

Temporal variation in development of ecosystem services from oyster reef restoration



Megan K. La Peyre^{a,*}, Austin T. Humphries^{b,c}, Sandra M. Casas^d, Jerome F. La Peyre^d

^a U.S. Geological Survey, Louisiana Cooperative Fish and Wildlife Research Unit, School of Renewable Natural Resources, Louisiana State University AgCenter, Baton Rouge, Louisiana 70803, USA

^b School of Renewable Natural Resources, Louisiana State University AgCenter, Baton Rouge, Louisiana 70803, USA

^c Department of Zoology and Entomology, Rhodes University, Grahamstown, Eastern Cape 6140, South Africa

^d Department of Veterinary Science, Louisiana State University AgCenter, Baton Rouge, Louisiana 70803, USA

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ABSTRACT

Restoration ecology relies heavily on ecosystem development theories that generally assume development of fully functioning natural systems over time, but often fail to identify the time-frame required for provision of desired functions, or acknowledge different pathways of functional development. In estuaries, a decline of overall habitat quality and functioning has led to significant efforts to restore critical ecosystem services, recently through the creation and restoration of oyster reefs. Oyster reef restoration generally occurs with goals of (1) increasing water quality via filtration through sustainable oyster recruitment, (2) stabilizing shorelines, and (3) creating and enhancing critical estuarine habitat for fish and invertebrates. We restored over 260 m² of oyster reef habitat in coastal Louisiana and followed the development and provision of these ecosystem services from 2009 through 2012. Oysters recruited to reefs immediately, with densities of oysters greater than 75 mm exceeding 80 ind m⁻² after 3 years, and provision of filtration rates of 1002 ± 187 L h⁻¹ m⁻²; shoreline stabilization effects of the created reefs were minimal over the three years of monitoring, with some evidence of positive shoreline stabilization during higher wind/energy events only; increased nekton abundance of resident, but not larger transient fish was immediately measurable at the reefs, however, this failed to increase through time. Our results provide critical insights into the development trajectories of ecosystem services provided by restored oyster reefs, as well as the mechanisms mediating these changes. This is critical both ecologically to understand how and where a reef thrives, and for policy and management to guide decision-making related to oyster reef restoration and the crediting and accounting of ecosystem services.

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1. Introduction

Restoration trajectory models differ in their predictions of the timing and pathway of the recovery of ecosystem functions (Mori, 2011; Suding, 2011). These models tend to rely on succession theory as a framework for understanding restoration patterns within different settings (Clements, 1916; Odum, 1969; Connell and Slayter, 1977; Grime, 1977). One general theory assumes that restoration initiates a simple trajectory whereby ecosystem services approach those of a reference state over some time frame; alternative theories suggest punctuated delivery of services which may require active management over time, while others assume immediate restoration of services (Hobbs and Norton, 1996; Mitsch

et al., 1998; Weinstein et al., 2001; Lindig-Cisneros et al., 2003; Mayer and Rietkerk, 2004; Mathews et al., 2009; Mori, 2011). Different models are likely to apply to different services depending on the characteristics of the service in question and the restoration setting (Suding, 2011).

Understanding the time frame in which services may be fully restored, and perhaps more importantly, how local conditions and discrete events may affect the timing and development of services is critical for establishing development trajectory models for services of interest (Hobbs, 2007; Mathews et al., 2009). For example, it is suggested that plant biomass and wildlife use levels achieve reference goals within a decadal time scale for wetland restoration (Skelly et al., 1999; Batzer et al., 2006) but the recovery of soils may take considerably longer or never be restored at all (Craft et al., 1999; Ballantine and Schneider, 2009). Temporal ranges of the recovery of ecosystem services may relate to overall ecosystem development or may simply reflect local conditions (geographic and climate, or degradation of area) (Suding, 2011). However,

* Corresponding author at: 124 School of Renewable Natural Resources, Louisiana State University AgCenter, Baton Rouge, Louisiana 70803, USA. Tel.: +1 225 578 4180.
E-mail address: mlapeyre@agcenter.lsu.edu (M.K. La Peyre).

without a better understanding of mediating factors, it is difficult to identify trends or assign success to restoration efforts and determine when and where restoration is a viable option (Ballantine and Schneider, 2009; Holl and Aide, 2011; Mori, 2011). Understanding these developments is of more than just academic interest given the high rate of ecosystem restoration, the trade-offs of costs and benefits, and the crediting of services provided by restoration (Grabowski et al., 2012).

In estuarine shallow water areas, the recognition of habitat loss and related restoration of ecosystem services lags behind terrestrial activities, largely due to the hidden nature of lost underwater resources (Elliott et al., 2007). In particular, only recently has the loss and degradation of shellfish reefs been fully identified as a global issue, with significant losses (Beck et al., 2011; Zu Ermgassen et al., 2012a). This recognition, coupled with increased understanding of the valuable ecosystem services provided by oyster reefs, has resulted in significant focus on the restoration of oyster reefs in many regions (Coen and Luckenbach, 2000; Coen et al., 2007; Kennedy et al., 2011). Several of these projects focus on the ability of reefs to contribute to water quality maintenance through filtration, habitat provision by the addition of complex hard structure, and shoreline stabilization through wave attenuation (Coen et al., 2007). However, many projects fail to monitor the development of multiple ecosystem services after creation, especially on spatial and temporal scales relevant to restoration activities (Kennedy et al., 2011; Furlong, 2012). As such, it remains difficult to assess failure or success of oyster reef restoration activities, or to know when a restored reef may need active management to provide desired end goals.

While restoration activities are designed to initiate development of targeted communities and associated services, much uncertainty remains associated with how quickly some of the desired services will develop (Elliott et al., 2007; Suding, 2011; Maron et al., 2012). Specifically for restoration of oyster reefs, the provision of habitat, shoreline stabilization, and water quality maintenance services likely develop over very different time-scales. For example, contributions of restored oyster reefs to water quality maintenance are obviously dependent on recruitment and growth of a sustainable filter-feeding community. Thus, water quality maintenance services are predicted to develop over varying time frames, depending on how local conditions such as salinity, temperature, hypoxia, sedimentation vary and influence recruitment, growth, and survival of oyster populations on the reef (Lenihan, 1999; Beseres-Pollack et al., 2012). In contrast, the provision of habitat for nekton and shoreline stabilization services may occur more quickly, particularly if restoration itself involves the deployment of hard structure as a reef base. What is less clear, however, is how reef characteristics, including the complexity of the reef, existence of large live oysters and other sessile organisms, and reef location may affect the provision of these services, and how changes over time in reef characteristics may further affect the provision of these services (Grabowski et al., 2005; Geraldi et al., 2009; Scyphers et al., 2011; Humphries et al., 2011a). It is predicted, however, that for created oyster reefs, provision of habitat and shoreline stabilization services may occur to some extent, immediately upon reef creation.

This work examines the temporal development of three ecosystem services for oyster reef restoration projects, (1) increasing water quality through sustainable oyster recruitment, (2) stabilization of shorelines, and (3) enhancing critical estuarine habitat for fish and invertebrates. Specifically, using six experimentally restored shoreline fringing oyster reefs, we examine (a) the development of the oyster reef community and relate it to estimated filtration capabilities of the restored reef over time, (b) shoreline stabilization in the context of shoreline exposures based on wave

and wind energies, and (c) the enhancement of fish and invertebrate abundance, and track any changes that may occur over the three years of the study. Understanding these development trajectories is important both ecologically, to understand how and where a reef thrives, and for policy and management, to guide decision-making related to crediting and accounting of ecosystem services.

2. Methods

2.1. Study site

The study was conducted at Caillou Lake, located in Terrebonne Parish, Louisiana (29° 14' 11.09N, 90° 55' 16.48W) and locally known as Sister Lake (Fig. 1). Sister Lake is primarily an open-water, brackish system with a mean tidal range of 0.3 ± 0.03 m (SE) (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. Fetch distance can be quite large (>7.5 km) and daily mean (± 1 SE) water temperature, salinity, and water level in the study area from 2002 through 2012 was 23.6 ± 0.41 °C, 11.2 ± 0.1 , and 0.33 ± 0.03 m, respectively (LDWF/USGS 07381349–Caillou Lake southwest of Dulac, LA, U.S.A.). Surrounding marsh consists of *Spartina alterniflora* and *Juncus roemerianus* dominated marsh community, with some *Distichlis spicata* and *Spartina patens* interspersed. Adjacent soils are typical marsh soils with 12–30% organic matter, and bulk density ranging from 0.3–0.4 g cm³ (Coastwide Reference Monitoring System (CRMS); CRMS0383, CRMS4455). Sister Lake has served as a state public oyster seed reservation since 1940, and is an area of extreme interest for maintenance of sustainable oyster reefs with abundant shell bottom and managed subtidal oyster beds occurring throughout the system.

Six experimental oyster reefs were created in March 2009 within Sister Lake, LA, (Fig. 1). Reefs were located in three different locations across the lake, at sites paired as having either 'low' or 'medium' wave exposure based on shoreline orientation, prevailing winds, and fetch distances, using methods similar to La Peyre and Birdsong (2008). At each of the six selected shorelines, two sections of 25 m shoreline were selected, with a minimum of 50 m between the shorelines. A narrow ($25 \times 1 \times 0.7$ m, length \times width \times height) fringing reef using shell cultch was created as close to the shoreline as possible (5–10 m), while the second shoreline was used as a reference (mud-bottom). All reefs were intertidal; however, due

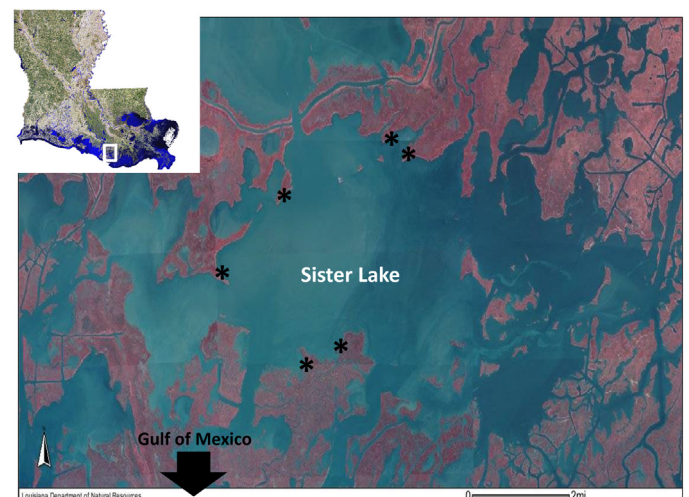


Fig. 1. Location of study areas (*) in Sister (Caillou) Lake, Louisiana. Reefs were created in 2009 using cultch oyster shell.

to the low tidal amplitude and water depth within our study area, the reefs were exposed less than 20% of the time over the study period. These narrow, small patches of reef are not unusual in this region, given the low tidal amplitude, shallow water depths across the estuaries and extensive soft bottoms. Reef creation methods involved placing shucked, unaggregated oyster shell using a barge and bucket dredge, similar to Piazza et al. (2005). Sampling occurred from March 2009 through March 2012.

2.2. Environmental variables

Continuous salinity, temperature (°C), water level data and meteorological conditions of wind direction (degrees) and speed (m s^{-1}) were obtained from the USGS recorder located in Sister Lake (LDWF/USGS 07381349 - Caillou Lake southwest of Dulac, LA, U.S.A.) from 2009 through 2012.

Discrete water quality samples were taken at each site approximately monthly. Dissolved oxygen (mg l^{-1}) was measured with a YSI 556 (YSI Inc., Yellow Springs, OH, U.S.A.). For chlorophyll *a* and total particulate matter measurements, two 250-mL water samples were collected in dark Nalgene bottles and placed on ice and returned to the lab for sampling. Under dim lights a 50 mL water sample was filtered through a pre-weighed Whatman 47 mm glass-fiber filter. The filter was placed in a labeled foil packet and store at -20°C until processing following EPA Method 445.0 for chlorophyll *a*. For total particulate matter, a 150-mL water sample was filtered through a pre-weighed Whatman 47 mm glass-fiber filter, washed three times with 20-mL dH_2O , and dried at 105°C for 1 h where it was weighed, and total particulate matter (TPM) calculated by subtracting the filter weight from the dried weight. The filter was then placed in a muffle furnace at 550°C for 30 min and weighed a third time. Particulate organic matter (POM) was calculated by subtracting the ashed weight (particulate inorganic matter, PIM) from the TPM weight (Taras 1971).

2.3. Reef sustainability

The number and size of live and dead oysters were estimated 1, 2 and 3 years post-reef creation in March 2010, 2011 and 2012. Three haphazard sample sites of approximately 0.25×0.25 m were located on each reef per sample period. Reef materials, down to a 10 cm depth were removed by hand and placed in a mesh bag (3-mm). Samples were placed on ice, transported back to the laboratory, and processed within 72 h. Materials were then processed by counting the number of live oysters, and measuring shell height (± 0.1 mm). Oyster density was determined for each sample. Within each sample, number and size of mussels and barnacles were also recorded.

Using the measured oyster sizes and densities, we calculated the potential filtration capacity of each reef over time using the

$$F_E = \frac{F(a) \times \cos(a) + \sum_{i=1}^3 F(a + 22.5i) \times \cos(a + 22.5i) + \sum_{i=1}^3 F(a - 22.5i) \times \cos(a - 22.5i)}{\cos(a) + 2 \left(\sum_{i=1}^3 \cos(a + 22.5i) \right)}$$

March oyster density and oyster shell height data from the reefs. We converted shell height (SH; cm) to dry tissue weight (DW; g) using an equation derived from measurements of oysters in cages located adjacent to each reef over the three years of this project ($\text{DW} = 0.0004(\text{SH})^{1.9217}$) (unpubl. data). We estimated

potential filtration rate using an equation derived from Riisgård (1988) for *Crassostrea virginica*, where filtration rate:

$$\text{Filtration rate}(\text{L h}^{-1}) = 6.79\text{DW}^{0.73}$$

corrected for temperature as written by Cerco and Noel (2005), resulting in the final equation of:

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

Bivalve filtration rate is a function of other variables including temperature, salinity and total suspended solids (review, Newell and Langdon, 1996; Dame, 2012). We used the median temperature from Sister Lake during the time of this study (23°C) to make our calculations. Salinity is believed to affect filtration through a step-like function, with lowered filtration rates below 7.5. We assumed the mean Sister Lake salinity of 11 (4 year study mean) for these rate calculations. Oysters have been shown to modulate feeding activity in response to seston concentrations, however, this occurs at concentrations below 5 mg L^{-1} or possibly, above 25 mg L^{-1} (review, Newell and Langdon, 1996; Dame, 2012); our field data over 3 years in this water body indicate that mean concentrations are well within this range. Thus, the filtration rates presented provide only a comparison between years, at 23°C , and under ideal salinity and food conditions, and actual filtration on any given day and time is likely lower than what is presented.

2.4. Marsh stabilization

Shoreline position change was measured using techniques similar to Meyer et al. (1997) and Piazza et al. (2005). Five transects were established within each site with permanent base stakes located in the marsh and in the water. For each sample, a tape measure was stretched level between base stakes and read at the shoreline marker. Shoreline edge is defined as the farthest waterward extent of the emergent wetland macrophytes. Shoreline position was measured quarterly and change in shoreline was calculated as the difference (cm) between measurements. Positive values indicate accretion, negative values indicate erosion. Data are expressed as mean erosion rate (cm d^{-1}).

Shoreline exposure is defined as the total effect of waves on marsh vegetation and was calculated using wind data and fetch measurements. Direct fetch (km) was measured using Landsat (2011) photographs from a single point (location of treatment) for 16 compass bearings, or at 22.5° intervals. Because the shape of a body of water will affect its wave generation (i.e. a large fetch value may be less meaningful if it represents a narrow arm rather than a large, open bay), we converted direct fetch into a measure of effective fetch, which takes into account adjacent fetch measures to correct for the shape of the opposite shore (U.S. Army Coastal Engineering Research Center, 1977). Each effective fetch value (F_E) was composed from weighted direct fetch values (F) for all adjacent fetches less than 45° away.

where α is set to zero for each F_E calculated (Keddy, 1982).

Climatic data were calculated using the downloaded wind speed and direction values from LDWF/USGS (#07381349) at daily, 15-min intervals. The data used in calculations were: (1) mean wind velocity for each 16 compass bearings; (2) directional percent frequency, or the percentage of time in which winds blew from each of

16 compass bearings; (3) exceedance, or the proportion of winds exceeding 35.4 km h^{-1} for each of 16 compass bearings, or those in the top 10% of all readings during the experiment. Exceedance might be important if only extreme conditions affect exposure. All values were generated for each treatment and site at daily time intervals, then averaged for each quarterly time period between samples of shoreline position (2 treatments \times 6 sites \times 12 quarterly samples = 144 observations).

The effects of exposure on shoreline erosion should be proportional to wave energy; however, in our study area wave energy is difficult to measure because of logistical reasons. Therefore, given that wave height is a function of fetch, wind speed, duration, water depth, we calculated a unit-less index of exposure to be able to rank our experimental treatments against one another in their degree of exposure. We first calculated exposure (E_M) using the effective fetch matrices of each treatment and mean wind velocity:

$$E_M = \sum_{i=1}^{16} \text{mean wind velocity}_{22.5i} \times \text{percent frequency}_{22.5i} \times \text{fetch}_{22.5i}$$

The summation occurs over 16 compass directions. We then calculated a second measure of exposure (E_E) based on exceedance, and since exceedance already incorporates the velocity component by considering only winds $>35 \text{ kmh}$, values based on exceedance are calculated as:

$$E_E = \sum_{i=1}^{16} \text{exceedance}_{22.5i} \times \text{fetch}_{22.5i}$$

Although duration is not directly included in these calculations, it is reflected in percent frequency. Fetch is measured in km, wind speed as km h^{-1} , and exceedance and percent frequency have no units. Since the objective is to produce a measure related to the magnitude of wave energy arriving at the marsh shoreline, integrated over a period of time, these units are not relevant and the values calculated are dimensionless units of exposure.

Treatment (mud-bottom versus oyster reef) was used as a fixed effect in one-way ANOVAs using generalized linear models (GLMs) to test for effects of exposure using mean wind velocity as well as exceedance on shoreline erosion rate. We also used a pairwise *t*-test with the calculated exposure values to determine whether the sites we chose within our study area differed significantly from one another in wave energy over the entire sampling period.

2.5. Habitat provision

To characterize nekton assemblages, we used a combination of sampling gears including gillnet, seine, and plastic substrate trays filled with shell cultch. Immediately after reef creation in March 2009, 18 plastic substrate trays ($63 \times 52 \times 11 \text{ cm}$ lined with 0.5 mm mesh screening), were filled with shell cultch and embedded haphazardly along the reef. At each mud-bottom control site, 3 plastic substrate trays were filled with mud and staked to the bottom with PVC poles.

Sampling occurred quarterly, beginning in June 2009, at each site and involved deployment of the gillnet ($50 \times 1.75 \text{ m}$ with 5, 7, 10, 12, 14 cm monofilament sections) forming a semicircular enclosure with the shoreline in order to capture larger organisms that may be leaving the treatment area during seining. A bag seine ($5 \times 2 \text{ m}$ with 3 mm square delta mesh) was then swept parallel to the shoreline along the edge of the reef for a distance of 25 m. One sweep was executed on the 'shore' side of the treatment, a second

sample was taken from the 'estuary' side of the treatment. Trays at reefs were sampled without replacement, while those at mud bottom were sampled with replacement. At each sample event, three trays were randomly sampled from each site by quickly lifting the trays and placing the contents in mesh bags (3 mm square delta mesh). Substrate tray contents were rinsed to remove excess sediment by sieving tray contents on site, and contents placed in labeled bags on ice for identification in the laboratory. The gill net was then removed and all nekton were identified, weighed to the nearest 10 g (wet weight), and total length measured to the nearest 1 cm before being released on site. Average gillnet soak time was approximately 2 h for each sampling event. In the laboratory, nekton from seine and substrate tray samples were identified to species or the lowest feasible taxon, total length and wet weight were recorded.

Catch per unit effort was examined for normality and homogeneity of variance, transformed as required and analyzed, by gear type, by treatment (reef, reference) and by year post-creation (Year 1: Summer 2009, Fall 2009, Winter 2009, Spring 2010; Year 2: Summer 2010, Fall 2010, Winter 2010, Spring 2011; Year 3: Summer 2012, Fall 2012) for gillnet and seine, and by sample period (5 sample periods: Summer, Fall, Winter 2009, Spring, Summer 2010) for tray data using a generalized linear model. Using gillnet and seine CPUE data, a linear regression was run to determine if CPUE was related to on-reef oyster density, using total oyster density, as well as by density of oysters $>25 \text{ mm}$ shell height.

Wilcoxon signed-rank tests were used to compare relative abundances of each species ($\geq 3\%$ of total gear catch, CPUE) between the paired oyster reef and mud bottom control treatments, by sample date. To further examine whether oyster reefs were recruiting and supporting unique fish and decapod communities, and if they changed over time, we applied a non-metric multidimensional scaling (nMDS) ordination of community structure (measured by the Bray-Curtis dissimilarity coefficient) on all gear types using catch per unit effort as the dependent variable (Clarke and Warwick, 2001). Using the Bray-Curtis distance matrices, we applied a permutational multivariate analysis of variance and associated *R*-squared and *p*-values are reported from the analysis of variance (Burnham and Anderson, 2002).

3. Results

3.1. Environmental variables

During 2009 through 2012, data from the continuous data recorder located in the middle of Sister Lake indicated that water temperature varied seasonally, with a daily mean of $22.7 \pm 0.1^\circ\text{C}$ (range: $2.2\text{--}34.4^\circ\text{C}$); salinity varied throughout the years and had a mean of 10.9 ± 0.01 (range $0.3\text{--}29.8$) and water level ranged from -3.1 to 5.8 NAVD with a mean of 0.3 ± 0.03 . Discrete sampling of dissolved oxygen, water clarity, total suspended solids and chlorophyll *a* concentrations varied, but generally indicated high dissolved oxygen, suspended solids and chlorophyll *a* concentrations, and low water clarity typical of this region (Table 1; Appendix A).

3.2. Reef sustainability

Overall oyster density did not increase through time, with highest density at one year post-creation ($1231 \pm 296 \text{ ind m}^{-2}$), and lowest density at 2 years post-creation ($487 \pm 45 \text{ ind m}^{-2}$) (Table 2). However, density of large oysters ($>75 \text{ mm}$) increased rapidly over time starting with a very low mean in 2010 ($3 \pm 2 \text{ ind m}^{-2}$), and reaching a high mean in 2012 ($80 \pm 12 \text{ ind m}^{-2}$). Differences in

Table 1
Mean SE (range) and N of discrete water quality samples collected at each site during each sample event. Samples were taken approximately bi-monthly at all sites from March 2009 through March 2012 at reefs created in March 2009 in Sister Lake, Louisiana, and at adjacent reference mud-bottom sites.

	Reef	Reference
Dissolved oxygen (mg L^{-1})	7.8 ± 0.2 (0.4–17.3); 199	7.6 ± 0.3 (0.4–14.0); 178
Secchi depth (cm)	43.2 ± 1.3 (9.1–102.0); 192	43.4 ± 1.6 (10–112.0); 164
TPM (mg L^{-1})	39.2 ± 2.5 (4.0–296.0); 257	32.6 ± 4.1 (10.0–251.3); 125
TOM (mg L^{-1})	10.7 ± 0.4 (2.0–45.3); 257	8.8 ± 0.6 (2.0–34.7); 125
Chlorophyll <i>a</i> ($\mu\text{g L}^{-1}$)	14.6 ± 0.4 (1.8–43.6); 306	14.8 ± 0.6 (1.1–47.9); 171

Table 2
Mean density ($\# \text{ ind m}^{-2}$; SE) and size (mm) of dominant sessile organisms on created reefs one (2010), two (2011), and three (2012) years post reef creation. The target organism, *Crassostrea virginica* (“oyster”) is divided by size class (spat <25 mm; seed >25 mm; <75 mm; market >75 mm).

Year	Oyster by size class ($\# \text{ ind m}^{-2}$)				Mussels		Barnacles	
	Reef	Spat	Seed	Market	Density	Size	Density	Size
2010	1231 (296)	610 (208)	619 (116)	3 (2)	319 (239)	15.0 (1.3)	8816 (4618)	5.1 (0.2)
2011	487 (45)	104 (18)	369 (30)	14 (3)	410 (149)	15.9 (2.7)	12532 (3131)	5.8 (0.5)
2012	738 (96)	431 (87)	227 (13)	80 (12)	348 (167)	8.0 (1.6)	11706 (4275)	5.7 (0.6)

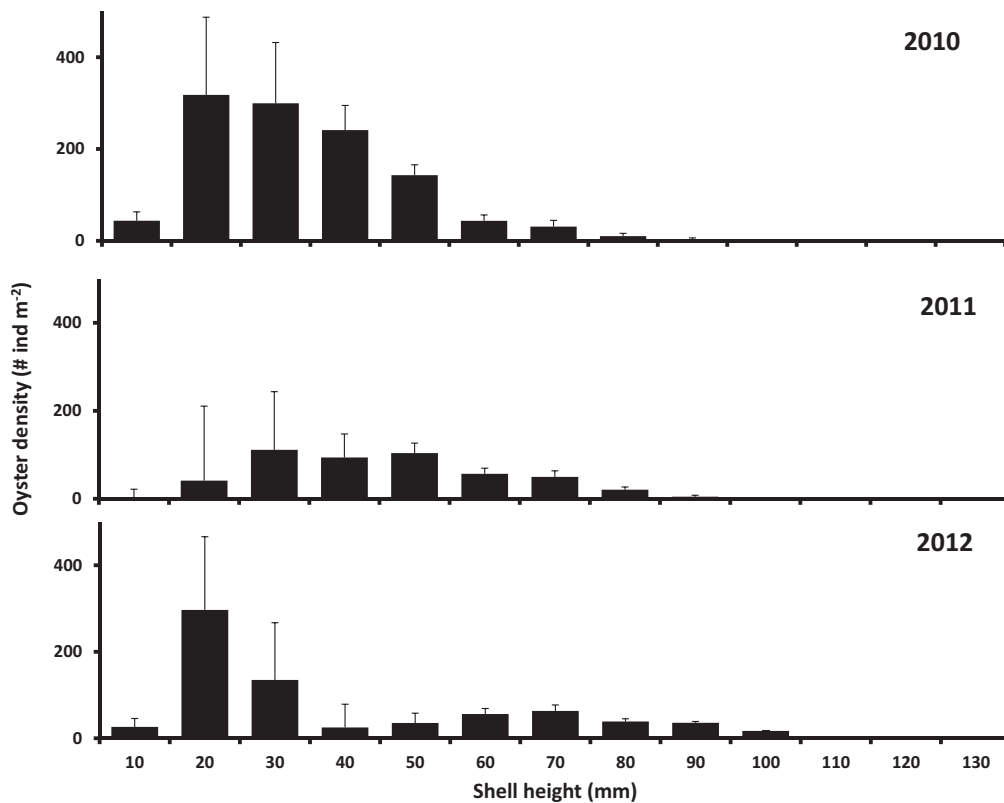


Fig. 2. Mean (SE) of oyster density ($\# \text{ ind m}^{-2}$) by size class (10 mm) measured on all experimental reefs in March 2010, 2011 and 2012, 1, 2 and 3 years post-creation of reef.

overall on-reef oyster density are best explained by variation in smaller sized oysters (i.e. <30 mm) which likely reflects recruitment from the previous year as spawning in this region may occur from May through November (Fig. 2, Table 2). Other sessile organisms recruited to the reef during this time; of filtering organisms, barnacles and mussels were the most dominant organisms with densities of $8816 \pm 4618 \text{ ind m}^{-2}$, and $319 \pm 239 \text{ ind m}^{-2}$ the first year, and remaining high through the three years of the study (Table 2). With the exception of the 2012 mussel population which had significantly smaller mean size (mm), mean size (mm) of barnacles and 2010 and 2011 mussels remained the same through the three years (Table 2).

Filtration rate: while overall oyster density did not increase over time, calculated filtration rates increased over time (Fig. 3). After 1 year, filtration rate was $404 \pm 107 \text{ L h}^{-1}$ of water filtered per square meter of reef, increasing to 607 ± 77 in Year 2, and reaching a high of $1002 \pm 187 \text{ L h}^{-1}$ of water per square meter of reef in year 3 (Table 3). Spat (<25 mm) contributed up to 24% of the filtration capacity of the reef through the three years; in all years, seed sized (25–75 mm) oysters contributed the most to reef filtration capacity (from 50% in 2010 to 86% in 2011) while market sized (>75 mm) oysters only contributed just over 30% of filtration capacity by the third year (Table 3).

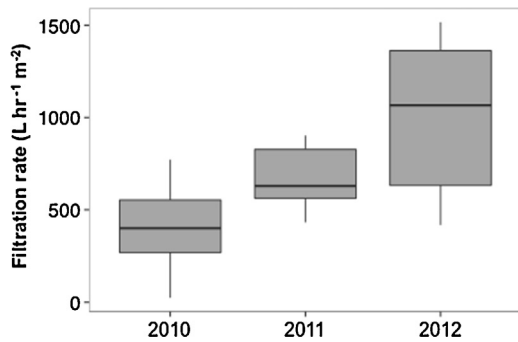


Fig. 3. Calculated filtration capacity ($L\ h^{-1}\ m^{-2}$) of the experimental reefs, based on measured oyster density and size in March 2010, 2011, and 2012; one, two and three years post-reef creation.

Table 3

Calculated filtration rate ($L\ h^{-1}\ m^{-2}$) of the oysters on the reef, 1 (2010), 2 (2011), and 3 (2012) years post reef creation. Numbers represent mean (standard error). Reef presents the filtration rate (m^{-2}) on the reefs; spat presents the filtration contribution of oysters <25 mm shell height; seed presents the filtration contribution of oysters >25 mm, <75 mm shell height and market presents the filtration contribution of oysters >75 mm.

Year	Filtration rate ($L\ h^{-1}\ m^{-2}$)			
	Reef	Spat	Seed	Market
2010	404 (107)	96 (56)	305 (73)	4 (4)
2011	671 (77)	51 (14)	570 (60)	44 (21)
2012	1002 (187)	193 (78)	467 (64)	342 (87)

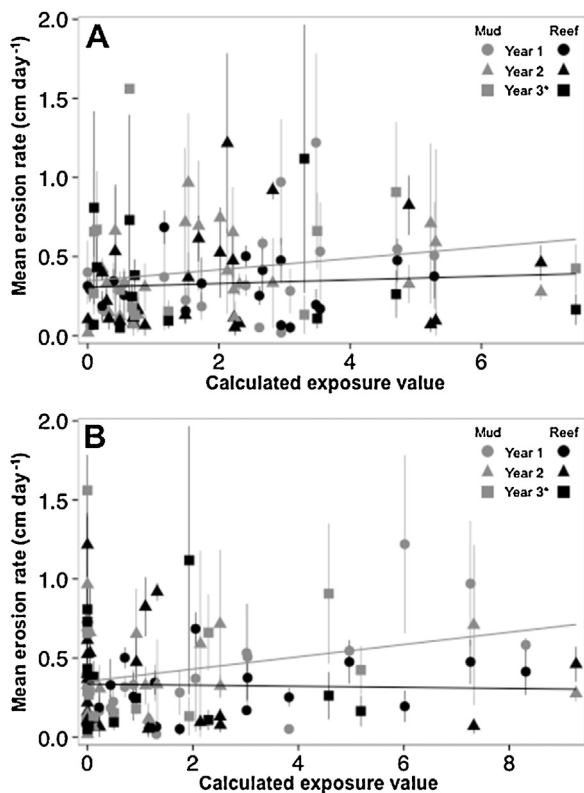


Fig. 4. Mean (SE) erosion rate ($cm\ day^{-1}$) plotted as a function of the calculated exposure value of each reef location. Exposure value is a function of the wind direction and speed, and shoreline orientation during each sample period. (A) All data collected during the project; (B) only uses exposure rates during exceedance periods (winds $>35.4\ km\ h^{-1}$).

3.3. Marsh stabilization

Using the calculated exposure index, oyster reefs did a better job of preventing shoreline erosion when compared to mud-bottom, especially at the higher levels of exposure in our study (Fig. 4). However, oyster reefs failed to have a significant effect on marsh stabilization using both calculated measures of exposure, with continued retreat at all sites through the monitoring period ($>1\ cm\ d^{-1}$). Pairwise t -test indicated that calculated exposure values at our sites was significantly different ($p < 0.001$), with a mean exposure value of 0.79 (± 0.12) at low energy sites, and 3.31 (± 0.24) at medium energy sites, which indicates that we did represent a significant gradient in selecting shorelines for variable wind and wave energy.

3.4. Habitat provision

A total of 1,381 individuals from 25 species were collected in 128 gillnet samples throughout the study. In 250 seine samples, a total of 13,968 individuals were collected that represented 50 species. Not all substrate trays were recovered for sampling due to loss of trays; a total of 99 substrate trays were recovered and sampled (June 2009 = 23; August 2009 = 31; December 2009 = 25; March 2010 = 13; June 2010 = 7). The 99 tray samples resulted in 1,356 individuals and 20 species.

Catch per unit effort (CPUE) of gillnets was significantly higher at reefs as compared to reference mud bottom sites ($F_{5,114} = 13.4$, $p = 0.0004$; Fig. 5A) however there was no increase in CPUE by year. Furthermore, there was no relationship between transient fish CPUE and the density of all oysters on the reef, or density of oysters greater than 25 mm shell height. Hardhead catfish (*Arius felis*), Gulf menhaden (*Brevoortia patronus*), blue crab (*Callinectes sapidus*), Atlantic croaker (*Micropogonias undulatus*), black drum (*Pogonias cromis*) and red drum (*Sciaenops ocellatus*) were all significantly more abundant at oyster reefs ($p < 0.05$; Fig. 6A). However, the composition of communities was not significantly different from one another between oyster reefs and mud bottom according to the nMDS analyses (stress = 0.21; PERMANOVA $R^2 = 0.02$; p -value = 0.19).

Catch per unit effort (CPUE) for seine data did not indicate any difference between treatment (reef, mud) or by year (Fig. 5B). Furthermore, there was no significant relationship with oyster density (total density, or oysters > 25 mm). Species richness did not differ between reef and mud bottom sites, but did decline for both treatments after the first year of the study. There were few differences in abundances of species between treatment types and overall community composition did not differ significantly between habitat types (nMDS stress = 0.26; PERMANOVA $R^2 = 0.005$ and p -value = 0.27; Fig. 6B).

There was a significant reef effect for tray catch with greater densities on reef, as compared to mud bottom reference (Fig. 5C). CPUE at oyster reef sites had a mean of $57.0 \pm 7.5\ ind\ m^{-2}$ compared to reference mud bottom with a mean of $9.1 \pm 1.7\ ind\ m^{-2}$. Atlantic and Flatback mud crabs (*Panopeus herbstii*, *Eurypanopeus depressus*) and skillettfish (*Gobiosox strumosus*) were more common at reefs as compared to mud bottom; bay anchovy was found more at mud bottom treatments as compared to reefs ($p < 0.05$; Fig. 6C). The species composition of communities was also significantly different from one another between oyster reefs and mud bottom reference treatments according to community analyses (nMDS stress = 0.19; PERMANOVA $R^2 = 0.19$ and p -value = 0.001). Driving these differences are the Atlantic and Flatback mud crabs and skillettfish.

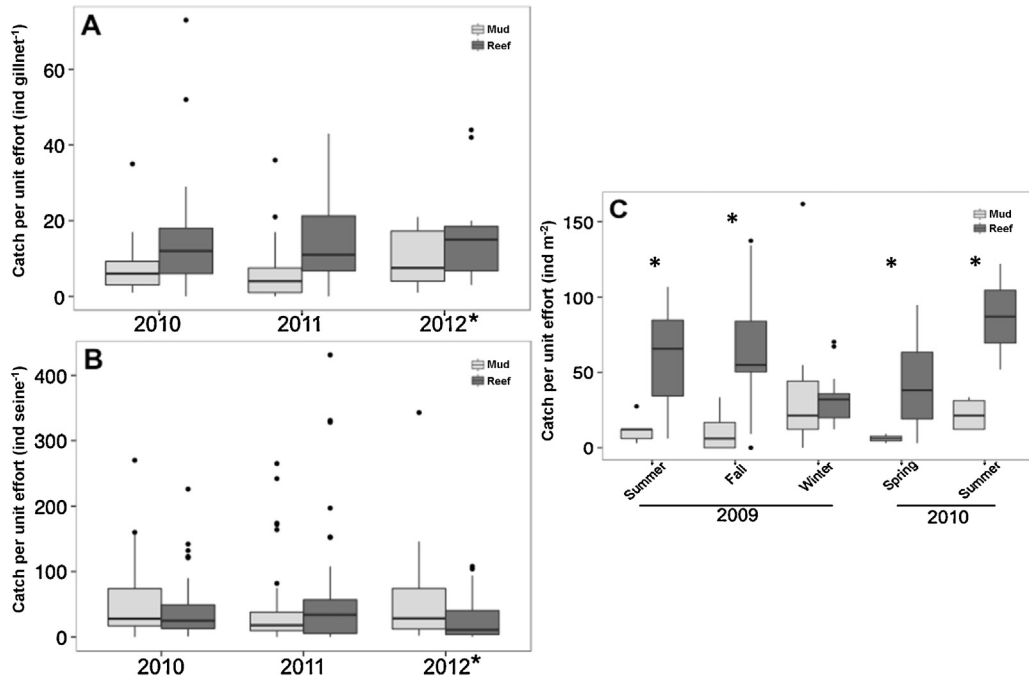


Fig. 5. Mean (SE) catch per unit by gillnet (A), seine (B) and substrate trays (C), comparing experimental reefs and reference mud-bottom sites over time. Asterisks indicate significant pairwise *t*-tests ($p < 0.05$).

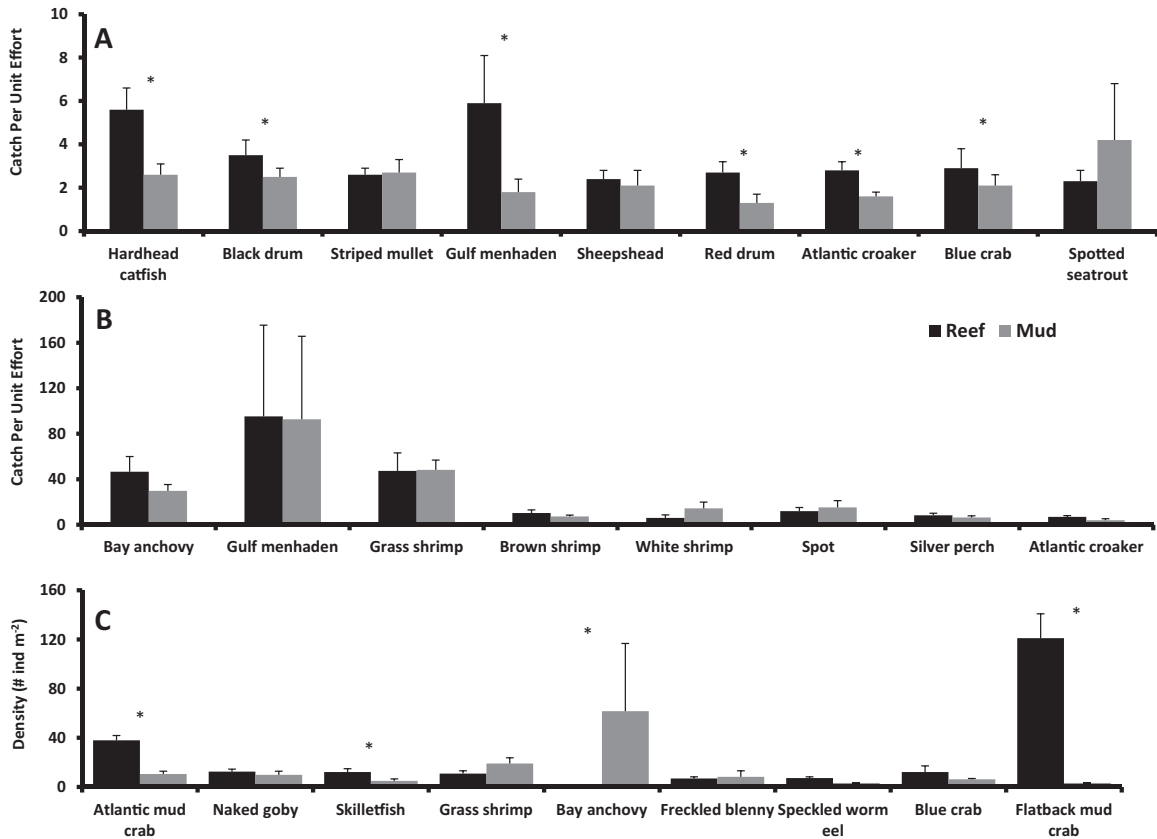


Fig. 6. Catch per unit effort of dominant species caught by gillnet (A), seine (B), and substrate tray (C) at reef and mud-bottom sites. Asterisks indicate significant pairwise *t*-tests ($p < 0.05$).

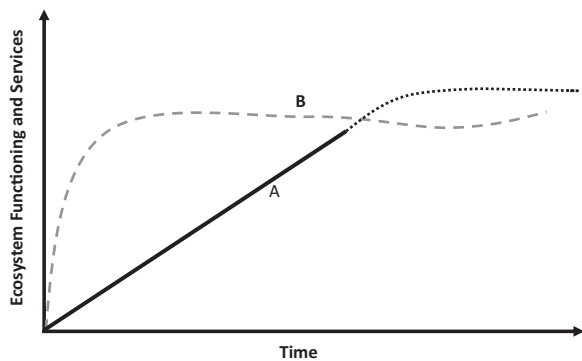


Fig. 7. Trajectories describing development of ecosystem function and service provision for created oyster reefs. This trajectory approach is adapted from previously published work for restoration theory (i.e., Craft et al., 2003; Van Andel and Aronson, 2006; Falk et al., 2006). Trajectory “A” describes processes linked to living oyster populations on reef (i.e., filtration). Trajectory “B” describes services linked to addition of hard structure (i.e., habitat provision). Time frame varies depending on local site conditions. This model assumes correct site placement for long-term maintenance of an oyster population.

4. Discussion

Development trajectories of ecosystem services provided by the restored oyster reefs differed substantially among one another. Within the first year, reefs immediately recruited oysters and other filtering feeding organisms, which provided immediate water filtration services. This trend was persistent through time as the oyster and filter feeding community continued to develop. Reefs failed to provide unequivocal shoreline stabilization services; reef effects on shoreline stabilization occurred only during periods of high exposure (fetch and wind/wave energy). This questions the value of restored reefs as an erosion mitigation tool in low energy interior waters. Reefs immediately supported higher abundances of resident nekton species, however, abundance remained constant through time. There were no measured effects of increased habitat support for larger transient or facultative resident fish species during the 3 years of monitoring.

4.1. Reef sustainability

The establishment and continual development of a sustainable oyster population is imperative for restored oyster reefs to provide desired ecosystem services of water filtration, shoreline protection, and habitat provision. Maintenance of such an oyster population is dependent on suitable environmental conditions for oyster survival (e.g., temperature, salinity, dissolved oxygen), (Lenihan, 1999; Paynter et al., 2010; Beseres-Pollack et al., 2012). Within the time-frame of this study (3 years), despite a low recruitment during the second year of the project, the created reefs maintained live oyster densities ($728.1 \pm 101.9 \text{ ind m}^{-2}$). Mean density of all live oysters on individual reefs over the 3 years ranged from 203 to 2586 ind m^{-2} , which was similar to densities reported at existing reefs located in the Calasahootche Estuary in Florida ($102\text{--}2345 \text{ ind m}^{-2}$; Volety et al., 2009), and to densities reported for patch reefs in the Chesapeake Bay ($477\text{--}1364 \text{ ind m}^{-2}$; Ross and Luckenbach, 2009) and Pamlico Sound in NC ($686\text{--}3782 \text{ ind m}^{-2}$; Puckett and Eggleston, 2012). The similarity in oyster density among comparable reefs in the region and along the Atlantic coast suggests environmental conditions were adequate to facilitate successful recruitment and reef growth.

Development of a market-size oyster population ($\text{ind} > 75 \text{ mm}$ shell height) took a full 3 years to establish. Specifically, while reef oyster density was similar throughout the 3 years, the range of

sizes expanded over time, with the density of market-size oysters ($>75 \text{ mm}$) reaching $80 \pm 12 \text{ ind m}^{-2}$ (11% of reef density) after 3 years. This proportion (11%) is similar to results reported for 2006–2008 in North Carolina no-take reserves (range 0.5–17% of reef population oysters $>75 \text{ mm}$) (Puckett and Eggleston, 2012). Created reefs in Mobile Bay, AL, reported on oyster reef densities approximately 2 years post-creation, indicating that reef density of adult oysters ($>30 \text{ mm}$) consisted of approximately 14–29% of the reef density which would be comparable to our combined densities of seed (25–75 mm) and market sized ($>75 \text{ mm}$) oysters (Scyphers et al., 2011). Timing of samples can significantly affect these percentages as a recent high recruitment event can dramatically lower the percent reef composition of large oysters.

An established sustainable oyster population potentially contributes to water quality maintenance within an estuary due to its filter feeding (Dame et al., 1984; Cerco and Noel 2007; Grizzle et al., 2008; Zu Ermgassen et al., 2012b). In this study, while oyster density did not increase over time, increases in the mean size of oysters over time are correlated with increases in filtration capacity. Assuming that filtration calculations apply equally to small to medium sized oysters ($<75 \text{ mm}$), the majority of filtration capacity during these three years is attributed to the smaller oysters, with only 30% of filtration attributed to larger oysters ($>75 \text{ mm}$) in the third year. While not completely comparable, the calculated filtration rates exceeded that for calculated filtration for 13 U.S. estuaries (Zu Ermgassen et al., 2012b). Zu Ermgassen et al. (2012b) however excluded all oysters $<25 \text{ mm}$ due to lack of consistent metadata, and were extrapolating across entire estuaries which likely included areas with limited to no oysters, reducing their population densities (less than 160 ind m^{-2} in all cases). This comparison, however, does provide a strong argument for the potential high value of created or protected reefs in helping maintain water quality in estuaries as much of the metadata used was likely from significantly impacted or harvested areas.

There has been some debate in past attempts to calculate and estimate filtration rates within estuaries, with varying success at measuring rates in the field (Grizzle et al., 2008; Plutchak et al., 2010) and controversies over the extrapolation of laboratory derived filtration rates to the field (Powell et al., 1992; Newell and Langdon, 1996). Our calculations were based on actual on-reef measurements of oyster sizes, but relied on published equations for filtration rates of the eastern oyster (Riisgård, 1988), none of which have been measured in-situ within the Gulf coast region where we were working. For these calculations, we assume adequate food concentrations based on data collected on chlorophyll *a* concentrations but do not account for the potential effects of high sediment loads in the water column on filtration rates (i.e., Ren, 2009; Barille et al., 2011). Powell et al. (1992) suggested a lower filtration to be used, which reduced our filtration rates by approximately 80% across all years. Despite significant densities of other filter feeders (barnacles, mussels), we did not include them in our filtration calculations but it is likely that they contribute to water filtration (Riisgård, 1988), and our calculations provide a conservative estimate.

A number of studies suggest further contributions of reefs to water quality through denitrification and nutrient assimilation in shell (Dame et al., 1989; Newell et al., 2002; Piehler and Smyth, 2011; Beseres-Pollack et al., 2013; Kellogg et al., 2013; Smyth et al., 2013). However, differences in approaches and questions related to the long-term relevance of shell nutrient assimilation make extrapolating existing data or comparing data between studies difficult. For example, site-specific measurements are needed on how N and P assimilation relate to oyster size and density, or how temperature, salinity or submergence time contribute to denitrification rates (but see Smyth et al., 2013). This is an important ecosystem

service of oyster reefs, however, this was beyond the scope of this study.

4.2. Shoreline stabilization

Across a range of locations and conditions, reefs have been shown over the short term to provide some beneficial shoreline stabilization effects, and modeling efforts have estimated that subtidal oyster bottoms within a bay can significantly reduce wave energies, providing some protection to coastal marshes (Meyer et al., 1997; Piazza et al., 2005; Stone et al., 2005; Scyphers et al., 2011). In this study, effects of reefs on shoreline erosion were highly variable through time, and differences may have been masked when comparing treatments without accounting for spatial and temporal variability of reef location and exposure (wave energy and fetch). When specific shoreline retreat rates were examined with respect to actual exposure (fetch + wave energies; Keddy, 1982), the reefs reduced erosion rates in comparison to adjacent controls, but only significantly during periods of high exposure (i.e., storms or fronts). This finding is similar to that of Meyer et al. (1997) who found that fringing reefs in North Carolina reduced shoreline erosion only during storm events. As large storms have been shown to be responsible for massive erosion along the northern shore of the Gulf of Mexico (Kahn and Roberts, 1982; Stone et al., 1997), the effectiveness of these small fringing reefs during high energy periods shows promise for storm generated erosion assuming they remain intact during these events. In contrast, the use of fringing oyster reefs for shore stabilization to address chronic erosion within shallow water estuaries and bays resulting from processes other than large storm events may have limited value.

4.3. Habitat provision

The created oyster reefs provided immediate habitat and supported an overall increase in abundance of resident (800% increase) and some known reef-attracted transient species, but failed to increase overall transient or facultative species abundances. Perhaps the most unexpected finding was how abundances failed to increase through time as the reefs matured, or how increased resident species abundance failed to translate into increased abundances at the higher trophic levels.

Increasing structure and its associated complexity is thought to provide increased refuge areas for residents, but it remains unclear whether this translates into increased prey survivorship, or increased foraging efficiency (Heck and Thoman, 1981; Grabowski and Powers, 2004; Humphries et al., 2011b). Ultimately, the interaction of both possibilities may serve to limit the overall effect of reef habitat in enhancing nekton abundances, particularly of mid-level fish species, and suggests that despite assumptions of increasing habitat value over time (i.e., Peterson et al., 2003), restored reefs provide immediate value that may only increase in time if the reef footprint, or complexity increases. Several studies have indicated that the refuge or habitat value may be critically dependent on reef complexity, including for example, shell orientation, which may influence settlement processes and predation pressure (Lenihan et al., 2001; Soniat et al., 2004; Grabowski et al., 2008; Humphries et al., 2011b). While the reefs clearly changed in terms of oyster size distributions on the reefs, it is not clear if there were actual changes in reef complexity or habitat provision that would affect reef value for fish and invertebrates within the 3 year time frame of this study.

The assumption of fisheries enhancement by the creation of oyster reefs assumes that fish production is limited by reef habitat. Within the complex marsh and shallow water estuarine complexes

of coastal Louisiana, determining which habitats may limit or support greater production can be difficult. In coastal Louisiana, while marsh extent is declining dramatically, and oyster reefs are considered threatened or declining on a global scale (Beck et al., 2011), this has not resulted in a decline of all Gulf estuarine-dependent fish and invertebrates (i.e., red drum, Powers et al., 2012). In our study, the potential for functional redundancy of the extensive and adjacent salt marsh habitat may have played an important role in results by mediating habitat availability and the recruitment processes that control fish and invertebrate production (Minello et al., 2003; Grabowski et al., 2005; Geraldi et al., 2009). For example, Grabowski et al. (2005) found that while reefs enhanced juvenile fish prey biomass, regardless of setting, juvenile fish abundance was only enhanced on restored reefs located within mudflats, and not when near saltmarsh or seagrass habitats. The positive effect of reefs located on mudflats may be due to a combination of the increased resource availability provided by the reefs, combined with the reefs isolation from functionally equivalent habitats (Grabowski et al., 2005). Geraldi et al. (2009) failed to find evidence of enhanced fishery use of oyster reefs restored in marsh tidal creeks, and concluded that this might be due to the reef being functionally redundant to the existing marsh complexity. For fisheries, presence not only of similar oyster reef habitat, but the value of surrounding habitat types and bio-physical environment may be critically important in determining the enhancement value of created reefs, and affect the development trajectory of these reefs (Grabowski et al., 2005; Geraldi et al., 2009).

4.4. Conceptual model of oyster reef development and conclusions

Provision of three key ecosystem functions attributed to the restoration of oyster reefs exhibited different temporal development trajectories. Services linked directly to the presence of a live oyster population, such as reef sustainability and water quality maintenance increased linearly over time and reached equivalence with oyster populations of other natural reefs reported in the literature within the first 3 years (e.g., Volety et al., 2009; Ross and Luckenbach, 2009; Puckett and Eggleston, 2012; Fig. 7). These processes are linked to provision of appropriate substrate for recruitment of oysters, and, importantly, the location of this substrate in appropriate conditions (salinity, temperature, DO) for development of viable oyster populations. This last caveat is important as reefs placed in areas not conducive to reef sustainability may either see no recruitment and development of an oyster population, or rapid recruitment but high mortality. Created reefs studied by Scyphers et al. (2011) experienced high oyster recruitment, but substantial mortality which they suggest may be due to high predation, or physical disturbance. Similarly, reefs created in a high salinity area in Louisiana found high recruitment, but no survival to market-size due to predation (La Peyre et al., 2013a), and reefs created in an area which frequently experiences monthly mean salinities less than 2 failed to develop long-term sustainable communities (La Peyre et al., 2013b).

Services associated more with the provision of structure, such as habitat provision and shoreline stabilization developed rapidly as predicted and these are linked to the direct result of providing added habitat complexity and hard bottom habitat within an area dominated by soft-bottoms. Use of this added habitat by fish and decapod crustaceans was immediate, and for known resident and reef-associated transient fish, abundances compared to nearby references were increased immediately but this did not change with time. If monitored for longer periods of time, it is possible that further enhancement would occur as reef

size or complexity approaches some threshold (Humphries et al., 2011b); it is also possible that in certain locations, redundancy of habitats may limit further augmentation of abundances over time (Grabowski et al., 2005; Geraldini et al., 2009; Stunz et al., 2010).

Shoreline stabilization is also related to the provision of structure, and occurred immediately, but the reefs were only effective when exposure conditions were high. This service is highly influenced by local conditions; only longer term monitoring will determine if further reef expansion and development will increase the provision of this service by the reefs. In identifying locations for reefs to provide shoreline protection, the use of exposure calculations to identify appropriate areas would be valuable given the relationship we found between high exposure and shoreline erosion reduction. Shoreline protection services of these restored reefs occurred not necessarily as a function of time and reef development, but were more related to energy exposure in the interior shallow estuarine areas of Louisiana, and may be further impacted by reef design and long-term sustainability as measured by changes in reef height and footprint. A similar project using created loose shell reefs suggested that the addition of a more rigid base for the created reef might be beneficial in ensuring long-term viability of these reefs, particularly in areas where the oyster population may not develop quickly (Scyphers et al., 2011).

Development trajectories of oyster reef function varied by function with those related to establishment of a viable oyster population increasing over time, and those related only to provision of a base structure occurring immediately. The development time-frame of oyster populations will vary depending on the location of the reef, and requires correct site location; the continued provision of services related to structure is dependent over time on the maintenance of the structure through the development of a viable oyster population. While the shape of the development trajectory likely remains true across sites with very different conditions, similar to restoration in other systems, the time frame of development may vary enormously at different sites, and be critically affected by local conditions (Suding, 2011). Understanding the factors driving development of services for any restoration project is critical to identify successful restoration trajectories, and to determine a priori, when and where restoration is a viable option (Holl and Aide, 2011; Mori, 2011).

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Appendix A.

Mean daily temperature, salinity and gauge height in Sister Lake, Louisiana from 2009 through 2012 during the study. Data taken from LDWF/USGS Continuous Data Recorder 07381349 - Caillou Lake southwest of Dulac, LA, U.S.A.

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