

## Sediment-mediated suppression of herbivory on coral reefs: Decreasing resilience to rising sea levels and climate change?

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### Abstract

We describe a mechanistic basis for maintaining an alternative degraded stable state on coral reefs: sediment-laden algal turfs. Using remote underwater video cameras we quantified rates of herbivory by coral reef fishes on epilithic algal turfs with natural and experimentally reduced sediment loads. Removal of sediment increased overall fish feeding rates 3.8-fold, and resulted in a decrease in mean algal turf length of 64% within 4 h. After 4 h, sediment accumulated in the treatment plots, but only returned to 41% of the original depth. A total of 20 species actively fed on the sediment removal plots, compared with 12 species in control plots. Of the five numerically abundant herbivorous fish species, all increased feeding by at least 225% in the absence of sediment. Only juvenile *Scarus* spp. fed to any extent (28% of bites) on control plots. We suggest that naturally occurring sediment loads in epilithic algal turfs can suppress herbivory and that sediment-laden algal turfs may be an alternative stable state on coral reefs. This may provide a mechanistic basis for the geological evidence of a sediment-induced turn-off of coral reef growth. With projected global sea-level rises due to climate change, reef-based sediment loads may be a critical factor in differentiating the relative resilience of coral reefs and identifying reef ecosystems that are at highest risk to rising sea levels.

Throughout the world's tropical oceans there is increasing evidence of detrimental changes on coral reefs. In many areas coral reefs are exhibiting a progressive deterioration as systems become increasingly affected by human activities such as overfishing, habitat loss, or increased terrigenous input (Hughes et al. 2003; Pandolfi et al. 2003). Some of these areas exhibit more catastrophic changes marked by phase shifts, where the system flips rapidly from one ecosystem state to another (McClanahan et al. 2001; Bellwood et al. 2004). In many cases these changes have been associated with, or are exacerbated by, global climate change (Hughes et al. 2003).

For coral reefs, ecosystem changes, whether gradual or rapid, are often associated with a shift from a coral-dominated to an algal-dominated state. One of the most widely recognized shifts is the coral–macroalgal phase shift, which has been reported on reefs from the tropical Atlantic, Indian, and Pacific oceans (McClanahan et al. 2001; McCook et al. 2001; Mumby et al. 2006). However, this is only one of a range of possible ecosystem transitions on coral reefs (Bellwood et al. 2004). Which of these states or

transitions occurs is dependent on both the biological and physical environment. Although coral reef deterioration is often marked by a shift to a macroalgal-dominated state, this can only occur within certain constraints. Tropical macroalgae have specific limitations shaped by their depth, light, and sediment tolerance and their susceptibility to wave-induced water motion (Hay 1981; Steneck and Dethier 1994). Moreover, algal distribution is strongly shaped by patterns of herbivory, especially fish herbivory (McCook et al. 2001; Burkepile and Hay 2006; Littler et al. 2006). Similar constraints apply to crustose coralline and epilithic “turf” algae (Steneck and Dethier 1994; Airoidi 1998, 2003).

On both Indo-Pacific and Caribbean coral reefs, large areas of substratum are covered by an algal turf or epilithic algal matrix (EAM; Wilson et al. 2003); on flat open areas this is often manifested as a sediment-rich epilithic algal turf or “hard pan” (Steneck et al. 1997; Purcell and Bellwood 2001). This substratum configuration often appears to be a relatively stable state (Kench and Brander 2006), with little evidence of it being a transitory state shifting to coral, crustose coralline, or macroalgal domination, at least in the short term. Although this type of benthic cover may be expected in areas with low herbivore densities, why such habitats persist in herbivore-rich areas, such as mid-shelf reefs on the Great Barrier Reef (GBR), is unclear. How can 1–2-cm-thick epilithic algal mats persist on coral reefs in areas with a high density and diverse array of mobile fish herbivores?

It has been suggested that some sediment types on coral reefs can act as a deterrent to herbivory and that herbivory

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### Acknowledgments

We thank the staff of Lizard Island Research Station, A. Gonzalez-Cabello, J. Johansen, and R. Kushner for field assistance; A. Hoey, J. H. Choat, S. Wismer, and P. Kench for helpful discussions; and two anonymous reviewers for valuable comments on the manuscript.

This work was supported by the Australian Research Council.

is inversely related to sediment load (Steneck et al. 1997; Purcell and Bellwood 2001). Comparable modification of the benthic substratum through an interaction between benthic organisms and sediments has been reported in numerous aquatic ecosystems from freshwater streams to rocky coasts (Statzner et al. 2000; Airolidi 2003; Gorgula and Connell 2004). In the majority of cases, sediment appears to have a direct negative effect on grazing activity. The resultant long turf algae trap further sediment, which results in a stable sediment-rich turf.

If sediments do prevent herbivory, then sediment-rich epilithic algal turfs may represent a stable alternative state on coral reefs, with a positive feedback between sediment load and reduced herbivory leading to a grazing-resistant algal mat. Central to this scenario, however, is the assumption that it is the sediment that prevents herbivory in these areas. For coral reefs, this assumption is based largely on inferential data (Airolidi 2003), although the highest herbivorous and detritivorous fish densities are found on the reef crest, where sediment loads are lowest (Purcell and Bellwood 2001; Wilson et al. 2003; Fox and Bellwood 2007). A direct relationship between fish grazing rates and sediment load, however, has not been demonstrated in a reefal system. The goal of this study, therefore, was to experimentally evaluate the effect of natural sediment loads on rates of herbivory in an intact coral reef ecosystem. Furthermore, by using remote video we are able to identify and directly quantify the relative contribution of the taxa responsible for changes in algal standing stock after sediment removal.

## Methods

*Visual fish and benthic surveys*—Surveys were conducted in February 2006 at three sites, 100–150 m apart, along the reef flat between South and Palfrey Islands in the Lizard Island Group, northern GBR (14°41'5"S, 145°26'55"E). Fish surveys focused on roving herbivorous or detritivorous (or both) species from the families Acanthuridae, Pomacentridae, Kyphosidae, Labridae (parrotfishes), and Siganidae. During a 5-min timed swim (estimated distance  $64.2 \pm 7.8$  m SE,  $n = 4$ ), all individuals of these species encountered within a 5-m-wide transect were recorded in 5-cm total length (TL) size categories. This was repeated four times at each site (all surveys by C.J.F.). In addition, a point line-transect method was used to survey the benthos at each site, using a 10-m line transect. Benthic organisms or substrata were identified and classified into one of seven categories (sediment, EAM, macroalgae, crustose coralline algae, live scleractinian coral, soft coral, and damselfish territory) at 33 points along the transect, i.e., every meter starting from zero and 1 m either side. Six replicate transects were surveyed at each site.

*Sediment removal experiments*—Experimental plots were established at each of the three reef flat sites described above. A chain was first used to demarcate adjacent control and treatment plots (each plot was  $0.7 \times 1.4$  m =  $0.98$  m<sup>2</sup>) on an area of reef flat pavement dominated by a sediment-rich EAM that was devoid of any large holes or pits. Sediment was then removed from within the treatment plot

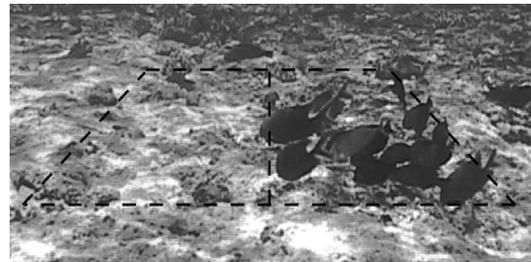


Fig. 1. A single frame from the digital video footage showing the experimental layout. The dashed lines mark the location of the control (left) and treatment (right) plots (each  $0.7 \times 1.4$  m). Note the concentration of feeding activity within the sediment-reduced treatment plot. The plots were marked by chains that were removed at the start of filming (to delimit the borders on the screen).

using a compressed-air uplift (this caused minimal disruption to the EAM while still removing the majority of entrapped sediment). The chain outlines for each plot were then removed so that no marks other than the cleaned patch of reef flat pavement remained, with each experiment initiated almost simultaneously at all three sites ( $08:30$  h  $\pm$  20 min). Herbivore feeding rates were recorded for the following 6 h using stationary underwater video cameras (Sony TRV-950 MiniDV cameras in Amphibico housings) on tripods located approximately 4 m away from the experimental plots (Fig. 1). Each site was undisturbed apart from 5-min battery and tape changes every 90 min. Subsequent experimental plots were established at each site over five consecutive days (with similar tidal conditions, i.e., on a falling tide with a similar tidal range; February 2006), with new treatment and control plots selected haphazardly without replacement, i.e., no overlap with previous treatment or control areas (at least 20 m away).

*Video analysis of herbivore feeding rates*—Pilot studies established that most feeding occurred in the first 3 h. To provide an overview of feeding activity during the first 3 h, the first 15 min of each hour (0+, 1+, 2+, and 3+ h) after sediment removal was examined. During each 15-min interval, the time each individual fish entered and left the control or treatment plot was recorded along with the genus (species where possible), estimated total length (one of seven 5-cm TL size classes: 5–10, 10–15, to 35+ cm), and total number of bites taken. Individual bites were defined as those with an accompanying rapid movement of the head toward and away from the substratum, as this provided the most consistent means of recording the activity of all fish taxa found at these sites. It should be noted that for taxa such as *Ctenochaetus* and *Siganus*, this provides a conservative measure of actual bites taken, as these fishes often feed in “forays,” i.e., taking several rapid bites in between a single approach–retraction of the head from the substratum. Feeding activity was recorded only from individuals of 5-cm TL or larger, as individual bites by fishes smaller than this length were difficult to distinguish accurately.

*Sediment loadings and algal turf height*—To avoid disturbing fish feeding, the sediment removal experiment

was repeated under similar tidal and wave conditions (May 2006), and sediment loadings and algal turf height within the control and treatment plots were measured over a 4-h period. First, sediment depth and algal turf heights were measured using the wire depth probe of a precision dial caliper, which was pushed into the sediment–turf matrix until solid reef pavement was reached. This permitted equivalent measurements of sediment depth and turf height (to nearest 0.1 mm) between the control and treatment plots. These measurements were repeated at five locations within each plot every hour.

In addition to the above measurements, extractive samples of sediment loadings were taken within the control and treatment plots at four time intervals (before sediment removal, immediately after, +2 h, and +4 h) using an electronic submersible pump fitted with a removable prefilter (following Purcell and Bellwood 2001). For each sample, a polyvinyl chloride ring (86 mm Ø, 60 cm<sup>2</sup> area) was secured on the substratum, then sediment vacuumed from within the sampling ring into a plastic bag along with approximately 4 L of seawater. The prefilter and plastic bag were removed from the pump and sealed in a plastic bag. All samples were returned to the field station within 6 h of collection, where each sample was poured into settling containers and left undisturbed for 36 h. Sediment samples were then air dried for transportation to the laboratory. To remove any organic material, each sample was placed in a bleach solution (12% sodium hypochlorite), the volume being at least three times the volume of the sediment. The sediment was stirred three times a day and the solution changed twice over 3 d. Samples were then rinsed twice with fresh water. Great care was taken to minimize loss of fine sediment particles when pouring off the bleach solution and water. Samples were oven-dried at 50°C for 10 d, then air-dried until they reached constant mass (less than 1% change).

*Statistical analyses*—The abundance of substratum categories among the three sites was compared using a one-way multivariate analysis of variance (MANOVA), as were the abundances of herbivorous fishes among sites. Site was a fixed factor in each analysis. Data transformations ( $\log_{10}[x + 1]$ ) were used to minimize deviations from normality and homogeneity of variances. In addition, Pillai's trace was chosen as the principal statistic for multivariate analyses as it provides the most robust index to any violations of such assumptions (Johnson and Field 1993). Sediment depth and turfing algae heights were compared for control and treatment plots over the four time intervals using a three-way MANOVA, with site, time interval, and sediment treatment as fixed factors in a fully orthogonal design.

For the video analysis of herbivorous grazing activity, each day was treated as a single replicate, being composed of four 15-min intervals summed to make 60 min of footage analyzed per replicate day per site. Statistical analyses of fish bite data focused on six species or species groups that displayed the highest overall bites (treatment and control data pooled), which were those species or species groups displaying more than 6500 total bites (cf. less

Table 1. Mean densities of the 11 most abundant herbivorous fishes (from a total 21 species) censused, pooled across sites (MANOVA no-site effect: Pillai's trace 1.438,  $F_{18,4} = 0.568$   $p = 0.819$ ), with family indicated in parentheses (L, Labridae; S, Siganidae; A, Acanthuridae). Average number of bites taken by each species per hour also indicated (pooled across treatment and control, averaged across 5 d,  $n = 5$ ). Note that density rankings are not reflected in mean number of bites recorded, especially *Siganus doliatus*.

Species	Density $\pm$ SE (ha <sup>-1</sup> )	Bites $\pm$ SE (h <sup>-1</sup> )
<i>Scarus</i> spp. (L)*	890.6 $\pm$ 172	3379 $\pm$ 852
<i>Scarus psittacus</i> (L)*	537.5 $\pm$ 113	1383 $\pm$ 602
<i>Siganus</i> spp. (S)*	418.8 $\pm$ 81	2372 $\pm$ 1037
<i>Scarus rivulatus</i> (L)	162.5 $\pm$ 44	18 $\pm$ 11
<i>Ctenocheatus striatus</i> (A)*	153.1 $\pm$ 9	1703 $\pm$ 1129
<i>Naso brevirostris</i> (A)	150.0 $\pm$ 3	476 $\pm$ 414
<i>Acanthurus nigrofuscus</i> (A)*	146.9 $\pm$ 44	1397 $\pm$ 866
<i>Chlorurus sordidus</i> (L)	125.0 $\pm$ 31	468 $\pm$ 290
<i>Acanthurus olivaceus</i> (A)	71.9 $\pm$ 38	37 $\pm$ 31
<i>Acanthurus</i> spp. (A)	62.5 $\pm$ 13	512 $\pm$ 525
<i>Siganus doliatus</i> (S)*	40.6 $\pm$ 3	1548 $\pm$ 625

\* Species used in feeding activity analyses.

than 2600 total bites in all other species). Together, these species took 71% of all bites over the 5 d of observation. This was done for two main reasons: to concentrate on those species that had the greatest effect, and to remove those species with high incidences of zero bites, which severely depletes the power of parametric analyses. Bites taken per hour in each experimental plot were then compared using a two-way MANOVA, with site and sediment treatment as fixed factors in a fully orthogonal design.

## Results

A sediment-laden EAM was the dominant substratum type, covering an estimated 76.1%  $\pm$  1.6% of the study area ( $n = 3$ , averaged across sites,  $\pm$ SE), with soft coral being the second most abundant category at 5.7%  $\pm$  0.9%, with no significant difference in substratum composition between sites (Pillai's trace 0.624,  $F_{20,14} = 0.317$ ,  $p = 0.99$ ). The visually censused roving herbivore fauna in this area contained 21 species. Parrotfishes were the most abundant group, comprising more than half (54.9%) of the individuals recorded (Table 1). Rabbitfishes (Siganidae) were the second most abundant group, with *Siganus doliatus* and *Siganus* spp. (*Siganus spinus* and *Siganus argenteus*) alone comprising 14.7% of all individuals.

The sediment removal treatment reduced sediment loads within the EAM from approximately 8.1 to 1.1 kg m<sup>-2</sup> (Table 2), equating to a decrease in depth from 18.0 to 0.9 mm (Fig. 2). The reduction in sediment was highly consistent among sites (Table 3). This resulted in a rapid increase in fish feeding rates within the treatment plots. There was a 3.8-fold increase in the number of bites taken within the low-sediment (11,702  $\pm$  1917 bites h<sup>-1</sup>) plots compared with control (3077  $\pm$  360 bites h<sup>-1</sup>) plots when taking all species and sizes together (mean  $\pm$  SE,  $n = 5$ ; sites

Table 2. Change in sediment mass loadings within the epilithic algal matrix over time for both control and treatment plots (averaged across sites,  $n = 3$ ).

Time (h)	Sediment mass ( $\text{g } 60 \text{ cm}^{-2}$ )	
	Control ( $\pm$ SE)	Treatment ( $\pm$ SE)
0- (before)	50.3 ( $\pm$ 5.1)	48.4 ( $\pm$ 6.0)
0+ (immediately after)	49.1 ( $\pm$ 3.6)	6.7 ( $\pm$ 1.5)
2+	54.4 ( $\pm$ 4.5)	24.3 ( $\pm$ 1.3)
4+	51.8 ( $\pm$ 4.8)	41.6 ( $\pm$ 1.2)

pooled within days). On the basis of the six most important species (bites taken), there was a highly significant treatment effect but no significant site effect (Table 4). The increase in feeding rates was most marked in the acanthurids and siganids. In *Acanthurus nigrofuscus* and *S. doliatus*, feeding rates increased from 129.6 to 1267.4 bites  $\text{h}^{-1}$  and from 13.8 to 1534.0 bites  $\text{h}^{-1}$  respectively, representing a 977% and 11,115% increase in feeding rates. Notably, the relative abundance of species in the visual censuses was a poor predictor of their feeding rates in the experimental plots (Table 1). The smallest increases were in *Scarus* spp. (primarily immature *Scarus psittacus*), with only a 229% increase (Fig. 3). The total number of species actively feeding ( $>2$  bites  $\text{h}^{-1}$ ) was 1.7 times greater in treatment plots (20 species) than in control plots (12 species).

Feeding by herbivorous fishes in treatment plots reduced algal length by approximately 64% within 4 h of sediment removal (Fig. 2). Nevertheless, sediment movement on the reef flat was pronounced and sediment loads returned to approximately 41% of the original depth within 4 h (Fig. 2A). No significant site effect was detected in the reduction of algal height, nor the rates of subsequent sediment accumulation among sites (Table 3). The next day treatment plots were visually indistinguishable from controls.

## Discussion

Reduction of the overlaying sediment load on experimental plots resulted in a rapid and dramatic increase in grazing rates by herbivorous fishes. Algal length decreased by more than 60% within 4 h. The rapid and substantial increase in fish feeding within areas of reduced sediment load strongly supports the suggestion that natural densities of sediments can suppress herbivory on coral reefs. Indeed, the uncovered algal filaments may have been grazed even further if not for the rapid ( $<4$  h) redeposition of sediment to around 40% of the previous depth. It may be no coincidence that sediment returned to 40% of the initial sediment depth when approximately 40% of the initial algal length remained. The lack of a significant site effect suggests that this is a widespread response at Lizard Island. Moreover, the increase in feeding rates was seen in all five numerically dominant local herbivorous or detritivorous fish species; only juvenile *Scarus* spp. showed minimal response. This limited response may be because they feed on individual algal filaments and are unlikely to be deterred by sediment (Chen 2002).

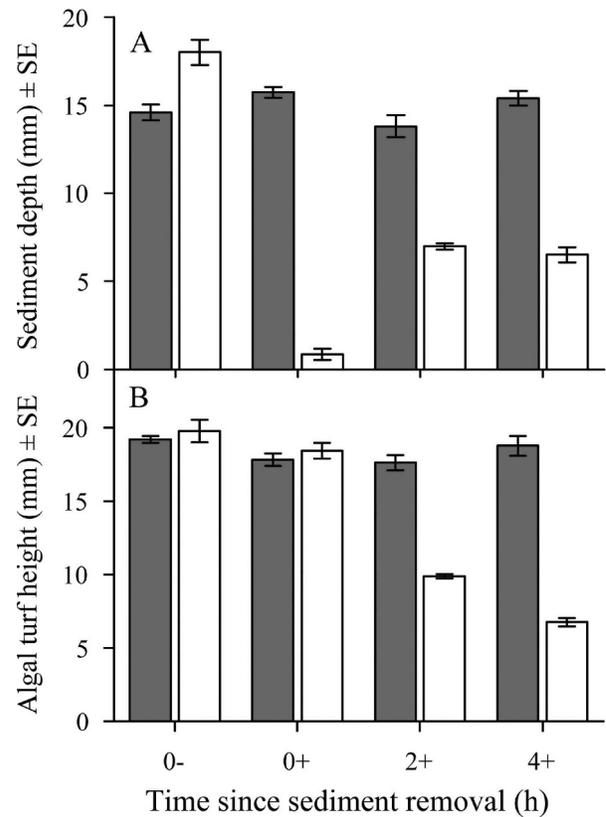


Fig. 2. Temporal changes in sediment depth and algal height. (A) Sediment depth and (B) algal turf length: before sediment removal (0-), immediately after removal (0+), after 2 h (2+), and after 4 h (4+). Open bars, treatment plots; shaded bars, control plots (three plots per site, three sites, errors based on five replicate days).

There are several reasons why carbonate sediments may deter fish feeding. The traditional explanation is that carbonates interfere with digestion, calcium carbonate in reefal sediments buffering the acid stomachs of fishes. This may be the case for siganids and those acanthurids that have acidic stomachs (Choat and Clements 1998). Indeed, these two groups did display the greatest increase in feeding

Table 3. Summary of three-way MANOVA of sediment depth and turf height within experimental plots (sediment removed or control with natural sediment loads) at each of three sites, measured over four time periods (before and immediately after, 2+ h, and 4+ h after establishment of plots). Sediment treatment, time, and site were fixed factors.

Factor	Pillai's trace	F	df	p-value
Sediment	0.610	74.30	2,95	$<0.01$
Time	0.880	25.16	6,192	$<0.01$
Site	0.007	0.17	4,192	0.956
Sediment $\times$ time	0.954	29.16	6,192	$<0.01$
Sediment $\times$ site	0.018	0.44	4,192	0.779
Time $\times$ site	0.039	0.32	12,192	0.985
Sediment $\times$ time $\times$ site	0.031	0.25	12,192	0.995

Table 4. Summary of two-way MANOVA of bites taken by six species of herbivorous reef fishes within each experimental plot (sediment removed or control with natural sediment loads) at each of three sites. Sediment treatment and site were fixed factors.

Factor	Pillai's trace	F	df	p-value
Sediment	0.735	8.777	6,9	<0.01
Site	0.689	1.752	12,40	0.092
Sediment × site	0.150	0.270	12,40	0.991

activity with sediment removal. However, such physiological constraints cannot apply to the parrotfishes, which lack stomachs but do possess a highly modified pharyngeal apparatus that can triturate food with high sediment loads (Bellwood 1996). Interestingly, adult parrotfishes rarely fed in control areas but did feed in treatment areas. It is likely that as adults these fishes cannot target individual algal filaments and, although they can cope with high-carbonate diets, they actively select surfaces with low-carbonate loads and high concentrations of organic material (Purcell and Bellwood 2001; Wilson et al. 2003). As predominantly detrital feeders, parrotfishes in the genera *Scarus* and *Chlorurus* appear to selectively feed in areas where inorganic sediments comprise a smaller proportion of the particulate matter in the EAM (Purcell and Bellwood 2001; Wilson et al. 2003). Thus, even for grazing parrotfishes, a high-sediment EAM may be an undesirable and ultimately a nutritionally inadequate foraging location. The rapid reaction of most herbivores and detritivores to the reduced sediment load (all species present and feeding within 20 min and algae halved within 2 h) emphasizes the quick recognition of the low-sediment areas as desirable foraging locations and suggest that the presence of sediment normally renders it unavailable, unapparent, or undesirable. The grazing rates in the experimental plots were abnormal and unsustainable. However, they do show that resident algae are palatable to a wide range of species and, given the opportunity, most algae would be rapidly consumed.

The experiments were undertaken on the outer reef flat. This habitat experiences one of the highest rates of water movement (Fulton and Bellwood 2005; Kench and Brander 2006). Here, macroalgae are rarely encountered (except *Turbinaria*). Unlike temperate exposed shores, reduced rates of herbivory are unlikely to result in a switch to macroalgae, as tropical algae appear to have a limited capacity to cope with the turbulence and scour experienced in these exposed wave-swept locations (Kendrick 1991). The presence of a sediment-laden EAM may be a characteristic of high-wave-energy locations. This benthic assemblage is highly resistant to dislodgement by wave action, but it does need a sediment reservoir (adjacent reef flat or lagoon) (Kench and Brander 2006; Stamski and Field 2006). Without this reservoir the area is likely to be dominated by a short EAM, with coral or crustose coralline algae (or both). The key is probably the interaction between sediment movement and availability, microtopography, and, to a lesser extent, herbivore densities (Irving and Connell 2002). Overall, a sediment-laden EAM is

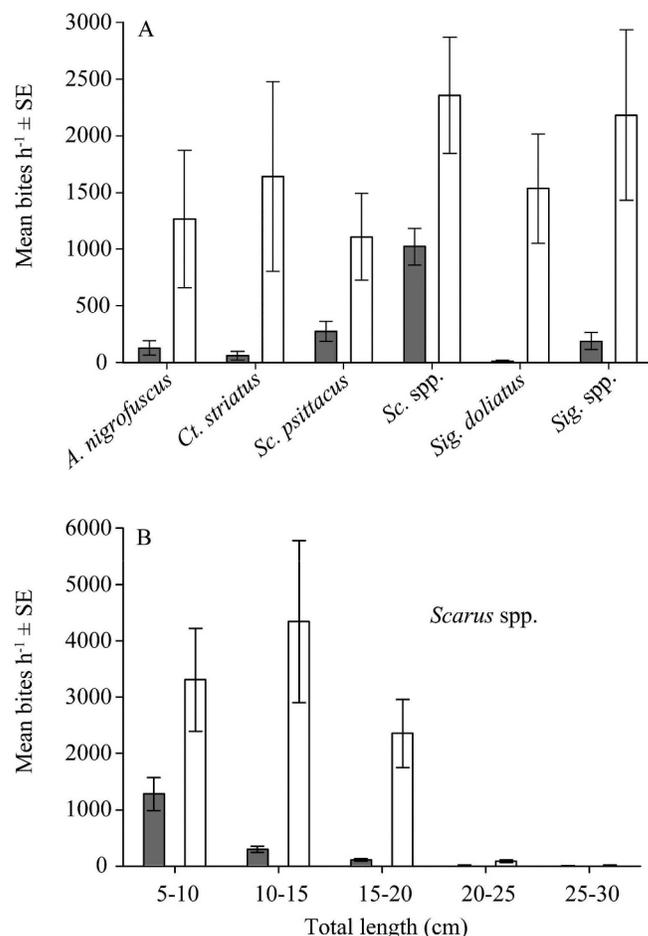


Fig. 3. Herbivore feeding rates in control and treatment plots. (A) The five dominant herbivorous fish species and *Scarus* spp. (pale initial phase specimens; probably *S. psittacus*). (B) Among-size class variation in feeding by *Scarus* spp. Open bars, treatment plots; shaded bars, control plots (three sites, errors based on five replicate days). *A.*, *Acanthurus*; *Ct.*, *Ctenochaetus*; *Sc.*, *Scarus*; *Sig.*, *Siganus*.

compatible with and may even be a characteristic of moderately high-wave-energy locations, and may persist regardless of potential rates of local herbivory.

A sediment-laden EAM may represent an alternative stable state for coral reefs, a high-energy alternative to the macroalgal-dominated states found in lower-energy locations (although sediment-laden EAMs also occur in low-energy locations; Kench and Brander 2006). A shift to macroalgae is one of the most conspicuous and widely documented phase shifts on coral reefs. Sediment-laden EAMs are less conspicuous but may represent another alternative degraded state. This is likely to be a very stable, resilient, alternative state. An extensive turf with high sediment loads will limit both coral and macroalgal colonization (Hunte and Wittenberg 1992; McCook et al. 2001), preventing shifts to coral or macroalgal domination, whereas suppression of grazing will prevent a shift to coralline algae (Steneck 1988). With the exception of periodic storms, the benthic composition is unlikely to be disturbed (Kendrick 1991; Airoldi 1998, 2003). The

extensive hard pan on Caribbean reefs may be a characteristic feature of this positive feedback.

Nevertheless, a sediment-laden EAM may be prevented from forming. Parrotfishes and surgeonfishes in the genus *Ctenochaetus* can play an important role in modifying the EAM composition and reducing sediment loads. Unlike many other taxa that selectively remove algae when grazing (e.g., many acanthurids), most parrotfishes scrape the surface while ingesting algae and detritus (especially *Scarus*, *Chlorurus*, and *Hipposcarus*; Bellwood and Choat 1990). This not only reduces algal length (and thus reducing its capacity to hold sediment; Purcell and Bellwood 2001; Stamski and Field 2006) but also directly removes sediment. Sediment ingestion and processing by parrotfishes and *Ctenochaetus* reduces particle sizes and results in a net loss from the system, especially if defecation is away from the reef (Bellwood 1996). Parrotfish grazing on the inner GBR can scrape the entire reef crest surface every 19 d (Fox and Bellwood 2007; Hoey and Bellwood 2008). Such intense grazing may provide the critical feedback required to maintain the low-sediment EAMs found in heavily grazed reef crest locations (Purcell and Bellwood 2001; Fox and Bellwood 2007). Parrotfishes may thus modify the nature of the EAM, lowering sediment loads and increasing the probability of further herbivory and, indirectly, increasing the potential for coral recruitment and survival (Hunte and Wittenberg 1992; Birrell et al. 2005).

Many studies have documented the negative effect of increasing sediment on coral reefs, usually as a result of anthropogenic disturbance (Hunte and Wittenberg 1992; Jones et al. 2004). However, the experiments presented herein demonstrate the potential effect of natural loads of reef-based sediment on fish grazing patterns. The role of these sediments in the EAM provides a mechanistic basis for the geological phenomenon of “drowned reefs.” It has been hypothesized in the geological literature that a sediment-filled lagoon can smother a reef; reef growth is “turned off” as a result of being smothered from behind by sediment (Blanchon and Shaw 1995). The reef is, in effect, choked by its own waste. The flow of sediment onto a reef, and its persistence in a stable sediment-laden EAM, would decrease herbivory, resulting in a stable condition characterized by low coral recruitment and, as a result, low rates of framework-building carbonate deposition and reef growth. Faced with rising sea levels these reefs would fail to keep up with the sea level and effectively drown. This is a sobering scenario given the current state of many of the world’s coral reefs, which have experienced overfishing and extensive coral bleaching and now face predicted global sea-level rises.

In the Caribbean many reefs possess large areas of sediment-laden EAMs commonly referred to as hard pan. Although less prominent on Indo-Pacific coral reefs, such expanses of sediment-laden EAM are frequently encountered in shallow-wave exposed locations. Although they probably represent a natural alternative benthic configuration, a significant increase in the area of such habitats may be a sign of reef degradation and any increase must be viewed with concern. Characterized by low topographic

complexity and low fish abundance, this benthic configuration is probably highly resilient. It would therefore reduce options for reef reorganization in the face of climate change, and may represent a decrease in the overall resilience of the coral reef ecosystem. Sediment-laden turfs may thus represent an easily overlooked but highly dangerous stable state on coral reefs. In the face of global climate change, sediments, algae, and herbivory may hold the key to the survival of many of the world’s coral reefs.

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*Received: 31 January 2008*

*Accepted: 20 May 2008*

*Amended: 16 June 2008*