Inferring labrid functional roles through morphological and ecological traits

G. C. Cardozo-Ferreira1,*, R. M. Macieira1,2, R. B. Francini-Filho3, J. C. Joyeux1

1Laboratório de Ictiologia, Departamento de Oceanografia e Ecologia, Universidade Federal do Espírito Santo, Vitória ES, Brazil
2Laboratório de Ecologia Marinha, Complexo Biopráticas, Universidade Vila Velha, Vila Velha ES, Brazil
3Departamento 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, Kuitert 2010). Parrotfishes and odacines (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. Doratontus), planktivores (e.g. Clepticus) and predators of benthic invertebrates (e.g. Bodianus, Halichoeres and Xyrichtys).

*Corresponding author: gabrielccf@gmail.com
© Inter-Research 2018 · www.int-res.com
The evolution of many traits closely linked to feeding habits and swimming ability is detectable in Labridae phylogeny (Choat 1991, Steelman 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 (Haipern & 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 (Guilmot 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 (Du-may 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 (SLmax) 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 < 1/3 of SLmax medium-size (M) were between 1/3 and 2/3 of SLmax, and large-sized fishes (L) showed SL > 2/3 of SLmax (Nagelkerken & van der Velde 2002).
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).

### Table 1

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

<sup>a</sup>Brazilian Province endemic species; <sup>b</sup>Red listed species (MMA 2014)

---

### Morphometric measurements and functional traits

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

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

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 ‘clusig’ 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 (CPI) and pectoral fin relative area (PFRA). Within parrotfishes, BEI
<table>
<thead>
<tr>
<th>Functional group</th>
<th>Characteristic functional traits</th>
<th>Examples</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Coalesced teeth, higher positioned eye and thicker caudal peduncle</td>
<td><em>Sparisoma amplum</em> (S) and <em>Sp. axillare</em> (S)</td>
</tr>
<tr>
<td>2</td>
<td>Coalesced teeth, deeper body, smaller species, smaller eye and thicker caudal peduncle</td>
<td><em>Sparisoma rocha</em> (M/L) and <em>Sp. radians</em> (M/L)</td>
</tr>
<tr>
<td>3</td>
<td>Larger species, thicker caudal peduncle and lower positioned eye</td>
<td><em>Scarus trispinosus</em> (M), <em>Sp. amplum</em> (L) and <em>S. axillare</em> (L)</td>
</tr>
<tr>
<td>4</td>
<td>Elongated body, coalesced tooth and narrow mouth.</td>
<td><em>Cryptotomus roseus</em> (S/M)</td>
</tr>
<tr>
<td>5</td>
<td>Narrow mouth, shallow and elongated body, smaller eye, and smaller species</td>
<td><em>Halichoeres rubrovirens</em> (M) and <em>H. poeyi</em> (M)</td>
</tr>
<tr>
<td>6</td>
<td>Thinner caudal peduncle, higher positioned eye, canine teeth and larger species</td>
<td><em>H. brasiliensis</em> (L) and <em>H. dimidiatus</em> (L)</td>
</tr>
<tr>
<td>7</td>
<td>Broader mouth, canine teeth and thicker caudal peduncle.</td>
<td><em>Bodianus</em> spp. (M) and <em>Doratonotus megalepis</em> (L)</td>
</tr>
<tr>
<td>8</td>
<td>Larger eyes and canine teeth</td>
<td><em>Thalassoma noronhanum</em> (S/M/L) and <em>Halichoeres</em> spp. (S)</td>
</tr>
<tr>
<td>9</td>
<td>Long and wide pectoral fin, deeper and fusiform body and lower positioned eye</td>
<td><em>Clepticus brasiliensis</em> (M/L)</td>
</tr>
</tbody>
</table>

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.

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*: *Dorato- notus megalepis*; *Hal bra*: *Halichoeres brasiliensis*; *Hal dim*: *Halichoeres dimidiatus*; *Hal pen*: *Halichoeres penrosei*; *Hal poe*: *Halichoeres poeyi*; *Hal rub*: *Halichoeres rubrovirens*; *Tha nor*: *Thalassoma noronhanum*; *Xyr nov*: *Xyrichtys novacula*; *Xyr spl*: *Xyrichtys splendens*. Drawings modified from Menezes & Figueiredo (1985) with permission.
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 *Sc. 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 amplus 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).

Clavérie & 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 (Scarinii) from invertivores/planktiivores (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 Scarini (Baliga & Law 2016), which may plausibly lead to functional divergences. Considered to mostly feed on seagrass, C. roseus and Nicholosina 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.

Acknowledgements. We thank the Brazilian Navy (Marinha do Brasil – 1° Distrito Naval) for logistical support at Trindade Island, National Council for Research for partial funding (CNPq: grant 405426/2012-7 to J.C.J.), Juan Quimbayo for his help in collecting specimens at Trindade Island; N. A. Menezes and J. L. Figueiredo for authorizing the use and his help in collecting specimens at Trindade Island, National Council for Research for partial funding. We are indebted to the curators of MZUSP (Osvaldo Oyakawa), ZUEC (Karina Almeida), and CIUFES (Larissa J. Benevides and Bianca Cruz) for their
assistance, and to L. J. Benevides, A. Crosbie and the 3 anonymous reviewers for their comments on the manuscript. Financial support to G.C.C.F. was provided by a MSc fellowship from CAPES/Brazilian Ministry Educational Council.

LITERATURE CITED


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


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


Fulton CJ, Bellwood DR, Wainwright PC (2001) The rela-
sionship between swimming ability and habitat use in wrasses (Labridae). Mar Biol 139:25–33


Longo GO, Morais RA, Martins CDL, Mendes TC and others (2013) 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


Cardozo-Ferreira et al.: Inferring labrid functional roles


Editorial responsibility: Charles Birkeland, Honolulu, Hawaii, USA

Submitted: June 26, 2017; Accepted: November 19, 2017
Proofs received from author(s): January 20, 2018