



Digital Commons@

Loyola Marymount University
LMU Loyola Law School

Biology Faculty Works

Biology

2014

Effects of sediment depth on algal turf height are mediated by interactions with fish herbivory on a fringing reef

Sarah Joy Bittick

Loyola Marymount University, sarah.bittick@lmu.edu

Follow this and additional works at: https://digitalcommons.lmu.edu/bio_fac

Digital Commons @ LMU & LLS Citation

Bittick, Sarah Joy, "Effects of sediment depth on algal turf height are mediated by interactions with fish herbivory on a fringing reef" (2014). *Biology Faculty Works*. 147.

https://digitalcommons.lmu.edu/bio_fac/147

This Article is brought to you for free and open access by the Biology at Digital Commons @ Loyola Marymount University and Loyola Law School. It has been accepted for inclusion in Biology Faculty Works by an authorized administrator of Digital Commons@Loyola Marymount University and Loyola Law School. For more information, please contact digitalcommons@lmu.edu.

Effects of sediment depth on algal turf height are mediated by interactions with fish herbivory on a fringing reef

R. J. Clausing*, C. Annunziata, G. Baker, C. Lee, S. J. Bittick, P. Fong

Department of Ecology and Evolutionary Biology, University of California, Los Angeles,
California 90095-1606, USA

ABSTRACT: Closely cropped algal turfs support key ecosystem functions on healthy coral-dominated reefs, yet how this important reef component is affected by sedimentation, a key stressor on reefs worldwide, is relatively unknown. We used a 2-factor caging experiment to evaluate the effects of varying sediment depth and presence of herbivorous fish on algal turf height on a fringing reef in Mo'orea, French Polynesia. Without herbivory, 2 mm of sediment reduced turf growth by ~50% compared to sediment removal treatments; in contrast, growth with 4 mm of sediment was low or negligible regardless of herbivory treatment. Negative effects of sediment were linked to the development of black basal layers of sediment, indicating accumulation of hydrogen sulfide. Black sediment occurred in 60 to 70% of all 4 mm plots and in 43% of caged 2 mm plots but was not found in open 2 mm plots, implying that grazing ameliorated development of black sediment under 2 mm loads. Sediment levels of 2 mm did not deter herbivory, evidenced by the significant decrease in turf height in open compared to caged plots. Under 4 mm of sediment, black sediment inhibited both growth and herbivory where it occurred. Without black sediment, however, fish grazing balanced algal growth, resulting in negligible algal height changes across 4 mm plots but with differing underlying mechanisms. Field surveys on other sedimented reefs with healthy herbivore communities confirmed an increase in the presence of black sediment at depths over 3 mm. Thus, deeper sediment depths inhibit turf growth, yet under moderate levels of sedimentation, intact herbivorous fish communities may maintain closely cropped, healthy turf communities by preventing the negative effects of black sediment.

KEY WORDS: Sediments · Algal turf · Herbivory · Fringing reef · Tropical algae

INTRODUCTION

Healthy coral reefs are dominated by benthic communities of corals, crustose calcareous red algae, and closely cropped algal turfs (reviewed by Fong & Paul 2011). The global decline in coral reefs is often associated with phase shifts from these communities to those of longer turfs and larger fleshy macroalgae (Hughes et al. 2007); thus, research on factors that sustain healthy benthic communities is imperative. Corals have been studied extensively, yet little is

known about how anthropogenic impacts affect algal turfs (for a review, see Fong & Paul 2011). Algal turfs are important components of coral reefs as they support key ecosystem functions including high rates of primary production, trophic support, and nitrogen fixation (McCook 1999, Russ 2003, Fong & Paul 2011); thus, they are often used as an indicator of reef health (e.g. Carpenter 1986, McCook 1999). In healthy, coral-dominated reef systems, herbivory is typically high and algae of almost all species are usually grazed down to form diverse turfs <1 cm tall,

*Corresponding author: rclausing@ucla.edu

with the exception of areas and species with spatial, chemical, or temporal refuges (e.g. Fong et al. 2006, Smith et al. 2010a). Reduction of herbivory is often associated with shifts to larger macroalgae (Bellwood et al. 2004, Hughes et al. 2007, Smith et al. 2010b), and past research suggests that closely cropped algal turfs will dominate the algal community under conditions of low nutrient supplies and relatively high herbivory pressure (e.g. Littler & Littler 1984, McClanahan et al. 2003). Interactions between nutrients and herbivory and other controlling factors such as sediment loads, however, may confound these relationships (Airoldi 2003).

Sediments blanket algal turf tissue and, as a result, may block herbivore access, enhancing the risk of increased turf height and resultant negative community-level effects. Goatley & Bellwood (2013) showed that a pulse of sediment added to turfs on a high-energy reef crest was as effective as a cage at increasing net turf growth rates on the Great Barrier Reef (GBR). Bellwood & Fulton (2008) measured a 64% increase in fish bite rates on algal turfs when sediment loads were experimentally reduced from 18 to 0.9 mm, suggesting high sediment loads were deterring consumption; this effect was later shown to extend across 3 reef zones from crest to flat (Goatley & Bellwood 2012). However, another study on the GBR found that lower levels of sediment may have been insufficient to deter herbivory on turfs (Bonaldo & Bellwood 2011). If sediments reduce herbivory on turfs and promote turf elongation, this may inhibit reef resilience by direct and indirect negative effects on coral (McCook 1999). For example, taller less-grazed turfs can prevent settlement of new coral recruits (Birrell et al. 2005). While deeper sediment loads have been shown to diminish herbivore control of algal turfs on the GBR, it is still unclear at what sediment depth this control may no longer be efficacious. We hypothesize that herbivorous fish may tolerate sediment loads on algal turf to a critical tipping point before consumption is significantly deterred.

Sediment loads also have inherent costs to algae, though these costs have usually been studied for fleshy macroalgae, not turfs. For example, while the macroalga *Sargassum microphyllum* is tolerant of current sediment loads on nearshore reefs of the GBR, experimental increases in sediment depth reduced recruitment, growth, survival, and vegetative regeneration (Umar et al. 1998). A review documented numerous additional negative effects of sediment on algae and other marine organisms, including physical damage from scouring or abrasion and burial (Airoldi 2003). One study on temperate

turf assemblages found that negative effects of sediment are strongly modulated by light availability (Irving & Connell 2002). Sediment burial of embryos of the temperate rocky shore macroalga *Fucus serratus* limited light availability and diffusion of metabolic waste products, creating localized areas with black sediment that contained hydrogen sulfide (H_2S), which not only inhibited growth, but also limited survival (Chapman & Fletcher 2002). Extrapolation from these studies indicates that the negative effects of sediment on tropical algal turf growth may also depend on sediment depth.

Although evidence exists that both inhibition and facilitation of algal turf growth may occur with sedimentation, no studies have directly examined these effects across a range of sediment depths, despite evidence suggesting they may be dependent on sediment depth and mediated by herbivory. To address this knowledge gap, we conducted an experiment examining how varying sediment depths affected algal turf net growth under ambient and reduced levels of fish herbivory on a fringing reef flat.

MATERIALS AND METHODS

This study was conducted in May 2012 on a fringing reef along the north shore of Mo'orea, French Polynesia. The experimental site was located within the lagoon on the northeast side of Opunohu Bay, in patch reefs roughly 50 m from shore ($17^{\circ}29'30''N$, $149^{\circ}51'4''W$). To determine how sediment depth and herbivory affected change in algal turf height, a 2-factor fully crossed experiment was conducted manipulating sediment depth (0, 2, or 4 mm) and access to herbivorous fish (\pm complete cages) using haphazardly chosen plots. Replication was 10-fold except for 2 treatments where replicates were lost to physical damage (open 4 mm: $n = 8$; caged 2 mm: $n = 7$). In order to ensure results were realistic approximations of local sediment conditions, sediment treatment levels were chosen within the range measured on 2 fringing reefs of Mo'orea (average = 2.49 ± 0.17 mm, range = 0–7 mm, $n = 94$), including the study reef (average = 1.89 ± 0.19 mm, range = 0–4 mm, $n = 51$). Herbivorous fish communities were measured as the number of acanthurids and scarids (no kyphosids or siganids were observed) within 1 m on either side of a 50 m transect tape while swimming at a constant speed ($n = 12$). The length of each individual was recorded as 1 of 4 size classes: <5, 5 to <10, 10 to <15, and >15 cm. All experimental plots were located between 1 and 2 m depth. Plots were

established on the algal turf-covered tops of dead colonies of *Porites* sp. that were killed during a recent *Acanthaster planci* outbreak (Kayal et al. 2012). Semi-isolated heads of mainly *Porites* sp. are characteristic of the fringing and back reef systems in this area (Hench et al. 2008).

Water sample (via Niskin bottles) data collected within this fringing reef system twice yearly (summer and winter) from 2005 to 2013 showed physical parameters similar to other fringing reefs in the South Pacific (data obtained with permission from the Mo'orea Coral Reef Ecosystem LTER; Alldredge & Carlson 2013). Water temperature ranged from 25.7 to 29.2°C, averaging 26.2°C in the winter and 28.3°C in the summer. Salinity was 36.1 ± 0.04 PSU (mean \pm SE). Nutrients were variable with no consistent seasonal pattern, ranging from 0.26 to 1.40 $\mu\text{mol l}^{-1}$ nitrite + nitrate (0.55 ± 0.03 mean \pm SE) and 0.09 to 0.27 $\mu\text{mol l}^{-1}$ phosphate (0.17 ± 0.006). Turbidity averaged 0.61 ± 0.01 V. Previous work in this reef system has shown that water exchange over the reef crest and in the shallow back reef is wave-driven and flushing is rapid (Hench et al. 2008). Although no data are available for the fringing reef, flow is likely much slower in this area (see also Schmitt & Holbrook 2002, who measured 1.6 cm s^{-1} flow in the lagoon).

Each experimental unit was delineated by a cylinder (15 cm diameter by 6 cm high) constructed of thin metal mesh (hardware cloth, <1 mm thick) with 1 cm^2 openings. A random selection of half the plots chosen to exclude herbivorous fish were topped with mesh lids (hereafter referred to as 'caged' plots); the other half of the plots ('open' plots) lacked lids. Visual observations of fish herbivory (measured as bite rates) within open-topped cages compared to fully open but otherwise similar substrate (50 replicate 5 min intervals) confirmed fish were not significantly deterred by cage sides (data taken at the study site in April 2014, *t*-test, $p = 0.70$; V. Phan unpubl. data). This is likely because acanthurids, the dominant herbivorous fish in this system, prefer to feed on flat surfaces on which they bite down (see Choat & Bellwood 1985). 'Urchin barriers' (sensu Carpenter 1986) were constructed around open plots (extended mesh panels folded back) to ensure exclusion of other herbivores larger than 1 cm^2 (mainly echinoids). Fully open cage controls were not used in this experiment as previous work utilizing this caging material found no reduction of flow or any effects on the biota (Wartian 2006, Muthukrishnan & Fong 2014). Moreover, subsequent measurements of flow within compared to outside cages at the study site found no difference

in flow rate among partial cages, full cages, or completely open plots (ANOVA, $F_{2,26} = 0.53$, $p = 0.59$, $n = 10$; S. Bittick unpubl. data). The reduction of irradiance by the caging material was <10% (R. Clausing unpubl. data).

Prior to beginning the experiment, algal turf height was measured in each plot using a steel wire marked at 1 mm intervals. Initial heights were averages of turf height measured at 10 haphazardly chosen points inside each experimental unit. Mean initial turf height across treatments was 1.45 ± 0.059 mm (mean \pm SE). Sediment was removed from all treatment plots with gentle fanning. Sediment additions were applied by sifting sediment from the benthos surrounding each experimental unit with a 1 mm sieve to reach the assigned treatment depth, also measured with the calibrated wire. Sediment composition was 43% sand, 18% clay and 39% silt, with $2.24 \pm 0.05\%$ organic material (mean \pm SE, $n = 3$). Natural sediment used in this experiment likely contained a complex assemblage including detrital material, small invertebrates, microbes, and inorganic materials such as adsorbed nutrients. While hereafter we refer to this assemblage as sediments for simplicity, it is important they are distinguished from sediments that have been cleaned of other constituents. Sediment depths for all replicates were maintained twice over the course of 11 d by adding or removing sediment as needed. Only 0 mm plots needed sediment removal; sediment depths in 2 and 4 mm plots never exceeded the treatment depth. While maintaining the treatments, black sediment was observed in the basal sediment layers of some plots. Black sediment is a well-established and commonly used indicator of the presence of H_2S and low oxygen conditions in estuarine sediments (e.g. Rhoads & Germano 1982, Nilsson & Rosenberg 1997, Cicchetti et al. 2006, Sutula et al. 2014). Shifts in sediment color as an indicator for H_2S have also been used in experiments on juvenile temperate intertidal algae, where sediment treated with seawater containing H_2S changed from light to dark within 5 d (Chapman & Fletcher 2002). Thus, we considered the shift from light to black sediment to indicate the transition from oxidized to hypoxic sediments (Rhoads & Germano 1982, Cicchetti et al. 2006). At the end of the experiment, final algal height was measured as above. All measurements were made at least 2 cm from the cage barriers around each plot to avoid potential edge effects. After measuring final turf height, sediment was brushed from each experimental unit and the presence or absence of black sediment near the benthos noted.

Change in average turf height over the course of the experiment was calculated by subtracting average initial height in each plot from the average final height. Because the assumptions of factorial ANOVA were not met (data could not be transformed to achieve normality), data were analyzed using a bootstrapped 2-way factorial ANOVA to simulate the null hypothesis and examine the significance level of individual and interacting effects of sediment depth and herbivory on algal turf net growth (Davison & Hinkley 1997, Manly 1997). Proportion data of presence/absence of black sediment were also analyzed using a bootstrapped 2-factor ANOVA. Because the presence of H₂S has strong negative effects on algal growth, particularly at early life stages (e.g. Chapman & Fletcher 2002), we examined differences in change in turf height within treatments between plots with vs. those without black sediment. Since black sediment developed as a result of experimental treatments rather than as a controlled factor, only 2 and 4 mm caged, and 4 mm open treatments had enough plots with black sediment to analyze (see Fig. 2 caption for sample size). Examining change in turf height between 4 mm caged and open plots as a function of the presence of black sediment allowed us to differentiate between negative effects on height due to herbivory versus those due to inhibition of growth. Differences in turf height between 2 mm caged plots with and without black sediment were analyzed with a *t*-test, while differences among 4 mm caged and open plots were analyzed with a 2-factor ANOVA, with access to herbivorous fish and black sediment as factors. These data met assumptions of normality and homogeneity of variance.

To evaluate the relationship between sediment depth and the presence of black sediment, we conducted surveys of sediment depth and noted the color of the sediments near the benthos on 2 near-shore fringing reefs of Mo'orea, one of which was our study site. The sites were located at the mouths of the 2 northern bays. Within these areas, measurements and observations were made at randomly selected points along 50 m transects haphazardly placed within the 1 to 2 m depth contour (*n* = 51 and 43 replicate points at the experimental site and a similar fringing reef, respectively). As a result, sediment depths were measured on all types of substrate upon which the transect line landed, including both dead coral heads and flatter, hard benthos. Data from the 2 reefs were combined and frequency histograms of sediment depth and presence/absence of black sediment constructed. All data were analyzed using the R programming language version 2.15.1 (R Development Core Team 2012).

RESULTS

The presence of sediment had strong negative effects on algal turf growth, but this was only detectable in the absence of herbivorous fish (caged plots), resulting in an interaction between sediment and herbivore access (Fig. 1; bootstrapped 2-way factorial ANOVA, interaction *p* = 0.0089). In caged plots, sediment drastically reduced turf growth. When sediment was removed (0 mm), turf grew nearly 4 mm in 11 d, but natural levels of sediment (~2 mm treatment) reduced growth by ~50%, and there was virtually no growth under 4 mm of sediment. In contrast, turfs exposed to herbivorous fish (open plots) changed little (if at all) in height, demonstrating strong top-down control by herbivores rather than by sediment, at least in the 0 and 2 mm treatments where open plots showed substantially lower change in height compared to caged plots (90 and >80% reduction in 0 and 2 mm treatments, respectively).

There was a significant effect of sediment depth on the development of black sediment (bootstrapped 2-way factorial ANOVA, sediment depth *p* = 0.029) (Fig. 2a). In caged plots with no access to herbivorous fish, black sediment was found in 43% of 2 mm plots (3 of 7), but the activity of fish in 2 mm open plots prevented black sediment from ever occurring. In contrast, in 4 mm plots, there appeared to be no effect of fish activity as open and caged plots showed similar frequencies of black sediments (63%; 5 of 8 and 70%; 7 of 10, respectively).

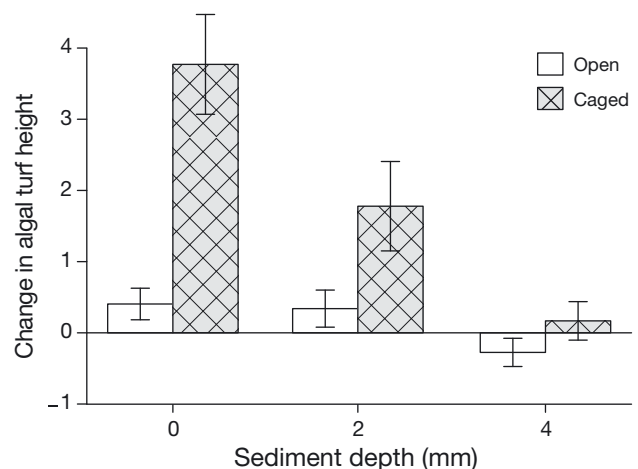


Fig. 1. Change in average turf height over 11 d (\pm SE) in each combination of sediment depth (0, 2, and 4 mm) and herbivore treatment (open or caged plots). Replication was *n* = 10 for all combinations except 2 mm caged (*n* = 7) and 4 mm open plots (*n* = 8).

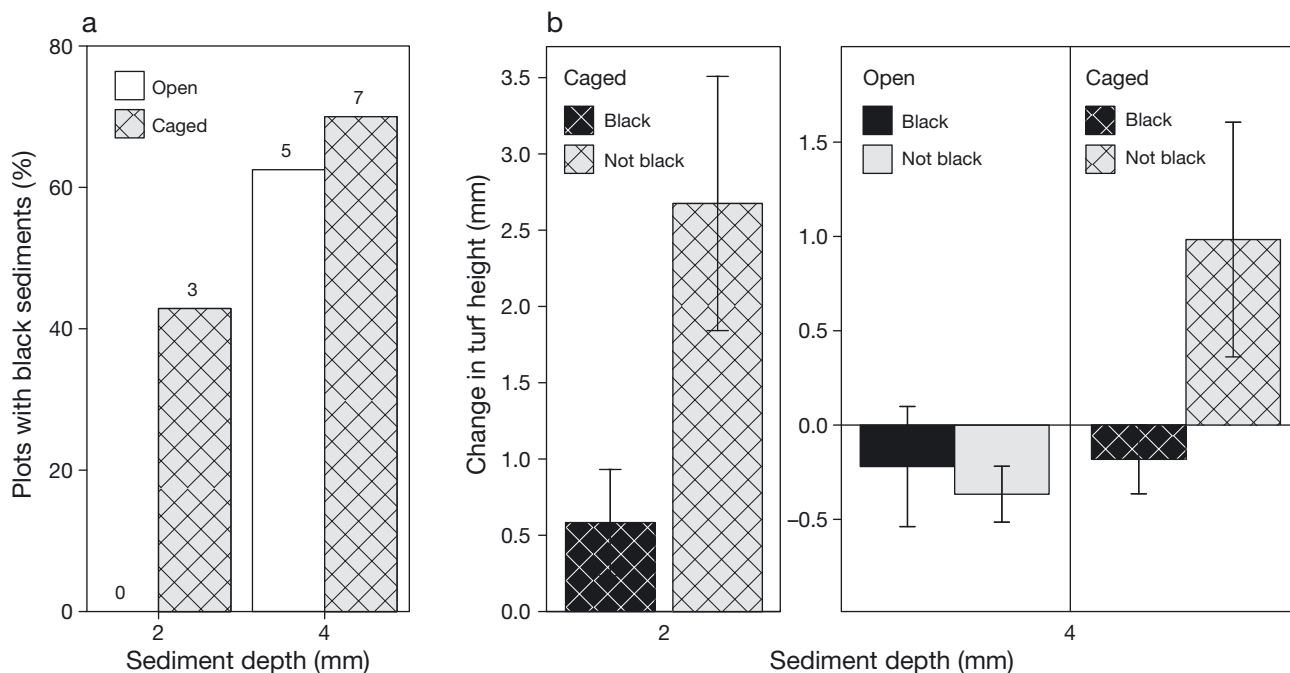


Fig. 2. Presence and effects of black sediments on growth. (a) Percent of experimental plots with black sediment in each combination of sediment depth and herbivory treatment. Number of plots with black sediment is above each bar. Turfs in experimental plots without sediment additions showed no black sediment. (b) Change in average turf height (\pm SE) with (Black) and without black sediment (Not black). Only treatment combinations where black sediment developed (2 mm caged, 4 mm open and caged) could be analyzed. Caged plots with 2 mm of sediment (n = 3 with black sediment, n = 4 without), or all plots with 4 mm of sediment (open with black sediment: n = 5, without: n = 3; caged with black sediment: n = 7, without: n = 3)

The presence of black sediment appeared to have effects on change in algal turf height, though significance of tests were marginal due to low sample size (Fig. 2b). In 2 mm caged treatments, the presence of black sediment reduced growth to roughly 20% of that of the plots without black sediment (Fig 2b; *t*-test, $p = 0.082$). We did not analyze 2 mm open plots, as black sediment was not observed. In plots with 4 mm of sediment, herbivory was only apparent in units where black sediment did not occur (Fig. 2c; 2-way ANOVA, interaction $p = 0.064$). In plots where black sediment developed, algal turf did not grow regardless of the presence of fish herbivores. In contrast, with neither herbivorous fish (caged plots) nor black sediment, turf grew about 1 mm, whereas in open plots with no black sediment, fish herbivores significantly consumed turf, reducing turf height by about 0.35 mm from initial height. This indicates that where 4 mm sediment loads did not develop black basal layers, herbivory remained substantial, although overall herbivore control was weaker than in 2 mm plots where sediment had smaller negative effects on growth.

Field surveys of sediment depth showed a threshold pattern, where sediment depths of 3 mm or

greater frequently had black sediment at their base (Fig. 3a) while at depths less than 3 mm, none of the plots showed any evidence of black sediment. Fish communities were comparable to other Mo'orean fringing reefs: high densities of smaller acanthurids and very small scarids in lower numbers (Adam et al. 2011, Fig. 3b).

DISCUSSION

Sediment had a strong negative effect on net algal growth in this experiment, likely as a result of anoxic conditions that promoted the production and accumulation of H_2S . Kawamata et al. (2012) also documented strong negative effects of sediment on the macroalga *Sargassum duplicatum* on temperate rocky reefs, where sediment depths as thin as 0.5 mm limited growth while 2 to 4 mm of sediment decreased growth by 90%. Likewise, Chapman & Fletcher (2002) found that 3 mm of fine sediment significantly reduced embryo survival of the temperate macroalga *Fucus serratus*, and even 1 mm of organically-rich sediment was enough to impact recruit survival. Moreover, they found that H_2S alone was suffi-

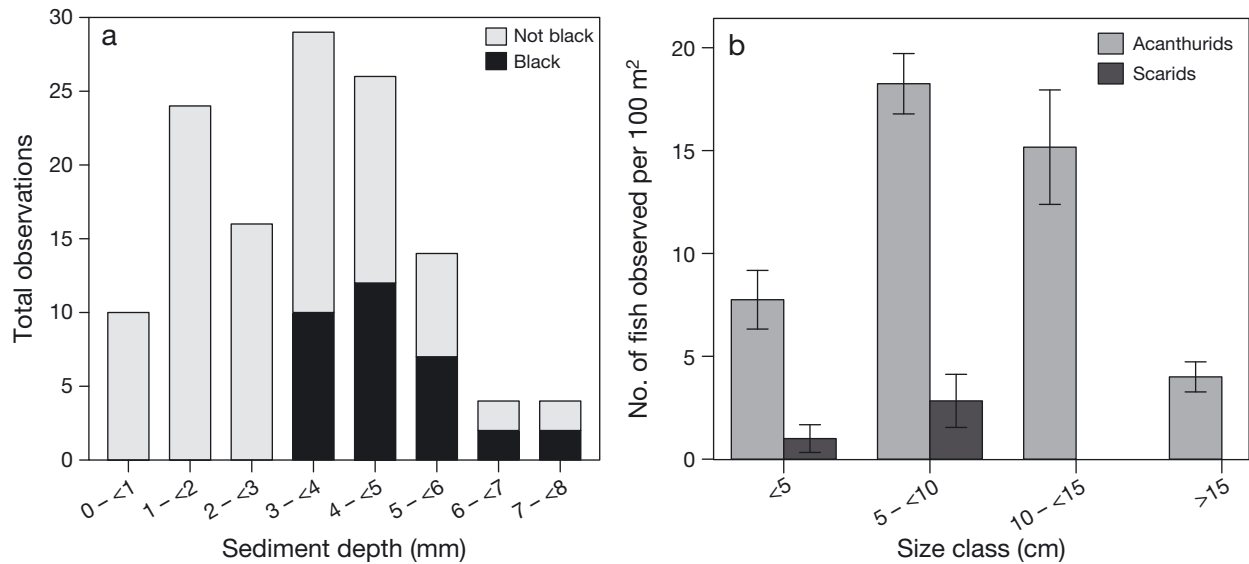


Fig. 3. Surveys of sediment depth and herbivorous fish communities. (a) Frequency distributions of sediment depths measured on 2 fringing reefs in Mo'orea, French Polynesia. Basal sediment layers were checked for demarcation from not black to black sediment. Sediment depths were placed into 1 mm categories. (b) Number (mean \pm SE) of herbivorous fish (acanthurids and scarids) per 100 m² (1 m on either side of a 50 m transect tape, n = 12)

cient to cause algal mortality, whereas low oxygen levels alone were not. When covering coral on tropical reefs, sediment has also been found to produce anoxia and H₂S (Weber et al. 2012). Sediment may promote conditions for anoxia by reducing light penetration and thereby photosynthesis, restricting oxygen diffusion and removal of metabolic waste products, and providing more organic material for decomposition and production of H₂S. Moreover, because natural sediment was used in this experiment, increased metabolic activity resulting from moderate organic content (2.25%) and intact microbial communities may have contributed to the depletion of oxygen (Barott & Rohwer 2012). In addition, previous work in Mo'orea demonstrated that natural sediments retained on macroalgal thalli had substantially higher organic matter and smaller grain size than the surrounding benthic sediment (R. J. Clausen & P. Fong unpubl. data); if turf algae also differentially retain smaller grain sizes, this could amplify negative effects. Anoxic conditions resulting from sediment are likely to negatively affect all benthic communities. Thus, further research is needed to determine the environmental conditions and sediment characteristics under which black sediment is likely to occur, as well as the mechanism (H₂S or hypoxia) by which turfs and other benthic organisms are negatively affected.

The presence of herbivorous fish ameliorated the occurrence of black sediment up to a critical sediment depth. While similar frequencies of black sedi-

ment were observed in 4 mm plots regardless of the caging treatment, herbivory prevented the occurrence of black sediment in turfs with 2 mm of sediment. As a significant amount of turf was consumed under 2 mm of sediment, this suggests herbivorous fish may be preventing H₂S production or accumulation at this depth by disturbing and thus oxygenating the sediment as they forage. Some species of acanthurids have the capability to ingest large quantities of sediments while grazing (Goatley & Bellwood 2010, Krone et al. 2011), suggesting they may contribute to bioturbation. The inability of fish to reduce instances of black sediment under 4 mm of sediment indicates that foraging no longer provided sufficient bioturbation to prevent anoxia, whether by ineffective or simply reduced levels of foraging. Surveys supported this conclusion, providing evidence that black sediment did not occur until depths of at least 3 mm when herbivore fish communities were present. In contrast, in studies of rocky reef turf assemblages in the Mediterranean, sediment deposition was found to promote dominance of several filamentous turf species, either with direct increases in growth rates (Balata et al. 2007) or indirectly by adaptations in turf to reduce negative impacts relative to erect algae (Airoldi & Cinelli 1997, but sediment had no effect on turf dominance in Airoldi 1998). The lack of negative effects of sediment on temperate algal turf may be related to increased flow or bioturbation (see also Gorgula & Connell 2004 for a study in South Australia). Regardless, our results

demonstrated that in moderate sedimentation regimes, intact fish assemblages may reduce the negative effects of sediment on tropical reefs by preventing the development of low or no-oxygen conditions, thus maintaining the existence of productive algal turf communities while limiting turf height.

Our results suggest a novel mechanism by which sediments inhibit herbivory on coral reefs: the development of hypoxia and H_2S . In our study, only black sediment appeared to deter herbivores. Herbivory was strong under 2 mm of sediment, and even in 4 mm plots; as long as there was no black sediment, herbivores readily consumed turf. In contrast, several studies on the GBR found that deeper depths of oxygenated sediment (e.g. 15 to 18 mm) deterred herbivores (Bellwood & Fulton 2008, Goatley & Bellwood 2012, 2013). Bellwood & Fulton (2008) showed that after sediment removal, fish continued to reduce turf height until the accumulation of 7 mm of sediment roughly 4 h later, indicating inhibition of herbivory began between 7 and 18 mm—deeper depths than were examined in our study. The lack of development of black sediment in these studies was likely caused by the high-flow environments in which they were conducted (outer reef flat: Bellwood & Fulton 2008; reef crest: Goatley & Bellwood 2013, reef base, crest and flat: Goatley & Bellwood 2012) and the relatively coarse calcareous sediments. Our study took place on a nearshore fringing reef where lower flow, sediment turnover, and grain size as well as increased organic content may all amplify the chance of anoxia developing. The effects of sediment on suppression of herbivory may also differ with herbivore community composition and size–frequency distribution, as some species and sizes of fish may be more adapted to ingesting sediment than others (Goatley & Bellwood 2010, Krone et al. 2011). Thus, our results combined with work on the GBR suggest that sediment alone may only deter herbivory while facilitating turf growth if substantially deep sediments accumulate without anoxia developing. In contrast, under conditions in which heavy sediment loads lead to H_2S accumulation, sediment may ultimately inhibit turf growth rather than stabilize an alternate turf state as Bellwood & Fulton (2008) suggest.

In summary, our results suggest that under even moderate loads of natural sediment, algal turf communities may be susceptible to a toxic build-up of H_2S . Intact communities of herbivores may ameliorate these negative effects, acting to maintain important ecosystem functions while preventing development of tall algal turfs that may negatively affect

coral. While burrowing infauna are known to be important for oxygenation of marine sediments (see review by Kristensen 2000), to our knowledge the importance of fish foraging in preventing anoxic conditions on reefs has not been demonstrated. Studies directly observing fish feeding behaviors and measuring sediment oxygen levels are needed to better understand this relationship. Moreover, the positive effects of herbivory are dependent on sediment depth; this relationship is likely dependent on environmental context including hydrodynamics, fish community composition and abundance, and sediment type and organic content. With higher sediment loads, fish activity may no longer ameliorate negative effects, and low-oxygen conditions may degrade benthic communities, further inhibiting herbivory and reducing ecosystem function. While we found no indication that sediments facilitate algal turfs, it could be that lower-flow, fringing reefs close to substantial human activity (such as this study reef) may be more susceptible to degradation by sediment due to greater availability of organic matter for decomposition and low sediment disturbance and turnover. If anthropogenic sources of sedimentation are to increase as projected (UNEP 2006), a greater understanding of how sediment loads affect entire benthic communities will be essential to maintain reef health.

Acknowledgements. We thank the Department of Ecology and Evolutionary Biology and the Office of Instructional Development at the University of California, Los Angeles, for financial support. Writing was completed with support by the National Science Foundation Graduate Research Fellowship Program. Water column data on the reef were provided by the Mo'orea Coral Reef Ecosystem LTER, funded by the US National Science Foundation (OCE-0417412). This is contribution #206 of the University of California Berkeley's Gump South Pacific Research Station.

LITERATURE CITED

- Adam TC, Schmitt RJ, Holbrook SJ, Brooks AJ, Edmunds PJ, Carpenter RC, Bernardi G (2011) Herbivory, connectivity, and ecosystem resilience: response of a coral reef to a large-scale perturbation. *PLoS ONE* 6:e23717
- Airoldi L (1998) Roles of disturbance, sediment stress, and substratum retention on spatial dominance in algal turf. *Ecology* 79:2759–2770
- Airoldi L (2003) The effects of sedimentation on rocky coast assemblages. In: Gibson RN, Atkinson RJA (eds) *Oceanography and marine biology: an annual review*, 41st edn. CRC Press: Taylor & Francis Group, Boca Raton, FL, p 161–236
- Airoldi L, Cinelli F (1997) Effects of sedimentation on subtidal macroalgal assemblages: an experimental study from a Mediterranean rocky shore. *J Exp Mar Biol Ecol* 215:269–288

- Allredge A, Carlson C (2013) Moorea Coral Reef LTER: coral reef, water column, nearshore water profiles, CTD, primary production, and chemistry, ongoing since 2005. Marine Science Institute, University of California, Santa Barbara, CA. <http://metacat.lternet.edu/knb/metacat/knb-lter-mcr.10.32/lter>
- Balata D, Piazzoli L, Cinelli F (2007) Increase of sedimentation in a subtidal system: effects on the structure and diversity of macroalgal assemblages. *J Exp Mar Biol Ecol* 351: 73–82
- Barott KL, Rohwer FL (2012) Unseen players shape benthic competition on coral reefs. *Trends Microbiol* 20:621–628
- Bellwood DR, Fulton CJ (2008) Sediment-mediated suppression of herbivory on coral reefs: decreasing resilience to rising sea levels and climate change? *Limnol Oceanogr* 53:2695–2701
- Bellwood DR, Hughes TP, Folke C, Nystroem M (2004) Confronting the coral reef crisis. *Nature* 429:827–833
- Birrell CL, McCook LJ, Willis BL (2005) Effects of algal turfs and sediment on coral settlement. *Mar Pollut Bull* 51: 408–414
- Bonaldo RM, Bellwood DR (2011) Spatial variation in the effects of grazing on epilithic algal turfs on the Great Barrier Reef, Australia. *Coral Reefs* 30:381–390
- Carpenter RC (1986) Partitioning herbivory and its effects on coral reef algal communities. *Ecol Monogr* 56: 345–364
- Chapman AS, Fletcher RL (2002) Differential effects of sediments on survival and growth of *Fucus serratus* embryos (Fucales, Phaeophyceae). *J Phycol* 38:894–903
- Choat JH, Bellwood DR (1985) Interactions amongst herbivorous fishes on a coral reef: influence of spatial variation. *Mar Biol* 89:221–234
- Cicchetti G, Latimer JS, Rego SA, Nelson WG, Bergen BJ, Coiro LL (2006) Relationships between near-bottom dissolved oxygen and sediment profile camera measures. *J Mar Syst* 62:124–141
- Davison AC, Hinkley DV (1997) Bootstrap methods and their application, Vol 8. Cambridge University Press, Cambridge
- Fong P, Paul VJ (2011) Coral reef algae. In: Dubinsky Z, Stambler N (eds) *Coral reefs: an ecosystem in transition*. Springer, New York, NY, p 241–272
- Fong P, Smith TB, Wartian MJ (2006) Epiphytic cyanobacteria maintain shifts to macroalgal dominance on coral reefs following ENSO disturbance. *Ecology* 87: 1162–1168
- Goatley C, Bellwood D (2010) Biologically mediated sediment fluxes on coral reefs: sediment removal and off-reef transportation by the surgeonfish *Ctenochaetus striatus*. *Mar Ecol Prog Ser* 415:237–245
- Goatley CHR, Bellwood DR (2012) Sediment suppresses herbivory across a coral reef depth gradient. *Biol Lett* 8: 1016–1018
- Goatley CHR, Bellwood DR (2013) Ecological consequences of sediment on high-energy coral reefs. *PLoS ONE* 8: e77737
- Gorgula SK, Connell SD (2004) Expansive covers of turf-forming algae on human-dominated coast: the relative effects of increasing nutrient and sediment loads. *Mar Biol* 145:613–619
- Hench JL, Leichter JJ, Monismith SG (2008) Episodic circulation and exchange in a wave-driven coral reef and lagoon system. *Limnol Oceanogr* 53:2681–2694
- Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D and others (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr Biol* 17:360–365
- Irving A, Connell S (2002) Sedimentation and light penetration interact to maintain heterogeneity of subtidal habitats: algal versus invertebrate dominated assemblages. *Mar Ecol Prog Ser* 245:83–91
- Kawamata S, Yoshimitsu S, Tokunaga S, Kubo S, Tanaka T (2012) Sediment tolerance of *Sargassum* algae inhabiting sediment-covered rocky reefs. *Mar Biol* 159:723–733
- Kayal M, Vercelloni J, de Loma T, Bosserelle P and others (2012) Predator crown-of-thorns starfish (*Acanthaster planci*) outbreak, mass mortality of corals, and cascading effects on reef fish and benthic communities. *PLoS ONE* 7:e47363
- Kristensen E (2000) Organic matter diagenesis at the oxic/anoxic interface in coastal marine sediments, with emphasis on the role of burrowing animals. *Hydrobiologia* 426:1–24
- Krone R, Paster M, Schuhmacher H (2011) Effect of the surgeonfish *Ctenochaetus striatus* (Acanthuridae) on the processes of sediment transport and deposition on a coral reef in the Red Sea. *Facies* 57:215–221
- Littler MM, Littler DS (1984) Model of tropical reef biogenesis: the contribution of algae. In: Round FE, Chapman DJ (eds) *Progress in phycological research*, 3rd edn. Bioscience Press, Bristol, p 323–364
- Manly BFJ (1997) *Randomization, bootstrap and Monte Carlo methods in biology*, 2nd edn. Chapman and Hall, Boca Raton, FL
- McClanahan TR, Sala E, Stickels PA, Cokos BA, Baker AC, Starger CJ, Iv SHJ (2003) Interaction between nutrients and herbivory in controlling algal communities and coral condition on Glover's Reef, Belize. *Mar Ecol Prog Ser* 261:135–147
- McCook LJ (1999) Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. *Coral Reefs* 18: 357–367
- Muthukrishnan R, Fong P (2014) Multiple anthropogenic stressors exert complex, interactive effects on a coral reef community. *Coral Reefs* 33:911–921
- Nilsson HC, Rosenberg R (1997) Benthic habitat quality assessment of an oxygen stressed fjord by surface and sediment profile images. *J Mar Syst* 11:249–264
- R Development Core Team (2012) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- Rhoads D, Germano J (1982) Characterization of organism-sediment relations using sediment profile imaging: an efficient method of remote ecological monitoring of the seafloor (Remots™ System). *Mar Ecol Prog Ser* 8: 115–128
- Russ GR (2003) Grazer biomass correlates more strongly with production than with biomass of algal turfs on a coral reef. *Coral Reefs* 22:63–67
- Schmitt R, Holbrook S (2002) Spatial variation in concurrent settlement of three damselfishes: relationships with near-field current flow. *Oecologia* 131:391–401
- Smith TB, Fong P, Kennison R, Smith J (2010a) Spatial refuges and associational defenses promote harmful blooms of the alga *Caulerpa sertularioides* onto coral reefs. *Oecologia* 164:1039–1048
- Smith JE, Hunter CL, Smith CM (2010b) The effects of top-down versus bottom-up control on benthic coral reef community structure. *Oecologia* 163:497–507

- Sutula M, Green L, Cicchetti G, Detenbeck N, Fong P (2014) Thresholds of adverse effects of macroalgal abundance and sediment organic matter on benthic habitat quality in estuarine intertidal flats. *Estuaries Coasts* 37:1532–1548
- Umar MJ, McCook LJ, Price IR (1998) Effects of sediment deposition on the seaweed *Sargassum* on a fringing coral reef. *Coral Reefs* 17:169–177
- UNEP (2006) Global international waters assessment: challenges to international waters—regional assessments in a global perspective. United Nations Environment Programme, Nairobi
- Wartian MJ (2006) Determinants of community structure and resilience on tropical Eastern Pacific coral reefs. PhD dissertation, University of California, Los Angeles, CA
- Weber M, de Beer D, Lott C, Polerecky L and others (2012) Mechanisms of damage to corals exposed to sedimentation. *Proc Natl Acad Sci USA* 109:E1558–E1567

*Editorial responsibility: Charles Birkeland,
Honolulu, Hawaii, USA*

*Submitted: March 13, 2014; Accepted: September 2, 2014
Proofs received from author(s): November 30, 2014*