter = 3.84, and maximum partial F to remove = 2.71 was used. Correlation within functional traits was tested through Spearman's rank correlation test (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m588p135_supp.pdf) using R (R Core Team 2017).

RESULTS

The trait-based consensus tree segregated the 21 labrid species into 9 functional groups. Discriminant analyses performed *a posteriori* to the SIMPROF test revealed the body elongation index (BEi) to be the most important trait (Table 3) for separating parrotfishes (tribe Scarini) from wrasses (other tribes), followed by caudal peduncle throttling (CPt) and pectoral fin relative area (PFra). Within parrotfishes, BEi

Table 3. Functional traits characterizing each functional group and examples of species that fit in each group. Groups listed in the first column correspond to the groups assigned in Figs. 2 & 3. Significant traits were detected through discriminant analysis testing each single group against all others. S: small; M: medium; L: large

| Functional group	Characteristic functional traits	Examples
1	Coalesced teeth, higher positioned eye and thicker caudal peduncle	*Sparisoma amplum* (S) and *Sp. axillare* (S)
2	Coalesced teeth, deeper body, smaller species, smaller eye and thicker caudal peduncle	*Sparisoma rocha* (M/L) and *Sp. radians* (M/L)
3	Larger species, thicker caudal peduncle and lower positioned eye	*Scarus trispinosus* (M), *Sp. amplum* (L) and *S. axillare* (L)
4	Elongated body, coalesced tooth and narrow mouth.	*Cryptotomus roseus* (S/M)
5	Narrow mouth, shallow and elongated body, smaller eye, and smaller species	*Halichoeres rubrovirens* (M) and *H. poeyi* (M)
6	Thinner caudal peduncle, higher positioned eye, canine teeth and larger species	*H. brasiliensis* (L) and *H. dimidiatus* (L)
7	Broader mouth, canine teeth and thicker caudal peduncle.	*Bodianus* spp. (M) and *Doratonotus megalepis* (L)
8	Larger eyes and canine teeth	*Thalassoma noronhanum* (S/M/L) and *Halichoeres* spp. (S)
9	Long and wide pectoral fin, deeper and fusiform body and lower positioned eye	*Clepticus brasiliensis* (M/L)
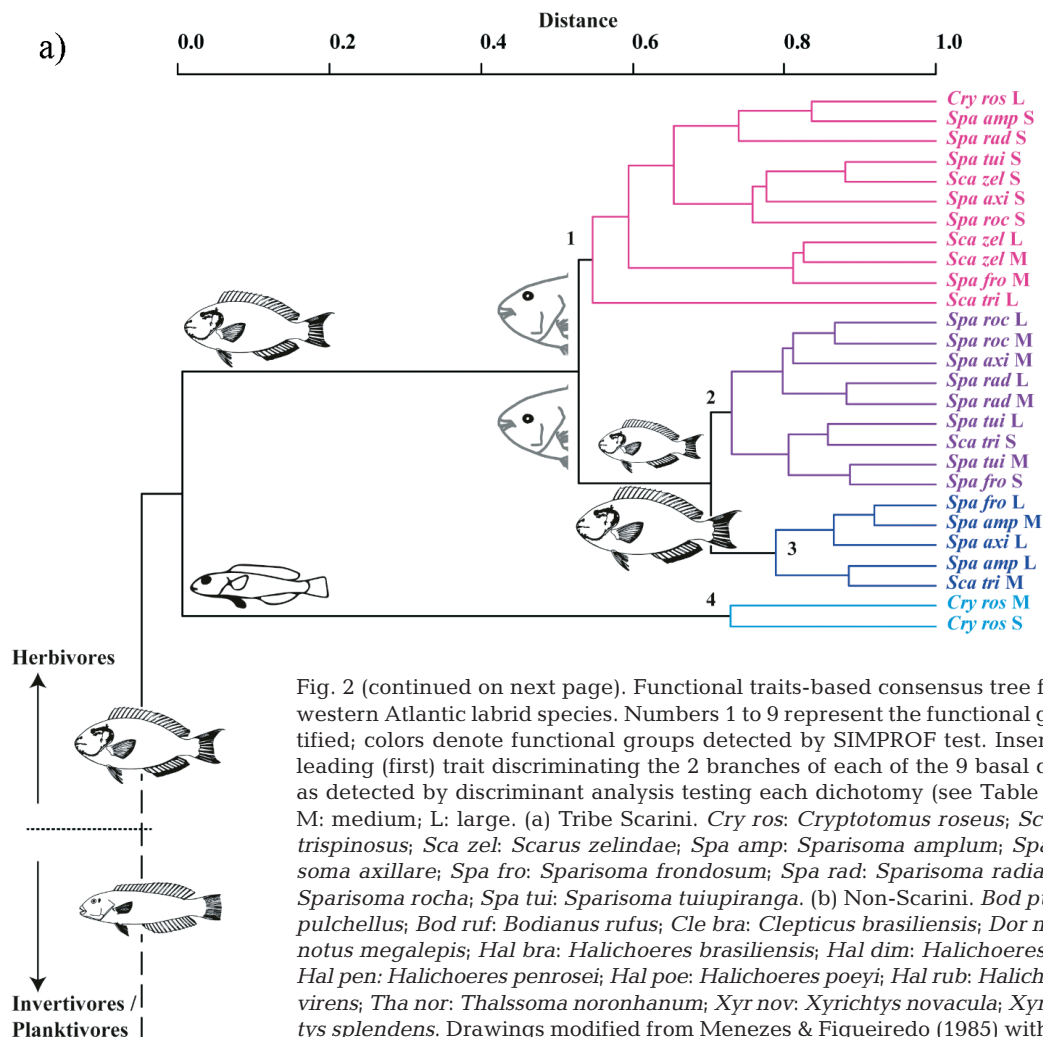
Fig. 2 (continued on next page). Functional traits-based consensus tree for 21 southwestern Atlantic labrid species. Numbers 1 to 9 represent the functional groups identified; colors denote functional groups detected by SIMPROF test. Inserts show the leading (first) trait discriminating the 2 branches of each of the 9 basal dichotomies, as detected by discriminant analysis testing each dichotomy (see Table 3). S: small; M: medium; L: large. (a) Tribe Scarini. *Cry ros*: *Cryptotomus roseus*; *Sca tri*: *Scarus trispinosus*; *Sca zel*: *Scarus zelindae*; *Spa amp*: *Sparisoma amplum*; *Spa axi*: *Sparisoma axillare*; *Spa fro*: *Sparisoma frondosum*; *Spa rad*: *Sparisoma radians*; *Spa roc*: *Sparisoma rocha*; *Spa tui*: *Sparisoma tuiupiranga*. (b) Non-Scarini. *Bod pul*: *Bodianus pulchellus*; *Bod ruf*: *Bodianus rufus*; *Cle bra*: *Clepticus brasiliensis*; *Dor meg*: *Doratonotus megalepis*; *Hal bra*: *Halichoeres brasiliensis*; *Hal dim*: *Halichoeres dimidiatus*; *Hal pen*: *Halichoeres penrosei*; *Hal poe*: *Halichoeres poeyi*; *Hal rub*: *Halichoeres rubrovirens*; *Tha nor*: *Thalssoma noronhanum*; *Xyr nov*: *Xyrichtys novacula*; *Xyr spl*: *Xyrichtys splendens*. Drawings modified from Menezes & Figueiredo (1985) with permission
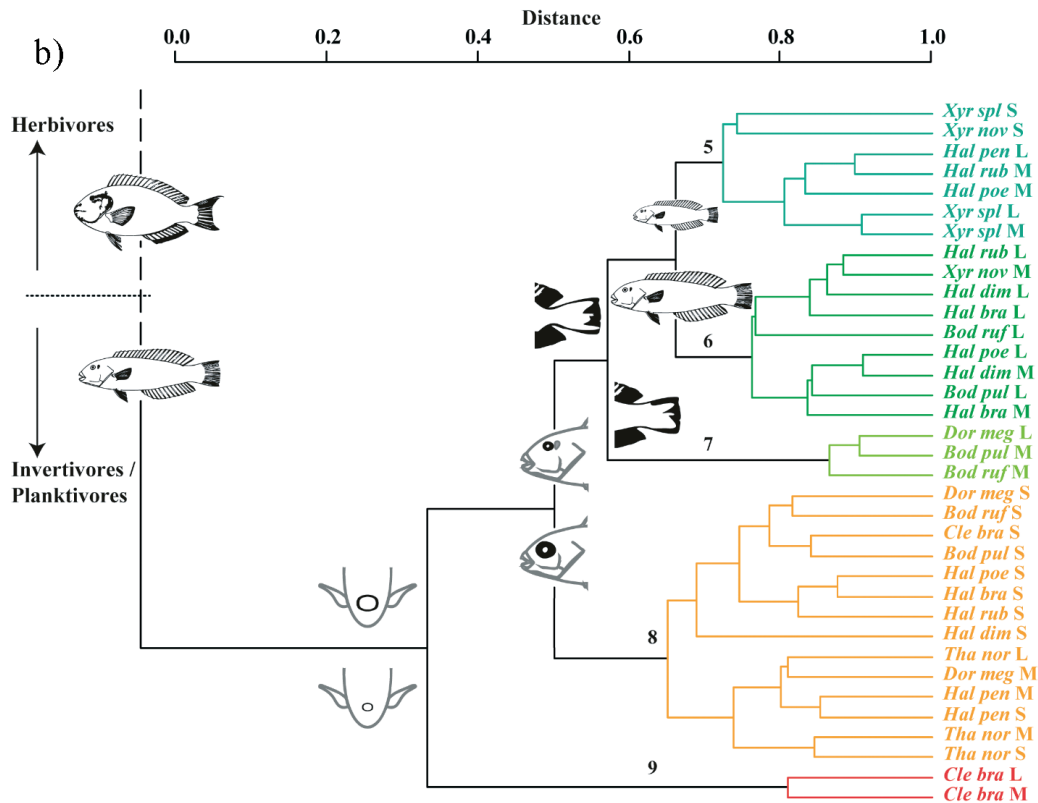
Fig. 2 (continued)

separated the most elongated species, *Cryptotomus roseus*, from all others (Fig. 2). Spearman tests showed that a number of traits were inter-correlated (see Fig. S1 in the Supplement), with a particularly strong negative relationship between eye size and size class limit (Figs. S1 & S2). Scarini segregated into 4 functional groups (Fig. 2a), with one single-species group (group 4). With eyes higher-positioned on the head and small mouth area, group 1 comprised almost all small-sized individuals, the medium-sized *Sparisoma frondosum* and *Scarus zelindae*, and the large-sized *C. roseus* and *Scarus trispinosus*. Medium and large-sized individuals of most species and small ones of *Sc. trispinosus* and *Sp. frondosum* formed groups 2 and 3, with traits opposite to those of group 1. The fourth group comprised small and medium individuals of the slim-bodied *C. roseus*, which are even more elongated than larger specimens.

Within wrasses, most medium and large-sized specimens assembled into groups 5, 6 and 7 due to their small eyes, with further segregation linked to depth of the caudal peduncle (Fig. 2b). However, small *Xyrichtys* spp., which have laterally compressed and deep bodies were also included in group 5. Small-size classes of all other species, along with medium

Doratonotus megalepis, *Halichoeres penrosei* and *Thalassoma noronhanum* were clustered into group 8 due to disproportionally large eyes. Medium and large size classes of the planktivore *Clepticus brasiliensis* were isolated from carnivores in group 9 primarily because of their small oral gape, high body and long pectoral fins.

DISCUSSION

After evaluating the morphological similarities among 21 labrid species and 3 size classes based on functional traits and ecological attributes, we were able to infer their functional role on SW Atlantic Ocean reefs. Our findings indicate that species that are generally classified in the literature as belonging to different trophic groups may perform similar functional roles (i.e. high morphological overlap), reinforcing the difference between these 2 concepts (Blondel 2003). The current segregation of parrotfishes into different functional groups, based on field observations and dietary analysis (e.g. browsers, scrapers, excavators and herbivorous–detritivorous; Bonaldo & Bellwood 2009, Francini-Filho et al. 2010,

Cordeiro et al. 2016), was not retrieved here. Our analysis therefore suggests that closely related species may not always perform similar functional roles. A similar pattern was recorded for cichlids by Cochran-Biederman & Winemiller (2010), who showed that closely related species were not the most ecologically similar. We found that parrotfish functional groups based on morphological features (groups 1 to 4; Fig. 2a) were composed of a mix of species from previous functional classifications (e.g. large *Sparisoma amplum* and *Scarus trispinosus* — excavators — grouped with scrapers *Sparisoma* spp.; see Fig. 2a). Recent evidence suggests that parrotfishes may target distinct food sources, such as endo- and epilithic microorganisms (Clements et al. 2017) and even copepods (Kramer et al. 2013). Thus, more detailed studies integrating ecomorphology, foraging behavior and diet will be necessary for attaining a comprehensive trophic/functional classification of parrotfish and other labrids, and to better understand the impacts over the benthic community and resource/use partitioning.

The most striking discordance between phylogenetic proximity and functional roles was between *Bodianus* and *Clepticus*. Baliga & Law (2016) suggest that *Clepticus* is the sister group of *Bodianus*, despite the difference in trophic ecology, swimming mode and habitat use (see Kuiter 2010). Here, the nominally planktivorous *Thalassoma noronhanum* is clustered with mobile invertebrate feeders (*Bodianus*, *Halichoeres* and *Xyrichtys*), which is in accordance with observations showing that it does feed on mobile invertebrates (Rocha et al. 2001, Longo et al. 2015) and ectoparasites (Francini-Filho et al. 2000) rather than only plankton (Ferreira et al. 2004, Floeter et al. 2007). According to Fulton et al. (2017), *Thalassoma* presents efficient high-speed swimming combined with trophic versatility which allows it to dominate extreme coral reef habitats around the world (Fulton et al. 2017). In the Labridae phylogeny (see Baliga & Law 2016), *Thalassoma* groups are interspersed with other wrasse groups, including the Caribbean *Halichoeres maculipinna* (Müller & Troschel, 1848), a sister species of the Brazilian endemic *Halichoeres penrosei*. Thus, phylogenetic constraints within the Labridae family may be significant only for groups with small morphological variations and represented by few lineages (Bellwood et al. 2006).

The ontogenetic approach clearly segregated small from large fishes in this family, where size is generally correlated with the initial (female) and terminal (male) sexual phases. Labrids usually form harems (Streelman et al. 2002) in schools with medium and large-sized males, and functional redundancy was expected within these sizes once they explore similar resources. All the *Halichoeres* species in our analysis had the small-sized individuals in the same functional group (group 8; Fig. 2b). Wainwright (1988) reported a difference in prey items between Caribbean *Halichoeres* spp. and between ontogenetic stages related to jaw crushing strength, with juveniles eating soft-bodied prey. The exception to our smaller individuals in the labrid groups were *Xyrichtys* spp., in which smaller phases clustered with medium and larger-size groups, including those from *X. splendens* and *X. novacula* (group 5; Fig. 2b). The *Xyrichtys* group is related (but not closely so) to the *Halichoeres* + *Thalassoma* groups (Baliga & Law 2016), which may be the cause of such a morphological differentiation (all *Xyrichtys* species and size classes are in groups 5 and 6; Fig. 2b).

Although different traits segregate small-sized individuals across the labrid spectra (i.e. eye position, eye size and class size limit), these traits are highly correlated (see Fig. S1 in the Supplement). In fishes, eyes grow throughout the life of the individual through the addition or elongation of retinal cells (Fernald 1991, Wilkens 2007) but become proportionally smaller with increasing size (Gould 1966). However, visual acuity is expected to improve as the absolute eye diameter increases, leading to higher capacity of prey or predator detection (Albouy et al. 2011). This typical ontogenetic allometry is probably associated with approaching the optimal functioning of the organ early in life (Boyle & Horn 2006) or to physiological energy requirements in early life stages (Post & Parkinson 2001). The presence of large-sized classes among small-sized ones in several functional groups produced here (e.g. large *Cryptotomus roseus*, Fig. 2a; *T. noronhanum*, Fig. 2b) may represent cases of neoteny (i.e. retention of juvenile characteristics in adults) (Shea 1983).

Claverie & Wainwright (2014) showed that the BEi is the main driver of diversification within 56 families of tropical Indo-Pacific reef fishes. Such a feature is also directly linked to swimming speed and endurance, mainly in fishes with rigid bodies that minimize undulation during swimming (Walker et al. 2013). For species in which the main power for propulsion is provided by pectoral fins, such as Labridae (Bellwood & Wainwright 2001), flexible bodies and high caudal throttling (e.g. compared to scombrids) would also promote more maneuverability and the acceleration needed to feed or flee from predators in the highly-complex 3-dimensional maze of reef environments. Here, BEi showed a remarkable influence in

some of the deepest cluster dichotomies, such as the segregation of herbivores (Scarini) from invertivores/planktivores (wrasses), evidencing its importance in food acquisition (Walker et al. 2013). BEi also isolated the early (S and M size classes) developmental phases of *C. roseus* from other parrotfishes (Fig. 2a), possibly a result of evolutionary history within Labridae species. *Cryptotomus* is older than *Sparisoma* and *Scarus* (Robertson et al. 2006, Smith et al. 2008) and appears phylogenetically isolated from other Scarinii (Baliga & Law 2016), which may plausibly lead to functional divergences. Considered to mostly feed on seagrass, *C. roseus* and *Nicholsina usta* (Valenciennes, 1840) are the only Scarini to harbor teeth not fully coalesced and caniniform at the top (Westneat 2002), suggesting that they also explore non-vegetal food sources. Beside the expected allometry in body proportions typical of the high growth rates found in juveniles (Gould 1966), slender bodies (i.e. high BEi) are useful to the burying habits at the settlement stage (Lara 2008, Leis et al. 2011). While this behavior is known to persist into adulthood of many wrasses, *C. roseus* is the only known parrotfish that buries itself (Bolhke & Chaplin 1968), an activity certainly facilitated by its slender body. This species also produces a mucus cocoon (after burrowing into the sand) in which to sleep, probably protecting itself from predators and parasites during the night (Sazima & Ferreira 2006, Grutter et al. 2011).

No clear differentiation in functional morphology among *Sparisoma* and *Scarus* species was found (except for those linked to size classes), reinforcing the hypothesis that the functions played by these species are strongly size-dependent (Bonaldo & Bellwood 2008, Francini-Filho et al. 2008, Bonaldo et al. 2014). This is especially clear in *Scarus* spp., with large *S. trispinosus* acting as excavators while small ones are scrapers (Francini-Filho et al. 2008, Bonaldo et al. 2014). *Scarus* species also showed clear differences in body shape and size, features that may lead to differences in habitat use and food selection, thus possibly reducing competition and facilitating species coexistence (McAfee & Morgan 1996, Streit et al. 2015).

Functional redundancy would vary in accordance with assemblage composition, where the absence of a species (or its rarity) could allow another species to thrive owing to reduced competition. Lower-than-expected redundancy would also be attained if species clustered into the same functional group (see groups 1 to 3) played different roles. Further studies could use more refined traits (see Wainwright & Bellwood 2002, Schmitz & Wainwright 2011) and

approaches (Clements et al. 2017) to better elucidate functional relationships within SWA labrids.

Excavating is a critical functional role for the maintenance of resistance and resilience of coral reef ecosystems (Bellwood et al. 2003, 2004). This is only performed by large and medium-sized *Sc. trispinosus* and *Sp. amplum* in the SWA (Francini-Filho et al. 2010, R. B. Francini-Filho unpubl. data). This low redundancy highlights their fragility and regional susceptibility to natural and anthropogenic impacts such as overfishing (Francini-Filho & Moura 2008). However, the abundance and biomass of scrapers and excavators tend to differ depending on site (see Ferreira et al. 2004), and thus the combined impact of these 2 groups over the substratum should vary in accordance with their relative importance in the community. Therefore, the fishery management strategy of implementing size limits for catches clearly cannot be applied casually to excavating parrotfishes, as their functional role changes with size and they have a striking importance to bioconstruction, e.g. through sediment accretion (see Perry et al. 2015).

Overfishing of parrotfishes led Brazilian authorities to red list most large-sized parrotfishes (MMA 2014). Because species may exert particular roles and functional redundancy is null (as for *C. roseus* and *Clepticus brasiliensis* within Atlantic labrids), low or unrecognized, one should not overestimate redundancy levels (Guillemot et al. 2011), and conservation measures need to evaluate each species within an ecosystem framework. Other labrid assemblages that are more diverse (e.g. Caribbean and Indo-Australian) may be more redundant, more stable and less prone to function loss caused by extinction of a single species (Guillemot et al. 2011). The functional approach to identify the ecological roles that labrids play in SWA reefs provides valuable insights into the interlaced effects of morphology and size and highlights a number of possible conservation pitfalls. The complementation of the analysis with other approaches (e.g. diet, stable isotopes, population demography) is fundamental to enhance our understanding and sharpen our tools to support conservation programs for species, communities and whole habitats.

LITERATURE CITED

Albouy C, Guilhaumon F, Villéger S, Mouchet MA and others (2011) Predicting trophic guild and diet overlap from functional traits: statistics, opportunities and limitations for marine ecology. Mar Ecol Prog Ser 436:17–28

Alfaro ME, Bolnick DI, Wainwright PC (2005) Evolutionary consequences of many-to-one mapping of jaw morphology to mechanics in labrid fishes. Am Nat 165: E140–E154

Baliga VB, Law CJ (2016) Cleaners among wrasses: phylogenetics and evolutionary patterns of cleaning behavior within Labridae. Mol Phylogenet Evol 94:424–435

Bellwood DR, Choat JH (1990) A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. Environ Biol Fishes 28:189–214

Bellwood DR, Wainwright PC (2001) Locomotion in labrid fishes: implications for habitat use and cross-shelf biogeography on the Great Barrier Reef. Coral Reefs 20: 139–150

Bellwood DR, Wainwright PC, Fulton CJ, Hoey AS (2002) Assembly rules and functional groups at global biogeographic scales. Funct Ecol 16:557–562

Bellwood DR, Hoey AS, Choat JH (2003) Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. Ecol Lett 6:281–285

Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. Nature 429:827–833

Bellwood DR, Wainwright PC, Fulton CJ, Hoey AS (2006) Functional versatility supports coral reef biodiversity. Proc R Soc B 273:101–107

Blondel J (2003) Guilds or functional groups: Does it matter? Oikos 100:223–231

Bolhke JE, Chaplin CCG (1968) Fishes of the Bahamas and adjacent tropical waters, 1st edn. Livingston Publishing Company, Wynnewood, PA

Bonaldo RM, Bellwood DR (2008) Size-dependent variation in the functional role of the parrotfish Scarus rivulatus on the Great Barrier Reef, Australia. Mar Ecol Prog Ser 360: 237–244

Bonaldo RM, Bellwood DR (2009) Dynamics of parrotfish grazing scars. Mar Biol 156:771–777

Bonaldo RM, Hoey AS, Bellwood DR (2014) The ecosystem roles of parrotfishes on tropical reefs. Oceanogr Mar Biol Annu Rev 52:81–132

Boyle KS, Horn MH (2006) Comparison of feeding guild structure and ecomorphology of intertidal fish assemblages from central California and central Chile. Mar Ecol Prog Ser 319:65–84

Choat JH (1991) The biology of herbivorous fishes on coral reefs. In: Sale PE (ed) The ecology of fishes on coral reefs. Academic Press, San Diego, CA, p 120–155

Clarke KR, Somerfield PJ, Gorley RN (2008) Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. J Exp Mar Biol Ecol 366:56–69

Claverie T, Wainwright PC (2014) A morphospace for reef fishes: elongation is the dominant axis of body shape evolution. PLOS ONE 9:e112732

Clements KD, Alfaro ME, Fessler JL, Westneat MW (2004) Relationships of the temperate Australasian labrid fish tribe Odacini (Perciformes; Teleostei). Mol Phylogenet Evol 32:575–587

Clements KD, German DP, Piché J, Tribollet A, Choat JH (2017) Integrating ecological roles and trophic diversification on coral reefs: multiple lines of evidence identify parrotfishes as microphages. Biol J Linn Soc 120:729–751

Clifton KB, Motta PJ (1998) Feeding morphology, diet, and ecomorphological relationships among five Caribbean labrids (Teleostei, Labridae). Copeia 1998:953–966

Cochran-Biederman JL, Winemiller KO (2010) Relationships among habitat, ecomorphology and diets of cichlids in the Bladen River, Belize. Environ Biol Fishes 88:143–152

Cordeiro CAMM, Mendes TC, Harborne AR, Ferreira CEL (2016) Spatial distribution of nominally herbivorous fishes across environmental gradients on Brazilian rocky reefs. J Fish Biol 89:939–958

Dumay O, Tari PS, Tomasini JA, Mouillot D (2004) Functional groups of lagoon fish species in Languedoc Roussillon, southern France. J Fish Biol 64:970–983

Fernald RD (1991) Teleost vision: seeing while growing. J Exp Zool Suppl 5:167–180

Ferreira CEL, Gonçalves JEA (2006) Community structure and diet of roving herbivorous reef fishes in the Abrolhos Archipelago, south-western Atlantic. J Fish Biol 69: 1533–1551

Ferreira CEL, Floeter SR, Gasparini JL, Ferreira BP, Joyeux JC (2004) Trophic structure patterns of Brazilian reef fishes: a latitudinal comparison. J Biogeogr 31:1093–1106

Fey DP, Hare JA (2005) Length correction for larval and early-juvenile Atlantic menhaden (Brevoortia tyrannus) after preservation in alcohol. Fish Bull 103:725–727

Floeter SR, Krohling W, Ferreira CEL, Zalmon IR (2007) Reef fish community structure on coastal islands of the southeastern Brazil: the influence of exposure and benthic cover. Environ Biol Fishes 78:147–160

Floeter SR, Rocha LA, Robertson DR, Joyeux JC and others (2008) Atlantic reef fish biogeography and evolution. J Biogeogr 35:22–47

Fox CJ (1996) Length changes in herring (Clupea harengus) larvae: effects of capture and storage in formaldehyde and alcohol. J Plankton Res 18:483–493

Francini-Filho RB, Moura RL (2008) Dynamics of fish assemblages on coral reefs subjected to different management regimes in the Abrolhos Bank, eastern Brazil. Aquat Conserv 18:1166–1179

Francini-Filho RB, Moura RL, Sazima I (2000) Cleaning by the wrasse Thalassoma noronhanum, with two records of predation by its grouper client Cephalopholis fulva. J Fish Biol 56:802–809

Francini-Filho RB, Moura RL, Ferreira CM, Coni EOC (2008) Live coral predation by parrotfishes (Perciformes: Scaridae) in the Abrolhos Bank, eastern Brazil, with comments on the classification of species into functional groups. Neotrop Ichthyol 6:191–200

Francini-Filho RB, Ferreira CM, Coni EOC, Moura RL, Kaufman L (2010) Foraging activity of roving herbivorous reef fish (Acanthuridae and Scaridae) in eastern Brazil: influence of resource availability and interference competition. J Mar Biol Assoc UK 90:481–492

Fulton CJ, Bellwood DR (2002) Ontogenetic habitat use in labrid fishes: an ecomorphological perspective. Mar Ecol Prog Ser 236:255–262

Fulton CJ, Bellwood DR, Wainwright PC (2001) The rela-

tionship between swimming ability and habitat use in wrasses (Labridae). Mar Biol 139:25–33

Fulton CJ, Wainwright PC, Hoey AS, Bellwood DR (2017) Global ecological success of *Thalassoma* fishes in extreme coral reef habitats. Ecol Evol 7:466–472

Gasparini JL, Joyeux JC, Floeter SR (2003) *Sparisoma tuiupiranga*, a new species of parrotfish (Perciformes: Labroidei: Scaridae) from Brazil, with comments on the evolution of the genus. Zootaxa 384:1–14

Gatz AJ (1979) Community organization in fishes as indicated by morphological features. Ecology 60:711–718

Gomon MF (2006) A revision of the labrid fish genus *Bodianus* with descriptions of eight new species. Rec Aust Mus Suppl 30:1–133

Gould SJ (1966) Allometry and size in ontogeny and phylogeny. Biol Rev Camb Philos Soc 41:587–640

Grutter AS, Rumney JG, Sinclair-Taylor T, Waldie P, Franklin CE (2011) Fish mucous cocoons: the 'mosquito nets' of the sea. Biol Lett 7:292–294

Guillemot N, Kulbicki M, Chabanet P, Vigliola L (2011) Functional redundancy patterns reveal non-random assembly rules in a species-rich marine assemblage. PLOS ONE 6:e26735

Halpern BS, Floeter SR (2008) Functional diversity responses to changing species richness in reef fish communities. Mar Ecol Prog Ser 364:147–156

Heiser JB, Moura RL, Robertson DR (2000) Two new species of creole wrasse (Labridae: *Clepticus*) from opposite sides of the Atlantic. Aqua 4:67–76

Kramer MJ, Bellwood O, Bellwood DR (2013) The trophic importance of algal turfs for coral reef fishes: the crustacean link. Coral Reefs 32:575–583

Kuiter RH (2010) Labridae fishes: wrasses, 1st edn. Aquatic Photographics, Seaford

Lara MR (2008) Development of the nasal olfactory organs in the larvae, settlement-stages and some adults of 14 species of Caribbean reef fishes (Labridae, Scaridae, Pomacentridae). Mar Biol 154:51–64

Leis JM, Hay AC, Gaither MR (2011) Swimming ability and its rapid decrease at settlement in wrasse larvae (Teleostei: Labridae). Mar Biol 158:1239–1246

Longo GO, Morais RA, Martins CDL, Mendes TC and others (2015) Between-habitat variation of benthic cover, reef fish assemblage and feeding pressure on the benthos at the only atoll in South Atlantic: Rocas Atoll, NE Brazil. PLOS ONE 10:e0127176

McAfee ST, Morgan SG (1996) Resource use by five sympatric parrotfishes in the San Blas Archipelago, Panama. Mar Biol 125:427–437

Menezes N, Figueiredo JL (1985) Manual de peixes marinhos do Sudeste do Brasil. V. Teleostei (4). Museu de Zoologia da Universidade de São Paulo, São Paulo

MMA (2014) Portaria N° 445 de 17 de dezembro de 2014 - Lista nacional oficial de espécies da fauna ameaçadas de extinção - peixes e invertebrados aquáticos. Diário Of da União

Mouchet MA, Guilhaumon F, Villéger S, Mason NWH, Tomasini JA, Mouillot D (2008) Towards a consensus for calculating dendrogram-based functional diversity indices. Oikos 117:794–800

Moura RL, Figueiredo JL, Sazima I (2001) A new parrotfish (Scaridae) from Brazil, and revalidation of *Sparisoma amplum* (Ranzani, 1842), *Sparisoma frondosum* (Agassiz, 1831), *Sparisoma axillare* (Steindachner, 1878) and *Scarus trispinosus.* Bull Mar Sci 68:505–524

Nagelkerken I, van der Velde G (2002) Do non-estuarine mangroves harbour higher densities of juvenile fish than adjacent shallow water and coral reef habitats in Curaçao (Netherlands Antilles)? Mar Ecol Prog Ser 245: 191–204

Nishi G (1989) Locomotor activity rhythm in two wrasses, *Halichoeres tenuispinnis* and *Pteragogus flagellifera*, under various light conditions. Jpn J Ichthyol 36:350–356

Parker RR (1963) Effects of formalin on length and weight of fishes. J Fish Res Board Can 20:1441–1455

Perry CT, Kench PS, O'Leary MJ, Morgan KM, Januchowski-Hartley F (2015) Linking reef ecology to island building: parrotfish identified as major producers of island-building sediment in the Maldives. Geology 43: 503–506

Post JR, Parkinson EA (2001) Energy allocation strategy in young fish: allometry and survival. Ecology 82:1040–1051

Potts GW (1973) The ethology of *Labroides dimidiatus* (Cuv. & Val.) (Labridae, Pisces) on Aldabra. Anim Behav 21: 250–291

Pouilly M, Lino F, Bretenoux JGG, Rosales C (2003) Dietary-morphological relationships in a fish assemblage of the Bolivian Amazonian floodplain. J Fish Biol 62:1137–1158

Quignard JP (1966) Recerces sur les Labridae des côtes européennes: systématique, et biologie. Nat Monspel Série Zool 5:7–248

R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Randall JE (1967) Food habits of reef fishes of the West Indies. Stud Trop Oceanogr 5:665–847

Robertson DR, Karg F, Moura RL, Victor BC, Bernardi G (2006) Mechanisms of speciation and faunal enrichment in Atlantic parrotfishes. Mol Phylogenet Evol 40:795–807

Robins CR, Ray GC (1986) A field guide to Atlantic coast fishes of North America. Houghton Mifflin Company, Boston, MA

Rocha LA, Rosa RS (2001) *Halichoeres brasiliensis* (Bloch, 1791), a valid wrasse species (Teleostei: Labridae) from Brazil, with notes on the Caribbean species *Halichoeres radiatus* (Linnaeus, 1758). Aqua 4:161–166

Rocha LA, Guimarães RZP, Gasparini JL (2001) Redescription of the Brazilian wrasse *Thalassoma noronhanum* (Boulenger, 1890) (Teleostei: Labridae). Aqua 4:105–108

Rocha LA, Pinheiro HT, Gasparini JL (2010) Description of *Halichoeres rubrovirens*, a new species of wrasse (Labridae: Perciformes) from the Trindade and Martin Vaz Island group, southeastern Brazil, with a preliminary mtDNA molecular phylogeny of New World *Halichoeres*. Zootaxa 2422:22–30

Sabaj Pérez MH (2014) Standard symbolic codes for institutional resource collections in herpetology and ichthyology: an online reference. American Society of Ichthyologists and Herpetologists, Washington, DC

Sazima I, Ferreira CEL (2006) A cocoon-producing parrotfish in the southwestern Atlantic. Coral Reefs 25:212

Schmitz L, Wainwright PC (2011) Ecomorphology of the eyes and skull in zooplanktivorous labrid fishes. Coral Reefs 30:415–428

Shea BT (1983) Paedomorphosis and neoteny in the pygmy chimpanzee. Science 222:521–522

Smith LL, Fessler JL, Alfaro ME, Streelman JT, Westneat MW (2008) Phylogenetic relationships and the evolution of regulatory gene sequences in the parrotfishes. Mol Phylogenet Evol 49:136–152

Streelman JT, Alfaro ME, Westneat MW, Bellwood DR, Karl SA (2002) Evolutionary history of the parrotfishes: biogeography, ecomorphology, and comparative diversity. Evolution 56:961–971

Streit RP, Hoey AS, Bellwood DR (2015) Feeding characteristics reveal functional distinctions among browsing herbivorous fishes on coral reefs. Coral Reefs 34:1037–1047

Wainwright PC (1988) Morphology and ecology: functional basis of feeding constraints in Caribbean labrid fishes. Ecology 69:635–645

Wainwright PC (2007) Functional versus morphological diversity in macroevolution. Annu Rev Ecol Evol Syst 38: 381–401

Wainwright PC, Bellwood DR (2002) Ecomorphology of feeding in coral reef fishes. In: Sale PF (ed) Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, San Diego, CA, p 33–56

Walker JA, Westneat MW (2002) Performance limits of labriform propulsion and correlates with fin shape and motion. J Exp Biol 205:177–187

Walker JA, Alfaro ME, Noble MM, Fulton CJ (2013) Body fineness ratio as a predictor of maximum prolonged-swimming speed in coral reef fishes. PLOS ONE 8:e75422

Westneat MW (1995) Phylogenetic systematics and biomechanics in ecomorphology. Environ Biol Fishes 44: 263–283

Westneat MW (2002) Labridae: wrasses. In: Carpenter KE (ed) The living marine resources of the western central Atlantic, Vol 3: Bony fishes, part 2 (Opistognathidae to Molidae), sea turtles and marine mammals, 1st edn. FAO, Rome, p 1375–2127

Westneat MW, Alfaro ME (2005) Phylogenetic relationships and evolutionary history of the reef fish family Labridae. Mol Phylogenet Evol 36:370–390

Whitaker D, Christman M (2014) clustsig: significant cluster analysis. R package, Version 1.1, available at: https://cran.r-project.org/web/packages/clustsig/index.html

Wikramanayake ED (1990) Ecomorphology and biogeography of a tropical stream fish assemblage: evolution of assemblage structure. Ecology 71:1756–1764

Wilkens H (2007) Regressive evolution: ontogeny and genetics of cavefish eye rudimentation. Biol J Linn Soc 92: 287–296

Winemiller KO (1991) Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. Ecol Monogr 61:343–365