

# Effects of habitat heterogeneity in seagrass beds on grazing patterns of parrotfishes

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**ABSTRACT:** Habitat heterogeneity, particularly patchiness in seagrass cover, greatly affects the community dynamics of seagrass ecosystems. Heterogeneity in seagrass habitats can also be caused by unvegetated patches within the otherwise continuous seagrass cover. Blowouts are bare areas with an eroding edge that forms a vertical wall, often with overhanging seagrass roots and rhizomes. Fishes, including parrotfishes, aggregate in these blowouts. These aggregations of herbivorous fishes might influence the structure of the adjacent seagrass habitat. We compared parrotfish *Sparisoma* spp. grazing patterns at different distances from the edge of blowouts in seagrass beds (mainly *Thalassia testudinum*) at St. Ann's Bay, Jamaica, by counting and measuring the number of bite marks on the seagrass blades. The percentage of grazed blades, number of bites per blade, and total area of seagrass removed by grazing all increased with increasing distance from the edge of the blowout. However, the size of the bite marks, which is indicative of the size of the fish that made them, was significantly larger near the blowout than at further distances. Few large bites were found at distances greater than 4 m from the blowout, while small bites were more abundant at distances further from the edge. These data suggest that larger fishes feed in closer proximity to the shelter of the blowouts, while smaller fishes avoid the blowout edge. Both seagrass morphology and parrotfish grazing characteristics were significantly different among the blowouts used in the study, indicating that blowouts in and of themselves increase the structural heterogeneity of seagrass beds. Thus, blowouts affect the structure of seagrass ecosystems directly and indirectly (via their effects on the grazing behavior of parrotfishes).

**KEY WORDS:** Habitat heterogeneity · Grazing · Blowouts · Parrotfishes · *Thalassia testudinum* · Seagrass

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## INTRODUCTION

Habitat heterogeneity can have important effects on the structure and function of seagrass beds. Patchiness in bottom cover can affect seagrass growth and survivorship (Ramage & Schiel 1999) and shoot density (Hovel et al. 2002). In addition, seagrass patchiness affects the broader community through changes in local sediment size (Bowden et al. 2001), abundance of fishes and shrimps (Murphey & Fonseca 1995, Hyndes et al. 2003, Salita et al. 2003), survivorship, growth and

predation rates of bivalves and crabs (Irlandi & Peterson 1991, Irlandi 1994, Irlandi et al. 1995, Hovel et al. 2002), and infaunal species richness (Bowden et al. 2001). The aforementioned studies have considered habitat heterogeneity in terms of size, shape and connectivity of isolated patches of seagrass. Small, unvegetated areas within an otherwise continuous seagrass bed also increase habitat heterogeneity. Such bare areas can be caused by localized grazing (Bjornedal 1980, Williams 1988, Valentine & Heck 1991), by bioturbation (Fonseca et al. 1996, Townsend & Fonseca

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1998), or by abiotic factors (Scoffin 1970, Patriquin 1975). The heterogeneity caused by these bare areas, however, has received relatively little attention.

Blowouts are bare or sparsely vegetated open areas in an established seagrass bed (Patriquin 1975). Blowouts are most commonly caused by persistent wave or current activity that erodes part of the sediment and seagrass root/rhizome mat (Scoffin 1970, Patriquin 1975). These bare areas are often crescent-shaped, with a vertical wall (scarp) along a clearly defined eroding edge. The unvegetated area of the blowout is usually deeper than the surrounding seagrass bed, and the scarp may have a vertical relief of up to 80 cm (Patriquin 1975, and present study). Sections of the root/rhizome mat often hang over and down along the scarp, creating crevices in which many fishes can be found (M. P. Robinson pers. obs.).

The presence of blowouts creates unique microhabitats within the continuous canopy of a dense seagrass bed. Some of these microhabitats, such as the seagrass root/rhizome mats that overhang the scarp, could be used by various fishes as refugia for avoiding predators. At least 23 species from 14 families of fishes are found in blowouts during the day (M. P. Robinson et al. unpubl. data). If used as refugia by herbivorous fishes, blowouts could have significant effects on the surrounding seagrass. Because smaller fishes can hide more easily within the seagrass canopy than can larger fishes, the effectiveness of blowouts relative to the seagrass canopy as protection from predators probably depends on the size of the fish. Accordingly, we predict that larger fishes spend more time near blowouts than in the seagrass. In particular, the parrotfishes *Sparisoma radians*, *S. chrysopteron*, and *S. rubripinne*, which are associated with seagrass habitats and graze live seagrass blades (Randall 1965, 1967, Lobel & Ogden 1981, Macintyre et al. 1987, Montague et al. 1995, McAfee & Morgan 1996) are often found in and around seagrass blowouts (M. P. Robinson et al. unpubl. data).

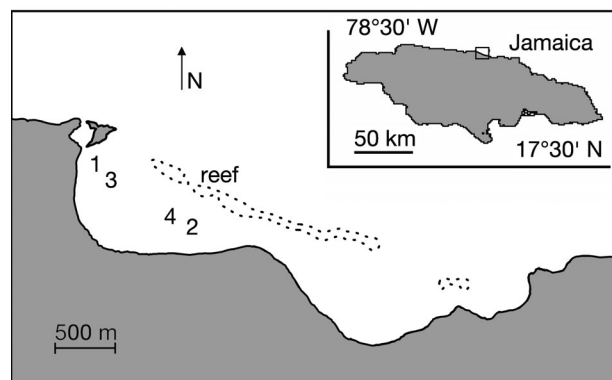


Fig. 1. Study site in St. Ann's Bay, north coast of Jamaica. 1 to 4: blowouts examined in this study

Our study was designed to answer the following questions: (1) do parrotfishes of different sizes use blowouts differently and, if so, (2) is there a difference in grazing effects on the seagrass at different distances from the blowouts? Parrotfishes are well-camouflaged and difficult to observe in seagrass beds. When feeding on seagrass blades, however, these fishes leave a distinct hemispherical bite mark on the blade (Greenway 1976, Montague et al. 1995, Kirsch et al. 2002). Therefore, we used an indirect approach to answer our research questions, with bite marks acting as a proxy for direct observations of the fishes themselves. This is the first study to investigate the use of blowouts by fishes and its potential consequences for the nearby seagrass population.

## MATERIALS AND METHODS

**Study site.** We conducted our study in the seagrass beds of St. Ann's Bay, Jamaica (Fig. 1). Bottom cover in St. Ann's Bay consists primarily of dense *Thalassia testudinum* beds (aboveground biomass = 1100 to 1400 g m<sup>-2</sup>, S. Maciá unpubl. data). We identified 11 blowouts in the western side of the bay, and randomly selected 4 whose eroding edge was isolated by at least 50 m from the next nearest blowout. These 4 blowouts were of varying size and depth (Table 1).

**Parrotfish grazing and seagrass morphometrics.** Because we used bite size as a proxy for actual fish size, it was necessary to definitively establish the relationship between bite size and fish length. We used a drop-net to capture 5 individuals of the parrotfish *Sparisoma chrysopteron*, 8 *S. rubripinne*, and 3 *S. radians*. We measured total length (TL) and placed the fish individually into 90 l outdoor aquaria with an open seawater system. Each tank had 4 seagrass 'shoots' consisting of 3 or 4 blades (approximately 200 mm length) of unbitten *Thalassia testudinum* held together with a clothespin such that the blades floated upright in the water column. We maintained the fishes in the aquaria until they had made at least 10 bites each on the seagrass blades (1 to 2 d). We then removed the seagrass leaves from the tanks, dried them, flattened

Table 1. Characteristics of blowouts examined in this study

Blowout	Length (m)	Width (m)	Scarp height (cm)	Water depth (m)
1	15	3–8	30–60	1.5
2	62	5–10	30–60	1.3
3	13	1	30–50	0.5
4	19	1–2	20–30	3.0

them on a scanner and digitized their image into a computer (sensu Kirsch et al. 2002, O'Neal et al. 2002). We randomly selected 10 complete bites from each aquarium and, using SigmaScan (Jandel Scientific) image-analysis software, measured their maximum width. Bites were considered complete when they were hemispherical and the entire arc of both sides was evident.

To quantify parrotfish grazing in the field, we laid out 8 transects of 10 m perpendicular to the eroding edge of each blowout. The transects were approximately 1.5 m apart at the edge of the blowout but fanned outwards, as the blowouts were crescent-shaped. Seagrass samples were collected at 5 distances along each transect: 0, 2, 4, 7 and 10 m from the eroding edge. At each distance we hand-collected all seagrass blades within a 0.01 m<sup>2</sup> quadrat. The non-bitten blades of 1 quadrat at Blowout 1, 7 m distance from the eroding edge, were lost prior to counting.

We measured the length and width of 2 randomly selected seagrass blades from each of the above quadrats from Blowouts 2, 3 and 4. All other analyses used samples from all 4 blowouts. We counted the total number of bites (complete and incomplete) on every blade. Because there was a significant effect of distance from the blowout on seagrass length (see 'Results'), we standardized bite number as a function of seagrass length. We divided the number of bites on each blade by the average length of seagrass blades for that distance from the blowout. Seagrass blades with bites were patted dry and immediately scanned into a computer. We used image-analysis software to measure the maximum widths of all complete bites and the total area of each of 40 randomly selected bites (2 from each distance from each blowout). Within this subset of 40 bites, area increased with increasing bite width, and a second-order regression fit these data significantly ( $r^2 = 0.93$ ;  $p < 0.001$ ;  $n = 40$ ). We then used this regression to convert the width of each complete bite to an area.

**Statistical methods.** Individual parrotfishes tend to make multiple bites on the same seagrass blade while feeding (M. P. Robinson pers. obs.). To avoid pseudo-replication, we calculated a mean per quadrat for each type of grazing datum (i.e. number of bites per blade, proportion of blades grazed, bite width, total seagrass area grazed) and used these means as replicates in our statistical analyses. We performed a multivariate analysis of variance (MANOVA) using all seagrass and grazing data as dependent variables of the fixed factor distance and a blocked factor, blowout number. Blowouts were analyzed as blocks rather than as part of a fully factorial 2-way ANOVA, because replicates of a 2-way ANOVA must be completely randomized (Sokal & Rohlf 1995), an impossi-

bility in our case given the pre-existing differences among the blowouts (Table 1). In the MANOVA, the distance effect was significant (Wilk's  $\lambda = 0.628$ ,  $F_{8,149} = 11.017$ ,  $p < 0.001$ ); therefore we analyzed each variable independently. We analyzed all of the dependent factors from the MANOVA with separate randomized-block ANOVA, with the blowouts as blocks and distance as a fixed factor. Tukey's honest significant difference (HSD) test was used for post-hoc analyses. Seagrass blade length data were box-cox-transformed and the number of bites cm<sup>-1</sup> blade length was square-root-transformed prior to analysis. All other non-transformed data satisfied the assumptions of ANOVA.

Because the ANOVA of bite width found a significant effect of distance (Table 2), we examined more closely the relationships of large ( $\geq 7$  mm, see 'Results') and small ( $\leq 7$  mm) bites with distance from the blowout. We standardized the number of bites as number cm<sup>-1</sup> seagrass blade length. The number of small bites cm<sup>-1</sup> seagrass was square-root-transformed and analyzed with an ANOVA. Because there was a large number of quadrats without any large bites (i.e. resulting in many zeros in the data set), it was not possible to use parametric analyses. Therefore, we used a bootstrapped 1-way ANOVA to determine the overall significance of distance on the number of large bites. For post-hoc analyses we used multiple, Bonferroni-corrected ( $k = 10$ ) bootstrapped ANOVA comparing each pair of distances. This type of analysis is analogous (but not equivalent in calculation) to Tukey's HSD test, because we used unplanned comparisons to compare individual groups. Where noted, we corrected p-values with a Bonferroni correction calculated using the sequential Dunn-Šidák procedure (Sokal & Rohlf 1995).

## RESULTS

For each parrotfish species we calculated a linear geometric mean (GM) regression between TL and mean bite width in captivity. These regressions did not differ based on their 95% confidence intervals (Jolicoeur & Mosimann 1968); therefore we combined the data for the 3 species. The combined GM regression of bite width on fish TL was significant ( $r^2 = 0.83$ ;  $p < 0.001$ ;  $n = 16$ ) and positive (Fig. 2); therefore bite width is an appropriate indicator of the length of the fish that created the bite mark.

As distance from the blowout increased, the length of the seagrass blades increased significantly (Table 2, Fig. 3a). There was no effect of distance on the width of the blades, however (Table 2, Fig. 3b). The density of the seagrass blades increased significantly with increasing distance from the blowout (Table 2, Fig. 3c).

Table 2. Results of randomized-block univariate ANOVA on various seagrass *Thalassia testudinum* and parrotfish grazing parameters. Distance from edge of blowout is main factor and blowout is blocked factor

Seagrass/grazing parameter	Source	df	MS	F	p
Blade length	Distance	4	11473.860	5.514	<0.001
	Blowout	3	131122.015	63.012	<0.001
	Error	233	2080.904		
Blade width	Distance	4	2.452	0.872	0.482
	Blowout	3	48.205	17.327	<0.001
	Error	233	2.782		
Blade density	Distance	4	660.404	4.674	<0.001
	Blowout	3	5689.133	40.264	<0.001
	Error	151	141.296		
No. bites cm <sup>-1</sup> blade	Distance	4	0.034	5.645	<0.001
	Blowout	3	0.143	24.091	<0.001
	Error	152	0.006		
% Grazed blades	Distance	4	0.070	5.896	<0.001
	Blowout	3	0.439	36.704	<0.001
	Error	151	0.012		
Bite width	Distance	4	8.920	11.841	<0.001
	Blowout	3	11.921	15.825	<0.001
	Error	152	0.753		
No. small bites cm <sup>-1</sup> blade	Distance	4	0.113	14.892	<0.001
	Blowout	3	0.132	17.312	<0.001
	Error	152	0.008		
Total seagrass area removed	Distance	4	45910.216	6.986	<0.001
	Blowout	3	22181.407	3.375	0.020
	Error	152	6571.580		

These increases in length and density indicate an overall increase in above-ground biomass with increasing distance from the edge of a blowout. The blocked blowout factor significantly affected seagrass blade length, width, and density (Table 2).

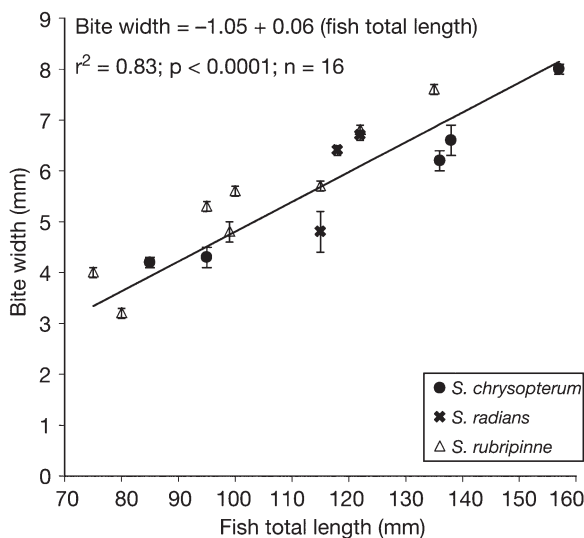


Fig. 2. *Sparisoma* spp. Regression between fish total length and bite width for 3 parrotfish species maintained in aquaria. Each data point represents mean bite width ( $\pm$ SE) for a single fish

Distance from the blowout had a strong effect on grazing intensity. There was a significant effect of distance from the blowout on the mean number of bites cm<sup>-1</sup> seagrass blade (Table 2). Seagrass blades at the edge of the blowout had significantly fewer bites per unit blade length than blades farther away (Fig. 4a). The proportion of blades with at least 1 bite also increased significantly with increasing distance from the blowout (Table 2, Fig. 4b). The blocked blowout factor significantly affected both number of bites cm<sup>-1</sup> blade and proportion of grazed blades (Table 2).

Distance from the blowout significantly affected the mean width of bites (Table 2). Bites at the edge of the blowout (0 m) were significantly wider than at all other distances, but there was no difference among the other 4 distances (Fig. 4c). Bite width was also significantly affected by the blocked blowout factor (Table 2). To test whether the frequency distributions of bite widths differed as a function of distance, we compared all possible combinations of distances with Bonferroni-corrected ( $k = 10$ ) 2-sample Kolmogorov-Smirnov tests. The distribution of bite widths at 0 m differed significantly from the distributions at all other distances (4 tests: all  $p < 0.008$ ), and the distribution at 4 m differed from the distribution at 7 m ( $p < 0.01$ ). None of the other distributions differed significantly from one another.

The distribution of bite widths at the edge of the blowout had a significant right skew ( $g_1 \pm SE = 1.183$

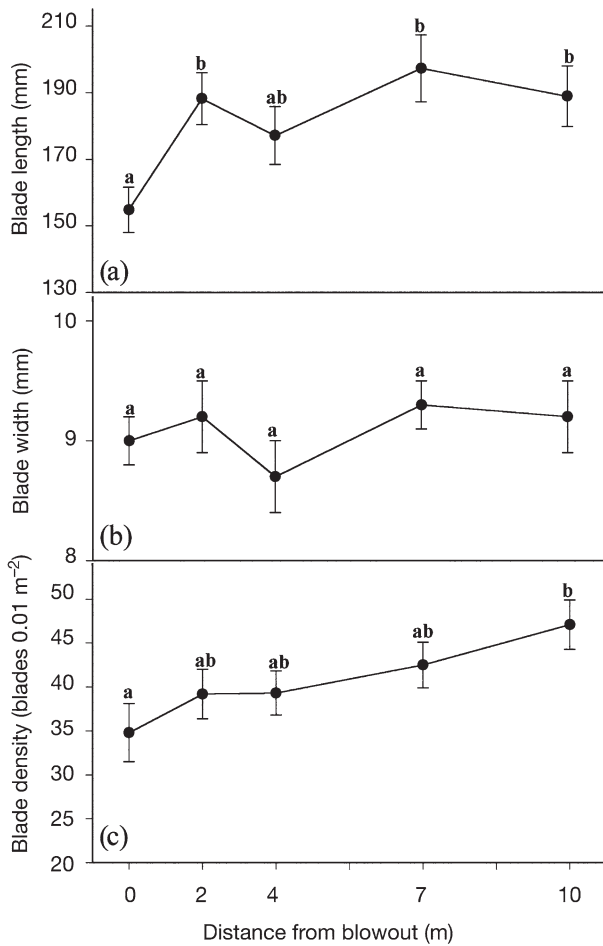


Fig. 3. *Thalassia testudinum*. Blade morphometrics and density as a function of distance from edge of blowout. Here and in Fig. 4, data points are mean  $\pm$  SE, and values with same letter are not significantly different from each other (Tukey's post-hoc analysis)

$\pm 0.120$ ), indicating a high frequency of large bites (Fig. 5). The widths of all observed bites ranged from 1.13 to 12.45 mm. Subsequently, we defined a large bite as being  $\geq 7$  mm, the approximate midpoint of this range. We square-root-transformed the number of small bites  $\text{cm}^{-1}$  seagrass blade. There were significantly more small bites per length of seagrass blade at 10 m from the blowout and fewer small bites at 0 and 2 m than at any other distance (Table 2; Fig. 5). The large number of quadrats without any large bites made parametric tests suspect. We therefore performed a bootstrapped 1-way ANOVA which found a significant effect of distance on the number of large bites per length of seagrass (10 000 iterations,  $F = 2.630$ ,  $p = 0.031$ ). Post-hoc analyses found that there were significantly more large bites in the quadrats at 0 m than at 4, 7 or 10 m (Fig. 5). No other distances

differed significantly. At distances beyond 2 m large bites were rare.

We used our second-order regression to convert each bite width to an area. We then summed the area of all bites in each quadrat to estimate the total seagrass blade area removed by grazing. These data showed a significant effect of distance from the blowout on total seagrass area removed (Table 2). The total area of seagrass blade material removed by grazing parrotfishes increased with increasing distance from the blowout (Fig. 4d). Total seagrass area removed differed significantly among the blowouts (Table 2).

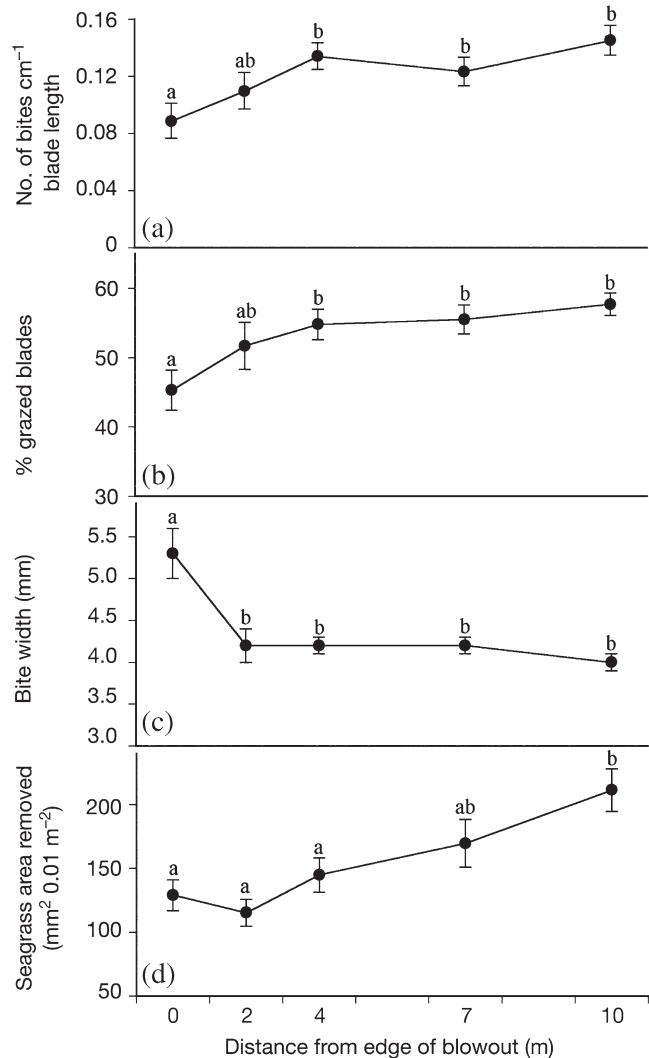


Fig. 4. *Thalassia testudinum*. Grazing effects by parrotfishes as a function of distance from edge of blowout. (a) Mean no. bites  $\text{cm}^{-1}$  seagrass blade length (back-transformed from original square-root-transformed data); (b) percentage seagrass blades with at least 1 bite; (c) mean width of parrotfish bites; (d) total seagrass blade area removed by parrotfish grazing (calculated by converting bite widths to bite area, then summing all bite areas for each 0.01 m<sup>2</sup> quadrat)



## DISCUSSION

Blowouts are common features of many seagrass beds, but until now their effect on the surrounding community has been largely ignored. Our data indicate that blowouts could have significant effects on the local seagrass community. Every dependent variable we measured, whether a characteristic of the seagrass or of the grazing of the parrotfishes, differed significantly among blowouts (Table 2). Despite the small

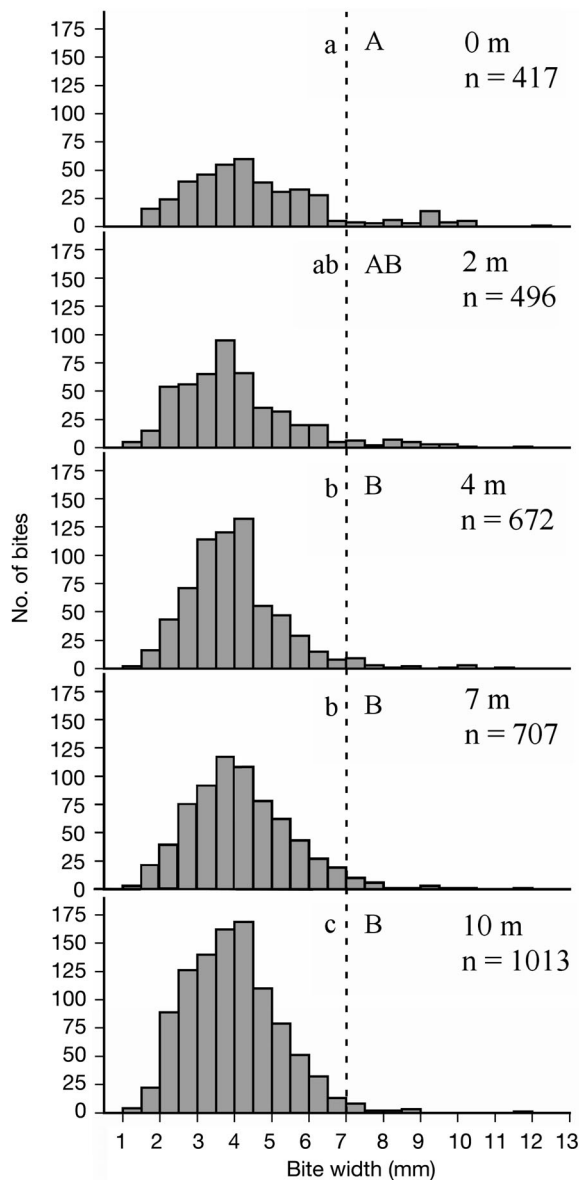


Fig. 5. *Thalassia testudinum*. Size-frequency histograms of width of bites made by parrotfishes on seagrass blades for each distance (0, 2, 4, 7, 10 m) from edge of blowout. Different letters indicate size-frequency distributions that are significantly different from each other for small bites (left of vertical line) and large bites (right of vertical line)

size of the blowouts relative to the surrounding seagrass bed, it appears that differences in size, shape, location, and possibly other unidentified features can lead to significantly different effects on the nearby seagrass community. The variation among blowouts had, in most cases, a stronger influence on the dependent variables than did the effect of distance from the edge of the blowout. Blowouts accounted for 5.3–42.6% of the variation in the dependent variables compared to 1.2–19.2% accounted for by distance (Table 2). Such a strong effect suggests that blowouts, despite their small size, could play important roles in seagrass ecosystems. Because of the many measured (Table 1) and unmeasured differences that were uncontrolled among the blowouts, however, it is difficult to interpret these effects in light of the differences among blowouts.

It is possible that the blowout-derived variation observed here is not specific to blowouts but simply results from edge effects common to sand–seagrass interfaces. Many seagrass beds have bare areas without the 3-dimensional complexity of blowouts. Although we did not investigate the effects of such bed edges, we believe that our results are specific to blowouts. In the Philippines, the abundance of fishes is not correlated with either the complexity of sand–seagrass edges nor with the shape of seagrass patches (Salita et al. 2003). More importantly, the blowout scarp, which can be up to 60 cm high and overhung by a complex mat of seagrass rhizomes, is a unique microhabitat. Simple edges between vegetated and unvegetated areas would not necessarily provide effective refugia from predation, and would not be likely to cause a difference in behavior of fishes of different sizes.

Parrotfish grazing was significantly affected by proximity to a blowout. Total grazing pressure increased with increasing distance from the edge of the blowouts, and this effect could be seen within as little as 4 m from the edge. There were significantly more bites 4 m from the blowout than immediately at the blowout edge. The proportion of blades with at least 1 bite was also significantly higher at distances at least 4 m from the blowout than at 0 or 2 m from the blowout. The size of the bites, however, was significantly larger at the edge of the blowout than at any of the farther distances. Although individual bites near the blowout were larger, they were also much fewer in number. Thus, the overall impact of grazing parrotfishes on the seagrass (total area of seagrass blade removed) increased significantly with increasing distance from the blowout. Compared to seagrasses farther from the blowout, seagrasses closer to the edge of the blowout lose less above-ground biomass to parrotfish grazers.

Grazing by parrotfishes in the Florida Keys is variable on a scale of 100s of meters (Kirsch et al. 2002). Such a

large area might include a number of different microhabitats and parrotfish populations. Our study has shown that there can be significant variability in grazing over much smaller scales (i.e. <10 m). Although parrotfishes of all sizes easily swim and feed over distances >10 m in less than 1 min (M. P. Robinson pers. obs.), the presence of a blowout appears to limit the foraging area and thus the spatial impact of certain grazers (larger parrotfishes) on the seagrass population.

Bites were significantly larger at the edge of the blowout than at all other distances. This pattern was caused by a greater number of large bites (i.e.  $\geq 7$  mm width) and fewer small bites near the blowout edge (Fig. 5). It is unlikely that the large bites at each blowout (which were relatively fewer than the small bites and were found mostly at 0 m), were created by a single large fish and represent pseudoreplication. These bites ranged from 7.0 to 12.4 mm in width (Fig. 5), corresponding to fishes of 137 to 230 mm TL, a relatively large range of 93 mm.

The decrease in bite size with increasing distance from the edge indicates that larger parrotfishes feed more along the edge of the blowout than at distances farther into the seagrass bed, whereas smaller parrotfishes exhibit the opposite pattern. There are several potential and non-exclusive explanations for this pattern. It is unlikely that smaller fishes are capable of excluding larger fishes from a preferred habitat. In addition, differences in resource availability with distance do not explain the more intense grazing of larger fishes near the blowout edge, because there is actually less above-ground seagrass biomass closest to the blowout. Therefore, it appears that larger fishes prefer the blowout edges. The remaining question then is whether the smaller fishes are excluded from the blowout edge by the larger fishes or whether the smaller fishes prefer to forage in the seagrass further from the blowout. Despite the significant differences in seagrass morphometrics, there is nevertheless a high biomass of seagrass at each distance. Therefore, competition for this resource seems an unlikely explanation for the greater presence of smaller fishes further from the blowout.

A better explanation of the differences between fish size classes in feeding is that larger fishes require the refuge provided by the blowout. Smaller parrotfishes that can penetrate and hide among the seagrass blades are probably less constrained in their needs for refugia and can feed further from the blowouts. These fishes might prefer the greater above-ground biomass farther from the blowout. Parrotfishes associated with coral reefs use the reef as a refuge when not feeding, but leave its shelter for feeding bouts in nearby seagrass beds (Randall 1965, Ogden & Zieman 1977, Tribble 1981, Macintyre et al. 1987). Furthermore, mean bite

size on seagrass blades decreases with increasing distance from a patch reef (Ogden & Zieman 1977), a pattern similar to that which we found for blowouts. Ogden & Zieman (1977) attributed this pattern to the fact that larger fishes (20 to 40 cm) cannot use the seagrass canopy itself as a refuge from predation, while smaller fishes (<15 cm) move freely through the seagrass canopy at all times of the day. A similar pattern occurs in beds of seagrasses with different morphologies (Hyndes et al. 2003). The seagrass *Amphibolis griffithii* has a dense canopy of leaves that is elevated above the sediment by the stems, creating an open space beneath. Fishes inhabiting this seagrass are larger than those in beds of *Posidonia* spp., the leaves of which emerge directly from the sediment surface. Hyndes et al. (2003) attribute this size difference to the ability of smaller fishes to penetrate the dense canopy of *Posidonia* spp. leaves, while the larger fishes are able to move about in the space underneath the *A. griffithii* canopy.

Our data suggest that blowouts, like coral reefs and the seagrass *Amphibolis griffithii*, increase habitat complexity and provide a refuge for larger parrotfishes that cannot hide within the canopy of strap-shaped seagrass blades. When using blowouts as a refuge, however, fishes appear to be more restricted in their movements than those using reefs. Our data show that larger parrotfishes graze primarily within a distance of <2 m from the blowout, whereas reef-associated parrotfishes venture as much as 90 m from the reef during their feeding bouts (Macintyre et al. 1987). This difference is likely to be at least partially explained by the lack of seagrass in the unvegetated halo (typically 10 m wide) often found near patch reefs (Randall 1965, Ogden 1976, Ogden & Zieman 1977). Such a halo does not exist in blowouts, as the seagrass can be found immediately at the eroding edge of the blowout.

Although seagrass blade-width was not affected by distance from the blowout, blade-length was significantly shorter at the edge of the blowout than further into the seagrass bed. Similarly, blade density increased with increasing distance from the blowout. Larger parrotfishes, however, grazed preferentially at the blowout edge, where seagrass blades were shorter and less dense. These fishes could easily swim the few meters to the area where seagrass length and density increase, but do not do so, suggesting that even the longer, more dense seagrass is insufficient to provide protection from predators.

Alternatively, our observed grazing pattern could result from ontogenetic changes in feeding behavior. Parrotfishes graze preferentially on epiphytized portions of seagrass blades (Lobel & Ogden 1981), nitrogen-enriched blades (McGlathery 1995) and seagrass species with lower levels of refractory compounds

(Mariani & Alcoverro 1999). Such feeding preferences might vary with age. Some *Scarus* spp. parrotfishes undergo ontogenetic shifts from carnivory to herbivory as juveniles (Bellwood 1988). Qualitative observations in our study area indicate little, if any, difference in the epiphyte load of blades at varying distances from the blowout. Older fishes may selectively graze the seagrass blades near the blowout because of some particular chemical composition of which we are unaware. Given the rhizomatous morphology of *Thalassia testudinum* and the short distances (<10 m) over which our patterns were observed, however, this explanation seems unlikely.

Another possible explanation for the observed patterns of grazing is social interaction. Parrotfishes exhibit diverse social systems both inter- and intra-specifically (Robertson & Warner 1978, Thresher 1984 [review], Shapiro 1991). *Sparisoma radians*, for example, is a territorial, harem species, although many reproducing individuals remain outside established harems (Robertson & Warner 1978, Farm 1993). If blowouts represent a significant resource (e.g. as a refuge), larger individuals might spend more time near a blowout, defending either the resource or the females that use the resource. Such behavior might explain the presence of more large bites close to the blowout as well as the increase in small bites farther from the blowout if the larger fishes are actively excluding the smaller fishes.

In conclusion, blowouts increase the habitat heterogeneity of seagrass beds and are potentially important refugia for larger parrotfishes. The grazing effects of herbivorous parrotfishes increase with increasing distance from the blowout, creating further complexity in the seagrass population. Furthermore, there appear to be important differences among individual blowouts, as shown by the significance of the blocked blowout factor in all our analyses. Although the effects of blowouts occur over a small scale (<10 m) relative to the size of the entire seagrass bed, many of the fish and invertebrate inhabitants of the seagrass bed spend their entire lives over such small scales. Thus, blowouts can contribute to overall heterogeneity in the structure and function of seagrass ecosystems.

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