UNIVERSITY OF CALIFORNIA, SAN DIEGO

The Ecology of Turf Algae on Coral Reefs

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

in

Marine Biology

by

Jill Lauren Harris

Committee in charge:

Professor Jennifer Smith, Chair
Professor Elsa Cleland
Professor David Holway
Professor Lisa Levin
Professor Stuart Sandin

2015

The Dissertation of Jill Lauren Harris is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Chair

University of California, San Diego

2015

DEDICATION

To my parents, Jeff and Joan, who support me in more ways than I can count.
To my sister, Janna, who is a role model in science and in life.

All three of you are really good dive and snorkel buddies.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

ACKNOWLEDGEMENTS

First and foremost, I thank my advisor, Jennifer Smith, for rigorous scientific training and for reminding me to appreciate the natural beauty that we are so fortunate to study. Jen gave me unparalleled opportunities to explore the world's coral reefs, teaching me that sticking my face in the water is often the best way to figure things out. Her love of seaweed must have deeply affected me, because somehow I ended up doing an entire dissertation on algae despite entering her lab with hopes of studying corals. And for their supportive words and scientific guidance, I owe a huge thank you to the rest of my committee Elsa Cleland, David Holway, Lisa Levin, and Stuart Sandin.

I am fortunate to be part of a big happy lab family that is full of good science and good adventure. I couldn't ask for a better group of people who erase the line between colleagues and friends. In particular, for help with data collection and always being willing to talk shop, thank you to Lindsay Bonito, Saray Dugas, Clint Edwards, Mike Fox, Kate Furby, Maggie Johnson, Emily Kelly, Susan Kram, Levi Lewis, Rachel Morrison, Nichole Price, Gareth Williams, and Brian Zgliczynski. I am grateful also for the friends I have made at SIO outside of my lab, especially Lauren Shipp, Joseph Campanale, Noelle Bowlin, Maya deVries, Christian Briseño, and Mindi Summers. You kept me sane through this all. I treasure our lady breakfasts and knitting brunches.

Thank you to many friends and colleagues at field stations and expeditions all over the world, including the Maui ohana, Palmyra Atoll, CARMABI in Curaçao, Korallionlab in the Maldives, the scientists and crew from the Northern Line Islands expedition, and the small group of seaweed loving scientists at the Jardim Botânico do Rio de Janeiro. It is a joy working alongside you.

I am thankful for the support I have received at SIO from Penny Dockry and the Center for Marine Biodiversity and Conservation, from the SIO Graduate Office, the SIO Development Office, and my funding sources, all of whom made it possible for me to get into the field and focus on my research.

My family is, and has always been, tremendously supportive. My grandfather, Jerry, celebrates his family's successes so much that he has travelled far and wide to attend every single one of my school graduations (I promise this is the last one!). My parents, Jeff and Joan, taught me to value education and to pursue my goals. They bought me my first set of SCUBA gear and didn't blink when I moved to the Bahamas for two years. My sister, Janna, has taught me many big sisterly things, not the least of which was paving the way as a PhD scientist and showing me that it can be done. Finally, I owe much to my fiancé Ed Vul. His love and support make all the difference in my life. I value his guidance on ideas great and small, personal and professional. I swear I am not using him for his technical expertise, but I certainly appreciate it.

Chapter 1, in part, is currently being prepared for submission for publication of the material. Harris, Jill and Jennifer Smith. "Tropical algal turfs: a review of their ecology and a framework for their analysis." The dissertation author was the principal researcher and author of this material.

Chapter 2, in full, is a reprint of the material as it appears in the Marine Ecology Progress Series 2015. Harris, Jill L., Levi S. Lewis, and Jennifer E Smith. The dissertation author was the principal researcher and author of this material.

Chapter 3, in part, is currently being prepared for submission for publication of the material. Harris, Jill, Lindsay Bonito, Maggie Johnson, Emily Kelly, and Jennifer

Smith. “An Experimental Analysis of the Context Dependent Effects of Nutrient Enrichment and Herbivore Exclusion on Coral Reef Turf Algae.” The dissertation author was the principal researcher and author of this material.

Chapter 4, in part, is currently being prepared for submission for publication of the material. Harris, Jill. “The role of small infaunal invertebrates in coral reef algal turfs.” The dissertation author was the principal researcher and author of this material.

VITA

2005	Bachelor of Arts, Dartmouth College
2009	Master of Marine Affairs, University of Washington
2015	Doctor of Philosophy, University of California, San Diego

PUBLICATIONS

Harris, JL, LS Lewis, and JE Smith. 2015. Quantifying scales of spatial variability in algal turf assemblages on coral reefs. *Marine Ecology Progress Series* 532:41-57

Barott, KL, GJ Williams, MJA Vermeij, **JL Harris**, JE Smith, FL Rohwer, and SA Sandin. 2012. Natural history of coral-algae competition across a gradient of human activity in the Line Islands. *Marine Ecology Progress Series* 460:1-2

ABSTRACT OF THE DISSERTATION

The Ecology of Turf Algae on Coral Reefs

by

Jill Lauren Harris

Doctor of Philosophy in Marine Biology

University of California, San Diego, 2015

Professor Jennifer Smith, Chair

Coral reefs are one of the most diverse and productive ecosystems on the planet. Globally, corals are declining and algae are increasing due to anthropogenic activities. While most research and conservation efforts focus on the proliferation of macroalgae, in fact most algae on coral reefs are turf algae: heterogeneous assemblages of many species of small algae. These ubiquitous and abundant algal “shag carpets” are typically overlooked or studied as a homogenous functional group. I examine characteristics that make turf algae functionally unique from other types of algae, focusing on their ecological importance as food for reef organisms, major sources of productivity, and competitors with reef-building corals. Further, I argue that turfs will become more abundant in the future because they respond positively to the many anthropogenic threats facing coral reefs, including overfishing, pollution, acidification and warming. First, I explore the spatial patterns in turf assemblages, showing that, although turfs appear visually homogenous to the naked eye, they are highly variable at the centimeter scale. This descriptive work provides a foundation for testing ecological processes that may be causing those small-scale patterns. Second, I use turf algae as a tool to demonstrate that the relative influences of top-down and bottom-up processes are context-dependent. I measured the greatest response to grazer exclusion where background herbivory was lowest, suggesting a positive feedback between the loss of herbivory and loss of resilience. Further, in contrast to high profile findings in other ecosystems, my data revealed that nutrient enrichment increased, and consumers reduced, turf diversity. Finally, I expand the traditional perspective of coral reef herbivores to include small infaunal invertebrates living in turf algae. By partitioning herbivory among fish and small invertebrates, I provide some of the first evidence that infaunal invertebrates significantly impact turf algae, but their role depends on either competition with or predation by fish. Overall, my dissertation provides a new perspective on turf algae and opportunities to test classic ecological concepts. Additionally, a better understanding of the ecology of turf algae has urgent conservation applications, including insight into how reefs of the future will function and how to best protect them.

Introduction

Coral reefs are incredibly diverse and productive, and they provide important ecosystem services such as fisheries and shoreline protection (Hatcher 1988; Moberg and Folke 1999; Knowlton et al. 2010). Globally, reefs are being lost because of human activities, and on these degraded coral reefs we see declines in coral cover along with increases in algal cover (Pandolfi et al. 2005; Jackson et al. 2014). While the shift toward more algae, and interactions between coral and algae, have received considerable research focus, that attention is focused largely on macroalgae. In fact, most algae on coral reefs are actually turf algae, which are heterogeneous assemblages of many species of small algae. Algal turfs are both ubiquitous and abundant on coral reefs, although they are typically overlooked in research and in conservation. Lumping turf algae together with macroalgae species ignores major differences in their ecology. In my dissertation, I explore the characteristics and ecological processes that make turf algae unique from macroalgae.

My dissertation begins with a synthesis of existing information about turf algae on coral reefs (Chapter 1). Using data from reefs all over the world, I argue that coral reef turf algae are ecologically important as the main food for herbivores, major sources of primary production, and the primary competitors with reef-building hard corals (Bruggemann et al. 1994; Ledlie et al. 2007; Hamilton et al. 2014). Turf algae are abundant on even the healthiest of coral reefs (Sandin et al. 2008), and I predict that turf algae will only become more abundant in the future as they benefit from the litany of anthropogenic stressors that threaten corals (Diaz-Pulido and McCook 2002; Bender et al. 2014). Turf algae are typically studied as a homogeneous functional group, but in this chapter I explain why they should be examined in greater detail. Grasslands and forests provide a helpful analogy: ecologists care not just about the spatial extent of grasses and trees, but also the density of plants, their canopy heights, and the species composition. Taking the same approach with algal turfs, I explain how each of these same characteristics informs us about ecological processes in turf algae and in the broader reef community. Finally, I present a novel framework for studying turf algae, providing a way for researchers to measure variability in turf assemblages, experimentally test processes that cause those patterns, and address potential implications of different types of turf algae for reef ecology.

One of the primary claims in Chapter 1 is that we should study turfs in greater detail than as homogenous functional group. Which details are most important, and how do they relate to specific ecological processes? A fundamental rule of ecology is that we must first understand pattern before we can investigate process (Levin 1992). In Chapter 2, I used this classical ecological perspective to improve our understanding of coral reef turf algae. By quantifying turf algae characteristics at four hierarchical spatial scales, I discovered that turfs are most variable at very small scales such that patches of turf algae separated by only a few centimeters were more different than were patches separated by meters or kilometers. Although algal turfs appear visually homogenous to the naked eye, my findings revealed that turfs are, in fact, highly heterogeneous and likely controlled by stochastic small-scale processes such as herbivory and competition. This descriptive work is an essential foundation for experimentally testing how these mechanisms scale up to determine the structure of coral reef benthos.

In particular, herbivory and nutrient availability are the two processes that exert the most control on the abundance and distribution of coral reef algae and primary producers in other marine, aquatic, and terrestrial ecosystems. The relative influences and context-dependence of top-down and bottom-up control has been tested and debated in many ecosystems – including numerous experiments in coral reefs (Burkepile and Hay 2006; Gruner et al. 2008). However, these experiments typically treat turf algae as a single response variable. Instead, in Chapter 3, I address how herbivory and nutrients influence multiple characteristics of the heterogeneous turf algae community. By replicating an experiment in three locations, I investigated how environmental context affects the relative strengths of top-down and bottom-up control. I measured the greatest response to grazer exclusion where background herbivory was lowest, suggesting a positive feedback between the loss of herbivory and loss of resilience: environments with few herbivores are likely to see rapid algal increases in response to further reduction in top-down control when additional grazers are removed, while environments with abundant herbivores will be more resilient to fluctuations in herbivory.

Chapter 4 builds upon the results from Chapter 3 by taking a more expansive view of herbivory on coral reefs to include small invertebrate grazers. Turf algae are not only important as coral competitors and food sources for fish and urchins, but also as complex, three-dimensional habitats for small invertebrates. Although small infauanal invertebrates receive little attention, recent studies suggest that they are abundant and diverse (Klumpp et al. 1988; Smith et al. 2001; Glynn and Enochs 2011). However, most research to date has focused on quantifying and identifying small invertebrates. In this chapter, I took the next step and examined their potential ecological roles as grazers and nutrient sources for turf algae. Here, I partitioned the effect of herbivory between fish/urchins and small infaunal invertebrates and present some of the first evidence that small invertebrates have a measurable impact on the abundance of turf algae on coral reefs. The effect of invertebrates depended on the presence of fish, which suggests that invertebrates are either competing with herbivorous fishes or being preyed upon by carnivores. These findings contradict several earlier studies that reported a negligible role for small invertebrates and pave the way for future experiments to directly test mechanisms.

My dissertation provides a new perspective on turf algae, which are common, but typically unexamined, components of a threatened ecosystem. This new knowledge about turfs as heterogeneous assemblages presents opportunities to test classic ecological concepts from other systems. Turf algae are global and abundant, so experiments are easily replicated. My dissertation also has urgent applications to coral reef conservation. Turf algae typically take over reefs following coral death, for example from the global bleaching event currently underway. If we want to know how reefs of the future will function, and how to best protect and restore them, then improved knowledge of the ecology of turf algae will become increasingly central to understanding, protecting, and restoring coral reefs.

References

Bender D, Diaz-Pulido G, Dove S (2014) Warming and acidification promote cyanobacterial dominance in turf algal assemblages. Mar. Ecol. Prog. Ser. 517:271–284

Bruggemann J, Kuyper M, Breeman A (1994) Comparative analysis of foraging and habitat use by the sympatric Caribbean parrotfish *Scarus vetula* and *Sparisoma viride* (Scaridae). Mar. Ecol. Prog. Ser. 112:51–66

Burkepile DE, Hay ME (2006) Herbivore vs. nutrient control of marine primary producers: context-dependent effects. Ecology 87:3128–39

Diaz-Pulido G, McCook LJ (2002) The fate of bleached corals: patterns and dynamics of algal recruitment. Mar. Ecol. Prog. Ser. 232:115–128

Glynn PW, Enochs IC (2011) Invertebrates and Their Roles in Coral Reef Ecosystems. In: Dubinsky Z., Stambler N. (eds) Coral Reefs: An Ecosystem in Transition. Springer Netherlands, Dordrecht, pp 273–325

Gruner DS, Smith JE, Seabloom EW, Sandin S a, Ngai JT, Hillebrand H, Harpole WS, Elser JJ, Cleland EE, Bracken MES, Borer ET, Bolker BM (2008) A cross-system synthesis of consumer and nutrient resource control on producer biomass. Ecol. Lett. 11:740–55

Hamilton S, Smith J, Price N, Sandin S (2014) Quantifying patterns of fish herbivory on Palmyra Atoll (USA), an uninhabited predator-dominated central Pacific coral reef. Mar. Ecol. Prog. Ser. 501:141–155

Hatcher BG (1988) Coral reef primary productivity: A beggar’s banquet. Trends Ecol. Evol. 3:106–111

Jackson JBC, Donovan MK, Cramer K, Lam V (2014) Status and trends of Caribbean coral reefs: 1970-2012. Global Coral Reef Monitoring Network, Washington, DC

Klumpp D, McKinnon A, Mundy C (1988) Motile cryptofauna of a coral reef: abundance, distribution and trophic potential. Mar. Ecol. Prog. Ser. 45:95–108

Knowlton N, Brainard RE, Fisher R, Moews M, Plaisance L, Caley MJ (2010) Coral Reef Biodiversity. In: McIntyre A.D. (eds) Life in the World’s Oceans. Blackwell Publishing Ltd., pp 65–77

Ledlie MH, Graham NAJ, Bythell JC, Wilson SK, Jennings S, Polunin NVC, Hardcastle J (2007) Phase shifts and the role of herbivory in the resilience of coral reefs. Coral Reefs 26:641–653

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73:1943–1967

Moberg F, Folke C (1999) Ecological goods and services of coral reef ecosystems. Ecol. Econ. 29:215–233

Pandolfi J, Jackson J, Baron N (2005) Are US Coral Reefs on the Slippery Slope to Slime? Science (80-.). 307:1725–26

Sandin SA, Smith JE, Demartini EE, Dinsdale E a, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder RE, Walsh S, Jackson JBC, Knowlton N, Sala E (2008) Baselines and degradation of coral reefs in the Northern Line Islands. PLoS One 3:e1548

Smith JE, Smith C, Hunter CL (2001) An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. Coral Reefs 19:332–342

Chapter 1 Tropical Algal Turfs: A Review of Their Ecology and a Framework for Their Analysis

Jill Harris and Jennifer Smith

What are turf algae?
Productive and abundant
On reefs everywhere

Abstract

Turf algae are diverse assemblages of small, mostly filamentous algae that are abundant and common on coral reefs worldwide. However, they are typically overlooked by scientists or considered only as a single homogenous functional group. Here I show that turf algae are essential to the ecological functioning of coral reef ecosystems as the primary food source for herbivores, major sources of production, and the most common competitors with reef-building corals. Further, because they respond positively to the many anthropogenic activities that threaten reefs such as overfishing, pollution, warming, and ocean acidification, I argue that turf algae will become increasingly important on the coral reefs of the future. Based on the first global meta-analysis of turf algae cover on coral reefs worldwide, I conclude that turf algae make up 39.7% of coral reefs today. Turf cover is between 20-60% in most countries, although there are many extreme examples of individual sites with < 5% or greater than 90% turf cover. Finally, I present a novel framework that provides a more detailed way to measure turf algae characteristics related to specific ecological processes such as herbivory, production, and competition.

Introduction

Turf algae are an ecologically important, abundant, and typically underappreciated component of coral reef ecosystems. In tropical marine systems, turf algae are a consortium of filamentous algae, cyanobacteria, microalgae (e.g. diatoms), and juvenile life stages or heavily cropped species of macroalgae, typically less than 2 cm tall. Here, we review the ecological roles of turf algae, arguing that they are one of the main sources of primary production on tropical coral reefs, the primary food source for most coral reef herbivores, and under certain conditions can overgrow reef-building corals and crustose coralline algae (CCA). We summarize data showing that turf algae respond positively to conditions that threaten coral health, such as frequent physical disturbances, coral bleaching and disease, overfishing of herbivores, ocean acidification, and warming. Given their widespread distribution, broad functional importance, and positive response to the many factors known to negatively affect coral reefs, we argue that turf algae are poised to play an increasingly central role in the ecological functioning of coral reef ecosystems in the future.

Turf algae can be particularly difficult to study due to the inconsistency in how researchers categorize them, their diversity in different ecosystems, and the tendency for scientists to group them together with other benthic organisms. Two common synonyms for turf algae are the ‘epilithic algal community (EAC)’ (Hatcher & Larkum 1983, McCook 1999) and ‘epilithic algal matrix (EAM)’ (Wilson et al. 2003), though the latter specifically includes invertebrates, detritus, and microbes in addition to algae. In temperate intertidal systems, algal turfs are often monospecific or dominated by articulated coralline algae that trap sand and debris. Sometimes, the term ‘turf’ actually refers to invertebrate assemblages that inhabit the turfs, not the algae themselves (Huff 2006). In this paper, the term “turf algae” specifically refers to only the algal component of the community. Some benthic studies and reef monitoring programs report cover of dead coral covered with algae, coral rubble, pavement, or the ambiguously broad “rubble” (Table 1), all of which are substrates that are almost always covered in some type of turf algae, even if sparse. Turf algae are also frequently grouped with macroalgae or lumped together with CCA and bare limestone as “CTB” (CCA / Turf / Bare Space). These broader groupings are inappropriate because they ignore significant functional differences in reef communities. Unlike turf algae, macroalgae are large enough to shade or abrade corals and are not the primary food source for most reef herbivores (McCook et al. 2001). CCA physically build reefs and provide settlement substrates for coral larvae, which turfs do not. Bare space does not trap sediment, compete with corals, or provide food for herbivores, and given the rapid colonization rates of benthic reef organisms, rarely exists on coral reefs. Tropical turf algae on coral reefs are functionally unique and should be classified separately from these other types of benthic algae and substrate types.

Table 1.1 Monitoring programs used as sources for global meta-analysis of turf algae coverage on coral reefs.

Source	**Method**	**Turf Definition**	**Other Categories That Could Include Turf Algae**
AGRRA Atlantic and Gulf Rapid Reef Assessment Marks 2007	Line Point Intercept (LPI)	Not specified.	Rock, Dead Coral (covered with biofilms or microalgae), Rubble ("ignore associated epibenthos like turf algae"), Cyanobacteria
Moorea LTER Long Term Ecological Research Carpenter 2013	Permanent quadrat, *in situ*	"Multi species aggregates." Damselfish turf (usually > 1 cm) recorded separately.	Bare Space, Coral Rubble, Cyanobacteria
CARICOMP Caribbean Coastal Marine Productivity Program Linton and BIOS 2013	LPI	"May look fleshy and/or filamentous but do not rise more than 1 cm above the substrate"	Bare Boulder/Coral Head, Recently Dead Coral, Rubble, Bare Rock
NOAA-CRED/ SIO Coral Reef Ecosystem Division with Scripps Inst. Oceanography	Photo quadrat	Multispecies algal assemblage < 1 cm where cannot distinguish individual plants in photograph.	N/A
CI Conservation International Erdmann and Mohan 2013 McKenna et al. 2009 McKenna et al. 2011 Mustika et al. 2012	LPI	When specified: turf "included filamentous and turf algae as well as bottom dwelling cyanobacteria." Bali: no explicit definition	Bali: Dead Coral With Algae, Rubble
CORDIO Coastal Oceans Research and Development – Indian Ocean Church and Obura 2006	LPI	Use definition from (English et al. 1997): "lush filamentous algae, often found inside damselfish territories."	Dead Coral, Rubble, Substrate, Dead Coral with Algae
GCRMN Global Coral Reef Monitoring Network Wilkinson 2008	LPI	Use definition from (English et al. 1997): "lush filamentous algae, often found inside damselfish territories."	Dead Coral, Rubble, Substrate, Dead Coral with Algae
NCRMP National Coral Reef Monitoring Network (U.S.) NCRMP 2015	Video transects	Not Specified.	Filamentous Algae / Cyanobacteria

One unifying characteristic of tropical turfs is their highly diverse, mixed-species algal assemblage. Given the taxonomic complexity and diversity often found within algal turf communities, few studies quantify the genus- or species-level composition of turf assemblages. Richness of algal turfs ranges from 1-10 genera per cm^2 (Harris et al. 2015), 15-20 species per 100 cm^2 (Diaz-Pulido & McCook 2002, Smith et al. 2010, Fricke et al. 2011), to 54 species in $25m^2$ (van den Hoek et al. 1975). Although turf algae may appear homogenous to the naked eye (Fig 1.1), across relatively small scales there may be high beta-diversity that asymptotes to approximately 30 genera across an entire atoll (Harris et al. 2015). In other cases, presence/absence taxonomic lists are assembled for turf assemblages (e.g. Carpenter 1981, 1985, Cheroske et al. 2000), but those lists lack quantitative or relative abundance metrics and measures of variability that are useful in describing, understanding, and comparing these communities across space and over time.

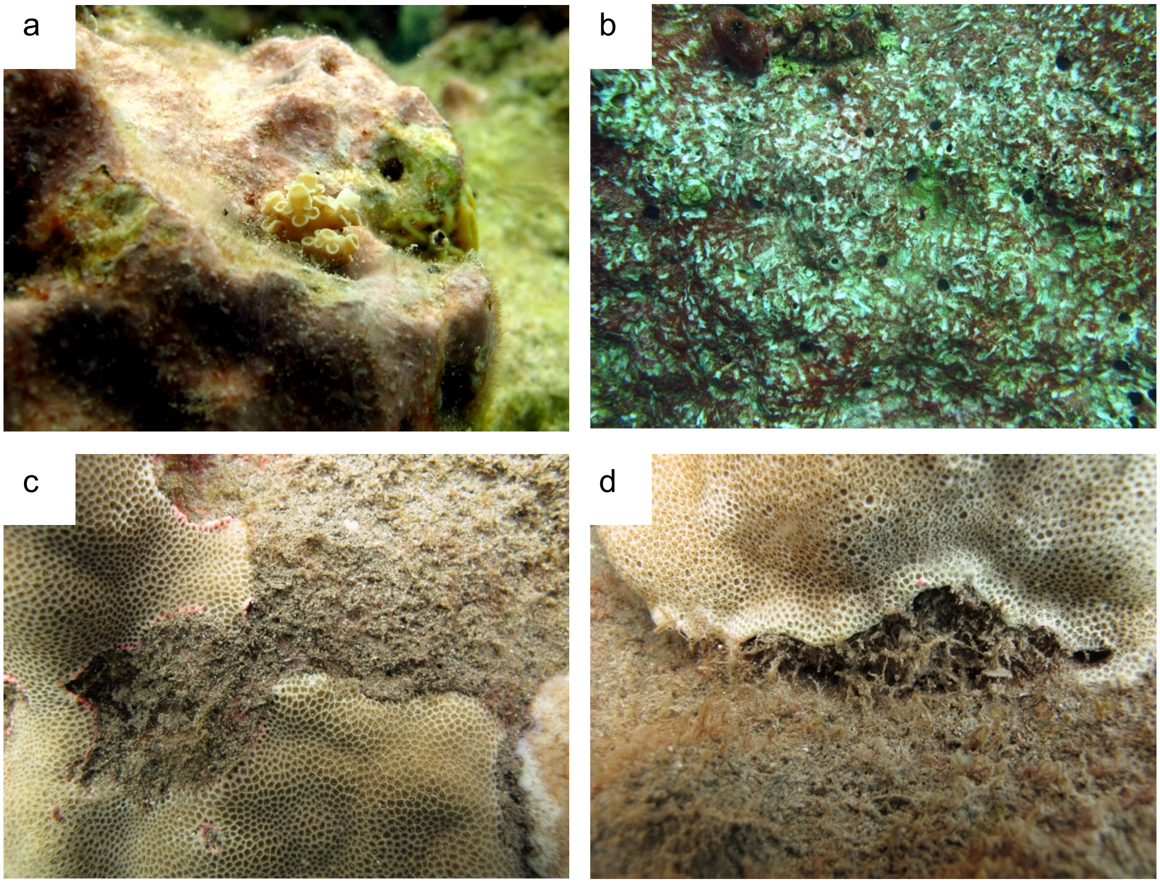

Figure 1.1 Turf algae are assemblages of many species of small, mostly filamentous algae. Although turf algae in general are common on coral reefs worldwide, specific types of turfs vary widely. a) Turf algae that have short canopies, are sparse, and do not retain sediment are relatively benign, and coral larvae can settle within these types of turfs. b) Visible grazing scars in turf algae indicate heavy grazing pressure that keeps turfs in cropped and productive early successional states and makes bare limestone available for larval settlement. c) In contrast, tall, dense turfs packed with sediment usually overgrow live corals, leaving visible signs of coral stress (discoloration at interface). d) Sometimes, though, specific coral morphologies allow corals to co-exist with dense, sediment-laden turfs.

Although few studies report the genus or species-level composition of turf algal assemblages, there is evidence that turfs are variable across space (Harris et al. 2015), depths and reef zones (Bonaldo & Bellwood 2011), across gradients of disturbance and through the process of succession (Diaz-Pulido & McCook 2002, Smith et al. 2010, Fricke et al. 2011). For example, early successional turfs are characterized by thin films of diatoms, other microalgae, and filamentous algae and cyanobacteria (Diaz-Pulido & McCook 2002, Fricke et al. 2011). These sparse, early successional turfs composed of simple and easily digestible taxa, such as *Cladophora* and *Hincksia*, can be maintained by heavy grazing, and they typically have negligible effects on coral (Burkepile & Hay 2010). However, where there is reduced herbivory or an herbivore assemblage dominated by urchins instead of fish, within weeks to months turf assemblages increase in cover and biomass, and also progress to include cyanobacteria and more upright and morphologically complex taxa, including *Polysiphonia*, *Herposiphonia, Ceramium*, *Centroceras*, and *Sphacelaria* (McClanahan 1997, Diaz-Pulido & McCook 2002, Fricke et al. 2011). In some cases, climax turf assemblages include juvenile stages of macroalgae, such as *Asparagopsis*, *Sargassum*, *Dictyota*, and *Lobophora*, although species composition varies among otherwise similar reefs separated by only 30 km (Diaz-Pulido & McCook 2002).

Another major source of variation among turf assemblages is within damselfish (Pomacentridae) territories, where farming behavior promotes turf algae and selects for preferred filamentous turf taxa over calcified algae or juvenile stages of macroalgae (Lobel 1980, De Ruyter van Steveninck 1984, Jones et al. 2006, Ceccarelli 2007). Damselfish turfs are generally taller, denser, more productive, and more diverse than ambient turfs (Hixon & Brostoff 1983, Sammarco 1983, De Ruyter van Steveninck 1984, Klumpp et al. 1987), and the turf algae within territories vary among damselfish species and across locations (Ceccarelli 2007). Additionally, the microbial communities associated with damselfish turfs are more pathogenic than those in ambient turfs (Casey et al. 2014). Curiously, although in some cases damselfish pluck back live coral to expand their territories, coral settlement may actually be greater inside some types of damselfish turfs, at least on the back reefs of Moorea where the damselfish *Stegastes nigricans* farms dense turfs dominated by the red alga *Polysiphonia* (Gleason 1996). Notably, damselfish are more abundant on fished reefs than on remote, unfished, or protected reefs (Edwards et al. 2013). Therefore, we might expect that as fishing pressure increases on coral reefs worldwide, damselfish and their dense, tall, and pathogenic turf algae patches will become more abundant. For all of these reasons, turfs within damselfish territories are functionally distinct from ambient turfs in the broader reef community and therefore deserve separate treatment beyond this review. Here, we focus on the ecology of ambient coral reef turf algae.

Part I: Ecological role of turf algae on coral reefs

Production

Turf algae are among the most productive members of reef benthos (Odum & Odum 1955, Hay 1981, Larkum 1983, Carpenter 1985, Klumpp & Mckinnon 1989, Wilson et al. 2003). Measured rates of primary production are up to 19.2 g O_2 m^2 day^{-1} on a backreef in the Caribbean and up to 6 g C m^2 day^{-1} on a forereef in the Great Barrier Reef, compared to 10 g O_2 m^2 d^{-1} and <1 g C m^2 d^{-1} for CCA (Larkum 1983, Carpenter

1985, Wanders 1976). In particular, dense turf communities have some of the highest production rates ever measured on a reef, equal to or greater than coral and crustose coralline algae (Wanders 1976). Mass-specific production rates of turfs are several times greater than both macroalgae and crustose coralline algae, and approximately equivalent to corals (Wanders 1976, Littler & Arnold 1982, Carpenter 1986, Steneck 1988).

Because coral reefs exist in oligotrophic environments, production is supported with "new" nitrogen from nitrogen fixation. The highest rates of N-fixation on coral reefs are typically found in cyanobacteria (Larkum et al. 1988, O'Neil & Capone 2008). Pure cyanobacterial mats are rare on healthy reefs, but cyanobacteria are a major component of algal turf assemblages, so per area, turf algae tend to be responsible for the largest fraction of N-fixation (Adey & Goertemiller 1987, Larkum et al. 1988, Rix et al. 2015). Further, algal turfs may trap and retain regenerated nutrients, increasing the availability of nitrogen for other reef organisms (O'Neil & Capone 2008). Grazing by fish and urchins further increases these already high rates of N-fixation in turf algae (Larkum et al. 1988, Williams & Carpenter 1997), underscoring the importance of turfs for overall reef production.

Grazing

The balance between high productivity and herbivory determines the abundance of turf algae, a relationship that was established by some of the earliest ecological studies of coral reefs (Odum & Odum 1955, Bakus 1966, Steneck 1988). Herbivores keep turf algae in a cropped, early successional, and highly productive state (Fong & Paul 2011), in which turfs contribute to the efficient transfer of energy to higher trophic levels.

Reducing herbivorous fish and urchin abundances can cause turfs to rapidly undergo succession, grow taller, potentially becoming less palatable and more dense (Morrison 1988). If they are able to outcompete corals and other benthic organisms, turf algae may also increase in cover. Taller and denser turf algae are less productive and transfer less energy through the food web, are able to trap more sediment, leak more dissolved organic carbon, and have higher microbial loads. Reducing herbivory also shifts turf composition to later successional taxa that are more morphologically complex, less palatable, resistant to grazing, and/or allelopathic (Hixon & Brostoff 1996, Smith et al. 2010). In some cases, turfs under reduced herbivory proceed through succession where they are eventually replaced by macroalgae (Aronson et al. 2002, Arthur et al. 2005). These processes combine to make turf algae more competitive in areas of lower herbivory. Although harder to manipulate and therefore less studied, the same process also happens in reverse: increased grazing pressure can shift benthic dominance from macroalgae to turf algae and eventually to CCA (Steneck 1988). In essence, intense grazing by herbivores prevents turf algae from expanding in area and taking over reefs.

On most reefs, grazing rates on turfs are high because turf algae are the preferred food for most reef herbivores, likely because turfs have simple and easily digestible growth forms with high surface area to volume ratios (Carpenter 1986, Bruggemann et al. 1994, Bonaldo et al. 2006, Ledlie et al. 2007, Vermeij, van Moorselaar, et al. 2010). For example, in the Indian Ocean more than 85% (Ledlie et al. 2007) and in the Caribbean more than 75% of herbivore bites were on turfs (Bruggemann et al. 1994), even though macroalgae dominated the benthos in both cases. On the unfished reefs of Palmyra Atoll in the central Pacific, each square centimeter of turf algae is bitten by an herbivore up to

6 times per day (Hamilton et al. 2014). On the Great Barrier Reef, turfs on the reef crest are completely removed by dominant herbivores an estimated 1.5 times per month, and Acanthurids alone consume 73% of daily turf algae productivity (Bonaldo & Bellwood 2009, Marshell & Mumby 2015). Detritivores, too, graze more heavily on turfs than on any other available substrate, consuming algal filaments along with organic matter and detritus (Wilson et al. 2003, Fox & Bellwood 2007, Bonaldo & Bellwood 2008). Turf algae are an important food source for herbivores, and, because of this, turfs are likely to increase on reefs where herbivore populations decline.

Response to disturbance

Turf algae respond rapidly to disturbance due to their highly productive, opportunistic life history strategies. For example, turfs rapidly colonize parrotfish grazing scars, preventing recovery of coral tissue on small spatial scales (Bonaldo & Bellwood 2009). At larger scales, turf algae rapidly colonize dead corals following large physical disturbances such as a bleaching events or hurricanes (Diaz-Pulido & McCook 2002, Houk et al. 2010). These early successional turfs are sparse (low density), have short canopy heights, and are composed mainly of diatoms, filamentous cyanobacteria, and other taxa with simple morphologies such as the green algae *Cladophora* and *Ulva* and brown algae *Hincksia* and *Feldmannia* (Diaz-Pulido & McCook 2002, Fricke et al. 2011). These early colonizing turfs prevent coral recovery, particularly where herbivory is low (Diaz-Pulido & McCook 2002, Arthur et al. 2005, Houk et al. 2010), and over time will progress to denser assemblages with more morphologically complex taxa.

Temperate turf algae regain space quickly and maintain dominance following physical disturbances on temperate rocky shores, regardless of the size, intensity, or timing of the disturbance (Airoldi 1998), which may explain the increasing dominance of turf algae on human impacted coastlines (Benedetti-Cecchi et al. 2001). Given the ability of turf algae to rapidly colonize and persist on exposed substrate, their ecological role on reefs is likely to become even more important in the future as disturbances on reefs become more frequent and more intense (Hoegh-Guldberg 1999).

Competitive interactions with adult corals

Competition between corals and algae in general has been an important topic in coral reef ecology and conservation (Knowlton 2001). While many studies on coral-algal interactions focus exclusively on coral and macroalgae (Tanner 1995, River & Edmunds 2001), the majority of direct coral-algal interactions are actually between coral and turf algae (Lirman 2001, Haas et al. 2010, Barott et al. 2011, Brown & Carpenter 2015). Whether a coral-turf interaction is antagonistic and indicates competition depends on grazing intensity, turf height, and composition, and therefore requires explicit testing and time-series observations (McCook et al. 2001). Compared to CCA and macroalgae, turf algae are generally superior competitors against corals (Vermeij, van Moorselaar, et al. 2010, Haas et al. 2010, Barott et al. 2012, Brown & Carpenter 2015). But sometimes turfs have no negative effect on corals and the observable turf algae-coral interaction zone may be simply a consequence of coral death from some other cause, such as predation or disease (Jompa & McCook 2003a, Vermeij, van Moorselaar, et al. 2010). In at least one case, the coral *Porites lobata* was competitively dominant and actually inhibited turf algae growth (McCook 2001). As turf algae proliferate on reefs, interactions between corals and turf algae will likely become even more common. Processes operating at the scale of the coral-turf algae interaction zone differ from processes operating where a macroalgal frond shades or physically abrades coral tissue, so coral-turf competitive interactions deserve particular attention to understand the contexts in which turf algae are able to damage and outcompete corals.

Turf algae primarily interact with adult corals by direct overgrowth (Table 1.2). Overgrowth is commonly reported as an inverse correlation between turf abundance and coral cover in experiments, but the specific mechanism is frequently unknown. When turf algae grow over live coral, they are typically led by one or two specific turf algae taxa advancing ahead of the mixed turf assemblage (e.g. the red algae *Anotrichium*, *Corallophila*, *Hypnea*, and *Gracilaria* and the green algae *Chlorodesmis* and *Bryopsis*), suggesting allelopathy (Bonaldo & Hay 2014). Another likely mechanism comes from the dense microbial populations harbored within turf algae: algae release dissolved organic carbon that fuels microbial respiration, creating a hypoxic microenvironment that can be detrimental to corals (Smith et al. 2006, Haas et al. 2009, Barott et al. 2011) and described as the DDAM model (Dissolved organic material, Disease, Algae, and Microbes) (Barott & Rohwer 2012). Hypoxia is more pronounced at the coral-turf interface between coral and CCA or between competing corals (Barott et al. 2009, 2011, Gregg et al. 2013), possibly due to microtopography (Wangpraseurt et al. 2012). In addition to detrimental hypoxia, microbial communities within algal turfs can be more virulent than other benthic microbial communities (Barott et al. 2009, 2011), exacerbating the negative influence of turf algae on corals.

Competition between coral and turf algae will ultimately be affected by numerous biotic and abiotic factors, although mechanisms have rarely been tested in experiments that can provide direct evidence of competitive inhibition between coral and algae (McCook 2001, Jompa and McCook 2002). In theory, environmental conditions that favor rapid algal growth (e.g., low grazing, high nutrients) should provide turfs with a competitive advantage over coral, while conditions that favor coral growth and/or inhibit algal growth (e.g., low turbidity, high grazing intensity, low nutrients) should provide corals with a competitive advantage. For example, under low flow at the turf algae-coral interface, a thicker diffusive boundary layer develops (Brown & Carpenter 2015), which is harmful to corals because of the increased retention time for algal exudates (fueling microbial respiration) and hypoxic water. Grazing rates also likely play a major role in determining the outcome of competition between coral and turfs, because low grazing should provide turfs with a competitive advantage, and vice versa. Further, there may be a tipping point in the ability of herbivores to mediate coral-turf algae competition: on reefs with low coral cover and high turf algal cover, grazing rates may need to be unnaturally high in order to facilitate a transition back to coral dominance (Williams et al 2001). In contrast, on high coral cover reefs, there is little space for turf algae to occupy so grazing is concentrated on a small area, turfs remain in an early successional state: cropped, highly productive, and more palatable, and positive feedbacks maintain the system in a coral-dominated state. Coral-turf algae competitive outcomes appear to be context-dependent and require more careful experimental analysis.

Table 1.2. Published studies on interactions between turf algae and a) adult and b) larval and juvenile corals. Interactions between coral and macroalgae are included when those macroalgal taxa are commonly found as members of mixed turf assemblages. Results of interactions are positive for corals (+), neutral (0), and/or positive for algae (-).

a)

Interaction Type	**Mechanism**	**Result**	**Notes**	**Source**
Overgrowth	Unknown	+	*Porites lobata* inhibited turf growth *in situ*	McCook 2001
Overgrowth Preventing re-growth	Unknown	-	Sedimentation increased turf overgrowth and prevented growth of *Siderastrea siderea, Colpophyllia natans*	Nugues and Roberts 2003
Overgrowth	Unknown	-, 0	*Anotrichium tenue* overgrew and killed live *Porites* spp. Mixed turf had no effect on *Porites* spp.	Jompa and McCook 2003a
Overgrowth	Unknown	-, 0	• *Corallophila huysmansii* overgrew, killed *Porites cylindrica* • *Hypnea pannosa* overgrew but did not kill *Porites cylindrica* • *Chlorodesmis* spp. did not kill live coral	Jompa and McCook 2003b
Overgrowth	Hypoxia at interface	-	• *Gracilaria* sp. and *Bryopsis pennata* overgrew live *Pocillopora verucosa* • Mixed turf overgrew live *Montipora* spp.	Barott et al. 2009
Overgrowth	Unknown	-	• Turf overgrew *Montastrea annularis in situ*, added nutrients enhanced rate of overgrowth • Turf reduced fitness (photochemical efficiency) of *M. annularis*	Vermeij et al 2010
Overgrowth	Unknown	-	Turf algae overgrew coral at a faster rate than did *Peyssonnelia* or *Caulerpa*	Haas et al. 2010
Overgrowth	Unknown	-	Turf algae more likely to overgrow corals than CCA or macroalgae species	Barott et al 2012
Overgrowth	Allelopathy	-	• Transplanted *Chlorodesmis fastigiata*, *Galaxaura filamentosa* damaged and sometimes overgrew *Acropora aspera* and *Pocillopora damicornis* • Transplanted *C. fastigiata*, *G. filamentosa* bleached but did not kill *Montipora digitata, Porites cylindrica*, *P. lobata*	Bonaldo and Hay 2014
Correlation	Unknown	-	Taller turfs (> 5 mm) correlated with increased coral mortality, decreased growth of *Porites porites, P. astreoides*	Burkepile and Hay 2010
Not specified	Microbes Hypoxia at interface	-	Hypoxia caused by microbial respiration at turf-coral interface (multiple species of coral)	Smith et al. 2006
Not specified	Microbes Hypoxia at interface	-	Turf algae reduced O_2, caused bleaching in transplanted and non-touching *Acropora* spp.; effect enhanced by glucose addition	Haas et al. 2009

Table 1.2. Published studies on interactions between turf algae and a) adult and b) larval and juvenile corals. Interactions between coral and macroalgae are included when those macroalgal taxa are commonly found as members of mixed turf assemblages. Results of interactions are positive for corals (+), neutral (0), and/or positive for algae (-), continued.

Interaction Type	**Mechanism**	**Result**	**Notes**	**Source**
Not specified	Microbes Hypoxia at interface	0	Thicker diffusive boundary layer at turf-*Porites* interface No significant hypoxia *in situ* at turf-*Porites* interface	Wangpraseurt et al. 2012
Not specified	Microbes Hypoxia at interface	-	• Hypoxia at interfaces between *Dictyota bartayresiana*, *Halimeda opuntia*, mixed turf and *Montastrea annularis* • More pathogenic and virulent microbes in turf algae growing up against *M.annularis*	Barott et al. 2011
Not specified	Microbes Hypoxia at interface	-	Turf algae exudates increased respiration (resulting in hypoxia) by microbial communities from *Montastrea annularis* and *Mussimilia hispida*	Gregg et al. 2013
Not specified	Microbes	-	Pathogenic bacteria, ciliates associated with white band disease found in turfs > 5 mm canopy height	Sweet et al. 2013
Overgrowth	Microbes	-	Turf algae overgrew massive *Porites* with lower water flow, higher microbial concentrations	Brown and Carpenter 2015

b)

Interaction Type	**Mechanism**	**Result**	**Notes**	**Source**
Mortality	Unknown	-	~30% mortality of juvenile corals transplanted into damselfish territory	Potts 1977
Mortality Space pre-emption	Unknown	-	Rapid settlement and growth of turf algae prevented coral settlement, increased mortality in recruits	Birkeland 1977
Indirect prevention of larval settlement on CCA	Unknown	-	Turf algae grew over CCA inside fish exclusion cages	Wanders 1977
Overgrowth Mortality	Unknown	-	Turf algae grew over previously living recruits *in situ*	Bak and Engel 1979
Overgrowth Mortality	Unknown	-	Certain turf taxa were a significant source of competitive losses for settling coral larvae	Sammarco 1991
Correlation	Unknown	-	Turf canopy height, density, sediment load inversely correlated with settlement success, directly correlated with post-settlement mortality	Birell et al 2005

Table 1.2. Published studies on interactions between turf algae and a) adult and b) larval and juvenile corals. Interactions between coral and macroalgae are included when those macroalgal taxa are commonly found as members of mixed turf assemblages. Results of interactions are positive for corals (+), neutral (0), and/or positive for algae (-), continued.

Interaction Type	**Mechanism**	**Result**	**Notes**	**Source**
Correlation	Unknown	-	Turf abundance correlates negatively with success of early coral settlers	Vermeij and Sandin 2008
Correlation	Unknown	-	Larval settlement rate inversely correlated with greater turf abundance (canopy height x percent cover)	Arnold et al. 2010
Correlation	Unknown	-	Higher mortality of coral recruits inside cages where 3x greater turf cover	Penin et al. 2011
Promoted coral settlement	Unknown	+	• Greater rates of coral settlement on tiles with turf algae (inside damselfish territories) than to tiles outside territories or in *Sargassum* bed	Gleason 1996
Avoidance behavior Mortality	Microbes or allelopathy	-	• *Moorea* (*Lyngbya*), *Dictyota*, *Lobophora* caused avoidance behavior in *Porites astreoides* larvae • *Lobophora, Dictyota* caused mortality in *P. astreoides* larvae	Kuffner et al. 2006
Reduced settlement	Microbes or allelopathy	+, -	• *Lobophora variegate* enhanced settlement of larval *Acropora millepora* • *Chlorodesmis fastigiata* delayed larval settlement • *Padina* sp. reduced larval settlement	Birrell et al. 2008
Avoidance behavior Mortality	Allelopathy	-	• *Ulva fasciata* increased mortality in larval *Montipora capitata* • *Sargassum polyphyllum, Pterocladiella caerulescens* reduced settlement of larval *M. capitata*	Vermeij et al 2009
Space pre-emption	Unknown	-	Turfs settle quickly in newly opened space following coral morality from bleaching	Diaz-Pulido and McCook 2002
Space pre-emption	Unknown	-	Turfs settle quickly in newly opened space following coral morality from bleaching	Arthur et al. 2005
Space pre-emption	Unknown	-	Turfs rapidly re-colonize open space in parrotfish grazing scars	Bonaldo and Bellwood 2009
Space pre-emption	Unknown	-	Turfs settle quickly in newly opened space following coral morality from hurricane	Houk et al. 2010

Effects on coral recruitment

Turf algae compete indirectly and directly with larval and juvenile corals by pre-emptively occupying space, changing larval behavior, or growing over coral recruits (Birkeland 1977, Birrell et al. 2005, Birrell, McCook, Willis, & Diaz-Pulido 2008, Vermeij & Sandin 2008, Vermeij et al. 2009, Arnold et al. 2010, Penin et al. 2011) (Table 1.2). Coral larvae typically settle on CCA or even bare limestone, but turfs preempt settlement by rapidly colonizing open space following disturbances (Diaz-Pulido & McCook 2002, Houk et al. 2010), being competitively dominant over CCA where grazing is low (Wanders 1977), and persisting where there is high sedimentation and low grazing (Bellwood & Fulton 2008). When turfs are abundant and these factors combine, there is less available space for coral settlement (Fabricius & De'Ath 2001, Belliveau & Paul 2002). However, coral larvae are sometimes able to settle in short, sparse turfs that contain little sediment (Birrell et al. 2005) (Fig 1.1A), although evidence of this phenomenon is based on post-hoc comparisons of turf assemblages. In one study, coral settlement on the back reef of Moorea was higher inside damselfish territories characterized by tall, dense turf dominated by the red alga *Polysiphonia,* likely because damselfish protected recruits from predation (Gleason 1996). Some turf algae taxa also prevent coral settlement directly by changing larval behavior or increasing mortality of early settlers, likely via allelopathy or microbial activity (Kuffner et al. 2006, Birrell, McCook, Willis, & Harrington 2008, Vermeij et al. 2009). While turfs do compete with larval and juvenile corals, not all turf assemblages should be considered equally damaging to corals. Turfs can become particularly detrimental to coral recruits when grazing is limited and/or sedimentation is high.

Where dense, tall, and sediment laden turfs persist, they impede settlement as part of a positive feedback loop that reduces reef resilience. For example, following the 1998 bleaching event on the Great Barrier Reef, turfs grew on dead coral skeletons and persisted for at least 2.5 years, preventing both re-growth of surviving corals and settlement of new recruits (Diaz-Pulido & McCook 2002). In that case, high algal turf cover was a consequence and not a cause of coral death, but the turfs remained dominant over existing corals, prevented coral recovery, and ultimately contributed to lower community resilience. In a future with fewer herbivores and more frequent disturbance events, turf algae will likely continue to ratchet up in abundance, persisting as an abundant benthic component on coral reefs.

Response to global stressors (warming and ocean acidification)

While information is limited, evidence to date suggests that both warming temperatures and ocean acidification benefit tropical turf algae. Both temperate and tropical turfs become more productive and more abundant in response to experimentally and naturally acidified conditions (Connell et al. 2013, Bender et al. 2014). Elevated temperature and CO_2 both increase the prevalence of red algae and some cyanobacteria in turf assemblages, two taxonomic groups with species that have negative effects on corals (Bender et al. 2014). Emerging evidence suggests that elevated CO_2 enhances photosynthesis, allowing turfs to become more productive and enabling them to either outcompete calcifiers (Short et al. 2014) or simply occupy space made available by the death/reduced growth of calcifiers (Connell et al. 2013). Finally, increasing CO_2 makes corals more susceptible to mortality due to direct overgrowth competition (Diaz-Pulido et al. 2011), but the effects of pH on the ability of turfs to overgrow CCA appear to be more complicated and not yet fully understood (Short et al. 2014). Although the effects of warming and ocean acidification on coral overgrowth by turf algae have not yet been fully tested, if corals and CCA become generally weaker competitors and fleshy algae become stronger competitors under ocean acidification (Johnson et al. 2014), then it is plausible that these key reef-building groups will become more susceptible to turf algae overgrowth under future global change scenarios (Diaz-Pulido et al. 2011).

In summary, turfs are an ecologically critical component of coral reef ecosystems, and their role will only become increasingly important in the future. Turfs are the preferred food for most coral reef herbivores and can withstand intense grazing because of extremely high rates of production. The high productivity of turf algae also allows them to rapidly colonize open substrate following disturbances, as well as outcompete many other benthic groups including corals and CCA. Once established, turf algae can persist for months or years by impeding settlement of corals, potentially leading to a positive feedback loop between declining coral cover and increasing turf cover. For these reasons, turf algae are poised to shape the ecology of coral reefs of the future.

Part II: Status and trends of turf algae on coral reefs

Studies routinely claim that turf algae are the most abundant benthic component on coral reefs, but those data are limited in geographic scope (Ledlie et al. 2007, Wismer et al. 2009, Bonaldo & Bellwood 2011). Turfs do tend to dominate the algal community or even the entire benthos on shallow (<10 m) reefs where herbivory is high (Odum &

Odum 1955, Bakus 1966, Morrissey 1980, Steneck 1988). Even on extremely remote and uninhabited islands in the central Pacific, turfs are a major component of the benthos, composing on average one-third of reef benthic cover across the Northern Line Islands (Sandin et al. 2008). However, there has never been a comprehensive, quantitative analysis of the abundance of turf algae on reefs worldwide.

Several recent regional meta-analyses of coral reef benthic communities have used hard coral cover as the sole metric of reef condition (Pandolfi 2003, Bruno & Selig 2007, Osborne et al. 2011). Percent coral cover is a useful metric for comparisons because it is widely reported and ecologically meaningful (Osborne et al. 2011). However, other members of the benthos are clearly important components of reef health and resilience. For example, two reefs with equal coral cover but with vastly different abundances of turf and CCA will likely function very differently: a reef composed of mainly coral and CCA is more likely to see future increases in coral cover and be more resilient to physical damage from storms compared to a reef composed mainly of coral and turf algae. Data on these additional benthic reef components provides essential information about current and future reef condition. Percent cover of turf algae correlates tightly with overall reef health and human impact (Vermeij, Dailer, et al. 2010), so quantitative data on turf algae cover and other metrics such as canopy height can contribute to informative metrics.

Here, for the first time, we present global turf algae cover, using data compiled from multiple coral reef monitoring programs over the last 20 years (Table 1.1). We included only monitoring programs that regularly collect data on coral reef benthic communities and that record turf algae separately from other benthic categories. Because there are few monitoring programs in the Indian Ocean, for that region we also included published data from individual surveys that followed standard protocols from the Global Coral Reef Monitoring Network (GCRMN). From each location and year, we recorded percent cover of turf algae, survey location, survey method, and, where available, survey depth, reef strata, and definition of what counted as turf algae (Tables 1.1, 1.2). Survey depth and strata were not available for all locations, so we pooled all data together for analysis.

We synthesized data from eight different monitoring programs and regional networks (Table 1.1). We had a total of 176 records from 35 countries spanning 1993-2014. Each record is the mean turf cover from one country (or island) for one year, with some exceptions. Australia data are reported by region of the Great Barrier Reef. United States data include both Flower Garden Banks and the Florida Keys, but the US Virgin Islands and the following Pacific islands and territories are reported separately: main Hawaiian Islands, American Samoa, Mariana Islands, and the Pacific Remote Islands (Baker Island, Howland Island, Jarvis Island, Johnston Atoll, Kingman Reef, Palmyra Atoll, and Wake Atoll).

About half of the monitoring programs (Moorea LTER, CARICOMP, NOAA/SIO, GCRMN, and AIMS) provide explicit definitions of turf algae, but all programs except NOAA/SIO and AIMS record multiple benthic categories that likely include turf algae, for example dead coral, bare space, coral rubble, dead coral with algae, substrate, cyanobacteria, and turfs within damselfish territories (Table 1.1). For example, in the Atlantic and Gulf Rapid Reef Assessment (AGRRA) protocol, rock and dead coral are defined as “covered with biofilms or microalgae” and, when recording rubble, divers are instructed to “ignore associated epibenthos like turf algae” (Lang et al. 2010). In contrast, the Australian Institute of Marine Science’s long-term monitoring program explicitly states that coral rubble and bare space are only recorded as separate categories when these substrates are not colonized by turf algae. Further, because turf algae colonize open space within just a few weeks (Diaz-Pulido & McCook 2002), true bare space is rare on coral reefs unless there has been a very recent bleaching or predation event. Much of what is recorded as bare space or limestone is more likely colonized by early successional turf algae (e.g. biofilms or sparse filaments). To be conservative, we only included data specifically assigned to the turf algae category. Therefore, our data are likely an underestimate as turf algae are usually present on “rubble” and “dead coral” on most reefs.

Our data span more than 20 years of monitoring efforts. However, we did not quantify changes over time in turf algae cover because not all locations were repeatedly sampled in a balanced way (Table 1.3). To get a sense of average turf cover on reefs worldwide, we calculated regional and global means from the most recent years: 2010-2012 in the Caribbean, 2012-2014 in the Pacific, and 2000-2010 in the data sparse Indian Ocean.

Mean cover of turf algae in individual countries, averaged across all survey years, ranges from 2.5-74%. Generally, individual countries have between 20-60% of all coral reef benthos (Figure 1.2). The highest recorded cover of turf algae in a single year at the island scale was 94% (on Lehua Island, Hawaii in 2008). Several surveys also recorded less than 1% cover of turf algae (Jamaica 1994, Nicaragua 1997 and 1998, and Venezuela 1998). In the most recent years, turf cover was 39.7% globally (mean weighted by sample sizes in each ocean basin), 30.5% in the Caribbean, 48.4% in the Pacific, and 37.3% in the Indian Ocean.

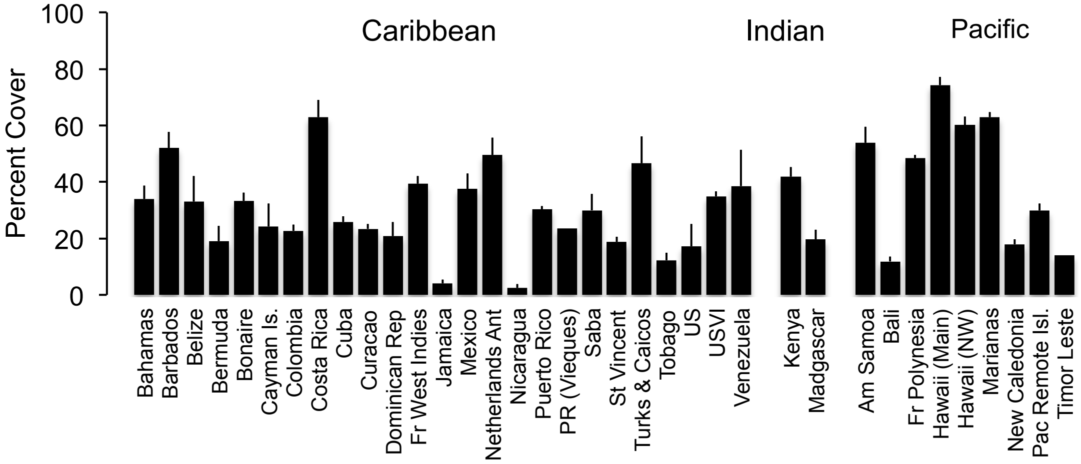

Figure 1.2 Mean (± SE) percent cover of turf algae based on data from eight regional long-term monitoring programs (Table 1). Depth and other meta-data in Table 1.2, sample sizes and sampling years for each country in Table 1.3

Table 1.3 Metadata for surveys from long-term monitoring programs used for global meta-analysis of turf algae on coral reef. Organization and Method acronyms as in Table 1.1.

Country	Region	Site Name	Organization	Year	Habitat	Depth (m)	Method
Bahamas	Carib.		CARICOMP	1994		10	LPI
Bahamas	Carib.		CARICOMP	1995		10	LPI
Bahamas	Carib.		CARICOMP	1996		10	LPI
Bahamas	Carib.		AGRRA	1997	Forereef	8.6	LPI
Bahamas	Carib.		AGRRA	1997	Reef Crest	2.0	LPI
Bahamas	Carib.		CARICOMP	1997		10	LPI
Bahamas	Carib.		AGRRA	1998	Forereef	8.0	LPI
Bahamas	Carib.		AGRRA	1998	Reef Crest	5.2	LPI
Bahamas	Carib.		AGRRA	1998	Patch	4.1	LPI
Bahamas	Carib.		AGRRA	1998	Forereef	9.9	LPI
Bahamas	Carib.		AGRRA	1998	Reef Crest	1.2	LPI
Bahamas	Carib.		CARICOMP	1998		10	LPI
Bahamas	Carib.		AGRRA	1999	Reef Crest	3.7	LPI
Bahamas	Carib.		AGRRA	1999	Forereef	6.5	LPI
Barbados	Carib.		CARICOMP	1993		10	LPI

Table 1.3 Metadata for surveys from long-term monitoring programs used for global meta-analysis of turf algae on coral reef. Organization and Method acronyms as in Table 1.1, continued.

Country	Region	Site Name	Organization	Year	Habitat	Depth (m)	Method
Barbados	Carib.		CARICOMP	1994		10	LPI
Belize	Carib.		CARICOMP	1994		10	LPI
Belize	Carib.		CARICOMP	1995		10	LPI
Belize	Carib.		CARICOMP	1996		10	LPI
Belize	Carib.		CARICOMP	1997		10	LPI
Belize	Carib.		AGRRA	1999	Forereef	8.3	LPI
Belize	Carib.		AGRRA	1999	Patch	6.2	LPI
Belize	Carib.		AGRRA	1999	Forereef	7.8	LPI
Bermuda	Carib.		CARICOMP	1993		10	LPI
Bermuda	Carib.		CARICOMP	1993		10	LPI
Bermuda	Carib.		CARICOMP	1995		10	LPI
Bermuda	Carib.		CARICOMP	1997		10	LPI
Bermuda	Carib.		CARICOMP	1998		10	LPI
Bonaire	Carib.		CARICOMP	1994		10	LPI
Bonaire	Carib.		CARICOMP	1995		10	LPI
Bonaire	Carib.		CARICOMP	1996		10	LPI
Bonaire	Carib.		CARICOMP	1997		10	LPI
Cayman	Carib.		CARICOMP	1995		10	LPI
Cayman	Carib.		CARICOMP	1997		10	LPI
Cayman	Carib.		AGRRA	1999	Forereef	10.8	LPI
Cayman	Carib.		AGRRA	1999	Reef Crest	2.7	LPI
Cayman	Carib.		AGRRA	2000	Patch	8.6	LPI
Cayman	Carib.		AGRRA	2000	Forereef	9.2	LPI
Colombia	Carib.		CARICOMP	1993		10	LPI
Colombia	Carib.		CARICOMP	1994		10	LPI
Colombia	Carib.		CARICOMP	1995		10	LPI
Colombia	Carib.		CARICOMP	1996		10	LPI
Colombia	Carib.		CARICOMP	1997		10	LPI
Colombia	Carib.		CARICOMP	1998		10	LPI
Costa Rica	Carib.		CARICOMP	1995		10	LPI
Costa Rica	Carib.		AGRRA	1999	Forereef	5.5	LPI
Costa Rica	Carib.		AGRRA	1999	Patch	2.0	LPI
Costa Rica	Carib.		AGRRA	1999	Bank	7.0	LPI
Cuba	Carib.		CARICOMP	1994		10	LPI
Cuba	Carib.		CARICOMP	1995		10	LPI
Cuba	Carib.		CARICOMP	1996		10	LPI
Cuba	Carib.		CARICOMP	1997		10	LPI
Cuba	Carib.		AGRRA	1999	Forereef	7.7	LPI
Curacao	Carib.		CARICOMP	1994		10	LPI

Table 1.3 Metadata for surveys from long-term monitoring programs used for global meta-analysis of turf algae on coral reef. Organization and Method acronyms as in Table 1.1, continued.

Country	Region	Site Name	Organization	Year	Habitat	Depth (m)	Method
Curacao	Carib.		CARICOMP	1995		10	LPI
Dominican Republic	Carib.		CARICOMP	1994		10	LPI
Dominican Republic	Carib.		CARICOMP	1996		10	LPI
Dominican Republic	Carib.		CARICOMP	1997		10	LPI
FrWIndies	Carib.		GCRMN	1995			photoquad or LPI
FrWIndies	Carib.		GCRMN	1999			photoquad or LPI
FrWIndies	Carib.		GCRMN	2001			photoquad or LPI
FrWIndies	Carib.		GCRMN	2002			photoquad or LPI
FrWIndies	Carib.		GCRMN	2003			photoquad or LPI
FrWIndies	Carib.		GCRMN	2004			photoquad or LPI
FrWIndies	Carib.		GCRMN	2005			photoquad or LPI
FrWIndies	Carib.		GCRMN	2006			photoquad or LPI
FrWIndies	Carib.		GCRMN	2007			photoquad or LPI
Jamaica	Carib.		CARICOMP	1993		10	LPI
Jamaica	Carib.		CARICOMP	1994		10	LPI
Jamaica	Carib.		CARICOMP	1995		10	LPI
Jamaica	Carib.		CARICOMP	1996		10	LPI
Jamaica	Carib.		CARICOMP	1997		10	LPI
Mexico	Carib.		CARICOMP	1993		10	LPI
Mexico	Carib.		CARICOMP	1994		10	LPI
Mexico	Carib.		CARICOMP	1995		10	LPI
Mexico	Carib.		CARICOMP	1996		10	LPI
Mexico	Carib.		CARICOMP	1997		10	LPI
Mexico	Carib.		CARICOMP	1998		10	LPI
Mexico	Carib.		AGRRA	1999	Forereef	11.3	LPI
Mexico	Carib.		AGRRA	1999	Patch	1.3	LPI
Mexico	Carib.		AGRRA	1999	Forereef	7.5	LPI
Mexico	Carib.		AGRRA	1999	Forereef	10.4	LPI
NethAnt	Carib.		AGRRA	1998	Forereef	10.0	LPI
NethAnt	Carib.		AGRRA	1999	Forereef	10.0	LPI
NethAnt	Carib.		AGRRA	1999	Bank	17.6	LPI
NethAnt	Carib.		AGRRA	1999	Forereef	12.4	LPI
NethAnt	Carib.		AGRRA	2000	Forereef	15.0	LPI
Nicaragua	Carib.		CARICOMP	1993		10	LPI
Nicaragua	Carib.		CARICOMP	1995		10	LPI

Table 1.3 Metadata for surveys from long-term monitoring programs used for global meta-analysis of turf algae on coral reef. Organization and Method acronyms as in Table 1.1, continued.

Country	Region	Site Name	Organization	Year	Habitat	Depth (m)	Method
Nicaragua	Carib.		CARICOMP	1997		10	LPI
Nicaragua	Carib.		CARICOMP	1998		10	LPI
Puerto Rico	Carib.		CARICOMP	1994		10	LPI
Puerto Rico	Carib.		CARICOMP	1995		10	LPI
Puerto Rico	Carib.		CARICOMP	1996		10	LPI
Puerto Rico	Carib.		CARICOMP	1997		10	LPI
Puerto Rico	Carib.		CARICOMP	1998		10	LPI
Puerto Rico	Carib.		NCRMP	2001			video transects
Puerto Rico	Carib.		NCRMP	2002			video transects
Puerto Rico	Carib.		NCRMP	2003			video transects
Puerto Rico	Carib.		NCRMP	2004			video transects
Puerto Rico	Carib.		NCRMP	2005			video transects
Puerto Rico	Carib.		NCRMP	2006			video transects
Puerto Rico	Carib.		NCRMP	2007			video transects
Puerto Rico	Carib.		NCRMP	2008			video transects
Puerto Rico	Carib.		NCRMP	2009			video transects
Puerto Rico	Carib.		NCRMP	2010			video transects
Puerto Rico	Carib.		NCRMP	2011			video transects
Puerto Rico	Carib.		NCRMP	2012			video transects
Puerto Rico (Vieques)	Carib.		NCRMP	2007			video transects
Saba	Carib.		CARICOMP	1993		10	LPI
Saba	Carib.		CARICOMP	1994		10	LPI
Saba	Carib.		CARICOMP	1995		10	LPI
Saba	Carib.		CARICOMP	1996		10	LPI
Saba	Carib.		CARICOMP	1998		10	LPI
St Vincent	Carib.		AGRRA	1999	Forereef	10.5	LPI
St Vincent	Carib.		AGRRA	1999	Reef Crest	3.3	LPI
TCI	Carib.		AGRRA	1999	Patch	3.9	LPI
TCI	Carib.		AGRRA	1999	Bank	18.2	LPI
TCI	Carib.		AGRRA	1999	Forereef	13.7	LPI
Tobago	Carib.		CARICOMP	1994		10	LPI
Tobago	Carib.		CARICOMP	1995		10	LPI
Tobago	Carib.		CARICOMP	1996		10	LPI
Tobago	Carib.		CARICOMP	1997		10	LPI
Tobago	Carib.		CARICOMP	1998		10	LPI

Table 1.3 Metadata for surveys from long-term monitoring programs used for global meta-analysis of turf algae on coral reef. Organization and Method acronyms as in Table 1.1, continued.

Country	**Region**	**Site Name**	**Organization**	**Year**	**Habitat**	**Depth (m)**	**Method**
US	Carib.	Florida	AGRRA	1999	Bank	20.9	LPI
US	Carib.	Flower Garden Banks	NCRMP	2006			video transects
US	Carib.	Flower Garden Banks	NCRMP	2007			video transects
US	Carib.	Flower Garden Banks	NCRMP	2010			video transects
US	Carib.	Flower Garden Banks	NCRMP	2011			video transects
US	Carib.	Flower Garden Banks	NCRMP	2012			video transects
USVI	Carib.	St Croix	NCRMP	2001			video transects
USVI	Carib.	St Croix	NCRMP	2002			video transects
USVI	Carib.	St Croix	NCRMP	2003			video transects
USVI	Carib.	St Croix	NCRMP	2004			video transects
USVI	Carib.	St Croix	NCRMP	2005			video transects
USVI	Carib.	St Croix	NCRMP	2006			video transects
USVI	Carib.	St Croix	NCRMP	2007			video transects
USVI	Carib.	St Croix	NCRMP	2008			video transects
USVI	Carib.	St Croix	NCRMP	2009			video transects
USVI	Carib.	St Croix	NCRMP	2010			video transects
USVI	Carib.	St Croix	NCRMP	2011			video transects
USVI	Carib.	St Croix	NCRMP	2012			video transects
USVI	Carib.	St John	NCRMP	2001			video transects
USVI	Carib.	St John	NCRMP	2002			video transects
USVI	Carib.	St John	NCRMP	2003			video transects
USVI	Carib.	St John	NCRMP	2004			video transects
USVI	Carib.	St John	NCRMP	2005			video transects
USVI	Carib.	St John	NCRMP	2006			video transects
USVI	Carib.	St John	NCRMP	2007			video transects
USVI	Carib.	St John	NCRMP	2008			video transects
USVI	Carib.	St John	NCRMP	2009			video transects
USVI	Carib.	St John	NCRMP	2010			video transects
USVI	Carib.	St John	NCRMP	2011			video transects
USVI	Carib.	St Thomas	NCRMP	2012			video transects
USVI	Carib.		AGRRA	1998	Forereef	11.1	LPI

Table 1.3 Metadata for surveys from long-term monitoring programs used for global meta-analysis of turf algae on coral reef. Organization and Method acronyms as in Table 1.1, continued.

Country	Region	Site Name	Organization	Year	Habitat	Depth (m)	Method
USVI	Carib.		AGRRA	1999	Forereef	9.9	LPI
USVI	Carib.		AGRRA	2000	Backreef	13.1	LPI
USVI	Carib.		AGRRA	2000	Forereef	8.4	LPI
Venezuela	Carib.		CARICOMP	1995		10	LPI
Venezuela	Carib.		CARICOMP	1996		10	LPI
Venezuela	Carib.		CARICOMP	1997		10	LPI
Venezuela	Carib.		CARICOMP	1998		10	LPI
Venezuela	Carib.		AGRRA	1999	Forereef	9.9	LPI
Venezuela	Carib.		AGRRA	1999	Reef Crest	3.1	LPI
Venezuela	Carib.		AGRRA	1999	Patch	1.6	LPI
Kenya	Indian		CORDIO	1998	Back / Patch	0-5	RE
Kenya	Indian		CORDIO	1998	Forereef	8-25	RE
Kenya	Indian		CORDIO	1998	Fringing	0-15	RE
Kenya	Indian		CORDIO	1999	Back / Patch	0-5	LPI
Kenya	Indian		CORDIO	1999	Forereef	8-25	LPI
Kenya	Indian		CORDIO	1999	Fringing	0-15	LPI
Kenya	Indian		CORDIO	2000	Back / Patch	0-5	LPI
Kenya	Indian		CORDIO	2000	Forereef	8-25	LPI
Kenya	Indian		CORDIO	2000	Fringing	0-15	LPI
Kenya	Indian		CORDIO	2001	Back / Patch	0-5	photo quadrat
Kenya	Indian		CORDIO	2001	Forereef	8-25	photo quadrat
Kenya	Indian		CORDIO	2001	Fringing	0-15	photo quadrat
Kenya	Indian		CORDIO	2002	Back / Patch	0-5	photo quadrat
Kenya	Indian		CORDIO	2002	Forereef	8-25	photo quadrat
Kenya	Indian		CORDIO	2002	Fringing	0-15	photo quadrat
Kenya	Indian		CORDIO	2003	Back / Patch	0-5	photo
Kenya	Indian		CORDIO	2003	Forereef	8-25	photo
Kenya	Indian		CORDIO	2003	Fringing	0-15	photo
Madagascar	Indian	Northeast	CORDIO	2010		1-15	by eye
Madagascar	Indian	Northwest	CORDIO	2002		4-6	LPI
Madagascar	Indian	Northwest	CORDIO	2002		12-16	LPI
Madagascar	Indian		CORDIO	2005			LPI
Bali	Pacific	Nusa Penida	CI	2008		10-14	LPI
Bali	Pacific	Nusa Penida	CI	2008		5-7	LPI
Bali	Pacific		CI	2011		10-14	LPI
Bali	Pacific		CI	2011		5-7	LPI
FrPolynesia	Pacific	Moorea	LTER	2006	Backreef		permanent quad

Table 1.3 Metadata for surveys from long-term monitoring programs used for global meta-analysis of turf algae on coral reef. Organization and Method acronyms as in Table 1.1, continued.

Country	Region	Site Name	Organization	Year	Habitat	Depth (m)	Method
FrPolynesia	Pacific	Moorea	LTER	2006	Forereef		permanent quad
FrPolynesia	Pacific	Moorea	LTER	2006	Forereef	10	permanent quad
FrPolynesia	Pacific	Moorea	LTER	2006	Forereef	17	permanent quad
FrPolynesia	Pacific	Moorea	LTER	2007	Backreef		permanent quad
FrPolynesia	Pacific	Moorea	LTER	2007	Forereef		permanent quad
FrPolynesia	Pacific	Moorea	LTER	2007	Forereef	10	permanent quad
FrPolynesia	Pacific	Moorea	LTER	2007	Forereef	17	permanent quad
FrPolynesia	Pacific	Moorea	LTER	2008	Backreef		permanent quad
FrPolynesia	Pacific	Moorea	LTER	2008	Forereef		permanent quad
FrPolynesia	Pacific	Moorea	LTER	2008	Forereef	10	permanent quad
FrPolynesia	Pacific	Moorea	LTER	2008	Forereef	17	permanent quad
FrPolynesia	Pacific	Moorea	LTER	2009	Backreef		permanent quad
FrPolynesia	Pacific	Moorea	LTER	2009	Forereef		permanent quad
FrPolynesia	Pacific	Moorea	LTER	2009	Forereef	10	permanent quad
FrPolynesia	Pacific	Moorea	LTER	2009	Forereef	17	permanent quad
FrPolynesia	Pacific	Moorea	LTER	2010	Backreef		permanent quad
FrPolynesia	Pacific	Moorea	LTER	2010	Forereef		permanent quad
FrPolynesia	Pacific	Moorea	LTER	2010	Forereef	10	permanent quad
FrPolynesia	Pacific	Moorea	LTER	2010	Forereef	17	permanent quad
FrPolynesia	Pacific	Moorea	LTER	2011	Backreef		permanent quad
FrPolynesia	Pacific	Moorea	LTER	2011	Forereef		permanent quad
FrPolynesia	Pacific	Moorea	LTER	2011	Forereef	10	permanent quad
FrPolynesia	Pacific	Moorea	LTER	2011	Forereef	17	permanent quad
FrPolynesia	Pacific	Moorea	LTER	2012	Backreef		permanent quad
FrPolynesia	Pacific	Moorea	LTER	2012	Forereef		permanent quad
FrPolynesia	Pacific	Moorea	LTER	2012	Forereef	10	permanent quad
FrPolynesia	Pacific	Moorea	LTER	2012	Forereef	17	permanent quad
FrPolynesia	Pacific	Moorea	LTER	2013	Backreef		permanent quad
FrPolynesia	Pacific	Moorea	LTER	2013	Forereef		permanent quad
FrPolynesia	Pacific	Moorea	LTER	2013	Forereef	10	permanent quad

Table 1.3 Metadata for surveys from long-term monitoring programs used for global meta-analysis of turf algae on coral reef. Organization and Method acronyms as in Table 1.1, continued.

Country	**Region**	**Site Name**	**Organization**	**Year**	**Habitat**	**Depth (m)**	**Method**
FrPolynesia	Pacific	Moorea	LTER	2013	Forereef	17	permanent quad
FrPolynesia	Pacific	Moorea	LTER	2014	Backreef		permanent quad
FrPolynesia	Pacific	Moorea	LTER	2014	Forereef		permanent quad
FrPolynesia	Pacific	Moorea	LTER	2014	Forereef	10	permanent quad
FrPolynesia	Pacific	Moorea	LTER	2014	Forereef	17	permanent quad
Marianas	Pacific	Agrihan	CRED/ SIO	2003			photo quadrat
Marianas	Pacific	Agrihan	CRED/ SIO	2005			photo quadrat
Marianas	Pacific	Agrihan	CRED/ SIO	2007			photo quadrat
Marianas	Pacific	Agrihan	CRED/ SIO	2009			photo quadrat
Marianas	Pacific	Aguijan	CRED/ SIO	2003			photo quadrat
Marianas	Pacific	Aguijan	CRED/ SIO	2005			photo quadrat
Marianas	Pacific	Aguijan	CRED/ SIO	2007			photo quadrat
Marianas	Pacific	Alamagan	CRED/ SIO	2003			photo quadrat
Marianas	Pacific	Alamagan	CRED/ SIO	2005			photo quadrat
Marianas	Pacific	Alamagan	CRED/ SIO	2007			photo quadrat
Marianas	Pacific	Alamagan	CRED/ SIO	2009			photo quadrat
Marianas	Pacific	Asuncion	CRED/ SIO	2003			photo quadrat
Marianas	Pacific	Asuncion	CRED/ SIO	2005			photo quadrat
Marianas	Pacific	Asuncion	CRED/ SIO	2007			photo quadrat
Marianas	Pacific	Asuncion	CRED/ SIO	2009			photo quadrat
Marianas	Pacific	Farallon de Pajaros	CRED/ SIO	2003			photo quadrat
Marianas	Pacific	Farallon de Pajaros	CRED/ SIO	2005			photo quadrat
Marianas	Pacific	Farallon de Pajaros	CRED/ SIO	2009			photo quadrat
Marianas	Pacific	Guam	CRED/ SIO	2003			photo quadrat
Marianas	Pacific	Guam	CRED/ SIO	2005			photo quadrat
Marianas	Pacific	Guam	CRED/ SIO	2007			photo quadrat
Marianas	Pacific	Guam	CRED/ SIO	2009			photo quadrat
Marianas	Pacific	Guguan	CRED/ SIO	2003			photo quadrat
Marianas	Pacific	Guguan	CRED/ SIO	2007			photo quadrat
Marianas	Pacific	Guguan	CRED/ SIO	2009			photo quadrat
Marianas	Pacific	Maug	CRED/ SIO	2003			photo quadrat
Marianas	Pacific	Maug	CRED/ SIO	2005			photo quadrat
Marianas	Pacific	Maug	CRED/ SIO	2007			photo quadrat
Marianas	Pacific	Maug	CRED/ SIO	2009			photo quadrat
Marianas	Pacific	Pagan	CRED/ SIO	2003			photo quadrat
Marianas	Pacific	Pagan	CRED/ SIO	2005			photo quadrat
Marianas	Pacific	Pagan	CRED/ SIO	2007			photo quadrat

Table 1.3 Metadata for surveys from long-term monitoring programs used for global meta-analysis of turf algae on coral reef. Organization and Method acronyms as in Table 1.1, continued.

Country	Region	Site Name	Organization	Year	Habitat	Depth (m)	Method
Marianas	Pacific	Pagan	CRED/ SIO	2009			photo quadrat
Marianas	Pacific	Rota	CRED/ SIO	2003			photo quadrat
Marianas	Pacific	Rota	CRED/ SIO	2005			photo quadrat
Marianas	Pacific	Rota	CRED/ SIO	2007			photo quadrat
Marianas	Pacific	Rota	CRED/ SIO	2009			photo quadrat
Marianas	Pacific	Saipan	CRED/ SIO	2003			photo quadrat
Marianas	Pacific	Saipan	CRED/ SIO	2005			photo quadrat
Marianas	Pacific	Saipan	CRED/ SIO	2007			photo quadrat
Marianas	Pacific	Saipan	CRED/ SIO	2009			photo quadrat
Marianas	Pacific	Sarigan	CRED/ SIO	2003			photo quadrat
Marianas	Pacific	Sarigan	CRED/ SIO	2005			photo quadrat
Marianas	Pacific	Sarigan	CRED/ SIO	2007			photo quadrat
Marianas	Pacific	Sarigan	CRED/ SIO	2009			photo quadrat
Marianas	Pacific	Tinian	CRED/ SIO	2003			photo quadrat
Marianas	Pacific	Tinian	CRED/ SIO	2005			photo quadrat
Marianas	Pacific	Tinian	CRED/ SIO	2007			photo quadrat
Marianas	Pacific	Tinian	CRED/ SIO	2009			photo quadrat
MHI	Pacific	French Frigate	CRED/ SIO	2002			photo quadrat
MHI	Pacific	French Frigate	CRED/ SIO	2004			photo quadrat
MHI	Pacific	French Frigate	CRED/ SIO	2006			photo quadrat
MHI	Pacific	French Frigate	CRED/ SIO	2008			photo quadrat
MHI	Pacific	Hawaii	CRED/ SIO	2005			photo quadrat
MHI	Pacific	Hawaii	CRED/ SIO	2006			photo quadrat
MHI	Pacific	Hawaii	CRED/ SIO	2008			photo quadrat
MHI	Pacific	Kauai	CRED/ SIO	2005			photo quadrat
MHI	Pacific	Kauai	CRED/ SIO	2006			photo quadrat
MHI	Pacific	Kauai	CRED/ SIO	2008			photo quadrat
MHI	Pacific	Kure Atoll	CRED/ SIO	2002			photo quadrat
MHI	Pacific	Kure Atoll	CRED/ SIO	2004			photo quadrat
MHI	Pacific	Kure Atoll	CRED/ SIO	2006			photo quadrat
MHI	Pacific	Kure Atoll	CRED/ SIO	2008			photo quadrat
MHI	Pacific	Lanai	CRED/ SIO	2005			photo quadrat
MHI	Pacific	Lanai	CRED/ SIO	2006			photo quadrat
MHI	Pacific	Lanai	CRED/ SIO	2008			photo quadrat
MHI	Pacific	Laysan	CRED/ SIO	2002			photo quadrat
MHI	Pacific	Laysan	CRED/ SIO	2004			photo quadrat
MHI	Pacific	Laysan	CRED/ SIO	2006			photo quadrat
MHI	Pacific	Laysan	CRED/ SIO	2008			photo quadrat
MHI	Pacific	Lehua	CRED/ SIO	2005			photo quadrat

Table 1.3 Metadata for surveys from long-term monitoring programs used for global meta-analysis of turf algae on coral reef. Organization and Method acronyms as in Table 1.1, continued.

Country	**Region**	**Site Name**	**Organization**	**Year**	**Habitat**	**Depth (m)**	**Method**
MHI	Pacific	Lehua	CRED/ SIO	2006			photo quadrat
MHI	Pacific	Lehua	CRED/ SIO	2008			photo quadrat
MHI	Pacific	Lisianski	CRED/ SIO	2002			photo quadrat
MHI	Pacific	Lisianski	CRED/ SIO	2004			photo quadrat
MHI	Pacific	Lisianski	CRED/ SIO	2006			photo quadrat
MHI	Pacific	Lisianski	CRED/ SIO	2008			photo quadrat
MHI	Pacific	Maro Reef	CRED/ SIO	2004			photo quadrat
MHI	Pacific	Maro Reef	CRED/ SIO	2006			photo quadrat
MHI	Pacific	Maro Reef	CRED/ SIO	2008			photo quadrat
MHI	Pacific	Maui	CRED/ SIO	2005			photo quadrat
MHI	Pacific	Maui	CRED/ SIO	2006			photo quadrat
MHI	Pacific	Maui	CRED/ SIO	2008			photo quadrat
MHI	Pacific	Midway	CRED/ SIO	2002			photo quadrat
MHI	Pacific	Midway	CRED/ SIO	2004			photo quadrat
MHI	Pacific	Midway	CRED/ SIO	2006			photo quadrat
MHI	Pacific	Midway	CRED/ SIO	2008			photo quadrat
MHI	Pacific	Molokai	CRED/ SIO	2005			photo quadrat
MHI	Pacific	Molokai	CRED/ SIO	2006			photo quadrat
MHI	Pacific	Molokai	CRED/ SIO	2008			photo quadrat
MHI	Pacific	Necker Island	CRED/ SIO	2002			photo quadrat
MHI	Pacific	Necker Island	CRED/ SIO	2006			photo quadrat
MHI	Pacific	Niihau	CRED/ SIO	2005			photo quadrat
MHI	Pacific	Niihau	CRED/ SIO	2006			photo quadrat
MHI	Pacific	Niihau	CRED/ SIO	2008			photo quadrat
MHI	Pacific	Oahu	CRED/ SIO	2005			photo quadrat
MHI	Pacific	Oahu	CRED/ SIO	2006			photo quadrat
MHI	Pacific	Oahu	CRED/ SIO	2008			photo quadrat
MHI	Pacific	Pearl & Hermes	CRED/ SIO	2004			photo quadrat
MHI	Pacific	Pearl & Hermes	CRED/ SIO	2006			photo quadrat
MHI	Pacific	Pearl & Hermes	CRED/ SIO	2008			photo quadrat
New Caledonia	Pacific	Northeast	CI	2005		> 12	LPI
New Caledonia	Pacific	Northeast	CI	2005		7-10	LPI
New Caledonia	Pacific	Northeast	CI	2005		< 7	LPI
New Caledonia	Pacific	Northwest	CI	2005		< 6	LPI
New Caledonia	Pacific	Northwest	CI	2005		6-10	LPI
New Caledonia	Pacific	Northwest	CI	2005		> 12	LPI
Pacific Remote Islands (US)	Pacific	Baker	CRED/ SIO	2004			photo quadrat
Pacific Remote Islands (US)	Pacific	Baker	CRED/ SIO	2006			photo quadrat

Table 1.3 Metadata for surveys from long-term monitoring programs used for global meta-analysis of turf algae on coral reef. Organization and Method acronyms as in Table 1.1, continued.

Country	Region	Site Name	Organization	Year	Habitat	Depth (m)	Method
Pacific Remote Islands (US)	Pacific	Baker	CRED/ SIO	2008			photo quadrat
Pacific Remote Islands (US)	Pacific	Baker	CRED/ SIO	2010			photo quadrat
Pacific Remote Islands (US)	Pacific	Howland	CRED/ SIO	2004			photo quadrat
Pacific Remote Islands (US)	Pacific	Howland	CRED/ SIO	2006			photo quadrat
Pacific Remote Islands (US)	Pacific	Howland	CRED/ SIO	2008			photo quadrat
Pacific Remote Islands (US)	Pacific	Howland	CRED/ SIO	2010			photo quadrat
Pacific Remote Islands (US)	Pacific	Jarvis	CRED/ SIO	2004			photo quadrat
Pacific Remote Islands (US)	Pacific	Jarvis	CRED/ SIO	2006			photo quadrat
Pacific Remote Islands (US)	Pacific	Jarvis	CRED/ SIO	2008			photo quadrat
Pacific Remote Islands (US)	Pacific	Jarvis	CRED/ SIO	2010			photo quadrat
Pacific Remote Islands (US)	Pacific	Johnston	CRED/ SIO	2006			photo quadrat
Pacific Remote Islands (US)	Pacific	Johnston	CRED/ SIO	2010			photo quadrat
Pacific Remote Islands (US)	Pacific	Kingman	CRED/ SIO	2004			photo quadrat
Pacific Remote Islands (US)	Pacific	Kingman	CRED/ SIO	2006			photo quadrat
Pacific Remote Islands (US)	Pacific	Kingman	CRED/ SIO	2008			photo quadrat
Pacific Remote Islands (US)	Pacific	Kingman	CRED/ SIO	2010			photo quadrat
Pacific Remote Islands (US)	Pacific	Palmyra	CRED/ SIO	2004			photo quadrat
Pacific Remote Islands (US)	Pacific	Palmyra	CRED/ SIO	2006			photo quadrat
Pacific Remote Islands (US)	Pacific	Palmyra	CRED/ SIO	2008			photo quadrat
Pacific Remote Islands (US)	Pacific	Palmyra	CRED/ SIO	2010			photo quadrat
Pacific Remote Islands (US)	Pacific	Wake	CRED/ SIO	2006			photo quadrat
Pacific Remote Islands (US)	Pacific	Wake	CRED/ SIO	2007			photo quadrat
Pacific Remote Islands (US)	Pacific	Wake	CRED/ SIO	2008			photo quadrat
Pacific Remote Islands (US)	Pacific	Wake	CRED/ SIO	2009			photo quadrat
American Samoa	Pacific	Ofu	CRED/ SIO	2004			photo quadrat
American Samoa	Pacific	Ofu	CRED/ SIO	2006			photo quadrat
American Samoa	Pacific	Ofu	CRED/ SIO	2008			photo quadrat
American Samoa	Pacific	Ofu	CRED/ SIO	2010			photo quadrat
American Samoa	Pacific	Olosega	CRED/ SIO	2004			photo quadrat
American Samoa	Pacific	Olosega	CRED/ SIO	2006			photo quadrat
American Samoa	Pacific	Olosega	CRED/ SIO	2008			photo quadrat
American Samoa	Pacific	Olosega	CRED/ SIO	2010			photo quadrat

Table 1.3 Metadata for surveys from long-term monitoring programs used for global meta-analysis of turf algae on coral reef. Organization and Method acronyms as in Table 1.1, continued.

Country	Region	Site Name	Organization	Year	Habitat	Depth (m)	Method
American Samoa	Pacific	Rose	CRED/ SIO	2004			photo quadrat
American Samoa	Pacific	Rose	CRED/ SIO	2006			photo quadrat
American Samoa	Pacific	Rose	CRED/ SIO	2008			photo quadrat
American Samoa	Pacific	Rose	CRED/ SIO	2010			photo quadrat
American Samoa	Pacific	Swains	CRED/ SIO	2004			photo quadrat
American Samoa	Pacific	Swains	CRED/ SIO	2006			photo quadrat
American Samoa	Pacific	Swains	CRED/ SIO	2008			photo quadrat
American Samoa	Pacific	Swains	CRED/ SIO	2010			photo quadrat
American Samoa	Pacific	Tau	CRED/ SIO	2004			photo quadrat
American Samoa	Pacific	Tau	CRED/ SIO	2006			photo quadrat
American Samoa	Pacific	Tau	CRED/ SIO	2008			photo quadrat
American Samoa	Pacific	Tau	CRED/ SIO	2010			photo quadrat
American Samoa	Pacific	Tutuila	CRED/ SIO	2004			photo quadrat
American Samoa	Pacific	Tutuila	CRED/ SIO	2006			photo quadrat
American Samoa	Pacific	Tutuila	CRED/ SIO	2008			photo quadrat
American Samoa	Pacific	Tutuila	CRED/ SIO	2010			photo quadrat
Timor Leste	Pacific		CI	2012			by eye

Table 1.4 Number of survey sites in each sampling year for turf algae percent cover in Fig 1.2.

Region	**Country**	**Year**	**Sites**	**Region**	**Country**	**Year**	**Sites**
Caribbean	Bahamas	1994	1	Caribbean	Saba	1993	1
Caribbean	Bahamas	1995	1	Caribbean	Saba	1994	1
Caribbean	Bahamas	1996	1	Caribbean	Saba	1995	1
Caribbean	Bahamas	1997	3	Caribbean	Saba	1996	1
Caribbean	Bahamas	1998	6	Caribbean	Saba	1998	1
Caribbean	Bahamas	1999	2	Caribbean	St Vincent	1999	2
Caribbean	Barbados	1993	1	Caribbean	Turks and Caicos	1999	3
Caribbean	Barbados	1994	1	Caribbean	Tobago	1994	1
Caribbean	Belize	1994	1	Caribbean	Tobago	1995	1
Caribbean	Belize	1995	1	Caribbean	Tobago	1996	1
Caribbean	Belize	1996	1	Caribbean	Tobago	1997	1
Caribbean	Belize	1997	1	Caribbean	Tobago	1998	1
Caribbean	Belize	1999	3	Caribbean	US	1999	1
Caribbean	Bermuda	1993	2	Caribbean	US	2006	1
Caribbean	Bermuda	1995	1	Caribbean	US	2007	1
Caribbean	Bermuda	1997	1	Caribbean	US	2010	1
Caribbean	Bermuda	1998	1	Caribbean	US	2011	1
Caribbean	Bonaire	1994	1	Caribbean	US	2012	1
Caribbean	Bonaire	1995	1	Caribbean	USVI	1998	1
Caribbean	Bonaire	1996	1	Caribbean	USVI	1999	1
Caribbean	Bonaire	1997	1	Caribbean	USVI	2000	2
Caribbean	Cayman	1995	1	Caribbean	USVI	2001	2
Caribbean	Cayman	1997	1	Caribbean	USVI	2002	2
Caribbean	Cayman	1999	2	Caribbean	USVI	2003	2
Caribbean	Cayman	2000	2	Caribbean	USVI	2004	2
Caribbean	Colombia	1993	1	Caribbean	USVI	2005	2
Caribbean	Colombia	1994	1	Caribbean	USVI	2006	2
Caribbean	Colombia	1995	1	Caribbean	USVI	2007	2
Caribbean	Colombia	1996	1	Caribbean	USVI	2008	2
Caribbean	Colombia	1997	1	Caribbean	USVI	2009	2
Caribbean	Colombia	1998	1	Caribbean	USVI	2010	2
Caribbean	Costa Rica	1995	1	Caribbean	USVI	2011	2
Caribbean	Costa Rica	1999	3	Caribbean	USVI	2012	2
Caribbean	Cuba	1994	1	Caribbean	Venezuela	1995	1
Caribbean	Cuba	1995	1	Caribbean	Venezuela	1996	1
Caribbean	Cuba	1996	1	Caribbean	Venezuela	1997	1
Caribbean	Cuba	1997	1	Caribbean	Venezuela	1998	1
Caribbean	Cuba	1999	1	Caribbean	Venezuela	1999	3
Caribbean	Curacao	1994	1	Indian	Kenya	1998	3

Table 1.4 Number of survey sites in each sampling year for turf algae percent cover in Fig 1.2, continued.

Region	Country	Year	Sites	Region	Country	Year	Sites
Caribbean	Curacao	1995	1	Indian	Kenya	1999	3
Caribbean	Dominican Republic	1994	1	Indian	Kenya	2000	3
Caribbean	Dominican Republic	1996	1	Indian	Kenya	2001	3
Caribbean	Dominican Republic	1997	1	Indian	Kenya	2002	3
Caribbean	Fr West Indies	1995	1	Indian	Kenya	2003	3
Caribbean	Fr West Indies	1999	1	Indian	Madagascar	2002	2
Caribbean	Fr West Indies	2001	1	Indian	Madagascar	2005	1
Caribbean	Fr West Indies	2002	1	Indian	Madagascar	2010	1
Caribbean	Fr West Indies	2003	1	Pacific	Am Samoa	2004	6
Caribbean	Fr West Indies	2004	1	Pacific	Am Samoa	2006	6
Caribbean	Fr West Indies	2005	1	Pacific	Am Samoa	2008	6
Caribbean	Fr West Indies	2006	1	Pacific	Am Samoa	2010	6
Caribbean	Fr West Indies	2007	1	Pacific	Bali	2008	2
Caribbean	Jamaica	1993	1	Pacific	Bali	2011	2
Caribbean	Jamaica	1994	1	Pacific	Fr Polynesia	2006	4
Caribbean	Jamaica	1995	1	Pacific	Fr Polynesia	2007	4
Caribbean	Jamaica	1996	1	Pacific	Fr Polynesia	2008	4
Caribbean	Jamaica	1997	1	Pacific	Fr Polynesia	2009	4
Caribbean	Mexico	1993	1	Pacific	Fr Polynesia	2010	4
Caribbean	Mexico	1994	1	Pacific	Fr Polynesia	2011	4
Caribbean	Mexico	1995	1	Pacific	Fr Polynesia	2012	4
Caribbean	Mexico	1996	1	Pacific	Fr Polynesia	2013	4
Caribbean	Mexico	1997	1	Pacific	Fr Polynesia	2014	4
Caribbean	Mexico	1998	1	Pacific	Hawaii (Main)	2002	6
Caribbean	Mexico	1999	4	Pacific	Hawaii (Main)	2004	7
Caribbean	Neth Antilles	1998	1	Pacific	Hawaii (Main)	2005	8
Caribbean	Neth Antilles	1999	3	Pacific	Hawaii (Main)	2006	16
Caribbean	Neth Antilles	2000	1	Pacific	Hawaii (Main)	2008	15
Caribbean	Nicaragua	1993	1	Pacific	Marianas	2003	13
Caribbean	Nicaragua	1995	1	Pacific	Marianas	2005	12
Caribbean	Nicaragua	1997	1	Pacific	Marianas	2007	12
Caribbean	Nicaragua	1998	1	Pacific	Marianas	2009	12
Caribbean	Puerto Rico	1994	1	Pacific	New Caledonia	2005	6
Caribbean	Puerto Rico	1995	1	Pacific	Pac Remote Isl	2004	5
Caribbean	Puerto Rico	1996	1	Pacific	Pac Remote Isl	2006	7
Caribbean	Puerto Rico	1997	1	Pacific	Pac Remote Isl	2007	1
Caribbean	Puerto Rico	1998	1	Pacific	Pac Remote Isl	2008	6
Caribbean	Puerto Rico	2001	1	Pacific	Pac Remote Isl	2009	1
Caribbean	Puerto Rico	2002	1	Pacific	Pac Remote Isl	2010	6

Table 1.4 Number of survey sites in each sampling year for turf algae percent cover in Fig 1.2, continued.

Region	**Country**	**Year**	**Sites**
Caribbean	Puerto Rico	2003	1
Caribbean	Puerto Rico	2004	1
Caribbean	Puerto Rico	2005	1
Caribbean	Puerto Rico	2006	1
Caribbean	Puerto Rico	2007	1
Caribbean	Puerto Rico	2008	1
Caribbean	Puerto Rico	2009	1
Caribbean	Puerto Rico	2010	1
Caribbean	Puerto Rico	2011	1
Caribbean	Puerto Rico	2012	1
Caribbean	PR (Vieques)	2007	1
Pacific	Timor Leste	2012	1

Part III: A quantitative framework for tropical turf algae

Turf algae are rarely studied beyond a functional group level because of their diversity and the fact that species-level algae identification often requires microscopic investigation and presence of reproductive structures (Steneck 1988). The functional group approach is based on the idea that morphologically similar species function more similarly than taxonomically related species with different morphologies, and it allows for comparisons among systems and across wide geographic ranges that may have little overlap at the species level (Steneck & Dethier 1994, Fong & Paul 2011). However, there are two drawbacks to using such an approach to describe turf algae as a single homogenous functional group: turfs do not all have the same ecological functions (Fig 1.1), and lumping them together ignores the species diversity in any given turf assemblage. Acknowledging the diversity of turfs allows us to account for processes driven by species interactions or species-specific characteristics, such as rapid growth rates and chemical defense.

The two most common algae functional group schemes are based on susceptibility to grazing, production, and characteristics that describe broader ecological performance such as nutrient uptake and turnover rate (Littler & Littler 1984, Steneck & Dethier 1994) (Table 1.3). Both of these classification systems arrange algae taxa along a morphological continuum from fast growing and easily grazed to slow growing and grazer resistant. However, these existing functional schemes are insufficient to accurately and meaningfully describe turf algae, because turf assemblages include representatives from almost all groups within both of these classification systems (Table 1.3). Instead of describing turfs as a homogenous group, general physical characteristics are a more informative and practical way to describe turf algae. Other analogous assemblages across terrestrial and marine ecosystems are commonly described under taxonomic or functional frameworks (Appendix). A recent review of temperate and tropical algal turfs proposed a set of physical characteristics of turf algae to facilitate comparisons among studies and ecosystems (Connell et al 2014). The authors maintained that we currently do not know enough about turf algae to predict which traits will occur within a particular set of environmental conditions. However, temperate and tropical turfs differ sufficiently such that each deserves a unique empirical approach, and we argue that we do know enough about tropical turfs to establish a quantitative classification scheme for the different types of turf assemblages associated with specific ecological conditions.

Table 1.5 The two most common functional classification schemes for algae are based on traits such as susceptibility to grazing, production, nutrient uptake, and turnover rates. However, diverse algal turfs include representatives from almost all functional groups under both schemes.

Rapid growth
Susceptible to grazing
Simple morphologies
↓
Slow growth
Resistant to grazing
Complex morphologies

Steneck and Dethier 1994	**Littler and Littler 1984**	**Representatives in turf assemblages?**
Microalgae (single-celled)	Sheet-like	Yes
Filamentous (uniseriate)	Filamentous	Yes
Foliose (single layer)	n/a	Yes
Corticated foliose	Coarsely branched	Yes
Corticated macroalgae	n/a	No (only when juvenile)
Leathery macroalgae	Thick leathery	No (only when juvenile)
Articulated calcareous	Articulated calcareous	Yes
Crustose	Crustose	Yes

We present a simple, practical, and accessible framework for measuring and describing turf algae based on their three primary ecological functions: as a source of primary production, as a food source for herbivores and as space competitors with corals.

The framework consists of four turf assemblage characteristics that are related to these two functions, easily measured, and comparable across systems: canopy height, sediment content, density, and presence of diagnostic taxa. The absolute value of each of these characteristics is useful to understand the current state of a reef system and to compare among locations, and relative changes in these characteristics are indicators of ecosystem shifts. This universal and qualitative framework will allow researchers to measure variability in turf assemblages, experimentally test processes that cause those patterns, and address potential implications of variable turf assemblages for reef ecology.

Canopy Height

We propose that turf canopy height is the single most informative metric because it relates directly to both herbivory (short turfs reflect high grazing pressure, Morrison 1988, Fong & Paul 2011) and competition with coral (tall turfs are stronger competitors against corals, Birrell et al. 2005, Burkepile & Hay 2010). Canopy height also responds quickly to environmental change and is a sensitive metric: changes of only several millimeters cause measurable changes in the thickness of the diffusive boundary layer (DBL) (Carpenter & Williams 1993), within which there are different oxygen, pH, and allelochemical conditions (Larkum et al 2003, Wangpraseurt et al. 2012). Tall turfs are more productive per unit area (Wanders 1976), host pathogenic bacteria and the ciliates associated with the coral white band disease (Sweet et al. 2013), and are more competitive with corals because they reduce larval settlement success (Birell et al. 2005) and increase mortality of adult corals (Burkepile and Hay 2010). While the mechanism behind tall turfs' competitive advantage has not been explicitly tested, we expect that it is related to their ability to trap sediment and organic matter that host microbes, creating a hypoxic and/or pathogenic microenvironment that is damaging to corals.

Canopy height is easily measured using plastic or stainless steel calipers *in situ* or in preserved or fresh samples in the lab, because filament height is a conserved quality even when turf algae are scraped from the substrate. Canopy height is highly variable over small spatial scales (Harris et al. 2015), so we recommend at least 5 measurements per cm^2 or >10 per 100 cm^2. The canopy height that distinguishes tall and short turfs depends on local conditions and the ecological function of interest. For example, DBL thickness varies with flow speed, so turfs in a high flow environment with a 10 mm canopy could create a DBL of similar thickness to turfs in a low flow environment with a 5 mm canopy. Further, if one were interested in turf algae's ability to prevent successful settlement of coral larvae, it would make sense to define turf canopy heights based on the size of coral propagules (microns to millimeters).

We define tropical short turfs as 1-5 mm and tall turfs as > 5 mm. Turfs < 1 mm are more accurately described as a biofilm or microalgae. At a canopy height of 5 mm and greater, turfs retain enough sediment to affect coral settlement and herbivory (Fig 1.1, Birrell et al. 2005, Bellwood and Fulton 2008), negatively affect the survival of adult corals (Burkepile and Hay 2010), are twice as productive per unit area as turfs <3 mm tall (Wanders 1976), and host different bacterial communities compared to turfs < 5 mm (Sweet et al. 2013). Additionally, turfs with canopy height < 5 mm are typical of those grazed by both urchins and fish, while taller turfs indicate grazing only by fish grazers (Carpenter and Williams 1993), so measuring canopy height potentially tells us not only how much herbivory exists, but also what type of herbivores are present.

Many of these quantitative cutoffs that distinguish among turfs' functions are defined either arbitrarily, *post hoc*, or both (Rasher et al. 2012, Birell et al 2005). Therefore, it would be valuable to robustly test the effect of experimentally manipulated canopy height on any number of response variables. Until then, however, the 5 mm cutoff is a useful hypothesis against which to test ecological functions of the turf assemblage and the larger reef community and a benchmark for comparing turf algae among locations.

In some cases, measuring changes in canopy height is more informative than classifying absolute turf algae height as tall or short. Canopy height is the first metric of a turf assemblage to change in response to changing environmental conditions, because vegetative growth of existing filaments can be rapid: more than 0.5 mm per day under moderate herbivory (Bonaldo and Bellwood 2009), or 50-100% growth within a few weeks under experimental sediment addition (Goatley and Bellwood 2013). The rate of change in canopy height is greater than either expansion over new substrate (changes in cover or density) or new recruitment (changes in diagnostic species). Therefore, canopy height is the single most informative turf algae metric to monitor a reef ecosystem's current status and trajectory.

Sediment Content

Turf canopy height is also important because it controls the amount of sediment and detritus that becomes trapped within the turf algae matrix (Hatcher 1983, Purcell 2000, Bonaldo and Bellwood 2001), which is both a cause and effect of grazing pressure and makes turfs stronger competitors against coral. Sediment within turfs is either inorganic (e.g. carbonate) and/or organic (e.g. detritus), and in some cases, the turf matrix contains as much sediment as it does algae (Purcell and Bellwood 2001). While inorganic particles deter herbivory (Bellwood and Fulton 2008), organic detritus actually attracts detritivorous fish (Crossman et al. 2001, Purcell & Bellwood 2001, Wilson et al. 2003, Bonaldo & Bellwood 2011, Choat 1991, Goatley and Bellwood 2001) and determines the type of infaunal invertebrate assemblage present (Kramer et al. 2014). Much of what we recognize as grazing on turf algae may actually be consumption of organic matter and invertebrates living within the turf matrix (Wilson et al. 2003, Bonaldo & Bellwood 2011).

There is a complex relationship between sediment content, canopy height, and herbivory that is not yet entirely understood. Experimentally removing fish increases the amount of sediment in turfs (Rasher et al 2012), perhaps by allowing turf algae to grow taller and physically trap more sediment, or because the sediment within turfs is no longer removed by fish. In turn, sediment-laden turfs grow taller, because adding sediment reduces herbivory (Bellwood and Fulton 2008, Goatley and Bellwood 2012). Further, thick sediment benefits turf algae by creating microrefuges for the base of algal filaments, allowing turfs to regrow rapidly after grazing (Steneck 1988). While this seems like positive feedback that would lead to a persistent stable state of tall, sediment-laden, herbivore-resistant turfs, there is conflicting evidence. Experimentally adding sediment may reduce herbivory, but it also increases detrivory, particularly when the sediment is high in organic matter (Crossman et al. 2001, Purcell & Bellwood 2001, Wilson et al. 2003, Bonaldo & Bellwood 2011). Therefore, the relationship could also be a negative feedback loop in which tall turfs trap sediment and get targeted by detritivores that crop the algae, thereby reducing their ability to trap sediment and attracting herbivory. Experiments designed to test for effects in both directions would help to clarify this relationship, which may depend on the relative abundances of herbivores and detritivores in the fish assemblage and inorganic and organic sediments in turfs.

Sediment content also affects the outcome of competition between turfs and coral (Fig 1.1C-D). Turfs with higher sediment loads negatively affect current and future coral survival by preventing the settlement of CCA and coral larvae (Steneck 1997, Birell et al 2005) and developing anoxic layers (Clausing et al 2014). Sedimentation also indirectly benefits turf alge by causing coral stress or mortality, opening space for turf algae proliferation (Nugues & Roberts 2003). Therefore, greater sediment content in turfs indicates negative prospects for future coral cover. Finally, sediment content is controlled by flow, so it varies spatially across reef zones: taller, higher sediment turfs are found in low energy areas like lagoons and reef flats (Bonaldo & Bellwood 2011). Therefore, measures of sediment content are only valid for comparisons within reef zones or flow regimes.

Both sediment type and sediment content should be quantified as proportion organic and inorganic/sand by rinsing turf algae onto a filter and measuring dry weight and ash-free dry weight. While sediment content is typically reported as a qualitative measure (e.g. “sediment-laden” vs. “sediment-free”), only quantitative measures let us detect potential threshold responses to sediment content in turfs. One possible metric is sediment depth, measured with the depth measuring faces of calipers. However, there are limited data on ecological thresholds of sediment depth: a small change of several millimeters suppressed turf algae growth but does not deter herbivory (Clausing et al.

2014), while larger changes of 15-17 mm reduced grazing and increased canopy height by approximately 50% (Bellwood and Fulton 2008, Goatley and Bellwood 2013). As with canopy height thresholds, categorizing sediment depth appears to be arbitrary or *post hoc*, so it would be informative to test ecosystem responses to a range of experimentally manipulated sediment depths. Finally, quantitative sediment depth measurements are most useful when reported relative to turf canopy height to account for the relationship between these turf algae characteristics.

Density

Turf density, although highly spatially variable (Harris et al. 2015), is weakly correlated with sediment content (Purcell and Bellwood 2001) and inversely correlated with coral settlement success (Birrell et al. 2005). Dense and tall turfs are twice as productive as shorter, sparser turfs (Wanders 1976), although density and canopy height have also been hypothesized to introduce self-shading and reduce productivity (Carpenter 1985). Therefore, we expect denser turfs to reflect lower grazing and to be strong competitors with coral because dense turfs grow more and retain more sediment, both of which negatively impact coral.

While rarely quantified as number of filaments per unit area, density is sometimes described qualitatively as sparse/dense (Wanders 1976), tightly woven/loosely branched (Birrell et al. 2005), or thin/thick (Casey et al. 2014). One labor-intensive way to quantify turf density is via microscopic examination, using mini-quadrats or visual inspection to quantify percent cover of algal filaments over replicate 1 square-cm plots (Harris et al. 2015). Two metrics that are more widely accessible are biomass per area, measured by scraping turf algae from a known area, then decalcifying, drying, and weighing (Purcell and Bellwood 2001) and qualitative descriptions of the amount of visible underlying limestone (Wanders 1976).

There is currently limited quantitative data on how turf density relates to herbivory, production, and competition, so studies that empirically measure or test this relationship would go far in advancing our understanding and setting numerical bounds on "dense" and "sparse" algal turfs. From qualitative studies, though, we know that sparse turfs with visible limestone reflect high herbivory and contain less sediment (Wanders 1976) (Fig 1.1B), suggesting that these types of turf algae will not outcompete adult or larval corals (Birrell et al. 2005). In contrast, dense turfs, with little visible limestone and potentially packed with sediment (Fig 1.1C), are likely to be more productive, present in environments with low herbivory, and superior competitors to larval and adult corals.

Specific Diagnostic Taxa / Community Composition

Detailed analyses of the entire turf assemblage are rare and labor intensive (but see Smith et al. 2010, Harris et al. 2015, Diaz-Pulido and McCook 2002, Fricke et al. 2011, van den Hoek et al. 1975), but the presence and prevalence of a few diagnostic turf taxa with specific distinguishing characteristics is sufficient for understanding both grazing pressure and likelihood of competitive success against corals. For example, an abundance of simple, easily digestible turf taxa indicates either minimal grazing pressure (Scott and Russ 1997) or early succession turfs (Diaz-Pulido & McCook 2002, Fricke et al. 2011). Specific taxa that indicate low grazing are the siphonous green algae *Acetabularia* and *Taeniomia,* taxa with simple morphologies such as *Cladophora* and

Ulva (*Entermorpha*), and morphologically plastic *Lobophora*, which grows as either uncalcified crusts or blades (Scott and Russ 1997, Smith et al 2010, Harris Ch. 3). Notably, none of these taxa are calcified. The absence or rarity of these taxa coupled with high abundance of calcified branches or CCA (Scott and Russ 1997) indicates high grazing intensity, or high grazing coupled with high nutrients (Smith et al. 2010). Additionally, species richness tends to be higher where grazing is lower or experimentally removed (Scott and Russ 1997, Smith et al. 2010, Harris Ch. 3).

Several turf algae taxa are known to actively overgrow or kill adult corals including the red algae *Corallophila*, *Anotrichium* (Jompa & McCook 2003a, b) and *Gracilaria* (Barott et al. 2009), the green alga *Chlorodesmis* (Bonaldo and Hay 2014), and the brown alga *Dictyota* (Barott et al. 2011). Turf assemblages that include these species should have superior competitive abilities over corals, even though other species in the turf assemblage could be weaker competitors. The cyanobacteria *Moorea* (*Lyngbya*), brown algae *Dictyota* and *Lobophora* (Kuffner et al 2006), and the green alga *Ulva* (Vermeij et al 2009) cause mortality or avoidance behavior settling coral larvae. There are varying, and sometimes unknown, mechanisms for these negative effects on corals, including allelochemical activity (Bonaldo and Hay 2014) and microbially-mediated hypoxia (Barott et al 2011).

Interestingly, *Ulva, Dictyota* and *Lobophora* are all both indicative of low grazing pressure and can negatively affect coral. While these taxa (along with *Gracilaria* and *Chlorodesmis*) grow as macroalage, their early life stages are frequently found in turf assemblages. Therefore, these taxa could be particularly important as early indicators of positive feedback loops in which low grazing allows them to increase in abundance, their presence reduces coral abundance, turfs gain a competitive advantage, and coral abundance continues to decrease.

The entire turf assemblage or just the above focal taxa can be identified and quantified in via microscopic inspection: either directly on pieces of carbonate submerged in seawater or by scraping a known area with a razor blade onto a microscope slide, then staining with aniline blue for easier identification of cellular structure. Quantitative assemblage structure (e.g. relative percent cover of taxa) is more informative than presence/absence lists.

Summary

Turf algae are an abundant, important, and overlooked component of coral reef ecosystems. Here we have synthesized data showing that turfs are abundant members of reef benthos all over the world, and we hypothesize that turf algae are increasing in prevalence in response to disturbances that degrade coral reef health. However, turf algae are typically overlooked in ecological studies of coral reefs. Where turfs are measured, they are treated as a single homogenous functional group and measured as a percentage of the benthos. In fact, turfs are multispecies assemblages with heterogeneous characteristics that respond to the biotic and abiotic environment in predictable and informative ways. Our proposed framework for studying turf algae captures the most essential elements of the ecological role of turf algae in coral reef systems.

Measuring all four of the framework metrics outlined above provides the most complete picture of the ecology of both the turf assemblage itself and of the broader reef ecosystem, allowing for quantitative comparisons among locations and over time.

However, such a detailed analysis is unnecessary for many purposes. Instead, just one or two of these metrics provides sufficient information for specific research interests and is far better than the previous standard protocol of treating turfs as a homogenous functional group (Table 1.4). For example, those interested in biodiversity and chemical ecology should record taxonomic assemblage, while insight into the ecology of microbes and meiofauna comes from measuring canopy height, sediment content, and assemblage.

Table 1.6 Guidelines for adapting the turf algae framework to specific research needs.

If you're interested in	And you want to know about	Then measure these turf metrics
Biodiversity	Species diversity	Assemblage
Chemical ecology	Specific taxa with chemical activity	Assemblage
Microbial ecology	Microbial abundance	Sediment content, canopy height
	Microbial communities	Canopy height
Meiofauana	Meiofaunal communities	Density, sediment content
	Meiofaunal abundance	Canopy height, sediment content
Herbivores	Grazing intensity	Canopy height, density
	Grazing type	Density, assemblage
Competition	Turf-coral competition	Canopy height, sediment content, assemblage
	Larval settlement	Canopy height, sediment content, density

Coral cover and fish abundance are already routinely measured in most monitoring programs, so managers should add to existing monitoring protocols, in order of decreasing importance and increasing difficulty: turf canopy height, density, and sediment content. These metrics reflect grazing type, grazing intensity, and degree of competition with adult and larval corals. Further, changes in these metrics, particularly canopy height, can be sensitive indicators about changes in reef condition. For example, a slight reduction in canopy height could be the first indication that a marine reserve has improved benthic reef condition via enhanced herbivore consumption, even before there are measurable changes in fish populations, or cover of turfs and coral.

This framework is targeted toward ecology of coral reefs, so it provides little direct information about, for example, productivity or reef carbonate chemistry. However, some metrics are proxies for processes outside ecology. For example, changes in canopy height can be translated into ecosystem productivity (e.g. g C / area / time) and assemblage measurements can be geared toward proportion of calcifying and non-calcifying taxa.

Ultimately, measuring any (or all) of these turf algae metrics is a significant improvement in understanding the ecological processes on a coral reef. Turf algae are a diverse group that is far from homogenous. The old way of studying turfs – that is, to lump them together and describe only spatial extent or, worse, ignore them entirely or group them with macroalgae, CCA or bare space– ignores their role as food for herbivores, competitors with corals, and contributors to reef productivity. Coral reefs are facing increasing threats, and research to understand how these threats impact reefs should be based in understanding the ecology of the reef system, which includes the ecology of the prevalent and important turf algae.

Appendix: Frameworks/classification schemes in analogous systems

There are many assemblages in different ecosystems in which simple abundance or percent cover metrics are insufficient to describe their important ecological functions.

For example, stream invertebrates, grasslands, microalgal biofilms, periphyton, and bacteria are all most easily described using abundance metrics. However, in each of these systems there is a rich history of frameworks to measure and describe function, such as indicating pollution or ecosystem productivity. In some cases, species-level identification is too difficult or not possible given current tools (e.g. aquatic invertebrates, unculturable bacteria), while in other cases, abundance metrics simply do an inadequate job of addressing the question at hand.

Freshwater streams were one of the first systems for which a robust set of metrics based on richness of the flora and fauna was developed as an indicator of pollution (Patrick 1950). The original scheme has been repeatedly updated, refined, and adjusted to additional environments (Chutter 1972, Patrick and Palavage 1994). These frameworks reduced the hundreds of freshwater stream taxa from many phyla to a manageable set of indicator taxa that could be adapted to different locations or processes of interest (Metcalf 1989), thereby streamlining the processes for describing a complex community.

Descriptive frameworks based on function have been perhaps most widely used in grasslands. There are numerous frameworks (reviewed in Lavorel et al 1997), but just a few key functions are directly related to both community productivity and invasion resistance (Tilman et al 1997, Diaz and Cabido 2001, Dukes 2001), thus descriptions of complex communities to just a few metrics. While most grassland functional frameworks are based on physiology (e.g. C3 or C4, nitrogen fixation), physical characteristics (e.g. root depth, canopy morphology) are also closely related to ecosystem production (Hooper and Dukes 2004). Therefore, using these frameworks to describe grasslands provides more information than does biomass alone, but retains the simplicity of a small set of metrics.

In communities for which abundance is not particularly informative, there are new frameworks emerging. For example, freshwater diatom communities can be described using biomass or diversity, but metrics like growth form and reproductive type are even more useful in understanding ecosystem processes (Patrick 1976). Nematodes in soils can be classified as colonizers or persisters, resulting in a "maturity index" of the soil condition (Bongers 1990), while seed banks in soils are classified under a range of metrics that move well beyond abundance, including seed size, depth, chemical defense, and life history (Thompson 2000). Marine invertebrate assemblages in infaunal (Waldbusser et al 2004) and benthic (Bremner et al 2006) habitats are classified by functions such as feeding mode, size, and attachment. Each of these frameworks allows scientists to gather more information than we could get from only measuring biomass or diversity.

More recently, genetic tools provide a way to move beyond abundance measures for microscopic taxa, for example measuring how biofilm diversity changes over time in response to abiotic conditions in freshwater (Moss et al. 2006) and marine (Witt et al 2012) systems. Even newer metagenomic techniques for bacterial communities quantify community function, instead of taxonomic diversity (Riesenfeld et al 2004). For example, recent efforts have described and compared bacterial communities from wildly diverse ecosystems using physiological metrics like virulence, metabolism, mobility, production of secondary metabolites (Tringe et al 2005, Dinsdale, Edwards et al 2008). This type of framework for describing and comparing bacterial communities is both more practical and more informative than a simple species or abundance comparison.

Chapter 1, in part, is currently being prepared for submission for publication of the material. Harris, Jill and Jennifer Smith. “Tropical algal turfs: a review of their ecology and a framework for their analysis.” The dissertation author was the principal researcher and author of this material.

References

Adey WH, Goertemiller T (1987) Coral reef algal turfs: master producers in nutrient poor seas. Phycologia 26:374–386

Airoldi L (1998) Roles of disturbance, sediment stress, and substratum retention on spatial dominance in algal turf. Ecology 79:2759–2770

Arnold SN, Steneck RS, Mumby PJ (2010) Running the gauntlet: Inhibitory effects of algal turfs on the processes of coral recruitment. Mar Ecol Prog Ser 414:91–105

Aronson RB, Precht WF, Toscano MA, Koltes KH (2002) The 1998 bleaching event and its aftermath on a coral reef in Belize. Mar Biol 141:435–447

Arthur R, Done TJ, Marsh H (2005) Benthic recovery four years after an El Niño-induced coral mass mortality in the Lakshadweep atolls. Curr Sci 89:694–699

Bak RPM, Engel MS (1979) Distribution, abundance and survival of juvenile hermatypic corals (Scleractinia) and the importance of life history strategies in the parent coral community. Mar Biol 54:341–352

Bakus G (1966) Some relationships of fishes to benthic organisms on coral reefs. Nature 210:280–84

Barott KL, Rodriguez-Mueller B, Youle M, Marhaver KL, Vermeij MJ a, Smith JE, Rohwer FL (2011) Microbial to reef scale interactions between the reef-building coral *Montastraea annularis* and benthic algae. Proc R Soc B Biol Sci 279:1655–64

Barott KL, Rohwer FL (2012) Unseen players shape benthic competition on coral reefs. Trends Microbiol 20:621–628

Barott K, Smith JE, Dinsdale EA, Hatay M, Sandin S, Rohwer F (2009) Hyperspectral and physiological analyses of coral-algal interactions. PLoS One 4:e8043

Barott K, Williams G, Vermeij M, Harris J, Smith J, Rohwer F, Sandin S (2012) Natural history of coral−algae competition across a gradient of human activity in the Line Islands. Mar Ecol Prog Ser 460:1–12

Belliveau SA, Paul VJ (2002) Effects of herbivory and nutrients on the early colonization of crustose coralline and fleshy algae. Mar Ecol Prog Ser 232:105–114

Bellwood D, Fulton C (2008) Sediment-mediated suppression of herbivory on coral reefs: decreasing resilience to rising sea levels and climate change? Limnol Oceanogr 53:2695–2701

Bender D, Diaz-Pulido G, Dove S (2014) Warming and acidification promote cyanobacterial dominance in turf algal assemblages. Mar Ecol Prog Ser 517:271–284

Benedetti-Cecchi L, Pannacciulli F, Bulleri F, Moschella PS, Airoldi L, Relini G, Cinelli F (2001) Predicting the consequences of anthropogenic disturbance: Large-scale effects of loss of canopy algae on rocky shores. Mar Ecol Prog Ser 214:137–150

Birkeland C (1977) The importance of rate of biomass accumulation in early successional stages of benthic communities to the survival of coral recruits. Proc 3rd Int Coral Reef Symp

Birrell CL, McCook LJ, Willis BL (2005) Effects of algal turfs and sediment on coral settlement. Mar. Pollut. Bull. 51:408–414

Birrell CL, McCook LJ, Willis BL, Diaz-Pulido G (2008) Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. Oceanogr Mar Biol an Annu Rev 46:25–63

Birrell CL, McCook L, Willis B, Harrington L (2008) Chemical effects of macroalgae on larval settlement of the broadcast spawning coral *Acropora millepora*. Mar Ecol Prog Ser 362:129–137

Bonaldo R, Bellwood D (2008) Size-dependent variation in the functional role of the parrotfish *Scarus rivulatus* on the Great Barrier Reef, Australia. Mar Ecol Prog Ser 360:237–244

Bonaldo RM, Bellwood DR (2009) Dynamics of parrotfish grazing scars. Mar Biol 156:771–777

Bonaldo RM, Bellwood DR (2011) Spatial variation in the effects of grazing on epilithic algal turfs on the Great Barrier Reef, Australia. Coral Reefs 30:381–390

Bonaldo RM, Hay ME (2014) Seaweed-coral interactions: variance in seaweed allelopathy, coral susceptibility, and potential effects on coral resilience. PLoS One 9:e85786

Bonaldo RM, Krajewski JP, Sazima C, Sazima I (2006) Foraging activity and resource use by three parrotfish species at Fernando de Noronha Archipelago, tropical West Atlantic. Mar Biol 149:423–433

Brown AL, Carpenter RC (2015) Water flow influences the mechanisms and outcomes of interactions between massive *Porites* and coral reef algae. Mar Biol 162:459–468

Bruggemann J, Kuyper M, Breeman A (1994) Comparative analysis of foraging and habitat use by the sympatric Caribbean parrotfish *Scarus vetula* and *Sparisoma viride* (Scaridae). Mar Ecol Prog Ser 112:51–66

Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. PLoS One 2:e711

Burkepile DE, Hay ME (2010) Impact of herbivore identity on algal succession and coral growth on a Caribbean reef. PLoS One 5:e8963

Carpenter R (1981) Grazing by *Diadema Antillarum* (Philippi) and its effects on the benthic algal community. J Mar Res 39:749–766

Carpenter R (1985) Relationships between primary production and irradiance in coral reef algal communities. Limnol Oceanogr 30:784–793

Carpenter R (1986) Partitioning herbivory and its effects on coral reef algal communities. Ecol Monogr 56:345–364

Carpenter, R of Moorea Coral Reef LTER (2013) MCR LTER: Coral Reef: Long-term Population and Community Dynamics: Benthic Algae and Other Community Components, knb-lter-mcr.8.26 [Database]

Carpenter RC, Williams SL (1993) Effects of algal turf canopy height and microscale substratum topography on profiles of flow speed in a coral forereef environment. Limnol Oceanogr 38:687–694

Casey JM, Ainsworth TD, Choat JH, Connolly SR (2014) Farming behaviour of reef fishes increases the prevalence of coral disease associated microbes and black band disease. Proc R Soc B Biol Sci 281:20141032

Ceccarelli DM (2007) Modification of benthic communities by territorial damselfish: A multi-species comparison. Coral Reefs 26:853–866

Cheroske A, Williams S, Carpenter R (2000) Effects of physical and biological disturbances on algal turfs in Kaneohe Bay, Hawaii. J Exp Mar Bio Ecol 248:1–34

Church J, Obura D (2006) Sustaining Coral Reef Ecosystems and their Fisheries in the Kiunga Marine National Reserve, Lamu, Kenya. Proc 10th Int Coral Reef Symp, Okinawa. pp. 1381-1390.

Connell S, Kroeker KJ, Fabricius KE, Kline DI, Russell BD (2013) The other ocean acidification problem: CO2 as a resource among competitors for ecosystem dominance. Philos Trans R Soc B 368:20120442

Crossman DJ, Choat JH, Clements KD, Hardy T, McConochie J (2001) Detritus as food for grazing fishes on coral reefs. Limnol Oceanogr 46:1596–1605

Diaz-Pulido G, Gouezo M, Tilbrook B, Dove S, Anthony KRN (2011) High CO2 enhances the competitive strength of seaweeds over corals. Ecol Lett 14:156–62

Diaz-Pulido G, McCook LJ (2002) The fate of bleached corals: patterns and dynamics of algal recruitment. Mar Ecol Prog Ser 232:115–128

Edwards CB, Friedlander AM, Green AG, Hardt MJ, Sala E, Sweatman HP, Williams ID, Zgliczynski B, Sandin SA, Smith JE (2013) Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects. Proc R Soc B Biol Sci 281:20131835

English SS, Wilkinson CC, Baker VV (1997) Survey manual for tropical marine resources., 2nd edn. Australian Institute of Marine Science (AIMS), Townsville

Erdmann MV, Mohan C, eds (2013) A Rapid Marine Biological Assessment of Timor-Leste, RAP Bulletin of BiologicalAssessment 66, Coral Triangle Support Partnership, Conservation International Timor- Leste, Dili. 166 p

Fabricius K, De'Ath G (2001) Environmental factors associated with the spatial distribution of crustose coralline algae on the Great Barrier Reef. Coral Reefs 19:303–309

Fong P, Paul VJ (2011) Coral reef algae. In: Dubinsky Z, Stambler N (eds) Coral Reefs: an ecosystem in transition. Springer Netherlands, Dordrecht, p 242–272

Fox R, Bellwood D (2007) Quantifying herbivory across a coral reef depth gradient. Mar Ecol Prog Ser 339:49–59

Fricke A, Teichberg M, Beilfuss S, Bischof K (2011) Succession patterns in algal turf vegetation on a Caribbean coral reef. Bot Mar 54:111–126

Gleason MG (1996) Coral recruitment in Moorea, French Polynesia:the importance of patch type and temporal variation. J Exp Mar Bio Ecol 207:79–101

Gregg A, Hatay M, Haas A, Robinett N, Barott K, Vermeij M, Marhaver K, Meirelles P, Thompson F, Rohwer F (2013) Biological oxygen demand optode analysis of coral reef-associated microbial communities exposed to algal exudates. PeerJ 1:e107

Haas A, Al-Zibdah M, Wild C (2009) Effect of inorganic and organic nutrient addition on coral – algae assemblages from the Northern Red Sea. J Exp Mar Biol Ecol 380:99–105

Haas A, El-Zibdah M, Wild C (2010) Seasonal monitoring of coral–algae interactions in fringing reefs of the Gulf of Aqaba, Northern Red Sea. Coral Reefs 29:93–103

Harris JL, Lewis LS, Smith JE (2015) Quantifying scales of spatial variability in algal turf assemblages on coral reefs. Mar. Ecol. Prog. Ser. 532:41–57

Hamilton S, Smith J, Price N, Sandin S (2014) Quantifying patterns of fish herbivory on Palmyra Atoll (USA), an uninhabited predator-dominated central Pacific coral reef. Mar Ecol Prog Ser 501:141–155

Hatcher BG, Larkum AWD (1983) An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. J Exp Mar Bio Ecol 69:61–84

Hay ME (1981) The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. Ecology 62:739–750

Hixon MA, Brostoff W (1983) Damselfish as keystone species in reverse: intermediate disturbance and diversity of reef algae. Science 220:511–513

Hixon MA, Brostoff WN (1996) Succession and herbivory: effects of differential fish grazing on Hawaiian coral-reef algae. Ecol. Monogr. 66:67

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. Mar Freshw Res 50:839–66

Hoek C van den, Cortel-Breeman AM, Wanders JBW (1975) Algal zonation in the fringing coral reef of Curaçao, Netherlands Antilles, in relation to zonation of corals and gorgonians. Aquat Bot 1:269–308

Houk P, Musburger C, Wiles P (2010) Water quality and herbivory interactively drive coral-reef recovery patterns in American Samoa. PLoS One 5:e13913

Huff TM (2006) Impacts of human trampling and periodic sand inundation on Southern California intertidal algal turf communities: Implications for conservation and management of rocky shores. Scripps Institution of Oceanography, La Jolla, CA, USA

Johnson MD, Price NN, Smith JE (2014) Contrasting effects of ocean acidification on tropical fleshy and calcareous algae. PeerJ 2:e411

Jompa J, McCook LJ (2002) Effects of competition and herbivory on interactions between a hard coral and a brown alga. J Exp Mar Bio Ecol 271:25–39

Jompa J, McCook LJ (2003a) Contrasting effects of turf algae on corals: massive *Porites* spp. are unaffected by mixed-species turfs, but killed by the red alga *Anotrichium tenue*. Mar Ecol Prog Ser 258:79–86

Jompa J, McCook LJ (2003b) Coral-algal competition: macroalgae with different properties have different effects on corals. Mar Ecol Prog Ser 258:87–95

Jones G, Santana L, McCook L, McCormick M (2006) Resource use and impact of three herbivorous damselfishes on coral reef communities. Mar Ecol Prog Ser 328:215–224

Klumpp DW, Mckinnon AD (1989) Temporal and spatial patterns in primary production of a coral-reef epilithic algal community. J Exp Mar Bio Ecol 131:1–22

Klumpp DW, Mckinnon D, Daniel P (1987) Damselfish territories: zones of high productivity on coral reefs. Mar Ecol Prog Ser 40:41–51

Knowlton N (2001) The future of coral reefs. Proc Natl Acad Sci U S A 98:5419–5425

Kuffner IB, Walters LJ, Becerro MA, Paul VJ, Ritson-Williams R, Beach KS (2006) Inhibition of coral recruitment by macroalgae and cyanobacteria. Mar Ecol Prog Ser 323:107–117

Lang JC, Marks KW, Kramer PA, Kramer PR, Ginsburg RN (2010) AGRRA Protocols Version 5.4. [http://www.agrra.org/method/methodhome.html]

Larkum AWD (1983) The primary productivity of plant communities on coral reefs. In: Barnes DJ (ed) Perspectives on Coral Reefs. Australian Institute of Marine Sciences, p 221–230

Larkum AWD, Kennedy I, Muller W (1988) Nitrogen fixation on a coral reef. Mar Biol 98:143–155

Ledlie MH, Graham N a. J, Bythell JC, Wilson SK, Jennings S, Polunin NVC, Hardcastle J (2007) Phase shifts and the role of herbivory in the resilience of coral reefs. Coral Reefs 26:641–653

Linton, D and Bermuda Institute of Ocean Sciences (2013) A unified, long-term, Caribbean-wide initiative to identity the factors responsible for sustaining mangrove wetland, seagrass meadow, and coral reef productivity, February 1993 - October 1998 (NODC Accession 0000501). National Oceanographic Data Center, NOAA. Dataset. [26 June 2015]

Lirman D (2001) Competition between macroalgae and corals: effects of herbivore exclusion and increased algal biomass on coral survivorship and growth. Coral Reefs 19:392–399

Littler MM, Arnold KE (1982) Primary productivity of marine macroalagal functional-form groups from southwestern North America. J Phycol 18:307–311

Littler M, Littler D (1984) Relationships between macroalgal functional form groups and substrata stability in a subtropical rocky-intertidal system. J Exp Mar Bio Ecol 14:13–34

Lobel PS (1980) Herbivory by damselfishes and their role in coral reef community ecology. Bull Mar Sci 30:273–289

Marks, KW (2007) AGRRA Database, version (10/2007). Available online <www.agrra.org/Release_2007-10>

Marshell A, Mumby PJ (2015) The role of surgeonfish (Acanthuridae) in maintaining algal turf biomass on coral reefs. J Exp Mar Bio Ecol 473:152–160

McClanahan TR (1997) Primary succession of coral-reef algae: Differing patterns on fished versus unfished reefs. 218:77–102

McCook LJ (1999) Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. Coral Reefs 18:357–367

McCook LJ (2001) Competition between corals and algal turfs along a gradient of terrestrial influence in the nearshore central Great Barrier Reef. Coral Reefs 19:419–425

McCook LJ, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. Coral Reefs 19:400–417

McKenna SA, Baillon N, Spaggiari J (2009) Rapid Marine Biodiversity Assessment of the coral reefs of the northwest lagoon, between Koumac and Yandé, Province Nord, New Caledonia. RAP Bulletin of Biological Assessment 53. Conservation International, Arlington, VA, USA

McKenna SA, Hosken M, Baillon N (2011) Evaluation rapide de la biodiversité marine du lagon Nord-est de Touho à Ponérihouen, province Nord, Nouvelle-Calédonie.

Morrison D (1988) Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. Ecology 69:1367–1382

Morrissey J (1980) Community structure and zonation of macroalgae and hermatypic corals on a fringing reef flat of Magnetic Island (Queensland, Australia). Aquat Bot 8:91–139

Mustika PL, Ratha IMJ, Purwanto S, eds. (2012) The 2011 Bali Marine Rapid Assessment (2nd English edition August 2012). RAP Bulletin of Biological Assessment 64. Bali Marine and Fisheries Affairs, South East Asia Center for Ocean Research and Monitoring, Warmadewa University, Conservation International Indonesia, Denpasar. 137 pp.

National Coral Reef Monitoring Program, National Centers for Coastal Ocean Science, NOAA [24 June 2015]

Nugues MM, Roberts CM (2003) Coral mortality and interaction with algae in relation to sedimentation. Coral Reefs 22:507–516

O'Neil JM, Capone DG (2008) Nitrogen Cycling in Coral Reef Environments. In: Capone DG, Bronk DA, Mulholland MR, Carpenter EJ (eds) Nitrogen in the Marine Environment, 2nd edn. Academic Press, San Diego, p 949–989

Odum HT, Odum EP (1955) Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecol Monogr 25:291–320

Osborne K, Dolman AM, Burgess SC, Johns KA (2011) Disturbance and the dynamics of coral cover on the Great Barrier Reef (1995-2009). (B Gratwicke, Ed.). PLoS One 6:e17516

Pandolfi JM (2003) Global Trajectories of the Long-Term Decline of Coral Reef Ecosystems. Science 301:955–958

Penin L, Michonneau F, Carroll A, Adjeroud M (2011) Effects of predators and grazers exclusion on early post-settlement coral mortality. Hydrobiologia 663:259–264

Petersen D, Laterveer M, Schuhmacher H (2005) Spatial and temporal variation in larval settlement of reefbuilding corals in mariculture. Aquaculture 249:317–327

Potts DC (1977) Suppression of coral populations by filamentous algae within damselfish territories. J Exp Mar Bio Ecol 28:207-216

Purcell SW, Bellwood DR (2001) Spatial patterns of epilithic algal and detrital resources on a windward coral reef. Coral Reefs 20:117–125

River GF, Edmunds PJ (2001) Mechanisms of interaction between macroalgae and scleractinians on a coral reef in Jamaica. J Exp Mar Bio Ecol 261:159–172

Rix L, Bednarz V, Cardini U, Hoytema N van, Al-Horani F, Wild C, Naumann M (2015) Seasonality in dinitrogen fixation and primary productivity by coral reef framework substrates from the northern Red Sea. Mar Ecol Prog Ser 533:79–92

De Ruyter van Steveninck ED (1984) The composition of algal vegetation in and outside damselfish territories on a Florida reef. Aquat Bot 20:11–19

Sammarco PW (1983) Effects of fish grazing and damselfish territoriality on coral reef algae. I. Algal community structure. Mar. Ecol. Prog. Ser. 13:1–14

Sammarco PW (1991) Geographically specific recruitment and postsettlement mortality as influences on coral communities: The cross-continental shelf transplant experiment. Limnol Oceanogr 36:496–514

Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder RE, Walsh S, Jackson JBC, Knowlton N, Sala E (2008) Baselines and degradation of coral reefs in the Northern Line Islands. PLoS One 3:e1548

Short J, Kendrick GA, Falter J, McCulloch MT (2014) Interactions between filamentous turf algae and coralline algae are modified under ocean acidification. J Exp Mar Bio Ecol 456:70–77

Smith JE, Hunter CL, Smith CM (2010) The effects of top-down versus bottom-up control on benthic coral reef community structure. Oecologia 163:497–507

Smith JE, Shaw M, Edwards RA, Obura D, Pantos O, Sala E, Sandin SA, Smriga S, Hatay M, Rohwer FL (2006) Indirect effects of algae on coral: algae-mediated, microbe-induced coral mortality. Ecol Lett 9:835–845

Steneck RS (1988) Herbivory on Coral Reefs: A Synthesis. In: Proc 6th Int Coral Reef Symp.p 37–49

Steneck RS, Dethier MN (1994) A functional group approach to the structure of algal-dominated communities. Oikos 69:476–498

Tanner JE (1995) Competition between scleractinian corals and macroalgae: An experimental investigation of coral growth, survival and reproduction. J Exp Mar Bio Ecol 190:151–168

Vermeij MJA, Dailer ML, Walsh SM, Donovan MK, Smith CM (2010) The effects of trophic interactions and spatial competition on algal community composition on Hawaiian coral reefs. Mar Ecol 31:291–299

Vermeij MJ, Moorselaar I van, Engelhard S, Hörnlein C, Vonk SM, Visser PM (2010) The effects of nutrient enrichment and herbivore abundance on the ability of turf algae to overgrow coral in the Caribbean. PLoS One 5:e14312

Vermeij MJA, Sandin SA (2008) Density-dependent settlement and mortality structure the earliest life phases of a coral population. Ecology 89:1994–2004

Vermeij MJA, Smith JE, Smith CM, Vega Thurber R, Sandin SA (2009) Survival and settlement success of coral planulae: independent and synergistic effects of macroalgae and microbes. Oecologia 159:325–36

Wanders JBW (1976) The role of benthic algae in the shallow reef of Curaçao (Netherlands Antilles). I: primary productivity in the coral reef. Aquat Bot 2:235–270

Wanders JBW (1977) The role of benthic algae in the shallow reef of Curaçao (Netherlands Antilles) III: the significance of grazing. Aquat Bot 3:357–390

Wangpraseurt D, Weber M, Røy H, Polerecky L, Beer D de, Suharsono, Nugues MM (2012) In situ oxygen dynamics in coral-algal interactions. PLoS One 7:e31192

Wilkinson C (2008) Status of Coral Reefs of the World: 2008. Global Coral Reef Monitoring Network and Reef and Rainforest Research Center, Townsville, Australia, 296 p

Williams S, Carpenter R (1997) Grazing effects on nitrogen fixation in coral reef algal turfs. Mar Biol:223–231

Wilson SK, Bellwood DR, Choat JH, Furnas M (2003) Detritus in the epilithic algal matrix and its use by coral reef fishes. Oceanogr Mar Biol Annu Rev 41:279–309

Wismer S, Hoey A, Bellwood D (2009) Cross-shelf benthic community structure on the Great Barrier Reef: relationships between macroalgal cover and herbivore biomass. Mar Ecol Prog Ser 376:45–54

Chapter 2 Quantifying Scales of Spatial Variability in Algal Turf Assemblages on Coral Reefs

Jill Harris, Levi Lewis, and Jennifer Smith

Turfs all look the same
But are they homogeneous
or does scale matter?

Abstract

Quantifying variability over multiple spatial scales is a fundamental goal in ecology, providing insight into which scale-dependent processes most strongly influence community structure. On coral reefs, the ubiquitous turf algae are the primary food source for herbivores and competitors for space with corals. Turf algae will likely increase in the future, because they thrive under conditions that reduce coral cover. Turfs are typically treated as a single homogeneous functional group, but analyzing them as a variable assemblage is more informative. We used a hierarchical sampling design to quantify 4 scales of variability in turf assemblages from centimeters (within single dead coral heads) to kilometers (across islands) on the rarely studied Lhaviyani Atoll, Maldives. We used 4 metrics, each reflecting different ecological processes: percent cover, canopy height, richness, and assemblage composition. For most of these metrics, variability was significant at multiple spatial scales. However, for all metrics, the smallest scale (centimeters) explained the greatest proportion of overall variability. The least variability in cover, canopy height, and richness occurred among sites (100s meters), suggesting that processes such as com- petition, predation, and vegetative growth are heterogeneous at small scales. In contrast, assemblage composition was least variable at the largest scale (kilometers), suggesting that oceanographic processes or a well-mixed propagule supply reduce variability. With declining coral and increasing cover of turf on reefs worldwide, it will become increasingly important to understand the dynamics of

coral–turf competitive interactions. However, because turf assemblages are highly variable at small spatial scales, these interactions require more detailed consideration.

Introduction

Spatial heterogeneity is an intrinsic feature of ecological communities, and quantifying the hierarchical scales of this variability is a fundamental goal of ecology (Levin 1992). Numerous ecological and environmental factors, acting on different spatial scales, affect the variable abundance and distribution of species across a landscape (Menge & Olson 1990). Heterogeneity in community or assemblage structure is driven by succession (Odum 1969), which in turn is driven by disturbance (Connell 1978). Mechanisms behind the relationship between disturbance, succession, and community structure include life history strategies, nutrient uptake, reproductive potential, and interspecific competition (Connell & Slatyer 1977). Therefore, identifying scales of the greatest heterogeneity can elucidate which scale-dependent processes exert the most influence on community structure.

In many ecosystems, the smallest scales are characterized by stochastic events or processes, while at larger scales these random processes and patchy distributions even out and become more generalizable as biogeographic patterns (Levin 1992, Coleman 2002, Fraschetti et al. 2005). However, small-scale patchiness is not simply random, ecological noise (Coleman 2002) . In terrestrial, aquatic, and marine systems, small-scale heterogeneity and community diversity is driven by dispersal ability (Levin 1992, Marhaver et al. 2013), micro-patchiness in the physical habitat or substrate and both facilitative and inhibitive biological interactions (Pacala & Levin 1997). At larger scales (e.g., >100 kilometers), biogeographic factors, such as habitat and long-distance dispersal, appear to be more important (Underwood & Chapman 1996, Fraschetti et al. 2005). This spatial variability can be either compounded or counteracted by temporal variation, particularly in systems where small-scale spatial heterogeneity is the largest source of variation (Underwood 1991). However, interactions between spatial and temporal scales of variation require explicit examination of nested scales in both dimensions, which was beyond the scope of this study. Therefore, here we examine only the spatial aspects of variability as a foundation for future investigation into temporal variability.

Marine benthic community structure is typically, but not always, most spatially variable at small scales (Fraschetti et al. 2005). Grazing and competition (Steneck & Dethier 1994) are two of the most dominant processes that drive succession and thus heterogeneity in community structure. However, the effects of grazing are widely variable at scales ranging from meters (Iveša et al. 2010, Poray & Carpenter 2014) to local (Fletcher 1987) and regional scales (Foster 1990). Disturbance has long been known to play a major role in driving variability among communities separated by several meters in the rocky intertidal and subtidal habitats (Sousa 1979, Smale et al. 2010), and large scale disturbances such as storms, fires, or El Niño events can create heterogeneity over a scale of 10's or 100's of meters (Kennelly 1987, Collins 1992, Dayton et al. 1992). Propagule dispersal and recruitment contribute to community heterogeneity at both small (meters) (Andrew & Viejo 1998) and very large (100's km) spatial scales (Deysher & Norton 1981), depending on the type of reproduction (Bellgrove et al. 2004).

Many of these processes contribute to heterogeneity in marine algal assemblages, which can be most variable at scales ranging from centimeters (Rowan & Knowlton 1995) to kilometers (Tribollet et al. 2010). Importantly, though, marine algal assemblages appear to not be consistently structured at a global scale. One of the most widely applicable trends in global diversity patterns, the latitudinal diversity gradient, is a broad pattern of high species diversity at the equator and decreasing diversity as latitude increases (Pianka 1966). While the latitudinal diversity gradient is observed in almost every group of organisms in marine, terrestrial, and aquatic environments (Witman & Roy 2009), it, notably, does not apply to marine macroalgae (Santelices et al. 2009). Therefore, smaller scale processes may be more important in driving variability in algal communities. Specifically, heterogeneous recruitment and recovery from disturbance appear to be the most influential in structuring temperate algal turfing assemblages, which are most heterogeneous at smaller scales (Chapman & Underwood 1998).

Turf algae comprise a multi-species assemblage of taxonomically diverse algae and cyanobacteria. The definition of algal turf varies among temperate and tropical systems (Hatcher & Larkum 1983, Connell et al. 2014), sometimes including associated invertebrates (Huff 2006) and organic matter (Wilson et al. 2003). Here, tropical turf refers to only the algal component of the community with a canopy height of less than 1 centimeter. On coral reefs, turf algae are typically found growing on the calcium carbonate substrata of dead corals and rubble.

Turf assemblages are ecologically important, abundant, and significantly understudied components of the coral reef ecosystem. Turf algae are the main source of primary production on reefs (Wanders 1976), the primary food source for most coral reef herbivores (Carpenter 1986, Ledlie et al. 2007), can reduce the abundance of both adult and juvenile corals directly (i.e. overgrowth, allelochemicals) and indirectly (i.e. preemption of space, overgrowth of crustose coralline algae) (Birrell et al. 2005, 2008, Vermeij et al. 2010), and are rapid colonizers of open space after physical disturbances (Fong & Paul 2011), coral bleaching and disease (Diaz-Pulido & McCook 2002), and corallivory (Bonaldo & Bellwood 2009). Turf algae are more abundant than both coral and macroalgae on many coral reefs (Wismer et al. 2009). Turf algae are likely to become more abundant in the future, because they thrive under conditions that threaten coral health such as overfishing of herbivores, nutrient pollution (Smith et al. 2010), ocean acidification (Falkenberg et al. 2013), and sedimentation (Birrell et al. 2005). As anthropogenic impacts become more frequent and more extreme, turf algae will likely play an increasingly central role in the coral reef communities of the future. Therefore, a more comprehensive understanding of the structure and variability of turf assemblages is needed to better understand the overall ecology of reef ecosystems.

Most ecological studies treat turf algae as a single homogenous functional group. However, there is mounting evidence that different turf assemblages may play variable ecological roles. Turf assemblages at different successional stages vary in canopy height, density, and heterogeneity, causing variable effects on coral larval settlement (Birrell et al. 2005). Canopy height in particular may be an important physical trait of turf algae as taller turf assemblages trap more sediment, making them less susceptible to herbivory and possibly triggering a positive feedback loop leading to a persistent state of ungrazed, sediment-laden turf that is inhospitable to coral settlement (Bellwood & Fulton 2008). In addition to canopy height, morphologically distinct species within a turf assemblage have predictable differences in productivity, longevity, and susceptibility to herbivory (Steneck & Dethier 1994, Padilla & Allen 2000). For example, turf assemblages dominated by simple, filamentous algae would likely respond more quickly to nutrient enrichment but be more susceptible to herbivory compared to more complex corticated or calcified species. Individual turf algae species that are superior competitors to corals (Jompa & McCook 2003a) might be more likely to overgrow existing corals or prevent coral recovery following a disturbance event, while presence of taxa that are preferred by herbivores would indicate low levels of herbivory. A closer examination of both the physical traits and taxonomic composition of turf assemblages is needed.

There are few studies that have explicitly addressed how tropical turf assemblages vary across spatial scales, and the results are thus far conflicting. Diversity and assemblage structure vary across ocean basins (Anderson et al. 2005), across 10's of kilometers (Diaz-Pulido & McCook 2002, Stuercke & McDermid 2004) or 100's of kilometers (Chapman & Underwood 1998), with depth (Anderson et al. 2005), based on successional stage following a coral bleaching event (Diaz-Pulido & McCook 2002) and within damselfish territories (Lison de Loma & Ballesteros 2002), and in response to experimental manipulations of herbivory and nutrients (Smith et al. 2010). These results demonstrate quantifiable spatial patterns in turf assemblages and suggest that turf assemblage composition could be related to ecological function or environmental conditions. However, it remains unclear to what degree tropical turf assemblages vary at different spatial scales within a given system. A quantitative understanding of spatial variation in turf assemblages would help elucidate the spatial patterns of the biological and physical processes driving benthic reef community structure (Table 2.1). Once spatial patterns are understood, we can begin to examine both the processes that cause those patterns and the effects of those patterns on the community and ecosystem. Here we take the first step by quantifying the spatial patterns of a tropical turf assemblage.

Specifically, the purpose of this study was to describe a variety of turf assemblage characteristics at a greater level of detail than typically studied and to identify how these characteristics vary across spatial scales. To identify any scale-dependent processes that contribute most to the structure of tropical algal turf assemblages, we compared four functionally distinct metrics (total percent cover, canopy height, composition, richness, and assemblage composition) that each reflect different dimensions of the ecological role of turf algae, identifying the spatial scale (mm, cm, m, km) that explained the majority of variation for each metric.

Table 2.1 Sampling strategy at hierarchical spatial scales and the processes that likely contribute the most heterogeneity at each scale.

Scale	Distance between replicates		n	Processes
Punch	10 cm	(1×10^{-1} m)	256	Microhabitat suitability, vegetative growth, competition, herbivory
Colony	1 m	(1×10^{0} m)	64	Vegetative growth, morphology, competition, herbivory, time since coral death
Site	100 m	(1×10^{2} m)	16	Herbivory, abiotic environment
Island	5–10 km	(1×10^{4} m)	4	Currents, propagule dispersal, herbivory, nutrient availability

Methods

Site Description and Sample Collection

Turf algae were collected from the lagoonal reef flat of Lhaviyani Atoll (also called Faadhippolhu), Republic of the Maldives (Fig. 2.1). Lhaviyani is in the northern part of the Maldivian Archipelago in the Indian Ocean. The atoll is approximately 35 km in diameter and made up of 54 islets, 5 of which are inhabited with a total atoll population of approximately 9,000 (Maldives Population and Housing Census, 2006). The lagoon is physically sheltered but open to ocean flushing and swell and dominated by massive *Porites* and branching *Acropora* corals. Lagoon depths of approximately 50m have been reported. The tropical climate is driven by seasonal monsoons, with westerly winds over the wet summer and easterly winds in the drier winter.

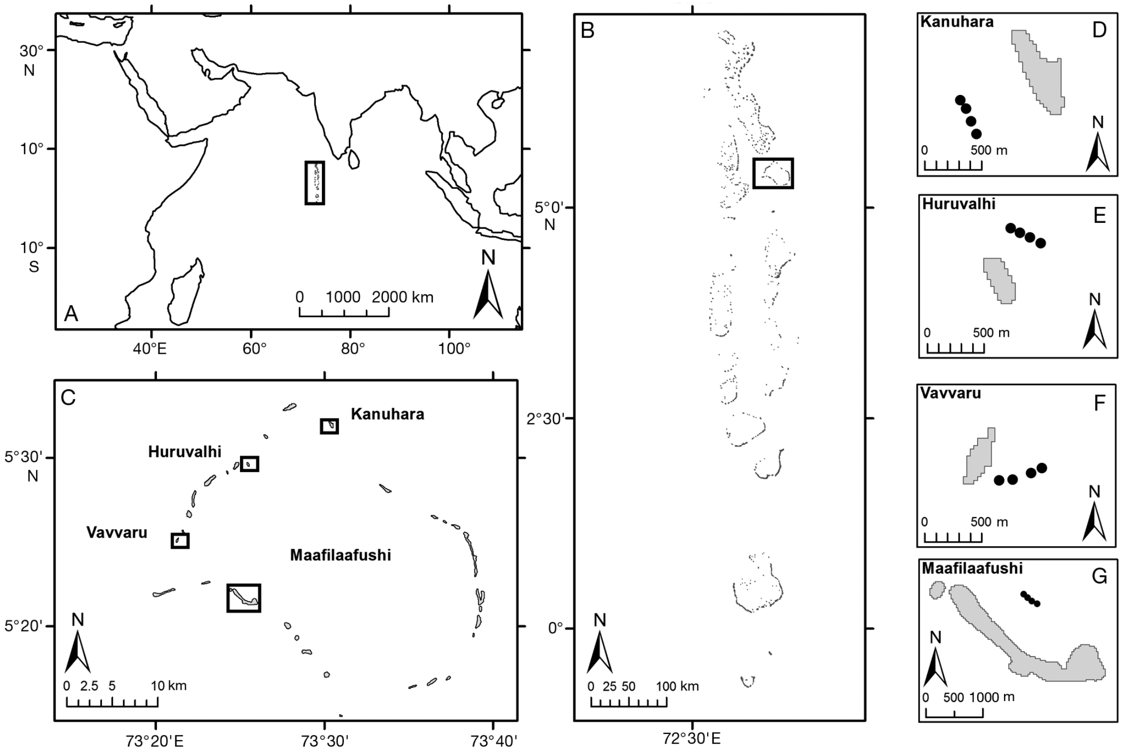

Figure 2.1 Hierarchical spatial arrangement of sampling locations. Algal turf samples were collected (A) from the Republic of the Maldives in the Indian Ocean, (B) from Lhaviyani Atoll in the northern part of the Maldives archipelago, (C) at four islands within Lhaviyani Atoll, and (D-G) from four sites at each island.

Reefs in Lhaviyani Atoll were recently affected by two major disturbance events: a massive bleaching event in 1998 and a tsunami in 2004. The bleaching event resulted in almost complete loss of branching and tabular corals in the portion of the atoll that was investigated (Loch et al. 2002, 2004). The tsunami completely washed over Lhaviyani's islands (Fritz et al. 2006, Kalhey, pers. comm.), which reach a maximum elevation of 1.5 m above sea level, but it was less damaging there than in more southern parts of the Maldives. While scientific data are lacking for Lhaviyani's reefs, these two significant disturbances likely 'reset' much of the reef ecosystem, killing many corals and opening up space for turf colonization. Algal turf assemblages in Lhaviyani are likely representative of algal turfs on other reefs that have experienced similar large-scale disturbances in the past few decades.

To quantify spatial variability in turf assemblages, replicate samples were collected using identical methods at four different scales: sample/punch (separated by ~10 cm), colony (separated by ~1 m), site (separated by ~100 meters), and island (separated by ~10 kilometers). Smaller scales reflect stochastic biological events and processes, such as different algal growth morphologies or individual herbivore grazing scars, while larger scales reflect broader population or landscape level processes including herbivore populations, propagule supply, and the abiotic environment (including thermal histories and bleaching events; Table 2.1).

Each scale was sampled with four replicates for a total of 256 turf samples. Samples were collected on SCUBA using a 1.3-cm diameter steel hollow punch and mallet, resulting in an area of 1.27 cm^2 per replicate. As the thalli of most tropical turf species are less than 1 mm in diameter, this allowed for a hypothetical assemblage of >100 densely packed filaments per punch. Importantly, this punch size was selected to allow the collection of four independent, non-adjacent punches from visually similar turf (Fig. 2.2A). To minimize variability due to light availability, exposure to herbivores, and edge effects, punches were all collected from massive *Porites* spp. coral colonies with at least 0.5m^2 partial mortality overgrown with turf algae, as flat as possible and oriented directly upward (i.e., perpendicular to incident irradiance). Sites were interior lagoonal reefs at depths of 4-5 m. Islands were individual islets comprising Lhaviyani Atoll. Samples were collected in July 2013 over the course of 11 days to minimize effects of temporal variability as much as possible. Upon collection, individual samples were placed in pre-labeled Ziploc bags and held in an ambient seawater bath. Once ashore, individual samples were preserved in 10% formalin and stored for analysis.

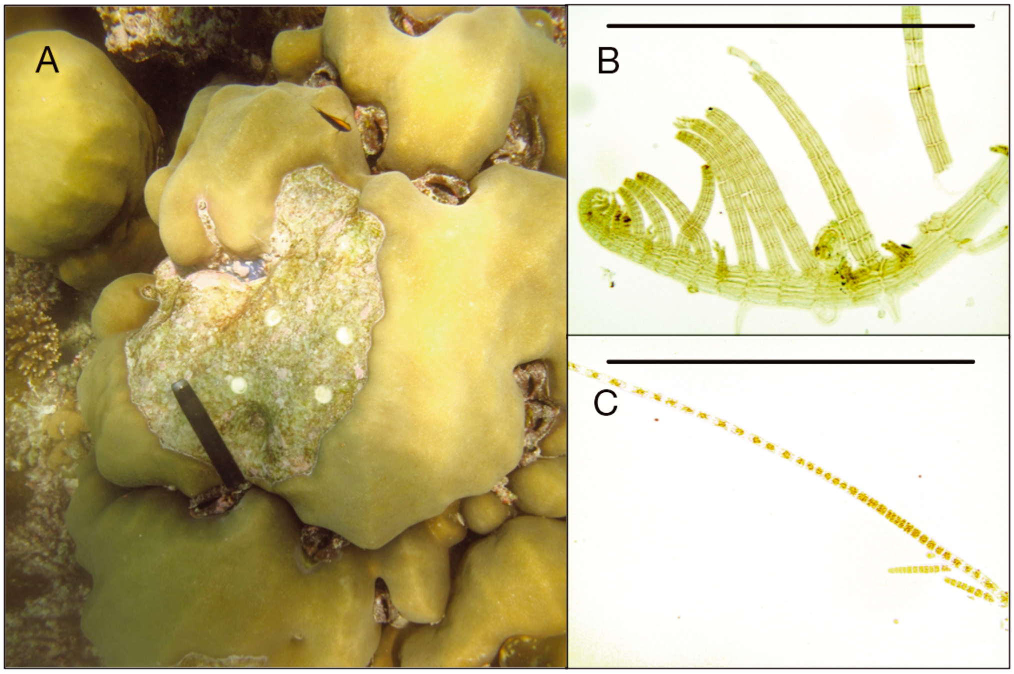

Figure 2.2 Photographic examples of turf communities. (A) The typical sampling area appeared visually homogenous (scale: black punch tool is 11.5 cm). (B) The uncorticaged, terete alga *Herposiphonia* (scale bar = 1 mm) was one of the most abundant and widespread taxa. In contrast, (C) uniseriate filamentous algae in the order Ectocarpales (scale bar = 0.5mm) were widespread but, due to their small size and growth habit, contributed a very small amount to percent cover.

We used four different metrics to analyze turf algae: total percent cover, canopy height, generic richness, and a multivariate comparison of assemblage composition. Total percent cover and canopy height are reflections of grazing pressure and algal growth rates, which can vary with nutrient availability and disturbance regimes. Differences in taxonomic richness and composition indicate an assemblage's potential ecological function or propagule dispersal. For example, dominance by heavily calcified or chemically defended taxa would characterize a turf assemblage heavily defended from grazing pressure, while dominance by fast-growing or larger taxa might suggest nutrient enrichment or signal an assemblage that would be competitively dominant over coral.

Samples were analyzed under a dissecting microscope for physical characteristics (% cover and canopy height) and taxonomic composition (to genus when possible). Total percent cover was visually estimated to the nearest 5%. Canopy height of six haphazardly selected algal filaments per sample was measured to the nearest 0.01 mm using digital calipers. Taxonomic composition was visually estimated to the nearest 1% (for taxa with cover ≤ 10%) and to the nearest 5% (for taxa with cover > 10%) and recorded as a fraction of total cover, providing descriptions of relative abundance of each taxon (taxa-specific cover as a percentage of total algal cover on a given sample). Closely related algal taxa that could not be consistently identified to genus due to lack of reproductive material were grouped together as follows: CCA (several species of crustose coralline algae), cyanobacteria (separated into cyanobacterial filaments and film-like cyanobacterial mats), Ectocarps (including the brown genera *Ectocarpus* spp. and *Hincksia* spp.), *Gelidium* and *Gelidiella* spp., and *Chondria* spp. and *Laurencia* spp. Following analysis, all taxa were coded as one of seven functional groups following the classification scheme of Steneck & Dethier (1994).

Statistical Analysis

To determine if heterogeneity of turf algae was related to spatial scale, univariate metrics (mean canopy height, total percent cover, and total number of taxa at the genus level unless otherwise noted) were each compared using hierarchical nested ANOVA, with colony nested within site and site nested within island. All factors were treated as random. To force non-negative variance components, a restricted maximum likelihood estimation model (REML) was used to calculate variance components. Because we used a completely balanced design, REML is equivalent to a 3-way nested hierarchical ANOVA (Fletcher & Underwood 2002). To understand what proportion of total variation was due to variability at each scale, variance for the three metrics is presented as both absolute variance and as a percent of total variation for each response variable separately (the 'magnitude of effect', Graham and Edwards 2001), thus allowing us to quantify total variability attributed to each scale and to determine the proportion of total variability that occurs between specific scales, respectively (Edwards 2004). While presenting variance components as proportions prevents direct comparisons across metrics (Underwood 1997) it does allow for a clearer picture of patterns of variability across scales within a given metric. To provide an estimate of the uncertainty in the variance components, 95% confidence intervals of variance components were calculated using parametric bootstrapping. Hierarchical ANOVAs and bootstrapping were performed using the *lmer* and *confint* functions (lme4 package), respectively, in R 3.1.2 (R Development Core Team, http://www.r-project.org).

Multivariate approaches were used to test whether spatial variability in turf assemblage composition, at the genus level, was related to scale. A hierarchical nested

PERMANOVA (permutation-based multivariate analysis of variance, Anderson 2001) with three factors (island, site, and colony) was run on a Bray-Curtis similarity matrix of relative percent cover data using PRIMER-E (v6). As with univariate metrics, colony was nested within site and site was nested within island; all factors were treated as random. Variance components for each spatial scale were calculated from the PERMANOVA mean squares, and statistical significance was tested under a reduced model with 9999 permutations. As with the univariate metrics, PERMANOVA variance components are presented as both absolute variance (square roots of estimates of components of variation, Anderson et al. 2008) and as a proportion of total variability within each response variable separately (Underwood & Chapman 1996).

To visually represent the similarity in turf assemblage structure within and among spatial scales, non-metric multidimensional scaling (nMDS) plots of all 256 samples were created based on ranked Bray-Curtis similarities. To visually represent the structure of turf assemblages for each island separately, individual nMDS plots were created for each of the four islands based on Bray-Curtis similarities of genus-level percent cover data.

We used a square-root transformation to increase the influence of less common taxa that could have unique ecological functions. We performed all analyses on both transformed and untransformed data. However, because the transformation made no material difference in the results or interpretation, we present only the untransformed data below.

Results

Turf Assemblage Composition

We identified 29 taxa (including the few higher order taxa that were indistinguishable to finer genus level) from 11 orders across four algal phyla (Table 2.2). Red algae were both the most common, accounting for 16 of the 29 taxa, and most abundant taxa, accounting for 56% of the total algal assemblage by cover. These patterns of red algal occurrence were driven by the abundant and diverse order Ceramiales, which accounted for 9 taxa and 40% of algae by cover. Seven of the 8 functional groups identified by Steneck and Dethier (1994) were represented, excluding only leathery macrophytes, which typically include only large macroalgae species not commonly found in turf assemblages. The most common functional group, in terms of prevalence in samples, was corticated terete algae, which included most of the taxa from the order Ceramiales.

Table 2.2 All algal taxa found, including percent cover (of all 256 punches) and percent occurrence (percentage of punches in which each taxon occurred). Functional groups are after Steneck and Dethier (1994): MIC: single-celled microalgae and cyanobacteria; FIL: simple uniseriate filaments; FOL: foliose (sheet of cells); CFL: complex foliose (multiple layers of cells); CRT: complex or corticated terete; ART: articulated calcified; CRU: calcified crusts; SPH: siphonous; CCA: crustose coralline algae. Abundances of the taxa shown in **bold** are presented in Fig 4.

Taxon	% Cover	% Occurrence	Order	Phylum	Functional group
Cyanobacterial filaments	30.0	93.4	–	Cyanophyta	MIC
Polysiphonia	28.9	93.0	Ceramiales	Rhodophyta	CRT
Gelidium/-iella	8.7	62.1	Gelidiales	Rhodophyta	CRT
Herposiphonia	7.9	67.6	Ceramiales	Rhodophyta	CRT
Dictyota	6.9	16.8	Dictyotales	Ochrophyta	CFL
CCA	5.0	27.7	Corallinales	Rhodophyta	CRU
Ectocarpales (multiple families)	2.8	30.1	Ectocarpales	Ochrophyta	FIL
Caulerpella	<2	41.0	Bryopsidales	Chlorophyta	SPH
Ceramium	<2	22.7	Ceramiales	Rhodophyta	CRT
Ulva	<2	16.0	Ulvales	Chlorophyta	FOL
Anotrichium	<2	12.9	Ceramiales	Rhodophyta	FIL
Gelidium – blades	<2	11.3	Gelidiales	Rhodophyta	CFL
Cladophora	<1	18.0	Cladophorales	Chlorophyta	FIL
Corallophila	<1	8.6	Ceramiales	Rhodophyta	CRT
Cyanobacterial mats	<1	5.5	–	Cyanophyta	MIC
Caulerpa	<1	4.3	Bryopsidales	Chlorophyta	SPH
Sphacelaria	<1	4.3	Sphacelariales	Ochrophyta	FIL
Bryopsis	<1	3.9	Bryopsidales	Chlorophyta	SPH
Jania	<1	3.1	Corallinales	Rhodophyta	ART
Centroceras	<1	2.3	Ceramiales	Rhodophyta	CRT
Chondria/Laurencia	<1	<2	Ceramiales	Rhodophyta	CRT
Champia	<1	<2	Rhodomeniales	Rhodophyta	CRT
Lobophora	<1	<2	Dictyotales	Ochrophyta	CFL
Rhipidosiphon	<1	<2	Bryopsidales	Chlorophyta	SPH
Condrophycus/Laurencia	<1	<1	Ceramiales	Rhodophyta	CRT
Griffithsia	<1	<1	Ceramiales	Rhodophyta	FIL
Peyssonnelia	<1	<1	Peyssonneliales	Rhodophyta	CRF
Unknown red blade	<1	<1	–	Rhodophyta	CRF
Unknown sp.	<1	<1	–	–	–

The single most abundant taxa were filamentous cyanobacteria (30 ± 22% cover, occurring on 93% of individual punches) and *Polysiphonia* spp. (29 ± 22% cover, occurring on 93% of punches) (Figs. 2.3 and 2.4). The next most abundant taxa, *Gelidium/-iella* spp., *Herposiphonia* spp. (Fig. 2B), and *Dictyota* spp., each had mean cover of less than 9% (Figs. 3 and 4). *Gelidium/-iella* spp. and *Herposiphonia* spp. were both abundant and widespread and were found on 62% and 68% of punches, respectively (Figs. 2.3 and 2.4). In contrast, while *Dictyota* spp. was abundant, it was not widespread and found in just 17% of punches (Figs. 2.3 and 2.4). However, when it was present it covered a large proportion of the substrate.

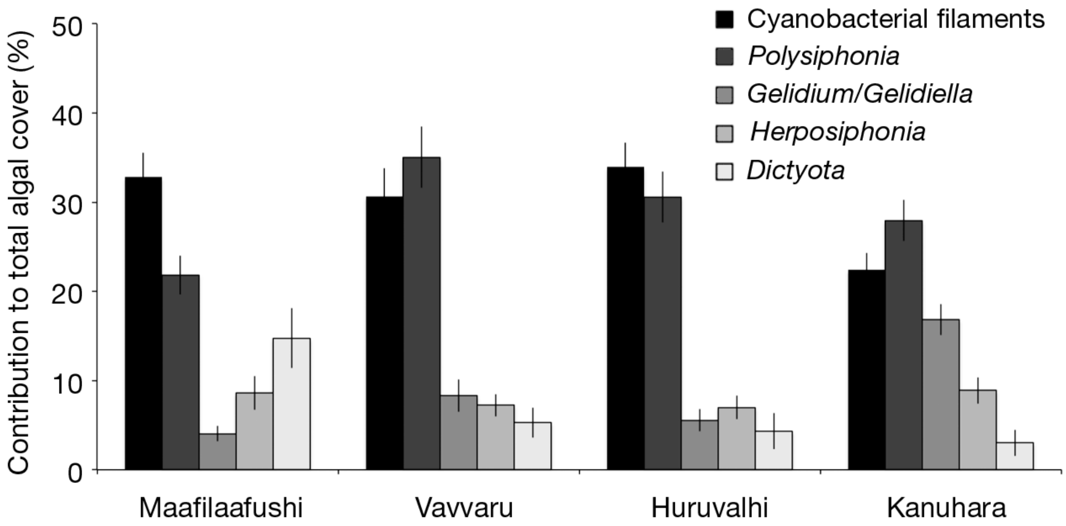

Figure 2.3 Relative contribution by cover (mean ± SE) of the five most abundant taxa on each island. Means and standard errors were calculated by treating all 64 punches on an island as individual replicates.

Most taxa were rare: 17 taxa had less than 1% cover (Table 2.2), either because they were physically small filaments that, due to their growth habit, did not cover much of the substrate (e.g. *Cladophora* spp., *Sphacelaria* spp., and Ectocarpales, Fig. 2.2C) or because they were only found on one or two individual punches (e.g. *Griffithsia* spp., *Peyssonnelia* spp., and two unidentified taxa).

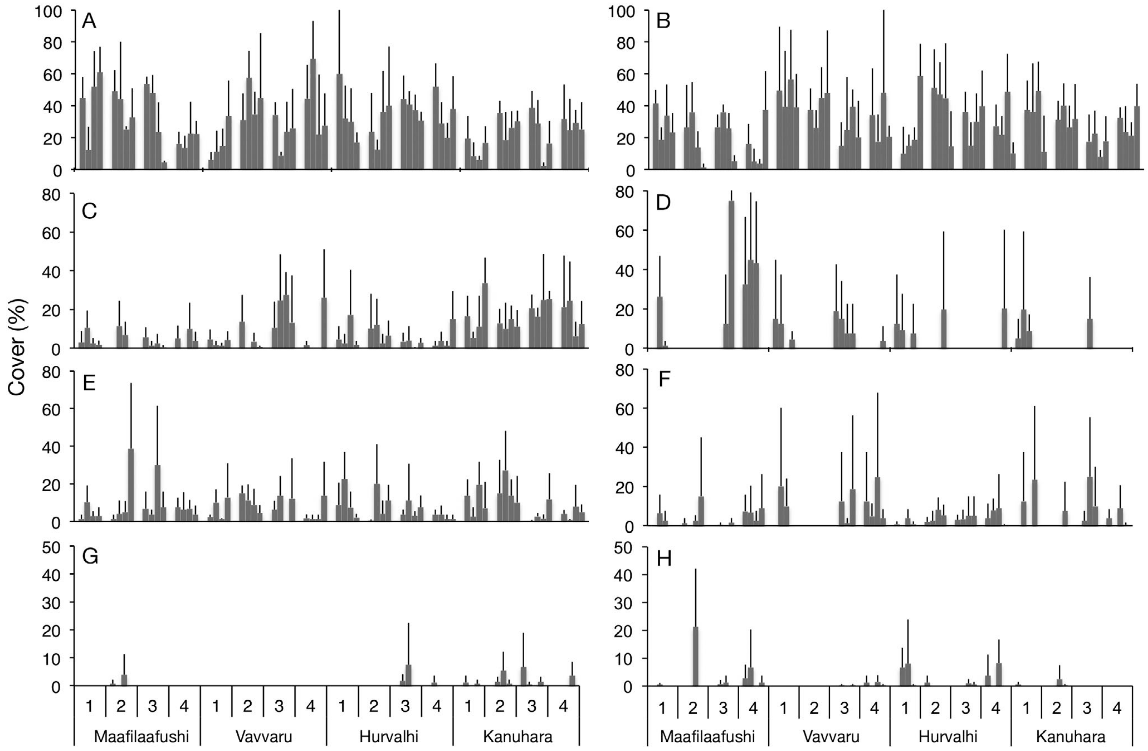

Figure 2.4 Mean (± SD) cover of eight key taxa by colony (n=4 colonies per site) at each of four sites on each island: (A) cyanobacterial filaments, (B) *Polysiphonia* spp., (C) *Gelidium/-iella* spp., (D) *Dictyota* spp., (E) *Herposiphonia* spp., (F) crustose coralline algae (CCA), (G) *Corallophila* spp., and (H) *Anotrichium* spp. Taxa selected were the most abundant (A-E), known to have positive effects on corals (F), or known to have negative effects on corals (G, H).

Turf Cover, Height and Richness

Total cover, canopy height, and richness were all approximately normally distributed based on distributions and quantile-quantile plots, thereby satisfying the assumptions for ANOVA. Mean total algal cover across all punches was 57.5% (± 1.6 SE), ranging from 10% to 100%. The remaining space was either bare limestone or microbial films. ANOVA revealed significant variation in total cover at the scales of island and colony but not among sites (Table 2.3a).

Table 2.3 Results of the hierarchical nested ANOVA tests, using a restricted maximum likelihood estimation model, on total algal cover, canopy height, and richness. All factors treated as random factors. Significance effects for α = 0.05 are shown in **bold**. Confidence intervals were calculated by bootstrapping. The proportion of variance explained by each spatial scale is presented in Fig. 2.6.

Source	df	MS	*F*	p	Variance component	95% CI
Total percent cover						
Island	3	2809	4.815	**0.020**	28.2	[0, 102.9]
Site (Island)	12	583.3	0.5279	0.89	0	[0, 45.6]
Colony (Site (Island))	48	1105	2.160	**0.0001**	122.2	[43.0, 191.1]
Residual = Punch	192	511.6			511.7	[432.8, 604.5]
Total	255					
Mean canopy height						
Island	3	0.9592	2.163	0.15	0.008	[0, 0.03]
Site (Island)	12	0.4435	1.310	0.24	0.006	[0, 0.03]
Colony (Site (Island))	48	0.3386	3.574	**<0.0001**	0.061	[0.03, 0.09]
Residual = Punch	192	0.0947			0.095	[0.08, 0.1]
Total	255					
Taxonomic richness						
Island	3	33.9	9.555	**0.0017**	0.49	[0, 1.5]
Site (Island)	12	3.553	0.9094	0.55	0	[0, 0.19]
Colony (Site (Island))	48	3.908	2.332	**0.0001**	0.54	[0.02, 0.8]
Residual = Punch	192	1.676			1.68	[0, 2.0]
.	255					

Eight key taxa were selected to more closely investigate ecologically-relevant variability across scales. These taxa included the five most abundant taxa (cyanobacterial filaments, *Polysiphonia* spp., *Herposiphonia* spp., *Gelidium/-iella* spp., *Dictyota* spp., Table 2.2), one “ecologically positive” taxon known to be beneficial to reef accretion and coral settlement (CCA), and two “ecologically detrimental” taxa known to have harmful effects on coral (*Corallophila* spp. and *Anotrichium* spp., Jompa & McCook 2003a). Cover of all of these representative taxa was highly variable across sites, with no discernible patterns in abundance at the colony, site, or island level (Fig. 2.4).

Mean canopy height across all punches was 1.3 mm (± 0.03 SE), ranging from 0.4 to 3.8 mm. Mean canopy height varied significantly only among colonies and not at greater scales among sites or islands (Table 2.3b).

Mean generic richness of all punches was 5.5 (± 0.1 SE) taxa per punch (per 1.3 cm^2). Richness ranged from 1 to 10 taxa per punch. Punches from Vavvaru had the lowest mean richness at all spatial scales, but also had the single punch with the highest richness. There was significant variation in number of taxa at the scales of island and colony, but not among sites (Table 2.3c). The cumulative number of unique taxa increased with sampling area and appeared to approach an asymptote (n = 29 taxa) across all 256 punches (approximately 340 cm^2 sampled, Fig. 2.5).

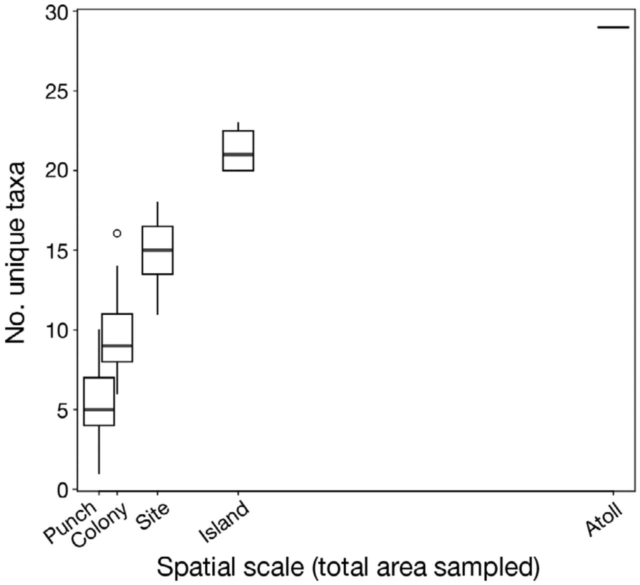

Figure 2.5 Cumulative number of unique taxa at each spatial scale. Horizontal bars show medians, boxes are drawn at the first and third quartiles, whiskers display the range of the data, and outliers (open circles) are more than 1.5 times the interquartile range outside the box.

Variance components for all three of these univariate measures were greatest at the smallest scale (Table 2.3), such that the smallest spatial scale explained the largest proportion of the total variation (Fig. 2.6). Estimates of residual variance were always greater than variance at any other scale and accounted for more than 50% of the total variability, indicating that there was high variation among individual punches. Both absolute and proportional variability decreased as spatial scale increased from the punch to the site level, which always contributed the least to total variance (Table 2.3, Fig. 2.6). In fact, among-site variability contributed nearly 0% to overall variability for both total cover and richness. Among-island variability always explained a greater proportion of total variation than among-site variability. Although variability was highly significant at all spatial scales, the 95% confidence intervals of variance components were overlapping among many of the larger scales. However, the confidence interval around variance at the punch level did not overlap any other confidence intervals for either percent cover or mean canopy height.

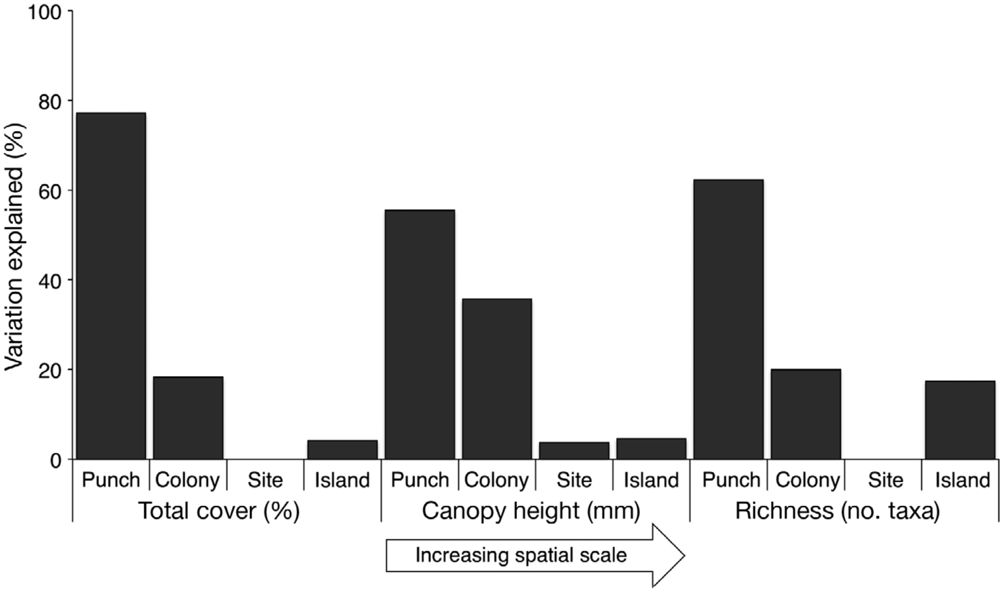

Figure 2.6 Percent of total variation in three turf characteristics explained by each spatial scale. Percent variation explained was calculated as the 'magnitude of effect' of each scale: individual variance components divided by the sum of all variance components for each metric. Estimates of uncertainty around variance components in Table 2.3.

Scales of Assemblage Variation

Variability in taxonomic similarity among assemblages was significant at all spatial scales based on nested PERMANOVA (Table 2.4). As with the univariate metrics, multivariate variability was greatest at the smallest scales, and variance components decreased (assemblages became more homogenous) as spatial scale increased (Table 2.4, Fig. 2.7d). There was approximately 32% residual variability unexplained by the scales sampled, indicating the greatest proportion of multivariate heterogeneity was among individual punches. The variance components were significantly different from zero at all spatial scales based on 9999 permutations (Table 2.4) and followed the same pattern as the results obtained from the nested univariate ANOVAs.

Table 2.4 Permutational multivariate ANOVA based on Bray-Curtis dissimilarities of relative percent cover of turf algae genera. Analysis was based on 9999 permutations. Significance effects for α = 0.05 are shown in **bold**. The proportion of variance explained by each spatial scale is presented in Fig. 2.7.

Source	df	MS	Pseudo-*F*	p (perm)	Variance component
Island	3	9231.6	1.943	**0.0198**	70.02
Site (Island)	12	4750.3	1.681	**0.0037**	120.25
Colony (Site (Island))	48	2862.4	2.052	**0.0001**	362.27
Residual = Punch	192	1377.3			1377.3
Total	255				

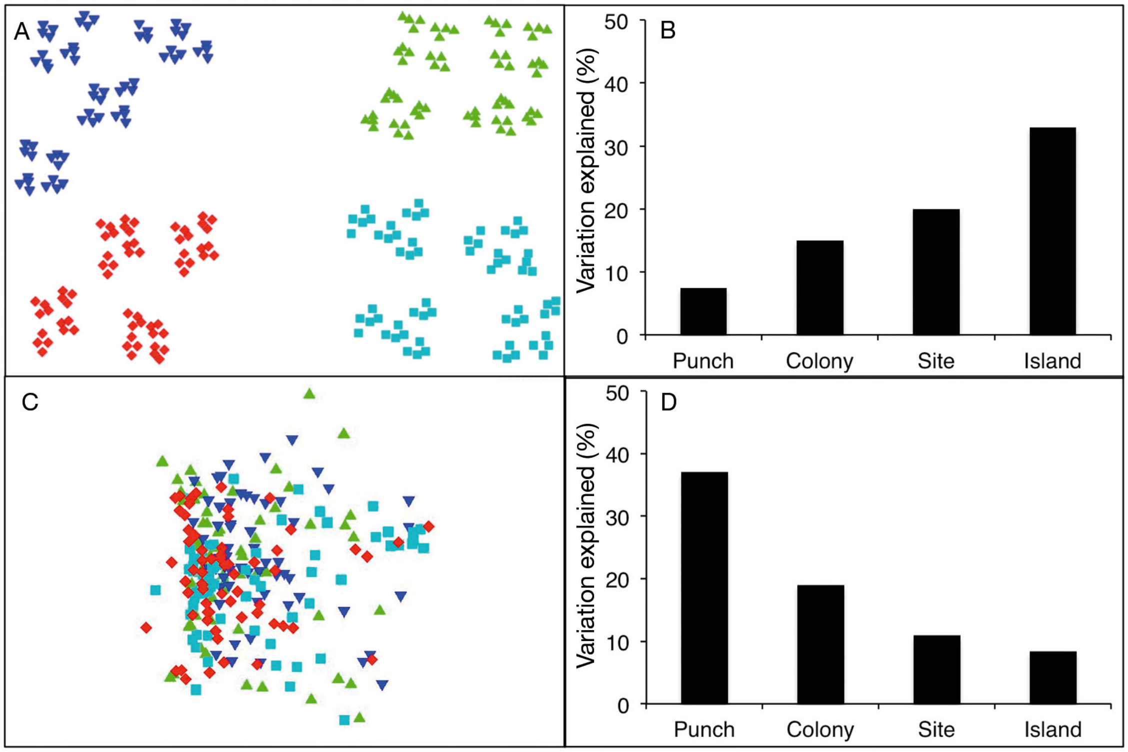

Figure 2.7 Comparison of two possible relationships between variability and spatial scale. (A) Theoretical non-metric multidimensional scaling (nMDS) plot of similarity among samples from 4 different spatial scales in which communities are most similar at smaller scales (e.g. within a single colony) and most dissimilar at larger scales (among islands). Symbols differentiate the 4 islands: green triangles = Vavvaru; blue inverted triangles = Kanuhara; light blue squares = Maafilaafushi; red diamonds = Huruvalhi. This clustering pattern in an MDS plot would correspond to (B) a theoretical positive relationship between spatial scale and percent of total variation in taxonomic composition, where the greatest amount of variation in community composition occurs among samples from different islands. (C) Actual nMDS plot of all samples (n = 256) based on Bray−Curtis similarities (stress = 0.2) of untransformed relative abundances. Symbols dif- ferentiate the 4 islands as in A. (D) Actual percent of total variation in turf communities explained by each spatial scale from square roots of estimates of variance components from PERMANOVA (Table 4)

The clear pattern of variability decreasing as spatial scale increases is reflected in the nMDS plot of all 256 samples (Fig 2.7c), which shows no clear grouping among samples at the colony, site, or island level. Instead, individual punches are fairly evenly scattered such that larger scale groups overlap completely (i.e. islands almost completely overlap all other islands).

The same inverse relationship between variability and spatial scale are visible in nMDS plots of assemblage structure at individual islands (Fig. 2.8). There is no clear visual separation between sites because variability is greater within than among sites. Note, however, that with such large sample sizes (n=64) the nMDS stress ranges from 0.16-0.19, and therefore these configurations should be interpreted conservatively.

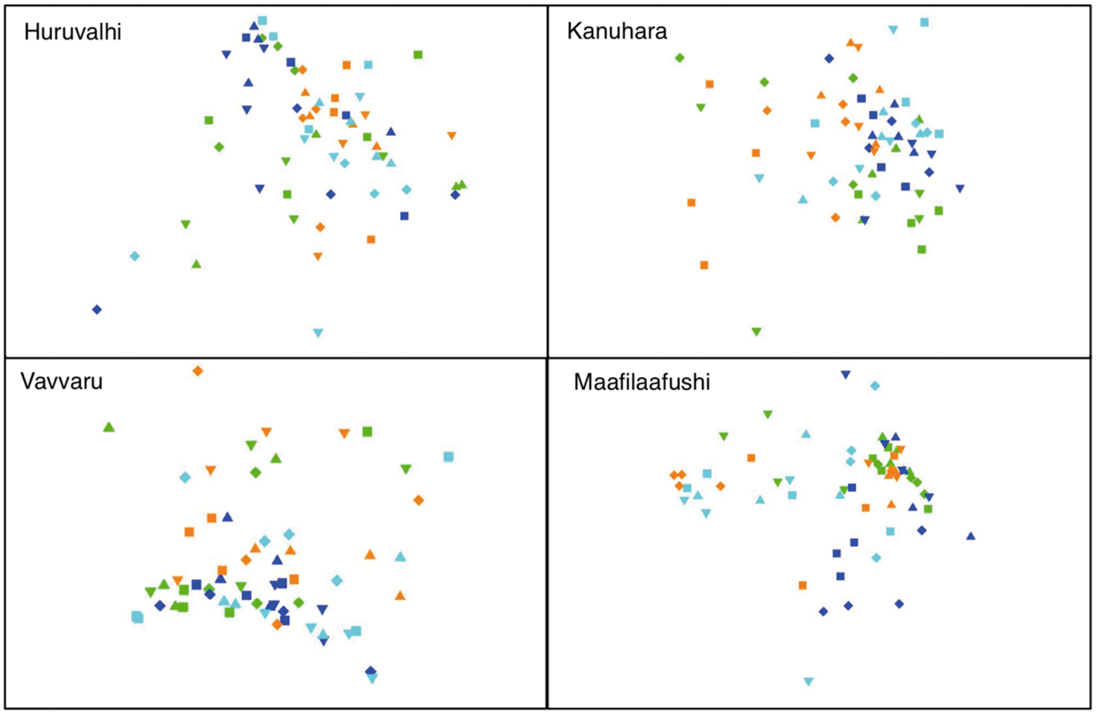

Figure 2.8 Non-metric multidimensional scaling plots of untransformed relative abundance on punches (n = 64) from each island. Colors indicate site (for all islands, green = site 1, orange = site 2, dark blue = site 3, light blue = site 4) and shapes indicate colony (for all islands, square = colony 1, diamond = colony 2, triangle = colony 3, inverted triangle = colony 4). Stress values are 0.16 (Huruvalhi, Vavvaru, Maafilaafushi) and 0.19 (Kanuhara).

Discussion

All of the turf algal parameters measured here show the greatest variability at the smallest spatial scales, among assemblages separated by centimeters. While, in some cases, there was statistically significant variability at other spatial scales (and in fact, variance was highly significant at all spatial scales under the PERMANOVA model with 9999 permutations, Table 2.4), by far the largest proportion of total variability always occurred at the smallest scale. This inverse relationship between spatial scale and variability suggests that at least some processes operating at small scales, such as grazing by herbivores, competition, propagule settlement, and vegetative growth, are important in structuring turf algal assemblages on these Maldivian coral reefs. Alternately, turf algae assemblages may vary over time and although we controlled for it here, temporal variability can actually conflate spatial variability on very small scales (Underwood 1991). However, the relative strengths of temporal and spatial variation are inconsistent (e.g. see opposite results in Hughes et al. 1999 and Kelaher & Levinton 2003). Therefore, here we limit our interpretation to processes that drive spatial patterns.

Other studies that have examined structure of marine algal and benthic invertebrate assemblages at hierarchical spatial scales have documented similar inverse relationships between variability and spatial scale (reviewed in Fraschetti et al. 2005; see also Wiens 1989, Underwood & Chapman 1996, Smale et al. 2010, O’Leary & Potts 2011). Most heterogeneity in benthic marine taxa occurs at small, but not always the smallest, scales (tens of centimeters to several meters) (Fraschetti et al. 2005). For example, temperate turf algal assemblages display the greatest variation at the centimeter scale (Coleman 2002), and in tropical marine environments specifically, coral reef fish assemblages are heterogeneous among individual patch reefs and become more homogenous at larger scales (Wiens 1989). In contrast, however, coral cover varies widely among reefs separated by several kilometers, though this effect depends on reproductive strategy (brooders vs. spawners) (Hughes et al. 1999).

Such spatial patterns in benthic organisms can be driven by recruitment variability. There is experimental evidence that variable recruitment drives small-scale heterogeneity at the scale of 10's of centimeters in temperate macroalgae (Bellgrove et al. 2004, Smale et al. 2010) and invertebrates living in temperate turf algae (Kelaher 2005). As a general rule, marine animals with limited dispersal are most variable at the centimeter to meter scale (Underwood & Chapman 1996). Organisms with planktonic larvae vary at larger scales than do organisms with direct development (Fraschetti et al. 2005). Turf algae, specifically, have been show to vary at the centimeter scale due to recruitment patterns (Coleman 2002). However, since algal dispersal can be hyper-local (<1 km) or more regional (up to 100 km) (Shanks et al. 2003), and algal recruitment varies temporally in species-specific ways (Bellgrove et al. 2004), we can expect recruitment to drive species-specific spatial patterns among algae that would sum to the heterogeneous assemblages measured here.

In addition to recruitment, disturbance events influence spatial patterns because space is one of the most limiting resources in benthic communities. We can expect benthic communities to be variable at small scales where isolated chance events or biological interactions dominate a landscape, and at larger spatial scales where the physical disturbances such as bleaching events, wave energy, storms, or tsunamis are the main driving forces. For example, following a large scale bleaching event in Australia, turf succession varied among locations depending upon both the bleaching severity and the local site environment (Diaz-Pulido & McCook 2002). Recolonization after a space-clearing disturbance drives small-scale variability in temperate intertidal turf (Benedetti-Cecchi & Cinelli 1994) and their infaunal invertebrate assemblages (Olabarria 2002).

However, physical disturbances are less important than interspecific competition in structuring temperate turf assemblages (Maggi et al. 2012), and anthropogenic disturbances seem to structure turf variability on larger scales (kilometers) (Benedetti-Cecchi et al. 2001). As the largest variability we measured in tropical turf algal assemblages was at the scale of centimeters, we propose that smaller-scale disturbances are more important in structuring tropical turf communities.

Herbivorous grazing is one such spatial disturbance that structures benthic reef communities (Steneck & Dethier 1994, Poray & Carpenter 2014) and, due to its mechanics, is likely to drive small-scale patchiness of algal turf assemblages. Grazing bites can be considered centimeter-scale “disturbances” that completely reset turf succession by cropping or entirely scraping the algae down to the underlying carbonate substrate (Bonaldo & Bellwood 2009), but this effect depends on the type of grazer (Ceccarelli et al. 2011). The effect of grazing is pronounced for turf algae, because turf algae are the preferred food source for most reef herbivores (Carpenter 1986, Ledlie et al. 2007), and consequently on unfished reefs, each square centimeter of turf is bitten up to 6 times per day (Hamilton et al. 2014). Since such intense grazing and its effects on algae are spatially variable due to behavioral and ecological variation among types of grazers (Carpenter 1986, Bonaldo & Bellwood 2011, Sandin & McNamara 2012), one might expect grazing to contribute to a patchy mosaic of turf assemblages at different points in succession, as has been observed in temperate intertidal algae (Benedetti-Cecchi & Cinelli 1993). If herbivore assemblages are consistent across reefs, this pattern would be repeated at the site and island scale, such that variability decreases as spatial scale increases. As the scale of greatest variability measured here, centimeters, approximates the bite size of dominant reef grazers (herbivorous fishes and urchins), one plausible explanation for the observed scales of spatial variability in turf algae is that turf assemblages are patchy in response to the distribution of herbivores across the landscape.

Although herbivores influence the spatial distribtion of benthic primary producers in most ecosystems, such effects tend to vary with the idiosyncratic circumstances of each system. For instance, selective herbivory on specific morphologies or life stages can act as a special type of disturbance that increases plant diversity (Hulme 1996). Grazing has been experimentally measured to be more important than physical factors in driving assemblage variability in subtropical intertidal microalgae (Christofoletti et al. 2011) and in some temperate turf systems (Benedetti-Cecchi et al. 2000). However, grazing is a negligible factor in other temperate turf systems (e.g. see Benedetti-Cecchi et al. 2012), so this comparison may not be particularly informative for predicting processes that drive spatial patterns in tropical coral reef turf algae. And while spatially patchy grazing increases heterogeneity in corals (O'Leary & Potts 2011), terrestrial vegetation (Adler et al. 2001), unicellular benthic marine algae (Sommer 2000), and intertidal coralline algae (Wai & Williams 2006), it seems to *reduce* spatial homogeneity of algae in a stream even at very small scales (Sarnelle et al. 1993). Therefore, while there are compelling reasons why grazing patterns might yield small-scale patchiness in turf algal assemblages, such effects are not assured.

An alternative explanation is that small-scale patchiness is simply an inherent feature of mixed-species assemblages due to the diverse growth forms represented in a typical turf algal assemblage, analogous to the way that differences in life history strategies contribute to patchiness in terrestrial plant assemblages (Shmida & Ellner

1985). For example, *Polysiphonia*, *Gelidiella/Gelidum*, and *Herposiphonia* were some of the most abundant and widespread taxa observed here. Where these red terete algae occurred, they branched out and crept across the substrate, leaving open space for other algae. In contrast, *Dictyota* was also one of the most abundant taxa, but it was not widespread. As a foliose alga, it grows in a much different pattern than do terete filaments. In the few samples where it occurred, it grew as a thick mat, covering 100% of the substrate and leaving no room for other taxa. Smaller brown filamentous algae from the order Ectocarpales, which grow singly as simple filaments, and red calcified crustose coralline algae, which grow as thick crusts, are further extreme examples of the morphological diversity within the mixed species turf assemblage. Such variable morphologies could explain the heterogeneity in existing assemblages, while random settlement processes could be responsible for starting individual turf assemblages on different trajectories. Both the 'lottery hypothesis' (Sale 1977) and the 'carousel' model (van der Maarel & Sykes 1993) rely on some amount of stochastic settlement, allowing many species with similar traits to take turns occupying the same niche space. These models explain small-scale patchiness in temperate intertidal algae (Bastow Wilson et al. 1992), and they could be equally applicable in tropical turf algae. The observed patterns of small-scale patchiness could be a straightforward result of stochastic settlement processes that are amplified as algae grow in different ways.

Comparing the richness of turfs on Maldivian reefs measured here to turf diversity reported elsewhere is not straightforward due to unknown relationships between α and β diversity of turf algae and the distribution of species at different spatial scales. Here, the smallest unit measured was 1.27 cm^2 and, with 256 samples, the total area sampled was

324 cm^2 across more than 20 km of reef. Other studies have used different areas, but it is not appropriate to simply standardize by area. Still, taxonomic richness reported here falls within the range of richness reported elsewhere for tropical turf algae (Stuercke & McDermid 2004, Anderson et al. 2005, Smith et al. 2010).

Total cover, canopy height, and taxonomic richness all displayed the same pattern: decreasing variability as spatial scale increased from punch to colony to site, then *greater* variability at the island level. Therefore, these characteristics of turf assemblages were relatively homogenous within and among sites on a given island, but there was larger variability among the four islands. That there was no discernible variation among sites (separated by 100-300m) implies homogeneous environmental conditions within a given island, with dispersal barriers and/or different disturbance regimes (e.g. wave forcing or bleaching history) among islands. Therefore, we propose that both very small-scale processes, such as vegetative growth, herbivory, and competition, and larger scale processes, such as propagule dispersal, likely play important roles in differentiating turf assemblages on coral reefs.

Whatever processes drive the observed variation in canopy height may in part determine the ecological role of turf algae. Turf canopy height is rarely manipulated experimentally or even measured at a resolution matching the resolution presented here, but there is indirect evidence that differences of just a few millimeters in canopy height could make a difference in the ecology of turf on a coral reef. For example, an increase in turf canopy height of 3 mm (from <1 to 4 mm) increased the thickness of the benthic boundary layer (Carpenter & Williams 1993), within which there are measured changes in pH, O_2, and rates of photosynthesis and respiration (Larkum et al. 2003). Further, thicker and taller turfs trap more sediment and organic matter than thinner and shorter turfs, which has negative effects on survival of coral larvae (reviewed in Birrell et al. 2008). Sediment within turf assemblages has strong effects on survival of canopy-forming macroalgae in temperate systems (Alestra et al. 2014), the infaunal invertebrate community living in turf (Prathep et al. 2003), and coral settlement success (Birrell et al. 2005). Differences of millimeters in the amount of accumulated sediment within turf reduces the survival of macroalgal recruits (Chapman & Fletcher 2002) and matches the scale of a proposed threshold for the creation of anoxic sediment (Clausing et al. 2014). Though it has not been experimentally tested, we expect that millimeter changes in turf canopy height could negatively affect the settlement and survival of coral larvae, which are in the micron to millimeter size range, via either sediment retention, smothering or other mechanisms. Our measured range of 0.4 to almost 4 mm matches the range in canopy height shown to cause impacts in other studies. As there was significant variation in canopy height only among colonies, any effects of variation in turf canopy height are acting on individual coral colonies. In future studies, it would be interesting to experimentally test the effect of turf canopy height on sediment retention, turf competitive ability, and coral larval settlement.

In contrast to the variability in canopy height and the other univariate measures, multivariate variability in turf assemblage decreased monotonically as spatial scale increased, with variance in assemblage at the island scale explaining the smallest proportion of the total variability. These different patterns of spatial variability for multivariate and univariate metrics suggest that processes governing these different parameters act at separate scales. Any small-scale processes that determine assemblage structure are repeated and balanced out across larger spatial scales, while small-scale processes that determine cover, canopy, or richness increase slightly in variability from the site to the island scale.

In addition to examining whole-assemblage characteristics, spatial patterns of key taxa may be particularly informative about ecological processes. For example, two red algae known to be harmful to corals, *Corallophila* spp. and *Anotrichium* spp., were neither common nor abundant throughout the study (Table 2). However, closer inspection of their individual spatial patterns (Fig 4g-h) points to a handful of individual coral colonies where one or both of these taxa were relatively abundant. Therefore, we can predict that those individual colonies may either have active coral-algal interaction zones or may, in fact, be losing space to aggressive turf assemblages laden with toxic red algae. And while among-island variability was the smallest proportion of overall assemblage variability, abundance patterns of these two red algae taxa points to individual islands where corals may be susceptible to turf overgrowth: turf assemblages on Kanuhara and Maafilaafushi have relatively consistent amounts of *Corallophila* spp. and *Anotrichium* spp., respectively. These taxa were low in abundance and so contributed little to variability in the total assemblage, but examining them separately from the whole assemblage provides important insight into potentially critical ecological processes underway at these two islands.

Taxa-specific insights, combined with the overall small-scale variability of turf algal assemblages, present a suite of implications for future analysis of coral reef communities. Knowing that turf assemblages on coral reefs can be highly variable at a scale of centimeters highlights a need for appropriate spatial sampling. Describing a 1-m quadrat by its overall turf cover may be insufficient to capture the highly variable turf assemblage. Instead, detailed samples replicated across centimeters are needed to sufficiently describe the complexity and diversity of turf assemblages, especially if different taxa within the turf assemblage have unique roles in coral-algal competition such as producing allelochemicals that can kill corals (e.g. Jompa and McCook 2003a).

With declining coral and increasing turf cover on reefs worldwide, understanding coral-turf interaction dynamics will become increasingly central to coral reef ecology and conservation. However, turf assemblages are variable at scales smaller than a single coral colony, so these interactions deserve more detailed consideration. Turf algae represent a dominant, diverse, and highly productive component of coral reef communities, so a better understanding of the processes that drive turf assemblage structure and spatial dynamics is needed.

Chapter 2, in full, is a reprint of the material as it appears in the Marine Ecology Progress Series 2015. Harris, Jill L., Levi S. Lewis, and Jennifer E Smith. The dissertation author was the principal researcher and author of this material.

References

Adler PB, Raff DA, Lauenroth WK (2001) The effect of grazing on the spatial heterogeneity of vegetation. Oecologia 128:465–479

Alestra T, Tait L, Schiel D (2014) Effects of algal turfs and sediment accumulation on replenishment and primary productivity of fucoid assemblages. Mar Ecol Prog Ser 511:59–70

Anderson MJ (2001) A new method for non-parametric multivariate analysis of variance. Austral Ecol 26:32–46

Anderson MJ, Gorley R, Clarke K (2008) PERMANOVA+ for PRIMER: Guide to Software and Statistical Methods. PRIMER-E, Plymouth, UK

Anderson RJ, McKune C, Bolton J, Declerck O, Tronchin E (2005) Patterns in subtidal seaweed communities on coral-dominated reefs at Sodwana Bay on the KwaZulu-Natal coast, South Africa. African J Mar Sci 27:529–537

Andrew N, Viejo R (1998) Ecological limits to the invasion of *Sargassum muticum* in northern Spain. Aquat Bot 60:251–263

Bastow Wilson J, James R, Newman J, Myers T (1992) Rock pool algae: species composition determined by chance? Oecologia 91:150–152

Bellgrove A, Clayton MN, Quinn GP (2004) An integrated study of the temporal and spatial variation in the supply of propagules, recruitment and assemblages of intertidal macroalgae on a wave-exposed rocky coast, Victoria, Australia. J Exp Mar Bio Ecol 310:207–225

Bellwood D, Fulton C (2008) Sediment-mediated suppression of herbivory on coral reefs: decreasing resilience to rising sea levels and climate change? Limnol Oceanogr 53:2695–2701

Benedetti-Cecchi L, Bulleri F, Cinelli F (2000) The interplay of physical and biological factors in maintaining mid-shore and low-shore assemblages on rocky coasts in the northwest Mediterranean. Oecologia 123:406–417

Benedetti-Cecchi L, Cinelli F (1993) Early patterns of algal succession in a midlittoral community of the Mediterranean sea : a multifactorial experiment. J Exp Mar Bio Ecol 169:15–31

Benedetti-Cecchi L, Cinelli F (1994) Recovery of patches in an assemblage of geniculate coralline algae - Variability at different successional stages. Mar Ecol Prog Ser 110:9–18

Benedetti-Cecchi L, Pannacciulli F, Bulleri F, Moschella PS, Airoldi L, Relini G, Cinelli F (2001) Predicting the consequences of anthropogenic disturbance: Large-scale effects of loss of canopy algae on rocky shores. Mar Ecol Prog Ser 214:137–150

Benedetti-Cecchi L, Tamburello L, Bulleri F, Maggi E, Gennusa V, Miller M (2012) Linking patterns and processes across scales: the application of scale-transition theory to algal dynamics on rocky shores. J Exp Biol 215:977–985

Birrell CL, McCook LJ, Willis BL (2005) Effects of algal turfs and sediment on coral settlement. Mar Pollut Bull 51:408–414

Birrell CL, McCook LJ, Willis BL, Diaz-Pulido G (2008) Effects of benthic algae on the replenishment of corals and the implications for the resilience of coral reefs. Oceanogr Mar Biol an Annu Rev 46:25–63

Bonaldo RM, Bellwood DR (2009) Dynamics of parrotfish grazing scars. Mar Biol 156:771–777

Bonaldo RM, Bellwood DR (2011) Spatial variation in the effects of grazing on epilithic algal turfs on the Great Barrier Reef, Australia. Coral Reefs 30:381–390

Carpenter R (1986) Partitioning herbivory and its effects on coral reef algal communities. Ecol Monogr 56:345–364

Carpenter RC, Williams SL (1993) Effects of algal turf canopy height and microscale substratum topography on profiles of flow speed in a coral forereef environment. Limnol Oceanogr 38:687–694

Ceccarelli DM, Jones GP, McCook LJ (2011) Interactions between herbivorous fish guilds and their influence on algal succession on a coastal coral reef. J Exp Mar Bio Ecol 399:60–67

Chapman AS, Fletcher RL (2002) Differential effects of sediments on survival and growth of *Fucus serratus* embryos (Fucales, Phaeophyceae). J Phycol 38:894–903

Chapman M, Underwood A (1998) Inconsistency and variation in the development of rocky intertidal algal assemblages. J Exp Mar Bio Ecol 224:265–289

Christofoletti RA, Almeida TV V, Ciotti ÁM (2011) Environmental and grazing influence on spatial variability of intertidal biofilm on subtropical rocky shores. Mar Ecol Prog Ser 424:15–23

Clausing R, Annunziata C, Baker G, Lee C, Bittick S, Fong P (2014) Effects of sediment depth on algal turf height are mediated by interactions with fish herbivory on a fringing reef. Mar Ecol Prog Ser 517:121–129

Coleman MA (2002) Small-scale spatial variability in intertidal and subtidal turfing algal assemblages and the temporal generality of these patterns. J Exp Mar Bio Ecol 267:53–74

Collins SL (1992) Fire frequency and community heterogeneity in tallgrass prairie vegetation. Ecology 73:2001–2006

Connell JH (1978) Diversity in tropical rain forests and coral reefs. Science 199:1302–10

Connell S, Foster M, Airoldi L (2014) What are algal turfs? Towards a better description of turfs. Mar Ecol Prog Ser 495:299–307

Connell JH, Slatyer RO (1977) Mechanisms of succession in natural communities and their role in community stability and organization. Am Nat 111:1119–1144

Dayton PK, Tegner MJ, Parnell PE, Edwards PB (1992) Temporal and spatial patterns of disturbance and recovery in a kelp forest community. Ecol Monogr 62:421

Deysher L, Norton TA (1981) Dispersal and colonization in *Sargassum muticum* (Yendo) Fensholt. J Exp Mar Bio Ecol 56:179–195

Diaz-Pulido G, McCook LJ (2002) The fate of bleached corals: patterns and dynamics of algal recruitment. Mar Ecol Prog Ser 232:115–128

Edwards MS (2004) Estimating scale-dependency in disturbance impacts: El Niños and giant kelp forests in the northeast Pacific. Oecologia 138:436–47

Falkenberg LJ, Russell BD, Connell SD (2013) Contrasting resource limitations of marine primary producers: implications for competitive interactions under enriched CO2 and nutrient regimes. Oecologia 172:575–83

Fletcher WJ (1987) Interactions among subtidal Australian sea urchins, gastropods, and algae: effects of experimental removals. Ecol Monogr 57:89–109

Fletcher D, Underwood A (2002) How to cope with negative estimates of components of variance in ecological field studies. J Exp Mar Bio Ecol 273:89–95

Fong P, Paul VJ (2011) Coral reef algae. In: Dubinsky Z, Stambler N (eds) Coral Reefs: an ecosystem in transition. Springer Netherlands, Dordrecht, p 242–272

Foster MS (1990) Organization of macroalgal assemblages in the Northeast Pacific: the assumption of homogeneity and the illusion of generality. Hydrobiologia 192:21–33

Fraschetti S, Terlizzi A, Benedetti-Cecchi L (2005) Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation. Mar Ecol Prog Ser 296:13–29

Fritz HM, Synolakis CE, McAdoo BG (2006) Maldives field survey after the December 2004 Indian Ocean tsunami. Earthq Spectra 22:S137–S154

Graham M, Edwards M (2001) Statistical significance versus fit: estimating the importance of individual factors in ecological analysis of variance. Oikos 93:5060513

Hamilton S, Smith J, Price N, Sandin S (2014) Quantifying patterns of fish herbivory on Palmyra Atoll (USA), an uninhabited predator-dominated central Pacific coral reef. Mar Ecol Prog Ser 501:141–155

Hatcher BG, Larkum AWD (1983) An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. J Exp Mar Bio Ecol 69:61–84

Huff TM (2006) Impacts of human trampling and periodic sand inundation on Southern California intertidal algal turf communities: Implications for conservation and management of rocky shores. Scripps Institution of Oceanography, La Jolla, CA, USA

Hughes T, Baird A, Dinsdale EA, Moltschaniwskyj NA, Pratchett MS, Tanner JE, Willis BL (1999) Patterns of recruitment and abundance of corals along the Great Barrier Reef. Nature 397:10–14

Hulme P (1996) Herbivory, plant regeneration, and species coexistence. J Ecol 4:609–615

Iveša L, Chapman MG, Underwood AJ, Murphy RJ (2010) Differential patterns of distribution of limpets on intertidal seawalls: Experimental investigation of the roles of recruitment, survival and competition. Mar Ecol Prog Ser 407:55–69

Jompa J, McCook LJ (2003a) Coral-algal competition: macroalgae with different properties have different effects on corals. Mar Ecol Prog Ser 258:87–95

Kelaher BP (2005) Does colonization contribute to spatial patterns of common invertebrates in coralline algal turf? Austral Ecol 30:40–48

Kelaher BP, Levinton JS (2003) Variation in detrital enrichment causes spatio-temporal variation in soft-sediment assemblages. Mar Ecol Prog Ser 261:85–97

Kennelly S (1987) Physical disturbances in an Australian kelp community. II. Effects on understorey species due to differences in kelp cover. Mar Ecol Prog Ser 40:155–165

Larkum AWD, Koch MW, Ku M (2003) Diffusive boundary layers and photosynthesis of the epilithic algal community of coral reefs. Mar Biol 142:1073–1082

Ledlie MH, Graham N a. J, Bythell JC, Wilson SK, Jennings S, Polunin NVC, Hardcastle J (2007) Phase shifts and the role of herbivory in the resilience of coral reefs. Coral Reefs 26:641–653

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73:1943–1967

Lison de Loma T, Ballesteros E (2002) Microspatial variability inside epilithic algal communities within territories of the damselfish *Stegastes nigricans* at La Réunion (Indian Ocean). Bot Mar 45:316–323

Loch K, Loch W, Schuhmacher H, See WR (2002) Coral recruitment and regeneration on a Maldivian reef 21 months after the coral bleaching event of 1998. Mar Ecol 23:219–236

Loch K, Loch W, Schuhmacher H, See WR (2004) Coral recruitment and regeneration on a Maldivian reef four years after the coral bleaching event of 1998. Part 2: 2001-2002. Mar Ecol 25:145–154

Maarel E van der, Sykes MT (1993) Small-scale plant species turnover in a limestone grassland: the carousel model and some comments on the niche concept. J Veg Sci 4:179–188

Maggi E, Bulleri F, Bertocci I, Benedetti-Cecchi L (2012) Competitive ability of macroalgal canopies overwhelms the effects of variable regimes of disturbance. Mar Ecol Prog Ser 465:99–109

Marhaver KL, Vermeij MJ, Rohwer FL, Sandin S (2013) Janzen-Connell effects in a broadcast-spawning Caribbean coral: distance-dependent survival of larvae and settlers. Ecology 94:146–60

Menge B, Olson A (1990) Role of scale and environmental factors in regulation of community structure. Trends Ecol Evol 5:52–7

O'Leary JK, Potts DC (2011) Using hierarchical sampling to understand scales of spatial variation in early coral recruitment. Coral Reefs 30:1013–1023

Odum E (1969) The strategy of ecosystem development. Science 164:262–270

Olabarria C (2002) Role of colonization in spatio-temporal patchiness of microgastropods in coralline turf habitat. J Exp Mar Bio Ecol 274:121–140

Pacala SW, Levin SA (1997) Biologically generated spatial pattern and the coexistence of competing species. In: Tilman D, Kareiva P (eds) Spatial Ecology: the role of space in population dynamics and interspecific interaction. Princeton University Press, Princeton, NJ, p 204–232

Padilla D, Allen B (2000) Paradigm lost: reconsidering functional form and group hypotheses in marine ecology. J Exp Mar Bio Ecol 250:207–221

Pianka ER (1966) Latitudinal gradients in species diversity: a review of concepts. Am Nat 100:33–46

Poray AK, Carpenter RC (2014) Distributions of coral reef macroalgae in a back reef habitat in Moorea, French Polynesia. Coral Reefs 33:67–76

Prathep A, Marrs R, Norton T (2003) Spatial and temporal variations in sediment accumulation in an algal turf and their impact on associated fauna. Mar Biol 142:381–390

Rowan R, Knowlton N (1995) Intraspecific diversity and ecological zonation in coral-algal symbiosis. Proc Natl Acad Sci U S A 92:2850–3

Sale P (1977) Maintenance of high diversity in coral reef fish communities. Am Nat 111:337–359

Sandin S a, McNamara DE (2012) Spatial dynamics of benthic competition on coral reefs. Oecologia 168:1079–90

Santelices B, Bolton J, Meneses I (2009) Marine algal communities. In: Witman JD, Roy K (eds) Marine Macroecology. The University of Chicago Press, Chicago, p 424

Sarnelle O, Kratz K, Cooper S (1993) Effects of an invertebrate grazer on the spatial arrangement of a benthic microhabitat. Oecologia 96:208–218

Shanks AL, Grantham BA, Carr MH (2003) Propagule dispersal distance and the size and spacing of marine reserves. Ecol Appl 13:S159–S169

Shmida A, Ellner S (1985) Coexistence of plant species with similar niches. In: Plant Community Ecology: Papers in Honor of Robert H. Whittaker. Springer Netherlands, p 275–301

Smale DA, Kendrick GA, Wernberg T (2010) Assemblage turnover and taxonomic sufficiency of subtidal macroalgae at multiple spatial scales. J Exp Mar Bio Ecol 384:76–86

Smith JE, Hunter CL, Smith CM (2010) The effects of top-down versus bottom-up control on benthic coral reef community structure. Oecologia 163:497–507

Sommer U (2000) Benthic microalgal diversity enhanced by spatial heterogeneity of grazing. Oecologia 122:284–287

Sousa WP (1979) Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. Ecol Monogr 49:227

Steneck RS, Dethier MN (1994) A functional group approach to the structure of algal-dominated communities. Oikos 69:476–498

Stuercke B, McDermid K (2004) Variation in algal turf species composition and abundance on two Hawaiian shallow subtidal reefs. Crypotogamie Algol 25:353–365

Tribollet AD, Schils T, Vroom PS (2010) Spatio-temporal variability in macroalgal assemblages of American Samoa. Phycologia 49:574–591

Underwood A (1991) Spatial and Temporal Problems with Monitoring. In: Calow P (ed) Rivers Handbook: The Science and Management of River Environments. Wiley-Blackwell, Hoboken, NJ, p 101–123

Underwood AJ (1997) Ecological experiments: their logical design and interpretation using analysis of variance. Cambridge University Press, Melbourne

Underwood AJ, Chapman MG (1996) Scales of spatial patterns of distribution of intertidal invertebrates. Oecologia 107:212–224

Vermeij MJ, Moorselaar I van, Engelhard S, Hörnlein C, Vonk SM, Visser PM (2010) The effects of nutrient enrichment and herbivore abundance on the ability of turf algae to overgrow coral in the Caribbean. PLoS One 5:e14312

Wai T-C, Williams GA (2006) Monitoring spatio-temporal variation in molluscan grazing pressure in seasonal, tropical rock pools. Mar Biol 149:1139–1147

Wanders JBW (1976) The role of benthic algae in the shallow reef of Curaçao (Netherlands Antilles). I: primary productivity in the coral reef. Aquat Bot 2:235–270

Wiens J (1989) Spatial scaling in ecology. Funct Ecol 3:385–397

Wilson SK, Bellwood DR, Choat JH, Furnas M (2003) Detritus in the epilithic algal matrix and its use by coral reef fishes. Oceanogr Mar Biol Annu Rev 41:279–309

Wismer S, Hoey A, Bellwood D (2009) Cross-shelf benthic community structure on the Great Barrier Reef: relationships between macroalgal cover and herbivore biomass. Mar Ecol Prog Ser 376:45–54

Witman JD, Roy K (2009) Marine Macroecology (JD Witman and K Roy, Eds.). University of Chicago Press, Chicago

Chapter 3 An Experimental Analysis of the Context Dependent Effects of Nutrient Enrichment and Herbivore Exclusion on Coral Reef Turf Algae

Jill Harris, Lindsay Bonito, Maggie Johnson, Emily Kelly, Jennifer Smith

Nutrient supply
versus herbivore demand
Which limits the turfs?

Abstract

Consumer pressure and resource availability together determine the biomass of primary producers, and the relative strengths of these top-down and bottom-up factors vary among ecosystems and environmental contexts. On coral reefs, herbivory is generally a stronger control than nutrients on algal biomass. However, experiments on coral reefs reach conflicting conclusions, perhaps because they are rarely replicated in different environmental contexts. I used common, abundant heterogeneous turf algae assemblages as a tool to examine the influences of herbivory and nutrients on multiple metrics of primary producers. By replicating a factorial experiment in three locations with different herbivore and nutrient regimes, I show that producers respond most strongly to herbivore removal where background herbivory pressure is weakest, suggesting positive feedback between loss of herbivory and loss of ecosystem resilience. Further, although nutrients had negligible influence on the abundance of algae over this short-term experiment, grazer consumption remained constant under algae enrichment, suggesting that herbivores will not be able to consume excess algae production in scenarios of chronic nutrient pollution on coral reefs. Finally, in contrast to high profile findings in terrestrial ecosystems, I show that enrichment actually increases, and consumers reduce, producer diversity. My results demonstrate that turf algae are informative experimental subjects, that the relative influences of top-down and bottom-up are context-dependent, and the alarming potential for both herbivore losses and nutrient

pollution to trigger positive feedback loops that lead to turf algae proliferation and coral reef degradation.

Introduction

The relative strengths of resource and consumer control of community structure have been the focus of considerable research in terrestrial, aquatic, and marine environments (Hillebrand et al. 2007; Gruner et al. 2008). There is generally weaker top-down control and stronger bottom-up control in terrestrial systems compared to aquatic and marine systems (Hillebrand et al. 2007; Gruner et al. 2008; Cleland and Harpole 2010). This issue has important implications on coral reefs, where the removal of herbivores and the addition of inorganic nutrients are among the most significant local-scale anthropogenic impacts. The interaction between herbivory and nutrients drives algal biomass on reefs, altering community structure and promoting the abundance of fleshy algae over reef-building hard corals and crustose coralline algae (CCA) (Belliveau and Paul 2002; Littler et al. 2006; Smith et al. 2010). Despite the large body of work investigating the separate and combined effects of herbivory and nutrients on coral reef benthic communities, experimental results are variable and this topic has been the subject of a contentious debate in the literature (e.g. Hughes et al. 1999; Lapointe 1999).

Grazing has a large impact on the spatial distribution and abundance of algae in tropical marine systems (Odum and Odum 1955; Steneck 1988; Fong and Paul 2011). Experimental removal of herbivores is a stronger, more consistent control than nutrient addition, and it almost always leads to an increase in fleshy algal biomass or cover (Miller et al. 1999; Diaz-Pulido and McCook 2003; McClanahan 2003; Burkepile and

Hay 2006; Gruner et al. 2008; Smith et al. 2010; Jessen et al. 2013). The process also works in reverse, where returning herbivores to a system reduces macroalgae biomass in both experimental and natural systems (Bellwood et al. 2006; Carpenter and Edmunds 2006). There have been rare exceptions where removing herbivores had no measureable effect on reef algal biomass (Muthukrishnan and Fong 2014). The effect of herbivore removal varies across macroalgal taxa (Diaz-Pulido and McCook 2003), with the most palatable taxa generally responding most positively to herbivore exclusion (Thacker et al. 2001).

Compared to herbivore removal, the effect of nutrient pollution on benthic reef communities is more variable across experiments and locations, and frequently only has an impact when interacting with low herbivory. On some reefs, inorganic nutrient enrichment alone increases the biomass or cover of fleshy algae, but the effect is usually limited to small, filamentous turf algae, not macroalgae (Hatcher and Larkum 1983; McClanahan et al. 2003; Muthukrishnan and Fong 2014). Nutrient enrichment alone increases macroalgal biomass in reef-associated environments with low herbivory (e.g. lagoons, patch reefs, mangroves) (Lapointe et al. 2004). In other cases, nutrient pollution makes fleshy algae more palatable to grazers (Boyer et al. 2004; Russell and Connell 2005) so that where there is high herbivory, increased nutrients actually reduce fleshy algae biomass, often in conjunction with an increase in herbivore-resistant CCA (Belliveau and Paul 2002; Smith et al. 2010). However, this interactive effect is less consistent than the effect of each parameter independently (Miller et al. 1999; Jessen et al. 2013; Muthukrishnan and Fong 2014) and sometimes is nonexistent (McClanahan et al. 2003).

The inconsistent response of benthic reef communities to herbivore removal or nutrient addition may be due to experimental manipulations set in a range of environmental conditions and typically not interpreted with respect to the natural context. Fully testing the outcomes of top-down and bottom-up control requires comparative experiments across systems, which may have fundamental differences that can explain seemingly inconsistent experimental responses (Littler and Littler 2007; Roff and Mumby 2012). For example, we might expect herbivore removal to have a weaker effect in an algal-dominated lagoon with few herbivores than on a coral-dominated forereef with high herbivory. Similarly, we should expect different responses to nutrient enrichment on high islands or in systems that experience natural upwelling events (Leichter et al. 2003) versus low (carbonate) islands because phosphorous and, to some extent, nitrogen are more limiting on the latter (Littler et al. 1991). However, out of 12 factorial coral reef experiments in two recent meta-analyses on top-down versus bottom-up control (Burkepile and Hay 2006; Gruner et al. 2008), only two were replicated in different environmental settings (Hatcher and Larkum 1983; Lapointe et al. 2004) (Table 3.1). Considering these experiments within their environmental context may explain some of the variation in benthic community responses.

Table 3.1 Coral reef experiments included in recent meta analyses on the effects of herbivory and nutrient control of ecosystem structure.

Meta Analysis	**source**	**Experiment replicated in multiple contexts?**	**Measured turf algae response?**	**Turf metrics**
Burkepile and Hay 2006	Burkepile and Hay 2009	no	yes	% cover
Burkepile and Hay 2006	Diaz and McCook 2003	no	no	n/a
Burkepile and Hay 2006	Sotka and Hay 2009	no	yes	% cover
Both	Belliveau and Paul 2002	no	no	fleshy algae AFDM
Both	Hatcher and Larkum 1983	yes (but did not quantify ambient conditions)	yes	chlorophyll, nutrient content, AFDM
Both	McClanahan et al 2003	no	yes	% cover
Both	Miller et al 1999	no	yes	% cover, biomass, taxa
Both	Smith et al 2001	no	yes	biomass, sediment, inverts
Both	Thacker et al 2001	no	no	n/a
Gruner et al 2008	Gobler et al 2006	no	yes	taxa, % cover, growth rate, canopy height
Gruner et al 2008	Lapointe et al 2004	yes, nutrient gradient	no	only algal biomass
Gruner et al 2008	Smith et al 2010	no	yes	% cover, community

One way to replicate experiments across a range of environmental settings is to use turf algae, the small (< 1 cm), filamentous, multi-species assemblages of algae that are common on reefs worldwide. Algal turfs are highly productive, are the primary food source for herbivorous fishes and urchins, and are often the most common space competitors with adult and larval corals (Steneck 1988; Ledlie et al. 2007; Haas et al. 2010; Barott et al. 2012; Hamilton et al. 2014). Turf algae also thrive under conditions that degrade coral reefs, including overfishing, pollution, sedimentation, warming, and ocean acidification (Diaz-Pulido and McCook 2002; Bellwood and Fulton 2008; Vermeij et al. 2010; Connell et al. 2013), so turf algae are likely to become more abundant in the future as reefs face increasingly severe and frequent anthropogenic stressors. Because overfishing and nutrient pollution are also likely to affect turf algae, understanding how these factors affect turf assemblages provides insight into how coral reefs as a whole will respond to future human impacts.

Despite their importance, abundance, and ubiquity on reefs globally, turf algae are typically not studied in much detail in the many studies that have looked at effects of nutrient enrichment and overfishing on benthic reef communities. Indeed, out of 12 coral reef experiments reviewed in two recent meta-analyses that examined the response of coral reef benthic communities to top-down and bottom-up control (Burkepile and Hay 2006; Gruner et al. 2008), 8 experiments measured turf algae, and of those, five (Hatcher and Larkum 1983; Miller et al. 1999; Smith et al. 2001, 2010; Gobler et al. 2006) examined any turf algae metric beyond percent cover, even though every single one of these experiments took place on reefs with abundant turf algae (Table 3.1).

Algal turfs are heterogeneous assemblages, so quantifying how multiple turf metrics respond to experimental manipulation is important in understanding potentially complex and nuanced ecological processes. Turf algae canopy height, biomass and patchiness in percent cover are all influenced in part by grazer type and intensity (Carpenter and Williams 1993; Sandin and McNamara 2012). Specifically, turf algae biomass and canopy height may be the two best predictors of the ability of turfs to outcompete reef-building corals (Nugues and Roberts 2003; Harris et al. 2015).

Interestingly, though, in one study these two metrics responded differently to experimental manipulations: canopy height was more influenced by nutrient addition, while biomass was more influenced by herbivore removal (McClanahan et al. 2003). However, few studies have measured multiple metrics simultaneously, underscoring the need to measure multiple metrics across different environmental contexts.

Additionally, individual taxa within the turf assemblage may respond differently to top-down and bottom-up control (McClanahan et al 2003; Diaz-Pulido and McCook 2003). Changes in herbivore pressure could shift the turf algal assemblage toward more or less palatable taxa (Thacker et al. 2001), while increased nutrient availability might spur the growth of weedy taxa or those with high surface area to volume ratios. Turf species composition matters because assemblages containing taxa detrimental to corals, such as those that produce allelochemicals or influence microbial communities, are likely to exert stronger negative influences on corals and on the broader coral reef community (Jompa and McCook 2003). Turfs are diverse and heterogeneous assemblages, and evidence suggests that multiple metrics such as canopy height, biomass, cover, and relative species abundances are responsive to different processes and can potentially serve as multiple indicators of top-down and bottom-up influences in the broader coral reef system.

We tested how the relative strengths of top-down and bottom-up effects vary with environmental context in a series of replicated experiments at three different locations that differed in herbivore biomass and nutrient conditions. First, we hypothesized that both removing herbivores and adding nutrients would increase the amount of turf algae, whether measured as an increase in canopy height, biomass, or cover. Second, we hypothesized that treatments would cause predictable changes in algal turf assemblage structure: removing herbivores would reduce the relative abundance of grazer-resistant taxa (e.g. calcified, crusts, complex blades, etc.) and nutrient addition would increase the relative abundance of weedy taxa (e.g. simple filaments). Further, we predicted that treatment effects would be context-dependent: effects of herbivore removal would depend on each site's herbivore biomass, and the effects of nutrient addition would depend on each site's ambient nutrient levels. Turf algae should be poised to quickly increase in abundance following herbivore removal at locations with the highest herbivory, because heavy herbivory keeps turf algae cropped and productive (Fong and Paul 2011). On the other hand, if turfs are overly cropped from extremely heavy grazing, then any increases in abundance following herbivore removal would necessarily result from the slower processes of recruitment and succession, not more rapid regrowth. In that case, we would expect slower changes in turf abundance following herbivore removal at locations with the highest herbivory. Responses to nutrient enrichment should be directly related to ambient nutrient levels if high nutrient environments select for nutrient-limited turf taxa. Alternatively, we would see the greatest response to nutrient enrichment at low-nutrient sites if those turfs exist far from their physiological maximum and therefore have a greater capacity for increased production.

Methods

To examine how the response of turf algae to herbivore removal or nutrient addition varies across environmental contexts, we replicated an experiment in three locations with different herbivore-nutrient regimes (Table 3.2, Fig 3.1). The separate and combined effects of herbivore exclusion and nutrient enrichment were tested in factorial at two locations, and the effect of herbivore exclusion alone was tested in a third location. Palmyra Atoll (U.S.A.) and Millennium Atoll (Republic of Kiribati), both part of the Line Islands in the central Pacific, are both uninhabited atolls far from major human populations. Palmyra is a National Fish and Wildlife Refuge that is managed by the U.S. Fish and Wildlife Service and is part of the Pacific Remote Islands Marine National Monument. In contrast, Curaçao, in the southern Caribbean, has a population of 155,000 (Central Bureau of Statistics, Curaçao, http://www.cbs.cw). The herbivore biomass on Palmyra (45 g m^{-2}) and Millennium (48 g m^{-2}) is more than double that on Curaçao (20 g m^{-2}) (Edwards et al. 2013). Palmyra and Curaçao are both typical low-nutrient tropical islands, while Millennium has nutrient-rich upwelled water due to its location in the South Equatorial Countercurrent (Table 3.1, Fig 3.1) (Karnauskas and Cohen 2012).

Table 3.2 Summary of experiments. Herbivore biomass data for all sites from Edwards et al. (2013). Nutrient data for Millennium from Kelly et al. (2014 PNAS), for Palmyra and Curaçao from this study.

Location	**Palmyra Atoll**	**Curaçao**	**Millennium Atoll**
Date	Exp. 1: Sept 2009 Exp. 2: Oct 2012	July 2014	Nov 2013
Duration	Exp. 1: 12 days Exp. 2: 14 days	28-30 days	30 days
Depth	5 m	5 m	10 m
n	Exp. 1: 16 (4 per treatment) Exp. 2: 28 (7 per treatment)	28 (7 per treatment)	10 (5 per treatment)
Treatments	Factorial: Herbivore removal x Nutrient addition	Factorial: Herbivore removal x Nutrient addition	Herbivore removal
Response variables	% cover canopy height biomass assemblage (functional)	% cover canopy height biomass assemblage	% cover canopy height biomass assemblage
Herbivore biomass	High: 45 g m^{-2}	Medium: 20 g m^{-2}	High: 48 g m^{-2}
Water column nutrients	Medium: 1.1 μM DIN 0.23 μM Phosphate	Low: 0.65 μM DIN 0.05 μM Phosphate	High: 2.9 μM DIN 0.2 μM Phosphate

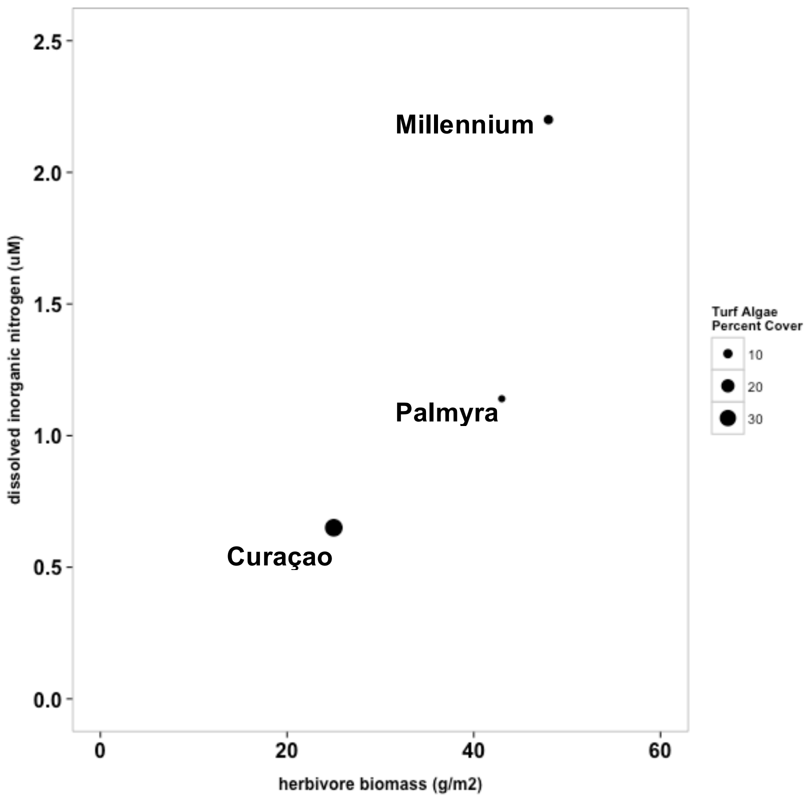

Figure 3.1 Herbivore biomass, water column DIN, and turf cover at the three experiment sites. Herbivore biomass data for all sites from Edwards et al. (2013). Nutrient data for Millennium from Kelly et al. (2014 PNAS), for Palmyra and Curaçao from this study.

Experimental setup

Intact turf assemblages growing on carbonate plates (dead coral fragments approximately 10 x 10 cm, n = 4-7 per treatment) were attached in pairs to PVC frames, with one turf plate inside and one outside a 25 x 25 x 25 cm enclosure of 0.5 cm clear plastic mesh (Figure 3.2). On Palmyra and Curaçao, half of the frames were allocated to the nutrient enrichment treatment by adding 12 g of Osmocote brand slow-release fertilizer (19:6:12 N:P:K) in nylon mesh bags to the middle of the frames, equidistant from the two turf plates. Nutrient treatments were placed at least 5m from non-enriched treatments and Osmocote was replaced every 10-14 days for the duration of the experiment.

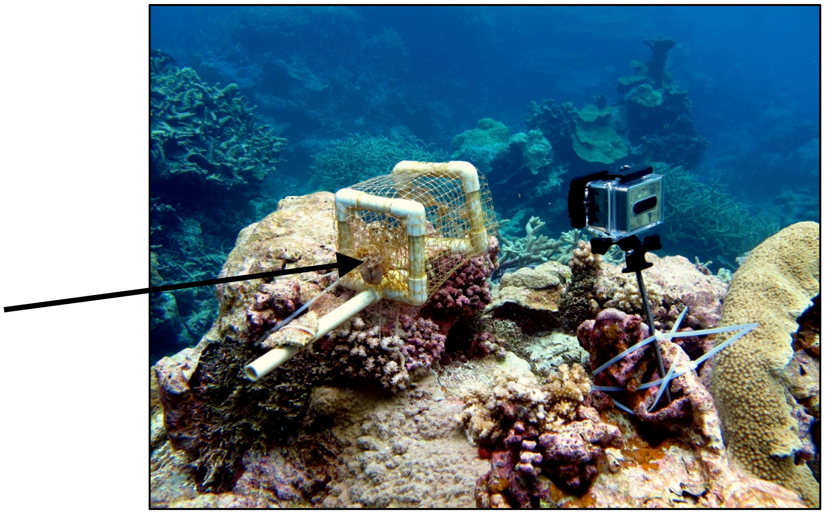

Figure 3.2 Experimental setup with plates of dead coral covered in turf algae placed outside and inside mesh cages. Arrow indicates nylon mesh bag containing fertilizer located equidistant from turf inside and outside cage as part of the nutrient addition treatment.

The experiment on Palmyra Atoll ran for 12 days in September 2009 and was replicated for 14 days in October 2012. Turf plates on Palmyra were collected from, and deployed on, the shallow reef terrace at 5 m depth. The experiment on Curaçao ran for 30 days in July 2014. Turf plates on Curaçao were collected from, and deployed on, the shallow fringing reef on the leeward side of the island at 5-6 m depth. The experiment on Millennium Atoll ran for 30 days in November 2013. Turf plates on Millennium were collected from, and deployed on, the reef slope at 10-12 m depth.

In the nutrient enrichment experiments, water column nutrients were measured at a random subset of enriched plots (n=4), control plots (n=2), and ambient locations (n=2, >10 m from all plots) every two weeks (n=2 time points on Palmyra, n=3 time points on Curaçao). Water samples were collected <1 cm from the surface of the turf plates using

50 mL syringes that were rinsed 3 times with ambient seawater. Samples were filtered through GF/C filters and stored in the dark in on ice until returned to shore, then frozen for analysis. Within 1 month of collection, samples were analyzed for nitrate and nitrite, phosphate, and ammonium by flow injection analysis at the Marine Science Institute Analytical Lab at the University of California, Santa Barbara. Nitrogen is reported as total dissolved inorganic nitrogen (DIN; sum of nitrate, nitrite, and ammonium).

To quantify potential shading effects from cages, light intensity was recorded every 10 minutes on HOBO Pendant temperature/light data loggers (Onset Computer Corporation, USA) attached inside and outside cages. Light intensity was not measured inside cages on Millennium. However, as the cage design was identical and experiment depth similar to that on Palmyra and Curaçao, we expect that shading effects were similar. Cages were brushed clean and data loggers were switched to new cages every 1-2 days.

Response variables

Turf plates were analyzed for canopy height, biomass, total algal cover, and taxonomic composition. Canopy height was calculated by submerging turf plates in seawater and using manual calipers to measure the height, to the nearest 0.05 mm, of 6 randomly selected filaments per plate. To measure biomass, we used a razor blade to scrape all algae from a 2 x 2 cm area off each plate, decalcified the biological matter in 5% HCl, used fresh water to rinse the algae onto pre-weighed filters, dried at 60°C to a constant weight, and re-weighed the filters. Following these analyses, the remaining samples were preserved in 10% formalin in seawater.

Algal cover and assemblage structure were analyzed under a dissecting microscope, providing high resolution at the millimeter scale. A 1 x 1 cm monofilament grid was overlaid on turf plates, and the total cover of all algae inside 5 randomly selected cells was recorded. Note that this provided a high resolution, precise measurement of percent cover on a sub-centimeter scale, analogous to density or thickness of turfs. Within each grid cell, percent cover of algae was recorded at the genus level. Crustose coralline algae (CCA) were recorded separately from all other algae (upright filaments, blades, non-calcified crusts, and cyanobacteria) to allow for analysis of *a priori* expectations that there would be less CCA when herbivores were excluded and more CCA with herbivores present and nutrients added (Littler and Littler 1984; Smith et al. 2001). Where necessary for identification, algae were stained with aniline blue dye, mounted onto permanent slides, and examined under higher magnification on a compound microscope.

Statistical analysis

Total daily light intensity was calculated for each measured plot, and mean total daily light intensity was calculated per treatment. The difference in light intensity inside and outside cages was compared using a paired one-tailed t-test, pairing experimental and control measurements within day. Within each treatment, water column nutrients from the beginning and end of experiment on Palmyra and from the beginning, middle, and end of experiment on Curaçao were compared using a t-test and ANOVA, respectively. There were no changes over time in nutrient levels within experimental treatments on either Palmyra (Phosphate: $t(6.77) = -1.35$, $p = 0.22$; Total N: $t(6.01) = -1.52$, $p = 0.18$))

or Curaçao (Phosphate: F(2,18) = 2.274, p = 0.132; Total N: F(2,18) = 3.151, p = 0.067), so time points were grouped together to compare overall nutrient levels between enriched and control plots.

All three univariate metrics (canopy height, biomass, and cover) were approximately normal within location based on the distribution of residuals. A t-test was used to compare canopy height, biomass, and cover inside and outside cages on Millennium, and a two-factor factorial ANOVA was used to compare each metric across treatments for each year on Palmyra and on Curaçao, with herbivore removal and nutrient addition both treated as fixed factors.

For each location, we compared assemblage structure within and among treatments using a two-way factorial PERMANOVA (one-factor on Millennium), treating herbivore removal and nutrient addition as fixed factors. Multivariate dispersions were tested for homogeneity using the PERMDISP routine in PRIMER-E, using Bray-Curtis dissimilarities and calculating p-values based on permutation. Assemblages were compared using raw percent cover data at the lowest possible taxonomic level, typically genus. We used SIMPER analysis to identify taxa that cumulatively contributed at least 50% of the difference among treatments. Additionally, we calculated taxonomic richness for each sample in each location and used two-factor ANOVAs (t-test on Millennium) to compare richness among treatments. The PERMANOVA and SIMPER analyses used here are based on the relative abundance of each taxon (i.e. two assemblages will be more similar if they share taxa in similar abundances) and richness is based only on presence/absence, so the combination of these two methods provided us with two different perspectives on turf algae diversity.

We used two methods to directly compare responses among all three locations. The three locations are in different biogeographic regions and there is little overlap in turf algal taxonomy. Therefore, to compare the turf assemblage response to treatments across all locations, we grouped taxa into seven morphological functional groups based on calcification (calcified or uncalcified) and growth form (crust, upright, blade) as proxies for susceptibility to grazing and weediness in response to nutrient addition (Table 3.3). We used these broad functional groups in a PERMANOVA analysis and for non-metric multidimensional scaling ordination to visualize community structure across locations.

Table 3.3 All algal taxa and corresponding functional groups of turf from each location.

Taxon	**Curaçao**	**Palmyra**	**Millennium**	**Functional Group**
Cyanobacteria	X	X	X	cyanobacteria
Acetabularia	X	X		non-calcified upright
Anotrichium	X		X	non-calcified upright
Antithamnionella	X		X	non-calcified upright
Bryopsis	X		X	non-calcified upright
Caulerpa	X			non-calcified upright
Centroceras	X			non-calcified upright
Ceramium	X	X	X	non-calcified upright
Chaetomorpha	X			non-calcified upright
Champia	X			non-calcified upright
Chondria/Laurencia	X	X	X	non-calcified upright
Cladophora	X	X		non-calcified upright
Corallophila	X	X	X	non-calcified upright
Derbesia	X			non-calcified upright
Dictyosphaeria		X		non-calcified upright
Ectocarpales	X	X		non-calcified upright
Enteromorpha	X	X	X	non-calcified upright
Gelidiella	X	X	X	non-calcified upright
Griffithsia	X		X	non-calcified upright
Herposiphonia	X	X	X	non-calcified upright
Laurencia	X			non-calcified upright
Polysiphonia	X	X	X	non-calcified upright
Rhipiliopsis	X			non-calcified upright
Sphacelaria	X			non-calcified upright
Taenioma	X			non-calcified upright
Unknown sp. 1	X			non-calcified upright
Unknown sp. 2	X			non-calcified upright
Amphiroa	X			calcified upright
Jania	X	X	X	calcified upright
Neomeris	X			calcified upright
unknown Corallinales	X			calcified upright
Dictyota	X			non-calcified blade
Gelidiopsis blade	X			non-calcified blade
Martensia	X			non-calcified blade
Microdictyon	X			non-calcified blade
Padina	X			calcified blade
Peyssonnelia	X	X		non-calcified crust
Unknown brown crust	X			non-calcified crust
Unknown green/brown	X			non-calcified crust
CCA	X	X	X	calcified crust

Second, to compare how canopy height, biomass, and cover changed in response to treatments, we calculated an effect size as the response ratio of the mean log response variable in treatment compared to control samples. The logarithm of the response ratio is a common metric, behaves better statistically than does raw data, and allowed us to compare what, if any, statistical interaction exists between each treatment (Hedges et al. 1999, Gruner et al. 2008). While meta-analyses typically weight response ratios by sample variance to account for differences in sample size or study quality, here we instead used a direct comparison of sample means because sample sizes, methods, and experimenters were nearly identical across all three locations. Further, because we have the raw data and not just treatment means, we used the mean of the logarithms of the canopy heights, biomasses, and covers of the caged and unfertilized (X_{C1F0}), caged and fertilized (X_{C1F1}), uncaged and fertilized (X_{C0F1}), and uncaged and unfertilized (X_{C0F0}) samples to calculate the response ratio for herbivore removal (RR_{Cage}), nutrient addition ($RR_{Nutrients}$), and for the interaction effect (RR_{Int}), modified from Gruner et al. (2008):

$$RR_{Cage} = \text{mean}[(\ln(X_{C1F0}), \ln(X_{C1F1})] - \text{mean}[(\ln(X_{C0F0}), \ln(X_{C0F1})]$$

$$RR_{Nutrients} = \text{mean}[(\ln(X_{C0F1}), \ln(X_{C1F1})] - \text{mean}[(\ln(X_{C0F0}), \ln(X_{C1F0})]$$

$RR_{Int} = \text{mean}[(\ln(X_{C0F1}), \ln(X_{C1F0})] - \text{mean}[(\ln(X_{C1F1}), \ln(X_{C0F0})]$. For each log response ratio, a 95% confidence interval was calculated (Hedges et al. 1999). Response ratios were constructed so that a positive value indicates an increase in the response variable with treatment (e.g. $RR_{Cage} > 0$ means a greater canopy height inside cages compared to outside cages). Response ratios for interaction effects were constructed such that $RR_{Int} > 0$ suggests a super-additive effect, $RR_{Int} = 0$ suggests an additive effect (no interaction), and $RR_{Int} < 0$ suggests a sub-additive effect of interaction (Gruner et al. 2008).

Statistical analyses were performed in JMP 11.0, R 3.1.2 (R Development Core Team, http://www.r-project.org), and PRIMER-E (v6).

Results

Ambient turf algae assemblages

A total of 44 taxa were identified in the algal turf assemblages from all three locations (Table 3.3). Some taxa could not be reliably identified to genus without reproductive segments and were therefore grouped into higher taxonomic categories: cyanobacteria, CCA, small brown filamentous species in the order Ectocarpales, and the red genera *Chondria* and *Laurencia*.

Physical characteristics of ambient algal turfs (from control treatments) varied among locations in correlation with the herbivore abundance at each site. Millennium and Palmyra, which each have nearly twice the abundance of herbivores compared to Curaçao (Figure 3.1), both had less turf algae than Curaçao: shorter canopy height, lower biomass, and more sparse cover (Figure 3.3, Figure 3.4). Cover of CCA within turfs was low in all locations: 1.9 ± 1.1 % on Millennium, 1.0 ± 0.6 % on Palmyra, and 0.9 ± 0.6 % on Curaçao (all values mean ± SE).

Figure 3.3 Examples of the drastically different turf algae assemblages on Curaçao (top) and Palmyra (bottom). Turfs in Curaçao were taller, denser, and typically packed with sediment while Palmyra turfs were extremely sparse, retained almost no sediment, and typically had visible grazing scars. These turf plates are from control treatments (outside cages, no nutrients added). Scale: both plates 8-10 cm wide.

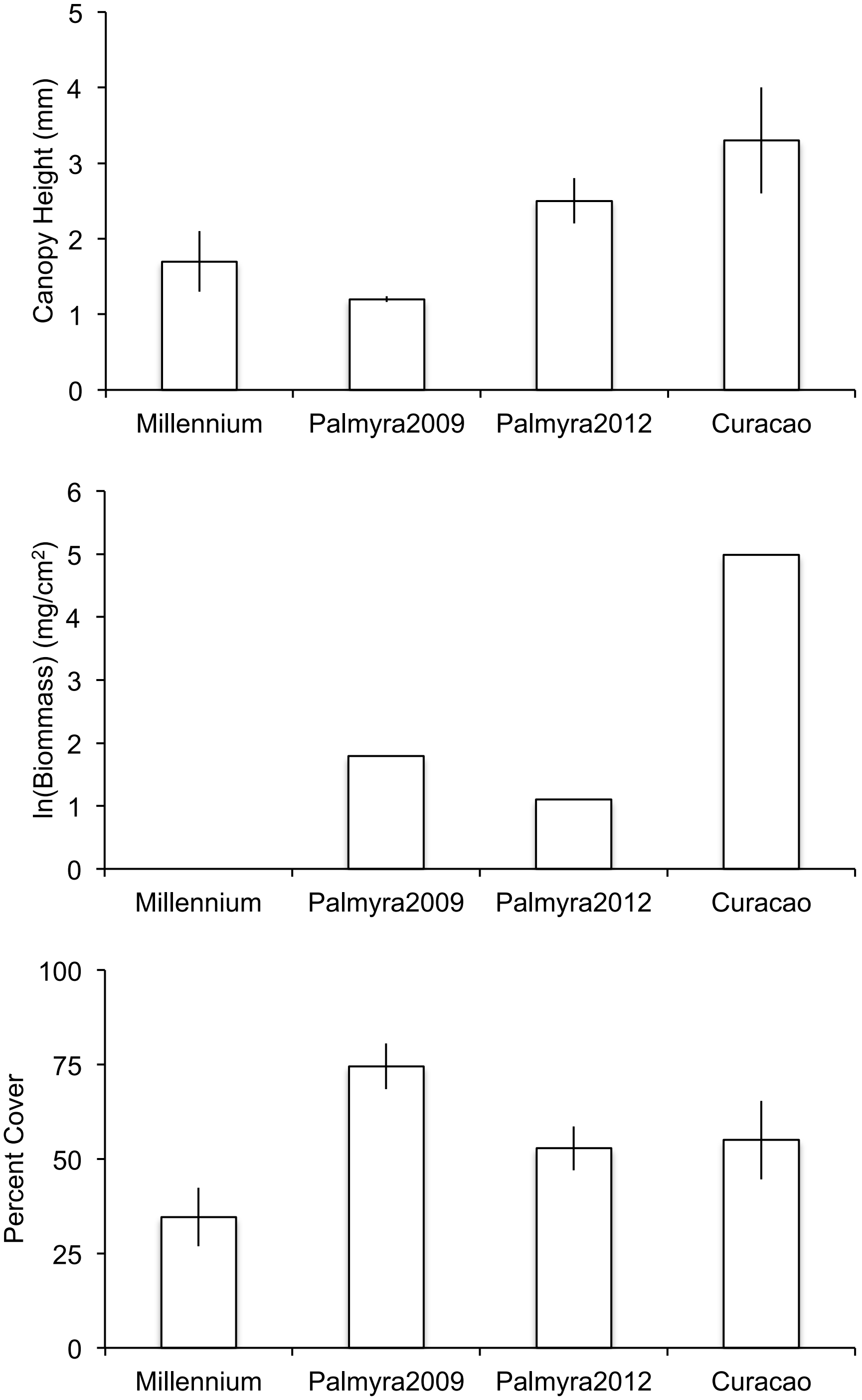

Figure 3.4 Physical characteristics of ambient turf algae at each location, quantified in terms of a) canopy height, b) biomass, and c) percent cover. Means ± SE reported for each metric. Note that biomass on Millennium was 0.001 g/cm^2, so its log does not show up on this scale.

Treatment conditions

Caging treatments reduced light inside cages by approximately 60% on Palmyra and 25% on Curaçao (Figure 3.5). Total daily lux was greater outside than inside cages on both Palmyra (one-tailed paired t-test, t(21) = 4.73, $p < 0.0001$) and on Curaçao (one-tailed paired t-test, t(30) = 2.07, $p = 0.02$).

On Palmyra, nutrient addition significantly increased the levels of both phosphate (F(2,40) = 10.13, $p = 0.0003$) and DIN (F(2,40) = 9.01, $p = 0.0006$) at experimental enrichment plots. Post-hoc Tukey HSD tests showed that phosphate and nitrogen differed (at $\alpha = 0.05$) only for nutrient addition treatments and not between ambient measurements and control treatments. On average, phosphate was 9x greater and nitrogen 27x greater in treatment plots compared to control plots. Despite identical nutrient addition methods in the two locations and observing Osmocote dissolving and washing through the samples, on Curaçao we did not detect any significant differences in either phosphate (F(2,44) = 0.326, $p = 0.723$) or total nitrogen (F(2,44) = 1.700, $p = 0.194$) (Table 3.4).

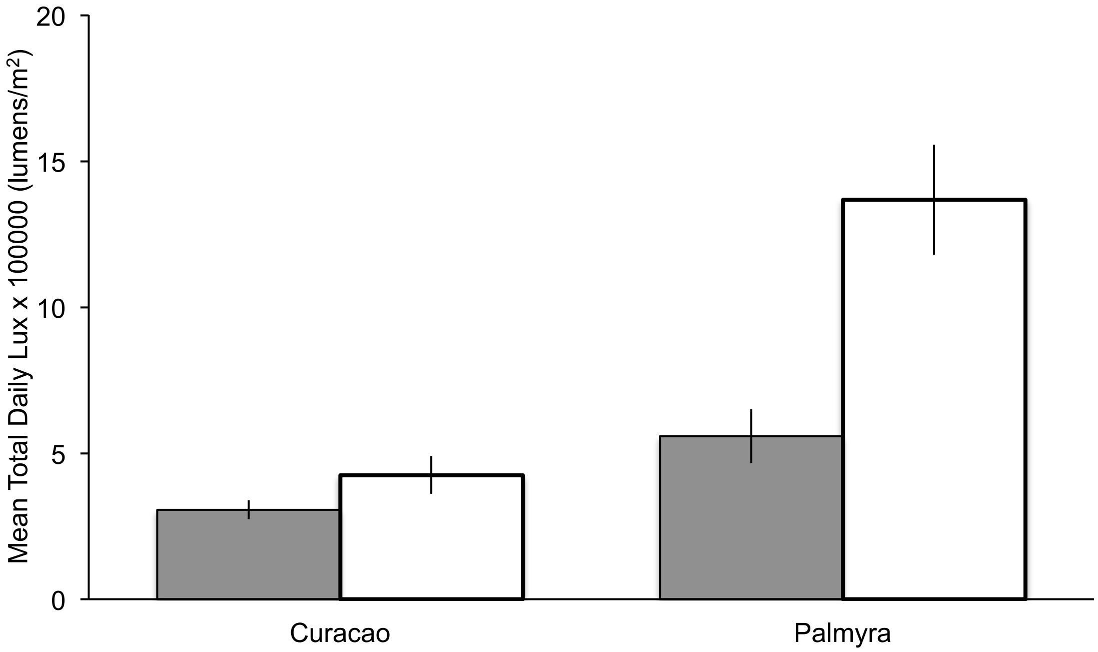

Figure 3.5 Mean (± SE) daily total light levels (lux) inside (gray) and outside (white) cages in experiments on Curaçao and Palmyra.

Table 3.4 Mean (± SE) phosphate and nitrogen ($NO_3^- + NO_4^+ + NH_4^+$) from the water in ambient (> 10m from experiments), control, and nutrient addition treatments in experiments on Palmyra and Curaçao. Letters indicate differences that were significant at α=0.05 from post-hoc Tukey HSD tests.

	Phosphate (µM)			**DIN (µM)**		
	Ambient	**Control**	**Treatment**	**Ambient**	**Control**	**Treatment**
Palmyra	0.3 ± 0.004 a	0.2 ± 0.006 a	2.4 ± 0.8 b	1.7 ± 0.4 a	1.7 ± 0.3 a	43.8 ± 55.6 b
Curaçao	0.05 ± 0.01 c	0.04 ± 0.01 c	0.04 ± 0.009 c	0.9 ± 0.2 c	1.3 ± 0.2 c	1.0 ± 0.1 c

Treatment effects

On Palmyra, herbivore exclusion increased both turf canopy height and biomass, and nutrient addition increased biomass (in 2009 only; 2012 ns). However, there were no significant interaction effects (Table 3.5, Figure 3.6). Multivariate dispersion was not significantly different among treatments (PERMDISP F = 1.0, p = 0.56). Herbivore removal on Palmyra (2012) also significantly shifted the turf assemblage (PERMANOVA pseudo-F(1) = 4.6, p = 0.001), but there was no effect of nutrient addition on assemblage structure: turf assemblages inside cages tended to be more similar to each other than to turf assemblages outside cages, regardless of nutrient treatment (Figure 3.7a). SIMPER analysis revealed that three taxa (Corallophila, *Gelidium*/*Gelidiella*, and *Peyssonellia*) together accounted for 57% of the dissimilarity between assemblages inside and outside of cages, with all three taxa more abundant inside cages. There were no differences in richness among any treatments (Table 3.5).

Herbivore removal on Curaçao increased turf canopy height ($p < 0.0001$) and marginally increased biomass (p = 0.09), but there were no effects of nutrient addition alone or in combination with herbivore removal (Table 3.5, Figure 3.6). Multivariate dispersion was not significantly different among treatments (PERMDISP F = 0.50, p = 0.79). There were significant shifts in the Curaçao turf assemblage due to both herbivore removal (PERMANOVA pseudo-F(1) = 1.8, p = 0.05) and nutrient addition (PERMANOVA pseudo-F(1) = 2.1, p = 0.02), and the interaction between these two treatments had a marginally significant effect on the turf assemblage (PERMANOVA pseudo-F(1) = 1.8, p = 0.058). These patterns are evident in the nMDS plot (Figure 3.7c) in which turf assemblages outside cages were generally more similar to each other than to assemblages inside cages, and turf assemblages inside cages separated according to nutrient treatment. SIMPER analysis revealed that the taxa primarily responsible for driving the majority of the differences among treatments were also the most abundant: cyanobacteria, CCA, *Dictyota*, and *Polysiphonia*. All four of those taxa were more abundant in fertilized treatments, and *Dictyota* was also more abundant when herbivores were excluded. There were no differences in richness due to either removing herbivores or adding nutrients alone, but there was a marginally significant interaction such that turf algae richness was highest with nutrient addition and without cages (Table 3.5).

Herbivore exclusion on Millennium marginally increased turf cover (from 34.6 ± 7.7% to 58.0 ± 7.5%, t(8.0) = 2.17, p = 0.06) but had no effect on turf canopy height, biomass, or cover of CCA (all p-values > 0.05). Multidimensional scaling revealed no clear patterns of assemblage differences inside cages compared to outside cages (Figure 3.7c, PERMANOVA pseudo-F(1) = 1.25, p = 0.27), and there were no differences in multivariate dispersion among treatments (PERMDISP F = 4.1, p = 0.09). However, richness was significantly greater inside than outside cages (t(9) = 13.3, p <0.001).

Table 3.5 Results from factorial ANOVA of the separate and combined effects of herbivore removal and nutrient enrichment on algal turf canopy height, biomass, and cover in experiments on Palmyra and Curaçao. **Bold** values indicate significance at α = 0.05, *italics* indicate significance at α = 0.1.

Treatment	**Response Variable**	df	**Palmyra 2009**		**Palmyra 2012**		**Curaçao**	
			F	p	F	p	F	p
Herbivore Removal (H)	**Canopy Height**	1	25.31	**0.0001**	24.57	**<0.0001**	38.2	**<0.0001**
	Biomass	1	10.00	**0.004**	0.001	0.98	3.02	*0.09*
	% Cover	1			17.01	**0.0004**	1.38	0.25
	Richness	1			0.19	0.67	1.47	0.24
Nutrients (N)	**Canopy Height**	1	3.77	0.07	1.15	0.30	0.40	0.53
	Biomass	1	4.65	**0.04**	1.71	0.20	0.19	0.66
	% Cover	1			0.003	0.96	0.05	0.82
	Richness				0.42	0.52	0.45	0.51
H x N	**Canopy Height**	1	2.55	0.13	0.97	0.34	1.24	0.27
	Biomass	1	1.39	0.26	2.73	0.11	0.004	0.95
	% Cover	1			0.74	0.40	0.86	0.36
	Richness				0.05	0.83	3.01	*0.096*

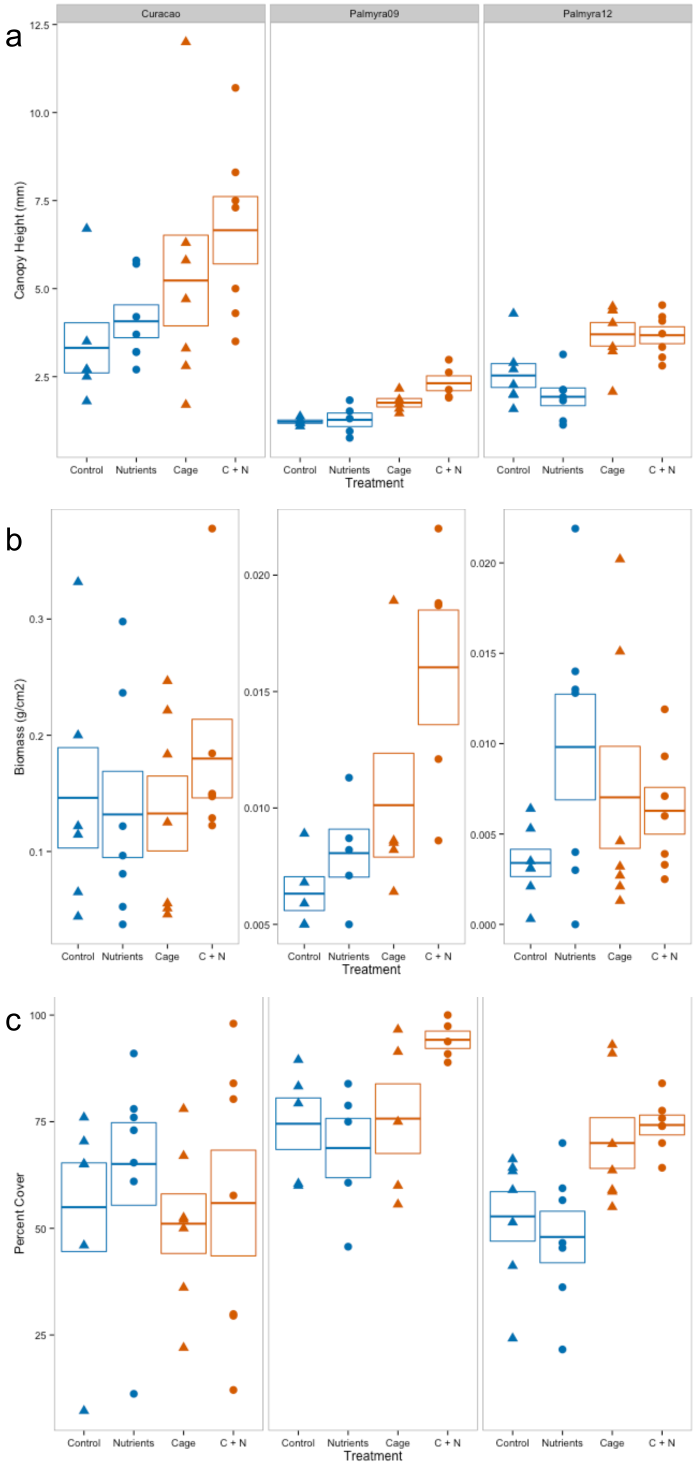

Figure 3.6 a) Canopy height, b) biomass, and c) percent cover of algal turf in factorial experiment of caging (blue = outside cages, red = inside cages) and nutrient addition (triangles = no nutrients, circles = nutrients added), on Curaçao (left panels) and Palmyra (center and right panels). Boxes show means and standard errors. Note different y-axis scales in (b).

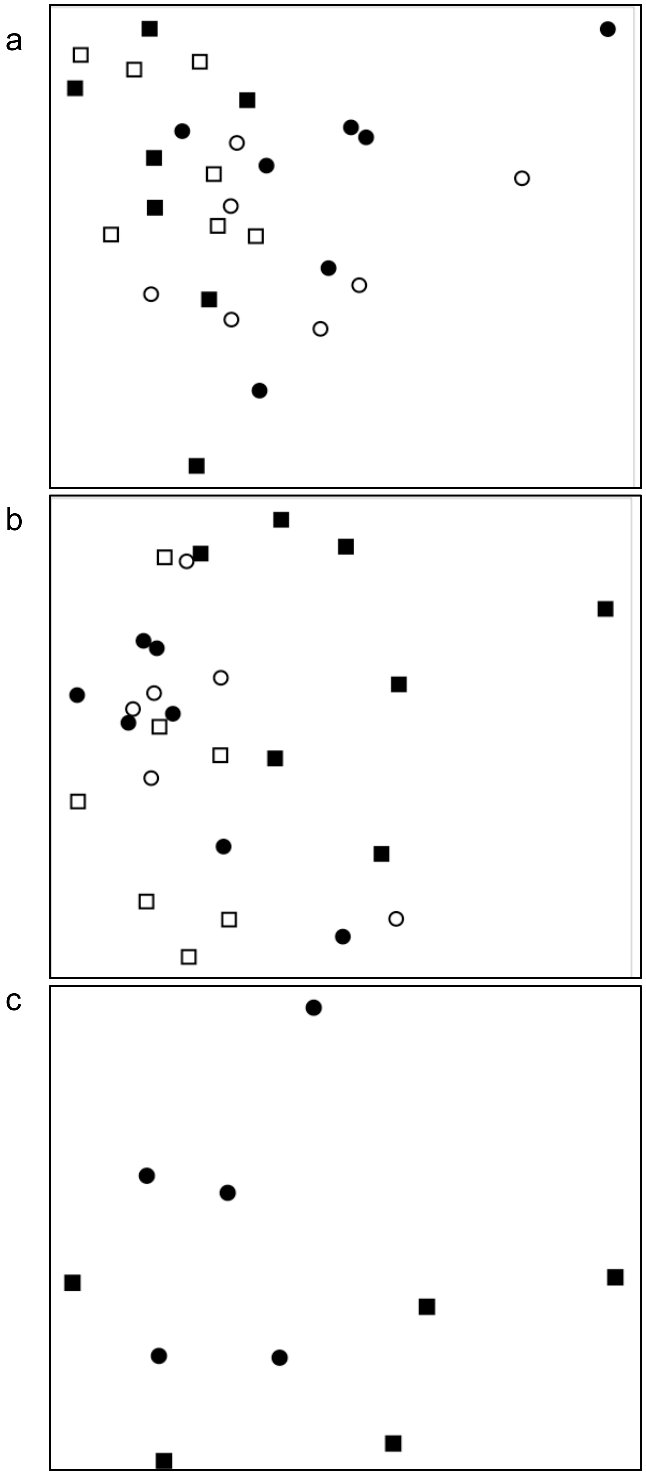

Figure 3.7 nMDS plots based on Bray-Curtis similarities of turf assemblages at the genus level from an herbivore removal x nutrient addition factorial experiment on a) Palmyra Atoll (stress = 0.14) and b) Curaçao (stress = 0.15) and an herbivore removal experiment on c) Millennium Atoll (stress = 0.11). Shape indicates herbivore treatment and fill indicates nutrient treatment: ○ = control, ● = nutrient addition, □ = herbivore removal, ■ = herbivore removal + nutrient addition.

Effect size: comparison of responses across locations

Herbivore removal had a consistently positive effect on almost all response variables in all locations ($RR_{Cage} > 0$), and this effect was particularly strong on canopy height in Curaçao (Figure 3.8). The effect of nutrient enrichment was less strong and less consistent than the effect of caging: the effect on canopy height was stronger in Curaçao than in Palmyra, while the effect on turf biomass was stronger in Palmyra (Figure 3.8). Nutrient addition had a positive effect on turf biomass and cover on Palmyra in 2009, but this effect was not repeated in 2012. The interaction effect of caging and nutrients was additive or sub-additive ($RR_{Int} \leq 0$) for nearly all response variables across locations (Figure 3.8). The one exception was a slightly super-additive interaction effect on percent cover in Curaçao, which is in sharp contrast to the additive and sub-additive interaction effects on canopy height and biomass in Curaçao (Figure 3.8). Treatments had no consistent effects on turf assemblage at the level of broad functional groups based on susceptibility to grazing and weediness (Table 3.3). Indeed, when visualizing turf assemblages across all locations and all treatments, assemblages primarily grouped according to location with variation among treatments within each location (Figure 3.9).

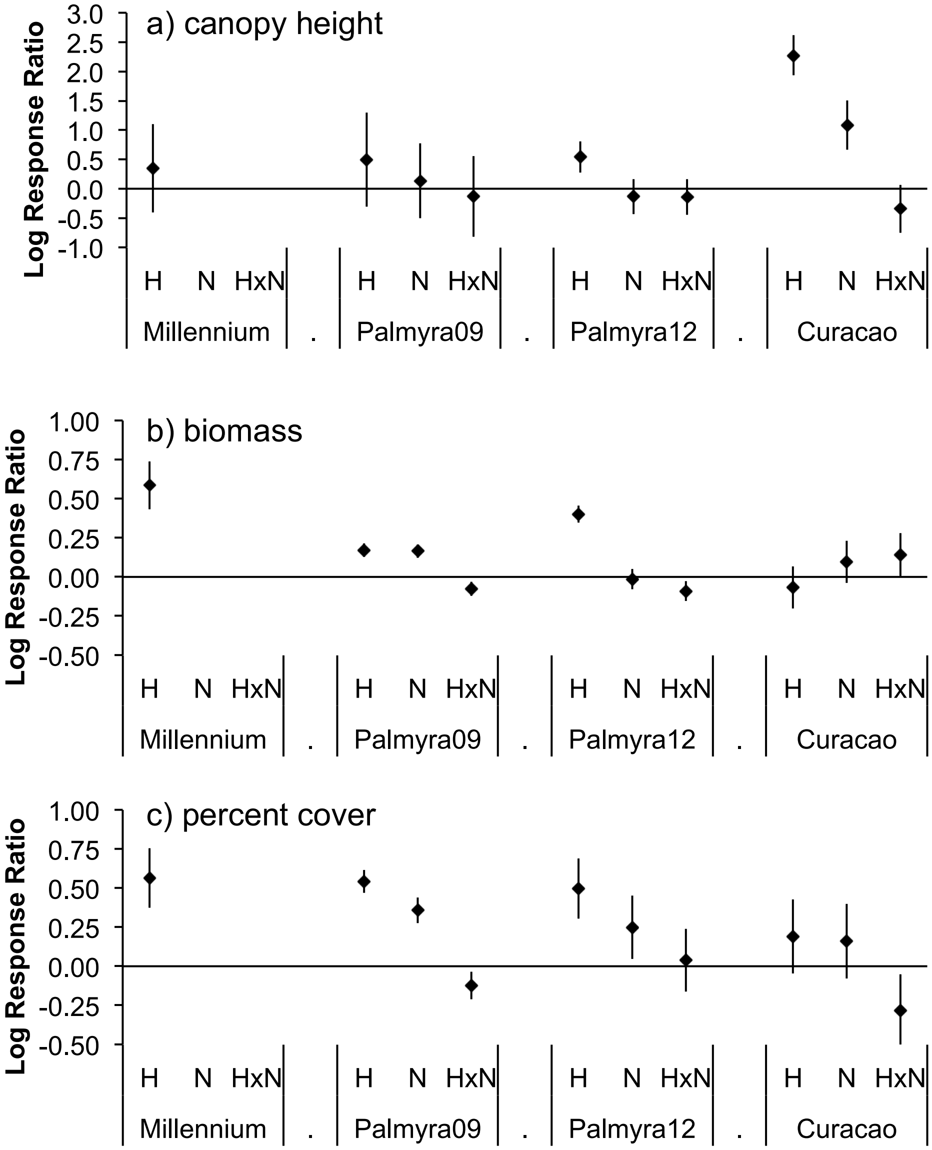

Figure 3.8 Effect sizes (and 95% CI) of herbivore removal (H), nutrient addition (N) and the interaction of these treatments (HxN) on three separate algal turf metrics at the three experiment locations.

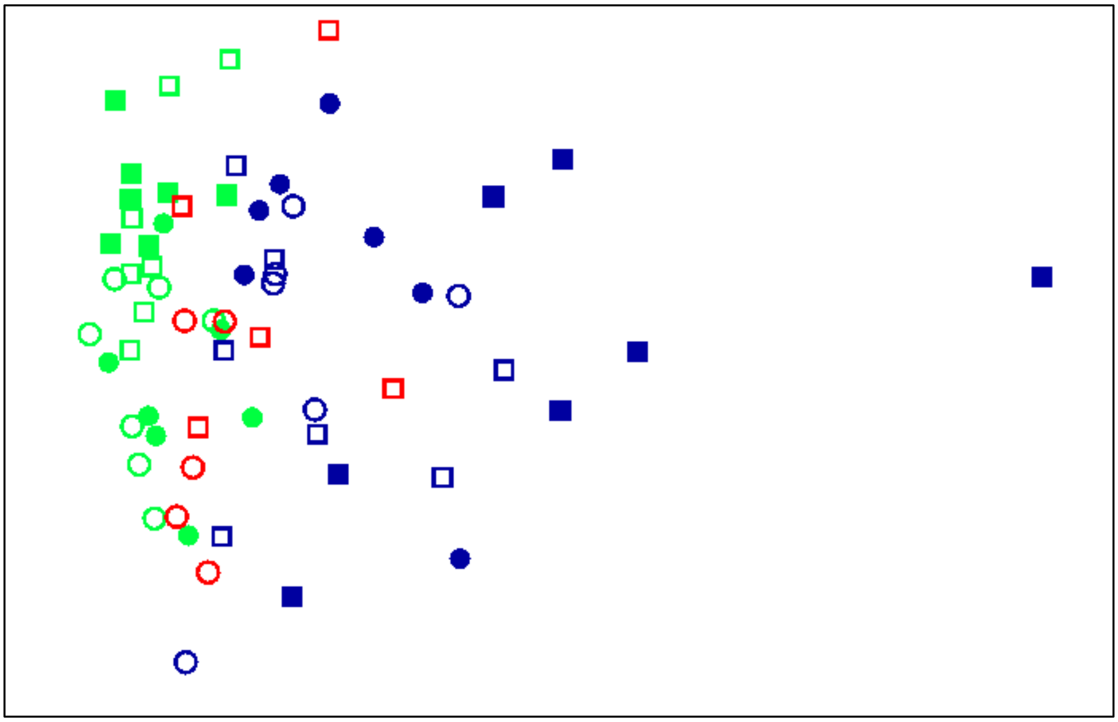

Figure 3.9 nMDS of turf assemblages based on Bray-Curtis similarities of broad functional groups (Table 3.3) in response to experimental treatments at all three locations. Color represents locations (blue = Curaçao, green = Palmyra, red = Millennium), shape indicates herbivore treatment and fill indicates nutrient treatment (○ = control, ● = nutrient addition, ☐ = herbivore removal, ■ = herbivore removal + nutrient addition). Assemblages differentiate by location along x-axis, and within each location differentiate by treatment along the y-axis. Stress = 0.12.

Discussion

Our study examined how the impacts of top-down and bottom-up control vary with environmental context, using turf algae, the abundant and widespread primary producers on tropical reefs, as a study organism. We found that removing herbivores increased the amount of turf algae in all locations, and the results varied depending upon the specific metrics we used (canopy height, cover, or biomass). Nutrient enrichment had almost no effect on turf algae abundance.

Other studies have also found that herbivory has a strong effect on turf algae, both on healthy coral reefs (Hatcher and Larkum 1983; Smith et al. 2001; Rasher et al. 2012;

Jessen et al. 2013) and on more degraded reefs with high cover of turf and macroalgae (Miller et al. 1999; Thacker et al. 2001; McClanahan et al. 2003; Burkepile and Hay 2009). For example, herbivore exclusion increased turf height on a turf-dominated reef in Florida (Burkepile and Hay 2009), but not on a coral-dominated reef in the Pacific (Rasher et al. 2012).

Nutrient addition had almost no effect on turf algae canopy height, biomass, or cover in any location, which agrees with many other studies that have failed to find any effect of nutrient enrichment on turf algae (Miller et al. 1999; Burkepile and Hay 2009; Jessen et al. 2013). We suggest that responses to nutrient enrichment were limited because grazing activity swamped the more subtle effects of elevated nutrients. Ambient nutrient levels were well within the measured global range of coral reefs (Kleypas et al. 1999), so it is unlikely that these were eutrophic sites where nutrients were not limiting.

On Curaçao, we were unable to detect any elevation in either phosphate or nitrogen, a common challenge in similar experiments on coral reefs where nitrogen is generally quite variable spatially and temporally (e.g., McClanahan et al. 2003, Burkepile and Hay 2009). We are confident that nutrients were successfully delivered to the system because fertilizer was observed dissolving into the water column and washing through the experimental units, and the fertilizer pellets were visibly reduced in size when they were replenished. However, even where elevated nutrients were detected, hydrodynamics could have prevented enriched water from penetrating the boundary layer and actually contacting turf algae filaments. We collected water samples from within 1 cm of the turf canopy, but boundary layers above turf algae are at most 2 mm thick (Larkum et al. 2003). Turf algae on Curaçao are highly productive (den Haan et al. 2014) and quickly take up excess nutrients, so if excess nutrients were available, we expect that turfs would respond. Therefore, we propose that one reason nutrient enrichment rarely affects turf algae is simply because nutrients in the water column do not physically contact the algal surfaces.

Our results differ for several reasons from a similar experiment in a shallow backreef in Belize, in which nutrient enrichment did increase turf cover (McClanahan et al. 2003). First, our turf "cover" measurements captured changes at a sub-centimeter scale and can also be described as turf density, in contrast to their *in situ* measurements of turf "cover" as lateral expansion. Second, there may be unique turf algae assemblages in each location that have different nutrient limitations and therefore respond differently to enrichment, and by chance we conducted our experiment in three locations with turfs that are unaffected by nutrients.

The interaction between herbivore removal and nutrient enrichment had no effect on turf canopy height, cover or biomass in any location, which supports the findings of many other studies (Gruner et al. 2008; Burkepile and Hay 2009). However, one observational study that monitored the broader reef community found that the interaction between water quality and herbivore biomass was the best predictor of turf abundance over a four year period (Houk et al. 2010). We suggest that the key difference is between experiments focused on turf algae and observational studies of turfs as one component in a coral reef benthos. The interaction between herbivory and nutrients may indirectly influence turf algae, such that turfs increase as a result of changes in the broader reef ecosystem, but not as a direct result of the interaction between top-down and bottom-up control.

Both assemblage structure and diversity of turf assemblages responded to treatments, but the type of response was different in each location. Nutrient enrichment increased turf diversity where nutrients were lowest (Curaçao), while herbivores reduced diversity where herbivory was highest (Millennium). This is partially, but not entirely, in agreement with Worm et al.'s (2002) hypothesis that herbivore effects on diversity depend on system productivity. Like us, they found that enrichment increased diversity at low productivity sites (our experiment on Curaçao). But our data contradict their findings that consumers increase diversity at high productivity sites (our experiment on Millennium). Studies at locations with moderate herbivory have also found that herbivores reduce turf diversity (Scott and Russ 1987; Smith et al. 2010). However, our data are in contrast to the effect of nutrient enrichment in grasslands, a terrestrial analogue to turf assemblages, where nitrogen enrichment decreases species richness (Tilman 1987). We suggest the mechanism for this interactive effect of herbivory and nutrients on diversity is driven by selective grazing, and turf richness increases when herbivores do not consume their preferred turf taxa. At locations with high herbivory (e.g. Millennium), this occurs due to caging. At locations with lower herbivory (e.g. Curaçao), enrichment promotes the growth of nutrient-limited turf algae taxa that are either not targeted by herbivores, or herbivory is too low to keep pace with turf growth. Examining top-down and bottom-up effects in different contexts provided this insight into potential mechanisms.

Our results point to emergent relationships between the physical characteristics and diversity of turf algae, although these relationships do not strictly follow the relationships among diversity, productivity, grazing, and nutrients established in terrestrial ecosystems. If turf assemblages followed classic succession from terrestrial models, then we would expect peak productivity in mid-successional, high diversity turfs (Odum 1969). This seemed to apply on Millennium, where turfs with the greatest cover also had the greatest richness herbivore exclusion – equivalent to less disturbance. However, on Curaçao, greatest productivity actually occurred in lower diversity turfs, because biomass and canopy height were both highest in the lower-diversity turfs inside cages. In at least one other study, turf diversity had no relationship to successional patterns of biomass and production (Fricke et al. 2011). Successional patterns in diversity, biomass, and production of turf algae appear to not precisely follow traditional models.

Our results clarify which are the most informative metrics of heterogeneous turf algae. Canopy height generally responded most strongly to all treatments, suggesting that, at least in the short term, growth of existing filaments is more responsive to environmental changes than is lateral expansion, which requires recruitment of new individuals. Although turf canopy height and biomass both increased in response to caging, we propose that canopy height is a more useful indicator of herbivory because it responds more rapidly, to a larger degree, and is easier to measure than biomass.

As we compare responses among sites, one important caveat is that the experiment durations on Curaçao and Millennium were approximately twice that on Palmyra. This could explain why the response magnitudes were larger on Curaçao than on Palmyra, but it does not explain why the response sizes were different on Curaçao and Millennium. Therefore, we conclude that differences among locations were due to environmental context, not experiment duration.

Turf algae responded to caging most strongly where herbivory was lowest and ambient turf communities started with the greatest canopy height, biomass, and cover. This could be due to major differences between Pacific and Caribbean reefs, because algal responses to caging are typically more rapid in the latter (Roff and Mumby 2012). We suggest that turf algae on Millennium and Palmyra are so heavily grazed, particularly by scraping and excavating herbivores (Hamilton et al. 2014), that there are very few basal filaments from which turfs can quickly regrow (Figure 3.3). Therefore, turf algae responses in high-herbivore environments may require recruitment of new individuals and subsequent succession versus the much quicker regrowth of existing plants in Curaçao. Importantly, this suggests a positive feedback between the loss of herbivory and loss of resilience, in which environments with few herbivores are likely to experience rapid responses to further reduction in top-down control when additional grazers are removed, while environments with abundant herbivores will be more resilient to fluctuations in herbivory.

This issue is further exacerbated by the fact that, on Millennium and Palmyra, herbivory remained constant under increased nutrients, evidenced by the near-zero response ratios of the interaction treatments. This suggests that herbivores did not increase consumption enough to keep up with even small levels of excess production caused by enrichment (Gruner et al. 2008). Therefore, we expect that over longer time scales turf algae would increase slowly in response to enrichment, although nutrients had no effect on turf abundance over a 9 month experimental period in the Florida Keys, where herbivores are considerably less abundant than in our experiment locations

(Burkepile and Hay 2009). More studies are needed on the longer-term successional trajectories of turf assemblages.

In summary, algal turfs are ubiquitous on coral reefs worldwide, but turf algae differ among locations in their responses to top-down and bottom-up control. Because turfs are heterogeneous algal assemblages, measuring multiple dimensions of turfs is the best way to get a complete understanding of the broader reef ecosystem. In particular, canopy height is sensitive to herbivory, so small increases in canopy height can be an early warning sign for marine resource managers that herbivores are declining. Turf algae on coral reefs are primarily controlled by herbivory, but herbivores cannot always graze down excess production due to prolonged nutrient enrichment. Importantly, loss of grazing services creates a positive feedback on the growth of turfs, so we are likely to see increasing amounts of turf algae on degraded reefs with few herbivores.

Chapter 3, in part, is currently being prepared for submission for publication of the material. Harris, Jill, Lindsay Bonito, Maggie Johnson, Emily Kelly, and Jennifer Smith. “An Experimental Analysis of the Context Dependent Effects of Nutrient Enrichment and Herbivore Exclusion on Coral Reef Turf Algae.” The dissertation author was the principal researcher and author of this material.

References

Barott K, Williams G, Vermeij M, Harris J, Smith J, Rohwer F, Sandin S (2012) Natural history of coral−algae competition across a gradient of human activity in the Line Islands. Mar. Ecol. Prog. Ser. 460:1–12

Belliveau SA, Paul VJ (2002) Effects of herbivory and nutrients on the early colonization of crustose coralline and fleshy algae. Mar. Ecol. Prog. Ser. 232:105–114

Bellwood D, Fulton C (2008) Sediment-mediated suppression of herbivory on coral reefs: decreasing resilience to rising sea levels and climate change? Limnol. Oceanogr. 53:2695–2701

Bellwood DR, Hughes TP, Hoey AS (2006) Sleeping functional group drives coral-reef recovery. Curr. Biol. 16:2434–9

Boyer KE, Fong P, Armitage AR, Cohen RA (2004) Elevated nutrient content of tropical macroalgae increases rates of herbivory in coral, seagrass, and mangrove habitats. Coral Reefs 23:530–538

Burkepile D, Hay M (2009) Nutrient versus herbivore control of macroalgal community development and coral growth on a Caribbean reef. Mar. Ecol. Prog. Ser. 389:71–84

Burkepile DE, Hay ME (2006) Herbivore vs. nutrient control of marine primary producers: context-dependent effects. Ecology 87:3128–39

Carpenter RC, Edmunds PJ (2006) Local and regional scale recovery of *Diadema* promotes recruitment of scleractinian corals. Ecol. Lett. 9:271–280

Carpenter RC, Williams SL (1993) Effects of algal turf canopy height and microscale substratum topography on profiles of flow speed in a coral forereef environment. Limnol. Oceanogr. 38:687–694

Cleland EE, Harpole WS (2010) Nitrogen enrichment and plant communities. Ann. N. Y. Acad. Sci. 1195:46–61

Connell S, Kroeker KJ, Fabricius KE, Kline DI, Russell BD (2013) The other ocean acidification problem: CO2 as a resource among competitors for ecosystem dominance. Philos. Trans. R. Soc. B 368:20120442

Diaz-Pulido G, McCook LJ (2002) The fate of bleached corals: patterns and dynamics of algal recruitment. Mar. Ecol. Prog. Ser. 232:115–128

Diaz-Pulido G, McCook LJ (2003) Relative roles of herbivory and nutrients in the recruitment of coral-reef seaweeds. Ecology 84:2026–2033

Edwards CB, Friedlander AM, Green AG, Hardt MJ, Sala E, Sweatman HP, Williams ID, Zgliczynski B, Sandin SA, Smith JE (2013) Global assessment of the status of coral reef herbivorous fishes: evidence for fishing effects. Proc. R. Soc. B Biol. Sci. 281:20131835

Fong P, Paul VJ (2011) Coral reef algae. In: Dubinsky Z., Stambler N. (eds) Coral Reefs: an ecosystem in transition. Springer Netherlands, Dordrecht, pp 242–272

Gobler CJ, Thibault DB, Davis TW, Curran PB, Peterson BJ, Liddle LB (2006) Algal assemblages associated with *Stegastes* sp. territories on Indo-Pacific coral reefs: Characterization of diversity and controls on growth. J. Exp. Mar. Bio. Ecol. 336:135–145

Gruner DS, Smith JE, Seabloom EW, Sandin S a, Ngai JT, Hillebrand H, Harpole WS, Elser JJ, Cleland EE, Bracken MES, Borer ET, Bolker BM (2008) A cross-system synthesis of consumer and nutrient resource control on producer biomass. Ecol. Lett. 11:740–55

Den Haan J, Visser PM, Ganase AE (2014) Nitrogen fixation rates in algal turf communities of a degraded versus less degraded coral reef. Coral Reefs 33:1003–1015

Fricke A, Teichberg M, Beilfuss S, Bischof K (2011) Succession patterns in algal turf vegetation on a Caribbean coral reef. Bot Mar 54:111–126ß

Haas A, El-Zibdah M, Wild C (2010) Seasonal monitoring of coral–algae interactions in fringing reefs of the Gulf of Aqaba, Northern Red Sea. Coral Reefs 29:93–103

Hamilton S, Smith J, Price N, Sandin S (2014) Quantifying patterns of fish herbivory on Palmyra Atoll (USA), an uninhabited predator-dominated central Pacific coral reef. Mar. Ecol. Prog. Ser. 501:141–155

Harris JL, Lewis LS, Smith JE (2015) Quantifying scales of spatial variability in algal turf assemblages on coral reefs. Mar. Ecol. Prog. Ser. 532:41–57

Hatcher BG, Larkum AWD (1983) An experimental analysis of factors controlling the standing crop of the epilithic algal community on a coral reef. J. Exp. Mar. Bio. Ecol. 69:61–84

Hedges L V., Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. Ecology 80:1150–1156

Hillebrand H, Gruner DS, Borer ET, Bracken MES, Cleland EE, Elser JJ, Harpole WS, Ngai JT, Seabloom EW, Shurin JB, Smith JE (2007) Consumer versus resource control of producer diversity depends on ecosystem type and producer community structure. Proc. Natl. Acad. Sci. U. S. A. 104:10904–10909

Houk P, Musburger C, Wiles P (2010) Water quality and herbivory interactively drive coral-reef recovery patterns in American Samoa. PLoS One 5:e13913

Hughes TP, Szmant AM, Steneck RS, Carpenter RC, Miller SL (1999) Algal Blooms on Coral Reefs: What Are the Causes? Limnol. Oceanogr. 44:1583–1586

Jessen C, Roder C, Villa Lizcano JF, Voolstra CR, Wild C (2013) In-situ effects of simulated overfishing and eutrophication on benthic coral reef algae growth, succession, and composition in the central Red Sea. PLoS One 8:e66992

Jompa J, McCook LJ (2003) Contrasting effects of turf algae on corals: massive *Porites* spp. are unaffected by mixed-species turfs, but killed by the red alga *Anotrichium tenue*. Mar. Ecol. Prog. Ser. 258:79–86

Karnauskas KB, Cohen AL (2012) Equatorial refuge amid tropical warming. Nat. Clim. Chang. 2:530–534

Kelly LW, Williams GJ, Barott KL, Carlson CA, Dinsdale EA, Edwards RA, Haas AF, Haynes M, Lim YW, McDole T, Nelson CE, Sala E, Sandin SA, Smith JE, Vermeij MJA, Youle M, Rohwer F (2014) Local genomic adaptation of coral reef-associated microbiomes to gradients of natural variability and anthropogenic stressors. Proc Natl Acad Sci U S A 111.28 (2014): 10227-10232.

Kleypas JA, McManus JW, Meñez LAB (1999) Environmental Limits to Coral Reef Development: Where Do We Draw the Line? Integr. Comp. Biol. 39:146–159

Lapointe BE (1999) Simultaneous top-down and bottom-up forces control macroalgal blooms on coral reefs - (Reply to the comment by Hughes et al.). Limnol. Oceanogr. 44:1586–1592

Lapointe BE, Barile PJ, Yentsch CS, Littler MM, Littler DS, Kakuk B (2004) The relative importance of nutrient enrichment and herbivory on macroalgal communities near Norman's Pond Cay, Exumas Cays, Bahamas: a "natural" enrichment experiment. J. Exp. Mar. Bio. Ecol. 298:275–301

Larkum AWD, Koch MW, Ku M (2003) Diffusive boundary layers and photosynthesis of the epilithic algal community of coral reefs. Mar. Biol. 142:1073–1082

Ledlie MH, Graham NAJ, Bythell JC, Wilson SK, Jennings S, Polunin NVC, Hardcastle J (2007) Phase shifts and the role of herbivory in the resilience of coral reefs. Coral Reefs 26:641–653

Leichter JJ, Stewart HL, Miller SL (2003) Episodic nutrient transport to Florida coral reefs. Limnol. Oceanogr. 48:1394–1407

Littler M, Littler D, Brooks B (2006) Harmful algae on tropical coral reefs: bottom-up eutrophication and top-down herbivory. Harmful Algae 5:565–585

Littler MM, Littler DS (1984) Models of tropical reef biogenesis: The contribution of algae. In: Round/Chapman (eds) Progress in Phycological Research. Biopress Ltd., pp 323–364

Littler MM, Littler DS (2007) Assessment of coral reefs using herbivory/nutrient assays and indicator groups of benthic primary producers: A critical synthesis, proposed protocols, and critique of management strategies. Aquat. Conserv. Mar. Freshw. Ecosyst. 17:195–215

Littler MM, Littler DS, Titlyanov EA (1991) Comparisons of N- and P-limited productivity between high granitic islands versus low carbonate atolls in the Seychelles Archipelago: a test of the relative-dominance paradigm. Coral Reefs 10:199–209

McClanahan TR (2003) The near future of coral reefs. Environ. Conserv. 29:460–483

McClanahan TR, Sala E, Stickels PA, Cokos BA, Baker AC, Starger CJ, Jones SH (2003) Interaction between nutrients and herbivory in controlling algal communities and coral condition on Glover's Reef, Belize. Mar. Ecol. Prog. Ser. 261:135–147

Miller MW, Hay ME, Miller SL, Malone D, Sotka EE, Szmant AM (1999) Effects of nutrients versus herbivores on reef algae: A new method for manipulating nutrients on coral reefs. Limnol. Oceanogr. 44:1847–1861

Muthukrishnan R, Fong P (2014) Multiple anthropogenic stressors exert complex, interactive effects on a coral reef community. Coral Reefs 33:911–921

Nugues MM, Roberts CM (2003) Coral mortality and interaction with algae in relation to sedimentation. Coral Reefs 22:507–516

Odum HT, Odum EP (1955) Trophic structure and productivity of a windward coral reef community on Eniwetok Atoll. Ecol. Monogr. 25:291–320

Odum EP (1969) The strategy of ecosystem development. Science. 164:262–270

Rasher DB, Engel S, Bonito V, Fraser GJ, Montoya JP, Hay ME (2012) Effects of herbivory, nutrients, and reef protection on algal proliferation and coral growth on a tropical reef. Oecologia 169:187–98

Roff G, Mumby PJ (2012) Global disparity in the resilience of coral reefs. Trends Ecol. Evol. 27:404–13

Russell BD, Connell SD (2005) A novel interaction between nutrients and grazers alters relative dominance of marine habitats. Mar. Ecol. Prog. Ser. 289:5–11

Sandin SA, McNamara DE (2012) Spatial dynamics of benthic competition on coral reefs. Oecologia 168:1079–90

Scott F, Russ G (1987) Effects of grazing on species composition of the epilithic algal community on coral reefs of the central Great Barrier Reef. Mar. Ecol. Prog. Ser. 39:293–304

Smith JE, Hunter CL, Smith CM (2010) The effects of top-down versus bottom-up control on benthic coral reef community structure. Oecologia 163:497–507

Smith JE, Smith C, Hunter CL (2001) An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. Coral Reefs 19:332–342

Steneck RS (1988) Herbivory on coral reefs: a synthesis. 37–49

Thacker R, Ginsburg D, Paul V (2001) Effects of herbivore exclusion and nutrient enrichment on coral reef macroalgae and cyanobacteria. Coral Reefs 19:318–329

Tilman D (1987) Secondary Succession and the Pattern of Plant Dominance Along Experimental Nitrogen Gradients. Ecol. Monogr. 57:189

Vermeij MJ, van Moorselaar I, Engelhard S, Hörnlein C, Vonk SM, Visser PM (2010) The effects of nutrient enrichment and herbivore abundance on the ability of turf algae to overgrow coral in the Caribbean. PLoS One 5:e14312

Worm B, Lotze HK, Hillebrand H, Sommer U (2002) Consumer versus resource control of species diversity and ecosystem functioning. Nature 417:848–51

Chapter 4 **The Role of Small Infaunal Invertebrates in Coral Reef Algal Turfs**

Jill Harris

On tiny algae
and tiny invertebrates:
Small things matter, too

Abstract

Herbivory is a strong determinant of turf algae abundance and assemblage structure, but most researchers only consider grazing by fish. In fact, algal turfs provide habitat for abundant and diverse small infaunal invertebrates that are rarely examined for their ecological role. I hypothesized that these small invertebrates could be 1) grazing on turf algae, 2) benefitting turfs via nutrient enrichment from excretions, and/or 3) indirectly impacting turf algae by competition with or predation by fish. Here, by partitioning herbivory between fish and small infaunal invertebrates, I present some of the first evidence that small invertebrates have a measurable impact on coral reef turf algae. The direction of this effect depended on the presence of fish: invertebrates had a positive effect on turf algae when fish were present, but the positive effect disappeared when fish were excluded. I suggest that invertebrates are either being preyed upon by or competing with fish, and in the absence of fish, invertebrates increase their consumption of turf algae. These findings contradict several earlier studies that concluded invertebrates had a negligible influence on coral reef turfs and lay the foundation for future direct tests of the mechanisms by which small infaunal invertebrates either directly or indirectly influence turf algae.

Introduction

Herbivory and nutrients together influence the structure of coral reef benthic communities. Numerous experiments and observational studies have demonstrated that herbivory is generally a stronger control on algal biomass in the broader reef community, although there are also synergistic effects between herbivores and nutrients (Burkepile and Hay 2006). However, we know little about how these top-down and bottom-up factors specifically influence algal turfs, the diverse multispecies assemblages of small (< 1 cm) algae that are ubiquitous and abundant on coral reefs. Turf algae are useful subjects with which to investigate top-down and bottom-up impacts because, in addition to measuring responses in overall growth and biomass, we can examine impacts on assemblage diversity and structure. Further, herbivorous fishes and urchins are typically considered the only significant grazers on reefs, so we know even less about consumption by the diverse and abundant small invertebrates that live infaunally in turf algae.

Small benthic invertebrates, also called cryptofauna, epifauna, and meio/mesofauna (Brostoff 1988; Dulvy et al. 2002; Logan et al. 2008; Glynn and Enochs 2011; Kramer et al. 2012), are rarely studied. Their small size and cryptic habitat makes them difficult to see and collect, while their considerable diversity makes them difficult to identify. While herbivorous coral reef fishes primarily belong to two families (Acanthuridae and Scaridae), small benthic invertebrate fauna represent a hugely diverse spectrum of taxa across multiple phyla, including larvae of larger invertebrates (Glynn and Enochs 2011). Harpacticoid copepods are the most common member of infaunal communities in algal turfs, with gammarid amphipods, tanaids, other crustaceans, nematodes, polychaetes, and gastropods also common (Carpenter 1986; Klumpp et al. 1988; Zeller 1988; Smith et al. 2001; Dulvy et al. 2002; Logan et al. 2008; Kramer et al. 2014; Head et al. 2015). Limited, but rapidly emerging, evidence points to small benthic invertebrates on coral reefs as not only diverse, but also abundant and potentially variable.

Small invertebrates are especially abundant in turf algae, where widely varying biomass and density estimates are as high as 1.36 g / m^2 (Klumpp et al. 1988) or 290,000 individuals / m^2 (Logan et al. 2008), respectively (Table 4.1). Some of the uncertainty in abundance estimates is likely due to limited samples from a variety of geographic regions, depths, and reef zones, though it might also reflect actual variability. Mesoinvertebrate communities in turf algae are spatially variable over 100's of kilometers (Kramer et al. 2014) but not on scales of 100's of meters (Logan et al. 2008) or across reef zones in the same location (Kramer et al. 2012). Mesofauna are 2-3.5 times more abundant in algal turfs inside damselfish territories compared to outside, which contributes to their spatial variability over small scales (Lobel 1980; Klumpp et al. 1988). Data on temporal variation are even more limited: one study found significant seasonal variation in abundances in Hawaii (Klumpp et al. 1988), while another found no seasonal variation on the Great Barrier Reef (Logan et al. 2008).

Table 4.1 Published estimates of the biomass and abundance of small benthic infaunal invertebrates in algal turfs on coral reefs.

Density individuals m^{-2}	**Biomass** g m^{-2}	**Depth** **Reef zone**	**Location**	**Source**
32,700 (polychaetes only)	-	<1 m back reef / crest	Eniwetok Atoll	Bailey-Brock et al. 1980
16,300 - 58,300	0.6-1.36	10 m damselfish territories on reef flat, back reef, reef slope	Davies Reef, Great Barrier Reef	Klumpp et al. 1988
300	-	damselfish territories on patch reefs	Orpheus Island, GBR	Zeller 1988
20,000 - 70,000				Smith et al. 2001
18,900	-	7 m barrier reef	Fiji	Dulvy et al. 2002
40,000 - 290,000	-	10-12 m reef slope	Heron Island, GBR	Logan et al. 2008
-	0.4-0.6	0-8 m reef flat/crest/base	Orpheus Island, GBR	Kramer et al. 2012

In other marine systems, small benthic invertebrates are also diverse, abundant, and exert significant grazing pressure. In kelp forests, for example, experimentally removing carnivorous fish increases the abundance and grazing intensity of small grazers, which in turn reduces the growth and physiological performance of algae (Kennelly 1983; Davenport and Anderson 2007). Grazing by abundant small invertebrates controls the colonization, and sometimes also adult biomass, of fucoid-dominated macroalgal communities in the Baltic Sea (Korpinen et al. 2007). In freshwater streams and lakes, invertebrate grazers control both the biomass and diversity of microalgae (McCormick and Stevenson 1989; Hillebrand 2003). Small herbivorous invertebrates are also abundant, and highly variable spatially and temporally, in temperate intertidal ecosystems (Ruesink 2000).

Among all marine and aquatic ecosystems, small invertebrate grazers are arguably most important and well studied in seagrass beds, which provide a particularly informative analog to coral reefs: both are shallow coastal ecosystems subject to overfishing and nutrient enrichment. Seagrass plants are the foundational species in seagrass beds, and their biomass is reduced by predator loss and nutrient enrichment (via increased epiphyte load) (Heck et al. 2000), just as corals are the foundational species on reefs, and loss of herbivores and nutrient enrichment together facilitate algal proliferation (McCook 1999). In seagrass beds, abundant amphipods control the growth of the green algae that is epiphytic on seagrass (Duffy 1990; Duffy and Hay 2000). Amphipods can even consume excess epiphyte production caused by nutrient enrichment, thereby preventing losses of seagrass (Myers and Heck 2013). Amphipod abundance is primarily controlled by fish predation (Heck et al. 2000; O'Connor and Bruno 2007; Douglass et al. 2008), making these invertebrates an important trophic link in seagrass food webs (Williams and Heck Jr 2000).

Despite the key role that small invertebrates play in other marine ecosystems and their abundance on coral reefs, they have only rarely been investigated for their ecological role on reefs. One early study on a back reef in the Caribbean concluded that small invertebrates have a negligible effect on coral reef algae (Carpenter 1986), but a growing body of more recent studies has hinted that they may actually be important food sources and herbivores. Infaunal invertebrates in algal turfs can comprise more than 50% of the diet for common reef fishes, including invertivores/omnivores (wrasses, gobies) and taxa that are typically considered herbivores (parrotfish, damselfish) (Kramer et al. 2013), and are an obligate food source for juveniles of herbivorous fishes (Choat 1991).

These small invertebrates are also potentially significant grazers, estimated to consume 31% of turf algae production or up to 1.9 g dry weight m^{-2} day^{-1} (Klumpp et al. 1988; Klumpp and Polunin 1989). In an experimental mesocosm, amphipods at densities of > 1 cm^{-2} – far lower than typical estimates of *in situ* densities (Table 4.1) – reduced biomass and altered assemblage structure of turf algae (Brawley and Adey 1981). In a different experiment, removing invertebrate grazers from seaweed beds actually reduced algal biomass as epiphyte load increased, suggesting that small invertebrates actually have a positive effect on seaweed – whether by consuming epiphytic microalgae or some other unknown mechanism (Brostoff 1988).

The evidence suggesting small invertebrates are significant grazers on coral reefs is contradicted by several studies where small invertebrate abundance and/or biomass correlate positively with turf algae biomass (Klumpp et al. 1988; Zeller 1988; Smith et al. 2001; Kramer et al. 2012), which is opposite of what we would expect if invertebrates exerted strong grazing pressure. One potential explanation is that the relationship between invertebrates and turf algae is only correlative, not causative: perhaps they both increase in abundance and biomass, respectively, inside fish exclusion cages (Zeller 1988; Smith et al. 2001) as a result of protection from invertivorous and herbivorous fishes, respectively. For example, the thick algal turfs in damselfish territories are a refuge for infaunal invertebrates (Lobel 1980; Klumpp et al. 1988), but this would occur either if the abundant turf provided ample food for invertebrates or if the thick turf and damselfish behavior together protected invertebrates from predation.

Based on the limited information available, we have identified three potential ecological roles for mesoinvertebrates on coral reefs: herbivores, prey resources for fish, and sources of nutrient enrichment to algal turfs. First, if mesoinvertebrates are significant consumers of turf algae (Klumpp et al. 1988), they might compete with larger herbivores, while if they consume primarily epiphytic microalgae (Glynn and Enochs 2011), they might be beneficial to turf algae in the same way amphipods benefit seagrasses by grazing epiphytes. The latter seems plausible because most infaunal invertebrate assemblages are dominated by harpacticoid copepods, which primarily eat benthic microalgae (Klumpp et al. 1988; Zeller 1988; Logan et al. 2008; Kramer et al. 2012, 2014). Even if small invertebrate grazers have minimal impacts on algal biomass, they might increase algal diversity by imposing intermediate grazing pressure, at which levels algal diversity peaks (Carpenter 1981; McCormick and Stevenson 1989). Second, invertebrates in turf algae could be significant prey sources for invertivorous and carnivorous fish which are more abundant and diverse than herbivores on some reefs (Glynn and Enochs 2011). If this is the case, infaunal invertebrates in algal turfs would be a key trophic link in coral reefs just like they are in seagrass ecosystems (Edgar and Shaw 1995; Williams and Heck Jr 2000; Kramer et al. 2013), and they may actually increase turf consumption by attracting omnivorous fish that consume invertebrates together with algae and particulate organic matter (Wilson et al. 2003; Bonaldo and Bellwood 2011). A third and new idea is that infaunal invertebrates could be fertilizing turf algae via excretion, in a similar but more localized manner to how fish excretion fertilizes algae and suppresses corals (Burkepile et al. 2013). Algal fertilization by grazers has been hypothesized for snails and freshwater algae and for urchins on coral reefs (Williams and Carpenter 1988; McCormick and Stevenson 1989; McClanahan 1997). Much of our existing insight into the ecology of small benthic invertebrates on coral reefs is based on limited experiments, observational studies, and insight from other ecosystems. Therefore, we need more direct tests of how small invertebrates affect primary producers.

To test how bottom-up and top-down factors influence turf algae communities on coral reefs, and to specifically compare the roles of infaunal invertebrates and herbivorous fish, we tested the effects of nutrients, fish grazing, and small invertebrate grazing in a three-way fully factorial experiment. We predicted that nutrients and herbivore exclusion would both increase the amount of turf algae, but that herbivores would have a stronger effect. In one of the first studies to directly test for effects of small benthic invertebrates on a coral reef, we partitioned the effects of herbivory from small invertebrates and from larger fish by using a combination of fish exclusion cages and insecticide. Invertebrate removal decreasing turf algae abundance would suggest that small invertebrates are benefiting turfs by consuming epiphytic microalgae, fertilization, or thinning to increase assemblage productivity. Alternatively, invertebrate removal increasing turf algae would suggest that these small invertebrates are consuming turfs directly. Additionally, we tested how algal diversity and community structure are affected by nutrients and by different grazing types and intensities.

Methods

Experimental Setup

To test the separate and combined effects on turf algae of nutrients, fish, and small invertebrates, we deployed a three-factor factorial experiment on the shallow (5-6 m) fringing reef on the leeward side of Curaçao. The experiment ran for 30 days in July-

August 2014. The experimental setup is identical to that described in Chapter 3, with the addition of a third treatment to remove small infaunal invertebrates from turfs.

Visually similar turf algae communities growing on approximately 10 x 10 cm carbonate plates were attached to PVC frames, with two plates per frame. To exclude fish, one end of the frame had a 25 x 25 x 25 cm enclosure of 0.5 cm clear plastic mesh. Cages were brushed clean every 1-2 days. Half the frames were assigned to the nutrient enrichment treatment by adding 12 g of Osmocote brand slow-release fertilizer (19:6:12 N:P:K) in nylon mesh bags, and, orthogonally, half were assigned to the invertebrate removal treatment by adding insecticide in slow-release plaster in nylon mesh bags. Insecticide-infused plaster was mixed after Poore et al. (2009) and Johnston and Keough (2002). We used Sevin (active ingredient carbaryl), a commercially available cholinesterase inhibitor that is frequently used in liquid form to remove small invertebrates from aquaculture, mesocosm, and seagrass experiments, or incorporated into plaster for slow-release in *in situ* experiments (Duffy and Hay 2000; Douglass et al. 2008; Poore et al. 2009). Carbaryl has no effect on algal growth or productivity (Shacklock and Croft 1981; Carpenter 1986; Poore et al. 2009). It is very effective at removing amphipods, has mixed results in removing other crustaceans, and is generally considered ineffective against molluscs and polychaetes (Shacklock and Croft 1981; Duffy and Hay 2000; Dumbauld et al. 2001; Poore et al. 2009; Whalen et al. 2013). However, a 5-minute weekly treatment with 50% Sevin caused a >80% reduction in all mesoinvertebrates in algal turfs (Carpenter 1986), and it is toxic at certain doses to both crustaceans and molluscs (Stewart et al. 1967). A concentration of 10% carbaryl by weight in slow-release plaster is effective up to 60 cm (Reynolds et al. 2014), so we diluted concentrated liquid Sevin insecticide to a 10% solution, mixed with plaster for a total volume of 200 mL, and air-dried for two days.

The nutrient and insecticide treatments were applied to the center of the frames, equidistant from both turf plates, replaced every 10-14 days, and located > 5 m from control treatments. There were a total of 51 samples, n = 6-7 samples in each of eight treatments: Control, Invert Grazers only (fish excluded using cages), Fish Grazers only (invertebrates excluded using insecticide), No Grazers (both fish and invertebrates excluded), Nutrients, Invert Grazers + Nutrients (fish excluded, nutrients added), Fish Grazers + Nutrients (invertebrates excluded, nutrients added), and No Grazers + Nutrients (both fish and invertebrates excluded, nutrients added). Seven additional procedural control samples were collected at the beginning of the experiment and stored for processing.

Treatment Measurements and Response Variables

To quantify the effectiveness of experimental nutrient enrichment, water samples were collected from a random subset of enriched and control frames and ambient locations (> 10 m away) at the beginning, midpoint, and end of the experiment. Using syringes rinsed three times with ambient seawater, water was collected < 1 cm from turf canopy, filtered through GF/C filters, and stored on ice in the dark until frozen. Within 1 month, samples were analyzed for phosphate and for nitrate, nitrite, and ammonium (reported together as dissolved inorganic nitrogen, DIN) by flow injection analysis at the Marine Science Institute Analytical Lab at the University of California, Santa Barbara. To test for potential shading inside cages, HOBO pendant temperature/light data loggers

(Onset Computer Corporation, USA) recorded light intensity every 10 minutes inside and outside cages.

We measured canopy height, biomass, and assemblage of each turf algae sample. Canopy height was measured at the beginning and end of the experiment using calipers *in situ* to measure the length to the nearest 0.5 mm of 6 randomly selected turf filaments per sample. The difference in mean canopy height from the beginning to the end of the experiment is reported as change in canopy height. To measure algal biomass, we used a razor blade to scrape all algae from a 2 x 2 cm area, decalcified biological matter in 5% HCl, rinsed with freshwater onto pre-weighed filters, dried filters at 60°C to a constant weight, and re-weighed the filters. Biomass was normalized to the mean biomass of procedural control samples and is reported here as change in biomass per month.

Turf assemblage at the genus level were analyzed under a dissecting microscope beneath a 1 x 1 cm monofilament grid. Within 5 grid cells per sample, percent cover of each taxon was recorded. Where necessary for identification, algae were stained with aniline blue dye, mounted on permanent slides, and examined at higher magnification.

Data Analysis

Nutrient levels within each treatment did not change over time (Phosphate: $F_{2,18} = 2.3$, $p = 0.13$; DIN: $F_{2,18} = 3.2$, $p = 0.067$), so time points were grouped together to compare overall nutrient levels between ambient, control, and enriched plots using ANOVA. Total daily light intensity was calculated for each HOBO logger, and mean total daily light intensity was calculated per treatment (inside or outside cages). The difference in light intensity inside and outside cages was compared using a paired one-tailed t-test, pairing caged and control measurements within day.

Canopy height and biomass were approximately normal based on the distribution of residuals. A three-factor factorial ANOVA was used to compare each metric within and among treatments, with nutrient addition, fish removal, and invertebrate removal all treated as fixed factors.

We compared assemblage structure within and among treatments using a three-way factorial PERMANOVA, again treating nutrient addition, fish removal, and invertebrate removal as fixed factors. Assemblages were compared using untransformed percent cover data at the lowest possible taxonomic level, typically genus. We used SIMPER analysis to identify taxa that cumulatively contributed 50% of the difference among treatments. Additionally, we compared taxonomic richness among treatments with three-factor ANOVAs. The PERMANOVA and SIMPER analyses are based on the relative abundance of each taxon (i.e. two assemblages will be more similar if they share taxa in similar abundances) and richness is based only number of taxa, so the combination of these two methods provided us with two different perspectives on turf algae diversity.

Results

Treatment Conditions

There were no detectible differences among nutrient treatments in levels of either phosphate ($F_{2,44} = 0.33$, $p = 0.72$) or nitrogen ($F_{2,44} = 1.7$, $p = 0.19$). Light was greater outside than inside cages (one-tailed paired t-test, $t_{30} = 2.07$, $p = 0.02$); caging treatments reduced light inside cages by approximately 25% (Table 4.2).

Table 4.2 Experimental conditions at control and treatment plots. Mean (± SE) phosphate and DIN ($NO_3^- + NO_4^+ + NH_4^+$) from ambient (> 10 m from experiments), control, and nutrient addition treatments, and mean (± SE) total daily light from controls (outside cages) and treatments (inside cages).

	Ambient	**Control**	**Treatment**
Phosphate (µM)	0.05 ± 0.01	0.04 ± 0.01	0.04 ± 0.009
DIN (µM)	0.9 ± 0.2	1.3 ± 0.2	2.0 ± 0.1
Light (lumens / m^2)		4.3 ± 0.7	3.1 ± 0.3

Turf Canopy Height, Biomass Response to Treatments

When turf algae were exposed to invertebrate grazing only (inside cages), there was a significant ($p < 0.001$) increase in canopy height and a marginally significant ($p = 0.089$) increase in biomass compared to turfs exposed to both fish and invertebrate grazers (Figure 4.1a-b). The interaction between caging and invertebrate removal was also significant, such that the effect of small invertebrate grazers depended on whether or not fish were present (Table 4.3). The only treatment to cause a significant decrease in canopy height was when turf algae were exposed to fish (outside cages) and invertebrates were removed. In contrast, when fish were excluded (inside cages), invertebrate removal increased canopy height. The greatest increase in canopy height occurred when both types of grazers were removed (Figure 4.1a).

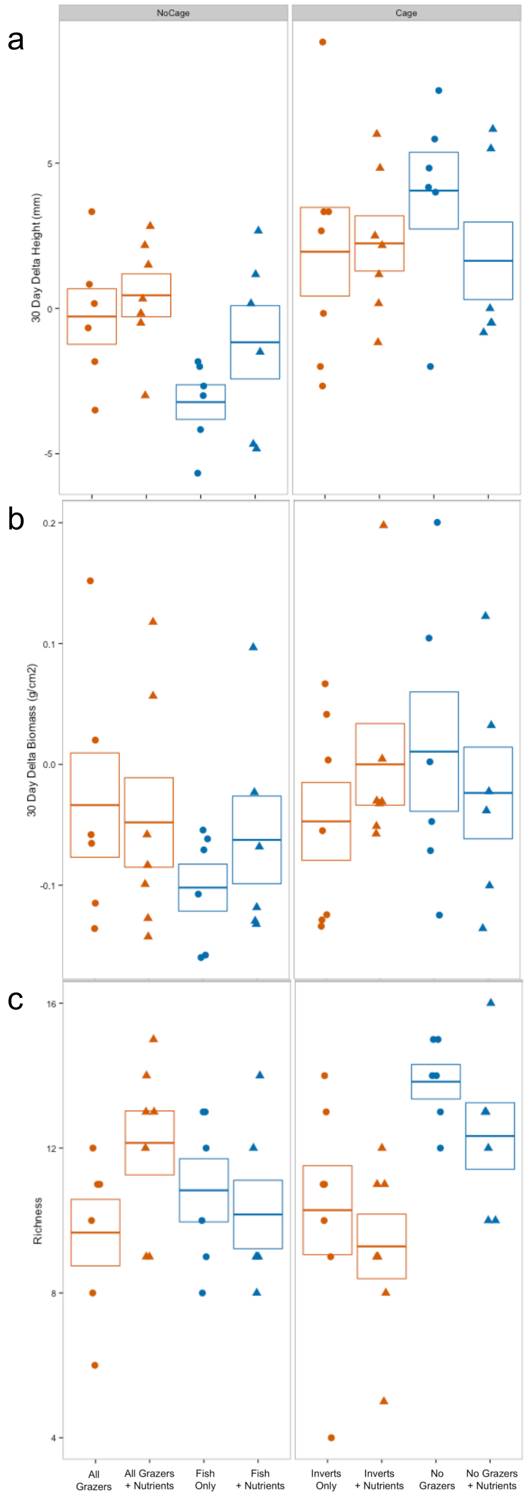

Figure 4.1 Change in a) canopy height, b) biomass, and c) richness of algal turf from a 30-day three-way factorial experiment of fish removal (left panel = outside cages; right panel = inside cages), nutrient addition (circles = no nutrients, triangles = nutrients added), and invertebrate removal (red = no insecticide, blue = insecticide added). Boxes show means and standard errors.

Table 4.3 Results from three-factor factorial ANOVAs on the 30-day change in turf canopy height and biomass, and taxonomic richness. **Bold** values indicate significance at α < 0.05, *italics* at α < 0.1.

		Delta Canopy Height			Delta Biomass			Richness		
	df	MS	F	p	MS	F	p	MS	F	p
Cage (C)	1	**151**	**18.5**	**<0.001**	*0.0262*	*3.0*	*0.090*	3.8	0.69	0.41
Nutrients (N)	1	0.64	0.078	0.78	0.0016	0.19	0.67	0.28	0.050	0.82
Insecticide (I)	1	7.1	0.87	0.36	0.0016	0.18	0.67	**26**	**4.7**	**0.036**
C x N	1	18	2.2	0.14	0.000031	0.004	0.95	*16*	*3.0*	*0.092*
C x I	1	*29*	*3.5*	*0.067*	0.011	1.2	0.28	**45**	**8.1**	**0.0066**
N x I	1	1.7	0.20	0.65	0.00072	0.083	0.77	10	1.9	0.18
C x N x I	1	13	1.6	0.22	0.015	1.7	0.20	5.5	1.0	0.32
residuals	43	8.2			0.0087			5.5		

Turf Assemblage Response to Treatments

Turf algae richness was affected by the interaction between invertebrate removal and fish exclusion and by the interaction between fish exclusion and nutrient addition. There was no change in turf richness when either invertebrates or fish were removed, but when both types of grazers were removed, richness significantly increased (Table 4.3, Figure 4.1). The greatest richness among all treatments was with no grazers present (mean S = 10.8 and 13.3 inside cages, invertebrates removed, with and without nutrients, respectively). There was a marginally significant (p=0.092) interaction between fish exclusion and nutrient addition such that the effect of nutrient addition depended on fish: outside cages, adding nutrients increased diversity (from mean 9.9 to 11.4 taxa), while inside cages, adding nutrients decreased diversity (from mean 12.5 to 10.4 taxa) (Figure 4.1c).

Assemblage structure was also affected both by the interaction between invertebrate removal and fish exclusion and by the interaction between invertebrate removal and nutrient addition (Table 4.4). As with canopy height and richness, the effect of fish depended on whether or not invertebrates were removed: all turf samples with invertebrates removed were similar to each other, regardless of whether they were inside or outside cages. In contrast, when invertebrates were present, samples outside cages were quite similar to each other while samples inside cages were much more variable (Figure 4.2). The effect of nutrient addition also depended on whether or not invertebrates were removed: when invertebrates were removed, there was very little variation among samples regardless of whether nutrients were added. However, when invertebrates were present, there were greater differences among samples with and without added nutrients (Figure 4.2).

Table 4.4 Results from three-factor factorial PERMANOVA on turf assemblage composition. **Bold** values indicate significance at $\alpha < 0.05$.

	df	**MS**	**Pseudo-F**	**p**	**permutations**
Cage (C)	1	3151	1.6	0.1	999
Nutrients (N)	1	2752	1.4	0.18	997
Insecticide (I)	**1**	**3943**	**1.9**	**0.047**	**999**
C x N	1	3252	1.6	0.10	999
C x I	**1**	**3873**	**1.9**	**0.054**	**998**
N x I	**1**	**4421**	**2.2**	**0.018**	**999**
C x N x I	1	2588	1.3	0.19	998
Residuals	43	2035			

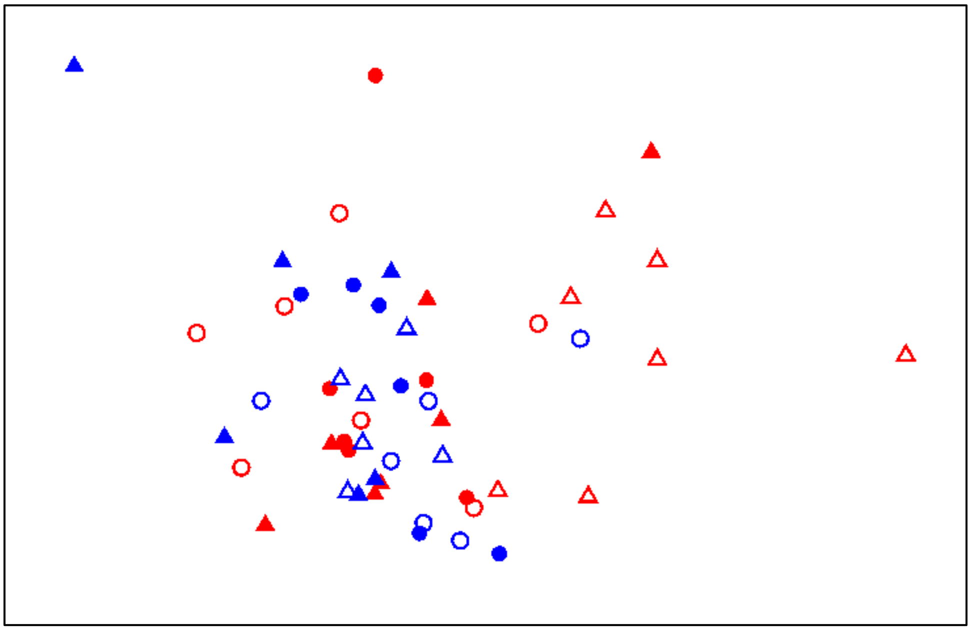

Figure 4.2 nMDS plot based on Bray-Curtis similarities of turf algae assemblages at the genus level from a three-way factorial experiment of herbivore removal, invertebrate removal, and nutrient addition (stress = 0.18). Fill indicates herbivore treatment (fill = no cage, open = cage), shape indicates nutrient treatment (circle = no nutrients, triangle = nutrient addition), color indicates invertebrate treatment (red = invertebrates present, blue = invertebrates removed).

The four most abundant taxa (CCA, *Polysiphonia*, *Herposiphonia*, and cyanobacteria) together contributed approximately 50% of the dissimilarities among treatments. When invertebrates were excluded, *Herposiphonia* and cyanobacteria were relatively more abundant. When fish were excluded, CCA was more abundant. In samples where nutrients were added, CCA, *Polysiphonia*, and *Herposiphonia* were all more abundant. Several less abundant taxa were present in significantly different abundances depending on whether invertebrates or fish were excluded. Specifically, *Sphacelaria* and an unidentified brown crust were more abundant in assemblages without invertebrates, while *Dictyota* and *Jania* were both more abundant in samples where fish were excluded. One taxon, *Ceramium*, was more abundant when either invertebrates, fish, or both were excluded compared to turfs exposed to all grazers.

Discussion

Our goal was to examine top-down and bottom-up influences on turf algae assemblages on coral reefs, specifically partitioning the consumer roles of fish and small, infaunal invertebrates that live within turfs. Small invertebrates are well known as important grazers and food sources in other marine ecosystems, but our study is one of the first to explicitly examine their ecology on a coral reef. We found that fish and invertebrates together controlled the biomass and canopy height of turf algae, but, in our system at least, nutrients had no effect on the amount of turf.

Most notably, we present some of the first evidence that small invertebrates have a measurable effect on turf algae on coral reefs, in contrast to two earlier studies that reported negligible impacts of small invertebrates (Carpenter 1986; Brostoff 1988). Fish and invertebrates had impacts of similar magnitude and opposite direction: when invertebrates were removed, canopy height decreased by about 3 mm / month, and when fish were excluded, canopy height increased by about the same amount. Such a seemingly small difference in turf algae heights can have potentially large impacts on boundary layer thickness, sediment retention, and mortality of settling coral larvae (Carpenter and Williams 1993; Birrell et al. 2005). Therefore, we propose that small invertebrates play an important role in the ecology of turf algae and the broader coral reef community.

However, the way that invertebrates affected turf algae depended on the presence of fish; small invertebrates alone had little effect on turfs, but their interactions with fish affected both the amount and composition of turf assemblages. When turfs were exposed to fish, invertebrates actually had a positive effect on canopy height; the invertebrate removal treatment was the only one in which canopy height decreased. This positive effect of invertebrates on turfs explains why several studies have found a positive relationship between turf algae biomass and invertebrate abundance or biomass (Klumpp et al. 1988; Zeller 1988; Smith et al. 2001; Kramer et al. 2012). However, the positive effect disappeared when fish were excluded.

We propose two explanations for the context-dependent effects of invertebrates on turf algae. First, in the absence of fish predators and/or competitors, invertebrate consumption of turf may increase, thus causing a negative effect on turf algae abundance. In kelp forests, exclusion of carnivorous fish increases invertebrate grazing intensity and reduces algal growth (Kennelly 1983; Davenport and Anderson 2007). Second, omnivorous fish that consume both turf algae and infaunal invertebrates may increase their algal consumption in the absence of invertebrates, such that invertebrates “protect” turf from being grazed. This would result in an observed positive effect of invertebrates on turf algae abundance in the presence of fish. Omnivorous fishes and small invertebrates are both abundance on coral reefs (Bailey-Brock et al. 1980; Glynn and Enochs 2011; Kramer et al. 2012, 2013), so we suggest that this may be an important trophic link. Future experiments should explicitly test whether the interaction between fish and invertebrates is due to invertebrate competition with herbivorous fish or predation by carnivorous fish.

In addition to measuring controls on the amount of turf algae, we also examined community-level responses and found some evidence of intermediate grazing effects on turf diversity. Richness was greater at low levels of grazing (all grazers excluded) than with only invertebrates, only fish, or both present. This effect confirms a mesocosm experiment in which turf diversity increased in the absence of both fish and amphipod grazers (Brawley and Adey 1981), but it contradicts several studies where diversity was greatest at intermediate levels of grazing (Carpenter 1981; McCormick and Stevenson 1989). However, in both of those cases intermediate grazing intensity was due to intermediate density of a single grazer, whereas we manipulated the type of grazer. Just as herbivorous fish guilds have different feeding preferences, and algae susceptibility to grazing varies with both grazer type and among algae species (Lewis 1985; Burkepile and Hay 2008), we extend this analogy to fish and small invertebrates representing a diversity of grazing types and suggest that turf algae diversity is affected differently by variations in grazing intensity than by variations in grazer type.

If these differences in turf assemblage structure were due to the grazing preferences of fish and invertebrates, then there are both specific preferences and at least some diet overlap. Small invertebrates preferred smaller and simpler taxa like *Sphacelaria* and *Herposiphonia*, just as they did in two other experiments that quantified turf assemblage structure in the presence and absence of small invertebrate grazers (Brawley and Adey 1981; Brostoff 1988). Fish preferred more complex and calcified taxa like CCA, *Dictyota*, and *Jania*. Both fish and invertebrates consumed *Ceramium*, which was abundant only when both types of grazers were excluded. While CCA were rare (<10%) in all treatments, our finding that CCA were more abundant when fish were excluded is a surprising contrast to previous studies where grazing promoted the abundance of CCA over filamentous turfs (Smith et al. 2010).

Algal turfs also varied in richness with nutrients and fish herbivory: nutrients increased turf diversity in the presence of fish but decreased diversity when fish were excluded. In other words, the effect of consumers was context-dependent and only increased diversity where there were excess nutrients (Worm et al. 2002). These two effects match some previous studies while contradicting others. In Chapter 3, enrichment also increased turf diversity only in the presence of fish, and the decreased diversity that we observed inside cages matches results from terrestrial grasslands where nutrient enrichment also reduces primary producer richness (Tilman 1987). However, our findings that fish herbivory alone had no effect on diversity were in contrast to two other studies in which excluding fish did increase richness of coral reef turfs (Scott and Russ 1987; Smith et al. 2010). In multispecies assemblages of primary producers, such as coral reef algal turfs, it appears that consumers and nutrients together control diversity, perhaps via interspecific competition and interactions among different types of grazers.

In summary, herbivory by both fish and small invertebrates controls the amount of turf algae on coral reefs. Nutrients have no effects on turf algae abundance over short (1 month) time scales, but they do interact with herbivory to drive turf algal community structure. On coral reefs, turf algae are both habitats and food sources for numerous and diverse small invertebrates. These invertebrates can exert either negative or positive influences on turf algae depending on their interactions with fish, which may act as competitors, predators, or both. Thus, the ecological effects of overfishing may be more complicated than previously thought if there are indirect effects on turf algae via interactions with small invertebrates. Infaunal invertebrates and turf algae are both diverse assemblages composed of small taxa that are typically overlooked in coral reef ecology. Both are diverse groups that should be considered for their heterogeneity, not as single functional groups: small invertebrates include herbivores, detritivores, and carnivores, while turfs include taxa that are allelopathic or harmless, calcified or uncalcified, crusts or uprights, and retain thick sediments or virulent microbial communities depending on conditions. Future studies should consider these details in examining interactions between the infaunal invertebrate and turf algae communities to better understand how they each fit into competitive interactions and trophic ecology of the broader reef community.

Chapter 4, in part, is currently being prepared for submission for publication of the material. Harris, Jill. “The role of small infaunal invertebrates in coral reef algal turfs.” The dissertation author was the principal researcher and author of this material.

References

Bailey-Brock JH, White JK, Ward LA (1980) Effects of algal turf and depressions as refuges on polychaete assemblages of a windward reef bench at Enewetak Atoll. Micronesica 16:43–58

Birrell CL, McCook LJ, Willis BL (2005) Effects of algal turfs and sediment on coral settlement. 51:408–414

Bonaldo RM, Bellwood DR (2011) Spatial variation in the effects of grazing on epilithic algal turfs on the Great Barrier Reef, Australia. Coral Reefs 30:381–390

Brawley SH, Adey WH (1981) The effect of micrograzers on algal community structure in a coral reef microcosm. Mar. Biol. 61:167–177

Brostoff WN (1988) Seaweed community structure and productivity: the role of mesograzers. Proc. 6th Int. Coral Reef Symp. 2:1–6

Burkepile DE, Allgeier JE, Shantz A a, Pritchard CE, Lemoine NP, Bhatti LH, Layman CA (2013) Nutrient supply from fishes facilitates macroalgae and suppresses corals in a Caribbean coral reef ecosystem. Sci. Rep. 3:1493

Burkepile DE, Hay ME (2006) Herbivore vs. nutrient control of marine primary producers: context-dependent effects. Ecology 87:3128–39

Burkepile DE, Hay ME (2008) Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. Proc. Natl. Acad. Sci. U. S. A. 105:16201–6

Carpenter RC (1981) Grazing by *Diadema antillarum* (Philippi) and its effects on the benthic algal community. J. Mar. Res. 39:749–766

Carpenter RC (1986) Partitioning herbivory and its effects on coral reef algal communities. Ecol. Monogr. 56:345–364

Carpenter RC, Williams SL (1993) Effects of algal turf canopy height and microscale substratum topography on profiles of flow speed in a coral forereef environment. Limnol. Oceanogr. 38:687–694

Choat J (1991) The biology of herbivorous fishes on coral reefs. In: Sale P.F. (eds) The Ecology of Reef Fishes on Coral Reefs. Academic Press, Inc., San Diego, pp 120–155

Davenport AC, Anderson TW (2007) Positive indirect effects of reef fishes on kelp performance: the importance of mesograzers. Ecology 88:1548–1561

Douglass JG, Duffy JE, Bruno JF (2008) Herbivore and predator diversity interactively affect ecosystem properties in an experimental marine community. Ecol. Lett. 11:598–608

Duffy JE (1990) Amphipods on seaweeds: partners or pests? Oecologia 83:267–276

Duffy JE, Hay ME (2000) Strong impacts of grazing amphipods on the organization of a benthic community. Ecol. Monogr. 70:237–263

Dulvy NK, Mitchell RE, Watson D, Sweeting CJ, Polunin NVC (2002) Scale-dependant control of motile epifaunal community structure along a coral reef fishing gradient. J. Exp. Mar. Bio. Ecol. 278:1–29

Dumbauld BR, Brooks KM, Posey MH (2001) Response of an estuarine benthic community to application of the pesticide carbaryl and cultivation of Pacific oysters (*Crassostrea gigas*) in Willapa Bay, Washington. Mar. Pollut. Bull. 42:826–844

Edgar GJ, Shaw C (1995) The production and trophic ecology of shallow-water fish assemblages in southern Australia III. General relationships between sediments, seagrasses, invertebrates and fishes. J. Exp. Mar. Bio. Ecol. 194:107–131

Glynn PW, Enochs IC (2011) Invertebrates and Their Roles in Coral Reef Ecosystems. In: Dubinsky Z., Stambler N. (eds) Coral Reefs: An Ecosystem in Transition. Springer Netherlands, Dordrecht, pp 273–325

Head CEI, Bonsall MB, Koldewey H, Pratchett MS, Speight M, Rogers AD (2015) High prevalence of obligate coral-dwelling decapods on dead corals in the Chagos Archipelago, central Indian Ocean. Coral Reefs 34:905–915

Heck KL, Pennock JR, Valentine JF, Coen LD, Sklenar SA (2000) Effects of nutrient enrichment and small predator density on seagrass ecosystems: An experimental assessment. Limnol. Oceanogr. 45:1041–1057

Hillebrand H (2003) Opposing effects of grazing and nutrients on diversity. Oikos 100:592–600

Johnston EL, Keough MJ (2002) Direct and indirect effects of repeated pollution events on marine hard-substrate assemblages. Ecol. Appl. 12:1212–1228

Kennelly SJ (1983) An experimental approach to the study of factors affecting algal colonization in a sublittoral kelp forest. J. Exp. Mar. Bio. Ecol. 68:257–276

Klumpp D, McKinnon A, Mundy C (1988) Motile cryptofauna of a coral reef: abundance, distribution and trophic potential. Mar. Ecol. Prog. Ser. 45:95–108

Klumpp DW, Polunin NVC (1989) Partitioning among grazers of food resources within damselfish territories on a coral reef. J. Exp. Mar. Bio. Ecol. 125:145–169

Korpinen S, Honkanen T, Vesakoski O, Hemmi A, Koivikko R, Loponen J, Jormalainen V (2007) Macroalgal communities face the challenge of changing biotic interactions: review with focus on the Baltic Sea. AMBIO A J. Hum. Environ. 36:203–211

Kramer MJ, Bellwood DR, Bellwood O (2012) Cryptofauna of the epilithic algal matrix on an inshore coral reef, Great Barrier Reef. Coral Reefs 31:1007–1015

Kramer MJ, Bellwood DR, Bellwood O (2014) Large-scale spatial variation in epilithic algal matrix cryptofaunal assemblages on the Great Barrier Reef. Mar. Biol. 161:2183–2190

Kramer MJ, Bellwood O, Bellwood DR (2013) The trophic importance of algal turfs for coral reef fishes: the crustacean link. Coral Reefs

Lewis SM (1985) Herbivory on coral reefs: algal susceptibility to herbivorous fishes. Oecologia 65:370–375

Lobel PS (1980) Herbivory by damselfishes and their role in coral reef community ecology. Bull. Mar. Sci. 30:273–289

Logan D, Townsend KA, Townsend K, Tibbetts IR (2008) Meiofauna sediment relations in leeward slope turf algae of Heron Island reef. Hydrobiologia 610:269–276

McClanahan TR (1997) Primary succession of coral-reef algae: Differing patterns on fished versus unfished reefs. 218:77–102

McCook LJ (1999) Macroalgae, nutrients and phase shifts on coral reefs: scientific issues and management consequences for the Great Barrier Reef. Coral Reefs 18:357–367

McCormick P, Stevenson RJ (1989) Effects of snail grazing on benthic algal community structure in different nutrient environments. J. North Am. Benthol. Soc. 8:162–172

Myers J, Heck K (2013) Amphipod control of epiphyte load and its concomitant effects on shoalgrass *Halodule wrightii* biomass. Mar. Ecol. Prog. Ser. 483:133–142

O’Connor NE, Bruno JF (2007) Predatory fish loss affects the structure and functioning of a model marine food web. Oikos 116:2027–2038

Poore AGB, Campbell AH, Steinberg PD (2009) Natural densities of mesograzers fail to limit growth of macroalgae or their epiphytes in a temperate algal bed. J. Ecol. 97:164–175

Reynolds PL, Paul Richardson J, Emmett Duffy J (2014) Field experimental evidence that grazers mediate transition between microalgal and seagrass dominance. Limnol. Oceanogr. 59:1053–1064

Ruesink JL (2000) Intertidal mesograzers in field microcosms: Linking laboratory feeding rates to community dynamics. J. Exp. Mar. Bio. Ecol. 248:163–176

Scott F, Russ G (1987) Effects of grazing on species composition of the epilithic algal community on coral reefs of the central Great Barrier Reef. Mar. Ecol. Prog. Ser. 39:293–304

Shacklock P, Croft G (1981) Effect of grazers on *Chondrus crispus* in culture. Aquaculture 22:331–342

Smith JE, Hunter CL, Smith CM (2010) The effects of top-down versus bottom-up control on benthic coral reef community structure. Oecologia 163:497–507

Smith JE, Smith C, Hunter CL (2001) An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. Coral Reefs 19:332–342

Stewart NE, Millemann RE, Breese WP (1967) Acute toxicity of the insecticide Sevin® and its hydrolytic product 1-Naphthol to some marine organisms. Trans. Am. Fish. Soc. 96:25–30

Tilman D (1987) Secondary succession and the pattern of plant dominance along experimental nitrogen gradients. Ecol. Monogr. 57:189

Whalen M, Duffy J, Grace J (2013) Temporal shifts in top-down vs. bottom-up control of epiphytic algae in a seagrass ecosystem. Ecology 94:510–520

Williams S, Carpenter R (1988) Nitrogen-limited primary productivity of coral reef algal turfs: potential contribution of ammonium excreted by *Diadema antillarum*. Mar. Ecol. Prog. Ser. 47:145–152

Williams SL, Heck Jr KL (2000) Seagrass Community Ecology. In: Bertness M.D., Gaines S.D., Hay M.E. (eds) Marine Community Ecology. Sinauer Associates Inc., pp 317–337

Wilson SK, Bellwood DR, Choat JH, Furnas M (2003) Detritus in the epilithic algal matrix and its use by coral reef fishes. Oceanogr. Mar. Biol. Annu. Rev. 41:279–309

Worm B, Lotze HK, Hillebrand H, Sommer U (2002) Consumer versus resource control of species diversity and ecosystem functioning. Nature 417:848–51

Zeller D (1988) Short-term effects of territoriality of a tropical damselfish and experimental exclusion of large fishes on invertebrates in algal turfs. Mar. Ecol. Prog. Ser. 44:85–93

Conclusion

The key takeaway from my dissertation is that turf algae are worth studying in greater detail than previous research, because they are abundant, widespread, heterogeneous, offer useful a testing ground for ecological theory, and impact pressing conservation issues. Turf algae are ecologically important on coral reefs and distinct from what is also called ‘turf algae’ in other ecosystems (Chapter 1). In particular, I offer the first global quantitative meta-analysis of turf algae abundance on coral reefs. Published articles commonly include bold statements that turf algae are one of, or the, most abundant benthic group, but those claims either go uncited or reference single location studies. To remedy this lack of quantitative data, I gathered global reef monitoring data from 35 countries over 20 years to provide an actual quantitative estimate of global turf algae cover. My analysis necessarily relied on a broad stroke to estimate turf algae cover, because many monitoring programs either do not record data on turf algae or use multiple ambiguous benthic categories (e.g. dead coral, rubble, and pavement, all of which are likely covered in turfs). Therefore, I hope that this meta-analysis motivates monitoring programs and managers to begin recording turf algae data, and that it might serve as a baseline for analyzing future temporal changes in global turf algae abundance. Additionally, as my data become publicly available, they will offer opportunities to investigate both spatial and temporal trends in turf algae abundance.

The heterogeneous nature of turf algae communities is a theme that runs throughout my dissertation. When turfs are measured in experiments or by monitoring programs, spatial coverage is typically the only metric that is reported. This approach treats turfs as single homogeneous functional groups, instead of the heterogeneous communities they truly are. In my dissertation, I describe and measure other turf metrics that I expect to have the most significant ecological interpretations. For example, turf canopy height reflects grazing pressure, but it also influences diffusive boundary layer thickness and the ability of turfs to retain sediment. Therefore, I predict turf canopy height to be an important indicator of competition between turf algae and corals. However, it is important to note that this is only a prediction based on personal field observations and results from observational studies. There have never been direct tests of the ecological effects of turf canopy height, or of any other turf metrics I introduce, in a manipulative study. The relationships between these multiple aspects of heterogeneous turf assemblages and various facets of reef community ecology merit explicit experimental treatment. Such experiments would provide insight into both ecological processes and effective conservation actions.

From my two manipulative experiments (Chapters 3 and 4), I learned that each turf metric responds in different ways to changes in grazers, nutrients, and small cryptic invertebrates. Broadly speaking, I was interested in what controls the “amount” of turf algae on coral reefs. I learned that the answer depends on how we define the “amount” of algae: canopy height almost always increased under reduced herbivory or increased nutrients, while turf biomass and density exhibited different patterns. My findings further highlight the inherent heterogeneity in turf algae assemblages. I hope that future work will reveal more about the processes that control and are influenced by each of these metrics. Based on my dissertation research and field observations, I suspect that turf canopy height is the most informative metric because it is directly linked to grazing and competition, but I look forward to new information that supports or refutes this claim.

These different characteristics of the heterogeneous turf assemblage make turf algae a convenient testing ground for ecological theory. For example, individual species of coral reef macroalgae have been commonly used to test the relative influences of top-down and bottom-up control on primary producer biomass. Instead, using turfs as the focal group (Chapter 3) allowed me to test for responses beyond changes in biomass: changes in canopy height, density, and community composition. In particular, I find it exciting that the way turf assemblages respond to consumer pressure and resource availability does not follow rules from either terrestrial grasslands or other marine systems (Chapter 3). These findings point to the potential of turf algae to provide new insight into bigger picture ecological processes.

We know that there is heterogeneity within turf assemblages, and I underscore the point that there are also differences among patches of turf algae. Not all algal turfs fulfill the same ecological role. Specifically, it is tempting to categorize turf algae as indicators of ecosystem degradation: more coral and crustose coralline algae indicate reef health, so more turf algae should indicate an unhealthy ecosystem. However, distinct types of turf communities are indicators for different types of coral reef ecosystems. Continuing with the previous example of turf canopy height, short and sparse turfs are relatively benign and can be considered components of healthy reefs. In contrast, tall and dense turfs with heavy sediment loads are likely to prevent settlement of juvenile corals, be dominant competitors over adult corals, and be resistant to grazers. These types of turfs can be considered signs of a more degraded reef.

Turf canopy height is particularly sensitive to changes in herbivore abundance (Chapter 3), so sparse, short turfs are indicative of reefs with high herbivore biomass.

More generally, turf algae grow quickly (i.e., rapid increases in biomass, spatial coverage, etc.), especially compared to corals and other reef benthic groups. This characteristic of rapid growth is most useful for conservation practitioners and reef managers. For example, it takes many years for coral cover to increase in response to new management practices. In contrast, changes in turf algae height (or spatial extent, density, composition, etc.) could change within weeks of increases in herbivore biomass or improvements in water quality. Monitoring for multiple turf algae metrics can be a useful way to quantify impacts and demonstrate measurable progress on conservation actions.

In summary, the ecology of turf algae is a central component of broader coral reef ecology. Turfs are abundant, will likely become more abundant in the future, and exhibit strong interactions with herbivores and corals, two functional groups essential to healthy reef ecosystems. Studying the ecology of coral reefs is an essential precursor to effective reef conservation, and turf algae are an essential component of coral reef ecosystems, so effective coral reef conservation must include a better understanding of the ecology of turf algae.