

# Restoration of oyster reefs in an estuarine lake: population dynamics and shell accretion

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**ABSTRACT:** Restoration activities inherently depend on understanding the spatial and temporal variation in basic demographic rates of the species of interest. For species that modify and maintain their own habitat such as the eastern oyster *Crassostrea virginica*, understanding demographic rates and their impacts on population and habitat success are crucial to ensuring restoration success. We measured oyster recruitment, density, size distribution, biomass, mortality and *Perkinsus marinus* infection intensity quarterly for 3 yr on shallow intertidal reefs created with shell cultch in March 2009. All reefs were located within Sister Lake, LA. Reefs were placed in pairs at 3 different locations within the lake; pairs were placed in low and medium energy sites within each location. Restored reefs placed within close proximity (<8 km) experienced very different development trajectories; there was high inter-site and inter-annual variation in recruitment and mortality of oysters, with only slight variation in growth curves. Despite this high variation in population dynamics, all reefs supported dense oyster populations ( $728 \pm 102$  ind.  $m^{-2}$ ) and high live oyster biomass ( $>14.6$  kg  $m^{-2}$ ) at the end of 3 yr. Shell accretion, on average, exceeded estimated rates required to keep pace with local subsidence and shell loss. Variation in recruitment, growth and survival drives local site-specific population success, which highlights the need to understand local water quality, hydrodynamics, and metapopulation dynamics when planning restoration.

**KEY WORDS:** Oyster reef restoration · *Crassostrea virginica* · Population demographics · Spatial variability · Temporal variability · Shell accretion · Louisiana · Gulf of Mexico

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## INTRODUCTION

A central tenet of restoration involves the need to ensure adequate conditions for the sustained recruitment, growth and survival of the species or communities of interest. Understanding how populations establish, change and sustain themselves over time requires basic demographic data at different spatial and temporal scales (Schemske et al. 1994, Drechsler & Burgman 2004, Mann & Powell 2007). While these data have been integrated into conservation of rare species and habitats, often through the use of population viability or metapopulation models, they are

less used within the restoration community despite similar information needs (Possingham et al. 2000). In many instances, the basic data to construct such models are lacking for the species or habitat of interest and for the suggested locations, making acquisition of these population data a high priority for developing effective and reliable restoration plans (Schemske et al. 1994, Possingham et al. 2000). With continuing restoration and conservation of habitats on a global scale, combined with the need to ensure efficient and effective restoration activities, there is a real need to integrate these approaches more widely into restoration planning.

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Along the northern coast of the Gulf of Mexico, reefs formed by the eastern oyster *Crassostrea virginica* are one of the few biogenic natural hard habitats in the region. In recent decades, recognition of the contributions of oyster reefs to valuable ecosystem services (Grabowski & Peterson 2007, Scyphers et al. 2011, M. La Peyre et al. 2014a) combined with evidence of a functional decline in shellfish reefs (Beck et al. 2011, Zu Ermgassen et al. 2012) has led to hundreds of small-scale efforts to build or enhance oyster reefs, with mixed results (Schulte et al. 2009, Kennedy et al. 2011, M. La Peyre et al. 2014b). Success of these efforts is dependent on understanding site-specific variation in the range and timing of key physical, chemical and biological factors that control oyster recruitment, growth and survival.

Oysters create and maintain their own habitat via recruitment, growth and mortality, resulting in 2 necessary criteria for successful restoration: sustainability of oyster populations, and sustainability of substrate (Mann & Powell 2007). Predicting sustainability of oyster populations requires a site- and population-specific understanding of recruitment, growth and mortality rates across multiple years; recruitment being marked by infrequent large events, with growth and mortality affected by a myriad of potential factors including water quality, disease, predation and harvesting (Paynter & Burreson 1991, Lenihan & Peterson 1998, Powell et al. 2006, Mann et al. 2009, Soniat et al. 2012, Munroe et al. 2013). Sustainability of substrate is dependent on shell accretion through oyster recruitment and growth, and thus is affected by oyster population dynamics as outlined above, but is also affected by shell loss through reef spreading, subsidence, sedimentation, dissolution, or fragmentation from wave energies or anthropogenic activities (Powell et al. 2006). Estimating shell loss not tied directly to fishery harvest requires a site specific understanding of factors that may affect shell budgets, including interactions of reef characteristics (height, shape) with site specific habitat characteristics (flow, depth, water quality, adjacent habitats).

Reef characteristics (height, shape), reef location (intertidal, subtidal) and habitat variability (water quality, landscape design, hydrodynamics) interact to control oyster populations, with salinity and temperature being 2 of the most important variables. However, comparisons of site-level oyster population dynamics within similar salinity and temperature regimes have demonstrated widely varying results. Puckett & Eggleston (2012) showed that in a small geographic area (20 km<sup>2</sup>), oyster sites varied in their

demographic rates. Similarly, recent restoration projects located in areas deemed suitable based on salinity and temperature regimes have had mixed success, with some sites lacking recruitment and others experiencing high recruitment but 100% mortality (La Peyre et al. 2013a). Other studies have examined how reef characteristics such as reef height, material and adjacent habitats may also affect sustainability of oyster substrate, and ultimately of the reefs themselves (Lenihan 1999, Nestlerode et al. 2007, Gregalis et al. 2008). Factors such as reef location in relation to larval supply or predator abundance can affect settlement densities and mortality rates. Energy and water currents may influence recruitment and growth by affecting larval and food supply as well as influence shell movement. Furthermore, oyster diseases can affect growth and mortality, making it essential to better predict population viability by using models which include hydrodynamics and metapopulation dynamics, and allow for inter-annual variation (Barnes et al. 2007, North et al. 2010, Southworth et al. 2010, Beseres Pollack et al. 2012).

We examined oyster population dynamics on newly created reefs to document (1) inter-site and inter-annual population dynamics of oysters, and (2) the variation in population dynamics and shell accretion in relation to location and site energy within one estuarine lake area. Specifically, we quantified oyster recruitment, density, size distribution, biomass, mortality, *Perkinsus marinus* infection, and shell accretion on 6 newly created reefs over 3 yr. Understanding how oyster population dynamics may vary within close proximity and the effects on oyster reef development are critical for properly selecting sites for restoration, and ensuring long-term sustainability of these resources.

## MATERIALS AND METHODS

### Study site

The study was conducted at Sister (Caillou) Lake, located in Terrebonne Parish, Louisiana (29° 14' 11.09" N, 90° 55' 16.48" W) (Fig. 1). Sister Lake is primarily an open-water, mesohaline system with a mean ( $\pm$ SE) tidal range of 0.3  $\pm$  0.03 m (National Geodetic Vertical Datum). Water levels are driven primarily by wind events; dominant winds are typically from the southeast, except during the winter when northerly winds accompany cold fronts. Daily mean ( $\pm$ SE) water temperature and salinity in the

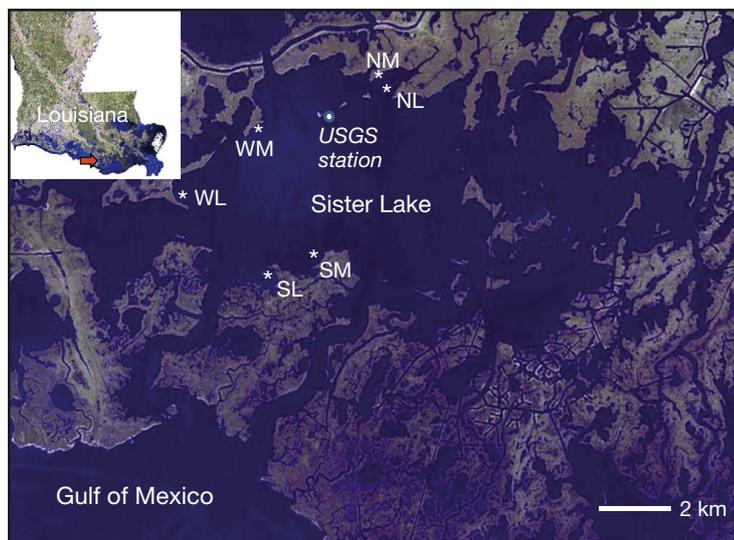


Fig. 1. Locations of 6 reefs created using loose disarticulated shell in Sister Lake, Terrebonne Parish, Louisiana. Based on location and shoreline exposure, reefs were designated as: north medium energy reef (NM), north low energy reef (NL), west medium energy reef (WM), west low energy reef (WL), south medium energy reef (SM), south low energy reef (SL)

study area between 1997 and 2009 were  $23.5 \pm 1.9^\circ\text{C}$  and  $12.0 \pm 2.8$ , respectively (from USGS recorder 07381349). Sister Lake has served as a state public oyster seed reservation since 1940, and oyster beds are abundant within the system (LDWF 2011). Public oyster seed reservations in Louisiana are areas designated by the state for the development of wild-oyster seed stocks. Seed reserves are publically harvested during very short (typically 1 to 5 d) periods in late fall only during years designated by the state management agency.

Three study locations were chosen in Sister Lake, along the north end, south end, and west side of the Lake (<8 km apart; Fig. 1). Within each study location, paired shorelines were identified as having either 'low' or 'medium' energy exposure, based on a combination of wave fetch, direction and wind speeds (M. La Peyre et al. 2014a). In March 2009, fringing reefs ( $25 \times 1 \times 0.7$  m; 1 to 1.5 m water depth; <50 m from shoreline) were created using shucked oyster shell placed by a bucket dredge (3 locations  $\times$  2 energies = 6 reefs), which we designated as 'north medium energy' (NM), 'north low energy' (NL), 'west medium energy' (WM), 'west low energy' (WL), 'south medium energy' (SM) and 'south low energy' (SL) reefs. As the gulf coast is microtidal, intertidal reefs here indicate reefs that are exposed on an irregular basis, and not due to regular tidal action. In

general, reef exposure occurs during winter and fall months when cold fronts push water out of the estuaries. Reefs were sampled for water quality and on-reef oyster population dynamics including oyster recruitment, density, size distribution, biomass, mortality and *Perkinsus marinus* infection prevalence and intensity from March 2009 through March 2012.

### Environmental variables

Water quality variables were taken at each site concurrent with oyster sampling. Discrete salinity, temperature ( $^\circ\text{C}$ ) and dissolved oxygen ( $\text{mg l}^{-1}$ ) were measured with a YSI 556 (YSI Inc.). For measurement of chlorophyll *a* (chl *a*), total particulate matter (TPM), particulate organic matter (POM) and particulate inorganic matter (PIM), two 250 ml water samples were collected approximately 0.5 m from the surface in dark Nalgene bottles, placed on ice and returned to the lab for sampling fol-

lowing standard methods (Eaton et al. 2005). Under dim lights, a 50 ml water sample was filtered through a Whatman 47 mm glass fiber filter. The filter was placed in a labeled foil packet and stored at  $-20^\circ\text{C}$  until processing following EPA Method 445.0 for chl *a*. A 150 ml water sample was filtered through a pre-weighed Whatman 47 mm glass fiber filter, washed 3 times with 20 ml distilled  $\text{H}_2\text{O}$ , dried at  $105^\circ\text{C}$  for 1 h and then weighed. TPM was calculated by subtracting the filter weight from the dried weight (mg). The filter was then placed in a muffle furnace at  $550^\circ\text{C}$  for 30 min and weighed a third time. POM was calculated by subtracting the ashed filter weight (PIM) from the TPM weight (Taras 1971). Continuous salinity, temperature ( $^\circ\text{C}$ ), wind speed ( $\text{m s}^{-1}$ ) and wind direction (degrees) were also obtained from the USGS data recorder located in Sister Lake (USGS 07381349; Fig. 1). A survey of reef top elevation using an electronic total station (TopCon GTS-220) was conducted once in November 2009 at all 6 sites.

Salinity, temperature, chl *a*, TPM and POM were examined for normality and homogeneity of variance, and transformed as required. Differences in these environmental variables among reef location and wave energy were analyzed with a general linear model (GLM) with 2 fixed factors (location, energy) and a random factor (sample date). When significant results were obtained ( $p < 0.05$ ), the mul-

multiple-comparison Tukey's test was used to examine differences. All statistical analyses were done using Minitab® release 14 statistical software (Minitab). Data are reported as mean  $\pm$  SE.

### Reef sampling

Recruitment was quantified from April through October 2009, 2010 and 2011. Four unglazed clay tiles ( $0.31 \times 0.31$  m) were haphazardly placed on each reef. Tiles were laid horizontally on top of the reef and kept in place by attaching them to PVC pipes buried in the substrate. Every 4 to 6 wk, tiles were collected and replaced with new, clean tiles. Sampled tiles were returned to the laboratory where they were air dried for 1 to 2 d and gently rinsed to remove sediment. Spat were counted on both sides of the tiles using a magnifying glass for a total of 816 counts (4 tiles  $\times$  2 sides = 8 counts  $\times$  6 reefs  $\times$  17 dates). Counts were scaled to spat  $m^{-2}$ . Only months with mass spawning events (May, September and October 2009, August and October 2010, April and May 2011) were used for the statistical analyses that were done as described earlier with a GLM with 2 fixed factors (location, energy) and a random factor (sample date).

From June 2009 through March 2012, 3 haphazard samples of approximately  $0.25 \times 0.25$  m and a depth of 0.1 m were taken from each reef every 3 mo for a total of 216 samples (3 samples  $\times$  6 reefs  $\times$  12 sampling times). Samples were removed by hand from the reef, placed in a mesh bag (3 mm), stored on ice and processed within 72 h to determine oyster density, size distribution, biomass, mortality and *Perkinsus marinus* infection intensity as described below.

All live and recently dead oysters in each sample were counted, and their shell height measured with a Vernier caliper (Scienceware Bel-Art products;  $\pm 0.1$  mm). Counts were scaled to no. ind.  $m^{-2}$  based on size class (spat:  $<25$  mm; seed: 25 up to 75 mm; market:  $\geq 75$  mm). The effects of location and energy on the density of each size class were analyzed with a GLM with 2 fixed factors (location, energy) and a random factor (sample date). Total oyster density analyses were calculated by including only seed and market size oysters to diminish the effect of recruitment peaks on density. From March 2010 to March 2012, the whole oyster wet weight (shell + tissue) of all live oysters contained in the quarterly sampled trays was recorded, and weights were scaled to kg of live whole oyster wet weight per reef square meter. Biomass was analyzed with a GLM with 2 fixed factors (location, energy) and a random factor (sample date).

Oysters from the August 2010 cohort were selected to estimate on-reef oyster growth by site. This cohort was selected for growth rate determination because it had high survival during the first year, and it was distant in time from the September 2009 and May 2011 spawning events, differentiating their sizes from previous and later recruitments (see the Appendix). For each location, shell height data for the low and medium wave energy sites were combined to increase the sample size because of the reduced number of oysters in the older classes; while this may overlook some site-specific differences in growth, there is no reason to suspect large differences in food availability (i.e. chl *a*, POM) that would affect growth rates between sites within a location. Flow patterns may vary at each site based on their location, however we assumed that food was not limiting even under the lowest flow conditions. The selected shell heights of the August 2010 cohort from the west, north and south reefs were represented versus oyster age (*x*), and the age-to-size relationship was estimated with a quadratic equation.

Quarterly mortality was calculated by dividing the number of recently dead oysters by the sum of live and recently dead oysters in the sample. Recently dead oysters were defined as oysters that were thought to have died since the previous sampling based on fouling criteria such as algae growth, size of barnacles inside the shell, and on comparisons to a reference bag of oysters killed during the previous sampling.

Cumulative mortality (CM) in the 2009 cohort was estimated by considering the total number of spat recruited in May, September and October 2009 ( $Live_{t_0}$ ), and the number of live oysters in the range of 18 to 65 mm in June 2010 ( $Live_{t_1}$ ), 69 to 95 mm in June 2012 ( $Live_{t_2}$ ) and 100 to 130 mm in March 2012 ( $Live_{t_3}$ ) (see the Appendix). Cohort analyses were conducted following Haddon (2011). Cumulative mortality of the ~1, 2 and 3 yr old 2009 cohort was calculated using the following equations:

$$CM1yr = (Live_{t_0} - Live_{t_1})/Live_{t_0} \quad (1)$$

$$CM2yr = (Live_{t_0} - Live_{t_2})/Live_{t_0} \quad (2)$$

$$CM3yr = (Live_{t_0} - Live_{t_3})/Live_{t_0} \quad (3)$$

The same calculations were used for the 2010 cohort for a 2 yr time frame. In the 2010 cohort,  $Live_{t_0}$  corresponded to the oysters recruited in August and October 2010. The number of oysters reaching ~1 and 2 yr old was calculated as the number of live oysters in the range of 22 to 72 mm in June 2011, and 62 to 102 mm in March 2012 (see the Appendix). Comparisons of cumulative mortalities (CM1yr, CM2yr

and CM3yr) among reefs for the 2009 and 2010 cohorts were run separately by cohort, using chi-squared analysis.

A total of 10 oysters per reef and sampling time were processed to determine *P. marinus* infection intensity using the whole-oyster procedure described by Fisher & Oliver (1996) and modified by La Peyre et al. (2003). Infection intensity of individual oysters was reported as number of parasites per gram of oyster tissue wet weight. Comparisons of parasite prevalence (i.e. % of oysters infected) and percentages of infected oysters in each intensity category (parasites  $g^{-1}$  wet oyster tissue, light: 1 to <10 000; moderate: 10 000 to 500 000; heavy: >500 000) among reefs were performed with a chi-squared test. *P. marinus* body burden was analyzed with a GLM with 2 fixed factors (location, energy) and a random factor (sample date).

Shell accretion was estimated using data from recently dead oysters and relationships of shell wet weight (SWW, g; no meat) and shell height (SH, mm) based on the following:

$$SWW = 0.0005 \times SH^{2.6898} \quad (4)$$

( $R^2 = 0.7$ ,  $n = 228$ , SH range: 29–99 mm)

SWW of all live oysters in March 2010, March 2011 and March 2012, and SWW from all recently dead oysters as defined above (quarterly mortality) from each quarterly sampling were added to determine annual shell accretion (SA,  $g\ m^{-2}\ yr^{-1}$ ) using the following equation:

$$SA_t = Jun_{RDt} + Sep_{RDt} + Dec_{RDt} + Mar_{RDt} + Mar_{LIVEt} - Mar_{LIVEt-1} \quad (5)$$

where  $SA_t$  = shell accretion at time  $t$  (units of 1 yr),  $Jun_{RDt}$  = SWW of oysters dead between March and June of year  $t$ ,  $Sep_{RDt}$  = SWW of oysters dead between June and September of year  $t$ ,  $Dec_{RDt}$  = SWW of oysters dead between September and December of year  $t$ ,  $Mar_{RDt}$  = SWW of oysters dead between December and March of year  $t$ ,  $Mar_{LIVEt}$  = SWW of live oysters on-reef in March of year  $t$  and  $Mar_{LIVEt-1}$  = SWW of live oysters on-reef in March of year  $t - 1$ .

Reef height and reef footprint were compared between March 2009 and March 2012. Reef height was calculated by measuring depth to the water bottom adjacent to the reef and at the top of the reef at 3 locations, and determining the difference. Reef footprint was outlined using a GPS (Garmin), by walking the edge of the reef (based on the presence of solid shell substrate to identify reef edges). The difference between final and initial dimensions was used to calculate change in reef footprint and overall reef volume.

## RESULTS

### Environmental variables

Discrete temperature sampling indicated no significant differences across sites; salinity differed significantly by site but not by energy level, with decreasing salinity associated with increasing distance from the Gulf of Mexico (Table 1, Fig. 2). Dissolved oxygen, TPM, POM and chl *a* concentrations differed significantly by site and energy level, but with no sig-

Table 1. Mean  $\pm$  SE (range in parentheses) of discrete water quality samples collected at each site during each sample event ( $N = 627$ ). Lowercase superscript letters indicate significant differences between sites (Tukey's HSD,  $p < 0.05$ ). See Fig. 1 for site location descriptions. TPM: total particulate matter; POM: particulate organic matter

Site	Temperature (°C)	Dissolved oxygen (mg l <sup>-1</sup> )	Salinity	Secchi depth (cm)	TPM (mg l <sup>-1</sup> )	POM (mg l <sup>-1</sup> )	Chl <i>a</i> (µg l <sup>-1</sup> )
WM	23.8 $\pm$ 0.8 (9.6–36.0)	8.1 $\pm$ 0.2 <sup>ab</sup> (4.5–15.9)	8.9 $\pm$ 0.5 <sup>b</sup> (1.4–19.9)	40.9 $\pm$ 1.4 <sup>b</sup> (13.0–74.0)	36.0 $\pm$ 2.5 <sup>bc</sup> (8.7–158.7)	9.3 $\pm$ 0.4 <sup>bc</sup> (1.3–30.7)	16.3 $\pm$ 0.6 <sup>ab</sup> (1.7–35.6)
WL	23.6 $\pm$ 0.9 (10.1–34.4)	7.9 $\pm$ 0.3 <sup>ab</sup> (4.2–16.2)	10.1 $\pm$ 0.6 <sup>b</sup> (1.6–17.4)	37.2 $\pm$ 1.8 <sup>b</sup> (9.1–77.0)	52.8 $\pm$ 7.4 <sup>a</sup> (7.3–296.0)	11.6 $\pm$ 1.0 <sup>a</sup> (1.0–43.3)	16.8 $\pm$ 0.9 <sup>a</sup> (2.2–47.9)
NM	24.3 $\pm$ 0.7 (10.0–34.7)	7.8 $\pm$ 0.2 <sup>bc</sup> (2.8–12.6)	10.2 $\pm$ 0.5 <sup>b</sup> (1.2–20.9)	40.8 $\pm$ 1.6 <sup>b</sup> (14.0–80.0)	42.5 $\pm$ 4.3 <sup>ab</sup> (2.0–380.0)	11.2 $\pm$ 0.7 <sup>ab</sup> (1.3–51.3)	13.8 $\pm$ 0.5 <sup>bc</sup> (1.8–36.0)
NL	24.6 $\pm$ 0.9 (10.0–36.1)	7.8 $\pm$ 0.2 <sup>bc</sup> (4.6–12.8)	10.3 $\pm$ 0.6 <sup>b</sup> (1.1–21.1)	41.9 $\pm$ 2.1 <sup>b</sup> (12.8–76.0)	33.1 $\pm$ 3.1 <sup>bc</sup> (4.7–141.3)	10.1 $\pm$ 0.8 <sup>bc</sup> (1.3–32.0)	12.9 $\pm$ 0.8 <sup>c</sup> (2.4–37.1)
SM	23.6 $\pm$ 0.8 (10.5–33.3)	8.0 $\pm$ 0.2 <sup>ab</sup> (4.5–17.3)	13.2 $\pm$ 0.6 <sup>a</sup> (3.6–23.8)	49.5 $\pm$ 1.9 <sup>a</sup> (15.0–86.0)	27.8 $\pm$ 2.1 <sup>c</sup> (2.7–142.0)	9.1 $\pm$ 0.7 <sup>c</sup> (0.4–50.7)	14.1 $\pm$ 0.7 <sup>abc</sup> (4.5–55.2)
SL	23.4 $\pm$ 0.9 (10.9–32.8)	7.6 $\pm$ 0.3 <sup>c</sup> (1.5–15.9)	13.1 $\pm$ 0.6 <sup>a</sup> (3.2–24.4)	45.7 $\pm$ 1.9 <sup>a</sup> (11.0–73.0)	26.8 $\pm$ 2.4 <sup>c</sup> (5.3–100.0)	8.6 $\pm$ 0.6 <sup>c</sup> (0.7–28.0)	14.0 $\pm$ 0.9 <sup>abc</sup> (1.1–41.0)

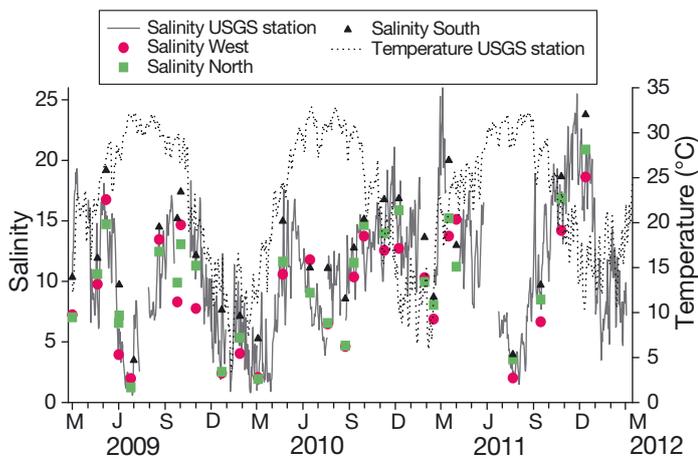


Fig. 2. Mean daily temperature and salinity in Sister Lake during the studied period, March 2009 to 2012. Data taken from the Louisiana Department of Wildlife and Fisheries/USGS continuous data recorder 07381349, Caillou Lake southwest of Dulac, LA. Graph also includes salinity in the west, north, and south locations measured every 4 to 6 wk using a YSI meter

nificant trend (Table 1). Reefs were more likely to be exposed during low water events in the fall/winter months (Fig. 3). Reef tops were exposed annually from 11% (NL, NM), and 13% (WL, WM) to as much as 18% (SL) and 19% (SM) of the time in 2009; reef elevations were not measured in subsequent years. Mean daily winds ranged from 4.7 to >30 km h<sup>-1</sup>, and were predominantly southern winds during the period of this study (Fig. 3).

**Reef sampling**

Recruitment occurred throughout the 3 yr of the study (Fig. 4). Spat were observed in 94% of the tile deployments in the south and west sites and 65% of the north sites, and were characterized by mass spawning events evidenced by a minimum of 2 peaks of spat density each year (i.e. May, September and October 2009; August and October 2010; April and May 2011); most of the months during the spawning season had low recruitment densities (<100 spat m<sup>-2</sup>). When comparing recruitment densities for the months with mass spawning events, there was a significant site by energy interaction for recruitment ( $F_{2,253} = 44.45, p < 0.001$ ). Both south sites had significantly higher recruitment than both west sites, which had significantly

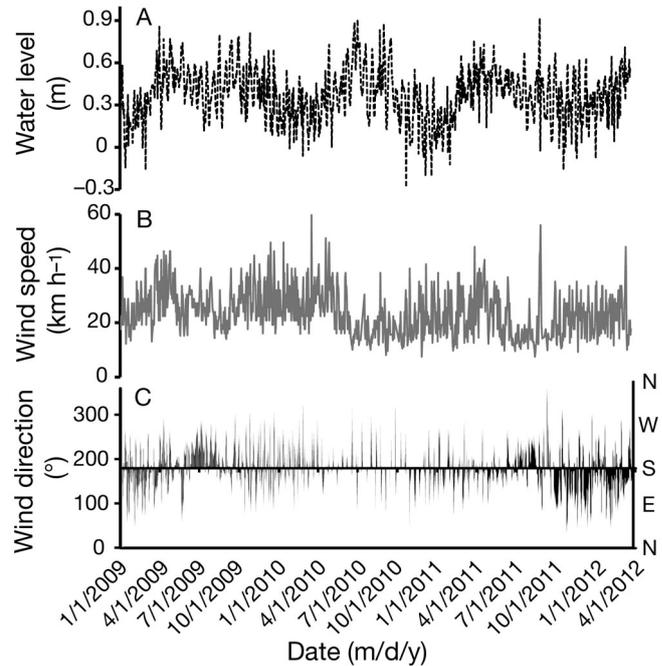


Fig. 3. (A) Daily water level (m; relative to National Geodetic Vertical Datum of 1929), (B) daily wind speed (km h<sup>-1</sup>) and (C) direction (degrees on left axis, cardinal directions on right axis) during the study period. All data were obtained from the US Geological Services recorder in Sister Lake (LDWF/USGS 07381349, Caillou Lake southwest of Dulac, LA)

higher recruitment than both north sites. The interaction was due to higher recruitment in the low energy compared with the medium energy in the north location (Table 2).

Inter-annual variation in recruitment density and timing was also evident. Specifically, averaged across all sites and all recruitments within a year, recruitment in 2009 ( $17\,361 \pm 6\,959$  spat m<sup>-2</sup>) was sig-

Table 2. *Crassostrea virginica*. Mean ( $\pm$ SE) oyster spat recruitment densities (no. m<sup>-2</sup>) for the months with mass spawning events, and overall mean densities of spat, seed and market-size oysters at reef sites in Sister Lake, Louisiana, for the study period March 2009 to May 2012. Lowercase superscript letters indicate significant differences between sites (GLM,  $p < 0.05$ ). See Fig. 1 for site location descriptions

Site	Spat density (mass-spawning)	Overall spat density	Overall seed density	Overall market-size oyster density
WM	1809 $\pm$ 326 <sup>b</sup>	729 $\pm$ 148 <sup>b</sup>	501 $\pm$ 70 <sup>a</sup>	23 $\pm$ 7 <sup>a</sup>
WL	3935 $\pm$ 997 <sup>b</sup>	630 $\pm$ 71 <sup>b</sup>	380 $\pm$ 44 <sup>a</sup>	17 $\pm$ 4 <sup>ab</sup>
NM	160 $\pm$ 36 <sup>d</sup>	121 $\pm$ 28 <sup>d</sup>	211 $\pm$ 34 <sup>b</sup>	13 $\pm$ 3 <sup>ab</sup>
NL	793 $\pm$ 180 <sup>c</sup>	240 $\pm$ 53 <sup>c</sup>	414 $\pm$ 52 <sup>a</sup>	26 $\pm$ 8 <sup>a</sup>
SM	9557 $\pm$ 1956 <sup>a</sup>	1913 $\pm$ 513 <sup>a</sup>	606 $\pm$ 92 <sup>a</sup>	6 $\pm$ 1 <sup>b</sup>
SL	7879 $\pm$ 1737 <sup>a</sup>	642 $\pm$ 151 <sup>b</sup>	505 $\pm$ 52 <sup>a</sup>	22 $\pm$ 5 <sup>a</sup>

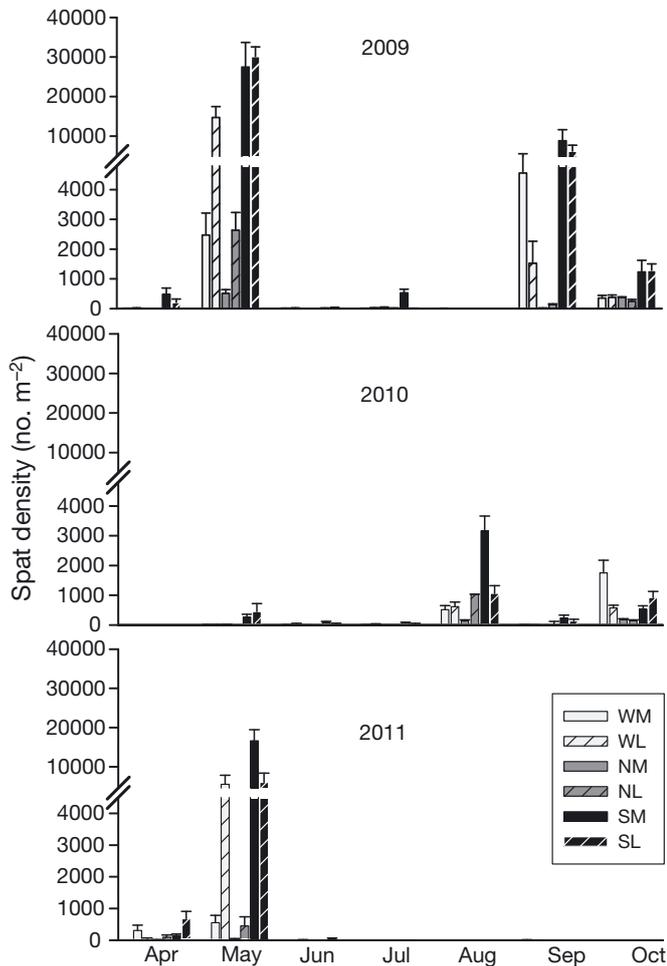


Fig. 4. *Crassostrea virginica*. Mean (+SE) density of recruits on tiles placed on the 6 reefs every 4 to 6 wk during April to October of 2009, 2010 and 2011. See Fig. 1 for site location descriptions

nificantly higher than in 2010 and 2011 ( $1616 \pm 580$  and  $5111 \pm 2614$  spat  $m^{-2}$ , respectively).

Oyster spat (<25 mm) was present on the reefs at all sampling times, and increases in spat densities followed the recruitment numbers recorded with the tiles method. Seed oysters were present on all reefs beginning in September 2009, and peaks tended to lag 3 mo behind recruitment events. Market size oysters ( $\geq 75$  mm) were measured beginning as early as December 2009, but did not become established until December 2010, at which point densities increased through time at all sites. By March 2012, market size oyster density ranged between 16 and 135 ind.  $m^{-2}$  (Fig. 5).

There was significant location by energy interaction for on-reef spat, seed and market size density. For spat, all south and west locations had higher spat density compared to the northern locations, which

differed from one another, with the NL reef having higher spat density than the NM (Table 2). Southern locations differed from one another with the spat density in the SM reef significantly greater than in the SL reef (Table 2). For seed, only the NM reef differed from all other reefs with lower seed density (Table 2). For market size oysters, the SM reef was significantly lower than all the others, except for the

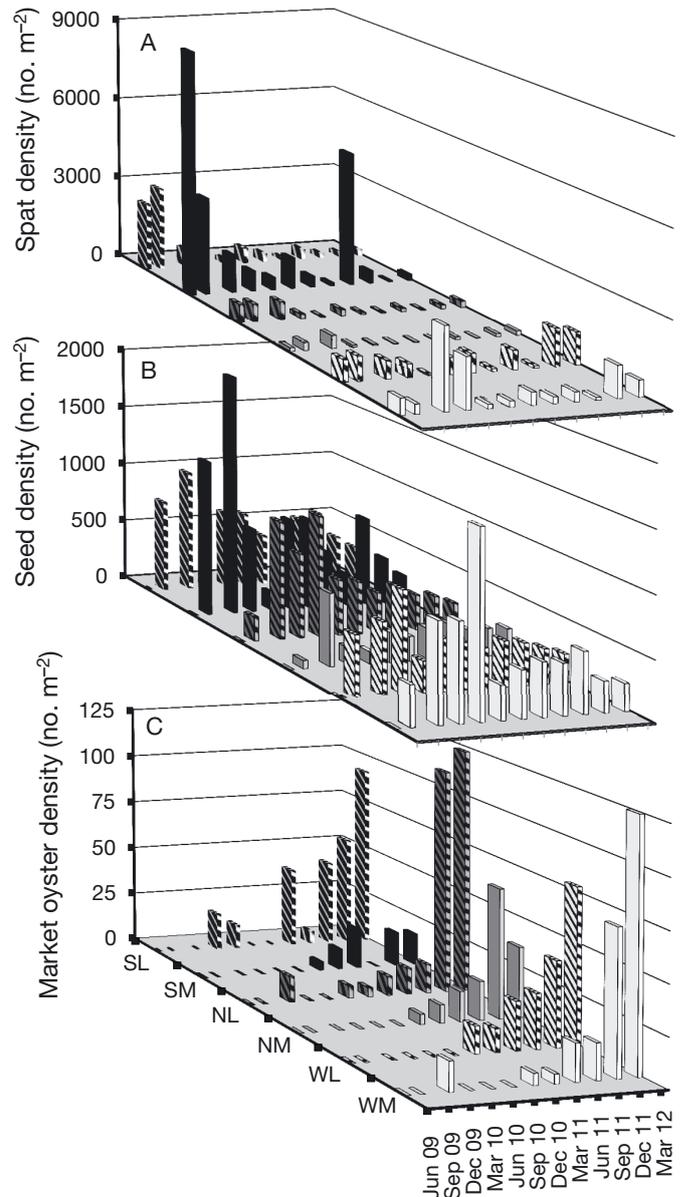


Fig. 5. *Crassostrea virginica*. Mean density of (A) spat (<25 mm), (B) seed (25 up to 75 mm) and (C) market size ( $\geq 75$  mm) oysters on 6 reefs created in March 2009 and monitored quarterly from June 2009 to March 2012. Note that y-axes have different scales for the different size classes. See Fig. 1 for site location descriptions

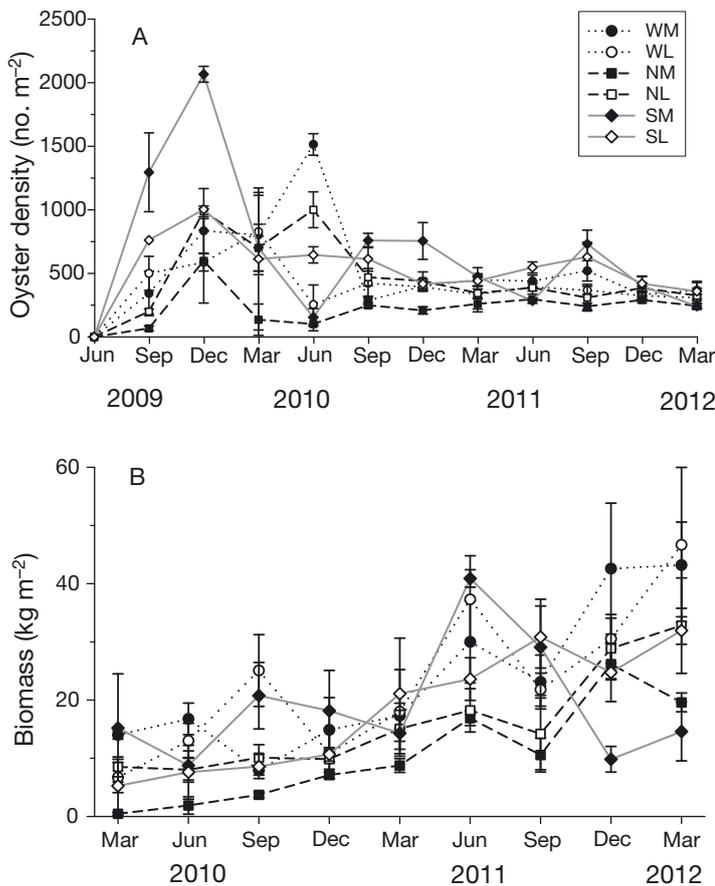


Fig. 6. *Crassostrea virginica*. Mean ( $\pm$ SE) (A) oyster density ( $\geq 25$  mm shell height, i.e. seed and market-size oysters) measured quarterly on 6 reefs created in March 2009 and monitored until March 2012 and (B) biomass (live whole oyster wet weight per area, for all sizes combined, in kg m<sup>-2</sup>) monitored from March 2010 until March 2012. See Fig. 1 for site location descriptions

WL and NM reefs, which did not differ from any reef (Table 2). Comparisons of total oyster density (seed + market) over time showed that density appeared to only vary following periods of high recruitment (Fig. 6A).

Except for SM, all reefs increased in live oyster biomass from March 2010 through March 2012 (Fig. 6B). SM increased initially, but the reef population experienced a significant decline in the last quarter of 2011. There was a significant effect of location ( $F_{2,134} = 11.79$ ,  $p < 0.0001$ ) on overall live oyster biomass accretion, with west reefs having higher biomass than south and north reefs. No differences by energy level were detected.

Growth curves described the size-at-age relationship for the August 2010 oyster cohort at the 3 sites ( $R^2 > 0.78$ ; Fig. 7, Appendix). The estimated SH of differently aged oysters from all sites were  $28.2 \pm$

1.0 mm (3 mo),  $40.5 \pm 1.9$  mm (6 mo),  $51.9 \pm 1.0$  mm (9 mo),  $62.3 \pm 0.8$  mm (12 mo),  $71.9 \pm 0.8$  mm (15 mo), and  $80.4 \pm 0.5$  mm (18 mo).

In the 2009 cohort, the percentage of oysters that died before reaching 1 yr differed among all reefs, and ranged between  $98.7 \pm 0.7\%$  at the SM reef and  $50.9 \pm 6.4\%$  at the NL reef (Fig. 8). There were no significant differences among reefs in cumulative mortality in Year 2, with greater than 95% mortality at all reefs. By Year 3, no oysters from the 2009 cohort survived at the SM and NM reefs, and less than 1% survived at the remaining 4 reefs. In the 2010 cohort, there was a significant difference by site and energy in cumulative mortality in Year 1 and Year 2 (Fig. 8). Cumulative mortality in Year 1 ranged from approximately 10 to 95%, with north reefs having the lowest mortality. In March 2012, SM reef had highest cumulative mortality ( $99.1 \pm 0.6\%$ ), which was significantly higher than WL ( $93.0 \pm 0.7\%$ ), and SL ( $91.5 \pm 1.0\%$ ) reefs. Cumulative mortality was lowest and similar between NM ( $78.4 \pm 8.4\%$ ), WM ( $74.4 \pm 5.5\%$ ), and NL ( $59.9 \pm 9.5\%$ ) reefs.

Differences in *P. marinus* infection prevalence (data not shown) among reefs were not detected, with percentages of infected oysters ranging between 54 and 75%. Similarly, *P. marinus* infection intensity did not vary between reefs, with most of the infected oysters (83 to 100%) in the light intensity category (1 to <10 000 parasites g<sup>-1</sup> wet oyster tissue). An effect of location or energy on the body burden was not detected.

Annual shell accretion on reefs ranged from a loss of shell to a high of  $13\,410$  g m<sup>-2</sup> yr<sup>-1</sup> (Table 3). Accre-

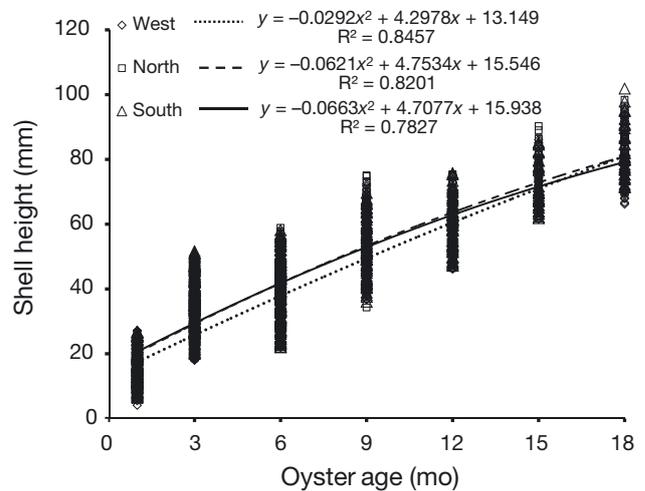


Fig. 7. *Crassostrea virginica*. Oyster growth curves at north, south and west reefs, with best fit models to estimate the age to shell height relationship at each location

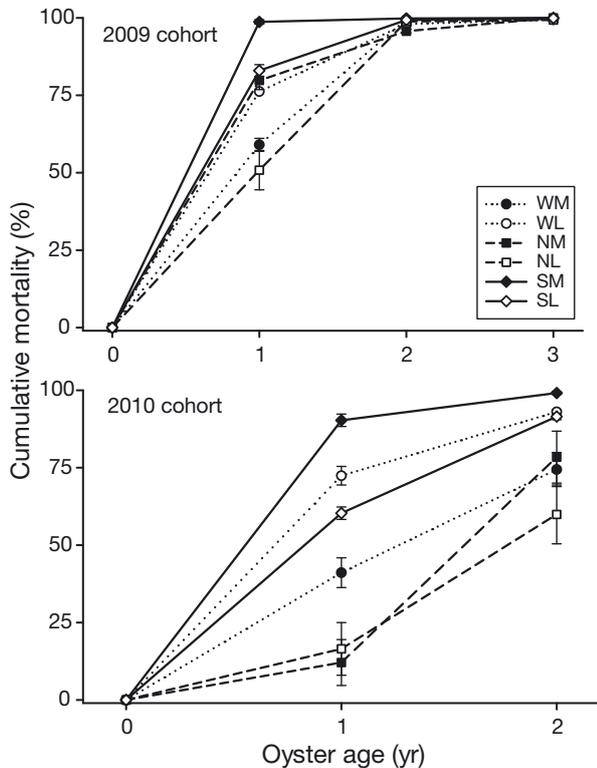


Fig. 8. Cumulative mortality (%) 1, 2 or 3 yr after recruitment of the 2009 and 2010 cohorts in the 6 reefs using data from on-reef shell height measurements, shown in the Appendix. See Fig. 1 for site location descriptions

Table 3. Estimation of shell accretion ( $\text{g m}^{-2} \text{yr}^{-1}$ ) for the 6 reefs (see Fig. 1 for site location descriptions) from March 2009 to March 2012

	WM	WL	NM	NL	SM	SL
Mar 2009–2010	9358	6277	3766	6778	12869	12044
Mar 2010–2011	218	3262	7765	7329	2611	3054
Mar 2011–2012	13410	7599	2205	9428	-114	5002

Table 4. Area and height of the 6 reefs (see Fig. 1 for site location descriptions), 2 mo after their creation (May 2009) and at the end of the study (March 2012)

	WM	WL	NM	NL	SM	SL
<b>Area (<math>\text{m}^2</math>)</b>						
May 2009	45	38	36	41	38	37
Mar 2012	234	132	88	91	264	130
<b>Height (m)</b>						
May 2009	0.61	0.33	0.39	0.37	0.35	0.45
Mar 2012	0.37	0.19	0.21	0.18	0.18	0.28

tion varied by year and site, with no detectable pattern.

During the 3 yr post-construction, the reefs experienced a 2- to 7-fold increase in reef area and a 28 to 51 % loss of reef height (Table 4). Assuming rectangular reef shapes, total reef volumes more than doubled at all west and south sites, and increased slightly at both northern sites.

## DISCUSSION

Inter-annual and inter-site variation affected the trajectories of individual reef development, with reefs exhibiting different patterns of recruitment and survival over the 3 yr study period. Reefs closest to the Gulf of Mexico experienced the highest recruitment and mortality while reefs furthest from the Gulf had the lowest recruitment, but highest survival rates. These differences may be attributed to a small salinity gradient across the study area, and possible unmeasured differences in food availability and hydrodynamics. Despite the differences in recruitment and survival between reefs, all reefs had a similar density and population structure at the end of the 3 yr, suggesting density-mediated outcomes.

Despite high inter-site and inter-annual variation in oyster population dynamics, all 6 reefs supported dense, multiple-size-class oyster populations 3 yr after reef creation. Average density of all sizes combined at the end of the study was  $728 \pm 102 \text{ ind. m}^{-2}$  (range 203 to 2586  $\text{ind. m}^{-2}$ ), with an average of 80 market size  $\text{ind. m}^{-2}$ . Reefs supported densities similar to those reported in other regions, including reefs in Florida, North Carolina, South Carolina and Delaware (Tolley et al. 2005, Taylor & Bushek 2008, Hadley et al. 2010, Puckett & Eggleston 2012). For example, Hadley et al. (2010) reported that the density of oysters in a 3 yr old South Carolina reef ranged from 1500 to 2900  $\text{ind. m}^{-2}$ , and for large oysters (>60 mm), density was estimated at 25 to 40  $\text{ind. m}^{-2}$ . The lower density of large oysters after 3 yr is likely explained by slower growth rates along the east coast compared to the Gulf Coast (Kraeuter et al. 2007).

Our study reefs exceeded thresholds identified for assessing success of restored oyster reefs, and over the 3 yr of the study met the abundance biological reference point ( $dN/dt \geq 0$ , where  $N$  = no. of oysters) suggested by Powell & Klinck (2007), and exceeded values of oyster density that have been suggested as a benchmark for reef success (i.e. 10  $\text{ind. m}^{-2}$ ; Powers et al. 2009). Variation in oyster density (i.e. Fig. 6A), however, indicates that reefs did not meet the

requirement of equivalent or increasing oyster abundance ( $dN/dt \geq 0$ ) across all time periods, and clearly, the time frame of measurement could affect determination of reef success. For example, while oyster density increased during Year 1, Year 2 (2010) had low recruitment and salinity, and most of the reefs decreased in population density during that year. However, using abundance of oysters may not be the best approach on new reefs, as live oyster biomass increased continuously across all reefs and years with the exception of one reef (SM) that lost biomass during the last 6 mo of sampling, most likely because of scattering of reef shells and associated loss of reef height (Table 2) and elevated mortality (Fig. 8).

Environmental conditions in the northern Gulf of Mexico provide for fast growth rates compared to reported rates along the east coast (Kraeuter et al. 2007). There are few studies of oyster growth rates on the bottom of oyster beds or directly on reefs, and most of the information about oyster growth has been obtained with animals maintained in off-bottom conditions (Kraeuter et al. 2007). Our on-reef data collection and cohort analyses estimated shell height of a 3 mo old oyster to be 28 mm, 62 mm at 12 mo, and 80 mm at 18 mo in an area of moderate salinity (mean  $\sim 13$ ). Harvest size ( $\geq 75$  mm) under this on-bottom condition was reached 18 mo after setting, sooner than the more than 2 yr reported in on-bottom higher salinity water studies in the Chesapeake Bay (Harding et al. 2010, Paynter et al. 2010, Southworth et al. 2010) or 4 to 5 yr in Delaware Bay (Kraeuter et al. 2007), but later than reported in off-bottom culture in similar salinity waters in Louisiana (12 mo; Leonhardt 2013), and corroborating previous conclusions of more rapid oyster growth in the northern Gulf of Mexico than on the east coast (Kraeuter et al. 2007). The elevated densities and fast growth produced oyster biomass between 14.6 and 46.7 kg m<sup>-2</sup> after 3 yr. These values exceed the range of values previously used to determine ecological and fishery success of reefs ( $>0$  to 10 kg m<sup>-2</sup>; Powers et al. 2009)

Recruitment varied significantly between reef locations, with higher recruitment associated with the higher salinity site (SM, SL), which was also more exposed to the Gulf of Mexico. It is possible that the relatively small difference in salinity between the southern site (mean  $\sim 13$ ) and the northern site (mean  $\sim 10$ ) could explain some of the difference in recruitment between locations, as a salinity of 10 is the minimum required for larval metamorphosis (Davis 1958). Unmeasured factors such as hydrodynamics combined with metapopulation dynamics, however, cannot be excluded as additional causes of differ-

ences in population dynamics between sites. A field and modeling study in Alabama suggested that within a shallow estuary, larval supply and retention near spawning areas may explain observed gradients in oyster populations (Kim et al. 2010). In contrast, mean dispersal distance in North Carolina for a 21 d larval duration ranged from 5 to 40 km (Puckett et al. 2014). It is difficult to extrapolate results from these studies to other water bodies without local hydrodynamic models, which could track local larval supply, but also potential larval recruitment from adjacent bays.

Regardless of inter-site recruitment patterns which remained consistent throughout the 3 yr study (south site  $>$  west  $>$  north), inter-annual variability was high, with almost no recruitment observed in 2010. This low recruitment in 2010 matches other studies across the coast (LDWF 2011, La Peyre et al. 2013b), and may be normal variation in oyster population dynamics in this region, as recruitment is well-known to vary enormously; however, we lack long-term quantitative data for this region. While 2010 was the year of a massive oil spill off the Louisiana coast (Deepwater Horizon), no oil was reported in our study estuary (J. La Peyre et al. 2014), and this event also followed an extended period of low salinity ( $<5$ ) from January through April 2010 that did not occur in any of the other years (Fig. 2) and might have interfered with normal gonadal development (Butler 1949).

While all reefs experienced high overall recruitment, cohort survival to 2 yr of age was low (0.2 to 4.3% of the 2009 cohort, 0.9 to 40.1% of the 2010 cohort; Fig. 8), with most mortality occurring with smaller size classes (spat mortality = 60 to 85% of the quarterly mortality) similar to results of other studies in different environments (Finucane & Campbell 1968, Newell et al. 2000). An early study reported that typical annual mortality of  $\geq 1$  yr old oysters in Louisiana is between 50 to 70% (Mackin 1959). Mortalities reported in the present study were elevated compared with other population studies, which found survival of 2 yr old oysters to range from 25 to 59% over a 9 yr period in the Chesapeake Bay (Mann et al. 2009), and 2 yr cohort survival in North Carolina no-take reserves to range between 20 and 50% (Puckett & Eggleston 2012). Although mortality rates may approach 100% under certain adverse environmental conditions (i.e. 2009 cohort mortality), the sustainability of the populations in Sister Lake is ensured by the reproductive capabilities of oysters in the area, even in years of low spatfall (i.e. 2010 spawning) and as long as the habitat is not limited as a consequence of burial or dredging of the reefs. Nei-

ther predation by oyster drills or *P. marinus* infection intensities (<10 000 parasites  $g^{-1}$  of oyster tissue) likely explain the observed mortality rates due to the moderate salinity waters in Sister Lake (Garton & Stickle 1980, La Peyre et al. 2006).

The high cohort mortality in our study may have been due to density-dependent processes given our high recruitment numbers (up to 8916 spat  $m^{-2}$ ), which were significantly higher than recruitment densities reported in the Chesapeake (64 to 538 oysters  $m^{-2}$ ; ~4 mo old; Mann et al. 2009) and NC reefs (150 to 2374 spat  $m^{-2}$ ; Puckett & Eggleston 2012). Population structure in *Crassostrea virginica* is determined by density-dependent mortality when recruitment is not limited (Knights & Walters 2010, Puckett & Eggleston 2012). When recruitment rates exceed mortality (as in the case of Sister Lake), low and intermediate recruitment rates are associated with increased oyster densities, while high recruitment is associated with decreasing densities caused by density-dependent mortality and the limited space and food capacity of the system (Chatry et al. 1983, Knights & Walters 2010).

Reef accretion and sustainability are dependent on oyster recruitment, growth and survival to a large size in order to accumulate adequate shell for reef creation. A second biological reference point identified for reef sustainability suggests that, similar to oyster abundance, shell resources should also be maintained, or accrete over time (Powell & Klinck 2007; i.e.  $dS/dt \geq 0$ ). Our data indicate shell accretion through the years at all sites, with the exception of SM during the last year (Table 3), again suggesting that accretion may not have to occur every year to ensure sustainable reefs as long as accretion rates prevent a reef from dropping below an elevation threshold required to maintain a viable oyster population (Lenihan 1999, Gregalis et al. 2008). The difficulty remains in determining what minimum elevation is necessary for long-term reef sustainability, particularly in the rapidly subsiding Louisiana environment where local subsidence rates exceed 6 mm  $yr^{-1}$  (Coastal Protection and Restoration Authority 2013).

Shell accretion must be adequate to keep up with local subsidence rates, and account for local shell dissolution and loss from shell scattering, dissolution and fragmentation or human removal (Powell et al. 2006). In the Chesapeake Bay, Southworth et al. (2010) estimate that with a regional mean rate of sea level rise (RSLR) of 3.5 mm  $yr^{-1}$  and 30% shell loss rate, shell must accumulate at a rate of 4.55 l  $m^{-2} yr^{-1}$ , which converts to 2672  $g m^{-2} yr^{-1}$  of shell accretion in

order to be sustainable (1 l wet shell = 587.3 g; Mann et al. 2009). If the same calculations and assumptions are applied to our Louisiana sites, using a minimum RSLR of 6 mm  $yr^{-1}$  with a 30% annual shell loss rate, we would require a minimum shell accretion of 4581  $g m^{-2} yr^{-1}$ . This calculation assumes that shell loss rates are similar to estimates made in Chesapeake Bay (i.e. Powell et al. 2006, Powell & Klinck 2007, Mann et al. 2009) despite the very different temperature and salinity conditions at our sites, and does not account for shell loss from wave energies experienced by our intertidal reefs created using loose shell. While on average all sites exceeded this calculated minimum accretion rate, many sites experienced loss of height and shell scattering as evidenced by a 28 to 51% decrease in reef height, and a 2- to 7-fold increase in reef footprint. Understanding local site energy conditions, effects on shell loss, and local dissolution rates are key to estimating shell accretion and reef sustainability rates.

## CONCLUSIONS

Restored reefs placed within close proximity to one another experienced very different development trajectories. Understanding how differences in population recruitment, growth and survival affect population development, and in the case of oysters, reef creation, is critical for ensuring successful restoration. Comparisons of oyster reefs within similar regions and in other regions clearly demonstrate and support the contention that all conservation is site specific. Clear differences in recruitment densities, growth curves and survivorship within our set of reefs, between our reefs and east coast oyster reefs, and between years suggest a need for better understanding of local site conditions such as water quality, hydrodynamics, and metapopulation dynamics when planning local restoration.

Efforts to restore oyster reefs typically begin with the placement of hard substrate to serve as base for oyster recruitment. Timing of both substrate placement within the oyster's life cycle and timing of data collection can significantly influence conclusions drawn regarding the success of restored reefs. For example, long delays between larval settlement and reef monitoring can overestimate the importance of recruitment versus mortality in determining the number of adults (Caley et al. 1996). Although recruitment and mortality are principal mechanisms regulating the size of natural populations of animals, they are difficult to measure in wild marine animals and

are poorly understood. In Louisiana, there are few published studies on wild-set oyster population dynamics; the few that exist tend to focus on recruitment rates (Pollard 1973) or mortality rates (Owen 1953), and to our knowledge there are no comprehensive studies of *Crassostrea virginica* recruitment, growth, and mortality. Knowledge of these population mechanisms is needed to estimate the sustainability of future created reefs.

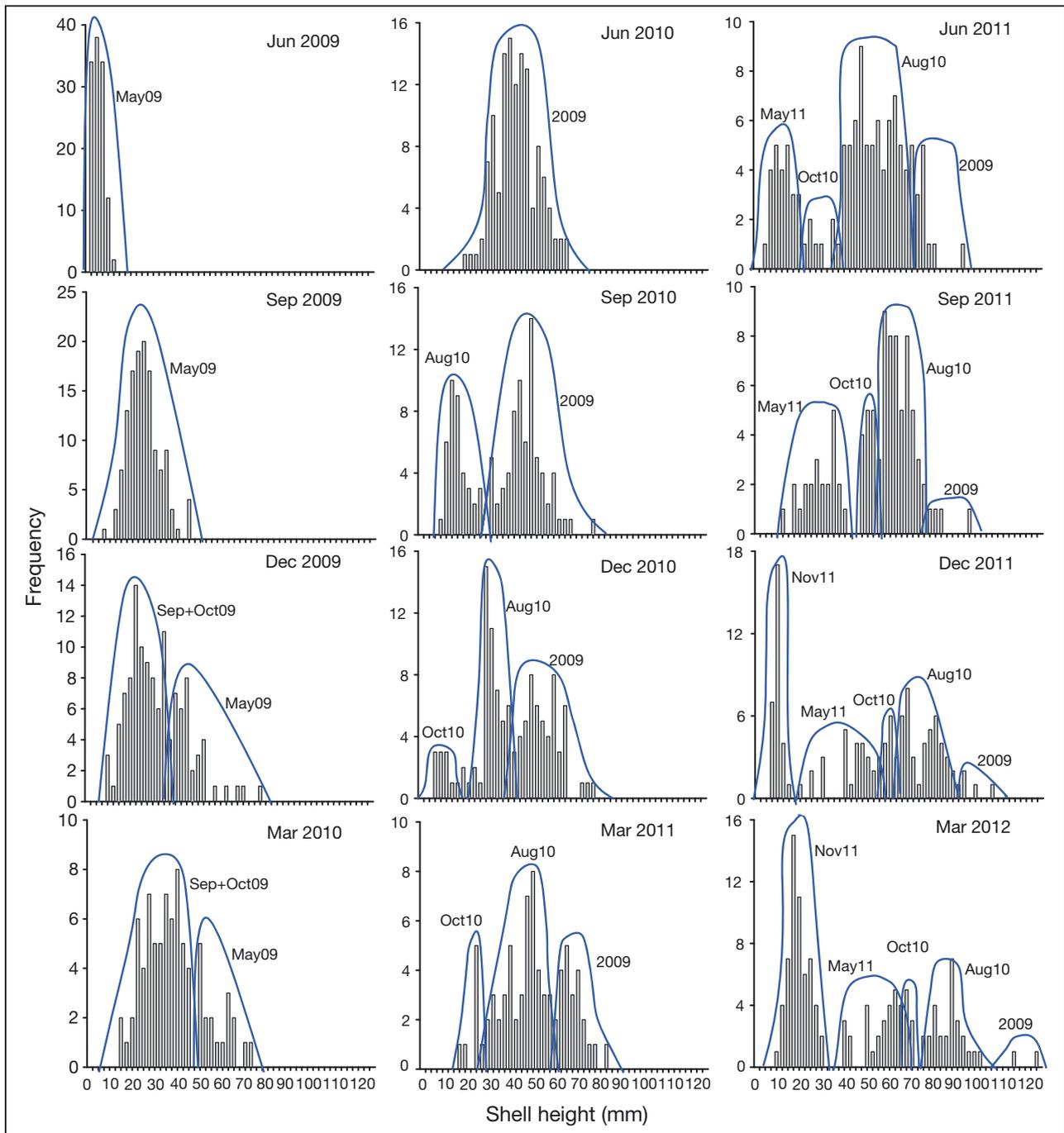
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**Appendix.** Shell height frequency histogram obtained from 3 quadrat samples collected quarterly in the north medium energy (NM) reef. The 2009 cohorts (May09, Sep+Oct09), 2010 cohorts (Aug10, Oct10) and 2011 cohorts (May11, Nov11) are identified by lines fitting the histogram patterns. Cohort separation was completed following methods outlined in Haddon (2011)



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