Parrotfish abundance and selective corallivory on a Belizean coral reef

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Abstract

Parrotfish are important members of coral reef communities because they consume macroalgae that would otherwise outcompete reef-building corals for space. However, some Caribbean parrotfish species also feed directly on live corals, and thus have the potential to negatively impact coral fitness and survival. This study investigates selective grazing by parrotfish on particular coral species, differences in grazing incidence among reef habitats and intraspecific discrimination among colonies of several coral species. We also investigate spatial and temporal patterns of parrotfish species abundance across habitats on the Belize barrier reef, and examine correlations between parrotfish abundance and grazing intensity across reef habitats. We found that members of the *Montastraea annularis* species complex, major builders of Caribbean reefs, were preferred targets of parrotfish grazing across all reef habitats, while *M. cavernosa*, *Agaricia agaricites*, *Diploria strigosa*, *Porites astreoides* and *Porites porites* were not preferred; *Siderastrea siderea* was preferentially grazed only in the spur and groove habitats. Parrotfish grazing preferences varied across habitats; *M. annularis* was grazed most often in shallow habitats, whereas *M. franksi* was consumed more at depth. Although it was not possible to directly observe parrotfish grazing on corals, we did find a positive correlation between *Sparisoma aurofrenatum* abundance and *M. franksi* grazing incidence across habitats. Finally, when we compared our results to parrotfish abundances measured by a previous study, we found that *Sparisoma viride* and *Sp. aurofrenatum*, two species known to be corallivorous, had increased abundances between 1982 and 2004. In light of escalating threats on Caribbean reef corals, it would be important for future studies to evaluate the impact of parrotfish corallivory on coral survival.
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1. Introduction

Scleractinian corals are ecosystem engineers (sensu Jones et al., 1994) of tropical reefs, providing a structural base for one of the most diverse ecosystems world-wide. Parrotfish play an important role in the maintenance of coral reefs; as herbivores, they consume macroalgae that otherwise outcompetes reef-building corals for space (Lewis, 1986; Hughes, 1994; Bellwood et al., 2004). Parrotfish are known to feed selectively on different types of algae (Lewis, 1985; Bellwood and Choat, 1990; Bruggemann et al., 1994a). In addition, some Caribbean parrotfish species, including *Sparisoma viride*, *Scarus vetula*, *Sc. guacamaia* and *Sparisoma aurofrenatum*, have been reported to feed

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directly on living corals (Gygi, 1975; Frydl, 1979; Littler et al., 1989; Bruggemann et al., 1994b; Miller and Hay, 1998; Bruckner et al., 2000; Garzon-Ferreira and Reyes-Nivia, 2001; Sanchez et al., 2004; Rotjan and Lewis, 2005). Because of the potential negative effects such parrotfish corallivory may have on coral fitness (Van Veghel and Bak, 1994; Meesters et al., 1996; Rotjan and Lewis, 2005), it is important to understand whether parrotfish feed selectively on coral, as might be predicted by their algal diet selectivity. However, little is known about parrotfish feeding selectivity among coral species and only a few studies have quantified spatial patterns of parrotfish corallivory (Littler et al., 1989; Bruggemann et al., 1994b; Garzon-Ferreira and Reyes-Nivia, 2001).

In this study, we investigated whether parrotfish discriminate among coral species, and whether coral grazing intensity changes across different habitats on the Belizean barrier reef. We also explored whether or not grazing is uniform or varies across colonies of particular coral species, as well as the spatial and temporal patterns of parrotfish species abundance across reef habitats. Finally, we correlated parrotfish abundance with grazing intensity across reef habitats to provide insight into which parrotfish species might be responsible for observed patterns of corallivory.

2. Methods

2.1. Study and transect locations

This study was conducted in February 2004 at Carrie Bow Cay (16°48′N and 88°05′W) on the Belizean barrier reef. Six major habitats were examined for parrotfish species abundances, as well as the incidence and extent of coral grazing: the backreef (1–2 m depth), lagoon (2–4 m), upper spur and groove (3–8 m), lower spur and groove (8–20 m), inner reef slope (20–30 m) and the crest of the outer ridge (15–25 m) (described in detail by Rüetzler and Macintyre, 1982). Within each reef habitat, we measured parrotfish and coral abundances, grazing incidence and extent within the same five 30 m × 2 m belt transects. Transect locations were chosen haphazardly (wherever the anchor landed), but were oriented towards areas with the greatest live coral cover (as opposed to sand or rubble substrate).

2.2. Parrotfish species abundances

There are 14 species of Caribbean reef parrotfish (Humann and Deloach, 2002). We measured abundance of all parrotfish species encountered by conducting four consecutive passes over each 30 m × 2 m transect ($n = 5$ per reef habitat), then summing counts to yield individuals per 240 m², following the methods of Lewis and Wainwright (1985). We summed four consecutive passes in order to increase the probability of including highly mobile parrotfishes; it is possible, but not likely, that some individuals could have been counted more than once. We separately counted adults and juveniles for each species, distinguished by body size and coloration as described in Humann and Deloach (2002). Because only adult parrotfish are known to consume live coral (Bruggemann et al., 1994c,b), we present data here only for adults (both initial and terminal phase). Caribbean parrotfish are mainly considered to be herbivorous, yet *Sp. viride*, *Sp. aurofrenatum* and *Sc. vetula* also consume some live coral as part of their diet. In particular, *Sp. viride* adults allocate 1–1.3% of their bites to live corals in shallow reef zones in Bonaire, Netherlands Antilles (Bruggemann et al., 1994a,b), and we have observed that about 2% of all *Sp. viride* bites are taken on live *Porites astreoides* corals on the back-reef habitat of Carrie Bow Cay, Belize (S. Lewis, unpublished data). We compared the abundance of each parrotfish species across habitats using Kruskal–Wallis non-parametric comparisons.

2.3. Relative coral abundance

In assessing coral species abundance across reef habitats, we focused on nine scleractinian corals that have been identified as the main targets of parrotfish grazing in the Caribbean (Garzon-Ferreira and Reyes-Nivia, 2001): *Agaricia agaricites*, *Diploria strigosa*, *Montastraea annularis*, *M. cavernosa*, *M. faveolata*, *M. franksi*, *Porites porites*, *P. astreoides* and *Siderastrea siderea*. Although other coral species have been reported as grazed (Frydl, 1979; Bruckner and Bruckner, 2000), we did not observe any additional coral species with grazing scars in our transects in Belize. *M. annularis*, *M. faveolata* and *M. franksi* are very closely related, and are commonly grouped together as the *M. annularis* species complex (Weil and Knowlton, 1994); this complex has been reported to be grazed throughout the tropical Atlantic (Bythell et al., 1993; Bruggemann et al., 1994b; Bruckner and Bruckner, 1998; Bruckner et al., 2000; Sanchez et al., 2004). Caribbean *Porites* spp. have also been reported as grazed in Barbados, Belize, Florida and the Virgin Islands (Frydl, 1979; Littler et al., 1989; Bythell et al., 1993; Miller and Hay, 1998; Rotjan and Lewis, 2005). For each of these individual coral species, we quantified coral abundance along five 30 m × 2 m transects in each habitat (the same transects
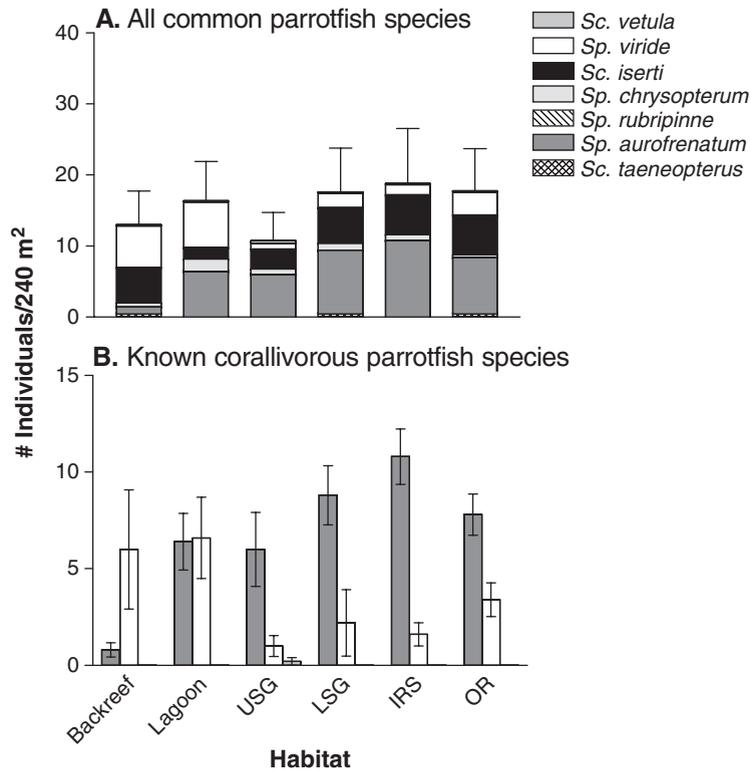
Fig. 1. (A) Adult parrotfish densities across six reef habitats (means for $n=5$ transects in each habitat+1 S.E. for total parrotfish density). (B) Densities of known corallivorous parrotfish species (*Sp. aurofrenatum*, *Sp. viride* and *Sc. vetula*) across reef habitats. Bars show mean±1 S.E. for $n=5$ transects per habitat.

as used for assessing parrotfish abundance). It should be noted that, for *M. annularis*, we included all ramets together as a single colony. Coral abundance (# colonies per 60 m^2) was measured by counting all colonies greater than 25 cm^2 (maximum size was 400 dm^2) within 1 m on either side of the transect line. Relative abundance was calculated as the number of colonies of each species divided by the total number of coral colonies counted per transect.

2.4. Estimating the incidence and extent of coral grazing

Parrotfish produce distinctive grazing scars as they excavate portions of the skeleton along with coral tissue (Gygi, 1975; Frydl, 1979; Bruckner et al., 2000; Sanchez et al., 2004; Rotjan and Lewis, 2005); shallow spot-biting scars are usually paired (average bite size=25.4± 2.04 mm^2 on *Montastraea* spp. corals, $n=15$ bites), reflecting marks made by the upper and lower jaws (Frydl, 1979; Bellwood and Choat, 1990). Because direct observations of parrotfish consuming live coral are infrequent, we have followed Frydl (1979) and numer-

ous others (Littler et al., 1989; Miller and Hay, 1998; Sanchez et al., 2004) in using the presence of these paired scars as an indicator of spot-biting by parrotfish. Focused biting, whereby parrotfish repeatedly excavate deep portions of a single coral colony (Bruckner et al., 2000), has only been observed on *P. astreoides* in the backreef habitat (Rotjan and Lewis, 2005). The majority of grazing observations reported here, with the exception of *P. astreoides*, are of spot-biting scars. Although focused biting has been implicated in territorial marking by adult, terminal phase *Sp. viride* males, spot-biting does not appear to be associated with territoriality (Bruckner et al., 2000). We determined parrotfish grazing incidence (percentage of colonies grazed) for each of the nine coral species in each transect. Colonies were classified as grazed if they showed at least two distinct parrotfish grazing scars: intact colonies lacked such scars. Both freshly made and recovering grazing scars were counted. To determine grazing extent, we counted the number of distinct parrotfish bites and estimated coral colony surface area (length × width) for each grazed colony; grazing extent was then calculated as the number of bites per dm^2.
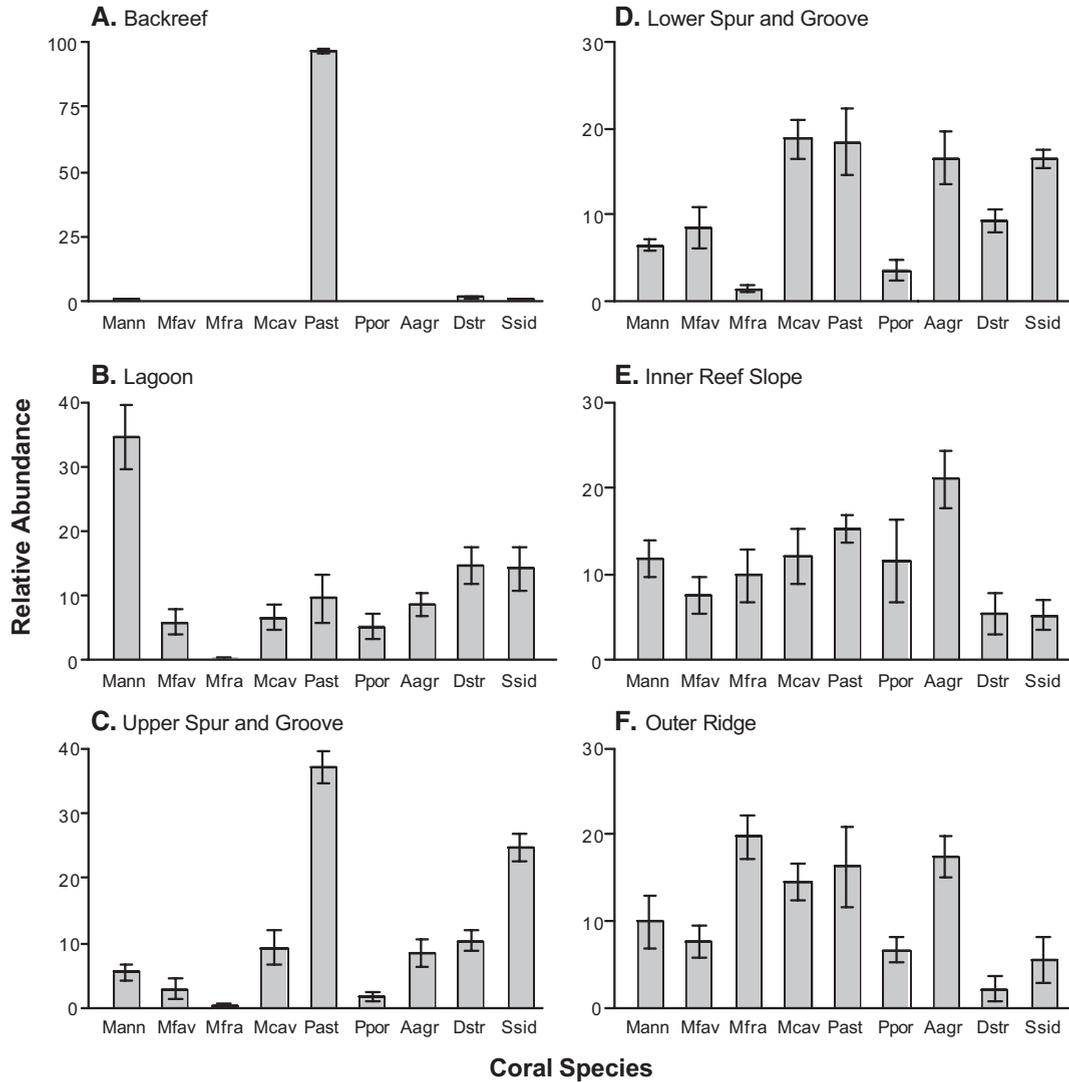
Fig. 2. Relative abundances of nine coral species in six habitats along the Belize barrier reef (A–F). Means ± 1 S.E. shown for $n = 5$ 60 m² transects in each habitat.

2.5. Grazing selectivity

To determine parrotfish selectivity for different coral species, we calculated Ivlev's electivity index (E_i) (Ivlev, 1961) for each habitat as:

$$E_i = \frac{r_i - n_i}{r_i + n_i}$$

where r_i is the proportion of all parrotfish bites that were taken on the ith coral species, and n_i is the proportional abundance of the ith coral species (based on colonies). For each habitat, we summed the data across the five 60-m² transects to yield electivities based on a 300-m² area. Electivity varies from -1.0 to $+1.0$, with negative

values indicating avoidance and positive values indicating preference. Coral species grazed in direct proportion to their abundance have electivities of zero. To determine if grazing extent was uniform across all colonies of a given coral species within each habitat (for species with >10 grazed colonies), we used a Kolmogorov–Smirnov test to a uniform distribution.

2.6. Correlating parrotfish abundances with coral grazing incidence

Although we have seen *Sp. viride* consume live *P. astreoides* and *Montastraea* spp. corals, direct observations of such grazing events are rare. Thus, it is impossible

to use behavioral observations to quantify preferences of particular parrotfish for different coral species. Instead, we used an indirect method that examined the correlation between parrotfish species abundances and differences in grazing incidence across habitats with Spearman rank correlation tests. For these correlational tests, we focused on those parrotfish that we or others have directly observed feeding on live corals (*Sp. viride*, *Sp. aurofrenatum* and *Sc. vetula*), and focused on corals in the *M. annularis* species complex, based on their high electivity indices. To compare parrotfish abundance across time, we compared our data to similar data collected in 1982 in the same habitats at Carrie Bow Cay (Lewis and Wainwright, 1985); four consecutive passes of 50 m×2 m transects were summed to yield counts of individuals per 400 m^2.

3. Results

3.1. Parrotfish abundances and distribution

There were marked differences in species abundances of adult parrotfish across habitats (Fig. 1A and B). *Sc. iserti* was highly abundant in most habitats, but these small parrotfishes are not known to be corallivorous. *Sc. vetula*, which has been reported to graze live coral, showed low abundance across all habitats. Of the remaining corallivorous parrotfish species, *Sp. viride* and *Sp. aurofrenatum* were abundant across many reef habitats (Fig. 1B). *Sp. aurofrenatum* reached its highest level on the inner reef slope (Kruskal–Wallis H=15.865, df=5, p=0.007), while *Sc. vetula* and *Sp. viride* abundances did not differ across habitats (*Sc. vetula*: H=5.000, df=5, p=0.416; *Sp. viride*: H=8.925, df=5, p=0.112).

3.2. Coral abundances and distribution

Relative abundances of the nine scleractinian species commonly targeted by parrotfish varied across reef habitats (Fig. 2); *P. astreoides* was dominant in the shallow backreef habitat, while all of the coral species were present in the remaining habitats. Different species within the *M. annularis* species complex dominated different habitats, with *M. annularis* being more abundant than the others in shallower habitats (the lagoon and upper spur and groove), while *M. franksi* predominated in the deepest habitat (outer ridge).

3.3. Parrotfish grazing selectivity

Parrotfish grazing incidence was highest on *M. annularis* corals (over 55% of colonies across all hab-

Table 1
Parrotfish grazing incidence on scleractinian coral species (calculated across all reef habitats) on the Belizean barrier reef

Species	% Grazed (total # colonies)
M. annularis	55.86 (222)
M. franksi	39.02 (82)
M. faveolata	37.23 (94)
S. siderastrea	10.41 (221)
A. agaricites	3.77 (212)
P. porites	2.33 (86)
P. astreoides	1.93 (931)
M. cavernosa	1.07 (187)
D. strigosa	0.68 (146)

Species are ordered from highest to lowest grazing incidence.

itats showed evidence of parrotfish grazing), followed by *M. franksi* and *M. faveolata*, respectively (Table 1). Similarly, parrotfish electivity indices for nine coral species indicate selective grazing on particular coral species (Fig. 3). Across all reef habitats, three *Montastraea* species were preferentially grazed, while *M. cavernosa* consistently had low electivity and grazing incidence (Fig. 3, Table 1). Contrary to expectation, coral species heavily grazed by parrotfish in a backreef habitat such as *P. porites* (Littler et al., 1989) and *P. astreoides* (Rotjan and Lewis, 2005), showed low electivity indices, indicating that fewer colonies were grazed than expected based on their abundance. *S. siderea* corals showed moderately high electivity indices in the spur and groove habitats, although these did not exceed *M. annularis* species complex electivities in any habitat.

However, even for preferred *Montastraea* species, grazing extent was not uniform across all colonies within a coral species (Fig. 4). In most habitats, a few colonies of *Montastraea* spp. were more heavily grazed by parrotfishes (9–12 bites/dm^2), while the majority showed little or no parrotfish grazing (1–3 bites/dm^2) (Fig. 4). The frequency distributions of *Montastraea* spp. grazing extent deviated significantly from a uniform distribution (Table 2), with the exception of *M. annularis* on the inner reef slope. In the latter case, the overall levels of grazing were low (maximum grazing extent=1.5 bites/dm^2), compared to grazing on this and other members of the *M. annularis* species complex in other habitats (up to 14 bites/dm^2).

When we examined the correlation between species abundances of known corallivorous parrotfish and grazing incidence on corals in the *M. annularis* species complex across six reef habitats, we found that grazing incidence on *M. franksi* was positively correlated with *Sp. aurofrenatum* abundance (Fig. 5, Spearman rank r_s=0.886, n=6, p=0.05). There were no other significant correlations between *Sp. aurofrenatum* or *Sp. viride*
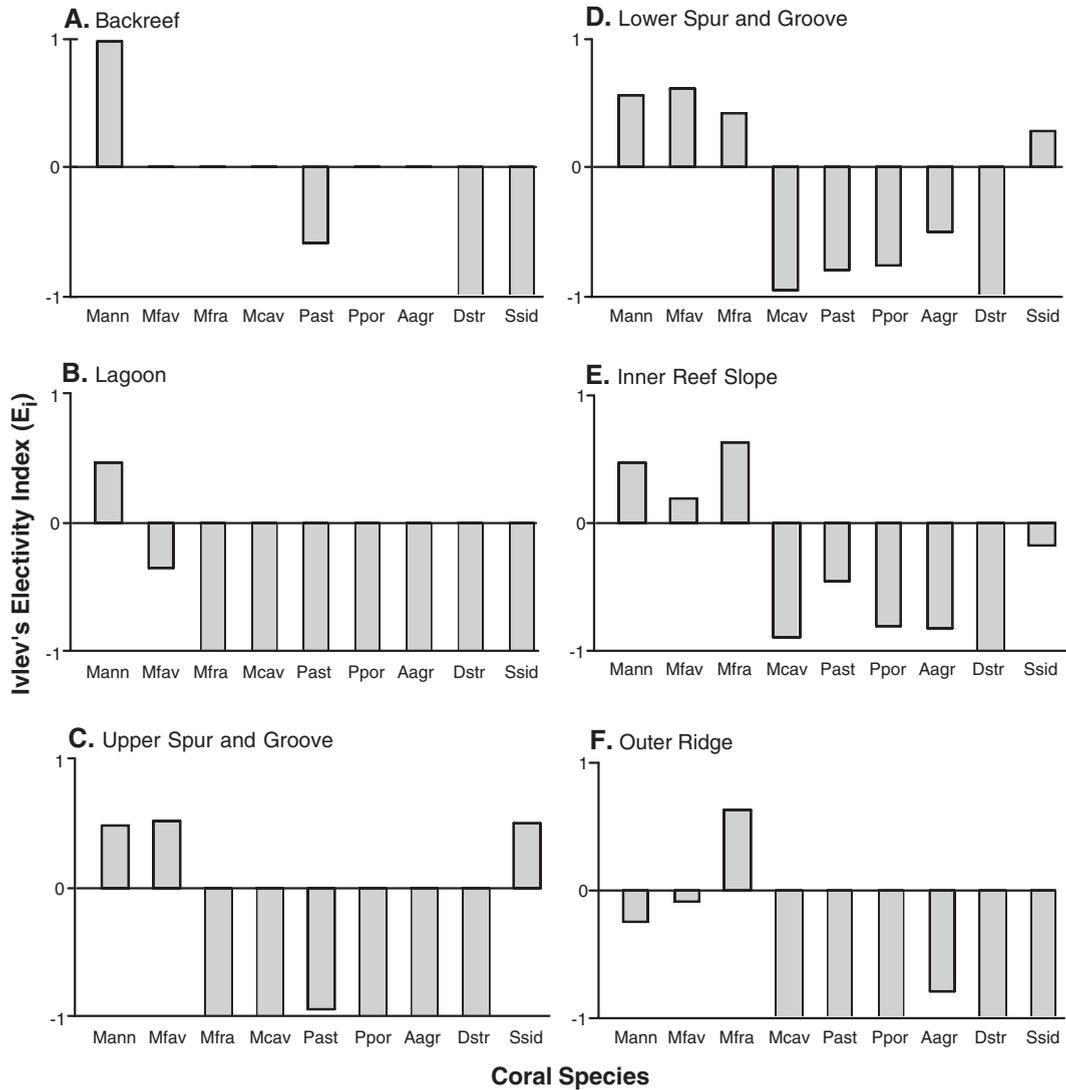
Fig. 3. Feeding selectivity by parrotfish on nine coral species within each of six habitats (A–F). Ivlev's electivity index ($E_i > 0$ is preferred, $E_i < 0$ is avoided) was calculated based on each coral species' relative abundance and relative bite frequency, both measured within a 300-m^2 area within each habitat.

parrotfish abundance and grazing incidence for any other *Montastraea* species (all $p > 0.1$). Comparisons of transect data between 1982 and 2004 indicated reduced abundances of *Sc. iserti*, *Sc. vetula*, *Sp. chrysopterum* and *Sp. rubripinne* (Fig. 6). The only parrotfish species that increased in abundance across most habitats were *Sp. viride* and *Sp. aurofrenatum* (Fig. 6).

4. Discussion

The results of this study demonstrate that parrotfish preferentially graze corals in the *M. annularis* species complex, based on higher grazing incidence than expected given their relative abundance. These results

offer the most comprehensive study to date of parrotfish grazing preferences on corals across reef habitats. Our findings are in accord with others that have described particularly high levels of parrotfish grazing on live *Montastraea* spp. corals (Frydl, 1979; Bythell et al., 1993; Bruckner and Bruckner, 2000; Garzon-Ferreira and Reyes-Nivia, 2001; Sanchez et al., 2004). Some previous studies have also reported intense parrotfish grazing on *P. astreoides, P. porites* and *P. porites furcata* (Gygi, 1975; Littler et al., 1989; Miller and Hay, 1998; Rotjan and Lewis, 2005). For example, parrotfish predation appears to be responsible for both partial and total colony mortality of *P. astreoides* in the back-reef habitat in Belize (Rotjan and Lewis, 2005).
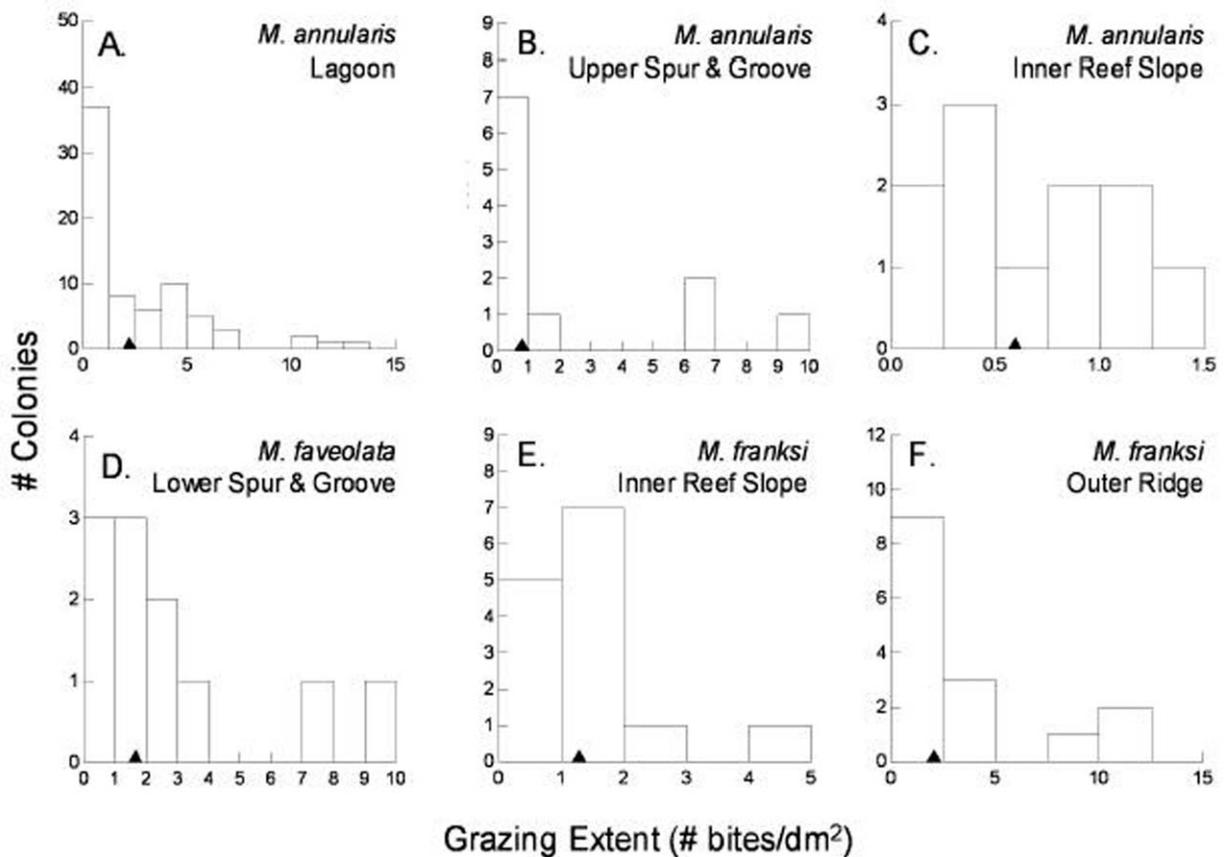
Fig. 4. Frequency histograms of parrotfish grazing extent per colony across individual colonies of three *Montastrea* species in various habitats (A–F). Black triangles along the x-axis represent the median grazing extent. Data shown for all habitats with >10 colonies grazed for a given species. Differential grazing was examined using a Kolmogorov–Smirnov goodness-of-fit test to a uniform distribution (Table 1).

However, as the present results indicate that these corals are grazed less often than would be expected based on their abundance, *Porites* spp. may only be subject to high levels of grazing when more preferred coral species are absent. This may represent an example of associational resistance, in which palatable but less preferred species are protected in habitats where preferred species are more abundant (reviewed by Huntly, 1991). Differences in coral species composition, therefore, are likely to contribute to observed variation across habitats in grazing incidence on a given coral species.

Members of the *M. annularis* species complex may be preferred due to a possible lack of defensive characteristics, high nutritional quality or both. Despite parrotfish preference for grazing algae off dead corals with low skeletal density (Littler et al., 1989; Bruggemann et al., 1996), a comparison across species from the literature revealed no clear patterns between the incidence of parrotfish grazing on live corals and skeletal densities of different species (Highsmith, 1981; Littler et al., 1989;

Garzon-Ferreira and Reyes-Nivia, 2001). Instead, parrotfish preferences for different coral species may be related to differences in nutritional quality. Parrotfish have been shown to prefer algal diets with higher nitrogen content (Bruggemann et al., 1994b; Goecker et al., 2005). It would be interesting to see if preferred coral species in the *M. annularis* species complex have higher nutritional quality compared to non-preferred

Table 2
Results of Kolmogorov–Smirnov goodness-of-fit tests to uniform distributions of parrotfish bites (# bites/dm^2) across all coral colonies of different *Montastrea* species in different reef habitats

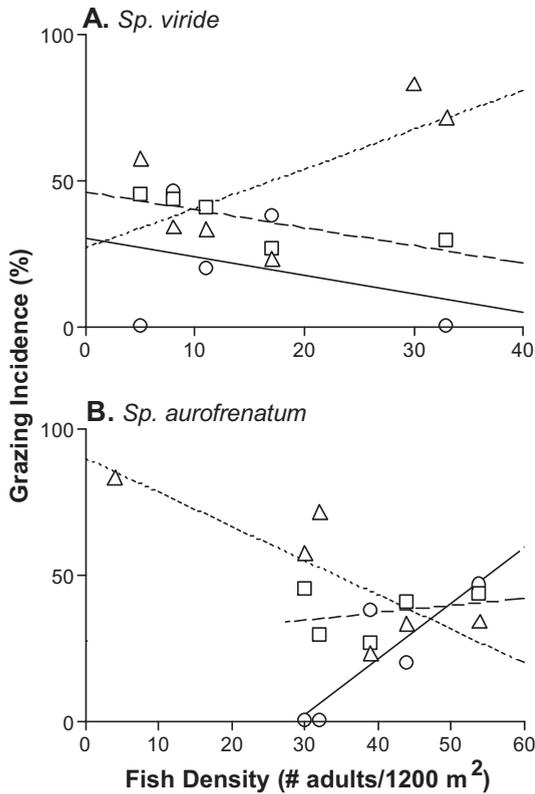| Species	Habitat	N	MaxDif	P
M. annularis	Lagoon	73	0.575	0.0001**
M. annularis	USG	11	0.429	0.0230*
M. annularis	IRS	11	0.273	0.3250
M. faveolata	LSG	11	0.727	0.0001**
M. franksi	IRS	14	0.643	0.0001**
M. franksi	OR	15	0.695	0.0001**

Fig. 5. Correlation of parrotfish grazing incidence on *Montastrea* corals with known corallivorous parrotfish densities (# fish per 240 m²) across six reef habitats: (A) *Sp. viride* and (B) *Sp. aurofrenatum*. Triangles and dotted lines represent *M. annularis*; squares and dashed lines indicate *M. faveolata*; circles and solid lines indicate *M. franksi*. Linear regression lines are plotted.

corals. Interestingly, *M. cavernosa* seems to be avoided by parrotfish in all habitats, suggesting that it may lack such nutritional benefits, or be chemically or structurally defended against parrotfish predation. Furthermore, although it is possible that different *Symbiodinium* spp. types may contribute to differences in parrotfish grazing preferences, recent work has shown that it is more likely that parrotfish grazing influences *Symbiodinium* type (Rotjan et al., in press). Regardless, it is clear from our study that certain *Montastraea* spp. are most likely to be consumed by corallivorous parrotfish. Although the direct fitness costs of corallivory have yet to be determined, previous studies have shown reduced coral growth and reproduction from artificial lesions (Meesters et al., 1994, 1996; Van Veghel and Bak, 1994), which mimic parrotfish grazing scars. Corallivory may thus have major consequences because *Montastraea* spp. are major reef-building corals on Caribbean reefs.

Interestingly, parrotfish grazing preferences shifted across reef habitats, even when coral species composition

remained the same. For example, different members of the *M. annularis* species complex were preferred in different reef habitats, even though they coexist in Belize from depths of 3–30+ m. *M. annularis* was the most abundant and also the most preferred *Montastraea* species in shallow habitats, whereas *M. franksi* was more abundant in deeper habitats. The distributional differences we observed are similar to distributions of the *M. annularis* species complex in Panama, where *M. annularis* exists mainly in shallower depths and *M. franksi* is found consistently deeper than the others (Weil and Knowlton, 1994). Although all members of the *M. annularis* species complex are available and preferred in intermediate depths (the lower spur and groove and the inner reef slope), only *M. franksi* is preferentially consumed in the deepest habitat (on the outer ridge). This suggests that each species may offer different advantages (perhaps nutritional) in each habitat. Alternatively, shifts in grazing preferences may reflect differences in fish species composition across habitats. Although this study did not determine which parrotfish species were responsible for observed coral grazing, we found a positive correlation between *Sp. aurofrenatum* density in different habitats and grazing on *M. franksi*, suggesting that this parrotfish may be responsible for observed grazing. Further investigation is needed to quantify grazing preferences of particular parrotfish species.

In addition, when we compared data from 1982 with our data, we found that parrotfish species abundance did not change uniformly across habitats over time. The upper spur and groove and outer ridge habitats experienced an overall increase in parrotfishes, perhaps because they are the most structurally complex habitats on the Belizean reef (Rüetzler and Macintyre, 1982). On the other hand, the backreef and inner reef slope habitats declined in overall parrotfish abundance. We found that *Sp. viride* and *Sp. aurofrenatum* increased in abundance across habitats from 1982 to 2004. Given that both *Sp. viride* and *Sp. aurofrenatum* are known corallivores (Frydl and Stearn, 1978; Bythell et al., 1993; Bruggemann et al., 1994b; Miller and Hay, 1998; Bruckner et al., 2000), it would be important for future studies to determine the impact of potentially increased corallivory on coral survival.

Parrotfish populations are changing rapidly throughout the Caribbean due to a variety of natural and anthropogenic forces, including commercial and artisinal overfishing, disease, and loss of habitat due to increased incidence of major storms (Munro, 1980; Hughes, 1994; Aronson and Precht, 2000; Hawkins and Roberts, 2004; Valentine and Heck, 2005). This study highlights the need to include the full dietary range of parrotfishes into models of reef trophodynamics because parrotfish corallivory
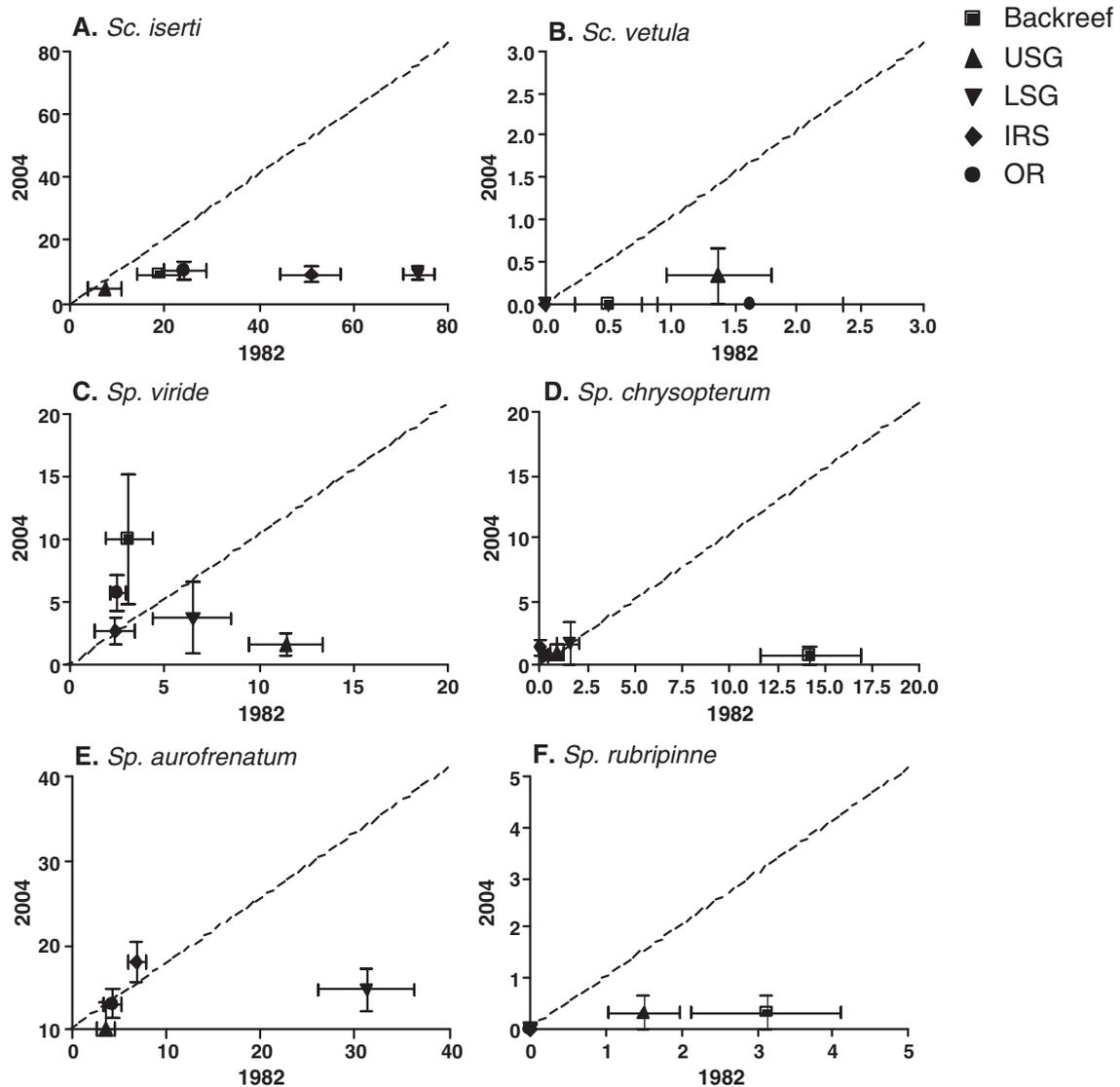
Fig. 6. Comparison of parrotfish species abundances (A–F) measured as # fish per 240 m^2 across different reef habitats at Carrie Bow Cay, Belize between 1982 ($n=8$ transects, mean ± 1 S.E. shown) to 2004 ($n=5$ transects, mean ± 1 S.E. shown). Dashed lines represent a line of equality (no change in parrotfish species abundance over time).

may have direct negative effects on corals, while parrotfish herbivory will simultaneously have indirect positive effects on corals. As reef conservation efforts focus on maintaining redundancy in herbivorous guilds through marine protected areas (Bellwood et al., 2003; Mumby et al., 2006), additional attention needs to be paid to the broader ecological role of parrotfish in reef communities.

Acknowledgements

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