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Effects of Salinity on Eastern Oysters: Locating Lower-Salinity Tolerant Populations and Defining Resource Zones Suitable to Restoration, Fisheries, and Aquaculture.

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EFFECTS OF SALINITY ON EASTERN OYSTERS: LOCATING LOWER SALINITY TOLERANT POPULATIONS AND DEFINING RESOURCE ZONES SUITABLE TO RESTORATION, FISHERIES AND AQUACULTURE

A Thesis

Submitted to the Graduate Faculty of the
Louisiana State University and
Agriculture and Mechanical College
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in

The School of Renewable Natural Resources

by
Lauren Michelle Swam
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ABSTRACT

Eastern oysters (*Crassostrea virginica*) provide valuable ecosystem services and support a productive commercial industry in the northern Gulf of Mexico. Declining abundance from water quality changes and other factors drives development of management and restoration strategies focused on a comprehensive, metapopulation approach. Identifying oyster resource zones based on water quality combined with selective breeding of oysters adapted to specific conditions provides strategies to support aquaculture development and ensure resilient oyster populations and high production. Using 2015-2019 satellite-derived continuous salinity and temperature data for coastal Louisiana, this work created maps defining oyster resource zones supportive of (1) broodstock sanctuary reefs, (2) productive reefs during dry and (3) wet years, and (4) off-bottom aquaculture development. Unique salinity regimes occurred across estuaries, with high salinity variation critically limiting broodstock sanctuary areas. Further, these maps suggest consideration of offshore areas for aquaculture development and identify a need to shift restoration areas down-estuary due to up-estuary freshening. Accounting for variable water quality conditions over time acknowledges temporally variable reef success as individual populations in different zones will thrive in different years, thus promoting overall oyster persistence and production long-term. Reef persistence and oyster production would also benefit from ensuring oyster populations within zones or identified for use in aquaculture are uniquely adapted to decreasing salinities. A second study assessed unique Louisiana oyster populations from assumed low-salinity areas for population-specific low salinity tolerance. Progeny of these populations were grown at an intermediate (10-20) and low salinity (<8) field site for twelve months, tracking growth, mortality, and condition. While oyster growth was similar between populations, one population experienced low mortality (<20%) compared to the other three (40-70%) at the low salinity site. The identification of populations tolerant to low salinity would facilitate the use of stocks specifically suited to areas where they will be grown, promoting restoration, development of aquaculture, and industry interests. Together, these two approaches could help maximize oyster restoration and harvest through the selective breeding and placement of adapted populations in areas identified to typically experience a given condition, both within traditional oyster areas and in areas predicted to support future production and aquaculture.

CHAPTER 1. INTRODUCTION

The eastern oyster, *Crassostrea virginica*, is a critical estuarine species that supports ecosystems and commercial industries along the Atlantic and Gulf coasts of the United States. Oysters provide critical ecosystem services including water filtration, shoreline stabilization, carbon sequestration, and habitat provision as well as support over 45% of the commercial oyster production in the USA (Shumway 1996, Coen et al. 2007, LDWF 2019). Despite their importance, oyster populations are declining globally (Beck et al. 2011). Possible reasons for this decline include overharvesting, increased prevalence of disease, and habitat destruction, but a primary source of oyster decline in Gulf of Mexico estuaries specifically is the occurrence of increasingly variable water quality conditions (NRC 2004, Beck et al. 2011, Beseres Pollack et al. 2012).

Eastern oysters reside in estuaries which are naturally spatially and temporally variable. Influenced by both marine and terrestrial inputs, estuaries create a gradient of water quality conditions ranging up-estuary to down-estuary (Dugas and Roussel 1983, Dekshenieks et al. 1993). This gradient can fluctuate over time when riverine input and precipitation are greater in some years compared to others, creating relatively “wet” or “dry” conditions (Melancon et al. 1998). Additionally, increased freshwater inputs from changing climate patterns, and consequent long-term water quality changes, are predicted for the northeastern Gulf of Mexico creating more intense and extreme conditions in the near future (Keim and Powell 2015). Further, coastal land loss mitigation strategies such as riverine diversions may deposit additional freshwater into specific estuaries, causing further changes to oyster habitat (DWH NDRA 2017).

This current and projected increase in water quality variability, particularly in salinity, is especially relevant to oysters. As osmoconformers, oysters regulate osmolytes through intracellular and extracellular regulation of fluids, changes in cell volume, and through closure of their shells under extreme water quality conditions (Shumway 1996). Therefore, increased salinity variability is detrimental to oysters because it is energetically costly to constantly osmoconform (Lavaud et al. 2017) and, while shell closure can be maintained for several days without harm, it reduces feeding rates and will weaken the individual causing mortality over long time periods (Shumway 1996). Several water quality conditions including temperature, turbidity, chlorophyll-*a* concentration, and dissolved oxygen are critical to oyster growth and survival, but in Louisiana, salinity is the most locally critical influencing water quality condition for oysters (Heilmayer et al. 2008, Rybovich et al. 2016, Casas et al. 2018).

Oysters are generally tolerant to a large range of water quality conditions, with optimum conditions promoting fast growth and low mortality. Eastern oysters can survive a wide salinity range from 5 – 40 with Louisiana populations showing optimal growth and lowest mortality in ranges between 10.7 – 16.1 (Shumway 1996, Lowe et al. 2017). As salinity decreases, oysters may have reduced growth from decreased feeding, with extreme events resulting in mortality, while higher salinities may result in increased mortality from predation or disease (Shumway 1996, McCarty et al. 2020). Oysters are traditionally farmed along the estuarine salinity gradient to allow for production in wet, dry, and average condition years (Melancon et al. 1998), as wet, dry and average condition years are reflected in shifting salinities up or down estuary. This approach, used for decades by oyster farmers, acknowledges that not all locations will be productive for oysters every year, and relies on the metapopulation connectivity of oyster resources within specific estuaries, and can be expanded to restoration activities and aquaculture development. Rather than focusing on single reefs or sites, this framework acknowledges this spatial and temporal variation in water quality conditions result in shifting production and resource zones for oysters.

While metapopulation connectivity enables oyster reefs to remain linked and productive along the estuarine salinity gradient despite temporally changing conditions, there is also evidence that some discrete oyster populations are better able to tolerate low salinity than others. This population specific adaptation may allow for the strategic placement of oyster populations tolerant to lower salinity in areas that more often experience those conditions to assist in reef persistence over time. This identification of specific oyster populations may be most effective if used by the oyster aquaculture industry on the Louisiana coast. Development of low salinity tolerant population broodstock able to survive and grow in low salinity areas would improve the ability of oysterfishers to maintain crops along the estuarine salinity gradient and improve the chances of some oysters being viable in all years despite variable conditions. With continued high market demand and declining oyster abundance, the aquaculture industry is developing rapidly in this region.

The concept of metapopulation connectivity as a management tool and population specific adaptation as a mechanism of improving oyster survival and productivity for both restoration and commercial production were examined in this work through two studies. The second chapter of this thesis outlines the development of a method to identify static zones of oyster suitability based on local salinity conditions known to impact oyster growth and survival across the Louisiana coast over time. Coastwide salinity and temperature profiles were generated and then filtered based on five salinity condition thresholds to determine discrete areas suitable to oyster metapopulations across Louisiana estuaries with varying freshwater input over time. The third chapter of this thesis explores the potential for low salinity adaptation of discrete oyster populations for their use in both restoration and aquaculture placement and development across the Louisiana coast. Identification of populations tolerant to lower salinity can facilitate their use as broodstock to support aquaculture, restoration, and management. Through a combination of these two studies, we explore the critical relationship between oysters and low salinity exposure over time to identify specific means of combating the pervasive challenges of decreasing salinity averages and increasing salinity variability in Gulf of Mexico estuaries.

CHAPTER 2. DEFINING OYSTER RESOURCE ZONES FOR RESTORATION, FISHERIES AND AQUACULTURE IN COASTAL LOUISIANA

2.1. INTRODUCTION

Across the northern Gulf of Mexico (nGoM), the eastern oyster, *Crassostrea virginica*, provides vital ecosystem services and supports over 45% of eastern oyster production in the United States (LDWF 2019, NMFS 2020). Eastern oysters provide unique hard-bottom habitat, water filtration, carbon sequestration, coastline stabilization, increased landscape diversity, and benthic-pelagic coupling to estuarine ecosystems (Coen et al. 2007, Beck et al. 2011, Grabowski et al. 2012, La Peyre et al. 2014). Despite their ecological and commercial importance, eastern oyster populations are declining globally (Beck et al. 2011). This decline is caused by extensive overharvesting, disease, shoreline alteration, changes in freshwater flows, and changing climate conditions (NRC 2004, Beck et al. 2011, Beseres Pollack et al. 2012). In the face of these declines, many states are investing in oyster reef restoration as a component of coastal restoration and land loss mitigation and are calling for development of a reef network with areas for sanctuary or broodstock reefs (Lipcius et al. 2008, Lipcius et al. 2015, DWH NDRA 2017). In addition, the nGOM is investing heavily in off-bottom aquaculture to grow oysters for harvest with seed produced from hatcheries to address the challenges faced by on-bottom oyster leases (Maxwell et al. 2008, Walton et al. 2013, Frank-Lawale et al. 2014, Campbell and Hall 2019). Research to find strategic locations to place these restoration reefs and off-bottom aquaculture is critical to ensure the success of these strategies.

Eastern oysters occur over a large latitudinal range and can tolerate wide ranges of water quality conditions (Casas et al. 2018). In Louisiana, salinity and temperature are the primary water quality variables impacting eastern oyster survival (Dugas and Roussel 1983, Heilmayer et al. 2008, Rybovich et al. 2016). Eastern oysters can survive temperatures ranging -2 – 36°C throughout their geographical range, but Louisiana populations have exhibited optimal growth within 20 - 26°C (Shumway 1996, Lowe et al. 2017). Eastern oysters can survive a wide salinity range from 5 – 40 with Louisiana populations showing optimal growth and lowest mortality in ranges between 10.7 – 16.1 (Shumway 1996, Lowe et al. 2017). Both salinity and temperature vary up-estuary to down-estuary and sessile organisms, such as the eastern oyster, are inherently susceptible to these changing conditions (Melancon et al. 1998, Lowe et al. 2017). As a result, Louisiana oyster farmers have traditionally maintained leases along the natural gradient allowing for productive on-bottom operation in wet, dry, and average condition years (Melancon et al. 1998). With predicted long-term changes in critical water quality parameters (Keim and Powell 2015), more intense and extreme conditions may threaten eastern oysters in nGoM in the near future.

In estuarine environments, high spatial and temporal variability from both terrestrial and marine influences affect critical water quality parameters, impacting ecosystem functioning and fisheries production (Dugas and Roussel 1983, Dekshenieks et al. 1993). Temporal variability arises from seasonal, annual, and long-term climatic cycles (Orlando et al. 1993). For example, water quality conditions in nGoM are impacted by the El Niño Southern Oscillation, which creates lower than average up-estuary salinities (Orlando et al. 1993, Kennedy et al 2007). Spatial variability in estuaries across the nGoM results from differences in riverine input, basin geomorphology, coastal land loss, and restoration activities (Orlando et al. 1993). For example, variation in freshwater river inputs from the Mississippi, Atchafalaya, and Pearl rivers in Louisiana result in some estuaries with high salinity but low nutrients and others with low and variable salinity but high nutrients (Skylar et al. 1998). Additional variability from climate change including sea level rise and increased precipitation and runoff may exacerbate these effects (Keim et al. 2011, Keim and Powell 2015). These numerous sources of variability cause individual estuaries to experience water quality changes in different directions and magnitudes, resulting in unique estuarine environments across Louisiana. As a result, management of ecosystems and fisheries requires consideration of local conditions and how local populations of organisms can adapt (Mulholland et al. 1997, Bible et al. 2017).

Numerous habitat suitability indices (HSI) models have been developed to inform locally specific management of oyster resources and placement of restoration projects (Cake 1983, Soniat et al. 2013, Denapolis 2018, Theuerkauf et al. 2019). HSI's vary from models using a few to fifteen parameters to assess habitat suitability for oysters and have been used for environmental impact assessments (Cake 1983), to assess changes from proposed restoration (Soniat et al. 2013), and to inform restoration site placement (Theuerkauf et al. 2019). HSI models have also been implemented in geospatial frameworks and developed as web-based platforms (Beseres Pollack et al. 2012, Beseres Pollack et al. 2019, Wickliffe et al. 2019).

However, to identify locations for sustainable oyster metapopulations, conditions over multiple years and across the spatial gradient must be considered to account for variation of water quality conditions over time (Lipcius et al. 2015). Melancon et al. (1998) suggested a set of oyster resource zones for Barataria and Terrebonne estuaries in Louisiana based on long-term salinity patterns and input from oyster farmers. This approach responds to not only the spatial and temporal variation within an estuary but incorporates metapopulation connectivity between oyster reefs as well. Recent studies suggest that recognition of oyster population connectivity and focus on development of sanctuaries and aquaculture improves maintenance of oyster resources (Lipcius et al. 2008, Lipcius et al. 2015, DWH NDRA 2017). A spatial tool to identify areas (zones) differentially suitable for aquaculture, restoration for sites suitable across wet or dry years, and for sanctuary or broodstock would critically inform an approach to manage oysters as metapopulations (Theuerkauf et al. 2019).

Increased focus on restoration, conservation, and development of off-bottom oyster aquaculture requires increased focus on marine spatial planning. This spatial planning for oyster resilience and production requires determining suitable habitat conditions, largely driven by salinity in this region, for oysters to thrive. The objective of this study is to define zones based on the last 5-years (2015-2019) environmental conditions in estuaries across Louisiana to determine areas where a network of oyster reefs would survive and be most productive over time. Specifically, this work aims to develop a coastwide map identifying four distinct oyster resource zones to support decision making related to the selection of locations for aquaculture operations, reef restoration, and broodstock sanctuaries.

2.2. METHODS

Oyster resource zones were defined based on five-year salinity parameters relevant to oyster survival in coastal Louisiana. Salinity and temperature (°C) from continuous data recorders and satellite-derived data were used to generate coastwide profiles that were then filtered based on condition thresholds. The filtered water quality data was used to define areas across estuaries suitable to oyster conditions with varying freshwater inputs over time.

2.2.1. Study area

The study area for this analysis was defined using the Louisiana basin boundaries (CPRA 2017) (Figure 2.1.), extended 5 km from the coastline, and manually simplified in order to extend the boundary beyond the state territorial waters out into the Gulf of Mexico. The Louisiana coast is composed of multiple estuaries, which vary in freshwater river influence, tidal exchange, and magnitude of salinity variability (Orlando et al. 1993, Solis and Powell 1999) (Figure 2.1.). The eastern half of the state is dominated by the Mississippi River Delta while the western half consists of the Chenier Plains and many estuarine lakes. These estuaries represent a large range of spatially and temporally varying conditions resulting from differing riverine inputs, basin morphology, and management.

Projected Coordinate System: NAD83 UTM Zone 15N
Map Prepared By: Lauren Swam

Figure 2.1. Louisiana basin boundaries as defined by the Coastal Protection and Restoration Authority.

2.2.2. Zone definition

Four oyster resource zones were defined to identify areas that would support (1) development of broodstock spawning sanctuaries, (2) restoration of oyster reefs across areas supportive of oyster growth, survival, and reproduction, and (3) aquaculture operations. Key variables that could inform the zones were identified (Table 2.1.) for potential inclusion in the zone definitions, however, due to lacking data availability, only water coverage, salinity, and season (temperature (°C)) were used in defining the zones (Table 2.2.).

Table 2.1. Water quality parameters considered to generate oyster resources zones in coastal Louisiana.

Variable	Measure
Land/water coverage	Presence/absence of water
Salinity	Seasonal mean, variation, min, max
Water temperature °C	Seasonal mean, variation, min, max
Turbidity	Annual mean
Chlorophyll-*a*	Annual mean
Exposure (fetch + wind)	Seasonal mean
Adjacent land use	Level of impact; accessibility

The four zones identified covered both aquaculture, and potential restoration sites, including broodstock sanctuary zones, dry, and wet year restoration zones. The Aquaculture Zone was designed to capture conditions best suited for high oyster growth and low mortality, while disregarding concerns for reproduction (based on assumption that seed would come from hatcheries) and predation at high salinity (as oysters would be grown in baskets). The Broodstock Sanctuary Zone was designed to optimize reef establishment and long-term persistence with a focus on spawning month mean salinity, annual mean salinity, and low annual salinity variation. The Restoration Dry and Restoration Wet Zones were designed for optimum reef survival, growth, and reproduction during years with lower or higher than average freshwater inputs into estuaries. These zones would contain oyster populations that may recruit and reproduce only once every few years but still allow some to survive through the years in between.

Accounting for conditions in dry and wet years was based on zones described by Melancon et al. (1998). A dry year, with lower-than-average freshwater input, results in higher inshore salinities providing conditions for optimal oyster growth, survival and reproduction at more inshore sites during these years; a wet year, with higher-than-average freshwater input, results in lower offshore salinities providing conditions for optimal oyster growth, survival and reproduction at more offshore sites during these years (Figure 2.2.). To define these zones, annual mean salinity, annual salinity variation, spawning season salinity, and summer and winter minimum salinity were defined for each zone explicitly (Table 2.2.). The aquaculture zone was defined by salinities that generally support high oyster growth, low mortality, and assumed aquaculture stock would be hatchery produced.

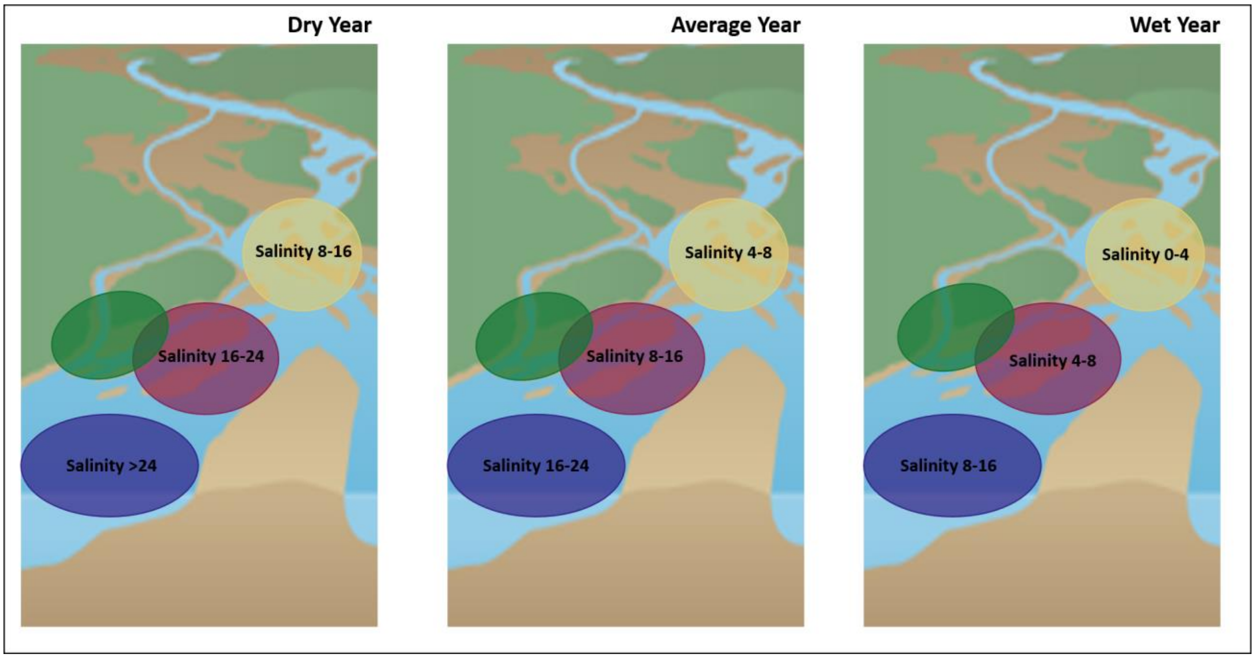


Figure 2.2. Salinity conditions within an estuary in dry, wet, and average years. Yellow areas would be included in the Dry Restoration Zone, red areas would be included in the Broodstock Sanctuary Zone, blue areas would be included in the Wet Restoration Zone and green areas would be an example of areas included in the Aquaculture Zone.

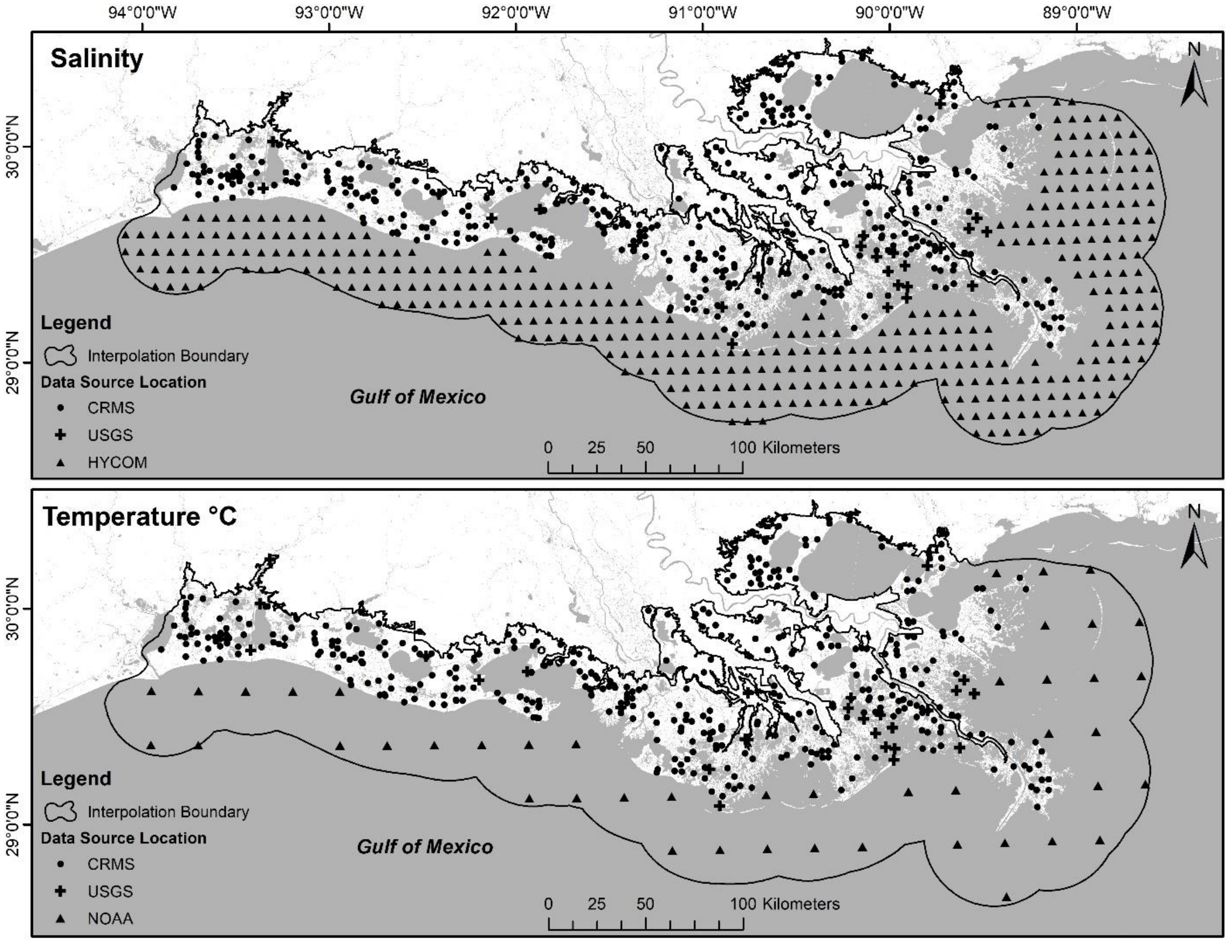
2.2.3. Coastwide data acquisition

We obtained daily inshore salinity and temperature (°C) data from continuous data recorders maintained by the state of Louisiana Coastwide Reference Monitoring System (CRMS, CPRA 2020) and the United States Geological Survey (USGS 2020) (Figure 2.3.). Offshore data were obtained from the Hybrid Coordinate Ocean Model for salinity (GODAE 2020) and the National Oceanographic and Atmospheric Administration (NOAA) Optimum Interpolation Sea Surface Temperature dataset for temperature (NOAA 2020) (Figure 2.3.). CRMS and USGS data were accessed by public online websites databases, HYCOM and NOAA data were derived from remote sensing raster coverage and accessed through the data catalog of Google Earth Engine, an online computing platform for geospatial analysis using Google's infrastructure. From all sources, daily salinity and temperature means were obtained for January 1, 2015 through December 31, 2019. There were thirty-two dates that did not contain data in the HYCOM dataset; the salinity mean for these days was estimated by averaging the means of the two surrounding dates.

In order to compare the 5-year data set used for these maps to a longer historical timeframe, six locations with continuous long-term data recorders available were identified: Calcasieu Lake, Vermilion Bay, Terrebonne Bay, Barataria Bay, Breton Sound, and Biloxi. Monthly salinity means for 2002 – 2019 were compared to monthly salinity means for 2015 – 2019 to identify differences in short-term versus long-term salinity trends (USGS 2020). The data was adjusted to directly show the disparity between the two data sets (salinity anomaly). The longer 2002 – 2019 timeframe was not used to develop oyster resource zones in this study due to a focus on developing maps reflective of current estuarine conditions and a lack of long-term, coastwide daily data to inform the spatial interpolations.

Table 2.2. Environmental conditions included in oyster resource zone definition. Time is defined as the number of months and/or years out of the relevant time period required to meet the zone conditions. Spawning months are defined as Apr-Nov, summer is defined as Jun-Sep, and winter is defined as Dec-Feb for each year in the analysis.

	Spawning months mean salinity		Minimum monthly summer mean salinity		Minimum monthly winter mean salinity		Annual mean salinity		Annual salinity variation	
	Value	Time	Value	Time	Value	Time	Value	Time	Value	Time
Broodstock Sanctuary Zone	≥12	2+/8 months for 3/5 years	≥8	16+/20 summer months	≥8	12+/15 winter months	8-16	4/5 years	1SD ≤ 4.416	4/5 years
Dry Restoration Zone	≥12	1+/8 months for 1/5 years	≥2	16+/20 summer months	≥2	12+/15 winter months	4-12	3/5 years	1SD ≤ 8.832	3/5 years
Wet Restoration Zone	≥12	1+/8 months for 1/5 years	≥5	16+/20 summer months	≥5	12+/15 winter months	12-20	3/5 years	1SD ≤ 8.832	3/5 years
Aquaculture Zone			≥8	16+/20 summer months	≥8	12+/15 winter months	≥12	4/5 years		



Projected Coordinate System: NAD 83 UTM Zone 15 N
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Figure 2.3. Salinity: locations of 457 CRMS and 27 USGS data recorders and 392 approximate data locations from remote sensing raster coverage (HYCOM) for 2015-2019 for a total of 876 data points. Temperature °C: locations of 462 CRMS and 27 USGS data recorders and 45 approximate data locations from remote sensing raster coverage (NOAA) for 2015-2019 for a total of 534 data points.

2.2.4. Spatial layer development

Interpolations for full spatial coverage across the study area were generated in ArcGIS v.10.7 using the spline with barriers technique with a 500 m resolution. The spline technique estimates values using a mathematical function to create the smoothest possible surface curve that passes through the input points exactly. Barriers included levees, impoundments, and basin boundaries affecting hydrologic flow to prevent interpolation across hydrologic boundaries (Figure 2.4.; DeMarco et al. 2018). We interpolated daily salinity and temperature means to create daily raster surfaces for the Louisiana coast from 1/1/2015 through 12/31/2019. Interpolations were uploaded into Google Earth Engine where daily salinity and temperature data were used to calculate monthly means, annual means, and annual standard deviation per pixel. Each pixel in the raster surface is 250,000 m^2 (500 m-sided square) which was selected to maximize spatial resolution while minimizing processing time.

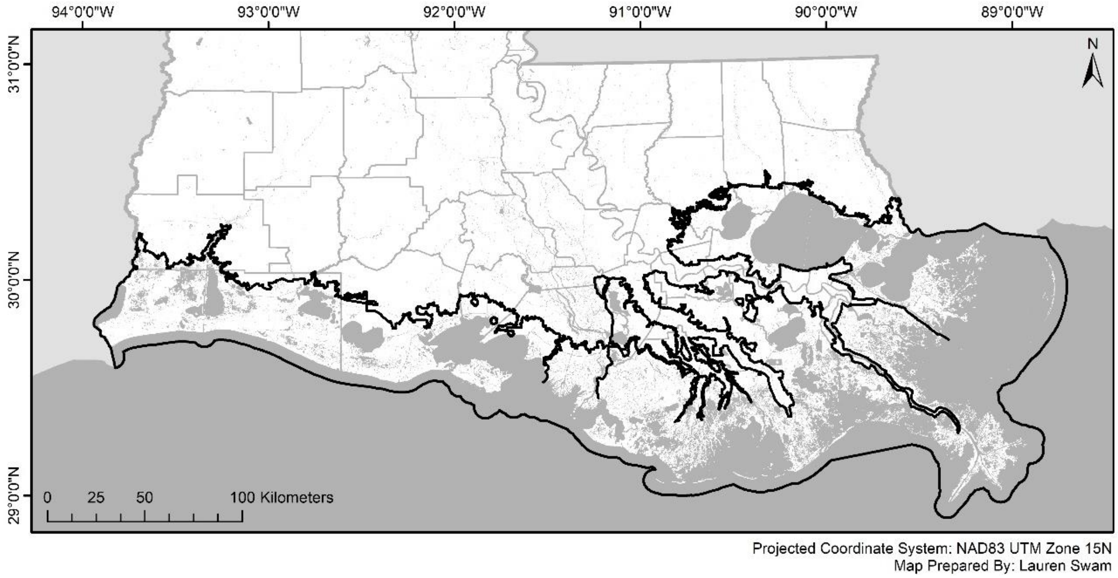

Figure 2.4. Location of hydrologic barriers used to define oyster resource zones.

2.2.5. Zone generation

Monthly and annual salinity values generated in Google Earth Engine were filtered to include appropriate ranges and thresholds for five variables for each of the four oyster resource zones. Each of the five variables (spawning month mean salinity, minimum monthly summer mean salinity, minimum monthly winter mean salinity, annual mean salinity, and annual salinity variation) were defined with a salinity value and a time component to represent the relevant salinity required and for the time which is was required for. Due to large temporal salinity variation in Louisiana estuaries, the time component was added to the zone definitions to allow for sufficient, less-restrictive coverage.

Spawning month mean salinity represents the Louisiana oyster spawning season (April – November), and specifies the amount of time during that season each year of 2015 – 2019 that the minimum monthly mean salinity of 12 is observed. The minimum monthly summer mean salinity represents the lowest mean salinity allowable per month for oyster survival in Louisiana summer months (June – September) for all five years combined. The minimum monthly winter mean salinity represents the same but for Louisiana winter months (December – February). The annual mean salinity variable represents the range of mean yearly salinity allowable for some or most years from 2015 – 2019. The annual salinity variation variable represents the maximum standard deviation allowable for some or most years from 2015 – 2019. The standard deviation threshold was calculated based on the five-year standard deviation mean for the entire Louisiana coast area (SD = 2.208) and multiplied by a factor of 2 or 4 to allow sufficient area to be included in the zones.

Once filtered to each zone's specifications, the five variables were stacked to create multi-variable oyster resource zones that include all relevant, zone-specific salinity criteria. Overlapping zone coverage was mapped to show the full range of oyster suitability across the Louisiana coast.

Coverage (km^2) was calculated in ArcGIS for each zone using the Calculate Geometry tool and simplified to two significant figures.

2.3. RESULTS

Salinity and temperature along the Louisiana coast are highly spatially and temporally variable. This variation is what allows for variable oyster survival under different freshwater input scenarios. Quantifying this variation has facilitated the definition of discrete oyster resource zones for use in oyster restoration, production, and aquaculture.

2.3.1. Environmental data

Five-year mean salinity from 2015 – 2019 across the Louisiana coast ranged from 0 to 34.7 with increasing salinity moving down-estuary and offshore, mapped up to 5 km (Figure 2.5., Panel A.). Five-year mean salinity standard deviation ranged from 0 to 6.5, with differences in variation evident across the coast, by estuary. Specifically, higher variation was seen in Calcasieu, Barataria, Breton Sound, and Biloxi basins (Figure 2.5., Panel B.).

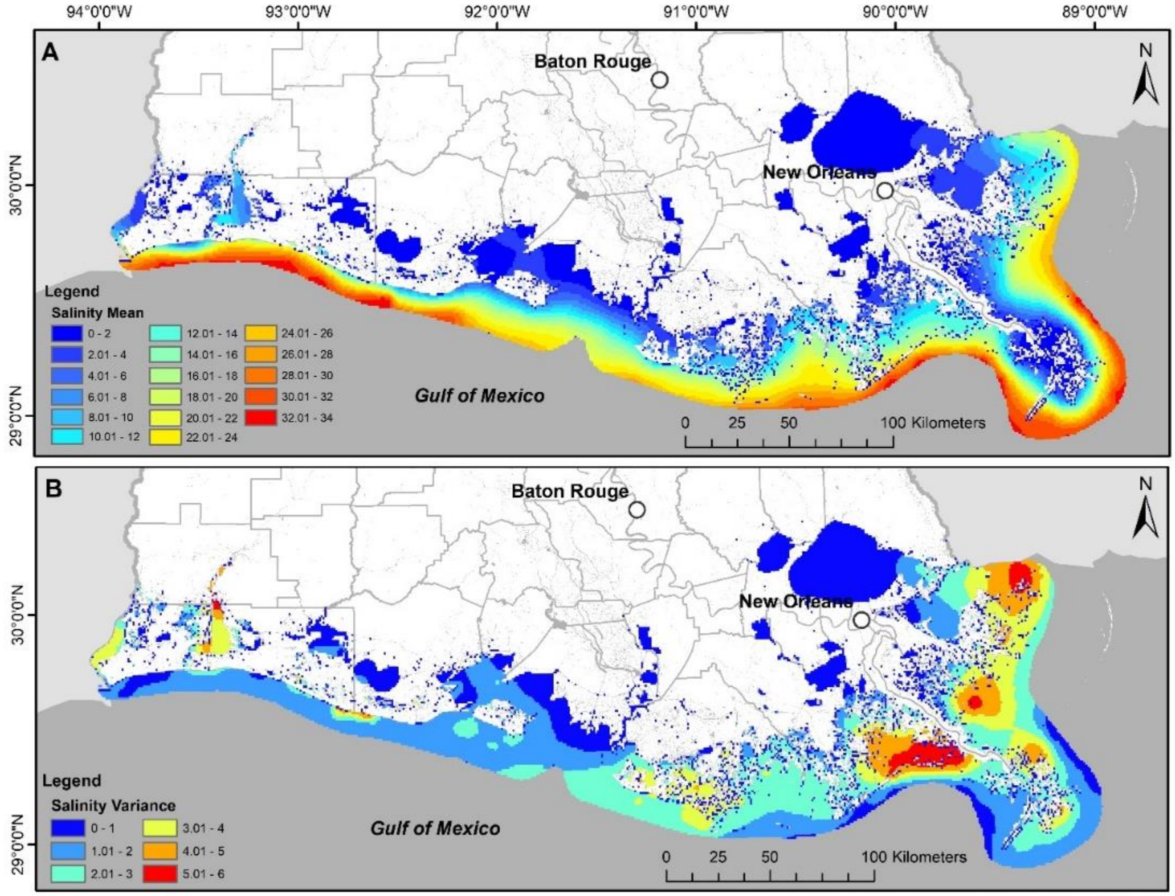

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Figure 2.5. Louisiana coast salinity profile from years included in oyster resource zone definition. Panel A: mean annual salinity 2015-2019. Panel B: mean annual salinity standard deviation 2015-2019.

Five-year mean temperature from 2015 – 2019 across the Louisiana coast ranged from <20°C to 25°C with temperature increasing slightly moving offshore (Figure 2.6., Panel A.). Five-year mean temperature standard deviation ranged from 0 to 8°C with highest variation around the Mississippi River Delta (Figure 2.6., Panel B.).

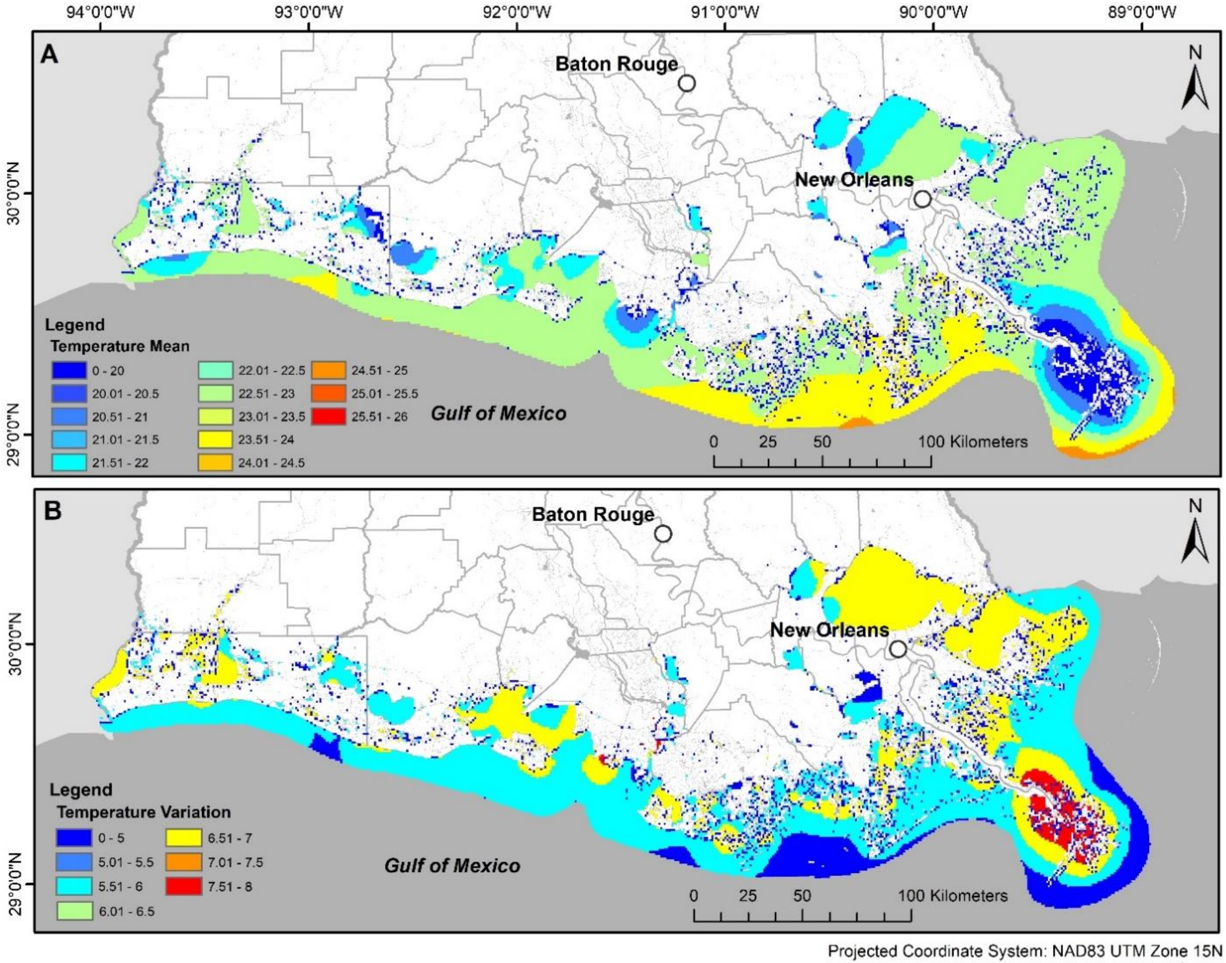

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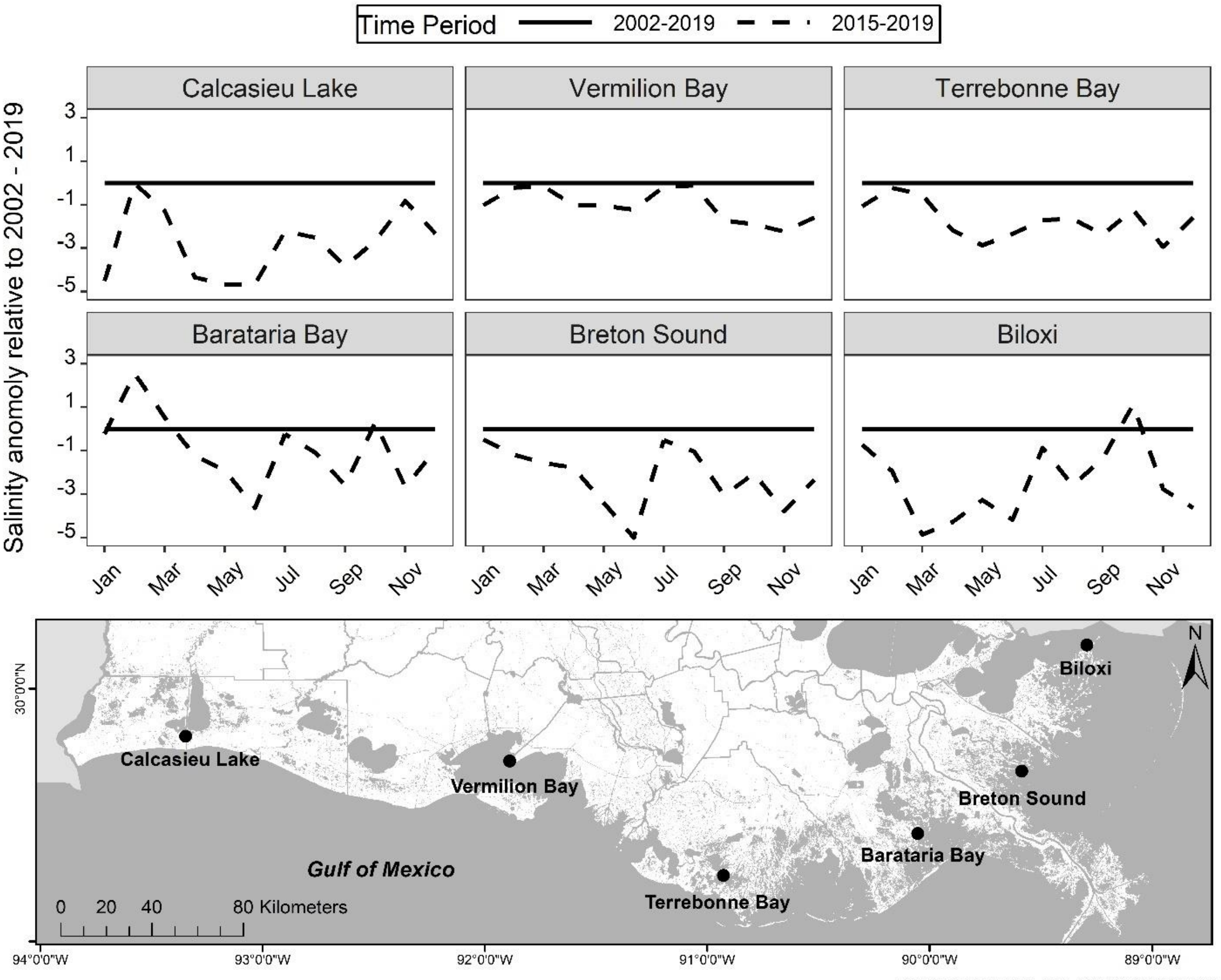
Figure 2.6. Louisiana coast temperature (°C) profile from years included in oyster resource zone definition. Panel A: mean annual temperature 2015-2019. Panel B: mean annual temperature standard deviation 2015-2019.

Comparison of salinity means at six continuous data recorders with daily data from 2002-2019 to their salinity means from 2015-2019 indicated that the years for zone development were generally fresher than the long-term salinity at critical oyster resource locations (Figure 2.7.).

2.3.2. Oyster resource zones

The four oyster resource zones span the Louisiana coast and depict predicted areas of optimum oyster performance based on water quality conditions (Figure 2.8.). The four zones combined cover 18,000 km^2 of water bottom out of 37,000 km^2 total within our study area. The least prevalent zone was the Broodstock Sanctuary Zone accounting for 1,100 km^2. In general, the Broodstock Sanctuary Zone occurred where the Dry and Wet Restoration Zones overlap and



Projected Coordinate System: NAD83 UTM Zone 15N
Map Prepared By: Lauren Swam

Figure 2.7. Monthly salinity means of most recent five years (2015-2019) compared to the past eighteen years (2002-2019) at six critical oyster resource locations along the Louisiana coast. Salinity anomaly represents the 2002-2019 mean salinity minus the 2015-2019 salinity mean. Negative values indicate the salinity mean was lower in 2015-2019 compared to the 2002-2019 mean. Salinity data used are daily means taken from USGS recorders: 08017118 – Calcasieu River at Cameron, LA; 07387040 – Vermilion Bay near Cypremort Point, LA; 07381349 – Caillou Lake (Sister Lake) SW of Dulac, LA; 073802512 – Hackberry Bay NW of Grand Isle, LA; 07374526 – Black Bay near Snake Island near Pointe-A-La-Hache, LA; 300722089150100 – Mississippi Sound near Grand Pass.

represented a smaller range of water quality conditions. The Dry Restoration Zone accounted for 3,600 km^2 and covered up-estuary areas across the coast, including areas that would be fresher in an average year (Figure 2.8.). The Wet Restoration Zone accounted for 4,000 km^2 and covered down-estuary areas across the coast, including areas that would be saltier in an average year (Figure 2.8.). The largest area was covered by the Aquaculture Zone, accounting for 9,600 km^2, due to less restrictive water quality conditions (Figure 2.8.).

Zone representation has a general gradient pattern from inshore to offshore estuary, changing from Dry Restoration Zone, to Broodstock Sanctuary Zone, to Wet Restoration Zone, to Aquaculture Zone with areas of overlap between each (Figure 2.9.). Aquaculture Zone overlaps with many of the other zones due to its less restrictive water quality requirements (Figure 2.9.).

Existing reefs and cultch plants were captured within these layers and largely exist within the Dry Restoration Zone (Figure 2.9.).

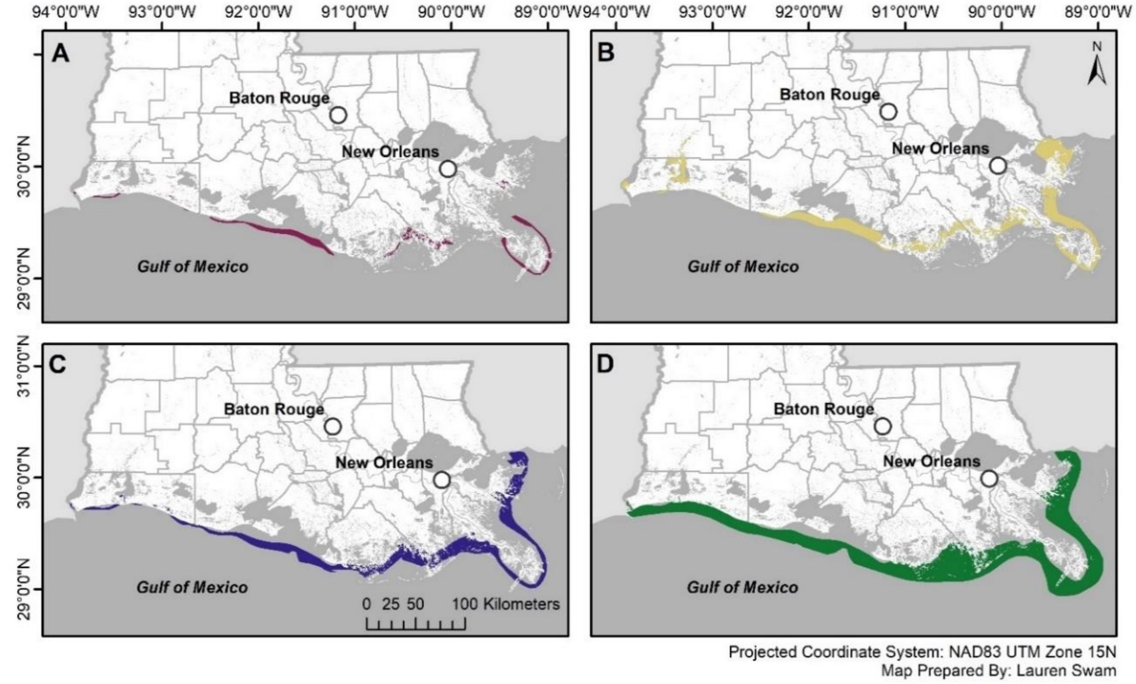


Figure 2.8. Oyster resource zones across coastal Louisiana based on mean salinity parameters from 2015-2019 separated to show all areas included within each zone. A: Broodstock Sanctuary Zone, B: Dry Restoration Zone, C: Wet Restoration Zone, D: Aquaculture Zone.

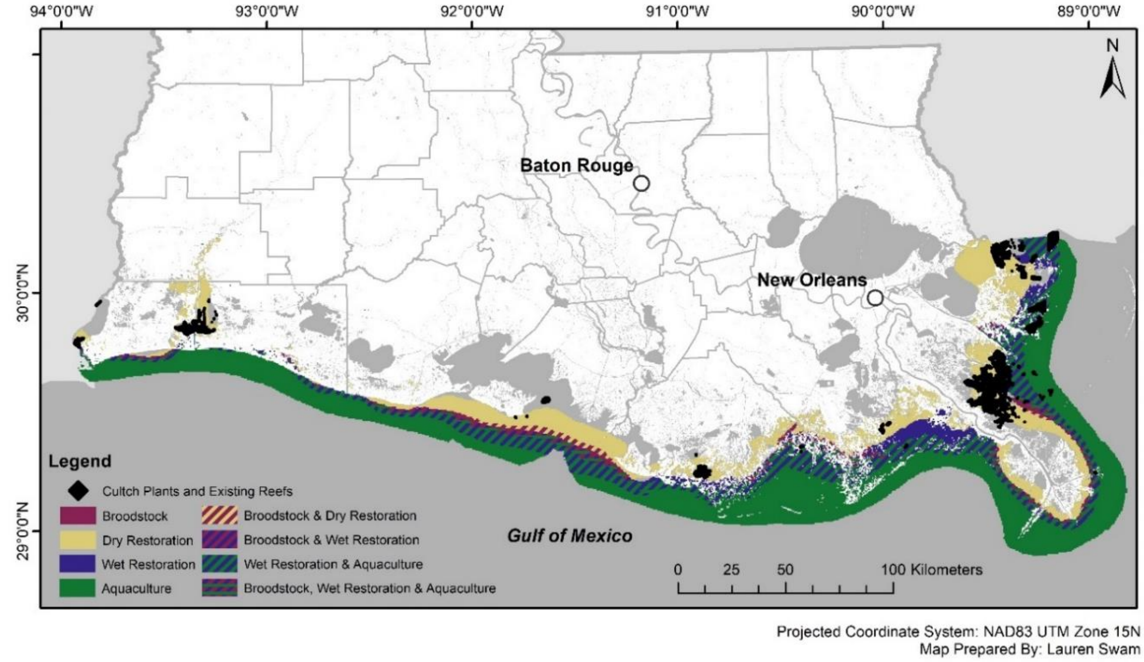


Figure 2.9. Oyster resource zones across coastal Louisiana based on mean salinity parameters from 2015-2019 including overlapping resource areas. Areas identified by the Louisiana Department of Wildlife and Fisheries as existing reefs and for cultch plants are included.

2.4. DISCUSSION

Increased investment in oyster restoration for both conservation and harvest requires broad resource-level planning. There is extensive area supportive of oyster production across coastal Louisiana (up to 18,000 km^2), limited potentially by water bottom type and competing uses including shipping and oil. The identification of broad resource zones within this area provides a means to ensure successful planning critical to the maintenance and advancement of oyster restoration and commercial productivity. Based on coastwide water quality data, we predicted areas to support oyster broodstock sanctuaries, restoration sites, and aquaculture development. The development of these oyster resource zones for coastal Louisiana (1) identifies unique estuarine salinity signatures with salinity variation playing a critical role in determining sanctuary areas, (2) identifies a potential shift in oyster restoration areas with changing freshwater inputs from management and climate change, (3) highlights the mismatch between static single reef management and shifting optimal oyster zones, and (4) suggests potential areas for offshore aquaculture development.

These coastwide salinity maps show trends of an increasing salinity gradient moving offshore in all estuaries, estuary-specific salinity variation, and mean five-year salinities as fresher than the previous 18 years. The fresher years captured in these data (2015 – 2019) may have shifted the Dry and Wet Restoration zones further down-estuary; a slight down-estuary shift can be seen in comparison to maps generated in Barataria and Terrebonne estuaries in 1998 (Melancon et al. 1998). This down-estuary shift in these fresher years may explain why existing mapped reefs provided by LDWF are all located in the Dry Restoration Zone and have had lower than average production during these years (LDWF 2018, LDWF 2019, LDWF 2020). The salinity interpolations matched Louisiana Department of Wildlife and Fisheries (LDWF) discrete data (Supplementary Figure B) with the largest incongruence actually showing higher predicted salinities for 2019 than were observed by LDWF, suggesting that the zones created may not reflect the full scope of freshening within the estuaries (Figure A.2.). Additionally, increased precipitation and runoff are predicted in the Gulf of Mexico region in future years (Keim et al. 2011, Keim and Powell 2015) suggesting that the zones determined in this study may represent future conditions more accurately than they would with inclusion of longer-term historic data. In addition to mean salinity decreases in the future, more salinity extremes and higher variation are predicted, emphasizing the importance of including salinity variation in the zone definition.

Salinity variation, measured by annual standard deviation, critically limited the Broodstock Sanctuary Zone, which covered only 6% of the identified area suitable for oysters. Previous studies and models indicate that variation likely plays a critical role in the overall success and population dynamics of eastern oysters but is rarely accounted for in habitat suitability models (Livingston et al. 2000, La Peyre et al. 2014, La Peyre et al. 2015). Salinity variability plays a large role in the energetic cost’s oysters face as osmoconformers (Lavaud et al. 2017). Eastern oysters regulate osmolytes through intracellular and extracellular regulation of fluids, changes in cell volume, and through closure of their shells under extreme water quality conditions (Shumway 1996). Therefore, oysters are susceptible to salinity variation, over both long and short time periods, because it is energetically costly to constantly osmoconform (McCarty et al 2020). Given predictions of increasing variability and extreme storm events, and that salinity variability is detrimental to oyster persistence, the idea of static broodstock sanctuary reefs is imperfect and must incorporate temporally dynamic water quality conditions.

Local oyster populations exist as part of a larger metapopulation, dependent on the persistence and success of nearby reefs (Lipcius et al. 2015). At any given time, suitable habitat for oysters may shift between different zones, as defined within this study. Dry Restoration areas may provide suitable oyster habitat for the oyster metapopulation during drier, high salinity years, while Wet Restoration areas may provide suitable habitat to ensure overall oyster persistence during wetter, low salinity years. This suggests a possible need for investment into reefs in the Wet Restoration Zone to preserve reef connectivity as current reefs are mostly up-estuary. Conservation and restoration science have demonstrated that connectivity of populations promotes species persistence and conserves ecological functions (D'Aloia et al. 2019). For management and restoration of oyster resources, this involves moving away from single reef management and accounting for variable water quality conditions to allow for temporally variable reef success (Kininmonth et al. 2010, Gerber et al. 2014, Spiecker et al. 2016, D'Aloia et al. 2019) (DWH NDRA 2017). Including both permanent (*ie*. Broodstock Sanctuary Zone) and dynamic (*ie*. Dry and Wet Restoration zones) conservation areas would encompass a larger range of conditions and facilitate oyster persistence over time (D'Aloia et al. 2019).

Similar to HSI's, salinity was the primary driver of the zones developed in these maps (Cake 1983, Denapolis 2018, Theuerkauf et al. 2019) but other factors such as food availability, temperature, suspended sediments, and hypoxia may help further refine zones. For example, area around the Mississippi River Delta is generally not suitable oyster habitat due to high suspended sediments, so the identification of Broodstock Sanctuary area there would likely be removed with the addition of a turbidity or sedimentation threshold. Increasing periods of hypoxia may also be problematic for suitable areas identified down-estuary and offshore, particularly if occurring for extended periods of time or if moving into up-estuary areas (Hagy and Murrell 2007, Rabalais and Turner 2019). However, a down-estuary suitability shift can be seen under high freshwater input scenarios demonstrated by modeled oyster production under scenarios of climate change and river diversions, further supporting that investment in the Wet Restoration Zone may be critical (Wang et al. 2017). Although these and other variables may become increasingly relevant, these zones overlap with prior outputs of HSI's across estuaries (Cake 1983, Soniat et al. 2013) and match well with a similar mapping effort in Barataria-Terrebonne estuaries, with a slight but overlapping down-estuary shift in suitability (Melancon et al. 1998). A further understanding of relationships between oyster population dynamics and environmental factors, along with increasing availability of daily data to support coastwide interpolations remains critical to better defining these zones.

Further development is also needed for off-bottom aquaculture in the region. The Aquaculture Zone defined in this study is extensive, and accounts for approximately 50% of the identified area suitable for oysters. However, it is often outside areas generally considered for oyster aquaculture, suggesting a need to examine the current approach to aquaculture site selection, and for local buy-in to considering more off-shore sites. Offshore oyster aquaculture exists in other regions (*ie*. New Zealand, Southern California; Cheney et al. 2010) but the Gulf of Mexico faces frequent and extreme severe weather challenges that must be considered. Technology modifications to address these challenges (*ie*. sinking baskets) plus the inclusion of logistics such as water depth, distance from shore, and use of the nearby waterways should be considered for aquaculture development, but we currently lack data for these parameters (Theuerkauf et al. 2019). Offshore areas in Vermilion-Teche and Terrebonne basins in the Gulf of Mexico, where extensive oyster reefs were historically present before being mined, may be promising for aquaculture operations if these considerations are accounted for.

2.5. CONCLUSION

With competing uses for restoration funding and expenses associated with oyster reef restoration and aquaculture establishment in the Gulf of Mexico, guidance on site selection provides critical data to ensure continued production and persistent oyster populations. A move away from single reef or site planning, and towards spatial planning, and managing oysters with both permanent and dynamic reefs, would better reflect and account for how metapopulations persist particularly within highly variable habitats. This spatial planning can further be aided through other restoration techniques including seeding reefs with low salinity adapted broodstock (Swam et al. 2020), use of supplementary hatchery produced seed especially in broodstock sanctuary areas, and long-term evaluation of current restoration efforts (LeBlanc et al. 2020). The use of a combination of these suggestions to inform management based on the maps developed in this study would promote efficient and effective restoration and aquaculture system establishment.

CHAPTER 3. ASSESSMENT OF UNIQUE LOUISIANA OYSTER POPULATIONS FOR ADAPTATION TO LOW SALINITY

3.1. INTRODUCTION

The eastern oyster, *Crassostrea virginica*, is an estuarine keystone species found along the Atlantic coast and in the Gulf of Mexico (Casas et al. 2018a). They are a critical economic resource in many coastal regions with Louisiana production comprising 34% of the nations' and 55% of the Gulf of Mexico's landings (LDWF 2019). Oysters are experiencing drastic population declines from overharvesting, habitat destruction, and increased disease prevalence (NRC 2004, Beck et al. 2011, Beseres Pollack et al. 2012). To balance high market demand with declining abundance, aquaculture production has become increasingly popular (Maxwell et al. 2008, Walton et al. 2013, Frank-Lawale et al. 2014, Campbell and Hall 2019).

Aquaculture systems are dependent on the suitability of local water conditions for their product because they are fixed in place. Conditions including temperature, salinity, dissolved oxygen, chlorophyll-*a*, turbidity, and wave exposure influence oyster growth and survival (Rybovich et al. 2016, Casas et al. 2018a). The two most important interacting conditions for oysters in Louisiana are temperature and salinity (Dugas and Roussel 1983, Heilmayer et al. 2008, Rybovich et al. 2016). Louisiana oysters survive in temperatures between 20°C and 26.3°C (Lowe et al. 2017), although oysters can be found in waters with average temperatures between -2°C and 36°C (Shumway 1996). The optimal salinity for wild, on-bottom Louisiana oyster growth and survival is between 10.7 – 16.1 (Lowe et al. 2017) but oysters can survive a wide salinity range from 5 – 40 (Shumway 1996). Overall, salinity is the most critical environmental factor impacting the success of natural oyster populations and oyster aquaculture systems (McCarty et al. 2020).

Although aquaculture systems require stable conditions, estuaries in the Gulf of Mexico (GOM) are variable and face further salinity changes. Climate models predict increased precipitation and runoff in the southeastern United States and more frequent extreme events causing increased exposure to both general and acute low salinity (Dugas and Roussel 1983, Mulholland et al. 1997, Keim and Powell 2015). Increasingly low salinities will be experienced along the northeastern GOM, but Louisiana estuaries face additional low salinity events from land loss management which involves large-scale river diversions into estuaries (CPRA 2017, LDWF 2019). Decreasing salinity across oyster producing locations may lead to increased mortality of natural oyster populations, traditional oyster leases, and aquaculture systems within these areas (Das et al. 2012, Lavaud et al. 2021).

Salinities outside of oyster tolerance ranges both high and low can cause major physiological stress to oysters. When exposed to low salinity, oysters' physiological and behavioral responses as osmoconformers include the regulation of osmolytes through intracellular and extracellular regulation of fluids, changes in cell volume, and through closure of their shells under extreme water quality conditions (Shumway 1996, Lavaud et al. 2017). Shell closure can be maintained for several days without harm, but over a long period of time, reduced feeding rates will limit growth and weaken the oyster causing mortality (Shumway 1996). While low salinity environments pose these physiological challenges for oysters, they offer refuge from predation and disease and would allow for farming in areas affected by increasing freshwater, creating an opportunity for aquaculture system development in previously unconsidered areas if these low salinity challenges can be overcome (La Peyre et al. 2003, McCarty et al. 2020).

One management strategy to address increased freshwater and low salinity events while maintaining high oyster production and ensuring oyster persistence is to locate and specifically farm oyster populations with low salinity tolerance. Oysters exist across a gradient of environmental conditions through their large latitudinal range, including salinity, and there has been some evidence for genetic subpopulations or population-specific adaptation to local conditions (Barber et al. 1991, Dittman et al. 1998, Burford et al. 2014). In Louisiana estuaries specifically, mean salinity from 2015 – 2019 ranged from 0 – 34.7, increasing with distance from shore (Swam et al. in review). Additionally, mean annual salinity standard deviation for 2015 – 2019 ranged from 0 – 6.5, differentiating by estuary (Swam et al. 2021). Within the Gulf of Mexico, studies have shown differential growth and survival between populations depending on the parent's site of origin when transplanted to a different grow-out location (Leonhardt et al. 2017, Miller et al. 2017). A recent study using east coast oyster populations also found evidence of heritability for the trait of low salinity tolerance (McCarty et al. 2020).

Oysters exist in many Louisiana estuaries that differ significantly in salinity means and variation. While public oyster grounds exist in areas which have historically experienced optimal salinity conditions for on-bottom oyster production and supported highly productive oyster reefs, significant oyster resources have persisted outside of these areas. As these areas represent a range of salinity regimes, uniquely adapted populations may exist that can support the selection of oyster populations likely to survive freshwater events and future low salinity conditions. This study compares the performance of three oyster populations that exist in areas of Louisiana estuaries suspected to frequently have lower than optimal salinity conditions for oyster growth and survival, by comparing the growth, mortality, and condition of their progeny at a low and high salinity site to a control population. Identifying oyster populations tolerant of low salinity can help in developing broodstock to support aquaculture and management, especially in the increasingly fresh Gulf of Mexico estuaries.

3.2. METHODS

This field study quantified growth (mm mo^{-1}), mortality (%), *Perkinsus marinus* infection (%), and body condition of four Louisiana oyster populations when exposed to different salinities. One population was from a highly productive region which served as our control. Three populations were suspected to be from low salinity regions, with two in areas that receive high river input potentially contributing to salinity regimes experienced by present oyster reefs.

3.2.1. Oyster collection sites

C. virginica used in this study were the progeny of oysters collected from four sites along the Louisiana coast: Calcasieu Lake, Sabine Lake, Pass a Loutre, and Point Au Fer (Figure 3.1.). Natural reefs exist across these locations, which represent a wide range of environmental conditions and riverine influence (Figure 3.2.).

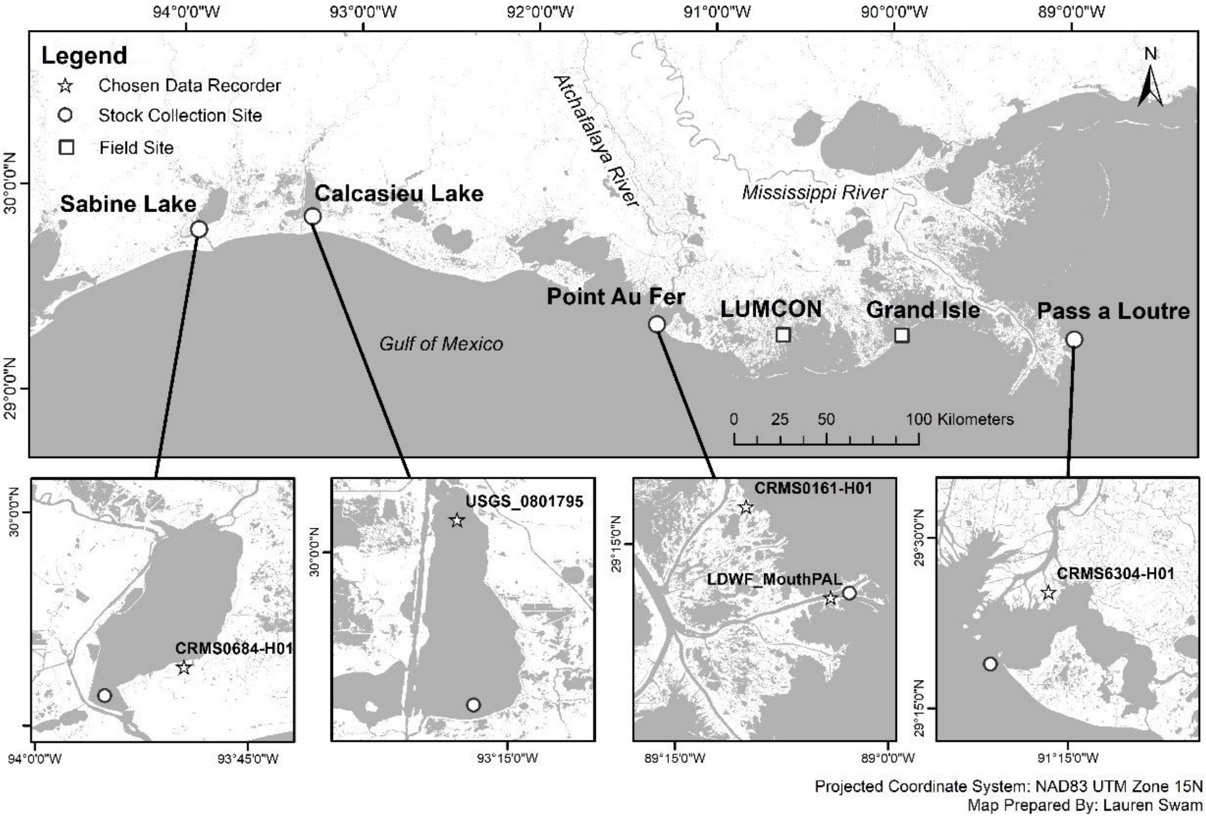


Figure 3.1.Locations of original broodstock collection sites and sites of progeny grow out field experiment (Grand Isle, LA and LUMCON in Cocodrie, LA). Zoomed panels depict the collection site and chosen associated daily data recorder. Calcasieu Lake values were obtained from USGS recorder 08010795 (daily data; highest correlation to LDWF monthly data at collection site $R^2 = 0.7583$, 10-year mean salinity difference was 0.2). Sabine Lake values were obtained from CRMS recorder 0684-H01 (daily data; highest correlation to LDWF twice-monthly data directly at collection site $R^2 = 0.5774$, 10-year mean salinity difference was 5.6). Pass a Loutre values were obtained from CRMS recorder 0161-H01 (daily data nearest to collection site, LDWF data was infrequent but pictured for reference). Point Au Fer values were obtained from CRMS recorder 6304-H01 (daily data, nearest to collection site).

Calcasieu Lake is an estuarine lake located at the southern end of the Calcasieu River Basin that experiences freshwater inflow from the Calcasieu River, consists of 58,260 acres of water bottom with oyster reefs, and supports extensive oyster harvesting (LDWF 2019). In Calcasieu Lake, according to USGS recorder representing this site, the range of monthly mean salinities from 2009 – 2019 was 8.7 – 17.5 with daily salinities ranging from 0.1 – 29.0 and will be used as a control to compare to untested populations (Figure 3.1.) (USGS 08010795 – North Calcasieu Lake near Hackberry, LA, U.S.A).

Sabine Lake is a fresher estuarine bay located at the southern end of the Sabine River Basin that experiences freshwater inflow from the Neches and Sabine rivers, consists of 55,057 acres of water bottom with oyster reefs only in the southernmost portion of the lake, and supports minimal oyster harvesting (there has been no oyster season in Sabine Lake since the early 1960s) (LDWF 2019). In Sabine Lake, according to USGS recorder representing this site, the range of monthly mean salinities from 2009 – 2019 was 4.7 – 11.1 with daily salinities ranging from 0.2 – 25.6 (Figure 3.1.) (CRMS0684-H01, LA, U.S.A.).

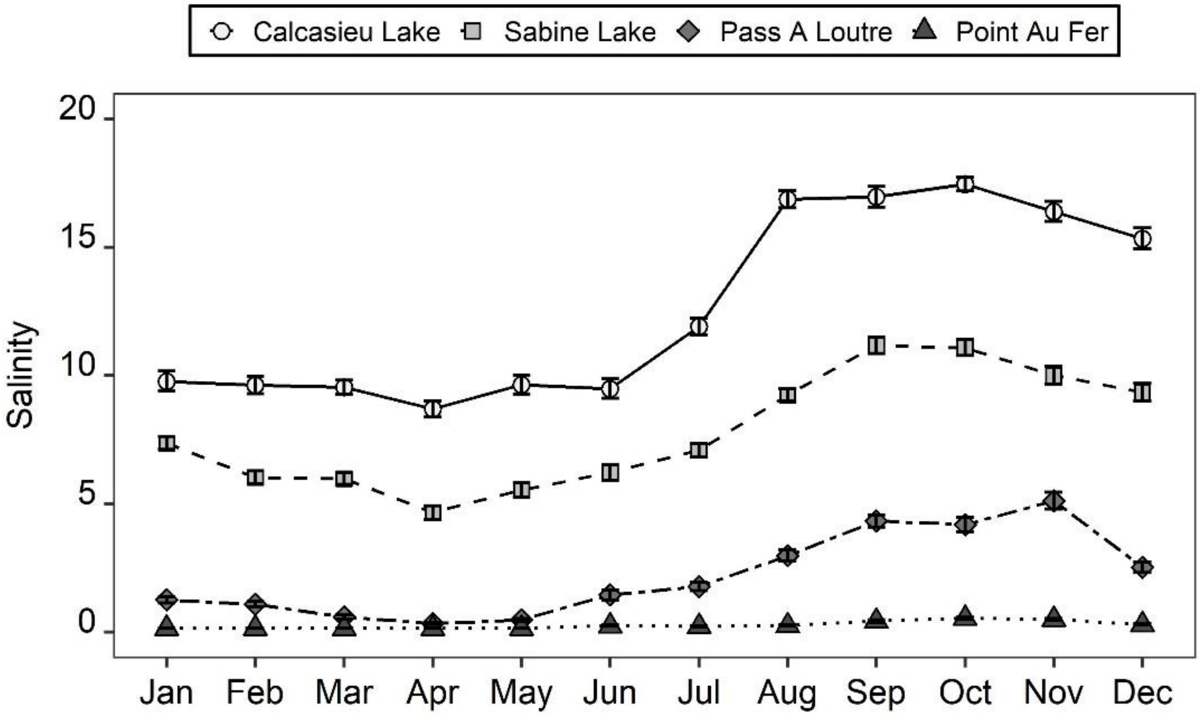


Figure 3.2. Estimated mean monthly salinity (±1 SEM) at broodstock origin locations from 2009 – 2019 (n=10 for each month).

Pass a Loutre is an area on the eastern side of the Mississippi River Delta that experiences freshwater inflow from the Bohemia Spillway, Caernarvon and Bayou Lamoque freshwater diversion structures and main-stem river distributaries and consists of nearby intermittent public oyster reefs enhanced through the placement of cultch material on suitable water bottoms (LDWF 2019). At the Pass a Loutre stock collection site, the range of monthly mean salinities from 2009 – 2019 was 0.3 – 5.1 with daily salinities ranging from 0.1 – 23.9 (Figure 3.1.) (CRMS0161-H01, LA, U.S.A.). At Pass a Loutre, there is some evidence of a possible salt wedge allowing oyster reefs to persist at monthly mean salinity ranges of 9.2 – 17.1 rather than 0.3 – 5.1 but this is currently unknown (Figure 3.3.) (LDWF Mouth of Pass a Loutre).

Point Au Fer is a primarily open water brackish system that experiences freshwater inflow from the Atchafalaya and Vermilion rivers, consists of nearby public oyster seed grounds that experience extensive oyster mortalities except in years with reduced freshwater from the Atchafalaya River and, therefore, support intermittent oyster harvests (LDWF 2019). At the Point

Au Fer stock collection site, the range of monthly mean salinities from 2009 – 2019 was 0.1 – 0.5 with daily salinities ranging from 0.1 – 10.3 (Figure 3.1.) (CRMS6304-H01, LA, U.S.A.).

3.2.2. Oyster spawning

In April 2019, approximately 200 market-sized oysters were collected from each of the four sites and transported to the Michael C. Voisin Louisiana Sea Grant Oyster Research Farm located in Grand Isle, LA. Oysters were placed in baskets suspended on an adjustable long-line system nearshore (ALS, BST Oyster Co., Cowell, South Australia). In summer and early fall 2019, individuals from each broodstock were kept in controlled conditions and exposed to an increase in water temperature to induce natural spawning at the Louisiana Sea Grant Oyster Research Hatchery in Grand Isle, LA (Table 3.1.) (Wallace et al. 2008). Once individual oysters (both male and female) had spawned, gametes were combined to form larvae (Wallace et al. 2008). Larvae were fed algae and allowed to grow in aerated tanks until they developed an eyespot and were large enough to set (>290 µm) on microcultch to promote single oysters (Wallace et al. 2008). Once large enough for mesh baskets, the progeny of individuals from the four stocks were placed in color-coded baskets by stock, moved to a long-line system adjacent to the hatchery, and allowed to grow until the start of this experiment in December 2019.

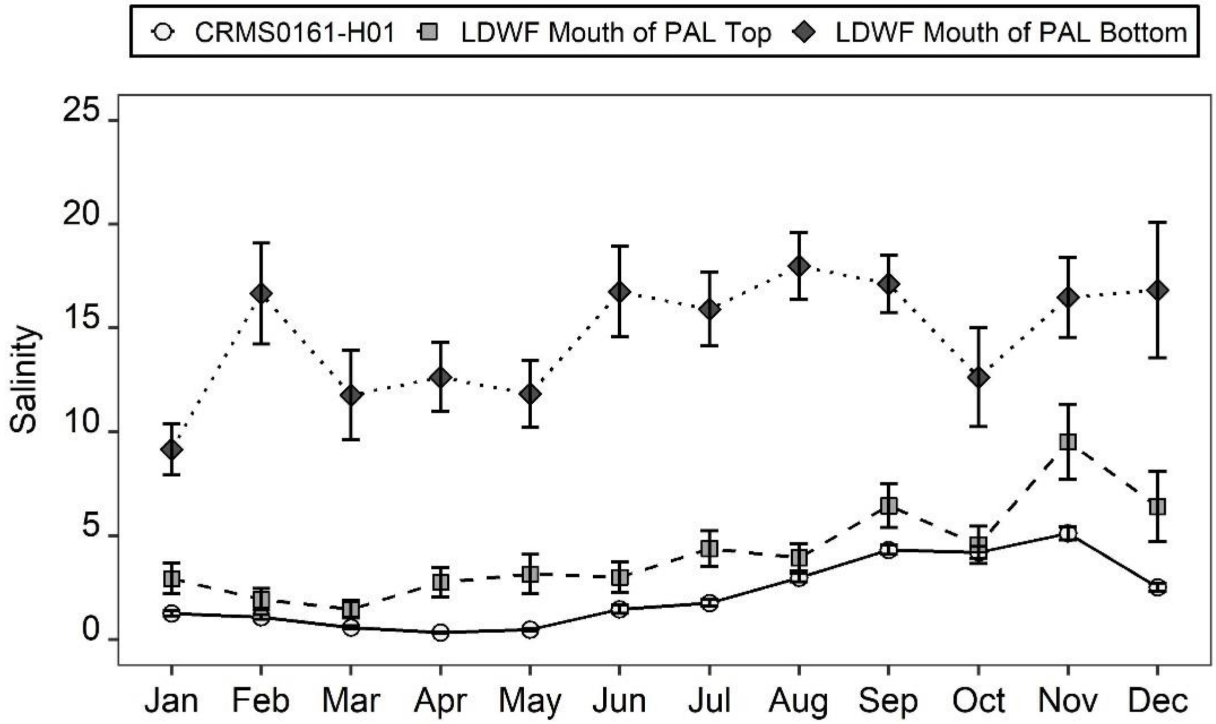


Figure 3.3. Estimated mean monthly salinity (2009 – 2019) of salinity data collected bi-monthly by hand-held meter at top and bottom of the water column nearest oyster broodstock collection site (LDWF Mouth of PAL, n=207) compared to the nearest continuous salinity data recorder to the oyster broodstock collection site (CRMS0161-H01n=3407).

Table 3.1. Number of males and females spawned at Grand Isle oyster hatchery to produce progeny of populations.

	Males	Females
Calcasieu Lake	3	5
Sabine Lake	9	9
Pass a Loutre	13	13
Point Au Fer	17	15

3.2.3. Oyster grow out sites

In December 2019, progeny from the four spawned broodstocks were deployed in oyster baskets suspended on long-line systems at two sites with one representing a lower salinity, upper estuary environment and the second representing a higher salinity, lower estuary environment. Four baskets of 100 oysters each were deployed at each site for the four broodstocks (4 populations x 4 baskets x 2 sites x 100 oysters). Baskets were placed on the long line in a randomized block design to account for unmeasured variation from water movement.

3.2.4. Water quality

Daily mean salinity and temperature from December 2019 through November 2020 were obtained for the Grand Isle grow out site from USGS continuous data recorder (Barataria Pass at Grand Isle, LA; 073802516). Missing data points were filled in from a second USGS continuous data recorder (Barataria Bay near Grand Terre Island, LA; 291929089562600), which had a correlation of $R^2 = 0.8797$ to the original daily dataset. Data from the same period for the LUMCON grow out site was obtained from a continuous data recorder at LUMCON. Interval salinity and interval temperature (averages between sampling dates) were compared to quantify differences in environmental conditions between the two grow out sites over the twelve-month study period.

3.2.5. Mortality

At each monthly sampling from December 2019 through November 2020 the number of live and dead oysters in each bag were recorded, dead oysters were discarded, and interval mortality was calculated as [interval percent mortality = (# dead / # total) * 100]. Cumulative percent mortality was then calculated as [cumulative mortality = (# dead / # total) * (100-previous sampling cumulative mortality) + (previous sampling cumulative mortality)]. A multiple linear regression analysis was used to explore causal connections between interval mortality and interval salinity, interval temperature, and interval initial shell height of all stocks combined and each stock separately.

3.2.6. Growth

At each monthly sampling shell height, the distance from shell umbo to distal edge, was measured for a random subset of 25 oysters per cage (La Peyre et al. 2013). Initial average shell height of each stock is summarized in Table 2. Monthly interval growth rate was calculated and standardized to a 30-day month as [interval growth = (change in height from previous sampling) / (days since previous sampling) * 30]. Mean interval growth rate was calculated using [(height from completion of experiment – height from start of experiment) / (days of experiment duration) * 30]. A multiple linear regression analysis was used to explore causal connections between interval growth and interval salinity, interval temperature, and interval initial shell height of all stocks combined and each stock separately.

3.2.7. **Perkinsus marinus** *infection intensity*

In October 2020, near the completion of this study, fatal sampling of five oysters per cage of each population was conducted to assess *Perkinsus marinus* infection intensity and body condition index. The infection intensity of *P. marinus* of individual oysters was measured as the number of parasites per gram of oyster tissue following protocols outlined in Fisher and Oliver (1996) and updated by La Peyre, et al. (2019). Infection prevalence (%) indicates the number of infected oysters out of the total number of oysters sampled (infected + uninfected).

Table 3.2. Mean (± standard error) shell height at start of experiment (Dec 2019).

	Grand Isle	LUMCON
Calcasieu Lake	23.1 ± 0.6	22.1 ± 0.7
Sabine Lake	11.3 ± 0.3	10.8 ± 0.3
Pass a Loutre	17.0 ± 0.4	17.3 ± 0.4
Point Au Fer	16.9 ± 0.4	16.4 ± 0.4

3.2.8. Condition index

Condition index was calculated as [CI = (dry tissue weight) / (whole wet oyster weight) – (shell wet weight * 100)] (Casas et al. 2017, Casas et al. 2018a). For each oyster, a 10mL aliquot of oyster homogenate created for *P. marinus* infection intensity was dried at 65°C for 48 hours and the total dry weight was calculated based on the total volume of oyster homogenate (La Peyre et al. 2003). The condition index value reflects the physiological and nutrition status of an individual as it assesses its use of the available internal space for somatic and gonadal tissue growth (Casas et al. 2018a).

3.2.9. Statistical analyses

All statistical analyses were conducted using R v.3.6.3 (R Core Team, 2020). A p-value of <0.05 was used to determine significance for all tests. Results from daily salinity and temperature data were analyzed using an independent t-test to compare sites. Cumulative mortality at the end of the study were compared using a series of chi-square analyses using the Bonferroni adjustment on p-values to assess differences between stocks at each site. Interval mortality of all stocks combined and each stock individually at both sites were analyzed using a multiple linear regression using interval salinity and interval temperature as predictor variables. Mean annual growth rate (mm mo-1) for each stock at both sites was analyzed using a two-factor ANOVA (site, stock) followed by a Tukey post-hoc test. Interval growth of all stocks combined and each stock individually at both sites were analyzed using a multiple linear regression using interval salinity, interval temperature, and interval initial shell height as predictor variables. Interval initial shell height is defined as the average shell height at the start of each sampling interval. P. marinus infection intensity and condition index near the end of the experiment (October 2020) were compared using a two-factor ANOVA (site, stock) followed by a Tukey post-hoc test.

3.3. RESULTS

Several significant differences in growth and mortality of four oyster broodstocks were found throughout the duration of this experiment.

3.3.1. Water quality

Daily mean salinity at Grand Isle was significantly higher than mean daily salinity at LUMCON in Cocodrie, LA ($p < 0.001$, Figure 3.4.). During the study (Dec 12, 2019- Nov 19, 2020), the Grand Isle, LA site had a mean daily salinity of 16.8 ± 0.32 SEM with a range of 4.8 – 29.9. The Louisiana Universities Marine Consortium (LUMCON) site had a mean daily salinity of 8.7 ± 0.24 SEM with a daily range of 1.2 – 19.0. Salinity generally decreased from December through April, increased from April through September, and plateaued from September through December at both sites (Figure 3.4.).

Daily temperature followed expected seasonal trends and was within expected ranges for this region with no difference found between grow out sites ($p = 0.6$, Figure 3.4.). Grand Isle, LA had a mean annual temperature of 23.7 ± 0.3 SEM with a daily range of 10.7 – 32.5. LUMCON had a mean annual temperature of 23.9 ± 0.31 SEM with a daily range of 9.9 – 32.6. Temperature generally increased from December through June, plateaued from June through August, and decreased from August through December at both sites (Figure 3.4.).

3.3.2. Mortality

At the study’s completion, significant differences in cumulative mortality were only found between stocks at LUMCON ($p < 0.001$). At this site, the cumulative mortality of the Point Au Fer stock was significantly higher than the cumulative mortality of Calcasieu Lake and Sabine Lake stocks (Figure 3.5.), and the cumulative mortality of the Pass a Loutre stock was significantly higher than the Sabine Lake stock.

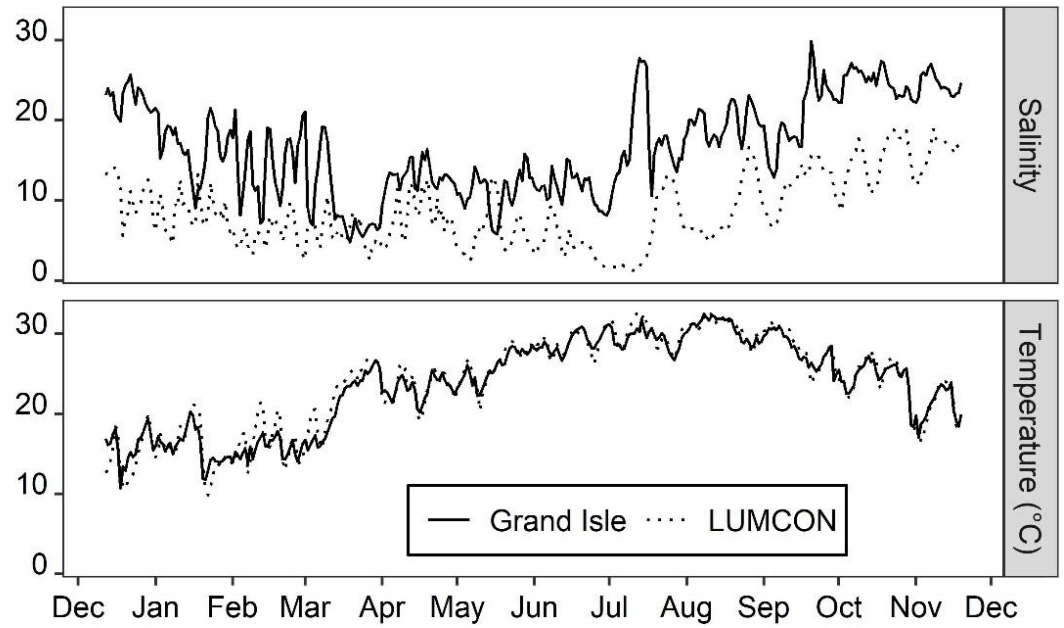


Figure 3.4. Daily water salinity and temperature (°C) from December 12, 2019 to November 19, 2020 from continuous recorders at LUMCON (DeFelice Marine Center Environmental Monitoring Station Data, 2019 & 2020) and Grand Isle (USGS Barataria Pass at Grand Isle, LA with missing data points filled in using USGS Barataria Bay near Grand Terre Island, LA).

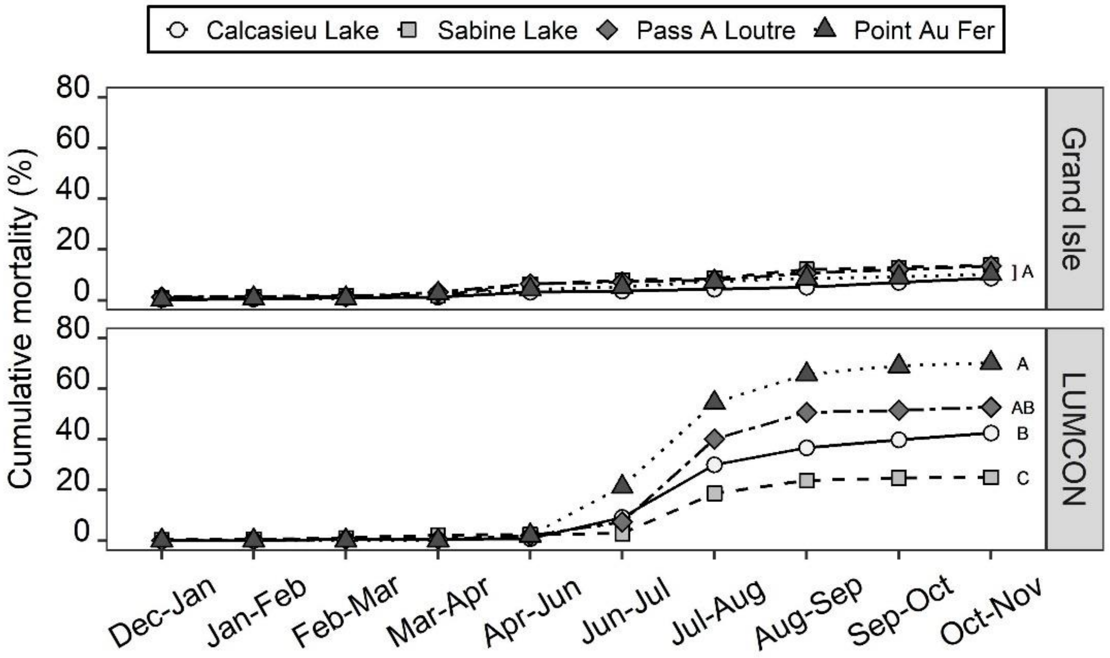


Figure 3.5. Cumulative mortality (%) of oysters from Calcasieu Lake, Sabine Lake, Pass a Loutre, and Point Au Fer stock populations. Different letters denote statistical differences (sites analyzed separately).

For all stocks combined, a significant regression equation with an R^2 of 0.25 was found (Table 3.3.). Significant regression equations were also found for each stock individually with R^2 ranging from 0.20 to 0.38 (Table 3.3.).

Table 3.3. Regression results examining interval mortality as a function of interval salinity and interval temperature, for all stocks combined, and by individual population, over experiment duration without interaction.

	All Stocks	Calcasieu Lake	Sabine Lake	Pass a Loutre	Point Au Fer
Interval salinity	0.07	0.14	0.15	0.28	0.13
Interval temperature	0.89*	0.75*	0.48*	1.13*	1.51*
Interval initial shell height	-0.17*	-0.17*	-0.11*	-0.27*	-0.31*
Intercept	-12.10*	-9.23	-7.97*	-16.39*	-20.42*
Df	316	76	76	76	76
Adj. R^2	0.25	0.26	0.20	0.25	0.38
F-statistic	36.7*	10.46*	7.59*	9.85*	17.36*

*indicates significance
$p<0.05$

3.3.3. Growth

There was a significant site by stock interaction for mean growth rate from beginning to end of the experiment duration ($p = 0.002$). Average interval growth was significantly higher at Grand Isle than at LUMCON for all stocks ($p < 0.001$). At Grand Isle, only the Point Au Fer stock had a significantly higher growth rate from the Calcasieu Lake and Sabine Lake stocks ($p = 0.007$ and $p = 0.03$ respectively).

For all stocks combined, a significant regression equation with an R^2 of 0.45 was found (Table 3.4.). Significant regression equations were also found for each stock individually with R^2 ranging from 0.37 to 0.51 (Table 3.4.).

Table 3.4. Regression results examining interval growth as a function of interval salinity, interval temperature, and interval initial shell height over experiment duration without interaction.

	All Stocks	Calcasieu Lake	Sabine Lake	Pass a Loutre	Point Au Fer
Interval salinity	0.34*	0.28*	0.35*	0.39*	0.37*
Interval temperature	0.15*	0.07	0.20*	0.17*	0.16*
Interval initial shell height	-0.04*	-0.02	-0.06*	-0.05*	-0.03
Intercept	-2.21*	-0.33	-3.17*	-2.85*	-3.08*
Df	316	76	76	76	76
Adj. R^2	0.45	0.37	0.41	0.49	0.51
F-statistic	89.04*	16.43*	19.58*	25.94*	28.52*

*indicates significance,
$p<0.05$

3.3.4. **Perkinsus marinus** *infection intensity*

At the completion of the experiment in November 2020, stocks at LUMCON had significantly lower prevalence and intensity of *P. marinus* infection than stocks at Grand Isle ($p < 0.001$, Figure 3.6.). There were no significant differences detected between stocks at either site ($p = 0.09$, Figure 3.6.).

There were more uninfected oysters for all stocks at LUMCON compared to Grand Isle. There were also instances of moderately and highly infected oysters at Grand Isle for all stocks, which did not occur at LUMCON (Figure 3.7.).

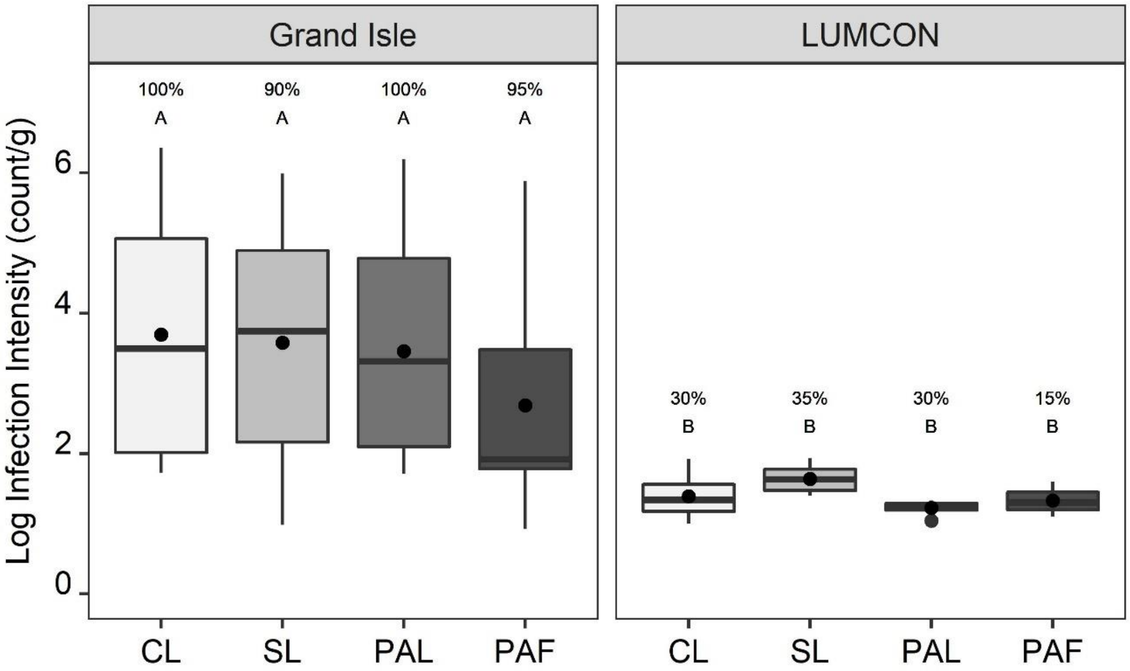


Figure 3.6. Infection intensity of oysters ($\log_{10}$ parasites g^{-1}) from Calcasieu Lake (CL), Sabine Lake (SL), Pass a Loutre (PAL), and Point Au Fer (PAF) stock populations. Only infected oysters are included. Different letters denote statistical differences at both sites. For each boxplot, the black circle indicates mean, whiskers represent first and fourth quartiles, the box represents second and third quartiles, and the horizontal line represents the median.

3.3.5. Condition index

At the completion of the experiment in November 2020, there was a significant site by stock interaction on the condition index of oysters ($p < 0.001$). There were no significant differences in condition index between the four stocks at Grand Isle but at LUMCON, the Calcasieu Lake stock had a significantly lower condition index than the stocks from Sabine Lake, Pass a Loutre, and Point Au Fer (Figure 3.8.).

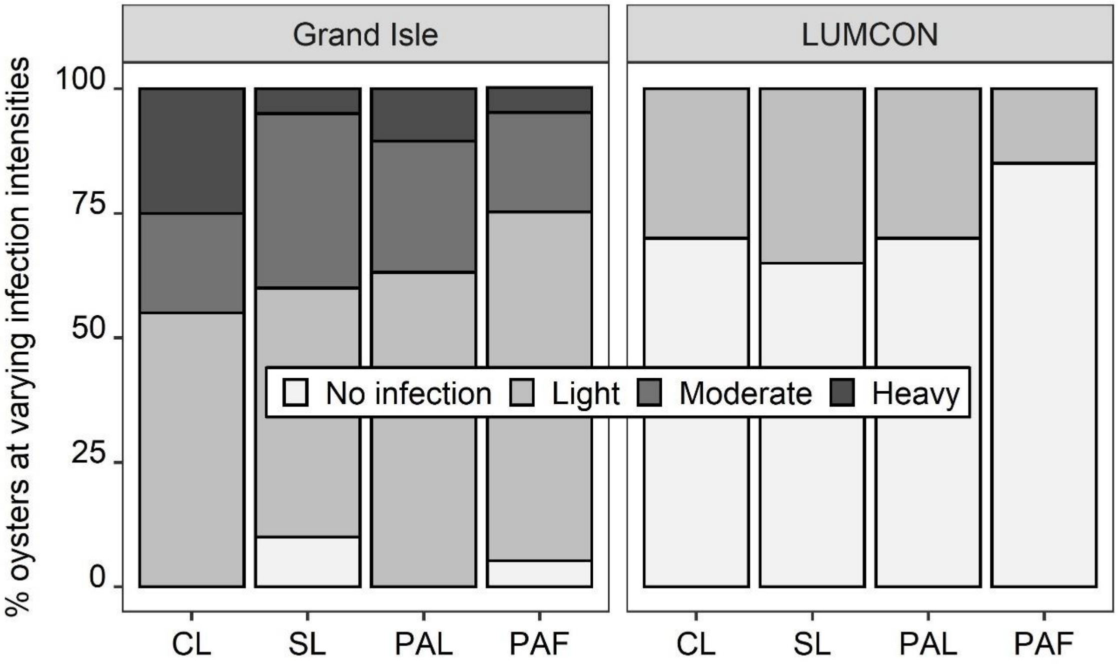


Figure 3.7. Percentage of oysters from Calcasieu Lake (CL), Sabine Lake (SL), Pass a Loutre (PAL), and Point Au Fer (PAF) stock populations with no *Perkinsus marinus* infection, with light (<10,000 parasites per g wet tissue), moderate (10,000 – 500,000 parasites per g wet tissue), and heavy (>500,000 parasites per g of wet tissue) infection sampled in October 2020 at both sites.

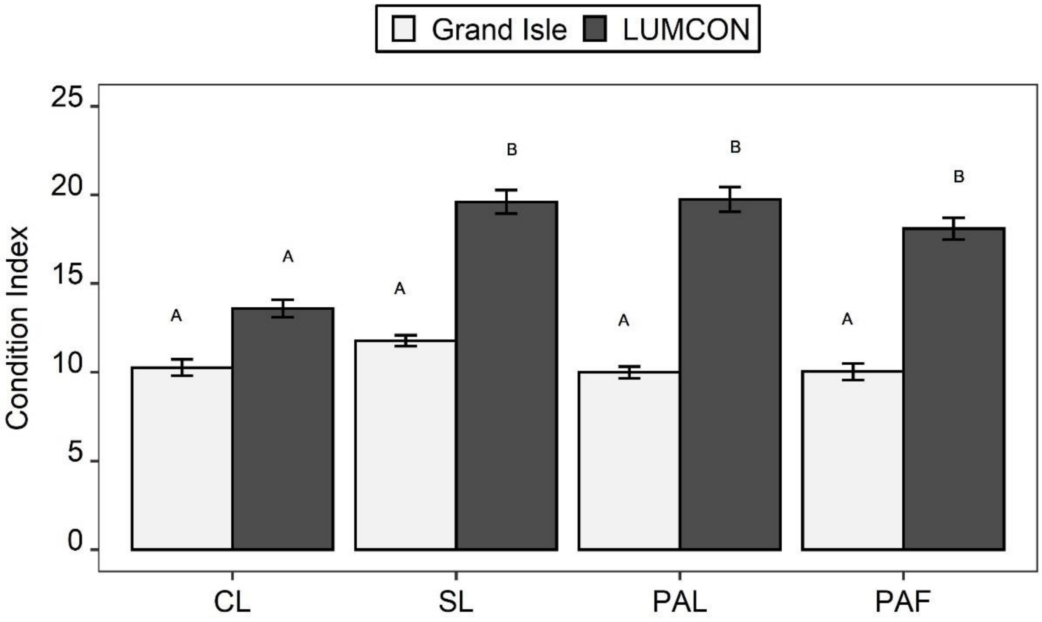


Figure 3.8. Condition index of oysters from Calcasieu Lake (CL), Sabine Lake (SL), Pass a Loutre (PAL), and Point Au Fer (PAF) stock populations sampled in October 2020 at Grand Isle and LUMCON, Louisiana (±1 SEM). Different letters denote statistical differences at both sites.

3.4. DISCUSSION

Progeny of four unique Louisiana oyster populations were assessed for phenotypic adaptation to low salinity. The most significant differences between populations in our study were their mortalities at the low salinity site, specifically between June and September, during peak summer temperatures (>29°C) and following months with low salinity (<8). Observed differential mortality between populations suggests that discrete populations of oysters can be better suited to low salinity areas or events, potentially through population-specific tolerance to a given conditions. This adaptation can be exploited for the selection of broodstock better suited to specific conditions to facilitate efficient aquaculture and management.

Significant differences in mortality between populations at the low salinity site largely occurred between June and September, a period characterized by high temperatures (30.1 ± 0.16) and low salinity (7.3 ± 0.45). Both high temperatures and low salinities have been shown to be lethal to oysters, especially when occurring together (Shumway 1996, Rybovich et al. 2016). In this study, the Sabine Lake oysters had significantly lower mortality at the low salinity site compared to the other populations. The three test populations used in this experiment (Sabine Lake, Pass a Loutre, and Point Au Fer) were selected due to their suspected exposures to low salinity, with the hypothesis that population performance would reflect how well exposure conditions matched site of origin conditions. Based on available data, the Sabine Lake site of origin had the closest matching salinity regime to the low salinity site used in this study, and oysters from this site had significantly lower cumulatively mortality compared to the other sites. This suggests that lower mortality could be due to local adaptation to the low salinity, explained by decreased environmental difference between the site of origin and the testing site.

The Pass a Loutre and Point Au Fer populations were suspected to be from low salinity sites based on data from their nearest continuous data recorders. However, the nearest data recorders are located on the marsh surface and may not accurately reflect salinity at the bottom of the water column if there is stratification in these areas. Both sites exist in locations that receive large amounts of riverine input, with Pass a Loutre being located at the mouth of the Mississippi River and Point Au Fer being located at the mouth of the Atchafalaya River. While Louisiana estuaries are generally described as shallow, well-mixed estuaries, it is possible that high river inflow in some locations results in some stratification, with nearby marshes being flooded with freshwater while bottom waters are more influenced by marine waters (Laevastu & Hela 1970). Evidence to support this for at least one location comes from discrete data collection at Pass a Loutre, which records a surface and bottom water mean salinity difference of 4.7 (higher on bottom at 7.7) over 32 years with that difference being greater in summer (6.1 higher on bottom) compared to the other three seasons (LDWF Pass a Loutre discrete water quality data 4/13/2021). This seasonal salinity difference can be explained by the increased freshwater flow from the Mississippi River due to snow melt in the spring and from generally higher precipitation. Temperature stratification often accompanies salinity stratification in estuaries due to thermal heating on the surface (Laevastu & Hela 1970) and, although not significantly demonstrated in the monthly dataset available (LDWF Pass a Loutre discrete water quality data 4/13/2021), plausible lower mean temperatures at the Pass a Loutre and Point Au Fer sites of origin could have possibly affected their mortality at higher experimental temperatures. While Louisiana has a large network of marsh-based continuous data recorders (*i.e.,* CPRA 2020), increased monitoring of open-water areas, including bottom water salinity and temperature would help better inform oyster management.

Mean growth rate was lowest at the low salinity site between June and August, coinciding with highest temperatures and lowest salinity experienced through the experiment duration. Since all populations had equal access to resources (*i.e.,* food) within sites, individuals from all populations that could withstand mortality-inducing events were able to maintain size or continue growing, albeit at lower rates. Regressions of interval growth rates found salinity to be a significant predictor variable for all four populations. Lowered salinity can cause reduced oyster feeding through both extended valve closures to water quality stressors and through changes in food quality and availability (Shumway 1996, Riekenberg et al. 2015, Casas et al. 2018b).

In contrast to growth results, oysters at the low salinity site had a higher condition index than the high salinity site, but in all cases, condition index was relatively high (> 10), and it is unlikely that the small difference impacted overall oyster survival (Casas et al. 2017). Condition index indicates how well an oyster uses its' shell cavity for tissue growth, reflects overall health status, and estimates meat quality (Haven 1960, Lawrence and Scott 1982, Mann 1992). Condition index is often decreased after gametogenesis, which is reduced, or delayed with lower salinity (< 10) which could explain some of the lowered condition index at the higher salinity site (Butler 1949, Loosanoff 1953).

Although they present physiological challenges to oysters, low salinity sites are a refuge for mortality from *Perkinsus marinus* infection, which has been shown to have limited or delayed development at lower salinities (Chu and La Peyre 1993, La Peyre et al. 2003, Ragone Calvo and Burreson 2003, Bushek et al. 2012, McCarty et al. 2020). This is likely reflected in our study both through lower infection prevalence and lighter infection intensity when infected at the low salinity site compared to the high salinity site, although both sites tended to have overall light to moderate infection intensities. With higher mortalities seen at the site with lighter infection, we concluded that infection was not a leading cause of differing mortality between populations seen in this study. Further, infection intensity high enough to cause mortality (>500,000 parasites per g wet tissue) did not occur in a majority of individuals in this experiment (La Peyre et al. 2019).

3.5. CONCLUSION

Overall, our findings are supportive of the idea of population-specific adaptation of oyster populations to low salinity. Oysters found in Sabine Lake indicate tolerance to low salinity based on exposure at their site of origin, and we should continue assessing other populations along the Louisiana coast in low-salinity areas for similar adaptation. Although untested in this study specifically, there is likely a genetic component to low salinity tolerance in oysters (Eierman and Hare 2014, McCarty et al. 2020). In this study, the use of progeny oysters rather than the parents collected at our sites of origin suggest a genetic component as well, and the underlying genetic mechanisms of this adaptation should be explored further. Adaptation to low salinity is a useful consideration for aquaculture as the progeny from adapted oysters could generate seed for use on oyster leases affected by low salinity events (freshwater runoff, sediment diversions, etc.) and for aquaculture farms to be set up in lower salinity areas of the coast. This potential would be best capitalized upon with the identification of other low-salinity tolerant oyster populations to ensure genetic diversity in broodstocks used for seed development.

CHAPTER 4. SUMMARY AND CONCLUSIONS

Eastern oysters are a critical estuarine species that have major impacts on the ecosystems and industries that rely on their production and survival. Due to rapidly freshening estuaries in the Gulf of Mexico, oyster populations have been declining for decades and novel management strategies would help restore them. The studies outlined here explored two such strategies specifically aimed at ensuring resilient oyster populations and high production in the face of lower salinities and increasing variability across Louisiana estuaries.

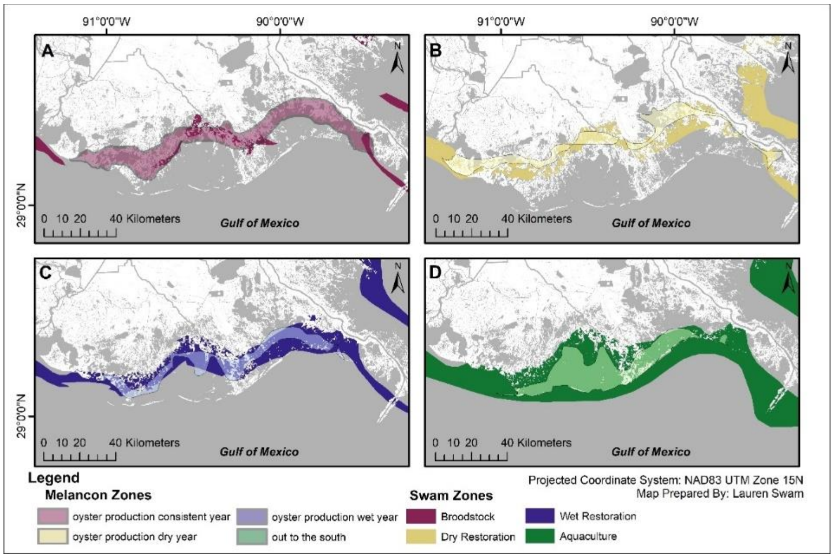
This work emphasizes the importance of using a comprehensive, metapopulation approach to designing oyster management and restoration strategies. Some oyster populations can exist independently from others, but if reefs are near one another, they are reproductively connected. This connection is what allows connected oyster populations to persist through periods with adverse water quality conditions (*i.e.*, if one reef experiences optimal conditions while another experiences sub-optimal conditions, gametes from the reef able to reproduce at that time can repopulate the other reefs for the next year when optimal conditions may shift location). This work spatially mapped open-water areas with salinities matching oyster habitat needs and used these maps to identify oyster resource zones across the Louisiana coast which, together, enable the movement away from single reef management to management and restoration of oyster resources as an integrated set of reefs. This oyster zone identification is the first step towards a spatial management approach to use both constantly and variably productive oyster reefs by including both permanent and dynamic conservation areas to promote long-term sustainable oyster populations and restoration projects.

This work also highlights the probability of discrete oyster populations to be uniquely adapted to local water quality conditions. This study specifically explored the potential for increased tolerance to low salinity in several Louisiana populations, identifying one population which outperformed the other tested populations. While breeding oysters with the ability to tolerate low salinity, other potential adaptations are plausible and should be explored further. If more adapted populations can be identified, this adaptability of specific oyster populations to local conditions could facilitate the strategic placement of adapted broodstock to areas experiencing a certain adverse condition for generic oysters. This would promote the persistence of oysters through variable conditions, which would then continue to repopulate other nearby reefs to maintain the larger metapopulation over time.

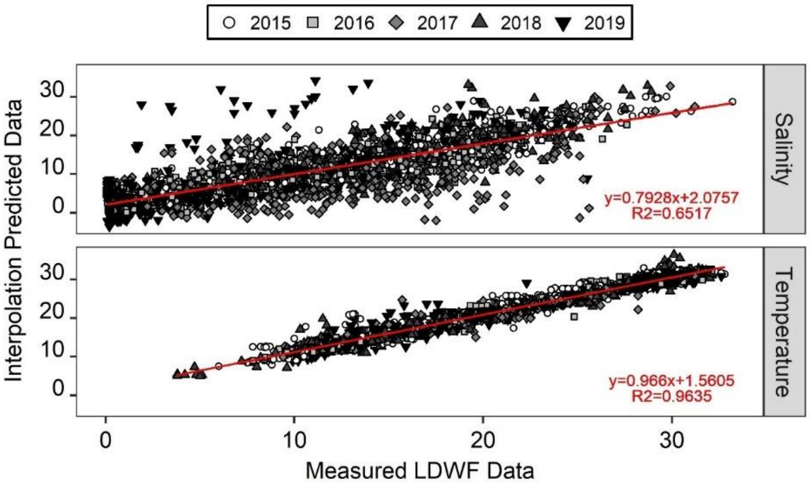
These two approaches could, together, help maximize the efficacy of oyster restoration efforts and harvest through the selective breeding and placement of adapted populations in areas identified to typically experience a given condition. This combined approach can be additionally maximized through the parallel development of oyster aquaculture in Louisiana. Adapted oyster populations could be matched to aquaculture grow out sites with similar conditions as their sites of origin to promote viability across a range of possible water quality conditions. Oyster production and restoration would benefit from novel strategies to restore native oyster populations and increase the efficacy of oyster harvest, especially considering continued abundance declines, persistent market demand, and coastal land loss. Continued research targeted at selective breeding of oysters to match existing and predicted future conditions may be valuable in ensuring oysters are able to adapt to quickly changing water quality in this region. Further, acknowledging reef connectivity and moving from single-reef management and restoration will promote long-term oyster reef and production sustainability despite temporally variable water quality conditions.

APPENDIX A. SUPPLEMENTARY FIGURES FOR CHAPTER 2

These figures provide supporting evidence for the oyster resource zones developed in the second chapter of this thesis. The oyster resource zones were conceptually based on maps created by Melancon et al. (1998), which mapped similar dry, wet, wet-dry, and high salinity zones in Barataria and Terrebonne estuaries in coastal Louisiana. Figure A.1. depicts the comparison between these original maps and the maps generated in this study. Figure A.2. depicts the linear relationship and regression equation between the LDWF physically sampled salinity and temperature data across coastal Louisiana (not included in the coastwide interpolations) and the interpolation predicted values, showing a reasonably high correlation of salinity and a high correlation of temperature.



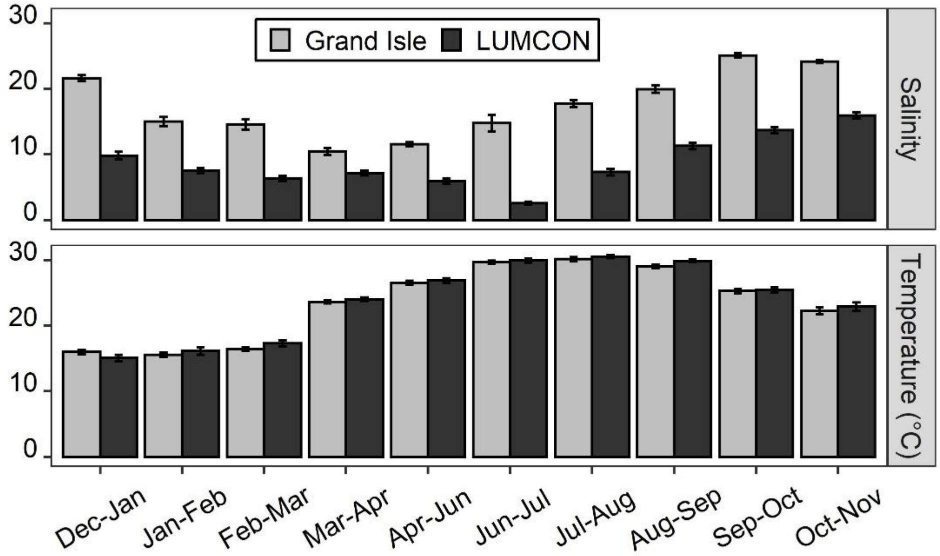
A.1. Oyster resource zones across coastal Louisiana based on mean salinity parameters from 2015-2019 separated to show all areas included within each zone overlaid with extents of zones from Melancon and Barras maps (1998). A: Broodstock Sanctuary Zone, B: Dry Restoration Zone, C: Wet Restoration Zone, D: Aquaculture Zone.



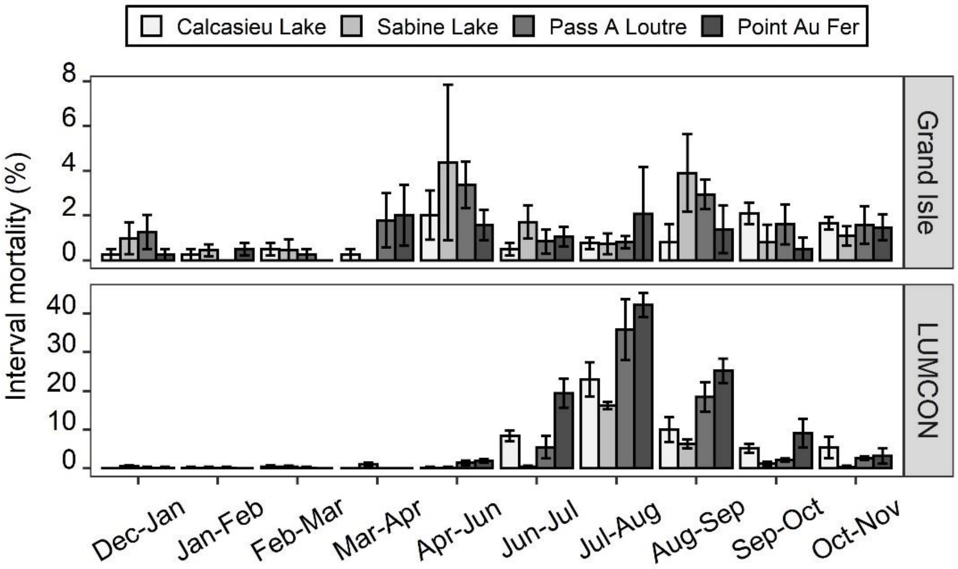
A.2. Validation of salinity and temperature interpolation outputs using *in situ* Louisiana Department of Wildlife and Fisheries water quality data for comparison (not used in interpolation generation).

APPENDIX B. SUPPLEMENTARY FIGURES FOR CHAPTER 3

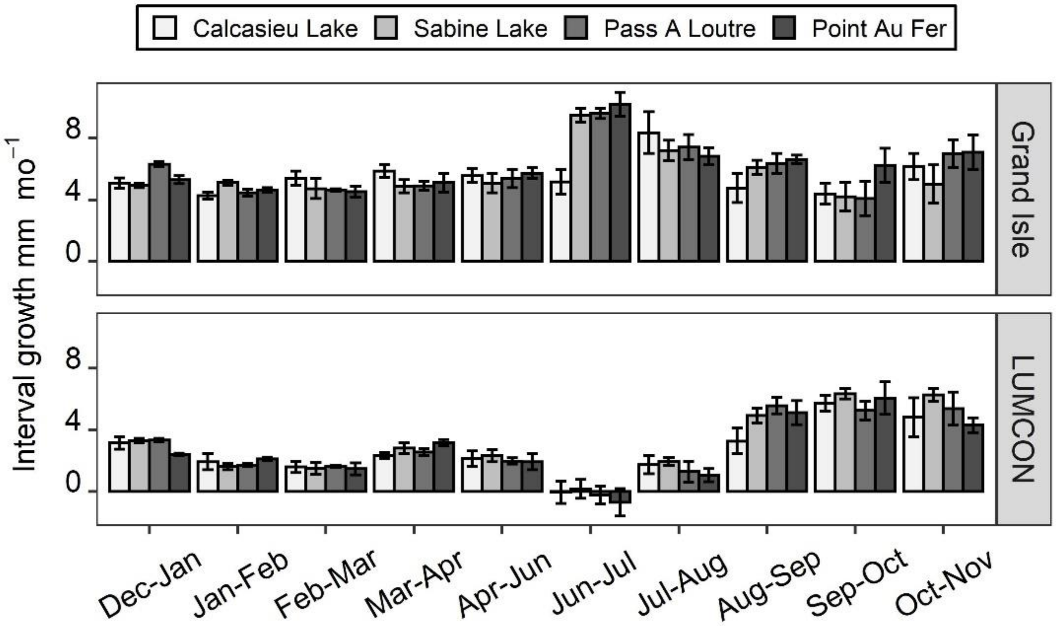
The figures included in this appendix visually showcase data supporting the claims made in chapter 3 of this thesis. Interval water quality conditions were used to generate linear regressions to show the effect of conditions on oyster interval growth and interval mortality (Fig. B.1., Fig. B.2., Fig. B.3.). While interval growth calculations were used to assess growth rate of oyster populations throughout this experiment, mean shell height can show the general size comparison between populations (Fig. B.4). Finally, oyster growth



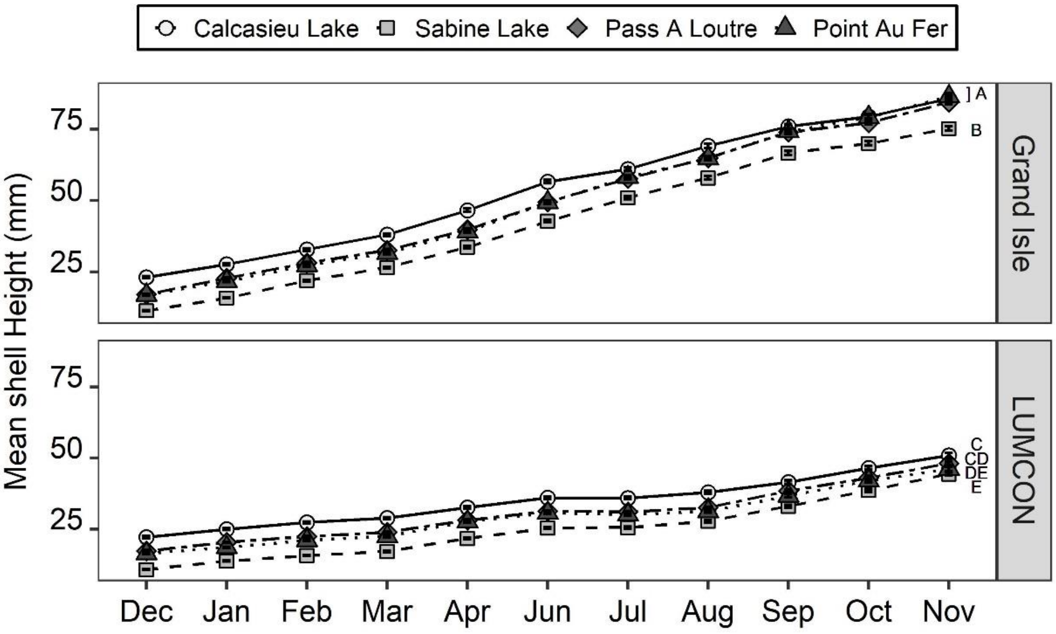
B.1. Interval salinity and temperature (°C) from December 12, 2019 to November 19, 2020 from continuous recorders at LUMCON (DeFelice Marine Center Environmental Monitoring Station Data, 2019 & 2020) and Grand Isle (USGS Barataria Pass at Grand Isle, LA with missing data points filled in using USGS Barataria Bay near Grand Terre Island, LA). Intervals are based on sampling dates.



B.2. Mean interval mortality (%) of oysters from Calcasieu Lake Sabine Lake, Pass a Loutre, and Point Au Fer stock populations (±1 SEM).



B.3. Mean interval growth rates (mm mo^{-1}) of oysters from Calcasieu Lake Sabine Lake, Pass a Loutre, and Point Au Fer stock populations (±1 SEM).



B.4. Mean shell height (mm) of oysters from Calcasieu Lake Sabine Lake, Pass a Loutre, and Point Au Fer stock populations (±1 SEM). Different letters denote statistical differences.

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VITA

Lauren Michelle Swam was born in Westminster, Maryland to parents Michael and Kimberly Swam. She has a brother, Ben (18) and a sister, Nikki (14) and a large extended family whom she loves very much. She also enjoys reading, cooking, crafting, and traveling in her free time. After attending Manchester Valley High School, she received her B.S. in Biology with a minor in Environmental Studies from St. Mary's College of Maryland in St. Mary's City, Maryland. During her undergraduate education, she participated in several research projects including cataloging dolphin movement off Bimini Island, Bahamas, studying the effects of ocean acidification on tropical crabs in a laboratory and on Carrie Bow Cay off the coast of Belize, and analyzing the long-term abundance of two arctic clam species for her senior thesis.

After her graduation in May 2019, she enrolled in a graduate program in the School of Renewable Natural Resources at the Louisiana State University AgCenter. She anticipates earning her M.S. in Renewable Natural Resources with a concentration in Fisheries and Aquaculture in August 2021. At LSU, her research has focused on the effects of low salinity on eastern oyster growth and survival in order to develop oyster resource zones to inform future restoration and aquaculture efforts as well as investigate oyster populations for local adaptation to low salinity.