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Analysis of temperature and salinity effects on growth and mortality of oysters (Crassostrea virginica) in Louisiana

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Analysis of temperature and salinity effects on growth and mortality of oysters (*Crassostrea virginica*) in Louisiana

A Thesis

Submitted to the Graduate Faculty of the
University of New Orleans
in partial fulfillment of the
requirements for the degree of

Master of Science
in
Biological Sciences

by

Troy Schlinger

B.S. Louisiana State University, 2012

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Abstract

Salinity (S) and temperature (T) control every facet of the eastern oyster (*Crassostrea virginica*) life cycle, principally reproduction, development, growth, and mortality. Previous studies conducted in the Breton Sound (BR) and Barataria (BA) estuaries have reported differences in growth and mortality rates between the basins. In the present study, environmental conditions were synchronized to compare growth and mortality rates between basins at similar combinations of T and S. Results indicate that when T and S are the same (synchronized), seasonal oyster growth and mortality rates differ between BR and BA. Seasonal analyses revealed that as salinities increased in both estuaries, growth rates generally increased, while mortality rates generally decreased. These findings suggest that basin-wide adaptations to local environmental conditions may exist.

Keywords: *Crassostrea virginica*, Louisiana, growth, mortality, temperature, salinity
Introduction

The importance of oysters in estuaries

The eastern oyster (*Crassostrea virginica*; hereafter, “oyster”) is a sessile bivalve that inhabits estuaries along the Gulf and Atlantic coasts of North America (Stanley and Sellers 1986). As classically defined, estuaries are semi-enclosed coastal bodies of water with a free connection to the open sea, and where sea water is measurably diluted with fresh water derived from land drainage (Pritchard 1967). Estuaries are transition habitats between inland freshwater and coastal marine environments, where the distribution of flora and fauna is correlated with salinity levels (Gunter 1961, Rakociński et al. 1992, Hastings 2009). The fresh water deposits large quantities of nutrients and sediment into the estuary, and leads to high levels of primary production and increased sustainability of marsh habitat (Pritchard 1967, Kennedy 1996, Chesney et al. 2000, Lopez et al. 2014, Wang et al. 2017). This primary production is transferred to secondary consumers like zooplankton and oysters, which in turn support species occupying high trophic levels, including many of commercial importance (Gunter 1961, Livingston et al. 1975, Weinstein 1979, Malone et al. 1986, Deegan 1993, Houde and Rutherford 1993, Kennedy 1996, Murrell et al. 2007, Hastings 2009).

The spatial and temporal distributions of estuarine species vary. In general, motile organisms enter the estuary in winter, spawn in shallow areas of the estuary during spring and early summer, then as they mature, move to deeper areas in the fall when the water begins to cool (Livingston et al. 1975, Weinstein 1979, Rogers et al. 1984). While some estuarine-dependent species are commercially important, such as Gulf menhaden (*Brevoortia patronus*), black drum (*Pogonias cromis*), sheepshead (*Archosargus probatocephalus*), southern flounder (*Paralichthys lethostigma*), blue crab (*Callinectes sapidus*), oysters, and various shrimp species (Penaeidae). Others are valued for recreational purposes, such as spot (*Leiostomus xanthurus*), Atlantic croaker (*Micropogonias undulatus*), red drum (*Sciaenops ocellatus*), and spotted seatrout (*Cynoscion nebulosus*) (Cake et al. 1983, Lassuy 1983, Muncy et al. 1984, Rogers et al. 1984, Jennings et al. 1985, Reagan et al. 1985, Gilbert et al. 1986, Stanley and Sellers 1986, Sutter et al. 1986, Houde and Rutherford 1993, Lowe et al. 2012).

Since 2000, commercially harvested species in the Gulf of Mexico, most of which are estuarine-dependent, have generated $13.1 billion (NMFS 2007). Specifically, Louisiana leads the nation in commercial oyster production and provides 40% of its national landings (Dugas et al. 1977, LDWF 2015, Banks et al. 2016) with an annual dockside value of nearly $67 million (Dugas et al. 1977, LDWF 2015). Gulf of Mexico estuaries provide the hydrodynamic and geomorphological features necessary for oyster proliferation, including hard substrates, shifting water currents, high solar radiation, shallow depths, and high rates of primary production (Butler 1954, Malone et al. 1986, Stanley and Sellers 1986, Kennedy 1996, Alber 2002, Murrell et al. 2007).


**Biology and environmental requirements of the oyster**


Oyster gonadal tissues begin to develop within 8 to 12 weeks of larval settlement (Coe 1934, Eble and Scro 1996), and gonads in juveniles contain both spermatogonia and oogonia (Coe 1934). Spermatogonia will develop faster than oogonia, resulting in initial higher abundances of males, but larger juveniles develop into females (Coe 1934). Oysters are protandric hermaphrodites, and as they grow, most will become female (Eble and Scro 1996). Individuals develop mature female cells faster as their metabolism increases, resulting in larger, predominantly female oysters (Coe 1934, 1944). Sexual differentiation occurs during winter when oysters are sexually inactive, and sex is influenced by food limitations, environmental stress, and proximity and sex of nearby oysters (Coe 1934, 1944, Thompson et al. 1996). As oysters continue to develop and grow, their gonads increase in size until they reach a “ripe” stage that precedes spawning (Eble and Scro 1996). Once gametes are fully ripe, and temperatures reach a certain minimum (>25°C in the Gulf of Mexico) spawning begins (Hopkins 1931, Dugas et al. 1977, Lorio and Malone 1994, Shumway 1996, Wilson et al. 2005, La Peyre et al. 2013, Swannack et al. 2014).


The fertilized egg (zygote) develops into a blastula within about 3 hours and subsequently into a gastrula within about 5 hours. Within 10 hours the free-swimming trochophore larva hatches from the zygote and possesses a girdle of cilia used for propulsion (Galtsoff 1964, Loosanoff


In Louisiana, oyster growth rates vary among years and locations, but growth generally increases at higher temperatures and moderate salinities, with optimum growth occurring between 20°C-25°C and salinities of 10-15 (Menzel 1951, Loosanoff 1953, Harding 2007, Kraeuter et al. 2007, Wang et al. 2008, Rybovich 2016, Lowe et al. 2017). The combined effects of early sexual development and year-round warm temperatures result in rapid growth rates in the northern Gulf of Mexico (Menzel 1951, Shumway 1996), and in Louisiana newly attached spat may reach
seed-size in less than 2 months (Moore 1899, Menzel 1951, Mackin 1959, Cake 1983, Kraeuter et al. 2007, La Peyre et al. 2016). In contrast, Atlantic coast spat may take 4 months to do the same (Paynter and Dimichele 1990, Kraeuter et al. 2007). As oysters mature, growth rates tend to slow due to an ontogenetic shift of energy being diverted from growth to reproduction (Butler et al. 1954, Kraeuter et al. 2007, Wang et al. 2008, Kelly et al. 2011, Lowe et al. 2017). Growth rate ranges for Louisiana spat, seed, and market-sized oysters are: 3.5-16.93 mm per month (mo^(-1)), 1.28-6.0 mm mo^(-1), and 1.0-1.5 mm mo^(-1), respectively (Kraeuter et al. 2007, Lowe et al. 2017).

In the Gulf of Mexico, maximum growth rates correlate with areas having lower salinities and higher water temperatures than in Atlantic populations (Menzel 1951, Loosanoff 1953, Galtsoff 1964, Shumway 1996, Kraeuter et al. 2007, La Peyre et al. 2016, Proestou et al. 2016, Rybovich et al. 2016, Lowe et al. 2017). When conditions are favorable in the Gulf of Mexico, oysters can reach market size in 12 months, whereas in Atlantic populations, market-size can take 3-5 years (Menzel 1951, Mackin 1959, Paynter and Dimichele 1990, Lorio & Malone 1994).

Oysters can withstand extreme temperatures, both low and high; however, the rates at which these changes occur play a more important role than temperature alone (Shumway 1996). A short exposure to high temperatures or a long exposure to low temperatures can both be fatal (Garton and Stickel 1980, Shumway 1996, La Peyre et al. 2003, Lowe et al. 2017). Higher salinities (>20) and temperatures (>25°C) can promote faster growth, but can also result in greater predation and disease (Butler 1954, Garton and Stickel 1980, Ewart and Ford 1993, Shumway 1996, La Peyre et al. 2003, Mann and Powell 2007, Soniat et al. 2012, Lowe et al. 2017). Major predator species include sheephead, black drum, blue crab, and the southern oyster drill (Stramonita haemastoma) (Butler 1954, Nichy and Menzel 1960, Galtsoff 1964, Jennings et al. 1985, Sutter et al. 1986, Shumway 1996, Hastings 2009, Kulp et al. 2011). Predators generally prey on spat and seed oysters due to their smaller and thinner shells (Sutter et al. 1986), whereas market-sized oysters’ larger, thicker shells make them less susceptible to predation (White and Wilson 1996).


Shifting estuarine environmental conditions can lower salinities and temperatures below a survivable threshold (<8 and <15°C) for predatory and disease-causing organisms (Butler 1954, Shumway 1996, Mann and Powell 2007). Such low salinities will, however, stress oysters and cause them to reduce filtration, osmoregulation, and metabolic rates (Loosanoff 1953, Andrews 1958, Shumway 1996, Wilson et al. 2005, La Peyre et al. 2013, Rybovich et al. 2016). Reductions in osmoregulation can lead to an imbalance in the equilibrium of internal body fluids surrounding the heart, and reduce its water pumping and respiration rates (Galtsoff 1964, Hand and Stickel 1977, Shumway 1996, Swanson 1998). When environmental conditions exceed...
tolerance limits, oysters will close their valves to conserve energy to avoid adverse conditions (Newell and Langdon 1996, Mann and Powell 2007, Parker et al. 2013). If this is sustained for prolonged periods, mortality will ensue (Shumway 1996).

**Wetland loss and freshwater diversions**

Coastal wetlands offer numerous ecosystem services that benefit both humans and the environment. They provide natural buffers against storm surges, protect inland areas that harbor fisheries, and enhance nutrient cycling and water filtration (Rakocinski et al. 1992, LDNR 1998, Alber 2002, Seo et al. 2008, Engle 2011, Couvillion et al. 2013, La Peyre et al. 2016). Coastal Louisiana marshes are frequently degraded by saltwater intrusion, erosion by wave action, and land subsidence (USACE 1984, Rybczyk and Cahoon 2002, Morton et al. 2003, Cowan et al. 2008, Couvillion 2013). Since 1932, Louisiana has lost over 1,800 square miles of coastal wetlands (LDNR 1998, Couvillion et al. 2011). To combat coastal erosion in Louisiana and provide federal funding for wetland restoration, the United States Congress enacted the Coastal Wetlands Planning, Protection, and Restoration Act (CWPPRA) in 1990. After Hurricanes Katrina and Rita devastated coastal Louisiana in 2005, the Coastal Protection and Restoration Authority (CPRA) was formed by restructuring and combining Louisiana’s various wetland conservation and restoration authorities to form a more centralized governing organization (CPRA 2012). CPRA created the “Coastal Master Plan” in 2012, with the goal of “reducing economic losses to homes and business from storm surge-based flooding, promoting sustainable ecosystems, providing habitats for a variety of commercial and recreational activities coast-wide, strengthening communities, and supporting businesses and industry in Louisiana” (CPRA 2012). The Coastal Master Plan implements FDS, levee and floodwall systems, sediment diversion structures (SDS), shoreline and marsh creation activities, and other coastal restoration projects.

Mississippi River FDS were constructed to manage flood stages and isohalines to enhance marsh vegetation growth, reduce marsh loss, and increase fisheries productivity (USACE 1984, LDNR 2003, Hastings 2009, CPRA 2012, Lopez et al. 2014). The FDS can deliver massive amounts of freshwater in short periods of time, resulting in drastically altered temperatures and salinity levels. For example, the Davis Pond FDS can deliver up to 300 m³ s⁻¹ of freshwater to the Barataria Estuary when running at full capacity (USACE 1984). Over the years, management practices have influenced the timing and quantities of freshwater pulses delivered to estuaries (Cake 1983, La Peyre et al. 2003, Wilson et al. 2005, Parker et al. 2013, Lopez et al. 2014, La Peyre et al. 2016). In coastal estuaries, salinity gradients define the distributions of marine organisms, specifically sessile organisms, like the eastern oyster (Butler 1954, Gunter 1961, Melancon et al. 1998, Wagner 1999, Livingston et al. 2000, La Peyre et al. 2003). Changes in salinity regimes resulting from freshwater diversions portend a seaward shift in oyster distributions (Soniat et al. 2012).

Current oyster management combines annual stock assessments, environmental parameters, and biological information to predict the success of oyster populations (LDNR 2003, LDWF 2015). Oyster management uses habitat suitability index (HSI) models to examine environmental parameters of an area and assess their suitability to support oysters (Cake 1983, Soniat et al. 2013, LDWF 2015, La Peyre et al. 2016). These models, however, provide no information on historical trends of salinity patterns that affect oyster populations (Dugas et al. 1977, United

Decline of the public fishery


In an effort to evaluate the health of the public resource and better inform management decisions, a Sustainable Oyster Shellstock Budget Model (SOSBM) was developed by Soniat et al. (2012). The SOSBM is a numerical model for sustainable management of oysters in Louisiana which emphasizes the primacy of managing for no net shell loss over management of sustainable abundances (Soniat et al. 2012, 2014). Primary model components calculate growth, natural mortality, fishing mortality, culch density, and sacks of seed- and market-sized oysters harvested. Soniat et al. (2012) recommended that the SOSBM be refined by developing new growth and mortality equations to account for regional variations in environmental conditions. Lowe et al. (2017) refined those equations established in the SOSBM by analyzing long-term coast-wide oyster reef monitoring programs in relation to the combined effects of temperature and salinity on growth and mortality. By improving the parameterization of stock assessments and habitat suitability models, work done by Lowe et al. (2017) helps managers mitigate the potential impacts of climate change and freshwater inputs on the valuable public oyster resource.

**Objectives**

The purpose of this work is to build upon the natural mortality and growth rates defined in Lowe et al. (2017) by analyzing long-term environmental and biological data from LDWF Nestier trays in the Breton Sound and Barataria estuaries. Understanding the dynamic effects of local environmental conditions on growth and mortality rates is critical in predicting oyster population dynamics (Shumway 1996, Mann and Powell 2007, Soniat et al. 2012, La Peyre et al. 2013, 2016, Puckett and Eggleston 2016, Lowe et al. 2017). Due to variable releases of the Davis Pond FDS in Barataria Estuary and Caernarvon FDS in Breton Sound Estuary, temperatures and salinities may differ between basins. Studying the differences, if present, will quantify the effects of two important environmental drivers on local oyster population dynamics. By analyzing the growth and mortality rates of each basin and relating those to the range of seasonal salinities and temperatures, periods of maximum growth and minimum natural mortality can be identified. These regional growth and mortality rates can then be integrated into equations that drive the SOSBM, with the potential of using the updated model as an environmentally driven predictor for future management practices.

**Methods and Materials**

**Study sites**

The study area encompasses two of the most important public oyster management areas in coastal Louisiana (LDWF 2015), Breton Sound and Barataria Estuary (Figure 1). While the southern section of Breton Sound is historically the most productive oyster seed ground (LDWF 2011), Barataria Estuary oyster production has expanded in recent years. Barataria Estuary is a 628,000 hectare (ha) mesohaline estuary located south of New Orleans, Louisiana and bounded by Bayou Lafourche to the west and the Mississippi River on the eastern edge (Hopkinson and Day 1979). The basin is characterized by bottomland hardwoods upstream and extensive barrier islands downstream, and is home to major natural and artificial oyster producing areas (LDWF 2015). The basin is strongly influenced by the Davis Pond FDS which was constructed in 2002 to reduce the effects of saltwater intrusion and create more marsh habitat for fish and wildlife populations. The Davis Pond FDS can deliver up to 300 m$^3$ s$^{-1}$ of freshwater to the Barataria
Estuary, but has a mean annual outflow of 63 m$^3$ s$^{-1}$. Breton Sound is a 271,000 ha estuary consisting of micro-tidal bays and bayous ranging from fresh water habitats to saline marshes (La Peyre et al. 2013) with an abundance of POSG and oyster reservations. The Breton Sound Estuary is located east of the Mississippi River and below the Mississippi River Gulf Outlet (MRGO). Local hydrology is influenced by the Bohemia Spillway and the Caernarvon FDS, and main-stem Mississippi River distributaries in the southern areas (LDWF 2011). Caernarvon was constructed in 1991 by the United States Army Corps of Engineers (USACE) with an initial goal of improving estuarine environments by reducing saltwater intrusion and retarding the rate of coastal land loss (USACE 1984). Over the years, however, management practices have varied in response to anthropogenic influences, with experimental pulses being delivered at different times of the year (La Peyre et al. 2016). Breton Sound differs from the Barataria Estuary in that there are fewer barrier islands protecting Breton Sound, making it more vulnerable to saltwater intrusion from fronts, tides, and wind-driven advection (La Peyre et al. 2016).

Figure 1. Study area with locations for monthly Nestier tray stations (triangles), continuous data recorders (closed circles), and freshwater diversion structures (FDS) (open circles).
**Experimental tray construction**

With the development of FDS programs, oyster resources in both estuaries were monitored using experimental trays of individually marked oysters (hereafter, “Nestier trays”) with the explicit goal of understanding the effects of FDS on oyster growth and mortality (LDNR 2003). The Nestier tray monitoring program began in 1988 in Breton Sound and then replicated in Barataria Estuary beginning in 1998. For this study, we treat 1998 as the initial year of the study in both basins. Both studies concluded in 2013. The Barataria Estuary contained 12 study sites and Breton Sound contained 26 (Figure 1). Large seed- (> 50 mm shell height) and market-sized (≥ 75 mm shell height) oysters from commercial oyster fishermen within each estuary were used to construct experimental trays. Oyster were culled and cleaned at LDWF facilities. A smooth surface was created on the oyster shell for marine epoxy to connect a cable tie from the oyster to a 23” x 23” x 2-7/8” Buckhorn Oyster Grow Out Tray®. Each January, two trays with a new set of 20 oysters each were deployed on the bottom at each site and attached to PVC poles by a 15’ rope. To differentiate trays, 3 knots were tied in one of the ropes of one tray, where the rope met the tray, thus creating “knot” and “no-knot” trays. Oysters were numbered from 1-20 in each tray and growth and mortality were monitored at different time intervals (see “Oyster growth and mortality” below).

**Environmental data**

A combination of discrete and continuous environmental data was used to derive daily salinity and temperature profiles for each station. Discrete bottom water temperature and salinity data were collected monthly at each Nestier tray site with a YSI Professional Series handheld multimeter. At deeper sites (>1 m depth), temperature and salinity readings were taken at 0.3 m below the water surface and 0.3 m above the bottom and averaged for analyses. Discrete monthly data represent the end points between sample dates, and fail to capture the full range of environmental conditions experienced over the interval (i.e., daily variation in water quality during the days between measurements). To fully capture the range of environmental conditions to which experimental oysters were exposed, discrete data from other LDWF fisheries independent monitoring programs from 1998-2013 (133 stations; hereafter “external data”) were combined with the environmental data from each Nestier tray site. These programs included monthly oyster dredge, finfish gillnet, seine, and trammel, and bottom trawl programs conducted monthly by LDWF since 1966. For external data to be included in the set of discrete data points, they had to be within 3 km from the Nestier tray station and have a direct hydrological connection (i.e., not separated by a land mass). Temperature and salinity values that were out of range for the time of year were discarded. After removal of erroneous data points mentioned above, a daily time series of salinity and temperature for each station was constructed following the approach below.

A natural polynomial smoothing spline was fit to the time-series of discrete temperature and salinity data points from all data sources. Smoothing splines are series of linear segments connected at points of inflection (i.e., “knots”) and are commonly used to smooth data (see Appendix). In our case, smoothing splines were used to interpolate daily temperature and salinity values between sampling dates for each oyster station. To balance ecological realism and
limit over-fitting the model to the data, a limited number of knots (< 20/year) were used to smooth the data. The smoothing spline was forced through or near the discrete data points associated with each Nestier tray by weighting the data such that Nestier trays had a weighting factor of 1.0 and external data a factor of 0.75.

To verify the accuracy of constructed splines, daily temperature and salinity observation from nearby United States Geological Survey (USGS) data recorders (hereafter, “continuous data”) were regressed against predicted daily temperature and salinity splines from each study site. Continuous data recorders included were: Barataria Estuary (USGS 73802512, USGS 292800090060000, USGS 292859090004000, USGS 291929089562600, USGS 73802516) and Breton Sound (USGS 07374527, USGS 07374526, and USGS 073745258) (Figure 1).

**Synched environmental stanza identification**

Temperatures throughout the year did not differ between the two basins (Lowe et al. 2017); therefore, seasonality was used as a proxy for temperature. Salinity was greater in Barataria Estuary than in Breton Sound (Lowe et al. 2017). However, Breton Sound had more available data from Nestier trays than Barataria Estuary (Tables 1 and 2). For each year and season combination, constructed splines were first visually inspected to identify stations within each estuary where oysters were experiencing the same salinity (assuming similar temperatures) conditions (hereafter “synched environmental stanzas”). Upon initial identification of these stanzas, a forward selection stepwise removal of outliers was employed to 1) remove stations within each estuary with out-of-range salinity values that could not be reliably paired to a station in the other estuary, and 2) equalize sample sizes. By isolating synched stanzas, we could test the hypothesis that growth and mortality does not differ between the estuaries when oysters experience the same environmental conditions.

**Oyster growth and mortality**

Nestier tray oysters were used to calculate standardized growth and mortality at each station. Shell height (SH) for each individual oyster was measured to the nearest millimeter at initial deployment and then again in March, June, September and December roughly corresponding to: winter (January-March), spring (March-June), summer (June-September) and fall (September-December) seasons. Growth was calculated as the difference between successive SH measurements and standardized to monthly growth rates (mm mo⁻¹) by dividing the total growth by the number of days in the measurement interval and then multiply by the number of days in an average month (30.4 day mo⁻¹) (Table 1). Oyster mortality (# live/# dead) was recorded monthly and instantaneous mortality was calculated between sampling dates. If two consecutive counts were recorded as dead, then that oyster was removed from the analysis. By doing this, artificial inflation or deflation of mortality estimates were prevented. Monthly mortality was calculated [#dead/(#live+#dead)] and reported as proportion of dead to total oysters per site (Table 2). Data from each estuary were removed from analyses when trays were lost due to storm events or theft, when 100% mortality occurred, when oysters were inexplicably missing, or when Nestier trays were not monitored (La Peyre et al. 2016).
Prior to analysis, the assumptions of normality and homogeneity of variance for oyster growth and mortality were checked using Shapiro-Wilk and Levene’s tests, respectively. Data regularly violated both assumptions and were subsequently transformed. Several common transformations were explored, and the square root transformation performed best for normalizing both salinity and growth data across all seasons (Table 3). A logit transformation was used for the binomial mortality data rather than an arcsin transformation because interpretations were more natural and simple, and the power tended to be higher across all seasons (Table 4) (Warton and Hui 2011). Though the transformed data do not meet the assumptions of normality or heterodescacity, they are much improved (Table 2) and both analysis of variance and analysis of covariance are robust to all but the most extreme violations of these assumptions (Olejnik and Algina 1984, 1985; Schmider et al. 2010). Transformed salinity data were statistically compared and mean values

### Table 1
**Summary of data used in growth calculations.**

<table>
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</thead>
</table>

**Total stations** refers to total number of sample stations for each basin. "Stations used" refers to the actual number of stations which had useable data for the analyses. "Season" corresponds to sampling periods: winter (January-March), spring (March-June), summer (June-September), and fall (September-December). "Years" refers to the range for years in which data was collected and useable in analyses.

### Table 2
**Summary of data used in mortality calculations.**

<table>
<thead>
<tr>
<th>Basin</th>
<th>Total Stations</th>
<th>Stations Used</th>
<th>Season</th>
<th>Years Included</th>
<th>Total Measurements Used</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>26</td>
<td>14</td>
<td>Fall</td>
<td>1998-2004, 2007-2011</td>
<td>168</td>
</tr>
</tbody>
</table>

**Total stations** refers to total number of sample stations for each basin. "Stations used" refers to the actual number of stations which had useable data for the analyses. "Season" corresponds to sampling periods: winter (January-March), spring (March-June), summer (June-September), and fall (September-December). "Years" refers to the range for years in which data was collected and useable in analyses.

**Statistical analyses**

Prior to analysis, the assumptions of normality and homogeneity of variance for oyster growth and mortality were checked using Shapiro-Wilk and Levene’s tests, respectively. Data regularly violated both assumptions and were subsequently transformed. Several common transformations were explored, and the square root transformation performed best for normalizing both salinity and growth data across all seasons (Table 3). A logit transformation was used for the binomial mortality data rather than an arcsin transformation because interpretations were more natural and simple, and the power tended to be higher across all seasons (Table 4) (Warton and Hui 2011). Though the transformed data do not meet the assumptions of normality or heterodescacity, they are much improved (Table 2) and both analysis of variance and analysis of covariance are robust to all but the most extreme violations of these assumptions (Olejnik and Algina 1984, 1985; Schmider et al. 2010). Transformed salinity data were statistically compared and mean values
were retrieved from these analyses. An analysis of variance (ANOVA) was run for each season in order to compare salinity by basin. Tukey’s HSD was used to further examine significant differences within each independent variable.

<table>
<thead>
<tr>
<th>Season</th>
<th>p-value</th>
<th>Growth</th>
<th>Shapiro-Wilks</th>
<th>Levene’s</th>
<th>Salinity with Growth</th>
<th>Shapiro-Wilks</th>
<th>Levene’s</th>
<th>Salinity with Mortality</th>
<th>Shapiro-Wilks</th>
<th>Levene’s</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>Raw</td>
<td>log</td>
<td>Reciprocal</td>
<td>SQRT</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Growth</td>
<td>4.34E-07</td>
<td>0.0153</td>
<td>0.04139</td>
<td>4.61E-15</td>
<td>0.0169</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Salinity with Growth</td>
<td>7.77E-04</td>
<td>0.00023</td>
<td>3.37E-15</td>
<td>0.2204</td>
<td>0.0195</td>
<td>0.008818</td>
<td>0.92</td>
<td>3.26E-05</td>
<td>0.0002</td>
<td>1.50E-14</td>
</tr>
<tr>
<td>Spring</td>
<td>Growth</td>
<td>0.0014</td>
<td>0.0044</td>
<td>9.21E-15</td>
<td>0.61</td>
<td>0.00299</td>
<td>0.4003</td>
<td>0.03855</td>
<td>0.2818</td>
<td>0.0126</td>
</tr>
<tr>
<td>Salinity with Mortality</td>
<td>0.038</td>
<td>4.37E-09</td>
<td>2.20E-16</td>
<td>0.05</td>
<td>0.04</td>
<td>0.84</td>
<td>0.86</td>
<td>0.37</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer</td>
<td>Growth</td>
<td>8.90E-05</td>
<td>9.32E-05</td>
<td>2.20E-16</td>
<td>0.813</td>
<td>0.404</td>
<td>0.5377</td>
<td>0.5337</td>
<td>0.421</td>
<td>0.0516</td>
</tr>
<tr>
<td>Salinity with Mortality</td>
<td>1.82E-04</td>
<td>0.07888</td>
<td>6.16E-15</td>
<td>0.5764</td>
<td>0.02575</td>
<td>0.1155</td>
<td>0.3146</td>
<td>0.04908</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fall</td>
<td>Growth</td>
<td>0.1455</td>
<td>0.01777</td>
<td>1.97E-08</td>
<td>0.3564</td>
<td>0.318</td>
<td>0.2863</td>
<td>0.18</td>
<td>0.2749</td>
<td>0.1105</td>
</tr>
<tr>
<td>Salinity with Mortality</td>
<td>0.07</td>
<td>0.001</td>
<td>5.08E-12</td>
<td>0.14</td>
<td>0.32</td>
<td>0.72</td>
<td>0.85</td>
<td>0.52</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Values were transformed to meet assumptions of normality and homogeneity of variance. Multiple transformations were tried and results show that the square-root (SQRT) transformation performed best. The robustness of the data compensated for non-significance when square-root transformations did not result in p-values >.05. Salinity was uniformly transformed for both growth and mortality analyses. Bold numbers represent significant (p<.05) values. Raw, original data; log, log-normal [log(10)]; reciprocal, 1/x; SQRT, square-root √(x).
A full factorial analysis of covariance (ANCOVA) was used to compare the linear relationship between salinity (covariate) and oyster growth or mortality (response variable) between estuaries (independent variable). Models for growth and mortality were developed for each season separately. In models where there was no significant interaction between salinity and estuary, a Tukey’s HSD posthoc test was used to compare estimated marginal means (i.e., at a common salinity value) for monthly growth and mortality rates. However, if there was a significant interaction (i.e., the regression lines were not parallel), comparing estimated marginal means would be inappropriate and an independent t test to compare slope values for each level of the

<table>
<thead>
<tr>
<th>Season</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>Raw</td>
</tr>
<tr>
<td>Mortality Shapiro-Wilks</td>
<td>2.20E-16</td>
</tr>
<tr>
<td>Levene's</td>
<td>0.09</td>
</tr>
<tr>
<td>Spring</td>
<td>Shapiro-Wilks</td>
</tr>
<tr>
<td>Mortality Levene's</td>
<td>0.022</td>
</tr>
<tr>
<td>Summer</td>
<td>Shapiro-Wilks</td>
</tr>
<tr>
<td>Mortality Levene's</td>
<td>0.7226</td>
</tr>
<tr>
<td>Fall</td>
<td>Shapiro-Wilks</td>
</tr>
<tr>
<td>Mortality Levene's</td>
<td>0.003</td>
</tr>
</tbody>
</table>

Values were transformed to meet assumptions of normality and homogeneity of variance. Multiple transformations were tried and results show that the logit transformation performed best. The robustness of the data compensated for non-significance when square-root transformations did not result in p-values >.05. **Bold** numbers represent significant (p<.05) values. Raw, original data; logit, log-odds \([x/(1-x)]\); arcsin, \(y=sin^{-1}x=arcsinx\).
independent variable was used. Summary models were created for growth and mortality for each season and adjusted means were back-transformed to display differences properly.

All spatial analyses and products were developed in Qgis (Qgis Development Team 2011). All statistical analyses were performed in R version 3.3.3 (R Core Team 2015). Packages used include ‘pspline’ (Ripley 2015) for the interpolated temperature and salinity splines, ‘pastecs’ for descriptive statistics, ‘compute.es’ for effect size, ‘effects’ for adjusted means, ‘multcomp’ for posthoc tests, ‘WRS2’ for robustness tests, ‘car’ for Levene’s test and Type III sum of squares and ‘ggplot2’ for graphing.

Results

Environmental conditions

Temporal cycles of water temperature varied within estuaries due to seasonality (see Appendix). However, mean water temperatures were consistent across sites within each season (i.e., no spatial variability). When water temperatures were analyzed during synched environmental stanzas, there were no differences between estuaries for either growth (Table 5; $F_{1, 362} = 0.064; p = 0.80$) or mortality (Table 6; $F_{1, 592} = 0.77; p = 0.38$).

### TABLE 5
Mean (range) of environmental conditions for growth analysis by season after synchronization.

<table>
<thead>
<tr>
<th>Basin</th>
<th>Winter</th>
<th>Spring</th>
<th>Summer</th>
<th>Fall</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean (°C)</td>
<td>Mean (°C)</td>
<td>Mean (°C)</td>
<td>Mean (°C)</td>
</tr>
<tr>
<td></td>
<td>(Range)</td>
<td>(Range)</td>
<td>(Range)</td>
<td>(Range)</td>
</tr>
<tr>
<td>Temperature</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Barataria</td>
<td>16.4 (11.1-25.4)</td>
<td>25.2 (22.7-27.7)</td>
<td>28.3 (15.8-31.6)</td>
<td>21.7 (18.0-32.2)</td>
</tr>
<tr>
<td>Breton</td>
<td>16.9 (11.3-24.9)</td>
<td>24.7 (22.9-28.1)</td>
<td>28.9 (24.9-30.9)</td>
<td>20.8 (17.2-23.8)</td>
</tr>
<tr>
<td>Salinity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Barataria</td>
<td>9.5 (1.3-22.3)</td>
<td>10.1 (3.0-19.5)</td>
<td>12.2 (4.8-23.4)</td>
<td>12.7 (5.0-18.4)</td>
</tr>
<tr>
<td>Breton</td>
<td>8.8 (1.6-22.0)</td>
<td>8.7 (3.0-20.0)</td>
<td>11.0 (3.9-20.9)</td>
<td>10.7 (3.3-17.0)</td>
</tr>
</tbody>
</table>

Mean conditions, with range in parentheses, for each season using interpolated data after synched stanzas were created.

### TABLE 6
Mean (range) of environmental conditions for mortality analysis by season after synchronization.

<table>
<thead>
<tr>
<th>Basin</th>
<th>Winter</th>
<th>Spring</th>
<th>Summer</th>
<th>Fall</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Mean (%)</td>
<td>Mean (%)</td>
<td>Mean (%)</td>
<td>Mean (%)</td>
</tr>
<tr>
<td></td>
<td>(Range)</td>
<td>(Range)</td>
<td>(Range)</td>
<td>(Range)</td>
</tr>
<tr>
<td>Temperature</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Barataria</td>
<td>16.6 (11.1-30.9)</td>
<td>24.2 (18.1-31.8)</td>
<td>29.1 (26.3-31.6)</td>
<td>21.9 (16.2-32.2)</td>
</tr>
<tr>
<td>Breton</td>
<td>16.5 (11.4-21.6)</td>
<td>24.5 (18.9-27.7)</td>
<td>29.5 (26.5-31.3)</td>
<td>21.0 (17.7-25.0)</td>
</tr>
<tr>
<td>Salinity</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Barataria</td>
<td>9.8 (1.3-22.3)</td>
<td>9.7 (0.7-19.4)</td>
<td>10.7 (1.5-23.4)</td>
<td>12.4 (2.2-21.8)</td>
</tr>
<tr>
<td>Breton</td>
<td>8.4 (2.4-22.0)</td>
<td>8.3 (1.0-20.0)</td>
<td>9.3 (3.1-20.9)</td>
<td>10.7 (3.8-22.3)</td>
</tr>
</tbody>
</table>

Mean conditions, with range in parentheses, for each season using interpolated data after synched stanzas were created.
Salinity cycles varied temporally, but, this was not due to seasonality (see Appendix). Salinity levels throughout the estuaries generally increased extending seaward and downstream (Figure 1). For each season, synched environmental stanzas revealed no differences in salinities between estuaries for the growth and mortality analyses (Table 7).

**TABLE 7**
Summary of transformed seasonal salinity during the periods of time in which useable oyster data were available

<table>
<thead>
<tr>
<th>Growth - Season</th>
<th>df</th>
<th>Sum Sq</th>
<th>F</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>1, 140</td>
<td>0.46</td>
<td>0.81</td>
<td>0.37</td>
</tr>
<tr>
<td>Spring</td>
<td>1, 85</td>
<td>1.19</td>
<td>3.35</td>
<td>0.07</td>
</tr>
<tr>
<td>Summer</td>
<td>1, 82</td>
<td>0.55</td>
<td>1.4</td>
<td>0.24</td>
</tr>
<tr>
<td>Fall</td>
<td>1, 48</td>
<td>1.19</td>
<td>3.56</td>
<td>0.07</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Mortality - Season</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
</tr>
<tr>
<td>Spring</td>
</tr>
<tr>
<td>Summer</td>
</tr>
<tr>
<td>Fall</td>
</tr>
</tbody>
</table>

df, degrees of freedom; Sum Sq, sum of squares value; F, F-statistic; p, p-value (<0.05)

**Growth**

**Winter**

Growth rates were determined from 108 Nestier tray samples from 9 stations in Barataria Estuary and from 180 samples from 15 stations in Breton Sound (Table 1). Growth rate increased significantly with salinity, and basin had a significant effect on oyster growth, but there was no interaction between independent variables (Table 8; Figure 2A). During the winter, growth rates ranged from 0.12 to 4.5 mm mo\(^{-1}\), and oysters consistently grew faster in Barataria Estuary (mean = 1.51 mm mo\(^{-1}\)) than in Breton Sound (mean = 1.06 mm mo\(^{-1}\)) (Figure 3A).

**Spring**

One hundred ten Nestier tray samples from 10 stations in Barataria Estuary and 154 samples from 14 stations in Breton Sound were used for spring growth analysis (Table 1). Both salinity and basin were significant drivers of market-sized oyster growth, but the interaction was not significant (Table 8; Figure 2B). Overall, oysters in Barataria Estuary grew faster than in Breton Sound (mean = 1.96 mm mo\(^{-1}\), 1.17 mm mo\(^{-1}\); respectively) (Figure 3A), with growth rates ranging from 0.11 to 4.02 mm mo\(^{-1}\).

**Summer**
Growth rates were determined from 120 Nestier tray samples from 12 stations in Barataria Estuary and from 140 samples from 14 stations in Breton Sound (Table 1). Summer growth rates ranged from 0.03 to 5.33 mm mo\(^{-1}\). Neither salinity nor basin had a significant effect on summer oyster growth (Table 8). There was, however, a salinity*basin interaction, but the slopes of the regressions did not significantly differ \( t (77.96) = -0.194, p > 0.85 \) (Figure 3B). At low salinities (<5), oysters grew faster in Barataria Estuary, than in Breton Sound. For instance, at a salinity of 5, Breton Sound oysters grew at a predicted rate of 0.92 mm mo\(^{-1}\), whereas oysters in Barataria Estuary grew at a predicted rate of 1.56 mm mo\(^{-1}\). However, at high salinities (>15), oysters grew faster in Breton Sound than in Barataria Estuary (Figure 2C). At a salinity of 15, Breton Sound oysters grew at a predicted rate of 2.05 mm mo\(^{-1}\), and oysters in Barataria Estuary grew at a predicted rate of 1.49 mm mo\(^{-1}\).

\textit{Fall}

In the Barataria Estuary, 88 Nestier tray samples from 8 stations were used for the fall growth analysis, and 91 Nestier tray samples from 13 stations were used from Breton Sound (Table 3). Salinity was the only significant driver of market-sized oyster growth, and basin and the interaction between independent variables were not significant (Table 8; Figure 2D). Fall growth rates ranged from 0.45 to 6.13 mm mo\(^{-1}\) and oysters grew slightly faster in Breton Sound (mean = 2.79 mm mo\(^{-1}\)) than in Barataria Estuary (mean = 2.38 mm mo\(^{-1}\)) (Figure 3A).
Figure 2. Seasonal regression models for market-sized growth rates. Data were transformed using a square-root function to fit the assumptions of normality and homogeneity of variance. Transformed data were statistically compared and mean values were retrieved from these analyses. Winter (January-March), Spring (April-June), Summer (July-September), and Fall (October-December).
<table>
<thead>
<tr>
<th>Season</th>
<th>df</th>
<th>Sum Sq</th>
<th>Mean Sq</th>
<th>F value</th>
<th>Pr(&gt;F)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>sqrtS</td>
<td>1</td>
<td>4.414</td>
<td>4.414</td>
<td>40.032</td>
</tr>
<tr>
<td></td>
<td>Bay</td>
<td>1</td>
<td>1.364</td>
<td>1.364</td>
<td>12.371</td>
</tr>
<tr>
<td></td>
<td>sqrtS:Bay</td>
<td>1</td>
<td>0.054</td>
<td>0.054</td>
<td>0.489</td>
</tr>
<tr>
<td></td>
<td>Residuals</td>
<td>138</td>
<td>15.218</td>
<td>0.11</td>
<td></td>
</tr>
<tr>
<td></td>
<td>sqrtS</td>
<td>1</td>
<td>1.292</td>
<td>1.2916</td>
<td>11.207</td>
</tr>
<tr>
<td></td>
<td>Bay</td>
<td>1</td>
<td>2.13</td>
<td>2.13</td>
<td>18.481</td>
</tr>
<tr>
<td></td>
<td>sqrtS:Bay</td>
<td>1</td>
<td>0.078</td>
<td>0.0779</td>
<td>0.676</td>
</tr>
<tr>
<td></td>
<td>Residuals</td>
<td>83</td>
<td>9.566</td>
<td>0.1153</td>
<td></td>
</tr>
<tr>
<td>Summer</td>
<td>sqrtS</td>
<td>1</td>
<td>0.379</td>
<td>0.3794</td>
<td>2.094</td>
</tr>
<tr>
<td></td>
<td>Bay</td>
<td>1</td>
<td>0.028</td>
<td>0.0277</td>
<td>0.153</td>
</tr>
<tr>
<td></td>
<td>sqrtS:Bay</td>
<td>1</td>
<td>0.728</td>
<td>0.7276</td>
<td>4.016</td>
</tr>
<tr>
<td></td>
<td>Residuals</td>
<td>80</td>
<td>14.493</td>
<td>0.1812</td>
<td></td>
</tr>
<tr>
<td>Fall</td>
<td>sqrtS</td>
<td>1</td>
<td>1.732</td>
<td>1.7316</td>
<td>11.204</td>
</tr>
<tr>
<td></td>
<td>Bay</td>
<td>1</td>
<td>0.193</td>
<td>0.1925</td>
<td>1.246</td>
</tr>
<tr>
<td></td>
<td>sqrtS:Bay</td>
<td>1</td>
<td>0</td>
<td>0.0001</td>
<td>0.001</td>
</tr>
<tr>
<td></td>
<td>Residuals</td>
<td>46</td>
<td>7.109</td>
<td>0.1545</td>
<td></td>
</tr>
</tbody>
</table>

sqrtS, salinity effect on growth; Bay, basin effect on growth; sqrtS:Bay, interaction between salinity and basin; Sum Sq=Sum of squares; Mean Sq=mean squared error. Significance values are in **bold**.
Figure 3A. Seasonal estimated marginal means (±SE) for market-sized oyster growth rates by basin. Winter (January-March), Spring (April-June), Summer (July-September), and Fall (October-December). “A” denotes significant salinity effect. “B” denotes significant basin effect. “AB” denotes significant salinity:basin effect. Statistical comparison was only valid if the interaction term (salinity:basin) in the model was not significant; however, using the mean seasonal salinity value (Table 5), mean seasonal growth rates for Summer could be determined. A standard error could not be calculated for significant interaction seasons. Growth values are reported as “mm per month”.

Figure 3B. ANCOVA (Table 8) indicated a significant interaction between salinity and basin. Pairwise comparisons of regression slope values (±SE) for summer growth analysis.
Mortality

Winter

One hundred ten Nestier tray samples from 10 stations in Barataria Estuary and 165 samples from 15 stations in Breton Sound were used for the winter mortality analysis (Table 2). Both salinity and basin were significant drivers of market-sized oyster growth, but the interaction was not significant (Table 9; Figure 4A). As salinity levels rose, mortality rates in both Barataria Estuary and Breton Sound decreased (Figure 4A). Overall, oysters in Barataria Estuary (mean = 0.098) had higher mortality rates than in Breton Sound (mean = 0.048) (Figure 5A).

Spring

Spring mortality rates were determined from 130 Nestier tray samples from 10 stations in Barataria Estuary and from 195 samples from 15 stations in Breton Sound (Table 2). Salinity, basin, and the interaction between both independent variables (salinity*basin) had a significant effect on oyster mortality (Table 9). The slopes of regression were significant $t(143.08) = 4.82$, $p<.05$ (Figure 5B), indicating that as salinity increases, mortality rates in Breton Sound lower more than in Barataria Estuary (Figure 4B). At low salinities (<5), Breton Sound experienced higher mortality rates (0.34) than in Barataria Estuary (0.31), and as salinities increased (>15), both estuaries’ mortality rates decreased, and Breton Sound (0.03) had lower mortality rates than Barataria Estuary (0.22) (Figure 4B).

Summer

Mortality rates were determined from 156 Nestier tray samples from 12 stations in Barataria Estuary and from 182 samples from 14 stations in Breton Sound (Table 2). Basin, salinity, and the salinity*basin interaction significantly affected oyster mortality during the summer months (Table 9). However, the regression slopes did not differ $t(144.15) = 1.84$, $p=0.068$ (Figure 5B), and only represented a small effect $r = 0.15$ (Figure 4C). At low salinity (5), oysters in Breton Sound (0.461) experienced higher mortality rates than in Barataria Estuary (0.459), and as salinities increased, both mortality rates decreased (Figure 4C). At a salinity of 15, mortality rates were higher in Barataria Estuary (0.22) than in Breton Sound (0.07).

Fall

In the Barataria Estuary, 108 Nestier tray samples from 9 stations were used for the fall mortality analysis, and 168 samples from 14 stations were used from Breton Sound (Table 2). The independent variable basin and the interaction of salinity*basin had significant effects on oyster mortality (Table 9). The regression slopes were significant $t(106.66) = 4.84$, $p<.05$ (Figure 5B), indicating that as salinity increases, mortality rates in Breton Sound will increase while Barataria Estuary mortality rates will decrease (Figure 4D). At a low salinity (5), predicted mortality rates were 0.05 in Breton Sound and 0.22 in Barataria Estuary. At a salinity of 15, predicted mortality rates in Breton Sound would be 0.09, but would still be lower than Barataria Estuary (0.16) (Figure 4D).
Figure 4. Seasonal regression models for market-sized mortality rates. Data were transformed to fit the assumptions of normality and homogeneity of variance. Using a square-root function for salinity and a logit function for mortality, data were statistically compared and mean values were retrieved from these analyses. Winter (January-March), Spring (April-June), Summer (July-September), and Fall (October-December).
TABLE 9
Seasonal results for basin comparison of market-sized oyster mortality
based on available, transformed Nestier tray data.

<table>
<thead>
<tr>
<th>Season</th>
<th>sqrtS</th>
<th>Df</th>
<th>Sum Sq</th>
<th>Mean Sq</th>
<th>F value</th>
<th>Pr(&gt;F)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>sqrtS</td>
<td>1</td>
<td>11.53</td>
<td>11.53</td>
<td>11.44</td>
<td><strong>0.000893</strong></td>
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<tr>
<td></td>
<td>Bay</td>
<td>1</td>
<td>25.13</td>
<td>25.131</td>
<td>24.935</td>
<td><strong>1.47E-06</strong></td>
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<tr>
<td></td>
<td>sqrtS:Bay</td>
<td>1</td>
<td>3.02</td>
<td>3.017</td>
<td>2.993</td>
<td>0.085443</td>
</tr>
<tr>
<td></td>
<td>Residuals</td>
<td>169</td>
<td>170.33</td>
<td>1.008</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Spring</td>
<td>sqrtS</td>
<td>1</td>
<td>22.1</td>
<td>22.11</td>
<td>9.923</td>
<td><strong>0.00197</strong></td>
</tr>
<tr>
<td></td>
<td>Bay</td>
<td>1</td>
<td>74.1</td>
<td>74.09</td>
<td>33.243</td>
<td><strong>4.48E-08</strong></td>
</tr>
<tr>
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<td>sqrtS:Bay</td>
<td>1</td>
<td>19.2</td>
<td>19.25</td>
<td>8.637</td>
<td><strong>0.00382</strong></td>
</tr>
<tr>
<td></td>
<td>Residuals</td>
<td>150</td>
<td>334.3</td>
<td>2.23</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer</td>
<td>sqrtS</td>
<td>1</td>
<td>64.7</td>
<td>64.69</td>
<td>24.063</td>
<td><strong>2.43E-06</strong></td>
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<tr>
<td></td>
<td>Bay</td>
<td>1</td>
<td>19.6</td>
<td>19.65</td>
<td>7.309</td>
<td><strong>0.00766</strong></td>
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<tr>
<td></td>
<td>sqrtS:Bay</td>
<td>1</td>
<td>12.3</td>
<td>12.26</td>
<td>4.56</td>
<td><strong>0.03438</strong></td>
</tr>
<tr>
<td></td>
<td>Residuals</td>
<td>148</td>
<td>397.9</td>
<td>2.69</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fall</td>
<td>sqrtS</td>
<td>1</td>
<td>1.59</td>
<td>1.593</td>
<td>1.417</td>
<td>0.2364</td>
</tr>
<tr>
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<td>22.918</td>
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<tr>
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<td>sqrtS:Bay</td>
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<td>5.387</td>
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<td>Residuals</td>
<td>111</td>
<td>124.75</td>
<td>1.124</td>
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<td></td>
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</tbody>
</table>

sqrtS, salinity effect on growth; Bay, basin effect on growth; sqrtS:Bay, interaction between salinity and basin; Sum Sq=Sum of squares; Mean Sq=mean squared error. Significance values are in **bold**.
Figure 5A. Seasonal estimated marginal means (±SE) for market-sized oyster mortality rates by basin. Winter (January-March), Spring (April-June), Summer (July-September), and Fall (October-December). “A” denotes significant salinity effect. “B” denotes significant basin effect. “AB” denotes significant salinity:basin effect. Statistical comparison was only valid if the interaction term (salinity:basin) in the model was not significant; however, using the mean seasonal salinity value (Table 6), mean seasonal growth rates for Summer could be determined. A standard error could not be calculated for significant interaction seasons. Mortality values are reported as #dead/(#dead+#live).

Figure 5B. ANCOVA (Table 8) indicated a significant interaction between salinity and basin. Pairwise comparisons of regression slope values (±SE) for mortality analyses with basin-salinity interaction. * denotes a significant difference in slopes of the regressions.
Discussion

Salinity and temperature control every facet of the oyster life cycle, principally reproduction, development, growth, and mortality (Butler 1954, Galtsoff 1964, Garton and Stickle 1980, Shumway 1996, Brown et al. 2004, Harding et al. 2008, Rybovich et al. 2016, Lowe et al. 2017). Growth and mortality rates have previously been reported in the Breton Sound and Barataria estuaries (Butler 1954, Kraeuter et al. 2007, La Peyre et al. 2016, Rybovich et al. 2016, Lowe et al. 2017). Lowe et al. (2017) provided a coast-wide model for environmentally-driven oyster growth and mortality rates in Louisiana. This study, however, synchronized environmental conditions to compare growth and mortality rates between two economically- and ecologically-important oyster-producing areas. Understanding regional temperature and salinity effects on oyster growth and mortality rates is critical for oyster management (Shumway 1996, Mann and Powell 2007, Soniat et al. 2012, La Peyre et al. 2013, 2016, Puckett and Eggleston 2016, Lowe et al. 2017). By analyzing long-term Nestier tray data, growth and mortality were found to vary across multiple years and seasons in both estuaries. This study suggests that even when two key environmental conditions (i.e., water temperature and salinity) are the same, seasonal oyster growth and mortality rates differ between Breton Sound (BR) and Barataria (BA) estuaries. These findings suggest that basin-wide adaptations to local environmental conditions may exist.

Oysters in both estuaries experienced extremes in temperature (>30°C or <5°C) and salinity (>30 or <5) and uncharacteristic seasonal conditions (e.g., relatively high winter temperatures). Analyses revealed there were highest combined mean temperatures during the summer (mean = BA: 28.7°C, BR: 29.2°C) and lowest combined mean temperatures during the winter (BA: 16.5°C, BR: 16.7°C), as was expected (Tables 5 and 6). Water temperature is a main driver of physiological processes such as ciliary activity, and temperatures exceeding 32°C lead to a rapid decline in feeding behavior (Galtsoff 1964). In Breton Sound and Barataria estuaries, temperatures exceeded 30°C no more than 46% of the time during summer (Lowe et al. 2017), making the possibility of a complete and continuous shutdown in feeding unlikely. Higher temperatures are often accompanied by low oxygen concentrations, which amplify the cumulative effects of interacting environmental stressors (Lenihan 1999, Levinton et al. 2013, Rybovich et al. 2016). At higher temperatures (>25°C) during the summer, Louisiana oysters can tolerate low salinity (0-5) for more than a month (Loosanoff 1953, Garton and Stickle 1980, White and Wilson 1996, La Peyre et al. 2003, Swannack et al. 2014, Leonhardt et al. 2017, Lowe et al. 2017). Seasonal analyses found the highest mean salinities during fall (BR: 10.7, BA: 12.7) and lowest during winter (BR: 8.4, BA: 9.8) (Tables 5 and 6). This study synched environmental conditions to analyze growth and mortality rates when temperature and salinity levels were the same during each season (Tables 3 and 4). These temperature and salinity levels are not the exact ranges or the extremes that oysters experienced in the Breton Sound and Barataria estuaries. The ranges of the synched stanzas are, however, comparable to those found in previous studies in the Gulf of Mexico and Louisiana (Butler 1954, Nichy and Menzel 1960, Soniat et al. 2012, La Peyre et al. 2013, 2016, Rybovich et al. 2016, Leonhardt et al. 2017, Lowe et al. 2017).

Louisiana market-sized oysters experience increased growth between 20°C-25°C and salinities between 10-15, and decreased mortality between 12°C-18°C and salinities between 9-13 (Butler 1954, Shumway 1996, La Peyre et al. 2016, Leonhardt et al. 2017, Lowe et al. 2017). Compared to spat and seed in Louisiana, market-sized oysters are reported to have a narrower range of tolerance for salinities and a broader range of tolerance for temperatures with respect to growth rates (Rybovich et al. 2016, Lowe et al. 2017). Seasonal analyses revealed that at higher salinities during each season, growth rates generally increase in both estuaries, with the exception of summer growth rates in Barataria Estuary which declined (Figure 2). The mortality analysis showed that mortality rates generally decreased as estuaries experienced higher salinities, except in Breton Sound where fall mortality rates increased (Figure 4). These results support the need for a better understanding of differences in environmental conditions that affect oyster performance in Louisiana estuaries (Shumway 1996, Mann and Powell 2007, Soniat et al. 2012, La Peyre et al. 2013, 2016, Leonhardt et al. 2017, Lowe et al. 2017).

Winter growth rates in the Barataria Estuary (mean = 1.51 mm mo⁻¹) were generally higher than in Breton Sound (mean = 1.07 mm mo⁻¹), regardless of salinity levels (Figure 2A and 3A), however, Barataria Estuary oysters also had higher mortality rates (0.098) than Breton Sound oysters (0.048) (Figure 4A and 5A). Compared with previous studies, the results of the combined mean winter growth (1.29 mm mo⁻¹) and mortality (0.073) rates are within the range of similar Louisiana data (Mackin 1961, La Peyre et al. 2003, Casas et al. 2005, Kraeuter et al. 2007, La Peyre et al. 2009, 2013, 2015, Rybovich et al. 2016, Lowe et al. 2017, Leonhardt et al. 2017, Munroe et al. 2017). The variables “basin” and “salinity” had significant effects on both growth and mortality levels (Tables 7 and 8). For both growth and mortality analyses, winter temperatures remained around 16.5°C and salinities remained around 8-10 (Tables 5 and 6). Mean temperature and salinity levels in synched stanzas (Table 5) were below the optimal range (temperatures: 20°C-25°C; salinities: 10-15) for successful oyster growth as previously defined in literature (Menzel 1951, Loosanoff 1953, Garton and Stickle 1980, White and Wilson 1996, La Peyre et al. 2003, Harding 2007, Kraeuter et al 2007, Wang et al. 2008, Rybovich 2016, Lowe et al. 2017).


Oysters can also experience decreased mortality during the winter due to mean temperatures and salinities being below the optimal level (>20°C and >12-15 salinities) for predator and Dermo

Spring environmental data used mean temperatures ranging from 24.2°C-25.2°C and mean salinities ranging from 8.3-10.1 (Tables 5 and 6). With mean temperatures near the upper end of the optimal range (20°C-25°C), salinity levels play a critical role in growth and mortality rates in both estuaries (Gunter 1952, Butler 1954, Gunter 1961, Galtsoff 1964, Cake 1983, Chatry et al. 1983, USACE 1984, Melancon et al. 1998, Engle and Summers 1999, Wagner 1999, Livingston et al. 2000, La Peyre et al. 2003, Casas et al. 2005, Kraeuter et al. 2007, La Peyre et al. 2009, 2013, 2015, Rybovich et al. 2016, Lowe et al. 2017, Leonhardt et al. 2017, Munroe et al. 2017). For both growth and mortality analyses, the variables salinity and basin had significant effects, and the interaction was significant in the mortality analysis (Tables 7 and 8). As salinities increased in both estuaries, growth rates increased (Figure 2B). Higher mean growth rates in the Barataria Estuary (1.96 mm mo⁻¹ versus BR: 1.17 mm mo⁻¹) might be attributed to higher mean salinities in Barataria Estuary (10.1) than in Breton Sound (8.7), which are within the optimal range for increased oyster growth (10-15) (Menzel 1951, Loosanoff 1953, Garton and Stickle 1980, White and Wilson 1996, La Peyre et al. 2003, Harding 2007, Kraeuter et al. 2007, Wang et al. 2008, Rybovich 2016, Lowe et al. 2017). The combined spring mean growth rate (1.57 mm mo⁻¹) was second highest behind the combined fall mean growth rate (2.58 mm mo⁻¹) (Figure 3A).


Using the mean spring salinities of each estuary (Table 6), the mortality analysis showed mean mortality rates (Figure 5A) in both estuaries (BA: 0.24, BR: 0.24) to be on the lower end of the range of similar data collected in previous Louisiana studies (Mackin 1961, La Peyre et al. 2003, Casas et al. 2005, Kraeuter et al. 2007, La Peyre et al. 2009, 2013, 2015, Rybovich et al. 2016, Lowe et al. 2017, Leonhardt et al. 2017, Munroe et al. 2017). Mean spring mortality rates in Breton Sound during periods of high salinities (15) were the lowest of all season/basin combinations (0.03). Mortalities can be low during the spring due to salinities being below the optimal level (>12-15) for Dermo and predator success (Butler 1954, Galtsoff 1964, Garton and Stickle 1980, Ewart and Ford 1993, Shumway 1996, Livingston et al. 2000, La Peyre et al. 2003, Wilson et al. 2005, Mann and Powell 2007, Harding et al. 2008, La Peyre et al. 2009, Soniat et al. 2012, Levinton et al. 2013, Lowe et al. 2017, Powell 2017). The spring FDS releases will also help deter Dermo infection, and lower mortality rates, by depositing freshwater into the estuaries during periods of Dermo proliferation (i.e., increasing temperatures) (Galtsoff 1964, Ewart and Ford 1993, La Peyre et al. 2003, Wilson et al. 2005, Harding et al. 2008, La Peyre et al. 2009, Levinton et al. 2013, Powell 2017). Mortality rates were lower in Barataria Estuary than in Breton Sound, however, as salinities increased, Barataria Estuary oysters experienced higher mortality than Breton Sound oysters (Figure 4B). As salinities increased, a shift in mean mortality rates occurred, suggesting a possible genetic adaptation to local environmental conditions, with better oyster survival in Breton Sound at higher salinities than in the Barataria Estuary (Figure 4B).

During July-September, the interaction of basin and salinity had a significant effect on both growth and mortality (Tables 7 and 8), resulting in a unique shift in growth and mortality rates as salinities changed (Figures 2C and 4C). At low salinities, Barataria Estuary oysters experienced higher growth rates and lower mortality rates than in Breton Sound, however, as salinities increased, Breton Sound oysters experienced higher growth rates and lower mortality rates than in the Barataria Estuary (Figures 2C and 4C). Barataria Estuary oysters appear to grow faster and better survive at low to mid-salinities, whereas Breton sound oysters tend to proliferate at higher salinities. These shifts in growth and mortality rates provide evidence that basin-specific growth and mortality are determined by local environmental conditions, and that regional adaptations might exist.

During the summer, using the mean seasonal salinities to compare, mean growth rates varied between estuaries (BA: 1.75 mm mo⁻¹, BR: 1.51 mm mo⁻¹), and were second highest for all seasons (mean = 1.63 mm mo⁻¹) (Figure 3A). Although salinities were within the optimum range for increased growth (10-15) (Table 5), summer mean temperatures (BA: 28.3°C, BR: 28.9°C) were above the optimum temperature range (20°C-25°C) (Menzel 1951, Loosanoff 1953, Garton and Stickle 1980, White and Wilson 1996, La Peyre et al. 2003, Harding 2007, Kraeuter et al 2007, Wang et al. 2008, Rybovich 2016, Lowe et al. 2017). As temperatures near and exceed 30°C (Table 5), oysters become physiologically stressed, which causes them to divert energy to survival instead of tissue and valve growth (Loosanoff 1953, Andrews 1958, Shumway 1996, Wilson et al. 2005, La Peyre et al. 2013, Rybovich et al. 2016). Using the mean seasonal salinities for each estuary, mean summer mortality rates were the highest of all seasons (BA: 0.30, BR: 0.20) (Figure 5A). Oysters can expend a majority of their energy in reproductive


The synched stanzas for the fall used mean temperatures ranging from 20.8°C-21.9°C and mean salinities ranging from 10.7-12.7 (Tables 5 and 6). The variable salinity was the only significant driver of market-sized oyster growth (Table 8). As a result, oyster growth rates in both estuaries increased as salinities increased (Figure 2D). During the fall, mean growth rates in Breton Sound (mean = 2.79 mm mo⁻¹) were generally higher than in Barataria Estuary (mean = 2.38 mm mo⁻¹), regardless of salinity levels (Figure 2D). Fall growth rates for Breton Sound and Barataria Estuary were higher than corresponding growth rates in other seasons (Figure 3A). The months October-December were the only ones when salinity and temperature (Table 5) were within the optimal range for growth, and explain why growth rates were the highest for any season (Figure 3A) (Menzel 1951, Loosanoff 1953, Garton and Stickle 1980, White and Wilson 1996, La Peyre et al. 2003, Harding 2007, Kraeuter et al 2007, Wang et al. 2008, Rybovich 2016, Lowe et al. 2017). In comparison to previous studies in Louisiana, the combined seasonal growth rate (2.58 mm mo⁻¹) is slightly higher than other reported rates (Mackin 1961, La Peyre et al. 2003, Casas et al. 2005, Kraeuter et al. 2007, La Peyre et al. 2009, 2013, 2015, Rybovich et al. 2016, Lowe et al. 2017, Leonhardt et al. 2017, Munroe et al. 2017).

For the mortality analysis, the variable basin and the interaction of variables salinity*basin showed significant effects (Table 9), and indicate that when salinities increase or decrease,
mortality rates vary within and between basins. Using mean seasonal salinities, mean monthly mortality rates differed between basins (BA: 0.17, BR: 0.07) (Figure 5A), and at low salinities (5), Breton Sound oysters had lower mortality rates than in Barataria Estuary (BR: 0.05, BA: 0.22). The increase in Breton Sound mortality rates with increasing salinities was the only season/basin combination that showed this effect. All other season/basin combinations showed decreased mortality with increasing salinities (Figure 4). These different mortality responses to shifting environmental conditions provide evidence that genetic adaptations to local environmental conditions may exist. Fall mortality might be more likely from predation than disease or environmental stress. Environmental stress was unlikely, because conditions were optimal for increased growth (20°C-25°C and 10-15), and temperatures were only slightly higher than optimal (12°C-18°C and 9-13) for decreased mortality (Butler 1954, Shumway 1996, La Peyre et al. 2016, Leonhardt et al. 2017, Lowe et al. 2017). For Dermo disease to thrive, salinities must be above 15 and temperatures must be above 20°C (Galtsoff 1964, Ewart and Ford 1993, Wilson et al. 2005, Harding et al. 2008, La Peyre et al. 2009, Levinton et al. 2013, Powell 2017). During the fall, mean salinities were in the 10-12 range and mean temperatures were only slightly above the optimal level (20.8°C-21.9°C), so potentially, the degree of Dermo intensity was lower. Mean temperatures and salinities, however, were in the range for increased predator presence and feeding activity (Butler 1954, Nichy and Menzel 1960, Galtsoff 1964, Jennings et al. 1985, Sutter et al. 1986, Shumway 1996, Hastings 2009, Kulp et al. 2011). In combination, low salinities and temperatures result in lower mortality rates than low salinity and high temperature conditions (La Peyre et al. 2015, Lowe et al. 2017). Fall releases of freshwater from a FDS into estuaries can increase primary production (USACE 1984, Livingston et al. 2000, LDNR 2003, Hastings 2009, CPRA 2012, Lopez et al. 2014), however, decreased water temperatures and salinities might shift environmental conditions out of their optimal ranges and result in decreased growth rates.

This work highlighted differences in growth and mortality rates between two Louisiana estuaries at similar (synched) temperatures and salinities. Since environmental conditions were synched in the analyses, other environmental factors might be contributing to differences in regional growth and mortality rates. These might include differences between the two basins: 1) food availability (Murrell et al. 2007, Wang et al. 2017), 2) suitable available habitat (Dugas et al. 1977, Melancon et al. 1998, Livingston et al. 2000, Soniat et al. 2013, Lopez et al. 2014), 3) variations in FDS discharges causing varying rates of nutrient loading and sedimentation (USACE 1984, LDNR 2003) and 4) genetic differences between oyster populations (Leonhardt et al. 2017). By keeping these differences in mind, oyster managers can balance each estuary’s oyster habitat demands, and administer proper adaptive management for oyster populations. Freshwater releases could be controlled to establish the optimum salinity levels over oyster grounds (Chatry et al. 1983, La Peyre et al. 2016, Lorio and Malone 1994). Freshwater releases can negatively impact oysters by delivering large quantities of sediment and decrease salinity below optimal levels (Lenihan 1999, Day et al 2003, Livingston et al. 2000, Snedden et al. 2007, Wang et al 2017). Thus, the timing and magnitude of FDS releases play a critical role in the success of present, and future, oyster populations.

A genetic analysis of population differences within local areas would help determine drivers of growth and mortality rates. Finding the source of where the oyster stocks are from, which was difficult for this study, would help improve future comparative genetic studies. Coupling
hydrodynamic and biological data could advance the predictive potential of biological response models to alterations in environmental factors, and thus provide a more effective tool for the management of oyster resources (Livingston et al. 2000, Soniat et al. 2012). Using the methods above, more accurate growth and mortality rates can potentially be identified in other coastal estuaries and incorporated into the SOSBM. By combining the results of this study with Lowe et al. (2017) and Louisiana HSI models (USFWS 1981, Cake 1983, Barnes et al. 2007, Soniat et al. 2013), oyster managers will not only have information on possible areas where oysters will successfully grow and survive in Louisiana, but also insight on how future freshwater diversion strategies can minimize damage to oyster reefs. This study suggests that growth and mortality may be basin specific and thus supplement parameterization of the coast-wide model of Soniat et al. (2012), as refined by Lowe et al. (2017).

Through this study, the synergistic effects of temperature and salinity on oyster growth and mortality are quantified for application to HSI and sustainable harvest models for improved management of oyster resources. Future work should be conducted on how FDS releases affect oyster populations and how releases could be managed for minimal impact on existing Louisiana oyster populations and relocating future populations as FDS come online (USFWS 1981, Cake 1983, Barnes et al. 2007, Soniat et al. 2013).
References


Figure S1. Interpolated natural polynomial temperature splines for Breton Sound Nestier tray 1. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S2. Interpolated natural polynomial temperature splines for Breton Sound Nestier tray 2. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S3. Interpolated natural polynomial temperature splines for Breton Sound Nestier tray 3. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S4. Interpolated natural polynomial temperature splines for Breton Sound Nestier tray 4. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S5. Interpolated natural polynomial temperature splines for Breton Sound Nestier tray 6. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S6. Interpolated natural polynomial temperature splines for Breton Sound Nestier tray 7. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S7. Interpolated natural polynomial temperature splines for Breton Sound Nestier tray 8. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S8. Interpolated natural polynomial temperature splines for Breton Sound Nestier tray 9. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S9. Interpolated natural polynomial temperature splines for Breton Sound Nestier tray 10. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S10. Interpolated natural polynomial temperature splines for Breton Sound Nestier tray 11. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S11. Interpolated natural polynomial temperature splines for Breton Sound Nestier tray 12. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S12. Interpolated natural polynomial temperature splines for Breton Sound Nestier tray 13. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S13. Interpolated natural polynomial temperature splines for Breton Sound Nestier tray 17. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S14. Interpolated natural polynomial temperature splines for Breton Sound Nestier tray 18. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S15. Interpolated natural polynomial temperature splines for Breton Sound Nestier tray 19. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S16. Interpolated natural polynomial temperature splines for Breton Sound Nestier tray 20. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S17. Interpolated natural polynomial temperature splines for Breton Sound Nestier tray 21. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S18. Interpolated natural polynomial temperature splines for Breton Sound Nestier tray 22. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S19. Interpolated natural polynomial temperature splines for Breton Sound Nestier tray 24. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S20. Interpolated natural polynomial temperature splines for Breton Sound Nestier tray 25. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S21. Interpolated natural polynomial temperature splines for Breton Sound Nestier tray 26. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S22. Interpolated natural polynomial temperature splines for Barataria Estuary Nestier tray 201. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S23. Interpolated natural polynomial temperature splines for Barataria Estuary Nestier tray 202. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S24. Interpolated natural polynomial temperature splines for Barataria Estuary Nestier tray 203. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S25. Interpolated natural polynomial temperature splines for Barataria Estuary Nestier tray 203. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S26. Interpolated natural polynomial temperature splines for Barataria Estuary Nestier tray 206. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S27. Interpolated natural polynomial temperature splines for Barataria Estuary Nestier tray 206. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S28. Interpolated natural polynomial temperature splines for Barataria Estuary Nestier tray 207. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S29. Interpolated natural polynomial temperature splines for Barataria Estuary Nestier tray 208. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S30. Interpolated natural polynomial temperature splines for Barataria Estuary Nestier tray 209. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S31. Interpolated natural polynomial temperature splines for Barataria Estuary Nestier tray 210. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S32. Interpolated natural polynomial temperature splines for Barataria Estuary Nestier tray 211. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S33. Interpolated natural polynomial temperature splines for Barataria Estuary Nestier tray 212. Splines were used to interpolate daily temperature values between sampling dates for each NT station. Discrete data was included to fully capture the range of environmental conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily temperature data from each study site.
Figure S34. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 1. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S35. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 2. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S36. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 3. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S37. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 4. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S38. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 6. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S39. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 7. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S40. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 8. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S41. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 9. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S42. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 10. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S43. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 11. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S44. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 12. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S45. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 13. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S46. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 17. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S47. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 18. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S48. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 19. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S49. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 20. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S50. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 21. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S51. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 22. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S52. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 23. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S53. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 24. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S54. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 25. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S55. Interpolated natural polynomial salinity splines for Breton Sound Nestier tray 26. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S56. Interpolated natural polynomial salinity splines for Barataria Estuary Nestier tray 201. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S57. Interpolated natural polynomial salinity splines for Barataria Estuary Nestier tray 202. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S57. Interpolated natural polynomial salinity splines for Barataria Estuary Nestier tray 203. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S58. Interpolated natural polynomial salinity splines for Barataria Estuary Nestier tray 204. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S59. Interpolated natural polynomial salinity splines for Barataria Estuary Nestier tray 205. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S60. Interpolated natural polynomial salinity splines for Barataria Estuary Nestier tray 206. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S61. Interpolated natural polynomial salinity splines for Barataria Estuary Nestier tray 207. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S62. Interpolated natural polynomial salinity splines for Barataria Estuary Nestier tray 208. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S63. Interpolated natural polynomial salinity splines for Barataria Estuary Nestier tray 209. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S64. Interpolated natural polynomial salinity splines for Barataria Estuary Nestier tray 210. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S65. Interpolated natural polynomial salinity splines for Barataria Estuary Nestier tray 211. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
Figure S66. Interpolated natural polynomial salinity splines for Barataria Estuary Nestier tray 212. Splines were used to interpolate daily salinity values between sampling dates for each NT station. Discrete data was included to fully capture the range of temperature conditions to which experimental oysters were exposed. Interpolations were expanded to the entire time series for each station. To verify the accuracy of constructed splines, continuous data were regressed against predicted daily salinity data from each study site.
VITA

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