Dynamics of fish assemblages on coral reefs subjected to different management regimes in the Abrolhos Bank, eastern Brazil

RONALDO BASTOS FRANCINI-FILHO[a,b,*] and RODRIGO LEÃO DE MOURA[b]

[a] *Grupo de Pesquisas em Recifes de Corais e Mudanças Globais, Universidade Federal da Bahia, Rua Caetano Moura 123, 40210-340 Salvador, BA, Brazil*

[b] *Conservation International Brazil, Marine Program, Rua das Palmeiras 451, 45900-000 Caravelas, BA, Brazil*

ABSTRACT

1. Marine protected areas (MPAs) range from multiple-use areas (MUA) to absolute no-take reserves (NTR). Despite their importance for fisheries management, there are few long-term studies comparing benefits from different types of MPAs within the same region.

2. Fish assemblages were monitored for five years (2001–2005) in the largest coral reefs in the South Atlantic (Abrolhos Bank, Brazil). Monitoring included one community-based MUA, two NTRs (one established in 1983 and another in 2001), and one unprotected area. Benthic assemblages at these areas, as well as fish assemblages on unprotected deeper reefs (25–35 m), were monitored from 2003 onwards.

3. Habitat characteristics strongly influenced fish assemblages' structure. This, together with the lack of data from before establishment of the MPAs, did not allow an unequivocal analysis of the effects of the MPAs.

4. Biomass of commercially important fish, particularly small carnivores, was higher in the older NTR. Biomass of black grouper *Mycteroperca bonaci* increased by 30-fold inside NTRs during the study period, while remaining consistently low elsewhere.

5. A single herbivore species, the parrotfish *Scarus trispinosus*, dominated fish assemblages (28.3% of total biomass). Biomass of this species increased in 2002 on the younger NTR and on the MUA, soon after establishment of the former and banning of the parrotfish fishery in the latter. This increase was followed by a decline from 2003 onwards, after increased poaching and reopening of the parrotfish fishery.

6. Fish biomass increased in 2002 across the entire region. This increase was stronger in sites closer to deeper reefs, where fish biomass was up to 30-times higher than shallow reefs: movement of fish from deeper to shallower areas may have played a role.

7. The effective use of MPAs in the Abrolhos Bank is still dependent on adequate enforcement and the protection of critical habitats such as deep reefs and mangroves.
Copyright © 2008 John Wiley & Sons, Ltd.

*Correspondence to: R. B. Francini-Filho, Rua das Palmeiras 451, 45900-000 Caravelas, BA, Brazil. E-mail: rofilho@yahoo.com

INTRODUCTION

Overfishing is one of the three most significant threats to coral reefs, as it causes dramatic and lasting negative effects on reef assemblages (Roberts, 1995a; Jennings and Lock, 1996). Worldwide, increases in fishing pressure over the past decade has caused a severe reduction in the abundance of target reef fish species (Hawkins and Roberts, 2004), changes in their size composition and life-history characteristics (Roberts and Polunin, 1993), shifts in trophic structure (Jennings et al., 1995), and interruption of key ecological processes (Bellwood et al., 2004).

Marine protected areas (MPAs) are a form of spatial resource management that regulates human activities at different levels, from multiple-use areas (where fishing and other types of exploitation may occur) to absolute no-take reserves (all types of exploitation prohibited) (Mora et al., 2006). The establishment of MPAs, particularly no-take reserves, is widely recognized as an important conservation and fisheries management tool (Roberts and Polunin, 1993; Chape et al., 2005). Increased protection may promote the recovery of critical fish spawning stock biomass (Roberts, 1995b; Russ and Alcala, 1996a), the re-establishment of critical ecological processes (Micheli et al., 2005), and the maintenance of adjacent fishing grounds via exportation of biomass (Russ and Alcala, 1996b; McClanahan and Mangi, 2000). Particular interest in using no-take reserves for managing tropical reef fisheries arose owing to the inefficiency of conventional management strategies, such as catch and effort restrictions (Polunin and Roberts, 1993; Russ and Alcala, 1996a). Despite some recent encouraging developments (Roberts et al., 2001; Russ et al., 2004), the ability of MPAs to conserve reef biodiversity and to sustain fish harvests over large spatial and temporal scales is still controversial (Willis et al., 2003; Sale et al., 2005; Walters et al., 2007).

Habitat characteristics are known to strongly influence fish assemblages and their response to fishing pressure (McClanahan and Arthur, 2001). For example, several studies have found a positive effect of coral cover and benthic complexity on the abundance and diversity of coral reef fish (Luckhurst and Luckhurst, 1978; Bell and Galzin, 1984). Therefore, a complex habitat with high coral cover may delay negative impacts of fishing and/or facilitate recovery of fish populations after initiation of protection. Fishing pressure may also modify habitat characteristics through direct and cascading processes. For example, overfishing of grazing parrotfish probably facilitated rapid shifts from coral to macroalgae-dominated benthic assemblages throughout the Caribbean (Hughes, 1994; Bellwood et al., 2004).

Spatial variability in habitat characteristics may lead to misleading interpretations on the effects of MPAs, especially so because bias in the process of establishing MPAs generally leads to the selection of areas with exceptionally high-quality or low-quality habitats (Edgar et al., 2004). Thus, the relative effects of MPAs and habitat characteristics on exploited populations can only be unequivocally evaluated when information from before and after initiation of protection is available and when monitoring includes both MPAs and control sites (Russ, 2002; Edgar et al., 2004).

Besides several biological aspects, the success of MPAs is also highly dependent on a number of socio-economic variables (Bunce et al., 1999; Russ and Alcala, 1999). For example, it has been emphasized that for any process of establishment and management of a given MPA to be successful it should be community-based (Russ and Alcala, 1999; Alcala and Russ, 2002). The idea behind community-based management is that a high degree of involvement of local people in the elaboration and implementation of regulations would lead to a better management of resources (Johannes, 1978). Despite the enthusiasm behind community-based MPA management, there are few long-term studies that compare ecological outcomes from community-based versus other types of management regimes within the same region (but see Russ and Alcala, 1999).

Brazilian reefs represent a priority area for biodiversity conservation in the Atlantic Ocean owing to their relatively high endemism levels (about 25% in fish and 50% in corals) concentrated in a small reef area (5% of West Atlantic reefs; Moura, 2002). Artisanal small-scale fisheries account for an estimated 70% of total fish landings on the eastern Brazilian coast (Cordell, 2006), where coral reefs are concentrated (Leão et al., 2003). Despite their importance, Brazilian reefs are increasingly suffering from overfishing, pollution, sedimentation, unplanned industrial development and intense tourism (Leão and Kikuchi, 2005; Marchioro et al., 2005; Dutra et al., 2006; Floeter et al., 2006).

This study aims to evaluate the effects of different types of MPAs on the structure and dynamics of reef fish assemblages in the Abrolhos Bank, eastern Brazil. The region encompasses the largest and richest coral reef complex in the South Atlantic Ocean and the oldest among the few networks of MPAs in the country. The units of this network were established at different times and show different management histories and protection levels, covering less than 10% of the total coral reef area of the Abrolhos Bank (Dutra et al., 2006). Given that MPAs, particularly no-take reserves, may represent the last viable option for the effective conservation of coral reefs, as well as for the sustainable management of reef fisheries, it is imperative to understand factors influencing their performance. Although an ad hoc zoning scheme may not constitute the perfect experiment, it can be treated as an experiment, as has been done here.

METHODS

Areas sampled and management regimes

The Abrolhos Bank (16° 40′/19° 40′S–39° 10′/37° 20′W) is a wide portion of the continental shelf (42 000 km²), with depths rarely exceeding 30 m and a shelf edge at about 70 m. Reef structures display a characteristic form of mushroom-shaped pinnacles, which attain 5 to 25 m in height and 20 to 300 m across their tops. Eight of the 16 reef corals commonly recorded in the Abrolhos Bank occur only in Brazil, and one species (*Mussismilia braziliensis*) is endemic to the Abrolhos region alone (Leão and Kikuchi, 2001). The reef and shore fish fauna includes about 270 species (Moura and Francini-Filho, 2006).

Monitoring of reef fish assemblages was undertaken from 2001 to 2005 in four areas (Figure 1), as follows: Area 1–No-take reserve of Timbebas Reef—Located within the National Marine Park of Abrolhos (NMPA), created by the Brazilian government in 1983. The NMPA comprises two discontinuous portions, one closer to shore and poorly enforced (Timbebas Reef), and another farther from shore and more intensively enforced (Abrolhos Archipelago and Parcel dos Abrolhos Reef). Poaching occurred frequently in Timbebas until 2001, but decreased between 2002 and 2003, when a short-term project sponsored by the Brazilian Government and non-governmental organizations (NGOs) promoted enforcement and an outreach campaign focused on local fishermen. Enforcement levels decreased in 2004, when the project ended and the nautical infrastructure (boats and equipments) of the NMPA deteriorated severely. Areas 2 and 3–Multiple-use and no-take zones of Itacolomis Reef—Itacolomis Reef is the largest reef complex (∼50 km²) within the Marine Extractive Reserve of Corumbau (MERC) (see Castro and Segal, 2001 for a description of this reef).
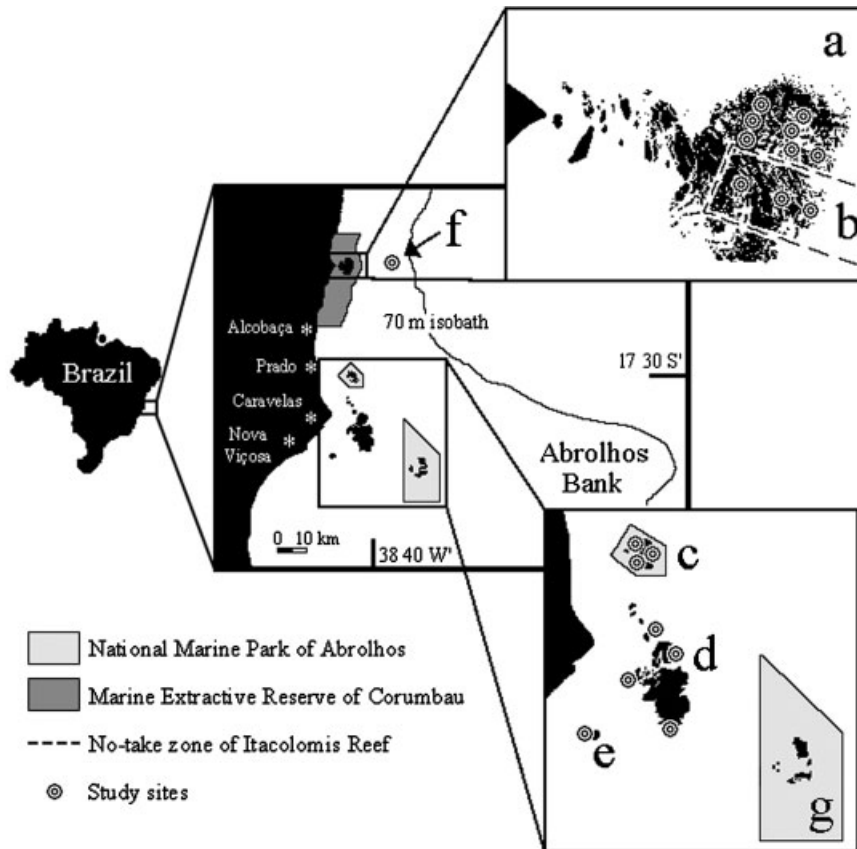

Figure 1. Map of the Abrolhos Bank showing MPAs and study sites. (a) Itacolomis Reef (multiple-use; established in 2000), (b) Itacolomis Reef (no-take; established in 2001), (c) Timbebas Reef (no-take; established in 1983), (d) Parcel das Paredes Reef (open access), (e) Sebastião Gomes Reef (open access), (f) Deep reefs (open access), (g) Abrolhos Archipelago and Parcel dos Abrolhos Reef (no-take; established in 1983). Main municipalities along the coast are highlighted: Alcobaça (∼200 fishing boats; 22 500 habitants), Caravelas (∼150 boats; 20 500 habitants), Nova Viçosa (∼40 boats and 34 100 habitants) and Prado (∼100 boats; 27 700 habitants).

The MERC is a co-managed MPA created in 2000 by the initiative of local fishermen with support from the Federal environmental agency (IBAMA) and NGOs (Moura *et al.*, 2007). Management practices are established through decisions of a deliberative council on which local fishermen occupy 50% plus one additional chair. Exploitation of marine resources is allowed only for locals, with rules of use (e.g. zoning and gear restrictions) defined by the council and endorsed by IBAMA. Fishing pressure decreased sharply after MERC's creation, owing to the banning of hundreds of fishers from neighbouring municipalities (mainly Alcobaça; see Figure 1). Aquarium trade and destructive fishing practices such as drive-nets above the reefs were prohibited. Only handlines, spears and various types of nets are still allowed. The parrotfish fishery was prohibited in the entire MERC from November 2001 to July 2002 through an informal agreement built by the local fishing community. The Itacolomis Reef is divided in two main zones: multiple-use (Area 2) and no-take (Area 3) (Figure 1). The no-take zone (~20% of Itacolomis Reef's total area) was established in November 2001, aiming to restore fish populations within its boundaries and sustain fish harvests on adjacent fishing grounds. Fishing pressure decreased sharply soon after its establishment, but increased again in 2003 because of increased poaching. Area 4–Open-access (i.e. unprotected) area — It encompasses two coastal reefs (Parcel das Paredes and Sebastião Gomes) subjected to the highest fishing pressure in the region (more than 200 boats from four municipalities operating regularly). Most frequent fishing gears are hand lines, spears and various types of nets. Although located within the State Protected Area Ponta da Baleia/Abrolhos (SPA), a MPA created by the Bahia State Government in 1993, the SPA has never been implemented and it is not staffed nor equipped, being in fact a 'paper park'.

One additional area on unprotected deeper reefs (25–35 m) was surveyed from 2003 to 2005 (Figure 1). Deeper reefs are composed of scattered drowned reefs surrounded by extensive flat plains covered by rhodoliths of calcareous algae and macroalgae.

Sampling design and field measurements

Samples were obtained from between three and seven sites within each area, except for deep reefs where only one site was sampled (Figure 1). Distance between adjacent sites ranged from 0.5 to 17 km. Each site was about 200 m in diameter and included one to three interconnected reef pinnacles. Surveys were always done in the summer (January–March), thus avoiding seasonal artefacts. Two habitats were sampled within each site: pinnacle tops (2–6 m depth) and walls (3–15 m depth). Fish counts were made using a nested stationary visual census technique adapted from Bohnsack and Bannerot (1986). Different size categories of fishes were counted in two

different sampling radii, with a size limit for individuals to be included in each count. Each sample started with an identification period of 5 min in which all species within a 4 m radius (defined by a tape rule laid immediately before censusing) were listed. After this period, quantitative data were recorded separately for each species. Individuals $\leqslant 10$ cm total length (TL) were counted in a 2 m radius, and recorded in two different size categories: $\leqslant 2$ and 2–10 cm. Individuals > 10 cm TL were counted in a 4 m radius, and recorded in four size categories: 10–20, 20–30, 30–40, > 40 cm. Individuals $\leqslant 2$ cm TL for small-bodied species ($\leqslant 25$ cm maximum TL) and individuals $\leqslant 10$ cm TL for large-bodied species (> 25 cm maximum TL) were not included in the analysis in order to reduce errors (Bellwood and Alcala, 1988). Extensive training in fish size estimation was undertaken prior to sampling with use of fish models to minimize operator variability (Samoilys, 1997). Between 15 and 20 samples were obtained per habitat per site per year, totaling 2820 samples during the entire study period.

Habitat measurements were undertaken from 2003 to 2005 at the same sites where fish assemblages were surveyed (except for deeper reefs). Benthic cover was estimated using two distinct methods, one for each habitat. Point-intercept lines (10 m length; 100 points) were haphazardly laid on pinnacle tops, and groups of four quadrats (50 × 50 cm; 25 intercepts) equally distributed within a 10 m line were haphazardly laid on pinnacle walls. Each group of quadrats was considered as a single sample. Organisms immediately below each point were recorded and classified as follows: algal turf, crustose calcareous algae, fleshy algae, live coral, octocoral, sea urchin and zoanthid. Topographic complexity on pinnacle tops was estimated with the deployment of a 10 m chain following all contours and crevices of the bottom. Surface length relative to linear chain length was used as an index of complexity (Luckhurst and Luckhurst, 1978). Eight benthic cover samples (four in each habitat) and four complexity samples were obtained per site per year.

Data analysis

Species were grouped as targeted and non-targeted by fisheries. Target species were further subdivided into three trophic categories: large carnivores, small carnivores and large herbivores (Table 1). Quantitative analyses were performed for each trophic category and for the most abundant target species ($> 1\%$ of total fish biomass). The 13 species retained for analysis belong to five families (Carangidae, Haemulidae, Lutjanidae, Scaridae and Serranidae) and represented 94% of total fish biomass recorded in this study (Table 1).

Fish counts were converted to biomass using length–weight relationships (Froese and Pauly, 2006). Estimates were calculated by multiplying the weight from the midpoint of

Table 1. Reef fish species recorded in the Abrolhos Bank from 2001 to 2005

Family/species	OF	TC	%
Synodontidae			
Synodus intermedius	N	—	0.7
Ogcocephalidae			
Ogcocephalus vespertilio	N	—	<0.1
Muraenidae			
Gymnothorax funebris	T	SC	<0.1
Gymnothorax moringa	T	SC	<0.1
Gymnothorax vicinus	T	SC	<0.1
Holocentridae			
Holocentrus ascensionis	N	—	0.15
Scorpaenidae			
Scorpaena brasiliensis	N	—	<0.1
Scorpaena plumieri	N	—	<0.1
Sphyraenidae			
Sphyraena barracuda	T	LC	0.9
Sphyraena guachancho	T	SC	<0.1
Serranidae			
Cephalopholis fulva	T	SC	<0.1
Epinephelus adscensionis	T	LC	<0.1
Epinephelus itajara	T	LC	<0.1
Epinephelus morio	T	LC	0.4
Mycteroperca bonaci	T	LC	1.5
Rypticus saponaceus	N	—	<0.1
Serranus baldwini	N	—	<0.1
Serranus flaviventris	N	—	0.1
Grammatidae			
Gramma brasiliensis	N	—	<0.1
Cirrhitidae			
Amblycirrhitus pinos	N	—	<0.1
Carangidae			
Carangoides bartholomaei	T	LC	0.4
Carangoides crysos	T	LC	1.9
Carangoides ruber	T	LC	0.2
Caranx latus	T	LC	<0.1
Pseudocaranx dentex	N	—	0.1
Lutjanidae			
Lutjanus analis	T	LC	<0.1
Lutjanus jocu	T	LC	2.7
Lutjanus synagris	T	LC	0.4
Lutjanus alexandrei	T	LC	<0.1
Ocyurus chrysurus	T	SC	3.1
Haemulidae			
Anisotremus moricandi	T	SC	<0.1
Anisotremus surinamensis	T	SC	0.6
Anisotremus virginicus	T	SC	1.9
Haemulon aurolineatum	T	SC	4.3
Haemulon parra	T	SC	0.8
Haemulon plumieri	T	SC	0.9
Haemulon squamipinna	T	SC	<0.1
Haemulon steindachneri	T	SC	<0.1
Sparidae			
Archosargus probatocephalus	T	SC	<0.1
Calamus pennatula	T	SC	0.1
Sciaenidae			
Odontoscion dentex	T	SC	<0.1
Mullidae			
Pseudupeneus maculatus	T	SC	0.2
Chaetodontidae			
Chaetodon sedentarius	N	—	<0.1
Chaetodon striatus	N	—	0.6
Pomacanthidae			
Holacanthus ciliaris	N	—	0.9

Table 1 (*continued*)

Family/species	OF	TC	%
Holacanthus tricolor	N	—	<0.1
Pomacanthus arcuatus	N	—	5.1
Pomacanthus paru	N	—	4.7
Pomacentridae			
Abudefduf saxatilis	N	—	2.5
Chromis jubauna	N	—	<0.1
Chromis marginata	N	—	<0.1
Microspathodon chrysurus	N	—	0.6
Stegastes pictus	N	—	<0.1
Stegastes spp.[†]	N	—	3.2
Ephippidae			
Chaetodipterus faber	T	SC	0.1
Labridae			
Bodianus pulchellus	T	SC	<0.1
Bodianus rufus	T	SC	<0.1
Clepticus brasiliensis	N	—	<0.1
Halichoeres brasiliensis	T	SC	0.3
Halichoeres dimidiatus	N	—	<0.1
Halichoeres penrosei	N	—	<0.1
Halichoeres poeyi	N	—	0.5
Thalassoma noronhanum	N	—	<0.1
Scaridae			
Cryptotomus roseus	N	—	<0.1
Scarus trispinosus	T	LH	28.3
Scarus zelindae	T	LH	0.9
Sparisoma amplum	T	LH	3.2
Sparisoma axillare	T	LH	3.1
Sparisoma frondosum	T	LH	1.5
Labrisomidae			
Labrisomus nuchipinnis	N	—	<0.1
Labrisomus cricota	N	—	<0.1
Malacoctenus sp.	N	—	<0.1
Gobiidae			
Coryphopterus spp.[‡]	N	—	0.2
Elacatinus figaro	N	—	<0.1
Bleniidae			
Ophioblennius atlanticus	N	—	<0.1
Parablennius marmoreus	N	—	<0.1
Scartella cf. *cristata*	N	—	<0.1
Acanthuridae			
Acanthurus bahianus	T	LH	2.5
Acanthurus chirurgus	T	LH	7.8
Acanthurus coeruleus	T	LH	9.8
Balistidae			
Balistes vetula	T	SC	0.3
Monacanthidae			
Aluterus scriptus	N	—	<0.1
Cantherhines macrocerus	N	—	<0.1
Cantherhines pullus	N	—	<0.1
Tetraodontidae			
Canthigaster figueiredoi	N	—	<0.1
Sphoeroides spengleri	N	—	<0.1
Diodontidae			
Diodon hystrix	N	—	0.1

Occurrence in fisheries (OF): T, target and N, non-target. Trophic category (TC): LH, large herbivores, LC, large carnivores and SC, small carnivores. Percentage of total biomass (%).
[†]Data pooled for *Stegastes fuscus* and *S. variabilis*.
[‡]Data pooled for *Coryphopterus dicrus*, *C. glaucofraenum* and *C. thrix*.

each size class by the number of fish per size category, and then summing size categories (cf. McClanahan and Kuanda-Arara, 1996). When length–weight information was not available, parameters from similarly sized congeners were used. Counts of benthic organisms were converted to percentages.

Analysis of variance (ANOVA) was used to evaluate spatial and temporal variations in fish biomass and habitat characteristics, with management areas and years as fixed factors. In order to satisfy ANOVA assumptions of normality and homoscedasticity, fish biomass was converted to log $(x + 1)$, while benthic cover percentages were converted 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 (MDS) ordination was used to summarize spatial and temporal similarities (Bray–Curtis) on the structure of target fish assemblages, and two-way analysis of similarities (ANOSIM) was used to evaluate significant differences according to management regimes and years (Clarke and Warwick, 1994).

Canonical correspondence analysis (CCA; ter Braak, 1996) was used to evaluate the influence of habitat characteristics on the structure of target fish assemblages. Two additional explanatory variables, latitude and distance offshore, were added to the habitat variables already described above. A forward selection procedure was used to select the five most important independent variables affecting fish assemblages. Fishing pressure was included as an explanatory variable in a second CCA run, with sites dummy-coded as follows: 1 for the older no-take reserve, 2 for the younger no-take reserve, 3 for multiple-use reefs and 4 for open-access reefs.

RESULTS

Fish assemblages

In total, 90 species of fishes belonging to 30 families were recorded (Table 1), representing nearly 60% of the known reef fish species pool of the Abrolhos Bank (Moura and Francini-Filho, 2006). Predominant target species in terms of biomass ($>1\%$ of total fish biomass) are shown in Table 1. Large herbivorous fish dominated (71.4% of total target fish biomass), followed by small carnivores (16.4%) and large carnivores (12.2%).

Total biomass of both target and non-target fish was higher in the older no-take reserve (Timbebas Reef) (Tables 2 and 3), but different responses were observed when species and trophic categories were analysed separately. Biomass of small carnivores was notably higher in Timbebas Reef than elsewhere (Figure 2(c)), as was the biomass of two parrotfish (*Sparisoma amplum* and *S. frondosum*), the yellowtail snapper *Ocyurus chrysurus* (Figure 3(a)) and the blue surgeonfish *Acanthurus coeruleus* (Table 3). Biomass of large carnivores, particularly that of the dog snapper *Lutjanus jocu* (Figures 2(b) and 3(d)), as well as the biomass of the parrotfish *Sparisoma axillare* was higher on open-access reefs. Biomass of the parrotfish *Scarus trispinosus* increased sharply between 2001 and 2002 on the multiple-use and the no-take zones of Itacolomis Reef, but decreased on the former from 2003 on, and on the latter from 2004 on (Figure 3(c)). Biomass of the black grouper *Mycteroperca bonaci* increased 30-fold inside the two no-take reserves during the study period, remaining consistently low in other areas (Figure 3(b)). An opposite

Table 2. Analysis of variance (ANOVA) testing the effect of reef areas and years on reef fish biomass

Species	Reef area (df = 3)		Year (df = 4)		Reef area × year (df = 12)	
	F	P	F	P	F	P
Acanthurus bahianus	17.35	***	5.98	***	2.13	*
Acanthurus chirurgus	3.37	*	7.63	***	2.84	***
Acanthurus coeruleus	36.49	***	2.40	***	2.40	**
Carangoides crysos	2.46	ns	4.70	***	3.19	***
Anisotremus virginicus	54.48	***	2.45	*	1.19	ns
Haemulon aurolineatum	114.30	***	26.15	***	3.65	***
Lutjanus jocu	81.92	***	5.98	***	3.64	***
Ocyurus chrysurus	221.39	***	11.70	***	5.45	***
Scarus trispinosus	9.64	***	7.16	***	3.98	***
Sparisoma amplum	8.52	***	1.84	ns	5.36	***
Sparisoma axillare	11.66	***	4.53	**	2.12	*
Sparisoma frondosum	105.01	***	4.59	**	2.17	*
Mycteroperca bonaci	7.29	***	3.41	**	3.11	***
Large herbivores	35.11	***	9.77	***	3.28	***
Large carnivores	34.23	***	10.73	***	4.28	***
Small carnivores	194.86	***	20.91	***	1.67	ns
Total target	97.37	***	18.81	***	2.77	***
Total non-target	27.22	***	8.36	***	0.87	ns

$*P < 0.05$, $**P < 0.01$, $***P < 0.001$, ns — not significant.

Table 3. Significant differences in fish biomass according to reef areas and years, as determined by Student–Newman–Keuls (SNK) *post-hoc* comparisons (groups arranged in decreasing order of fish biomass)

Species	SNK	
	Reef area	Year
Acanthurus bahianus	NTO = OA > NTN = MU	05 = 04 = 02 = 03 > 03 = 01
Acanthurus chirurgus	NTO = MU = OA > OA = NTN	02 > 05 = 04 > 04 = 03 = 01
Acanthurus coeruleus	NTO > OA > MU = NTN	02 > 05 = 03 = 04 = 01
Carangoides crysos	ns	02 > 01 = 05 = 03 = 04
Anisotremus virginicus	OA = NTO > MU > NTN	02 = 04 = 03 > 04 = 03 = 05 = 01
Haemulon aurolineatum	OA = NTO > MU > NTN	02 > 04 = 03 = 01 > 05
Lutjanus jocu	OA > NTO = NTN = MU	02 = 05 = 03 > 05 = 03 = 04 > 03 = 04 = 01
Ocyurus chrysurus	NTO > OA > NTN = MU	04 = 02 > 05 = 03 = 01
Scarus trispinosus	NTN > MU = NTO = OA	02 = 03 = 05 > 03 = 05 = 04 > 04 = 01
Sparisoma amplum	NTO > NTN = MU = OA	ns
Sparisoma axillare	OA > MU > NTO = NTN	02 = 04 = 05 > 03 > 01
Sparisoma frondosum	NTO > OA > MU = NTN	04 = 05 = 02 > 05 = 02 = 01 = 03
Mycteroperca bonaci	NTN > NTO = MU > OA	04 = 05 = 02 = 03 > 02 = 03 = 01
Large herbivores	NTN = MU = NTO > OA	02 > 04 = 03 = 05 > 01
Large carnivores	OA > NTN = NTO = MU	02 = 05 > 05 = 04 > 04 = 03 > 03 = 01
Small carnivores	NTO > OA > MU > NTN	02 > 04 > 03 > 01 = 05
Total target	NTO > OA > NTN = MU	02 > 04 = 03 > 03 = 05 > 01
Total non-target	NTO > OA > MU > NTN	02 > 03 = 01 = 05 = 04

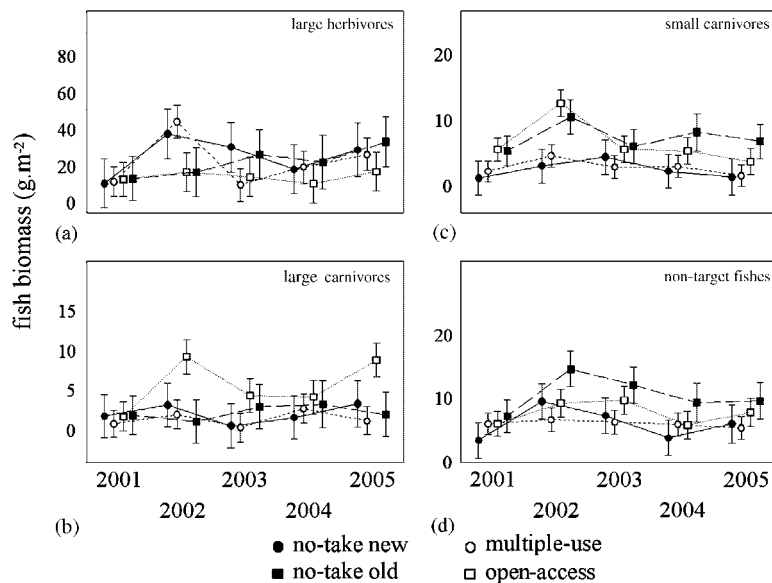Reef areas: no-take old (NTO), no-take new (NTN), multiple-use (MU) and open-access (OA). ns — not significant.

Figure 2. Biomass (mean ± 95% confidence limits) of target and non-target reef fish in four areas over 5 years. Target fish are grouped according to trophic category.

pattern (i.e. increases only on unprotected reefs) was recorded for *S. axillare* and *L. jocu* (Figure 3d). Interaction between management area and year was significant for most species, except for the haemulid *Anisotremus virginicus*, indicating that spatial variation related to management regimes was not consistent through time in most cases (Tables 2 and 3).

The structure of target reef fish assemblages differed significantly according to management regime (ANOSIM global test: $R = 0.21$; $P = 0.001$). Only the two adjacent management zones within Itacolomis Reef (multiple-use and no-take) were not significantly different from each other (pairwise comparison: $P > 0.05$). The stress value associated
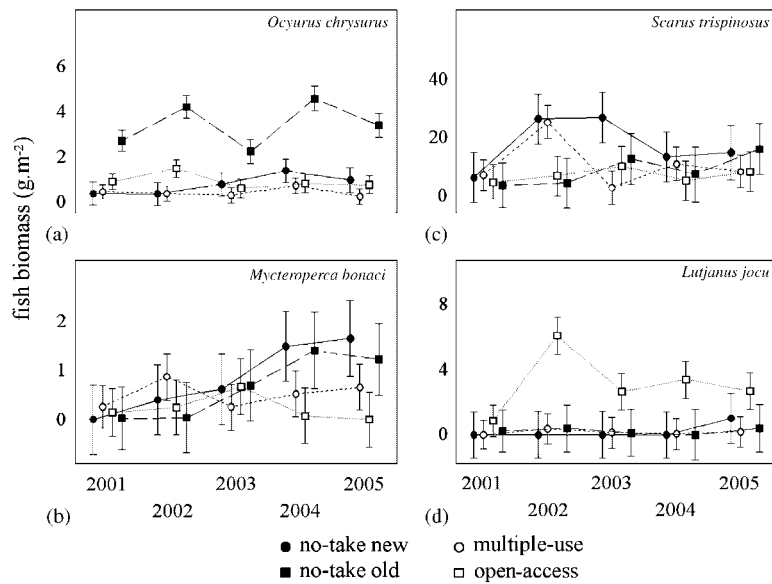
Figure 3. Biomass (mean ± 95% confidence limits) of four primary target reef fish species in four areas over 5 years.
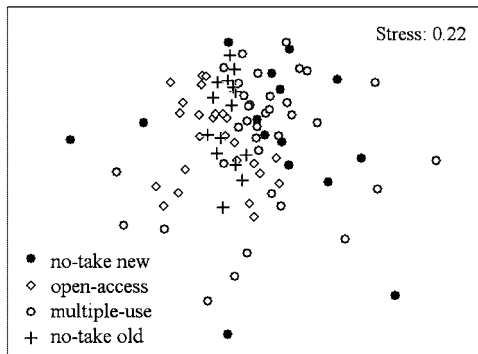

Figure 4. Multidimensional scaling (MDS) of 18 sites over 5 years based on Bray–Curtis similarities of reef fish assemblages.
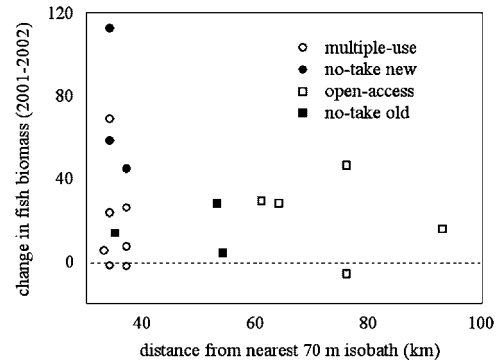

Figure 5. Relationship between distance from deeper reefs (nearest 70 m isobath) and absolute change in reef fish biomass at 18 sites between 2001 and 2002. Negative values (sites below dashed line) indicate inter-annual decrease in fish biomass and positive values (sites above dashed line) indicate increase.

with the final MDS plot (0.22) indicates that the final solution was useful for explaining the relationship between sites (Clarke and Warwick, 1994). However, a high overlap among sites was noted in the two-dimensional plot, particularly for the two management zones within Itacolomis Reef (Figure 4), indicating only slight differences related to management regimes.

Biomass of both target and non-target fish increased sharply between 2001 and 2002 throughout the entire region (see Figure 2). In general, this increase was more pronounced on sites closer to deeper reefs (as measured by the distance

from the nearest 70 m isobath) (Figure 5). Despite the significant temporal variation in the biomass of most species (Table 2), no significant temporal variation was detected in the structure of target fish assemblages as a whole ($R = 0.03$; $P = 0.13$).

Additional surveys from 2003 to 2005 showed that unprotected deeper reefs contained up to 30 times greater biomass of target fish than shallow coastal areas, with SNK post-hoc comparisons detecting significantly greater values of biomass on deeper reefs for the three trophic categories (Figure 6; one-way ANOVA: $P < 0.001$ in all cases).
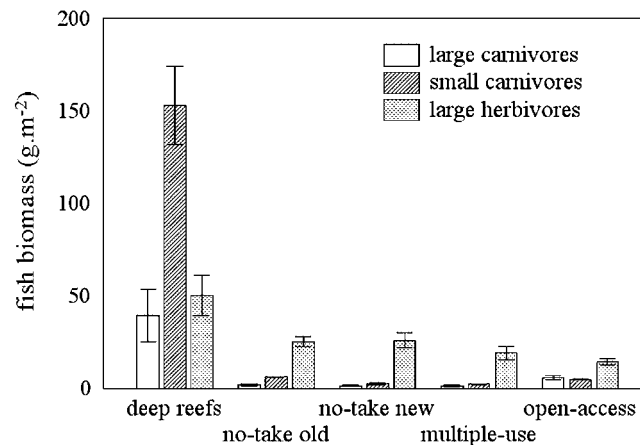
Figure 6. Biomass (mean ± SE) of target reef fish in five areas. Data pooled for three consecutive years (2003–2005).

Table 4. Analysis of variance (ANOVA) testing the effect of reef areas and years on habitat characteristics

Category	Reef area (df = 3)		Year (df = 2)		Reef area × year (df = 6)	
	F	P	F	P	F	P
Calcareous algae	29.23	***	8.44	***	0.97	ns
Complexity	3.81	*	0.13	ns	1.37	ns
Fleshy algae	17.89	***	1.46	ns	1.81	ns
Live coral	31.26	***	0.17	ns	0.63	ns
Octocoral	3.27	*	0.68	ns	1.08	ns
Turf algae	10.63	***	2.69	ns	2.60	*
Sea urchin	8.06	***	0.58	ns	1.92	ns
Zoanthid	15.20	***	0.31	ns	1.84	ns

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ns — not significant.

Table 5. Significant differences in habitat characteristics according to reef areas and years, as determined by Student–Newman–Keuls (SNK) *post-hoc* comparisons (groups arranged in decreasing order of benthic cover/complexity)

Category	SNK	
	Reef area	Year
Calcareous algae	OA = NTO = NTN > MU	03 = 05 > 04
Complexity	OA = NTO > NTO = MU = NTN	ns
Fleshy algae	MU = NTN > OA = NTO	ns
Live coral	OA > NTO > MU > NTN	ns
Octocoral	OA = MU = NTO > NTN	ns
Turf algae	MU = NTN = NTO > OA	ns
Sea urchin	NTN > MU = OA = NTO	ns
Zoanthid	NTO = OA > NTN > MU	ns

Reef areas: no-take old (NTO), no-take new (NTN), multiple-use (MU) and open-access (OA). ns — not significant.

Habitat characteristics

Turf algae (35.9%) was the dominant benthic cover type in all areas over the three years of benthic monitoring (2003–2005), followed by fleshy algae (13.8%), live corals (13.3%), crustose calcareous algae (12.4%), zoanthids (11.3%), octocorals (1.2%) and sea urchins (0.4%). All benthic cover categories, as well as benthic complexity differed significantly between management areas. Significant interannual variability was detected only for crustose calcareous algal cover, which decreased in 2004 and increased again in 2005 (Tables 4 and 5).

Benthic complexity and zoanthid cover were higher in the older no-take reserve (Timbebas Reef) and in the open-access area, while live coral cover was higher in the open-access area, followed by the older no-take reserve. The two management zones within Itacolomis Reef (no-take and multiple-use) were characterized by a relatively high cover of fleshy algae, turf algae and sea urchins, lower coral and octocoral cover, as well

as lower benthic complexity. Some sites were dominated (>50% of relative cover) by fleshy brown algae (mainly *Dictyota* and *Sargassum*) (Figure 7). Considering all sites, a significant negative relationship between live coral and fleshy algal cover was recorded in 2003. This negative relationship became not significant in 2004 and disappeared in 2005, mainly due to a decrease in fleshy algal cover in two sites within the no-take zone of Itacolomis Reef and one site within its multiple-use zone (Figure 7(a)). Biomass of large herbivores increased significantly within two of these three sites between 2003 and 2005 (Figure 7(b)).

Influence of habitat characteristics and fishing pressure on fish assemblages

Results from the first CCA run (only habitat characteristics included) showed that depth, latitude, distance offshore, fleshy algal cover and live coral cover were, in decreasing order, the
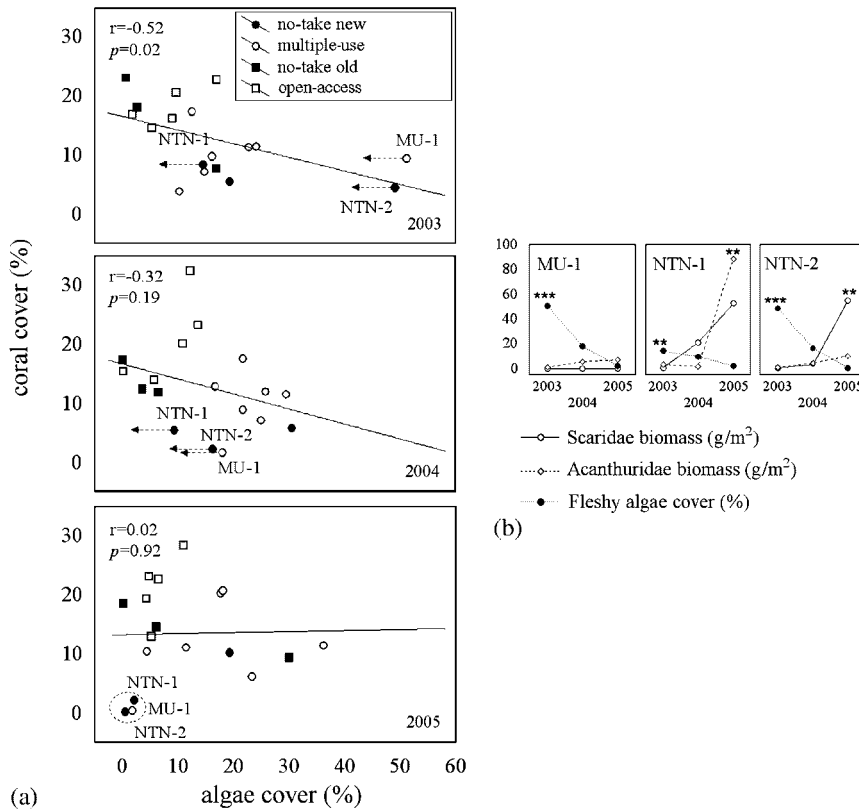
Figure 7. (a) Relationship between fleshy algae cover and coral cover in 18 sites over 3 years. (b) Temporal change in biomass of large herbivorous fishes (Acanthuridae and Scaridae) and fleshy algae cover in three selected sites. (NTN) no-take new and (MU) multiple-use.
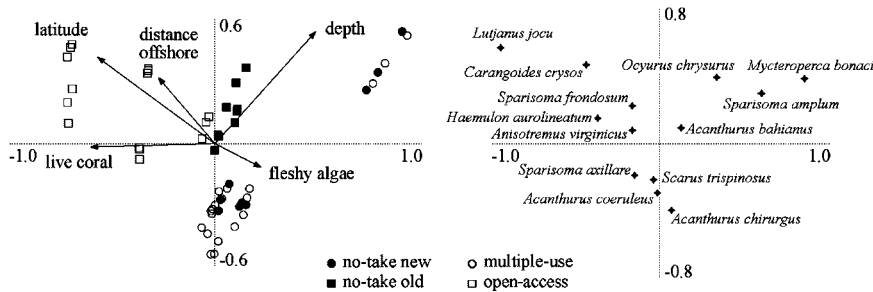

Figure 8. Canonical correspondence analysis (CCA) plot showing (a) relationship between habitat variables (arrows) and the 18 monitored sites over 5 years, and (b) distribution of 13 target reef fish species in the two-dimensional ordination space.

main predictors of fish assemblage structure. The first two axes explained 76.2% of the relationship between habitat characteristics and fish assemblage structure. The CCA plot showed that sites were distributed along two main axes, one related to depth, and another to a gradient in which high fleshy algal cover is to one side and high coral cover, high latitude and greater distance offshore are to the other (Figure 8(a)). Sites within the no-take reserve of Timbebas

Reef were near the interception of the two axes, showing intermediate levels of coral and fleshy algal cover, as well as depth, latitude and distance offshore. Sites within the open-access area were more distant offshore and concentrated in the southern portion of the Abrolhos Bank (i.e. higher latitude), showing high levels of coral cover and intermediate depths. Sites within the multiple-use and the no-take zones of Itacolomis Reef showed a high overlap in the ordination

space, with their strongest response varying with depth. Most sites at Itacolomis Reef were relatively shallow (except for two deeper sites between 15 and 20 m) and dominated by fleshy algae (Figure 8(a)).

Target fish species showed different habitat association patterns. Five species (*A. virginicus*, *C. crysos*, *H. aurolineatum*, *L. jocu* and *S. frondosum*) were associated with middle-depth sites and intermediate to high levels of coral cover; *A. bahianus*, *M. bonaci*, *O. chrysurus* and *S. amplum* with deeper sites and intermediate to high levels of fleshy algal cover; *A. coeruleus*, *S. trispinosus* and *S. axillare* with shallower sites and intermediate levels of coral and fleshy algal cover; *A. chirurgus* with shallower sites and high fleshy algal cover (Figure 8(b)).

When fishing pressure was included as an explanatory variable (second CCA run), 77.5% of the relationship between independent variables and fish assemblage structure was explained by the first two axes. Depth, latitude, distance offshore, fishing pressure and live coral cover became, in decreasing order, the main predictors of reef fish assemblage structure.

DISCUSSION

This is the first temporal analysis of reef fish monitoring data in Brazil covering areas under different management regimes within a single biogeographical unit (Abrolhos Bank). Marine zoning on the Abrolhos shelf is extensive, and allows this region to be considered as a 'marine management area' (MMA) with at least the beginnings of a holistic management plan. Although experimental conditions were not homogeneous for the entire time of this study, with low and/or unstable compliance levels, the results obtained suggest that under adequate enforcement, impacts of fishing were apparently attenuated in totally and partially protected tiles within the MMA mosaic. However, it is important to note that a great amount of variability in the structure of reef fish assemblages was explained by variability in habitat characteristics, particularly depth, latitude and distance offshore. This strong influence of habitat, together with the lack of data from before the establishment of the MPAs indicate that inferences on the effects of MPAs must be made with caution, since many of the observed patterns may be attributed also to intrinsic differences between the monitored areas (Russ, 2002; Edgar *et al.*, 2004).

Supposed benefits derived from protection include higher biomass of several target species, particularly small carnivores, in the older no-take reserve (Timbebas Reef), and a 30-fold increase in the biomass of the black grouper *Mycteroperca bonaci* inside the two no-take reserves during the study period. Despite these benefits, some results were contrary to the prediction of increased biomass of target fish within MPAs. For example, biomass of the dog snapper *Lutjanus jocu*, the most abundant large carnivorous fish, as well as the biomass of the parrotfish *Sparisoma axillare*, was relatively higher on open-access reefs. In addition, biomass of these two species increased significantly in the open-access area from 2002 onwards, remaining consistently low elsewhere. Possible explanations include greater habitat integrity on open-access reefs, coupled with habitat preferences by these two species that showed unexpected responses. Coral cover and benthic complexity were higher on open-access reefs, while fleshy and turf algae cover were lower. Results from the CCA showed that both *L. jocu* and *S. axillare* were preferentially associated with sites with intermediate to high levels of coral cover.

Regional differences in habitat characteristics clearly influenced other trends observed in the present study. Coral cover and benthic complexity were higher in the same areas (older no-take reserve and open-access area) in which target fish biomass was higher. In addition, the multiple-use and the no-take zones of Itacolomis Reef presented extremely low levels of fish biomass for most species, as well as poor habitat conditions (as indicated by the relatively high fleshy algae cover, as well as low coral cover and benthic complexity). Itacolomis Reef is also closer to land in comparison with the other monitored areas, resulting in an extremely high influx of terrigenous sediment (34–78 mg cm^{-2} day^{-1}; Garzón-Ferreira *et al.*, 2002), which may lead to detrimental effects on the reef community (Dodge and Vaisnys, 1977; McClanahan and Obura, 1997).

Some negative changes were detected following certain community-based decisions and events of compliance failure. For example, biomass of the parrotfish *Scarus trispinosus*, the most abundant target species in the region, increased sharply between 2001 and 2002 on the newer no-take reserve and on the multiple-use area, soon after initiation of protection in the former and the banning of the parrotfish fishery in the latter. This increase was followed by a sharp decline from 2003 on, after poaching levels increased in the no-take reserve and local fishermen decided to reopen the parrotfish fishery in the multiple-use area. These results indicate that legal protection alone, without effective enforcement and continued engagement from the local fishing communities on the implementation of regulations, is not enough to guarantee the success of MPAs. In fact, MPAs worldwide are rarely accompanied by effective enforcement (Mora *et al.*, 2006), which may seriously compromise people's willingness to employ them as a fisheries management tool in the long term.

Brazilian reefs are characterized by an impoverished fauna, but with a high proportion of endemic species concentrated in a small area (Moura, 2002). This low species richness implies a limited functional redundancy when Brazilian reefs are compared with other species-rich regions (e.g. Caribbean and

central Indo-Pacific). Under these special conditions there is a greater chance of losing critical ecosystem functions due to overfishing, as few species will be available to replace possible losses within functional groups (Bellwood *et al.*, 2004). A disproportionately low redundancy is noted for large-bodied parrotfish. Only five species occur in Brazil, while there are at least ten such large-bodied parrotfish in the Caribbean (Moura *et al.*, 2001). Moreover, only one species, *S. trispinosus*, contributed 76.6% of total parrotfish biomass in the Abrolhos Bank. Given that grazing intensity is expected to increase with parrotfish biomass (Mumby, 2006), algae removal by fish in Abrolhos may strongly rely on the foraging activity of *S. trispinosus*, highlighting the disproportional contribution of a single species to the resilience of these reefs.

Overfishing of parrotfishes is one of the most important issues related to coral reef conservation worldwide (Hughes, 1994; Pandolfi *et al.*, 2003; Mumby, 2006). In the Abrolhos Bank the situation is no different, with parrotfish increasingly contributing to fishery yields, especially because other traditional resources such as serranids and lutjanids are becoming scarce (Costa *et al.*, 2005). *Scarus trispinosus* is not a traditional fishery resource, and was not used even for subsistence a decade ago. Spearfishing was introduced in the region in the early 1980s as a recreational activity, and commercial spearfishing dates back only to the 1990s. However, in the last five years *S. trispinosus* has become one of the most important fishery resources and is now being sold to regional markets in the nearest larger cities (e.g. Vitória and Porto Seguro), and even overseas (authors' personal observations). Overfishing of this and other large herbivorous fish is possibly contributing to the high fleshy algal cover ($> 50\%$) recorded at some reefs, and although more detailed information is needed to clarify factors influencing algal overgrowth, precaution in managing the parrotfish fishery must be urgently introduced.

Fish biomass increased sharply between 2001 and 2002 across the entire region (Figure 2). This increase was more pronounced on sites closer to deeper reefs (Figure 5). Data on size structure of fish and long-term information on the abundance of young of the year individuals indicate that variability in recruitment was not a plausible explanation for such an increase. No mass recruitment events were detected in this period and most individuals recorded in 2002 were relatively large ($\geqslant 20$ cm TL) (Francini-Filho and Moura, unpublished data). The additional surveys undertaken from 2003 to 2005 showed that the biomass of target fish is up to 30-times higher on deeper reefs than shallower coastal areas (Figure 6). Thus, regional-scale movements of fish from deeper to shallower areas may have played an important role in this unique event during the 5 years of monitoring. McClanahan and Mangi (2000) presented evidence of movement of exploitable fish from deeper reefs to a shallow protected area

in Kenya, highlighting the role of deeper reefs in sustaining fish populations in coastal areas. There is a clear need to enhance knowledge on the scale and patterns of reef fish movement, and to better estimate not only the rates of fish spillover from no-take reserves, but also the rates of spill in from neighbouring habitats (Sale *et al.*, 2005).

The World Summit on Sustainable Development, the World Conservation Union (IUCN) Commission on Protected Areas, and the Convention on Biological Diversity have all called for the establishment of an effective global system of MPAs network by the year 2012. Although Brazil is committed to this target, there have been few studies on the effects of MPAs in this country (Floeter *et al.*, 2006). Results from the present study indicate that despite some positive signs at a local scale, the effective use of MPAs as fishery management tools in the Abrolhos Bank is still dependent on a larger network of MPAs with adequate enforcement and including several critical but still unprotected habitats such as deep reefs and mangroves (McClanahan and Mangi, 2000; Mumby *et al.*, 2004). At present, only 2% of the Abrolhos Bank are set as no-take, and even this small fraction still lacks adequate enforcement. In addition, the fragile marine and coastal habitats within the region are highly threatened by oil development, channel dredging and shrimp-farming projects in the mangroves, as well as by a steady increase in fishing effort (Leão and Kikuchi, 2005; Marchioro *et al.*, 2005; Dutra *et al.*, 2006). Larger and better-equipped boats are coming to the Abrolhos Bank from the north-eastern and south-eastern coasts, where fish stocks are already depleted owing to habitat degradation, mismanagement, and overall open-access regimes (Costa *et al.*, 2005; authors' personal observations). Thus, a planned increase in the number of MPAs, adequate implementation of the existing MPAs, as well as the implementation of some other forms of management outside MPAs (e.g. restriction of parrotfish catches and markets) should be part of the agenda of governmental, nongovernmental and multilateral development organizations aiming to conserve and use in a sustainable manner the unique biodiversity of the Abrolhos Bank. Community engagement, as well as outreach and long-term monitoring programmes, are equally important and must be on the priority list for urgent action.

REFERENCES

Alcala A, Russ G. 2002. Role of socioeconomic factors in coral reef protection and management. *Proceedings of the 9th International Coral Reef Symposium*, vol. 1; 29–32.

Bell JD, Galzin R. 1984. Influence of live coral cover on coral reef fish communities. *Marine Ecology Progress Series* **15**: 265–274.

Bellwood DR, Alcala AC. 1988. The effect of a minimum length specification on visual estimates of density and biomass of coral reef fishes. *Coral Reefs* **7**: 23–27.

Bellwood DR, Hughes TP, Folke C, Nÿstrom M. 2004. Confronting the coral reef crisis. *Nature* **429**: 827–833.

Bohnsack JA, Bannerot SP. 1986. A stationary visual census technique for quantitatively assessing community structure of coral reef fishes. NOAA Technical Report 41, Washington DC.

Bunce L, Gustavson K, Williams J, Miller M. 1999. The human side of reef management: a case study analysis of the socioeconomic framework of Montego Bay Marine Park. *Coral Reefs* **18**: 369–380.

Castro CB, Segal B. 2001. The Itacolomis: large and unexplored reefs at the arrival point of the first Europeans in Brazil. *Coral Reefs* **20**: 18.

Chape S, Harrison J, Spalding M, Lysenko I. 2005. Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. *Philosophical Transactions of the Royal Society of London* **360**: 443–455.

Clarke KR, Warwick RM. 1994. *Change in Marine Communities*: *An Approach to Statistical Analysis and Interpretation*. Plymouth Marine Laboratory: Plymouth.

Cordell J. 2006. Brazil: dynamics and challenges of marine protected area development and coastal protection. In *Scaling up Marine Management*: *The Role of Marine Protected Areas*. The World Bank: Washington DC; 58–77.

Costa PAS, Martins AS, Olavo G (eds). 2005. *Pesca e potenciais de exploração de recursos vivos na região central da Zona Econômica Exclusiva Brasileira*. Série Livros, Documentos REVIZEE/Score Central: Rio de Janeiro.

Dodge RE, Vaisnys JR. 1977. Coral population and growth patterns: responses to sedimentation and turbidity associated with dredging. *Journal of Marine Research* **35**: 715–730.

Dutra GF, Allen GR, Werner T, McKenna SA (eds). 2006. A rapid marine biodiversity assessment of the Abrolhos Bank, Bahia, Brazil. RAP Bulletin of Biological Assessment 38. Conservation International: Washington DC.

Edgar GJ, Bustamante RH, Farina JM, Calvopina M, Martinez C, Toral-Granda MV. 2004. Bias in evaluating the effects of marine protected areas: the importance of baseline data for the Galapagos Marine Reserve. *Environmental Conservation* **31**: 212–218.

Floeter SR, Halpern BS, Ferreira CEL. 2006. Effects of fishing and protection on Brazilian reef fishes. *Biological Conservation* **128**: 391–402.

Froese R, Pauly D (eds). 2006. *FishBase*. http://www.fishbase.org. Version13 June 2006.

Garzón-Frreira J, Cortés J, Croquer A, Guzmán H, Leão ZMAN, Rodríguez-Ramírez A. 2002. Status of coral reefs in southern tropical America in 2000-2002: Brazil, Colombia, Costa Rica, Panama and Venezuela. In *Status of Coral Reefs of the World*: *2002*, Wilkinson C (ed.). Australian Institute of Marine Science: Townsville; 343–360.

Hawkins JP, Roberts CM. 2004. Effects of artisanal fishing on Caribbean Coral Reefs. *Conservation Biology* **18**: 215–226.

Hughes TP. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* **265**: 1547–1551.

Jennings S, Lock JM. 1996. Population and ecosystem effects of reef fishing. In *Reef Fisheries*, Polunin NVC, Roberts CM (eds). Chapman & Hall: London; 193–218.

Jennings S, Grandcourt EM, Polunin NVC. 1995. The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. *Coral Reefs* **14**: 225–235.

Johannes RE. 1978. Traditional marine conservation methods in Oceania and their demise. *Annual Review of Ecology and Systematics* **9**: 349–364.

Leão ZMAN, Kikuchi RKP. 2001. The Abrolhos Reefs of Brazil. In *Coastal Marine Ecosystems of Latin America*, Seeliger U, Kjerfve B (eds). Springer-Verlag: Berlin; 83–96.

Leão ZMAN, Kikuchi RKP. 2005. A relic coral fauna threatened by global changes and human activities, Eastern Brazil. *Marine Pollution Bulletin* **51**: 599–611.

Leão ZMAN, Kikuchi RKP, Testa V. 2003. Corals and coral reefs of Brazil. In *Latin America Coral Reefs*, Cortés J (ed.). Elsevier Science: Amsterdam; 9–52.

Luckhurst BE, Luckhurst K. 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Marine Biology* **49**: 317–323.

Marchioro GB, Nunes MA, Dutra GF, Moura RL, Pereira PGP. 2005. Avaliação dos impactos da exploração e produção de hidrocarbonetos no Banco dos Abrolhos e adjacências. *Megadiversidade* **1**: 225–310.

McClanahan TR, Arthur R. 2001. The effect of marine reserves and habitat on populations of east African coral reef fishes. *Ecological Applications* **11**: 559–569.

McClanahan TR, Kaunda-Arara B. 1996. Fishery recovery in a coral-reef marine park and its effect on the adjacent fishery. *Conservation Biology* **10**: 1187–1199.

McClanahan TR, Mangi S. 2000. Spillover of exploitable fishes from a marine park and its effect on the adjacent fishery. *Ecological Applications* **10**: 1792–1805.

McClanahan TR, Obura DO. 1997. Sedimentation effects on shallow coral communities in Kenya. *Journal of Experimental Marine Biology and Ecology* **209**: 103–122.

Micheli F, Halpern BS, Botsford LW, Warner RR. 2005. Trajectories and correlates of community change in no-take marine reserves. *Ecological Applications* **14**: 1709–1723.

Mora C, Andréfouët S, Costello MJ, Kranenburg C, Rollo A, Veron J, Gaston KJ, Myers RA. 2006. Coral reefs and the global network of marine protected areas. *Science* **312**: 1750–1751.

Moura RL. 2002. Brazilian reefs as priority areas for biodiversity conservation in the Atlantic Ocean. *Proceedings of the 9th International Coral Reef Symposium*, vol. 2; 917–920.

Moura RL, Francini-Filho RB. 2006. Reef and shore fishes of the Abrolhos Region, Brazil. In *A Rapid Marine Biodiversity Assessment of the Abrolhos Bank, Bahia, Brazil*, Dutra GF, Allen GR, Werner T, McKenna AS (eds). RAP Bulletin of Biological Assessment 38. Conservation International: Washington DC; 40–55.

Moura RL, Figueiredo JL, 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 RL, Dutra GF, Francini-Filho RB, Minte-Vera CV, Curado IB, Guimarães FJ, Oliveira RF, Alves DC. 2007. Fisheries management in the Marine Extractive Reserve of Corumbau, Bahia. In *Aquatic Protected Areas as Fisheries Management Tools*. Ministério do Meio Ambiente: Brasília; 175–187.

Mumby PJ. 2006. The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. *Ecological Applications* **16**: 747–796.

Mumby PJ, Edwards AJ, Arias-Gonzalez JE, Lindeman KC, Blackwell PG, Gall A, Gorczynska MI, Harborne AR, Pescod CL, Renken H, Wabnitz CCC, Llewellyn G. 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* **427**: 533–536.

Pandolfi JM, Bradburry RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman NJH, Paredes G, Warner RR, Jackson JBC. 2003. Global trajectories of the long-term decline of coral reef ecosystems. *Science* **301**: 955–958.

Polunin NVC, Roberts CM. 1993. Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Marine Ecology Progress Series* **100**: 167–176.

Roberts CM. 1995a. Effects of fishing on the ecosystem structure of coral reefs. *Conservation Biology* **9**: 988–995.

Roberts CM. 1995b. Rapid build-up of fish biomass in a Caribbean marine reserve. *Conservation Biology* **9**: 815–826.

Roberts CM, Polunin NVC. 1993. Marine reserves: simple solutions to managing complex fisheries? *Ambio* **22**: 363–368.

Roberts CM, Bohnsack JA, Gell FR, Hawkins JP, Goodridge R. 2001. Effects of marine reserves on adjacent fisheries. *Science* **294**: 1920–1923.

Russ GR. 2002. Yet another review of marine reserves as reef fishery management tools. In *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*, Sale PF (ed.). Academic Press: San Diego; 421–443.

Russ GR, Alcala AC. 1996a. Marine reserves: rates and patterns of recovery and decline of large predatory fish. *Ecological Applications* **6**: 947–961.

Russ GR, Alcala AC. 1996b. Do marine reserves export adult fish biomass? Evidence from Apo Island, Central Philippines. *Marine Ecology Progress Series* **132**: 1–9.

Russ GR, Alcala AC. 1999. Management histories of Sumilon and Apo Marine Reserves, Philippines, and their influence on national marine resource policy. *Coral Reefs* **18**: 307–319.

Russ GR, Alcala AC, Maypa AP, Calumpong HP, White AT. 2004. Marine reserve benefits local fisheries. *Ecological Applications* **14**: 597–606.

Sale PF, Cowen RK, Danilowicz BS, Jones GP, Kritzer JP, Lindeman KC, Planes S, Polunin NVC, Russ GR, Sadovy YJ, Steneck RS. 2005. Critical science gaps impede use of no-take fishery reserves. *Trends in Ecology and Evolution* **20**: 74–80.

Samoilys M. 1997. *Manual for Assessing Fish Stocks on Pacific Coral Reefs*. Department of Primary Industries: Brisbane.

ter Braak CJF. 1996. *Unimodal Models to Relate Species to Environment*. DLO-Agricultural Mathematics Group: Wageningen.

Walters CJ, Hilborn R, Parrish R. 2007. An equilibrium model for predicting the efficacy of marine protected areas in coastal environments. *Canadian Journal of Fisheries and Aquatic Sciences* **64**: 1009–1018.

Willis TJ, Millar RB, Babcock RC, Tolimieri N. 2003. Burdens of evidence and the benefits of marine reserves: putting Descartes before des horse? *Environmental Conservation* **30**: 97–103.

Zar JH. 1999. *Biostatistical Analysis*, 4th edn. Prentice-Hall: New Jersey.