Harnessing positive interactions at multiple scales for seagrass restoration.

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Abstract

Restoration is increasingly utilized as a strategy to reverse the loss and degradation of coastal habitats globally. Restoring foundation species that create habitat and facilitate the settlement and survivorship of other organisms is crucial for rebuilding ecosystems. Current methods in restoration science emphasize minimizing competition and interactions among transplants despite an extensive body of literature demonstrating that positive species interactions are critical for the recovery of foundation species following intense disturbance. Here, we experimentally tested how both intra- and interspecific species interactions can be applied in seagrass restoration by incorporating i) interspecific facilitation (clam additions) into seed plantings, and ii) both intraspecific (aggregated vs. dispersed layouts) and interspecific facilitation (clam additions) into shoot plantings. In the seed study, clam additions were significantly associated with greater shoot lengths, as well as patch expansion and belowground biomass. Clams were also found to enhance total aboveground biomass as well as reproductive effort. In contrast, we did not find support for a facilitative effect of clams on adult seagrass transplants. 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. Both intraspecific and interspecific interactions positively influenced seagrass productivity in our study. We demonstrate that slight modifications to restoration designs to include positive interactions can greatly enhance seagrass growth and expansion with little to no additional costs and that interspecific facilitation inclusion can increase seagrass growth but the effect can differ based upon the life stage being restored. Incorporation of positive interactions thus has the potential to further confer multiple benefits to community organization and the provisioning of ecosystem services. Because restoring seagrasses with seeds is increasing in occurrence and likely represents the wave of the future, as a result of lower costs, our results suggest that scientists should test for the impact of adding clams to the soil at the same time they outset seeds.

Introduction

Coastal ecosystems increasingly face a number of anthropogenic stressors that threaten their health, extent, and the services they provide. Climate change, pollution, habitat destruction, overharvest, 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). The decline of these habitats has massive implications for fisheries production, storm and flood mitigation, carbon storage such that the United States invests millions of dollars annually towards coastal conservation efforts (Edwards et al. 2013, BenDor et al. 2015). Restoration, in particular, has recently been elevated by nations, corporations, and non-profit organizations as a means for increasing coastal defenses (Sutton-Grier et al 2018), combatting habitat losses in response to large-scale disturbances (RESTORE Act), compensation for adverse impacts (Clean Water Act), and providing employment (Edwards et al 2012).

Unfortunately, restoration is a costly endeavor. A hectare of restored salt marshes cost on average over 67,000 USD per year (107-28,800,000 USD*year^{-1}), restored seagrasses costs over 106,000 USD per year (3,966-1866,385 USD*year^{-1}), and restored oyster reef costs over 66,000 USD per year (4,490-1,419,856 USD*year^{-1}) (Bayraktarov et al. 2016). Despite high initial costs in investment, across all habitats, ecosystem restoration can increase the biodiversity and ecosystem services conferred by 44% and 35% compared to degraded habitats (Benayas et al. 2009). Regardless, the need to make restoration more affordable and effective is paramount. Thus far, efforts to restore habitats have primarily had a botanical focus on restoring habitat-forming foundation species and placed an emphasis on attaining the correct physical environment for restoration to succeed (Zhang et al. 2018).

Planting designs in coastal restoration have historically been derived from forestry science. Ordinarily, outplants are placed in a dispersed arrangement in order to minimize competition (Halpern et al. 2007, Gedan and Silliman 2009b) and to account for the rate of canopy closure. However, many ecological studies have overturned this paradigm in coastal systems and found that positive interactions among closely planted propagules may enhance growth and productivity, especially in situations of physical stress as is often the case after systems are heavily degraded (Angelini et al. 2011, Silliman et al. 2015, Gittman et al. 2017). Thus, incorporating interactions that have been shown to be critical for enhancing ecosystem response to physical stressors, such as facilitation among organisms, may drastically increase restoration success (He et al. 2013, He and Bertness 2014). Calls are increasingly being made for restoration to include biotic considerations into restoration designs including spatial subsidies from nearby or adjacent habitats (Halpern et al. 2007), planting arrangement (Silliman et al. 2015), and restoration of associated of organisms (Palmer et al. 1997). However, few organizations or studies have included facilitation into their restoration designs despite growing amounts of evidence indicating it can increase restoration yields (Silliman et al. 2015, Zhang et al. 2018).

In response to global loss trends, efforts to restore seagrass beds globally have increased dramatically in popularity over the last 2 decades (Zhang et al. 2018). Case studies from the Virginia coastal bays, USA, have found that historical lack of seagrass regrowth was due to recruitment limitation and not due to environmental constraints (Orth et al. 2012), leading to a renewed focus on planting efforts. In combination with widespread efforts to decrease estuarine nutrient enrichment and turbidity, re-seeding efforts have led to the successful restoration of over 17,000 ha of seagrass beds (Orth et al. 2012, Lefcheck et al. 2018) that support a diverse array of fishes, invertebrates, and algal species (Lefcheck et al. 2017). These studies emphasize the importance of ecosystem rather than single-species restoration. Community organization and succession are critical theories for restoration ecology; thus, methodologies, such as including facilitation among organisms, that may enhance whole ecosystem development will be critical for success (Palmer et al. 1997).

One potential way to harness facilitation in seagrass restoration 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, the strategic use of bivalves in seagrass restoration has the high potential to improve restoration success, potentially 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 et al diversity). One of the most abundant clams in NC is the quahog, *Mercenaria mercenaria,* which is also the subject of extensive aquaculture. 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.

Methods

Our original proposal was to plant seagrasses adjacent to and isolated from restored oyster reefs. Due to physical limitations at the sites, namely that sandflats adjacent to restored reefs were too shallow for seagrasses to succeed, we altered our project to test how planting success varied with the addition of infaunal hard clams and with planting arrangement. In particular, we conducted two distinct experiments to test i) clam effects on seeds and ii) clam effects on adult shoots with respect to planting arrangement.

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 stored until December 2017 until planting. Prior to planting, seed viability was tested using tetrazolium staining and found to have 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. For clam treatments, 10 seed clams were added within the plot. 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 entirely 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.

Adult Transplants

To directly test for potential differences between intra and inter-specific facilitation, 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 support seagrass beds in the past at south Core Banks, NC. Each patch was a total of 0.0625 m^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 pressed monthly to maintain clam density and monitored for seagrass density and patch dimensions. Experiments were concluded in September 2018 as a result of Hurricane Florence.

Results

Seed Planting

When planted alone, seagrasses were significantly shorter in length than when planted with clams ($p = 0.013$, Figure 1A). Additionally, patches with clams expanded on average 400% from their original size; whereas, patches without clams did not change significantly in size ($p=0.023$, Figure 1B). This greater patch size was concomitant with a significantly greater belowground biomass ($p=0.011$, Figure 1C). Aboveground biomass was similarly greater in the presence of clams, and the difference was marginally significant ($p=0.074$, Figure 2A). 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 2B and 2C, respectively). Subsequently, we found that clams were associated with a marked 276% increase in reproductive shoot length, 500% reproductive shoot biomass increase, and 480% enhancement of spathe abundance within patches; however, the difference was not significant (p-value = 0.1156, p-value = 0.1575, p-value = 0.1519, Figures 3A-C, respectively).

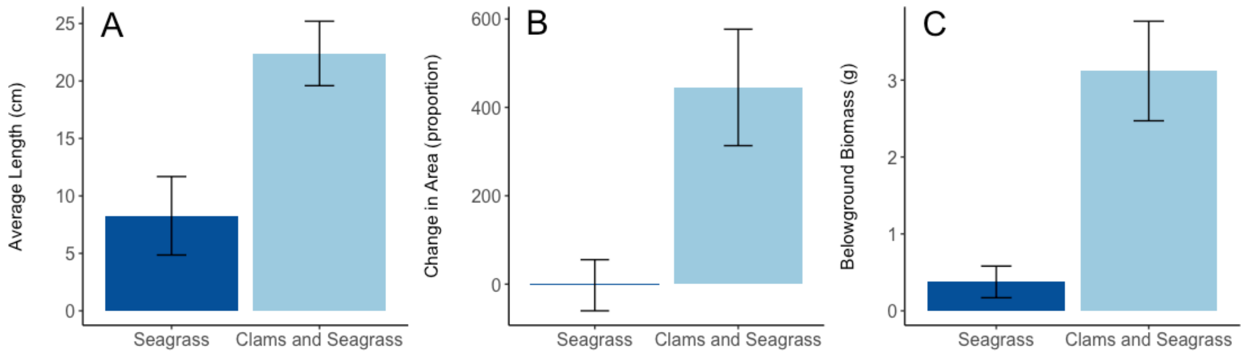

Figure 1. Adding clams to seagrass seeds was found to significantly increase the a) average shoot length, p-value = 0.013, b) proportional change in patch area, p-value = 0.023, and c) belowground biomass, p-value = 0.011.

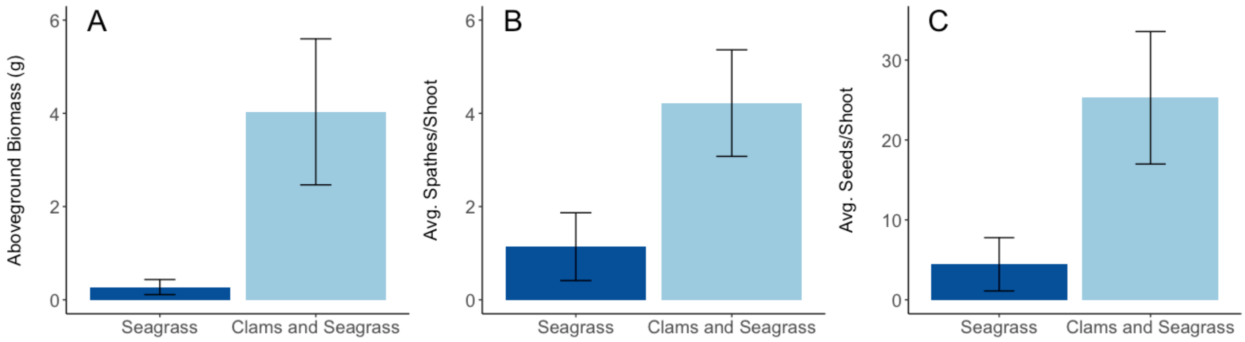

Figure 2. Adding clams to seagrass seeds was found to marginally increase the a) aboveground biomass, p-value = 0.074, and patch reproductive effort measured as the b) average number of spathes per reproductive shoot, p-value = 0.058, and c) average number of seeds per reproductive shoot, p-value = 0.065. Error bars represent 1 standard error.

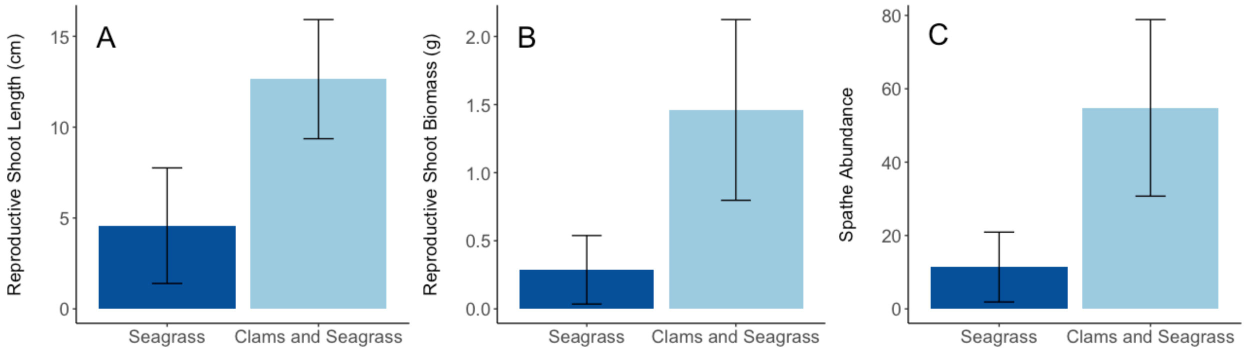

Figure 3. Clam additions were found to lead to a) 276% increase in reproductive shoot length and subsequent b) >500% increase in reproductive shoot biomass, and c) 480% increase in patch spathe abundance. Error bars represent 1 standard error.

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 layout was significantly associated with the proportional change in shoot density at experiment end (p<0.001, Figure 4A). 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 4B). 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 4C). Aggregated patches tended to increase in patch size over the experiment duration; whereas, dispersed treatments all declined in area.

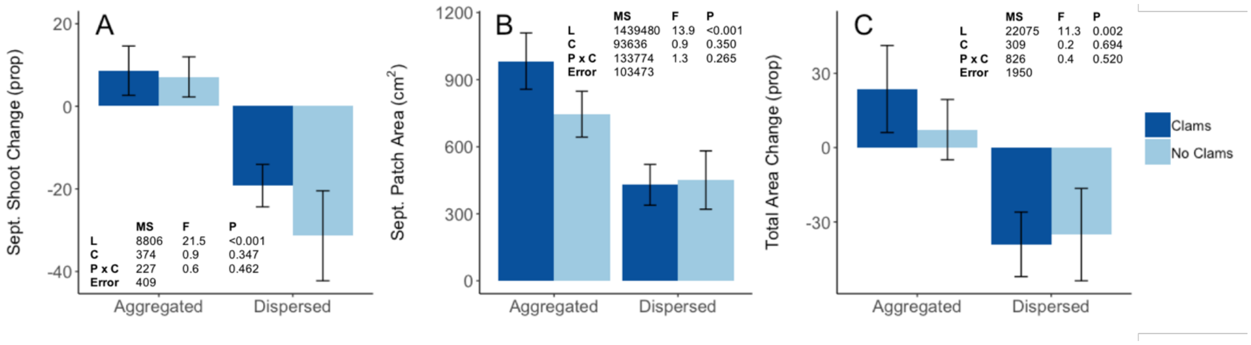

Figure 4. Interactive and separate effects of planting configuration and clam addition on a) the proportional change in shoot density from August to September, b) patch area at experiment end in September, c) total change in patch area over experimental duration from June to September. Probability value given for two-way ANOVAs testing for main and interactive effects. L is the main effect of planting layout, and C is the main effect of clams. Error bars represent 1 standard error.

Discussion:

Facilitations and mutualisms are powerful, structuring species interactions in coastal systems. Foundation species, such as seagrasses, marsh cordgrasses, oyster reefs, and forest trees, facilitate whole-ecosystem generation by providing habitat and ameliorating stressful environmental conditions for countless organisms (Angelini et al. 2011, Angelini et al. 2015, Thomsen et al. 2018). Multiple studies have further demonstrated the keystone role of positive interactions for enhancing ecosystem resistance to and recovery from disturbance (Angelini and Silliman 2012, He and Bertness 2014). For example, salt marsh grasses that grow with mussels can more readily withstand the negative effects of drought, and surviving marsh patches act as nuclei for marsh recovery and expansion (Angelini and Silliman 2012, Silliman et al. 2015). Facilitative interactions in coastal systems can be critical for resisting ecosystem transformations to less desirable alternative stable states.

Because restoration is an inherently stressful endeavor, it is necessary for methodologies to consider and include approaches that can enhance resistance to physical stressors. Here we demonstrate that 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. However, clam addition was not found to significantly affect the productivity of transplanted adult seagrass patches. Organic matter deposited as feces from bivalves may constitute a significant proportion of nutrients available to seagrasses (Peterson and Heck Jr 2001). 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 play a particularly vital role in the early stages of seagrass development and expansion by seed. Seagrass germination, in particular, is correlated with temperature, salinity and sediment oxygen levels (Orth et al. 2000), of which bioturbation by infaunal bivalves may facilitate.

Intraspecific facilitation is particularly likely 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 (Marbà et al. 2006). When planted as adult shoots, we found that intraspecific interactions 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 and excess. First, seagrasses planted in low nutrient soils can more efficiently utilize and retain nutrients under stressful conditions via leaf abscission and loss – nutrient reclamation through resorption. Thus, larger patches may be able to self-sustain low-nutrient conditions better than small patches (Pedersen and Borum 1993).

Moreover, 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. Moreover, oxygen released from roots to rhizospheres of submerged macrophytes contribute 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 positively facilitate one another to relieve anoxia stress at the patch level. However, empirical evidence is still needed to determine if, similarly to salt marsh grasses, passive diffusion of oxygen into the substrate can be used be neighboring plants (Howes et al. 1986, Bertness 1991).

Although our findings suggest that interspecific facilitation affects early-stage seagrasses; whereas, intraspecific facilitation enhances late-stage/adult seagrass productivity, use of these restoration techniques in other scenarios or at other sites may provide additional benefits. For example, restoration of seagrasses in areas with sulfide-reducing lucinid bivalves may further enhance restoration yields (van der Heide et al. 2012). Moreover, planting in clumped, high-density configurations may be advantageous for withstanding shear stress from waves (Chen et al. 2007). The 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 incorporating positive interactions into coastal restoration designs.

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 (Rietkerk et al. 2004, van de Koppel et al. 2005) where there are significant environmental and temporal constraints on organism establishment and growth. 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 where positive interactions that promote resilience to environmental stress are likely more prevalent. However, more experimentation is needed to determine how ubiquitous our intra- and interspecific interactions are across seagrass ecosystems and the underlying mechanisms that drive changes in productivity.

Our experiments provide further evidence and rationale for including facilitation into restoration designs. 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). 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 (Silliman et al. 2015, Zhang et al. 2018) into restoration designs. 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, 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.

Outreach

I have made a concerted effort to present preliminary findings at international and local conferences including the International Marine Conservation Congress, university symposiums, the Benthic Ecology Meeting, and the upcoming meeting for the Society for Ecological Restoration. On a more local level, I have given talks to local chapters of the eastern North Carolina Boys and Girls Clubs discussing my research motto, "teamwork makes the dream work" in coastal restoration. I will also serve as a mentor for several (6) high school students via a Duke Marine Lab – Carteret County High School partnership to engage students in local marine science research. These students will be shadowing me in Summer 2019, and though the experiment for which I was awarded the fellowship has concluded, many of the experimental patches have persisted. Students will be involved in ongoing monitoring of plots as well as taught basic ecological research techniques.

Students Supported

Our study was a collaborative effort with researchers from the UNC Institute of Marine Science, East Carolina University, and a local shellfish hatchery (Morris Farms). Through this project, I have also mentored and involved several research technicians (2) and undergraduate research students (6) including an NSF REU and NOAA Hollings Scholar. Former mentees are actively involved in the manuscript preparation and have also gone on to graduate programs where they are researching the inclusion of facilitation in coastal restoration designs.

Data Management Plan Progress

Our data management plan has not deviated from the initial proposal. Original data was initially maintained and written in field notebooks prior to transfer to electronic spreadsheets for storage and analysis. These spreadsheets are stored on an online server (Dropbox). The collected data will be made available to the public upon request, beginning October 1, 2019.

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