



Seasonal Feeding Behavior of Aquaculture Eastern Oysters (*Crassostrea virginica*) in the Mid-Atlantic

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Abstract

The Eastern Oyster (*Crassostrea virginica*) is a commercially important aquaculture species and food resource along the Atlantic and Gulf coasts of the USA. In addition to its economic value, oyster aquaculture provides ecological value such as water quality improvement. Oyster filtration is highly variable as filtration behavior is influenced by environmental conditions, oyster size, and oyster energetic demands. However, average rates generated in laboratory experiments are often used to estimate the ecological impact of oyster filtration, and there is a need for field-based, farm-specific estimates of filtration that account for this variation. In this study, field experiments were conducted between September 2020 and September 2021 to estimate seasonal oyster filtration physiology at oyster farms in three different bays in the Mid-Atlantic (Barnegat Bay and Delaware Bay in New Jersey and Rehoboth Bay in Delaware). The physiological activity of oysters at each farm varied such that oysters at Barnegat Bay were the most active and oysters at Rehoboth Bay were the least active. Seasonal physiological trends were observed such that filtration behavior generally increased in warmer months. An increase in physiological activity across all farms was associated with an increase in salinity and temperature, but physiological activity at each farm was associated with a different suite of environmental variables including total particulate matter and the organic content of seston. This study provides a robust dataset which can be incorporated into models estimating ecological filtration rates in the Mid-Atlantic and adds to the growing body of evidence supporting bivalve aquaculture as a nutrient reduction strategy.

Keywords Oyster · Aquaculture · Ecosystem service · Water quality

Introduction

Oysters are critically important for maintaining healthy coastal ecosystems, and the impact of anthropogenic stressors on oyster reefs is well documented (Beck et al. 2011).

Globally, it is estimated that 85% of oyster reef ecosystems have been lost over the past 130 years as a result of overharvesting, changes in freshwater inflows, alterations to shorelines, disease, and other factors (Beck et al. 2011). This decline has resulted in a loss of the ecosystem services oysters provide such as water quality improvements (Grabowski et al. 2012). This ecosystem service is particularly important as eutrophication, the condition of excessive nutrients in a water body, continues to be a global water quality concern for aquatic environments (Howarth 2008; Wurtsbaugh et al. 2019). Eutrophication can be harmful to aquatic life and has been linked to environmental problems such as hypoxia, algal blooms, and fish kills (Bricker et al. 1999; de Jonge et al. 2002; Ferreira et al. 2011). Restoration of natural oyster reefs can help reduce excess nutrients (Hernández et al. 2018; Duarte et al. 2020), and studies suggest oyster aquaculture could provide equivalent or greater water quality benefits than reefs (Zu Ermgassen et al. 2012; Froehlich et al. 2017; Campbell and Hall 2019).

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A growing body of evidence demonstrates the value of bivalve aquaculture to mitigate eutrophication in the USA and abroad via bioextraction (Lindahl et al. 2005; Rose et al. 2014, 2015; Ferreira and Bricker 2016; Bricker et al. 2018; Clements and Comeau 2019; van der Schatte Olivier et al. 2020). Bioextraction refers to the permanent removal of nutrients contained in the bodies of cultivated shellfish and seaweeds when they are harvested. As suspension feeders, bivalves remove nutrients from the water column directly (i.e., feeding on microscopic nutrient rich particles) and indirectly (i.e., feeding on phytoplankton, which have already assimilated nutrients into their cellular structure). Bioextraction is an affordable and innovative option to mitigate nutrient pollution when implemented into water quality management strategies (Rose et al. 2014), and cultivated bivalves are beginning to be introduced into such strategies (Cornwell et al. 2016; Reitsma et al. 2017).

While it is clear that bivalve aquaculture can mitigate eutrophication, the scale at which oyster farms provide water quality benefits is not well understood (Gentry et al. 2019). One reason is that estimates of oyster physiological rates including clearance rates (CR), filtration rates (FR), and others of interest (Table 1) often do not account for seasonal variation in suspension feeding. Site-specific environmental variables are known to influence oyster feeding behavior (Cranford et al. 2011) such as hydrodynamics (Campbell and Hall 2019), water temperature (Comeau et al. 2008; Pernet et al. 2008), salinity (Casas et al. 2018a), and quantity and quality of suspended particles (Navarro and Iglesias 1993). Although suspension feeding is variable over both space and time, average physiological rates that do not account for these variables are often used in estimates of ecological filtration. Furthermore, traditional methods for measuring oyster CRs and FRs may overestimate oysters' water quality benefits due to biases in sampling protocol where static water or laboratory diets, or both, were used (Kreeger et al. 2018). Comprehensive strategies for measuring oyster feeding behavior have been developed recently that overcome

these biases (Galimany et al. 2011; Hoellein et al. 2015). Therefore, a detailed understanding of oysters' CRs and FRs, under site-specific conditions, is possible and essential for a comprehensive estimation of oysters' impact on water quality (Ehrich and Harris 2015). Understanding the influence of site-specific conditions on oyster physiology is also important for farm lease siting decisions as oyster farmers are most interested in locations that produce quality market-sized oysters quickly.

Oyster aquaculture also serves as a mechanism for benthic-pelagic coupling such that oyster feces and pseudofeces (collectively known as "biodeposits") settle to the sediment beneath and near oyster farms. These biodeposits introduce a new source of energy and nutrients to the benthic environment. Some studies have expressed concern for the potential negative effects of excessive biodeposits to local ecosystems and water quality such that biodeposits may inhibit denitrification processes at the benthic-pelagic boundary, cause benthic anoxia, or be resuspended into the water column via local hydrology (Dame and Libes 1993; Kreeger et al. 2018). Additional studies have shown that these effects can be minimized if biodeposits are adequately dispersed and aquaculture gear appropriately stocked with oysters (Testa et al. 2015) and that overall oyster aquaculture is considered ecologically sound in its specific location (Hilborn et al. 2018). Moreover, in certain locations, biodeposits from restored or farmed oysters can enhance sediment denitrification thus providing another means to reduce nutrient pollution separate from bioextraction (Humphries et al. 2016; Donnelly 2021; Rose et al. 2021). The negative impacts that have been observed tend to be associated with areas of high oyster density, are found in poorly flushed ecosystems, and are limited to localized areas directly adjacent to the oyster farm (Lunstrum et al. 2018; Turner et al. 2019). To more holistically understand the role of oyster aquaculture in a coastal ecosystem, it is important to quantify what oysters are taking out of the water column via suspension feeding

Table 1 Definitions of the physiological components of absorptive balance for oysters (Iglesias et al. 1998). Modified from Galimany et al. (2017b)

Parameter	Units	Definition	Calculation
Clearance rate (CR)	L h ⁻¹	The volume of water cleared of particles per unit of time.	(mg inorganic matter from feces and pseudofeces per unit of time [mg h ⁻¹]) / (mg particulate inorganic matter (PIM) in bay water [mg L ⁻¹])
Filtration rate (FR)	mg h ⁻¹	The biomass of particles removed from water column per unit of time.	CR × total particulate matter (TPM) in bay water [mg L ⁻¹]
Rejection rate (RR)	mg h ⁻¹	TPM that has been retained in the gills but rejected prior to ingestion.	mg inorganic and organic matter from pseudofeces per unit of time
Absorption rate (AR)	mg h ⁻¹	Biomass of organic particles ingested and not egested as feces per unit of time.	(CR × particulate organic matter (POM) in bay water) - (mg organic matter from pseudofeces [mg h ⁻¹]) - (mg organic matter from feces [mg h ⁻¹])

and putting back into the environment via biodeposition. This can be achieved by analyzing various physiological components of oyster feeding behavior.

The present study quantifies farm-specific year-round filtration behavior of Eastern Oysters (*Crassostrea virginica*) at three farms in the Mid-Atlantic and provides insights into the physiological differences in aquaculture oysters as well as the environmental drivers of oyster filtration capacity. To do this, filtration experiments were conducted seasonally in the field using ambient farm water to estimate CR, FR, rejection rate (RR), and absorption rate (AR) (hereafter, collectively “filtration physiology”) of aquaculture oysters (Table 1). Oyster filtration physiology was analyzed under a range of environmental conditions (i.e., temperature, salinity, total particulate matter, and the organic content of suspended solids in the water column), and associations with oyster behavior were explored. These experiments provide a robust dataset of oyster filtration physiology observed under natural conditions across farms and may be used in a broader framework to inform development of nutrient management strategies in the region.

Methods

Study Site and Frequency

Seasonal filtration experiments were conducted in the field at three different oyster farms in the Mid-Atlantic between September 2020 and September 2021 (13 months). These farms were located in Barnegat Bay (39° 36′ 10.8″ N, 74° 18′ 7.2″ W), Delaware Bay (39° 4′ 16.4″ N, 74° 54′ 47.5″ W), and Rehoboth Bay (38° 39′ 0.3″ N, 75° 7′ 41.8″ W) (Fig. 1). Each location had two sites: the oyster farm where oysters were collected and the experiment site where the filtration experiments were conducted. Each farm and experiment site pair were less than 1.4 km apart (1.27, 1.03, and 1.36 km, respectively) such that no significant difference in water temperature was found between each farm/experiment pair (Barnegat Bay: $t(2) = -1.07$, $p = 0.40$; Delaware Bay: $t(3) = -0.61$, $p = 0.58$; Rehoboth Bay: $t(1) = 0.20$, $p = 0.87$) (Table S1). The three farms represent a range of water quality conditions and used different farming methods: a coastal backbay habitat supporting

Fig. 1 Locations of the three Eastern Oyster farms where filtration experiments were conducted (created with Datawrapper). The northern site is a coastal backbay habitat in Barnegat Bay, NJ, using subtidal floating and bottom cage culture (blue dot); the central site is a mudflat habitat in Delaware Bay, NJ, using intertidal rack-and-bag culture methods (orange dot); and the southern site is an inland bay habitat in Rehoboth Bay, DE, using subtidal floating and longline culture (gray dot). Three experiments were conducted at Barnegat Bay, four experiments at Delaware Bay, and four experiments at Rehoboth Bay



a subtidal farm using floating and bottom cage culture, a mudflat habitat supporting an intertidal farm using rack-and-bag culture methods, and an inland bay habitat supporting a subtidal farm using floating and longline culture, respectively.

Three filtration experiments were conducted at Barnegat Bay (July 2021; September and November 2020), four experiments at Delaware Bay (April, June, and August 2021; October 2020), and four experiments at Rehoboth Bay (April, July, and September 2021; November 2020) such that experiments generally occurred once every 2 months.

Physiology Experiments

A flow-through filtration chamber with ambient water was used during each experiment ($n = 11$) to calculate filtration physiology values for three oyster farms following protocols detailed in Galimany et al. (2011). The flow-through filtration chamber consisted of a central polyvinyl chloride (PVC) reservoir tank and twenty smaller PVC feeding chambers (Fig. 2). Ambient bay water was pumped from approximately 30 cm below the surface through a coarse filter (100 μm mesh) into the reservoir tank. The coarse filter prevented large pieces of detritus from clogging the connection tubing between reservoir tank and feeding chambers, and the sealed reservoir served to maintain constant water pressure and flow. Water flow through each of the twenty feeding chambers was set at 12 L h^{-1} . This flow rate allowed a homogeneous distribution of particles among feeding

chambers and precluded water recirculation within a feeding chamber (Galimany et al. 2011). The reservoir tank was aerated with two air stones to suspend particles throughout the tank allowing equal distribution of particles to each feeding chamber, and covers (i.e., shade boxes) were used to shade the feeding chambers.

Oysters were collected from the farm no more than 4 h prior to the start of each experiment. Once collected, oysters were rinsed in ambient bay water, cleaned of all detritus, and all fouling organisms removed. Oysters used in each experiment represented the full range of sizes (Barnegat Bay: 42.7–92.3 mm; Delaware Bay: 32.3–96.1 mm; Rehoboth Bay: 44.2–101.3 mm in shell length) on the farm and were held out of water in a shaded area until the experiment began.

Prior to the start of an experiment, oyster gut transit time (GTT) was estimated following the methods detailed in Galimany et al. (2018) with the exception that water flow in the gut transit chamber (GTC) was achieved with recirculation. In summary, five oysters from the farm were placed in a 30-L GTC filled with 13 L of ambient bay water filtered to 1 μm (Fig. S1). Each oyster was placed into one of five smaller containers ($14 \times 14 \times 5 \text{ cm}$) located in the GTC with left shells flush to bottom of chamber. An aquarium pump (EHEIM CompactON 300, 79 GPH) continually circulated the filtered bay water through a baffle into each of the smaller containers, creating posterior to anterior flow over each oyster. This created a flow-through environment similar to that in the filtration chamber, while allowing cultured

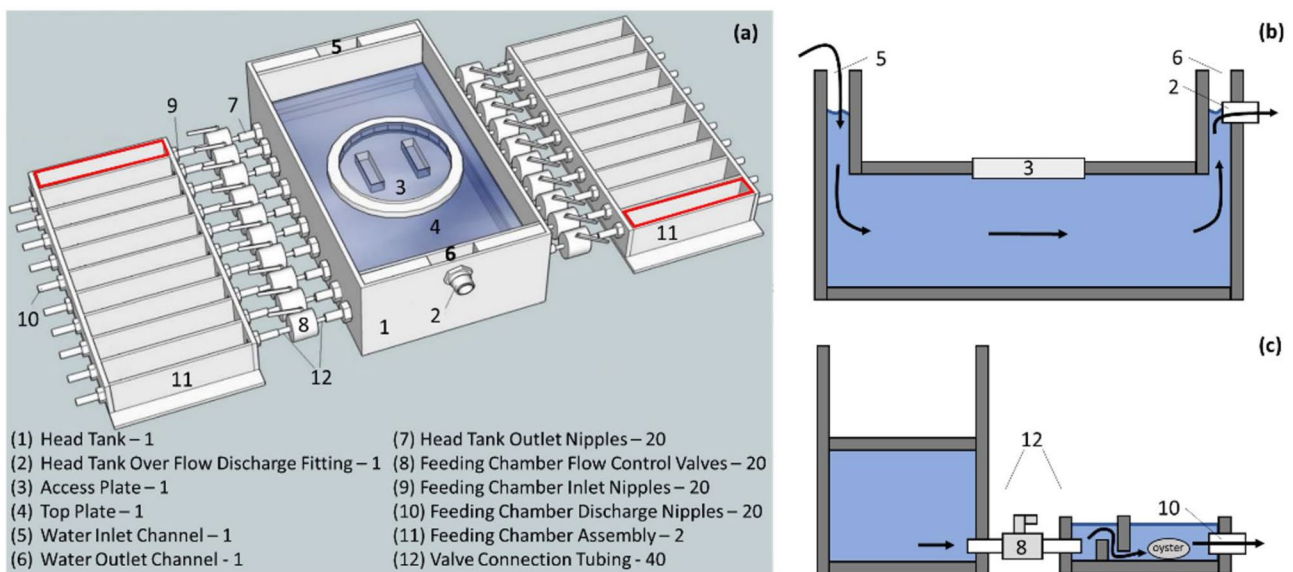


Fig. 2 Schematic of flow-through filtration chamber design. (a) shows the entire apparatus including reservoir tank with 20 feeding chambers (modified from Galimany et al. 2018), (b) shows the side view of the head tank with arrows indicating flow of water, and (c) shows the

front view with arrows indicating the flow of water from head tank to feeding chamber with baffles to provide appropriate water turbulence. (a) Feeding chambers outlined in red indicate location of oyster blanks during experiments

algae to be used. Oysters were acclimated to the GTC for 10 min before algae (LPB Frozen Shellfish Diet of whole-cell *Tetraselmis*, *Thalassiosira weissflogii*, *Thalassiosira pseudonana*, and *Schizochytrium*, Reed Mariculture) was introduced to the system at a concentration of 300,000 cells mL⁻¹. GTT was determined based on the time an oyster opened to the time the oyster started to produce green feces. When valve opening could not be accurately observed, the time elapsed between initial and green feces deposition was used as GTT. The mean GTT of oysters in the GTC was used to offset the time of biodeposit collection in the filtration chamber. Oysters in the GTC that did not produce biodeposits, or produced biodeposits that did not turn green, were omitted from the final GTT calculation.

To begin each experiment, 18 oysters were placed in the filtration chamber between 120 and 10 min before high tide ($t=0$). Experiments began on a rising high tide to preclude tidal cycle as a variable among farm sites that may influence oyster feeding behavior. Nine oysters were placed in feeding chambers on either side of the reservoir tank, and one oyster blank (empty, clean shells glued together) was placed in the remaining feeding chambers indicated in red in Fig. 2a. Oyster blanks were used to account for particle deposition due to hydrodynamics around each oyster. Temperature, dissolved oxygen (DO), total dissolved solids (TDS), salinity, and pH of the incoming water were measured every 20 min starting at $t=0$ using a YSI handheld multiparameter meter (YSI ProDSS Water Quality Meter #626973) submerged adjacent to the submersible pump.

When the GTT had elapsed ($t=GTT$), all detritus and biodeposits that settled to the bottom of each feeding chamber were removed with minimal disturbance to the oysters. For the remainder of the experiment, the feces and pseudofeces produced by each oyster were carefully collected with a glass transfer pipette and stored separately in 50-mL Falcon tubes. When biodeposits could not be conclusively identified as feces or pseudofeces, the biodeposit was not collected. After 2 h had elapsed ($t=GTT+2$ h), oysters were removed from feeding chambers and the experiment terminated. Two hours was generally sufficient time to collect enough biodeposits for processing; however, when needed, biodeposits were collected for an additional 20 min.

Bay water samples (250 mL each) were collected every 20 min starting from $t=0$ from three sources: the filtration chamber inflow (after the 100 μ m filter) and the outflow of the two feeding chambers holding oyster blanks. If the experiment ran for 2 h and 20 min, an additional water sample was taken. Oysters, biodeposits, and water samples were stored on ice and transported to the lab for filtering and further processing.

Each oysters' CR, FR, RR, AR, absorption efficiency (AE), inorganic egestion rate (IER), organic egestion rate (OER), inorganic rejection rate (IRR), and organic rejection

rate (ORR) were calculated using the biodeposition method detailed in Iglesias et al. (1998). This required the total particulate matter (TPM), particulate organic matter (POM), and particulate inorganic matter (PIM) content of the (1) 250 mL water samples, (2) pseudofeces samples, and (3) feces samples (hereafter "biological samples") to be measured for each oyster in each experiment. To do this, each biological sample was filtered through a pre-ashed (450 °C), pre-weighed (10^{-5} g) 1.2- μ m glass microfiber filter (GF/C 25-mm diameter) using a filtration manifold and vacuum pump (MultiVac 300-MS 3-Branch Stainless Steel Manifold, filtration flask, and Rocker 300 oil-free vacuum pump) consistent with Galimany et al. (2011). All feces and pseudofeces samples were diluted using isotonic 1 μ m filtered seawater to achieve a volume suitable to filter. When biological samples contained a greater mass than one filter paper could support, a subsample was processed. Once filtered, biological samples were rinsed with 5 mL of isotonic ammonium formate. All biological samples were processed within 13 h of experiment termination then stored frozen. Frozen filters were then dried at 60 °C until a constant weight was achieved (~4.5 days). TPM, PIM, and POM (mg L⁻¹) of each biological sample were then calculated consistent with Galimany et al. (2011).

Oyster shell length measurements, umbo to growing edge of the right valve, were taken. Oyster dry tissue weight (DTW) and dry shell weight were measured after drying for 72 h at 60 °C. Oyster condition (= DTW [g]/dry shell weight [g]) was also calculated. All physiological variables were standardized to 1 g DTW using the following equation:

$$Y_s = Y_e(1/W_e)^b$$

where Y_s is the standardized physiological rate, Y_e is the experimentally determined rate, W_e is the measured dry tissue weight (DTW), and $b=0.73$ as determined by Riisgård (1988).

Physiology values were only determined for oysters that produced both feces and pseudofeces during an experiment. The number of oysters that produced both feces and pseudofeces at any point during an experiment was recorded as actively feeding for the duration of the experiment as the feeding chambers with shade boxes made it difficult to observe gaping.

To compare CR (L h⁻¹ g⁻¹) with the often-quoted estimate that oysters can filter up to 50 gallons of water per day (Freeman et al. 2010; Karel 2019), individual oyster CRs were converted to gal day⁻¹.

Farm Environmental Conditions

The water quality measurements made during each experiment (temperature, salinity, DO, pH, TDS, TPM, and the

organic content of suspended solids in the water column (i.e., WC.Org) were also made monthly at each experiment location starting in May 2021 to quantify the environmental conditions oysters experienced between experiments. WC.Org (%) was calculated by dividing POM of a water sample by TPM. All discrete samples were taken in 3 h before high tide.

Loggers (Onset HOBO Conductivity Logger) were deployed at each farm to measure temperature and salinity data at 30-min intervals between July 2020 and September 2021.

Statistical Analyses

All analyses were performed using RStudio version 4.1.1 (R Core Team 2020), and a p -value less than 0.05 was considered significant, while a p -value between 0.05 and 0.10 was considered marginally significant. Assigning marginal significance to a p -value greater than 0.05 was used to account for the expected high noise in environmental data and better ascertain physiology signal from noise (Smith 2020). Median filtration physiology values were used in all analyses, as opposed to oyster-specific filtration physiology values, to avoid pseudoreplication and better represent the central tendency of oyster behavior in each experiment.

Water Quality

To test if there were differences in water quality among aquaculture farms, a one-way analysis of variance (ANOVA) was used. The following water quality parameters were compared: temperature, salinity, DO, pH, TDS, TPM, and WC.Org. If significant differences in water quality were detected, a Tukey's post hoc test was used to assess pairwise comparisons among farms. The mean of water and seston measurements collected during an experiment were used in each ANOVA.

Differences in Oyster Filtration Physiology

To test if there were differences in oyster filtration physiology among aquaculture farms, an ANOVA was used. The following median filtration physiology values were compared: CR, FR, RR, and AR as well as mean oyster condition. If significant differences in median filtration physiology were detected, a Tukey's post hoc test was used to assess pairwise comparisons among farms.

Drivers of Oyster Filtration Physiology

To test if changes in water quality were associated with changes in oyster filtration physiology at each farm, linear regressions were used to relate the environmental

characteristics (mean temperature, salinity, TPM, and WC.Org) to median CR, FR, RR, and AR ($n=3$ at Barnegat Bay, $n=4$ at Delaware Bay, $n=4$ at Rehoboth Bay).

These four water quality parameters were compared against oyster filtration physiology to mitigate autocorrelation biases in analyses. TPM and WC.Org were found to be inversely correlated, but both seston variables remained in analyses to elucidate how quantity and quality seston, respectively, impacted oyster filtration physiology.

To test if changes in water quality were associated with changes in regional (i.e., Mid-Atlantic) oyster filtration physiology, analyses of covariance (ANCOVA) were used to relate the environmental characteristics (mean temperature, salinity, TPM, and WC.Org) to median CR, FR, RR, and AR ($n=11$). Variables were examined for normality (Shapiro-Wilk test) and homogeneity of variance (Bartlett's test) and were square root transformed as required. ANCOVAs were not performed with more than one covariate due to small sample size. To test if changes in water quality were associated with an increase or decrease in regional oyster filtration physiology, linear regressions were used to determine the directionality of these relationships (e.g., an increase in FR corresponds to an increase in salinity).

Coefficient of variation (CV) values was also calculated for each experiment to quantify the dispersion of CR, FR, RR, and AR values (hereafter, CR.CV, FR.CV, RR.CV, and AR.CV).

Results

Water Quality

No significant difference in water quality was found between Barnegat and Rehoboth Bays (Fig. 3). Temperature, DO, and pH were not significantly different among the three farm locations. Delaware Bay, in comparison to Barnegat and Rehoboth Bays, had 22 and 23% lower salinity, 21 and 28% lower WC.Org, 15 and 17% lower TDS, and 298 and 818% higher TPM, respectively (salinity: $F(2,17)=23.84$, $p<0.0001$, Tukey HSD, $p=0.00014$ and $p<0.0001$; WC.Org.: $F(2,17)=3.14$, $p=0.02$, Tukey HSD, $p=0.29$ and $p=0.07$; TDS: $F(2,17)=4.39$, $p=0.03$, Tukey HSD, $p=0.10$ and $p=0.04$; TPM: $F(2,17)=4.90$, $p=0.02$, Tukey HSD, $p=0.06$ and $p=0.04$) (Fig. 3). Seasonal trends in temperature and DO were evident at all farms with increased temperature and decreased DO in the summer (Figs. 3, and S2).

Differences in Oyster Filtration Physiology

Oyster filtration physiology varied across farms (Fig. 4). Oysters from Barnegat Bay were the most active, Delaware

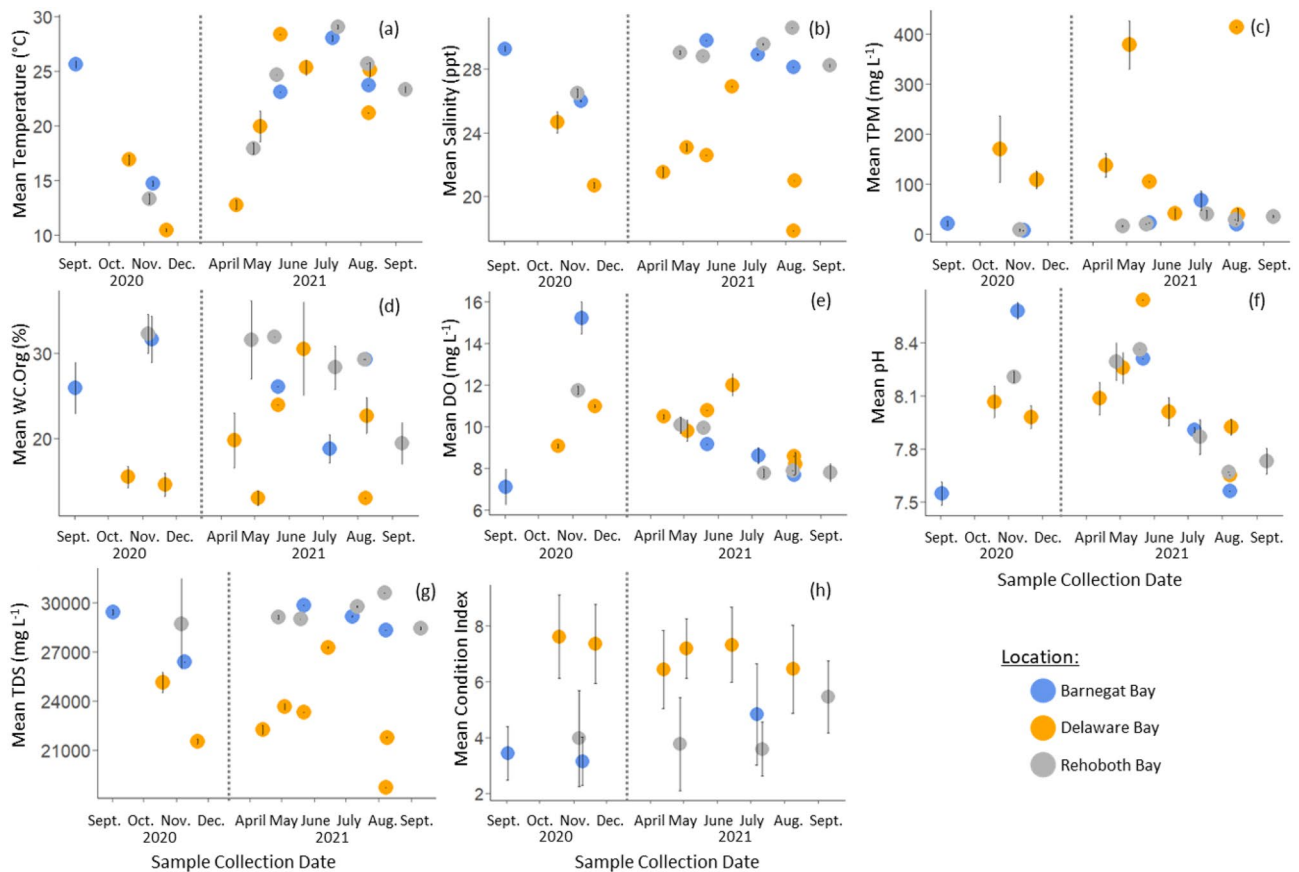


Fig. 3 Water quality measurements recorded at three oyster farms during, and between, filtration experiments including (a) temperature, (b) salinity, (c) TPM, (d) WC.Org, (e) DO, (f) pH, and (g) TDS. Points represent mean values (measurements collected during experiments were averaged over ~3.5-h period) with standard deviation (SD) bars. Measurements collected between experiments were opportunistic and

have no SD bars. All water quality measurements were taken within 3 h of high tide. (h) Oyster condition (or condition index (CI)) was also measured for the oysters in each experiment. In each panel, data to the left of the vertical dashed line were collected in 2020, and data to the right of the vertical dashed line were collected in 2021

Bay oysters were moderately active, and Rehoboth Bay oysters were the least active (Fig. 4). Median CR for oysters at Barnegat Bay was 235% higher than Delaware Bay oysters and 217% higher than Rehoboth Bay oysters ($F(2,8) = 4.01$, $p = 0.06$; Tukey HSD, $p = 0.08$ and $p = 0.09$, respectively). No significant difference in oyster median FR ($F(2,8) = 1.36$, $p = 0.31$), RR ($F(2,8) = 1.12$, $p = 0.37$), or AR ($F(2,8) = 1.84$, $p = 0.22$) among farms was found. When comparing AE for actively feeding oysters at each farm, the median AE for Barnegat and Delaware Bay oysters were the highest (72.6 and 82.9%, respectively), and median AE for Rehoboth Bay oysters was the lowest (56.7%). Results for IER, OER, IRR, and ORR can be found in the electronic supplementary material (Fig. S3).

Seasonal trends in filtration physiology were also observed. The Barnegat and Rehoboth Bay oysters showed a general seasonal trend in mean filtration physiology where mean CR, FR, RR, and AR were largest in the summer (June to September 2021) (Fig. 4). Similarly, the oysters that were

estimated to clear the greatest volume of water in 1 day were in Barnegat Bay (34.1 gal day⁻¹) and Rehoboth Bay (28.2 gal day⁻¹) in the summer (Table S2). This seasonal trend was not observed from Delaware Bay oysters as mean filtration physiology was lower in August relative to the values observed in June and October. Mean AE for oysters from Delaware Bay followed the same trend with 54.5, 87.3, and 85.6% AE, respectively. Mean oyster condition increased seasonally at Delaware Bay (i.e., 6.44 to 7.32 from April to June) and dropped to 6.45 in August (Fig. 3). Delaware Bay oysters had 70% higher oyster condition index than the other farms ($F(2,227) = 90.6$, $p < 0.0001$; Tukey HSD, $p < 0.0001$) (Fig. 3).

A range of physiological activity was observed during each experiment regardless of farm and time of year as indicated by the large standard deviation evident in Fig. 4. Indeed, qualitatively, oysters were observed to either never, intermittently, or constantly produce biodeposits over the duration of each experiment. At no point during a filtration

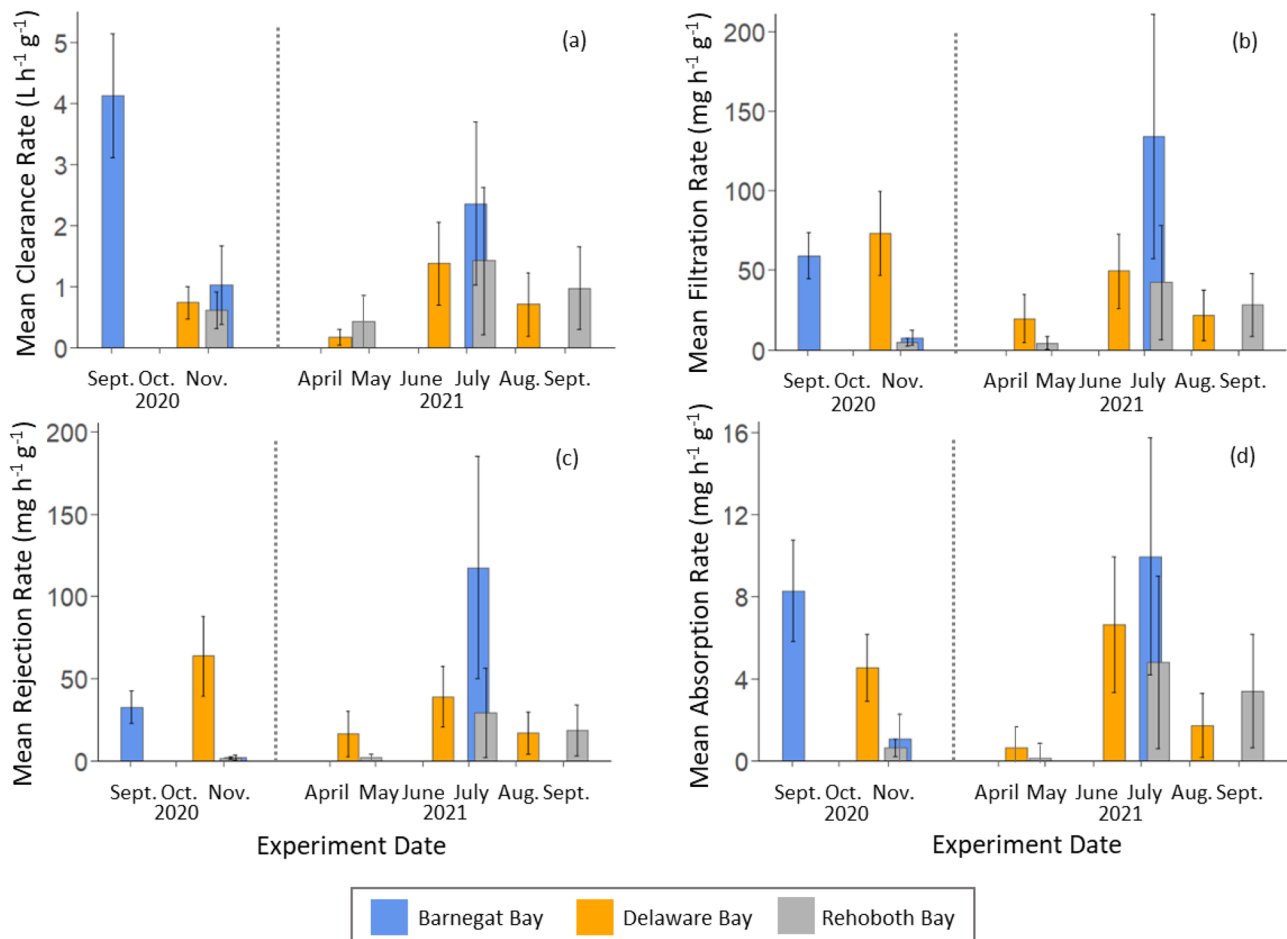


Fig. 4 Seasonal patterns in mean filtration physiology parameters measured at three oyster farms including mean (a) clearance rate (CR), (b) filtration rate (FR), (c) rejection rate (RR), and (d) absorption rate (AR). Filtration physiology was measured in the field during 11 seasonal experiments. Color indicates farm location (blue represents

Barnegat Bay, orange represents Delaware Bay, and gray represents Rehoboth Bay), and error bars indicate standard deviation. In each panel, data to the left of the vertical dashed line were collected in 2020, and data to the right of the vertical dashed line were collected in 2021

experiment did all oysters ($n = 18$) actively filter. The mean proportion of oysters that fed during a filtration experiment was 0.70 ± 0.20 SD. Additionally, CVs at Rehoboth Bay were largest across all filtration physiologies, and CVs at Barnegat Bay were consistently the smallest (Table S3).

Drivers of Oyster Filtration Physiology

Locally, the oyster population at each farm had unique physiological responses to environmental conditions (Table 2). While linear regressions indicated few significant relationships between environmental parameters and a given filtration physiology, the strongest correlations for each site are enlightening. Median filtration physiology of oysters from Delaware Bay was positively correlated with salinity (Table 2). Median filtration physiology of oysters from Rehoboth Bay was positively correlated with temperature, with median RR and median AR also being positively

correlated with TPM (Table 2). However, oysters from Barnegat Bay showed the greatest mixed response such that median FR was negatively correlated with WC.Org and median CR, RR, and AR were positively correlated with salinity, TPM, and temperature, respectively (Table 2).

Regionally when all three farms were analyzed together, temperature, salinity, TPM, and WC.Org were found to influence oyster filtration physiology, but salinity and temperature had the greatest influence (Table 3). Salinity had at least a marginally significant influence on all four median filtration physiologies, and temperature had at least a marginally significant influence on three of the four median filtration physiologies, with the exception that temperature did not have a marginally significant influence median FR (Table 3). Increases in salinity and temperature corresponded to an increase in filtration physiology, and increases in WC.Org corresponded to a decrease in filtration physiology (Table S4). Increases in TPM corresponded

Table 2 Results of linear regression of median physiology and environmental variables at each farm location. Significant correlations are highlighted in gray and denoted with two asterisks (**). Marginally significant correlations are highlighted in gray and denoted with one

asterisk (*). Gray highlighted correlations without asterisks indicates the environmental parameter that is most correlated with a filtration physiology but is not statistically significant. Correlations are positive unless specified by a “(-)” sign at the start of the cell

Physiological Variable Median	Barnegat Bay	Delaware Bay	Rehoboth Bay
CR	Temp: F(1,1)=1.3, p=.46 Salinity: F(1,1)=4.4, p=.28 TPM: F(1,1)=.04, p=.87 (-)WC.Org: F(1,1)=.22, p=.72	Temp: F(1,2)=2.0, p=.30 Salinity: F(1,2)=7.1, p=.12 (-)TPM: F(1,2)=.45, p=.57 (-)WC.Org: F(1,2)=1.1, p=.40	Temp: F(1,2)=4.1, p=.18 Salinity: F(1,2)=.59, p=.52 TPM: F(1,2)=2.2, p=.28 (-)WC.Org: F(1,2)=.04, p=.86
FR	Temp: F(1,1)=3.8, p=.30 Salinity: F(1,1)=1.2, p=.47 TPM: F(1,1)=31.0, p=.11 **(-)WC.Org: F(1,1)=263.4, p=.04	Temp: F(1,2)<.001, p=.98 Salinity: F(1,2)=2.2, p=.27 TPM: F(1,2)=.39, p=.59 (-)WC.Org: F(1,2)=.10, p=.78	*Temp: F(1,2)=16.4, p=.06 Salinity: F(1,2)=1.3, p=.38 TPM: F(1,2)=7.4, p=.11 (-)WC.Org: F(1,2)=.31, p=.64
RR	Temp: F(1,1)=1.9, p=.40 Salinity: F(1,1)=.63, p=.57 **TPM: F(1,1)=2026, p=.01 (-)WC.Org: F(1,1)=20.5, p=.14	Temp: F(1,2)=.001, p=.97 Salinity: F(1,2)=1.7, p=.32 TPM: F(1,2)=.52, p=.54 (-)WC.Org: F(1,2)=0.18, p=.71	**Temp: F(1,2)=19.9, p=.047 Salinity: F(1,2)= 1.4, p=.37 *TPM: F(1,2)=8.6, p=.099 (-)WC.Org: F(1,2)=.35, p=.61
AR	**Temp: F(1,1)=1956, p=.01 Salinity: F(1,1)=15.8, p=.16 TPM: F(1,1)=1.6, p=.43 (-)WC.Org: F(1,1)=4.6, p=.28	Temp: F(1,2)=.32, p=.63 **Salinity: F(1,2)=39.2, p=.02 (-)TPM: F(1,2)=.006, p=.94 (-)WC.Org: F(1,2)=.29, p=.64	*Temp: F(1,2)=10.8, p=.08 Salinity: F(1,2)=.66, p=.50 *TPM: F(1,2)=11.0, p=.08 (-)WC.Org: F(1,2)= .82, p=.46

Table 3 Results of ANCOVA testing whether changes in water quality were associated with changes in regional oyster filtration physiology. Analysis included the mean environmental conditions observed during each experiment (temperature, salinity, TPM, and WC.Org) and the median oyster CR, FR, AR, and RR for each experiment

(n = 11). A shaded cell indicates a given environmental variable had at least a marginally significant influence on a given physiological variable at these three farms. All influences were positive (e.g., an increase in temperature corresponded with an increase in CR) unless noted by a “(-)” at the start of a cell

	Clearance Rate	Filtration Rate	Absorption Rate	Rejection Rate
Temp.	F(1,7)=9.22, p=.019	F(1,7)=3.19, p=.117	F(1,7)=7.51, p=.029	F(1,7)=4.82, p=.064
Salinity	F(1,7)=8.33, p=.023	F(1,7)=4.31, p=.076	F(1,7)=14.2, p=.007	F(1,7)=4.84, p=.064
TPM	(-) F(1,7)=.057, p=.816	F(1,7)=5.01, p=.060	F(1,7)=.448, p=.525	F(1,7)=5.14, p=.058
WC.Org	(-) F(1,7)=.017, p=.900	(-) F(1,7)=3.12, p=.121	(-) F(1,7)=.951, p=.361	(-) F(1,7)=3.65, p=.098

to an increase in median CR, RR, and AR and a decrease in CR (Table S4).

Discussion

Oyster Filtration Physiology

The filtration physiology of oysters analyzed in this study differed among locations and across seasons. The range in physiological activity observed in this study is generally within the range of filtration physiology values reported across the Eastern Oyster range under comparable conditions with published mean FRs ranging from 17.9 (Galimany et al. 2017a, subtidal farm oyster averaged between March

and August) to 111.2 mg h⁻¹ g⁻¹ (Hoellein et al. 2015, subtidal reef oyster measured in July) and mean ARs ranging from 3.4 (Galimany et al. 2017a) and 26.7 mg h⁻¹ g⁻¹ (Hoellein et al. 2015). Reported RRs are limited and have a narrower range (i.e., 24.9 to 33.1 mg h⁻¹ from Galimany et al. 2017b) than those in this study. Mean CRs observed in this study overlapped with the low range of mean CRs reported elsewhere (Fig. 5). Additionally, no oyster in this study was estimated to clear more than 34.1 gallons per day which is lower than the often referenced 50 gallons per day value.

The difference in filtration physiology evident among farms suggests the oyster populations analyzed in this study were acclimated to their own unique environment and could alter their feeding behavior to meet changing metabolic

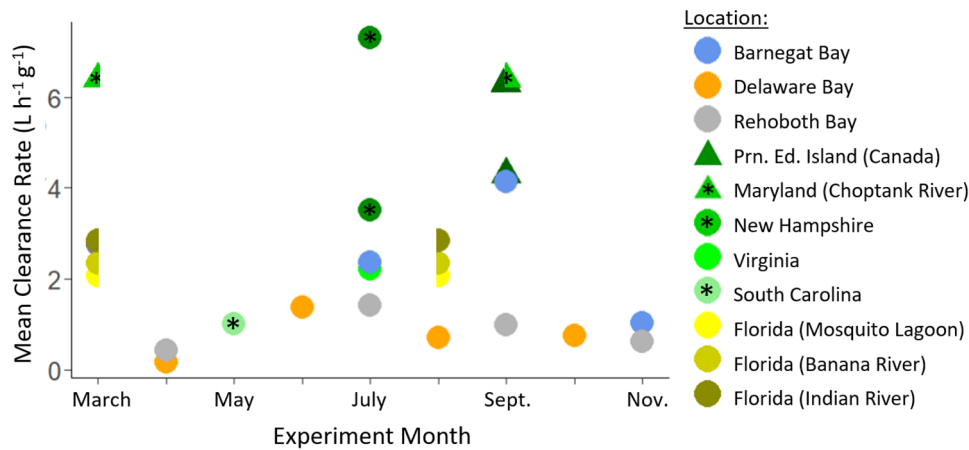


Fig. 5 Mean CR values for Eastern Oysters derived from this study and reported elsewhere, including Prince Edward Island (Comeau 2013), Maryland (Newell and Koch 2004), New Hampshire (Hoellein et al. 2015), Virginia (Kelly et al. 2011), South Carolina (Grizzle et al. 2008), and Florida (Galimany et al. 2017a, b). All oysters were exposed to a natural diet: triangles represent studies conducted in a laboratory environment, and circles represent studies conducted

in nature. Oysters from wild reefs are denoted with an asterisk (*), except for the South Carolina value which is an average CR of five constructed and three natural intertidal reefs. All oysters were subtidal except for the Delaware Bay site and South Carolina study. Symbols cut in half represent reported values that were averaged over two experiment dates

demands. Indeed, Barnegat and Delaware Bay oysters had higher median AE, 72.6 and 82.9%, respectively, which suggests these oyster populations optimized feeding when exposed to endogenous and exogenous stressors (Bayne et al. 1987, 1988; Ibarrola et al. 2000; Hall et al. 2020). Barnegat and Delaware Bay oysters had the greatest physiological activity and the lowest CVs, further supporting the acclimation of these populations to their habitat. Oysters from Rehoboth Bay had a median AE of 56.4% suggesting these oysters did not take up particles optimally as reflected in the overall lower physiological activity at that farm, which could be linked to oyster acclimation to the high WC.Org values seen in Rehoboth Bay (Cammen 1980; Galimany et al. 2017a; and in contrast Taghon 1981; Bayne et al. 1984). The site-specific nature of oyster physiology is recognized broadly (Fig. 5).

Across the farms analyzed in this study, temperature, salinity, TPM, and WC.Org were associated with changes in filtration physiology, but temperature and salinity had the most prominent association. As temperature and salinity decreased so did median FR, CR, RR, and AR, regardless of farm location.

This positive relationship between temperature and oyster physiological activity is well known (Casas et al. 2018b; Kinsella 2019). In this study, a linear and consistently positive relationship was observed between temperature and filtration physiology. However, previous literature suggests the presence of an optimum temperature range for oysters, above and below which physiological activity declines rapidly and in a nonlinear fashion (Yu et al. 2017). Seasonal CR experiments using farmed *Crassostrea angulata* oysters in southern China showed a non-linear trend between CR

and temperature with CR measurements made in the field between 16.7 and 30.2 °C with a maximum oyster CR at 24.9 °C (Yu et al. 2017).

Studies suggest the optimal temperature for all Eastern Oyster physiology lies between 16 and 28 °C (Loosanoff 1958; Casas et al. 2018a) as warmer water with corresponding low oxygen levels may require oysters to transition to anaerobic respiration (less energetically favorable than aerobic respiration) (Pörtner 2010), while cooler temperatures slow the ectothermic oyster metabolic rate and reduces growth (Zuo et al. 2012) and the viscosity of the cooler water increases the energy necessary for cilia to function (Ward and Shumway 2004; Humphries 2013). This study likely exhibited a linear relationship between temperature and filtration physiology because the oysters did not experience thermal stress beyond the 16–28 °C thermal optimum. The highest experimental temperature in this study was 29 °C in Rehoboth Bay which may not have been high enough to see a decrease in oyster physiological activity. The water used in this study was also aerated which likely precluded the oysters from needing to transition to anaerobic respiration under warm conditions. Moreover, the lowest temperature in this study was recorded for Delaware Bay oysters examined in November 2020 (10.5 °C, Fig. 3) at a time when biodeposit production was too low for a successful experiment.

It is also possible that the thermal tolerance of oysters examined in this study influenced how strongly oyster filtration physiology was associated with temperature. Oysters in Delaware Bay may have had a higher thermal tolerance because the farm was intertidal and the oysters were exposed to extremely high temperatures during summer low tide exposure, whereas oysters from the other subtidal farms were not.

Delaware Bay oysters did not show signs of chronic stress, including thermal, as the oysters' condition were higher than the oysters at the other two farm sites. This elevated thermal tolerance may explain why filtration physiology of oysters from the Delaware Bay farm was not associated with temperature. In contrast, filtration physiology of oysters from Rehoboth Bay increased more with temperature than did the oysters at the other two farms. This may be related to the genetic diversity of Rehoboth and Barnegat Bay oyster stocks. Rehoboth Bay oyster seed largely came from one supplier, while Barnegat Bay seed came from multiple suppliers: this may lead the oyster population at Rehoboth Bay to be less genetically diverse than at Barnegat Bay. Greater genetic diversity, presumably, would allow an oyster population to be physiologically resilient over greater temperature extremes because each genetic strain may have a unique thermal tolerance. It is therefore possible the Rehoboth Bay oyster population was dominated by a genetic strain with lower thermal tolerance and was thus more sensitive to local changes in temperature.

Increased oyster physiological activity with increased salinity has been previously reported (Gray and Langdon 2019). Seasonal experiments conducted in Louisiana found oysters kept at about 22.8 parts per thousand (ppt) and subsequently exposed to 3 weeks of low salinity conditions (i.e., 3, 6, 9, 15, and 25 ppt) had greater CRs at 15 and 25 ppt than in the lower salinity conditions (Casas et al. 2018a). In contrast, a Florida field study of oysters naturally exposed to salinity between 21.9 and 33.1 ppt found that while salinity was positively correlated with absorption efficiency, no correlation was found with CR, FR, or AR but oyster physiological rates were highest in experiments with the highest salinity (Galimany et al. 2017a).

Oysters are known to tolerate 5 to 40 ppt (Shumway 1996) with an optimum salinity range estimated between 10 and 28 ppt (Loosanoff 1965). Low salinity conditions are harmful to oysters because the water chemistry hinders metabolism and intracellular ion and acid base regulation (Ballantyne and Berges 1991; Dickinson et al. 2012). As such, it is expected that filtration physiology of oysters examined in this study would be depressed by low salinity, which is evident in the positive association between median filtration physiology and mean salinity found in this study. The filtration physiology of oysters from Delaware Bay was the most influenced by salinity, which may be due to the fact that Delaware Bay had significantly lower salinity than the other two locations. Bivalves that experience conditions closer to the thresholds of their environmental optimum (like the 10–28 ppt optimum salinity for oysters) have been found to be more sensitive to changes in those environmental conditions (Galimany et al. 2017a).

The trends in filtration physiology were not uniform among locations with respect to TPM and WC.Org. While

an increase in TPM corresponded to an increase in median FR, RR, and AR, this relationship was clearest in Barnegat and Rehoboth Bays for median RR. Furthermore, while an increase in WC.Org was linked with a decrease in median FR and RR at all farms, the relationship to WC.Org and median FR was strongest in Barnegat Bay. These trends are likely related to the selective feeding ability of oysters. Oysters have several mechanisms by which they can maximize the organic/inorganic ratio of particles ingested (Newell and Jordan 1983; Shumway et al. 1985; Ward et al. 1998; Espinosa and Allam 2021) including rejecting excess inorganic matter as pseudofeces through pre-ingestive selection (Newell and Jordan 1983; Hawkins et al. 1996; Ward and Shumway 2004). Pre-ingestive selection is particularly beneficial in turbid environments with elevated TPM (Hawkins et al. 1996), and evidence suggests oysters can be more effective at this selection mechanism compared to other bivalves (Galimany et al. 2017b). Oysters in Barnegat and Rehoboth Bays performed according to what has been observed in other studies: as TPM increased so did RR, suggesting efficient pre-ingestive selection (Galimany et al. 2017b). This trend was not seen in oysters from Delaware Bay, possibly because environmental conditions there preclude efficient pre-ingestive selection. Delaware Bay had significantly higher TPM and lower organic content than the other two farms. Studies show high particle concentrations can clog oyster gills making it energetically unfavorable for oysters to feed (Widdows et al. 1979; Bayne and Newell 1983; Gray and Langdon 2019). *Crassostrea gigas*, for example, can maintain constant feeding up to a natural seston TPM of 50 mg L⁻¹, but CR declines as TPM increases above that threshold (Barillé and Prou 1993). In this way, the environmental conditions at the Delaware Bay site may be less favorable to oysters that may also be experiencing low salinity as discussed earlier.

The lack of a seasonal trend in oyster filtration physiology at Delaware Bay may be explained by rain events that occurred the day before the August 2021 experiment which resulted in a higher than mean TPM (413.7 mg L⁻¹) at the Delaware Bay site (as well as a lower mean salinity of 17.8 ppt and WC.Org of 13.0%). While conditions during the August experiment date were relatively normal, it is possible the storm the day prior disturbed the oysters in such a way that depressed feeding behavior the following day. Indeed, short-term environmental perturbations including increased TPM have been associated with reduced bivalve physiological activity during and in the days following the stress event (Poirier et al. 2021). This underscores the value of making conservative estimates of ecological filtration to account for days of low physiological activity triggered by increased sedimentation (Poirier et al. 2021) or other environmental stressors. Indeed, as the intensity and frequency of rainfall events along the east coast of the USA increase with climate change (Sanderson et al. 2019; Maxwell et al.

2021), conservative estimates of ecological filtration may be necessary.

A range of filtration physiology values was observed among individual oysters during each experiment. Previous studies have anticipated feeding rates in nature would vary more than in a laboratory physiology experiment (Grizzle et al. 2008). Individual oyster feeding rates are rarely reported, and those that are reported show a range of filtration physiology values similar to this study including do Nascimento et al. (2022) showing about $\pm 0.6 \text{ L h}^{-1} \text{ g}^{-1}$ of SD for CR of *Crassostrea* species and with Galimany et al. (2017a, b) showing about $\pm 1.4 \text{ L h}^{-1} \text{ g}^{-1}$ of SD for CR of *Crassostrea virginica*. As such, this study is on par with the range of filtration physiology exhibited in similar experiments and demonstrates the individual variability of oyster feeding behavior.

Implications to the Biodeposition Method

Improvements can be made to the biodeposition method that may increase the accuracy of future filtration physiology studies. The largest inconsistency among biodeposition experiments concerns when to start collecting biodeposits. In this study, biodeposits were collected after an experiment-specific GTT had elapsed to ensure biodeposits collected were a product of ambient water flowing through the filtration chamber. The GTT protocols used in this study provide a good estimate of GTT, but the methods herein assumed all oysters in the filtration chamber started to feed when submerged in the filtration chamber. Qualitative observations indicated some oysters did not begin to feed until the final 20-min of the experiment, but those biodeposits were still analyzed because the time of initial biodeposit production was not recorded. This likely contributed to some of the variation observed in filtration physiology during each experiment as initial biodeposits produced by an oyster in the flow-through chamber could have been generated from farm water in the hours or day before an experiment (oysters can remain closed for 8 h under ambient conditions (Poirier et al. 2021), and seston can remain in an oyster's digestive system for more than 7 h (Bayne et al. 1984)) when farm water may have been drastically different.

Other oyster filtration studies have used varying approaches which may, likewise, bias experimental results by omitting oysters from analyses based on specific behavioral traits, such as removing oysters from analyses if biodeposits were not produced in the first hour (Hoellein et al. 2015), removing a set of oysters from a physiological model when measured CRs at 20 °C were too low (Newell and Koch 2004), or not accounting for GTT at all. While no method may overcome all biases, possible solutions to minimize bias include taking biodeposits from multiple oysters at once and averaging those values (Zu Ermgassen et al.

2013; Gray and Langdon 2019) or measuring filtration over a period of days (Palmer 1980; Yu et al. 2017).

Implications to Ecological Estimates of Filtration

The filtration physiology data collected in this study will help to improve ecological estimates of oyster water quality benefits in several ways. First, the observed relationships between environmental parameters and filtration physiology could be used to improve the process of modifying built-in “maximum CR” values in models. When site-specific data are unavailable, models for estimating the water quality benefits of oysters typically use a maximum CR from the literature derived under laboratory conditions (e.g., Gray et al. 2022) and modify the maximum CR value based on environmental variables (Ehrich and Harris 2015; Gray et al. 2022). It is well understood that models estimating ecological filtration need to incorporate the influence of environmental drivers on individual oyster CRs rather than using average physiological rates (Ferreira et al. 2007; Ehrich and Harris 2015; Cubillo et al. 2018; Gray et al. 2022), but some existing models do not include sensitivity thresholds reflective of those observed in this study. For example, CR at the farms examined in this study decreased in salinities ranging from between 21.0 and 29.6 ppt, yet previous models have assumed salinities above 7.5, 10.3, and 12.1 ppt have no impact on CR (Powell et al. 1992; Cerco and Noel 2005; Fulford et al. 2007; Ehrich and Harris 2015). Temperature and salinity had the largest influence on oyster filtration physiology in this study, and models may therefore benefit from physiological model parameters that respond to these two environmental variables.

Incorporating information regarding the proportion of oysters that are actively feeding at any given time would also improve the accuracy of models estimating ecological filtration. In this study, an average of 70% of oysters fed during a filtration experiment indicating oysters in a population do not all feed at the same time. Although the proportion of oysters open has been used previously to model clearance in oyster populations (Comeau 2013), it remains an important yet frequently overlooked component of modeling oyster ecological filtration.

Finally, the filtration physiology collected in this study captures seasonal information regarding what oysters remove from the water column and what they put back into the environment via biodeposition. Traditional models estimating population- or ecosystem-scale oyster filtration tend to focus on CR and FR, without also estimating the biomass of deposits to the benthic system. While the impacts of bivalve aquaculture are localized (Lunstrum et al. 2018; Turner et al. 2019) and biodeposits can effectively enhance net ecosystem losses of nitrogen and phosphorus (Newell et al. 2005; Humphries et al. 2016; Rose et al. 2021), the reintroduction

of nutrients to the benthos should not be ignored. Indeed, a recent study found juvenile oysters (< 14 months) contribute more nutrient rich biodeposits to the benthic environment than older oysters (Locher et al. 2021) which could be relevant to the young age classes typically found on oyster farms. Furthermore, reporting CR and FR estimates alone may give the false impression that bivalves absorb all of what they take in, whereas a comparison of FR and RR is more accurate for bioextraction purposes. For example, an oyster observed in July 2021 from Barnegat Bay deposited $218.1 \text{ mg h}^{-1} \text{ g}^{-1}$ of pseudofecal biodeposits while removing $253.6 \text{ mg h}^{-1} \text{ g}^{-1}$ of particulate matter from the water column when feeding. While stand-alone models to predict biodeposition at bivalve farms (Hayakawa et al. 2001; Weise et al. 2009; Testa et al. 2015) and models to connect estimates of water quality improvements and settling biodeposits (Granada et al. 2018) exist, additional models are needed to provide a more holistic understanding of oyster farms' ecological influence (Newell 2007).

Implications to Aquaculture

The seasonal feeding behavior described in this study via CR, FR, AR, and RR supports the use of aquaculture as a tool for nutrient management in coastal water bodies. The impact of oyster farms to local water quality can be negligible given site-specific conditions like high flushing rates that dilute improvements over a greater volume of water (Turner et al. 2019), but understanding how individual farms contribute to water quality improvement can help water quality managers incorporate oyster aquaculture into robust nutrient reduction strategies. A robust nutrient reduction strategy is one that compares the expected water quality benefits generated by all feasible nutrient reduction best management practices (BMPs) for an area on a per-acre basis. In reality, the nutrient reduction strategy for a water body will be a combination of complementary BMPs that achieve the greatest water quality improvement while maintaining, or improving, ecosystem health.

The oyster filtration physiology and environmental data collected in this study will help water quality managers and farmers plan future farms that maximize environmental benefit as well as oyster productivity. Interest is growing to use multifaceted and inclusive models to improve siting decisions for farm leases such that the models consider both conflict minimization (e.g., competing uses for potential farm sites) and good conditions for growing shellfish to market size quickly (Bricker et al. 2016; Snyder et al. 2017). This study identifies local environmental conditions that correspond with increased oyster feeding behavior that could inform the development of growth experiments and subsequent models for farm siting in the Mid-Atlantic.

Our results support the use of oyster aquaculture to reduce excess nutrients in coastal water bodies and provide data modelers can use to improve ecological estimates of aquaculture water quality benefits. This study provides one of the first estimates of year-round filtration activity of Eastern Oysters and will inform the sustainable growth of the USA oyster aquaculture industry.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s12237-023-01293-9>.

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Data Availability The data collected in this manuscript is not publicly available, but may be made available upon request by contacting the primary author.

Declarations

Conflict of Interest The authors declare that they have no conflict of interest.

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