

Community structure and diet of roving herbivorous reef fishes in the Abrolhos Archipelago, south-western Atlantic

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Community structure and diet of roving herbivorous reef fishes were analysed in 13 study sites around the five islands of the Abrolhos Archipelago, north-eastern Brazil (17°58' S; 38°42' W). This area has been part of the Abrolhos Marine National Park since 1983. Abundances and diets of fishes within the families Scaridae, Acanthuridae and Kyphosidae were compared among groups of sites differing in benthic community structure and exposure regime. The abundance of roving herbivorous fishes was higher in shallower sites than in deeper sites. At all study sites, observations of total herbivorous reef fish community structure revealed that 64% of fishes were acanthurids, 33% were scarids and only 4% were kyphosids. This pattern was predominant in all study sites. The majority of fishes examined in this study had the bulk of their diet based on both algae (35–90%) and detritus (35–65%). Among groups of algae, filamentous algae were the most commonly consumed as the majority of roving herbivorous fishes in Abrolhos feed as scrapers and excavators. The exceptions were the kyphosids, which had a diet consisting primarily of macroalgae (mainly Phaeophyta), and *Acanthurus coeruleus* that consumed mainly turf algae and very little detritus. The data collected indicate that roving herbivorous fishes in the Abrolhos Archipelago are more abundant at calm sites where detritus and delicate algae, their major food resources, are more abundant. The results presented here, along with underwater observations, suggest that the abundance and diet of these three fish families are associated with substratum cover.

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Key words: Abrolhos Archipelago; community structure; fish diet; herbivorous reef fishes; substratum diversity.

INTRODUCTION

Herbivorous reef fishes are important members of the coral reef community, accounting for a large proportion of the fish biomass. These fishes have been shown to substantially affect the standing crop, productivity and community structure of reef algae (Hatcher, 1983; Carpenter, 1986; Klumpp & Polunin,

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1990; Choat, 1991; Hay, 1991). Although the influence of herbivorous fishes on algae and associated organisms are very well documented (Horn, 1989; Choat, 1991; Hay, 1991), their trophic role has been recently re-assessed (Choat & Clements, 1998; Crossman *et al.*, 2001, 2005; Choat *et al.*, 2002, 2004; Wilson *et al.*, 2003). As the epilithic algal community is recognized as an efficient sediment and detritus trap, the epilithic algal matrix (EAM) includes a variety of potential food resources (Crossman *et al.*, 2001; Wilson *et al.*, 2003), some of which can be of higher nutritional value than algae (Crossman *et al.*, 2001; Wilson, 2002). Some herbivorous species are specifically adapted to rasp and excavate the substratum in a non-selective manner (Bellwood & Choat, 1990), thus ingesting not only algae, but also a great amount of detritus contained within the EAM. Intentionally or non-intentionally, herbivorous fishes are likely to play an important role in the detritus pathway of coral reef systems (Choat & Clements, 1998).

While herbivorous fish diets have been extensively analysed in the Indo-Pacific (Crossman *et al.*, 2001, 2005; Choat *et al.*, 2002, 2004; Wilson *et al.*, 2003), only a few studies have been conducted on south-western Atlantic reefs (Ferreira *et al.*, 1998; Dias *et al.*, 2001; Aragão, 2003; Bonaldo *et al.*, 2006). Studies in the Caribbean demonstrated that a large proportion of detritus is ingested (Randall, 1967; Bruggemann, 1994), but they did not indicate to what extent these fishes are targeting living plant material and detritus.

Roving coral reef herbivores in the Atlantic include the families Scaridae, Acanthuridae and Kyphosidae (Horn, 1989; Choat, 1991). The Atlantic fauna contains representatives of the sparisomatine clade, which is poorly represented on Indo-Pacific reefs. The sparisomatines are the predominant scarids on south-western Atlantic reefs (Ferreira *et al.*, 2004). Moreover, the Brazilian fauna is of considerable interest as it sustains a high rate of endemic herbivorous fishes (Floeter & Gasparini, 2000; Moura & Sazima, 2003), including several newly described scarids (Moura *et al.*, 2001; Gasparini *et al.*, 2004). In addition to the endemic fish fauna, the Brazilian reefs have some unique characteristics. Coral and algal reefs extend for almost half of the coastline (the tropical north-eastern coast), forming structures significantly different from most of the well-known coral reef models (Maida & Ferreira, 1997; Leão & Dominguez, 2000; Leão & Kikuchi, 2001). In the warm subtropical south-eastern and southern coasts, where nutrient-rich upwelling events occur seasonally, rocky shores form the main habitat for the reef-associated biota (Ekau & Knoppers, 1999; Floeter *et al.*, 2001). The north-eastern reef fish fauna is characteristically tropical (Floeter *et al.*, 2001), with roving herbivores presenting the higher biomass along a middle stretch of the Brazilian coast (Ferreira *et al.*, 2004; Floeter *et al.*, 2005).

Herbivorous fishes are generally restricted to shallow environments (Bouchon-Navaro & Harmelin-Vivien, 1981; Russ, 1984; Lewis & Wainwright, 1985), closely linked with the distribution of algae, which are in turn highly dependent on incident light. Other factors shown to influence the distribution of these fishes include wave surge, predator avoidance and territorial fish abundance (Lewis & Wainwright, 1985; Horn, 1989; Choat, 1991; Williams & Polunin, 2001; Gust, 2002). In a recent study, Russ (2003) found larger herbivorous fishes to be strongly associated with reef zones of highest algal turf production.

It is still unclear, however, how herbivorous fishes respond to habitat-specific differences, but correlating fish diet and local distribution patterns with the spatial dynamics of benthos is an important part of understanding the significance of grazing fish faunas in reef systems.

This study collected data on the abundance, distribution and dietary preferences of roving herbivorous fishes in distinct habitats of the Abrolhos Archipelago, providing specific patterns of benthos distribution. The data gathered were used to answer the following questions: What are the dominant families of herbivorous fishes in the different reef habitats? How is the abundance of roving herbivorous fishes correlated to the benthos, and to different algal morphological groups? What is the proportion of algae and detritus ingested by each fish species?

MATERIAL AND METHODS

STUDY AREA

This study was carried out in the austral summer of 1995 to 1996 at the Abrolhos Archipelago (17°58' S; 38°42' W). The Abrolhos Archipelago lies 60 km off the southern Bahia State, consisting of five volcanic islands (Fig. 1) bordered by fringing reefs. The archipelago is included in the Abrolhos Marine National Park, protected by federal law since 1983. No kind of fishing activity is permitted inside park limits. These fringing reefs are not remarkable coral constructions, but a veneer of reef organisms growing on a hard ground formed by the growth and cementation of coralline algae and other encrusting organisms, and the infilling of the internal voids with cemented sediment (Leão, 1996). These reefs extend from shallow water to depths of *c.* 10 m, ending in a sand or gravel substratum, where seaweeds (*Sargassum* spp. and other brown and green macroalgae) dominate. In some places, the reefs are surrounded by seagrass meadows dominated by *Halodule wrightii* or by extensive *Caulerpa prolifera* beds. Contrary to most typical tropical coral reefs, Abrolhos is an example of reefs surrounded by sediments containing considerable proportions of siliceous sand and mud (Leão & Kikuchi, 2001). Therefore, water turbidity around Abrolhos is high during most of the year, due mainly to carbonate sediment re-suspension *via* winds and currents. The inner parts of the archipelago, however, are protected from prevailing northerly and north-easterly winds, providing a better water visibility (mean of 15 m) and a calm coral reef 'oasis'. The water is clearer during warmer months (summer), when the average annual temperature ranges from 23 to 28° C. Thirteen sites were chosen for sampling around the five islands, in order to encompass contrasting environmental conditions and to search for differences in community structure of roving herbivorous fishes. Five sites were located at Santa Barbara Island, three at Redonda Island, two at Siriba Island, two at Sueste Island and one at Guarita Island (Fig. 1). These sites were chosen to encompass a range of exposure regimes so that large-scale patterns could be examined, while differences within reefs zones will be assessed later.

DATA COLLECTION

Substratum diversity

Composition and per cent cover of reef substratum organisms were assessed by laying a chain 1 m long with links of 2 cm in length parallel to the depth contour of the reef substratum. The number of chain links covering each organism was recorded and used to determine the proportional reef substratum composition (Porter, 1972). Replicated transects ($n = 8$) were performed in each study site using scuba, with data recorded on acrylic sheets.

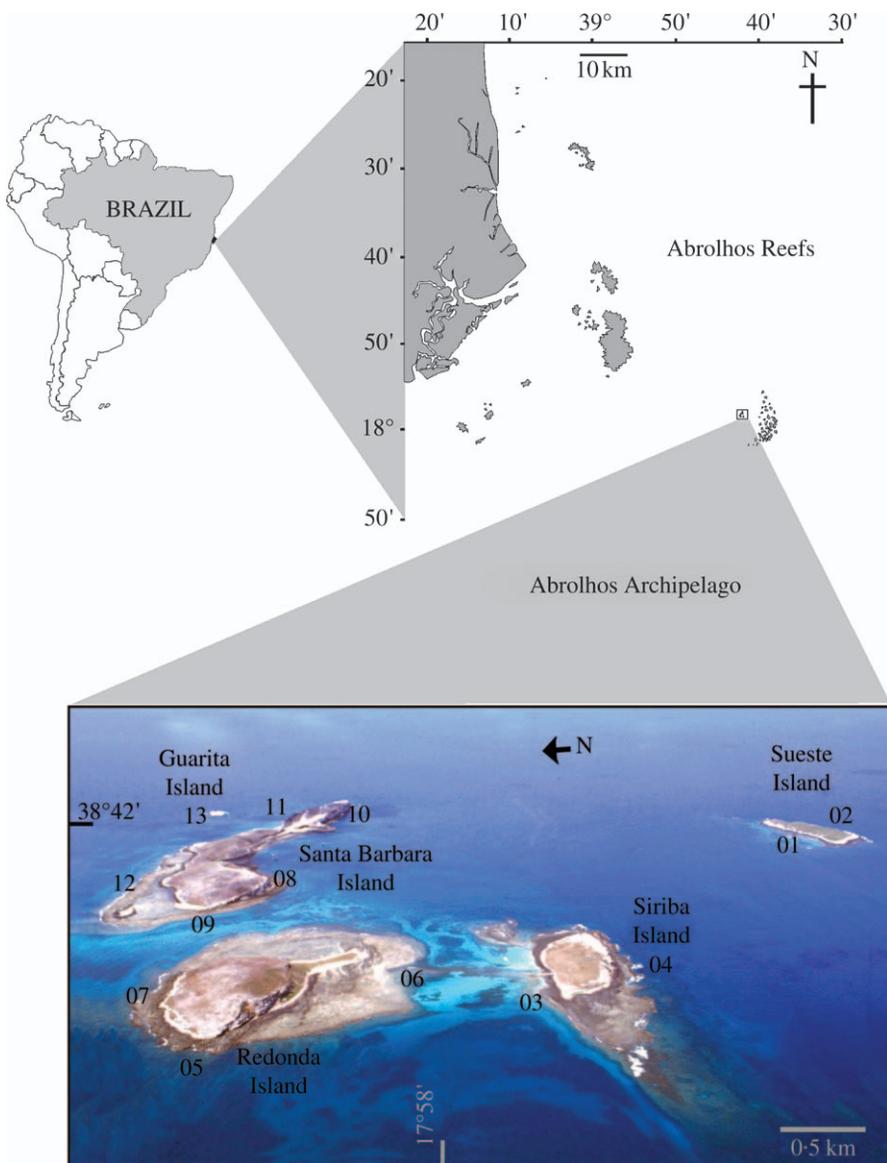


FIG. 1. Map of Abrolhos Archipelago showing study sites (1–13).

Fish abundance

The abundance of fishes in the families Scaridae, Acanthuridae and Kyphosidae was assessed by visual census technique using replicate strip transects ($n = 25$), running vertically on the reef at each site. A single diver using scuba swam along the transect recording fish species abundance and size within 2 m on each side of a 100 m long transect (400 m^2). Juvenile fishes ($<10 \text{ cm}$ total length, L_T) were excluded from the census as a conservative approach, in order to maximize the precision of counts of adults. Pilot studies were conducted to determine the number of replicates and swimming velocity utilizing the cumulative fish species number. Care was taken to do all censuses at high tide periods, in order to avoid bias due to tidal variations in fish distribution.

The two small parrotfishes, *Sparisoma radians* (Valenciennes) and *Cryptotomus roseus* Cope, were not considered herein, as they are predominantly inhabitants of seaweed beds. *Sparisoma frondosum* (Agassiz) and *Sparisoma amplum* (Ranzani) were combined in the abundance results, since in the initial phase of work there were problems in distinguishing the two species underwater. The same was done for the kyphosids.

Fish diet

Fishes were sampled for diet analysis at each study site ($n = c. 20$ per species) using hand spears. Only fishes >20 cm L_T were collected in order to minimize variance due to ontogenetic differences in diet of juvenile fishes. Collections were confined to mid-afternoon, when feeding rates were observed to be higher and guts were full. The L_T (cm) and wet mass (g) of each fish were recorded, and gut contents were removed and fixed in 10% formalin for later analysis. In the laboratory, gut contents were homogenized on a Dolphus plate and per cent content of food items and sediment were counted on 100 random squares with a stereomicroscope ($\times 50$). Algae were identified to at least genus and sorted into morphological groups according to Littler & Littler (1984). These functional-group approaches are of particular value in categorizing algae into ecologically meaningful groups. This approach has been successfully used in order to understand the variability of algal communities in order to differentiate gradients of productivity and disturbance (Steneck & Dethier, 1994). Difficulties in distinguishing *S. frondosum* and *S. amplum* underwater were resolved in the laboratory, so their diets were analysed separately. The diets of the two species of kyphosids were analysed together, however as previous analysis revealed very similar food habits.

STATISTICAL ANALYSIS

A correspondence analysis ordination was performed with data from all study sites using reef substratum cover to characterize groups of sites with similar substratum cover features. These procedures synthesize the presentation of fish abundance data based only on the outcome of similar sites clustered (= group of sites). A one-way ANOSIM permutation test was used *a posteriori* to test for significant differences among assembled groups. Both procedures were carried out utilizing Primer 5.0 software. Differences in per cent cover of reef substratum organisms among different groups of sites were analysed with a one-way ANOVA.

Differences in per cent contribution in abundance of target fish families among study sites were analysed using a two-way ANOVA, and a χ^2 test was used to test differences within sites. Fish abundance was compared among groups of sites with a one-way ANOVA, using all transects of similar study sites as replicates.

Diets were compared among fishes and study sites by using a two-way ANOVA. In all ANOVAs the data were transformed to \log_{10} , square root or arcsine in order to stabilize the variances when necessary (Underwood, 1997), and additional Student–Newman–Keuls multiple comparisons of means tests were performed as a *post hoc* test (Zar, 1999).

RESULTS

SUBSTRATUM DIVERSITY

The correspondence analysis ordination extracted 47% of the variance for the first two vectors, indicated three major groups of sites based on reef benthic organisms (Fig. 2). The one-way ANOSIM test identified the groups 1, 2 and 3 as significantly different ($r = 0.88$; $P < 0.1\%$). Differences among those groups for per cent cover of reef benthic organisms are illustrated in Table I. Algal species found in reef substratum and guts are listed in Table II. Group 1

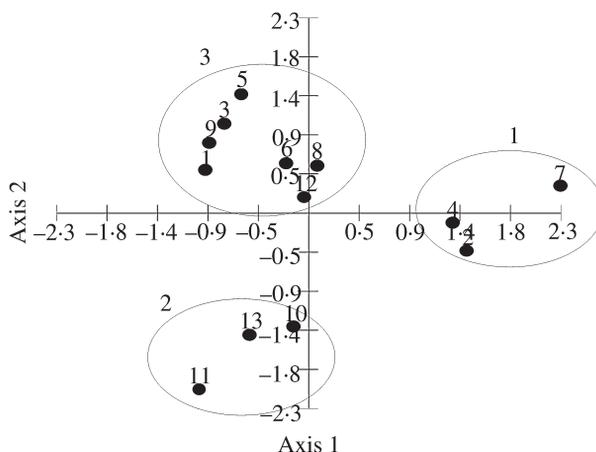


Fig. 2. Correspondence analysis based on per cent cover of reef substratum organisms from study sites on Abrolhos Archipelago (see locations on Fig. 1), showing the three groups of sites considered for analysis in this study.

included sites with high abundance of seaweeds, mainly *Dictyota* spp., *Dictyopteris* spp. and *Stypopodium zonale*, and low abundance of corals. Sites 2 and 4, included in group 1 (Fig. 2), are typically exposed to strong southerly and south-westerly winds (those associated with cold fronts), being comparatively deeper and consisting of hard substratum ending in sand habitat with extensive macroalgal beds. Site 7 on Redonda Island, although typically dominated by shallow habitats, also sustains an extensive macroalgal bed and low abundance of corals, thus being associated with sites 2 and 4. Group 2 comprised of sites with high coral cover, including millepores, stony corals and octocorals. Although site 10 sustains a high macroalgal cover, the abundance of stony corals and millepores are also high, resulting in it being clustered with sites 11 and 13, which are the sites where corals are more abundant (Table I). Urchins, predominantly *Echinometra lucunter*, were also more abundant in sites of group 2. Group 3 included calm and shallow sites, where the density of filamentous algae was higher. Seagrasses, specifically *H. wrightii*, the most widespread in Abrolhos Archipelago, were not considered in the analysis of Table I, since it forms specific habitats, which frequently function as dividing habitats between islands, the most extensive being located between Redonda and Siriba Islands.

COMMUNITY STRUCTURE OF FISHES

All roving herbivorous fishes found in the Abrolhos Archipelago, including three acanthurids, seven scarids and two kyphosids are listed in Table III. The per cent contribution of roving herbivorous fishes was significantly different among families ($P < 0.001$ for all comparisons). Approximately 64% of all observed fishes were acanthurids, 32% were scarids and only 4% were kyphosids; this pattern was consistent at all sites ($F_{2,36}$, $P < 0.001$).

TABLE I. Summary of comparative substratum reef organisms per cent coverage (mean \pm s.e.), plus the ANOVA (one-way) and Student–Newman–Keuls (SNK) multiple means comparison results among different group of sites

	Group of sites			ANOVA + SNK results
	1	2	3	
Filamentous algae	13.11 \pm 3.82	19.51 \pm 3.83	43.57 \pm 6.02	$F = 7.23; P < 0.01$
Sheet-like algae	32.2 \pm 2.01	13.72 \pm 6.87	12.04 \pm 1.65	$F = 10.6; P < 0.05$
Thick-leathery algae	18.29 \pm 4.51	1.93 \pm 0.97	9.15 \pm 2.15	$F = 6.26; P < 0.05$
Articulated coralline algae	2.98 \pm 1.20	2.54 \pm 0.75	2.41 \pm 0.85	$F = 0.08; P = 0.92$
Crustose coralline algae	5.44 \pm 1.73	4.84 \pm 0.47	2.76 \pm 0.72	$F = 2.27; P = 0.15$
Coarsely branched algae	10.49 \pm 4.83	1.71 \pm 0.78	5.61 \pm 2.0	$F = 1.78; P = 0.22$
Sponges	1.38 \pm 0.84	2.03 \pm 0.15	1.25 \pm 0.29	$F = 0.79; P = 0.48$
Millepores	1.44 \pm 0.87	8.30 \pm 1.21	3.63 \pm 0.27	$F = 22.9; P < 0.001$
Stony corals	9.05 \pm 3.0	25.43 \pm 8.15	11.64 \pm 1.84	$F = 4.12; P < 0.05$
Zoanthids	2.50 \pm 0.93	2.81 \pm 0.6	1.24 \pm 0.42	$F = 2.19; P = 0.16$
Octocorals	1.54 \pm 0.78	17.91 \pm 6.14	10.36 \pm 1.87	$F = 5.68; P < 0.05$
Urchins	0.88 \pm 0.28	6.95 \pm 2.13	3.09 \pm 0.96	$F = 4.31; P < 0.05$

TABLE II. Algae species found in the Archipelago of Arolhos during study development and assignment to morphological groups (modified from Littler & Littler, 1984) used for statistical analysis

Filamentous	Sheet-like	Thick-leathery	Articulated coralline	Coarsely branched
<i>Chaetomorpha clavata</i>	<i>Enteromorpha flexuosa</i>	<i>Halimeda tuna</i>	<i>Corallina officinalis</i>	<i>Anadyomene stellata</i>
<i>Cladophora</i> sp.	<i>Ulva lactuca</i>	<i>Penicillus capitatus</i>	<i>Jania adhaerens</i>	<i>Dictyosphaeria cavernosa</i>
<i>Bryopsis pennata</i>	<i>Dictyopteris delicatula</i>	<i>Udotea flabellum</i>	<i>Amphiroa beauvoisii</i>	<i>Valonia aegagropila</i>
<i>Caulerpa webbiana</i>	<i>Dictyopteris justii</i>	<i>Colpomenia sinuosa</i>		<i>Codium</i> sp.
<i>Caulerpa ambigua</i>	<i>Dictyopteris plagiogramma</i>	<i>Lobophora variegata</i>		<i>Caulerpa racemosa</i>
<i>Bodleopsis pusilla</i>	<i>Dictyota bartayresiana</i>	<i>Padina gymnospora</i>		<i>Gelidium pusillum</i>
<i>Hinckia breviarticulata</i>	<i>Dictyota cervicornis</i>	<i>Styopodium zonale</i>		<i>Pterocladia capillacea</i>
<i>Hinckia mitchelliae</i>	<i>Dictyota menstrualis</i>	<i>Sargassum</i> spp.		<i>Gelidiella acerosa</i>
<i>Sphacelaria rigidula</i>		<i>Galaxaura</i> sp.		<i>Hypnea musciformis</i>
<i>Callithamnion</i> sp.		<i>Tricleocarpa cylindrica</i>		<i>Hypnea spinella</i>
<i>Centroceras clavulatum</i>		<i>Gracilaria</i> sp.		<i>Laurencia papillosa</i>
<i>Ceramium deslongchampsii</i>		<i>Gracilaria cervicornis</i>		
<i>Ceramium diaphanum</i>		<i>Champia parvula</i>		
<i>Chondria</i> sp.		<i>Osmundaria obtusiloba</i>		
<i>Herposiphonia secunda</i> f. <i>secunda</i>				
<i>Herposiphonia secunda</i> f. <i>tenella</i>				
<i>Ophidocladus simpliciisculus</i>				
<i>Polysiphonia ferulacea</i>				
<i>Polysiphonia howei</i>				
<i>Calothrix crustacea</i>				
<i>Calothrix contarenii</i>				
<i>Lyngbya semipruena</i>				
<i>Plectonema terebrans</i>				
<i>Cyanoecystis sphaerica</i>				
<i>Brachytrichia quoyi</i>				
<i>Phomidium tenue</i>				
<i>Entophysaus deusta</i>				
<i>Blennothrix lyngbyaceae</i>				
<i>Xenococcus kermeri</i>				

TABLE III. List of roving herbivorous reef fishes found in the Abrolhos Archipelago

Family	Species	Suggested feeding mode	Mean \pm s.d. L_T (cm)/mass (g)
Acanthuridae	<i>Acanthurus bahianus</i> Castelnau	Scraper	19.6 \pm 3.1/232.6 \pm 188.3
Acanthuridae	<i>Acanthurus chirurgus</i> Bloch	Scraper	23.4 \pm 2.6/301.4 \pm 109.2
Acanthuridae	<i>Acanthurus coeruleus</i> Bloch & Schneider	Browser	24.8 \pm 4.3/462.2 \pm 281.6
Scaridae	<i>Scarus trispinosus</i> Valenciennes	Excavator/scraper	48.2 \pm 3.7/1766.3 \pm 539.2
Scaridae	<i>Scarus zelindae</i> Moura, Figueiredo & Sazima	Excavator/scraper	26.9 \pm 2.1/454.7 \pm 235.6
Scaridae	<i>Sparisoma axillare</i> Steindachner	Excavator/scraper	22.6 \pm 3.5/254.12 \pm 133.5
Scaridae	<i>Sparisoma amplum</i> Ranzani	Excavator/scraper	23.2 \pm 1.8/382.1 \pm 166.8
Scaridae	<i>Sparisoma frondosum</i> Agassiz	Excavator/scraper	24.3 \pm 1.9/298.8 \pm 113.1
Scaridae	<i>Sparisoma radians</i> * Valenciennes	Browser	—
Scaridae	<i>Cryptotomus roseus</i> * Cope	Browser	—
Kyphosidae	<i>Kyphosus sectatrix</i> Cuvier	Browser	36.3 \pm 6.7/963.4 \pm 681.3
Kyphosidae	<i>Kyphosus incisor</i> L.	Browser	33.9 \pm 5.3/890.3 \pm 368.4

*Not included in analysis; L_T , total length.

Analysing the archipelago as whole, *Scarus trispinosus* Valenciennes and *Sparisoma axillare* (Steindachner) were the dominant scarids in all groups of sites, while among acanthurids, the three species occurred in similar densities (Fig. 3). When fish abundance was compared among different groups of sites, the most notable difference detected was between group of sites 1 and the other two (Table IV). Thus, *S. trispinosus*, *Sparisoma* spp., *Acanthurus bahianus* Castelnau, *Acanthurus chirurgus* (Bloch) and *Acanthurus coeruleus* Bloch & Schneider, showed significant lower densities in group of sites 1, while *S. axillare*, *Scarus zelindae* (Moura, Figueiredo & Sazima) and *Kyphosus* spp. did not (Fig. 3 and Table IV). The only fish that differed significantly between group of sites 2 and 3 was *A. coeruleus*, but the mean abundances were very similar (Table IV).

FISH DIET

The diet of the majority of fishes examined consisted primarily of both algae (35–90% of gut contents) and detritus (35–65% of gut contents). Additionally, there was a low proportion of seagrasses (0.2–11%) and animal material (1.3–3.5%) (Fig. 4). *Kyphosus* spp. and *A. coeruleus* were exceptions in that their guts

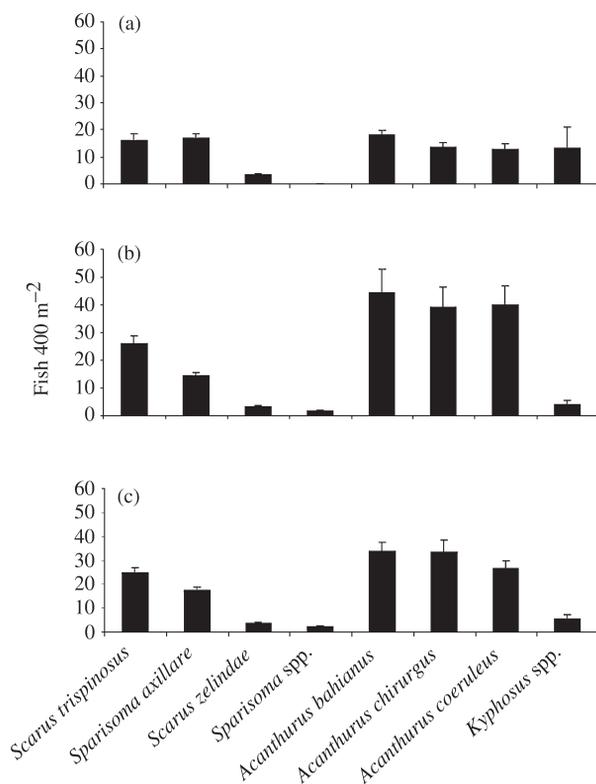


FIG. 3. Comparative abundance of roving herbivorous fishes (mean + s.e.) among group of sites (a) 1, (b) 2 and (c) 3.

contained mainly algae (83 and 91%, respectively) (Fig. 4). Scarids ingested significantly more detritus and less algae than *A. chirurgus* and *A. bahianus* ($F_{8,117}$, $P < 0.001$). Notably, *S. amplum* had significantly more detritus in their guts than all other fishes (63%). The amount of animal material in guts (1–4%) was similar for all fishes ($F_{8,117}$, $P > 0.05$), while only kyphosids ingested a significantly greater amount of seagrasses than other fishes ($F_{2,117}$, $P < 0.001$) [Fig. 4(b)].

Of the algae ingested, the bulk was filamentous species (35–65% of total algae), except in *Kyphosus* spp. and *S. axillare* ($F_{8,117}$, $P < 0.001$), where sheet-like species predominated [Fig. 4(b)]. Kyphosids also ingested significantly more thick-leathery algae than all other fishes ($F_{8,117}$, $P < 0.001$). Scarids, excluding *S. axillare*, ingested proportionally more articulated algae than acanthurids and kyphosids ($F_{8,117}$, $P < 0.001$).

DISCUSSION

The Abrolhos Archipelago comprises the most diverse set of habitats within the Abrolhos reef complex (c. 6000 km²). A distinct characteristic is that all

TABLE IV. Summary of comparative fish species abundance (mean \pm s.e.), plus the ANOVA (one-way) and Student–Newman–Keuls (SNK) multiple means comparison results among different group of sites

Fish species	Group of sites			ANOVA + SNK results
	1	2	3	
<i>Scarus trispinosus</i>	16.0 \pm 2.6	26.1 \pm 2.5	24.8 \pm 2.3	$F = 3.60; P < 0.05$ 1 < 2 = 3
<i>Sparisoma axillare</i>	16.1 \pm 1.7	14.3 \pm 1.1	17.5 \pm 1.1	$F = 1.53; P = 0.22$ 1 = 2 = 3
<i>Scarus zelindae</i>	3.1 \pm 0.5	3.0 \pm 0.6	3.9 \pm 0.4	$F = 0.89; P = 0.41$ 1 = 2 = 3
<i>Sparisoma</i> spp.	0.5 \pm 0.1	1.7 \pm 0.1	2.3 \pm 0.4	$F = 36.69; P = 0.001$ 1 < 2 = 3
<i>Acanthurus bahianus</i>	17.9 \pm 1.9	44.64 \pm 8.3	34 \pm 3.6	$F = 5.42; P < 0.01$ 1 < 2 = 3
<i>Acanthurus chirurgus</i>	13.5 \pm 1.9	34.2 \pm 7.1	33.6 \pm 4.7	$F = 3.79; P < 0.05$ 1 < 2 = 3
<i>Acanthurus coeruleus</i>	16.6 \pm 1.9	38.5 \pm 6.5	31.5 \pm 3.2	$F = 7.28; P < 0.001$ 1 < 3 < 2
<i>Kyphosus</i> spp.	13.3 \pm 2.8	4.1 \pm 1.3	5.5 \pm 1.6	$F = 1.23; P = 0.31$ 1 = 2 = 3

reef habitats in the Archipelago are relatively shallow and short in length (mean of 60 m), quite different from typical reefs of the Caribbean and Pacific, where reef zones are larger and clear niche partitioning can be observed within herbivorous fishes among zones (Bouchon-Navaro & Harmelin-Vivien, 1981; Russ, 1984, 2003; Lewis & Wainwright, 1985; Crossman *et al.*, 2005). Therefore, fishes in the Archipelago are likely to be able to move among distinct habitats, containing different algal species and forms (plus additional detritus and associated microorganisms), with little energy expenditure. Characteristically, when a site is short in extension, the depth gradient is comparatively more pronounced (most of exposed sites), conversely when the reef is extensive (maximum 100 m), the depth gradient is quite smooth (most of calm sites).

Distinct feeding and resting areas were observed, the former including several areas, and the latter, mainly shallow sites, generally with high coral cover, especially those where *Millepora alcicornis* was abundant. Juveniles seemed to be restricted to shallow areas and habitats with more complexity, such as seaweed beds, while adults were prone to exploring large areas (including low relief areas). As the distances among islands are also not large (Fig. 1), and because seagrass and seaweed beds border most of the islands (together with rubble), fishes can easily migrate from one island to another, increasing the availability of food resources. The only island that seems to be isolated from the others is Sueste Island, *c.* 2.5 km apart from Santa Barbara Island. Nevertheless, the presence of ‘Chapeirões’ (conspicuous and unique coral pinacles that grows in a mushroom shape; Leão, 1996) between Redonda and Sueste Island, could function as ‘stepping stones’ for fish migration.

The observed differences in fish abundance between group of sites 1 and group of sites 2 and 3 appear related to biotic and abiotic factors. The sites

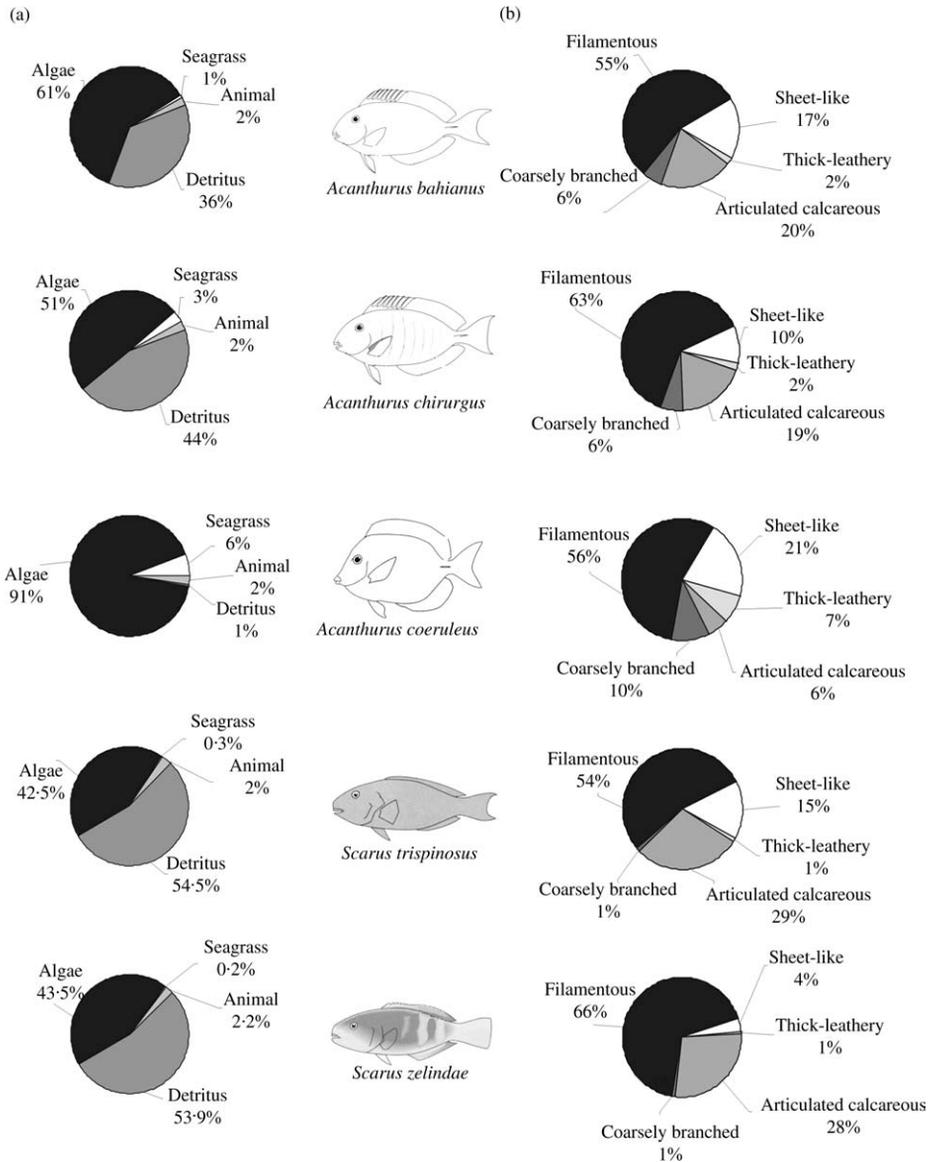


FIG. 4. Diet based upon (a) gut contents with (b) a further break down of composition of algal portion of the diet.

of group 1 are comparatively deeper than the others (except site 7), with low availability of filamentous algae (and associated trapped detritus), the main component in the diet of most herbivorous fishes (Fig. 4). These sites are exposed to strong southern and south-western cold fronts which promote high wave surge. Physically resistant forms of algae, such as thick-leathery, sheet-like and coarsely branched algae, proliferate there (Table I). This pattern of algal distribution is similar to the proposed model of Steneck & Dethier (1994) for high productivity and low disturbance (herbivory) environments.

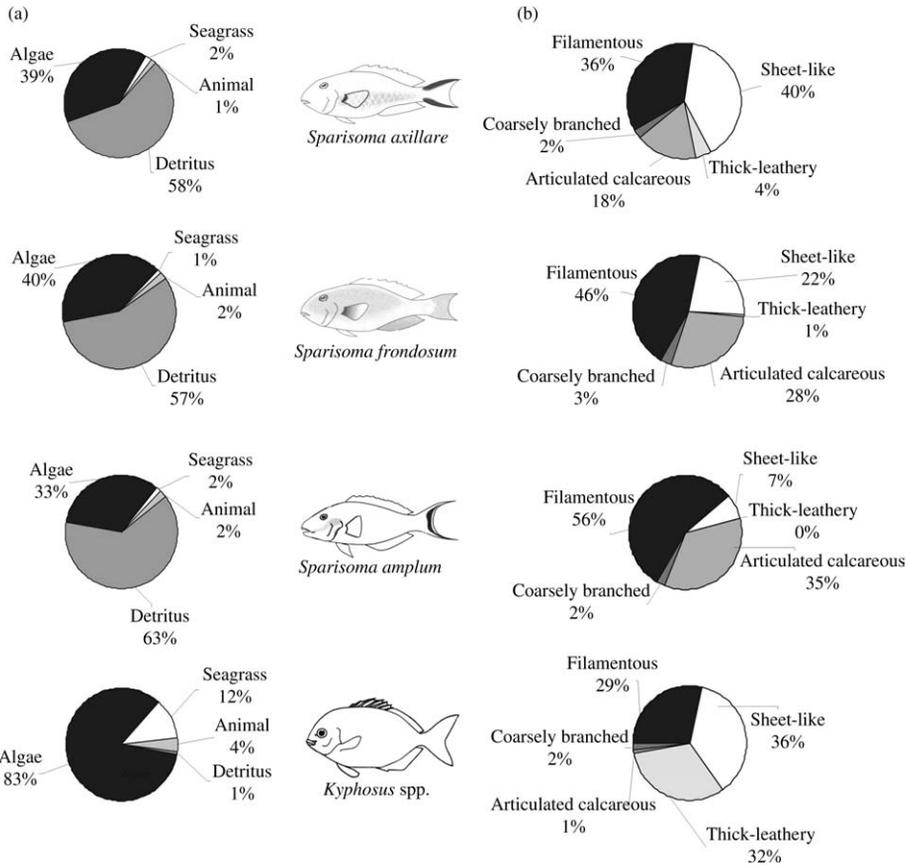


FIG. 4. Continued

These sites, however, also include corticated foliose algae (Steneck & Dethier, 1994) such as *Dictyota* spp. and *Dictyopteris* spp. In sites of group 1, the algal distribution pattern is similar to that described for other local subtidal environments, where leathery macrophytes (*Sargassum* spp.) dominate the shallowest areas, with corticated and foliose algae somewhat deeper. Crustose coralline algae are spread over boulders in deeper reef zones. In addition, the complexity derived from extensive coral cover, which provides optimal refuges for fishes, is not present. Moreover, the abundance of predators is higher; notable in the region is *Mycteroperca bonaci* (Poey), which was observed to swallow an entire *S. axillare* c. 30 cm in length captured and yet transpierced by a spear (C. E. L. Ferreira, pers. obs.). Although not analysed here, the mean size of roving herbivorous fishes observed at these deep sites are larger, generally abundant schools composed of terminal-phase males and large females. Otherwise, these habitat-specific characteristics of group of sites 1 appear preferable to kyphosids (Fig. 3), which are well adapted to feed on thick-leathery and sheet-like algae with a small amount of associated detritus [Fig. 4(b); Horn, 1989, 1992]. *Sparisoma axillare* is an abundant scarid that feeds on a large variety of algal forms, and seems to be the roving herbivore most adapted to exploiting

all the different habitats (Fig. 3). Indeed, this fish is conspicuous along the whole Brazilian coast (Floeter *et al.*, 2001; Bonaldo *et al.*, 2006), suggesting a high competitive ability (diet plasticity).

In shallow, calm habitats of group of sites 2 and 3, the density of damselfishes [predominantly *Stegastes fuscus* (Cuvier)] is high. There, reef zonation is clear with higher densities occurring in shallower parts (C. E. L. Ferreira, unpubl. data). These fishes certainly have a social influence on other fishes, although direct observations showed that schools of large scarids, as well as very large schools of acanthurids, frequently venture inside their territories to feed on the EAM. Although their territories are more abundant in calm sites, this factor appears not to influence the abundance of roving herbivores when the group of sites 1 and the other groups were compared.

The community structure of roving herbivorous fishes in the Abrolhos Archipelago seems to be largely influenced by food and refuge availability. The abundance and distribution results indicate that roving herbivorous fishes in the Abrolhos Archipelago are more abundant at calm sites such as the group of sites 2 and 3. In group of sites 3, detritus and delicate turf algae, their major food resource, are more abundant. This differs from results of Gust's (2002) study on scarids in the Great Barrier Reef, who found poor correlations between fish biomass and habitat. Although these fishes are unlikely to respond to differences in species composition of algal turfs as claimed by Russ (2003), they apparently are able to optimize their nutrient intake by utilizing a diversified diet (Crossman *et al.*, 2005). Boyer *et al.* (2004) had also added evidence of fishes' ability to respond to changes in food quality according to a differential gradient in nutrient input. The higher abundance of fishes at calm sites could also be concurrent with higher biomass of algae and even higher algal and detrital production there.

With the exception of the kyphosids and *A. coeruleus*, the diets of roving herbivorous fishes in the Abrolhos Archipelago are composed of both algae and detritus. Detritus includes both organic and inorganic material. Inorganic components have most of their origin from CaCO_3 derived from corals and coralline algae that make up the reef framework. Organic material is reported to originate from algae, fish faeces and coral mucus, and includes microbes, microalgae and associated meiofauna (Crossman *et al.*, 2001). Compared to algae, detritus is known to have greater concentrations of amino acids, suggesting that a significant portion of the fish biomass on coral reefs claimed to be herbivorous in an extensive body of literature, seems instead to be directly supported by the detrital food web (Crossman *et al.*, 2001, 2005; Choat *et al.*, 2002, 2004). The EAM has a high capacity to trap sediment and organic matter, providing an excellent habitat for the development of a rich associated fauna and flora (Choat, 1991), which in turn is ingested by the supposedly herbivorous fishes. This fact has important consequences for the trophic pathways reported on coral reefs, where there is a consistent pattern of a high proportion of algal turf production being consumed by grazers (Hatcher, 1981; Carpenter, 1986; Klumpp & Polunin, 1989; Polunin & Klumpp, 1992).

Most acceptable digestibility concepts concerning herbivorous fishes were based on Lobel's work (1981), which demonstrated that a low pH in the stomachs of some fishes could lyse algae cell walls, thus making algal contents

available for assimilation. Recent experiments by Zemke-White *et al.* (1999), however, clearly showed that once lysed, algal cell contents are not necessarily assimilated by fishes. Recent work on Indo-Pacific herbivorous fishes has demonstrated that carbohydrates are fermented by bacteria under anaerobic conditions to produce short chain fatty acids (SCFAs), which in turn could be absorbed by the gut, enabling the host animal to gain energy from dietary components not generally susceptible to endogenous digestive enzymes (Stevens & Hume, 1998). It seems that fermentation benefits species that feed on material that contains large amounts of structural carbohydrates, which bacteria can break down to produce acetate, which the fish can use as a source of energy. Indeed, species that feed largely on detritus show little evidence of fermentation (Clements & Choat, 1995; Choat *et al.*, 2002, 2004; Mountfort *et al.*, 2002). Based on those concepts, the great majority of roving herbivorous fishes in Abrolhos, classified as scrapers and excavators (Bellwood & Choat, 1990), are included in the group which ingests large amounts of bacterial and meiofaunal biomass (low levels of acetate and high levels of isovalerate; Choat *et al.*, 2002), with rapid feeding rates and turnover of gut contents (Choat *et al.*, 2004). Exceptions to that are the kyphosids and *A. coeruleus*. The former feeds mostly on brown algae, most of them well reported as 'chemically defended' (Hay & Fenical, 1988; Paul, 1992; Steinberg, 1992). Kyphosids are known to sustain strong microbial fermentation, including endemic endogenous protozoans (Rimmer & Wiebe, 1987), and to be the dominant groups in temperate and subtropical reef environments (Horn, 1989; Choat, 1991). *Acanthurus coeruleus*, as distinct from kyphosids, is restricted to the tropics (Ferreira *et al.*, 2004) and seems to be included in a different SCFA digestion profile group (high to intermediate levels of SCFAs; Choat *et al.*, 2002). It appears that *A. coeruleus* has a similar nutritional strategy to *Acanthurus lineatus* (L.) (Choat *et al.*, 2004; Crossman *et al.*, 2005), in which moderate levels of fermentation produce acetate from red and green algae with acid lysis occurring in the thin-walled stomach, in contrast to the thick-walled stomach with a muscular gizzard of the detrital feeding surgeonfishes (*A. bahianus* and *A. chirurgus*).

The extensive underwater observations clearly detected food selection by the fishes studied, especially in the parrotfishes. As an example, *S. amplum* together with *S. trispinosus* seem to spend much of the daytime foraging over the extensive crustose coralline flats of the Abrolhos Archipelago (*Porolithon pachydermun* being the dominant species; Figueiredo & Steneck, 2003). *Sparisoma amplum* is not a conspicuous scarid in the region, while the largest scraper, *S. trispinosus*, is abundant not only in the archipelago, but in the whole region (Ferreira & Gonçalves, 1999). In the Caribbean, the conspecific of *S. amplum*, *Sparisoma viride* (Bonnaterre), is the most important excavator in some coral reefs (Bruggemann, 1994), also consuming high proportions of endolithic and crustose corallines. As crustose coralline algae form a large proportion of the Abrolhos reef framework (Figueiredo, 1997; Villaça & Pitombo, 1997), this implies that scrapers like *S. trispinosus* may play an important role as bioeroders on local reefs. Another example of differential use and selectivity by specific food resources takes place daily during high tide periods. In the shallow water of most islands, a complex zone of small basaltic boulders covered by a thin and profuse cyanobacterial layer is commonly a place for intense foraging by

multispecific herbivorous fish schools (acanthurids, scarids, pomacentrids and others), including the large *S. trispinosus*. These observations indicate that roving herbivorous fishes move daily among different habitats around the islands (e.g. coral reefs, rocky reefs, seaweed and seagrass beds and crustose coralline flats) benefiting from different food resources. Although fishes like *S. trispinosus* could comparatively be classified as a scraper (Bellwood & Choat, 1990) with a non-selective bite (Choat *et al.*, 2002), underwater observations clearly detected them inspecting and foraging over crustose coralline flats, coralline nodules, cyanobacteria covering rocky boulders and also biting large, sheet-like macroalgae. The foraging plasticity of *S. trispinosus* acting either as scraper, excavator and browser indicates the need for reconsideration of the classification of fish feeding modes. This suggests that, depending on environmental heterogeneity, these fishes have the capacity to exercise some level of selectivity over their primary food, and are thus adapted to foraging in different modes (Table III). Another important consideration regarding foraging mode is related to fish size. Large scarids, often considered scrapers, were observed to leave profound marks on the reef framework (unpubl. obs.). Thus, the excavator capacity seems to be strongly related to size. The ecological and physiological significance of this requires further study.

Although many of the species considered in this study have high proportions of detritus in their diets, there were also more algae in the diets of parrotfishes and sediment feeding surgeonfishes than would have been expected from previous studies (Randall, 1967; Bruggemann, 1994; Crossman *et al.*, 2001; Choat *et al.*, 2002). Underwater observations also corroborate these patterns (this study and Bonaldo *et al.*, 2006).

As most Brazilian scarids are endemic, further studies on diet and selectivity in different places are ultimately important to aid in the understanding of their feeding plasticity and their methods of meeting their energetic requirements. Also, their similarity with Caribbean and Indo-Pacific counterparts suggest opportunities for interesting comparisons.

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