Long-term assessments are critical to determining persistence and shoreline protection from oyster reef nature-based coastal defenses

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A R T I C L E   I N F O

A B S T R A C T

Nature-based coastal defense using bivalve reefs provides a potentially self-sustaining approach for regions facing high coastal land loss, relative sea level rise and increasing frequency and intensity of storms. Success of such nature-based coastal defense depends on the reef-building species' life history, habitat requirements, and ability to thrive through short-term and longer-term environmental variation, yet few projects have reported on outcomes beyond the first few years. In coastal Louisiana, USA, *Crassostrea virginica* (oyster) is an ecosystem engineer, creating self-sustaining, vertically accreting reefs that also provide ecosystem services. Here, we examine the short ($<$ 3 years) and medium ($>$ 10 years) term outcomes of experimental reefs constructed in 2009 for nature-based coastal defense in a Louisiana, USA estuarine lake. Oyster reef density, demography, along with adjacent salt marsh, and shoreline movement were compared at six fringing shoreline reefs and paired reference sites over the first three years post-construction (2009–2011), and a decade later (2019–2020). Oyster density measured in 2019–2020 ($<$ 60 ind m^{-2}) was less than 10% of density measured during 2009–2011 ($>$ 1000 ind m^{-2}). This density difference largely reflected a lack of new recruits and small oysters ($<$ 75 mm shell height) in later samples, with adult oyster densities similar between 2011, 2019 and 2020. Lack of smaller oysters in recent sampling likely reflected the impact of multiple extended low salinity events in this region in recent years, including the record-breaking low salinity in 2019. No differences in shoreline characteristics were detected in marsh vegetation, soil properties or nutrient concentrations between reef and reference sites during early and later years. Similarly, shoreline erosion at both reef and reference sites immediately post-construction, and 10 years later, was high ($\sim$1 m y^{-1}) indicating a lack of shoreline protection from these reefs. These findings highlight the need to consider both current and future conditions, including the effect of extreme years, when implementing nature-based coastal defense. On the other hand, the persistence of reproductive-sized oysters on the reef 10 years post creation, indicate reef resilience and potential for reef development and shoreline benefits, should better site conditions return in future years. Determining restoration success within variable and dynamic environments requires frequent monitoring which is required to understand responses to short and longer-term environmental variation.

1. Introduction

Rising sea levels and increasing storminess impact coastal habitats and the human populations living along the coast (Syvitski et al., 2009; Knutson et al., 2010; Bukvic et al., 2020). Globally, growing support for the use of nature-based coastal defenses has led to numerous schemes relying on the use of vegetated foreshore ecosystems (i.e., saltmarshes, mangroves, vegetated dunes) and lower intertidal or subtidal ecosystems (i.e., seagrass, shellfish beds) to facilitate and enhance coastal stability (Walles et al., 2015a; Bilkovic et al., 2017; Morris et al., 2018,

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2020; Chowdhury et al., 2021; Fivash et al., 2021). This approach assumes these systems are persistent and self-sustaining over time with no or low maintenance requirements (Temmerman et al., 2013; Bouma et al., 2014; Walles et al., 2016a; Bilkovic et al., 2017; Morris et al., 2018, 2020). These nature-based approaches are also valued because they provide ecosystem services including biodiversity support, fisheries enhancement, habitat provision, carbon sequestration, nutrient mitigation, and resilience in the face of rising sea levels and repeated storms (Ysebaert et al., 2019; Chowdhury et al., 2021). While such projects are valued for their ability to self-sustain, most reports document only the short-term (< 3 years) outcomes, and long-term sustainability and provision of services are rarely determined (Walles et al., 2016a; Ridlon et al., 2021).

Along the U.S. Gulf of Mexico coast (GoM), coastal defense remains a priority as storm frequency and intensity increase, and subsidence, sea level rise (SLR) and wetland loss rates remain high (CPRA, 2017; Chen et al., 2021). An important component of these restoration activities involves the use of nature-based coastal defense composed of reefs created by the native eastern oyster (*Crassostrea virginica*, hereinafter "oyster"; CPRA, 2017; DWH NRDA, 2017). Eastern oysters are noted ecosystem engineers, and valued for coastal defense because they build and maintain their own habitat (reefs), and may grow vertically, thus potentially keeping pace with SLR (La Peyre et al., 2014; Rodriguez et al., 2014; Ridge et al., 2015). Further, fringing oyster reefs may support adjacent marsh stability through wave attenuation (Borjse et al., 2011; Walles et al., 2015a; Morris et al., 2018), and nutrient and sediment subsidies from oyster filtration and trapping and stabilization of sediments (Walles et al., 2015a; Chowdhury et al., 2019a, 2019b).

Nature-based defense that is sustainable over the long-term depends on the ability of the ecosystem engineer (i.e., oyster) to maintain its structure through recruitment, growth, and mortality (Soniat et al., 2012a; Walles et al., 2016a; Yurek et al., 2021). For most of their life cycle, oysters remain sessile, and their growth, survival, and reef persistence are dependent on environmental conditions including water temperature, salinity and water movement affecting the delivery of food (Shumway, 1996; Coen and Humphries, 2017; Bayne, 2017). Oysters are considered tolerant to a wide range of salinity and temperature, however, oyster growth and survival in coastal Louisiana are highest within an annual mean salinity range of 10–15 (Soniat et al., 2013; Lowe et al., 2017; Lindquist et al., 2021). Below a salinity of 10, oysters start reducing feeding, and growth and reproduction decrease (Rybovich et al., 2016; Casas et al., 2018); above a salinity of 15, predators and disease increase mortality of oysters in this region (Menzel et al., 1966; Garton and Stickle, 1980; Brown and Haight, 1992).

Oysters survive temperatures ranging from −2 to 36 °C throughout their geographical range (Shumway, 1996), with temperatures above 36 °C reported as being acutely lethal (Galtsoff, 1964). However, a recent study with GoM oysters found oysters sensitive to temperatures as they increased above 30 °C, particularly with lower salinity (i.e., 4.0) (Marshall et al., 2021a). Oysters are also sensitive to water movement, as they are dependent on water currents for the provision of food for filter feeding, but with evidence indicating higher energy environments may result in a cessation of feeding (Dame et al., 1989; Bayne, 2017). Variation in these environmental conditions outside of the oyster tolerance range may impact the persistence and viability of this nature-based coastal defense approach through direct impacts on oyster growth, reproduction and survival.

Estuaries across the GoM experience a wide range of environmental conditions varying both spatially and temporally (Orlando et al., 1993). Existing climate models predict increasing frequency and intensity of extreme climatic events including precipitation and large storm events, which impact water quality, including salinity variability and extremes (Biasutti et al., 2012; Powell and Keim, 2015; Prein et al., 2017). Along the GoM, El Niño Southern Oscillation (ENSO), with an average 3–4 year periodicity (Graham and White, 1988), influences oyster mortality from disease (Soniat et al., 2012b), as well as reef oyster demography and

biodiversity support (Beseres Pollack et al., 2021); this finding suggests a minimal 5 years of monitoring is critical to determine reef persistence through short-term variability, and medium-term climatic cycles (i.e., ENSO). A recent review of oyster (*Ostrea lurida*) restoration on the west coast of Canada and the U.S. also concluded that restoration monitoring over a broader spatial (beyond restoration substrate) and temporal scale (5–10 yrs) was necessary to more accurately document impact and sustainability (Ridlon et al., 2021). As environmental conditions change over the long-term from both climate change and anthropogenic activities, tracking restored oyster reef outcomes over extended time frames is increasingly important and dependent on frequent monitoring.

Nature based coastal defense, initially conceived as a tool using only building blocks of the natural environment (i.e., oyster shell, adjacent marsh), involve enhancing, restoring or creating oyster reefs in strategic locations for shoreline protection specifically. Initial studies identified site characteristics including conditions supportive of oyster reef building, and landscape position (i.e., bathymetry, fetch, wind, or "exposure") to be key variables which address both reef persistence, and effectiveness in protecting shorelines (Meyer et al., 1997; Piazza et al., 2005). Despite many potential advantages from more recent bio-engineered reefs for nature based coastal defense (i.e., Morris et al., 2019; Chowdhury et al., 2021), mimicking natural reefs in terms of location and reef characteristics, and determining how exposure might influence both the living component and the shoreline protection services of these reefs created only with native materials remains important in informing site selection and design of both natural reefs, and bio-engineered reefs.

Here, we examine oyster reef density, demography, along with adjacent foreshore marsh vegetation, soils and movement on six created fringing shoreline reefs, designed to mimic natural fringing reefs in this region. Six reefs were created in 2009 at low and medium exposure shorelines in coastal Louisiana, USA (La Peyre et al., 2014). Using data collected to assess the reefs over the short-term (2009–2011; La Peyre et al., 2014), and data collected for this study documenting outcomes in the medium-term (2019–2020), reef oyster density and demography, and water filtration potential are examined. Shoreline marsh characteristics (vegetation, soils, soil nutrients) and shoreline movement are also compared between experimental reef and paired reference sites to examine effects of the reef on the adjacent foreshore habitat. Using these data, we examined the short (< 3 yrs) and medium-term (10–11 yrs) term outcomes of these reefs built for coastal defense. These data can help improve our understanding of potential reef persistence, and provision of coastal defense services across an extended time frame.

2. Materials and methods

2.1. Study site and experimental design

Sister Lake (also referred to as Caillou Lake), located in Terrebonne Parish, Louisiana, supports one of Louisiana's most productive public oyster grounds (LDWF, 2018) (29° 14′ 11.09 N, 90° 55′ 15.48 W). Sister Lake is a primarily open-water, brackish system, with water level influenced predominantly by southeastern winds and a mean tidal range of 0.3 ± 0.03 m (Fig. 1). Sister Lake displays minimal bathymetric relief with the few features evident identified as reefs, or shoals from recent erosion (Freeman, 2020). Mean water depth across the 8.9 km² lake is 1.5 ± 0.6 m (range 0.8–8.9 m; Freeman, 2020). Oyster reefs in this region are predominantly subtidal with limited vertical reef; Sister Lake reefs have been characterized with having less than 0.20 m vertical relief (Beck and La Peyre, 2015). As an estuarine interior lake, Sister Lake is partially protected from Gulf of Mexico fetch and winds through the marsh landscape on its southern end (Fig. 1). This region however is vulnerable to large tropical storms and hurricanes. From January 2010 through December 2020, wind speed averaged 20.6 kmh, ranging from 0 to 116 kmh, with a dominant southeastern wind (station DCLL1, https ://mesonet.agron.iastate.edu/sites; accessed 12/17/2021).
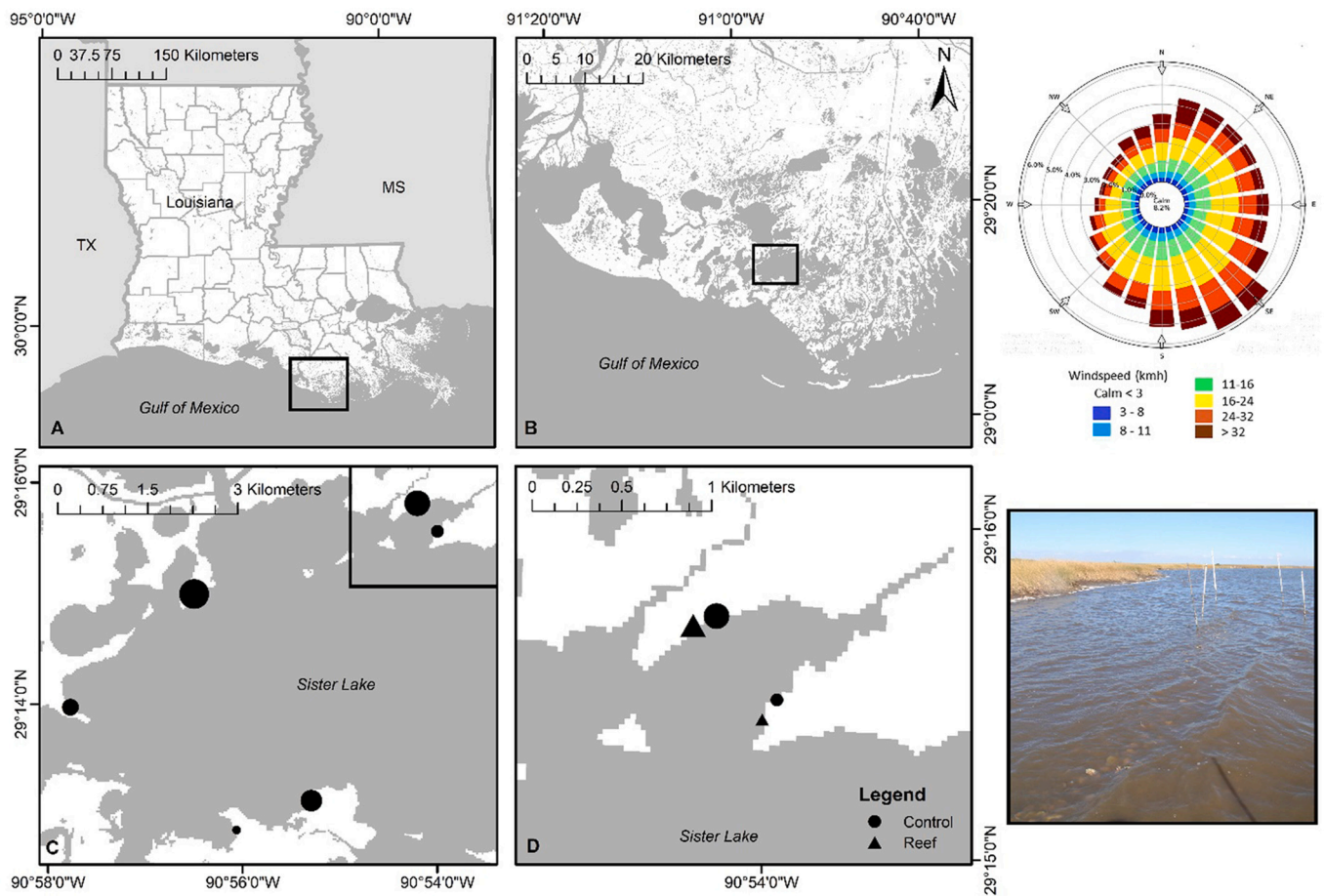
Fig. 1. Study Site Map. (A) Location map of study sites within Louisiana, USA, (B) Location map showing the location of the study sites within the estuarine lake, Sister Lake, within the marsh-water complex of south Louisiana, (C) Specific site locations within Sister Lake with size of site locator scaled to the relative exposure of the site calculated using fetch + wind speed + wind direction from 2010 to 2020, (D) Zoomed in view of the northern most sites showing location of reference and reef sites at low and moderate exposure site. On the right top is a wind rose for Sister Lake (2010–2020; Station DCLL1, https://mesonet.agron.iastate.edu/sites), and the right bottom is a picture from 2010 of the reef site in the forefront, and the reference site (poles) in the background from the north moderate exposure site (Photo: M. La Peyre, November 2010). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Annual mean ($\pm$ SE) salinity, temperature, and gauge height in Sister Lake from 2009 to 2020 was 10.5 ± 0.3, $23.0 \pm 0.4\,°C$, and 1.3 ± 0.01 m respectively (USGS Continuous Data Recorder 07381349; USGS 2021). Annual mean salinity and temperature ranged from 7 to 14 and 22–24 °C respectively during 2009–2020. Sister Lake sits within a complex of extensive marsh dominated by *Spartina alterniflora* and *Juncus roemerianus* with *Spartina patens*, *Batis maritima*, and *Distichlis spicata* interspersed throughout. Marsh soils are composed of 13–22% organic matter with bulk density ranging between 0.3 and 0.4 g cm^{-3} (Coastwide Reference Monitoring System (CRMS) sites CRMS0383, CRMS4455; CPRA, 2021). This region has high subsidence rates, ranging from 6 to 22 mm y^{-1} (Fitzpatrick et al., 2020).

In March 2009, six experimental intertidal oyster reefs (25 m $\times$ 1 m $\times$ 0.7 m, length x width x height) were constructed parallel to, and 5–10 m away from the marsh shoreline using unconsolidated clean, dry oyster shell. Three reefs were located along shorelines identified as having a lower exposure, based on their orientation with respect to dominant winds, and fetch; three were located along shorelines identified as having a higher exposure (see La Peyre et al., 2014). Briefly, exposure for each of the six reefs was calculated using effective fetch which uses direct fetch (km) for 36 compass bearings, at 10 degree intervals, mean wind velocity (kmh) for each of the 36 compass bearings, and directional percent frequency as described fully in La Peyre et al. (2014). Fetch measurements were calculated as maximum potential fetch using Arc-GIS (v. 10.0) while wind speed (kmh) and direction data were downloaded from a continuous data recorder located in Sister Lake, from 2010 to 2020 (DCLL1, https://mesonet.agron.iastate.edu/sites). This calculation provided a unitless measure of exposure, and exposure of higher energy sites was, on average, 4 times higher than at lower energy sites (La Peyre et al., 2014). Wave data were not available for these sites.

For each experimental reef and adjacent shoreline, a reference bottom and shoreline were established 50 m away. Monitoring of oyster reef sustainability, shoreline vegetation, soils, and shoreline movement, was conducted in late summer (August/September) in 2009, 2010, 2011 (La Peyre et al., 2014). In 2019 and 2020, all sites were revisited, replicating the late summer sampling events, as described below, to quantify reef persistence and filtration capacity, shoreline vegetation and soil characteristics, and shoreline movement 10- and 11-years post-reef creation.

2.2. Sampling and data collection

2.2.1. Reef characteristics

Three 0.25×0.25 m (0.0625 m^2) quadrat samples were taken at each reef and control site (12 sites $\times$ 3 quadrats $\times$ 5 years = 180 samples) using a weighted quadrat and buoy. Upon arrival on site, three quadrats were haphazardly thrown from the boat over the reef. Divers removed the top 10 cm of reef material by hand, placing each sample in a mesh bag which was rinsed, kept cool, and returned to the lab at

Louisiana State University (LSU) for processing. In the lab, reef material was separated into categories of live oysters, dead oysters, and shell hash within 72 h of collection. Total number of oysters, and shell height (SH) of live oysters were measured. Data were used to calculate total live oyster density (ind. m^{-2}), and live oyster density by size class (spat <25 mm, seed 25 ≤ SH <75 mm, market ≥75 mm).

Reef oyster density by oyster size class was used to estimate potential filtration services provided by each reef over time. Shell height was converted to dry tissue weight (DW; g) with the regression equation derived from Sister Lake oysters (La Peyre et al., 2014).

$$DW = 0.0004*(SH)^{1.9217} \qquad (1)$$

Potential filtration rate was estimated with the temperature corrected equation provided by Cerco and Noel (2005), originally based on Riisgård (1988), that calculates filtration rate based on regressions of filtration rate (Lh^{-1}) on temperature:

$$\text{Filtration rate } (Lh^{-1}) = 6.79 \, DW^{0.73} e^{(-0.15(temperature-27)^2)} \qquad (2)$$

The mean 11-year temperature (23.0° ± 0.1 °C) for Sister Lake was used to make the temperature adjustment. Bivalve filtration is also affected by salinity, with lower rates occurring below 7.5 (Newell and Langdon, 1996; Dame, 2012). The mean salinity in Sister Lake over the 11-year period (10.5 ± 0.1) was above 7.5 for all years except 2019, and thus the equation was applied without adjusting for salinity. Daily fluctuations for both variables can result in either higher or lower rates of filtration, and thus, the rates presented provide only a comparison between years, assuming a temperature of 23.0 °C, and salinity above 7.5.

2.2.2. Marsh characteristics

Vegetation and soil characteristics on shorelines adjacent to the reefs were quantified in triplicate 1 m^2 plots located haphazardly within 5 m of the marsh edge at each site (12 sites × 3 replicates × 5 years = 180 samples). Vegetation and soil characteristics determined for all five years include species-specific percent cover (%), stem height (cm), total above ground vegetation biomass (g m^{-2}), soil bulk density (g m^{-2}), and soil percent organic matter (%), following protocols listed below. In 2019, total (live and dead) belowground vegetation biomass (gdw m^{-2}) and soil extractable nutrients (NO$_x$, NH$_4^+$, PO$_4^{3-}$) concentrations were quantified to examine long-term effects of adjacent reefs on these vegetation and soil properties. In 2020, soil shear strength (kpa) was quantified with a shear vane (Geotechnics Geovane #2285) in each of the 1 m^2 plots within the root zone (15 cm depth) using the approach described in Lin et al. (2016).

Species-specific percent cover was estimated for each plot using Braun-Blanquet (1932). In 2009–2011, each sample plot was destructively sampled for live and dead aboveground biomass (g m^{-2}). In 2019–2020, a 0.25 m × 0.25 m quadrat was haphazardly placed inside the 1 m^2 plot and destructively sampled for live and dead aboveground biomass (g m^{-2}) following the same methods as in 2009–2011.Vegetation was cut at the marsh surface, placed in a labelled bag and returned to LSU for processing. In the lab, samples were identified to the species level, and then live and dead stems were separated and dried to a constant weight at 60 °C. Dry weight (g) of live and dead material for each species was recorded.

Within each sample plot, one sediment core (6.7 cm dia. x 15 cm depth) was collected for measurement of bulk density (g m^{-3}) and organic matter (%). Cores were placed in plastic labelled bags and returned to the lab at LSU for processing. In the lab, homogenized subsamples (~10 g) were weighed wet, dried to a constant mass at 60 °C, reweighed, then placed in a muffle furnace at 400 °C for 4 h to determine organic content by mass loss on ignition (Marton and Roberts, 2014). Bulk density was calculated as the dry mass of the core divided by core volume (g m^{-3}).

In 2019 only, total belowground biomass (g m^{-2}) was measured in the destructively sampled quadrat. Belowground biomass was collected by taking one auger core (6.35 cm dia. x 30 cm depth), placing it in a labelled bag on ice, and processing in the laboratory. In the laboratory, the 30 cm core was rinsed free of sediment, sorted into live and dead biomass following procedures detailed in Hill and Roberts (2017), and then dried to a constant weight at 80 °C. A separate surficial sediment (0–5 cm) core (6.7 cm diameter) was taken to quantify extractable nutrient (NO$_x$, NH$_4^+$, PO$_4^{3-}$) concentrations. Approximately 2 g of soil was added to each of two 50-mL centrifuge tubes, one tube for extractable dissolved inorganic nitrogen (DIN), and the other for dissolved inorganic phosphorus (DIP) as described in Schutte et al. (2020). A total of 30 mL of 2 N KCL was added to the DIN tube and shaken at 250 rpm for 2 h. The DIN tube was then centrifuged at 3000 rpm for 10 min, filtered (0.2 μm), and stored frozen until analysis. Similarly, 30 mL of 0.5 M NaHCO$_3$ was added to the DIP tube and shaken for 16 h at 250 rpm, centrifuged at 3000 rpm for 10 min, filtered (0.2 μm), and stored frozen until analysis. NO$_x$ was analyzed using Cu—Cd reduction followed by azo colorimetry with a Lachat Instruments QuickChem ® FIA + 8000 series automated Ion analyzer with an ASX-400 series XYZ Autosampler (APHA, 1992). Samples were analyzed for dissolved NH$_4^+$ (with phenate cloriometry) and PO$_4^{3-}$ (with ascorbic acid reduction method) on a Shimadzu UV-1800 spectrophotometer (APHA, 1992). Standard curves were prepared by diluting NO$_3^-$, NH$_4^+$, and PO$_4^{3-}$ stock solutions (Hach, Loveland, CO) and yielded r^2 values of >0.99 for each analyte.

2.2.3. Shoreline movement

Shoreline movement adjacent to each control and reef site was analyzed using aerial imagery from U.S. Geological Survey Earth-Explorer website (https://earthexplorer.usgs.gov) from 2005 to 2019 following McClenachan et al. (2020). Selected images were imported into ArcGIS v10, and resolution ranged from 0.3 to 1.0 m. Each study shoreline was hand digitized in years 2005, 2010, 2014 and 2019 when clear, winter images (November–January) were available for all sites, and vegetation dieback had occurred for the growing season. Shoreline position was determined by the location of vegetation edge. After delineating shoreline locations, the Digital Shoreline Analysis System (DSAS; Thieler et al., 2009) was used to quantify net shoreline change (m yr^{-1}) for "pre-reef" (2005–2010), "early reef" (2010–2014), and "late reef" (2014–2019) periods by running perpendicular transects every 1 m and calculating the distance between delineated shorelines.

2.3. Statistical analyses

Data were analyzed with two-way ANOVAs (R 3.6.3; R Foundation for Statistical Computing, 2018). For all analyses, data were examined for normality and homogeneity of variance, and an alpha value of less than 0.05 was used to determine significance. For oyster density and filtration, a two-way ANOVA with factors being exposure (medium, low) and year (2009, 2010, 2011, 2019, 2020) was run on total, spat, seed and market sized density, and filtration rate, examining the single and interactive effects. For shoreline characteristics collected for all five years (percent cover (%), total above ground vegetation (g m^{-2}), soil bulk density (g m^{-2}), and soil percent organic matter (%)), a two-way ANOVA including treatment (reef, reference), and year was run separately for each exposure (medium, low). For parameters collected only in 2019 (belowground biomass, nutrients) or 2020 (soil shear strength), data were analyzed with a one-way ANOVA (factor: treatment) by exposure. A two-way ANOVA by exposure (medium or low) examined shoreline erosion (m y^{-1}) by treatment (reef, control) and time period (pre-reef, early-reef, and late reef). Where significant differences occurred, a post-ANOVA LSMeans test was used.

3. Results

Mean daily salinity ranged from 0.4 to 30, with mean monthly

salinity ranging from 2 to 24 (Fig. 2). Mean annual salinity in 2009 (10.4 ± 0.3), 2010 (9.8 ± 0.2), and 2011 (13.2 ± 0.4) was greater compared to 2019 (6.9 ± 0.2; F = 50.2, p < 0.001) and 2020 (8.5 ± 0.4; F = 15.2, p < 0.001; Fig. 3a). Mean monthly salinity varied by year and month with lower salinities occurring during spring when freshwater inflow tended to be higher from riverine input, and precipitation events (i.e., 2019, Gledhill et al., 2020). Mean daily temperature ranged from 2.2 to 34.4 °C, with mean monthly temperature ranging from 9 to 32 °C, following typical seasonal patterns for this region. Mean annual temperature did not vary significantly with an overall mean of 22.8 ± 0.4 °C (Fig. 3b).

3.1. Reef characteristics

Across the years and sites, mean total oyster density was 926.8 ± 149.0 ind m^{-2}, ranging from a high of 2216.1 ± 605.0 ind m^{-2} (2009) to a low of 48.9 ± 17.7 ind m^{-2} (2019) with spat density accounting for over 50% of total density across all years (Table 1). Spat and total oyster density were highly correlated (r = 0.97, p < 0.0001), and thus only statistical results by individual size class are presented. Spat and seed oyster differed significantly only by year and not by site. Spat density was significantly greater in 2009 as compared to the other four years, which did not differ from one another (F$_{4,79}$ = 9.35, p < 0.0001). Seed density was significantly greater in 2009–2011 as compared to 2019 and 2020 (F$_{4,79}$ = 18.44, p < 0.0001). Market density differed by the interaction of year and exposure (F$_{4,7\,9}$ = 4.41 p = 0.0029). The 2011 low exposure sites had significantly greater market oyster density compared to all other year and exposure combinations.

Total estimated reef filtration potential ranged from a high of 5381.7 ± 1421.3 L h^{-1} m^{-2} (2009) to a low of 251.7 ± 86.3 L h^{-1} m^{-2} (2019) (Table 2). In 2009–2011, estimated total filtration potential contributed by size class ranged from 18 to 72% (spat), 27–77% (seed) and 0–5% (market). In contrast, in 2019–2020, percent contribution ranged from 41 to 61% (spat), 9–55% (seed) and 4–31% (market) of total filtration potential.

3.2. Shoreline characteristics

Vegetation percent cover ranged from 33.5 ± 2.2% to 51.6 ± 2.5%, with *S. alterniflora* accounting, on average for 23.6 ± 1.2% and *J. roemerianus* for 13.3 ± 1.6% of total cover across all sites. *S. patens*, *B. maritima* and *D. spicata* were present throughout most years and sites, but generally accounted for less than 5% of total percent vegetation cover. At medium exposure sites, percent cover differed only by year (F = 9.1, p = 0.0004) with 2011 having significantly less cover as compared to all other years (Table 3). At low exposure sites, there was a significant treatment by year interaction (F = 4.8, p = 0.0016),

Fig. 2. Monthly mean salinity and temperature. Monthly mean salinity and temperature from 2009 through 2020 in Sister Lake, Louisiana (USGS #07381349; https://waterdata.usgs.gov/la/nwis/nwismap/?site_no=07381349&agency_cd=USGS).

explained by 2019 when reference sites had a significantly greater percent cover as compared to the reef sites.

Total live aboveground biomass differed only by year in both medium and low exposure settings (medium: F = 4.7, p = 0.00516; low: F = 2.9, p = 0.041). For medium exposure sites, aboveground vegetation biomass was similar in 2010, 2019 and 2020, all having higher biomass than in 2009 and 2011, which were similar to one another (Table 3). In low exposure sites, 2009, 2019, 2020 had significantly greater biomass than 2011; 2010 did not differ from any other years. Total live belowground vegetation biomass, measured in 2019 only, ranged from 60.9 to 3882.6 g m^{-2} and was significantly greater at medium exposure reference sites (1816.0 ± 413.7 g m^{-2}; F = 5.1, p = 0.0385) compared to medium exposure reef sites (723.7 ± 138.3 g m^{-2}), with no difference between treatments at low exposure sites (526.4 ± 53.5 g m^{-2}).

Soil percent organic matter ranged from 17 to 30% (Table 3), soil bulk density from 0.2 to 0.4 g m^{-2} and soil moisture content from 30.8 to 89.1%. Soil percent organic matter, bulk density and moisture content did not differ by year, treatment, or their interaction in either low or high exposure sites. Soil extractable nutrient (NO$_3^-$, PO$_4^{3-}$, NH$_4^+$) concentrations and soil shear strength did not differ by treatment, or exposure.

3.3. Shoreline movement

All sites showed shoreline retreat (erosion) throughout the period of study, with an overall average retreat of 1.1 ± 0.07 m y^{-1} (Fig. 4). Shoreline movement of medium exposure shorelines did not differ significantly by treatment (F = 1. 6, p > 0.05), year (F = 3.008, p > 0.05), or the interaction of year by treatment (F = 1.2, p > 0.05), with an overall average of 1.1 ± 0.1 m y^{-1}. In contrast, shoreline movement of low exposure shorelines differed significantly for the interaction of year and treatment (F = 8.631, p = 0.000266). This interaction was largely explained by the large difference reported between the pre-reef reference and the early reef reference site (pre-reef: 1.6 ± 0.2 m y^{-1}, early reef: 0.6 ± 0.1 m y^{-1}).

4. Discussion

Nature-based coastal defenses provide a potentially low maintenance approach to stabilize shorelines and keep pace with SLR but assume persistence and resilience of the natural ecosystem engineer. Despite this assumption, few studies have considered the persistence of many nature-based coastal defense projects for more than a few years; this is increasingly relevant given the rapid coastal changes in environmental conditions experienced in many areas. In this study, significant reduction in individual reef oyster populations, as measured by oyster density and demography, was evident between the first years (1–3 years) and after a decade (10–11 years) across experimental reefs. During the time of this study, this region experienced several historic freshwater events and extended reduced salinity (USACE, 2019; Gledhill et al., 2020; Swam et al., in review), resulting in estuarine salinity below the oysters' ideal range which contributed to this reduced oyster population, and prevented reefs from building (Fig. 2, Supplementary Table 1). In addition, the reefs failed to impact the adjacent foreshore marsh, or reduce marsh erosion over the period of study. As this failure was evident in the early and late years, reef location, or design may contribute largely to this lack of shoreline protection. A lack of consistent and more frequent monitoring across the full 11 years however limits our ability to place the current status of the reefs within full range of normal reef development, and functioning. Tracking changes in nature-based coastal defense outcomes would benefit from sustained and continued monitoring of the ecosystem engineer, the resulting nature-based coastal defense and associated ecosystem services and would have the added benefit of enabling adaptive management to maximize positive outcomes.

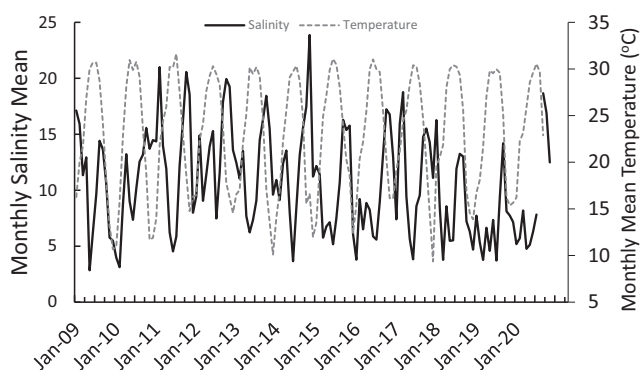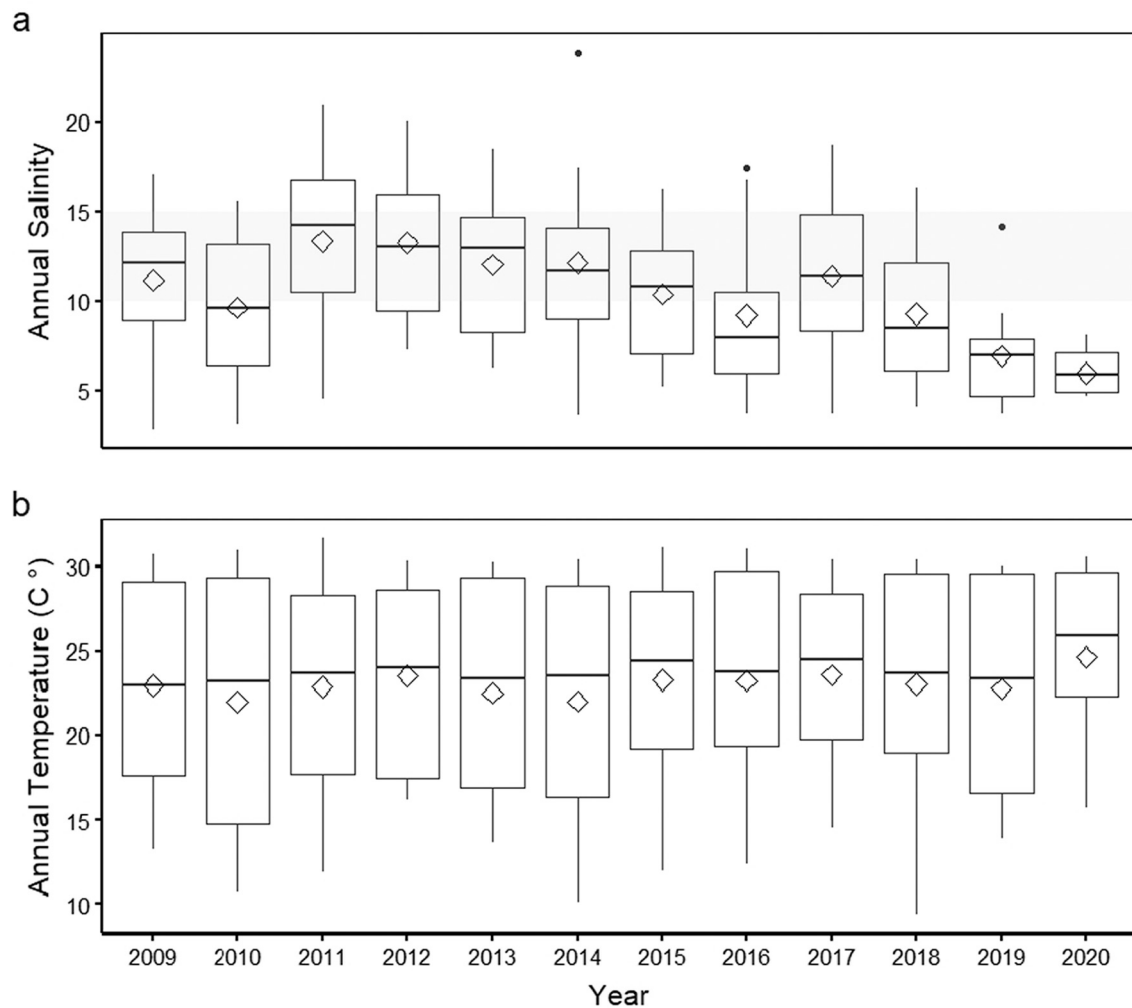Continued development and sustainability of restored oyster reefs

Fig. 3. Annual Mean Salinity and Temperature. A: Box and whisker plot (mean, quartiles, outliers) showing mean annual salinity for 2009–2020. Diamonds denote mean, line denotes median, shaded region denotes annual mean salinity range where oyster habitat suitability has a value of 1 (Lindquist et al., 2021) B: Box and whisker plot showing mean (diamond) and median (line) annual temperature for 2009–2020. Data from (USGS #07381349; https://waterdata.usgs.gov/la/nwis/nwismap/?site_no=07381349&agency_cd=USGS).

Table 1
Oyster densities by size class (spat, SH < 25 mm; seed, $25 \leq SH < 75$ mm; market, $SH \geq 75$ mm) and reef exposure for all created reefs (mean ± SE) from 2009, 2010, 2011, 2019, and 2020. Superscript letters denote significant statistical differences between years and exposure (2-way ANOVA, alpha value = 0.05) within each oyster size class (spat, seed, market).

Year	Exposure	Spat	Seed	Market	Total Density
		Ind. m^{-2}	Ind. m^{-2}	Ind. m^{-2}	Ind. m^{-2}
2009	Medium	1881 ± 821[a]	766 ± 294[a]	0 ± 0[a]	2646 ± 1109
	Low	1258 ± 277[a]	474 ± 88[a]	0 ± 0[a]	1732 ± 343
2010	Medium	638 ± 247[b]	587 ± 124[a]	0 ± 0[a]	1225 ± 370
	Low	565 ± 94[b]	618 ± 59[a]	3 ± 1[b]	1185 ± 133
2011	Medium	324 ± 112[b]	830 ± 129[a]	23 ± 6[b]	1177 ± 227
	Low	197 ± 43[b]	834 ± 129[a]	59 ± 10[c]	1090 ± 530
2019	Medium	14 ± 8[b]	2 ± 2[b]	7 ± 4[b]	23 ± 13
	Low	46 ± 20[b]	16 ± 14[b]	12 ± 6[b]	75 ± 32
2020	Medium	46 ± 31[b]	62 ± 36[b]	4 ± 2[b]	112 ± 67
	Low	55 ± 34[b]	28 ± 17[b]	7 ± 7[b]	91 ± 55

Table 2
Estimated potential filtration rate (L h^{-1} m^{-2}) by oyster size class (spat, SH < 25 mm; seed, $25 \leq SH < 75$ mm; market, $SH \geq 75$ mm) by exposure and year.

Year	Exposure	Spat	Seed	Market
2009	Medium	2568 ± 1120	3915 ± 1505	0 ± 0
	Low	1718 ± 402	2425 ± 475	0 ± 0
2010	Medium	871 ± 337	3004 ± 634	0 ± 0
	Low	771 ± 129	3160 ± 304	28 ± 15
2011	Medium	443 ± 153	4245 ± 660	232 ± 63
	Low	269 ± 59	4266 ± 660	593 ± 101
2019	Medium	2 ± 2	73 ± 42	72 ± 39
	Low	22 ± 19	227 ± 103	107 ± 54
2020	Medium	75 ± 47	145 ± 89	69 ± 69
	Low	63 ± 42	318 ± 182	25 ± 17

depends on maintenance of suitable environmental conditions (i.e., salinity and temperature) and the physical characteristics of a site through time. In this case, the restored oyster reefs persisted over 11 years, although oyster density and filtration potential were significantly lower in years 10 and 11, compared to the first three years post-creation. While oysters are well adapted to variable estuarine conditions tolerating large ranges and changes in water salinity and temperature, prolonged or repeated exposure to unfavorable conditions often leads to high mortality and loss of ecosystem services (La Peyre et al., 2013; Munroe et al., 2013; Rybovich et al., 2016; Du et al., 2021). Total oyster density was an estimated 96% lower compared to initial densities in 2009. During the period from 2013 to 2019, oyster densities reported on

Table 3

Mean ± SE for soil organic matter, vegetation percent cover (%), aboveground (AG) biomass (g m^{-2}) 2009, 2010, 2011, 2019, and 2020, for belowground (BG) biomass, soil extractable NO$_{3-}$, NH$_{4+}$ and PO$_4^{2+}$ for 2019 only, and soil shear strength, for 2020 only. Samples were collected each year between August 20 and September 15. Superscript letters (a, b) denote significance between years and treatment within each exposure (low, medium) for percent cover, and above and belowground biomass. No significant differences existed for other parameters.

Year	Treatment	Organic Matter (%)	Percent Cover (%)	AG Biomass (g m^{-2})	BG Biomass (g m^{-2})	NO$_3^-$ (uM dwg^{-1})	PO$_4^{2+}$ (uM dwg^{-1})	NH$_4^+$ (μM dwg^{-1})	Shear Strength kPa m^{-2}
Medium Exposure									
2009	Reef	22 ± 5	53 ± 9[a]	520 ± 162[a]	–	–	–	–	–
	Reference	24 ± 5	44 ± 7[a]	812 ± 141[a]	–	–	–	–	–
2010	Reef	24 ± 6	66 ± 9[a]	1254 ± 180[b]	–	–	–	–	–
	Reference	24 ± 5	57 ± 4[a]	1119 ± 192[b]	–	–	–	–	–
2011	Reef	15 ± 4	28 ± 8[b]	712 ± 134[a]	–	–	–	–	–
	Reference	19 ± 4	23 ± 4[b]	785 ± 135[a]	–	–	–	–	–
2019	Reef	23 ± 3	48 ± 4[a]	760 ± 123[ab]	1285 ± 188[a]	0.09 ± 0.02	13 ± 2.3	10.8 ± 0.7	–
	Reference	19 ± 4	47 ± 6[a]	1233 ± 162[ab]	2307 ± 413[b]	0.1 ± 0.04	10.6 ± 1.6	12.9 ± 0.8	–
2020	Reef	18 ± 3	52 ± 2[a]	1704 ± 206[ab]	–	–	–	–	8.9 ± 1.1
	Reference	20 ± 4	45 ± 2[a]	1340 ± 107[ab]	–	–	–	–	14.1 ± 2.2
Low Exposure									
2009	Reef	27 ± 4	41 ± 5[b]	1127 ± 128[ab]	–	–	–	–	–
	Reference	31 ± 6	33 ± 5[b]	829 ± 205[ab]	–	–	–	–	–
2010	Reef	24 ± 3	51 ± 3[ab]	1324 ± 149[b]	–	–	–	–	–
	Reference	30 ± 6	53 ± 3[ab]	1297 ± 169[b]	–	–	–	–	–
2011	Reef	22 ± 2	33 ± 4[c]	946 ± 131[a]	–	–	–	–	–
	Reference	24 ± 3	31 ± 2[c]	737 ± 62[a]	–	–	–	–	–
2019	Reef	27 ± 3	44 ± 3[a]	1096 ± 190[ab]	1019 ± 130[a]	0.11 0.02	10.7 ± 1.8	11.1 ± 1.8	–
	Reference	35 ± 5	71 ± 7[b]	1089 ± 226[ab]	878 ± 157[a]	0.07 0.02	11.1 ± 1.6	10.3 ± 0.4	–
2020	Reef	27 ± 3	46 ± 3[b]	1339 ± 196[ab]	–	–	–	–	10.4 ± 1.5
	Reference	33 ± 5	48 ± 4[b]	1676 ± 300[ab]	–	–	–	–	7.7 ± 1.7
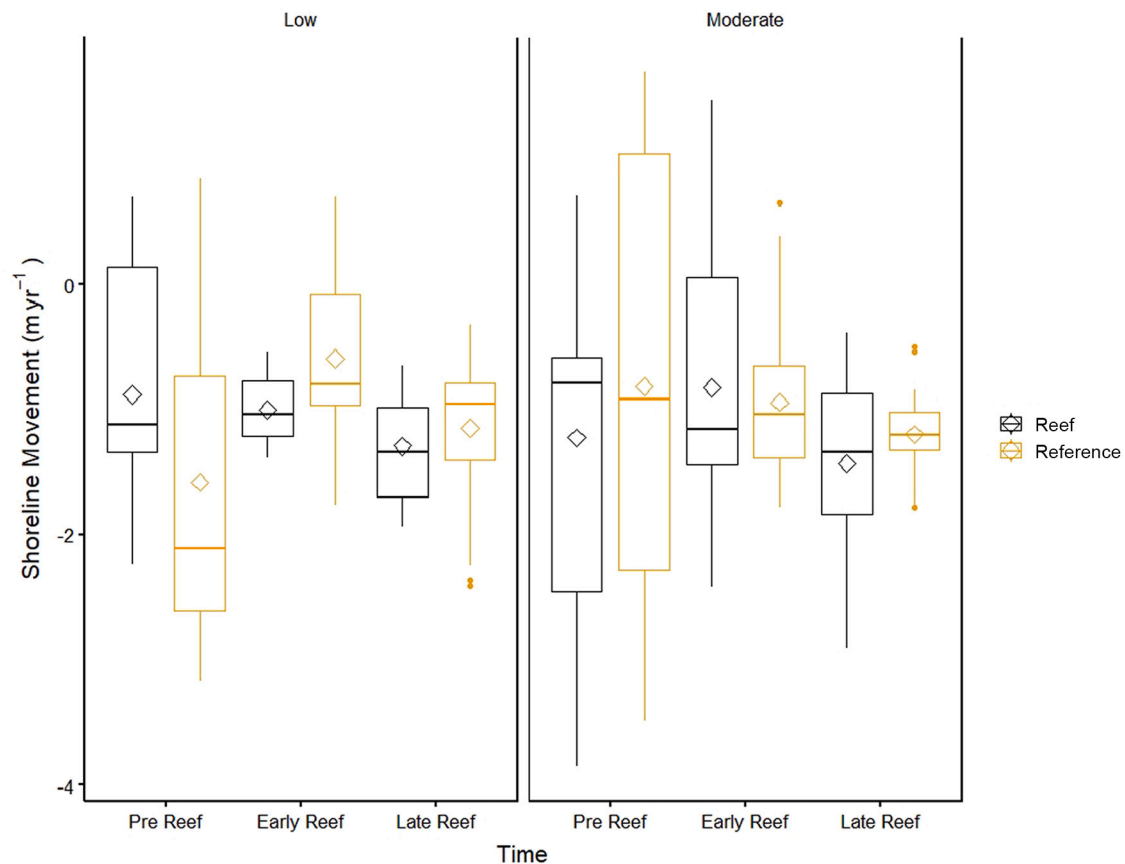
Fig. 4. Shoreline movement. Box and whisker plot (median, quartiles) of shoreline movement (m y^{-1}) by treatment (reef, reference) located at low and moderate exposure shorelines. Diamonds denote mean. Negative shoreline movement indicates shoreline erosion. Time period represents pre-reef (2005–2010), early reef (2010–2014) and late reef (2014–2019) periods. Reefs were created in late 2009.

adjacent subtidal reefs from fisheries independent monitoring showed a wide range of oyster densities ranging from a low of <20 ind m^{-2} (2019) to a high of >200 ind m^{-2} (2017) (LDWF, 2019, 2020, 2021). The low densities reported in this study match fisheries independent data from 2019 and 2020, which may be due to the unprecedented freshwater into the system during these latter two years, with large periods of salinity below 8, which is not supportive of recruitment (i.e., Gledhill et al., 2020; Supplementary Table 1). While the low salinity would generally inhibit mortality from disease or predation, it may however cause mortality in larger oysters when occurring during hot weather months (i. e., > 32 °C) (Rybovich et al., 2016; Marshall et al., 2021b). Combined effects of low salinity and high temperatures have well-documented synergistic effects on oyster reproduction, mortality and physiology (Shumway, 1996; La Peyre et al., 2013; Munroe et al., 2013; Rybovich et al., 2016; Bayne, 2017; Marshall et al., 2021a, 2021b). Repeated and extended exposure to low salinity during recent years likely explain much of the decrease of total oyster density compared to earlier years, but the maintenance of adult oysters suggests potential reef persistence. A key component of reef maintenance over time is population demography, including recruitment (Soniat et al., 2012a; Walles et al., 2015b; Yurek et al., 2021). Although data were only collected in the last two years of this period, the low spat and seed density numbers recorded (2019–2020 < 10% of 2009–2011) suggest that these reefs experienced limited recruitment during the later years. This matches general trends across Louisiana as historically productive oyster areas (including Sister Lake where this study occurred) have experienced significant declines in production (i.e., LDWF, 2019). Interestingly, on these study reefs, market oyster density was similar in 2019 and 2020 compared to 2011, suggesting reef persistence and the potential for reef building and development with improved water quality conditions. As larger oysters tend to be more sensitive to extreme conditions, including low salinity and high temperatures (La Peyre et al., 2013; Rybovich et al., 2016), the observed population demography in 2019 and 2020 likely reflected the effects of reduced reproduction due to the low, but not lethal salinity conditions over the last few years. As oyster populations reflect the accumulation of spat falls over many years (He et al., 2012), poor reproduction or recruitment over a short period of time may not be detrimental to the long-term persistence of a population, unless associated with high mortality of adult oysters. More frequent (annual) monitoring of oyster populations on restoration projects could provide more insight into variation in population demography.

Filter feeders, including oysters, contribute numerous ecosystem services to estuarine habitat, including local improvements in water quality through filtration (Coen et al., 2007; Coen and Humphries, 2017). However, lack of favorable environmental conditions results in decreased filtration potential, by impacting clearance rates. For example, a 90–95% reduction in eastern oyster clearance rate has been noted after continuous exposure to salinities of 6 and 3 (Casas et al., 2018); because clearance rates also represent feeding by oysters, such a reduction will result in reduced growth, and energy available for reproduction (Lavaud et al., 2017), further exacerbating the impacts. Reduced total filtration potential calculated in this study between 2009 (5000 L h^{-1} m^{-2}) and 2019 (250 L h^{-1} m^{-2}), was calculated based on a 10-year mean salinity, thus reduced filtration reflected only the decrease in oyster densities and change in oyster size distribution. If annual salinities were also used to calculate each year, the filtration provided in the lower salinity years (i.e., 2019) would be further reduced. In addition to direct impacts on clearance rates, these extended low salinity conditions may reduce food quality by altering phytoplankton community composition, and promoting cyanobacterial growth (Bargu et al., 2019) which may impact overall population dynamics and the observed population demography discussed above.

Nearshore reefs for coastal defense such as these are hypothesized to protect shorelines from erosion through multiple potential mechanisms including direct wave attenuation, and through sediment trapping and provision of nutrients (Bilkovic et al., 2017; Ysebaert et al., 2019;

Chowdhury et al., 2021; Morris et al., 2021). The provision of nutrients and sediments are hypothesized to result from both the hypothesized wave attenuation, and the packaging of materials from oyster filtration, and creation of feces and pseudofeces, although evidence to support this remains limited (Walles et al., 2015a; Bilkovic et al., 2017; Chowdhury et al., 2019a, b). The net expected outcome, if effective, would be reduced shoreline erosion, and potentially enhanced vegetative production, and altered sediment characteristics from increased mineral and nutrient inputs. Minimal differences were found in this study on the adjacent marsh vegetation and soils when comparing reef and adjacent reference sites. This lack of effect on the adjacent foreshore marsh vegetation, soils and nutrient concentrations, combined with reduced oyster populations on the reefs likely contributed to the lack of impact on shoreline erosion along these reefs from trapping of sediments or nutrient provision.

In addition to ensuring site conditions support the reef-building organism, numerous site-specific characteristics have been suggested as critical to consider when locating reefs for shoreline protection specifically, including site exposure, and adjacent habitat, and reef demography, and architecture (Walles et al., 2015a, 2015b; Van de Koppel et al., 2015; La Peyre et al., 2015; Chowdhury et al., 2019, 2020, 2021; Marin-Diaz et al., 2021). For example, a number of studies have demonstrated wave attenuation impacts with lower wave energies measured behind the reef compared to the front of the reef (Meyer et al., 1997; Borsje et al., 2011; Chowdhury et al., 2019a, b), however, this finding has not always translated to reduced shoreline erosion (i.e., Morris et al., 2018) with a meta-analysis identifying trade-offs between oyster recruitment and growth, reef inundation, and wave attenuation impacts (Morris et al., 2021). These trade-offs remain difficult to explicitly identify given that every study differs in specific reef architecture (i.e., reef height, footprint), oyster demography (i.e., oyster density, size distribution), and local subsidence and SLR, which are also impacted by site morphology, and environmental conditions (Walles et al., 2016a, 2016b; Morris et al., 2018, 2021; Marin-Diaz et al., 2021).

In this study, the lack of measured stabilization benefits or impacts on shoreline vegetation and soils may reflect a combination of factors including reef size (length, crest, width), reef oyster population dynamics, and shoreline morphology and exposure. For example, several studies have found that reefs may influence adjacent areas and upland salt marsh habitats, but this effect was found to be reduced as the shoreline slope increased (i.e., Walles et al., 2015a, 2015b; Ysebaert et al., 2019). Across coastal Louisiana, rapid erosion, combined with high subsidence (6–20 mm y^{-1}; Reed and Yuill, 2017) and SLR (0.28–1.66 cm y^{-1}; Pahl, 2017) coincide with vertical marsh edges as the marsh platform is eroded from underneath. This setting thus may require significantly different design or positioning of the reef as compared to those designed for areas with gentle slopes, and less rapid erosion. Ultimately, identifying appropriate locations for reef nature-based coastal defense may require more effort to carefully define appropriate settings, including analyzing short and longer -term environmental conditions to ensure they are supportive of adequate oyster population maintenance and growth, as well as consideration of exposure, shoreline morphology, and local subsidence, SLR and erosion rates.

5. Conclusions

Highly variable and dynamic ecosystems, such as estuaries, provide a challenge when working to restore with nature. While oysters and the reefs they create are considered ideal for coastal defense, their success for nature-based coastal defense depends on their ability to not only stabilize the shoreline, but also the ability of the ecosystem (in this case reef) to be resilient through short and longer-term environmental changes. In this study, the experimental reefs created using native materials failed to reduce shoreline erosion over the short and medium-term. Reef effectiveness in shoreline protection is highly site specific, but some common determinants identified across studies include reef

size, architecture, shoreline slope, inundation duration and local sedimentation (Walles et al., 2016a, b; Morris et al., 2019; Chowdhury et al., 2021; Fivash et al., 2021). Over this study, reef sustainability was at risk from unprecedented low salinity years, which likely resulted in the observed low or no oyster recruitment critical for the long-term survival of the reefs, particularly in a rapidly subsiding area experiencing high rates of SLR.

Continued frequent monitoring (i.e., annual) could provide more insight into the normal variation in reef demography and highlight potential adaptive management opportunities to ensure reef persistence and shoreline protection in this and similar nature-based coastal defense projects. Determining not just oyster population dynamics under historic and current conditions, but also incorporating the effects of short-term environmental variability, and ensuring future conditions are supportive of continued reef growth are critical for selecting locations for the use of oyster reefs in nature-based coastal defense.

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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.

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MKL and BJR conceived the ideas, designed the methodology and analyses. RR and SCLB collected data, ran analyses, and analyzed the data. MKL and SCLB wrote the original draft. All authors contributed critically to the subsequent drafts and gave final approval for publication.

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