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Sponge Community Biocomplexity, Competition, and Functional Significance in Hard-Bottom Habitats of the Florida Keys, FL (USA)

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SPONGE COMMUNITY BIOCOMPLEXITY, COMPETITION, AND FUNCTIONAL SIGNIFICANCE IN HARD-BOTTOM HABITATS OF THE FLORIDA KEYS, FL (USA)

by

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ABSTRACT

SPONGE COMMUNITY BIOCOMPLEXITY, COMPETITION, AND FUNCTIONAL SIGNIFICANCE IN HARD-BOTTOM HABITATS OF THE FLORIDA KEYS, FL (USA)

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Sponges can have powerful effects on ecosystem processes in shallow, tropical marine ecosystems and are an integral component of the bentho-pelagic cycle of nutrients, via filtering of dissolved and particulate organic matter from the water column. The diversity of marine communities is thought to play a determining role in intensity of ecosystem processes; thus the loss of taxa alters community function and by extension ecosystem processes. Coastal sponge populations worldwide are increasingly exposed to declining water quality that in several regions has resulted in mass sponge mortalities and reduced sponge diversity. In the Florida Keys (Florida, USA), for example, frequent cyanobacteria blooms have decimated coastal sponge communities. There were two objectives for this research. First, to experimentally establish the baseline effects of Florida Keys sponges, at ecologically relevant biomass levels, on various shallow water ecosystem processes and functions, and richness on water column properties. The results of this work demonstrated the importance of sponge biomass and species-specific filtration rates on the intensity of water column nutrient cycling, and its constituents. The second objective of this research was to develop an understanding of how sponges might interact in the wild, ultimately affecting the ecosystem processes and functions measured previously. The results of field manipulations, and sponge measurements plus water column sampling, conducted at multiple sites within Florida Bay showed clearly that the sponges of these back-water lagoons competed

intensely for food, particularly in areas of higher biomass and slower water movement. Overall, this dissertation highlighted how reductions in the abundance and diversity of sponges in coastal ecosystems can drastically alter water column properties.

This dissertation is dedicated to my father, Dr. John Valentine, for his unwavering support and unconditional love. He has inspired in me a passion for exploration of the unknown and instilled in me the value of science.

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CHAPTER 1

INTRODUCTION

Confronted with an ever-increasing rate of biodiversity loss in the Anthropocene epoch, many scientists now seek to tease apart the causes and relative effects of this loss on ecosystem structure and processes. Exposure to changing long-term ecological forces and stochastic disturbance events cumulatively influence the community structure, species diversity, and ecosystem processes of marine environments. These ecosystems are under constant threat on both local and global scales, from stressors such as pollution, climate change, and habitat fragmentation (Naeem 2002; Pereira et al. 2010). Degradation of these essential ecosystems often results in the loss of critical species. When important species (e.g. foundation species *sensu* Dayton, 1971) are lost, weakened ecosystems are susceptible to invasion, spread of disease, decreased productivity, and the loss of other vital ecosystem services and functions (Petchey et al. 2004); which can have further detrimental and cascading effects. Loss of foundational species and their ecosystem functions further erodes environmental stability, creating a negative feedback loop. With the rate of species extinction rapidly increasing, there has been growing interest in determining how the loss of biodiversity might alter the rates of ecological processes that are essential to their respective ecosystems (Cardinale et al. 2000).

Darwin (1872) first hypothesized that communities that are more diverse should be more productive than less diverse communities. This hypothesis is a highly debated topic in ecology (Naeem et al. 2012); many have sought to document the link between biodiversity and ecosystem function in hopes of demonstrating the effects of species loss at a community and ecosystem

level (e.g. Cardinale et al. 2011). The validity of this fundamental ecological concept has been heavily scrutinized mostly in terrestrial plant communities (e.g. Tilman & Downing, 1994; Naeem et al. 1994, 1996; Hooper & Vitousek 1997; Petchy et al. 2004), but also in microbial communities (e.g. Finlay et al. 1997; Griffiths et al. 1997; McGrady-Steed et al. 1997; Naeem & Li, 1997), and to a lesser extent, in the marine environment (Bolam et al. 2002; Stachowicz et al. 2007; Perea-Blazquez et al. 2013). Not all of these studies have found a positive relation between biological diversity and ecosystem function (e.g. Hooper & Vitousek, 1997; Finlay et al. 1997) and many investigators remain skeptical of the relationship (e.g. Wardle et al. 2000). A recent review of such studies by Cardinale et al. (2011), however, found that on average, more diverse communities had 1.4 times the productivity of monocultures.

There may also be an asymptotic relationship between biodiversity and ecosystem function. In a study of herbaceous plant communities, Tilman (1996) found that gains in ecosystem function diminished after the first ten species were added to an experimental assemblage. These results, and those of other studies indicate that in species-rich communities, there is a high level of redundancy that potentially buffers communities against disturbances and losses of species (e.g. Bracken & Williams, 2013). However, should the most productive members of the community be lost, peak productivity or function may not be achieved.

Increasingly, scientists are recognizing that species diversity may not play as large a role as does functional group diversity and species identity in controlling for ecosystem processes (e.g. Hooper & Vitousek, 1997; Hector et al. 1999; Lefcheck & Duffy, 2016). The effects of biodiversity on production can depend on both the number of functional groups present and the identity of the species (Naeem, 1999). High levels of functional redundancy may also portend

greater competition among species if resources are limited, especially for sessile organisms that cannot migrate for resources, thus confounding the interpretation of biological diversity studies.

In highly diverse or dense communities, competition for growth-limiting resources can be intense. Competition for critical, limited resources such as food or space can restrict the growth and fitness of many sessile marine organisms with overlapping resource requirements (e.g. Branch, 1975; Chadwick & Morrow, 2011). As such, the relative strengths of intra- versus interspecific competition can play a key role in determining population demography and community composition (Branch, 1975). If intraspecific competition is greater than interspecific competition, then many species may coexist, but at limited densities and smaller individual sizes (Underwood, 1979; Connell, 1983). The effect of food limitation on marine sponge assemblages is now fiercely debated, although the more recent studies have been conducted to fore reefs environments where water movement is great (see Pawlik et al. 2018).

Over 8,500 species of sponges (phylum Porifera) have been described thus far and 90% of these species are assigned to the family Demospongiae (van Soest, 2015). These organisms are sessile metazoans, one of the earliest diverging multicellular sponge clades. Sponges are a dense amalgamation of tissues interspersed with canals through which water is filtered for essential food and nutrients (Bell, 2008). Some sponges also have photosynthetic endosymbionts that provide additional energy to their sponge hosts (Slattery & Lesser 2015). Choanocytes (flagellated cells) lining the inner chambers of canals drive the movement of water into and then out of these sponges. Captured food particles are then phagocytized and transferred to the body of the sponge via vesicles. Sponges rapidly regenerate damaged, or lost, tissue due to their totipotent cells, with regeneration rates of sponge species reaching 2,900 times their somatic growth rates (Ayling, 1983). Tissue regression also occurs when sponges are exposed to stressful

conditions (Simpson 1984) and spatial competition via allelopathic compounds (Pawlik et al. 2018), although little is known on whether food limitation would result in the same response.

Marine sponge assemblages serve various ecological functions including their effects on substrate (e.g. bioerosion and cementation), bentho-pelagic coupling, habitat provisioning, and food for spongivorous species (Bell 2008). Via filtration, sponges consume bacteria, viruses, and picoplankton in a size range mainly from 0.5 to 50 µm, as well as nutrients in the form of dissolved organic material (DOM) (Reiswig 1971; Pile 1996; Ribes et al. 1999). By feeding on plankton and absorbing waterborne nutrients, sponges have historically formed a critical bentho-pelagic link, fixing organic and inorganic matter from the water column into forms usable by other organisms. Per day, a 1 kg sponge, such as *Speciospongia vesparium,* can filter 24,000 l of water (Vogel 1977) or 50,000 times their tissue volume (Reiswig 1971). The barrel sponge (*Xestospongia muta*), a common large sponge on Caribbean reefs can overturn a volume of water 1.7-12.9 m^3 a day (McMurray et al. 2018). An entire sponge assemblage in Discovery Bay, Jamaica can purportedly filter 15.5 to 40 m of the water column per day (Reiswig 1974). By estimating and extrapolating filtration and retention rates of sponges in Florida Bay, Peterson et al. (2006) proposed that the loss of a single species of sponge that once controlled the biological structure of the water column has resulted in an increase in cyanobacterial blooms. Although the effects of some individual species of sponges on the water column has been estimated, there is little information on how mixtures of sponge species of varying densities affect nutrients and water column communities.

In filter-feeding communities, functional redundancy is typically assumed to be high (Perea-Blázquez et al. 2013); although some filter feeders, such as ascidians, have been shown to partition food resources (Stuart and Klump 1984). Across the board, sponge species usually feed

on similarly sized particles; however, some studies have shown that when sponges are compared at higher taxonomic levels, they indeed differentiate among particle sizes (Yahel et al. 2006; Thurber 2007; Bell 2008). Different species of sponges also fix nutrients at different concentrations (e.g. Weisz et al. 2007; De Goji et al. 2013), a process that is often dependent on microbial constituents. As such, increasing biodiversity may well have an additive effect, thereby increasing ecosystem function in more diverse communities (i.e. as additional species are added to a system, there should be more comprehensive nutrient fixation and plankton removal). Indeed, when Perea-Blázquez et al. (2013) performed *in situ* feeding trials in New Zealand with seven species of sponges, they found that each species had different retention efficiencies for different types of picoplankton based on particle size and type, and that there was low functional redundancy across species. As sponges are rarely found in monoculture, it is likely that this niche partitioning results in increased ecosystem function (e.g. removal or fixation of nutrients).

Analogous to the microbial loop (Azam et al. 1983), the 'sponge loop' serves to transfer and convert nutrients and energy through oligotrophic food webs (Figure 1). This 'sponge loop' is hypothesized to help explain Darwin's paradox of how highly productive and diverse coral reef ecosystems occur in desert-like tropical seas (McMurray et al. 2018). Sponges assimilate dissolved organic matter from the water column, constituting up to 90% of the sponge total carbon uptake (McMurray et al. 2018). This DOM is produced by primary producers such as phytoplankton and is converted within the sponge to particulate organic matter, in the form of cellular detritus that then becomes a food source for detritivores, other sponges, and a variety of marine organisms such as corals (De Goji et al. 2013). Of the assimilated dissolved organic carbon (DOC), approximately 40% is released as POC through cellular shedding (de Goeij et al. 2013; Rix et al. 2016; 2017).

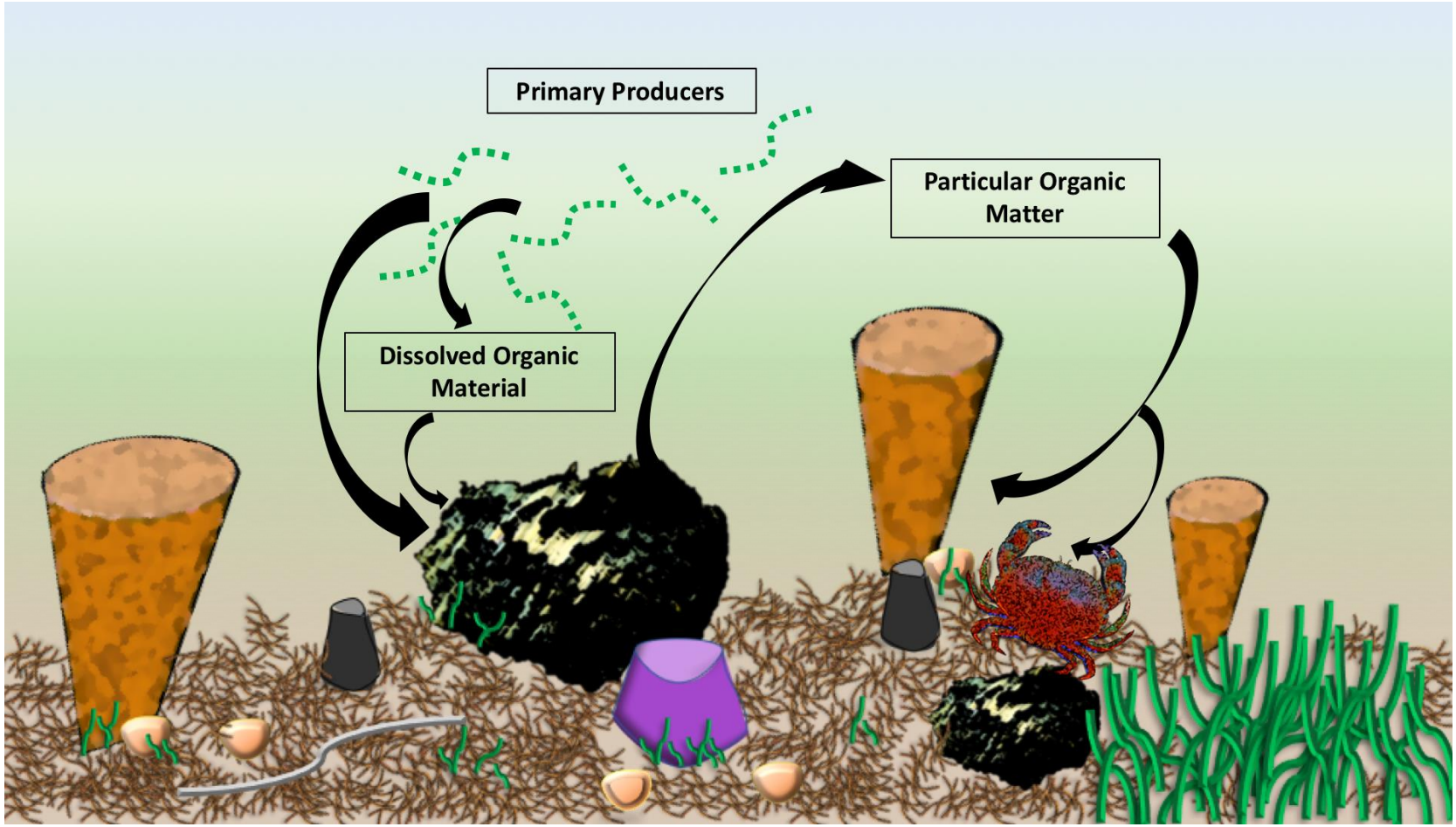

Figure 1. Pictographic description of the sponge loop. Sponges consume dissolved organic material and planktonic organisms such as primary producers. This is then processed within the sponge and released as particulate organic matter which is then consumed by detritovores and other organisms

Sponges also alter inorganic nutrient cycling by acting as both sources and sinks of bioavailable compounds. In nutrient-limited environments, the quantities released are ecologically relevant and can stimulate the growth of nearby primary producers (Pita et al. 2018). Marine ecosystems are often nitrogen limited; however, nitrogen is excreted in large quantities by sponges (Pita et al. 2018; Valentine & Butler, 2018). Sponges also release phosphate, (Valentine & Butler 2018), another limiting resource, and in areas where sponges are still abundant, this may provide neighboring organisms a release from nutrient limitation. Many of these functions (e.g. biogeochemical cycling) are the product of a diverse community of sponge symbionts (Weisz et al. 2007).

A key function of sponge assemblages is their ability to fix or concentrate nutrients such as carbon, nitrogen, silica, and phosphorus (Taylor et al. 2007; Webster & Taylor 2012), much of which can be attributed to the sponges' multifaceted relationships with bacteria, archaea, and some eukaryotes (fungi and microalgae) (Webster & Taylor 2012). Marine microbes play a key role in ecosystem biogeochemical cycling and we are only now beginning to understand how these microbes interact with their sponge hosts to affect the surrounding environments. These microbial symbionts purportedly play a role in sponge nutrition (including autotrophic and heterotopic nutrient pathways), the production of chemical defenses, and host immunity (Pita et al. 2018). These symbionts are hypothesized to have specifically evolved for life within their sponge hosts. Most symbionts lack the genes that encode for flagella and are encapsulated in mucus envelopes to prevent phagocytosis by the host and produce defensive compounds to shield them from pathogens and toxins introduced via the sponge hosts' filtration of water (Pita et al. 2018). Each species of sponge hosts a core microbiome, but also a loosely associated suite

of microbial constituents that vary across individuals and with environmental conditions (Pita et al. 2018).

Because of this ecologically important relationship between symbionts and their host sponges, sponges have been divided into two functional groups based on their associated microbe abundance and density. The first group, the bacteriosponges (Reiswig 1981), harbor diverse and abundant microbial communities, and are referred to as high microbial abundance (HMA) sponges (Hentschel et al. 2003). In areas where sponges are found, these organisms tend to be dense and have large areas of anaerobic activity that can comprise up to 40% of their volume (Webster & Taylor 2012). HMAs have low pumping/clearance rates and high rates of nutrient fixation because much of their energetic needs are provided by their microbial constituents (Weisz et al. 2007). Most of the microbial symbionts in HMA sponges play a role in nitrogen metabolism and ammonia oxidation, whereas the sponges themselves provide internal zones for both aerobic (nitrification and nitrogen fixation) and anaerobic (denitrification, anammox) processes (Hoffman et al. 2009; Bayer et al. 2014; Pita et al. 2018). In addition, cyanobacterial symbionts can provide >50% of some sponge species' energy requirements (Wilkinson 1983).

The second functional group of sponges contains a relatively depauperate microbial community and are known as low microbial abundance (LMA) sponges (Hentschel et al. 2003). This functional group tends to be abundant on coral reefs and rely primarily on uptake of particulate organic matter (Reiswig 1974), in contrast to the HMA sponges that also take up dissolved organic material required by their microbial symbionts. However, there is recent evidence that LMA sponges also consume DOC (Morganti et al. 2017; Valentine & Butler 2018).

The resistance (i.e. withstanding perturbation unchanged) and resilience (i.e. capacity to recover following disturbance) of the sponge-microbiome mutualism remains a hotly debated topic (Pita et al. 2018). Within species, the host microbiome diversity and relative abundance appears stable across geographic distance, season, and depth (Erwin et al. 2012; Pita et al. 2013; Erwin et al. 2015; Steinert et al. 2016). Conversely, there is evidence that the microbiome (particularly the variable quotient) is affected by environmental conditions such as temperature, depth, and water depth (Morrow et al. 2016; Weigel et al. 2017; Pita et al. 2018). However, little is known about the resistance of sponge microbiomes to environmental perturbations such as the harmful algal blooms that have become increasingly persistent in the Florida Keys (Berry et al. 2015).

In shallow, hard-bottom habitats of the Florida Keys, Florida (USA), a diverse and abundant assemblage of large sponges presumably serve as foundation species for the ecosystem (Butler et al. 1995). Florida Bay is a shallow (~1-3 m), subtropical bay, encompassing approximately 2,850 km^2 of the seafloor between the Florida Keys and the mainland. The Bay is open to the West to the Gulf of Mexico and seawater is also exchanged through tidal passages in the Florida Keys from the Atlantic Ocean. Freshwater input to the bay is variable and often limited to precipitation because much of the historical riverine contribution from the Everglades has been diverted for agricultural and storm-protection purposes. Florida Bay is not an open system, but instead is composed of discrete embayments divided by an interconnected network of carbonate banks and shoals that restrict the exchange of water between approximately 40 semi-isolated basins (Boyer et al. 1999; Phlips et al. 1999). This restricted exchange in shallow waters reduces rates of flushing and increases residence time, often resulting in hot, hypersaline

eutrophic conditions (Cotnet et al. 2000; Nuttle et al. 2003). Exchange is instead dominated by winds rather than tidal movements (Gilbert et al. 2009; Lee et al. 2016).

Marine habitats in the shallow waters surrounding the Florida Keys and in Florida Bay, include patchily distributed mangroves, seagrass, sand-mud bottom, patch reefs, and hard-bottom. Hard-bottom is characterized by low relief (<0.5 m), limestone bedrock overlain by a thin veneer of sediment (Schomer & Drew 1982; Chiappone 1996); however, in some locations, sediment depth can be much deeper (approximately 15 cm) (Schomer & Drew 1982; Chiappone 1996). This habitat serves as an important nursery for many commercially and recreationally valuable fishes and invertebrates including, but not limited to, the Caribbean spiny lobster (*Panulirus argus*) and stone crab (*Menippe mercenaria*) (Butler et al. 1995). Hard-bottom habitat is home to the region's second most diverse sponge assemblage (second only to nearby coral reefs). Some 60 species of sponges are found on these hard-bottom substrates and their composition is largely distinct from the composition of sponges found on coral reefs (Stevely et al.2011). HMA Demosponges dominate the sponge complex on hard-bottom habitats where their densities, in some places, can exceed 300,000 sponges per hectare (Herrnkind et al. 1997; Torres et al. 2004; Stevely et al. 2010; 2011; Butler et al. 2018). Some of these sponges support a small, artisanal commercial sponge fishery (Butler et al. 2016) that in the late 1800s-early 1900s was once one of Florida's most valuable fisheries. In recent times, the abundance of sponges in this region has been greatly diminished by environmental change (Stevely et al. 2011; Butler et al. 2018), but the effects of the loss of sponge biocomplexity on ecosystem function is poorly understood.

The diverse, shallow-water sponge assemblages of the Florida Keys are under constant threat of mortality due to a multitude of stressors, including recurrent cyanobacteria blooms,

temperature extremes, and variable salinity that are now common place and caused by management of freshwater 'upstream' in the Everglades (Stevely et al. 2011; Butler et al. 2018). Cyanobacteria, the only form of prokaryotes that can produce oxygen, blooms are now common and represent a major threat to ecosystem resiliency in Florida Bay and are responsible for major regional losses of sponges (Butler et al. 1995). Prior to these events, the hard-bottom communities of Florida Bay were largely dominated by sponges (Stevely et al. 2011), both in terms of biomass and spatial coverage. The first documented cyanobacteria bloom in the region occurred in 1991 (Butler et al. 1995; Boyer et al. 1999) and resulted in a mass sponge die-off. Additional blooms occurred in 2007 and 2013 and destroyed sponges in an area > 500km^2 with >90% mortality of most sponges at the most severely affected sites (Stevely et al. 2011). Given the foundational role that sponges arguably play in tropical hard-bottom communities, it seems certain that the nearly complete loss of sponges in this area had a deleterious impact on ecosystem structure and function.

Despite the plethora of sponge-related benefits, and their sudden and extensive losses, we know very little about sponges, especially within Florida Bay, mostly due to the difficulty in working with and identifying cryptic species. Within Florida Bay, restoration attempts are being made, but questions remain: What role did these once-abundant sponges play in structuring the Florida Bay ecosystem? How did abundance and diversity of sponges alter their services? What is the relationship among sponge biodiversity, community resilience, and ecosystem function? The vast majority of scientific work on marine sponges has been carried out on coral reefs, where sponges are strong interspecific competitors for attachment space with other sponges and other sessile taxa (Aerts 1998). Importantly, the catastrophic impacts that harmful algal blooms (HAB's) had on sponges in Florida Bay, did not extend to reef sponges. In contrast, no work has

been performed on intraspecific and interspecific interactions among sponge species in nearshore hard-bottom communities where ecological conditions and sponge assemblage composition differ markedly from those of coral reefs. Here, I propose to explore how the loss of sponge diversity and abundance in Florida Bay has altered ecosystem function and services.

Aims and Outlines

The overall aim of this dissertation is to investigate the ecological interactions of sponges with the water column and how these interactions affect the ecosystems in which they are found. These interactions were studied for sponge species with varying life histories to further understand the effect of multiple sponge populations on ecosystems rather than focusing on the behavior of model organisms.

Chapter 2. Sponges Structure Water Column Characteristics In Shallow, Tropical Coastal Ecosystems

Florida Bay was once populated by a diverse assemblage of sponge species before perturbations largely eliminated them from the area. What consequences these reductions in sponge density, and probably species diversity, may have had on ecosystem structure and function until now have remained unknown. As such, it is reasonable to hypothesize that, given the reports of their impressive filtration rates and abilities to fix nutrients, the effects of these losses must have been great.

To examine this possibility, I manipulated sponge biomass in replicated mesocosm experiments of varying flow rates to determine how varying populations sizes, and sponge species identity behave to control the composition and abundance of planktonic (phytoplankton, virus, and bacteria) assemblages and water column nutrient cycling.

Chapter 3. Functional Poverty in Marine Ecosystems: How Loss of Species Diversity in Marine Sponges Diminishes the Health of Tropical Waters

Sponges do not occur naturally in monoculture, but rather patchily distributed densely populated and diverse groupings. The effect of these remaining diverse sponge groupings on water column composition and nutrient cycling has not previously been studied in such a controlled setting. Until this study, no one had attempted to test for non-additive emergent effects of interacting sponge species on filtration, thus any projections of sponges influence on ecosystems seem of little empirical value. In this study, I manipulated sponge diversity in mesocosm experiments to determine what extent sponge species diversity might control plankton composition and nutrient concentration.

Chapter 4. Exploitative Competition for Planktonic Resources Limits Growth of Tropical Sponges.

Based on the results of Chapters 2 and 3, I hypothesized that it is conceivable that sponges may compete for those resources. Although Pawlik et al. (2014) argue that there is little or no evidence for competition for food among sponges for food in coral reef communities, their conclusions cannot be generalized to include shallow, hard-bottom sponge assemblages where

species composition, and hydrological conditions, are very different. To test my hypothesis, I transplanted sponge clones into replicated areas of variable sponge density and documented their growth to assess the extent to which in an effort to determine whether local conditions or competition have a stronger effect on sponge fitness.

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CHAPTER 2

SPONGES STRUCTURE WATER COLUMN CHARACTERISTICS IN SHALLOW, TROPICAL COASTAL ECOSYSTEMS (Valentine & Butler 2018)

Introduction

In many coastal ecosystems benthic suspension feeders control rates of biogeochemical cycling and the strength of benthic-pelagic coupling via removal of dissolved and particulate organic matter (DOM and POM) (Gili & Coma 1998; Peterson 2004; Jiménez & Ribes 2007). These influential suspension feeders (e.g. bivalves, ascidians, bryozoans, polychaetes, cnidarians, echinoderms, and sponges) also alter turbidity, oxygen concentration, and sedimentation levels in a wide range of ecosystems, from tropical waters to Antarctica (Grebmeier & Barry 1991; Barnes & Clarke 1995; Orejas et al. 2000; Jonsson et al. 2005). When sufficiently dense, aggregations of suspension feeders exert strong top-down control of pelagic plankton communities, and sometimes experience density-dependent regulation (i.e. competition) due to depletion of limiting water column resources (Hily 1991: Newell 2004: Dame & Olenin 2005; Wulff 2017).

Sponges are important filter feeders in many marine ecosystems (Riisgård & Larsen 2010), but until recently there have been few studies of density-dependent and species-specific effects of sponge assemblages on water column filtration (Reiswig 1974). Contemporary studies of sponge feeding show that they can have stronger effects on nutrient processes than bivalves, especially in shallow, subtropical and tropical ecosystems (Lesser 2006; Bell 2008; Alexander et al. 2014; McMurray et al.2014; Easson et al.2015). Sponges consume a diverse array of

suspended picoplankton including bacteria and viruses in sizes ranging mainly from 0.5 to 50 μm, and their filtration efficiencies (i.e. particle removal) typically exceed 75% (Reiswig 1971; Pile et al. 1997; Ribes et al. 1999; Hadas et al. 2009). Where abundant, sponges form an important benthic-pelagic link (Diaz & Ward 1997) by altering organic and inorganic matter acquired from the water column into forms (i.e. chemical states, organic particles) that are used by other benthic organisms (Diaz & Rützler 2001; Webster & Taylor 2012; De Goeij et al. 2013).

Much of the nutrient conversion efficiency of sponges is attributable to their multifaceted relationships with symbiotic bacteria, archaea, and some eukaryotes (fungi and microalgae) living within the interstices of their tissues (Weisz et al. 2007; Webster & Taylor; 2012, Thomas et al. 2015). For this reason, sponges have been categorized into one of two broad functional groups based on their microbial communities. The bacteriosponges (Reiswig 1981) harbor diverse and abundant microbial communities and are referred to as high microbial abundance (HMA) sponges (Hentschel et al. 2003). HMA sponges often have dense tissues that contain large anaerobic areas and microbial biomass that can comprise up to 40% of their volume (Webster & Taylor 2012). They also have low pumping/clearance rates, cycle dissolved organic carbon, and fix nitrogen; thus, most of their energetic requirements are hypothesized to be provided by symbiotic microbes (Taylor et al. 2007; Weisz et al. 2007). In contrast, low microbial abundance (LMA) sponges (Hentschel et al. 2003) harbor comparatively depauperate microbial communities and are thought to rely on the filtration of particulate organic matter from the water column to meet their nutritional needs (Reiswig 1974). However, recent studies (Rix et al. 2016; Morganti et al. 2017; de Goeij et al. 2017) have shown that some LMA sponges also consume DOM. Due to the unique, species-specific differences in microbial community

composition among sponge species (Lee et al. 2011), the effect of each species on water column parameters is likely to be idiosyncratic and environmentally dependent.

To date, studies of the effects of sponges and their associated symbionts on nutrient cycling have relied on the use of either incubator-based or *in situ* measurements on individual sponges. Incubator-based measurements may overestimate nutrient cycling and particle filtration (e.g. Pile et al. 2003; Jiménez & Ribes 2007) if sponges filter the same water repeatedly. Alternatively, if oxygen and nutrient availability decline and wastes buildup unnaturally within the incubator, then sponge filtration is likely to be suppressed (Hadas et al. 2009; Maldonado et al. 2012). *In situ* measurements of changes in water column constituents are made by comparing water entering and leaving the incurrent and excurrent canals of a sponge (Yahel et al. 2003, Maldonado et al. 2012); these measurements provide a more natural approximation of a sponge's effect on the water column. But such results are based on single-specimen measurements and are usually short in duration. Thus, they do not capture variability in feeding rates and cannot be easily manipulated to measure the effects of intra- or interspecific competition (Patterson et al. 1997). Moreover, the possible synergistic or inhibitory effects of multiple individuals or species on filtration cannot be ascertained from single individual experiments, whether measured in incubators or *in situ*. These experimental drawbacks limit the extrapolation of filtration to community- or ecosystem-scales, or to estimates of the effect of changes in filter feeder abundance or diversity due to natural or anthropogenic perturbation.

Although some investigators have scaled up measurements made on individuals to communities based on total sponge biomass (see McMurray et al. 2014; McMurray et al. 2017), this does not account for potential interactions and emergent effects among individuals in sponge communities. Most studies of sponge filtration have also been conducted on coral reefs or rocky

bottoms in water that is several to tens of meters deep but extrapolating the effects of sponge filtration on water column characteristics in those environments is likely to underestimate their effects in shallow water habitats where sponges filter a larger fraction of the water column.

In the shallow waters surrounding the Florida Keys, Florida (USA) including portions of Florida Bay, sponge assemblages are threatened by the persistent effects of a multitude of stressors including recurrent cyanobacteria blooms, highly variable temperature and salinity regimes, and, to a much lesser extent, commercial sponge fishing (Cropper & DiResta 1999; Stevely et al. 2011; Kearny et al. 2015; Butler et al. 2017). Repeated cyanobacteria blooms, first documented in 1991 (Butler et al. 1995; Boyer et al. 1999), have had the most dramatic impact on sponges. Each has triggered sponge die-offs over large areas (up to 500 km^2) in south central Florida Bay where sponge densities and diversity have been reduced by 90% or more (Herrnkind et al. 1997; Torres et al. 2006; Stevely et al. 2011). The large-scale losses of sponges is thought to have dramatic consequences for water column geochemistry and plankton community composition (Lynch & Phlips 2000; Peterson et al. 2006; Weisz et al. 2007), but those conclusions are based on experiments that did not take into account intra- and interspecies interactions that may occur in dense sponge assemblages.

The goal of my study was to determine potential effects of the loss of sponge biomass and species composition on the structure of planktonic communities and nutrient cycling in the shallow water Florida Keys ecosystem. To do so, I conducted experiments in flow-through mesocosms uniquely designed to quantify the effects of changes in sponge biomass and species identity on water column properties at ecologically relevant water velocities.

Materials and Methods

Origin and preparation of sponges

To assess the effects of species-specific sponge loss on water column constituents and nutrient concentration, I conducted a series of experiments in custom-made, flow-through mesocosms using 10 species of sponge common in Florida Bay and representing both major functional groups (most HMA and some LMA) (Table 1) (Weisz et al. 2008; Hardoim et al. 2009; Gloeckner et al. 2014). Some species have not been categorized as HMA or LMA sponges, so I assumed classifications based on other species within the same genus. To procure the large numbers of sponges needed to conduct these experiments, individual sponges of each species were collected from the seafloor and cut into multiple smaller pieces (~ 300 cm^3). Sufficient tissue (~ 2 cm thick) from each individual 'source' sponge was left attached to the seafloor to facilitate regrowth (Stevely 1985). The experimental sponge 'cuttings' were then attached with plastic cable ties to individually tagged concrete brick baseplates then returned to the seafloor for a few months to heal, adhere to the baseplate, and grow. An equivalent number of brick baseplates without sponges were placed for an equivalent period of time on the seafloor for use as experimental controls to account for the potential effects of fouling microorganisms on the bricks used to anchor sponges.

Table 1. Mean percent change (±1 SD) in chl a and nutrients (NO_2^- ; NO_3^- ; NH_4^+; PO_4^{3-}; DOC) in seawater exiting mesocosms containing sponges compared to that in control treatments with no sponges. The top portion of the table presents species-specific data depicted by the scientific and common names of sponges along with their microbial associations (HMA: high microbial abundance; LMA: low microbial abundance). The bottom portion of the table summarizes data by biomass and water flow treatments

Grouping	Common name	Microbial association	Chl *a*	$NO^- + NO^-$	NH^+	PO_4^{3-}	DOC
Species							
Spheciospongia vesparium[a,b]	Loggerhead	HMA	−30.00±25.60	90.51±118.81	−26.14±17.15	115.18±147.20	−34.09±15.14
Ircinia campana[a,c]	Vase	HMA	−22.75 ± 24.22	55.54 ± 65.81	−63.30 ± 14.21	88.20 ± 85.76	−49.10 ± 20.47
Spongia barbara[d]	Yellow	HMA	−48.01 ± 16.16	86.28 ± 47.64	−42.29 ± 24.27	48.57 ± 33.99	−56.10 ± 23.51
Hippospongia lachne[d]	Sheepswool	HMA	−51.33 ± 20.83	55.82 ± 72.32	−62.39 ± 22.88	47.40 ± 37.77	−35.37 ± 12.29
Ircinia sp.[a,b]	Brown branching	HMA	−47.26 ± 33.29	106.97 ± 101.55	−61.40 ± 16.95	66.01 ± 53.03	−70.80 ± 24.83
Spongia graminea[d]	Glove sponge	HMA	−45.44 ± 17.00	84.73 ± 82.97	−51.67 ± 25.19	59.73 ± 72.43	−43.59 ± 21.70
Niphates erecta[b]	Lavender rope	LMA	−27.25 ± 18.98	64.99 ± 50.14	−23.52 ± 16.65	172.82 ± 238.01	−19.90 ± 11.91
Cinachyrella alloclada[a,b]	Golf ball	LMA	−28.26 ± 17.29	93.81 ± 68.14	−37.10 ± 18.15	44.89 ± 33.95	−22.02 ± 20.36
Tectitethya crypta[a,c]	Green volcano	LMA	−39.78 ± 17.53	130.02 ± 78.97	−38.50 ± 14.62	103.03 ± 138.58	−28.98 ± 17.96
Aplysina fulva[f]	Yellow rope	HMA	−46.53 ± 20.29	62.30 ± 55.49	−32.50 ± 14.03	36.38 ± 27.65	−44.91 ± 15.47
Treatment							
High biomass, high flow			−37.04 ± 22.51	99.28 ± 89.66	−44.76 ± 27.50	112.98 ± 175.50	−42.06 ± 24.45
Low biomass, high flow			−30.16 ± 21.26	99.15 ± 88.73	−36.08 ± 15.88	58.01 ± 69.25	−36.92 ± 27.67
High biomass, low flow			−46.56 ± 24.51	64.75 ± 50.08	−46.33 ± 27.34	109.87 ± 115.33	−40.71 ± 21.43
Low biomass, low flow			−41.56 ± 23.96	71.00 ± 82.48	−51.04 ± 19.93	40.01 ± 29.26	−41.85 ± 21.50

Mesocosms

I constructed six flow-through rectangular mesocosms (fiberglass tanks; 25 cm high x 30 cm wide x 2.4 m long) for use in my experiments on Long Key, FL (USA) (Figure 2). The mesocosms were set-up outdoor under a 50% shade-cloth canopy. A ‘flume-like’ design was employed instead of round tanks (Maldonado et al. 2012) to reduce water recirculation during my experiments, thus minimizing the confounding effects of water re-filtering by sponges. This design enabled the standardization of flow rate and ensured that possible changes in water quality due to the presence of other organisms (e.g. algae, sediment microbial community, etc.) were minimized. I was not attempting to achieve laminar flow in the mesocosms, merely the unidirectional movement of seawater to mimic the natural, tidally-driven flow of seawater through a stand of sponges on the seafloor. Unfiltered seawater drawn from Florida Bay (2 m depth) by a 1.5 hp pump was introduced at one end of each mesocosm through three 5-cm dia

pipes that were equipped with valves to adjust flow. The water delivery system was new, and custom built for this experiment, so the chemical and biological constituents of the water entering the mesocosms was probably minimally impacted by fouling organisms in the piping system. A honeycomb-like baffle (7.5 cm long pieces of 1.3 cm diameter PVC stacked to the water surface) was installed in each mesocosm15 cm from the supply pipes to more evenly disperse the water through the 1.8 m long x 0.3 m wide working area in each mesocosm. A weir was installed at the opposite end of the mesocosm at a 70° angle relative to the bottom to prevent water from striking the rear wall and rebounding through the working area of the mesocosm. Seawater drained behind the weir into a reservoir through two 5-cm drain lines where a hand-operated valve was used to collect samples from the seawater effluent. Water was not recirculated after passing through the mesocosm. After each trial, the walls of the mesocosms were cleaned of fouling organisms and seawater could flow through each mesocosm for at least 12 hrs. without sponges being present. To reduce the buildup of fouling organisms in the intake pipes, the system was intermittently drained and left empty.

Experimental treatments

A three-factor, fully-crossed design was used to test for the effects of differences in sponge biomass (high biomass, low biomass, and a sponge-free control), sponge species identity (one of ten species plus one sponge-free control) and flow regime (high, low turnover). This design resulted in a total of 44 treatments, each of which was replicated seven times.

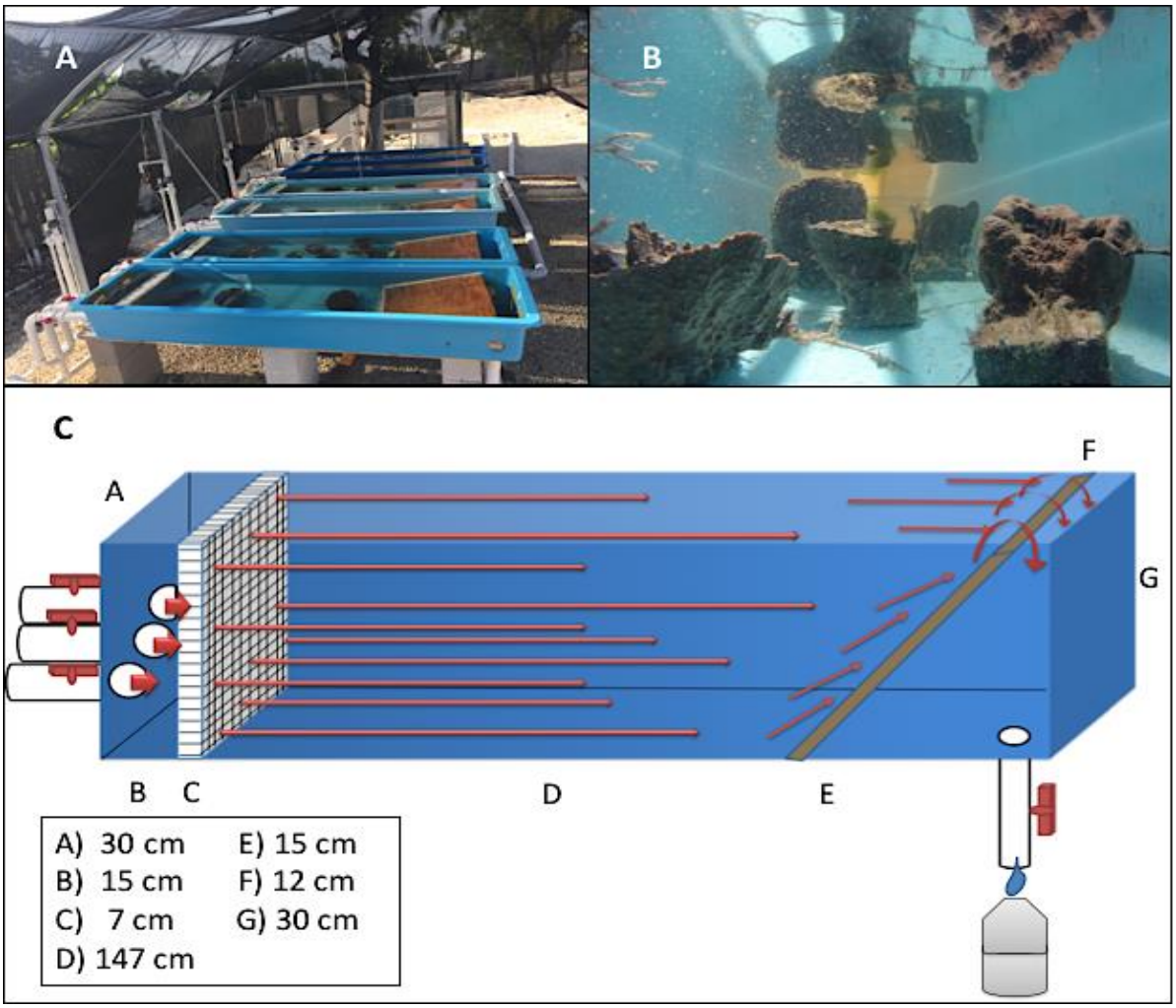


Figure 2. (A) Photo of six mesocosm flume tanks in operation, (B) underwater photo of sponge cuttings within a mesocosm flume tank, (C) diagram of mesocosm flume tank showing water movement (depicted by red arrows) through mesocosm. Unfiltered seawater enters the mesocosm at left, passes through a baffle to reduce turbulence, flows through the working section of the mesocosm and then spills over a weir (which reduces backflow) into the drain section where a subsample of the water is collected in a flask for analysis. The dimensions at various locations around the mesocosm diagram are listed by letters at the bottom left of the diagram

The sponge biomass levels and the identity of species selected for use in my experiments were based on sponge surveys conducted at sites located throughout the Florida Keys (Butler et al. 2015). Estimates of the volume of individual species derived from those 100 m^2 surveys were

scaled to the size of the mesocosms, so that the high and low sponge biomass treatment levels used in my experiments represented the upper and lower quartiles (i.e. 25% and 75%) of the estimated natural sponge biomass in an equivalent water volume. Natural biomass was calculated as the average volumes of sponge (based on height and diameter) based on length, width, and depth of survey area. Based on these calculations natural sponge volumes were on average 14,337 cm^3 at 25% and 43,012 cm^3 at 75%. These estimates were scaled to the mesocosm volume, so that experimental sponge volumes were 2136 cm^3 and 6408 cm^3 in the low and high biomass treatments, respectively. Using this approach, the biomass of each experimental replicate was equivalent in each treatment. Sponge biomass in the two treatments was standardized using total volume displacement of all sponges in the mesocosm to control for differences in sizes and shapes of the sponge species selected for use in these trials. To estimate biomass by volume displacement, experimental sponges (attached to brick bases) were submerged in buckets and the displaced water was measured using a graduated cylinder. To compensate for water displaced by the bricks to which sponges were attached, the volume of control bricks was measured and subtracted from the volume measured for the sponge plus brick replicates. To achieve the treatment biomass, and because the displacement volumes varied greatly among the sponge species, sponge density varied across the treatments.

Flow regimes in my experiments mimicked the range of flows observed during typical tidal changes in Florida Bay (Wang et al. 1994). To better estimate common velocities in nearshore Florida Bay hard-bottom areas, I made a series of vertical velocity profiles at eight hard-bottom sites (2-3 m deep) during spring tides using a WaterMark USGS Current Meter (Model 6205) ™. Based on those field measurements, mean velocity in the center of the mesocosms was set at 3 cm sec^{-1} in the low flow regime treatment and 12 cm sec^{-1} in the high

flow regime treatment. Water turnover rate through the flume tanks (approximate volume 180 L) without sponges present averaged 4 L min^{-1} (45 min) and 16 L min^{-1} (11 min), respectively. When sponges were present and there was no replenishment, high biomass treatments turned over the mesocosm volume at a rate of 34.6 L min^{-1} and low biomass treatments at 11.53 L min^{-1}. The turnover presence of sponges in my treatments, low-flow, high-biomass (HBLF); low-flow, low-biomass (LBLF); high-flow, high-biomass (HBHF); high-flow, low-biomass (LBHF), were projected to be 5.88 min, 23.89 min, 9.67 min, and -40.32 L min, respectively. In the LBHF treatment, water replenishment exceeded the rate of sponge filtration. The velocity slowed near the walls of the mesocosms, thus sponges were placed no closer than 5 cm from the sides of each mesocosm and sponges were raised ~ 5 cm from the bottom because of their attachment to brick baseplates.

The high flow regime reduced the residence time of water in the mesocosm, which presumably increased the supply of POM, DOM, and nutrients to sponges and reduced the recycling of water by sponges as it would in nature. Although my mesocosm design reduced the amount of water reprocessed by sponges, difference in sponge biomass in the treatments and filtration rates among species means that some refiltration may have occurred, particularly in the low flow regime treatment. Based on estimates of filtration by *Spheciospongia vesparium* (0.09 l s^{-1} l of sponge $biovolume^{-1}$; Wall et al. 2012), I estimated the possible re-filtration of water within mesocosms for each of my treatment groups (Table 2). These estimates are likely to represent an upper bound because *S. vesparium* filters water at a higher rate than is suspected for most of the other species tested. In my low flow + high biomass treatment, I estimate that sponges may have filtered the water in the mesocosm at approximately eight times the rate of replenishment. In the low flow + low biomass treatment, they perhaps could have filtered the

water twice as fast as it was replenished in the mesocosm. However, in my high flow treatments, I estimate that when at high biomass, sponges could possibly filter the water in the mesocosm about twice the rate of its replenishment but less than once in the low biomass treatment.

Table 2. Estimated rates of water flow through mesocosms and filtered by sponges at each treatment level based upon filtration rates of *S. vesparium*. Sponge volume is the estimated liters of sponge per high and low biomass treatments. Mesocosm turnover is the estimated time for mesocosm water volume (180 L) to be completely cycled without sponges present. Sponge turnover is the estimated time sponges would need to turn over the water in the mesocosm with no input of fresh water based on reported sponge filtration rates of 0.09 l s^{-1} l of sponge biovolume^{-1} (Wall et al. 2012). Estimated treatment turnover is the combined time of sponge turnover based on treatment volume and tank turnover without sponges to project the length of time it would take sponges to clear a mesocosm of water during the experiment. The negative value of the Low Biomass High Flow indicates that sponges are never able to completely process mesocosm volume

	Sponge Volume	Mesocosm Turnover	Sponge Turnover	Estimated Treatment Turnover
High Biomass Low Flow	6.408 L	4 L/min	34.60 L/min	5.88 min
Low Biomass Low Flow	2.136 L	4 L/min	11.53 L/min	23.89 min
High Biomass High Flow	6.408 L	16 L/min	34.60 L/min	9.67 min
Low Biomass High Flow	2.136 L	16 L/min	11.53 L/min	-40.32 min

Preliminary trials

Preliminary trials were conducted in February-April 2015. Using *S. vesparium* and *Ircinia campana* in all combinations of high and low biomass and flow regime to determine the appropriate acclimation period and sampling interval for my experiments. To determine the time needed for sponges to begin filtering, fluorescein dye was injected into the water near the incurrent canals of representative sponges on an hourly basis. I observed that all of the sponge species began filtering within an hour of their placement into the mesocosms.

During preliminary trials, water was collected at the mesocosm outlets at 4-hr intervals over three consecutive days, and the concentrations of nitrite + nitrate (NO_2^-+NO_3^-), ammonium (NH_4^+), and phosphate (PO_4^{3-}) were analyzed to determine if sponge effects on water chemistry were consistent over time or affected by diel cycles (Patterson et al. 1997). Those results revealed that the most distinct filtration effects occurred during mid-afternoon; minimal differences from controls were detected at night and in the morning. Based on these preliminary results, I used an acclimation period of 24 hrs and collected water from experimental treatments at 1400 hrs. I would have preferred to sample water periodically throughout each experimental trial, but such an approach was cost prohibitive given the large number of treatment combinations and replicates.

Experimental Design

To initiate an experiment, sponge cuttings (Figure 2) were haphazardly selected from those established earlier and left on the seafloor to grow. Any flora or fauna (e.g. algae or other encrusting sponges) attached to the sponges or to the brick baseplate (including control bricks without sponges) were removed underwater and the sponges then placed in aerated, seawater-filled coolers for transport (~ one hour) to the mesocosm facility. Treatments were randomly assigned to each mesocosm before trials began. Sponges were placed in the mesocosms and allowed to acclimate for 24 hrs. at the determined treatment flow regime. I had six mesocosms, so I ran four experimental treatments and two controls (i.e. seasoned bricks placed in the mesocosms, at high and low flow regime) simultaneously. Trials were not conducted if rain occurred during the 24-hr period preceding trials, or if winds exceeded 30 kph, to minimize the effects of freshwater run-off and wind-mixing of sediments on seawater chemistry. After each 24

hr trial, 2 L of seawater was collected from the outlet of each mesocosm. At the end of each trial, sponges were returned to their original locations on the seafloor and were not used again for a period of at least three weeks; over 3,000 separate sponge cuttings were used in this experiment.

Nutrient analysis and plankton counts

All glassware used in this study was acid washed, rinsed with DI water, and sterilized in a muffle furnace prior to use. Each sample container was rinsed with treatment seawater three times before aliquots were collected from the mesocosms. Water collected for nutrient and dissolved organic carbon (DOC) analysis was filtered through a 0.7-micron GF/F filter and stored at -30° C for no longer than two months before processing. Treatment effects on NO_2^- $+NO_3^-$, NH_4^+, and total PO_4^{3-} concentrations were documented using a SAN^{++} automated wet chemistry analyzer. For chlorophyll analysis, filters were extracted using 10 ml of acetone for 24 hrs and then processed using a TD-700 fluorometer (Turner Designs, San Jose, CA). DOC samples were processed using a Shimadzu total organic carbon analyzer (TOC-V). The instrument was calibrated after each run of 30 samples over 200 runs, standardized from a 1000 ppm standard of potassium biphthalate. The accuracy of each run varied between 0.08-0.2ppm (checked for drift every 5 samples) and individual samples were repeatedly tested until a CV of <2% was reached.

Samples from treatments containing the sponges *S. vesparium, I. campana, Ircinia* spp. *Cinachyrella alloclada,* and *Tectitethya crypta,* were selected to assess the extent to which bacteria were removed from the water column by each separate sponge species. To quantify treatment effects on bacterial cells in the water column (Shibata et al. 2006), 10 ml of water was collected from each mesocosm water sample and fixed with 1 ml of filtered formalin (37%

formaldehyde). For bacterial analysis, fixed water was filtered onto Whatman™ black Nuclepore filters and filters were mounted and stained using Vectashield DAPI stain with mounting medium. Slides were sealed with clear nail polish and frozen at -80°C for storage. All slides were analyzed within one month of fixation to minimize sample degradation. I used an epifluorescent microscope and 377 nm cube to count the presence of bacteria; 25 images were haphazardly taken from each prepared slide for bacterial enumeration (Patel et al. 2007).

Statistical analysis

To test for treatments effects on the multiple dependent variables measured in this study, I used a three-factor multivariate analysis of variance (MANOVA), the factors being: sponge species identity, sponge biomass, and flow regime whereas the response variables tested were: bacterioplankton, DOC, PO_4^{3-}, NO_2^-+NO_3^-, NH_4^+, and chl *a*. Because of the number of treatments and replicates in the study, trials were conducted across multiple months thus daily fluctuations in the concentrations of dependent variables were normalized by subtracting dependent variable concentrations from the corresponding daily values in control mesocosms. Therefore, water column constituent values used in these analyses are based on the differences in water column parameters measured concurrently in the outflows from control mesocosm and the mesocosms containing sponge treatments. The MANOVA assumptions of normality, homogeneity of variances, and collinearity were tested, and the data were rank transformed because the MANOVA assumption of non-collinearity was not met. An additional MANOVA was performed to test the differences between HMA and LMA sponges for each treatment group. For this, eight levels were created representing the four treatment groups classified as HMA and four treatments classified as LMA. An ANCOVA was also performed using control mesocosm

water constituent values as covariates to determine the relative effect of ambient conditions on changes to nutrient concentrations attributable to sponge filtration in the four treatments (i.e. high and low sponge biomass x high and low water turnover).

When treatment effects were significant ($p < 0.05$), post-hoc Tukey's tests were used to examine differences among species and microbial associations (HMA, LMA) across four sponge biomass/water turnover treatments: HBHF, HBLF, LBHF, and LBLF. A Bonferroni correction of P-critical values was made to control for experiment-wise error when testing for each response variable, so only Tukey test P-values < 0.008 were considered significant. Effect sizes and LSD (least significant difference error bars) were also plotted to inspect for significant relationships among treatments (Williams 2010, Hector 2015). To assess whether sponge filtration rates depended upon ambient concentrations of water column constituents, I performed a linear regression analysis for each species and treatment group and separate linear regression analyses for all species and treatments combined (McMurray et al. 2016). All statistical analyses were conducted using SPSS V.22 (IBM Corp).

Results

The results of the MANOVA conducted on the main effects (species identity, biomass, and water turnover) showed that all treatments significantly ($p<0.008$) affected the concentrations of water column constituents with the exception of turnover effects on NO_2^- $+NO_3^-$ ($p= 0.249$) and DOC ($p= 0.148$) and biomass on $NO_2^-+NO_3^-$ ($p=0.011$) (Table 3). In general, regardless of sponge species or biomass, concentrations of chl *a*, NH_4^+, DOC and bacterioplankton were lower (Figures 3 & 4), whereas $NO_2^-+NO_3^-$ and PO_4^{3-} (Figure 5) concentrations were higher in mesocosms with sponges relative to control mesocosms. The

strength of these effects, however, was heavily dependent upon species identity (Table 3, Figure 6) and a particular response variable. When comparisons of sponge effects were based on functional classification (HMA or LMA), clear differences were detected between the treatments (Figure 7). HMA sponges removed relatively greater concentrations of chl *a*, NH_4^+, DOC, whereas LMA sponges produced relatively greater concentrations of NO_2^-+NO_3^- and PO_4^{3-}.

Table 3. MANOVA results for differences from controls for treatments, biomass, flow, and species

Source	*Dependent Variable*	*Type III Sum of Squares*	*df*	*Mean Square*	*F*	*Sig.*
Species	Chla (ug/L)	1.215	9	0.135	202.031	<0.001
	NO_2^-+NO_3^- (µM)	3.545	9	0.394	36.771	<0.001
	NH_4^+ (µM)	203.292	9	22.588	325.789	<0.001
	PO_4^{3-} (µM)	0.115	9	0.013	34.253	<0.001
	DOC (µM)	1643265.03	9	182585.00	245.56	<0.001
Flow	Chla (ug/L)	0.343	1	0.343	513.737	<0.001
	NO_2^-+NO_3^- (µM)	0.014	1	0.014	1.337	0.249
	NH_4^+ (µM)	36.041	1	36.041	519.82	<0.001
	PO_4^{3-} (µM)	0.009	1	0.009	25.075	<0.001
	DOC (µM)	1565.93	1	1565.93	2.106	0.148
Biomass	Chla (ug/L)	0.104	1	0.104	155.559	<0.001
	NO_2^-+NO_3^- (µM)	0.071	1	0.071	6.629	0.011
	NH_4^+ (µM)	24.103	1	24.103	347.643	<0.001
	PO_4^{3-} (µM)	0.143	1	0.143	382.356	<0.001
	DOC (µM)	15144.738	1	15144.738	20.369	<0.001
Species x Flow	Chla (ug/L)	0.861	9	0.096	143.15	<0.001

	$NO_2^-+NO_3^-$ (µM)	1.441	9	0.16	14.946	<0.001
	NH_4^+ (µM)	37.886	9	4.21	60.715	<0.001
	PO_4^{3-} (µM)	0.136	9	0.015	40.508	<0.001
	DOC (µM)	148034.95	9	16448.33	22.122	<0.001
Species x Biomass	Chla (ug/L)	1.174	9	0.13	195.22	<0.001
	$NO_2^-+NO_3^-$ (µM)	1.335	9	0.148	13.845	<0.001
	NH_4^+ (µM)	94.92	9	10.547	152.116	<0.001
	PO_4^{3-} (µM)	0.126	9	0.014	37.384	<0.001
	DOC (µM)	777258.72	9	86362.08	116.151	<0.001
Flow x Biomass	Chla (ug/L)	0.006	1	0.006	8.745	0.003
	$NO_2^-+NO_3^-$ (µM)	0.226	1	0.226	21.079	<0.001
	NH_4^+ (µM)	8.849	1	8.849	127.629	<0.001
	PO_4^{3-} (µM)	0.007	1	0.007	19.817	<0.001
	DOC (µM)	11147.81	1	11147.81	14.993	<0.001
Species x Flow x Biomass	Chla (ug/L)	0.713	9	0.079	118.628	<0.001
	$NO_2^-+NO_3^-$ (µM)	1.075	9	0.119	11.144	<0.001
	NH_4^+ (µM)	30.667	9	3.407	49.145	<0.001
	PO_4^{3-} (µM)	0.117	9	0.013	34.808	<0.001
	DOC (µM)	247595.91	9	27510.66	37.00	<0.001
Error	Chla (ug/L)	0.165	247	0.001		
	$NO_2^-+NO_3^-$ (µM)	2.646	247	0.011		
	NH_4^+ (µM)	17.125	247	0.069		
	PO_4^{3-} (µM)	0.092	247	0		
	DOC (µM)	183652.03	247	743.53		
Total	Chla (ug/L)	19.142	287			
	$NO_2^-+NO_3^-$ (µM)	48.357	287			
	NH_4^+ (µM)	1385.061	287			
	PO_4^{3-} (µM)	1.924	287			
	DOC (µM)	10758448.6	287			

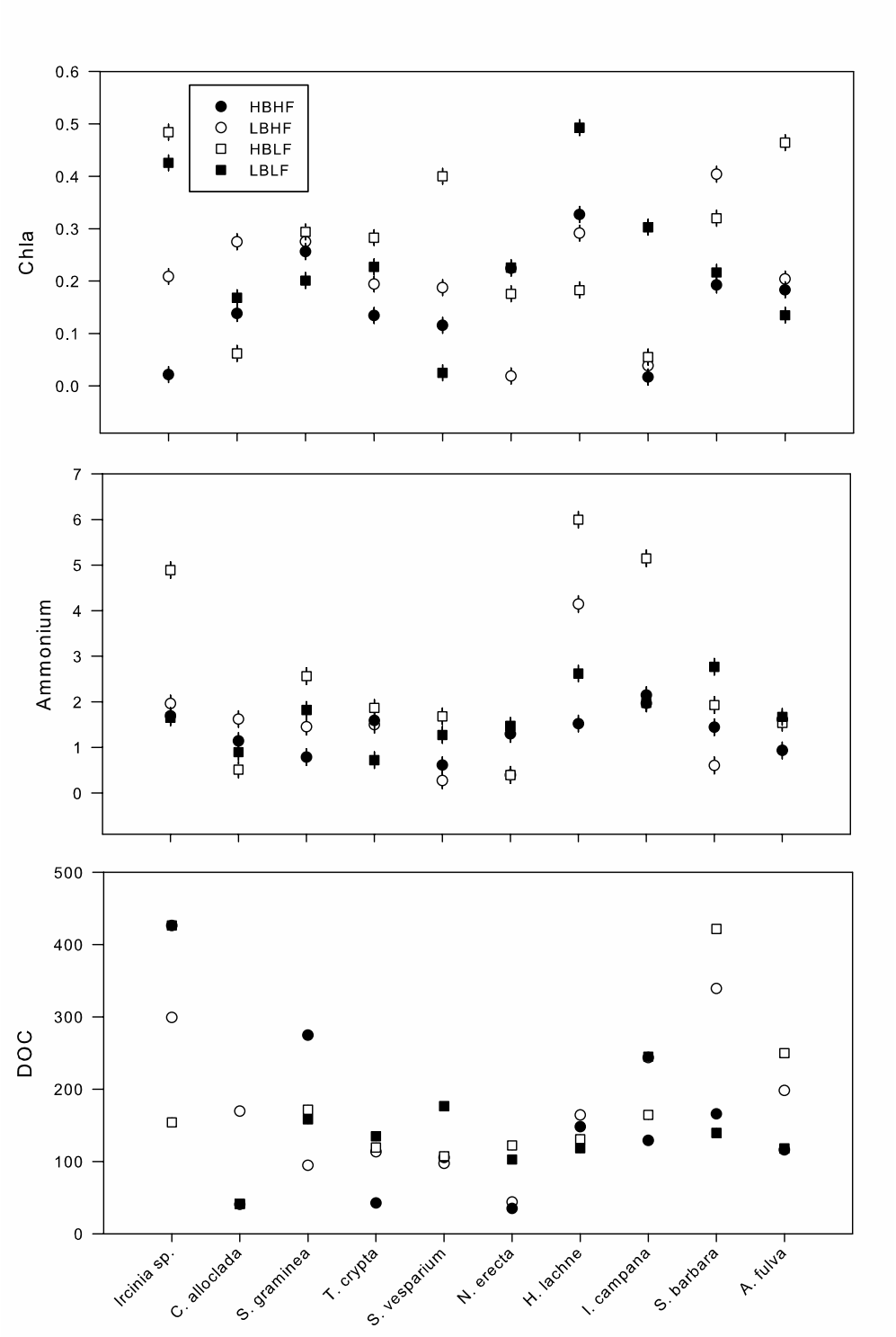


Figure 3. Effects of sponge biomass and flow treatments; high-flow, high-biomass (HBHF); low-flow, high-biomass (HBLF); high-flow, low-biomass (LBHF); and low-flow, low-biomass (LBLF), on the mean decrease of three water quality constituents: chl *a* (a), NH_4^+(b), and DOC(c). Values represent the mean decrease of each variable relative to controls and error bars represent least significant differences

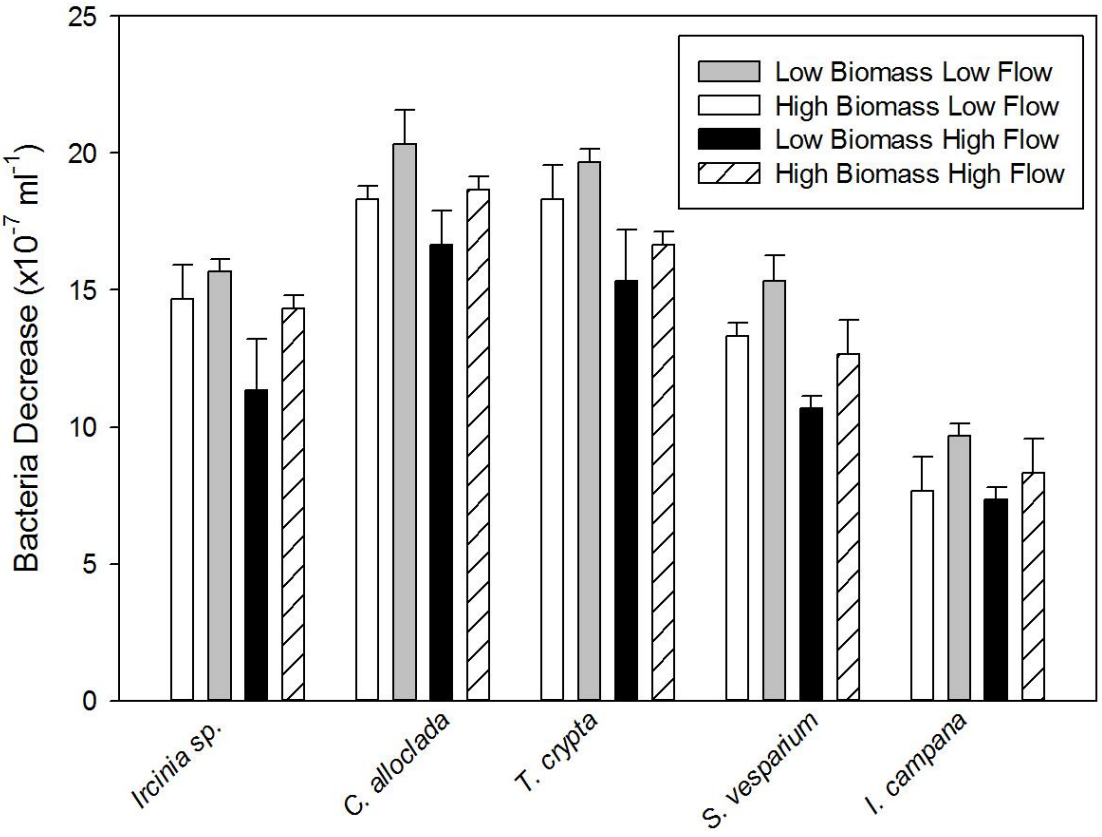


Figure 4. Effects of sponge biomass and flow on bacteria concentrations in the water column for five species. Values represent the mean decrease of each bacterioplankton in comparison to controls and $\pm$ 1standard error

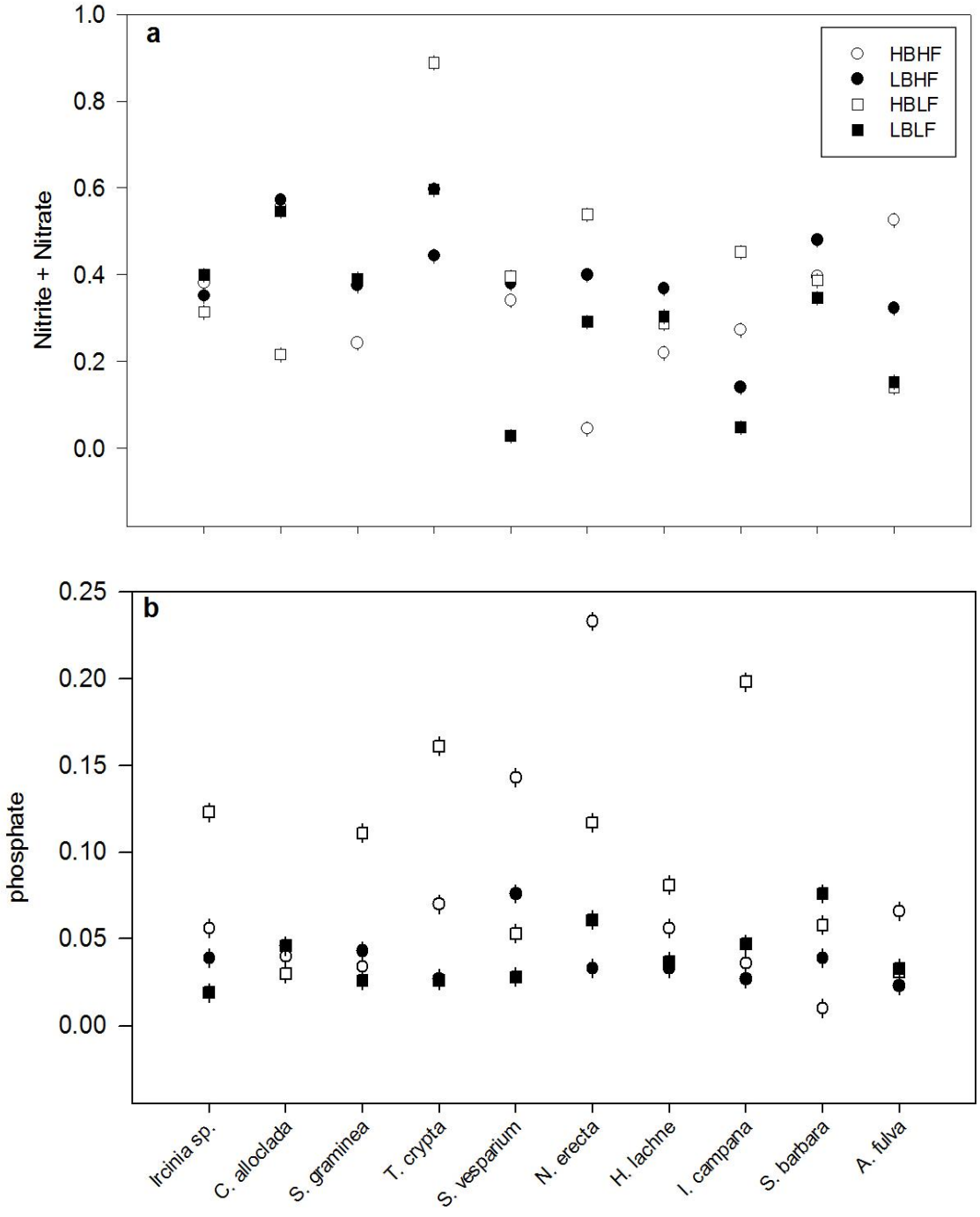


Figure 5. Mean treatment effect, high-flow, high-biomass (HBHF); low-flow, high-biomass (HBLF); high-flow, low-biomass (LBHF); and low-flow, low-biomass (LBLF), on the concentrations of two water quality constituents: NO_2^-+NO_3^-(a) and PO_4^{3-}(b). Values represent the mean increase of each variable in comparison to controls and error bars represent least significant differences

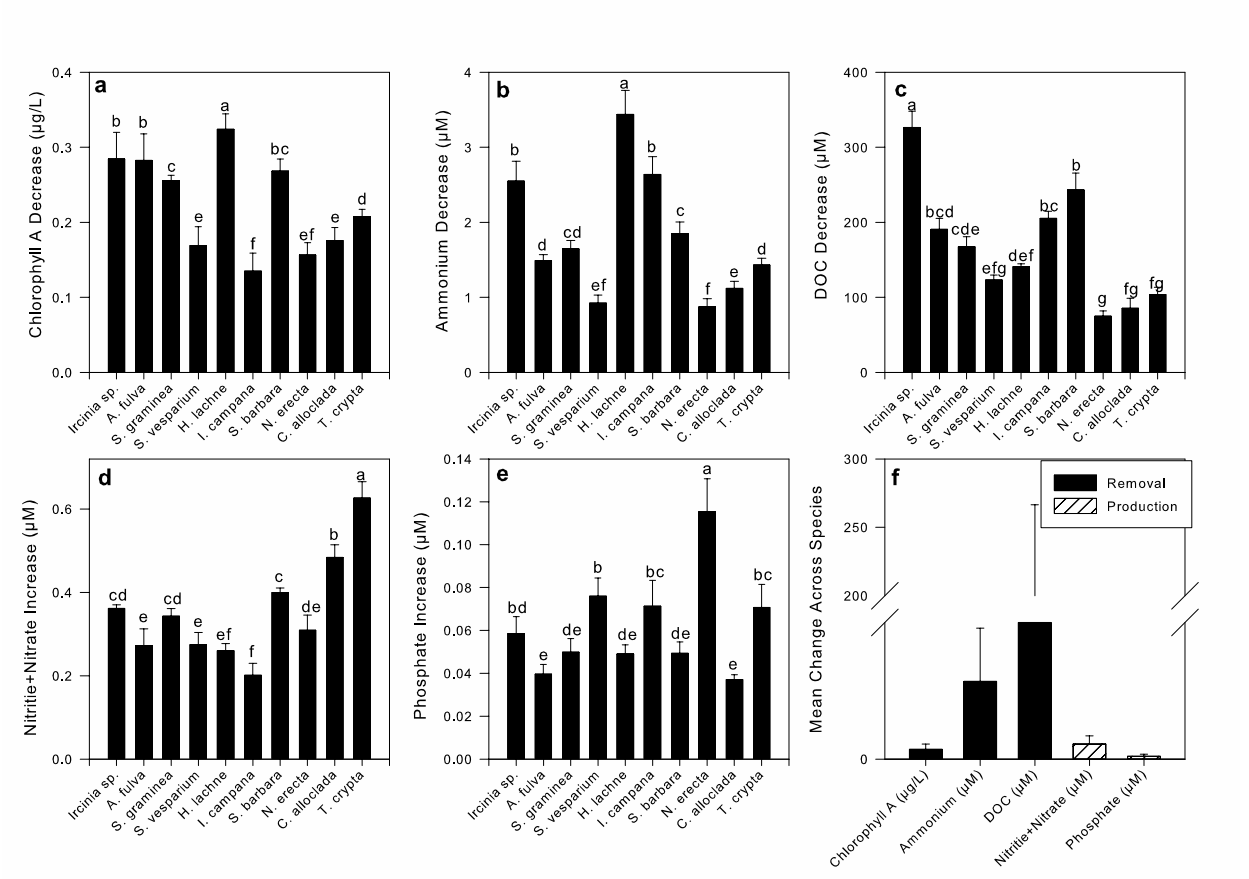


Figure 6. Species-specific effects of sponge biomass and velocity on the mean decrease or increase of water quality constituents: chl *a*(a), NH_4^+(b), DOC(c), NO_2^-+NO_3^- (d), PO_4^{3-} (e), and mean across all species (f). Values represent the mean change of each variable in comparison to controls and standard error. Lower case letters represent statistical significant differences among treatments ($p<0.008$)

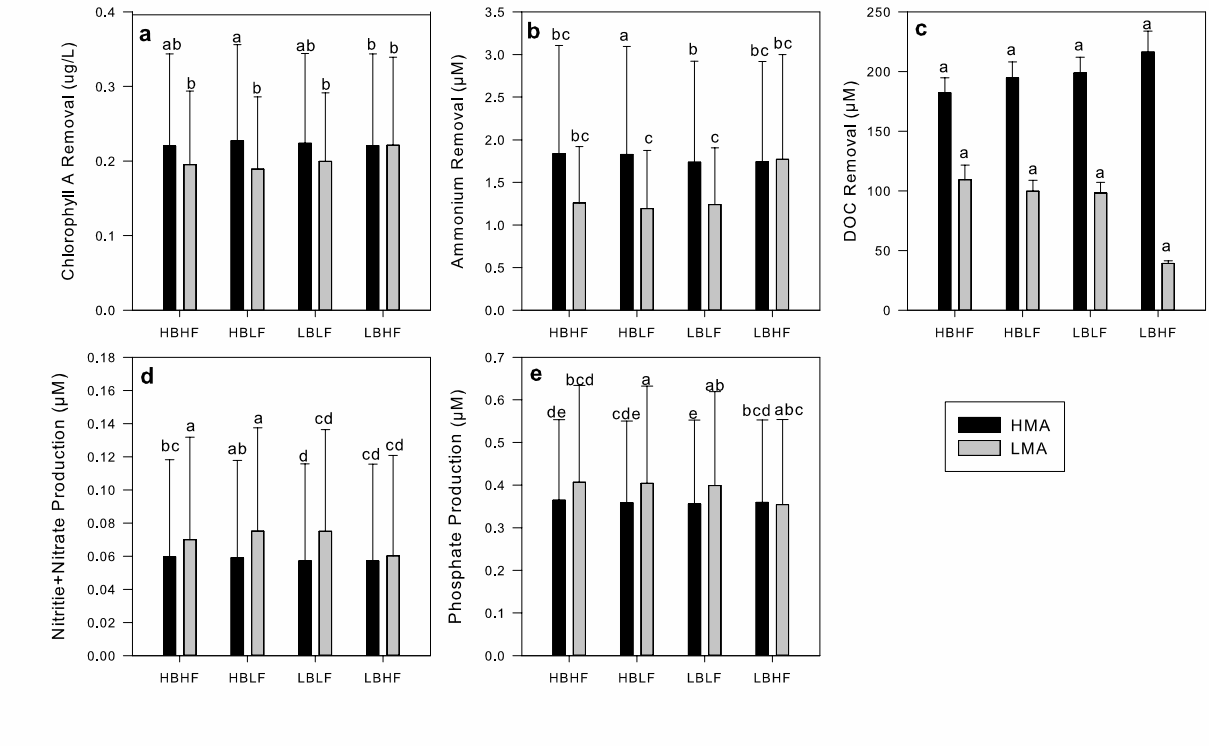


Figure 7. The mean decrease of chl *a*(a), NH_4^+(b), and DOC(c), and increase of NO_2^- +NO_3^-(d) and PO_4^{3-} (e) by sponges in high and low biomass and flow treatments shown by sponge functional group (HML, LMA). Values represent the mean increase of each variable in comparison to controls and standard error. HBHF= High Biomass High Flow HBLF= High Biomass Low Flow LBHF=Low Biomass High Flow LBLF= Low Biomass Low Flow

Pooling all species effects to estimate the cumulative effect of a natural multi-species situation, pairwise comparisons showed the interaction of biomass and water turnover significantly increased the change in concentrations of PO_4^{3-} ($p<0.008$), NO_2^-+NO_3^- ($p<0.008$), and NH_4^+ ($p<0.008$), DOC ($p<0.008$), and chl *a* ($p=0.003$) (Table 4, Figure 8). High sponge biomass had a significant positive effect on PO_4^{3-} ($p<0.008$) but not NO_2^-+NO_3^- ($p=0.011$), and a significant negative effect on the concentrations of chl *a* ($p<0.008$), NH_4^+ ($p<0.008$), and DOC ($p<0.008$). The magnitude of each response was generally greater in the low turnover regime

treatment than the high turnover regime treatment. The linear regression analyses showed that there is a positive relationship between ambient water quality conditions and sponge effects on those response variables (Figure 9). The greater the concentration of a nutrient in the control, the greater the change in the response variable.

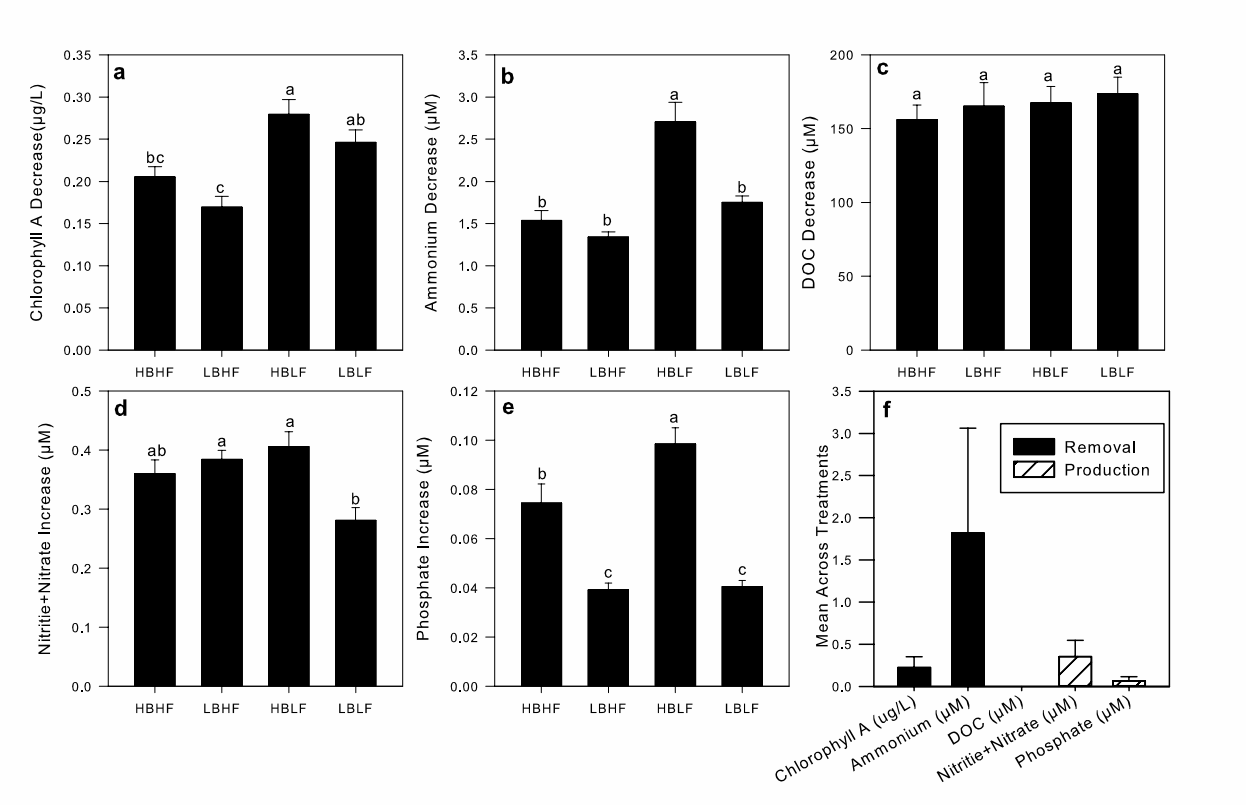


Figure 8. Mean effects of sponge biomass and flow on the response variables chl *a*(a), NH_4^+(b), and DOC(c), and increase of NO_2^-+NO_3^-(d), PO_4^{3-} (e) for all species and the mean across all species (f). Values represent the mean increase of each variable in comparison to controls and standard error. Letters represent statistical significance ($p<0.008$). HBHF= High Biomass High Flow HBLF= High Biomass Low Flow LBHF=Low Biomass High Flow LBLF= Low Biomass Low Flow

Table 4. Results from multiple regression analysis between sponge uptake and ambient conditions for each nutrient variable. R-squared values are presented. For all treatments $p<0.008$

	*Chl*a (ug/L)	$NO_2^-+NO_3^-$ (μM)	NH_4^+ (μM)	PO_4^{3-} (μM)	*DOC* (μM)
Spheciospongia vesparium	0.791	0.873	0.987	0.556	0.924
Ircinia campana	0.952	0.966	0.739	0.932	0.940
Spongia barbara	0.945	0.896	0.884	0.773	0.384
Hippospongia lachne	0.969	0.422	0.676	0.922	0.982
Ircinia sp.	0.944	0.607	0.873	0.931	0.554
Spongia graminea	0.949	0.268	0.825	0.913	0.774
Niphates erecta	0.871	0.952	0.857	0.982	0.914
Cinachyrella alloclada	0.807	0.688	0.885	0.94	0.932
Tectitethya crypta	0.811	0.864	0.976	0.379	0.918
Aplysina fulva	0.236	0.919	0.798	0.894	0.897
All Species	0.871	0.834	0.555	0.712	0.716

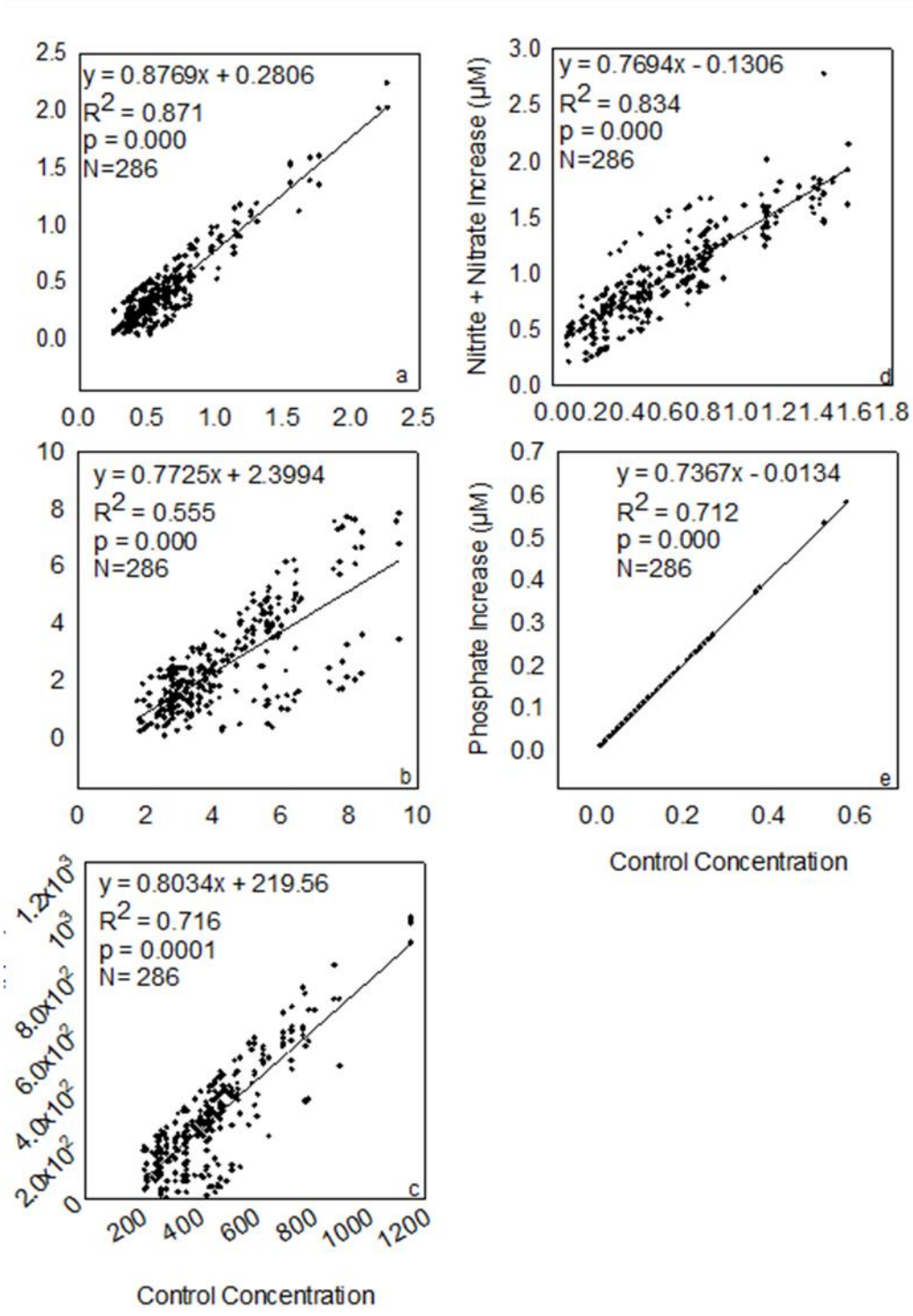


Figure 9. Results from multiple regression analysis between changes when sponge were present and ambient conditions for each nutrient variable, chl *a*(a), NH_4^+(b), and DOC(c), and increase of NO_2^-+NO_3^-(d) and PO_4^{3-} (e). R-squared values are presented

Chlorophyll *a*

I observed a mean decrease in the concentration of chl *a* across all species and treatments of 0.23 µg/L (0.01 se), an approximately 41% decrease from the control treatments. In the HBHF treatment, the mean decrease was 0.21 µg/L (0.01 se), in HBLF it was 0.28 µg/L (0.02 se), in the LBHF treatment it was 0.17 µg/L (0.01 se), and in the LBLF treatment the mean was 0.25 µg/L (0.01 se). Pairwise comparisons showed that the decrease of chl *a* was significantly greater **(**$p<0.008$**)** in the HBLF treatment than in any of the other treatments, whereas the smallest decrease was documented in the LBHF treatment. HMA sponges decreased chl *a* concentration about 0.26 µg/L (0.01 se) and LMA sponges about 0.20 µg/L (0.01 se); a statistically significant difference ($p<0.008$). All LMA sponges were statistically similar in their effects on chl *a*; *Hippospongia lachne* had the greatest **(**$p<0.008$ effect on chl *a* and *I. campana, N. erecta, S. vesparium, and C. allocolada* the least.

Ammonium

The mean decrease of NH_4^+ across all species and treatments was 1.82 µM (0.07 se), a value approximately 51% lower than measured in the controls. In the HBHF treatment, the mean decrease was 1.54 µM (0.12 se), in HBLF it was 2.73 µM (0.23 se), in LBHF it was 1.34 µM (0.06 se), and in LBLF the mean was 1.75 µM (0.08 se). Pairwise comparisons showed that the decrease of NH_4^+ was significantly greater in the HBLF treatment than in any of the other treatments **(**$p<0.008$). No other significant differences among the remaining treatments were detected. The mean decrease of NH_4^+ across HMA sponges was 2.48 µM (0.12 se) as compared to 1.23 µM (0.05 se) in LMA sponges. HMA sponges had a significantly greater effect on NH_4^+

decrease than LMA sponges **(**$p<0.008$**).** Of the ten sponges tested in this study, *H. lachne* had the greatest ($p<0.008$**)** effect on NH_4^+ decrease and *N. erecta* the least.

Dissolved Organic Carbon

The mean decrease in DOC across all species and treatments was 165 μM (101 se), a concentration that was approximately 40% lower than those measured in the controls. The decrease in the HBHF treatment was 156 μM (9.90 μM se), in the HBLF treatment it was 167 μM (9.28 μM se), in LBHF it was 165 μM (15.91 μM se), and the mean in the LBLF treatment was 173 μM (11.22 μM se). There was no statistically significant difference between treatment combination effects on DOC decrease. HMA sponges decreased DOC by an average of 197 μM (7.08 μM se), approximately double that of LMA sponges 89 μM (5.72 μM se), which was a significant effect **(**$p<0.000$**).** Of the 10 species, *Ircinia* sp. *and S. barbara.* had the largest effect on DOC decrease and *N. erecta* the least.

Nitrite + Nitrate

Sponges increased nitrogen (NO_2^-+NO_3^-) concentration across all species and treatments (mean = 0.36 μM; 0.01 se), an approximately 43% increase over controls. In the HBHF treatment the mean increase was 0.36 μM (0.02 se), it was 0.41 μM (0.03 se) in the HBLF treatment, in the LBHF treatment it was 0.38 μM (0.02 se), and it was lowest in the LBLF treatment at 0.28 μM (0.02 se). Among treatments, HBLF and LBHF had a larger but non-significant effect on NO_2^-+NO_3^- concentration. LMA sponges had a significantly greater effect on NO_2^-+NO_3^- concentration **(**$p<0.008$**)** increase than HMA sponges, registering a mean value of

0.41 μM (0.02 se) compared to 0.30 μM (0.01 se) in HMA sponges. *Tectitethya crypta* had the greatest **(**$p<0.008$**)** effect on $NO_2^-+NO_3^-$ increase and *I. campana* the least.

Phosphate

Across all species and treatments, sponges increased PO_4^{3-} concentrations by 43% (mean = 0.06 μM; se = 0.003). Concentration increases in PO_4^{3-} were greatest ($p<0.05$**)** in the HBLF (mean = 0.10 μM; 0.01 se) and HBHF (mean = 0.07 μM; 0.01 se) treatments as compared to those in both the LBHF and LBLF (both averaged 0.04 μM; 0.002 se). The LMA sponges created a significantly ($p<0.008$) greater increase on PO_4^{3-} (mean 0.07 μM; 0.004 se) than did HMA sponges (mean =0.05 μM; 0.003 se). *Niphates erecta* had the greatest **(**$p<0.008$**)** effect on PO_4^3 concentrations whereas *A. fulva* had the least.

Bacterioplankton

Sponge identity, biomass, and water turnover each had significant independent effects ($p< 0.001$) in decreasing the bacterioplankton concentrations in the mesocosms in comparison to the controls, but the two-way interactions between species and biomass ($p=0.064$) and the three-way interaction of species x biomass x turnover ($p=0.553$) were non-significant. However, when water turnover was crossed with either biomass or species, there was a significant effect on bacterioplankton reduction ($p=0.003$ and $p<0.001$, respectively). In general, *T. crypta* and *C. alloclada* were the most efficient filterers of bacterioplankton, whereas *I. campana* had the least effect on bacterioplankton concentrations.

Discussion

My results show that sponge species identity, functional group (i.e. HMA vs. LMA), and biomass interacted in complex ways with rates of water turnover to control biogeochemical cycling and the concentrations of water column constituents. In general, the strength of the effects of sponges on response variables were greatest when sponge biomass was high and water turnover low, the latter mimicking conditions during slack tides in Florida Keys hard-bottom areas. That said, the effects varied greatly from species to species and among dependent variables. No one species of sponge had consistently strong effects on all response variables. This demonstrates the complex effect of sponge structure (i.e. species biomass, identity, and functional group) and its interaction with water residence time on the biochemical character of the water column. Therefore, the effect of sponges on the water column will likely be context-dependent and vary with location, but in ways that can be predicted from community structure and water flow. Moreover, my results highlight the important biochemical cycling function of sponges that is lost when sponges are eradicated or when their diversity is diminished by HABs.

I observed a net decrease in the presence of NH_4^+ in comparison to my controls and, similar to results reported by Morganti et al. (2017), there was a larger decrease in nitrogenous waste products when HMA sponges were present relative to LMA sponges. However, other incubation studies (Southwell et al. 2008) of similar sponge species (*I. campana* and *N. erecta*) found an increase in NH_4^+. I also observed much lower concentrations of NO_2^-+NO_3^- after filtration by *I. campana* but higher concentrations after filtration by *N. erecta* (0.201 μM l^{-1} s^{-1} and 0.309 μM l^{-1} s^{-1}, respectively) in comparison to incubation studies (0.833 μM l^{-1} s^{-1} and 0.014 μM l^{-1} s^{-1}, respectively) (Southwell et al. 2008). In incubation experiments, *S. vesparium* reduced chl *a* by 0.2-0.3 μg l^{-1} of over a 60-minute period (Peterson et al. 2006), whereas I

recorded 0.17 µg l^{-1} s^{-1}. If I extrapolated my data to an hourly scale, the rate would have been 10.2 µg l^{-1} h^{-1}, much higher than documented in Peterson et al. (2006). Peterson et al. (2006) indicated that this plateau in chl *a* reduction was likely due to food concentrations falling below a threshold density and my results confirm that such a mechanism exists.

Common attributes of ecosystem structure and function can be altered or lost when the density and diversity of suspension feeders are reduced, often resulting in cascades through an ecosystem (Ellison et al. 2005, Hooper et al. 2005). It is clear from my results that sponges (and their microbial symbionts) likely play an important role in mediating the nitrogen cycle (particularly nitrification) in the shallow waters surrounding the Florida Keys. Sponge filter feeding also profoundly reduced concentrations of DOC, chl *a*, and bacterioplankton in my mesocosms. Individual species strongly affected just a single response variable. For example, *I. campana* - a large vase sponge that is highly sensitive to HABs - dramatically reduced water column concentrations of NH_4^+ but had a negligible effect on chl *a* in comparison with other species. In contrast, the presence of the hardy sponge *T. crypta* elevated concentrations of NO_2^- +NO_3^- but had little effect on DOC compared to other species,

The variable effects of sponge species on nutrient concentrations observed in my experiments was likely driven by distinct microbial constituents associated with sponge species. I cannot yet separate the confounding effects of sponge genotype from the unique microbial symbionts associated with each individual sponge. But my inability to differentiate host versus microbial effects does not diminish the significance of species-specific ecosystem effects, especially since sponge-microbial community associations are often stable over time (Erwin et al. 2012). My results also highlight the interactive influence of water flow and turnover on the effects of sponge filtration.

My experiments show that sponge effects on water quality properties were harder to detect when the rate of water turnover was higher. When turnover was low, the filtration signal was more pronounced, indicating that sponges were actively depleting the water column of resources at a rate that exceeded replenishment. These data suggest that the shallow water sponges I studied may be better adapted and more efficient filterers at low rates of water turnover. However, I did not address feeding efficiency of individual sponges in this experiment, thus I must attribute some of the greater depletion in low flow treatments to refiltration. Other studies have found that increased water velocity or turnover has inconsistent effects on the rates of filtration by suspension feeders (Peterson & Black, 1987, Jonnson et al. 2005). For example, Lasson and colleagues (2006) reported that at low water velocities, when turnover is limited, concentrations of phytoplankton are diminished and in response, bivalves maintain high rates of filtration to maximize uptake of POC. My results indicate that sponge filtration rates generally increased with increasing concentrations of the response variables, which further complicates the interactive effects of sponge abundance, water flow, and food availability on rates of filtration. Previous studies have also found a positive relationship between the concentration of available resources and sponge filtration and retention rates (Archer et al. 2017; McMurray et al. 2017).

My study included only high and low water flow regimes meant to bracket the common tidally-driven flow present in the shallow water habitats of the Florida Keys. Further testing across a broader range of tidal flows is needed to more fully characterize the effect of flow regime and turnover on species-specific sponge filtration efficiencies. Data on tidal regime and species-specific response to flow versus turnover will permit more accurate projections of filtration rates of sponges at ecosystem scales, dynamics that are now ignored when estimating the effects of sponge filtration over large spatial scales. When I created a low flow environment

that mimicked shallow water, slack tide conditions, there was likely refiltration of water by sponges, especially at high biomass. Refiltration by sponges was probably minimal in my high flow treatments, especially when sponge biomass was low. Although my mesocosms were designed to minimize container effects and back-eddies, my apparatus likely did not exclude such effects in their entirety. To overcome any limitations posed by experimental containers, I conducted similar experiments *in situ*, to better emulate the effect of ambient conditions on sponge ecosystem effects.

Although it is clear that local hydrodynamics play an important role in determining the effects of sponges on water column constituents, the effects of species identity and sponge biomass are even more pronounced. As resource-rich water passes over a sessile filter feeding community, the organisms that first encounter the water mass experience minimal re-filtration, whereas those located 'downstream' in the community will receive water depleted of some resources (O'Riordan et al. 1995; Jones et al. 2011). Therefore, in high biomass communities, as the water mass is cleared of food particles and usable nutrients are fixed into other forms, resource availability could become a limiting factor to growth and reproduction. Indeed, I have evidence from field experiments that sponge growth in Florida Bay is strongly dependent on the local density of this rather enclosed sponge community (Chapter 4). However, the notion that sponge growth can be limited by planktonic resource availability runs counter to the prevailing paradigm that sponges on deeper coral reefs are generally not nutrient limited (Pawlik et al. 2015).

The species richness of shallow, hard-bottom sponge assemblages in the Florida Keys (Stevely et al. 2011) is far lower than on nearby coral reefs (Pawlik 2011), but it is nonetheless highly variable among locations (2 to > 25 species per site) as is sponge density (Coefficient of

variation = 172). Those assemblages can also change rapidly and dramatically over time. In the past 30 years, sponge assemblages have been devastated in areas of persistent environmental degradation (e.g. HAB-induced sponge die-offs) or when subject to hurricanes, and, to a lesser extent, commercial harvest (Stevely et al. 2011; Butler et al. 2017). Although HAB-associated mortality is relatively uniform among sponge species, commercial harvest alters the relative abundances of sponges because fishers target just a few species (e.g. *H. lachne, S. Barbara, S. graminea*). These spatio-temporal fluctuations in sponge composition and density will thus be reflected in species-specific effects on water column properties. In short, because sponges are not equal in their effect on ecosystem processes, neither are the implications of community assembly or sponge loss.

My experiments also show that commercially targeted sponges, such as *H. lachne,* decrease the concentration of NH_4^+ and chl *a* more than any other sponge species. The commercially valuable sponge species are also among those most sensitive to destruction by HABs (Butler et al. 2015; 2017). In contrast, some widespread sponge species of no commercial importance and which are resistant to HABs (e.g. *C. alloclada*) had minimal effects on water column nutrients in my mesocosms. Thus, reductions in the natural diversity as well as the density of these important filter feeders significantly alters biogeochemical cycling and thus benthic-pelagic linkages (Peterson et al. 2006). Management and restoration of sponge assemblages after HAB-associated die-offs should consider the implications of species-dependent effects and perhaps focus on finding and restoring those that are most resilient and useful to ecosystem processes.

In summary, my study established that sponge species identity and biomass along with water flow influence a range of water column properties, including nitrogen and carbon cycles.

Extrapolating my mesocosm-based results to natural sponge assemblages suggests that differences in sponge assemblages as well as the loss of sponges due to environmental change is likely to trigger idiosyncratic shifts in plankton communities and nutrient concentrations. I only tested one species at a time in this set of mesocosm experiments, each at two different biomass and flow regime treatments. What remains to be documented is whether the ecosystem effects of sponge filtration and nutrient conversion differ across the range of naturally occurring sponge assemblages, that is, between diverse, species-rich, assemblages and the monospecific assemblages that I explored here. The question is not only whether sponge diversity matters, but also whether more diverse assemblages interact in synergistic or inhibitory ways that affect ecosystem function. I explored that question in another study whose results follow.

CHAPTER 3

FUNCTIONAL POVERTY IN A DEGRADED MARINE ECOSYSTEM: LOSS OF SPONGE DIVERSITY DIMINISHES THE QUALITY OF TROPICAL WATERS

Introduction

For decades, ecologists have debated the relative importance of various aspects of community structure in determining the stability of ecosystems. Chief among these is the importance of biological diversity (i.e. species richness). Biological diversity is hypothesized to be a key determinant of the health and productivity of most ecological communities through the control of ecosystem structure and function (i.e. the more species present in a system, the greater the diversity of functions they provide and processes they influence) (Cardinale et al. 2011). This is of great consequence in the current Anthropocene epoch during which the rates of local and global losses of biodiversity have been extraordinary and continue to increase (Naeem 2002; Pereira et al. 2010). Dramatic losses of species have altered community structure and composition in most marine ecosystems, triggering alarm in the scientific community because such large shifts in community composition can lead to dramatic alterations of ecosystem functions. Importantly, the majority of what is known about diversity-ecosystem function relationships comes from the terrestrial literature (e.g. Tilman and Downing 1994; Naeem et al. 1994, 1996; Hooper and Vitousek 1997; Petchy et al. 2004), but there is growing evidence for concern from experimental studies of biodiversity effects on ecosystem function in shallow water marine communities in the world's oceans as well (Duffy 2002; Stachowitz et al. 2007). Yet, the

importance of biodiversity to ecosystem function remains a much-debated topic (e.g. Hooper and Vitousek 1997; Finlay et al. 1997; Wardle et al. 2000).

It is widely hypothesized that the more species present in an ecosystem, the more productive the ecosystem will be and the more diverse its ecological functions (Tilman 1997; Naeem 2012). This supposition is based on the idea that the effects of individual species on ecosystem functions are functionally unique and therefore additive (Tilman 1997). Depending on the strength of a community's constituent interactions with the environment, the consequences of species losses from a community can result in crucial reductions of ecosystem functions and services. Among the ecosystem functions that could be affected are production (both primary and secondary), respiration, biomass production, and consumer feeding, which in turn can negatively affect ecosystem services, which are those activities that are considered to be of some value to humanity (Duffy 2009). Among the questions that remain for consideration is how many species does an ecosystem have to lose before its structure and functions are negatively affected?

Given the uncertainty about the strength of the predictive power of current biodiversity theory, some have argued that scientists should embrace the fact that there can be high degrees of overlap within the constituent members of many ecological communities. Functional redundancy (i.e. the presence of species with high levels of diet overlap or that make equivalent contributions to ecosystem function) is also hypothesized by some to be widespread within ecological communities (Duarte 2000), potentially masking some of the effects of species loss and thus explaining the contradictory results of some biodiversity studies (Naeem et al. 2012). Thus, functional redundancy may act as an ecological 'insurance' policy that may mitigate (via competitive release) the effect of species losses caused by natural and anthropogenic perturbations (Duarte 2000; Palumbi et al. 2009). That said, some contend that species diversity

may not play as large a role in controlling the efficiency of ecosystems function as does functional group diversity (e.g. Hooper and Vitousek 1997; Hector et al. 1999; Naeem 1999; Naeem 2011). This, at least in part, may be because diverse communities can exhibit emergent, non-additive, effects on ecosystem functions as a result of interspecific competition, facilitation, mutualism, cannibalism, and intraguild consumption that cannot be predicted based solely on assessments of monocultures (Didham et al. 2007; Ball et al. 2008).

The effects of biodiversity on ecosystem function can depend on both the number of functional groups present and the identity of the species within a given functional group (Naeem 1999), thus identification of functional criteria can be a tricky proposition. For example, to define functional groups objectively, Grime (1979) developed a triangular model that sorted species into functional groups based on competitive prowess, 'weediness', and survival traits. Westoby (1998) developed a similar categorical approach that sorted plant species by leaf area, canopy height, and seed size. Other organisms, such as the marine sponges that are the subject of my study, might be sorted based on easily identifiable traits that exhibit potentially strong ecological expression, such as: morphological features (e.g. vase, branching, ball), microbial associations (e.g. high or low microbial abundance); and life history (e.g. rapidly recruiting weedy taxa versus slower recruiting climax taxa).

In this dissertation, I introduce a new term 'functional poverty' to refer to the ecosystem-wide loss of functional diversity. More specifically, I define functional poverty as an ecosystem state in which many species, or trophic guilds that formerly contributed fundamentally to ecosystem functions are lost, leading to a breakdown of essential ecosystem functions. This state ensues when the loss in diversity is not counterbalanced by a high level of functional redundancy (i.e. multiple species with a high level of diet overlap or function), therefore these impoverished

ecosystems begin to reach an alternative stable-state where they cease to function as they did historically prior to perturbation and are resistant to recovery (Oliver et al. 2015). To identify functional poverty and understand how the loss of species affects ecosystem quality, it is essential that we move beyond simple metrics of lost diversity and incorporate measures of lost or altered ecosystem function. As a model system to explore the concept of functional poverty, I examined experimentally whether changes in species and functional diversity of a suite of abundant, closely related filter-feeding species (Porifera: Demospongidae) influenced fundamental water column properties in a shallow, tropical marine ecosystem (Florida Keys, Florida, USA) that has been recently buffeted by drastic changes in environmental quality and biodiversity.

Marine sponges and their associated microbiome serve several fundamental ecological functions via habitat conditioning and the provisioning of three-dimensional complexity (Butler et al. 1995), bentho-pelagic coupling (both nutrient cycling and water column plankton concentrations) (Riisgard and Larsen 2010; De Goji 2013), and availability of food for spongivorous species (Loh and Pawlik 2014). Sponge assemblages are a mixture of species and functional groups that may interact positively through ecological facilitation or negatively via inhibition and interspecific competition for space and food. At least some of the ecosystem functions (e.g. biogeochemical cycling) performed by sponges are the products of an even more diverse assemblage of sponge endosymbionts composed of bacteria, archaea, and eukaryotes (fungi and microalgae) (Weisz et al. 2007; Taylor et al. 2007; Webster & Taylor, 2012).

However, the loss of species from filter-feeding assemblages such as sponges are predicted by some to have little effect on ecosystem function, because of the presumed high degree of functional redundancy and diet overlap of non-selective filter feeders (Perea-Blázquez

et al. 2013). In contrast, there is evidence that filter feeders, including organisms like ascidians and sponges, can differentially partition food resources among species, selectively removing particles from the water column based on size and type (Reiswig 1971). Sponges can also alter ambient nutrient concentrations by changing available types of nitrogen and carbon (Reiswig 1974; Stuart & Klumpp; 1984 De Goji et al. 2013; Valentine & Butler 2018). Sponges are rarely found in monoculture in nature, so the dietary partitioning of water-column constituents by sponges in diverse sponge assemblages could be an adaptive response to interspecific competition for food that has also increased the complexity of their ecosystem functions they currently provide (e.g. removal or fixation of nutrients) (Bell 2008). That is, increasing biodiversity in sponge assemblages presumably has a commensurately additive effect on the diversity of ecosystem functions in which sponges have a role. But shallow coastal seas - where marine filter feeders are abundant and their role in ecosystems probably most prevalent - are among the most anthropogenically degraded ecosystems on earth (Halpern et al. 2008).

The widespread losses of mangroves, coral reefs, and seagrass beds are broadly recognized as serious threats to the stability and persistence of tropical coastal marine ecosystems and the many ecosystem services they provide (e.g. fisheries, water filtration, protection from erosion; Duarte 2000; Orth et al. 2006; Feller et al. 2010; Bozec et al. 2016; Lamb et al. 2017). Sponges can dominate the sessile faunal biomass on submerged mangrove roots, on coral reefs, and in a lesser known tropical marine habitat: hard-bottom, which often intersperses with seagrass meadows in shallow, back-reef environments (Stevely et al. 2011).

Yet, like other coastal habitats, hard-bottom habitat in places like the Florida Keys have been beset by environmental change and degradation (e.g. nutrient enrichment, changing freshwater inputs, harmful algal blooms, climate change; Fourquerean & Robblee 1999; Boyer et

al. 2006; Blakey et al. 2015; Kearney et al. 2015; 2016) that have collectively decimated the once widespread and diverse, shallow-water sponge assemblages in portions of the Florida Keys. This area is an important nursery habitat for many commercially and recreationally valuable fishes and invertebrates including, but not limited to, the Caribbean spiny lobster (*Panulirus argus*) and stone crab (*Menippe mercenaria*) (Butler et al. 1995). Cyanobacteria blooms, in particular, have represented a major threat to water quality and ecosystem resiliency and, more specifically, to sponge assemblages (Butler et al. 1995; Boyer et al. 1999; Stevely et al. 2011; Wall et al. 2012). Although the hard-bottom sponge assemblages in Florida are less diverse (~ 80 species) than those on nearby coral reefs (>300 species; Diaz & Rutzler 2001), they dominate the animal biomass in hard-bottom areas where their density can exceed 80,000 per hectare with some species larger than 1 m diam. (Torres et al. 2006; Stevely et al.2011). However, repeated occurrences of blooms, with especially large and persistent episodes in 1991, 2007, and 2013 (Butler et al. 1995; 2018), resulted in > 90% mortality of sponges in an area > 500km^2. Those dramatic blooms, along with other environmental changes and commercial sponge fishing, have altered patterns of sponge abundance and species diversity in the Florida Keys (Butler et al. 2017; 2018). Given their abundance and foundational role in tropical hard-bottom communities, it is certain that the nearly complete loss of sponges in such a large area has had deleterious ecological consequences, although many of those functions are unquantified (Butler et al. 1995; 2016; Peterson et al. 2006).

To date, most studies of the effects of sponges on water column nutrient concentrations have been conducted on ***individual*** sponges, one species at a time, using either incubator-based measurements (Peterson et al. 2006; Southwell et al. 2008) or sampling of water as it enters and leaves a sponge (Yahel et al. 2005; Weisz et al. 2008; Perea-Blazquez et al. 2013; Fiore et al.

2017). But sponges do not occur naturally in monoculture and no study has directly tested how changes in sponge assemblage composition affects planktonic communities and water chemistry. Tropical sponges coexist in dense aggregations and could indirectly interact with one another through either exploitative consumption of water column resources or allelopathic suppression of filtration capabilities leading to non-additive effects on water column properties.

In this study I sought to determine if filter- feeding by sponge assemblages differing in species richness or functional group diversity determined planktonic composition and nutrient concentration in the shallow waters of the Florida Keys. To do so I used flow-through seawater flumes to explore how monocultures and polycultures of sponges altered plankton assemblages (phytoplankton, virus, and bacteria) and water chemistry. I hypothesized that sponge species richness and functional group richness played key roles in maintaining ecosystem multifunctionality via their separate effects on nutrient cycling and planktonic communities. I also hypothesized that functional poverty exists in portions of Florida Bay and that the loss of sponge abundance and diversity in the region has reduced and altered nutrient cycling and plankton removal.

Materials and Methods

Origin and preparation of sponges

My experiments were conducted using 10 species of sponge common in the Florida Keys and representing two major functional groups: most were HMA sponges, but some were LMA (Table 5). Some species have not been categorized as HMA or LMA sponges, so I assumed classifications based on species within the same genus. Many individual sponges of each species were needed for these experiments, so to minimize my sampling effects on natural sponge

populations, I created multiple sponge cuttings from large sponges of each species that I harvested from natural sponge communities. I divided each sponge into multiple smaller pieces (~ 300 cm^3), attached each piece with plastic cable ties to concrete bricks, and returned them to the seafloor to allow them to heal, attach to the brick, and regrow large enough for use in my experiments (Valentine & Butler 2018). An approximately 2 cm thick base of each harvested sponge was left attached to the seafloor to regrow (Stevely 1985). Bricks without sponges were also placed on the seafloor for later use as experimental controls for the effects of fouling organisms.

Flow-through Flumes

Six flow-through 'flumes' or mesocosms (fiberglass tanks; 25 cm high x 30 cm wide x 2.4 m long) were constructed and set-up outdoor under a 50% shade-cloth canopy on Long Key, FL (USA) (Figure 10). A flume design was employed to reduce water recirculation, thus minimizing the confounding effects of water re-filtering by sponges. The design was not meant to achieve laminar flow, but to mimic the largely unidirectional, tidally-driven flow of seawater through a stand of sponges on the seafloor. Unfiltered seawater pumped from Florida Bay (2 m depth) was introduced at one end of each flume through three 5-cm diam pipes that were equipped with valves to adjust flow. A honeycomb-like baffle (a wall of 7.5 cm long pieces of 1.3 cm diameter PVC) was installed 15 cm from the supply pipes to disperse the water evenly through the 1.8 m long x 0.3 m wide working area in each flume. A weir (70° angle) at the downstream end of the flume prevented water from striking the rear wall and rebounding into the flume. Seawater drained into a reservoir behind the weir through two 5-cm drain lines where a hand-operated valve was used to collect samples from the seawater effluent. After each trial, the walls of the

flumes were cleaned of fouling organisms, and seawater could flow through each flume for at least 12 hrs without sponges being present.

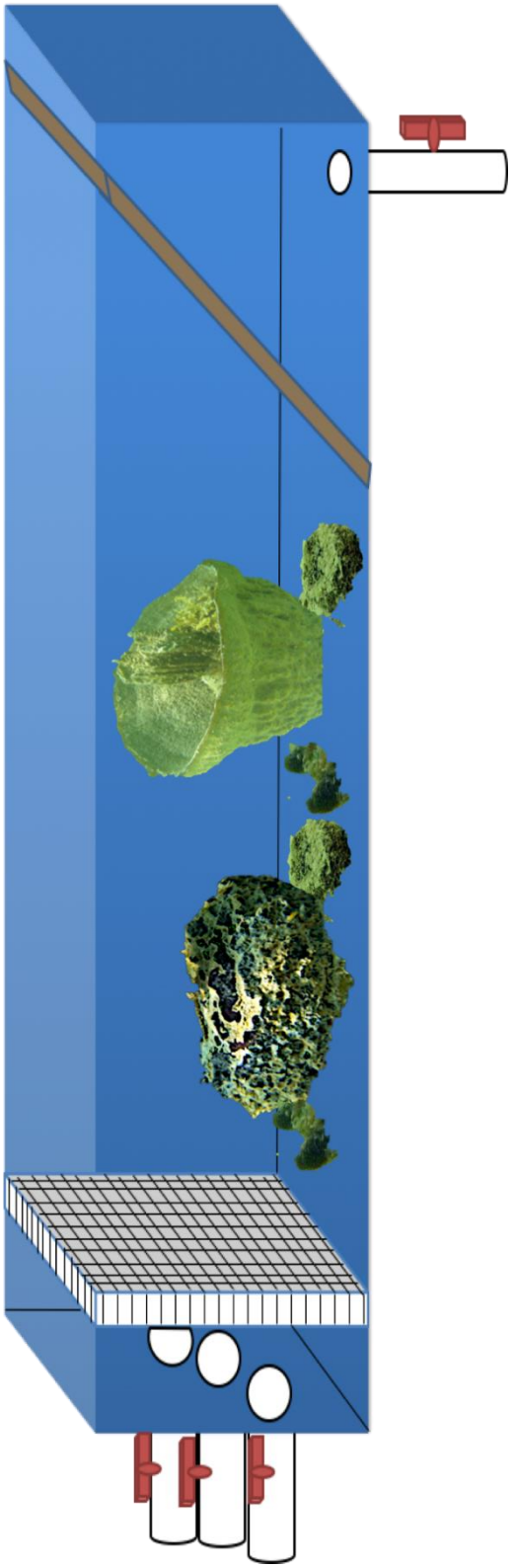


Figure 10. Diagram of tank set up. Sponges were haphazardly place in a unidirectional flow mesocosm between a baffle system and rear weir

Experimental Design

I employed a traditional replacement experimental design (cf. Stachowiz 2007) to quantify the effects of species richness and functional group richness on nutrient concentrations and plankton composition in the water column. To determine if functional group diversity was more important than species richness in determining plankton composition and biogeochemical processes, I also assigned each species to 20 functional groupings for comparative statistical analysis (Table 5; 6). Functional groups were based on four characteristics that might affect the measured response variables: relative body size, morphology, life history, and microbial association (i.e. HMA vs. LMA) (Figure 11; Tables 5; 6). This resulted in 20 unique functional group combinations.

Table 5. Functional characteristics of 10 sponge species adapted from (Valentine & Butler, 2018). * indicates four species used in present study

Species	Relative Size	Abundance	Microbiology	Morphology	Functional Group By Attribute
Aplysina fulva	M	weedy	HMA	Branching	1
Callyspongia tenerrima	S	weedy	LMA	Branching	2
*Cinachyrella alloclada**	S	weedy	LMA	Ball	3
Hippospongia lachne	M	sparse	HMA	Ball	4
*Ircinia campana**	L	sparse	HMA	Vase	5
Ircinia sp.	L	weedy	HMA	Branching	6
*Spheciospongia vesparium**	L	sparse	HMA	Ball	7
Spongia barbara	M	sparse	HMA	Ball	4
Spongia graminea	M	sparse	HMA	Ball	4
*Tectitethya crypta**	S	weedy	LMA	Volcano	8

Table 6. The percent change from controls in five response variables (chl *a*, NO_2^-+NO_3, NH_4^+, PO_4^-, DOC) listed by treatments groups and functional group division. '<' indicates observed values significantly greater than expected values; '>' indicates expected values significantly greater than observed

Treatments	Functional group	chl *a*	NO_2-NO_3	NH_4	PO_4	DOC
Spheciospongia vesparium Cinachyrella alloclada	*10*	<41.62	<51.40	<57.16	<18.50	59.67
Spheciospongia vesparium Ircinia campana	*11*	47.28	>38.28	50.33	>3.41	71.62
Ircinia campana Cinachyrella alloclada	*13*	<42.12	36.24	>49.28	<13.02	>52.03
Ircinia campana Tectitethya crypta	*14*	40.76	>51.82	>56.03	>10.09	>59.48
Tectitethya crypta Cinachyrella alloclada	*9*	<51.45	<65.33	<44.40	>2.98	<60.67
Spheciospongia vesparium Tectitethya crypta	*12*	>64.81	<61.72	<67.08	<19.80	>63.47
Spheciospongia vesparium Cinachyrella alloclada Tectitethya crypta	*15*	<67.19	<64.69	<67.47	<23.67	<65.01
Ircinia campana Cinachyrella alloclada Tectitethya crypta	*17*	<69.16	52.75	61.19	<20.21	62.19
Spheciospongia vesparium Ircinia campana Tectitethya crypta	*16*	64.75	<69.60	<79.54	<14.80	>76.36
Spheciospongia vesparium Ircinia campana Cinachyrella alloclada	*18*	>63.16	<69.23	<80.59	<19.96	78.36
Spheciospongia vesparium Ircinia campana Cinachyrella alloclada Tectitethya crypta	*19*	<92.55	<70.17	<74.26	<32.86	<87.68
All Species	20	<79.43	<80.38	<94.37	<39.00	<85.24

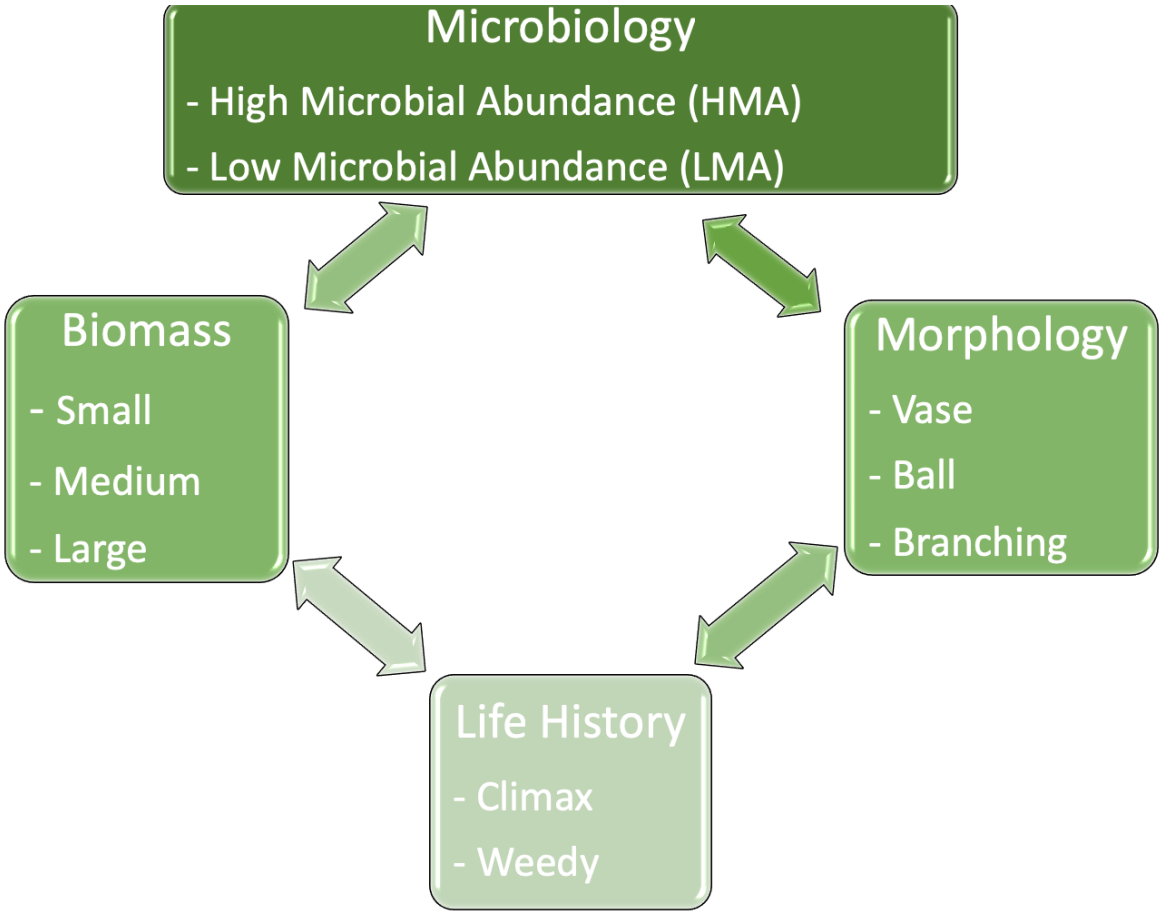


Figure 11. Graphical description of four functional traits I examined in sponges (microbiome, morphology, biomass, life history) and the subcategories considered within each

Four of these species (*Spheciospongia vesparium*, *Ircinia campana*, *Cinachyrella alloclada*, and *Tectitethya crypta*) were selected from the 10 species pool to represent distinct functional groupings (Figure 11). Employing a fully-crossed design, the treatments consisted of combinations of these four species from monoculture to polyculture so as to establish a diversity gradient (e.g. pairs, triplets, and quadruplet). A 12th treatment consisted of a combination of all 10 species to examine the additive effects of species and functional diversity of response variables.

I did not test the effects of sponge biomass or water flow effects in combination with diversity effects, because I had already established in a previous study (Chapter 2) that dense sponge assemblages in low-current velocities produced the largest changes in response variables. The sponge biomass used in each experiment was therefore held constant (6.408 L) in my experiments and was based on mean total sponge biomass determined from surveys conducted at sites located throughout the Florida Keys (Butler et al. 2015). Sponge biomass was standardized using total volume displacement of all sponges in the flume to control for differences in sizes and shapes of the sponge species selected for use in each trial.

Similarly, the flow regimes in these experiments were the same and mimicked the average that I observed after taking a series of vertical velocity profiles at eight hard-bottom sites (2-3 m deep) during spring tides using a WaterMark USGS Current Meter (Model 6205) ^{TM}. Mean velocity in the center of the flumes was set at 4 L min^{-1} (45 min), but slowed near the walls of the flumes, so sponges were placed no closer than 5 cm from the sides of each flume. Water turnover rate through the flume tanks with sponges present averaged 5.88 min. Preliminary trials (see Chapter 2) were conducted to determine the appropriate acclimation period and sampling interval once sponges were introduced into the flumes. Based on those results, sponges were

acclimated in each flume with flow-through seawater for 24 hrs and collected water from experimental treatments at 1400 hrs. I would have preferred to sample water periodically throughout each experiment, but such an approach was cost prohibitive.

To begin a trial, I haphazardly selected experimental sponge cuttings from the field, scraped all fouling organisms from the brick baseplates, then randomly assigned them to flumes according to treatment. Five experimental treatments were run simultaneously with one control (seasoned bricks without sponges) in the six available flumes. Following the 24-hr acclimation period, 2 L of water was collected in acid-washed containers from the outflow of each of the size flumes (five treatments and control) for comparison. The water collected was filtered and analyzed for treatment effects on chl *a*, DOC, NO_2^-+NO_3^- , NH_4^+, and total PO_4^{3-}.

Water Quality

Water collected for nutrient and dissolved organic carbon (DOC) analysis was filtered through a 0.7-micron GF/F filter and stored at -30° C for no longer than two months before processing. Treatment effects on NO_2^-+NO_3^- , NH_4^+, and total PO_4^{3-} concentrations were documented using a SAN^{++} automated wet chemistry analyzer. DOC samples were processed using a Shimadzu total organic carbon analyzer (TOC-V). For chlorophyll analysis, filters were extracted using 10 ml of acetone for 24 hrs and then processed using a TD-700 fluorometer (Turner Designs, San Jose, CA). Bacteria were enumerated using the methods in Valentine and Butler (2018); water filtered onto Whatman™ black Nuclepore filters and then mounted and stained using Vectashield DAPI and processed with an epifluorescent microscope and 377 nm cube.

Data Analysis

Species richness versus functional traits

To determine the relative influence of species diversity, microbiome, life history, biomass, and morphology effects on each response variable, a 1-factor fixed effect Multivariate Analysis of Variance (MANOVA) was used. The study was conducted over several months because of the many experimental trials and replicates needed for this study (July-August 2015), so there was potential for daily variation in water quality and thus the dependent variables I measured. Therefore, the data were normalized by taking the difference between the dependent variable values measured in the treatment flumes and the simultaneously run control flumes that only contained seasoned bricks. The assumptions of homogeneity of variances and normality were tested with Levene's and Kolmogorov–Smirnov tests (respectively), but due to collinear variance in the means over time, the data were then rank transformed to produce non-parametric analyses (Conover & Iman 1981). When the results of the MANOVA were significant, a Tukey's post-hoc test was performed for each response variable

To assess the overall effect of species richness on ecosystem function (i.e. dependent variables), treatment effects were ranked 1-22 (12 experimental polycultures, 10 previous monocultures) based on the mean value for each response variable (Table 7). The ranks for each response variable were then averaged for the five species richness treatments tested: 1, 2, 3, 4, and 10 species combination treatments. These ranks were used to determine the overall strength of species richness of ecosystem function. I then averaged all monocultures together and then all polycultures to establish a baseline effect of mono- versus poly-cultures to determine which

treatments exceed their means. Log regression was conducted independently on mean nutrients produced and removed. All statistical analyses were conducted using SPSS V.22 (IBM Corp).

Substitutive versus additive ecosystem effects

I also sought to detect if emergent properties (i.e. competition or facilitation) in diverse assemblages affected response variables and whether these effects were substitutive or additive. I calculated observed versus expected values in a series of steps based on species richness using semi-random simulations of species combinations. First the monoculture response values (Chapter 2) were summed for the species in each polyculture treatment (e.g. for a simulation of a pair consisting of *I. campana* and *T. crypta*, a random value for each species would be selected and added together). These sums were then normalized to the standard treatment biomass (for a pairing divided in half). This simulation was run 10,000 times. Then the number of simulations greater or less than observed pairs were calculated as significant if greater or less than 500 (e.g. p=0.05). This was repeated for the three species and four species groups, and then repeated for the 10 species polyculture. Simulations were conducted in MATLAB R2018b.

Results

Species richness and functional trait effects on water quality

MANOVA results revealed that both species richness and overall functional grouping had significant effects on the five response variables (Table 8). Generally, increasing the number of species resulted in a larger effect on response variables (Figure 12). Post-hoc tests indicated that species richness treatments containing either four or ten species had the strongest effects on the five response variables compared to sponge groups composed of one or two species. The

sponge polyculture assemblage with 10 species provided the highest increases in concentrations of NO_2^-+NO_3^-, and PO_4^{3-}, and a decrease in NH_4^+ concentrations relative to the controls. With respect to the removal of chl *a*, the only treatment to significantly outperform the 10 species polyculture was the four species polyculture. All the polyculture treatments outperformed the monocultures, in terms of treatment effects. Only one monoculture (data from Chapter 2) significantly outperformed the effects of higher diversity treatment groups, a case of 'transgressively over-yielding' (Schmid et al. 2008). In that case, a population of *Spongia barbara* alone removed significantly more DOC than any multispecies sponge assemblage tested.

Table 7. MANOVA results for species richness, functional groups, microbiome, morphology, size, and life history

	Dependent Variable	Type III Sum of Squares	df	Mean Square	F	Sig.
Species Richness	Chl*a* (ug/L)	8.858	4	2.215	56.908	<0.001
	NO_2^-+NO_3^- (µM)	7.043	4	1.761	40.837	<0.001
	NH_4^+ (µM)	176.836	4	44.209	18.339	<0.001
	PO_4^{3-} (µM)	6.571	4	1.643	182.403	<0.001
	DOC (µM)	35.672	4	8.918	11.305	<0.001
Functional Group	Chl*a* (ug/L)	13.856	19	0.729	266.796	<0.001
	NO_2^-+NO_3^- (µM)	12.687	19	0.668	309.861	<0.001
	NH_4^+ (µM)	434.314	19	22.859	38.317	<0.001
	PO_4^{3-} (µM)	7.749	19	0.408	875.297	<0.001
	DOC (µM)	94.058	19	4.95	12.155	<0.001
Microbiome	Chl*a* (ug/L)	10.363	8	1.295	45.025	<0.001
	NO_2^-+NO_3^- (µM)	9.879	8	1.235	53.489	<0.001
	NH_4^+ (µM)	306.958	8	38.370	25.499	<0.001
	PO_4^{3-} (µM)	6.979	8	0.872	140.323	<0.001
	DOC (µM)	79.130	8	9.891	20.360	<0.001

Morphology	Chl*a* (ug/L)	0.815	5	0.163	59.935	<0.001
	$NO_2^-+NO_3^-$ (µM)	1.827	5	0.365	168.206	<0.001
	NH_4^+ (µM)	41.496	5	8.299	13.806	<0.001
	PO_4^{3-} (µM)	0.174	5	0.035	74.302	<0.001
	DOC (µM)	5.210	5	1.042	2.538	0.032
Size	Chl*a* (ug/L)	0.001	1	0.001	0.515	0.475
	$NO_2^-+NO_3^-$ (µM)	0.106	1	0.106	48.912	<0.001
	NH_4^+ (µM)	39.331	1	39.331	65.426	<0.001
	PO_4^{3-} (µM)	0.028	1	0.028	60.572	<0.001
	DOC (µM)	4.600	1	4.600	11.202	0.001
Life History	Chl*a* (ug/L)	0.004	1	0.004	1.588	0.210
	$NO_2^-+NO_3^-$ (µM)	0.000	1	0.000	0.055	0.815
	NH_4^+ (µM)	0.042	1	0.042	0.070	0.792
	PO_4^{3-} (µM)	3.000E-05	1	3.000E-05	0.064	0.801
	DOC (µM)	0.003	1	0.003	0.008	0.928

Table 8. Example of simulations in which random values are selected from each species for $NO_2^-+NO_3^-$ (µM). These values are then summed and normalized for biomass. These values were then compared as less than or greater than the observed values. Matching colors indicate which values were randomly selected for the sum

I. campana	*T. crypta*	Sum	Normalization (sum/2)	Observed (0.53 µM)
0.06226	0.468	0.48378	0.24189	<
0.05113	0.437	0.47315	0.236575	<
0.037	0.437	0.5093	0.25465	<
0.053	0.43265	0.48	0.24	<
0.043	0.43	0.49	0.245	<
0.0413	0.43615	0.49226	0.24613	<

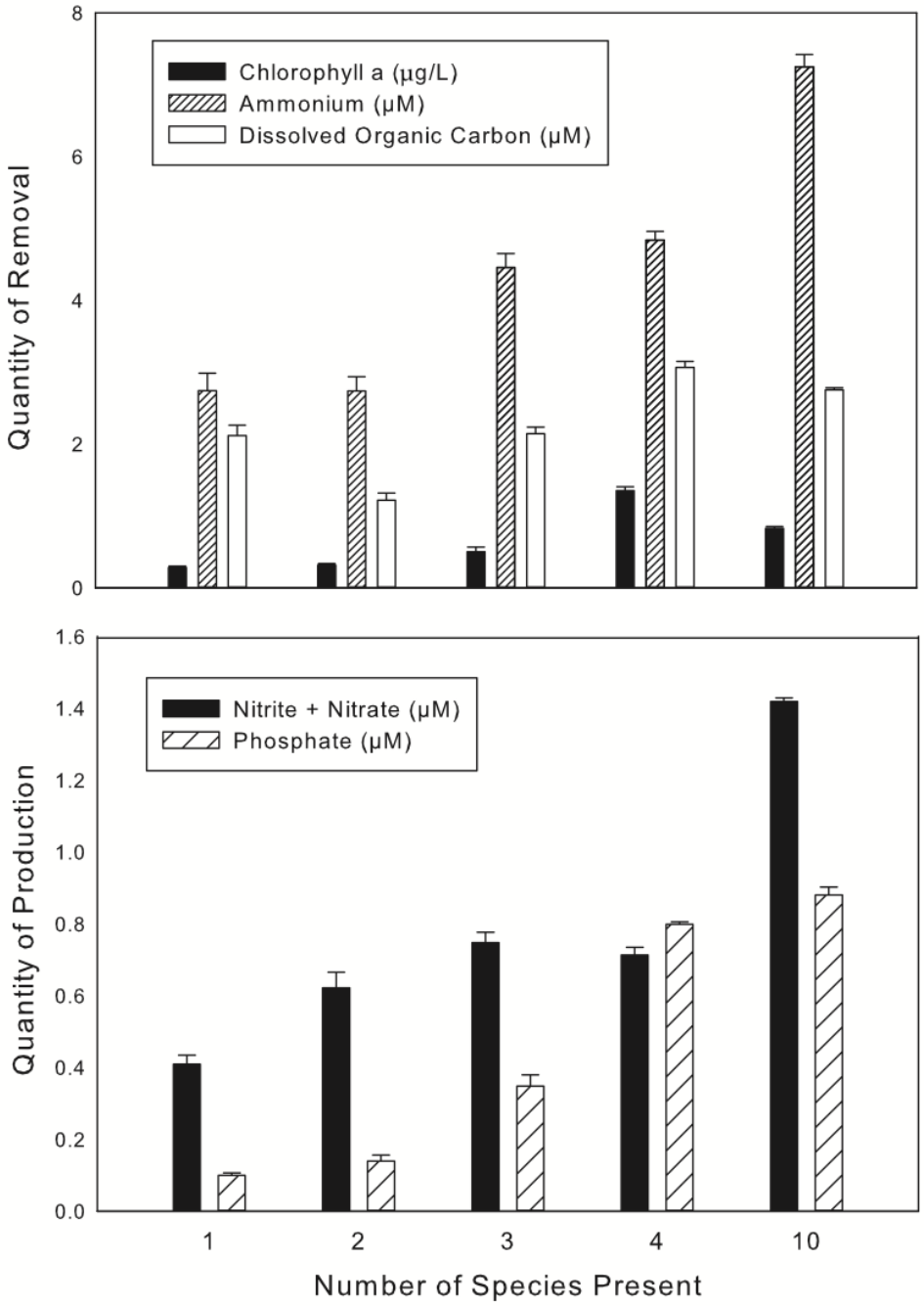


Figure 12. Change in five response variables based on their removal from the water by sponges (top panel; chl *a*, NH_4^+, DOC) or their release into the water by sponges (bottom panel; NO_2^- $+NO_3^-$, PO_4^-) as a function of the number of sponge species present in the mesocosm. Means and error bars ($\pm$1 standard error of the mean) are shown. Lower case letters signify significant differences for each response variables at $p<0.05$ level

As richness increased so too did the strength of response on ecosystem function, in this case: water quality. By ranking the average change of all response variables for the number of species present, I estimated the number of sponge species necessary in an assemblage to promote maximum ecosystem function (Figure 13). Averaging the effect of each species richness group for each response variable gave a clearer picture of how the number of species present affected ecosystem function (Figure 14). The effect of species richness on all of the response variables combined was greatest when between four to 10 species were present. However, the relationship was asymptotic for both removal and production of response variables. The 10 species polyculture only slightly outperformed the four species polyculture. This relationship suggests either the presence of competition in a diverse sponge assemblage that limits their function, or that additional species are functionally redundant at some level. By performing log regression on both production and removal, I assessed the ideal number of species in this ecosystem. The two regression lines met when approximately eight species were present.

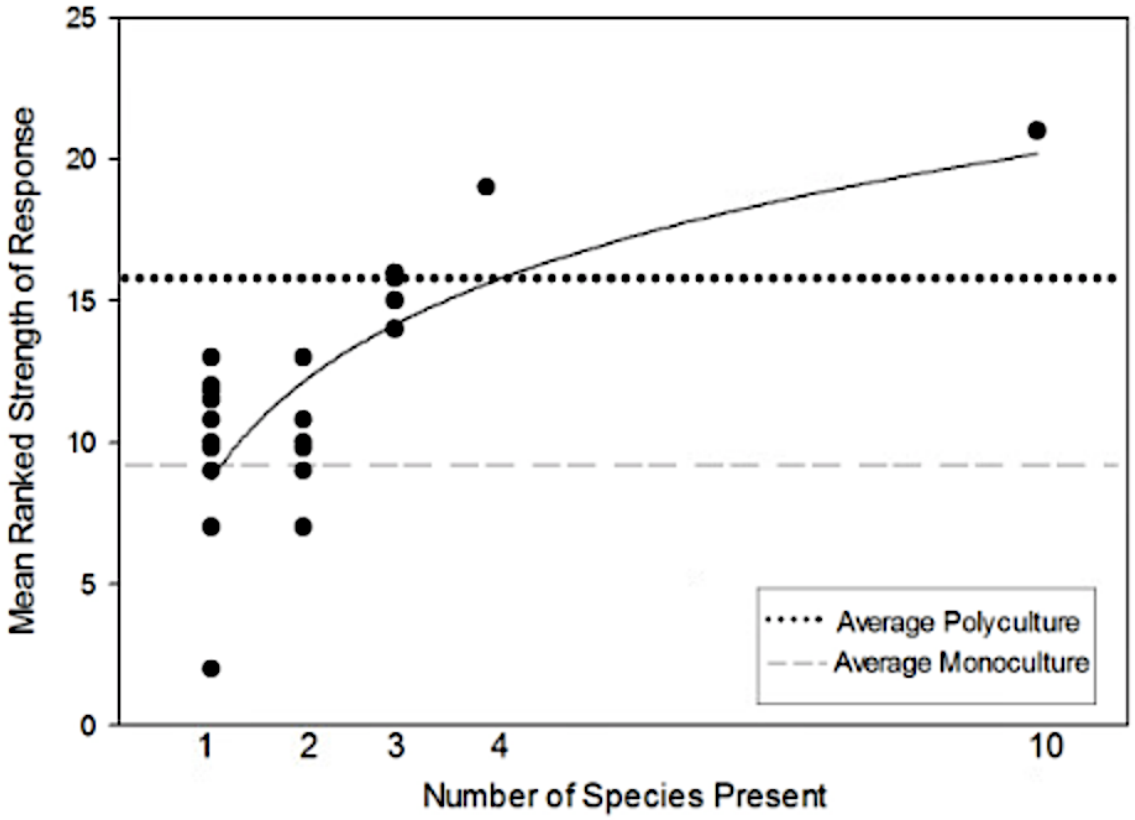


Figure 13. The mean ranked strength of response for the five species richness treatments tested: 1, 2, 3, 4, and 10 species combination treatments. The logistic regression based on species richness across all response variables. The averaged monocultures and polycultures to establish a baseline effect of mono- versus poly cultures to determine which treatments exceed their means

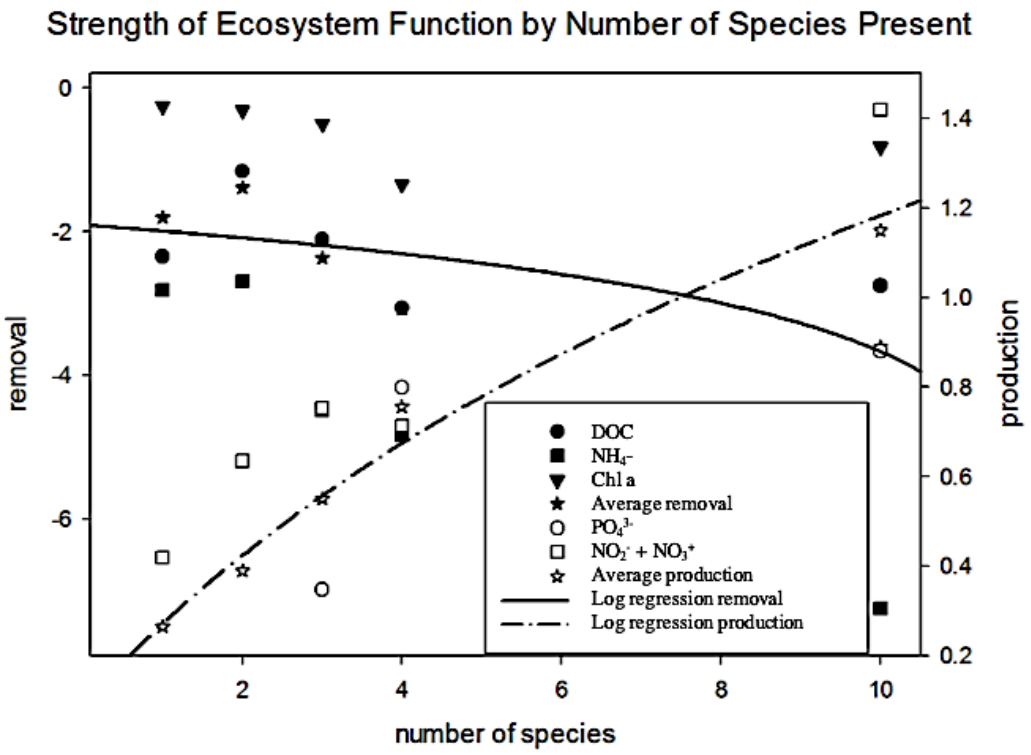


Figure 14. Mean quantity of removal (chl *a*, NH_4^-, DOC; solid line) or production (NO_2-NO_3^+, PO_4^{3-}; dashed-dotted line) of response variables for species richness treatments. Asymptote based on logistic regression indicates that eight species may be the ideal number of sponge species in an ecosystem

Functional traits

Microbial association and morphology had a significant effect on the five response variables (Table 7). Size did not significantly affect chl *a* ($F = 0.515$ df = 1, $p=0.475$), but did significantly affect $NO_2^-+NO_3^-$, NH_4, PO_4^3, and DOC ($p<0.001$, Table 7). Life history did not significantly affect chl *a*, $NO_2^-+NO_3^-$, NH_4 , PO_4^3, or DOC ($F = 1.588$, df = 1, $p=0.210$; $F = 0.055$, df = 1, $p=0.815$; $F = 0.064$, df = 1, $p=0.79$; $F = 0.064$ df = 1, $p=0.801$; $F = 0.008$, df = 1, $p=0.928$). Although each functional trait significantly influenced each of the response variables, the results mirrored the trends observed for species richness. Treatments containing all sizes, morphologies, life histories, and microbial associations tended to perform better than other mixtures, which performed better than monocultures across all response variables (Figure 15).

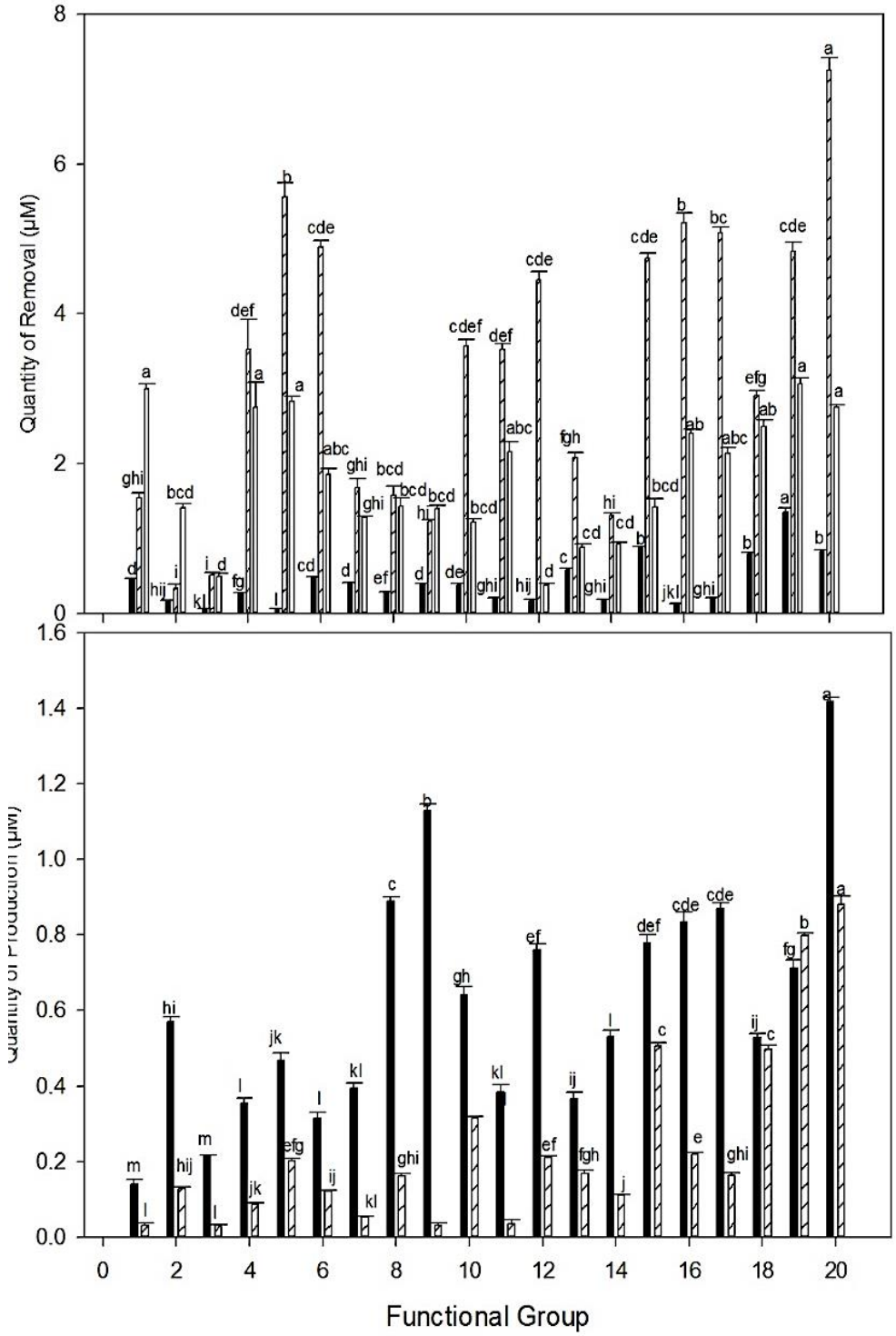


Figure 15. Effect of functional group treatments on response variables, for unique functional groups present in mesocosms. Error bars are standard error of the mean. Lower case letters signify significant differences for each response variables when $p<0.05$. Numbering on x-axis refers to functional group codes

Microbial Symbionts

Treatments with unique mixtures of microbial symbionts (HMA vs. LMA) had a significant effect on all response variables (Table 7; Figure 16). Post hoc analysis indicated the increase of NO_2^-+NO_3^- was significantly greater when seven HMA and three LMA species were present, as compared to all other treatment groups. Phosphate production was similar in combinations of seven HMA and three LMA species and two HMA and two LMA species, and significantly greater than all other treatment groups. Chlorophyll *a* removal was significantly greatest in combinations of two HMA and two LMA species. Combinations of seven HMA and three LMA species had a significantly greater effect in NH_4^+ removal than all other treatments groups but was similar to combinations of two HMA and two LMA, and two HMA and one LMA species. Nitrification was greatest among HMA sponges, but denitrification was greatest in LMA sponges.

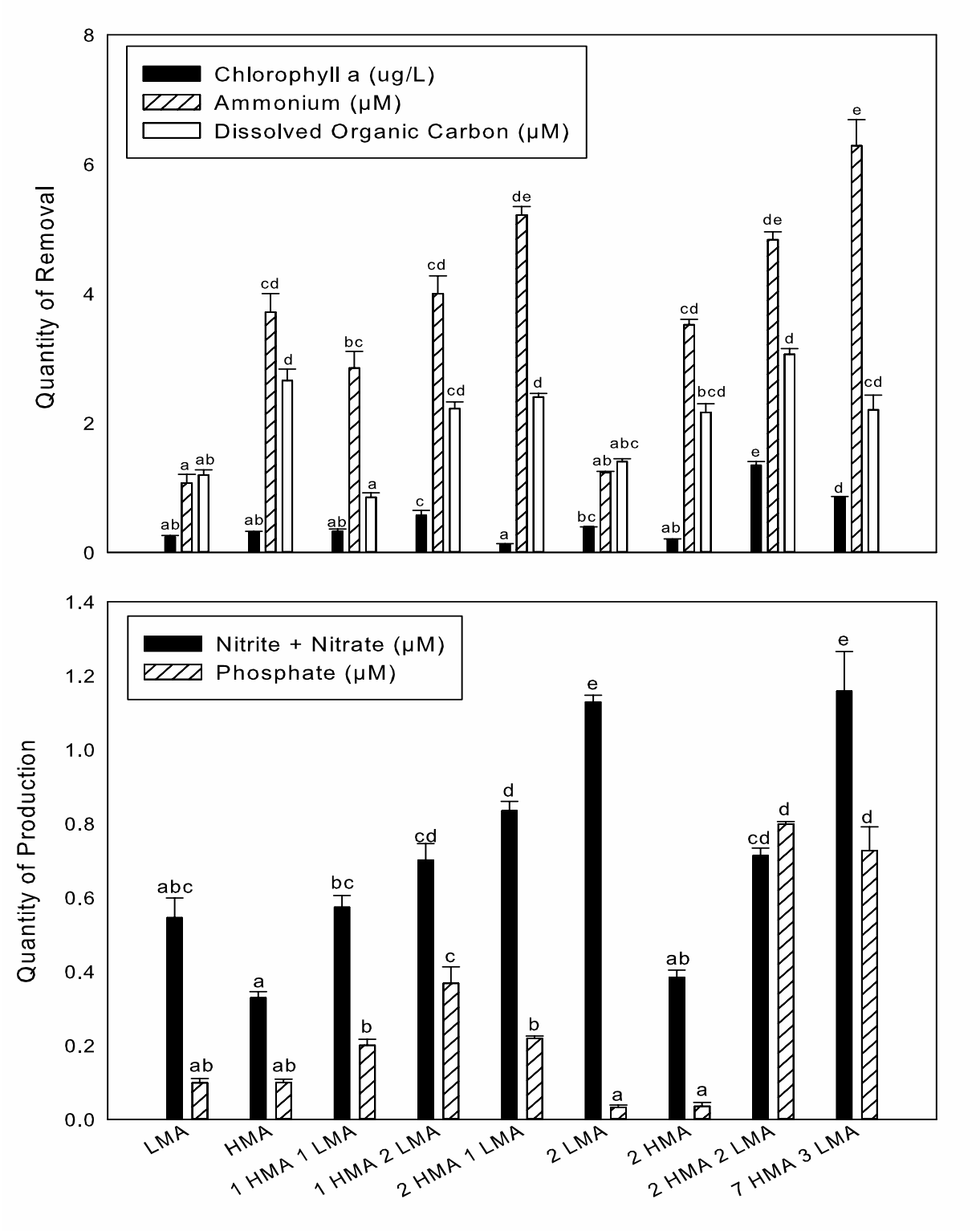


Figure 16. Effect of combinations of sponge species defined by their microbial associations (LMA, HMA) on five response variables. Mean + 1 S.E. Lower case letters signify significant differences or each response variables when $p<0.05$

Size

The terminal size of sponges (i.e. large, medium, and small) had a significant effect on response variables, except for effects on chl *a* ($F = 0.515$, $df = 1$, $p=0.475$), (Table 7; Figure 17). Based on post hoc analysis, mixtures containing small, medium, and large sponge species or those containing two small sponge species had the largest effect on $NO_2^-+NO_3^-$. Combinations containing all three sizes of sponge also had the largest effect on NH_4^+. Phosphate also differed most in the size class mixture with three species and when two large and two small sponge species were present. DOC concentrations were similarly altered by combinations of two large and two small, medium, two large and two small sponge species, as well as the size class mixture with three species.

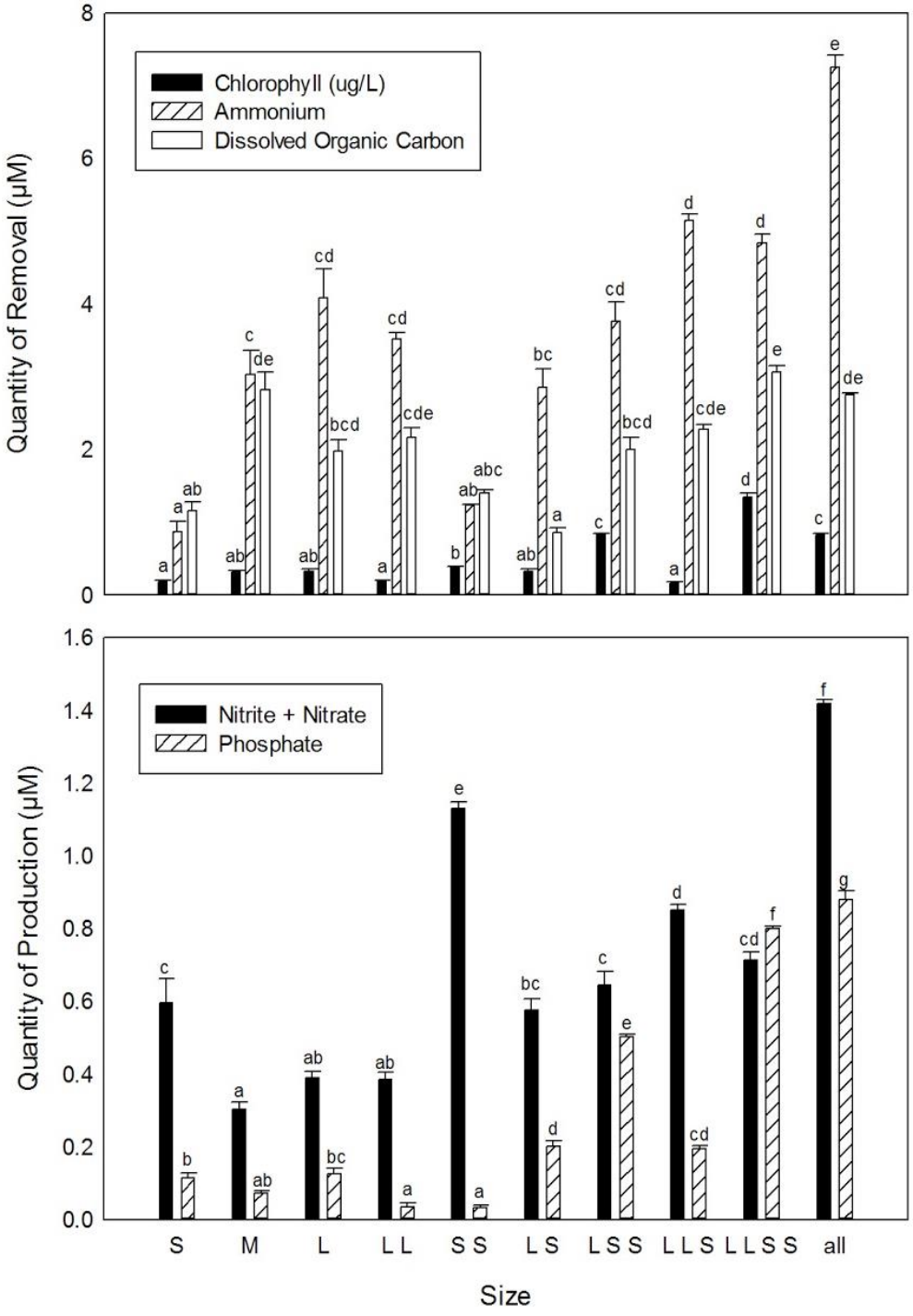


Figure 17. Effect of combinations of sponge size classes on five response variables. Change in five response variables based on their removal from the water by sponges (top panel; chl *a*, NH_4^+, DOC) or their release into the water by sponges (bottom panel; NO_2^-+NO_3^-, PO_4^-) as a function of sponge size (S = small, M = medium, L = large) the number combinations present in the mesocosm. Error bars are standard error of the mean. Lower case letters signify significant treatment differences for each response variables when $p<0.05$

Morphology

Sponge morphology significantly affected all response variables (Table 7; Figure 18). Based on post hoc analysis, combinations of all four morphologies and combinations of ball, vase, and volcano (Table 5) sponges had the largest effect on chl *a*. The treatment containing all four morphologies had the largest effect on NO_2^-+NO_3^- , NH_4^+ and PO_4^{3-}. DOC was similarly affected by vase, branching, and ball species, combinations of ball, vase, and volcano species, and combinations of all four morphologies.

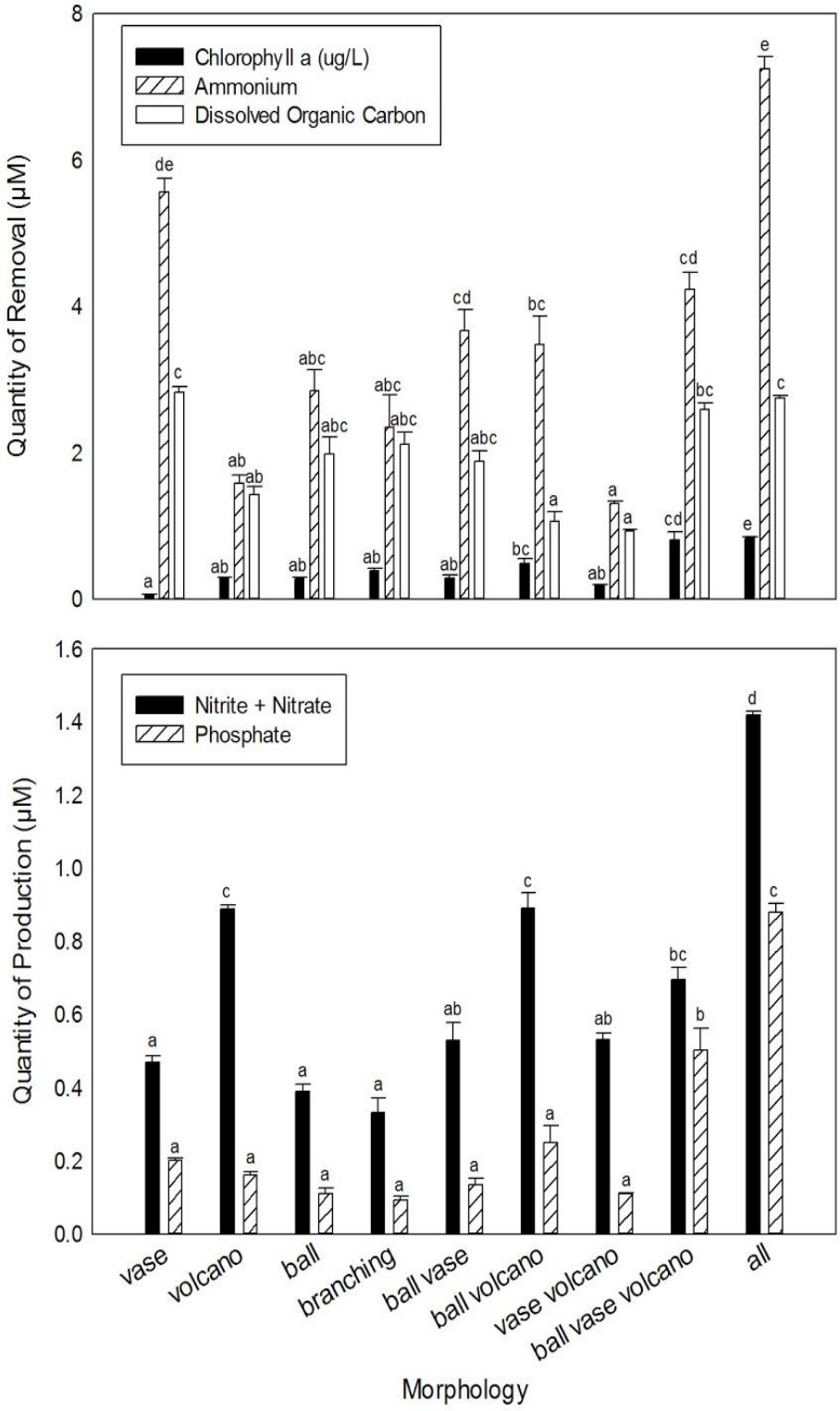
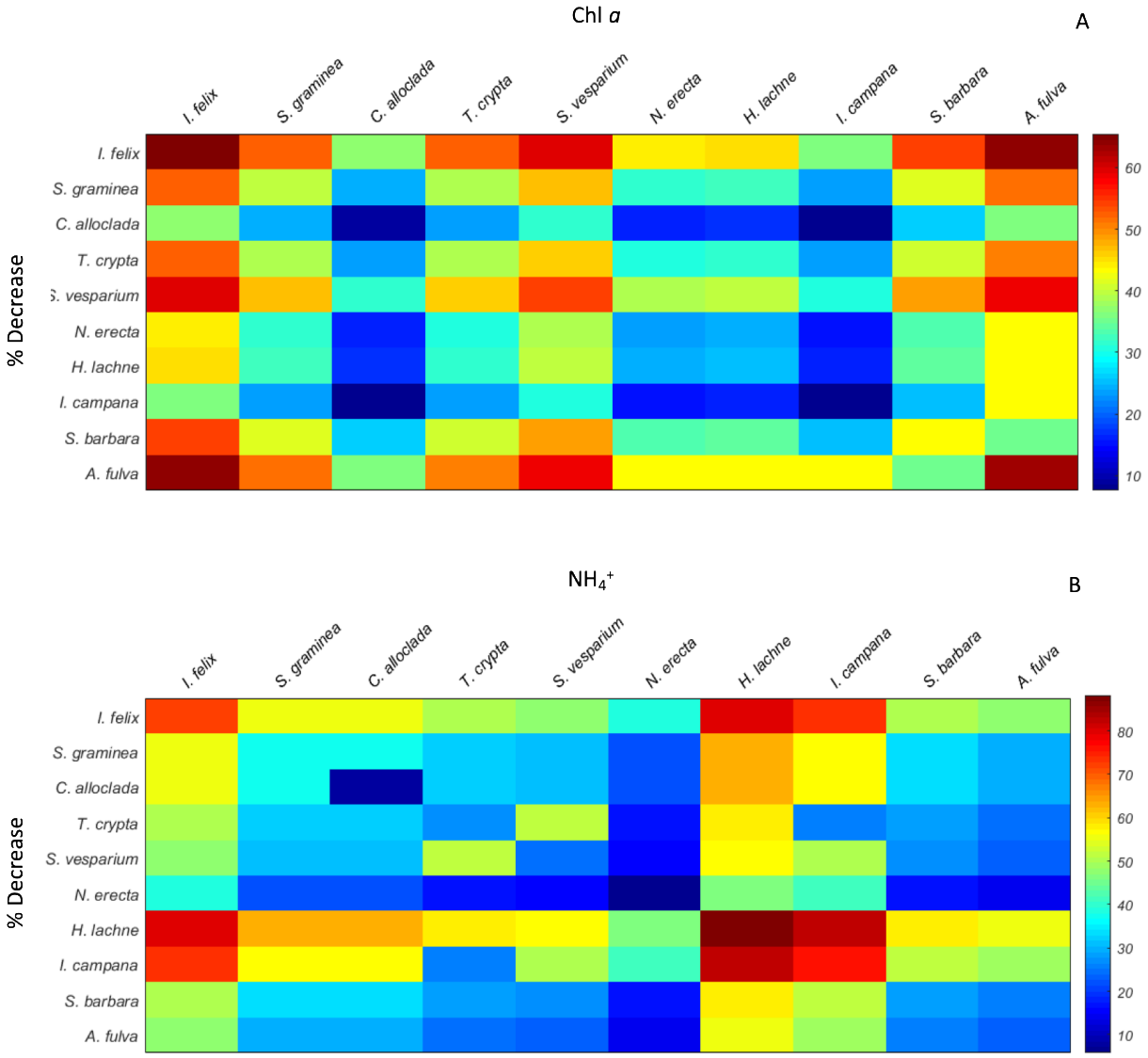
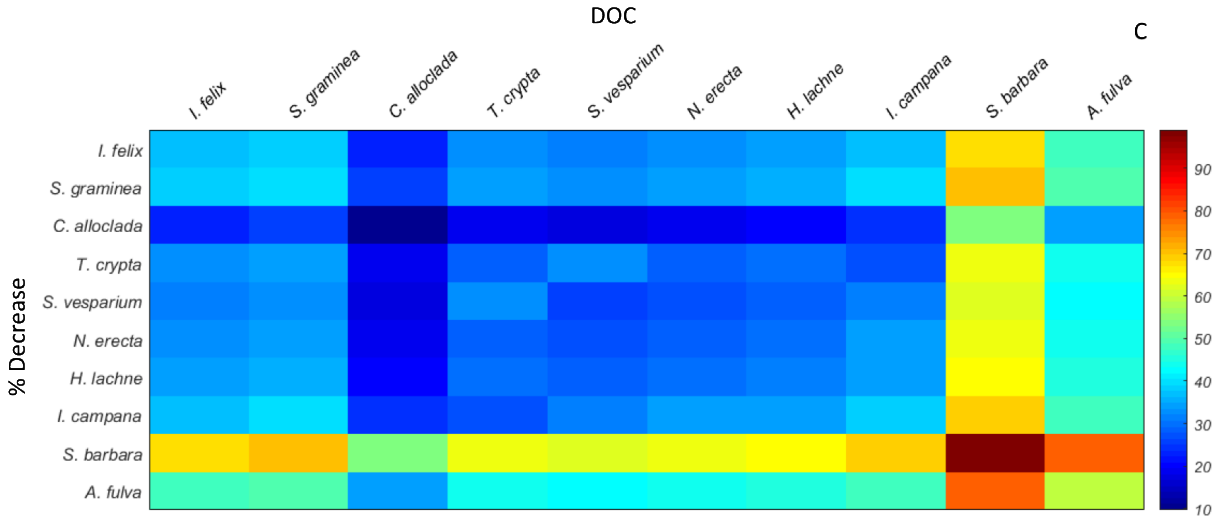


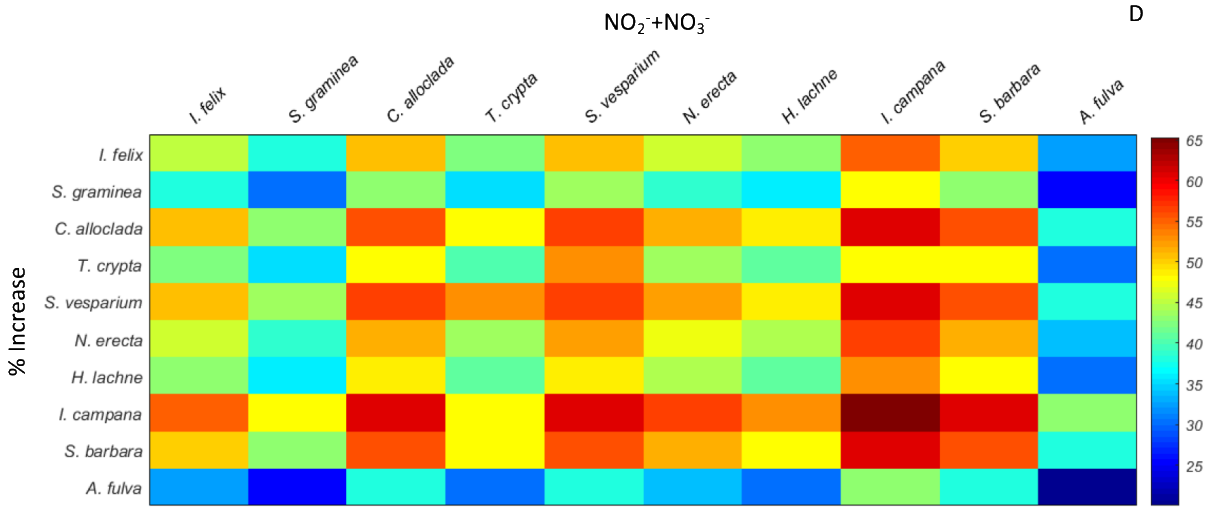
Figure 18. Effect of combinations of different sponge morphologies (ball, branching, vase, volcano) on five response variables. Error bars are standard error of the mean. Lower case letters signify significant differences for each response variables when $p<0.05$

Substitutive versus additive ecosystem effects

The simulations of expected treatment responses allowed me to predict how species combinations should affect selected response variables if the species effects were purely additive. In addition, they reveal which species combinations would have the greatest influence on particular water quality parameters. For example, sponge assemblages consisting of *S. barbara* and *I. campana* had the largest effect on concentrations of chl *a* (Figure 18), whereas concentrations of NH_4^+ were most affected by combinations containing *A. fulva* and *I. felix*. These simulations of species combinations indicated that polycultures typically outperform the expected values (Table 5; Figure 19).


Chl a
A
I. felix
S. graminea
C. alloclada
T. crypta
S. vesparium
N. erecta
H. lachne
I. campana
S. barbara
A. fulva
% Decrease
60
50
40
30
20
10
NH4+
B
80
70
60
50
40
30
20
10


DOC
C
I. felix
S. graminea
C. alloclada
T. crypta
S. vesparium
N. erecta
H. lachne
I. campana
S. barbara
A. fulva
% Decrease
90
80
70
60
50
40
30
20
10


NO2-+NO3-
D
I. felix
S. graminea
C. alloclada
T. crypta
S. vesparium
N. erecta
H. lachne
I. campana
S. barbara
A. fulva
% Increase
65
60
55
50
45
40
35
30
25

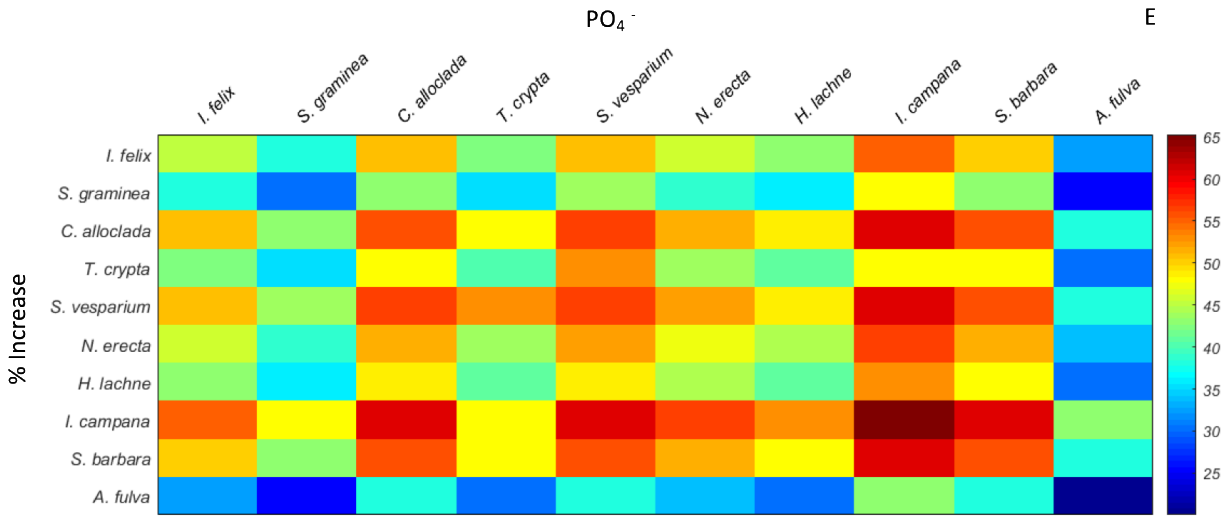


Figure 19. Heatmap of predicted response to species combinations on selected nutrients. The color bar indicates predicted percent increase or decrease based on two species combinations on each of five water column characteristics: chl *a*, NH_4^+, DOC, NO_2^-+NO_3^-, and PO_4^-

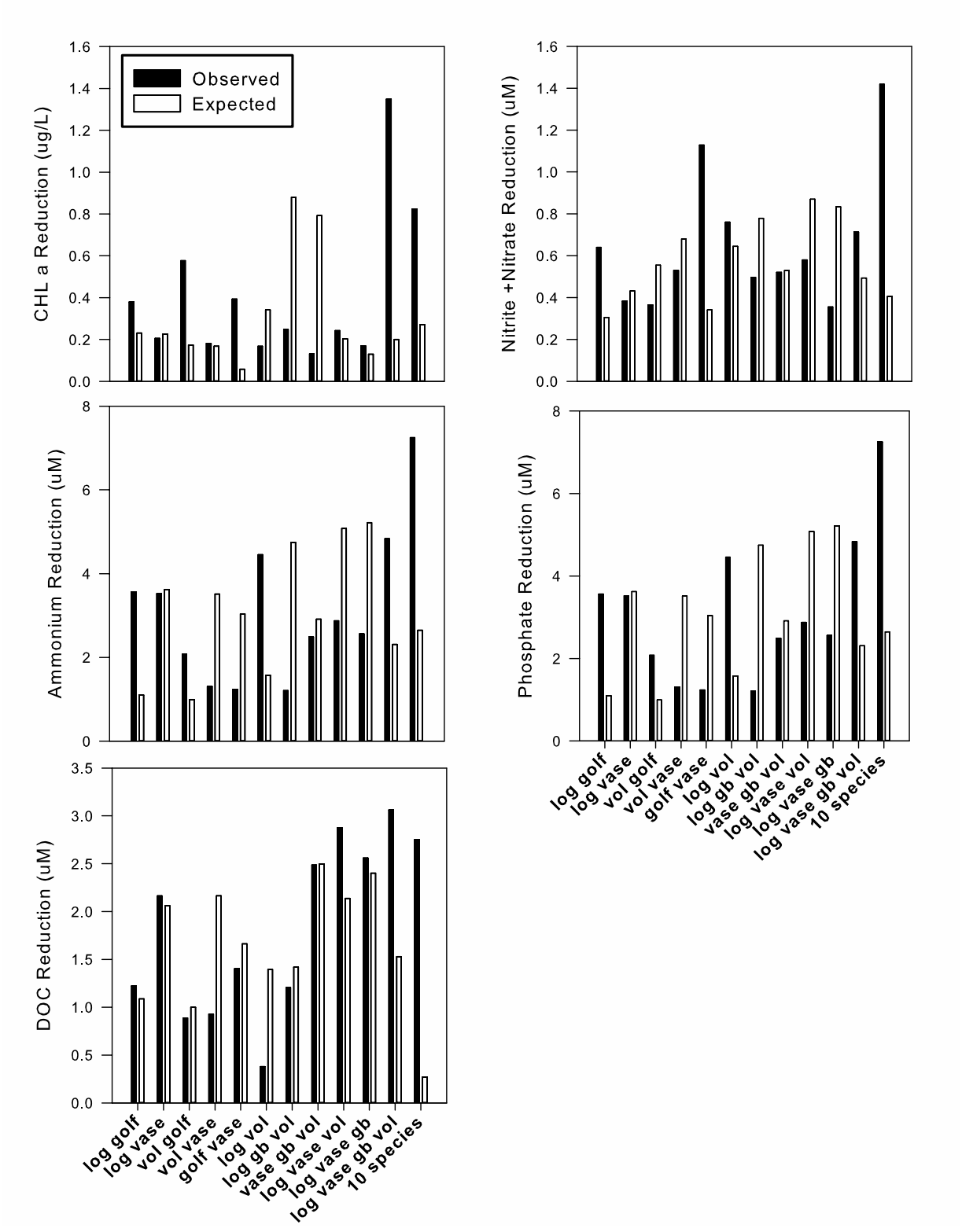


Figure 20. Observed values (filled histograms) of treatment effects (species-specific assemblies) on five response variables (panels) versus expected values from simulations of simple additive species effects

Discussion

Most of what is known about the effects of sponges on nutrient cycling and plankton composition have come from studies based on measurements of individual species of sponges, (e.g. Peterson et al. 2006; Valentine & Butler 2018), and indeed, individual sponges. Because resource selectivity varies greatly among sponge species, it is likely that not all species contribute equally to ecosystem functioning. Given widespread reports that diverse mixtures of consumers exhibit emergent, non-additive properties (Didham et al. 2007; Ball et al. 2008), it is possible that exploitative consumption of resources or allelopathic suppression of feeding occurs among diverse groups of sponges. My study is the first to explicitly test, using a manipulative experiment, the effects of sponge diversity on ecosystem function, and to parse those effects into those due to species, microbiome, morphology, and life history. I found that sponge biodiversity has an additive, but asymptotic relationship with many ecosystem functions that determine water quality and plankton community structure. However, explanation of this relationship is limited to the selected response variables measured during this experiment and the relationship could be different if other responses such as sound (e.g. Butler et al. 2017) were selected. Among tropical demosponges, functional diversity (i.e. microbiome, life history, or morphology) better predicted resource consumption and biochemical cycling than did species richness, echoing the results of a review of 94 diversity ecosystem function studies by Lefcheck et al. (2015). Contrary to my predictions, I found that the largest multispecies assemblages were rarely subject to transgressive overyielding by monocultures.

There are a number of criticisms of studies on the relationship between biodiversity and ecosystem function. The first concerns 'sampling effects', the idea that studies with large numbers of species are statistically more likely to contain species with high functional effects

(Huston, 1997; Tilman 1997). My experimental design explored the concept of multifunctionality by combining multiple treatments and response variables. The results from these analyses show that depending on which resource is targeted, different species were quantitatively 'better' than others. However, in aggregations of multiple species, the ecosystem effects were even stronger (Figure 21). Thus, these results support the conclusions of others (e.g. Duffy et al. 2003; Bracken & Stachowitz 2006; Gamfeldt et al. 2008) that multivariate complementarity occurs in marine ecosystems. A secondary criticism focuses on whether study species are selected randomly. The sponges used in this study were selected specifically for their abundance in the Florida Bay seascape and manipulability (i.e. large enough to create cuttings). These represented only a small proportion of the available species, approximately 5-12% of those found in Florida Bay. For the polyculture treatments, two species were selected that are resilient to HABS and two that are not but are larger in biomass. Hence, my selection of species underrepresented rare or cryptic sponge species and their effects on water column properties.

The initial linear trajectory of the effect of species additions on water column resources observed in this study (Figure 13), suggests that the accumulation of just a few species enhances community ecosystem functioning through some kind of ecological facilitation (Wall & Nielsen 2012). The asymptotic nature of the relationship also indicates that functional redundancy eventually ensues in even more diverse communities. However, the ten species treatment sets the asymptote to what could be a steeper curve, potentially skewing the results. But, these tests of other numbers of species combinations were not possible. Perhaps if these trials had been continued longer (i.e. weeks or months, rather than days) and manipulated on a larger scale or with even more species, the community may have developed further, and the asymptote associated with species richness may not have occurred (Duffy 2009). But several results argue

against that alternative outcome. First, the preliminary experiment that I conducted ran for a week, during which time I could detect no difference in sponge effects from those measured after a day's acclimation. In addition, the asymptote in the biodiversity-ecosystem response curve occurred regardless of the response variable measured (Figure 13). Finally, I tested experimental model communities of up to 10 common sponge species - nearly all of the large sponge species and approximately 10-15% of all sponge species in the habitat - but saw no evidence of a parabolic relationship, which would have provided evidence for interspecific competition for water column resources. However, in a separate field study of sponge growth as a function of sponge biomass (not necessarily diversity), I discovered evidence for competition among sponges for food (Chapter 2).

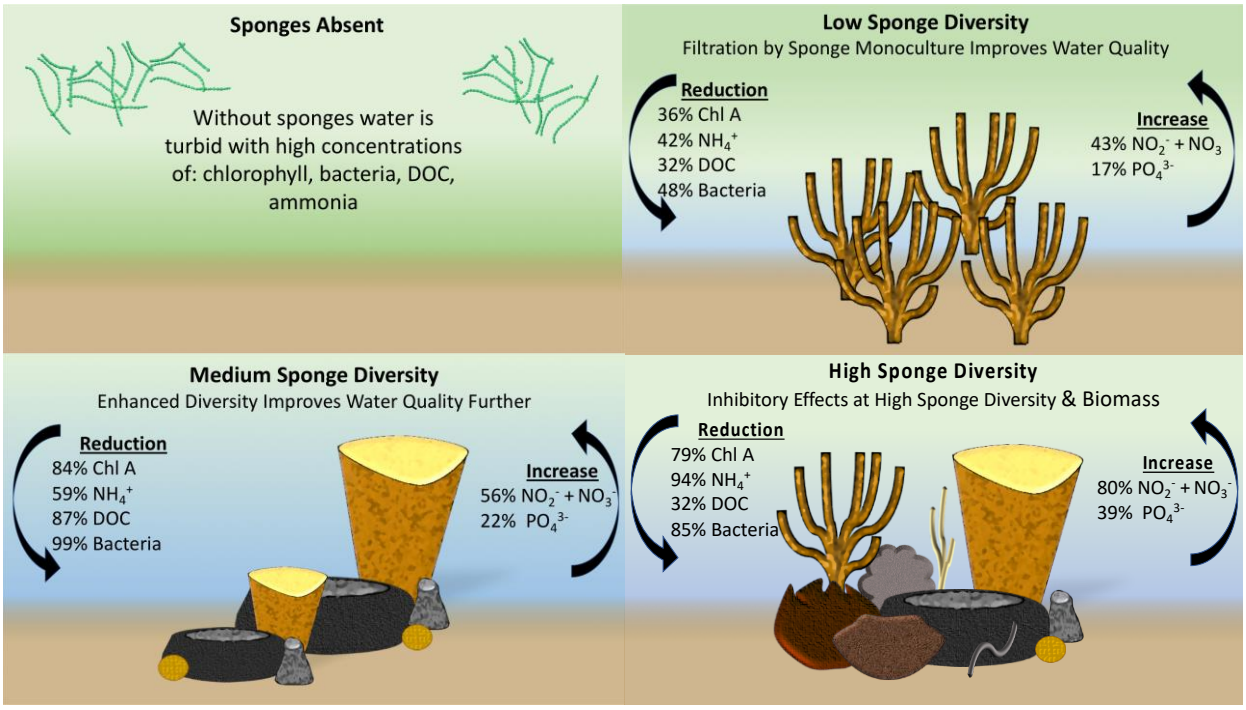


Figure 21. Graphical representation of the effects of sponge assemblage diversity on response variables. Changes in water column constituents is greatly affected by the types and concentrations of sponges present

In a number of important ways, sponge assemblages are probably one of the marine faunal assemblages most comparable to the historically well-studied terrestrial plant communities. Sponges are sessile and, similar to plants, compete for 'community property' as nutrients and other consumable resources are dispersed in a common medium (e.g. soil for angiosperms and water for sponges). In the original study of the effect of diversity on productivity in herbaceous plant communities, Tilman (1996) found that gains in ecosystem function diminished after the first ten species were added to the assemblage. While fewer sponge species were used in this study than Tilman's plots (combinations of 1, 2, 4, 8, and 16 plant species out of 18 species), this may indicate greater redundancy in tropical demosponge assemblages that potentially buffers sponge assemblages against disturbances (e.g. Bracken and Williams 2013). However, functional redundancy may also portend greater interspecific competition if resources are limited. Alternatively, should the most productive members of the community be lost, as has occurred in large portions of Florida Bay, peak productivity or function may not be achieved. The idiosyncratic relationship between each species means that while most species have the same functional abilities, they each enhance functioning differentially. Because sponges remove different-sized particles and differentially cycle nutrients (Pile et al. 1997; De Caralt et al. 2008), it is unsurprising that combinations of species have more comprehensive effects on response variables than individuals. So, it is likely that when sponges from two different species or functional groups are found together, resources will be used more completely, resulting in a stronger effect on the ecosystem.

Although not addressed in this study because location of sponges within flumes was haphazard, a subtle benefit of multispecies assemblages is the potential effect of morphology and size on small-scale hydrodynamics. While hydrodynamic effects of sponge assemblages were not

measured per se, both morphology and size significantly affected response variables. A possible explanation of this may be the movement of water around the sponges in mesocosms. Large sponges (e.g. *S. vesparium*) may cause 'current shading' with two possible outcomes: (a) they may be decelerating water flow, permitting a greater fraction of resources to be utilized in the slower current, or (b) they may enhance turbulent mixing, reduce the depth of the boundary layer, and thus increase resource supply to smaller sponges (Cardinale et al. 2000). Height of sponges may also support differential feeding. Taller sponges may be able to filter from higher in the water column, reaching planktonic communities unavailable to smaller sponges. Those smaller sponges may in turn be more affected my sediment nutrient concentrations than those further from the sea floor.

This body of work suggests how the Florida Keys ecosystem may change over the coming decades if sponge assemblages naturally rebound or are restored. Most studies on the effect of biodiversity on ecosystem function are concerned with how continuing species loss will alter future productivity and ecosystem functioning. The sponge assemblages in Florida Bay and the Florida Keys are a prime example and have already experienced widespread declines in sponge biomass and diversity due to recurrent cyanobacteria blooms, extreme temperatures and salinities, and commercial fishing (Stevely et al. 2011; Butler et al. 2017). Following intense or persistent HABs, species such as *I. campana* are first to be lost and often the last to recover, whereas other more resilient species such as *T. crypta* are likely to survive. Yet, the loss of just one species such as *I. campana*, which strongly reduced chl *a* and DOC, could conceivably result in ecosystem-wide changes in biogeochemistry if not counter-balanced by some other process. In the aftermath of intense HABs and the loss of most sponge species, I expect that the few remaining resilient species (e.g. *C. alloclada*) might become more dominant and thus would

continue to alter concentrations of nitrate and nitrite, while also resulting in increased concentrations of chl *a*, ammonium, and DOC.

An understanding of mixed-species effects on ecosystem parameters is especially important in places like the Florida Keys where restoration efforts have begun in an effort to rebuild lost sponge populations and revitalize their ecosystem functions. But most marine restoration research has focused on the restoration of systems dominated by a single foundation species (e.g. oysters, salt marsh grasses, mangroves), and often with the goal of improving 'essential fisheries habitat' (Levin and Stunz, 2005). Even on coral reefs, restoration is focused on a few shallow water framework- building species (e.g. *A. cervicornis* and *A. palmata* in the Caribbean). But an alternative approach would be for ecosystem managers to determine what functions are most important to the ecosystem and its recovery. For example, water quality in Florida Bay is highly degraded and has substantial deleterious effects on many species. Perhaps the restoration of species that reduce concentrations of NH_4 or bacterioplankton may be more useful for overall ecosystem recovery than those that provide habitat for a few fishery species.

Understanding the drivers and consequences of changes to ecosystem metrics, both structural and functional, in comparison to non-perturbed or pre-perturbed conditions enables us to project the future state and potential resilience of ecosystems (Schaeffer et al. 1988; Palmer and Febria 2012). This study indicates that certain sponge species have a disproportionately large effect on function in comparison to the number of species present, allowing us to predict the likely effect of sponge restoration on a variety of essential ecosystem functions in Florida Bay. Using historic distributions of sponges and water quality data across Florida Bay, restoration managers can select species that are: a) most likely to survive future perturbations, b) provide habitat for target species, and c) improve overall ecosystem water quality. Not only does this

study have important implications for the restoration of the Florida Keys marine ecosystem, it also reinforces the biodiversity-ecosystem functional relationship and perhaps its universality that has been so richly described for terrestrial plant communities.

CHAPTER 4

EXPLOITATIVE COMPETITION FOR PLANKTONIC RESOURCES LIMITS GROWTH OF TROPICAL SPONGES

Introduction

Exploitative competition occurs among species or functional groups, with overlapping niches and similar limiting resource requirements (Branch 1975; Gotelli 2008). When critical resources are restricted (e.g. space, light, or food), the consequences of such shortages for inferior competitors can be dramatic, often resulting in decreased growth and recruitment along with increased mortality (Amundsen et al. 2007; Gross & Cardinale 2007). Evidence of the negative relationship between density and growth due to exploitative competition of food or nutrients is widespread in the literature (Tilman 1982; Violle et al. 2009) with examples from many taxa, including: bacteria (Chao et al.1977; Smith & Davey 1993; Celiker & Gore 2012), phytoplankton (Sommer 1985; Vrede et al. 2009; Borics et al. 2012), bryozoans (Buss & Jackson, 1981), mollusks (Frechette et al. 1992; Grant et al. 2008; Guyondet et al. 2010), amphibians (Petranka & Sih 1986), fishes (Einum et al. 2006; Amundsen et al. 2007; Ward et al. 2007), trees (Pretzsch et al. 2007), and ungulates (Sinclair et al. 2003) among others. It is especially prevalent in rocky intertidal populations (Connell 1961; Dayton 1971; Menge & Sutherland 1987) where this form of competition is hypothesized to be a key determinant of community structure.

One of the prevailing paradigms in marine ecology is that abundance and growth of sessile, suspension feeding organisms (Buss & Jackson 1979; Witman & Dayton 2001; Ferguson

et al. 2013) is limited by the availability of space (Connell 1961; Lesser et al. 1992; Dubois et al. 2007; Grant et al. 2008), whereas competition for other resources (e.g. food) is considered to be minimal or reduced in intensity by predation or physical disturbances (e.g. Connell 1961; Dayton1971; Sousa 2001; Svensson & Marshall 2015). These assumptions remain despite evidence that removal of growth-limiting nutrients and food by suspension-feeding organisms can result in the depletion of those resources in the water column (Peterson & Black 1987; Troost et al. 2008; Lesser & Slattery 2013). Indeed, nutrients and plankton are exploitable water column resources, especially in oligotrophic ecosystems where their concentrations can decline steeply within dense aggregations of suspension-feeding populations (Menge & Sutherland 1987; Newell 2004).

Although research in this area is dominated by studies on bivalves, filtering by marine sponges can also have powerful effects on water column properties and ecosystem function (Gili & Coma 1998; Bell 2008; Perea-Blazquez et al. 2013; Valentine & Butler 2018). Sponges consume a diverse array of suspended picoplankton, including bacteria and viruses in sizes ranging from 0.5 to 50 μm with filtration efficiencies (i.e. particle removal) that typically exceed 75% of the available resources (Reiswig 1971; Pile et al. 1997; Ribes et al. 1999; Hadas et al. 2009). Where sponges are abundant, their ability to efficiently remove particulate and dissolved materials from the water makes them an important benthic-pelagic link in tropical, temperate, and polar regions (Webster & Taylor 2012; McMurray et al. 2014; Easson et al. 2015).

To date, most of what is known about the effects of sponges on water column processes has been the result of research conducted on rocky reefs in the Mediterranean Sea and on the fore reefs of coral-dominated ecosystems, where sponges are prolific and diverse (Diaz & Rützler 2001; Knapp et al. 2016) and planktonic food is readily available (Pawlik 2011; Pawlik et al.

2015). In these habitats, the importance of food limitation for marine sponges is likely diminished by deep water and oceanographic processes (e.g. upwelling, internal waves) that provide a ready supply of food and nutrients (Leichter et al. 2003; Lesser 2006). On coral reefs, in particular, interspecific competition for attachment space (Paine 1966; Menge & Farrell 1989; Aerts 1998; Wulff 2006; Norström et al. 2009) combined with the presence of spongivorous predators are thought to limit sponge abundance and drive their production of chemical defenses (Pawlik 2011; Pawlik et al. 2015). Therefore, in predator-rich environments, predators may obscure relationships between resources and population dynamics by keeping the biomass of suspension feeders so low that the carrying capacity is not reached and competition less likely (Owen-Smith et al. 2005; Chamaillé-Jammes et al. 2008).

The ecological processes controlling the assemblage and functioning of sponges in shallow coastal areas, where ecological conditions differ markedly from those offshore or in deeper waters, remain inadequately studied (but see Peterson et al. 2006; Butler et al. 2018). For example, environmental conditions of sponge assemblages in nearshore, back-reef lagoonal habitat where sponges can dominate the animal biomass are very different from those present on coral reefs found in deeper waters. In the Florida Keys (USA), approximately 60 species of sponges are found in the back-reef lagoon where their densities can exceed 80,000 sponges/ha and some individuals can exceed 1 m in diameter (Torres et al. 2006; Stevely et al. 2010; 2011). In contrast to reef-dwelling sponges, most lagoonal sponges lack chemical defenses from spongivory but harbor large concentrations of symbiotic bacteria (hence they are referred to as 'high microbial abundance' sponges; HMA) that strongly influence sponge biochemical cycling of waterborne nutrients (Hentschel et al. 2003; Weisz et al. 2007). In back-reef ecosystems such

as Florida Bay, the water is also shallower (< 3m) and water residence times typically longer than on fore reefs (Leichter et al. 2003; Nuttle et al. 2003; Lee et al. 2016).

Under these hydrodynamic conditions, it is conceivable that filtration by dense assemblages of sponges could deplete the water column of picoplankton and dissolved organic material (DOM), creating an environment where exploitative competition for food resources among sponges may become limiting (Bacher et al. 2003; Peterson et al. 2006). If the sponges consume local water-column constituents faster than they can be replenished by wind, tidal exchange, or water-column productivity, exploitative competition for food among sponges is possible (Cranford et al. 2008). Still, the local effect of variation in sponge volume on the immediate water column is likely to vary with abiotic conditions such as water depth, temperature, nutrients, and water turnover, leading to localized exploitative competition for water-column nutrients (Gagern et al. 2008; Archer et al. 2017; Butler et al. 2018).

Based on a limited number of studies that have described the effects of sponge filtration on water column constituents, nutrient geochemistry, and habitat provisioning (Butler et al. 1995; 2007; Lynch & Phlips 2000; Peterson et al. 2006; Valentine & Butler 2018) it is likely that sponges of hard-bottom habitats of the Florida Keys represent a heretofore unappreciated foundation species (*sensu* Dayton 1972; Ellison et al. 2005) that are key determinants of ecosystem composition and productivity in the lagoonal waters of the Florida Keys. Here, I report the results of two field studies. I first documented the effects of naturally occurring sponge assemblages on nutrient concentrations and water-column constituents across a range of sponge abundances. I then compared the growth of clonal sponge transplants of three species over 2.5 years in areas that differed in sponge abundance. I hypothesized that sponge growth and

available water-column resources would be reduced in areas of high sponge abundance because of sponge filtration and exploitative competition.

Materials and Methods

Site Surveys

To test the hypothesis that sponge growth is density dependent, I deployed sponge transplants cut from known genotypes to nine shallow-water lagoonal sites in the Florida Keys, Florida (Figure 22) that varied in sponge species abundance and size structure (hence, total sponge volume). I documented their growth for up to two years to measure the effects of ambient sponge volume on transplanted sponge growth and, by inference, competition for food. This region is dominated by a patchy mosaic of hard-bottom and seagrass habitats with hard-bottom covering some 30% of the area (Zieman et al. 1989; Herrnkind and Butler 1997). Hard-bottom in the region is characterized by low-relief limestone bedrock overlain by a thin veneer of sediment with a mean water depth of ~ 2 m and maximum depths < 4 m (Schomer & Drew 1982; Chiappone & Sullivan 1996). Water turnover and vertical mixing in this region of the Florida Keys is largely wind driven (Nuttle et al. 2003, Gilbert et al. 2009; Lee et al. 2016). Sponges are the dominant suspension feeder on these substrates throughout the Florida Keys except in areas that have experienced persistent, recurrent harmful algal blooms (Butler et al. 1995; Torres et al. 2006; Stevely et al. 2010; 2011).

Sites for my experiment were selected based on diver surveys in which I measured the density and richness of all sponges larger than 40 cm^3 found within four, 25 m long by 2 m wide belt transects (100 m^2 search area). Based on these surveys, 9 sites were identified and divided

equally into three sponge treatments for use in this study: high sponge volume, medium sponge volume, and low sponge volume (n = 3 sites per treatment). The low sponge volume sites where those within an area that had experienced a recent mass sponge mortality event due to harmful algal blooms (HAB). The blooms killed all large sponges leaving only a few small, resilient species (e.g. *Cinachyrella alloclada*, *Tectitethya crypta*) that are ubiquitous and occurred in similar abundances on high and medium sponge volume sites. All sites were separated by ~ 0.5 km to reduce environmental variability) (Figure 22). One high volume site was the original donor location where sponges were collected. At least 5 km separated each of the three regions to establish unique study sites with minimal to know exchange of water. After the start of the experiment, a third biomass treatment was added into a fourth region decimated by HABS. These low volume sponge sites were grouped together, and each site was separated by at least 1.5 km. The sites selected were similar in depth (~2 m) to reduce the effects of light and temperature variability on sponge growth and to standardize distance from shore (~15 km).

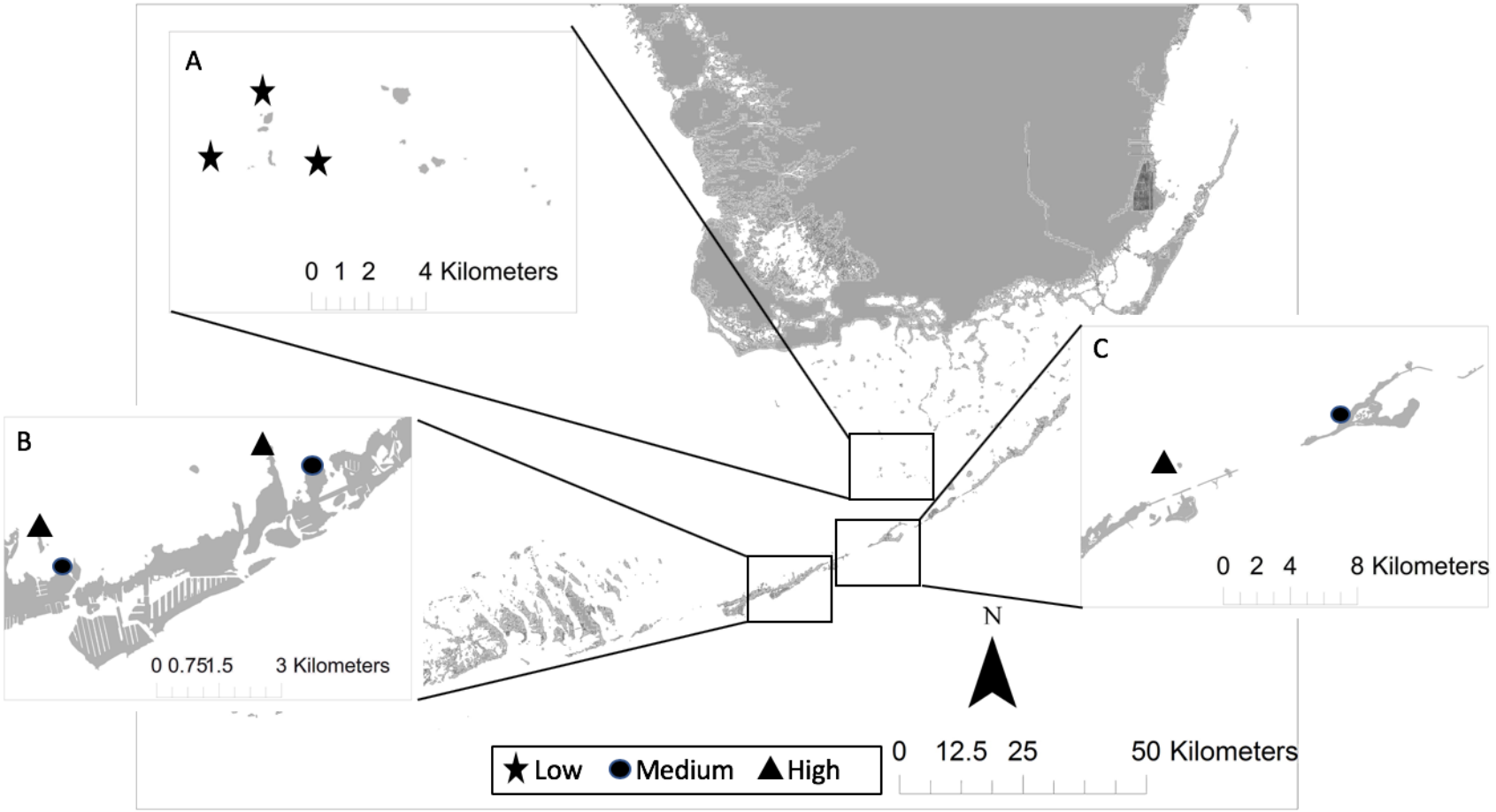


Figure 22. Map of study locations in the middle, Florida Keys, Florida (USA). (A) Location of low density sponge sites that were established in an area that contained dense sponge assemblages prior to mass die-offs caused by blooms of cyanobacteria. (B, and C) Paired high and medium sponge density sites

Sponge Growth

I selected three locally abundant species of sponges (maximum size > 30 cm^3diameter and height) for use in this study: *Ircinia campana* (vase sponge), *Spongia barbara* (yellow sponge), and *Spongia graminea* (glove sponge). The study initially only used *I. campana* and *S. barbara*; *S. graminea* was added to the experiment after one year. To reduce genotypic and local environmental variability among sponges, tissue from wild sponges was collected by divers from a single 'donor' site and individual sponges were cut into 12 pieces (each ~ 15 cm x 15 cm x 10 cm) to create clonal sponge 'cuttings' for transplantation. Each cutting was then strapped to a concrete brick (20 cm x 10 cm x 10 cm) with a plastic cable tie and left on the seafloor at the donor site for 3 months to heal and attach to the brick baseplate before it was moved to experimental sites. The original donor sponges were left intact to re-grow. My original design called for equal numbers of each sponge species and individual (i.e. genotype) to be transplanted to each experimental site, but some mortality occurred during the 3-month healing period resulting in a decrease in my source stock an inability to set up a completely orthogonal design. Thus, not every genotype was transplanted to every site and genotypes were haphazardly deployed among sites. Still, my experimental sponge units were reasonably uniform in that they came from the same location and consisted of 14 individual sponges per species. The sponges were transplanted into six initial study sites (high and medium volume sites) and after one year, a third of the individuals of all three species were transplanted into three additional sites (low volume sites) to take advantage of a recent algal bloom that created a virtually sponge-free environment. In March 2015, sponges were placed randomly into a 30 m^2 grid established on the seafloor at each site with individuals spaced 0.5 m apart (Figure 23. A-B).

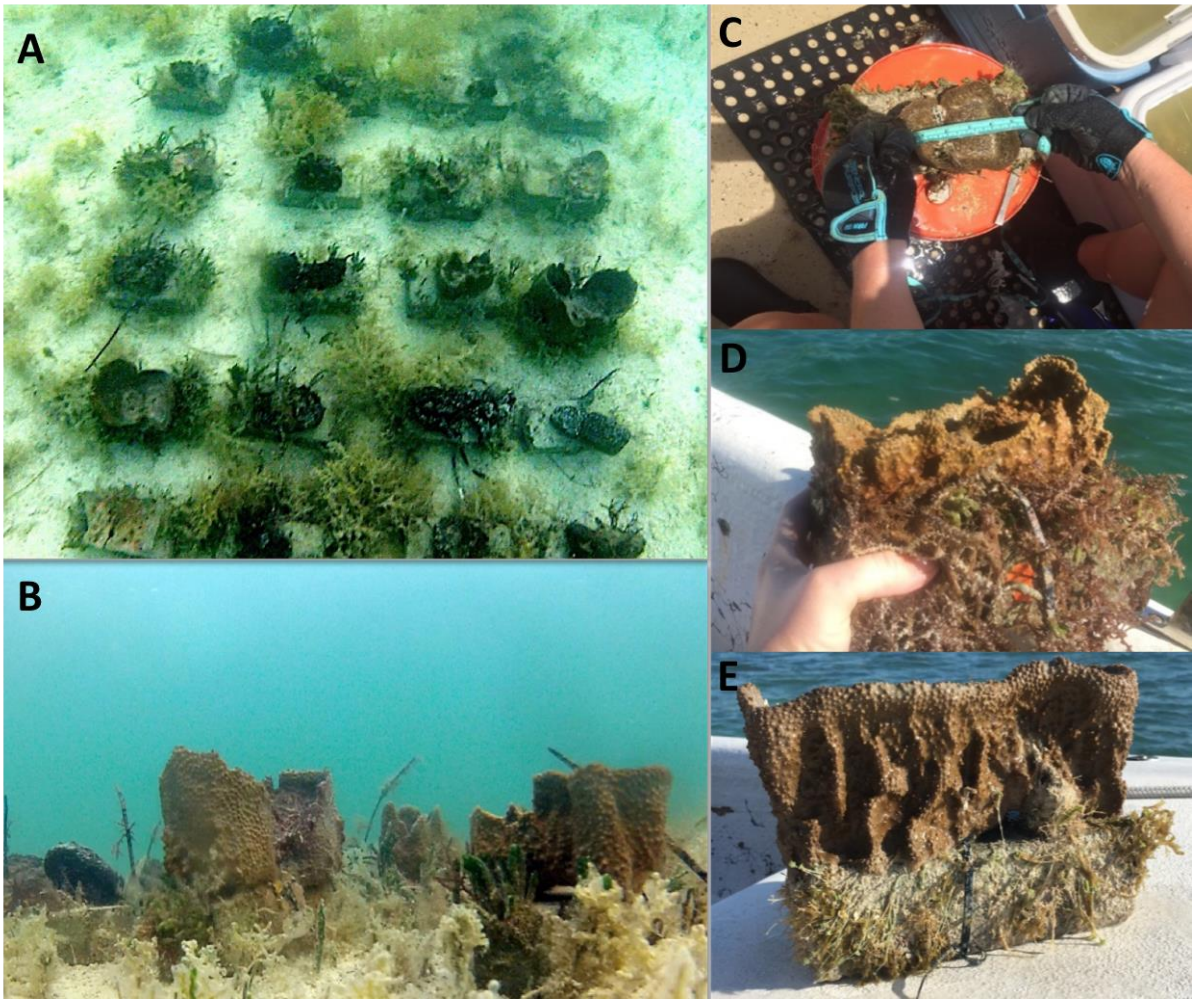


Figure 23. Top (A) and side (B) view photos of transplanted sponges at one of the experimental sites. (C) Measuring a sponge (*I. campana*) cutting when first transplanted, and photos of the growth of the same individual after 6 months (D) and 18 months (E)

To measure sponge growth (measured as an increase in estimated volume), individual cuttings were measured (height, diameter, and width) prior to placement into the treatment sites and then again, every six months for 2.5 years (March 2015, August 2015, March 2016, August 2016, March 2017, August 2017), for a total of five repeated measurements post-transplantation (Figure 23. C-E). Mortality was also documented during the sampling events and the sponges and brick baseplates cleaned of epizoic organisms that could inhibit their growth. The

experiment was terminated when an algal bloom spread across the three low volume sites, where all experimental sponges were killed.

Water Column Characteristics

To document the potential relationship between sponge effects on water column characteristics at each of my experimental sites (i.e. low, medium, and high natural sponge volume sites), I took water samples at each site in August 2017 at slack tide during a week in which prevailing winds were less than 5 m/s. A total of 1 L of seawater was collected in polyurethane bottles 1 m from the seafloor by sampling 200 ml of water from five locations in the 30 m^2 experimental area. Storage and preservation of water samples for analysis of dissolved organic carbon (DOC) using a Shimadzu TOC 5050 analyzer and particulate organic matter (POC) using a CE Elantech NC2100 elemental analyzer followed those methods presented in McMurray et al. (2016). Using a BD FACSCalibur Flow Cytometer, water samples were excited at 488 nm to measure picoeukaryotes, *Synechococcus*, and total planktonic concentrations the presented by McMurray et al. (2016). Aliquots of each sample were stained with Sybr Green-1 to measure high nucleic acid (HNA) bacteria, low nucleic acid (LNA) bacteria, and viruses prior the use of flow cytometer.

In the laboratory, water was filtered using precombusted 7 micron GF/F filters and 100 ml aliquots were stored in polyurethane bottles at -20 °C for nutrient analysis. To quantify concentration of particulate organic carbon (POC) and DOC at sites of varying sponge density, seawater was filtered through a precombusted 7 micron GF/F filters and 20 ml of filtrate was stored in acidified (100 ul of 50% phosphoric acid) glass vials at -20 °C. Total dissolved nitrogen (TDN) was quantified using an Antek 9000N analyzer that was run in tandem with the Shimadzu

TOC 5050 used to measure DOC; nutrients (nitrate, ammonia, phosphate) were measured with a Bran+Luebbe AutoAnalyzer III, and dissolved organic nitrogen was calculated as the difference between TDN and dissolved inorganic nitrogen (DIN).

Statistics

I compared growth and mortality of experimental sponges: (a) between paired sites (high and medium) within each region, (b) among high, medium, and low sponge volume treatments, and (c) among species and genotypes. To calculate volumes of each species, general morphology was used to select a geometric formula. *Ircinia campana* volume was calculated as a cone, whereas *S. graminea* and *S. barbara* were calculated as spheres based on field measurements. Although similar in size at the start of the study, the sponge cuttings were not identical in size, so growth was converted to the proportional increase in volume for each cutting to control for different starting volumes.

Repeated-measures general linear model Analyses of Variance (ANOVA)s were performed for each species to compare mortality and growth across treatments, sampling events (season), and genotypes. Genotype was assigned as a covariate for this ANOVA to determine its effect on individual growth patterns. Tukeys tests were performed post-hoc on significant ANOVA effects. When comparing growth rates from the second year of deployment of *S. graminea* and the three initial sites, the first six months of growth of *S. graminea* (August 2016-March 2017) were compared to the initial six months of growth of *I. campana* and *S. barbara* in the first year of the experiment (March 2015- August 2015). If an individual died during the experiment, its growth rate was excluded from statistical analysis. To determine if genotype influenced growth, I also conducted repeated-measures ANOVAs using genotype as a random factor, blocking for individuals. Because 'site' is a random effect, the proportion of variation

explained by the site effect was compared to the treatment effect for each species. One-way ANOVAs were used to compare all water column constituents among treatments. Analyses were conducted in SPSS V.22 (IBM Corp).

Results

Site Surveys

There were significant differences in natural sponge volume among the high, medium, and low sponge volume treatments ($F = 63.2$, $df = 2$, $p<0.001$) (Figure 24) in accord with my classifications of the sites. High sponge volume sites contained an average of 231 (2.31/ m^2) individual sponges > 20 cm diameter with mean sponge biomass 706 cm^3 of sponge/m^2 from 13 species. At the medium sponge volume site there was a mean of 174 (1.75/ m^2) sponges with mean sponge biomass 307 cm^3 of sponge/m^2 and 15 species. In comparison, low volume sponge sites had a mean of only 81 (0.82/ m^2) sponges with a mean biomass 102 cm^3 of sponge/m^2 from 11 species Species richness was similar among the three treatment groups, although some rarer species were found only at a few sites. For example, *Dysidea etheria* was only present at low volume sites and some medium volume sites, whereas *Spongia obscura* was only found at high sponge volume sites.

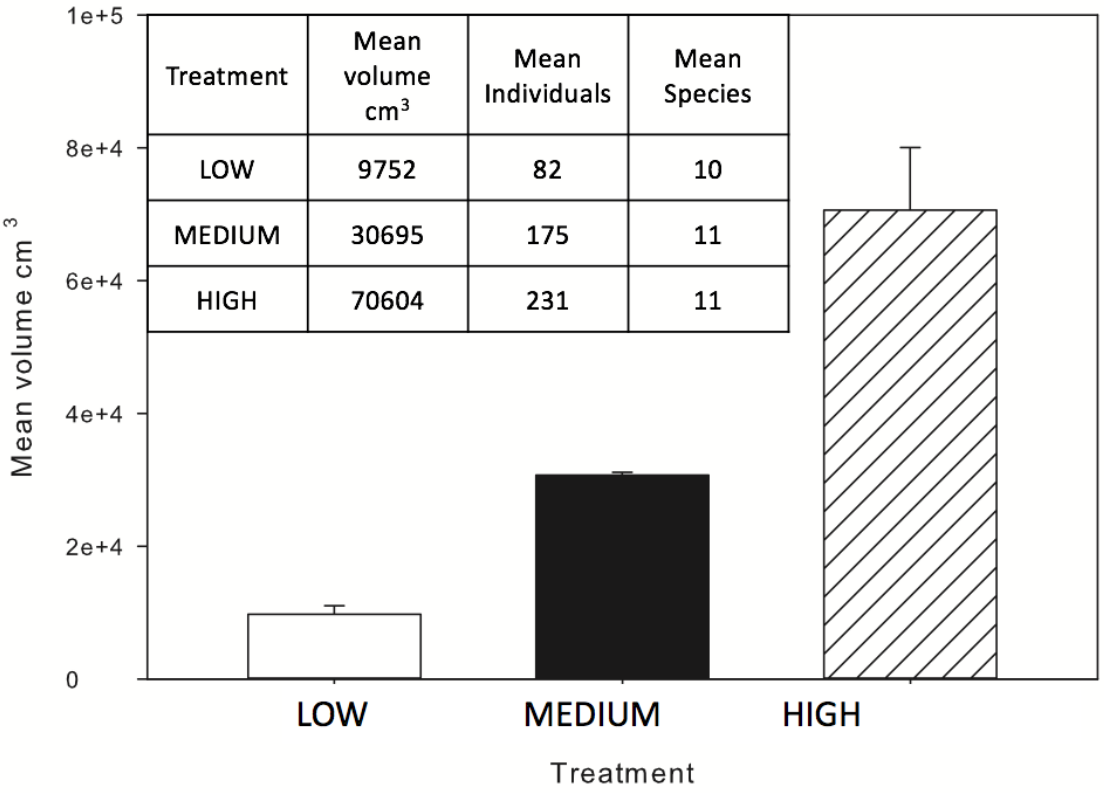


Figure 24. Mean volume of sponges summed across all species for each treatment (error bars represent ± 1 standard deviation). Inset table with mean volume, individuals, and species at each treatment

Sponge Growth

Spongia barbara and *I. campana* were monitored at the medium and high sponge volume sites for 30 months, while *S. graminea* was only monitored for 18 months. At the low sponge volume sites, the three sponges were monitored for only 6 months, a consequence of the aftermath of an algal bloom. In general, all of the deployed sponges increased in volume over the course of this study; however, changes in volume were correlated with season (Figure 25, Table 9). Spring-summer periods were characterized by large proportional increases in total volume, while changes in volume during the autumn and winter were negligible. Over the course of the

two-year study, the pattern of growth for the three species was similar, with higher growth on sites with medium volumes of natural sponges compared to sites with high sponge volumes. *Spongia barbara* increased by 31,958% (N=29) and 9949% (N=37) (respectively) at the medium and high sponge volume treatments; growth for *I. campana* at medium volume sites was 25,726% (N=22) and much less 3357% (N=29) at high sites. After deployment one year into the study, the volume of *S. graminea* increased by 1328% (N=11) and 5057% (N=13) in the high and medium sponge volume treatments, respectively.

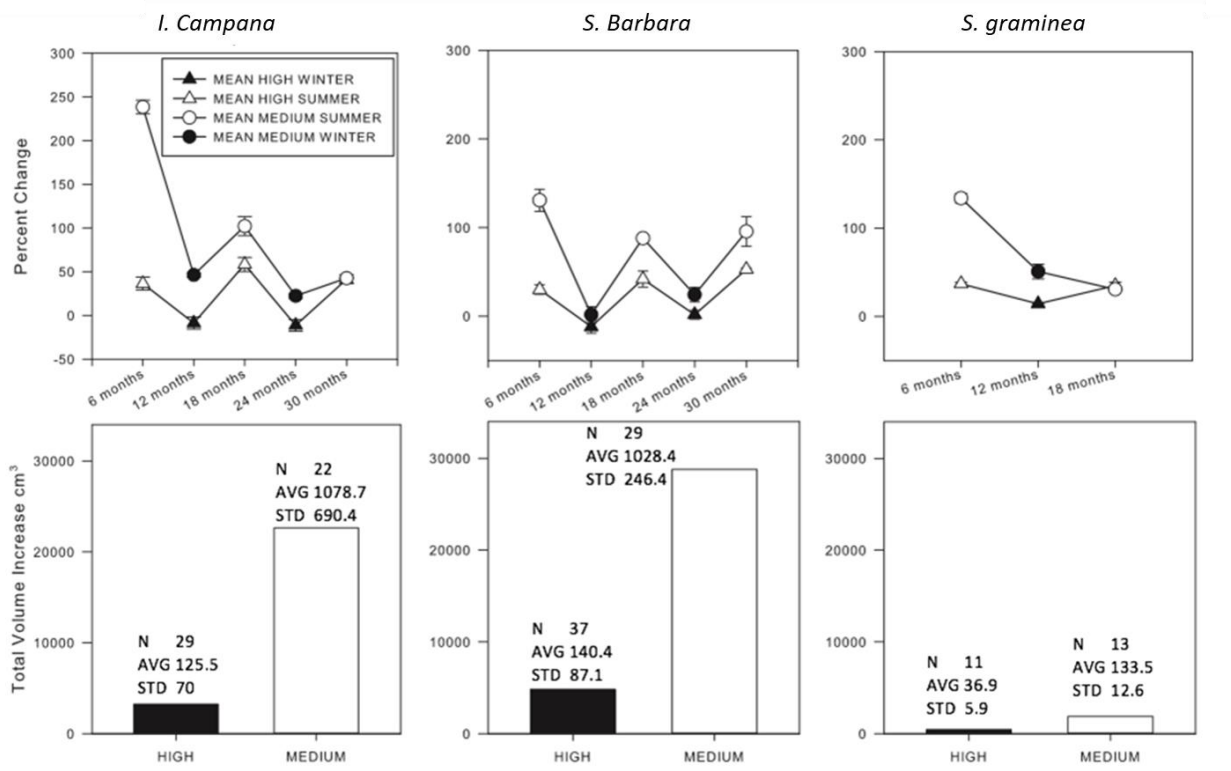


Figure 25. (Top) Mean (± standard deviation) percent change in growth of three sponge species (*I. campana*, *S. barbara*, S. graminea) over the 30-month long monitoring period during summer (open symbols) and winter (filled symbols) when transplanted to sites with high (triangle) and medium (circle) natural sponge densities. (Bottom) Total increase in the volume of all transplanted sponges of three species when moved to high (dark bar) and medium (open bar) density sponge sites. Sample size, mean volume increase, and ± 1 standard deviation for each sponge species over the study period is listed above each histogram

Table 9. Total percent change in volume for all individuals at each survey period in comparison to the previous month. Mean change in volume across each individual at each site is in parentheses

		6	12	18	24	30	Total
I. campana	High	1240.03 (41.33)	-239.54 (-7.98)	1609.24 (55.49)	-220.58 (-8.48)	894.81 (34.42)	5862 (225)
	Medium	4162.28 (215.30)	1113.38 (53.02)	1832.60 (87.27)	534.18 (26.71)	452.76 (22.64)	27196 (1295)
	Low			11039.16 (1103.92)			
S. barbara	High	1205.78 (31.73)	446.85 (-11.76)	1685.56 (44.36)	67.60 (1.78)	2008.82 (52.86)	9949 (261)
	Medium	3772.19 (130.08)	57.13 (1.97)	2553.47 (88.05)	730.61 (25.19)	2806.27 (96.77)	31985 (1102)
	Low			10791.76 (830.14)			
S. graminea	High			2311.60 (88.91)	885.39 (34.05)	844.41 (32.48)	442 (36)
	Medium			1869.42 (133.53)	713.87 (50.99)	427.28 (30.52)	1869 (133)
	Low			3855.24 (275.37)			

Six months after the initial deployment of sponges at treatment sites, changes in *S. barbara* volume were significantly greater ($F = 618.5$, $df=1$, $p<0.0005$) at the medium sponge volume sites than at the high-volume treatment sites; the trend was similar for *I. campana* ($F = 112.6$, $df=1$, $p<0.0005$) (Table 10; Figure 26). Although increases in sponge volume continued to be significantly greater at the medium sponge volume sites for both *S. barbara* ($F = 34.04$, $df=1$, $p<0.0005$) and *I. campana* ($F = 222.541$, $df=1$, $p<0.0005$) during the first winter of the experiment 12 months after deployment, sponge growth slowed dramatically across all species and in some instances, decreased during winter. Measurements made during the second summer period, 18 months after deployment, showed that the rate of increase in sponge growth was markedly less than recorded in the first summer period, but continued to be significantly greater in the medium sponge volume treatment than in the high treatment for *S. barbara* ($F = 206.73$, $df=1$, $p<0.001$) and *I. campana* ($F = 17.73$, $df=1$, $p<0.001$). Change in volume during the second winter period after 24 months was again negligible. At the high-volume sites, the volume of sponges decreased rather than increased; however, at the medium sponge volume sites there was a small, but significant increase in volume for *S. barbara* ($F = 132.73$, $df=1$, $p<0.001$) and *I. campana* ($F = 57.87$, $df=1$, $p<0.001$). After 30 months, growth of *I. campana* was similar in the two treatments ($F = 3.10$, $df=1$, $p=0.085$), but again significantly greater at medium sponge volume sites for *S. barbara* ($F = 132.63$, $df=1$, $p<0.001$). In summary, growth of both species was initially high, but tapered off during the course of the study, particularly during winter. However, growth rates were always higher in the medium sponge volume treatment compared to the high-volume treatment, with only one exception (*I. campana* at 30 months). Twelve months after initial deployment, a third sponge species, *S. graminea,* was added to the experiment and its patterns of growth were the same as the other species: growth was always significantly greater at

the medium sponge volume sites after six months (F = 546.96, df=1, p<0.001), twelve months (F = 130.54, df=1, p<0.001), and 18 months (F = 5.67, df=1, p=0.025).

Table 10. ANOVA results for biomass treatment (high, medium, and low) and six treatment sites for initial experiment for three selected species

Biomass		Sum of Squares	df	Mean Square	F	Sig.
I. campana	six	328771.072	1	328771.072	112.642	<0.001
	twelve	44670.448	1	44670.448	200.729	<0.001
	eighteen	10604.230	1	10604.230	17.731	<0.001
	twentyfour	14000.839	1	14000.839	57.874	<0.001
	thirty	1247.545	1	1247.545	3.102	0.085
S. barbara	six	159076.426	1	159076.426	618.598	<0.001
	twelve	3100.304	1	3100.304	34.044	<0.001
	eighteen	31401.323	1	31401.323	206.734	<0.001
	twentyfour	9017.185	1	9017.185	132.738	<0.001
	thirty	31704.680	1	31704.680	132.635	<0.001
S. graminea	six	60398.152	1	60398.152	546.968	<0.001
	twelve	8702.138	1	8702.138	130.547	<0.001
	eighteen	116.201	1	116.201	5.674	0.025
Site						
I. campana	six	434822.976	5	86964.595	155.486	<0.001
	twelve	48332.073	5	9666.415	63.074	<0.001
	eighteen	26346.203	5	5269.241	19.936	<0.001
	twentyfour	17566.370	5	3513.274	19.852	<0.001
	thirty	15910.228	5	3182.046	41.985	<0.001
S. barbara	six	164612.761	5	32922.552	179.650	<0.001
	twelve	7029.204	5	1405.841	43.084	<0.001
	eighteen	34559.675	5	6911.935	62.792	<0.001
	twentyfour	11899.404	5	2379.881	94.675	<0.001
	thirty	39858.912	5	7971.782	65.863	<0.001
S. graminea	six	60856.128	5	12171.226	111.042	<0.001
	twelve	9753.031	5	1950.606	71.071	<0.001
	eighteen	296.478	5	59.296	3.810	0.014

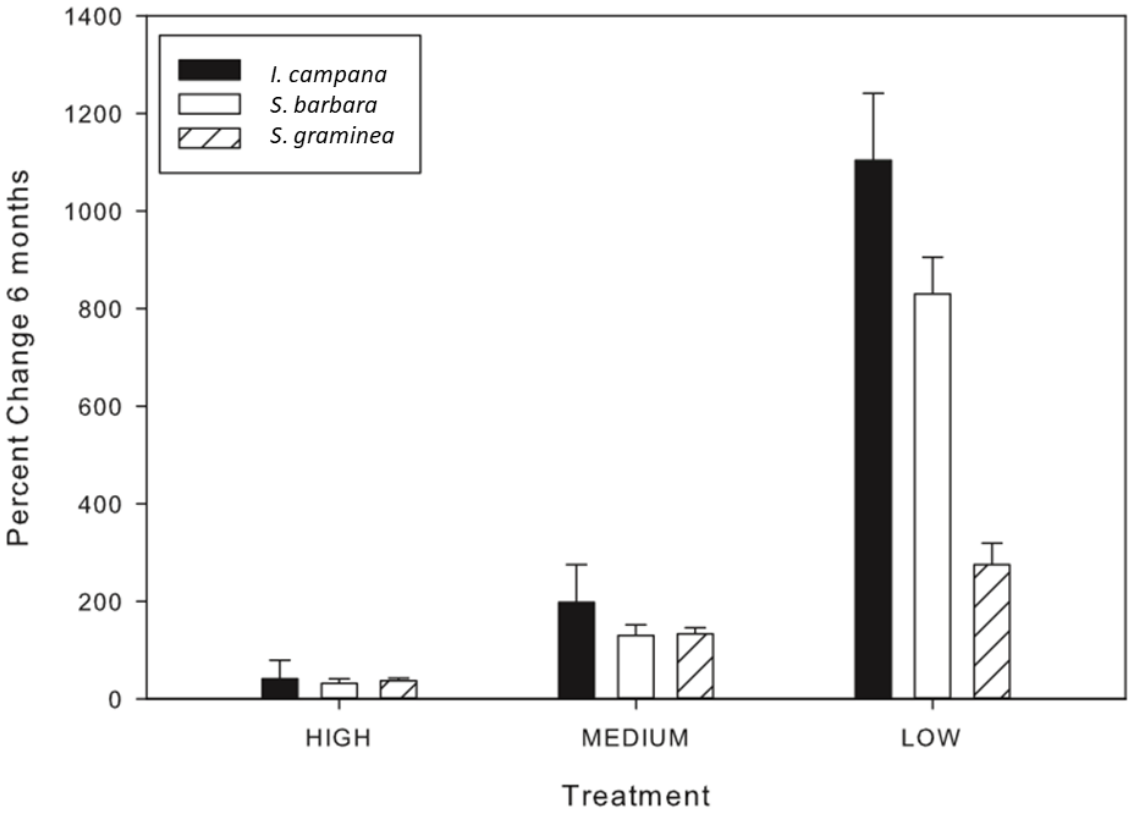


Figure 26. Percent change in the growth of three sponge species (*I. campana, S. barbara, S. graminea*) six months after transplantation onto sites with high, medium, and low natural sponge density

A third treatment (low sponge volume) was established with the three selected species 12 months after the start of the experiment. When compared with the initial six months of growth at the high and medium sponge volume treatments, growth was significantly greater for *S. barbara* ($F = 2717.73$, $df=2$, $p=0.025$) and *I. campana* ($F = 5.67$, $df=2$, $p<0.025$) at the low sponge abundance sites. A second comparison, which now included the three treatments, during the same time period showed that change in volume was significantly greater at the low sponge volume sites for *S. barbara* ($F = 2965.79$, $df=2$, $p<0.025$), *I. campana* ($F = 1025.68$, $df=2$,

p<0.025), and *S. graminea* (F = 232.75, df=2, p<0.001), indicating a consistent decrease in sponge growth along a gradient of increasing natural sponge abundance.

Water Column Characteristics

One-factor ANOVA analyses revealed that concentrations of picoeukaryotes (p=0.044), *Synechococcus* (p<0.001), HNA bacteria (p<0.001), LNA bacteria (p=0.001), and concentrations of total plankton in the water column (p<0.001) were all significantly greater at low sponge volume treatment sites than at the medium and high sponge volume sites (Figure 27). No significant differences among treatments were detected for prokaryotes (p=0.721) and viruses (p=0.916). POC and particulate organic nitrogen (PON) were significantly greater (p<0.0005) at low sponge volume sites than at high and medium sponge volume sites, consistent with increasing nutrient uptake along a gradient of increasing sponge volume. Results were less clear with respect to other water column constituents. Total phosphate, POC, and PON differed significantly among treatments (p=0.015, 0.001, and 0.043; respectively). Concentration of phosphate was similarly lower at the high and medium sites than at the low sites.

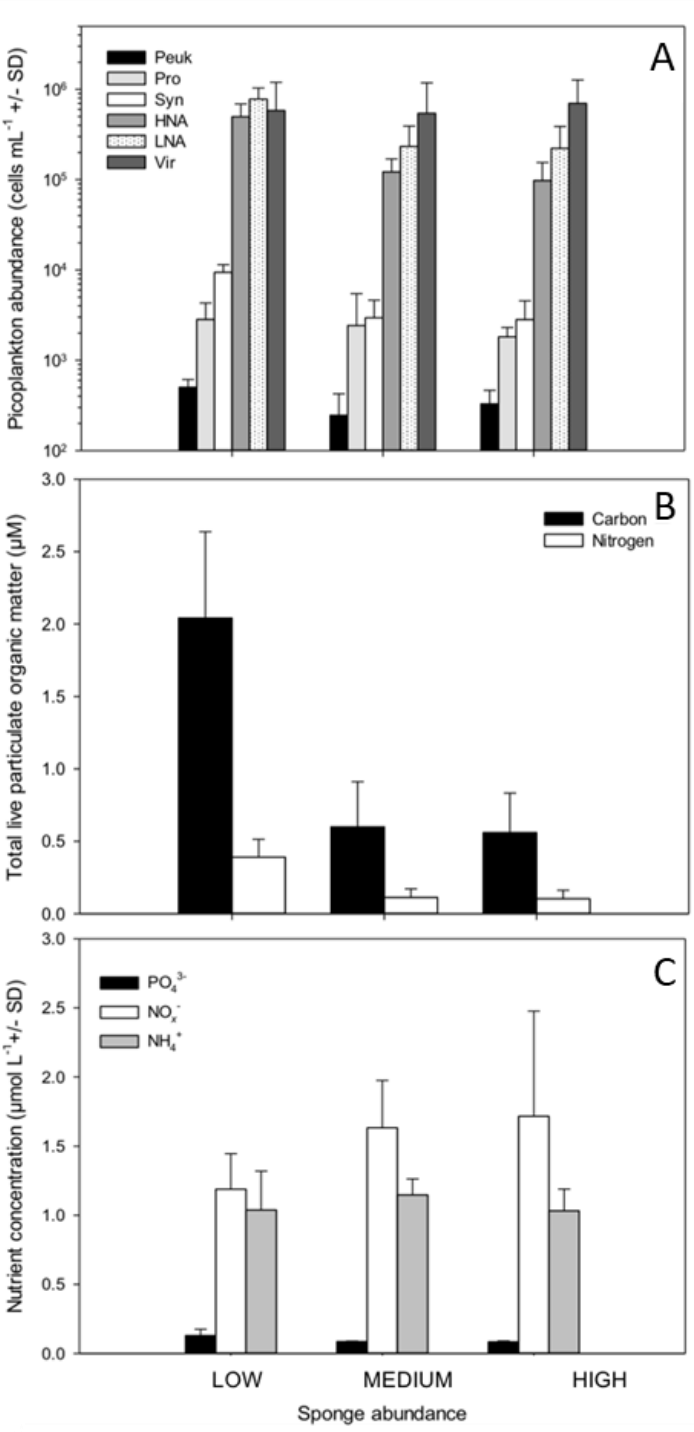


Figure 27. (A) Mean abundance (± sd) of picoplankton in seawater over sites of varying sponge density (low, medium, high). Peuk = picoeukaryotes, Syn = *Synechococcus*, Pro = *Prochlorococcus*, HNA = high nucleic acid bacteria, LNA = low nucleic acid bacteria, and Vir = viruses, (B) mean concentration (± sd) of total ambient particulate organic matter in seawater over sites of varying sponge density in Florida Bay (C) mean concentration (± sd) of PO_4^{3-}, NO_x^-, and NH_4^+

Discussion

Competition is greatest among closely related species with overlapping resource requirements, especially when those resources are limited (e.g. Branch 1975; Perea-Blazquez et al. 2013), a condition that my research shows applies to sponges in the shallow, tropical waters of the Florida Keys. Different sponge species feed on similarly sized particles (Reiswig 1971; Valentine & Butler 2018), thus creating the possibility of resource depletion among dietarily similar sponge species and density-dependent competition where planktonic food resources are limited (e.g. in oligotrophic water with slow water column turnover). In this study, I found a negative relationship between the volume of sponges in natural sponge assemblages and water column planktonic resources within the same areas, and I further documented an inverse relationship between the growth of transplanted sponges and the volume of sponges in natural communities. When moved from dense sponge assemblages into areas with less dense assemblages, all three species of sponges I transplanted exhibited a similarly rapid acceleration in growth, which fluctuated seasonally but still differed by orders of magnitude among areas of low, medium, and high sponge abundance. However, patterns of sponge mortality were idiosyncratic across treatments and were not dependent upon the abundance (volume) of natural sponges at each site.

These results suggest that planktonic and water chemistry conditions in the shallow, back-reef hard-bottom environments of the Florida Keys are strongly influenced by sponge abundance, which in turn indirectly affects individual sponge growth via exploitative competition for limited planktonic resources. I found that sponge growth, at least for the three species included in this study, was highly variable seasonally and those differences seemed best

explained by variability in the concentration of planktonic food resources. Sponge growth increased during warmer months and decreased or was stagnant during winter. Summer months were characterized by increased water column productivity, providing more planktonic food for sponge consumption (Richardson et al. 2003). Decreases in sponge growth in winter were likely the result of lower food availability and sloughing of the outer pinacoderm, a well-documented winter phenomenon (Alexander et al. 2015).

Because cyanobacteria are a common food source for sponges (Lynch & Phlips 2000; Peterson et al. 2006), unprecedented rates of growth at low sponge abundance sites were driven both by the absence of sponges and the sudden increased food availability during the developing HAB. Beginning in October 2016 and continuing through February 2017, a cyanobacteria bloom persisted in the Everglades National Park and spread south through Florida Bay with peak chl *a* concentrations ranging from 50 to 60 µg/L (SFNRC. 2017). Interestingly, the strong growth recorded in the low sites occurred at the same time as an increase in chl *a*, indicating growing cyanobacteria blooms in the region. The cyanobacteria bloom was densest and spread more extensively over the three low volume sites than the other sites for a period of three months (Oct-Dec 2016). During the initial six-months of this treatment, the cyanobacteria bloom was minimal and centered in nearby embayments; however, there was likely tidal exchange and flushing that led to elevated levels of cyanobacteria at the low volume sites.

The effect of sponge volume on water column constituents was pronounced across my treatments. Overall, concentrations of picoplankton, bacteria, and POC were lower where natural sponge volume was higher, indicative of greater water column depletion. However, the similarity between the medium- and high-sponge volume treatment sites indicates that even when at moderate densities, sponge assemblages can deplete picoplankton abundance sufficiently to

trigger exploitative competition among sponges, and perhaps for other unstudied suspension feeders in the system as well (e.g. bivalves). Indeed, similar scenarios of planktonic resource depletion leading to exploitative competition have been reported in shallow, bivalve-dominated coastal systems (Newell, 2004; Grizzle et al. 2006).

Clearly, water column depletion of POM and DOM can only occur if those resources are cleared faster than they can be replaced either by tidal exchange or autochtonous primary production (Cranford et al. 2008). Shallow, oligotrophic waters with little tidal exchange offer ideal conditions for such a phenomenon - circumstances largely met by the environmental and oceanographic conditions in the waters surrounding the Florida Keys (Lee et al. 2016; Butler et al. 2018). Yet, such depletion is undoubtedly spatio-temporally variable and affected not only by suspension feeder abundance but also by other factors such as feeding behavior, benthic habitat type, season, and tidal cycle. Identifying those independent influences on sestonic water column characteristics requires more intensive sampling than my study provided (Strohmeier et al. 2005; Grant et al. 2008). Indeed, the time required for sampling water masses over a large spatial scale can be longer than the persistence of the effect, given rapid resource renewal (Grant et al. 2008). For example, it is reasonable to expect that the measurable effect of a patch of suspension feeders on water column constituents would diminish during periods of high tidal flow that rapidly replenish waterborne resources. Yet even those predictions are complicated by non-linear relationships between abundance and rates of filter feeding, as has been documented in some sponges that increase filtration at higher plankton concentrations (Archer et al. 2017; McMurray et al. 2017). Several studies have found that flow velocity and direction affect the growth of sessile species (Lohse 2002; Palardy & Witman 2014; Svensson & Marshall 2015) and that biomass of suspension-feeding populations scales with current direction to offset depletion. My

water sampling above sponge assemblages was purposefully conducted during slack tide to ascertain whether any effect of sponge filtration was obvious under 'ideal' conditions, and because I had insufficient fiscal resources for a more synoptic sampling regime. Yet, the remarkable differences in the growth of sponge transplants on those same sites provide strong evidence of persistent patterns in water column depletion with increasing natural sponge abundance.

The mesocosm studies that I conducted (described in chapters 2 and 3) in which I manipulated sponge biomass and diversity showed differential use of nutrients and uptake of planktonic bacteria by different sponge species and combinations of species (Valentine & Butler 2018*)*. In those trials, relatively high sponge biomass greatly reduced chlorophyll *a,* ammonium, and dissolved organic carbon in the water and increased concentrations of nitrites, nitrates, and phosphates in comparison to low biomass treatments. Those studies also revealed that sponge species identity had differential effects on water column constituents. Thus, both the biomass and diversity of sponges in coastal ecosystems can drastically alter water column properties in complex ways.

Although competition for planktonic resources may help shape the structure of sponge assemblages in back-reef lagoonal habitats, just as predation and competition for space does on reefs, disturbance too can play a role in community assembly (Sousa 1979). Epizootics have periodically decimated sponges in the Mediterranean and Caribbean, as have cyanobacteria blooms in Florida (Butler et al. 1995; Berry et al. 2015; Blakey et al. 2015), essentially 'wiping the community slate ‘clean' by killing nearly all sponges present in a region. Recovery of sponge assemblages takes decades and tends to follow a successional sequence that begins with small, rapidly colonizing 'weedy' species and culminates with a speciose community replete with large,

late successional species (Stevely et al. 2010; 2011). My findings suggest that the reestablishment of those communities may be enhanced by the release from exploitative competition for planktonic resources that occurs following a mass sponge die-off. In fact, I have observed that early colonizing sponge species (e.g. *Tedania ignis*) in sponge die-off areas are typically much larger than their counterparts in sponge-rich areas, suggesting that they too have been released from food competition. The artisanal sponge fishery of the Florida Keys (Butler et al. 2018) can be viewed similarly in that the culling of large, commercial sponges from the community could increase ambient food availability for the remaining sponges and thus increase their growth.

Although a growing body of evidence suggests that competition for food among sponges occurs in some environments with dramatic consequences on their population structure (Reed & Pomponi 1997; Lesser 2006; Lesser & Slattery 2013), on rocky and coral reefs the mechanisms organizing sponge assemblages are predominantly attributed to space availability and the presence of spongivores rather than food depletion (Wulff 1997; Dayton 1971; Hill 1998; Svensson & Marshall 2015; Pawlik et al. 2018). In the shallow, coastal ecosystem where my study was conducted, water residence time is longer than on nearby coral reefs, spongivores are largely absent, and environmental conditions more variable. Thus, sponge fitness in this back-reef system is likely influenced less by predation and space availability than food resource availability and fluctuating environmental conditions (Butler et al. 2018). I am not suggesting that competition for food or space, avoidance of predation, or resilience to environmental conditions are mutually exclusive mechanisms, but their relative importance in driving sponge community structure appears to differ among habitats.

In summary, this study demonstrated how sponge populations in shallow, tropical waters can deplete planktonic resources and, in turn, were affected by density-dependent competition for food. I provide strong experimental evidence that competition for planktonic food resources limits the growth and presumably fitness (through reproductive output) of these shallow, tropical sponge species. Thus, there appears to be a cost to individuals living in or recruiting into dense groups. My results for back-reef, hard-bottom habitats contrast with the prevailing paradigm that competition for space, along with predation and its associated cost of anti-predator chemical defenses, limits sponge populations on coral reefs.

CHAPTER 5

CONCLUSIONS

Biological diversity at the organizational levels of species, functional groups, and genomes is widely hypothesized to support a diverse array of ecosystem processes and services on both local and global scales (Naeem et al. 2012). As anthropogenic perturbations continue to degrade the health of marine ecosystems, losses of biological diversity have reached unprecedented rates (Worm et al. 2006). As both biological and functional diversity in ecosystems are lost, so too are integral processes and functions that determine primary and secondary production, along with biogeochemical cycling (Bracken et al. 2008). Thus, understanding the effects of, and developing the new tools to evaluate these changes in ecosystem constituents is of critical importance.

Importantly, most of what we know about the relationship between biodiversity and ecosystem function is derived from studies conducted in terrestrial ecosystems (Naeem et al. 2012). Because of the enormous logistical challenges associated with conducting such studies in the submerged realm, the diversity-ecosystem function relationship has been drastically understudied in marine ecosystems. In this dissertation I sought to evaluate the efficacy of this emerging ecological paradigm to predict the effects of the basin-wide losses of sponges on water column structure and productivity. To do this, I conducted a series of studies designed to examine the effects and interactions of biological and functional diversity of marine sponges at multiple levels in the nearshore coastal ecosystems of the Florida Keys, Florida (USA).

In the Florida Keys, shallow hard-bottom habitats were occupied historically by diverse and abundant assemblage of large sponges. These sponges presumably served as foundation

species for ecosystem health via the strength of their roles in benthic-pelagic coupling, biogeochemical cycling, and habitat provisioning (Butler et al. 1995). Due to environmental fluctuations, harmful algal blooms, and other anthropogenic disturbances (e.g. commercial harvesting of sponges) their once great abundances and diversity have been diminished (Stevely et al. 2011). To date, scientists have understudied the consequences of declining sponge biocomplexity for ecosystem structure and function. Although many sponge populations have been decimated, recovery efforts and natural replenishment efforts are attempting to restore some semblance of what once normal populations were. However, these restored populations are also under constant threat of mortality due to a multitude of stressors, including recurrent cyanobacteria blooms, temperature extremes (presumably due to climate change), and variable salinity caused by the poor management of freshwater 'upstream' in the Everglades (Butler et al. 1995; Stevely et al. 2011; Kearney et al. 2015).

The first of my studies simulated the effects of sponge species identity at varying levels of density across a realistic range of flows on ecosystem process (i.e. nutrient cycling) and structure (planktonic community structure). This was a novel study, because the findings of previous work relied on extrapolations from measurements of individual sponges to estimate ecosystem effects, and they largely ignored hydrodynamic forces such as current rate. The historical approach also assumed that sponge effects on the water column and associated ecosystem processes are simply additive, ignoring the potential interactive effects of multiple individuals or species on ecosystem properties (Bell 2008). The results of my experiments showed that dense aggregations of sponges, particularly in areas where hydrodynamic effects are less dynamic, can have significant effects on nutrient concentration and planktonic composition. The results of this study highlight how changes in the abundance and diversity of sponges in

coastal ecosystems can drastically alter a number of water column properties but that these effects are context specific. For example, each species interacts differently with each water column property under each treatment condition.

I demonstrated in Chapter 2 that the effects of sponges on ecosystem functions and processes can vary greatly among sponge taxa. Put simply, species identity matters. Moreover, my results highlight the important biogeochemical function of sponges and illustrate how the dramatic reductions in sponge abundance and their diversity diminished these functions. As with my first study, what can be predicted about the effects of sponges on the water column is probably context-dependent and varies according to local conditions. Based on these results demonstrating the unique effects of individuals examined in monoculture, Chapter 3 was developed to explore how these ecosystem processes and functions would be affected by mixtures of species.

Historically, sponges did not occur in low-density monocultures; they were once ubiquitous throughout Florida Bay and found in dense, diverse assemblages (Stevely et al. 2011). Thus, exploring how species once interacted in complex groupings is fundamental to grasping how ecosystems have been transformed when species composition is altered by both natural and anthropogenic perturbations. Results of Chapter 3 revealed that species and functional diversity had an additive, but asymptotic relationship with ecosystem processes and functions.

The results reported in Chapter 2, in conjunction with those found in Chapter 3, showed that sponge degradation alters the essential ecosystem process of nutrient cycling by structuring planktonic communities. Sponges, regardless of species identity or functional groups, play an important role in mediating the nitrification and nitrogen oxidation cycling, as well as the state conversions between dissolved and particulate organic carbon in the shallow waters surrounding

the Florida Keys. Yet, there is a discrepancy between additions to cumulative biomass and diversity on the amplitude of ecosystem effects. The results of Chapters 2 and 3 indicate that some emergent effect (i.e. competition, facilitation, mutualism) or functional redundancy prevents sponge assemblages from being truly additive.

Recovery of sponges takes decades and follows a successional sequence that starts with the establishment of small, rapidly colonizing species and ultimately culminates in a diverse community replete with large, climax species (Stevely et al. 2010; 2011). My findings in Chapter 4 suggest that the reestablishment of those communities may be determined by the intensity of interspecific, exploitative competition for water column resources they experience if recruitment occurs into existing sponge assemblages.

Intra- and interspecific competition for food and nutrients reduces the growth and survival of many marine organisms, (Branch 1975), so I hypothesized that at high density, interspecific competition among sponges in diverse assemblages could suppress individual fitness via reductions in growth. I therefore designed an experiment assessing the effects of local density and genotype on individual growth in three sponge species. The magnitude of growth of experimental sponges in low-density populations was astronomical in comparison to sponge growth in densely aggregated areas. Water column constituents composed of picoeukaryotes, *Synechococcus*, *Prochlorococcus,* bacteria, and viruses were also depleted in larger quantities in areas with dense aggregations. The results of this study showed that remaining patches of sponges with high densities deplete water column constituents, and this finding is correlated spatially with lower growth rates of sponges transplanted into the high-density sites.

Chapter 4 focused on my experimental assessment of the extent to which sponges in shallow ecosystems can deplete planktonic resources in realistic field conditions and, if so, I

sought to determine if there was evidence that this hypothesized depletion could affect the growth of sponges. In a number of ways, this field experiment validated the findings of the two mesocosms reported on above. The results of these robust experiments provided evidence supporting my supposition that sponge assemblages are controlled by competition for planktonic food resources, which limits new sponge growth depending on the intensity of sponge competition. Hence, it is possible that dense concentrations of sponges reduce fitness of new recruits because growth is often considered a good proxy for fitness. As such, it is likely that while ecosystem effects (as demonstrated in Chapters 2 and 3) increased with increasing assemblage density and diversity, there is a negative cost for individuals living or recruiting into areas with higher densities of sponges.

Discovering the patterns that exist in sponges and their function under changing environmental conditions is useful for marine spatial planning, the prediction of future effects of climate change and habitat alteration, the identification of potential sites for conservation and protection, and the potential for mitigating ecosystem-wide impacts through restoration (McPherson & Jetz 2007; Rouse et al. 2014). My work makes clear the implications of a reduction in the natural density and diversity of sponges in terms of significant alterations in the ecosystem's natural biogeochemical cycles and benthic-pelagic linkages (Peterson et al. 2006). This is especially important because most restoration efforts have largely ignored the uses of diverse communities, instead focusing on the restoration of habitat structure provided by one or a few dominant species. But the management of sponge populations and the restoration of sponges after perturbations should consider the implications of species-dependent ecosystem effects and focus on those combinations of species most useful to ecosystem processes and functions, as well as those species most resilient to HABs.

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