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Mitigation of Negative Effects of Ocean Change on Oysters by Eelgrass and its Implications for Aquaculture in Midcoast Maine

An Honors Paper for the Department of Biology

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Bowdoin College, 2022

Abstract

Species interactions are important to organisms and to the ecosystems they inhabit. These interactions, sometimes facilitations, can result in increased resiliency for both species. When facilitation occurs, organisms co-assist with physiological and environmental stressors. As anthropogenic impacts become more stressful for modern organisms, these interactions could offer a solution for many species. Ocean acidification has been shown to be detrimental to many calcifying organisms including oysters. More acidic conditions can slow the process of shell calcification, which can slow growth rates. This effect could directly impact the robust oyster farming business in Midcoast Maine. Because of its possible importance to oyster crops, we assessed the potential of *Zostera marina*, or eelgrass, to ameliorate the stresses of ocean acidification on farmed Eastern Oysters (*Crassotrea virginica*).

Photosynthesizing organisms such as seagrasses have been shown to locally raise pH, which could create growth refugia for calcifying organisms. While eelgrass has the potential to enhance oyster growth rates, its meadows could also be influencing food availability. To better understand these dynamics, we grew *C. virginica* in two locations in Harpswell, ME. *Crassostrea virginica* were split into three habitats at each location: seagrass, fringe, and mudflat, and placed on surface or benthic arrays. We found that seagrass presence and depth interacted to increase shell growth rate. Similarly, *Z. marina* improved condition index of *C. virginica.* As ocean acidification worsens, oyster farmers might have to turn to mitigation strategies to ensure profit yield from their labors. *Zostera marina* could be the solution to their future problems.

Introduction

The world's oceans are warming and acidifying at an alarming rate due to anthropogenic CO_2 emissions. On average, ocean surface waters maintained a pH ~8.2 before the Industrial Revolution but are projected to be about pH = 7.8 by the end of this century (Feely *et al.*, 2009). The Gulf of Maine is being particularly impacted by the consequences of ocean warming and acidification. The Northwest Atlantic has been warming at a faster rate than most other bodies of water, with the Gulf of Maine warming at a rate of 0.7°C per decade (Durack *et al*., 2018). Although these warming and acidifying increments seem to be insignificant, when put in an evolutionary context, the increases can be catastrophic. The speed at which the oceans are changing currently outpaces the rate at which most organisms can adapt (Tan *et al.,* 2018). The Gulf of Maine contains many species that are particularly vulnerable to warming and acidification including commercially important shellfish, such as the Eastern Oyster (*Crassostrea virginica*) (Salisbury and Jönsson 2017; Siedlecki *et al.,* 2021).

Midcoast Maine is home to a robust aquaculture economy, which may soon be, if not already, under duress due to ocean change. Ocean acidification occurs when anthropogenic inputs of carbon dioxide dissolve into the ocean and react with water to form bicarbonate and hydrogen ions. These hydrogen ions make the oceans more acidic on their own, but also react with carbonate to form more bicarbonate, making ocean conditions less favorable for carbonate ion formation. Because many marine organisms use calcium carbonate to build shells and exoskeletons, less carbonate in the ocean makes the biogenic synthesis of calcium carbonate more difficult and thus impacts the growth of organisms such as mollusks, corals, and echinoderms who depend on this process (Caldiera and Wickett 2003; Hoegh-Guldberg *et al.*, 2017; Salisbury and Jönsson 2017). In fact, mollusks have experienced up to a 40% reduction in calcification due to ocean acidification (Kroeker *et al*., 2013). Declines in calcification rates translate to smaller mollusk shell sizes. This could be problematic for oyster farmers as they profit from larger oysters. It is thought that by 2060, ocean acidification could reach a point of noticeable negative impact to mollusk aquaculture across the world (Stewart- Sinclair *et al*., 2020). Time is of the essence to implement mitigation strategies to preserve the value ($9.6 million in 2019; Maine Sea Grant) of oyster farms in the Midcoast region. While acidification is negatively impacting marine calcifying organisms, marine macrophytes that require carbon dioxide for photosynthesis may grow and thrive in low pH environments (Kroeker *et al*., 2013), and via photosynthesis may provide essential buffering capacity to the negative effects of ocean acidification on marine calcifiers.

One species interaction that may help buffer the negative effects of ocean acidification on oysters is their relationship with eelgrass (*Zostera marina*). Eelgrass is an aquatic flowering plant that is widespread in the northern hemisphere. It can be found in varying habitats and is a foundation species that creates a unique ecosystem that serves as a refuge, nursery, and home to many species (Nielsen *et al*., 2018). Through photosynthesis, autotrophs, such as eelgrass, pull in carbon dioxide from the environment to metabolize into sugars used for cellular processes. In regions of high eelgrass biomass, rates of photosynthesis can exceed rates of cellular respiration. In these cases, more carbon dioxide is being taken out of the system than is being put in, resulting in a locally increased pH during the day (Ricart *et al*., 2021). This creates localized refuges from low pH, which could be beneficial for calcifying organisms such as oysters. Along the coast of California, eelgrass has been found to raise pH in its meadows 65% of the time when compared to unvegetated areas. In some cases, the ability of eelgrass to raise pH was found to be long-lasting and effective, meaning that the benefits may translate to better outcomes for organisms that live in eelgrass meadows (Ricart *et al.,* 2021). However, to achieve these positive impacts, seagrass meadows need optimal light conditions (i.e. limited shading and/or longer photoperiods) and water residence time (Nielsen *et al*., 2018). Intermediate water residence time will allow for seawater with elevated pH to stay in the meadow long enough to cause an effect but not too long as to become stagnant. These effects might have seasonal variation, in that they are more pronounced during the summer, when many macrophytes are most productive (Hendriks *et al.,* 2014; Ricart *et al.,* 2021). It is possible that the effects of both oysters and eelgrass could be harnessed into a synthetic facilitative interaction.

The promise of a relationship between photosynthesizing organisms like eelgrass with calcifying organisms such as oysters is well documented, but quite complex and possibly difficult to implement (Bergstrom *et al*., 2019; Ricart *et al.,* 2021). The pH modifying qualities of marine macrophytes often directly translate into increased calcification rates for calcifying organisms. For example, species of *Halimeda,* a genus of calcifying algae, have been shown to double their calcification rates when in the presence of *Halodule wrightii*, a seagrass species native to Brazil (Bergstrom *et al.,* 2019). Similarly, *Crassostrea gigas*, the Pacific oyster, experienced up to a 40% increase in shell growth rate when in the presence of high eelgrass biomass (Ricart *et al.,* 2021). It is possible that macrophyte restoration could be used as a strategy to mitigate the effects of ocean acidification on calcifying organisms, though in the case of eelgrass, there are issues to the implementation of a mitigation strategy of this kind in Maine. Since eelgrass meadows are so ecologically important, they are protected by the State of Maine through ME LD593. This law calls for the statewide mapping of eelgrass meadows to restore and protect current stands of eelgrass (ME LD593). Shading from oyster racks could pose an issue for light limited eelgrass meadows. Additionally, eelgrass populations have fluctuated throughout recorded history due to wasting disease and other unknown factors (Wipplehauser 1996). A robust eelgrass meadow could disappear from one growing season to the next. In less ideal conditions, diel fluctuations in photosynthesis and cellular respiration have the possibility of exacerbating low pH instead of ameliorating it (Pacella *et al.,* 2018). Work done by Groner *et al.,* (2018) found that eelgrass was able to lessen but not ameliorate low pH in co-culture with oysters. They saw that in low pH conditions, eelgrass benefitted from co-culture with oysters more than oysters benefitted from eelgrass. Because these interactions are complex, more research is needed to understand how eelgrass meadow restoration or conservation could have implications for improving future oyster farming.

While eelgrass often seems to improve environmental conditions enough for calcifying organisms to grow faster and more effectively, it has also been shown to impact food availability. Eelgrass blades increase roughness in meadows and thus reduce water flow. The decreased flow to the system causes interruptions in food delivery and subsequent decreases in food availability (Reusch 1998). Work done by Lowe *et al.,* (2019) showed that food availability, not pH, was the limiting factor in bottom-up ecosystem control. In some eelgrass meadows in that study, eelgrass improved food availability through either increased resuspension or support of epiphyte communities important to oyster diet. Seagrass-associated impacts on food availability were site specific and dependent on other factors such as salinity. Allen and Williams (2003) corroborated the importance of food availability when they saw increased *Musculista senhousia* growth in eelgrass meadows after the addition of plankton to the system. Access to food seems to be important to growth rates of oysters and other bivalves. Since they are sessile organisms, the conditions of their ecosystem that effect food availability directly enhance or impede their ability to thrive. In this way, environmental stressors, including pH, and biotic factors, such as the presence of an eelgrass meadow, likely interact to influence oyster growth rates.

In this study our goal was to determine if proximity to eelgrass meadows aided oysters in calcifying and increasing tissue. We hypothesized that oysters grown in aquaculture cages in or near eelgrass meadows would grow to have greater shell surface area and condition indices than oysters placed in mudflats, far from eelgrass meadows. To test this hypothesis, we used image analysis to compare growth before and after an 11-week exposure to presence or absence of eelgrass. Additionally, we performed condition indexing on each surviving oyster to determine if eelgrass exposure had a quantifiable effect on tissue. The overall goal of this study was to understand how the restoration and planting of eelgrass meadows could be coupled with oyster farming to enhance production and outcome for oyster farms and mitigate the projected impacts of climate change.

Methods

Study Sites

We selected two study sites as locations for our experiment due to their proximity to the Schiller Coastal Studies Center and to one of The Quahog Bay Conservancy's oyster farms (Fig 1). The locations, which will hereafter be referred to as Widgeon Cove (43.798427 N, -69.972102 W) and Dog's Head (43.793894 N, -69.953851 W), contained a robust eelgrass meadow, an adjacent mudflat, and an in-between fringe area (Fig 1). Dog’s Head is a peninsula on Orr’s Island in Harpswell, ME. It partially forms Brewer Cove, which is home to a healthy eelgrass meadow. Below low tide at Brewer Cove, which is where we performed maintenance on the arrays, seawater level at the seagrass habitat was at 5 ft, the fringe habitat was at 7 ft, and the mudflat habitat was at 9 ft. Widgeon Cove is located on the opposite side of Harpswell Sound, directly west of the Schiller Coastal Studies Center. It also features a dense eelgrass bed. Below low tide at Widgeon Cove, the seawater level at the eelgrass habitat was at 6 ft, the fringe habitat was at 8 ft, and the mudflat habitat was at 10 ft.

Oyster Collection

The Quahog Bay Conservancy’s Snow Island Oyster Farm in Quahog Bay in Harpswell, Maine supplied 360 triploid oysters, bred for aquaculture for this study. Oysters were approximately 2 cm in length at the start of the study (Timepoint 1).

Experimental Design

We glued six oysters to each of sixty Trex composite deck board plates (Fig 2). We attached five plates each to one of twelve PVC arrays (Fig 3). To test the effect of depth on oyster shell growth, six of the arrays were designed to float on the water (Surface Arrays), while the other six were anchored to the ocean floor and held oyster plates approximately one meter above the sediment (Benthic Arrays).

We selected mudflat, fringe, and seagrass habitats at each location (Widgeon Cove or Dog’s Head) and deployed a paired benthic and surface array in each habitat (i.e., three benthic and three surface arrays at each location) (Fig 3). We constructed the benthic arrays using a coated steel aquaculture cage on a PVC frame, which was affixed to the benthos with cinder blocks. We also constructed the surface arrays with a coated steel aquaculture cage attached to two buoys with a PVC frame, these floating arrays were fixed in place with a cinder block anchor. The aquaculture cage served to limit predation on the oysters.

Before deployment, we took images of each oyster plate with a scale. We numbered the plates and recorded their locations. We gave every oyster a letter from A to E and tracked their growth throughout the course of the study. We analyzed the images at three timepoints throughout the study. Timepoint 1 was June 21, 2021, Timepoint 2 was July 29, 2021, and Timepoint 3 was September 6, 2021 (Fig 2).

On July 29, 2021, we pulled all the oyster arrays of the ocean and took images of each individual oyster plate. These images served as Timepoint 2 in oyster shell growth change (Fig 2). Collection date of each oyster was recorded.

On September 6, 2021, we pulled arrays from the ocean for a second time. At this point we removed all oyster plates from the arrays and brought back to the lab for imaging. These images were used to find surface areas for Timepoint 3, which was the final timepoint in the oyster shell growth study (Fig 2). Once photographed, we froze all remaining oysters at -80°C for condition indexing. Any dead oysters were noted throughout the time of the study. In all, the study took place over 11 weeks from June 21, 2021, to September 6, 2021 (77 days).

Change in projected area as a proxy for growth rate

At each timepoint, we took top-down photographs of each of the oyster plates with a camera placed at a fixed height. Two-dimensional shell surface area was quantified for each oyster using ImageJ, following Ricart *et al.* (2021) (ImageJ v1.8, NIH). Mean change in surface area over 77 days was calculated by subtracting oyster surface area at Timepoint 1 from oyster surface area at Timepoint 3 for each individual.

Condition Indexing

We quantified oyster condition index using protocols adapted from Ricart *et al.* (2021) and Davenport and Chen (1987). First, oyster tissue was removed from the shell and weighed. Oyster shell and tissue were then both dried in a 60°C drying oven for one week and then weighed. Condition Index (CI) was calculated as: CI= (Tissue dry weight / (Shell dry weight + Tissue dry weight)) * 100. Thus, CI is a ratio that determines how much of an oyster's weight is found in its tissue. This value is commonly used in aquaculture as it is a way to visualize how physiological stress translates to changes in somatic tissue growth (Sasikumar and Krishnakumar, 2011).

Statistical Analysis

We performed statistical analyses in RStudio v.3.6.0 (RStudio Team). A three-way ANOVA followed by a post-hoc Tukey's Honestly Significant Different test was used to assess the additive impacts of depth (surface vs. benthic) and location (Dog's Head vs. Widgeon Cove), and the interactive effects of habitat (fringe, mudflat, seagrass) on the change in oyster surface area. A four-way ANOVA followed by a post-hoc Tukey's Honestly Significant Different test was used to assess the additive effects of date, habitat, and location and the interactive effect of depth on oyster condition index.

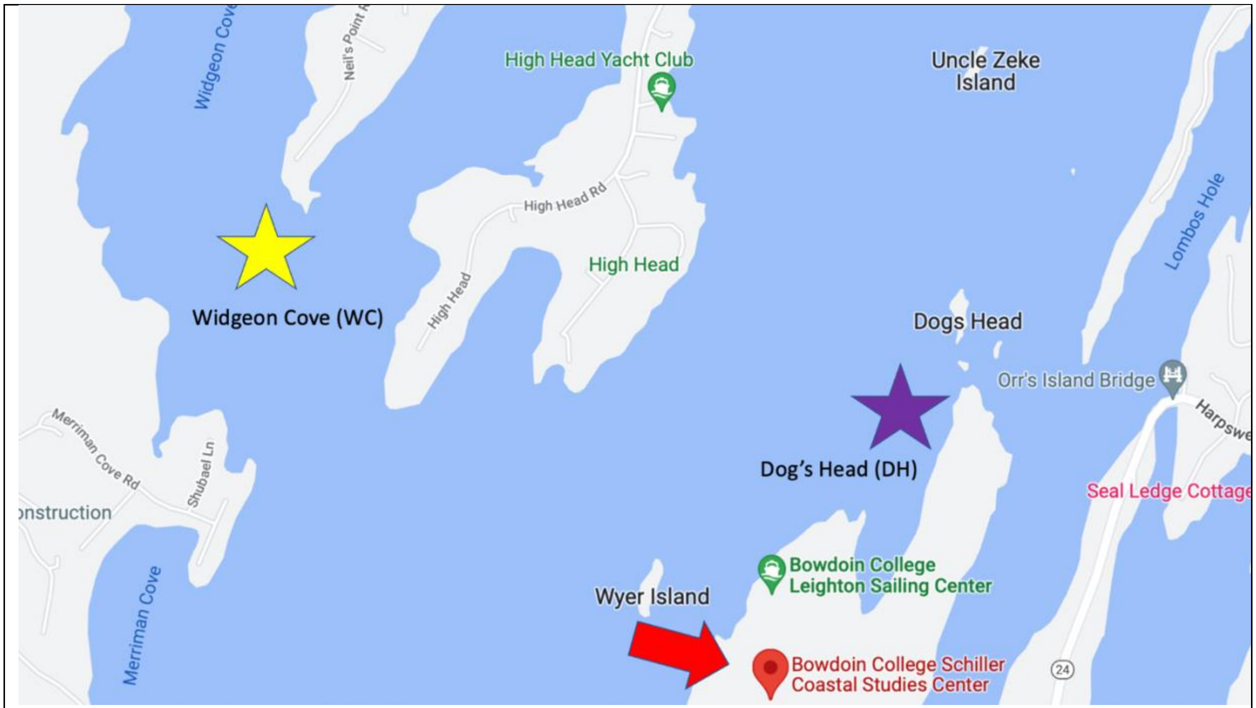

Figure 1| **Map of Array Locations.** Google Maps image of the Bowdoin Schiller Coastal Studies Center along with the two study locations, Widgeon Cove shown by a yellow star and Dog's Head, indicated by a purple star.

Figure 2| **Images of oyster plates at 3 timepoints**. (a) Timepoint 1 (June 21) (b) Timepoint 2 (July 29) (c) Timepoint 3 (September 6). Red circles highlight one individual oyster over the 77-day study.

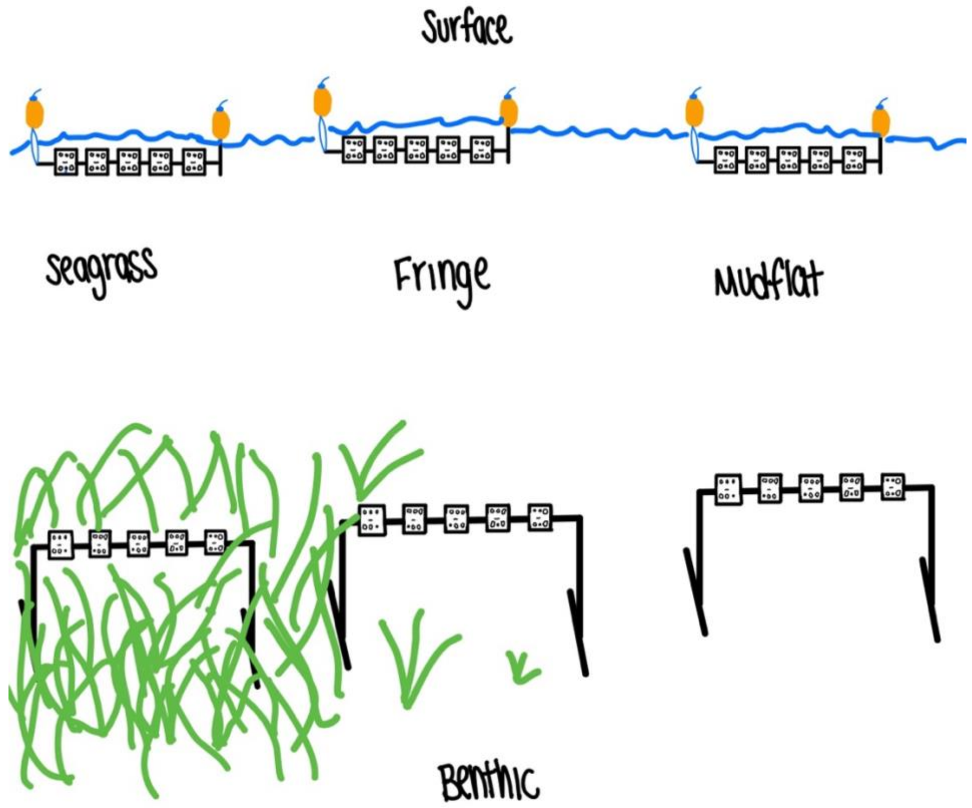

Figure 3| **Schematic of experimental design.** We placed paired benthic and surface arrays in each habitat (seagrass, fringe, mudflat) at each location (Dog's Head and Widgeon Cove). We adhered five plates with six oysters to each of the twelve arrays.

Results

Oyster Surface Area

Oysters in all treatments grew over the course of the experiment, exhibiting 2-3-fold increases in surface area (Fig 4). Changes in oyster surface area over the course of the experiment were dependent upon both depth (benthic vs. surface) and the interaction of depth and habitat (Table 1). Specifically, overall benthic oysters grew more over 77 days experiment than did surface oysters (Table 1; Fig 4). Interestingly, there was no significant difference between surface and benthic oysters in the mudflat or fringe habitats, but surface oysters in the seagrass habitats grew significantly less than benthic oysters in both the seagrass and fringe habitats (Table 1; Fig 5). There was no significant effect of location (Brewer Cove vs. Dog's Head) on change in oyster surface area (Table 1; Fig 5).

Oyster Condition Indexing

Oysters grown in seagrass habitats had significantly greater condition indices than did those grown in the mudflat and fringe habitats (Table 2; Fig 6). Condition index was not affected by location (Dog's Head vs. Widgeon Cove) or depth (benthic vs. surface) (Table 2). Additionally, condition index did not vary across date of collection (Timepoint 2 vs Timepoint 3) (Table 2).

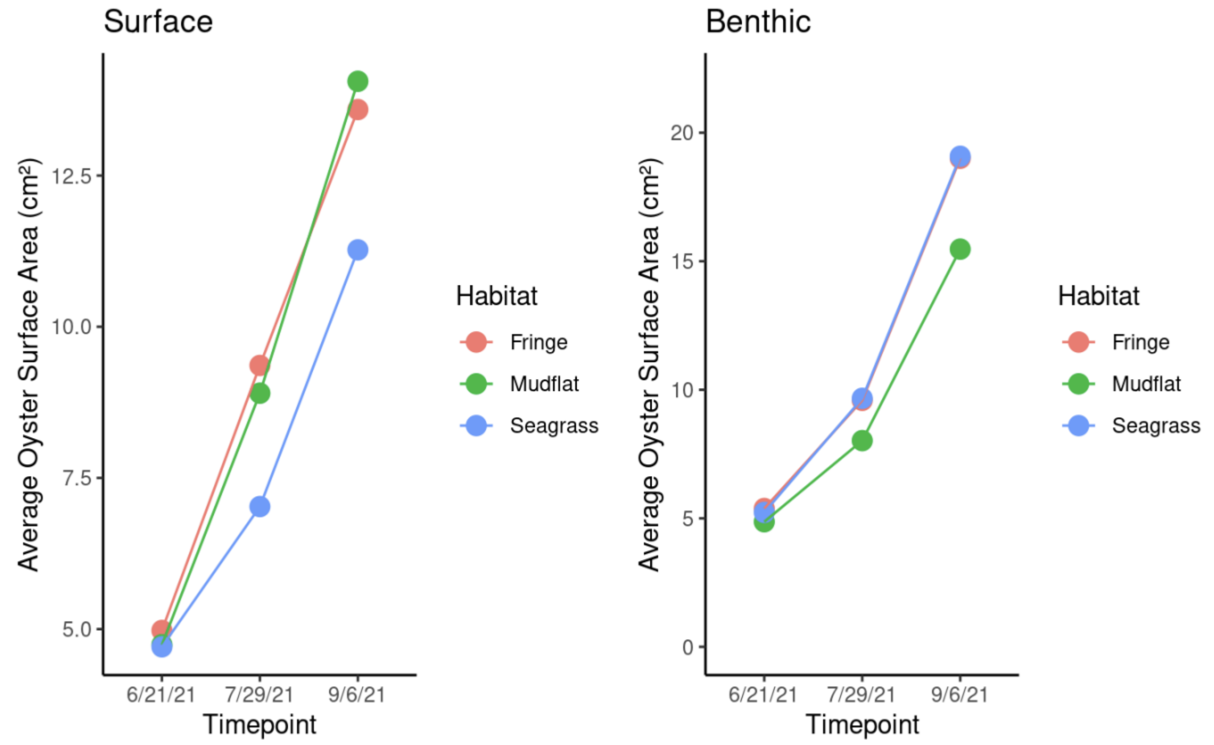

Figure 4 | **Oyster shell growth over 11 weeks, broken down by habitat and depth.** Oyster shell surface area, measured in cm^2,was averaged by habitat at each time point (June 21, July 29, and September 6). Each habitat is shown in a different color (fringe = red, mudflat = green, seagrass = blue). N = 132.

	Df	Sum Sq	Mean Sq	F	*p*-value	Tukey/ANOVA
Depth	1	739	739.1	15.200	0.000144*	ANOVA
Location	1	0	0.0	0.001	0.981410	
Habitat	2	7	3.4	0.069	0.932896	
Habitat:Depth	2	253	126.6	2.604	0.077243	
Seagrass:Surface-Fringe:Benthic					0.0143202*	Tukey
Seagrass:Surface-Seagrass:Benthic					0.0033975*	

Table 1 | **Summary of ANOVA and Tukey HSD of effects of habitat, depth, and location on change in oyster surface area.** Significant values (*p* <0.05) are denoted with asterisks.

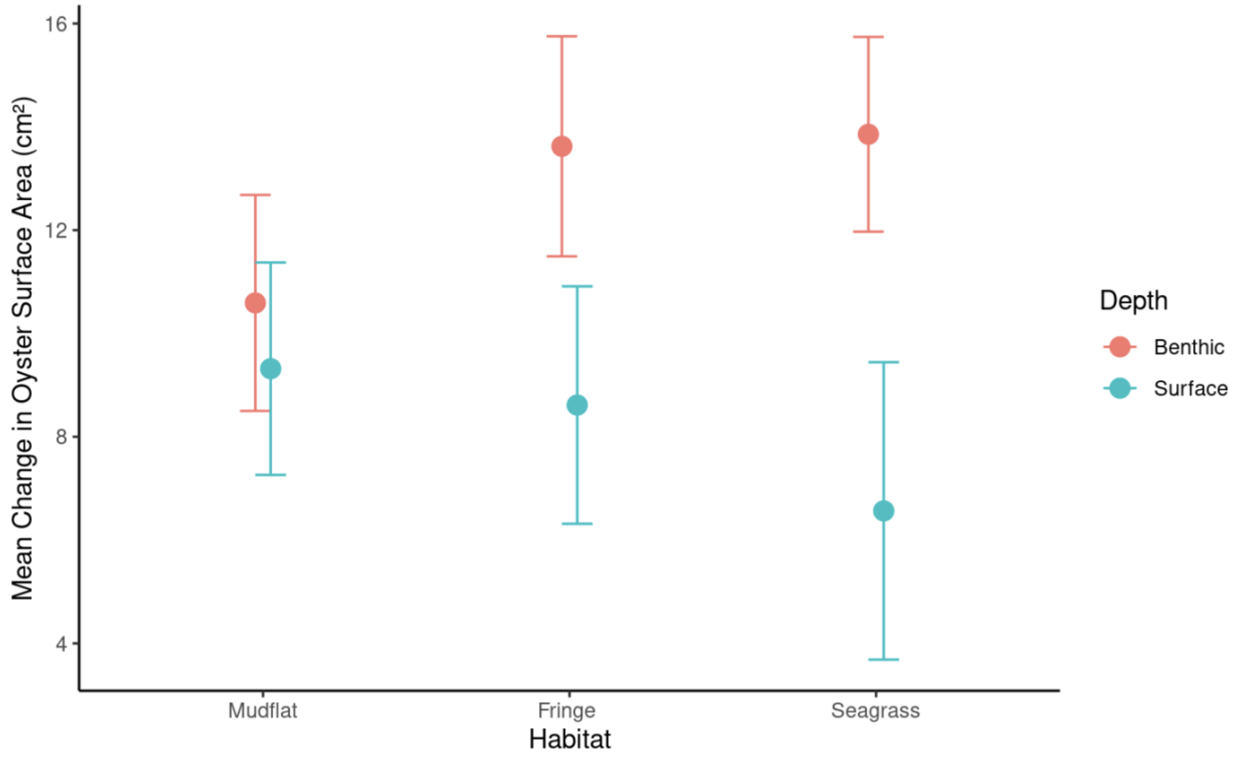

Figure 5 | **Mean change in oyster shell growth by depth and habitat from Timepoint 1 to Timepoint 3 (77 days).** The difference between initial oyster surface area (Timepoint 1) was subtracted from final surface area (Timepoint 3) and then averaged across arrays (considering both habitat and depth). There was a significant difference in mean change in oyster surface area between depths in the seagrass habitat (post hoc comparison: $p < 0.01$). Error bars represent standard error. N = 132.

	Df	Sum Sq	Mean Sq	F	*p*-value	Tukey/ANOVA
Date	1	32.7	32.69	2.622	0.1079	ANOVA
Location	1	0.0	0.03	0.003	0.9585	
Depth	1	2.2	2.17	0.174	0.6774	
Habitat	2	96.6	48.32	3.876	0.0233*	
Habitat:Depth	2	5.6	2.80	0.224	0.7993	
Mudflat:Fringe					0.9991	Tukey
Seagrass:Fringe					0.0305*	
Seagrass:Mudflat					0.0194*	

Table 2 | **Summary of ANOVA and Tukey HSD of effects of date, location, depth, and habitat on oyster condition indexing.** Significant values ($p < 0.05$) are reported with asterisks.

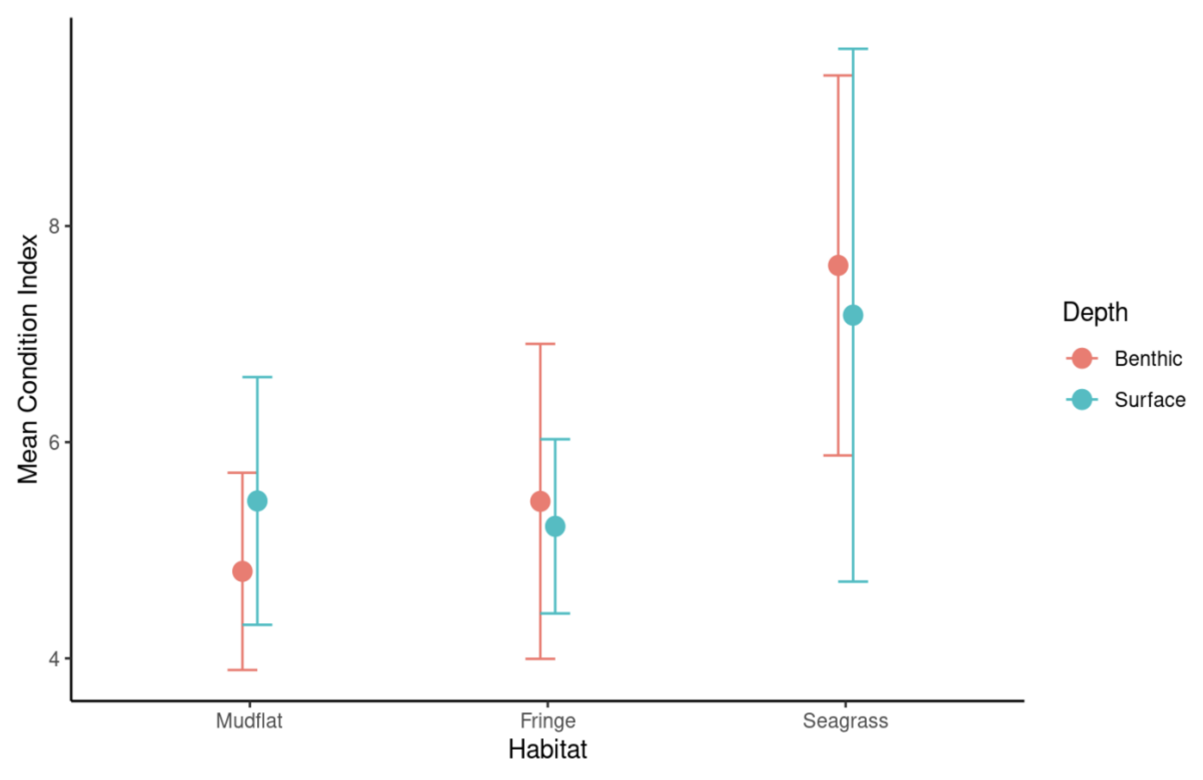

Figure 6 | **Mean Condition Index of oysters by habitat and depth.** We averaged condition indices across arrays (including habitat and depth). There were significant differences in mean condition index of oysters between seagrass and fringe habitats as well as seagrass and mudflat habitats (post hoc comparison $p < 0.05$, $p < 0.05$). These results occurred regardless of depth. Error bars represent standard error. N = 132

Discussion

The positive association between oyster growth and exposure to eelgrass indicate that a facilitative interaction is occurring between the two species. This interaction can likely be explained by eelgrass manipulating both pH and food availability in its meadows. It is unclear which of these two mechanisms has more control over this interaction and it is possible that the importance of the mechanisms varies across depths and habitats. Our results reveal that eelgrass may enhance the growth of oysters in the field in certain contexts through increased shell surface area and/or increased condition index(tissue:shell), which holds importance to the oyster farming industry in Midcoast Maine.

While not statistically significant, it appears that oysters in surface seagrass arrays trended toward having the lowest growth rates of any oysters in our experiment (Fig 4). The lack of growth seen by surface seagrass oysters could be attributed to warm temperatures in the shallowest water in the study. Previous studies have shown that high temperatures reduce oyster growth rates and increase mortality (Rybovich *et al.,* 2016, Speights *et al.*, 2017). Taken together, these results suggest that proximity to eelgrass may provide benefits to oyster growth but that some of these benefits are lost if oysters are above rather than in seagrass meadows. Site and condition specific differences, including hydrodynamics and community structure have been shown to influence ocean acidification buffering in other work as well (Fernandez *et al.,* 2018). Notably, differences in growth parameters between benthic and surface arrays are lost when the arrays are not placed above or in eelgrass meadows, suggesting that both surface and benthic aquaculture methods are equally as effective in mudflats and even adjacent to eelgrass meadows.

These findings have implications for both commercial oyster aquaculture and eelgrass restoration and management practices in the Gulf of Maine. Within eelgrass meadows both physical and biological conditions are different than outside meadows, which could explain variation across habitats. Eelgrass meadows are known to locally elevate pH long enough to have lasting ecological effects (Ricart *et al.,* 2021). In mesocosm experiments, calcifying organisms have shown increased calcification rates due to exposure to eelgrass (Ricart *et al.,* 2021). Additionally, many factors including predator abundance, food availability, and oxygen concentration, to name a few, are altered (Nielsen *et al.,* 2018).

Increased access to food could play a large role in the differences we observed in condition index between eelgrass meadows and the other habitats. It is likely that a combination of increased food availability and pH amelioration caused better conditions for oysters in seagrass habitats. Since condition index was still high in the surface seagrass habitat, although shell growth was low, it is possible that access to nutrition was able to make up for less-than-ideal shell-forming conditions at the surface of the eelgrass meadows (Fig 5, 6). These findings are like work done by Reusch (1998) who found that *Mytillus edulis* growth rates in seagrass meadows were significantly less than those in mudflats, but recruitment rates were higher in seagrass meadows than in mudflats. Because of its control over food availability, seagrass caused concurrent enhancement of one parameter and depression of another. Both food availability and pH amelioration are playing roles in this relationship and have varying effects depending on other conditions.

The results in this study complicate both current oyster aquaculture practices and pushes for eelgrass restoration in the state of Maine. Oyster farming in Maine utilizes several aquaculture methods: floating oyster arrays, submerged bags and/or cages, and scattering of individuals on the benthos. Little work has been done to compare the different methods of oyster aquaculture and their benefits for oyster shell and tissue growth. There is no clear best method for oyster farming widely accepted by the oyster farming community in Maine. Most methods are categorized as off-bottom, meaning that oysters are held in some fashion above the seafloor (Walton *et al.,* 2012). While according to the industry both our surface and benthic arrays would be considered off-bottom methods, we have shown that there are differences within this categorization and when oysters are placed in eelgrass beds there is a clear difference in oyster growth parameters between the two. The presence of eelgrass adds even more complexity to this situation.

The improved condition and growth of oysters within eelgrass beds poses an issue since eelgrass is protected in Maine and can be harmed by shading and dredging (Wipplehauser 1996; Neckles *et al.,* 2005). In oyster aquaculture in the Pacific Northwest where oysters are often grown on-bottom, meaning they are spread on the seafloor and then harvested by dredging or hand-picking, eelgrass and oysters often compete for space, and increasing oyster density causes decreases in eelgrass biomass (Tallis *et al.,* 2009) More research needs to be done to determine how an aquaculture approach can be developed to minimize shading and dredging while maximizing proximity of oysters to eelgrass, thus increasing both growth rate and condition index (Tan and Zheng 2020). Eelgrass's status as a protected habitat-forming organism in Maine means that planning and implementing strategies to benefit oysters and farmers will not be easy, but the positive interactions between the two species need more work and attention, especially as ocean conditions become less favorable to the farming of oysters. Eelgrass meadows can be planted strategically around submerged oyster racks or reefs to achieve these ends. Creating and restoring eelgrass meadows is known to be a "no regrets" coastal management strategy, meaning there cannot be a bad outcome associated with a plan of this kind (Nielsen *et al.,* 2018). Thoughtful planning and cooperation between researchers, conservationists, and oyster farmers could result in benefit to the oyster farming industry as well as to eelgrass recovery.

Potentially, oysters could positively impact eelgrass growth, creating the possibility for positive feedback between these two species. Oysters could potentially improve water quality by removing seston from the water column, making light and turbidity conditions more favorable for eelgrass restoration. Since oysters filter feed, it is possible that they are positively contributing to seagrass growth and biomass, resulting in a mutualistic relationship between the two species (Smith *et al.,* 2009). There are possibilities for oyster reefs enhancing water quality enough to restore seagrass meadows (Sharma *et al*., 2016). It has even been found that the presence of oysters could improve eelgrass health by filtering out *Labrinthula zosterae*, which causes eelgrass wasting disease (Groner *et al*., 2018). This relationship could form a positive feedback loop, in which more eelgrass biomass means more oyster growth, that benefits both species and the stakeholders invested in them.

Future studies could more deeply explore the connection of proximity of oysters to eelgrass meadows. Implementation of a mitigation strategy of this kind would require determining the extent of positive effect of eelgrass on oysters, the magnitude of shading allowed by eelgrass, and the best method for oyster farming with eelgrass present. An economic cost-benefit analysis of the monetary benefit of this positive interaction to oyster farmers would likely be necessary for implementation. If the positive relationship we found between oyster rack depth and oyster shell growth is corroborated by other work, it might be beneficial to rethink the current practices of oyster farming in Midcoast Maine, especially as climate change exacerbates ocean acidification’s impacts on calcifying organisms.

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