Herbivorous fishes and the potential of Caribbean marine reserves to preserve coral reef ecosystems

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SUMMARY

1. The development of macroalgae to the detriment of corals is now one of the major threats to coral reefs. Herbivorous fishes are partly responsible for algal regulation on coral reefs and their overexploitation favours the shift from scleractinian coral-dominated systems towards macroalgae-dominated systems.

2. Marine Protected Areas (MPAs) that have been established worldwide may benefit coral reefs through the maintenance of high densities of herbivorous fishes which regulate algal growth.

3. Here we assess whether small MPAs in the Caribbean are able to enhance herbivorous fish stock and by controlling macroalgae help to maintain reef ecosystems. A visual census using band-transects was undertaken around Guadeloupe island where marine reserves have been in place since 1979. We examined the effects of MPAs on both benthic communities and herbivorous fishes.

4. Inside MPAs, herbivorous fish biomass was almost twice as high as outside MPAs and macroalgal cover was significantly lower. Fish size class distributions revealed that large individuals mainly occurred inside MPAs and that few male individuals were found outside MPAs.

KEY WORDS: marine protected areas; canonical analysis of principal coordinates; sex change; coral reefs; phase shifts; Caribbean

INTRODUCTION

The degradation of habitats and the decrease of biodiversity are undoubtedly two of the main causes of the global environmental crisis. In tropical areas, global warming, land-based pollution and over-fishing threaten coral reef integrity and their ability to provide goods and services upon which human welfare depends (Nyström *et al*., 2000; Jackson *et al*., 2001; Gardner *et al*., 2003; Hughes *et al*., 2003; Pandolfi *et al*., 2003; Mumby, 2006). Scleractinian coral-dominated systems are being supplanted at an increasing rate by macroalgae-dominated systems, the latter being favoured by eutrophication and reduction of herbivores as a result of disease and over-fishing (Miller *et al*., 1999; Costa Jr *et al*., 2000; Smith *et al*., 2001; Fabricius *et al*., 2005). Over-fishing is known to induce a decline in fish body size and density (Hughes, 1994; Jackson *et al*., 2001), but an even more insidious effect occurs when it prevents sequential hermaphrodite fishes from growing large enough to undergo sex change, leading some populations to become non-reproductive (Buxton, 1993; Coleman *et al.*, 1996).

To sustain the resilience of coral reef ecosystems, Marine Protected Areas (MPAs) have been established worldwide with the aim of protecting species and habitats. MPAs are known to have several positive effects on fish assemblages such as increasing the mean size of individuals (Rakitin and Kramer, 1996; Chapman and Kramer, 1999; Halpern, 2003; Hawkins and Roberts, 2003), increasing fish density and biomass (Rakitin and Kramer, 1996; McClanahan, 1997; Wantiez *et al*., 1997; Chapman and Kramer, 1999; Halpern, 2003; Mumby *et al*., 2006), providing a source of recruitment for surrounding areas and enhancing local fisheries in adjacent unprotected areas through adult fish spillover (Man *et al*., 1995; Russ and Alcala, 1996; Roberts, 1997; but see Gardmark *et al*., 2006 and Kulbicki *et al*., 2007 for another view). These positive effects have been directly related to the prohibition of fishing in marine reserves.

MPAs also have positive effects on the welfare of coral reefs (Hughes *et al*., 2003; Mumby *et al*., 2006). Indeed, herbivorous fishes may present higher densities inside protected areas and consequently may regulate algal growth (Williams *et al*., 2001; Williams and Polunin, 2001; McClanahan *et al*., 2002; Mumby *et al*., 2006; Newman *et al*., 2006; Stockwell *et al*., 2009). Conversely, on unprotected reefs, non-consumed algae may develop and supplant scleractinian corals. Recently, Mumby *et al*. (2006) demonstrated that large (456 km^2) and old (established in 1959) MPAs of the Bahamas archipelago have positive impacts on their resident herbivorous fishes and consequently on coral reefs. Here we test whether two small marine reserves (4 and 21 km^2), that were established twenty years ago, enhance fish stocks and are able to control macroalgae at a level sufficient to sustain coral reef ecosystem. This question has important implications for the future planning of marine reserve establishment because the design of marine reserve networks still lacks information about the spatial extent and the duration needed for protected areas to provide adequate protection to coral reef ecosystems.

We tested the effect of two MPAs on herbivorous fish density, biomass and size. As the influence of marine reserves on benthic assemblages is less studied than that on fish assemblages, we also aimed to demonstrate the importance of examining simultaneously fish assemblages and macroalgal benthic cover in assessing the role of MPAs for the conservation of coral reefs. Indeed, most studies showing MPA effects focus on fish while overlooking interacting effects with benthos (but see Mumby *et al.*, 2006). Since herbivorous fishes are partly responsible for algal regulation on coral reefs (Hatcher, 1981; Carpenter, 1986; Paddack *et al.*, 2006; Hughes *et al.*, 2007b; Mörk *et al.*, 2009), we tested whether macrophyte development is related to herbivorous fish rarefaction.

For that purpose, herbivorous fish assemblages were compared across several coral reefs, either protected from fishing or not, located around the Caribbean island of Guadeloupe. Number of individuals, species biomass and size distribution were compared, as well as the percentage of scarid terminal male individuals observed inside and outside protected areas. Finally, benthic cover was measured to investigate whether a correlation can be established between the protection of fish assemblages and habitat characteristics (i.e. balance between macroalgae and coral reefs).

METHODS

Study site

Guadeloupe is located in the Eastern Caribbean Sea (16°15′N, 61°35′W) and is composed of two islands, Basse-Terre and Grande-Terre, separated by a narrow sea channel called Rivière Salée. Coral reefs are abundant around these two islands (Bouchon *et al.*, 2008) and some of them have been protected since the 1980s. On protected coral reefs, human activities such as fishing, diving and anchoring are restricted and often forbidden. The MPAs studied are located around Ilets Pigeon (4 km^2) on the western coast and in the bay of the Grand Cul-de-Sac Marin (21 km^2) which forms the northern embayment between the two islands (Figure 1). In these two MPAs, fishing has been forbidden since 1979 and 1987 respectively. Five reef sites in these MPAs were sampled between 1 and 10m depth, (S1 to S3 in Grand Cul-de-Sac Marin and S4 – S5 in Ilets Pigeon) (Figure 1). Five non-protected reefs (S6 to S10) were also studied for comparison with MPAs (Figure 1). These sites were also located between 1 and 10 m depth. Every site was sampled both during the dry and rainy season (respectively May and November 2004).

Around the islands, water temperature varies little over the year, ranging from 25.8 to 29.9°C (Bouchon-Navaro, 1997). The climate in Guadeloupe is typical of the tropical zone with a dry and a wet season. Sampling areas are not under any influence of freshwater discharges and nutrient concentrations (nitrate and phosphate) are very low (respectively under 0.05 and 0.02 μmol.l^{-1}; Kopp, 2007).

Fish surveys

Visual surveys of a 150 x 2 metres transect were carried out on each reef site using scuba diving to estimate fish abundances, in terms of both density and biomass. Each transect was replicated two times in each season. Counts were done for each site, at the same hour of the day, and only when environmental conditions were optimal, i.e. no swell and low wind. All species of Scaridae and Acanthuridae present on the coral reefs of Guadeloupe were studied: *Scarus iserti* Bloch,1789, *Scarus taeniopterus* Desmarest, 1831, *Scarus vetula* Bloch & Schneider, 1801, *Sparisoma aurofrenatum* (Valenciennes, 1840), *Sparisoma chrysopterum* (Bloch & Schneider, 1801), *Sparisoma rubripinne* (Valenciennes, 1840), *Sparisoma viride* (Bonnaterre, 1788), *Acanthurus bahianus*

Castelnau, 1855, *Acanthurus chirurgus* (Bloch,1787) and *Acanthurus coeruleus* Bloch & Schneider, 1801. Herbivorous fish individuals observed on transects were identified to the species level, counted and their sizes estimated (total length). Lengths were recorded in 5 cm size classes for fish under 20 cm and 10 cm size classes for fish larger than 20 cm and phases were noted for scarid fish (i.e. initial or terminal; Robertson and Warner, 1978). Fish biomass was estimated using weight-length relationships (WLR) available in literature (Bohnsack and Harper, 1988; Claro and Garcia-Arteaga, 1994; Bouchon-Navaro, 1997).

Survey of benthic communities

Surveys of the benthic communities were carried out to determine whether any observed difference among fish assemblages was related to differences in habitats. Simultaneously with all fish surveys, we estimated the benthic community composition on each transect (in percentage) by recording benthic organisms present at point intercepts distributed every meter along the 150 m long transect (Lucas and Sebber, 1977; Eberhardt, 1978; Liddell and Ohlhorst, 1987). The recorded benthic categories were: Cyanobacteria, algal turf, soft Chlorophyta, calcareous Chlorophyta, Phaeophyta, Rhodophyta, encrusting crustose coralline algae, seagrasses, sponges, gorgonians, corals, actinarians, zoanthids, tunicates.

Analysis of data

A Canonical Analysis of Principal coordinates (CAP) (Anderson and Willis, 2003) was carried out to investigate the influence of reserve effects on fish assemblage structures. CAP is a constrained ordination procedure that initially calculates unconstrained principal coordinate axes, followed by a canonical discriminant analysis on the principal coordinates to maximize separation between predefined groups. CAP analysis is a flexible method which allows a constrained ordination to be done on the basis of any distance. Here, the Bray-Curtis dissimilarity index was used to measure dissimilarity between assemblages since it was recognized as one of the most appropriate distance measure for species abundance data (Legendre and Legendre, 1998). We also performed an ANOVA-like permutation test (9999 statistics were computed under the null hypothesis) for the CAP analysis. More precisely, we used a one-factor design to assess the significance of an MPA's effect on fish assemblage structures for both fish density and biomass. We used a CAP analysis instead of a more classical PERMANOVA because Anderson and Willis (2003) noticed that PERMANOVA may lead to some odd results compared to a CAP analysis. CAP analyses were processed using the R software package 'vegan'.

After analysing the responses of the whole fish assemblage we carried out a species by species approach. We implemented Mann-Whitney U-tests where the null hypothesis was the absence of MPA's effects on two quantitative variables for each species: number of individuals (density) and biomass.

The percentage of benthic cover (coral, algal turf and macroalgae, mainly composed of *Dictyota* spp.) between the two types of areas was also compared inside and outside the reserves. The non-parametric Spearman rank correlation coefficient was used to search for correlations between benthic cover and herbivorous fish biomass.

Chi-square contingency tests (Sokal and Rohlf, 1995) were used to compare fish sex ratio between MPAs and fished areas.

RESULTS

Fish abundances

CAP analysis (whole assemblage) revealed that the structure of herbivorous fish assemblage differed significantly in terms of density and biomass according to reserve ($p<0.01$). Mann-Whitney U-tests results for fish abundances using reserve as the independent factor are reported in Table 1. Overall, in MPAs, the mean number of individuals per $100m^2$ was 87.4 ± 19.8 (SE) whereas it was 86.3 ± 22.3 (SE) outside MPAs ($p=0.93$). Mean biomass of herbivorous fishes per $100m^2$ was 5645 g ± 1426 (SE) inside MPAs whereas it was 3283 g ± 958 (SE) outside ($p=0.007$), indicating significantly larger fish inside the MPAs. Inside MPAs, the mean number of scarid individuals per $100m^2$ was 50.7 ± 10.4 (SE) whereas it was 50.5 ± 12.4 (SE) outside MPAs ($p=0.58$). Mean biomass of scarid fishes per $100m^2$ was 3944 g ± 932 (SE) inside MPAs whereas it was 1196 g ± 291 (SE) outside ($p<0.0001$). The mean number of acanthurid individuals per $100m^2$ was 36.6 ± 9.5 (SE) in MPAs whereas it was 35.9 ± 9.9 (SE) outside MPAs ($p=0.38$). Mean biomass of acanthurid fishes per $100m^2$ was 1701 g ± 495 (SE) inside MPAs whereas it was 2087 g ± 667 (SE) outside ($p=0.85$).

Figure 2 shows the results of density and biomass for each fish species inside and outside MPAs. Results from Mann-Whitney U-tests showed that *Scarus taeniopterus* and *Sparisoma chrysopterum* densities were higher outside MPAs than inside (Table 1 and Figure 2A). Conversely, abundance for *S.aurofrenatum, S. viride and Scarus vetula* were higher inside than outside MPAs indicating a significant reserve effect on these species (p<0.05 in Table 1; Figure 2A). The three species of Acanthuridae did not present significant differences in abundance between the sites located inside or outside MPAs.

Scarid biomass was consistently higher within the marine protected areas than outside (Figure 2B), except for *Sparisoma chrysopterum*, *S. rubripinne* and *Scarus iserti* for which we did not detect any reserve effect on biomass values (Table 1). Biomass of *Sparisoma aurofrenatum* and *Scarus taeniopterus* were 4 times higher inside than outside MPAs, the mean biomass of *S. vetula* was 22 times higher in MPAs than in fished areas and biomass of *Sparisoma viride* was 7 times higher inside than outside MPAs (Figure 2B). A significant reserve effect was also found for *Acanthurus bahianus* where the biomass was two times higher inside than outside MPAs.

Size class distribution

Non-protected areas yielded numerous individuals of small size, *i.e.* under 10 cm length. *Scarus iserti*, *S. taeniopterus*, *Sparisoma chrysopterum* and *S. rubripinne* occurred in high densities of small individuals outside the reserve, whereas inside MPAs they were of larger size, *i.e.* up to 45 cm (Figure 3). Large adults of *Scarus vetula*, *Sparisoma rubripinne* or *S. viride* which had reached their terminal phase were only present in MPAs. There were no differences in the size class structure of the surgeonfishes, *Acanthurus chirurgus* and *A. coeruleus* between those inside and outside MPAs; *A. bahianus,* however, was present at high densities of medium-sized individuals only inside marine reserves (Figure 3).

Proportion of scarid individuals in terminal phase

The mean percentage of terminal males as determined by their colour phase was 22% inside marine protected areas and only 10% in fished areas. Four scarid species present terminal phase individuals outside MPAs: two species in high abundance (*Scarus iserti* and *Sparisoma aurofrenatum*; 16% and 17% respectively) and 2 species in low abundance (*Scarus taeniopterus* and *Sparisoma viride*; 3% and 2% respectively). Three species (*Sparisoma chrysopterum*, *S. rubripinne* and *Scarus vetula*) did not present TP individuals outside MPAs (Figure 3). Chi-square tests showed that there is a significant difference in the sex ratio between inside and outside MPAs for five species: *Scarus taeniopterus*, *Sparisoma aurofrenatum*, *S. rubripinne*, *S. viride* ($p<0.001$) and *S. chrysopterum* ($p=0.02$).

Correlation between herbivorous fishes and benthic cover

There was a significant difference in macroalgal cover ($p<0.0001$) inside and outside MPAs for Phaeophytae mainly comprising *Dictyota* spp., with more cover in the non-protected areas (35.7%) than in the MPAs (13.2%). A Spearman rank correlation coefficient between benthic macroalgal cover and the biomass of large herbivorous fish (>20cm), revealed a significant negative correlation between these two variables (r_s = -

0.660; p=0.002) (Figure 4A). A significant difference was also found for coral cover between protected and non-protected areas (p=0.002) with more coral cover inside MPAs (25.6%) than outside (18.1%). A Spearman rank correlation coefficient revealed a significant positive correlation between coral cover and the biomass of large herbivorous fish (r_s = 0.757; p<0.0001) (Figure 4B). Finally, algal turf cover inside and outside MPAs showed a significant difference (p=0.017) with 47.5% and 35.1% of the benthic cover respectively. No correlation was found between large herbivorous fishes and algal turf cover (Figure 4C) but a significant negative correlation was found between macroalgae and algal turf (r_s = -0.769; p<0.001).

DISCUSSION

Herbivorous fish abundance and biomass

This study shows there is a difference between the herbivorous fish guild composition inside and outside marine protected areas. Although reef protection has only a slight effect on the number of individuals, it has a strong influence on fish biomass as it is almost two times higher inside MPAs than outside. Parrotfishes and surgeonfishes are particularly vulnerable to trap- and spear- fishing (Koslow *et al.*, 1988), but the positive effect of MPAs on herbivorous fish biomass does not seem to extend over reserve boundaries. Indeed, numerous small individuals are found outside the reserve while large individuals live almost exclusively inside MPAs. Although there appears to be little emigration of adult fish from within to outside the MPAs they are likely to provide a source of recruitment for non-protected areas (but see Kulbicki *et al*., 2007 for another point of view).

In their synthesis on the relationships between MPAs, herbivores and coral reef resilience, Hughes *et al*. (2007a) assert that marine reserves are essential to increase herbivorous fish biomass. Other authors have pointed out the importance of Caribbean marine reserves to maintain herbivorous fish biomass. According to Mumby *et al*. (2006), biomass of scarid fishes is between 30 and 60% higher in Bahamian MPAs than in non-protected areas. In St Lucia, the total parrotfish biomass increased significantly over time in both fishing grounds (doubled in five years) and reserves (quadrupled in five years) since the establishment of marine reserves, albeit higher biomass was observed in protected areas than in fishing grounds (Hawkins and Roberts, 2003). In Barbados, Rakitin and Kramer (1996) also noticed that scarid fishes were significantly more abundant in the less exploited areas as scarids are particularly vulnerable to coastal trap fishing. In the Indo-Pacific region herbivorous fish biomass varied between 5000 and 7000 g.100m^{-2} on protected reefs whereas it was only 200g.100m^{-2} in non-protected zones (McClanahan, 1997). However, in McClanahan's studied sites only a slight increase of individual density was observed after 20 years of protection. In the Philippines, Stockwell *et al.* (2009) observed a 9- and 15-fold increase in density and biomass of herbivorous fishes in the MPAs. In the New Caledonian region, the protection of coral reefs led to the recovery of fish biomass as well as fish densities after the reserve establishment (Wantiez *et al*., 1997) suggesting that MPAs have also a positive effect on individual density.

It should be noted that other factors may contribute to the differences in the structure of herbivorous fish assemblages: e.g. sampling strategy, environmental variables and habitat characteristics. Fish were counted along 2 metres wide transects because at widths greater than 2 m, it was difficult to sample the small juvenile fish. A 2 m width transect is rather narrow for large species and that it may have biased the frequency of observation of shy species, especially large individuals inside MPAs (Kulbicki, 1998). The non-random location of reserves as a result of the necessity to include particular features make spatial comparisons rather difficult when trying to assess a reserve effect. However, the magnitude of the observed difference between herbivorous fish biomass inside and outside the MPAs seems sufficient for it to be attributed at least in part to a reserve effect rather than to ecological differences among sites (Willis *et al.*, 2003). Indeed, the mean scarid biomass was three times higher inside than outside MPAs, greatly exceeding the 100% threshold suggested by Edgar and Barett (1997) to accept the existence of a real reserve effect and disregard any flaws in the sampling design.

Size frequencies

Large individuals of scarid fish were mainly found in marine reserves. For medium size species (*Scarus iserti*, *S. taeniopterus* and *Sparisoma aurofrenatum*), individuals never reached their theoretical maximum lengths outside MPAs, where only individuals less than 20 cm long were observed. A similar disparity was seen for large species (*Scarus vetula*, *Sparisoma rubripinne* and *S. viride*) which reached larger size inside MPAs. Only *Sparisoma chrysopterum* reached its maximum size outside as well as inside the reserve. Small individuals of scarid fish were dominant in the assemblages outside MPAs. The surgeonfish, *A. bahianus* occurred in high densities of large individuals inside marine reserve. According to Edgar and Barrett (1997), a 10% increase in the mean size of fish is sufficient to indicate that a significant change has occurred with MPAs establishment. Inside Guadeloupe MPAs, the mean size of herbivorous fish is more than 10 % greater than outside (respectively 16.3 ± 1.3 cm and 11.9 ± 1.0 cm; Kopp *et al*., 2009) suggesting that the reserve effect plays a significant role.

Hawkins and Roberts (2003) did not study the direct impact of marine reserves on parrotfish but evaluated the effect of fishing on scarids in several Caribbean islands. They found that the mean size of all species, except *Scarus vetula*, decreased with increasing fishing pressure. For all species, fishing pressure appears to reduce fish size. The same phenomenon was observed by Ferry and Kohler (1987) in Haiti where scarid fishes were significantly smaller when under higher exploitation.

Proportion of terminal male

The present results suggest that marine reserves have a positive impact on the number of scarid terminal phase individuals occurring on coral reefs. Terminal male individuals were relatively abundant inside MPAs whereas outside MPAs terminal phase individuals of some species were virtually absent. This means that species populations would potentially become non-reproductive, unless they can compensate by changing sex earlier, and would disappear from heavily fished areas. However, non-protected areas shelter numerous juvenile parrotfishes. According to Thresher (1984) and Roberts (1997), the large majority of marine species have a pelagic larval dispersal phase, which means that ocean currents can carry the progeny of protected stocks outside reserves to replenish fishing grounds. As Scaridae have a pelagic larval dispersal phase (Reeson, 1983; Bellwood and Choat, 1989), this is probably what happens in our studied areas. Marine reserves, where male individuals occur, export eggs and larvae outside the protected areas. Such dependence on external sources of recruitment highlights the need of marine protected areas within depleted regions, and that such marine reserves should be spaced so as to enable a significant proportion of larvae to disperse to surrounding fished areas (Sale *et al.,* 2005). In Guadeloupe, some fished areas may not benefit from such dispersion of larvae as they are located relatively far from MPAs and other factors such as ocean currents may have an effect.

Hawkins and Roberts (2003) found that the fraction of terminal males of *Sparisoma viride*, *Scarus vetula*, and *Sparisoma aurofrenatum* decreased with increasing fishing pressure. Other species did not show such clear trends in relation to fishing pressure. Hawkins and Roberts (2003) also demonstrated that the creation of marine reserves allows scarids to undergo sex change at larger sizes both in marine reserves and in fishing grounds (except for *Sparisoma viride*), supporting the hypothesis that parrotfishes can undergo sex change earlier in non-protected areas in order to maintain their reproductive success.

Control of algae

One of the basic questions broached in this study was to know whether the intensive macrophyte development is due to the rarefaction of herbivores which leads to the decrease of herbivory pressure over algae. Unambiguously, we found that the larger herbivorous fishes mainly occur on coral reefs where macroalgae are controlled, i.e.

with low abundance compared to sites outside MPAs. Two hypotheses can be proposed: i) herbivorous fishes, feeding mainly on algal turf, do not occur on coral reefs dominated by macroalgae ii) macroalgae develop in areas where herbivorous fishes, absent or scarce, are unable to control their growth. Experiments may be performed to disentangle these two hypotheses. Some authors already used caging experiments to exclude herbivorous fish from coral reefs (Earle, 1972; Wanders, 1977; Foster, 1987; Lirman, 2001; McClanahan *et al*., 2002) and described an intensive macroalgal development. Over-fishing act in the same way, excluding herbivorous fishes, and all the observations on different coral reefs located all around the world (Jones, 1992; Williams *et al*., 2001; Williams & Polunin, 2001; McClanahan *et al*., 2002; Mumby *et al*., 2006; Newman *et al*., 2006; Hughes *et al*., 2007b) show that the exclusion of herbivorous fishes by intense harvesting leads to an increase of macroalgal cover on coral reefs. Areas, formerly dominated by healthy fish assemblages and algal turf, are now dominated by macroalgae, as herbivorous fish stocks are becoming depleted. In this study, we compared the effect of abundant herbivorous fishes observed in MPAs to those observed in non-protected areas. We obtained a negative correlation between the number of large herbivorous fish and macroalgal cover suggesting that large herbivorous fishes effectively control macroalgal benthic cover inside MPAs. In non-protected areas fishes are exploited and those remaining cannot reach big size. In turn, they cannot prevent the development of macroalgae neither control algal growth.

This study supports the idea that even small MPAs play a significant role in maintaining fish stocks and by cascade contribute to maintain a fairly low algal cover via the herbivorous fish grazing and sustain coral reefs. Such benefits make marine reserves an important tool for managing artisanal fisheries which, in the Caribbean, often target herbivorous fishes and impede the effects of marine protected areas to exceed reserve boundaries.

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Table 1: Comparison of fish density and biomass between MPAs and unprotected sites using Mann-Whitney U-tests. Significant results are in bold.

	U value	p-value
Number of individuals		
All species	196.5	0.93
Scarus iserti	169.0	0.41
Scarus taeniopterus	**277.0**	**0.04**
Scarus vetula	**286.5**	**<0.01**
Sparisoma aurofrenatum	**344.0**	**<0.01**
Sparisoma chrysopterum	**114.5**	**0.02**
Sparisoma rubripinne	170.5	0.38
Sparisoma viride	**278.0**	**0.04**
All scarids	220.5	0.58
Acanthurus bahianus	241.0	0.27
Acanthurus chirurgus	172.5	0.42
Acanthurus coeruleus	152.0	0.19
All acanthurids	167.5	0.38
Biomass		
All species	**299.0**	**<0.01**
Scarus iserti	210.0	0.79
Scarus taeniopterus	**327.0**	**<0.01**
Scarus vetula	**289.5**	**<0.01**
Sparisoma aurofrenatum	**352.5**	**<0.01**
Sparisoma chrysopterum	149.0	0.15
Sparisoma rubripinne	204.5	0.89
Sparisoma viride	**366.0**	**<0.01**
All scarids	**380.0**	**<0.01**
Acanthurus bahianus	**289.0**	**0.02**
Acanthurus chirurgus	171.0	0.39
Acanthurus coeruleus	191.0	0.81
All acanthurids	193.0	0.85

Figure captions

Figure 1. Map of the study area and location of the sampling sites.

Figure 2. Mean abundance (.100m^{-2} ± SE) and biomass (g. 100m^{-2} ± SE) of herbivorous fishes with black bars for outside MPA and grey bars for inside MPA. A: abundance, B: biomass. Mann-Whitney U-tests were used to test the difference: * $p<0.05$; ** $p<0.01$.

Figure 3. Size class (cm) frequency distribution for each herbivorous fish species with grey bars for inside MPA and black bars for outside MPA.

Figure 4. Macroalgal (A), coral (B) and turf (C) covers, versus biomass of large individuals (in g.100m^{-2}) inside (◊) and outside (■) the MPA.

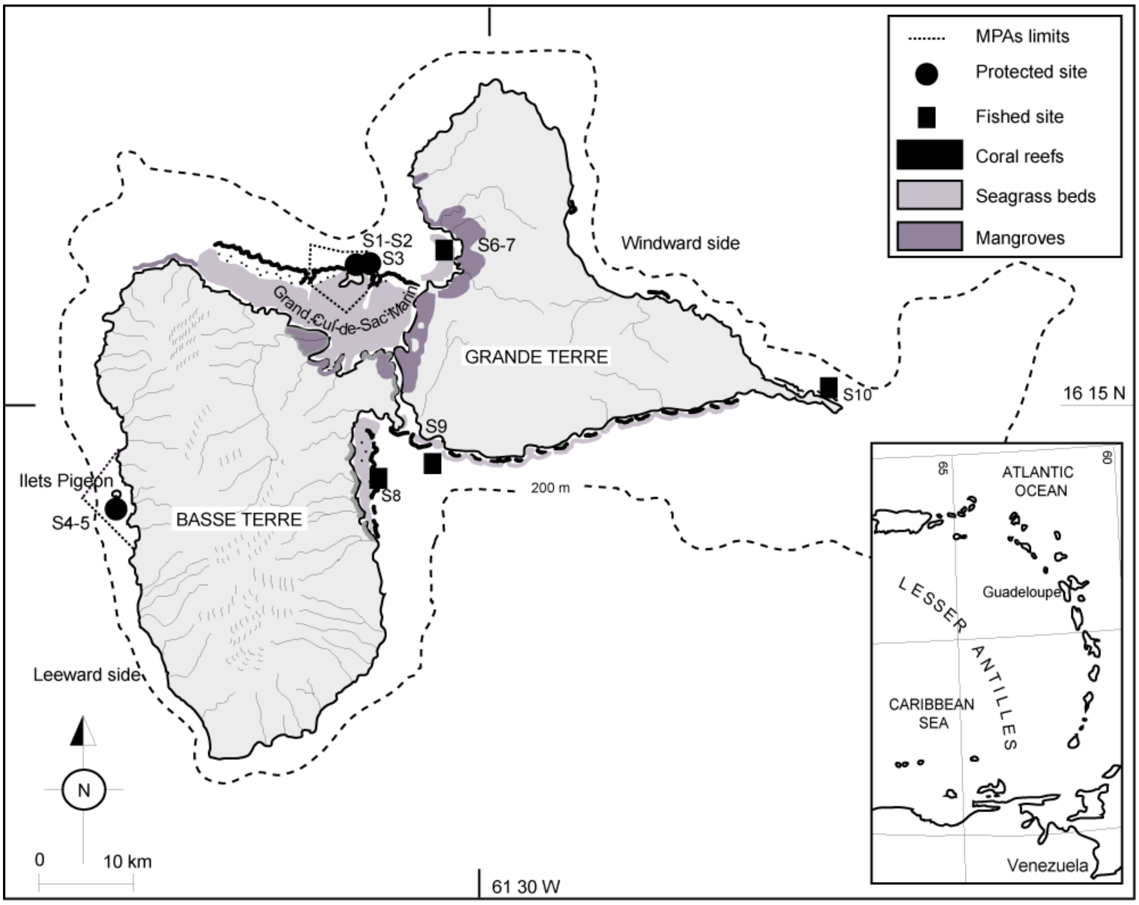
MPAs limits
Protected site
Fished site
Coral reefs
Seagrass beds
Mangroves
S1-S2
S3
S6-7
Windward side
Grand Cul-de-Sac Marin
GRANDE TERRE
S10
16 15 N
S9
S8
200 m
Ilets Pigeon
S4-5
BASSE TERRE
Leeward side
N
0
10 km
61 30 W
65
60
ATLANTIC OCEAN
Guadeloupe
LESSER ANTILLES
CARIBBEAN SEA
Venezuela

Figure 1

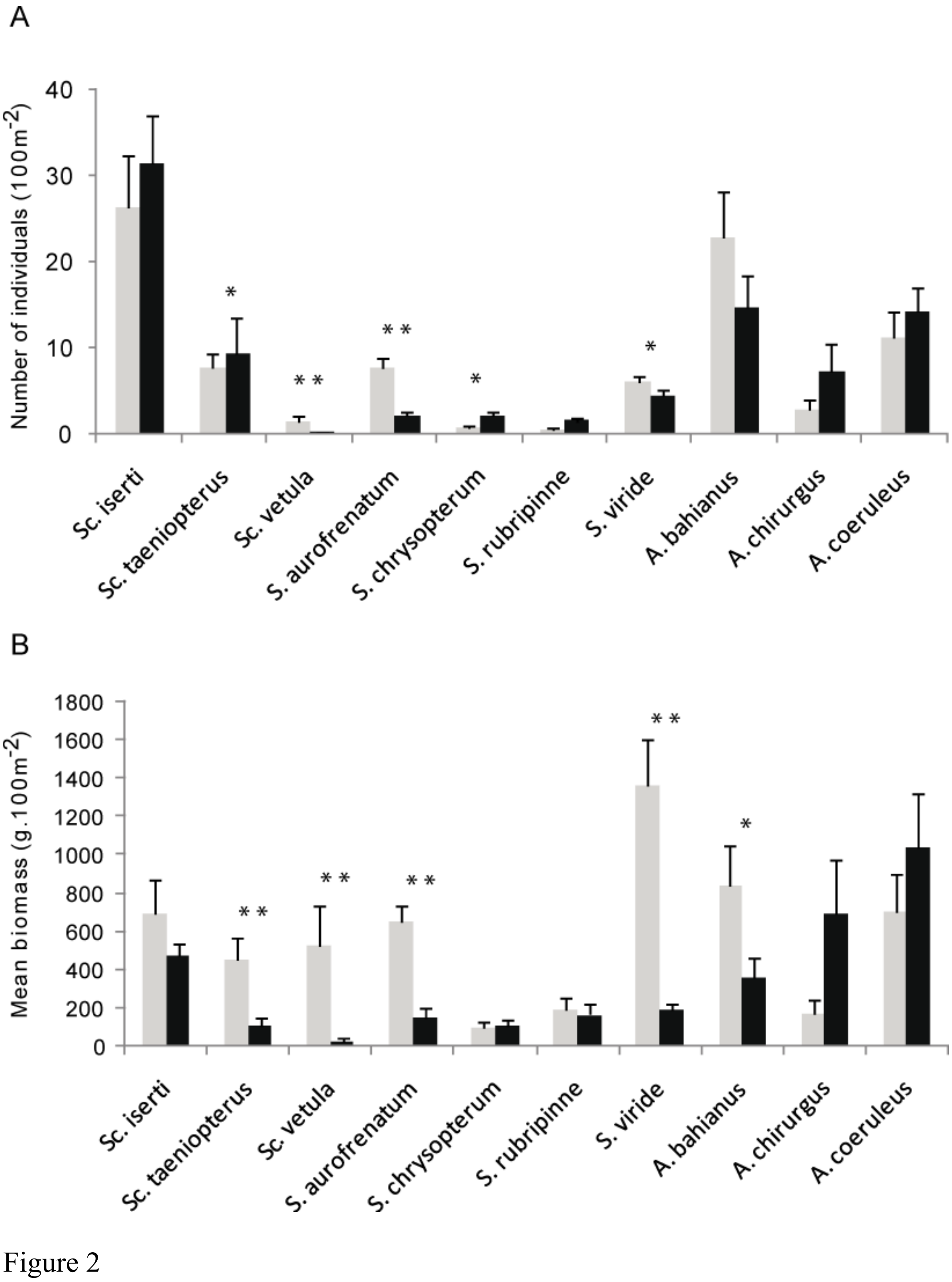
A
Number of individuals (100m^{-2})
0
10
20
30
40
*
* *
* *
*
*
Sc. iserti
Sc. taeniopterus
Sc. vetula
S. aurofrenatum
S. chrysopterum
S. rubripinne
S. viride
A. bahianus
A. chirurgus
A. coeruleus
B
Mean biomass (g.100m^{-2})
0
200
400
600
800
1000
1200
1400
1600
1800
* *
* *
* *
* *
*
Sc. iserti
Sc. taeniopterus
Sc. vetula
S. aurofrenatum
S. chrysopterum
S. rubripinne
S. viride
A. bahianus
A. chirurgus
A. coeruleus

Figure 2

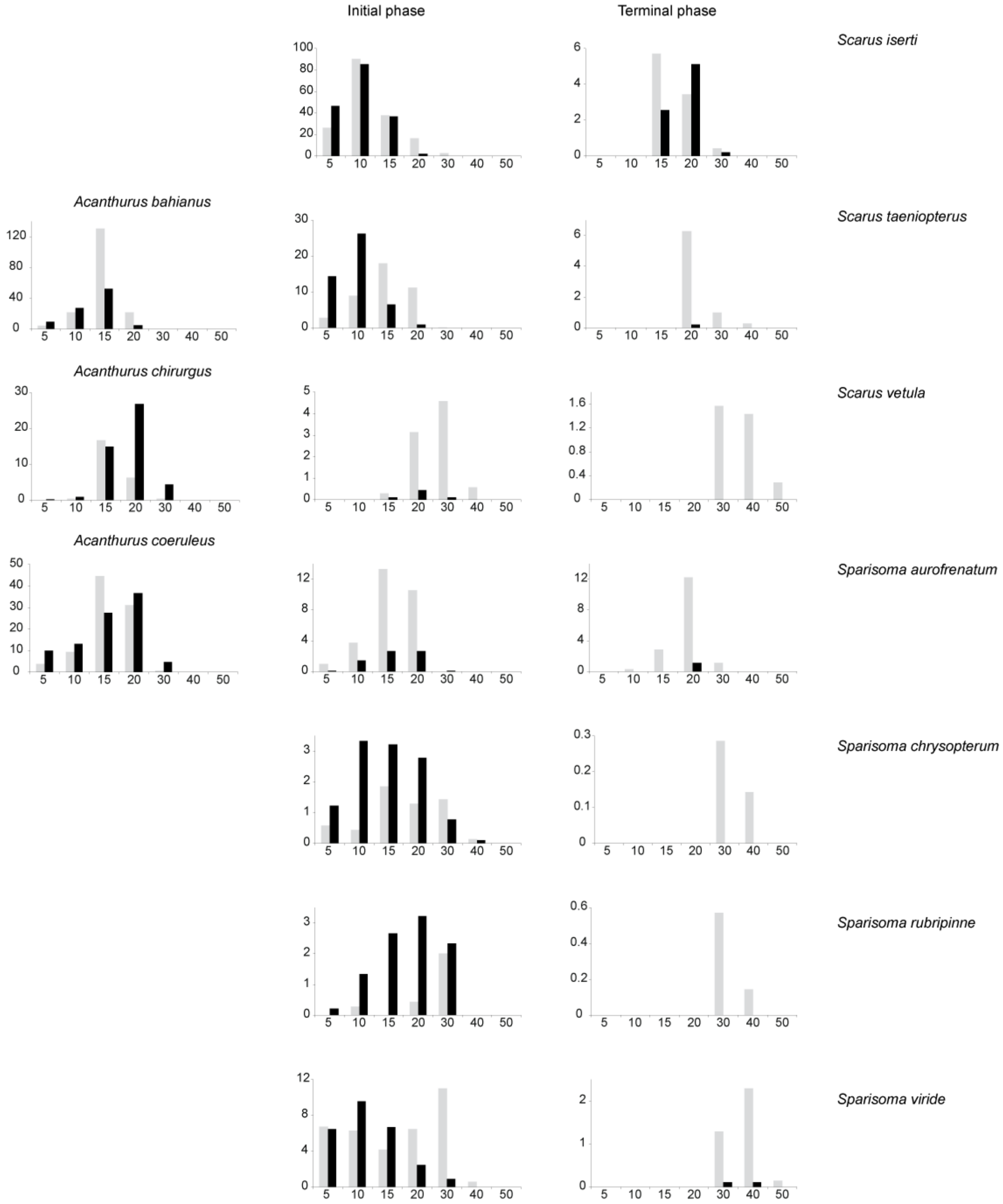
Initial phase
Terminal phase
Scarus iserti
Acanthurus bahianus
Scarus taeniopterus
Acanthurus chirurgus
Scarus vetula
Acanthurus coeruleus
Sparisoma aurofrenatum
Sparisoma chrysopterum
Sparisoma rubripinne
Sparisoma viride
5 10 15 20 30 40 50

Figure 3

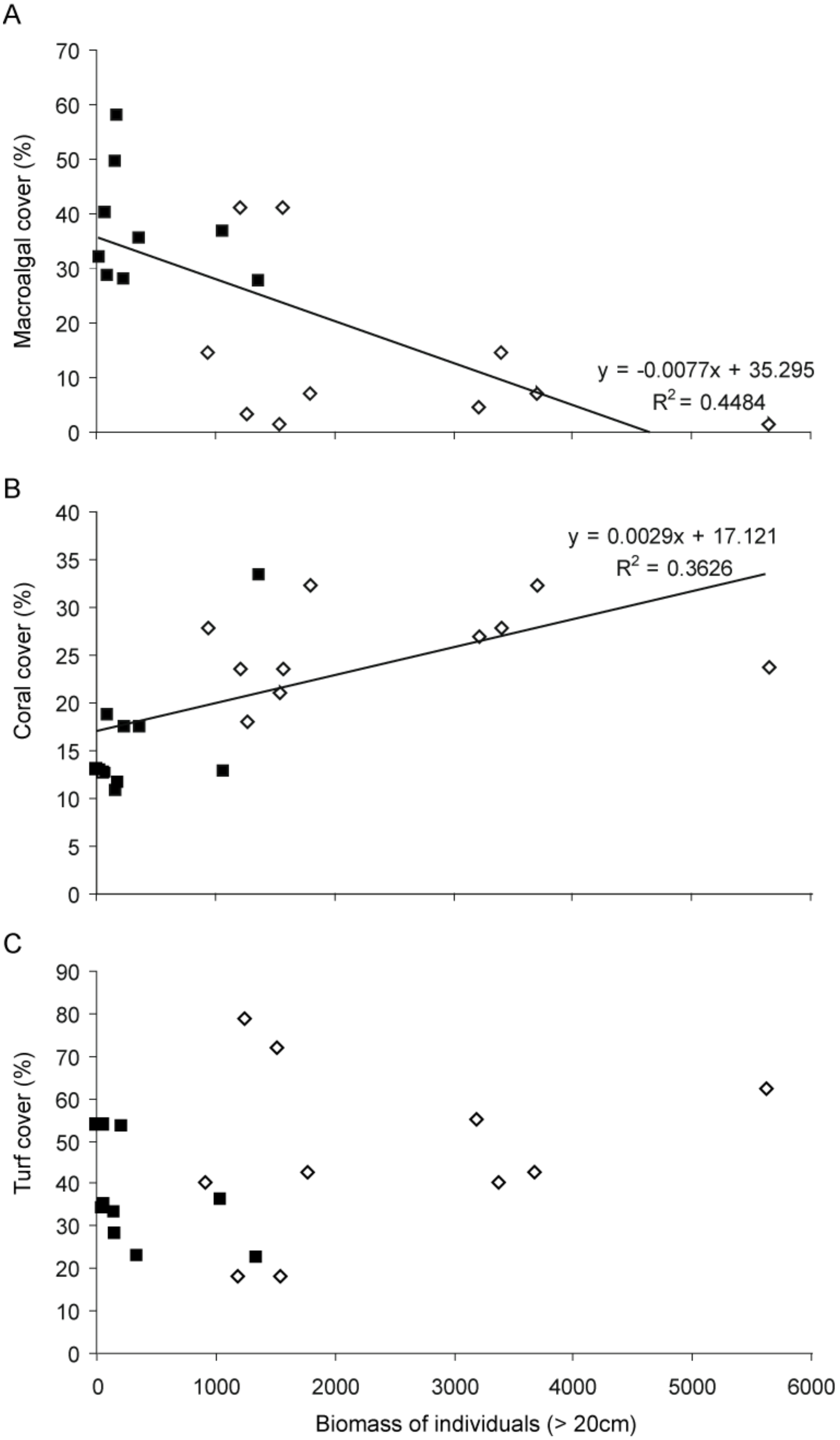
A
Macroalgal cover (%)
70
60
50
40
30
20
10
0
y = -0.0077x + 35.295
R^2 = 0.4484
B
Coral cover (%)
40
35
30
25
20
15
10
5
0
y = 0.0029x + 17.121
R^2 = 0.3626
C
Turf cover (%)
90
80
70
60
50
40
30
20
10
0
0
1000
2000
3000
4000
5000
6000
Biomass of individuals (> 20cm)

Figure 4