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Discordance between diet analysis and dietary macronutrient content in four nominally herbivorous fishes from the Southwestern Atlantic

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Abstract

Herbivorous fishes are an important component of coral reef systems worldwide, but their nutritional ecology is poorly understood, particularly the relationships between the taxonomic composition and the nutritional composition of their diets. We compared dietary composition with % carbon, % nitrogen and C:N ratios of diet in four species of nominally herbivorous fishes from the Southwestern Atlantic and used literature values to calculate proportional contributions of dietary items to total nitrogen intake. Both *Sparisoma axillare* (Labridae, Scarinae) and *Acanthurus chirurgus* (Acanthuridae) had a diet composed mainly of detritus, with contributions of red algae. However, the diet of *S. axillare* displayed higher %N and a lower C:N ratio, although animal material made only a slightly greater contribution to total nitrogen intake than in *A. chirurgus*. *Kyphosus sectatrix* (Kyphosidae) ingested mainly carbon-rich corticated algae, while *Diplodus argenteus* (Sparidae) had a varied, omnivorous diet. These results indicate that conventional diet analysis may not reveal important interspecific differences in nutrient intake and that a reassessment of the nutrient intake of different herbivorous fishes is required to fully understand their ecology. This finding highlights the fact that foods of nominally herbivorous fishes vary greatly in nutritional quality. Moreover, conventional dietary categories such as detritus may exhibit considerable heterogeneity in taxonomic and nutritional composition, suggesting a previously unrecognised level of dietary selectivity in this fish assemblage.

Introduction

One of the main goals of ecological research is to determine how nutrients and energy flow through ecosystems and are partitioned among different trophic levels (Paine 1996; Rooney et al. 2006; Bierwagen et al. 2018). The study of nutritional ecology is central to ecological research since it deals with the relationship between animals and their food, encompassing aspects such as food composition, acquisition and processing (Raubenheimer et al. 2009). In this sense, herbivorous animals represent an important group for nutritional research as they transfer nutrients and energy from primary producers to higher trophic levels. Our understanding of herbivory in terrestrial systems is underpinned by a vast literature on the selection and processing of nutritional resources by vertebrate groups including mammals (Van Soest 1994), lizards (Bjorndal 1997) and birds (Levey and Martínez del Rio 2001).

Nominally herbivorous fishes are recognised as an important ecological component of reef environments due to their high contribution to the total biomass of different habitats and their influence on the benthic communities (Horn 1989; Choat and Clements 1998; Ferreira et al. 2004; Cordeiro et al. 2016). Through their intense feeding activity, herbivorous fishes can influence the composition of benthic biota (Carpenter 1986; Smith et al. 2001; Burkepile and Hay 2006) and are generally regarded as one of the most important groups of fish on tropical reefs (Bellwood et al. 2004). Most of the research on herbivorous

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reef fishes classify them in discrete categories that can be broadly clustered into browsers/algivores and scrapers/grazers/detritivores (e.g. Burkepile & Hay 2006; Green & Bellwood 2009; Bonaldo et al. 2014; Adam et al. 2015). Nevertheless, among herbivores there are species that feed on different food sources, including macroalgae, turfing algae, cyanobacteria, detritus and zooplankton, among others (Choat et al. 2002, 2004; Ferreira and Gonçalves 2006). This variety is better demonstrated as a continuum, with macroalgivores with carbohydrate-rich diets at one end of the spectrum and detritivorous protein-scavengers at the other (Crossman et al. 2005).

Gut content analysis has been used for decades to assess diet in herbivorous fishes (e.g. Randall 1967), but since species possess different food processing modes, the extent to which this method reflects nutritional resources is likely to be variable depending on the species studied. As an example, parrotfishes (Labridae, Scarinae) possess pharyngeal jaws, which grind ingested material to very small fragments, hampering the identification of gut contents (Choat et al. 2002). Moreover, the identification of food items does not indicate their nutritional content or how they may contribute to overall nutrient intake. Many studies consider that algae represent low-quality food compared to animal material (Lobato et al. 2014), despite great variation in their nutritional composition (Montgomery and Gerking 1980; Barbarino and Lourenço 2009; Angell et al. 2015). Furthermore, interspecific variation in post-ingestive processing may influence the extent to which various species can extract nutrients from different food items. Although recent studies using stable isotope and fatty acid analyses (Piché et al. 2010; Dromard et al. 2015; McMahon et al. 2016) recognized that herbivorous fishes have distinct nutritional profiles, many studies do not consider diet beyond broad categories and fail to capture the complexity of the resource used (Clements et al. 2017). An integrative, multi-faceted approach is required that takes into account what foods are ingested, the nutritional composition of these foods and post-ingestive processing to understand the trophic ecology of this fish assemblage (Choat et al. 2004; Clements et al. 2009, 2017).

The objective of the present study was to examine the relationships between diet as quantified by traditional gut content analysis and diet as quantified by carbon and nitrogen content (as nutritional proxies). We examined four nominally herbivorous fish species from the Southwestern Atlantic that differ in food processing modes, and that are usually classified in different functional groups: one browser/algivore, two scraper/detritivores and one omnivore known to feed heavily on algae. Our main goal was to test the hypothesis that conventional methods used to characterise diet reflected interspecific differences in nutrient intake and nutritional targets among these fishes.

Materials and methods

Study area

Sampling was carried out between February and March 2013 (Austral Summer) at Arraial do Cabo (22°57′S, 42°01′W) on the southeastern coast of Brazil. This region is of great ecological and biogeographic importance as it accumulates species with both tropical and temperate affinities (Ferreira et al. 2001, 2004). Reefs in the region are predominantly rocky and covered by a rich epilithic algal community (EAC) and the zoanthid *Palythoa caribaeorum*, while corals and other invertebrates occupy a lesser proportion of the substratum (Ferreira et al. 1998a; Rogers et al. 2014). The richness of reef-associated fish fauna in the region is relatively high (within the Brazilian province), with the occurrence of at least 13 species of nominally herbivorous fishes (Cordeiro et al. 2016). Although local upwelling brings up waters colder than 18 °C (Valentin 1984), the study sites are protected from this upwelling and generally experience temperatures between 18 and 25 °C.

Study species

The Southwestern Atlantic has a depauperate fish fauna compared to other biogeographical regions such as the Indo-Pacific and the Caribbean (Kulbicki et al. 2013), and this is reflected in the number of herbivorous fishes in this area. Fish herbivory is restricted to a few families, most importantly Kyphosidae, Acanthuridae, Labridae (Scarinae) and Pomacentridae (Ferreira et al. 2004; Floeter et al. 2005), with contributions from omnivorous species belonging to the families Sparidae, Monacanthidae and Pomacanthidae (Ferreira et al. 2004; Dubiaski-Silva and Masunari 2006; Mendes et al. 2015). Four species were selected as they represent different feeding modes and phylogenetic affinities: the macroalgivore *Kyphosus sectatrix* (Kyphosidae), the detritivore-herbivores *Sparisoma axillare* (Labridae, Scarinae) and *Acanthurus chirurgus* (Acanthuridae), and the omnivore *Diplodus argenteus* (Sparidae). Previous work on the diets of these study species identified *K. sectatrix* as eating mainly brown macroalgae (Ferreira and Gonçalves 2006), *S. axillare* and *A. chirurgus* ingesting mainly detritus and filamentous algae (Ferreira and Gonçalves 2006) and *D. argenteus* as an omnivore that ingests a broad range of food items (Dubiaski-Silva and Masunari 2006). All these species are known to ingest algae to some extent and are abundant throughout the study area (Cordeiro et al. 2016).

Adult fish were collected with a speargun at different sites throughout the study area (Table 1) with all

Table 1 Sample number (N) for each species, with ranges of length (mean fork length, minimum and maximum) and weight (average, minimum and maximum)

Family	Species	N	Fork length (mm) Average (min − max)	Weight (g) Average (min − max)
Kyphosidae	*Kyphosus sectatrix*	22	289.9 (199–392)	576.8 (304–991)
Labridae	*Sparisoma axillare*	10	333.5 (196–394)	768.5 (145–1030)
Acanthuridae	*Acanthurus chirurgus*	18	292.1 (198–336)	674.9 (381–840)
Sparidae	*Diplodus argenteus*	13	220.2 (170–249)	283.6 (189–396)

collections restricted to the afternoon, when feeding rates of most herbivorous fishes attain their peak and guts are full (Ferreira et al. 1998b; Zemke-White et al. 2002; Choat et al. 2004). The number of individuals sampled varied among species in accordance to their availability during sampling (22 *K. sectatrix*, 10 *S. axillare*, 18 *A. chirurgus*, 13 *D. argenteus*). Sample size was tested to ensure that the diet of each species was accurately represented (Fig ESM1). Once collected, specimens were removed from water, killed by pithing (when necessary) and placed on ice prior to transportation to the laboratory where they were measured (fork length), weighed (in grammes) and had their alimentary tracts removed (see Table 1). In species with a distinct stomach (*K. sectatrix*, *A. chirurgus* and *D. argentus*) just the stomach content was stored, but in *S. axillare*, which lacks a distinct stomach (Clements and Choat 2018), the proximal unsacculated region of the intestine was sampled. Gut contents were divided in two equivalent subsamples: one used to identify dietary items (gut content analysis) and the other for nutritional analysis. The former subsample was frozen (− 20 °C) until analysis, and the latter immediately placed in liquid nitrogen, then freeze-dried to constant mass and stored in a freezer (− 20 °C). Handling time between collection and processing was as short as possible to prevent changes in nutrient concentration (following Crossman et al. 2005).

Dietary analysis

Material for diet analysis was thawed at the laboratory before analysis. The subsample of gut content material for dietary analysis from each individual was evenly spread on a Petri dish positioned over a grid with 50 marked points. The items over each point were recorded and counted under a stereoscopic microscope (50 × magnification). Dietary items were identified to the lowest taxonomic category and sorted into groups (Table 2) according to taxonomy and morphological structure (Steneck and Dethier 1994). Although detritus can be defined as “dead and decaying primary producer material, which normally becomes detached from the primary producer after senescence” (Lartigue and Cebrian 2012; Hundt and Simons 2018), it is often difficult to visually discriminate living components such as bacteria, diatoms and cyanobacteria from the non-living component (Wilson et al. 2003). We thus applied this term broadly and identified detritus in the dietary analyses as any amorphic organic material found.

Nutritional analysis

Freeze-dried samples used in nutritional analysis were homogenised on a Retsch MM301 ball and mill homogenizer at 25 repetitions/second for 15 s. Immediately before grinding, samples were bathed in liquid nitrogen to avoid over-heating, which can change nutrient content. Measurements of percentage values for carbon, hydrogen and nitrogen were assessed in duplicate using an elemental analyser Exeter CE-440 located at the Auckland University of Technology (AUT). Nitrogen content is usually related to protein, which represents an important nutrient for fishes (Weber and Haman 1996). Likewise, diets with high concentration of carbon are usually associated with the ingestion of carbohydrate-rich plant material (Crossman et al. 2005). From the values of nitrogen and carbon, the C:N ratios for each individual diet were obtained. The C:N ratio is widely used in ecology as a proxy for the relative nutritional value of a food type, with lower values generally thought to indicate more nutritious dietary sources of protein (Wilson et al. 2003). Thus, nitrogen and carbon measurements from the gut contents, along with C:N ratios, were used here as proxies for the nutritional value of the foods ingested by the study species.

We also estimated the proportional contribution to total nitrogen intake of each of the major food categories in the four study fish species by combining: (1) the dietary proportions of food categories from gut content analysis, (2) the total nitrogen content of the diet in each of the four species and (3) literature data on nitrogen concentration in each of the main food categories in the fish diets. This was done as follows. First, we surveyed the literature for the nitrogen content of each of the most important food item categories found in our gut content analysis. Second, we took the proportional contribution made by each food item to the total diet of each fish species and divided these values by the total nitrogen content of the diet for each study fish species. Third, we multiplied this value by the nitrogen content of each food item as follows: $\mathrm{NI}_i = (D_i/\mathrm{N}) \times \mathrm{FN}_i$, where NI_i is the nitrogen intake of the item i to the diet of a given species, D_i is

Table 2 Relative contribution of each taxonomic group of food items identified in gut contents of the four study species with their respective group

Food item	Group	*A. chirurgus*	*S. axillare*	*K. sectatrix*	*D. argenteus*
Cyanophyta	Large filamentous cyanobacteria	0.78	6.00	2.00	0.51
Rhodophyta					
Polysiphonia spp.	Red filamentous	5.22	6.33	6.36	8.72
Herposiphonia sp.	Red filamentous	2.67	2.00	0.91	
Ceramium spp.	Red filamentous	3.11	5.00		
Centroceras clavulatum	Red filamentous	1.00	2.67		
Jania spp.	Red calcareous	18.89	22.33	4.55	10.36
Amphiroa sp.	Red calcareous	0.56			
Spyridia hypnoides	Red corticated	2.44		0.09	3.26
Champia sp.	Red corticated	0.78			
Gelidiella acerosa	Red corticated	8.56	4.67	7.45	2.72
Gelidium pusillum	Red corticated	1.89	3.33	8.36	3.28
Gelidiopsis sp.	Red corticated	0.22			
Pterocladiella capillacea	Red corticated	0.11		9.45	2.92
Hypnea spp.	Red corticated	0.22		8.00	
Plocamium brasiliense	Red corticated	1.67			
Chlorophyta					
Cladophora sp.	Green filamentous	2.00	0.33	0.64	1.59
Bryopsis sp.	Green filamentous	8.44	2.67	2.00	3.00
Chaetomorpha sp.	Green filamentous	0.78			1.03
Ulva sp.	Green corticated	0.56		1.82	11.28
Phaeophyceae					
Sphacelaria sp.	Brown filamentous	1.11	1.33	2.55	2.82
Hincksia sp.	Brown filamentous	0.33	0.33		
Dictyota sp.	Brown corticated	0.67		14.82	
Sargassum sp.	Brown corticated	2.44		30.91	1.33
Porifera	Porifera	0.11			0.31
Bryozoa	Bryozoa	2.44		0.09	
Arthropoda					
Cirripedia	Arthropoda				1.08
Gammaridae	Arthropoda	0.78	4.67		2.05
Caprellidae	Arthropoda	0.67			7.79
Insecta	Arthropoda				5.54
Polychaeta	Polychaeta				1.54
Mollusca					
Gastropoda	Mollusca	0.11			3.46
Bivalvia	Mollusca	0.22			7.87
Echinodermata	Echinodermata				7.69
Detritus	Detritus	31.22	38.33		9.85

the contribution of the item *i* to the diet of a given species, N is the amount of dietary nitrogen and FN_i is the value of nitrogen content of each food type *i*. This value was finally turned into a percentage to give the relative contribution made by each dietary food category to total nitrogen intake for each of the study fish species.

Data analysis

Because our data did not meet parametric assumptions of normality and homogeneity of variances, we performed a one-way permutation-based Analysis of Variance (ANOVA) to compare the contribution of the different food items for each one of the four study species using the package 'lmPerm'(Wheeler and Torchiano 2016), followed by a Tukey HSD post hoc test to assess the differences. In order to visualise the similarities and differences in the diets of the four fish species, a Principal Components Analysis (PCA) was applied to gut content analysis data using the package 'vegan' (Oksanen et al. 2017). We used the Schoener index (Wallace 1981) to assess dietary overlap between each pair of species using the package 'spaa' (Zhang 2016). This index varies between 0 and 1 with higher values indicating higher overlap. We also used a one-way permutation-based ANOVA for each nutrient (%C, %N and C:N ratio) with Tukey HSD post hoc test to compare nutrient concentrations among species using a similar aforementioned approach. All analyses were performed using the software R (R Core Team 2017).

Results

Thirty-four different food items were identified in the diet of the four study fish species (Table 2), and these were grouped into 15 categories. The species with the most diverse diet was *A. chirurgus* with 30 food items, followed by *D. argenteus* (23), *K. sectatrix* (16) and *S. axillare* (14). Of the 34 food items identified, only eight were present in the diet of all four fish species (i.e. Cyanobacteria, *Polysiphonia* spp., *Jania* spp., *Gelidiella acerosa*, *Gelidium pusillum*, *Cladophora* sp., *Bryopsis* sp. and *Sphacelaria* sp.), and only *A. chirurgus* and *D. argenteus* ingested exclusive food items not found in other species (three and four, respectively) (Table 2).

We detected a large variation in the diets of all four study species (Table ESM1). The most abundant food item in the diet of *A. chirurgus* ($F=87.56$, $P<0.001$) was detritus, with four groups of algae having secondary importance (i.e. articulated calcareous, filamentous and corticated red algae, and green filamentous categories). Other items such as brown algae, bryozoans and arthropods were also present in very small quantities (Fig. 1, Table ESM2). Detritus was also the dominant food item in *S. axillare* ($F=68.22$, $P<0.001$), followed by both articulated calcareous and filamentous red algae. Cyanobacteria, red corticated algae and arthropods were also abundant in gut contents, while others items such as green and brown filamentous algae were present in lower amounts (Fig. 1, Table ESM3). The diet of *K. sectatrix* ($F=66.51$, $P<0.001$) was dominated by brown and red corticated algae, with other algae (mainly filamentous) composing a small fraction (Fig. 1, Table ESM4). *D. argenteus* ($F=4.25$, $P<0.001$) exhibited the most variable

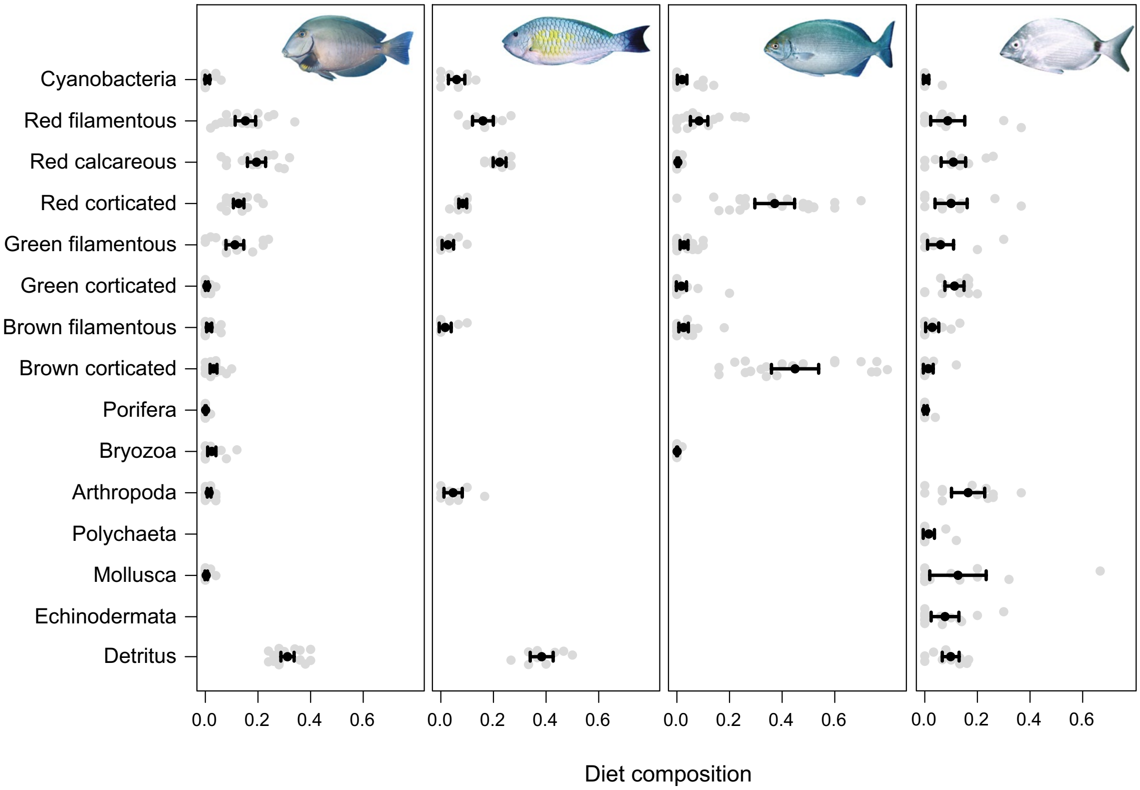

Fig. 1 Diet composition of the four study species by food categories. From left to right: *Acanthurus chirurgus*, *Sparisoma axillare*, *Kyphosus sectatrix*, and *Diplodus argenteus*. In grey are the individual values and in black average ± 95% CI

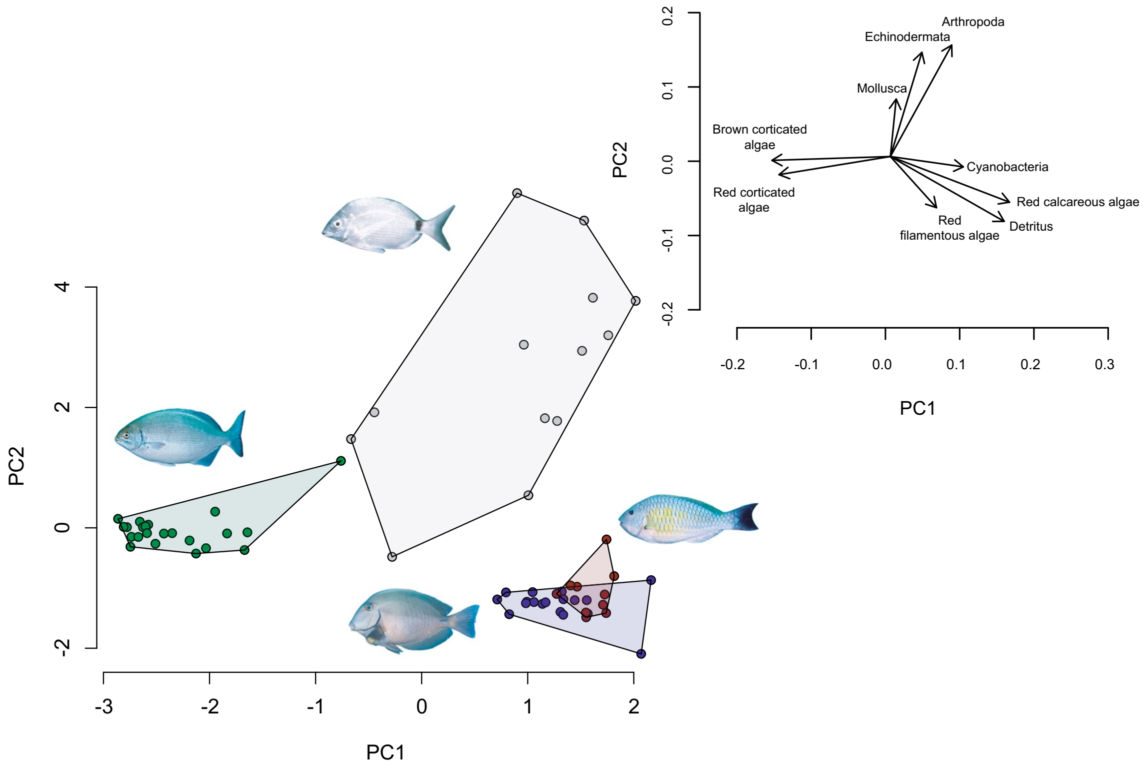

Fig. 2 Principal component analysis based on dietary content of the four study species. Each point represents one individual fish. Convex hulls were drawn for each species to highlight differences among species: *Acanthurus chirurgus* (blue), *Sparisoma axillare* (red), *Kyphosus sectatrix* (green), *Diplodus argenteus* (grey) (color figure online)

Table 3 Diet overlap of each pair of species Schoener index

	S. axillare	*K. sectatrix*	*D. argenteus*
A. chirurgus	0.805	0.301	0.511
S. axillare		0.234	0.472
K. sectatrix			0.276

diet among the study species, with no obvious dominant component. While arthropods, echinoderms and molluscs were the most important items of animal origin, green corticated, red calcareous, and corticated composed the bulk of algal categories (Fig. 1, Table ESM5).

The PCA with data from diet composition highlighted differences and similarities among the nutritional strategies of the four study fish species (Fig. 2). The diet of *Kyphosus sectatrix* was positively related to red and brown corticated algae with negative values along the first component axis. *S. axillare* and *A. chirurgus* overlapped in diet and had positive values along the first component axis being related to detritus, red and calcareous filamentous algae. Among the study species, *D. argenteus* has the most variable diet, with data scattered on both axis and spread positively along the second component axis. It was related to different animal material such as Arthropoda, Echinodermata and Mollusca (Fig. 2). Dietary overlap was the highest between *A. chirurgus* and *S. axillare* (Schoener index = 0.81). *Kyphosus sectatrix* presented the most dissimilar diet when comparing with *S. axillare* (0.30), *A. chirurgus* (0.23) and *D. argenteus* (0.28) (Table 3).

Carbon content differed significantly between all fish species ($F = 53.05$, $P < 0.001$), with the highest values in the diet for *S. axillare* followed by *K. sectatrix*, while *D. argenteus* exhibited the greatest variation and *A. chirurgus* the lowest (Fig. 3a, Table ESM6). *S. axillare* exhibited the highest %N, followed by both *D. argenteus* and *K. sectatrix* ($F = 55.28$, $P < 0.001$), with *A. chirurgus* displaying the most nitrogen-poor diet (Fig. 3b, Table ESM6). C:N ratio was highest in *A. chirurgus* and lowest in *S. axillare* ($F = 15.44$, $P < 0.001$), with both *K. sectatrix* and *D. argenteus* exhibiting intermediate and similar ratios (Fig. 3c, Table ESM6).

The calculations of proportional nitrogen intake from each dietary food category indicated that detritus was the main source of dietary nitrogen in both *A. chirurgus* and *S. axillare*, contributing 36% and 37.8% of total nitrogen intake, respectively (Table 4). Large filamentous cyanobacteria were also a significant contributor to total nitrogen intake in *S. axillare* at 11.1%. The contribution of animal material to total dietary nitrogen intake was highest in *D. argenteus* (76.5%), intermediate in *S. axillare* (16.6%) and *A. chirurgus*

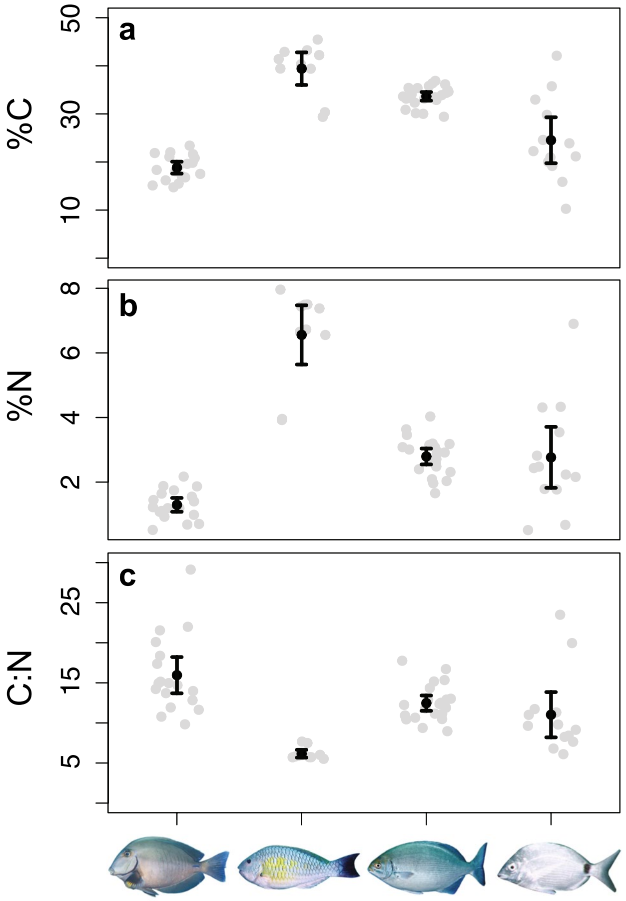

Fig. 3 Percent composition of dietary **a** carbon, **b** nitrogen, and **c** C:N ratios of the four study species. From left to right: *Acanthurus chirurgus*, *Sparisoma axillare*, *Kyphosus sectatrix*, *Diplodus argenteus*. In grey are the individual values and in black average ± 95% CI

(13.2%) and lowest in *K. sectatrix* (0.2%) (Table 4). The main components of this animal material differed between the fish species: arthropods, molluscs and echinoderms in *D. argenteus*, arthropods in *S. axillare*, bryozoans and arthropods in *A. chirurgus* and bryozoans in *K. sectatrix* (Table 4). Brown and red corticated algae were the main source of nitrogen for *K. sectatrix*, and although having a very varied diet, *D. argenteus* acquired most of its total nitrogen intake (76.5%) from invertebrates (Table 4).

Discussion

In this study, we present data on gut content analyses and dietary nutrient concentration of four nominally herbivorous fish species from the Southwestern Atlantic. The four fish species analysed had distinct diets in relation to the percentage contribution of the different food categories, with the greatest overlap between *A. chirurgus* and *S. axillare*. While *K. sectatrix* had a diet dominated by corticated algae with intermediate levels of carbon and nitrogen, and *D. argenteus* the most variable diet and nutrient concentration, the diets of both *A. chirurgus* and *S. axillare* included high proportions of detritus in addition to red algae. Despite the apparent similarity in the diets of *A. chirurgus* and *S. axillare*, they had very distinct nutritional dietary profiles with the former containing roughly four times the nitrogen and double the carbon content of the latter.

High nitrogen concentration is usually associated with protein-rich food items, especially from animal origin. Organic detritus associated with algal turfs in reef systems can also have high levels of nitrogen and protein (Crossman et al. 2001; Wilson et al. 2003; Clements and Choat 2018), but this fact alone would not explain the discrepancy between *S. axillare* and *A. chirurgus* diets in C:N ratio since the dietary contribution of detritus was similar in both species. Endogenous mucus produced from the pharynx, which is considerable in parrotfishes, can also elevate nitrogen content of material in the anterior gut (Holley et al. 2015), but not sufficiently to explain the magnitude of differences seen here. Rather, our data indicate that detritus as identified by gut content analysis in this study does not represent a homogeneous category. The high taxonomic and nutritional heterogeneity of detritus in algal turfs (Crossman et al. 2001; Wilson et al. 2003; Crossman et al. 2005), combined with the mechanical processing of ingested material by the pharyngeal mill in parrotfishes (Choat et al. 2002; Carr et al. 2006), clearly complicate accurate assessment of diet by traditional gut content analysis in some of these fishes.

Despite the similarities in the proportions of food categories in gut contents, the differences between *S. axillare* and *A. chirurgus* in dietary nutritional profiles suggest that these two species have distinct feeding strategies that result in profound differences in the nutritional composition of their diets. Although both *S. axillare* and *A. chirurgus* actively select algal turf substrata when feeding (Bonaldo et al. 2006; Francini-Filho et al. 2010), our results suggest that they feed selectively on different components of this resource. *Sparisoma axillare* obviously selects material with a higher proportion of protein (e.g. large filamentous cyanobacteria), whereas *A. chirurgus* ingests material with higher carbon content. This supports the view that parrotfishes do not actively select macroalgae as their primary food source (Clements et al. 2017; Clements and Choat 2018). This view is reinforced by the fact that another Brazilian parrotfish, *Scarus trispinosus*, apparently has little or no capacity to digest macroalgae, since a large number of algae species survived the entire digestive process and were viable in culture from fish faeces (Tâmega et al. 2016). Indeed, recent advances in parrotfish nutritional ecology suggest that these fishes are best described as microphages targeting protein-rich cyanobacteria and other endolithic and epilithic autotrophic microorganisms (Clements et al. 2017; Clements and

Table 4 Diet contribution (% diet) and estimated relative contribution of total nitrogen intake (% total N) of major food items for the four study fish species

	N content	*A. chirurgus*		*S. axillare*		*K. sectatrix*		*D. argenteus*	
		% diet	% total N	% diet	% total N	% diet	% total N	% diet	% total N
Detritus	2.12[a]	31.2	34.0	38.3	37.8	–	–	9.8	5.2
Large filamentous cyanobacteria	3.99[b]	0.8	1.6	6.1	11.1	1.9	4.8	0.5	0.5
Red filamentous algae	2.16[c,d]	15.2	16.9	15.9	16.1	8.5	11.0	8.7	4.7
Red calcareous algae	0.75[e]	19.4	7.5	22.3	7.8	0.4	0.2	10.9	2.0
Red corticated algae	1.82[c,f,g]	12.7	11.8	8.3	7.0	37.2	40.6	10.1	4.5
Green filamentous algae	2.02[d,f]	11.2	11.7	2.7	2.5	2.7	3.3	6.2	3.0
Green corticated algae	1.58[c,f,g]	0.6	0.5	–	–	1.7	1.6	11.3	4.4
Brown filamentous algae	1.41[e]	1.4	1.0	1.4	1.1	2.5	2.2	2.8	1.0
Brown corticated algae	1.34[c,d,f,g]	3.1	2.1	–	–	45.1	36.1	1.3	0.4
Porifera	3.58[g]	0.1	0.2	–	–	–	–	1.1	0.3
Bryozoa	4.30[h]	2.4	5.4	–	–	0.1	0.2	–	–
Arthropoda	7.67[b]	1.4	5.7	4.7	16.6	–	–	16.5	31.4
Polychaeta	9.34[i]	–	–	–	–	–	–	1.5	3.6
Mollusca	9.07[g]	0.3	1.6	–	–	–	–	12.6	28.5
Echinodermata	5.42[j]	–	–	–	–	–	–	7.7	10.4
N in diet (mean)		1.30		6.56		2.79		2.77	

N content refers to nitrogen content (%N dry weight) of each food based on literature sources

Sources for N content: [a]Crossman et al. (2001); [b]Yamamuro (1999); [c]Burkholder et al. (1971); [d]Diniz et al. (2012); [e]Munda and Gubenšek (1976); [f]McDermid et al. (2007); [g]Barbarino and Lourenço (2009); [h]Hepburn et al. (2012); [i]Kikuchi and Wada (1996); [j]Diniz et al. (2014)

Choat 2018). The high nitrogen concentration and C:N ratios found on the diet of *S. axillare* at least partly reflect the presence of these microorganisms in the detrital component of their diets. Although microscopic endolithic and epilithic cyanobacteria were not assessed in our gut content analyses, large filamentous cyanobacteria were a frequent food item in *S. axillare* (being registered in eight out of ten individual analysed), but were identified in the guts of only two (out of 18) *A. chirurgus*. This reinforces the idea that *S. axillare* targets protein-rich autotrophs as their main food. The detritus in *A. chirurgus* appears to be of a different origin. The dominant monounsaturated fatty acid in *A. chirurgus* is 16:1n-7 palmitoleic acid (Phleger and Laub 1989), which is a biomarker for diatoms (Kelly and Scheibling 2012). This indicates that the detritus in *A. chirurgus* is rich in diatoms and likely also in dead algal material colonised by heterotrophic bacteria.

The differences observed in dietary nutritional composition of *S. axillare* and *A. chirurgus* reflect distinct levels of selectivity by these fishes within the same habitat and highlight the low redundancy in their feeding ecology. Such a pattern of selectivity would be similar to that seen between grazing ruminants and equids (Duncan et al. 1990, Edwards 1991) and between wallabies and kangaroos (Freudenberger et al. 1989, Hume 1999). In the former example the higher intake requirements of equids forces them to be less selective of forage quality than grazing ruminants, which are more efficient at digesting forage of intermediate quality than equids, and thus require lower daily food intake rates. In the latter example, kangaroos are able to subsist on a diet with higher fibre content than wallabies by having lower intake rates which enable lengthy retention times, thus facilitating efficient digestion of forage through fermentation by microorganisms in the tubiform forestomach. Alimentary morphology in *A. chirurgus* and *S. axillare* resembles that of related "detritivorous" acanthurid and scarine taxa, which appear to be largely reliant on endogenous digestive mechanisms (Choat et al. 2004, Crossman et al. 2005). In terms of their feeding behaviour, *A. chirurgus* has a feeding rate consistently higher than *S. axillare* (Francini-Filho et al. 2010), a pattern that resembles the aforementioned mammal examples. Similarly, in the same study region, Ferreira et al. (1998b) found that *Acanthurus bahianus* has a feeding rate up to five times higher and ingestion by weight higher than *Sparisoma tuiupiranga*, reinforcing the discrepancies between surgeonfishes and parrotfishes. *A. chirurgus* would thus require higher intake rates than *S. axillare* to fulfil its nutritional requirements, especially in terms of protein intake.

The higher %C in the diet of *S. axillare* compared to *A. chirurgus* is likely to include inorganic carbon from articulated calcareous algae such as *Jania* spp. and *Amphiroa* spp. These algae are the most important components in the turf communities in the sampling region and are ingested by a number of grazing species (Ferreira et al. 1998a; Mendes et al. 2009). Although articulated calcareous algae comprised similar proportions of the diet in both *S. axillare* and *A. chirurgus*, the dietary proportion of these algae are more likely to be underestimated by visual examination in *S. axillare* due to the action of the pharyngeal mill. The inclusion of inorganic carbon from calcareous algae in *S. axillare* is likely to mean that the differences we note between this species and *A. chirurgus* in both C:N ratio and %N intake are actually underestimates in terms of nutrient intake.

The diet of *K. sectatrix* was largely dominated by brown and red corticated algae. Most *Kyphosus* species worldwide eat brown algae (Clements and Choat 1997; Ferreira and Gonçalves 2006), which possess highly refractory carbohydrates (Littler et al. 1983; White et al. 2010). Herbivorous *Kyphosus* species arguably display the most effective mechanisms for algal processing and digestion seen among marine herbivorous fishes, relying on both endogenous and exogenous strategies for nutrient acquisition (Mountfort et al. 2002, Crossman et al. 2005). The large, acidic stomach lyses macroalgal cell walls, allowing digestive enzymes access to cell contents (Zemke-White et al. 2000), while the hindgut microbiota converts refractory carbohydrates into short-chain fatty acids that are assimilated by the fish for energy and lipid synthesis (Mountfort et al. 2002; Fidopiastis et al. 2006). These strategies allow *K. sectatrix* to extract energy from corticated algae that most other fish species cannot process effectively. The nature of their food and the lack of significant mechanical digestion mean that conventional gut content analysis is a reliable indicator of diet in *Kyphosus* spp.

The omnivorous *D. argenteus* ingested a great variety of food items, with some individuals ingesting almost exclusively algae while others ingested mainly animal material as previously described for this species in the Southwestern Atlantic (Dubiaski-Silva and Masunari 2006). Most species from the family Sparidae are considered omnivores and display considerable trophic plasticity (e.g. Dubiaski-Silva and Masunari 2006; Soares et al. 2012; Sheaves et al. 2014). The genus *Diplodus* is characterised by a relatively small acidic stomach followed by a long intestine and produce a range of digestive enzymes enabling the utilisation of both animal and plant matter (Tramati et al. 2005). Although little information is available about the drivers of selectivity on highly omnivorous fishes, other sparid species show differences in amylase activity which are related to their diets, suggesting a high physiological plasticity (Fernández et al. 2001). Whether this plasticity is solely related to opportunity or is triggered by sex or developmental stage is yet to be determined.

It is important to note that all the sampling for this work was carried out in summer, and thus our results do not incorporate seasonal variation. Seasonal dietary variation in the study fish species is likely to occur in the study area due to seasonal variation in food availability (Ferreira et al. 1998b). For example, throughout the entire study area brown algae (mainly *Sargassum* and *Dictyota*) are much more abundant during spring and summer than autumn and winter, when *Sargassum* retains only its holdfast and almost disappears (Guimaraes and Coutinho 1996; Villaça et al. 2008). Thus, in winter *K. sectatrix* in particular would need to either spend more time foraging or explore different food sources. Similarly, nothing is known about the seasonal dynamics of algal turf communities and its components, or how its composition and nutritional properties vary over time. It is possible that *D. argenteus* modulates the intake between animal and plant material seasonally depending on availability, reproductive period or nutritional composition of their food.

In summary, the four herbivorous fish species studied displayed diets that were broadly consistent with previously used dietary categories: macroalgae (*K. sectatrix*), omnivory (*D. argenteus*) and detritivory (*S. axillare* and *A. chirurgus*) (Longo et al. 2014; Cordeiro et al. 2016). However, the dietary nutritional analysis presented here clearly shows that the latter two species have distinct diets, and thus their trophic ecology requires reassessment. It is likely that they represent distinct functional groups, with *S. axillare* acting as microphage targeting protein-rich autotrophic microorganisms (such as cyanobacteria) and *A. chirurgus* ingesting larger quantities of dead algal material colonised by bacteria and diatoms. In this sense, the present study reinforces the view that conventional gut content analysis is not sufficient to identify the diet of some herbivorous species. More detailed information on the nutritional composition of foods and how different nutrients are utilised by herbivorous species is still required to understand the nutritional ecology of this important group of fishes on reefs worldwide. These four species represent only a fraction of the relatively species-poor fauna of reef fishes that occur in Brazil. Little is known about how herbivorous fishes in the Atlantic process ingested foods, since by far most of the work on nutritional ecology of herbivorous fishes has been performed in the Pacific (Choat et al. 2002, 2004; Crossman et al. 2005). The high diversity of endemic herbivorous genera restricted to the Atlantic (like *Sparisoma*) provides great potential for comparative study of food processing modes and the description of novel nutritional strategies within this assemblage.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval All collections were performed under environmental and ethical permits of responsible agencies (ICMBIO permit #46271).

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