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# Parrotfish functional morphology and bioerosion on SW Atlantic reefs

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ABSTRACT: Parrotfishes (Labridae: Scarini) have jaws formed by teeth fused into a beak-like structure in most species, and are classified into 3 functional groups (browsers, scrapers and excavators) based on jaw morphology, foraging behavior and feeding impact on the benthos. We compared the feeding morphology of 3 parrotfish species in the Abrolhos Bank, SW Atlantic. We also estimated rates of bioerosion caused by the largest and most abundant parrotfish in the region, *Scarus trispinosus*, and compared them to literature estimates from 12 species. The 3 studied species differed in dentary, suspensorium and mouth/head height. Large (>40 cm) *Sc. trispinosus* individuals were functionally classified as excavators because of their body size, robust premaxilla and jaws with simple joints, in addition to the large proportion of their bites leaving pronounced marks on the substratum. Large (>40 cm) adult *Sparisoma amplum* were also classified as excavators because of their mouth/head height, dentary and suspensorium size and robust jaws (dentary) with simple joints. *Sc. zelindae* had the most mobile jaw among the 3 species and was functionally classified as a scraper, as were juveniles or initial phases of the other 2 species. Body size and feeding rates of *Sc. trispinosus* were positively correlated with the volume of substratum removed, with large adults removing 207 $cm^3$ $d^{-1}$ and eroding ~75 500 $cm^3$ $yr^{-1}$. Our results reinforce the importance of studies on jaw morphology and osteology for the assessment of parrotfish feeding modes, and indicate that large adult *Sc. trispinosus* and *Sp. amplum* play unique roles as excavating fishes in the Abrolhos Bank.

KEY WORDS: Labridae · Scarini · Herbivory · Osteology · Jaw morphology · Abrolhos Bank

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## 1. INTRODUCTION

Tropical reefs face increasing impacts from local disturbances, such as eutrophication and overfishing, and from global changes, such as ocean warming (Hughes et al. 2003, Bellwood et al. 2004). Several studies over the last 2 decades have focused on the identification of key species and processes in tropical reefs, as this information can provide a better understating of the factors underlying ecosystem functioning and the maintenance of reef health and diversity (e.g. Bellwood et al. 2003, 2006, Hoey & Bellwood 2008).

The parrotfishes (Labridae: Scarini) are one of the dominant components of fish assemblages on coral reefs, and may represent up to 50% of the herbivorous fish biomass in these systems (Horn 1989, Bellwood et al. 2004, Francini-Filho & Moura 2008). Most species within this group have unique and robust oral jaws composed of teeth fused into beak-like structures, which are used to scrape algae, corals and detritus from the reef matrix (Bellwood & Choat

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1990, Bonaldo et al. 2014, Clements et al. 2017). This unique feeding morphology, along with the high parrotfish biomass in reef fish assemblages, renders the parrotfishes one of the main consumers of benthic algae and other primary producers on tropical reefs (Horn 1989, Fox & Bellwood 2007). Some large parrotfishes are also among the most important bioeroders in these systems, as they ingest large portions of consolidated substratum during feeding. This material is triturated by the pharyngeal apparatus of these fishes and discharged as sediment with feces onto the reef and nearby areas (Bellwood 1995a,b, Bruggemann et al. 1996, Alwany et al. 2009).

The parrotfishes do not comprise a uniform group in terms of their influence on the benthos where they forage, since their feeding morphology and impact greatly vary within and among species (Bellwood & Choat 1990, Bonaldo & Bellwood 2008, 2009, 2011, Lokrantz et al. 2008). For this reason, parrotfishes are classified into 3 main functional groups; browsers, scrapers and excavators, based on their oral jaw structure and the quantity of substratum removed during feeding (Bellwood & Choat 1990, Bruggemann et al. 1996). Browsers have relatively weak jaws that are used to crop algae, while scrapers and excavators remove algae and portions of the underlying substratum when feeding. Excavators have more robust jaws than scrapers (Bellwood & Choat 1990), and their excavating bites leave deeper marks on the substratum than scraping bites (Bruggemann et al. 1996, Bonaldo & Bellwood 2008, 2009, 2011, Lokrantz et al. 2008).

The type of the bite delivered by an individual parrotfish also depends on the body size of the fish, because small individuals, even of large excavating species, are not able to excavate the benthos (Bruggemann et al. 1994, 1996, Lokrantz et al. 2008, Bonaldo & Bellwood 2009, Bonaldo et al. 2011). Parrotfishes may also differ in their feeding preferences and foraging behavior within and among species (Choat et al. 2002, Francini-Filho et al. 2010, Bonaldo et al. 2014). For example, some parrotfish species are protogynous hermaphrodites, which change their behavior after transitioning from initial phase (IP) individuals (females or males) to terminal phase (TP) males when adults (Bruggemann et al. 1994, Lokrantz et al. 2008).

Despite the extensive literature on parrotfish feeding, studies on ecomorphology in this group are rare. Apart from a few studies in the Pacific (e.g. Gobalet 1989, Bellwood & Choat 1990, Bellwood 1994, Wainwright et al. 2004) and in the Mediterranean (e.g. Board 1956), no studies have examined in detail the potential relationships between parrotfish oral jaw morphology and functionality, especially by comparing species and ontogenetic phases (but see Nanami 2016). The few studies on this subject, however, indicate that information on ecomorphological attributes (particularly size and weight of the head and mouth bony structures), associated with data on foraging patterns (e.g. bite rate, bite size, amount of substrate removed), are useful proxies for defining parrotfish impacts on the benthos (e.g. Bellwood & Choat 1990).

Another weakness in the parrotfish literature is the dominance of studies in coral reefs in the Caribbean and Indo-Pacific. Therefore, the functional ecology of this group remains largely unknown for other regions such as the SW Atlantic (Bonaldo et al. 2014). In this area, although some aspects of parrotfish foraging behavior (e.g. Bonaldo et al. 2006, Francini-Filho et al. 2010, Pereira et al. 2016), diet (e.g. Ferreira & Gonçalves 2006) and coral predation (e.g. Francini-Filho et al. 2008) have been assessed, nothing is known about the relationships between jaw morphology and feeding performance. This lack of information is particularly relevant for SW Atlantic reefs because of the relatively low species richness and high endemism of corals and reef fishes, including the parrotfishes, compared to other common regions for which parrotfish studies are available (Floeter et al. 2008). Additionally, the physical structure of SW reefs is unique, as true coral reefs are rare in this region and, when present, are predominantly constituted of *Montastraea cavernosa*, which grows over a complex framework building system composed mainly of bryozoans (Bastos et al. 2018), or *Madracis decactis* colonies cemented by crustose coralline algae (Pereira-Filho et al. 2019). Because of these particularities, parrotfish behavior and ecology may differ in Brazilian reefs compared to other studied reefs. Therefore, extrapolations of parrotfish functional roles from studies performed in the Caribbean and Indo-Pacific to the SW Atlantic may be misleading (Bonaldo et al. 2014, Bellwood et al. 2018, Hoey et al. 2018).

We aimed to fill some of the gaps in the knowledge on parrotfish feeding ecology by assessing the ecomorphology of 3 parrotfish species endemic to Brazil: *Scarus trispinosus*, *Sc. zelindae* and *Sparisoma amplum*. These species were chosen because they attain relatively large body sizes (40–70 cm total length, TL) and, combined, represent 32% of the total reef fish biomass and 57% of the large, roving, herbivorous fish biomass at our study site in the tropical Abrolhos Reefs of northeastern Brazil (Moura & Francini-Filho 2006, Francini-Filho & Moura 2008). In addition, previous studies indicated that relatively large individuals of 2 of these species, namely *Sp. amplum* and *Sc. trispinosus*, act as excavators (Francini-Filho et al. 2010) and thus possibly exert a marked influence on the benthos (Francini-Filho et al. 2008, 2010). We assessed the structure of the jaws (but not of associated muscles) among the 3 species and among different-sized individuals within species. We used this information, along with previous information on these species' feeding behaviors and feeding impacts on the substratum (see Francini-Filho et al. 2010), to infer the feeding mode of each species by classifying them as functional scrapers or excavators. In this classification, we also accounted for possible ontogenetic variation in each species. For *Sc. trispinosus,* we also assessed feeding rates, substratum preferences and bioerosion rates in different life phases, because of the large body size (up to 80 cm TL) and the relatively high abundance of this species in the study reefs. Our study thus addresses the following 4 questions: (1) Do *Sc. trispinosus, Sc. zelindae* and *Sp. amplum* differ in their feeding mode and morphology? (2) Do the morphology and associated feeding mode of these species change ontogenetically? (3) At what size does *Sc. trispinosus* start to act as an excavator? and (4) What are the annual bioerosion rates for *Sc. trispinosus* at the studied reefs?

## 2. MATERIALS AND METHODS

### 2.1. Study site

This study was conducted in the Abrolhos Bank, northeastern Brazil (16–20° S, 37–39° W; Fig. 1), at 4 sites within the altiphotic reef habitat (i.e. <40 m depth, cf. Baldwin et al. 2018) (Moura et al. 2013). Two of these sites are biogenic reefs in coastal areas (~12 km offshore): Timbebas Reef, which is inside a discontinuous portion of the National Marine Park of Abrolhos (NMPA) and is protected from fishing (but with poor enforcement), and Pedra de Leste, which is inside a 'paper park' (Environmental Protected Area Ponta da Baleia/Abrolhos) and thus is unprotected from fishing (Francini-Filho & Moura 2008). The other 2 sites are inside a better enforced portion of the NMPA and are located on the mid-shelf: the rocky reefs of the Abrolhos Archipelago, and the biogenic reefs of Parcel dos Abrolhos (both ~60 km offshore). Biogenic reefs (Timbebas, Pedra de Leste and Parcel dos Abrolhos) comprise mushroom-shaped pinnacles that extend to 2–6 m below the surface and extensive platforms formed by fused pinnacles, while the Abrolhos Archipelago is a rocky shore covered by corals, algae and other benthic components (Laborel 1969, Francini-Filho et al. 2013). The extent and distribution of benthic mega habitats in the Abrolhos region (e.g. shallow reefs, rhodolith beds) was characterized using extensive side scan sonar sampling in combination with ground-truthing through remotely operated vehicles and mixed-gas diving operations (Moura et al. 2013).

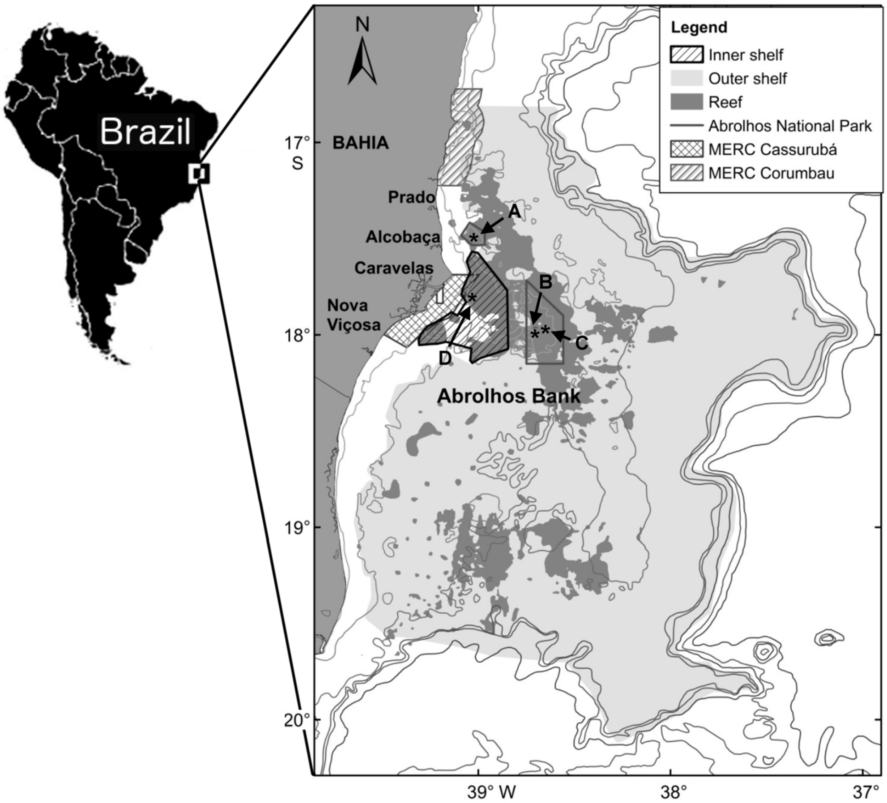

Fig. 1. Abrolhos Bank in eastern Brazil, South America. The Abrolhos National Marine Park, where fishing is forbidden, includes Timbebas (inner-shelf, site A), the Abrolhos Archipelago and Parcel dos Abrolhos (both at mid-shelf, sites B and C, respectively). Pedra de Leste, the unprotected site (D), is enclosed within Parcel das Paredes (inner-shelf). MERC: Marine Extractive Reserve of Corumbau (map modified from Freitas et al. 2017)

### 2.2. Ecomorphology

To assess potential differences in parrotfish oral jaw morphology, we used fresh fish specimens obtained from local fishermen (Prado, Alcobaça and Caravelas municipalities, Fig. 1). For interspecific comparisons, we considered 2 body size categories ('small' and 'large') within each species. We used 5–25 specimens from each size category and species to account for allometric growth effects within categories (Wikramanayake 1990). Because the study species differ in their maximum body sizes, different ranges of 'small' and 'large' were considered for each species. *Scarus zelindae* and *Sparisoma amplum* also have 2 distinct adult phases, the IP and the TP, with clear color and shape distinctions between them. In contrast, *Sc. trispinosus* does not have different adult phases (Moura et al. 2001), so that we used available information on gonad maturation related to fish body size to classify individuals of this species as 'small' (i.e. juveniles and females) or 'large' (i.e. adult males). At the study site, estimates of *Sc. trispinosus* body size at first maturity (i.e. 50% mature) was about 40 cm TL, with 100% of individuals mature at 48 cm TL (Freitas et al. 2012 [unpubl. report] cited by Salz 2015). For *Sc. zelindae*, we considered individuals ≤22 cm TL as small (n = 6, all of them IP) and individuals ≥31 cm TL as large (n = 6, all of them TP). For *Sp. amplum,* TLs for small (IP) and large (TP) individuals were ≤28 cm (n = 5) and ≥31 cm (n = 12), respectively. As *Sc. trispinosus* does not have different adult phases (Moura et al. 2001), individuals ≤40 cm TL (n = 25) and ≥47 cm TL (n = 14) were classified as small and large, respectively, based on the time of maturation as explained above.

Because of the relatively large size, relatively high abundance and the potential key ecological role as a bioeroder played by *Sc. trispinosus* in the studied reefs (Francini-Filho & Moura 2008), we did a more detailed ontogenetic assessment for this species. In this analysis, individuals were classified into 6 size classes for a comprehensive assessment of intraspecific differences in feeding activity and bioerosion. We used 4–9 individuals for each of the following 6 size classes (TL): ~10–20 (n = 8), 21–30 (n = 8), 31–40 (n = 9), 41–50 (n = 5), 51–56 (n = 5) and >58 cm (n = 4) (total n = 39). Although fish size is a continuous variable, we used size categories (discrete) in our main analysis for life phase comparisons and also because our long-term data for the Abrolhos region (Francini-Filho & Moura 2008, Francini-Filho et al. 2010) on fish density and feeding rates were obtained considering size categories, with no absolute measurements available. Thus, the potential functional roles played by parrotfishes across the region could be more easily inferred by using data from the present study based on size categories, especially for *Sc. trispinosus*. Absolute size values were only used in the ANCOVA testing for the effect of body size in between-species comparisons of osteo-morphological attributes (see below).

The morphology of the 2 body size categories within each species, and of the 6 *Sc. trispinosus* size classes considered, were compared (cf. Keast & Webb 1966, Winemiller 1991) considering the following 5 ecomorphological attributes (i.e. linear distances), measured in each fresh specimen (following Gatz 1979, but see also Gibran 2007, 2010): (1) mouth width, defined as the interior lateral dimension of the mouth (fully opened); (2) mouth height, defined as the interior dorsal–ventral dimension of the mouth (fully opened, i.e. mouth gape); (3) head width, corresponding to a horizontal measurement of the head between the center of the eyes; (4) head height, defined as the head depth measured vertically through the center of the eyes; (5) head length, corresponding to the maximum length of the head (i.e. from the tip of the snout to the end of the operculum). Moreover, to allow for functional interpretations, we extracted and weighed 6 principal bony structures of the jaw. Fish heads were boiled and dried, and the following parts were subsequently weighed (cf. Bellwood & Choat 1990): (1) premaxilla; (2) maxilla; (3) dentary; (4) articular bone; (5) hyomandibular; and (6) suspensorium. The operculum was also weighed and included in interspecific comparisons as a control, because it represents a structure unrelated to feeding (Bellwood & Choat 1990). The rationale behind our approach is based on the positive relationship between the weight of bony structure(s) and jaw strength, with more robust and heavier bones plausibly leading to greater impacts on the benthos (Bellwood & Choat 1990).

### 2.3. Feeding activity of *Sc. trispinosus* and consequent bioerosion

The feeding activity of *Sc. trispinosus* and the resulting bioerosion were assessed over 15 non-consecutive days by SCUBA divers, for a total of 523 min of direct observation in February 2012 and 2013. Observations were evenly distributed throughout the day and started immediately after sunrise, before the initiation of parrotfish feeding, and finished at 18:00 h, when parrotfish feeding ceased. Daily feeding rates of *Sc. trispinosus* were quantified by divers who followed individual fish for 1 min (n = 298 replicates, cf. Francini-Filho et al. 2010). Fish were grouped into one of the following size categories: <10, ~20, ~30, ~40, ~50 and >60 cm TL. The total number of bites per foray was also recorded for each individual (n = 225 forays). A foray consists of a series of bites with no discernable interval between them (cf. Bellwood & Choat 1990). Observations were discarded if the individual was lost from sight or showed signs of disturbance due to the presence of divers. Additional observations of *Sc. trispinosus* (n = 226) were conducted to assess the percentage of bites leaving visible marks on the substratum (hereafter referred to as 'significant bites') from fish of different sizes. To accomplish this, divers followed parrotfish individuals (10–70 cm TL) until a bite was delivered, and then recorded how many of the observed bites left visible marks on the substratum per foray (Bruggemann et al. 1996).

Bioerosion rates were only estimated for *Sc. trispinosus* individuals >30 cm TL, as individuals below this size rarely leave significant bite marks (Francini-Filho et al. 2008 and observations in the present study). For assessing theses rates, we followed these individuals and, once a significant bite was left, it was measured and the piece of consolidated substratum containing the fresh mark was collected using a hammer and chisel. A total of 39 fresh bite marks were measured and collected. To standardize our methods, we only considered bites on calcareous matrix covered by crustose calcareous algae (CCA) and the epilithic algae matrix (EAM). These samples were brought to the surface, labeled, photographed, fixed in 4% formalin and subsequently stored in 10% ethanol. In the laboratory, bite volume was assessed using alginate impressions with chlorhexidine (cf. Bellwood 1995a). Five molds of each bite mark were made to minimize variation in measurements. After drying, molds were removed and weighed, and the volume of each bite was calculated from the mean weights of the 5 molds.

Feeding day length (FDL) was used to assess the total activity time of *Sc. trispinosus* $d^{-1}$. FDL is defined as the time between the first and the last recorded bite (in min) by a species in a given day (Bellwood 1995a). For FDL estimates, time was standardized to minutes after midnight, and day length (DL) was considered as the period between sunrise and sunset (Bellwood 1995a). The proportion of the day spent performing feeding activities was calculated as FDL × 100/DL (Bellwood 1995a). The total number of bites $d^{-1}$ was then calculated by plotting feeding rate against time (bites $min^{-1}$). As feeding initiation and termination were abrupt, all zeros were removed. A quadratic polynomial line was fitted to the data, and the area under the line represented the duration of feeding and was used to estimate the total number of bites taken on a given day (cf. Bellwood 1995a). To ensure a representative sample size, calculations were made for 2 pooled size categories (TL <30 and >30 cm).

Erosion rates of *Sc. trispinosus* were estimated using bite volumes, significant bites per foray and daily feeding rates for individuals >30 cm TL, as they frequently left significant bite marks, and thus potentially contribute more to bioerosion than do smaller individuals (Francini-Filho et al. 2008). Bioerosion rates were estimated as follows (cf. Bellwood 1995a, Bruggemann et al. 1996):

$$\text{ERB (cm}^3\text{ bite}^{-1}) = \text{MBV} \times \text{PSB} \tag{1}$$

$$\text{ERD (cm}^3\text{ ind.}^{-1}\text{ d}^{-1}) = \text{ERB} \times \text{MDBR} \tag{2}$$

where ERB = erosion rate per bite, MBV = mean bite volume, PSB = proportion of significant bites, ERD = erosion rate per day, MDBR = mean daily bite rate.

Yearly erosion rates were then calculated by multiplying daily rates by 365, and overall error terms were calculated using Goodman's estimator (Travis 1982). Regional extrapolation of total bioerosion by *Sc. trispinosus* was calculated by using mean fish density data collected in a previous study during 5 successive summers (2005–2009) at 18 sites in the study area (see Francini-Filho & Moura 2008 and Francini-Filho et al. 2013 for details). Fifteen to 30 censuses were obtained per site per year using the stationary visual census technique (Minte-Vera et al. 2008), and individual fish were recorded in the 5 following size classes: <10, 10–20, 20–30, 30–40 and >40 cm TL. Mean *Sc. trispinosus* density (ind. $m^{-2}$) for fish >30 cm was estimated for each of the 3 studied portions of the Abrolhos Bank (i.e. inner-shelf, mid-shelf biogenic reefs and mid-shelf rocky reefs; see Moura et al. 2011). Absolute abundances were then extrapolated for each area/portion (ind. $m^{-2}$ × each reef total area) by obtaining total reef area through extensive side scan sonar surveys (see Moura et al. 2013). Annual erosion rates in the Abrolhos Bank were then obtained by multiplying the absolute abundance of *Sc. trispinosus* (>30 cm TL) by the annual bioerosion rate per individual.

### 2.4. Statistical analyses

To assess morphological and osteological similarities among species and among body size categories within each species, as well as among the 6 size classes of *Sc. trispinosus*, rectangular data matrices with the original values of morphometric (mm) and osteological (g) attributes were first submitted to a normalization technique to scale data, thus removing allometric effects of body size (cf. Lleonart et al. 2000). As size and shape are important properties of organisms with important functional and ecological implications (Marroig 2007), the use of this normalization technique allows morphological comparisons adjusting one measure of body size ($Y$) to another ($X$) in the following form: $Y_i^* = Y_i \left[\frac{X_0}{X_i}\right]^b$, where $Y_i^*$ is the predicted value of $Y$ for individual $i$ after correcting for the underlying scaling relationship between $Y$ and $X$; $X_i$ and $Y_i$ are the observed values of $X$ and $Y$ for individual $i$; $b$ is the slope from the ordinary least squares regression on log transformed $Y$ and $X$ variables, and $X_0$ and arbitrary $X$ values are the mean for the study population (see Lleonart et al. 2000, Peig & Green 2009).

Second, the data contained in the normalized matrices were then standardized to $Z$-scores for a normal distribution and, third, they were submitted to a linear discriminant analysis (LDA ordination) and MANOVA, as groups are known *a priori*. Normalization and standardization were performed with Excel, and LDAs/MANOVAs were conducted using the R software version 3.5.2 (R Core Team 2014). The use of normalized and standardized data allows for the interpretation of the first LDA axes as shape-related rather than size-related axes, reducing the chance of bias due to body size (see Lleonart et al. 2000). Two-way ANOVAs were then used to compare each morphometric and osteological attribute, with species (3 levels) and size categories (2 levels) used as fixed factors and the morphometric and osteological attributes as the response variables. Separate 2-way ANOVAs were used for each variable. For a more detailed ontogenetic analysis of *Sc. trispinosus*, 1-way ANOVA was used to evaluate variations in ecomorphological attributes among the 6 size classes. For these evaluations, the critical p-value was corrected using the Bonferroni adjustment for 11 different tests (i.e. $p = 0.0045$ for a test aiming a type I error of 5%; Quinn & Keough 2002). We also used 1-way ANOVAs to test whether feeding rates, proportion of significant bites, bite volume and feeding periods differed among *Sc. trispinosus* size classes. To meet ANOVA assumptions of normality and homoscedasticity, we used the same normalization and standardization procedures as for LDA. When significant differences were found, post hoc Tukey tests were used to detect the sources of variation and potential interactions. ANOVA and post hoc tests were also conducted using the same R software.

As a complementary approach, we used ANCOVAs to compare the 3 species as fixed factors and absolute log transformed data for body size (TL, measured to the nearest millimeter) as a continuous variable, as covariates, for each of the morphological (length) and osteological (head/bone weight) variables. These latter analyses were also conducted with the R software. In this case, we aimed to compare the results obtained with the allometric model of Lleonart et al. (2000) and a classical model in which size is statistically controlled (ANCOVA). This is because different species may show differences for a given size class due to differences in the proportions of osteo-morphological variables, while different size classes may show differences because of size *per se* (i.e. different length ranges). To meet ANCOVA assumptions, we first tested if the 3 species significantly differed in body size (with size as a continuous variable) using ANOVA, with results ($F_{2,65} = 1.8$; $p = 0.173$) showing that ANCOVA could be applied.

The relationship between body size and rates of bioerosion of *Sc. trispinosus* and 12 other parrotfish species from the literature was explored using generalized additive models (GAMs). Models were built using a Gaussian distribution, an identity link and cubic regression splines (Hastie & Tibshirani 1990).

## 3. RESULTS

### 3.1. Osteology

Jawbone morphology differed markedly among species, especially between genera (Figs. 2 & 3). In the 2 *Scarus* species, the mouth closes with the premaxilla in front of the dentary, while in *Sparisoma amplum*, the pattern is the opposite. The premaxilla structure also differed between genera, as the *Scarus* species have a longer ascending process than *Sp. amplum* and a complete absence of maxillary fossa in the alveolar process, which was present in the latter. Furthermore, the 2 *Scarus* species have larger and deeper dental plates with multiple overlapping small teeth, in contrast to a single row of larger teeth in *Sp. amplum*. *Sc. trispinosus* has a relatively thick layer of blue-green cement, while large *Sc. zelindae* have 3 lateral canines on the premaxilla at the end of the tooth row in the anterior portion of the alveolar process. Two lateral canines are also present in *Sp. amplum*, but absent in *Sc. trispinosus*. The dentary of the 2 *Scarus* species has a coronoid process with rounded cutting edges, which are crenate in *Sp. amplum*, and a poorly developed articular socket that

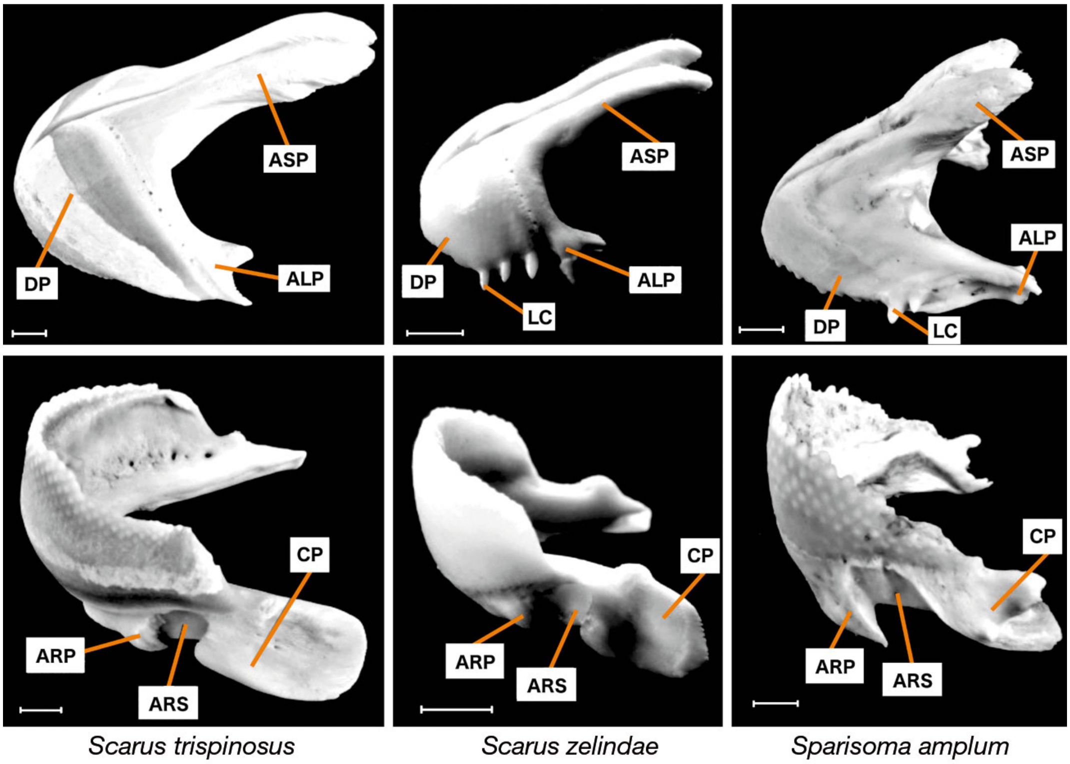

Fig. 2. Premaxilla (upper row) and dentary (lower row) jaw bones of 3 parrotfish species endemic to the SW Atlantic. DP: dental plates; ASP: ascending process; ALP: alveolar process; LC: lateral canine; ARP: articular process; ARS: articular socket; CP: coronoid process. Scale bars = 5 mm

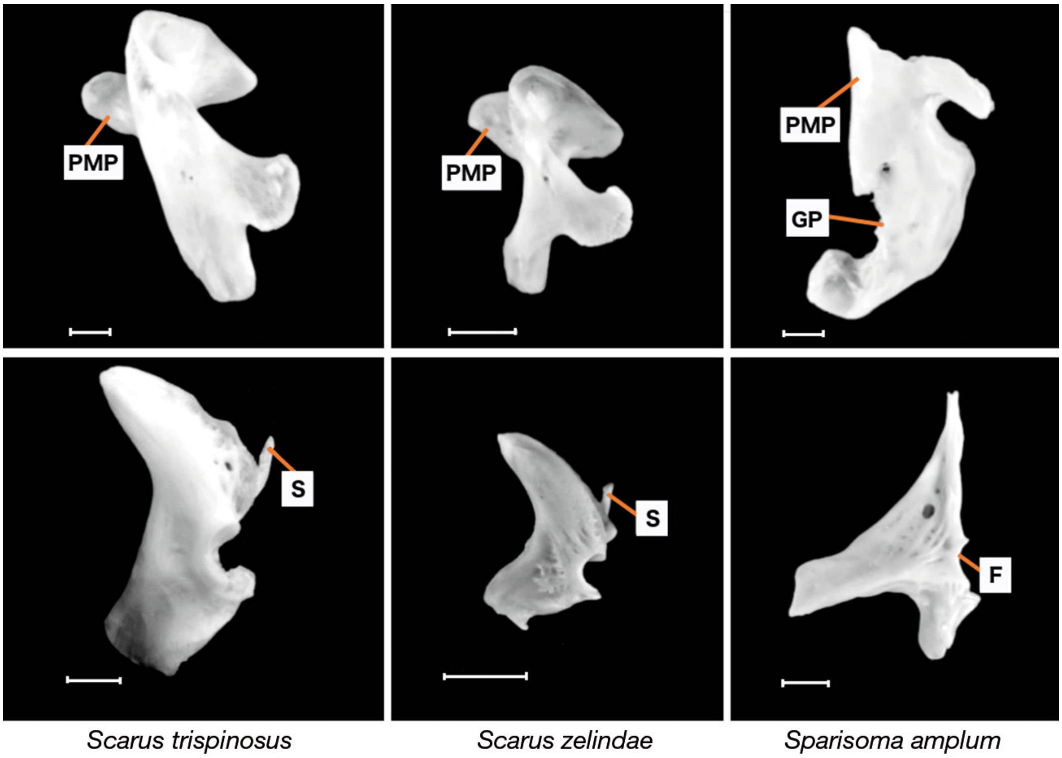

Fig. 3. Maxilla (upper row) and articular (lower row) jaw bones of 3 parrotfish species endemic to the SW Atlantic. PMP: premaxillary process; GP: grooved process; S: spine; F: flange. Scale bars = 5 mm

is more extensive and well-developed in *Sp. amplum*. The maxilla of *Sp. amplum* has an unusual grooved process, where the maxillary arm abuts the premaxilla, and the maxillary arm is limited to the alveolar process of the premaxilla. The premaxillary process is broad and elongate and extends vertically to the middle of the bone. The articular bone of *Sp. amplum* is triangular, with a medial flange on the descending process extending up to the anterior ascending process (the flange is reduced to an articular medial spine in the *Scarus* species; Figs. 2 & 3).

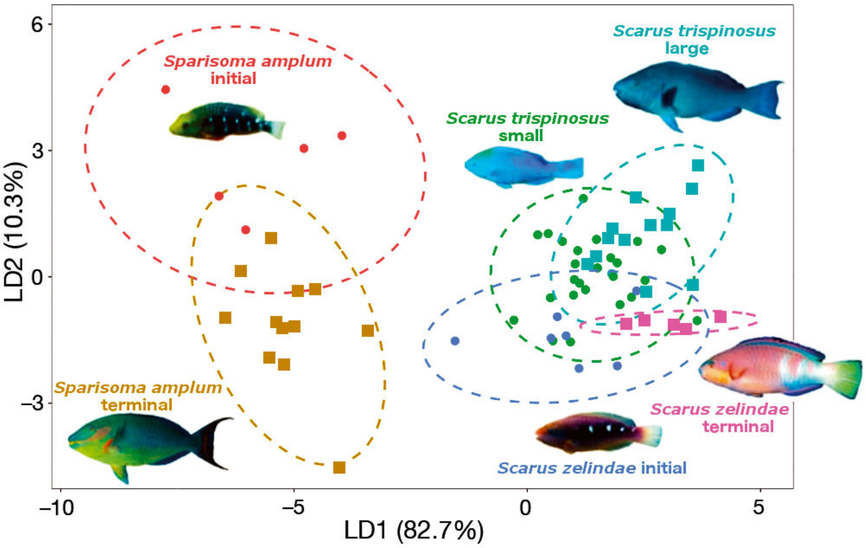

Fig. 4. Distribution of fish individuals considering 2 size categories ('small' and 'large', as defined in Section 2.2) for 3 parrotfish species based on scores from the 2 first linear discriminant analysis (LDA) axes for both morphometric and osteological attributes. Dashed ellipses are 95% confidence intervals. 'Initial' and 'terminal' refer to life cycle phases

### 3.2. Ecomorphology

In the LDA ordination with 5 morphometric and 7 osteological attributes, species and size categories, the first (LD1) and second (LD2) axes accounted for 93% of the cumulative variation (Fig. 4). These first 2 axes were mainly influenced by premaxilla, maxilla, dentary, articular and suspensorium weights (Table S1 in the Supplement, www.int-res.com/articles/suppl/m629p149_supp.pdf) with the parrotfish species and size categories distinguished by mouth and head height, as well as dentary, suspensorium and operculum weights (LDA MANOVA $F_{5,62} = 3.42$; $p < 0.001$; Fig. S1 in the Supplement). There is a clear discrimination of genera (*Scarus* spp. to the right on the LD1 axis versus *Sp. amplum* to the left), with *Sc. trispinosus* presenting the heaviest premaxilla and *Sp. amplum* having the heaviest dentary and suspensorium (Fig. 4, Table S1, Fig. S1). There is also a clear discrimination between small (IP) versus large (TP) individuals of *Sc. zelindae* (also by LD1 axis), and a clear discrimination between small (IP) versus large (TP) individuals of *Sp. amplum* (higher and lower on the LD2 axis, respectively; Fig. 4). We also found a positive relationship between bone weight and body size for all species. The results of this ordination also corroborate the need for a more detailed analysis for *Sc. trispinosus* (Fig. 4).

We found no significant differences between size categories for the 3 parrotfish species. Interactions between species and size categories were observed for head height, maxilla, articular and suspensorium weights, with the variables head height and suspensorium weight also presenting differences among species (Table 1). Significant differences between species were only detected for mouth height and dentary and operculum weights, with *Sp. amplum* presenting the highest mouth and strongest and heaviest dentary (Table 1, Fig. S1). Considering pairwise comparisons for species, we found some differences in mouth height (only between *Sc. trispinosus* and *Sp. amplum*, $p < 0.01$); head height (between *Scarus* spp. and *Sp. amplum*, $p < 0.01$); dentary (between *Scarus* spp. and *Sp. amplum*, $p < 0.001$); suspensorium (between *Scarus* spp. and *Sp. amplum*, $p < 0.01$); and operculum (only between *Sc. trispinosus* and *Sp. amplum*, $p = 0.05$). Considering the 2 unique variables with differences among species and interactions between species and size categories (head height and suspensorium weight, Table 1), we found differences for head height between small (IP) versus large (TP) *Sp. amplum* (Tukey post hoc, $p < 0.05$), and between small (IP) *Sp. amplum* versus small or large *Scarus* spp. (Tukey post hoc, $p < 0.05$). We also found differences between large individuals of *Sc. trispinosus* versus *Sp. amplum* for suspensorium (Tukey post hoc, $p < 0.05$). Head height, premaxilla, dentary and hyomandibular have different growth rates for each species (Table S2).

For *Sc. trispinosus* size classes, we also found a positive relationship between bone weight and body size. A clear distinction was recorded only between small individuals (<40 cm TL, left of 0.5 units on

Table 1. Two-way ANOVA for body size category (small and large; see Section 2.2 for definitions) of 3 parrotfish species (*Scarus trispinosus*, *Scarus zelindae* and *Sparisoma amplum*) on 12 ecomorphological attributes. **Bold**: significant differences ($p < 0.05$)

| Source | df | MS | *F* | p |
|---|---|---|---|---|
| Mouth width | | | | |
| Species | 2 | 0.0518 | 0.052 | 0.949 |
| Size category | 1 | 0.0000 | 0.000 | 0.994 |
| Species × Size category | 2 | 2.8235 | 2.864 | 0.065 |
| Residuals | 62 | 0.9859 | | |
| Mouth height | | | | |
| Species | 2 | 4.925 | 5.527 | **0.006** |
| Size category | 1 | 0.644 | 0.722 | 0.399 |
| Species × Size category | 2 | 0.590 | 0.662 | 0.519 |
| Residuals | 62 | 0.891 | | |
| Head width | | | | |
| Species | 2 | 0.1722 | 0.162 | 0.851 |
| Size category | 1 | 0.2466 | 0.232 | 0.632 |
| Species × Size category | 2 | 0.2448 | 0.231 | 0.795 |
| Residuals | 62 | 1.0619 | | |
| Head height | | | | |
| Species | 2 | 5.847 | 8.332 | **<0.001** |
| Size category | 1 | 0.171 | 0.244 | 0.623 |
| Species × Size category | 2 | 5.809 | 8.277 | **<0.001** |
| Residuals | 62 | 0.702 | | |
| Head length | | | | |
| Species | 2 | 0.0446 | 0.045 | 0.956 |
| Size category | 1 | 1.0617 | 1.070 | 0.305 |
| Species × Size category | 2 | 2.1020 | 2.118 | 0.129 |
| Residuals | 62 | 0.9926 | | |
| Premaxilla weight | | | | |
| Species | 2 | 2.2049 | 2.297 | 0.109 |
| Size category | 1 | 0.4068 | 0.424 | 0.517 |
| Species × Size category | 2 | 1.0865 | 1.132 | 0.329 |
| Residuals | 62 | 0.9600 | | |
| Maxilla weight | | | | |
| Species | 2 | 0.186 | 0.178 | 0.837 |
| Size category | 1 | 0.256 | 0.246 | 0.621 |
| Species × Size category | 2 | 3.435 | 3.291 | **0.043** |
| Residuals | 62 | 1.044 | | |
| Dentary weight | | | | |
| Species | 2 | 8.134 | 10.151 | **<0.001** |
| Size category | 1 | 0.002 | 0.003 | 0.957 |
| Species × Size category | 2 | 0.546 | 0.681 | 0.509 |
| Residuals | 62 | 0.801 | | |
| Articular weight | | | | |
| Species | 2 | 0.547 | 0.570 | 0.568 |
| Size category | 1 | 0.061 | 0.064 | 0.801 |
| Species × Size category | 2 | 3.251 | 3.388 | **0.040** |
| Residuals | 62 | 0.959 | | |
| Hyomandibular weight | | | | |
| Species | 2 | 2.7299 | 2.636 | 0.079 |
| Size category | 1 | 0.0478 | 0.046 | 0.830 |
| Species × Size category | 2 | 0.3409 | 0.329 | 0.720 |
| Residuals | 62 | 1.0356 | | |
| Suspensorium weight | | | | |
| Species | 2 | 6.641 | 8.541 | **<0.001** |
| Size category | 1 | 0.162 | 0.208 | 0.649 |
| Species × Size category | 2 | 2.572 | 3.308 | **0.043** |
| Residuals | 62 | 0.777 | | |
| Operculum weight | | | | |
| Species | 2 | 3.285 | 3.788 | **0.028** |
| Size category | 1 | 0.000 | 0.000 | 0.994 |
| Species × Size category | 2 | 2.186 | 2.521 | 0.088 |
| Residuals | 62 | 0.867 | | |

the LD1 axis) versus large individuals (>40 cm TL, right of 0.5 units on the LD1 axis, especially those >58 cm TL) (Fig. 5, Table S1). Combined, the 2 first LDA axes accounted for 85% of the total variation (Fig. 5). Large individuals (≥40 cm TL) with large, heavy and strong jaw apparatuses are on the right side of LDA axis 1 (Fig. 5; LDA MANOVA $F_{5,33} = 1.58$; $p < 0.05$); therefore, a greater force of bite is more evident for the largest sizes of *Sc. trispinosus*, as they also show wider mouths and greater head height only due to growth (i.e. no significant differences after Bonferroni corrections were recorded for any variable after removing allometric effects of body size), corroborating the ontogenetic gradient due to body dimensions.

### 3.3. Feeding activity of *Sc. trispinosus* and consequent bioerosion

The feeding rates of *Sc. trispinosus* decreased with body size (Table 2), although bites of all size classes were mostly (97%) on EAM and CCA. In contrast, the proportion of significant bites (i.e. the ones leaving scars) per foray increased with fish body size, ranging from 9–30% for the smallest sizes (~10–30 cm TL), and 59–75% for the largest sizes (~40–60 cm TL). Bite volume also increased with body size, with ~50–60 cm TL individuals removing up to 5-fold more substratum per bite than individuals with ~30–40 cm TL (mean ± SE: 0.12 ± 0.09 versus 0.04 ± 0.03 cm$^3$, respectively) (Table 2). Feeding rates, the proportion of significant bites, bite volume and feeding periods differed ontogenetically ($p \leq 0.01$).

*Sc. trispinosus* feeding rates varied significantly throughout the day, with a peak between 09:00 and 12:00 h (Fig. 6). Estimated number of bites d$^{-1}$ was 5585 and 4995 for individuals <30 and >30 cm TL, respectively (Table 2). Estimated bioerosion rate per bite for individuals >30 cm TL was 207 cm$^3$ of substratum d$^{-1}$, and annual erosion rate was 75 534 cm$^3$ (overall Goodman's error term = 1710.98).

Reef area, density and total abundance were used as parameters for estimating bioerosion rates of *Sc. trispinosus* in the Abrolhos Bank (Table 3). Higher densities of this species were recorded in the rocky reefs of the Archipelago, followed by the mid-shelf biogenic reefs of Parcel dos Abrolhos. Reefs on the inner shelf had lower fish densities. Bioerosion rates were highest in the Parcel dos Abrolhos (biogenic reefs, mid-shelf), followed by the inner arc biogenic reefs of Pedra de Leste and the rocky reefs of the Abrolhos Archipelago (mid-shelf) (Table 3). However,

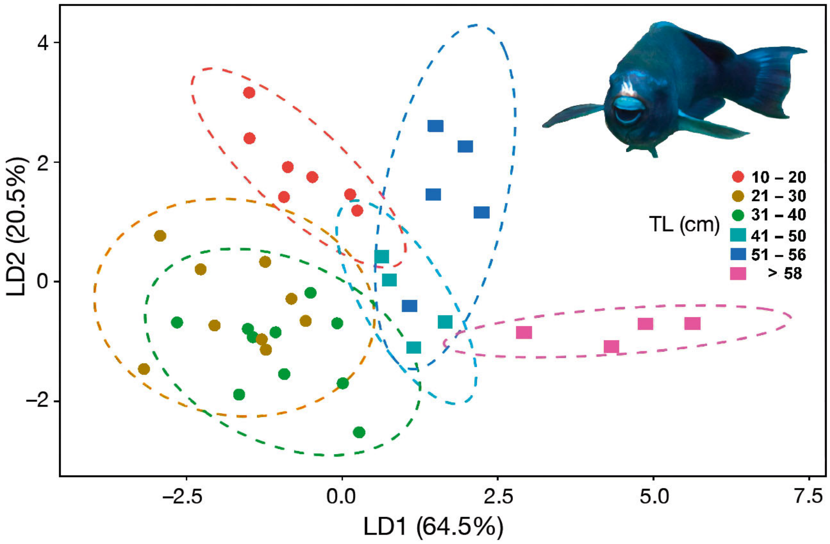

Fig. 5. Distribution of *Scarus trispinosus* individuals from 6 size classes of total length based on scores from the 2 first LDA axes for both morphometric and osteological attributes. Circles are small individuals and squares are large individuals (see Section 2.2 for size definitions). Dashed ellipses are 95% confidence intervals

Table 2. Feeding rates (mean ± SE), proportion of significant bites (i.e. those leaving visible marks), bite volume and daily feeding rates for each size class of *Scarus trispinosus* in the SW Atlantic. Within columns, means followed by the same lowercase letters indicate similar groups ($p > 0.05$). Individuals with total length (TL) <20 cm only left superficial bite marks, and so bite volume was not estimated

| Size class (cm TL) | Feeding rate (bites min$^{-1}$) | Significant bites per foray (%) | Bite volume (cm$^{3}$) | Daily feeding rates (bites d$^{-1}$) |
|---|---|---|---|---|
| <10 | 8.54 ± 3.6$^{a}$ | 09$^{a}$ | – | 5584.86 |
| ~20 | 8.49 ± 7.3$^{a}$ | 11$^{a}$ | – | (<30 cm TL) |
| ~30 | 7.54 ± 4.8$^{a}$ | 30$^{a}$ | 0.025 ± 0.03 | |
| ~40 | 6.84 ± 4.8$^{a}$ | 59$^{b}$ | 0.046 ± 0.03 | 4995.25 |
| ~50 | 3.06 ± 3.4$^{b}$ | 60$^{b}$ | 0.13 ± 0.12 | (>30 cm TL) |
| >60 | 1.52 ± 1.8$^{b}$ | 75$^{b}$ | 0.11 ± 0.07 | |

rates of annual bioerosion per reef area were 1.5-fold higher in the Archipelago than in the Parcel dos Abrolhos, and 2.6-fold higher in the Archipelago than in the inner shelf reefs (Table 3).

## 4. DISCUSSION

Our results provide the first ecomorphological comparison among 3 parrotfishes endemic to the SW Atlantic: *Scarus trispinosus, Sc. zelindae* and *Sparisoma amplum* (Moura et al. 2001, Robertson et al. 2006). We also provide the first estimates of bioerosion combined with the ecomorphology and feeding activity of *Sc. trispinosus*. The heavy premaxilla and large body size of *Sc. trispinosus* and the strong dentary of *Sp. amplum*, along with previous information on their feeding behavior (see Francini-Filho et al. 2010), suggest that these species play unique roles as excavating parrotfishes in the Abrolhos region. This information is relevant considering that only 2 other large parrotfish species occur in the study area (*Sp. axillare* and *Sp. frondosum*), both predominantly browsers and scrapers (Francini-Filho et al. 2010). Our results reinforce that studies on oral jaw morphology and osteology, associated with field observations, are valid tools to assess parrotfish feeding modes and potential impacts on the benthos.

Despite the several roles played by parrotfish in tropical reefs (see Bonaldo et al. 2014 for a review), body size is, within species, probably directly related to jaw force when biting the substratum (Bruggemann et al. 1994, Bonaldo & Bellwood 2008, Lokrantz et al. 2008, Cardozo-Ferreira et al. 2018). As we found

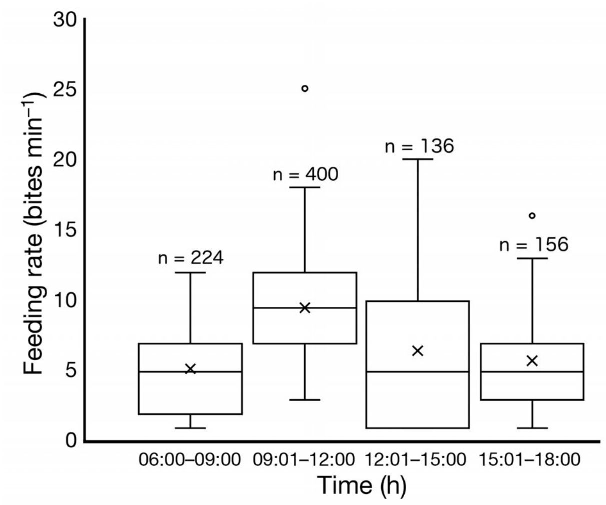

Fig. 6. *Scarus trispinosus* daily feeding rates from 06:00 to 18:00 h in the Abrolhos Bank, SW Atlantic, showing the number of bites for each 3 h interval considering only individuals >30 cm in total length. Whiskers denote minimum and maximum values (empty circles are outliers). Box denotes the first and third quartiles. Middle line indicates the median, and '×' indicates the mean

Table 3. Parameters used for estimating bioerosion rates of *Scarus trispinosus* (only for individuals with total length >30 cm) in the Abrolhos Bank

| Study site | Reef area ($km^2$) | Mean density (ind. $m^{-2}$) | Total abundance | Daily erosion ($cm^3$ $d^{-1}$) | Annual erosion ($cm^3$ $yr^{-1}$) |
|---|---|---|---|---|---|
| Inner-shelf (biogenic) | 38.7 | 0.003 | $11.1 \times 10^6$ | $26.5 \times 10^6$ | $9.7 \times 10^9$ |
| Mid-shelf (biogenic) | 292.2 | 0.005 | $144.9 \times 10^6$ | $344.2 \times 10^6$ | $125.6 \times 10^9$ |
| Mid-shelf (Archipelago) | 2.3 | 0.007 | $1.7 \times 10^6$ | $4.0 \times 10^6$ | $1.5 \times 10^9$ |

no differences between individuals of the same body size category, and head height, dentary, premaxilla and hyomandibular showed different growth rates for each species, we can conclude that *Sc. trispinosus* and *Sp. amplum* shift their ecological roles mostly due to growth (i.e. larger mouths and heads, and heavier jaw bones, promoting stronger and wider bites that are more capable of removing the substratum when compared to weaker structures of juveniles or IP individuals). These results corroborate previous studies in other locations, in which parrotfishes also shifted from browsers and scrapers to excavators as they grow, and reinforce that the functional roles of parrotfishes are largely size-dependent (Bruggemann et al. 1994, Bonaldo & Bellwood 2008, Lokrantz et al. 2008, Cardozo-Ferreira et al. 2018, Smith et al. 2018).

In our study, discrimination of species and sizes in the ecomorphological space was largely influenced by mouth/head height, and dentary and suspensorium weights, features associated with bite force and ability to excavate hard substrata (Bellwood & Choat 1990). In contrast, small individuals of *Sc. trispinosus* and *Sp. amplum* and all individuals of *Sc. zelindae* had relatively weaker jaw bones. This result is consistent with previous reports of scraping or browsing feeding modes for IP or juveniles of parrotfishes (e.g. Bellwood & Choat 1990, Bruggemann et al. 1994, 1996, Lokrantz et al. 2008), and of scraping habits of *Sc. zelindae* irrespective of the ontogenetic phase (Francini-Filho et al. 2010, Pereira et al. 2016, Cardozo-Ferreira et al. 2018). Therefore, our results reinforce the importance of the relative weights of oral structures for assessing parrotfish feeding, and corroborate previous studies (e.g. Francini-Filho et al. 2008, 2010), suggesting that large *Sc. trispinosus* and *Sp. amplum* are the main functionally excavating parrotfishes in the SW Atlantic (Hoey et al. 2018).

Because *Sc. trispinosus* is far more abundant than *Sp. amplum* in Abrolhos and is thus plausibly the most important functionally excavating parrotfish in local reefs, population declines may have profound impacts on the benthic dynamics. Indeed, recent studies indicate that *Sc. trispinosus* have suffered massive declines in abundance in Brazil, particularly in the Abrolhos region, and, as a consequence, this species is considered Endangered by the IUCN (Padovani-Ferreira et al. 2012). Considering the unique ecological roles of *Sc. trispinosus* in the Abrolhos reefs, losses and even reductions of populations of this species may directly affect the dynamics of these systems, possibly impairing reef resistance/resilience in face of major disturbances. Therefore, measures aimed at protecting this species and recovery of its populations are key to the conservation and healthy functioning of SW Atlantic reefs.

In the present study, small *Sc. trispinosus* (<40 cm TL) had the highest feeding rates, while large individuals (>40 cm TL) delivered all observed significant bites. These results agree with previous studies comparing different-sized parrotfishes in other locations (e.g. Bruggemann et al. 1996, Bonaldo & Bellwood 2008, Lokrantz et al. 2008, Adam et al. 2018), and support the hypothesis that body size is key in shaping parrotfish function (Bruggemann et al. 1994, Mumby et al. 2006, Ong & Holland 2010, Cardozo-Ferreira et al. 2018). In this sense, the feeding of small individuals seems more related to the control of (or impacting) algal growth by grazing, whereas feeding by large excavators opens areas on the reef that can facilitate the settlement of corals and other benthic organisms (Bonaldo & Bellwood 2008, 2009, Bonaldo et al. 2014). The highest feeding rates for *Sc. trispinosus* were observed from late morning until midday, a common pattern for herbivorous reef fish (Zemke-White et al. 2002, Bonaldo & Bellwood 2008). This trend likely stems from daily variation in the nutritional quality of algae, which increases in the morning, peaks at midday and remains constant in the afternoon (Zemke-White et al. 2002). However, *Sc. trispinosus* may also ingest other food items associated with substratum coverage, including microorganisms and small crustaceans (cf. Kramer et al. 2013, Clements et al. 2017). Thus, further studies are needed to better understand drivers of daily patterns in foraging activity and feeding of parrotfishes.

Estimates of parrotfish bite volumes may vary greatly depending on substratum type, abundance and size of fishes (Bellwood 1995a, Bruggemann et al. 1996, Bonaldo & Bellwood 2008, Alwany et al. 2009, Ong & Holland 2010), ranging from 0.002 $cm^3$

Table 4. Bioerosion rates for parrotfishes in different regions of the world. Only studies with the same metric used in the present study (i.e. volume removed per individual per year) were considered. Size of studied individuals (Fish size), maximum known sizes (Max size) for studied species (obtained from Froese & Pauly 2019), annual bioerosion rates and data sources are given. TL: total length; na: not available

| Location | Species | Fish size (cm; TL) | Max size (cm; TL) | Annual bioerosion rate ($cm^3$ $yr^{-1}$) | Reference |
|---|---|---|---|---|---|
| Abrolhos, Brazil, Atlantic Ocean | *Scarus trispinosus* | 30–65 | 86[a] | 75 500 | Present study |
| Great Barrier Reef, Australia, Pacific Ocean | *Chlorurus gibbus* | 35–44 | 70 | 410 000 | Bellwood (1995a) |
| Great Barrier Reef, Australia, Pacific Ocean | *Chlorurus sordidus* | 15–20 | 40 | 9700 | Bellwood (1995a) |
| Great Barrier Reef, Australia, Pacific Ocean | *Bolbometopon muricatum* | na | 130 | 2 330 000 | Bellwood et al. (2003) |
| Hawaii, USA, Pacific Ocean | *Scarus rubroviolaceus* | 25–54 | 70 | 126 667 | Ong & Holland (2010) |
| Hawaii, USA, Pacific Ocean | *Chlorurus perspicillatus* | 25–54 | 69[b] | 230 000 | Ong & Holland (2010) |
| Red Sea, Egypt, Indian Ocean | *Cetoscarus bicolor* | na | 59[b] | 178 704 | Alwany et al. (2009) |
| Red Sea, Egypt, Indian Ocean | *Chlorurus gibbus* | na | 70 | 205 860 | Alwany et al. (2009) |
| Red Sea, Egypt, Indian Ocean | *Chlorurus sordidus* | na | 40 | 30 660 | Alwany et al. (2009) |
| Red Sea, Egypt, Indian Ocean | *Scarus ferrugineus* | na | 41 | 30 222 | Alwany et al. (2009) |
| Red Sea, Egypt, Indian Ocean | *Scarus frenatus* | na | 47 | 31 098 | Alwany et al. (2009) |
| Red Sea, Egypt, Indian Ocean | *Scarus ghobban* | na | 75 | 180 456 | Alwany et al. (2009) |
| Red Sea, Egypt, Indian Ocean | *Scarus niger* | na | 40 | 10 950 | Alwany et al. (2009) |

[a] Size recorded by the author for 1 individual obtained from fish landings in the Abrolhos Bank, Brazil

[b] Sizes converted from standard length (SL) to total length (TL) using equations from Froese & Pauly 2019

(*Sc. niger*, Red Sea; Alwany et al. 2009) to 1.6 $cm^3$ (*Bolbometopon muricatum*, Indo-Pacific and Red Sea; Bellwood et al. 2003). The bite volume of *Sc. trispinosus* is about 0.08 $cm^3$ with all sizes pooled, and this value increases to 0.12 ± 0.09 (mean ± SE) when considering only individuals >50 cm TL. Thus, the contribution of large individuals to bioerosion is disproportionate, and the loss of large parrotfishes reduces bioerosion even if the overall parrotfish biomass remains the same (Bruggemann et al. 1996, Bonaldo & Bellwood 2008, Ong & Holland 2010).

Estimates of annual bioerosion for *Sc. trispinosus* (0.076 $m^3$ $ind^{-1}$ $yr^{-1}$) were smaller than those for congeners such as *Sc. rubroviolaceus* (0.126 $m^3$ $ind.^{-1}$ $yr^{-1}$) (Ong & Holland 2010), as *Sc. trispinosus* presents lower bite rates (4955 vs. 9154 bites $d^{-1}$) and a smaller proportion of significant bites than *Sc. rubroviolaceus* (51 vs. 68 %, respectively). A broader comparison, using literature data with the same metric used here (i.e. volume removed per species per unit of time) showed that maximum size attained by each species is an important predictor of bioerosion rates, even when not considering huge species such as *B. muricatum* (Table 4; Fig. 7). This result was expected and corroborates the idea that large-sized parrotfishes may play key ecological roles on coral reefs (Bonaldo & Bellwood 2008, Ong & Holland 2010).

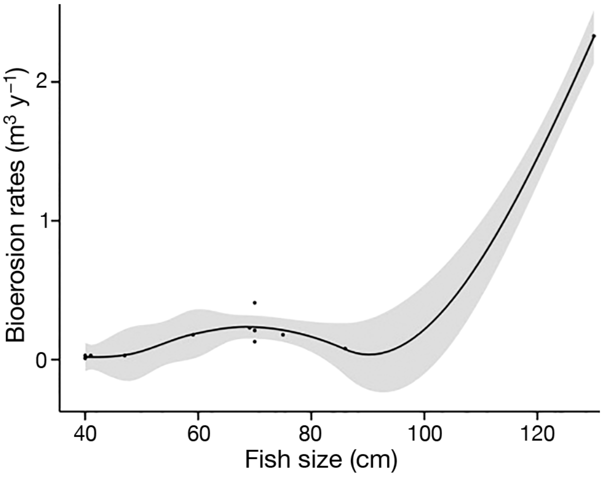

Fig. 7. Generalized additive model showing the relationship between maximum fish size (total length, TL) and annual bioerosion rates for different parrotfish species (see list of species and locations in Table 4) ($p < 0.05$). Gray shading indicates the 95 % confidence interval

Biogenic reefs grow with the deposition of calcium carbonate by reef builders such as corals and CCA. Excavating parrotfishes are important agents of bioerosion (i.e. the removal of carbonate by living organisms) and sediment transportation (Bellwood & Choat 1990, Bonaldo et al. 2014). The mean carbonate production for the same study sites in Abrolhos (2012–2014) measured by using calcification accretion units (CAUs) was 579 ± 98 (SD) g $m^{-2}$ $yr^{-1}$, with CCA as the main reef builder (Reis et al. 2016). Unfortunately, because we did not measure the density of substrates removed and used volume instead of mass, it was not possible to perform comprehensive comparisons between bioerosion by *Sc. trispinosus* and reef accretion rates. Future studies using similar metrics for estimating both reef bioerosion and accretion may help to understand variations in carbonate budgets on coral reefs of the Abrolhos region.

SW Atlantic reefs have low fish richness compared to other biogeographical provinces (Floeter et al. 2008, Bowen et al. 2013), which implies potentially lower functional diversity and redundancy for parrotfishes (Francini-Filho et al. 2008, 2010, 2013, Halpern & Floeter 2008). For instance, only 5 large-bodied parrotfish species (>30 cm TL) occur in Brazil, in contrast to 10 species in the Caribbean and at least 16 in the Indo-Pacific (Bellwood 1995a, Moura et al. 2001, Bonaldo et al. 2014). Furthermore, 9 and 3 parrotfish species are excavators in the Indo-Pacific and the Caribbean, respectively, while only 2 (*Sc. trispinosus* and *Sp. amplum*) are able to act as excavators in the SW Atlantic (Francini-Filho et al. 2010, Bonaldo et al. 2014, present study). The low functional redundancy of large-bodied parrotfishes in the SW Atlantic may influence the dynamics of benthic assemblages, since the roles of these 2 excavating parrotfishes cannot be replaced by any other species (Ferreira & Gonçalves 2006, Francini-Filho et al. 2008, 2010, Cardozo-Ferreira et al. 2018). In contrast, Brazil has a higher richness of parrotfish functional groups, with more browsing and scraping species, than the Eastern Pacific, but still has fewer species and functional groups than other regions where parrotfish ecology has been more frequently studied, such as the Caribbean, Great Barrier Reef and the Red Sea (Bellwood et al. 2018).

Reduction or extirpation of excavating species due to intensive overfishing (Aswani & Hamilton 2004) leads to declines in rates of bioerosion and sediment production, with subsequent potential changes in ecosystem dynamics (Bellwood et al. 2003, 2012, Hoey & Bellwood 2008). Parrotfish overfishing is one of the most important global issues in coral reef conservation (Hughes 1994, Bellwood et al. 2003, 2012), and has become increasingly problematic in Abrolhos in recent years (Francini-Filho & Moura 2008, Freitas et al. 2011). This is particularly concerning given that the area has low fish species richness and, as a consequence, likely has low functional redundancy; these factors together suggest lower ecosystem resilience after reductions or losses of unique species in the system (McCann 2000, Adam et al. 2018).

Our results reinforce the importance of studies on jaw morphology and osteology for the assessment of parrotfish feeding modes and indicate that large adult *Sc. trispinosus* and *Sp. amplum* play unique roles as excavating reef fishes in SW Atlantic reefs.

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