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CONSEQUENCES OF SALINITY CHANGE, SALINITY HISTORY, AND SHELL MORPHOLOGY ON EARLY GROWTH OF JUVENILE OYSTERS

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ABSTRACT Estuaries provide valuable habitat for the eastern oyster (*Crassostrea virginica*). Although salinity at a given location fluctuates regularly with tides, upbay and downbay salinity differences span a broad estuarine salinity gradient. Higher salinity habitats downbay support faster oyster growth, whereas lower salinities upbay act as a refuge from predation and disease but slows growth. Two experiments were performed to investigate the effect of salinity, postsettlement salinity changes, and shell morphology on juvenile oyster growth. One experiment used wild oyster spat collected from three distinct Delaware Bay salinity zones that were then transplanted into various salinity conditions in the laboratory, where growth was monitored. Transplanting into low salinity led to decreased growth compared with transplanting to higher salinity, and growth of oyster spat was overall highest for spat from the lowest salinity source. Growth did not differ among shell morphologies. A second experiment used hatchery reared larvae set in one of four different salinity conditions. Those spat were maintained in settlement salinities 22, 16, 10, and 6 for 2–3 wk postsettlement, then measured before fully factorial transfer into new salinity conditions with measurement 3 wk later. Lower final salinity treatments were associated with lower growth, lower initial salinity treatments were associated with faster final treatment growth, and final growth depended on the interaction between initial and final salinity. Therefore, in addition to the effects of acute salinity changes on growth, early postsettlement hyposalinity stress can generate compensatory juvenile oyster growth. As increased freshwater events due to climate change are expected in the Delaware Bay and regionally in the Northeast, these results indicate that nonlinear early life stress responses are important to quantify to better understand oyster stock resilience and plan management.

KEY WORDS: Oyster, spat morphology, salinity, growth, carryover effects

INTRODUCTION

Oysters (*Crassostrea virginica* Gmelin, 1791) provide many economic benefits and ecosystem services to the east coast of the Americas. They are euryhaline and can sustain populations in salinities ranging from 5 to 35 (Galtsoff 1964), with an optimal range from 14 to 28 (Shumway 1996), which makes estuaries ideal habitat. Higher salinity (downbay) favors faster growth and larger oyster size but brings with it higher predation and disease prevalence (Kraeuter et al. 2007, Powell et al. 2008, Munroe et al. 2013). In lower salinity (upbay), oysters grow slower and, therefore, take longer to reach fishable size but are less affected by disease and predation (La Peyre et al. 2003, Kraeuter et al. 2007, Powell et al. 2008, Munroe et al. 2013). Oysters grow slower upbay because environmental conditions, such as low salinity, are more frequently unfavorable in ways that trigger valve closure. Valve closure limits feeding opportunities (Galtsoff 1964) and eventually leads oysters to switch from aerobic to less efficient anaerobic respiration (Shumway & Koehn 1982, Michaelidis et al. 2005, Lombardi et al. 2013).

Although oysters cannot move postsettlement, the environment can change around them. Salinity at a given oyster bed will vary regularly in association with tidal flux, but sometimes changes more extremely due to a freshet: precipitation causing a rapid salinity decrease. Extreme storm events are expected to increase in frequency due to climate change (Najjar et al. 2000, 2009, Sanderson et al. 2019), which could alter the frequency and duration of extreme low salinity conditions at oyster beds. As a consequence, growth and survival may be reduced for oysters, with greater impacts at upbay beds because those beds are already near the lower limit of salinity tolerance during average conditions (Munroe et al. 2013). Fitness effects of episodic freshets may go beyond the mortality caused by low salinity, and have counter intuitive influences along the salinity gradient because of carryover effects. Carryover effects occur when the ability of an individual to grow and reproduce is affected by environmental experiences earlier in life (O'Connor et al. 2014). Understanding how previous environments could affect spat growth is important for managing oyster stocks in the face of increasing frequency of extreme storms. Additionally, a better understanding of carryover effects could support innovations in husbandry and culture techniques that seek to optimize growth of young oyster seed.

Growth rate of oysters is known to vary predictably with size such that smaller (early development) individuals exhibit faster growth (Mason et al. 1998). Oyster size increases relatively linearly in their first year of postsettlement growth, then slows as they age (Munroe et al. 2017). This occurs because smaller oysters have fewer homeostatic needs, or put another way, they have a lower surface area to volume ratio giving them a larger scope for growth (Shumway & Koehn 1982). Given that growth rate varies with oyster size, when investigating the influence of other factors (i.e., salinity) on growth, appropriate measures should be used to minimize the potentially confounding influence of size (Carroll & Finelli 2014).

Initially, as oysters grow postmetamorphosis, they build their shell flat to the settlement substrate, a morphology known as "spat." As they grow larger, they transition from growing flat to growing in a 3-dimensional shape. The triggers for this shape change have not been well-studied; however, in Delaware Bay, the shell size at which oysters transition from spat to 3-dimensional morphology (herein referred to as popped) increases from upbay to downbay (i.e., with increasing salinity)

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(Ashton-Alcox et al. 2016). Oysters with flat spat morphology presumably have a higher surface area to volume ratio, which may lead to different growth rates than a 3-dimensional spat (Harding 2007). Generally, multiple factors influence oyster growth rate simultaneously along a salinity gradient, and these covarying influences have not been adequately studied in the laboratory to date.

This study examined a subset of factors (salinity, salinity history, or shell morphology) that influence spat growth and how these factors interact with each other. This was tested using two experiments, one using wild spat placed into different salinity treatments in the laboratory (referred to as Wild Spat Experiment) and another using hatchery raised spat, which grew from larvae set in different salinities, then transferred into new salinities after 3 wk postset (referred to as Hatchery Spat Experiment). Wild spat provided observations linked to preexperiment conditions in the wild (larval dispersal, settlement, and early postset growth) to provide results of greater potential relevance to understanding effects of the natural estuarine gradient. Since wild spat potentially experience differences in food availability, predation, and disease along the salinity gradient, the Hatchery Spat Experiment used larval culture under standardized conditions to isolate just the influence of salinity at settlement and early postset. Knowing what factors alter spat growth provides a means of anticipating changes in growth due to environmental stressors.

MATERIALS AND METHODS

Wild Spat Experiment

The Delaware Bay is a tidally controlled Mid-Atlantic estuary located between the Delaware River and Atlantic Ocean (Fig. 1). The oyster beds in the Delaware Bay were divided into three zones based on average salinity. These salinity zones were used to delineate collection locations for spat used in the Wild Spat Experiment. Spat were collected using an oyster dredge, and only solitary spat smaller than 30 mm on a piece of shell were kept for this experiment (meaning that there was no crowding by adjacent spat as they grew).

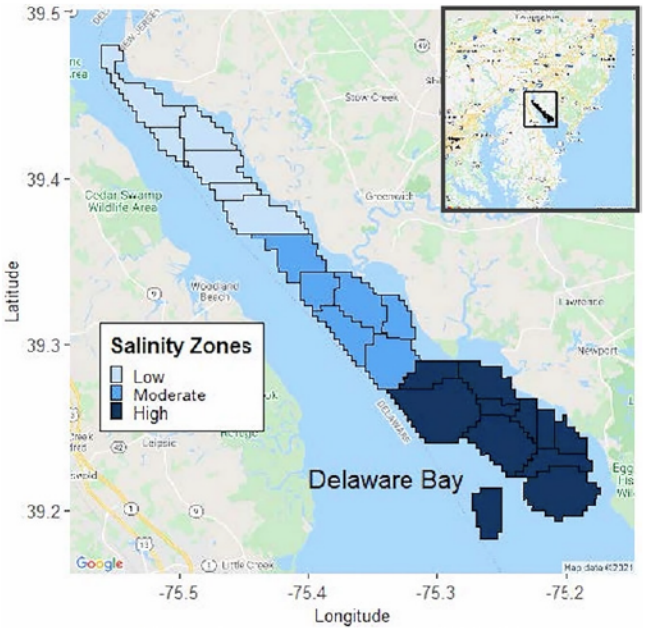

Figure 1. Map of Delaware Bay showing oyster bed regions, with colors indicating salinity source region from which spat were collected.

In year 1, 74 spat were collected on October 1, 2019, from the high salinity zone, and 42 from the moderate salinity zone (Table 1). Using modeled estimates of bottom salinity, from July to September 2019, spat experienced average daily salinities of 16–20 in the high salinity zone and 13–18 in the moderate salinity zone (Howlader 2022). The spat were returned to the laboratory, and haphazardly assigned to one of nine 40-L tanks filled with one of three experimental salinities (19, 13, and 7), with three replicates of each salinity treatment. The highest salinity treatment was consistent with salinity conditions in the high salinity zone, middle salinity treatment was consistent with the moderate salinity zone, and lowest salinity treatment could occur during a freshet event in either salinity zone. Tanks were filled with filtered seawater (filtered to 1 µM and diluted to each salinity treatment level with unchlorinated freshwater) and kept at ambient room temperature (averaging 22 ± 2°C). Partial water changes were performed weekly and one full water change was done halfway through the experiment. Length and width measurements were collected initially and weekly for 6 wk tracking the same individual over time using calipers. Similarly, shape observations were categorized weekly as flat, which was completely flush against the substrate, or popped where the shell growing edge was starting to curve upward. Shape was, therefore, a binary variable categorized as flat or popped.

In year 2, 83 spat were collected on October 1, 2020, from the high salinity zone, 19 spat from the moderate salinity zone, and 66 spat from the low salinity zone (Table 1). Using modeled estimates of bottom salinity, from July to September 2020, spat likely experienced average salinities of 18–19 in the high salinity zone, 14–17 in the moderate salinity zone, and 8.5–12.5 in the low salinity zone (Howlader 2022). The spat were haphazardly assigned to one of 12 10-L tanks filled with one of four experimental salinity treatments (22, 16, 10, and 6), with three replicates per salinity treatment. The highest experimental salinity treatment was representative of the salinity conditions consistent within the high salinity zone, the second highest salinity treatment was consistent with the moderate salinity

TABLE 1.

The number of wild spat from each source environment and allocated to each treatment in years 1 and 2.

	Salinity treatment	High salinity zone	Moderate salinity zone	Low salinity zone	Total
Year 1	19	24	15	–	39
	13	22	15	–	37
	7	38	12	–	50
Year 2	22	23	4	17	44
	16	21	4	16	41
	10	18	7	16	41
	6	21	6	17	44
	Total	167	63	66	–

zone, the third highest salinity treatment was consistent with the low salinity zone, and the lowest salinity could occur during a freshet. Tanks were filled with filtered seawater (filtered to 1 µM and diluted to each salinity treatment level with unchlorinated freshwater) and kept at ambient room temperature (24.3 ± 2.8°C) with full water changes once per week. Tanks were kept at ambient temperature. Length and width measurements were made initially and every other week for 6 wk tracking the same individual over time using calipers. As in the 2019 experiment, shape was categorized as flat or popped every second week for 6 wk.

In both years, spat were fed 0.6 mL of algae paste (Frozen LPB Shellfish Diet, Reed Mariculture™) daily, which was equivalent to approximately 15,000 cells/mL in 2019 and approximately 60,000 cells/mL in 2020. In 2019, spat were fed 0.3 mL of algae paste twice per day and in 2020, they were fed all 0.6 mL once per day. Temperature and salinity were recorded daily using a VWR Traceable Pen in all tanks, and temperature was recorded with a temperature probe every 15 min in three tanks. Spat that did not survive the duration of the experiment were removed from analysis ($n = 2$ in 2019, $n = 0$ in 2020).

Hatchery Spat Experiment

Two oyster strains were used to produce larvae for this experiment by performing two crosses. One, a Rutgers University disease resistant NEH (N1) line, hereafter referred to as the Selected Line, and the other, a cross between the disease resistant NEH strain and a Wild Delaware Bay line (D2), hereafter called the Hybrid Line. The Hybrid Line was spawned using 21 males and 39 females on June 10, 2020. The Selected Line was spawned 1 wk later using 39 males and 21 females on June 17, 2020. In both spawns, oysters were strip spawned and all eggs were rinsed and combined, whereas sperm was separated by individual. A sample of sperm from each individual male beaker was added to an aliquot of combined eggs. After fertilization, all embryos were combined and fertilization rate calculated (95% in the Selected Line and 93% in the Hybrid Line). This spawning method helps ensure equal opportunity of fertilization by sperm from each male and limits the chances of one male outcompeting the others. All larvae from the two crosses were hatchery raised in a salinity of 22 following standard hatchery protocols (Helm & Bourne 2004).

Upon reaching competency, eyed larvae were separated into four different salinity treatments (22, 16, 10, and 6) and allowed to set on plastic tags over 2 days. Once set, both oyster strains were held together in one of four 4-L treatment tanks, each with a different initial salinity making the initial salinity treatments unreplicated. Due to the difference in spawning date, the Selected Line were set 1 wk later than the Hybrid Line and were only in initial salinity conditions for 2 wk, whereas the Hybrid Line spat were in initial salinity conditions for 3 wk. Water was fully changed in the initial salinity tanks every other day and they were fed once per day using algae paste (Shellfish Diet 1800, Reed Mariculture™) targeting 110,000 cells/mL. After 2–3 wk in initial salinity conditions, 10 haphazardly selected spat from each of the four initial salinity levels and each oyster strain were photographed using an Infinity1 Lumenera camera with an Olympus SZX10 microscope, and the number of spat in each initial salinity tank was recorded. Spat from each initial salinity were fully crossed into four replicates each of four final salinity treatments (22, 16, 10, and 6) for a total of 64 1-L experimental units. Each unit received full water changes twice per week and was maintained in a 20°C temperature-controlled room. The spat remained in the final salinity treatments for 3 wk before being counted again and a haphazardly selected group of 10 spat from each experimental unit per oyster strain were photographed again. Photographs were analyzed using ImageJ (Schneider et al. 2012) to measure shell length, width, and area. These spat were within 5–6 wk of settlement, therefore, shell morphology was not recorded because all spat remained flat for the duration of the experiment.

Data Analysis

For the Wild Spat Experiment, shell area (mm^2) was calculated using length and width measurements (Eq. 1), whereas for the Hatchery Spat Experiment shell area (μM^2) was measured directly using ImageJ (Schneider et al. 2012). Change in shell area over time was used to calculate growth rate (Eq. 2). Due to unequal experimental design between years, interactions between salinity treatment and salinity zone source were unable to be tested. Additionally, mortality was calculated for each of the salinity treatments in the Hatchery Spat Experiment (Eq. 3). All statistical analysis was performed in R Studio (R Core Team 2020).

$$Shell\ Area = \pi \times length\,(mm) \times width\,(mm); \quad (1)$$

$$Growth\ Rate = \frac{final\ area - initial\ area}{time\,(days)}; \quad (2)$$

$$Mortality\,(\%) = \frac{number\ of\ spat\ at\ 6\ weeks}{number\ of\ spat\ at\ 3\ weeks} \times 100; \quad (3)$$

RESULTS

Wild Spat Experiment

None of the wild spat died during the experiment in either year. In year 1, experimental water temperature ranged from approximately 20°C to 24°C and did not differ between salinity treatments ($F_{(1, 691)} = 0.07$, $P = 0.8$). In year 2, experimental water temperature ranged from approximately 17°C to 28°C and did not differ between salinity treatments ($F_{(1, 430)} = 0.05$, $P = 0.82$). Because temperature did not vary among salinity treatments, it was not considered further. Likewise, growth rate was not affected by initial size ($n = 53$, $P = 0.15$, adjusted $r^2 = 0.02$; Fig. 2), therefore, initial size was not included in subsequent analyses. Growth rate decreased as salinity treatment decreased ($n = 51$, $P = 7.46 \times 10^{-4}$; Fig. 3); however, spat growth rate did not differ between salinity zones when compared with the high salinity zone ($n = 51$, moderate: $P = 0.40$; low: $P = 0.08$; Fig. 3). Additionally, spat shell morphology did not influence growth rate ($n = 51$, $P = 0.64$).

Hatchery Spat Experiment

The Hatchery Spat Experiment took place in a temperature-controlled room (temperature ranged from 19.5°C to 21.7°C) and, therefore, temperature was not tested as a factor influencing

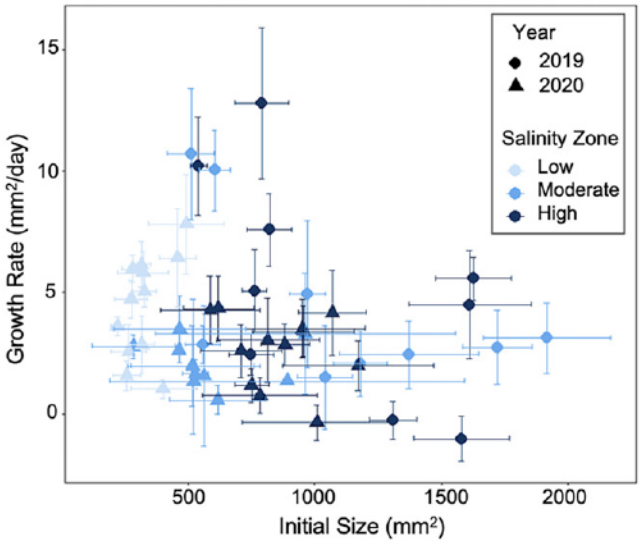

Figure 2. The influence of initial shell area (mean ± SE) on growth rate (mean ± SE) for wild spat. Each point represents the average growth and size per salinity zone from each experimental unit. Circles denote observations from 2019 and triangles denote observations from 2020. Colors represent the salinity zone from which the spat were collected.

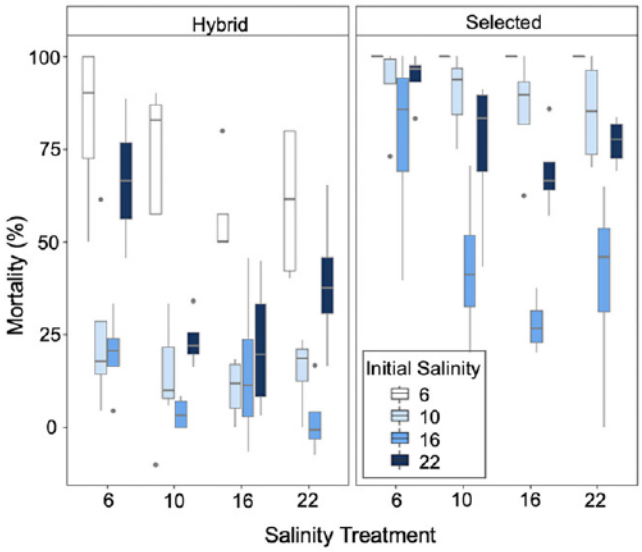

Figure 4. Percent mortality of the hatchery spat in the different final salinity treatments colored by initial salinity conditions. Panels display the Hybrid Line (left) and Selected Line (right). Boxes show upper and lower quartiles with median line inside box, and whiskers extend to 1.5 times the interquartile range from the upper and lower quartiles, respectively.

growth rate. Mortality increased as both initial salinity (n = 126, P = 0.01; Fig. 4) and final salinity (n = 126, P = 0.06; Fig. 4) decreased; however, no interaction between initial and final salinities (n = 126, P = 0.43) was evident. The Selected Line experienced higher mortality than the Hybrid Line (n = 126, $P = 7.35 \times 10^{-16}$; Fig. 4), with the initial salinity 6 experiencing 100% mortality across all final salinities and initial salinity 10 experiencing greater than 80% mortality across final salinities.

During the initial salinity period, spat had highest growth in the higher salinity treatments (22 and 16), moderate growth in 10 and lowest growth in 6. Growth rate was not significantly affected by initial size (n = 102, P = 0.43, adjusted $r^2 = -3.77 \times 10^{-3}$; Fig. 5), so initial size was not considered in further analysis. Growth rate decreased as final salinity decreased (n = 102, $P = 6.16 \times 10^{-7}$; Fig. 6), and as initial salinity increased (n = 102, P = 0.03; Fig. 6).

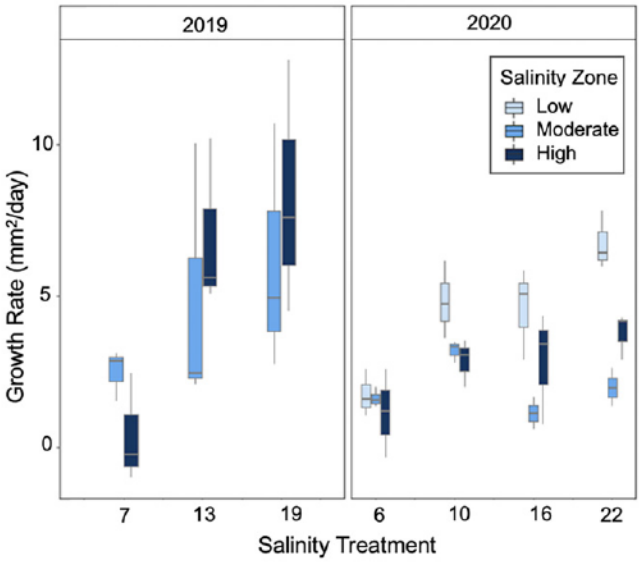

Figure 3. Wild spat growth rate as it varied by salinity treatment and by salinity zone (indicated by the colors). Panels display growth from the two experimental years: 2019 (left) and 2020 (right). Boxes show upper and lower quartiles with median line inside box, and whiskers extend to 1.5 times the interquartile range from the upper and lower quartiles, respectively. Spat from the low salinity zone were unable to be collected in 2019.

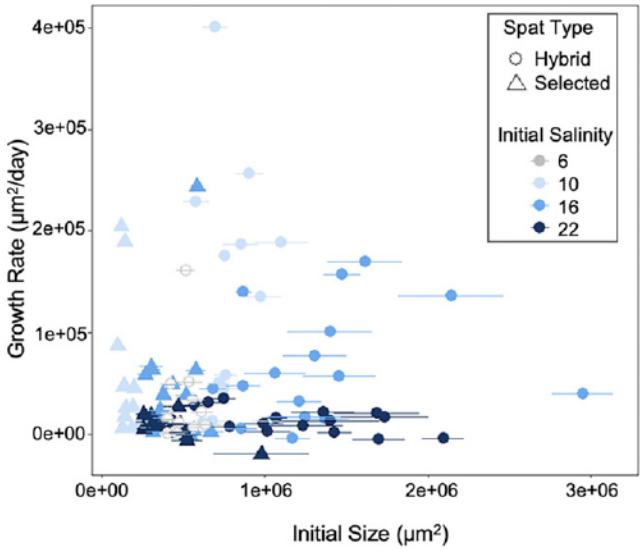

Figure 5. The influence of initial shell area (mean ± SE) on growth rate (mean) in hatchery spat. Error for growth rate could not be calculated because it reflected population level growth instead of individual growth. Each point represents the average growth rate and size per initial salinity from each experimental unit and including growth for the duration of the final salinity treatment. Circles denote observations from the Hybrid Line and triangles denote observations from the Selected Line. Colors represent the initial salinity conditions.

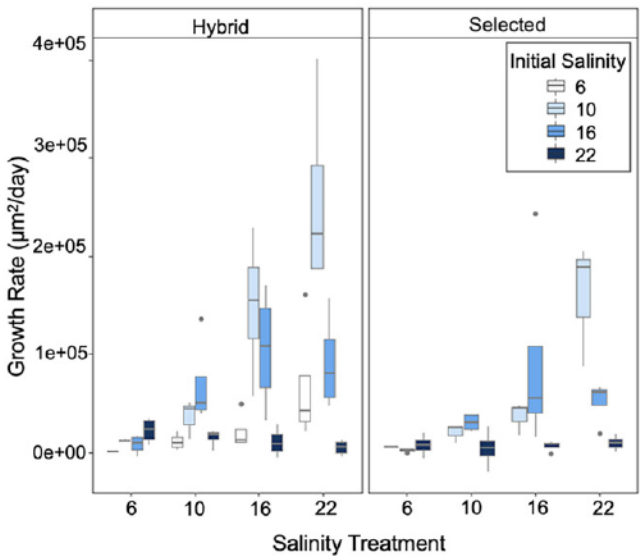

Figure 6. Hatchery spat growth rate as it relates to final salinity colored by initial salinity. Panels display the Hybrid Line (left) and Selected Line (right). Boxes indicate upper and lower quartiles with median line inside box, and whiskers extend to 1.5 times the interquartile range from the upper and lower quartiles, respectively. Spat from initial salinity 6 in the Selected Line did not survive the transfer into final salinity.

The interaction between initial and final salinity indicates a difference in growth rate in final salinity based on the initial salinity ($n = 102$, $P = 2.98 \times 10^{-4}$; Fig. 6). The most striking contribution to this interaction was that initial salinity 22 treatment showed uniformly poor growth at all final salinities, but the other initial treatments also varied in their response to final treatments. Both hatchery lines showed the largest plastic growth rate response to final salinity treatment when initial salinity was 10 (Fig. 6).

DISCUSSION

Salinity

In both the Wild and Hatchery Spat Experiments, our results showed a significant reduction of spat growth at lower salinity treatments. This finding is consistent with multiple observational (Kraeuter et al. 2007, Levinton et al. 2011, La Peyre et al. 2013) and experimental studies (Loosanoff 1953, McFarland et al. 2022) linking growth rate to salinity and its interaction with temperature. Oysters are osmotic conformers, which means their hemolymph gets adjusted to have the same osmotic pressure as the surrounding seawater. Their range of physiological plasticity is quite broad, often described as ranging across average salinities of 5–40 but with life stage, temperature, and acclimation also important factors determining limits (Galtsoff 1964, Barnes et al. 2007). Initially, after a large salinity reduction below the physiological capacity to conform, the rapid way for oysters to reduce osmolyte loss from their tissues is to close their valves (Anderson & Anderson 1975), immediately losing the ability to feed and ultimately transitioning to less efficient anaerobic respiration if the extreme low salinity is chronic (Munroe et al. 2013). Due to these physiological constraints, the stress and lack of feeding during low salinity can reduce growth, and even be fatal under extended duration of extreme low salinity exposure.

For eastern oysters, 3–5 salinity has been estimated as the threshold below which extended periods of exposure is fatal because valve closure prevents feeding and expelling of waste products, although temperature strongly interacts with salinity to determine lethality (Loosanoff 1953, Galtsoff 1964). Observations of survival across salinity gradients indicate that tolerance to extreme hyposalinity events is greater for smaller eastern oysters (LaPeyre et al. 2013, Munroe et al. 2013; but see McFarland et al. 2022). It is unknown to what degree tolerance to salinity extremes, and its variance across life history stages, is a function of variation in osmotic homeostatic abilities or vulnerability to extended anaerobic respiration (McCarty et al. 2020). The latter was hypothesized to be key by La Peyre et al. (2013) and Bible et al. (2020).

In both the Wild and Hatchery Spat Experiments, care was taken to choose salinities that were relevant to estuarine conditions but would avoid spat mortality. However, high mortality was observed for Hatchery Spat assigned to the lowest initial salinity (6). This high mortality could be attributed to a lack of selection for low salinity tolerance in the selected strain oysters (represented in both the "Hybrid" and "Selected" crosses). Alternatively, the higher mortality in the Selected Line could be attributed to a trade-off between increased disease resistance (the main selected trait) and low salinity tolerance (Munroe et al. 2015), or due to the smaller size and younger age of selected spat (1 wk difference in spawn date), possibly making them relatively more susceptible to poor environments (Dove & O'Connor 2007, McFarland et al. 2022). Although no mortality was observed during the Wild Spat Experiments, differential mortality in the bay prior to spat collection may have resulted in genetic differences, as has been seen in field studies (Hofmann et al. 2009), that could be related to growth potential in the groups of oysters used in that experiment.

Spat collected for the Wild Spat Experiment were slightly larger in 2019 than 2020 (Fig. 2) Assuming that the spat collected for the Wild Spat Experiment settled at the same time in both years, storm episodes with elevated freshwater input and consequent decreased salinity in 2020 (Robinson 2021, USGS 01463500 Delaware River at Trenton NJ 2021) could have depressed growth in 2020 spat before collection relative to 2019. The different conditions across years also could have influenced food supply and general physiological condition of spat. Oddly, the low salinity zone source population most subject to stress from these 2020 storms showed the greatest response to salinity treatments and overall, the highest growth rate.

In the Hatchery Spat Experiment, the Selected Line tended to respond worse to the experimental conditions in terms of growth and survival than the Hybrid Line, suggesting a possible heterosis effect from sheltering of recessive deleterious alleles in the hybrid offspring. The Selected Line was spawned 1 wk after the Hybrid Line, making the initial size of Selected Line spat slightly smaller, and possibly helping to explain the difference in performance if younger spat are generally less tolerant to salinity changes (McFarland et al. 2022). Size affects potential for growth due to individual scope for growth (Shumway & Koehn 1982); therefore, differences in initial size could confound the ability to detect the influence of other factors on growth if the initial size differs among treatment groups. Although initial

size was not controlled for in the Wild Spat Experiment or made uniform across spat in initial salinity treatments for the Hatchery Spat Experiment, initial size variation was not correlated with overall growth rate in either experiment. In future studies, attention should be paid to gathering sufficient spat to allow size to be controlled for among salinity zones.

Carryover Effects

The impacts of low salinity conditions can be exacerbated by stressful temperatures or limited food availability, especially in field experiments (Brown & Hartwick 1988). As much as possible, in both the Wild and Hatchery Spat Experiments, the measurement of salinity effects was done while removing other potential stressors by holding temperature and food constant in the laboratory. Both experiments involved a change of environment such that a range of prior salinity exposures, estimated or imposed, could potentially affect measured growth rate responses to final salinity treatments—carryover effects. In both the Wild and Hatchery Spat Experiments, the array of early salinity exposures started at settlement and extended for 2–8 wk postsettlement. Thus, the carryover effect here is based on conditions experienced by early postset spat versus a several week older spat stage. Only approximate predictions for early salinity exposures are possible for the Wild Spat Experiment given the uncertainty about when larvae settled, and of course salinity exposures during larval dispersal are unknown. In the Wild Spat Experiment, both the larvae and early postsettlement spat experienced natural environmental variation in salinity as well as temperature and food availability. Wild spat from different salinity zones showed different growth responses to salinity treatments but no statistical interaction was detected. In contrast, the Hatchery Spat Experiment involved growing larvae in constant benign culture environments until competency, then establishing the four "initial" salinity exposures at settlement and maintaining that environment over 2–3 wk before initiating the final salinity treatments. With this more controlled experimental design, the interaction between initial and final salinities was a significant factor, indicating growth rate differed in the final salinity treatments in response to the initial salinity exposures.

In all experimental contexts except 2019, wild spat that previously experienced relatively low salinity had the fastest growth overall and showed the greatest variance in growth (plasticity) across final salinity treatments. For the 2020 wild spat, it was the low salinity source spat that outperformed those from higher salinity zones in every salinity treatment except 6, where all sources had equally slow growth. The 2019 Wild Spat Experiment did not include low source samples. Considering the moderate and high salinity source spat in both years, the relative growth performance and degree of plasticity had the reverse ranking than that suggested by the low source results, with high source spat tending to grow faster than moderate source spat. In the Hatchery Spat Experiment, it was the 10 initial salinity exposure that had the highest growth rate and plasticity among final salinity treatments. Initial salinity 6 all died in the Selected Line and had the highest mortality in the Hybrid Line. Even though surviving Hybrid salinity 6 spat had low maximum growth (<50,000 μM^2/day compared with maximum values of 110,000 and 210,000 in the best performing groups), suggesting lack of recovery from initial salinity stress, they retained some plasticity as demonstrated by increasingly faster growth in higher salinities. Unexpectedly, initial salinity 22 had uniformly poor growth in both lines even though the larval cultures were at 22. We are unable to explain why this group grew poorly, even at final salinity 22.

The carryover effects that generated strong oyster growth performance after low salinity exposure in this study have few parallels in the literature. For invertebrates, carryover effects typically entail positive correlations between performance measured during early and later environments, often measured across a metamorphic transition (Pechenik 2006). Thus, larvae with poor food resources tend to have delayed settlement and relatively poor juvenile performance. For example, Hettinger et al. (2013) found significant effects on spat growth due to the initial pH conditions that larvae were cultured in, but not the final pH conditions the spat were moved to postsettlement. In cases where there is a reverse of fortune, such as previously starved fish "catching up" with nonstarved controls after feeding is resumed, the phenomenon is more typically described in terms of compensatory growth that can mitigate negative carryover effects (e.g., Morgan & Metcalfe 2001). Growth compensation was found in oyster spat at various times during extended diel-cycling hypoxia or pH (Keppel et al. 2016). In the cycling experiments, compensation was hypothesized to result from elevated feeding rates during the high oxygen part of the cycle, but compensation mechanisms after prior static stressors are much less clear (O'Connor et al. 2014). One potentially insightful mechanistic framework is hormesis, a process that explains overcompensation in growth as a disruption in homeostasis (Calabrese 1999). Even though mechanisms are opaque, the carryover and compensation effects found here for eastern oysters may have practical value. Similar to thermal treatments found to strengthen resilience of corals later in life (DeMerlis et al. 2022), results here suggest that low salinity exposures postsettlement may be able to generate hatchery cohorts with greater tolerance and growth plasticity when confronted later with a wide array of environmental conditions. Similarly, nonlinear responses to early life stressors need to be taken into account in models predicting oyster stock resilience. Experiments with more extended poststressor observations may help determine how long compensation effects continue and at what cost (e.g., Parker et al. 2015).

The initial size of the animals used in the Wild Spat Experiment suggest they likely spawned a few months before collection in the summer. In both years, spat were collected on October 1 and experienced similar average salinities before collection; however, differences in storm events between years may have generated functionally meaningful differences in salinity history of the two cohorts. There were two tropical storms (July 10 and August 4) in 2020 that affected the Delaware River watershed (Robinson 2021). The storms in 2020 each caused levels of freshwater discharge in the Delaware River to spike for 7–10 days afterward, probably at times when larvae would have been affected. Whereas in 2019, river discharge decreased steadily throughout the summer (USGS 01463500 Delaware River at Trenton NJ 2021). These differences in freshwater input and, consequently, patterns of salinity variation at the oyster beds between years could have contributed to differences in experimental wild spat responses to salinity treatments in 2019 and 2020.

Shell Morphology

Spat shell shape was only measured in the Wild Spat Experiment because the Hatchery Spat were too small to undergo a shape change. Even though the popped spat have a higher surface area to volume ratio (Harding 2007), we observed no relationship between shell morphology and growth. Spat growth did not vary with shell shape in this experiment, in contrast to results reported by Harding (2007) who found shape to affect shell length. However, Harding (2007) did not calculate a growth rate, and instead measured discrete differences in length, and made observation over a longer experimental duration. Harding (2007) also suggested that the size at which morphology changes was related to oyster density as well as temperature and salinity. Here, spat density was held constant among treatments.

CONCLUSION

Oysters are highly plastic and well-adapted to tolerate a variety of salinities, but not all estuarine salinities are conducive to the fast growth associated with high fitness. For the salinity range tested here, salinity positively affected growth to a degree that depended on salinity conditions experienced during settlement and early postset development. Even though low salinities (6–10) reduced growth rates relative to moderate and high salinity (16, 22), early exposure to low salinity generated the fastest growth across salinity treatments several weeks later in both Wild Spat and Hatchery Spat Experiments. These varying growth responses to short-term environmental change become increasingly important to understand as climate change brings more frequent and severe storm events to the Northeast US region (Najjar et al. 2000, Sanderson et al. 2019, Maxwell et al. 2021), which generate perturbations in salinity that could affect population dynamics of oyster beds regionally.

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