Incorporation of Species Interactions in

Seagrass Conservation and Restoration

by

Yin San Stacy Zhang

Marine Science and Conservation
Duke University

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Dean L. Urban

Dissertation submitted in partial fulfillment of
the requirements for the degree of
Doctor of Philosophy
in the Division of Marine Science and Conservation
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ABSTRACT

Coastal ecosystems and the valuable services they provide have and continue to be degraded by anthropogenic stressors across the globe. Conservation efforts to mitigate deleterious impacts have largely failed at aiding ecosystem recovery such that restoration has become a predominant approach to stem the loss of critical habitats and the communities they support. Globally, it is estimated that 29% of seagrass beds have been lost or converted. In this dissertation, I evaluate how ecological interactions can shift seagrass community dynamics and alter restoration trajectories. Namely, I focus on how facilitative and trophic interactions among seagrasses, bivalves, and their associated nekton and mesograzer communities propagate through seagrass ecosystems. To do this, I employ a combination of scientific literature review, surveys, and manipulative field experiments to test ecological theories of species interactions in seagrass restoration and conservation.

Systematic reviews of current coastal restoration research reveal a paucity of studies that consider biological interactions as important factors that may determine restoration success and a critical lack of emphasis on- and communication of knowledge across restoration sectors and geographies (Chapter 1). Because restoration of foundation species, such as seagrasses, can promote the success and survival of numerous other organisms through facilitation, I further tested if and how a density-dependent facilitation cascade among seagrasses and pen clams, *Atrina rigida*, may affect biodiversity and ecosystem functions (Chapter 2). In this instance, I found that seagrasses promote the survival of pen clams that then act as secondary foundation species that locally enhance

species richness and abundance. Since studies have, in fact, shown that positive interactions can also enhance the restoration of coastal foundation species, I investigated how the inclusion of intra- and interspecific facilitation can affect seagrass restoration from seed and adult shoots (Chapter 3). I find that interspecific facilitation from hard clams can greatly enhance the growth and restoration of seagrasses from seed, and in contrast, intraspecific facilitation that capitalizes on density-dependence in planting configurations, rather than the addition of bivalves, is the predominant promoter of seagrass resilience in restoration with adult shoots. Finally, given that top-down influences can also affect the restoration of declining bivalve stocks and seagrass resilience, I explored how large predator removals (via exclusion stockades) may shift seagrass community structure and propagate onto primary producers. Exclusion of large predators was associated with greater mesopredator and scallop abundance, but we did not find direct evidence that large-predators exerted indirect influences on seagrasses over the duration of our experiment.

The research findings presented in this dissertation demonstrate the pervasive and critical role that species interactions, direct and indirect, trophic and facilitative, play in structuring seagrass ecosystems. Facilitative interactions can promote not only the settlement and survivorship of bivalve populations, but that in some instances, bivalves can, in turn, facilitate the growth of seagrasses. Similarly, alteration to diversity and species dominance at higher trophic levels can have evident top-down impacts on bivalve and mesopredator populations. Whereas biological interactions have historically been understudied in the ecological restoration literature, my dissertation research makes the argument that consideration and incorporation of species interactions is necessary for

understanding the ecology that underlies the stability, recovery, and resilience of coastal

ecosystems.

DEDICATION

For my siblings—Nancy, Lucy, and Justin.

Thank you for always encouraging me to pursue my dreams, travel,

and live a full life.

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I am deeply thankful and grateful to the many people who have supported and assisted me throughout my graduate career and doctoral research. I could not have accomplished this feat without the assistance and feedback from my graduate advisor, committee members, collaborators, friends, and family. You have all taught me how pervasive and critical positive interactions truly are.

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INTRODUCTION

A primary goal of ecology is to understand how physical and biological factors regulate ecological communities. Early studies identified physical forces as primary controls of species distributions. Later experimental and observational work found biotic interactions, with a heavy focus on negative interactions such as competition and predation, could also play a strong role in determining species distributions and diversity (MacArthur 1958, Hutchinson 1959). For instance, early studies on biotic interactions demonstrated that predators and dominant space competitors controlled species diversity and ecosystem productivity (e.g. seastars and barnacles in the rocky intertidal as demonstrated in Connell (1961), Paine (1980)). Since then, indirect (trophic cascades) and direct impacts of predation have been well-documented across a diverse set of ecosystems including kelp communities (Estes et al. 1998), temperate salt marshes (Silliman et al. 2005), temperate forests (Paine et al. 1997), African savannahs (Dublin et al. 1990), and mangrove forests (McKee et al. 2002).

Within the last few decades, ecological studies have also revealed the importance of positive species interactions on community structure. Positive species interactions, where species benefit rather than harm one another (e.g. mutualisms, facilitations, and facilitation cascades), were noted in the early ecological literature (Clements 1916, Gause and Witt 1935) but generally viewed as unimportant in regulating ecosystems (Tilman 1982, Menge and Sutherland 1987). This belief persisted until the 1990s when experimental work began to show that positive interactions were key drivers of species

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diversity patterns. For example, work in intertidal systems found that intraspecific facilitation allows mussels to expand their range limitations and live higher in the rocky intertidal by reducing mortality from winter ice and crab predators (Bertness and Grosholz 1985). Similarly, interspecific facilitation between marsh grasses allows salt marsh plants to extend their distribution to lower intertidal habitats by sharing oxygen in the root layer (Bertness and Hacker 1994, Hacker and Bertness 1995).

Trophic facilitation, in contrast, occurs when a species is indirectly and positively impacted via the feeding activities of another. In trophic cascades, predators can indirectly promote the diversity and productivity of primary producers by feeding on primary consumers. Trophic cascades have been demonstrated across a variety of aquatic, terrestrial, and marine systems such as in the case of wolves on vegetation in Yellowstone National Park (Fortin et al. 2005), and otters in kelp forests. Another example of trophic facilitation occurs when consumers facilitate species that are otherwise competitively inferior. For instance, herbivores that feed on competitive macroalgae in coral reefs can facilitate coral growth (Hay 1984, Burkepile and Hay 2008), and epiphytic algae grazers can facilitate seagrass productivity (van Montfrans et al. 1984, Moksnes et al. 2008, Hughes et al. 2013).

In addition to positive interactions by foundation species (*sense* Dayton 1972) and trophic cascades, facilitation cascades have recently been found to be critical in promoting species abundance and diversity within ecological communities. Facilitation cascades, where a habitat-forming, or foundational species colonizes an area and then facilitates a secondary foundation species in a hierarchical manner, lead to enhanced structural

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complexity, multifunctionality, stress amelioration and biodiversity (Altieri et al. 2007, Angelini et al. 2015). Facilitation cascades have been demonstrated in cordgrass-mussel (Altieri et al. 2007, Angelini et al. 2015), tropical forest-epiphyte (Cruz-Angón and Greenberg 2005), mangrove-oyster (Bishop et al. 2012) and epibenthic invertebrate communities (Yakovis et al. 2008). While there is increasing awareness, from both theoretical and applied perspectives that positive interactions are key for regulating communities, most research on positive species interactions has been conducted in terrestrial and intertidal systems. Much less work has focused on subtidal marine systems and how positive interactions might shape these ecosystems.

Positive interactions in seagrass and bivalve ecosystems

In shallow subtidal areas around the world, seagrasses are among the most important foundation species (Bahr and Lanier 1981, Short et al. 2007). Seagrass beds provide habitat for many marine organisms as well as multiple ecosystem services including wave attenuation, carbon storage, sediment stabilization, and nutrient filtration, among others (Orth et al. 2006, Barbier et al. 2011). Over the past 50 years, seagrass research has followed the arc of ecological history and found physical factors (Lee et al. 2007 and references therein) and negative species interactions to be important determinants of seagrass distribution and productivity (McGlathery 1995, Valentine and Heck 1999). Although positive interactions have been shown to impact and benefit seagrasses, less work has examined how facilitation and mutualisms shape seagrass ecosystems.

The most conspicuous co-occurring organisms in seagrass beds are often bivalves. Within seagrass beds, bivalves occur both as randomly dispersed individuals and in small

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aggregations. Similarly to mussels in salt marshes (Angelini et al. 2016), infaunal bivalves may act as secondary foundation species in seagrasses by increasing local diversity, enhancing nutrient transfer from the water column to the sediment, and increasing seagrass productivity. For example, positive interactions between sulfur-oxidizing clams and seagrasses have been shown to enhance seagrass biomass while also providing refuge for clams (van der Heide et al. 2012). Similarly, where reef-building bivalves grow adjacent to seagrass beds, research has shown enhanced water quality (Newell and Koch 2004) and reduced wave stress that could otherwise uproot seagrasses (Scyphers et al. 2011).

Early observational studies have suggested a facilitation cascade exists between bivalves and seagrasses. Compared to sandflats and unvegetated areas, bivalves have been shown to grow faster, occur in greater densities (Peterson et al. 1984) and experience reduced mortality rates in seagrass habitats (Peterson and Heck Jr, 2001a). Similarly, in the presence of mussel aggregations, tropical seagrasses showed enhanced growth rates, lower epiphyte loads, and reduced C:N:P ratios in seagrass leaf tissues (Peterson and Heck Jr. 2001b). Bivalves that colonize within seagrass beds have further been shown to enhance species abundances locally (Kuhlmann 1998). However, the commonality of this effect remains unclear. Whether bivalves in seagrass beds constitute a facilitation cascade that enhance ecosystem functions such as primary productivity, nutrient transfer and retention, and biodiversity, remains a significant knowledge gap.

Trophic interactions in seagrass conservation

Trophic cascades are predator-driven indirect effects on two or more lower trophic levels that have been shown to regulate numerous ecosystems (Hairston et al. 1960, Paine

1980, Menge 1995). Shifts in predator abundance can propagate through food webs and drastically alter population dynamics and the dominance of species interactions in ways that can alter whole ecosystem biodiversity and vegetation (Sih et al. 1985, Menge 1995, Jackson et al. 2001, Burkholder et al. 2007, Estes et al. 2011). Once released from predation, prey populations, particularly of grazers, can overconsume foundation-forming primary producers and induce shifts to alternative stable states (Carpenter et al. 1985, Terborgh et al. 2001, Silliman and Bertness 2002).

Numerous examples of trophic cascades in seagrass beds have focused on what is known as the Mutualistic Mesograzer Model (MMM). In the MMM, large predators consume smaller mesopredators that feed upon algal grazers that consume algae that can otherwise compete with seagrasses for resources and space (Moksnes et al. 2008). Large predators thus indirectly facilitate the presence of seagrasses by promoting the presence of algal grazers. Recent studies have also demonstrated that sea otters can enhancing seagrass bed expansion and resilience, in a path that similarly follows the MMM. Otters (top predators) were shown to promote seagrass growth by reducing the number of crabs (small predators) that would otherwise feed upon algal grazers that can shift competitive dominance in a eutrophic estuary to seagrasses over macroalgae (Hughes et al. 2013).

Another example of a trophic cascade in seagrass beds is from Myers et al. (2007) that used historical data to infer a trophic cascade induced by large, apex, predatory sharks on seagrass communities of the western Atlantic. Myers hypothesized that the loss of apex sharks led to a dramatic increase in smaller elasmobranchs, namely cow nose rays, *Rhinoptera bonasus*, that then overconsumed bay scallops, *Argopecten irradians*

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concentricus, causing their populations to crash. Recent studies, however, have challenged Myers et al. (2007) and shown a spatiotemporal disjunction in population shifts across trophic levels and a lack of evidence demonstrating that cownose rays frequently consume bay scallops (Grubbs et al. 2016). Neither study, however, considers how these top-down effects may alter the the primary producer and foundation species critical to this trophic cascade, seagrasses. Given that rays are known to bioturbate and create large bare patches within seagrass beds while foraging for prey, they have the potential to further impact seagrasses in addition to feeding upon bivalves. In light of continual declines in seagrass extent and multiple efforts to restore diminishing bay scallop populations, there is a pressing need to experimentally test this trophic cascade to determine how human interventions to food webs alter seagrass community structure.

Harnessing positive interactions for restoration

While multiple studies have demonstrated the critical role of positive interactions for ecosystem resilience, few have directly tested if positive interactions can be incorporated into restoration practice to promote the establishment and recovery of foundation species. Restoration has traditionally focused on minimizing negative interactions, e.g., competition among transplants; however, recent studies have indicated that inclusion of positive interactions into methodologies could enhance restoration success at multiple spatial scales (Halpern et al. 2007, He et al. 2013, van de Koppel et al. 2014, Silliman et al. 2015). At small spatial scales (i.e., short-distance facilitation), planting seagrasses, marsh cordgrasses and mangroves in aggregate can increase belowground oxygen supplies (Silliman et al. 2005, Huxham et al. 2010) and resilience to wave stress

(Angelini et al. 2011), thus enhancing growth of conspecifics. Across coastal habitats (i.e., long-distance or cross-habitat facilitation) water filtration provided by suspension-feeding bivalves may increase water clarity (Newell and Koch 2004) and reduce epiphyte loads on seagrasses (Peterson and Heck Jr 2001b), thus creating more favorable physical conditions for seagrass growth. Moreover, wave attenuation provided by coastal habitats is not only a highly valuable ecosystem service (Barbier et al. 2008) but can also facilitate the growth and development of neighboring habitats (Barbier et al. 2011).

Unfortunately, a leaky pipeline exists between ecological theories of positive interactions and their application in restoration methodologies despite studies calling for their inclusion (Halpern et al. 2007, Silliman et al. 2015). Despite their proven benefits for ecosystem resilience, there are few studies that directly test how facilitations and mutualisms can be easily incorporated into methodologies to enhance restoration success.

In this dissertation, I examine how species interactions, both positive and negative, indirect and direct, affect the ecology of seagrass beds and their subsequent conservation and restoration. In Chapter 1, I conduct a global meta-analysis to determine what knowledge gaps may exist in coastal restoration research. Specifically, I ask i) how frequent is cross-sector authorship in coastal restoration research; ii) what is the geographic distribution of coastal restoration research; and, iii) are abiotic and biotic factors equally emphasized in the literature and how does this vary with time? I focus on the extent to which managing or considering species interactions is recommended for restoration success in order to demonstrate that the vast majority of restoration is conducted without consideration of biological interactions. In Chapter 2, I use a combination of survey and

experimental tests to determine if a facilitation cascade occurs among eelgrass (*Zostera marina*), pen clams (*Atrina rigida*), and community diversity in temperate seagrass bed in North Carolina, U.S.A., and if this sequence of direct positive interactions created feedbacks that affected various metrics of seagrass ecosystem function and structure. In Chapter 3, I we experimentally tested how both intra- and interspecific positive species interactions can be applied in seagrass restoration by incorporating i) clam additions into seed plantings, and ii) outplanting adult shoots in aggregated versus dispersed layouts with clam additions. Lastly, in Chapter 4, I investigate how large bodied predators (animals over 25 cm in width) may exert top-down controls on seagrass community structure and function. I experimentally manipulated predator presence using exclusion stockades over a two-year period to test for top-down impacts of large predators on biodiversity, bivalve survivorship, and seagrass edge expansion/retraction and cover. I conclude this dissertation with a summary of important findings from the review and experimental studies and provide a discussion of how facilitation and trophic cascades may regulate seagrass ecosystem stability and ways in which biotic interactions can be harnessed in the management and restoration of these critical ecosystems.

CHAPTER 1. A GLOBAL SYNTHESIS REVEALS GAPS IN COASTAL HABITAT RESTORATION RESEARCH

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1.1 Introduction

Coastal ecosystems and the valuable services they provide have been lost and degraded as a result of human-induced disturbances, land-use change, alteration of food webs, and climate-related stressors, among others (Jackson et al. 2001, Leemans and Groot 2003). Coastal habitat change and loss over the 20th century alone has been extensive, with hundreds of thousands of acres lost across the globe (Jackson et al. 2001, Lotze et al. 2006, Waycott et al. 2009, Beck et al. 2011). The magnitude of coastal and estuarine degradation

has generated a pressing need for conservation strategies that actively combat decline. Early conservation efforts primarily focused on reducing human impacts and physical stressors (as reviewed in (Young 2000, Young et al. 2005)), but with increasing rates of habitat degradation, conservation alone may not be sufficient to protect and reestablish coastal ecosystems.

Habitat restoration has recently been promoted, along with other conservation strategies, such as spatial planning and reducing direct destruction of habitat, as a tool to combat habitat and biodiversity loss (Jordan et al. 1990, Dobson et al. 1997, Young 2000). For restoration to be effective and employed as a primary method of coastal conservation, we must improve its efficiency (Suding 2011). One crucial step will be to identify when and where conservation paradigms have already been applied in habitat restoration and gauge their success. Knowledge and effort gaps need to be identified promptly to better align current ecological theory and research efforts with restoration priorities and best practices.

Relatively long-established coastal conservation strategies, such as protected areas and endangered species management, can be stymied by limited communication across institutions and interested parties (i.e., non-governmental organizations, governmental organizations, and academia (Tallis and Lubchenco 2014)), mismatches between conservation priorities and regions where efforts and resources have been focused (Fisher et al. 2011, Jenkins et al. 2015), lack of adaptive management, and incorporation of ecological advances (Williams et al. 2007). In conservation science and practice, it is broadly recognized that collaboration across sectors can facilitate the transfer of both

knowledge and resources in addition to promoting complex problem-solving in policy and management (Dietz et al. 2003, Hardy et al. 2003). Research and information must be effectively communicated and congruent with the priorities of decision makers (National Research Council 1989), and cross-sector collaboration can help to facilitate the assimilation of knowledge. Traditional conservation efforts have unfortunately been hindered by a general paucity of strategic and lasting cross-sector partnerships (Stinchcombe et al. 2002, du Toit et al. 2004, Nature Publishing Group 2007, Sunderland et al. 2009, Bennett et al. 2017). This lack of connection can impede the development and implementation of standardized methods for conducting and monitoring restoration making broad-scale comparison of restoration success difficult (Bernhardt et al. 2005, Juffe-Bignoli et al. 2016). Moreover, slow-to-publish or pay-wall journals can inhibit small non-governmental organizations from accessing recently developed restoration research (Kareiva et al. 2002), and language barriers may further widen the research-implementation gap (Knight et al. 2008). Emphasis has recently been placed on addressing these conservation challenges and enhancing dialogue between interested parties (Imperial 1999, Kareiva et al. 2014), but the extent to which cross-sector collaborations occur in peer-reviewed and published restoration research is unknown.

For effective conservation, it is also essential to identify and fill gaps in knowledge that are relevant to saving threatened species and habitats (Knight et al. 2008). One simple approach to address this need is to map the distribution of conservation efforts and determine regions where additional action may be needed in response to biological threat or lack of research emphasis. For example, conservation societies have called on

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researchers to conduct studies where animals and habitats are most endangered (Wilcove et al. 1998, Kappel 2005). Despite this recommendation, conservation science has historically done the opposite and focused efforts in areas that do not geographically align with areas that have the greatest number of threatened species (Lawler et al. 2006). Mismatches between the biological need for protection and conservation efforts have been well-documented in coral reefs (Fisher et al. 2011, Mouillot et al. 2016), avian conservation (Brito and Oprea 2009), amphibians (Lawler et al. 2006) and terrestrial protected lands in the United States (Jenkins et al. 2015), among others (Lawler et al. 2006). In addition, conservation is especially emphasized and practiced in the western hemisphere despite the global distribution of ecosystems in need of protection (Lawler et al. 2006). Determining if similar geographic gaps and/or habitat mismatches exist in coastal restoration will be crucial for informing and adapting future restoration priorities and efforts.

Another manner in which conservation science may move forward is by actively testing and incorporating new ecological theories and understanding. Coastal ecosystems were historically thought to be controlled primarily by abiotic and physical factors (see Teal 1962, Odum et al. 1971)). Thus, conservation approaches were similarly focused on the preservation and restoration of pristine physical conditions (Fazey et al. 2005). Empirical research in coastal ecosystems over recent decades, however, has shown that biotic interactions such as predation, competition, and, more recently, positive species interactions are also important controls, especially under high physical stress scenarios (Bertness and Grosholz 1985, Bertness and Callaway 1994, Bertness and Hacker 1994, He et al. 2013). In particular, recent small-scale, experimental tests in marsh restoration have

demonstrated that incorporating indirect positive interactions among transplants and between foundation species can increase ecosystem recovery and resilience (Silliman et al. 2015, Angelini et al. 2016). These results indicate that expanding restoration designs to also consider trophic controls and indirect species interactions in addition to the physical template may enhance restoration efficacy and yield (Halpern et al. 2007, Silliman et al. 2015). Despite this, the extent to which direct and indirect interactions are put forth as considerations in the restoration literature has not been assessed.

We synthesized the peer-reviewed literature on seagrass, salt marsh, and oyster reef restoration in order to better identify knowledge gaps related to collaboration, distribution, and methodology. In particular, we examined author affiliations to better describe the amount of interaction that occurs between conservation research and practice. To determine if current restoration research occurred in at-risk areas, we examined the geographic distribution of study sites. Finally, to determine whether factors considered in restoration tracked with advances in ecological theory, we compared the incorporation of biotic and abiotic variables over time.

1.2 Methods

We conducted an extensive literature search and synthesis of the Web of Science™ (all databases and all years) using the query "Topic = (habitat restoration) AND Topic = (oyster* OR salt marsh*)". This search resulted in 952 publications as of October 2016. We later expanded our study to include seagrass restoration studies and conducted a second literature search in March 2017 using the query "Topic = (habitat restoration) AND Topic

= (seagrass*)", which resulted in 302 publications (Appendix A), excluding papers that were discovered in the first search (24 studies). We focused our search on habitat restoration as opposed to ecosystem restoration because we were primarily interested in research that pertained to the restoration of habitat-forming foundation species (Dayton 1972b). Moreover, restoration of foundation species can be an avenue by which to restore ecosystems and ecosystem functions. This specific choice of search terms, however, may have led to the underrepresentation of multi-habitat and ecosystem enhancement restoration studies in our results.

Given the large number of studies on the topic, we randomly selected half of all articles to be scored (Pigott 2012). Articles were randomly assigned to nine individuals for evaluation to minimize potential reader biases. To be included in our analysis the study (i) must have been published in a peer-reviewed, English-language journal; and (ii) must have pertained to restored salt marshes, oyster reefs, or seagrasses, or made explicit recommendations for the restoration of those habitats. Our analysis included only the published scientific literature because it is readily accessible and serves as a comprehensive documentation of substantiated restoration research, advancements, and priorities. From each study, we extracted author affiliations, funding sources and acknowledged organizations, journal of publication, article accessibility (open access or paywall), publication year, study location, habitat type, restoration/management phase represented (site selection, implementation, or monitoring), methodology (experimental, model, observational, or review), measured response variables (focal foundation species growth, abiotic factors, or biotic factors), and factors emphasized, tested, or employed. We utilized

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a vote-counting approach to provide an assessment of the state and development of the published restoration literature, the monitoring protocols and study methodologies employed, and the variables emphasized or considered in analyses.

1.2.1. Cross-Sector Collaborations

To determine the extent to which cross-sector collaborations occur in restoration research, we categorized author affiliations as one of three sectors: Academia, Non-Governmental Organizations (NGOs), and Governmental Organizations (GOs). Additionally, we extracted the affiliation category of any funders, organizations, and individuals mentioned in the acknowledgements section of each paper. Individuals whose affiliation was not stated in the acknowledgements were not included. Since we cannot accurately ascertain the extent of involvement for those listed in the acknowledgements, we focused primarily on authorship and funding as an indication of collaboration.

1.2.2. Restoration Geography

To determine the geographic distribution of published restoration studies, we extracted information regarding study locations by continent (or global study), country, and region if conducted in the United States. It is important to note that although our dataset includes some of the most recognized and prominent published papers in restoration research, it likely does not include all influential restoration literature due to the nature of randomly selecting half of the studies. Furthermore, because we also excluded non-English-language studies, studies conducted by and in non-English-speaking entities and countries are likely to be under-represented in our dataset. In addition, our vote-count

examined only where published restoration research occurred, which may differ from where restoration efforts as a whole may be conducted.

1.2.3. Factors Considered in Restoration Methodologies

In order to address our third objective, we first defined 35 potential biotic and abiotic restoration factors a priori based upon preliminary literature reviews and recorded if a factor was stated as a consideration for restoration (Appendix B). A factor was marked as an important consideration if the article stated the factor must be addressed for restoration of salt marshes, seagrasses, or oyster reefs to succeed, or that manipulating the factor could lead to positive or negative restoration outcomes. We further distinguished if a study explicitly tested a factor's effect on restoration and noted whether the factor was found to be significant or not.

1.3 Results

In total, 301 papers met the criteria for inclusion in the study—we assessed 177 salt marsh, 75 oyster reef, and 82 seagrass publications (Figure 1a, Appendix A). Of these, 8% of papers discussed two habitats, and 2% of papers discussed all three habitats. Additionally, the number of published papers on coastal restoration increased dramatically over the last 15 years (Figure 1b). The majority of restoration studies were observational in approach (55%, Figure 1c) and roughly 1/3 conducted experimental restoration. Across all studies, 57% made recommendations regarding restoration methodology and implementation, 46% for restoration monitoring, and 32% on site selection (Figure 1d).

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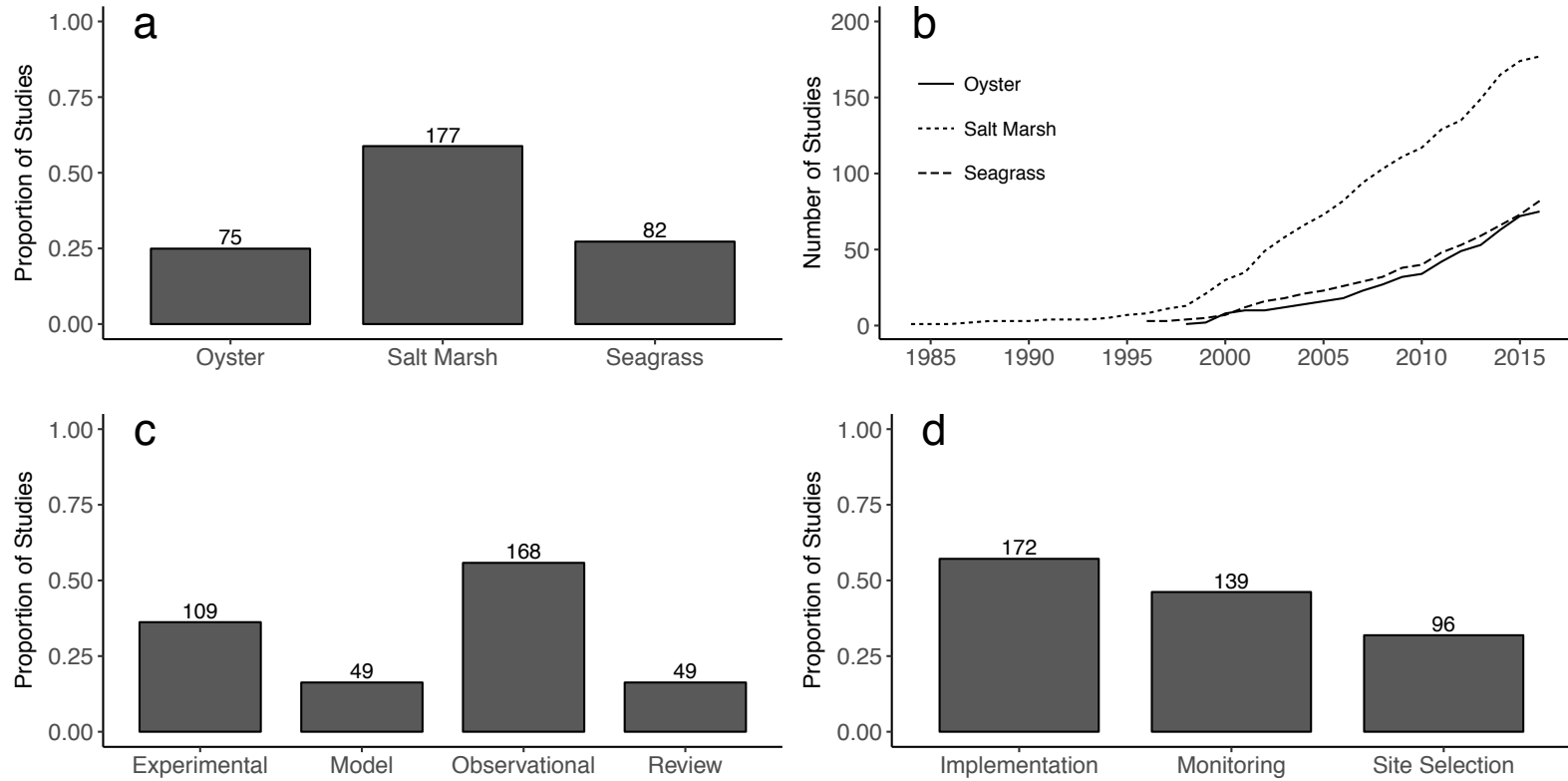
Figure 1: Journal article characteristics by (a) habitat, (b) publication date, (c) study methodology, and (d) restoration phase.
Values above bars indicate the explicit quantity of studies. Note different y-axis on Figure 1b.

The vast majority of studies were authored by at least one researcher associated with a university (84%). Of our studies, 60% were published by authors representing only one sector; 34% were published by authors representing two sectors; and 6% had authors from academia, non-governmental organizations, and governmental organizations (Figure 2a). In contrast, government organizations alone accounted for nearly half (47%) of funding for restoration research, and 14% of studies did not state a funding source (Figure 2b). Approximately one-third of studies received funding from two or more sectors. When authors, funding sources, and acknowledgements were combined, cross-sector collaborations occurred in 89% of studies (Table 1). Of the 88 different journals in which studies were published, however, only nine were fully open-access (Appendix C). Open-access articles, including those published as open-access in an otherwise subscription journal, accounted for less than 9% of all included studies.
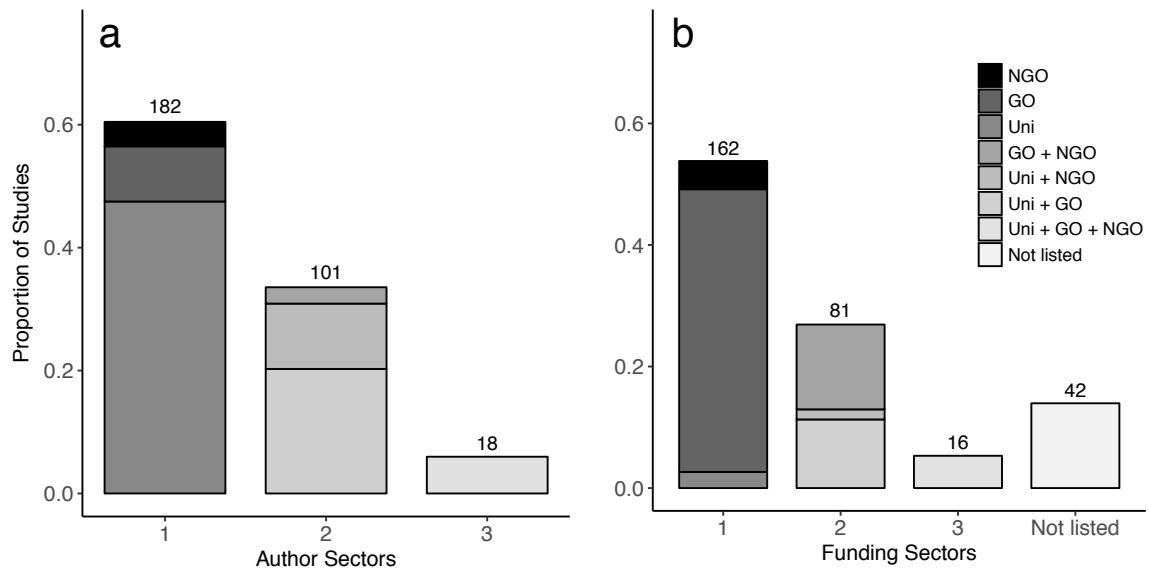
Figure 2: Collaborations in restoration research quantified by (a) listed authors and (b) acknowledged funding sources.

Table 1: Authors, funders and acknowledged collaborations

Affiliations	Frequency	Percent
University	16	5.3
Government Org.	14	4.7
Non-Governmental Org.	3	1.0
Uni + GO	116	38.5
Uni + NGO	20	6.6
GO + NGO	17	5.6
Uni + GO + NGO	115	38.2

Globally, the vast majority of peer-reviewed restoration studies published in our database were conducted in North America followed by Europe and Asia (74%, 14% and 5% respectively; Figure 3a, Table 2). An additional 4% of studies in our dataset were conducted across multiple continents. No studies that we reviewed occurred in either Africa

or South America. In the United States, just over one third (36%) of all peer-reviewed restoration studies occurred in the northeastern United States followed by the Gulf and Pacific coasts (27% and 24%, respectively, Figure 3b). The majority of published salt marsh studies were conducted on the northeastern and Pacific coasts (both 33%), whereas seagrass studies were most often conducted on the northeastern and Gulf coasts (35% and 33%, respectively). Similarly, oyster restoration studies were predominantly conducted on the northeastern, Gulf, and southeastern coasts of the United States (39%, 27%, and 27%, respectively).

While the authors in our database were affiliated with organizations from 25 different countries (Table 3 and Appendix B), 70% of articles were published by authors solely affiliated with institutions in the United States; this bias likely affects our analysis of where restoration research has been conducted but likely has less influence on our study of what factors are emphasized or the extent of collaboration.
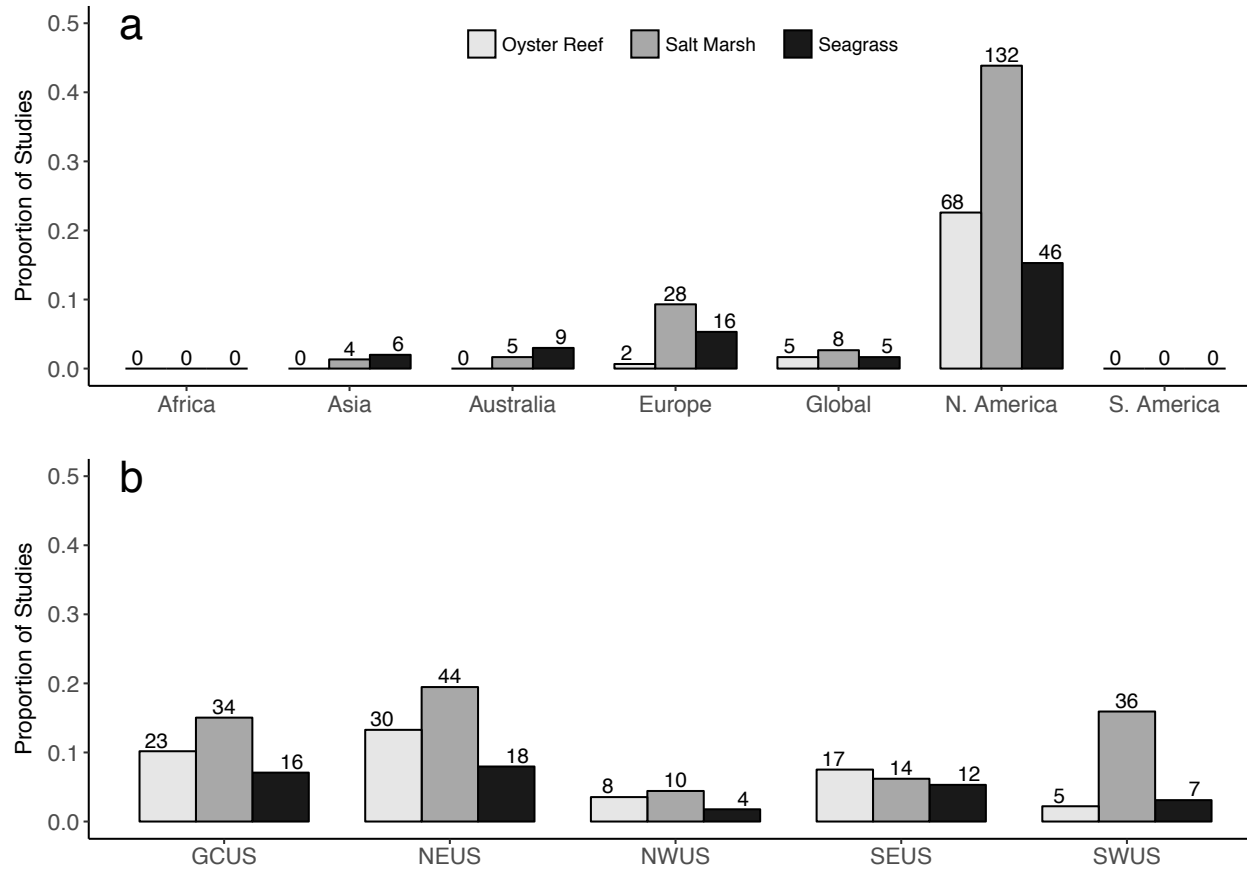
Figure 3: Oyster reef, salt marsh, and seagrass restoration study locations (a) **by continent or globally and** (b) **by United States region.**
NEUS = Northeast United States, SEUS = Southeast United States, GCUS = Gulf Coast United States, PCUS = Pacific Coast United States. Values above bars indicate the explicit quantity of studies.

Table 2: Author affiliations by continent

Continent	Number	Percent
North America	218	72.4
Europe	36	12.0
Global	24	8.0
Australia	9	3.0
Asia	9	3.0
Africa	0	0.0
South America	0	0.0

Table 3: Author affiliations by country excluding the United States

Location	Frequency	Percent
Australia	18	6.0
United Kingdom	15	5.0
Netherlands	12	4.0
Spain	11	3.7
Portugal	10	3.3
China	8	2.7
France	7	2.3
Belgium	6	2.0
Canada	6	2.0
Italy	4	1.3
Mexico	2	0.7
New Zealand	2	0.7
Panama	2	0.7
Philippines	2	0.7
Sweden	2	0.7
Czech Republic	1	0.3
Denmark	1	0.3
Finland	1	0.3
Germany	1	0.3
Hungary	1	0.3
South Korea	1	0.3
Malaysia	1	0.3
Poland	1	0.3
Singapore	1	0.3
Taiwan	1	0.3

Nearly two-thirds of examined studies (64%, Figure 4a) discussed both biotic and abiotic factors as important considerations for restoration success. Studies that discussed only abiotic or physical factors as restoration considerations far outnumbered those that only discussed biotic considerations (Figure 4b). Across all habitats and factors, water depth/elevation, human interactions, tidal flow, temperature, and salinity were the most commonly recommended considerations for restoration (Figure 5, Appendix A). The top three biotic factors considered for restoration success were human interactions, recruitment, and consumption (includes both predation and grazing). Salinity, water depth/elevation, and temperature were most often tested experimentally. Of the tested factors, salinity, water depth/elevation, and nutrients were most frequently found to have significant effects on restoration success across all habitats.

In contrast, the factor most frequently stated as critical for restoration success differed by habitat. Water depth/tidal elevation was most often stated as important for salt marsh restoration (50% of salt marsh papers). Human interactions and disturbances were the most considered factors for seagrasses (57% of seagrass studies), and recruitment was the most frequent consideration for oyster restoration (49% of oyster reef studies).

There was little to no lag between when trophic interactions were first recommended as important considerations (1996) compared to non-trophic species interactions (Figure 6). However, less than one-fourth of studies mentioned either positive species interactions or top-down forcing in their studies. Only 3% of all studies in our dataset specifically tested for the impacts of incorporating positive species interactions into

restoration designs, and 1% experimentally tested for the effects of top-down controls on

restoration success.
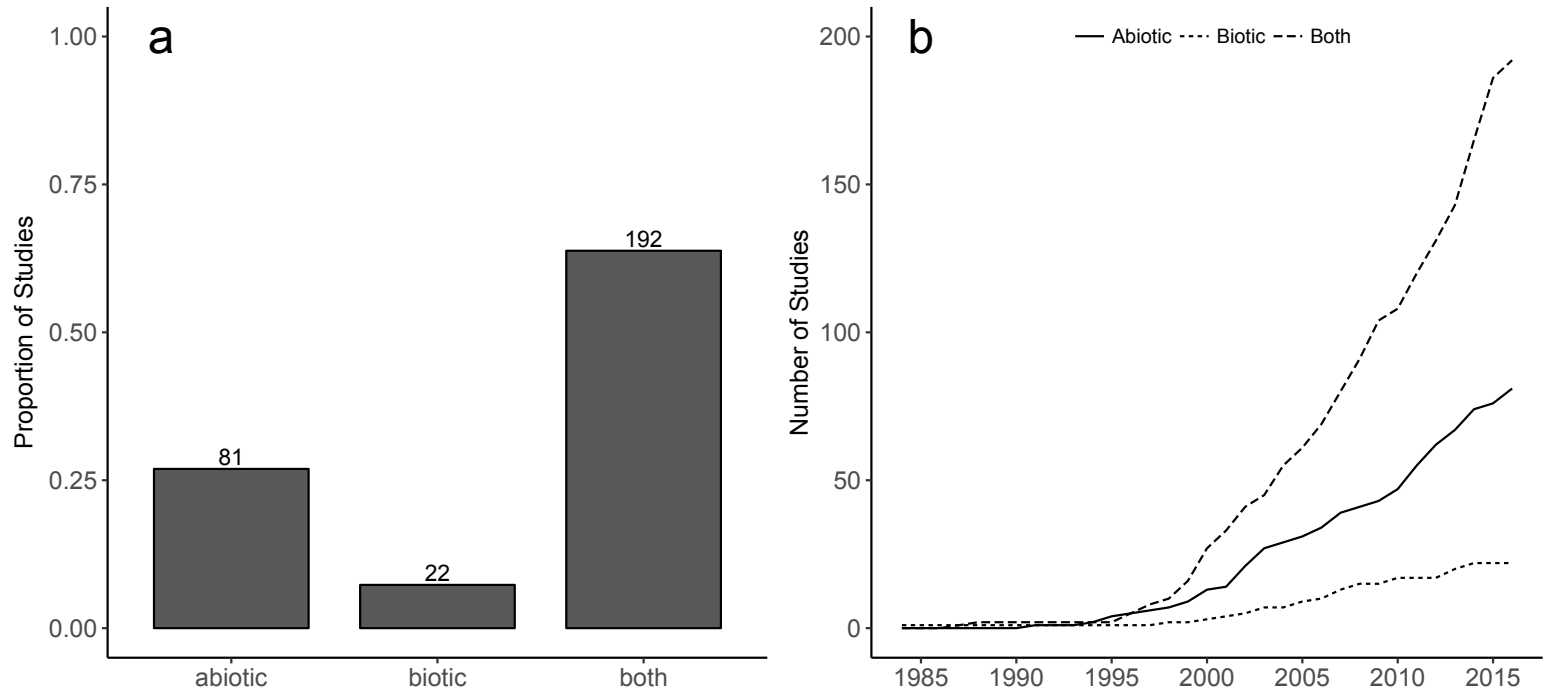
Figure 4: Quantification of physical or biological factors recommended in salt marsh, oyster reef, and seagrass restoration literature (a) total and (b) over time.
Values above bars indicate the explicit quantity of studies.
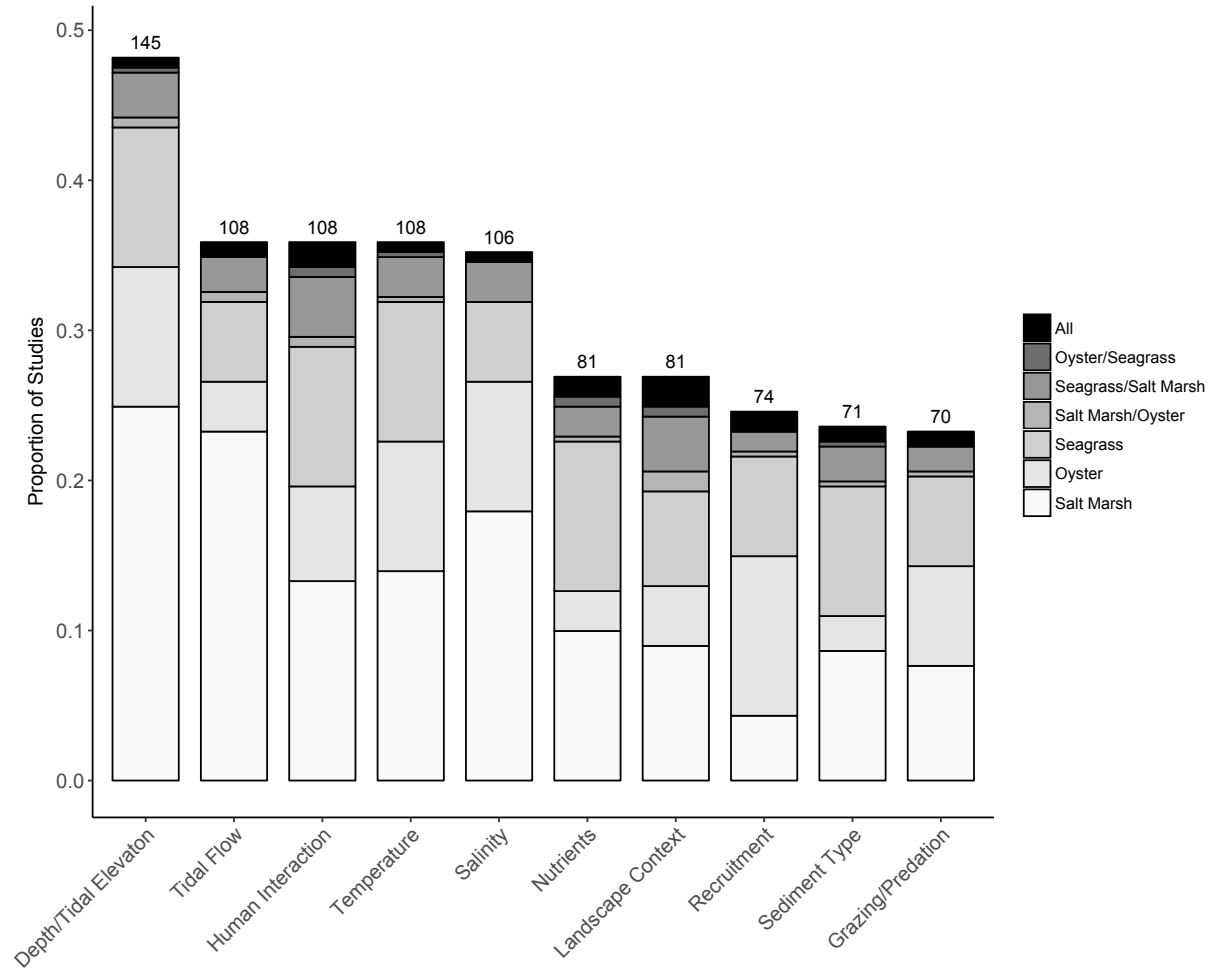
Figure 5: Top 10 factors considered for habitat restoration by ecosystem.
Values above bars indicate the explicit quantity of studies.
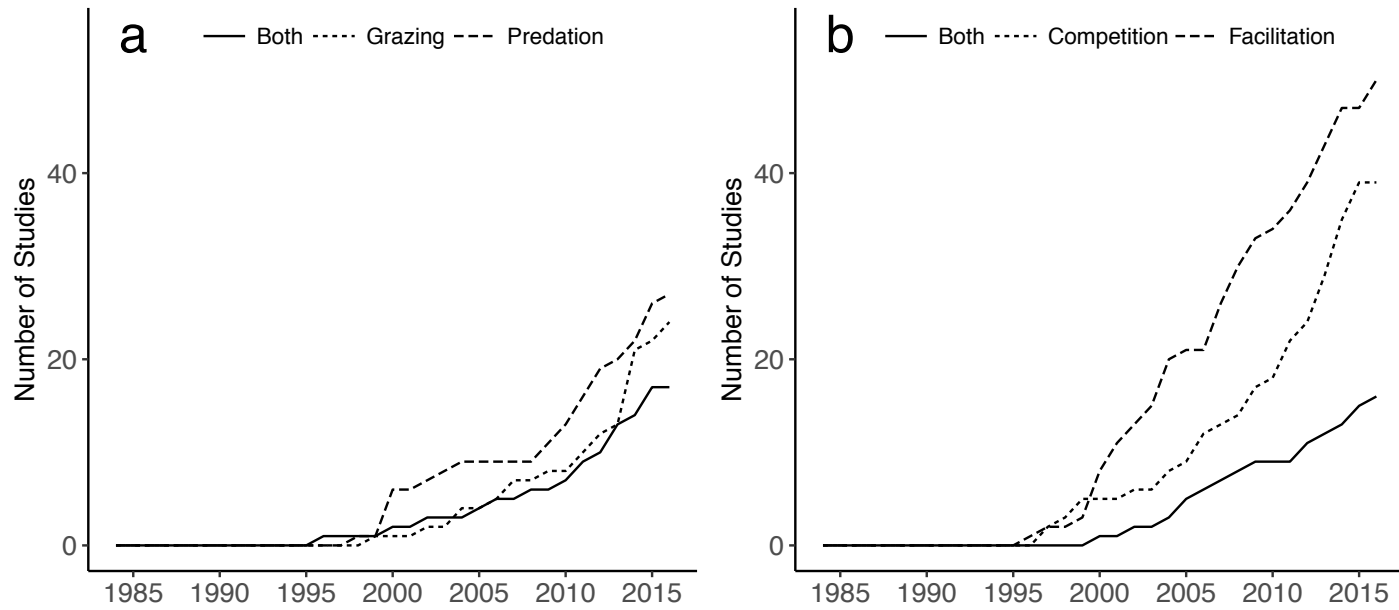
Figure 6: Cumulative number of coastal restoration studies over time that recommend considering biotic interactions.
a) Top-down trophic forcing and b) non-trophic species interactions, specifically competition or facilitation.

1.4 Discussion

We conducted this synthesis of peer-reviewed journal publications to identify potential knowledge gaps and areas of improvement in coastal habitat restoration with respect to collaboration, location, and implementation methodology. Our vote-count revealed three major findings: (i) cross-sector collaboration as assessed by author affiliation occurred in about one-third of the studies examined and 89% of studies when authors, funders, and acknowledged organizations were considered; (ii) there is a dearth of peer-reviewed English-language studies from Africa, South America, Asia, and Australia; and (iii) abiotic factors were more frequently stated as important considerations for restoration success than biotic factors, but studies often addressed both. In particular, there was little difference in timing between when direct and indirect species interactions began to be recommended as important considerations in the restoration literature, however, very few of the studies specifically tested for their effects (<5%).

1.4.1. Cross-Sector Collaborations

Multiple studies have shown that the establishment of relationships between individuals, organizations, or sectors can facilitate the formation of common goals and lead to more effective and coordinated conservation efforts (Jones et al. 1997, Robins et al. 2011). Our finding that roughly one-third of peer-reviewed restoration studies listed authors from at least two sectors, and 85% of papers represented a form of collaboration with respect to authorship, funding, and acknowledged work, suggests that previous restoration efforts have been collaborative. The sectors considered in this paper (i.e., NGO, GO, and academia) differentially specialize in implementation, policy, and innovation, and

the nature of the collaboration ranges dramatically with respect to length, investment of resources, power, and involvement (Guerrero et al. 2015). Given past findings from conservation studies, it is very likely that strategic approaches that form and support well-integrated and lasting relationships across individuals and organizations will increase the effectiveness of future restoration initiatives (Lubell 2004, Guerrero et al. 2015).

Cross-sector collaborations can offer a number of benefits in conservation efforts, including knowledge transfer, resource sharing, and cooperative problem-solving (Hardy et al. 2003, Suding 2011). As researchers decipher the complex interactions involved in restoring ecological communities, the information often does not get integrated into the practice of habitat restoration and vice-versa (Hobbs 2007, Cook et al. 2013). The research-implementation gap has been well-documented and criticized in conservation as a whole (Nature Publishing Group 2007, Chapron and Arlettaz 2008, Knight et al. 2008, Toomey et al. 2016). For example, many small NGOs may not have the financial resources to subscribe to scientific journals, and few studies are published open access. In contrast, many university researchers do not have the financial (Holl and Howarth 2000) or human-power to conduct broad-scale restoration, and both NGOs and academics often rely on government agencies to provide the financial means to restore habitats. Given these differential specialties and resources for all three sectors, bringing them together in lasting collaboration is likely to promote positive cooperative interactions and outcomes.

Although most listed authors were affiliated with academic institutions, our method of quantifying substantial collaboration does not take into account authors who may have multiple affiliations or collaborations that may occur between universities and other entities

outside the domain of authorship. For example, we found that governmental agencies and NGOs were the predominant sources of funding for restoration research, but this contribution does not necessarily warrant authorship. However, because grantors ultimately determine what is funded, they likely play a disproportionately large role in determining restoration priorities and the scope of the projects to ensure they align with regulatory or management needs (Holl and Howarth 2000). In addition, because we only included peer-reviewed articles, it is possible that studies by non-academics in general may be underrepresented in our dataset, as they publish more frequently in white or gray papers.

1.4.2. Restoration Geography

Our synthesis revealed that peer-reviewed restoration studies were strongly concentrated in the western hemisphere, and little to no research on coastal habitat restoration has occurred elsewhere. Most studies occurred in North America (74%), followed by Europe (14%), and few to no studies took place in Asia, Africa, or South America (3%, 0%, and 0%, respectively). The dearth of studies may be partially attributed to our selection of English-language journals, but may also be the result of fewer research universities as well as less funding opportunities in these areas. There may alsobe an emphasis on restoration and research of other coastal habitats, such as coral reefs or mangroves on some of these continents rather than on salt marsh, oyster reef, or seagrass meadows. Regardless, it is evident that the majority of restoration research published in peer-reviewed journals on temperate coastal habitats has occurred in North America and Europe. Restoration inherently occurs in high-stress or degraded areas (Prach and Hobbs 2008, Holmgren and Scheffer 2010), and, as a result, success can be highly variable (Zedler

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2007, Maron et al. 2012). For restoration research and experimentation to be broadly applicable, it should be conducted under similar environmental conditions and constraints, as larger restoration projects and aid in selecting areas with the highest likelihood of successfully restoring ecosystems and their services (Grabowski and Peterson 2007, Palmer and Filoso 2009). Where research has occurred, however, is likely influenced by multiple factors such as disaster response, local investment, and researcher concentration, among others.

Though we cannot directly ascertain whether restoration research has occurred in the appropriate locations, particularly with respect to areas with the greatest likelihood for success, our study sheds light on where there is an overall lack of restoration knowledge geographically. Few studies have provided estimates of coastal habitat extent and change in Africa, Asia, and South America (An et al. 2007, Waycott et al. 2009, Beck et al. 2011); thus, it is not surprising that we similarly found a lack of restoration studies. Studies that quantified global changes in seagrass, salt marsh, and oyster reefs estimate that declines range from 20–95% based upon region (An et al. 2007, Silliman et al. 2009, Waycott et al. 2009, Beck et al. 2011), suggesting that there is a pressing biological need for restoration research and transference of knowledge as a means of conservation. In response, the restoration community should redirect research and efforts to better address areas of threat where little is known regarding habitat loss and recovery.

1.4.3. Factors Considered in Restoration Methodologies

In our vote-count, we found that variables related to physical stress were by far the most considered factors in restoration studies. This is striking given that our knowledge of

ecological systems suggests species interactions are fundamental in determining the structure and function of ecosystems (Hairston et al. 1960, Paine 1966, Dayton 1971, Platt 1975, McNaughton 1985). Notably, marine restoration literature seems to recapitulate early ecological conventions and best practices from terrestrial restoration that prioritized abiotic over biotic forces for decades. When species interactions are included, there is often a focus on minimizing negative interactions, such as competition, rather than promoting positive interactions, such as facilitation. Furthermore, restoration practice has historically been influenced by forestry science, which emphasizes intra- and inter-specific competition as limiting forces for seedling recruitment success (Halpern et al. 2007). For decades, the paradigm of terrestrial restoration designs was to minimize competition between out-planted propagules by planting them at constant and dispersed distances (Silliman et al. 2015). In contrast, recent research demonstrated that salt-marsh restoration yield doubled simply by planting marsh grass plugs in aggregate (thus ameliorating abiotic stressors via increased intraspecific facilitation) (Silliman et al. 2015). This example underscores the idea that best practices learned from other terrestrial restoration projects may not necessarily be appropriate guidelines for marine restoration. Moreover, incorporating facilitation into restoration schemes has the potential to increase success with little additional expense.

Top-down control of transplants directly by grazers and predators has historically been recognized as another influential negative biological force. Consequently, we found many studies considered predation (15%) and grazing (14%) as important factors for restoration success. Grazers, for example, are known to exert strong control upon habitats.

There are multiple examples where release of consumers from natural regulation by predators has led to complete habitat loss across a wide variety of grazer organisms (e.g., insects, echinoderms, small and big mammals, birds) and habitats (e.g., forests, savannas, kelp forests, mangroves, salt marshes, coral reefs; see (Silliman et al. 2013) for a review). Thus, it is not surprising that consumers can strongly influence restoration success. In some cases, restitution of natural predators can be the only way to achieve habitat restoration by means of a trophic cascade, as in the case of the re-introduction of wolves in Yellowstone (Kauffman et al. 2010). Although the ecological literature recognized the importance of top-down interactions, our study found that they were not commonly stated as considerations in coastal habitat restoration, potentially because top-down interactions are not always practical to manipulate, and their effects can be difficult to predict. However, when top-down interactions were directly employed and tested in restoration (4 studies, 1%), they were consistently found to have a significant effect on restoration success. Future studies in temperate marine systems should continue to investigate how accounting for and managing species interactions can affect restoration outcomes. In particular, testing and incorporating positive species interactions such as tri-trophic and facilitation cascades may greatly enhance restoration productivity and yield.

1.4.4. Recommendations for Coastal Habitat Restoration

Maximizing multi-functionality in habitat restoration, especially in coastal areas where there are a multitude of conflicting ecological, economic, and social priorities, is increasingly emphasized as a goal of conservation (Douvere 2008). While restoration in and of itself should continue to be a priority, restoration schemes can be tailored to

incorporate additional human priorities (e.g., shoreline erosion protection and aquaculture). For example, ecologists and restoration practitioners have recently begun to advocate for the use of shoreline stabilization strategies often referred to as "living shorelines" that prioritize coastal ecosystem restoration (e.g., salt marshes and oyster reefs), as well as coastal erosion protection. Living shorelines employ long-distance, intraspecific facilitation in the restoration scheme, whereby an offshore restored oyster reef attenuates wave energy and allows the persistence and potential expansion of a landward salt marsh where one might not be able to exist on its own. Living shorelines have been shown to enhance the services provided by coastal ecosystems (Scyphers 2012, Gittman et al. 2016). Furthermore, the promotion of bivalve aquaculture in eutrophic areas has been proposed as a mechanism for promoting the restoration of seagrass beds via the reduction of water column turbidity (Peterson and Heck Jr 2001b), while at the same time providing an economic and social benefit.

Proper site selection is also crucial for restoration success (Miller and Hobbs 2007); however, the means by which potential restoration sites are identified, prioritized, and selected are only beginning to be developed. Roughly one-fourth of the studies in our dataset researched factors that would inform the site-selection stage of restoration. Whether this represents a paucity of knowledge, or that there has been adequate research on this subject, cannot be discerned by our study, as we do not have information regarding long-term success of restoration studies, which is also a large gap in restoration knowledge. Restoration science and practice would benefit from more systematic, long-term monitoring that can be incorporated into predictive site-selection models (Ruiz- Jaen and

Mitchell Aide 2005, Wortley et al. 2013). Similarly, conducting basic research in regions where little is known regarding coastal habitat change will be crucial for identifying priority areas.

Ultimately, successful restoration will rely in part on minimizing per-unit restoration cost and enhancing our ability to restore at large scales (Holl and Howarth 2000, Holl et al. 2003, Holl 2017). This can potentially be achieved by promoting collaborative restoration efforts (Bodin and Crona 2009), incorporating planting strategies that can increase yield (i.e., utilizing aggregated over dispersed planting arrangements in wetland restoration) (Silliman et al. 2015), and/or by designing restoration to simultaneously address multiple human priorities (Aronson et al. 2010). The fact that the most-frequently mentioned and tested factors in this study were abiotic in nature highlights the fact that re-creating the physical template remains the top priority for restoration. The inclusion of biotic factors, specifically species interactions, may greatly enhance restoration success when included in addition to the physical template (Halpern et al. 2007, Fodrie et al. 2014, Silliman et al. 2015, Gittman et al. 2017a). Restoration efforts based solely on the re-creation of physical site characteristics may fail due to biotic issues like recruitment limitation (Bell et al. 1997) or underperform because of a failure to consider facilitation (Halpern et al. 2007, Silliman et al. 2015, Bilkovic et al. 2017).

For restoration science and practice to advance as a method of conservation at large spatial scales, it is crucial to continually identify and address knowledge gaps, as well as develop and implement the most cost- and time-effective techniques. This includes actively developing and incorporating relevant ecological theories into designs and improving

collaboration and communication across sectors. Thus, we suggest that the field of restoration science and practice could benefit from:

1. A broad discussion of the extent to which cross-sector collaborations with significant intellectual contributions from all participants occur as well as their effects on knowledge transference and adaptive management of restoration projects.

2. A greater emphasis on- and communication of restoration research that occurs outside of the western hemisphere.

3. The inclusion of biotic interactions, in addition to the physical template (specifically, top-down effects and facilitation) as a potential means to further enhance restoration yields.

CHAPTER 2. A FACILITATION CASCADE ENHANCES LOCAL BIODIVERSITY IN SEAGRASS BEDS

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Y.S. Zhang and B.R. Silliman conceived and designed the study. Y.S. Zhang conducted the investigation, analyzed the data, and acquired funding. Y.S. Zhang and B.R. Silliman wrote and edited the paper.

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2.1 Introduction

It has long been recognized that cascades of species interactions can indirectly alter ecosystem processes and community organization (Hairston et al. 1960, Paine 1966). Tritrophic cascades are one well-known example that occur when double-negative feeding interactions result in predators indirectly increasing plant populations by suppressing populations of otherwise voracious grazers (Estes and Duggins 1995, Silliman and Zieman 2001, Terborgh et al. 2001). Facilitation cascades generated by sequences of direct positive effects between habitat-forming ecosystem engineers can also have powerful, indirect effects on marine ecosystems (Thomsen et al. 2010). In habitat cascades, primary foundation species, such as mangroves and salt marsh cordgrasses, ameliorate stressful

physical conditions and provide habitat for secondary foundation species such as oysters and mussels (Altieri et al. 2007, Thomsen et al. 2010, Angelini et al. 2011). In turn, secondary foundation species further modify ecosystem structure and functioning and enhance community diversity via their own engineering and niche space provisioning (Angelini and Silliman 2014).

Despite their likely influence on ecosystem functioning and resilience, ecological models often do not include positive interactions (Bruno et al. 2003). Moreover, the generality of habitat-mediated facilitation cascades and their application in conservation has only gained traction in the last two decades (Halpern et al. 2007). In salt marshes, facilitation cascades between ecosystem-engineering grasses and mussel aggregations have been found to enhance multiple functions including soil accretion and infiltration rate in addition to plant biomass and local biodiversity (Angelini et al. 2015). Similarly, facilitation cascades and mutualisms among mangroves, algae, and oysters have been demonstrated to increase growth rates, niche provisioning, and epifaunal diversity and abundance (Ellison et al. 1996, Bishop et al. 2012). Recent syntheses have further found that positive interactions (He et al. 2013) and facilitation cascades (Thomsen et al. 2018) are especially important for enhancing resilience to physical stressors and driving patterns of biodiversity across marine, aquatic and terrestrial ecosystems.

Studies have only recently begun to examine how biodiversity in seagrass beds may alter ecosystem functioning (Duffy et al. 2003, Duffy et al. 2015), and the role of facilitation cascades in determining seagrass biodiversity has similarly been under-studied. Prior studies of positive interactions between seagrasses and bivalves have focused

primarily on the direct effects of bivalves on seagrass productivity (Reusch et al. 1994, Peterson and Heck Jr 2001a, Vinther et al. 2008, van der Heide et al. 2012, Castorani et al. 2015). These studies also did not first examine the role of seagrasses as primary foundation species prior to testing for bivalve impacts or whether bivalves may have indirect effects on tertiary species via a multi-level facilitation cascade. Secondary foundation species in seagrass beds, such as algae and bivalves, may also independently and directly facilitate fish and invertebrate settlement. (Angelini et al. 2015, Thomsen et al. 2018). Thus, it is possible that habitat cascades between seagrasses and secondary foundation species may also be prevalent drivers of biodiversity patterns in shallow water marine systems (Wall et al. 2008, Gribben et al. 2017). However, further examination is required to determine how common and the extent to which facilitation cascades influence seagrass community structure and ecosystem functions.

Bivalves commonly occur in seagrass ecosystems across the globe (van der Heide et al. 2012). Seagrasses have been shown to first facilitate bivalves by attracting bivalve larvae and decreasing the intensity of physical and biological stressors (Eckman 1987, Bologna and Heck 2000, Williams and Heck 2001). Bivalves, in turn, may positively affect seagrasses by increasing water clarity and beneficially altering sediment nutrient chemistry, and soil oxygenation (Reusch et al. 1994, Peterson and Heck Jr 2001b, Wall et al. 2008, van der Heide et al. 2012). Lucina clams, for example, can reduce otherwise toxic sediment sulfide concentrations and enhance seagrass biomass via a mutualism with sulfide-oxidizing bacteria that reside within their gills (van der Heide et al. 2012). Reef-building bivalves such as oysters or mussels may act as both primary or secondary

foundation species depending on whether they occur within or adjacent to seagrass meadows. Oyster reefs, for example, may facilitate nearby seagrass growth by ameliorating wave stress (Sharma et al. 2016). In addition to directly impacting seagrass productivity and functioning, bivalves can also act as ecosystem engineers and create habitat that supports greater biodiversity (Altieri et al. 2007, Angelini et al. 2015). Such a habitat cascade could support the formation of tertiary habitats that may only have detectable impacts at high densities of secondary foundation species (Thomsen et al. 2018).These indirect impacts may be density-dependent and increase with density or even disappear (Gascoigne et al. 2005, Gribben et al. 2017). For example, secondary foundation species may provide positive effects on biodiversity at low densities but may compete for space or resources beyond a threshold density (Bertness 1984, Angelini et al. 2011).

Clams in the *Pinedale* family, collectively known as pen shells or fan clams, are large, habitat-forming bivalves that occur within seagrass meadows and adjacent sand flats in many of the world's oceans and estuaries. In some regions, such as Baja, California, Mexico, they occur in extremely high densities and constitute a critical and profitable fishery (Ahumada-Sempoal et al. 2002, Basurto 2006, García-March et al. 2006). However, little scientific knowledge exists regarding the ecological role pen clams may play in marine systems. Previous studies have shown that pen clams can provide primary habitat and nest sites for many epifaunal organisms and fish species, particularly post-mortem (Keough 1984b, Gribben et al. 2017). More recently, Gribben et al (2017) found that pen clam presence increased local diversity, but the effect was not density-dependent. This contrasts with previous studies that indicate greater facilitation with increasing density (van

Hulzen et al. 2007, Irving and Bertness 2009, Harley and O'Riley 2011, Bishop et al. 2012). These studies have indicated that pen clams may act as secondary foundation species in seagrass ecosystems; however, whether the initial step in this potential facilitation cascade occurs, i.e. seagrass facilitation of pen clams, has not been tested. Moreover, whether the density-dependent effects of pen clams are general across other species is not known.

In coastal North Carolina, there are two commonly-occurring species of pen clam, *Atrina rigida* and *Atrina serrata* (i.e. the rigid and the sawtooth pen clam, respectively). Pen clams in NC are functionally both infaunal and epifaunal with only the upper ~1/4 of their shell above the sediment surface. Exposed portions of the shells are frequently colonized by multiple species of invertebrates and algae. Though edible, pen clams in NC are not commonly harvested. The purpose of this study was to first determine the relative distribution and abundance of pen clams in the southern Outer Banks of North Carolina, and second, to ascertain if a facilitation cascade exists between seagrasses - pen clams - and local biodiversity. In particular, we tested if seagrasses enhanced pen shell success (i.e. density and survivorship) and if pen clams in turn impacted community diversity and ecosystem functioning. We further sought to determine if impacts were density dependent.

2.2 Materials and Methods

To examine how and if seagrasses and pen clams form the basis for a facilitation cascade we conducted a survey of seagrass beds in the southern Outer Banks of North Carolina and two field experiments. For all experiments, pen clams were collected from seagrass beds in Back Sound, NC and field manipulations conducted in Middle Marsh, Beaufort, NC, USA.

To obtain an estimate of pen clam densities in NC, we surveyed 13 seagrass beds and adjacent sand flats in Back, Bogue, and Core Sounds (Figure 7). Pen clam density was quantified using two survey methods. We first surveyed for clams by haphazardly tossing a 1 m^2 quadrat across a seagrass meadow and neighboring sandflat, and recording seagrass species and number of pen clams within the quadrat (n=25 per site). We also took a more systematic approach and conducted eight 25 m belt transect surveys in both seagrass and sandflat for a total of 16 transect surveys at each of the 13 sites. All pen clams that occurred along the transect were noted, and seagrass species was recorded at 2 m intervals.
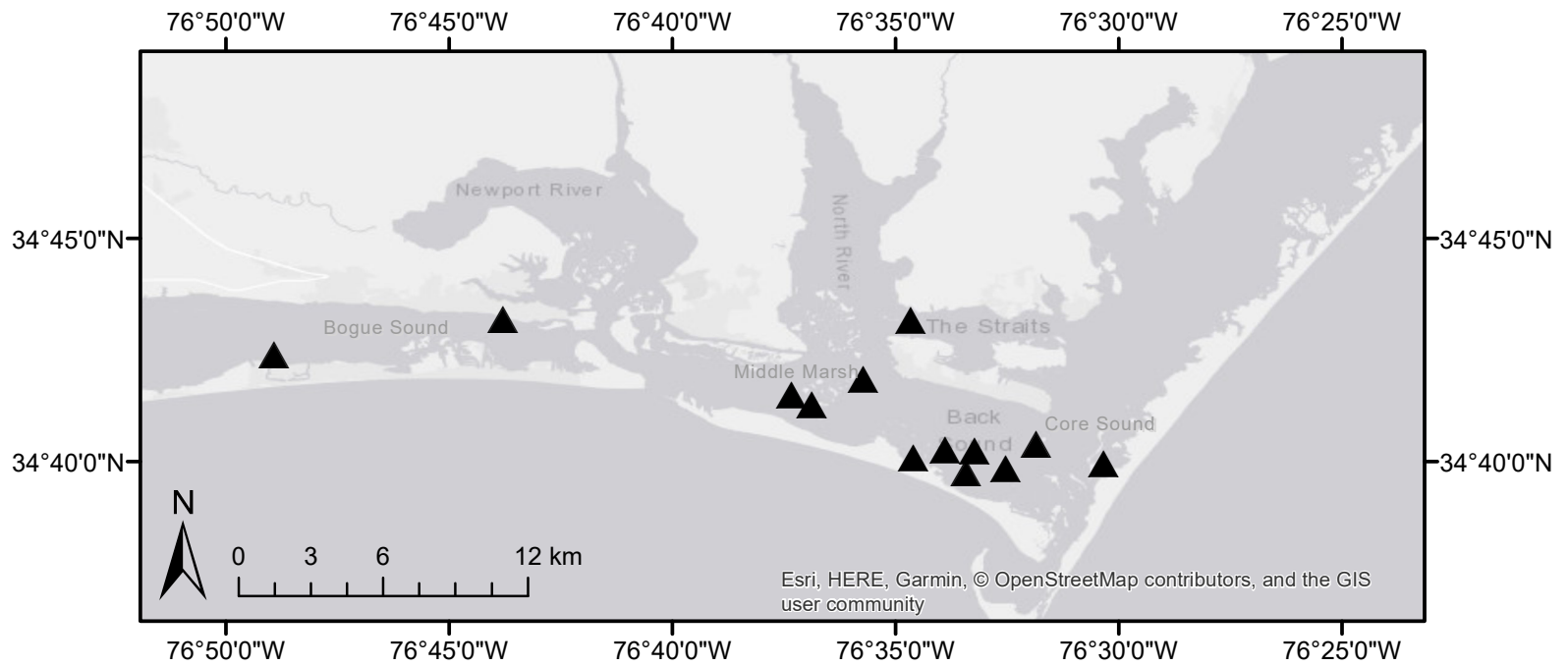
Figure 7: Survey locations of seagrass beds and adjacent sand flats (N=13).

To assess if seagrasses can facilitate pen clam survivorship, we conducted a reciprocal transplant experiment. Pen clams (n=10 per habitat type) were collected from seagrass bed interiors and transplanted into the interior of a seagrass bed or sandflat in June 2017. Mortality, shell condition, and potential cause of death was assessed weekly for the first 4 weeks and monthly thereafter through October 2018.

In order to test for the presence of a density-dependent facilitation cascade, we manipulated pen clam density within plots to 0, 1, or 4 clams per m^2 (n=5) within a seagrass bed in Middle Marsh, Beaufort, NC to represent densities observed from surveys. Experiments were conducted from November 2015 through August 2017. Seagrass percent cover was measured prior to experiment implementation to ensure similar conditions across plots. Seagrass density, height, growth, and reproductive effort were measured in May 2016 and 2017 to coincide with the period of greatest eelgrass productivity in NC. Seagrass density and reproductive shoots were counted *in situ* within 0.25 m^2 quadrats inside plots within which ten stems were measured for growth. Seagrass growth was measured by marking 10 separate seagrass shoots approximately 1 cm below the sheath. After two weeks, marked shoots were collected and brought to lab for processing. New and old growth area and biomass were measured to determine proportional growth. We also quantified aboveground seagrass decomposition to determine if pen clams affected seagrass decay rates. Decomposition bags were constructed from 1x1mm mesh screen cloth and packed and massed onshore with 50 g of live, aboveground *Z. marina* collected from the same meadow but 30 m away from the experiment area (Walker et al. 2001). Bags

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were deployed within plots in June 2017 for 6 months then collected and remaining material was massed.

To assess community composition within plots, we quantified mobile nekton, seagrass epibiont, macroalgal species and associated fauna, and pen clam epibiont communities. Nekton and macroalgal species present were quantified via *in situ* snorkeler surveys at mid-tide (~1.5 m water depth) once a month from April-August in 2016 and 2017. Observers floated above plots and enumerated all nekton that entered the plots over a 3-minute duration after a 2-minute acclimation period (Edgar et al. 2001). To determine if pen clams/pen clam density affected benthic, free-growing macroalgal biomass, we collected algal samples from plots in May 2016 and 2017. A 25x25 cm quadrat was randomly placed within the plot, and all macroalgae within the quadrat was collected and taken back to the lab for processing. Macroalgal samples were rinsed through a 500 μm sieve, dried, and weighed (Kendrick and Lavery 2001, Sidik et al. 2001). Algal-associated organisms within samples were also enumerated and identified to species. To quantify seagrass epibiont communities, 10 random stems were collected from plots and epibiota identified to family and quantified in June 2016 and 2017 to coincide with documented periods of high epibiont coverage in NC. Clam epibiont communities were assessed from photos taken in the field in August 2016 to minimize damage to plots. In August 2017, (experiment end), clams were collected and epibiont communities on clams were identified to species and enumerated. In instances where species are known to be colonial, e.g. bryozoans, organisms were recorded as present/absent rather than enumerated.

2.3 Results

Pen clams were significantly more abundant and dense in seagrass beds compared to adjacent sandflats (Student's t-Test $p<0.001$, Figure 8a) at an average of roughly 1818 per hectare in seagrasses; whereas, there was on average 100 clams per hectare in adjacent sandflats. When clams were observed (13.2% of all observations in seagrass beds), they were typically solitary, however, densities of up to 7 m-2 were observed (Figure 8b). Transplantation into seagrass beds and sandflats found that 16 months post-transplant, there was a significant effect of seagrasses on pen clam survivorship with 80% mortality observed in sand flats and no pen clam mortality observed in seagrass beds (Figure 8c). Assessment of shell condition post-mortem revealed that clams typically remain buried in the sediment with intact shells, potentially indicating death by senescence or due to physical stressors. In our experiments, two clams showed potential signs of predation (shell was crushed), and two were not recovered. When mortality by predation was observed, shells/shell fragments were found within one meter of where clams were originally transplanted.

Transplantation experiments at varying densities revealed no significant effects of pen clams on aspects of seagrass ecosystem function and structure, i.e. seagrass growth seagrass density, or decomposition (ANOVA $p=0.642$, $p=0.393$, and $p=0.814$ respectively, Figures 9a-c). We also failed to detect a relationship between algal biomass and pen clam density (ANOVA $p=0.321$, Figure 3d). Because no metric of seagrass productivity differed across treatments, we did not further quantify sediment or seagrass nutrient content.
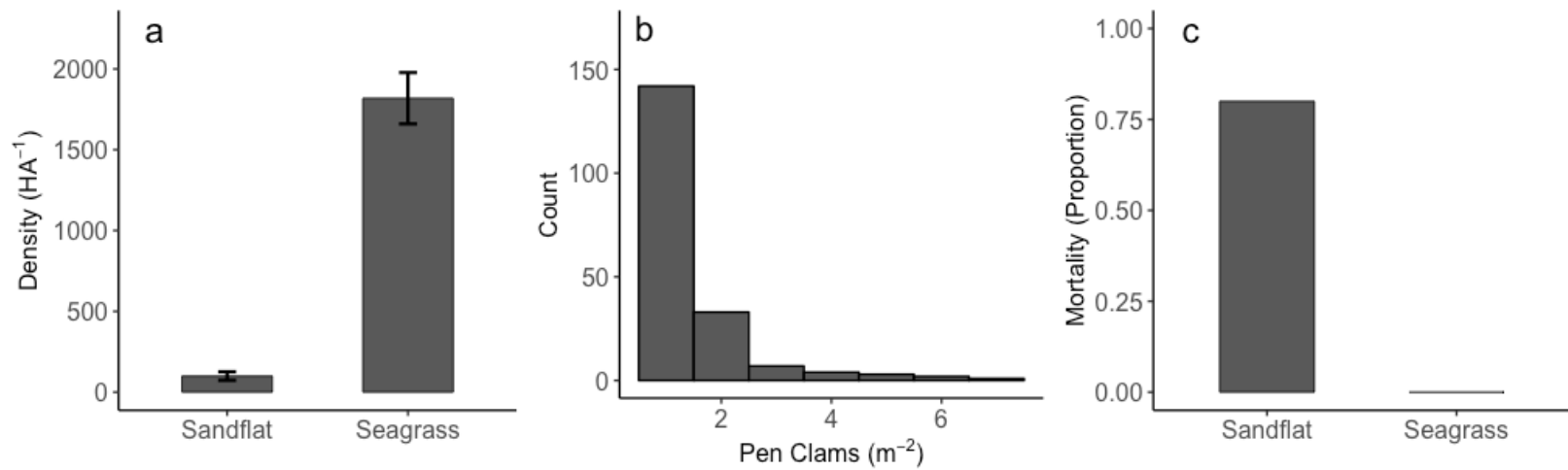
Figure 8: Pen clam surveys and survivorship of transplants.
a) Distribution and density from surveys of 13 seagrass beds and adjacent sandflats, b) Histogram of observed pen clam occurrences, and c) Observed mortality and location of transplanted pen clams. Error bars represent standard errors.
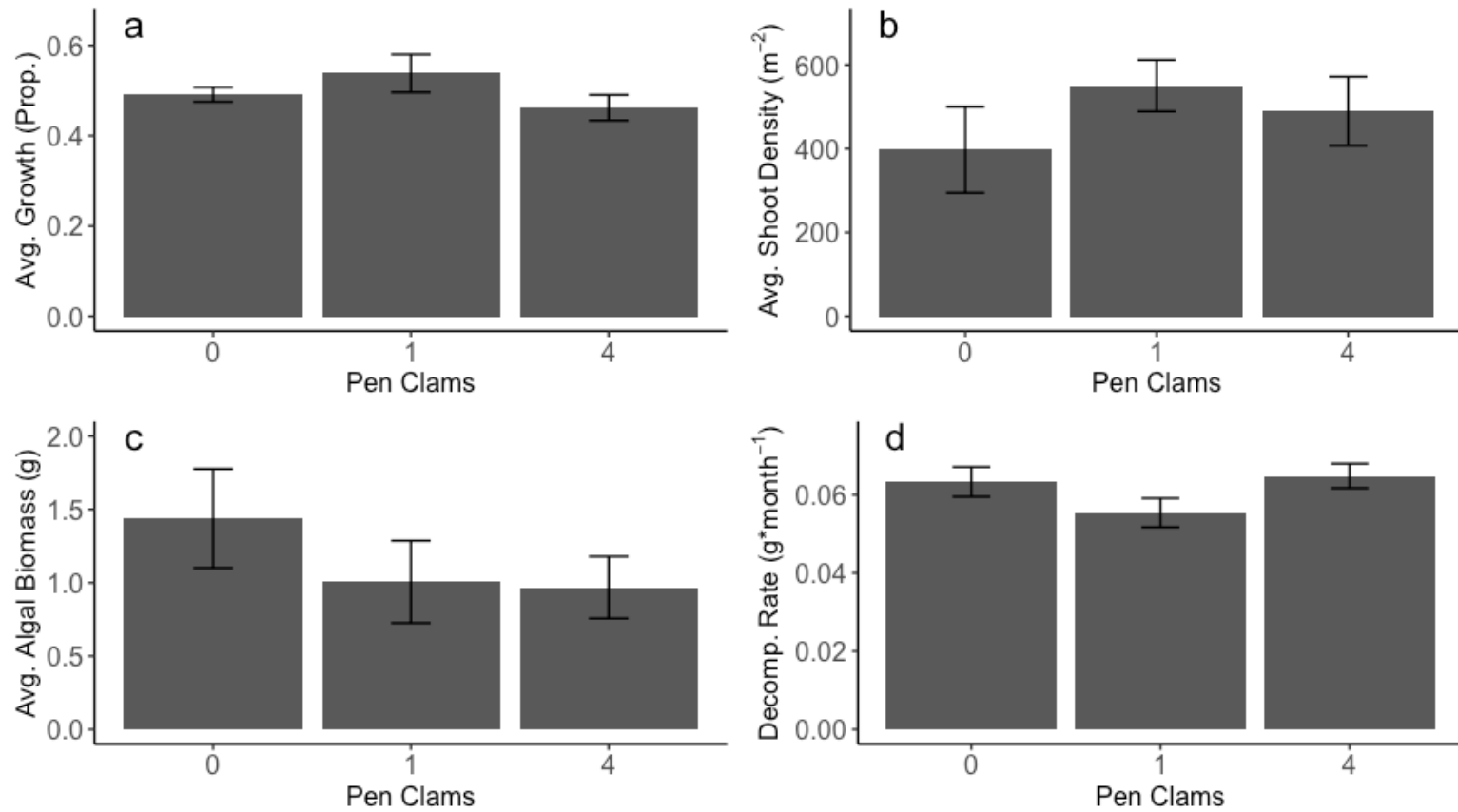
Figure 9: Ecosystem function responses from density-dependent pen clam transplant experiment.
a) Average proportional growth of seagrasses, b) average seagrass shoot density per m^2, c) average algal biomass per m^2, and d) decomposition rate (g/month).

Across all replicates, the number of unique species found increased with pen clam density with 37 species identified in the clam-absent treatment, and 41 and 59 species present in the one- and four-clam treatments, respectively. Moreover, community diversity measured as average species richness increased stepwise with increasing pen clam density and was significantly different between the zero versus four and one versus four pen clam treatments (ANOVA p=0.0043, Tukey Honest Significant Difference 0 vs. 4 p=0.002, and 1 vs. 4 p=0.016, Figure 10a). In particular, fouling invertebrates associated with epibiont communities (i.e. corals, anemones, barnacles, tunicates, sessile polychaetes, etc., ANOVA p<0.00, Figure 10b) and algal species significantly increased in richness with increasing pen clam density (ANOVA p<0.001). In contrast, species richness for other functional groups or communities assessed (e.g. nekton, seagrass, and algae-associated) did not vary significantly across treatments.

Total organismal abundance was not significantly different across treatments (ANOVA p=0.359). Because mesograzers (amphipods, isopods, and tanaids) constituted the vast majority of the community, and their abundance did not differ with respect to clam density, we removed mesograzers from the abundance analysis to more closely examine how the rest of the community varied with respect to clam density. In the absence of mesograzers, we found that overall organismal abundance was significantly greater with four pen clams present compared to the no-clam and one-clam treatments (ANOVA p=0.009, Tukey Honest Significant Difference 0 vs. 4 p=0.044 and 1 vs. 4 p=0.009, Figure 5a). Across all taxa, Shannon–Wiener diversity was greater at high pen clam density than both absent and one-clam treatments (ANOVA p=0.037, Figure 11b).

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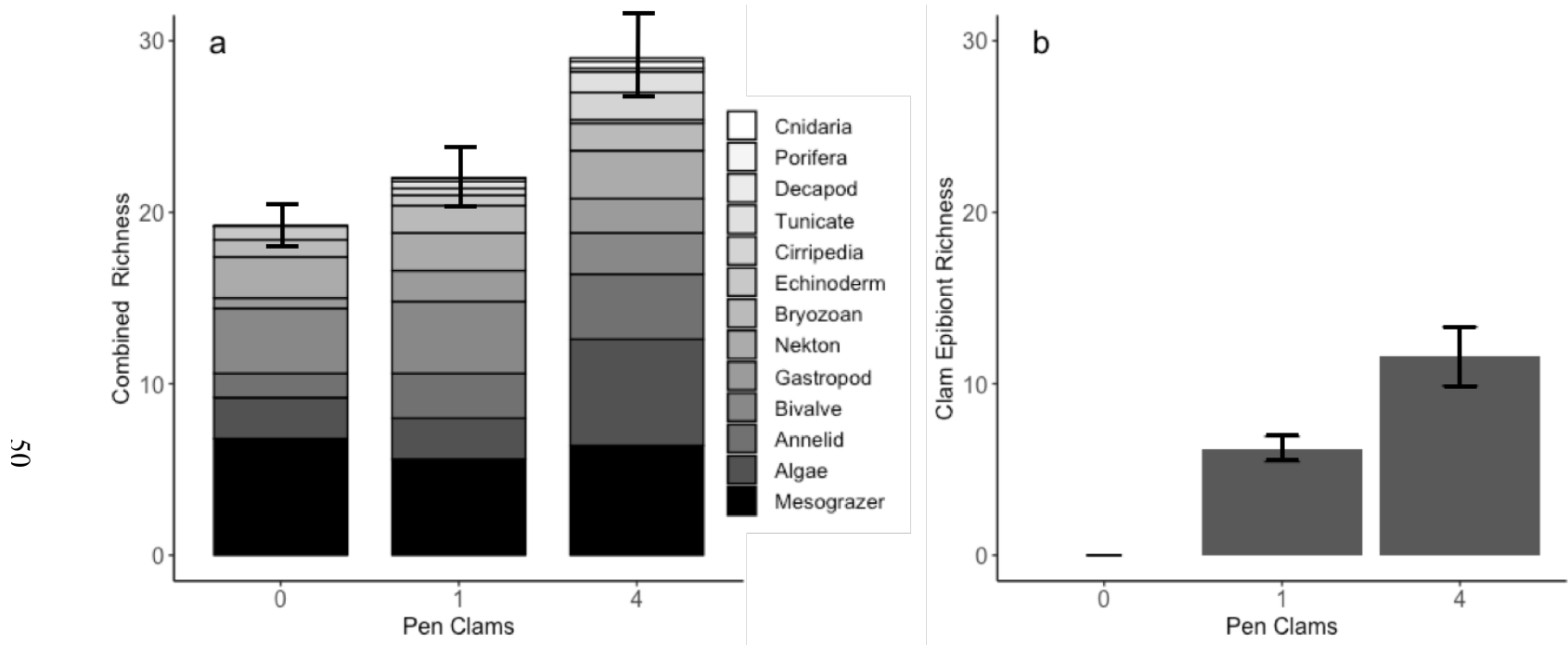
Figure 10: Quantified species richness in pen clam plots.
a) Nekton, algal, and shell communities averaged across treatments, gray-toned by taxonomic group, and b) Species richness of clam epibiont communities alone. Error bars represent standard errors.
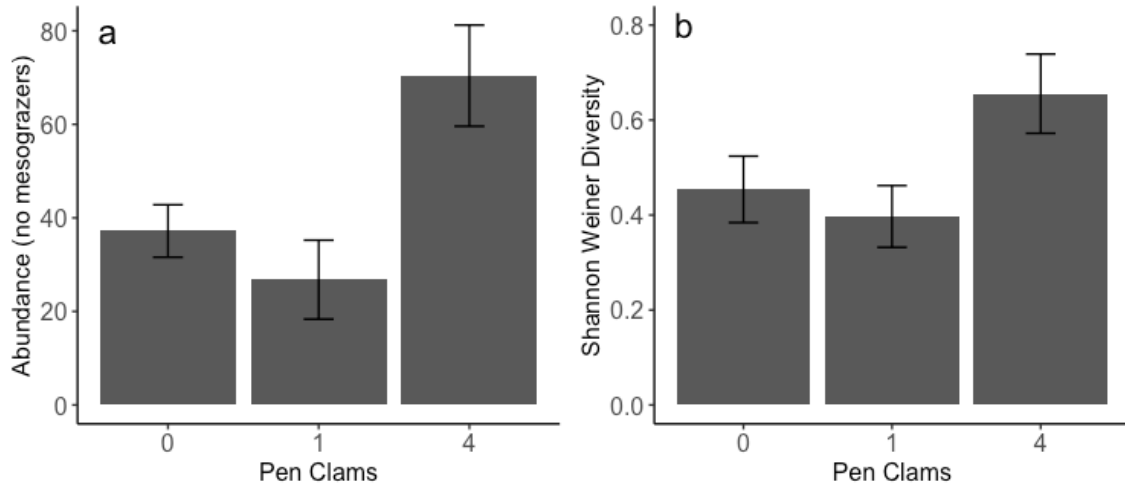
Figure 11: Effects of pen clams on a) abundance and b) Shannon-Wiener diversity.
Error bars represent standard errors.

Non-metric multidimensional scaling (NMDS) further indicated that there were differences between the community composition found across treatments (stress = 0.187, Figure 12) with communities sorting most strongly by pen clam density (NMDS 1, $R^2 = 0.88$, p=0.01) followed by algal biomass (NMDS 2, $R^2 = 0.61$, p=0.04). Species indicator analysis further identified that a barnacle (*Balanus eburneus*) and worms in the family, Terebellidae, were strongly associated with high-density clam treatments (p=0.001, and p=0.038, respectively) but not low density treatments.
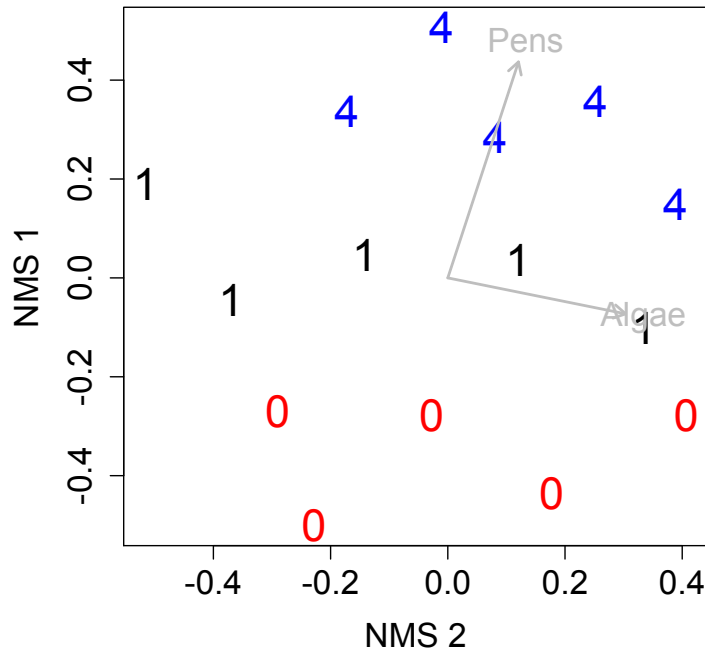
Figure 12: Nonmetric multidimensional scaling plot of pen clam communities.
Numbers and colors indicate clam density per plot (treatment). Gray arrows represent
correlation vectors where p<0.1. Stress = 0.187.

2.4 Discussion

2.4.1 A facilitation cascade enhances local biodiversity

Facilitation cascades between ecosystem engineers have been shown in numerous studies and habitats (e.g. salt marsh, temperate and tropical forests, mangroves, among others) to enhance ecosystem functions, biodiversity, and resilience to physiological stressors (Thomsen et al. 2010). Using a combination of observational and experimental studies, we found support for a facilitation cascade among seagrasses and pen clams in coastal North Carolina by showing that i) seagrasses support higher survivorship and densities of pen clams, and ii) pen clams act as secondary foundation species that enhance

local diversity, which scales positively with clam density. Our findings provide further evidence that under certain scenarios, beneficial interactions, such as habitat cascades, can play a structuring role in determining biodiversity in seagrass ecosystems.

Our survey data supports the conclusion that seagrasses positively influence pen clam density and survivorship, as pen clams were primarily found within seagrass habitats and not within neighboring sand flats. Our transplantation study further demonstrated that seagrasses promote the survivorship of pen clams, as 8/10 clams in sand flats died while all survived in seagrasses as of October 2018. There are likely multiple mechanisms by which seagrasses facilitated pen clam populations in our study. First, when seagrasses colonize an area they act as ecosystem engineers and, through their three-dimensional structure, alter the physical environment in ways that can facilitate clams including dampening wave energy, altering turbulence, and changing flow velocity among others (Fonseca et al. 1982, Ward et al. 1984, Gacia and Duarte 2001). Second, studies have shown that settlement of bivalve larvae is higher in seagrass beds compared to unvegetated habitats, (Bologna and Heck 2000), and bivalves within seagrass beds grow at faster rates than those in nearby sandflats (Peterson et al. 1984). Finally, structural complexity provided by seagrass roots, rhizomes, and canopies can mediate predator-prey interactions and has been shown in numerous studies to reduce predator efficiency and increase bivalve survivorship (as reviewed in Orth et al. 1984b, Heck and Orth 2006).

After secondary foundation species have established in seagrass beds, like pen clams, they can further provide microstructure that positively influences settlement of epibiota (Bologna and Heck 2000). Despite only exposing a small portion of their shell,

pen clams provide substantial sources of hard substrate when they establish on sand- or mud-dominated bottoms. This biogenic structure can promote the diversity of fouling organisms and macroalgae that require solid substrates for attachment (Keough 1984a). Our results supported this hypothesis, as plots with a higher density of pen clams had significantly greater species richness than low density plots. Thus, our findings highlight the often hierarchical structure of community organization, and the value of foundation species overlap in promoting local biodiversity.

2.4.2 Effects of functional diversity versus diversity *per se*

In our study, we found that pen clams increased diversity overall, but this increase occurred primarily in certain functional groups. Specifically, we found that pen clams increased the diversity of fouling organisms, including tunicates, barnacles, and encrusting sponges and bryozoans. There was, however, no difference detected in either amphipods or nekton across pen clam densities. This finding is consistent with the type of habitat pen shells provide relative to their occurrence in seagrass beds. Hard substrate for fouling organisms to settle upon and colonize is relatively rare in seagrasses, thus pen clams may selectively promote organisms reliant on attachment substrate. Complex, three-dimensional structure that amphipods and and fish depend upon for refuge and forage did not vary across treatments as both algal and seagrass biomass remained the same. Had plant structure and abundance differed, we would have expected to observe a greater change in mesograzer and nekton density that may have affected ecosystem functioning.

Although greater overall diversity did not directly translate into enhanced seagrass ecosystem functioning, we cannot definitively conclude that pen clams cannot alter

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ecosystem functions. Our findings do beg the question of the importance of overall diversity versus functional diversity. Many of the species promoted by pen clams were directly associated with the clam epibiont communities. However, several of these organisms (e.g. barnacles, bryozoans, boring sponges, etc.) may not functionally benefit seagrasses. Similarly, we also found an increase in macroalgae richness, but again, these organisms have generally been found to suppress rather than enhance seagrass growth (Hauxwell et al. 2001).

Though many previous studies have found links between diversity and enhanced seagrass productivity (Hughes and Stachowicz 2004, Reynolds et al. 2014, Duffy et al. 2015), these studies found that the key force underlying changes in primary productivity was an increase in epiphytic grazer diversity, which was more efficient in consuming epiphytic algae that could otherwise overgrow and suppress seagrass growth. In contrast, we did not find that pen clams increased mesograzer (i.e. amphipods, isopods, tanaids) diversity or abundance (Duffy et al. 2015). Had we observed an increase in mesograzers in relation to pen clam density, we hypothesize that we would have seen a concomitant increase in ecosystem function (Cardinale et al. 2002).

2.4.3 Bivalves as key drivers of seagrass structure and function

Bivalves play unique and foundational roles across multiple marine and aquatic systems (Vaughn and Hoellein 2018). The functional role bivalves play within an ecosystem, however, is context-dependent and strongly related to differences in life-history strategy, i.e. whether they are epibenthic or infaunal, solitary or reef-building, intertidal or subtidal, etc. (Vaughn and Hoellein 2018). As filter feeders, they affect benthic-pelagic

coupling, alter nutrient cycling, affect food webs and modify trophic subsidies to nearby habitats (Dame 2011). Many reef-building species also act as ecosystem engineers by creating and modifying habitat (Wells 1961, Bahr and Lanier 1981, Lenihan et al. 2001). Epibenthic and reef-building bivalves, such as oysters and mussels, may act as autogenic ecosystem engineers that create niche space for many small invertebrates thus enhancing local diversity (Wells 1961, Bahr and Lanier 1981, Grabowski and Peterson 2007, Gedan et al. 2014). They may also serve as substrate for algal epibionts which, in turn, may act as secondary engineers or foundation species (Gutiérrez et al. 2019). At high densities, however, they may compete with other foundation species for space (Menge 1976). In contrast, infaunal bivalves more often function as allogenic ecosystem engineers and can modify the physical environment by providing nutrient subsidies via pseudofeces, increasing oxygen penetration into the sediment, and stimulating microbial metabolism via bioturbation (Levinton 1995, Vaughn and Hakenkamp 2001, Mermillod-Blondin and Rosenberg 2006, Kristensen et al. 2012, Vaughn and Hoellein 2018). Moreover, many infaunal clams can further facilitate seagrasses by reducing sulfides in the sediment via a mutualistic interaction with bacteria that reside in their gills (van der Heide et al. 2012).

Our study examined a bivalve that is a mix of both infaunal and epibenthic. Though pen clams in our study region do not occur in high enough densities to form reefs, we found densities of up to 7 m^{-2} in our surveys, and in other regions of the world, pen clams have been found in aggregations of 14 m^{-2} (Escamilla-Montes et al. 2017). Despite having the majority of their shell buried beneath the sediment surface, bivalves can provide a substantial source of hard substrate for colonization in an otherwise soft bottom (Beckett

et al. 1996, Gribben et al. 2009). Post-mortem they can also serve as refugia for many small fish and crustacean species as their shells can remain intact and partially buried in the sediment for many months before degrading (Kuhlmann 1998, Gribben et al. 2017). Thus, we predict that the impacts of bivalves on seagrass functions are likely to vary not only with density but also with functional group. Specifically, we hypothesize that, while alive, infaunal bivalves will facilitate seagrass primarily by increasing nutrient availability in sediments and reduce sulfide stress in contrast to epifaunal bivalves that are more likely to promote biodiversity and nursery functions. Post-mortem, however, both infaunal and epifaunal bivalve shells that rise to the sediment surface can promote biodiversity via the provision of refugia and hard substrate (Gutiérrez and Iribarne 1999).

2.5 Conclusions

A large body of ecological research has focused on how cascades of negative trophic or competitive interactions can structure communities and are mediated by biodiversity (Finke and Denno 2004). Ecological studies have only begun to elucidate the important role of positive interactions and facilitation cascades in generating habitats and determining the distribution and abundance of biodiversity (Altieri et al. 2007, Angelini et al. 2011, Angelini et al. 2015, Thomsen et al. 2018). Our findings suggest that biodiversity in North Carolina seagrass communities is influenced by a facilitation cascade whereby seagrasses facilitate bivalves and in turn those bivalves facilitate fouling and algal diversity.

Our results also have implications for the conservation and restoration of seagrass ecosystems. Restoration of seagrasses that includes the simultaneous planting of both

primary and secondary foundation species such as seagrasses and bivalves is likely to yield greater biodiversity. Greater emphasis should be placed on the enhancement of habitat cascade units (secondary foundation species/ecosystem engineers) and whole ecosystems, not just primary foundation species, that promote positive interactions and ecosystem functioning (Zhang et al. 2018). We suggest that future ecological studies and conservation actions further incorporate facilitation cascades, as they are likely key but underappreciated drivers of spatial and temporal variation of biodiversity and function in seagrass beds.

CHAPTER 3. INCLUSION OF INTRA- AND INTERSPECIFIC FACILITATION REVERSES TRAJECTORY OF SEAGRASS RESTORATION FROM DECLINE TO GROWTH

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3.1 Introduction

Coastal ecosystems increasingly face a number of anthropogenic stressors that threaten their health, extent, and the numerous services they provide (Millenium Ecosystem Millenium Ecosystem Assessment 2005). Climate change, pollution, habitat destruction, overharvest of predators, among others, have contributed to the global loss or conversion of roughly 29% of seagrasses (Waycott et al. 2009), 85% of oyster reefs (Beck et al. 2011), and 42% of North American salt marshes (Gedan and Silliman 2009a). Because the decline of these habitats has massive implications for coastal services including fisheries production, storm and flood mitigation, pollution control, and carbon storage, countries

invest millions of dollars annually towards coastal conservation effort (Edwards et al. 2013, BenDor et al. 2015). Restoration has recently been elevated as a primary coastal conservation strategy by nations, corporations, and non-profit organizations to bolster shoreline ecosystems and communities, combat habitat losses in response to large-scale disturbances, compensate for adverse impacts, , and create jobs (CWA 1972, ERA 2000, RESTORE Act 2012, Edwards et al. 2013, Sutton-Grier et al. 2015, Sutton-Grier et al. 2018).

Unfortunately, coastal restoration is usually a costly endeavor. A hectare of restored salt marshes cost on average over 67,000 USD (107-28,800,000 USD), restored seagrasses cost on average over 106,000 USD (3,966-1866,385 USD), and restored oyster reef cost on average over 66,000 USD (4,490-1,419,856 USD) (Bayraktarov et al. 2016). Despite high initial costs in investment, restored ecosystems can increase the biodiversity and ecosystem services conferred by 44% and 35% compared to degraded habitats (Benayas et al. 2009). Regardless of these benefits, the need to make restoration more affordable and effective is paramount to not only increase return on investment but also to make these interventions more easily achievable and accessible to a greater number of coastal communities.

Planting designs in coastal habitat restoration have historically been derived from forestry science (Gedan and Silliman 2009b, Silliman et al. 2015, Shaver and Silliman 2017). This theoretical framework for restoration places an emphasis on maximizing outplanting yields by managing for the correct physical environment and planting propagules in designs aimed at minimizing competitive interactions (Halpern et al. 2007,

Gedan and Silliman 2009b). For example, for salt marshes, seagrasses and mangroves, the vast majority of coastal conservation agencies in the United States outplant propagules in dispersed, or plantation style arrangements in order to minimize resource competition (Silliman et al. 2015). In contrast, many ecological studies in coastal ecosystems have found that plants experienced increased growth when planted in clumps adjacent to neighbors of the same species, especially in situations of high physical stress as is often the case after systems are heavily degraded (Van Keulen et al. 2003, Bos and Van Katwijk 2007, Angelini et al. 2011, Silliman et al. 2015, Gittman et al. 2017b). This positive effect of neighbors during ecosystem recovery can be generated by multiple mechanisms, including group benefits associated with reducing oxygen stress in sediments (Howes et al. 1981, Howes et al. 1986) and decreasing erosional stress around transplants edges (Balke et al. 2012, Silliman et al. 2012). Incorporating positive species interactions such as these and other mutualisms has the potential to drastically increase restoration success and reduce costs (He et al. 2013, He and Bertness 2014). Indeed, small scale studies in salt marsh systems have shown that incorporating intraspecific facilitation can enhance outplant growth by over 100% (Silliman et al. 2015), and interspecific facilitation with mussels can increase resistance to climate stress (Angelini et al. 2015). Whether integrating such positive interactions can increase restoration success in other marine ecosystems, however, is not well explored (Zhang et al. 2018).

Seagrass systems are among the most productive marine ecosystems and provide numerous essential ecosystem services to coastal communities (Costanza et al. 1998, Barbier et al. 2011). In response to accelerated declines in seagrasses across the globe

(Waycott et al. 2009), efforts to restore seagrass beds have increased dramatically in popularity over the last 2 decades (Zhang et al. 2018). For example, re-seeding efforts in combination with widespread efforts to decrease estuarine nutrient enrichment and turbidity have led to the successful restoration of over 17,000 hectares of seagrass beds in coastal Virginia (Orth et al. 2012, Lefcheck et al. 2018) that support a diverse array of fishes, invertebrates, and algal species (Lefcheck et al. 2017). Similarly, efforts to restore seagrasses, particularly *Zostera noltii*, in combination with natural expansion of extant beds led to a three to four-fold increase in seagrass area in the Northfrisian Wadden Sea (Reise and Kohlus 2008). However, seagrass restoration success is highly variable; a meta-analysis of restoration trials found a 37% trial survival rate, potentially due to the small scale of restoration (van Katwijk et al. 2016). The mixed results of these studies emphasize that seagrass restoration can be successful at large scales but that there is also much room for improvement. Given that intra- and interspecific mutualisms and facilitations are common in seagrass systems, incorporating positive species interactions by design has the potential to substantially enhance conservation success (Palmer et al. 1997, Bos and Van Katwijk 2007, Halpern et al. 2007).

One potential way to harness facilitation in seagrass restoration is to plant them in aggregated rather than dispersed designs. Studies have shown that seagrasses planted in high densities or large patches self-facilitate to resist hydrodynamic stress (Van Keulen et al. 2003, Bos and Van Katwijk 2007). Moreover, clonal organisms such as seagrasses may more readily resist abiotic stressors via internal resource translocation that alleviates competition within populations (de Kroon 1993). Another technique to harness facilitation

is to utilize secondary foundation species such as bivalves. As filter feeders, bivalves have the capability to enhance benthic-pelagic coupling and benefit seagrass ecosystems (Officer et al. 1982, Dame et al. 1985, Smaal and Prins 1993). Removal of suspended solids can increase water clarity above oyster reefs, for example (Grizzle et al. 2008), and deposition of nutrient-rich pseudo-feces into the sediment by infaunal bivalves can also enhance seagrass growth (Wall et al. 2008). Studies that have added hard clams to extant beds have further found that clam addition can enhance overall bed reproductive effort (Poray et al pending). Additionally, some bivalve species that harbor sulfide-oxidizing bacteria on their gills, can facilitate seagrass growth by reducing soil sulfide stress (van der Heide et al. 2012). Thus, like aggregating outplants, the strategic use of bivalves in seagrass restoration has the high potential to improve restoration success, likely by allowing grasses to devote energetic resources towards seed and spathe production rather than photosynthesis. This is especially true if native bivalves are readily available through low-cost harvesting/relaying or through aquaculture that already focuses on cultivating bivalves for release into nature.

In North Carolina, USA, anecdotal accounts estimate that seagrass extent has declined by 50% from historical levels (Barrett et al. 2016). Large storms, ocean warming, construction, and nutrient and sediment runoff have all contributed to the loss of seagrass meadows (Barrett et al 2016, NC Sea Grant) that provide a multitude of ecosystem benefits including sediment retention, wave attenuation, and fisheries habitat. In particular, eelgrass and shoalgrass beds provide habitat for a diverse set of bivalves, and recent work has theorized that infaunal clams may facilitate seagrass growth and enhance community

diversity (Zhang and Silliman 2019). One of the most abundant clams in NC is the quahog, *Mercenaria mercenaria,* which is also the subject of extensive aquaculture such that large quantities of juvenile seed clams are readily available at low cost. We sought to determine the effects of intraspecific and interspecific facilitation between hard clams*, Mercenaria mercenaria,* and the seagrasses, *Zostera marina* and *Halodule wrightii* (eelgrass and shoal grass, respectively). In particular, we tested how i) hard clams affected germination and growth of seagrasses from seed, and ii) the separate and interactive effects of clam addition and seagrass planting configuration (aggregated vs. dispersed) on transplant growth, expansion, and persistence.

3.2 Materials and Methods

To examine the effects of intra- and inter-specific facilitation on seagrass restoration, we conducted two separate field experiments in the southern Outer Banks of North Carolina, USA.

3.2.1 Seed Planting

Reproductive eelgrass shoots were collected in April and May 2017 from a donor seagrass bed near Harker's Island, NC, USA. Shoots were stored within an indoor, flow-through seawater system at the Duke Marine Lab in Beaufort, NC, USA with a 12-hour light timer. When seeds had dropped from the spathes and shoots, excess plant material was strained from the tanks. Seeds were maintained in flow-through tanks until December 2017. Prior to planting, seed viability was tested using tetrazolium staining. We found that this seed collection had an average viability of 80%.

Seed planting experiments consisted of four treatments: bare, clam addition only, seeds only, and clams & seagrass (n=5). Because large clams could adversely bioturbate seagrass seeds, seed clams (<1cm width, ~0.8 cm umbo height) were purchased from a local aquaculture farm, Morris Farms, located in Sealevel, NC. Seed clams were stored in the same facility as seagrass seeds for 24 hours prior to deployment. Eelgrass seeds were planted at Oscar Shoals, NC in December 2017 at a density of 65 seeds (50 viable seeds) within a 20 x 20 cm quadrat to emulate naturally occurring seed densities in North Carolina (Livernois et al. 2017). For clam treatments, 10 seed clams were added within the plot to align with personal observations of naturally high clam densities. Both seeds and clams were manually covered with a thin layer of sediment (<5 cm) after planting.

Plots were monitored monthly from December through March, and biweekly in April, and May. In April and May, patch dimensions, shoot density, and grass growth were quantified. Seagrass growth was measured by marking 10 separate seagrass shoots approximately 1 cm below the sheath. After two weeks, marked shoots were collected and brought to the lab for processing. New and old growth area and biomass were measured to calculate proportional growth. At the end of May, plots were excavated and processed in lab to determine above and belowground biomass, shoot density, average shoot length, and reproductive effort measured as flowering shoot abundance, spathe abundance, and seed abundance.

Because bivalves can increase the supply of nitrogen available to seagrasses through biodeposition, we further measured the carbon content (%C), nitrogen content (%N) and carbon to nitrogen ratio (C:N) by clipping, drying, grinding, and acidifying (to

remove inorganic nitrogen) samples of above and belowground biomass. CHN analyses were run by the Duke Environmental Stable Isotope Laboratory on a CE FlashEA 1112 (ThermoFisher Scientific, Waltham, Massachusetts, USA).

Statistical differences across treatments were calculated using a Student's T-test comparing seed-only and clam & seed treatments, as no seagrass growth was observed at either bare or clam-only treatments.

3.2.2 Adult Transplants

To directly test for potential differences between intra and inter-specific facilitation on adult shoot transplant growth, we conducted a fully-factorial experiment crossing planting arrangement (aggregated versus dispersed) with clam additions (n=7 replicates). Patches were transplanted from a nearby seagrass bed into an adjacent sandflat (<400 m away) that was determined from historical maps to have supported seagrass beds in the past at south Core Banks, NC. Each patch was a total of 625 cm^2 in area. Harvest-sized clams were purchased from local fishers and stored in flow-through seawater facilities for 24 hours prior to deployment. Experiments were conducted from June through September 2018. Plots were monitored for seagrass density and patch dimensions, and pressed monthly to maintain clam density when obvious signs of mortality (shell fragments) were observed. We were unable to obtain samples for Carbon: Nitrogen analyses as experiments were abruptly concluded in September 2018 as a result of Hurricane Florence.

3.3 Results

3.3.1 Seed Planting

When planted alone, seagrasses were significantly shorter in length than when planted with clams (p = 0.013, Figure 13A). Additionally, patches with clams expanded on average 400% from their initial (March) area; whereas, patches without clams did not change significantly in size (p=0.023, Figure 13B). This greater patch size occurred concomitantly with a significantly greater belowground biomass in plots with clams at experiment end (p=0.011, Figure 13C). Total aboveground biomass was similarly greater in the presence of clams, and the difference was marginally significant (p=0.074, Figure 14A). Reproductive effort, measured as both the average number of spathes per shoot and average number of seeds per shoot, was also marginally enhanced in the presence of clams (p=0.058 and p=0.065, Figure 14B and 14C, respectively). Subsequently, we found that clams were associated with a marked 276% increase in average reproductive shoot length, 500% total plot reproductive shoot biomass increase, and 480% enhancement of total plot spathe abundance; however, the difference was not significant (p-value=0.1156, p-value=0.1575, p-value=0.1519, Figures 15A-C, respectively). C:N content in leaves and rhizomes was also significantly different between clam addition versus absent treatments (p-value=0.0047, p-value=0.0053, Figures 16A and 4B).
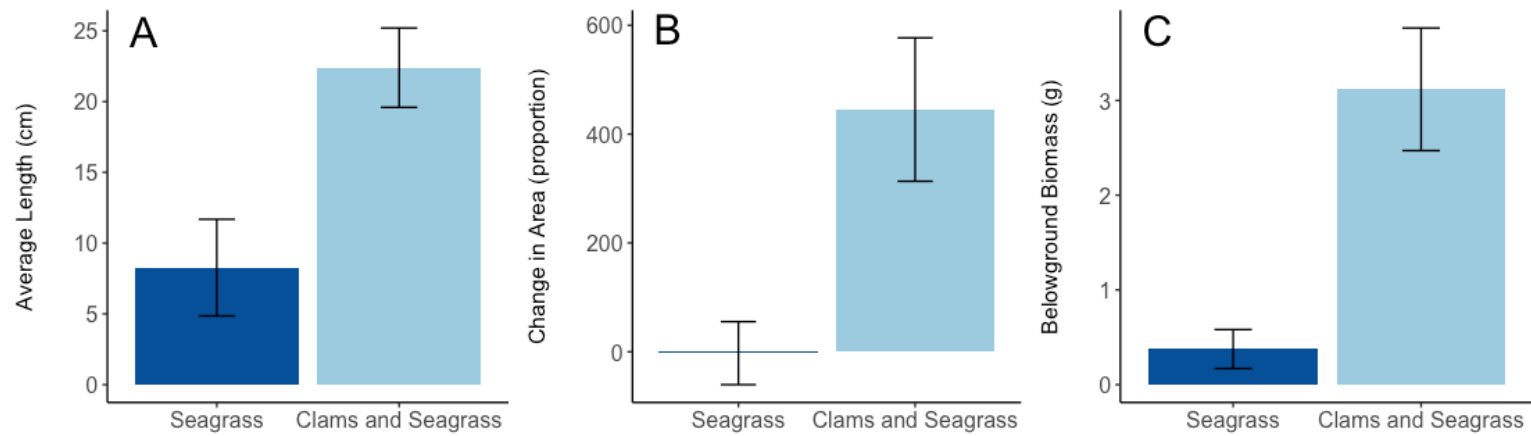
Figure 13: Statistically significant effects of clam additions.
Adding clams to seagrass seeds was found to significantly increase the A) average shoot length, p-value = 0.013, B) proportional change in patch area, p-value = 0.023, and C) belowground biomass, p-value = 0.011. Error bars represent 1 standard error.
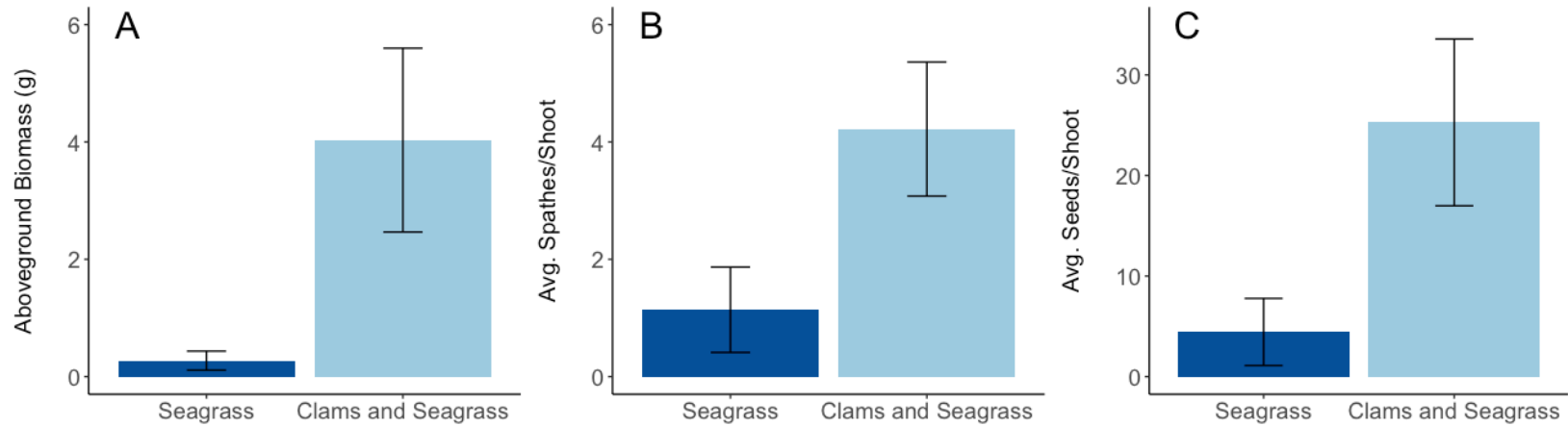
Figure 14: Marginally significant effects of clam additions.
Adding clams to seagrass seeds was found to marginally increase the a) aboveground biomass, p-value = 0.074, and patch reproductive effort measured as the b) average number of spathes per reproductive shoot, p-value = 0.058, and c) average number of seeds per reproductive shoot, p-value = 0.065. Error bars represent one standard error.
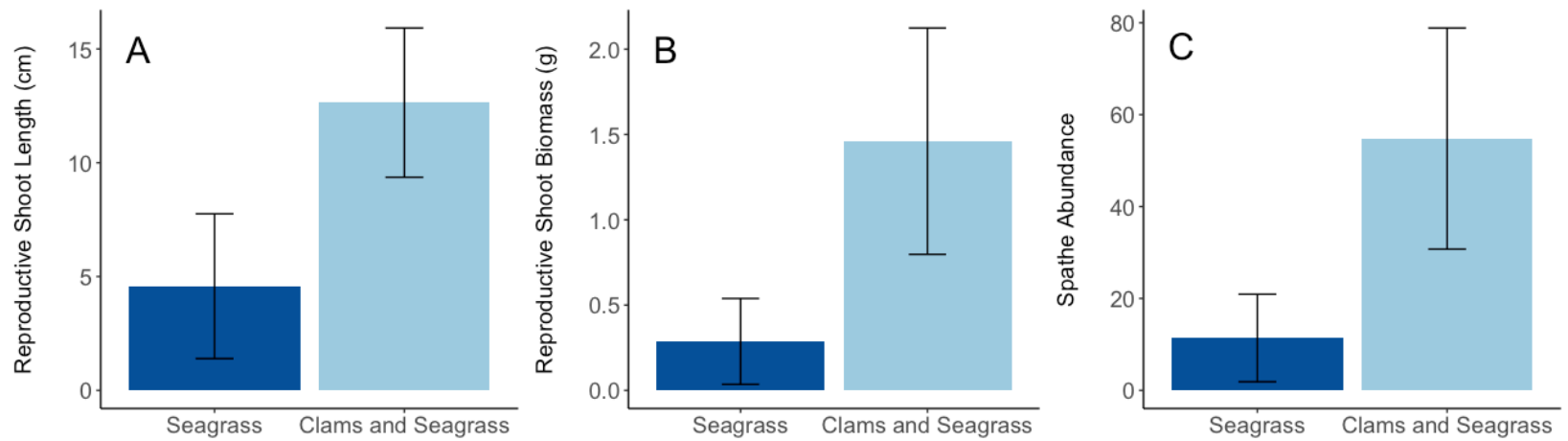
Figure 15: Non-significant clam-enhanced response variables.
Clam additions were found to lead to a) 276% increase in reproductive shoot length and subsequent b) >500% increase in reproductive shoot biomass, and c) 480% increase in patch spathe abundance. Error bars represent one standard error.
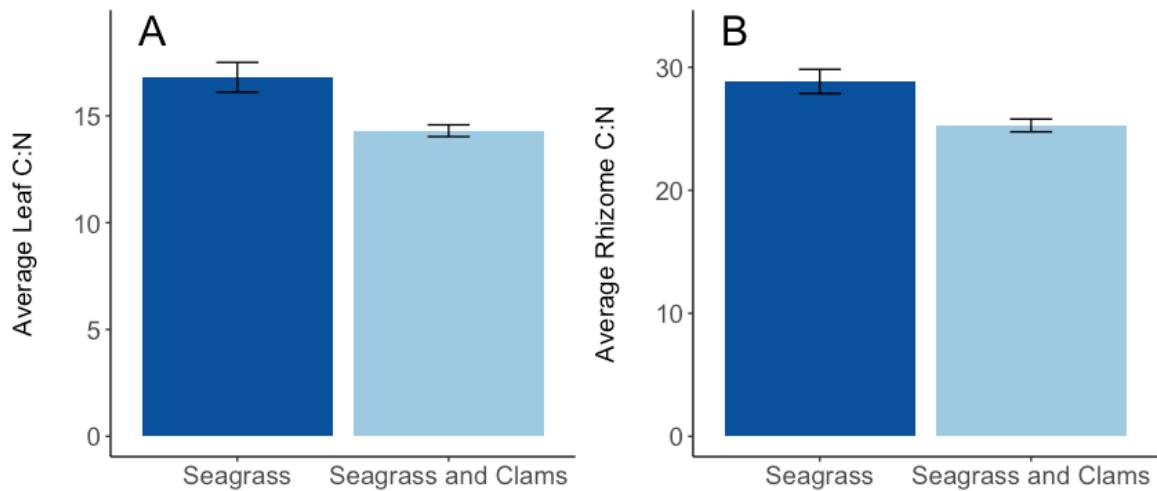
Figure 16: Carbon: Nitrogen ratios from seagrasses grown from seed.
A) Aboveground, p-value=0.0047, and B) Belowground biomass, p=0.0053. Error bars represent one standard error.

3.3.2 Adult Seagrass Planting

Our experiment did not find evidence to support an effect of clams on the success of adult seagrass transplants. In contrast, planting configuration was significantly associated with the proportional change in shoot density at experiment end (p<0.001, Figure 17A). Transplants that were configured in a dispersed arrangement consistently lost shoots throughout the experiment duration; whereas, aggregated transplants gained shoots. Subsequently, patch area was significantly greater for aggregated transplants compared to dispersed at experiment end (p<0.001, Figure 5B). The overall proportional amount of area change over the duration of the entire experiment from June to September was also significantly greater for aggregated patch configurations compared to dispersed (p=0.002, Figure 5C). Aggregated patches tended to increase in patch size over the experiment duration; whereas, dispersed treatments all declined in area.
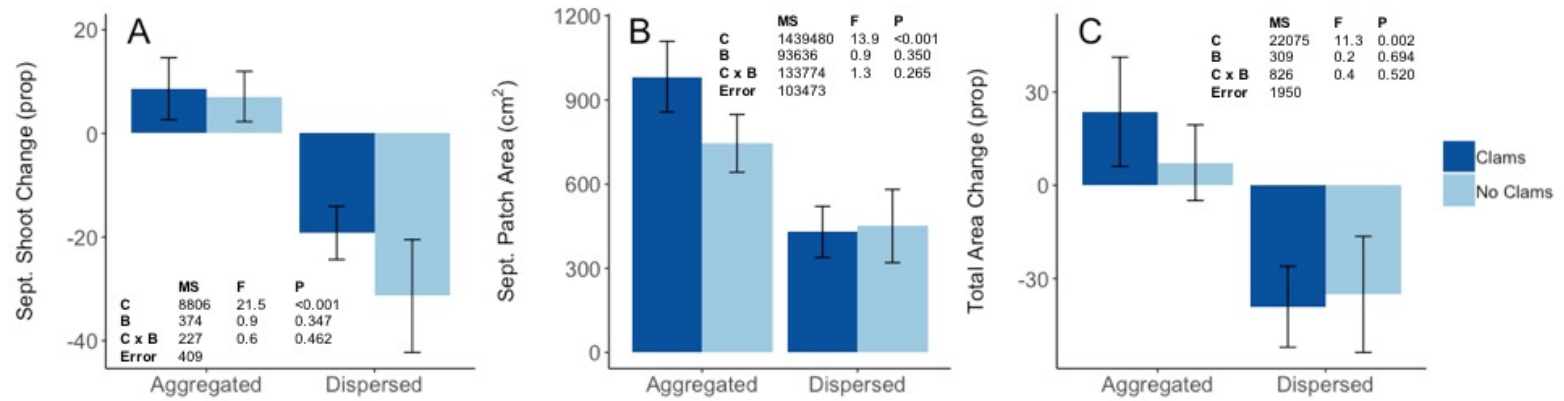
Figure 17: Figure 5. Interactive and separate effects of adult planting configuration and clam addition.
A) Proportional change in shoot density from August to September. B) Patch area at experiment end in September. C) Total change in patch area over experimental duration from June to September. Probability value given for two-way ANOVAs testing for main and interactive effects. C is the main effect of planting configuration, and B is the main effect of clams. Error bars represent one standard error.

3.4 Discussion

Facilitations and mutualisms are powerful species interactions that play important roles in the organization and resilience of coastal systems. Foundation species, such as seagrasses, marsh cordgrasses, oyster reefs, and forest trees, facilitate the generation of whole-ecosystems by providing habitat and ameliorating stressful environmental conditions for countless organisms (Dayton 1972a, Bruno et al. 2003). Multiple studies have further demonstrated the keystone role of positive interactions for enhancing ecosystem resistance to and recovery from disturbance (He et al. 2013, He and Bertness 2014, Thomsen et al. 2018). Facilitative interactions in coastal systems can be critical for resisting ecosystem transformations to alternative stable states (Holmgren et al. 1997).

Positive interactions have been shown to be more common in environmentally stressful regions where drought or heat stresses are frequently high (He et al. 2013). Natural, self-organized patchiness is also more frequent in intertidal ecosystems where there are significant environmental and temporal constraints on organism establishment and growth (Rietkerk et al. 2004, van de Koppel et al. 2005). In North Carolina, the two dominant species of high-salinity submerged aquatic vegetation, *Z. marina* and *H. wrightii*, co-exist at the limit of their thermal tolerances. Given these conditions, positive interactions that promote resilience to environmental stress are likely to be more prevalent and important for seagrass persistence and recovery from physical disturbance.

Because restoration usually takes place in areas that have or currently experience increased physical stress, it is necessary for methodologies to consider and include approaches that can enhance resistance to physical stressors. Here we demonstrate that

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including positive interactions at two different seagrass life stages reverses seagrass restoration trajectories from decline to growth. At the seed stage, we found that interspecific interactions with clams was associated with greater shoot length as well as patch expansion, and belowground biomass. In contrast, clam addition was not found to significantly affect the productivity of transplanted adult seagrass patches. Nitrogen content in both leaves and rhizomes of seagrasses grown from seeds with clams, however, was significantly greater than without clams, suggesting that organic matter deposited as feces from bivalves may elevate early seagrass growth (Peterson and Heck Jr 2001b). Combined with results from other studies that have found clam addition to existing seagrass beds leads to greater reproductive effort but not growth (Poray et al, *in prep*), our findings further suggest that the addition of nutrients via pseudofeces from clams may have a particularly vital role in the early stages of seagrass development and expansion by seed but shift in effect for later life-stages. In addition to nitrogen deposition, bivalves may facilitate seagrasses by reducing epiphyte loads (Peterson and Heck Jr 2001b, a). In the context of infaunal bivalves and our experiment, two additional mechanisms may occur: 1) bivalves consume epiphyte propagules prior to attaching to seagrass blades, or 2) enhanced growth rates lead to greater leaf turnover and thus less accumulation of epiphytes on grass blades (Peterson and Heck Jr 2001b, a).

Intraspecific facilitation is particularly important in clonal plants, such as seagrasses, as clonal integration allows for more efficient recycling and distribution of resources via the continuous recruitment and mortality of shoots within the same individual (Duarte et al. 2005). When planted as adult shoots, we found that intraspecific interactions

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between seagrass transplants played a greater role in patch persistence and expansion than clam presence. Patches planted in an aggregated rather than dispersed layout all increased in both shoot density and area. We hypothesize that when planted as a clump with rhizomes intact, multiple mechanisms may occur related to intraspecific facilitation and nutrient limitation. First, seagrasses planted in low nutrient soils can more efficiently utilize and retain nutrients under stressful conditions via leaf abscission and loss i.e. nutrient reclamation through resorption (Cebrian 1999, 2002). Internal recycling of nitrogen can reduce annual nitrogen requirements by 25% in eelgrass beds (Hemminga et al. 1991). Thus, larger patches may be able to self-sustain low-nutrient conditions better than small patches (Pedersen and Borum 1992, 1993). Moreover, nitrogen reclamation has been found to account for at least 12% of nitrogen incorporated into newly grown tissues, as is often the case for restoration outplants (Pedersen and Borum 1993).

Another mechanism by which clumping could have increased grass growth is via reduction of sediment redox stress. Organic carbon and oxygen release from the roots and rhizomes of seagrasses can have a major influence on sediment conditions and processes (J. O'Donohue et al. 1991, Pollard and Moriarty 1991, Blackburn et al. 1994). Given that coastal sediments can become anaerobic just a few millimeters to centimeters below the sediment surface (Terrados et al. 1999), the shunting of oxygen from seagrass leaves to rhizomes represents a significant source of oxygen to the rhizosphere. Oxygen loss to the rhizosphere is vital to protect root tissues by oxidizing reduced phytotoxins (Mendelssohn and Postek 1982, Armstrong et al. 1996, Hemminga 1998), contributing significantly to aerobic mineralization of organic matter within the sediments (Sand-Jensen et al. 1982),

and sulphide reoxidation (Lee and Dunton 2000). Thus, clumped and densely planted seagrasses may also positively facilitate one another by relieving anoxia stress at the patch level. However, empirical evidence is still needed to determine if passive diffusion of oxygen into the substrate can be used be neighboring plants similarly to marsh grasses (Howes et al. 1986, Bertness 1991). Although our findings suggest that interspecific facilitation affected early-stage seagrasses, whereas intraspecific facilitation enhanced late-stage/adult seagrass productivity, use of these restoration techniques in other scenarios or at other sites may provide additional benefits and results. For example, restoration of seagrasses in areas with sulfide-reducing lucinid clams may further enhance restoration yields of restored adult seagrasses (van der Heide et al. 2012). Moreover, planting in clumped, high-density configurations is advantageous for withstanding shear stress from waves (Peterson et al. 2004, Bos and Van Katwijk 2007). The general, applied implications of our study are that clumping and clam additions are likely to enhance restoration yields, especially under high stress scenarios. Therefore, it is important to consider site characteristics and variations in facilitation strength when determining whether to incorporate positive interactions into coastal restoration designs and to test for both clumping and clam addition at the seedling and adult stage at other sites.

Our experiments provide further evidence and rationale for including facilitation into restoration designs of all seagrass restoration projects. Although we were limited in size and time, our study has multiple implications for larger scale restoration efforts. In particular, our findings that planting seagrass seeds with seed clams resulted in a 4-fold increase in patch size and a 5-fold increase in reproductive effort has the potential to greatly

reduce the number of seeds needed to ensure whole meadow restoration. Though supplementing seagrass restoration with infaunal bivalves adds an additional cost to restoration, the cost is likely minimal compared to other restoration techniques (e.g. regrading in salt marshes, restoring oyster reefs with pre-seeded materials, etc., (Bayraktarov et al. 2016) or replanting after a failed restoration attempt. Moreover, the purchase of clams may also present a significant boon and chance for collaboration with shellfish hatcheries, particularly if they are local to the restoration area.

Our study adds to the growing amount of literature that calls for the inclusion of positive interactions and facilitation theory into restoration designs of all coastal ecosystems (Silliman et al 2015, Shaver and Silliman 2018, Zhang et al 2018, Renzi et al 2019, Valdez et al in review). Whereas, many coastal restoration methodologies focus on reducing competition or threats to outplants by minimizing species interactions (Halpern et al 2007), our findings suggest that utilizing inter- and intraspecific facilitation has the potential to greatly increase restoration yields. These small changes in methodology represent could significantly enhance restoration efficiency at little to no extra cost. Moreover, as restoration moves towards an ecosystem- rather than single-species approach (Palmer et al. 1997), designs that incorporate whole-community facilitation and restoration, such as restoring primary and secondary foundation species or multi-habitat restoration, are more likely to improve the scale and success of restoration efforts as a whole.

CHAPTER 4. LARGE PREDATOR REGULATION OF MESOCONSUMERS IN A SEAGRASS ECOSYSTEM

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4.1 Introduction

The degradation of marine ecosystems over the last century has been extensive with far-reaching ecological effects (Jackson et al. 2001), Millenium Ecosystem Assessment (2005), (Lotze et al. 2006). Anthropogenic impacts including habitat destruction, eutrophication, climate change, and overfishing can have dramatic direct and indirect effects on coastal systems (Jackson et al. 2001, Lotze et al. 2006). Determining the drivers, mechanisms, and thresholds of ecosystem collapse and recovery is a fundamental tenant of ecology and crucial for implementing effective marine conservation. Understanding how

species interactions and changes in consumer populations in particular, is of paramount importance for stabilizing shifting food webs and preventing further ecosystem degradation (Pauly et al. 1998, Alheit 2009)

Trophic cascades are indirect, top-down effects on two or more trophic levels of ecosystems (Hairston et al. 1960, Paine 1980, Menge 1995). Shifts in trophic diversity and dominance at the top of food webs can propagate downward and laterally to induce drastic changes in overall ecosystem biodiversity and vegetation (Sih et al. 1985, Menge 1995, Jackson et al. 2001, Burkholder et al. 2007, Estes et al. 2011). When predators do not suppress prey populations, booming prey populations, especially of herbivores, can drastically reduce plant biomass and overgraze crucial habitat-forming foundation species (Carpenter et al. 1985, Terborgh et al. 2001, Silliman and Bertness 2002). Consumer fronts can cause large-scale degradation across ecosystems and has been documented in snails and crabs in temperate marshes (Silliman et al. 2005, Holdredge et al. 2009), bark beetles in forests (Hard et al. 1983), insects in mangroves (Anderson and Lee 1995), urchins grazing on kelp forests (Estes and Palmisano 1974, Scheibling et al. 1999), among others (see Silliman et al 2013).

The harvest and removal of large predators in marine systems has been linked to massive food web shifts and alternative stable states (Pauly et al. 1998, Jackson et al. 2001, Essington et al. 2006, Myers et al. 2007, Estes et al. 2011). Multiple controlled experiments (Menge 1995) as well as inferences from historical data (Dayton et al. 1998, Jackson et al. 2001) and fisheries data (Botsford et al. 1997, Pinnegar et al. 2000) have demonstrated that top-down forces can have community-wide impacts. One of the most well-known

examples of trophic cascades is that of the decline of the great sharks in the western Atlantic (Myers et al 2007). Decades of overfishing is hypothesized to have depleted populations of large coastal sharks, releasing their prey, specifically cownose rays (*Rhinoptera bonasus*), from predation. Subsequent increases in cownose ray populations and feeding caused the collapse of bay scallop (*Argopecten irradians concentricus*) populations (Myers et al. 2007). In North Carolina, cownose rays are known to immigrate into the region from warmer, southern waters in mid-spring, disperse throughout the estuary while in transit to the Chesapeake Bay in the summer, and emigrate back south in late Autumn (Goodman et al. 2011). During their migration, cownose rays travel in large schools i.e. "fevers," with estimated sightings ranging from 500 to upwards of 1000 in one day of surveying a single estuary (Goodman et al. 2011). Small-scale experiments (1 m^2 plots) have found that exclusion stockades can prevent rays and other potential predators from causing localized bay scallop extinctions (Peterson et al 2001).

However, the shark-ray-scallop trophic cascade has been challenged in recent years with competing datasets suggesting a lack of temporal correlation among population shifts (Grubbs et al. 2016). Moreover, scallops are consumed by multiple different species in addition to cownose rays. Small invertebrate consumers such as xanthid crabs amphipods, isopods, and shrimp can exert strong top-down control on juvenile scallops (Milke and Kennedy 2001, O'Connor et al. 2008, Rindone and Eggleston 2011, Lefcheck et al. 2014), and larger crustacean predators such as blue crabs, *Callinectes sapidus*, are also major consumers of bay scallops (Eggleston et al. 1992, Seitz et al. 2001, Floyd and Williams 2004, Miron et al. 2005). These mesopredator populations are also strongly controlled by

apex predators such as sharks and other large finfish that aren't considered in the trophic cascade, thus a more comprehensive view and test of direct and indirect effects of large consumers within seagrass food webs is needed.

Here, we report the results from a large-bodied predator exclusion experiment in coastal seagrass beds. Whereas previous studies in this system have employed observational data to infer a trophic cascade or used small mesocosm experiments to test species interactions, we sought to take our experiments a step further and directly examine how removing large predators (via exclusion stockades) would alter whole community dynamics, including the seagrass bed itself. Specifically, we asked how and if predator exclusion from seagrass beds 1) altered nekton community dynamics, and 2) scallop abundance and 3) seagrass productivity. Using a combination of surveys, mapping, and mark-recapture techniques within manipulative plots, we found support for a large-predator driven trophic cascade that affected mesopredator and scallop populations but did not propagate down to observed effects on the primary producer.

4.2 Methods

4.2.1 Study Location and Stockades

We conducted our experiment in seagrass beds in Core Sound, North Carolina, adjacent to the southern Core Banks (Figure 18). Seagrass beds in North Carolina are largely seasonal and dominated by eelgrass, *Zostera marina* (Linnaeus, 1753), shoalgrass, *Halodule wrightii* (Ascherson, 1868), and widgeongrass, *Ruppia maritima* (Linnaeus, 1737). In North Carolina, both shoalgrass and eelgrass are at their geographic and thermal

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limits such that peak productivity occurs in spring through summer (March-September)

(Thayer et al. 1984).

Figure 18: Map of large predator exclusion plots in South Core Sound, NC.

To test for effects of large predators at the edge of seagrass beds, we conducted a large predator exclusion experiment at the edge of an extensive, continuous seagrass meadow from May 2017-August 2018. We built 5x5 m exclusion stockades, exclusion controls, and open control plots (n=9 after removal of outlier plots) along the edge of an extensive seagrass meadow known to have high cownose ray densities from previous surveys. Full exclusion stockades were built from 2.5 m tall bamboo poles (average diameter 6 cm), sunk at least 60-80m into the ground, with one pole every 25 cm. Exclusion/cage controls consisted of one pole every meter, and open/control plots were marked by one pole at each corner. Thus, organisms wider than 25 cm were excluded or deterred from entering plots, but smaller organisms could freely pass through cages.

4.2.2 Seagrass Mapping and Characterization

Prior to the experiment and at the beginning and end of each growing season (i.e. May and October 2017 and 2018), we surveyed plots for overall seagrass percent cover, fine-scale seagrass cover, seagrass biomass. The edge of the seagrass bed within plots was mapped in May and October 2018 using a Trimble® Real Time Kinematic (RTK) Global Positioning System (GPS). The RTK base station was located on a published benchmark (865-6539 D).

Fine-scale cover by seagrass species was estimated from three randomly placed 0.5 x 0.5 m quadrats within each plot. We further collected one 30 cm diameter core (10 cm deep) from each plot per survey. Cores were brought back to the laboratory for processing where all seagrass was sorted by species and enumerated, and the heights for 10 random

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shoots per species were measured to the nearest millimeter. Aboveground biomass, divided by species, and belowground biomass was separated and dried at 60ºC for at least 48 hours.

Because caging can cause indirect effects on water flow, we further quantified alteration to fluid dynamics using gypsum blocks made of plaster of Paris glued to Vexar attached to paving bricks. Blocks were pre-weighed and deployed within cage centers for 48 hours. Loss in weight was calculated and used as a relative measure of flow within cages.

4.2.3 Seagrass Community Surveys

To determine how and if seagrass community composition was altered by exclusion cages, we quantified both infaunal macroinvertebrates, epifaunal bivalves, and mobile nekton using a variety of survey techniques. Macroinvertebrate fauna (larger than 0.5 cm) within cores was identified to species and noted for presence-absence. Epifaunal bivalves, specifically bay scallops, were quantified from snorkel surveys in May and October of 2017 and 2018. Mobile nekton was quantified monthly in summer 2018 (June-September) using scientific gill nets and minnow traps placed within plots. Nekton samples were standardized to catch per unit effort (CPUE) comprised of one gill net survey and two minnow traps. Gill nets were 7 m long x 1.5 m tall composed four 1.5 m panels of 0.65 cm, 1.27 cm, 2.5 cm, and 5 cm mesh. Nets were soaked at night during falling tides for five hours to capture animals as they egressed from the seagrass beds. Moreover, we soaked 2 minnow traps per cage to quantify smaller nekton during the day. Minnow traps were soaked for six hours from mid-rising tide to mid-falling tide to coincide with dusk.

4.2.4 Predation Assays

To assess if exclusion cages reduced bivalve predation or affected survivorship, as opposed to potentially altering settlement, we conducted mark-recapture experiments with bay scallops. Bay scallops were collected locally, brought to the lab and marked with paint for recapture. Within each cage, we deployed 10 scallops and monitored survivorship daily for the first three days and then weekly for the month after. When mortality was observed, shell condition was recorded (crushed, intact, etc.). Scallops were not replaced.

4.3 Results

4.3.1 Nekton Communities

Survey efforts were standardized Catch Per Unit Effort (CPUE) such that each sample community was the representation of one gill net and two minnow traps. Nekton size (i.e. length) was significantly different across treatments (ANOVA p = 0.003, Figure 19A). Specifically, we found a significant difference between exclusion plots and open control plots (TukeyHSD p=0.002) and a marginally significant difference in nekton size between exclusion and exclusion control plots (Tukey HSD p=0.074). Exclusion plots had, on average, smaller nekton sizes than both exclusion control and open control plots.

Nekton diversity measured as species richness was also significantly different across treatments (ANOVA P=0.0204, Figure 19B). Higher diversity was observed in exclusion plots compared to exclusion control and open control plots. (Tukey HSD p=0.002 and p=0.108, respectively). Nekton biomass calculated as grams per catch was not significantly different across treatments (ANOVA P=0.955, Figure 20A). In contrast, nekton abundance per unit effort was significantly different across treatments (ANOVA

P=0.0267, Figure 20B). Specifically, we found that exclusion plots had, on average, greater abundance than open control plots (Tukey HSD p=0.020), and nekton abundance in exclusion control plots was marginally greater than open control plots (Tukey HSD p=0.108). Further examination of changes with respect to size-delimited functional groups revealed significant differences in mesopredator abundance (ANOVA P = 0.041, Figure 21). Exclusion plots had significantly more fish mesopredators and marginally more crustacean mesopredators than exclusion control and open control plots (Tukey HSD p = 0.043, p = 0.087, respectively).
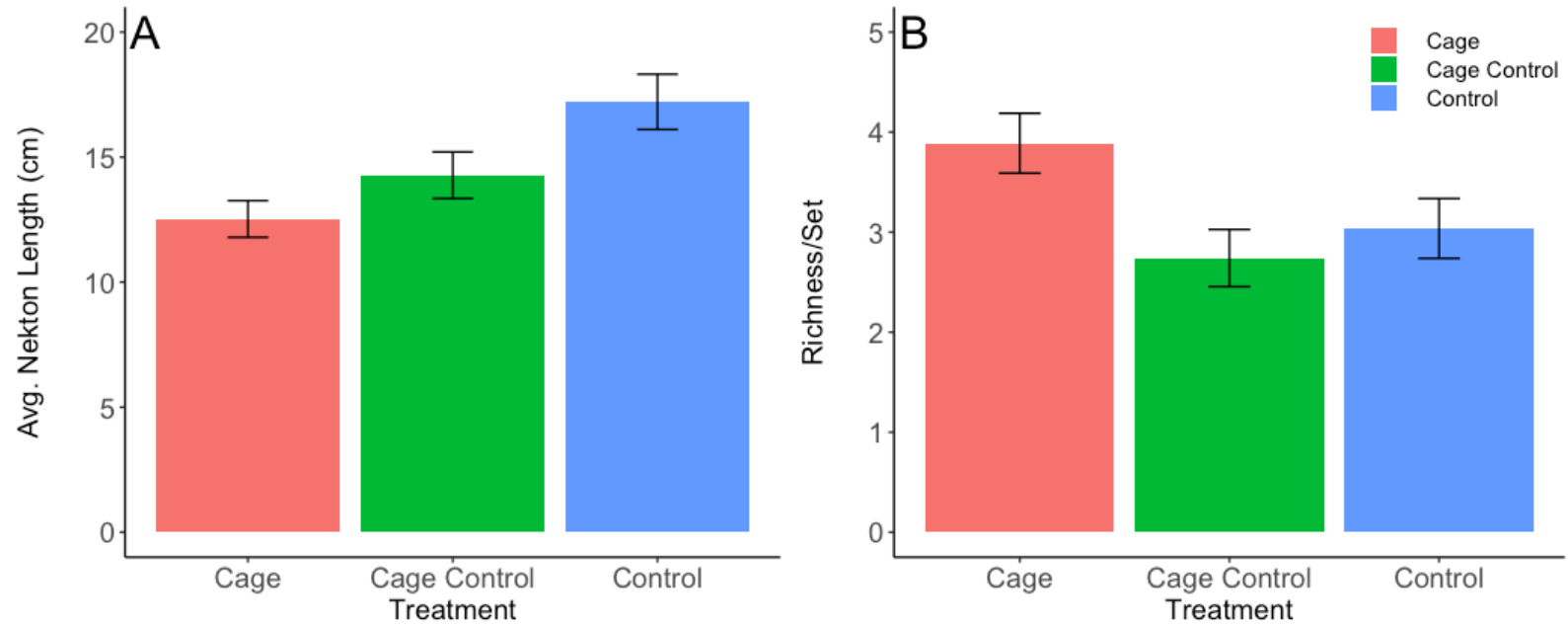
Figure 19: Changes in nekton community with respect to treatment.
A) Average nekton length per set was significantly different across treatments, ANOVA, p = 0.003. B) Nekton diversity, measured as species richness, was significantly different across treatments, ANOVA p = 0.020. Error bars represent standard errors.
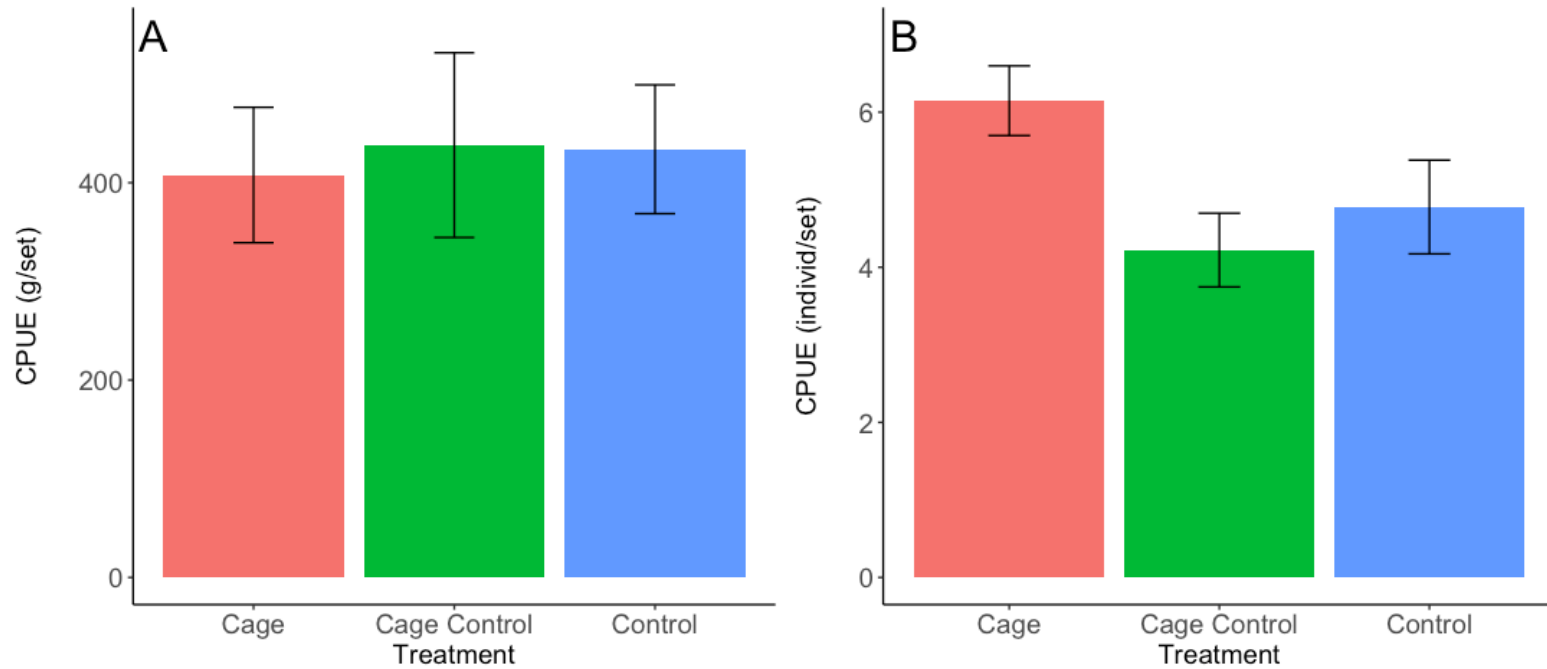
Figure 20: Nekton catch per unit effort.
A) grams per set, ANOVA P = 0.955. B) individuals per set, ANOVA P = 0.027. Across treatments, nekton biomass caught per set was not significantly different. In contrast, nekton abundance in exclusion plots was significantly greater than exclusion controls and marginally greater than control plots. Error bars represent standard errors.
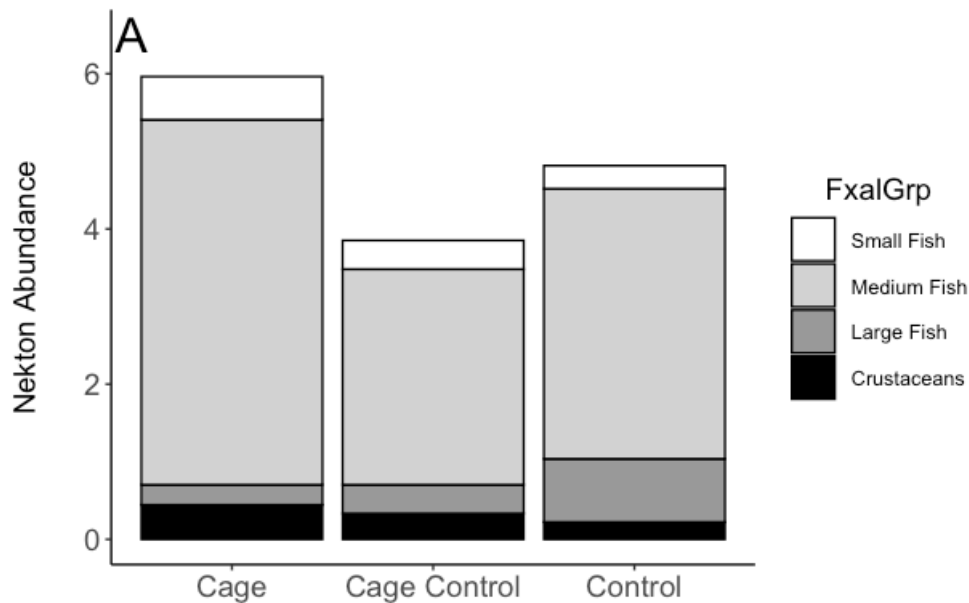
Figure 21: Nekton abundance per catch separated by size-delimited functional groups.
Exclusion plots had significantly more fish mesopredators than both exclusion control and control treatments and marginally more crustacean mesopredators than open control plots (Tukey HSD p = 0.043, p = 0.087, respectively).

Non-metric multidimensional scaling (NMDS) did not distinctly indicate differences in community composition across treatments (3D stress = 0.197, Figure 22). Rather, communities sorted most strongly based upon aboveground biomass, cage direction, and percent cover of seagrass within plots (NMDS1 R^2 = 0.538, NMDS2 R^2 = 0.648, and NMDS3 R^2 = 0.788 respectively). Mantel correlations further found that within the NMDS axes, treatment was partially correlated with NMDS1 (R^2 = -0.239). Indicator species analysis revealed that spottail pinfish, sergeant majors, and planehead filefish were strongly associated with exclusion treatments only (*Diplodus holbrookii* p=0.013, *Abudefduf saxatilis* p=0.002, and *Stephanolepis hispidus,*p=0.037, respectively), and

Atlantic menhaden were significantly associated with exclusion control treatments (*Brevoortia tyrannus* p=0.037).
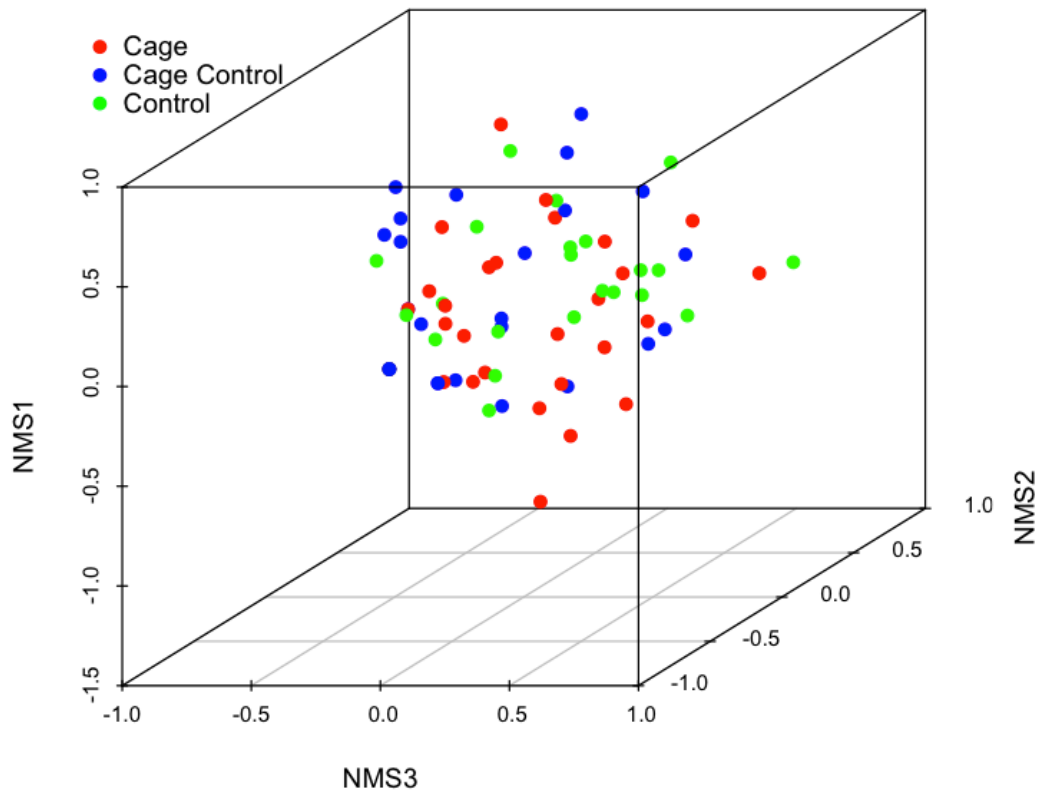
Figure 22: Three-dimensional nonmetric multidimensional scaling plot of nekton communities.
NMDS1 was most strongly associated with aboveground biomass while NMDS2 was correlated with cage direction and NMDS3 was correlated with percent cover of seagrass with plots ($R^2 = 0.538$, $R^2 = 0.648$, and $R^2 = 0.788$, respectively, 3D stress = 0.197).

4.3.2 Scallop surveys and mark-recapture

Prior to experiment set-up we conducted scallop surveys and found no significant difference in natural scallop abundance across treatments plots (ANOVA, P = 0.88, Figure 23A, Table 1). Post-installation of cages, scallop abundance did not change significantly

within cages or cage controls from May 2017 to October 2018 (Student's t-test, P = 0.63 and P = 0.15, respectively) but did significantly decline in open plots (P < 0.01). Declines in natural scallop abundance were observed across all treatments, but abundances in exclusion plots remained significantly higher than that of open control plots throughout the monitoring period (Student's t-test Cage: Control October 2017 p=0.04, Cage:Control May 2018 p=0.008, Cage:Control October 2018 p=0.03). Survivorship of marked scallops in exclusion plots remained steady from day one until day 28 (ANOVA P=0.348, Figure 23B). Whereas, survivorship in both cage control and control plots declined significantly within a week post-deployment (Students t-test Cage Control Day 1: Day 7 p < 0.01, and Control Day 1: Day 7 p < 0.01, respectively).

4.3.3 Effects on Seagrass

Exclusion of large-bodied organisms was not found to significantly alter the above or belowground biomass of seagrass within plots over the duration of the experiment (ANOVA P = 0.41, Figure 7A and 7B). However, we did detect a significant difference in both below- and aboveground biomass with respect to year (ANOVA P < 0.01, P<0.01, Table 1). Similarly, the overall density of shoots was significantly different between years but not across treatments (ANOVA P < 0.01 and P = 0.88, Figure 8).

We are confident that this lack of treatment effect is not related to cage artifacts. Based on our measured rates of dissolution of gypsum blocks, our experimental treatments had no measurable effect on flow dynamics (ANOVA P=0.351).
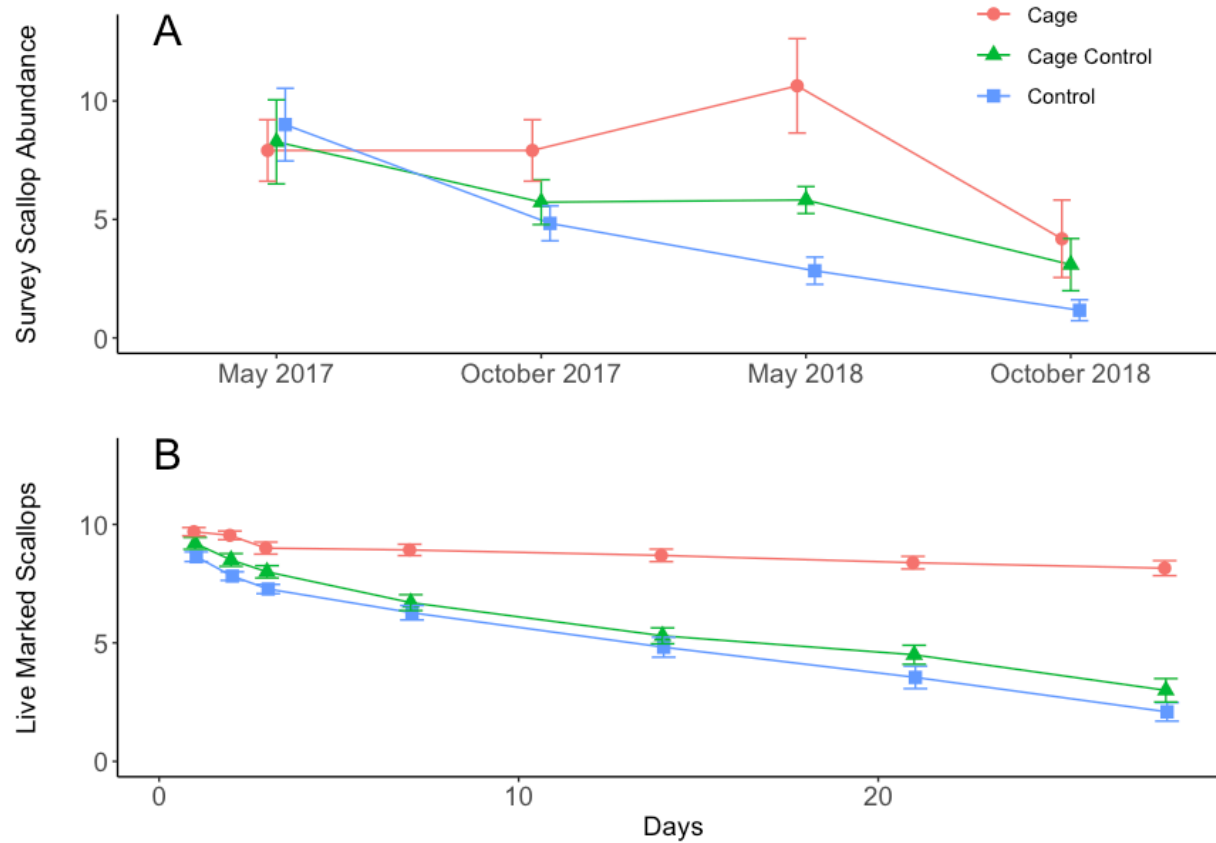
Figure 23: Observed changes in scallop abundances.
A) surveys and B) scallops deployed for mark-recapture. Natural scallop abundances were variable across the observation period. No significant difference was observed in scallop abundances prior to experiment set-up. The number of scallops within cages during the month of May was significantly greater in 2017 than 2018. However, the opposite was true for cage controls and controls, where scallops were observed to decrease from 2017 to 2018. P = 0.03 Treatment * Year in May. P = 0.04 Treatment * Year in October.

Table 4: Repeated measures ANOVA table of predator exclusion response variables

Response	Independent Variable	Df	Sum Sq	Mean Sq	F value	P-value
Aboveground Cage Biomass	Treatment	2	723824.68	361912.34	0.92	0.41
	Residuals	29	11418544.37	393742.91		
	Sampling Date	3	2194366073.6	73145357.88	265.76	<0.01
	Treatment : Sampling Date	6	990993.75	165165.63	0.6	0.73
	Residuals	95	26147250.48	275234.22		
Belowground Cage Biomass	Treatment	2	1927623.89	963811.94	0.14	0.87
	Residuals	29	198641756.5	6849715.74		
	Sampling Date	3	1145718260	381906086.8	79.52	<0.01
	Treatment : Sampling Date	6	18222788.97	3037131.5	0.63	0.7
	Residuals	95	456222644.2	4802343.62		
Cage Shoot Abundance	Treatment	2	80321314.67	40160657.33	0.13	0.88
	Residuals	29	8696785364	299889150.5		
	Sampling Date	3	1.7625E+11	58750383040	193.85	<0.01
	Treatment : Sampling Date	6	578942033.5	96490338.92	0.32	0.93
	Residuals	95	28792364012	303077515.9		
Natural Scallop Abundance	Treatment	2	237.23	118.61	5.48	0.01
	Residuals	29	627.78	21.65		
	Sampling Date	3	556.43	185.48	11.47	<0.01
	Treatment : Sampling Date	6	234.19	39.03	2.41	0.03
	Residuals	95	1536.13	16.17		
Cage Percent Cover	Treatment	2	63.04	31.52	0.17	0.84
	Residuals	29	5317.34	183.36		
	Sampling Date	3	12658.59	4219.53	55.75	<0.01
	Treatment : Sampling Date	6	271.06	45.18	0.6	0.73
	Residuals	95	7190.66	75.69		
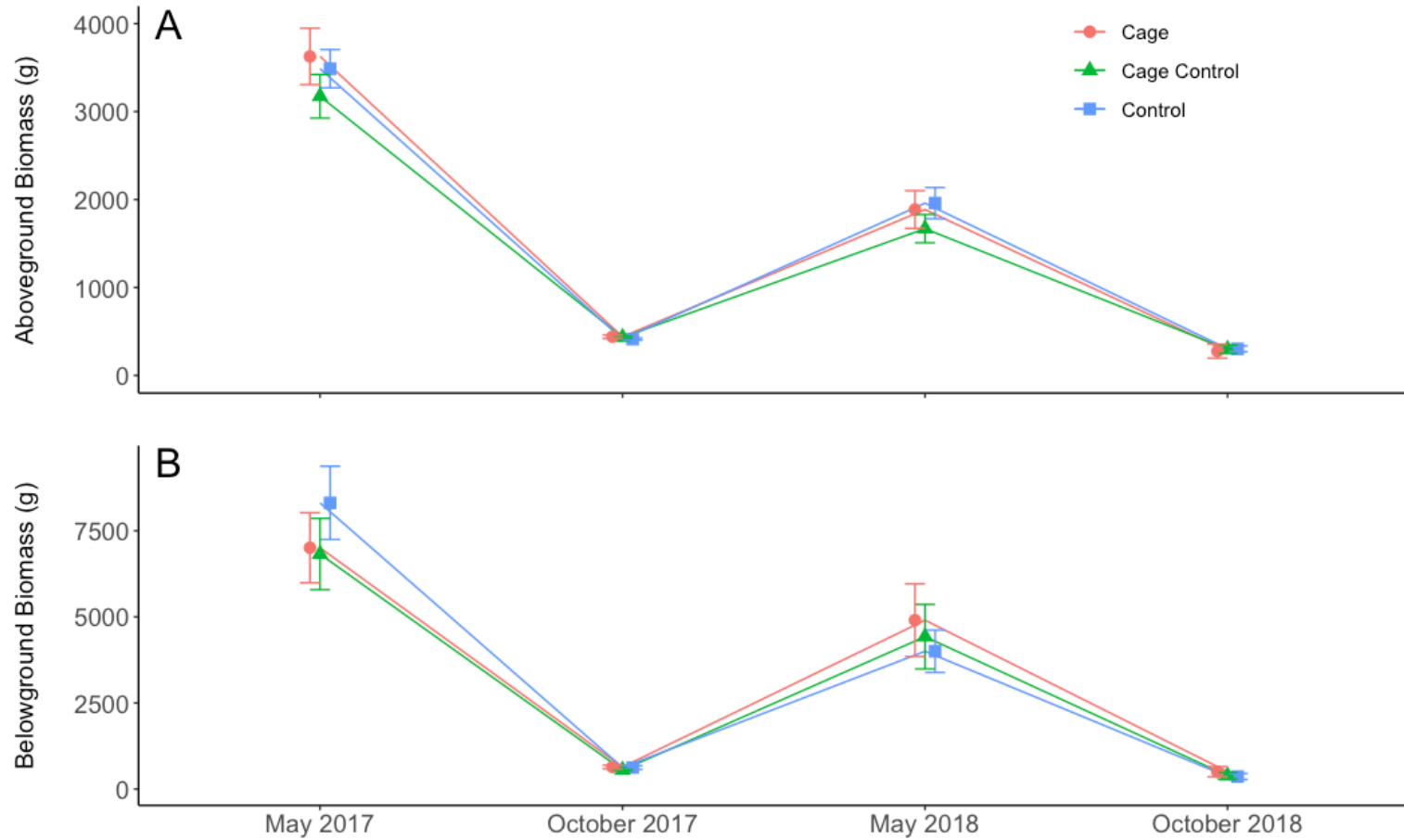
Figure 24: Changes in A) above and B) belowground biomass over time.
Neither above or belowground biomass was found to be significantly different as a result of treatment (ANOVA P=0.41, and P=087, respectively) but did differ significantly with respect to year (ANOVA P<0.01, and P<0.01, respectively).
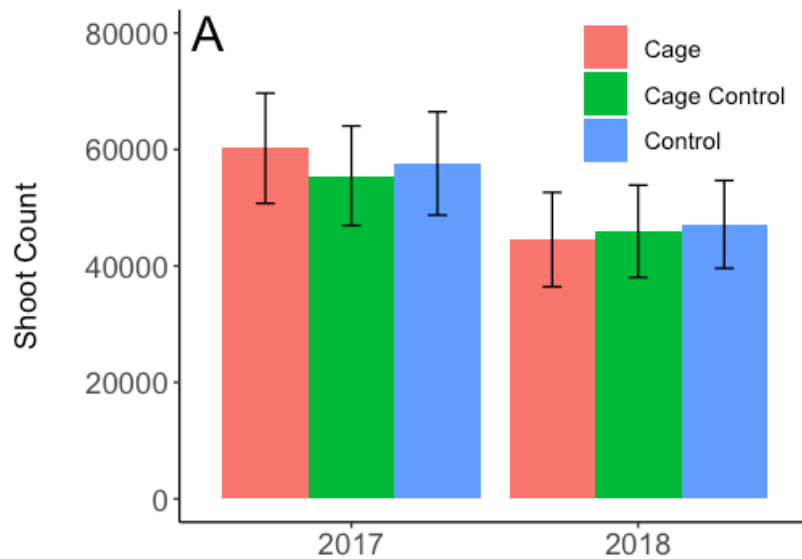
Figure 25: Shoot count in experimental plots.
Shoot count in cages was significantly different between years (ANOVA P <0.01) but did
not differ across treatments (ANOVA P=0.88).

4.4 Discussion

Overfishing or the removal of large-bodied predators and nekton has been linked
to modifications of ecosystems ranging from shifts in food web and predator-prey
population dynamics to declines in critical foundation species (Pauly et al. 1998, Jackson
et al. 2001). Numerous factors can regulate marine species populations, including food
resources, predation pressure, recruitment, and shifts in human management of fisheries.
By taking an experimental approach, we were able to isolate the effects of large predator
exclusion from other potential spatial features that may limit or enhance interactions
between trophic levels such as landscape context and habitat heterogeneity. Results from
our large predator exclusion experiment did not find support for a multi-tiered trophic
cascade that propagated down to the primary foundation species (Figure 26). However, we

did find that exclusion of large predators shifted both nekton and bivalve community assemblages. In the context of our experiment, we cannot directly these shifts in mesopredator and bivalve abundances to predation by large sharks or cownose rays as opposed to large consumers as a whole, but we provide experimental support for top-down effects of large predators in Atlantic seagrass ecosystems, specifically on scallop abundances.
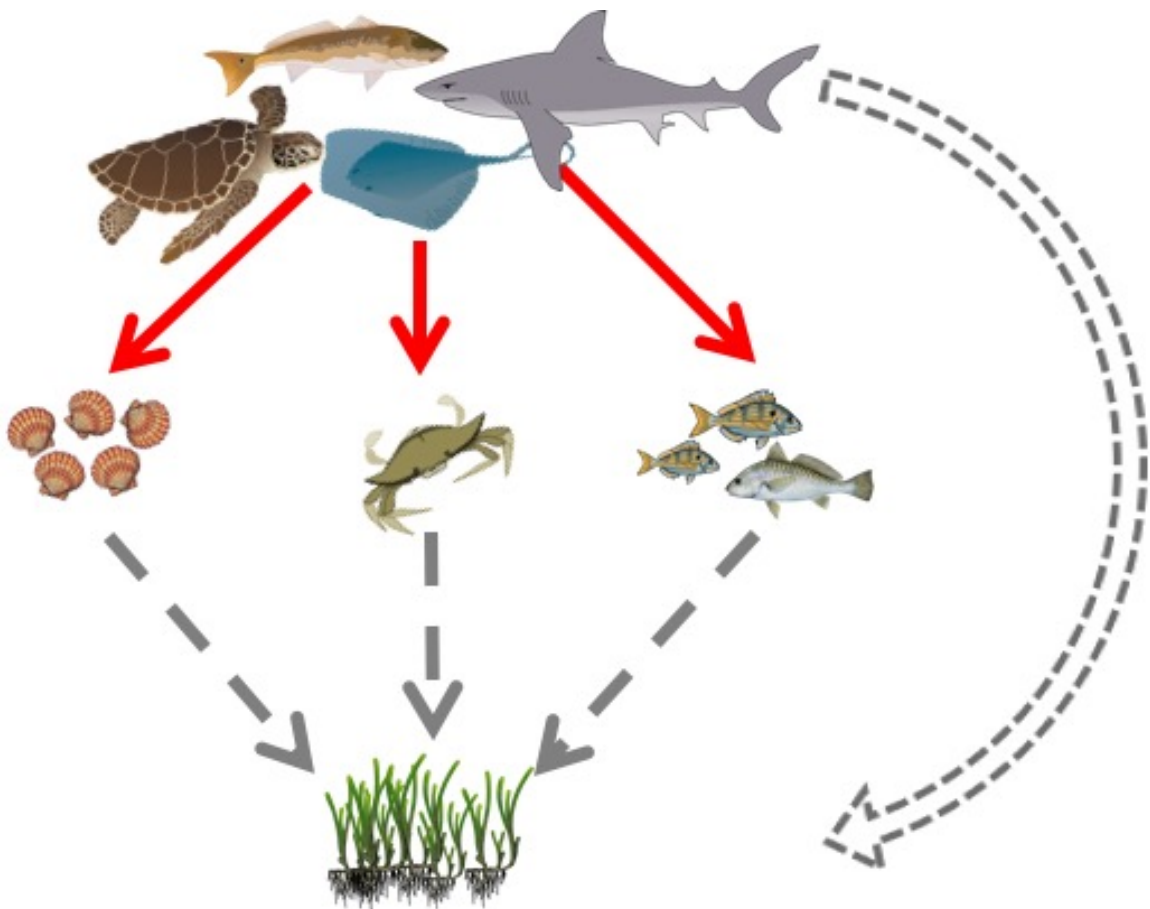
Figure 26: Hypothesized seagrass food web interactions.
Interactions tested by large consumer exclusions. Red arrows indicate statistically supported effects of top-down control on scallops, large decapod crustaceans, and smaller fish species. Dashed gray arrows indicate lack of statistical support for species interaction effects.

Field-based experiment of large consumers and predators are plagued by the issue of scale- both spatially and temporally. Experimental tests of biotic interactions where focal species densities have been manipulated typically occur within a small portion of the species' habitat and assume that results can be extrapolated to larger scales (Diamond and Case 1986, Hairston 1989). However, predation rates can be spatially heterogeneous and variable, and movement rates of both predator and prey can strongly influence predation rate (Englund 1997). In an effort to encompass more area for consumer home ranges, tests of predator effects have been conducted at large scales on the order of several hectares in size; however, these studies often lack replicative power (Hairston 1989). Moreover, many studies of biotic interactions manipulate predator presence by caging predators in rather than exclusion and risk the potential for amplified predation rates within cages compared to open areas (Hairston 1989). In comparison, exclusion plots may show a weaker biotic interaction. We chose to conduct our experiment as an exclusion of large consumers at a relatively small scale in order to maintain replicative power as well as capture a large overall extent of the experimental seagrass meadow. While large consumers and mesopredators migrate on scales larger than the 5x5 m cages that we erected, our design was conducted such that should consumers have an impact on bivalve species, or seagrasses (via bioturbation), the effects could be readily quantified.

4.4.1 Large consumer exclusion effects on mesoconsumers

Few studies have taken an experimental approach to demonstrate the role of large predators in generating a trophic cascade in marine systems (as summarized in Shurin et al. 2002, Halpern et al. 2005, Baum and Worm 2009). Whether experimental or

observational, studies that have examined top-down effects have primarily concluded that substantial reductions in large marine predators leads to mesopredator and invertebrate predator increases (Baum and Worm 2009). Thus, in regards to direct effects of predator exclusion on prey species, I hypothesized that large predator exclusion would correspond with increases in mesopredator, e.g. pinfish, croaker, spot, abundances. My findings supported this hypothesis as we caught both a greater number and diversity of small nekton in exclusion plots than in open or exclusion-control plots. Interestingly, the subsequent increase in smaller fish taxa resulted in equivalent nekton biomasses across treatments.

I further found that differences in nekton communities among treatments were driven primarily by the presence of three species of small (<10 cm) mesopredators that were strongly associated with exclusion plots and one species of small mesopredator that was indicative of exclusion control treatments. Specifically, spottail pinfish, sergeant majors, and planehead filefish (*Diplodus holbrookii*, *Abudefduf saxatilis*, and *Stephanolepis hispidus*, respectively) were found predominantly in exclusion treatments and Atlantic menhaden (*Brevoortia tyrannus*) were caught mainly in exclusion control treatments. Studies have shown that all of the aforementioned species are frequently predated upon by large predators including multiple sport fish species, pelagic rays, as well as large estuarine predators including red drums, black drums, and striped bass (*Sciaenops ocellatus*, *Pogonias cromis*, and *Morone saxatilis*, respectively) (Rudershausen et al. 2005, Rudershausen et al. 2010, Peacock 2014, Weidner et al. 2017). Moreover, spottail pinfish, sergeant majors, and planehead filefish are benthic omnivores and feed upon plant remains,

copepods, amphipods, and invertebrate eggs (Livingston 1982, Lewis and Peters 1994, Pike and Lindquist 1994).

Our findings suggest that large predators, either by directly consuming or indirectly through fear, may exert top-down controls on seagrass nekton communities, but in contrast to other studies of predator control, we did not observe a marked shift towards a single competitively dominant mesopredator species. It is possible that our exclusion stockades attracted nekton that are drawn to structure as planehead filefish, spottail pinfish, and sergeant majors are also associated with high relief habitats. Though we did not find any species that were common indicators of both exclusion control and control plots, we cannot rule out the possibility that exclusion control plots acted as an intermediate level of structure rather than disproving an effect of structure (Schmidt and Warner 1984, Steele 1996). Further studies are needed to assess specific rates of predation on these fishes within and outside of exclusion plots.

4.4.2 Direct and indirect impacts on bivalve and crustacean communities

In concert with increases in mesopredator abundances, I found that large predator exclusions also corresponded with a marked increase in bay scallop, *Argopecten irradians concentricus*, abundance and survivorship and an increase in crustacean abundance. Bay scallop populations in North Carolina have dropped precipitously. Surveys conducted by the North Carolina Division of Marine Fisheries report low abundances across all estuaries and no viable annual stock assessment (NC DEQ 2017). Similarly, blue crab harvests and spawning stock biomass has fluctuated greatly over the last two decades but has shown a steadily declining trend in population (NC DEQ 2017). Multiple factors including

overfishing, declines in seagrass habitats, and changing climate conditions, likely contribute to declines in both bivalve and crustacean populations (Deaton et al. 2010). Previous studies have similarly found that predator exclusion stockades can effectively increase scallop survivorship at a small scale and have been suggested as a potential means to elevate declining bay scallop populations. Our study provides further support for the top-down influence of large nektonic predators on bivalve abundances but to our knowledge, is the first to demonstrate that the combination of predation-release and increasing food availability is also associated with greater crustacean abundances.

Surveys prior to experiment implementation indicated no initial differences in bay scallop abundance across the experimental seagrass meadow. Subsequent surveys of natural scallop abundance within plots were variable with respect to time, but scallop abundances within exclusion plots were consistently greater than in open control plots. Survey abundances declined across all treatments over the duration of our experiment. Because we could not initially determine if changes in scallop abundance were due to interannual recruitment variability or changes in survivorship, we further conducted a mark-recapture study within our plots. Pilot testing of scallop tethers versus mark-recapture indicated that although mobile, scallops did not move significant distances from where they were deployed, thus we did not tether scallops and allowed scallops to move freely given the large size of our exclusion stockades. Our mark-recapture study provided further evidence that rates of predation were significantly less in the absence of large predators. Marked scallops within exclusion plots showed significantly greater rates of survivorship than both exclusion control and control plots. Further examination of shell fragments also

revealed that the predominant cause of mortality was consumption by shell-crushing predators.

Concomitant with an increase in food resources (i.e. greater scallop abundance), we also found consumption by large predators to be a potential factor influencing crustacean abundances. We predicted that large predator exclusion would be associated with an increase in crustacean bivalve-predators. Our surveys revealed that two crustacean predators, blue crabs, *Callinectes sapidus*, and stone crabs, *Menippe mercenaria*, were indeed more abundant in the absence of large predators. Moreover, the majority of crustaceans caught in our surveys were juveniles and small adults (<7 cm carapace width). Diet studies of large estuarine predators have found that juvenile blue crabs and stone crabs are frequently consumed by large foraging predators including red drum, bonnethead sharks, (*Sciaenops ocellatus*, *Sphyrna tiburo*, respectively) (Cortes et al. 1996, Guillory and Prejean 2001) as well as larger mesopredators including adult pinfish (Darnell , Reid Jr 1954). Our findings thus suggest that removal of large nektonic predators may release crustacean prey from top-down control.

Furthermore, both stone crabs and blue crabs are known to be voracious bivalve predators and may preferentially feed upon bay scallops (Ebersole and Kennedy 1995, Bishop et al. 2005). Outside of stone crab burrows, we frequently observed signs of predation on bivalve molluscs, i.e. shell fragments of hard clams, cross-barred venus clams (*Mercenaria mercenaria* and *Chione cancellata*), and bay scallops, including scallops deployed for mark-recapture. We hypothesize that the concomitant release from predation and increase in food availability are associated with elevated crustacean abundances

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Studies have similarly shown that the presence of medium-sized mesopredators, such as the pinfish, *Lagodon rhomboides*, can indirectly increase the survivorship of bay scallop recruits by depressing the feeding activity of blue crabs (Bishop and Wear 2005). However, our experimental approach does not allow us to draw direct conclusions regarding the direct strength and impact of predation by crustaceans compared to large nekton.

4.4.3 Attenuated effects of top-down control on primary producers

The results reported here encompass the effects of large predator exclusion after only two years, and thus it is difficult to parse out effects of exclusion on seagrass productivity from inter-annual variability. We found that seagrass percent cover within cages did not differ significantly between treatments but varied significantly with respect time. No changes were observed immediately after plot installation, but declines in overall percent cover were observed from October 2017 through October 2018. Moreover, no ray pits or evidence of bioturbation was observed within our plots over the study duration.

Prior studies of top-down effects on seagrasses have been limited to manipulations of a few, typically lower-trophic level species. These studies have primarily examined the effects of small epigrazers such as isopods and amphipods on seagrass productivity and found that greater epigrazer diversity can suppress algal growth and enhance the growth of eelgrass (Reynolds et al. 2014, Duffy et al. 2015). Seagrass cores from our exclusion cages did not indicate a difference in small grazer richness across treatments. Moreover, studies have shown that plant biomass is more variable with longer food chains in marine systems (Halpern et al. 2005). Meta-analyses have further found that the magnitude of trophic cascades attenuates down the food chain such that lower trophic levels are frequently

buffered from the effects of changing diversity at higher trophic levels (Shurin et al. 2002). Here, we report on the effects of a 4+ level trophic cascade, and thus, it is likely that large-predator driven effects attenuate further down the food web or that effects on primary productivity require longer time scales.

Most evidence for top-down control in marine systems comes from salt marshes where experimental studies in salt marshes have shown that predator removal can lead to the formation of large grazing fronts that denude habitat-forming vegetation (Silliman and Bertness 2002, Altieri et al. 2012, Coverdale et al. 2012, Silliman et al. 2013). Though large grazing fronts of sea turtles, herbivorous mammals, fishes, and sea urchins are known to clear seagrass beds in tropical regions (Camp et al. 1973, Valentine and Heck 1991, Valentine and Duffy 2007), such high accumulations and strong impacts of herbivores are not as common in temperate seagrass ecosystems (Valentine and Duffy 2007). Waterfowl and herbivorous fishes can locally denude seagrass beds, but the predominant primary consumers are smaller invertebrate mesograzers, i.e. amphipods and isopods, that feed upon epiphytic algae on seagrass blades (Kikuchi 1974, Orth et al. 1984a, Klumpp et al. 1992, Jernakoff et al. 1996). However, studies conducted by Hughes et al. (2013), (2016) provided experimental evidence for a large-predator driven trophic cascade in coastal California seagrass beds. The studies found that sea otters in a nutrient-enriched estuary can enhance seagrass resilience by reducing the number of mesopredator- and algal-grazing crabs which then released epiphytic mesograzers from predation. In both these instances, large predators preferentially exert strong top-down control on mesopredator prey populations that are strongly associated with declines in epiphytic grazers. Given the

transient nature of much of the nektonic seagrass community in North Carolina, finding a definitive effect of large predators that propagates to primary producers requires much more direct and comparative testing of species interactions and interaction cascades as well as examinations of historical fisheries data that includes both large elasmobranchs as well as other large nektonic predators.

4.5 Conclusion

Taken together, the results provided here provide support for the presence of complex top-down effects of large predators on seagrass communities. Our findings add to a growing body of literature that demonstrates the importance of consumer controls in structuring seagrass ecosystems (Heck et al. 2000, Duffy 2006, Valentine and Duffy 2007, Moksnes et al. 2008, Lewis and Anderson 2012, Hughes et al. 2013). In this case, the exclusion of large-bodied predators was associated with an increase in both fish and crustacean mesopredators as well as an increase in scallops. The concurrent increase in top-down control by bivalve-consuming crustaceans, either as a result of predation-release or increase in food resources, however, was not equivocal to that exerted by large-bodied predators.

Our findings do not put to rest the debate over the validity of large apex predator driven trophic cascades in the western Atlantic Ocean (Myers et al. 2007, Grubbs et al. 2016). Because our exclusion stockades are size-selective and not species-selective, we cannot definitively state that the presence or absence of either great sharks or cownose rays was the contributing factor towards observed shifts in seagrass communities. Rather, we provide experimental support suggesting that large predators in seagrass beds can exert

top-down controls across multiple trophic levels, but further experimentation and is needed

to determine direct and indirect effects on seagrass primary productivity.

CONCLUSIONS

Centuries of human activities have induced drastic changes in global ecosystems with cascading effects on coastal habitats (Jackson et al. 2001, Lotze et al. 2006). Despite their critical role as nursery habitats, and the numerous ecosystem services and resources they provide for coastal communities, seagrass beds have declined precipitously in both health and extent over the last century (Orth et al. 2006, Waycott et al. 2009). It is estimated that 29% of historical seagrass beds have already been lost or converted and continue to be lost at a rate of 7% per year (Waycott et al. 2009). Understanding how biotic interactions can contribute to and may regulate efforts to conserve and restore seagrass beds and the communities they support are fundamental for success.

In this dissertation, I evaluated how ecological interactions between seagrasses and other organisms, namely bivalves and nekton, affect overall community dynamics and impact the success of restoration efforts. Using a large-scale review of the scientific literature, I elucidate critical knowledge gaps in the restoration literature related to collaboration, study locations, and factors emphasized for success (Chapter 1). My vote-count review indicated that one-third of the journal-published studies listed authors from at least two sectors, and 6% listed authors from all three sectors. Across all habitat types, there was a dearth of studies from Africa, Asia and South America. Finally, despite many experimental studies demonstrating that species interactions can greatly affect the recovery and persistence of coastal foundation species, only one-fourth of the studies we examined discussed their effects on restoration. Results from Chapter 1 reveal a pressing need for more collaborative restoration studies that occur outside of the western hemisphere that

research ways in which biological interactions can be harnessed to promote restoration success.

Given this lack of studies that directly research biological interactions in restoration success, Chapters 2, 3, and 4 experimentally tested how facilitative interactions interactions may alter restoration trajectories and seagrass community structure. In Chapter 2, we found that pen clam density and survivorship was significantly greater in seagrass beds, indicating that eelgrass facilitates pen clams. Pen clams in turn enhanced local diversity and increased both the abundance and species richness of organisms (specifically, macroalgae and fouling invertebrate fauna)—the effect of which scaled with increasing clam density. However, we failed to detect an impact of pen clams on other seagrass functions and hypothesize that functioning may more likely be enhanced in scenarios where secondary foundation species specifically increase the diversity of key functional groups such as epiphyte grazers and/or when bivalves are infaunal rather than epifaunal. Our findings add to the growing amount of literature that demonstrate secondary foundation species are important drivers of local biodiversity in marine ecosystems. Further experimentation is needed that directly examines i) the role of functional versus overall diversity on seagrass functions, and ii) the relative importance of life-history strategy in determining when and where engineering bivalves increase biodiversity and/or functioning of seagrass beds.

To directly test if and how bivalves can facilitate or enhance seagrass restoration, we experimentally manipulated both intra- and interspecific positive species interactions by incorporating i) clam additions into seed plantings, and ii) outplanting adult shoots in aggregated versus dispersed layouts with clam additions. In the seed study, clam additions

increased seagrass productivity including length, above- and belowground biomass, patch expansion, nitrogen content, and reproductive effort (seed production). Without clams, seagrass patches grown from seed did not change from initial measurements or decreased in area over time; whereas, with clams, patches grown from seed increased on average by 400%. In contrast, we did not find support for a facilitative effect of clams on adult outplants. Instead, our results demonstrated a strong impact of intraspecific facilitation, as seagrasses planted in aggregated rather than dispersed designs grew twice as fast in terms of shoot density and patch area coverage. Indeed, dispersed configurations consistently declined in coverage throughout the experiment, while aggregated ones increased on average 47% from initial patch area. These results demonstrate that slight modifications to restoration designs (switching from dispersed to clumped, adding small clams to seed additions) to allow for positive species interactions can greatly enhance seagrass restoration success with no or little increase in cost. More broadly, these findings highlight different types of positive species interactions can increase restoration success for different life stages and growth variables of the restored species.

Trophic facilitations as a result of large-predator direct and indirect interactions can also impact seagrass community structure by controlling mesopredator populations in addition to having massive implications for bivalve populations. In particular, the historical and precipitous decline of large apex predators in the western Atlantic Ocean has been observationally linked to significant changes in coastal seagrass communities. Little experimental evidence, however, exists demonstrating that large consumers indeed exert strong top-down controls on western Atlantic seagrass ecosystems. Results of Chapter 4

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demonstrate that exclusion of large-bodied consumers was associated with a greater number of fish- and crustacean- mesopredators as well as increased bivalve abundance, but overall macroinvertebrate diversity was not affected. However, these upper-level trophic changes we did not observe a cascading impact on the primary producer, the seagrass itself. Our results suggest that large consumers may in fact exert top-down control on seagrass food webs; however, further testing of mechanistic species interactions is needed to separate out the effects of interannual seagrass variability and increased structure from that of large predator exclusion.

The combined results of my research demonstrate the pervasive and strong structuring effects of both facilitative and trophic interactions in seagrass ecosystems. These findings are reminiscent of those from other ecosystems that have similarly found that species interactions can greatly influence restoration success, and positive interactions can particular can greatly enhance yields but are infrequently included in restoration schemes (Silliman et al. 2015, Gittman et al. 2017b). Similarly, our findings add to a growing body of literature that demonstrates the importance of consumer controls in structuring seagrass ecosystems (Heck et al. 2000, Duffy 2006, Valentine and Duffy 2007, Moksnes et al. 2008, Lewis and Anderson 2012, Hughes et al. 2013). Through the research presented in this dissertation, I argue that species interactions that may mutually benefit seagrass restoration and health should be systematically investigated, tested, and incorporated into coastal conservation, restoration and management.

APPENDIX A

Papers included in restoration synthesis (Chapter 1):

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* Fonseca 1996a and Fonseca 1996b counted as one study

APPENDIX B

Table B1. Restoration factors quantified (% of studies)

Category	Factor	All Habitats	Salt Marsh	Oyster	Seagrass
	Tidal Flow	35.9	46.4	19.7	31.7
	Water depth/Tidal Elevation	48.2	49.7	43.4	48.8
	Sediment Type	23.3	20.1	15.8	43.9
	Wave Energy	14.6	11.7	18.4	26.8
	Slope	8.6	11.2	7.9	13.4
	Pre-existing substrate	17.9	13.4	35.5	13.4
	Add or Remove Substrate	20.9	17.3	40.8	13.4
	Flow velocity and direction	21.6	16.2	26.3	40.2
Abiotic	Salinity	35.2	35.8	36.8	31.7
Factors	Nutrients	26.9	23.5	19.7	51.2
	Oxygen	17.9	14.5	22.4	22.0
	Landscape Context	26.9	26.8	31.6	46.3
	Drainage	16.3	25.7	0.0	3.7
	Turbidity	18.6	10.6	19.7	41.5
	Sedimentation Rate	18.9	19.6	21.1	24.4
	Time of year of restoration	13.3	9.5	14.5	20.7
	Climate Change Predictions	10.6	12.3	13.2	14.6
	Environmental Disturbance	17.9	15.1	15.8	34.1

	Climate Oscillations	6.0	6.1	6.6	6.1
	Temperature	35.9	29.6	39.5	47.6
	Landscape/Habitat heterogeneity	22.9	29.6	22.4	15.9
	Development of soil parameters	16.9	26.3	2.6	3.7
	Groundwater penetration & flow	9.3	12.3	2.6	4.9
	Scale/arrangement of restoration project	19.3	20.7	21.1	17.1
	Human Interactions/ disturbances	35.9	33.5	36.8	57.3
	Consumption	23.3	17.9	31.6	31.7
	Pathogens and Parasitism	11.3	4.5	32.9	13.4
	Recruitment	24.6	12.8	48.7	34.1
Biotic	Intraspecific Competition	4.7	1.7	3.9	11.0
Factors	Interspecific Competition	14.6	14.5	10.5	18.3
	Intraspecific Facilitation	8.0	3.9	15.8	6.1
	Interspecific Facilitation	16.6	19.6	18.4	22.0
	Invasive Species	13.6	17.9	11.8	8.5
	Historical Ecology	15.9	16.2	18.4	17.1
	Microphytobenthos	1.0	1.1	0.0	1.2
	Total Number of Studies	301	179	75	82

APPENDIX C

Table C1. Article Accessibility

Accessibility	Journal	# of Studies
Open Access Article	Journal Of Applied Ecology	1
	Journal Of Coastal Conservation	1
	Marine Ecology Progress Series	6
Open Access Journal	Aquatic Biology	2
	Ecology And Society	1
	Ecosphere	1
	European Mosquito Bulletin	1
	Peerj	1
	Plos One	10
	San Francisco Estuary & Watershed Science	1
	Scientific Reports	1
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Zhang, Y. S., and B. R. Silliman. 2019. A Facilitation Cascade Enhances Local Biodiversity in Seagrass Beds. Diversity **11**:30.

BIOGRAPHY

Yin San Stacy Zhang

<u>**Education**</u>

Dr. Zhang obtained a Bachelor of Science in Biology with a minor in Chemistry from the University of North Carolina at Chapel Hill in 2012 where her undergraduate thesis investigated the relationship between coral community diversity and resilience to disturbance. Her dissertation research, conducted at Duke University from 2014 to 2019, explores how facilitative and trophic interactions affect seagrass ecosystem structure and functioning, and the application of biological interactions in habitat restoration.

<u>**Publications**</u>

Zhang, Y.S., and B. R. Silliman. A facilitation cascade enhances biodiversity but not function in a seagrass community. 2019. Diversity. 11(30); DOI: [10.3390/d11030030](10.3390/d11030030)

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Gittman, Rachel K., F.J. Fodrie, C. Baillie, M. Brodeur, C. Currin, D. Keller, M. Kenworthy, J. Morton, J. Ridge, and **Y.S. Zhang.** 2018. Living on the edge: Thresholds in environmental stress and scale determine the fate of coastal habitat restoration. Estuaries and Coasts. 41(3); DOI: [10.1007/s12237-017-0302-6](10.1007/s12237-017-0302-6)

Clark, J.S., D. Nemergut, B. Seyednasrollah, P. Turner, and **Y.S. Zhang**. 2017. Generalized joint attribute modeling for biodiversity analysis: Median-zero, multivariate, multifarious data. Ecological Monographs. 87(1). DOI: [10.1002/ecm.1241](10.1002/ecm.1241)

Zhang, Y.S., K. Speare, Z. Long, K. McKeever, M. Gyoerkoe, A. Ramus, Z. Mohorn, K. Atkins, S. Hambridge, N. Graham, K. Nash, E. Selig, and J. Bruno. 2014. Is coral richness related to community resistance to and recovery from disturbance? PeerJ. DOI: 10.7717/peerj.308

Honors and Awards

Duke University Summer Research Fellowship, 2017 & 2018
Duke University Marine Lab Graduate Fellowship, 2017-2018
North Carolina Sea Grant and Albemarle-Pamlico National Estuary Partnership Fellowship, "Harnessing positive interactions at multiple scales for seagrass restoration," $9,970.00, 2016-2018
Duke Wetlands Center Graduate Student Research Grant, "Evaluating multi-scale positive interactions for enhancing biodiversity and ecosystem resilience," $4,914.53, 2015-2016
Duke Ramus Fund for Estuarine Research, "Investigating interactions between bivalves and seagrasses" $2,539.00, 2015
Carolina Covenant Scholar, The University of North Carolina at Chapel Hill 2008-2012