EVALUATING SUCCESS OF OYSTER REEF RESTORATION

A Dissertation

by

BRITTANY NICOLE BLOMBERG

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This dissertation meets the standards for scope and quality of
Texas A&M University-Corpus Christi and is hereby approved.

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ABSTRACT

Oyster reefs are the most degraded marine habitat type, with estimated global losses of 85% from historic abundances. Restoration efforts have increased to restore important ecosystem functions and services associated with oyster reefs. The objective of this study was to evaluate the success of oyster reef restoration projects from a variety of perspectives. The importance of oyster reefs, causes of degradation, and methods of restoration were reviewed (Chapter I). Oyster reef restoration projects across the United States were analyzed to examine temporal trends and influences of national policies (Chapter II). Oyster reef habitat was restored in Copano Bay, Texas and monitored for two years to examine habitat value (Chapter III), oyster diet composition (Chapter IV), and nutrient regulation functions (Chapter V). Finally, the results and implications of each chapter are summarized (Chapter VI).

In Chapter II, data were compiled from the National Estuaries Restoration Inventory to analyze oyster reef restoration projects. Over $45 million has been invested for the restoration of more than 150 ha of oyster reef habitat. Trends over time indicate projects are being implemented at larger scales with improved cost efficiency. However, this analysis revealed a lack of available monitoring data or project assessments. In Chapter III, an oyster reef complex was constructed in Copano Bay, Texas. The restored reef and natural reference habitats were monitored for two years to examine oyster and nekton communities. The restored reef had substantial oyster recruitment and growth, with oyster abundance and size comparable to reference conditions within the first year. Fishes and crustaceans recruited to the restored reef within six months post-construction, and abundance and diversity were comparable to reference habitats. High densities of oysters and nekton relative to other studies indicate this restored reef complex was successful in providing important ecological functions associated with habitat

provision and oyster production. In Chapter IV, a dual stable isotope ($\delta^{13}C$ and $\delta^{15}N$) approach was employed to assess oyster diet composition. Oysters and potential composite food sources — water column and sediment surface organic matter — were sampled from restored and reference habitats. Oyster diet composition was similar among habitats, but changed over time with increasing contributions of sediment organic matter. Results demonstrate that benthic food resources are important components of oyster diets, and that oysters may enhance the development of benthic algal food resources. In Chapter V, nitrogen removal attributed to the burial and mineralization of oyster deposits was quantified at the restored and natural oyster reefs through emergy analysis. Emergy evaluations can represent environmental and economic values of a system in equivalent units based on solar energy, and thus present an ecological approach to quantify ecosystem services. Results demonstrate that the restored reef was providing a greater function per unit area compared to the natural reef within the second year post-restoration.

This study provides insight into the effects of national policies on restoration trends, and stresses the importance of project assessments and data sharing to ensure future restoration projects make meaningful scientific contributions. The restored reef in Copano Bay was successful in supporting high densities of oysters, fishes and crustaceans. Much of this success could be attributed to the design of the reef complex, and thus will support the planning of future restoration efforts. Benthic organic matter was determined to be an important food resource for oysters, which will improve the development of food web and population dynamic models. This work also demonstrates the application of emergy analysis to quantify ecosystem functions and services, which can complement traditional economic valuation methods. Overall, the work presented here makes novel contributions to the broader knowledge of oyster reef restoration practice and theory.

DEDICATION

To my Dad

Warren Lee Blomberg

April 13, 1963 – December 23, 1992

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CHAPTER I: INTRODUCTION

1.1. Importance of oyster reefs in terms of ecosystem functions and services

Eastern oysters, *Crassostrea virginica*, are the most common oysters in North America, forming extensive reefs in estuaries throughout their range (Atlantic coast from Canada to Brazil) (EOBRT 2007; Beck et al. 2009). As a foundational species, oysters contribute to the integrity and functionality of estuarine ecosystems, and are an important ecological and economic resource. Though traditionally prized as an important food source, oysters have gained greater recognition for providing numerous other ecological functions and ecosystem services (Luckenbach et al. 1999; Brumbaugh et al. 2006; Grabowski & Peterson 2007; Coen et al. 2007). Ecosystem services are contributions from ecosystems that, directly or indirectly, support and enrich the lives of humans (Costanza et al. 2007; MEA 2005). The concept of ecosystem services provides a framework for examining linkages between the environment and human societies, and has gained popularity since the 1990s when seminal papers on the topic were published (de Groot 1992; Costanza et al. 1997; Daily et al. 1997). Basic categories and classifications of ecosystem services are now widely accepted, and include provisioning, regulating, cultural and supporting functions and services (de Groot et al. 2002; Hassan et al. 2005; Farber et al. 2006; Barbier et al. 2011).

Oyster reefs can have 50 times the surface area of an equally sized flat bottom, and provide important structure in often otherwise barren, muddy landscapes (Coen et al. 1999; Henderson & O'Neil 2003). Young oysters depend upon the hard shell substrate provided by reefs for attachment and growth, and this is the mechanism by which oyster reefs are formed and maintained. The complex structure of oyster reefs provides essential habitat for many fish and other invertebrates (Zimmerman et al. 1989; Breitburg 1999; Peterson et al. 2003; Plunket & La

Peyre 2005; Tolley & Volety 2005; Stunz et al. 2010; Reese Robillard et al. 2010). Many commercially important species depend on oyster reefs during some part of their life, whether as nursery habitat, refuge from predators or foraging areas (Beck et al. 2003; Coen & Grizzle 2007). Thus, oyster reefs can enhance tertiary productivity of estuaries and fishing opportunities for humans.

As filter feeders, oysters can regulate nutrients and wastes and play a significant role in estuarine nutrient cycles (Dame et al. 1984; Newell 1988; Beseres Pollack et al. 2013). Filtration rates of *C. virginica* have been estimated as high as 10 L hr^{-1} g^{-1} dry tissue weight (Newell & Langdon 1996). Based on filtration rates estimated by Beseres Pollack et al. (2011) in Texas, an individual oyster can filter over 26 liters of water each day. As oysters filter bay waters, they remove excess nutrients, pollutants and heavy metals, sediments, bacteria, plankton, and may play an important role in decreasing the occurrence of harmful algal blooms (Cerato et al. 2004; Grizzle et al. 2006). This filtering activity can improve water clarity and quality, which can subsequently enhance surrounding habitats. For example, increased water clarity allows more light penetration, which can have positive effects on nearby vegetated habitats, such as seagrass beds (Peterson & Heck 1999; Peterson & Heck 2001; Newell & Koch 2004).

1.2. Degradation of oyster reefs

Oyster populations are considered functionally extinct in many places worldwide. Even if oysters are present in a system, they may not be abundant enough to provide the ecosystem services associated with oyster reefs. Remaining oyster populations are often too dispersed or fragmented to support sufficient spawning and recruitment to maintain or build strong populations (EOBRT 2007; Beck et al. 2009). Compared to historical population estimates, oyster reefs in Europe are currently considered to be in poor condition (90-99% lost) or functionally extinct (> 99% lost). Oyster reefs in Australia are now classified as functionally extinct (> 99% lost). Some areas in South America report oyster reefs in good condition (< 50% lost); however, there is a lack of data availability in these areas. In North America, oyster reefs on the Atlantic and Pacific coasts of the United States are in poor condition (90-99% lost) or functionally extinct (> 99% lost) (Beck et al. 2009). The Gulf of Mexico is the largest ecoregion globally where oyster reefs are considered in fair condition (50-89% lost); the region also supports the world's largest natural oyster fishery (Beck et al. 2009; Beck et al. 2011).

The decline of oyster populations was initiated with historical overharvesting. The oyster fishery in the United States began with aboriginal Native Americans, and expanded with European colonization (Dugas et al. 1997; Kirby 2004). Commercial oyster harvesting began in the 1600s in the Hudson River Estuary, New York (Kirby 2004). By the early 1800s, the oyster fishery in the Hudson River Estuary had collapsed, and exploitation spread south into Mid-Atlantic States. In the 1880s, oyster landings were greatest in Chesapeake Bay (Maryland and Virginia). By the early 1900s, Chesapeake Bay landings had begun to decrease, and exploitation spread further south and into the Gulf of Mexico (Kirby 2004). Commercial oyster harvesting started in Texas after 1870 (Quast et al. 1988). The largest oyster fisheries have been in Gulf States since the 1940s. By 2000, 83% of the nation's oyster harvest was landed in the Gulf of Mexico (western Florida through Texas), and Chesapeake Bay landings had decreased to approximately 2% of their record-high landings in the 1880s (Kirby 2004). From 2000 to 2009, 51% of the U.S. oyster harvest came from Louisiana, 19% from Texas, and 30% from the remainder of the United States (NMFS 2010).

Intense harvesting and destructive fishing methods (e.g., bottom dredging, tonging) degraded the complex structure of oyster reefs and reduced vertical relief (i.e., height of reef from bay bottom) (Rothschild et al. 1994; MacKenzie et al. 1997; Luckenbach et al. 1999). In addition to harvesting oysters as a food resource, dredging was also used in some areas to harvest the ancient shell matrix buried in the sediment (Dugas et al. 1997; Luckenbach et al. 1999). Oyster shell itself is a valuable resource, and has many uses for construction (e.g., building material, road pavement), agricultural (e.g., fertilizer, poultry feed) and commercial purposes (e.g., lime production) (Doran 1965; Ceci 1984; Yoon et al. 2004). These activities have depleted the shell substrate available in estuaries. Larval oysters depend on the hard shell substrate of oyster reefs to settle and colonize; this is the mechanism by which reefs are formed (Galtsoff 1964; Stanley & Sellers 1986). Thus, as oysters are removed for harvest, their habitat is similarly reduced.

In addition to harvesting pressure, oysters have faced increased anthropogenic stressors. Coastal development and land use changes have increased upland erosion and runoff, leading to increased turbidity and pollution along shorelines and in estuaries (MacKenzie et al. 1997; EOBRT 2007). Pollution and nutrient loading degrade water and sediment quality, leading to eutrophication and accumulation of toxic pollutants (Stegeman & Solow 2002; Bricker et al. 2008). Eutrophication is prevalent in estuaries and along coastlines worldwide, and can lead to hypoxic conditions, increased occurrences of harmful algal blooms, and changes in community structure (Howarth et al. 2000; EOBRT 2007; Bricker et al. 2008; Montagna & Froeschke 2009). Hypoxic conditions can be stressful to oysters, and have caused massive mortalities (Lenihan & Peterson 1998). Harmful algal blooms (HABs) are occurring more often and persisting longer (Anderson et al. 2000). HABs can be stressful to oysters, and have also led to closures of oyster fisheries due to accumulation of HAB toxins that cause shellfish poisoning (Loosanoff 1953;

Anderson et al. 2000). Closure of oyster reefs to harvest can increase harvest pressure on oyster populations in other areas (EOBRT 2007).

Demands for freshwater and energy sources have increased with growing human populations. River flows have undergone substantial alterations since the first large dams were built in the 1920s (Aubrey 1993; Montagna et al. 2002). Decreases in freshwater inflow alter salinity characteristics of an estuary, often increasing salinities beyond the tolerable range of oysters (5-35 psu; optimum range 10-20 psu) (Bergquist et al. 2006; Montagna et al. 2009). Oil and gas drilling has expanded into coastal areas, and exploration continues further offshore. In 2010, the Deepwater Horizon oil blowout occurred in the northern Gulf of Mexico. In an effort to flush oil away from vulnerable marsh habitats, large amounts of freshwater were released into the estuaries of Louisiana. This effectively dropped the salinity below the tolerable range for oysters (< 5 psu), and resulted in massive mortalities (estimated 50% loss) of Louisiana's oyster population (Upton 2011).

Natural environmental changes and disasters also have a significant impact on oyster populations. Hurricanes and other severe storms have been known to cause large oyster mortalities. In 2008, Hurricane Ike struck Galveston Bay and covered an estimated 60% of the oyster reef area (3,885 ha) with large amounts of sediment, effectively smothering and burying oysters (McKinley & Crawley 2009). Climate change and sea level rise may alter habitat suitable for oysters, leading to mortality and changes in distribution of oysters and other species, particularly predators and parasites (EOBRT 2007). The southern oyster drill, *Stramonita haemastoma*, is a common predator of oysters in the Atlantic and Gulf of Mexico (Butler 1985; EOBRT 2007). This carnivorous gastropod can decimate oyster populations, and is more abundant at salinities greater than 15-20 psu (Butler 1985). The protozoan parasite, *Perkinsus* *marinus*, is the most common pathogen of oysters in the Gulf of Mexico, causing severe oyster mortalities (Ray 1966; Soniat et al. 2012). *P. marinus* infections are initiated by parasites released from the disintegration of infected dead oysters (Soniat 1996). The parasites accumulate in oyster tissue over time and infections tend to be size-specific, with large oysters having higher infection levels and disease-related mortality than small individuals (Andrews & Ray 1988). The disease proliferates rapidly at temperatures above 25° C and salinities greater than 15-20 psu (Powell et al. 1992). Decreased freshwater inflows, in conjunction with increased occurrences of drought conditions, result in salinity increases that are favorable to disease and predators affecting oyster reefs.

In summary, historical overharvesting initiated the degradation of oyster reefs, and additional anthropogenic and natural stressors have led to the current state of oyster populations worldwide.

1.3. Oyster reef restoration

In the United States, oystermen began replacing harvested oyster shell on reefs during the 1800s to maintain harvestable oyster stocks (Dugas et al. 1997; Luckenbach et al. 1999). Since then, much of the restoration efforts were managed by the states. Focus has been on maintaining harvestable reefs by planting cultch material to restore the hard substrate habitat necessary for oyster settlement (MacKenzie et al. 1997; Luckenbach et al. 1999). In the last 20 years, restoration of oyster reef habitat has become a broader priority for restoring a variety of important ecosystem services (Grabowski & Peterson 2007; Brumbaugh & Coen 2009; Beck et al. 2009). Common goals of such projects include habitat creation, shoreline stabilization, water quality improvement, broodstock enhancement and educational outreach (Coen et al. 2007; Grabowski & Peterson 2007; Brumbaugh & Coen 2009). Sustaining or enhancing the fishery resource may or may not be included as a goal. Oyster restoration projects are rarely, if ever, motivated by the need to protect the species itself, as persistence of the species is not currently believed to be at risk (EOBRT 2007).

A variety of restoration methods are employed to restore oyster reef habitat (Brumbaugh et al. 2006; EOBRT 2007; Brumbaugh & Coen 2009). Lack of suitable hard substrate habitat is the major problem facing oyster populations. Restoration projects to address this problem primarily involve replenishing degraded reefs with cultch material, or constructing new reefs. A variety of materials have been used. Clean oyster shell is one of the most common and desired materials because it most closely resembles natural reef structure and interstitial space. Traditionally, local shucking houses were the main source of oyster shell. However, with declines in harvest and canning operations, the availability of oyster shell has become limited (Leard et al. 1999; Brumbaugh & Coen 2009). Oysters shipped out of state for the half-shell market represent the loss of an important resource belonging to the state in which the oysters originated. To compensate for this loss, some states have established laws that require shells to be returned, or a tax or fee is paid for unreturned shells (Leard et al. 1999; EOBRT 2007).

Oyster shell recycling programs have become a common mechanism to collect oyster shell for use in restoration projects. Through such programs, shells are reclaimed from restaurants or local citizens and stockpiled and dried on land for 3-6 months. The drying period ensures that shells are clean and free of tissue, minimizing the risk of introducing disease or pathogens upon return to the water (Bushek et al. 2004; Cohen & Zabin 2009; Brumbaugh & Coen 2009). North and South Carolina established programs nearly a decade ago, in which shell recycling stations were set up throughout coastal counties (Brumbaugh & Coen 2009; SCDNR 2012; NCDENR 2012). Similar programs have been initiated in most U.S. states along the

Atlantic coast, and are now becoming common in the Gulf of Mexico (Brumbaugh & Coen 2009; GoMF 2012; FDEP 2012; HRI 2012).

Fossil shells of oysters and other molluscs (e.g., *Rangia* clam shell, calico scallop shell) dredged from bays and quarries have also been a common cultch material for reef restoration (MacKenzie et al. 1997; Luckenbach et al. 1999; EOBRT 2007). These resources are limited as well, and dredging activities have been restricted to reduce further environmental degradation (Leard et al. 1999; Brumbaugh & Coen 2009). A variety of other materials have been experimented with as cultch material, with varying degrees of success. Limestone has proven to be an effective and economically feasible alternative to shell cultch, with high spat settlement observed (Chatry et al. 1986; Haywood et al. 1999; George et al. 2015). Crushed concrete, granite and river rock have also been used as cultch materials (Dugas et al. 1991; MacKenzie et al. 1997; Luckenbach et al. 1999; Brumbaugh & Coen 2009; George et al. 2015). Typically, deployment of cultch materials to restore or construct reefs is done one of two ways. Subtidal restoration efforts generally involve the transportation and deployment of loose cultch materials via barges and excavators. For small-scale, intertidal restoration projects, cultch is often bagged into small mesh bags for deployment. This minimizes loss or spreading of cultch in areas of high wave energy or currents (Luckenbach et al. 1999; Brumbaugh et al. 2009). In recent years, new methods have been developed for the construction of large-scale intertidal reefs. Dome-shaped structures made of concrete (e.g., reef balls) and rebar cages (e.g., Reef BLK) have been used in oyster reef restoration projects that aim primarily to improve shoreline stabilization (Brumbaugh & Coen 2009).

In areas where restoration is also hampered by recruitment limitation, seed planting may be implemented (Luckenbach et al. 1999; Mann & Powell 2007; Brumbaugh & Coen 2009).

This is typically done one of two ways: wild seed transplanting and hatchery seed planting. Wild seed transplanting involves large-scale additions of oyster shell or other hard substrate in areas where natural spat settlement is known to be high, but where other factors may prevent oyster survival or harvest potential (e.g., polluted waters, high prevalence of disease). Shells and attached spat are collected from grow-out areas after spawning and spat settlement periods, and are then transplanted to restored reefs (Brumbaugh & Coen 2009; ORET 2009). Hatchery seed planting involves the production of oyster larvae in hatcheries from broodstock. The larvae are provided with shell for settlement in the hatchery, and then the spat-on-shell are planted on restoration reefs (Brumbaugh & Coen 2009; ORET 2009).

1.4. Monitoring and assessment of restoration projects

Monitoring a restoration project after implementation is critical to assess project success. Ecological restoration has expanded globally for its ability to stimulate recovery of degraded or disturbed ecosystems (Aronson & Alexander 2013; Menz et al. 2013) and plays a key role in natural resource management and policy decisions (Suding 2011). Synthesis and evaluation of previous restoration activities can provide key insights as to whether restoration approaches should be continued or changed, and can be used to support an adaptive resource management framework (Gregory et al. 2006; Wortley et al. 2013). Although thousands of hours and millions of dollars have been invested in oyster restoration projects (Mann & Powell 2007; zu Ermgassen et al. 2012), much skepticism surrounds their effectiveness (Mann & Powell 2007; Choi 2007; but see Schulte et al. 2009; Powers et al. 2009), and comprehensive project assessments are sparse (Hackney 2000; Kennedy et al. 2011; La Peyre et al. 2014).

Comprehensive monitoring plans and project assessments are necessary to examine return on investment, particularly with regard to ecosystem services (Brumbaugh et al. 2006;

Rey Benayas et al. 2009; Suding 2011; Menz et al. 2013), and to implement adaptive management strategies that maintain or correct the trajectory of a restoration project (Hackney 2000; Thayer et al. 2005; Suding 2011; Baggett et al. 2014). Monitoring structural and functional changes of restored reefs and surrounding environments should be incorporated in every project. Ultimately, effective mechanisms for data dissemination are essential to improve future restoration efforts and advance the field of restoration ecology (Thayer et al. 2003; Bjorndal et al. 2011; Menz et al. 2013).

1.5. Purpose and study approach

The purpose of this study was to assess the success of oyster reef restoration efforts. Exponential increases in restoration efforts have occurred in the past 20 years. However, many restoration projects end after the construction phase. Thus, relatively little is known about the success of these efforts in restoring ecological function. Monitoring is a critical step in the restoration process, not only for assessing restoration success, but also for informing adaptive management strategies. The objective of this study was to evaluate success of oyster reef restoration from a variety of perspectives.

Four studies were conducted to address this objective. First, a meta-analysis was conducted to examine trends in oyster reef restoration projects across the United States (Chapter II). Data for 187 restoration projects were compiled from the National Estuaries Restoration Inventory. Data were examined to understand temporal trends of project implementation and monitoring over the past decade (2000-2011). Regression analyses were utilized to quantify changes in project size and per unit cost over time. Hypotheses tested in this chapter were: 1) project implementation would become more efficient over time in terms of both size (e.g., project scale would increase) and cost (e.g., per unit restoration costs would decrease), 2) more ecologically meaningful success metrics would be included in monitoring plans over time, and 3) restoration-related policies would influence project trends over time.

The following three studies are based on a restoration project implemented in the Mission-Aransas Estuary, Texas. A 1.5 ha reef complex was designed and constructed in Copano Bay within the Mission-Aransas Estuary during the summer of 2011. A variety of parameters were monitored at the restored reef in addition to natural reference habitats (i.e., natural oyster reef and unrestored bottom) for two years post-construction. In Chapter III, structural and functional characteristics were measured to determine the success of the restored reef in terms of habitat value and oyster production. Oysters were collected to quantify oyster recruitment, density and size class structure. Resident and transient fishes and crustaceans were sampled to examine density and community similarity. In Chapter IV, relative contributions of potential water column and benthic food resources to oyster diets were examined at restored and reference habitats. Oysters and potential composite food sources — suspended particulate organic matter (SPOM) and sediment surface organic matter (SSOM) — were sampled, and compositions were determined using a dual stable isotope ($\delta^{13}C$ and $\delta^{15}N$) approach. In Chapter V, nutrient regulating functions were quantified using an energetic approach. While feeding, oysters transfer nutrients and organic matter to the sediments, where burial and mineralization can occur. Nitrogen removal attributed to the burial and mineralization of oyster deposits is quantified at the restored and natural oyster reefs through emergy analysis. Emergy is a measure of total energy necessary to produce a good or service, and thus can be thought of as 'energy memory.' Emergy evaluations can be used to represent environmental and economic values of a system in equivalent units, generally solar energy units, and provide a more complete alternative to traditional economic methods employed to value ecosystem services. Overall hypotheses for these chapters were: 1) differences in ecosystem structure and function would be observed between restored and reference habitats and 2) the restored reef would become more similar to the natural oyster reef reference over time.

Overall, this work demonstrates the value of assessing restoration success through a variety of perspectives: economic and policy analysis, habitat assessment, determination of oyster diets, and quantification of nutrient regulation functions. Chapter II presents restoration trends across the United States, and Chapters III, IV and V present ecological assessments of one of the first oyster reef restoration projects implemented in South Texas. Collectively, this work will serve to inform future oyster reef restoration efforts.

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CHAPTER II: TRENDS IN U.S. OYSTER REEF RESTORATION PROJECTS: PROGRESS, CHALLENGES AND OPPORTUNITIES

Abstract

Recent research revealing the extent of marine habitat degradation has ignited a surge of restoration efforts globally. In the U.S., restoration of estuarine habitats became a national priority with the Estuary Restoration Act (ERA) of 2000, and the National Estuaries Restoration Inventory (NERI) was developed in response to ERA requirements to track and disseminate project data. Oyster reefs, the most imperiled marine habitat, have received much funding and support, but oyster restoration projects have faced more scrutiny in recent years. I investigated the NERI to analyze U.S. oyster reef restoration projects. More than $45 million has been invested for the implementation of 187 non-compensatory oyster reef restoration projects. Over 150 ha of oyster reef habitat have been restored across the U.S., with projects most heavily concentrated in the Chesapeake Bay area and the Florida Gulf coast. Trends over time indicate that projects are being implemented at larger scales, increasing from an average of less than 0.4 ha in 2000 to over 1 ha on average in 2011. Costs per unit decreased from an average of more than $2.1 million per ha in 2000 to just over $500,000 per ha in 2011. However, this analysis confirms one major problem hindering the field of restoration ecology: a lack of available monitoring data or project assessments of success. Billions of dollars will be dedicated solely to ecosystem restoration projects and related scientific endeavors through the RESTORE Act, providing unprecedented opportunities to for advancements in the field of restoration ecology. Perhaps most important are improved monitoring and data sharing practices.

2.1. Introduction

Environmental change, natural perturbation, and anthropogenic activities have degraded marine habitats compared to historic levels (Kirby 2004; Lotze et al. 2006; McCauley 2015). Coastal wetlands, seagrasses, and oyster reefs alone have declined by 65-91% (Jackson 2008). Marine habitat loss is of particular concern because of cascading effects on biodiversity (Jones et al. 2004; Airoldi et al. 2008; Polidoro et al. 2010) and ecosystem service provision (Worm et al. 2006; Grabowski & Peterson 2007; Rey Benayas et al. 2009). In response, ecological restoration has expanded globally for its ability to stimulate recovery of degraded or disturbed ecosystems (Aronson & Alexander 2013; Menz et al. 2013) and plays a key role in natural resource management and policy decisions (Suding 2011). Synthesis and evaluation of previous restoration activities can provide key insights as to whether restoration approaches should be continued or changed, and can be used to support an adaptive resource management framework (Gregory et al. 2006; Wortley et al. 2013).

In the United States, restoration of estuarine habitats became a national priority with the Estuary Restoration Act (ERA) of 2000 (Title 1 within the Estuaries and Clean Waters Act of 2000). ERA goals include: promotion of estuarine habitat restoration, use of common monitoring standards, development of effective partnerships, improved cost-efficiency, and enhancement of monitoring and research capabilities to ensure sound science (ERA 2000). Monitoring is mandated, and monitoring standards and guidance were compiled into two volumes (Thayer et al. 2003, 2005) to help standardize metrics and methods for measuring structural and functional characteristics. In response to ERA requirements to track restoration projects and publicly disseminate project information, the National Oceanic and Atmospheric

Administration (NOAA) developed and maintains the National Estuaries Restoration Inventory (NERI, https://neri.noaa.gov), a database of estuary restoration projects around the country.

Oyster reefs, once dominant habitats in temperate estuaries world-wide, have experienced losses in abundance and extent greater than any other marine habitat (Beck et al. 2011; zu Ermgassen et al. 2012). Management efforts to maintain productive oyster fisheries have been widespread for centuries (MacKenzie et al. 1997; Breitburg et al. 2000; Kennedy et al. 2011), yet only recently have oysters gained greater recognition for the non-food benefits they provide that support and sustain human welfare (e.g., water filtration, shoreline stabilization, recreational fishing opportunities). Restoration efforts are increasingly focused on returning these valuable ecosystem services to society (Breitburg et al. 2000; Brumbaugh et al. 2006; Grabowski & Peterson 2007; Schulte et al. 2009; Powers et al. 2009; Beck et al. 2011; Beseres Pollack et al. 2013).

Although thousands of hours and millions of dollars have been invested in oyster restoration projects (Mann & Powell 2007; zu Ermgassen et al. 2012), much skepticism surrounds their effectiveness (Mann & Powell 2007; Choi 2007; but see Schulte et al. 2009; Powers et al. 2009), and comprehensive project assessments are sparse (Hackney 2000; Kennedy et al. 2011; La Peyre et al. 2014). In this study, I examined oyster reef restoration efforts in the U.S.A. to determine restoration progress, challenges, and opportunities since the ERA was enacted. A database was built of all oyster reef restoration projects funded through the ERA by compiling data from the NERI to examine 1) spatial distribution of restoration effort and funding, 2) trends in project size and cost, and 3) parameters used to determine success.

2.2. Methods

I compiled the database through queries of the NERI because it represents a national summary of restoration efforts, was developed in accordance with ERA mandates, and includes projects funded by ERA Council agencies (e.g. NOAA, EPA, Army Corps of Engineers, U.S. Fish and Wildlife Service and the USDA National Resources Conservation Service). Although the database does not encompass all restoration efforts across the Nation, it provides a uniform dataset for which to compare project variables and examine overall trends, particularly as they relate to federal policies and funding programs. The ERA defines restoration as "an activity that results in improving degraded estuaries or estuary habitat or creating estuary habitat (including both physical and functional restoration), with the goal of attaining a self-sustaining system integrated into the surrounding landscape" (ERA 2000). For inclusion in the NERI, projects must have been implemented after the ERA was signed into law (7 November 2000) and must not be mitigation or legally mandated restoration. Additionally, all projects must include monitoring to assess restoration success, and the monitoring plan must meet ERA monitoring standards (NERI 2012).

The NERI was queried on 17 April 2014 using the habitat filter "oyster reef/shell bottom." Full reports were examined for each project, and relevant data were collected (see Table 2.1). Project size was reported several times for each project, and was not always consistent. In an effort to facilitate uniform data collection, I used the value provided under "estimated acres to be restored." I assume this was the size expected for the funding awarded, and thus provides a better match to examine funding information. To examine restoration trends in relation to project size, acres were converted to hectares, and each project was assigned to one of four size classes: enhancement (0 ha), small (< 0.4 ha), medium (0.4–2.0 ha), or large (> 2.0

ha). Data for project costs consisted of the "original proposed project cost estimate" designated between federal and non-federal funding sources. For each project with acreage and funding data, cost per hectare was calculated.

Regression analyses were performed to examine trends over time (R version 3.0.1; R Core Team 2013) for number of projects, area restored, funding, mean hectares per project, mean cost per project and mean cost per hectare. Dollar values were converted into the same year dollars according to:

$$Cost_y = (Cost_x)*(CPI_y/CPI_x),$$

where *CPI* is the consumer price index and *Cost* is the project cost. Subscripts *x* and *y* denote the year of project implementation and year for which all values are converted to, respectively. Average CPI values for each year were obtained from the Bureau of Labor Statistics (BLS 2015). Data for number of projects, area restored and funding were $\log_{10}$ transformed, and all rate data —hectares per project, cost per project and cost per hectare— were square root transformed prior to analysis to improve statistical performance.

2.3. Results

A total of 192 projects were returned in the search. Despite ERA definitions and rules for project inclusion in the NERI, five compensatory projects were identified. I chose to follow the ERA definition of restoration, and thus excluded these compensatory projects from this analysis. The NERI did not contain any projects implemented after 2011, and 19 projects did not include a date. Although the rules for inclusion in the NERI stated that only projects implemented after the enactment of the ERA were to be included, eight projects were implemented between 1995 and 1999. To examine trends since the ERA, regression analyses included projects implemented during or after 2000. Only one project in the dataset did not provide any budget information.

Other than the distinction between federal and non-federal sources, no other funding metadata were provided. The report format provided a place for "total cost estimate for monitoring," but this was not reported for any project examined. Although all project records indicate a monitoring plan was developed, no data or assessments of restoration success were found. Within each project summary, a table was devoted to "Monitoring Parameters and Success Criteria" and a space reserved for a URL for monitoring data. However, in every project examined, no data were available.

2.3.1. Distribution of effort

The NERI contains 187 non-compensatory oyster restoration projects spanning all coastal states of the contiguous U.S. except Maine (Fig. 2.1; Table 2.1). Number of projects varied among states, with half of all projects implemented in Florida, Maryland and Virginia (43, 26 and 25 projects, respectively). Over 150 ha of oyster habitat have been restored, of which nearly 62% occurred collectively in Florida, Virginia and North Carolina (42.6, 26.2 and 24.1 ha, respectively).

Florida, Virginia and North Carolina also received approximately 53% of the total $45.3 million awarded. Overall, nearly two-thirds of total funding originated from federal sources, and one-third from non-federal dollars. Alabama and Louisiana relied most heavily on federal funding, with non-federal contributions of only 5.9% and 7.3% of total funds received in each respective state. Washington and Texas received the most non-federal support, which contributed 67.8% and 66.3% of total funding received by each state, respectively.

2.3.2. Project size and cost

Nearly 20% of projects involved enhancement activities, such as seeding extant reefs with oyster larvae or implementing restoration-related programs (e.g., shell recycling programs, education and outreach). The remainder of projects ranged in size from 0.004–19.8 ha, with an average project size of 0.99 ha (median = 0.24). The small (< 0.4 ha) size class contained the most projects (43%), yet accounted for only 5% of total area restored. The majority (64%) of total area restored has been accomplished through large (> 2.0 ha) projects, which represent less than 10% of all projects (Table 2.2).

Projects ranged in total cost from $500-$5,000,000, with an average project cost of $243,731 across all size classes (median = $105,250). Mean cost per hectare decreased exponentially with increased project size, from $3,477,339 for small projects (median = $1,235,527) to $97,989 for large projects (median = $41,043). In general, larger projects were supported primarily by federal funds, while small projects and enhancement activities were funded largely by non-federal dollars (Table 2.2).

Linear regression analyses indicated weak to moderate trends for project size and cost per hectare (Fig. 2.2). Average project size increased over time ($r^2 = 0.32$, $p = 0.055$), from 0.36 ha in 2000 to 1.07 ha in 2011 (Fig. 2.2A). Average cost per hectare decreased over time ($r^2 = 0.60$, $p = 0.003$), from $2,169,042 in 2000 to $517,950 in 2011 (Fig. 2.2B).

2.4. Discussion

2.4.1. Progress

Ecological restoration has become a global priority, with considerable implications for science, society and policy (Cairns & Heckman 1996; Suding 2011; Aronson & Alexander 2013). However, restoration efforts to date have generally been ad hoc and site- or project-specific. Individual oyster reef restoration projects are frequently small scale (< 0.4 ha), implemented by relatively small groups, and have occurred within short-term grant funding periods of 1-2 years (EOBRT 2007). Although these characteristics often make small projects desirable to funders by allowing broad distribution of available resources, it is unlikely that large functioning ecosystems will ever be achieved through the cumulative effects of small-scale projects (Manning et al. 2006; EOBRT 2007; Choi 2007; Mann & Powell 2007). Some large scale restoration projects are ongoing, including the Great Wicomico River, Chesapeake Bay (Schulte et al. 2009), the network of oyster reserves in Pamlico Sound, North Carolina (Puckett & Eggleston 2012) and the coast of Alabama (100-1000: Restore Coastal Alabama, 2015) . More projects of this size and scale are needed (Hobbs & Norton 1996; Soulé & Terborgh 1999).

Examination of restoration projects for other habitats within the NERI indicates that oyster reef projects may be particularly small. Within the submerged habitat category, 44% of projects comprise oyster reef (one of nine habitat types), yet these only account for 2% of area restored (NERI 2012). The total area of oyster reef restored by projects in this analysis represents only 0.17% of an estimated 86,000 ha lost from 28 bays across the U.S.A. (zu Ermgassen et al. 2012). The small scales at which most projects are implemented may not effectively sustain, enhance or restore ecosystem services, and the relatively large costs per unit size can be inefficient or even wasteful (Aronson et al. 2006; Rey Benayas et al. 2009).

ERA-funded oyster reef restoration projects have increased in size and decreased in per unit costs over the past decade. There are significant fixed costs associated with most restoration projects, and as a result, the cost-per-unit-area for relatively small projects can be exceptionally high while the cost-per-unit-area for large scale projects can be relatively low (King & Bohlen 1994; Spurgeon & Lindahl 2000). This is not an unusual phenomenon in restoration. For example, beach nourishment projects follow the same economies of scale principle. In a summary of beach nourishment projects on the Atlantic and Gulf Coasts of the United States, high density (e.g., volume per unit length) projects have smaller per unit costs than low density projects. (Dixon & Pilkey 1991; Valverde et al. 1999). Larger projects are frequently more cost efficient because of declining average fixed costs that includes construction costs such as mobilization, demobilization, and loading facility set-up (Chitkara 1998). Research to identify optimal scales of restoration activities and to remove barriers to large scale restoration projects would help to maximize efficiency and impact of investment (Cairns & Heckman 1996; Spurgeon & Lindahl 2000; Manning et al. 2006; Menz et al. 2013).

Lack of funding for large scale restoration projects is an obstacle that is linked to social and political goals and priorities (RAE 2002). In other words, society will continue life as usual until a loss of valued goods and services is realized and science and restoration are spurred into action (Hilderbrand et al. 2005). In 2009, over $10 million was awarded for the purposes of oyster reef restoration through the American Recovery and Reinvestment Act (ARRA) (zu Ermgassen et al. 2012). The dataset compiled in the present study contained seven ARRA projects implemented in 2009 and 2010, with six of them directly engaging in reef construction activities. The effect of this large influx of funding, accompanied by goals for funding large-scale projects, was significant. During 2009, when the largest ARRA projects were implemented, mean project size increased from 1.4 to 4.0 hectares. In addition, economic benefits were provided to local and regional economies (Pendleton 2010; Schrack et al. 2012; Edwards et al. 2013; BenDor et al. 2015). Every $1 million invested in oyster reef restoration through ARRA funding created on average 16.6 jobs and included workers such as fishermen, scientists, biologists, barge and tug operators, divers, and truck drivers (Edwards et al. 2013). The number of jobs created is relatively higher than other industrial coastal activities, such as oil and gas development, which generate approximately five jobs per $1 million invested (Edwards et al. 2013; BenDor et al. 2015). Proof-of-concept techniques were also scaled up to effect ecosystem-level changes (Pendleton 2010; Schrack et al. 2012), better facilitating future large-scale restoration efforts.

The move to a larger-scale framework for restoration does not mean that small-scale restoration should be dismissed but that smaller efforts should fit into a larger, coordinated guiding structure (Soulé & Terborgh 1999). Techniques such as backcasting are well suited to this goal, where an appropriate end point is envisioned, and then a pathway to attainment is worked out retrospectively by identifying key elements and projects required for success (Robinson 1988; Cinq-Mars & Wiken 2002). Community-based restoration projects, though small in scale, are vital in providing valuable experiences that have large social impacts (Cairns & Heckman 1996; Leigh 2005), connecting contemporary societies to these cultural keystone species, educating the public, and fostering environmental stewardship (Leigh 2005; Miller & Hobbs 2007). Inclusion of smaller community-based efforts in larger plans for system restoration could maximize the long-term contribution and effectiveness of such efforts while maintaining the unique social benefits these projects provide. Transparency and public inclusion in the restoration process is important for building support (Hackney 2000; Miller & Hobbs 2007; Suding 2011).

2.4.2. Challenges

A major hurdle to the advancement of restoration science, confirmed in this analysis, is the lack of available project data. In contrast, the ERA heavily emphasized the importance of monitoring and data sharing, with explicit goals to measure project effectiveness and enable adaptive management. Two comprehensive volumes were produced in association with the ERA to guide project implementation and assessment (Thayer et al. 2003, 2005), and the NERI was subsequently developed to facilitate data dissemination. It is not suspected that this lack of data accurately portrays monitoring activities, but rather, reflects obstacles in data dissemination, whether by lack of data provision or database maintenance.

Other studies have compiled regional databases of habitat restoration projects by direct contact with individual scientists, practitioners and agencies, and have similarly reported on the absence of project data. Kennedy et al. (2011) and La Peyre et al. (2014) described how less than one-half and one-quarter of oyster reef restoration projects in the Chesapeake Bay and northern Gulf of Mexico, respectively, were monitored or reported, hindering evaluation of project effectiveness. Similarly low monitoring and reporting rates were found for salt marsh restorations in northwestern Europe (Wolters et al. 2005) and U.S. river restoration efforts (Bernhardt et al. 2005). To maximize restoration success, we must be able to learn from past projects. As restoration efforts increase, this inability to assess project outcomes is particularly troublesome (Suding 2011; La Peyre et al. 2014).

The scarcity of monitoring data and project assessments have led to a patchwork of restoration projects without a strong scientific foundation (Suding 2011; Wortley et al. 2013). Because every restoration project is an ecological experiment, informing later efforts is critical to identify effective solutions for recovering degraded species and habitats (Cairns & Heckman 1996; Breitburg et al. 2000). Future restoration outcomes may be positively influenced by the availability, comprehensiveness, and up-to-date nature of monitoring data that can be used to create practitioner handbooks to guide future activities (e.g. Brumbaugh et al. 2006; Baggett et al. 2014).

Monitoring timeframes are also often too short to capture development of restored habitats to a mature state, when ecological functions and provision of ecosystem services may become more similar to reference habitats with time (Cairns & Heckman 1996; Hackney 2000).

Inclusion of ecosystem services and socio-economic metrics in monitoring plans, and measurement of such metrics over sufficient time periods to assess habitat function and service provision, would increase knowledge of the development and function of restored habitats and inform future efforts (Thayer et al. 2005; Brumbaugh et al. 2006; Wortley et al. 2013). For example, a network of restored oyster reefs in Pamlico Sound, NC initially supported high oyster densities and restoration was determined to be successful (Powers et al. 2009; Puckett & Eggleston 2012). However, nearly a decade after reef construction, monitoring efforts revealed extensive declines in oyster populations concurrent with increased prevalence of boring sponges (*Cliona*) (Dunn et al. 2014a, 2014b). This demonstrates the need for long-term monitoring. Additionally, capturing the costs and benefits of restoration activities on human well-being and community resilience, via ecosystem services, could garner support for additional protection and restoration of reefs (Spurgeon & Lindahl 2000; Pendleton 2010; Wortley et al. 2013).

Without effective use of, and contribution to science, projects are merely random acts of restoration (Gaskill 2014). Monitoring structural and functional changes of the restored reef and surrounding environment should be incorporated in every project. To this end, a sufficient proportion of the project budget should be devoted to monitoring and assessment. Based on experience, I suggest allocating a minimum of 10% of project funds to monitoring activities. Submission of data to a data portal, such as the NERI, should be a requirement for grant compliance (Bjorndal et al. 2011; McNutt 2015). Some funders withhold a percentage of grant funds until data are submitted and wide adoption of such practice could increase data availability. Additionally, a standardized data template or explicit data/metadata reporting requirements, like that available from the National Oceanographic Data Center, could make database population and maintenance more efficient.

Another hurdle to increasing project efficiency over time is that restoration cost data are frequently vague or unavailable (Spurgeon & Lindahl 2000; Bernhardt et al. 2005; BenDor et al. 2015). In this analysis, only total project cost, delegated between federal and non-federal funding sources, was identified. No other details were provided to identify various cost components by task (e.g. pre-construction, construction, post-construction) or input category (e.g. labor, materials, equipment). Making informed private and public funding decisions about habitat restoration projects calls for reliable restoration cost data (King & Bohlen 1994; BenDor et al. 2015). It is also important for new practitioners and scientists entering the field of restoration ecology to be able to determine reliable estimates of the costs of designing, implementing, and monitoring restoration projects to ensure project completion and monitoring success.

2.4.3. Opportunities

Large investments are being made for restoration of oyster reefs, among other habitats, yet, the piecemeal assessment information available limits evaluation of return on investment, or better yet the impact of investment. It is known, however, that habitat restoration can bring long-term benefits of improved fishing, recreational opportunities, storm surge buffering, and carbon sequestration, amongst others. Unlike 'gray infrastructure' that begins to depreciate early in its life, coastal 'green infrastructure' can appreciate over time increasing the quantity and quality of ecosystem services. Other important economic benefits include the creation of jobs as well as new opportunities for businesses (Stokes et al. 2012; Edwards et al. 2013; BenDor et al. 2015).

There is a need for improved strategies to ensure effective project implementation, comprehensive monitoring, and data dissemination so that restoration projects make meaningful contributions to science and society (Bjorndal et al. 2011; Aronson & Alexander 2013). This is particularly timely in the Gulf of Mexico with the 2012 Resources and Ecosystems Sustainability, Tourist Opportunities, and Revived Economies of the Gulf Coast States (RESTORE) Act, which allocates 80% of all fines paid under the Clean Water Act in response to the Deepwater Horizon disaster to the Gulf Coast Restoration Trust Fund. Billions of dollars will be dedicated solely to ecosystem restoration efforts and related scientific endeavors, providing an unprecedented opportunity for comprehensive habitat restoration and scientific advancement. "It would be very easy for states to use RESTORE funds as merely a way to pay for projects for which they did not have sufficient funding from other sources. That would be a great disappointment and clearly not what was intended by the legislation. We have a rare opportunity to address ecosystem issues on a grand scale, and to step away from that opportunity in order to address more provincial needs may be understandable but would be a singular failure" (McKinney 2014).

Now more than ever, the means exist to implement comprehensive restoration plans on a regional scale. There is great potential for these efforts to advance restoration science throughout the U.S.A. and globally. This opportunity must be embraced, and responsibilities that have been neglected must be fulfilled. Every on-the-ground effort should contribute to scientific knowledge, both natural and social, but improvements in data sharing and communication remain the biggest hurdles. Methods for monitoring restored habitats and sharing data are known; what is needed is the initiative and determination to actualize not only the legal obligations under the U.S. ERA and RESTORE Acts, but also scientific duties. To continue with a business-as-usual attitude in the face of unparalleled possibilities would be a great misfortune for marine habitat restoration and the field of restoration ecology.

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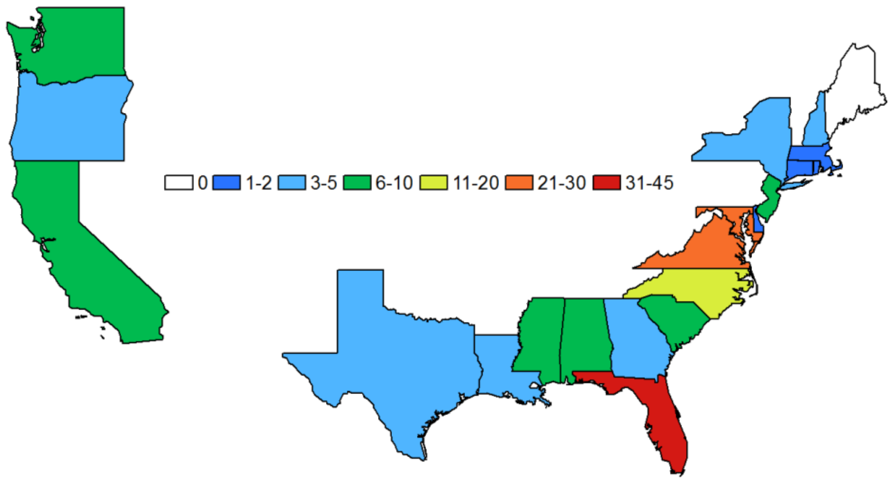

Fig. 2.1. Number of oyster reef restoration projects from the National Estuaries Restoration Inventory implemented in each state.

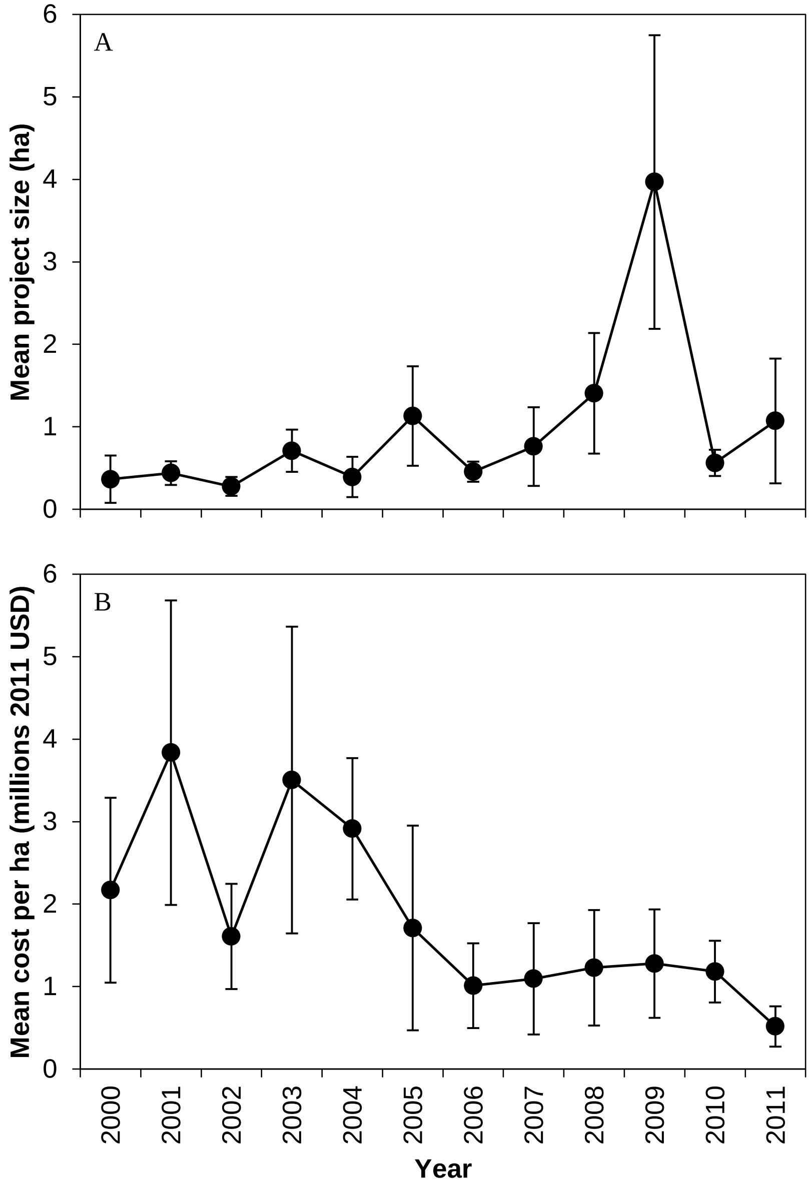

Fig. 2.2. Temporal trends in average (A) project size and (B) cost per hectare. Error bars represent SE.

Table 2.1. Summary, by state, of oyster restoration effort and funding from projects used in this analysis.

State	Number of projects	Total area restored (ha)	Mean project size (ha)	Total funding (US$)	Federal funding (US$)	Non-federal funding (US$)	Mean project cost (US$)	Mean cost per ha (US$)
NH	3	1.42	0.47	$362,446	$181,834	$180,612	$120,815	$7,498,670
MA	2	1.21	0.61	$111,767	$49,367	$62,400	$55,884	$89,617
RI	2	0.15	0.08	$117,208	$49,154	$68,054	$58,604	$379,944
CT	1	0.27	0.27	$29,750	$14,875	$14,875	$29,750	$111,385
NY	3	0.10	0.03	$268,739	$142,375	$126,364	$89,580	$494,082
NJ	7	4.58	0.65	$1,862,931	$742,084	$1,120,847	$266,133	$4,979,006
DE	1	0.09	0.09	$22,000	$11,000	$11,000	$22,000	$236,362
MD	26	10.45	0.40	$3,415,879	$1,376,469	$2,039,410	$136,635	$1,192,132
VA	25	26.16	1.05	$5,575,608	$3,685,509	$1,890,100	$223,024	$417,920
NC	20	24.09	1.20	$8,452,242	$6,226,708	$2,225,534	$422,612	$1,532,966
SC	6	0.23	0.04	$737,670	$449,573	$288,097	$122,945	$1,623,883
GA	3	0.12	0.04	$240,269	$115,249	$125,020	$80,090	$8,834,464
FL	43	42.58	0.99	$9,935,520	$6,342,324	$3,593,196	$231,059	$2,202,203
AL	9	7.11	0.79	$3,791,428	$3,567,137	$224,291	$421,270	$6,397,179
MS	7	14.30	2.04	$679,878	$337,097	$342,781	$97,125	$1,233,799
LA	5	2.15	0.43	$4,550,017	$4,216,997	$333,020	$910,003	$1,964,943
TX	3	1.62	0.54	$2,433,646	$819,408	$1,614,238	$811,215	$704,379
WA	7	5.87	0.84	$967,695	$311,415	$656,280	$138,242	$136,969
OR	4	6.30	1.58	$352,934	$156,844	$196,090	$88,234	$249,796
CA	10	1.87	0.19	$1,426,408	$797,566	$628,842	$142,641	$714,961
Total	**187**	**150.68**	**0.81**	**$45,334,035**	**$29,592,985**	**$15,741,051**	**$243,731**	**$1,953,196**

Table 2.2. Summary of oyster restoration projects by size class.

Size class	Number of projects	Total area restored (ha)	Funding			Mean cost (USD)	
			Total (millions USD)	Federal (%)	Non-federal (%)	per project	per ha
Enhancement (0 ha)	35	0	6.5	37%	63%	$185,180	N/A
Small (< 0.4 ha)	80	7.5	9.6	52%	48%	$121,774	$3,477,339
Medium (0.4 - 2.0 ha)	55	46.7	15.3	66%	34%	$278,328	$337,399
Large (> 2.0 ha)	17	96.4	13.9	87%	13%	$819,090	$97,989

CHAPTER III: HABITAT ASSESSMENT OF A RESTORED OYSTER REEF IN SOUTH TEXAS

Abstract

Oyster reefs are important foundational habitats and provide many ecosystem services. A century of habitat degradation caused the ecological extinction of oysters in many estuaries, thus spurring restoration efforts. In this study, a 1.5 ha oyster reef complex was constructed in Copano Bay, Texas to restore habitat for oysters and associated fauna. Oysters and resident and transient fishes and crustaceans were monitored at the restored reef in addition to natural oyster reef and unrestored bottom reference habitats for two years following reef construction. The restored reef had substantial oyster recruitment and growth, with oyster abundance and size comparable to reference conditions within the first year. Resident and transient fauna communities recruited to the restored reef within six months post-construction, and abundance and diversity were comparable to reference habitats. The high densities of oysters and resident nekton relative to other studies indicate that this restored reef was successful in restoring several ecological functions. Additionally, the present study provides insight regarding restoration trajectories and implications for monitoring timeframes. Significant changes observed in oyster densities between the first and second year post-restoration demonstrate the importance of monitoring over multiple years to capture multiple recruitment cycles and growth to market size. Nekton densities did not change significantly after the first year, but changes in community assemblages were observed through the end of the study. Overall, the restored reef in this study showed near-term success in providing important ecological functions associated with habitat provision and oyster production.

3.1. Introduction

Marine ecosystems have experienced critical levels of degradation and loss over the past century through various natural and anthropogenic stressors (e.g., climate change, coastal development, increased nutrient loading, extraction of natural resources) (Aubrey 1993; Montagna et al. 2002; Stegeman & Solow 2002; Lotze et al. 2006; Bricker et al. 2008). Seagrass and mangrove habitats have experienced global losses of about 30% from historic estimates. Salt marsh habitats have declined by 50% world-wide (Jackson 2008; Barbier et al. 2011). Oyster reefs are the most imperiled marine habitat on Earth, exhibiting losses of 85% from historic abundances (Beck et al. 2011, zu Ermgassen et al. 2012). Habitat degradation and loss is of particular concern because of associated losses in biodiversity and the provision of ecosystem services (Worm et al. 2006; Grabowski & Peterson 2007; Rey Benayas et al. 2009). Restoration projects have increased in an effort to reverse losses of habitat and decreases in ecosystem service provision.

Eastern oysters (*Crassostrea virginica*) are the most common oysters in North America, forming extensive reefs in estuaries throughout their range (Atlantic coast from Canada to Brazil) (EOBRT 2007; Beck et al. 2009). As foundational species, oysters contribute to the integrity and functionality of estuarine ecosystems, and are an important ecological and economic resource. Oysters have been an important food source for humans for centuries, but have recently gained recognition for many other services they provide (Luckenbach et al. 1999; Brumbaugh et al. 2006; Grabowski & Peterson 2007; Coen et al. 2007). In particular, the complex structure of oyster reefs provides essential habitat for a variety of fish and other invertebrates (Zimmerman et al. 1989; Breitburg 1999; Peterson et al. 2003; Plunket & La Peyre 2005; Tolley & Volety 2005; Stunz et al. 2010; Reese Robillard et al. 2010). Oyster reefs can have 50 times the surface area of an equally sized flat bottom, and provide important structure in often otherwise barren landscapes (Coen et al. 1999; Henderson & O'Neil 2003). Young oysters depend upon the hard shell substrate provided by reefs for attachment and growth, and this is the mechanism by which oyster reefs are formed and maintained. Many commercially important fishes and crustaceans depend on oyster reefs during some part of their life, whether as nursery habitat or foraging areas (Beck et al. 2003; Coen & Grizzle 2007). Thus, oyster reefs can enhance tertiary productivity of estuaries and fishing opportunities for humans.

Efforts to restore oyster reef habitat have increased, and often include goals of providing suitable habitat for the many resident and transient fishes and crustaceans that utilize reefs (Breitburg 1999; Peterson et al. 2003; Plunket & La Peyre 2005). However, relatively little is still known about the trajectories of reef and community development following restoration. It is important to understand how long it may take for the goals to be met, if they are met, and whether oyster reef restoration is a good investment (Grabowski et al. 2012, La Peyre et al. 2014a). Better understanding will improve knowledge of what metrics to monitor and at which timescales. Additionally, a better understanding of restoration trajectories will provide insight regarding the production-attraction debate. Artificial reefs are known to support increased abundances of fishes and other organisms, but it is highly debated as to whether these reefs merely attract organisms from other areas, or whether they enhance production (Grossman et al. 1997; Powers et al. 2003; Brickhill et al. 2005).

The goal of this study is to determine success of a restored oyster reef in Copano Bay, Texas, in terms of habitat provision and oyster production. Oysters and resident and transient fishes and crustaceans were monitored at the restored reef in addition to natural oyster reef and unrestored bottom reference habitats. The natural oyster reef represents the minimum end goal of restoration, while the unrestored bottom provides a reference of conditions prior to reef construction. An understanding of the dynamics of habitat provisioning by restored reefs is essential for assessing whether these habitats can function similarly to natural reefs, how long it takes for the restored reef to provide the similar habitat functions, and how these functions may change during reef development.

3.2. Material and methods

3.2.1. Study area

The Mission-Aransas Estuary is a bar-built estuary in South Texas composed of several shallow bays, the largest being Copano Bay and Aransas Bay (Fig. 3.1A). The area is characterized by a semi-arid, subtropical climate with infrequent rain events. The average tidal range is small (0.15 m) and water movement is predominantly wind-influenced (Evans & Morehead Palmer 2012). Oyster reefs are common throughout the system (Fig. 3.1A). Reefs are primarily subtidal, and more prominent in areas of low to moderate salinity (Beseres Pollack et al. 2011). The Mission-Aransas estuary is the southern-most extent of commercial oyster harvest in Texas, and oysters are the most profitable fishery in the estuary (NMFS 2009).

3.2.2. Reef construction

An oyster reef complex was constructed in Copano Bay in July-August, 2011, to restore habitat for oysters and associated fauna (Fig. 3.1B). The restoration site (28.13°N, 97.05°W) was chosen based on previous efforts to identify suitable areas for oyster reef development (e.g., water quality, oyster health, substrate characteristics) (Beseres Pollack et al. 2012). The three-dimensional reef complex was designed to maximize available resources and create a structurally complex habitat that incorporates hills and valleys as essential design elements (Lenihan &

Peterson 1998; Lenihan 1999; Stunz et al. 2010). These valleys create important corridors that can increase habitat use across a larger spatial scale (Lenihan & Peterson 1998; Lenihan 1999; Stunz et al. 2010). Eight reef mounds, each measuring 20 x 30 m (0.06 ha), were constructed of a concrete rubble base topped with oyster shell to achieve a vertical relief of 0.3 m. Concrete was reclaimed from chutes and hoppers of concrete trucks and crushed to class 3 riprap size to resemble the size of large oysters and maintain natural interstitial space within the reef. Oyster shell was reclaimed from Alby's seafood wholesaler in Fulton, Texas and through the Oyster Recycling Program founded by the Harte Research Institute (HRI 2009). All shell material was sun-bleached for at least six months before use to ensure all shells were free of oyster tissue and harmful bacteria (Bushek et al. 2004; Cohen & Zabin 2009). Construction occurred via barges and excavators during July 2011. The footprint of the restored reef complex encompasses approximately 1.6 ha, and is situated in close proximity to a subtidal natural oyster reef complex (Fig. 3.1B). Commercial harvesting via oyster dredges maintains a low vertical relief (~ 0.1 m) across much of the reef. The surrounding unrestored bottom is characterized by muddy sediments with dense shell hash and few scattered oysters, and provides a reference of conditions prior to reef construction.

3.2.3. Experiment setup

Six sites were haphazardly chosen at the restored reef as well as at natural reef and unrestored bottom reference habitats for a total of 18 fixed sampling sites (depth 0.6-1.7 m; Fig. 3.1B). Plastic sampling trays (0.64 x 0.70 m; 0.44 m^2) were lined with 0.6 cm aquaculture mesh and used to assess colonization and habitat use by oysters and resident crustaceans and fishes (Eggleston et al. 1998; Plunket & La Peyre 2005; Rodney & Paynter 2006; Gregalis et al. 2009). In August, 2011, following reef construction, trays were filled with approximately 20 L of corresponding substrate and secured in place with rebar hooks by divers. Trays deployed on restored reefs were filled with reclaimed oyster shell to match the veneer of the constructed reefs. An oyster dredge was used to collect natural reef material (i.e., oysters and dead shells), and this material was used to fill trays deployed on the natural reference reef. For the unrestored bottom reference habitat, trays were first deployed, secured and then filled with surrounding substrate (i.e., mud, shell hash, oysters) by divers using shovels. Six trays were deployed at each site so that sampling could occur for two years without tray replacement. This was done to ensure that sampling captured successional trends in reef development. Three additional sites were haphazardly chosen within each habitat type (9 sites total; Fig. 3.1B) for sampling of transient crustaceans and fishes using a beam trawl (2 m wide, 6 mm stretch mesh; Froeschke 2011).

3.2.4. Field sampling

Sampling commenced in February 2012 (six months following experiment setup) and occurred three times per year through September 2013, for a total of six sampling periods (February 2012, June 2012, September 2012, March 2013, June 2013, and September 2013). Environmental parameters were measured at each tray sampling site. Water temperature (°C), salinity (psu) and dissolved oxygen (mg L^{-1}) were measured 0.1 m from the bottom with a handheld Hydrolab data sonde. Water clarity was measured by Secchi depth (m). Discrete water quality samples were collected 0.1 m from the bottom using a horizontal van Dorn water sampler. Water samples were stored in amber Nalgene bottles and placed on ice until further processing in the lab to quantify chlorophyll-*a* and total suspended solids (TSS).

One tray was retrieved by divers from each site during each sampling period (i.e., total of six trays per habitat type per sampling period). Tray contents were rough sorted in the field. Oysters were thoroughly rinsed within buckets to dislodge mobile fauna and then stored on ice for transport to the lab. All crustaceans and fish were then collected and preserved in buffered formalin (10%) for laboratory analysis. Transient species were sampled at each habitat type using a beam trawl. The trawl was towed at approximately 1 m $second^{-1}$ for an average of 90 seconds at each site (average sampled area of 174 m^2). Samples were rough sorted in the field, and all fishes and crustaceans were preserved in buffered formalin (10%).

3.2.5. Laboratory analyses

In the laboratory, water samples were analyzed for chlorophyll-*a* using a non-acidification technique (Welschmeyer 1994; EPA method 445.0), and total suspended solids were also quantified (EPA method 160.2). Oysters were counted and measured for shell height from the umbo to posterior margin of the right valve (nearest 0.1 mm). Oyster abundance was transformed to density (ind. m^{-2}). Nekton samples were rinsed through a 1 mm-mesh sieve, identified to the lowest relevant taxonomic unit, enumerated and measured (standard length (or carapace width for crabs) to nearest 0.1 mm). For abundant species groups, a randomly selected subset (22 individuals, including smallest and largest specimens) was measured (Stunz et al. 2010). For each tray and trawl sample, faunal abundance was transformed to density (ind. m^{-2}), and diversity was calculated using Hill's N1 diversity (Hill 1973).

3.2.6. Data analysis

The effects of sampling period and habitat type on environmental parameters, oyster densities, oyster size, nekton densities, and N1 diversity were analyzed using two-way analysis of variance (ANOVA, $\alpha = 0.05$) models. Data were tested for normality and homogeneity of variances using Shapiro-Wilk and Levene tests, respectively. Fourth-root transformations were applied where needed to improve normality and homogeneity of variances. Significant interactions were examined using simple main effects analyses. Tukey's honestly significant different (HSD) multiple-comparison test was used to examine differences among treatment levels. Additional analyses were performed separately for the most abundant families and species. All data were analyzed in R 3.0.1 (R Core Team 2013).

Similarities in nekton communities among habitat types and sampling periods were examined in PRIMER version 7 (Clark & Gorley 2015). Non-metric multidimensional scaling (MDS) was performed based on a Bray-Curtis similarity matrix. The SIMPROF routine was used to determine significant differences among clusters, and cluster groups were superimposed on the plot for interpretation. ANOSIM was used to determine significant differences in communities among habitat types and sampling periods (Clark & Warwick 2001).

3.3. Results

3.3.1. Environmental parameters

Salinity ranged from 26.6-38.8 psu, water temperature from 13.8-30.1 °C, and dissolved oxygen from 4.6-8.7 mg L^{-1} over the course of the study period. Chlorophyll-*a* levels ranged from 0.1-7.8 μg L^{-1}. TSS concentrations ranged from 6.8-50.3 mg L^{-1} across all sampling dates. No significant differences in environmental parameters were observed between habitat types. Differences observed between sampling periods reflected expected seasonal trends.

3.3.2. Oysters

Oysters were analyzed by size class: spat (< 25 mm), submarket (25-76 mm), and market (> 76 mm). Significant interaction terms between habitat type and sampling period in the two-way ANOVA models for both spat and submarket oyster densities required simple main effects analysis. Throughout 2012, spat oyster densities remained low (< 600 ind. m^{-2}) and did not differ significantly between habitat types during any of the three sampling periods (Fig. 3.2A).

In March 2013, spat densities at the restored reef were significantly higher than densities observed at the natural reef ($p = 0.005$) and unrestored bottom reference ($p < 0.001$). Substantial recruitment was observed in June 2013, with spat densities greater than 1,000 ind. m^{-2} across all habitats. Spat density at the restored reef surpassed that at the natural reef and unrestored bottom reference habitats by September 2012 and remained highest through the end of the study period.

Submarket oyster density was significantly higher at the natural reference reef in February 2012 compared to the unrestored bottom reference habitat ($p = 0.011$; Fig. 3.2B), but not significantly different from the restored reef ($p = 0.067$). In June 2012, oyster densities decreased across all habitats, followed by increased densities in September 2012. No significant differences were observed between habitat types during June or September 2012. In March 2013, submarket oyster densities at the restored reef increased greatly. Submarket oyster density was significantly greater at the restored reef compared to unrestored bottom reference habitats ($p < 0.032$) throughout 2013, but was not significantly greater compared to the natural reference reef ($p > 0.15$). Similar to the pattern demonstrated by spat oysters, submarket oyster density at the restored reef surpassed that at the natural reef and unrestored bottom reference habitats by September 2012 and remained highest through the end of the study period.

Densities of market-sized oysters differed significantly among sampling periods ($p < 0.0001$), but not between habitats ($p = 0.078$) over the study (Fig. 3.2C). Market oysters were first observed at the restored reef during September 2012, approximately 13 months following reef construction. Market-sized oyster density at the restored reef surpassed that at the natural reef and unrestored bottom reference habitats by March 2013 and remained higher than the natural reef through the end of the study period. The lowest densities of market oysters were observed during June 2012, and were significantly lower than densities observed throughout

2013 ($p < 0.02$). No significant differences were observed between habitats during any sampling periods.

Shell height was examined for submarket and market oysters combined (Fig. 3.3). A significant interaction existed between habitat type and sampling period in the two-way ANOVA model for oyster shell height, and thus analysis of the main effects was required. At the beginning of the study (February 2012), oyster size was significantly different between all habitats ($p < 0.003$), with largest oysters (50.9 ± 1.9 mm) collected from the unrestored bottom habitat, and smallest oysters (30.4 ± 0.3 mm) at the restored reef habitat (Fig. 3.3). Oysters at the restored reef continued to be significantly smaller than those at both the natural reef and unrestored bottom reference habitats ($p < 0.005$) in June 2012. In September 2012, there were no significant differences in oyster size among habitats ($p > 0.18$). Oyster sizes remained largest at the unrestored bottom reference habitat throughout the remainder of the study, and in March 2013 were significantly larger compared to the restored ($p = 0.024$) and natural ($p = 0.046$) reef habitats. At the end of the study in September 2013, oyster shell height was comparable across all habitats ($p \geq 0.99$). In general, oyster size increased over the duration of the study from an average of 41.6 mm in February 2012 to 55.7 mm in September 2013 across all habitats.

3.3.3. Nekton

A total of 1,245 fish from 25 species and 21,832 crustaceans from 17 species groups were collected from tray and trawl samples throughout the study (Table 3.1). The greatest numbers of organisms were collected from the restored reef, with 556 fish from 21 species and 8,381 crustaceans from 14 species (Tables 3.2 and 3.3). The unrestored bottom reference habitat had the next highest abundance overall, with 391 fish from 21 species and 6,769 crustaceans from 15 species collected throughout the study (Tables 3.2 and 3.3). The fewest organisms were collected from the natural reef, with 298 fish from 19 species and 6,682 crustaceans from 15 species (Tables 3.2 and 3.3). However, the natural reef appears to be performing just as well as the unrestored bottom reference habitat when excluding a school of Atlantic croaker (n = 70) that was captured at the unrestored bottom habitat in February 2012. Across all habitats, the most abundant crustaceans were porcelain crabs (*Porcellanidae*, 46.8% RA (relative abundance)), mud crabs (*Xanthidae*, 34.6% RA) and snapping shrimp (*Alpheus heterochaelis*, 4.3% RA) (Table 3.1). The most abundant fishes were the code goby (*Gobiosoma robustum*, 1.3% RA) and the Gulf toadfish (*Opsanus beta*, 0.9% RA) (Table 3.1). Densities of resident nekton (i.e., tray samples) were much greater than densities of transient nekton (i.e., trawl samples) across all habitat types and sampling periods (Fig. 3.4). Additionally, crustaceans were much more abundant than fishes, for both tray and trawl samples.

3.3.3.1. Nekton Densities

Resident crustacean density averaged 1,097 ind. m^{-2} across habitats in February 2012, and was significantly lower throughout the rest of the study, averaging 190-384 ind. m^{-2} ($p <$ 0.001, Fig. 3.4A). No significant differences in total resident crustacean densities were observed between habitat types during the study ($p = 0.085$). The most abundant resident crustacean was the porcelain crab (*Porcellanidae*), and densities were significantly higher in February (average 601 ind. m^{-2}) than any other sampling period (range 101-201 ind. m^{-2}; $p < 0.0001$). Significant differences in porcelain crab densities were observed between habitat types, with the natural and restored reef habitats similar to each other ($p > 0.2$) but both greater than the unrestored bottom reference habitat ($p < 0.05$). Over the duration of the study, porcelain crab densities averaged 140 ind. m^{-2} at unrestored bottom reference habitats, 238 ind. m^{-2} at the natural reference reef, and 275 ind. m^{-2} at the restored reef. Mud crabs (*Xanthidae*) were the second most abundant resident crustacean, and were also significantly more abundant in February 2012 (average 475 ind. m^{-2}) than any other sampling period (range 46-135 ind. m^{-2}; $p < 0.001$). Throughout 2012, mud crab densities were significantly higher at the unrestored bottom reference habitat compared to the natural oyster reef reference ($p < 0.01$). Throughout 2013, no significant differences in mud crab densities were observed between habitats. Snapping shrimp (*Alpheus heterochaelis*) were the third most dominant crustacean. Densities of snapping shrimp were initially low (average 5.1 ind. m^{-2} in February 2012) and increased over the course of the study (range 14.3-33.4 ind. m^{-2}). In general, snapping shrimp were more abundant in natural and restored reef habitats (24.6-29.7 ind. m^{-2}) compared to the unrestored bottom reference habitat (16.2 ind. m^{-2}) over all sampling periods. The only significant difference between habitat types was observed during March 2013, when snapping shrimp densities were significantly higher at the restored reef (43.6 ind. m^{-2}) compared to the unrestored bottom reference (11.3 ind. m^{-2}; $p = 0.016$).

Resident fish densities were highest at the restored reef during February 2012 (mean 30.8 ind. m^{-2}) (Fig. 3.4C). Significant differences were observed between sampling periods ($p = 0.035$) and between habitats ($p = 0.049$) in the two-way ANOVA model. Tukey's post-hoc test identified the only significant difference in resident fish densities occurred between the restored reef in February 2012 and the unrestored bottom habitat in June 2012 ($p = 0.034$; Fig. 3.4C). Resident fish assemblages were dominated by *Gobiidae* species. Significant differences in *Gobiidae* densities were observed between habitats during February 2012 ($p < 0.04$) due to high densities at the restored reef (mean 30.4 ind. m^{-2}) compared to unrestored bottom (7.9 ind. m^{-2}) and natural reef (8.6 ind. m^{-2}) reference habitats. During the remainder of the study, goby densities ranged from 5.6-12.5 ind. m^{-2} across all habitat types. The oyster toadfish (*Opsanus beta*) was the second most abundant resident fish species. Densities of *O. beta* increased over the course of the study across all habitat types, from an average of 2.3 ind. m^{-2} in February 2012 to 10.1 ind. m^{-2} in September 2013. Densities observed in September 2013 were significantly higher than in February (p = 0.044) and June (p = 0.004) 2012. No differences between habitat types were observed over the duration of the study (p > 0.5).

Transient faunal densities observed in trawl samples were much lower than resident faunal densities observed in trays (Fig. 3.4A-D). A significant interaction term in the two-way ANOVA model for transient crustaceans required simple main effects analysis. High densities of crustaceans were observed at the unrestored bottom reference habitat during February 2012 (Fig. 3.4B), and crabs from the *Xanthidae* and *Portunidae* families were dominant. Over the remainder of the study, transient crustacean densities were generally highest at the restored reef (except during June 2013) and were dominated by grass shrimp (*Palaemonetes* spp.). No significant differences in transient crustacean densities were observed between habitat types during any sampling period.

Significant differences in transient fish densities were observed between sampling periods (p < 0.0001), but not habitats (p = 0.097) (Fig. 3.4D). These differences were attributable to high densities observed at the unrestored bottom reference habitats during February 2012 and at the restored reef during June 2012 (Fig. 3.4D). Atlantic croaker (*Micropogonias undulatus*) represented over half of all fishes identified at the unrestored bottom habitats in February 2012. In June 2012, high fish densities observed at the restored reef were due to the collection of a school of spot croaker (*Leiostomus xanthurus*). Lowest densities of transient fishes were observed in June and September 2013 (Fig. 3.4D).

3.3.3.2. Nekton Diversity

A significant interaction term between sampling period and habitat in the two-way ANOVA model for resident faunal diversity required simple main effects analysis. A general trend of increased diversity over time was observed for resident nekton (Fig. 3.4E). During June 2012, diversity observed at the natural reference reef was significantly higher than at the restored reef or unrestored bottom reference habitats ($p < 0.02$). No other significant differences between habitat types were observed during the study.

Transient faunal diversity was slightly higher and more variable than resident faunal diversity (Fig. 3.4E-F). Transient faunal diversity showed significant differences between sampling periods ($p < 0.0001$) in the two-way ANOVA model. Faunal diversity was significantly lower during June 2013 than during any of the previous four sampling periods ($p < 0.002$), and remained low in September 2013 (Fig. 3.4F). No significant differences were observed between habitat types overall ($p = 0.326$), nor within any sampling period.

MDS analysis of resident faunal communities identified two distinct clusters, with communities at least 60% similar to each other (SIMPROF: $p = 0.001$; Fig. 3.5A). Resident communities were significantly different among sampling periods (ANOSIM: $R = 0.619$, $p = 0.001$), but not among habitat types (ANOSIM: $R = 0.069$; $p = 0.826$). One cluster contains all habitat types during the first sampling period (February 2012) and unrestored bottom reference habitat communities observed during the second sampling period (June 2012). The other cluster is segregated into two groups: all remaining communities observed in 2012 are on the left, and all communities observed during the second year of the study (March, June and September 2013) are together on the right (Fig. 3.5A). Communities within each of these groupings are at least 75% similar to each other (SIMPROF: $p = 0.058$). MDS analysis of transient faunal communities identified five clusters, with communities at least 50% similar to each other (SIMPROF: $p < 0.05$; Fig. 3.5B). Transient communities were significantly different among sampling periods (ANOSIM: $R = 0.255$, $p = 0.01$), though not as strongly separated as resident communities. No significant differences were observed among habitat types (ANOSIM: $R = 0.065$, $p = 0.204$).

3.4. Discussion

A major goal of oyster reef restoration is to restore suitable habitat to support oyster recruitment and growth, and also the fauna communities associated with oyster reefs (Brumbaugh et al. 2006; Baggett et al. 2014). Oysters and associated fauna communities support desired ecosystem functions, such as providing critical habitat and supporting secondary and tertiary production (Coen et al. 1999; Peterson et al. 2003), and are often linearly associated with ecosystem services such as nutrient regulation, augmented potential oyster harvest and recreational fishing opportunities (Breitburg 1999; Grabowski et al. 2012). The results of this study indicate success of the restored oyster reef. Recruitment both of oysters and reef-associated fauna was observed in comparable numbers to reference habitats.

3.4.1. Oyster production

As restoration efforts continue to increase, restoration projects face more scrutiny (Mann & Powell 2007; Choi 2007). Oyster densities observed at the restored reef in the present study are at the high end of the spectrum of observations from other restoration projects. By the end of the study, oyster densities totaled over 4,000 ind. m^{-2} (Fig. 3.2). A restoration effort in Virginia regarded as highly successful reported oyster densities at high-relief (0.25-0.45 m) and low-relief (0.08-0.12 m) reefs just over 1,000 and 250 ind. m^{-2} respectively (Schulte et al. 2009). The restoration of these reefs in Virginia is considered unprecedented (Schulte et al. 2009; Bullock et al. 2011; Nyström et al. 2012). Thus, the oyster densities observed at the restored reef in the present study reflect tremendous success. Oyster densities observed in this study were substantially higher than any of the restored reefs sampled across the Gulf of Mexico by La Peyre et al. (2014b), who reported oyster densities across Texas, Louisiana, Mississippi and Alabama ranging from 0-392 ind. m^{-2} (La Peyre et al. 2014b). Oyster densities observed at a suite of constructed reefs within oyster sanctuary areas in North Carolina were generally lower than densities observed in the present study, with spat oyster densities less than 40 ind. m^{-2} and submarket oyster densities less than 250 ind. m^{-2} (Powers et al. 2009). Densities of market-sized oysters at the most successful reefs were over 100 ind. m^{-2} (Powers et al. 2009). These reefs have been protected for 3-30 years in no-harvest sanctuaries, and observed densities of market-sized oysters reflect the success of sanctuary designation (Powers et al. 2009).

In the present study, declines in oyster densities were observed across all size classes and habitats during June 2012. This was particularly evident for submarket oysters at the natural reference reef (Fig. 3.2B). This may have been due to mortality induced by the protozoan parasite, *Perkinsus marinus*, which causes the disease known as dermo (Ray 1966; Andrews & Ray 1988; Soniat 1996). Oysters collected from the natural reef in the study area exhibited high weighted prevalence values in both submarket and market-sized oysters (2.65 and 4.71, respectively) in January 2012 (Oyster Sentinel 2015). In June 2012, submarket oysters exhibited similar weighted prevalence values (2.65) and no market oysters were observed (Oyster Sentinel 2015). Market oysters were observed in November 2012, and exhibited high weighted prevalence values (3.21), as did submarket oysters (3.07) during this period (Oyster Sentinel 2015). Sharp increases in salinity coincident with increasing temperatures observed during summer 2012 indicate favorable conditions for the proliferation of *P. marinus* disease (Powell et al. 1992). Fortunately, subsequent increases in oyster density were observed across all size classes and habitats during September 2012. Highest oyster densities across all size classes were observed at the restored reef throughout 2013 (Fig. 3.2).

Submarket oysters were observed at similar densities at the restored reef during 2013 as were observed at the natural reef during the first sampling period (>300 ind. m^{-2}; Fig. 3.2B). This is a great indicator of success, as it would be expected to observe similar oyster densities at natural and successfully restored reefs (Brumbaugh et al. 2006; Baggett et al. 2014). However, it is unclear why submarket oyster densities at the natural reef do not return to former densities. Sedimentation was observed at the natural reef sites, though was not quantitatively measured. At the restored reef, sedimentation was not observed to the extent as observed at the natural reef. The restored reef complex was designed to achieve relatively high vertical relief (~0.3 m) to avoid as much as possible the effects of sedimentation (Lenihan 1999; Soniat et al. 2004). A previous restoration attempt in Copano Bay, constructed of oyster shell spread across mud bottom with minimal vertical relief, suffered from sedimentation (Beseres Pollack et al. 2009). Three years post-construction, densities of oysters averaged 44 ind. m^{-2} (± 26.3 SE; La Peyre et al. 2014b).

General trends of increased oyster size were observed over the course of the present study (Fig. 3.3). An unexpected observation was the larger size of oysters at the unrestored bottom reference sites. During the harvest process, oyster clumps must be culled (e.g., broken apart) and submarket oysters are required to be returned to the water (Quast et al. 1988). Many submarket oysters may be deposited on sediments surrounding the reefs from which they were collected, where they can then continue to grow. These non-reef areas likely experiences less pressure during oyster harvest compared to reefs. It is possible that these areas may be serving as an important sanctuary for large oysters (Puckett & Eggleston 2012). Larger oysters contribute more eggs with each spawn, and thus their reproductive effort, or fecundity, is greater than smaller oysters (Galtsoff 1964; Hayes & Menzel 1981; Thompson et al. 1996; Dame 2012). Thus, these large oysters on sediments surrounding reefs may be an important source of larvae for the colonization of nearby reefs. More research in this area could further examine this hypothesis and offer insight on the designation of oyster sanctuaries.

3.4.2. Habitat use

Many estuarine species depend on structured habitats, such as oyster reefs (Zimmerman et al. 1989; Beck et al. 2003; Coen & Grizzle 2007). Habitat provision for crustaceans and fishes is often a primary goal of oyster reef restoration efforts (Breitburg 1999; Peterson et al. 2003; Plunket & La Peyre 2005). The results of this study indicate that the restored reef is successful in providing suitable nekton habitat. Over the course of the study, average densities of resident fishes (18.4 ± 2.1 SE ind. m^{-2}) and decapod crustaceans (453.9 ± 66.8 SE ind. m^{-2}) observed at the restored reef were consistent with, or greater than observed at natural and restored reefs elsewhere. Stunz et al. (2010) observed similar fish densities (17.2 ± 1.9 SE ind. m^{-2}) and lower crustacean densities (62.3 ± 9.9 SE ind. m^{-2}) at reef plots constructed of live oysters in Galveston Bay, Texas. Fish and decapod crustacean densities ranged from 80-100 ind. m^{-2} at live oyster cluster treatments in Florida (Tolley & Volety 2005). Fish and crustacean densities observed at natural subtidal oyster reefs in Lavaca Bay and Sabine Lake, Texas were low (< 5 ind. m^{-2}; Reese Robillard et al. 2010; Nevins et al. 2014). Low densities were particularly surprising in Sabine Lake, considering the sampled reef represents the largest unfished oyster reef in the United States and is characterized by high vertical relief and substantial structural complexity (Nevins et al. 2014). However, the complexity of these reefs was so great that sampling was difficult, and low nekton densities are likely a reflection of poor gear efficiency (Nevins et al. 2014).

Over the course of the present study, differences in species assemblages between tray and trawl samples, and between habitat types, were observed. The most pronounced difference was observed for small swimming crabs (*Portunidae*). They represented the only crustacean to be collected exclusively in trawl samples, and were relatively abundant (1.2% RA). They were observed at all habitats, with mean densities higher at the unrestored bottom sites (0.05 ± 0.04 ind. m^{-2}) compared to the natural and restored reef sites (both 0.02 ± 0.01 ind. m^{-2}). Additionally, they were almost exclusively observed during winter (67.7% of total catch observed in February 2012) and early spring (29.7% of total catch observed in March 2013) sampling periods. This indicates that the bare sediment and shell hash habitats may be important settlement habitats for juvenile blue crabs (*Callinectes sapidus*), which are an important commercial species and have shown troubling declines over the past decade in this area (Sutton & Wagner 2007).

A surprising finding in this study was the high degree of nekton use of the unrestored bottom reference habitats. This is in contrast to many studies that have compared relative habitat density among estuarine habitats of various structural complexities, which overwhelmingly indicate higher nekton densities associated with structured habitat compared to bare sediment (Harding & Mann 2001; Lenihan et al. 2001; Tolley & Volety 2005; Plunket & La Peyre 2005; Stunz et al. 2010; Reese Robillard et al. 2010; Humphries et al. 2011). However, it has been shown that shell hash or rubble is an important and highly utilized habitat for estuarine species (Lehnert & Allen 2002; Shervette & Gelwick 2008). Bare sediments have also been shown to support similar or higher abundances of transient species compared to reefs (Gregalis et al. 2009; Pierson & Eggleston 2014).

It is possible that the unrestored bottom sites in this study performed so well due to their proximity or connectivity to the natural and restored reef sites. For example, Gregalis et al. (2009) observed higher numbers of transient fishes at unrestored bottom reference sites following reef construction compared to observations prior to construction. Similarly, Grabowski et al. (2005) observed increased fish abundances at mudflat habitat following the construction of oyster reefs in the area. Due to the fact that sampling at unrestored bottom and natural reef sites in the present study did not start before the construction of the restored reef, it is not possible to determine whether observed densities were due to increased use of the nearby restored reef. However, it has been widely demonstrated that landscape connectivity is critical to the dispersal and colonization of organisms, and that bare habitats can serve as important corridors, facilitating the movement of organisms between other habitats (Taylor et al. 1993; Anderson & Danielson 1997; Kindlmann & Burel 2008).

Additionally, it has been shown that the presence of live oysters does not necessarily affect the habitat value for resident fishes and crustaceans (Tolley & Volety 2005). The micro-structure provided by oyster shells and shell hash may be enough structure to provide refuge for some species (Lehnert & Allen 2002). Also, it might be desirable habitat for certain functions. For example, empty shells are desired spawning substrate for several reef resident fishes (Crabtree & Middaugh 1982; Tolley & Volety 2005). During spawning, less structured habitat consisting of empty shells and shell hash may be a critical habitat for fishes such as gobies, blennies, and skilletfish.

Structured habitats (e.g., oyster reefs, seagrass beds, coastal marshes) receive more attention when discussing essential fish habitat, particularly for juveniles as nursery habitats (Beck et al. 2003; Coen & Grizzle 2007). Restoration efforts are increasing around the U.S. and globally to recreate structured habitats. In this study, bare sediments, or at least those with some micro-structure via shell hash, are providing similar habitat value as more structured reef habitats. Thus, further research to understand the relative value of bare substrates is warranted. Additionally, I suggest that bare sediments be included in restoration assessments. This will support return on investment analysis, and will be increasingly important as restoration efforts face more scrutiny for the large expense and perceived failure of some projects (Mann & Powell 2007; Choi 2007).

3.4.3. Restoration trajectories

It is important to understand trajectories of reef and community development following restoration in order to determine how long it takes for restoration goals to be met, and also to provide insight regarding the appropriate timeframes for monitoring various metrics of restoration success. In the present study, monitoring lasted for two years following reef construction in an effort to capture year-to-year variability and at least two oyster recruitment cycles. Interesting patterns were observed for oyster density and size from the first year to the second. It is evident that to assess the successful growth of adult oysters, monitoring needs to occur for at least two years. Oyster size and densities of submarket and market oysters did not approach similar values observed at the natural reef until after one year post-restoration. In colder waters where oyster growth is slower (Shumway 1996; EOBRT 2007), longer monitoring timeframes (e.g., five years) may be warranted. Additionally, substantial increases in spat recruitment were observed across all habitats during the second year of monitoring. Spat recruitment can vary greatly from year to year (Kennedy 1996). Thus, monitoring over multiple years is important for understanding recruitment dynamics at restored reefs.

An interesting pattern was observed in relative densities between size classes. Spat, submarket, and market-sized oysters exhibit approximately an order of magnitude difference in densities (Fig. 3.2), indicating approximately 10% survival rates between size classes. This observation is supported by survival estimates of oysters in Texas (Quast et al. 1988) and other molluscs in Copano Bay (Cummins et al. 1986). Better understanding of survival rates between size classes of oysters could improve monitoring efficiency. For example, observations of spat oyster densities over short time frames could provide a basis for estimating potential densities of larger oysters that could only be observed over longer time frames.

Temporal variations in resident crustacean and fish densities were also observed. The highest densities of resident crustaceans and fishes at the restored reef were observed during the first sampling period (six months post-construction). A significant decline in resident nekton densities was observed during the following sampling period, and levels were sustained for the remainder of the study. This observation indicates that monitoring of nekton should be conducted for at least one full year post-restoration. Personal observations during experiment setup (one month post-restoration) lead me to believe resident nekton densities may have been even higher immediately following reef construction. During placement of the trays at the restored reef, substantial noise was observed, indicating high use of the habitat by resident species (Lillis et al. 2014). The soundscape of the restored reef was considerably loud compared to the natural reef and unrestored bottom reference habitats during experiment setup, and the same level of noise was not observed during any subsequent sampling periods, including the first sampling event in February 2012. This evidence supports the hypothesis that new structure attracts nekton, rather than causing increased nekton production (Powers et al. 2003; Humphries et al. 2011). Attraction to the new reef habitat could also explain the relatively low numbers of nekton collected at the natural reef. Recruitment to the restored reef is likely due to movement from the nearby natural reef, resulting in a net loss of organisms from the natural reef habitat they previously occupied.

These observations also highlight important implications of replacing sampling trays between sampling events. Replacement of sampling units and substrates is common (Eggleston et al. 1998; Lehnert & Allen 2002; Tolley & Volety 2005; Plunket & La Peyre 2005; Gregalis et al. 2009; but see Humphries et al. 2011), and is likely due to budget constraints. However, I argue that replacement of sampling units between sampling events does not allow observations of succession patterns or development trajectories that are important to assessing success of restored habitats. This is further supported by analysis of resident community assemblages. As time progress, community assemblages become increasingly similar, and by the second year of monitoring, all samples exhibited 75% similarity to each other. By replacing sampling units between sampling events, observations may continually reflect initial attraction rather than sustained use.

3.5. Conclusion

In conclusion, the restored reef habitat shows remarkable success in terms of providing suitable habitat for oysters and nekton. Within the first year post-restoration, oyster densities observed at the restored reef were similar or greater than observations at reference habitats. Oyster sizes were similar between natural and restored reefs after one year post-restoration. Nekton densities were similar between all habitats throughout the study and community assemblages among the restored and reference habitat became more similar over time. The high densities of oysters and resident nekton relative to other studies indicate that this restored reef was highly successful.

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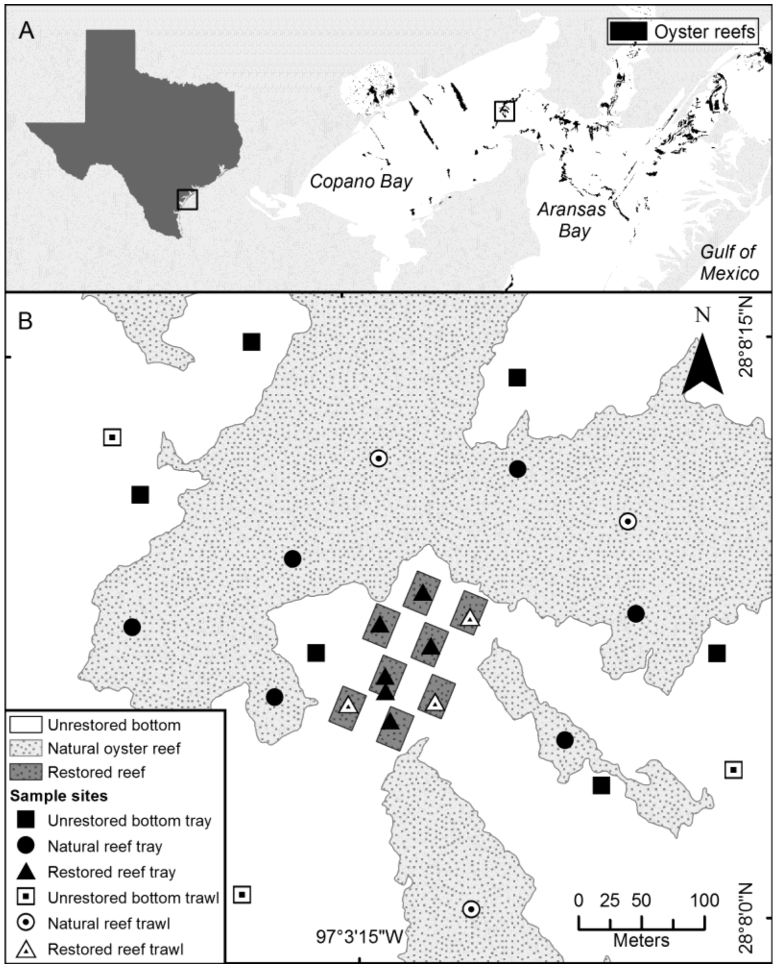

Fig. 3.1. Study area. A) Mission-Aransas Estuary, Texas; oyster reefs shown in black. The location of the restored reef complex in Copano Bay is indicated by the black box. B) Sampling sites.

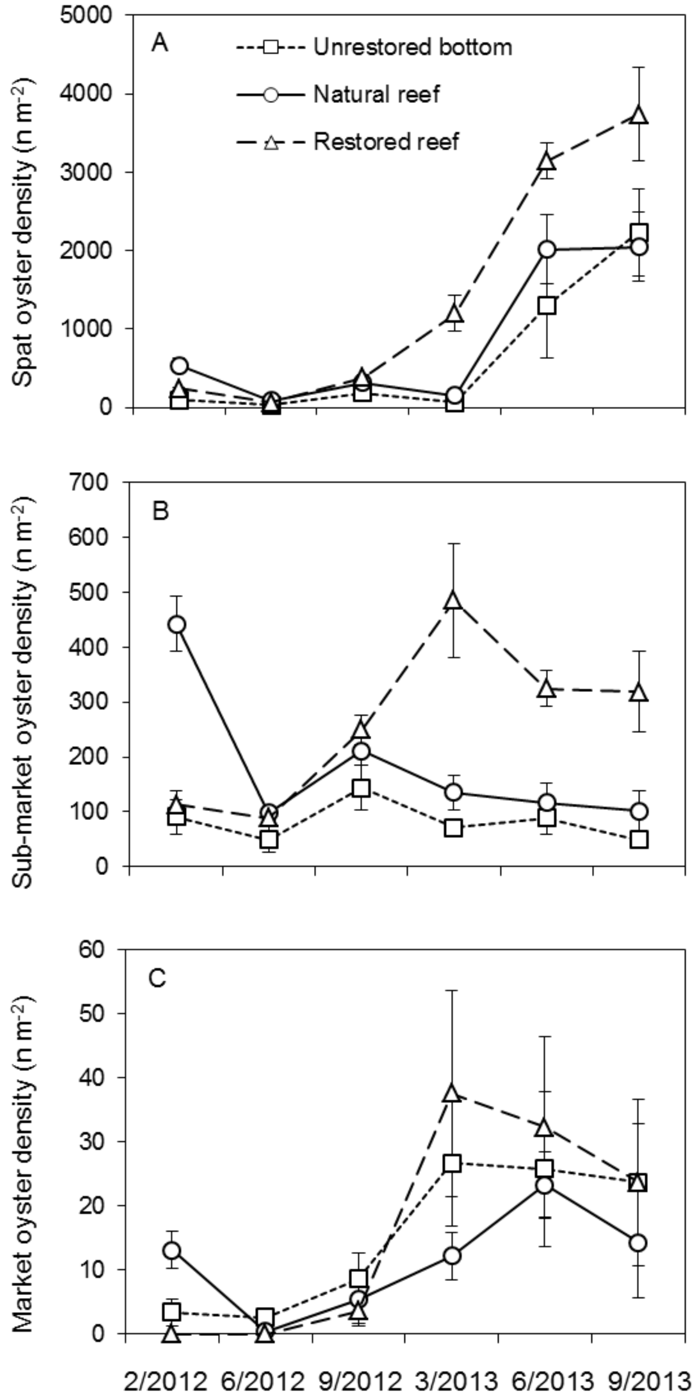

Fig. 3.2. Oyster density (mean ± SE) observed at unrestored bottom, natural reef and restored reef habitat types during each sampling period. A) Spat oysters (<25 mm). B) Sub-market oysters (25–76 mm). C) Market-sized oysters (>76 mm).

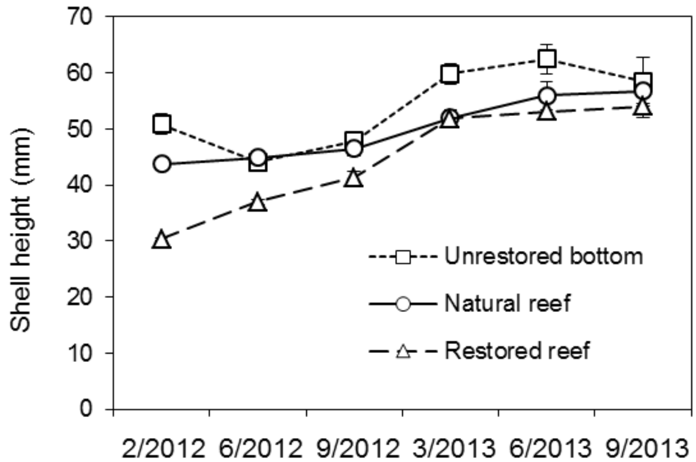

Fig. 3.3. Shell height (mean ± SE) of submarket and market oysters (> 25 mm) from unrestored bottom, natural reef and restored reef habitat types during each sampling period.

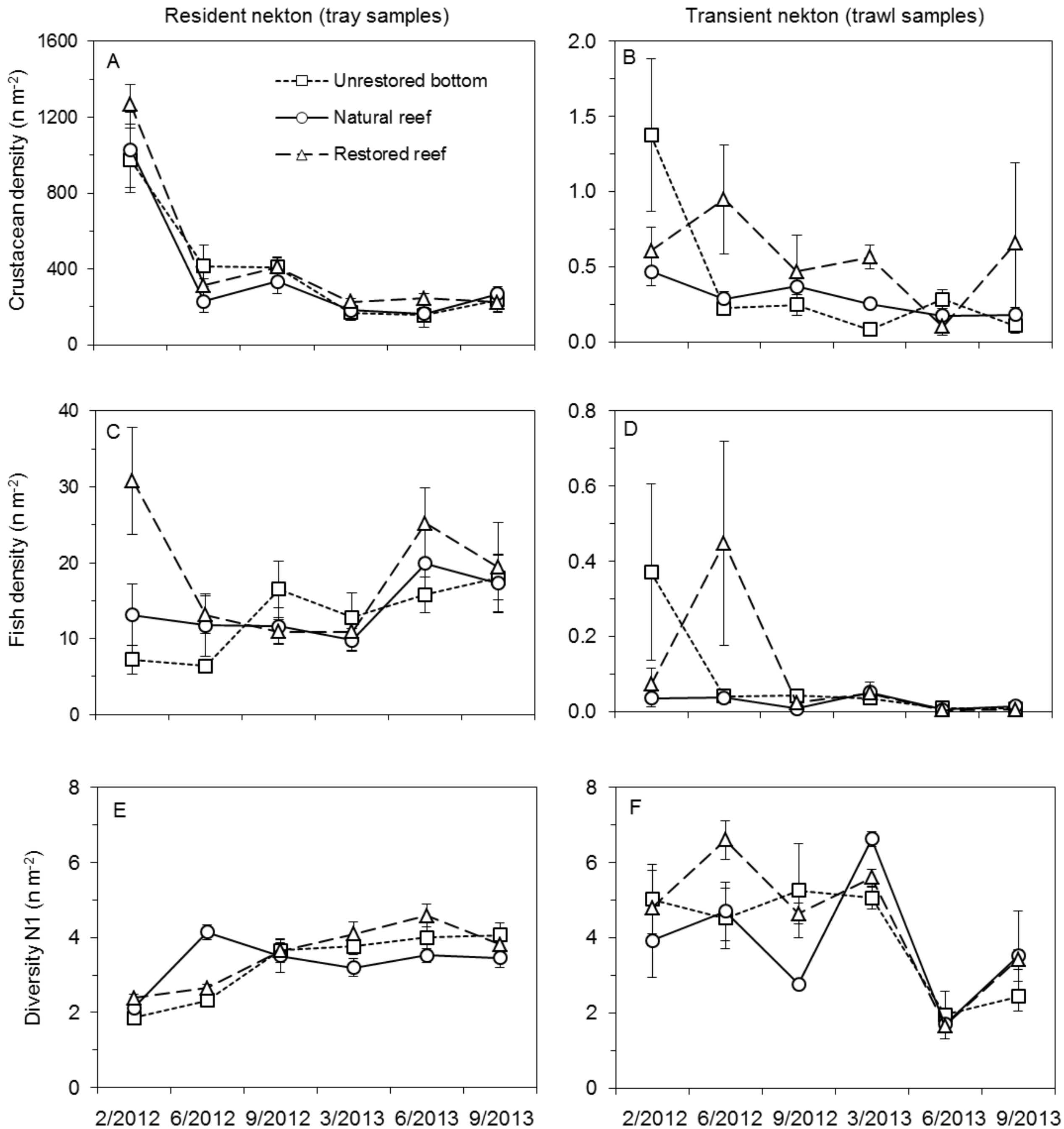

Fig. 3.4. Resident (A) and transient (B) crustacean density, resident (C) and transient (D) fish density, and diversity of resident (E) and transient (F) communities. Density reported in number of individuals per square meter; diversity reported as Hill's N1; all values reported as mean±SE.

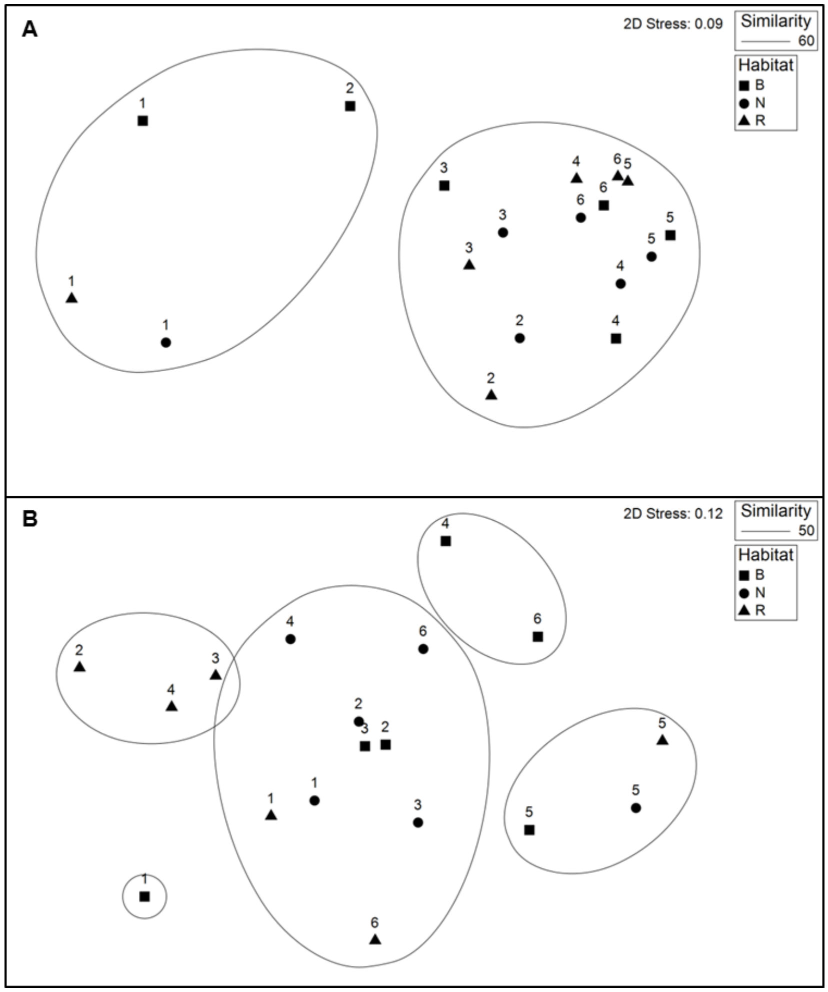

Fig. 3.5. Non-metric multidimensional scaling analysis of mean community structure of fish and crustaceans collected via trays (A) and trawls (B) for each habitat and sampling period combination. Symbols indicate unrestored bottom (B, squares), natural reef (N, circles) and restored reef (R, triangles) habitats. Numbers indicate sampling period, starting in February 2012 (1) through September 2013 (6). Lines show similarity grouping results related to community differences; similarity numbers indicate percent similarity of samples encompassed within each grouping.

Table 3.1. Total catch, relative abundance (RA), and gear, habitat and seasonal occurrence of fish and crustaceans collected during the study.

Common name	Scientific name	Total catch	RA (%)	Gear occurrence	Habitat occurrence	Seasonal occurrence					
						Feb-12	Jun-12	Sep-12	Mar-13	Jun-13	Sep-13
Total fish		**1,245**	**5.4**								
Code goby	*Gobiosoma robustum*	289	1.3	tray, trawl	B, N, R	X	X	X	X	X	X
Gulf toadfish	*Opsanus beta*	209	0.9	tray, trawl	B, N, R	X	X	X	X	X	X
Spot	*Leiostomus xanthurus*	177	0.8	tray, trawl	B, N, R		X	X			
Darter goby	*Ctenogobius boleosoma*	114	0.5	tray, trawl	B, N, R	X	X	X	X	X	X
Naked goby	*Gobiosoma bosc*	101	0.4	tray, trawl	B, N, R	X	X	X	X	X	X
Goby species	*Gobiidae*	95	0.4	tray, trawl	B, N, R	X	X	X	X		X
Atlantic croaker	*Micropogonias undulatus*	88	0.4	trawl	B, N, R	X			X		
Skilletfish	*Gobiesox strumosus*	73	0.3	tray, trawl	B, N, R	X	X	X	X	X	X
Green goby	*Microgobius thalassinus*	28	0.1	tray, trawl	B, N, R	X	X	X	X	X	
Stretchjaw blenny	*Chasmodes longimaxilla*	16	0.1	tray, trawl	B, N, R	X	X	X		X	X
Pipefish	*Sygnathidae*	14	0.1	tray, trawl	B, N, R	X	X	X	X		X
Bay whiff	*Citharichthys spilopterus*	12	0.1	trawl	B, N, R	X		X		X	X
Blackcheek tonguefish	*Symphurus plagiusa*	4	0.0	trawl	B, N, R				X		
Freckled blenny	*Hypsoblennius ionthas*	3	0.0	tray	N, R	X			X	X	
Gray snapper	*Lutjanus griseus*	3	0.0	tray	B, N				X		
Least puffer	*Sphoeroides parvus*	3	0.0	trawl	B, N, R		X				X
Pigfish	*Orthopristis chrysoptera*	3	0.0	tray	B, N			X			X
Speckled worm eel	*Myrophis punctatus*	3	0.0	tray, trawl	B, N, R		X		X		X
Feather blenny	*Hypsoblennius hentz*	2	0.0	tray	B, N	X					
Pinfish	*Lagodon rhomboides*	2	0.0	trawl	B, R			X			
Sheepshead	*Archosargus probatocephalus*	2	0.0	trawl	B, R	X	X				
Bay anchovy	*Anchoa mitchilli*	1	0.0	trawl	R				X		
Blackwing searobin	*Prionotus rubio*	1	0.0	trawl	R	X					
Spotfin mojarra	*Eucinostomus argenteus*	1	0.0	tray	B						X
Unidentified larval fish	*Unidentified larval fish*	1	0.0	tray	R			X			
Total crustaceans		**21,832**	**94.6**								
Porcelain crabs	*Porcellanidae*	10,791	46.8	tray, trawl	B, N, R	X	X	X	X	X	X
Mud crabs	*Xanthidae*	7,977	34.6	tray, trawl	B, N, R	X	X	X	X	X	X
Snapping shrimp	*Alpheus heterochaelis*	990	4.3	tray, trawl	B, N, R	X	X	X	X	X	X
PL penaeid shrimp	*Postlarval Penaeidae*	542	2.3	tray, trawl	B, N, R	X	X	X	X	X	X
Marsh grass shrimp	*Palaemonetes vulgaris*	442	1.9	tray, trawl	B, N, R	X	X	X	X		X
Grass shrimp	*Palaemonetes spp.*	390	1.7	tray, trawl	B, N, R	X	X	X	X		X
Gulf stone crab	*Menippe adina*	320	1.4	tray, trawl	B, N, R	X	X	X	X	X	X
Swimming crabs	*Portunidae*	266	1.2	trawl	B, N, R	X	X	X	X		X
Arrow shrimp	*Tozeuma carolinense*	57	0.2	tray, trawl	B, N, R	X	X	X	X		X
Brown shrimp	*Farfantepenaeus aztecus*	25	0.1	tray, trawl	B, N, R	X	X	X		X	
Olivepit porcelain crab	*Euceramus praelongus*	7	0.0	tray, trawl	B, N, R		X			X	X
Cleaner shrimp	*Hippolytidae*	7	0.0	tray, trawl	N, R				X		X
Daggerblade grass sh.	*Palaemonetes pugio*	6	0.0	tray, trawl	B, R	X	X				X
White shrimp	*Litopenaeus setiferus*	5	0.0	tray, trawl	B, N, R	X		X			X
Blue crab	*Callinectes sapidus*	3	0.0	tray, trawl	N				X		X
Longnose spider crab	*Libinia dubia*	3	0.0	tray	B, N	X		X		X	
Ghost shrimp	*Callianassa spp.*	1	0.0	tray	B	X					

RA = (no. individuals/total)*100. Habitat types: unrestored bottom (B), natural reef (N), restored reef (R). X indicates species was collected during sampling date.

Table 3.2. Overall mean species density and SE, mean size and SE, and total number collected from trays in unrestored bottom, natural reef and restored reef habitats during the study.

		Unrestored bottom					Natural reef					Restored reef				
Common name	**Scientific name**	**Mean density**	**SE**	**Mean size**	**SE**	***n***	**Mean density**	**SE**	**Mean size**	**SE**	***n***	**Mean density**	**SE**	**Mean size**	**SE**	***n***
Total fish						**186**					**217**					**285**
Code goby	*Gobiosoma robustum*	3.35	0.62	20.9	0.9	49	3.67	0.63	21.0	0.8	57	3.41	0.69	21.5	0.7	53
Gulf toadfish	*Opsanus beta*	4.37	0.66	91.9	8.1	64	4.44	0.84	56.9	6.8	69	4.77	1.02	40.8	3.2	74
Spot	*Leiostomus xanthurus*	-	-	-	-	-	0.06	0.06	38.5	-	1	-	-	-	-	-
Darter goby	*Ctenogobius boleosoma*	1.64	0.38	18.6	1.3	24	0.84	0.23	19.7	1.7	13	1.35	0.38	20.5	1.2	21
Naked goby	*Gobiosoma bosc*	0.75	0.32	25.6	1.9	11	1.67	0.54	26.2	0.9	26	3.09	0.84	24.7	0.7	48
Goby species	*Gobiidae*	1.64	0.98	18.1	1.5	24	0.39	0.24	11.0	2.4	6	3.29	1.95	24.5	0.8	51
Skilletfish	*Gobiesox strumosus*	0.34	0.14	26.5	4.3	5	1.55	0.45	28.7	2.5	24	1.42	0.56	28.4	1.8	22
Green goby	*Microgobius thalassinus*	0.14	0.14	17.6	0.9	2	0.19	0.14	19.7	1.4	3	0.77	0.26	21.6	1.7	12
Stretchjaw blenny	*Chasmodes longimaxilla*	0.07	0.07	30.9	-	1	0.71	0.34	44.7	4.2	11	0.06	0.06	33.3	-	1
Pipefish	*Sygnathidae*	-	-	-	-	-	0.06	0.06	57.5	-	1	-	-	-	-	-
Freckled blenny	*Hypsoblennius ionthas*	-	-	-	-	-	0.06	0.06	49.4	-	1	0.13	0.09	51.2	28.0	2
Gray snapper	*Lutjanus griseus*	0.14	0.10	86.1	8.4	2	0.06	0.06	59.7	-	1	-	-	-	-	-
Pigfish	*Orthopristis chrysoptera*	0.07	0.07	190.0	-	1	0.13	0.09	132.0	12.0	2	-	-	-	-	-
Speckled worm eel	*Myrophis punctatus*	0.07	0.07	172.1	-	1	0.06	0.06	203.0	-	1	-	-	-	-	-
Feather blenny	*Hypsoblennius hentz*	0.07	0.07	35.3	-	1	0.06	0.06	48.7	-	1	-	-	-	-	-
Spotfin mojarra	*Eucinostomus argenteus*	0.07	0.07	16.9	-	1	-	-	-	-	-	-	-	-	-	-
Unidentified larval fish	*Unidentified larval fish*	-	-	-	-	-	-	-	-	-	-	0.06	0.06	-	-	1
Total crustaceans						**5,676**					**5,769**					**7,046**
Porcelain crabs	*Porcellanidae*	140.19	20.78	4.8	0.0	2,052	237.76	47.87	5.2	0.0	3,691	275.31	44.58	5.8	0.0	4,274
Mud crabs	*Xanthidae*	218.14	43.52	7.8	0.1	3,193	94.95	18.59	9.8	0.1	1,474	126.06	26.41	9.0	0.1	1,957
Snapping shrimp	*Alpheus heterochaelis*	14.28	2.48	15.3	0.4	209	21.13	3.18	14.5	0.3	328	28.02	3.19	16.3	0.3	435
PL penaeid shrimp	*Postlarval Penaeidae*	6.76	1.88	5.6	0.1	99	4.19	1.18	5.6	0.3	65	9.28	1.95	5.0	0.1	144
Marsh grass shrimp	*Palaemonetes vulgaris*	3.62	1.66	13.4	0.5	53	6.76	2.49	14.4	0.3	105	3.86	1.17	14.3	0.4	60
Grass shrimp	*Palaemonetes spp.*	1.30	0.56	11.6	1.0	19	0.84	0.42	12.8	1.5	13	0.71	0.30	12.2	1.3	11
Gulf stone crab	*Menippe adina*	2.80	0.56	36.1	3.2	41	5.48	1.02	25.5	1.8	85	10.50	2.23	17.5	0.9	163
Arrow shrimp	*Tozeuma carolinense*	0.07	0.07	13.6	-	1	0.06	0.06	14.8	-	1	-	-	-	-	-
Brown shrimp	*Farfantepenaeus aztecus*	0.07	0.07	-	-	1	0.06	0.06	56.9	-	1	-	-	-	-	-
Olivepit porcelain crab	*Euceramus praelongus*	0.20	0.15	10.0	1.0	3	-	-	-	-	-	-	-	-	-	-
Cleaner shrimp	*Hippolytidae*	-	-	-	-	-	0.13	0.13	7.7	0.5	2	-	-	-	-	-
Daggerblade grass sh.	*Palaemonetes pugio*	0.14	0.14	9.1	0.4	2	-	-	-	-	-	0.06	0.06	6.9	-	1
White shrimp	*Litopenaeus setiferus*	-	-	-	-	-	0.13	0.13	10.2	0.1	2	0.06	0.06	15.1	-	1
Blue crab	*Callinectes sapidus*	-	-	-	-	-	0.06	0.06	33.1	-	1	-	-	-	-	-
Longnose spider crab	*Libinia dubia*	0.14	0.10	5.4	0.6	2	0.06	0.06	9.0	-	1	-	-	-	-	-
Ghost shrimp	*Callianassa spp.*	0.07	0.07	14.8	-	1	-	-	-	-	-	-	-	-	-	-

Mean values were calculated from 33 samples for unrestored bottom and 35 samples each for natural reef and restored reef habitats. Density values in number ind. m^{-2}. Size values in mm. Dash indicates no catch.

Table 3.3. Overall mean species density and SE, mean size and SE, and total number collected from trawls in unrestored bottom, natural reef and restored reef habitats during the study.

		Unrestored bottom					Natural reef					Restored reef				
Common name	**Scientific name**	**Mean density**	**SE**	**Mean size**	**SE**	***n***	**Mean density**	**SE**	**Mean size**	**SE**	***n***	**Mean density**	**SE**	**Mean size**	**SE**	***n***
Total fish						**205**					**81**					**271**
Code goby	*Gobiosoma robustum*	0.01	0.00	20.2	1.0	42	0.01	0.01	23.4	1.2	43	0.01	0.01	22.0	1.2	45
Gulf toadfish	*Opsanus beta*	-	-	-	-	-	0.00	0.00	43.8	-	1	0.00	0.00	150.0	-	1
Spot	*Leiostomus xanthurus*	0.00	0.00	25.9	-	1	-	-	-	-	-	0.07	0.05	32.1	0.7	175
Darter goby	*Ctenogobius boleosoma*	0.01	0.01	17.6	0.9	32	0.00	0.00	20.5	1.8	9	0.00	0.00	18.8	2.1	15
Naked goby	*Gobiosoma bosc*	0.00	0.00	29.0	1.4	5	0.00	0.00	27.3	2.7	8	0.00	0.00	26.9	1.0	3
Goby species	*Gobiidae*	0.00	0.00	19.9	1.5	13	-	-	-	-	-	0.00	0.00	5.0	-	1
Atlantic croaker	*Micropogonias undulatus*	0.04	0.03	15.1	0.9	79	0.00	0.00	15.6	3.6	2	0.00	0.00	18.0	2.8	7
Skilletfish	*Gobiesox strumosus*	0.00	0.00	31.4	3.1	7	0.00	0.00	24.2	1.7	8	0.00	0.00	30.1	4.0	7
Green goby	*Microgobius thalassinus*	0.00	0.00	18.5	1.3	9	0.00	0.00	16.4	1.2	2	-	-	-	-	-
Stretchjaw blenny	*Chasmodes longimaxilla*	-	-	-	-	-	0.00	0.00	52.3	2.5	2	0.00	0.00	55.5	-	1
Pipefish	*Sygnathidae*	0.00	0.00	89.0	8.5	4	0.00	0.00	134.7	38.8	3	0.00	0.00	62.5	1.4	6
Bay whiff	*Citharichthys spilopterus*	0.00	0.00	39.2	10.2	8	0.00	0.00	15.7	-	1	0.00	0.00	20.7	5.5	3
Blackcheek tonguefish	*Symphurus plagiusa*	0.00	0.00	18.9	0.3	2	0.00	0.00	14.1	-	1	0.00	0.00	19.0	-	1
Least puffer	*Sphoeroides parvus*	0.00	0.00	36.7	-	1	0.00	0.00	72.3	-	1	0.00	0.00	39.1	-	1
Speckled worm eel	*Myrophis punctatus*	-	-	-	-	-	-	-	-	-	-	0.00	0.00	147.0	-	1
Pinfish	*Lagodon rhomboides*	0.00	0.00	45.1	-	1	-	-	-	-	-	0.00	0.00	120.0	-	1
Sheepshead	*Archosargus probatocephalus*	0.00	0.00	54.7	-	1	-	-	-	-	-	0.00	0.00	109.8	-	1
Bay anchovy	*Anchoa mitchilli*	-	-	-	-	-	-	-	-	-	-	0.00	0.00	19.3	-	1
Blackwing searobin	*Prionotus rubio*	-	-	-	-	-	-	-	-	-	-	0.00	0.00	45.8	-	1
Total crustaceans						**1,093**					**913**					**1,335**
Porcelain crabs	*Porcellanidae*	0.10	0.02	4.7	0.1	267	0.10	0.02	4.7	0.1	300	0.12	0.05	4.4	0.1	207
Mud crabs	*Xanthidae*	0.20	0.08	8.1	0.2	593	0.13	0.02	8.4	0.2	431	0.12	0.03	7.8	0.2	329
Snapping shrimp	*Alpheus heterochaelis*	0.00	0.00	18.3	3.7	5	0.00	0.00	13.9	1.9	8	0.00	0.00	14.4	1.7	5
PL penaeid shrimp	*Postlarval Penaeidae*	0.01	0.01	12.5	1.3	22	0.01	0.01	11.7	0.8	23	0.08	0.03	6.6	0.2	189
Marsh grass shrimp	*Palaemonetes vulgaris*	0.00	0.00	12.9	0.8	10	0.01	0.00	15.4	1.0	23	0.07	0.02	14.5	0.3	191
Grass shrimp	*Palaemonetes spp.*	0.01	0.01	8.0	0.4	26	0.01	0.00	8.6	0.3	34	0.11	0.04	8.1	0.1	287
Gulf stone crab	*Menippe adina*	0.00	0.00	15.4	2.2	9	0.00	0.00	16.7	2.4	15	0.00	0.00	21.8	8.9	7
Swimming crabs	*Portunidae*	0.05	0.04	9.0	0.6	133	0.02	0.01	9.4	0.7	65	0.02	0.01	8.6	0.7	68
Arrow shrimp	*Tozeuma carolinense*	0.00	0.00	12.5	0.8	14	0.00	0.00	12.9	2.2	6	0.01	0.01	13.7	0.5	35
Brown shrimp	*Farfantepenaeus aztecus*	0.00	0.00	47.9	2.5	11	0.00	0.00	39.5	4.0	3	0.00	0.00	46.4	4.2	9
Olivepit porcelain crab	*Euceramus praelongus*	0.00	0.00	6.3	-	1	0.00	0.00	7.7	0.6	2	0.00	0.00	8.8	-	1
Cleaner shrimp	*Hippolytidae*	-	-	-	-	-	0.00	0.00	9.2	-	1	0.01	0.01	17.4	4.7	4
Daggerblade grass sh.	*Palaemonetes pugio*	-	-	-	-	-	-	-	-	-	-	0.00	0.00	13.0	3.7	3
White shrimp	*Litopenaeus setiferus*	0.00	0.00	30.8	5.4	2	-	-	-	-	-	-	-	-	-	-
Blue crab	*Callinectes sapidus*	-	-	-	-	-	0.00	0.00	45.9	3.1	2	-	-	-	-	-

Mean values were calculated from 18 samples per habitat type. Density values in number ind. m^{-2}. Size values in mm. Dash indicates no catch.

CHAPTER IV: THE IMPORTANCE OF SEDIMENT ORGANIC MATTER IN THE DIET OF OYSTERS, WITH IMPLICATIONS FOR HABITAT RESTORATION.

Abstract

As foundational species, oysters can exert a strong influence on trophodynamics in estuarine systems, and there is great potential for oysters to mediate benthic-pelagic coupling. By assessing oyster diets, a better understanding of the trophic dynamics within oyster reefs and the role of oysters in regulating flows of organic matter can be developed. In the present study, a dual stable isotope ($\delta^{13}C$ and $\delta^{15}N$) approach was employed to assess temporal and habitat variability of oyster diet composition at a restored reef compared to surrounding natural reef and unrestored bottom reference habitats. Oysters and potential composite food sources — suspended particulate organic matter (SPOM) and sediment surface organic matter (SSOM) — were sampled from restored and reference habitats seasonally for two years post-restoration. Composite food resources were distinguishable based on their respective $\delta^{13}C$ values, with SPOM being more depleted in ^{13}C (-24.2 ± 0.6‰) than SSOM (-21.2 ± 0.8‰) throughout the study. SPOM composition is likely dominated by autochthonous phytoplankton production, while SSOM is a combination of trapped phytoplankton and benthic microalgae. Oyster diet composition was similar among restored and reference habitats, but changed over time. SSOM is an important component of oyster diets, contributing larger proportions relative to SPOM over time. This trend held true even with the higher vertical relief of the restored reef (0.3 m) compared to reference conditions (0.1 m). These results support growing evidence that benthic organic matter can be an important food resource for suspension-feeders, such as oysters. This information should be used to improve existing population dynamics models, and for restoration and management of shellfish populations, by accounting for all potential food resources.

4.1. Introduction

Coastal environments face continued habitat loss, degradation and alteration, making it increasingly important to understand, and even predict, resulting changes in trophodynamics and ecosystem functions. Trophic dynamics drive many ecosystem processes, and form the basis of matter, nutrient and energy cycles in the greater environment (de Ruiter et al. 2005). As foundational species, oysters can exert a strong influence on the trophic dynamics in a system. Oyster reefs provide structured habitat for numerous organisms and support complex trophic webs (Grabowski & Peterson 2007; Coen et al. 2007; Beck et al. 2011). Through their suspension-feeding activities, oysters help regulate nutrient dynamics (Dame et al. 1984; Newell 2004; Beseres Pollack et al. 2013), and there is great potential for oysters to mediate benthic-pelagic coupling. Oysters filter large amounts of particulate matter from the water column and excrete excess particles as biodeposits, thereby transferring organic matter from the water column to the benthos (Dame et al. 1984; Prins et al. 1998; Newell 2004; Dame 2012). Determining the diet of suspension-feeding shellfish, such as oysters, has broad applications for management, conservation, and restoration of shellfish populations.

Oyster reefs have been severely degraded worldwide, and are now considered to be the most imperiled marine habitat (Beck et al. 2011; zu Ermgassen et al. 2012). Restoration efforts are increasingly focused on restoring one or more of the valuable ecosystem services oysters provide (Grabowski & Peterson 2007; Coen et al. 2007). Ecosystem services related to nutrient regulation are of particular interest because of the potential for oysters to remove excess nutrients and enhance water quality (Cerco & Noel 2007; zu Ermgassen et al. 2013; Beseres Pollack et al. 2013). Recent studies have developed estimates of the impacts of restored oyster populations on water quality via their filter-feeding activities (e.g. Cerco & Noel 2007; Grizzle et al. 2008;

Plutchak et al. 2010; Kellogg et al. 2013), yet information on the food resources of oysters is lacking or limited to phytoplankton (measured as water column chlorophyll-*a*) production (Armstrong 1987; Powell et al. 1995; Dekshenieks et al. 2000). Filtration rate models to estimate the impact of oyster populations of nutrient regulation dynamics are also limited to water column organic matter (Dame & Prins 1998; Dame 2012; Beseres Pollack et al. 2013). Much of what is known about oyster diets has come from studies on cultured populations, as the need to ensure adequate food resources and to understand the carrying capacity of the system is critical to supporting aquaculture operations (Dame & Prins 1998).

Analysis of stable isotope composition can be used to elucidate the different food resources utilized by consumers (Fry 2006). In particular, carbon isotope composition has proven useful for identifying original food sources (Fry & Sherr 1984; Peterson 1999). Stable isotope analyses have been widely employed to determine food sources of oysters in Europe (Riera & Richard 1996; Riera et al. 2002; Dubois et al. 2007; Leal et al. 2008) and Asia (Hsieh et al. 2000; Kang et al. 2003; Xu & Yang 2007; Fukumori et al. 2008). Contrary to traditional assumptions that suspension-feeding bivalves feed solely on phytoplankton and other organic matter suspended in the water column (Dame et al. 1984; Newell 2004), there is a growing body of work showing evidence that benthic organic matter, which includes microphytobenthos, can also be an important food resource for suspension-feeders (Riera & Richard 1996; Riera et al. 2002; Kang et al. 2003; Dubois et al. 2007; Leal et al. 2008; Abeels et al. 2012).

By assessing oyster diets, a better understanding of the trophic dynamics within oyster reefs and the role of oysters in regulating flows of organic matter can be developed. Restoration activities provide unique opportunities to study oyster diets by enabling examination of food resources utilized by oysters over the course of reef development. Additionally, as nutrient regulating ecosystem services are increasingly cited as restoration goals, it is important to compare oyster diets at restored and natural reefs to assess the success of restoration projects in restoring these ecosystem services. The objectives of this study were to determine relative contributions of water column and benthic food resources to the diets of subtidal oysters in a Texas estuary using a dual stable isotope ($\delta^{13}C$ and $\delta^{15}N$) approach. Comparisons were made between oyster diets at a restored oyster reef and reference habitats over a two year period to examine how oyster diets may change during the course of reef development.

4.2. Materials and Methods

4.2.1. Study Area

The Mission-Aransas Estuary is a bar-built system in the Texas coastal bend (Fig. 4.1A). The estuary occupies approximately 463 km^2 and is composed of several shallow (average 2 m depth) bays (Armstrong 1987). The area is characterized by a semi-arid, subtropical climate with infrequent rain events. Evaporation typically exceeds precipitation (62.7 cm $year^{-1}$ net water loss) (Armstrong 1987). Two rivers feed the system: the Mission River flows through Mission Bay into Copano Bay and the Aransas River flows directly into Copano Bay. Average freshwater inflow to the estuary is low (< 0.5 km^3 $year^{-1}$) (Armstrong 1987; Montagna et al. 1996). The estuary is microtidal (0.15 m tidal range) and water movement is predominantly wind-influenced (Evans & Morehead Palmer 2012). Mixing with the Gulf of Mexico occurs through two tidal inlets at the northern and southern ends of the system. High winds characteristic of the region maintain well-mixed conditions throughout the system (Evans & Morehead Palmer 2012). Average residence time is 360 days, but can be as long as three years (Montagna et al. 1996; Beseres Pollack et al. 2011).

Oyster reefs are common in the estuary (Fig. 4.1A). Reefs are primarily subtidal, and are more prominent in areas of low to moderate salinity. This study was conducted at a restored oyster reef complex in Copano Bay (Fig. 4.1B). The reef complex consists of eight reef mounds (20 x 30 x 0.3 m) constructed of a crushed concrete base and topped with reclaimed oyster shell. Construction occurred during summer 2011. The restored complex is situated near a natural reference oyster reef of low vertical relief (approximately 0.1 m). Surrounding sediments are muddy with dense shell hash and scattered oysters and provide a reference of conditions prior to reef construction (i.e., unrestored bottom). Oysters and potential composite food resources — suspended particulate organic matter (SPOM) and surface sediment organic matter (SSOM) — were sampled at the restored reef complex and surrounding natural reef and unrestored bottom habitats for reference. Average depth of sampling sites was 1.1 m. Sampling commenced in February 2012 (approximately six months after reef construction) and continued seasonally through September 2013 for a total of six sampling periods (February 2012, June 2012, September 2012, March 2013, June 2013, and September 2013).

4.2.2. Abiotic environmental data

Continuous environmental data were obtained from Centralized Data Management Office of the National Estuarine Research Reserve System (NERRS 2015). Data were collected near the study site (Copano Bay East station) as part of the NERRS system-wide monitoring program, and included measurements of temperature (°C), salinity (psu), dissolved oxygen (mg L^{-1}), wind speed (m $second^{-1}$) and turbidity (Formazin Nephelometric Unit (FNU)/Nephelometric Turbidity Unit (NTU)). Additional environmental data were collected during each sampling period using a handheld Hydrolab data sonde: water temperature (°C), salinity (psu) and dissolved oxygen (mg L^{-1}). Freshwater inflows into the system were obtained from the U.S. Geological Survey

(USGS) gauge stations in the Mission (USGS station 08189500) and Aransas (USGS station 08189700) Rivers (USGS 2015). Continuous environmental data and freshwater inflow data were collected for the entire study period, starting in July 2011 when reef construction began, and continuing until October 2013 when the study was complete.

4.2.3. Sampling and preparation of water chlorophyll-*a* and composite food source samples

Bottom water samples were collected 0.1 m above the sediment-water interface at each sampling site using a horizontal van Dorn water sampler for quantification of chlorophyll-*a* and stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$). Water was filtered on Whatman GF/F glass fiber filters (0.7 µm porosity) to collect SPOM for chlorophyll-*a* analysis. Filters were stored at -20 °C until analysis. SPOM samples for stable isotope analyses were sieved on a 300-µm screen to eliminate large detrital particles and zooplankton, and then filtered on two different precombusted Whatman GF/F glass fiber filters (0.7 µm porosity) to determine stable isotope composition. Filters were frozen at -20 °C and freeze-dried. Carbonates were removed from filters for $\delta^{13}C$ and %C analyses by contact with HCl fumes in a vacuum-enclosed system. $\delta^{15}N$ and %N analyses were carried out on raw samples.

Three cylindrical sediment cores (37.4 cm^2) were collected by divers from each habitat type for stable isotope analysis ($\delta^{13}C$ and $\delta^{15}N$) of SSOM. Cores were collected and handled with minimal disturbance, and the top 2 cm were sliced and stored at -20 °C until further processing. Samples were thawed and sieved wet on a 500 µm mesh screen to eliminate macrofauna, shell pieces and large detrital particles. Sieved sediment was freeze-dried and ground using a mortar and pestle. Carbonates were removed from sediment for $\delta^{13}C$ and %C analyses using 2 M HCl. HCl was added drop-by-drop until cessation of bubbling. Samples were then dried at 60 °C using a dry block heater under air flow. Dried samples were rehomogenized into ultrapure water using an ultrasonic bath, freeze-dried and ground again. $\delta^{15}N$ and %N analyses were carried out on raw samples.

4.2.4. Sampling and preparation of oysters

Oysters were collected from each habitat type by divers and stored on ice for transport to the laboratory. They were cleaned of epibionts and kept alive for up to 36 hr in filtered seawater to allow for gut content evacuation (Dubois et al. 2007). Oysters were frozen at -20 °C and then dissected to collect digestive gland material. We aimed to collect three medium-sized oysters (> 25 mm shell height) and three spat oyster (≤ 25 mm) samples from each habitat type during each sampling event. Spat oysters were pooled in groups (2-4 individuals) when possible to obtain enough material for stable isotope analysis. Low oyster density at unrestored bottom sediment habitats often limited the number of oysters collected. In total, 52 oysters and 44 spat groups (111 individual spat) were analyzed for this study, ranging in size from 25.4 mm to 76.8 mm (47.2 ± 13.4 mm, mean ± SD) and from 11.5 mm to 25.0 mm (18.4 ± 3.4 mm), respectively.

Digestive gland samples were freeze-dried and ground to a homogenous powder using a ball mill (MM400, Restch, Germany). Digestive glands are known to contain high amounts of lipids, which are highly depleted in ^{13}C relative to other tissues due to the different biochemical pathways involved in their respective synthesis (DeNiro & Epstein 1977). As a result, the $\delta^{13}C$ value of a raw sample does not only reflect the diet of a consumer. Thus, lipids were extracted from samples for $\delta^{13}C$ and %C analyses using two successive extractions with cyclohexane. Samples were then dried at 45 °C and ground again. $\delta^{15}N$ and %N analyses were carried out on raw samples.

4.2.5. Chlorophyll-*a* and stable isotope ratio measurements

Chlorophyll-*a* was extracted from filters overnight using a non-acidification technique and read on a Turner Trilogy fluorometer (Welschmeyer 1994; EPA method 445.0). Elemental stable isotope compositions were determined using an elemental analyzer (Flash EA 1112, Thermo Scientific, Milan, Italy) coupled to an isotope ratio mass spectrometer (Delta V Advantage with a Conflo IV interface, Thermo Scientific, Bremen, Germany). Analyses were conducted at the stable isotope facility at the University of La Rochelle, France. Results are expressed in δ notation as deviations from standards (Vienna Pee Dee Belemnite for $\delta^{13}C$ and N_2 in air for $\delta^{15}N$) following the formula: $\delta^{13}C$ or $\delta^{15}N = [(R_{sample}/R_{standard}) - 1] \times 10^3$, where R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$. Calibration was done using reference materials (USGS-24, IAEA-CH6, -600 for carbon; IAEA-N2, -NO-3, -600 for nitrogen). Analytical precision was < 0.15 ‰ based on the analyses of acetanilide (Thermo Scientific) used as laboratory internal standard.

4.2.6. Data analysis and statistics

Statistical analyses were performed using R 2.12.2 (R Foundation for Statistical Computing 2011). Comparisons between stable isotope values were conducted using nonparametric procedures (Zar 2010). Kruskal-Wallis tests (*kruskal.test*) were used to compare stable isotope compositions of SPOM, SSOM and oysters among seasons and habitat types. Kruskal–Wallis tests were followed by multiple comparisons of means (*kruskalmc* in *R pgirmess* package) by using the *pgirmess* package (Giraudoux 2011). Isotopic ratios of oysters and food sources were compared considering a trophic fractionation factor of 0.3 ± 1.3 ‰ (mean ± SD) for $\delta^{13}C$ values and of 2.3 ± 1.6 ‰ for $\delta^{15}N$ values (Vander Zanden & Rasmussen 2001). Theoretical oyster diets were computed by subtracting the trophic fractionation values from observed $\delta^{13}C$ and $\delta^{15}N$ values of oysters to correct for fractionation. Contributions of SPOM and SSOM to oyster diets were estimated by solving mixing models within a Bayesian framework (*siarmcmcdirichlety4* in *R siar* package) (Parnell *et al.* 2010; Parnell &Jackson 2014). Models were run for 500,000 iterations and the first 50,000 iterations were discarded. Credibility intervals (CI) of 0.95, 0.75 and 0.25 were computed and are displayed on figures (Parnell & Jackson 2014).

4.3. Results

4.3.1. Environmental parameters

Monthly average water temperature ranged from 13.8 °C during January 2013 to 31.0 °C during August 2011. Monthly average salinity ranged from 25.2 psu during May 2012 to 38.8 psu during November 2011. Monthly freshwater inflow varied during the study, with monthly total inflows ranging from 200,644 m^3 during August 2011 to 27,648,897 m^3 during May 2013. Despite the high volume of freshwater inflow during late May 2013, salinity in the study area was relatively high (33.8 psu) and continued to increase during the following months.

4.3.2. Composition of potential food resources

Mean $\delta^{13}C$ values for SPOM ranged from -24.8 to -23.5 ‰; mean $\delta^{15}N$ values ranged from 7.3 to 8.7 ‰ (Fig. 4.2). Some significant differences were observed for $\delta^{13}C$ and $\delta^{15}N$ values between sampling periods (p = 0.016 and 0.010, respectively). No clear temporal patterns were evident for $\delta^{13}C$ values. $\delta^{15}N$ values were generally more enriched during September sampling periods. Mean C:N ratios of SPOM ranged from 6.4 to 12.8. C:N ratios were lowest during September sampling periods in both 2012 and 2013 (7.8 ± 1.8 and 6.4 ± 0.5, respectively) compared to all other sampling periods (Fig. 4.3), though no significant differences were observed (p = 0.086).

Chlorophyll-*a* concentrations ranged from 0.7 to 4.3 μg L^{-1} (mean 3.0 ± 1.7). Significant differences were observed among sampling periods ($p < 0.001$), with lower values observed in February 2012 (0.7 ± 0.6) and higher values observed in September 2012 and 2013 (4.3 ± 1.3 and 3.8 ± 0.9, respectively). Mean C:Chlorophyll-*a* ratios ranged from 58.8 to 328.8, and were significantly greater in February 2012 than in September 2012 and 2013 ($p = 0.023$) (Fig. 4.3).

Mean $\delta^{13}C$ values for SSOM ranged from -22.6 to -20.1 ‰ (Fig. 4.2). Significant differences were evident among sampling periods ($p < 0.001$), with a general pattern of enrichment over time. Mean $\delta^{15}N$ values ranged from 7.5 to 8.5 ‰ (Fig. 4.2). Mean C:N ratios ranged from 7.7 to 10.6. No significant differences were observed for $\delta^{15}N$ values or C:N ratios among sampling periods ($p = 0.186$ and 0.228, respectively).

4.3.3. Stable isotope composition of oysters

Mean $\delta^{13}C$ values for oysters ranged from -23.5 to -20.2 ‰ (Fig. 4.2). Spat and larger oysters did not differ significantly ($p = 0.478$). Mean $\delta^{15}N$ values ranged from 8.1 to 11.6 ‰, and differed significantly between spat (mean 10.2 ± 1.0) and larger oysters (mean 9.5 ± 1.0) ($p = 0.003$), with spat being more enriched. Oysters were more enriched in both ^{13}C and ^{15}N during June and September 2013 compared to other months ($p < 0.001$ for both $\delta^{13}C$ and $\delta^{15}N$). Significant differences between habitats occurred only during the first sampling period (February 2012); oysters from the natural reef were more enriched in both ^{13}C ($p = 0.010$) and ^{15}N ($p = 0.044$) than oysters at unrestored bottom sites. Theoretical oyster diets, corrected for trophic fractionation by subtracting 0.3‰ from $\delta^{13}C$ values and 2.3‰ from $\delta^{15}N$ values of oysters, are illustrated with shaded areas (Fig. 4.2) and overlap predominantly with SSOM food resources across all habitats.

4.3.4. Mixing model estimations of food source contributions to oyster diets

Mixing model results revealed a general trend of decreasing SPOM and increasing SSOM contributions with time (Fig. 4.4). This trend was evident across all habitats. In February 2012, SPOM contributed from 20 to 98% (95% CI range) and SSOM contributed from 2 to 80%. By the end of the study (September 2013), the relative importance of food sources switched with SPOM contributions ranging from 2 to 54% and SSOM from 47 to 98%.

4.5. Discussion

4.5.1. Origin and composition of potential food resources

A distinct separation of $\delta^{13}C$ values between SPOM and SSOM was observed, with average $\delta^{13}C$ values of SPOM being more depleted (-24.2 ± 0.6‰) than SSOM (-21.2 ± 0.8‰) throughout the study. The range of $\delta^{13}C$ values observed from SPOM (-25.1 to -23.6‰) fall within ranges typical of river-estuarine phytoplankton (-30 to -24‰) and C_3 marsh (-26 to -23‰) and terrestrial (-30 to -23‰) plants (Fry & Sherr 1984). Recent work in the Mission-Aransas Estuary determined $\delta^{13}C$ values for C_3 plants (-29 to -27‰) and estuarine SPOM (-27 to -21‰) (Lebreton et al. in review). C:N ratios less than 20 and C:Chlorophyll-*a* ratios less than 200 indicate a dominant influence of fresh organic matter (e.g., fresh phytoplankton) rather than degraded matter (e.g., decayed phytoplankton, terrestrial or saltmarsh plant detritus) (Cifuentes et al. 1988; Leal et al. 2008). Considered together, the $\delta^{13}C$ values of SPOM and low C:N and C:Chlorophyll-*a* ratios observed throughout much of the study indicate a dominant influence of autochthonous phytoplankton production on SPOM (Fry & Sherr 1984; Lebreton et al. in review). Some variations observed reflect expected seasonal trends. Lowest ratios of C:N and C:Chlorophyll-*a* are observed during September sampling periods, indicating that quality of SPOM was high. This strong influence of fresh organic matter is likely a result of higher primary production during summer. Low primary productivity during winter months, and thus less fresh organic matter in the SPOM pool, explains the high C:Chlorophyll-*a* ratios observed during February 2012. C:N and C:Chlorophyll-*a* ratios are higher in June 2013 than in June 2012, which may indicate an influence of detrital material delivered with the higher inflow of freshwater during May 2013. However, salinity does not decrease with the high freshwater inflows, indicating that the influence of freshwater inflow at the study site is minimal.

$\delta^{13}C$ values of SSOM (ranging from -22.6 to -20.1‰) indicate potential influences from a variety of sources (Fry & Sherr 1984). C:N ratios remain very low (generally < 10), indicative of very fresh organic matter (Kang et al. 2003), and thus suggest that riverine and terrestrial sources of organic matter play a very minor role in the composition of SSOM. Thus, we infer that SSOM is largely composed of fresh organic matter sources, such as trapped phytoplankton (-24‰; Fry & Sherr 1984), but also benthic microalgae, which are more ^{13}C-enriched, with $\delta^{13}C$ values of -17‰ in Fry and Sherr (1984), and ranging from -21.7 to -12.0‰ in Lebreton et al. (in review). The distinctly separate ranges of $\delta^{13}C$ values observed for SSOM and SPOM further indicate that SSOM is not only composed of settled SPOM, but is more likely benthic microalgae. A temporal pattern of $\delta^{13}C$ values was observed for SSOM, with values most depleted in ^{13}C during February 2012 and becoming more enriched through September 2013. This pattern may reflect an increasing influence of benthic microalgae on SSOM across the sampling dates.

4.5.2. Food resources utilized by oysters

The results of the isotope analyses indicate that oysters do not feed exclusively on SPOM, but rather utilize both SPOM and SSOM food resources. The range of $\delta^{13}C$ values observed in oysters overlaps mostly with SSOM $\delta^{13}C$ values, indicating that SSOM is an important food resource for oysters. Additionally, SSOM becomes more ^{13}C-enriched over time and at all habitats, suggesting that the proportion of benthic algae in SSOM increases while the proportion of trapped phytoplankton or detrital material decreases. Mixing model results indicate that the contribution of SSOM to oyster diets increases over the duration of the study across all habitats.

This large influence of SSOM in oyster diets can be instigated by oysters themselves. Oysters can have a strong influence on the degree of benthic-pelagic coupling within a system (Newell 2004; Dame 2012). As suspension-feeders, oysters remove suspended particles from the water column, and also those resuspended from the sediment, and deposit feces and pseudofeces, or biodeposits, onto the sediment, thereby linking organic matter and nutrient flows between pelagic and benthic habitats (Hsieh et al. 2000; Newell 2004, Quan et al. 2012). Feces and pseudofeces excreted by oysters may stimulate benthic production as this organic matter is remineralized by bacteria (Miller et al. 1996). This production can provide important food sources to benthic organisms, and may provide an alternative food source to filter-feeders, including oysters (Miller et al. 1996; Leal et al. 2008). Augmented oyster populations supported through restoration activities may stimulate this process by increasing sediment organic matter and fueling production of benthic microalgae. The increasing influence of SSOM on oyster diets throughout the study period may be related to the increase of oyster biomass at the restored reef through recruitment and growth. Increased oyster biomass equates to increased biodeposits, which can fuel benthic production, leading to an increase in benthic organic matter that can then be available to oysters (Miller et al. 1996; Leal et al. 2008).

SSOM becomes accessible to oysters via resuspension during water movement (Miller et al. 1996). Minimal tidal ranges and freshwater inflows, coupled with consistently strong winds in the region, suggest that wind-induced waves are the predominant forcing factor causing resuspension in this system (Armstrong 1987; Evans & Morehead Palmer 2012). Resuspension allows oysters at varying elevations to access similar food resources (Kang et al. 2003). This is likely the reason that no significant differences were observed in oyster diets at the three habitats sampled in this study. The natural reef in the sampling area is very low (< 0.1 m), and thus, oysters have easy access to SSOM food resources no matter the mixing conditions. The restored reef is of higher vertical relief (0.3 m), and it could be hypothesized that SSOM food resources may be more difficult for oysters to access (Hsieh et al. 2000). However, oysters at both the natural and unrestored bottom habitats have very similar $\delta^{13}C$ values (Fig. 4.2), and thus diets. Temporal trends observed in SSOM of increased enrichment of $\delta^{13}C$ values over time are similarly reflected in oyster $\delta^{13}C$ values across habitats, indicating that the difference in vertical relief is not enough to prevent consumption of SSOM.

Composition of organic matter resources can be influenced by various environmental factors, and may also affect the assimilation of these food resources by consumers (Fry 2006; Michener & Kaufman 2007). In particular, freshwater inflow can be a strong environmental forcing factor by altering the quantity and quality of available food resources (Palmer et al. 2011; Beseres Pollack et al. 2011; Mooney & McClelland 2012; Paudel & Montagna 2014; Lebreton et al. in review). Freshwater inflows may affect SPOM composition within the Mission-Aransas Estuary, likely due to the influence of freshwater delivered from San Antonio Bay via the Intracoastal Waterway (Lebreton et al. in review). During the present study, a rain event in late May 2013 led to a decrease of the quality of SPOM and probably indirectly influenced the diet of oysters in June 2013. The lower quality of the SPOM probably lead to higher assimilation of the organic matter from the SSOM after the rain event, indicating that the SSOM can be preferentially used when the quality of the SPOM is reduced.

4.5.3. Implications for the restoration of oyster reef habitat

These observations, highlighting the role of SSOM in oyster diets, have important implications for the design and placement of restoration or cultivation activities, and deserve further research. For example, at what vertical relief are oysters prevented from accessing benthic food resources? The answer to this question is likely to be highly variable between systems, because of differences in sediments, inflow regimes, and tidal regimes. Resuspension of SSOM is dependent on tidal and wind conditions that vary between systems, but also spatially and temporally within systems. The physical characteristics of oyster reefs (e.g., depth, vertical relief, orientation) and surrounding environments (e.g., sediment grain size, connectivity) can also influence resuspension of SSOM, and may have very localized effects (Quan et al. 2012). For example, Dubois et al. (2007) determined that tidal height, which affects the amount of time oysters are inundated, and thus able to feed, had no effect on oyster diet composition. However, percent mud partly explained variations observed in $\delta^{13}C$ values of oysters (Dubois et al. 2007). There is in fact a close relationship between the sediment grain size and population structure of benthic algae: muddy sediment is dominated by epipelic diatoms, which can be easily suspended into the water column, whereas sandy sediment is dominated by epipsammic diatoms, which stick to sediment particles, and are therefore much less suspended in the water column (Sundbäck, 1984).

Seasonal and temporal variations have also been shown to affect food resources available to oysters (Riera & Richard 1996; Leal et al. 2008). In the present study, temporal variations occur, but do not show strong seasonal patterns at an annual scale. Further research to examine seasonal variations over longer time frames (e.g., El Niño Southern Oscillation (ENSO) cycles) could provide more insight in year-to-year variability. Additionally, longer-term monitoring of restored reef systems would enhance understanding of potential feedback effects related to reef development. Finally, as shellfish populations face continued alterations through natural and anthropogenic influences, the use of population dynamics models as tools to predict population changes is increasingly important (Powell et al. 1995; Dekshenieks et al. 2000; Dame 2012). Food resource inputs are a major component of such models, and it is important to improve model inputs as new information becomes available.

4.6. Conclusions

Food sources of *C. virginica* are not well characterized, despite the important role oysters play in estuarine dynamics. The results of the present study build on evidence that oysters can access and consume benthic food resources, such as microphytobenthos or trapped phytoplankton (Riera & Richard 1996; Riera et al. 2002; Kang et al. 2003; Dubois et al. 2007; Leal et al. 2008; Abeels et al. 2012). Research related to oyster-mediated benthic-pelagic coupling has typically focused on phytoplankton consumption (Prins et al. 1998; Newell 2004; Dame 2012). It is necessary to incorporate consumption of resuspended benthic food sources in food web models so that trophodynamics and food availability can be examined more accurately. A more complete understanding of suspension-feeders diets has the potential to significantly alter understanding of food web and population dynamics in shellfish-dominated habitats. Oyster-mediated benthic-pelagic coupling can exert strong influences over the entire ecosystem. As systems continue to face alterations, either through the continued loss of shellfish populations, or through the augmentation of shellfish populations through restoration or cultivation, phase shifts can occur between planktonic systems and benthic-pelagic coupling

(Dame 2012). As new information is gained regarding food resources of shellfish, improvements can be made in food web and population dynamics models to increase their accuracy.

Prior to implementation of cultivation activities or restoration efforts, it is important to assess the carrying capacity of the system to support augmented shellfish populations (Prins et al. 1998; Leal et al. 2008; Fukumori et al. 2008). Food availability is critical, and most often, phytoplankton is the only food source considered (Prins et al. 1998; Newell 2004). Thus, benthic food resources should be taken into account in studies carried out prior to the implementation of oyster reef restoration projects. Further research exploring shellfish diets in relation to available food sources would improve population dynamic models and carrying capacity estimates. This would support better design and implementation of cultivation and restoration efforts, and would improve management of shellfish populations.

As research increasingly focuses on quantification of ecosystem services provided by oysters, calculation of filtration rates and nutrient regulation dynamics need to incorporate a more accurate view of system dynamics. Nutrient regulating ecosystem services are traditionally quantified via filtration rate models. Fundamental components of any bivalve filtration model include water mass residence time, phytoplankton primary productivity, and bivalve clearance rates (Dame 2012). Sediment dynamics should be included to accurately depict bivalve filtration rates.

Despite traditional assumptions that oysters feed solely from the water column, evidence of the importance of sediment organic matter to oyster diets is increasing. Measurement of sediment organic matter should become an integral part of any monitoring or management program.

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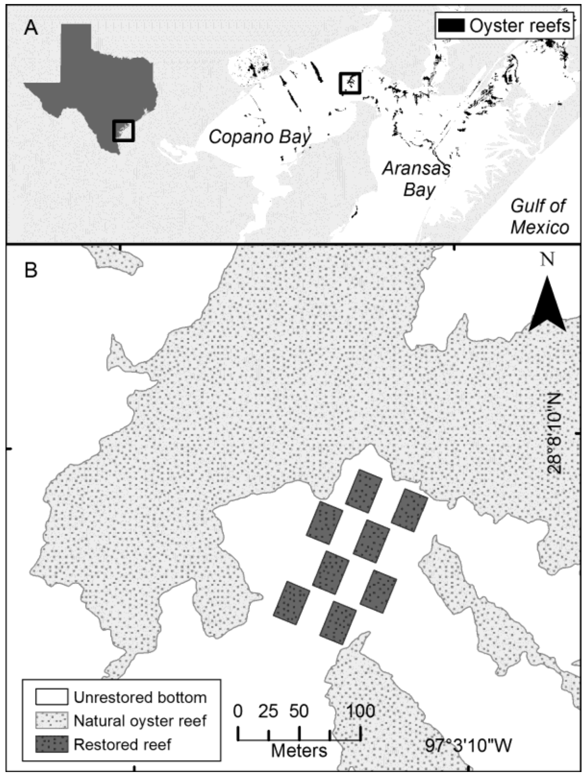
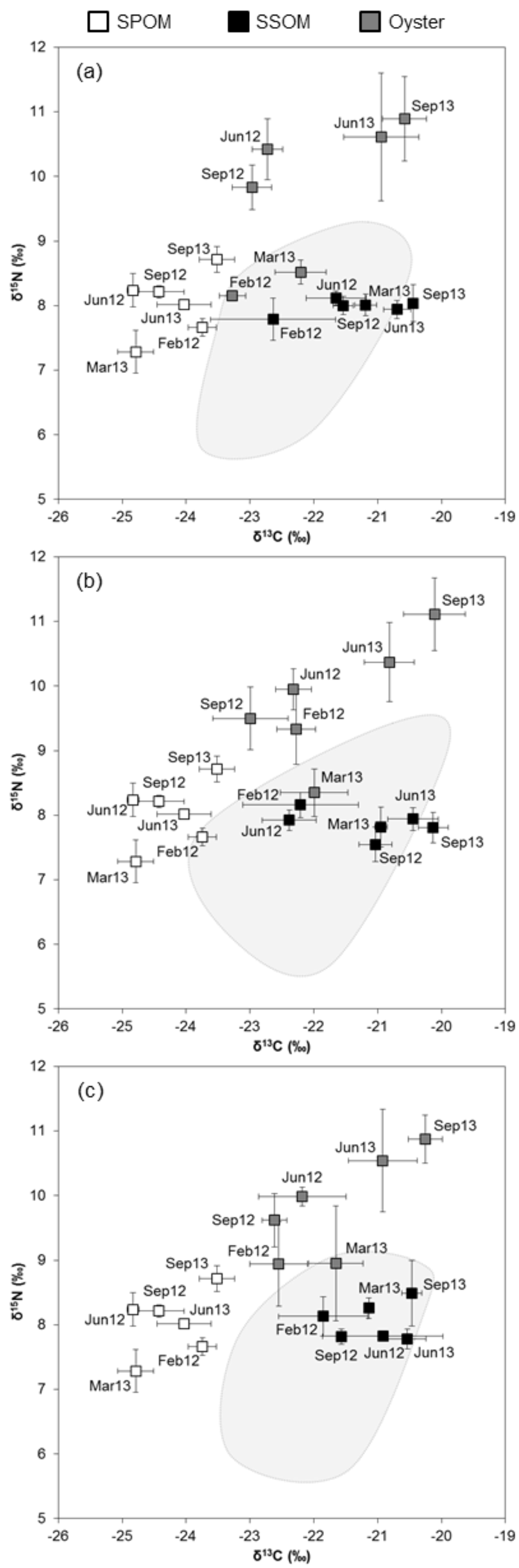


Fig. 4.1. Study area. (A) Location of study site within the Mission-Aransas Estuary, Texas, USA. (B) Extent of sampling area.

Fig. 4.2. Variability of $\delta^{13}C$ and $\delta^{15}N$ (mean ± SD) of SPOM, SSOM, and oysters during each sampling date. (A) Unrestored bottom. (B) Natural reef. (C) Restored reef. SPOM: suspended particulate organic matter; SSOM: surface sediment organic matter. Grey areas represent the range of theoretical oyster food source stable isotope composition accounting for trophic fractionation.



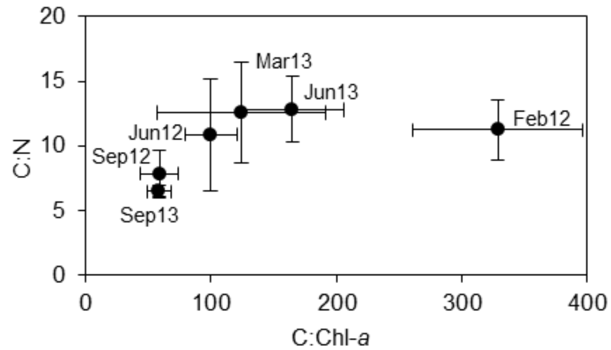


Fig. 4.3. C:N and C:Chl-*a* ratios (mean ± SD) observed for suspended particulate organic matter sampled across the study area during each sampling period.

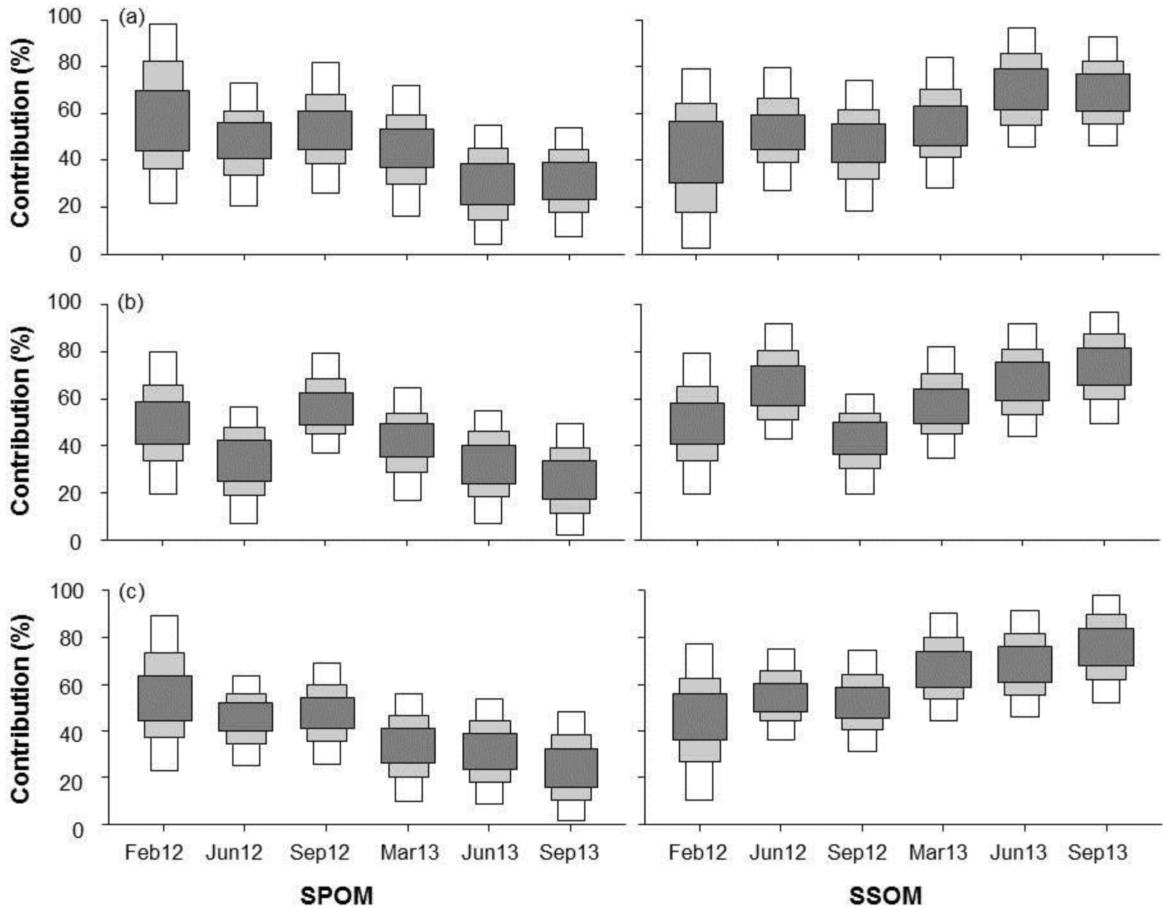


Fig. 4.4. Seasonal comparison of contributions (%) of potential food resources (SPOM: suspended particulate organic matter, SSOM: surface sediment organic matter) to oyster diets resulting from the mixing model SIAR. (A) Unrestored bottom. (B) Natural reef. (C) Restored reef. 0.95, 0.75, 0.25 credibility intervals are shown in white, light grey, and dark grey, respectively.

CHAPTER V: EVALUATION OF NUTRIENT REGULATING FUNCTIONS PROVIDED BY A RESTORED OYSTER REEF: AN ENERGETIC APPROACH

Abstract

Oyster reefs are an important component of estuarine ecosystems and provide many ecological and economic benefits. Though traditionally prized as an important food source, oysters have gained greater recognition for providing numerous other ecosystem services (e.g., cultural and regulating services). The degradation and loss of oyster reef systems during the past century has prompted efforts to restore these systems and associated functions and services. Nutrient regulating ecosystem services are highly cited as goals of oyster reef restoration efforts. As oysters filter water to feed, they excrete excess particles as biodeposits. Nitrogen shunted from the water column to sediments via oyster biodeposits and waste may then undergo burial or denitrification, resulting in nitrogen removal from the system. In the present study, nitrogen removal attributed to oysters is quantified at a restored oyster reef in comparison to a nearby natural oyster reef in Copano Bay, Texas. Emergy analysis is performed to compare relative value of nitrogen removal functions at the restored and natural reefs. Emergy is a measure of total energy necessary to produce a good or service, and thus can be thought of as 'energy memory.' Emergy evaluations can be used to represent environmental and economic values of a system in equivalent units, generally solar energy units, and thus present ecological approach to quantify market and non-market services in common units. The results of the present study demonstrate that within the second year post-restoration, the reef is providing a greater function per unit area compared to the natural reef. Thus, the restored reef has proven to be successful in performing the ecological functions necessary for providing ecosystem services related to nutrient removal.

5.1. Introduction

As a foundational species, oysters contribute to the integrity and functionality of estuarine ecosystems, and are important ecological and economic resources. Though traditionally prized as an important food source, oysters have gained greater recognition for providing numerous other ecosystem services that, directly or indirectly, support and enrich the lives of humans (Luckenbach et al. 1999; Brumbaugh et al. 2006; Grabowski & Peterson 2007; Coen et al. 2007). As filter feeders, oysters can regulate nutrients and wastes and play a significant role in estuarine nutrient cycles (Dame et al. 1984; Newell 1988; Cerato et al. 2004; Grizzle et al. 2006; Dame 2012; Beseres Pollack et al. 2013). This filtering activity can help to improve water quality and clarity, which can have cascading effects on a variety of ecosystem services. For example, improvements in water quality and clarity have been shown to enhance the value of recreational boating, swimming, beach use and aesthetic values by millions of dollars (Bockstael et al. 1989; Leggett & Bockstael 2000; Henderson & O'Neil 2003; Poor et al. 2007)

Oyster reefs have been lost at distressing rates, with current extent and biomass estimated to be less than 15% of historic levels (Beck et al. 2011; zu Ermgassen et al. 2012). Loss of oysters and oyster reef habitats results in the loss of associated ecological functions necessary for the provision of a variety of ecosystem services (zu Ermgassen et al. 2013). Thus, restoration of oyster reef habitat has become a broader priority for restoring important functions and services (Coen et al. 2007; Grabowski & Peterson 2007; Cerco & Noel 2007; Plutchak et al. 2010). Quantification of ecosystem services is an emergent goal for restoration projects. Several methods can be utilized to quantify market and non-market ecosystem services. Valuation of market goods provided by ecosystems is relatively simple: economic markets exist and humans pay a particular price for such goods. Methods for valuing ecosystem services in which a market does not exist are more difficult. Non-market valuation techniques often rely on revealed or stated preferences. Revealed preference methods value ecosystem services based on real actions and choices people make (e.g., expenditures; Pendleton 2010). Stated preference methods are based on hypothetical values (e.g., willingness to pay) obtained from surveys (Pendleton 2010). While economic valuation can be useful, such methods can be incomplete because ecological functions that support the provision of ecosystem services are not necessarily accounted for.

In the present study, emergy analysis is employed to quantify nitrogen removal at restored and natural oyster reefs. Emergy accounting methods are desirable because they can quantify a variety of goods and services in common energy-based units, typically solar energy (Odum 1996; Odum & Odum 2000). Emergy analysis accounts for work necessary to transform energy into a product or service, and thus, can be thought of as "energy memory" (Scienceman 1987; Odum 1996). Solar emergy is quantified in units of solar emjoules (sej; Odum 1996). Emergy is unique from energy because it quantifies the energy used to produce products or services, rather than available potential energy (Odum 1996). This is accomplished with the application of transformity values. Solar transformitity values (sej J^{-1}) describe the solar emergy (sej) necessary to produce an energetic unit (J) of a product or service (Odum 1996). The novelty of emergy approaches to value ecosystem services compared to traditional economic methods lies in the perspectives from which goods and services are valued. Emergy accounting methods evaluate goods and services from a donor perspective, by incorporating the work done by the natural environment, rather than the value perceived by receivers (Odum 1996; Kangas 2004). Thus, emergy analysis can complement economic methods by providing a more complete approach for quantifying ecosystem service values (Odum 1996; Hau & Bakshi 2004).

The objectives of the present study are to quantify nutrient regulating functions, in terms of nitrogen removal, performed by a restored oyster reef in South Texas. Comparison is made to a natural oyster reef to evaluate the success of the restoration project in providing these functions and services. First, a conceptual model is developed to evaluate ecological flows associated with nutrient regulating functions provided by oyster reefs. Steady-state conditions are determined and then used to calculate solar transformity values for functional flows. Emergy analysis methods are then applied to quantify nitrogen removal functions provided by the restored and natural reefs during the first two years following the construction of the restored reef.

5.2. Methods

5.2.1. Study Area

Copano Bay is located within the Mission-Aransas Estuary in the Texas coastal bend (Fig. 5.1A). The estuary occupies approximately 463 km^2 and is composed of several shallow (average 2 m depth) bays (Armstrong 1987). The area is characterized by a semi-arid, subtropical climate with infrequent rain events. Evaporation typically exceeds precipitation (62.7 cm $year^{-1}$ net water loss) (Armstrong 1987). Two rivers feed the system: the Mission River flows through Mission Bay into Copano Bay and the Aransas River flows directly into Copano Bay. Average freshwater inflow to the estuary is low (< 0.5 km^3 $year^{-1}$) (Armstrong 1987; Montagna et al. 1996). Nitrogen loading is relatively low, averaging 1.93 g m^{-3} $year^{-1}$ (Russell & Montagna 2007). The estuary is microtidal (0.15 m tidal range) and water movement is predominantly wind-influenced (Evans & Morehead Palmer 2012). Mixing with the Gulf of Mexico occurs through two tidal inlets at the northern and southern ends of the system. Average residence time of water in Copano Bay can be as long as three years (Montagna et al. 1996; Russell & Montagna 2007; Beseres Pollack et al. 2011).

Oyster reefs are common in the estuary. Reefs are primarily subtidal, and are more prominent in areas of low to moderate salinity. This study focuses on Lap Reef, a natural oyster reef complex occupying approximately 387,000 m^2 in Copano Bay (Fig. 5.1A). A restoration project completed in August 2011 involved the construction of eight reef mounds (each 20 x 30 m) within the Lap Reef complex (Fig. 5.1B). Reef mounds were constructed of a crushed concrete base topped with reclaimed oyster shell, and resulted in the addition of 4,800 m^2 of reef habitat. Average depth of the study area is approximately 1 m.

5.2.2. Field sampling and laboratory analyses

Monitoring of the restored and natural reefs was conducted throughout 2012 and 2013. A handheld Hydrolab data sonde was used to measure environmental parameters, including water temperature (°C), salinity (psu) and dissolved oxygen (mg L^{-1}). Bottom water samples were collected 0.1 m above the reefs using a horizontal van Dorn water sampler and chlorophyll-*a* and total suspended solids (TSS) were quantified in the laboratory (EPA methods 445.0 and 160.2, respectively). Oysters were collected from restored and natural reef sites to determine oyster density (ind. m^{-2}) and shell height (mm).

5.2.3. Conceptual model and calculation of unit emergy values

A conceptual model of ecological flows associated with nitrogen removal from the oyster reef system was developed (Fig. 5.2). Boundaries of the modeled system are defined as the extent of the reef, including the overlying water column (1 m) and the surface sediments (2 cm depth). Inputs to the system include solar energy and nutrients delivered with river inflows. Nutrient regulating ecosystem services are represented by the functional flows that result in the removal of bio-deposited nitrogen from the system, either through burial into deep sediments or denitrification and release to the atmosphere as nitrogen gas (Fig. 5.2). Steady-state values of system components and flows were estimated from the literature and converted to energetic units (J m^2 day^{-1}). Equations were written to express flows into and out of each model component according to the conceptual model:

$$N_t = N_{(t-1)} + J_N + k_4 P + k_8 F + k_{12} D - k_1 RN - k_{13} N$$

$$P_t = P_{(t-1)} + k_2 RN - k_3 P - k_5 PF$$

$$F_t = F_{(t-1)} + k_6 PF - k_7 F$$

$$D_t = D_{(t-1)} + k_9 PF - k_{10} D - k_{11} D - k_{12} D$$

where *N* represents nitrogen, *P* represents primary producers, *F* represents oysters, and *D* represents the detritus pool. *J* describes the solar energy input to the system, with *R* representing the proportion of solar energy reflected from the system. J_N represents nitrogen inputs to the system. Coefficients are described as follows: k_0 and k_1 represent solar energy and nitrogen uptake during gross primary production; k_2 represents net primary productivity; k_3 and k_4 describe losses of primary producers and recycling of nitrogen; k_5 describes clearance of primary production by oysters; k_6 describes assimilation of cleared nitrogen; k_7 describes metabolic processes of oysters and k_8 describes recycling of nitrogen during these processes; k_9 describes deposition of excess nitrogen; k_{10} describes the proportion of deposited nitrogen that is buried into deeper sediments and effectively removed from the system; k_{11} represents the proportion of deposited nitrogen that is mineralized by denitrifying bacteria, and is released from the system as nitrogen gas; k_{12} represents the recycling of nitrogen by bacteria to the nitrogen pool; and k_{13} describes losses from the nitrogen pool associated with water flow and other ecological processes not depicted in the model. The flows of interest for describing ecosystem services are the flows resulting in nitrogen burial and nitrogen gas release. The model was simulated over three years to ensure steady-state conditions were achieved.

Energy flows depicted in the steady-state model were set up in matrix form based on flows to and from each model component. The Microsoft Excel Solver tool was used to calculate solar transformities for each energy transformation process represented in the matrix. Solver utilizes optimization algorithms to determine resource allocations to model components (Frontline Systems Inc. 2014). Unknown transformities were manipulated subject to the constraints set (e.g., emergy in = emergy out). The model was run for 100,000 iterations (precision = 0.01). This method has been proven to be a valid way to estimate solar transformities for use in emergy analyses (Bardi et al. 2005).

5.2.4. Emergy evaluation

Flows of nitrogen removal from the natural and restored reefs during 2012 and 2013 were quantified based on data collected from the field. Clearance rates were calculated according to methods outlined in Beseres Pollack et al. (2013). Approximately 50% of all nitrogen cleared from the water column by oysters is voided as biodeposits (Newell & Jordan 1983; Beseres Pollack et al. 2013). Laboratory and field studies have estimated that 20% of bio-deposited nitrogen undergoes denitrification (Newell et al. 2002; Beseres Pollack et al. 2013), and approximately 10% of bio-deposited nitrogen is buried in deeper sediments (Boynton et al. 1995; Beseres Pollack et al. 2013). These rates were applied to calculate amounts of deposited nitrogen that are effectively removed from the system through burial and denitrification. All processes quantified in units of nitrogen were converted to energy (J) according to the following conversion factors (Redfield 1958; Campbell 2004):

$$Nitrogen\ x\ 6.625 = Carbon\ x\ 10 = kcal\ x\ 4186 = J$$

Solar transformities calculated from the steady-state model were then applied to the energy flows of nitrogen removal to quantify the nutrient regulating functions in emergy terms according to (Odum 1996):

$$Emergy\ (sej) = Energy\ (J) x\ Solar\ Transformity\ (sej\ J^{-1})$$

Emergy values obtained on a per square meter basis were scaled up to examine the total relative contributions of the entire reef complexes. Enhancement of ecosystem service provision was examined by quantifying the relative contributions of the restoration project in terms of reef extent and nitrogen removal.

5.3. Results

Solar transformities for the nitrogen removal functions were determined to be 4.35 E+10 and 1.81 E+10 sej J^{-1} for denitrification and burial, respectively (Table 5.1). Transformity values increase as more transformations are necessary to produce a good or service (Odum 1996). The transformity values obtained for these flows reflect the magnitude of work required to remove nitrogen from the system. Denitrification requires more transformation processes (Kellogg et al. 2013), and thus has a higher transformity value compared to nitrogen burial. The solar transformity values calculated in the present study (Table 5.1) can contribute to the growing Emergy Society database of unit emergy values (2014; www.emergydatabase.org).

Solar transformities were applied to calculated rates of nitrogen removal to determine the solar emergy values of these ecological functions (Table 5.1). During 2012, the first year post-restoration, the natural reef outperformed the restored reef in terms of nitrogen removal (Fig. 5.3, Table 5.1). Solar emergy values of nitrogen burial and denitrification at the natural reef were determined to be 3.15 E+15 sej m^{-2} $year^{-1}$ and 1.51 E+16 sej m^{-2} $year^{-1}$, respectively. The restored reef was providing the same services at approximately 50%, with emergy values of nitrogen burial and denitrification estimated at 1.54 E+15 and 7.40 E+15 sej m^{-2} $year^{-1}$, respectively. During 2013, ecosystem service provision declined slightly at the natural reef, with emergy values of nitrogen burial and denitrification determined to be 2.32 E+15 sej m^{-2} $year^{-1}$ and 1.12 E+16 sej m^{-2} $year^{-1}$, respectively. Ecosystem service values provided by the restored reef increased greatly from 2012 to 2013 (Fig. 5.3), with emergy values of nitrogen burial and denitrification determined to be 6.15 E+15 sej m^{-2} $year^{-1}$ and 2.96 E+16 sej m^{-2} $year^{-1}$, respectively.

Emergy values of nitrogen removal processes were scaled up to examine total value of services provided by the entire reef complex. The restoration project increased the extent of the Lap Reef complex by 4,800 m^2, and thus represents 1.23% of the new total area (Table 5.2). During 2012, the restored reef accounted for only 0.60% of the nitrogen removal ecosystem services provided by the combined Lap Reef complex. During 2013, the restored reef accounted for 3.18% of the total services provided by the complex.

5.4. Discussion

The valuation of ecosystem services provides a framework for integrating natural and human systems that should result in better management practices to ensure environmental, social and economic demands are met in the future (Farber et al. 2006; Daily et al. 2009; de Groot et al. 2010; Grabowski et al. 2012). One major challenge is the development of methods to properly value ecosystems and the services they provide (Odum & Odum 2000; Kangas 2004). A variety of studies have attempted to estimate the economic, or monetary, value of ecosystems with respect to the services they provide (Costanza et al. 1997; Henderson & O'Neil 2003; Barbier et al. 2011; Grabowski et al. 2012). Monetary estimates of ecosystem value can be insightful for several reasons. Management of ecosystems and natural resources requires decisions to be made that involve spending and tradeoffs in resource use (Costanza et al. 1997; Brumbaugh et al. 2006; Farber et al. 2006). Also, monetary values help capture the attention of policy makers and the general public that may have no interest in ecological or inherent values (Ledoux & Turner 2002, Stegeman & Solow 2002). However, market prices are subject to great fluctuation, and do not necessarily represent the complete value of a product or service (Lipton et al. 1995; Odum 1996; Odum & Odum 2000; Ledoux & Turner 2002). Ecosystems can be severely undervalued when only market prices are considered. Additionally, putting a "price tag" on nature can create a slippery slope. For example, it can always be argued that infrastructure can replace certain ecosystem services. Replacement cost methods have been utilized to compare nutrient regulating services of oyster reefs to the cost of operating waste water treatment plants that can accomplish similar services (Beseres Pollack et al. 2013).

The present study demonstrates the application of emergy analysis to quantify ecosystem functions and services on the basis of solar energy. Results demonstrate that the restoration of oyster reef habitat has increased the value of nutrient regulating ecosystem services (i.e., nitrogen removal through denitrification and burial of oyster biodeposits) provided by the Lap Reef complex in Copano Bay. During the first year post-restoration (2012), the restored reef provided approximately half of the value of the evaluated functions compared to the natural reef. The smaller contribution of the restored reef was expected during the first year as the reef was developing. In the second year post-restoration, the restored reef was contributing approximately twice the value of nitrogen removal functions as the natural reef on a per unit area basis. The differences observed between 2012 and 2013 reflect development of oyster populations at the restored reef (see Chapter III). The restoration project created 4,800 m^2 of new oyster habitat, representing a 1.2% increase of reef area to the Lap Reef complex. The contribution of the restored reef in terms of nitrogen removal functions is more than twice the contribution in area within the second year post-restoration. This again is likely a reflection of higher densities of oysters at the restored reef during 2013 compared to the natural reef. Overall, these results demonstrate the near-term success of the restoration project in terms of providing suitable habitat to support oyster production and related nutrient regulating functions and services.

The present study also provides insight regarding the trajectories of ecological functions during reef development. It is important to understand how long it may take for ecosystem service related goals to be met, if they are met, and whether oyster reef restoration is a good investment (Bullock et al. 2011; La Peyre et al. 2014). Yet, relatively little is still known about the development trajectories of restored oyster reefs and associated functions or services (but see Grabowski et al. 2012; La Peyre et al. 2014). The present study indicates that the values of ecosystem services related to nitrogen removal are similar between restored and natural reefs within the second year post-restoration. Thus, nutrient removal services can be attained in a relatively short time frame. Other services may take much longer to develop, and the timeframe for the development of ecosystem services can vary greatly depending on system-specific attributes and inputs. For example, vegetation biomass of marsh or forest ecosystems can take decades to reach levels equivalent to natural reference systems (Bullock et al. 2011; La Peyre et al. 2014). An analysis of no-take marine reserves demonstrated that while ecosystem structure and biomass may be restored relatively quickly (e.g., several years), it may take much longer (e.g., decades) to restore ecosystem function (Micheli et al. 2004; Bullock et al. 2011).

Emergy analysis may present a particularly unique approach for examining restoration trajectories by allowing for the incorporation of external influences on ecosystem development and function. Principles of self-organization are important in emergy theory (Odum 1996), and are a critical factor in the development of systems and ecosystem services. Recent studies have examined relationships of emergy and ecosystem services (Pulselli et al. 2011; Coscieme et al. 2013). The efficiency of emergy inputs to produce ecosystem services was examined, and relationships were categorized in two dimensions (Pulselli et al. 2011) and three dimensions (Coscieme et al. 2013). These studies demonstrated how systems can change and mature in a thermodynamic context, and the methods outlined could prove useful for examining restoration trajectories.

There are many unique advantages to the application of emergy analysis to value ecosystem services (Odum 1996; Odum & Odum 2000; Brown & Ulgiati 2004; Hau & Bakshi 2004; Pulselli et al. 2011; Coscieme et al. 2013). Emergy analysis can effectively link ecological and economic systems (Odum 1996). Market and non-market goods and services can be evaluated objectively from an ecocentric, or integrated, perspective, independent of monetary values (Odum & Odum 2000; Hau & Bakshi 2004). Based on thermodynamic principles, emergy methods allow for ecological and economic systems to be evaluated in common energy-based units. Thus, systems can be evaluated more holistically with emergy analysis compared to traditional economic methods.

5.5. Conclusion

The present study demonstrates the application of emergy analysis methods to the quantification of two nutrient regulating functions provided by oyster reefs. As habitat restoration becomes a broader priority for restoring ecosystem services, it is important to quantify the ecological functions that support the provision of ecosystem services. Problems inherent with monetary analysis of ecosystem services and values are increasingly being recognized, and research directed at non-monetary approaches to valuation of ecosystems and the services they provide is likely to increase. Emergy theory provides an ecocentric approach for valuing ecosystem services that can complement traditional economic methods.

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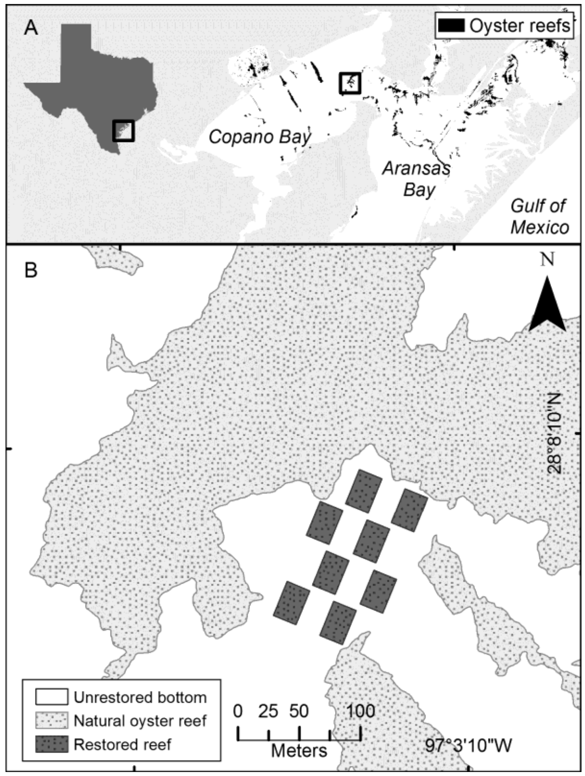

Fig. 5.1. Study area. (A) Location of Lap Reef complex in Copano Bay, Texas, USA. (B) Location of restored reef within Lap Reef complex.

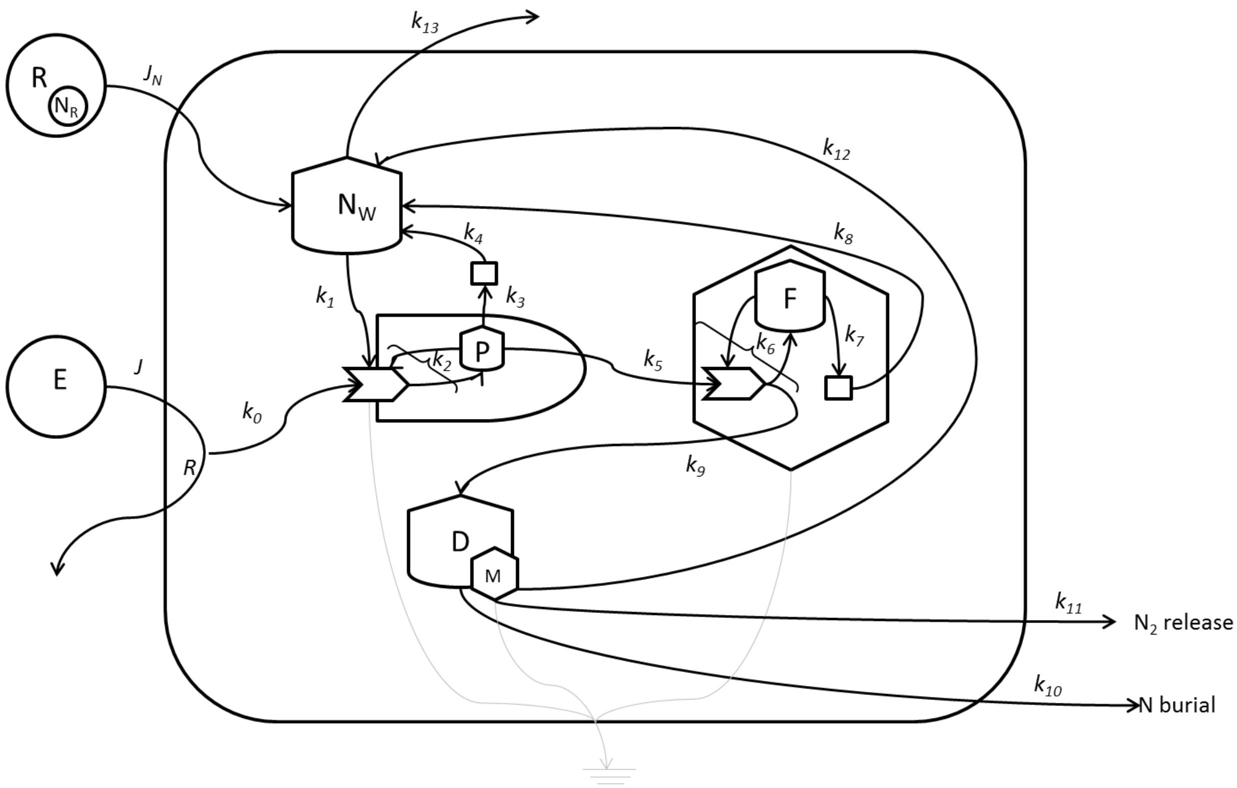

Fig. 5.2. Conceptual model of nutrient regulating ecosystem services (i.e., nitrogen removal) provided by an oyster reef. Inputs include solar energy (E) and nitrogen delivered with river flows (N_R). Nitrogen available in the water column (N_W) is utilized by primary producers (P), which are available as food for oysters (F). Oyster deposits contribute to the pool of detritus (D) in sediments. Deposited nitrogen is removed from the system either through burial into deep sediments (N burial), or through denitrification by mineralizing bacteria (M) and subsequent release of nitrogen gas (N_2 release). Flows from primary producers, oysters, and mineralizers to the N_W pool represent recycling pathways within the system (e.g., metabolites, mineralization). Light gray flows exiting at the bottom of the diagram represent energy losses.

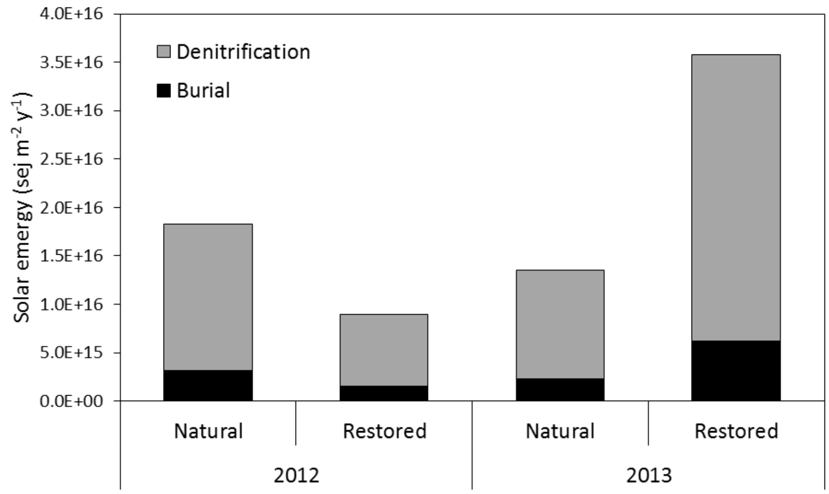

Fig. 5.3. Emergy values (sej m^{-2} $year^{-1}$) of nitrogen removal through burial and denitrification provided by the natural and restored reefs during 2012 and 2013.

Table 5.1. Emergy analysis of nitrogen removal functions provided by the natural and restored reefs during 2012 and 2013.

	Energy (J m^{-2} y^{-1})	Transformity (sej J^{-1})	Emergy (sej m^{-2} y^{-1})
Denitrification			
2012			
Natural reef	3.47E+05	4.35E+10	1.51E+16
Restored reef	1.70E+05	4.35E+10	7.40E+15
2013			
Natural reef	2.57E+05	4.35E+10	1.12E+16
Restored reef	6.80E+05	4.35E+10	2.96E+16
Burial			
2012			
Natural reef	1.74E+05	1.81E+10	3.15E+15
Restored reef	8.51E+04	1.81E+10	1.54E+15
2013			
Natural reef	1.28E+05	1.81E+10	2.32E+15
Restored reef	3.40E+05	1.81E+10	6.15E+15

Table 5.2. Enhancement (%) of reef area (m^2) and provision of nutrient regulating functions (sej year^{-1}) via restoration.

	Natural reef	Restored reef	Combined	Contribution of restoration (%)
Reef area (m^2)				
	387,000	4,800	391,800	1.23%
Nitrogen removal (sej year^{-1})				
2012	7.07E+21	4.29E+19	7.11E+21	0.60%
2013	5.22E+21	1.72E+20	5.39E+21	3.18%

CHAPTER VI: CONCLUDING SUMMARY

Recent research revealing the extent of marine habitat degradation has ignited a surge of restoration efforts globally. Oyster reefs, once dominant habitats in temperate estuaries world-wide, have experienced losses in abundance and extent greater than any other marine habitat. The purpose of this study was to assess the success of oyster reef restoration. It was hypothesized that restoration projects have been implemented with increased efficiency during the past decade, and that there has been an increased use of ecologically-relevant success metrics to assess restoration projects. These hypotheses were tested in Chapter II by conducting a meta-analysis to identify trends in oyster reef restoration projects across the United States. Additional hypotheses regarding the effectiveness of various ecological metrics were tested in the following chapters by constructing oyster reef habitat in Copano Bay, Texas, and monitoring to assess the success of the restored reef in terms of various ecological functions. It was hypothesized that differences in ecosystem structure and function would be observed between restored and reference habitats and that the restored reef would become more similar to the natural oyster reef reference over time.

In the United States, restoration of estuarine habitats became a national priority with the Estuary Restoration Act (ERA) of 2000. A substantial amount of effort was expended to outline guidelines for the implementation and monitoring of restoration projects, and for disseminating resulting data. In Chapter II, data for oyster reef restoration projects were compiled from the National Estuaries Restoration Inventory to examine trends in projects since the ERA. More than $45 million has been invested for the implementation of 187 non-compensatory oyster reef restoration projects. Over 150 ha of oyster reef habitat have been restored across the U.S., with projects most heavily concentrated in the Chesapeake Bay area and the Florida Gulf coast.

Trends over time indicate that projects are being implemented at larger scales, increasing from an average of less than 0.4 ha in 2000 to over 1 ha on average in 2011. Costs per unit decreased from an average of more than $2.1 million per ha in 2000 to just over $500,000 per ha in 2011. Trends in project size and cost were driven heavily by the American Recovery and Reinvestment Act of 2009. However, this analysis confirms one major problem hindering the field of restoration ecology: a lack of available monitoring data or assessments of project success. While projects can be considered successful in terms of compliance (i.e., the project was physically completed), this does not provide information regarding ecological function, and thus does not allow for assessment of project goals related to ecological function. Billions of dollars will be dedicated solely to ecosystem restoration projects and related scientific endeavors through the RESTORE Act of 2012, providing unprecedented opportunities for advancements in the field of restoration ecology. This study provides insight into the effects of national policies on restoration trends, and stresses the importance of project assessments and data sharing to ensure that future restoration projects make meaningful contributions to science and society.

Efforts to restore oyster reef habitat are often implemented with goals to restore oyster production, and also to create suitable habitat to support the many resident and transient fishes and crustaceans that use reefs. During the summer of 2011, a 1.5 ha oyster reef complex was constructed in Copano Bay, Texas to restore habitat for oysters and associated fauna. The three-dimensional reef complex was designed to maximize available resources and create a structurally complex habitat that incorporates hills and valleys as essential design elements. In Chapter III, oysters and resident and transient fishes and crustaceans were monitored at the restored reef in addition to natural oyster reef and unrestored bottom reference habitats for two years following reef construction. The restored reef had substantial oyster recruitment and growth, with oyster abundance and size comparable to reference conditions within the first year. By the end of the study, approximately 25 months post-restoration, oyster densities totaled over 4,000 individuals per square meter. Resident and transient fishes and crustaceans recruited to the restored reef within six months post-construction, and abundance and diversity were comparable to reference habitats. Results indicate that the restored reef is successful in providing important ecological functions associated with habitat provision and oyster production. Densities of oysters and nekton were higher than observed in a majority of previous restoration efforts across the United States, and may be attributed to the complex reef design incorporating relatively high relief reefs and also valleys that create corridors important for nekton use and habitat connectivity. Additionally, the present study provides insight regarding restoration trajectories and implications for monitoring timeframes that should be considered in future restoration projects.

As foundational species, oysters can exert a strong influence on trophodynamics in estuarine systems, and there is great potential for oysters to mediate benthic-pelagic coupling. By assessing oyster diets, a better understanding of the trophic dynamics within oyster reefs and the role of oysters in regulating flows of organic matter can be developed. It has been demonstrated that areas of dense cultured oysters can have a positive feedback effect on sediment organic matter, fueling benthic microalgae growth. It was hypothesized that restoration could have the same effects, which may influence oyster diets. In Chapter IV, a dual stable isotope ($\delta^{13}C$ and $\delta^{15}N$) approach was utilized to assess temporal and habitat variability of oyster diet composition at a restored reef compared to surrounding reference habitats. Oysters and potential composite food sources — suspended particulate organic matter (SPOM) and sediment surface organic matter (SSOM) — were sampled from restored and reference habitats seasonally for two years post-restoration. Composite food resources were distinguishable based on their respective $\delta^{13}C$ values, with SPOM being more depleted in ^{13}C (-24.2 ± 0.6‰) than SSOM (-21.2 ± 0.8‰) throughout the study. SPOM composition is likely dominated by autochthonous phytoplankton production, while SSOM is a combination of trapped phytoplankton and benthic microalgae. Oyster diet composition was similar among restored and reference habitats, but changed over time. SSOM was found to be an important component of oyster diets, and contributed larger proportions relative to SPOM over time, likely due to an increase in availability of benthic microalgae present in SSOM. The higher vertical relief of the restored reef (0.3 m) compared to reference conditions (0.1 m) did not appear to affect oyster diets. This was unexpected, and will support future research regarding the design of restoration reefs. The results of this study support growing evidence that benthic organic matter can be an important food resource for oysters. This information should be used to improve existing population dynamics models, and for restoration and management of shellfish populations. By accounting for all potential food sources, better estimates of carrying capacity to support shellfish populations, and better understanding of the impact of shellfish populations on ecosystem functioning, can be achieved.

Enhancing or restoring nutrient regulating ecosystem services are highly cited as goals of oyster reef restoration efforts. Oyster reefs can play a major role in the acquisition, processing and storage of nutrients within estuaries, and help maintain ecologically-acceptable levels of major nutrients, such as nitrogen. As oysters filter water to feed, they excrete excess particles as biodeposits. Nitrogen shunted from the water column to sediments via oyster biodeposits and waste may then undergo burial or denitrification, resulting in nitrogen removal from the system. In Chapter V, nitrogen removal attributed to oysters was quantified using emergy analysis to compare relative value of nitrogen removal functions by the restored and natural reefs. Emergy is a measure of total energy necessary to produce a good or service, and thus can be thought of as 'energy memory.' Emergy evaluations can be used to represent environmental and economic values of a system in equivalent units, generally solar energy units, and thus present a more holistic way to value market and non-market ecosystem services in common units. The results of the present study demonstrate that within the second year post-restoration, the restored reef was providing a greater value of services per unit area compared to the natural reef. Thus, the restored reef has proven to be successful in providing ecosystem services related to nutrient removal.

Overall, the work presented here has contributed to the broader knowledge of oyster reef restoration practice and theory. For example, trends examined over time for projects implemented across the United States demonstrate that the implementation of oyster reef restoration projects has become more cost efficient. However, findings confirm a lack of available data, and suggestions are presented to improve data collection and sharing. The restoration project implemented in Copano Bay, Texas proved to be successful in restoring a variety of ecological functions. Much of this success could be attributed to the design of the reef complex, and thus will support the planning and design of future restoration efforts. Substantial densities of oysters and nekton were observed, and are at the high end of the spectrum of previous reports from other projects. Food sources of *Crassostrea virginica* are not well characterized, despite the important role oysters can play in estuarine dynamics. Stable isotope analyses presented in this work confirm that oysters can access and consume benthic food resources. This work can support the development of food web and population dynamic models by accounting for potential benthic food resources, and highlights important implications related to restoration, such as the design and placement of reefs. Finally, emergy analysis methods were applied to quantify nitrogen removal from oyster reef systems. The results of Chapter V indicate that the restored reef provides more service value per unit area compared to the natural reference reef, illustrating the success of the restoration project in providing these services. This work also demonstrates the application of emergy analysis to quantify ecosystem functions and services on the basis of solar energy, which can provide a complementary approach to traditional economic valuation methods.