

**EVALUATION OF SELECTIVELY BRED EASTERN OYSTER  
(*CRASSOSTREA VIRGINICA*) STRAINS IN DELAWARE BAY:  
IMPLICATIONS FOR LIVING SHORELINE ENHANCEMENT**

by

Raleigh Elizabeth Hudock

A thesis submitted to the Faculty of the University of Delaware in partial fulfillment of the requirements for the degree of Master of Science in Marine Studies

Fall 2025

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## ABSTRACT

Oyster-based restoration projects, particularly living shorelines, are being installed to protect coastal ecosystems and infrastructure. While these installations often successfully create aquatic habitats, further refinement in optimizing the growth potential of shellfish on shoreline installations will increase the success rate and efficiency of restoration projects. This study evaluated the growth and mortality of two farmed strains of oyster, NEH<sup>®</sup> (high salinity tolerant) and DBX (medium and low salinity tolerant), in the lower Delaware Bay. From July to October 2023, we monitored the growth and mortality of each strain cultured in rack-and-bag oyster aquaculture gear positioned at intertidal and subtidal environments. The effect of tidal position, temperature, salinity, and dissolved oxygen on oyster performance (average oyster length and weekly oyster mortality) was examined using Generalized Additive Models (GAMs) to determine covariate importance towards the growth and survival of both oyster strains. Our findings indicate that NEH<sup>®</sup> oysters exhibited better meat condition than DBX oysters (two-way ANOVA,  $p = 0.03$ ), as well as a significant difference in average weekly length (Growth GAM,  $p = 0.02$ ). Oyster weekly average length was influenced by average temperature and previous week's minimum dissolved oxygen, while weekly mortality was influenced by minimum and average salinity and minimum dissolved oxygen. Subtidal oysters exhibited greater growth (Growth GAM,  $p < 0.001$ ) and survival (Mortality GAM,  $p = 0.01$ ; Scheirer-Ray-Hare test,  $p < 0.001$ ; Wilcoxon rank-sum test,  $p < 0.001$ , adjusted with Bonferroni corrections) than intertidal oysters, suggesting the addition of subtidal design features

can enhance the likelihood of success for oyster restoration projects. These results emphasize the need to select an appropriate strain based on local environmental conditions and suggest that pre-seeding selectively bred oysters into living shoreline materials is a viable option to enhance restoration efficiency. Our results aid in our understanding of identifying important physical and environmental factors that determine oyster performance and provide insights via statistical models that can be applied to inform restoration and shellfish-based living shoreline planning.

# Chapter 1

## LITERATURE REVIEW

### 1.1 Introduction

The eastern oyster is both a commercially and ecologically important species to coastal regions in eastern North America. Eastern oysters are an important aquaculture species and provide a multitude of beneficial ecosystem services. With their increasing importance to coastal ecosystems, eastern oyster studies are becoming progressively more popular for experiments involving restoration, ecosystem services, and oyster aquaculture (Atwood & Grizzle, 2020; Grizzle et al., 2020; Martínez-Baena et al., 2022). However, some aspects of the population dynamics of eastern oyster are still highly debated (e.g., recruitment irregularities) or represent understudied processes, more specifically larval recruitment (Epifanio, 1988; Manley et al., 2008), and transport (Atwood & Grizzle, 2020), as well as the ecosystem services provided by eastern oyster reefs and aquaculture gear are less well understood. My literature review aims to document the current state of knowledge of eastern oyster life history, population, and size demographics, as well as ecosystem services and impacts of oyster aquaculture, helping to identify gaps in the literature that require further study. The outcomes of this review will offer valuable information for advancing future living shoreline studies and installation endeavors. Additionally, my research will support commercial oyster production and equip stakeholders with the means to enhance the effectiveness of their investments in oyster-based living shorelines, all while optimizing ecosystem benefits and fostering economic growth.

## 1.2 Taxonomy & Morphology

Eastern oysters occupy a vast range and are located throughout the coast of eastern North America, specifically ranging from the Gulf of Mexico to the Gulf of St. Lawrence (NOAA Fisheries EOBRT, 2007). *C. virginica* is classified in the phylum Mollusca, class Bivalvia, order Ostreida, and the family Ostreidae (NOAA Fisheries, 2022b). The eastern oyster is characterized by bilateral asymmetry, with the left valve being thicker and cupped deeper than the right valve (Galtsoff, 1964) and a reduced body cavity (Seed, 1983). Eastern oysters settle as spat on the left valve, which forces the right valve on top (NOAA Fisheries EOBRT, 2007; Figure 1.1). The interior of the shells have a purple-pigmented scar near the dorsal end where the adductor muscle is located (NOAA Fisheries EOBRT, 2007). Eastern oyster umbones point to the posterior end of the organism and have a curved shape (Stanley & Sellers, 1986). Ultimately, eastern oyster shell thickness and shape are inconsistent and are partially driven by environmental forcing (Stanley & Sellers, 1986). Specifically, shells of oysters grown in hard-bottom substrates tend to be thicker, while oysters grown in finer sediment have more delicate shells with straighter umbones (Stanley & Sellers, 1986). Shell morphology also differs between solitary oysters and oyster reefs. Solitary oysters that grow on rocky, hard substrate are typically rounded and have radial ridges and layered shells (Stanley & Sellers, 1986). Whereas oysters grown on reefs and soft substrates have fewer ridges and are slimmer in shape (Stanley & Sellers, 1986). Additionally, oyster morphology is more flexible during the adult stages compared to static morphology in the larval stage (Carriker, 1996).

### **1.3 Life History**

#### **1.3.1 Reproductive Strategies and Fecundity**

Eastern oysters exhibit protandry, where organisms mature as males but frequently transition to females in later life stages (Thompson et al., 1996). However, factors affecting sexual determination in eastern oysters are often complicated and variable. For instance, eastern oysters may annually change their sex in response to multiple stressors, such as environmental conditions, physiological responses, or nutrient availability (Ford et al., 1990). Additionally, Thompson et al. (1996) suggested eastern oyster sex determination can be affected by their proximity to adjacent oysters and community demographics. When oyster gonads are undifferentiated, sex reversal can occur during spawning events (Thompson et al., 1996). Not only is eastern oyster sex reversal a difficult process to predict, but oyster fecundity is also challenging to calculate, because oysters exhibit extended spawning periods with irregular spawning events (Thompson et al., 1996). Additionally, oyster gonadal tissue is internally dispersed and fused with other tissues (Thompson et al., 1996). Fecundity estimations have been made ranging from 2 to 115 million eggs per female; however, this number is dependent on the size of the female as well as where they are geographically located (Cox & Mann, 1992). Spawning initiation is influenced by a multitude of factors such as salinity, temperature, and other physiochemical cues, including chemical stimulation from gametes, as well as chemical induction by phytoplankton and hormones (Galtsoff, 1964). Due to the spatial variability of these factors, eastern oyster spawning times will vary based on geographic range. For instance, in the mid and North Atlantic, spawning is seasonal and often occurs in the summer, whereas the southern parts of their habitat range

experience spawning in all seasons except winter (Berrigan et al., 1991). Ultimately, the optimal spawning conditions occur above a salinity of 10 psu and water temperature at or above 20 °C (Breuer, 1962). Persistence of these conditions will allow for extensions of the spawning duration (Breuer, 1962).

### **1.3.2 Larval Background**

Once oyster sperm and egg unite, oysters mature through multiple larval stages until they adhere to substrate (Shumway, 1996). The rate of larval development is greatly dependent on water temperature (Shumway, 1996). Ultimately, oyster larval dispersion and recruitment processes are not well understood as they are largely based on oceanographic forcing conditions that vary at subtidal frequencies (Epifanio, 1988). Oyster larval retention is driven by both passive (i.e., hydrodynamic forcing) and active (i.e., vertical swimming) transport mechanisms (Dekshenieks et al., 1996). The eastern oyster larval stages can be further broken down into planktonic (not free swimming) and vertically migratory capable stages (NOAA Fisheries EOBRT, 2007). The trochophore stage, or the first larval planktonic stage, occurs 4 to 6 hours after fertilization and can last up to 2 days (Kennedy, 1996). Feeding does not occur during the first larval stage. In the second, ‘veliger’ stage, larvae are planktotrophic and feed on small animals and plants (Kennedy, 1996). These veliger stages last up to 2 months and involve significant morphological changes, including the development of larvae with a functioning foot (Hopkins, 1931). The foot is used to travel to settlement areas where they attach to the substrate; however, this foot is absorbed when metamorphosis occurs into a fully settled oyster (Hopkins, 1931). Veliger larvae utilize both internal and environmental cues to identify the substrate they wish to settle on (Kennedy, 1996). Larvae display

exploratory behavior to identify appropriate substrate, and this behavior can be performed again or reversed to find better substrate if metamorphosis has not occurred yet, since it is a permanent process that invokes morphological changes (Kennedy, 1996). Metamorphosis is triggered by water salinity, chemical cues from surrounding oysters, and biofilms from the substrate (Kennedy, 1996). Settlement, metamorphosis, and attachment typically take place two to three weeks post-hatching; however, these processes can be postponed up to two months in poor environmental circumstances (Stallworthy, 1979). Once attached, eastern oysters can reach a maximum size of 203.2 millimeters, but typically reach 76.2 to 127 millimeters (Wheaton, 2007; NOAA Fisheries, 2022b). Additionally, they can reach a maximum lifespan of up to 20 years (NOAA Fisheries, 2022b).

### **1.3.3 Historical Populations & Sources of Population Decline**

Locally, eastern oysters are an important resource within the Delaware Bay and mid-Atlantic region. Historically, European settlers discovered copious amounts of eastern oysters in Delaware Bay and proceeded to overharvest oysters, particularly over the latter part of the 19<sup>th</sup> century (Canzonier, 2004). The buildup of commercial fisheries and processing centers caused the oyster industry to accelerate as the regions surrounding Delaware Bay grew (Canzonier, 2004). Currently, oyster populations are weaker than they have historically been in the Delaware Bay due to historical overharvest and oyster diseases such as MSX and Dermo, but populations are continuing to grow (Canzonier, 2004; Wong, 2024). Historically, eastern oyster total landings have decreased significantly across the east coast of the United States since the 1890s (Clyde, 2007). In the 1890s, landings for eastern oysters totaled almost 27 million bushels; however, as time progressed, landings decreased to around 11.5

million bushels in 1940 and only 350 thousand bushels in 2004 (Clyde, 2007). In the Gulf of Mexico, there has been an estimated 50 to 80 percent decrease in eastern oyster populations compared to their historic levels (Beck et al., 2011).

Similar estimations of decrease have been gathered for the Chesapeake and Delaware Bay (Rothschild et al., 1994; Powell, 2008) caused by a variety of factors, including over-harvesting, water quality, habitat degradation, and parasitic invasion (Sarinsky et al., 2005; Carlsson et al., 2006; Beseres Pollack et al., 2012). However, historical overharvest has remained as the principal suggested cause of eastern oyster population decline (Clyde, 2007). Within the Chesapeake Bay, eastern oyster landings totaled 615,000 tons in 1884 and decreased to 12,000 tons in 1992 (Rothschild, 1994). Additionally, from the 1890s to around the 1930s, the harvest of market-sized oysters decreased to less than 2 million bushels per year (Schulte, 2017). Delaware Bay populations have seen a similar decline, with the highest landings occurring in the 1970s and the lowest landings taking place since the early 2000s (Powell, 2008). New York is also experiencing similar declines in harvest following the early 1900s (Sarinsky et al., 2005). Eastern oyster water quality and habitat degradation are primarily caused by pollution, coastal development, and storm impacts (Carlsson et al., 2006; Beseres Pollack et al., 2012).

Like other areas throughout the species range, Eastern oysters have been subject to parasitic invasions and disease such as MSX and Dermo (Canzonier, 2004). MSX was first documented in 1957, where it caused mass oyster mortality in the Delaware Bay (Ewart & Ford, 1993). By the 1960s, the MSX parasite was present in coastal bays ranging from North Carolina to Connecticut (Ewart & Ford, 1993). In 1980, the MSX parasite covered an overall range from Maine to Florida (Ewart &

Ford, 1993). Dermo disease was first discovered in 1949 within the Chesapeake Bay, where it was associated with high oyster mortality (Ewart & Ford, 1993). Until 1990, Dermo disease was primarily found in warmer waters from the Chesapeake Bay to the Gulf of Mexico (Ewart & Ford, 1993). Following 1990, a Dermo disease spike occurred in the Delaware Bay, which allowed for the parasite to spread to Connecticut, New York, Massachusetts, and Maine (Ewart & Ford, 1993). Dermo and MSX are the primary diseases that affect eastern oyster populations; however, new potential pathogenic threats are occurring, like Ostreid herpesvirus (Friedman et al., 2020).

Multiple management strategies have been implemented to overcome the declining trend, including the implementation of aquaculture-based practices and restoration projects. Restoration efforts are being put in place, as well as protection from federal and state regulations (Delaware Division of Fish & Wildlife, 2021; NOAA Fisheries, 2022b). The largest restoration effort currently taking place on the east coast is in the Chesapeake Bay through the Chesapeake Bay Program (NOAA Fisheries, 2022b). The goal of this effort is to restore the native oyster reefs in 10 Chesapeake Bay tributaries by 2025 (NOAA Fisheries, 2022b). These restoration areas are protected from harvest in order to augment wild oyster abundance (Chesapeake Bay Program, n.d.). Implementation of federal and state regulations plays a key role in restoring eastern oyster populations because they allow for oysters to be grown and harvested sustainably (NOAA Fisheries, 2022b). Shellfish aquaculture requires permitting that is controlled by the local, state, and federal government (NOAA Fisheries, 2022b). Some of the federal agencies that participate include the US Army Corps of Engineers, NOAA, U.S. Fish & Wildlife Service, the Environmental Protection Agency, and U.S. Department of Agriculture (NOAA

Fisheries, 2022a; NOAA Fisheries, 2022b). Additionally, these shellfish farms must follow federal regulations from the Magnuson-Stevens Fishery Conservation & Management Act, the Endangered Species Act, the National Environmental Policy Act, and the Clean Water Act (NOAA Fisheries, 2022b). Currently, the Delaware's Inland Bays and Delaware Bay have distinct shellfish programs, with Inland Bays having an existing leasing program and Delaware Bay operating on an annually renewed basis for harvesting and utilizing designated regions (NOAA Fisheries, 2021). The Delaware permitting process requires direct approval from the Department of Natural Resources and Environmental Control (DNREC) Wetlands and Subaqueous Lands Section, as well as the US Army Corps of Engineers Philadelphia district (NOAA Fisheries, 2021). To further protect oyster populations, state-by-state harvesting regulations are also put into place. Specifically, some states implement minimum harvesting sizes, oyster harvesting seasons, and bushel collection limits (Maryland Department of Natural Resources, n.d; Delaware Division of Fish & Wildlife, 2021; Worrell, 2022). For example, recreational oyster harvesting in Maryland can occur between October 1<sup>st</sup> and March 31<sup>st</sup>, with a quota of 100 harvestable-sized oysters per day (Maryland Department of Natural Resources, n.d.). However, recreational harvest in Delaware state waters is prohibited (Delaware Division of Fish & Wildlife, 2021).

#### **1.3.4 Population Dynamics**

Eastern oyster population dynamics are highly dependent on recruitment and physical forces (NOAA Fisheries EOBRT, 2007). However, oyster dispersal and recruitment methods are not well understood (Epifanio, 1988; North et al., 2006;

North et al., 2008). Specifically, there continues to be substantial spatial and temporal irregularity in local and seasonal recruitment (Epifanio, 1988). This variability has been associated with both biotic parameters, such as brood stock biomass, and abiotic parameters like tidal amplitude (Manley et al., 2008). Environmental factors like estuary characteristics, such as flow, also play a role in oyster recruitment. Estuaries that exhibit elevated tidal flushing usually have low, but consistent recruitment levels (Kennedy, 1996). Estuaries with decreased tidal flushing are associated with low circulation, which permits prolonged residence time and increased recruitment, but ultimately more irregular recruitment (Kennedy, 1996). Recruitment can also be impacted by larval retention, which can be affected by a combination of passive and active transport (Dekshenieks et al., 1996). Recruitment patterns have also been identified from a microhabitat scope at meter spatial scales; however, the causes of recruitment variability are not yet definite (Kennedy, 1996). Oyster mortality rates are more sensitive to changes in larval recruitment and survival compared to mature oyster fecundity and survivorship, with the exception of increased rates of disease (Brousseau, 2005). Once larvae have recruited and settled, oyster populations and reefs develop. Oyster reefs can be subtidal, continuously covered by water, or intertidal, revealed during low tide (Volety, 2013). Oyster reefs are capable of being exposed during low tide due to their increased tolerance to desiccation, or aerial exposure, for multiple hours (Volety, 2013). There is often variety in individual eastern oyster reef demographics. Reasons for this variety include fishing pressure, location, and predation (Peters et al., 2017; Geraldi et al., 2022). Heavy colonized reefs within the Chesapeake Bay have a density ranging from 28 to 168 oysters per m<sup>2</sup> of oyster reef surface area; the surface densities translate to approximately 1085

oysters per m<sup>2</sup> of river bottom (Lipcius & Burke, 2006). Average density is similar along the species range; however, regional variation is exhibited within sites (Peters et al., 2017). For instance, eastern oyster reefs sampled within Pamlico Sound, North Carolina, displayed significant differences in population densities between sampling sites (Peters et al., 2017). Specifically, the mean total eastern oyster density was approximately two times greater at sampling locations in the western Pamlico Sound compared to eastern locations (Peters et al., 2017). Additionally, the density of preharvest-sized eastern oysters (< 75mm) was four times greater in the western Pamlico Sound compared to eastern Pamlico Sound, possibly due to elevated mortality from predation in the eastern Pamlico Sound (Peters et al., 2017). The Peters et al. (2017) study also examined eastern oyster density within harvested reefs versus protected reserves. Protected reserves exhibited a mean total oyster density that was approximately 8 to 72 times greater than harvested reefs (Peters et al., 2017). Predation can also have an impact on eastern oyster density. Another study performed in Pamlico Sound, North Carolina, analyzed the effects of predator access on eastern oyster abundance (Geraldi et al., 2022). Specifically, this study determined eastern oyster abundance when different-sized predators were present versus excluded (Geraldi et al., 2022). Within this study, there was a statistically significant increase in oyster abundance when smaller predators, like oyster drills and mud crabs, were removed (Geraldi et al., 2022). Geraldi et al. (2022) suggested that mud crabs are the predators that have the greatest impact on eastern oyster abundance in intertidal regions, but in subtidal regions, these impacts are temporally and spatially controlled by large predators like sheephead (*Archosargus probatocephalus*).

### **1.3.5 Patch Demographics**

Overall, eastern oyster density demographics vary and are influenced by a multitude of factors. Within these populations, the size demographics also vary because of similar factors, specifically reefs that are harvested versus protected (Peters et al., 2017). Patch demographics, or patch dynamics, is a theoretical approach that states that an environment's structure and dynamics can be approximated through the analysis of smaller spatial sections or "patches" (Paine & Levin, 1981; Wu, 2019). Harvested reefs within the Pamlico Sound displayed a size structure where the majority of individuals were under the legal harvest size of 76 millimeters (Peters et al., 2017). Interestingly, the protected reefs consisted of larger individuals that were greater than the legal harvest threshold (Peters et al., 2017). Additionally, within this study, it was noted that relative size class abundance varied between protected and harvested oyster reefs (Peters et al., 2017). Specifically, 62.8% of the total number of individuals within protected reefs consisted of recruits compared to the 23.5% for harvested reefs (Peters et al., 2017). Ultimately, harvested reefs appear to contain a majority of oysters that are below the legal size, but they only make up about half of the total population density in protected reefs (Peters et al., 2017).

Currently, patch demographics of eastern oysters are not well studied and represent a large data gap. Studies successfully estimated intertidal oyster reef densities; however, present methods of obtaining oyster reef habitat area measurements are expensive and time-consuming (Windle et al., 2019). Recent use of newer technologies, such as unoccupied aircraft systems (UAS), has overcome both the efficiency and cost hurdles while providing a faster and more reliable technique for assessing intertidal oyster habitats (Windle et al., 2019). UAS technology utilizes remote sensing and aerial surveys to generate measurements of reef area and

morphology that can be compared to ground measurements (Windle et al., 2019). UAS can generate similar results compared to ground-based measurements (Windle et al., 2019). Additionally, UAS can be paired with terrestrial laser scanners to measure three-dimensional properties of intertidal ecosystems, which are processed using ‘Structure from Motion’ photogrammetry (Ridge et al., 2023). By comparing results from unoccupied aircraft systems and terrestrial laser scanners, reliable structural metrics of oyster reefs can be produced (Ridge et al., 2023). This modernized technology can be used as a non-invasive way to monitor oyster habitats (Windle et al., 2019).

The coupled UAS and laser scanner approach was recently used to estimate intertidal oyster reef density in the Rachel Carson National Estuarine Research Reserve in Beaufort, NC (Windle et al., 2022). Windle et al. (2022) found that the total oyster density across all sampled reefs varied from 768 to 6975 m<sup>-2</sup>, with an average of 1383 m<sup>-2</sup> (Windle et al., 2022). Density of recruit, market, and submarket oysters were also collected (Windle et al., 2022). Recruit density ranged from 33 to 3150 m<sup>-2</sup>, while market density ranged from 75 to 900 m<sup>-2</sup>, and submarket density ranged from 481 to 3475 m<sup>-2</sup> (Windle et al., 2022). Size demographics were also collected across all reefs, with average shell height being 46.5 mm and average left valve length ranging from 32.4 to 63.1 mm (Windle et al., 2022).

### **1.3.6 Optimal Covariate Ranges**

The eastern oyster is known to tolerate and adapt to an array of environmental conditions, which becomes increasingly important as climate change effects occur (NOAA Fisheries EOBRT, 2007). Environmental conditions like food availability,

temperature, and salinity have a large impact on oyster growth, but vary seasonally depending on latitude (NOAA Fisheries EOBRT, 2007). In order for eastern oyster populations to efficiently thrive and grow, their optimal environmental conditions must be met. These optimal conditions vary between larval and adult stages (NOAA Fisheries EOBRT, 2007). Eastern oyster larvae can grow at a minimum temperature of 17.5 °C but have an optimum temperature range of approximately 20 to 32.5 °C (Calabrese & Davis, 1970; Hofstetter, 1977). Adult eastern oysters have a higher temperature tolerance and have been reported to survive in temperatures ranging from -2 to 36 °C (Stanley & Sellers, 1986). However, adult eastern oysters have an optimum temperature range between 20 and 30 °C (Stanley & Sellers, 1986). Adults can survive in water temperatures as high as 49 °C, but only for short time periods, approximately 2 to 3 hours, due to high temperatures altering ciliary pumping rates and subsequent feeding rates (Stanley & Sellers, 1986; Shumway, 1996). The broad temperature tolerance of the eastern oyster is associated with heat shock proteins that help protect oysters from thermal stress (Encomio & Chu, 2005). Eastern oyster larvae can tolerate salinities ranging from 10 to 27.5 psu, but their optimum salinity occurs around 17.5 psu (Calabrese & Davis, 1970). Salinity tolerances for adult eastern oysters are broader and range from approximately 5 to 40 psu, with their optimum salinity ranging from 14 to 28 psu (Shumway, 1996; Calabrese & Davis, 1970). In order for efficient oyster growth to occur, water salinity must be a minimum of 10 psu; little growth has been recorded at salinities under 5 psu without a growth penalty (Shumway, 1996). Both eastern oyster larvae and adults can tolerate a dissolved oxygen range of 20-100% saturation, or levels above 1.51 mg/L (NOAA Fisheries EOBRT, 2007; Bradley, 2018). Vulnerability to low oxygen conditions

appears to decrease with increasing body size in settled oysters (Baker & Mann, 1994). However, the opposite relationship occurs for settling larvae, with vulnerability to low oxygen conditions increasing with body size (Baker & Mann, 1994). Additionally, eastern oyster larvae and adults tolerate pHs ranging from 6.75 to 8.75 but have a preferred pH of approximately 7.4 (Boulais et al., 2017; NOAA Fisheries EOBRT, 2007). Genetically based selections of eastern oyster families are created to increase tolerance to varying water temperatures and salinities, as well as disease (Standish et al., 1993; Bernatchez et al., 2018). These genetic improvements are heritable and can be utilized by breeding programs to develop regional resilience in aquaculture and aquaculture-based restoration projects (Yang et al., 2021).

### **1.3.7 Growth Rates**

The growth rate of the eastern oyster is highly reliant on food availability and temperature (Kennedy, 1996). During the initial six months of life, eastern oysters exhibit accelerated growth at approximately 10 mm per month (Quast et al., 1988). Following the first six months, the growth rate is reduced, and individuals grow to roughly 150 mm after five to six years (Quast et al., 1988; Berrigan et al., 1991). Growth to harvest size, or 76-90 mm, is variable depending on location. For instance, harvest size is typically reached in the Gulf of Mexico 18-24 months after settlement, but oysters in northern locations like Long Island Sound do not reach harvestable sizes between 76 and 90 mm until 4 to 5 years (Berrigan et al., 1991; Shumway, 1996). Inconsistent oyster shell growth is common, with the left valve growing faster than the right valve (Carriker, 1996). Though growth rate decreases with age, oysters do continue to grow throughout their life (Carriker, 1996). In the northeast, eastern

oysters can reach a maximum shell length of 206 to 355 mm (Galtsoff, 1964; Carriker, 1996). In southern parts of their range, like the Gulf of Mexico, eastern oysters can obtain shell lengths of up to 300 mm (NOAA Fisheries EOBRT, 2007). Oysters that reach the higher shell length threshold are often found in areas where commercial fishing is banned, and the bottom is rarely disturbed (Carriker, 1996).

Water flow is another significant factor that influences oyster growth rate (Newell & Langdon, 1996), as water flow affects the potential concentration of plankton food particles. Excess water flow ( $>10 \text{ cm s}^{-1}$ ) can cause food particles to move out of the water column before oysters can ingest them (Newell & Langdon, 1996). If water flow is too slow ( $< 1 \text{ cm s}^{-1}$ ), there will not be enough food particles to reinforce growth within the entire reef (Newell & Langdon, 1996). The effect of water flow on oyster growth is ultimately inconsistent and requires further study, but higher velocity hydrodynamics are beneficial for oyster growth because higher velocity currents will increase food delivery, enhance water quality, and stimulate biodeposit distribution (Campbell & Hall, 2018). Seasonal variation in oyster growth can be location-dependent. Specifically, oyster growth in northern regions slows or stops during the winter and reaches a peak in the fall and summer (Loosanoff & Nomejko, 1949; NOAA Fisheries EOBRT, 2007). However, in regions like the Gulf of Mexico, oysters are able to grow throughout the year (Stanley & Sellers, 1986). Ultimately, optimal growth rates are dependent on the interactions between food availability and environmental conditions (Shumway, 1996).

### 1.3.8 Recruitment Patterns

Eastern oyster recruitment patterns can vary in wild versus restored populations, as well as due to other factors. By identifying oyster recruitment patterns, it is possible to determine adequate harvest techniques, seed collection, and management plans for oyster restoration efforts and the aquaculture industry (Manley et al., 2008). However, the relationship between recruitment patterns and distribution potential on a large spatial scale is not well understood (Atwood & Grizzle, 2020). An oyster recruitment pattern study was performed in Sapelo Sound, Georgia, to identify natural spatial and temporal differences in recruitment along the Georgia coastline (Manley et al., 2008). Manley et al. (2008) found that spat recruitment was highest in the mouth of the Sapelo River with 98,132 spat per m<sup>2</sup> per month, while the lowest recruitment occurred in the headwaters of Ridge River with 482 spat per m<sup>2</sup> per month (Manley et al., 2008). Low recruitment levels within the headwaters of Ridge River were likely caused by high tidal amplitudes flushing the oyster larvae away from that region, as well as suboptimal salinity, temperature, turbidity, and available broodstock (Manley et al., 2008). An additional study was performed to monitor oyster recruitment in Wassaw Sound, Georgia, to understand appropriate natural spat collection for recreation and mariculture (O'Beirn et al., 1995). Within Wassaw Sound, three sites were chosen based on varying hydrographic characteristics (O'Beirn et al., 1995). The site with the least wave exposure has the highest recruitment, which was approximately 6,260 spat per m<sup>2</sup> per month; however, it was noted that this site had the highest temperatures as well as the greatest daily temperature fluctuations (O'Beirn et al., 1995). The site with the highest wave exposure had the least recruitment (686 spat per m<sup>2</sup>/month) and had the most consistent temperature (O'Beirn et al., 1995). On a monthly scale, the greatest observed spatfall occurred at mean low

water marks, while seasonal samples were greatest within the intertidal zone (O'Beirn et al., 1995).

Temperature and tidal zonation appear to have an influence on eastern oyster recruitment, as this concept was further examined in a study performed in the York River, Virginia (Roegner & Mann, 1995). Oyster recruits were not present in the mid-intertidal zone and above when the temperature was above 30 °C (Roegner & Mann, 1995). However, during autumnal colder periods, recruits were present in intertidal areas only when natural oyster populations were present (Roegner & Mann, 1995). Eastern oyster recruitment patterns are also impacted by salinity and depth. A study performed in the Pamlico and Core sounds, North Carolina, aimed to investigate the effects of depth, salinity, and location on eastern oyster recruitment over a two-year period (Ortega & Sutherland, 1992). Recruitment density was measured at 6 high-salinity and 6 low-salinity sites (Ortega & Sutherland, 1992). Sites were separated into two depths to measure density: a deeper depth (~3 meters) and a shallower depth (~1 meter) (Ortega & Sutherland, 1992). Oyster recruitment was generally greater in high-salinity areas at deeper depths, compared to the low-salinity, shallower depth sites (Ortega & Sutherland, 1992). Within the eastern oyster's northern range, a study was performed on natural oyster reefs in New Hampshire (Atwood & Grizzle, 2020). Spat collectors were placed directly on and 1 km from natural oyster reefs within New Hampshire to better understand the relationship between recruitment patterns and distribution potential (Atwood & Grizzle, 2020). Results of the Atwood and Grizzle (2020) study reveal that spat densities were 10-fold higher directly on reefs and in areas within 400 m of the reefs compared to densities that were more distant from the reefs, suggesting that oyster restoration projects may need to consider proximity to

spawning adults to maximize the probability of natural oyster recruitment (Atwood & Grizzle, 2020).

### **1.3.9 Mortality**

Eastern oyster mortality is highly influenced by environmental factors such as temperature, salinity, predation, and oyster diseases. One major factor concerning oyster mortality is the potential impacts of climate change, specifically global increases in temperature and freshwater intrusion among oyster populations (Gledhill et al., 2020). While some species have been shown to be resilient to major climate change effects such as pH, salinity, and temperature (Thiyagarajan & Ko, 2012), many studies have determined that temperature and salinity have the greatest influence on the eastern oyster life cycle and survival (Galtsoff, 1964; Shumway, 1996; Lowe et al., 2017; Sehlinger, 2018). Therefore, understanding local salinity and temperature effects on oyster mortality is important for management and restoration (Sehlinger, 2018). The results of Sehlinger's (2018) study suggest that when temperature and salinity are synchronized, mortality rates and seasonal growth rates vary between Breton Sound and Barataria estuaries. Additionally, with increasing salinity in both estuaries, mortality rates decreased while growth rates increased (Sehlinger, 2018). The findings of this study propose that estuary-wide adaptations to regional environmental conditions are possible (Sehlinger, 2018). However, the effects of combined low salinity and high temperature stress on Olympia oysters (*Ostrea lurida*) had a negative synergistic effect on survival when compared to eastern oyster (Bible et al., 2017).

The relationship between oyster mortality and environmental parameters like temperature and salinity can be size class dependent. A study performed on Louisiana's public oyster reefs applied this idea to create a model for temperature and salinity-driven mortality by using long-term monitoring data (Lowe et al., 2017). Tolerance to varying salinity and temperature conditions appeared to be size class dependent, with seed and spat-sized oysters having a broader tolerance compared to oysters greater than 75 mm (Lowe et al., 2017). However, based on the results of the model, the oysters sampled within this study demonstrated enhanced growth rates and decreased mortality in higher temperatures and lower salinities compared to previous models (Lowe et al., 2017). These findings suggest that growth rates and mortality reflect fluctuations in local temperatures and salinity, which result in possible localized, stage-specific adaptations (Lowe et al., 2017). A similar size class study was performed to better understand eastern oyster mortality when exposed to extended periods of low salinity and high temperature by Southworth et al. (2017). Specifically, oysters < 35 and > 35 mm were exposed to low salinities (1, 2, 3, and 4 psu) and water temperatures similar to Virginia Chesapeake Bay subestuaries (25-30 °C) in the summer for up to 30 days to better understand mortality (Southworth et al., 2017). The results of Southworth et al. (2017) suggest that cumulative oyster mortality occurs at critical values of salinities less than 2 psu and temperatures greater than 28 °C when exposed for more than one week. This data suggests that local oyster populations can develop different salinity tolerances (Southworth et al., 2017). Specifically, these low salinity tolerances appear to be a highly heritable trait that could possibly be used for selective breeding programs (McCarty et al., 2020).

### 1.3.10 Predation & Disease

Eastern oyster mortality is not only dependent on water quality but is also impacted by predation and oyster diseases. When eastern oysters are in planktonic life stages, they are subject to predation by various filter-feeding organisms, such as rotifers and ctenophores like sea walnuts and comb jellies (Galtsoff, 1964). Once spat settles to the substrate, juvenile oysters become immersed in the benthic food chain, where they become vulnerable to crab species that feed on oyster tissue (Galtsoff, 1964). Oysters are able to better resist predation as they grow and develop thicker shells (Galtsoff, 1964). In coastal locations, developed oyster populations are preyed upon by starfish, flatworm turbellarians, and carnivorous gastropods, like whelk and drills (Galtsoff, 1964). Fish species like black drum and cownose rays have been seen to cause notable damage to seeded eastern oyster beds (Galtsoff, 1964).

Eastern oyster populations are vulnerable to various parasitic diseases, with the two largest known contributors to mortality being Dermo and MSX. Dermo is a parasitic disease that is caused by the protozoan *Perkinsus marinus* (Mackin et al., 1950). Oysters are infected during the first year of their life, and the parasite continues to multiply (NOAA Fisheries EOBRT, 2007). Dermo infections are associated with 50% mortality in infected oysters during their second summer season and 80-90% mortality by the third season, with little to no survival by the fourth season (Hewatt & Andrews, 1954; NOAA Fisheries EOBRT, 2007). The parasite targets oyster immune cells and dampens the immune system response by decreasing the efficiency of oyster phagocytes, negatively impacting the ability to fight off opportunistic organisms (NOAA Fisheries EOBRT, 2007). Dermo has a reported range from southern Maine to the Yucatan Peninsula (Burreson et al., 1994). Increased Dermo disease levels are associated with high temperatures and high

salinities, especially during drought years (Burreson et al., 1994). This disease is transferred through the movement of infected oysters, and once an individual is infected, the disease will spread across the entire population (NOAA Fisheries EOBRT, 2007). Mass mortality events typically occur in the summer due to optimal temperature and salinity conditions for the parasite (NOAA Fisheries EOBRT, 2007).

The second most influential disease on oyster mortality is MSX. MSX is a pathogenic disease caused by the protozoan *Haplosporidium nelsoni* (Haskin et al. 1966). MSX was first reported in Delaware Bay and has since expanded along the Atlantic coast (Haskin et al. 1966). The expansion of MSX is linked to the movement of infected oyster seed between populations (Haskin et al. 1966). Intensity of MSX mortality appears to fluctuate but is commonly related to salinity increases during drought periods (Barber et al., 1997; NOAA Fisheries EOBRT, 2007). Early MSX infections typically start in mid to late summer, while mortalities continue until parasite and oyster metabolisms slow in winter temperatures (Barber et al., 1997; NOAA Fisheries EOBRT, 2007). Unlike Dermo, MSX is not directly transmitted from one infected oyster to another (Barber et al., 1988; NOAA Fisheries EOBRT, 2007). In order to sustain MSX infections within an oyster population, salinity must be above 15 psu, but appears to thrive in salinities above 18-20 psu (Barber et al., 1997; NOAA Fisheries EOBRT, 2007). Heavy MSX infections result in emaciated tissue followed by rapid death, typically occurring six weeks after infection (NOAA Fisheries EOBRT, 2007). Sublethal MSX infections result in a weakened metabolism and reduced fecundity, generating indirect population-level effects (Barber et al., 1988; NOAA Fisheries EOBRT, 2007). Both Dermo and MSX infections have caused historic oyster fishery crashes. The most notable MSX infection occurred in

the lower Delaware Bay in 1957, shortly followed by an MSX infection in the lower Chesapeake Bay in 1959 (Ewart & Ford, 1993). Dermo infections first caused mass mortality events within the Gulf of Mexico in the 1940s, where it then proliferated up the coast to the Chesapeake and Delaware Bay (Ewart & Ford, 1993). These historic mass mortality events for both diseases have influenced the selective artificial breeding of disease-resistant strains to help combat future outbreaks (Ewart & Ford, 1993; Standish et al., 1993).

## **1.4 Ecosystem Services**

### **1.4.1 Water Filtration**

Eastern oysters are considered a keystone species in estuaries along the Atlantic and Gulf coasts due to their enhancement of the functionality and stability of the aquatic community. Sustainable oyster reefs are capable of increasing species diversity, contributing to structural integrity, which affects water flow patterns and circulation, and performing services that recycle nutrients and help to enhance water quality (NOAA Fisheries EOBRT, 2007). Adult eastern oysters have been reported to have a maximum water clearance rate of  $10 \text{ L h}^{-1} \text{ g}^{-1}$  dry tissue weight under laboratory conditions (Newell & Langdon, 1996). However, results from field estimates of oyster water clearance rates suggest that lab estimates may be unreliable for field applications (Kreeger et al., 2018; Barr et al., 2023). These high clearance rates have caused eastern oysters to become assessed as a possible tool to decrease contaminant loading in estuary ecosystems (Breitburg et al. 2000). The filtration capacity of the eastern oyster populations, however, has decreased historically over time (zu Ermgassen et al., 2012). A model was proposed to estimate the volume of

water filtered by oyster populations in 13 U.S. estuaries to understand their contribution to past and present water quality (zu Ermgassen et al., 2012). The results of the model suggest that the population filtration capacity of oysters has universally declined approximately 85% among 12 of the 13 U.S. estuaries, including the Delaware Bay and Raritan Bay (zu Ermgassen et al., 2012). These estimates of filtration capacity represent a substantial decline when compared to the estimated historical levels of full estuary filtration (zu Ermgassen et al., 2012). The reduction in filtration capacity is associated with changes in the ecosystem function of estuaries (Dame et al., 2002).

#### **1.4.2 Nutrient Assimilation, Burial, and Denitrification Enhancement**

Eastern oyster reefs have been important in the assimilation, burial, and regeneration of carbon, nitrogen, and phosphorus (Hoellein et al., 2014; Ray et al., 2015). Oyster stocks graze on phytoplankton; some portion of the nitrogen and phosphorus from the phytoplankton is assimilated into tissue and shell, and some nutrients are regenerated into the water column through excretion and microbial decomposition of biodeposits (Newell et al., 2005). Investigation of oyster reefs as areas of carbon sequestration has become increasingly popular as atmospheric carbon dioxide levels rise (Filgueira et al., 2015; Morris & Humphreys, 2019). Oyster reefs accumulate organic matter through their biodeposits and vertical structure (Veenstra et al., 2021). Oyster biodeposits contain increased levels of carbon, nitrogen, and phosphorus, while their vertical structure enhances surface roughness, which allows for accumulation of fine sediment and organic matter burial (Chambers et al., 2017; Chowdhury et al., 2019). Similarly, oyster reefs are involved in nitrogen regulation via enhancement of sediment denitrification and nitrogen burial (Beseres Pollack et

al., 2013; Kellogg et al., 2013). A study performed in the Mission-Aransas Estuary, Texas, estimated  $502.5 \text{ kg N km}^{-2}$  was removed through denitrification of biodeposits and  $251.3 \text{ kg N km}^{-2}$  in biodeposit burial (Beseres Pollack et al., 2013). Considering nutrient reduction best management practices in the mid-Atlantic, the Chesapeake Bay Program now acknowledges nitrogen and phosphorus assimilation, along with enhanced sediment denitrification, associated with oyster reefs (Cornwell et al., 2023). While oyster reefs are being considered as areas for macronutrient accumulation, there are disagreements with this theory. Some studies propose that oyster reefs do not enhance carbon and nitrogen burial rates. Specifically, a study performed in Louisiana aimed to better understand the role of oyster reefs in nutrient mitigation (Westbrook et al., 2018). Nutrient mitigation was found to be minimal, with estimated burial rates of  $1.4\text{--}2.6 \text{ g N m}^{-2} \text{ year}^{-1}$  and  $26.9\text{--}43.8 \text{ g C m}^{-2} \text{ year}^{-1}$  (Westbrook et al., 2018). These low burial rates are most likely due to Louisiana sediments being very rich as well as redundant supplies of carbon and nitrogen from surrounding marshes (Westbrook et al., 2018). Therefore, the role of oyster reefs in nutrient burial is likely site-specific and difficult to accurately measure, highlighting a need for further exploration.

### **1.4.3 Habitat Provisioning**

Studies examining how oyster reefs provide habitat for a variety of coastal species have become an increasing area of interest in the scientific community. The impacts of oyster reefs on the enhancement of seagrass beds are still being studied, but current results show positive correlations. Specifically, the creation of oyster reefs was associated with a temporal increase in seagrass cover across the experimental reef areas, as well as into control plot regions (Sharma et al., 2016). Similar studies are being performed to better understand the interaction of oyster reefs and coastal bird

communities. Coastal bird communities can utilize oyster reefs for foraging due to the high density of benthic invertebrates found in reefs (Copertino et al., 2022). Current research has examined the utilization of live, restored, and dead oyster reefs by birds to understand how oyster reef restoration influences bird communities. Bird abundances appear to be lower in immediately restored reefs due to a lack of prey availability, but given time, they developed similar abundances to live reefs (Copertino, 2021). Ultimately, bird communities are utilizing live, restored, and dead oyster reefs in a variety of ways (Copertino, 2021). Impacts of oyster aquaculture on horseshoe crab communities are a point of conflict among conservationists. Some oyster farms are located in Atlantic horseshoe crab spawning areas, which were previously believed to negatively impact access to spawning grounds. However, a study performed during horseshoe crab spawning season indicated that horseshoe crabs were able to traverse rack and bag areas to reach spawning grounds with little to no behavioral interruptions caused by farming gear (Munroe et al., 2020). The impacts of oyster aquaculture on horseshoe crab communities are still being debated and require further research to draw more definitive conclusions.

However, the potential benefits of oyster aquaculture on habitat provisioning of juvenile and adult finfish species have become increasingly popular (Coen et al., 1999). Fishes that are found near oyster reefs utilize the grounds as either primary habitat, or represent facultative species, or transient species (Coen et al., 1999; Erbland & Ozbay, 2008; Marenghi et al., 2009; Shinn et al., 2021). Oyster reef surveys in Maryland, Virginia, North Carolina, South Carolina, and Texas identified 79 different fish species that were associated with oyster reef regions (Coen et al., 1999). In addition to oyster reefs, aquaculture-based practices have been found to

positively affect species richness. A study was conducted to examine fish communities between rack-and-bag and longline basket-based production methods (Martínez-Baena et al., 2022). Martínez-Baena et al. (2022) found that both rack and bag, and longline based aquaculture farming systems supported an equal number of fish species as surrounding natural habitats, but species richness was generally higher for racks compared to longline systems, suggesting that oyster aquaculture has the ability to support fish communities similar to natural biogenic habitat fish communities (Martínez-Baena et al., 2022). The Martínez-Baena et al. (2022) study also demonstrated that the oyster aquaculture method being used has an influence on habitat provisioning services (Gray et al., 2021).

#### **1.4.4 Shoreline Resilience**

On top of habitat provisioning, oyster reefs have been identified as possible sources of shoreline stabilization. Oyster reef structures have the ability to reduce erosion by collecting sediments and dispersing wave energy (Stricklin et al., 2010). Use of oyster reef structures, such as oyster castles or reef balls (Walters et al., 2022), for shoreline stabilization is becoming increasingly popular to replace current hardened structures, including seawalls and groins. Hardened structures are spatially static over time and often reflect wave energy, which induces benthic scour and trapped debris (Pilkey, 1988). By converting to shellfish-based living shorelines, coastal erosion could be mitigated while simultaneously implementing ecological services like nutrient cycling and habitat provisioning (Smaal, 2019). The effectiveness of oyster reefs for shoreline protection is still relatively uncertain and requires further application to better understand this service (Scyphers et al., 2011; La Peyre et al., 2022). The economic value of oyster reefs is typically only considered

from a commercial lens, and the value of their ecosystem services is often not acknowledged. A framework was created to assess the economic value of oyster reef services, specifically shoreline stabilization and water quality improvement (Grabowski et al., 2012). The economic value of shoreline stabilization and water quality improvement is estimated to be between \$5,500 and \$99,000 per hectare per year (Grabowski et al., 2012). This reef service value estimate is likely conservative because services such as nutrient burial and increased biodiversity were not considered (Grabowski et al., 2012).

### **1.5 Oyster Aquaculture**

Commercial production of farmed oysters has increased significantly in the United States over recent decades. Oyster aquaculture consists of two traditional methods: bottom and off-bottom culture. Bottom culture is a shellfish farming practice where organisms are directly grown on the sea floor (University of Maryland Extension, 2022). Off-bottom culture consists of a variety of techniques that allow for oysters to be grown throughout the water column. Off-bottom methods that are commonly used consist of floating bags, floating cage systems, adjustable long-line systems, bottom cages, and rack and bag culture (Davis et al., 2012). Off-bottom methods are advantageous as they allow for biofouling mitigation, increased survival, predator protection, improved shell shape, increased product consistency, and increased commercial value per weight (Walton et al., 2013). Within rack and bag culture, oysters are placed into either flat ('envelope') or boxed, rectangular Vexar bags that are attached to rebar racks, which are secured in the substrate (VIMS, n.d.). Rack and bag systems are typically used when growing oysters intertidally, where the bags are exposed during low tide and susceptible to waves during tidal shifts (VIMS,

n.d.). Farming methods vary by personal preference, regional regulatory constraints, and environmental limitations; therefore, research efforts discussing the influence of culture method on oyster performance is still in its infancy (< 40 years old) (Guo et al., 2015).

However, recent studies have been conducted that further analyze this topic (e.g., Mallet et al., 2013). A study performed in oyster farms in New Hampshire to assess the effects of different gear deployment configurations on oyster growth and mortality (Grizzle et al., 2020). The results of this study suggest that there was no significant difference in oyster growth between rack and bag versus bottom trays (Grizzle et al., 2020). However, final growth measurements were 18% higher for box-style bags compared to envelope-style Vexar bags (Grizzle et al., 2020). Grizzle et al. (2022) acknowledged that food supply and other physical factors have a strong effect on oyster growth, citing the importance of understanding this phenomenon when trying to refine gear deployment methods (Grizzle et al., 2020). A similar study was performed in New Brunswick, Canada, which analyzed oyster performance between horizontal rope and Vexar bags floating gear, which indicated that rope-grown oysters significantly outperformed oysters grown in floating bags (Mallet et al., 2013). Within one growing season, rope-grown oysters experienced approximately double the weight gain and 60% higher shell growth compared to floating bags (Mallet et al., 2013). Site-specific effects were suggested to have caused some of the variability in growth observed by Mallet et al. (2013); however, there was no data to support this claim. Another study was performed in York River, Virginia, that compared the growth rates of 4 strains of eastern oyster using two grow-out methods (Leggett, 1999). The grow-out methods consisted of traditional rack and bag culture and bottom trays on PVC

racks (Leggett, 1999). Growth for each strain was measured over 10 months, as well as the suitability of each grow-out method (Leggett, 1999). Between strains, there was little variance in growth rate; however, growth was more rapid for all strains when using the rack and bag method (Leggett, 1999). Based on the results of this study, rack and bag culture is better suited for oyster growth and has more benefits compared to rack and tray methods in the sample location (Leggett, 1999). Specifically, rack and bag methods are better suited for regions with firmer substrate (i.e., for walking at low tide), less susceptible to fouling, and relatively inexpensive compared to other methods (Leggett, 1999). Tidal positioning of aquaculture gear can also have an impact on the survival and growth of eastern oysters. A study performed in House Creek, Georgia, attempted to identify optimal bottom and tidal placement of oyster grow-out methods (Moroney & Walker, 2007). Oyster bags on rebar frames were placed in four different tidal positions, subtidal on-bottom, subtidal off-bottom, intertidal on-bottom, and intertidal off-bottom, at five sites in House Creek (Moroney & Walker, 2007). Oyster growth, survival, and spat fouling data were collected every three months (Moroney & Walker, 2007). Results indicated that on-bottom treatments were associated with decreased growth and survival but exhibited a lower degree of fouling compared to the intertidal off-bottom treatments (Moroney & Walker, 2007). However, intertidal off-bottom treatments experienced higher degrees of fouling during the recruitment period (Moroney & Walker, 2007). Therefore, maximized oyster growth and survival occurred during the non-recruitment period when oyster bags were placed intertidally and off-bottom (Moroney & Walker, 2007).

## 1.6 Conclusion

My review has examined relevant background literature on eastern oyster life history, population size and demographics, ecosystem services, and oyster aquaculture. Eastern oyster populations occur along the coast of eastern North America and have experienced a significant historical population decline. In order to combat this decline, oyster recruitment studies were conducted to assist in population development. However, substantial spatial and temporal irregularity in local and seasonal recruitment variability persists. Specifically, larval recruitment patterns and transport models suggest that environmental factors that impact these patterns are location-dependent. Ultimately, proximity to spawning adults to maximize the probability of natural oyster recruitment is of critical importance. Eastern oysters can tolerate a wide range of environmental characteristics and, therefore, are considered a resilient species. Optimal environmental conditions for oyster growth appear to be site-specific, and genetic improvements have been implemented to increase tolerance to disease and varying water temperatures and salinities. Eastern oyster mortality is influenced by environmental factors such as temperature, salinity, predation, and oyster diseases. To combat mass mortality events, artificial selection and breeding programs at hatcheries in the US have created oyster strains that are disease-resistant, as well as tolerant of varying temperatures and salinities. Eastern oyster reefs can provide an assortment of ecosystem services. Specifically, they are capable of increasing species diversity through habitat provisioning and performing services that recycle nutrients and help to enhance water quality. Not only are eastern oysters ecologically beneficial by providing ecosystem services, but they can also be economically important through commercial aquaculture production. Large knowledge gaps persist and debate concerning oyster population demographics,

ecosystem services, and oyster aquaculture, requiring further research. However, there is a common consensus that eastern oysters are both an ecologically and economically important species to ecosystems along eastern North America.

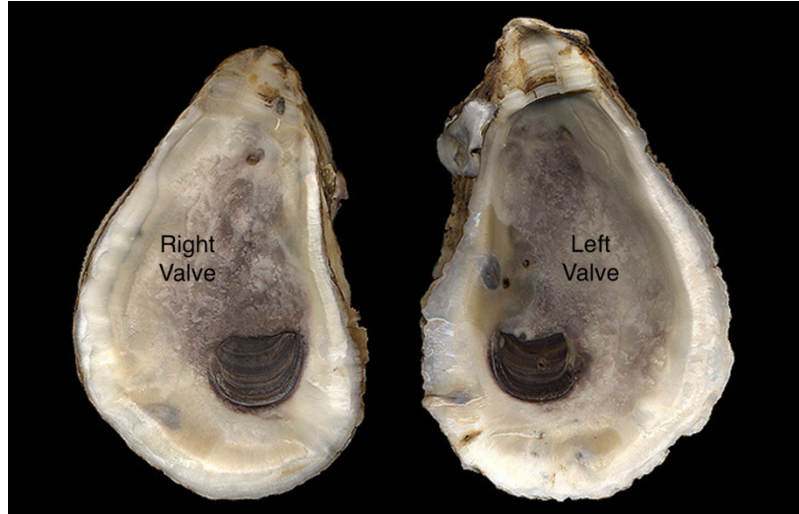


Figure 1.1 Eastern oyster right versus left valve. Photograph from Jacksonville Shells. (n.d.). *Crassostrea virginica* (Gmelin, 1791).

## Chapter 2

### PERFORMANCE OF TWO SELECTIVELY BRED STRAINS OF EASTERN OYSTER, *CRASSOSTREA VIRGINICA*, IN DELAWARE BAY, USA

#### 2.1 Introduction

With the growing impact of climate change and sea level rise, there is an urgent need for resilient and adaptive solutions to protect vulnerable shorelines that support growing coastal communities. Traditional hardened structures, such as riprap and seawalls, while effective in the short term, are not adaptive in dynamic environments (Pilkey, 1988, Nunn et al., 2021). As such, there has been increased interest in living shoreline approaches that are adaptable and provide ecological benefits. Among these approaches, oysters and other reef building shellfish species are gaining attention for their ability to reduce erosion by accreting sediment and dispersing wave energy (Piazza et al., 2005; Stricklin et al., 2010; Walles et al., 2015), while providing essential ecosystem services (Shumway et al., 2003).

Eastern oysters (*Crassostrea virginica*) are a keystone species in marine environments that contribute to habitat provisioning services (Coen et al., 1999; Erbland and Ozbay, 2008; Marenghi et al., 2009; Shinn et al., 2021), nutrient assimilation (Newell et al., 2005; Hoellein et al., 2014; Ray et al., 2015), and water filtration (Newell and Langdon, 1996; Kreeger et al., 2018; Barr et al., 2023). Sustainable oyster reefs also provide structural integrity that modifies water flow patterns and circulation (Morris et al., 2021; Tso et al., 2023; Stanley et al., 2024; Campbell et al., 2025). However, eastern oyster populations have experienced a

drastic depletion as a result of overharvesting (Canzonier, 2004; Sarinsky et al., 2005; Clyde, 2007), habitat degradation (Carlsson et al., 2006; Beseres Pollack et al., 2012), and disease (Canzonier, 2004; Friedman et al., 2020), requiring large-scale restoration efforts to aid in their recovery. Oysters are valuable not only ecologically but also economically. Oyster aquaculture is an important and rapidly expanding industry (Botta et al., 2020), valued at \$285 million in 2018 in the United States (USDA NASS, 2018). Oyster aquaculture provides not just economic benefits (Grabowski et al., 2012; Kumar et al., 2024) but also environmental services akin to natural reefs, including habitat provisioning (Martínez-Baena et al., 2022) and coastal resilience enhancement (Hossain et al., 2013).

Oysters and other shellfish are increasingly being used in restoration projects aimed at rebuilding reefs (Bersosa Hernández et al., 2018) and protecting shorelines (La Peyre et al., 2013). These restoration efforts can employ a range of techniques to capture wild spat by deploying alternate substrates to encourage recruitment where reef habitats have been lost (van den Brink et al., 2020; Rusydi et al., 2023) or through remote setting where juvenile oysters are seeded onto structures and then are released on existing reefs to increase their survival (Sunila et al., 2016). In Chesapeake Bay, where oyster populations have been severely reduced, these methods are being explored to accelerate the repopulation of native oyster reefs (USACE, 2012). Additionally, as of 2023, the cost to date of oyster restoration efforts in Maryland was approximately \$87.36 million, signaling the need to refine restoration efforts to reduce expenses (NOAA Fisheries, 2024). Although individual seed oysters have not been widely used in restoration projects, remote, ‘spat-on-shell’ approaches seem to be effective for large-scale applications (Maryland Oyster Restoration Interagency

Workgroup, 2024). Such gaps in understanding highlight the need for further research to improve the effectiveness of installing pre-seeded structures for restoration purposes across different environments, particularly in areas with low natural recruitment.

The growth and survival of oysters depend on a suite of environmental parameters, including temperature, salinity, and dissolved oxygen, making oyster-based restoration efforts closely linked with local water quality (NOAA Fisheries EOBRT, 2007). Since these environmental parameters vary spatially and temporally, understanding how the range of environmental conditions influence oyster performance is critical for developing effective restoration strategies. Oysters have specific thermal tolerances (Calabrese and Davis, 1970; Hofstetter, 1977; Stanley and Sellers, 1986), and extreme changes in temperature have been shown to disrupt their physiological functioning (Shumway, 1996). Similarly, salinity levels influence osmoregulation and can impact oyster health (Casas et al., 2024), while low dissolved oxygen can create additional physiological stress (Patterson et al., 2014). Understanding these interactions is key to making sure restoration sites are selected and managed to enable persistent oyster populations. Previous studies focused on the impact of genetic diversity and the comparison between different oyster strains as an approach to increasing survival and resilience to environmental stressors, where disease-resistant strains showed better survival than wild and susceptible lines (Rawson and Feindel, 2012; Frank-Lawale et al., 2014; Proestou et al., 2016; McCarty et al., 2021). Growth patterns were found to differ between oyster strains and across tidal positions (Bartol et al., 1999; Bishop and Peterson, 2005). These aspects highlight the importance of targeted oyster strain selection and tidal placement to

optimize restoration success, as well as additional studies on factors driving oyster growth and survival.

DBX and NEH<sup>®</sup> are two selectively bred oyster strains developed by Rutgers University's Haskin Shellfish Research Laboratory. NEH<sup>®</sup>, derived from Long Island Sound stocks, has undergone decades of selection for improved growth and survival in high-salinity environments and exhibits strong resistance to two major oyster pathogens, MSX (*Haplosporidium nelsoni*) and Dermo (*Perkinsus marinus*). DBX, bred primarily from Delaware Bay oyster lines, was developed to perform well in mesohaline and oligohaline environments and also carries resistance to both MSX and Dermo, though it is generally deployed in lower-salinity areas. Both strains are used in aquaculture and restoration due to their enhanced growth rates compared to wild oysters and adaptability to a range of estuarine conditions (Rutgers University, n.d.).

Our study examined how environmental variables (temperature, salinity, and dissolved oxygen), family strain, and tidal position impact oyster growth and survival using rack-and-bag oyster aquaculture gear as a proxy for living shoreline coastal restoration projects. We evaluated the performance of DBX and NEH<sup>®</sup> oyster strains in intertidal and subtidal environments within the Delaware Bay (Lewes) by sampling and modeling oyster growth and mortality as a function of the environment. We hypothesized that oyster performance will differ by strain and tidal position, dependent on environmental water quality parameters (temperature, salinity, and dissolved oxygen) experienced at the study site. Specifically, NEH<sup>®</sup> strain farmed oysters will perform better under high salinity site conditions (>25 psu), while DBX strain farmed oysters will perform better under medium salinity site conditions (12-20 psu). Additionally, oyster performance will be more successful in subtidal conditions

than in intertidal conditions. Evaluating these factors provides recommendations for optimal oyster strain selection and tidal placement to inform the design of shellfish-based living shorelines, contributing to more resilient and adaptive strategies for coastal restoration.

## **2.2 Methods**

### **2.2.1 Study Area**

The field study was conducted at the University of Delaware Hugh R. Sharp Campus boat basin (38.788081°N, 75.162194°W), located in Lewes, Delaware, on the southwest portion of Delaware Bay. Delaware Bay is connected to the Atlantic Ocean to the southeast and the Delaware River to the north. This system is considered a well-mixed estuary with an average depth of 8 m, an average tidal range of ~1.5 m (Aristizábal and Chant, 2013; Aristizábal and Chant, 2015; Hall et al., 2013), and an average residence time of 40 to 90 days depending on discharge, categorizing it as a moderately flushed system (Joeseof et al., 2015). The bay follows a strong salinity gradient, ranging from 0.1 to 31.5 psu (NOAA DBOFS, n.d.) and provides habitat for many aquatic species (Mathews et al. 2022; Oleynik et al. 2024).

### **2.2.2 Experimental Design**

We deployed triploid, disease-resistant, high-salinity tolerant (NEH<sup>®</sup>), and low-salinity tolerant (DBX) oysters produced by the New Jersey Aquaculture Innovation Center at Rutgers University (Cape May, NJ), using rack-and-bag culture systems throughout mid-summer (July 2023) to the fall (October 2023). Treatment groups consisted of six rack-and-bag installations within the boat basin, three placed in the intertidal zone and three in the subtidal zone. Each pair of intertidal and subtidal

racks ran parallel to the shoreline (with spacing adjusted for tidal range) and were at equal depths per respective tidal position. The racks were randomly allocated to their corresponding tidal positions, with 50-meter intervals between each pair of racks (Figure 2.1). Each rack was approximately 8 inches above the sediment. Oysters were graded at the start of the experiment and had an average shell length of  $8.42 \pm 1.88$  mm for NEH<sup>®</sup> and  $7.69 \pm 1.69$  mm for DBX. Although this difference was minor, and size grading was conducted to reduce variation, the initial size discrepancy is acknowledged as a potential source of bias in growth comparisons. Four rectangular Vexar bags containing 50 oysters each were attached to each rack and two bags of ~200 cultch were added as space-holders. The stocking density of these bags was low compared to commercial standards, which is typically around 800 oysters at that stocked size. The four bags were grouped by genetic strain, NEH<sup>®</sup> and DBX, with two bags per strain. The mesh size of the Vexar bag was originally 4 mm, based on the oysters' initial shell length, and then enlarged to 9 mm when the minimum shell length reached about 1.5 times that of the mesh size. To control biofouling, sea squirts (*Molgula manhattensis*) were removed, and bags were flipped weekly. Bags were replaced once at the 4 mm stage to control for extreme biofouling. Oysters within each pair of bags per strain were pooled per rack, and each rack served as replicate for that strain and tidal position. These data were then aggregated across all three racks per tidal position and strain (e.g., all NEH intertidal racks,  $n = 3$ ) to calculate final strain and tidal position level averages and metrics for statistical analysis.

### **2.2.3 Environmental Monitoring**

Continuous monitoring of temperature (°C), salinity (psu), and dissolved oxygen (mg/L) were conducted at subtidal rack locations, utilizing Onset<sup>®</sup> HOBO<sup>®</sup>

loggers (HOBO U24-002-C for temperature and salinity and HOBO U26-001 equipped with a U26-GUARD-2 anti-fouling guard for dissolved oxygen, Onset Computer Corporation, Bourne, MA U.S.A). Water quality loggers sampled at a 30-minute frequency, determined from the guidance provided by the HOBOWare® Pro software. Environmental time series data were aggregated to examine temporal patterns in water quality variables throughout the study period. To assess the stationarity of the data, we tested both daily (24 hours prior to the sampling event) and weekly intervals (the week prior to the sampling event), evaluating the maximum, minimum, and average values for each variable. Stationary variables included daily averages, minimums, and maximums for dissolved oxygen, temperature, and salinity, as well as weekly average temperature and weekly minimum dissolved oxygen. For stationary time series, no differencing was required, while non-stationary time series required first- or second-order differencing to achieve stationarity. Time series that were unable to achieve stationarity were removed from the analysis.

#### **2.2.4 Oyster Performance**

Oyster growth and survival were assessed weekly. For each bag, shell length, width, and depth of 20 individuals were measured at random. Mortality was assessed weekly by counting the number of dead oysters in each bag. A dead oyster was identified by the open separation of its valves, emitting a hollow sound when knocked against a live oyster, or by the absence of resistance when attempting to close its valves together. Dead oysters were removed from each bag weekly to prevent recounting, and no live oysters were added or replaced throughout the experiment. Following the completion of the field experiment, 10 individuals were randomly selected per rack and per strain across replicate bags to measure wet mass and estimate

their condition index (CI; Eqn. 1) using methods from Lawrence and Scott (1982). The ratio of dry tissue weight to dry shell provides an indication of the oyster meat quality and a proxy for tissue growth and performance.

$$\text{Eqn. 1: } CI = \frac{\text{dry tissue weight (g)} * 100}{\text{dry shell weight (g)}}$$

At the end of the experiment, final measurements of shell length and mortality were used to determine weekly average oyster length, instantaneous growth rate (IGR), and survivorship by strain and tidal position. IGR was calculated using Equation 2, where  $L_2$  and  $L_1$  correspond to the final and initial lengths, and  $t_2 - t_1$  is the duration of the experiment expressed in weeks. Since the duration of the experiment was less than one year, this formula was applied.

$$\text{Eqn. 2: } IGR = \frac{\log_e(\text{Length}_2) - \log_e(\text{Length}_1)}{t_2 - t_1}$$

### 2.2.5 Statistical Analysis

Univariate statistical analyses were conducted to understand the effects of oyster strain and tidal position on oyster performance metrics, including growth (average length, instantaneous growth rate, and condition index) and survivorship, and to provide context to aid in covariate selection for the preceding descriptive model. Normality was checked using Shapiro-Wilk tests to determine the use of standard or non-parametric equivalents to derive differences in performance. Condition index followed a normal distribution while growth and mortality did not. For each of the growth metrics and survivorship, Scheirer-Ray-Hare tests were implemented to compare significant differences between oyster strains and tidal positions. For the

statistically significant relationships, a post-hoc Wilcoxon rank sum test was used to define significantly different groups. For condition index data, a two-way ANOVA was used to find significant differences between oyster strains and tidal position, followed by Tukey's HSD test for significant relationships. Significance was determined using an alpha of 0.05 for normality checks and univariate statistical analyses.

We used Generalized Additive Models (GAMs) to analyze the effect of environmental variables on oyster growth and mortality. The goal was to understand how environmental covariates (temperature, salinity, and dissolved oxygen) influenced oyster performance across different strains and tidal positions. The response variables for the models included average oyster length and weekly mortality. Each weekly observation in the GAMs represented an average across both bags per strain, per rack, further aggregated by tidal position, resulting in one observation per strain and tidal position combination per week. Therefore, each GAM used repeated, temporally spaced observations from these four groups (NEH-intertidal, NEH-subtidal, DBX-intertidal, DBX-subtidal), but did not include a hierarchical or random-effects structure due to the data being pooled at the strain and tidal position level. Only stationary environmental time series, previously found to be correlated with the response variables through cross-correlation functions, were included as covariates in the models.

Collinearity tests among covariates were performed using Variance Inflation Factor (VIF) analysis using the "vif" function from the car package in R version 4.2.1 (R Core Team, 2022). We removed variables with a VIF score greater than 5 to reduce multicollinearity. Models were fitted using the "gam" function in the mgcv package in

R version 4.2.1 (Wood, 2017). The best family distribution was chosen based on scoring using Akaike's Information Criterion (AICc) for small sample size (Burnham and Anderson, 2022). After selecting the best family distribution based on global models, we applied the “dredge” function in the MuMIn package of R version 4.2.1 (Bartoń, 2025) for automatic model selection. This function selects the most relevant environmental covariates and identifies the tightest model construction. Predictive ability and k-fold cross-validation were assessed on models within 5 AICc points of the top model using the “predict” function in the car package in R version 4.2.1 (Fox & Weisberg, 2019). This method divides the data into  $k$  folds, with each fold serving as one validation set at a time, while the remaining folds were used for training data. The predictive accuracy for the models was determined by calculating the average root mean square error (RMSE) across all  $k$  folds. The model with the lowest average RMSE value was selected as the final model.

The GAM for oyster growth was fitted using the Gaussian family with the identity link function, using weekly average oyster length as the response variable (Equation 3). The model included smooth terms for average temperature and the previous week's minimum dissolved oxygen, as well as categorical terms for tidal position and strain. The formula for the final growth model was:

$$\begin{aligned} \text{Eqn. 3: Avg. Length} &\sim \text{factor(Tidal Position)} + \text{factor(Strain)} \\ &+ \text{s(Avg. Temperature)} \\ &+ \text{s(Previous Weeks Min. Dissolved Oxygen)} \end{aligned}$$

The GAM for oyster mortality was fitted using the Negative Binomial family with the log link function and weekly mortality as the response variable (Equation 4). The model included smooth terms for minimum salinity, average salinity, and minimum dissolved oxygen, as well as a categorical term for tidal position. The formula for the final mortality model was:

$$\text{Eqn. 4: Weekly Mortality} \sim \text{factor}(\text{Tidal Position}) + \text{s}(\text{Min. Salinity}) \\ + \text{s}(\text{Avg. Salinity}) + \text{s}(\text{Min. Dissolved Oxygen})$$

## 2.3 Results

### 2.3.1 Environmental Monitoring

The water temperature between 07/09/23 and 10/16/23 ranged from 15.80 to 29.12 °C (average 23.30±2.80 °C SD), with the highest temperatures observed in July and August. Temperature was fairly stable through the summer months, with a gradual drop in temperature starting in mid-September. Salinity ranged from 18.34 to 30.94 psu (28.30±1.40 psu) and remained steady throughout the study, aside from the normal daily fluctuations associated with tidal changes. Dissolved oxygen levels ranged from 0.40 to 13.53 mg/L (5±1.90 mg/L), with the lowest concentrations observed in late summer and early fall. Dissolved oxygen values declined steadily through September and early October, tracking seasonal trends expected between summer and fall.

Environmental time series data for temperature, salinity, and dissolved oxygen were checked for stationarity at both daily (24 hours prior to the sampling event) and weekly intervals (week prior to the sampling event). The stationarity tests revealed that all daily intervals (averages, minimums, and maximums) for all variables were

stationary, in addition to the weekly average temperature and weekly minimum dissolved oxygen. Variables that required no differencing consisted of average dissolved oxygen, minimum dissolved oxygen, minimum salinity, and weekly minimum dissolved oxygen. First-order differencing was required for maximum dissolved oxygen, average temperature, maximum temperature, average salinity, and maximum salinity, while second-order differencing was necessary for minimum temperature and weekly average temperature. Variables that were unable to achieve stationarity include weekly average dissolved oxygen, maximum dissolved oxygen, maximum temperature, minimum temperature, average salinity, maximum salinity, and minimum salinity. Cross-correlation functions (CCFs) were used to examine the relationships between the daily and weekly environmental variables and oyster performance response variables (i.e. weekly average length and weekly mortality). Significant correlations (values that exceed the 95% confidence interval) were observed for the following variables for weekly average oyster length: daily average dissolved oxygen, daily minimum dissolved oxygen, daily average temperature, daily minimum salinity, and weekly minimum dissolved oxygen. Significant correlations were observed for the following variables for weekly mortality: daily minimum temperature, daily average temperature, daily minimum dissolved oxygen, daily average dissolved oxygen, daily maximum dissolved oxygen, weekly minimum dissolved oxygen, daily minimum salinity, and daily average salinity.

### **2.3.2 Oyster Performance**

Mean oyster shell length was calculated weekly for each tidal position and farmed strain combination (Figure 2.2). NEH<sup>®</sup> subtidal oysters had the greatest final mean shell length (39.40 mm  $\pm$  5.60 SD, 95% CI: 38.10-40.80), followed by DBX

subtidal oysters ( $38.80 \text{ mm} \pm 6.50 \text{ SD}$ , 95% CI: 37.10-40.50). NEH<sup>®</sup> intertidal was similar, with a final value of  $37.40 \text{ mm} \pm 6.20 \text{ SD}$  (95% CI: 35.60-39.20). DBX intertidal showed the smallest final mean length with a value of  $30.10 \text{ mm} \pm 6.30 \text{ SD}$  (95% CI: 27.50-32.70). Mean shell length of oysters from different strains cultured in subtidal and intertidal positions did not differ according to the Scheirer-Ray-Hare test ( $p > 0.05$ ).

IGR was calculated weekly for each oyster group combination (Figure 3; Equation 2). Growth rates varied between groups. The NEH<sup>®</sup> subtidal oysters exhibited a mean growth rate of  $0.38 \text{ mm/week}$ ,  $\pm 0.12 \text{ SD}$  (95% CI: 0.30-0.50), followed closely by DBX subtidal oysters ( $0.37 \text{ mm/week}$ ,  $\pm 0.13 \text{ SD}$ , 95% CI: 0.30-0.40). Mean growth rate for NEH<sup>®</sup> intertidal oysters was  $0.36 \text{ mm/week} \pm 0.13 \text{ SD}$  (95% CI: 0.30-0.40), while DBX intertidal oysters had a mean growth rate of  $0.35 \text{ mm/week}$ ,  $\pm 0.12 \text{ SD}$  (95% CI: 0.30-0.40). However, the Scheirer-Ray-Hare test showed no significant effects of tidal position ( $p = 0.36$ ), strain ( $p = 0.66$ ), or their interaction ( $p = 0.74$ ) on IGR. Additionally, linear models were fit to evaluate the trend in growth rate over time for each strain and tidal position combination. Growth rates over time showed no statistical difference when analyzed using linear models. The DBX intertidal oysters had an R-squared value of 0.3 ( $p = 0.08$ ), DBX subtidal oysters had an R-squared of 0.25 ( $p = 0.11$ ), NEH<sup>®</sup> intertidal oysters had an R-squared value of 0.32 ( $p = 0.07$ ), and NEH<sup>®</sup> subtidal oysters had an R-squared of 0.24 ( $p = 0.12$ ).

Condition index was calculated through Eqn. 1. The average condition index value for intertidal DBX was  $5.40 \pm 0.61 \text{ SD}$  (95% CI: 5.20-5.60), while intertidal NEH<sup>®</sup> showed a condition index of  $5.88 \pm 0.80 \text{ SD}$  (95% CI: 5.50-6.20). Mean

condition index within the subtidal zone for DBX oysters was  $4.09 \pm 0.71$  SD (95% CI: 3.80-4.40), and NEH<sup>®</sup> oysters had a mean condition index of  $4.22 \pm 0.63$  SD (95% CI: 3.99-4.50). A two-way ANOVA was conducted to examine the effects of tidal position and strain on the condition index. Analysis indicated a significant effect of tidal position ( $p < 0.001$ ), suggesting that the condition index of oysters in the intertidal zone is significantly different from those in the subtidal zone. Strain also had a significant effect ( $p = 0.03$ ), with NEH<sup>®</sup> oysters showing a significantly different condition index than DBX oysters. However, the interaction between tidal position and strain was not significant ( $p = 0.18$ ), indicating that the effect of tidal position on the condition index did not significantly vary between strains. Results of subsequent pairwise comparisons using Tukey's HSD test indicated that subtidal oysters had a significantly lower condition index than intertidal oysters ( $p < 0.001$ ), and NEH<sup>®</sup> oysters exhibited a significantly higher condition index than DBX oysters ( $p = 0.03$ ). When comparing oysters of the same strain, subtidal DBX oysters had a significantly lower condition index than intertidal DBX oysters ( $p < 0.001$ ). Condition index of intertidal NEH<sup>®</sup> oysters was greater than subtidal DBX oysters ( $p < 0.001$ ) and subtidal NEH<sup>®</sup> oysters ( $p < 0.001$ ). The difference in condition index between intertidal NEH<sup>®</sup> oysters and intertidal DBX oysters was not statistically significant ( $p = 0.06$ ), meaning that the condition index of these two groups was similar. Intertidal oysters likely experienced better condition indices due to the chipping and tumbling experienced in the intertidal zone, in conjunction with condition index metrics being biased towards smaller shell lengths. These results indicate that oysters in the intertidal zone generally have better condition, as well as NEH<sup>®</sup> oysters compared to DBX

oysters, emphasizing that both tidal position and strain significantly influence the condition index.

The number of survivors was measured across the oyster group combinations (Figure 5), with mean survivors as follows: intertidal DBX had 174 survivors ( $\pm 55.90$  SD, 95% CI: 160-188), intertidal NEH<sup>®</sup> had 177 survivors ( $\pm 56$  SD, 95% CI: 163-191), subtidal DBX had 221 survivors ( $\pm 42.20$  SD, 95% CI: 211-231), and subtidal NEH<sup>®</sup> had 227 survivors ( $\pm 40.10$  SD, 95% CI: 217-236). A Scheirer-Ray-Hare test was conducted to examine the effects of tidal position, strain, and their interaction on survivorship. The results showed a strong effect of tidal position on survivorship ( $p < 0.001$ ), with the mean number of survivors for subtidal oyster groups being significantly different than intertidal oyster groups. Neither strain ( $p = 0.28$ ) nor the interaction between tidal position and strain ( $p = 0.83$ ) significantly affected survivorship, suggesting that the difference in survivorship between intertidal and subtidal oysters was independent of strain. A subsequent Wilcoxon rank-sum test verified that survivorship differs between intertidal and subtidal oysters ( $p < 0.001$ , adjusted with Bonferroni), with significantly higher survivorship observed in subtidal oysters compared to intertidal oysters (Figure 5). No significant differences were detected between strains within each tidal position.

### **2.3.3 Generalized Additive Models for Oyster Growth and Mortality**

Generalized Additive Models (GAMs) for weekly average oyster length were used to assess the effects of environmental covariates, including average temperature, previous week's minimum dissolved oxygen, tidal position, and strain. Multicollinearity was checked using VIF analysis prior to model fitting, and covariates with a VIF above five were excluded. The best fit was the Gaussian family distribution

according to AICc scoring (AICc = 311.18). Further model selection was finalized through automated model selection (Table 1) and k-fold cross-validation, which identified the model with the lowest mean RMSE. The best GAM for weekly average oyster length accounted for 89.4% of the deviance in oyster length (adjusted R-squared = 0.87). We found significant smooth terms for average temperature (effective degrees of freedom (edf) = 2.67,  $p < 0.001$ ) and previous week's minimum dissolved oxygen (edf = 3.52,  $p < 0.001$ ), both of which had a non-linear, positive association with oyster length (Figure 6). The temperature smoothing plot shows that higher temperatures result in decreased oyster length ( $>20$  °C), indicating optimal growth within a specific temperature range (10-20 °C). The GAM indicated an association between growth and lower dissolved oxygen, though this likely stems from limited data at those levels rather than a genuine growth optimum below 2 mg/L. The model showed significant effects of tidal position ( $p < 0.001$ ), with subtidal oyster's having significantly different mean length than intertidal oysters. Strain had a small, yet significant effect on average shell length growth ( $p = 0.02$ ), with NEH<sup>®</sup> oysters exhibiting significantly greater average length than DBX oysters. The GAM diagnostics revealed a well-fitting model, with full convergence after 10 iterations and a positive definite Hessian. The k-index was verified for the smoothing terms, indicating adequate basis dimensions for both temperature and dissolved oxygen ( $p < 0.001$ ).

The GAM for weekly oyster mortality was applied to investigate the effects of minimum salinity, average salinity, minimum dissolved oxygen, and tidal position on oyster mortality. Multicollinearity was checked with VIF analysis prior to model fitting, and covariates with a VIF above five were excluded. The best fitting model

used the negative binomial family with a log link function, accounting for the over-dispersed nature of the count data (though AICc comparison favored Poisson distribution). In this model, we applied the same automated model selection (Table 2) and cross-validation strategies. The best GAM accounted for 81.7% of deviance in weekly oyster mortality (adjusted R-squared = 0.72). Minimum salinity (edf = 2.90,  $p < 0.001$ ) and minimum dissolved oxygen (edf = 2.77,  $p < 0.001$ ) had significant smooth terms. This indicated lower salinity and dissolved oxygen levels were coupled with higher mortality counts, and the relationship between these environmental factors and mortality was non-linear. The minimum salinity (Figure 7) plot displays that mortality increased with decreasing salinities, while the minimum dissolved oxygen plot shows that lower mortality was observed as dissolved oxygen increased. Average salinity (edf = 1,  $p = 0.32$ ) was incorporated in the final model but was not statistically significant. The relationship between average salinity and mortality was somewhat flat, implying that changes in mean salinity had less impact on weekly mortality relative to minimum salinity. Tidal position was significant ( $p = 0.01$ ), with subtidal oysters exhibiting significantly lower weekly mortality than intertidal oysters. K-index values for smooth terms were within reasonable bounds (min salinity:  $p = 0.03$ , average salinity:  $p = 0.01$ , minimum dissolved oxygen:  $p = 0.09$ ), suggesting that the basis functions were correctly specified. The GAM diagnostics revealed full convergence after 10 iterations and a positive definite Hessian, signifying a stable solution.

## **2.4 Discussion**

This study evaluated the growth, condition index, and mortality of DBX and NEH<sup>®</sup> farmed oyster strains across different tidal positions (intertidal vs. subtidal)

within the lower Delaware Bay. NEH<sup>®</sup> and DBX exhibit both MSX and Dermo disease resistance, as well as enhanced growth and shell characteristics compared to wild eastern oysters. NEH<sup>®</sup> strain, derived from Long Island Sound oysters, thrives in high salinity (20-34 psu) environments, while DBX, derived from Delaware Bay oysters, is suited to medium and low salinity (18-23 psu) environments (Rutgers University, n.d.). NEH<sup>®</sup> oysters specifically appeared to perform better in the higher salinity of the lower Delaware Bay (study site salinity range: 18.34-30.94 psu). NEH<sup>®</sup> oysters exhibited significantly higher condition index values than DBX oysters, with a modest trend of greater growth in NEH<sup>®</sup> oysters (Figure 2), although this difference was not statistically significant in univariate tests. NEH<sup>®</sup> oysters also demonstrated increased performance, particularly in subtidal environments where covariate values were within the optimal range for this strain. Tidal position was also an important driver in our study, where subtidal oysters performed better than intertidal oysters, especially in survivability. However, intertidal oysters experienced a higher condition index than subtidal oysters. The higher overall performance of subtidal oysters may be due to a more stable environment, where the oysters are less exposed to environmental extremes compared to the intertidal treatment group that experiences wider temperature and dissolved oxygen fluctuations associated with episodic tidal desiccation (Heo et al., 2023; Masanja et al., 2023). Oyster growth and survival were significantly affected by environmental covariates, specifically temperature, dissolved oxygen, and salinity. Our results are consistent with other studies that found salinity and dissolved oxygen to be key determinants of oyster survival (Galtsoff, 1964; Shumway, 1996; Jeppesen et al., 2016; Lowe et al. 2017; Sehlinger, 2018; Davis et al., 2024). Additionally, our finding that temperature impacts growth also confirms

previous findings which demonstrate that although growth increases with higher temperatures, extreme heat ( $> 30\text{ }^{\circ}\text{C}$ ) can adversely affect oyster survival (Galtsoff, 1964; Shumway, 1996; Lowe et al. 2017; Sehlinger, 2018). Our results underscore the importance of strain selection, tidal location, and environmental conditions in ensuring optimal oyster performance in living shoreline and habitat restoration projects. Further research would be useful to provide more definitive recommendations for the use of specific oyster strains across salinity regimes and other environmental gradients.

Contrary to other studies (e.g., Manzi et al., 1977; Bartol et al., 1999; Moroney and Walker, 1999; Bishop and Peterson, 2005), we found that subtidal oysters consistently performed better than intertidal oysters. Likely due to the protection from daily air exposure and atmospheric temperature extremes experienced in the summer months (Clements et al., 2018; Heo et al., 2023), as well as high sensitivity of juvenile oysters within the intertidal zone (Overton et al., 2023). Research has demonstrated that subtidal habitats generally offer better conditions for oysters, being less likely to experience air exposure and experiencing more stable temperature and salinity regimes (Lowe et al. 2017; Sehlinger, 2018), which may translate to increased survival and growth of subtidal oysters. Minimum salinity and dissolved oxygen were key environmental factors associated with mortality in our study, consistent with prior work in estuarine systems (Jeppesen et al., 2016; Rybovich et al., 2016).

The differences observed in our study in the growth of DBX and NEH<sup>®</sup> oysters are largely underexplored in other literature. However, previous studies have looked at other selectively bred oyster lines (Leggett, 1999). Our results suggest that NEH<sup>®</sup> oysters, which are adapted for high-salinity environments, could be appropriate candidates for restoration in similar conditions, though further testing across broader

spatial and temporal scales would be beneficial. Our study also adds new information to the impact of tidal position on oyster performance. Although the impact of tidal position has been described in the literature (Manzi et al., 1977; Bartol et al., 1999; Moroney and Walker, 1999; Bishop and Peterson, 2005), our study provides a better understanding of how strain and tidal position interact to impact oyster growth and mortality. The performance of DBX and NEH<sup>®</sup> oysters in different tidal positions provides insight into how restoration strategies may be optimized based on such factors. Additional research across seasons would be valuable in determining if such interactions occur over longer time frames than a single growing season.

Unfortunately, overwintering can limit studies that extend into the winter months, as interannual overwintering mortality can be high (>35%) in farmed oysters depending upon region and year (Mayrand et al., 2017).

These findings can be used to inform strategies for oyster-based ecological restoration, aquaculture, and living shoreline development in estuarine habitats. NEH<sup>®</sup> oysters exhibited increased condition indices and may be suitable for candidates for restoration in higher salinity environments. While their disease resistance and growth patterns suggest potential advantages, broader validation across multiple sites and seasons would be needed to confirm long-term performance. Incorporating selectively bred strains into living shoreline efforts could enhance establishment success, particularly in areas subject to disease pressure. Our study emphasizes the need to match oyster strains to the environmental conditions of the restoration site, specifically salinity. By selecting the right strain to match salinity preferences, restoration practitioners can increase oyster survival and growth, thereby ensuring long-term success in sustainable oyster reefs. In addition, our findings suggest that the subtidal

zone appears to provide unique benefits to oyster performance. In this study subtidal oysters exhibited consistently higher survival than intertidal oysters, which may reflect greater protection from thermal and dissolved oxygen extremes during submersion. These submerged environments may offer oysters the stability needed to grow. Further, by establishing a subtidal oyster reef, there is a likelihood that subtidal reefs will continue to develop into intertidal regions as the reef expands and recruitment occurs. Since oyster reefs are dynamic structures, this allows them to provide a variety of ecosystem services that are not exclusive to the subtidal zone. Therefore, as the installation changes over time, these structures can contribute ecosystem services to the intertidal zone, such as sediment accretion (Salvador de Paiva et al., 2018) and wave attenuation (Wiberg et al., 2018), while simultaneously providing subtidal habitats.

Overall, these results offer important new insights into the various physical and environmental factors that can shape oyster performance, along with support for the development of tailored restoration strategies that take these factors into account. We must consider the oyster size range that was tested, as it represents a very sensitive portion of the oyster life cycle ( $\leq 25$  mm). Therefore, identifying the strains and conditions that favor the survival of these individuals up to 25 mm, represents the critical point in reef development (Powell et al., 1994). If it is possible to efficiently transition oysters out of that size range, where they are more protected against predation, disease, and environmental changes, the restoration process will have a greater chance of success. A promising area of growth in living shoreline restoration is the idea of pre-seeding these installations with the appropriate strain of oyster to match the environmental conditions of the installation site. Instead of relying on natural

oyster recruitment to populate the site, pre-seeding the installation with selectively bred strains (i.e., NEH<sup>®</sup>) would potentially allow for oyster establishment within a shellfish-based living shoreline in a shorter period (USACE Baltimore and Norfolk Districts, 2012). By introducing more oysters to the restoration area from the start, this approach may enhance habitat provisioning and coastal protection benefits. The benefits of this strategy are particularly applicable to sites where natural recruitment is limited or sporadic. Further exploration of water quality variables, tidal position, and strain selection will help improve the restoration process and maximize the effectiveness of shellfish-based living shorelines.

Although the data and models presented here yield insights into the complex relationships between environmental factors, oyster strain, and tidal position, a number of assumptions and limitations should be noted. Oyster growth and mortality data were collected at weekly intervals, so measurements were weekly averages and totals. This sampling frequency could have missed finer timescales of variations in oyster performance that may be significant. One important design limitation is that tidal position was spatially confounded with rack identity. Racks were installed in fixed locations at the start of the study, which means we could not statistically distinguish the effect of tidal exposure from potential site-level variation among individual rack locations. However, all racks were placed at consistent depths for their respective tidal positions, spaced approximately 50 meters within a semi-enclosed basin, minimizing expected environmental heterogeneity across replicates. Comparable spatial designs have been used in other estuarine oyster studies with limited microhabitat variation exhibited between gear sites (Campbell et al., 2025). The environmental data were recorded every 30 minutes across the whole study period, but these data have been

post-processed and filtered into two different time scales: daily values and weekly values. For daily values, the data were filtered to include only the 24-hour period prior to each oyster sampling event. For weekly values, data were all the environmental observations for the week before the oyster sampling event of the current week. We made this choice based on the assumption that environmental conditions in the days preceding the sampling event would be the most influential to oyster growth and mortality. This filtering approach is fairly reasonable but does not account for any integrated effects of longer-term environmental exposure. Additionally, the use of three replicate racks per tidal treatment limits the degree of statistical inference that can be drawn, particularly when exploring environmental interactions using GAMs. While model performance was cross-validated and overfitting was addressed through covariate screening and AICc-based selection, we acknowledge that the small number of spatial replicates may constrain the generalizability of some findings. However, this replication strategy aligns with recent experimental designs employed in comparable field-based oyster studies (e.g., Campbell and Gray, 2024), particularly when logistical and spatial constraints exist in estuarine settings.

The duration of this study was relatively short in the context of oyster performance metrics (4 months), thus only allowing us to observe oyster performance across a limited seasonal range of environmental conditions. The environmental variables included can vary greatly during the winter months, potentially influencing oyster metabolism, growth, and mortality (Mayrand et al., 2017). A longer-term study would provide more insight into how seasonal changes impact oyster performance, particularly concerning temperature extremes and variability in salinity. However, oyster farmers frequently adjust oyster gear before the late fall and winter months to

avoid extreme weather events and increased oyster mortality (Morse 2006). The study site reflects a distinct environment within Delaware Bay. Additional sites with different environmental conditions would help assess the generalizability of these findings. The Generalized Additive Models (GAMs) applied in this analysis assume that the relationships between environmental drivers (salinity, temperature, dissolved oxygen) and oyster performance (weekly average length and weekly mortality) are smooth and non-linear; and that the data are independent and identically distributed. Though the GAMs provide useful information on how environmental factors affect oyster performance, there may be other limiting factors not considered in the models, including predation, oyster behavior, or habitat interactions. Furthermore, although the GAMs incorporated repeated weekly averages as independent observations to improve temporal resolution, this approach may introduce some degree of pseudoreplication and potentially inflate significance levels in the GAM outputs. The resulting strain effect detected in the growth GAM, not seen in the univariate test, may reflect the influence of environmental covariates and increased statistical power, but should be interpreted cautiously. Despite these limitations, we were able to demonstrate the potential for future research utilizing GAMs to investigate the interactions among environmental variables influencing oyster performance, aiding in a series of recommendations to improve living shoreline designs and restoration efforts in estuarine environments.

Though this study provides insight into selectively bred oyster performance across different tidal positions and environmental conditions, several areas of future investigation would be useful for further consideration. First, the seasonal variability in environmental conditions, particularly temperature, salinity, and dissolved oxygen,

has been identified as a potential factor influencing oyster performance (NOAA Fisheries EOBRT, 2007). Future studies should extend monitoring to include more seasons (i.e., winter and spring months). Including a full annual cycle would help researchers understand how oysters respond to seasonal changes in their environmental conditions, particularly in growth and mortality. However, issues of overwintering mortality, particularly for intertidal installations, would need to be considered (Mayrand et al. 2017). Studies in additional estuaries or coastal systems could elucidate more generalized effects of salinity and temperature on strain performance and tidal position within estuaries. This information would be particularly applicable for restoration, aquaculture, or living shorelines, as their success is often dictated by site-specific characteristics.

Other future research directions should attempt to integrate additional environmental covariates that can affect oyster health (e.g., sediment type, turbidity, and pH). For example, oysters in areas with high sediment loads or elevated turbidity may face feeding and survival challenges (Barillé et al., 1997; La Peyre et al., 2020). Another potential avenue for future research would be to compare other selectively bred strains of oyster like the Virginia Institute of Marine Science (VIMS) DEBYs, LOLAs, or HNRYS, as these strains are characterized by genetic differences that allow them to thrive in different salinity regimes (Proestou et al., 2016). Despite these associated limitations, our study provides essential information regarding the importance of strain and tidal placement on oyster performance. A coupled approach to living shoreline designs featuring subtidal and intertidal oyster reef components, though underexplored, could be used as a prescriptive measure to enhance living shoreline resilience. Some shellfish-based living shoreline designs allude to the fact

that subtidal installations can result in the mitigation of shoreline retreat (Scyphers et al., 2011). However, intertidal reefs have been found to reduce wave height buffering shoreline erosion during storm events (Morris et al., 2021). The discrepancy between the functional differences of the two zones emphasizes the tradeoff between greater survival and suitable habitat of the subtidal zone compared to increased wave attenuation of the intertidal zone (Salatin et al., 2022). However, these elements should be considered synergistically to maximize the likelihood of shoreline resilience.

## **2.5 Conclusion**

Selectively bred oysters can help increase the success of oyster-based restoration and living shorelines. Our results strongly suggest that subtidal areas appeared to provide more optimal conditions for oyster growth and survival, suggesting their potential value for initiating reef formation in restoration efforts. Furthermore, NEH<sup>®</sup> oysters, selected for disease resistance and improved growth, perform better in the conditions of the lower Delaware Bay than DBX oysters. This emphasizes the importance of strain selection based on associated environmental conditions, though growth differences are smaller and model-dependent. However, these findings should be interpreted in the context of the study's limitations, including a short duration, single-site design, limited spatial replication, and potential lack of independence in weekly measurements. Despite these limitations, our results highlight the importance of tailoring oyster restoration strategies that consider environmental factors and genetic strain. More studies are needed to further optimize these approaches and explore interactions between oyster strains, tidal position, and environmental variables to increase the success and resilience of living shorelines in a changing climate.

Table 1 Generalized Additive Model selection table for average oyster length response variable. Based off selection output, variables kept in final model consist of average daily temperature, previous week's minimum dissolved oxygen, strain, and tidal position. Daily minimum salinity was not included.

Intercept	s(Average Temperature)	s(Minimum Salinity)	s(Previous Week Minimum Dissolved Oxygen)	Strain	Tidal Position	df	logLik	AICc	delta	weight
20	+		+	+	+	10	-140.667	308.9	0	0.663
20	+	+	+	+	+	11	-140.147	311.2	2.25	0.215
21.09	+		+		+	9	-144.299	312.9	4.01	0.089

Table 2 Generalized Additive Model selection table for weekly oyster mortality response variable. Based on the selection output, variables kept in the final model consist of minimum daily dissolved oxygen, minimum daily salinity, average daily salinity, and tidal position. Previous week's minimum dissolved oxygen and strain were not included.

Intercept	s(Average Salinity)	s(Minimum Dissolved Oxygen)	s(Minimum Salinity)	s(Previous Week Minimum Dissolved Oxygen)	Strain	Tidal Position	df	logLik	AICc	delta	weight
2.311		+	+			+	10	-124.511	275.4	0	0.497
2.146		+	+				8	-127.71	278.4	3.01	0.111
2.322	+	+	+			+	10	-125.276	278.7	3.3	0.096
2.31		+	+		+	+	10	-124.69	279.1	3.74	0.077
2.376			+	+		+	8	-129.318	280.7	5.33	0.035



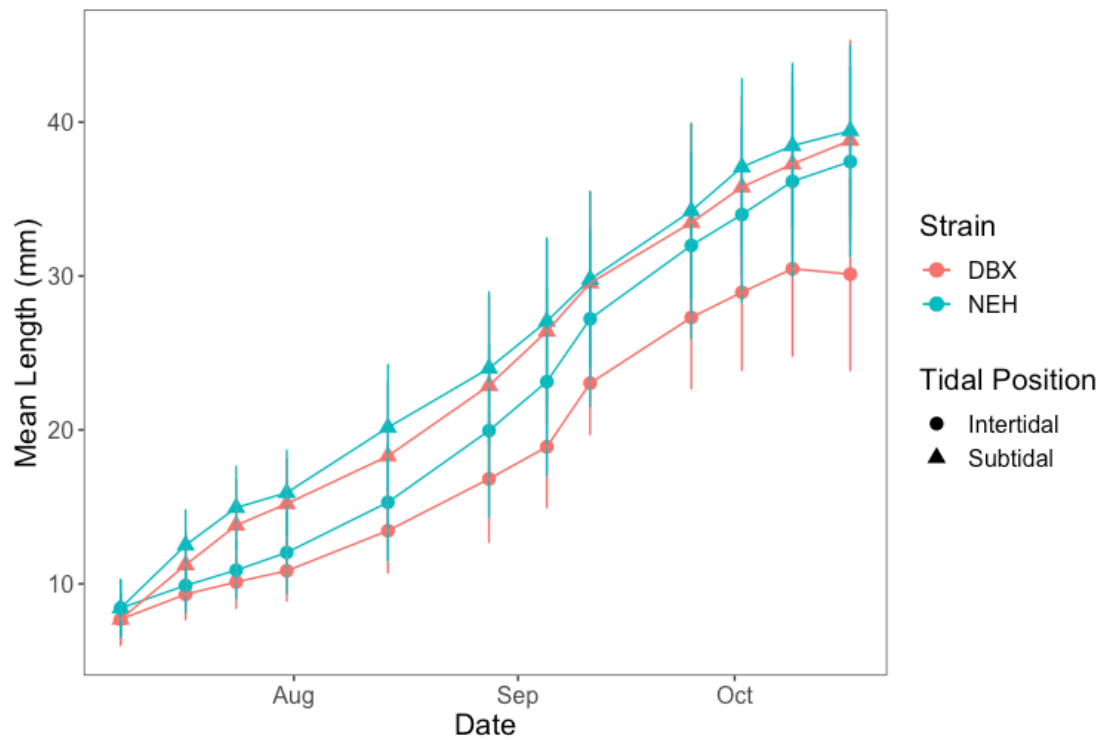


Figure 2.2 Mean oyster length between oyster strain and rack tidal position over time. Blue indicates NEH® oysters, while pink represents DBX oysters. Intertidal positioning is noted with circle symbols and subtidal positioning with triangle symbols. Error bars are  $\pm$  one standard deviation, ( $n = 3$  racks per strain x tidal combination).

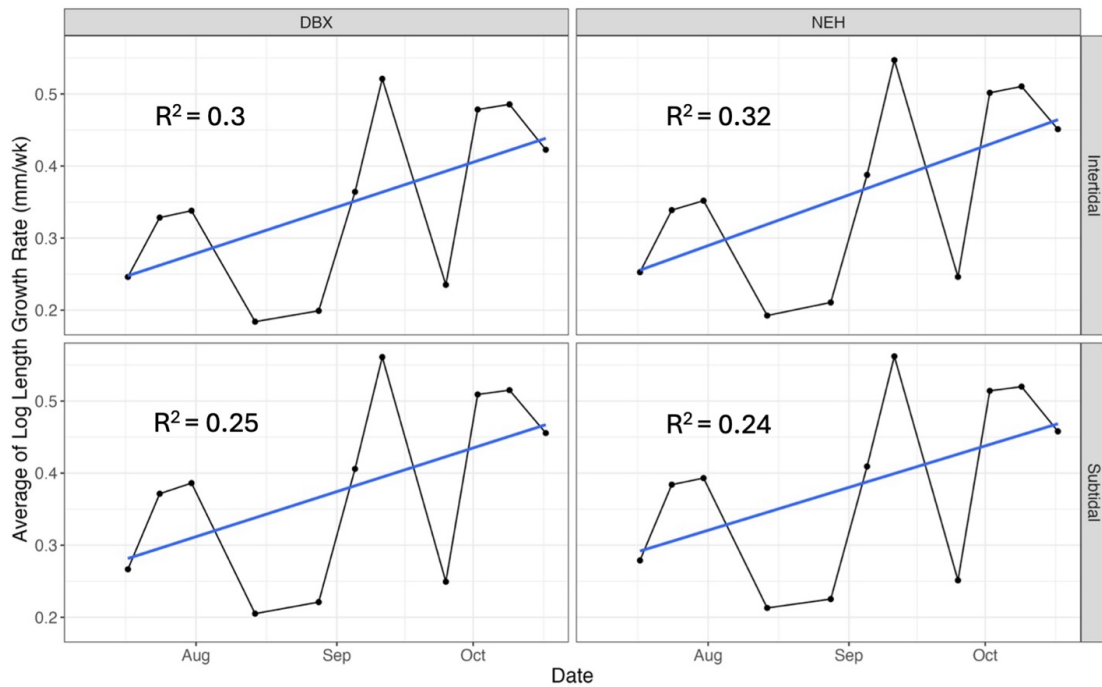


Figure 2.3 Instantaneous growth rate over time (mm/week) for each oyster strain and tidal position with a linear regression trendline found in blue ( $n = 3$  racks per strain x tidal combination). DBX intertidal oysters had an R-squared value of 0.3, while DBX subtidal oysters had an R-squared value of 0.25. NEH® intertidal oysters had an R-squared value of 0.32, while NEH® subtidal oysters had an R-squared value of 0.24.

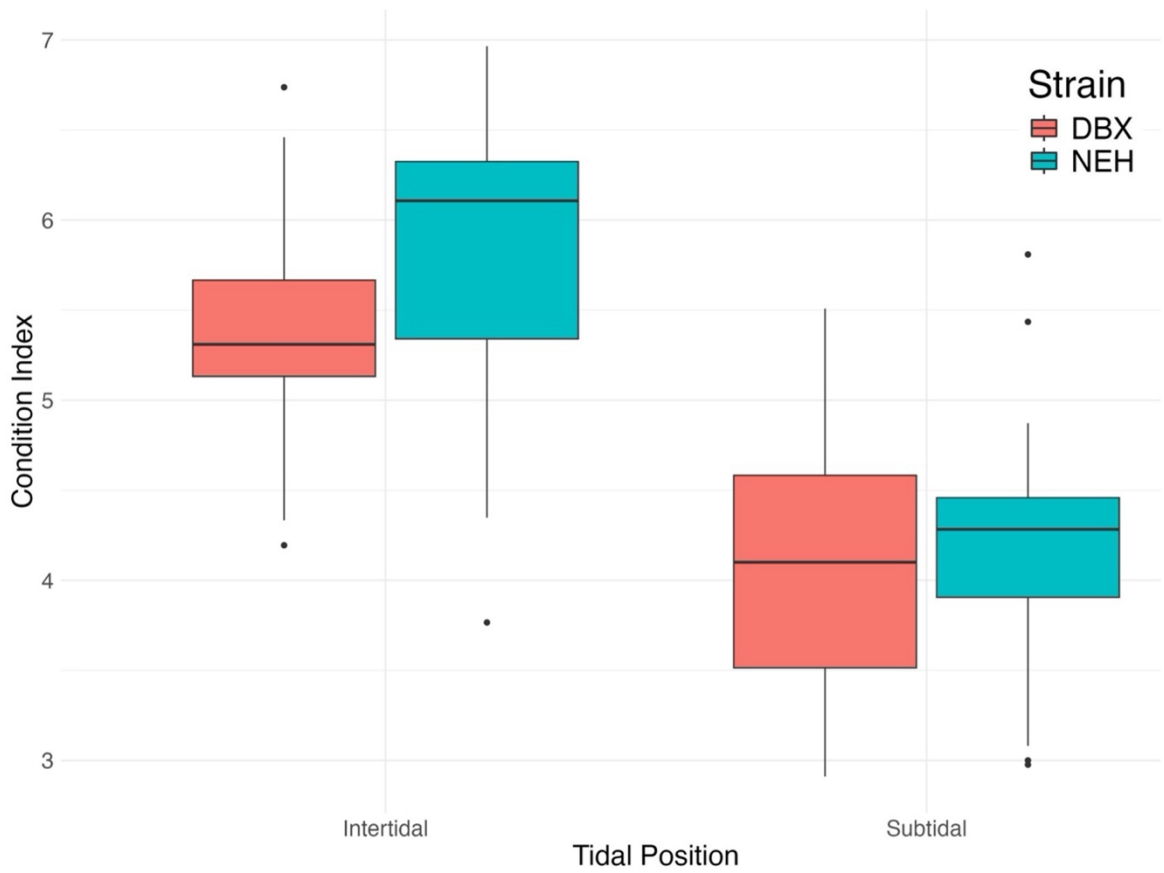


Figure 2.4 Final oyster condition index by tidal position and strain. Intertidal oysters appear to show an overall greater condition index than subtidal oysters (n = 3 racks per strain x tidal combination, 10 individuals each).

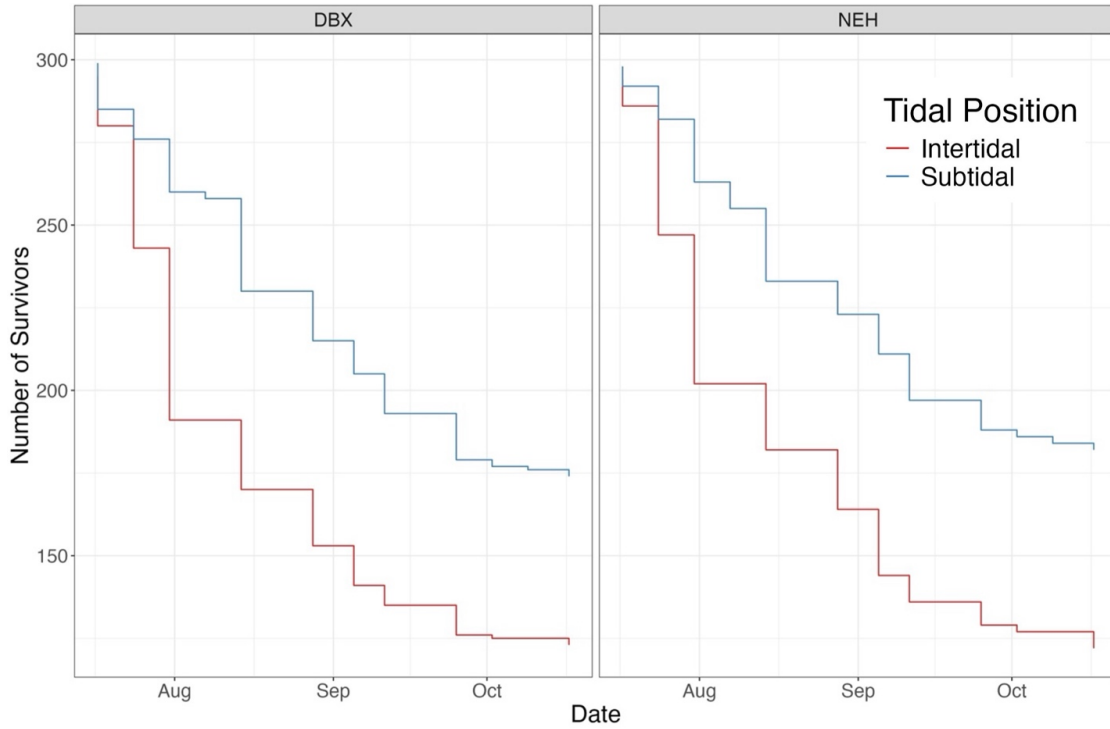


Figure 2.5 Oyster survivorship curve across strain and tidal position. Intertidal oysters survival is found in red, while subtidal oysters survival is found in blue ( $n = 3$  racks per strain x tidal combination). Trends in survivorship suggest that subtidal oysters had more survivors than intertidal oysters.

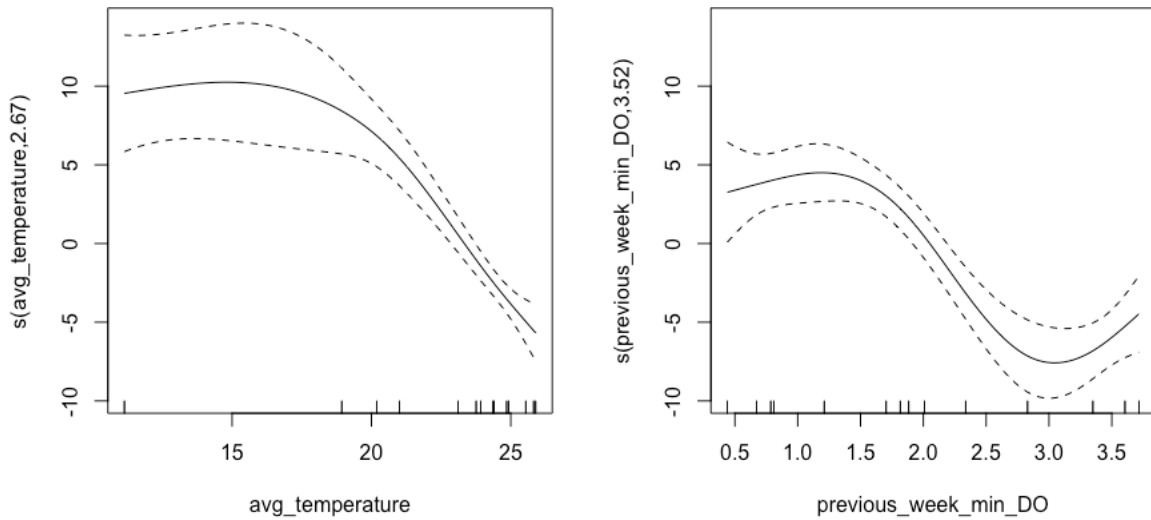


Figure 2.6 Plots of model smoothing terms for average temperature and minimum dissolved oxygen average oyster length ( $n = 3$  racks per strain  $\times$  tidal combination). The temperature smooth term indicates the partial effect of daily average temperature on average oyster length, while the previous weekly minimum dissolved oxygen smooth term demonstrates the partial effect on average oyster length. The temperature smoothing plot shows that higher temperatures have a decreasing effect on oyster length, indicating optimal growth within a specific temperature range less than  $20\text{ }^{\circ}\text{C}$ , while optimal growth of oysters occurred at periods when the weekly minimum dissolved oxygen was less than  $2.0\text{ mg/L}$ .

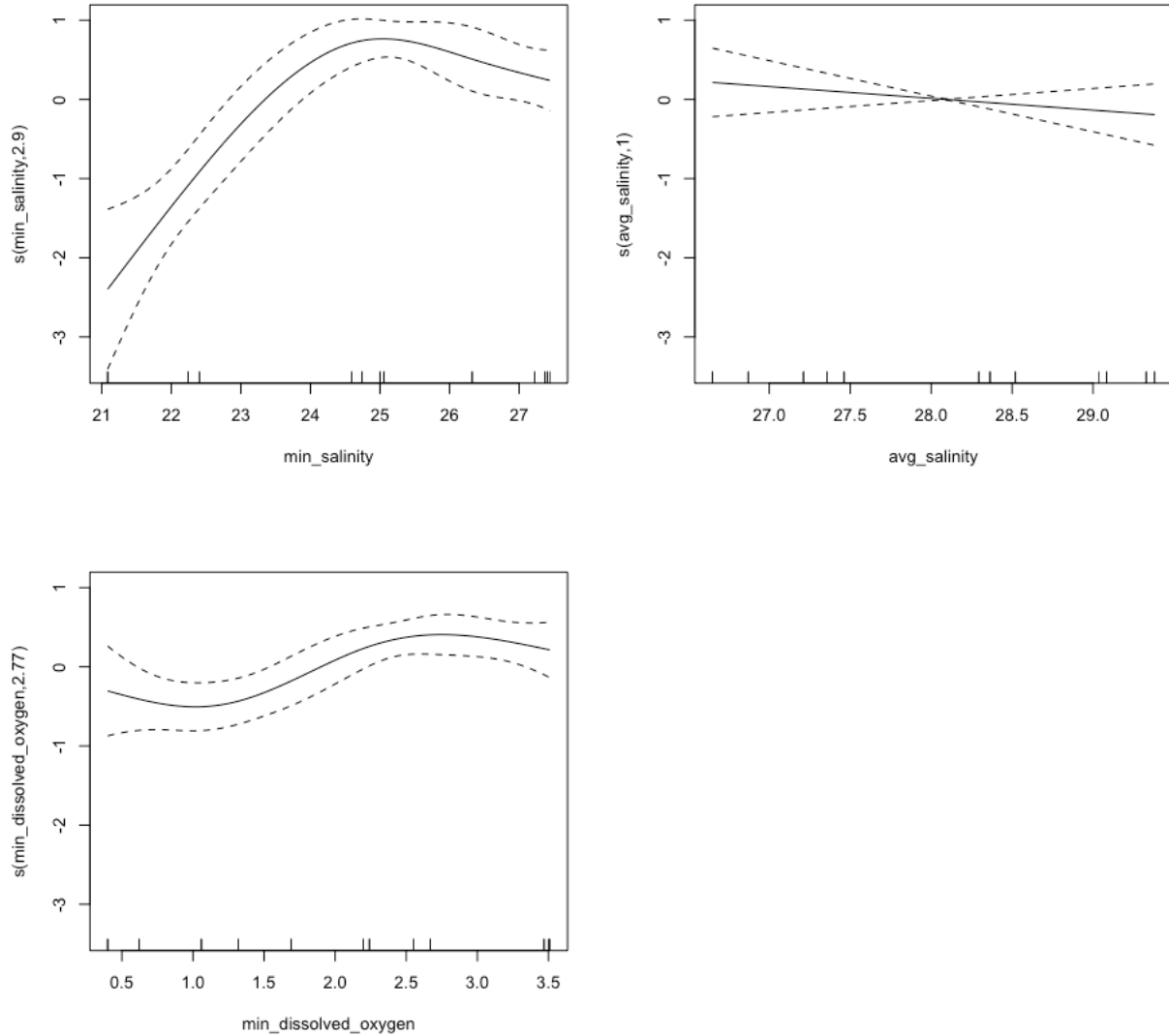


Figure 2.7 Plots of model smoothing terms for minimum salinity, average salinity, and minimum dissolved oxygen on average oyster mortality ( $n = 3$  racks per strain x tidal combination). The salinity smooth terms indicate the partial effect of daily minimum salinity and daily average salinity, respectively, on weekly oyster mortality. The dissolved oxygen smooth term shows the partial effect of daily minimum dissolved oxygen on weekly oyster mortality. The daily minimum salinity plot displays that mortality increased with decreasing salinities, while the daily minimum dissolved oxygen plot shows that lower mortality was observed as dissolved oxygen increased. Daily average salinity ( $\text{edf} = 1$ ,  $p = 0.32$ ) was incorporated in the final model but was not statistically significant.

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## Appendix A

### EXPLORATION OF OYSTER AQUACULTURE GEAR ACCELERATION IN RELATION TO ALONGSHORE WIND

#### **Methods:**

##### **Accelerometer Deployment Design**

To characterize oyster gear movement across tidal environments, 36 triaxial accelerometers were deployed across three paired intertidal and subtidal aquaculture installations in the University of Delaware Lewes Campus boat basin. Each installation contained six sensors arranged to capture rack-level and bag-level motion. Two accelerometers were attached to the rack itself—one on the left side and one on the right—to monitor for potential rack sway. The remaining four accelerometers were distributed across two oyster grow-out bags per installation. On each bag, one accelerometer was attached to the exterior, simulating the exposure that oysters experience, while another was placed loosely inside the bag, capturing the interior motion of the oysters. This sensor design allowed for fine-scale comparisons of movement exposure between distinct sensor positions and within two different settings: exposed intertidal sites and continuously submerged subtidal sites. All accelerometers were programmed to record motion data at 5-minute intervals over the study period. Only accelerometers fixed to the outside of the oyster bags (“On” sensors) were used in analyses, as these most accurately represented biologically relevant motion experienced by oysters in situ. Initial statistical analysis indicated significantly different acceleration magnitudes across sensor types (rack vs on vs in),

which justified the exclusion of structurally inconsistent replicates in favor of consistent, meaningful data.

### **Acceleration Data Processing**

Acceleration data consisted of triaxial values recorded along the X, Y, and Z axes. For each 5-minute reading, a sum vector was computed. This metric was selected as a univariate representation of total gear motion. To reduce the influence of outliers and sensor error, values beyond  $\pm 3$  standard deviations from the mean were removed. After outlier filtering, the dataset was subset to include only the accelerometers located on the outside of bags at both intertidal and subtidal positions. Acceleration data from each tidal position (intertidal vs. subtidal) were pooled across replicate installations prior to binning or analysis. All data processing and analysis were performed in R.

### **Wind Data Collection and Alongshore Wind Calculation**

Wind data were obtained from the National Data Buoy Center (NDBC) Station 44009, located off the coast of Delaware Bay, approximately 55 kilometers from the study site. This station provided continuous meteorological observations throughout the study period, including wind speed and wind direction, which were recorded at 10-minute intervals. These variables were used to characterize atmospheric conditions acting on oyster gear deployed in both intertidal and subtidal environments. To quantify wind effects relative to the orientation of the shoreline, an alongshore wind component was calculated. This involved determining the azimuthal angle of the shoreline near the oyster installations using GPS coordinates from rack-and-bag

installations that defined a representative stretch of coast. The resulting angle represented the orientation of the shoreline, measured in degrees from true north. Wind direction data were converted from the conventional “wind from” format (direction the wind is coming from) to a “wind to” format (direction the wind is blowing toward) by adding 180°. Next, wind speed and direction were decomposed into zonal (east-west) and meridional (north-south) vector components. These vectors were then projected onto the shoreline axis to compute the alongshore wind, which quantifies the portion of wind speed acting parallel to the coastline. Positive values of alongshore wind indicate wind flowing downcoast (aligned with shoreline orientation), while negative values indicate upcoast (against the shoreline). This derived variable provided a biologically and physically meaningful metric to examine the relationship between coastal wind forcing and oyster gear movement. The alongshore wind component was ultimately used in all cross-correlation analyses with acceleration data.

### **Temporal Binning and Stationarity Testing**

To evaluate how environmental motion influences oyster gear movement over various time scales, both wind and acceleration data were aggregated into discrete temporal bins ranging from 6 to 48 hours, at 6-hour increments (i.e., 6, 12, 18, 24, 30, 36, 42, and 48 hours). Binning was performed using `floor_date()` from the `lubridate` package to ensure temporal alignment between datasets. Prior to running time series analyses, both the binned acceleration and wind time series were tested for stationarity using statistical checks (e.g., augmented Dickey-Fuller tests). If non-stationary trends were identified, the series were detrended using differencing until stationarity was

achieved. All autocorrelation and cross-correlation analyses were performed on stationary datasets only.

### **Autocorrelation and Cross-Correlation Analysis**

Autocorrelation functions (ACFs) were calculated for each stationary time series of acceleration and wind data to evaluate the presence of temporal structure or periodic cycles. ACFs were assessed visually for repeating peaks or significant lags, as indicated by crossing the confidence boundary. Cross-correlation functions (CCFs) were calculated using the `ccf()` function in base R to determine the strength and direction of lagged relationships between alongshore wind velocity and gear acceleration. Analyses were performed independently for intertidal and subtidal datasets at each bin size. Only the alongshore component of wind was used as the explanatory variable in CCFs. Default settings were used in `ccf()` (`type = "correlation"`, `plot = TRUE`, `lag.max = NULL`), which includes a 95% confidence interval band for visual assessment of significance. Lags were interpreted in hours, with positive lags indicating wind conditions leading gear movement.

### **Results:**

Cross-correlation analyses revealed differences in the relationship between alongshore wind and oyster gear acceleration across tidal positions and temporal bin sizes (Table 1). Subtidal installations consistently exhibited stronger and more temporally extensive correlations with alongshore wind than intertidal installations. These patterns held across bin sizes, suggesting that hydrodynamic forcing from wind

plays a greater role in influencing gear movement at subtidal sites compared to intertidal locations.

### **Subtidal and Intertidal Gear Response to Alongshore Wind**

For all bin sizes (6-48 hours), subtidal gear showed statistically significant correlations between alongshore wind and sum vector acceleration (CCF crossing 95% confidence interval band). At the finest temporal resolution (6-hour bins), subtidal correlations were significant across a broad lag window (-10 to +10 hours), with a peak correlation occurring at lag 0 (correlation coefficient:  $r \approx 0.38$ ), indicating that acceleration increased concurrently with alongshore wind events. This trend of strong, zero-lag correlations persisted across bin sizes up to 48 hours, where significant lags narrowed slightly (e.g., -1 to +2 at 48-hour bins), but the strength of the peak correlation remained relatively high (e.g.,  $r \approx 0.44$  at lag 0).

The temporal alignment of these responses (i.e., lag 0 or +1) supports the interpretation that gear movement in subtidal positions responds rapidly to changes in wind forcing. This effect may be amplified by greater exposure to flow in deeper water. The absence of consistent drying periods may also enhance the sensitivity of gear movement to hydrodynamic drivers in subtidal areas.

In contrast, intertidal gear exhibited far fewer and weaker correlations with alongshore wind. At the 6-hour bin size, some significant correlations were present (-6 to +10 lags, peak  $r \approx .18$  at lag +1), suggesting a modest influence of wind, potentially during high tide conditions. However, the strength and extent of significant correlations decreased with increasing bin size. At 24 hours, only a single lag (0) showed significance ( $r \approx .21$ ), and at bin sizes of 30, 36, 42, and 48 hours, no

significant correlations were detected. These results indicate that wind forcing is not a primary driver of gear movement at intertidal sites, especially at longer temporal scales. This likely reflects the dominance of tidal exposure cycles in intertidal zones, where gear is periodically desiccated and thus decoupled from hydrodynamic forces for substantial portions of each day. The intermittent nature of immersion and drying could interrupt or mask correlations with wind-driven water movement.

### **Comparative Patterns Across Tidal Positions**

A consistent trend emerged across all bin sizes: subtidal gear movement was more sensitive to wind forcing than intertidal gear movement, and this difference became more pronounced at coarser temporal resolutions. For example, subtidal bins at 30-48 hours retained significant correlations (e.g., -2 to +3 at 30 hours, and -1 to +2 at 48 hours), while intertidal bins at the same scales exhibited no significant lags. This suggests that in subtidal environments, wind events leave a longer hydrodynamic signature, whereas intertidal gear movement is episodic and more constrained by tidal cycling. The presence of peak correlations at or near lag 0 across all subtidal CCFs further reinforces the interpretation that wind events have an immediate influence on gear acceleration. Conversely, intertidal peaks, when present, tended to occur at small positive lags, possibly reflecting a delay between wind forcing and gear re-immersion during high tide.

### **Biological and Morphological Considerations**

These findings have implications for the interpretation of biologically relevant activity in rack-and-bag oyster aquaculture. The decision to use only acceleration data

from sensors placed on oyster bags, rather than those inside the bag or on the rack, was based on the biological relevance of outer bag movement as a proxy for oyster exposure to physical disturbance. Given that gear movement is higher and more wind-correlated at subtidal sites, oysters grown in these environments may experience greater mechanical agitation, potentially affecting shell morphology and growth. In intertidal systems, where wind is a less dominant driver of gear movement, oyster exposure may be more structured around tidal cycles, which influence feeding windows, desiccation stress, and shell formation differently than in subtidal placements.

<b>Bin Size (hr)</b>	<b>Tidal Position</b>	<b>Peak Lag (hr)</b>	<b>Peak Correlation</b>	<b>Significant Lags (hr)</b>
6	Intertidal	+1	~0.18	-6 to +10
6	Subtidal	0	~0.38	-10 to +10
12	Intertidal	0	~0.20	-2 to +2, +5 to +6
12	Subtidal	0	~0.40	-6 to +6
18	Intertidal	0	~0.21	-3 to +3, +5
18	Subtidal	0	~0.42	-5 to +5
24	Intertidal	0	~0.21	0 only
24	Subtidal	0	~0.44	-3 to +5
30	Intertidal	0	~0.23	<i>None</i>
30	Subtidal	0	~0.44	-2 to +3
36	Intertidal	0	~0.22	<i>None</i>
36	Subtidal	0	~0.46	-1 to +3
42	Intertidal	0	~0.25	<i>None</i>
42	Subtidal	0	~0.45	-1 to +2
48	Intertidal	0	~0.24	<i>None</i>
48	Subtidal	0	~0.44	-1 to +2

Table A1 Cross correlation function (CCF) output between the alongshore wind component and oyster aquaculture gear acceleration. Wind and acceleration CCFs were analyzed at 6-hour bins, up to 48 hours for both intertidal and subtidal gear positions.

## Appendix B

### RAW HOBO LOGGER DATA

To better understand the broader environmental context of our study site, HOBO loggers were attached to the rack and bag oyster gear structures. A dissolved oxygen logger, as well as a temperature/salinity logger, was placed on the central subtidal rack. The loggers were set to sample at a 30-minute frequency for the entire study period (July 9, 2023-October 16, 2023). Within these time series, dissolved oxygen ranged from 0.40 to 13.53 mg/L, salinity ranged from 18.34 to 30.94 psu, and temperature ranged from 15.80 to 29.12 °C. Below are the graphical results of the environmental time series data.

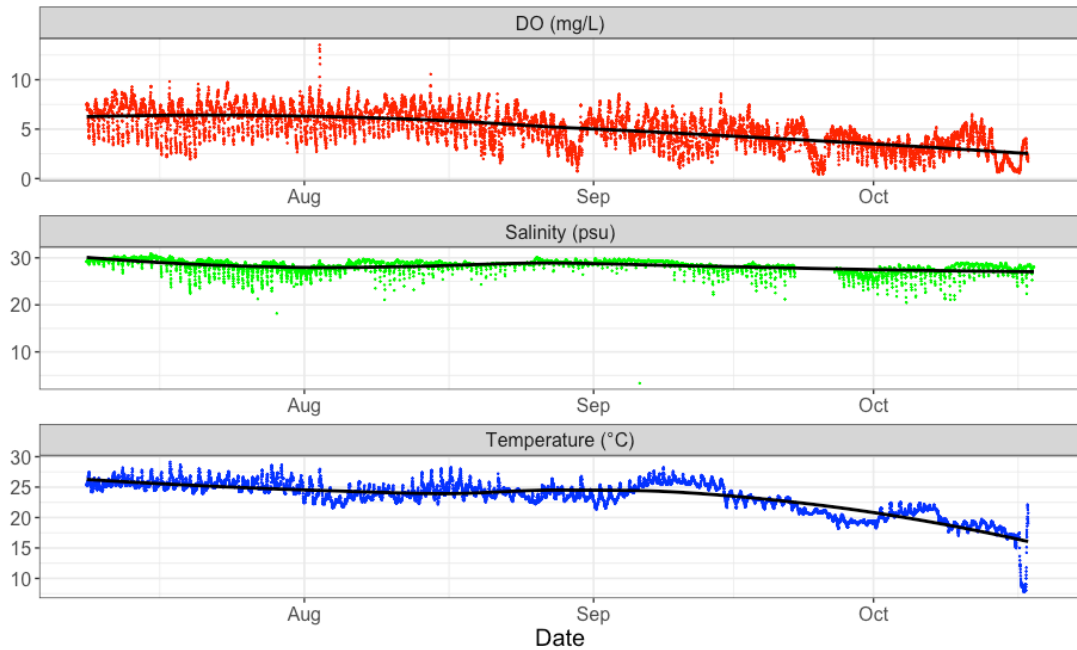


Figure B1 A figure of raw environmental time series for dissolved oxygen (mg/L), salinity (psu), and temperature (°C) at a 30-minute sampling interval.

## **Appendix C**

### **GENERALIZED ADDITIVE MODEL WORKFLOWS**

#### **Time Series Preparation and Stationarity Checks**

Environmental time series for salinity, dissolved oxygen, and temperature were first processed to evaluate their suitability for inclusion in subsequent analyses. Each variable was examined for stationarity at both daily (24-hour) and weekly temporal resolutions, summarized as maximum, minimum, or average values. Non-stationary series were differenced (first order and second order) until stationarity was achieved, and only those that could be successfully stabilized were retained for further analysis. This ensured that subsequent autocorrelation and cross-correlation analyses met the assumptions of temporal independence.

#### **Cross-Correlation Analyses (CCF)**

Cross-correlation functions (CCFs) were conducted between each stationary environmental variable and weekly average oyster shell length and weekly average oyster mortality. Analyses were performed for two temporal offsets: environmental variables 24 hours before sampling, and environmental variables one week before sampling. Variables showing significant correlations with the response variable were retained for model exploration. For weekly average growth, these included: average dissolved oxygen, minimum dissolved oxygen, average temperature, minimum salinity, and weekly minimum dissolved oxygen. For weekly average mortality, these included: average salinity, minimum salinity, average dissolved oxygen, max

dissolved oxygen, minimum dissolved oxygen, average temperature, minimum temperature, and weekly minimum dissolved oxygen.

### **Multicollinearity Screening**

Retained variables were tested for collinearity using Variance Inflation Factor (VIF) analysis. Variables with  $VIF > 5$  were excluded. Specifically for the growth model, average dissolved oxygen and minimum dissolved oxygen were removed. The remaining predictors used for growth modeling included: minimum salinity, average temperature, and previous week's minimum dissolved oxygen. For the mortality predictors, average dissolved oxygen, maximum dissolved oxygen, average temperature, and minimum temperature were removed. The remaining predictors used for mortality modeling included: average salinity, minimum salinity, minimum dissolved oxygen, and previous week's minimum dissolved oxygen.

### **Model Development and Selection**

For growth models, three GAM families were tested: Gaussian, Gamma (link = "log"), and Tweedie. The Gaussian family produced the lowest AICc values across smooth parameter settings. Model selection using the "dredge" function suggested that minimum salinity could be removed without loss of explanatory power. Comparative AICc analyses confirmed that excluding minimum salinity improved model fit, and the simplified Gaussian GAM was selected as the final growth model, along with significant tidal position and strain factored terms.

Mortality was analyzed using two response variables: average weekly mortality and instantaneous mortality rate. For weekly mortality, both Poisson and

Negative Binomial GAMs were evaluated. Although the Poisson model initially produced the best AICc, residual checks indicated overdispersion; therefore, the Negative Binomial model was chosen. The optimal model retained minimum salinity, average salinity, minimum dissolved oxygen, and tidal position as significant. For the instantaneous mortality rate, Gaussian and Tweedie families were tested. The Tweedie GAM yielded the lowest AICc, with the best performing structure excluding maximum salinity, minimum salinity, and strain. Although both mortality models fit well, the average weekly mortality GAM explained 81.7% of deviance (compared to 79.2% for instantaneous mortality rate). Because AICc scores were similar, the mean RMSE from predictive validation was used as a deciding metric. Based on this criteria, the weekly mortality GAM was selected as the final model. A similar model selection and comparison approach was used for the growth GAMs to ensure consistency across analyses.

All data processing, statistical analyses, and model selection procedures were performed in R (version 4.2.1; R Core Team, 2023). The complete annotated R script used in this workflow is available on GitHub at: [https://github.com/hudockr/Oyster-Performance\\_GAMs.git](https://github.com/hudockr/Oyster-Performance_GAMs.git)

Intercept	s(Average Temperature)	s(Minimum Salinity)	s(Previous Week Minimum Dissolved Oxygen)	Strain	Tidal position	df	logLik	AICc	Delta	Weight
20	+		+	+	+	10	-140.7	308.9	0	0.7
20	+	+	+	+	+	11	-140.1	311.2	2.2	0.2
21.1	+		+		+	9	-144.3	312.9	4	0.1

Table C1 Automated model selection table of final growth model predictor variables, ranked by highest explanatory power.

Intercept	s(Average Salinity)	s(Minimum Dissolved Oxygen)	s(Minimum Salinity)	s(Previous Week Minimum Dissolved Oxygen)	Strain	Tidal position	df	logLik	AICc	Delta	Weight
2.3		+	+			+	10	-124.5	275.4	0	0.5
2.1		+	+				8	-127.7	278.4	3.01	0.1
2.3	+	+	+			+	10	-125.3	278.7	3.3	0.1
2.3		+	+		+	+	10	-124.7	279.1	3.7	0.1
2.4			+	+		+	8	-129.3	280.7	5.3	0.03

Table C2 Automated model selection table of final mortality model predictor variables, ranked by highest explanatory power.