ECOLOGICAL STRUCTURE AND FUNCTION OF RESTORED HABITATS ACROSS A RANGE OF COASTAL ENVIRONMENTS

A Dissertation

by

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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

Coastal habitat loss represents a major threat to biodiversity and ecosystem services worldwide. Habitat restoration plays a key role in efforts to mitigate this loss by supporting the recovery of ecological communities (i.e., structure) and important ecosystem processes (i.e., functions). The objective of this dissertation was to evaluate the ability of constructed habitat restorations to support equivalent ecological communities and functions to reference habitats across a range of coastal environments. This was accomplished through an analytical framework combining community structure analysis with stable isotope based food web analysis.

In Chapter I, the scale and implications of coastal degradation, the use of constructed habitats for coastal restoration, and the use of stable isotope analysis to study food webs and function are outlined. In Chapter II, the development of a constructed subtidal oyster reef in the Mission-Aransas estuary was surveyed alongside a natural oyster reef over a 5- to 29-month post-restoration timeframe to evaluate recovery. The results demonstrated structural and functional recovery occurring between 12-15 months post-restoration, as oysters and predatory consumers increasingly colonized the developing reef.

In Chapter III, a constructed salt marsh was monitored alongside a natural reference marsh in Nueces Bay over a 4- to 6-year post-restoration timeframe. The results of this study demonstrated the ability of the restored marsh to support communities with similar composition as the natural marsh, however, stable isotope mixing models demonstrated that dominant macrofauna in the restored marsh consumed less organic matter originating from macrophyte production than their natural counterparts. This functional variation was attributed to the relatively low amounts of organic matter and detritus contained in the recently constructed salt marsh sediments.

In Chapter IV, I examined the epibenthic community and food web structure of subsurface "Rigs-to-Reefs" artificial reefs in comparison to standing operational platforms in the Texas offshore Gulf of Mexico shelf region. Reefed platforms were found to support similar communities as standing platform habitats at similar depths (30-m), however shallow standing platform sites (5-m) were found to support communities that were distinct from deeper standing platform and clearance-limited reefed platform sites. Reefed platform and standing platforms at 5- and 30-m depths were found to support similar food web structure, indicating that reefed platforms replicate the fundamental ecological functions associated with standing platforms. Although, the loss of shallow water substrate, associated with platform reefing, could be expected to reduce the biodiversity associated with these structures.

In Chapter V, I conclude with a summary of the findings in this dissertation and outline general patterns of functional recovery between different coastal habitat types that can be inferred from these results and established theory. This study provides strong evidence for the ability of constructed habitats to support similar communities as natural/pre-existing habitats across a range of coastal environments. The results suggest that constructed habitats in systems driven by microalgal producers are likely to functionally recover as community structure develops. However, functional recovery in systems driven by vascular plant production are limited by the recovery of detrital food web intermediaries. The insights obtained from this study have broad implications for coastal restoration practitioners and resource managers.

DEDICATION

In dedication to my parents, Ron and Julia, for their unwavering support and for instilling the values of science and rational thought in me from a young age.

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CHAPTER I: INTRODUCTION

Environmental degradation and ecological restoration

Habitat loss is one of the greatest threats to earth's life-support systems and humanity in the 21st century. The loss of natural environments through habitat destruction, fragmentation, and degradation is the primary threat to global biodiversity (Wilson 1988; Fahrig 1997; Pimm and Raven 2000) and ecosystem functioning (Daily et al. 1997; Dobson et al. 2006). Human alteration of the global environment is responsible for initiating the sixth major extinction event in earth's history, which has had profound effects on ecological functions and associated services necessary to sustain human civilization (Chapin et al. 2000; Costanza et al. 2014; Ceballos et al. 2017). Ecological degradation is expected to intensify in the near future under the additional pressures of expanding human populations (Sisk et al. 1994) and climate change (McCarty 2001). Substantial changes in policy and practices will be required to reverse this trend over the next 50 years in order to sustain the needs of future generations and avoid catastrophic global ecological disaster (MEA 2005).

Changing the practices that contribute to environmental degradation and protecting existing natural capital through conservation efforts are paramount to maintain ecological functioning and biodiversity (Young 2000). However, land transformations and other human disturbances have degraded many systems to the point in which natural recovery processes would take place over decades or centuries, if at all (Dobson et al. 1997). The sheer extent of human-induced damage to natural systems has rendered ecosystem repair an essential aspect of our future survival strategy (Hobbs and Harris 2001b). The emergence and rapid development of restoration ecology as a distinct academic discipline was largely a response to these challenges.

Ecological restoration has been defined as "the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SER 2004). The field of restoration ecology is an interdisciplinary practice that integrates theoretical aspects of community ecology, landscape ecology, physical geography, and other related fields, to guide and improve the practice of ecological restoration. The principal goals of ecological restorations are to re-establish ecological structure and ecological function of a degraded system to a close approximation to its pre-degraded state (SER 2004). Ecological structure describes the organizational attributes of communities, such as species composition, diversity, and abundance in a system (Palmer et al. 1997). Ecological function describes processes that occur over time such as nutrient cycling, production, and the transfer of organic matter through food webs (i.e. trophic structure) (Palmer et al. 1997). The ecological success of restoration projects is typically evaluated through post-restoration monitoring of ecological attributes in comparison to a natural reference system (Palmer et al. 1997, SER 2004).

In practice, post-restoration monitoring has largely focused on the analysis of variables related to the ecological structure of restored habitats; variables related to ecological function in restored habitats are rarely measured (Ruiz-Jaen and Aide 2005). There is growing consensus among researchers that a greater focus on evaluating the functional attributes of restored habitats is necessary to fully assess the ecological success of restorations (Ehrenfeld and Toth 1997; Kentula 2000; Ruiz-Jaen and Aide 2005). This is because ecological functions are closely related to ecosystem services provision (Barbier et al. 2011b) and the recovery of ecological structure can occur independently of functional recovery (Lockwood and Pimm 1994; Zedler and Lindig-Cisneros 2000; Cortina et al. 2006).

Habitat construction and restoration in coastal systems

Coastal habitats are among the most valuable on earth due to their support of critical ecosystem services such as food production, nutrient cycling, waste treatment and disturbance regulation (Costanza et al. 1997a; Barbier et al. 2011b). Unfortunately, coastal ecosystems are also among the most vulnerable to human alterations, as these regions have long been focal points of human settlements and resource extraction. Habitat loss in coastal regions associated with land transformation, resource extraction and pollution has substantially diminished the ability of these systems to provide basic ecosystem services (Lotze et al. 2006; Worm et al. 2006; Vitousek et al. 2008). The degradation of coastal ecosystems has resulted in a 33% reduction in the number of viable fisheries, a 69% reduction in the provision of nursery habitat (oyster reef, seagrass, and wetlands), and a 63% reduction in the water filtration and waste removal services provided by suspension feeders and wetlands (Worm et al. 2006).

Restoration has become an increasingly important tool for reversing ecological degradation in coastal systems. Coastal restoration techniques include the re-establishment of previously altered hydrological regimes, the reintroduction of native biota, re-establishing topographic features, and pollution control (NRC 1992). Urban coastal habitats are often severely impacted by activities that result in complete habitat destruction such as dredging, destructive fishing practices, and landscape alterations. These activities frequently result in a near or complete loss of the topographic features that define these habitats. In such cases, ecological restoration often requires the re-creation of these physical features through construction projects, such as the creation of artificial reefs and salt marshes (Race and Christie 1982; Grayson et al. 1999; Baggett et al. 2014).

Coastal habitat restoration and construction have become a national priority in the United States through the Estuary Restoration Act (ERA 2000) and the National Fishing Enhancement Act (NEFA 1984). The Estuary Restoration Act promotes a coordinated federal approach and provides financial and technical assistance for estuarine habitat restoration projects. The National Fishing Enhancement Act directed the development of the National Artificial Reef Plan (NOAA Technical Memorandum, NMFS OF-6, 1985) to establish national standards for artificial reef creation, and a reef-permitting system under the regulatory oversight of the U.S. Army Corps of Engineers. The goals of these legislations are to enhance ecological resources by encouraging the construction and restoration of coastal habitats, and to promote the monitoring and research necessary to improve these practices.

Stable isotope analysis in the study of food webs and ecosystem function

The growing interest in assessing the functional attributes of constructed coastal habitats has led researchers to incorporate stable isotope based food web analysis into restoration monitoring schemes. Stable isotope analysis is a powerful tool for studying the trophic structure and biogeochemical processes that underlie ecological functions. Stable isotope analysis is becoming an increasingly important tool for monitoring constructed habitats and has been successfully employed to study function in offshore (Kang et al. 2008; Cresson et al. 2014) and estuarine (Nordström et al. 2014; Dillon et al. 2015) environments. The isotopic composition of carbon and nitrogen change in predictable ways as these elements move through food webs, as many physiological reactions alter the ratio of heavy to light isotopes in a process known as isotopic fractionation (DeNiro and Epstein 1978; Peterson and Fry 1987). Physiological reactions often favor lighter isotopes (^{12}C, ^{14}N) because they react faster than their heavier counterparts (^{13}C, ^{15}N). These changes in isotopic composition can be measured with great accuracy using

isotope ratio mass spectrometry, and are exploited by ecologists to study elemental cycles in ecosystems.

The carbon isotopic composition ($^{13}C/^{12}C$) undergoes fractionation as it is assimilated by primary producers during photosynthesis. The stable isotope composition of carbon in primary producer tissue is related to its photosynthetic processes (e.g. C_3, C_4, CAM) and to the CO_2 reservoir from which its carbon was derived (e.g. atmosphere, ocean, freshwater) (DeNiro and Epstein 1978; Peterson and Fry 1987). The isotopic composition of C changes little with trophic transfers (0 to 1‰), and can be used to trace organic matter in consumer tissue to its primary producer origins. The stable isotope ratio of nitrogen in consumer tissue is enriched in ^{15}N relative to its food sources due to the preferential excretion of isotopically light nitrogen. This process results in a stepwise ^{15}N enrichment associated with trophic transfers (2 to 4‰) that can be used to determine consumer trophic levels (Minagawa and Wada 1984; Peterson and Fry 1987; Post 2002). These properties allow researchers to obtain time-integrated information about the sources of organic matter and ecological processes supporting secondary production (Fry 2006). When conducted on a community-wide scale, stable isotope analysis can establish a chemical outline of community trophic structure that can be used to evaluate and compare trophic diversity and ecological functioning between habitats and systems.

As the use of stable isotope analysis in food web studies has substantially increased in the last 2 decades, several important analytical tools have been developed for interpreting stable isotope data (reviewed by Layman et al. 2012). These methods include stable isotope mixing models for calculating consumer dietary components (Phillips and Gregg 2001; Parnell et al. 2010; Parnell et al. 2013) and stable isotope based community-wide metrics of trophic structure (Layman et al. 2007). The recent advance of analytical techniques that integrate community

isotope information with community biomass structure data (Rigolet et al. 2015; Cucherousset and Villéger 2015) is an important development for the study of food web structure and function, as the influence a species has on ecological function can be greatly influenced by its relative abundance (Grime 1998; Díaz and Cabido 2001).

These tools offer an analytical framework for the quantitative comparison of functional attributes between constructed habitats and natural or pre-existing reference habitats to evaluate functional recovery. Information gained through this approach can provide decision makers with critical information for judging proficiency of constructed habitats in meeting ecosystem service enhancement goals. Increasing our understanding of how habitat construction influences the structure and function of communities in the variety of coastal ecosystems where it is employed is essential to improve future habitat design and construction practices.

Coastal restorations take place across a continuum of ecosystems that include terrestrial, shallow benthic, and oceanic habitats. Substantial systematic differences in ecosystem functioning and trophic architecture occur along this gradient which have been linked to the relatively low nutritional quality and growth rate of terrestrial primary producers in comparison to those in aquatic systems (e.g. phytoplankton, benthic algae) (Cebrian et al. 1998). Due to the relatively greater lability of aquatic primary producers, the percent of production consumed by herbivores is much greater in aquatic than terrestrial systems, and the percent of production accumulated as detritus is much lower than in terrestrial systems (Cyr and Pace 1993; Cebrian et al. 1998). As a result, detrital organic matter pools and decomposer trophic intermediaries play a more important role in transferring primary production to consumers in coastal systems structured by vascular plants (Mann 1988; Shurin et al. 2006). As ecological processes underlying the development of detrital food webs occur over longer timeframes than grazer

trophic compartments (Mann 1988), investigating the process of trophic assembly in constructed habitats across a terrestrial-to-oceanic gradient can shed light on the importance of basal functional diversity in driving ecological functions essential for macrofauna community recovery (e.g. trophic transfer to consumers) across coastal systems.

Dissertation Approach, Study Systems, and Chapter Outline

The purpose of this dissertation is to evaluate the ecological structure and function of constructed habitats in the Texas Gulf of Mexico coastal region in comparison to natural or pre-existing habitats they are intended to recreate. To accomplish this, I employed a habitat monitoring framework using a combined approach of measuring variables of community structure (e.g. species diversity, biomass, density) alongside stable isotope based analysis of indicators of ecosystem function (e.g. basal resource use, trophic linkages, trophic diversity) in constructed habitats within three distinct environmental contexts. This was undertaken to examine the ability of these constructed habitats to achieve ecological equivalency with their respective reference systems, and to identify potential differences in community or functional attributes between constructed and reference habitats that can inform future management decisions and improve construction practices. The habitat types investigated in this study—constructed oyster reef, constructed salt marsh, and offshore decommissioned oil platform reef—were selected because they were created to mitigate the loss of threatened habitat and represent major areas of scientific and economic interest. In addition, these three unique systems were chosen because they exemplify the range of trophic typologies in which coastal restorations occur; extending from characteristically terrestrial intertidal saltmarsh to offshore artificial reefs. Examining ecological function in constructed habitats across these ecosystems provides a framework for investigating the diversity of successional processes that take place across coastal

systems and for establishing trends of ecological recovery relevant to the goals of restoration ecology that are broadly applicable to coastal ecoclines throughout the world.

Estuarine oyster reef habitats support a variety of important ecosystem functions and services. Oyster reefs improve water quality through filtration, enhance fisheries production through habitat provision and reduce erosion by stabilizing shorelines (Peterson et al. 2003; Grabowski et al. 2012; Beseres Pollack et al. 2013). Oysters themselves are also an economically important fishery resource. Oyster reefs have been subject to severe overexploitation and destructive fishing practices, resulting in an 85% loss of historic habitat a worldwide (Beck et al. 2011). Oyster reef restoration typically involves creating hard structure necessary for oyster recruitment through reef construction using various substrates types (George et al. 2015; Graham et al. 2017). Oyster reef restoration projects in the United States have received tens of millions of dollars in federal and non-federal funding and the size and expenditures associated with these projects are increasing (Blomberg 2015). However, a major hurdle in advancing oyster reef restoration practices is the lack of post-restoration monitoring and data sharing.

Oyster reefs support diverse fish and invertebrate assemblages that are distinct from other estuarine habitats (Robillard et al. 2010a; Stunz et al. 2010b; Nevins et al. 2014). Oyster reef food webs in the Gulf of Mexico are supported by a diverse suit of basal resources that include both pelagic (i.e. phytoplankton) and sediment associated benthic resources (i.e. benthic microalgae, phytodetritus) (Yeager and Layman 2011; Oakley et al. 2014; Blomberg et al. 2017a). Understanding how the links between these resources and consumer trophic compartments develop in constructed oyster reef habitats is critical to evaluating the success of oyster reef restoration in meeting functional equivalency goals.

In Chapter II, I focus on monitoring the development of community and food web structure in a recently constructed subtidal *Crassostrea virginica* oyster reef in comparison to a natural reference reef in the Mission-Aransas Estuary, TX. This study focused on concurrent monitoring of community and trophic assembly in a restored oyster reef over a 5 to 29 months post-restoration timeframe to determine the ecological success of the project, establish a timeframe of functional recovery, and study the relationship between community successional process and functional development. The results of this survey have important implications for resource managers, including the effects oyster reef restorations have on estuarine function and the timeframe over which the important trophic links that support ecosystem services can be expected to develop.

Salt marshes are highly productive habitats that occur at the interface between terrestrial and marine systems. Salt marshes provide critical nursery habitat for economically important fisheries species, coastline protection, water purification, and a variety of other ecosystem services (Stunz et al. 2010b; Barbier et al. 2011b; Nevins et al. 2014). Coastal development and hydrological alterations have resulted in a 50% reduction in U.S. salt marsh habitat from historic levels (Dahl 1990). Salt marsh restoration has become a major conservation enterprise in the Unites States with over 36,000 ha of salt marsh habitat restored through hundreds of millions of dollars in expenditures (Grabowski et al. 2012, neri.noaa.gov).

Salt marsh food webs are supported by unique array of primary producer groups that are characteristic of both terrestrial and marine environments including vascular plants (e.g. *Spartina* sp.) and their detrital products, pelagic phytoplankton, benthic microalgae, and epiphytic microalgae (Teal 1962; Currin et al. 1995; Fleeger et al. 1999; Riera et al. 2000). Although salt marsh construction is a common restoration technique, some attributes of these habitats, such as

sediment organic matter and detritus content, recover over very long timeframes, if at all (Craft et al. 1999; Craft et al. 2003). Few studies have directly addressed ecological functioning in constructed salt marshes (Zedler and Lindig-Cisneros 2000), and the proficiency of salt marsh construction in restoring the trophic links and ecological processes that support secondary production and ecosystem services is poorly understood.

In Chapter III, I investigate the ecological equivalency of a constructed *Spartina alterniflora* salt marsh in comparison to a natural reference marsh over a 2-year period beginning 4 years post-construction in the heavily urbanized Nueces Bay, TX. In this study, I investigate the relative importance of trophic links between various primary producers and macrofauna consumers in constructed versus natural salt marsh habitats. I also assess the influence of salt marsh flooding frequency on community and food web structure in natural and constructed salt marshes. The results of this study fill important knowledge gaps related to the pathways of organic matter flow supporting secondary production in constructed marshes and the influence of hydroperiod on trophic interactions in salt marsh communities in general. Based on these results, I make specific recommendations for salt marsh construction practices and identify research priorities which may inform methods for accelerating functional recovery in future restorations.

Offshore oil and gas platforms in the Gulf of Mexico continental shelf constitute the largest artificial reef system on earth (Dauterive 2000). The subtidal structural components of these platforms and their associated epibenthic communities provide refuge and feeding opportunities for a diverse array of species (Gallaway et al. 1979; Nelson and Bortone 1996; Beaver et al. 1997; Rauch 2004; Ajemian et al. 2015). Offshore platforms in the Gulf of Mexico are used extensively by fisherman and recreational divers, generating $324 million annually and supporting 5,560 full time jobs (MMS 2006). When platforms reach the end of their production

lifespans and are removed, valuable reef habitat is lost. Platform removal is occurring at a rate of 125 structures per year (Kaiser and Pulsipher 2005). State-run Rigs-to-Reefs programs have been established to mitigate this habitat loss by converting standing platforms into artificial reefs. The current reefing process involves removing the upper 26-m portion of platforms, to prevent navigational hazards, by platform toppling or partial platform removal (Macreadie et al. 2011).

Secondary production in offshore epibenthic platform communities in Louisiana waters have been shown to rely on allochthonous pelagic phytoplankton, with relatively little influence from benthic microalgal or macroalgal resources (Daigle et al. 2013). However, there is little information on how standing and reefed platform communities function in the comparatively oligotrophic Texas shelf waters. Epibenthic platform communities have been shown to exhibit compositional vertical zonation patterns (Lewbel et al. 1987). The effects removing shallow water substrate from standing platforms on epibenthic community structure and associated functions is not well known, and is an important area of inquiry as platforms are increasingly converted into artificial reefs.

In chapter IV, I survey the epibenthic communities on three reefed platforms at 30-m depths and on two standing platforms at 5- and 30-m depths in offshore Gulf of Mexico waters with the goal of comparing the community and trophic structure of these habitats. This study concentrates on identifying potential compositional and functional attributes of epibenthic communities that may differ between depths and/or structure types. The results of this study reveal variation in community structure along vertical gradients and yields important information pertaining to the effect of current reefing practices on biodiversity. This study also identifies and catalogs the diverse assemblage of sessile and motile macrofauna species inhabiting these unique anthropogenic ecosystems.

In Chapter V, I summarize the findings in previous chapters and highlight conclusions with important implications for restoration ecology and habitat construction. I also review the critical insights gained about the functional attributes of constructed habitats through monitoring frameworks that integrate community analysis and stable isotope based food web analysis. In addition, I outline general principles on the effects of habitat construction on ecological function along terrestrial-oceanic gradient based on the synthesis of information from previous chapters. These principals apply broadly to coastal systems, highlight important areas of study, and offer important insights that can serve to enhance ecosystem-based management of natural resources.

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CHAPTER II: HOW DOES A RESTORED OYSTER REEF DEVELOP? AN ASSESSMENT BASED ON STABLE ISOTOPES AND COMMUNITY METRICS

Abstract

Oyster reefs host complex food webs, as their three-dimensional biogenic structure provides habitat for a diverse range of invertebrates and fish. Oyster reefs have suffered severe degradation due to anthropogenic activities. Restoration projects aim to mitigate this habitat loss. We compared the development of a restored subtidal oyster reef to that of a natural reef for 29 months by assessing (1) community metrics (e.g., biomass, diversity), (2) the stable isotope composition of food sources and consumers, and (3) biomass-weighted isotopic diversity indices. A clear shift in restored reef community composition occurred 12–15 months after restoration, moving from a community dominated by opportunistic species to a more diverse and evenly distributed community, similar to that of the natural reef. Consumer stable isotope values indicated that the restored reef community was supported by similar food resources and had similar food chain length as the natural reef community by 5-month post-restoration. However, biomass-weighted isotopic diversity indices indicated that the magnitude of the main trophic pathways and characteristics of food web complexity in the restored reef did not recover to natural reef levels until 12–15 months after construction. The functional recovery of the restored reef community was driven by the homogenization of biomass distribution among trophic compartments as oysters and top predators increasingly colonized the reef. Results indicate that oyster reef restoration can support food web functions like those provided by natural reefs. We also demonstrate the importance of combining food web and community structure information in the study of ecological functioning.

Introduction

Oyster reefs are ecologically important constituents of estuarine systems worldwide and provide a number of ecosystem services (Rothschild et al. 1994; Kirby 2004; Flemer and Champ 2006; Grabowski et al. 2012). One service, provision of habitat for fish and invertebrate species, is supported by the complex biogenic structure formed by oyster reefs (Coen et al. 1999; Glancy et al. 2003; Tolley and Volety 2005; Stunz et al. 2010). Oyster reefs have been shown to support higher macrofaunal biomass and diversity as well as macrofaunal assemblages distinct, from other estuarine habitat types (Harding and Mann 2001; Glancy et al. 2003; Stunz et al. 2010; Nevins et al. 2014). Oyster reefs can support higher trophic levels and more complex food webs than other estuarine habitats (Quan et al. 2012; Oakley et al. 2014). The habitat complexity provided by oyster reefs mediates trophic transfer by providing refuge for intermediate predators and their prey and reducing interference competition at high densities (Posey and Hines 1991; Grabowski 2004; Grabowski and Powers 2004).

Oyster reefs have suffered severe degradation due to anthropogenic activities, with estimates of up to 91% lost compared to historic levels (Lotze et al. 2006). Significant efforts have focused on reef restoration to mitigate habitat loss and enhance ecosystem services (Harding and Mann 2001; Rodney and Paynter 2006; Schulte et al. 2009; Beseres Pollack et al. 2013). There is broad interest in determining how restored habitats develop and how long it takes for them to function like their natural counterparts. Dillon et al. (2015) observed conspecific consumers to have similar isotopic compositions within 2 years in natural and restored intertidal oyster reef communities, suggesting a relatively quick recovery of food web structure. However, the recovery of the food web structure in restored subtidal oyster reefs, which can support different species assemblages (Lehnert and Allen 2002), may be fueled by different food

resources (Kang et al. 2015), and may be more difficult to restore (Powers et al. 2009), has not been investigated in comparison to natural reference.

Habitat recovery has typically been evaluated based on community structure, comparing metrics, such as macrofauna abundance and biomass to those in natural or unrestored reference sites (Peterson et al. 2003; Baggett et al. 2015). However, these community metrics do not consider the relationships between and among the different trophic compartments in these habitats (i.e., food resources, consumers, and top predators) which are interrelated via flows of energy and organic matter (i.e., food web structure and functioning). Features of food web structure are believed to be the predominant mediator of the relationship between biodiversity and ecological function (Duffy 2003; Thébault and Loreau 2006). In this study, we take a system-wide approach based on the combination of community and food web analyses to provide a comprehensive framework for assessing different aspects of food web complexity relevant to ecosystem functioning.

Stable isotope analysis has become a standard tool in the study of organic matter flows within food webs in coastal ecosystems. Primary producers are characterized by different carbon isotopic composition in relation to their photosynthetic pathways and the reserve of CO_2 they rely on (e.g., air and seawater). This carbon isotopic composition changes relatively little (0–1‰) with trophic transfers. Thus, stable isotopes of carbon can be used to identify the origins of organic matter in consumers (Peterson and Fry 1987; Fry and Sherr 1989). The isotopic composition of nitrogen exhibits a step-wise enrichment in ^{15}N (2–4‰) associated with trophic transfers, permitting the calculation of trophic levels (Vander Zanden and Rasmussen 2001; Post 2002).

Recently, the role of stable isotope analysis has expanded from its use at the individual scale (i.e., determination of the food resources of a consumer), to its use for the study of community-wide food web characteristics. Community-wide indices based on the relative position of groups or individuals in multivariate isotope space have been developed to study the relationships between trophic structure and ecological functions (Layman et al. 2007; Jackson et al. 2011). Although these metrics have proven useful in the examination of community trophic structure (e.g., Jackson et al. 2012; Sagouis et al. 2015; Nordström et al. 2015), they are based on stable isotope data alone and assume that all species are equally important regardless of their relative abundance within a system. This can be a substantial limitation, as there is typically wide variation in biomass among community members and the effect of an individual species on ecosystem functioning is greatly influenced by its relative biomass (Grime 1998; Díaz and Cabido 2001). Isotopic diversity indices have recently been developed to incorporate species biomass information for quantifying different facets of food web complexity based on biomass-weighted stable isotope data (Cucherousset and Villéger 2015; Rigolet et al. 2015). These types of indices have successfully been employed to investigate functional changes associated with colonization by a benthic ecosystem engineering species (Rigolet et al. 2015) and the effect of macroalgal blooms on trophic diversity in sandy beach habitats (Quillien et al. 2016).

In this study, we used biomass-weighted isotopic diversity indices in combination with traditional community analysis (macrofauna density, biomass, and species richness) to assess the functional recovery of a restored subtidal oyster reef. Community metrics and isotopic diversity indices measured on the restored oyster reef were calculated over the course of its development in comparison with a natural reef counterpart, whose values were used as a benchmark for restoration success and establishing a timeframe of functional recovery.

Methods

Study site

The Mission-Aransas Estuary is a subtropical, shallow, bar-built estuary composed of several bays that drain into the Gulf of Mexico through Aransas Pass (Fig. 2.1). The total surface area of the Mission-Aransas Estuary is 46,279 ha and its average depth is 2 m (Armstrong 1987). It is a microtidal system and receives relatively low freshwater inflow from the Mission and Aransas Rivers outside of periodic storm events (Mooney and McClelland 2012). Water circulation is primarily wind driven.

The study site for this research project was a 0.6-ha subtidal restored oyster reef in Aransas Bay, TX constructed in July 2012 by deploying 600 m^3 of concrete rubble with a veneer of 50 m^3 of reclaimed oyster shell into four adjacent mounds (Fig. 2.1). Site selection was performed using a restoration suitability index model for the estuary (Beseres Pollack et al. 2012). The reef was designed to have 30 cm of vertical relief and the average mound size was ~680 m^2. A nearby natural oyster reef served as a reference habitat. Local environmental data (salinity, temperature, wind speed, turbidity, and chlorophyll *a*) were obtained from a NOAA National Estuarine Research Reserve System (NERRS) monitoring station located ~5 km east of the study location (Copano Bay East; NERRS 2016). Monthly means of environmental data based on data collected at 15-min intervals are reported.

Sample collection

Six sampling sites were selected at both the natural and restored oyster reefs. In October 2012 (3 months after reef restoration), four sampling trays filled with corresponding reef substrate (reclaimed oyster shell in the restored reef, natural reef substrate, including shell and live oysters in the natural reef) were deployed at each site. Sampling trays (45 × 30 × 11 cm;

0.135 m^2), were placed in a shallow excavated area in the existing reef, and affixed to the reef with rebar. Trays were used to sample oysters and motile macrofauna (reef-resident fishes and macroinvertebrates; hereinafter termed "macrofauna"), and were collected 5-, 9-, 12-, 15-, and 29-month post-restoration (i.e., January 20th 2013, May 11th 2013, August 16th 2013, October 28th 2013, and January 16th 2015, respectively). During each sampling period, sites in each reef were randomly designated to be used for community analysis (n = 3), stable isotope analysis (n = 2), or not sampled (n = 1). One tray from each site sampled was removed and all substrates (shell, sediment) were placed in buckets, transported to the lab, rinsed, and separated from macrofauna. Stable isotope analysis was not conducted in winter 2015, because there were only three trays per treatment left to be retrieved.

Macrofauna in community analysis trays were fixed in 10% buffered formalin, enumerated, and identified to lowest practical taxonomic level (usually species). Oysters (*Crassostrea virginica*) with shell heights of at least 25 mm (post-spat) were enumerated and measured for shell height. Macrofauna were dried for 24 h at 55 °C and combusted for 4 h at 450 °C to obtain ash free dry weight (AFDW) biomass. Macrofauna species in stable isotope analysis trays were separated and starved for 24 h in aerated artificial seawater to evacuate gut contents, and then stored at −20 °C. Mollusk shells were removed prior to stable isotope analysis and combustion for biomass.

During each sampling period, potential food sources were collected for stable isotope analysis. Surface sediment organic matter (SSOM) was collected with sediment cores (35.4 cm^2, 3-cm depth) adjacent to each reef type. Suspended particulate organic matter (SPOM) was sampled with two replicate bottom water collections (0.1 m above the sediment– water interface) on each reef, sieved through a 250-μm screen to remove large zooplankton, and then filtered

through pre-combusted Whatman GF/F filters (0.7-μm nominal pore size). SSOM and filters containing SPOM were brought back to the laboratory in coolers with ice packs. Sediment for SSOM analysis was sieved through a 500-μm screen to remove shell hash and large organic material. Oyster shell organic matter (OSOM) was sampled from lightly rinsed shells by brushing their surface into artificial seawater with a soft plastic brush. The collected solution was then sieved through a 250-μm screen to remove large particles and filtered through pre-combusted Whatman GF/F filters. SSOM and filters (SPOM and OSOM) were stored at −20 °C.

Stable isotope laboratory analysis

All materials were freeze-dried prior to stable isotope analysis. Macrofauna and SSOM were ground into a homogeneous powder with a ball mill, and a mortar and pestle, respectively. Samples possibly containing inorganic carbonates (SSOM, SPOM, OSOM, and organisms with shells) were acidified. $\delta^{15}N$ and $\delta^{13}C$ values were determined separately for acidified samples. $\delta^{15}N$ measurements were carried out on raw samples to avoid bias due to acidification. $\delta^{13}C$ measurements of SSOM and organisms with shells were carried out on samples decarbonated with 1 mol l^{-1} HCl and dried at 55 °C. Filters (SPOM and OSOM) were decarbonated by contact with HCl fumes under light vacuum for 4 h. Samples were precisely weighted (±1 μg), encapsulated in combustion cups, and analyzed with an elemental analyzer (NA 1500 Series 2, Carlo Erba, Milan, Italy) coupled with an isotope ratio mass spectrometer (Delta Plus XP with a Conflo III interface, Thermo-Finnigan, Bremen, Germany) at the Stable Isotope Geosciences Facility at Texas A&M University. Ratios of $^{13}C/^{12}C$ and $^{15}N/14N$ are expressed in the delta (δ) notation in parts per thousand (‰) as deviation from international standards (Vienna Pee Dee Belemnite for $\delta^{13}C$ and N2 in air for $\delta^{15}N$) and following the formula δX (‰) = [(*R*sample/*R*standard) − 1] × 10^3, where X is ^{13}C or ^{15}N and R is

$^{13}C/^{12}C$ or $^{15}N/^{14}N$ isotopic ratio, respectively. Two-point calibration was done using reference materials (l-glutamic acid: USGS-40 and USGS-41). Analytical precision based on repeated measurements of internal laboratory standards similar to the sample matrix (e.g., decarbonated sediment, acetanilide, rice) was <0.20‰ for carbon and nitrogen in most samples, analytical precision for some small samples was <0.25‰ for carbon and nitrogen (Online Resource 1).

Community data analysis

Macrofauna species richness was calculated in addition to oyster and motile macrofauna density and biomass. These univariate metrics were compared between reefs and within each sampling period using linear mixed effects analysis of variance (ANOVA) models, with reef-sampling period combinations as a fixed effect and site and season as random effects, using the lme4 package in R (Bates et al. 2015; R Core Team 2016). Planned contrasts were applied to compare parameters between natural and restored reefs within sampling periods with separate variance estimates for each treatment combination using the R package multcomp (Hothorn et al. 2008). Assumptions of normality were assessed with the Shapiro–Wilk tests and homoscedasticity was assessed with normalized residual vs. fitted value plots. Oyster density/biomass and macrofauna biomass data were square root transformed, and macrofauna density data were natural log-transformed to meet assumptions of normality. Oyster shell heights were compared using non-parametric Kruskal–Wallis ($\alpha = 0.05$) as they did not meet assumptions of normality after transformation. Post-hoc multiple comparisons were performed using Dunn's test (Dunn 1964) with Bonferroni *P*-value adjustments (R package: dunn.test, Dinno 2016).

Relationships among macrofauna community compositions between reefs over time were presented with nonmetric multidimensional scaling (nMDS) using Bray–Curtis similarities of

fourth-root-transformed species biomass data. Relationships among reef-sampling period combinations were highlighted using cluster analysis (group average). Multivariate relationships are interpreted based on their similarity (=1—dissimilarity). Multivariate analyses were conducted using PRIMER v6.0 statistical package (Clarke and Warwick 2001).

Stable isotope data analysis

Non-parametric Kruskal–Wallis and Mann–Whitney tests ($\alpha = 0.05$) were used to compare isotopic values of SPOM, SSOM, OSOM, and specific consumer trophic groups. Post-hoc multiple comparisons were performed using Dunn's test with Bonferroni *P*-value adjustments. Stable isotope compositions of primary producers (phytoplankton, microphytobenthos, and C_3 and C_4 plants) in the Mission- Aransas Estuary characterized by Lebreton et al. (2016) were included to complete the data set of potential food sources. Values of phytoplankton were estimated using SPOM values when C/N and C/chlorophyll *a* ratios of SPOM from Lebreton et al. (2016) indicated that it was primarily composed of fresh material. These represent average primary producer values and do not account for potential seasonal variation. Consumers were assigned to trophic groups based on recognized feeding strategy (Griffen and Mosblack 2011; Yeager and Layman 2011; Oakley et al. 2014).

A non-parametric multivariate analysis of variance (PERMANOVA) test (Anderson 2001) on mean consumer isotope values with planned contrasts was used to evaluate the variability in community isotope centroids between reefs within each sampling period. The PERMANOVA was conducted on a Euclidian distance matrix, with 9999 permutations of the raw data, using type III sums of squares (PRIMER v6.0). As PERMANOVA is sensitive to heterogeneity in multivariate dispersions, pairwise distance-based tests for homogeneity of

multivariate dispersions (PERMDISP; a multivariate extension of Levene's test) were used to test for differences in species isotope dispersions between reefs within each sampling period (Anderson 2006). Together, these tests provide an indication of niche overlap and a comparison of isotopic heterogeneity between reef communities.

Scaled consumer isotope values (0–1) and relative species biomass data (i.e., biomass data of each species (g AFDW m^{-2}) divided by the total biomass) obtained from community samples were combined to generate isotopic diversity indices. Indices were calculated using methods and adapted R-scripts provided by Cucherousset and Villéger (2015): (1) the $\delta^{13}C$ and (2) $\delta^{15}N$ isotopic positions ($\delta^{13}C$ IPos and $\delta^{15}N$ IPos, respectively), (3) the isotopic divergence (IDiv), and (4) the isotopic dispersion (IDis). $\delta^{13}C$ IPos is a biomass-weighted mean of scaled consumer $\delta^{13}C$ values that can be used to examine the distribution of biomass between species with relatively high vs. relatively low $\delta^{13}C$ values. This metric tends towards 1 as more biomass is found in ^{13}C-enriched species. $\delta^{15}N$ IPos is a biomass-weighted mean of scaled consumer $\delta^{15}N$ values and can be used to assess the distribution of biomass among trophic levels. This metric tends towards 1 as more biomasses are contained in top predators. IDiv is the average biomass-weighted distance of species to the unweighted isotope convex hull centroid. This metric tends towards 1 when most of the isotope values/weights are at extreme positions (e.g., when one or more species at extreme positions contains most of the biomass). IDis is the average distance of weighted species isotope values to the weighted community center of gravity (i.e., the intersect of $\delta^{13}C$ and $\delta^{15}N$ IPos) divided by the maximum distance to the center of gravity. This metric tends towards 1 when isotope values/weights are equally dispersed among extreme positions (e.g., similar biomass between predators and primary consumers). $\delta^{13}C$

and $\delta^{15}N$ IPos are both single axis indices with units of scaled ‰, whereas IDiv and IDis are based on multivariate isotope information and are unitless.

Stable isotope data encompassed a minimum of 95% of the total biomass collected within each reef-sampling period. To account for intra-specific isotope variability, 95% confidence intervals for differences in isotope diversity indices between reefs (i.e., natural—restored values) were generated by bootstrapping isotope values within each species (i.e., random selection of individuals) with 4999 resamples using the boot R package (Canty and Ripley 2016). Indices of isotopic diversity based on nearest neighbor distances (i.e., isotopic evenness and isotopic uniqueness; Cucherousset and Villéger 2015) are known to be sensitive to low numbers of species, odd numbers of species, and unbalanced species distributions (Brind'Amour and Dubois 2013; Rigolet et al. 2015). Because of this, these indices were not included in this study. Means are provided with ±1 standard deviation, unless specified otherwise.

Results

Environmental data

Monthly mean wind speed, turbidity, and chlorophyll *a* concentrations ranged from 4.0 to 7.8 ms^{-1}, 3.8 to 49.1 NTU, and 1.2 to 9.6 $\mu g\ L^{-1}$, respectively (Fig. 2.2). Turbidity and chlorophyll *a* concentrations followed repetitive seasonal patterns throughout from 2013 to 2015, with minima occurring in winter (December–January) and maxima occurring in spring/summer (April–July). Monthly mean salinity ranged from 30.6 to 39.5, with lowest values during winter (December–January) and highest ones during late summer/early fall (August–September). Monthly mean water temperature followed predictable seasonal patterns; lowest in December to January, and highest in August, ranging from 10.9 to 30.4 °C during the survey.

Community development

A total of 304 oysters with shell height ≥ 25 mm were collected from both reefs during the study, yielding 62.3 g (AFDW) of biomass. Mean oyster density and biomass ranged from 22 to 185 m^{-2} and from 5.9 to 50.1 g AFDW m^{-2} in the natural reef and from 5 to 212 m^{-2} and from 0.5 to 26.8 g AFDW m^{-2} in the restored reef. Oyster density was greater in the natural reef than in the restored reef 5-month post-restoration (i.e., January 2013, ANOVA contrast, $P < 0.001$) and did not differ between reefs after. Oyster biomass was greater in the natural reef than in the restored reef 5- and 9-month post-restoration (January 2013, ANOVA contrast, $P < 0.001$; May 2013, ANOVA contrast, $P = 0.028$) (Fig. 2.3a, b) and did not differ after. Oyster shell heights were greater in the natural reef 5-months' post-restoration (January 2013, Dunn's test, $P < 0.001$), and similar between reefs during all other sampling periods (Fig. 2.3c). In the restored reef, mean oyster shell heights increased as the reef developed, from 27.6 mm 5-month post-restoration (January 2013) to 45.3 mm 12-month post-restoration (August 2013), and decreased to 40.1 mm in January 2015 (29-month post-restoration) due to recruitment of small individuals. Temporal shell height trends were different in the natural reef, with mean shell heights consistently decreasing from 42.7 mm in August 2013 to 38.6 mm in January 2015.

A total of 14 different motile macrofauna taxa were collected over the course of the survey (Table 2.1). *Palaemonetes vulgaris* was the only species occurring more than once in the natural reef community samples that was not found in the restored reef. Mean macrofauna densities ranged from 820 to 3267 m^{-2} in the natural reef and from 664 to 6498 m^{-2} in the restored reef (Fig. 2.4a). Macrofauna density was significantly higher in the restored reef than in the natural reef 9-month post-restoration (i.e., May 2013, ANOVA contrast, $P = 0.006$). Mean biomass of motile macrofauna ranged from 51.9 to 124.0 g AFDW m^{-2} in the natural reef and

from 43.2 to 96.2 g m^{-2} in the restored reef, and did not differ between reefs within any sampling period (Fig. 2.4b). High variability in macrofauna densities and biomass in the restored reef in August 2013 (i.e., 12-month post-restoration) were caused by a sample containing an exceptionally high density of porcelain crabs (*Petrolisthes* spp., 14,459 m^{-2}). Mean species richness (per 0.135 m^2) ranged from 7 to 9 in the natural reef and from 4 to 8 in the restored reef. Species richness was significantly greater in the natural reef than in the restored reef 5–12- month post-restoration (i.e., January, May, and August 2013, ANOVA contrasts, $P \leq 0.015$); after which species richness was similar between reefs.

Biomass-based community composition on the initial sampling date (January 2013) in the restored reef was the least similar to any other community composition (58% similar) regardless of reef location or date (Fig. 2.5a). Community compositions between the natural and restored reefs among all other sampling periods were >66% similar. Macrofauna communities in the restored reef were >70% similar 9 months' after reef restoration and after. Community compositions in the restored and natural reefs were 75% similar 29 months' after reef restoration (i.e., January 2015). Biomasses of macrofauna in the natural reef were dominated by fish and Brachyuran crabs throughout the study (Fig. 2.5b). In the natural reef, the porcelain crab *Petrolisthes* spp. composed a maximum biomass proportion of 37% (20.7 g AFDW m^{-2}) in January 2013, with greatest total biomass occurring in August 2013 (37.0 g AFDW m^{-2}). *Petrolisthes* spp. dominated the restored reef community in the early sampling periods, composing 63% of total biomass (31.1 g AFDW.m^{-2}) 5-month post-restoration (January 2013), and 82% 9 and 12-month post-restoration (i.e., May 2013, 78.7 g AFDW m^{-2}, August 2013, 77.8 g AFDW m^{-2}). *Petrolisthes* spp. biomass was much lower 15-month post-restoration (October 2013, 27%; 12.6 g AFDW m^{-2}) and 29-month post-restoration (January 2015, 35%; 15.1 g

AFDW m^{-2}). Proportional biomass of motile macrofauna on the restored reef was dominated by fish and Brachyuran crab 15-month post-restoration and after, similar to the natural reef.

Stable isotope composition of potential food sources

SPOM $\delta^{13}C$ values ranged from −27.8 to −22.3‰ (mean = −24.7‰ ± 1.3, n = 16) and were similar between reefs and sampling periods (Figs. 2.6, 2.7). SPOM $\delta^{15}N$ values ranged from 4.4 to 10.2‰, and were similar between reefs, but were significantly higher 15- and 29-month post-restoration (i.e., October 2013, mean = 8.7‰ ± 1.3, n = 4, and January 2015, mean = 8.9‰ ± 0.9, n = 4) than 9-month post-restoration (May 2013, mean = 5.3‰ ± 1.0, n = 4) (Kruskal–Wallis test, P = 0.009; Dunn's test, $P \leq 0.018$). Isotope compositions were not determined for SPOM 5-month post-restoration (January 2013) due to technical problems. January 2015 ratios have been used in the place of January 2013 ratios, because similar hydrological conditions occurred prior to, and within, these two sampling periods (Fig. 2.2).

The $\delta^{13}C$ values of SSOM were similar among reefs and sampling periods (Figs. 2.6, 2.7: mean −19.8‰ ± 1.5, n = 21). SSOM $\delta^{15}N$ values ranged from 6.1 to 10.1‰ (Mean 8.1‰ ± 1.2, n = *22*). SSOM $\delta^{15}N$ values were significantly higher in the restored reef (Mean = 9.0‰ ± 0.8, n = 11) than in the natural reef (Mean = 7.2‰ ± 0.7, n = 11) (Mann–Whitney test, $P < 0.001$) but were similar among sampling periods. OSOM $\delta^{13}C$ values were higher in the natural reef (Mean = −21.8‰ ± 1.9, n = 8) than in the restored reef (Mean = −23.8‰ ± 1.2, n = 8; Fig. 2.6) (Mann–Whitney test, P = 0.046) but were similar among sampling periods. OSOM $\delta^{15}N$ values were similar between reefs and sampling periods (Fig. 2.6). The $\delta^{13}C$ and $\delta^{15}N$ values of OSOM ranged from −25.3 to −18.9‰ and 8.1 to 12.7‰, with inter-sampling period means of −22.8‰ ± 1.8 and 9.8‰ ± 1.2 *(*n = 16).

SPOM from both reefs was depleted in ^{13}C by a mean of 4.9‰ relative to SSOM (Mann–Whitney test, $P < 0.001$), whereas $\delta^{15}N$ values of SSOM and SPOM were similar. In the natural reef, OSOM $\delta^{13}C$ values were higher than SPOM values but similar to SSOM values (Kruskal–Wallis test, $P < 0.001$; Dunn's test, $P = 0.019$). In the restored reef, OSOM was significantly more depleted in ^{13}C than SSOM but similar to SPOM (Kruskal–Wallis test, $P < 0.001$; $P = 0.002$ for OSOM < SSOM). OSOM was significantly more enriched in ^{15}N than SPOM and SSOM from both reefs (Kruskal–Wallis test, $P < 0.001$; Dunn's test, $P = 0.001$) (Fig. 2.6).

Stable isotope composition of consumers

Individual organisms from 36 taxa were collected from both reefs and analyzed for stable isotope composition (Fig. 2.6, Table 2.2). Mean $\delta^{13}C$ values and $\delta^{15}N$ values for consumer taxa ranged from −27.9 to −13.6‰ and from 9.9 to 16.9‰, respectively. $\delta^{13}C$-$\delta^{15}N$ centroid values were similar during all 2013 sampling periods (PERMANOVA contrasts, $F1,149 = 1.4$, $P = 0.24$ for January; $F1,149 = 0.4$, $P = 0.66$ for May; $F1,149 = 0.2$, $P = 0.76$ for August; $F1,149 = 1.7$, $P = 0.18$ for October) (Fig. 2.6). Consumer isotope value dispersions were similar between reefs during all 2013 sampling periods (pairwise PERMDISP tests, $P \geq 0.16$).

Suspension feeders, omnivores, and predators/scavengers trophic groups had similar isotopic compositions between the natural and the restored reef in each sampling period (Dunn's tests, $P > 0.05$ for $\delta^{13}C$ and $\delta^{15}N$ pairwise comparisons within each group). Suspension feeders had $\delta^{13}C$ values ranging from −26.1 to −17.5‰ and $\delta^{15}N$ values ranging from 10.1 to 14.0‰ in the natural reef, and $\delta^{13}C$ values ranging from −27.9 to −17.6‰ and $\delta^{15}N$ values ranging from 9.6 to 15.0‰ in the restored reef. The range of omnivore $\delta^{13}C$ values in the restored reef (from −20.7 to −17.4‰) was narrower than in the natural reef (from −22.1 to −13.6‰), which is primarily attributable to the presence of *P. vulgaris* in the natural reef only. *P. vulgaris* had the

highest $\delta^{13}C$ value of all consumers during the summer of 2013 (Fig. 2.6). $\delta^{15}N$ values ranged from 11.6 to 15.4‰ in the natural reef and from 10.4 to 16.1‰ in the restored reef (Fig. 2.6). Predators/scavengers $\delta^{13}C$ values ranged from −20.6 to −16.4‰ and their $\delta^{15}N$ values ranged from 14.2 to 16.5‰ in the natural reef. Restored reef predator/scavenger taxa mean $\delta^{13}C$ values ranged from −20.3 to −17.2, and $\delta^{15}N$ values ranged from 14.5 to 16.9. Grazers/deposit feeders were sampled inconsistently between reefs over the course of the study; with some reef-seasons containing isotope values for only one representative taxa. Because of this, data were not sufficient for a comparison of this group between reefs within each season. Pooled (i.e., all sampling periods together) grazer/deposit feeder taxa mean $\delta^{13}C$ and $\delta^{15}N$ values did not differ significantly between reefs (Mann–Whitney test, $P = 0.829$ for $\delta^{13}C$; $P = 0.663$ for $\delta^{15}N$), with $\delta^{13}C$ values ranging from 25.9 to −19.3‰ and from −23.6 to −18.5‰ in the natural and in the restored reefs, respectively. $\delta^{15}N$ values ranged from 10.0 to 14.3‰ and from 9.9 to 14.0‰ in the natural and in the restored reefs, respectively. On both reefs, suspension feeders were more enriched in ^{13}C in August 2013 (12-month post-restoration) than in January, May, and October 2013 (Fig. 2.6) (Kruskal–Wallis test, $P < 0.001$; Dunn's test, $P \leq 0.035$). $\delta^{15}N$ values of suspension feeders also varied between sampling periods (Kruskal–Wallis test, $P = 0.001$); with higher $\delta^{15}N$ values in October 2013 than in January 2013 or May 2013 and higher $\delta^{15}N$ values in August 2013 than in January 2013 (Dunn's test, $P \leq 0.027$) (Fig. 2.6). $\delta^{13}C$ and $\delta^{15}N$ values of omnivores were stable among sampling periods in both the restored and natural reefs (Kruskal–Wallis test, $P = 0.157$ for $\delta^{13}C$; $P = 0.650$ for $\delta^{15}N$). $\delta^{13}C$ values of predators/scavengers from both reefs varied between sampling periods (Kruskal–Wallis test, $P = 0.015$), with higher $\delta^{13}C$ values in August 2013 than in May 2013 (Dunn's test, $P = 0.004$). Predators/scavengers $\delta^{15}N$ values were stable among sampling periods (Kruskal–Wallis test, $P = 0.368$).

Weighted isotopic diversity indices

The trophic structure in the restored reef showed a trend of increasing complexity over time, with all isotopic diversity indices becoming similar to natural reef values by the October 2013 sampling period (Figs. 2.7, 2.8; Table 2.3). In January 2013 (5 months post-restoration), IDiv and IDis were significantly greater in the natural reef than in the restored reef, while $\delta^{13}C$ IPos was greater in the restored reef. In May 2013 (9 months post-restoration), IDis and $\delta^{15}N$ IPos were greater in the natural reef and $\delta^{13}C$ IPos was greater in the restored reef (Fig. 2.7). In August 2013 (12 months post-restoration), IDis and $\delta^{15}N$ IPos were greater in the natural reef and IDiv was greater in the restored reef.

Discussion

Habitat and community recovery

The restored reef had similar habitat characteristics (oyster density, biomass, and shell heights) to the natural reef within 12 months of restoration and remained similar through the duration of the survey (29 months). Observed temporal variations in oyster populations were likely due to Dermo (*Perkinsus marinus*) infection (Beseres Pollack et al. 2011) and/or predation (Johnson and Smee 2014). Juvenile oyster densities were comparable to those reported for other restored reefs studied in the area (89–485 m^{-2}, Blomberg 2015; 1–400 m^{-2}; Graham et al. 2016) and other estuaries along the Gulf of Mexico (18–115 m^{-2}, Gregalis et al. 2008).

Motile macrofauna density, biomass, and species richness became similar to the natural reef by 15-month postrestoration. Development of benthic fauna on the restored oyster reef was characterized by two main phases. In the first phase, the initial 12-month post-restoration, community biomass was dominated by opportunistic porcelain crab species (*Petrolisthes* spp.) and species richness was low. During the second phase, comprising the final 15 months of the

study, a shift to a more even community composition occurred, with higher species richness, lower porcelain crab densities, and higher proportions of fish and carnivorous decapods. The reliability of determining the recovery of these metrics in the restored reef compared to natural reef levels depends on the variability of the measures; caution should be taken in interpreting comparisons where the standard error is high in one or both reefs.

Rapid colonization of motile macrofauna in the restored reef is consistent with other studies showing that resident fauna densities recovered within 1-year post-restoration (Peterson et al. 2003; Dillon et al. 2015; La Peyre et al. 2014). Mean motile macrofauna densities and biomass were comparable to those found in natural oyster reefs (40–144 *n* m^{-2}, Zimmerman et al. 1989; 31–211 g m^{-2}; Stunz et al. 2010) and restored oyster reefs (57 *n* m^{-2}, La Peyre et al. 2014; 50 g m^{-2}; Humphries and La Peyre 2015) in Gulf of Mexico estuaries. Species richness was similar to that observed for fish and decapod crustacean species in other Gulf of Mexico oyster reefs (8–12 m^{-2} Tolley and Volety 2005; 4–21 0.5m^{-2}; Stunz et al. 2010).

Stable isotope composition of potential food resources

The $\delta^{13}C$ values of SSOM and SPOM were stable throughout the survey, with SSOM values greater than SPOM values by ~5‰. OSOM had variable $\delta^{13}C$ values, which overlapped with SSOM and/or SPOM. Mean SPOM $\delta^{13}C$ values were relatively depleted (−24.7‰), indicating that SPOM composition in the Mission-Aransas Estuary is dominated by autochthonous phytoplankton with minimal influence of continental inputs of C3 plant material (Peterson and Fry 1987). These results are consistent with other studies reporting little influence of terrestrial organic matter on SPOM in this system (Mooney and McClelland 2012; Lebreton et al. 2016). ^{15}N enriched SPOM values observed in October and January are likely related to a greater influence of recycling processes leading to higher $\delta^{15}N$ values of inorganic nitrogen in

the water column (Cifuentes et al. 1988). $\delta^{13}C$ values of SSOM (−19.8‰) were closer to those of marine phytoplankton (−22.1‰) than to those of benthic microalgae (−13.8‰; Lebreton et al. 2016), indicating that SSOM comprises mostly trapped phytoplankton with a slight influence of benthic microalgae. Greater SSOM $\delta^{15}N$ values in the restored reef area may be attributable to differing meiofauna community composition (i.e., higher heterotrophic biomass). However, this was not examined explicitly in this study. Higher $\delta^{13}C$ values of OSOM in the natural reef indicate a greater influence of benthic organic matter than in the restored reef.

A food web fueled by benthic and pelagic resources

The $\delta^{13}C$ values of consumers clearly demonstrate that the benthic fauna community relies on food resources from both pelagic (i.e., SPOM) and benthic (i.e., SSOM/OSOM) compartments. Primary consumer feeding strategy generally determined the relative importance of pelagic (i.e., sessile suspension feeders) or benthic (i.e., motile omnivores) food resources assimilated. Most predators and higher trophic level omnivores were slightly enriched in ^{13}C, related to the ^{13}C-enrichment occurring between trophic levels, highlighting that these consumers were relying on both groups of primary consumers, showing a relatively flexible feeding strategy among this group. The reliance of macrofauna on both pelagic and benthic primary food resources has already been inferred by food web studies of oyster reefs in other subtidal systems (Quan et al. 2012; Oakley et al. 2014; Blomberg 2015), and highlights the strong bentho-pelagic coupling existing in these habitats.

Sessile suspension feeder and grazer/deposit feeder $\delta^{13}C$ values reflect a higher dependence on SPOM relative to the two other trophic groups. The relatively large range of isotopic composition of suspension feeders is indicative of resource partitioning, most likely due to differences in particle size selectivity (Lefebvre et al. 2009; Riisgård and Larsen 2010), but

may also be related to physiological differences between species (Martínez del Rio and Wolf 2005). The large influence of trapped phytoplankton into the composition of SSOM and the mean $\delta^{13}C$ values of suspension feeders (−21.8‰), closer to that of SSOM than SPOM overall, indicate that the pathway between pelagic production and suspension feeding consumers may be largely indirect; through the deposition and resuspension of phytoplankton/phytodetritus. This is supported by the facts that (1) SSOM is available all year long, as it is stored in the system and consumers can access it due to resuspension via hydrodynamic processes; and (2) SSOM is of relatively high nutritional quality as it can contain large amounts of liable microalgal resources (MacIntyre et al. 1996). This interpretation is consistent with other studies that have shown near-bottom seston and detritus to be the primary food sources for oysters and benthic fauna in Gulf of Mexico estuaries (Soniat et al. 1984; Gaston et al. 1997). Moreover, oysters can enhance these processes by releasing large quantities of biodeposits (Newell 2004; Hoellein et al. 2015). SPOM, on the contrary, is subject to high temporal variation in terms of biomass and quality (i.e., blooms in spring). Relatively high $\delta^{13}C$ values in suspension feeders in August (Fig. 2.6) are likely due to an increase in resuspension of sediment in late May and early August, as confirmed by turbidity peaks during these periods (Shideler 1984; MacIntyre and Cullen 1996; Fig. 2.2). Indeed, the 3 months leading up to the August 2013, sampling period had the highest average turbidity and chlorophyll *a* concentrations. These data demonstrate that the wind and resulting turbidity patterns may influence the food resources used by oysters and other suspension feeders (Soniat et al. 1984; Barillé et al. 1997; Grizzle et al. 2008; Blomberg 2015). The similarity of the $\delta^{13}C$ values between suspension feeders and grazer/deposit feeders indicates that the latest also importantly rely on trapped phytoplankton.

For omnivores, the higher $\delta^{13}C$ values in comparison with suspension and grazer/deposit feeders reflect a higher influence of benthic food resources (e.g., benthic microalgae) for this trophic group. Motile omnivores, such as Panopeid crabs and *Petrolisthes* spp. are preyed upon by a wide variety of reef-resident predators, including fish (Hollebone and Hay 2007; Yeager and Layman 2011). Given the ubiquity of *Petrolisthes* spp. (31% of the reef biomass), they likely play a major role in the transfer of organic matter from the benthos to higher trophic level consumers. As a result, consumer isotope data indicate that the food web comprises two main organic matter pathways: one dominated by the engineering species (i.e., oysters), other suspension feeders and grazer/deposit feeders, relying more strongly on SPOM, and a second driven by motile omnivores (i.e., opportunistic species) inhabiting the reef and relying more strongly on benthic primary food sources. The latter consumers have very high trophic plasticity and utilize the food resources which are most readily available (Caine 1975; McGlaun and Withers 2012).

Development of the restored reef community and changes in food web structure

Consumers in the restored and natural reef relied upon similar profile and range of food resources shortly after reef restoration (within 5 months), as indicated by raw isotope data, PERMANOVA and PERMDISP results. The restored reef community thus relied on similar pathways of organic matter flux and supported a similar food chain length, suggesting a rapid recovery of trophic structure within 5 months of restoration. This indicates that, soon after restoration, the restored reef was already accumulating organic matter in sufficient quantities to support motile primary consumers. SPOM is delivered by the water, and, therefore, is available regardless of reef development. SSOM availability is likely facilitated by the three-dimensional structure of the reef, which enhances its deposition (Reise 2002; Colden et al. 2016).

However, the examination of the isotopic diversity indices revealed that the magnitude of these energy fluxes and trophic diversity was quite different in the restored reef *vs*. the natural reef during the successional period (initial 12-month post-restoration). The lack of differences in consumer isotope values between reefs indicates that the variations in isotopic diversity indices and food web functioning were primarily related to the changes in the community structure associated with successional processes.

The $\delta^{13}C$ IPos tended to be greater in the restored reef due to the greater proportional of biomass of relatively enriched *Petrolisthes* spp. in comparison to the natural reef, which had greater biomass of relatively depleted *C. virginica*, during the first 9 months of sampling (Figs. 2.7, 2.8b). As *C. virginica* biomass became similar between reefs in August 2013 (12 months post-restoration; Fig. 2.3b), the $\delta^{13}C$ IPos converged. The $\delta^{15}N$ IPos was lower in the restored reef during the successional phase, because most of the biomass was consolidated in the ^{15}N depleted (low trophic level) *Petrolisthes* spp. vs. the natural reef with a higher proportion biomass of predators and mid-level consumers (Figs. 2.7, 2.8b). An exception to this was the January 2013 sampling period; when high oyster biomass in the natural reef reduced the $\delta^{15}N$ IPos to a similar level found in the restored reef. Similar $\delta^{15}N$ IPos values between reefs 15-month post-restoration (October 2013) reflected the increase in the relative biomass of higher trophic level consumers in the restored reef (Fig. 2.8b).

IDiv was initially lower in the restored reef vs. the natural reef (January 2013), as most of the biomass was consolidated near the convex hull centroid in *Petrolisthes* spp. and the dove snail *Costoanachis semiplicata*, with the relatively low biomass in species at extreme positions (*C. virginica*, Panopeidae spp. and predators) (Figs. 2.7, 2.8a). When *Petrolisthes* spp. moved to a more extreme position as the most ^{15}N depleted (lowest trophic level) motile consumer, IDiv in

the restored reef increased dramatically. Due to the consolidation of most restored community biomass in *Petrolisthes* spp., IDiv in the restored reef surpassed the more evenly distributed trophic-biomass structure of the natural reef in August 2013. IDiv was lower in the restored reef during its successional phase in comparison to the natural reef, reflecting a less complex trophic structure with an asymmetrical distribution of biomass across the food web (Figs. 2.7, 2.8b). The natural reef had relatively high isotopic dispersion values during this period as the, reflecting greater food web complexity, as community biomass was distributed more equally between trophic compartments.

Isotopic diversity metrics used in this study can be confounded by variations in primary producer isotope composition, which can lead to isotopic variability in consumers that are not related to trophic differences (Hoeinghaus and Zeug 2008). In such cases, additional transformations of consumer isotope values relating to their respective sources may be necessary to mitigate potential biases (Cucherousset and Villéger 2015). These biases were avoided in this study, as we compared communities that occupied similar isotopic space in the same system, that primarily rely on similar allochthonous resources delivered through the water column. Due to potential variation in primary producer isotope values resulting from seasonal environmental variation, temporal differences isotope diversity metrics were not interpreted.

Although consumers made use of a similar profile of food resources in restored reef and natural reef throughout the study, differences in the $\delta^{13}C$ IPos demonstrated that the developing reef community was more reliant on ^{13}C enriched benthic organic matter (e.g., microphytobenthos) than the natural reef due to the dominance of the motile primary consumer trophic compartment (i.e., omnivores) vs. oysters. The shift in community biomass composition from the initial dominance by opportunistic motile primary consumer species to a

more even vertical biomass distribution is related to increased top-down control of prey species by predators, which, in turn, increased in biomass due to the availability of prey. Although the restored reef supported predators throughout the successional period (initial 12-month post-restoration), isotopic diversity indices revealed that the trophic pathway between primary consumer compartments and secondary consumers was depressed during the successional phase in comparison to the natural reef.

The convergence of all isotopic diversity indices between reefs 15-month post-restoration (October 2013) reflects a transition in the restored reef to a more complex food web with a more even distribution of biomass among compartments, functionally similar to the natural reef. This event temporally coincided with the convergence of all community-based metrics. When sampled 29-month post restoration, the restored reef community retained structural characteristics of the natural reef, with biomass distributed evenly through different trophic compartments, indicating that the functional recovery of the restored reef was stable over this timeframe, assuming no major shifts in trophic position of important species. Although results demonstrated a recovery of all functional aspects examined, other processes that are important for long-term reef restoration success may not become apparent within the initial 2 years of restoration. Perhaps the most important process is the rate of shell accretion vs. sedimentation, which is vital for maintaining the habitat structure that supports reef communities (Coen and Luckenbach 2000). As this study was based on the comparison of two oyster reef complexes within the same estuary, the ability to predict timeframes of functional recovery based on these results, especially in reef systems with different species pools, may be limited. It will be of great importance in the near future to realize similar studies in different restored habitats (e.g., different trophic role of the engineering species,

different species pools, and different environmental contexts) to evaluate the functional recovery in these systems as well, and to define general patterns.

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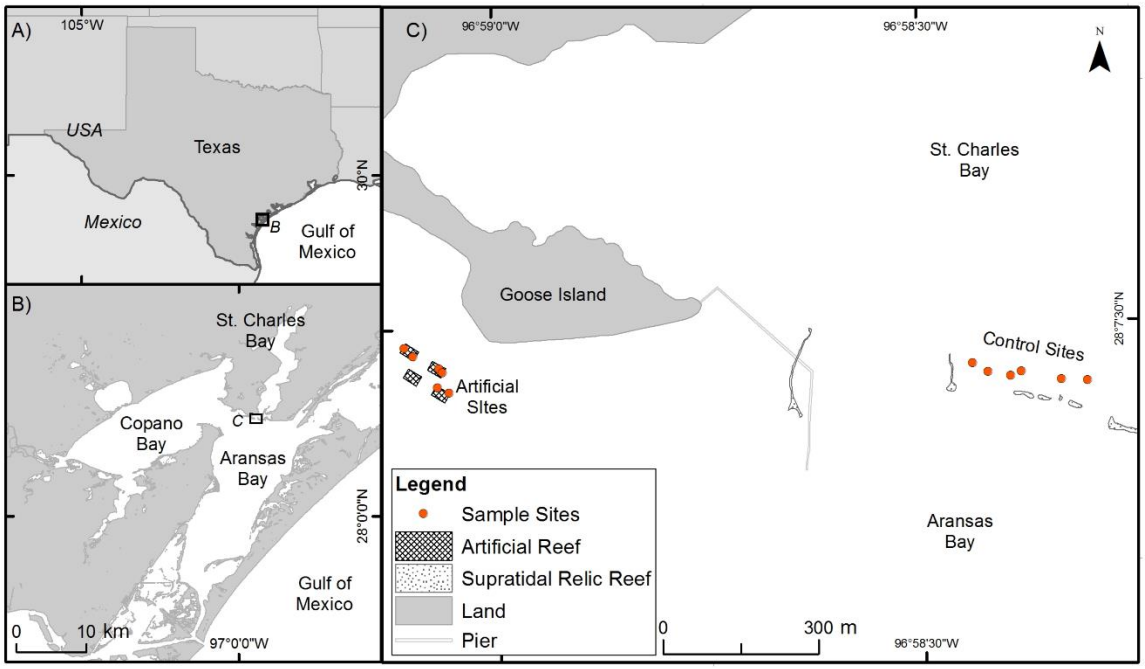

Figure 2.1: Location of the restored oyster reef in the Mission-Aransas Estuary, Texas, shown in state (a), estuary (b), and local (c) scales. Location of the NOAA National Estuarine Research Reserve System (NERRS) hydrological station is shown in b.

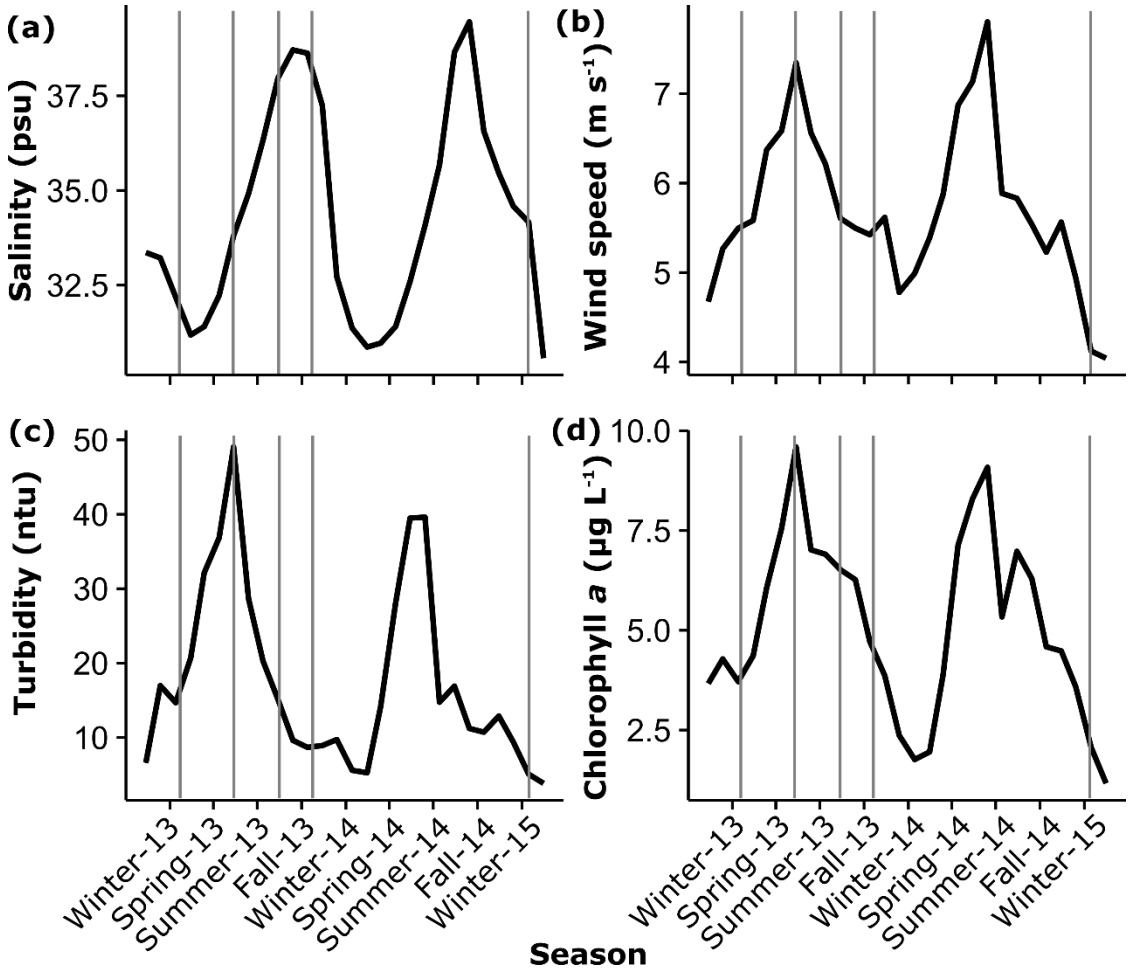

Figure 2.2: Mean monthly salinity, wind speed, turbidity, and chlorophyll a concentration in Mission-Aransas Estuary, Texas, over the course of the study. Sampling periods indicated with vertical gray lines. Data provided by the NOAA National Estuarine Research Reserve System (NERRS).

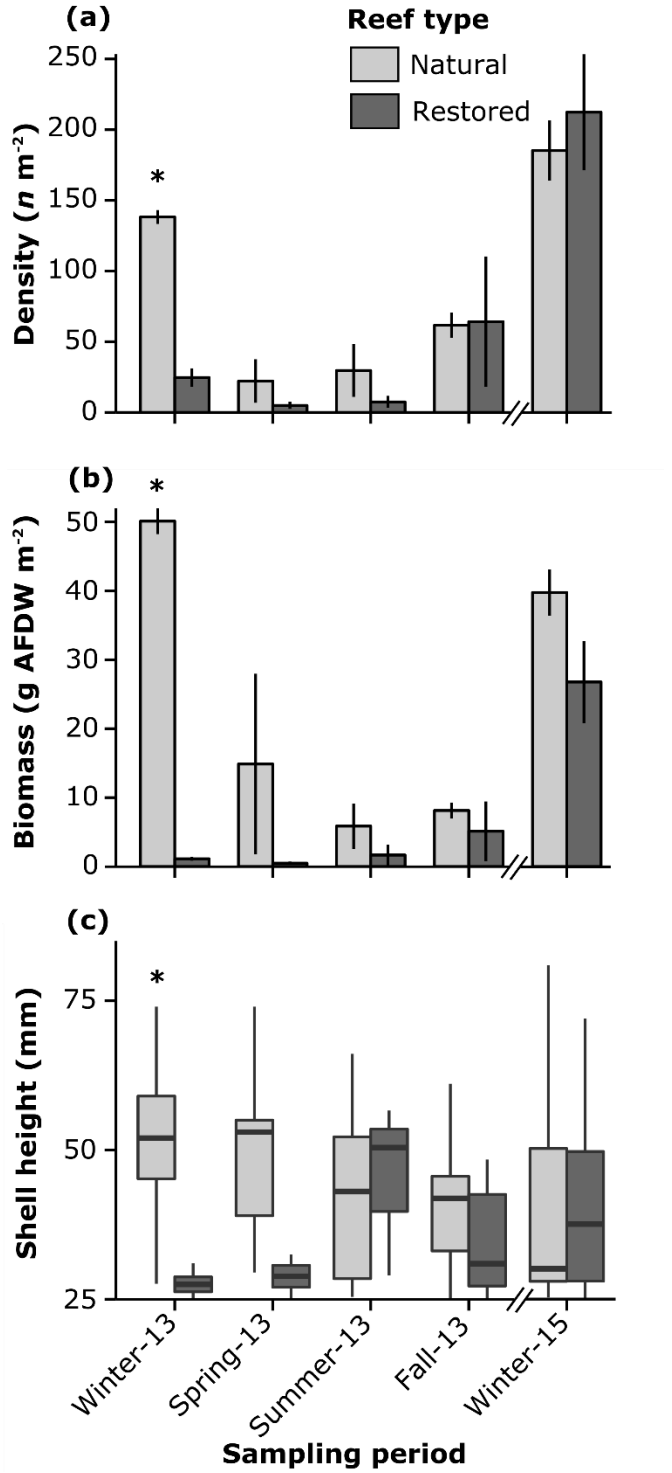

Figure 2.3: Mean ± standard error of oyster density (a) and biomass (b) in restored and natural oyster reef sites during sampling periods in the Mission-Aransas Estuary, Texas (n = 3). Shell height distribution (c) of oysters presented with boxplots indicating first quartile, median, second quartile, and 1.5 • inter quartile range. Significant differences between natural and restored reef values within sampling periods indicated by *asterisk* (Dunn's test, P-value ≤ 0.05 for shell height; ANOVA contrasts, P-value ≤ 0.05 for all else).

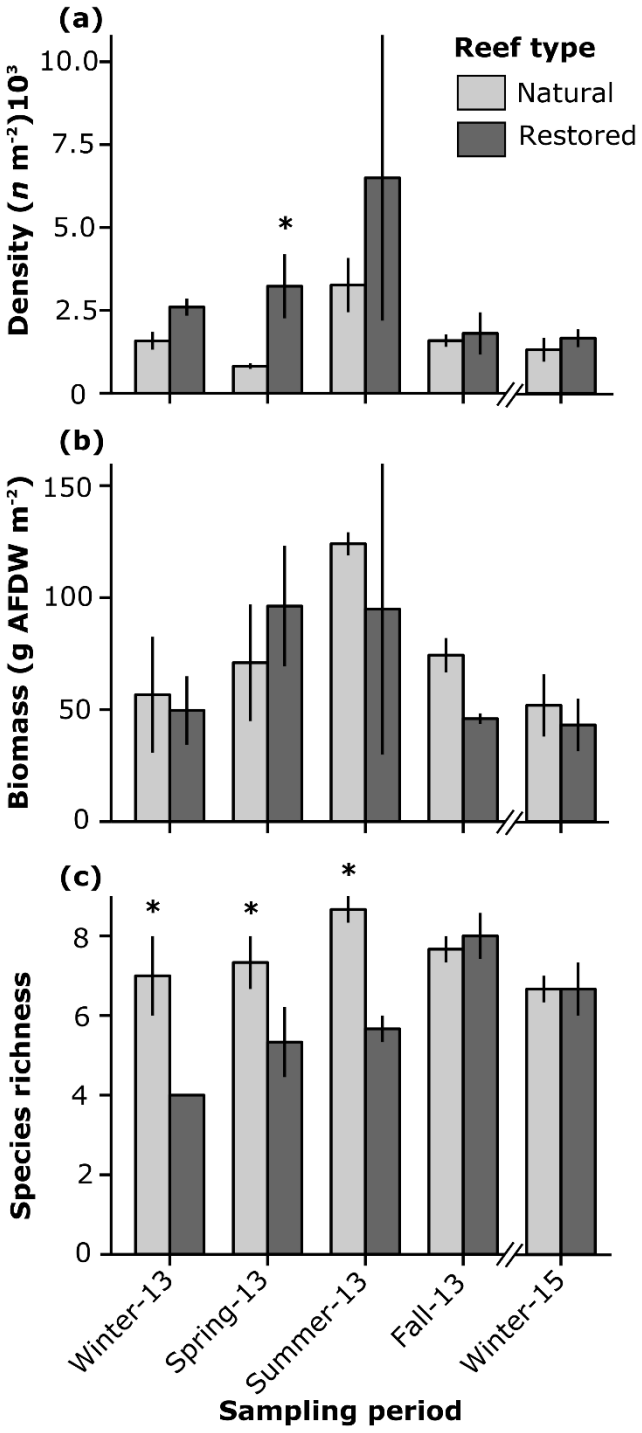

Figure 2.4: Mean ± standard errors of motile macrofauna density (a), biomass (b), and species richness (c), measured in restored and natural oyster reef sites during sampling periods in the Mission-Aransas Estuary, Texas (n = 3). Significant differences between natural and restored reef means within sampling periods are indicated by *asterisk* (ANOVA contrasts, P-value ≤ 0.05).

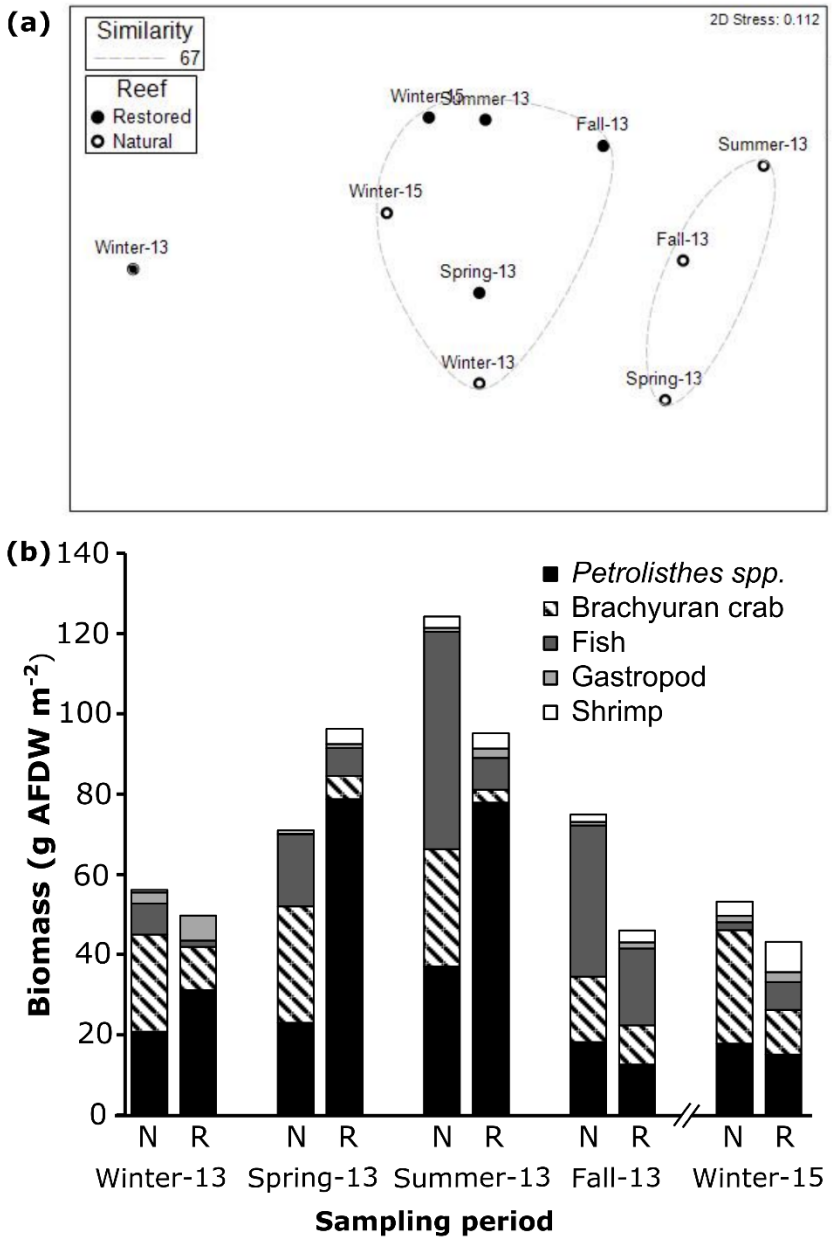

Figure 2.5: Non-metric multidimensional scaling (nMDS) of square root transformed motile macrofauna taxa biomass composition (a) and biomass contribution of motile macrofauna groups (b) in natural (N) and restored (R) oyster reefs aggregated by reef type and sampling periods in the Mission-Aransas Estuary, Texas.

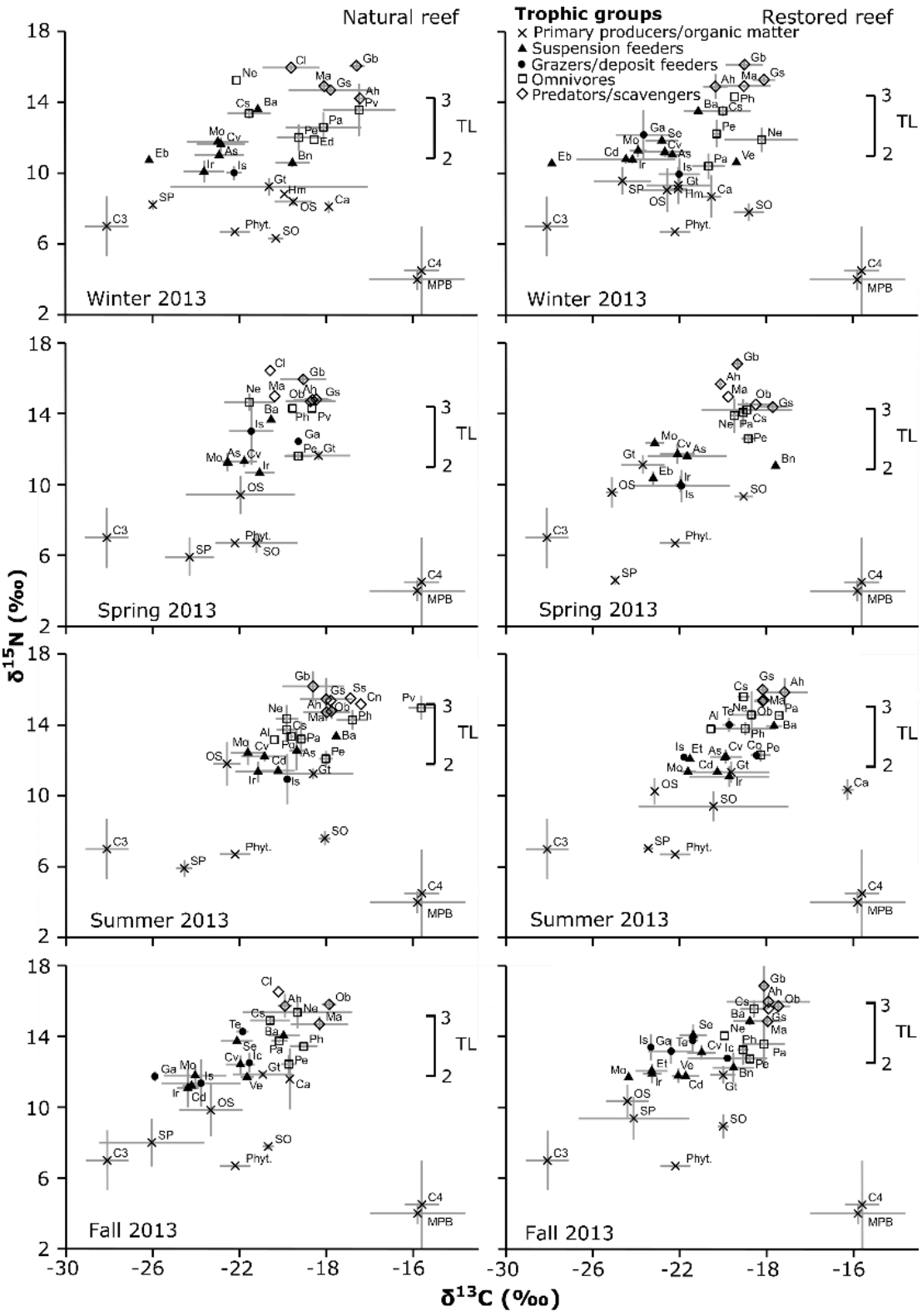

Figure 2.6: Mean $\delta^{13}C$ and $\delta^{15}N$ values (‰) ± standard deviation of potential food sources and consumers collected in natural (*left*) and restored (*right*) oyster reefs in the Mission-Aransas Estuary, Texas. Codes representing isotope values include: Ah, *Alpheus heterochaelis*; Al,

Astyris lunata; As, *Anomia simplex*; Ba, *Balanus* spp.; Bn, *Bugula neritina*; Ca, *Cladophora albida*; Cd, *Crepidula depressa*; Cl, *Chasmodes longimaxilla*; Cn, *Callinectes sapidus*; Co, *Corophiidae*; Cs, *Costoanachis semiplicata*; Cv, *Crassostrea virginica*; Eb, Encrusting bryozoan; Ed, *Eurypanopeus depressus*; Et, Encrusting tunicate; Ga, Gammaridae; Gb, *Gobiosoma bosc*; Gs, *Gobiesox strumosus*; Gt, *Gracilaria tikvahiae*; Hm, *Hincksia mitchellae*; Ic, *Ischnochiton* sp.; Ir, *Ischadium recurvum*; Is, Isopoda; Ma, *Menippe adina*; Mo, Molgulidae; Ne, Nereididae; Ob, *Opsanus beta*; OS, oyster shell organic matter (OSOM); Pa, Panopeidae spp.; Pe, *Petrolisthes* spp.; Ph, *Panopeus herbstii*; Po, *Parvanachis ostreicola*; Pv, *Palaemonetes vulgaris*; Se, Serpulidae; SO, surface sediment organic matter (SSOM); SP, suspended particulate organic matter (SPOM); Ss, *Syngnathus scovelli*; Te, Terebellidae; Ve, Vesiculariidae. Isotope values of Phyto: phytoplankton, C4: C_4 plants, C3: C_3 plants and MPB: microphytobenthos taken from Lebreton et al. (2016).

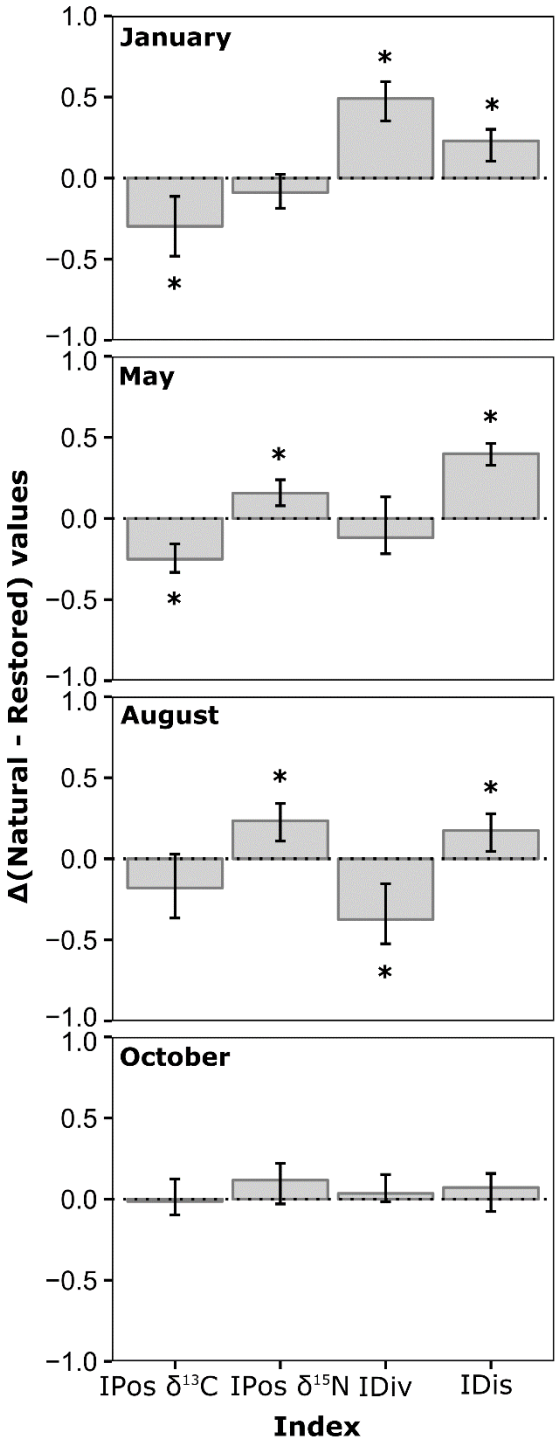

Figure 2.7: *Bar-plots* comparing in isotopic diversity index values from the natural vs. restored oyster reefs (natural—restored reef values) with 95% confidence intervals based on bootstrap resampling of species stable isotope data in each sampling period. Comparisons in which 95% confidence intervals do not include 0 are considered significantly different and indicated with *asterisk.*

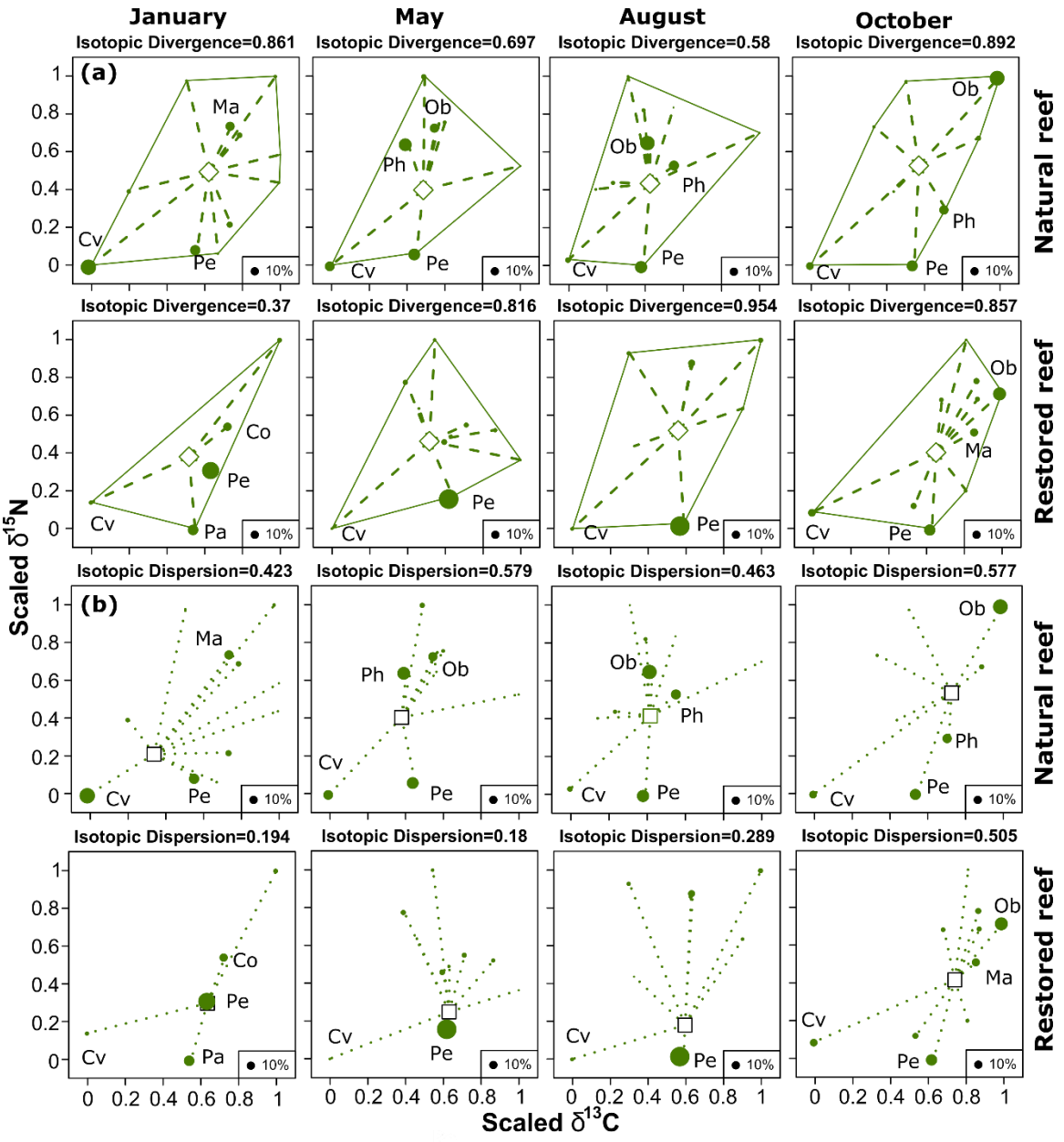

Figure 2.8: Graphical representation of isotopic divergence (IDiv) with diamonds representing unweighted convex hull centroid (a), and isotopic dispersion (IDis) with squares representing biomass-weighted $\delta^{13}C$ and $\delta^{15}N$ isotopic positions (IPos) (scaled ‰) in natural and restored oyster reefs over 2013 sampling periods. Isotope values are scaled between 0 and 1, and indices are based on mean species stable isotope values. *C. virginica* and macrofauna contributing at least 10% of community biomass are labeled (see Fig. 2.6 description for species codes)

Table 2.1: Motile macrofauna species total catch (*n*) and mean ± standard error of density and biomass in natural and restored oyster reefs in the Mission-Aransas Estuary, Texas.

	Natural reef			Restored reef		
Species	***n***	**Density (*n* m^{-2})**	**Biomass (g AFDW m^{-2})**	***n***	**Density (*n* m^{-2})**	**Biomass (g AFDW m^{-2})**
Fish						
Chasmodes longimaxilla	1	0.5 ± 0.5	0.11 ± 0.11	0		
Gobiesox strumosus	8	4.0 ± 1.6	1.21 ± 0.65	4	2 ± 0.9	1.01 ± 0.47
Gobiosoma bosc	27	13.3 ± 3.9	1.95 ± 0.62	13	6.4 ± 2	0.81 ± 0.33
Opsanus beta	19	9.4 ± 2.7	20.57 ± 7.24	7	3.5 ± 1.2	6.7 ± 2.52
Syngnathus scovelli	1	0.5 ± 0.5	0.04 ± 0.04	0		
Invertebrates						
Alpheus heterochaelis	111	54.8 ± 9.6	0.9 ± 0.3	179	88.4 ± 30.5	3.55 ± 0.8
Costoanachis semiplicata	274	135.3 ± 49.8	1.27 ± 0.55	616	304.2 ± 66.5	2.7 ± 0.66
Eurypanopeus depressus	19	9.4 ± 5.1	0.57 ± 0.24	1	0.5 ± 0.5	0.04 ± 0.04
Farfantepenaeus aztecus	0			1	0.5 ± 0.5	0.06 ± 0.06
Menippe adina	15	7.4 ± 2.5	7.42 ± 3.91	20	9.9 ± 3.4	3.33 ± 1.62
Palaemonetes vulgaris	44	21.7 ± 9	0.79 ± 0.34	0		
Panopeidae *spp.*	291	143.7 ± 36.8	3.51 ± 1.03	313	154.6 ± 26.5	4.12 ± 1.38
Panopeus herbstii	28	13.8 ± 3.1	13.92 ± 4.1	8	4.0 ± 2.2	0.62 ± 0.58
Petrolisthes spp.	2634	1300.7 ± 235.6	23.31 ± 3.13	5236	2585.7 ± 884.4	43.06 ± 14.83
Total	**3472**			**6398**		

Table 2.2: Species and organic matter mean ± standard deviation of $\delta^{13}C$, $\delta^{15}N$, and sample size (*n*) in each sampling period in natural and restored oyster reefs in the Mission-Aransas Estuary, Texas. Analytical precision was < 0.20‰ for carbon and nitrogen in most samples, analytical precision for some small samples was < 0.25‰ (indicated by *).

Taxa	**$\delta^{13}C$ (‰)**			**$\delta^{15}N$ (‰)**		
	Mean	**± SD**	***n***	**Mean**	**± SD**	***n***
Winter 2013						
Restored reef						
Primary producers						
Cladophora albida	-20.5	0.4	2	8.7*	1.2	2
Gracilaria tikvahiae	-22.0	1.5	3	9.3	1.1	3
Hincksia mitchellae	-22.1*	0.4	3	9.1*	0.2	3
Organic matter pools						
OSOM	-22.6	1.2	2	9.0	1.2	2
SSOM	-18.8	0.7	2	7.8	0.5	2
SPOM	-24.6	1.3	2	9.6	0.8	2
Suspension feeders						
Anomia simplex	-22.3	0.5	3	11.0	0.1	3
Balanus spp.	-21.1	0.7	3	13.5	0.1	3
Crassostrea virginica	-22.7	1.2	3	11.2	0.3	3
Crepidula depressa	-24.5	2.3	3	10.8	0.2	3
Encrusting bryozoan	-27.9		1	10.5*		1
Ischadium recurvum	-24.2	0.4	3	10.8	0.2	3
Molgulidae	-23.9	0.4	3	11.3	0.4	3
Serpulidae	-22.8	0.8	3	11.8	0.2	3
Vesiculariidae	-19.4		1	10.6		1
Grazers/Deposit feeders						
Gammaridae	-23.6*	1.3	3	12.2	1.4	3
Isopoda	-22.0	1.0	2	9.9	0.9	2
Omnivores						
Costoanachis semiplicata	-20.0	1.3	4	13.5	0.3	4
Nereididae	-18.2	1.7	3	11.9	0.7	3
Panopeidae spp.	-20.7	0.8	2	10.4	0.7	2
Panopeus herbstii	-19.4		1	14.3		1
Petrolisthes spp.	-20.3	0.2	3	12.2	0.8	3
Predators/Scavengers						
Alpheus heterochaelis	-20.3	0.6	2	14.9	0.7	2
Gobiesox strumosus	-18.1	0.5	3	15.3	0.2	3
Gobiosoma bosc	-19.0	0.9	3	16.1	0.2	3
Menippe adina	-19.0	1.2	2	14.9	0.1	2
Natural reef						
Primary producers						
Cladophora albida	-17.9	<0.1	2	8.1	0.4	2
Gracilaria tikvahiae	-20.6	4.5	3	9.2	0.5	3

Hincksia mitchellae	-19.9*		1	8.8*		1
Organic matter pools						
OSOM	-19.5	0.9	2	8.4	0.2	2
SSOM	-20.3*	0.3	2	6.3	<0.1	2
SPOM	-26.0	0.1	2	8.2	0.3	2
Suspension feeders						
Anomia simplex	-22.9	1.1	2	11.0	0.1	2
Balanus spp.	-21.1		1	13.6		1
Bugula sp.	-19.5*	0.8	2	10.6	0.2	2
Crassostrea virginica	-22.8	1.1	5	11.6	0.4	5
Encrusting bryozoan	-26.1		1	10.7*		1
Ischadium recurvum	-23.6	0.9	3	10.1	0.6	3
Molgulidae	-23.0	1.4	3	11.8	0.2	3
Grazers/Deposit feeders						
Isopoda	-22.2	0.4	3	10.0	0.4	3
Omnivores						
Costoanachis semiplicata	-21.5	1.0	2	13.4	0.3	2
Eurypanopeus depressus	-18.5		1	11.9		1
Nereididae	-22.1		1	15.2		1
Palamodes vulgaris	-16.5	1.7	3	13.6	1.5	3
Panopeidae spp.	-18.1	1.8	4	12.6	0.8	4
Petrolisthes spp.	-19.2	1.0	3	12.0	0.8	3
Predators/Scavengers						
Alpheus heterochaelis	-16.4	0.2	3	14.2	<0.1	3
Chasmodes longimaxilla	-19.6	1.3	3	16.0	0.2	3
Gobiesox strumosus	-17.8	1.9	2	14.7	0.2	2
Gobiosoma bosc	-16.6	0.4	3	16.1	0.3	3
Menippe adina	-18.1	0.2	3	14.9	0.3	3
Spring 2013						
Restored reef						
Primary producers						
Gracilaria tikvahiae	-23.7*	1.0	3	11.1	0.5	3
Organic matter pools	-22.5	3.2	7	8.0	2.4	7
OSOM	-25.1	0.3	2	9.6	0.8	2
SSOM	-19.0*	0.4	3	9.3*	<0.1	3
SPOM	-25.0	<0.1	2	4.6	0.2	2
Suspension feeders						
Anomia simplex	-21.6	1.8	3	11.6	0.2	3
Bugula sp.	-17.6		1	11.1		1
Crassostrea virginica	-22.1	0.8	6	11.7	0.6	6
Encrusting bryozoan	-23.2*	0.1	2	10.4*	0.4	2
Ischadium recurvum	-21.9	0.3	3	10.0	0.5	3
Molgulidae	-23.1	0.4	3	12.3	0.2	3
Grazers/Deposit feeders						
Isopoda	-21.9	2.2	2	9.9	0.9	2
Omnivores						

Costoanachis semiplicata	-18.9	2.1	3	14.2	0.5	3
Eurypanopeus depressus	-17.0		1	13.6		1
Nereididae	-19.5	0.2	3	13.9	1.0	3
Panopeidae spp.	-19.1	0.1	2	14.1	0.8	2
Petrolisthes spp.	-18.8	0.3	5	12.6	0.3	4
Predators/Scavengers						
Alpheus heterochaelis	-20.1	0.1	2	15.7	0.2	2
Gobiesox strumosus	-17.7	0.7	2	14.4	0.1	2
Gobiosoma bosc	-19.3	0.3	3	16.8	0.4	3
Menippe adina	-19.8		1	15.0		1
Opsanus beta	-18.5	0.8	2	14.5	<0.1	2
Natural reef						
Primary producers						
Gracilaria tikvahiae	-18.4	1.5	3	11.6	0.2	3
Organic matter pools						
OSOM	-21.9	2.5	2	9.4	1.1	2
SOM	-21.2	1.9	3	6.7*	0.5	3
SPOM	-24.3	1.1	2	5.9	1.1	2
Suspension feeders						
Anomia simplex	-22.5		1	11.2		1
Balanus spp.	-20.5	<0.1	2	13.7	<0.1	2
Crassostrea virginica	-21.8*	0.6	6	11.3	0.3	6
Ischadium recurvum	-21.1	0.7	3	10.7	0.2	3
Molgulidae	-22.5	0.3	2	11.3	0.5	2
Grazers/Deposit feeders						
Gammaridae	-19.3		1	12.4	0.2	3
Isopoda	-21.4	1.0	3	13.0	1.9	2
Omnivores						
Eurypanopeus depressus	-16.3		1	13.7		1
Nereididae	-21.5	1.2	3	14.6	0.5	3
Palamodes vulgaris	-18.7		1	14.3		1
Panopeus herbstii	-19.5		1	14.3		1
Petrolisthes spp.	-19.3	0.6	3	11.6	0.2	3
Predators/Scavengers						
Alpheus heterochaelis	-18.6	0.9	3	14.8	0.2	3
Chasmodes longimaxilla	-20.6		1	16.4		1
Gobiesox strumosus	-18.4	0.5	2	14.8	0.1	2
Gobiosoma bosc	-19.0	1.1	3	15.9	0.3	3
Menippe adina	-20.4		1	15.0		1
Opsanus beta	-18.7	1.2	3	14.7	0.2	3
Summer 2013						
Restored reef						
Primary producers						
Cladophora albida	-14.3*	0.3	2	10.4*	0.6	2
Gracilaria tikvahiae	-19.6	1.7	3	11.3	0.6	3
Organic matter pools						

OSOM	-23.1	<0.1	2	10.3	0.7	2
SSOM	-20.4	3.5	2	9.4	0.9	3
SPOM	-23.4	0.2	2	7.0	0.1	2
Suspension feeders						
Anomia simplex	-19.9		1	12.2		1
Balanus spp.	-17.6	0.4	2	14.0	0.1	2
Crassostrea virginica	-19.9	0.7	6	12.2	0.4	6
Crepidula depressa	-20.3	0.3	3	11.4	<0.1	3
Encrusting tunicate	-21.5	0.1	3	12.1	0.1	3
Ischadium recurvum	-19.7	1.8	3	11.1	0.6	3
Molgulidae	-21.6*	0.3	3	11.4	0.2	3
Grazers/Deposit feeders						
Corophiidae	-18.5		1	12.3		1
Isopoda	-21.8		1	12.2	0.2	2
Terebellidae	-19.7	0.3	3	14.0	0.4	3
Omnivores						
Astyris lunata	-20.6*		1	13.8		1
Costoanachis semiplicata	-19.1	0.3	2	15.6	0.1	2
Nereididae	-18.7	0.9	3	14.6	1.3	3
Panopeidae spp.	-17.4	0.1	2	14.5	0.1	2
Panopeus herbstii	-19.0	1.4	2	13.8	0.4	2
Petrolisthes spp.	-18.3	0.5	3	12.3	0.4	3
Predators/Scavengers						
Alpheus heterochaelis	-17.2	1.1	3	15.9	0.8	3
Gobiesox strumosus	-18.2	0.2	2	16.0	0.3	2
Menippe adina	-18.2	0.4	3	15.4	0.2	3
Opsanus beta	-18.1	0.4	3	15.4	0.3	3
Natural reef						
Primary producers						
Gracilaria tikvahiae	-18.6	1.8	3	11.3	0.3	3
Organic matter pools						
OSOM	-22.6	0.6	2	11.8	1.2	2
SSOM	-18.1	0.3	3	7.6	0.4	3
SPOM	-24.5	0.4	2	5.9	0.5	2
Suspension feeders						
Anomia simplex	-19.4	0.3	3	12.6	1.1	3
Balanus spp.	-17.5	0.2	3	13.4	0.1	3
Crassostrea virginica	-20.8	1.1	6	12.2	0.3	6
Crepidula depressa	-20.2	0.8	2	11.4	<0.1	2
Ischadium recurvum	-21.1	1.0	3	11.4	0.6	3
Molgulidae	-21.6	0.8	3	12.4	0.7	3
Grazers/Deposit feeders						
Isopoda	-19.8	0.2	2	10.9	1.4	3
Omnivores						
Astyris lunata	-20.4*		1	13.2		1
Costoanachis semiplicata	-19.8	0.5	2	13.7	0.6	2

Nereididae	-19.8	0.5	3	14.4	0.8	3
Palamodes vulgaris	-13.6	0.6	3	15.0	0.7	3
Panopeidae spp.	-19.1	0.3	3	13.2	1.0	5
Panopeus herbstii	-16.8	0.7	3	14.3	0.6	3
Parvanachis ostreicola	-19.6	0.1	2	13.4	0.2	2
Petrolisthes spp.	-18.0	0.3	3	12.1	0.4	3
Predators/Scavengers						
Alpheus heterochaelis	-18.0	1.2	3	15.5	1.2	3
Callinectes sapidus	-16.4		1	15.2		1
Gobiesox strumosus	-17.8		1	15.4		1
Gobiosoma bosc	-18.6	1.4	3	16.2	0.9	3
Menippe adina	-18.0	1.1	3	14.7	0.5	3
Opsanus beta	-17.8	0.2	3	14.8	0.4	3
Syngnathus scovelli	-16.9		1	15.5		1
Fall 2013						
Restored reef						
Primary producers						
Gracilaria tikvahiae	-20.0	0.6	3	11.8	0.5	3
Organic matter pools						
OSOM	-24.4	1.0	2	10.4	0.9	2
SSOM	-20.0*	0.2	3	8.9*	0.7	3
SPOM	-24.1	2.6	2	9.4	1.2	2
Suspension feeders						
Balanus spp.	-18.8	0.8	2	14.9	0.2	2
Bugula sp.	-19.5	1.0	5	12.2	0.9	5
Crassostrea virginica	-21.0	0.7	4	13.1	0.4	4
Crepidula depressa	-21.7	0.6	3	11.8	0.2	3
Encrusting tunicate	-23.3	0.7	5	12.1	0.1	5
Ischadium recurvum	-23.3	0.4	3	11.9	0.5	3
Molgulidae	-24.4		1	11.7		1
Serpulidae	-21.4	0.6	2	14.1	0.6	2
Vesiculariidae	-22.1	0.2	3	11.8	0.4	3
Grazers/Deposit feeders						
Gammaridae	-22.4	1.1	3	13.2	0.7	3
Ischnochiton sp.	-19.8	1.8	3	12.8	0.1	2
Isopoda	-23.3*		1	13.4	0.7	3
Terebellidae	-21.4	0.2	2	13.8	0.6	2
Omnivores						
Costoanachis semiplicata	-18.6	0.6	3	15.6	0.5	3
Nereididae	-19.9		1	14.0		1
Panopeidae spp.	-18.1	1.0	3	13.6	1.3	3
Panopeus herbstii	-19.1	0.3	3	13.2	0.8	3
Petrolisthes spp.	-18.8	<0.1	3	12.7	0.2	3
Predators/Scavengers						
Alpheus heterochaelis	-17.9	1.9	3	16.0	0.4	3
Gobiesox strumosus	-17.9		1	15.6		1

Gobiosoma bosc	-18.1*	0.2	2	16.9	1.2	2
Menippe adina	-18.0	0.6	3	14.9	0.2	3
Opsanus beta	-17.5	0.5	3	15.7	0.3	3
Natural reef						
Primary producers						
Cladophora albida	-19.7*	0.1	2	11.6*	1.7	2
Gracilaria tikvahiae	-20.9	1.4	2	11.9	0.2	2
Organic matter pools						
OSOM	-23.3	1.5	2	9.8	1.5	2
SSOM	-20.7*	0.3	3	7.8	0.2	3
SPOM	-26.0	2.4	2	8.0	1.4	2
Suspension feeders						
Balanus spp.	-20.0	0.7	3	14.0	0.3	3
Crassostrea virginica	-22.0	0.7	6	12.4	0.5	6
Crepidula depressa	-24.2	0.4	3	11.2	<0.1	3
Ischadium recurvum	-24.4	0.5	3	11.1	1.1	3
Molgulidae	-24.0*	1.5	3	11.8	0.6	3
Serpulidae	-22.1	0.7	2	13.7	0.1	2
Vesiculariidae	-21.7	0.3	3	11.7	0.1	3
Grazers/Deposit feeders						
Gammaridae	-25.9		1	11.7	0.3	3
Ischnochiton sp.	-21.6	0.2	2	12.5	0.5	4
Isopoda	-23.8	1.8	2	11.4	1.3	3
Terebellidae	-21.9	0.3	3	14.3	0.2	3
Omnivores						
Costoanachis semiplicata	-20.6	0.9	2	14.9	0.2	2
Nereididae	-19.3	2.5	3	15.3	0.9	3
Panopeidae spp.	-20.2	0.4	3	13.7	0.1	3
Panopeus herbstii	-19.0	0.7	2	13.4	0.1	2
Petrolisthes spp.	-19.7	0.4	3	12.4	0.5	3
Predators/Scavengers						
Alpheus heterochaelis	-19.9	0.3	3	15.7	0.7	3
Chasmodes longimaxilla	-20.2		1	16.5		1
Menippe adina	-18.3	1.3	3	14.7	0.4	3
Opsanus beta	-17.9	0.3	3	15.8	0.3	3

Table 2.3 : Isotope diversity indices of δ15N and δ13C isotopic position (scaled ‰) (IPos), isotopic divergence (IDiv), and isotopic dispersion (IDiv) based on mean species isotope values during 2013 sampling periods (month) in restored and natural oyster reef in the Mission- Aransas Estuary, Texas.

Index	**January**		**May**		**August**		**October**	
	Natural	Rest.	Natural	Rest.	Natural	Rest.	Natural	Rest.
IPos δ13C	0.337	0.634	0.379	0.630	0.416	0.596	0.726	0.740
IPos δ15N	0.208	0.297	0.403	0.248	0.414	0.179	0.533	0.416
IDiv	0.861	0.370	0.697	0.816	0.580	0.954	0.892	0.857
IDis	0.423	0.194	0.579	0.180	0.463	0.289	0.577	0.505

CHAPTER III: ECOLOGICAL STRUCTURE AND FUNCTION IN A RESTORED VERSUS NATURAL SALT MARSH

Abstract

Habitat reconstruction is commonly employed to restore degraded estuarine habitats and lost ecological functions. In this study, we use a combination of stable isotope analyses and macrofauna community analysis to compare the ecological structure and function between a recently constructed *Spartina alterniflora* salt marsh and a natural reference habitat over a 2-year period. The restored marsh was successful in providing habitat for economically and ecologically important macrofauna taxa; supporting similar or greater density, biomass, and species richness to the natural reference during all but one sampling period. Stable isotope analyses revealed that communities from the natural and the restored marshes relied on a similar diversity of food resources and that decapods had similar trophic levels. However, some generalist consumers (*Palaemonetes* spp. and *Penaeus aztecus*) were more ^{13}C-enriched in the natural marsh, indicating a greater use of macrophyte derived organic matter relative to restored marsh counterparts. This difference was attributed to the higher quantities of macrophyte detritus and organic carbon in natural marsh sediments. Reduced marsh flooding frequency was associated with a reduction in macrofaunal biomass and decapod trophic levels. The restored marsh edge occurred at lower elevations than natural marsh edge, apparently due to reduced fetch and wind-wave exposure provided by the protective berm structures. The lower elevation of the restored marsh edge mitigated negative impacts in sampling periods with low tidal elevations that affected the natural marsh. The results of this study highlight the importance of considering sediment characteristics and elevation in salt marsh constructions.

Introduction

Coastal salt marshes are among the most important habitats on earth in terms of ecosystem service provision (Costanza et al. 1997b). Salt marsh habitats are highly productive and provide fishery support, water purification, coastal protection, carbon sequestration and enhance biodiversity (Barbier et al. 2011a). The complex structure formed by salt marsh plants provides essential refuge habitat and feeding grounds for juvenile fish and crustacean species (Boesch and Turner 1984). In the Gulf of Mexico (GOM), salt marshes support economically important fisheries through the provision of refuge and trophic support for penaeid shrimp and blue crab (Rozas et al. 2005).

Salt marsh (hereafter "marsh") habitats in the GOM have experienced severe habitat loss and degradation relative to historic levels. Major drivers of marsh degradation include coastal development, agricultural land use, dredging, hydrologic alterations, and other anthropogenic impacts (Kennish 2001). As a result, approximately 50% of coastal marsh habitat in GOM states has been lost between 1780 and 1980 (Dahl 1990).

Marsh restoration is an important tool for enhancing ecological function and mitigating habitat loss in degraded coastal systems. Marsh restoration techniques include the restoration of previously restricted tidal regimes (Wozniak et al. 2006), invasive species removal (Gratton and Denno 2006), and the use of dredged or excavated material to construct marshes (Craft et al. 1999). Marsh construction has become a particularly common restoration method in urban coastal regions, and is often used to offset habitat losses associated with coastal development (Grayson et al. 1999).

The general goal of habitat restoration is to recover the ecological structure and function of natural habitats they are intended to recreate (SER (Society for Ecological Restoration International Science & Policy Working Group) 2004). Post-restoration monitoring is essential

for evaluating the ecological success of restoration projects and improving restoration practices (Kentula 2000). Post-restoration monitoring frequently includes assessing metrics of ecological structure (e.g. species composition, abundance) in restored habitats in comparison to a natural reference. However, the recovery of ecological functions, such as nutrient cycling and trophic pathways supporting secondary production, are rarely evaluated (Ehrenfeld and Toth 1997; Zedler and Lindig-Cisneros 2000).

Stable isotope based food web analysis is becoming an increasingly common technique used in studying aspects of functional recovery and equivalence in restored coastal habitats (Gratton and Denno 2006; Cravey 2011; Rezek et al. 2017). Primary producer carbon isotope composition varies in in relation to environmental and physiological factors associated with photosynthesis. The isotopic composition of carbon changes little as it moves through the food web and can be used to trace organic matter in consumer tissue to its primary producer source (Peterson and Fry 1987). The isotopic composition of nitrogen undergoes a predicable step-wise enrichment in ^{15}N with trophic transfers (2-4‰) and can be used to determine consumer trophic levels (Peterson and Fry 1987; Post 2002). These properties permit the study of important ecological functions related to trophic structure. In the context of restoration monitoring, stable isotope analysis can be used to examine the recovery of important trophic linkages driving secondary production and trophic diversity.

In this study, we examine the structural and functional characteristics of a recently constructed marsh in comparison to a natural reference marsh to evaluate the short-term ecological success of the restoration (4 to 5 years post-restoration). We employ a system-wide approach of evaluating traditional metrics of community structure in combination with stable isotope based food web analysis in each habitat. As tidal inundation and sediment organic matter

characteristics have been shown to influence aspects of marsh community structure and function (Craft et al. 1999; Minello et al. 2012; Baker et al. 2013; Nelson et al. 2015), these factors were also examined.

Methods

Study site

Nueces Bay is a shallow subtropical estuary located in the Texas Coastal Bend, U.S.A. This secondary bay drains into Corpus Christi Bay which is connected to the Gulf of Mexico through Aransas Pass (Fig. 3.1A). The surface area of Nueces Bay is 7,475 ha with an average depth of 0.7 m at mean low tide. Mean tide level in Nueces Bay is 0.242 m above NAVD 88 with an average tidal range of 0.12 m (Diener 1975). The bay receives most of its freshwater from the Nueces River and relatively little inflow outside of storm-related discharge events (Pennock et al. 1999). Nueces Bay supports approximately 24 ha of low marsh *Spartina alterniflora* (hereafter "*Spartina*") habitat which provides food and nursery habitat for economically important species (United States Army Corps of Engineers (USACE) 1971; Riera et al. 2000). Mid marsh vegetation in the study area was composed primarily of *Batis maritima* and *Salicornia bigelovii*.

Approximately 100 ha of salt marsh habitat were lost along the eastern margin of Nueces Bay during the construction of the Portland Causeway on U.S. Highway 181 in the late 1940's and through subsequent erosion (Cravey 2011). To compensate for this habitat loss, the Coastal Bend Bays and Estuaries Program (one of 28 areas in the National Estuary Program) initiated a marsh restoration project in 2011. The project created ~29 ha of salt marsh complex habitat consisting of protective berms and terraces planted with *Spartina* (25%) as well as protected open water (75%) (Fig. 3.1B). Berms and terraces were constructed by mechanically side casting

sediment from borrow trenches to create a surface ~ 3 m wide at 0.8 to 1.2 m elevation (NAVD 88) with ~ 6 m buffer zone from trenches.

Field sampling and measurements

Macrofauna (fish and decapod crustaceans) were sampled in *Spartina*-dominated marsh edge habitat at four sites within restored and natural habitats in Nueces Bay (Fig. 3.1B). Sampling was conducted seasonally during spring (May 27th) and summer (Aug 13th) of 2014 and winter (Feb 16th), spring (May 18th), and summer (Aug 17th) of 2015. Macrofauna were sampled at each site with triplicate tows of a modified epibenthic sled equipped with a 1-mm mesh conical plankton net (0.6 m width x 0.8 m height). Sampling sites were selected to occur on separate "islands" surrounded by open water. All 4 natural marsh islands in the area were sampled, 8 restored marsh berm islands supported sufficient *Spartina* coverage at the beginning of the study for sampling, and 4 were randomly selected as sites. The sled was pulled by hand along the fringe of *Spartina* marsh edge for 8.4 m, sampling an area of 5.0 m^2 (0.6 m width • 8.4 m tow). *Spartina* shoot counts were conducted at each site using triplicate 0.25 m^2 quadrats, samples were taken in the marsh edge (seaward 1 m of *Spartina*) within the length of each sled tow. Cores (35.4 cm^2) were used to collect above and below ground (0-20 cm) biomass of a randomly selected *Spartina* culm within each quadrat. A total of 120 *Spartina* (biomass/shoot count) and macrofauna community samples (3 replicates • 4 sites • 5 sampling periods • 2 marsh types) were taken over the course of the study. All necessary collecting permits were obtained from Texas Parks and Wildlife Department (Permit SPR-0911-344). No endangered species were collected in this study. Following approved Institutional Animal Care and Use Committee of Texas A&M University-Corpus Christi guidelines (IACUC #08-14), euthanasia occurred via rapid chilling (hypothermic shock) in an ice slurry in a cooler.

Suspended particulate organic matter (SPOM) was sampled with two replicate bottom water collections 0.1 m above the sediment-water interface at 3 sites (M2, M4 and R3; Fig 3.1). Water was sieved through a 250-µm screen to remove large zooplankton and particles and then filtered through pre-combusted Whatman GF/F filters (0.7-µm nominal pore size). Surface sediment (0 - 2 cm) was collected using cores (35.4 cm^2) on the marsh edge fringe at all sites. Nueces Bay tidal elevation data (in 30-minute intervals) from a nearby long-term data collection station were provided by the Conrad Blucher Institute for Surveying and Science at Texas A&M University Corpus Christi as part of the Texas Coastal Ocean Observation Network (TCOON) (http://www.cbi.tamucc.edu/TCOON). Three elevation measurements were taken along the marsh edge at the seaward *Spartina* fringe in each site in locations sampled with the epibenthic sled, using a real-time kinematic global positioning system (Altus Positioning Systems, Torrance, California). Marsh edge elevation data were related to water level data to create an index of flooding duration to estimate the proportion of time the marsh edge was flooded with at least 5 cm of water during the month prior to each sampling period. Five centimeters was considered the threshold in which the marsh edge was functionally accessible to macrofauna species.

Stable isotope analysis

All samples were transported to the laboratory in coolers with ice packs. Subsamples of each macrofauna species, 3 to 6 individuals if available, were selected for stable isotope analyses. All other macrofauna were fixed in buffered 10% formalin for abundance, richness, and biomass assessments. Organisms were enumerated and identified to the lowest practical taxonomic level. Live *Spartina* above- and below-ground materials collected in cores were rinsed thoroughly with tap water to remove detrital matter. Sediment samples were sieved

through a 500-µm screen to separate macrodetritus from surface sediment samples. *Spartina* above- and below-ground material, sediment macrodetritus and macrofauna were dried for 24 hours at 55 ˚C to obtain dry weight biomass.

For stable isotope analyses, small macrofauna (< 10 mm) were kept alive for 24 hours in artificial seawater to empty gut contents and whole individuals were used for isotope analysis. Larger macrofauna were dissected to obtain muscle tissue. All flora and fauna samples were rinsed with deionized water and then stored at -20 °C prior to analysis. Epiphytic microalgae were removed from *Spartina* stems with a scalpel and sorted under a dissecting microscope to remove detritus, macroalgae and macro/meiofauna. Stable isotope analysis was conducted on sieved (< 500 µm) sediment samples to determine the isotopic composition of surface sediment organic matter (SSOM) and on remaining sediment macrodetritus (> 500 µm). All samples were freeze-dried. Tissue samples were ground into a homogeneous powder using a ball mill and SSOM samples were ground using a mortar and pestle. Samples possibly containing inorganic carbonates (e.g. SPOM, SSOM, algal epiphytes and small crustaceans) were acidified prior to stable isotope analysis. Filters containing SPOM were decarbonated by contact with HCl fumes under light vacuum for 4 hours. All other samples were decarbonated with 1 mol l^{-1} HCl added drop by drop until cessation of bubbling. To avoid bias in $\delta^{15}N$ measurements due to acidification, $\delta^{15}N$ and $\delta^{13}C$ measurements were carried out on raw and decarbonated samples, respectively. Sediment organic carbon (OC) content was determined from acidified SSOM samples.

Samples were precisely weighed (± 1 µg), encapsulated in combustion cups and carbon/nitrogen isotopic compositions were determined using a Costech ECS4010 elemental analyzer (Valencia, CA) connected to a continuous flow Thermo Delta V Plus isotope ratio mass

spectrometer via a Thermo Conflo IV interface (Bremen, Germany). Replicate analyses of isotopic standard reference materials USGS 40 ($\delta^{13}C$ = -26.39 ‰; $\delta^{15}N$ = -4.52 ‰) and USGS 41 ($\delta^{13}C$ = 37.63 ‰; $\delta^{15}N$ = 47.57 ‰) were used to normalize preliminary isotopic values to the Air ($\delta^{15}N$) and Vienna Pee Dee Belemnite ($\delta^{13}C$) scales. Isotope values are expressed in δ notation following the formula $\delta X\ (‰) = [(R_{sample} / R_{standard}) - 1] \bullet 10^3$, where X is ^{13}C or ^{15}N and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$ isotopic ratio, respectively. Methionine standards (Costech) were analyzed after every 12 samples to monitor instrument performance and check data normalization. The precision of the laboratory standards was ± 0.2‰ for carbon and nitrogen.

Statistical analysis

All statistical analysis was conducted in R statistical software environment (R Development Core Team 2016). Differences in *Spartina* above- and below-ground biomass, macrofauna species richness and biomass between the restored and natural salt marsh within sampling periods and between sampling periods within each marsh were analyzed with linear mixed effects 2-way analysis of variance (ANOVA) models using the nlme package in R (Pinheiro et al. 2015). Marsh type and season were used as fixed effects with site as a random effect with a random intercept to account for spatial dependence within sites and across sampling periods (Zuur et al. 2009). For each parameter, a two-way ANOVA was fit using methods outlined in Zuur (Zuur et al. 2009). Planned contrasts established *a priori* were used to compare parameters between marsh types within each sampling period, and between sampling period within-marsh comparisons. *P*-values for within-marsh sampling period contrasts were adjusted for multiple comparisons using Westfall's modification of Tukey's HSD test with the multcomp R package (Hothorn et al. 2008). Assumptions of normality were assessed with Shapiro–Wilk tests and homoscedasticity was inspected with normalized residual *vs*. fitted value plots. *Spartina*

below-ground biomass data were square root transformed to meet assumptions of residual normality. Models were compared and selected based on corrected Akaike information criterion (AICc). Due to over-dispersion, *Spartina* and macrofauna density data were analyzed using generalized linear mixed effects two-way ANOVA models (negative binomial distribution) with the lme4 R package (Bates et al. 2015).

A Bray-Curtis similarity matrix of log(y+1) transformed of macrofauna species density data was used for multivariate community analysis and presented with a non-metric multidimensional scaling (nMDS) plot using the vegan R package (Oksanen et al. 2016). Multivariate macrofauna similarity between marsh types within each sampling period was evaluated with permutational multivariate analysis of variance tests (PERMANOVA, 9,999 permutations) (Anderson 2001). Community compositional heterogeneity was compared between marsh types using distance-based tests of homogeneity of multivariate dispersions (Anderson 2006) using the betadisper function. Four empty epibenthic sled samples, 2 within each marsh type during winter 2015, were omitted from multivariate analysis.

Spatial variation in stable isotope values (i.e. natural *vs*. restored) of potential food sources was analyzed using Wilcoxon rank sum tests and temporal variation was assessed using Kruskal-Wallis rank sum test with post-hoc multiple comparisons performed with Dunn's test (Dunn 1964) using Holm's p-value adjustment procedures with the dunn.test R package (Dinno 2016). Decapod $\delta^{13}C$ values and trophic levels (TLs) were compared between marshes with Wilcoxon rank sum tests. As marsh edge dwelling macrofauna generally exhibit high site fidelity outside of ontogenetic migrations (Fry et al. 2003; Green et al. 2012; Allen et al. 2015), consumer isotope values were expected to reflect the assimilation of locally available resources

within each marsh type. Isotope values of benthic diatoms in the Nueces Estuary were characterized by (Riera et al. 2000) and included as a potential food source in this study.

Consumer TLs (TL_i) were calculated based on the difference between $\delta^{15}N$ values of consumer and the average of major primary producer baselines using

$$TL_i = 1 + \frac{(\delta^{15}N_i - \delta^{15}N_b)}{TFF} \quad (1)$$

where $\delta^{15}N_i$ is the $\delta^{15}N$ value of consumer *i* and $\delta^{15}N_b$ is the $\delta^{15}N$ value of the baseline. A trophic fractionation factor (TFF) of 3.4‰ from literature was applied (Peterson and Fry 1987; Post 2002). $\delta^{15}N$ values of SPOM, *Spartina* (leaves/stems and roots), *Spartina* epiphytic microalgae, and benthic diatoms were used as baselines to calculate TLs. Stable isotope and TL means are given with ± standard deviation, all other means are given with ± standard error.

Stable isotope mixing models (SIMMs) were run to estimate the contribution of selected primary food resources to diets of dominant decapod consumers (*Palaemonetes spp.*, *P. aztecus* and *C. sapidus*) within each marsh during each sampling period using the simmr R package (Parnell 2015). SIMMs were used to estimate the contribution of SPOM, *Spartina* epiphytic microalgae, *Spartina* material (*Spartina*, *H. wrightii,* and *Spartina* detritus) and benthic diatoms. TFFs used for SIMMs were 3.4 ± 0.4‰ for $\delta^{15}N$ and 0.3 ± 1.3‰ for $\delta^{13}C$ (Zanden and Rasmussen 2001; Post 2002). The models were run for 10^4 iterations and the first 1,000 iterations were discarded. The source posterior distribution median was used as an unbiased estimate of dietary proportion, 95% and 50% credible intervals are also reported.

The effect of flood duration on average site spring and summer macrofauna biomass was analyzed with linear regression, biomass data was log(y+1) transformed for this analysis to meet assumptions of residual normality. The relationship between flood duration and spring and

summer TLs of dominant decapods (*Palaemonetes* spp., *Penaeus aztecus* and *Callinectes sapidus*) from both marshes were also evaluated with linear regression.

Results

Habitat characteristics

Mean water temperature ranged from 12.0 to 30.7 ˚C during sampling periods, with little spring and summer inter-annual variation (≤ 1 ˚C) (Table 3.1.). Salinity was 12.5 and 15.7 psu lower in spring and summer of 2015, respectively, than in spring and summer of 2014. Over the course of the survey, quantities of sediment OC in the natural marsh were from 2.4 to 5.1 times greater than in the restored marsh. Quantities of N in the natural marsh were from 2.5 to 6.0 times greater than in the restored marsh (Table 3.1.). Surface sediment in the natural marsh (0 - 2 cm) contained from 17 to 273 times as much dry weight detritus (g m^{-2}) than the restored marsh over the course of the study (Table 3.1.). Surface sediment OC, N and macrodetritus were greater in the natural marsh during all periods sampled (Table 3.1).

Mean monthly water level in Nueces Bay during the study period ranged from 0.15 m in January 2015 to 0.52 m (NAVD 88) in May 2015 (Fig. 3.2A). Mean water level during spring and summer sampling months was greater during 2015 than in 2014, with May 2015 0.19 m higher and August 2015 0.05 m higher than 2014 averages. The average water level during marsh sampling was 0.15 m in summer 2014 and 0.12 m in winter 2015 (Fig. 3.2B). The average water level during marsh sampling ranged from 0.38 to 0.59 m during all other sampling periods. The mean marsh edge elevation in natural marsh sites averaged 0.070 ± 0.020 m compared to 0.015 ± 0.018 (NAVD 88) in the restored marsh (Fig. 3.3A); or -0.172 m and -0.227 m relative to mean tide elevation, respectively. Mean marsh edge flooding duration in the natural marsh sites ranged from 61% in winter 2015 to 100% in spring 2015, and 74% in winter 2015 to 100%

in spring 2015 in the restored marsh (Fig. 3.3B). The lowest flood durations outside of winter occurred in summer of 2014, with mean flooding duration of 71% in the natural marsh and 87% in the restored marsh.

In the natural marsh edge, mean *Spartina* density varied seasonally (ANOVA contrasts, $P \leq 0.006$) ranging from 50.7 ± 5.6 *n* m^{-2} in summer 2015 to 106.3 ± 10.4 *n* m^{-2} in spring 2015 (Fig. 3.4A). Restored marsh edge *Spartina* density also varied seasonally (ANOVA contrasts, $P < 0.001$) ranging from 67.0 ± 6.2 *n* m^{-2} in summer 2015 to 148.7 ± 14.4 in *n* m^{-2} in spring 2015. *Spartina* density was similar between marsh types in all seasons except for summer 2014, where the restored marsh had higher densities of *Spartina* than the natural marsh (ANOVA contrast, $P = 0.040$) (Fig. 3.4A). In the natural marsh, *Spartina* above-ground biomass ranged from 3.6 ± 0.8 g $core^{-1}$ in winter 2015 to 5.8 ± 0.9 g $core^{-1}$ in spring 2015 (35.4 cm^2 core) and varied significantly between sampling periods (ANOVA contrasts, $P \leq 0.012$) (Fig. 3.4B). Natural marsh *Spartina* below-ground biomass (0-20 cm) ranged from 2.6 ± 0.5 g $core^{-1}$ in spring 2015 to 3.4 ± 0.5 g $core^{-1}$ in spring 2014 and was similar between sampling periods (Fig. 3.4C). Restored marsh *Spartina* above- and below-ground biomass were stable between sampling periods; with above-ground biomass ranging from 1.6 ± 0.3 g $core^{-1}$ in winter 2015 to 4.5 ± 0.8 g $core^{-1}$ in summer 2014 and below-ground biomass ranging from 1.6 ± 0.3 g $core^{-1}$ in winter 2015 to 2.9 ± 0.6 g $core^{-1}$ in spring 2014 (Fig. 3.4B and C). *Spartina* above-ground biomass was significantly greater in the natural marsh in spring 2015 (ANOVA contrast, $P = 0.029$) (Fig. 3.4B).

Macrofauna community

A total of 23,102 individuals from 27 species or taxa were collected from both natural and restored marsh habitats over the course of the study, yielding 921 g of dry weight biomass

(Table 3.2). Mean macrofauna density and biomass in the natural saltmarsh varied seasonally, ranging from 4.4 ± 1.8 *n* m^{-2} and 0.05 ± 0.02 g dry wt. m^{-2} in winter 2015 to 101.6 ± 14.3 *n* m^{-2} and 3.6 ± 1.1 g dry wt. m^{-2} in summer 2015 (Fig. 3.5A and B) (ANOVA contrasts, $P \leq 0.032$ for density; $P < 0.001$ for biomass). Mean species richness in the natural marsh also varied among seasons, ranging from 1.5 ± 0.4 in winter 2015 to 5.8 ± 0.6 in summer 2015 (Fig. 3.5C) (ANOVA contrasts, $P \leq 0.046$). Mean macrofauna abundance in the restored saltmarsh was stable among seasonal sampling periods, ranging from 23.8 ± 7.9 *n* m^{-2} in winter 2015 to 44.6 ± 8.8 *n* m^{-2} in summer 2014 (Fig. 3.5A). However, mean macrofauna biomass and species richness in the restored marsh varied seasonally—with biomass ranging from 0.3 ± 0.1 g dry wt. m^{-2} in winter 2015 to 2.0 ± 0.5 g dry wt. m^{-2} in summer 2014, and richness from 2.8 ± 0.6 in winter 2015 to 4.8 ± 0.4 in summer 2014 (ANOVA contrasts, $P \leq 0.003$ for biomass; $P = 0.022$ for species richness) (Fig. 3.5B and C). Mean macrofauna density, biomass and taxa richness were greater in the restored saltmarsh during summer 2014 (ANOVA contrasts, $P < 0.001$ for density; $P < 0.001$ for biomass; $P = 0.005$ for richness) and winter 2015 (ANOVA contrasts, $P < 0.001$ for density; $P = 0.031$ for biomass; $P = 0.040$ for richness), and greater in the natural marsh during summer 2015 (ANOVA contrasts, $P = 0.013$ for density; $P < 0.001$ for biomass; $P < 0.001$ for richness) (Fig. 3.5A-C).

The results of PERMANOVA showed natural and restored marsh macrofauna community composition were similar during both spring sampling periods and dissimilar during winter 2015 and summer sampling periods (Table 3.3 and Fig. 3.6A). Homogeneity of group dispersions (betadisper) tests indicated that macrofauna community variability was greater in the natural marsh during summer 2014 and summer 2015 (Table 3.3 and Fig. 3.6A). *Palaemonetes* spp. was the most numerically abundant consumer in both marsh types; mean densities ranged

from 2.8 to 84.0 *n* m^{-2} in the natural marsh and from 27.3 to 42.6 *n* m^{-2} in the restored marsh (Fig. 3.6B). *P. aztecus* was the second most abundant consumer species (natural: < 0.1 to 7.3 *n* m^{-2}; restored: 0.1 to 4 *n* m^{-2}) followed by *C. sapidus* (natural: < 0.1 to 4.4 *n* m^{-2}; restored: < 0.1 to 0.5 *n* m^{-2}) (Fig. 3.6B). Fish densities ranged from 0.2 to 6.8 *n* m^{-2} in the natural marsh and from 0.5 to 0.9 *n* m^{-2} in the restored marsh. Together, *Palaemonetes* spp., *P. aztecus* and *C. sapidus* composed 95.2% of the community biomass in the natural marsh and 94.7% of the biomass in the restored marsh. The remaining biomass was dominated by fish (Table 3.2).

Stable isotope analysis

No spatial differences in $\delta^{13}C$ or $\delta^{15}N$ values were found in primary producers (*Spartina*, *B. maritima*, *Spartina* epiphytic microalgae) or in *Spartina* detritus between marsh types over the course of the study (Wilcoxon tests, P > 0.05) (Fig. 3.7 and Table 3.4). *Spartina* $\delta^{13}C$ values varied between sampling periods; ranging from -14.3 ± 0.8‰ in spring 2014 to -13.2 ± 0.5‰ in summer 2015 (summer 2015 > spring 2014/2015; Dunn's tests, $P < 0.05$). *B. maritima* $\delta^{15}N$ values were lower in summer 2015 (6.3 ± 0.3‰) than in spring 2015 (12.5 ± 0.12‰) or summer 2014 (11.9 ± 1.2‰) (Dunn's tests, $P < 0.05$). *Spartina* epiphytic microalgae $\delta^{13}C$ values also varied temporally, ranging from -19.2 ± 2.1‰ in spring 2015 to -13.9 ± 2.6‰ in summer 2014 (summer 2014 > spring 2015; Dunn's test, $P = 0.006$). The $\delta^{15}N$ values of *Spartina* epiphytic microalgae were lower in summer 2014 (3.6 ± 2.3‰) than in spring 2015 (11.1 ± 1.7‰) (Dunn's test, $P = 0.007$).

Over the course of the study, SPOM samples taken in the restored marsh complex had higher $\delta^{15}N$ values (9.1 ± 0.4‰) than samples taken from natural marsh sites (8.2 ± 0.9‰) (Wilcoxon test, W = 20, $P = 0.006$). SSOM had higher $\delta^{13}C$ values in the natural marsh (-19.0 ± 1.7‰) than in the restored marsh (-22.0 ± 2.8‰) (Wilcoxon test, W = 216, $P = 0.001$). Sediment

macrodetritus in the natural marsh had lower $\delta^{13}C$ (-19.9 ± 4.6‰) values than in the restored marsh (-15.1 ± 3.1‰) (Wilcoxon test, W = 22, $P = 0.023$). SPOM $\delta^{13}C$ values varied over the course of the study; with SPOM ranging from -25.0 ± 0.6‰ in spring 2014 to -21.3 ± 1.0‰ in summer 2014 (summer 2014 > spring 2014/2015, summer 2015 > spring 2014; Dunn's tests, $P < 0.05$). SPOM, SSOM and sediment macrodetritus had mean C:N ratios of 10.8 ± 2.3, 9.2 ± 1.2 and 28.9 ± 5.4 in the natural marsh and 10.2 ± 3.0, 10.8 ± 2.3 and 36.4 ± 20.3 in the restored marsh, respectively.

Mean consumer $\delta^{13}C$ values ranged from -19.7‰ to -12.2‰ in the natural marsh and -19.5‰ to -12.2‰ in the restored marsh. Amphipod $\delta^{13}C$ and $\delta^{15}N$ values averaged -17.4‰ and 8.7‰ in the natural marsh and -17.3‰ and 9.1‰ in the restored marsh over the course of the study, respectively (Fig. 3.7). Isopods had the lowest average $\delta^{13}C$ values of all taxa; -19.7‰ in the natural marsh and -19.6‰ in the restored marsh. Mean Isopod $\delta^{15}N$ values were 8.7‰ in natural marsh and 11.1‰ in the restored marsh. Mean overall $\delta^{13}C$ values of major decapods (*Palaemonetes* spp., *P. aztecus* and *C. sapidus*) ranged from -17.2‰ to -15.0‰ in the natural marsh and from -17.5‰ to -16.0‰ in the restored marsh; $\delta^{15}N$ values ranged from 11.1‰ to 14.0‰ in the natural marsh and from 11.8‰ to 13.8‰ in the restored marsh (Fig. 3.7). Fish $\delta^{13}C$ values varied considerably between species. Greatest values were found in *Cyprinodon variegatus* (natural: -13.1‰, restored: -12.2‰) and lowest in *Gobiosoma bosc* (natural: -18.8‰, restored: -18.3‰). Mean fish $\delta^{15}N$ values also varied widely, with relatively low values in juvenile *Mugil* sp. (10.6‰) and *Cyprinodon variegatus* (10.21‰) in comparison to juvenile *Micropogonias undulatus* (15.4‰) and juvenile *Cynoscion nebulosus* (16.2‰).

Over the course of the study, mean $\delta^{13}C$ values of *Palaemonetes* spp. were higher in the natural marsh (-15.0 ± 1.5‰) than in the restored marsh (-16.0 ± 1.5‰) (Wilcoxon test, W =

397.5, $P = 0.010$) (Fig. 3.7). *P. aztecus* also had greater $\delta^{13}C$ values in the natural marsh (-15.7 ± 2.0‰) than in the restored marsh (-17.5 ± 1.8‰) (Wilcoxon test, W = 342.5, $P = 0.006$). *C. sapidus* $\delta^{13}C$ values in the natural marsh (-17.2 ± 1.8‰) were similar to those in the restored marsh (-17.1 ± 1.4‰) (Wilcoxon test, W = 57, $P = 0.872$). Among sampling periods, TLs of *Palaemonetes* spp., *P. aztecus,* and *C. sapidus* were 3.1 ± 0.5, 2.5 ± 0.4 and 2.2 ± 0.7 in the natural marsh and 3.0 ± 0.3, 2.6 ± 0.3 and 2.5 ± 0.5 in the restored marsh. There were no overall differences in TLs of decapod species between the restored and natural marshes (Wilcoxon tests, $P < 0.05$).

In summer 2014, decapods in the natural marsh had particularly high $\delta^{13}C$ values and low $\delta^{15}N$ values in comparison decapods in the restored marsh, and in the natural marsh during other sampling periods. Mean $\delta^{13}C$ value of major decapods ranged from -15.4 to -13.7‰ and $\delta^{15}N$ values ranged from 7.0 to 12.0‰ in the natural marsh during this sampling period (Fig. 3.7). Lowest decapod TLs also occurred during summer 2014 in the natural marsh (*Palaemonetes* spp. = 2.6, *P. aztecus* = 2.0, *C. sapidus* = 1.4).

Stable isotope mixing models

SIMM estimated dietary contributions to *Palaemonetes* spp. ranged from 26 to 58% for *Spartina* and 8% to 27% for SPOM in the natural marsh, and 17 to 56% for *Spartina* and 9 to 38% for SPOM in the restored marsh (Fig. 3.8A and Table 3.4). Contributions to *P. aztecus* ranged from 19 to 65% for *Spartina* and 6% to 27% for SPOM in the natural marsh, and 10 to 38% for *Spartina* and 16 to 54% for SPOM in the restored marsh (Fig. 3.8B). Contributions to *C. sapidus* ranged from 15 to 40% for *Spartina* and 18% to 31% for SPOM in the natural marsh, and 20 to 29% for *Spartina* and 19 to 29% for SPOM in the restored marsh (Fig. 3.8C). Contributions from benthic diatoms and *Spartina* epiphytic microalgae to decapod diets in the

natural marsh ranged from 10 to 29% and 14 to 22%, respectively, and from 16 to 27% and 13 to 24% in the restored marsh, respectively (Fig. 3.8A-C).

Hydroperiod influence

Regression models demonstrated a positive relationship between flood duration index and log(y+1) macrofauna biomass in spring and summer sampling periods ($F_{1,38} = 37.1$, $P < 0.001$, $R^2 = 0.50$) (Fig. 3.9A). Flood duration index was also positively related to the TLs of *Palaemonetes* spp. ($F_{1,12} = 6.8$, $P = 0.040$, $R^2 = 0.31$) and *P. aztecus* ($F_{1,12} = 10.6$, $P = 0.024$, $R^2 = 0.36$) (Fig. 3.9B). Flooding index did not significantly explain variation in *C. sapidus* TLs ($F_{1,12} = 2.3$, $P = 0.133$, $R^2 = 0.18$).

Discussion

Habitat restoration

Spartina density, above- and below-ground biomass were generally similar between the restored and natural marshes, demonstrating recovery within 4 years of marsh construction. However, surface sediment characteristics were substantially different between marsh types. Surface sediment OC, N and macrodetritus content in the restored marsh remained impoverished relative to the natural marsh throughout the study period. These results agree with previous research demonstrating the recovery of restored salt marsh *Spartina* characteristics (e.g. density, biomass) to natural marsh levels occur relatively quickly (5 to 15 years), while the recovery of restored marsh sediment characteristics occur over much longer timeframes (macro-organic matter: 15 years; OC and N: > 30 years) (Craft et al. 2003; Craft and Sacco 2003).

Although highest macrofauna density, biomass and species richness were observed in the natural marsh during summer 2015, these metrics were similar between marshes or greater in the restored marsh during all other sampling periods. The ability to determine the equivalency of

macrofauna community structural characteristics between restored and natural marshes was somewhat complicated by the high degree of temporal variability in the natural marsh used as a reference. Macrofauna densities in restored marsh were comparable to those reported in natural marshes in other bays in the Gulf of Mexico: Lavaca Bay (17.65 ± 2.38 *n* m^{-2}; (Robillard et al. 2010b)) and Galveston Bay (fish = 4.02 ± 0.69 *n* m^{-2}, crustaceans = 55.03 ± 8.80 *n* m^{-2}; (Stunz et al. 2010a)). Between-marsh multivariate similarity followed a comparable trend to that of density, biomass, and species richness. These results support previous research demonstrating the ability of constructed marsh restorations to enhance production of ecologically and economically important macrofauna species in degraded coastal systems (Rozas et al. 2005; Rozas and Minello 2009).

Isotopic composition of potential food sources

C_3 and C_4 marsh macrophytes were easily distinguished based on their $\delta^{13}C$ values: the relatively low values of *S. bigelovii* (-27.4‰) and *B. maritima* (-25.8‰) were typical of C_3 plants, and the relatively high values of *Spartina* (-13.8‰) were typical of C_4 plants (Peterson and Fry 1987). *S. bigelovii* and *Spartina* $\delta^{13}C$ values were similar to those reported by (Riera et al. 2000) in the Nueces estuary. SPOM $\delta^{13}C$ values (-23.6‰) were typical of marine and estuarine phytoplankton (Peterson and Fry 1987; Lebreton et al. 2016), indicating that the influence of terrestrial organic matter in the water column was relatively low in the study area. The $\delta^{13}C$ values of sediment macrodetritus in the restored marsh (-15.1‰) indicated that it was largely composed of recently deposited *Spartina* detritus (-14.2‰), whereas the lower $\delta^{13}C$ values of natural marsh macrodetritus (-19.9‰) were more characteristic of *Spartina* refractory compounds (e.g. lignin), which are generally more ^{13}C-depleted than fresh *Spartina* (e.g. -17.0‰ to -17.9‰; (Benner et al. 1987)), and accumulated in natural marsh sediments over an extended

timeframe. A greater influence of ^{13}C-depleted mid-marsh halophytes (i.e. C_3 plants) in natural marsh sediment macrodetritus could have also contributed to its relatively lower $\delta^{13}C$ values, as these plants were rare in the restored marsh. Isotopic composition of SSOM in the natural marsh (-19.0‰) reflected the $\delta^{13}C$ values of natural marsh sediment macrodetritus. SSOM $\delta^{13}C$ values in the restored marsh were lower (-22.0‰), indicating that it was primarily composed of deposited SPOM, and secondarily of benthic microalgae and/or of C_4 plant detritus.

Food web structure

Mean consumer $\delta^{13}C$ values in both marshes were within a 7.5‰ range, from -19.7 to -12.2‰, indicating that the secondary production in these habitats was potentially supported by a wide range of resources including *Spartina*, sediment macrodetritus, SPOM, benthic microalgae, and *Spartina* epiphytic microalgae. C_3 plants were markedly depleted in ^{13}C in comparison to consumers, with mean *S. bigelovii* and *B. maritima* $\delta^{13}C$ values 6.2‰ and 7.8‰ lower, respectively, than the most ^{13}C-depleted consumers (isopods). These results indicate a minimal contribution from C_3 plants to secondary production in this system, despite the abundance of these plants in natural mid-marsh areas and their potential contribution to natural marsh sediment macrodetritus.

The similar ranges in $\delta^{13}C$ and $\delta^{15}N$ values in natural and restored marsh consumers over the course of the study indicate these communities were supported by a similar diversity of basal resources, and had similar food chain lengths. However, *Palaemonetes* spp. and *P. aztecus* had slightly greater $\delta^{13}C$ values in the natural marsh (-15.0 and -15.7‰, respectively) than in the restored marsh (-16.0 and -17.5‰, respectively). This indicates that 1) these consumers significantly rely on SSOM, as SSOM is more enriched in ^{13}C in the natural marsh than in the restored marsh, and/or that 2) ^{13}C-enriched sources (i.e. *Spartina*, benthic microalgae, *Spartina*

epiphytic microalgae, sediment macrodetritus) are used more by these consumers in the natural marsh than in the restored marsh. The lack of systematic difference between marshes in *C. sapidus* $\delta^{13}C$ values may be related to their highly variable and opportunistic feeding strategies (Laughlin 1982), leading to greater intra-marsh dietary variability. A potential role of *Spartina* as an important food resource for decapods in both marshes would indeed be consistent with the established paradigm of marsh food webs being largely supported by *Spartina*-derived organic matter (Odum 1957; Teal 1962).

Benthic microalgae and *Spartina* epiphytic microalgae are also considered important components of salt marsh food webs (Riera et al. 2000; Quiñones-Rivera and Fleeger 2005). Both these algal resources were utilized relatively consistently across inter-seasonal and inter-annual periods. The similar isotope compositions of *Spartina* epiphytic algae and benthic diatoms during most sampling periods limits the ability of mixing models to discriminate between the use of these two food sources, potentially leading to an underestimated or overestimated contribution of either resource. In combination, models indicated that these microalgal resources were an important food resources for decapods in both marshes. The influence of SPOM generally increased during summer; reflecting an increase in bentho-pelagic coupling, possibly associated with seasonal phytoplankton blooms (Galván et al. 2008). SPOM was the most important food source for decapods in both marshes during summer 2015, likely due to an increase in pelagic production associated with greater influx of freshwater (reflected by low salinity in 2015) and associated nutrients earlier in the year (Pennock et al. 1999).

On average, contributions of *Spartina* as a food source to *Palaemonetes* spp. and *P. aztecus* were 17% and 18% higher in the natural marsh than in the restored marsh, respectively. In contrast, contributions of SPOM to *Palaemonetes* spp. and *P. aztecus* diets were 10% and

15% higher on average in the restored marsh than in the natural marsh, respectively. These differences are likely related to the much greater quantities of macrophyte macrodetritus and/or sediment organic matter accumulated in natural marsh surface sediments in comparison to the recently restored marsh. These results suggest that the relatively impoverished sediments, typical of young constructed marshes, resulted in lower contributions from macrophyte derived organic matter and a greater reliance on pelagic primary production subsidies by important restored marsh community members. Lower flooding durations in natural marsh sites potentially confound the ability to attribute inter-marsh differences in resource use to variations in sediment organic matter versus marsh elevation. However, macrofauna inhabiting marshes with lower flooding frequencies have been shown to consume less *Spartina* derived organic matter than macrofauna in more frequently flooded marshes across a range of systems (Baker et al. 2013), while the opposite trend was observed in the natural marsh. This indicates between-marsh dietary variations were likely related to differences in sediment organic matter content.

As the quality and abundance of SPOM can vary substantially over time, the reduced availability of macrophyte-derived organic matter in sediments may reduce the food web stability (Moore et al. 2004) and macrofauna carrying capacity (Edgar 1993) of recently restored marshes in comparison to their natural counterparts. Higher organic matter content in natural marsh sediments may enhance foraging opportunities for macrofauna and infauna prey compared to recently restored marshes (Craft 2000; Craft and Sacco 2003).

Habitat structure and hydroperiod influence

The physical design of the restored marsh created marsh edge habitat that was subject to much less exposure and fetch than the natural marsh. Exposure, fetch and associated wind-wave disturbance play an important role in determining the location and condition of marsh edge

habitat; *Spartina* in sheltered areas have been shown to occupy lower elevations than in areas exposed to higher wave energy (Delaney et al. 2000; Roland and Douglass 2005). The lower elevations occupied by restored marsh edge *Spartina* indicate the protection provided by the berm and terrace structures may have reduced disturbance associated with wave energy, leading to greater flooding durations.

Flooding duration had a substantial influence in macrofauna communities, explaining 50% of the variation in macrofauna biomass in spring and summer sampling periods. Sampling periods characterized by relatively low flood durations in the natural marsh (i.e. summer 2014, winter 2015) coincided with substantially reduced natural marsh macrofauna density, biomass, and richness. In contrast, the restored marsh macrofauna community was relatively stable, with no significant variation in macrofauna density, biomass or richness between spring and summer sampling periods. These results support the well-documented positive relationship between flood duration and macrofauna use of marsh edge habitat (Minello and Webb 1997; Minello et al. 2012).

Tidal inundation controls access to important prey that are more abundant (or only available) in marsh edge habitat, such as surface dwelling infauna (Whaley and Minello 2002) and *Spartina* epiphyte associated meiofauna (Gregg and Fleeger 1998). Our results indicated a significant positive relationship between TLs and flood duration index in *Palaemonetes* spp. and *P. aztecus*, demonstrating an association between reduced access to marsh edge habitat and lower TLs. These results are consistent with those of Nelson et al. (Nelson et al. 2015), who found a positive relationship between marsh flooding frequency and *Fundulus heteroclitus* TLs.

As this study examined the recovery of a single recently constructed marsh complex and does not account for potential between-system variability, the ability to make general inferences

about the overall effect of marsh restoration on community structure and function from these results is limited. Further research on functioning of constructed marshes across regional scales and at different stages of successional development (i.e. age) is warranted to fully appreciate the ability of constructed marshes to achieve long term functional recovery goals.

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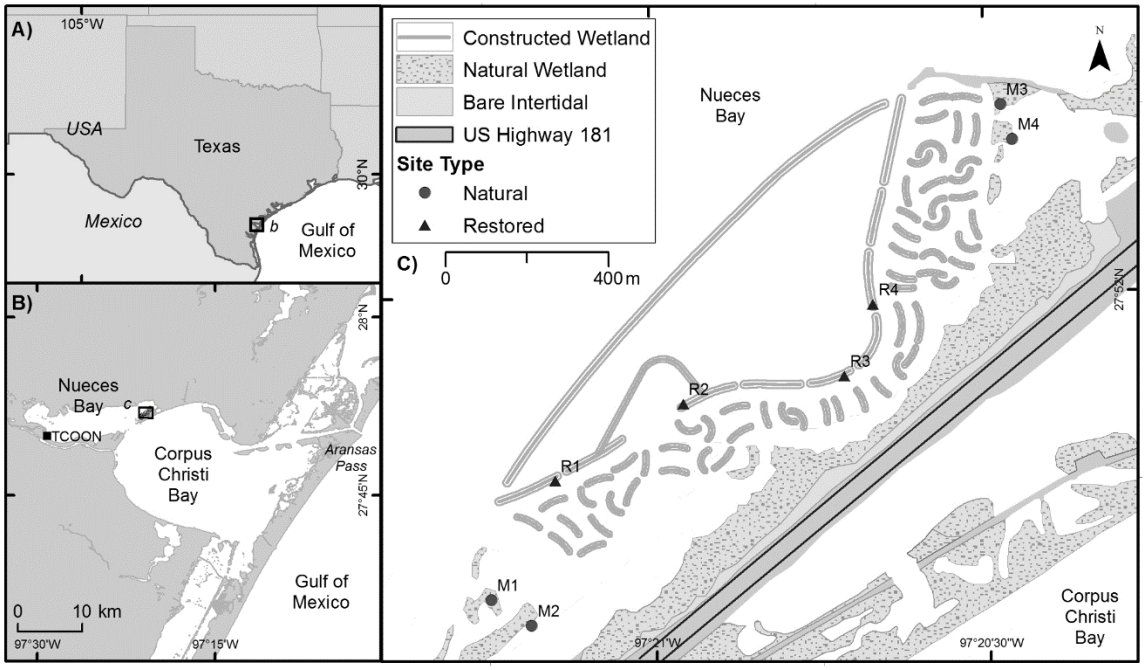

Figure 3.1: Map of study region (A) and study site with labeled restored and natural salt marsh sampling sites (B) in Nueces Bay, Texas. TCOON: Texas coastal ocean observation network.

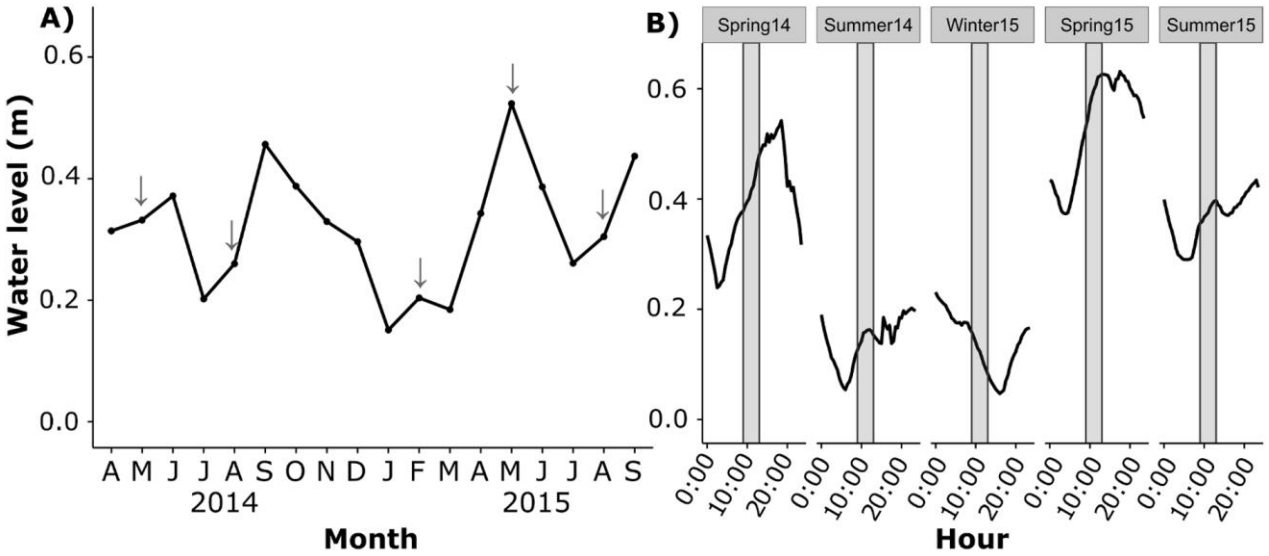

Figure 3. 2: Mean monthly water level (NAVD 88) throughout the study duration (sampling months indicated with arrows) (A) and water level during sampling days (approximate sampling duration indicated with gray boxes) (B) in Nueces Bay, Texas.

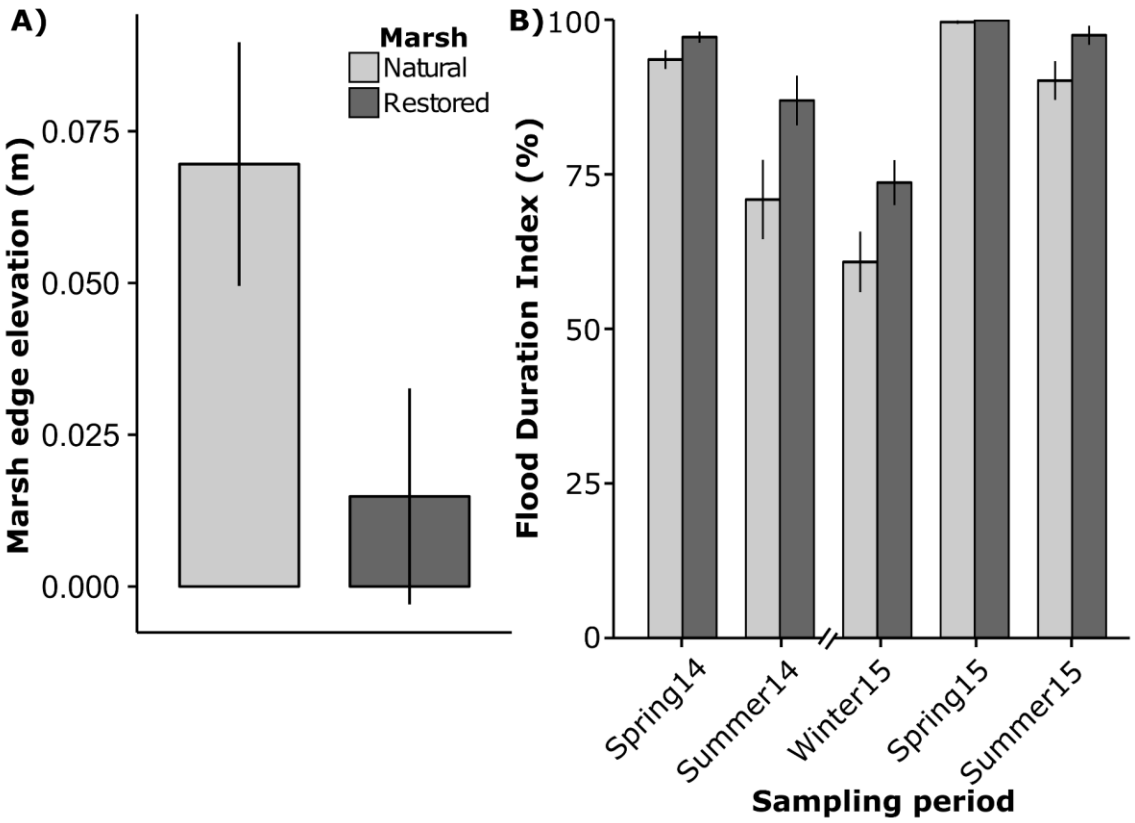

Figure 3.3: Mean ± standard error of marsh edge elevation in restored and natural marsh sites (A) and marsh edge flood duration (time water level > 5 cm + marsh elevation • total time-1) within one month prior to sampling period (B).

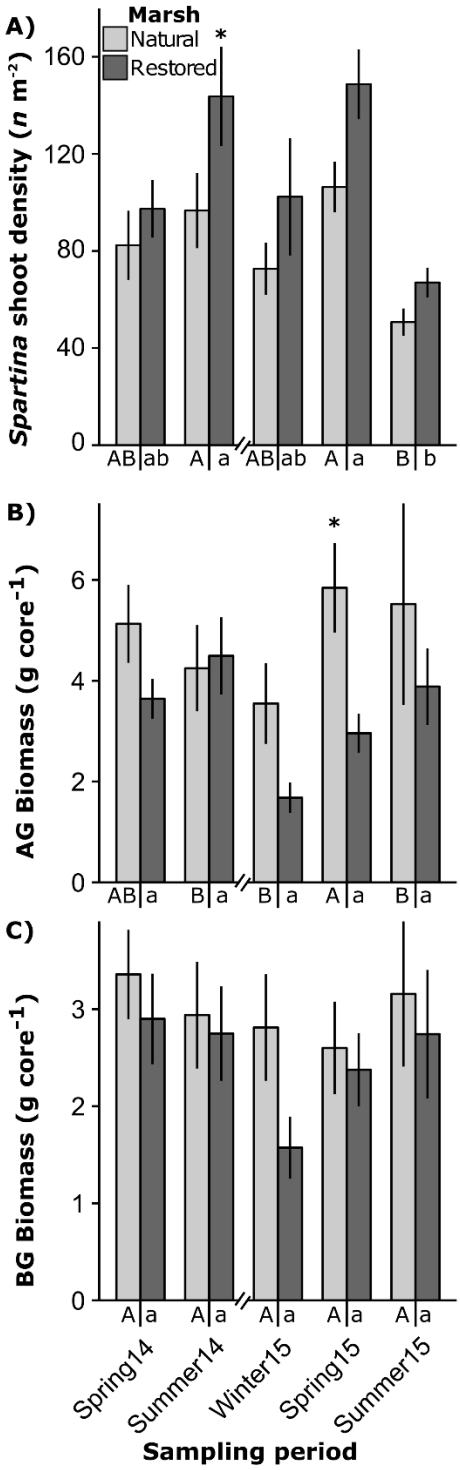

Figure 3.4: Mean ± standard error of *Spartina* shoot density (A), above ground (AG) biomass (B) and below ground (BG, 0 - 20 cm) biomass (dry weight) (C) of *Spartina* per 35.4 cm^2 core in restored and natural marsh sites in each sampling period in Nueces Bay, Texas. Significant differences between restored and natural marshes within seasons indicated by *, and within marsh seasonal contrast groupings indicated under x-axis (ANOVA contrasts $P < 0.05$).

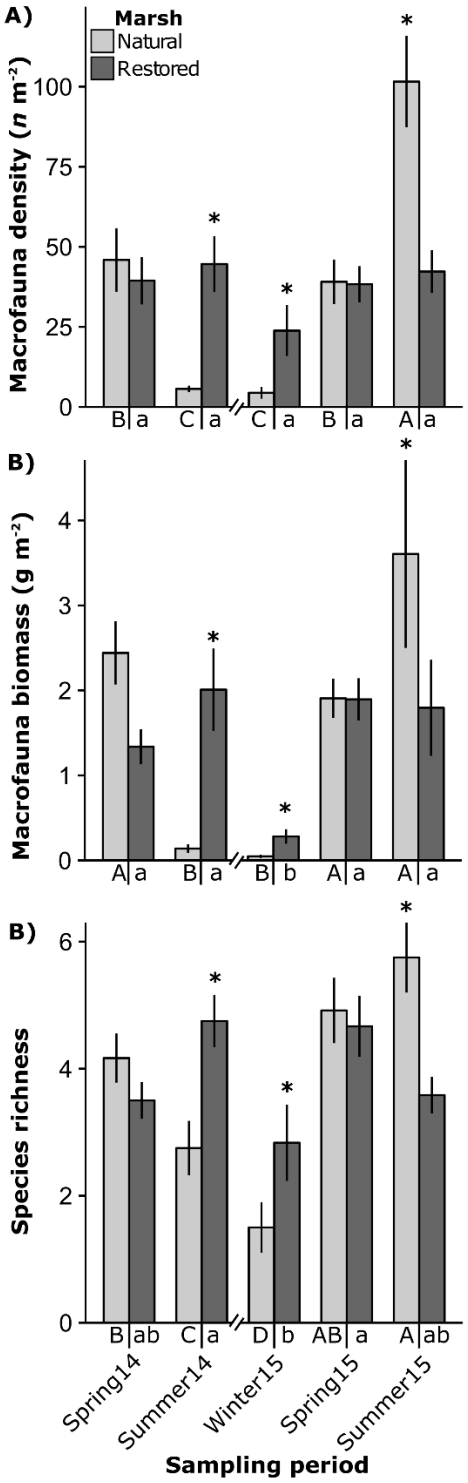

Figure 3.5: Mean ± standard error of macrofauna density (A), macrofauna biomass (dry weight) (B) and macrofauna species richness (C) in restored and natural marsh habitat during each sampling period in Nueces Bay, Texas. Significant differences between restored and natural marshes within seasons indicated by *, and within marsh seasonal contrast groupings indicated under x-axis (ANOVA contrasts $P < 0.05$).

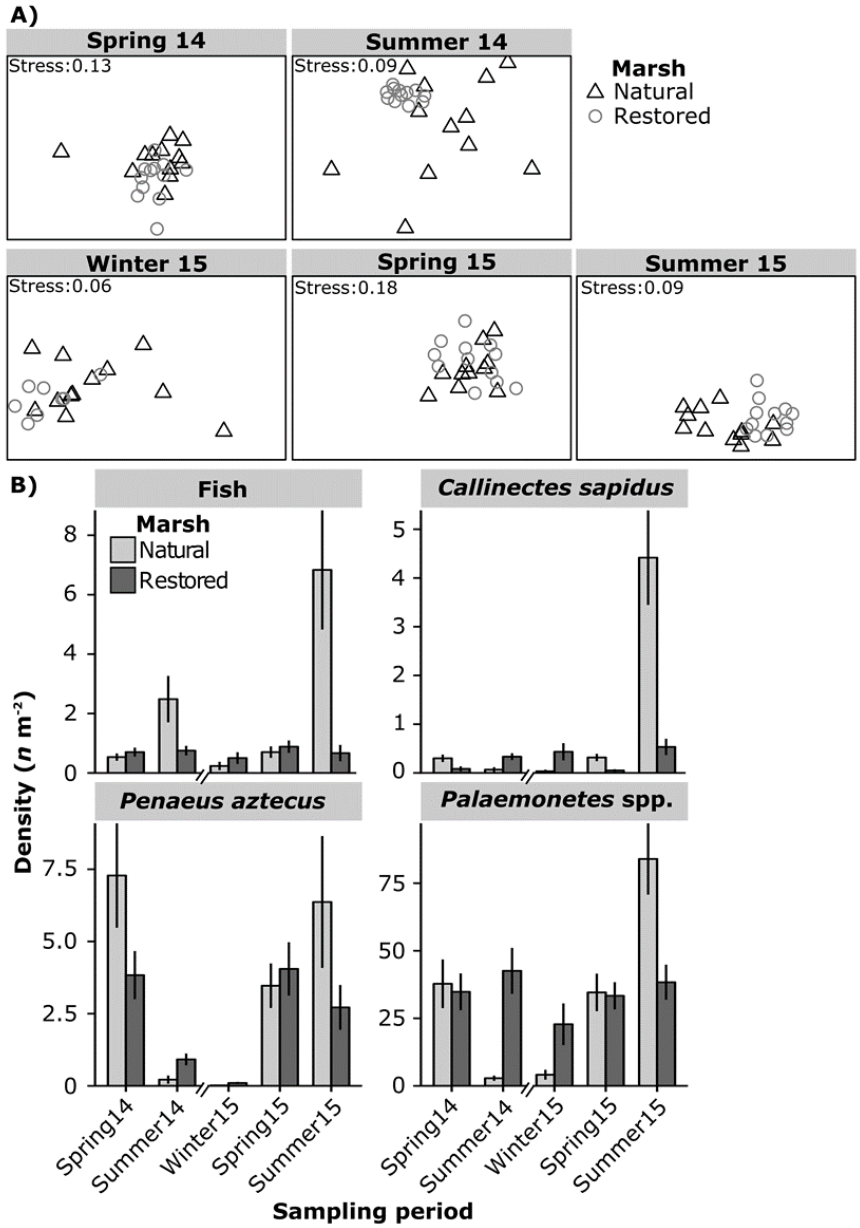

Figure 3.6: Non-metric multidimensional scaling plots of log(y+1) transformed multivariate macrofauna density data from the natural and restored marshes (A) and mean ± standard error of major taxa density within sampling periods in Nueces Bay, Texas (B).

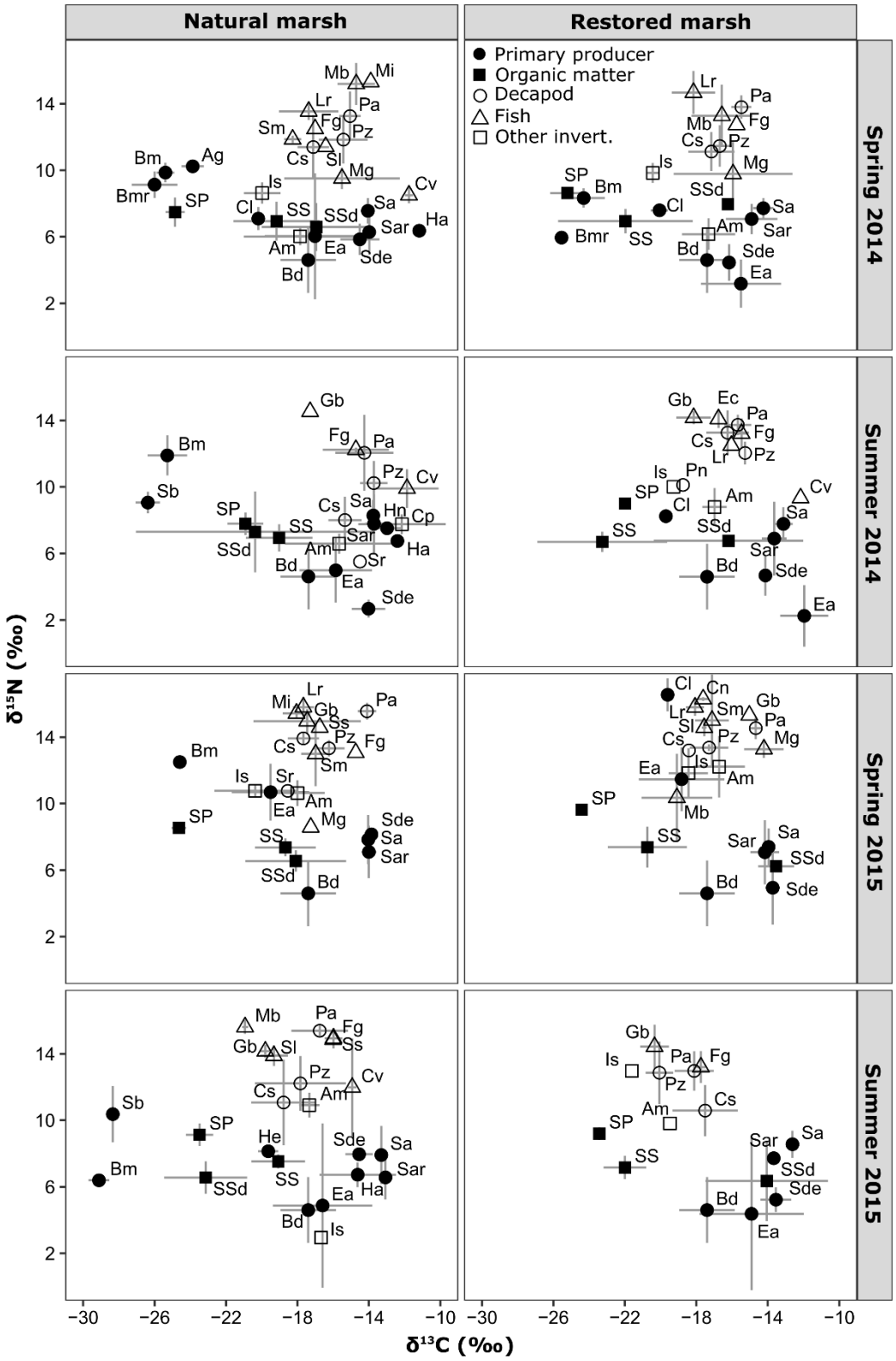

Figure 3.7: Mean ± standard deviation of $\delta^{13}C$ and $\delta^{15}N$ values of potential food resources and consumers in natural and restored marsh sites within each sampling period in Nueces Bay,

Texas. Labels representing samples - amphipods: Am, *Avicennia germinans*: Ag, *Batis maritima*: Bm, *Batis maritima* root: Bmr, *Callinectes sapidus*: Cs, *Cerithideopsis pliculosa*: Cp, Filamentous algae: Cl, *Cynoscion nebulosus*: Cn, *Cyprinodon variegatus*: Cv, *Etropus crossotus*: Ec, *Penaeus aztecus*: Pz, *Fundulus grandis*: Fg, *Gobiosoma bosc*: Gb, *H. wrightii* epiphyte: He, *Halodule wrightii*: Ha, *Halophila engelmannii*: Hn, Isopod: Is, *Lagodon rhomboides*: Lr. *Menidia beryllina*: Mb, *Micropogonias undulatus*: Mu, *Mugil sp*.: Mg, *Palaemonetes spp*.: Pa, Panopeidae: Pn, *Salicornia bigelovii*: Sb, *Sesarma reticulatum*: Sr, *Spartina alterniflora*: Sa, *Spartina alterniflora* root: Sar, *Spartina* detritus: Sde, *Spartina epiphytic algae*: Ea, SPOM: SP, Sediment detritus: SSd, SSOM: SS, *Strongylura marina*: Sm, *Syngnathus louisianae*: Sl, *Syngnathus scovelli*: Ss. Isotope values for benthic diatoms (Bd) were taken from Riera et al. (Riera et al. 2000).

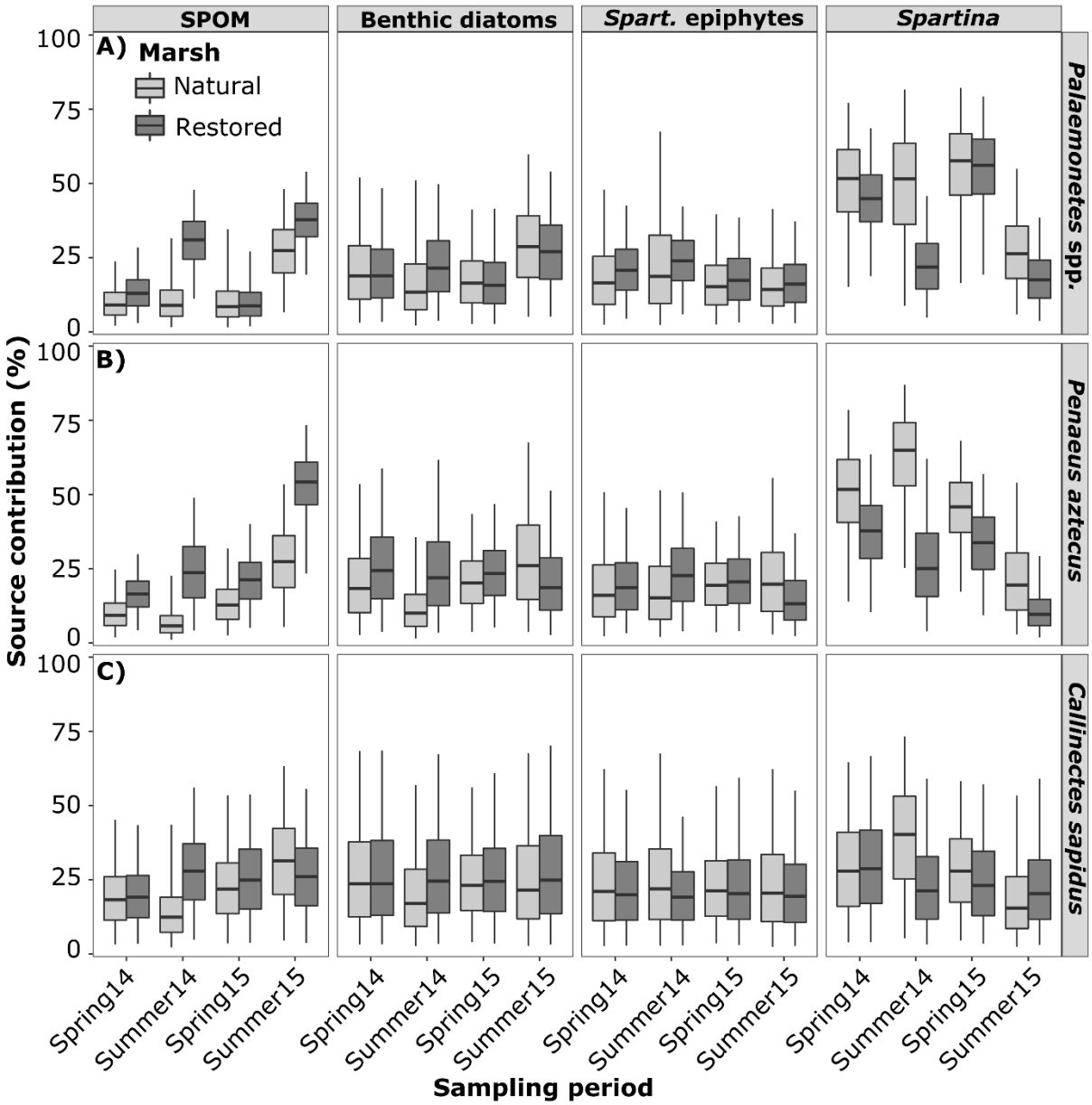

Figure 3.8: Estimated proportional contribution of suspended particulate organic matter (SPOM), benthic diatoms, *Spartina* epiphytic microalgae, and *Spartina* to the diets of *Palaemonetes* spp. (A) *P. aztecus* (B) and *C. sapidus* (C) in spring and summer sampling periods in natural and restored marsh sites. Plots indicate *posterior* dietary contribution estimate (median) with 50% (hinges) and 95% (whiskers) credibility intervals

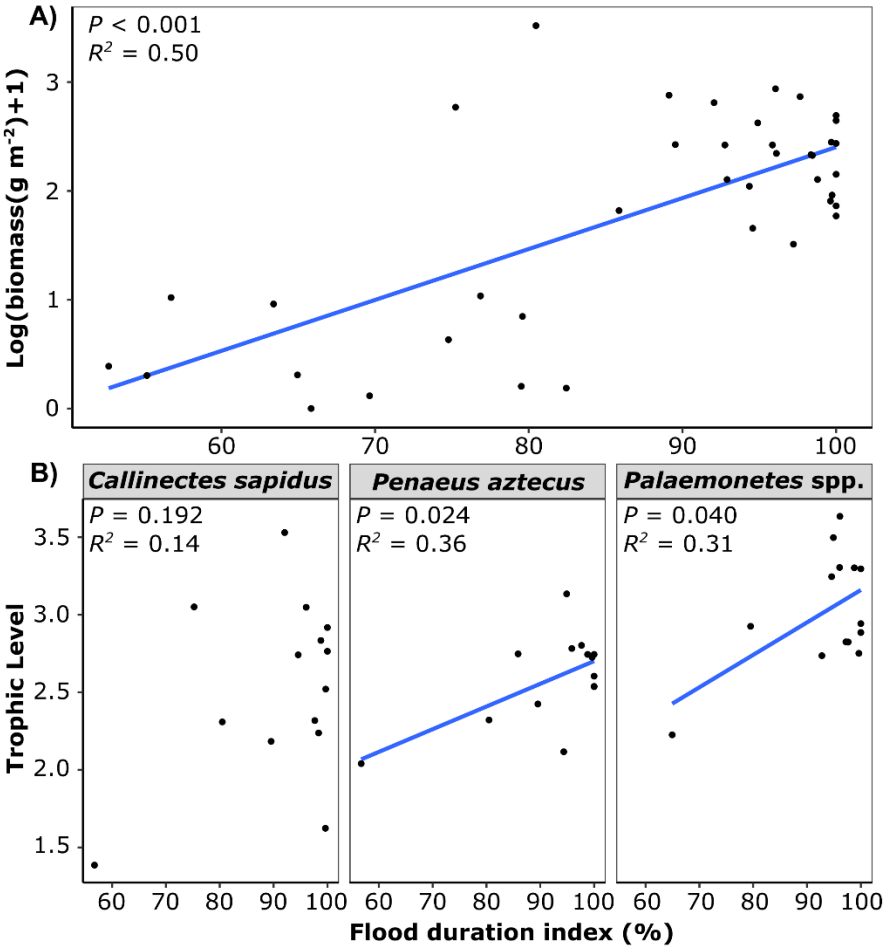

Figure 3.9: Relationship between macrofauna biomass (g m^{-2}) (A), decapod trophic levels (B), and flood duration index in restored and natural sites in spring and summer sampling periods in Nueces Bay, Texas

Table 3.1 Sediment and hydrographic data (mean ± standard error) from natural (Nat) and restored (Rest) marsh sites in spring and summer sampling periods in Nueces Bay, Texas. Sediment macrodetritus (> 500-μm) is represented in g dry weight m^{-2}, no data indicated with *hyphen*. Mean salinity and water temperature (temp.) values from samples at sites M2, R3 and M4.

	Marsh	**Spring 2014**	**Summer 2014**	**Winter 2015**	**Spring 2015**	**Summer 2015**
Sediment organic C (%)	Nat	0.81±0.27	0.45±0.13	-	0.46±0.15	0.52±0.11
	Rest	0.16±0.03	0.19±0.04	-	0.22±0.04	0.11±0.01
Sediment N (%)	Nat	0.10±0.03	0.05±0.01	-	0.06±0.01	0.06±0.01
	Rest	0.02±<0.01	0.02±0.01	-	0.03±0.01	0.01±<0.01
Sediment macrodetritus	Nat	218.5±57.5	50.6±18.8	-	49.4±16.9	53.1±17.8
	Rest	0.8±0.2	0.9±0.5	-	2.3±1.7	3.2±1.8
Salinity (psu)	Both	35.4±0.2	40.1±0.2	32.5±0.1	22.9±0.1	24.4±0.4
Temp. (˚C)	Both	26.8±0.8	30.7±0.8	12.0±0.3	27.8±0.7	30.3±1.0

Table 3.2: Total catch (*n*), species density (mean ± standard error, *n* m^{-2}) and dry weight biomass (mean ± standard error, g m^{-2}) in natural and restored marsh edge habitat in Nueces Bay, Texas

	Natural marsh			Restored marsh		
Species	***n***	***n* m^{-2} ±SE**	**g m^{-2} ±SE**	***n***	***n* m^{-2} ±SE**	**g m^{-2} ±SE**
Decapods						
Palaemonetes spp.	9797	32.66±5.13	0.74±0.11	10312	34.37±3.15	0.84±0.08
Penaeus aztecus	1041	3.47±0.7	0.52±0.09	697	2.32±0.35	0.32±0.05
Callinectes sapidus	308	1.03±0.29	0.28±0.18	86	0.29±0.06	0.23±0.12
Sesarma reticulatum	2	0.01±<0.01	<0.01±<0.01	0	0.00	0.00
Panopeidae	0	0.00	0.00	1	<0.01±<0.01	<0.01±<0.01
Fish						
Lucania parva	300	1±0.42	0.01±<0.01	0	0.00	0.00
Gobiosoma bosc	100	0.33±0.1	0.01±<0.01	96	0.32±0.08	0.01±<0.01
Cyprinodon variegatus	86	0.29±0.12	0.01±<0.01	5	0.02±0.01	<0.01±<0.01
Lagodon rhomboides	76	0.25±0.1	0.02±0.01	50	0.17±0.04	0.04±0.02
Fundulus grandis	24	0.08±0.03	0.01±<0.01	18	0.06±0.02	0.01±<0.01
Unidentified larval fish	16	0.05±0.03	<0.01±<0.01	1	<0.01±<0.01	<0.01±<0.01
Micropogonias undulatus	10	0.03±0.02	0.01±<0.01	0	0.00	0.00
Bairdiella chrysoura	6	0.02±0.01	<0.01±<0.01	0	0.00	0.00
Menidia beryllina	6	0.02±0.01	<0.01±<0.01	6	0.02±0.01	<0.01±<0.01
Syngnathus louisianae	5	0.02±0.01	<0.01±<0.01	8	0.03±0.01	<0.01±<0.01
Mugil sp.	4	0.01±0.01	<0.01±<0.01	9	0.03±0.01	<0.01±<0.01
Fundulus pulvereus	3	0.01±0.01	<0.01±<0.01	0	0.00	0.00
Strongylura marina	3	0.01±0.01	<0.01±<0.01	3	0.01±0.01	<0.01±<0.01
Adinia xenica	2	0.01±0.01	<0.01±<0.01	3	0.01±0.01	<0.01±<0.01
Leiostomus xanthurus	2	0.01±0.01	<0.01±<0.01	0	0.00	0.00
Syngnathus scovelli	2	0.01±<0.01	<0.01±<0.01	0	0.00	0.00
Centropristis philadelphica	1	<0.01±<0.01	<0.01±<0.01	0	0.00	0.00
Cynoscion nebulosus	1	<0.01±<0.01	<0.01±<0.01	2	0.01±<0.01	<0.01±<0.01
Alpheus heterochaelis	0	0.00	0.00	1	<0.01±<0.01	<0.01±<0.01
Etropus crossotus	0	0.00	0.00	2	0.01±<0.01	<0.01±<0.01
Larimus fasciatus	0	0.00	0.00	1	<0.01±<0.01	<0.01±<0.01
Membras martinica	0	0.00	0.00	4	0.01±0.01	<0.01±<0.01
Tozeuma carolinense	0	0.00	0.00	2	0.01±0.01	<0.01±<0.01

Table 3.3: Results of PERMANOVA and analyses of multivariate homogeneity of group dispersions (betadisper) comparisons of log(y+1) transformed multivariate community composition data between natural and restored marshes within each sampling period. Numerator and denominator degrees of freedom are given as subscript of *t*-values, significant *P*-values are indicated with *asterisk* ($\alpha = 0.05$).

Sampling period	**PERMANOVA**		**Betadisper**	
	t	***P*(perm)**	***t***	***P***
Spring 2014	$1.34_{(1,22)}$	0.118	$0.84_{(1,22)}$	0.408
Summer 2014	$2.65_{(1,22)}$	<0.001*	$5.59_{(1,22)}$	<0.001*
Winter 2015	$1.98_{(1,18)}$	0.009*	$1.52_{(1,18)}$	0.146
Spring 2015	$0.47_{(1,22)}$	0.096	$0.66_{(1,22)}$	0.519
Summer 2015	$2.22_{(1,22)}$	0.001*	$2.51_{(1,22)}$	0.020*

Table 3.4: $\delta^{13}C$ and $\delta^{15}N$ values (mean ± standard deviation) of potential food sources and consumers from restored and natural marsh sites during spring and summer sampling periods of 2014 and 2015 in Nueces Bay, Texas. If sample size (*n*) differs between elements, sample size for $\delta^{15}N$ measurement is given after comma.

Species / organic matter	***n***	**$\delta^{13}C$±SD (‰)**	**$\delta^{15}N$±SD (‰)**
Natural marsh			
Spring14			
Plant			
Avicennia germinans	2	-23.9±0.6	10.2±0.1
Batis maritima	3	-25.4±0.5	9.9±0.6
Batis maritima root	3	-26.0±1.3	9.1±0.8
Cladophora sp.	2	-20.2±0.2	7.1±0.7
Halodule wrightii	1	-11.2	6.4
Spartina alterniflora	3	-14.1±0.3	7.6±0.8
Spartina alterniflora root	3	-14.0±0.4	6.3±1.4
Spartina detritus	3	-14.5±1.1	5.8±0.9
Spartina epiphytic algae	5	-17.0±2.8	6.0±3.8
OM pool			
SPOM	4	-24.8±0.5	7.5±0.9
SSOM	4	-19.2±2.4	6.9±1.2
Sediment macrodetritus	2,4	-16.9±3.0	6.6±1.4
Other invertebrates			
Amphipod	3	-17.9±3.1	6.0±0.5
Isopoda	3	-20.0±1.0	8.6±0.6
Decapod			
Callinectes sapidus	3	-17.1±0.9	11.4±1.9
Penaeus aztecus	6	-15.4±1.4	11.8±1.4
Palaemonetes spp.	6	-15.1±0.6	13.3±1.5
Fish			
Cyprinodon variegatus	2	-11.8±0.2	8.5±0.5
Fundulus grandis	1	-17.0	12.5
Lagodon rhomboides	2	-17.4±1.7	13.5±0.5
Menidia beryllina	3	-14.7±1.0	15.2±1.3
Micropogonias undulatus	1	-13.9	15.3
Mugil sp.	3	-15.5±3.2	9.5±0.6
Strongylura marina	2	-18.3±0.5	11.9±0.2
Syngnathus louisianae	1	-16.4	11.4
Summer14			
Plant			
Batis maritima	3	-25.3±1.1	11.9±1.2
Halodule wrightii	3	-12.4±0.2	6.7±0.1
Halophila engelmannii	2	-13.0±0.9	7.5±0.1
Salicornia bigelovii	3	-26.4±0.7	9.0±0.6
Spartina alterniflora	3	-13.8±0.3	8.3±0.9

Spartina alterniflora root	3	-13.7±0.5	7.8±1.8
Spartina detritus	3	-14.0±0.9	2.7±0.5
Spartina epiphytic algae	3	-15.9±2.0	5.0±1.9
OM pool			
SPOM	4	-20.9±1.0	7.8±0.7
SSOM	4	-19.0±1.9	6.9±0.8
Sediment macrodetritus	4	-20.4±6.7	7.3±2.4
Other invertebrates			
Amphipod	2	-15.7±3.0	6.6±0.6
Cerithideopsis pliculosa	2	-12.2±2.4	7.7±0.6
Decapod			
Callinectes sapidus	3	-15.4±0.9	8.0±1.4
Penaeus aztecus	6	-13.7±0.8	10.2±1.3
Palaemonetes spp.	6	-14.3±1.6	12.0±2.3
Sesarma reticulatum	1	-14.5	5.5
Fish			
Cyprinodon variegatus	3	-11.9±1.8	9.9±1.2
Fundulus grandis	3	-14.7±1.9	12.2±0.1
Gobiosoma bosc	1	-17.3	14.5
Spring15			
Plant			
Batis maritima	3	-24.6±0.1	12.5±0.1
Spartina alterniflora	3	-14.0±<0.1	7.8±1.5
Spartina alterniflora root	4	-14.0±0.4	7.1±1.6
Spartina detritus	2	-13.9±0.2	8.1±0.0
Spartina epiphytic algae	3	-19.5±2.2	10.7±1.7
OM pool			
SPOM	4	-24.6±0.4	8.5±0.3
SSOM	4	-18.7±1.7	7.4±0.5
Sediment macrodetritus	3	-18.1±2.8	6.5±0.6
Other invertebrates			
Amphipod	3	-18.0±1.5	10.6±0.8
Isopoda	3	-20.4±2.3	10.8±0.4
Decapod			
Callinectes sapidus	3	-17.7±0.9	13.9±0.3
Penaeus aztecus	6	-16.2±0.9	13.3±0.5
Palaemonetes spp.	6	-14.1±0.5	15.6±0.5
Sesarma reticulatum	1	-18.5	10.8
Fish			
Fundulus grandis	1	-14.7	13.1
Gobiosoma bosc	2	-17.5±3.0	15.0±0.7
Lagodon rhomboides	3	-17.7±0.6	15.8±0.6
Micropogonias undulatus	3	-18.1±0.8	15.4±0.3
Mugil sp.	1	-17.3	8.6
Strongylura marina	2	-17.0±0.8	13.0±1.9

Syngnathus scovelli	1	-16.8	14.6
Summer15			
Plant			
Batis maritima	3	-29.1±0.6	6.4±0.3
Halodule epiphyte	3	-19.6±0.6	8.1±0.1
Halodule wrightii	3	-14.6±2.1	6.7±0.7
Salicornia bigelovii	3	-28.3±0.3	10.4±1.7
Spartina alterniflora	3	-13.3±0.3	7.9±1.7
Spartina alterniflora root	2	-13.1±0.1	6.6±1.3
Spartina detritus	2	-14.6±0.8	8.0±0.1
Spartina epiphytic algae	3	-16.6±2.8	4.9±4.9
OM pool			
SPOM	4	-23.5±0.8	9.1±0.7
SSOM	4	-19.1±1.5	7.5±0.4
Sediment macrodetritus	3	-23.1±2.3	6.6±1.0
Other invertebrates			
Amphipod	3	-17.3±0.6	10.9±0.7
Isopoda	1	-16.7	2.9
Decapod			
Callinectes sapidus	3	-18.8±1.8	11.1±2.6
Penaeus aztecus	5	-17.8±2.5	12.2±1.6
Palaemonetes spp.	5	-16.8±1.6	15.4±0.4
Fish			
Cyprinodon variegatus	3	-14.9±0.2	12.0±3.0
Fundulus grandis	2	-16.0±0.5	14.9±0.6
Gobiosoma bosc	3	-19.8±0.3	14.1±0.4
Menidia beryllina	2	-20.9±0.2	15.6±0.4
Syngnathus louisianae	2	-19.3±0.8	13.9±0.6
Syngnathus scovelli	1	-16.0	14.9
Restored marsh			
Spring14			
Plant			
Batis maritima	3	-24.3±1.2	8.3±0.6
Batis maritima root	1,3	-25.5	5.9±0.2
Cladophora sp.	4	-20.1±0.5	7.6±0.3
Spartina alterniflora	3	-14.2±0.6	7.7±0.6
Spartina alterniflora root	3,4	-14.9±1.4	7.1±0.9
Spartina detritus	1,3	-16.2	4.5±1.1
Spartina epiphytic algae	6	-15.5±2.2	3.2±1.4
OM pool			
SPOM	2	-25.2±1.0	8.6±0.0
SSOM	4	-22.0±3.8	6.9±0.7
Sediment macrodetritus	1	-16.2	8.0
Other invertebrates			
Amphipod	3	-17.3±1.5	6.2±0.9

Isopoda	2	-20.4±0.3	9.8±0.6
Decapod			
Callinectes sapidus	3	-17.2±1.3	11.1±1.2
Penaeus aztecus	6	-16.7±0.7	11.5±1.3
Palaemonetes spp.	6	-15.5±0.6	13.8±0.7
Fish			
Fundulus grandis	1	-15.7	12.7
Lagodon rhomboides	3	-18.2±1.2	14.7±1.3
Menidia beryllina	2	-16.6±1.7	13.3±1.9
Mugil sp.	3	-15.9±3.3	9.8±1.9
Summer14			
Plant			
Cladophora sp.	3	-19.7±0.1	8.2±0.4
Spartina alterniflora	2	-13.1±0.5	7.8±1.0
Spartina alterniflora root	3	-13.6±0.7	6.9±2.2
Spartina detritus	2	-14.1±0.2	4.7±1.2
Spartina epiphytic algae	3	-12.0±1.3	2.2±1.9
OM pool			
SPOM	2	-22.0±0.3	9.0±0.1
SSOM	4	-23.3±3.6	6.7±0.6
Sediment macrodetritus	4	-16.2±4.2	6.8±0.3
Other invertebrates			
Amphipod	3	-17.0±0.7	8.8±1.1
Isopoda	1	-19.3	10.0
Decapod			
Callinectes sapidus	3	-16.3±1.2	13.3±1.3
Penaeus aztecus	3	-15.3±0.0	12.0±0.7
Palaemonetes spp.	6	-15.7±0.8	13.7±0.6
Panopeidae	1	-18.7	10.1
Fish			
Cyprinodon variegatus	1	-12.2	9.3
Etropus crossotus	2	-16.8±0.0	14.1±0.6
Fundulus grandis	3	-15.5±0.3	13.2±0.9
Gobiosoma bosc	3	-18.2±1.0	14.2±0.4
Lagodon rhomboides	1	-16.0	12.5
Spring15			
Plant			
Cladophora sp.	3	-19.6±0.2	16.5±1.0
Spartina alterniflora	3	-14.0±0.1	7.4±1.1
Spartina alterniflora root	3	-14.2±0.8	7.1±1.9
Spartina detritus	1	-13.4	3.4
Spartina epiphytic algae	3	-18.8±2.4	11.5±1.9
OM pool			
SPOM	2	-24.4±0.2	9.6±0.0
SSOM	4	-20.7±2.2	7.4±1.2

Sediment macrodetritus	2	-13.5±1.0	6.2±0.2
Other invertebrates			
Amphipod	3	-16.7±1.4	12.2±1.9
Isopoda	3,2	-18.4±1.1	11.8±1.5
Decapod			
Callinectes sapidus	1	-18.4	13.2
Penaeus aztecus	6	-17.3±1.1	13.4±0.2
Palaemonetes spp.	6	-14.7±0.3	14.5±0.7
Fish			
Cynoscion nebulosus	2	-17.6±0.3	16.3±0.1
Gobiosoma bosc	1	-15.0	15.3
Lagodon rhomboides	3	-18.1±0.5	15.8±0.5
Menidia beryllina	3	-19.1±2.0	10.4±2.6
Mugil sp.	3	-14.2±1.1	13.3±0.5
Strongylura marina	2	-17.1±0.9	15.0±2.8
Syngnathus louisianae	3	-17.6±0.1	14.6±0.5
Summer15			
Plant			
Spartina alterniflora	3	-12.6±0.3	8.6±0.8
Spartina alterniflora root	3	-13.7±0.2	7.7±0.3
Spartina detritus	3	-13.5±0.9	5.2±0.7
Spartina epiphytic algae	3	-14.9±2.9	4.4±4.6
OM pool			
SPOM	2	-23.4±0.0	9.2±0.4
SSOM	4	-22.0±1.2	7.2±0.7
Sediment macrodetritus	2	-14.1±3.4	6.3±2.4
Other invertebrates			
Amphipod	1	-19.5	9.8
Isopoda	1	-21.6	13.0
Decapod			
Callinectes sapidus	3	-17.5±1.8	10.6±1.5
Penaeus aztecus	5	-20.1±0.8	12.9±1.9
Palaemonetes spp.	6	-18.1±1.1	13.0±1.2
Fish			
Fundulus grandis	2	-17.7±0.3	13.2±1.0
Gobiosoma bosc	2	-20.3±0.8	14.4±1.3

Table 3 5: Estimated source dietary contribution (%) with upper/lower bounds of 95% credibility intervals (in parentheses) for decapod consumers from natural and restored marshes over the course of the study.

Sampling period	SPOM	Benthic diatoms	*Spartina* epiphytes	*Spartina*
Natural Marsh				
Palaemonetes spp.				
spring14	9(2/24)	19(3/52)	16(2/48)	52(15/77)
summer14	9(2/32)	13(2/51)	19(2/67)	51(9/82)
spring15	8(1/35)	16(3/41)	15(2/40)	58(16/82)
summer15	27(7/48)	29(5/60)	14(3/41)	26(6/55)
Penaeus aztecus				
spring14	9(2/25)	18(3/54)	16(2/51)	52(14/79)
summer14	6(1/23)	10(1/36)	15(2/51)	65(25/87)
spring15	13(2/32)	20(4/43)	19(4/41)	46(17/68)
summer15	27(5/53)	26(4/68)	20(3/56)	19(3/54)
Callinectes sapidus				
spring14	18(3/45)	24(3/68)	21(3/62)	28(4/65)
summer14	12(2/43)	17(3/57)	22(3/68)	40(5/73)
spring15	22(4/53)	23(4/56)	21(4/57)	28(4/58)
summer15	31(5/63)	21(3/68)	20(2/62)	15(2/53)
Restored Marsh				
Palaemonetes spp.				
spring14	13(3/28)	19(3/48)	21(4/43)	45(19/69)
summer14	31(11/48)	21(4/50)	24(6/42)	22(5/46)
spring15	9(2/27)	16(3/41)	17(3/38)	56(19/79)
summer15	38(19/54)	27(5/54)	16(3/37)	17(4/38)
Penaeus aztecus				
spring14	16(4/30)	24(4/59)	19(3/45)	38(10/64)
summer14	24(4/49)	22(3/62)	23(4/51)	25(4/62)
spring15	21(5/40)	23(5/47)	21(4/43)	34(9/57)
summer15	54(23/73)	19(3/51)	13(2/37)	10(2/29)
Callinectes sapidus				
spring14	19(3/43)	24(3/68)	20(3/55)	29(4/67)
summer14	28(5/56)	25(3/67)	19(3/46)	21(3/59)
spring15	25(4/54)	24(4/61)	20(3/59)	23(3/57)
summer15	26(4/56)	25(3/70)	19(3/55)	20(3/59)

CHAPTER IV: STRUCTURAL AND FUNCTIONAL SIMILARITY OF EPIBENTHIC COMMUNITIES ON STANDING AND REEFED OIL AND GAS PLATFORMS IN THE NORTHWESTERN GULF OF MEXICO

Abstract

Offshore oil and gas platforms are an important habitat for fish and invertebrate species in the northwestern Gulf of Mexico, and are among the most productive systems per area of ocean due to their vertical relief. To mitigate the loss of habitat when active platforms are decommissioned, Rigs-to-Reefs programs maintain existing communities by removing the upper 26-m of platform structure and converting upper and lower portions into artificial reefs. We examined the epibenthic communities of two standing platforms at 5-m and 30-m depths and three reefed platforms at 30-m depths. A combination of stable isotope and community analysis was used to assess the structure and food web functioning of epibenthic communities among these site-types. Reefed platforms (30-m) supported communities with similar food web structure as 5-m and 30-m standing platform communities. However, community composition in standing platform and reefed platform sites at 30-m differed from those of standing platform sites at 5-m depths. Results indicate that, although loss of shallow water habitat associated with platform reefing may diminish some aspects of biodiversity, reefed platforms support similar fundamental ecological functions as standing platforms in the Gulf of Mexico.

Introduction

Artificial reefs have been employed across a variety of coastal and marine habitats for fisheries enhancement, ecological restoration, and recreational purposes (Bohnsack and Sutherland 1985; Buckley and Hueckel 1985; Baine 2001; Seaman 2007). Fossil fuel extraction in the Gulf of Mexico (hereafter "GOM") currently involves the use of ~2100 active oil and gas

production platforms (hereafter "platforms"; www.bsee.gov), constituting the largest *de facto* artificial reef system in the world (Dauterive 2000; Shipp and Bortone 2009). Platforms and other artificial reef structures provide a number of ecological functions, including support for diverse assemblages of epibenthic invertebrates (Gallaway and Lewbel 1982; Lewbel et al. 1987; Pickering and Whitmarsh 1997) and provision of food and refuge for a variety of fish species (Nelson & Bortone 1996, Beaver et al. 1997, Rooker et al. 1997, Szedlmayer & Lee 2004, Ajemian et al. 2015, Streich, et al. 2017a). Platforms are among the most productive marine fish habitats on earth, primarily due to the high ratio of structural surface area per area of seafloor (Claisse et al. 2014).

A large number of platforms are reaching the end of their productive lifespans, resulting in a predicted loss of 29% of platforms in the GOM between 1999 and 2023 (Pulsipher et al. 2001) and a substantial loss of complex marine habitat. To mitigate habitat loss, state-run Rigs-to-Reef programs repurpose decommissioned platforms into permitted artificial reefs. Current reefing guidelines require reefed platforms to maintain 26-m of clearance to avoid navigational hazards to large vessels. This is accomplished by: (1) partial platform removal; (2) toppling the structure in place; or, (3) toppling the structure after towing to an approved reefing site (Kaiser and Pulsipher 2005; Macreadie et al. 2011). As of 2015, 470 platforms have been converted to artificial reefs through Rigs-to-Reef programs in the GOM (www.bsee.gov). The conversion of platforms into artificial reefs substantially alters the structure of these habitats, resulting in a structure with lower relief and no physical connection with substrate in the upper water column. The effect of this physical transformation on platform-associated epibenthic communities in the GOM is not well known. As decommissioned platforms are increasingly converted into artificial

reefs, it is important evaluate the effectiveness of Rigs-to-Reef programs in preserving the communities and food webs that standing platforms support.

Stable isotope analysis is a powerful tool for investigating organic matter flows and trophic structure in marine ecosystems. The isotopic composition of carbon in primary producer tissues is influenced by their photosynthetic pathway and inorganic carbon source, and changes little with trophic transfers. This allows the carbon isotopic composition of consumer tissue to be traced back to its primary producer origins (DeNiro and Epstein 1978; Peterson and Fry 1987). The isotopic composition of nitrogen undergoes a predictable step-wise enrichment in ^{15}N with trophic transfers (2 to 4‰), which allows the evaluation of consumer trophic levels (Post 2002). Together, the isotopic compositions of carbon and nitrogen can be used to construct a time-integrated biochemical outline of organic matter pathways within food webs. Because of these properties, stable isotopes of C and N have been successfully employed to study trophic structure and ecological functions provided by food webs in artificial marine habitats (Daigle et al. 2013; Cresson et al. 2014; Rezek et al. 2017; Blomberg et al. 2017b).

In this study, we compare the structure and food web function of three artificial reef epibenthic communities by platform type and depth to evaluate the ability of current reefing practices to replace the habitat lost when platforms are removed or modified. To this aim, we compare: 1) the structure and the functioning of deep (30-m; i.e. lower than the 26-m guideline) communities from reefed platforms and standing platforms with shallow standing platform communities (5-m) to determine the effects of removing of the highest sections of platforms; and 2) the structure and functioning of deep (30-m) standing platform communities with reefed platforms (30-m) communities. To accomplish this, we employ a combination of traditional community analysis (macrofauna density, biomass, multivariate analysis) with stable isotope

based food web analysis. The results of this study will provide important information for resource managers to improve reefing practices with the goal of preserving the unique and diverse communities inhabiting platforms in the GOM.

Methods

Field sampling

Three reefed platforms (RP-A: BA-A-132A, RP-B: MU-A-85B, RP-C: MI-A-7A) and two standing platforms (SP-A: BA-A-133A, SP-B: MU-A-85A) were sampled within a study area located ~75 km off the Texas coast in the northwestern GOM (Fig. 4.1), at bottom depths ranging from 60 to 83 m (Table 4.1). All structures sampled were composed of conventional fixed steel jacket platforms. SCUBA divers sampled the epibenthic community on each structure by scraping ~20 cm x 20 cm (0.04 m^2) areas with hand tools and collecting all material in fine-mesh (< 1-mm) bags. Standing platforms were sampled at two depths (5-m and 30-m; hereafter SP5 and SP30, respectively) and reefed platforms were sampled at 30-m (near the top of the structure; hereafter RP30). Three replicate samples were taken from each site-type (i.e. structure type-depth combination). RP-A, RP-B and both standing platforms were sampled on June 5th, July 2nd, and October 15th of 2014, respectively, in conjunction with cruises for related studies (Streich 2017b). RP-C was sampled on August 10th, 2013 and again on July 14th, 2014—samples from the 2013 visit were not used for stable isotope analysis but were included in community analyses. Depth profiles of salinity and chlorophyll *a* concentration were measured during separate cruises within the study period (June 11th, July 29th, September 8th, and October 1st of 2014) with ~ 45 m vertical casts of a Hydrolab® DS5 sonde adjacent to RP-A and RP-C.

Water samples for stable isotope analyses of suspended particulate organic matter (SPOM) were collected at 5- and 30-m depths at each structure using a Van Dorn bottle and

sieved through a 250-µm screen to remove large zooplankton and particles. Epibenthic samples for community and stable isotope analyses were collected from separate jackets (legs) on structures. The sampled area was photographed with an Intova® Sport HD II underwater camera along with a scale. These photos were then analyzed with the image analysis software ImageJ® to obtain precise estimates of the area removed for areal macrofauna biomass and density calculations (Schneider et al. 2012). The trapezoid perimeter encompassing removed areas was measured with meter tape and used to calculate sample areas for the 2014 visit of RP-C due to camera loss. Grey triggerfish (*Balistes capriscus*) were opportunistically collected with spears for stable isotope analysis. Water samples were kept on ice and epibenthic community samples were kept in aerated seawater during transport to the laboratory (i.e. no longer than 10 hours).

Sample preparation for stable isotope analyses

Between 500 and 1500 ml of water were filtered through pre-combusted (4 hours, 450 °C) Whatman GF/F filters (0.7-µm nominal pore size) for analysis of SPOM. Oyster shell organic matter (OSOM) was collected by lightly brushing the shell surfaces of the dominant reef building taxa (*Hyotissa mcgintyi*) into artificial seawater. Collected material was sieved through a 250-µm screen to remove large particles and filtered through pre-combusted Whatman GF/F filters. Flora and macrofauna from epibenthic community samples were sorted and subsets of individuals of each taxon (3 or more if available) were selected. Red algae (Rhodophyta) were separated into three groups: Corallinaceae (articulated coralline algae), red macroalgae (mixed Rhodomelaceae and Gracilariaceae), and filamentous red algae. Among consumer taxa, corals, bivalves, barnacles, and small decapods (less than ~10 mm length) were kept alive in aerated artificial seawater for 24 hours to evacuate gut contents and then stored at -20 °C. Other taxa (i.e. large motile macrofauna) were frozen the same day of collection. For starved taxa, calcareous

shells were removed, and entire individuals were used for analysis. Muscle tissue was analyzed in large motile macrofauna.

All samples were freeze-dried. Flora and fauna samples were ground into a homogeneous powder with a ball mill (MM 400, Retsch). Samples potentially containing carbonates were acidified. SPOM and OSOM filters were decarbonated by contact with HCl fumes under light vacuum for 4 hours. Tissue samples containing carbonates were decarbonated with 1 mol l^{-1} HCl and dried at 55 °C. $\delta^{15}N$ and $\delta^{13}C$ measurements were carried out on raw and acidified samples, respectively, to avoid bias on $\delta^{15}N$ values due to acidification. Sample powders were precisely (±1 µg) weighed with a microscale (ME 5, Sartorius) and encapsulated in combustion cups for analysis.

Stable isotope analyses

Carbon and nitrogen isotopic compositions were determined using an elemental analyzer (ECS 4010, Costech) connected to a continuous flow isotope ratio mass spectrometer (Delta V Plus, Thermo Scientific) through a Conflo IV interface (Thermo Scientific) at the Texas A&M University-Corpus Christi Isotope Core Laboratory. Isotopic compositions are given in delta (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: $\delta X\ (‰) = [(R_{sample}/R_{standard}) - 1] \times 10^3$, where X is ^{13}C or ^{15}N and R is $^{13}C/^{12}C$ or $^{15}N/^{14}N$, respectively. Two-point calibration was performed with L-glutamic acid reference materials (USGS-40 and USGS-41). Methionine standards (Costech) were analyzed after every 12 samples to monitor instrument performance. Analytical precision was ± 0.2 ‰ for carbon and nitrogen based on repeated measurements of standards.

Sample preparation for community analysis

Macrofauna were fixed in buffered 10% formalin and then stored in 70% ethanol. Animals were enumerated and identified to the lowest practical taxonomic level. They were then dried for 48 hours at 55 °C, weighed (± 0.1 mg), and combusted at 450 °C for 4 hours to obtain ash free dry weight (AFDW) biomass. Ahermatypic cup coral density was assessed with polyp counts.

Data analysis

Differences in sessile and motile macrofauna density and AFDW biomass between site-types (i.e. SP5, SP30, and RP30) were analyzed with mixed effects one-way analysis of variance (ANOVA) tests with site as a random effect, using the nlme package in R (Pinheiro et al. 2015; R Development Core Team 2016). ANOVA models were fit using procedures described in Zuur et al. (2009). Residual normality and homoscedasticity assumptions were assessed with Shapiro–Wilk tests and normalized residual *vs*. fitted value plots, respectively. Models were compared and selected based on corrected Akaike information criterion (AICc) (Hurvich and Tsai 1989). Post hoc analysis was conducted with Westfall's modification of Tukey's HSD test (Westfall 1997) using the multcomp R package (Hothorn et al. 2008). Community structure was compared between site-types with non-parametric permutational multivariate analysis of variance (PERMANOVA; permutations = 9,999; Anderson 2001) tests on Hellinger distance matrix (Legendre and Gallagher 2001) of multivariate community abundance data with the adonis function in the R package vegan (Oksanen et al. 2016). Multiple PERMANOVA comparisons were corrected with Bonferroni *P*-value adjustments. The relationship between multivariate community composition and sites was presented with non-metric multidimensional scaling (nMDS) plots.

The $\delta^{13}C$ and $\delta^{15}N$ values of potential food sources were compared between site-types and each other using Wilcoxon rank-sum tests and Kruskal-Wallis tests. Post-hoc analysis for Kruskal-Wallis tests were conducted with Dunn's tests using the dunn.test R package (Dunn 1964; Dinno 2016) with Bonferroni *P*-value corrections for multiple comparisons. To detect community-wide shifts in isotope values, differences in isotope values of co-occurring taxa between site-types were compared with a stratified bootstrap paired test on mean differences (Konietschke and Pauly 2014). Confidence intervals for the average difference in isotope values of paired co-occurring taxa between sites were generated by bootstrapping isotope values within each consumer species/taxon (4,999 resamples) using the boot R package (Canty and Ripley 2016). Bonferroni adjustments were applied to 95% confidence intervals to obtain family-wise 95% confidence intervals for multiple comparisons. Confidence intervals (95%) for the mean of differences in isotope values of co-occurring taxa between site-types that did not include 0 were considered significantly different.

Consumer isotopic heterogeneity, a proxy for trophic diversity, was compared between site-types by analyzing variance among consumer mean $\delta^{13}C$ and $\delta^{15}N$ values with Levene's tests. Levene's test was also used to compare the variance of food source isotope values that were found in all site-types (SPOM, OSOM and Corallinaceae) to validate the assumption that between-site-type differences in consumer isotopic heterogeneity would reflect trophic variation, rather than potential between-site-type differences in the isotopic variance among food sources.

Results

Hydrological conditions

Salinity was relatively low in surface waters during June 2014, with average salinities of 32.6 ppt from 0 to 10 m, 32.7 ppt from 10 to 20 m and 34.1 ppt from 20 to 30 m (Fig. 4.2a).

Average salinity values from all other 10 m intervals during other hydrological sampling periods remained between 35.4 and 36.3 ppt and showed little variation with depth. Chlorophyll *a* concentration in surface waters were the greatest during June 2014, with mean concentrations of 0.22 μg l^{-1} between 0- and 10-m depths, and 1.62 μg l^{-1} between 20- and 30-m depths (Fig. 4.2b). For comparison, the greatest mean chlorophyll *a* concentration from July through October were 0.13 and 0.34 μg l^{-1} from 0 to 10-m and 20 to 30-m depths, respectively. In July through October, greatest chlorophyll *a* concentration occurred in 40 to 50-m depths, ranging from 0.48 to 2.10 μg l^{-1} (Fig. 4.2b).

Community analysis

Forty reef resident macrofauna taxa were identified from collections (Table 4.2, Table 4.3). Total macrofauna density (sessile and motile) ranged from 3960 ± 553 to 4584 ± 1199 *n* m^{-2} and were similar between site-types (ANOVA; $F_{2,17} = 0.4$, $P = 0.67$; Fig. 4.3a). Total macrofauna biomass (sessile and motile) ranged from 186.2 ± 13.0 to 330.4 ± 52.9 g m^{-2} and did not differ between site-types (ANOVA; $F_{2,17} = 0.4$, $P = 0.67$; Fig. 4.3a). Sessile macrofauna densities ranged from 3115 ± 429 to 3912 ± 1106 *n* m^{-2} and were similar between the three site-types (ANOVA; $F_{2,17} = 0.2$, $P = 0.85$; Fig. 4.3a). Sessile macrofauna biomass ranged from 172.7 ± 13.9 to 322.9 ± 50.1 g m^{-2} and were similar between site-types (ANOVA; $F_{2,17} = 0.9$, $P = 0.420$; Fig. 4.3c). Barnacles accounted for < 0.01% of total biomass (0.0042 g AFDW per individual; based on a subsample of 33) and were not included in community biomass analysis. Motile macrofauna density was greater in SP5 sites (1107 ± 83 *n* m^{-2}) than in SP30 (672 ± 115 *n* m^{-2}) and RP30 (677 ± 186 *n* m^{-2}) sites (ANOVA; $F_{2,17} = 6.1$ $P = 0.01$; Fig. 4.3b). Mean motile macrofauna biomass ranged from 13.4 ± 1.3 to 7.5 ± 3.1 g m^{-2} and did not differ between site-types (ANOVA; $F_{2,17} = 1.5$, $P = 0.25$; Fig. 4.3d).

Macrofauna community structure in SP5 sites differed from communities in SP30 and RP30 sites (PERMANOVA; SP5 vs. SP30: $t_{1,10} = 4.6$, $P < 0.01$; SP5 vs. RP30: $t_{1,16} = 3.5$, $P < 0.01$) (Fig. 4.4). Communities on standing and reefed platform sites at 30-m were similar (PERMANOVA; $t_{1,16} = 0.7$, $P = 1.00$). The sessile macrofauna community in SP5 sites were characterized by relatively high densities of tree oysters (*Isognomon* spp.) and relatively low densities of orange cup coral polyps (*T. coccinea*) in comparison to 30-m sites (Fig. 4.5a, Table 4.2). Motile macrofauna communities in SP5 sites had higher densities of the brittle star *Ophiactis savignyi* and sipunculid worms in comparison to sites at 30-m (Fig. 4.5b).

The bivalve *H. mcgintyi* was the greatest contributor to the community biomass in all sites (Fig. 4.6, Table 4.2), on average composing 73% of the SP5 (137.4 g m^{-2}), 77% of SP30 (250.8 g m^{-2}), and 57% of the RP30 biomass (187.3 g m^{-2}). Cup corals were the second greatest contributor to biomass at 30-m sites in both standing and reefed platforms; accounting for 16% of the SP30 biomass (54.3 g m^{-2}) and 34% of the RP30 biomass (113.2 g m^{-2}). Corals did not contribute substantially to SP5 biomass (< 1%). The bivalves *Chama macrophylla* and *Isognomon* spp. represented 10% (18.4 g m^{-2}) and 3% (5.9 g m^{-2}) of the SP5 biomass, respectively. These taxa contributed relatively little to SP30 and RP30 biomass (*C. macrophylla* = 1%; *Isognomon* spp. = < 1%).

Stable isotope data

SPOM $\delta^{13}C$ and $\delta^{15}N$ values were similar between 5-m and 30-m depths (Wilcoxon tests; $\delta^{13}C$: W = 8, $P = 0.42$; $\delta^{15}N$: W = 11, $P = 0.84$). SPOM (pooled 5-m/30-m) $\delta^{13}C$ values (-24.2 ± 0.6‰) did not differ between standing and reefed platform (Wilcoxon test; W = 11, $P = 0.91$), however, $\delta^{15}N$ values were lower at standing platforms (5.0 ± 1.1‰) than at reefed platforms (6.0 ± 1.2‰) (Wilcoxon test; W = 24, $P = 0.01$) (Fig. 7). OSOM $\delta^{13}C$ values (-21.4 ± 0.9‰)

were similar between site-types (Kruskal-Wallis test; $\chi^2 = 5.7$, $P = 0.06$); $\delta^{15}N$ values were lower at SP30 (4.0 ± 1.1‰) than at RP30 (6.2 ± 0.4‰) (Kruskal-Wallis test; $\chi^2 = 7.3$, $P = 0.03$).

Corallinaceae were the only macroalgae found at all sites-types (i.e. SP5, SP30, RP30), with $\delta^{13}C$ values and $\delta^{15}N$ values ranging from -25.9 to -22.4‰ and 3.2 and 6.4‰, respectively. Only one Corallinaceae sample was collected from SP30 sites, so RP30 samples were compared with SP5 samples. Corallinaceae $\delta^{13}C$ values were similar between RP30 and SP5 sites (-23.3 ± 1.5‰) (Wilcoxon test; W = 18, $P = 0.73$); $\delta^{15}N$ values were lower in SP5 sites (3.8 ± 0.5‰) than RP30 sites (5.4 ± 0.5‰) (Wilcoxon test; W = 42, $P < 0.01$). Other macroalgae were found sporadically. Filamentous red algae—found on SP5 and RP30 sites—had the lowest $\delta^{13}C$ values of all potential food sources (-31.3 ± 0.4‰) and had relatively low $\delta^{15}N$ values (2.5 ± 0.5‰) (Fig 7). $\delta^{13}C$ values of red macroalgae (found in SP5 and RP30 sites) ranged from -26.1 to -17.6‰. *Dictyota* sp. (found in RP30 sites) was relatively enriched in ^{13}C ($\delta^{13}C$: -19.7 ± 0.5‰) and had the lowest $\delta^{15}N$ values (1.4 ± 0.4‰) of any macroalgae. *Sargassum* sp. had the highest mean $\delta^{13}C$ value (-16.3 ± 0.3‰), and was found floating on surface waters around platforms. OSOM was more ^{13}C enriched than Corallinaceae and SPOM, which had similar $\delta^{13}C$ values; red macroalgae had highly variable $\delta^{13}C$ values and did not differ significantly from these sources (Kruskal-Wallis test; $\chi^2 = 8.5$, $P = 0.01$). SPOM and OSOM $\delta^{15}N$ values were greater than those of red macroalgae (Kruskal-Wallis test; $\chi^2 = 11.1$, $P = 0.01$).

Sessile filter feeders had mean $\delta^{13}C$ values ranging from -21.9 to -18.9‰ in SP5 sites (9 taxa), from -24.0 to -18.5‰ in SP30 sites (11 taxa), and from -25.1 to -19.6‰ in RP30 sites (14 taxa) (Fig. 7). Motile consumers mean $\delta^{13}C$ values ranged from -21.4 to -16.0‰ in SP5 sites (11 taxa), from -21.6 to -18.8‰ in SP30 sites (8 taxa), and -22.3 to -18.3‰ on RP30 sites (13 taxa). Fish had mean $\delta^{13}C$ values ranging from -19.8 to -19.2‰ in SP5 sites (2 taxa), of -19.0‰ in

SP30 sites (1 taxa), and from -20.2 to -18.5‰ on RP30 sites (2 taxa). Sessile filter feeders mean $\delta^{15}N$ values ranged from 3.8 to 8.9‰ in SP5 sites, from 3.2 to 8.1‰ in SP30 sites, and 5.3 to 9.2‰ in RP30 sites. Motile taxa mean $\delta^{15}N$ values ranged from 5.7 to 10.1‰ in SP5 sites, from 4.1 to 9.1‰ in SP30 sites, and from 6.6 to 10.4‰ in RP30 sites. Fish $\delta^{15}N$ values ranged from 8.5 (*Scorpaena plumieri*, RP30) to 12.3‰ (*Hypsoblennius invemar*, SP5).

$\delta^{13}C$ values of co-occurring taxa ($n = 14$) were on average 0.8‰ higher in SP5 sites than in RP30 sites (paired bootstrap comparison; upper, lower 95% CI = -1.1‰, -0.5‰; Fig. 8a) and 1.0‰ higher in SP5 sites than in RP30 sites (paired bootstrap comparison: upper, lower 95% CI = -1.3‰, -0.7‰). $\delta^{15}N$ values of co-occurring taxa were on average 0.5‰ lower in SP5 sites than in RP30 sites (Fig. 8b, paired bootstrap comparison: upper, lower 95% CI = 0.8‰, 0.2‰) and 0.7‰ lower in SP30 sites than in RP30 sites (paired bootstrap comparison: upper, lower 95% CI = 1.1‰, 0.3‰). Co-occurring taxa had similar $\delta^{13}C$ values and $\delta^{15}N$ values between 5-m (SP5) and 30-m (SP30) platforms sites (paired bootstrap comparisons: $\delta^{13}C$: mean = -0.2‰; upper, lower 95% CI = -0.5‰, 0.1‰; $\delta^{15}N$: mean = 0.2‰; upper, lower 95% CI = -0.2‰, 0.6‰).

Variance among co-occurring food source isotope values did not differ between site-types (Levene's tests; $\delta^{13}C$: $F_{2,33} = 0.7$, $P = 0.51$; $\delta^{15}N$: $F_{2,33} = 0.1$, $P = 0.93$). The variance among mean consumer taxa $\delta^{13}C$ values were similar between all site-types (Levene's test; $F_{2,65} = 0.7$, $P = 0.52$). The variance among mean consumer taxa $\delta^{15}N$ values were also similar between site-types (Levene's test; $F_{2,65} = 0.7$, $P = 0.49$).

Discussion

Community structure differs with depth, but not among structures

The sessile communities on the standing and reefed platforms assessed in this study were dominated by bivalves, a characteristic of offshore platforms previously surveyed in the GOM. *H. mcgintyi* was the most important reef building bivalve on all reefed and standing platform site-types surveyed, with *C. macerophylla* and *Isognomon* spp. contributing secondarily to bivalve biomass. Bivalve community structure on platforms and reefed platforms were comparable to those of offshore platforms near Louisiana (Gallaway et al. 1981, Lewbel et al. 1987), indicating these species are widely distributed on platform-like structures throughout the northwestern GOM. However, the identity of the dominant reef building bivalve species may vary, with some platform communities reportedly dominated by *C. macrophylla* (Gallaway et al. 1981; Lewbel et al. 1987).

Nearly all motile macrofauna identified in this survey have been collected on offshore platforms near Louisiana (Gallaway et al. 1981, Lewbel et al. 1987, Daigle et al. 2013), indicating that motile macrofauna assemblages may be relatively homogenous throughout offshore platforms in the northwestern GOM. The rough rubble crab (*P. agassizi*) is a dominant decapod species on platform-like structures in the GOM, with densities of 372 *n* m^{-2} measured in this study comparable to those previously reported on offshore platforms (up to 496 *n* m^{-2}, Gallaway et al. 1981; 336 *n* m^{-2}; Lewbel et al. 1987). Blenny density in SP5 sites were similar to those reported on other platforms at the same depth (7.9 *n* m^{-2}, Rauch 2004). A single post-larval spotted scorpionfish (*Scorpaena plumieri*, total length = 14.2 mm) was collected from RP-B, indicating that the complex interstitial space created by sessile macrofauna on offshore structures may provide settlement and nursery habitat for some fisheries species.

These results demonstrate that platforms provide similar deep-water habitat after they are transformed into artificial reefs. However, community variation between 5-m and 30-m sites indicate that current reefing practices result in the loss of unique shallow water communities. Although no significant differences were found between community biomass among site-types, possibly related to high variability, greater average biomass values found in 30-m sites indicate that *T. coccinea* may increase the overall biomass in deep epibenthic communities. Macrofauna community structure in SP5 sites were dissimilar from communities on SP30 and RP30 sites, indicating that depth is a major driver affecting community structure on offshore structures. These observations are consistent with previously documented vertical zonation patterns on offshore platforms. Relatively greater densities of *Isognomon* spp. bivalves and the ophiuroid *O. savignyi* were also found in shallower depths by Lewbel et al. (1987) (for 10-/30-m depths: *Isognomon bicolor:* 128/0 *n* m^{-2}, *O. savignyi:* 9472/432 *n* m^{-2}), and relatively greater densities of non-native coral *T. coccinea* were also found in deeper depths by Sammarco et al. (2014) (peak abundance at 35- to 40-m depths). The similarities between macrofauna community composition, density, and biomass between platforms and reefed platforms at 30-m indicate that comparable communities are able to develop at this depth regardless of physical links to shallow substrate.

Food web structure

Stable isotope data indicated that OSOM was an important food source for epibenthic macrofauna inhabiting these structures. Mean overall macrofauna taxa $\delta^{13}C$ values fell within a range from -21.4 to -17.4‰ (except for encrusting tunicates). SPOM $\delta^{13}C$ values found in this study (-24.2‰) were relatively low in comparison to macrofauna consumers. Macrofauna $\delta^{13}C$ values more closely resembled those of OSOM (-21.7‰), suggesting that, at the community scale, this resource had a high role in the food web functioning. It is possible that attached

benthic microalgae, bacteria, and trapped pelagic detritus contained in OSOM are consumed by suspension feeders after resuspension (Doi et al. 2008; Fukumori et al. 2008) and by motile consumers in these habitats.

The lower abundance of pelagic resources in this region may result in a greater reliance of platform communities on autochthonous epilithic production. These results differ from a stable isotope based food web study of offshore standing platforms in Louisiana waters conducted by Daigle et al. (2013). Although they found a similar range of macrofauna $\delta^{13}C$ values (-21.5 to -17.6‰), they found higher $\delta^{13}C$ values for SPOM (-20.8 to -19.7‰) and shell-attached microalgae (-18.7 to -15.8‰), indicating SPOM was the most important food source for platform consumers. These divergent results may reflect functional variation associated with regional differences in the availability (i.e. quality/quantity) of pelagic resources between the highly productive, Mississippi river influenced, Louisiana continental shelf (e.g. chlorophyll *a* concentrations from 5 to10 μg l^{-1}; Salmerón-García et al. (2011)) and relatively oligotrophic Texas shelf waters in the study area (chlorophyll *a* from 0.13 to 1.62 μg l^{-1}).

Several macroalgae had $\delta^{13}C$ values near or within OSOM $\delta^{13}C$ value range (e.g. red macroalgae: -22.2‰, *Dictyota* sp.: -19.7‰), limiting our ability to rule out the use of these resources. Very low $\delta^{13}C$ values of filamentous red algae (-31.3‰)—typical of macroalgae that are physiologically restricted to the use of CO_2—indicate a minimal contribution to secondary production.

Within-habitat variations among isotope values of sessile suspension feeders may be explained by variation in particle size selection (Riisgård and Larsen 2010; Cresson et al. 2016) and/or physiological processes (Martínez del Río and Wolf 2005). Encrusting tunicates had uniquely low $\delta^{13}C$ values in comparison with all other consumers. This may be related to the

assimilation of carbon derived from symbiotic cyanobacteria present in this taxon (Schmidt 2015), or to a unique suspension feeding mechanism. Markedly higher $\delta^{15}N$ values were found in azooxanthellate cup corals (*T. coccinea, P. americana)* and barnacles in comparison to most bivalve filter feeding taxa, indicating greater contributions from heterotrophic prey to their diets. Similar results have been obtained from stable isotope based studies demonstrating higher trophic position of barnacles in comparison to bivalves (Daigle et al. 2013; Richoux et al. 2014; Rezek et al. 2017). These results also support research indicating that some azooxanthellate cup corals rely largely on heterotrophic prey (Goreau et al. 1971; Houlbrèque et al. 2004; Houlbrèque and Ferrier-Pagès 2009). A large degree of overlap was found between $\delta^{15}N$ values of motile macrofauna and suspension feeding taxa. This is indicative of a motile macrofauna community largely composed of primary consumers, apart from a few ^{15}N enriched secondary consumers (e.g. *S. fritzmuelleri*, *S. haemastoma*, and blennies).

The slight community-wide shift in consumer isotope values in SP5 and SP30 sites compared to the RP30 sites was most likely related to the shift in isotopic compositions of food sources. The trend in C and N isotope variation between reefed and standing platform consumers was generally reflected in composite food sources—particularly OSOM, which was shown to be an important contributor to these food webs—and primary producers.

The variance in $\delta^{13}C$ and $\delta^{15}N$ values among consumer taxa was homogeneous between all site-types. Similar isotopic variability among consumer taxa indicate that each habitat supported similar trophic diversity; relying on a similar diversity of food resources and supporting food webs with similar trophic levels. This indicates epibenthic communities in SP30 and RP30 site-types relied on similar food sources as the shallower SP5 communities, despite the variation in community composition between these zones. These findings provide evidence that

platforms still play a role as a substrate for primary producers and for the trapping of organic matter after they are converted into artificial reefs.

Function of reefed and standing platform habitats

Standing and reefed platform habitats function as islands of productivity in the relatively unstructured soft bottom habitats typical of the northwestern GOM shelf (Rezak et al. 1985). A platform in 57 m of water can provide 2.2 ha of submerged surface area within a 0.2 ha footprint of ocean floor (MBC 1987). Based on mean areal macrofauna biomass found in these habitats (293 g AFDW m^{-2}); an offshore platform in the GOM at similar depths could support 6.4 tons of AFDW macrofauna biomass, or 3.2 kg AFDW biomass per m^2 of ocean floor, or 1.3 kg C per m^2 of ocean floor (assuming 40% organic carbon by weight). This is vastly greater than the biomass typically supported by unstructured benthic shelf habitats in the GOM (0.33 to 2.01 g C m^{-2}; Escobar-Briones and Soto, 1997). Further research is warranted to quantify the effect of reefing practices on the total biomass these structures support.

Standing and reefed platforms support macrofauna communities that provide a food source for fisheries species such as gray triggerfish (*B. capriscus*), rock hind (*Epinephelus adscensionis*), and spadefish (*Chaetodipterus faber*); as well as a variety of non-targeted reef fish (Gallaway et al. 1979; Vose and Nelson 1994; Nelson and Bortone 1996; Beaver et al. 1997). Higher growth rates of gray triggerfish (Nelson 1985) and red snapper (*Lutjanus campechanus*) (Streich et al. 2017b) have been reported on standing and reefed platforms compared to natural reef habitats in the GOM.

Epibenthic communities inhabiting natural hard banks in the northern GOM shelf differ substantially in composition from those on platform-like habitats. Natural hard bank communities have been found to be dominated by cnidarians, sponges and bryozoans (Thompson

et al. 1999; Sammarco et al. 2016), in contrast to the bivalve dominated communities characteristic of platform habitats. Much of the natural hard bottom substrate in this region has relatively low relief (>1 m) and supports relatively low sessile macrofauna abundance due to its exposure to a persistent turbid nepheloid layer that negatively affects many suspension feeding taxa (Rezak et al. 1985). Quantitative comparisons of the biomass supported by natural banks in comparison to platforms and reefed platform structures could yield important insights into the overall influence these artificial habitats have on macrofauna production in the GOM shelf.

Although our results indicate that platform and reefed platforms support structurally communities at equivalent depths (30-m), the distinct compositional characteristics of shallow platform communities are likely to be lost or diminished when standing platforms are converted into artificial reefs. Structures spanning the entire water column are likely to support greater biodiversity than structures with lower relief. This conclusion is consistent with those of a photo-transect based examination of platform and reefed platform epiphytic communities conducted in the same region (Dokken et al. 2000). Compositional dissimilarity in nektonic fish assemblages associated with standing platforms vs. reefed platforms in the GOM have also been documented, with greater abundance of pelagic planktivores (e.g. bermuda chub, blue runner) reported on standing platforms (Wilson et al. 2003; Ajemian et al. 2015). These fish are generally associated with the upper water column and are less likely to inhabit reefed platforms with relatively low relief.

Allowing platforms to remain standing would ameliorate the loss of biodiversity due to the loss of shallow water substrate. However, federal regulations would require a state agency responsible for managing fisheries to assume all liability and costs associated with maintaining

standing platforms in perpetuity (Kaiser and Pulsipher 2005). The high costs associated with maintaining standing platforms as artificial reefs would generally make this approach unfeasible.

Stable isotope data indicate that reefed platforms can be expected to support faunal communities with comparable food web structure to shallow (5-m) and deep (30-m) standing platform habitat. This conclusion has important implications for resource management, as it demonstrates the ability of reefed platforms to retain ecological functions that would otherwise be lost when decommissioned platforms are removed from the GOM. Although the 26-m clearance guidelines observed in current reefing practices may reduce some aspects of biodiversity associated with platforms, collectively our results indicate that Rigs-to-Reefs programs provide an effective means of preserving the highly productive epibenthic macrofauna assemblages associated with standing platforms. As offshore platforms in the GOM reach the end of their productive lives at an increasing rate, Rigs-to-Reefs programs can play a critical role in preserving the ecological functions and services associated with the largest anthropogenic marine habitat system on earth.

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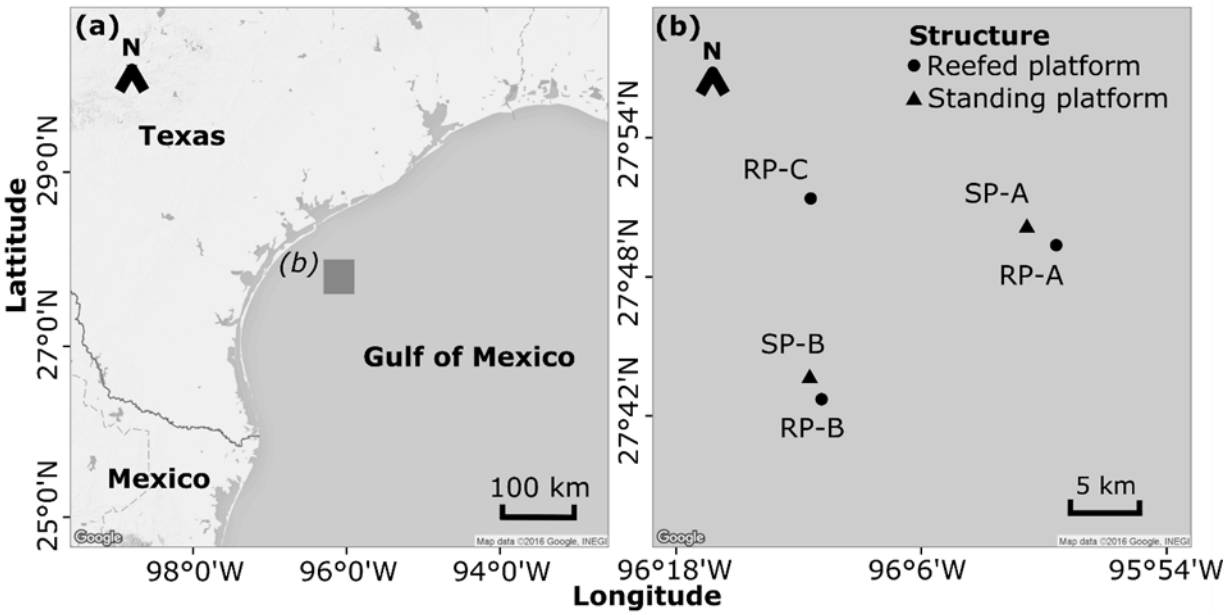

Figure 4.1: Location of the sampled standing platforms and reefed platform structures.

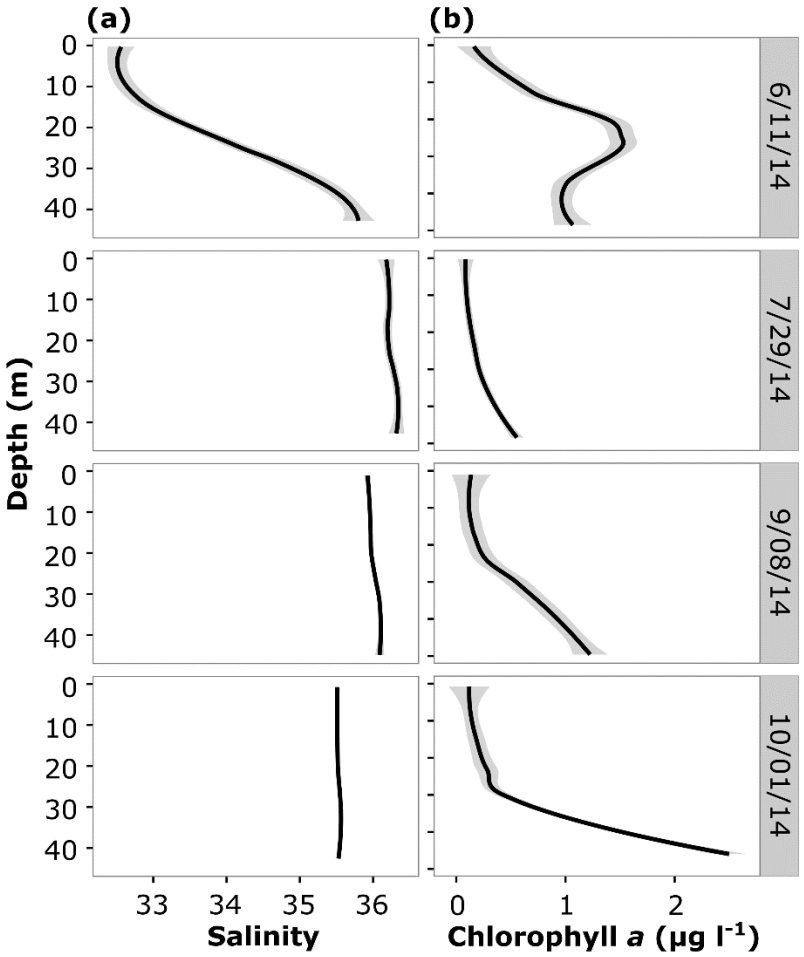

Figure 4.2: LOWESS-smoothed depth profiles of salinity and chlorophyll *a* concentration from sonde casts at RP-A and RP-C sites over the course of the survey. Shaded area represents 95% confidence intervals.

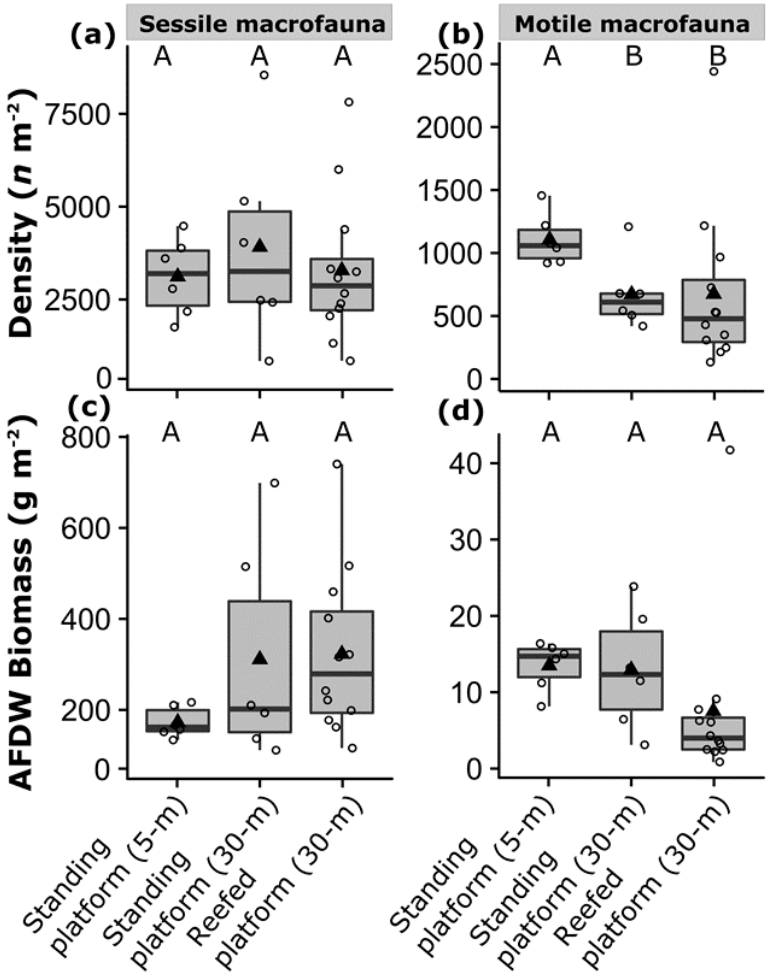

Figure 4.3: Density and ash free dry weight biomass of sessile macrofauna (a, c) and motile macrofauna (b, d) from standing platforms at 5- and 30-m depths, and reefed platforms at 30-m depth. Boxplots indicate median, interquartile range (IQR) and 1.5 • IQR. Raw data are indicated with open circles and means are indicated with triangle points. Tukey groupings obtained from ANOVAs post hoc tests indicated with letters above boxes ($\alpha = 0.05$).

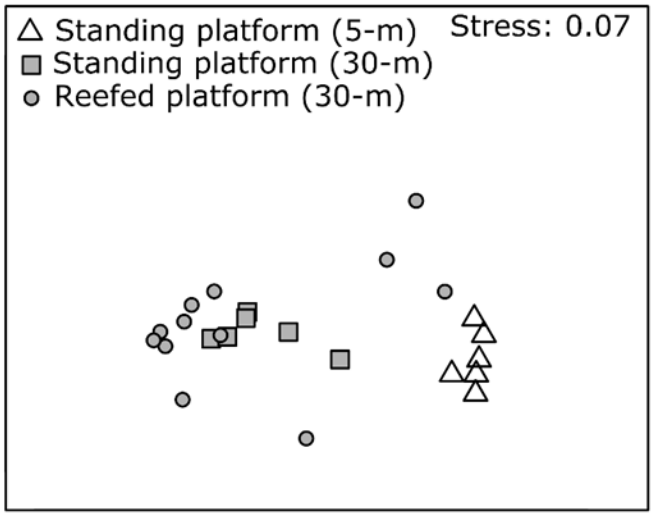

Figure 4.4: Non-metric multidimensional scaling plot of Hellinger transformed macrofauna community composition data from standing platforms at 5- and 30-m depths, and reefed platforms at 30-m depth.

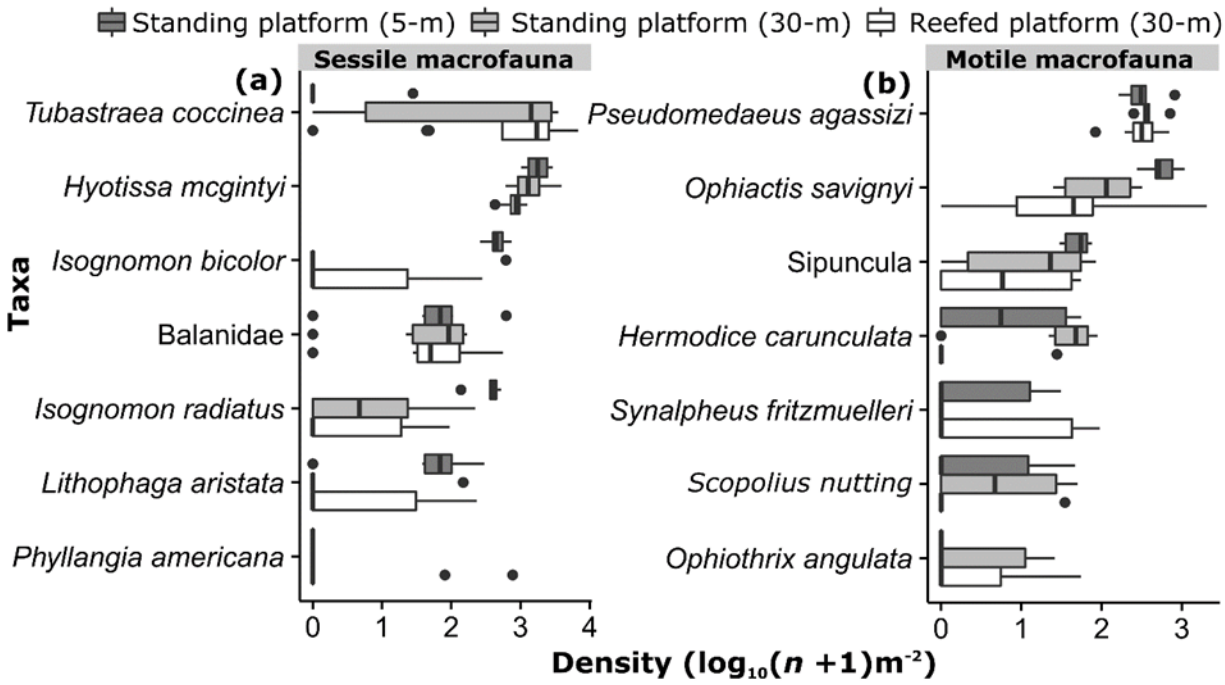

Figure 4.5: Densities of the 7 most abundant motile (a) and sessile (b) macrofauna taxa from standing platforms at 5- and 30-m depths, and reefed platforms at 30-m depth. Boxplots indicate median, interquartile range (IQR), and 1.5 • IQR. Data outside of 1.5 • IQR are represented with points.

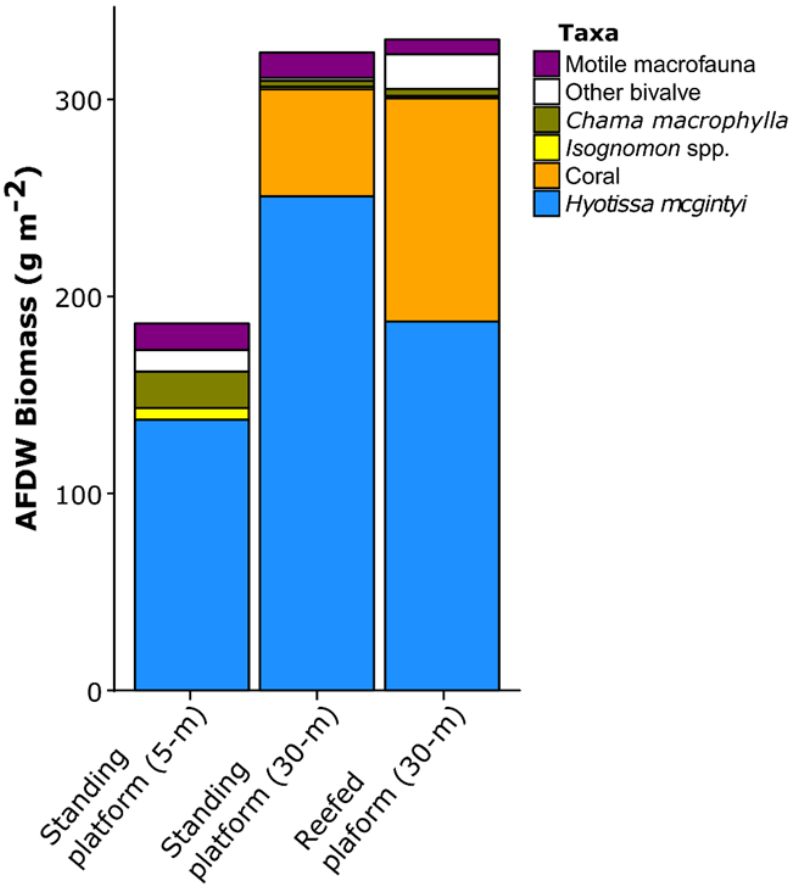

Figure 4.6: Mean AFDW biomass of major groups on standing platforms at 5- and 30-m depths, and reefed platforms at 30-m depth.

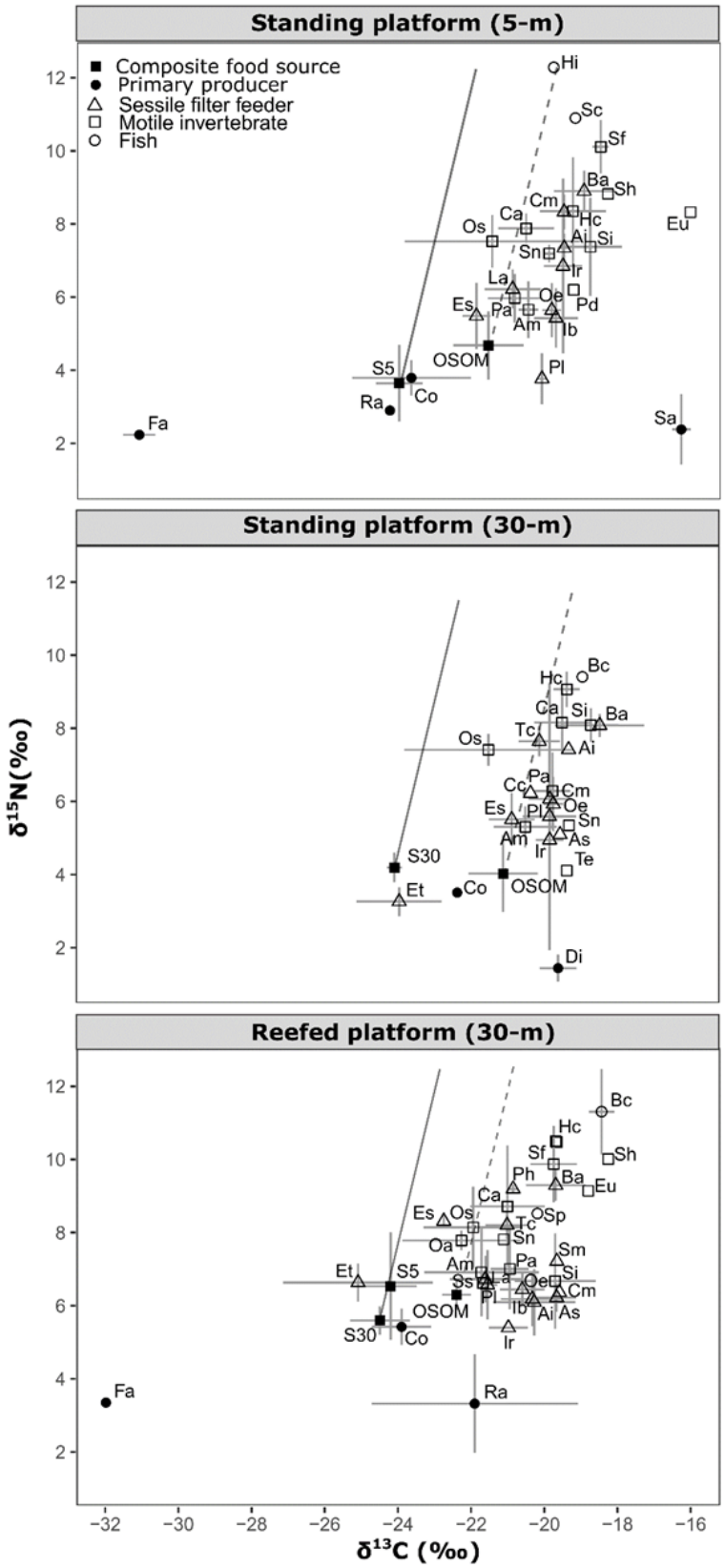

Figure 4.7: $\delta^{13}C$ and $\delta^{15}N$ values (‰, mean ± standard deviation) of primary producers, composite food sources and consumers on standing platforms at 5- and 30-m depths, and on

reefed platforms at 30-m depth. Code list: Ai: *Arca imbricate*; Am: amphipod; As: *Anomia simplex*; Ba: Balanidae; Bc: *Balistes capriscus*; Ca: Capitellidae; Cc: *Chama congregate*; Cm: *Chama macrophylla*; Co: Corallinaceae; Di: *Dictyota* sp.; Es: encrusting sponge; Et: encrusting tunicate; Eu: *Eucidaris tribuloides*; Hc: *Hermodice carunculate*; Hi: *Hypsoblennius invemar*; Hm: *Hyotissa mcgintyi*; Ib: *Isognomon bicolor*; Ir: *Isognomon radiatus*; La: *Lithophaga aristata*; Oa: *Ophiothrix angulate*; Os: *Ophiactis savignyi*; OSOM: Oyster shell organic matter; Pa: *Pseudomedaeus agassizi*; Pd: *Paraliomera dispar*; Ph: *Phyllangia americana*; Pl: Plumulariidae; Ra: red macroalgae; SPOM30: Suspended particulate organic matter (30-m); SPOM5: Suspended particulate organic matter (5-m); Sa: *Sargassum* sp.; Sc: *Scartella cristata*; Sf: *Synalpheus fritzmuelleri*; Sh: *Stramonita haemastoma*; Si: Sipuncula; Sm: *Spondylus americanus*; Sn: *Scopolius nuttingi*; Sp: *Scorpaena plumieri*; Ss: *Stenorhynchus seticornis*; Tc: *Tubastraea coccinea*; Te: *Teleophrys* sp. Lines indicate the influence of OSOM (dashed) and SPOM (solid) based on the relationship between $\delta^{13}C$ (0.5‰) and $\delta^{15}N$ (2.0‰) trophic fractionation factors.

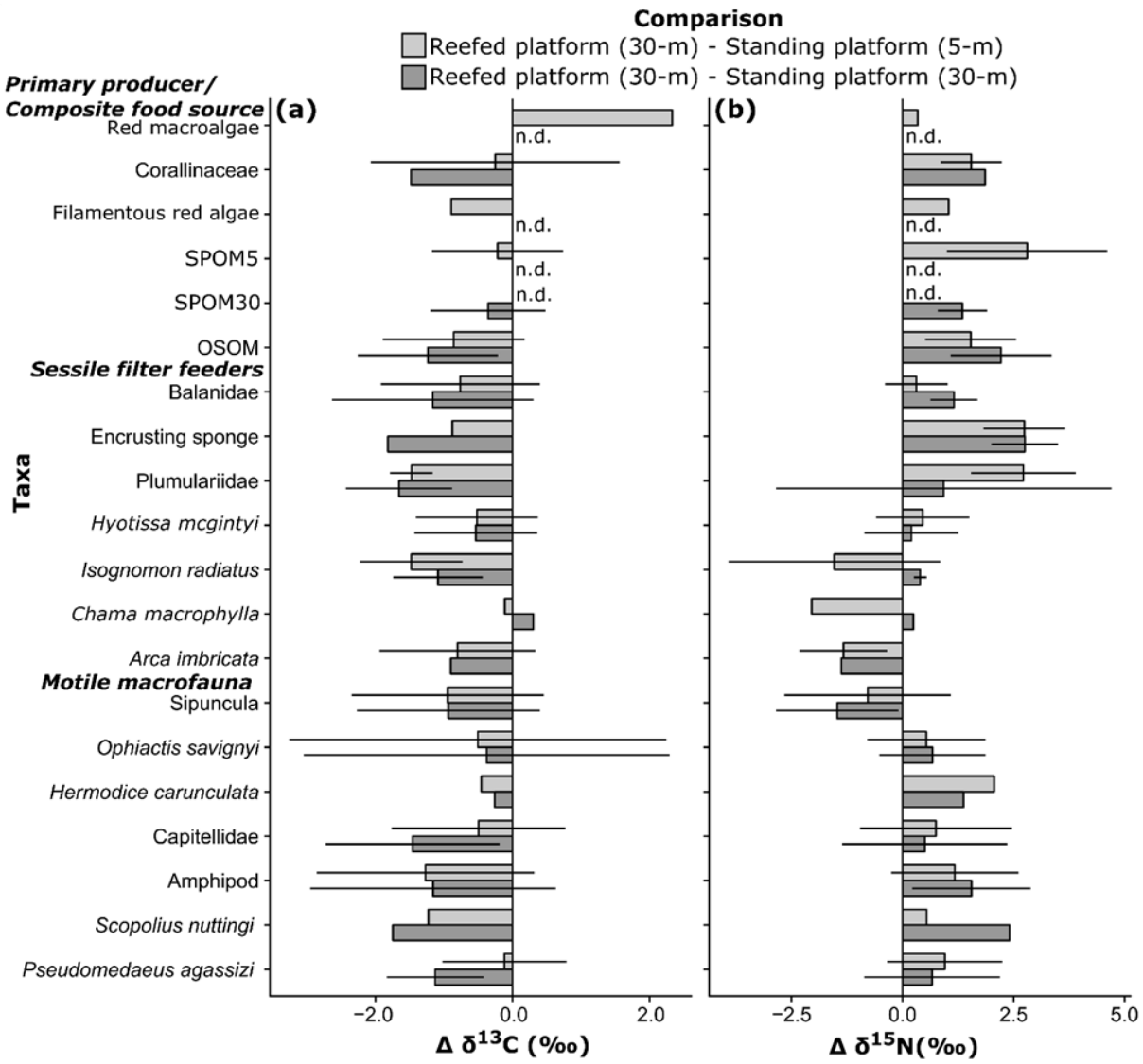

Figure 4.8: Differences (Δ) of $\delta^{13}C$ (a) and $\delta^{15}N$ (b) values (mean ± standard deviation) of primary producers, composite food sources and co-occurring taxa between standing platforms at 5-m depth and reefed platforms (30-m) and between standing platforms at 30-m depth and reefed platforms (30-m). Code list: OSOM: Oyster shell organic matter; SPOM30: Suspended particulate organic matter (30-m); SPOM5: Suspended particulate organic matter (5-m). No data indicated with n.d.

Table 4.1: Location and metadata for sampled standing platforms and reefed platforms. For reefed platforms, year constructed (Year const.) indicates year when the original platform was converted, and reefing method indicates if the structure is toppled platform (Topple) or a partially removed platform (Part. Rm.). Information obtained from the Bureau of Safety and Environmental Enforcement (www.bsee.gov) and Texas Parks and Wildlife Department (tpwd.texas.gov) databases.

ID	Structure name	Type	Reefing method	Latitude	Longitude	Year const.	Depth (m)	Relief (m)
RP-A	BA-A-132A	Reefed	Part. Rm.	27°49'22	-95°59'24	1992	61	34
RP-B	MU-A-85B	Reefed	Topple	27°42'43	-96°10'53	2006	83	54
RP-C	MI-A-7A	Reefed	Topple	27°51'23	-96°11'25	2002	60	32
SP-A	BA-A-133A	Platform	-	27°51'16	-96°02'11	1976	61	61
SP-B	MU-A-85A	Platform	-	27°43'37	-96°11'28	1977	79	79

Table 4.2: Density (*n* m^{-2}, mean ± standard error) and ash free dry weight biomass (g m^{-2}, mean ± standard error) of sessile and motile macrofauna species from standing platforms at 5-meter and 30-meter depths and from reefed platforms 30-meter depth. - indicates that parameter was not measured.

	Standing platform (5-m)			Standing platform (30-m)			Reefed platform (30-m)		
		Density	Biomass		Density	Biomass		Density	Biomass
Species	***n***	***n* m^{-2}**	**g m^{-2}**	***n***	***n* m^{-2}**	**g m^{-2}**	***n***	***n* m^{-2}**	**g m^{-2}**
Sessile macrofauna									
Anomia simplex	0	0	0	2	7.6 ± 4.8	<0.1 ± <0.1	3	4.6 ± 2.4	0.2 ± 0.2
Arca imbricate	14	51.4 ± 11.2	8.9 ± 4.9	1	4.9 ± 4.9	1.0 ± 1.0	9	20.9 ± 8.4	2.5 ± 1.8
Arcopsis adamsi	1	3.8 ± 3.8	<0.1 ± <0.1	0	0	0	0	0	0
Balanidae	43	150.5 ± 95.2	-	21	90.1 ± 29.9	-	42	110.2 ± 44.9	-
Chama congregata	10	34.8 ± 12.0	0.1 ± 0.1	7	29.2 ± 19.5	0.2 ± 0.2	14	27.9 ± 10.2	0.2 ± 0.1
Chama macrophylla	5	21.5 ± 5.3	18.4 ± 5.7	5	20.8 ± 7.6	3.1 ± 1.4	5	12.5 ± 7.2	3.7 ± 2.1
Hyotissa mcgintyi	49 0	1894.1 ± 313.7	137.4 ± 14.3	40 2	1674.0 ± 496.0	250.8 ± 88.4	380	841.5 ± 72.6	187.3 ± 28.4
Isognomon radiatus	10 5	378.4 ± 53.7	2.3 ± 0.5	11	44.3 ± 35.7	0.3 ± 0.2	5	13.0 ± 7.8	0.4 ± 0.3
Isognomon bicolor	12 7	479.4 ± 68.7	3.7 ± 0.9	25	102.6 ± 102.6	1.0 ± 1.0	10	30.3 ± 23.0	0.8 ± 0.8
Lithophaga aristata	29	97.0 ± 43.1	1.9 ± 1.6	6	24.6 ± 24.6	0.2 ± 0.2	10	30.8 ± 19.2	0.6 ± 0.5
Musculus lateralis	0	0	0	0	0	0	2	7.3 ± 4.9	<0.1 ± <0.1
Phyllangia americana	0	0	0	0	0	0	35	71.0 ± 64.0	3.8 ± 3.6
Pinna sp.	0	0	0	0	0	0	3	4.8 ± 3.3	<0.1 ± <0.1
Pteria colymbus	0	0	0	0	0	0	1	1.4 ± 1.4	<0.1 ± <0.1
Spondylus americanus	0	0	0	0	0	0	1	2.1 ± 2.1	14.0 ± 14.0
Tubastraea coccinea	1	4.5 ± 4.5	0.1 ± 0.1	45 1	1914.1 ± 522.2	54.3 ± 14.2	115 6	2105.1 ± 589.5	109.2 ± 41.4
Motile macrofauna									
Acteocina sp.	0	0	0	1	3.5 ± 3.5	<0.1 ± <0.1	1	2.2 ± 2.2	<0.1 ± <0.1
Eucidaris tribuloides	1	2.5 ± 2.5	<0.1 ± <0.1	0	0	0	1	2.2 ± 2.2	0.2 ± 0.2
Hermodice carunculata	5	20.4 ± 9.7	1.3 ± 0.8	10	42.2 ± 12.2	5.6 ± 1.8	1	2.2 ± 2.2	<0.1 ± <0.1
Hypsoblennius invemar	1	2.4 ± 2.4	0.1 ± 0.1	0	0	0	0	0	0
Majidae	0	0	0	1	4.6 ± 4.6	<0.1 ± <0.1	1	3.9 ± 3.9	<0.1 ± <0.1
Morula nodulosa	2	8.6 ± 6.2	<0.1 ± <0.1	1	4.1 ± 4.1	<0.1 ± <0.1	0	0	0
Ophiactis savignyi	15 2	617.8 ± 120.9	0.9 ± 0.3	35	145.8 ± 50.8	0.2 ± <0.1	70	242.3 ± 166.5	0.2 ± 0.1
Ophiothrix angulata	0	0	0	2	8.1 ± 5.1	0.1 ± 0.1	7	11.1 ± 5.8	0.4 ± 0.3
Paraliomera dispar	2	7.1 ± 4.7	0.2 ± 0.1	0	0	0	0	0	0
Pseudomedaeus agassizi	11 7	363.4 ± 95.7	9.2 ± 1.5	10 0	408.5 ± 69.1	6.6 ± 1.9	151	357.1 ± 52.2	3.5 ± 0.6
Scartella cristata	1	3.8 ± 3.8	0.5 ± 0.5	0	0	0	0	0	0
Scopolius nuttingi	3	12.2 ± 8.1	0.2 ± 0.1	4	16.3 ± 8.2	0.2 ± 0.1	2	2.9 ± 2.9	<0.1 ± <0.1
Scorpaena plumieri	0	0	0	0	0	0	1	1.4 ± 1.4	<0.1 ± <0.1
Sipuncula	13	51.8 ± 7.8	0.8 ± 0.4	8	33.4 ± 14.8	0.1 ± <0.1	11	21.5 ± 6.7	0.1 ± 0.1
Stenorhynchus seticornis	0	0	0	0	0	0	1	2.2 ± 2.2	<0.1 ± <0.1
Stramonita haemastoma	1	2.4 ± 2.4	0.2 ± 0.2	0	0	0	2	6.1 ± 4.3	2.7 ± 2.6
Synalpheus fritzmuelleri	4	9.8 ± 6.2	0.1 ± 0.1	0	0	0	8	21.4 ± 8.9	0.2 ± 0.1
Teleophrys ornatus	0	0	0	1	4.9 ± 4.9	0.2 ± 0.2	0	0	0
Trachypollia sclera	2	4.8 ± 4.8	<0.1 ± 0.1	0	0	0	0	0	0

Table 4.3: $\delta^{13}C$ and $\delta^{15}N$ values (‰, mean ± standard deviation) of primary producers, composite food sources and macrofauna from standing platform sites at 5-meter and 30-meter depths and from reefed platforms at 30-meter depth. $\delta^{15}N$ value sample size (*n*) is given after comma when isotope sample size (*n*) differs for $\delta^{13}C$ and $\delta^{15}N$ values.

	Standing platform(5-m)			Standing platform(30-m)			Reefed platform(30-m)		
Taxa	***n***	**$\delta^{13}C$ (‰)**	**$\delta^{15}N$ (‰)**	***n***	**$\delta^{13}C$ (‰)**	**$\delta^{15}N$ (‰)**	***n***	**$\delta^{13}C$ (‰)**	**$\delta^{15}N$ (‰)**
Primary producers									
Corallinaceae	5,6	-23.9 ± 1.7	3.8 ± 0.5	1	-22.4	3.5	7	-23.9 ± 0.8	5.4 ± 0.5
Dictyota sp.				3	-19.7 ± 0.5	1.4 ± 0.4			
Filamentous red algae	3	-31.1 ± 0.4	2.3 ± 0.1				1	-32.0	3.3
Red macroalgae	1	-24.2	2.9				7	-21.9 ± 2.8	3.3 ± 1.4
Sargassum sp.	3	-16.3 ± 0.3	2.4 ± 1.0						
Composite food sources									
OSOM	4	-21.5 ± 1.0	4.7 ± 0.9	4	-21.2 ± 0.9	4.0 ± 1.1	4	-22.4 ± 0.4	6.2 ± 0.4
SPOM (5-m)	2	-24.0 ± 0.6	3.7 ± 1.0				3	-24.2 ± 0.7	6.5 ± 1.5
SPOM (30-m)				2	-24.1 ± 0.2	4.2 ± 0.4	3	-24.5 ± 0.8	5.5 ± 0.4
Sessile filter feeders									
Anomia simplex				1	-19.6	5.1	2	-19.7 ± 0.5	6.2 ± 0.4
Arca imbricata	4	-19.5 ± 0.2	7.4 ± 0.4	1	-19.4	7.4	2	-20.3 ± 1.1	6.0 ± 0.9
Balanidae	3	-18.9 ± 0.8	8.9 ± 0.6	3	-18.5 ± 1.2	8.1 ± 0.3	3	-19.7 ± 0.8	9.2 ± 0.4
Chama congregata				1	-20.4	6.2			
Chama macerophylla	4	-19.5 ± 0.2	8.3 ± 0.5	2	-19.9 ± 0.6	6.1 ± 0.2	1	-19.6	6.3
Encrusting sponge	5	-21.9 ± 0.4	5.5 ± 0.9	7	-20.9 ± 0.6	5.5 ± 0.7	1,2	-22.7	8.2 ± 0.2
Encrusting tunicate				3	-24.0 ± 1.2	3.2 ± 0.4	6	-25.1 ± 2.1	6.6 ± 0.5
Hyotissa mcgintyi	9	-19.8 ± 0.3	5.7 ± 0.7	10	-19.8 ± 0.3	5.9 ± 0.7	14	-20.3 ± 0.9	6.1 ± 0.7
Isognomon bicolor	7	-19.7 ± 0.6	5.4 ± 0.8				5	-20.6 ± 0.6	6.4 ± 0.5
Isognomon radiatus	4	-19.5 ± 0.5	6.9 ± 2.4	2	-19.9 ± 0.4	4.9 ± 0.1	2	-21.0 ± 0.5	5.3 ± <0.1
Lithophaga aristata	6	-20.9 ± 0.8	6.2 ± 0.5				5	-21.6 ± 1.0	6.7 ± 0.6
Phyllangia americana							3	-20.8 ± 0.1	9.1 ± 0.1
Plumulariidae	4	-20.1 ± 0.1	3.8 ± 0.7	2	-19.9 ± 0.7	5.6 ± 3.7	7	-21.5 ± 0.3	6.5 ± 0.9
Spondylus americanus							1	-19.7	7.1
Tubastraea coccinea				3	-20.2 ± 0.6	7.6 ± 0.4	8	-21.0 ± 0.6	8.1 ± 0.4
Motile invertebrates									
Amphipod	5	-20.4 ± 0.3	5.7 ± 0.8	4	-20.6 ± 0.9	5.3 ± 0.6	7,8	-21.7 ± 1.6	6.8 ± 1.2
Capitellidae	4	-20.5 ± 0.8	7.9 ± 0.4	7	-19.5 ± 0.8	8.1 ± 0.8	8	-21.0 ± 1.0	8.6 ± 1.7
Eucidaris tribuloides	1	-16.0	8.3				1	-18.8	9.1
Hermodice carunculata	3	-19.2 ± 0.9	8.4 ± 1.5	6	-19.4 ± 0.4	9.1 ± 0.5	1	-19.7	10.4
Ophiactis savignyi	6	-21.4 ± 2.4	7.5 ± 0.7	6	-21.6 ± 2.3	7.4 ± 0.4	5	-21.9 ± 1.4	8.1 ± 1.1
Ophiothrix angulata							4	-22.3 ± 1.6	7.7 ± 0.3
Paraliomera dispar	1	-19.2	6.2						
Pseudomedaeus agassizi	6	-20.8 ± 0.7	6.0 ± 0.7	7	-19.8 ± 0.5	6.3 ± 1.0	10	-20.9 ± 0.5	6.9 ± 1.1
Scopolius nuttingi	2	-19.9 ± 0.2	7.2 ± 0.2	1	-19.4	5.3	1	-21.1	7.7
Sipuncula	6	-18.8 ± 0.9	7.4 ± 1.3	4	-18.8 ± 0.7	8.1 ± 0.5	5	-19.7 ± 1.1	6.6 ± 1.3
Stenorhynchus seticornis							1	-21.7	6.6
Stramonita haemastoma	1	-18.3	8.8				1	-18.3	9.9
Synalpheus fritzmuelleri	3	-18.5 ± 0.2	10.1 ± 0.7				5	-19.7 ± 0.6	9.8 ± 1.0
Teleophrys sp.				1	-19.4	4.1			
Fish									
Balistes capriscus				1	-19.0	9.4	6	-18.5 ± 0.3	11.3 ± 1.2
Hypsoblennius invemar	1	-19.8	12.3						
Scartella cristata	1	-19.2	10.9						
Scorpaena plumieri							1	-20.2	8.5

CHAPTER V: CONCLUDING SUMMARY

Chapter summary

Habitat restoration is likely to play a critical role in management strategies undertaken to reverse the trend of ecological degradation that has impacted coastal systems globally. However, questions persist about the ability of constructed habitat restorations to replicate the trophic structure and functions associated with natural or pre-existing reference habitats. The principal focus of this dissertation was to address important questions regarding the ability of constructed coastal habitats to restore communities and ecological functions associated with natural or pre-existing reference habitats. The hypothesis that constructed coastal habitats support equivalent communities and ecological functions to reference habitats was tested through the quantitative comparison of both community structure data (e.g. composition, abundance, diversity) and stable isotope-based ecological process data (e.g. trophic structure, resource use) between habitat types. The integrated investigative approach to habitat monitoring employed in this dissertation produced comprehensive information on the functioning of restored coastal habitats that could not have been obtained through either approach in isolation. These results broaden our understanding of how constructed habitats influence trophic functioning in coastal systems and provide novel information to resource managers that can be applied towards future coastal restoration projects. The synthesis of these results across habitat types highlight unique properties of different systems related to the recoverability of functional attributes that may apply generally across coastal ecoclines.

In Chapter II, I monitored the development of a restored subtidal *Crassostrea virginica* oyster reef in comparison to a natural reference reef and demonstrated the ability of the restored reef to reach structural and functional parity with the natural reference within 12 to 15 months

post-construction. The macrofauna community on the restored oyster reef exhibited a distinct early successional phase which lasted 12 months and was characterized by the dominance of motile pioneer species and relatively low diversity. This phase was followed by the recovery of oyster abundance, species richness and community composition to reference conditions.

Stable isotope evidence indicated similar resource use, food chain length, and community isotopic niche occupation between reefs as soon as 5-month post-restoration. However, integrating community structure and stable isotope process data with biomass-weighted isotopic diversity indices demonstrated that the magnitude of flux between organic matter sources, primary consumer groups, and secondary consumers differed in the restored reef during the successional period. Important aspects of ecological function, such as the transfer of organic matter to secondary consumers and bentho-pelagic coupling, were impoverished in the developing reef in comparison to the natural reference. The colonization of large bodied predators and oysters drove the functional recovery of the restored reef, resulting in a community biomass structure that was more evenly distributed across the food web—similar to the natural reference. The results of this study have important implications for resource management, as they demonstrate the ability of constructed subtidal oyster reefs to function as natural reefs remarkably soon after they are created. This study also highlights the importance of the relationship between community structure and trophic topology in determining ecosystem functions.

In Chapter III, I studied a constructed *Spartina alterniflora* salt marsh in comparison to a natural reference salt marsh. This study demonstrated the restored marsh was capable of supporting structurally similar macrofauna assemblages as in a natural habitat relatively rapidly (i.e. at most 4 years after construction), providing critical habitat to economically important

fisheries species. The restored marsh supported similar macrofauna trophic levels and the food web was supported by a similar diversity of resources as natural references. However, stable isotope mixing models showed that dominant omnivorous consumers (grass shrimp and brown shrimp) in restored salt marsh habitats had lower dietary contributions from macrophyte derived resources and higher contributions from pelagic microalgal resources than those in natural salt marshes throughout the survey. A diminished linkage existed between vascular plant production, detrital pools, and secondary production in the recently created salt marsh. This was attributed to the markedly lower concentrations of detritus and organic matter in the restored salt marsh surface sediments. The results of this study call attention to functional differences between recently constructed salt marshes and established natural marshes related to variations in the flux of terrestrial versus marine resources to consumers. Based on these findings, I recommend further research into methods of hastening the recovery of sediment characteristics to re-establish detrital pathways supporting secondary production in constructed salt marshes.

This study also demonstrated the influence of marsh edge accessibility on resident communities and food webs. Macrofauna biomass and the trophic levels of dominant decapods were found to be positively related to marsh edge flooding durations, likely due to the increased foraging opportunities associated with greater marsh access. These results highlight the importance of considering the relationship between marsh edge elevation and hydroperiod characteristics when constructing salt marshes.

In Chapter IV, I surveyed offshore Rigs-to-Reefs artificial reef habitats in comparison to standing platform habitats. I found that epibenthic communities associated with reefed platforms were similar in composition to those on platform habitats at equivalent depths (30 meters). However, compositional variation was observed between habitats at 30-m depths and platform

habitats at 5-m depth, demonstrating that depth is an important factor influencing epibenthic species composition in these habitats. Similar variance in $\delta^{13}C$ and $\delta^{15}N$ values among consumer taxa between habitats indicated the community trophic structure was similar between 5-m and 30-m standing platform and 30-m reefed platform sites.

Based on these results, we conclude that reefed platform communities are functionally similar to the standing platform habitats they are intended to replace. However, the loss of hardscape in the upper water column, due to 26-m clearance guidelines observed in current reefing practices, is likely reduce some aspects of biodiversity associated with platform structures after they are converted into artificial reefs. Results indicate that platform reefing is an effective means of preserving the unique and productive communities that inhabit standing platforms in the in the pelagic Gulf of Mexico environment.

Collectively, the results of my dissertation demonstrate that constructed habitats can be an effective tool for enhancing ecologically important communities. Constructed habitats in all systems demonstrated the ability support ecological structure attributes in close approximation of what was observed in natural habitats, or desirable pre-existing artificial habitats in the case of reefed platforms. Macrofauna density, biomass and species composition in constructed habitats became equivalent to reference habitats at some in point in all surveyed systems. These results demonstrate that habitat construction can provide managers with an effective means of supporting the production of economically/ecologically important macrofauna and enhance biodiversity in degraded coastal systems.

Functional development across habitat types

Although constructed habitats in all environments demonstrated the ability to support similar community structure to reference habitats, the relationship between the structural and

functional development varied between habitat types. Variations in trophic topology and function in oyster reefs were primarily mediated by variations in community structure that resulted in dissimilar allocation of biomass between consumer trophic compartments in constructed versus reference habitats. These functional variations diminished when community compositional similarity was reached. A high degree of trophic redundancy characterized offshore standing and reefed platform communities, and as a result, similar food web structure was found between deep and shallow habitats despite variations in community composition. In contrast, functional variation between constructed and reference salt marshes was primarily linked to variation in the dietary composition of important generalist consumers. This outcome may be related to the several important characteristics that distinguish vascular plants from microalgal producers.

Primary producer nutritional quality is an important mediator of the rapidity of nutrient and energy recycling, the trophic pathways linking producers to consumers, and the accumulation of stored carbon in ecosystems (Nielsen et al. 1996; Cebrian et al. 1998; Cebrian 1999; Cebrian and Lartigue 2004). Producers with high nutritional quality (i.e. low C:N, C:P ratios) such as microalgae generally have rapid growth rates, rapid turnover rates, and are readily consumed by herbivores. While producers with low nutritional quality such as vascular plants have slower growth rates, slower turnover rates, and higher proportions of their production are channeled as detritus (Cyr and Pace 1993; Nielsen et al. 1996; Cebrian 1999). Refractory detritus in salt marshes is of low nutritive value, and consumers generally rely on microbial decomposition to enhance its palatability (Haines and Hanson 1979).

The turnover rate of *Spartina alterniflora* ranges from 0.7 to 5.1 $year^{-1}$ (Dame and Kenny 1986), and sediment organic matter pools and detrital food resources can takes decades to recover in constructed salt marshes (Craft et al. 1999; Craft et al. 2003). This may explain why

the trophic link between *Spartina* and some consumers was diminished in the recently constructed marsh in comparison to natural marsh consumers (Chapter III).

Microalgae have a much faster turnover rate than vascular plants (e.g. 0.6 to 1.3 day^{-1}; Geider 1988) and autochthonous microalgal production (e.g. benthic diatoms) is an important component of consumer diets in coastal habitats structured by both vascular plants and suspension feeders (Haines and Montague 1979; Riera 1998; Lebreton et al. 2009). And these autochthonous microalgal resources can recover relatively rapidly in restored habitats (Craft et al. 2003; Nordstrom et al. 2014; Blomberg et al. 2017). High quality allochthonous microalgal resources (e.g. phytoplankton) transported through the water column are also an important food source in coastal habitats structured by both vascular plants and suspension feeding invertebrates (Haines and Montague 1979; Dame and Patten 1981; Galván et al. 2008), and can become available to consumers in restored habitats as soon as they are created. These important attributes of microalgal producers may explain why they were consumed by macrofauna in higher proportions in the recently restored marsh (Chapter III), and the rapid recovery of food web structure in the microalgal driven restored oyster reef community (Chapter II).

The rapidity that nutrients cycle through a producer compartment, linked to its nutritional quality and turnover rate, may be an important indicator of the speed in which trophic links between producer and consumer compartments can recover in constructed habitats. This indicates that consumers in restored coastal habitats structured by vascular plants (e.g. salt marsh, mangrove, and seagrass) may rely more heavily on microalgal resources, compared to natural counterparts, until local detrital food webs and organic matter pools recover. This relationship would have important implications for the influence of restored habitats on organic matter flux in coastal systems, and could be used to predict recovery time frames of specific

producer-consumer trophic links. This hypothesis could be tested by evaluating the recovery of trophic structure across restored coastal habitats that are supported by producers with a wide variety of nutritional content and turnover rates.

Due to increasing human populations and climate variability, coastal systems are transforming at a growing rate. In order to adapt to these changes, ecological restoration efforts must focus on interventions that sustain services within the context of future environmental conditions, and have alternative goals and trajectories to account for unpredictable endpoints (Choi 2007). Ecological restoration efforts need to account for increasing impacts of human populations by enhancing the ability of coastal habitats co-exist with urban environments and provide ecosystem services in increasingly developed coastal systems (Grimm et al. 2008; Standish et al. 2013; Elmqvist et al. 2015). Historic ecological conditions will become less suitable restoration endpoints as climate change increasingly alters the biophysical environment and regional species pools; restoration and maintenance of ecosystem function may take priority over the restoration of historical species composition and ecological structure (Hobbs and Harris 2001; Harris et al. 2006).

Habitat construction and coastal restoration will become an increasingly important feature of ecosystem-based management and it will be essential to implement adaptive management strategies to maintain ecosystem services and functions in a changing global environment. The results of these investigations describe the effect of habitat constructions on ecological processes and communities over a range of coastal environments. This study expands on the body of scientific work in coastal restoration necessary to inform the implementation of habitat construction as a component of comprehensive ecosystem-wide resource management plans.

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