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Discriminating causes from consequences of persistent parrotfish corallivory

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ABSTRACT

A detailed understanding of the dual role of parrotfish as both key herbivores and potentially important corallivores is essential to the study of coral health and reef trophodynamics. Some Caribbean parrotfish regularly consume live coral, and discriminate both among coral species and among colonies within a particular species. While they prefer *Montastraea* spp. corals, which are dominant Caribbean reef builders, causes of selective and persistent grazing of certain colonies remain unknown. We manipulated coral exposure to parrotfish grazing through a long-term cage exclusion experiment in Belize, comparing initially grazed vs. intact (non-grazed) *Montastraea* spp. colonies. We measured nutrition-related characteristics (C:N ratio, %C, and %N) as well as defensive characteristics (nematocyst density and skeletal hardness) to determine if any of these variables accurately predicted parrotfish grazing. There were substantial reductions in coral nutritional quality (C:N) associated with parrotfish grazing, although these changes appear to be a consequence rather than a cause of parrotfish selectivity. Likewise, nematocyst densities were suppressed in grazed corals, also likely a result of chronic grazing stress. We found no intraspecific differences in skeletal hardness related to grazing. These results provide further demonstration of the physiological consequences of grazing, but the cause of preferential grazing by parrotfishes on certain *Montastraea* spp. colonies still requires further investigation.

1. Introduction

Scleractinian corals constitute the foundation of tropical reef ecosystems, and therefore much attention has been given to factors influencing their performance. Corallivory, the consumption of live coral, can be an important determinant of coral growth, survival, and fitness, with potentially widespread implications since there are over 160 tropical corallivores worldwide (reviewed by Cole et al., 2008; Rotjan and Lewis, 2008). A growing body of evidence has documented that Caribbean parrotfish, classically regarded as important reef herbivores (Lewis, 1986; Hughes, 1994; McClanahan and Muthiga, 1998), are also regular corallivores (Gygi, 1975; Frydl, 1979; Littler et al., 1989; Bruggemann et al., 1994; Miller and Hay, 1998; Bruckner et al., 2000; Garzon-Ferreira and Reyes-Nivia, 2001; Sanchez et al., 2004; Rotjan and Lewis, 2005,2006; Rotjan et al., 2006). In the Caribbean, the ecological importance of parrotfish corallivory is controversial (Mumby, 2009), largely because common corallivorous species, for example *Sparisoma viride* (the stoplight parrotfish), only consume live coral as 2% of its diet, and coral colonies often recover from grazing incidents (reviewed by Henry and Hart, 2005; Rotjan and Lewis, 2008). Regardless, several Caribbean parrotfish species are known to preferentially graze particular coral species, specializing on colonies of *Montastraea* spp. (Garzon-Ferreira and Reyes-Nivia, 2001; Rotjan and Lewis, 2006). This grazing selectivity is particularly important, given that *Montastraea* spp. are major builders of Caribbean reefs (Veron, 2000). Yet, the explanations for selective parrotfish grazing on corals have only begun to be investigated.

Directly observing patterns of selective corallivory is difficult because underwater observations of parrotfish grazing mostly reveal patterns of herbivory (Lewis and Wainwright, 1985). Most studies of corallivory take an indirect approach by examining grazing scars on corals, but one limitation of indirect observations is the inability to determine corallivory cause from consequence at a single snapshot in time; in other words, to determine whether coral characteristics change in response to parrotfish grazing (consequence) or whether parrotfish grazing is instead driven by certain coral characteristics (cause). However, coupling repeated observations with corallivore-exclusion manipulations is one way to effectively distinguish cause from consequence without directly observing parrotfish corallivory.

Several coral characteristics may either incite or be affected by corallivory. Such features may be nutritional or defensive, with the rationale that corallivores should be attracted to colonies with high nutritional quality and/or low deterrence. Within coral species, parrotfish grazing intensity varies; some colonies experience very high levels of grazing, whereas others display only a few bites (Miller and Hay, 1998; Rotjan and Lewis, 2006). One explanation proposed

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for parrotfish selectivity among coral species (interspecific selectivity) is based on differences in coral skeletal hardness. Littler et al. (1989) found that parrotfish prefer *Porites porites* f. *furcata* over *Porites astreoides* in Belize, and found that this difference was due to species-level differences in skeletal hardness characteristics. Other defensive characteristics may include nematocyst stinging cells, which have been shown to deter grazing by butterflyfish in Pacific corals (Gochfeld, 2004). The presence of surface-visible macroborers such as serpulid polychaetes and barnacles explains intraspecific selectivity by parrotfish feeding on shallow *P. astreoides* in Belize (Rotjan and Lewis, 2005). For *Montastraea* spp., explanations of selective corallivory have thus far been limited to high gonad density during the reproductive season (Rotjan and Lewis, 2009), but no year-round explanation has been determined. On the other hand, several consequences of real or simulated corallivory have been documented, including partial or total colony mortality leading to suppressed colony growth (e.g. Meesters et al., 1994; Edmunds and Lenihan, 2010), changes in *Symbiodinium* spp. density and diversity (Rotjan et al., 2006), and decreased reproductive fitness (Rotjan and Lewis, 2009), but no direct changes in 1) coral nutritional quality or 2) defensive ability have yet been examined.

In this study, we investigated a suite of coral characteristics that might either cause or result from parrotfish corallivory on *Montastraea* spp. in Belize. We conducted an 18-month manipulative experiment to reduce grazing intensity on *Montastraea* spp. colonies that were either intact or that had been previously grazed by parrotfishes. We investigated several coral traits that might serve as predictors of parrotfish grazing, including nutritional characteristics (C:N ratio, %C, and %N) and defensive characteristics (nematocyst density and skeletal hardness). We first examined whether these coral traits differed between grazed and intact colonies. We then protected colonies from grazing using exclosure cages, and monitored whether initially grazed colonies showed signs of recovery over 8 months. Subsequent re-exposure of colonies to parrotfish grazing gave us the opportunity to examine what coral characteristics were associated with increased parrotfish grazing. Thus, our experimental approach allowed us to evaluate changes in the same coral colonies both in the presence and absence of predation stress over time, providing insight into whether changes in coral quality were causes or consequences of parrotfish grazing selectivity.

2. Methods

2.1. Study site

This study was conducted at ~18 m depth at Carrie Bow Cay, Belize (16° 48′ N, 88° 05′ W), on the outer ridge of the Belize barrier reef (described by Rüetzler and Macintyre, 1982). High densities of adults and juveniles of several parrotfish species are common in this habitat, including facultatively corallivorous species such as *Scarus vetula*, *S. viride*, *S. chrysopterum*, and *S. aurofrenatum* (Lewis and Wainwright, 1985). Of these, *S. viride* and *S. aurofrenatum* are likely to be the major corallivorous parrotfish grazers in the outer ridge habitat (Rotjan and Lewis, 2006). We focused this study on colonies of *Montastraea faveolata* and *Montastraea franksi* because they are the major reef building corals in this habitat and are the preferred prey of corallivorous parrotfish in Belize, with an estimated 35% of colonies in the outer ridge habitat experiencing grazing (Rotjan and Lewis, 2006).

We classified coral colonies as grazed if they showed at least 6 distinct grazing scars; most grazed colonies had more than 30 distinct bites. Intact colonies had no grazing scars. Colonies were individually marked with numbered aluminum tags nailed into dead portions of the coral. Small samples (~ 5 cm^2) were collected by SCUBA with a hammer and chisel; sampling locations on the top or sides of each colony were selected haphazardly, with no differences between grazed and intact colonies in sampling locations. When sampling grazed colonies, care was taken to remove tissue only from areas adjacent to grazing scars rather than from the scars themselves. Colony size (length × width) did not differ between groups (intact colonies $\bar{X} \pm SE = 1786 \pm 194$ cm^2; grazed colonies $\bar{X}$ 1950 ± 246 cm^2, $t = 0.5219$, $df = 77$, $p = 0.6032$).

2.2. Cage design

Forty-two 0.5 m × 0.5 m PVC-frame cages were each placed over a focal *Montastraea* spp. colony (Fig. 1B). Each cage had link-chain connected to the bottom of the mesh with cable ties, and we drilled screws through the chain to securely anchor cages to dead substrate on the outer ridge. The chain added weight to stabilize our cages, and also allowed tight conformation of the cage to the contoured reef substrate. Exclosures were surrounded by a 1-inch mesh polypropylene plastic netting coated with an environmentally-safe anti-fouling agent containing zinc pyrithione (Arch Chemicals, Inc.) to prevent overgrowth by algae (Turley et al., 2000; Turley et al., 2005). The 1-inch mesh size was chosen to exclude large adult corallivorous fishes such as scarid parrotfishes, but also to allow smaller herbivores such as small damselfish, small acanthurids, and non-corallivorous juvenile parrotfish grazing access to turf and macroalgae growing inside. Although our primary intent was to exclude large corallivorous parrotfish, the 1-inch mesh size undoubtedly excluded other large fishes from the caged area including adult corallivorous butterflyfish and other large fishes (such as herbivorous acanthurids and kyphosids, and serranids). We regularly observed small herbivorous fishes and invertebrates inside the cages, and no corals were observed to be overgrown by macroalgae, turf algae, or cyanobacteria during the experimental period.

Despite the relatively large mesh size, it is possible that caging might have altered water flow, light levels, or other physical characteristics. To test this, we measured water current direction, velocity, and turbulence immediately inside and outside an exclusion cage using an Acoustic Doppler Velocimeter (Sontek ADV Field) at 10 Hz every 10 s for 20 min. There was no measurable effect of the cage structure on water motion (paired *t*-test on principal component of the three variables, $t = 0.4594$, $df = 11{,}927$, $p = 0.6459$). We also measured light levels using the external light meter of a PAM fluorometer (Walz Gmbh, Germany) at noon. Light levels outside cages were significantly higher than inside (inside $\bar{X} \pm SE = 49.27 \pm 2.91$ μmol quanta m^{-2} s^{-1}, outside $\bar{X} \pm SE = 34.29 \pm 1.99$ μmol quanta m^{-2} s^{-1}; paired $t = 8.8694$, $df = 45$, $p < 0.001$). We examined the effects of these light differences with cage controls ($N = 4$) that were fully netted on top and had each side opened diagonally to allow corallivorous fishes access to the corals inside. For each dependent variable possibly impacted by incident light (C:N ratio, %C, and %N), we conducted Bonferroni-protected *t*-tests to compare cage-control colonies to uncaged colonies at each time point (both prior to, during, and after caging so that we could compare significant caging effects with initial and final differences between colonies). We found no significant effect of caging on nutritional parameters (for all, $p > 0.05$).

2.3. Experimental manipulation of parrotfish grazing

In order to compare nutrition-related and defensive coral characteristics (described below) between grazed and intact colonies, we first sampled individually-marked *Montastraea* spp. colonies in August 2004. To investigate whether these dependent variables changed in response to parrotfish grazing, or whether differences in these dependent variables incite parrotfish grazing, we used cages to prevent parrotfish access to colonies (described above). We conducted an 8-month experimental reduction of grazing intensity, manipulating colonies that were initially grazed or intact (condition) by treatment (cage or control) (Fig. 1A). Cages (Fig. 1B) were initially installed in August 2004, but were dislodged by storm surge from Hurricane Ivan in September 2004. Unseasonably high temperatures also characterized this time period (Rotjan et al., 2006). Cages were therefore re-installed in October

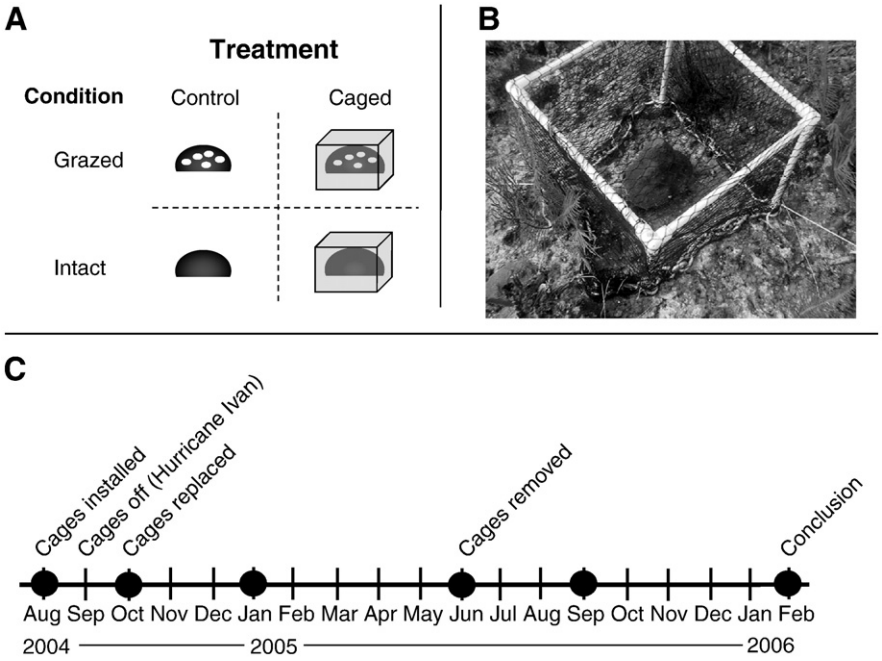

Fig. 1. Experimental setup. A. Experimental design showing *Montastraea* spp. coral colony condition (initially grazed or intact), and treatment (predator exclusion cages or controls): some colonies are protected from grazing by caging while others remain exposed to predation. B. Photograph of experimental cage displaying an intact experimental *Montastraea* spp. colony within cage that excluded large corallivorous fishes. C. Experimental timeline. Cages were installed in August 2004, left on to allow colonies to recover from grazing, and finally removed to re-introduce colonies to grazing. Black circles represent sampling dates.

and remained in place until June 2005 (the "recovery from grazing" phase, Fig. 1C); no major temperature anomalies were recorded during this time (http://nmnhmp.riocean.com/). To examine how corals responded to reduced grazing pressure, and how parrotfish responded to corals after caging, we continued to monitor colonies after cage removal until February 2006 (the "reintroduction of grazing" phase). We sampled experimental colonies of grazed and intact *M. faveolata* and *M. franksi* corals at six time points: August 2004 ($N=60$ colonies), October 2004 ($N=37$) mid-January 2005 ($N=60$), June 2005 ($N=59$), September 2005 ($N=63$), and in February 2006 ($N=48$). Sample sizes varied depending on our ability to re-locate tagged colonies, and on the integrity of exclusion cages.

2.4. Nutritional parameters

To determine if variation in coral nutritional quality among *Montastraea* spp. colonies might explain patterns of parrotfish predation, we conducted elemental analysis to measure % carbon (C), % nitrogen (N), and C:N ratio on coral tissue samples. C:N ratios have traditionally been used as an indicator of nutritional quality (reviewed by Crossman et al., 2000; Purcell and Bellwood, 2001) because they consider total (not dietary) carbon and nitrogen. We looked at %C and %N separately to provide additional insight into parrotfish grazing preferences.

From the sub-sample collected from each colony, we removed tissue with an airbrush created from a modified 1/4-inch blow gun (Craftsman tools) fitted to a SCUBA tank, so as to avoid dilution of tissue with seawater. We dried removed tissue at 60 °C until constant weight was achieved, then transported samples back to the laboratory for elemental analysis. All samples were analyzed with a NC-2500 Elemental Analyzer (CE Elantech) and run against an apple leaf standard, a technique that has been used previously to describe nutritional quality in *P. astreoides* (Rotjan and Lewis, 2005).

2.5. Defensive parameters

Nematocysts are stinging cells used in both coral defense and prey capture (Mariscal, 1974). As defensive structures, they release upon contact to barb or sting a potential predator, and some contain chemical toxins (Mariscal, 1974; Kass-Simon and Scappaticci, 2002). To examine whether nematocysts may help deter parrotfish predators directly, we measured the density of holotrich nematocysts, which are considered to be the most defensive nematocyst type. We followed the conventional identifications as determined by de Oliveira Pires (1997) for scleractinian cnidae, although what we call holotrichs here have also been elsewhere called both spirocysts and p-basic mastigophores. From the same coral sample collected from each colony, we airbrushed tissue off the skeleton and homogenized it with a small coffee bean grinder. Nematocysts were counted at 400× magnification using a hemacytometer (16 replicate subsamples). The remaining homogenate was then dried to a constant weight at 60 °C and weighed to calculate nematocysts per mg dry weight.

In addition to coral tissue characteristics, parrotfish may select or avoid certain corals based on the hardness of their underlying skeleton (Littler et al., 1989). Caribbean coral species vary in their compressive strength and elasticity (Chamberlain, 1978), but how colonies differ within a species (and may therefore influence intraspecific parrotfish selectivity) is not yet known. To evaluate differences in skeletal hardness, we used the skeletons from the coral samples collected above. Once the tissue was stripped from each sample, we bleached the remaining skeleton with a dilute bleach + seawater solution and then dried all skeletons in direct sunlight for at least 24 h before transport back to the laboratory. We used a diamond trim saw (Felker BayState) to cut skeletons so that polyps would have the same approximate orientation, cutting all pieces ~2–3 cm thick and flat. An Instron Model 4505 Universal Testing Instrument with digital control and data acquisition system was used to test how much compressive load (kilogram force) each skeleton could withstand with a standardized 2 mm of compressive extension (Fig. 2). We tested the hardness of 5 haphazardly selected calyxes and 5 haphazardly selected thecae (between-calyx areas) for each skeletal sample and analyzed both the maximum compressive load reached across all 5 trials for both calyxes and thecae separately, and the average compressive load across all 5 trials. To determine whether there were intraspecific (colony-level) differences in skeletal hardness, we conducted two-sample *t*-tests (Systat 11) comparing grazed vs. intact colonies.

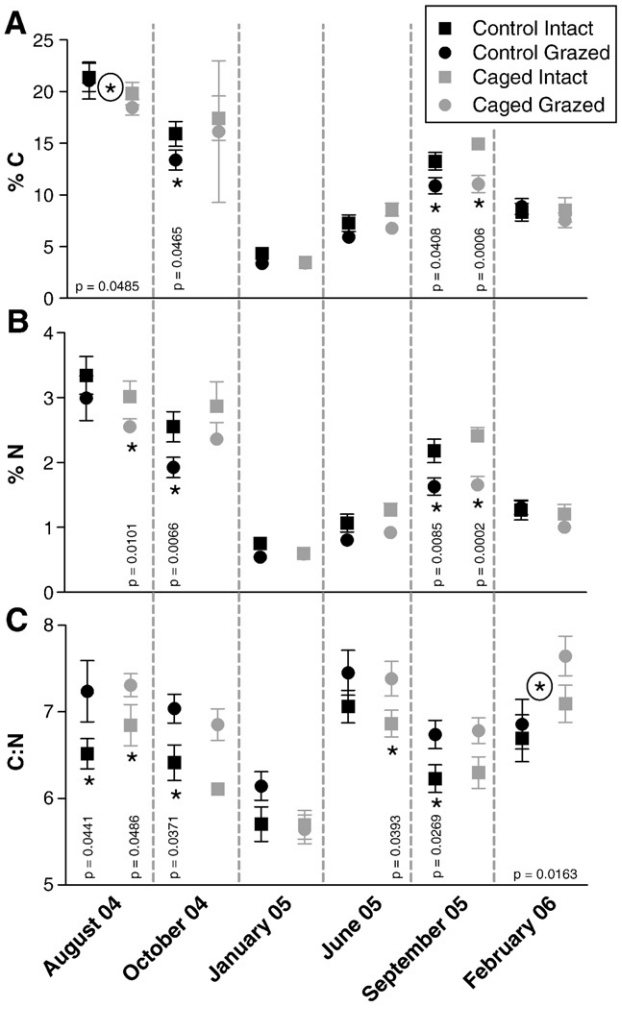

Fig. 2. Nutritional variables (mean ± SE), including % carbon (A), % nitrogen (B) and C:N ratio (C) in coral tissue sampled from initially grazed (circles) and intact (squares) *Montastraea* spp. colonies randomly assigned to control (black) and caged (grey) treatments. See Table 1 for model statistical results; significant linear contrast values within treatment between grazed and intact are indicated with an asterisk(*p*-values listed vertically), while significant contrasts between treatments are indicated with circled (grazed) asterisks (and horizontal *p*-values). All other contrasts $p > 0.05$. Control vs. caged points are offset for ease of interpretation, but were sampled simultaneously.

Coral color and *Symbiodinium* spp. (zooxanthellae) density were also measured. Since these variables did not contribute significantly to the logistic regression model, they were subsequently excluded from the analysis, but were initially included (see below). These data are discussed in Rotjan (2007) and *Symbiodinium* spp. cell densities are the subject of Rotjan et al. (2006).

2.6. Statistical analyses

To assess the influence of coral characteristics on whether or not *Montastraea* spp. coral colonies were initially grazed by parrotfish, stepwise logistic regression models (Systat 11) were built with the response variables grazed (1) or intact (0), with the predictors nutritional quality, coral color, *Symbiodinium* spp. cell density, and nematocyst density (all continuous variables). We ran logistic regression models on colonies prior to experimental manipulation (the initial data set), and on caged colonies only in June (immediately after cage removal). We defined the initial data set as the sum of all colonies in August and in October, since cages were removed by Hurricane Ivan in early September 2004. The odds ratios of the predictors in the final model were analyzed in order to understand the nature of the relationship between each predictor and the response variable. The odds ratio is a measure of association that approximates how much more likely (or unlikely) it is for a colony to be grazed with each unit increase of each predictor variable.

We also conducted stepwise multiple regressions (Systat 11) on the initial data set and on caged colonies in June to determine how a continuous response variable, grazing intensity (based on the number of bites on each colony) was influenced by each predictor variable. We ran backwards stepwise regression models with coral color, *Symbiodinium* spp. cell density, C:N ratios, and nematocyst density.

The caging design allowed us to manipulate parrotfish access to coral colonies, and to remove any visible signs of grazing by giving corals enough time to regenerate lost tissue. With this design, we then tested whether or not parrotfish re-graze the same individual colonies, even without a visual indication of prior grazing. In other words, are there characters inherent to specific coral colonies that parrotfish repeatedly choose or avoid, and is their choice based on any of the dependent variables we measured? To determine whether parrotfish re-graze the same colonies, we conducted contingency table analyses (chi square) comparing initial grazing status (August 2004) to final grazing status (February 2006) for both caged and control colonies. We used the regression analyses, as above, to determine whether parrotfish preference was predicted by any of our measured dependent variables.

To investigate how each dependent variable changed over the course of the experiment, we used a generalized linear mixed model approximating a 2-way mixed model ANOVA to determine condition (initially grazed vs. intact), and treatment (cage vs. control) as fixed effects, and time (month) as a random effect, as well as interaction effects (as in Bolker et al., 2009). To examine specific differences between initially grazed and intact colonies within each treatment (cage or control) during each sampling period, we used linear contrasts for planned comparisons (SAS). In the case of contrast analyses, we separately analyzed %C and %N to better understand how each of these elements change in response to parrotfish predation. For these analyses, *Symbiodinium* spp. cell densities were log transformed to satisfy normality assumptions.

3. Results

3.1. Initial differences in coral characteristics between grazed and intact colonies

We examined whether parrotfish predation was predicted by any of the dependent variables that we used to measure *Montastraea* spp. coral quality. At the outset of the experiment (before caging), a logistic regression model including C:N ratio, *Symbiodinium* spp. cell density, nematocyst density and coral color significantly predicted whether coral colonies were grazed by parrotfishes (likelihood ratio Chi Square = 13.43, 4 *df*, $p = 0.0093$). In this model, C:N ratio was the only significant predictor of initial parrotfish grazing (estimate ± SE = −0.97 ± 0.48, odds ratio = 0.38, $t = -2.02$, $p = 0.0433$), with colonies initially having higher C:N ratios more likely to be grazed.

For grazed *Montastraea* spp. colonies, we examined whether initial grazing intensity (based on the number of bites) was affected by any of the measured coral characteristics. Only C:N ratio predicted grazing intensity (multiple regression coefficient ± SE = 4.62 ± 1.97, $F = 5.47$, $df = 1, 88$, $p = 0.0219$; all other variables $p > 0.05$). Thus, at the outset of the experiment, increased C:N ratio significantly increased both the likelihood of a *Montastraea* spp. colony being grazed, as well as grazing intensity (number of bites) on initially grazed colonies.

3.2. Do parrotfish re-graze the same colonies?

Regardless of treatment, the majority of *Montastraea* spp. colonies that were not initially grazed by parrotfishes remained ungrazed at the end of the experiment (February 2006). Only 2 out of 27 initially

intact colonies were grazed in February 2006, 8 months after cage removal (caged $\chi^2 = 5.39$, $df = 1$, $p = 0.02$; control $\chi^2 = 3.74$, $df = 1$, $p = 0.05$). Overall, 83.3% of initially intact control colonies (10/12) remained intact by the end of the experiment, and 100% of intact caged colonies (15/15) remained intact throughout the experiment. Similarly, colonies that were grazed at the start of the experiment were often, but not always, re-grazed by the end of the experiment; 53.8% of initially grazed control (uncaged) colonies (7/13) were re-grazed by February, whereas 30.8% of initially grazed caged colonies (4/13) were re-grazed. Thus, intact colonies tend to stay intact, and initially grazed colonies are more likely to be re-grazed, suggesting that grazing may be a chronic recurrence for certain *Montastraea* spp. colonies.

When we removed cages in June 2005, we scored colonies for re-grazing after only 12 h of exposure to parrotfish. Parrotfish immediately grazed three colonies that had been caged, two of which had been initially grazed. Interestingly, the two previously grazed colonies showed high grazing intensity (>30 bites per colony), whereas the previously intact colony had only 6 bites.

3.3. Differences in coral characteristics immediately after cage removal

To investigate whether the presence or absence of parrotfish predation was affected by coral characteristics (C:N ratio, *Symbiodinium* spp. cell density, nematocysts, and coral color), we used logistic regression to analyze the dependent variables immediately after cage removal (in June) None of these variables significantly predicted the likelihood of parrotfish grazing (likelihood ratio Chi Square = 3.0609, 4 *df*, $p = 0.5477$).

Similarly, parrotfish grazing intensity (number of bites) in June after cage removal was not related to any measured coral characteristics (stepwise multiple regression coefficient ± SE = 2.95 ± 1.86, $t = 1.59$, $df = 1$, $p = 0.1281$; final step had only the constant remaining, all other variables removed). Taken together, these results suggest that after *Montastraea* spp. colonies were caged for 8 months, parrotfish re-grazing was not related to any of the measured coral characteristics. Even C:N ratio, the variable that differed between grazed and intact colonies at the outset of the experiment, no longer showed any difference after colonies recovered from grazing. Thus, it seems that parrotfish do not selectively graze colonies based on any of our measured coral characteristics, and the differences observed at the initial time point were likely a response to parrotfish grazing, not a cause.

3.4. Changes in coral nutritional quality

Montastraea spp. coral colonies experienced seasonal fluctuations in nutritional quality (Fig. 2), resulting in highly significant differences in C:N, %C, and %N over time (Table 1). Grazed vs. intact colonies (colony condition) differed significantly for all three variables measuring nutritional quality (Table 1), with grazed coral colonies showing lower %N and %C (but higher C:N) when averaged across all timepoints (Fig. 2). These results complement the findings from our regression models and suggest that lower coral nutritional quality is associated with parrotfish grazing. Although there were no significant effects of the corallivore-exclusion treatment alone for any variable, there were significant interactions between treatment and time for all nutritional variables (Table 1), suggesting that corallivore exclusion influenced these nutritional variables differently at each sampled timepoint.

Effects of colony condition on nutritional quality were further examined within each sampling date using linear contrasts, and revealed significant differences both in August and October 2004, prior to any experimental manipulation (Fig. 2). These results support our earlier findings and indicate that grazed and intact *Montastraea* spp. colonies differed in nutritional quality from the outset, although if we had only a single snapshot in time it would have been impossible to determine whether nutritional quality differences were a cause or an effect of parrotfish grazing. Upon cage removal, C:N ratio significantly differed between grazed and intact colonies only in the caged treatment, suggesting that these differences became more pronounced in the absence of corallivory (Fig. 2C), although this finding was not seen in %C or %N alone (Fig. 2A,B). It appears that seasonality had the strongest influence on coral nutritional differences between grazed and intact colonies, as these differences were most pronounced (regardless of treatment) in the warmest months (August and October 2004, and September 2005). It should be noted that there was no significant interaction between time and condition, likely due to the fact that grazed colonies always showed slightly higher C:N ratios compared to intact colonies within treatments (Fig. 2C).

Table 1
Changes in nutritional quality of *Montastraea* spp. colonies. Two-way ANOVA shows effects of coral condition (grazed vs. intact), experimental treatment (cage or control), sampling time, and interaction. Grazed vs. intact colonies were compared at each sampling month using planned linear contrasts; results shown on Fig. 2.

Nutritional variable	Source	SS	*df*	*F*	*p*
%C	Time (month)	9725.56	5	190.38	<0.0001**
	Condition (G vs. I)	141.09	1	13.81	0.0002**
	Treatment (cage vs. control)	2.45	1	.024	0.6247
	Condition*time	82.17	5	1.61	0.1574
	Treatment*time	129.04	5	2.53	0.0292*
	Condition*treatment	3.01	1	0.29	0.5874
	Condition*treatment*time	22.65	5	0.44	0.8181
	Error	3228.55	316		
	Total	10,650.29	23	45.32	<0.0001**
%N	Time (month)	215.02	5	129.19	<0.0001**
	Condition (G vs. I)	9.51	1	28.58	<0.0001**
	Treatment (cage vs. control)	0.004	1	0.01	0.9035
	Condition*time	3.66	5	2.20	0.0543
	Treatment*time	4.12	5	2.48	0.0321*
	Condition*treatment	0.06	1	0.17	0.6829
	Condition*treatment*time	0.52	5	0.31	0.9048
	Error	105.19	316		
	Total	241.40	23	31.53	<0.0001**
C:N	Time (month)	79.27	5	27.98	<0.0001**
	Condition (G vs. I)	16.24	1	28.66	<0.0001**
	Treatment (cage vs. control)	0.10	1	0.18	0.6754
	Condition*time	1.87	5	0.66	0.6535
	Treatment*time	6.40	5	2.26	0.0486*
	Condition*treatment	0.01	1	0.02	0.8941
	Condition*treatment*time	1.67	5	0.59	0.7093
	Error	179.04	316		
	Total	112.35	23	8.62	<0.0001**

3.5. Changes in nematocyst density

As with all other measured coral characteristics, seasonality had strong effects on nematocyst densities (Table 2). There were highly significant effects of condition (initially grazed vs. intact colonies) on nematocyst density, with intact colonies displaying more nematocysts throughout the experiment (Table 2, Fig. 3). There were no significant

Table 2
Changes in holotrich nematocyst density of *Montastraea* spp. colonies. Two-way ANOVA shows effects of coral condition (grazed vs. intact), experimental treatment (cage or control), sampling time, and interaction. Grazed vs. intact colonies were compared at each sampling month using planned linear contrasts; results shown on Fig. 3.

Source	SS	*df*	*F*	*p*
Time (month)	2,620,762,653	5	26.62	<0.0001**
Condition (G vs. I)	13,816,922	1	7.02	0.0085**
Treatment (cage vs. control)	453,934	5	0.02	0.8794
Condition*time	112,870,396	5	1.15	0.3359
Treatment*time	59,983,066	5	0.61	0.6929
Condition*treatment	1,885,892	1	0.10	0.7572
Condition*treatment*time	162,005,782	5	1.65	0.1478
Error	5,927,231,385	301		
Total	3,313,267,761	23	7.32	<0.0001**

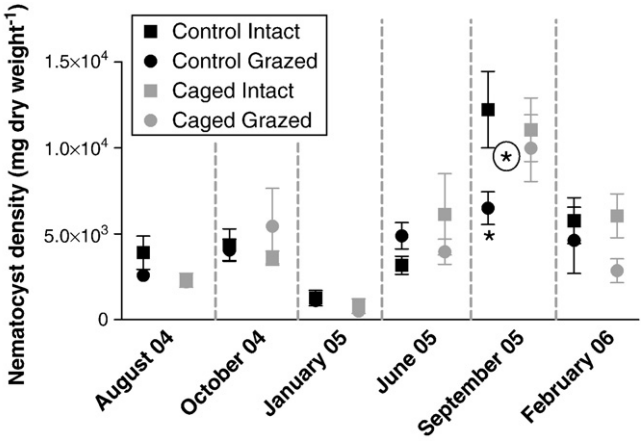

Fig. 3. Nematocyst density (mean ± SE) in coral tissue sampled from initially grazed (circles) or intact (squares) *Montastraea* spp. colonies randomly assigned to control (black) and caged (grey) treatments. See Table 2 for statistical results; significant linear contrast value between control grazed and intact indicated with an asterisk ($p = 0.0006$), while significant contrast between treatments is indicated with a circled (grazed) asterisk ($p = 0.0485$). All other contrasts $p > 0.05$. Control vs. caged points are offset for ease of interpretation, but were sampled simultaneously.

interaction effects, indicating that nematocyst densities varied similarly between treatment, condition, and time. Only in September 2005 were significant differences detected, with higher nematocyst densities in intact control colonies vs. grazed control colonies, and between grazed control and caged colonies (Fig. 3). Interestingly, September also showed the highest overall nematocyst densities compared to any other month.

3.6. Differences in coral skeletal hardness

We did not observe any difference in coral compressive strength between grazed and intact *Montastraea* spp. colonies, for either metric we examined (Fig. 4). Compressive strength exerted within calyces was similar for both grazed and intact colonies (grazed maximum strength $\bar{X} \pm SD = 88.22 \pm 43$ kgf, intact $\bar{X} = 78.14 \pm 25$ kgf, $t = -1.12$, $df = 61$, $p = 0.2678$; grazed average compressive strength $\bar{X} \pm SD = 54.84 \pm 27.56$ kgf, intact $\bar{X} = 51.45 \pm 17.20$; $t = -0.58$, $df = 61$, $p = 0.5653$). Measurements taken between calyces (on the thecae) handled higher compressive loads than within-calyx measurements (grazed maximum load $\bar{X} \pm SD = 100.09 \pm 50$ kgf, intact $\bar{X} = 90.21 \pm 26$ kgf; grazed average load $\bar{X} \pm SD = 66.33 \pm 32$, intact $\bar{X} = 62.33 \pm 21$ kgf), indicating that the area between calyces would be harder for a scraping or excavating parrotfish to get through. Nonetheless, there was no difference in hardness between grazed and intact colonies in the maximum compressive load tolerated on thecae ($t = -0.97$, $df = 61$, $p = 0.3348$), or the average compressive load ($t = -0.57$, $df = 61$, $p = 0.5686$).

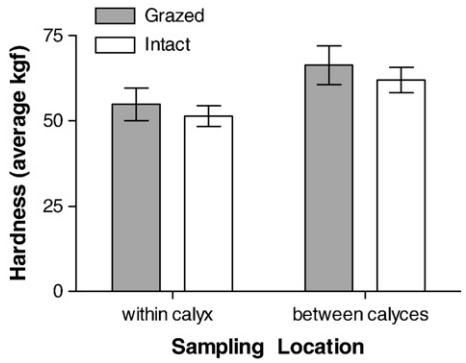

Fig. 4. Skeletal hardness (average kilogram force; mean ± SE) of grazed (grey) and intact (white) *Montastraea* spp. coral skeletons, measured within- and between-coral calyces. $N = 62$ skeletons.

4. Discussion

Caribbean parrotfish are known to selectively graze *Montastraea* spp. corals, yet the causes of selective and persistent grazing of certain colonies are not well understood. This study allowed us to discriminate whether changes in nutritional and defensive coral characteristics were causes or effects of selective parrotfish corallivory. Using a corallivore-exclusion caging design, our results re-affirm that *Montastraea* spp. coral characteristics are affected by grazing, but none of the measured characteristics thus far explain parrotfish selectivity. Decreases in coral nutritional quality (C:N) represented the most substantial changes resulting from grazing.

4.1. Parrotfish grazing influences coral nutritional quality

A key finding of this study is that reduced coral nutritional quality, including increased C:N ratio and decreased overall %C and %N, is associated with parrotfish grazing. This is somewhat surprising because parrotfish are known to prefer algal diets with higher nitrogen content (Bruggemann et al., 1994; Goecker et al., 2005); thus, we hypothesized that parrotfish would selectively graze coral colonies with higher percent nitrogen. Parrotfish are considered to be nitrogen-limited, since 98% of their diet consists of nitrogen-poor algae (Bruggemann et al. 1994). In some terrestrial plant–herbivore systems, herbivory has been shown to increase plant nutritional value by stimulating new shoot growth, thereby creating a feedback loop where chronic herbivory maximizes available nitrogen (e.g. McNaughton, 1979; Mattson, 1980; Paige and Whitham, 1987; Mauricio et al., 1993). Our data suggest the opposite in regard to parrotfish grazing on corals. Here, we found that chronic corallivory decreased coral percent nitrogen, but that parrotfish re-graze these colonies nonetheless. We did find, however, that parrotfish take more bites (higher grazing intensity) on corals with the highest C:N ratios, perhaps compensating for lower nutritional quality by higher consumption. Alternatively, parrotfish may be targeting lipid-rich coral gonads (Rotjan and Lewis, 2009) or mucous (Benson and Muscatine, 1974). It is important to note that we found decreases in nutritional quality resulting from parrotfish grazing in every analysis we conducted, suggesting that this result is a consequence of parrotfish grazing.

We found that the differences in nutritional quality (C:N, %C, and %N) between grazed and intact colonies (regardless of caging treatment) were only apparent during the warmest times of year (August and October 2004, and September 2005). Previous studies suggest that winter is the time when corals typically reach their highest host tissue mass, symbiont densities and photosynthetic capacity, which ultimately drives coral growth and reproductive output (Fitt et al., 2000; Warner et al., 2002). In this study, winter months correspond to the lowest concentrations of C and N in coral tissue. This is not surprising, as it is well documented in plants that during a growth phase, C:N increases (and %N decreases), and it is further thought that the nutritional status of a plant can, in turn, influence growth dynamics (Ingestad and Agren, 1991). One possible explanation for why grazed colonies have higher C:N compared to intact colonies in warmer months is that grazing initiates a wound response, since it is well known that corals allocate available energy and resources to regeneration above all other functions (including new colony growth, reproduction, etc.) (reviewed by Henry and Hart, 2005). Furthermore, grazing (like other stressors) may also induce corals to produce higher amounts of carbon-rich mucous (e.g. Krupp, 1984; Riegl and Branch, 1995). Intact colonies, in contrast, have no need for active regeneration. Thus, differences between grazed and intact colonies may be most pronounced in the summer months when

new growth is minimal and temperatures approach coral thermal tolerance thresholds (Jokiel and Coles, 1990; Fitt et al., 2000). In winter, nutritional differences between grazed and intact colonies are likely to be minimized because both colony types are not stressed by high temperatures and are actively allocating nutritional resources to new growth. Along these lines, Edmunds and Lenihan (2010) found that artificially damaged Pacific *Porites* spp. were more negatively affected at higher temperatures. If parrotfish are keeping colonies in a suspended state of wounding, then grazed colonies would be predicted to have less overall new growth each year, with related implications for coral fitness.

4.2. Grazing effects on nematocyst densities

Although we found that nematocyst densities are significantly lower overall in grazed compared to intact colonies, nematocysts do not seem to be important in predicting parrotfish grazing. Nematocysts had no influence on parrotfish grazing in any of our regression models, and after cage removal, parrotfish did not selectively target colonies with significantly lower nematocyst densities. Thus, the significant condition effect we observed (overall lower nematocyst densities in grazed colonies) is likely an effect of long-term parrotfish grazing on the coral, rather than a cause. We found some evidence that corals might raise nematocyst levels as a short-term response to corallivory. Shortly after cage removal in September, previously caged grazed colonies had significantly more nematocysts than grazed control colonies (Fig. 3). By February 2006, caged grazed colonies did not significantly differ from intact or control colonies. Furthermore, significantly lower nematocyst densities in grazed control colonies (vs. intact control colonies) cannot be explained by caging or seasonality, and may instead reflect another stressor or mechanical stimulus. Grazing by other corallivores, such as the Hawaiian butterflyfish *Chaetodon multicinctus*, has been shown to induce an increase in *Porites compressa* coral nematocyst density, which subsequently reduced grazing (Gochfeld, 2004). Since nematocysts do not appear to deter parrotfish grazing, increases in nematocyst density might reflect a generalized induced defense response mounted by the coral. Regardless, corals do not appear to sustain high nematocyst levels over the long-term (in fact, these levels are lower in grazed compared to intact colonies). The decrease in nematocyst density may be due to the energetic costs necessary to maintain high densities, or alternatively because nematocysts appear to be ineffective against parrotfish; further study is needed.

4.3. Skeletal properties of Montastraea spp.

Although some studies have found evidence for interspecific grazing selectivity based on skeletal properties (Littler et al., 1989; Bruggemann et al., 1996), there is no consistent correlation among Caribbean corals between skeletal density (Highsmith, 1981) and parrotfish grazing incidence (Littler et al., 1989; Garzon-Ferreira and Reyes-Nivia, 2001; Rotjan and Lewis, 2005). While it is known that different Caribbean coral species vary in their compressive strength and elasticity (Chamberlain, 1978), we were interested in the possibility that intraspecific differences in these characteristics might influence intraspecific parrotfish selectivity. However, no differences in coral skeletal hardness between grazed vs. intact *Montastraea* spp. colonies were observed, suggesting that coral skeleton compressive strength is not a determinant of intraspecific parrotfish grazing selectivity. Nonetheless, as stated above, it is likely to be important for interspecific parrotfish grazing selectivity. For example, when comparing across coral species, it has been demonstrated that parrotfish removed larger volumes of live coral on species with softer skeletons (Reyes-Nivia et al., 2004); similarly, Littler et al. (1989) found that parrotfish prefer grazing *Porites* spp. corals with softer skeletons.

4.4. What are the causes of selective corallivory by parrotfish?

We found evidence that parrotfish tend to repeatedly graze the same *Montastraea* spp. coral colonies, in accordance with previous findings (Bruckner and Bruckner, 1998; Bruckner et al., 2000; Sanchez et al., 2004; Rotjan and Lewis, 2005). This is in contrast to some butterflyfish, which prefer to feed on colonies that have not been recently grazed (Gochfeld, 2004). The only putative causes determined thus far for intraspecific parrotfish grazing selectivity are increased macroborer densities on shallow *P. astreoides* (Rotjan and Lewis, 2005) and high numbers of gonads immediately prior to spawning in *Montastraea* spp. (Rotjan and Lewis, 2009). However, gonads explain parrotfish choice for only a short part of the year; what explains their selectivity when gonads are absent? Corals may mount chemical defenses against corallivory, but no such chemical defenses in scleractinians have yet been found. Rotjan (2007) obtained inconclusive results from experimental fish feeding assays with coral extracts, but the potential role of chemical defenses requires further study. It should be noted that in some cases, parrotfish grazing selectivity on seagrasses is explained by nutritional, not defensive, characteristics (Goecker et al., 2005).

5. Conclusion

Parrotfish are complex reef inhabitants, on the one hand contributing to the maintenance of healthy reefs via herbivory and bioerosion (e.g. Lewis, 1986; Hughes, 1994; McClanahan and Muthiga, 1998), and on the other hand consuming live corals with known negative consequences (e.g. Cole et al., 2008, Rotjan and Lewis, 2008). The trophic role of parrotfishes on Caribbean reefs is complex (Mumby, 2009), and it is still unclear whether parrotfish grazing can substantially contribute to long-term coral decline. Nonetheless, corallivorous parrotfish abundance has been increasing on some Caribbean reefs (Rotjan and Lewis, 2006), while live coral cover has continually declined (Gardner et al., 2003). Thus, it is not unreasonable to suggest that the ecological role of parrotfish corallivory is both important and complex: corallivory is likely to have a negative impact in some instances (e.g. high corallivore abundance and low coral cover), while corallivory is likely tolerable in others (e.g. high coral cover). Understanding the mechanistic causes of selective parrotfish grazing is therefore important in order to predict the relative roles of corallivores on reefs with different coral species composition and percent live cover.

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