Ocean and Coastal Management 225 (2022) 106178

Contents lists available at ScienceDirect

Ocean and Coastal Management

journal homepage: www.elsevier.com/locate/ocecoaman

Defining oyster resource zones across coastal Louisiana for restoration and aquaculture

Lauren M. Swam [a], Brady Couvillion [b], Brian Callam [c], Jerome F. La Peyre [d], Megan K. La Peyre [e,*]

[a] *School of Renewable Natural Resources, Louisiana State University Agricultural Center, Baton Rouge, LA, 70803, USA*
[b] *U.S. Geological Survey, LSU Agricultural Center, Baton Rouge, LA, 70803, USA*
[c] *Louisiana Sea Grant College Program, Louisiana State University, Baton Rouge, LA, 70803, USA*
[d] *School of Animal Sciences, Louisiana State University Agricultural Center, Baton Rouge, LA, 70803, USA*
[e] *U.S. Geological Survey, Louisiana Fish and Wildlife Cooperative Research Unit, School of Renewable Natural Resources, Louisiana State University Agricultural Center, Baton Rouge, LA, 70803, USA*

ARTICLE INFO

Keywords:
Crassostrea virginica
Eastern oyster
Resource zones
Salinity
Management
Louisiana
Spatial mapping

ABSTRACT

Eastern oysters (*Crassostrea virginica*) are a critical ecological and commercial resource in the northern Gulf of Mexico facing changing environmental conditions from river management and climate change. In Louisiana, USA, development of restored reefs, and off-bottom aquaculture would benefit from the identification of locations supportive of sustainable oyster populations (*i.e.,* metapopulations) and high consistent production. This study defines four oyster resource zones across coastal Louisiana based on environmental conditions known to affect oyster survival, growth, and reproduction. Daily data from 2015 to 2019 were interpolated to generate salinity and temperature profiles across Louisiana's estuaries, which were then used to classify zones based on monthly and annual salinity mean and variance. Zones were classified as supportive of (1) broodstock sanctuary reefs (i.e., support reproductive populations), (2) productive reefs during dry (salty) years, (3) productive reefs during wet (fresh) years, and (4) off-bottom aquaculture development. Of the 38,000 km^2 investigated, over 11,000 km^2 of potential oyster zone area was identified across the Louisiana coast. The Broodstock Sanctuary Zone was the smallest (~540 km^2), as salinity variance limited this zone in many areas, as it is driven largely by riverine inputs across many estuaries. Located up-estuary (Dry Restoration Zone) and down-estuary (Wet Restoration Zone) of the Broodstock Sanctuary Zone, Dry and Wet Restoration Zone areas covered ~2400 km^2 and ~3900 km^2, respectively. Mapped reefs in Louisiana currently exist largely within the Dry Restoration zones, suggesting a potential strategy to focus reef development in Wet Restoration zones to ensure reef network sustainability through years with high precipitation and river inflow. The off-bottom Aquaculture Zone was the largest (~6400 km^2) zone identified, with much of this area located more down-estuary and off-shore. Accounting for variable water quality conditions enables the development of a network of reefs resilient to environmental variability, and more stable areas for consistent off-bottom aquaculture production. Spatial planning and identification of oyster resource zones reduces focus on individual reef success and supports management of oyster metapopulation outcomes, while identifying zones supportive of off-bottom aquaculture.

1. Introduction

In recent years, the use of spatial planning has emerged as an essential tool to support decision-making in coastal and marine systems vulnerable to rapid changes (Sousa et al., 2011; Halpern et al., 2012; Collie et al., 2013; Pittman and Brown, 2011; Lagabrielle et al., 2018). The identification and development of targeted resource zones can help reduce user conflict, improve restoration and management outcomes, integrate variable and future environmental conditions, and help strategically develop sustainable restoration strategies (*i.e.,* Agardy et al., 2011: Moura et al., 2013; Pinto and Martins, 2013). Over the last two decades, the United Nations Educational, Scientific and Cultural Organization (UNESCO)'s Marine Spatial Planning initiative has developed guidelines (mspglobal2030.org; accessed Jan 2022) and set an objective

* Corresponding author.
E-mail address: mlapeyre@agcenter.lsu.edu (M.K. La Peyre).

https://doi.org/10.1016/j.ocecoaman.2022.106178
Received 4 November 2021; Received in revised form 1 April 2022; Accepted 3 April 2022
Available online 22 April 2022

to triple areas benefitting from marine spatial planning. Spatial planning provides a means to support conservation and management of biodiversity and habitat connectivity and could be a valuable tool for management of benthic habitats created by economically and ecologically valuable species, such as shellfish populations which both create reef habitat, and support a valuable fishery.

Across the northern Gulf of Mexico (nGoM), the native eastern oyster (*Crassostrea virginica*; hereafter, "oysters") provides vital ecosystem services (*i.e.,* provision of habitat, water filtration, coastline stabilization, and benthic-pelagic coupling) and supports a highly productive seafood industry, with Louisiana alone contributing an average of 43% of annual landings (market value) of all oysters nationally (USA) from 1999 to 2018 (LDWF, 2021). Despite their ecological and commercial importance, nGoM oyster populations, as with others globally, have declined and continue to decline due to overharvesting, changes in freshwater flows, and changing climate conditions (Beck et al., 2011; Beseres Pollack et al., 2012; Zu Ermgassen et al., 2012). In the face of these trends, many states in the United States are investing in oyster restoration, focusing on reef networks with areas identified for restoration, and broodstock sanctuaries to support sustained natural reproduction and recruitment through environmental variation (Lipcius et al., 2008; Puckett and Eggleston, 2016; LDWF, 2020b; La Peyre et al., 2021). In addition, the nGoM oyster industry is focused on developing off-bottom aquaculture to grow oysters for harvest to address the challenges faced by on-bottom oyster production (Maxwell et al., 2008; Walton et al., 2013; Grice and Walton, 2018). Identifying strategic locations to place these restoration reefs and locate sites for off-bottom aquaculture would help ensure success of oyster restoration, and off-bottom aquaculture production.

For restoration and management of oysters in the United States, geospatial habitat suitability index (HSI) models are generally used to inform restoration planning (*i.e.,* Theuerkauf and Lipcius, 2016; Puckett et al., 2018; Theuerkauf et al., 2019; Reisinger et al., 2020; Lindquist et al., 2021; La Peyre et al., 2021). While often used to evaluate the suitability of restoration activities on oyster resources, an HSI type approach could be useful to identify specific zones that account for long-term mean and variance in environmental conditions. For example, Melancon et al. (1998) proposed oyster resource zones for Barataria and Terrebonne estuaries in Louisiana, USA based on long-term salinity patterns and oyster farmer input. This approach identified oyster zones for production during dry, wet, and average years, providing guidance for oyster farmers to ensure production across variable years by investing across the three zones. While this work focused solely on production, the development of a spatial tool to identify zones differentially suitable for aquaculture, restoration, and for broodstock sanctuaries across variable years would support restoration planning involving reef networks, broodstock sanctuaries, and off-bottom aquaculture (also called Alternative Oyster Culture in Louisiana) development (Lipcius et al., 2008, 2015; Deepwater Horizon Natural Resource Damage Assessment Trustees, 2017; LDWF, 2020a).

The development of spatial resource zones requires understanding of oyster population dynamics and their interaction with local habitat and environmental conditions. Oysters are tolerant to a wide range of environmental conditions, with salinity and temperature, and their interaction, affecting virtually every aspect of the oyster life cycle (Shumway, 1996; Bayne, 2017). While oysters can survive indefinitely in a wide salinity range from 5 to 40 (Shumway 1996), Louisiana populations show optimal performance (*i.e.,* growth, survival) in salinity ranging between ~10 and ~15 (Dugas and Roussel, 1983; Heilmayer et al., 2008; Soniat et al., 2013; Rybovich et al., 2016; Lowe et al., 2017). Oysters also survive temperatures ranging from -2 – 36 °C throughout their geographical range (Shumway, 1996), but Louisiana populations perform optimally (*i.e.,* growth) within 20–26 °C (Lowe et al., 2017), with upper thresholds of temperature tolerance highly dependent on salinity and oyster life stage (La Peyre et al., 2013; Rybovich et al., 2016; Marshall et al., 2021a, 2021b). In particular, low salinity (<5) and high temperatures (>30 °C) combined are increasingly lethal to oyster populations. Beyond salinity and temperature, other variables including chlorophyll-a, turbidity, and wave exposure could impact oyster survival and growth, but salinity and temperature are the dominant factors and currently drive most models of oyster growth and mortality for Louisiana (CPRA, 2017; Wang et al., 2017; Lavaud et al., 2021; La Peyre et al., 2021).

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 (Dekshenieks et al., 1993). Temporal variability arises from seasonal, annual, and long-term climatic cycles, such as the El Niño Southern Oscillation, which influences nGoM weather patterns on a 3–4 year average cycle (Graham and White, 1988; Orlando et al., 1993; Kennedy et al., 2007). Spatial variability between and within estuaries across the nGoM results from differences in influence from riverine input, basin geomorphology, coastal land loss, and restoration activities, which impacts salinity and nutrient status of estuaries (Orlando et al., 1993). Additional variability from climate change, including sea level rise and long-term predicted changes in upstream precipitation, may cause water quality changes in different directions and magnitudes in estuaries across the nGoM and within Louisiana, resulting in unique estuarine environments (Keim et al., 2011; Keim and Powell, 2015). As a result, management of ecosystems and fisheries requires consideration of local conditions, including annual and long-term environmental variation, and consideration of how local populations of organisms can adapt (Mulholland et al., 1997; Bible et al., 2017).

Increased focus on restoration, conservation, and development of off-bottom oyster aquaculture would benefit greatly from spatial planning, and the identification of critical resource zones. These zones would identify where optimal conditions for oyster survival, reproduction, or fisheries production may shift as environmental conditions vary across the years. The connectivity of individual populations (reefs) through larval dispersal between reefs (i.e., metapopulations) provides opportunity for populations located in optimal conditions in a given year to subsidize populations located in sub-optimal conditions (i.e., subsidize across zones). 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 environmental conditions over the last 5 years (2015–2019) in estuaries across subtropical Louisiana to identify areas potentially conducive to supporting a network of oyster reefs to ensure oyster resources survive and support a productive fishery through short-term and longer-term environmental variability. Specifically, this work aims to develop a coastwide map identifying four oyster resource zones to support decision making related to the selection of locations for aquaculture operations, reef restoration, and broodstock sanctuaries.

2. Methods

Oyster resource zones were defined based on five years of salinity and temperature (°C) data from continuous data recorders and satellite-derived data.

2.1. Study area

The study area for this analysis was defined using the Louisiana basin boundaries (CPRA, 2017, Fig. 1), extended 5 km from the coastline. The eastern half of the state is dominated by the Mississippi River, consisting of multiple estuaries and bays, while the western half consists of the Chenier Plains and many estuarine lakes (Fig. 1). These estuaries represent a large range of spatially and temporally varying conditions resulting from differing riverine inputs, basin morphology, and management (Orlando et al., 1993; Solis and Powell, 1999; CPRA, 2017).

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 suitable for oyster growth, survival, and reproduction in more extreme years, including wet and dry years, and (3) off-bottom aquaculture. We defined these zones using salinity and season, with season used as a proxy for the combined effects of temperature and salinity on the oyster life cycle. Five variables were included in the zone definition: annual mean salinity, annual salinity variation (in standard deviations), spawning months mean salinity (April–November), and summer (June–September) and winter (December–February) months mean salinity (Table 1). Each of these variables was defined with a salinity range or m\inimum threshold and a frequency component. The frequency component was included because strict application of thresholds across the 5-year time period resulted in highly limited oyster resource zones due to high inter-annual salinity variation in Louisiana estuaries. The high intra-annual variation in salinity was addressed by adding a threshold determined by annual salinity standard deviation, with lower thresholds for zones requiring more consistent results (i.e., Broodstock Sanctuary and Aquaculture Zone). The frequency and threshold restrictions reflect the fact that oysters can survive outside their optimal conditions for periods of time through closure of their shells, which can be maintained for several days to weeks depending on temperature without harm (Shumway, 1996; Lavaud et al., 2017).

The Broodstock Sanctuary Zone was designed to optimize reef sustainability and fecundity through inclusion of areas with conditions optimal for oyster growth and survival all or most of the time. Oysters on-bottom in Louisiana survive and grow optimally at mid-range (salinity: 10–15) and minimally variable salinities (Lowe et al., 2017). In the nGoM, oysters spawn multiple times throughout the year (Supan and Wilson, 2001) in response to suitable environmental conditions, which include warmer temperatures and its interaction with photoperiod and food supply (Bayne, 2017). Other factors, including salinity, impact the timing and occurrence of the reproductive cycle as low salinity has been associated with delayed gonad development and reduced larval survival, development, and settlement (Loosanoff, 1953; Calabrese and Davis, 1970; La Peyre et al., 2013). To ensure maximum growth and survival, the annual mean salinity range for the Broodstock Sanctuary Zone was defined as 8 to 16 for at least four out of five years (Table 1). Annual salinity variation had a maximum threshold of 2x the coastwide 5-year mean SD (2.208) for all five years to minimize impacts from high variation on reproduction. This 2x coastwide mean SD (salinity variation = 4.416) was selected because it captures the SD reported in field studies documenting oyster survival and growth across Louisiana estuaries (i.e., La Peyre et al., 2015; 2013; Rybovich et al., 2016). To maximize likelihood of reproduction, the spawning month mean salinity had to be greater than or equal to 12 for at least 25% of the season each year for at least three out of five years used in this study (Table 1). Generally, the interaction between temperature and salinity has an effect on oyster growth and mortality; however, for the Broodstock Sanctuary Zone, the minimum threshold for both the summer and winter month salinity was defined as a salinity of 8 for at least 80% of the season each year, because a salinity of 8 supports oyster growth and survival regardless of temperature (Table 1) (La Peyre et al., 2013; Rybovich et al., 2016; Lowe et al., 2017; Lindquist et al., 2021).

The Dry Restoration and Wet Restoration Zones were designed for optimum reef survival, growth, and reproduction during years with lower or higher than average freshwater input into estuaries, respectively (Melancon et al., 1998). As a result, the thresholds used for the five salinity variables represent slightly lower (Dry Restoration Zone) or higher (Wet Restoration Zone) than optimal conditions based on the hypothesis that optimal conditions would occur in those zones during dry or wet years (Melancon et al., 1998). The annual mean salinity range for the Dry Restoration Zone borders the optimum and was chosen to include areas with optimum salinity for oysters during dry years (less precipitation, higher inshore salinities) and lower salinities (4–12) during average years (Table 1). In contrast, the annual mean salinity range for the Wet Restoration Zone was chosen to include areas with optimum salinity during wet years (more precipitation, lower inshore salinities, optimal salinities farther offshore) and higher salinities (12–20) during average years (Table 1). Salinity was allowed to have a high variance (4x the coastwide 5-year mean SD, ~ salinity variation of 8) as these areas are expected to experience optimal and non-optimal years, and, in the absence of data to inform us of SD that are mortal to oyster reef survival on an annual basis, is non-restrictive across the Louisiana coast. 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. Therefore, the spawning month mean salinity had to be greater than or equal to 12 for at least 12.5% of the season for at least one out of five years used in this study (Table 1). To account for the effect of temperature-salinity interactions on oysters, minimum thresholds for the summer and winter months differed slightly between both seasons and zones. The Dry Restoration Zone summer month mean salinity minimum threshold was 4 while the winter month mean salinity minimum threshold was 2 to account for higher tolerance to low salinity in colder temperatures. The Wet Restoration Zone summer month mean salinity minimum threshold was 6 while the winter month mean salinity minimum threshold was 4.

The Aquaculture Zone was designed to capture conditions best suited for high oyster growth and low mortality while de-emphasizing

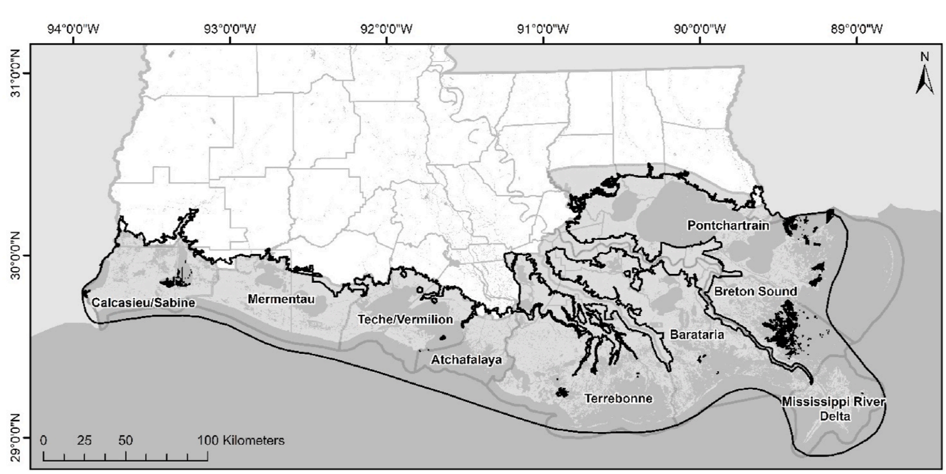

Fig. 1. Map of south Louisiana, U.S.A. showing coastal area used for this work. The black line represents the northern hydrologic barriers and southern boundary line used to define the interpolation area in this study. The Louisiana basin boundaries as defined by the Coastal Protection and Restoration Authority are outlined in gray and labeled. Current existing public reefs and cultch plants (i.e., substrate placed in oyster spawning areas to provide surface for oyster larvae to attach) maintained by Louisiana Department of Wildlife and Fisheries (LDWF) are shown as black areas. Map background is from the National Land Cover Dataset (NLCD, 2016).

Table 1
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. SD = standard deviation. One SD represents the coastwide 5-year mean SD for 2015–2019 (1SD = 2.208).

	Annual mean salinity		Annual salinity variation		Spawning month mean salinity		Summer month mean salinity		Winter month mean salinity	
	Value	Time	Value	Time	Value	Time	Value	Time	Value	Time
Broodstock Sanctuary Zone	8–16	4+/5 years	≤2 SD	All years	≥12	2+/8 months for 3/5 years	≥8	16+/20 summer months	≥8	12+/15 winter months
Dry Restoration Zone	4–12	3+/5 years	≤4 SD	All years	≥12	1+/8 months for 1/5 years	≥4	16+/20 summer months	≥2	12+/15 winter months
Wet Restoration Zone	12–20	3+/5 years	≤4 SD	All years	≥12	1+/8 months for 1/5 years	≥6	16+/20 summer months	≥4	12+/15 winter months
Aquaculture Zone	≥12	4+/5 years	≤2 SD	All years			≥8	16+/20 summer months	≥8	12+/15 winter months

reproduction and predation (oysters would be grown in predator-excluding baskets from hatchery provided seed). The annual mean salinity was defined as equal to or greater than 12 for at least four out of five years to represent ideal conditions for growth and survival (La Peyre et al., 2003; Bushek et al., 2012; Lowe et al., 2017). No maximum salinity was applied as the primary threat from higher salinity would be mortality from *Perkinsus marinus* and, given the fast growth and harvest within less than 1 year of oysters grown off-bottom in Louisiana waters, *P. marinus* is not generally a concern (Casas et al., 2017; Leonhardt et al., 2017). Additionally, annual salinity variation had a maximum threshold of 2x the coastwide 5-year mean SD for all five years similar to the Broodstock Zone to only include areas with the least salinity variation possible to promote optimal growth for harvest. Summer and winter month mean salinity had a minimum threshold of 8, based on Lindquist et al. (2021) which indicated a suitability over 1.0 at this salinity. Spawning month mean salinity was not included in this zone definition because seed used for aquaculture is anticipated to come from hatcheries.

2.3. Coastwide data acquisition

We obtained empirical daily inshore salinity and temperature (°C) data from continuous data recorders maintained by the state of Louisiana Coastwide Reference Monitoring System (Coastal Protection and Restoration Authority of Louisiana, 2021) and the U.S. Geological Survey (United States Geological Survey of US Department of the Interior, 2021) (Fig. 2). CRMS and USGS data were accessed by public online website databases. Daily offshore data were obtained from the Hybrid Coordinate Ocean Model (HYCOM) for salinity (GODAE, 2021) and the National Oceanographic and Atmospheric Administration (NOAA) Optimum Interpolation Sea Surface Temperature dataset for temperature (National Oceanic and Atmospheric Administration, NOAA, 2021) (Fig. 2). 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 nonconsecutive 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. Point data outside the study area for the analysis was included, as available, to incorporate as much data as possible in the salinity interpolations. Interpolations were conducted on this point data set for each day in the study period. These datasets include surface salinity and temperature data as bottom water quality data do not exist for this region. Within the estuaries where oysters exist, numerous analyses have demonstrated that there is no significant statistical difference between top and bottom water salinity (i.e., La Peyre et al., 2016). Generally, Louisiana estuaries are well-mixed, largely due to their shallow nature (average depth <2 m), however, we do acknowledge that in offshore areas included in this analysis, stratification may occur, however these offshore areas are likely only supportive of off-bottom oyster aquaculture.

In order to compare the 5-year data set used for these maps to a longer historical time frame, six locations with continuous long-term data recorders available were identified across six estuaries: Calcasieu Lake, Vermilion Bay, Terrebonne Bay, Barataria Bay, Breton Sound, and Mississippi (MS) Sound. Salinity data used are daily means taken from USGS recorders (USGS, 2021): Calcasieu: Calcasieu River at Cameron, LA (08017118); Vermilion Bay: Vermilion Bay near Cypremort Point, LA (07387040); Terrebonne Bay: Caillou Lake (Sister Lake) SW of Dulac, LA (07381349); Barataria Bay: Hackberry Bay NW of Grand Isle, LA (073802512); Breton Sound: Black Bay near Snake Island near Pointe-A-La-Hache, LA (07374526); MS Sound: Mississippi Sound near Grand Pass (300722089150100). Monthly salinity means for 2002–2019 were compared to monthly salinity means for 2015–2019 to

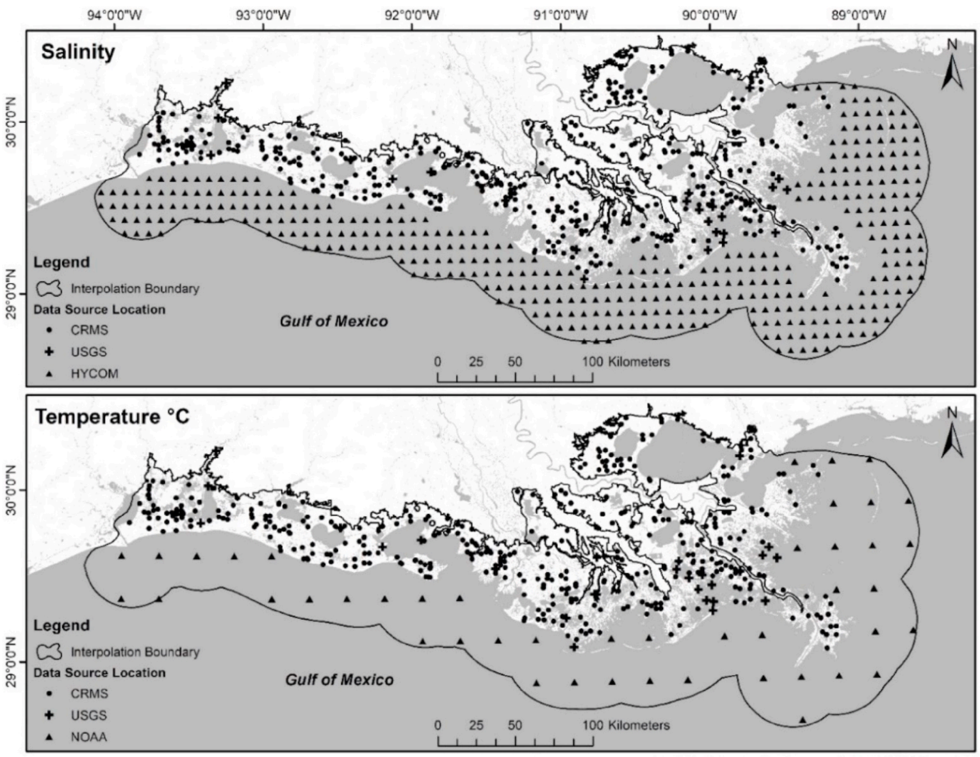

Fig. 2. Salinity (top panel): locations of 457 CRMS data recorders (Coastal Protection and Restoration Authority of Louisiana, 2021), 27 USGS data recorders (United States Geological Survey of US Department of the Interior, 2021), and 392 data points from remote sensing raster coverage (GODAE, 2021) for 2015–2019 for a total of 876 data points. Temperature (°C): locations of 462 CRMS data recorders (Coastal Protection and Restoration Authority of Louisiana, 2021), 27 USGS data recorders (United States Geological Survey of US Department of the Interior, 2021), and 45 data points from remote sensing raster coverage (National Oceanic and Atmospheric Administration, NOAA, 2021) for 2015–2019 for a total of 534 data points. Map background is from the National Land Cover Dataset (NLCD, 2016).

identify differences in short-term versus long-term salinity trends. A salinity anomaly index was calculated by subtracting the 2002–2019 monthly salinity mean from the 2002–2019 monthly salinity mean (to create the baseline of 0) and from the 2015–2019 monthly salinity mean (to show salinity differences between the two time periods). Negative values indicate the salinity mean was lower in 2015–2019 compared to 2002–2019. 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.

2.4. Spatial layer development

Interpolations 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 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 (Fig. 1; 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 validated by comparing 3466 points with discrete, fisheries independent salinity and temperature points collected (LDWF, 2018a). 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 500 m-sided square, which was selected to maximize spatial resolution while minimizing processing time.

2.5. Zone generation

Areas determined to be covered by water <20% of the time were excluded from the analysis, being less likely to support viable oyster reefs. Monthly and annual salinity values generated in Google Earth Engine were filtered to include appropriate ranges and thresholds for the five variables identified to differentiate the four oyster resource zones (Table 1). 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 for each zone using the Calculate Geometry tool and simplified to two significant figures.

3. Results

3.1. Environmental data

Five-year mean salinity from 2015 to 2019 across the Louisiana coast ranged from 0 to 34.7 with increasing salinity moving down-estuary and offshore across all estuaries (Fig. 3, Panel A; Appendix Fig. 1). 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 MS Sound basins (Fig. 3, Panel B).

Five-year mean temperature from 2015 to 2019 across the Louisiana coast ranged from 18.5 °C to 25 °C with temperature increasing slightly moving offshore (Fig. 4, Panel A). Five-year mean temperature standard deviation ranged from 0 to 8 °C with highest variation around the Mississippi River Delta (Fig. 4, Panel B).

Comparison of salinity means at six continuous data recorders with daily data from 2002 to 2019 to their salinity means from 2015 to 2019 indicated that the years for zone development were generally fresher than the long-term salinity at critical oyster resource locations (Fig. 5).

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 (Fig. 6). The four zones combined cover 11,000 km^2 of water bottom out of 38,000 km^2 total within our study area. The zone with the least coverage was the Broodstock Sanctuary Zone accounting for 540

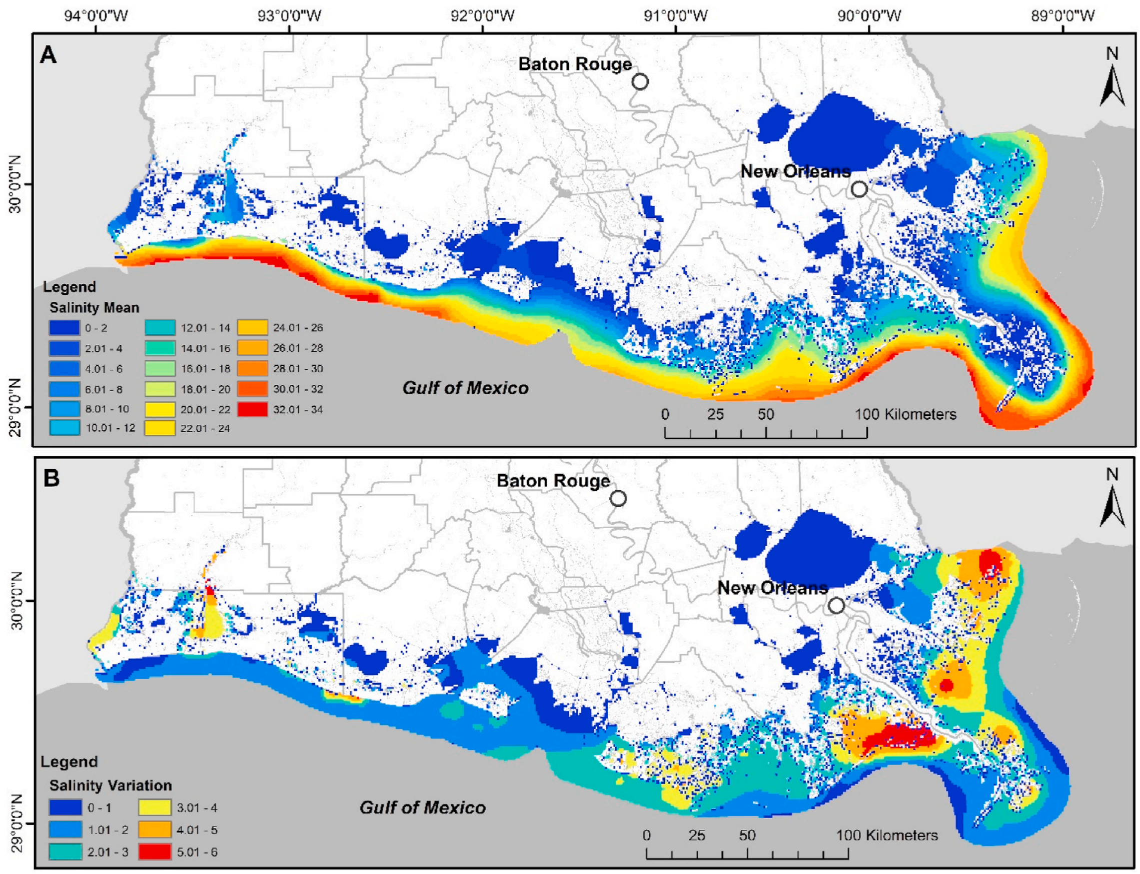

Fig. 3. Louisiana, U.S.A. coast salinity profile for 2015–2019. Panel A: mean annual salinity 2015–2019. Panel B: mean annual salinity standard deviation 2015–2019. Map background is from the National Land Cover Dataset (NLCD, 2016).

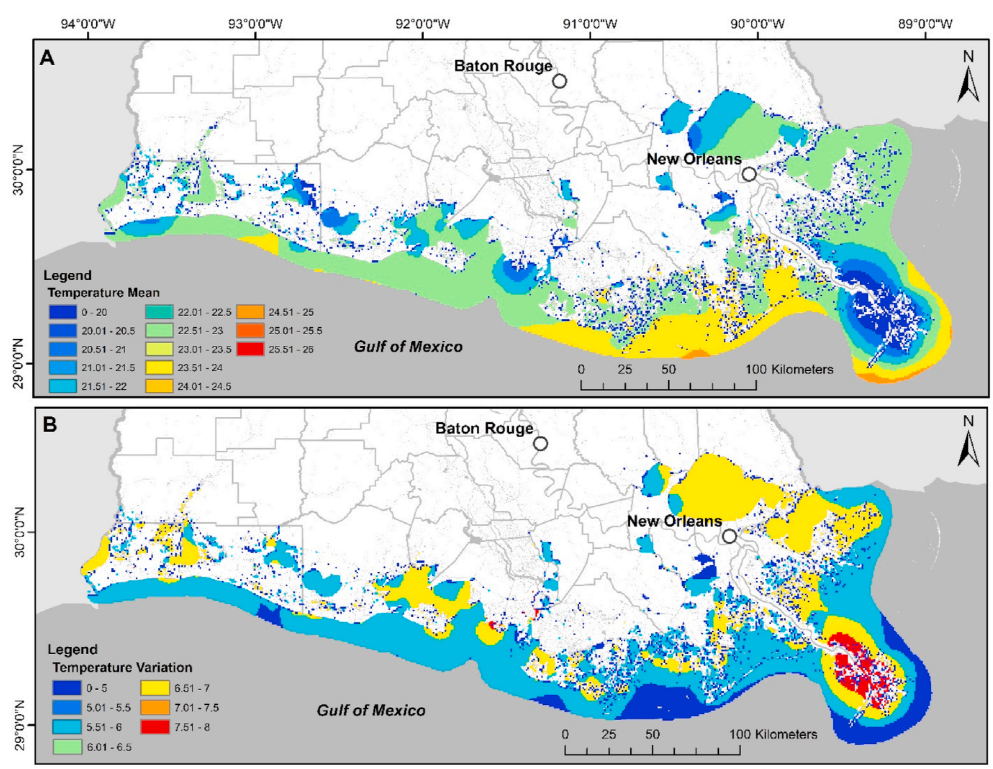

Fig. 4. Louisiana, U.S.A. coast temperature (°C) profile from 2015 to 2019. Panel A: mean annual temperature 2015–2019. Panel B: mean annual temperature standard deviation 2015–2019. Map background is from the National Land Cover Dataset (NLCD, 2016).

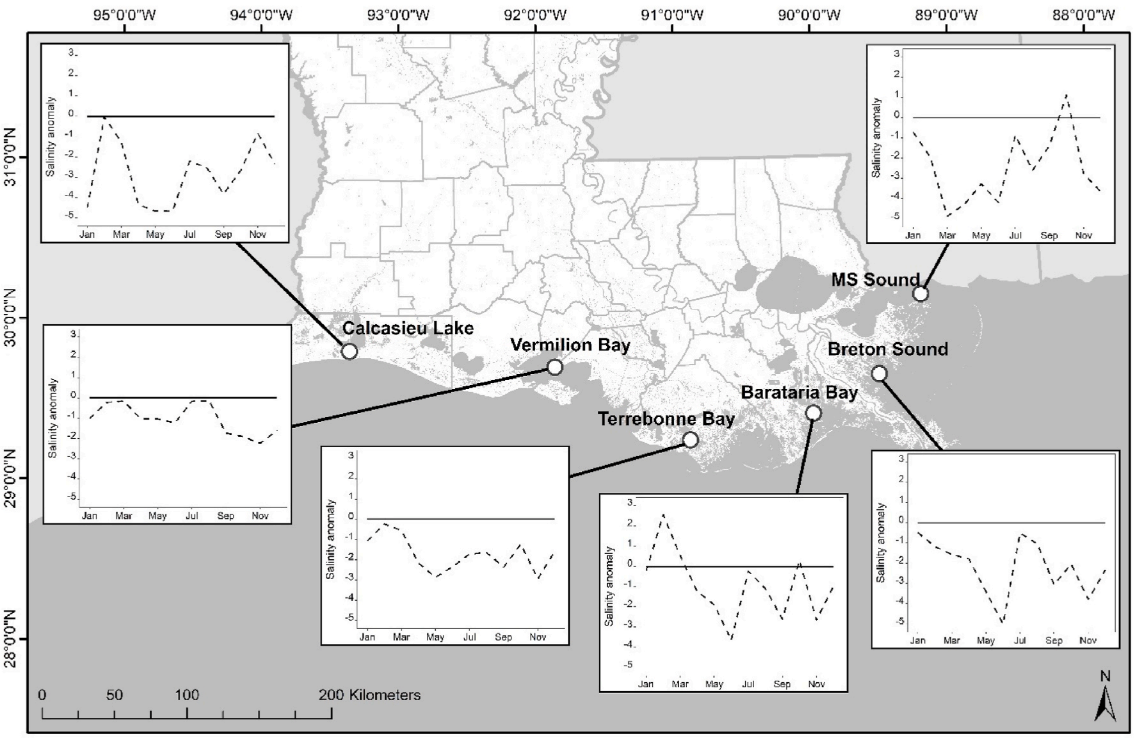

Fig. 5. Monthly salinity means of most recent five years (2015–2019; dashed line) compared to the past eighteen years (2002–2019; solid black line) at six critical oyster resource locations along the Louisiana coast, U.S.A. A salinity anomaly index (dashed line) was calculated by subtracting the longer-term (2002–2019) monthly salinity means from the most recent years (2015–2019) monthly salinity means. The solid line represents a salinity anomaly of 0 where the long-term and recent year monthly means are equal. 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 (USGS, 2021): Calcasieu: 08017118 – Calcasieu River at Cameron, LA; Vermilion Bay: 07387040 – Vermilion Bay near Cypremort Point, LA; Terrebonne Bay: 07381349 – Caillou Lake (Sister Lake) SW of Dulac, LA; Barataria Bay: 073802512 – Hackberry Bay NW of Grand Isle, LA; Breton Sound: 07374526 – Black Bay near Snake Island near Pointe-A-La-Hache, LA; MS Sound: 300722089150100 – Mississippi Sound near Grand Pass. Map background is from the National Land Cover Dataset (NLCD, 2016).

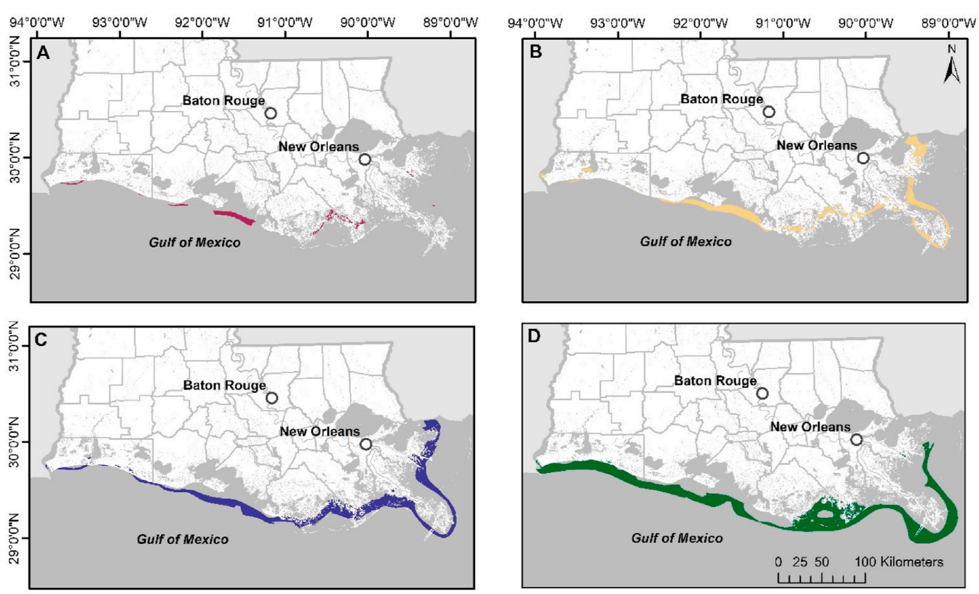

Fig. 6. Oyster resource zones across coastal Louisiana, U.S.A. based on mean salinity parameters from 2015 to 2019 separated to show all areas included within each zone. A: Broodstock Sanctuary Zone, B: Dry Restoration Zone, C: Wet Restoration Zone, D: Aquaculture Zone. Map background is from the National Land Cover Dataset (NLCD, 2016).

km^2. In general, the Broodstock Sanctuary Zone occurred where the Dry and Wet Restoration Zones overlap and represented a smaller range of water quality conditions. The Dry Restoration Zone accounted for 2400 km^2 and covered up-estuary areas across the coast, including areas that would be fresher in an average year (Fig. 6). The Wet Restoration Zone accounted for 3900 km^2 and covered down-estuary areas across the

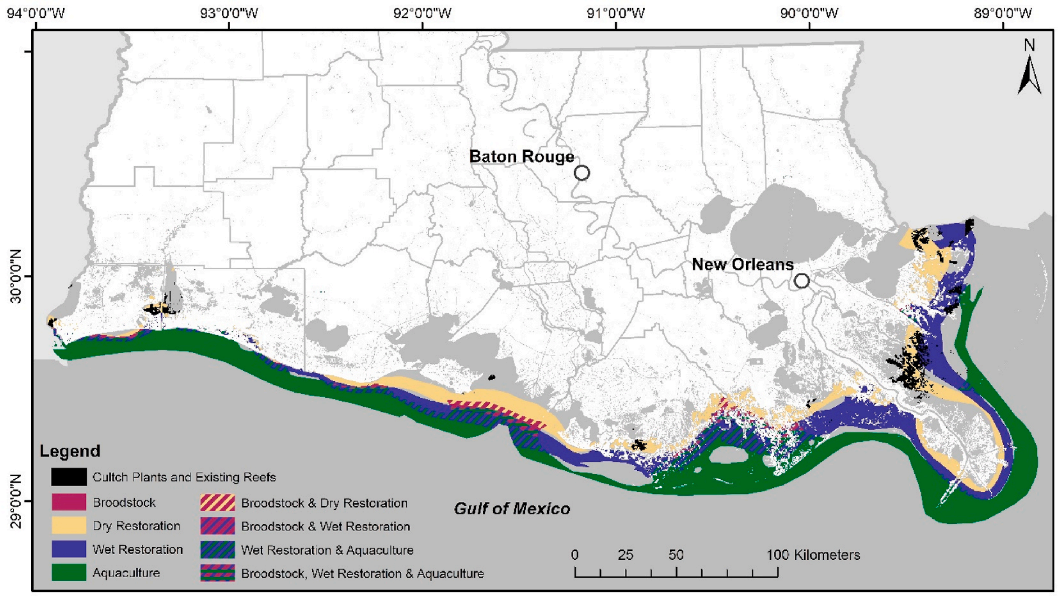

Fig. 7. Oyster resource zones across coastal Louisiana, U.S.A. based on mean salinity parameters from 2015 to 2019 including overlapping resource areas. Areas identified by the Louisiana Department of Wildlife and Fisheries as existing reefs and for cultch plants (i.e., substrate placed in oyster spawning areas to provide surface for oyster larvae to attach) are included. Map background is from the National Land Cover Dataset (NLCD, 2016).

coast, including areas that would be saltier in an average year (Fig. 6). The largest area was covered by the Aquaculture Zone, accounting for 6400 km^2, due to less restrictive water quality conditions (Fig. 6).

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 (Fig. 7). Aquaculture Zone overlaps with many of the other zones due to its less restrictive water quality requirements (Fig. 7). Existing public reefs and cultch plants (*i.e.,* substrate placed in oyster spawning areas to provide surface for oyster larvae to attach) were captured within these layers and largely exist within the Dry Restoration Zone (Fig. 7).

4. Discussion

Increased investment in oyster restoration for both conservation and harvest requires broad resource-level planning. There is extensive area potentially supportive of oyster restoration and aquaculture across coastal Louisiana (up to 11,000 km^2), limited potentially by water bottom type, water quality variables beyond salinity and temperature used here, and competing uses including shipping and oil. The identification of resource zones supportive of oyster restoration across dry and wet years and of off-bottom aquaculture may be used to support planning to ensure sustainability of a network of oyster reefs across zones and to support commercial oyster production. The development of these oyster resource zones, as a proof-of-concept, for coastal Louisiana (1) identifies unique estuarine salinity signatures with salinity variation determining sanctuary and aquaculture 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, and (5) identifies the need to better document how intra- and inter-annual variation in salinity may impact oyster reef maintenance over time.

Based on the development of coastwide salinity and temperature profiles for a five-year period, unique estuarine salinity signals were identified, with salinity variance dominating estuaries impacted by large rivers. The inclusion of salinity variance was critical in defining zones for broodstock sanctuary reefs and off-bottom aquaculture, as both zones call for locations likely to consistently support high oyster survival and growth, and the broodstock sanctuary zone also aims for high reproduction. In particular, salinity variance, defined here as 2x five-year mean SD, and matching the upper range identified in areas of oyster growth and survival in past field studies (i.e., La Peyre et al., 2015; 2013; Rybovich et al., 2016), critically limited the Broodstock Sanctuary Zone, which covered only 5% 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 or oyster population models (Livingston et al., 2000; Beseres Pollack et al., 2021; La Peyre et al., 2021). This lack of inclusion of salinity variance explicitly in models likely derives from a lack of daily salinity datasets across many of our estuaries, and limited studies exploring individual oyster or reef response to changing salinity specifically. Salinity variability plays a large role in the energetic costs oysters face as osmoconformers (Lavaud et al., 2017; McCarty et al., 2020). 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). Given predictions of increasing variability (Keim et al., 2011; Keim and Powell, 2015) and that salinity variability is detrimental to oyster persistence, reliance on static broodstock sanctuary reefs may require some flexibility and reliance on oyster populations located up (Dry Restoration Zone) and down (Wet Restoration Zone) estuary.

For restoration purposes specifically, acknowledging the need to move from single to networked reefs could better address the fact that local oyster populations exist as part of a larger metapopulation dependent on the persistence and success of nearby reefs within an estuary (Lipcius et al., 2015; Theuerkauf et al., 2021). At any given time, suitable conditions for oysters may shift between different zones, as defined within this study. Ensuring reefs exist across this range of conditions helps maintain the overall metapopulation. Interestingly, most mapped reefs, and those managed by the state of Louisiana, were found to be located within the Dry Restoration Zone (Fig. 6), suggesting investment in reefs (restoration) within the Wet Restoration Zone may help to promote metapopulation persistence through wetter years. The metapopulation management approach is based on the idea that one zone could subsidize or support reefs in adjacent zones depending on the conditions experienced that year (e.g. the Wet Restoration Zone could subsidize oyster reefs in the Broodstock and Dry Restoration zones in wet years) to allow reefs to persist until they experience suitable conditions. Moving from focused restoration of a single reef to restoration of a network of reefs may benefit from planning for both permanent (*i.e.* Broodstock Sanctuary Zone) and dynamic (*i.e.* Dry and Wet Restoration zones) restoration areas (D'Aloia et al., 2019). This approach may allow for flexibility in selecting sites, determining restoration success, and facilitate oyster resource persistence in the face of changing and variable environmental conditions.

The five-year period used for the coastwide salinity maps was found to be significantly 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 compared to using longer term (2002–2019), or older data as evidenced by a slight down-estuary shift in comparison to the dry and wet zones for Barataria and Terrebonne estuaries in 1998 (Appendix Fig. 2; Melancon et al., 1998). This down-estuary shift may explain why existing mapped reefs in Louisiana are all located in the Dry Restoration Zone and have had lower than average production during these recent years (LDWF, 2018b; LDWF, 2019; LDWF, 2020a; LDWF, 2021). While this five-year time frame may have captured fresher years than historically documented in this region, 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. An additional or alternative explanation for the observed lower than average production in existing cultch plants and public reefs within the Mississippi Delta region may also include the high annual salinity variation (4–8) documented in this region, which may relate to higher mortality, lower growth, or reduced recruitment to the reefs. Understanding how oysters are impacted by variation in salinity remains critically important as more salinity extremes and higher variation are predicted in the future, emphasizing the importance of including salinity variation in the zone definition. With conditions changing rapidly, the use of maps forecasting future conditions to develop oyster resource zones may be particularly helpful in establishing restoration and aquaculture projects suitable for long-term resilience.

Similar to HSIs and most oyster models, salinity was the primary driver of the zones developed in these maps (Lavaud et al., 2017; Wang et al., 2017; Puckett et al., 2018; Reisinger et al., 2020; Lindquist et al., 2021), but other factors such as food availability, temperature, suspended sediments, and hypoxia may all impact oysters, and their inclusion may help further refine zones. For example, the area around the Mississippi River Delta is generally not suitable oyster habitat due to high suspended sediments (Colden and Lipcius, 2015), so zone coverage in this region would likely be decreased 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). Overall, 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 HSIs 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 (Appendix Fig. 2; Melancon et al., 1998). Additional consideration of logistical constraints including distance from shore, bottom type, current technologies, current use, and regulatory limitations could also be considered and included in future modeling efforts (e.g. bioeconomic spatial modeling), as they represent potentially substantial hurdles to development of aquaculture and restoration in these zones. A further understanding of relationships between oyster population dynamics and environmental factors, along with increasing availability of daily data to support coastwide interpolations, may allow managers to better define these zones.

Off-bottom aquaculture is a rapidly expanding industry across the nGoM, credited with increasing oyster production in many nGoM states (Petrolia et al., 2017; Grice and Walton, 2018). While not a dominant means of production in Louisiana, increased investment and state support for the identification and development of aquaculture zones indicates a likely increase in activity (LDWF, 2020a). The Aquaculture Zone defined in this study is extensive, and accounts for approximately 50% of the identified area suitable for oysters. A large portion of the Aquaculture Zone identified in this work occurs in off-shore sites, which are generally not 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 (*i.e.*, New Zealand, Southern California, UK, France; Cheney et al., 2010; Heasman et al., 2020; Mascorda Cabre et al., 2021), but the Gulf of Mexico faces frequent and extreme severe weather challenges that may be important to consider. Technology modifications of gear to address these challenges (e.g., sinking cages and improved mooring systems), investment in appropriate boats and other equipment, plus the inclusion of logistical factors such as water depth, distance from shore, and use of the nearby waterways, in addition to regulatory challenges, could be considered for aquaculture development (Theuerkauf et al., 2019; Barillé et al., 2020). Offshore areas in Vermilion-Teche and Terrebonne basins in the nGOM, where extensive oyster reefs were historically present before being mined, may be promising for off-bottom aquaculture.

5. Conclusion

With competing uses for restoration funding and expenses associated with oyster reef restoration and aquaculture establishment in the nGOM, the use of spatial planning to inform a comprehensive site selection approach provides critical data to promote continued production and persistent oyster populations. A move away from single reef or site planning, and towards spatial planning would better reflect and account for how oysters persist as metapopulations within highly variable habitats. Further investigation into individual oyster and reef maintenance tolerance and response to changing salinity, along with further exploration of specific reef locations that facilitate larval connectivity of reefs between zones is the next step in implementing this approach for oyster reef management and aquaculture development. This spatial planning may further be aided through other restoration techniques including seeding reefs with low salinity adapted broodstock, use of supplementary hatchery produced seed especially in broodstock sanctuary areas, and long-term evaluation of current restoration efforts. Zones developed in this study provide a proof-of-concept for the use of a spatial planning moving forward for oyster restoration and production management; the use of spatial zones, combined with additional restoration techniques identified above may promote efficient and effective restoration and aquaculture system establishment.

Funding

This work was supported by the Louisiana Department of Wildlife and Fisheries [GR-00005587] to the Louisiana Fish and Wildlife Cooperative Research Unit.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We would like to thank Louisiana Department of Wildlife and Fisheries for funding this research through a grant to MKL. We thank Maurice Wolcott (LSU Agricultural Center) for his assistance with ArcGIS. We thank Dr. Earl Melancon, Louisiana Sea Grant, for continued discussions and his insightful comments. We thank Carolina Bourque and Brady Carter with LDWF who provided input and comments on earlier versions and assisted in and providing discrete data points to describe site salinities and compare the results of this study to current oyster reefs. Thanks to Dr. Seth Theuerkauf for constructive comments on an earlier version, discussions with Dr. Romain Lavaud, and comments from three reviewers who provided valuable comments that improved this manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ocecoaman.2022.106178.

References

Agardy, T., Di Sciara, G.N., Christie, P., 2011. Mind the gap: addressing the shortcomings of marine protected areas through large scale marine spatial planning. Mar. Pol. 35 (2), 226–232.
Barillé, L., Le Bris, A., Goulletquer, P., Thomas, Y., Glize, P., Kane, F., Falconer, L., Guillotreau, P., Trouillet, S., Palmer, P., Gernez, 2020. Biological, socio-economic, and administrative opportunities and challenges to moving aquaculture offshore for small French oyster-farming companies. Aquaculture 521, 735045.
Bayne, B.L., 2017. Biology of Oysters. Academic Press, London.
Beck, M.W., Brumbaugh, R.D., Airoldi, L., Carranza, A., Coen, L.D., Crawford, C., Defeo, O., Edgar, G.J., Hancock, B., Kay, M.C., Lenihan, H.S., Luckenbach, M.W., Toropova, C.L., Zhang, G., Guo, X., 2011. Oyster reefs at risk and recommendations for conservation, restoration, and management. Bioscience 61, 107–116.
Beseres Pollack, J., Cleveland, A., Palmer, T.A., Reisinger, A.S., Montagna, P.A., 2012. A Restoration Suitability Index Model for the Eastern Oyster (Crassostrea Virginica) in the Mission-Aransas Estuary, TX, USA. Public Library of Science 7:e40839.
Bible, J.M., Cheng, B.S., Chang, A.L., Ferner, M.C., Wasson, K., Zabin, C.J., Latta, M., Sanford, E., Deck, A., Grosholz, E.D., 2017. Timing of stressors alters interactive effects on a coastal foundation species. Ecology 98, 2468–2478.
Bushek, D., Ford, S.E., Burt, I., 2012. Long-term patterns of an estuarine pathogen along a salinity gradient. J. Mar. Res. 70, 225–251.
Cake, E.W., 1983. Habitat Suitability Index Models: Gulf of Mexico American Oyster. National Coastal Ecosystems Team, Division of Biological Services, Research.
Calabrese, A., Davis, H.C., 1970. Tolerances and requirements of embryos and larvae of bivalve molluscs. Helgoländer Wissenschaftliche Meeresuntersuchungen 20 (1), 553–564.
Casas, S., Walton, W., Chaplin, G., Rikard, S., Supan, J., La Peyre, J.F., 2017. Performance of oysters selected for dermo resistance compared to wild oysters in northern Gulf of Mexico estuaries. Aquaculture Environment Interactions 9, 169–180.
Cheney, D., Langan, R., Heasman, K., Friedman, B., 2010. Shellfish culture in the open ocean: lessons learned for offshore expansion. Mar. Technol. Soc. J. 44 (3), 55–67.
Coastal Protection and Restoration Authority (CPRA), 2017. Louisiana's Comprehensive Master Plan for a Sustainable Coast. OTS-State Printing, Baton Rouge, LA. https://coastal.la.gov/our-plan/2017-coastal-master-plan/. (Accessed January 2022).
Coastal Protection and Restoration Authority (CPRA), 2021. Coastwide Reference Monitoring System (CRMS) Data. Retrieved from Coastal Information Management System (CIMS) database. https://cims.coastal.louisiana.gov. August 2021.
Colden, A.M., Lipcius, R.N., 2015. Lethal and sublethal effects of sediment burial on the eastern oyster *Crassostrea virginica*. Mar. Ecol. Prog. Ser. 527, 105–117.
Collie, J.S., Beck, M.W., Craig, B., Essington, T.E., Fluharty, D., Rice, J., Sanchirico, J.N., 2013. Marine spatial planning in practice. Estuarine. Coast Shelf Sci. 117, 1–11.
D'Aloia, C.C., Naujokaitis-Lewis, I., Blackford, C., Chu, C., Curtis, J.M.R., Darling, E., Guichard, F., Leroux, S.J., Martensen, A.C., Rayfield, B., Sunday, J.M., Xuereb, A., Fortin, M.J., 2019. Coupled networks of permanent protected areas and dynamic conservation areas for biodiversity conservation under climate change. Front. Ecol. Evol 7. https://doi.org/10.3389/fevo.2019.00027.
Deepwater Horizon Natural Resources Damage Asssessment (DWH NRDA) Trustee Implementation Group, 2017. Deepwater Horizon Oil Spill Natural Resource Damage Assessment: Strategic Framework for Oyster Restoration Activities. Available: http://www.gulfspillrestoration.noaa.gov/restoration-planning/gulf-plan.
Dekshenieks, M.M., Hofmann, E.E., Powell, E.N., 1993. Environmental effects on the growth and development of eastern oyster, *Crassostrea virginica* (Gmelin, 1791), larvae: a modeling study. J. Shellfish Res. 12, 241–254.
DeMarco, K., Couvillion, B., Brown, S., La Peyre, M.K., 2018. Submerged aquatic vegetation mapping in coastal Louisiana through development of a spatial likelihood occurrence (SLOO) model. Aquat. Bot. 151, 87–97.
Dugas, R.J., Roussel, J., 1983. Report on Oyster Mortalities in Louisiana as a Result of Excessive Freshwater Intrusion - 1983. Seafood Division, New Orleans, Louisiana, pp. 1–65.
Global Ocean Data Assimilation Experiment (GODAE), 2021. Hybrid Coordinate Ocean model (HYCOM) data. Retrieved from Google Earth Engine database. https://code.earthengine.google.com/ee.ImageCollection. (Accessed 12 October 2021) ("HYCOM/sea_temp_salinity").
Graham, N.E., White, W.B., 1988. The El Nino cycle: a natural oscillator of the Pacific ocean-atmosphere system. Science 1988 (240), 1293–1301.
Grice, R., Walton, W., 2018. Alabama Shellfish Aquaculture Situation and Outlook Report: Production Year 2016. Auburn University Marine Extension and Research Center, AL.
Hagy, J.D., Murrell, M.C., 2007. Susceptibility of a northern Gulf of Mexico estuary to hypoxia: an analysis using box models. Estuar. Coast Shelf Sci. 74, 239–253.
Halpern, B.S., Longo, C., Hardy, D., McLeod, K.L., Samhouri, J.F., Katona, S.K., Kleisner, K., Lester, S.E., O'Leary, J., Ranelletti, M., Rosenbery, A.A., Scarborough, C., Selig, E.R., Best, B.D., Brumbaugh, D.R., Chapin, F.S., Crowder, L. B., Daly, K.L., Doney, S.C., Elfes, C., Fogarty, M.J., Gaines, S.D., Jacobsen, K.I., Karrer, L.B., Leslie, H.M., Neeley, E., Pauly, D., Polasky, S., Ris, B., St Martin, K., Stone, G.S., Sumaila, U.R., Zeller, D., 2012. An index to assess the health and benefits of the global ocean. Nature 488 (7413), 615–620.
Heasman, K.G., Scott, N., Ericson, J.A., Taylor, D.I., Buck, B.H., 2020. Extending New Zealand's marine shellfish aquaculture into exposed environments–adapting to modern anthropogenic challenges. Front. Mar. Sci. 751.
Heilmayer, O., Digialleonardo, J., Qian, L., Roesijadi, G., 2008. Stress tolerance of a subtropical *Crassostrea virginica* population to the combined effects of temperature and salinity. Estuarine. Coast Shelf Sci. 79, 179–185.
Keim, B.D., Fontenot, R., Tebaldi, C., Shankman, D., 2011. Hydroclimatology of the U.S. Gulf Coast under global climate change scenarios. Phys. Geogr. 32, 561–582.
Keim, B.D., Powell, E.J., 2015. Trends in daily temperature and precipitation extremes for the southeastern United States: 1948 – 2012. J. Clim. 28, 1592–1612.
Kennedy, A.J., Griffin, M.L., Morey, S.L., Smith, S.R., O'Brien, J.J., 2007. Effects of El Niño southern oscillation on Sea level anomalies along the Gulf of Mexico coast. J. Geophys. Res. 112 https://doi.org/10.1029/2006JC003904.
Lagabrielle, E., Lombard, A.T., Harris, J.M., Livingstone, T.C., 2018. Multi-scale multi-level marine spatial planning: a novel methodological approach applied in South Africa. Public Libr. Sci. 13 (7), e0192582.
La Peyre, M.K., Nickens, A.D., Volety, A.K., Tolley, G.S., La Peyre, J.F., 2003. Environmental significance of freshets in reducing *Perkinsus marinus* infection in eastern oysters *Crassostrea virginica*: potential management applications. Mar. Ecol. Prog. Ser. 248, 165–176.
La Peyre, M.K., Eberline, B.S., Soniat, T.M., La Peyre, J.F., 2013. Differences in extreme low salinity timing and duration differentially affect eastern oyster (*Crassostrea virginica*) size class growth and mortality in Breton Sound, LA. Estuarine. Coast Shelf Sci. 135, 146–157.
La Peyre, M.K., Geaghan, J., Decossas, G., La Peyre, J.F., 2016. Analysis of environmental factors influencing salinity patterns, oyster growth, and mortality in lower Breton Sound estuary, Louisiana, using 20 years of data. J. Coast Res. https://doi.org/10.2112/JCOASTRES-D-15-00146.1.
La Peyre, M.K., Serra, K., Joyner, T.A., Humphries, A., 2015. Assessing shoreline exposure and oyster habitat suitability maximizes potential success for sustainable shoreline protection using restored oyster reefs. Peer J. Life and Environ. 3, e1317.
La Peyre, M.K., Marshall, D.A., Sable, S.E., 2021. Oyster model inventory: identifying critical data and modeling approaches to support restoration of oyster reefs in coastal U.S. Gulf of Mexico waters. In: U.S. Geological Survey Open-File Report 2021–1063, p. 40. https://doi.org/10.3133/ofr20211063.
Lavaud, R., La Peyre, M.K., Casas, S.M., Bacher, C., La Peyre, J.F., 2017. Integrating the effects of salinity on the physiology of the eastern oyster, *Crassostrea virginica*, in the northern Gulf of Mexico through a Dynamic Energy Budget model. Ecol. Model. 363, 221–233.
Lavaud, R., La Peyre, M.K., Justic, D., La Peyre, J.F., 2021. Dynamic Energy Budget modelling to predict eastern oyster growth, reproduction, and mortality under river management and climate change scenarios. Estuar. Coast Shelf Sci. 251, 107188.
Leonhardt, J.M., Casas, S., Supan, J.E., La Peyre, J.F., 2017. Stock assessment for eastern oyster seed production and field grow-out in Louisiana. Aquaculture 466, 9–19.
Lindquist, D.C., Sable, S.E., D'Acunto, L., Hijuelos, A.C., Johnson, E.I., Langlois, S.R.M., Michel, N.L., Nakashima, L., O'Connell, A.M., Percy, K., Robinson, E.M., 2021. 2023 Coastal Master Plan: Habitat Suitability Index Model Improvements. Draft Final (189p. Coastal Protection and Restoration Authority, Baton Rouge, Louisiana.
Lipcius, R.N., Eggleston, D.B., Schreiber, S.J., Seitz, R.D., Shen, J., Sisson, M., Stockhausen, W.T., Wang, H.V., 2008. Importance of metapopulation connectivity to restocking and restoration of marine species. Rev. Fish. Sci. 16, 101–110.
Lipcius, R., Burke, R., McCulloch, D., Schreiber, S., Schulte, D., Seitz, R., Shen, J., 2015. Overcoming restoration paradigms: value of the historical record and metapopulation dynamics in native oyster restoration. Front. Mar. Sci. 2, 65.
Livingston, R.J., Lewis, F.G., Woodsum, G.C., Niu, X.F., Galperin, B., Huang, W., Christensen, J.D., Monaco, M.E., Battista, T.A., Klein, C.J., Howell, R.L., Ray, G.L., 2000. Modelling oyster population response to variation in freshwater input. Estuar. Coast Shelf Sci. 50, 655–672.
Loosanoff, V.L., 1953. Behavior of oysters in water of low salinities. Proc. Natl. Shellfish. Assoc. 43, 135–151.
Louisiana Department of Wildlife and Fisheries (LDWF), 2018a. LDWF Marine Fisheries Independent Sampling, Field Manual 2018. Baton Rouge, LA.

Louisiana Department of Wildlife and Fisheries (LDWF), 2018b. 2016 Oyster stock assessment of the public oyster areas of Louisiana. Oyster Data Rep. Ser. 22, 1–130. https://www.wlf.louisiana.gov/resources/category/stock-assessments/oyster. (Accessed August 2021).
Louisiana Department of Wildlife and Fisheries (LDWF), 2019. 2017 Stock assessment report of the public oyster seed grounds and reservations of Louisiana. Oyster Data Rep. Ser. 23, 1–74. https://www.wlf.louisiana.gov/resources/category/stock-assessments/oyster. (Accessed August 2021).
Louisiana Department of Wildlife and Fisheries (LDWF), 2020a. 2018 Stock assessment report of the public oyster seed grounds and reservations of Louisiana. Oyster Data Rep. Ser. 24, 1–61. https://www.wlf.louisiana.gov/resources/category/stock-assessments/oyster. (Accessed August 2021).
Louisiana Department of Wildlife and Fisheries (LDWF), 2020b. Louisiana Oyster Management and Rehabilitation Strategic Plan, pp. 1–17. Public Notice Draft. https://www.wlf.louisiana.gov/assets/Resources/Publications/Oyster/Final-Draft—Oyster-Strategic-Plan—12.30.20.pdf. (Accessed August 2021).
Louisiana Department of Wildlife and Fisheries (LDWF), 2021. 2019 Stock assessment report of the public oyster seed grounds and reservations of Louisiana. Oyster Data Rep. Ser. 25, 1–51. https://www.wlf.louisiana.gov/resources/category/stock-assessments/oyster. (Accessed August 2021).
Lowe, M.R., Sehlinger, T., Soniat, T.M., La Peyre, M.K., 2017. Interactive effects of water temperature and salinity on growth and mortality of eastern oysters, *Crassostrea virginica*: a meta-analysis using 40 years of monitoring data. J. Shellfish Res. 36, 683–697.
Mascorda Cabre, L., Hosegood, P., Attrill, M.J., Bridger, D., Sheehan, E.V., 2021. Offshore longline mussel farms: a review of oceanographic and ecological interactions to inform future research needs, policy and management. Rev. Aquacult. 13 (4), 1864–1887.
Marshall, D.A., Casas, S.M., Walton, W.C., Rikard, F.S., Palmer, T.A., Breaux, N., La Peyre, M.K., Pollack, J.B., Kelly, M., La Peyre, J.F., 2021a. Divergence in salinity tolerance of northern Gulf of Mexico eastern oysters under field and laboratory exposure. Conserv. Physiol. https://doi.org/10.1093/conphys/coab065.
Marshall, D.A., Coxe, N.C., La Peyre, M.K., Walton, W.C., Rikard, F.S., Pollack, J.B., Kelly, M.W., La Peyre, J.F., 2021b. Tolerance of northern Gulf of Mexico eastern oysters to chronic warming at extreme salinities. J. Therm. Biol., 103072
Maxwell, V.J., Supan, J., Schiavinato, L.C., Showalter, S., Treece, G.D., 2008. Aquaculture parks in the coastal zone: a review of legal and policy issues in the Gulf of Mexico state waters. Coast. Manag. 36, 241–253.
McCarty, A.J., McFarland, K., Small, J., Allen, S.K., Plough, L.V., 2020. Heritability of acute low salinity survival in the eastern oyster (*Crassostrea virginica*). Aquaculture 529, 735649.
Melancon, E., Soniat, T., Cheramie, V., Dugas, R., Barras, J., Lagarde, M., 1998. Oyster resource zones of the Barataria and Terrebonne estuaries of Louisiana. J. Shellfish Res. 17, 1143–1148.
Moura, R.L., Secchin, N.A., Amado-Filho, G.M., Francini-Filho, R.B., Freitas, M.O., Minte-Vera, C.V., Teixeira, J.B., Thompson, F.L., Dutra, G.F., Yuko, P., Sumida, G., Guth, A. Z., Lopes, R.M., Batos, A.C., 2013. Spatial patterns of benthic megahabitats and conservation planning in the Abrolhos Bank. Continent. Shelf Res. 70, 109–117. https://doi.org/10.1016/j.csr.2013.04.036.
Mulholland, P.J., Best, G.R., Coutant, C.C., Hornberger, G.M., Meyer, J.L., Robinson, P.J., Stenberg, J.R., Turner, R.E., Vera-Herrera, F., Wetzel, R.G., 1997. Effects of climate change on freshwater ecosystems of the southeastern United States and the Gulf Coast of Mexico. Hydrol. Process. 11, 949–970.
NLCD, 2016. Multi-resolution land characteristics consortium (U.S.). In: National Land Cover Dataset (NLCD), vol. 2016. Multi-Resolution Land Characteristics Consortium, Research Triangle Park, NC.
National Oceanic and Atmospheric Administration (NOAA). NOAA CDR OISST V02r01: Optimum Interpolation Sea Surface Temperature Data. Retrieved from: https://code.earthengine.google.com/ee.ImageCollection("NOAA/CDR/OISST/V2_1"). Accessed 12 October 2021.
Orlando, S.P.J., Rozas, L.P., Ward, G.H., Klein, C.J., 1993. Salinity characteristics of Gulf of Mexico estuaries. Natl. Ocean. Atmos. Adm. Off. Ocean. Resour. Conserv. Assess. 209.
Petrolia, D.R., Walton, W.C., Yehouenou, L., 2017. Is there a market for branded Gulf of Mexico oysters? J. Agric. Appl. Econ. 49 (1), 45–65.
Pinto, R., Martins, F.C., 2013. The Portuguese national strategy for integrated coastal zone management as a spatial planning instrument to climate change adaptation in the Minho River Estuary (Portugal NW-Coastal Zone). Environ. Sci. Pol. 33, 76–96.
Pittman, S.J., Brown, K.A., 2011. Multi-scale approach for predicting fish species distributions across coral reef seascapes. Public Libr. Sci. 6 (5), e20583.
Puckett, B.J., Eggleston, D.B., 2016. Metapopulation dynamics guide marine reserve design: importance of connectivity, demographics, and stock enhancement. Ecosphere 7 (6), e01322. https://doi.org/10.1002/ecs2.1322.
Puckett, B.J., Theuerkauf, S.J., Eggleston, D.B., Guajardo, R., Hardy, C., Gao, J., Luettich, R., 2018. Integrating larval dispersal, permitting, and logistical considerations within a validated habitat suitability index for oyster restoration. Front. Mar. Sci. 5 https://doi.org/10.3389/fmars.2018.00076.
Rabalais, N.N., Turner, R.E., 2019. Gulf of Mexico hypoxia: past, present, and future. Limnol. Oceanogr. Bull. 28 (4), 117–124.
Reisinger, A., Beseres Pollack, J., Gibeaut, J., 2020. Oyster reef restoration habitat suitability index of Texas bays & estuaries. In: Distributed by: Gulf of Mexico Research Initiative Information and Data Cooperative (GRIIDC). Harte Research Institute, Texas A&M University–Corpus Christi. https://doi.org/10.7266/n7-htxh-3g51.
Rybovich, M., La Peyre, M.K., Hall, S.G., La Peyre, J.F., 2016. Increased temperatures combined with lowered salinities differentially impact oyster size class growth and mortality. J. Shellfish Res. 35, 101–113.
Shumway, S.E., 1996. Natural Environmental Factors. In: Kennedy, V.S., Newell, R.I.E., Eble, A.F. (Eds.), Natural Environmental Factors.
Solis, R.S., Powell, G.L., 1999. Hydrography, mixing characteristics, and residence times of Gulf of Mexico estuaries. In: Bianchi, T.S., Pennock, J.R., Twilley, R.R. (Eds.), Biogeochemistry of Gulf of Mexico Estuaries. Wiley, New York.
Soniat, T.M., Conzelmann, C.P., Byrd, J.D., Roszell, D.P., Bridevaux, J.L., Suir, K.J., Colley, S.B., 2013. Predicting the effects of proposed Mississippi River diversions on oyster habitat quality; application of an oyster habitat suitability index model. J. Shellfish Res. 32, 629–638.
Sousa, L.P., Alves, F.L., Silva, J.V., 2011. Competing uses on marine space methodological aspects to consider in estuary management plans. J. Coast Res. 64, 1584–1588.
Supan, J.E., Wilson, C.A., 2001. Analyses of gonadal cycling by oyster broodstock, *Crassostrea virginica* (Gmelin), in Louisiana. J. Shellfish Res. 20 (1), 215–220.
Theuerkauf, S.J., Lipcius, R.N., 2016. Quantitative validation of a habitat suitability index for oyster restoration. Front. Mar. Sci. 3 (64) https://doi.org/10.3389/fmars.2016.00064.
Theuerkauf, S.J., Eggleston, D.B., Puckett, B.J., 2019. Integrating ecosystem services considerations within a GIS-based habitat suitability index for oyster restoration. Public Libr. Sci. 14, e0210936.
Theuerkauf, S., Puckett, B., Eggleston, D., 2021. Metapopulation dynamics of oysters: sources, sinks and implications for conservation and restoration. Ecosphere 12 (7), e03573.
United States Geological Survey (USGS) of US Department of the Interior, 2021. USGS Current Condition for the Nation. Retrieved from National Water Information System: Web Interface. https://nwis.waterdata.usgs.gov/usa/nwis/uv/?. (Accessed 23 August 2021).
Walton, W.C., Davis, J.E., Supan, J., 2013. Off-bottom Culture of Oysters in the Gulf of Mexico. Southern Regional Aquaculture Center.
Wang, H., Chen, Q., La Peyre, M.K., Hu, K., La Peyre, J.F., 2017. Predicting the impacts of Mississippi River diversions and sea-level rise on spatial patterns of eastern oyster growth rate and production. Ecol. Model. 352, 40–53.
Zu Ermgassen, P.S.E., Spalding, M.D., Blake, B., Coen, L.D., Dumbauld, B., Geiger, S., Grabowski, J.H., Grizzle, R., Luckenbach, M., McGraw, K., 2012. Historical ecology with real numbers: past and present extent and biomass of an imperiled estuarine habitat. Proc. Biol. Sci. 279, 3393–3400.