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Chronic parrotfish grazing impedes coral recovery after bleaching

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Abstract Coral bleaching, in which corals become visibly pale and typically lose their endosymbiotic zooxanthellae (*Symbiodinium* spp.), increasingly threatens coral reefs worldwide. While the proximal environmental triggers of bleaching are reasonably well understood, considerably less is known concerning physiological and ecological factors that might exacerbate coral bleaching or delay recovery. We report a bleaching event in Belize during September 2004 in which *Montastraea* spp. corals that had been previously grazed by corallivorous parrotfishes showed a persistent reduction in symbiont density compared to intact colonies. Additionally, grazed corals exhibited greater diversity in the genetic composition of their symbiont communities, changing from uniform ITS2 type C7 *Symbiodinium* prior to bleaching to mixed assemblages of *Symbiodinium* types post-bleaching. These results suggest that chronic predation may exacerbate the influence of environmental stressors and, by altering the coral-zooxanthellae

symbiosis, such abiotic-biotic interactions may contribute to spatial variation in bleaching processes.

Keywords Predation · Coral bleaching · Trophodynamics · Environmental stress · Zooxanthellae · *Symbiodinium*

Introduction

Coral reef ecosystems worldwide are in decline, associated with escalating stressors such as pollution, eutrophication, and increases in water temperature (Gardner et al. 2003; Pandolfi et al. 2003). These anthropogenic stressors have been implicated in coral bleaching events, during which corals become visibly pale typically due to declines in endosymbiont (zooxanthellae) density and/or changes in pigment concentration (Glynn 1991; Hoegh-Guldberg 1999). While it is well established that abnormally high seawater temperatures act as proximal triggers of coral bleaching (Coles and Brown 2003), other contributing factors including high light, pollution, low salinity, restricted water flow and disease have also been implicated (Lesser 2004). Even though the frequency of coral bleaching has increased dramatically over the past three decades (Hoegh-Guldberg 1999; Hughes et al. 2003), little is known concerning how key biological factors interact to influence coral survival and recovery during bleaching events.

Coral bleaching responses often vary substantially in their extent and severity, even for corals occupying the same physical environment (Rowan et al. 1997; Fitt et al. 2000; Baker 2003). Variation in bleaching susceptibility has been attributed to physiological and/or morphological differences within and between coral species (Edmunds 1994; Marshall and Baird 2000; Loya et al. 2001), and to small-scale variability in microhabitat conditions (Nakamura and van Woesik 2001; Finelli et al. 2006). Bleaching variability has also been attributed to genetic differences in the coral's community of photosymbiotic *Symbiodinium* (Rowan et al. 1997). The

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genus *Symbiodinium* is genetically diverse consisting of eight sub-generic clades (A-H), each comprised of numerous “types” (Baker 2003; LaJeunesse 2005). While these studies indicate that both intrinsic differences and external environmental heterogeneity can contribute to bleaching variability among corals, few studies have examined whether extrinsic biotic factors such as predation can influence coral bleaching susceptibility, intensity, and subsequent recovery.

In the Caribbean, herbivorous fishes (parrotfishes and surgeonfishes) are critical to maintaining healthy coral reefs, as they benefit corals by removing competitively superior macroalgae (Lewis 1986; Hughes 1994). However, some parrotfish also consume live coral, with direct detrimental effects on coral growth and survival (Meesters et al. 1994; McClanahan et al. 2005; Rotjan and Lewis 2005). Parrotfish preferentially graze certain coral species (Garzon-Ferreira and Reyes-Nivia 2001; Rotjan and Lewis 2006), as well as particular colonies within a species (Sanchez et al. 2004; Rotjan and Lewis 2005). Parrotfish predation produces characteristic, highly conspicuous grazing scars (Fig. 1a), and often results in partial colony mortality. Although the proximal cause of feeding selectivity is not known, parrotfish often repeatedly graze the same coral colonies (Bruckner and Bruckner 1998; Bruckner et al. 2000; Sanchez et al. 2004; Rotjan and Lewis 2005). Because corals are clonal organisms, partial predation by parrotfish is likely to be an important source of chronic stress for reef corals.

In this study, we document a non-catastrophic coral bleaching event in Belize in September 2004 that coincided with elevated seawater temperatures, storm surge from Hurricane Ivan, and seasonal variability in zooxanthellae densities. In the context of these stressors, we examined the effects of chronic parrotfish grazing on the coral-algal symbiosis. Specifically, we tested whether *Montastraea* spp. coral colonies exposed to chronic parrotfish grazing showed a greater reduction in symbiont density during this bleaching event compared to intact conspecific colonies over time. Finally, we investigated the genetic stability of *Symbiodinium* spp. communities in grazed versus intact coral colonies over the course of this bleaching event.

Materials and methods

Study site and sampling

This study was conducted at Carrie Bow Cay, Belize (16° 48' N and 88° 05' W) on the outer ridge of the Belize barrier reef (~18 m depth). *Montastraea faveolata* and *Montastraea franksi* are the major reef building corals in this habitat, and 21 out of 63 (~33%) colonies examined exhibited recent grazing scars. We sampled individually marked colonies of grazed and intact *M. faveolata* and *M. franksi* corals at three time periods: in August 2004 ($N = 64$ colonies), October 2004 ($N = 22$) and in mid-January 2005 ($N = 24$). August and October 2004

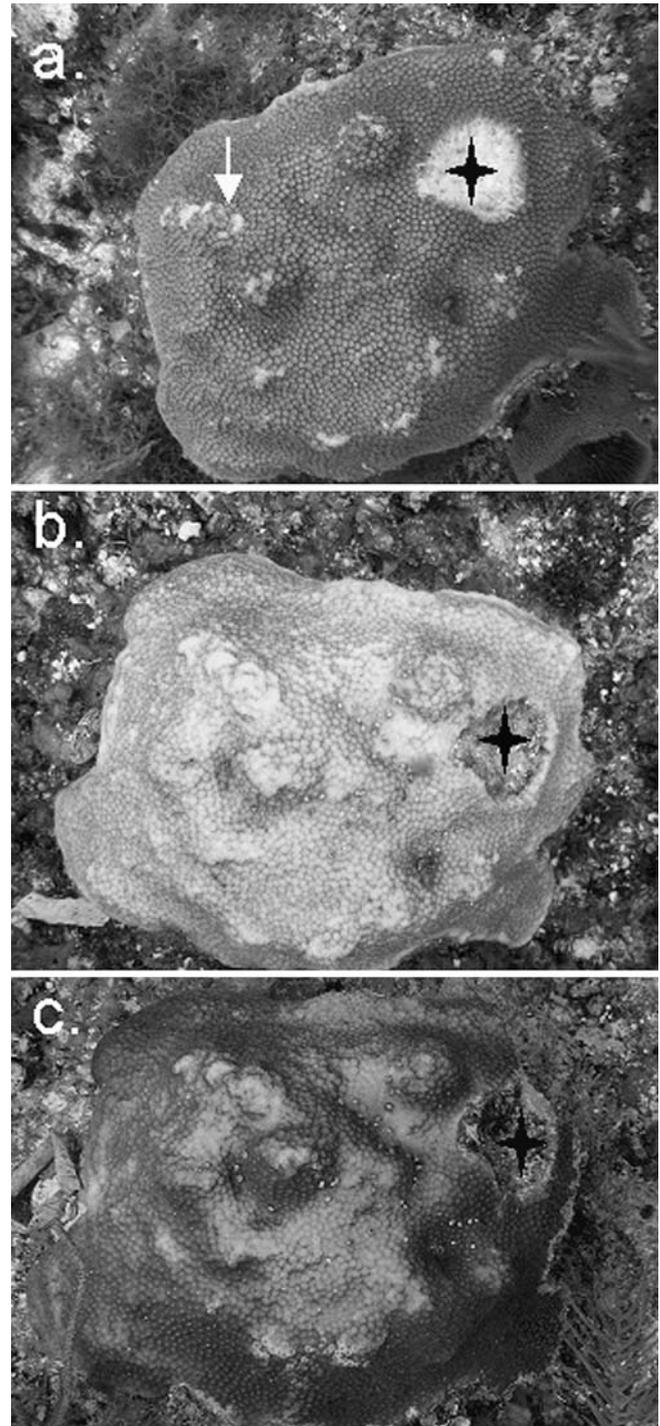


Fig. 1 Time series of a single grazed *Montastraea* spp. coral colony from **a** pre-bleaching in August 2004 to **b** October during bleaching to **c** recovery in January at Carrie Bow Cay, Belize. Relative bleaching levels can be visualized by contrasting the varying appearance of the colony to the reef floor. Arrows in (a) indicate representative grazing scars; the star in all three photos represents a sampling scar on the colony

sampling periods bracketed a period of considerable environmental disturbance characterized by unseasonably high temperatures concurrent with physical destruction caused by storm surge from Hurricane Ivan, in addition to

seasonal lows in zooxanthellae densities (described by Fagoonee et al. 1999; Fitt et al. 2000). The January/February 2005 sampling occurred during the coolest months of the year, when corals generally exhibit the fastest rates of skeletal growth and increase in tissue mass (Fitt et al. 1993; Fitt et al. 2000). 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. Small samples ($< 5 \text{ cm}^2$) 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. We measured each colony's size (length \times width using a flexible ruler) and colony size did not differ between groups: intact colonies $\bar{X} \pm \text{SE} = 1645 \pm 225 \text{ cm}^2$; grazed colonies $\bar{X} = 1934 \pm 282 \text{ cm}^2$, $t = 0.8049$, $df = 63$, $p = 0.4239$).

Temperature analysis

Ambient water temperatures were recorded from March 2000 through February 2005 using a combination of Onset Computer Corporation Stowaway, Tidbit, and Watertemp Pro loggers with 0.2°C resolution and a 1–5 min response time. These instruments sampled temperature every 0.5 s and recorded 10–16 min averages (except Watertemp Pro loggers which recorded 10–16 min interval points). Instruments were calibrated against a Seabird Electronic SBE 39 logger (0.001°C resolution, 20 s response time) in the laboratory and in the field, and were found to be within factory specifications. Daily average water temperatures for 2004 were compared to day-of-the-year averages calculated across the preceding 4 years.

Zooxanthellae density

To determine zooxanthellae density for *Montastraea* colonies, we completely removed approximately 5 cm^2 of coral tissue from colony samples using a WaterPik[®] with filtered seawater (Johannes and Wiebe 1970). Tissue was homogenized with a blender and zooxanthellae were counted at $100\times$ magnification using a hemacytometer (10 replicate subsamples). The total volume of the tissue homogenate was recorded and coral surface area was measured using aluminum foil (Marsh 1970) in order to calculate zooxanthellae density per cm^2 of coral tissue. A 2-way ANOVA was used to examine condition (grazed vs. intact), time (month), and interaction effects. To determine specific differences between grazed and intact colonies during each sampling period, we used linear contrast t -tests for pre-planned multiple comparisons (SAS); power analyses for linear contrasts (2-sample t tests) were conducted using SYSTAT 11.

Establishing *Symbiodinium* spp. ITS2 type

To determine the genetic identity of *Symbiodinium* spp. populations associated with the coral colonies, zooxanthellae (algal cells) were isolated from the remaining coral tissue by centrifugation at $\sim 6700 \text{ g}$ for 3–4 min. Algal pellets preserved in 70% ethanol were transported back to the U.S., and nucleic acids were extracted using the Wizard DNA preparation protocol (Promega) following the methods of LaJeunesse et al. (2003). The internal transcribed spacer 2 region (ITS 2) of nuclear ribosomal RNA was used to discriminate molecular types of *Symbiodinium* (LaJeunesse 2001, 2002). This region was amplified from the DNA extract for denaturing-gradient gel electrophoresis (DGGE) using primers “ITS 2 clamp” ($5' \text{CGCCCCGCCG CCGCGCC CGTCCCCGCC CCCCCGCC GGGATCCATA TGCTTAAGTT CAGCGGT-3'}$) and “ITSintfor 2” ($5' \text{GAATTGCAGA ACTCCGTG-3'}$). PCR amplification followed the “touchdown” thermal cycle protocol of LaJeunesse (2002). Products of these PCR reactions were checked by electrophoresis on agarose gels (0.8% agarose in 40 mM Tris-acetate, 1mM EDTA solution). Successfully amplified PCR products were subsequently electrophoresed on denaturing gradient gels (45–80% formamide, 8% acrylamide denaturing gradient gels; 100% consists of 7 M urea and 40% deionized formamide) following the protocol of LaJeunesse and Trench (2000), with the modifications of LaJeunesse et al. (2003).

Results

Temperature patterns

Coral bleaching was evident in that colonies appeared visibly pale in October compared to August, and re-gained considerable color by January (Fig. 1). The observed coral bleaching coincided with high seawater temperatures at 18 m depth, which were unusually high during August–November 2004 compared to the same periods in 2000–2003 (Fig. 2). Most coral bleaching models agree that bleaching occurs when corals are exposed to water temperatures $1\text{--}2^\circ\text{C}$ above the average local maximum for extended periods (Hoegh-Guldberg 1999). The HotSpot temperature threshold for this Belizean reef, reflecting the average local maximum temperature at 2 m depth, has previously been estimated to be 29.85°C (Aronson et al. 2002). Our data show that in 2004, daily average water temperature measured at 18 m exceeded this threshold for a total of 36 days, including a period of 19 consecutive days in 2004 (September 15–October 3). This is likely an underestimate of the number of potentially stressful days, as the 29.85°C threshold is based on 2 m depth, and the average local maximum temperature at 18 m is lower than this threshold. This factor is reflected by the observation that

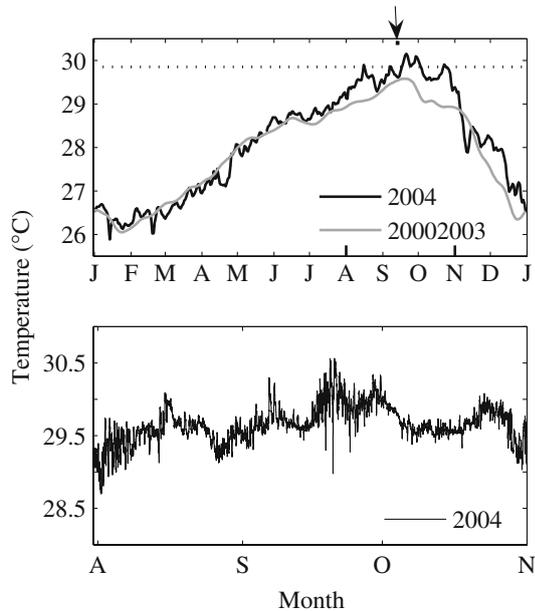


Fig. 2 Changes in water temperature over time at 18 m depth on the Belize Barrier Reef, Carrie Bow Cay (CBC), Belize. Top panel shows the average daily water temperatures for 2004 compared to a 7 day running mean of the day-of-the-year average for the previous 4 years (2000–2003). *Dashed line* represents the Pathfinder HotSpot threshold, 29.85°C, for 2 m depth at Carrie Bow Cay established by Aronson et al. (2002). Bottom panel shows a close-up of 10 min interval temperature data around the time of the bleaching event, August–November 2004. *Arrow* at the top indicates when storm surge from Hurricane Ivan first affected CBC (12–15 Sept 2004). *Bold ticks* along the bottom of the top panel indicate the period of the close-up shown in the lower panel

temperatures at 18 m were as much as 0.8°C warmer in September 2004 compared to temperatures recorded during the same times in previous (non-bleaching) years (Fig. 2). Coincident with this period of increased seawater temperatures, the Belizean barrier reef was affected in mid-September 2004 by storm surge from Hurricane Ivan; we therefore cannot de-couple these events. Hurricane Ivan was a Category 5 storm located approximately 600 km from Carrie Bow Cay at its closest point of 20.4°N, 84.1°W on September 13, 2004, with wind speeds of 140 kt (Stewart 2005).

Zooxanthellae density

Coral colonies experienced a major decline in zooxanthellae density between August and October 2004 (Fig. 3), resulting in highly significant differences in zooxanthellae density over time (Table 1). There was also a significant effect of *Montastraea* spp. colony condition (grazed vs. intact) on zooxanthellae density (Table 1), with grazed coral colonies showing lower zooxanthellae densities when averaged across all time-points (Fig. 3). When the effects of colony condition on zooxanthellae densities were examined at each sampling date using linear contrasts, no significant differences were found in either August (prior to the bleaching

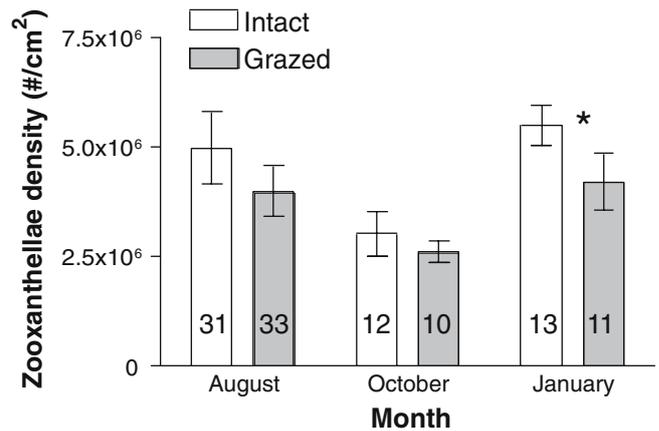


Fig. 3 Zooxanthellae densities within parrotfish-grazed versus intact *Montastraea* spp. colonies in 2004–2005 prior to the bleaching event (August), immediately following the bleaching event (October), and during recovery from bleaching (January). Sample sizes are represented within each bar; bars represent mean ± S.E. Linear contrasts were used to compare grazed and intact colonies for each month; *Indicates $p < 0.05$

event, power to detect an effect size of 0.80 = 0.87) or October (during the bleaching event; power to detect an effect size of 0.80 = 0.50), indicating that grazed and intact *Montastraea* spp. colonies were probably equally susceptible to bleaching. However, during recovery from bleaching in January 2005, intact *Montastraea* spp. colonies showed significantly higher zooxanthellae densities than grazed colonies (Table 1). It should be noted that the ANOVA revealed no significant interaction, likely due to the fact that grazed colonies always showed slightly reduced zooxanthellae densities compared to intact colonies (Fig. 2), suggesting that grazing may cause a weak chronic impact that becomes most acute in the post-bleaching recovery phase.

Table 1 Statistical analysis of changes in zooxanthellae density in *Montastraea* spp. corals in Belize

Source	SS	df	F	p
Condition (G vs. I)	11.809	1	5.43	0.0217
Time (Aug, Oct, Jan)	43.636	2	10.03	0.0001
Condition × Time	4.544	2	2.27	0.3556
Linear Contrasts:				
August (G vs. I)	1.193	1	0.55	0.4607
Pre-bleaching				
October (G vs. I)	2.220	1	1.02	0.3148
During-bleaching				
January (G vs. I)	9.967	1	4.58	0.0347
Post-bleaching recovery				
Error	228.48	105		
Total	57.76	5	5.31	0.0002

Two-way ANOVA shows effects of coral condition (grazed versus intact), sampling time, and interaction. Grazed versus intact colonies were compared at each sampling month using planned linear contrasts

Genetic identity of *Symbiodinium* spp.

Prior to the September bleaching event, we detected exclusively type C7 zooxanthellae in all *Montastraea* spp. corals ($N = 50$) (Fig. 4). In October, following the declines in zooxanthellae densities (Fig. 3), mixed symbiont assemblages of *Symbiodinium* type C7 with types B1, various C types, or D1a were detected in several *Montastraea* spp. colonies ($N = 6$ out of 36 colonies sampled). Furthermore, by recovery in January, colonies showed mixed symbiont assemblages ($N = 14$ out of 64), but grazed *Montastraea* spp. colonies were significantly more likely to have new *Symbiodinium* spp. types than intact colonies (Table 2, test of homogeneity of proportions, $\chi^2 = 8.317$, $p = 0.0063$). For those colonies in which new symbionts were detected, we always found *Symbiodinium* D1a in intact colonies, whereas we detected a greater diversity of symbiont types in grazed colonies including types B1, various C types, and D1a.

Discussion

This study documents a coral bleaching event in September 2004 in Belize associated with unusually high temperatures during the warmest season of the year, coupled with storm surge from Hurricane Ivan. Following this event, *M. franksi* and *M. faveolata* colonies that had been previously grazed by parrotfish showed both reduced zooxanthellae density and greater detect-

able diversity in *Symbiodinium* spp. populations compared to intact coral colonies. Although chronic parrotfish grazing appears to be associated with decreased zooxanthellae densities across all timepoints, we found no strong evidence that parrotfish grazing altered zooxanthellae densities prior to or during the bleaching event. Bleaching is an indicator of physiological stress in corals (Jones 1997; Hoegh-Guldberg 1999) that, combined with parrotfish predation, may alter coral-algal symbioses.

Reductions in zooxanthellae density are often associated with bleaching, though it has been shown that zooxanthellae densities fluctuate seasonally (Fagoonee et al. 1999; Fitt et al. 2000). Studies have documented regular reductions of symbiont density during the warmest times of year, a phenomenon assumed to be pantropical in corals (Fagoonee et al. 1999; Fitt et al. 2000). Although the bleaching extent did not reach catastrophic levels, the zooxanthellae reductions and visible bleaching that we observed likely go beyond seasonal lows, intensified by the abnormally high seawater temperatures and possibly by Hurricane Ivan storm surge as well. It is important to note that overall, the zooxanthellae densities that we observed before, during, and after bleaching are higher than reported elsewhere in the Caribbean for this genus (Fitt et al. 1993, 2000). Nonetheless, the pale appearance of our colonies in October (Fig. 1) along with the observed reduction in zooxanthellae density (Fig. 3) suggests that corals experienced considerable bleaching stress.

Fig. 4 PCR-DGGE profile of the *Symbiodinium* ITS 2 region showing symbiont types detected in representative grazed versus intact *Montastraea* spp. colonies ($N = 64$) sampled prior to bleaching (August 2004) and during bleaching recovery (January 2005). Profile is presented as a reverse image. Diagnostic bands are labeled for types B1, C7, and D1a

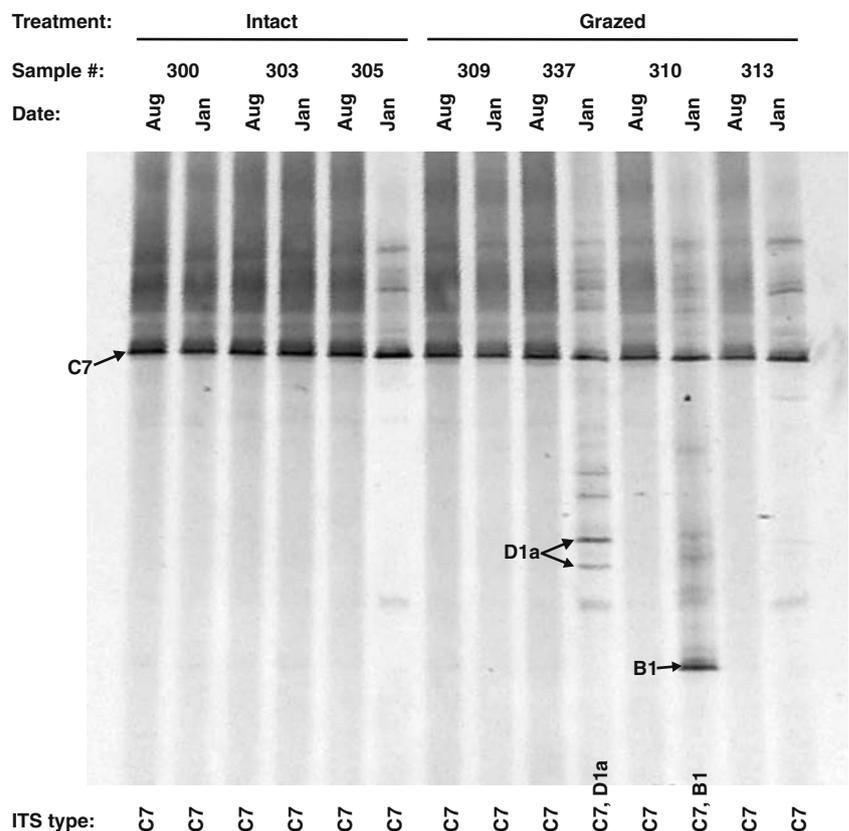


Table 2 Number and percentage of *Montastraea* colonies exhibiting increased diversity in *Symbiodinium* communities from August (pre-bleaching) to January (post-bleaching recovery)

	Increased clade diversity	No change	Percentage of change
Grazed	10	20	33
Intact	4	28	13

The same colonies were sampled at each time point. Grazed *Montastraea* spp. colonies were significantly more likely to display an increase in detectable *Symbiodinium* spp. types than intact colonies (test of homogeneity of proportions, $\chi^2 = 8.317$, $p = 0.0063$)

Additionally, it is possible that other mechanisms such as decreased symbiont pigmentation or decreased coral tissue thickness contributed to the colonies bleached appearance.

Although grazing did not appear to influence the susceptibility of colonies to bleaching, it did significantly affect recovery in January. 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). Szmant and Gassman (1990) found that the degree of recovery of zooxanthellae populations after a severe bleaching event determined whether or not a coral could complete gametogenesis the following year. In addition to zooxanthellae loss, physical damage also has reproductive consequences for corals: *Montastraea* spp. polyps adjacent to artificially damaged areas were shown to have lower fertility and fecundity compared to undamaged coral tissue (Van Veghel and Bak 1994). The combination of symbiont loss and physical damage may also interact. Meesters and Bak (1993) created artificial lesions on bleached and non-bleached *Montastraea annularis* colonies and found that bleached colonies exhibited less tissue growth, slower lesion recovery, slower tissue color restoration, and higher mortality. Since parrotfish grazing similarly removes coral tissue, grazed colonies are also likely to have slower tissue regrowth following bleaching. These findings, combined with our results, suggest that parrotfish grazing and bleaching may act synergistically to reduce coral fitness. However, as the relationship between symbiont density and fitness is non-linear (Fitt et al. 1993) and may be site-specific, further study is needed to determine the physiological and fitness consequences of the reduced symbiont densities we document here.

Environmental change has been previously shown to cause changes in *Symbiodinium* spp. communities (Rowan et al. 1997; Baker 2001; Lewis and Coffroth 2004). Prior to the bleaching event, we detected only type C7 *Symbiodinium* in our colonies, as expected since various types of clade C are frequently found in deep-water *Montastraea* spp. throughout the Western Atlantic (LaJeunesse 2002). After bleaching, we found that a

significantly greater proportion of grazed *Montastraea* spp. corals that had previously been subject to parrotfish grazing experienced a change in detectable symbiont diversity. While all colonies maintained a population of type C7 symbionts, many of the corals experienced changes in detectable symbiont communities. The reportedly stress-tolerant *Symbiodinium* type D1a (Toller et al. 2001a, b), was detected in 5 out of 63 colonies. Baker (2001) and Thornhill et al. (2006) observed *Symbiodinium* D1a in *Montastraea* spp. colonies following bleaching. Whether their newly detected symbionts were previously present at sub-detection densities or were newly acquired externally was not determined. It is also interesting to note that we detected *Symbiodinium* type B1 only in grazed corals; type B1 is commonly found throughout the Caribbean in *Montastraea* spp. colonies, and may also be considered somewhat of a generalist due to its symbiosis with a wide variety of cnidarian hosts (LaJeunesse 2002). In any case, parrotfish predation appears to increase detectable symbiont diversity.

These results suggest that parrotfish grazing may alter coral response to other stressors. An alternative explanation for the observed relationship between grazing and symbiont diversity is that parrotfishes might selectively graze coral tissue rich in C7 symbionts. However, it is unlikely that parrotfish are preferentially choosing colonies based on symbiont type because during August (pre-stress), both grazed and intact *Montastraea* spp. ($n = 50$) colonies uniformly showed exclusively type C7 *Symbiodinium* spp. (Fig. 4). While it is possible that corals with lower symbiont densities were preferentially grazed by parrotfish in August, perhaps based on differences in coral color, we did not detect any difference in zooxanthellae densities at this timepoint, even with a large sample size. Nonetheless, the possibility remains that parrotfish may selectively target colonies with lower zooxanthellae densities, although we consider it more likely that parrotfish grazing might influence zooxanthellae densities within a colony. Future experiments are needed to more explicitly address these hypotheses.

Our results suggest that chronic predation coupled with coral bleaching can exacerbate coral stress and significantly alter the coral-zooxanthellae symbiosis. Predation stress may thus contribute to spatial variation in the bleaching process. There has been much recent attention given to the role of parrotfish in coral reef resilience: although increased parrotfish abundance in marine protected areas indirectly benefits corals by decreasing macroalgal cover (Mumby et al. 2006), this study shows that parrotfish grazing may play a more complex role. It is well established that reef fish communities are rapidly changing, (Nystrom et al. 2000; Myers and Worm 2003), coral cover is declining (Gardner et al. 2003; Pandolfi et al. 2003), and the world's oceans are getting warmer (Hughes et al. 2003). As a result, it is crucial to understand the synergistic effects of multiple stressors, including chronic fish grazing, on coral survival and recovery.

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References

- Aronson RB, Precht WF, Toscano MA, Koltjes KH (2002) The 1998 bleaching event and its aftermath on a coral reef in Belize. *Mar Biol* 141:435–447
- Baker AC (2001) Reef corals bleach to survive change. *Nature* 411:765–766
- Baker AC (2003) Flexibility and specificity in coral-algal symbiosis: diversity, ecology, and biogeography of *Symbiodinium*. *Annu Rev Ecol Evol S* 34:661–689
- Bruckner AW, Bruckner RJ (1998) Destruction of coral by *Sparisoma viride*. *Coral Reefs* 17:350
- Bruckner AW, Bruckner RJ, Sollins P (2000) Parrotfish predation on live coral: “spot biting” and “focused biting”. *Coral Reefs* 19:50
- Coles SL, Brown BE (2003) Coral bleaching—capacity for acclimatization and adaptation. *Adv Mar Biol* 46:183–223
- Edmunds PJ (1994) Evidence that reef-wide patterns of coral bleaching may be the result of the distribution of bleaching-susceptible clones. *Mar Biol* 121:137–142
- Fagoonee I, Wilson HB, Hassell MP, Turner JR (1999) The dynamics of zooxanthellae populations: a long-term study in the field. *Science* 283:843–845
- Finelli CM, Helmuth BST, Pentcheff ND, Wetthey DS (2006) Water flow influences oxygen transport and photosynthetic efficiency in corals. *Coral Reefs* 25:47–57
- Fitt WK, Spero HJ, Halas J, White MW, Porter JW (1993) Recovery of the coral *Montastrea annularis* in the Florida Keys after the 1987 ‘bleaching event’. *Coral Reefs* 12:57–64
- Fitt WK, McFarland FK, Warner ME, Chilcoat GC (2000) Seasonal patterns of tissue biomass and densities of symbiotic dinoflagellates in reef corals and relation to coral bleaching. *Limnol Oceanogr* 45:677–685
- Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR (2003) Long-term region-wide declines in Caribbean corals. *Science* 301:958–960
- Garzon-Ferreira J, Reyes-Nivia MC (2001) Incidence of fish predation on stony corals at four atolls of the archipelago of San Andres and Providencia (Colombian Caribbean). *Bol Inv Mar Costeras* 30:133–150
- Glynn PW (1991) Coral reef bleaching in the 1980s and possible connections with global warming. *Trends Ecol Evol* 6:175–179
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world’s coral reefs. *Mar Freshwater Res* 50:839–866
- Hughes TP (1994) Catastrophes, phase shifts, and large scale degradation of a Caribbean coral reef. *Science* 256:1574–1551
- Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. *Science* 301:929–933
- Johannes RE, Wiebe WJ (1970) A method for determination of coral tissue biomass and composition. *Limnol Oceanogr* 15:822–824
- Jones RJ (1997) Zooxanthellae loss as a bioassay for assessing stress in corals. *Mar Ecol-Prog Ser* 149:163–171
- LaJeunesse TC (2001) Investigating the biodiversity, ecology, and phylogeny of endosymbiotic dinoflagellates in the genus *Symbiodinium* using the ITS region: in search of a “species” level marker. *J Phycol* 37:866–880
- LaJeunesse TC (2002) Diversity and community structure of symbiotic dinoflagellates from Caribbean coral reefs. *Mar Biol* 141:387–400
- LaJeunesse TC (2005) “Species” radiations of symbiotic dinoflagellates in the Atlantic and Indo-Pacific since the Miocene-Pliocene transition. *Mol Biol Evol* 22:570–581
- LaJeunesse TC, Trench RK (2000) The biogeography of two species of *Symbiodinium* (Freudenthal) inhabiting the intertidal anemone *Anthopleura elegantissima* (Brandt). *Biol Bull* 199:126–134
- LaJeunesse TC, Loh WKW, van Woesik R, Hoegh-Guldberg O, Schmidt GW, Fitt WK (2003) Low symbiont diversity in southern Great Barrier Reef corals, relative to those of the Caribbean. *Limnol Oceanogr* 48:2046–2054
- Lesser MP (2004) Experimental biology of coral reef ecosystems. *J Exp Mar Biol Ecol* 300:217–252
- Lewis SM (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecol Monogr* 56:183–200
- Lewis CL, Coffroth MA (2004) The acquisition of exogenous algal symbionts by an octocoral after bleaching. *Science* 304:1490–1492
- Loya Y, Sakai K, Yamazato K, Nakano Y, Sambali H, van Woesik R (2001) Coral bleaching: the winners and the losers. *Ecol Lett* 4:122–131
- Marsh JA (1970) Primary productivity of reef-building calcareous red algae. *Ecology* 51:255–263
- Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibility among taxa. *Coral Reefs* 19:155–163
- McClanahan TR, Maina J, Starger CJ, Herron-Perez P, Dusek E (2005) Detriments to post-bleaching recovery of corals. *Coral Reefs* 24:230–246
- Meesters EH, Bak RPM (1993) Effects of coral bleaching on tissue regeneration potential and colony survival. *Mar Ecol-Prog Ser* 96:189–198
- Meesters EH, Noordeloos M, Bak RPM (1994) Damage and regeneration: links to growth in the reef-building coral *Montastrea annularis*. *Mar Ecol-Prog Ser* 112:119–128
- Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, Gill AB (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311:98–101
- Myers RA, Worm B (2003) Rapid worldwide depletion of predatory fish communities. *Nature* 423:280–283
- Nakamura T, van Woesik R (2001) Waterflow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. *Mar Ecol-Prog Ser* 212:301–304
- Nystrom M, Folke C, Moberg F (2000) Coral reef disturbance and resilience in a human-dominated environment. *Trends Ecol Evol* 15:413–417
- Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman M, Paredes G, Warner RR, Jackson JBC (2003) Global trajectories of the long-term decline of coral reef ecosystems. *Science* 301:955–958
- Rotjan RD, Lewis SM (2005) Selective predation by parrotfishes on the reef coral *Porites astreoides*. *Mar Ecol-Prog Ser* 305:193–201
- Rotjan RD, Lewis SM (2006) Parrotfish abundance and selective corallivory on a Belizean coral reef. *J Exp Mar Biol Ecol* (in press). DOI 10.1016/j.jembe.2006.03.015

- Rowan R, Knowlton N, Baker AC, Jara J (1997) Landscape ecology of algal symbionts creates variation in episodes of coral bleaching. *Nature* 388:265–269
- Sanchez JA, Gil MF, Chasqui LH, Alvarado EM (2004) Grazing dynamics on a Caribbean reef-building coral. *Coral Reefs* 23:578–583
- Stewart SR (2005) Tropical cyclone report: Hurricane Ivan. National Hurricane Center. <http://www.nhc.noaa.gov/2004ivan.shtml>
- Szmant AM, Gassman NJ (1990) The effects of prolonged “bleaching” on the tissue biomass and reproduction of the reef coral *Montastrea annularis*. *Coral Reefs* 8:217–224
- Thornhill DJ, LaJeunesse TC, Kemp DW, Fitt WK, Schmidt GW (2006) Multi-year, seasonal genotypic surveys of coral-algal symbioses reveal prevalent stability or post-bleaching reversion. *Mar Biol* 148:711–722
- Toller WW, Rowan R, Knowlton N (2001a) Repopulation of zooxanthellae in the Caribbean corals *Montastraea annularis* and *M. faveolata* following experimental and disease-associated bleaching. *Biol Bull* 201:360–373
- Toller WW, Rowan R, Knowlton N (2001b) Zooxanthellae of the *Montastraea annularis* species complex: patterns of distribution of four taxa of *Symbiodinium* on different reefs and across depths. *Biol Bull* 201:348–359
- Van Veghel MLJ, Bak RPM (1994) Reproductive characteristics of the polymorphic Caribbean reef building coral *Montastrea annularis*. III. Reproduction in damaged and regenerating colonies. *Mar Ecol-Prog Ser* 109:229–233
- Warner ME, Chilcoat GC, McFarland FK, Fitt WK (2002) Seasonal fluctuations in the photosynthetic capacity of photosystem II in symbiotic dinoflagellates in the Caribbean reef-building coral *Montastrea*. *Mar Biol* 141:31–38