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Evaluating the influence of cage motion on the growth and shell characteristics of oysters (*Crassostrea virginica*) among several gear types

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ABSTRACT

An influx of new oyster culture gear provides growers with an expanded ability to grow oysters throughout the water column. Each gear type is exposed to a different regime of physical forces, which is thought to affect oyster production differently; however, there is a poor understanding of the physical conditions inside cages and how they influence the production rate and quality of oysters. A greater understanding of the fundamental relationships between cage motion, oyster growth, and shell shape could help to improve the efficiency of off-bottom oyster production. Such understanding is critical for tailoring gear selection and tuning gear performance to suit grower needs. To address this void, cage motion, internal oyster movement, and oyster growth among three common cultivation methods (Virginia-style bottom cages, Seapa® long-line baskets, and floating cages) were monitored over a single growing season to clarify the role of the physical environment on oyster performance (shell and tissue growth). The averages and variance in motion among each cultivation method were noticeably different, which resulted in significant differences in the growth rate and quality of oysters they produced. Movement of the floating cages and long-line baskets could largely be explained by wind waves generated from a single direction in the field ($r^2 = 0.49$, $r^2 = 0.36$, respectively), while bottom cage movement was far less affected by wind waves. The changes in physical conditions inside each cultivation method demonstrated a trade-off between shell growth rate (a metric of time to market) and shell and meat quality (representative of crop value). These results can help inform growers wishing to strategically adopt cultivation methods that are most aligned with their production goals.

1. Introduction

Within the global aquaculture industry, oyster aquaculture has been one of the fastest growing sectors (Botta et al., 2020). Off-bottom culture of oysters, which includes bottom cages, mid-column gear, and floating cages, has been increasing steadily in areas such as Maryland and Virginia (van Senten et al., 2019) and developing in areas such as the Gulf of Mexico (Walton et al., 2013a). Off-bottom aquaculture typically produces more uniform crops with a more desirable shell shape, which typically commands a premium from consumers in the raw, half-shell market (Mizuta and Wikfors, 2019). While oysters grown using off-bottom culture methods are believed to enhance the value of oysters and the overall profitability of a commercial operation, there is a much higher initial cost and considerable risk involved with this method (Huang and Lee, 2013; Engle et al., 2021). Factors that should be considered with starting-up an off-bottom farm include identifying a suitable area to lease and choosing the appropriate gear type, husbandry method, oyster species, and genetic family needed for that lease space (Walton et al., 2013a, 2013b). While some important water quality characteristics for growing oysters can be easily assessed (e.g., temperature and salinity), other site characteristics and how they interact with specific gear types are more cryptic. Specifically, there is a limited understanding of how physical forces influence oyster growth rate and product quality, especially within the context of caged oysters. There-

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fore, it can be difficult for growers to account for the role of physical forces when evaluating a site or predicting its effects on their yield.

Since oysters are filter feeders, they rely on the ambient physical environment to deliver food for growth and development (Grizzle et al., 1992; Lenihan et al., 1996; Wilson-Ormond et al., 1997; Lee et al., 2017; Cranford et al., 2011). While the relationship between oyster ecophysiology and ambient conditions has been well researched, how the environment interacts with gear and the animals growing within it is far less understood (Campbell and Hall, 2018; Gray et al., 2021). In past experiments and hydrodynamic models, the presence of aquaculture gear altered the local hydrodynamics (Grant and Bacher, 2001; Gaurier et al., 2011; Duarte et al., 2014; Dong et al., 2020), indicating it may be an important factor dictating oyster production (Stevens and Petersen, 2011; Lin et al., 2016; Liu and Huguenard, 2020). The growth and quality of oysters have also been found to change across culture gear types (Comeau, 2013; Mallet et al., 2013; Walton et al., 2013b; Mizuta and Wikfors, 2019; Thomas et al., 2019; Haché et al., 2021), although the mechanism driving growth differences was not identified. While the change in hydrodynamics and oyster production has been documented independently, few field studies have examined how gear motion varies among commercially available oyster cages. Additionally, relating internal cage conditions to oyster performance (i.e. meat growth and shell growth rate or shape) remains unresolved, but should improve management and production. Indeed, monitoring hydrodynamics among finfish farms has led to improved cage design (Klebert et al., 2013; Dong et al., 2020), production (Rabe et al., 2020), and environmental management (Henderson et al., 2001; Navas et al., 2011; Mayerle et al., 2020; Hartstein et al., 2021).

This study was designed to compare the internal movement of oyster cages and oyster performance across a series of commonly used oyster aquaculture cultivation methods (bottom, long-line, floating) in a low-energy environment. Using inexpensive accelerometers, we assessed physical forcing by monitoring the movement of both oyster cages as well as developed an indirect method to quantify internal motion of oyster with the cage. Oyster performance was monitored by tracking mortality, shell growth, tissue condition, and the shape ratio of oysters to assess oyster growth and quality using commercial standards (Galtsoff, 1964; Ward et al., 2005). The results of this work helped clarify how physical forces affect yield variability across various grow-out methods used in off-bottom oyster aquaculture. We also identified key physical factors that explained the variability in growth and quality between different culture methods.

2. Methods

Triploid, low salinity-tolerant oysters (LOLA), produced by Hooper's Island Oyster Company and wintered at the Horn Point Demonstration Farm (HPLDF), were deployed from June 2020 to November 2020 using three common grow-out methods (Virginia-Style bottom cages, Seapa® long-line baskets, OysterGro® floating cages). Throughout the duration of the experiment, oyster, and cage motion was monitored continuously. Oyster growth was measured at the middle and conclusion of the deployment period and condition was assessed immediately after the end of the experiment.

2.1. Study area

The field study was conducted at HPLDF, which is located along the southwest bank of the Choptank River, which has a water depth range of 1–2 m and is the largest tributary on the northeastern shore of Chesapeake Bay. The farm site is located upstream from a jetty and a large pier, which slows water flow through this area during incoming tides. During outgoing tides and wind-driven currents, water flow can be stronger, but typically the water velocity in the farm does not exceed 10 cm/s.

2.2. Experimental design

Oysters were deployed on a specialized line fit for holding bottom, long-line, and floating cages in parallel (Fig. 1). Three grow-out methods were used that span the vertical distribution of the water column (Virginia-Style bottom cages, Seapa® long-line baskets, OysterGro® floating cages). Three bottom and floating cages, and six long-line baskets were deployed along the line in two-meter intervals. The cages were not

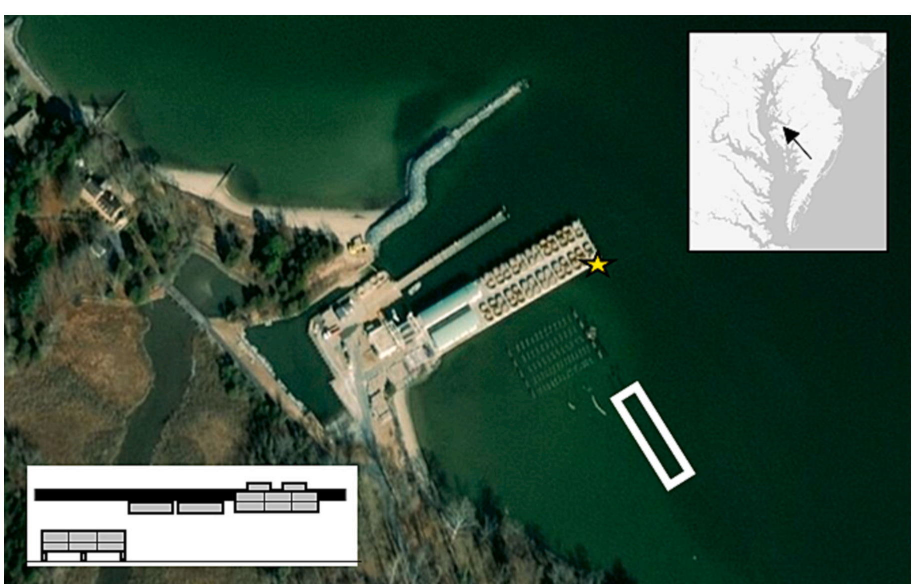

Fig. 1. Areal map of the experimental site in HPLDF and farm location on Choptank River (arrow). The location of the experiment is outlined in white and the location of the YSI is marked by the yellow star. The bottom left corner has a depiction of how cages were deployed during the experiment. One bottom cage (left) was deployed directly below the line followed by two Seapa® long-line baskets (center), then one OysterGro® floating cage (right). This pattern repeated three times along the same line for replication. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

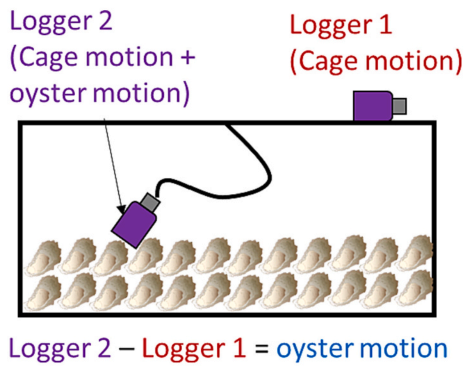

Fig. 2. Depiction of how HOBO accelerometers were placed in each cage. The first accelerometer was attached tightly to the exterior of the cage while the second was tethered to the inside center of the cage, free to move throughout the cage.

randomized since there were no obvious differences between cages across the footprint of the experiment and a randomized design was not practical for this specialized longline design. A single bottom and floating cage can hold up to six Vexar bags (three bags spaced evenly across two rows), however we only stocked three bags in the lower row of each cage. The three bags per cage were averaged to act as one replicate cage. Bottom cages are held eight inches above the seafloor and the floating cages are held at the surface of the water column. Seapa® long-line baskets were deployed approximately one foot below the surface of the water in three pairs. Since the long-line baskets are singular and thus hold roughly 1/3 of the oysters that were stocked in the floating and bottom cages, each pair of long-line baskets were averaged to act as one replicate to better match the sample size of the other cage types. At the start of the experiment, oysters were graded, and each bag was stocked with approximately 900 oysters per bag with an average shell length of 16.2 +/− 0.83 mm. This stocking density was initially light (~10% volume of each bag) compared to commercial standards and increased to nearly 50% volume by the end of the experiment. Stocking density was initially low to prevent having to remove animals throughout the season and intentionally compromise the sample size per bag. Despite a large natural set of biofouling accumulation on cages, there was no intentional effort to manage biofouling on cages however, there was some reduction in biofouling that occurred when cages were handled.

2.3. Oyster growth and performance

Oyster performance was assessed by taking measurements of the shell length (the distance between the hinge and the furthest point on the mantle), shell width (the widest distance perpendicular to the shell length), and shell depth (the widest point from the top shell to the bottom shell) of 150 random individuals of the whole population at the beginning of the experiment and 30 random individuals per bag in the middle, and end of the field deployment. Condition index of ten individuals was performed using methods by Lawrence and Scott (1982), (Eq. 1). Condition index is a common metric used as a proxy to describe the relative meat quality of an oyster compared to its shell weight. We assumed condition index to be positively correlated with oyster quality in our study, however, the specific range of optimal condition indexes likely varies among consumers and a standard, optimal condition index value has not been established. Using the shell measurements, a series of shell indices were calculated to assess the quality of the oysters grown in each method. Specifically, shape index, (Eq. 2), width index (Eq. 3), and elongation index (Eq. 4) were calculated (Galtsoff, 1964; Ward et al., 2005). Again, these shell indices are general metrics used for characterizing the relative quality and value of oysters grown and vary based on personal preference and market interests. The grading of the shape index scores was based on Ward et al. (2005) and Galtsoff (1964) where an average shape index score was 3 and shell shape was considered poor when >3. For the elongation index, values close to 1 were optimal, but values above 1 suggested a more elongated oyster, and values below 1 were rounder (Ward et al., 2005). Width index was considered 'good' above 0.63 (Brake et al., 2003).

$$CI = \frac{dry\ tissue\ weight\ (g)*100}{dry\ shell\ weight\ (g)} \quad (1)$$

$$SI = \frac{shell\ length\ (mm) + shell\ depth\ (mm)}{shell\ width\ (mm)} \quad (2)$$

$$WI = \frac{shell\ width\ (mm)}{shell\ length\ (mm)} \quad (3)$$

$$EI = \frac{2*shell\ length\ (mm)}{3*shell\ width\ (mm)} \quad (4)$$

2.4. Physical forcing

Two accelerometers (Onset HOBO Pendant G Logger: UA-004-64) per cage were deployed continuously throughout the experiment to monitor the movement of cages and the oysters they held in ten-minute intervals (Fig. 2). The first accelerometer (logger 1) was tightly fastened to the exterior of each cage and basket to monitor only cage and basket motion (gear only). The second accelerometer (logger 2) was tethered to the inside of each bag or basket and allowed enough slack to move freely inside each container to simulate oyster and cage motion (cage + oyster). The difference between the two accelerometers (logger 2 – logger 1) was considered representative of the net movement of one oyster inside the bag. Values that exceeded four standard deviations from the mean were removed from the dataset prior to analysis. To create a time series of cage motion that could be directly compared to wind direction and

Table 1
Southern and western winds have a stronger linear correlation with cage movement. Summary of the r^2 from each linear regression of cage motion and wind speed illustrated in Fig. 7 (* = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$).

	Range of Direction (degrees)	n	Floating Cage	Longline Basket	Bottom Cage
All data	0–360	805	0.241 ***	0.143 ***	8.62×10^{-3} **
North	337.5–22.5	64	3.05×10^{-3}	0.110 **	−0.0132
Northeast	22.5–67.5	79	-5.86×10^{-3}	0.0259	-5.08×10^{-3}
East	67.5–112.5	165	0.0338 *	0.0130	0.0490 **
Southeast	112.5–157.5	128	0.0366 *	-5.70×10^{-3}	5.14×10^{-3}
South	157.5–202.5	90	0.232 ***	0.197 ***	-8.95×10^{-3}
Southwest	202.5–247.5	89	0.487 ***	0.360 ***	−0.0139
West	247.5–292.5	87	0.243 ***	0.326 ***	0.0590 *
Northwest	292.5–337.5	103	0.164 ***	0.0571 *	0.0617 **

speed, data gaps were filled using the 'forecastML' package in R to produce data values at 10-min intervals. Once the time-series was established, four-hour averages, maximums, and minimums were calculated in parallel with the wind data to allow for further analysis.

2.5. Environmental monitoring

Water quality data, including water temperature, salinity, dissolved oxygen, and chlorophyll-a, were gathered from a nearby long-term fixed station (station ET5.2) and monitored monthly by the Maryland Department of Natural Resources' Eyes on the Bay Program (6.3 km upstream from the study site). Water quality data was averaged with depth and used to identify any points where average water quality may have influenced the growth of oysters. Wind speed and direction data were also obtained from station CAMM2 in Cambridge, MD from the National Data Buoy Center (5.7 km from the study site). To produce a 4-h average, maximum, and minimum of wind speed and wind direction, wind direction was converted to radian units. Once converted, averages, minimums, and maxima were calculated at four-hour intervals, then wind direction was converted back to degree units. Additionally, data were binned by average cardinal direction as shown in Table 1 to create eight divisions in direction.

2.6. Statistical analysis

The assumptions of normal distribution and homoscedasticity were tested using a Levene test and a Shaprio test. Most of the oyster growth data produced were not found to be normally distributed despite attempts to transform data, so non-parametric statistical approaches were used. Kruskal-Wallis tests with Scheirer-Ray-Hare Adjustments were used to determine statistical significance between the oyster performance and physical conditions among gear types. Of the comparisons that were significant, a post-hoc Dunn test using a Bonferroni correction was used to identify treatments responses that were significantly different from others.

To compare wind patterns and cage motion, each four-hour averaged time series were combined, and a correlation matrix was produced of all factors using the 'PerformanceAnalytics' package in R. Additionally, all data were binned into eight groups separated by the average cardinal wind direction. Within each bin, linear regression models were produced to compare the strength of the linear relationship between the average wind speed at each direction against the maximum cage movement experienced.

Lastly, a principal component analysis (PCA) was produced to determine any separation in physical conditions and changes in growth associated with different culture techniques. Since the number of measures were not equal for each parameter analyzed in this experiment, the PCA integrated the average shell growth, condition index, mortality, and physical parameters from each treatment to plot one point per treatment that was representative of all the data collected. The separation between points in scatter plot of the two major principal component axes described how the growth performance and physical environment were collectively different between these culture methods. All statistical metrics were based on an alpha value of 0.05.

3. Results

Internal conditions of three oyster culture methods and the potential implications on oyster growth and quality were evaluated. By growing oysters across a range of culture methods that span the depth of the water column, we aimed to determine if there were differences in the physical characteristics among cage systems and determine if those differences impose constraints on oyster growth or crop quality.

3.1. Environmental monitoring

Water quality varied greatly in HPLDF over the experimental period (Fig. 3). Water temperature decreased over the course of the study without any large, acute changes. Water temperature at the beginning of the experiment in June averaged near 30 °C and decreased to 10 °C by November. Salinity fluctuated across the time series but overall trended positively with time, then decreased suddenly in November. The observed range and seasonal trend in salinity (9–11 ppt) was comparable to the historic salinity observed in this region of the Chesapeake Bay from 1985 to 2020 (9–12 ppt) (Maryland Department of Natural Resources, 2022). A small increasing trend in optical dissolved oxygen

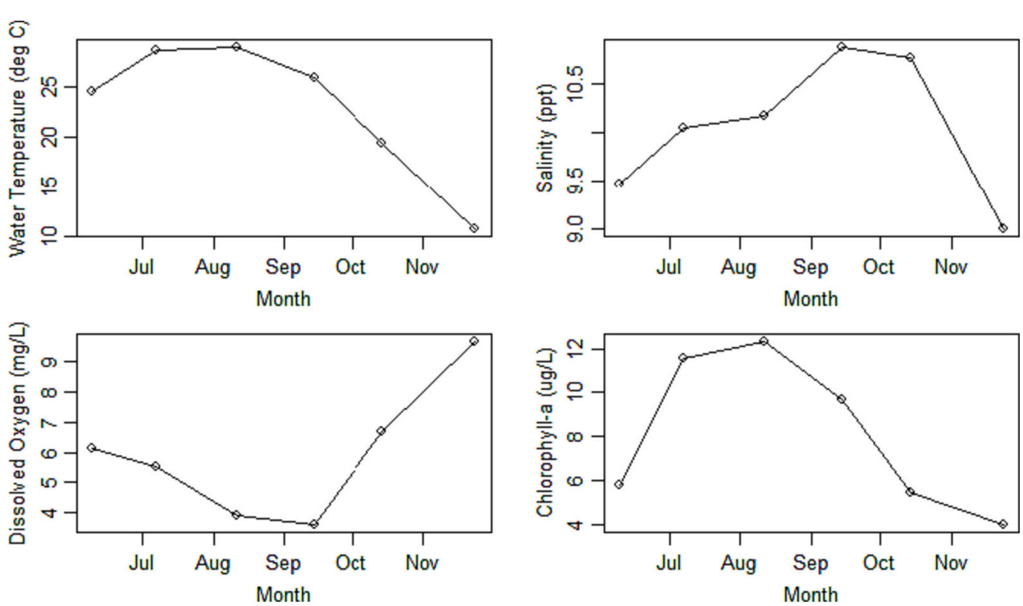

Fig. 3. Water quality fluctuated seasonally based on monthly point measurements from a nearby long-term fixed station (station ET5.2), which is monitored monthly by the Maryland Department of Natural Resources' Eyes on the Bay Program. Water quality was sampled monthly and was integrated with depth (0–10 m).

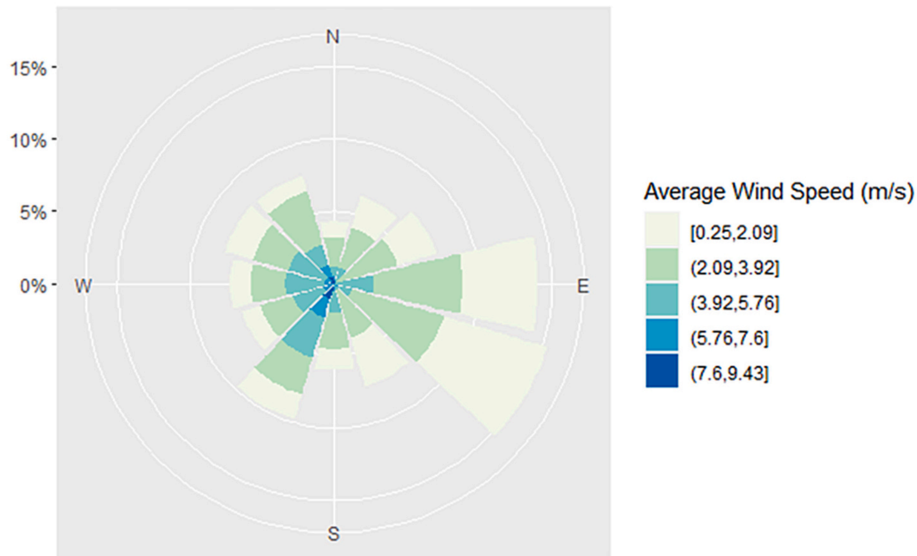

Fig. 4. Wind was most prevalent from the east but stronger winds occurred out of the southwest. Wind rose plot of the four-hour average wind speed at the nearby meteorological buoy, CAMM2, which is monitored by the National Data Buoy Center. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Average and confidence interval of all relevant parameters measured in this study separated by cultivation method. An alpha value of 0.05 was used to calculate confidence intervals. Superscript letters indicate significant ($p < 0.05$) treatments.

Culture Method	Shell Length (mm)	Shell Width (mm)	Shell Depth (mm)	Shape Index	Width Index
Bottom Cage	60.6 ± 2.41^{a}	48.6 ± 0.92^{a}	19.0 ± 0.34^{a}	1.65 ± 0.020^{a}	0.808 ± 0.011^{a}
Longline Cage	61.0 ± 1.56^{a}	50.6 ± 1.20^{a}	20.4 ± 0.64^{b}	1.61 ± 0.025^{b}	0.837 ± 0.014^{b}
Floating Cage	54.5 ± 1.01^{b}	48.9 ± 0.84^{a}	20.0 ± 0.38^{b}	1.53 ± 0.015^{c}	0.902 ± 0.009^{c}
Culture Method	**Elongation Index**	**Condition Index**	**Percent Mortality**	**Cage Motion (m/s^2)**	**Oyster Motion (m/s^2)**
Bottom Cage	0.836 ± 0.0111^{a}	7.19 ± 0.541^{a}	10.0^{ab}	10.0^{a}	0.539^{a}
Longline Cage	0.807 ± 0.0141^{b}	7.92 ± 0.528^{b}	21.8^{a}	10.1^{b}	0.427^{b}
Floating Cage	0.745 ± 0.0079^{c}	8.38 ± 0.674^{b}	6.0^{b}	9.82^{c}	0.279^{c}

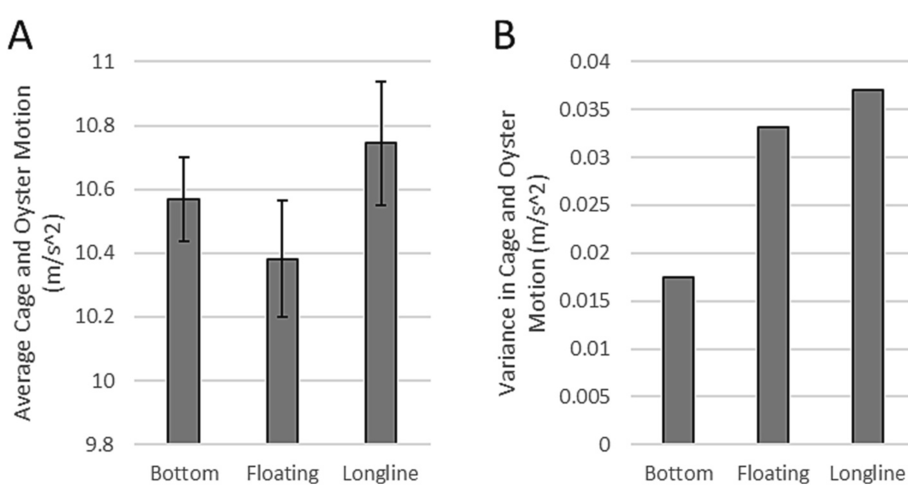

Fig. 5. Cage and oyster motion (A) and variance in motion (B) were the greatest among longline cages. Average and variance in the total movement was calculated from the 10-min averaged time series. Error bars represent one standard deviation from the average.

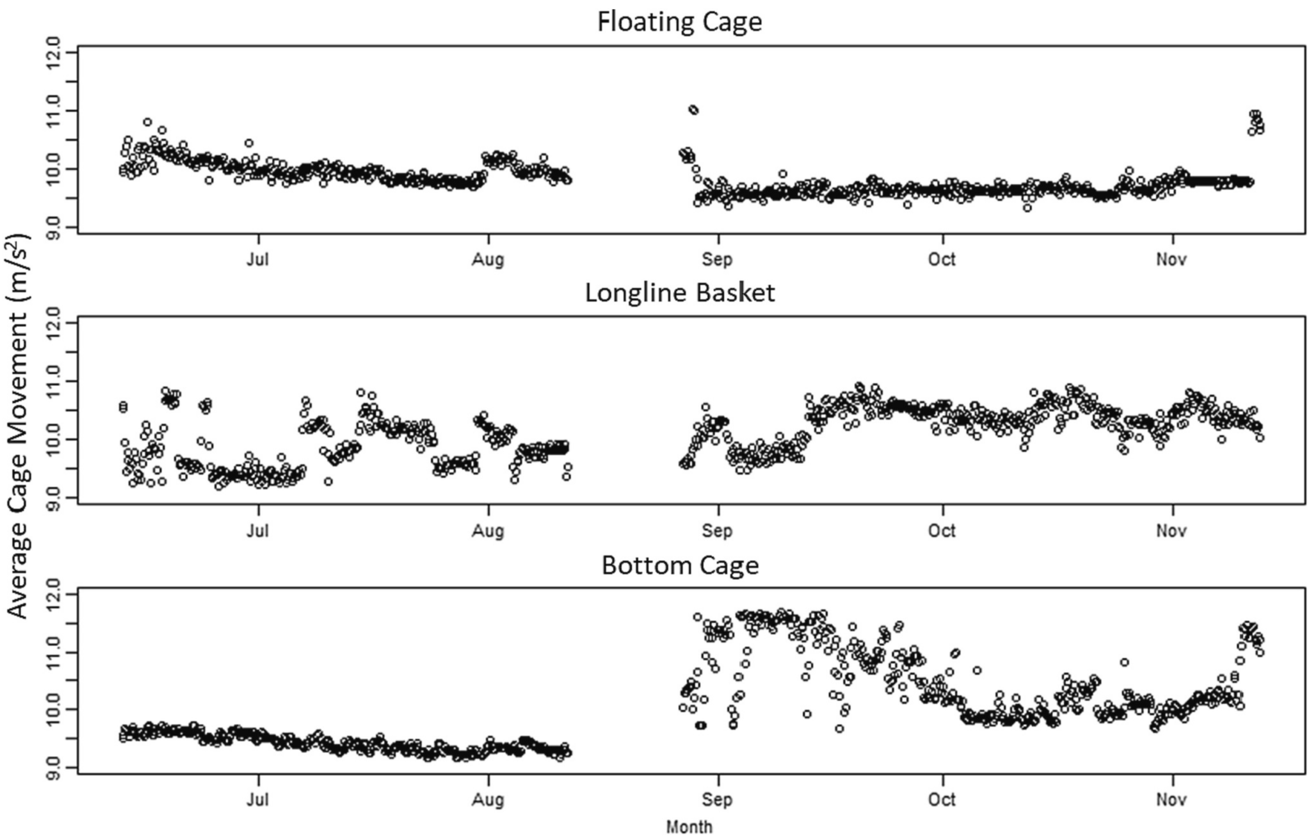

Fig. 6. Cage movement of floating (top), longline (middle), and bottom cages (bottom) varied greatly across the time series and showed no temporal trend. The data gap in the center of the time series occurred between accelerometer deployments.

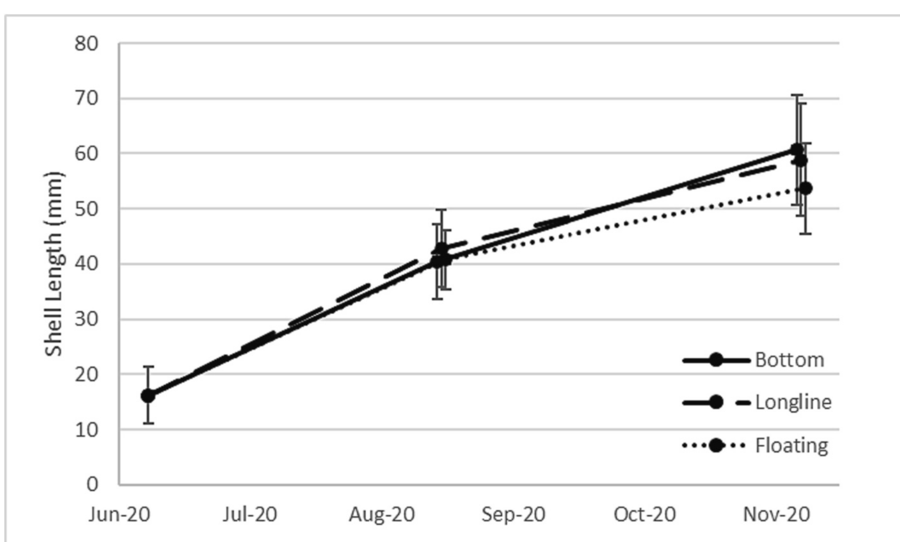

Fig. 7. Shell length of oysters per cage type began to deviate after the second sampling point. Averages consisted of 30 measurements per bag for each gear type included in the sample ($n = 270$ for floating and bottom cages, $n = 180$ for floating cages). Initial shell length was determined before splitting oysters into respective treatments, hence why all treatments have an identical initial shell length. Error bars represent one standard deviation among the mean. Sampling points were jittered to better show the individual points.

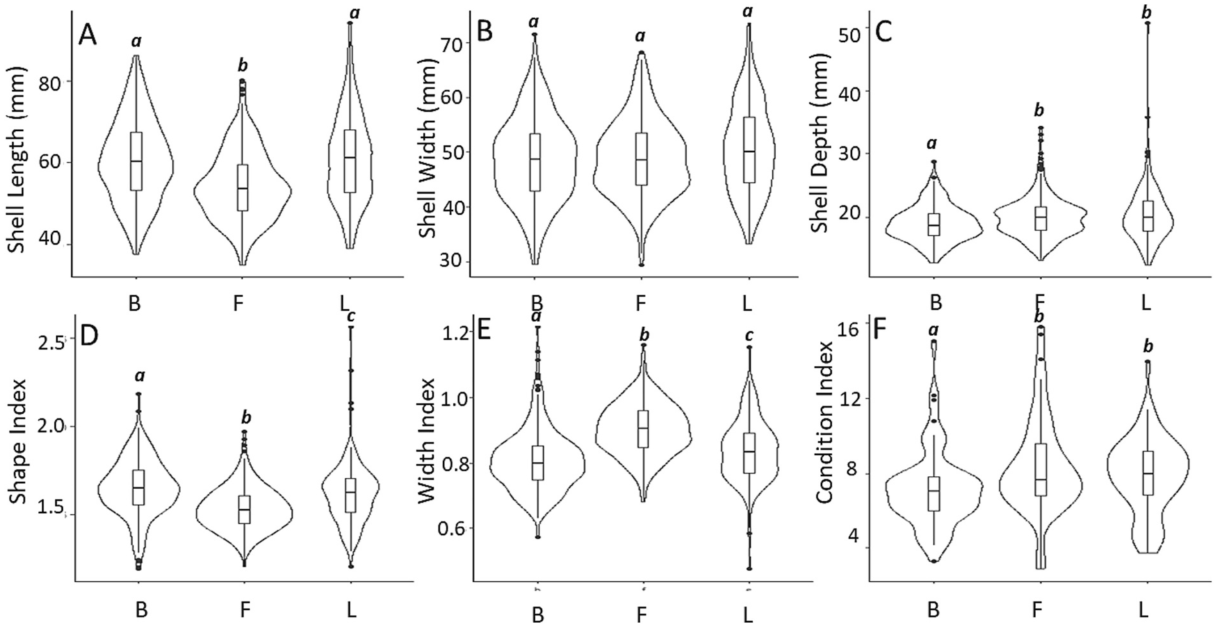

Fig. 8. While shell growth did not vary much between cages, the morphology and meat condition of oysters between gear types changed greatly. Violin plots of each measured shell performance metric for bottom cages (B), floating cages (F), and long-line baskets (L). A boxplot is centered within each violin and the spread of the violin represents the density of measurements along the y scale. Italicized letters above each violin indicate significantly separate treatments according to Kruskal-Wallis and Dunn tests ($p < 0.05$).

(ODO) was shown with high fluctuations ranging from 3 to 10 mg/L. Dissolved oxygen reached a minimum in the late summer dropping below 4 mg/L. Historic dissolved oxygen reaches an average minimum of 5 mg/L but follows a similar trend as our seasonal data. There was no seasonal trend in wind speed over time (Fig. 4). Winds predominantly came from the east and southeast; however, the stronger winds came from the west and southwest. Average wind speed on site was 3.14 m/s with a standard deviation of 1.68 m/s.

3.2. Physical forcing

There were significant differences in the average and variance in the cage movement among each cultivation method (Table 2). The long-line system had the greatest average cage motion followed by the bottom cage, then the floating cage (cage motion = 10.1 m/s^2, 10.0 m/s^2, 9.82 m/s^2, respectively, $p < 0.001$). However, net oyster movement within cages was greatest among the bottom cages, followed by the long-line baskets, then the floating cages (oyster motion = 0.539 m/s^2, 0.427 m/s^2, 0.279 m/s^2, respectively, $p < 0.001$). The variance in oyster movement per culture method was not proportionate to their respective average. While the long-line baskets had both the highest average and variance in cage plus oyster motion, the bottom cage had the least variance in cage motion and the floating cage had a similar variance comparable to the long-line baskets (variance = 0.037 m/s^2, 0.017 m/s^2, 0.033 m/s^2, respectively, Fig. 5b).

Cage movement for each gear type does not have any consistent temporal trend (Fig. 6). However, the motion of cages changes sporadically throughout the grow-out season. While the floating cages maintained consistent motion, the longline baskets showed an oscillatory pattern that increased over time. Additionally, the motion captured in the bottom cages increased greatly in the second half of the deployment compared to the first half. There was a minor positive significant correlation between 4-h maximum cage motion and 4-h average wind speed for all three cage types. The strength of the correlation declined with vertical position of gear in the water column (correlation coefficient: floating cage = 0.49, longline basket = 0.38, bottom cage = 0.10, $p < 0.01$ in all treatments). The strength of the correlation between the 4-h maximum cage motion and 4-h average wind speed was also dependent on wind direction. Winds from the south through the northwest had larger, significant correlations than winds from the north and eastern directions (Table 1). The regression slope of cage motion as a function of wind speed from the south and west was also higher than winds from the north and east (Fig. A.1).

3.3. Oyster performance

Mortality values for each gear type can be found in Table 2. The total mortality of oysters grown in long-line baskets were significantly greater than that of floating cages ($p = 0.034$); however, neither were significantly different from the mortality from bottom cages ($p = 0.11$, $p = 0.50$, respectively). Table 2 lists the average value of each measured attribute of oyster performance per treatment.

Oyster growth and performance were highly variable among each tested culture method. Based on the growth trends (Fig. 7), the growth of the oysters initially diverged between the second and third sampling dates. The shell length of the bottom and long-line oysters was significantly greater than those grown in floating cages ($p < 0.001$) (Fig. 8). While the mean shell length of the bottom and long-line basket was similar ($p = 0.096$), the floating cage had a smaller standard deviation in final shell length (bottom = 10.03 mm, long-line = 10.64 mm, floating = 8.47 mm). Shell width varied significantly among all treatments ($p = 0.041$; Fig. 9b). Longline baskets grew oysters with the largest shell

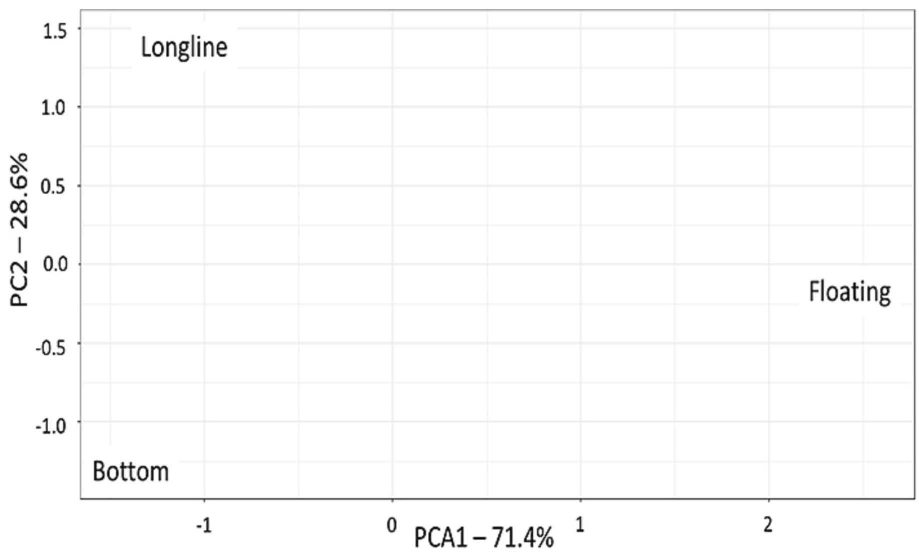

Fig. 9. PCA of the two primary components dictating oyster performance and physical forcing for each cultivation method.

width followed by floating, then bottom cages. Differences in shell depth were found to be statistically significant across all treatments ($p < 0.001$) and the long-line and floating cages were found to grow oysters with significantly deeper shells than in bottom cages ($p < 0.001$).

All shell shape indices varied significantly among treatments ($p < 0.001$). Shell shape indices for each gear type can be found in Table 2. The shape index of all treatments was <3 suggesting they are an appropriate shell shape for the half-shell market. However, the width index was >0.63 and the elongation index was less than one indicating that shells from all gear types were round and of 'good' quality according to Brake et al. (2003). Bottom cages exhibited the greatest shell shape index score (1.65) and elongation index (0.836), but the lowest width index score (0.808). Floating cages scored the highest in width index (0.902), but the lowest in shape index (1.53) and elongation index (0.745). Longline cages had median scores for all shell indices. Condition index of oysters grown in floating cages and long-line baskets was significantly greater than that of bottom cage oysters ($p = 0.013$, $p = 0.021$, respectively).

The results of a PCA illustrate the separation of oyster growth parameters and the ambient physical environment measured (Fig. 9). Across the first principal component (PCA1), similarities between the bottom and long-line baskets were found, which explained most of the difference in environment between these treatments (71.4%), however, there was a notable separation between all three cage types in the second component (PCA2) which accounted for 28.6% of the variance in the data.

4. Discussion

Within HPLDF, a relatively low-energy culture site, each oyster cultivation method responded differently to ambient physical forces, which led to different culture conditions and oyster performances among the tested gear. The gear types used in the study differ in their vertical position along the water column, which informs their response to winds and ultimately wave action that drives cage and oyster motion. The movement of oyster cages was influenced significantly by wind-driven wave action, but the strength of this relationship was reduced with water depth. The intensity of the effect of wind speed on cage movement was also influenced partially by wind direction, likely due to a combination of cage orientation and the surrounding fetch across the site location. As a result of the differences in cage movement due to environmental forces, each cultivation method produced oysters at varying growth rates with different shell dimensions. By accounting for physical forces acting on gear, such as wind-driven waves, this work demonstrates how growers may be able to more precisely manage crops to meet production goals when selecting and positioning gear or choosing grow-out sites.

The way that cages are deployed in the water column can create different types of physical resistance and can influence the average and variance of movement. For example, bottom cages are partially buried in bottom sediment, which was found to be most resistant to natural forces compared to the other gear types in this study. Any observed motion from this gear type is likely from the Vexar bags inside the bottom cage frame which would be accounted for by the oyster accelerometer unintentionally, explaining the large amount of oyster movement detected on this gear type. Unfortunately, we did not monitor the direct movement of the vexar bags themselves and future trials should consider bag movement as well to tease out oyster movement from that of the cage and the bag.

During early September, there was anomalously high cage motion in the bottom cages compared to the rest of the time series. It is likely that this behavior is a result of strong vertical mixing in the water column that is often present in the Chesapeake Bay at this time and is observed when dissolved oxygen rapidly depletes (Scully, 2016; see Fig. 3). While Scully (2016) observes this phenomenon in deeper waters (0–40 m), there is mention that there is a lagging northward advection of this signal. Furthermore, this northward advection might be strong enough to create lower-depth disruptions in shallower waters for the duration of the advection period which might have resulted in the movement observed in the bottom cages at that time, although a more resolved model in lower-depth waters would be required to make a concrete conclusion. The long-line baskets, which are clipped to a rope containing floats, are susceptible to water movement (Fig. 5). This arrangement allows the baskets to rotate nearly 45° about the rope and can sway up to two meters during low tide. The limited resistance to these forces explains why the bags had the highest movement and a variance very similar to the floating cages. It is important to note that there are many basket manufacturers and several ways to deploy long-line baskets that can offer increased resistance than the method used in this experiment. For example, a cage that was attached directly to a taught line or cable, like how adjustable longline systems (ALS) containing BST baskets are often deployed (see Hood et al., 2020), would be much more resistant to water movement and have different characteristics of motions. Lastly, the floating cages, which contain floats directly attached to the top of the structure, resist lower frequency motion by dampening the movement of the cage and bags inside. This layout likely offered little resistance in periods of high wave energy since the floats force the cage and internal bags to move in parallel with oncoming waves. Periods where wave height and frequency are high only occur in times with high winds or during storm conditions at our experimental site, which do not occur consistently over time. As a result, floating cages receive the least bag movement with high variance (Fig. 5).

Oyster performance varied significantly across each culture method in our experimental site. The differences among gear types highlight trade-offs among the growth, survival, and quality of the animals. Inside the HPLDF, bottom cages provided the fastest average shell length growth at the expense of tissue growth and a longer shell. Floating cages produced the most consistent oysters with high survival but resulted in slower shell growth. The long-line system produced oysters with high condition index and fast shell growth but incurred a cost of high mortality. This mortality was not observed in similar studies (see Walton et al., 2013a) however, the method that the longlines were deployed varied between our study and Walton et al. (2013a). Hood et al. (2020) suggests that the method baskets are secured to a longline should correspond to the characteristics of the local environment which can elucidate the differences in the results of these works.

When analyzing oyster performance from a commercial perspective, it is important to consider that 'ideal' oyster performance is subjective and can change widely across markets, growers, and individuals. Several indices have been developed to characterize oyster meat and shell quality (Galtsoff, 1964; Lawrence and Scott, 1982; Thomas et al., 2019). Brake et al. (2003) compared the predictability of several shell size ratios to determine the accuracy of these ratios against predetermined 'good' or 'bad' oysters. There are many additional characteristics to consider when comparing the quality of oysters that extend past shell growth, such as shell hardness, epibiont presence, and shell deformities (Mizuta and Wikfors, 2019), which was not considered in our study.

Few studies have compared the growth and performance of oysters across different cage systems. Walton et al. (2013a) conducted a similar experiment in Sandy Bay, AL comparing the growth between bottom cage, ALS, and two types of floating cages and found contrasting results in oyster performance. While their study does not describe the hydrodynamic conditions observed at the study site, the maximum tidal velocity appears to be slightly greater than HPLDF's overall maximum velocity (Passeri et al., 2015). Walton et al. (2013a) observed the lowest survival and slowest shell growth in the bottom cages and highest survival and medial shell growth in the floating cages. Interestingly, Thomas et al. (2019) compared bottom and floating cage systems across commercial farm sites closer to the main stem of the Chesapeake Bay, MD, an area that is more energetic than our field location at HPLDF and found similar results as Walton et al. (2013b) where floating cages experienced faster growth, greater survival, and higher shell quality compared to each bottom cage type. Both studies were conducted in higher energy environments than our study location, which could explain the disagreement in results.

The multitude of factors that influence oyster performance demonstrates that future studies of varying complexity are warranted. When comparing growth studies, the specific application of cage type, husbandry practices, and hydrodynamic characteristics needs to be considered to allow for a meaningful comparison. Future studies should exploit more energetic environments while comparing different gear types, species, and ploidy. A culmination of studies monitoring the physical conditions of cages across gear types in varying environments would be valuable to growers wishing to optimize their production. Also, for gear comparisons using lower depth cages, tidal activity should be considered further as a potential source driving bottom cage motion. Finally, because each gear type apparently provides different production benefits, it may be useful to evaluate if a rotational pattern of gear use could streamline production to optimize production.

5. Conclusion

The vertical distribution of cages along the water column significantly influences the physical forcing imposed on oysters. The frequency and variance of oyster movement and cage motion influence the growth and shell quality of oysters. The differences between the performance response of the oysters across each cultivation methods presents a potential cultivation technique that oyster growers can leverage to optimize animal growth and shell characteristics that reduces waste and are desirable to consumers. The results of this study represent a case study in a low-energy environment. The growth response of oysters may change in cages that are deployed in more energetic environments.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Matthew Gray reports financial support was provided by Maryland Sea Grant.

Data availability

Data will be made available on request.

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Appendix A. Appendix

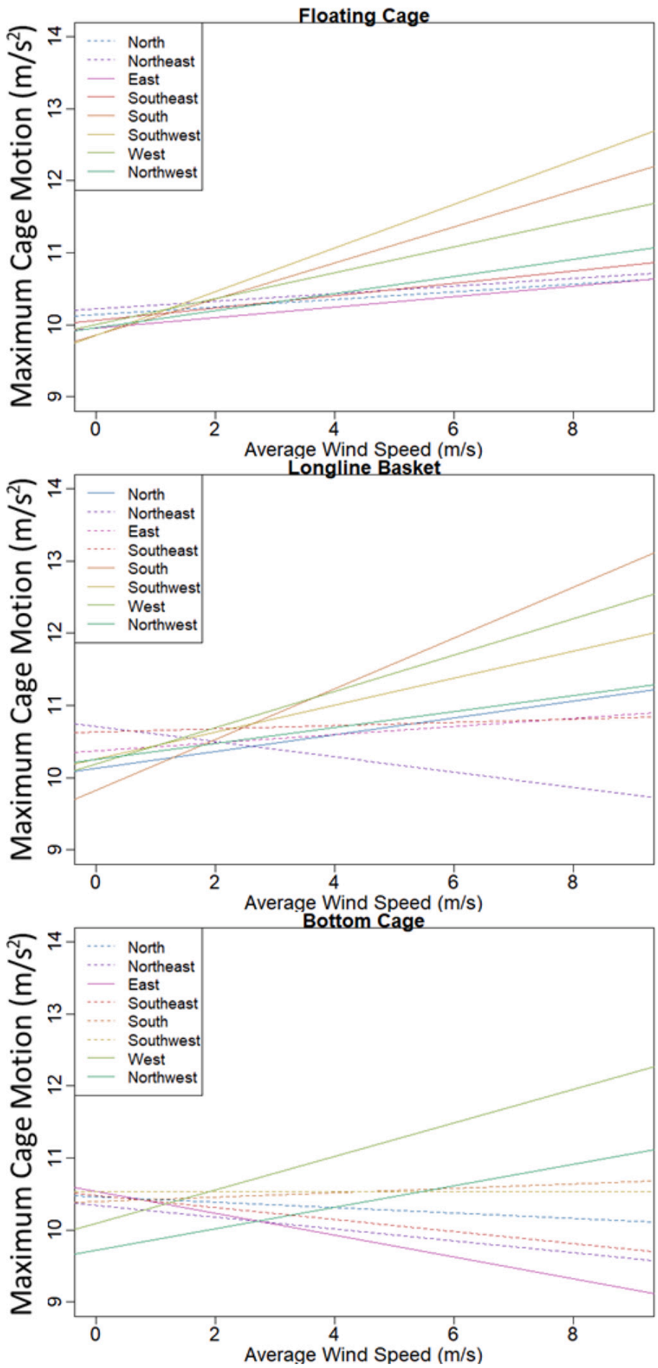

Fig. A.1. The motion of each cage type was affected differently by wind and wind direction. Linear regression of maximum cage movement as a function of average wind speed separated by bins of cardinal directions for floating cages (top), longline baskets (middle), and bottom cages (bottom). Statistically significant regression lines are represented by solid lines ($p < 0.05$) while dotted lines are used for insignificant regressions. Individual data points ($n = 908$) were removed for clarity.

References

Botta, R., Asche, F., Borsum, J.S., Camp, E.V., 2020. A review of global oyster aquaculture production and consumption. Mar. Policy 117, 103952. https://doi.org/10.1016/j.marpol.2020.103952.

Brake, J., Evans, F., Langdon, C., 2003. Is beauty in the eye of the beholder? Development of a simple method to describe desirable shell shape for the Pacific oyster industry. J. Shellfish Res. 22 (2), 767–771.

Campbell, M.D., Hall, S.G., 2018. Hydrodynamic effects on oyster aquaculture systems: a review. Rev. Aquac. 1-11 https://doi.org/10.1111/raq.12271.

Comeau, L., 2013. Suspended versus bottom oyster culture in eastern Canada: comparing stocking densities and clearance rates. Aquaculture. 410-411, 57–65. https://doi.org/10.1016/j.aquaculture.2013.06.017.

Cranford, P.J., Ward, J.E., Shumway, S.E., Shumway, S.E., 2011. Bivalve filter feeding: Variability and limits of the aquaculture biofilter. In: Shellfish Aquaculture and the Environment. John Wiley & Sons, United Kingdom, pp. 185–225.

Dong, S., You, X., Hu, F., 2020. Effects of wave forces on knotless polyethylene and chain-link wire netting panels for marine aquaculture cages. Ocean Eng. 207, 107368 https://doi.org/10.1016/j.oceaneng.2020.107368.

Duarte, P., Alvarez-Salgado, X.A., Fernández-Reiriz, M.J., Piedracoba, S., Labarta, U., 2014. A modeling study on the hydrodynamics of a coastal embayment occupied by

mussel farms (ria de Ares-Betanzos, NW Iberian Peninsula). Estuar. Coast. Shelf Sci. 147, 42–55. https://doi.org/10.1016/j.ecss.2014.05.021.
Engle, C., van Senten, J., Parker, M., Webster, D., Clark, C., 2021. Economic tradeoffs and risk between traditional bottom and container culture of oysters on Maryland farms. Aquac. Econ. Manag. 1-32 https://doi.org/10.1080/13657305.2021.1938295.
Galtsoff, P.S., 1964. The American oyster, *Crassostrea virginica* Gmelin. Fish. Bull. USA Fish Wildl. Serv. 64, 16–45.
Gaurier, B., Germain, G., Kervella, Y., Davourie, J., Cayocca, F., Lesueur, P., 2011. Experimental and numerical characterization of an oyster farm impact on the flow. Eur. J. Mech. B/Fluids 30, 513–525. https://doi.org/10.1016/j.euromechflu.2011.05.001.
Grant, J., Bacher, C., 2001. A numerical model of flow modification induced by suspended aquaculture in a Chinese bay. Can. J. Fish. Aquat. Sci. 58, 1003–1011. https://doi.org/10.1139/cjfas-58-5-1003.
Gray, M., Barbour, N., Campbell, B., Robillard, A.J., Todd-Rodriguez, A., Xiao, H., Plough, L., 2021. Ecolabels can improve public perception and farm profits for shellfish aquaculture. Aquac. Environ. Interact. 13, 13–20. https://doi.org/10.3354/aei00388.
Grizzle, R.E., Langan, R., Howell, W.H., 1992. Growth responses of suspension-feeding bivalve molluscs to changes in water flow: differences between siphonate and non siphonate taxa. J. Exp. Mar. Biol. Ecol. 162, 213–228. https://doi.org/10.1016/0022-0981(92)90202-L.
Haché, R., Plante, S., Doiron, S., 2021. Growth of eastern oyster (*Crassostrea virginica*) using two oyster – bag float configurations. J. Appl. Aquac. 1-12 https://doi.org/10.1080/10454438.2021.1955803.
Hartstein, N.D., Young, B., Anderson, M.R., Maxey, J.D., 2021. Hydrodynamic implications in and around a caged finfish farm and its implications on the dispersal of farm debris. Aquac. Eng. 93, 102154 https://doi.org/10.1016/j.aquaeng.2021.102154.
Henderson, A., Gamito, S., Karakassis, I., Pederson, P., Smaal, A., 2001. Use of hydrodynamic and benthic models for managing environmental impacts of marine aquaculture. J. Appl. Ichthyol. 17, 163–172 (ISSN: 0175-8659).
Hood, S., Webster, D., Meritt, D., Plough, L., Parker, M., 2020. Oyster Production Equipment Comparisons 2016-2018. Maryland Sea Grant. https://www.mdsg.umd.edu/sites/default/files/2020-08-11_OysterReport_FINAL.pdf.
Huang, J.F., Lee, J.M., 2013. Production economies and profitability analysis of horizontal rack culture and horizontal rack culture coupled with raft-string culture methods: a case study of Pacific oyster (*Crassostrea gigas*) farming in Chiayi and Yunlin Counties, Taiwan. Aquac. Int. 22, 1131–1147. https://doi.org/10.1007/s10499-013-9733-7.
Klebert, P., Lader, P., Gansel, L., Oppedal, F., 2013. Hydrodynamic interactions on net panel and aquaculture fish cages: a review. Ocean Eng. 58, 260–274. https://doi.org/10.1016/j.oceaneng.2012.11.006.
Lawrence, D.R., Scott, G.I., 1982. The determination and use of condition index of oysters. Estuaries. 5, 23–27. https://doi.org/10.2307/1352213.
Lee, Y.J., Kang, H.Y., Lee, W.C., Kang, C.K., 2017. Hydrodynamic effects on growth performance of the Pacific oyster *Crassostrea gigas* cultured in suspension in a temperate bay on the coast of Korea. Estuar. Coasts 40, 1551–1565. https://doi.org/10.1007/s12237-017-0252-z.
Lenihan, H.S., Peterson, C.H., Allen, J.M., 1996. Does flow speed also have a direct effect on growth of active suspension-feeders: an experimental test on oysters. Limnol. Oceanogr. 41 (6), 1359–1366. https://doi.org/10.4319/lo.1996.41.6.1359.
Lin, J., Li, C., Zhang, S., 2016. Hydrodynamic effect of a large offshore mussel suspended aquaculture farm. Aquaculture. 451, 147–155. https://doi.org/10.1016/j.aquaculture.2015.08.039.
Liu, Z., Huguenard, K., 2020. Hydrodynamic response of a floating aquaculture farm in a low inflow estuary. J. Geophys. Res. 125 https://doi.org/10.1029/2019JC015625 e2019JC015625.
Mallet, A.L., Carver, C.E., Thériault, M.H., 2013. Growth performance of eastern oysters *Crassostrea virginica* in Atlantic Canada: effect of the culture gear. Aquaculture. 396-399, 1–7. https://doi.org/10.1016/j.aquaculture.2013.02.019.
Mayerle, R., Niederndorfer, K.R., Jaramillo, J.M.F., Runte, K.H., 2020. Hydrodynamic method for estimating production carrying capacity of coastal finfish cage aquaculture in Southeast Asia. Aquac. Eng. 88, 102038 https://doi.org/10.1016/j.aquaeng.2019.102038.
Mizuta, D.D., Wikfors, G.H., 2019. Seeking the perfect oyster shell: a brief review of current knowledge. Rev. Aquac. 11, 586–602. https://doi.org/10.1111/raq.12247.
Navas, J.M., Telfer, T.C., Ross, L.G., 2011. Application of 3D hydrodynamic and particle tracking models for better environmental management of finfish culture. Cont. Shelf Res. 31, 675–684. https://doi.org/10.1016/j.csr.2011.01.001.
Passeri, D.L., Hagen, S.C., Medeiros, S.C., Bilskie, M.V., 2015. Impacts of historic morphology and sea level rise on tidal hydrodynamics in a microtidal estuary (Grand Bay, Mississippi). Cont. Shelf Res. 111, 150–158. https://doi.org/10.1016/j.csr.2015.08.001.
Rabe, B., Gallego, A., Wolf, J., Murray, R.O., Stuiver, C., Price, D., Johnson, H., 2020. Applied connectivity modeling at local to regional scale: the potential for sea lice transmission between Scottish finfish aquaculture management areas. Estuar. Coast. Shelf Sci. 238, 106716 https://doi.org/10.1016/j.ecss.2020.106716.
Scully, M.E., 2016. Mixing of dissolved oxygen in Chesapeake Bay driven by the interaction between wind-driven circulation and estuarine bathymetry. J. Geophys. Res. Oceans 121 (8), 5639–5654. https://doi.org/10.1002/2016JC011924.
Stevens, C.L., Petersen, J.K., 2011. Turbulent, stratified flow through a suspended shellfish canopy: implications for mussel farm design. Aquac. Environ. Interact. 2 (1), 87–104. https://doi.org/10.3354/aei00033.
Thomas, L.L., Allen Jr., S.K., Plough, L.V., 2019. The effect of aquaculture gear on the growth and shape of the oyster *Crassostrea virginica* during a “finishing period” in Chesapeake Bay, USA. Aquaculture. 508, 1–9. https://doi.org/10.1016/j.aquaculture.2019.03.061.
van Senten, J., Engle, C., Parker, M., Webster, D., 2019. Analysis of the Economic Benefits of the Maryland Shellfish Aquaculture Industry. Chesapeake Bay Foundation.
Walton, W.C., Davis, J.E., Supan, J.E., 2013a. Off-Bottom Culture of Oysters in the Gulf of Mexico, 4308. Southern Regional Aquaculture Center, pp. 1–6.
Walton, W.C., Rikard, F.S., Chaplin, G.I., Davis, J.E., Arias, C.R., Supan, J.E., 2013b. Effects of ploidy and gear on the performance of cultured oysters, *Crassostrea virginica*: survival, growth, shape, condition index and *Vibrio* abundances. Aquaculture. 414-415, 260–266. https://doi.org/10.1016/j.aquaculture.2013.07.032.
Ward, R.D., Thompson, P.A., Appleyard, S.A., Swan, A.A., Kube, P.D., 2005. Sustainable genetic improvement of Pacific oysters in Tasmania and South Australia. In: Fisheries Research and Development Corporation Final Report. Canberra, Australia, pp. 66–81.
Wilson-Ormond, E.A., Powell, E.N., Ray, S.M., 1997. Short-term and small-scale variation in food availability to natural oyster populations: food, flow and flux. Mar. Ecol. 18 (1), 1–34. https://doi.org/10.1111/j.1439-0485.1997.tb00424.x.