

Foraging activity of roving herbivorous reef fish (Acanthuridae and Scaridae) in eastern Brazil: influence of resource availability and interference competition

RONALDO BASTOS FRANCINI-FILHO^{1,2}, CAMILO MOITINHO FERREIRA³, ERICKA OLIVEIRA CAVALCANTI CONI³, RODRIGO LEÃO DE MOURA² AND LES KAUFMAN⁴

¹Departamento de Biologia, Centro de Ciências Biológicas e da Saúde, Universidade Estadual da Paraíba, Avenida das Baraúnas 351, 58109-753 Campina Grande, PB, Brazil, ²Conservation International Brazil, Marine Program, Rua das Palmeiras 451, 45900-000 Caravelas, BA, Brazil, ³Centro de Pesquisa e Conservação dos Ecossistemas Aquáticos – BIOTA Aquática, Rua Almirante Ernesto Jr, 41810-400 Salvador, BA, Brazil, ⁴Boston University Marine Program, 5 Cummington Street, Boston, MA 02215, USA

Foraging activity of roving herbivorous reef fish (RHs) from families Acanthuridae (surgeonfish; three species) and Scaridae (parrotfish; five species), and its relationship to resource availability and interference competition, was studied in the largest South Atlantic Reef complex (Abrolhos Bank, eastern Brazil). Observations were undertaken at four sites differing in resource availability and competitors' abundance (i.e. RHs and territorial herbivores from genus Stegastes). Turf algae (TA) were selected by most species in most sites, while other food items were generally avoided. Surgeonfish had higher feeding rates than parrotfish, the former grazing more frequently on fleshy algae (FA) and the latter on crustose calcareous algae (CCA). Both surgeonfish and parrotfish interacted agonistically most frequently with damselfish, followed by confamilial interactions. Despite these consistent patterns, feeding rates, food selection and frequency of agonistic interactions differed significantly between sites for most species. Bite rates on CCA and FA were disproportionately higher in sites where such items were more available, leading to significant spatial variation in grazing selectivity (i.e. positive rather than negative selection of CCA and 'lower avoidance' of FA). Although agonistic interactions were more frequent at sites where herbivorous fish (both roving and territorial) were most abundant, there was no clear relationship between interference competition and foraging patterns. These results indicate that the scarcity of other food may induce RHs to consume the dominant resources. They also support the hypotheses that RHs are unable to clear large tracts of reef surface of FA once these have proliferated, and that territorial herbivores do not limit the access of RHs to particular resources.

Keywords: parrotfish, surgeonfish, feeding rates, grazing selectivity, *Stegastes*, interference competition

Submitted 7 October 2008; accepted 10 July 2009; first published online 3 November 2009

INTRODUCTION

Roving herbivorous reef fish (RHs) from families Acanthuridae (surgeonfish) and Scaridae (parrotfish) are abundant and ecologically important members of the reef community. They feed primarily on algae and detritus and generally represent the predominant reef herbivores in terms of algal biomass consumption (Horn, 1989; Hay, 1991). Since their intense feeding activity reduces spatial competition between corals and algae, RHs are widely recognized as a critical functional group on coral reefs (Bellwood *et al.*, 2004).

Foraging activity of RHs is strongly related to morphology, with the recognition of three main functional groups: browsers, scrapers and excavators (Bellwood & Choat, 1990; Streelman *et al.*, 2002; Francini-Filho *et al.*, 2008a). Browsers use their discrete teeth to cut off macroalgae, leaving no scars on the

substrate. Scrapers feed at high rates and make shallow bites, leaving only a superficial scrape. Excavators feed at low rates and remove large portions of the substratum using their robust jaws, leaving noticeable scars (Bellwood & Choat, 1990; Streelman *et al.*, 2002). The recognition of species within each functional group helps to understand their relative effects in terms of bio-erosion, coral fitness and survival, habitat alteration and ecosystem dynamics (Bellwood & Choat, 1990; Bellwood *et al.*, 2004; Francini-Filho *et al.*, 2008a).

Foraging activity of RHs, particularly feeding rates, may also vary according to diet (Choat *et al.*, 2004). Despite the traditional hypothesis that RHs feed primarily on plant material, many species target organic detritus (e.g. diatoms and dinoflagellates) attached to turf algae rather than the algae themselves (Choat *et al.*, 2002; Wilson *et al.*, 2003). Currently four dietary groups of nominally herbivorous reef fish are recognized based primarily on the frequency of consumption of the following food items: macroalgae, turf algae, plankton and detritus (Choat *et al.*, 2002). Feeding rates of species ingesting mainly macroalgae and zooplankton are generally lower than that of detritivores, while feeding rates of species feeding primarily

Corresponding author:
R.B. Francini-Filho
Email: rofilho@yahoo.com

on turf algae are more variable. This relationship between diet and feeding rates, in turn, is mostly related to differences in digestive modes and rates of turnover of gut contents (Choat *et al.*, 2002, 2004; Crossman *et al.*, 2005).

Although feeding modes and diet differ interspecifically, many RH species prefer similar and high-quality food resources (Bruggemann *et al.*, 1994a, b), resulting in competition for food resources (e.g. Robertson & Gaines, 1986; Bruggemann *et al.*, 1994a). Roving herbivores also frequently compete with territorial herbivores, such as damselfish from genus *Stegastes*, which are highly aggressive toward conspecifics and heterospecifics with similar diet (Ceccarelli *et al.*, 2001; Osório *et al.*, 2006). Although interference competition is expected to intensify with increased density of herbivores, and availability of different food resources may vary considerably in space, the extent to which spatial variation in competitors' abundance and resource availability affect the foraging activity of RHs is still poorly known (but see Bruggemann *et al.*, 1994b).

Most studies on the foraging activity of RHs were done in the Caribbean and Indo-Pacific (Bruggemann *et al.*, 1994a, b; Bellwood *et al.*, 2003; Fox & Bellwood, 2007). The availability of detailed information for several species allowed the development of a reef trophic model (Van Rooij *et al.*, 1998) and an ecosystem level analysis on the impacts of RHs (Mumby, 2006) in the Caribbean, as well as quantitative assessments on the functional roles of RHs along depth and cross-shelf gradients in the Great Barrier Reef (Fox & Bellwood, 2007; Hoey & Bellwood, 2008).

In the impoverished tropical south-western Atlantic reefs (Brazil), three surgeonfish (genus *Acanthurus*) and seven endemic parrotfish species (five *Sparisoma* and two *Scarus*) are recognized (Moura *et al.*, 2001; Gasparini *et al.*, 2004; Robertson *et al.*, 2006). The diet of all acanthurids is described for a coastal beach-rock reef in north-eastern Brazil (Dias *et al.*, 2001). In addition, two studies in tropical rocky reefs provide information on the foraging activity (Bonaldo *et al.*, 2005) and diet (Ferreira & Gonçalves, 2006) of RHs in Brazil. Finally, a recent study reports on live coral predation by *Scarus trispinosus* Valenciennes, 1840 and *Sparisoma amplum* (Ranzani, 1841) in the Abrolhos Bank, eastern Brazil, and comments on the classification of these species into functional groups (Francini-Filho *et al.*, 2008a).

The present study investigates the foraging activity (i.e. feeding rates and food selection) of surgeonfish and parrotfish in the Abrolhos Bank, eastern Brazil. The particular hypotheses that spatial variability in interference competition and resource availability may lead to spatial variation in foraging patterns of RHs is tested. This is the first study to characterize the foraging activity of all RH species from families Acanthuridae and Scaridae in the same region, and the first comprehensive study of this type in Brazil. The detailed information for individual taxa provided here is critical for understanding the role of RHs in shaping reef benthic communities, in determining reef resilience, and to guide conservation and management measures (see Fox & Bellwood, 2007).

MATERIALS AND METHODS

Study region

The Abrolhos Bank occupies 42,000 km² of the continental shelf in eastern Brazil (Figure 1). Depths rarely exceed 30 m and reef

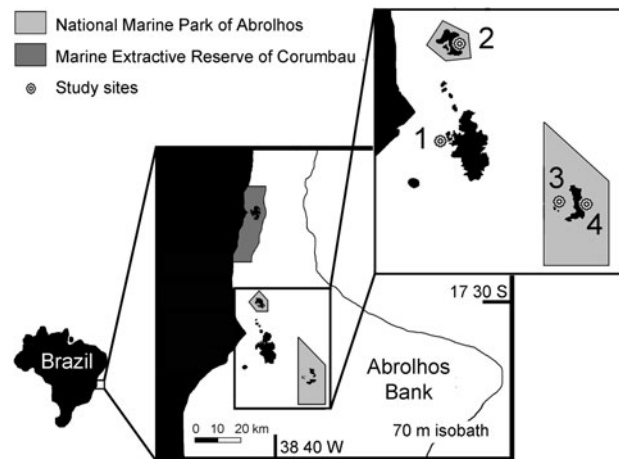


Fig. 1. Map of the Abrolhos Bank showing study sites and marine protected areas. (1) Pedra de Leste (PLES); (2) Timbebas (TIM); (3) Portinho Norte (PNOR; within the Abrolhos Archipelago); (4) Parcel dos Abrolhos (PAB).

structures display a characteristic form of mushroom-shaped pinnacles. The region encompasses the largest and richest coral reefs in the South Atlantic (Leão & Kikuchi, 2001). Three species of *Acanthurus* (*Acanthurus bahianus* Castelnau, 1855, *Acanthurus chirurgus* (Bloch, 1787) and *Acanthurus coeruleus* Bloch & Schneider, 1801), two of *Scarus* (*Scarus trispinosus* and *Scarus zelindae* Moura, Figueiredo & Sazima, 2001) and four of *Sparisoma* (*Sparisoma axillare* (Steindachner, 1878), *Sparisoma amplum*, *Sparisoma frondosum* (Agassiz, 1831), and *Sparisoma radians* (Valenciennes, 1840)) occur at the Abrolhos Bank (Moura & Francini-Filho, 2006). All species, except the small-bodied and peri-reefal dweller *S. radians*, were included in this study.

Underwater observations were conducted during the summer (January–April) of 2006 and 2007 at four sites (Parcel dos Abrolhos, Pedra de Leste, Portinho Norte and Timbebas). These sites vary greatly according to distance offshore, habitat characteristics and protection from fishing (Francini-Filho & Moura, 2008). Portinho Norte, within the Abrolhos Archipelago, is a rocky reef bordered by fringing coralline reefs, while the other sites are composed of typical coralline pinnacles. Two sites (Portinho Norte and Parcel dos Abrolhos) are further from the coast and located within the well enforced portion of the National Marine Park of Abrolhos (NMPA). Timbebas is located within a discontinuous portion of the NMPA that is closer to land and poorly enforced. Pedra de Leste is unprotected from fishing, closer to land and shallower than the other sites (Figure 1).

Field procedures

Food availability (i.e. benthic cover) at the study sites was assessed using photo-quadrats (N = 10 per site; see Francini-Filho *et al.*, 2008a,b for a detailed description of the method). Photographs were analysed using the Coral Point Count with Excel Extensions software (Kohler & Gill, 2006). Organisms were classified in the nine following categories: turf algae (i.e. multispecific stands of small epilithic algae), fleshy algae, crustose calcareous algae, *Halimeda* spp., live corals, fire-corals (*Millepora* spp.), octocorals, sand and zoanthids. Fish counts (N = 15 per site) were made using a nested stationary visual census technique (cf. Minte-Vera

et al., 2008). Counts for two species of territorial herbivores (*Stegastes fuscus* (Cuvier, 1830) and *Stegastes variabilis* (Castelnau, 1855)) were pooled.

Feeding rates were quantified using replicate 1-minute observation periods (cf. Francini-Filho *et al.*, 2008a), in which divers recorded the species identity, total number of bites on different benthic organisms and fish body size (total length, TL) to the nearest centimetre. Separate observations for initial phase (IP) and terminal phase (TP) males (Robertson & Warner, 1978) were only made for *Scarus zelindae*, *Sparisoma amplum* and *S. frondosum*, as *Scarus trispinosus* shows no clear colour and morphological changes according to life phase (Moura *et al.*, 2001) and no TP *Sparisoma axillare* individuals were recorded. A total of 641 independent observations were made. Frequency of agonistic interactions (cf. Robertson *et al.*, 1976; Risk, 1998) among RHs and between RHs and territorial herbivores was quantified in a separate set of 1-minute observation periods ($N = 492$). Detailed information on the sampling effort is shown in Table 1. Underwater observations were made in the same periods of day (0900–1600 h) for all species in the four sites, with samples distributed as evenly as possible between different hours of the day (cf. Ledlie *et al.*, 2007).

Data analyses

Student's *t*-test was used to evaluate significant differences in feeding rates between IP and TP individuals. Comparisons were made for each food item separately considering only the sites in which both IP and TP individuals were recorded (see Table 1). Since few significant differences were registered (see Results) data for IP and TP individuals were pooled in subsequent analyses. Sample size for a few species/sites remained relatively small even after pooling data for IP and TP individuals. Thus results for such particular cases must be interpreted with caution.

Selectivity for different benthic organisms was determined with Ivlev's electivity index (Ivlev, 1961), as follows:

$$E_i = (r_i - ni)(r_i + ni)^{-1}$$

where E_i = electivity measure for benthic organism i , r_i = proportion of bites taken on benthic organism i , and ni =

relative cover of benthic organism i in the studied habitat. Electivity index (E_i) varies from -1 to $+1$, in which values close to $+1$ indicate higher preferences and values close to -1 indicate lesser preference or avoidance.

One-way analysis of variance (ANOVA) was used to evaluate differences in fish density, benthic cover and frequency of agonistic interactions between sites, as well as differences in bite rates between species. Analysis of covariance (ANCOVA) was used to evaluate differences in bite rates and feeding selectivity (values of the E_i as the dependent variable) according to sites and benthic organisms for each species. Body size was used as covariate owing to neutralize the effect of fish size while evaluating spatial variability in bite rates and feeding selectivity. Normality and homocedasticity were improved by converting fish density and feeding rates to $\text{Log}_{10}(x + 1)$, grazing selectivity to $\text{Log}_{10}(E_i + 2)$ and benthic cover percentages to $\arcsin \sqrt{x}$. Student–Newman–Keuls (SNK) multiple comparisons of means were performed as a *post-hoc* test (Zar, 1999).

Non-metric multidimensional scaling (nMDS) ordinations were used to summarize spatial similarities (Bray–Curtis) in benthic cover, fish assemblages' structure and foraging activity (i.e. number of bites taken by each RH species on different benthic organisms). Two-way analyses of similarities (ANOSIM) were used to evaluate significant differences according to sites and species (Clarke & Warwick, 1994).

RESULTS

Benthic cover

Turf algae was the dominant benthic cover type (44.1%) considering the four sites, followed by live corals (14.9%), zoanthids (12.6%), crustose calcareous algae (12.4%), fleshy algae (10.8%), sand (1.8%), *Halimeda* spp. (1.4%), fire-corals (0.3%) and octocorals (0.04%). Habitat structure differed significantly between sites (ANOSIM global test: $R = 0.719$, $P = 0.001$). Turf algae cover was highest at Timbebas and Portinho Norte; coral cover (mainly *Mussismilia braziliensis* (Verrill, 1868)) at Portinho Norte; zoanthid (mainly *Palythoa caribaeorum* (Duchassaing & Michelotti, 1860)) and sand cover

Table 1. Number of samples (1-minute observation periods) obtained for feeding rates and agonistic interactions. Sites: PAB, Parcel dos Abrolhos; PLES, Pedra de Leste; TIM, Timbebas; and PNOR, Portinho Norte.

Species (life phase)	Sampling effort							
	Feeding rates				Agonistic interactions			
	PAB	PLES	TIM	PNOR	PAB	PLES	TIM	PNOR
<i>Acanthurus bahianus</i>	17	28	21	24	10	21	25	20
<i>Acanthurus chirurgus</i>	9	24	22	18	8	19	22	15
<i>Acanthurus coeruleus</i>	17	15	30	20	9	12	26	17
<i>Scarus trispinosus</i>	25	25	37	25	16	21	27	21
<i>Scarus zelindae</i> (IP)	18	4	26	11	8	2	20	9
<i>Scarus zelindae</i> (TP)	0	0	0	3	3	0	2	2
<i>Sparisoma axillare</i> (IP)	16	29	30	25	10	21	23	20
<i>Sparisoma axillare</i> (TP)	0	0	0	0	0	0	0	0
<i>Sparisoma frondosum</i> (IP)	18	14	28	14	9	6	18	12
<i>Sparisoma frondosum</i> (TP)	0	3	5	8	2	3	8	7
<i>Sparisoma amplum</i> (IP)	2	0	10	6	0	0	7	6
<i>Sparisoma amplum</i> (TP)	0	0	14	0	0	0	5	0

at Parcel dos Abrolhos; calcareous algae cover at Timbebas; fleshy algae (mainly *Dictyota* spp.) and fire-coral (mainly *Millepora nitida* Verrill, 1868) cover at Pedra de Leste. There were no spatial differences in cover of *Halimeda* spp. and octocorals (Figure 2).

Fish assemblages

Acanthurus bahianus was the dominant RH species in terms of density (0.11 ind m⁻²), followed by *Scarus trispinosus* (0.09 ind m⁻²), *A. coeruleus* (0.07 ind m⁻²), *Sparisoma axillare* (0.06 ind m⁻²), *A. chirurgus* (0.05 ind m⁻²), *S. frondosum* (0.23 ind m⁻²), *Scarus zelindae* (0.022 ind m⁻²) and *Sparisoma amplum* (0.005 ind m⁻²). The structure of RHs' assemblages differed significantly according to sites ($R = 0.218$; $P = 0.001$). Five species (*A. chirurgus*, *A. coeruleus*, *Scarus trispinosus*, *Sparisoma axillare* and *S. frondosum*) showed higher densities within the no-take area of Timbebas. *Acanthurus bahianus* was more abundant at Pedra de Leste and *Scarus zelindae* at Parcel dos Abrolhos (Figure 3). Territorial herbivores were more abundant at Portinho Norte and Parcel dos Abrolhos, followed by Timbebas and Pedra de Leste respectively (see Figure 8).

Foraging activity and feeding selectivity

Although body size differed significantly between life phases, with IP individuals attaining smaller sizes than TP ones (Table 2), there were no significant differences in bite rates between IP and TP individuals of *S. zelindae*, *Sparisoma amplum* and *S. frondosum* (t -test, $P > 0.05$ in all cases), except for relatively higher bite rates of IP *S. frondosum* on crustose calcareous algae ($t = 2.10$, $P = 0.03$). Turf algae was the most frequently grazed item considering all RH species (63.0% of all bites), followed by crustose calcareous algae (17.1%), fleshy algae (7.2%), *Halimeda* spp. (7.0%), live corals (2.1%), sand (1.3%), fire-corals (0.7%), zoanthids (0.6%) and octocorals (0.03%). *Sparisoma amplum*, as well as large individuals (>40 cm TL) of *Scarus trispinosus* and *S. zelindae*, employed a typical excavating feeding mode, while small *S. trispinosus* and *S. zelindae* individuals acted mainly as scrapers. The other five RH species acted mostly as browsers.

There were significant differences in the foraging activity of RHs according to sites ($R = 0.129$; $P = 0.001$) and species ($R = 0.191$; $P = 0.001$), with a clear distinction between surgeonfish and parrotfish in the two-dimensional ordination space (Figure 4). Significant ($P < 0.05$) pairwise between-species differences were obtained in all cases, except between *S. trispinosus* and *S. zelindae*. Surgeonfish, particularly *A. bahianus* and *A. chirurgus*, had consistently higher total bite rates than the two species of *Scarus* and the three species of *Sparisoma* respectively. A similar pattern was observed when analysing the turf algae category separately. *Scarus trispinosus*, *S. zelindae* and *Sparisoma amplum* grazed more frequently on crustose calcareous algae than the other species. Surgeonfish showed slightly higher bite rates on fleshy algae (10% of total bites) than parrotfish (9.4%). *Sparisoma amplum* showed the highest frequency of bites on live corals, although SNK *post-hoc* comparisons indicated a high overlap with the other species. *Acanthurus chirurgus* foraged more frequently over sand bottoms, while *A. bahianus*, *A. chirurgus* and *Scarus zelindae* grazed more frequently over fire-corals. There were no differences between species in frequency of bites in *Halimeda* spp. and octocorals (Figure 5; Table 3).

The interaction between site and food type was highly significant ($P < 0.001$) for all RH species, indicating that the different food items were not equally grazed in all sites (Table 4). In general, bite rates on two heavily grazed items (i.e. crustose calcareous algae and fleshy algae) were proportionally higher in sites where such items were more available. Crustose calcareous algae showed highest cover and grazing rates at Timbebas, while fleshy algae showed highest cover and grazing rates at Pedra de Leste (see Figures 2 & 5). Turf algae were frequently consumed at Timbebas and Parcel dos Abrolhos; *Halimeda* spp. and zoanthids at Timbebas; live corals at Pedra de Leste and Timbebas. There was no clear spatial grazing pattern for sand and octocorals (Figure 5).

Turf algae were positively selected by most species at Parcel dos Abrolhos and Portinho Norte, but avoided at the other two sites. Crustose calcareous algae were selected by *S. trispinosus*, *S. zelindae*, *Sparisoma amplum* and *S. frondosum* in at least one out of the three following sites: Parcel dos Abrolhos, Pedra de Leste and Timbebas. *Halimeda* spp. was positively selected by *A. chirurgus*, *S. axillare* and *S. frondosum* at

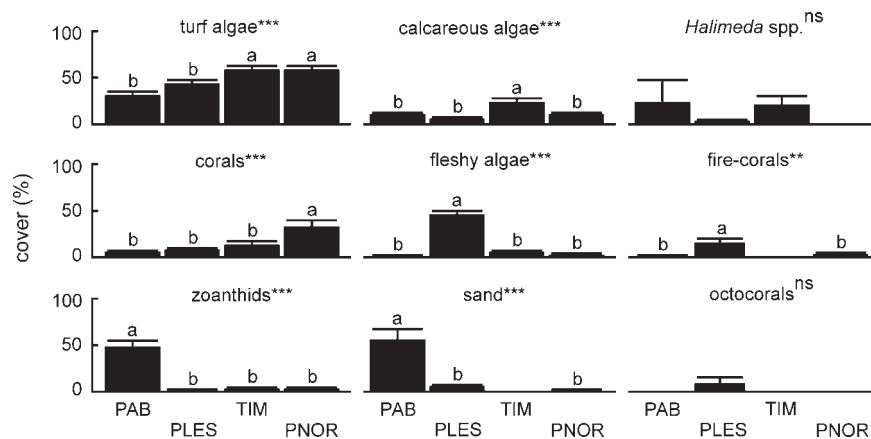


Fig. 2. Cover (mean + SE) of different benthic organisms in the four study sites. Analysis of variance results: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; n.s., not significant. Homogeneous groups are identified by equal letters. Site codes as in Figure 1.

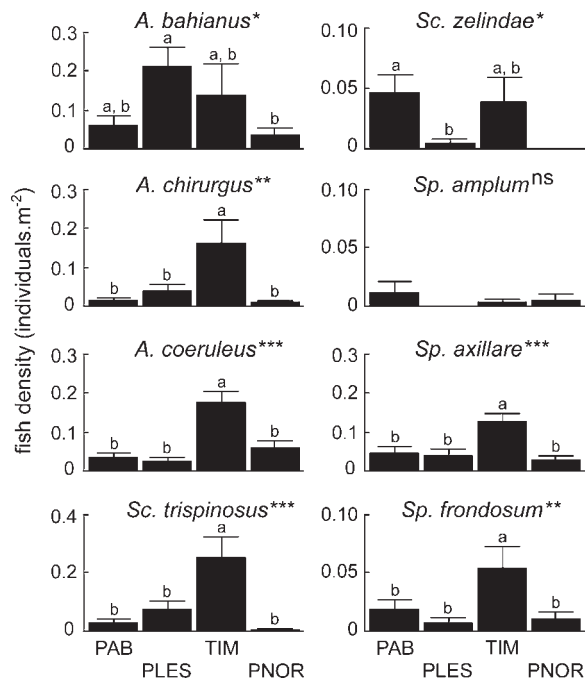


Fig. 3. Fish density (mean + SE) in the four study sites. Analysis of variance results: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; n.s., not significant. Homogeneous groups are identified by equal letters. Site codes as in Figure 1.

Timbebas. Slightly positive values of the E_i were also obtained for *Scarus zelindae* and *Sparisoma amplum* grazing over fire-corals at Timbebas. Negative values of the E_i were obtained in all other cases (Figure 6).

Grazing selectivity varied significantly according to food item and site for all species with significant interactions between the two factors recorded in all cases (Figure 6; Table 5).

Agonistic interactions

In total, 281 agonistic interactions were recorded. Both parrotfish and surgeonfish interacted agonistically most frequently with *Stegastes* spp., followed by interactions with members from the same family (Figure 7). In general, frequency of agonistic interactions was higher in sites with higher densities of herbivorous fish (Figure 8).

DISCUSSION

Inter-specific variation in the foraging activity of RHs within the same region, is well documented (e.g. Bellwood &

Choat, 1990; Bruggemann *et al.*, 1994a; Bonaldo *et al.*, 2005). Likewise, the foraging activity of the eight species of RHs that occur at the Abrolhos Bank differed significantly in many aspects. Some of these differences can be attributed to differences in feeding modes and morphology (Bellwood & Choat, 1990) and/or differences in digestive modes and diet (Choat *et al.*, 2004), but there are relevant residual differences once these fundamental considerations have been taken into account.

A comparative analysis on parrotfish jaw morphology and feeding behaviour found that excavating species have lower bite rates than scrapers (Bellwood & Choat, 1990). This difference is usually explained because excavators remove large pieces of the substratum and consequently more force and time is required to reapply the jaw (Bellwood & Choat, 1990). In Brazilian coral reefs, *Sparisoma amplum* is the main excavating parrotfish species (Bonaldo *et al.*, 2005; Francini-Filho *et al.*, 2008a), although large individuals of *Scarus trispinosus* and *S. zelindae* may act as excavators as well (Francini-Filho *et al.*, 2008a; this study). At the present study, the three *Sparisoma* species had similar and relatively low total feeding rates (see Figure 5 and Table 3). Thus the pattern of low feeding rates may be related not only to excavating potential, but also to other factors intrinsic to the Sparisomatinae clade (e.g. aspects of digestive physiology and biochemistry). In addition, the pattern of bite rates on turf algae was apparently correlated to the major taxa, as surgeonfish had the highest bite rates, *Scarus trispinosus* and *S. zelindae* intermediate values, and the three species of *Sparisoma* the lowest values.

Species within genus *Scarus*, as well as *Sparisoma viride* (Bonnaterre, 1788) and *S. amplum*, possess a robust jaw with fused teeth forming a dental plate (Bellwood & Choat, 1990; Streebman *et al.*, 2002; personal observations). The robust jaw, and consequent greater excavating potential, is consistent with the observation that *Scarus trispinosus*, *S. zelindae* and *Sparisoma amplum* grazed more frequently on crustose calcareous algae than other RH species. In addition, only *S. amplum* and large *Scarus trispinosus* individuals left noticeable bite scars while preying upon live corals. Although the other species also grazed over live corals, they left no discernible bite marks. Additional evidence for the relationship between jaw morphology and diet include the greater bite rates of the three species of surgeonfish on fleshy algae. These species have small discrete teeth with denticulated edges (Randall, 1955), which are better adapted for cutting off algae (Purcell & Bellwood, 1993), than for scratching the substratum.

Feeding rates of species ingesting mainly macroalgae are relatively lower than those of detritivores due mainly to difference in rates of food processing (Choat *et al.*, 2004). Although bites directed primarily to organic detritus could not be visually estimated during behavioural observations, information on the diet of RHs from the Abrolhos Bank is given by Ferreira & Gonçalves (2006). These authors showed that all RH species, except *A. coeruleus*, ingest large amounts of detritus. They also recognized *A. coeruleus*, *Sparisoma axillare* and *S. frondosum* as the main fleshy algae consumers. Similar findings were obtained by Dias *et al.* (2001), who also found larger amounts of sediment (possibly associated to detritus) in the guts of *A. bahianus* and *A. chirurgus* in comparison to *A. coeruleus* in north-eastern Brazil. In this study, the two surgeonfish recognized as detritivores by Ferreira & Gonçalves (2006) and Dias *et al.* (2001) (i.e. *A. bahianus* and

Table 2. Significant differences in body size (total length, in cm) between initial phase (IP) and terminal phase (TP) parrotfish as determined by Student's *t*-tests.

Species	Body size (mean \pm SE)		<i>t</i>	<i>P</i>
	IP	TP		
<i>Scarus zelindae</i>	23.3 \pm 1.2	46.7 \pm 3.6	26.6	<0.001
<i>Sparisoma amplum</i>	26.8 \pm 2.1	49.3 \pm 2.4	63.1	<0.001
<i>Sparisoma frondosum</i>	16.4 \pm 1.1	25.3 \pm 2.0	21.2	<0.001

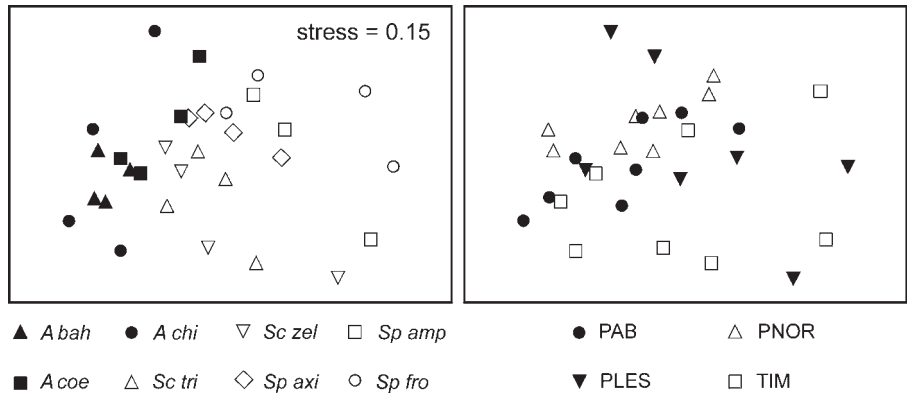


Fig. 4. Multidimensional scaling (MDS) of foraging activity (i.e. bites/min of each fish species on different benthic organisms) based on Bray–Curtis similarities. Left panel, samples classified according to species; right panel, samples classified according to sites.

A. chirurgus) had higher total feeding rates than *A. coeruleus*. Furthermore, *A. chirurgus* grazed more frequently over sand bottoms, in areas apparently saturated with detritus (see Dias *et al.*, 2001 for similar findings). Although these latter

results support the hypothesis of a relationship between diet and feeding rates (Choat *et al.*, 2002), results supporting the opposite hypothesis were also obtained. For example, the supposedly detritivore *A. chirurgus* had the highest feeding rates

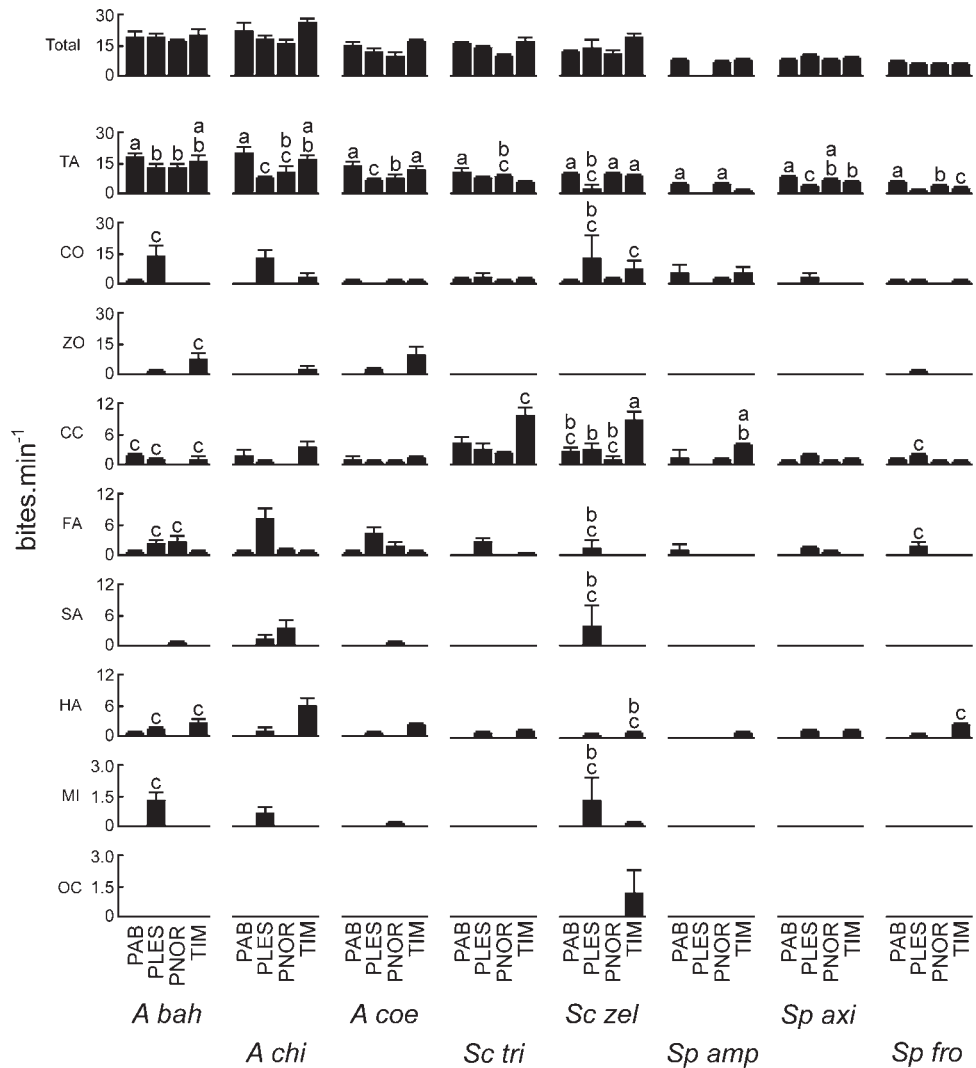


Fig. 5. Bite rates (mean + SE) of each fish species on different benthic organisms in the four study sites. Homogeneous groups for each species are identified by equal letters (only the first three groups are shown). Benthic organisms: TA, turf algae; CO, live corals; ZO, zoanthids; CC, crustose calcareous algae; FA, fleshy algae; SA, sand; HA, *Halimeda* spp.; MI, fire-corals (*Millepora* spp.); OC, octocorals. Site codes as in Figure 1.

Table 3. Significant interspecific differences in bite rates for different benthic organisms as determined by Student–Newman–Keuls (SNK) *post-hoc* comparisons. Homogeneous groups are linked by horizontal lines. Benthic organisms: TA, turf algae; CO, live corals; ZO, zoanths; CC, crustose calcareous algae; FA, fleshy algae; SA, sand; HA, *Halimeda* spp.; MI, fire-corals (*Millepora* spp.); OC, octocorals.

	F	P	Post-hoc (SNK)							
TA	18.44	***	<u>A bah</u>	A chi	A coe	Sc zel	Sc tri	Sp axi	Sp fro	Sp amp
CO	2.93	**	<u>Sp amp</u>	A chi	Sc zel	A bah	Sc tri	Sp axi	Sp fro	A coe
ZO	3.65	***	<u>A coe</u>	<u>A bah</u>	A chi	Sp fro	Sc zel	Sp axi	Sc tri	Sp amp
CC	22.64	***	<u>Sc tri</u>	<u>Sc zel</u>	<u>Sp amp</u>	Sp axi	Sp fro	A chi	A coe	A bah
FA	4.46	***	<u>A chi</u>	<u>A coe</u>	<u>A bah</u>	Sp axi	Sc tri	Sp fro	Sc zel	Sp amp
SA	3.66	***	<u>A chi</u>	Sc zel	A bah	Sp fro	A coe	Sp amp	Sc tri	Sp axi
HA	1.50	n.s.								
MI	3.39	**	<u>A bah</u>	<u>A chi</u>	<u>Sc zel</u>	<u>Sp amp</u>	A coe	Sp axi	Sp fro	Sc tri
OC	1.33	n.s.								
Total	33.68	***	<u>A chi</u>	<u>A bah</u>	Sc zel	Sc tri	A coe	Sp axi	Sp fro	Sp amp

on fleshy algae. In addition, the same species of parrotfish known to ingest large amounts of detritus (i.e. *S. axillare*, *S. amplum* and *S. frondosum*) showed the lowest feeding rates. It is important to note that Ferreira & Gonçalves (2006) pooled material of both organic and inorganic origin in their 'detritus' category. Thus the precise amount of organic detritus ingested by each species

is actually unknown, particularly for primarily excavating parrotfish such as *S. amplum*, which ingest large amounts of inorganic material.

The high consumption of turf algae by all RH species in the Abrolhos Bank was expected, since turf algae are more palatable (Hay, 1991, 1997) and contain higher protein levels than

the other considered food resources (Bruggemann *et al.*, 1994a, b). Most importantly, turf algae may trap protein-rich detritus, which is capable of providing a nutritional value twice as high as that of the algae themselves (Choat *et al.*, 2002; Crossman *et al.*, 2005). Such preference for small turf algae was also recorded for several RH species in Brazil (Bonaldo *et al.*, 2005) the Caribbean (Bruggemann *et al.*, 1994a,b; Paddock *et al.*, 2006) and Indo-Pacific regions (Bellwood & Choat, 1990; Bonaldo & Bellwood, 2008). So, this is probably a general pattern in the feeding ecology of herbivorous reef fish (Wilson *et al.*, 2003; Bellwood *et al.*, 2006; Ledlie *et al.*, 2007).

Table 4. Analysis of covariance (ANCOVA) testing the effect of site and food item on feeding rates (bites/min). Body size (total length) was used as covariate.

	Site		Food item		Site×food		Body size	
	F	P	F	P	F	P	F	P
<i>Acanthurus bahianus</i>	3.52	*	171.86	***	3.11	***	0.67	n.s.
<i>Acanthurus chirurgus</i>	1.41	n.s.	70.99	***	6.26	***	0.29	n.s.
<i>Acanthurus coeruleus</i>	2.73	*	141.76	***	2.73	***	4.44	*
<i>Scarus trispinosus</i>	4.85	**	176.59	***	8.05	***	0.14	n.s.
<i>Scarus zelindae</i>	2.62	*	47.49	***	3.93	***	0.69	n.s.
<i>Sparisoma amplum</i>	0.47	n.s.	15.33	***	3.60	***	0.18	n.s.
<i>Sparisoma axillare</i>	2.29	n.s.	174.31	***	5.05	***	0.01	n.s.
<i>Sparisoma frondosum</i>	1.28	n.s.	106.23	***	16.49	***	0.47	n.s.

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; n.s., not significant.

Despite the consistent inter-specific differences and similarities described above, feeding rates and food selection differed significantly between sites for most species. Possible explanations for such variability include between-sites differences in resource availability, nutritional quality of resources and intensity of interference competition.

Bite rates on two heavily grazed items (crustose calcareous algae and fleshy algae) were disproportionately higher in sites where these items were more available, leading to significant spatial variation in grazing selectivity (i.e. positive selection of CCA and 'lower avoidance' of FA; see Figures 5 & 6). This result indicates that the scarcity of other food may induce RHs to specifically target the dominant resources (see Bruggemann *et al.*, 1994b for similar conclusions). In areas dominated by low-quality food (e.g. fleshy algae), the costs of searching for high-quality items (e.g. turf algae) may be higher than the benefits of ingesting the more available low-quality resources. In extreme situations (i.e. very high dominance of low-quality resources), fish may be forced into a sub-optimal nutritional condition.

Turf algae were selected by most species at Parcel dos Abrolhos and Portinho Norte, but avoided in the other two sites. Possible explanations for this pattern include spatial differences in the nutritional quality of the food and variations in the amount of associated organic detritus. Differences in density of substrata covered by turf algae may also explain this pattern, as higher yields per bite are attained in low-density substrates than in high-density ones (Bruggemann *et al.*, 1994b).

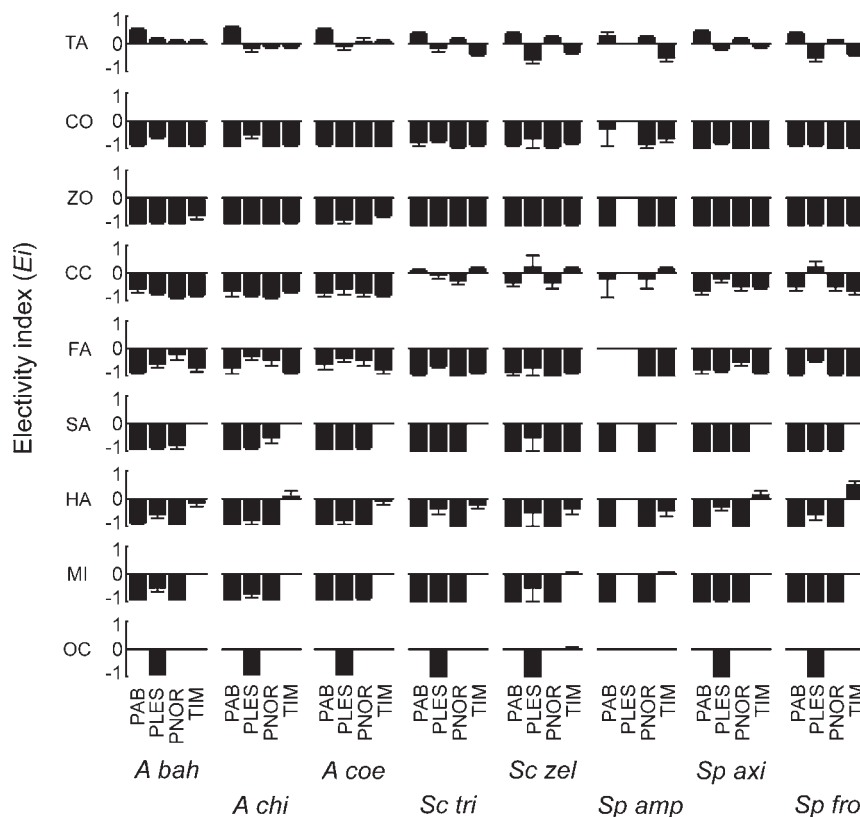


Fig. 6. Grazing selectivity (mean + SE) of each fish species for different benthic organisms in the four study sites. Benthic organisms: TA, turf algae; CO, live corals; ZO, zoanths; CC, crustose calcareous algae; FA, fleshy algae; SA, sand; HA, *Halimeda* spp.; MI, fire-corals (*Millepora* spp.); OC, octocorals. Site codes as in Figure 1.

Table 5. Analysis of covariance (ANCOVA) testing the effect of site and food item on feeding selectivity (values of the E_i). Body size (total length) was used as covariate.

	Site		Food item		Site × food		Body size	
	F	P	F	P	F	P	F	P
<i>Acanthurus bahianus</i>	25.3	***	61.6	***	14.1	***	1.3	n.s.
<i>Acanthurus chirurgus</i>	28.3	***	39.1	***	13.4	***	1.6	n.s.
<i>Acanthurus coeruleus</i>	47.1	***	67.1	***	16.3	***	2.4	n.s.
<i>Scarus trispinosus</i>	53.4	***	109.9	***	25.0	***	0.01	n.s.
<i>Scarus zelindae</i>	25.4	***	31.2	***	10.8	***	0.05	n.s.
<i>Sparisoma amplum</i>	8.29	***	11.8	***	7.0	***	0.6	n.s.
<i>Sparisoma axillare</i>	43.1	***	80.9	***	21.1	***	0.4	n.s.
<i>Sparisoma frondosum</i>	39.1	***	66.3	***	31.9	***	0.1	n.s.

*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; n.s., not significant.

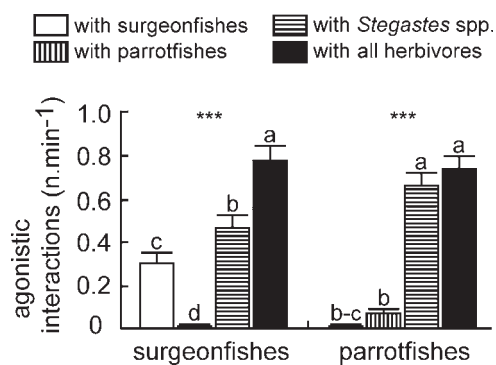


Fig. 7. Frequency of agonistic interactions (mean + SE) among roving herbivorous reef fish and between roving herbivores and territorial herbivores. Analysis of variance results: ***, $P < 0.001$. Homogeneous groups are identified by equal letters.

The effects of territorial herbivores on the foraging activity and ecological impacts of RHs are still controversial. The algal gardens created by some territorial damselfish have higher primary productivity than surrounding areas (Klump *et al.*,

1987). This encourages RHs to invade damselfish territories to obtain access to better food resources. Some studies indicate that competition with territorial herbivores may limit the access of RHs to algal resources (Robertson *et al.*, 1979), causing reduced feeding rates (Robertson *et al.*, 1976), lowered grazing pressure (Hixon & Brostoff, 1996), and ingestion of higher proportions of inferior food types (Bruggemann *et al.*, 1994b). On the other hand Ceccarelli *et al.* (2005), in an orthogonal experiment combining the exclusion of RHs and territorial herbivores in Papua New Guinea, obtained no evidence for an influence of territorial herbivores on the benthic community impacts of RHs. Similar results were obtained on an experiment in which RHs were excluded from areas occupied by two damselfish species in the Great Barrier Reef (Ceccarelli *et al.*, 2006). Although in the Abrolhos Bank, frequency of agonistic interactions was highest at sites where herbivorous fish (both roving and territorial) were abundant, only one example of the possible influence of territorial herbivores on the foraging activity of RHs was observed: the positive selection of *Halimeda* spp. at Timbebas, where competition between RHs and territorial herbivores was more intense. The preference for *Halimeda* spp. is noteworthy, as these algae possess several structural and chemical deterrents to herbivory (Hay, 1991).

During the last three decades coral reefs worldwide have experienced dramatic reductions in coral cover due to large-scale disturbances such as pollution, bleaching and disease (Gardner *et al.*, 2003; Bruno & Selig, 2007; Francini-Filho *et al.*, 2008b). Death of corals is often accompanied by a rapid proliferation of turf algae and if regular grazing is not maintained the benthic community is rapidly dominated by late successional stage fleshy algae such as *Dictyota* and *Sargassum* (Adey *et al.*, 1977; Steneck & Dethier, 1994; McClanahan, 1997). Fleshy algae dominance can negatively affect coral recruitment, growth and survivorship, both directly (McCook *et al.*, 2001) and indirectly (Nugues *et al.*, 2004). Although it is widely accepted that RHs are able to interrupt benthic succession, thus avoiding phase shifts from small turf algae to fleshy macroalgae (Paddack *et al.*, 2006; Hughes *et al.*, 2007), there is growing evidence that they are

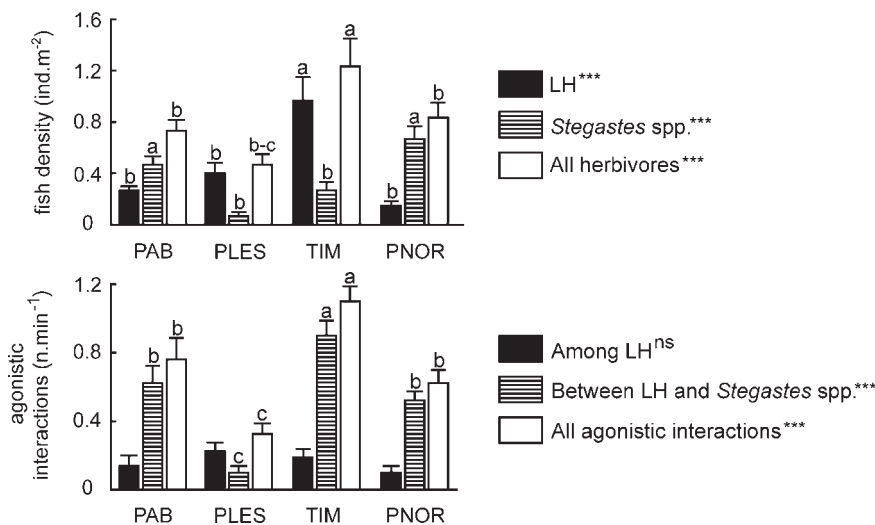


Fig. 8. Fish density (upper) and frequency of agonistic interactions (lower) in the four study sites. Values shown are mean + SE. Analysis of variance results (between-sites comparisons): ***, $P < 0.001$; n.s., not significant. Homogeneous groups are identified by equal letters. Site codes as in Figure 1.

unable to reverse a phase shift once it has occurred (Bellwood *et al.*, 2006). In other words, the absence of major macroalgal consumers 'locks down' the reef ecosystem as a fleshy algal pavement.

Results from the present study support these latter hypotheses, as in the Abrolhos Bank RHs greatly avoided grazing on fleshy algae. In most cases, bites were small and apparently limited to epiphytic material (see Bellwood *et al.*, 2006 for similar results). Even *Sparisoma* spp., which were recently recognized as possible candidates for a significant role in macroalgae consumption (Bellwood *et al.*, 2006), avoided grazing on fleshy algae. Most importantly, some parrotfish species frequently consume live corals (Rotjan & Lewis, 2008; Francini-Filho *et al.*, 2008a; this study). Thus their net effect on coral reef resilience has yet to be determined.

Organisms other than RHs may consume large amounts of fleshy algae. For example, sea urchins have the potential to play a major role in phase-shift reversal in the Caribbean (Edmunds & Carpenter, 2001). Also, a nominal invertivorous fish previously overlooked as a relevant player in determining benthic community structure (the batfish *Platax pinnatus* (Linnaeus, 1758), family Ephippidae) was recently recognized as a major macroalgal consumer in a simulated phase shift experiment in the Great Barrier Reef (Bellwood *et al.*, 2006). This latter example indicates that rules and species roles can both change profoundly during community transitions. Thus species once rare can become abundant and functionally significant in the new regime. Although in the western Atlantic the spadefish *Chaetodipterus faber* (Broussonet, 1782) (family Ephippidae) may be able to remove significant amounts of fleshy algae (Bellwood *et al.*, 2006), this latter species is relatively rare in the Abrolhos Bank. *Kyphosus* spp. may also be able to remove large amounts of fleshy algae (Ferreira & Gonçalves, 2006), but again these species are rare in the Abrolhos region (Francini-Filho & Moura, 2008).

It is noteworthy that fleshy algae cover in the unprotected site of Pedra de Leste (42.0%) was up to 600 times greater than that in the protected sites (0.1–1.1%), while RHs' biomass was 8 to 15 times lower (unpublished data). Although reduced herbivory due to over-fishing can lead to high fleshy algae abundance (Hughes *et al.*, 2007), the inverse can also occur (Fox & Bellwood, 2007). In this latter situation, high macroalgae abundance (determined in the first place by factors such as availability of space, nutrients and luminosity) reduces availability of high-quality food items, thus reducing abundance of herbivores. For example, shallow inshore sites such as Pedra de Leste (see Figure 1) generally have higher fleshy algae abundance than deep offshore sites (e.g. Klumpp & McKinnon, 1992; McCook & Price, 1997). Thus, additional studies are needed in order to better understand the factors leading to fleshy algae dominance on the Abrolhos Bank and elsewhere around the world.

Although simplistic, the phase shift paradigm is useful for devising conservation and management strategies to promote a return to the desired state of diverse, hard coral dominance. Roving herbivores clearly have an important role to play in this story, and the increasing and unsustainable demand for these fish is a worrying global trend (Bellwood *et al.*, 2004). If we hope to understand this role, however, we must inform the next generation of empirical studies with a rich historical perspective, and close attention to the influence of current reef conditions on future trajectories.

ACKNOWLEDGEMENTS

We thank R.M. Bonaldo for valuable comments and for reviewing the manuscript; G.F. Dutra for advice on the research. G. Fiuza-Lima, D. Lima Araújo, E. Marocci, C. Marques, P. Meirelles, R.M. Reis and I. Cruz for field assistance. Parque Nacional Marinho de Abrolhos/ICMBio (through M. Lourenço) for logistical support and research permits. Financial support was provided by the Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), International Society for Reefs Studies (ISRS), the Global Conservation Fund (GCF), CNPq/ProAbrolhos, NOAA Coral Reef Conservation Grants, BP Conservation Programme, and Conservation International. This is contribution no. 8 of the Marine Management Areas Science Programme, Brazil Node.

REFERENCES

- Adey W.H., Adey P.J., Burke R. and Kaufman L.S. (1977) The Holocene reefs of eastern Martinique, French West Indies. *Atoll Research Bulletin* 218, 1–40.
- Bellwood D.R. and Choat J.H. (1990) A functional analysis of grazing in parrotfish (family Scaridae): the ecological implications. *Environmental Biology of Fishes* 28, 189–214.
- Bellwood D.R., Hoey A.S. and Choat J.H. (2003) Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecology Letters* 6, 281–285.
- Bellwood D.R., Hughes T.P., Folke C. and Nystrom M. (2004) Confronting the coral reef crisis. *Nature* 429, 827–833.
- Bellwood D.R., Hughes T.P. and Hoey A.S. (2006) Sleeping functional group drives coral reef recovery. *Current Biology* 16, 2434–2439.
- Bonaldo R.M. and Bellwood D.R. (2008) Size-dependent variation in the functional role of the parrotfish *Scarus rivulatus* on the Great Barrier Reef, Australia. *Marine Ecology Progress Series* 360, 237–244.
- Bonaldo R.M., Krajewski J.P., Sazima C. and Sazima I. (2005) Foraging activity and resource use by three parrotfish species at Fernando de Noronha Archipelago, tropical West Atlantic. *Marine Biology* 149, 423–433.
- Bruggemann J.H., Kuyper M.W.M. and Breeman A.M. (1994a) Comparative analysis of foraging and habitat use by the sympatric Caribbean parrotfish *Scarus vetula* and *Sparisoma viride* (Scaridae). *Marine Ecology Progress Series* 112, 51–66.
- Bruggemann J.H., Oppen M.J.H. van and Breeman A.M. (1994b) Foraging by the stoplight parrotfish, *Sparisoma viride*. 1. Food selection in different, socially determined habitats. *Marine Ecology Progress Series* 106, 41–55.
- Bruno J.F. and Selig E.R. (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS One* 2, 1–8.
- Ceccarelli D.M., Hughes T.P. and McCook L.J. (2006) Impacts of simulated overfishing on the territoriality of coral reef damselfish. *Marine Ecology Progress Series* 309, 255–262.
- Ceccarelli D.M., Jones G.P. and McCook L.J. (2001) Territorial damselfishes as determinants of the structure of benthic communities on coral reefs. *Oceanography and Marine Biology: an Annual Review* 39, 355–389.
- Ceccarelli D.M., Jones G.P. and McCook L.J. (2005) Foragers versus farmers: contrasting effects of two behavioural groups of herbivores on coral reefs. *Oecologia* 145, 445–453.

- Choat J.H., Clements K.D. and Robbins W.D. (2002) The trophic status of herbivorous fishes on coral reefs. I. Diet analyses. *Marine Biology* 140, 613–623.
- Choat J.H., Clements K.D. and Robbins W.D. (2004) The trophic status of herbivorous fishes on coral reefs. II. Food processing modes and trophodynamics. *Marine Biology* 145, 445–454.
- Clarke K.R. and Warwick R.M. (1994) *Change in marine communities: an approach to statistical analysis and interpretation*. Plymouth: Plymouth Marine Laboratory.
- Crossman D.J., Choat J.H. and Clements K.D. (2005) Nutritional ecology of nominally herbivorous fishes on coral reefs. *Marine Ecology Progress Series* 296, 129–142.
- Dias T., Rosa I.L. and Feitoza B.M. (2001) Food resource and habitat sharing by the three western South Atlantic surgeonfishes (Teleostei: Acanthuridae: Acanthurus) off Paraíba Coast, northeastern Brazil. *Aqua Journal of Ichthyology and Aquatic Biology* 5, 1–10.
- Edmunds P.J. and Carpenter R.C. (2001) Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *Proceedings of the National Academy of Sciences of the United States of America* 98, 5067–5071.
- Ferreira C.E.L. and Gonçalves E.A. (2006) Community structure and diet of roving herbivorous reef fishes in the Abrolhos Archipelago, south-western Atlantic. *Journal of Fish Biology* 69, 1533–1551.
- Fox R.J. and Bellwood D.R. (2007) Quantifying herbivory across a coral reef depth gradient. *Marine Ecology Progress Series* 339, 49–59.
- Francini-Filho R.B. and Moura R.L. (2008) Dynamics of fish assemblages on coral reefs subjected to different management regimes in the Abrolhos Bank, eastern Brazil. *Aquatic Conservation: Marine and Freshwater Ecosystems* 18, 1166–1179.
- Francini-Filho R.B., Moura R.L., Ferreira C.M. and Coni E.O.C. (2008a) Live coral predation by parrotfishes (Perciformes: Scaridae) in the Abrolhos Bank, eastern Brazil, with comments on the classification of species into functional groups. *Neotropical Ichthyology* 6, 191–200.
- Francini-Filho R.B., Moura R.L., Thompson F.L., Reis R.D., Kaufman L., Kikuchi R.K.P. and Leão Z.M.A.N. (2008b) Diseases leading to accelerated decline of reef corals in the largest South Atlantic reef complex (Abrolhos Bank, eastern Brazil). *Marine Pollution Bulletin* 56, 1008–1014.
- Gardner T.A., Côté I.M. and Gill J.A. (2003) Long-term region-wide declines in Caribbean corals. *Science* 301, 958–960.
- Gasparini J.L., Floeter S.R. and Joyeux J.C. (2004) *Sparisoma tuiupiranga*, a new species of parrotfish (Perciformes: Labroidae: Scaridae) from Brazil, with comments on the evolution of the genus. *Zootaxa* 384, 1–14.
- Hay M.E. (1991) Fish–seaweed interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey. In Sale P.F. (ed.) *The ecology of fishes on coral reefs*. San Diego: Academic Press, pp. 96–119.
- Hay M.E. (1997) The ecology and evolution of seaweed–herbivore interactions on coral reefs. *Coral Reefs* 16, 67–76.
- Hixon M.A. and Brostoff W.N. (1996) Succession and herbivory: effects of differential fish grazing on Hawaiian coral-reef algae. *Ecological Monographs* 66, 67–90.
- Hoey A.S. and Bellwood D.R. (2008) Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs* 27, 37–47.
- Horn M.H. (1989) Biology of marine herbivorous fishes. *Oceanography and Marine Biology: an Annual Review* 27, 167–272.
- Hughes T.P., Rodrigues M.J., Bellwood D.R., Ceccarelli D., Hoegh-Guldberg O., McCook L., Moltschanivskyj N., Pratchett M.S., Steneck R.S. and Willis B. (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Current Biology* 17, 360–365.
- Ivlev V.S. (1961) *Experimental ecology of the feeding of fishes*. New Haven: Yale University Press.
- Klumpp D.W. and McKinnon A.D. (1992) Community structure, biomass and productivity of epilithic algal communities on the Great Barrier Reef: dynamics at different spatial scales. *Marine Ecology Progress Series* 86, 77–89.
- Klumpp D.W., McKinnon D. and Daniel P. (1987) Damselfish territories: zones of high productivity on coral reefs. *Marine Ecology Progress Series* 40, 41–51.
- Kohler K.E. and Gill S.M. (2006) Coral Point Count with Excel extensions (CPCe): a Visual Basic program for the determination of coral and substrate coverage using random point count methodology. *Computers and Geosciences* 32, 1259–1269.
- Leão Z.M.A.N. and Kikuchi R.K.P. (2001) The Abrolhos Reefs of Brazil. In Seeliger U. and Kjerfve B. (eds) *Coastal marine ecosystems of Latin America*. Berlin: Springer-Verlag, pp. 83–96.
- Ledlie M.H., Graham N.A.J., Bythell J.C., Wilson S.K., Jennings S., Polunin N.V.C. and Hardcastle J. (2007) Phase shifts and the role of herbivory in the resilience of coral reefs. *Coral Reefs* 26, 641–653.
- McClanahan T.R. (1997) Primary succession of coral-reef algae: differing patterns on fished versus unfished reefs. *Journal of Experimental Marine Biology and Ecology* 218, 77–102.
- McCook L.J., Jompa J. and Diaz-Pulido G. (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19, 400–417.
- McCook L.J. and Price I.R. (1997) Macroalgal distributions on the Great Barrier Reef: a review of patterns and causes. In *Proceedings of the Great Barrier Reef: science, use and management, a national conference*, Townsville, pp. 37–46.
- Minte-Vera C.V., Moura R.L. and Francini-Filho R.B. (2008) Nested sampling: an improved visual-census technique for studying reef fish assemblages. *Marine Ecology Progress Series* 367, 283–293.
- Moura R.L., Figueiredo J.L. and Sazima I. (2001) A new parrotfish (Scaridae) from Brazil, and revalidation of *Sparisoma amplum* (Ranzani, 1842), *Sparisoma frondosum* (Agassiz, 1831), *Sparisoma axillare* (Steindachner, 1878) and *Scarus trispinosus* Valenciennes, 1840. *Bulletin of Marine Science* 68, 505–524.
- Moura R.L. and Francini-Filho R.B. (2006) Reef and shore fishes of the Abrolhos region, Brazil. In Dutra G.F. et al. (eds) *A rapid marine biodiversity assessment of the Abrolhos Bank, Bahia, Brazil*. Washington DC: Conservation International, pp. 40–55. [RAP Bulletin of Biological Assessment no. 38.]
- Mumby P.J. (2006) The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecological Applications* 16, 747–769.
- Nugues M.M., Smith G.W., Van Hooindonk R.J., Seabra M.I. and Bak R.P.M. (2004) Algal contact as a trigger for coral disease. *Ecology Letters* 7, 919–923.
- Osório R., Rosa I.L. and Cabral H. (2006) Territorial defence by the Brazilian damselfish *Stegastes fuscus* (Teleostei: Pomacentridae). *Journal of Fish Biology* 69, 233–242.
- Paddock M.J., Cowen R.K. and Sponaugle S. (2006) Grazing pressure of herbivorous coral reef fishes on low coral-cover reefs. *Coral Reefs* 25, 461–472.
- Purcell S.W. and Bellwood D.R. (1993) A functional analysis of food procurement in two surgeonfish species, *Acanthurus nigrofuscus* and *Ctenochaetus striatus* (Acanthuridae). *Environmental Biology of Fishes* 37, 139–159.

- Randall J.E.** (1955) An analysis of the genera of surgeon fishes (Family Acanthuridae). *Pacific Science* 19, 359–367.
- Risk A.** (1998) The effects of interactions with reef residents on the settlement and subsequent persistence of ocean surgeonfish, *Acanthurus bahianus*. *Environmental Biology of Fishes* 51, 377–389.
- Robertson D.R. and Gaines S.D.** (1986) Interference competition structures habitat use in a local assemblage of coral reef surgeonfishes. *Ecology* 67, 1372–1383.
- Robertson D.R., Karg F., Moura R.L., Victor B.C. and Bernardi G.** (2006) Mechanisms of speciation and faunal enrichment in Atlantic parrotfishes. *Molecular Phylogenetics and Evolution* 40, 795–807.
- Robertson D.R., Polunin N.V.C. and Leighton K.** (1979) The behavioural ecology of three Indian Ocean surgeonfishes (*Acanthurus lineatus*, *A. leucosternon* and *Zebrasoma scopas*): their feeding strategies and social mating systems. *Environmental Biology of Fishes* 4, 125–170.
- Robertson D.R., Sweatman H.P.A., Fletcher E.A. and Cleland M.G.** (1976) Schooling as a mechanism for circumventing the territoriality of competitors. *Ecology* 57(6), 1208–1220.
- Robertson D.R. and Warner R.R.** (1978) Sexual patterns in the labroid fishes of the western Caribbean. II. The parrotfishes (Scaridae). *Smithsonian Contributions to Zoology* 255, 1–26.
- Rotjan R.D. and Lewis S.A.** (2008) Impact of coral predators on tropical reefs. *Marine Ecology Progress Series* 367, 73–91.
- Steneck R.S. and Dethier M.N.** (1994) A functional group approach to the structure of algal-dominated communities. *Oikos* 69, 476–498.
- Streelman J.T., Alfaro M., Westneat M.W., Bellwood D.R. and Karl S.A.** (2002) Evolutionary history of the parrotfishes: biogeography, ecomorphology, and comparative diversity. *Evolution* 56, 961–971.
- Van Rooij J.M., Videler J.J. and Bruggemann J.H.** (1998) High biomass and production but low energy transfer efficiency of Caribbean parrotfish: implications for trophic models of coral reefs. *Journal of Fish Biology* 53, 154–178.
- Wilson S.K., Bellwood D.R., Choat J.H. and Furnas M.J.** (2003) Detritus in the epilithic algal matrix and its use by coral reef fishes. *Oceanography and Marine Biology: an Annual Review* 41, 279–309.
- and
- Zar J.H.** (1999) *Biostatistical analysis*, 4th edition. New Jersey: Prentice-Hall.

Correspondence should be addressed to:

R.B. Francini-Filho
Departamento de Biologia
Centro de Ciências Biológicas e da Saúde
Universidade Estadual da Paraíba
Avenida das Baraúnas 351
58109-753 Campina Grande, PB, Brazil
email: rofilho@yahoo.com