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Environmental and biotic controls affecting recruitment and proliferation of algal turf communities in coral reef systems

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# Environmental and biotic controls affecting recruitment and proliferation of algal turf communities in coral reef systems

A dissertation submitted in partial satisfaction
of the requirements for the degree
Doctor of Philosophy in Biology

by

Camille Gaynus

2019

# ABSTRACT OF THE DISSERTATION

# Environmental and biotic controls affecting recruitment and proliferation of algal turf communities in coral reef systems

by

Camille Gaynus

Doctor of Philosophy in Biology

University of California, Los Angeles, 2019

Professor Peggy Marie Fong, Chair

Worldwide, coral reef communities are collapsing and shifting from coral to algal dominance. While human activities changing top-down (overfishing of grazers) and bottom-up (increases in nutrients and sediments) forces can initiate shifts, complex, non-linear interactions among stressors limit predictability (Hughes et al., 2007;Bellwood et al., 2004). Further, while top-down control is known to limit algal dominance (Knowlton & Jackson 2008; Jackson et al., 2001), less is known about bottom-up controls that may facilitate algae. One functional group of algae is turf algae, which are multi-species and often filamentous, ranging from 0.01-10cm in height (Fong & Paul 2011). Short, closely-cropped turf algae provide ecosystem functions such as primary productivity, trophic support, and nutrient cycling (Fong & Paul 2011). Under environmental

stress, however, turf algae can shift to long sediment-laden turf, which may be an alternative stable state that inhibits coral recovery (Adjeroud et al., 2009).

My first objective was to compare variation in the assembly of turf algae under a suite of top-down and bottom-up contexts at six sites on fringing reefs in Mo’orea French Polynesia. At each site, 10 settlement tiles were deployed and monitored for two-months and then after twelve months. During the first two months I also measured herbivore abundance, grazing pressure, sediment composition, nutrient availability, benthic community structure, and sediment deposition rates at each site. After two months turf did not vary among plots, despite significantly different herbivore abundances and nutrient availability. This implies that early successional forms are easily controlled, even by low numbers of herbivores, due to their high palatability. In contrast, after one year, tiles in highly grazed sites with low sedimentation rates were dominated by crustose coralline algae, and sites with low herbivores and high sedimentation rates dominated by long turf and macroalgae. As crustose coralline algae can facilitate coral recruitment, these results imply that herbivory can mediate the successional trajectory of algal communities toward recovery by coral or stability of the shifted algal state.

A robust herbivorous fish community is the paradigm of a healthy coral reef, however, altered sediment regimes can negatively influence their grazing patterns (Tebbett et al., 2018;Bellwood & Fulton 2008), leading to algal proliferation. While increases in sediment can lead to algal proliferation through reduced grazing and release from nutrient limitation, too much sediment can lead to negative turf responses (Tebbett et al., 2018) due to the buildup of anoxic-inducing bacteria (Clausing et al., 2014). Turf are particularly prone to the influence, both positive and negative, of sediment fluxes due to their filamentous nature that trap deposited sediment (Rogers 1990). The second objective of my dissertation was to establish the non-linear relationship between sediment and turf at two sites that varied in environmental context. Before manipulations commenced I conducted field surveys of sediment depth and turf height at seven fringing reef sites around Mo’orea. I found that sediment depth and turf height varied widely among sites and although longer turf did hold more sediment that shorter turf communities, it was not disproportionally more than expected. I then choose two sites that varied the greatest in turf and sediment and deployed tiles where I manipulated sediment depth (0,1,3, & 5mm) for 25 days. Because all tiles were open to herbivory, I quantified herbivorous fish communities through visual surveys. Interestingly, I found that sediment additions have overall negative impacts on turf, and that turf between sites did have different thresholds for sediment. As turf becomes a more conspicuous component of reefs worldwide, susceptible to increases in terrestrial fluxes, understanding the dynamics of this relationship will become crucial for predicting reef recovery and resilience.

In the Pacific, a healthy coral reef is characterized by intact herbivorous fish communities that reduce shifts to algal dominance through grazing (Hughes et al., 2007;Mumby et al., 2006). Sea urchins are an alternate grazing guild that are less studied, especially in the Pacific, but were found to maintain healthy algal communities on Caribbean reefs (Mumby et al., 2007;Lewis et al., 1987;Carpenter 1986; Carpenter 1985). My third objective was a novel exploration of the role urchins play in limiting algal proliferation in the South Pacific, and how this may be mediated by sediment, as sediment is known to deter fish grazing. Sediment (no addition, 3mm marine, or 3 mm terrestrial/marine mix) and presence of urchins (+/-) were manipulated in plots containing turf algae on a relatively overfished reef when compared to other Mo’orean fringing reefs (data

from Mo’orea Long Term Ecological Research Project). I found urchins maintained closely cropped turf even under high sediment conditions. Further, urchins removed added sediment, likely promoting consumption by fishes. Thus, urchins can be functionally redundant grazers as they can compensate for the loss of herbivorous fishes. Overall, turf is a dynamic community, sensitive to small environmental shifts dictating abundance, proliferation, and taxonomy, potentially altering its function in coral reefs.

The dissertation of Camille Gaynus is approved.

Paul Henry Barber

Kyle C. Cavanaugh

David K. Jacobs

Peggy Marie Fong, Committee Chair

University of California, Los Angeles

2019

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# EPIGRAPH

“*Those who cannot forget the past are destined to remix it*”

-Evie Shockley

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# ACKNOWLEDGEMENTS

I was unaware I could make a career out of studying something I enjoy, the ocean. In my early life, I believed success lied in law, medical or business degrees if you were not exceptional at sports or dubbed an entertainer. As a junior in college, I had some ideas as to where my life would go, but it was not until I met my advisor, Peggy Fong, participating in the UC-HBCU Diversity Project, that I truly realized I could become a research scientist. I was a good student and had research experience, but I assumed that I would get a masters then work a bit and return to school for a PhD; at the heart of it I did not think I was qualified to apply for a PhD program. Peggy dispelled this logic of mine quickly. The relationship I forged on with Peggy seven years ago made me question why I was limiting myself. For that Peggy, I will always be indebted to you. As a graduate student, Peggy consistently works to answer my questions, and encourages me to think freely, developing my research and writing style. Whether we are out in the field, collecting algae for a class, or just shooting the breeze, Peggy's dedication to education, strength as a person, and courage always shine through and I look forward to future collaborations. She has played a huge role in the researcher I am today and will be tomorrow.

Being funded as a UC-HBCU fellow has allowed me to not only make the best of my time here at UCLA, but helped me to meet other fellows and commune with UCOP staff and administrators. The UC-HBCU Initiative was Pamela Jennings' vision and she and her team members endless work behind the scenes has made it successful. Through the UCOP and the NSF PIRE grant ((#OISE1243541) funds, I have been fortunate to study the dynamic reefs of Mo'orea with minority undergraduate students. I have so many memories from these excursions many positive, and others I have grown from. I must thank Pamela and the UCOP office for these

experiences. Pamela has made herself personally available anytime I have needed advice or help navigating UCLA. I thank you Pamela for making your vast resource network available to me.

The UCLA Ecology and Evolutionary Biology department has helped me to develop as a researcher. I have been able to learn through departmental seminars and workshops. As I shout out the department, I instantly think of Tessa Villaseñor, the current Graduate Student Advisor, whose knowledge of the department has helped me secure TA positions and get paid on time. Tessa is a joy to be around personally, and is stellar at her position, which makes the hectic lives of graduate students easier.

Being a part of the Fong lab has been a great opportunity, and we are family. We may not always agree with one another, but at the end of the day, we all support each other in the best ways we know how. Whether it be going out to Catalina with Emily & Lauren, Carpentaria with Tiara, or the countless times I've spent with other lab members in Mo'orea; our love of natural systems has bound us all together. In particular, I must send a special shout out to Tiara, Kelcie and Ashlyn. Whether it be our dance adventures, or happy hour dates, Tiara and Kelcie, you both have always been there ready to listen and provide a laughing moment. Thank you both and I look forward to working together in the future. Tiara you and I have known and helped each other grow for quite some time, and you have always encouraged me to try new things and continue to be great. Love you always for that. Ashlyn, thank you for being my roommate/ Korean BBQ partner , I will truly miss you, and I look forward to dusting you in Skip-bo cards soon.

Through The Diversity Project I also met Paul Barber, another integral component of my success. The Diversity Project is not just a summer program, but a family and I am reminded of this any time we get together. Whether it be at Paul's home for ribs, a game of Spades at the

Gump Research station, or impromptu meetings on campus; we are bound together by a strong sense of community. Without Paul’s dedication, (and ability to play spades), this would have never happened and many, including myself might not be in graduate school. Thank you Paul, your program has changed lives. Having such a strong sense of community has been integral in my success and I will always remember that as I move forward in my career.

Finally, I must recognize my “day ones”, my family. From an early age, my family, especially my mom has encouraged me to explore, and pursue any (positive) endeavor I could dream of. She did this not just with her words, but more importantly her actions. My mom would forfeit her whole weekend to wake up at the crack of dawn and drive sometimes over two hours so that I could participate in swim meets throughout the Northeastern portion of the country. Although I wouldn’t get the most expensive or even the coolest, she made sure I had swimsuits, bathing caps, towel, and all the necessary supplies to perform at my best ability. She encouraged me to do my absolute best, and questioned why when I did not. I know there were many times my mom questioned the path I was going down, but she stood by me. She always made sure I was comfortable and provided me with all the unspoken support that mom’s do best. Without such support I know for a fact I would be a different person. She instilled the high self-esteem I have in myself, and encouraged me to be my biggest supporter. This has helped me navigate the many difficult and stressful times life has thrown my way and helped me to be a better person at the end of it all. I will always appreciate her unwavering love and for this reason, I dedicate this doctorate to my mom. She has been with me every step, and in many ways, this is her doctorate. I love you always mom.

**Chapter 1**: C.J. Gaynus, C. Fong, T. Moore, P. Barber, and P. Fong. Trajectories of turf algal community assembly diverse with differing herbivory pressure and sedimentation regimes among fringing reefs in Mo’orea, French Polynesia.  All authors aided in the collection of data. C. Gaynus analyzed the data. C. Gaynus wrote the manuscript with edits from P. Fong.

**Chapter 2:** C.J. Gaynus, C. Fong, S. Grier, P. Barber, J. Barber-Choi, and P. Fong. Can increased sediments destabilize algal turf communities on coral reefs? Evaluating functional response across a stress gradient. All authors aided in the collection of data. C. Gaynus analyzed the data and wrote the manuscript with edits from P. Fong & C. Fong.

**Chapter 3**: C.J. Gaynus, S. Bideau, M. Gasca, A. McDonald, P. Barber, C. Fong, S. Habtes, and P. Fong. Can sea urchins rise to the occasion? Assessing the capacity for functional redundancy among herbivore guilds on coral reefs subject to shifting environmental contexts. Submitted to Journal of Ecology. All authors designed and maintained the experiment collected data, and analyzed the data . C. Gaynus wrote the manuscript with edits from all authors.

# Vita/ Biographical Sketch

## Education

Hampton University, Hampton, VA 2014

- Bachelor of Science: Marine and Environmental Science
- GPA: 3.55/4.0

## Professional Experience

Fong Lab manager (2016-2018)

- Lab inspection preparation, and overall lab management

Graduate Research Assistantship (Summer 2018)

- Sample preparation for 16s Illumia Sequencing

The Diversity Project Mentor (Summer 2017)*

- Student led field experiment assessing urchin grazing under varying sediment regimes

Social Justice Learning Institute (Fall 2015-Spring 2016)*

- High school math, chemistry and biology tutor

The Diversity Project Mentor (Summer 2016)*

- Taxonomic diversity of turf algae

The Diversity Project Mentor (Summer 2015)*

- Environmental characterization of six fringing reef sites in Mo'orea French Polynesia

The Diversity Project Peer Mentor (Summer 2014)*

- Student- led project assessing impact of sediment-biota on turf algae

The Diversity Project participant Bali Indonesia (summer 2013)*

- Conduct independent research in Bali, Indonesia (work published below)

## Publications

**Gaynus, Camille**, Shamoy Bideau, Maria Gasca, Adrienne McDonald, Paul Barber, Caitlin Fong , Peggy Fong "Can sea urchins rise to the occasion/challenge? Assessing the capacity for functional redundancy of different herbivore guilds on coral reefs subject to shifting environmental contexts" *Submitted and under review Journal of Ecology*

Fong, Caitlin R., **Camille Gaynus**, Robert Carpenter, "Complex interactions among multiple anthropogenic stressors evolve over time to shift communities on reefs" *Submitted and under review Journal of Ecology*

Wilkinson, Grace M., **Camille Gaynus**, Tiara Moore, Sarah Rosengard, Hayley Schiebel, and Jacob Zwart. (2017) "Innovations and Solutions for ASLO Student Travel Grants." *Limnology and Oceanography Bulletin* 26, no. 2: 54-55.

Leasi, Francesca, **Camille Gaynus**, Angka Mahardini, Tiara N. Moore, Jon L. Norenburg, and Paul H.Barber. (2016) "Spatial and ecologic distribution of neglected microinvertebrate communities across endangered ecosystems: meiofauna in Bali (Indonesia)." *Marine Ecology* 37, no. 5: 970-987

## Teaching Experience (UCLA)

Teaching Associate: Introductory Marine Science lab and discussion (Summer 2018)

- Discussion instructor

Graduate Reader: Animal Behavior and Ecology

- Assignment and test grader

Teaching Associate: Introductory Marine Science (Fall 2018)

- Discussion instructor

Teaching Associate: Introductory Animal Behavior and Ecology (Winter 2017)

- Discussion instructor

Teaching Associate: Introductory Marine Science (Fall 2016)
- Lab and discussion instructor

Teaching Assistant: Introductory Ecology, Evolution and Biodiversity (Spring 2016)
- Dry lab instructor

Teaching Assistant: Marine Botany (Winter 2016)
- Lab instructor

Teaching Assistant: Introductory Marine Science lab and discussion (Fall 2015)
- Lab and discussion instructor of introductory marine science principles

## Conference Presentations

**Gaynus, Camille**, Caitlin Fong, Paul Barber, Peggy Fong *Understanding how turf algal communities transition to CCA dominated states.* Poster presentation Association for Sciences in Limnology and Oceanography 2018 Feb 11-16 Portland, Oregon

**Gaynus, Camille**, Caitlin Fong, Paul Barber, Peggy Fong *How does community context impact sediment tolerance of turf?* Poster presentation Association for Sciences in Limnology and Oceanography 2017 Feb 26-Mar 3 Honolulu, Hawaii

**Gaynus, Camille**, Tiara Moore, Paul Barber, Benjamin Cuker, Peggy Fong, *Turf algal recruitment and early growth did not differ across sites that varied greatly in herbivore and coral community structure.* Poster presentation Association for Sciences in Limnology and Oceanography 2016 Feb 21-26 New Orleans, Louisiana

**Gaynus, Camille**, Domonique Hatton, Christian Henry, Keeli Howard, Sahim Wallace, Melissa Kemp, Peggy Fong *Do sediment meiofaunal communities accelerate transitions of turf to macroalgal-dominated coral reef communities?* Poster presentation Association for Sciences in Limnology and Oceanography 2015 Feb 22-27 Granada, Spain

### Certifications

American Association for Underwater Sciences 60ft SCUBA certification (May 2013-present)
CPR/First Aid certification (current)

*Highlight activities targeting communities of color

# Chapter 1:

## Trajectories of turf algal community assembly diverge with differing herbivory pressure and sedimentation regimes among fringing reefs in Mo'orea, French Polynesia

## Abstract

We conducted a year-long observational study at sites across a range of environmental and biotic conditions along fringing reefs of Mo'orea in French Polynesia. Algal turf dominated all six study sites and the abundance of fishes varied by nearly an order of magnitude. Turf algae colonization, followed by short and long term dynamics were monitored using ceramic tiles. Despite environmental differences, after two months all sites were dominated by short algal turfs of similar height, that were heavily grazed by herbivorous fish, a result likely due to the high palatability of this early successional community. However, after one year, significant differences emerged. Sites with relatively little sedimentation and higher herbivore abundance transitioned to a more diverse turf associated with crustose coral algae (CCA). In contrast, sites with lower herbivore abundance and higher sediment loads developed longer, sediment-laden turf communities. We deployed turf proxies for three months and then collected sediment trapped within for grain size analysis at two sites that had the most differences in previously characterized biotic and abiotic conditions. Sediments accumulating on turf proxies at both sites were high in clay and silt, and differed from those collected from the benthos, which were largely sand. Results suggest that despite early similarities, long-term stressors likely drive the divergence of reef associated turf communities into either degraded (longer turf and macroalgae) or healthy (CCA dominant) compositions.

# Introduction

Increasing anthropogenic pressures on coral reefs have become a major research, management, and conservation concern over the past four decades. Today, reefs are experiencing severe disturbances at a higher frequency, and, due to anthropogenic stressors, their ability to recover is not guaranteed (Hughes et al., 2017;Hughes et al., 2007;Bellwood et al., 2004). Disturbances such as hurricanes, crown-of-thorns seastar outbreaks, and disease quickly remove corals, opening up space for an alternate community to dominate the benthos (Bellwood et al., 2004;Nyström et al., 2000). The return of a coral-dominated space relies heavily on robust herbivorous fish populations, which mitigate coral-algal competition by removing algae (Nyström et al., 2008; Hughes et al., 2007;Jackson et al., 2006, Mumby et al., 2006), and low nutrient availability, which limits algal growth (Fabricus et al., 2005;Gorgula & Connell, 2004).

Coral reefs can differ widely in herbivore abundances and nutrient supplies, leading to altered benthic composition even on small spatial scales (Mumby 2017;Edmunds & Bruno, 1996). While there are numerous manipulative studies that examine changes in benthic community structure under reduced herbivore pressure and increased nutrient and sediment loads on coral reefs (Muthukrishnan & Fong 2018;Muthukrishnan & Fong 2014; Clausing et al., 2014; Smith et al.,2010; Belliveau & Paul 2002), fewer studies examine how spatial variation in these factors can affect benthic algae after disturbance and influence long-term dynamics. Changes in coral and macroalgal abundance after disturbance are well documented (e.g. Smith et al., 2010;Burkepile & Hay 2009), less attention has focused on turf, an algal community that is becoming a dominant component of tropical reefs after disturbance-related coral loss (Smith et al., 2016;Goately et al., 2016).

On healthy coral reefs, closely cropped turf algae (e.g. 1-10mm) provide trophic support, aid in nutrient cycling, and support high photosynthesis rates (Fong et al.,2017; Fong & Paul 2011). However, changes in grazing pressure due to overfishing and altered nutrient and sediment regimes—characteristics of degraded reefs(Steneck et al., 2017;Goately et al., 2016; Adam et al., 2011;Fabricus 2005)—can promote proliferation of unhealthy algal communities characterized by longer, sediment-laden turfs and even macroalgae (Goately et al., 2016). Under extreme reductions in herbivores and altered nutrient patterns, these macroalgal assemblages can be dominated by as little as one species (Payri & Stiger 2001, but see Burkepile & Hay 2009), leading to altered ecosystem functions (Bulleri et al., 2013;Bittick et al., 2010). The potential for altered function due to one or two organisms dominating the benthos has strong implications for altered function (Arson et al., 2004), but is rarely studied outside of corals. There is relatively little information on the hidden diversity found within turf (but see Harris et al., 2015). Furthermore, little is known about how and if the taxonomic composition of turf is altered under increasing nutrients, sedimentation and reformed grazing patterns, all of which shape benthic macroalgae (Poore et al., 2012;Burkepile & Hay 2006). Understanding the relationship between spatial patterns in environmental biotic conditions and taxonomic composition of turf algae may be vital to understand future dynamics of turf, especially when it comes to their succession after large-scale disturbances.

Some experimental studies have demonstrated that herbivory, sedimentation and the interactions among these two variables can determine whether turf remain in a healthy state or transitions to longer turf or macroalgae (e.g., Muthukrishnan & Fong 2014, Adam et al., 2011). For example, reduced grazing pressure commonly leads to algal proliferation yet elevated sediment loads can alter this relationship by reducing grazing pressure exerted by herbivorous fishes (Goatley & Bellwood 2012;Bellwood & Fulton 2008). Similarly, at low loads, sediment can promote turf algal growth by releasing them from nutrient limitation, but at higher loads sediment can be detrimental by blocking light, reducing photosynthesis and smothering turf with anoxia-inducing bacteria (Clausing et al., 2014). These impacts, however, are dependent upon sediment composition and residence time (Bainbridge et al., 2018), which are dynamic processes.

As turf becomes a more conspicuous component of coral reefs, it is critical to understand the fine-scale processes that promote their proliferation. The objective of the present study is to compare assembly of turf on newly opened space on coral reefs that vary in herbivory pressure and sedimentation regime. To accomplish this objective, we characterized sites and monitored short-term (two months) and longer-term (one year) colonization, growth, and change in turf on recruitment tiles modeling newly opened space.

## Methods

### Study Location

Our research was conducted within fringing reefs along the northern shore of Mo'orea, French Polynesia (17.533° S, 149.833° W), a high volcanic island 16 kilometers northwest of Tahiti (Figure 1.1). The north shore has two large bay systems, Cook's Bay to the east, and Opunohu Bay to the west. There are two main coral reef systems within the barrier reef, the shallow fringing reef adjacent to shore and the back reef, which is separated from shore by a deeper lagoon. We conducted all of our research on fringing reefs as their close proximity to shore makes them more susceptible to terrestrial inputs.

We selected six sites to capture a range of variation in anthropogenic stressors. Three of these sites are within Cook's Bay (Sites 1, 2, & 3) which is adjacent to a watershed with substantial agricultural pressure, causing high inputs of terrestrial sediments and nutrients (Clausing & Fong 2016). These sites have higher sedimentation rates and lower herbivorous fish abundances than sites 4 and 5 those adjacent to Opunoho Bay, or site 6 at the mouth of Cooks Bay (Chapter 2). Sites 4-6 also have higher fish abundance and lower sediment loads than sites 1-3, creating an ideal comparison for this study.

### Site Characterization

Because herbivore populations and sediment loads can vary over time, we first reconfirmed site specific reef characteristics reported in Chapter 2 through site surveys and sediment nutrient analyses. We then conducted visual surveys of herbivorous fishes at each site. All herbivorous fishes were counted, categorized into one of four families/tribes of common reef herbivores, including Acanthuridae, Kyphosinae, Signidae, and the family Labridae, tribe Scarinae (formerly Scaridae) (Keeley et al., 2015;Clausing et al., 2014; Poray & Carpenter 2014). In addition, we divided herbivorous fishes into 2 size classes, ≥5cm and <5cm because algal removal is related to herbivore size (Jayewardene 2009; Bonaldo &Bellwood 2008; Mumby et al., 2006). However, because the fish on these fringing reefs are typically very small (Fong et al. 2016;Clausing et al., 2014), we grouped all sizes of each family/tribe bigger than 5cm into one class. Herbivorous fish counts occurred along a 2x30m belt transect haphazardly positioned at the same depth at each site. We then conducted 20 visual assessments along each transect, on snorkel, between 10 AM and 2PM when herbivorous fish are most active (Hobson 1991). We split these visual surveys equally between morning and afternoon to account for diurnal activity variation. After confirming that fish abundance data within categories met assumptions of parametric statistics, we analyzed data using a MANOVA with site as the independent factor and fish family/tribe within size categories as the response variables. A significant MANOVA was followed up by ANOVA's comparing each size class for each family between sites.

Benthic structure was quantified on SCUBA using the point intercept technique. After haphazardly placing a 30m transect along a depth isocline (3-6m), we categorized the benthos as turf, coral, sand, macroalgae, or "other" at ten random points along each transect using a 1m$^2$ quadrat with 81 intercepts. Since algae and coral require hard substrate to settle, sand points were not included in any analyses. After calculating percent cover for each quadrat, data were analyzed for differences in each of the three categories (turf, macroalgae, and coral). After testing that all data met assumptions for parametric statistics, we compared sites using a MANOVA framework, with all significant MANOVA's followed by ANOVA's on each category comparing differences among sites.

We characterized the benthic sediment as well as estimated the amount and characteristics of sediment deposited within the algal turf. We focused this comparison on sites 2 & 6 because of the large differences in herbivorous fishes, sediment depths, and turf heights found in a previous study (Gaynus Ch 2). At each site, we deployed 40 sediment collectors constructed of a commercial plastic grass substitute to capture ambient sediment (Stewart et al., 2006). We experimented with three different materials before selecting SIMPLE Turfs Gulf 46 Bi Color astro turf, selecting the latter because they were the most reliable design we believed would hold up during the full three month deployment period as an imitation of turf. To mimic naturally occurring turf, each experimental unit consisted of a 15.24x15.24 cm (232.26 $cm^2$) piece of astro turf with the “turf” height trimmed to 1-3mm. Four nails were used to secure each experimental unit to hard substrate (n = 20 per site). After maintaining sediment for 3 months, experimental turf sediment collectors were retrieved with minimal disturbance, placed into Ziploc bags, and then sealed underwater to prevent sediment loss. After returning to the lab, each sediment collector was individually rinsed with freshwater, such that rinse water and resuspended sediment could be collected into a bucket. Collectors were rinsed until all visible sediment was removed. Next, the rinse water and associated sediment were allowed to settle before excess water was carefully siphoned off and sediments sun-dried for >24hrs. We transported dried sediment samples back to UCLA, where we quantified sediment grain size and organic content following Bouyoucos (1962) and Dean (1974), respectively.

## Monitoring of Turf Assembly

To evaluate how turf structure developed over time, ten unglazed ceramic tiles (11.68 x11.68cm) were deployed in each of the 6 sites. We used unglazed ceramic tiles as they are commonly used to model newly opened space within a reef (Jouval et al., 2019;Harriot & Fisk 1987). Each tile was drilled with a hole in the center and secured to the benthos using a 7.8cm nail hammered through a metal washer, using a 2.5cm rubber stopper to make a flexible seal between the hole and the nail. Tiles were deployed 10-13 June, 2015 at 3-6m depth as our surveys demonstrated turf algae, rather than macroalgae, dominate the benthos in this depth range.

To estimate grazing pressure exerted by herbivores after a two month deployment, we quantified the percent cover of grazing scars on each tile at all sites. Through visual observation of herbivory, we confirmed that circular scars on turf algae covering the tiles were left by herbivorous fishes. To quantify the coverage of grazing scars, photos of each tile were taken using a SeaLife 1500 camera and housing unit, and then analyzed using ImageJ (Rasband 1997-2018). To determine the percentage of grazed turf on each tile, all bite mark areas were delineated using the lasso tool, total area of all marks was calculated, and that area was divided by the total tile area.

To assess the development and changes in turf communities over time, turf height was measured on SCUBA after 2 months and again after 1 year, using a calibrated measuring device. After 1 year, we also measured crustose coralline algal (CCA) cover, as CCA was present at one year monitoring, despite not being present at any site after 2 months, likely due to their long recruitment time (see Matsuda 1989). One year measurements were only collected at sites 1, 2, 3, & 6 as sites 4&5 were vandalized. Photos of each tile were taken using a SeaLife 1500 camera with accompanying underwater housing unit. Each tile was digitally analyzed using ImageJ (Rasband 1997-2018), to determine the percent cover of crustose coralline algae (CCA), following the methods described above.

Upon completion of data collection from tiles deployed for 1 year, we proceeded to cage each tile at sites 2 & 6 (the most different sites), allowing turf communities to continue to grow and develop in the absence of herbivory. After a full year of herbivore exclusion, we recovered each tile into a Ziploc bag, and returned to the lab for analysis of algae composition. Tiles were photographed and then rinsed gently to remove any sediment. Each tile were scraped using a paint scalpel and the contents placed in a large bowl of seawater. All visible algae were removed from the bowl and identified using a dissecting microscope, AlgaeBase, and a taxonomic key (Payri et al., 2000).

## Results

### Site Characterization

Abundances of herbivorous fishes differed significantly among sites, both in size and in taxonomic category (MANOVA **$p<0.0001$**)(Fig 1.2a). Abundance of the four herbivorous fish communities were significantly different among sites (ANOVA $p<0.05$ for 3 of 4 categories) except Labridae tribe Scarinae ≥5cm. Large (≥5cm) Acanthuridae were the most abundant category of fish at sites 2, 4 & 5, while sites 1,3, & 6 had more even distribution of fishes. Site 5 had the largest number of herbivorous fishes, which was dominated by large (≥5cm) Acanthuridae.

Although turf was dominant at all sites (e.g. at least 70 % of the benthos), benthic cover differed significantly among sites (MANOVA, **$p<0.0001$**) (Fig 1.2b). There was a significant difference in turf cover among sites (ANOVA, **$p<0.001$**), with sites 2 & 3 having significantly more turf cover compared to site 5 (HSD.test, **$p<0.01$** for both sites). Macroalgae cover was much lower than turf coverage, ranging from 0%-20% across the six sites. Macroalgal cover differed significantly across sites (ANOVA, **$p<0.0001$**). Site 3 had significantly more than sites 5, 4, & 1 (HSD.test, **$p<0.01$**, **$p<0.05$**, **$p<0.001$** respectively). Coral had the lowest percent cover at all sites with no significant differences among sites (ANOVA, $p=0.13$).

Astro turf sediment collectors collected 3-fold as much sediment over the 3 month period at site 2 compared to site 6 (Site 2= 757.77 g/m$^2$; Site 6= 213.80 g/m$^2$). Despite this difference, sediment composition was similar in both sites (Table 1.1), consisting of more silt and clay particles compared to benthic sediments which were dominated by sand. Organic content was more similar between sites than between collection locations (astro turfs vs benthic). This was also true for grain size, as sediments collected from the astro turf contained more silt and clay than samples collected from the benthos.

### Monitoring of Turf Assembly

After 2 months, more than half the surface area of each tile was covered in grazing scars (Fig 1.3a). However, there were significant differences in grazing scar cover among sites, with sites 4, 5, & 6 (29%-96%) all having similar grazing scar cover that were more than sites 2 & 3 (29%-77%). Site 1 was similar to both groupings. The lowest grazing scar cover was at site 3, which was 36% less than the highest percent cover found at site 6.

After two months, the mean turf height across all sites as was 1.29mm ± 0.009 (mean ± SE), and was not as variable (1-3mm) as more established plots can be (see Fong et al.,2018; Clausing et al.,2014; Gaynus Ch 2). There was no significant difference in turf height among sites after two months (one-factor ANOVA, p = 0.346)(Fig 1.3b, Table 1.2).

After one year, CCA cover on tiles differed significantly among sites (ANOVA **p<0.00001**). Sites located on the margins of Cook's Bay (sites 1,2,&3) did not differ significantly from each other in CCA coverage, but these sites had on average 94% less CCA cover compared to Site 6 (Fig 1.4a, Table 1.3) near the mouth of Cook's Bay. Moreover, after 1 year, sites within Cook's bay (sites

1,2,&3) also developed significantly longer turf than those at site 6 (ANOVA **$p<0.00001$,** Fig 1.4b, Table 1.4).

After 1 year of excluding herbivores, algal species richness on tiles was double at site 6 compared to site 2 (Table 1.5), although red algae was numerically dominant at both sites (Fig `1.5). Common genera at both sites included the macroaglae *Dictyota* and *Lobophora*, as well as the filamentous genera *Gelidiopsis* and *Polysiphoina*. Eleven of the 31 genera were found at both sites. The only genera that were noted at site 2 but not at site 6 were *Valonia* and *Grateloupia*, and a member of the green algal family *Cladophoraceae*.

## Discussion

Our results suggest that turf algae can be a transitional community after disturbance opens up space on a coral reef. Moreover this community can either develop into a short, healthy, biodiverse state associated with CCA or into less diverse, longer, sediment-laden turf. These different potentials are important because the former promotes recovery of corals while the latter can inhibit recovery (Fong & Paul 2011). Natural variations in herbivore abundance and composition as well as sediment loads deposited are likely strong mechanisms that regulate benthic succession. The importance of a natural herbivore community in benthic disturbance has been highlighted in multiple studies (Smith et al., 2010; Burkepile & Hay 2009; Belliveau & Paul 2002), however unlike these studies we examine how sediments and not just nutrients may influence benthic trajectories.

While transitions to longer turf in this study were relatively quick, transitions to CCA took much longer, being observed only after 1 year. High recruitment and cover of CCA serve as a signal for reef recovery, as some coral species (hard and soft) prefer to settle where there is high CCA cover (Golbuu & Richmond 2007;Hadfield & Paul 2001;Heyward & Negri 1999). Environmental factors such as high sediment loads can reduce CCA cover, creating more uncertainty for reef recovery (Fabricus & De'ath 2001) and as our results suggest provide the open space needed for an alternate turf dominated community to proliferate and be maintained over long periods of time. Other long-term benthic studies and manipulations suggest how important extended monitoring can be in understanding trajectories of successions after disturbances (Smith et al.,2010; Burkepile & Hay 2009; Belliveau & Paul 2002), and must be included to obtain complete understanding of reef recovery and resilience.

High sediment loads among sites may have contributed to transitions to longer turf overtime. Sediments can deter grazing by fishes (Goatley & Bellwood 2012;Fulton & Bellwood 2008) and release turf from nutrient limitation (Clausing et al. 2014), providing an opportunity for algal proliferation. Under high sediment loads, however, turf can have similarly negative response (Tebbett et al., 2018) as those discussed above for CCA, as sediment can become anaerobic and block light needed for photosynthesis (Clausing et al., 2014). This nonlinear relationship may lead to highly variable responses on small spatial scales (Bainbridge et al., 2018; Fong et al., 2018;Clausing et al., 2014). While our results do not pinpoint the inflection point of this nonlinear relationship, we do suggest the long-term negative implications high sediment loads can have on reefs, promoting algal proliferation and reducing algal diversity.

High sediment load did shape the different trajectories of benthic communities but benthic structure was at least partially driven by variation in herbivory between sites. Herbivory pressure is well-known mechanisms among healthy coral reefs, with high coral cover and low algal abundance (Adam et al., 2015;Hughes et al, 2007;Bellwood et al, 2004). Compromised herbivore communities due to overfishing can lead to reefs dominated by macroalgae (Steneck et al., 2017; Adam et al., 2015), especially after large-scale disturbances that open space for colonization. For example, following the death of 90% of the coral in the Seychelles in 1998 due to elevated sea surface temperatures (Wilkinson 2000), recovery was strongly tied to herbivore size and species composition (Nash et al., 2016). While herbivorous fishes in our study were much smaller than those in Nash et al. (2016), results still showed that sites with more and larger herbivores transitioned into a more diverse benthic turf and had more CCA cover.

Interestingly, short-term of turf communities after two months indicated that strong grazing pressure was exerted on new turf recruits irrespective of herbivore abundance or sediment load. This result is likely due to the high palatability of early successional stages of algal turf and the lack of time for turf to accumulate sufficient sediment to deter herbivory. Turf and sediments may have a nonlinear relationship that is dependent on sediment composition and quantity, influencing palatability. For example, naturally accrued sediments reduced turf grazing especially among parrotfish (Fulton & Bellwood 2008); however, at a similar reef in the Great Barrier Reef, some grazer members were not impacted by sediment additions (Tebbett et al., 2017). Given that algal turf is increasing in abundance and important on tropical reefs and that the dynamics of turf communities can be altered by sediment regimes, it is imperative to understand how small and large scale variation in sediments are impacting turf.

While strong herbivory pressure is a major factor limiting transitions of reefs to less desired algal states, it is increasingly clear that herbivory is not the only factor influencing recovery after large-scale disturbance. Changes in sediment deposition, residence time, and composition

(Bainbridge 2018) all shape reefs. Indeed, the results of this study demonstrate that turf readily occupies newly opened space after disturbance with the potential for multiple trajectories, either to a state that can facilitate coral recovery or one that inhibits it. As reef recovery slows and at times is lost completely, it is increasingly critical to understand the controls of this disparate outcomes. In particular, future research should focus on turf assembly after disturbance, and how this is modified by long-term stressors such as reduced herbivory and changes in sediment regimes.

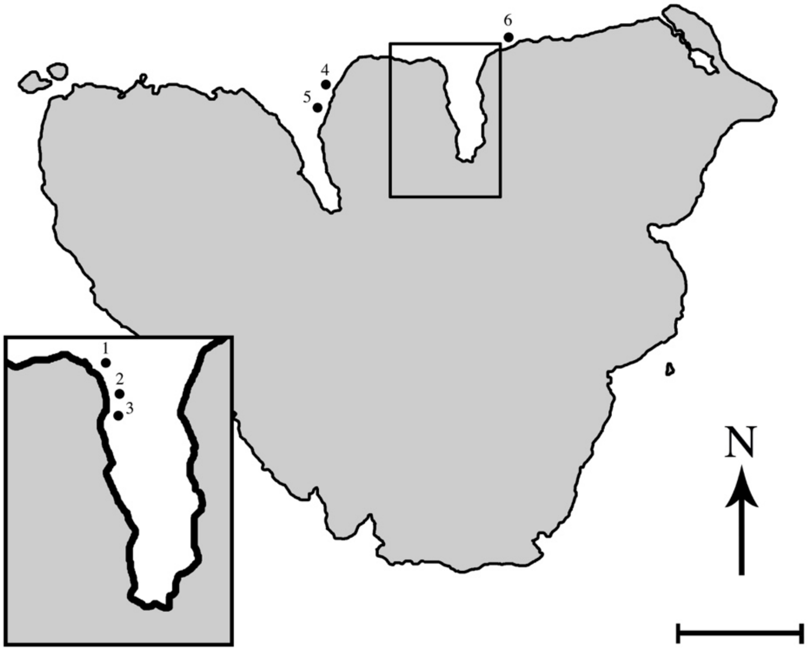

Fig 1. 1 Map of Mo’orea with six study sites marked

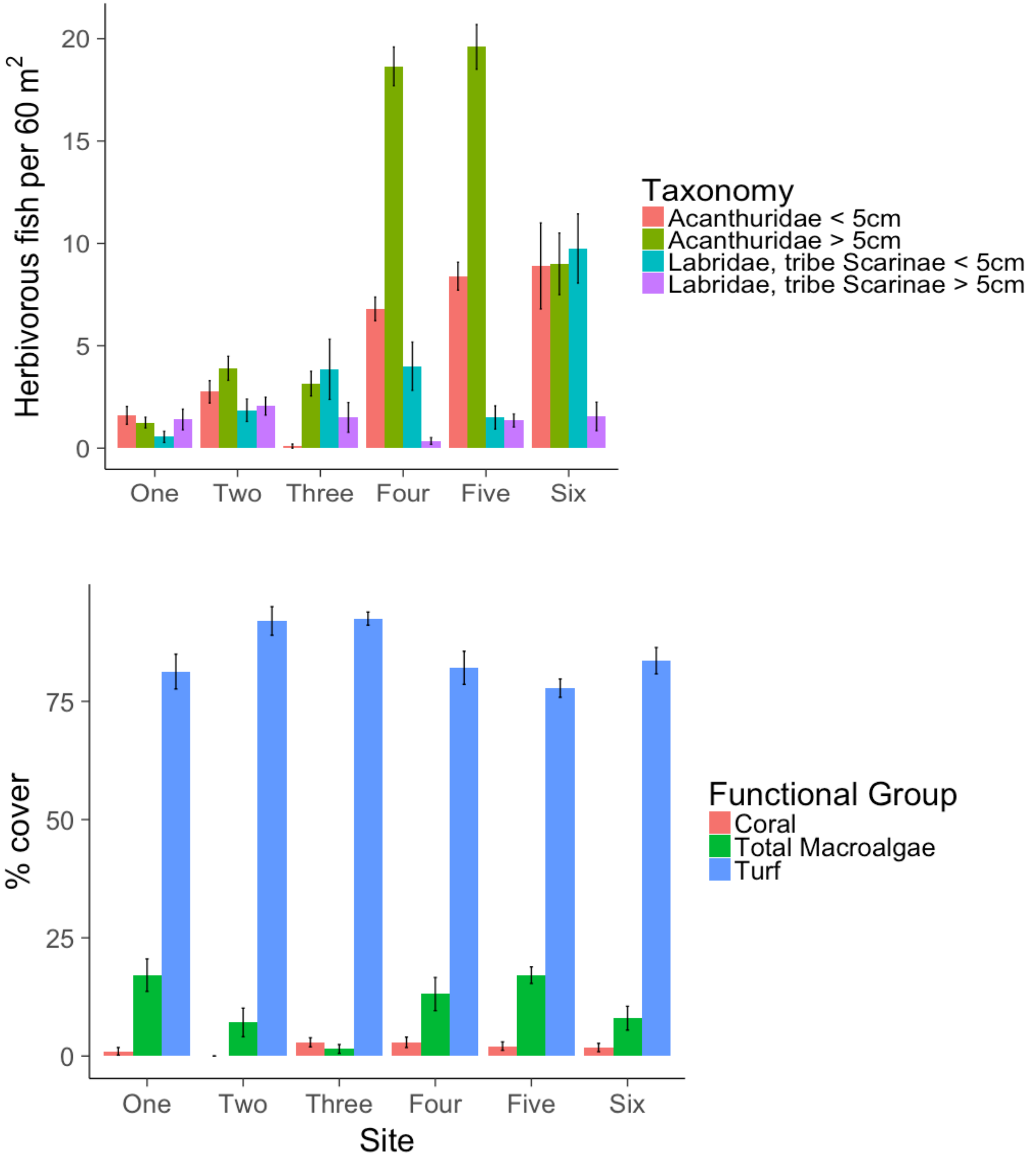

Fig 1.2: a) Herbivorous fish abundance at each site. Bars represent mean ± standard error. b) Benthic cover of three main functional groups among our six sites. Bars represent mean ± standard error.

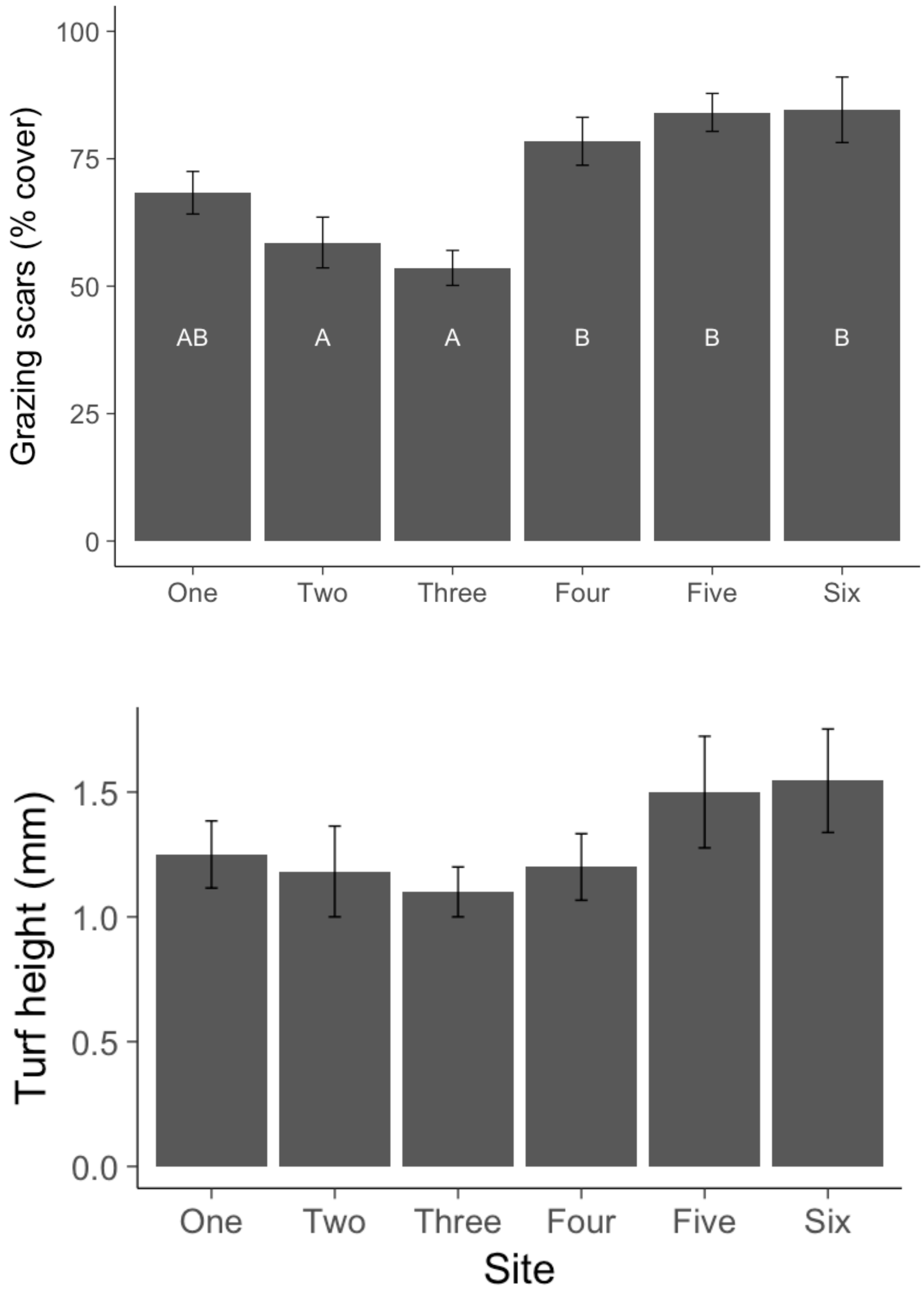

Fig 1.3: a) Mean percent of grazing scars on each tile 12 days after being deployed. Bars represent mean ± standard error. b) Turf height on tiles two months after being *in situ* at each site. Bars represent mean ± standard error.

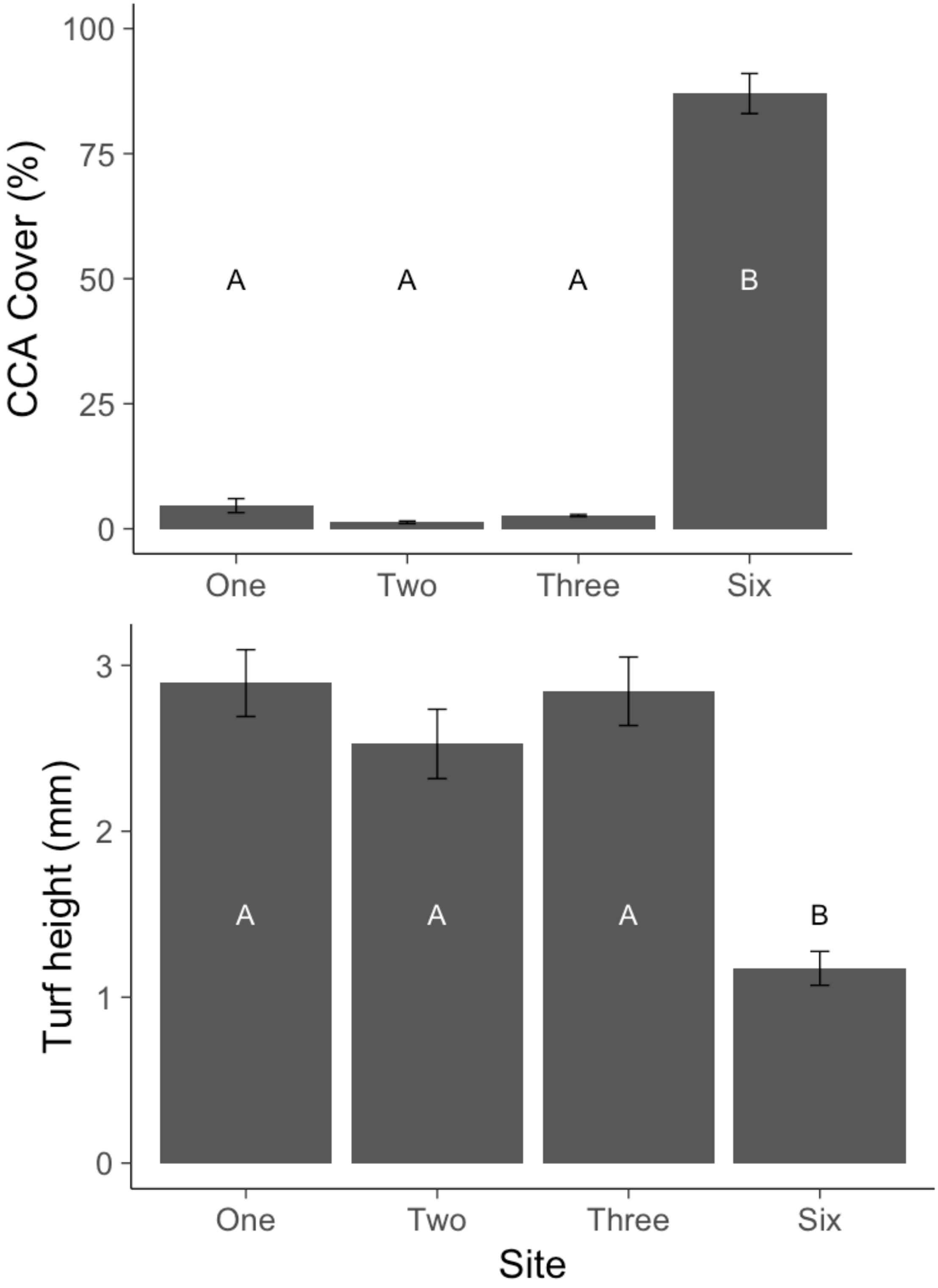

Fig 1.4: a) Mean percent of tile surface covered by CCA at each site and b) mean filament height after 1 year *in situ*. Bars represent mean ± standard error.

Fig 1.5: Picture taken under dissecting microscope of *Ceranium* spp of alga collected from a tile at site 6

Table 1.1: Comparison of sediment grain size and % organic content among sites and between sediment collected from the benthos and that maintained in astro turfs.

| Sediment Sample | Sand | Clay | Silt | % Organic Content |
|---|---|---|---|---|
| Site 2 astro turf | 32% | 28% | 40% | 5% |
| Site 2 benthic | 89% | 8% | 3% | 2% |
| Site 6 astro turf | 65% | 21% | 13% | 5% |
| Site 6 benthic | 92% | 8% | 0% | 2% |

Table 1.2: Results from a One-way ANOVA for turf height after two months, among sites.

|  | DF | Sum Sq | Mean Sq | F value | Pr (> F) |
|---|---|---|---|---|---|
| Site | 5 | 1.74 | 0.348 | 1.148 | 0.346 |
| Residuals | 56 | 16.989 | 0.3034 |  |  |

Table 1.3: Results from a One-way ANOVA for percent CCA cover after one year, among sites. Bolded values are significant

|  | DF | Sum Sq | Mean Sq | F value | Pr (> F) |
|---|---|---|---|---|---|
| Site | 3 | 24431 | 8144 | 282.6 | <0.00001 |
| Residuals | 12 | 346 | 29 |  |  |

Table 1.4: Results from a One-way ANOVA for turf height atop of tiles deployed for one year, among sites.

| | DF | Sum Sq | Mean Sq | F value | Pr (> F) |
|---|---|---|---|---|---|
| Site | 3 | 48.11 | 16.037 | 13.43 | <0.00001 |
| Residuals | 117 | 139.68 | 1.194 | | |

Table 1.5. Lowest possible classification (Family, genus, or functional group (CCA)) of algae found on ceramic tiles at two sites

| Genus | Site Two | Site Six |
|---|---|---|
| Amphiroa | | X |
| Anotrichium | | X |
| CCA | | X |
| Ceranium | X | X |
| Champia | X | X |
| Chondria | X | X |
| Cladophoraceae | X | |
| Colpomenia | | X |
| Cyanobacteria | | X |
| Dasphylla | | X |
| Dasya | | X |
| Dictyota | X | X |
| Dipterosiphonia | | X |
| Galaxaura | X | X |
| Gelidiella | | X |
| Gelidiopsis | X | X |

| | | |
|---|---|---|
| Gracilaria | X | X |
| Grateloupia | X | |
| Griffithsia | X | X |
| Heterosiphonia | X | X |
| Hypnea | | X |
| Lobophora | X | X |
| Lomentaria | | X |
| Padina | | X |
| Polysiphonia | X | X |
| Rosenvingea | | X |
| Sargassum | | X |
| Spyridia | | X |
| Ulva | | X |
| Unknown | | X |
| Valonia | X | |

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# Chapter 2:

## Can increased sediments destabilize algal turf communities on coral reefs? Evaluating functional responses across a stress gradient

## Abstract

Closely-cropped algal turfs are integral components of healthy tropical reef communities. However, because these can transition to longer, unhealthy turfs under high sedimentation rates, it is important to understand the functional relationship between sediment and turf. On seven reefs in Mo'orea French Polynesia, we surveyed sediment depth and turf height. We then conducted a two-factor experiment to evaluate how turf height responded to a range of sediment depths (0, 1, 3, 5 mm) maintained at two sites with different environmental conditions for 25 days. Results revealed a positive linear relationship between sediment depth and turf height, which demonstrates a proportional increase, but does not support the hypothesis that longer turf can hold disproportionally more sediment. Our experimental addition of sediment always negatively impacted turf height, though impacts were more severe at the site with more natural sediment and fewer herbivores. Our results show sediments always have a negative impact on turf algal communities and therefore their influx should be managed to maintain healthy a reef.

# Introduction

Historically, benthic coral reef communities have been dominated by mixed assemblages of corals, crustose coralline algae, and closely-cropped algal turf communities (Fong & Paul, 2011). However, phase shifts from this coral dominated state to a state dominated by algae with little to no live coral cover are increasingly common (D. R. Bellwood et al., 2004; Hughes et al., 2007). These phase shifts are linked to human activities that reduce herbivore populations (Jackson et al., 2006; Hughes et al., 2007), increase sedimentation and nutrient availability (Fabricius, 2005; Moberg & Folke 1999; Rogers 1990), and alter water chemistry (Hoegh-Guldberg et al., 2007), as well as interactions among these factors (Ban et al., 2014).What remains unknown is how disturbances work with environmental stressors typically found in conjunction to alter reefs .

Herbivory , nutrients, and sedimentation have a strong influence on benthic structure , inparticular the proliferation of algae (Erftemeijer et al., 2012;Burkepile & Hay 2010;Fabricus 2005; Hughes et al., 2004), which can negatively impact corals through indirect or direct competition (Barott et al.,2012;McCook et al.,2001). While the factors that lead to macroalgae-dominated reefs are important, there is growing documentation on the strong role turf can have in the transition from coral to algae dominated reefs (Jourfray et al., 2019;Fong et al., 2018; Fabricus 2011; Adjeroud et al., 2009).

Algal turfs are complex communities comprised of filamentous algae, cryptofauna, and associated sediments (Kramer et al., 2012;Fong & Paul 2011). Algal turfs are integral benthic space-holders on healthy tropical reefs, providing critical food web support , mediating nutrient cycling (Fong & Paul 2011) and can be an important transitional phase towards crustose coralline algae and recruitment of coral larvae (Smith et al., 2010; Burkepile & Hay 2009; Belliveau & Paul

2002;McClanahan 1997; Gaynus Chapter 1), promoting reef recovery. However, on some reefs, algal turfs have become increasingly dominant, taking over spaces previously dominated by coral, particularly after disturbance (Muthurkrishnan & Fong 2018; Adjeroud et al., 2009; Fulton & Bellwood 2008). Key to these alternate outcomes is algal turf height: short, closely-cropped turf (usually< 1cm height) promotes coral recovery (Fong & Paul 2011) while long sediment-laden turf may represent a degraded alternative stable state that prevents recovery of coral (Goately et al., 2016; Adjeroud et al., 2009; Birrell et al., 2005).

It is well established that loss of herbivory (Vermij et al., 2010;Jackson 2001) and eutrophication (Fabricus 2005) promote the growth of algal turf, but the impacts of sediment are more complex. Sediment is known to both increase (Goately & Bellwood 2013) and decrease turf growth (Tebbett et al., 2017;Clausing et al., 2014). Importantly, experimental and observational evidence supports the hypothesis that long sediment-laden turf may be an alternate reef stable state (Goately et al., 2016;Goately & Bellwood 2013;Bellwood & Fulton 2008). As such, algal turf height could represent a "tipping point" mediated by sediment, but the nature of this relationship between sediment load and turf height is unclear.

Tipping points are the inflexion point leading to alternative stable states (Scheffer et al., 2009;Scheffer et al., 2001). If a tipping point exists where turf is initially resistant to sediment stress then rapidly transitions to a long sediment-laden state, then these transitions may be difficult to predict, resulting in "ecological surprises" ( Nyström et al., 2000;Moberg & Folke, 1999) . Evidence to date suggests a non-linear relationship between sediment and turf, where at low levels sediments can be positive but at higher loads effects become negative. For example, at low levels, sediments can have a positive influence by transporting terrestrial nutrients to turf communities (Airoldi & Connell 2014; Gorgula & Connell 2004), thereby releasing turfs from nutrient-limitation. At moderate accumulations, sediments can deter grazing by herbivorous fishes (Clausing et al., 2014;Goately & Bellwood 2012; 2013; Bellwood & Fulton 2008), releasing turf from a key process maintaining healthy short turf communities and facilitating transitions to long turf that become laden with sediment (Fong et al., 2018). In turn, these deeper sediments can have negative effects by limiting incident light and reducing turf's typically high photosynthetic abilities (Fabricius et al., 2005). These deeper sediments can also become anoxic, causing loss in turf height (Clausing et al., 2014), likely through turf mortality. Taken together, these studies suggest that turf height may have a non-linear response to a gradient of sediment loads.

Because short, cropped turf are a hallmark of healthy reefs and foster coral recovery, while long turf communities may represent an alternative stable state that precludes recovery, it is critical to quantify their response across a gradient of sediment loads. In this study ,we characterize the natural variation in sediment depth and turf height among a range of fringing reef communities. We then directly test how turf communities on two of these reefs respond to a range of experimentally controlled sediment depths to determine how sediment depth may control algal turf height, and, in turn, impact the ability of reefs to recover from disturbance.

## Methods

### Survey Sites

To determine the relationship between turf height and sediment under ambient conditions, and to identify two sites that represent the extremes with respect to turf height and sediment depth, we surveyed 7 fringing reefs along the north shore of the island of Mo'orea in French Polynesia. Mo'orea lays approximately 11km northwest of Tahiti in the South Pacific and is home to the Mo'orea Coral Reef Long-Term Ecological Research (MCR LTER) Site, where reef processes have been studied for 15 years on a range of temporal and spatial scales. While Mo'orea has a diversity of reef habitats, we focused our surveys on fringing reefs because the shallower, nearshore fringing reef communities likely experience more terrestrial fluxes, particularly sediment loads. In addition, nearshore fringing reefs on Mo'orea are historically less resilient to disturbance than fore reef ecosystems (Edmunds et al. 2019; Adam et al. 2011;Adjeroud et al., 2009).

At each of seven survey sites, we measured sediment depth and turf height (Fig. 2.1). Ta'ahiamanu (17°29'27.9"S 149°51'03.4"W) and Opunohu West (17°29'50.3"S 149°51'47.5"W) were located in the more western Opunohu Bay while Gump (17°29'24.9"S 149°49'31.4"W) and Cook's Bay East (17°29'15.6"S 149°49'05.5W) were in the more eastern Cook's Bay. Maharepa (17°28'58.5"W 149°48'55.7"S) and Hilton (17°29'04.3"S 149°50'34.2"W) were located along the more open north shore and Melissa's Red Buoy [MRB] (17°28'38.01"S 149°49.2'2.35"W) was on the backreef (Fig. 1). Surveys were conducted during the dry season from April-May in 2016, and were conducted at 1-3m depth where turf is known to dominate (see Chapter 1 benthic survey results). At each site, a 50m transect was haphazardly deployed along a depth contour; at 20 randomly-chosen points along each transect, algal turf height and sediment depth were measured at 10 intersections within a 15cm x 15cm quadrat. If the random point was not comprised of turf, we measured the next closest turf patch. We measured each point by placing a galvanized steel mesh comb with teeth calibrated in 1mm increments (1-7mm) (Fong et al.,

2018) next to the attached turf community and recorded turf height and sediment depth to the nearest 0.5mm. We then calculated the mean of all 10 measurements within one quadrat, and each quadrat served as a replicate (n=20 per site, N= 140 over 7 sites). To minimize sediment disruption, we first measured sediment depth within our quadrat before taking turf measurements. All measurements were conducted on snorkel as to reduce SCUBA equipment sediment disturbances.

To compare turf height and sediment depth between sites, we used permutational analysis of variance (PERMANOVA) using the coin package in R as this technique has been found to be robust against non-normally distributed data (McARdle & Anderson, 2001; Anderson & Walsh, 2013). We then used linear regression to test for a relationship between sediment depth and turf height. To further explore potential sediment stabilizing mechanisms, we generated a second regression of turf height vs. proportion of sediment in the turf matrix to assess whether longer turf have a higher threshold for sediment than shorter turf heights.

### Experimental Sites

Based on the range of natural variation in sediment depth and turf height, we chose to conduct our sediment tolerance experiment at Gump and Maharepa reefs, which our surveys established to have different turf communities based on turf height and sediment depth. First, because all experimental units were open to herbivory, we quantified the abundance and size category of herbivorous fishes. We conducted visual fish assessments (n=20 at each site) on snorkel between 10am-2pm following the methods of Brock (1954). We counted and identified all herbivorous fishes in the families Acanthuridae, Kyphosidae, Siganidae, and the family Labridae, tribe Scarinae (formerly Scaridae) known to inhabit Mo’orean fringing reef communities (Adam et al. 2011; Clausing et al., 2014; Keeley et al., 2015). We binned fish into two categorizes, ≥5cm or <5cm because larger fish are known to have a greater impact in limiting algal proliferation (Mumby C.P. Dahlgren, C.P. et al., 2006). After testing the resulting data for assumptions of parametric statistics, we analyzed total herbivorous fish data using a MANOVA with site as the independent factor and fish family/tribe as the response variables (JMP©). A significant MANOVA result was followed by t-tests comparing means of each size class for each family between sites.

To characterize the sediment used in our experiment, we collected three 4-liter bags of sediment from the benthos of each site within 1m of where we conducted our experiment (see below). Sediments were sun dried for at least 48 hours, transported to UCLA, and dried at 60° C to achieve dry sediment weight. To quantify organic content, 3 subsamples from each of the 4-liter samples from each site were weighed using an analytical balance, placed in a muffle furnace at 480° C for 12 hours, then reweighed (Dean 1974). Mass of organic matter was calculated as the difference between the initial and final weight, then expressed as a percent of the initial mass. Percent organic content was averaged for all subsamples at each site and these entered as replicates in a t-test comparing sediment organic content between sites (n=3).

### Sediment Tolerance Experiment

To directly test the relationship between sediment depth and turf height, we conducted a two-factor experiment varying site (Gump & Maharepa) and sediment treatment, including sediment removal (0 mm) as well as 1mm, 3mm, & 5mm sediment additions. To ensure all turf communities developed under similar environmental conditions, unglazed ceramic tiles were preconditioned by deploying the tiles for five months at 2-3m depth on Gump Reef ~150 m from the Gump reef experimental site. Unglazed ceramic tiles are a good proxy for suitable hard substrate for coral recruits (Harriot & Fisk 1987), and are commonly used to replicate open space within coral reef communities (Hill & Wilkinson 2004). To start the experiment, tiles were and transported in seawater to each of the two experimental sites (Gump &Maharepa) where they were redeployed one week before sediment manipulations, which began on July 2nd. All tiles were placed at 2-3m depth at each site, on top of dead coral heads and outside of damselfish territories using a nail, a rubber stopper and a washer for attachment.

Five days before sediment treatments commenced (2 days after transport to experimental sites), initial turf heights were measured on all tiles to test for potential differences in turf height at the start of the experiment. To begin the experiment, we applied the 4 sediment treatments to randomly assigned tiles (n=10). Sediment treatments were reestablished (sediment reapplied or removed) every four days for 25 days. We used sediment collected no more than 1m away from a tile for the 1, 3, and 5mm sediment treatments. For the 0mm treatment, we removed naturally deposited sediment every four days through a slight wafting motion no more than 10cm above each tile. On the 25th day, turf heights were remeasured as described above. We measured 10 random points on the tile  and then calculated a mean turf height for each tile replicate. We calculated change in height per week (mm/week) by subtracting final heights from initial heights and dividing by number of weeks. After testing for the assumptions of parametric statistics, a two-way ANOVA was used to determine if there were significant differences among sediment treatments and between sites.

# Results

## Survey Sites

Turf height ranged widely (0-7mm) within survey sites and means differed significantly among reef sites (1-factor PERMANOVA, p < 0.0001) (Fig 2.2). Of all sites, Gump Reef in Cook's Bay had the longest filaments (0-7mm range), which were significantly longer than 4 of the other 6 sites. Only MRB and Opunohu West had turf communities with heights comparable to Gump (0-5mm, 0-7mm, respectively). In contrast, the other Cook's Bay site, Cook's Bay East grouped with the two open shore sites (Hilton and Maharepa), which had the shortest turf heights (0-4mm, 0-3mm respectively ). Turf in Ta'ahiamanu in Opunohu Bay was intermediate in height, grouping with all sites but Gump Reef.

Sediment depth also ranged from 0-6mm within sites and mean sediment depth differed significantly among reef sites (Fig 2.2b, 1-factor PERMANOVA, p < 0.0001). Although the pattern of sediment depth was similar to turf height, Tukey Post-Hoc tests revealed only two groups of means, with sediment on Gump, MRB, and Opunohu West Reefs significantly deeper (0-6mm) than on the other 4 reefs (0-3mm).

A linear regression indicated a significant positive linear relationship (Fig 3.3a) between turf height and sediment depth, with longer turf communities holding more sediment. Although, longer turf did contain sediment in a larger percent of its depth than shorter turf (Fig 3.3b), this relationship explained very little of the variance.

## Experimental Sites

At both experimental sites, only herbivorous fishes in the family Acanthuridae and Labridae, tribe Scarinae, were observed, with no Siganidae or Kyphosidae (Figure 2.4). Maharepa had over

3x (1973 total) the total herbivorous fish abundance compared to Gump (633 total). There were significant differences in the herbivorous fish community between sites (Table 2.2), but only Acanthuridae ≥5cm (t=test, $p < 0.0001$) and Scarinae <5cm (t=test, $p < 0.0001$) were significantly different between sites, with no other differences between sites.

Although mean organic content of the sediment appeared higher at Maharepa than Gump (9.4%, ±1.8 vs. 7.2%, ±2.8; mean, ± SE, respectively), it did not differ significantly between sites (t-test, $p = 0.5367$).

### Sediment Tolerance Experiment

At Maharepa Reef, mean filament height was shorter during the survey period (April- May 2016) compared to initials taken on tiles before sediment manipulations (July 2016) (1.2±0.1mm and 1.4±0.1mm respectively), although these differences were not significant (t-test, p-value=0.1115). Turf heights taken during both measurement times were extremely variable (range 1-4mm in both cases). In contrast, at Gump Reef, turf was significantly taller during our surveys than before the experiment commenced (2.7±0.2mm and 1.6±0.1mm respectively, Welch's t-test, $p < 0.0001$).

A 2-Factor ANOVA found no significant differences in initial turf height among treatments at both sites. Algal turfs at both sites showed a negative response to sediment addition across most sediment treatments (Fig 2.5), resulting in a significant main effect (Table 2.3). However, while both sites showed an overall negative response, there were important differences. Turf at Maharepa Reef grew longer in the cleared (0 mm) and 1 mm addition treatments, and only experienced negative growth when sediment depth was 3mm or greater. In contrast, turf on Gump Reef did not experience net growth in any treatment, although more sediment resulted in shorter turf. This difference between sites resulted in a main effect of site (Table 2.3). Response of turf to sediment was largely linear at Maharepa, but non-linear at Gump. As a result, there was a non-significant interaction between sediment and turf height (Table 2.3), despite a strong pattern of sediment producing negative effects on turf height across the entire range of sediment additions at both sites.

## Discussion

Our results did not support the current hypothesis that sediment-laden turfs are alternative states stabilized by positive feedbacks, as we documented none of the positive influences sediments can have on turf. This hypothesis has been reiterated through a number of observational and experimental studies that showed sediments deterred grazing and facilitated transitions to longer turfs, which in turn captured more sediments in a positive feedback (Fong et al.,2018; Goatley & Bellwood, 2012). While our surveys showed that longer turf did contain deeper sediments, our experiment showed that sediment additions had negative effects on turf height in the presence of herbivores similar to a study conducted in the GBR where sediment and herbivory were manipulated atop turf plots (Tebbett et al., 2017). Our study also aligns with one conducted in Mo'orea observing overall negative turf responses to high sediment loads (Clausing et al, 2014). In contrast to our Gump results, but in line with those results at Maharepa (1mm additions), Clausing and colleagues reported positive influence of low levels of sediment on turf algae, which deterred herbivory and promoted turf algal growth, a trend established in other fringing reefs ( Goately & Bellwood 2012, 2013). It is important to note that, while we found that increased sediments do not drive turfs on Mo'orean fringing reefs to an alternative stable state, this lack of turf stability is likely not a positive for coral reef recovery (Fabricius & De'ath 2001; Purcell 2000). Rather, overall decline in turf height with addition of sediment suggests that ecosystem functions such as increased productivity and food chain support may be disrupted, a hypothesis that warrants critical evaluation.

The high organic content of sediments from both of our experimental sites may provide one possible explanation for their strong negative effects on algal turfs. In comparison, sediment organic content both within the Great Barrier Reef as well as from other fringing reefs of Mo'orea were much lower than our values. For example, sediments used in our experiments contained 9-14 times more organic content compared to sites within the GBR (Yamamoto et al., 2001), and were 73% higher in organic content than at a different Mo'orean fringing reef site seven years earlier (Clausing et al., 2014). The high organic content may have fueled similar negative effects witnessed in a previous study, where negative effects were associated with localized anoxic conditions (Clausing et al., 2014), as bacterial decomposition of organic matter is an oxygen consuming process (Glud, 2008;Jɸrgensen, 1977). Sediments with high organic content can also locally reduce pH, are easily resuspended, and alter light attenuation (Fabricius et al., 2016, Storlazzi , et al.,2015), thereby reducing turf's ability to successfully recycle nutrients. The high organic content within our sediments may have further reduced turf functionality by reducing or deterring herbivory, as some fish communities within the GBR were deterred by turf algal communities containing fine sediments (Tebbett et al., 2018; Gordon et al., 2016). Thus, our results imply that the nature of the sediment themselves may be key to their impacts, with sediments high in organic content being particularly disruptive to reef ecosystem functioning.

Differences between sites in our study suggest the negative effects of sediment may be ameliorated by higher water flow or other environmental condition, as effects were more strongly negative within the bay than the more open north shore. Physical and biogeochemical properties such as water flow, rainfall, and coastline bathymetry simultaneously regulate sediment residence time, potentially altering how benthic organisms interact with organic-heavy sediments (Bainbridge et al., 2018). More study is needed on the relationship between sediment characteristics and algal turf growth in order to understand what is driving variance in this negative relationship.

Algal turfs are dynamic communities (Connell & Airoldi 2014) that are influenced by sediment in a suite of ways, highly dependent on both community and environmental characteristics. As the documented occurrences of sediment-laden turf increase among reefs, in particular among fringing reef communities (Adams et al., 2011; Adjeroud et al.,2009), it will become ever more pressing to study the environmental mechanisms that shift this community.

Fig 2.1: Survey sites along six fringing reef sites where turf height and sediment depth was measured; two sites along the north shore (Maharepa, and Hilton), two within Cook's Bay (Gump, Cook's Bay East) and two within Opunohu Bay (Ta'ahiamanu, Opunohu West). One backreef site (MRB) was also included.

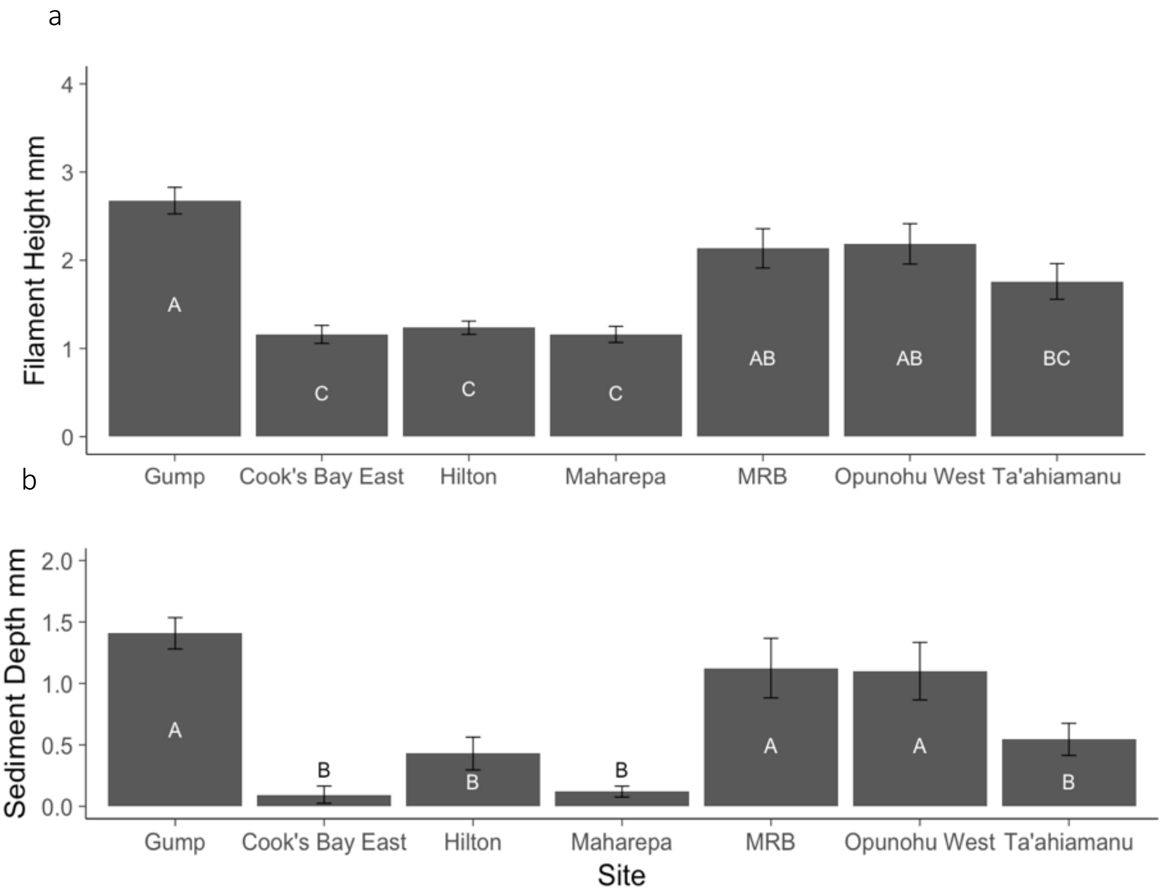

Fig 2.2: Average turf height (a) and sediment depth (b) at seven fringing reef sites. Bars represent mean ± standard error.

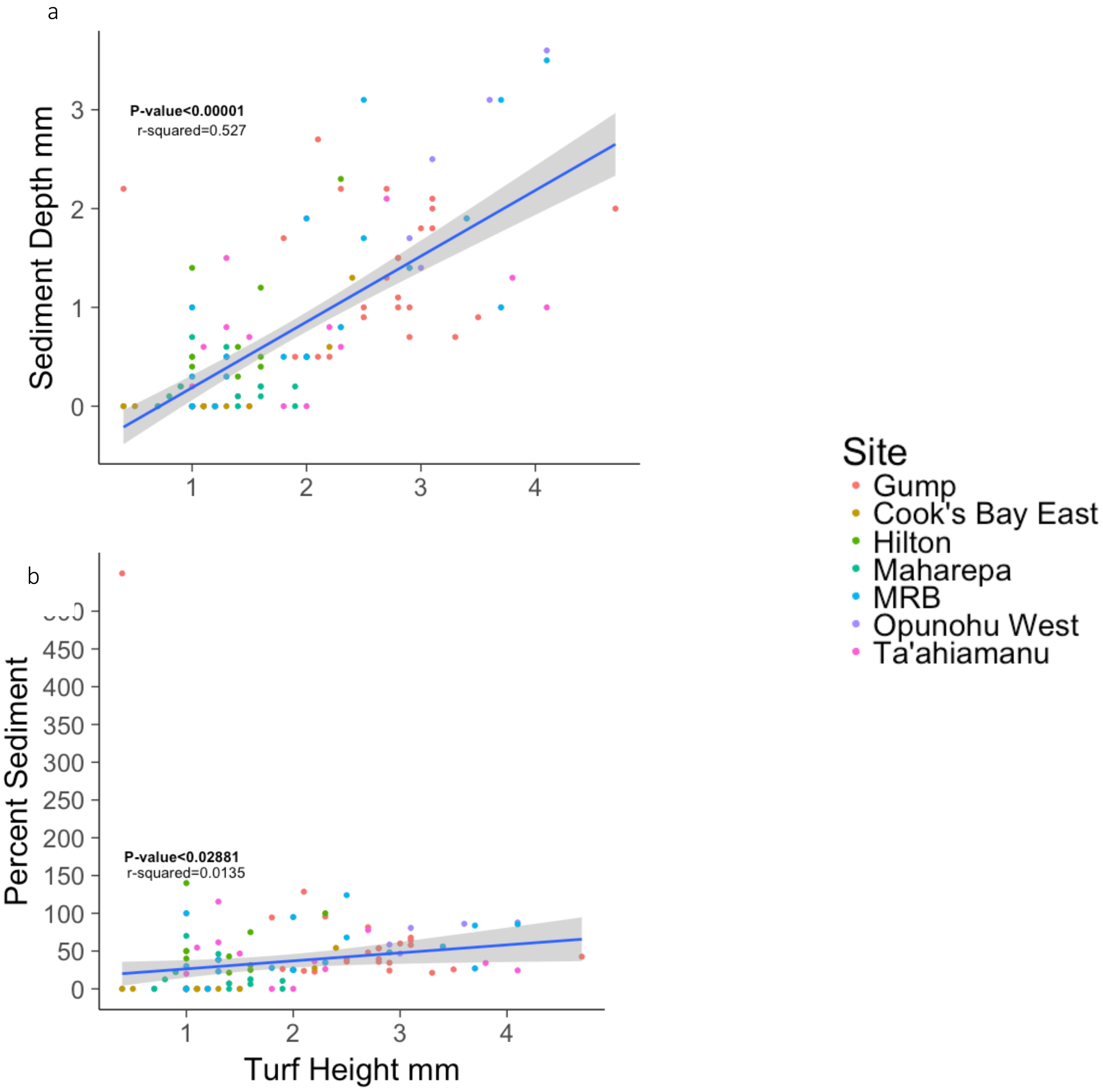

Fig 2.3: a) Simple linear regression between turf height and sediment depth across all sites. Gray area represents 95% confidence interval surrounding the linear model. b) Linear regression between turf height and the proportion of turf height occupied by sediment. Gray area represents 95% confidence interval surrounding the linear model.

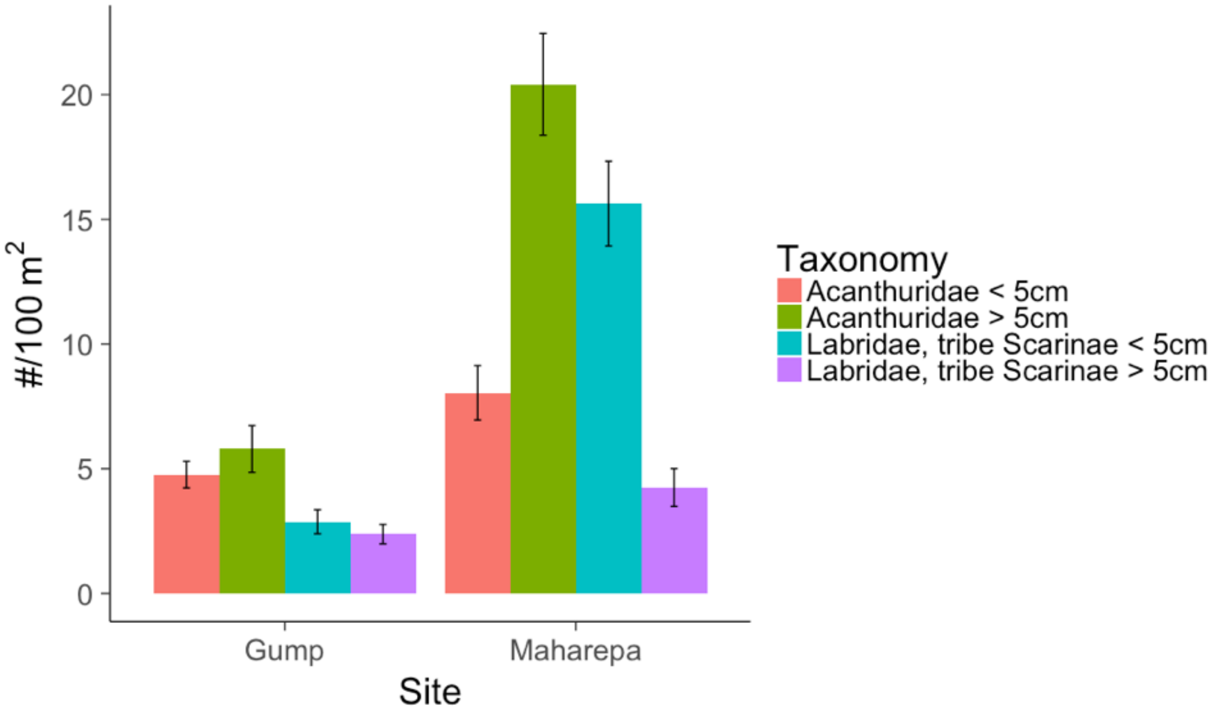

Fig 2.4: Mean number of herbivorous fish per 100m$^2$. Black bars represent standard error.

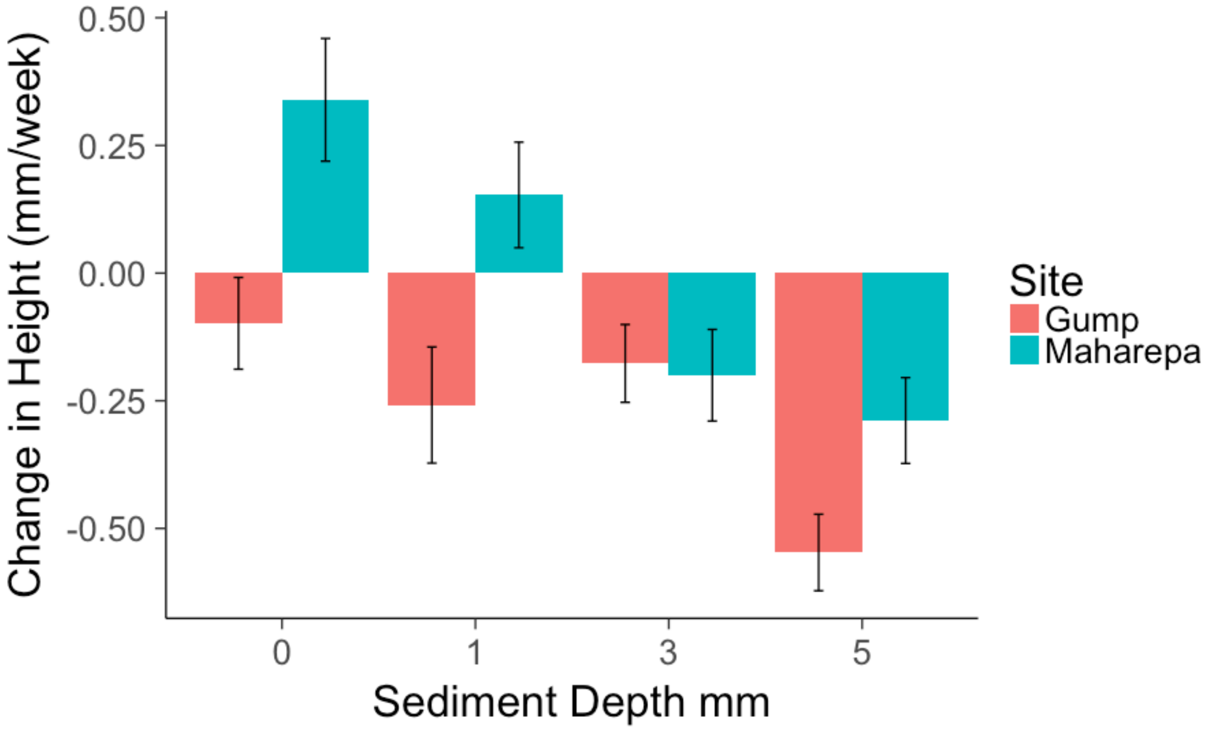

Fig 2.5: Mean change in filament height per week at each site by sediment treatment. Bars are means ± SE. Letters represent Tukey Post-Hoc designations of similar treatments at each site.

Table 2.1: Results from permutational ANOVA on sediment depth and turf height among survey sites. Bolded values are significant.

| | Df | SumSq | MeanSq | F value | Pr(>F) |
|---|---|---|---|---|---|
| **Sediment Depth** | | | | | |
| Site | 6 | 35.30 | 5.884 | 11.82 | **<0.000001** |
| Residuals | 138 | 68.67 | 0.498 | | |
| **Turf Height** | | | | | |
| Site | 6 | 47.18 | 7.863 | 14.05 | **<0.000001** |
| Residuals | 138 | 77.25 | 0.560 | | |

Table 2.2: Results from MANOVA for count of fish by grouping, between sites. Bolded values are significant

| | Value | Exact F | NumDF | DenDF | Pr (> F) |
|---|---|---|---|---|---|
| Whole Model | 1.275199 | 24.5476 | 4 | 77 | **<0.001** |
| Intercept | 4.1160306 | 79.2336 | 4 | 77 | **<0.001** |
| Site | 1.275199 | 24.5476 | 4 | 77 | **<0.001** |

Table 2.3: Results from a Two-Way ANOVA on change in turf height in mm/week between sites and among treatments. Bolded values are significant

| | Df | Sum Sq | Mean Sqq | F value | Pr(>F) |
|---|---|---|---|---|---|
| Sediment Treatment | 3 | 3.098 | 1.0327 | 11.371 | **<0.000001** |
| Site | 1 | 1.469 | 1.4692 | 16.179 | **<0.0001** |
| Sediment Treatment : Site | 3 | 0.670 | 0.2235 | 2.461 | 0.06951 |
| Residuals | 72 | 6.538 | 0.0908 | | |

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# Chapter 3:

## Can sea urchins rise to the occasion? Assessing the capacity for functional redundancy among herbivore guilds on coral reefs subject to shifting environmental contexts

## Abstract

The importance of herbivorous fishes in maintaining coral reef health has been globally established. While overfishing is impacting reefs worldwide, it is unknown whether urchin grazing compensates for overfishing on tropical Pacific reefs, and particularly on reefs subjected to multiple human stressors. We conducted a two-factor field experiment varying access to urchins (+/-) and sedimentation (ambient, +3mm marine, +3mm mixed terrestrial and marine) on algal turf communities on an overfished coral reef in Mo'orea, French Polynesia. Urchins maintained shorter algal turf, prevented accumulation of natural sediments, and removed added sediments. In contrast, turf height increased in the absence of urchins, especially after the addition of marine sediments, possibly due to increased nutrients supplied by sediments. However, mixed terrestrial sediments did not enhance turf growth. The results of this study demonstrate that urchins contribute to the maintenance of healthy turf in the Pacific, and may generally play an important compensatory role on overfished coral reefs through grazing and removing sediment, potentially promoting coral reef resilience.

# Introduction

Ecological communities are experiencing the loss of key ecosystem functions worldwide due to anthropogenic removals of major functional guilds (Laliberté et al., 2010;Rosenfeld 2002). When species that perform key functions are removed from communities, ecosystem changes can be dramatic. For example, mammal poaching in tropical forests decreases seed dispersal, leading to less diverse forests (Wang & Smith 2002; Wunderle 1997). Large-scale reductions in crustaceans in acidified lakes leads to detritus accumulation, slowing nutrient cycling and availability (Hořická et al., 2006).

However, high functional overlap among species can increase ecosystem resilience (Holling 1973), which includes both resistance, or the ability to maintain ecosystem structure and function under disturbance, and recovery, or the ability of an ecosystem to return to its original structure and function after disturbance (Suding et al., 2008; Hooper et al., 2005; Elmqvist et al., 2001; Walker 1992). For example, sister species of flying foxes were found to be functionally redundant seed dispersers when a cyclone removed one species (Elmqvist et al., 2001;Pierson et al., 1996). Very different species can also be functionally redundant; for example, beetles were able to maintain seed dispersal functions in a tropical rain forest when poaching decreased mammal abundances (Wright et al., 2000). Whether integral ecological functions are lost or maintained within ecosystems subject to species removal is of key importance; thus, it is imperative to explore the capacity of different species or guilds to compensate for the loss of others that share functional roles.

Anthropogenic shifts in environmental drivers can affect the ability of one species or guild to compensate for the loss of others (Elmqvist et al., 2003); however, if there is enough response diversity to environmental stressors within a functional group, this may provide a buffer to loss of ecosystem functions (Nyström 2006). When there is a high range of response diversity among members of the same guild, ecosystems are more resilient to disturbances and are less likely to lose key functional capacity. While many organisms respond strongly to environmental stressors in freshwater (Jackson et al., 2016), marine (Gunderson et al., 2016), and terrestrial (Munn & Maarouf 2005) ecosystems, it is still an open question how such stressors may impact ecosystem function. Some evidence suggests temporal variation in environmental conditions can drive different guilds to perform the same ecosystem function, but under different environmental contexts. For example, variation in pH and pollution regimes can cause abundances of detritivorous stoneflies and crustaceans in freshwater systems to alternate, as crustaceans have a low tolerance for acidic pH and stoneflies a low tolerance for pollution. These two guilds are functionally redundant, with high response diversity, as alternation in their abundance under changing environmental conditions did not change the overall function of detritus cycling (Dangles & Guérold, 1999). As many communities are experiencing shifts in multiple environmental and biotic factors (Côté et al., 2016;Crain et al., 2008), studies that focus on the interaction between functional redundancy, response diversity, and environmental context are imperative.

Herbivory is a strong and well-established ecological force supporting the resilience of coral reefs (e.g., Nyström et al.,2008;Hughes et al., 2007;Jackson et al., 2001) and multiple guilds of herbivores support this ecosystem function, including herbivorous fishes and a suite of grazing invertebrates (Nash et al., 2016;Carpenter, 1986). Herbivorous fishes are critical in supporting healthy coral reefs, as they consume algae that can compete directly and indirectly with coral

(Smith et al., 2006; McCook et al., 2001;McCook1999;). Fish herbivory is especially important on Pacific reefs (Nyström et al.,2008;Hughes et al., 2007) where fish provide the majority of grazing pressure on algae (Rasher et al., 2012; Hughes et al., 2007). However, in the Pacific, the role of other herbivorous guilds, such as sea urchins (hereafter urchins), is less well known.

The first documented case of urchins compensating for reduced fish populations due to overfishing occurred on Caribbean coral reefs (Mumby et al.,2007;Hughes, 1994; Lessios 1988). This compensatory role, however, was only discovered after the mass mortality of urchins, which released algae from top-down control, resulting in rapid algal growth (Lessios 1988). Subsequent work on Caribbean reefs showed a negative relationship between algal and urchin abundances (Edmunds & Carpenter 2001), that urchins could remove more algal biomass than fish (Carpenter 1986), and that urchins were the dominant grazers on Belizean reefs (Brown-Saracino et al.,2006) reefs. With many reefs impacted by overfishing (Bellwood et al., 2004), documented cases of urchins replacing fish as the dominant grazer are also increasing in the Pacific (Graham et. al, 2017). However, high urchin abundances have negative effects as well, such as eroding reef structure and reducing rugosity and available niche spaces for fishes and crustaceans (McClanahan 1994;Bak,1990). With many reefs facing reductions in herbivores (Rasher et al., 2012; Hughes et al., 2007), sea urchin grazing may become a more dominant component of coral reefs, necessitating research on the ability of urchin to maintain reef resilience.

While fish herbivory can be reduced through loss of herbivorous fish populations (Nyström, Graham, Lokrantz, & Norström, 2008), herbivory can also be reduced through abiotic processes. In particular, influxes of sediments significantly reduce fish herbivory as sediment accumulation on algae makes it less palatable (e.g., Bellwood & Fulton 2008). However, since sediment makes up a significant portion of the stomach contents of some Pacific urchins (McClanahan & Muthiga 2006), it is likely that sediment does not deter herbivory by these consumers. Overall, altered sediment regimes due to increasing precipitation and land-usage can threaten the health and stability of coastal marine ecosystems (Bainbridge et al., 2018; Scavia et al., 2002). Increased sedimentation rates are known to negatively impact corals (Pait et al., 2018;Rogers, 1990) but have a more complex relationship with algae as sediments can bring nutrients to these oligotrophic communities (Gorgula & Connell, 2004), but can also block light and harbor anoxia-inducing bacteria (Clausing et al., 2014). While the ability of urchins to compensate for reduced fish herbivory due to overfishing in reef ecosystems like the Caribbean has been well established, it is unclear if urchins can also compensate for reduced herbivory resulting from environmental stressors like increased sedimentation. What is remains unknown is whether urchins are also deterred by sediments, or if there is sufficient response diversity to this stressor for urchins to continue to fulfill the herbivory function on reefs.

In this study we test whether urchins are functionally redundant with herbivorous fishes on an overfished reef of the South Pacific, and whether their ability to compensate for loss of fishes is affected by shifts in sediment regimes. Specifically, we 1) evaluate the strength of top-down controls exerted by grazing urchins on algal turf communities in a site with relatively low abundances of herbivorous fishes, 2) determine whether accumulation of sediment (marine and terrestrial) on algal turf communities reduces urchin grazing, and 3) explore possible feedbacks between urchin grazing and sediment accumulation.

# Methods

## Site Description and Characterization

We conducted our study on the north shore of Mo’orea, a French Polynesian island located approximately 11 km northwest of Tahiti in the South Pacific. Our study site was conducted at Gump Reef (17.533$^{o}$ S, 149.833$^{o}$ W), a shallow fringing patch reef adjacent to the UC Berkeley Richard Gump South Pacific Research Station. This reef lies within Cook’s Bay, one of the two northern bays along which a large proportion of the human population lives. Along with many reefs of Mo’orea, Gump Reef was impacted by an outbreak of the coralivorous sea star *Acanthaster planci* that caused widespread coral mortality in Mo’orea (Holbrook et al, 2018); this reef is currently characterized by low live coral cover and many dead coral heads interspersed with sand patches at 1-1.5 m depth and covered in turf and macroalgae (Clausing, Bittick, Fong, & Fong, 2016). Although Gump is a no-take Marine Protected Area, there are relatively low fish abundances, likely due to poor water quality due to agricultural activity that causes inputs of nutrients and sediments to Cook’s Bay (Gaynus 2019;Clausing & Fong 2016).

To characterize the grazing community on this reef, we surveyed both herbivorous fishes and urchins. We quantified herbivorous fish communities on snorkel using underwater visual censuses (e.g. Colton & Swearer, 2010;Brock, 1954) along 2m x 50m belt transects (100m$^2$) randomly located within the study site. After deploying the transect, we waited 5 minutes before swimming along and counting fish to allow fish time to resume normal behavior. We counted and identified all fish in the families Acanthuridae, Kyphosidae, Siganidae (Clausing, et al., 2014; Keeley et al.,2015), and the family Labridae, tribe Scarinae. We did not estimate sizes of fishes; however we observed that the majority of fish on Gump Reef are small, with most less than

15cm as is true on other fringing reefs in Mo’orea (Adam et al. 2011). We conducted all fish surveys between 10am-2pm during June and July of 2017, and the same individual conducted all surveys to eliminate inter-observer variability. To contextualize these surveys, we compared these data to long-term monitoring data showing patterns in fish abundance on the other reef types of Mo’orea compiled by the Mo’orea Coral Reef Long Term Ecological Research Program (hereafter LTER) (Brooks MCR LTER 2017 & Carpenter MCR LTER 2017). Reef communities (organism diversity and benthic habitat) are extremely variable around the island of Mo’orea, both among sites and within habitats in a particular site, so we chose the closest location, LTER 1 (17.486 ° S, 149.845 ° W), which was comprised of three habitat types: fringing, back, and outer reefs. After meeting assumptions, a one-way Analysis of Variance (ANOVA) followed by a Tukey’s honestly significant difference (HSD) post-hoc test was used to analyze differences in total fish abundance data (No./100m$^2$) among all habitat types with data collected at Gump Reef.

To quantify urchin density, we counted all urchins encountered within 0.25 m$^2$ quadrats (N=29) placed on randomly selected dead coral heads along a 50 m transect within our study location. If the random point selected was within a sandflat, urchins were counted on the closest dead coral head within a circle of 0.5 m diameter. To ensure we counted urchins along the sides and bases of dead coral heads, we used the quadrat to form a belt transect from the highest point on each dead coral head to the base and counted urchins within this belt; we then standardized abundance to 1m$^2$. To compare our study site to other Mo’orean reefs, we used data collected at LTER site 1, which included the same three habitat types as in our analysis of fish abundance. We compared average urchin abundance data collected in 2017 in these 3 habitat types at LTER site 1 to average urchin abundances at Gump reef during our study. After meeting all assumptions, data were analyzed using a one-way ANOVA, with site as a factor.

### Field Experiment Testing the Effects of Urchins and Sediments

To determine the impacts of urchins and sediment on herbivory, we conducted a fully-crossed two-factor field experiment where grazing by urchins (present, absent) and sediment deposition (3 levels: ambient, addition of marine sediments, and addition of a terrestrial/marine mixture) were manipulated on experimental plots over three weeks spanning June and July of 2017. This design resulted in 6 treatments, each replicated 10 times for 60 total plots.

To limit variability caused by non-manipulated factors, all experimental plots were placed on naturally occurring turf communities found on the tops of dead coral heads, which were selected based on three criteria. First, to limit variation generated by depth gradients (as discussed by Wellington, 1982), all plots were between 1-1.5 m depth. Second, because turf-farming damselfish impact turf within their territory (Klumpp, & Polunin, 1989; Ferreira et al.,1998), we excluded dead coral heads with damselfish territories. Third, all plots were placed within 10 cm of at least one visible urchin hole, typically found within an eroded crevice of the dead coral heads. Each plot comprised a 10 cm x 10 cm area (100 cm$^2$).

Prior to initiating the experiment, we characterized initial height of the algal turf community and its associated sediment depth in each plot to establish a baseline. We used a measuring device made of galvanized mesh shaped like a comb with teeth calibrated in 1mm increments up to 7mm. In each plot, we measure 10 turf heights and sediment depths by placing our measuring device next to a turf filament and turf height or sediment depth was recorded to the nearest 0.5 mm. The mean for all measurements within one plot (n=10) was calculated and each plot served as a replicate (N=60).

To manipulate urchin presence/absence, we constructed urchin exclusion cages (*sensu* Carpenter, 1986) by creating a 4cm tall cube that ringed each plot with open tops and bottoms. We constructed cages from galvanized mesh with 1 cm x 1 cm openings and included a 3 cm outwardly curving horizontal skirt at the top and bottom of each cage. We used this caging material in our experiment because it produced limited cage effects in previous experiments (Clausing et al., 2014). We contoured the bottom of each skirt along the dead coral head surface to prevent entry by urchins under the cage bottom, while allowing access to herbivorous fish. The top horizontal skirt prevented urchins from entering cages from the top following Carpenter (1986). Cages that allowed urchin access were identical, but had only 3 sides, with the open side facing the nearest urchin hole.

All cages were open to allow for grazing by herbivorous fishes. Fish grazing in cages of similar design was confirmed to be no different than grazing in open plots by previous studies on another Mo'orean fringing reef (Fong et al., 2015;Clausing et al., 2014), and our cages were 2 cm shorter than in this study. To confirm that our cages did not deter fish herbivory, in May of 2019 we deployed identical cages and watched or videotaped cages and nearby open areas of the same size. We counted herbivorous fishes entering cages/open plots and counted the number of bites of turf take for 15 one hour periods for open and urchin exclusion plots. T-tests confirmed no differences between either mean number of fishes entering each plot type (grand mean 9.5 fish entering per hour ± 1.6 SE, N=30) or number of bites (grand mean 32.1 bites per hour ± 11.5 SE, N=30).

We also spent over 200 hours observing our plots to confirm that our cages did not act as refuges from predators for urchins. Urchins were never found grazing in urchin access cages during the day. Rather, their foraging behavior was confined to night time, as described in another study conducted in Mo'orea (Mills et al., 2000). We also did not observe urchins to congregate in cages compared to outside cages during the night.

Our three experimental sediment treatments modeled present conditions (ambient sediments), increased sediment deposition by resuspension of marine sediment (additions of 3mm of 100% marine sediment), and increased influx of terrestrial sediment (additions of 3mm of a mixture of 80% marine sediment and 20% riverine sediment). To ensure sediment additions were as natural as possible, we collected marine sediments at Gump Reef within 50m of our site and riverine sediment from a stream at the head of Cook's Bay (17.507131$^o$ S, 149.821629$^o$ W) that is the main source of freshwater and terrestrial sediment entering the bay. Sediments at Gump reef were of 43% sand, 18% clay and 39% silt and had an average organic content of 2.24% (± 0.05 SE) (Clausing et al. 2014).

We created the terrestrial/marine sediment mixture by adding one-part riverine sediment to four parts of Gump sediment (by volume). To apply sediment treatments, sediments of both types were placed in Ziploc bags with one corner cut; these acted as piping bags used to apply sediments to our plots. Sediments were applied to plots to a height of 3mm and reapplied on average every four days, which is based off previous work where 5 day reapplications consistently maintained sediment treatments (Clausing et al, 2014; Fulton & Bellwood 2008;Kendrick 1991)

We continued our treatments for 21 days, and then re-measured sediment depths and turf heights to calculate change from initial values. Because turf height and sediment depth data were normally distributed and variances were homogeneous, we used a two-way ANOVA to determine treatment effects and interactions. However, we did not include ambient sediment treatment data in the sediment depth ANOVA because it was not reasonable to test for differences in depths among treatments designed to be different. Thus, we only compared sediment depths with ANOVA in treatments where we added 3mm of the different sediment types. Sediment depths in ambient sediment plots were compared with a t-test between +/- urchin treatments.

## Results

### Site Characterization

Total herbivorous fish abundances were 46-59% lower on Gump reef compared to LTER 1 fringing, back and outer reef sites (one-way ANOVA, p<0.0001). On Gump reef, herbivorous fishes of the family Labridae, tribe Scarinae were the most visually abundant, followed by Acanthuridae and Siganidae (Fig. 1a).

There were significant differences in urchin abundances between sites (one-way ANOVA, p<0.0001) (Fig. 1b). At Gump reef, the abundance of urchins was more than 3-fold higher compared to the back and fringing reefs and an order of magnitude higher than on the outer reef. *E. mathaei* was the dominant species of urchin at Gump Reef as well as in both the fringing and back reef habitats in LTER 1 during 2017.

### Field Experiment Testing the Effects of Urchins and Sediments

Initial turf height was extremely variable within a given plot, ranging from 0 to 4mm; average initial turf height within our plots was 1.2mm (±0.5mm SE). At the beginning of the experiment, sediment made up 50% of the initial turf algae's vertical profile, with average sediment depth of 0.6mm (±0.4mm SE).

Urchins had a strong negative effect on turf height (Table 3.1, Fig. 3.2). Overall, turf height increased across all treatments, with average growth ranging from 0mm to almost 2mm. Turf growth averaged 174% in the absence of urchins compared to an average increase of 83% in their presence. There was also a nonsignificant trend between sediment treatment and increased average turf height. Average turf height increased by 0.7mm (±0.25 SE) in ambient sediment treatments, 1.3mm (0.3± SE) in 100% marine sediment additions, and 1.2mm (0.36± SE) with mixed sediment additions. The largest difference between + and - urchin treatments occurred in the ambient sediment treatment, suggesting urchin reduction of turf height is most effective under ambient sediment treatments. However, results from ANOVA showed no significant interaction between sediment and urchin treatments.

Sediment was lost in all of the sediment addition treatments in the 4 days after addition; however, sediments remained deeper with experimental additions than when allowed to accumulate naturally (Fig. 3.3). The presence of urchins prevented sediment accumulation in the no sediment addition treatments, keeping it approximately at initial levels, and reduced sediment on experimental addition plots (Table 3.2). Urchins significantly reduced sediment accumulation by about 50% in the naturally accumulating treatments (t-test, p =0.00736). Similarly, with urchins plots retained only 45-59% of total sediment added sediment over a 4-day period, while plots without urchins retained 65-83% over the same time period. Sediment loss was higher in sediment treatments with marine/terrestrial components than in treatments with all marine sediment treatments, although this effect was not statistically significant.

# Discussion

Our results show that sea urchins play a critical role in reducing algal abundance, providing functional redundancy that may compensate for loss of ecological function associated with reduced herbivorous fish populations (Bellwood & Fulton, 2008;Nyström et al., 2008; Hughes et al., 2007). Moreover, this functional redundancy was maintained under elevated sedimentation, conditions that can reduce fish herbivory (Bellwood & Fulton, 2008). Thus, urchins had sufficient response diversity to the environmental stress of sedimentation that they could maintain grazing under conditions that would inhibit fishes. Combined with studies from the Caribbean (Carpenter 1985, 1986, & 1989), these results suggest that urchins likely provide functional redundancy broadly across coral reef ecosystems, preventing the complete loss of ecosystem function under biotic and abiotic conditions that typically reduce herbivory and disrupt the balance between algae and coral in tropical marine ecosystems.

Not only did urchins compensate for reduced fish herbivory, but this grazing also significantly reduced sediment accumulation on algal turf. Given that sediment accumulation on turf algae reduces fish herbivory (Bellwood & Fulton, 2008), the sediment clearing resulting from urchin grazing should facilitate increased fish herbivory. Thus, urchin herbivory may play both a compensatory and facilitative role in maintaining herbivory on coral reefs.

## Urchins and Functional Redundancy

Due to the top-down pressures they exert on algal communities, a great deal of attention has focused on the importance of herbivorous fishes on coral reefs (Nyström et al.,2008;Hughes et al., 2007;). Through "natural experiments" resulting from overfishing in the Caribbean

(Carpenter 1985, 1986, & 1989) as well as controlled field experiments around the globe (e.g., Fong et al., 2018;Muthukrishnan & Fong 2014), results have consistently shown that herbivorous fishes play a vital role in maintaining healthy algal communities on coral reefs. These studies have resulted in a dominant paradigm that fishes are the most important grazers on coral reefs (Adam, et al., 2014; Burkepile & Hay, 2008; Hughes, et al., 2007;Jackson, et al., 2001). However, the results of this study combined with previous work in Kenya (Carriero-Silva, & McClanahan, 2001), Belize (Brown-Saracino et al., 2006) and the other parts of the Caribbean (Lewis & Wainwright 1985; Carpenter1989) demonstrate that urchins are also providing a significant grazing function on coral reefs, particularly in ecosystems with depleted populations of herbivorous fish.

Although large herbivorous fishes of the families Acanthuridae, Siganidae and Labridae, tribe Scarinae, clearly play an important role in maintaining low algal abundance on the reefs of the Pacific Ocean (Hughes, et al., 2007; Bellwood et al., 2004;Jackson, et al., 2001), fishing is substantially reducing herbivorous reef fish populations around the globe (Edwards et al., 2014), potentially compromising ecosystem function. This study suggests that if overfishing continues to occur, urchins may be able to compensate, fulfilling at least a portion of this lost herbivory function, much like urchins did on Caribbean coral reefs prior to the mass urchin die-off of the 1980's.

Past research on functional redundancy of coral reef herbivores has largely focused on functional redundancies among different species of herbivorous fish (Burkepile & Hay 2008;Bellwood et al., 2003), rarely considering other grazers (but see Carpenter 1989). Some recent studies of functional redundancy of herbivory on coral reefs focus not on species, but life stages, demonstrating the role of smaller juvenile fishes in reducing algal proliferation through intense grazing (Cernohorsky et al.,2015). Additional examples of grazer overlap in marine ecosystems comes from seagrass communities, where different species of crustaceans removed comparable epiphyte loads (Duffy et al.,2001). Taken together, these results highlight how diverse grazer communities may provide functional redundancy on coral reefs, contributing to overall reef resilience, much like functional redundancy maintains critical ecological processes in terrestrial communities, (Wright et al., 2000; Elmqvist et al., 2003;Pierson et al.,1996).

## Response Diversity Facilitates Compensation Across Stressors

Ecological control of algae on coral reefs can be disrupted through a diversity of stressors, including processes that negatively impact grazing (e.g. reduction of herbivore populations or increased sedimentation; Hughes et al. 2007), and/or processes that positively impact algal growth (e.g. eutrophication; Fabricius, 2005). Our results suggest environmental conditions that reduce functionality in one guild may not affect the functionality in the redundant guild as strongly. Specifically, while fish herbivory is negatively impacted by increased sediments (Bellwood & Fulton 2008), results of our study showed that urchin grazing was only weakly deterred by sediments—rather, urchins actively removed sediments. Evidence from other ecosystems also suggests that response diversity to differing environmental contexts can affect the relative roles of functionally redundant guilds. For example, environmental drivers had differential effects on two guilds of detritivores in rivers (Dangles & Guérold 1999), and this determined which redundant guild fulfilled the ecosystem function of detritivory. Bacterial and fungal communities also exhibited similar role-shifts, with pH dictating what community fulfilled the primary role in carbon remineralization (Rousk et al.,2009).

In the context of our study, removal of sediment by urchins may be especially important as added sediments had an overall positive, albeit weak, effect on algal turf growth. Sediments have a nonlinear relationship with algal turf fitness. At certain levels, sediments increase algal growth by increasing nutrient availability (Fabricius, 2005;Rogers, 1990). However, thicker sediment layers can induce anoxic zones within the algal turfs reducing algal growth (Clausing et al., 2014). Thus, not only might urchin presence maintain grazing function despite sedimentation and reduced fish herbivory, it may also reduce growth potential by removing nutrients supplied through sediment.

## Urchins as Facilitators of Herbivory

While urchin grazing provides functional redundancy on coral reefs, compensating for reduced herbivory associated with diminished fish populations, results also showed that urchins likely facilitate herbivory of fish that are still present. That urchins remove sediment from algal turf through grazing could be a net positive for reef resilience as decreased sediment can make turf more palatable to herbivorous fishes (Bellwood & Fulton, 2008). Thus, removal or reduction of sediment from algal turf may increase fish grazing, further reducing net algal growth. Given that reef communities are increasingly impacted by multiple environmental stressors ( Côté et al., 2016; Crain et al., 2008), if urchins truly facilitate increased fish herbivory, this process could provide an additional critical buffer in maintaining healthy coral reef ecosystems.

## The Potential for Long Term Consequences

While urchins demonstrated the capacity to fulfill a critical functional role on overfished reefs, with a response diversity to increased sedimentation that may facilitate fish herbivory, their compensatory role may not be without costs. Urchins are not just grazers, but bioeroders (McClanahan & Muthiga 2006) that can reduce reef structural complexity (McClanahan 1994). In extreme cases, bioerosion can exceed reef accretion, raising doubt about reef viability over the long term, as in the Galapagos (Reaka-Kudla et al., 1996). Further, while urchin herbivory may be little affected by sediments in the short term, others have found that sediment-laden turf reduces urchin recruitment (Dumas et al., 2007), casting doubt on the sustainability of urchins to compensating for fish herbivory.

As ecological communities worldwide face degradation, it is imperative to better understand how these shifts in community dynamics and environmental contexts impact the functional redundancy of different guilds. The loss of dominant guilds that perform critical ecosystem functions is unlikely to end. Rather, these losses are projected to increase (for a review see Hooper et al., 2012), necessitating more research on how other guilds may compensate, providing functional redundancy to maintain “healthy” communities. In the case of a continuously changing coral reef community, these functions must be studied in conjunction with shifting environmental factors, as we know that many reefs are experiencing multiple environmental and biotic alterations. Only through such integrative approaches will we understand how multiple stressors are impacting these vital ecosystems, providing critical insights for their sustainable management.

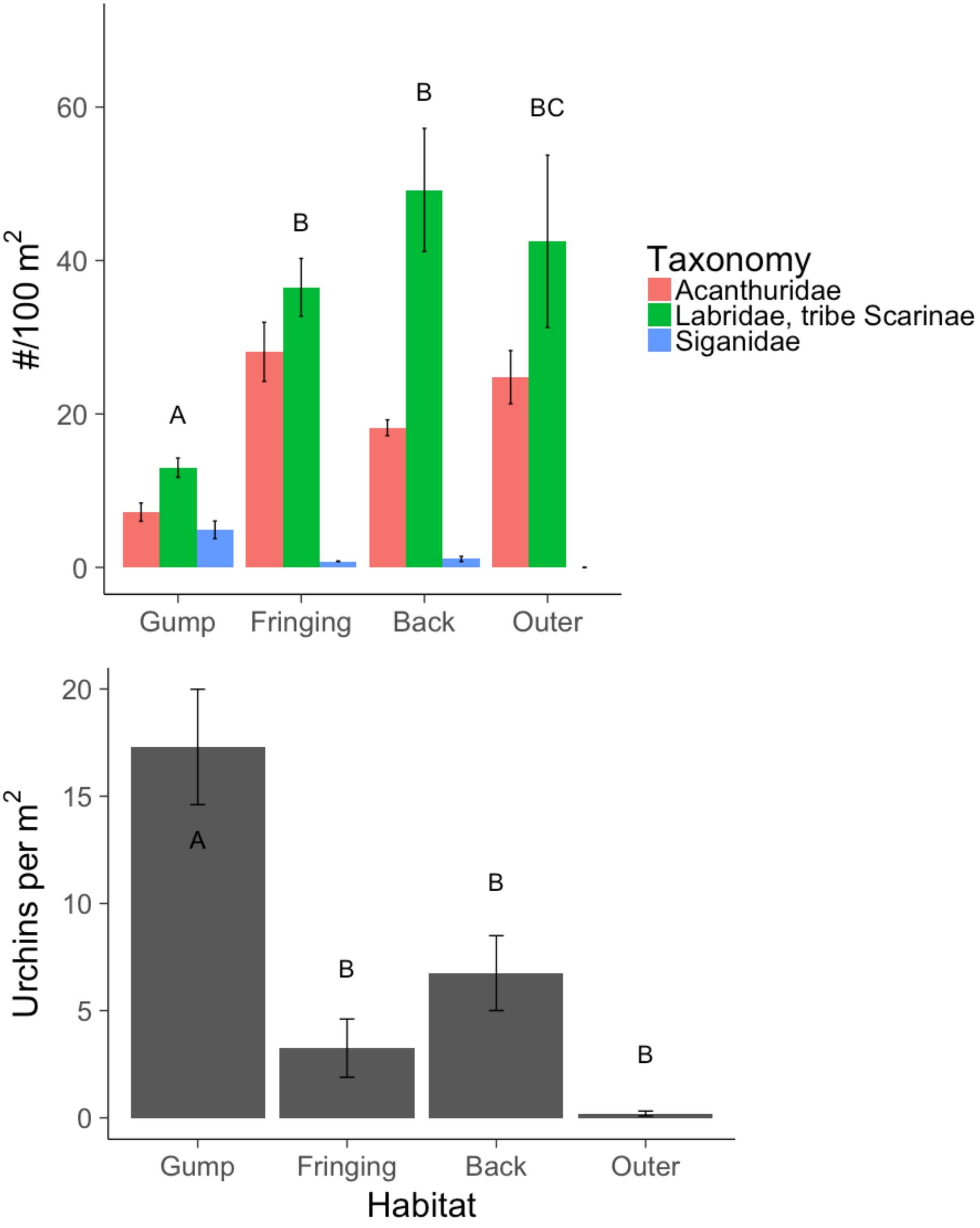

Fig 3.1: Comparison of a) mean herbivorous fish by Family and b) urchin abundances in 2017 at our study site (Gump), and all 3 LTER 1 habitats (Back, Fringing and Outer Reefs). Bar are means ± SE. Letters above bars are from Tukey's post-hoc test assignments based on total fish and urchin abundances. Bars sharing the same letter are not significantly different.

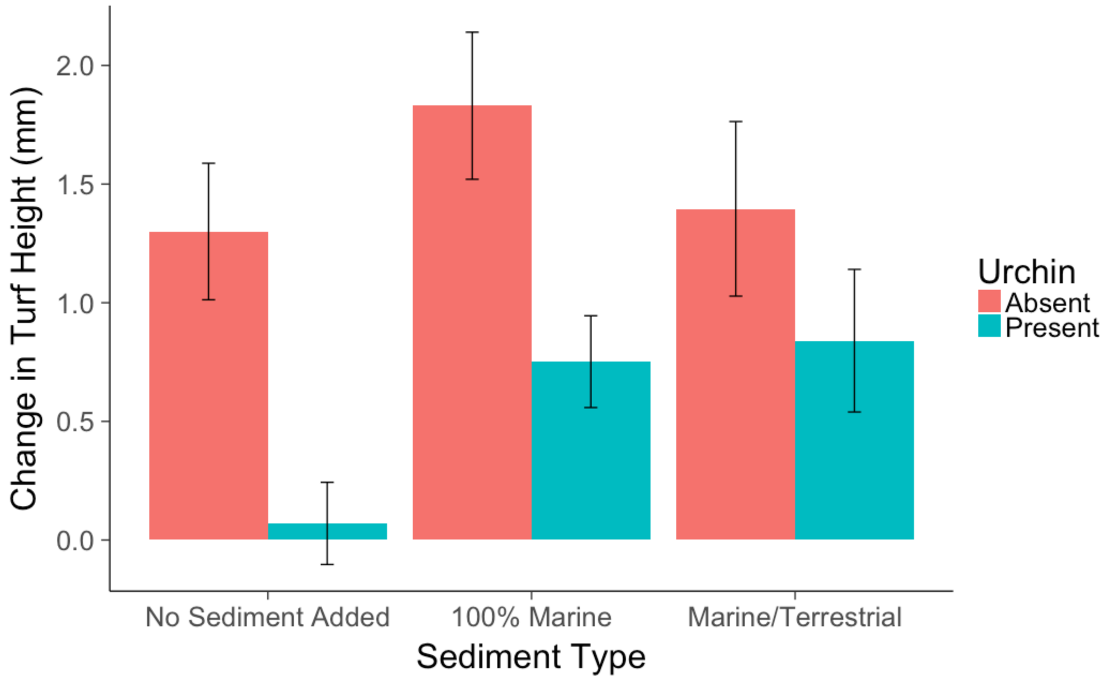

Fig 3.2: Average difference (mm) from initial turf height by treatment after 21 days. Bars are means ± SE.

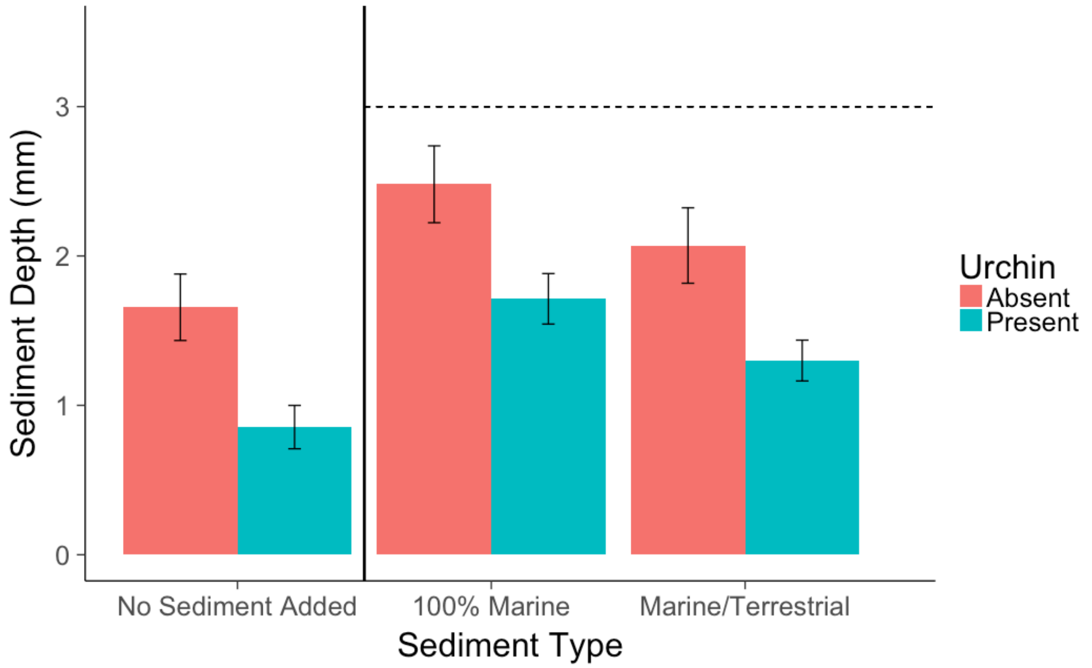

Fig 3.3: Final sediment depth 3 days after application. The dotted line represents the depth of sediment added to plots with sediment additions. Bars are means ± SE.

Table 3.1: Results from Two-Way ANOVA on change turf height after 21 days.

| | DF | Sum Sq | Mean Sq | F value | Pr(>F) |
|---|---|---|---|---|---|
| Sediment | 2 | 2.928482 | 1.4642407 | 3.118191 | 0.05229 |
| Urchins | 1 | 13.760074 | 13.7600741 | 29.302923 | **<0.00001** |
| Sediment: Urchins | 2 | 1.560482 | 0.7802407 | 1.661571 | 0.19940 |
| Residuals | 54 | 25.357333 | 0.4695802 | NA | NA |

Table 3.2: Results from Two-Way ANOVA of sediment retention on plots with added sediment (Mixture and Marine) 4 days after final reapplication.

| | DF | Sum Sq | Mean Sq | F value | Pr(>F) |
|---|---|---|---|---|---|
| Sediment | 1 | 1.6947 | 1.6947 | 3.8259 | 0.05826 |
| Urchins | 1 | 5.9034 | 5.9034 | 13.3273 | **0.00082** |
| Sediment: Urchins | 1 | 0.0000 | 0.0000 | 0.0001 | 0.9937 |
| Residuals | 36 | 15.9463 | 0.4430 | NA | NA |

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## My Final Thoughts

The rate at which natural systems are changing has intensified over the last four decades. Hotspots of diversity such as coral reefs and tropical rainforests are particularly susceptible to degradation spurred by human activity and climate change (Halpern 2008;Reaka-Kudla 1997;Connell 1978). Very few ecosystems, however, are immune to change, and we see documented cases of complete loss, altered habitat range, species richness, and diversity in mangroves (Cavanaugh et al., 2014), savannas (Murphy & Bowman 2012), and alpine tundra's (Wipf et al., 2009). Changes are occurring at all ecological levels, including the individual, population, community, ecosystem,& globally. In response, scientists have focused research at each level in the hopes to predict how future natural systems will look and function.

The service to space ratio for many coastal ecosystems is high (Barbier et al., 2011). Although coastal marine systems take up a small portion of our planet, we are able to extract a multitude of goods and services from them. For example, although coral reefs represent less than 0.1% of the total world's oceans, they are home to 25% of all marine life (Burke et al., 2011;Spalding et al., 2011;Knowlton 2001). Globally their loss will lead to the degradation and potential loss of fisheries worldwide (Jackson et al., 2001;Knowlton 2001). On a local scale, these diverse oases are important from an economic standpoint (ecotourism), culturally, and for food security (Bellwood et al., 2004;Ceasar et al.,2003;Moberg & Folke 1999; Wilkinson 1996). There is no doubt in the literature that reefs are being lost at an alarmingly fast rate (Hughes et al., 2017; Hughes 2007;Bellwood et al., 2004); however the mechanisms that reduce resilience and recovery, drivers of irreversible loss, are less concrete.

## Coral Reef Loss

At this moment in time, many reefs will never be able to return to a previously documented, 'healthy' state, depicted as a benthos dominated by a diverse assemblage of coral species, laying the foundation for a multitude of diverse marine organisms (Hughes et al., 2017). Threats such as less diverse herbivorous fish abundances due to overfishing (Hughes et al., 2007;Jackson 2001), fluxes in terrestrial input because of increased land-usage (Fabricus 2005; Roger 1990), increases in water temperature , and ocean acidification (Lough 2016;O Hoegh-Guldberg 2007) not only complicate recovery trajectories after large-scale disturbances (Cheal et al., 2017),but leave an abundance of open space ready for colonization by an alternate organism(Bellwood et al., 2004, Nyström et al., 2008). This, paired with long-term stressors, many induced by human activity, make it harder to predict community and population level responses (C Ô T É et al., 2016;Crain et al., 2008), all needed to forecast future reef system functionality.

## Turf and Herbivory

Turf algal communities are becoming a more conspicuous component of the coral reef benthos. Turf is often the first successional state after large scale disturbances(Gaynus Chapter 1; Smith et al., 2010; Burkepile & Hay 2009). High grazing pressure, however, is a well-known mitigator of algal growth, maintaining turf to a closely-cropped level, thereby reducing coral-algal competition (Fong & Paul 2011), all the while still providing turf functions (e.g., trophic support, nutrient cycling). Herbivorous fishes are important in mitigating algal proliferation in some reef systems (Jackson et al.,2001; Knowlton 2001), though there are alternate guild of herbivores that may perform redundant functions (Carpenter 1988; Lessios 1988;Gaynus Chapter 3). While herbivorous fishes are important, they may not all be the same when it comes to their grazing ability. Bellwood and collaborators found that a grazing function may be heavily dependent on one species (the humphead parrotfish) irrespective of counts/ biomass of other herbivore guild members (Bellwood et al., 2003). To maintain strong resiliency within a community requires not only functional redundancy, but there must be response diversity within each function (Nyström 2006;Elmqvist et al.,2003).

Herbivorous fishes are being depleted due to overfishing (Bellwood 2004; Jackson 2001), leading to a compromised grazing guild, forging a path for alternate grazing guilds to dominate this function. Caribbean reefs are a well-known example of just how strong a functionally redundant grazing community can be in reducing algae. During the 1980's many overfished Caribbean reefs remained low in algal abundance, as urchins a 'sleeping' guild member were able to exert strong grazing pressures on algae (Carpenter 1986), and it was only when their populations died-off due to disease that reefs began to transition quickly to algal dominance (Carpenter 1988;Lessois 1988). While the reduction in algae was found to be a positive, large urchin populations can reduce reef structure, leading to bioerosion (Carreiro-Silva & McClanahan 2001) that spurs biodiversity loss due to a reduction in available niches (Glynn & Manzello 2016). Herbivory is not the only function with documented compromises in redundancies and diversity (e.g., loss of coral morphology & species, reductions in zooxanthellae clades) and as human stressors intensify, secondary and tertiary members of a guild will play a stronger role in shaping coral reefs, shifting the baseline for what we as a profession consider a 'healthy' reef.

### Turf and Sediment

Changes in sediment composition, deposition and residence time lead to reductions in light, altered nutrient regimes and the smothering of organisms, reducing the fitness of many coastal organisms (Fabricus et al., 2011;Burkholder et al.,2007; Airoldi 2003;Rogers 1990). The adverse effects of these changes are particularly noted in benthic communities that are unable to remove themselves from an unsuitable environment (Ambrogi et al.,1990;Rogers 1990; Fresi et al.,1983). Among coral reefs, altered sediment regimes can undertow the proliferation of algae. The non-linear relationship between sediment and algae is highly dependent on small spatial and temporal scale differences as well as other stressors distressing the environment. For example, sediment had a continuing positive effect on naturally tall (<10mm) turf proliferation , that lasted three months even after additions ceased (Goately & Bellwood 2013). However another study, found similar to my second chapter that sediment additions may reduce turf proliferation altogether, potentially due to the anoxic bacteria transported within, and/or reducing light needed for photosynthesis due to smothering (Chapter 2;Tebbett et al., 2017). It is unclear, however if the addition of sediment leads to algal proliferation due to its release from nutrient limitation, or because herbivores are deterred from grazing by sediment, and one could argue it is neither in solitude. Complicating the relationship however is the diversity of responses herbivores have to grazing turf-laden sediment (for term definition see Bellwood & Fulton 2008). More accepted, however is that low quality sediment reduce turf palatability (Gordon et al., 2016), but species are known to respond differently (Tebbett et al ., 2018a). While sediment-laden turfs have been proposed as an alternative stable state (Goately & Bellwood 2013; Bellwood & Fulton 2008), more research must be conducted on the environmental mechanisms that regulate this community, especially as turf & sediment become more conspicuous components of reefs that are facing multiple environmental stressors.

## Ubiquity of Turf

Algal turfs are main components within subtidal and intertidal coast from temperate to tropical latitudes. Comparing associated turf algae experiments proves daunting, however, as loose definitions plague the literature and there high variability in turf described turf characteristics(Connell & Airoldi 2014).In coral reef communities, the term generally refers filamentous alga that range in length (<1mm->15cm) (Clausing et al., 2014; Bellwood & Fulton 2008), but can be comprised of a multitude of species (Harris et al., 2015), and non-alga counterparts such as invertebrates (referred to as cryptofauna in reef systems) (Kramer et al.,2012) and sediment load (Tebbett et al., 2018b). Turfs' importance as a successional stage after disturbance and threat as a coral competitor in degraded states, make it imperative to examine in more detail the characteristics associated with long sediment laden turf and healthy turf communities.

Poorly understood hidden alga diversity may prove important in understanding degraded vs healthy turf. Given that diverse alga communities have higher primary production rates ( Bruno et al., 2006 & 2005) the loss of alga diversity could compromise vital turf functions (Fong & Paul 2011). The lack of knowledge on turf diversity could serve as a cursory sign in predicting future benthic structure. As I move forward as a researcher, my research will begin to focus on understanding how hidden diversity in turf relates to the vital functions of primary production, trophic support and nutrient cycling (Fong & Paul 2011) over a range of impacted reefs.

## Diversity in nature to diversity of researchers

Researchers agree that the loss of diversity within our natural systems reduces their value. Such a broad idea is ever present in many disciplines that study natural systems. The group of people who unite, however, to study such natural diversity is rarely as diverse as the system. Being a black female, this troubles me, and it becomes even more troublesome when you are consistently reminded that the education system at all levels overwhelmingly fails black and brown students on a daily basis. Maintaining the integrity of our natural systems is a gargantuan problem that will not be solved by one. I see the space and need to involve black and brown communities, not just as researchers, but all professions tasked with studying and preserving nature. This spans a wide range and dare I say it, "leaves no one behind". Similar to the rapid negative changes occurring in nature, this problem will not be solved by one or two. There are however simple choices that can make a difference and moving forward this will become a major component of what I do as a researcher. Participating in science fairs, providing opportunities for minorities to engage in research, speaking to youth about research and how important the ocean is in their daily lives, or just simply being present in their space, open to questions and conversations are all valid ways I believe I can be apart of a larger solution. I say these words as someone who has directly benefited from targeted minority exposure to marine science, and will continue to contribute my time, my energy, and my thoughts to this cause.

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