ORIGINAL ARTICLE

Trophic structure patterns of Brazilian reef fishes: a latitudinal comparison

C. E. L. Ferreira[1]*, S. R. Floeter[2]†, J. L. Gasparini[3], B. P. Ferreira[4] and J. C. Joyeux[3]

[1]*Departamento de Oceanografia, IEAPM, Arraial do Cabo, RJ,* [2]*Laboratório de Ciências Ambientais, Universidade Estadual do Norte Fluminense, Campos dos Goytacazes, RJ,* [3]*Departamento de Ecologia e Recursos Naturais, Universidade Federal do Espírito Santo, Vitória, ES and* [4]*Laboratório de Nécton, Departamento de Oceanografia, Universidade Federal de Pernambuco, Recife, PE, Brasil*

ABSTRACT

Aim To investigate how reef fish trophic structure responds to latitudinal changes, using a simple model: the extensive Brazilian coast.

Location Six Brazilian tropical and subtropical coral and rocky coastal reefs, and the oceanic island of Atol das Rocas, between latitudes 0° and 27° S.

Methods Underwater visual census data collected by the authors (five locations) or obtained from the literature (two locations) were used to estimate the relative abundance of 123 fish species belonging to 33 reef-associated families. Cryptic species were excluded from the analysis. Fishes were grouped in eight trophic categories: roving herbivores, territorial herbivores, mobile invertebrate feeders, sessile invertebrate feeders, omnivores, planktivores, piscivores and carnivores. After a series of detailed predictions based on phylogeny, physiological constraints and anthropogenic impacts was established, the community trophic structure was analysed along a latitudinal gradient and among coastal, mid-shore and oceanic sites.

Results The trophic structure of Brazilian reef fish assemblages clearly changed with latitude. Roving herbivores such as scarids and acanthurids were proportionally more abundant at low latitudes. The browsing herbivores kyphosids followed an opposite latitudinal pattern. The parrotfish genus *Sparisoma*, more plastic in its feeding habits than *Scarus*, presented wider distribution. The relative abundance of territorial herbivores did not decrease towards higher latitudes. Mobile invertebrate feeders were the most important (in low latitudes) or the second most important trophic guild (in high latitudes) at all coastal sites. Sessile invertebrate feeders did not show any clear latitudinal trend, despite an expected increase in abundance towards low latitudes. Omnivores dominated high latitude reefs (27° S) and planktivores the oceanic island Atol das Rocas. Piscivores and carnivores were proportionally better represented in high latitudes.

Main conclusions Latitudinal patterns seem to be influenced by phylogeny, physiological constraints (mainly related to temperature), and also by anthropogenic impacts. Grazing scarids and acanthurids are largely restricted to tropical reefs and show an abrupt decline beyond 23° S. This does not reflect the amount of algae present, but probably temperature-dependent physiological constraints. Other herbivores seem to overcome this through symbiotic microbial digestive processes (kyphosids), manipulating the structure of algal turfs or increasing animal protein from within the territory (pomacentrids). Omnivores dominate the southern sites Arraial do Cabo and Arvoredo, being more adapted to environment constraints related to seasonal and/or stochastic shifts. Large carnivores (including piscivores) extend farther into high-latitude habitats, apparently not constrained by thermal thresholds that limit the herbivores.

*Correspondence: C.E.L. Ferreira, Departamento de Oceanografia, IEAPM, Rua Kioto 253, Arraial do Cabo, RJ 28930-000, Brasil. E-mail: kadu@alternex.com.br
†Present address: S.R. Floeter, National Center for Ecological Analysis and Synthesis, University of California, 735 State Street Suite 300, Santa Barbara, CA 93101-5504, USA.

Overfishing and/or ornamental harvesting certainly has been modifying local fish communities, but could not be detected properly at the large-scale patterns found in this study. The data presented put in evidence for the first time how reef fish trophic structure behave in the extensive south-western Atlantic latitudinal gradient.

INTRODUCTION

The Brazilian reefs are part of the tropical Atlantic reef system and have some unique characteristics. They are partially separated from the Caribbean to the north by the Amazon outflow, which results in numerous examples of regional endemism (Floeter & Gasparini, 2000, 2001; Joyeux *et al.*, 2001; Rocha, 2003). The coastal fauna is in dynamic state following glaciation-driven changes in sea level, with range expansions occurring in a number of taxa (Joyeux *et al.*, 2001; Rocha, 2003). The Brazilian coast is large enough to cover a substantial latitudinal gradient (*c.* 27°) in which coastal coral and rocky reef systems co-vary with latitude (Maida & Ferreira, 1997; Floeter *et al.*, 2001).

Coral and algae reefs extend for almost half of the coastline (the tropical north-eastern coast) and form structures significantly different from most of the well-known coral reef models (Maida & Ferreira, 1997; Leão & Dominguez, 2000; Leão & Kikuchi, 2001). Rocky shores represent the main habitat for the reef-associated biota in the warm subtropical south-eastern and southern coasts where cold, nutrient-rich upwelling events occur seasonally (Ekau & Knoppers, 1999; Floeter *et al.*, 2001).

Very few works dealing with quantitative latitudinal gradients in reef fishes were published to date (e.g. Meekan & Choat, 1997; Munday, 2002). In this paper, we explore quantitative information on reef fish communities from localities with biotic histories very different from those of most other coral reef systems. We aim to investigate how reef fish trophic structure responds to latitudinal changes along the extensive Brazilian coastline. For this purpose, we hypothesized that a series of factors including species phylogeny, physiological constraints and anthropogenic impacts (mainly fishing and ornamental harvesting) are the major forces that may drive trophic patterns along the Brazilian coast. After a brief description of each trophic category that will be used, a set of predictions is pointed out as guidelines for the discussion of how the proposed factors may influence the trophic structure of the reef fish community.

Roving herbivores (ROVH) include large herbivores like scarids, acanthurids and kyphosids. These fishes can include in their diet a rich mass of detritus, turf algae and macroalgae (Choat, 1991; Choat *et al.*, 2002). The three hypotheses for this group specifically refer to physiological constraints and phylogeny. (1) Higher numbers of detritus and filamentous algae feeders are predicted to occur at low latitudes. This prediction is based on the fact that the tropics sustain higher primary productivity and turnover rates of turf algae (Carpenter, 1986; Hatcher, 1988; Choat, 1991), both of which contribute to an accumulation of detritus as a product of high decomposition rates. The role of turf algae as organic matter and detritus trapping and processing devices is well established and results from their delicate tridimensional structure that facilitates decomposition (Horn, 1989; Choat, 1991; Wilson *et al.*, 2003). ROVHs are suggested to be unable to maintain populations on high latitude reefs due to the low productivity of turf assemblages and/or to problems related to their digestive mechanisms in colder water. This could limit nitrogen intake and impede the maintenance of the fish high metabolic needs (Horn, 1989; Choat, 1991; Wood, 1995). (2) Browsing herbivores such as kyphosids, which rely on efficient digestive mechanisms such as fermentation (symbiotic microbial processes; Choat & Clements, 1995), are expected to present a positive relationship with latitude. Macroalgae, mainly fucoids, are known to increase in biomass with latitude (Choat & Schiel, 1982; Horn, 1989) and to compose the bulk of the kyphosids diet. (3) Parrotfishes of the genus *Sparisoma* are predicted to present wider distributions, including higher latitudes, than other scarids. Sparisomatinae fishes are considered a plesiomorphic subfamily and exhibit a full range of feeding modes (browsing and biting), differently from the apomorphic and specialist scraping *Scarus* (Bernardi *et al.*, 2000, Streelman *et al.*, 2002; Gasparini *et al.*, 2003).

Territorial herbivores (TERH) include pomacentrids of the genus *Stegastes* and *Microspathodon* that have the bulk of their diet consisting of turf algae farmed within a vigorously defended territory. Diet also includes a low percentage of detritus found in the turf matrix. As for ROVH, a higher number of filamentous algae and detritus territorial feeders is predicted to occur at low latitudes (see prediction 1). However, one specific hypothesis is proposed for this group. (4) Due to smaller size and greater capacity of feeding choice (i.e. increase in protein intake through exploitation of the fauna of their territories) than most of the other tropical herbivores, it is expected that TERH show a more gradual decline with latitude when compared with grazing ROVHs (Choat, 1991).

Mobile invertebrate feeders (MIFs) are fishes that feed primarily on small benthic mobile invertebrates (e.g. crustaceans, molluscs, worms, etc.) associated to hard and nearby

soft substrates. (5) This group is predicted to be dominant in all sites studied. Fishes preying on mobile invertebrates are reported as the major trophic group on both tropical and temperate reefs (Ebeling & Hixon, 1991; Jones *et al.*, 1991; Wainwright & Bellwood, 2002). This wide-ranging dominance of MIF results from their preys being a high caloric food resource abundant on both hard and adjacent soft substratum (Jones *et al.*, 1991; Harmelin-Vivien, 2002).

Sessile invertebrate feeders (SIF) feed on a diverse array of sessile benthic invertebrates (e.g. cnidarians, hidrozoans, bryozoans, ascidians and sponges) that are mostly associated to hard substrate. (6) A negative relationship with latitude is expected for such specialist feeders. The higher diversity and abundance of SIFs in lower latitudes could be viewed as a reflection of a progressive adaptation to using low-caloric food sources and to circumventing structural and chemical defences against predators (Paul, 1992; Pawlik, 1993; Harmelin-Vivien, 2002). Such evolutionary process was only possible in the tropics because stability over geological time permitted fish specialization in respect to high levels of competition, herbivory and predation (Harmelin-Vivien, 2002).

Omnivores (OMN) feed on a variety of organisms, including animal and plant material. (7) Fishes belonging to this group are expected to dominate in high latitudes reef areas. These fishes are extremely plastic in their diet and can shift between food sources as a result of seasonal (and historical) environmental disturbances. Omnivorous fishes are reported to dominate in cold peripheral sites (e.g. Canaries and Mediterranean) (Fasola *et al.*, 1997; Sala & Boudouresque, 1997; García-Charton & Pérez-Ruzafa, 1998). We suggest that these fishes could only explore low-energy resources if associated with substantial portions of highly digestible animal protein in order to fulfil their metabolic needs (cf. Bowen *et al.*, 1995).

Planktivores (PLK) feed primarily on macro- and microzooplankton. (8) A greater number of planktivores is predicted to occur at offshore and/or in exposed environments. Reef sites or zones constantly influenced by strong water motion and currents concentrate a great amount of transient macrozooplankton (e.g. copepods, larvaceans and fish eggs). Characteristically, these habitats present good water transparency. In fact, diurnal planktivorous fishes are known to feed on individual preys based on visual cues, a process profoundly influenced by the variation in incident light (Thresher, 1983; Hobson, 1991).

Piscivores (PIS) feed only on live fishes; and carnivores (CAR) eat a variety of mobile organisms, including benthos and fishes. (9) Both groups are expected to be proportionally better represented in high latitudes due to a decrease in the abundance of guilds such as ROVH, TERH and SIF. In addition, the abundance of piscivorous and carnivorous fishes is expected to vary along the coast according to fishing pressure level. Various families of reef fishes included in these categories are main targets of fisheries (e.g. Serranidae, Lutjanidae and Carangidae). Most often, characteristics of the life cycle (e.g. long life span, ontogenetic migrations) and reproduction (e.g. sex reversal) make them highly vulnerable to even low levels of exploitation (Roberts, 1995; Coleman *et al.*, 2000; Sadovy, 2001).

METHODS

Data collection

Strip transects by means of underwater visual censuses (UVC) were conducted by the authors in five sites along the Brazilian coast (see Table 1 for a detailed description of the sites and methods). The sampling design contemplated different habitats in each site, covering reefs of various depths, exposures, and complexity profiles because reef fish exhibit high demographic plasticity, with consistent differences in growth, mortality and longevity within reefs (Gust *et al.*, 2002). Point count censuses from Manuel Luiz Reefs (Rocha & Rosa, 2001) and Atol das Rocas (Rosa & Moura, 1997) were also included. Data from Manuel Luiz Reefs was obtained from a single reef type habitat, and the area sampled was the central portion of

Table 1 Characteristic features of the studied Brazilian reef sites

Reef site (coordinates)	Distance from coast (km)	SWT*† winter–summer	Reef type	UVC type	Protection status
North-eastern Brazil					
Manuel Luis Reefs (0°52′ S; 44°15′ W)	86	26–28	Mid-shelf coralline algae	Point count 7.5 m radius‡	Full protection
Tamandaré (8°45′ S; 34°50 W)	–	25–28	Coastal fringing	Transect 20 × 5 m	None
Abrolhos Reefs (17°20′ S; 39° W)	50	22–27	Coastal and mid-shelf coral	Transect 30 × 2 m	Full protection
South-eastern Brazil					
Guarapari Islands (20°40′ S; 40°22′ W)	5	19–24	Coastal rocky	Transect 20 × 2 m	None
Arraial do Cabo (23° S; 42° W)	–	18–23	Coastal rocky	Transect 30 × 2 m	None
Arvoredo Island (27°17′ S; 48°28′ W)	6	17–21	Coastal rocky	Transect 20 × 2 m	Full protection
Oceanic Island					
Atol das Rocas (3°50′ S; 33°49′ W)	267	25–28	Coralline algae	Point count 7.5 m radius§	Full protection

SWT, surface water temperature (°C); UVC, underwater visual census.
Sources: *Maida & Ferreira (1997); †Ekau & Knoppers (1999); ‡Rocha & Rosa (2001); §Rosa & Moura (1997).
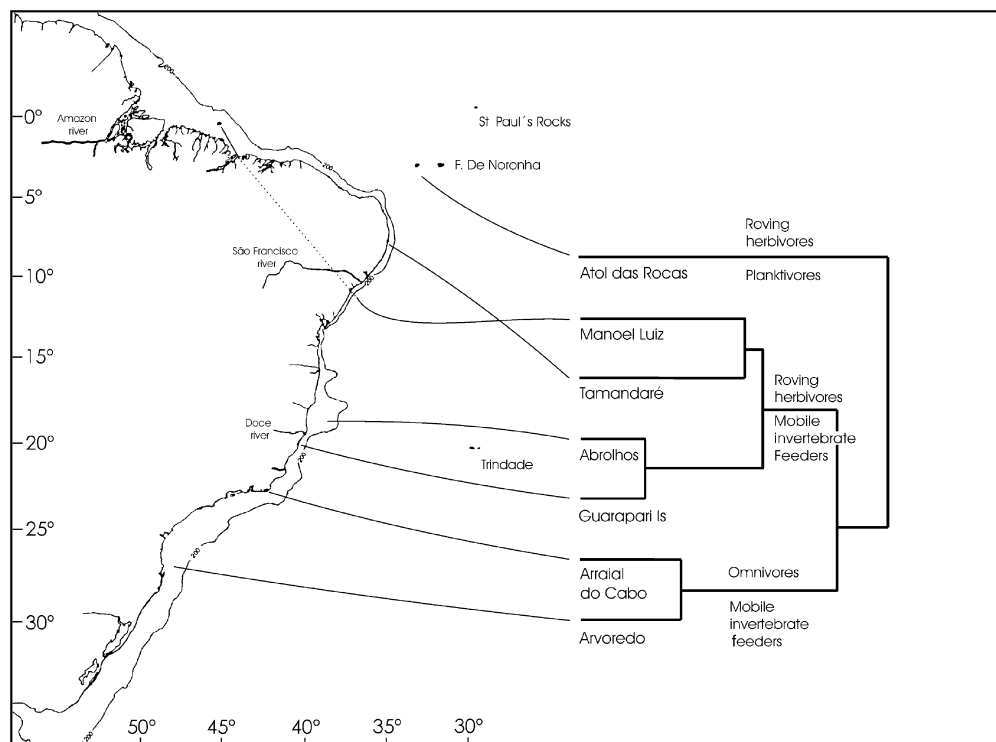
Figure 1 Map of the reef sites and cluster analysis (Bray-Curtis and UPGMA) based on the relative abundance of trophic groups. The two dominant trophic groups of each site are shown in the nodes.

the reef, over rocky and coral bottom, between 8 and 15 m depth (Rocha & Rosa, 2001).

A database of relative abundances including 123 species from 33 reef-associated families[1] was assembled based on number of individuals per species in UVC. Cryptobenthic species are generally underestimated in UVC (Ackerman & Bellwood, 2000, 2002; Willis, 2001), and to avoid inherent biases and errors, those were eliminated from all analyses. Our comparisons are based on relative abundance in order to homogenize data collected through different methods (see Table 1). Expressed as a percentage, relative abundance contemplates a proportion based on the total number of individuals of all species, pooled from different habitats within a site.

Trophic categories

The problem of grouping reef fishes in trophic categories has been widely discussed (Parrish, 1989; Jones *et al.*, 1991). Diet plasticity and ontogenetic shifts hinder the categorization of independent trophic groups. In this study, however, we assigned every species recorded in UVC to one of eight major

[1]Acanthuridae, Aulostomidae, Balistidae, Belonidae, Carangidae, Centropomidae, Chaetodontidae, Cirrhitidae, Dactylopteridae, Diodontidae, Fistulariidae, Grammidae, Haemulidae, Holocentridae, Kyphosidae, Labridae, Lutjanidae, Malacanthidae, Mullidae, Monacanthidae, Ogcocephalidae, Ophichthidae, Ostraciidae, Pomacanthidae, Pomacentridae, Priacanthidae, Scaridae, Serranidae, Sphyraenidae, Sciaenidae, Sparidae, Synodonthidae, Tetraodontidae.

feeding categories (based on the main diet of adults) in order to search for general patterns. Thereafter, a cluster analysis based on a matrix of relative abundance (percentage) for trophic guilds was performed. The Bray-Curtis dissimilarity index was used, and localities were clustered according to the UPGMA method (Pielou, 1984). Dominant food items were determined from direct behavioural observations, stomach content analysis, as well as the available literature (C.E.L. Ferreira, S.R. Floeter, J.L. Gasparini, B.P. Ferreira & J.C. Joyeux, unpubl. data; Randall, 1967; Moura, 1998).

RESULTS AND DISCUSSION

Major patterns in trophic structure

Sites clustered in three major groups according to the relative abundance of trophic guilds, delineating a clear latitudinal gradient (Fig. 1). The ROVH and MIF tend to dominate in low latitude sites (Manuel Luiz Reefs, Tamandaré, Abrolhos and Guarapari Is.). Omnivores gradually substitute ROVH with increasing latitude. Omnivores and MIF are the dominant trophic groups in Arraial do Cabo and Arvoredo. Although both Arraial do Cabo and Guarapari Is. present rocky shores and are influenced by subtropical currents, a clear dominance of OMN is only evident in Arraial do Cabo. A more subtle difference is found between the two main tropical groups, Manuel Luiz Reefs plus Tamandaré and Abrolhos plus Guarapari Is. The former sites are dominated by ROVH (followed by MIF) and the latter by MIF (followed by ROVH).
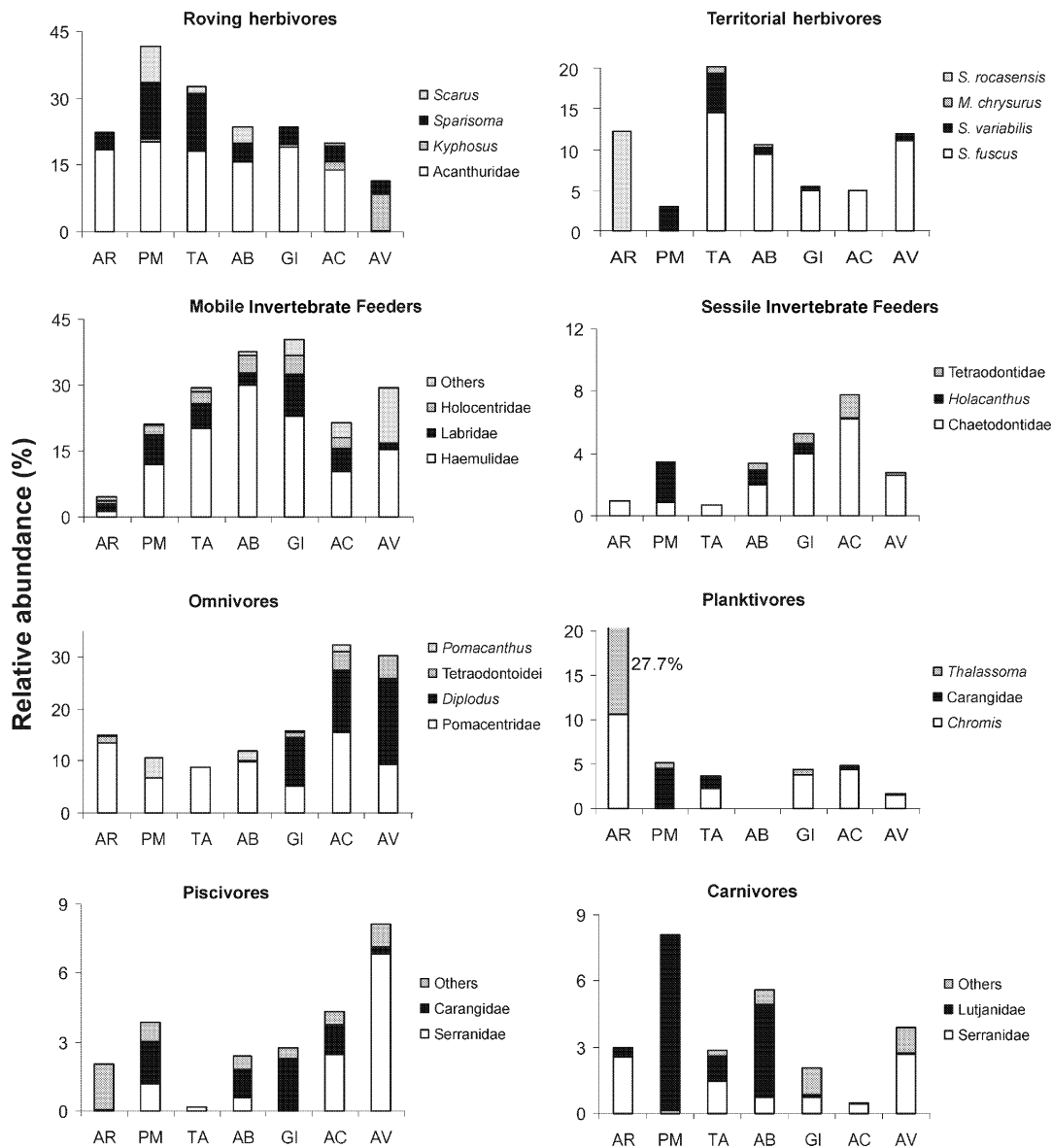
Figure 2 Relative abundance of the trophic groups along the Brazilian coast. Sites – AR, Atol das Rocas; PM, Manuel Luiz Reefs; TA, Tamandaré; AB, Abrolhos Reefs; GI, Guarapari Is.; AC, Arraial do Cabo; AV, Arvoredo. Refer to Table 1 for details on sites.

Trophic structure patterns in oceanic sites seem to be different from coastal and mid-shelf sites, with ROVH and PLK being dominant in Atol das Rocas.

Roving herbivores

The ROVH show a clear increase in abundance towards the tropical zone (Fig. 2), mainly due to the high abundance of scarids at low latitudes. Acanthurids present similar abundance throughout the analysed continuum and are more abundant than scarids in all sites, except at Arvoredo where both families are infrequent (Fig. 3a). As expected, kyphosids abundance increases at high latitudes (Horn, 1989; Choat, 1991) (Fig. 3a) as well as in harsh environments such as oceanic islands (C.E.L. Ferreira *et al.*, unpubl. data; B.M.

Feitoza, unpubl. data). Their favourite food, brown seaweeds (mainly fucoids), proliferate in these marginal sites (Hay, 1991). While kyphosids prefer seaweeds, most of South Atlantic scarids and acanthurids include in their diet a mixture of detritus and turf algae (Dias *et al.*, 2001; C.E.L. Ferreira & J. Gonçalves, unpubl. data). ROVH abundance patterns thus seem to be correlated with higher biomass and higher productivity of turf algae and consequently detritus production in the tropics (Carpenter, 1986; Hatcher, 1988; Choat, 1991; Cebrian, 2002) (for scarids and acanthurids), and seaweed biomass accumulation towards high latitude sites (Hay, 1991) (for kyphosids).

Among scarids, the genus *Sparisoma* is considered to be more plastic in its feeding habits than *Scarus*. In the Indo-Pacific, the genus *Scarus* is pretty much restricted to coral reefs
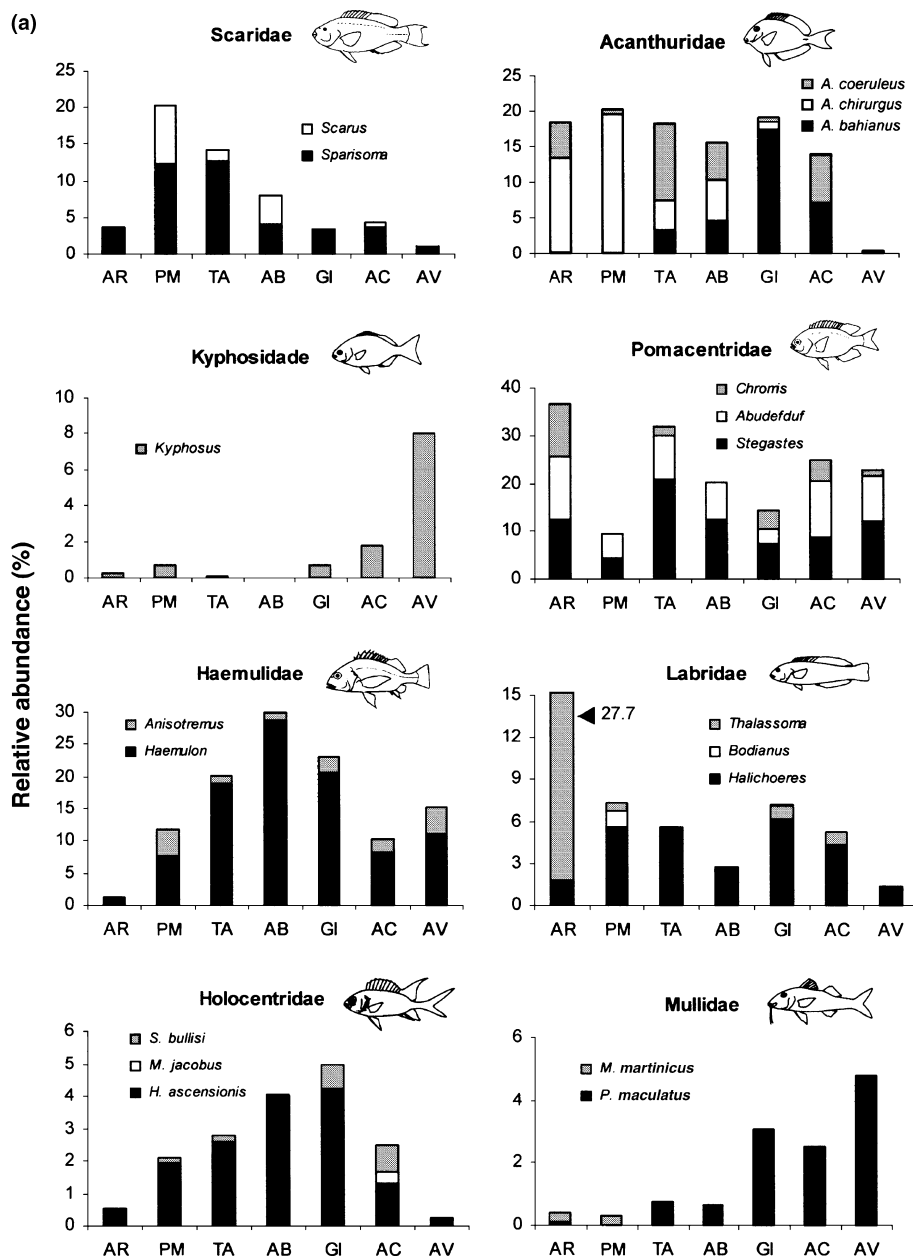
Figure 3 Relative abundance of the main reef-fish families along the Brazilian coast. Refer to Fig. 2 for site legends. Refer to Table 1 for details on sampling methods.

(Choat, 1991), while in the South Atlantic they penetrated into the rocky reef systems of the south-east coast (Fig. 3a). However, in oceanic islands, the scraper *Scarus* are absent (Floeter *et al.*, 2001). However, members of the genus *Sparisoma* are present on the offshore islands and are more abundant at higher latitude than *Scarus*. This reflects the broader feeding habits of this group (Bernardi *et al.*, 2000; Streelman *et al.*, 2002). The endemic Brazilian *Scarus* species (*S. trispinosus* and *S. zelindae*) are not obligate coral feeders, and if specific restrictions to habitat use are poorly known, are clearly not correlated with coral availability. Preliminary feeding studies and field observations indicate high abundance of detritus in *Scarus* diet, with additional material from

calcareous incrusting algae (C.E.L. Ferreira and J. Gonçalves, unpubl. data). Most Brazilian sparisomatines, including larger species like *Sparisoma axillare*, *S. frondosum*, and small species, like *S. radians*, *Cryptotomus roseus* and *Nicholsina ulsta*, show wide latitudinal distribution along the coast. *S. atomarium* was long thought to present a typical disjunct, anti-north-eastern distribution, but the southern component is actually a newly described species (J.L. Gasparini *et al.*, 2003). It differs from its Caribbean sister species by feeding either as browser or scraper. In that respect, it is very similar to *S. cretense* in the Mediterranean and *S. strigatum* in Ascension and St Helena islands (Bernardi *et al.*, 2000), both species living in harsh or subtropical conditions (Bortone *et al.*, 1991; Falcón *et al.*,
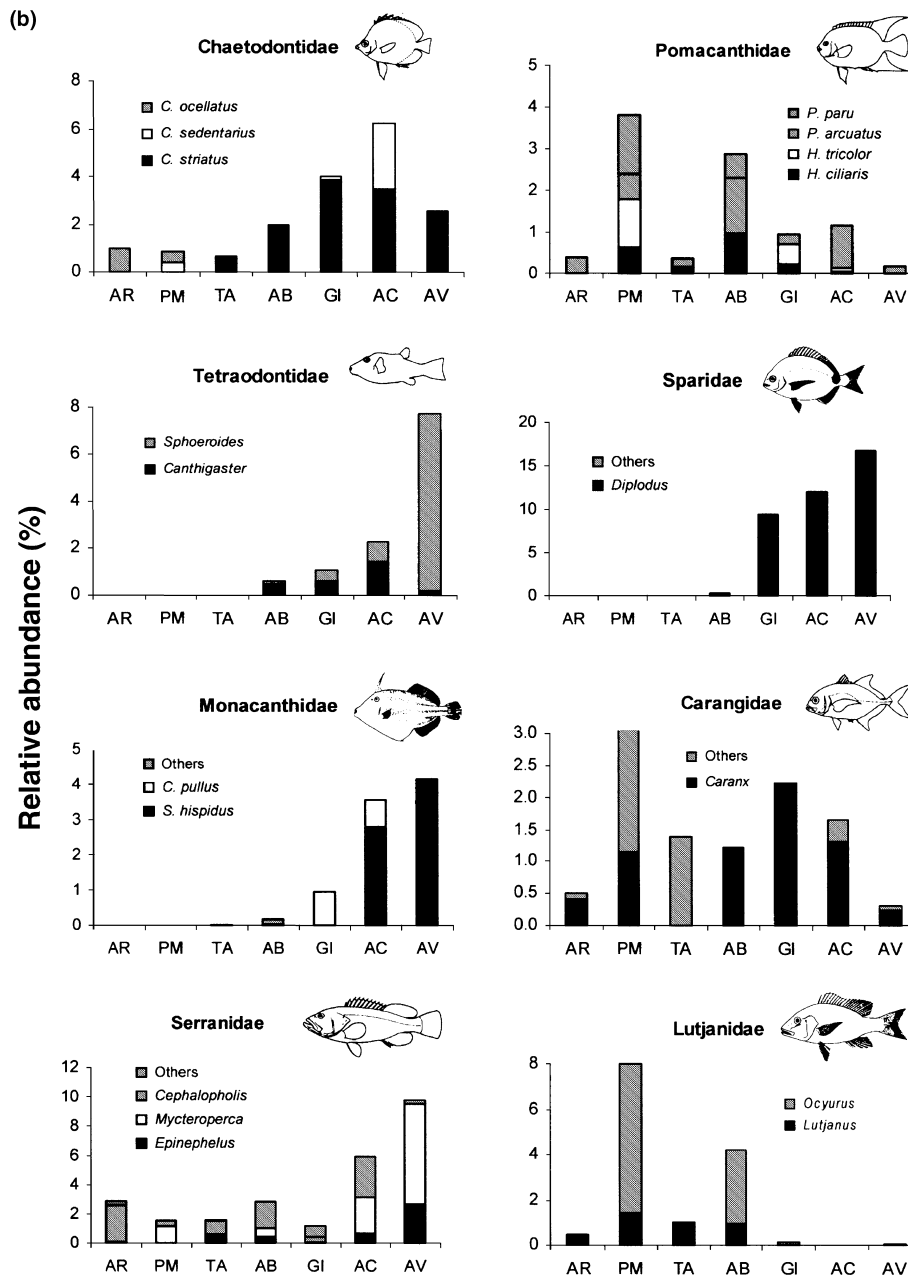
(b)

Figure 3 *continued*

1996; Mazoldi & Girolamo, 1997; García-Charton & Pérez-Ruzafa, 1998). This emphasizes sparisomatines plasticity, and those are the only scarids that could reach such marginal sites. However, the large endemic species *Sparisoma amplum* is more abundant in the tropics and in exposed oceanic sites than the other sparisomatines (Rosa & Moura, 1997; Gasparini & Floeter, 2001; Rocha & Rosa, 2001; S.R. Floeter & J.L. Gasparini, pers. obs.; F. de Noronha), a fact that may be related to its feeding apparatus, similar to that of its Caribbean sister species, *S. viride*. This species is known to possess distinct excavator characteristics (Bernardi *et al.*, 2000) that allow it to include corals in its diet (Bruckner *et al.*, 2000). Otherwise, *S. amplum* was observed to heavily feed on

incrusting calcareous algae in Brazilian coral reefs (C.E.L. Ferreira, pers. obs.).

Acanthurids are found at similar relative abundance from Atol das Rocas to Arraial do Cabo, then declining southwards to Arvoredo (Fig. 3a). The two species *Acanthurus bahianus* and *A. chirurgus* present similar diets, typically consisting of turf algae and detritus (Dias *et al.*, 2001). Both species showed unpredictable patterns of abundance along the coast (Fig. 3a). The third species, the browser *A. coeruleus*, is a strict turf algae feeder and does not ingest detritus as the other acanthurids and most sparisomatine scarids (Randall, 1967; C.E.L. Ferreira & J. Gonçalves, unpubl. data). This species decreases in abundance southwards from Abrolhos (Fig. 3a).

Territorial herbivores

They are mainly represented by the genus *Stegastes*, as the large *Mycrosphatodon chrysurus* only occurs in some NE sites (Fig. 2). Along the coastline, from Tamandaré to Arvoredo, *Stegastes fuscus* is by far the most abundant TERH (Fig. 2). Interestingly, this species is not found in Manuel Luiz Reefs, where *Stegastes* aff. *variabilis* abounds (Rocha & Rosa, 2001). Prediction 4 was corroborated, as the data show a more gradual decline in abundance of TERH towards the south Brazilian coast than for scarids and acanthurids (Fig. 2). *Stegastes fuscus* has wealthy established populations at Arvoredo. Thus, its presence is continuous along almost the entire latitudinal gradient studied, even in the Abrolhos mid-shelf reefs where it shares some habitats with *S. variabilis*.

On many tropical reefs, territorial fishes are extremely abundant and the areas they defend can occupy more than 70–80% of the surface of some reef habitats (e.g. Ferreira *et al.*, 1998a; Ceccarelli *et al.*, 2001). However, herbivore territoriality appears to be rare in temperate latitudes (Horn, 1989), where defending food resources seems not to be energetically viable. This rarefaction towards higher latitudes is not a consequence of lower algae biomass but, probably, of decreasing competition with other herbivorous fishes. We expect that complete disappearance of TERH occurs where temperature falls to that of typical temperate habitats. This would place TERH southern distribution limit around latitude 30°S (in the state of Rio Grande do Sul), where low water temperatures and the lack of available hard substratum contribute to the general depletion of tropical-warm reef fish populations.

Mobile invertebrate feeders

The MIFs include fishes adapted to explore both hard and complex substratum, and adjacent sandy flat bottoms (cf. McCormick, 1995). The diversity of the trophic category, and the consequently diversified ecomorphological types, make such group prone to be abundant in different environmental conditions. MIF are the most abundant trophic guild in all sites studied, but present a peculiar peak at 17–20° S (Abrolhos and Guarapari Is., Fig. 2). This peak is strongly dependent from locally high abundance of haemulids (Figs 2 & 3a). The genus *Haemulon* shows a peak at Abrolhos with an interesting pattern of species overlap and replacement along the coast. For example, *Haemulon aurolineatum* is dominant from Tamandaré to Arvoredo; *H. steindachneri* is mainly restricted to high latitudes and coastal habitats; *H. parra* is only found in the north-east (including Abrolhos, where it is very abundant); *H. chrysargyreum* is restricted to Atol das Rocas (and Fernando de Noronha), and the Brazilian-endemic *H. squamipinna* is only found in the north-eastern coast (north of Abrolhos). Only *H. plumieri* and *Anisotremus* spp. are widely distributed along the entire coast.

Patterns of distribution within the labrids are essentially uniform, except for offshore and southernmost sites (Atol das Rocas and Arvoredo). This family is second in contribution to the observed pattern of MIF. The widespread labrid genus *Bodianus* poorly participates to the definition of latitudinal patterns (Fig. 3a). *Halichoeres poeyi* is the most abundant species and occurs from Manuel Luiz Reefs to Arvoredo. *Halichoeres* aff. *cyanocephalus* and the Brazilian-endemic *H. brasiliensis* occupy the whole Brazilian coast, but the former shows low abundance at high latitudes. *Haemulon bivittatus* is restricted to low latitudes and is not found below 10° S. The same could occur with *H. maculipinna*, being known in the south-east only as vagrant (C.E.L. Ferreira, pers. obs.). The Caribbean *H. radiatus* only occurs in Atol das Rocas (and F. de Noronha), while *H.* aff. *bathyphilus* is very much associated with the deep habitats of south-eastern cold waters.

The holocentrids are less abundant than haemulids and labrids and show a peak at Abrolhos and Guarapari Is. southward from Guarapari, Holocentrids show a marked decrease in abundance (Fig. 3a). *Holocentrus ascensionis* is the most abundant and widely distributed holocentrid while *Myripristis jacobus*, that also presents a wide distribution, is less detectable by visual census technique (Fig. 3a). *Sargocentrun bullisi* seems to be more restricted in distribution, being detected in appreciable numbers only in Arraial do Cabo.

Mullids are represented by two species (Fig. 3a). The typically tropical *Mulloidichthys martinicus* is the least abundant. The abundant and widely distributed *Pseudupeneus maculatus* increases in relative abundance towards high latitudes (Fig. 3a).

Sessile invertebrate feeders

Although this guild was expected to increase in abundance towards low latitudes, it did not show any clear latitudinal trend (Fig. 2). Chaetodontidae and Pomacanthidae are the two most important families contributing to the observed patterns. Chaetodontids seem to peak at Arraial do Cabo (Fig. 3b), while Pomacanthids are patchily distributed. The chaetodontid *Chaetodon striatus*, the most widely distributed at coastal sites, sustains higher abundance in rocky shore systems. *Chaetodon ocellatus* seems to 'replace' *C. striatus* in some northern sites (e.g. Manuel Luiz Reefs and Atol das Rocas), and *Chaetodon sedentarius* exhibits an apparently anti-NE hump of Brazil distribution (Rocha, 2003), with highest abundance in Arraial do Cabo (Fig. 3b). There, they are commonly observed in pairs feeding on benthos, even at shallow depths. However, they also form large schools when feeding on macro-plankton in locations of intense water flux (C.E.L. Ferreira, pers. obs.). In most non-protected sites, pomacanthids are prone to be influenced by ornamental collection and, especially at Tamandaré, lower abundances could indicate overharvesting (B.P. Ferreira, pers. obs.; J.L. Gasparini, S.R. Floeter, C.E.L. Ferreira, I. Sazima, unpubl. data). The specialist spongivore pomacanthid genus *Holacanthus* shows an increase in abundance towards the tropics. Interestingly, the rock beauty *H. tricolor* is apparently absent from Abrolhos, where *H. ciliaris* and *Pomacanthus* spp. are found in high numbers (Fig. 3b). This kind of absence or replacement is recurrently detected along the Brazilian coast and

in the south-western Atlantic as a whole (this paper; Joyeux *et al.*, 2001) and probably results from the association of various ecological factors such as competition and larval supply. Deciphering Pomacanthids abundance patterns along the Brazilian coast necessitates a better knowledge on sponge distribution and feeding preferences of these fishes. At last, the tetraodontid genus *Canthigaster* are found from Abrolhos to Arvoredo, peaking at Arraial do Cabo.

Omnivores

These fishes tend to be relatively more abundant in the southernmost sites, including Arraial do Cabo and Arvoredo (Fig. 2) and this suggests some agreement with prediction 7. The sparid *Diplodus argenteus* is by far the most important species driving the observed patterns (Fig. 3b). The species is typically subtropical and appears to reach its higher biomass in Arraial do Cabo (Ferreira *et al.*, 2001). Other abundant and ubiquitously distributed omnivore is the pomacentrid *Abudefduf saxatilis* (Fig. 3a). This species is well adapted to different reef environments and possesses a flexible diet. It commonly feeds on benthos but, depending upon water currents and wave exposure, it can aggregate in huge schools to graze on plankton. The Brazilian endemic Pomacentrid *Stegastes pictus* is also included in OMN and, despite occurring in all coastal sites, reaches peak abundance from Abrolhos to Arraial do Cabo. The Pomacanthids *Centropyge* and *Pomacanthus* (Fig. 3b) seem to include algae in their diet, about 90% for the former and about 10% for the latter (Randall, 1967; Moura, 1998; C.E.L. Ferreira, unpubl. data). Percentage may vary with environmental conditions. Underwater observations suggest that the spongivore/herbivore genus *Pomacanthus* could explore marginal sites better than *Holacanthus* (SIF) (C.E.L. Ferreira *et al.*, pers. obs). *Centropyge aurantonotus* has established populations on Guarapari Is. and Arraial do Cabo and is rare southwards. In the north-eastern coast, it is only found on deep reefs (L.A. Rocha, pers. com.), to 'reappear' in the southern islands of the Caribbean (Humann & Deloach, 2002). *Pomacanthus paru* is comparatively more abundant along the coast than *P. arcuatus*. The latter species is abundant only at some north-eastern coastal sites.

Among monacanthids, the species *Stephanolepis hispidus* is very abundant in Arraial do Cabo and Arvoredo (Fig. 3a), and shows a typical anti-NE distribution. The whole family diminishes in abundance in northern regions (Fig. 3a).

Planktivores

Overall, reef planktivores are poorly represented in coastal sites (Fig. 2), and their great abundance in the oceanic Atol das Rocas corroborates prediction 8. The most important fishes in this group are the pelagic holoplankton feeders *Chromis multilineata* and *Paranthias furcifer*. Unexpectedly, these two species and other classic planktivores (e.g. *Clepticus, Thalassoma*) are not found to have established populations within the 6000 km^2 area of Abrolhos reefs. The Abrolhos reef complex is characterized by high rates of sedimentation of biogenic origin (Leão, 1996) and

consequent low water transparency in some months of the year. This suggests a preclusion of optimal foraging by these fishes, which are reported to depend highly on visual cues to feed on plankton (Thresher, 1983; Hobson, 1991). Carangid planktivores are important in some specific habitats. However, they are generally poorly censused because of their high mobility and pelagic behaviour. In Atol das Rocas, the two planktivores *C. multilineata* and the endemic labrid *Thalassoma noronhanum* dominate many exposed reef habitats (Rosa & Moura, 1997; Fig. 2), a characteristic shared with Fernando de Noronha and Trindade (Gasparini & Floeter, 2001; S.R. Floeter & J.L. Gasparini, pers. obs.).

Piscivores

Together with CAR and SIF, it is one of the least abundant (proportionally) trophic groups. Despite that, and following the prediction 9, the relative abundance of piscivores tends to increase towards the south. The pattern is primarily influenced by serranids (Fig. 2). The comb grouper *Mycteroperca acutirostris* is mainly responsible for the southward increase in CAR (Fig. 3b), and actually displays an anti-NE distribution. Northwards, *Mycteroperca bonaci* is the dominant serranid in most sites, and is targeted by many local fisheries (Ferreira *et al.*, 1995; Costa *et al.*, 2003). Carangids presented high variability along the coast, with *Caranx* being the main representative genus. Species in this family, specially the genus *Caranx*, are subject to high fishing pressure along the coast. It is important to note that abundance estimates by means of visual census are strongly biased by the high mobility shown by most of these species. Consequently, the observed latitudinal pattern in this family was primarily determined by fishing pressure and methodological limitation (Fig. 3b). Analysed sites that hold some protection status are Atol das Rocas, Manuel Luiz Reefs (solely by distance from coast), Abrolhos and Arvoredo (Table 1). Except for Arvoredo, these sites do not show higher proportion of piscivores (Fig. 2). Local ecological factors and fishing pressure may have varying influence on distributional patterns. However, the distinction of natural from anthropogenic effects is not obvious in the context of this study. Nevertheless, the bulk of piscivores in Atol das Rocas is composed of sharks and barracudas (Rosa & Moura, 1997), which seems to indicate that oceanic sites may be the best examples of 'relatively pristine' reef systems. Actually, it is incontestable that in the past such large piscivores (and carnivores) were the dominant top predators in most reef systems along the entire Brazilian coast (Isy-Schwart, 1954), and that overfishing is undoubtedly one of the main responsible for today's patterns.

Carnivores

These fishes are best represented by serranids and lutjanids that are, as PIS, highly influenced by fishing. Consequently, all previous considerations in regard to fishing impact are also applicable to this group. The data presented show no detectable latitudinal pattern (Fig. 2). Other carnivores like some sciaenids,

scorpaenids and priacanthids are fully distributed along sites and perform an important role as predators where large carnivores have declined. Among serranids, *Epinephelus marginatus*, restricted to south-eastern sites, is gradually 'replaced' by *E. adsensionis*, dominant in north-eastern sites. *Cephalopholis fulva* is the dominant carnivore in Atol das Rocas (and nearby Fernando de Noronha; S.R. Floeter, pers. obs.), and in some tropical coastal sites like Tamandaré and Guarapari Is. (Fig. 3b) Lutjanids variation in relative abundance is driven by the snapper *Ocyurus chrysurus* (Fig. 3b), especially abundant in mid-shelf sites (Manuel Luiz Reefs and Abrolhos). In Abrolhos, as in many Caribbean sites (Bohnsack *et al.*, 1994), it composes the bulk of local fisheries captures (e.g. Costa *et al.*, 2003, C.E.L. Ferreira, pers. obs.). Few lujanid species are captured by fisheries in the south-eastern and southern reef systems, although these may be abundant in estuarine systems (e.g. *Lutjanus synagris*, *L. analis* and *L. jocu*; P. Costa, C.E.L. Ferreira, L. Gerhardinger, J.C. Joyeux, pers. comm.).

CONCLUSIONS AND REMARKS

The data presented herein revealed interesting latitudinal patterns of reef fish trophic structure along the Brazilian coast, from 0° to 27° S. The analyses encompassed coastal, mid-shore and oceanic sites, including coral reefs in low latitudes (north and north-eastern coasts) and rocky shores in high latitudes (south and south-eastern coasts). This comparison is unique in the Atlantic as it deals with an extensive coastal shore (*c.* 8000 Km) and examines a diverse set of reef systems (Table 1). Based on predictions grounded on the available literature as well as authors (and colleagues) extensive observations, some degree of predictability was assumed to exist in the trophic patterns exhibited.

The MIFs were confirmed as the most widespread and dominant trophic group. This group preys on high caloric food resources, exploits either hard or associated soft substratum (Jones *et al.*, 1991; Harmelin-Vivien, 2002), and is reported to be abundant both in tropical and temperate reef systems (Ebeling & Hixon, 1991; Jones *et al.*, 1991). MIF (together with ROVH) dominate the tropical coral reefs of the north-eastern Brazilian coast and the rocky shores of Guarapari Islands (south-eastern coast), a site that displays an interesting transition in benthic organisms coverage between the two types of environments (S.R. Floeter and W. Krohling, unpubl. data). Why MIF are still dominant in this site should be investigated. Basically, the same MIF species are present in Abrolhos and Guarapari Is. This indicates that bottom-up and top-down processes could be very similar in those morphologically and ecologically different systems.

The ROVHs are the other dominant trophic group, being very abundant in five of the six sites analysed. These fishes are known to compose the bulk of fish biomass on coral reefs and play a vital role transferring energy from the base to the top of the food web (Horn, 1989; Choat, 1991). Although less diverse than other trophic groups, their huge biomass exerts a strong influence on the abundance of the epilithic algae community

and on sediment transport (Bruggemann, 1994; Bellwood, 1995). Various studies have evidenced that most of the net primary production (NPP) on coral reefs goes to the herbivory food chain *via* the strong pressure performed by herbivorous fishes (Carpenter, 1986; Polunin & Klumpp, 1992; Ferreira, 1998; Ferreira *et al.*, 1998b). Long considered strict herbivores (Randall, 1967; Hobson, 1974), these fishes also hold an important detritivorous role (Choat & Clements, 1998; Choat *et al.*, 2002; Wilson *et al.*, 2003). The tropics appear to be an optimal system as these 'herbivorous' fishes (i.e. those foraging on turf and detritus) find there high NPP and high intensity of detrital trophic processing (Hatcher, 1988; Cebrian, 2002). Our data clearly indicate that ROVH decrease in relative abundance as latitude increase (Fig. 2). How temperature and algae digestibility influence herbivorous fish distribution is still an important topic to be elucidated (Horn, 1989; S.R. Floeter and C.E.L. Ferreira, unpubl. data).

The high abundance of PLK in the exposed site of Atol das Rocas was clearly anticipated, and this prevalence also characterizes other Brazilian oceanic sites as PLK benefit from strong currents, abundant plankton and good water transparency. In fact, exposed reefs in the oceanic islands Atol das Rocas (Fig. 2), Fernando de Noronha and Trindade (Rosa & Moura, 1997; Gasparini & Floeter, 2001) are essentially dominated by a low-diversity planktivorous community that includes *Chromis multilineata*, *Thalassoma noronhanum*, *Clepticus brasiliensis* and *Paranthias furcifer*.

Omnivores and MIF, are the most representative groups at the southern sites Arraial do Cabo and Arvoredo. Theoretically, to be an omnivore is overall a question of being better adapted to environment constraints, which are generally related to periodic or unpredictable events (e.g. seasonal, annual, or stochastic shifts). Indeed, omnivorous fishes are frequently predominant in marginal reef systems (Fasola *et al.*, 1997; García-Charton & Pérez-Ruzafa, 1998). However, to categorize fishes as omnivores is a hard task as food items could strongly vary with benthic composition, fish size/age, exposure/currents and behaviour (e.g. spawning, nest guarding and ontogenetic shifts). On the Brazilian coast, *Diplodus argenteus* is the main species responsible for the increase of OMN in high latitudes. The genus *Diplodus* originated in the Mediterranean and the Eastern Atlantic (Summerer *et al.*, 2001), where its diversity and abundance are uniquely high (Fasola *et al.*, 1997; La Mesa & Vacchi, 1999). The Mediterranean is known to have suffered from continuous and intensive environment shifts due to successive glaciation and deglaciation events (Bellwood & Wainwright, 2002), thus preventing specialists to evolve (Harmelin-Vivien, 2002). Both Arraial do Cabo and Arvoredo (and also Guarapari Is.) are under influence of subtropical as well as tropical currents, and show reef fish fauna components from both systems. Arvoredo is the critical point of the gradient where overall abundance and diversity of reef fishes decrease (Floeter *et al.*, 2001; C.E.L. Ferreira *et al.*, unpubl. data), basically due to the collapse of tropical oceanographic conditions (e.g. temperature and transparency).

Further investigations on actual fish densities and biomass as well as abundance and biomass of food sources (i.e. macrofauna associated to hard and soft substratum, algal turfs, seaweeds, plankton, and small fishes), will certainly help to decipher the complex patterns in reef fish distribution and trophic structure along the Brazilian coast. In addition, the trophic role of cryptic species and the patterns in community structure of deep reefs are barely known, if at all. Cryptic fishes are abundant and potentially active participants of the energy transfer that are usually disregarded because of problematic sampling (Munday & Jones, 1998; Ackerman & Bellwood, 2000; Willis, 2001). The rarity of fish surveys in Brazilian deep reefs has been alleged to bias perceived disjunct distributions (L.A. Rocha, pers. comm.; B.M. Feitoza, pers. comm.; C.E.L. Ferreira *et al.*, pers. obs.). Deep reefs of the NE seem to sustain rich reef fish populations and could potentially operate as stepping stones for gene flow between the Caribbean and Brazil (Rocha *et al.*, 2000, 2002).

Fishing deserves a special attention among the factors within the frame of this study (phylogeny, physiological constraints and anthropogenic impacts). The lack of studies in major Brazilian reef impedes the detection of even clear-cut impacts, but large scarid species, such as *Scarus trispinosus* (and others), have suffered strong population declines in Tamandaré, Guarapari Is. and Arraial do Cabo because of spearfishing (C.E.L. Ferreira *et al.*, pers. obs.). Local or generalized disappearance of large herbivorous may not have induced significant changes into the large-scale pattern of trophic structure, resulting in that presently observed (Fig. 1). In Tamandaré and Guarapari Is., ROVH still are the dominant group. In Arraial do Cabo, scarid overfishing could have altered the original trophic pattern (probably once characterized by ROVH) towards the now detected OMN dominance (Fig. 1). However, the increasing abundance of OMN, such as *Diplodus* and Monacanthids, towards southern latitudes and the concomitant decreading representativeness of ROVH plead for a natural shift in structure (possibly exacerbated by anthropogenic effects).

The importance of fishing pressure as a shaping mechanism for contemporaneous reef fish communities has been emphasized in the recent literature (Russ & Alcala, 1989; Pauly, 1990; Roberts, 1995, 1997; Jennings & Lock, 1996; Steneck, 1998). Communities in least impacted reefs (oceanic and mid-shelf) depict the effects of man-made modifications that all natural systems have suffered. Typically, fishing impacts and other threats such as eutrophication, intensive tourism, etc., decrease with distance from the coast. In times when nearly 60% of the world fisheries stocks are under threat (Pauly & Christensen, 1995), information on fishing pressure levels along the coast is primordial to the interpretation of trophic patterns. Fundamentally, management and conservation actions should be based on data similar to that collected for the present study. The present-day scenario is <1% of the Brazilian coastline officially protected (A.P. Prates & B.P. Ferreira, pers. comm.), declining fishing stocks, and generalized reef disturbance (Leão, 1996; Ferreira & Gonçalves, 1999; Leão & Dominguez, 2000). Within this context, our expanding knowledge of species distribution and abundance and of patterns of trophic structure supports the urgent establishment of marine protected areas.

REFERENCES

Ackerman, J.L. & Bellwood, D.R. (2000) Reef fish assemblages: a re-evaluation using enclosed rotenone stations. *Marine Ecology Progress Series*, **206,** 227–237.

Ackerman, J.L. & Bellwood, D.R. (2002) Comparative efficiency of clove oil and rotenone for sampling tropical reef fish assemblages. *Journal of Fish Biology*, **60,** 893–901.

Bellwood, D.R. (1995) Direct estimate of bioerosion by two parrotfish species, *Chlorurus gibbus* and *C. sordidus*, on the Great Barrier Reef, Australia. *Marine Biology*, **121,** 419–429.

Bellwood, D.R. & Wainwright, P.C. (2002) The history and biogeography of fishes on coral reefs. *Coral reef fishes dynamics and diversity in a complex ecosystem* (ed. by P.F. Sale), pp. 5–32. Academic Press, San Diego, CA.

Bernardi, G., Robertson, D.R., Clifton, K.E. & Azzurro, E. (2000) Molecular systematics and evolutionary ecology of the Atlantic parrotfish genus *sparisoma*. *Molecular phylogenetics and Evolution*, **15,** 292–300.

Bohnsack, J.A., Harper, D.E. & McClellan, D.B. (1994) Fisheries trends from Monroe Country, Florida. *Bulletin of Marine Science*, **54,** 982–1018.

Bortone, S.A., Van Tassell, J., Brito, A., Falcón, J.M. & Bundrick, C.M. (1991) A visual assessment of the inshore fishes and fishery resources off El Hierro, Canary Islands: a baseline survey. *Scientia Marina*, **55,** 529–541.

Bowen, S.H., Lutz, E.V. & Ahlgren, M.O. (1995) Dietary protein as determinants of food quality: trophic strategies compared. *Ecology*, **76,** 899–907.

Bruckner, A.W., Bruckner, R.J. & Sollins, P. (2000) Parrotfish predation on live coral "spot biting" and "focusing biting". *Coral Reefs*, **19,** 50.

Bruggemann, J.H. (1994) Parrotfish grazing on coral reefs: a trophic novelty. PhD Thesis, University of Groningen, The Netherlands.

Carpenter, R.C. (1986) Partitioning herbivory and its effects on coral reef algal communities. *Ecological Monographs*, **56**, 345–363.

Cebrian, J. (2002) Variability and control of carbon consumption, export, and accumulation in marine communities. *Limnology and Oceanography*, **47**, 11–22.

Ceccarelli, D.M., Jones, G.P. & 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.

Choat, J.H. (1991) The biology of herbivorous fishes on coral reefs. *The ecology of fishes on coral reefs* (ed. by P.F. Sale), pp. 120–155. Academic Press, San Diego, CA.

Choat, J.H. & Clements, K.D. (1998) Vertebrate herbivores in marine and terrestrial environments: a nutritional perspective. *Annual Review in Ecology and Systematics*, **29**, 375–403.

Choat, J.H. & Schiel, D.R. (1982) Patterns of distribution and abundance of large brown algae and invertebrate herbivores in subtidal regions of northern New Zealand. *Journal of Experimental Marine Biology and Ecology*, **60**, 129–162.

Choat, J.H., Clements, K.D. & Robbins, W.D. (2002) The trophic status of herbivorous fishes on coral reefs. 1: dietary analyses. *Marine Biology*, **140**, 613–623.

Coleman, C.F., Koenig, C.C., Huntsman, G.R., Musick, J.A., Eklund, A.M., McGovern, J.C., Chapman, R.W., Sedberry, G.R. & Grimes, C.B. (2000) Long-lived reef fishes: the grouper-snapper complex. *Fisheries*, **25**, 14–20.

Costa, P.A.S., Braga, A.C. & Frota, L.O.R. (2003) Reef fisheries in Porto Seguro, eastern Brazilian coast. *Fisheries Research*, **60**, 577–586.

Dias, T.L.P., Rosa, I.L. & Feitoza, B.M. (2001) Food resource and habitat sharing by the three Western Atlantic surgeonfishes (Teleostei: Acanthuridae: *Acanthurus*) off Paraíba coast, north-eastern Brazil. *Aqua, Journal of Ichthyology and Aquatic Biology*, **5**, 1–10.

Ebeling, A.W. & Hixon, M.A. (1991) Tropical and temperate reef fishes: comparison of community structure. *The ecology of fishes on coral reefs* (ed. by P.F. Sale), pp. 509–563. Academic Press, San Diego, CA.

Ekau, W. & Knoppers, B. (1999) An introduction to the pelagic system of the north-east and east Brazilian shelf. *Archives of Fishery Marine Research*, **47**, 113–132.

Falcón, J.M., Bortone, S.A., Brito, A. & Bundrick, C.M. (1996) Structure of and relationships within and between the littoral, rock-substrate fish communities off four islands in the Canarian Archipelago. *Marine Biology*, **125**, 215–231.

Fasola, M., Canova, L., Foschi, F., Novelli, O. & Bressan, M. (1997) Resource use by a Mediterranean rocky slope fish assemblage. *P.S.Z.N. Marine Ecology*, **18**, 51–66.

Feitoza, B.M., Rocha, L.A., Luiz–Júnior, O.J., Floeter, S.R. & Gasparini, J.L. (2003) Reef fishes of St. Paul's Rocks: new records and notes on biology and zoogeography. *Aqua, Journal of Ichthyology and Aquatic Biology*, **7**, 61–82.

Ferreira, C.E.L. (1998) Resource partitioning by herbivores in a tropical rocky shore. PhD Thesis, Universidade Federal de São Carlos, São Paulo, Brazil. (in Portuguese)

Ferreira, C.E.L. & Gonçalves, J.E.A. (1999) The unique Abrolhos reef formation (Brazil): need for specific management strategies. *Coral Reefs*, **18**, 352.

Ferreira, B.P., Maida, M. & Souza, A.E.T. (1995) Levantamento inicial das comunidades de peixes recifais da região de Tamandaré – PE. *Boletin Técnico Científico CEPENE, Tamandaré*, **3**, 211–230.

Ferreira, C.E.L., Gonçalves, J.E.A., Coutinho, R. & Peret, A.C. (1998a) Herbivory by the dusky damselfish, *Stegastes fuscus* (Cuvier, 1830). *Journal of Experimental Marine Biology and Ecology*, **229**, 241–264.

Ferreira, C.E.L., Peret, A.C. & Coutinho, R. (1998b) Seasonal grazing rates and food processing by tropical herbivorous fishes. *Journal of Fish Biology*, **53**, 222–235.

Ferreira, C.E.L., Gonçalves, J.E.A. & Coutinho, R. (2001) Fish community structure and habitat complexity in a tropical rocky shore. *Environmental Biology of Fishes*, **61**, 353–369.

Floeter, S.R. & Gasparini, J.L. (2000) The southwestern Atlantic reef-fish fauna: composition and zoogeographic patterns. *Journal of Fish Biology*, **56**, 1099–1114.

Floeter, S.R. & Gasparini, J.L. (2001) The Brazilian endemic reef fishes. *Coral Reefs*, **19**, 292.

Floeter, S.R., Guimarães, R.Z.P., Rocha, L.A., Ferreira, C.E.L., Rangel, C.A. & Gasparini, J.L. (2001) Geographic variation in reef-fish assemblages along the Brazilian coast. *Global Ecology and Biogeography*, **10**, 423–433.

García-Charton, J.A. & Pérez-Ruzafa, A. (1998) Correlation between habitat structure and a rocky reef fish assemblage in the southwest Mediterranean. *P.S.Z.N. Marine Biology*, **19**, 111–128.

Gasparini, J.L. & Floeter, S.R. (2001) The shore fishes of Trindade Island, southwestern Atlantic. *Journal of Natural History*, **35**, 1639–1656.

Gasparini, J.L., Floeter, S.R. & Joyeux, J.C. (2003) *sparisoma tuiupiranga*, a new species of parrotfish (Perciformes: Labroidae: Scaridae) from Brazil, with comments on the evolution of the genus. *Zootaxa*, **384**, 1–14.

Gust, N., Choat, H.H. & Ackerman, J.L. (2002) Demographic plasticity in tropical reef fishes. *Marine Biology*, **140**, 1039–1051.

Harmelin-Vivien, M.L. (2002) Energetics and fish diversity on coral reefs. *Coral reef fishes: dynamics and diversity in a complex ecosystem* (ed. by P.F. Sale), pp. 265–274. Academic Press, San Diego, CA.

Hatcher, B.G. (1988) Coral reef primary productivity: a beggar's banquet. *Trends in Ecology and Evolution*, **3**, 106–111.

Hay, M.E. (1991) Fish-seaweed interactions on coral reefs: effects of herbivorous fishes and adaptations of their prey. *The ecology of fishes on coral reefs* (ed. by P.F. Sale), pp. 96–119. Academic Press, San Diego, CA.

Hobson, E.S. (1974) Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fishery Bulletin*, **72**, 915–1031.

Hobson, E.S. (1991) Trophic relationships of fishes specialised to feed on zooplankters above coral reefs. *The ecology of*

fishes on coral reefs (ed. by P.F. Sale), pp. 69–95. Academic Press, San Diego, CA.

Horn, M.H. (1989) Biology of marine herbivorous fishes. *Oceanography and Marine Biology: an Annual Review*, **27**, 167–272.

Humann, P. & Deloach, N. (2002) *Reef fish identification: Florida, Caribbean and Bahamas*. New World Publications, Jacksonville.

Isy-Schwart, M. (1954) *Hunting big fish*. Burke Publishing Co., London.

Jennings, S. & Lock, J.M. (1996) Population and ecosystem effects of reef fishing. *Reef fisheries* (ed. by N.V.C. Polunin and C.M. Roberts), pp. 193–218. Chapman & Hall, London.

Jones, G.P., Ferrel, D.J. & Sale, P.F. (1991) Fish predation and its impact on the invertebrates of coral reefs and adjacent sediments. *The ecology of fishes on coral reefs* (ed. by P.F. Sale), pp. 156–179. Academic Press, San Diego, CA.

Joyeux, J.C., Floeter, S.R., Ferreira, C.E.L. & Gasparini, J.L. (2001) Biogeography of tropical reef fish: the South Atlantic puzzle. *Journal of Biogeography*, **28**, 831–841.

La Mesa, G. & Vacchi, M. (1999). An analysis of the coastal fishes assemblage of the Ustica Island Marine Reserve (Mediterranean Sea). *P.S.Z.N. Marine Ecology*, **20**, 147–165.

Leão, Z.M.A.N. (1996) The coral reefs of Bahia: morphology, distribution and the major environmental impacts. *Anais da Academia Brasileira de Ciências*, **68**, 439–452.

Leão, Z.M.A.N. & Dominguez, J.M.L. (2000) Tropical coast of Brazil. *Marine Pollution Bulletin*, **41**, 112–122.

Leão, Z.M.A.N. & Kikuchi, R.K.P. (2001) The Abrolhos reefs of Brazil. *Ecological studies*, Vol. 144, Coastal Marine Ecosystems of Latin America (ed. by U. Seeliger and B. Kjerfve), pp. 83–96. Springer-Verlag, Berlin.

McCormick, M.I. (1995) Fish feeding mode on mobile benthic invertebrates: influence of spatial variability in habitat associations. *Marine Biology*, **49**, 317–323.

Maida, M. & Ferreira, B.P. (1997) Coral reefs of Brazil: an overview. *Proceedings of the 8th International Coral Reef Symposium, Panama*, **1**, 263–274.

Mazoldi, C. & Girolamo, M. (1997) Littoral fish community of the island Lampedusa (Italy): a visual census approach. *Italian Journal of Zoology*, **65**, 275–280.

Meekan, M.G. & Choat, J.H. (1997) Latitudinal variation in abundance of herbivorous fishes: a comparison of temperate and tropical reefs. *Marine Biology*, **128**, 373–383.

Moura, R.L. (1998) Activity, distribution and feeding tactics of a fish community from Atol das Rocas. MSc Thesis, Universidade de São Paulo, São Paulo. (in Portuguese)

Munday, P.L. (2002) Does variability determine geographical-scale abundances of coral-dwelling fishes? *Coral Reefs*, **21**, 105–116.

Munday, P.L. & Jones, G.P. (1998) The ecological implications of small body size among coral-reef fishes. *Oceanography and Marine Biology: an Annual Review*, **36**, 373–411.

Parrish, J.D. (1989) Fish communities of interacting shallow-water habitats in tropical oceanic regions. *Marine Ecology Progress Series*, **58**, 339–350.

Paul, V.J. (1992) Chemical defences of benthic marine invertebrates. *Ecological roles of marine natural products* (ed. by V.J. Paul), pp. 164–188. Cornel University Press, New York.

Pauly, D. (1990) On Malthusian overfishing. *Naga, the ICLARM Quarterly Journal*, **13**, 3–4.

Pauly, D. & Christensen, V. (1995) Primary production required to sustain global fisheries. *Nature*, **374**, 255–257.

Pawlik, J.R. (1993) Marine invertebrate chemical defences. *Chemical Reviews*, **93**, 1911–1922.

Pielou, E.C. (1984) *The interpretation of ecological data: a primer on classification and ordination*. John Wiley & Sons, Inc., New York.

Polunin, N.V.C. & Klumpp, D.W. (1992) Algal food supply and grazer demand in a very productive coral reef zone. *Journal of Experimental Marine Biology and Ecology*, **164**, 1–15.

Randall, J.E. (1967) Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography*, **5**, 665–847.

Roberts, C.M. (1995) Effects of fishing on the ecosystem structure of coral reefs. *Conservation Biology*, **9**, 988–994.

Roberts, C.M. (1997) Ecological advice for the global fisheries crisis. *Trends in Ecology and Evolution*, **12**, 35–38.

Rocha, L.A. (2003) Patterns of distribution and processes of speciation in Brazilian reef fishes. *Journal of Biogeography*, **30**, 1161–1171.

Rocha, L.A & Rosa, I.L. (2001) Baseline assessment of reef fish assemblages of Parcel Manuel Luiz Marine State Park, Maranhão, north-east Brazil. *Journal of Fish Biology*, **58**, 985–998.

Rocha, L.A., Rosa, I.L. & Feitoza, B.M. (2000) Sponge-dwelling fishes of northeastern Brazil. *Environmental Biology of Fishes*, **59**, 453–458.

Rocha, L.A., Bass, A.L., Robertson, D.R. & Bowen, B.W. (2002) Adult habitat preferences, larval dispersal, and the comparative phylogeography of three Atlantic surgeonfishes (Teleostei: Acanthuridae). *Molecular Ecology*, **11**, 243–252.

Rosa, R.S. & Moura, R.L. (1997) Visual assessment of reef fish community structure in the Atol das Rocas Biological Reserve, off northeastern Brazil. *Proceedings of the 8th International Coral Reef Symposium*, **1**, 983–986.

Russ, G.R. & Alcala, A.C. (1989) Effects of intense fishing pressure on an assemblage of coral reef fishes. *Marine Ecology Progress Series*, **56**, 13–27.

Sadovy, Y. (2001) The threat of fishing to highly fecund fishes. *Journal of Fish Biology*, **59**, 90–108.

Sala, E. & Boudouresque, C.F. (1997) The role of fishes in the organization of a Mediterranean sublittoral community. I: algae communities. *Journal of Experimental Marine Biology and Ecology*, **212**, 25–44.

Steneck, R.S. (1998) Human influences on coastal ecosystems: does overfishing create trophic cascade? *Trends in Ecology and Evolution*, **13**, 429–430.

Streelman, J.T., Alfaro, M., Westneat, M.W., Bellwood, D.R. & Karl, S.A. (2002) Evolutionary history of the parrotfishes: biogeography, ecomorphology, and comparative diversity. *Evolution*, **56**, 961–971.

Summerer, M., Janel, R. & Sturmbauer, C. (2001) Mitochondrial phylogeny and phylogeography affinities of seabreans of the genus *Diplodus* (Sparidae). *Journal of Fish Biology*, **10**, 1–23.

Thresher, R.E. (1983) Environmental correlates of the distribution of planktivorous fishes in the One Tree Reef lagoon. *Marine Ecology Progress Series*, **10**, 137–145.

Wainwright, P.C. & Bellwood, D.R. (2002) Ecomorphology of feeding in coral reef fishes. *Coral reef fishes: dynamics and diversity in a complex ecosystem* (ed. by P.F. Sale), pp. 33–55. Academic Press, San Diego, CA.

Willis, T.J. (2001) Visual census methods underestimate density and diversity of cryptic reef fishes. *Journal of Fish Biology*, **59**, 1408–1411.

Wilson, S.K., Bellwood, D.R., Choat, J.H. & 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.

Wood, R. (1999) *Reef evolution*. Oxford University Press, Oxford.

BIOSKETCHES

Dr Carlos Eduardo L. Ferreira works as a marine researcher at IEAPM Institute (Brazilian Navy), and has been dealing with various aspects of the ecology of Brazilian reefs and fishes for more than a decade.

Dr Sergio R. Floeter has been granted a post-doctoral fellowship by the National Center for Ecological Analysis and Synthesis, Santa Barbara, CA, USA, to work with the distributional data base for the tropical Atlantic reef fishes.

João Luiz Gasparini is affiliated to the Universidade Federal do Espírito Santo, and has been working for the last 15 years on the taxonomy, systematics and natural history of Brazilian reef fishes.

Dr Beatrice P. Ferreira is head professor in coral reef fish ecology and fishing at Pernambuco Federal University and is currently working in the development of marine protected areas in the north-eastern Brazil.

Dr Jean-Christophe Joyeux is a Professor of ecology at the Universidade Federal do Espírito Santo and is currently leading various projects on larval fish ecology.