REPORT

Parrotfish predation on massive *Porites* on the Great Barrier Reef

R. M. Bonaldo · D. R. Bellwood

Abstract Parrotfish grazing scars on coral colonies were quantified across four reef zones at Lizard Island, Northern Great Barrier Reef (GBR). The abundance of parrotfish grazing scars was highest on reef flat and crest, with massive *Porites* spp. colonies having more parrotfish grazing scars than all other coral species combined. Massive *Porites* was the only coral type positively selected for grazing by parrotfishes in all four reef zones. The density of parrotfish grazing scars on massive *Porites* spp., and the rate of new scar formation, was highest on the reef crest and flat, reflecting the lower massive *Porites* cover and higher parrotfish abundance in these habitats. Overall, it appears that parrotfish predation pressure on corals could affect the abundance of preferred coral species, especially massive *Porites* spp, across the reef gradient. Parrotfish predation on corals may have a more important role on the GBR reefs than previously thought.

Keywords Reef fish · Labridae · Grazing scar · Corallivory · Coral reef · Habitat

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Introduction

Coral reefs around the world face an uncertain future with the threat of ocean acidification, global warming, and more direct human disturbances (Nystrom et al. 2000; Baird and Marshall 2002; Hughes et al. 2003; Hoegh-Guldberg et al. 2007; De'ath et al. 2009). The potential loss of biodiversity in these systems has highlighted the need to better understand the key factors maintaining reef diversity and underpinning coral reef resilience (Bellwood et al. 2004; Nystrom et al. 2009). In this context, several studies on coral predation by reef fishes have been conducted recently (e.g., Rotjan and Lewis 2008, 2009; Francini-Filho et al. 2008; Alwany et al. 2009; Mumby 2009; Jayewardene et al. 2009), reflecting the importance of predation as one of the main natural factors affecting coral distribution and abundance on coral reefs (Littler et al. 1989; Hixon 1997; Rotjan and Lewis 2005).

Although parrotfishes have been considered one of the main coral predators on tropical reefs (Littler et al. 1989; Hixon 1997; Rotjan and Lewis 2005; Francini-Filho et al. 2008; Alwany et al. 2009; Mumby 2009), little information on coral consumption by this group is available to the Indo-Pacific region. For example, no studies have evaluated whether parrotfish predation affects the distribution, growth and survivorship of coral colonies in the Great Barrier Reef (GBR). Most studies on corallivory in this region have focused on coral predation by chaetodontids (e.g., Berumen et al. 2005; Pratchett 2005), a group that appears to have a limited influence on coral standing crops (Harmelin-Vivien and Bouchon-Navarro 1983) and a small impact on the physical structure of corals compared to parrotfishes, tetradontids, and balistids (Cole et al. 2008; Jayewardene et al. 2009).

In contrast, vast literature on coral predation by parrotfishes is available for the Caribbean (reviewed by Rotjan

and Lewis [2008]; Mumby [2009]) and, as a consequence, this detailed information makes system-level analyses of the impact of parrotfishes possible for coral colonies in this region (e.g., Mumby [2006]; Rotjan and Lewis [2005]). Reefs of the GBR and the Caribbean, however, differ greatly in their structure, species richness, and biodiversity. For example, the main coral predators in the Caribbean are *Sparisoma* spp. parrotfishes (Bruckner and Bruckner [1998]; Bruckner et al. [2000]; Rotjan and Lewis [2005], [2008]; Cole et al. [2008]), which are completely absent in the Indo-Pacific. There is also a much larger number of corallivorous reef species in the Indo-Pacific, and the evolution and ecology of coral predation in these two regions are likely to differ (Ferry-Graham et al. [2001]; Cole et al. [2008]; Rotjan and Lewis [2008]; Mumby [2009]; Bellwood et al. [2010]). Thus, extending general conclusions from the Caribbean to the Indo-Pacific may be unwise (Mumby [2009]). Studies of the high-diversity reefs in the Indo-Pacific, therefore, are critically important if we wish to understand the importance of parrotfishes on coral consumption and the potential impact of these fishes on coral colonies on this region.

This study provides a preliminary overview of coral predation by parrotfishes on an Indo-Pacific reef, examining four zones (backreef, flat, crest, and slope) at Lizard Island, on the GBR, Australia. Our specific objectives were (1) to quantify the density of parrotfish grazing scars on corals for coral standardized area (grazing scars m^{-2} of coral surface), (2) to evaluate parrotfish grazing selectivity on scleractinian corals, and (3) to quantify the rate of parrotfish predation on massive *Porites* spp. colonies across the reef gradient. Massive *Porites* spp. were chosen for the main focus of this study as initial observations at the study site showed that they are one of the most widespread coral groups among reef zones and have a high abundance of parrotfish grazing scars.

Materials and methods

Study sites and general methodology

This study was conducted during October and December 2008 at Lizard Island, a mid-shelf reef in the northern section of the GBR (14°40′S, 145°28′E). Two sites between South and Palfrey Islands were chosen for this study. Within each study site, four reef zones were selected: backreef (5–8 m deep), flat (0.5–1 m), crest (0.7–2 m), and slope (7–10 m). October and December were chosen for our data collection because corals at Lizard Island usually present different sexual maturation stages in each of these months (Harriott [1983]). Mass coral spawning in the GBR usually occurs between late November and early December (Harriott [1983]; Babcock et al. [1986]). As a

consequence, coral colonies have a significant increase in the quality and size of gametes from September to early December (Harriott [1983]). Coral colonies in October and December at the study site probably presented, respectively, the highest and lowest number of mature gonads and eggs.

Two major methodologies were used to assess coral predation by parrotfishes: a "still" measure, in which individual coral colonies were photographed only once, and a "dynamic" measure, in which a same coral colony was photographed over 14 consecutive days. The "still" methodology was used to assess coral abundance, density of parrotfish grazing scars on corals, parrotfish grazing selectivity, number of massive *Porites* spp. grazed colonies, and grazed area of massive *Porites* spp. colonies. The "dynamic" measure was applied to quantify the rates of coral predation events by parrotfishes on massive *Porites* spp. colonies over 14 days. Details of both methodologies are presented below.
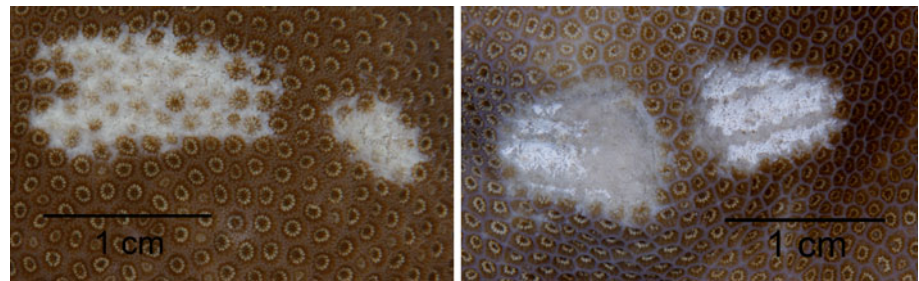
Coral abundance

A photoquadrat method was used to evaluate coral abundance in each reef zone at the two study sites. Six 20-m transects were laid within each of the four reef zones, at the two sites and at the two time periods ($n = 112$ transects). In each transect, the substratum was photographed every meter at a standardized distance of 1 m (240 photo frames per studied location). Subsequently, 10 random points were haphazardly selected in each photograph with the program CPCe 3.6 for windows to evaluate the coral cover and the abundance of different coral species ($n = 24{,}000$ points).

Abundance and distribution of parrotfish grazing scars on corals

Because direct observations of parrotfishes consuming live coral are infrequent, the presence of the distinctive grazing scars made by parrotfishes on live coral was used as an indicator of parrotfish feeding on corals (following Littler et al. [1989]; Rotjan and Lewis [2005]). However, before starting our data collection, we followed parrotfish individuals to observe the shape of their grazing scars on coral colonies (See Appendix 1 in Electronic Supplementary Material; ESM). Based on these observations, only very clear parrotfish grazing scars (i.e., presenting the typical jaws marks of parrotfishes, Fig. 1) were classified as parrotfish grazing scars (see Bellwood and Choat [1990]; Bonaldo and Bellwood [2009]). This methodology results in a conservative estimate of coral predation by parrotfishes and avoids the confusion with grazing scars left by other organisms, such as monacanthids, tetradontids, and labrids (cf. Jayewardene and Birkeland [2006]; Cole et al. [2008];

Fig. 1 Grazing scars of parrotfishes on massive *Porites* spp.

Jayewardene et al. 2009). However, non-scarid or unconfirmed scars represented less than 1% of all scars located.

The number of parrotfish grazing scars on corals was determined by the same surveys undertaken for the coral abundance assessments. Photographs were analyzed to verify the presence of parrotfish grazing scars on coral and, when present, scars were classified according to the coral species (or the lowest taxonomic category possible). Counts of number of parrotfish grazing scars in the photographs were calibrated by comparing counts in the photographs and counts in the field of a same coral area. The similarity between the two counts averaged 94.72% (2.16 ± % SE, $n = 33$).

Parrotfish grazing selectivity on scleractinian corals was assessed by comparing the number of grazing scars on each coral type and the availability of that coral type within each reef zone at each study site. For this analysis, coral colonies were classified into the following groups: Acroporidae, Faviidae, Mussidae, Pocilloporidae, and massive *Porites* spp.

Parrotfish abundance

Parrotfish abundance was assessed at each study site to examine the relationship between parrotfish abundance and coral predation pressure. Nine 50 m × 2 m tape transects were surveyed within each of the four zones at the two sites in the two studied months ($n = 96$). Censuses used two dives, one to count and the other to measure the distance. Counts were based on all parrotfish individuals over 10 cm total length (See Appendix 2 in ESM for the list of parrotfish species recorded in the transects). Because there is little information on parrotfish species feeding on live coral colonies (e.g., Bellwood and Choat 1990; Bellwood et al. 2003), all parrotfish species were considered in the counts as potential coral predators. All visual censuses were conducted within 2 h of the high tide in the morning to minimize any tide or time of day effects.

Number of grazed colonies and relative grazed area of massive *Porites* spp.

The number of grazed coral colonies and relative grazed area of coral colonies were measured for massive *Porites*

spp. colonies only. This group was chosen as it was consistently present in all four reef zones, exhibited clearly distinguishable grazing scars, and presented the highest grazing selectivity by parrotfishes and highest abundance of grazing scars at the study sites. A number of studies have also found *Porites* spp. to be among the main corals preyed on by parrotfishes (e.g., Littler et al. 1989; Rotjan and Lewis 2005, 2006; Cole et al. 2008). Because of the difficulty in distinguishing massive *Porites* species on the GBR, colonies were classified as 'massive *Porites* spp.'.

The relative number of grazed colonies and the grazed area of massive *Porites* spp. colonies were assessed with six independent 20-m transects within each reef zone, site, and month ($n = 112$). All colonies of massive *Porites* spp. found in the transects were photographed at a standardized distance of 1 m. Photographs were analyzed to verify the presence of parrotfish grazing scars and, when present, scars were counted and measured with the software Image Tool (version for Windows 3.0).

Dynamics of parrotfish grazing on massive *Porites* spp.

The dynamics of parrotfish grazing on massive *Porites* spp. colonies was evaluated in terms of (1) the frequency of new grazing scars over 14 days and (2) changes in the relative coral grazed area over 14 days. For this component, 20 individual massive *Porites* spp. colonies were haphazardly chosen in each reef zone of each study site and were photographed over 14 consecutive days in both months ($n = 320$ colonies, 4,480 photographs). To ensure that the same colonies were photographed every day, identification tags were placed about 50 cm from each colony. Photographs were always taken of the same region of each colony, which was delimited using a 22 cm × 22 cm plastic frame. For each colony, the external corners where the plastic frame was placed were marked with black pencil to allow divers to find the exact area of each colony to be photographed. Photographs were examined regarding the number of parrotfish grazing scars and the grazed area of each colony over the 14-day period. New and old scars were counted and measured with the software Image Tool (version for Windows 3.0). Dynamics of parrotfish grazing on massive *Porites* spp. colonies was evaluated in terms of

rate of new parrotfish grazing scars and area of *Porites* grazed per m² of *Porites* surface over the 14-day period. Rates of increase in the grazed area of massive *Porites* spp. in 14 days were extrapolated to calculate the yearly removal of *Porites* spp. tissue by parrotfishes in each study site.

Statistical analyses

Coral abundance among locations was compared with a two-way analysis of variance (ANOVA), with site and reef zone as fixed factors. The same test was used to compare the abundance of massive *Porites* spp. among zones and sites. Data on coral cover and *Porites* spp. abundance were square root–transformed to meet test assumptions.

The number of parrotfish grazing scars m⁻² on coral tissue was analyzed with a three-way ANOVA, with month, site, and reef zone as fixed factors. Data were log-transformed to meet test assumptions. A three-way ANOVA was also undertaken on parrotfish grazing scars on massive *Porites* spp. colonies only, although data were square root–transformed to meet test assumptions. To examine the relationship between parrotfish grazing predation and coral cover, two Spearman rank correlation tests were examined: (1) total coral cover vs. number of parrotfish grazing scars m⁻² of coral tissue and (2) massive *Porites* spp. cover vs. number of parrotfish grazing scars m⁻² of *Porites* tissue. In both correlations, coral cover was arcsine-transformed before to meet test assumptions.

Grazing selectivity of different groups of scleractinian corals by parrotfishes was measured based on Strauss's Linear Resource Selection Index (*L* in Strauss 1979). Non-parametric bootstrapping procedures were used to generate a 95% confidence interval around the observed *L* of each coral type, in which number of bites per coral type was used as sample units (10,000 randomizations). The confidence limits were determined using the percentile method (Manly 1997).

Parrotfish abundance in the study sites was compared with a three-way ANOVA, with month, site, and reef zone as fixed factors. Data were square root–transformed to meet assumptions. The relationship between the abundance of massive *Porites* spp. and parrotfishes was again examined using Spearman rank correlation tests. The number of grazed colonies of massive *Porites* spp. was also compared with a three-way ANOVA with month, site, and reef zone as fixed factors. This test was also applied to the relative grazed area of massive *Porites* spp. colonies (arcsine transformed to meet normality assumptions).

A three-way ANOVA was used to compare the rate of new parrotfish grazing scars on massive *Porites* spp. with month, site, and reef zones as fixed factors. The same analysis was used to examine the area of massive *Porites* spp.

grazed by parrotfishes over 14 days. For the analyses of rate of new grazing scars and area of massive *Porites* grazed in 14 days, data were respectively log $(n + 1)$ and arcsine-transformed to meet normality assumptions.

Before each parametric test, data were examined for normality and homogeneity of variances using residual analyses. When significant differences were found, post hoc tests (Tukey) were used to verify the specific sources of variation.

Results

Coral cover showed significant variation across the reef gradient ($F_1 = 13.04$, $P < 0.001$, Fig. 2). In both sites, the reef crest presented the highest coral cover, while the flat presented the lowest coral cover. No site effect was detected ($F_1 = 0.25$, $P = 0.62$), but a site vs. zone
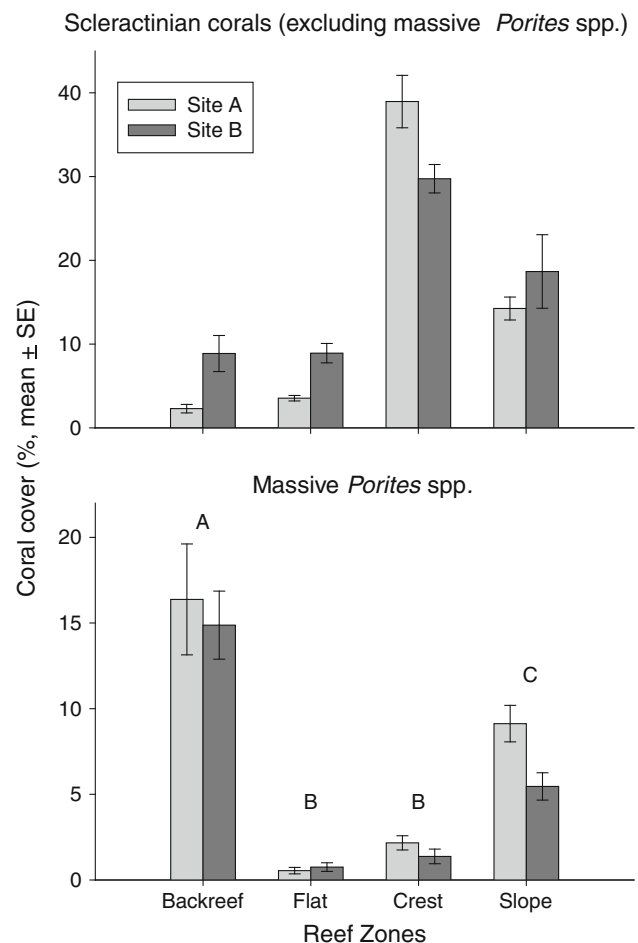
Fig. 2 Coral cover in the four reef zones at Lizard Island, Great Barrier Reef. *Upper bars* represent cover of all scleractinian corals, excluding massive *Porites* species, while *lower bars* represent cover of massive *Porites* spp. only. *Lower bars* marked with same letters showed no significant differences
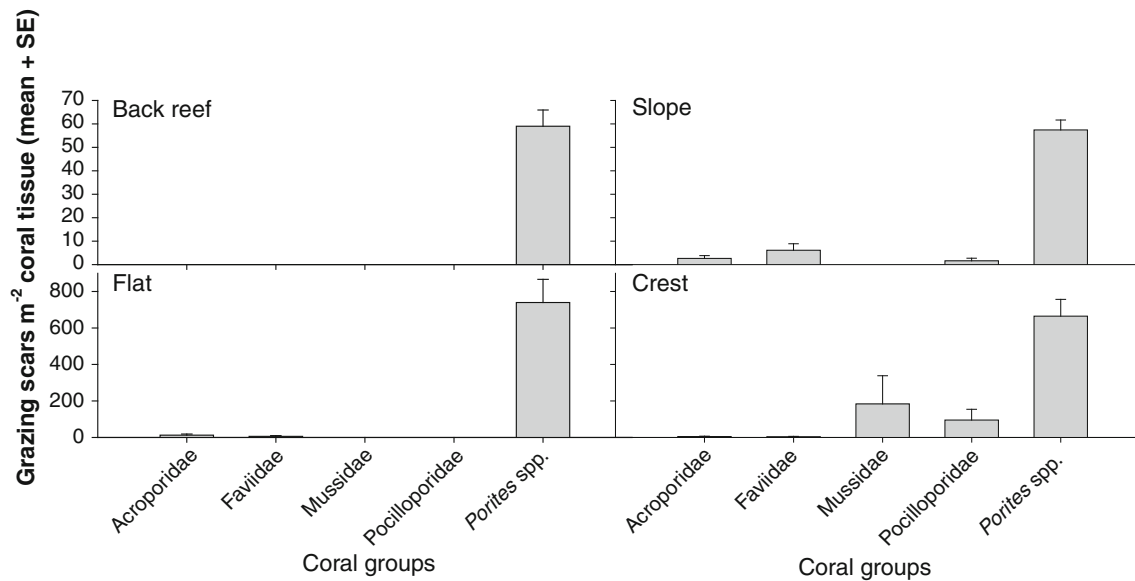
Fig. 3 Number of parrotfish grazing scars m^{-2} of coral on the main scleractinian coral groups at Lizard Island, GBR. For massive *Porites* spp., *bars* marked with same letters showed no significant differences. Note different *y* axis scales

interaction was significant as the flat in site B presented higher coral cover than in site A ($F_3 = 7.73$, $P < 0.001$). No significant correlation was found between total coral cover and number of parrotfish grazing scars m^{-2} of total coral tissue (Spearman rank $r_s = -0.11$, $P = 0.69$).

For abundance of massive colonies of *Porites* species only, backreef and slope presented higher values than reef flat and crest ($F_1 = 45.01$, $P < 0.001$), with no site effect ($F_1 = 1.99$, $P = 0.16$) or interaction between site and zone ($F_1 = 0.65$, $P = 0.59$, Fig. 2). The abundance of massive *Porites* spp. was negatively correlated with the number of parrotfish grazing scars m^{-2} of *Porites* in the four studied zones (Spearman rank $r_s = -0.81$, $P < 0.001$), indicating that reef zones with low *Porites* cover, i.e., the crest and flat, have higher coral predation by parrotfishes.

General patterns of abundance of parrotfish grazing scars on coral colonies were similar for the two study sites in the 2 months considered. Mean number of bites of parrotfish m^{-2} of coral surface varied among reef zones, ranging from 58.98 in the backreef to 952.48 in the reef flat. All reef zones presented higher number of parrotfish grazing scars on massive *Porites* spp. than on all other coral species combined (Fig. 3). Coral selectivity by parrotfishes varied among the reef zones, as some coral types were positively selected in some zones and avoided in others. Massive *Porites* spp. was the only coral type preferred by parrotfishes in all studied zones (Fig. 4).
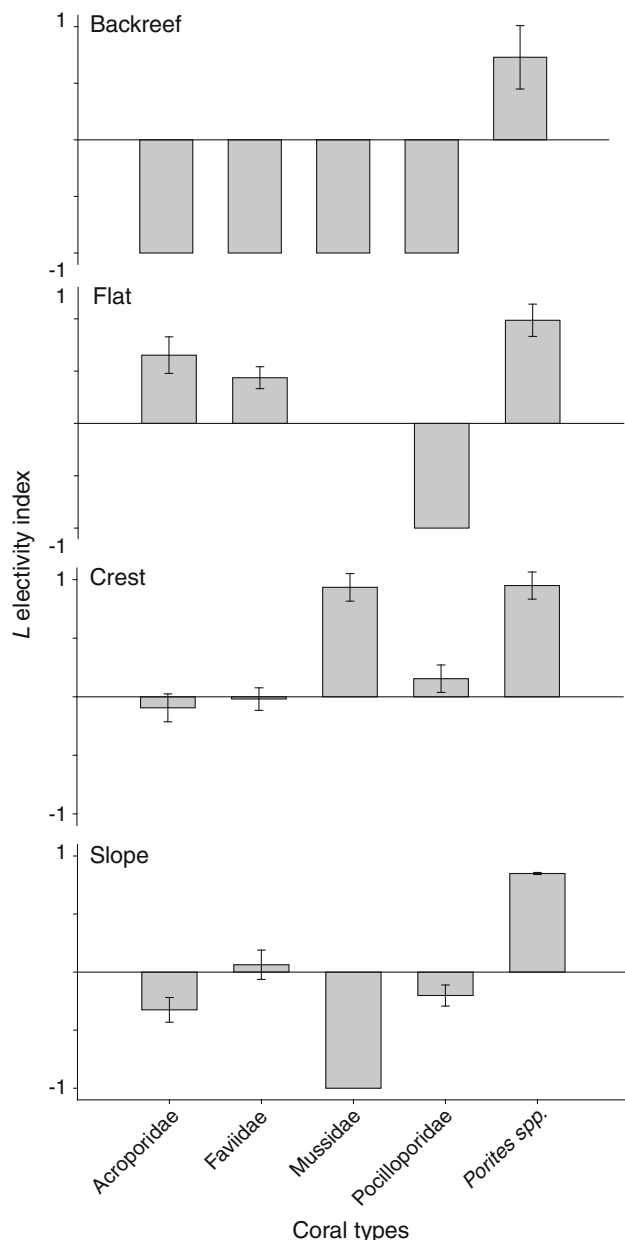
The number of parrotfish grazing scars m^{-2} of massive *Porites* spp. varied significantly among reef zones, as flat and crest presented higher number of parrotfish grazing scars m^{-2} *Porites* spp. than slope and backreef ($F_3 = 18.43$, $P < 0.001$, Fig. 3). No month ($F_1 = 0.47$,

$P = 0.50$) or site effects ($F_1 = 0.03$, $P = 0.86$) were detected, and all factor interactions were not found to be significant ($P \geq 0.87$ for all possible factor interactions).

The abundance of parrotfishes was variable among reef zones ($F_3 = 14.72$, $P < 0.001$), similar between the 2 months considered ($F_1 = 1.39$, $P = 0.24$), and slightly different between the two study sites, as values on the reef flat in site B were higher than in site A ($F_1 = 5.55$, $P = 0.02$, Fig. 5). The number of parrotfish grazing scars on massive *Porites* spp. was positively related to parrotfish abundance among reef zones (Spearman rank $r_s = 0.71$, $P = 0.002$).
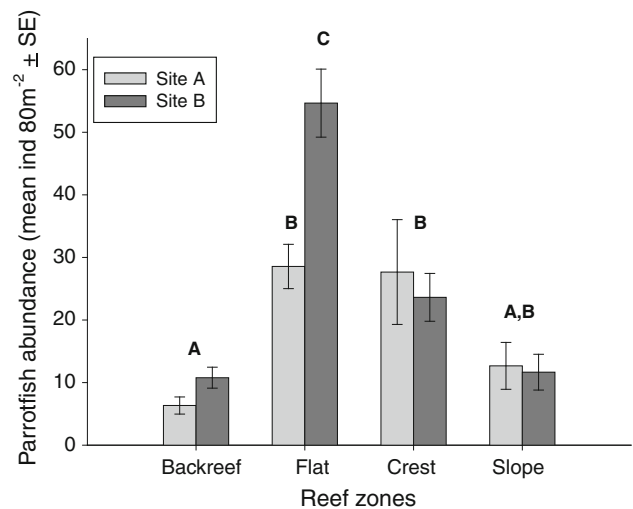
Grazed area of massive *Porites* spp. colonies varied among reef zones, but month and site effects and interactions between factors were not found to be significant ($P > 0.07$ for all possible comparisons). As with the number of grazing scars, massive *Porites* spp. colonies on the crest and flat had higher grazed area ($2.63\% \pm 0.74$ and $3.65\% \pm 2.55$, mean $\pm$ SE, respectively) compared to backreef and slope ($1.26\% \pm 0.40$ and $0.67\% \pm 0.16$, respectively).

The rate of new parrotfish grazing scars mirrored the static distributions. The rate of new parrotfish predation scars on massive *Porites* spp., in terms of the number of new grazing scars and area grazed by parrotfishes in 14 days, had similar results. In both analyses, no month or site effect were detected ($P > 0.10$ for all cases) and all interactions were not found to be significant ($P \geq 0.17$ for all possible interactions in both analyses). The reef flat had the highest number of new scars, followed by the crest, which had more than five times as many bites as the backreef and slope (Fig. 6a). The reef crest and flat also

Fig. 4 Feeding selectivity by parrotfishes on scleractinian corals (L Electivity Index ± 95% CI) at Lizard Island, Great Barrier Reef. Values of the 95% CI above/below zero indicate preference/avoidance

Fig. 5 Abundance of parrotfishes (mean ± SE) across a reef gradient on two study sites at Lizard Island, Northern Great Barrier Reef. *Bars* marked with same letters showed no significant differences

Discussion

This is the first study, to our knowledge, to quantify coral predation by parrotfishes in a high-diversity coral reef system in the Indo-Pacific. Overall, our results suggest that grazing by parrotfishes on corals is widespread (among habitats) and frequent on the GBR. The rates appear to be comparable to, or higher than, other coral reef regions. For example, predation pressure on massive *Porites* spp. on the GBR is up to four times higher than in the Colombian Caribbean, 60 times than in Belize, and 238 times than in Hawaii (Table 2). In all these locations, coral predation by reef fishes has been suggested to have important implications for coral distributions and survivorship (Littler et al. 1989; Bruckner and Bruckner 1998; Rotjan and Lewis 2005; Jayewardene et al. 2009). Parrotfish predation on corals may have a more important role on the GBR reefs than previously thought.

Our results suggest that total coral cover is not a good indicator of the abundance of parrotfish grazing scars across the reef gradient. In contrast, when considering just massive *Porites* colonies, a strong negative correlation was found between coral cover and the abundance of parrotfish bite marks. This difference is probably explained by the high selectivity of parrotfish for *Porites* when compared to other corals. As massive *Porites* spp. are highly targeted by parrotfishes, it is possible that grazing by parrotfishes directly affects the distribution of massive *Porites* spp. across the studied reef. This hypothesis is reinforced by a number of studies that suggest that coral predation by reef fishes may reduce or even prevent the development of target coral species on coral reefs (e.g., Neudecker 1977, 1979; Cox 1986; Littler et al.

had the highest grazed area and did not differ ($P = 0.55$), with at least three times the grazed area as the slope and backreef (Fig. 6b). Estimated annual loss of coral tissue reflected this among-habitat variation, with corals in the reef flat in site B having, approximately, 78% of total *Porites* spp. surface area grazed each year (Fig. 7). Losses in the other habitats were proportionally lower, ranging from 1.5% on the backreef at site A to 25% on the flat at site A (Table 1).
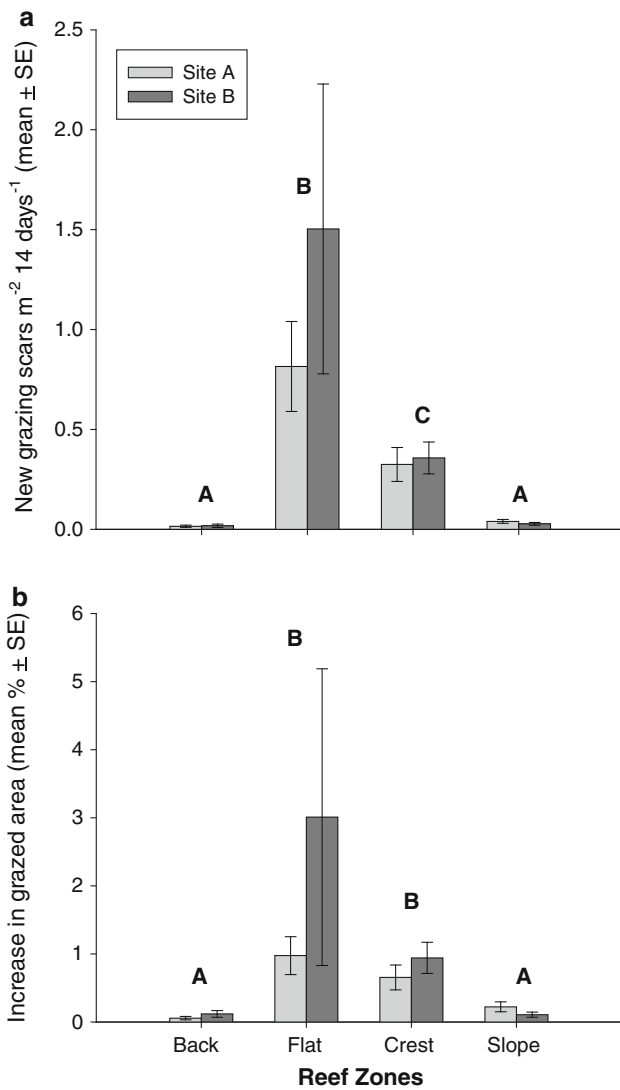
Table 1 Estimated area (%, average $\pm$ SE) of massive *Porites* spp. colonies grazed by parrotfishes in 1 year at Lizard Island, GBR

Reef zone	Area of massive Porites spp. grazed in 1 year (%, average)	
	Site A	Site B
Backreef	1.5 ± 0.6	3.1 ± 1.3
Flat	25.3 ± 7.2	78.2 ± 56.7
Crest	17.0 ± 4.7	24.5 ± 5.9
Slope	5.8 ± 1.9	2.8 ± 1.0

Jayewardene et al. 2009). Thus, our findings suggest that, as in the Caribbean and Hawaii, growth and development of coral colonies on the GBR are also negatively affected by fish feeding activity.

A number of previous studies have reported the use of *Porites* species by parrotfishes (e.g., Littler et al. 1989; Rotjan and Lewis 2005, 2008; Francini-Filho et al. 2008; Cole et al. 2008; Mumby 2009). Furthermore, other reef fish groups, such as bleniids, chaetodontids, gobids, labrids (wrasses), pomacentrids, monacanthids, and tetradontids, also positively select *Porites* spp. colonies when feeding on corals (Jayewardene and Birkeland 2006; Cole et al. 2008; Jayewardene et al. 2009). The morphological structure of *Porites* spp. is highly variable in terms of polyp size and position of tissue and fat in relation to the skeleton (Stimson 1987; Veron 2000; Cole et al. 2008). Hence, explanations for the selectivity for this coral genus by reef fishes would be too speculative, especially on the GBR, a region of high species richness of massive *Porites* (Veron 2000). Whatever the reasons for this selectivity, our results (as well as previous studies) suggest that *Porites* may be one of the most important coral groups in terms of a food source for reef fishes on coral reefs.

Levels of coral predation by parrotfishes in the present study were much higher than values reported in previous studies. This difference is particularly clear when comparing coral grazing pressure on the GBR with the Caribbean

Fig. 6 a Rate of new parrotfish grazing scars on massive *Porites* spp. (number of scars m^{-2} of coral tissue, mean $\pm$ SE) and **b** area of massive *Porites* spp. grazed by parrotfishes in 14 days (%, mean $\pm$ SE) at Lizard Island. *Bars* marked with same letters showed no significant differences

Fig. 7 A massive *Porites* spp. colony on the reef flat, site B, in two different occasions: 1st day of observation (*left*) and 14 days later (*right*). *Porites* colonies at this habitat were estimated to have, on average, 78.2% of their area consumed by parrotfishes every year

1989; Grottoli-Everett and Wellington 1997; Hixon 1997;

and Hawaii. The number of parrotfish grazing scars m^{-2} of

Table 2 Comparison of coral predation by fish scarring on coral reefs around the world

Region	Grazing scars m^{-2} of coral tissue (mean)	Monthly increase in coral grazed area (%)	% Colonies with recent parrotfish grazing scars	Coral species	Reference
GBR	58–952[a]	1.34–7.30[a]	17.08–64.81[a]	*Porites* spp.	This study
Hawaii	117	–	–	*Pocillopora meandrina*	Jayewardene et al. (2009)
	69	–	–	*Porites compressa*	
	4	–	–	*Porites lobata*	
Colombian Caribbean	–	0–1	–	*Montastrea annularis*	Sánchez et al. (2004)
Belize	0–300[a]	–	0–4.2[a]	*Montastrea annularis*	Rotjan and Lewis (2006)

[a] Values vary according to the reef zone/microhabitat

coral tissue on the GBR is up to 238 times higher than grazing scars in Hawaii and up to 60 times higher than in Belize. Experimental studies at these two locations found that corallivorous fishes have a significant role in shaping the distribution of targeted coral colonies, as transplanted coral nubbins were completely consumed by fishes within 1–5 days in some reef habitats (Littler et al. 1989; Jayewardene et al. 2009). As coral predation rates in the present study were comparable to or even higher than in Hawaii and Belize, parrotfish predation on corals probably affects the distribution of coral colonies, especially massive *Porites* spp., on the GBR.

The differences in the number of parrotfish grazing scars between the GBR and the Caribbean may be explained by the abundance of parrotfishes at each study location. In Belize, parrotfish mean abundance was about 20 individuals per 240 m^{-2} of reef (Rotjan and Lewis 2006). Converting our results to the same scale used by Rotjan and Lewis (2006), mean abundance of parrotfishes would range from about 30 to 180 individuals per 240 m^{-2} depending on the reef zone. Thus, the abundance of parrotfishes may be a strong indicator of the extent of corallivory among coral reef regions. This suggestion is reinforced by the fact that parrotfish abundance has been positively correlated with the number of parrotfish grazing scars on corals in both the present study and in Belize (Rotjan and Lewis 2006). However, this kind of relationship must be interpreted with care. In the present study, two of the most abundant parrotfish species, *S. psittacus* and *S. rivulatus*, have not been observed to prey either on corals or only on very rare occasions.

The low number of fish grazing scars m^{-2} of coral tissue in Hawaii compared to the GBR and even the Caribbean (Rotjan and Lewis 2006) may be related to the differences in corallivorous fish assemblages at these locations (probably a result of biogeography and local fishing pressure or coral assemblages). Fish predation in Hawaii is predominant on

non-massive *Porites* and is caused by tetradontids and monacanthids, which have lower feeding rates and are usually less abundant in coral reefs than parrotfishes (Guzmán and Robertson 1989; Jones et al. 1991), which are the main coral predators on *Montastrea annularis* in the Caribbean (Rotjan and Lewis 2006, 2008) and on massive *Porites* spp. on the GBR (Bellwood et al. 2003; Hoey and Bellwood 2008). These comparisons suggest that, in addition to abundance, identity of corallivorous fishes in coral reefs, and the coral prey species, may be factors shaping the intensity and nature of coral predation by fishes.

The rates of parrotfish scarring mirrored these static patterns. The rate of parrotfish predation on massive *Porites* spp. in the present study was higher than rates of coral consumption recorded at Rosario Islands, Colombian Caribbean (Sánchez et al. 2004). At Rosario Islands, increase in the grazed area of *M. annularis* usually did not exceed 1% of coral tissue per month (Sánchez et al. 2004). In contrast, on the GBR, colonies of massive *Porites* spp. have, on average, 1.34–7.30% of their total area consumed by parrotfishes every month, depending on the reef zone. The marked differences between these two studies suggest that rates of predation events by parrotfishes in the GBR are also high compared to the Caribbean and other regions.

One of the most marked patterns, for all analyses, of predation on massive *Porites* spp. in the present study was the variation in the impact of parrotfishes across the reef gradient. The crest and flat consistently presented higher *Porites* consumption than the back and reef slope. These results were similar to patterns of herbivory and grazing pressure of parrotfishes on algal communities in the Caribbean (Hay et al. 1983; Lewis and Wainwright 1985) and GBR (Russ 2003; Fox and Bellwood 2007; Hoey and Bellwood 2008). This relationship reinforces the well-recognized importance of parrotfishes in shaping the benthic community structure of coral reefs and the extent of spatial variation in their roles within these systems (Fox and

Bellwood 2007; Bellwood et al. 2004; Bonaldo and Bellwood 2009). To date, most studies emphasizing the importance of differential pressure of feeding by parrotfishes among reef habitats have been conducted on algae, especially in the Indo-Pacific (e.g., Russ 2003; Fox and Bellwood 2007; Bonaldo and Bellwood 2008, 2009). In the Caribbean and Hawaii, variation in coral predation by parrotfishes may lead to different coral communities among reef habitats, as the coral species that are positively selected for foraging by parrotfishes are usually rarer in areas where these fishes are more abundant (e.g., Neudecker 1979; Littler et al. 1989; Grottoli-Everett and Wellington 1997). The present study thus corroborates previous findings in the Caribbean and provides the first evidence for the potential importance of parrotfishes in shaping the distribution and abundance of coral colonies across reef zones on the GBR.

Although the overall results of the present study suggest that coral predation by reef fishes on the GBR is more intense than in the Caribbean and Hawaii, this does not necessarily means that corallivorous reef fishes have a higher impact on coral communities on the GBR than on the previously studied locations. Coral reefs on the GBR are markedly different in terms of geomorphological structure, coral species diversity, and structure of the corallivorous fish assemblages when compared to reefs in the Caribbean and Hawaii (Veron 2000; Cole et al. 2008; Rotjan and Lewis 2008; Jayewardene et al. 2009). As a consequence, conclusions from comparisons between these systems should be made with care, as the intensity or rate of a given process in each of this location does not necessarily mirror its relative importance in each ecosystem.

Yearly consumption rates of massive *Porites* spp. by parrotfishes in the present study reached mean values of up to 78.2% and maximum values as high as 134.9% of total colony area. Previous studies show that the healing of parrotfish grazing scars on corals is highly variable and can take from 2 months to 3 years to be completed (Bak and Steward-Van Es 1980; Bruckner and Bruckner 2000; Sánchez et al. 2004). Continuous predation is an energy drain for corals through the allocation of resources to tissue regeneration, and injured coral colonies usually have lower growth and recovery rates than intact colonies (Rotjan and Lewis 2005; Meesters et al. 1994). As a consequence, predation by parrotfishes may have a negative impact on the survival and energetics of massive *Porites* spp. colonies on the GBR, especially in habitats with low abundance of this coral. In recent years, massive *Porites* colonies on the GBR exhibited a significant decrease in calcification rates, possibly as a result of ocean acidification (Cooper et al. 2008; De'ath et al. 2009). The reduction in coral calcification has a direct impact on coral growth rates (De'ath et al. 2009), and as a consequence, it is possible that the negative effects of parrotfish grazing on coral growth may

have an even more profound impact on the development and survivorship of corals on reefs that are responding to ocean acidification.

The lack of significant differences, in all of the comparisons, between the two studied months (October and December) suggests that parrotfish feeding rates on massive *Porites* spp. colonies are not affected by different maturation states of polyps and coral colonies. Coral mass spawning for massive *Porites* spp. colonies happened during November 2008 on the GBR (A. Baird pers. comm.), suggesting that coral colonies would have higher number of gametes and mature reproductive structures in October compared to December. In the Caribbean, parrotfishes have been found to selectively graze reproductive structures in coral colonies, biting areas where there is a higher concentration of gametes and mature gonads (Rotjan and Lewis 2009). As we have not sampled coral colonies to verify the maturation stage of areas where bites were taken, it is not possible to know whether coral areas with parrotfish grazing scars had higher reproductive value than areas clear of grazing scars. However, although we cannot account for the specific location of grazing scars, our results suggest that overall patterns of coral predation by parrotfishes are not affected by differential maturation of coral colonies on the GBR.

The present study represents to the first detailed assessment of the importance of parrotfishes as coral predators in the GBR. Our results indicate that these fishes may have an important role in shaping the distribution of preferred coral types across the reef gradient. However, further studies are needed. For example, little is known about the species identity of corallivorous parrotfish, apart from a detailed study on *Bolbometopon muricatum* (e.g., Bellwood et al. 2003) and on the selectivity of corals as a foraging substratum and diet item by individual parrotfish species (e.g., Bellwood et al. 2003; Fox and Bellwood 2007). Also, although our studies do suggest that parrotfishes may be one of the main factors controlling the distribution of massive *Porites* spp. across the reef gradient on the GBR, further studies are necessary to evaluate the relative contribution of other factors, such as wave exposure, depth, and light intensity. The former, wave exposure, in particular, may limit the size of colonies in shallow, high-energy locations.

Overall, our study indicates that coral reefs in the GBR have high coral predation by parrotfishes compared to other areas where studies on coral predation by reef fishes have been conducted. Additionally, this study provides the first evidence for the potential importance of parrotfish predation in shaping the abundance and distribution of coral colonies among reef habitats on the GBR, as previously recorded for the Caribbean (Neudecker 1979; Cox 1986; Littler et al. 1989; Grottoli-Everett and Wellington 1997;

Hixon 1997). Parrotfishes may play a significant role in controlling the composition and structure of benthic communities, including corals, on most tropical Indo-Pacific reefs. The high parrotfish grazing pressure on corals on the GBR suggests that the extrapolation of general patterns from the Caribbean and Hawaii, where most studies on corallivory by parrotfishes have been conducted, may lead to an underestimation of the intensity of fish–coral interactions on coral reefs in the Indo-Pacific. Further studies in this region are essential if we are to obtain a better understanding of the impact of parrotfishes on high-diversity coral reefs.

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