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Comparative feeding morphology and diet of SW Atlantic surgeonfishes

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Herbivores are a key functional group. We used an ecomorphological approach and a dietary analysis to compare the *Acanthurus* species that occur at the largest reef bank of the South Atlantic. We compared the dimensions of heads and mouths, the length and characteristics of the digestive tubes, the dentitions and weights of the jaw bones, and the stomach contents of *Acanthurus bahianus*, *A. chirurgus*, and *A. coeruleus*. They form two ecomorphological groups that reflect their phylogenetic relationships. The detrital feeders *A. bahianus* and *A. chirurgus* have gizzard-like stomachs and are more similar to each other, feeding on a lower ratio of algae. In contrast, *A. coeruleus* has the ecomorphological features and diet of a cropper, as a heavier premaxilla and dentary, and the absence of a gizzard. Contrasting to previous studies for the same reef bank, there was a greater proportion of detritus for *A. bahianus* and *A. chirurgus* (~58%), in addition to 30 times more detritus for *A. coeruleus* and a greater proportion of invertebrates for all species (7.5–13 times), including salps. A lower proportion of algae was found, even for *A. coeruleus*. These finds may be due to their versatile diets and to the neglected importance of detritus composition.

Keywords: Abrolhos Bank, Acanthuridae, Ecomorphology, Herbivory, Jaw morphology.

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Herbívoros são um grupo funcional chave. Utilizamos uma abordagem ecomorfológica, juntamente com análise da dieta, para compararmos as espécies de peixes *Acanthurus* do maior banco recifal do Atlântico Sul. Comparamos as dimensões das cabeças e bocas, as características e comprimentos dos tubos digestórios, as dentições e os pesos dos ossos maxilares, além dos conteúdos estomacais de *Acanthurus bahianus*, *A. chirurgus* e *A. coeruleus*. Essas espécies formam dois grupos ecomorfológicos que refletem suas relações filogenéticas. Os detritívoros *A. bahianus* e *A. chirurgus* têm estômagos com moelas e são mais semelhantes entre si, alimentando-se em menor proporção de algas. Em contraste, *A. coeruleus* tem as características ecomorfológicas e dieta de um podador, com uma pré-maxila e dentário mais pesados, e a ausência de moela. Contrastando com estudos anteriores no mesmo banco recifal, encontramos uma maior proporção de detritos para *A. bahianus* e *A. chirurgus* (~58%), além de 30 vezes mais detritos para *A. coeruleus* e uma maior proporção de ingestão de invertebrados para todas as três espécies (7,5–13 vezes), incluindo salpas. Uma menor proporção na ingestão de algas também foi registrada, mesmo para *A. coeruleus.* Estes resultados podem ser consequência de suas dietas versáteis e à importância negligenciada da composição dos detritos.

Palavras-chave: Acanthuridae, Banco dos Abrolhos, Ecomorfologia, Herbivoria, Morfologia bucal.

INTRODUCTION

Herbivorous fishes are a key functional group in tropical reef communities (Bellwood *et al*., 2004). In addition to their major contribution to fish biomass, these fishes affect the distribution, abundance, and biomass of algae and the epilithic algae matrix (EAM), which comprises turfing algae, detritus, cryptofauna, microorganisms, unicellular algae, and inorganic sediment (Purcell, Bellwood, 2001; Kramer *et al*., 2012). In addition to algae, many herbivorous fishes also ingest fauna and detritus associated with the EAM, which might account for 10 to 78% of all food items in the algal matrix, likely playing a significant nutritional role for these species (Crossman *et al*., 2001; Choat *et al*., 2002; Wilson, 2002; Wilson *et al*., 2003; Bos *et al*., 2017). As primary consumers of these resources, herbivorous fishes are important links, transferring energy from the algal matrix/detritus to secondary consumers (Wilson *et al*., 2003), thereby essential for structuring and maintaining coral reef communities (Hay, 1991; Bellwood, 2003; Cordeiro *et al*., 2016).

Among the dominant nominally herbivorous fishes in coral reefs (Horn, 1989; Bellwood *et al*., 2004; Francini-Filho *et al*., 2010), surgeonfishes (Acanthuridae) representing over a quarter of tropical marine herbivorous fishes (Vergés *et al*., 2014). With approximately 85 species (Tebbett *et al*., 2022), they have inhabited reef habitats since the Middle Eocene (Bellwood, 1996; Bellwood, Wainwright, 2002; Tebbett *et al*., 2022). Their long evolutionary history is closely linked with that of coral reef ecosystems and has resulted in the emergence of species with varied morphological, physiological, and behavioral characteristics (Choat *et al*., 2002; Friedman *et al*., 2016; Tebbett *et al*., 2022). These morphological variations significantly influence the potential use of nutritional resources, as variations in morphological traits result in differences in function and performance (Karr, James, 1975; Wainwright, 1991, 1994; Motta *et al*., 1995). In this sense, differences in morphology among closely related species might indicate both evolutionary and ecological divergence, especially in sympatric and congeneric species (Van der Klaauw, 1948; Winemiller, 1991; Winemiller *et al*., 1995), as suggested by variations in dental and stomach morphology (Horn, 1989; Choat, 1991; Bellwood *et al*., 2014a,b; Siqueira *et al*., 2019a; Tebbett *et al*., 2022), as well as differences in the relative length of the digestive tube (Elliott, Belwood, 2003) and mouth size (Norton, 1991). For morphological (head morphology) and functional traits (jaw motion and feeding kinematics associated to biting and pull algae off the substrate) specifically relating to surgeonfishes, see Mihalitsis, Wainwright (2024), Mihalitsis *et al.* (2025), and Perevolotsky *et al.* (2025).

Within the South Atlantic, the Abrolhos Bank, Bahia State, Brazil, is the largest and most biodiverse reef system (Joly *et al*., 1969; Leão, Kikuchi, 2001; Dutra *et al*., 2005; Segal, Castro, 2011), encompassing approximately 11% nominally herbivorous fish species among its ichthyofauna (Moura, Francini-Filho, 2006). Three species of *Acanthurus*, *Acanthurus bahianus* Castelnau, 1855, *A. chirurgus* (Bloch, 1787), and *A. coeruleus* Bloch & Schneider, 1801, are especially abundant in this region, being widely distributed along the Brazilian coast, playing key ecological roles in various habitats (Menezes *et al*., 2003; Francini-Filho *et al*., 2010). These species present distinct feeding habits, with *A. coeruleus* being largely associated with algae and EAM ingestion (see Ferreira, Gonçalves, 2006; Francini-Filho *et al*., 2010; Siqueira *et al*., 2019a), while *A. chirurgus* and *A. bahianus*, two phylogenetically closer species (Sorenson *et al*., 2013; Friedman *et al*., 2016; Siqueira *et al*., 2019b), are considered sediment suckers (Tebbett *et al*., 2022). This variation in feeding ecology offers valuable insights into their functional roles, which is crucial for understanding the dynamics of herbivorous fishes in this reef bank.

Coral reefs, the most biodiverse of all marine ecosystems, are at the forefront of environmental changes (Barlow *et al*., 2018), and the configurations of these ecosystems will continue to change as coral cover decreases due to anthropogenic impacts and climate change (Bellwood *et al*., 2019a; Vercelloni *et al*., 2020; Tebbett *et al*., 2022). In this sense, the roles played by different functional groups may change, and defining the main ecosystem functions to be preserved may depend on context (Bellwood *et al*., 2019b; Tebbett *et al*., 2022). Despite extensive research on herbivorous fish in Indo-Pacific reefs (Siqueira *et al*., 2019a; Tebbett *et al*., 2022), studies in the South Atlantic remain limited. So, considering the close link between form and function, related to how fish species use food resources (see Karr, James, 1975; Wainwright, 1991, 1994; Motta *et al*., 1995), we describe and compare the feeding morphology and diet of the three *Acanthurus* species in the Abrolhos coral reef system. Our study thus addresses three main questions within the context of the ecomorphological hypothesis that species with similar feeding morphologies share similarities in ecology: (1) How do these *Acanthurus* species differ in their feeding morphology? (2) Do such differences reflect differences in the use of food resources? (3) Do their diet compositions differ in the proportions and categories of ingested items? By answering these questions, we aim to contribute to understanding the functional roles of surgeonfishes in the Brazilian

Province. We expect to find the closest similarities between *A. bahianus* and *A. chirurgus* due to their close evolutionary relationships (see Sorenson *et al*., 2013; Friedman *et al*., 2016; Siqueira *et al*., 2019b).

MATERIAL AND METHODS

Study site and collections. A field study was conducted in the Abrolhos Bank, northeastern Brazil (16–20°S 37–39°W), at sites up to 20 m deep. The Abrolhos bank is an enlargement of the continental shelf with an area of approximately 46,000 km² (Moura *et al*., 2013). The main coral reef formations consist of mushroom-shaped pinnacles 5–25 m in height and 20–300 m in length at their top (Francini-Filho *et al*., 2013). Due to its relatively high degree of endemism and specificity, the Abrolhos Marine National Park (AMNP) was created in 1983 to promote environmental protection against fishing activities in two discontinuous areas: Timbebas and the Archipelago and Parcel dos Abrolhos. The field activities detailed below were conducted at AMNP and the coastal Parcel das Paredes (PP), within the Ponta da Baleia Environmental Protected Area (Fig. 1).

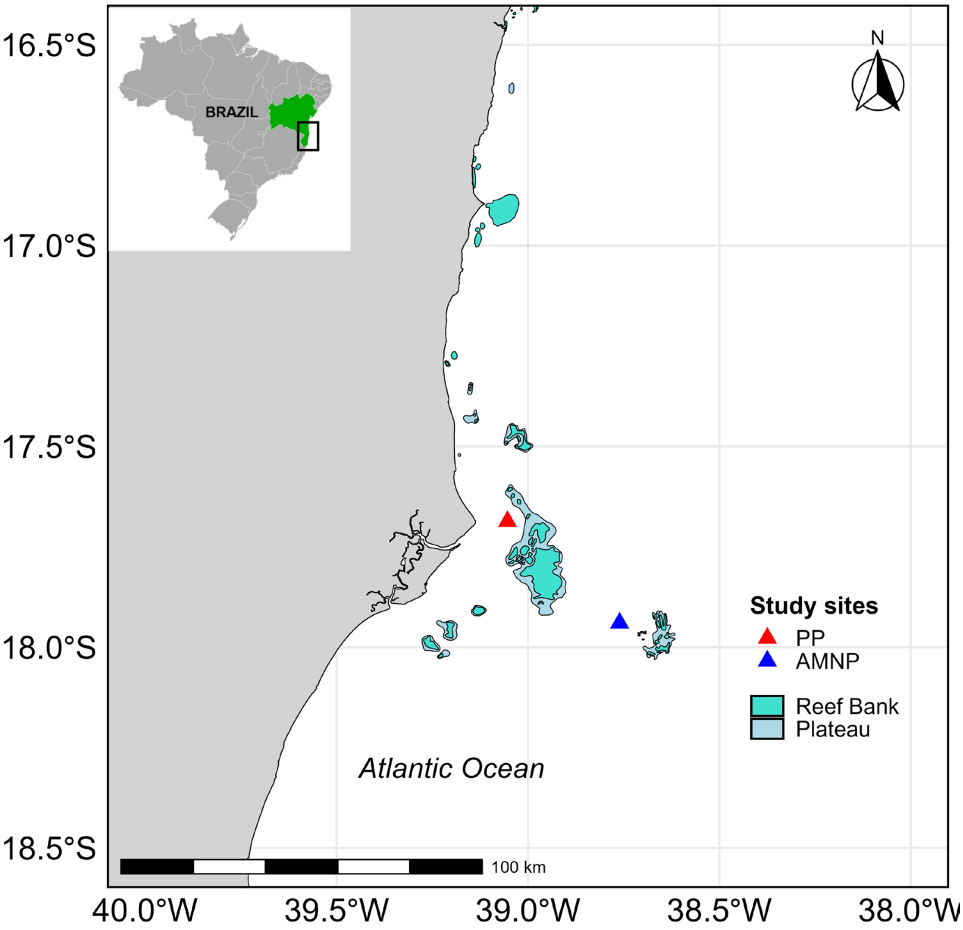

FIGURE 1 | Map of the Abrolhos Bank, northeastern Brazil, showing study sites and marine protected areas. AMNP = Abrolhos Marine National Park; PP = Parcel das Paredes.

Fish collections were conducted during the austral summer (February 2016, March 2017) and spring (October 2017), totaling 25 sampling days. Fresh fish specimens were collected by speargun during their diurnal foraging activity at the study site (between 08:00–17:00 h; FZG, 2016, pers. obs.), always after ingestion events, and were immediately euthanized by pithing. As references for confirmation of species identification see, *e.g.*, MZUSP 60836 for *A. bahianus*, MZUSP 60500 for *A. chirurgus*, and MZUSP 60521 for *A. coeruleus*, at Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil. A total of 14 individuals of *A. coeruleus* (188–370 mm ± 13.27 of total length, TL; total weight: 137–1,150 g ± 70.90) and 16 individuals of both *A. bahianus* (115–245 mm ± 9.82 TL; total weight: 31–295 g ± 17.61) and *A. chirurgus* (133–280 mm ± 9.93 TL; total weight: 53–550 g ± 35.50) were collected. All specimens were weighted to the nearest 0.1 g, measured with a digital caliper to the nearest 0.1 mm, and then fixed in 10% formalin within 1 h of capture to preserve the digestive tube and gut contents.

Osteology and ecomorphology. We compared the natural size and shape of the heads and mouths (see Keast, Webb, 1966; Belwood, Choat, 1990; Winemiller, 1991; Motta *et al*., 1995) of the three *Acanthurus* species considering linear distances of ecomorphological dimensions (see Tab. **S1**; following Gatz, 1979, and, where applicable, Gibran, 2007, 2010). The ecomorphological measures considered included head length (HL), head height (HH), head width (HW), head width on the eyes line (HWE), mouth width (MW), mouth height (MH), and digestive tube length (DTL), expressed in millimeters, which were chosen based on their functional interpretations – mouth dimensions use to be related to bite size and the amount of food; head dimensions, together with mouth dimensions, jaw bones and articulations, are related to feeding kinematics; head dimensions, as the relation of length and height, may be related to space utilization during biting, as more elongated and laterally compressed heads, associated with body shape, function as a control surface when biting, for fishes that feeding biting the substrate; and DTL is expected to be related to diet composition and trophic ecology (see Keast, Webb, 1966; Gatz, 1979; Mihalitsis, Wainwright, 2024; Mihalitsis *et al*., 2025; Perevolotsky *et al*., 2025).

For osteological analysis, premaxilla, maxilla, dentary, and articular weight were considered. All jaw bones evaluated were extracted from freshly collected specimens via boiling and dissection (*cf.* Belwood, Choat, 1990). The osteological analyses were based on the weights of jaw bones and related articulations following Purcell, Bellwood (1993), and Lellys *et al*. (2019); for this analysis, four adult specimens for both *A. bahianus* and *A. chirurgus* and three adult specimens for *A. coeruleus* were used. The comparative analysis also considered a visual description of the dentition, jaw bones, and of the general digestive tube morphology.

To assess morphological similarities among species, rectangular data matrices with values of morphometric attributes and weight of the jaw bones were first adjusted to body size and weight by removing allometric effects (*cf.* Lleonart *et al*., 2000; Marroig, 2007) according to the following function:

$$Y_i^* = Y_i \; [X_o / X_i]^b$$

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 means for the study population (see Lleonart *et al*., 2000; Peig, Green, 2009; Lellys *et al*., 2019).

To properly test for differences across species, we normalized the adjusted data to Z scores (Gauch, 1982; Ludwig, Reynolds, 1988; Quinn, Keough, 2002; Legendre, Legendre, 2012; Lellys *et al*., 2019). The use of normalized and standardized data allows for the interpretation of data as shape-related rather than size-related, reducing the chance of bias due to body size (Lleonart *et al*., 2000; Lellys *et al*., 2019).

Diet and feeding morphology. We analyzed the stomach contents of all collected specimens. We removed the digestive tubes, individualized each stomach, and separated the food items into three main categories under a stereomicroscope: algae, fauna, and sediment, including both detritus and inorganic sediment. Organic (detritus) and inorganic sediment were then separately quantified by the difference in weight before and after burning sedimentary material in a muffle furnace at 500°C for 5 h, to acquire the dry weight of inorganic sediment. As the three studied species are nominally herbivorous and details on algae composition are known for the three species in the same studied region (see Ferreira, Gonçalves, 2006), we focused here on a comprehensive detailed description of the fauna ingested. We calculated the percent composition (*cf*. Hynes, 1950) of food groups from the total weight of each category and the frequency of occurrence of the faunal food items (*cf*. Bowen, 1992), representing the number of fish in which each food item occurs, listed as a percentage. It is important to note that, since no observations of ingestion were included in this study, it is not possible to determine whether fragments found in the stomach contents were the results of direct ingestion or incidental consumption of detrital material from the substrate. In this context, all animal parts identified in the stomach contents were categorized as "fauna", while only the organic sediment was classified as detritus.

Statistical analysis. All data was tested for normality and homoscedasticity using the Shapiro-Wilk and Levene tests; two (fauna and inorganic sediment) out of 30 variable combinations did not follow a normal distribution. Therefore, data were either log-transformed or standardized to Z-scores before analysis. Morphological differentiation among species was initially assessed using linear discriminant analysis (LDA) (see Gauch, 1982; Ludwig, Reynolds, 1988; Quinn, Keough, 2002; Legendre, Legendre, 2012; Lellys *et al*., 2019). LD1–LD2 scores from model predictions were plotted with species-specific convex hulls, and the percentage of variance explained by each discriminant axis was calculated from the model eigenvalues. To test whether there are significant differences in morphology among species we used a PERMANOVA from a distance matrix using Euclidean distance. To verify which variables contributed to the morphological differences observed between each pair of species we performed a similarity percentage test (SIMPER). Differences in osteological comparisons (weight of the jaw bones) were visualized using a principal component analysis (PCA) and tested using a PERMANOVA. Additionally, one-way ANOVA was applied to each bone variable, followed by Tukey's post hoc test when $p < 0.05$. To verify which variables contributed to the osteological differences observed between each pair of species, we also performed SIMPER. Each morphometric variable and each category of food items was also analyzed separately using one-way ANOVA, to test differences among species, followed by Tukey's post hoc test when $p < 0.05$. For each PERMANOVA, the PERMDISP test was applied to ensure no differences in dispersion among groups. To explore the correspondence between fish species morphology, and diet composition, we performed a canonical correspondence analysis (CCA), and the significance of the correspondence was tested using Monte Carlo procedure (Legendre, Legendre, 2012). All analyses were conducted using the R software (R Development Core Team 2019, v. 3.5.3: multivariate analyses, including PERMANOVA and CCA were conducted using the "vegan" package; additional multivariate procedures were carried out with functions from the "ade4" package; when appropriate, LDA and generalized linear models were implemented with tools from the "MASS" package; model assumptions and diagnostics, including tests for homogeneity of variances, were assessed using functions from the "car" package).

RESULTS

Osteology. The morphological analysis of the three *Acanthurus* species revealed distinct traits that may influence their feeding ecology. In all evaluated species, the mouth closes with the premaxilla positioned in front of the dentary. The premaxilla of *A. coeruleus* has a longer ascending process, which is shorter and more rounded in *A. bahianus* and more pointed in *A. chirurgus* and *A. coeruleus* (Fig. 2). The alveolar process is rounded in *A. bahianus* and *A. chirurgus* and more flattened in *A. coeruleus*. *Acanthurus coeruleus* also presents a projection at the premaxilla, which is lacking from the other species. Compared with those of *A. bahianus* and *A. chirurgus*, the maxilla of *A. coeruleus* has an elongated premaxillary condyle (shorter in the other species) and a more flattened cranial condyle. For *A. bahianus* and *A. chirurgus*, the maxillary arm is more curved, while in *A. coeruleus,* the jaw insertion fossa is more evident. Dentaries of the three species exhibit similar sizes compared to their respective premaxilla, and *A. coeruleus* stands out for having a longer and wider ventral process with a larger lateral flange. The articular of *A. coeruleus* has a longer ascending process (shorter and more triangular in *A. bahianus* and *A. chirurgus*), a wider articulatory fossa, and a larger and less sharp descending process. The teeth of the three species are similar, elongated and spatulated, with multi-denticles on their margins (an average of ~9–10 denticles, depending on wear) (Fig. 2).

Ecomorphology. Results on ecomorphological features suggest that three species represent two ecomorphological groups. *Acanthurus coeruleus* differed from the other two species mainly because it had the highest head (head height is defined as the head depth measured vertically through the center of the eyes, see Gatz, 1979; Lellys *et al*., 2019) on LD1 (pseudo-$F_{2,43} = 4.16$; $p = 0.01$) and the longest digestive tube, while *A. chirurgus* differed from *A. bahianus* on LD2, with *A. chirurgus* having the longest and widest head and the highest mouth (mouth height is defined as the interior dorsal-ventral dimension of the mouth, fully opened, *i.e.*, mouth gape, see Gatz, 1979; Lellys *et al*., 2019) (Fig. 3; Tabs. **S2**, **S3**).

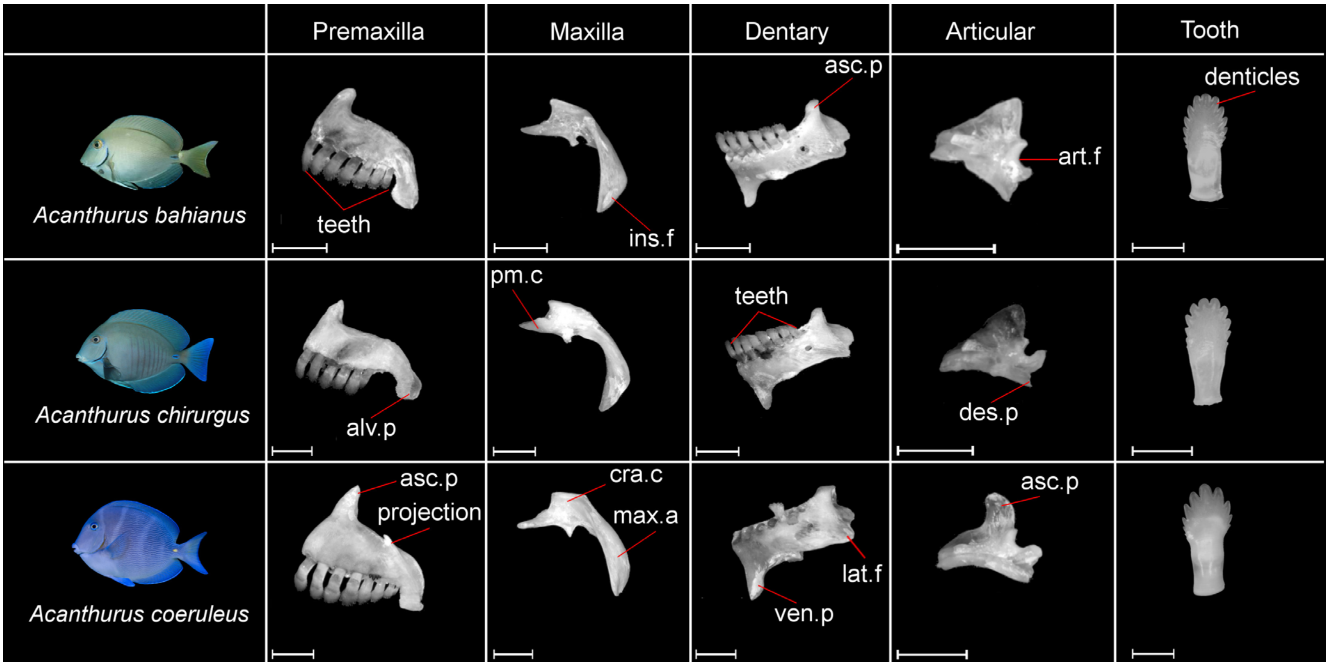

FIGURE 2 | Lateral view of the jaw bones and frontal view of the teeth of *Acanthurus bahianus*, *A. chirurgus*, and *A. coeruleus*. Legends: asc.p: ascending process, alv.p: alveolar process, cra.c: cranial condyle, pm.c: premaxillary condyle, max.a: maxillary arm, ins.f: jaw insertion fossa, lat.f: lateral flange, ven.p: ventral process, art.f: articular fossa of the jaw, des.p: descending process. Scale bars = 4.0 mm for jaw bones and 1.0 mm for tooth.

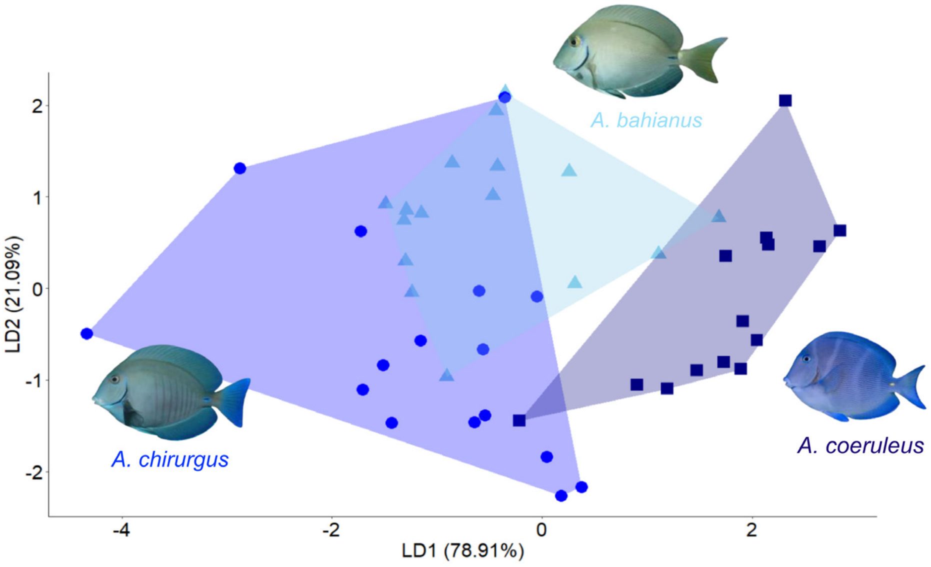

FIGURE 3 | Linear discriminant analysis (LDA) considering seven morphological attributes of the three surgeonfish species of the Abrolhos reefs, Brazil.

The discriminant function had a prediction capacity of 80.43%. The variables mouth height and width, head height, and digestive tube length contributed most to the morphological differences among the three species of the studied *Acanthurus* (Fig. 3; Tabs. **S2**, **S3**). The digestive tubes of the three species are similar, with the main difference being in the stomach. *Acanthurus bahianus* and *A. chirurgus* present stomachs with thick and brawny walls associated with a gizzard-like region. In contrast, *A. coeruleus* has no gizzard (Fig. **S4**). There was no significant difference in the total length of the digestive tubes among species ($F_{2,43} = 0.504$; $p = 0.608$; Fig. 7). Regarding the jaw bones, the weights of the dentary and premaxilla contributed to the differences among the three species ($p < 0.05$; see Fig. 4; Tab. **S5** for statistical tests).

The first two axes of the PCA accounted for 92% of the cumulative variation when using the four osteological attributes (bone weights) (Fig. 5), distinguishing *A. coeruleus* from the other two species mainly because of a heavier premaxilla and dentary (Pseudo-$F_{28} = 15.02$; $p = 0.03$; Fig. 5; see Tabs. **S6**, **S7**).

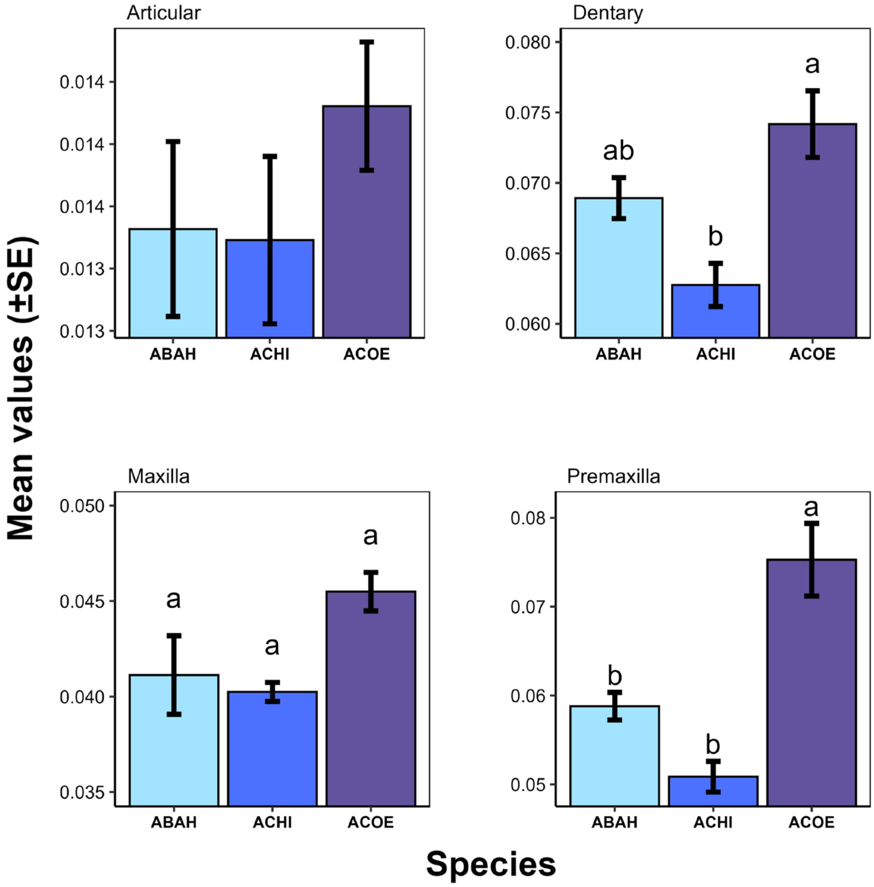

FIGURE 4 | Mean ± SE of the weights (g) of the jaw bones of *Acanthurus bahianus* (ABAH, n = 4), *A. chirurgus* (ACHI, n = 4), and *A. coeruleus* (ACOE, n = 3). Letters above the error bars represent homogeneous groups at $p < 0.5$, as defined by Tukey's test.

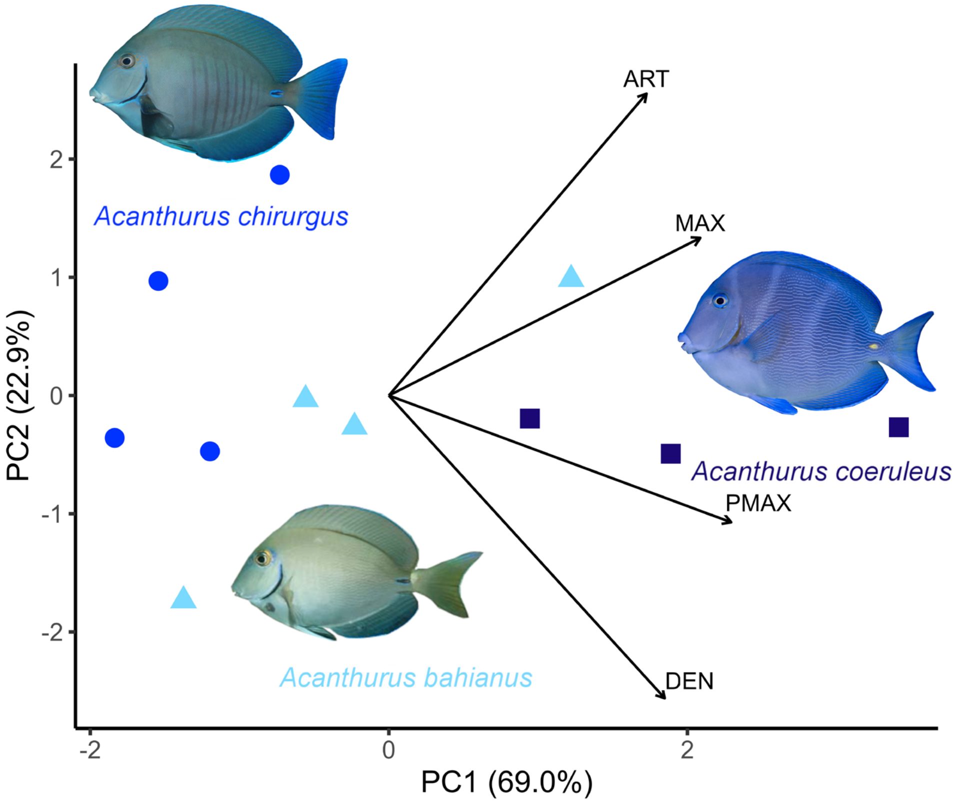

FIGURE 5 | Distribution of individuals of the three surgeonfish species studied based on scores from the first two principal component analysis (PCA) axes for osteological attributes (weight of the jaw bones). ART = articular; MAX = maxilla; PMAX = premaxilla; DEN = dentary.

Diet and feeding morphology. *Acanthurus bahianus* and *A. chirurgus* ingested mainly sediment with organic components (detritus), while *A. coeruleus* ingested mainly algae; and all three species ingested approximately 15–25% of invertebrates (Fig. 6). Among the fauna, sponges were the most frequent (94%) in the *A. chirurgus* and *A. bahianus* stomachs, while salps (Salpidae) were the most frequent (64%) in the *A. coeruleus* stomachs (Tab. 1). In addition to sponges, *A. bahianus* ingested more frequently on crustaceans and gastropods, and *A. chirurgus* ingested more frequently on gastropods, polychaeta worms, crustaceans and salps. In addition to salps, *A. coeruleus* ingested more frequently on crustaceans and sponges and exhibited less diverse faunal ingestion. Parasitic nematodes were frequent in the stomachs of all species (63–86%) (Tab. 1).

In the analysis of morphometric attributes and food items, the head height, head length, head width on the eyes line, mouth height, proportion of algae and proportion of inorganic and organic (detritus) sediments contributed to the differences among the species ($p < 0.05$; Fig. 7; see Tab. **S8**).

The first two CCA axes explained 27.9% of the variation in the diets considering feeding morphology (Fig. 8). Permutation tests confirmed that the CCA was significant (global test: $p = 0.001$). The first three canonical axes explained most of the constrained variation and were all significant (CC1: $p = 0.001$; CC2: $p = 0.001$; CC3: $p = 0.001$), indicating that more than two axes contribute to the relationship between diet

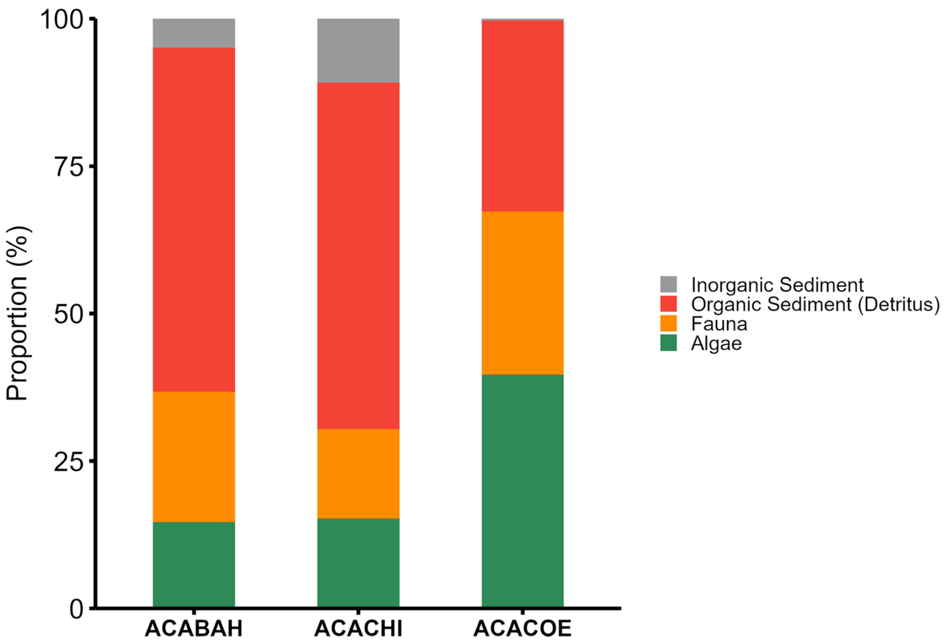

FIGURE 6 | Diet composition (%) of *Acanthurus* species whose stomach contents were grouped into three food categories (organic sediment with detritus, invertebrates/fauna, and algae), also showing the proportion of inorganic sediment. *Acanthurus bahianus* (ACABAH, n = 16), *A. chirurgus* (ACACHI, n = 16), and *A. coeruleus* (ACACOE, n = 14).

TABLE 1 | Frequency of occurrence (%) of faunal items in the stomachs (alphabetical order) of *Acanthurus* species ("-" indicates absence). *Parasite worms.

	A. bahianus **(n = 16)**	***A. chirurgus*** **(n = 16)**	***A. coeruleus*** **(n = 14)**
Amphipoda	19	31	43
Bryozoa	6	19	-
Copepoda	6	19	14
Cumacea	19	13	7
Gastropoda	50	75	7
Hydrozoa	13	-	7
Isopoda	-	13	7
Nematoda*	75	63	86
Ostracoda	31	44	-
Phyllocarida	-	6	14
Polychaeta	25	69	-
Porifera	94	94	44
Salpidae	19	56	64
Tanaidacea	50	63	21

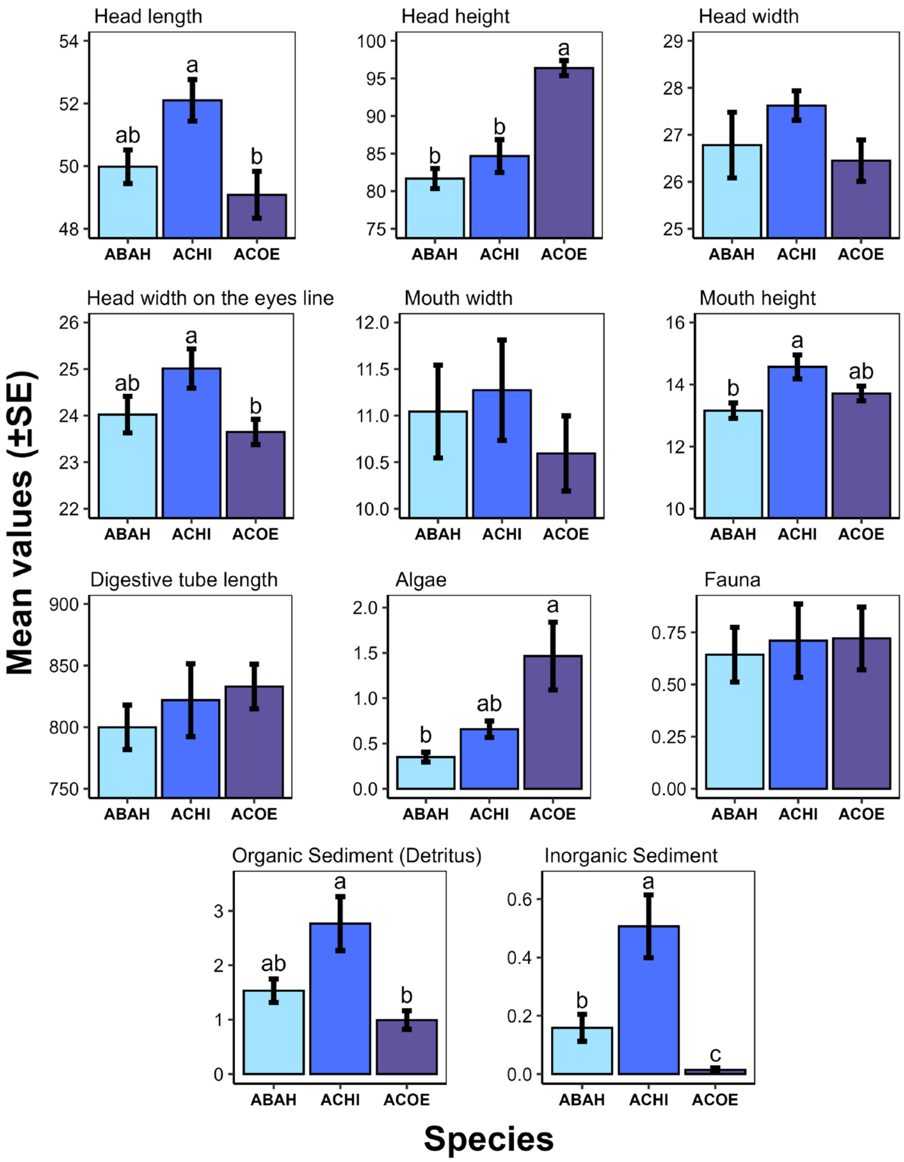

FIGURE 7 | Tests for each variable of morphometric measurements (mm) and for each category of food items (measured in mg and expressed as proportion,) of *Acanthurus bahianus* (ABAH, n = 16), *A. chirurgus* (ACHI, n = 16), and *A. coeruleus* (ACOE, n = 14). Letters above the error bars represent homogeneous groups at p < 0.05, as defined by Tukey's test.

composition and morphology. Marginal tests showed that all diet components (algae, fauna, detritus, and sediment) significantly influenced the ordination (p = 0.001 for all variables), while morphological traits displayed weaker effects, with only head length showing marginal significance (p = 0.089). Therefore, although visual patterns in the first two axes suggest associations between diet categories and certain morphological dimensions, these relationships should be interpreted cautiously because additional axes contribute significantly to the explained variation. There was a relationship between morphology and diet (pseudo-F = 2.301; p = 0.04) for the three species. The amount of fauna in the stomach contents was positively related to the digestive tube length, head width and mouth height (Fig. 8), and we also found a high correlation between algae intake and digestive tube length (r = 0.991) for the three species. The proportion of organic detritus showed a weak association with all morphological variables, being close to the center of the CCA. In contrast, inorganic sediment was positively related to head width, head width at the eye line, and mouth height. Lastly, the proportion of algae was positively related to head height, but negatively related to head width and head length (Fig. 8). *Acanthurus coeruleus* had the highest proportion of algae and the lowest proportion of inorganic and organic sediments (detritus), in contrast to the other two species, which had higher proportions of organic sediment and fauna (Fig. 6).

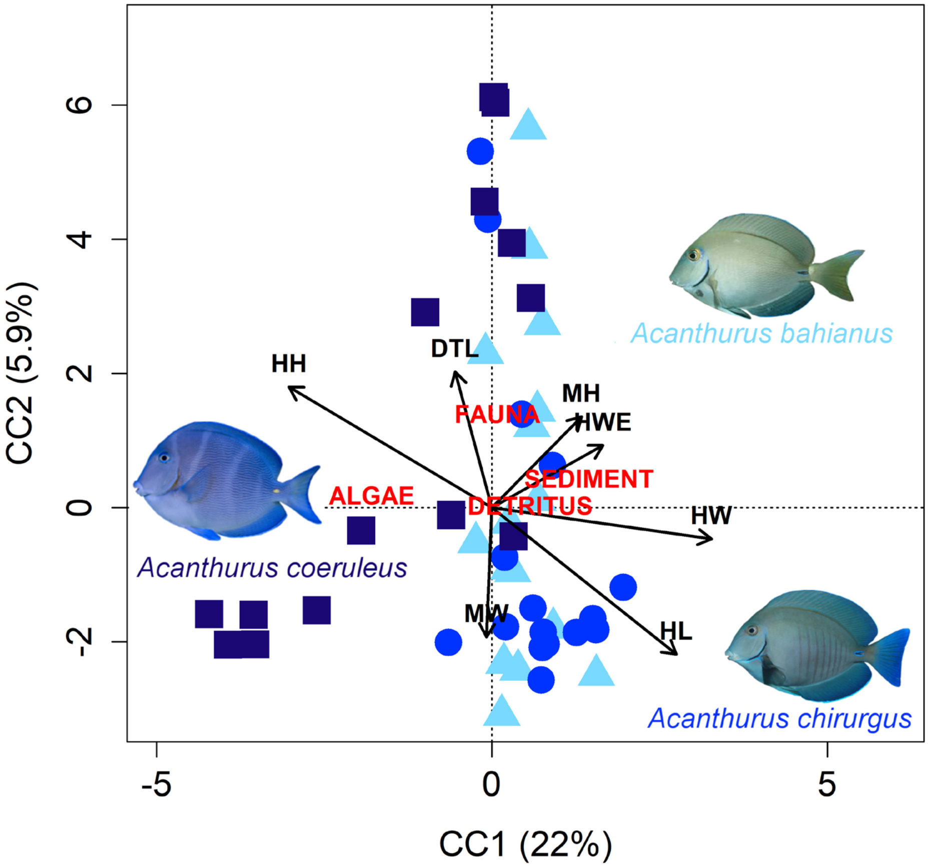

FIGURE 8 | Canonical correspondence analysis showing the relationship between the morphology and diet composition (proportions of food items) of the three *Acanthurus* species in the Abrolhos Reefs, Brazil. DTL: digestive tube length, MH: mouth height, HWE: head width on the eye line, HW: head width, HL: head length, MW: mouth width, HH: head height. “Detritus” refers to organic sediment and “Sediment” to the inorganic sediment portion of the diet contents.

DISCUSSION

Functional analyses have revealed a strong relationship between morphology and feeding behavior in herbivorous reef fishes, highlighting clear links between feeding mode and head morphology (*e.g.*, Bellwood *et al*., 2014a; Mihalitsis, Wainwright, 2024; Mihalitsis *et al*., 2025; Perevolotsky *et al*., 2025). Our study provides the first ecomorphological comparison of feeding and diet among three surgeonfish species co-occurring in the Abrolhos reefs. Based on morphology and diet, the three species were categorized into two ecomorphological groups that reflect their phylogenetic relationships and have a differentiated contribution to the percentage of food item categories. The *A. coeruleus* morphotype primarily differs in head height and the length of digestive tubes, while *A. chirurgus* and *A. bahianus*, despite significant overlap, show differences in head length, width, and mouth height. As expected, there were greater similarities in morphology and diet between the two detrital feeders, *A. chirurgus* and *A. bahianus*. In contrast, *A. coeruleus*, displayed characteristics of a cropper (see Tebbett *et al*., 2022), an herbivorous fish that feeds on filamentous algae, with a higher, shorter, and rounded head, and heavier premaxilla and dentary providing a greater potential for bite strength for turf removal, as observed by Barel (1983, *apud* Purcell, Bellwood, 1993) for *A. nigrofuscus*, a species with a diet more similar to *A. coeruleus*.

The shorter relative head length and higher head in *A. coeruleus* seem to limit biting over the reef, in contrast to *A. chirurgus* and *A. bahianus*, which have more elongated heads (and more elongated bodies and snouts) and wider mouths that allow them to bite, suck, and explore different types of surfaces inside and outside the reef, such as flat sand bottoms covered with biofilm adjacent to the reef (FZG, 2016, pers. obs., but see also Francini-Filho *et al*., 2010; Brandl *et al*., 2015; Tebbett *et al*., 2022), high-energy locations, and also complex surfaces and reef crevices (see Bellwood *et al*., 2014a), a more elongated and laterally compressed head, associated with body shape, function as a control surface when biting, for fishes that feeding biting the substrate (Perevolotsky *et al*., 2025). *Acanthurus coeruleus* has a more circular body and reaches a larger size (up to 39 cm TL; *cf*. Lessa, Nóbrega, 2000) than the other species. Such differences can be related to the phylogenetic history of these species, since *A. bahianus* has the Caribbean *A. tractus* Poey, 1860, as a sister taxon, forming a clade with *A. chirurgus* (Bernal, Rocha, 2011; Friedman *et al*., 2016; Fernandes *et al*., 2021), while sister taxon of *A. coeruleus* is the Indo-Pacific *A. guttatus* Forster, 1801 (see Sorenson *et al*., 2013). The radiation of *A. coeruleus* occurred in the early Miocene, ~21 million years ago, 11 million years earlier than that of *A. chirurgus* and *A. bahianus* (Sorenson *et al*., 2013; Tebbett *et al*., 2022). On modern coral reef fishes, the ability to access exposed reef flats, which had high abundance of EAM, likely gave rise to the detritus-feeding specialists (Bellwood *et al*., 2014a,b). In this sense, *Acanthurus chirurgus* and *A. bahianus* diverged from the ancestral body shape pattern and function after the rise of the genus *Acanthurus* within the rise of the clade of sediment suckers with a gizzard-like stomach (Sorenson *et al*., 2013; Tebbett *et al*., 2022). Additionally, understanding tooth structure is fundamental for interpreting dietary preferences and feeding mechanisms (Bellwood *et al*., 2014b). The morphology of the elongated and spatulated teeth with multi-denticles of the three studied species is a common and conservative feature within the genus *Acanthurus* (Tyler, 1970; Fishelson, Delarea, 2013).

Variation in feeding morphology among the studied surgeonfishes explained 31% of the variation in diet among the species. Morphological and osteological differences may also explain the differences in the functions that they exert in natural reef systems, despite their generally conservative morphology (*e.g*., Brandl *et al*., 2015; Tebbett *et al*., 2022). The most frequent and abundant category in the diet of *A. coeruleus* was algae, accounting for approximately 40% of its diet composition, at least three times more than in the other two species. Although the predominance of algae as the main food item of *A. coeruleus* was reported for the same reef bank 20 years ago (Ferreira, Gonçalves, 2006), we found only half of the values reported by Ferreira, Gonçalves (2006). Despite that, ecomorphological attributes suggest that *A. coeruleus* may play important roles in the removal of EAM and algae (Siqueira *et al*., 2019a). The heavier premaxilla and dentary in *A. coeruleus* are possibly a feature that descends from more ancient lineages of the Eocene, with relatively robust jawed morphologies, as this clade belongs to an older lineage than *A. chirurgus* and *A. bahianus* (Siqueira *et al*., 2019b), without a gizzard, but with a change that may reflect a shift from browsing on macroalgae to cropping short algal turfs in more open EAM-dominated areas, as seen in many extant surgeonfishes (Bellwood *et al*., 2014a). Its role is further supported by its thin-walled acidic stomach and the capacity for fermentative digestion (Purcell, Bellwood, 1993; Choat *et al*., 2004; Tebbett *et al*., 2017), key features separating these fishes from other surgeonfishes that also graze over an open substrate, namely the brushers and sediment suckers (Tebbett *et al*., 2022). However, detailed experimental studies are still needed to corroborate this inference.

Regarding gut morphology, gut length is strongly associated with feeding habits and overall digestive physiology (Jones, 1968). When there is a greater intake of algae matter, the gut is generally more elongated, and the stomach more acidic with thinner walls, as these traits facilitate the breakdown and fermentation of fibrous algal material, which requires longer retention times for effective nutrient extraction (Jones, 1968; Elliott, Belwood, 2003).

Nonetheless, *A. coeruleus* had the highest intake of algae, with a relatively, but not significantly, longer gut. It is possible that the higher acidity in thin-walled stomachs, together with intestinal symbionts, may contribute to the digestion of algae (Lobel, 1981; Horn, 1989; Choat *et al*., 2004; Miyake *et al*., 2015, 2016; Scott *et al*., 2020). In addition, intestinal traits seem to be highly conserved across reef herbivorous fishes (Duque-Correa *et al*., 2024), and in functional studies, intestinal surface area may better reflect ecological differences than intestinal length (Ghilardi *et al*., 2021). *Acanthurus coeruleus* has larger pyloric caeca, and adaptations to increase gut surface area in fishes, such as long intestines and the development of caeca, are alternative features to achieve similar masses of absorptive tissue (Buddington, Diamond, 1986). Alternatively, *A. bahianus* and *A. chirurgus*, as well as all *Acanthurus* species within the same subclade, have a differentiated gizzard-like region in their stomach that is used for the mechanical trituration of detritus (Choat *et al*., 2004). This feature is associated with the emergence of sediment suckers in the Indo-Pacific, which contributes to changes in the trophodynamics of coral reefs, as it allows the exploration of both soft and mixed substrates (Bellwood *et al*., 2017; Tebbett *et al*., 2022). The feeding behavior of sediment-sucking surgeonfishes in the Atlantic is also unique and includes the exploitation of EAM on hard substrates (Robertson, 1991; Francini-Filho *et al*., 2010; Duran *et al*., 2019).

In contrast to previous studies on the *Acanthurus* diet in Abrolhos (Ferreira, Gonçalves, 2006), we found that for both *A. bahianus* and *A. chirurgus,* algae are the least abundant item in the diet, apart from inorganic sediment ingestion. Both species had a greater contribution of fauna (~22% and 15%, respectively) and organic sediment (detritus), accounting for 58% for both species as the main food category. A high proportion of detritus in the diet of both species agrees with previous studies (*e.g*., Dias *et al*., 2001; Ferreira, Gonçalves, 2006; Mendes *et al*., 2018). The differences observed compared to previous studies conducted at the same reef bank two decades ago may be attributed to the study site, as Ferreira, Gonçalves (2006) analyzed the diet in mid-reef areas, while in this study, data include both outer areas as more coastal reefs. Nonetheless, detritus – a heterogeneous complex composed of dead organic matter, protein-rich, derived from living sources, inorganic matter, and microorganisms associated with meiofauna and biofilm (Wilson, 2002; Wilson *et al*., 2003), has nutritional value that may even surpass that of "turf" algae (Choat *et al*., 2002; Crossman *et al*., 2001, 2005; Purcell, Bellwood, 2001; Wilson, 2002). Indeed, Mendes *et al*. (2018) suggested that detritus is the main source of nitrogen for *A. chirurgus*. Likewise, other authors corroborate that micro-photoautotroph organisms, such as diatoms and cyanobacteria, are important components of detritus for herbivorous fishes, including *Acanthurus* species (Cissell *et al*., 2019; Cardozo-Ferreira *et al*., 2023).

We also found greater amounts of fauna than the study of Ferreira, Gonçalves (2006) (~13 times greater for *A. bahianus* and *A. coeruleus*, and ~7.5 times for *A. chirurgus*). Most of the fauna, however, are clearly epifauna associated within algae, EAM, and the substrate. Exceptionally, the presence of salps in more than half of our samples, with nine of the 14 individuals of *A. coeruleus* analyzed and 16 of *A. chirurgus*, with some of them containing more than 50 individuals of salp in a single *Acanthurus* stomach, indicates that this is not a case of accidental ingestion but rather an opportunistic feeding strategy (*i.e*., "trophic adaptability" or the ability of fish to take advantage of the most abundant food items in the environment at a given time; *cf*. Gerking, 1994). This suggests that the proportions of food categories in the diets of *Acanthurus* can be strongly related to the local context of food availability and, thus, to reef temporal dynamics. Furthermore, some *Acanthurus* might exhibit morphological characteristics of generalists, enabling them to explore many alternative resources (Motta *et al*., 1995; Brandl *et al*., 2015; Tebbett *et al*., 2022). Accordingly, studies performed with algivorous surgeonfishes around the world have shown that zooplankton are ingested at a relatively high macroscopic planktonic density (Fishelson, Delaria, 2013).

Another frequent food item here was sponge fragments. During foraging, *A. bahianus* and *A. chirurgus* bite EAM and other reef coverages composed of many organisms or their fragments, which can influence the ingestion of detritus and sponges (FZG, 2016, pers. obs.). The presence of sponge spicules, but not tissue, might suggest incidental ingestion while targeting epilithic photoautotrophic microorganisms (Clements *et al*., 2016). However, sponges can host or harbor high densities of cyanobacteria and zooxanthellae (Easson, Thacker, 2014), nutrient-rich resources that are known to be targeted by other herbivorous fish species (Clements *et al*., 2016; Nicholson, Clements, 2020). There are no reports of intentional ingestion of sponges by the studied Acanthuridae, but sponge predation is mostly neglected due to poor resolution in dietary analyses (Oricchio *et al*., 2016). Ingestion of crustaceans and mollusks may accompany algae and EAM, and they may have important nutritional value for the studied *Acanthurus* species. Phytal fauna, including hydrozoans, bryozoans, foraminifera, and many types of microcrustaceans, are common in several analyzed contents of surgeonfishes around the world (Fishelson, Delaria, 2013). However, the nutritional value of all these items for surgeonfishes is largely unknown, which may lead to underestimations of the level of resource partitioning and trophic innovation on coral reefs (see Clements *et al*., 2016).

Although we have contributed to a better understanding of the feeding morphology and diet of surgeonfishes in Abrolhos, further studies are needed to understand their nutritional ecology, especially in reefs with high natural sedimentation rates and SW Atlantic subtropical reefs, in contrast to the Indo-Pacific reefs (Tebbett *et al*., 2022). Unlike those of specialized herbivorous terrestrial mammals, the nutritional, physiological, metabolic, and gut microbiota of herbivorous fishes are still poorly studied (Choat, Clements, 1998; Clements *et al*., 2009, 2016; but see Thompson *et al*., 2024). Therefore, little is known about how much of the nutrients of algal origin are truly used and assimilated in nominally herbivorous fishes, as little is known about the composition and nutritional value of detritus, and even fauna, for *Acanthurus* species (see Mendes *et al*., 2018; Delgado-Pech *et al*., 2020).

Coral reefs worldwide are at the forefront of environmental changes (Barlow *et al*., 2018), and the configurations of these ecosystems will continue to change as coral cover decreases due to human actions (Bellwood *et al*., 2019a; Vercelloni *et al*., 2020). For example, it is estimated that 50% of the reefs around the world have a greater inflow of terrestrial sediment (Burke *et al*., 2011). This new context is important for understanding reef dynamics and determining which functional ecological roles will be critical in the future (Bellwood *et al*., 2019b; Tebbett *et al*., 2022). Therefore, understanding the role of surgeonfishes will also depend on the future of the Anthropocene reef context (Marshell, Mumb, 2015; Bellwood *et al*., 2019b; Tebbett *et al*., 2022). Thus, decisions regarding the conservation of Anthropocene reefs will require better knowledge of the nutritional ecology of all nominally herbivorous fishes, especially in the SW Atlantic, where the reefs are distinct from those of the Indo-Pacific and Caribbean in terms of structure, biodiversity, and environmental conditions (Mendes *et al*., 2018; Lellys *et al*., 2019; Tebbett *et al*., 2022).

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REFERENCES

- **Barel CDN.** Towards a constructional morphology of cichlid fishes (Teleostei, Perciformes). Neth J Zool. 1983; 33:357–424.
- **Barlow J, França F, Gardner TA, Hicks CC, Lennox GD, Berenguer E *et al*.** The future of hyperdiverse tropical ecosystems. Nature. 2018; 559:517–26. https://doi.org/10.1038/s41586-018-0301-1
- **Bellwood DR.** The Eocene fishes of Monte Bolca: the earliest coral reef fish assemblage. Coral Reefs. 1996; 15:11–19. https://doi.org/10.1007/BF01626074
- **Bellwood DR.** Origins and escalation of herbivory in fishes: a functional perspective. Paleobiology. 2003; 29(1):71–83. https://www.jstor.org/stable/4096875
- **Bellwood DR, Choat JH.** A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. Environ Biol Fishes. 1990; 28:189-214. https://doi.org/10.1007/BF00751035
- **Bellwood DR, Goatley CHR, Bellwood O.** The evolution of fishes and corals on reefs: form, function and interdependence. Biol Rev Camb Philos Soc. 2017; 92:878–901. https://doi.org/10.1111/brv.12259
- **Bellwood DR, Goatley CHR, Brandl SJ, Bellwood O.** Fifty million years of herbivory on coral reefs: fossils, fish and functional innovations. Proc R Soc B. 2014a; 281:20133046. https://doi.org/10.1098/rspb.2013.3046
- **Bellwood DR, Hoey AS, Bellwood O, Goatley CHR.** Evolution of long-toothed fishes and the changing nature of fish-benthos interactions on coral reefs. Nat Commun. 2014b; 5:3144. https://doi.org/10.1038/ncomms4144
- **Bellwood DR, Hughes TP, Folke C, Nyström M.** Confronting the coral reef crisis. Nature. 2004; 429:827–33. https://doi.org/10.1038/nature02691
- **Bellwood DR, Pratchett MS, Morrison TH, Gurney GG, Hughes TP, Á lvarez-Romero JG *et al*.** Coral reef conservation in the Anthropocene: confronting spatial mismatches and prioritizing functions. Biol Conserv. 2019a; 236:604–15. https://doi.org/10.1016/j.biocon.2019.05.056
- **Bellwood DR, Streit RP, Brandl SJ, Tebbett SB.** The meaning of the term ‘function’ in ecology: a coral reef perspective. Funct Ecol. 2019b; 33(6):948–61. https://doi.org/10.1111/1365-2435.13265
- **Bellwood DR, Wainwright PC.** The history and biogeography of fishes on coral reefs. In: Sale PF, editor. Coral reef fishes: dynamics and diversity in a complex ecosystem. San Diego: Academic Press; 2002. p.5–32.
- **Bernal MA, Rocha LA.** *Acanthurus tractus* Poey, 1860, a valid western Atlantic species of surgeonfish (Teleostei, Acanthuridae), distinct from *Acanthurus bahianus* Castelnau, 1855. Zootaxa. 2011; 2905(1):63–68. https://doi.org/10.11646/zootaxa.2905.1.5
- **Bos AR, Cruz-Rivera E, Sanad AM.** Herbivorous fishes *Siganus rivulatus* (Siganidae) and *Zebrasoma desjardinii* (Acanthuridae) feed Ctenophora and Scyphozoa in the Red Sea. Mar Biodivers. 2017; 47:243–46. https://doi.org/10.1007/s12526-016-0454-9
- **Bowen SH.** Quantitative description of the diet. In: Nielsen LA, Johnson DL, editors. Fisheries techniques. Blacksburg: American Fisheries Society; 1992. p.325–36.
- **Brandl SJ, Robbins WD, Bellwood DR.** Exploring the nature of ecological specialization in a coral reef fish community: morphology, diet and foraging microhabitat use. Proc R Soc B. 2015; 282(1815):20151147. https://doi.org/10.1098/rspb.2015.1147
- **Buddington RK, Diamond JM.** Aristotle revisited: the function of pyloric caeca in fish. PNAS. 1986; 83(20):8012–14. https://doi.org/10.1073/pnas.83.20.8012
- **Burke L, Reytar K, Spalding M, Perry A.** Reefs at risk revisited. Washington: World Resources Institute; 2011.
- **Cardozo-Ferreira GC, Ferreira CEL, Choat JH, Mendes TC, Macieira RM, Rezende CE *et al*.** Seasonal variation in diet and isotopic niche of nominally herbivorous fishes in subtropical rocky reefs. Mar Ecol Prog Ser. 2023; 722:125–43. https://doi.org/10.3354/meps14442

- **Choat JH.** The biology of herbivorous fishes on coral reefs. In: Sale PF, editor. The ecology of fishes on coral reefs. San Diego: Academic Press; 1991. p.120–55.
- **Choat JH, Clements KD.** Vertebrate herbivory in marine and terrestrial environments: a nutritional ecology perspective. Annu Rev Ecol Syst. 1998; 29:375–403. https://doi.org/10.1146/annurev.ecolsys.29.1.375
- **Choat JH, Clements KD, Robbins WD.** The trophic status of herbivorous fishes on coral reefs. Mar Biol. 2002; 140:613–23. https://10.1007/s00227-001-0715-3
- **Choat JH, Robbins WD, Clements KD.** The trophic status of herbivorous fishes on coral reefs II: food processing modes and trophodynamics. Mar Biol. 2004; 145:445–54. https://doi.org/10.1007/s00227-004-1341-7
- **Cissell EC, Manning JC, McCoy SJ.** Consumption of benthic cyanobacterial mats on a Caribbean coral reef. Sci Rep. 2019; 9:12693. https://doi.org/10.1038/s41598-019-49126-9
- **Clements KD, German DP, Piché J, Tribollet A, Choat JH.** Integrating ecological roles and trophic diversifcation on coral reefs: multiple lines of evidence identify parrotfishes as microphages. Biol J Linn Soc. 2016; 120:729–51. https://doi.org/10.1111/bij.12914
- **Clements KD, Raubenheimer D, Choat JH.** Nutritional ecology of marine herbivorous fishes: ten years on. Funct Ecol. 2009; 23(1):79–92. https://doi.org/10.1111/j.1365-2435.2008.01524.x
- **Cordeiro CAMM, Mendes TC, Harborne AR, Ferreira CEL.** Spatial distribution of nominally herbivorous fishes across environmental gradients on Brazilian rocky reefs. J Fish Biol. 2016; 89(1):939–58. https://doi.org/10.1111/jfb.12849
- **Crossman DJ, Choat JH, Clements KD.** Nutritional ecology of nominally herbivorous fishes on coral reefs. Mar Ecol Prog Ser. 2005; 296:129–42. https://www.jstor.org/stable/24868626
- **Crossman DJ, Choat JH, Clements KD, Hardy T, McConochie J.** Detritus as food for grazing fishes on coral reefs. Limnol Oceanogr. 2001; 46(7):1596–605. https://doi.org/10.4319/lo.2001.46.7.1596
- **Delgado-Pech B, Almazán-Becerril A, Peniche-Pérez J, Caballero-Vázquez JA.** Facultative scavenging feeding habits in *Acanthurus chirurgus* (Bloch, 1787) (Acanthuriformes: Acanthuridae). Biodivers Data J. 2020; 8:e53712. https://doi.org/10.3897/BDJ.8.e53712
- **Dias T, Rosa IL, Feitoza BM.** Food resource and habitat sharing by the three Western South Atlantic surgeonfishes (Teleostei: Acanthuridae: *Acanthurus*) off Paraiba Coast, northeastern Brazil. Aqua. 2001; 5:1–10.
- **Duque-Correa MJ, Clements KD, Meloro C, Ronco F, Boila A, Indermaur A *et al*.** Diet and habitat as determinants of intestine length in fishes. Rev Fish Biol Fish. 2024; 34:1017–34. https://doi.org/10.1007/s11160-024-09853-3
- **Duran A, Adam TC, Palma L, Moreno S, Collado-Vides L, Burkepile DE.** Feeding behavior in Caribbean surgeonfishes varies across fish size, algal abundance, and habitat characteristics. Mar Ecol. 2019; 40:e12561. https://doi.org/10.1111/maec.12561
- **Dutra GF, Allen GR, Werner T, McKenna SA.** A rapid marine biodiversity assessment of the Abrolhos Bank, Bahia, Brazil, RAP Bulletin of Biological Assessment 38. Washington, D.C.: Conservation International; 2005.
- **Easson CG, Thacker RW.** Phylogenetic signal in the community structure of host-specific microbiomes of tropical marine sponges. Front Microbiol. 2014; 5:532. https://doi.org/10.3389/fmicb.2014.00532
- **Elliott JP, Bellwood DR.** Alimentary tract morphology and diet in three coral reef fish families. J Fish Biol. 2003; 63(6):1598–609. https://doi.org/10.1111/j.1095-8649.2003.00272.x
- **Ferreira CEL, Gonçalves JEA.** Community structure and diet of roving herbivorous reef fishes in the Abrolhos Archipelago, south-western Atlantic. J Fish Biol. 2006; 69(5):1533–51. https://doi.org/10.1111/j.1095-8649.2006.01220.x
- **Fernandes MA, Cioffi MB, Bertollo LAC, Costa GWWF, Motta-Neto CC, Borges AT *et al*.** Evolutionary tracks of chromosomal diversification in surgeonfishes (Acanthuridae: *Acanthurus*) along the world's biogeographic domains. Front Genet. 2021; 12:1–12. https://doi.org/10.3389/fgene.2021.760244

- **Fishelson L, Delarea Y.** Comparison of the oral cavity architecture in surgeonfishes (Acanthuridae, Teleostei), with emphasis on the taste buds and jaw “retention plates”. Environ Biol Fishes. 2013; 97:173–85. https://doi.org/10.1007/s10641-013-0139-1
- **Francini-Filho RB, Coni EOC, Meirelles PM, Amado-Filho GM, Thompson FL, Pereira-Filho GH *et al*.** Dynamics of coral reef benthic assemblages of the Abrolhos Bank, eastern Brazil: inferences on natural and anthropogenic drivers. PLoS ONE. 2013; 8(1):e54260. https://doi.org/10.1371/journal.pone.0054260
- **Francini-Filho RB, Ferreira CM, Coni EOC, Moura RL, Kaufman L.** 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. 2010; 90:481–92. https://doi.org/10.1017/S0025315409991147
- **Friedman ST, Price SA, Hoey AS, Wainwright PC.** Ecomorphological convergence in planktivorous surgeonfishes. J Evol Biol. 2016; 29:965–78. https://doi.org/10.1111/jeb.12837
- **Gatz AJ.** Ecological morphology of freshwater stream fishes. Tulane Stud Zool Bot. 1979; 21:91–124.
- **Gauch HG.** Multivariate analysis in community ecology. New York: Cambridge University Press; 1982.
- **Gerking SD.** Feeding ecology of fishes. San Diego: Academic Press; 1994.
- **Ghilardi M, Schiettekatte NMD, Casey JM, Brandl SJ, Degregori S, Mercière A *et al*.** Phylogeny, body morphology, and trophic level shape intestinal traits in coral reef fishes. Ecol Evol. 2021; 11(19):13218–31. https://doi.org/10.1002/ece3.8045
- **Gibran FZ.** Activity, habitat use, feeding behavior, and diet of four sympatric species of Serranidae (Actinopterygii: Perciformes) in southeastern Brazil. Neotrop Ichthyol. 2007; 5(3):387–98. https://doi.org/10.1590/S1679-62252007000300018
- **Gibran FZ.** Habitat partitioning, habits and convergence among coastal nektonic fish species from the São Sebastião Channel, southeastern Brazil. Neotrop Ichthyol. 2010; 8(2):299–310. https://doi.org/10.1590/S1679-62252010000200008
- **Hay ME.** Fish-seaweed interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey. In: Sale PF, editor. The ecology of fishes on coral reefs. San Diego: Academic Press; 1991. p.96–119.
- **Horn MH.** Biology of marine herbivorous fishes. Oceanogr Mar Biol. 1989; 27:167–272.
- **Hynes HBN.** The food of fresh-water sticklebacks (*Gasterosteus aculeatus* and *Pygosteus pungitius*), with a review of methods used in studies of the food of fishes. J Anim Ecol. 1950; 19:36–57. https://doi.org/10.2307/1570
- **Joly AB, Oliveira-Filho EC, Narchi W.** Projeto de criação de um parque marinho na região de Abrolhos. An Acad Bras Cienc. 1969; 41:247–51.
- **Jones RS.** Ecological relationships in Hawaiian and Johnston Island Acanthuridae (surgeonfishes). Micronesica. 1968; 4:309–61.
- **Karr JR, James FC.** Eco-morphological configurations and convergent evolution of species and communities. In: Cody ML, Diamond JM, editors. Ecology and evolution of communities. Cambridge: Harvard University Press; 1975. p.258–91.
- **Keast A, Webb D.** Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. J Fish Res Board Can. 1966; 23(12):1845–74. https://doi.org/10.1139/f66-175
- **Kramer MJ, Bellwood DR, Bellwood O.** Cryptofauna of the epilithic algal matrix on an inshore coral reef, Great Barrier Reef. Coral Reefs. 2012; 31:1007–15. https://doi.org/10.1007/s00338-012-0924-x
- **Leão ZMAN, Kikuchi RKP.** The Abrolhos reefs of Brazil. In: Seeliger U, Kjerfve B, editors. Coastal marine ecosystems of Latin America. Berlin: Springer-Verlag; 2001. p.83–96.
- **Legendre P, Legendre L.** Numerical ecology. 3rd ed. Amsterdam: Elsevier; 2012.
- **Lellys NT, Moura RL, Bonaldo RM, Francini-Filho RB, Gibran FZ.** Parrotfish functional morphology and bioerosion on SW Atlantic reefs. Mar Ecol Prog Ser. 2019; 629:149–63. https://doi.org/10.3354/meps13102
- **Lessa RP, Nóbrega MF.** Guia de identificação de peixes marinhos da região nordeste do Brasil. Recife: Programa REVIZEE, Relatório Síntese; 2000.

- **Lleonart J, Salat J, Torres GJ.** Removing allometric effects of body size in morphological analysis. J Theor Biol. 2000; 205(1):85–93. https://doi.org/10.1006/jtbi.2000.2043
- **Lobel PS.** Trophic biology of herbivorous reef fishes: alimentary pH and digestive capabilities. J Fish Biol. 1981; 19(4):365–97. https://doi.org/10.1111/j.1095-8649.1981.tb05842.x
- **Ludwig JA, Reynolds JF.** Statistical ecology: a primer on methods and computing. New York: Wiley-Interscience Publications; 1988.
- **Marroig G.** When size makes a difference: allometry, life-history and morphological evolution of capuchins (Cebus) and squirrels (Saimiri) monkeys (Cebinae, Platyrrhini). BMC Evol Biol. 2007; 7:20. https://doi.org/10.1186/1471-2148-7-20
- **Marshell A, Mumby PJ.** The role of surgeonfish (Acanthuridae) in maintaining algal turf biomass on coral reefs. J Exp Mar Biol Ecol. 2015; 473:152–60. https://doi.org/10.1016/j.jembe.2015.09.002
- **Mendes TC, Ferreira CEL, Clements KD.** Discordance between diet analysis and dietary macronutrient content in four nominally herbivorous fishes from the Southwestern Atlantic. Mar Biol. 2018; 166:2. https://doi.org/10.1007/s00227-018-3448-2
- **Menezes NA, Buckup PA, Figueiredo JL, Moura RL.** Catálogo das espécies de peixes marinhos do Brasil. São Paulo: Museu de Zoologia da Universidade de São Paulo; 2003.
- **Mihalitsis M, Wainwright PC.** Feeding kinematics of a surgeonfish reveal novel functions and relationships to reef substrata. Commun Biol. 2024; 7:13. https://doi.org/10.1038/s42003-023-05696-z
- **Mihalitsis M, Yamhure-Ramirez D, Beil MH, Chan H, Cole NJ, Luenenborg A *et al*.** Lateral jaw motion in fish expands the functional repertoire of vertebrates and underpins the success of a dominant herbivore lineage. PNAS. 2025; 122(19):e2418982122. https://doi.org/10.1073/pnas.2418982122
- **Miyake S, Ngugi DK, Stingl U.** Diet strongly influences the gut microbiota of surgeonfishes. Mol Ecol. 2015; 24(3):656–72. https://doi.org/10.1111/mec.13050
- **Miyake S, Ngugi DK, Stingl U.** Phylogenetic diversity, distribution, and cophylogeny of giant bacteria (*Epulopiscium*) with their surgeonfish hosts in the Red Sea. Front Microbiol. 2016; 7:285. https://doi.org/10.3389/fmicb.2016.00285
- **Motta PJ, Clifton KB, Hernandez P, Eggold BT.** Ecomorphological correlates in ten species of subtropical seagrass fishes: diet and microhabitat utilization. Environ Biol Fishes. 1995; 44:37–60. https://doi.org/10.1007/BF00005906
- **Moura RL, Francini-Filho RB.** Reef and shore fishes of the Abrolhos Region, Brazil. In: Dutra GF, Allen GR, Werner T, Mckenna SA, editors. A rapid marine biodiversity assessment of the Abrolhos Bank, Bahia, Brazil. RAP Bulletin of Biological Assessment 38. Washington, D.C.: Conservation International; 2006. p.40–55.
- **Moura RL, Secchin NA, Amado-Filho GM, Francini-Filho RB, Freitas MO, Minte-Vera CV *et al*.** Spatial patterns of benthic megahabitats and conservation planning in the Abrolhos Bank. Cont Shelf Res. 2013; 70:109–17. https://doi.org/10.1016/j.csr.2013.04.036
- **Nicholson GM, Clements KD.** Resolving resource partitioning in parrotfishes (Scarini) using microhistology of feeding substrata. Coral Reefs. 2020; 39:1313–27. https://doi.org/10.1007/s00338-020-01964-0
- **Norton SF.** Capture success and diet of cottid fishes: the role of predator morphology and attack kinematics. Ecology. 1991; 72(5):1807–19. https://doi.org/10.2307/1940980
- **Oricchio FT, Pastro G, Vieira EA, Flores AAV, Gibran FZ, Dias GM.** Distinct community dynamics at two artificial habitats in a recreational marina. Mar Environ Res. 2016; 122:85–92. https://doi.org/10.1016/j.marenvres.2016.09.010
- **Peig J, Green AJ.** New perspectives for estimating body condition from mass/length data: the scaled mass index as an alternative method. Oikos. 2009; 118(12):1883–91. https://doi.org/10.1111/j.1600-0706.2009.17643.x

- **Perevolotsky T, Brotman-Krass JM, Ratner Y, Avigad Y, Summers AP, Donatelli CM *et al*.** Twist and snout: head and body morphologies determine feeding kinematics in substrate-biting fishes. Integr Org Biol. 2025; 7(1):obaf032. https://doi.org/10.1093/iob/obaf032
- **Purcell SW, Bellwood DR.** A functional analysis of food procurement in two surgeonfish species, *Acanthurus nigrofuscus* and *Ctenochaetus striatus* (Acanthuridae). Environ Biol Fishes. 1993; 37:139–59. https://doi.org/10.1007/BF00000589
- **Purcell SW, Bellwood DR.** Spatial patterns of epilithic algal and detrital resources on a windward coral reef. Coral Reefs. 2001; 20:117–25. https://doi.org/10.1007/s003380100150
- **Quinn GP, Keough MJ.** Experimental design and data analysis for biologists. 2nd ed. Cambridge: Cambridge University Press; 2002.
- **R Development Core Team.** R: a language and environment for statistical computing - Version 3.5.3 [internet]. R Foundation for Statistical Computing; 2019. Available from: https://www.R-project.org/
- **Robertson DR.** Increases in surgeonfish populations after mass mortality of the sea urchin *Diadema antillarum* in Panamá indicate food limitation. Mar Biol. 1991; 111:437–44. https://doi.org/10.1007/BF01319416
- **Scott JJ, Adam TC, Duran A, Burkepile DE, Rasher DB.** Intestinal microbes: an axis of functional diversity among large marine consumers. Proc R Soc B. 2020; 287:20192367. https://doi.org/10.1098/rspb.2019.2367
- **Segal B, Castro CB.** Coral community structure and sedimentation at different distances from the coast of the Abrolhos Bank, Brazil. Braz J Oceanogr. 2011; 59(2):119–29. https://doi.org/10.1590/S1679-87592011000200001
- **Siqueira AC, Bellwood DR, Cowman PF.** The evolution of traits and functions in herbivorous coral reef fishes through space and time. Proc R Soc B. 2019a; 286:20182672. https://doi.org/10.1098/rspb.2018.2672
- **Siqueira AC, Bellwood DR, Cowman PF.** Historical biogeography of herbivorous coral reef fishes: the formation of an Atlantic fauna. J Biogeogr. 2019b; 46(7):1611–24. https://doi.org/10.1111/jbi.13631
- **Sorenson L, Santini F, Carnevale G, Alfaro ME.** A multilocus timetree of surgeonfishes (Acanthuridae, Percomorpha) with revised family taxonomy. Mol Phylogenet Evol. 2013; 68(1):150–60. https://doi.org/10.1016/j.ympev.2013.03.014
- **Tebbett SB, Goatley CHR, Bellwood DR.** Clarifying functional roles: algal removal by the surgeonfishes *Ctenochaetus striatus* and *Acanthurus nigrofuscus* on coral reefs. Coral Reefs. 2017; 36:803–13. https://doi.org/10.1007/s00338-017-1571-z
- **Tebbett SB, Siqueira AC, Belwood DR.** The functional roles of surgeonfishes on coral reefs: past, present and future. Rev Fish Biol Fish. 2022; 32:387–439. https://doi.org/10.1007/s11160-021-09692-6
- **Thompson C, Silva R, Gibran FZ, Bacha L, Freitas MAM, Thompson M *et al*.** The Abrolhos nominally herbivorous coral reef fish *Acanthurus chirurgus*, *Kyphosus* sp., *Scarus trispinosus*, and *Sparisoma axillare* have similarities in feeding but species-specific microbiomes. Microb Ecol. 2024; 87:110. https://doi.org/10.1007/s00248-024-02423-x
- **Tyler JC.** Osteological aspects of interrelationships of surgeon fish genera (Acanthuridae). Proc Acad Nat Sci Phila. 1970; 122:87–124. https://www.jstor.org/stable/4064651
- **Van der Klaauw CJ.** Ecological studies and reviews. IV. Ecological morphology. Acta Biotheor. 1948; 4:27–111.
- **Vercelloni J, Liquet B, Kennedy EV, González-Rivero M, Caley MJ, Peterson EE *et al*.** Forecasting intensifying disturbance effects on coral reefs. Glob Chang Biol. 2020; 26:2785–97. https://doi.org/10.1111/gcb.15059
- **Vergés A, Steinberg PD, Hay ME, Poore AG, Campbell AH, Ballesteros E *et al*.** The tropicalization of temperate marine ecosystems: climate-mediated changes in herbivory and community phase shifts. Proc R Soc B. 2014; 281:20140846. https://doi.org/10.1098/rspb.2014.0846

- **Wainwright PC.** Ecomorphology: experimental functional anatomy for ecological problems. Am Zool. 1991; 31(4):680–93. https://doi.org/10.1093/icb/31.4.680
- **Wainwright PC.** Functional morphology as a tool in ecological research. In: Wainwright, PC, Reilly SM, editors. Ecological morphology: integrative organism biology. Chicago: The University of Chicago Press; 1994. p.42–59.
- **Wilson SK.** Nutritional value of detritus and algae in blenny territories on the Great Barrier Reef. J Exp Mar Biol Ecol. 2002; 271(2):419–30. https://doi.org/10.1016/S0022-0981(02)00035-7
- **Wilson SK, Bellwood DR, Choat JH, Furnas M.** Detritus in the epilithic algal matrix and its use by coral reef fishes. Oceanogr Mar Biol Annu Rev. 2003; 41:279–309.
- **Winemiller KO.** Ecomorphological diversification in lowland freshwater fish assemblages from five biotic regions. Ecol Monogr. 1991; 61(4):343–65. https://doi.org/10.2307/2937046
- **Winemiller KO, Kelso-Winemiller L, Brenkert AL.** Ecomorphological diversification and convergence in fluvial cichlid fishes. Environ Biol Fishes. 1995; 44:235–61. https://doi.org/10.1007/BF00005919

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ETHICAL STATEMENT

Collection licenses of SISBIO number 50872–1 and 50872–2, ethical guidelines for species collection were followed, but our work did not involve animal experimentation.

DATA AVAILABILITY STATEMENT

The data supporting the findings of this study are available from the corresponding author, upon reasonable request.

AI STATEMENT

ChatGPT (OpenAI) was used to assist with some grammatical corrections and as support for the R software. DeepL was also used for linguistic issues.

COMPETING INTERESTS

The authors declare no competing interests.

SUPPLEMENTARY MATERIAL

Supplementary material **S1**
Supplementary material **S2**
Supplementary material **S3**
Supplementary material **S4**
Supplementary material **S5**
Supplementary material **S6**
Supplementary material **S7**
Supplementary material **S8**

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