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The effects of oyster harvest on resident oyster reef communities and reef structure in coastal Louisiana proper

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THE EFFECTS OF OYSTER HARVEST ON RESIDENT OYSTER REEF COMMUNITIES AND REEF STRUCTURE IN COASTAL LOUISIANA

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ABSTRACT

Harvest of the eastern oyster (*Crassostrea virginica*) is a primary contributor to oyster reef habitat disturbance in the northern Gulf of Mexico. The impacts of oyster dredging on reef substrate and resident fauna have not been thoroughly examined on the extensive sub-tidal oyster reefs of Louisiana. Several reef structure and resident community metrics were compared on unharvested and harvested reefs during the spring, summer, and fall of 2010. Unharvested reefs had higher amounts of oyster clusters, solid reef substrate, and more large oysters, while harvested reefs had higher amounts of loose shell, mixed shell/mud substrate, and elevated chlorophyll-*a* levels. Overall, faunal densities did not differ with harvest status and dominant species were similar, although greater invertebrate diversity was found on harvested reefs. Several resident species were found to primarily associate with live oysters [freckled blenny (*Hypsoblennius ionthas*) and skilletfish (*Gobiesox strumosus*)] and chlorophyll-*a* levels [Harris mud crab (*Rhithropanopeus harrisii*) and snapping shrimp (*Alpheus* sp.)], indicating the importance of live oysters in determining reef microhabitat preferences by regulating types of available food sources. Condition (weight:length ratio) of naked gobies (*Gobiosoma bosc*) was greater on unharvested reefs, while other common fish species showed no difference. Large interstitial spaces associated with oyster clusters appear to enable several fish species to reach larger sizes at unharvested reefs and promote retention of age = 0 *G. bosc*. Stable isotope values ($\delta^{13}C$ and $\delta^{15}N$) of dominant species and basal food sources were used to compare food web characteristics between sites. Non-pelagic source contributions and trophic positions of dominant species were elevated at harvested sites. Trophic order did not differ suggesting that no major shifts in feeding behavior occur at harvested reefs with the exception of zooplankton (trophic position increased substantially at harvested sites). While not changing total refuge capacity, oyster harvest appears to decrease the number of large oysters and also fragment solid

reef area, resulting in elevated phytoplankton abundance, decreased benthopelagic coupling, and increased habitat heterogeneity. A larger forage base in the water column and mixed shell/mud substrate could account for increased invertebrate diversity and trophic position elevations on harvested oyster reefs.

CHAPTER 1: INTRODUCTION

Reef structures created by shellfish play an important role in aquatic ecosystems by supporting dense aggregations of organisms. Of these shellfish species, oysters are one of the few biogenic reef building species that are actively harvested for human consumption. Beck et al. (2011) conducted the only known global oyster reef assessment that identified oyster reefs as one of the most endangered aquatic habitats in the world, resulting primarily from overharvest, coastal degradation, and disease and it is estimated that 85% of oyster reefs have been lost globally. This of great concern because of the diverse ecosystem services that oyster reefs provide in estuaries, especially the ability to create foraging and refuge habitat for many aquatic organisms. Beck et al. (2011) found that the most extensive oyster reefs left in the world are those created by the eastern oyster (*Crassostrea virginica*) in the northern Gulf of Mexico (GOM), making this area a recent focal point for oyster reef research.

The productive coastal waters of Louisiana contain extensive sub-tidal oyster beds that support a large, culturally unique oyster fishery managed by the Louisiana Department of Wildlife and Fisheries (LDWF). This fishery regularly contributes over 30% of the total (eastern) oyster landings in the United States, more than any other state (LDWF 2010). The ultimate result of oyster overharvest may be the complete destruction and removal of oyster reef habitat. When overharvest is combined with oyster mortality caused by disease and poor water quality, such as what has occurred in the Chesapeake Bay, oyster populations are slow to recover (Rothschild et al. 1994). The impacts of intermediate or sustainable levels of oyster harvest on reef habitat and reef dependent (resident) organisms are still unclear. There are no oyster reefs remaining in Louisiana that have not been impacted by anthropogenic activities at some point in the past, but the oyster reefs in this region currently range from unharvested areas to heavily

harvested reefs, offering an excellent opportunity to study the effects of oyster harvest on oyster reef communities.

Ecosystem Services of Oyster Reefs:

The importance of oyster reefs in estuarine ecosystems has been thoroughly documented, and can be grouped into three categories: filtration services [water quality maintenance and benthopelagic coupling, altering wave/current velocities, and habitat provision (complex foraging and refuge habitat and hard substrate) (Kennedy 1996, Newell 2004, Coen et al. 2007). Oysters are well known for their ability to maintain water quality through filtration of the water column. Cressman et al. (2003) found that the presence of oyster reefs contributed to the reduction of chlorophyll-*a* and fecal coliform concentrations in tidal creeks. Dame et al. (1984) and Nelson et al. (2004) reported similar results for chlorophyll-*a*, and Dame et al. (1989) found that oyster reefs play an important role in nutrient uptake by removing carbon, nitrogen, and phosphorous from the water column at high rates, thus assisting in the prevention of eutrophication (Officer et al. 1982). Most recently, Wall et al. (2011) found that the filter-feeding activities of oysters can mediate the effects of nutrient loading, which has both positive and negative effects on other organisms. By filtering large quantities of water daily to feed on seston (Cloern 1982), oysters simultaneously deposit significant amounts of feces and undigested phytoplankton (pseudofeces) onto the surrounding benthos (Newell and Jordan 1983) which provides a food source to benthic fauna and results in benthopelagic coupling of nutrients (Coen et al. 2007). The ability of oyster reefs to attenuate wave action can help stabilize shorelines through sediment accumulation and prevention of marsh erosion. Piazza et al. (2005) found that artificial oyster shell reefs slowed shoreline retreat at low energy locations, while Meyer et al. (1997) showed that oyster shell cultch areas can lead to sediment accretion in salt marshes.

Gedan et al. (2011) highlights the potential benefits of using artificial oyster reefs to supplement shoreline protection measures.

The creation of complex foraging and refuge habitat is arguably the most important ecosystem service that oyster reefs provide, as oyster reefs support resident reef species, transient species, and also provide nursery functions for the larval and juvenile stages of species that complete their life histories in non-estuarine habitats (Beck et al. 2001). The ability of oyster reefs to alter currents creates areas of low-flow and provides refuge for larval fishes, contributing to nursery functions or oyster reefs (Breitburg et al. 1995). Oyster reef habitat is unique in that it often forms the only hard substrate in estuaries typically dominated by soft sediments and vegetation, providing attachment surfaces for other (secondary) sessile organisms and algae. In the northern Gulf of Mexico, several studies have compared the habitat function of various estuarine habitats to oyster reefs. Glancy et al. (2003) found that oyster reefs support a unique decapod crustacean assemblage compared to seagrass and marsh-edge habitats. A number of studies have compared the habitat function of oyster reefs to mud-bottom and marsh-edge habitats and found that oyster reefs support more abundant, diverse, and unique nekton assemblages than other habitat types (Shervette and Gelwick 2008, Stunz et al. 2010), although differences may be influenced by the proximity of other structured habitats [seagrass and marsh-edge (Grabowski et al. 2005)]. Interestingly, one study comparing fish and invertebrate abundance on harvested reefs versus mud bottom in Barataria Bay, Louisiana found greater benthic fish and invertebrate abundances over harvested reef habitat, showing that even altered oyster reefs provide important habitat functions for estuarine organisms (Plunket and La Peyre 2005).

Documented Impacts of Oyster Harvest:

Common oyster harvesting practices in sub-tidal reef areas include dredging and using hand tongs. These harvest methods have been shown to decrease habitat complexity and create two-dimensional (flat) reefs (Lenihan and Peterson 2004). On experimental reefs, hand-tonging oysters has been shown to decrease the vertical relief (height above adjacent substrate) of oyster reefs by 23%; but dredging was shown to be the most destructive oyster harvesting method, decreasing vertical relief by 34% (Lenihan and Peterson 2004). When oyster density is high, oysters growing in clusters will compete for space and the resulting shape of the oyster will be long and narrow. To prevent this, oyster fishermen will typically break apart any oyster clusters they encounter and deposit them back onto the reef, enabling young oysters to grow into a round shape more desirable to consumers, but further decreasing the vertical relief of harvested reefs (Earl Melancon, Nicholls State University, pers. comm.).

Additional alteration to harvested reef substrate in Louisiana comes with the deposition of clean oyster shell and non-shell cultch materials, such as limestone gravel, onto reef areas by state managers to enhance spat settlement and oyster recruitment (LDWF 2010). These cultch plants have likely played an important role in preventing the Louisiana oyster fishery from collapsing. While complete removal of oyster reef and shell habitat is the result of extreme overharvest, the substrate differences between unharvested reefs and reefs that have been successfully harvested for decades have not been studied in detail. Prior to this study, differences in oyster reef substrate between unharvested and harvested reef areas have been documented using side-scan sonar data to map oyster reefs in several areas of Louisiana (Encos 2008), and annual surveys quantifying live oyster stock size in publicly managed state oyster

grounds (LDWF 2010); which typically note the larger stock size of market-size oysters on unharvested reef areas.

Depending on the level of effort and effectiveness of management practices, oyster harvest may possibly alter, decrease, and even eliminate the important ecosystem services that oyster reefs provide. The most immediate documented effect of oyster overharvest is the removal of live oysters and the associated reduction of filtration and removal of nutrients and particulates from the water column. Elevated levels of decomposing phytoplankton increase the occurrence of hypoxic conditions and levels of bacteria (Rothschild et al. 1994, Lenihan and Peterson 1998). It can be predicted that conversion of oyster reef habitat to mud bottom habitat following extreme oyster overharvest would result in the reduction of reef dependent species based on the findings of other studies comparing shell and mud bottom substrates (Plunket and La Peyre 2005, Shervette and Gelwick 2008, Stunz et al. 2010); however, how harvest activities that maintain shell substrate affect the resident oyster reef community is still unclear.

Most existing oyster reef research focuses on comparing species abundance and diversity of artificial or natural reefs to other estuarine habitats (Meyer and Townsend 2000, Glancy et al. 2003, Grabowski et al. 2005, Plunket and La Peyre 2005, Shervette and Gelwick 2008, Stunz et al. 2010) or oyster aquaculture operations (Erbland and Ozbay 2008). Lenihan et al. (2001) mimicked harvest stress using specially constructed reefs that differed in reef height and found no difference in reef community abundance or diversity except when exposed to hypoxic conditions, where higher (6 m) reefs provided increased refuge compared to lower (3 m) reefs. Tolley and Volety (2005) attempted to quantify the role of live oysters in structuring reef communities but found little evidence of species preferences for live oyster clusters versus clusters containing articulated dead oyster shells. Refuge provided by the vertical structure of

oysters has been shown to increase biodiversity in experimental settings (Soniat et al. 2004). Humphries (2010) used variations in reef height as a proxy for complexity and found that a threshold may exist where above a certain point; increasing complexity does not result in increased species abundance and diversity. A number of controlled laboratory studies demonstrate how changes in habitat complexity can alter trophic dynamics among oyster reef species (Grabowski 2004, Grabowski et al. 2008). While the studies mentioned above all provide insight into how oyster harvest could affect reef structure and resident organisms, there are no field studies known that explicitly compare the reef structure and resident community characteristics between established unharvested and harvested oyster reef systems, nor any that examine the more subtle issue of whether moderate harvest activities can alter habitat quality, affect the condition of resident species, and change the structure of the resident community food web.

Species Condition:

Numerous measures of fish condition have been used to effectively evaluate the quality of aquatic habitats (Lloret et al. 2005, Amara et al. 2007, La Peyre et al. 2007). The use of these measures assumes that higher quality habitats provide more food sources, which is reflected morphologically and biochemically in fishes. The weight-length relationships of fish are frequently used as a condition metric due to their accessibility and have been used to compare habitat quality of restored versus natural marsh habitats in southwest Louisiana (La Peyre et al. 2007) and how freshwater pulses effect fish condition in southeast Louisiana (Piazza and La Peyre 2010). Length frequency distributions are also considered a fish condition metric that reflects the ability of a species to survive and reach larger sizes. These distributions are frequently used to determine population structure and inform fisheries management decisions

such as determining harvest size. Length distributions are useful for large, commercial fish species such as swordfish (Vega et al. 2009) where human predation (harvest) is the main controlling factor influencing population structure, but are also useful for small, non-game fish species (Ye et al. 2006) where population structure is determined more by habitat conditions and *in situ* predator-prey interactions.

Additional measures of fish condition include total lipid content, comparing growth rates, RNA:DNA ratios, and relative DNA content (Weber et al. 2003, Gilliers et al. 2004). Total lipid content in adult fishes increases when food sources are abundant (Reznick and Braun 1987, Morgan et al. 2002, Sogard and Spencer 2004). Comparisons of habitat quality using total lipid content have been conducted in the Mediterranean Sea (Lloret et al. 2005). More specific use of lipid content as an indicator of fish condition involves comparing quantities of triacylglycerols (nutritional lipids) to quantities of sterols (structural lipids), which defines available energy reserves (Amara et al. 2007). However, separating individual lipid classes is a more tedious process better suited for studies on fish energetics and often yields similar results as total lipid content (Weber et al. 2003). Growth rates can be determined by examining otolith structure (Amara et al. 2007), which is difficult on small fishes. Analysis of RNA:DNA ratios and relative DNA content is extremely accurate in controlled laboratory experiments; however, high sensitivity and variability limit their applicability to field studies. It has been recommended that combinations of fish condition indices be used to achieve conclusive results (Gilliers et al. 2004); however, most biochemical indices require laboratory facilities and equipment not readily available. Establishing weight-length relationships and length frequency distributions of fish species common across sites should indicate whether oyster harvest influences habitat quality by altering food availability and survivability.

Stable Isotope Analysis:

Stable isotope analysis (using $\delta^{13}C$ and $\delta^{15}N$ values) is becoming an increasingly common technique used to explore the trophic structure of various ecosystems (Fry 2006). The stable isotopes of carbon and nitrogen can identify the importance of various basal food sources and clarify trophic linkages throughout entire food webs (Fry 2006). Stable isotope values have been used to identify the primary basal food sources of mussels in San Francisco Bay (Howe and Simenstad 2007), to compare how estuarine restoration projects affect food webs (Weinstein et al. 2000, Wozniak et al. 2006, Quan et al. 2011), and to identify the trophic position of individual organisms by using nitrogen trophic fractioning to compare $\delta^{15}N$ levels between consumers and basal food sources (Post 2002). Layman et al. (2007) suggested that comparison of the sizes of the various convex hull areas imposed on $\delta^{13}C$ and $\delta^{15}N$ bi-plots can used to estimate trophic diversity of the entire food web as well as niche size (or niche breadth) of individual organisms. Stable isotope analysis is also well suited for impact studies, having recently been used to elucidate the effects of impoundments and non-native species on riverine food webs (Mercado-Silva et al. 2009) and the effects of oyster aquaculture operations on associated food webs (Dubois et al. 2007a, Carlier et al. 2009).

Overall, existing stable isotope methodologies have not been thoroughly applied to different types of oyster reef communities, especially in the northern GOM. Yeager and Layman (2011) have clarified trophic pathways of two oyster reef consumers, and Quan et al. (2011) have identified important basal food sources to oysters reefs and reported elevated trophic positions in organisms found on artificial oysters reefs compared to those found on adjacent salt marshes; indicating that oyster reef food webs may be more complex than surrounding habitats. Dubois et al (2007a, b) determined rates of trophic fractionation and food source partitioning for oysters

and other suspensivors, respectively. Comparing the importance of basal food source contributions, species trophic positions and niche breadths, and community trophic diversity at harvested and unharvested oyster reefs should help to reveal if and how oyster harvest activities alter the food web structure of resident oyster reef communities.

Resident versus Transient Oyster Reef Species:

Oyster reefs serve as important habitat for certain life stages of many estuarine and marine organisms, supporting both resident species and more mobile species that frequent other estuarine habitats. When comparing oyster reef communities, these transient species can complicate analyses (for example, a passing school of fish that was present during a single sampling event can create extreme variation in abundances among sampling events). Transient species are also not appropriate subjects for comparisons of condition or stable isotopes between sites in close proximity. The condition of transient species and their stable isotope values reflect influences from a variety of habitats, not specific oyster reefs. Focusing on the resident oyster reef community fauna that consists primarily of cryptic benthic fish and invertebrate species should isolate effects of harvest on oyster reef habitat function. With the exception of pelagic larval stages, resident species live and spawn on the oyster reef, making them appropriate candidates for fish condition comparisons and stable isotope analysis because their small home ranges reduces variations in food resource consumption and types of predator-prey interactions; enabling condition estimates and food web mapping that accurately characterizes specific locations. These resident species include oysters, mussels, grass shrimp, snapping shrimp, mud crabs, stone crabs, skilletfish, gobies, blennies, and toadfish. Many of these species exclusively use oyster reef habitat (McDonald 1982, Wilson et al. 1982, Lardies et al. 1998, Ross and Rhode 2004, Duci et al. 2009). These organisms are common on Louisiana oyster reefs (Plunket and La

Peyre 2005), making this community an excellent food web for which to examine the effects of oyster harvest activities.

Objectives:

The goal of this study was to quantify and describe the effects of oyster harvest on oyster reef habitat and the resident oyster reef community by comparing harvested and unharvested reef areas. Specific objectives included: 1) characterize and compare reef habitat (substrate/water quality parameters), 2) compare the resident community structure and species-habitat relationships, 3) compare size and condition of dominant species, and 4) compare food web dynamics using stable isotopes.

CHAPTER 2: METHODS

Study Areas:

This study was conducted in four areas of coastal Louisiana that contain extensive sub-tidal oyster reefs: Sabine Lake, Calcasieu Lake, Sister (Caillou) Lake, and Black Bay (Figure 1). All oyster reefs studied are located within public oyster seed grounds and are managed by the Louisiana Department of Wildlife and Fisheries (LDWF). Sabine Lake and northern Calcasieu Lake are currently closed to oyster harvest, while southern Calcasieu Lake, Sister Lake, and Black Bay are actively harvested. Long-term monitoring indicates that salinity and temperature regimes are similar between all selected sites (Table 1). All sites are micro-tidal (< 1m) systems located in remote open-water areas surrounded by coastal marsh. Differences in anthropogenic impacts (e.g. industrial, agricultural, urban runoff, navigation channel maintenance) may exist; however, the dominant difference between sites that affects oyster reef communities is assumed to be the substrate disturbance associated with oyster harvest activities.

Table 1: Long-term mean temperature and salinity (± SE) data for selected project areas. Data provided by the United States Geological Service (USGS).

Site	Temperature (°C)	Salinity	Time Period	USGS Station
Sabine Lake*	24.6 (0.6)	8.0 (0.3)	2007 - 2010	CRMS0684
Calcasieu Lake	22.6 (0.1)	13.5 (0.1)	2002 - 2011	USGS8017095
Sister Lake	22.5 (0.1)	11.6 (0.1)	2002 - 2011	USGS7381349
Black Bay	21.8 (0.1)	11.9 (0.1)	2002 - 2011	USGS7374526

*The only long term data available were pore water measurements taken from adjacent marsh.

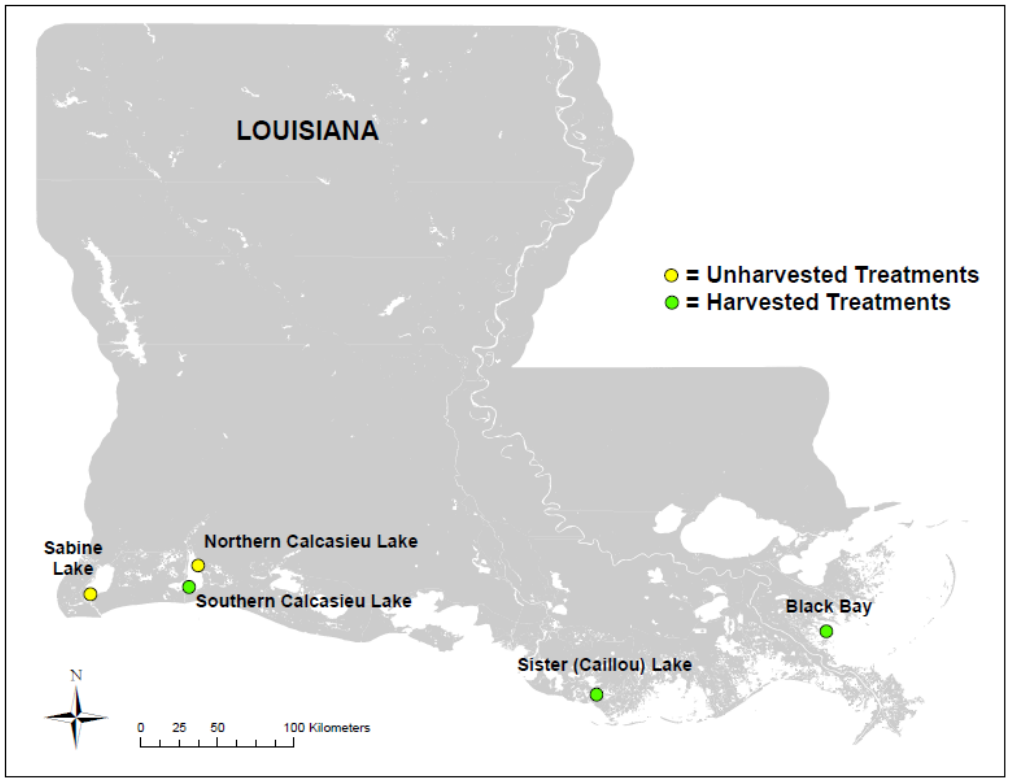

Figure 1: Project sites across coastal Louisiana depicting harvest status.

Unharvested Sites:

Sabine Lake: Sabine Lake is located on the Louisiana-Texas border in southwest Louisiana and this area is jointly managed by the LDWF and the Texas Parks and Wildlife Department (TPWD). There has been no recorded oyster harvest in Sabine Lake since 1965 (TPWD 2010). Side-scan sonar data indicates approximately 599 ha of oyster reef is present in the Louisiana portion of Sabine Lake with an estimated stock size of 1,391,246 sacks of oysters, including seed and market oysters (Encos 2008). These reefs have been closed to harvest in the past due to previously high levels of fecal coliform bacteria released from nearby sewage treatment plants. With coliform levels now in acceptable range, the LDWF and the TPWD are

considering opening Sabine Lake to public oyster harvest [Patrick Banks (LDWF) and Jerry Mambretti (TPWD), pers. comm.].

Northern Calcasieu Lake: Calcasieu Lake is also located in southwest Louisiana, east of Sabine Lake. Northern Calcasieu Lake has remained closed to harvest because fecal coliform levels in this area do not meet standards established by the Louisiana Department of Health and Hospitals (LDHH). In 1969, oyster shell cultch was placed off of Commissary Point in a rectangular area approximately 650 x 100m (6.5 ha) and has presumably remained undisturbed, establishing a substantial reef network of unknown size in the northern portion of Calcasieu Lake (side-scan sonar data is not available for this area).

Harvested Sites:

Southern Calcasieu Lake: Southern Calcasieu Lake has been open to oyster harvest using hand-tongs since 1975. In 2004, the use of small hand dredges (<1 m wide) was permitted. Actual acreage of oyster reef in southern Calcasieu Lake is estimated at 1,581 ha based on 2008 side-scan sonar data. In the 2009-2010 season, 137,074 sacks of oysters were harvested, with the annual LDWF stock assessment predicting a current stock size of 1,327,445 sacks of oysters in this public seed ground.

Sister Lake: Sister Lake is located on the south-central Louisiana coast. Oysters have been harvested in this area since before state record-keeping began. The earliest known cultch deposition occurred in 1906, with recent cultch materials deposited in 2004 (27 ha) and 2009 (63 ha). Side-scan sonar data indicates 922 ha of oyster reef are present in Sister Lake. The 2009-2010 season yielded 13,676 sacks of oysters with an estimated remaining stock size of 295,438 sacks, which represents a 12% increase in stock size from 2009 (LDWF 2010).

Black Bay: Black Bay is located within Breton Sound in southeast Louisiana. Breton Sound typically contributes more than any other area to statewide oyster landings. In 2009, limestone cultch was deposited in Black Bay covering an area of 98 ha. The estimated oyster reef acreage of Breton Sound is 7,037 ha (no side-scan sonar data available). The 2009-2010 seasons yielded 166,495 sacks of oysters with an estimated remaining stock size of 145,576 sacks. The 2010 standing oyster stock of Breton Sound is down approximately 50% from 2009 (LDWF 2010), likely due to the impacts of high freshwater inflow associated with precautionary measures enacted during the 2010 Deepwater Horizon oil spill. During this time, freshwater diversions were opened for extended periods in an effort to prevent oil from entering coastal areas.

Sample Design:

Within each study site, three sample stations were established on the largest oyster reefs located at each site. Reefs were located using data provided by LDWF: side-scan sonar data was available for Sabine, Southern Calcasieu, and Sister Lakes, and GPS coordinates of cultch deposits and historic reef areas were available for northern Calcasieu Lake and Black Bay. Stations (10 x 10m) were located greater than 100 m from the marsh to remove potential marsh edge habitat effects. Sampling occurred between April and October 2010. Figures 2-6 contain maps of oyster reef areas and station locations within each project site.

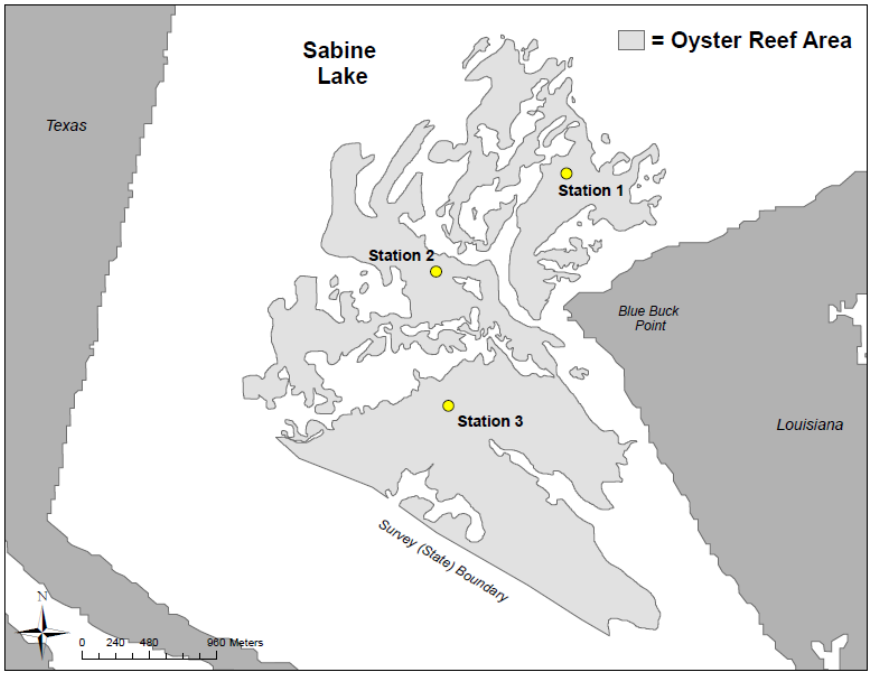

Figure 2: Oyster reef areas and stations within Sabine Lake (unharvested site).

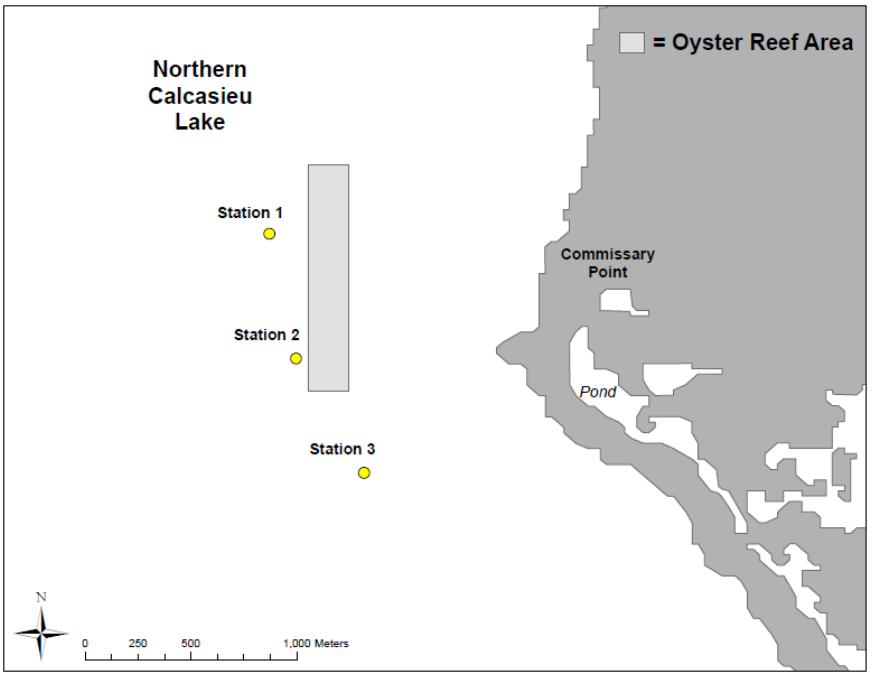

Figure 3: Oyster reef areas and stations within northern Calcasieu Lake (unharvested site).

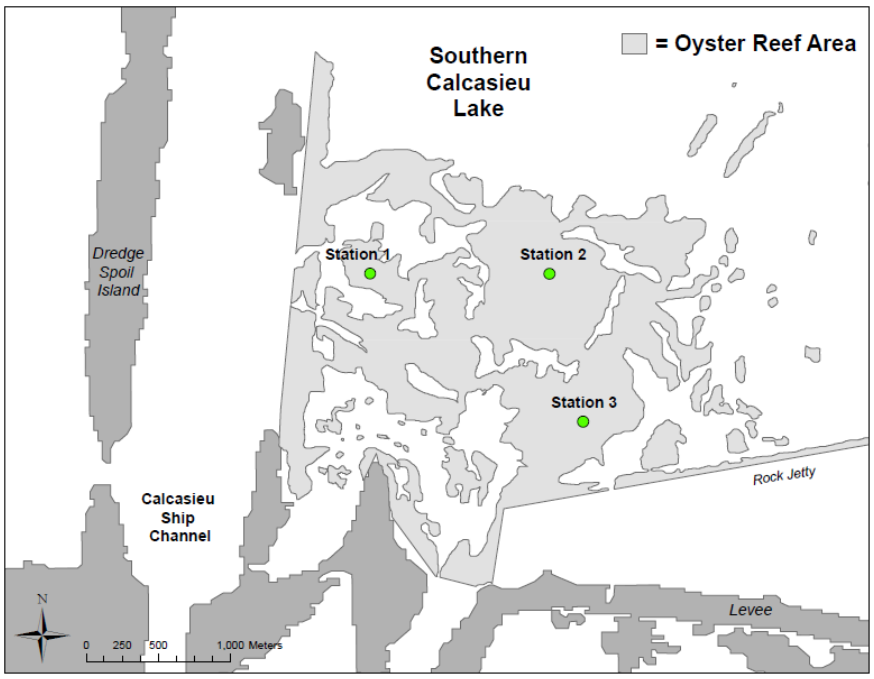

Figure 4: Oyster reef areas and stations within southern Calcasieu Lake (harvested site).

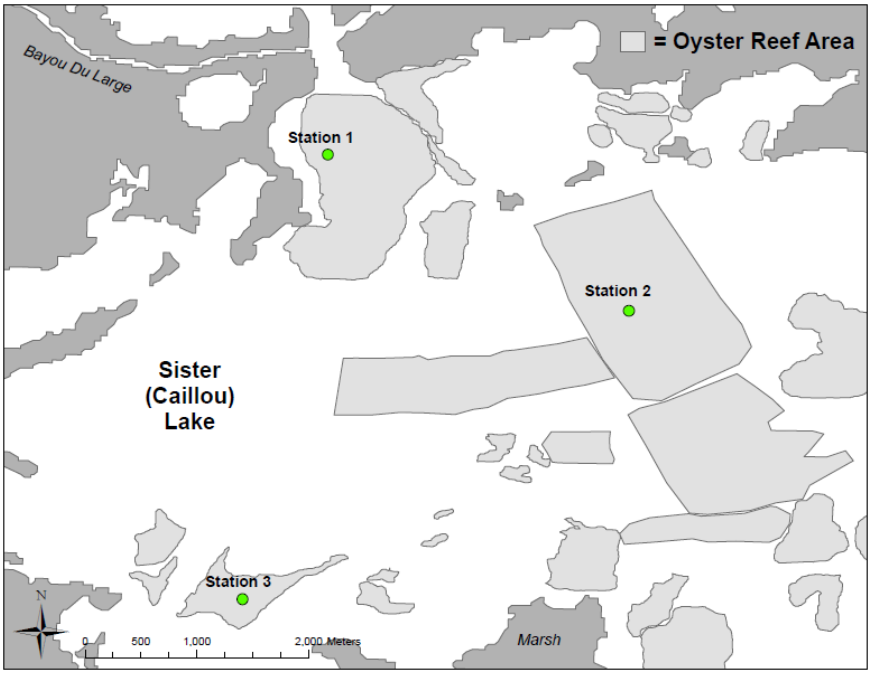

Figure 5: Oyster reef areas and sample stations within Sister Lake (harvested site).

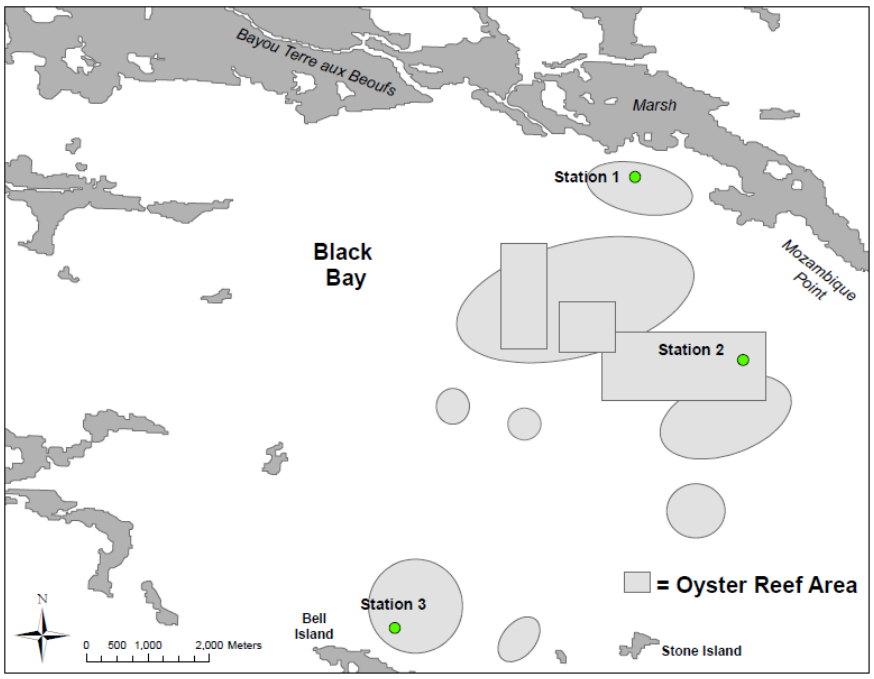

Figure 6: Oyster reef areas and sample stations within Black Bay (harvested site).

Data Collection:

Resident Community:

To collect resident oyster reef fauna, modified benthic trays filled with reef substrate were used. Trays are frequently used to sample oyster reef residents (Lehnert and Allen 2002, Plunket and La Peyre 2005, Yeager and Layman 2011) due to the impracticality of using nets to capture the cryptic species that live within the complex oyster reef matrix. Depths exceeded those required to use lift nets (Tolley and Volety 2005) or a drop sampler (Rozas and Minello 1997, Stunz et al. 2010). Each tray (0.22 m^2) was modified by attaching a drawstring bag net with fine mesh (2.6 mm^2). The sides of this net are gathered at the base of the tray while it is deployed and prior to retrieval, the net is drawn tight to enclose the tray contents before bringing

the tray to the surface, preventing the escape of more mobile organisms (Figure 7). Each tray was filled with 5.0 L of oyster reef substrate collected at adjacent reefs near each study site using a hand dredge. In this manner differences in reef substrate at each site were represented in each tray, and substrate within each tray had similar habitat complexity as the surrounding reef. Trays were deployed in the spring, summer, and fall (temporal change was not of interest). Four (spring/fall) or three (summer) replicate trays were deployed at each station. Each season consisted of two subsequent tray sets. Deployment (soak) times ranged from 1-3 weeks due primarily to weather, but we also found that tray losses were minimized with shorter deployment times. Lehnert and Allen (2002) found that tray soak times of 2-7 days were adequate to sample resident nekton at sub-tidal oyster shell habitats. Upon retrieval, all organisms within the drawstring net were collected, placed on ice, and returned to the laboratory where they were identified to the lowest practical taxon, measured (total length or carapace width, wet-weight), and frozen at -20°C. If a tray was dumped during retrieval (i.e., some tray contents lost due to improper net function), organisms were still collected and identified, but not included in species abundance comparisons.

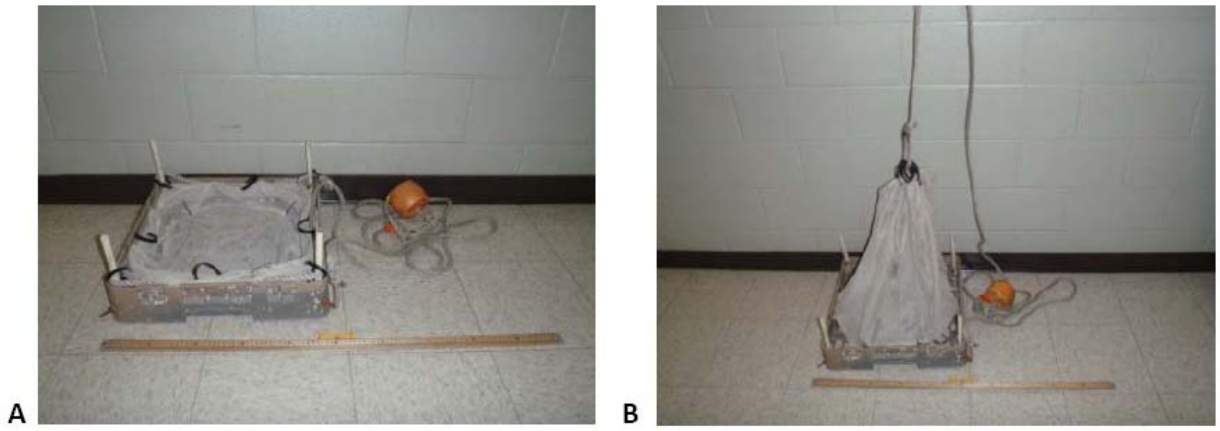

Figure 7: Modified sampling tray used to sample resident oyster reef fauna. An anchor line and drawstring line both connect to buoy. Upon retrieval: drawstring pulled tight, net encloses tray contents, tray pulled to surface. A.) Deployed. B.) Retrieval.

After the spring sampling event, the sampling design changed due to a variety of factors beyond our control, including: 1) the Deepwater Horizon oil spill and associated freshwater impacts to Black Bay during the summer of 2010, and 2) high tray loss (likely resulting from heavy boat traffic) and poor weather conditions at northern Calcasieu which prompted the additional fall sampling event within Calcasieu Lake and the addition of the southern Calcasieu Lake site. A sampling summary can be found in Table 2.

Table 2: Sampling summary showing which how sites were sampled over the course of the study (SA = Sabine Lake, NC = Northern Calcasieu Lake, SC = Southern Calcasieu Lake, SI = Sister Lake, BL = Black Bay).

	Spring	**Summer**	**Fall**	**Total**
Sites Sampled	SA, NC, SI, BL	SA, SI	NC, SC	-
Stations (#)	3	3	3	-
Trays/Station (#)	4	3	4	-
Deployment Time (weeks)	3	1	1	-
Sample Events (#)	2	2	2	6
Total Trays Deployed (#)	96	54	48	198
Total Trays Successfully Retrieved (#)	44	26	32	102

Water Quality:

Prior to tray retrieval during each sampling event, dissolved oxygen (DO, mg L^{-1}), salinity, and temperature (°C) were collected at each station at the surface (~10 cm below the surface) and bottom (~10 cm from the bottom) of the water column using a YSI-85 multi-

parameter sensor. One surface water sample was collected at each station using 250 mL opaque Nalgene bottles, placed on ice, returned to the laboratory, and immediately analyzed for chlorophyll-*a* (µg L^{-1}) (Arar 1997) and total particulate matter (mg L^{-1})(Taras 1971).

Reef Structure:

During the summer and fall tray deployment, reef substrate (5.0 L) in each tray was characterized. Volume and number of oyster clusters, market oysters ($\geq$ 75 mm shell height), seed oysters (25-74 mm), spat ($\leq$ 24 mm), loose shell and box shells (articulated dead oysters) were determined. Oyster clusters were defined as having at least three fused oyster shells (live or dead) of at least seed oyster size. *Geukensia demissa* (ribbed mussels) were collected from 1 L of reef substrate from one tray at each station and number and shell height were recorded. At each station, 20 random depth and pole measurements were taken to determine variation in vertical relief (rugosity) and the spatial extent and type of reef coverage. Pole measurements were grouped into three categories: solid oyster reef, mixed shell/mud substrate, and mud bottom. Each pole measurement consisted of striking the water bottom twice with a PVC pole. If both hits struck shell, the measurement was recorded as solid oyster reef. If only one hit struck shell, mixed shell/mud substrate was recorded. If both hits struck mud, mud substrate was recorded. Totals for each pole category were compared between sites.

Stable Isotope Analysis:

Sample Collection:

Resident organisms used for stable isotope analysis were taken from tray samples. Only species that were found across all sites were used, resulting in the use of samples only from Sabine and Sister Lakes (summer 2010) and northern and southern Calcasieu Lake (fall 2010).

Organisms used included polychaete worms, amphipods, *C. virginica* (eastern oyster), *G. demissa* (ribbed mussels), *Palaemonetes* spp. (grass shrimp), *Eurypanopeus depressus* (flatback mud crab), *Gobiosoma bosc* (naked goby), *Hypsoblennius ionthas* (freckled blenny), and *Gobiesox strumosus* (skilletfish). Two potential basal food sources were also collected for each station: fine particulate organic matter (FPOM, <200µm) and dominant marsh plants. For FPOM samples (representing a pelagic basal food source), 1 L of water was collected from each station, filtered through 200 µm mesh to remove larger particles, placed on ice, and returned to the laboratory. At the adjacent marsh edges of Calcasieu Lake, Sister Lake, and Black Bay, *Spartina alterniflora* was the dominant plant species (> 75% coverage), where at Sabine Lake, *Spartina patens* was dominant (both are C4 species). At each site, the above-ground portions of three plants were collected from the nearest marsh edge (plants being at least 10 m apart), and placed on ice. Marsh plants represented a non-pelagic basal food source. To collect coarse particulate organic matter (CPOM, >200µm, representing a zooplankton sample), a plankton tow fitted with 200 µm mesh was pulled at each station for 2 minutes at a speed of 5 knots. Plankton tow contents were bottled after removing visible detritus and placed on ice. FPOM and CPOM samples were filtered through Whatman glass microfiber filters (GF/F, pre-combusted for 3 hours at 450°C) until clogging and frozen at -20°C.

Composite samples of 15 individuals were used for polychaete worms and amphipods due to their small size. Similar size organisms from each site were chosen for stable isotope analysis (to remove possible ontogenetic dietary shift effects) and rinsed with tap water to remove debris (Fry et al. 2008). Entire *G. demissa* individuals were used once the shell was removed, and adductor muscle tissue was used for *C. virginica* samples. For *Palaemonetes* spp. and *E. depressus* the entire organism was used for stable isotope analysis. For *G. bosc* and *G.*

strumosus, tail portions (all post-anus tissue) were used. Epaxial muscle tissue was used for *H. ionthas* samples. Segments from the base of the stem were used for marsh plant samples.

All samples were dried for 48 hours at 60°C, then ground to a powder. For all samples, lipids were extracted and for organisms containing calcareous exoskeletons, inorganic carbonates were removed (Jacob et al. 2005, Carabel et al. 2006, Soreide et al. 2006, Post et al. 2007, Mateo et al. 2008, Serrano et al. 2008). Lipids were removed by soaking samples in hexane at room temperature, removing the hexane-lipid solution after 24 hours, and repeating this procedure once. Inorganic carbonates (found in shell and exoskeletons) are formed by absorbing ambient carbon, not through digestion, and thus do not reflect dietary patterns of interest (Mateo et al. 2008). Samples containing these carbonates (shrimp, crabs, FPOM, CPOM), were treated with minute quantities (drops) of 1 N hydrochloric acid until fizzing ceased. Samples were then dried for 48 hours at 60°C and packaged into 5 x 9 mm tin capsules. The samples were analyzed for $\delta^{15}N$ and $\delta^{13}C$ by the University of California Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer interfaced with a PDZ Europa 20-20 isotope ratio mass spectrometer.

The δ notation used to report results in this study is determined using the following equation:

$$\delta^{15}N \text{ or } \delta^{13}C = [(R_{Sample}/R_{Standard}) - 1) \times 1000$$

R is ^{15}N: ^{14}N or $\delta^{13}C$: $\delta^{12}C$. The global standard for $\delta^{15}N$ is atmospheric nitrogen and for $\delta^{13}C$ is PeeDee Belemnite (Post 2002).

Isotope values of $\delta^{15}N$ to $\delta^{13}C$ were used to determine basal food source (marsh plant, FPOM) contributions and consumer trophic positions. Fractional source contributions (F) of each organism were determined using the following two source mixing model (Fry 2006):

$$F_{Marsh} = (\delta^{13}C_{Organism} - \delta^{13}C_{FPOM}) / (\delta^{13}C_{Marsh} - \delta^{13}C_{FPOM})$$

$$F_{FPOM} = 1 - F_{Marsh}$$

The $\delta^{13}C_{FPOM}$ and $\delta^{13}C_{Marsh}$ values used were the mean for each basal food source from each site.

Trophic position (TP) was determined using the following equation (Post 2002):

$$TP = 1 + (\delta^{15}N_{Organism} - \delta^{15}N_{Base})/TEF$$

TEF is the trophic enrichment factor, which is the amount of $\delta^{15}N$ enrichment that occurs through each trophic transfer. The TEF can differ by taxa and environment. The overall mean TEF of 2.54‰ reported by Vanderklift and Ponsard (2003) was used as this was similar to marine fish and invertebrate TEFs reported in Caut et al. (2009). Trophic enrichment of $\delta^{13}C$ also occurs through trophic transfer; however, it is too minor to differ ecologically from 0‰ (Post 2002), and thus $\delta^{13}C$ values were not corrected for trophic enrichment. The $\delta^{15}N_{Base}$ value used was determined by plotting mean marsh plant, FPOM, and organism isotope values from each site on a $\delta^{15}N$ (y-axis) and $\delta^{13}C$ (x-axis) bi-plot using ESRI ArcGIS 9 software (ArcMap version 9.3.1). Marsh plant and FPOM points were connected with a "basal" line, and a perpendicular line was drawn from each organism point to the basal line. The $\delta^{15}N$ value at the intersection of the basal line and the perpendicular was used as the $\delta^{15}N_{Base}$ value for each organism, similar to the method used in Post (2002). Isotope bi-plots were also used to generate species and community convex hull areas to compare total trophic diversity of communities and niche breadth of individual organisms (Layman et al. 2007). Convex hull areas were constructed using the convex hull option in the XTools Pro toolbar in ArcGIS. In order to supplement convex hull area analysis, ranges of $\delta^{13}C$ and $\delta^{15}N$ values of the sampled communities and individual organisms were used to compare the diversity of basal food sources ($\delta^{13}C$ range), and trophic position ($\delta^{15}N$ range) (Layman et al. 2007).

Statistical Analyses:

For this study, a significance level of alpha = 0.05 was used. Unless otherwise indicated, SAS Software version 9.2 was used for all analyses.

Water Quality:

To select variables for subsequent analysis, Spearman Correlation Analysis was performed for surface and bottom DO, salinity, and temperature data. Surface and bottom measurements were correlated, so all further analyses were performed only on bottom DO, salinity, and temperature measurements, and chlorophyll-*a* and TPM values. Water quality variables were analyzed separately using generalized mixed models (GLMMs) to test for harvest treatment effects, with sites and stations included in the models as random effects. A negative binomial distribution was used with a log link to compensate for overdispersion in the data. Water quality variables for Sabine Lake and Sister Lake were also analyzed for seasonal (spring, summer) differences using the same GLMM.

Reef Structure:

Substrate data used in analyses include oyster cluster volume, shell volume, live oyster abundance (spat, seed, market, total), number of box shells, mussel abundance, rugosity and pole measurements. For all substrate variables except rugosity, analysis of harvest effects was conducted using separate GLMMs for each variable (random effects: site, station), using a negative binomial distribution with a log link. To determine harvest effects on rugosity, the coefficient of variation for all 20 depth measurements at each station was used as the dependent variable and compared between harvest treatments using a two-sample t-test.

Resident Community:

Abundance and biomass were significantly correlated when examined by Spearman Correlation Analysis, and the number of species was significantly correlated with Shannon diversity index values. Therefore, resident community variables used in further analysis included catch per unit effort, number of species, and abundances of common species (species comprising >1% total abundance). Analysis of harvest effects on resident community variables was conducted using separate GLMMs for each variable (random effects: site, station), using a negative binomial distribution with a log link. Resident community variables for Sabine Lake and Sister Lake were analyzed for seasonal (spring, summer) differences using the same GLMM.

To examine species-environment relationships, canonical correspondence analysis (CCA, CANOCO Software version 4.5) was used to analyze the relationship of resident species abundances and environmental variables (water quality and reef structure variables). Variables used for the CCA were chosen using backward selection. All water quality and reef structure variables were included in the initial CCA and the variable that contributed least to the model was removed. The CCA was re-run and this process was repeated until model assumptions for the proper number of variables were satisfied. Rare species (species comprising <1% total abundance) were removed and remaining common species abundance data was log(x +1) transformed. A Monte Carlo test was used to determine statistical significance of canonical axes using 1000 simulations on the full model.

Species Condition:

Analysis of harvest effects on the mean size (total length or carapace width) of the most abundant species (*G.bosc, E. depressus, Palaemonetes* spp., *G. strumosus, H. ionthas*) was

conducted using separate GLMMs for each species (random effects: site, station), using a negative binomial distribution with a log link. Data from the summer (Sabine and Sister Lake) and fall (Calcasieu Lake) were analyzed both combined and separately. Size (total length or carapace width) distributions were determined for these species between harvest treatments. Individuals were grouped into 5 mm size classes and the frequency of individuals in each class was determined and compared between treatments.

In addition, a measure of the condition of three numerically dominant fish species (*G.bosc, G. strumosus, H. ionthas,*) was calculated using a univariate analysis of covariance (ANCOVA) to investigate length-weight relationships (Vila-Gispert et al. 2000, Oliva-Paterna et al. 2003, La Peyre et al. 2007). Log (x + 1) transformed length and weight data were used, with weight as the dependent variable and length as the covariate. Homogeneity of slopes was tested using an ANCOVA model that included the pooled covariate-factor interaction. A standard ANCOVA model was used to test for differences in y-intercept between treatments if slopes were homogeneous. When slopes were heterogeneous, equality of mean weights was compared at the overall mean covariate value. Again, only data from the summer and fall were used to remove potential seasonal cohort use differences.

Stable Isotope Analysis:

Differences in basal food source (marsh, FPOM) $\delta^{15}N$ and $\delta^{13}C$ values by harvest treatment were tested using two sample t-tests. For most species and community isotope data (species trophic positions, convex hull areas, $\delta^{15}N$ range, and $\delta^{13}C$ range), separate two sample t-tests were used to test for differences between harvest treatments. Data unable to be transformed to normality ($\delta^{15}N$ range for *G. strumosus* and *C. virginica*, basal contributions and trophic

position for *G.bosc* and *Palaemonetes* spp., and trophic position for *C. virginica*) were compared between harvest treatments using a non-parametric Wilcoxon Rank Sum test.

CHAPTER 3: RESULTS

Water Quality:

Chlorophyll-*a* levels were significantly lower at the unharvested treatment than the harvested treatment ($p < 0.0001$) and mean values ranged from 6.95 µg L^{-1} at Sabine Lake to 19.23 µg L-1 at Black Bay (Table 3). There were no differences in DO, salinity, temperature, depth, or total particulate matter (TPM) between harvested and unharvested treatments. While significant seasonal differences were observed only for temperature at Sabine Lake and Sister Lake, temperatures were similarly elevated at each site in the summer and therefore season was not included as a variable in the harvest effect model.

Table 3: Mean water quality measurements (± standard error) taken over the course of the study. Parameters that differed significantly by harvest treatment are indicated in bold.

	Unharvested Sites			**Harvested Sites**			
Parameter	**Sabine Lake**	**Northern Calcasieu Lake**	**Treatment**	**Southern Calcasieu Lake**	**Sister Lake**	**Black Bay**	**Treatment**
Temperature (°C)	27.23 (0.78)	26.14 (0.73)	26.80 (0.55)	24.86 (1.07)	27.63 (0.93)	23.06 (0.65)	25.32 (0.57)
Salinity	12.81 (0.82)	20.68 (0.51)	15.89 (0.78)	19.15 (0.11)	14.70 (0.98)	15.17 (0.65)	16.20 (0.49)
Dissolved Oxygen (mg L^{-1})	5.34 (0.20)	6.62 (0.16)	5.84 (0.16)	6.34 (0.24)	4.77 (0.18)	5.35 (0.10)	5.43 (0.14)
Total Particulate Matter (mg L^{-1})	49.86 (8.22)	69.70 (3.55)	57.62 (5.69)	90.16 (5.33)	54.70 (3.93)	51.11 (5.91)	64.67 (3.74)
Chlorophyll-*a* (µg L^{-1})	6.95 (0.34)	8.36 (0.36)	7.50 (0.27)	16.93 (0.43)	16.59 (1.23)	19.23 (1.56)	17.54 (0.70)
Depth (m)	2.44 (0.02)	1.23 (0.02)	1.96 (0.09)	1.90 (0.03)	2.03 (0.07)	2.31 (0.05)	2.08 (0.39)

Reef Structure:

Volume of oyster clusters was significantly greater on unharvested reefs than harvested reefs ($p = 0.0078$, Table 4, Figure 8). Market oysters were more significantly abundant at unharvested sites ($p = 0.0296$). Remaining reef structure measurements were not significantly different between harvest treatments. Mussel abundance was also greater on unharvested reefs ($p = 0.0573$). Volume of oyster shell was greater on harvested reefs than unharvested reefs ($p = 0.0506$). There were no significant differences in spat, seed, or total oyster abundance, number of box shells, and rugosity and pole measurements between harvest treatments (Table 4, Figure 9). Pole measurements did indicate that more solid reef substrate was present at unharvested sites, where more mixed shell/mud substrate was present at harvested sites (Table 4, Figure 10).

Table 4: Mean reef structure measurements (± standard error) taken over the course of the study. Parameters that differed significantly by harvest treatment are indicated in bold.

Parameter	Unharvested Sites			Harvested Sites		
	Sabine Lake	**Northern Calcasieu Lake**	**Treatment**	**Southern Calcasieu Lake**	**Sister Lake**	**Treatment**
Tray Measurements						
Cluster Volume (L)	3.9 (0.1)	4.4 (0.1)	4.1 (0.1)	1.8 (0.1)	2.9 (0.2)	2.3 (0.1)
Shell Volume (L)	0.3 (0.1)	0	0.14 (0.04)	2.0 (0.1)	0.8 (0.2)	1.5 (0.1)
Oyster Spat (#)	0	9.9 (2.4)	5.1 (1.6)	2.1 (0.7)	4.2 (0.4)	3.0 (0.5)
Seed Oysters (#)	34.7 (2.3)	43.1 (3.9)	39.0 (2.4)	6.0 (0.7)	101.5 (16.54)	45.5 (11.1)
Market Oysters (#)	32.3 (1.8)	17.5 (0.36)	24.6 (1.7)	12.6 (0.7)	9.2 (1.1)	11.2 (0.7)
Total Live Oysters (#)	67.0 (2.9)	70.5 (4.5)	68.8 (2.7)	20.7 (1.1)	114.8 (16.4)	59.7 (11.0)
Box Shells (#)	5.3 (0.5)	1.6 (0.3)	3.4 (0.5)	7.9 (0.59)	1.8 (0.4)	5.4 (0.7)
Mussels (#)	636.7 (61.0)	1,424.7 (22.5)	1,044.1 (80.7)	54.7 (5.7)	319.2 (79.2)	164.1 (40.5)
Station Measurements						
Pole: Reef (#)	14.2 (1.1)	15.5 (1.3)	14.9 (0.8)	12.1 (1.0)	7.3 (1.5)	10.1 (1.0)
Pole: Mixed (#)	5.1 (0.7)	4.5 (1.3)	4.8 (0.7)	7.9 (1.0)	10.7 (0.8)	9.0 (0.7)
Pole: Mud (#)	0.6 (0.3)	0	0.3 (0.2)	0	2.0 (0.9)	0.8 (0.4)
Rugosity (depth CV)	6.4	4.5	2.8	5.14	13.9	2.4

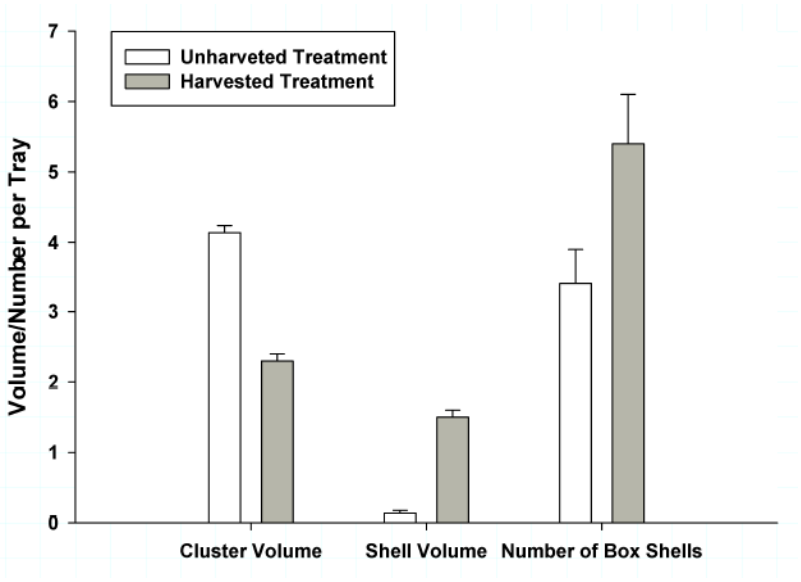

Figure 8: Tray substrate differences between harvest treatments. Values are mean (± standard error) tray values (per 5 L of substrate). Volume of oyster clusters was greater at unharvested reefs, where shell volume was greater at harvested reefs. No significant difference in the number box shells was found between treatments.

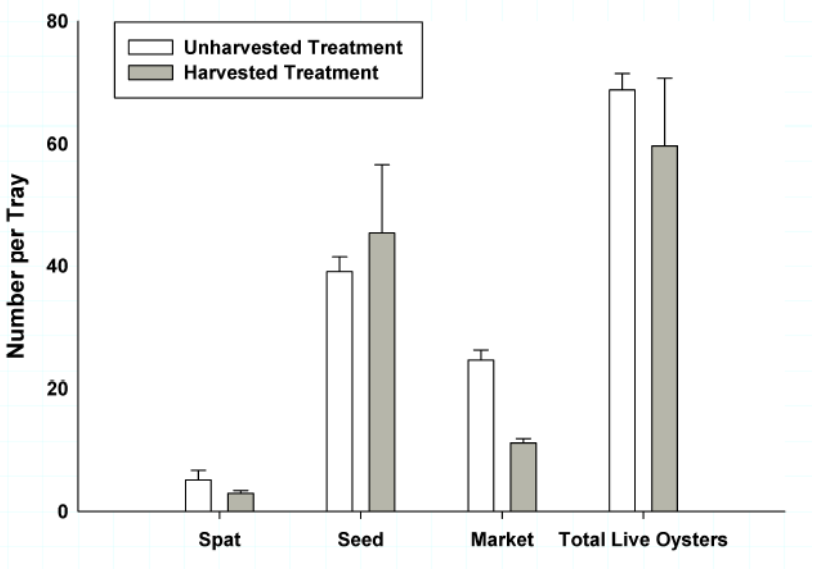

Figure 9: Oyster size class differences by harvest treatment. Values are mean (± standard error) tray values (per 5 L of substrate). The number of market oysters was significantly greater at unharvested reefs. No significant differences for the number of spat, seed, or total live oysters were observed between treatments.

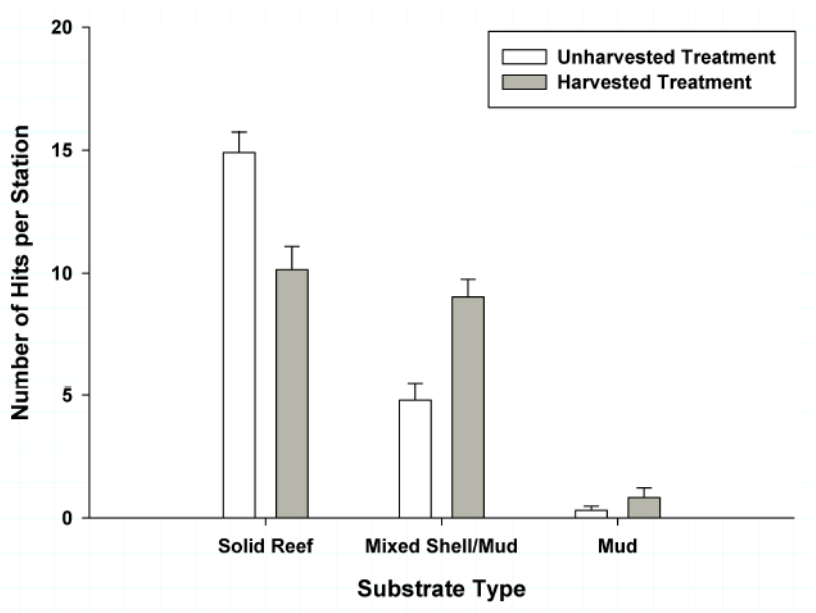

Figure 10: Pole measurements showing amount and type of reef coverage by harvest treatment. Values shown are mean (± standard error) number of hits per station on each substrate type. No significant differences in amount of reef coverage for each type were found between treatments.

Resident Community:

A total of 102 tray samples (52% of 198 possible samples) were successfully collected over the course of this project, with 56 samples from harvested areas and 46 samples from unharvested areas. A total of 6,574 organisms (1,253 fish, 5,321 invertebrates) were collected representing 21 taxa (10 fish taxa, 11 invertebrate taxa; see Table 5). Numerically dominant species included the *Eurypanopeus depressus* (flatback mud crab, 2,418 individuals), *Palaemonetes* spp. (grass shrimp, 2,180 individuals) and *G. bosc* (naked goby, 1,016 individuals), which comprised 85% of all collected organisms. Mean catch per unit of effort (CPUE) for all species was 64.5 ± 3.3 organisms (12.3 ± 1.2 fish, 52.2 ± 2.7 invertebrates) per tray, which converts to an overall estimated mean density of 293.2 organisms (55.9 fish, 237.3

invertebrates) per square meter of oyster reef habitat. Species that contributed most to biomass include *Panopeus herbstii* (Atlantic mud crab, 909.5 g), *E. depressus* (750.7 g), and *Opsanus beta* (gulf toadfish, 638.0 g); which comprised 52% (2.3 kg) of the total biomass collected (4.4 kg). Mean tray biomass was 43.4 $\pm$ 2.8 g, which converts to an estimated mean biomass of 197.3 g per square meter of oyster reef habitat.

There was no difference in total CPUE ($p = 0.8421$), fish CPUE ($p = 0.1538$), or invertebrate CPUE ($p = 0.6810$) between harvest treatments (Figure 11). Mean total, fish, and invertebrate CPUE at unharvested reefs was 60.8 $\pm$ 4.5, 6.7 $\pm$ 0.8, and 54.1 $\pm$ 4.2, respectively; converting to an estimated density of 276.4 organisms (30.5 fish, 247.3 invertebrates) per square meter of unharvested oyster reef habitat. Mean total, fish, and invertebrate CPUE at harvested reefs was 67.5 $\pm$ 4.7, 16.9 $\pm$ 2.0, and 50.6 $\pm$ 3.6 respectively; converting to an estimated density of 306.8 organisms (76.8 fish, 230.0) invertebrates) per square meter of harvested oyster reef habitat.

The mean number of invertebrate species was significantly greater at harvested treatments (4.8 $\pm$ 0.2 species) than unharvested treatments (3.2 $\pm$ 0.1 species, $p = 0.0002$). There were no significant differences in the number of fish species or total number of species between harvest treatments (Figure 12). While significant seasonal differences were observed in species abundances and richness at Sabine Lake and Sister Lake, these variables were similarly elevated at each site in the summer and therefore season not included as variable in the harvest effect model.

For individual species comparisons, *Palaemonetes* spp. CPUE was significantly greater at unharvested reefs (27.9 $\pm$ 3.3) than harvested reefs (16.0 $\pm$ 2.2, $p = 0.0174$); however the

CPUE of other numerically dominant species (*G. bosc* and *E. depressus*) did not significantly differ with harvest treatment (Figure 13). Mean *Alpheus* sp. CPUE was significantly greater at harvested reefs (1.3 ± 0.2) than unharvested reefs (0.1 ± 0.04, $p < 0.0001$). No other species showed a significant difference by harvest treatment.

Table 5: Species abundances (N) , mean catch per unit effort (CPUE ± standard error, unit effort = 0.22 m^2 tray filled with 5 L of reef substrate), and total tray samples collected over the course of the study. Species with significantly different CPUEs by harvest treatment are indicated in bold.

	Unharvested Sites						Harvested Sites								Project	
	Sabine Lake		Northern Calcasieu Lake		Treatment		Southern Calcasieu Lake		Sister Lake		Black Bay		Treatment			
Species	**N**	**Mean**	**N**	**Mean**	**N**	**Mean**	**N**	**Mean**	**N**	**Mean**	**N**	**Mean**	**N**	**Mean**	**N**	**Mean**
Chaetodipterus faber	1	<0.1	0	0	1	<0.1	0	0	1	<0.1	0	0	1	<0.1	2	<0.1
Chasmodes bosquianus	2	0.1(<0.1)	5	0.3(0.1)	7	0.2(0.1)	3	0.2(0.1)	6	0.3(0.1)	0	0	9	0.2(0.1)	16	0.2(0.1)
Gobiesox strumosus	12	0.4(0.1)	15	0.8(0.2)	27	0.6(0.1)	3	0.2(0.1)	31	1.5(0.4)	18	1.0(0.5)	52	0.9(0.2)	79	0.8(0.1)
Gobionellus boleosoma	1	<0.1	0	0	1	<0.1	0	0	3	0.1(0.1)	0	0	3	<0.1	4	<0.1
Gobiosoma bosc	52	1.9(0.2)	167	9.3(1.4)	219	4.8(0.8)	194	11.4(0.6)	413	19.7(3.5)	190	10.6(2.7)	797	14.2(1.7)	1016	10.0(1.1)
Hypsoblennius ionthas	27	1.0(0.3)	5	0.3(0.1)	32	0.7(0.2)	3	0.2(0.1)	54	2.6(0.8)	0	0	57	1.0(0.3)	89	0.9(0.2)
Lutjanus griseus	0	0	2	0.1(0.1)	2	<0.1	0	0	1	<0.1	0	0	1	<0.1	3	<0.1
Myrophis punctatus	1	<0.1	2	0.1(0.1)	3	0.1(<0.1)	0	0	12	0.6(0.2)	2	0.1(0.1)	14	0.3(0.1)	17	0.2(0.1)
Opsanus beta	14	0.5(0.1)	1	0.1(0.1)	15	0.3(0.1)	1	0.1(0.1)	8	0.4(0.1)	2	0.1(0.1)	11	0.2(0.1)	26	0.3(0.1)
Paralichthys lethostigma	1	<0.1	0	0	1	<0.1	0	0	0	0	0	0	0	0	1	<0.1
Fish Total	111	4.0(0.5)	197	10.9(1.4)	308	6.7(0.8)	204	12.0(0.6)	529	25.2(4.1)	212	11.8(2.7)	945	16.9(2.0)	1253	12.3(1.2)
***Alpheus* sp.**	2	0.1(<0.1)	2	0.1(0.1)	4	0.1(<0.1)	17	1.0(0.4)	33	1.6(0.4)	22	1.2(0.3)	72	1.3(0.2)	76	0.7(0.1)
Callinectes sapidus	0	0	47	2.6(0.8)	47	1.0(0.4)	58	3.4(1.1)	54	2.6(0.7)	37	2.1(0.4)	149	2.7(0.5)	196	1.9(0.3)
Clibanarius vittatus	0	0	0	0	0	0	0	0	6	0.3(0.2)	10	0.6(0.3)	16	0.3(0.1)	16	0.2(0.1)
Eurypanopeus depressus	405	14.5(1.6)	614	34.1(3.9)	1019	22.2(2.3)	639	37.6(3.1)	513	24.4(4.6)	247	13.7(3.6)	1399	25.0(2.6)	2418	23.7(1.7)
Farfantepenaeus aztecus	1	<0.1	0	0	1	<0.1	3	0.2(0.1)	4	0.2(0.1)	0	0	7	0.1(0.1)	8	0.1(<0.1)
Litopenaeus setiferus	2	0.1(0.1)	0	0	2	<0.1	0	0	0	0	0	0	0	0	2	<0.1
Menippe mercenaria	1	<0.1	7	0.4(0.1)	8	0.2(0.1)	21	1.2(0.3)	13	0.6(0.2)	10	0.6(0.2)	44	0.8(0.1)	52	0.5(0.1)
Rhithropanopeus harrisii	2	<0.1	1	0.1(0.1)	3	0.1(<0.1)	0	0	85	4.0(1.0)	23	1.3(0.7)	108	1.9(0.5)	111	1.1(0.3)
***Palaemonetes* spp.**	839	30.0(4.8)	443	24.6(4.0)	1282	27.9(3.3)	245	14.4(2.8)	422	20.1(5.0)	231	12.8(2.6)	898	16.0(2.2)	2180	21.4(2.0)
*Panopeus herbstii**	118	4.2(0.4)	3	0.2(0.1)	121	2.6(0.4)	59	3.5(0.5)	62	3.0(0.6)	19	1.1(0.4)	140	2.5(0.3)	261	2.6(0.2)
Petrolisthes armatus	0	0	0	0	0	0	1	0.1(0.1)	0	0	0	0	1	<0.1	1	<0.1
Invertebrate Total	1370	48.8(5.3)	1117	62.1(6.4)	2487	54.1(4.2)	1043	61.4(4.9)	1192	56.8(6.7)	599	33.3(4.5)	2834	50.6(3.6)	5321	52.2(2.7)
Project Total	1481	52.9(5.5)	1314	73(6.9)	2795	60.8(4.5)	1247	73.4(5.4)	1721	82.0(9.5)	811	45.1(5.3)	3779	67.5(4.7)	6574	64.5(3.3)
Total Tray Samples	28		18		46		17		21		18		56		102	

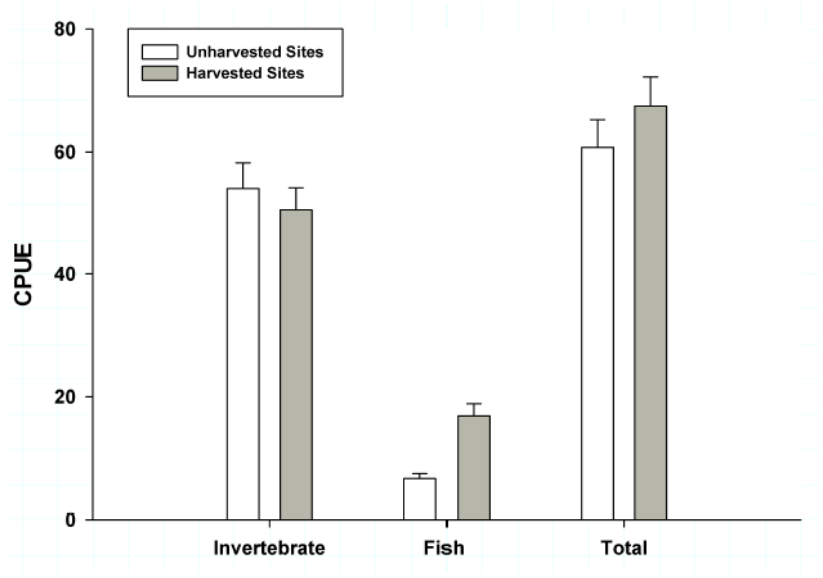

Figure 11: Mean catch per unit effort mean (CPUE ± standard error, unit effort = 0.22 m^2 tray filled with 5 L of reef substrate) for resident organisms by harvest treatment. No significant differences in invertebrate, fish, or total CPUE were found between treatments.

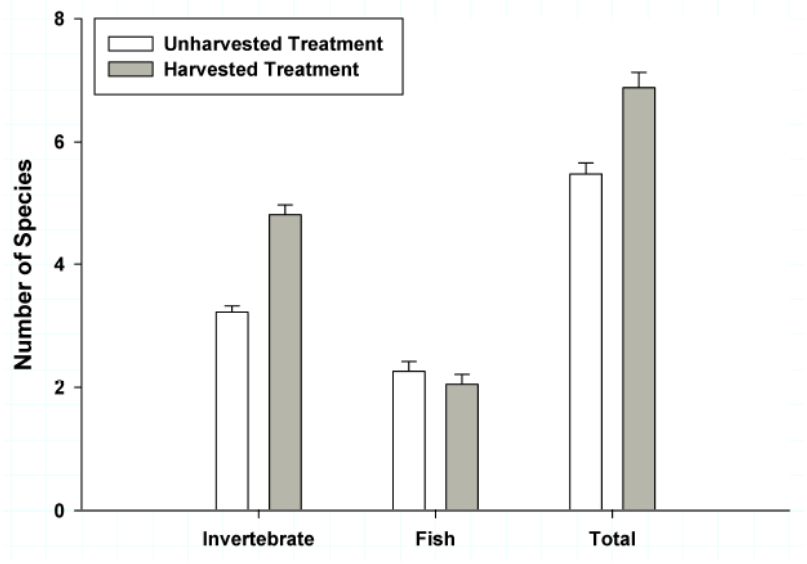

Figure 12: Mean number of species (± standard error) per tray (0.22 m^2 tray filled with 5 L of reef substrate) for resident organisms by harvest treatment. Significantly more invertebrate species were found at harvested reefs. No significant differences in the number of fish species or total species were found between harvest treatments.

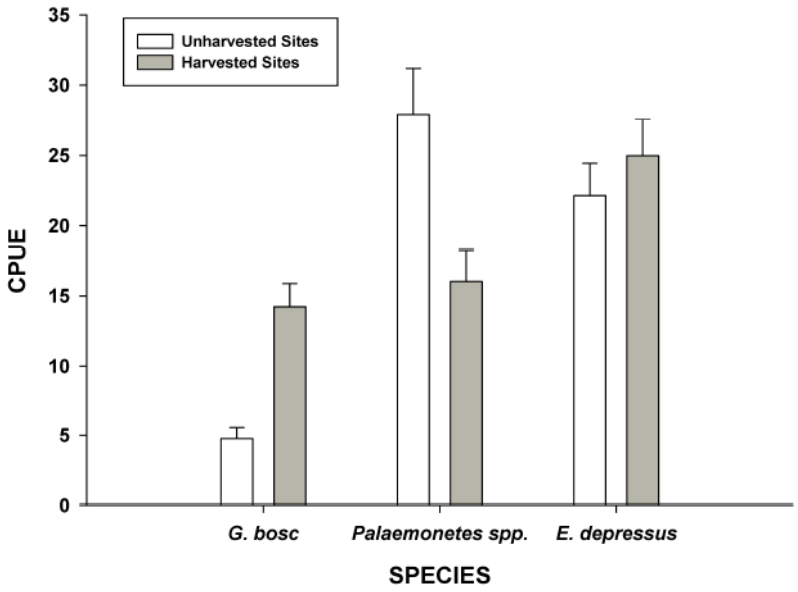

Figure 13: Mean catch per unit effort (CPUE ± standard error, unit effort = 0.22 m^2 tray filled with 5 L of reef substrate) for dominant species by harvest treatment. Significantly more *Palaemonetes* spp. were collected at unharvested reefs. No significant differences in *G. bosc* or *E. depressus* abundance were found between treatments.

Species-Environment Relationships:

The dominant environmental variables remaining in the CCA after backward selection were volume of shell, total number of live oysters, reef pole measurements, and chlorophyll-*a* levels; indicating that these variables were most important in determining the abundances of the common resident species included in the analysis. Monte Carlo simulations resulted in significant relationship between these variables and species abundance ($p = 0.001$, Figure 14). The first two axes of the CCA explained 86.0% of the species-environment variation. Axis 1 explained 58.3% of the species-environment variation (eigenvalue = 0.11) and was negatively associated with reef pole measurements ($r = -0.69$), and positively associated with chlorophyll-*a* levels ($r = 0.65$), distinguishing species that may be associating with solid reef areas or reefs with

low filtration rates. *Alpheus* sp. and *R. harrisii* were associated with higher chlorophyll-*a* levels and not associated with solid reef structure. Axis 2 explained 27.7% of the species-environment variation (eigenvalue = 0.05) and was negatively associated with shell volume (r = -0.70), and positively associated with the total number of live oysters (r = 0.70), distinguishing species that may associate with live oysters versus hard structure. *H. ionthas* and *G. strumosus* were strongly associated with the number of live oysters. Other species were not found to associate with any of these variables.

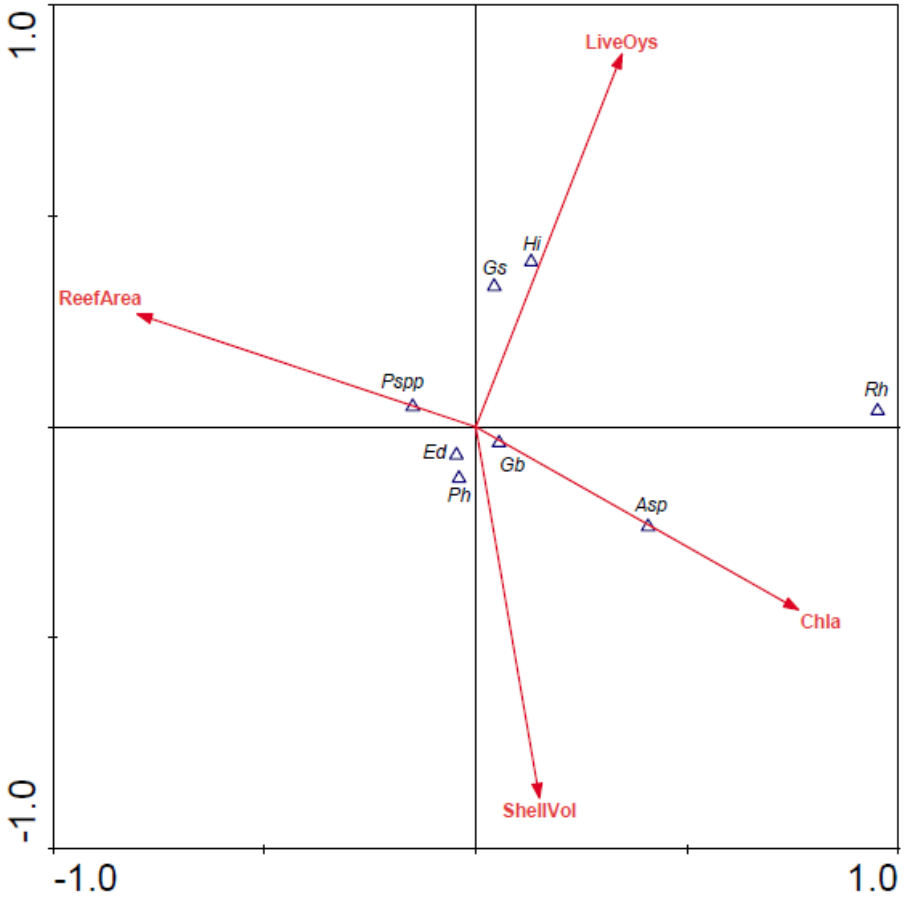

Figure 14: Canonical correspondence bi-plot relating species abundances with habitat variables. Species abbreviations: *Asp = Alpheus* sp., *Ed = E. depressus*, *Gb = G. bosc*, *Gs = G. strumosus*, *Hi = H. ionthas*, *Ph = P. herbstii*, *Pspp = Palaemonetes* spp., *Rh = R. harrisii*. Environmental abbreviations: **Shellvol** = volume of oyster shell, **Chla** = chlorophyll-*a*, **LiveOys =** total number of live oysters, **ReefArea =** number of solid reef pole measurements.

Species Condition:

There were no differences observed in the mean sizes of numerically dominant species and common fish species by harvest treatment (Table 6). Size frequency distributions (Figure 15) for *G. bosc* suggest that a spawning event recently occurred in Calcasieu Lake, primarily in the northern unharvested site as evidenced by the large number of age = 0 individuals. When Calacasieu Lake sites were removed, a higher proportion of large individuals were found at the remaining unharvested site (Sabine Lake) than the remaining harvested site (Sister Lake). Similarly, size frequency distributions of *G. strumosus* and *H. ionthas* show that a higher proportion of larger individuals were present at unharvested sites. Size frequency distributions of *E. depressus* and *Palaemonetes* spp. were similar between harvest treatments.

Table 6: Mean organism size (± standard error) for each site. Sizes (mm) reported are total length (fish, shrimp), carapace width (crabs), and shell height (mussels).

	Unharvested Sites			**Harvested Sites**		
Species	**Sabine Lake**	**Northern Calcasieu Lake**	**Treatment**	**Southern Calcasieu Lake**	**Sister Lake**	**Treatment**
Gobiosoma bosc	32.6 (1.8)	18.3 (0.8)	20.5 (0.8)	23.3 (0.6)	28.2 (0.3)	26.0 (0.4)
Gobiesox strumosus	32.3 (0.8)	44.7 (2.9)	39.3 (2.1)	38.3 (4.3)	26.7 (0.7)	27.8 (1.0)
Hypsoblennius ionthas	47.4 (1.9)	67.2 (2.0)	50.8 (2.2)	60.0 (4.5)	35.8 (1.4)	37.3 (1.5)
Eurypanopeus depressus	9.6 (0.2)	8.7 (0.2)	9.0 (0.1)	8.0 (0.1)	9.3 (0.2)	8.4 (0.1)
Palaemonetes spp.	22.3 (0.1)	20.8 (0.6)	21.6 (0.3)	21.5 (0.3)	24.5 (0.4)	22.7 (0.2)

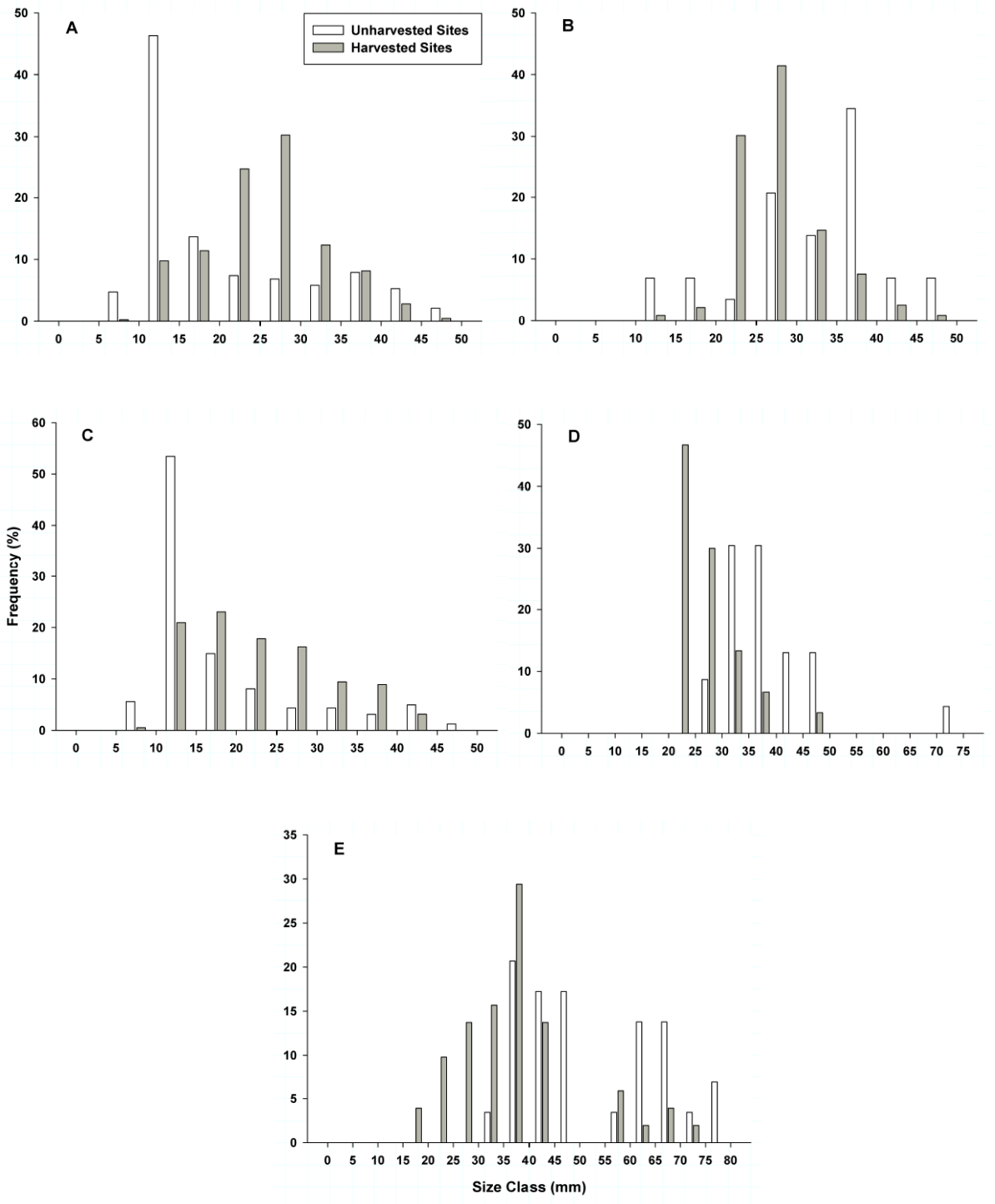

Figure 15: Size frequency distributions (% total treatment abundance) for common fish species by harvest treatment. Size classes are in 5 mm increments. **A:** *G. bosc* (all sites) **B:** *G. bosc* (excluding Calcasieu Lake sites) **C:** *G. bosc* (only Calcasieu Lake sites) **D:** *G. strumosus* **E:** *H. ionthas*.

G. bosc condition was greater at unharvested sites than harvested sites ($p < 0.0001$, Table 7). Because Calcasieu Lake sites contained abundunt age = 0 gobies, the ANCOVA was rerun excluding these sites to prevent possible bias from ontogenetic morphological changes. Condition comparisons among remaining sites still showed higher *G. bosc* condition at the unharvested site (Sabine Lake) than harvested site (Sister Lake, $p = 0.006$). The condition of *G. strumosus* and *H. ionthas* did not differ between harvest treatments. The weight-length relationships of *G. bosc* and *G. strumosus* contained heterogeneous slopes, so least-square means were used to test for differences in weight at the mean length value for each species. Slopes of the weight-length relationship for *H. ionthas* were homogeneous, so y-intercepts were used to determine condition.

Table 7: Weight-length ANCOVA regressions and harvest comparison p-values of the three dominant fish species used to determine and compare condition. Significant differences are in bold.

Species	Treatment	Regression	ANCOVA p
Gobiosoma bosc	Harvested	y = 3.290x – 5.334	**<0.0001**
	Unharvested	y = 3.022x – 4.928	
Gobiosoma bosc (excluding Calcasieu Lake sites)	Harvested	y = 2.861x – 4.692	**0.0060**
	Unharvested	y = 2.617x – 4.298	
Gobiesox strumosus	Harvested	y = 2.537x – 4.091	0.9211
	Unharvested	y = 3.031x – 4.834	
Hypsoblennius ionthas	Harvested	y = 2.890x – 4.598	0.0615
	Unharvested	y = 2.921x – 4.640	

Stable Isotope Analysis:

Mean $\delta^{13}C$ and $\delta^{15}N$ values of marsh and FPOM (basal food sources) did not differ between harvest treatments or sites (Table 8, Figure 16). Two-source mixing model results (Figure 17, Table 9) for determining basal food source contributions indicate that pelagic basal food sources (FPOM) contributes more to the resident oyster reef community food web than non-pelagic sources (marsh plant) regardless of harvest treatment (all FPOM source fractions > 0.50). When comparing harvest treatments, harvested sites showed significantly elevated mean non-pelagic and lower mean pelagic source fractions than unharvested sites for most species (CPOM [$p = 0.0159$], *C. virginica* [$p < 0.0001$], *Palaemonetes* spp. [$p < 0.0001$], *G. bosc* [$p < 0.0001$], and *H. ionthas* [$p = 0.0187$]). Mean source fractions for *E. depressus* did not differ with harvest treatment. Insufficient numbers of amphipods, polychaete worms, and *O. beta* were collected to conduct stable isotope analysis on these organisms. CPOM samples were dominated by ctenophores.

Table 8: Sample sizes (N) and mean $\delta^{13}C$ and $\delta^{15}N$ values (± standard error) for samples collected over the course of the study.

	Unharvested Sites						Harvested Sites					
	Sabine Lake			Northern Calcasieu Lake			Southern Calcasieu Lake			Sister Lake		
Sample	**N**	**$\delta^{13}C$**	**$\delta^{15}N$**	**N**	**$\delta^{13}C$**	**$\delta^{15}N$**	**N**	**$\delta^{13}C$**	**$\delta^{15}N$**	**N**	**$\delta^{13}C$**	**$\delta^{15}N$**
Basal Food Sources												
Marsh Plant	3	-12.81 (0.10)	7.09 (1.32)	3	-13.16 (0.21)	5.34 (0.28)	3	-13.35 (0.18)	6.64 (0.61)	3	-12.87 (0.07)	5.40 (0.54)
FPOM	3	-28.94 (0.24)	7.31 (0.01)	3	-24.97 (0.39)	5.47 (0.88)	3	-26.04 (1.13)	4.19 (2.95)	3	-28.16 (0.20)	3.02 (1.44)
Community												
CPOM	3	-25.81 (0.62)	-25.81 (0.62)	3	-23.83 (0.21)	11.42 (0.98)	3	-23.22 (0.42)	14.71 (0.32)	3	-24.51 (0.57)	10.82 (1.46)
Geukensia demissa	15	-25.69 (0.11)	8.99 (0.09)	15	-23.97 (0.08)	9.17 (0.07)	0	-	-	15	-24.83 (0.15)	6.94 (0.06)
Crassostrea virginica	15	-23.70 (0.12)	11.54 (0.07)	15	-22.54 (0.08)	11.64 (0.20)	15	-20.49 (0.08)	12.01 (0.08)	15	-23.20 (0.13)	9.36 (0.06)
Eurypanopeus depressus	15	-21.03 (0.59)	11.60 (0.30)	15	-21.61 (0.50)	11.42 (0.13)	15	-20.66 (0.30)	12.50 (0.12)	15	-22.86 (0.43)	8.92 (0.16)
Palaemonetes spp.	15	-23.47 (0.16)	12.90 (0.15)	15	-21.31 (0.18)	12.91 (0.21)	15	-20.08 (0.09)	13.87 (0.08)	15	-23.05 (0.11)	10.71 (0.14)
Gobiesox strumosus	3	-21.93 (0.20)	13.88 (0.09)	3	-21.03 (0.07)	13.40 (0.17)	3	-19.85 (0.07)	14.91 (0.09)	3	-22.17 (0.49)	11.89 (0.18)
Hypsoblennius ionthas	3	-23.15 (0.30)	14.30 (0.24)	3	-21.67 (0.22)	13.70 (0.16)	3	-20.12 (0.12)	15.16 (0.11)	3	-23.00 (0.18)	11.92 (0.25)
Gobiosoma bosc	15	-23.12 (0.14)	14.51 (0.14)	15	-21.56 (0.06)	14.42 (0.18)	15	-19.87 (0.07)	15.77 (0.08)	15	-22.86 (0.20)	12.03 (0.13)

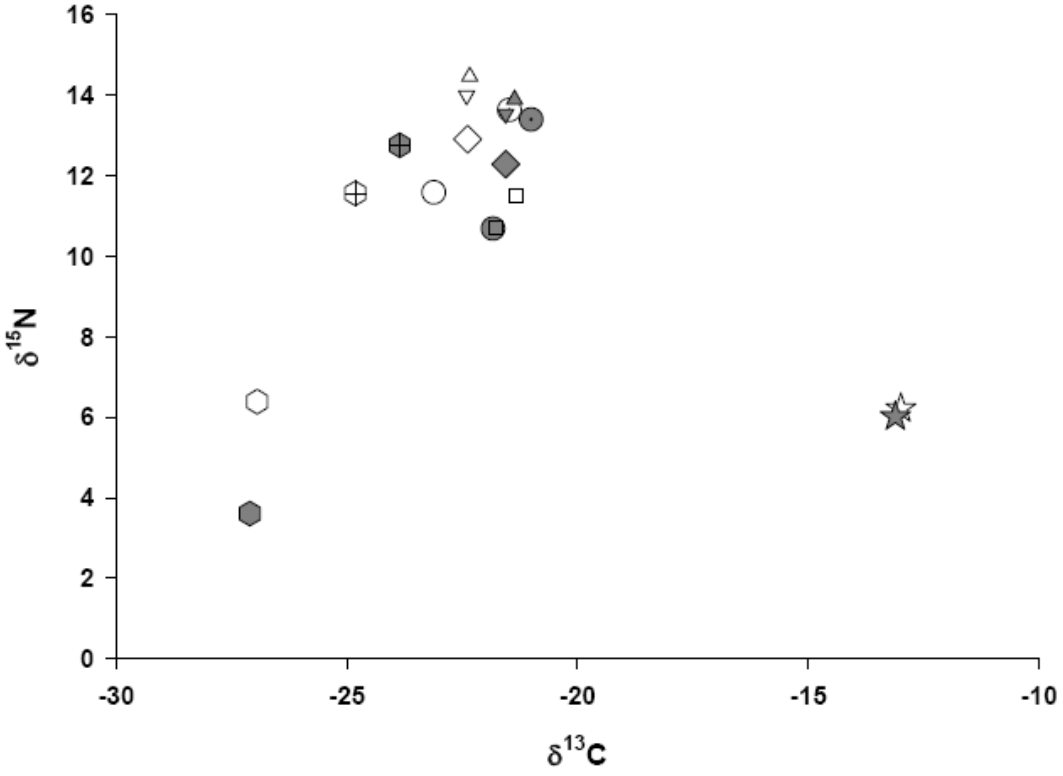

Figure 16: Bi-plot of basal food source and resident species mean δ values. Shaded symbols indicate harvested site means and hollow symbols indicate unharvested site means. Hexagons = FPOM, stars = marsh plant, crossed hexagons = CPOM, circles = C. virginica, squares = E. depressus, diamonds = Palaemonetes spp., dotted circles = G. strumosus, inverted triangles = H. ionthas, and triangles = G. bosc.

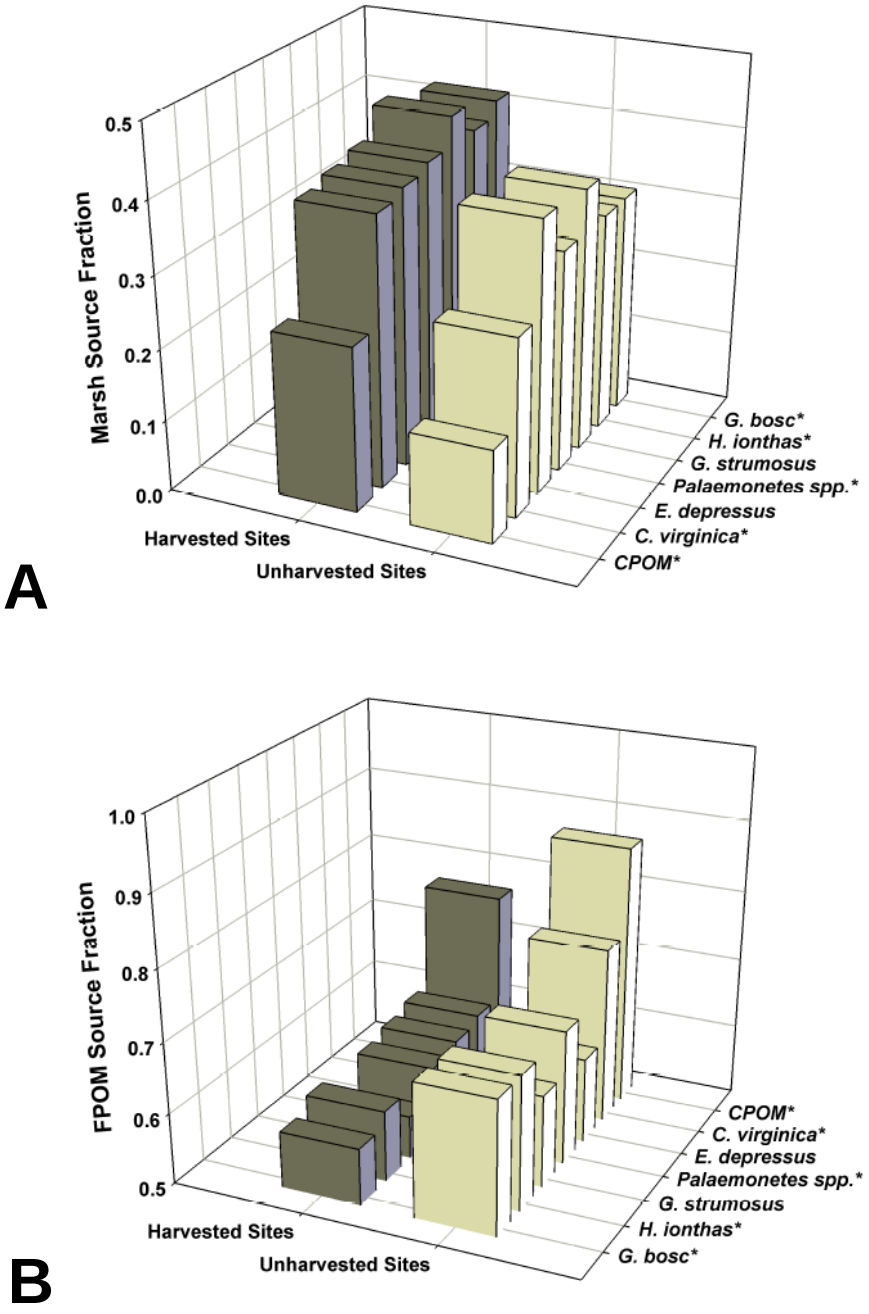

Figure 17: Two-source mixing model results showing source fractions of marsh (A) and fine particulate organic matter (FPOM; B) for sampled organisms at harvested and unharvested sites. Organisms with significant source fraction differences between harvest treatments are indicated with an asterix (*). Note scale and label changes in part B.

Table 9: Mean basal food source contributions (± SE) for organisms sampled over the course of the study. F_{Marsh} = marsh plant (non-pelagic) source fraction and F_{FPOM} = fine particulate organic matter (pelagic) source fraction.

	Unharvested Sites				**Harvested Sites**			
	Sabine Lake		**Northern Calcasieu Lake**		**Southern Calcasieu Lake**		**Sister Lake**	
Sample	**F_{Marsh}**	**F_{FPOM}**	**F_{Marsh}**	**F_{FPOM}**	**F_{Marsh}**	**F_{FPOM}**	**F_{Marsh}**	**F_{FPOM}**
CPOM	0.17 (0.04)	0.83 (0.04)	0.10 (0.02)	0.90 (0.02)	0.22 (0.03)	0.77 (0.03)	0.24 (0.04)	0.76 (0.04)
Geukensia demissa	0.18 (0.01)	0.82 (0.01)	0.08 (0.01)	0.92 (0.01)	-	-	0.22 (0.01)	0.78 (0.01)
Crassostrea virginica	0.30 (0.01)	0.70 (0.01)	0.21 (0.01)	0.79 (0.01)	0.44 (0.01)	0.56 (0.01)	0.33 (0.01)	0.67 (0.01)
Eurypanopeus depressus	0.47 (0.04)	0.53 (0.04)	0.28 (0.04)	0.72 (0.04)	0.42 (0.02)	0.58 (0.02)	0.35 (0.03)	0.65 (0.03)
Palaemonetes spp.	0.31 (0.01)	0.69 (0.01)	0.31 (0.02)	0.69 (0.02)	0.47 (0.01)	0.53 (0.01)	0.33 (0.01)	0.67 (0.01)
Gobiesox strumosus	0.41 (0.01)	0.59 (0.01)	0.33 (0.01)	0.67 (0.01)	0.49 (0.01)	0.51 (0.01)	0.39 (0.03)	0.61 (0.03)
Hypsoblennius ionthas	0.33 (0.02)	0.67 (0.02	0.28 (0.02)	0.72 (0.02)	0.47 (0.01)	0.53 (0.01)	0.34 (0.01)	0.66 (0.01)
Gobiosoma bosc	0.34 (0.01)	0.66 (0.01)	0.29 (0.01)	0.71 (0.01)	0.49 (0.01)	0.51 (0.01)	0.35 (0.01)	0.65 (0.01)

Mean trophic positions of all species (Figure 18, Table 10) except *H. ionthas* were significantly elevated at harvested sites (all p-values < 0.035). The mean trophic position of *H. ionthas* was higher at harvested sites, but it was not significant (p = 0.0583). The trophic order of sampled organisms was very similar between harvest treatments (from lowest trophic position to the highest: *C. virginica/E. depressus, Palaemonetes spp., G. strumosus, H. ionthas, and G. bosc*), with the exception of CPOM. The CPOM samples shifted from the second lowest trophic position at unharvested sites to a position closer to that of fish at harvested sites and showed the greatest variability (highest standard error) of all sample types at all stations. Table 10 also contains mean $\delta^{13}C$ and $\delta^{15}N$ bi-plot measurements (convex hull areas, $\delta^{13}C$ and $\delta^{15}N$ ranges) for sampled organisms and communities. There was no difference in convex hull areas, or $\delta^{13}C$ and $\delta^{15}N$ ranges for species or communities between harvest treatments.

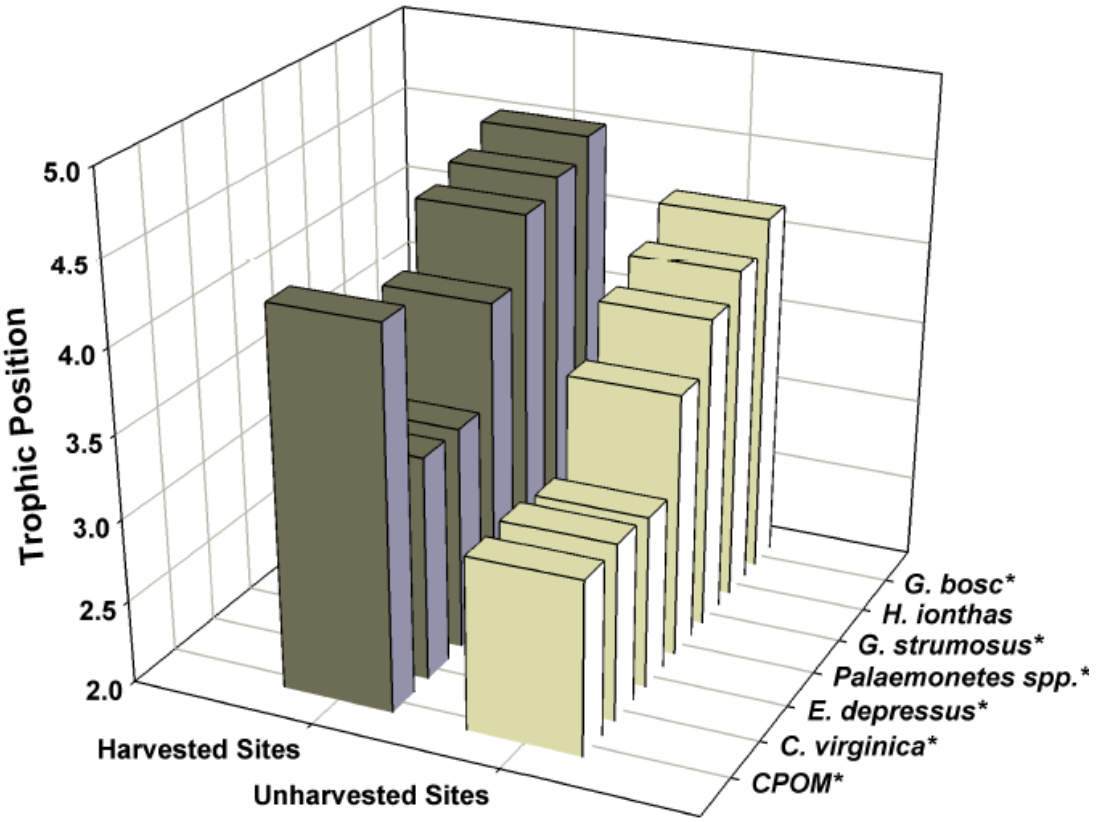

Figure 18: Mean trophic positions for sampled organisms at harvested and unharvested sites. Organisms with significant trophic position differences between harvest treatments are indicated with an asterix (*).

Table 10: Mean trophic position (TP, ± SE), convex hull areas (CH), and ranges of $\delta^{13}C$ (CR) and $\delta^{15}N$ (NR) for organisms sampled over the course of this study. *Community totals exclude *G. demissa* since it was not collected at all sites.

	Unharvested Sites								**Harvested Sites**							
	Sabine Lake				**Northern Calcasieu Lake**				**Southern Calcasieu Lake**				**Sister Lake**			
Sample	**TP**	**CH**	**CR**	**NR**	**TP**	**CH**	**CR**	**NR**	**TP**	**CH**	**CR**	**NR**	**TP**	**CH**	**CR**	**NR**
CPOM	2.75 (0.22)	1.61	2.02	1.83	3.34 (0.39)	1.08	0.67	3.4	4.78 (0.12)	0.69	1.43	1.00	3.77 (0.54)	3.55	1.98	5.04
Geukensia demissa	1.68 (0.04)	1.15	1.55	1.07	2.46 (0.03)	0.60	1.02	0.87	-	-	-	-	2.30 (0.02)	0.57	1.85	0.63
Crassostrea virginica	2.69 (0.03)	0.92	1.75	0.88	3.44 (0.08)	1.83	1.08	3.48	3.56 (0.03)	0.66	1.06	1.00	3.14 (0.02)	0.70	1.47	0.91
Eurypanopeus depressus	2.73 (0.11)	13.34	5.61	3.92	3.36 (0.05)	6.81	6.85	1.59	3.76 (0.06)	2.64	3.66	1.67	2.95 (0.06)	8.30	1.48	2.05
Palaemonetes spp.	3.23 (0.06)	1.72	1.82	2.07	3.94 (0..08)	4.40	2.77	3.2	4.24 (0.03)	0.73	1.24	1.12	3.65 (0.05)	1.82	5.49	1.67
Gobiesox strumosus	3.62 (0.04)	0.10	0.68	0.31	4.14 (0.07)	0.05	0.23	0.59	4.61 (0.04)	0.01	0.24	0.30	4.05 (0.04)	0.06	1.54	0.58
Hypsoblennius ionthas	3.78 (0.10)	0.08	1.03	0.81	4.25 (0.06)	0.18	0.75	0.49	4.73 (0.03)	0.01	0.42	0.37	4.11 (0.10)	0.22	0.59	0.80
Gobiosoma bosc	3.87 (0.05)	2.08	1.74	2.05	4.54 (0.07)	0.99	0.91	2.46	4.94 (0.03)	0.74	0.70	1.02	4.14 (0.04)	1.57	2.00	1.50
Community*	-	29.50	8.88	5.43	-	24.05	6.85	6.64	-	15.63	7.29	4.64	-	25.24	6.57	5.40

CHAPTER 4: DISCUSSION

Oyster harvest appears to influence reef habitat both physically and biologically by altering reef structure and the level of filtration provided by the presence of live oysters. Overall refuge capacity was not substantially altered between reef types, however certain species showed preferences for reef microhabitat conditions. The abundance of large living oysters, substrate heterogeneity, and interstitial space size appear to be the dominant reef characteristics that regulate resident community structure (Figure 19).

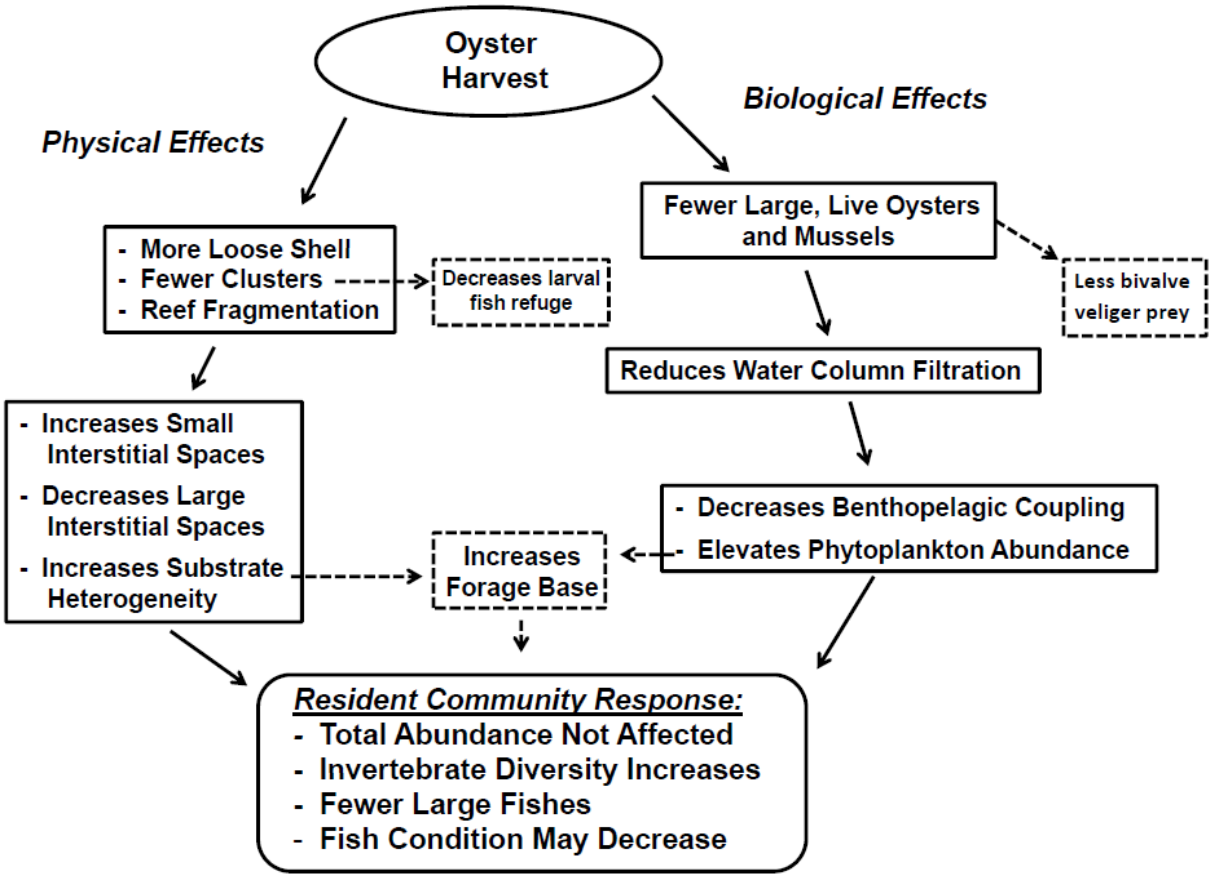

Figure 19: Summary of how harvest activities affect reef structure and the resident community. Dashed boxes indicate potential additional effects that require further study.

Harvest Effects on Oyster Reef Habitat:

The primary effect of oyster harvest activities on water quality is elevated phytoplankton abundance. The significantly lower amount of large market-size oysters at harvested reefs decreases the amount of phytoplankton and excessive particulates that are removed from the water column by the filter-feeding habits of oysters, enabling phytoplankton to increase in abundance and elevate observed chlorophyll-*a* levels. The rates at which oysters can remove phytoplankton from the water column fluctuate seasonally as a function of temperature, oyster size, and phytoplankton abundance and size class (Fulford et al. 2010). Filtration rates increase with oyster size; and it is still unclear how different oyster size classes proportionally contribute to total filtration (Pollack et al. 2011). In the absence of abundant suspensivors (i.e. oysters), excessive organics decompose, increasing biological oxygen demand and lowering dissolved oxygen levels, eventually resulting in hypoxic conditions. Prevention of this phenomena is one of the important services that oyster reefs provide (Officer et al. 1982) and has been observed in numerous field studies (Dame et al. 1984, Dame et al. 1989, Cressman et al. 2003, Nelson et al. 2004, Wall et al. 2011). Whether the filtration capacity of reefs with abundant live oysters is adequate to prevent harmful algal blooms is currently under debate (Pomeroy et al. 2006, Newell et al. 2007, Pomeroy et al. 2007) and highly dependent on urban/agricultural inputs vs. oyster population structure and size. Hypoxic waters, where dissolved oxygen levels were less than 2 mg L^{-1} (Rabalais et al. 2001), were not observed over the course of this study. While hypoxia is the ultimate result of excessive organics in the water column, before hypoxic conditions exist, elevated phytoplankton abundances could be exploited by infaunal and planktonic basal consumers in harvested reef systems, possibly increasing the abundance and diversity of these basal consumers. The relationship between phytoplankton and zooplankton is still relatively

unpredictable despite extensive study, and research focusing on how oyster predation influences plankton communities is lacking, focusing instead on non-suspensivore predation, nutrient levels, and dispersion (Brett and Goldman 1997, Shurin 2001). However, it has been shown that there is a negative correlation between copepod abundance and the abundance of clams and mussels through direct predation of copepod eggs (Lonsdale et al. 2009).

Other possible explanations for increased chlorophyll-*a* levels observed at harvested reefs could be elevated nutrient input at harvested reefs, as nitrogen concentrations are often correlated with chlorophyll-*a* levels in Louisiana (Lane et al. 2011). This is unlikely as all harvested sites had similar $\delta^{15}N$ values for basal food sources as unharvested sites, and significant differences in nitrogen levels at one site would have been reflected in all stable isotope samples from that site. The only known water quality issue related to this study is that unharvested reefs were located in areas closed to oyster harvest due to previously high levels of fecal coliform bacteria, suggesting that unharvested sites should be more subject to elevated nutrient levels than the harvested sites. Current levels are in acceptable ranges due to wastewater treatment improvements, and the state is considering opening these areas to harvest (Patrick Banks, LDWF, pers. comm.). This bacteria is not harmful to oysters, as oysters are used to reduce fecal coliform levels in coastal waters (Cressman et al. 2003), and these typically nutrient-rich waters support abundant fish and invertebrate communities (Van Dolah et al. 2003).

Oyster reef substrate was substantially altered by oyster harvest practices. Unharvested reefs were characterized as having abundant oyster clusters and live oysters, with minimal amounts of loose shell and large areas of solid reef with more abundant secondary sessile organisms. Harvested reefs were characterized as having abundant amounts of loose shell, with smaller amounts of oyster clusters and live oysters, and similar proportions of solid reef and

mixed shell/mud substrate. The structural differences between reefs possessing oyster clusters versus loose shell include fewer, larger interstitial spaces in cluster dominated reefs, where shell dominated reefs contain more numerous, smaller interstitial spaces. Where clusters are larger and likely to be firmly attached to the rest of the reef, loose shell is more likely to be scattered and/or buried if strong currents exist. As oyster harvest reduces the number of oyster clusters and increases the amount of loose shell, there is a change in the type of refuge available to reef-associated organisms (amount, size and permanence of interstitial spaces). In addition, the increase in surface area found with loose shell versus oyster cluster could provide more attachment surfaces for sessile and fouling organisms, thus increasing the forage base for resident organisms.

The increase in mixed shell/mud habitat found at harvested oyster reefs is indicative of the reef fragmentation caused by oyster dredging activities. The occurrence of soft, mud sediments throughout the reef matrix could create a more heterogeneous habitat than solid oyster reef, being able to support organisms that rely on hard substrate as well as infaunal organisms that thrive in soft sediments. Coral reef fragmentation has been shown to increase abundance and diversity and is thought to reduce interspecific competition (Bonin et al. 2011). The fragmentation effect could create conditions similar to reef-edge habitat, where proximity to another habitat results in elevated species diversity. Coral reef fish diversity is often greater on the reef-edge (Acosta and Robertson 2002). There is a threshold with this fragmentation effect, as excessive reef fragmentation results in the eventual conversion of reef habitat into soft-bottom (mud/sand substrate).

No differences in reef rugosity were observed between harvested and unharvested reefs over the course of this study. This could be attributed to the coarseness of depth measurements

(0.1 m); however, it appears from side-scan sonar data and personal observation that the unharvested subtidal reef systems in this study lack small-scale changes in vertical relief that are often observed in intertidal reef systems. The unharvested reefs in this study and at Sabine Lake in particular appear to form large domes and ridges where changes in vertical relief are gradual and occur on larger scales than captured in this study.

Resident Community Response to Habitat Alteration:

The lack of an oyster harvest effect on the total abundance of resident organisms suggests that there is an upper limit to the refuge function that oyster reefs can provide, and that oyster harvest activities that maintain reef substrate do not drastically impact the resident community. Lenihan et al. (2001) also reported no difference in the abundance of oyster reef community species between artificial reefs of varying height (representing harvest impact) or natural reefs. These findings on established reefs support those of Humphries (2010) who conducted manipulative lab and field experiments using micro-reefs constructed at different heights as a proxy for habitat complexity and found a limit to refuge function.

Invertebrate, fish, and total abundance and did not differ with harvest treatment, and only the abundance of one species (*Palaemonetes* spp.) appeared to be negatively affected by harvest, occurring in significantly greater numbers at unharvested reefs. This could be due to increased refuge available on harvested reefs in the form of larger interstitial spaces among oyster clusters, but the lack of a clear association of *Palaemonetes* spp. with any reef habitat variable indicate that there may be additional factors not studied contributing to abundance differences (i.e. water chemistry). Many species showed elevated mean abundances at harvested reefs, though differences were not statistically significant. While the number of fish species and total species

did not differ with harvest treatment, the number of invertebrate species was significantly greater at harvested reefs. Elevated species diversity in estuarine and coral reef systems is linked with increased habitat heterogeneity of structurally complex habitats which decrease interspecific competition (Shervette and Gelwick 2008, Stunz et al. 2010, Bonin et al. 2011). This explains why oyster reefs and marsh edge habitats provide similar habitat functions in estuaries (Grabowski et al. 2005). The results of this study suggest that disturbance to reef substrate attributed to oyster harvest increases reef heterogeneity, which is exploited primarily by resident invertebrates.

One mechanism causing increased diversity in disturbed habitats is referred to as the intermediate disturbance hypothesis (IDH) (Connell 1978, Roxburgh et al. 2004, Shea et al. 2004). The IDH applies where moderate levels of disturbance allow the simultaneous existence of competitively inferior and superior species (high diversity). Whereas in the absence of disturbance, competitively superior species would dominate (low diversity) and with frequent disturbance, competitively inferior species would dominate and superior would never become established (low diversity). The IDH would explain how the increased habitat heterogeneity via the inclusion of mud substrate into the reef matrix after harvest disturbance could influence invertebrate diversity. In the absence of harvest, the mud bottom infaunal community would likely be outcompeted as the oyster reef community would expand and create an area of solid reef. This decrease in forage base diversity could explain the decrease in invertebrate species diversity observed at unharvested oyster reefs.

Organisms select appropriate habitats based on the availability of preferred refuge and prey items. Species-environment relationships indicate that common species found in greater abundances at harvested sites were associated with the elevated area of mixed shell/mud

substrate and phytoplankton abundances found in these areas. *R. harrisii* and *Alpheus* sp. while requiring shell for refuge, likely prey upon basal consumers associated with high phytoplankton abundances and/or soft mud substrates. While *G. strumosus* and *H. ionthas* did not differ in abundance between harvest treatments, they were strongly associated with the number of live oysters and the amount of oyster clusters; appearing to prefer the larger interstitial spaces offered by clusters and likely feeding upon basal consumers abundant in areas where oysters provide benthopelagic coupling services (e.g. deposition of pseudofeces). Larval blennies and gobies have been shown to preferentially feed upon bivalve veligers (Harding 1999), and veliger abundances should be positively correlated with live oyster abundance. *G. bosc, Palaemonetes* spp., *E. depressus,* and *P. herbstii* appear to be oyster reef generalists, as indicated by their similar high abundances between harvest treatments and weak reef micro-habitat preferences. While some feeding and habitat specialization has been observed in *E. depressus* and *P. herbstii* in South Carolina (McDonald 1982), none was observed in this study.

The ability of live oysters to limit phytoplankton abundance and influence resident community dynamics revealed in this study contrast to the findings reported by Tolley and Volety (2005), which concluded that the presence of live oysters had no apparent effect on the resident community other than the creation of oyster shell. This contrast could result from the small scale of the 2005 study which took place entirely on a single reef and the non-living oyster treatments could have been obscured by surrounding live oysters on the reef. It appears that benthopelagic coupling services provided by abundant live oysters have the ability to influence the resident community, limiting the amount phytoplankton available to support infaunal and planktonic basal consumers that resident organisms may prey upon. Oyster harvest may increases basal consumer abundance and diversity 1) through the reduction of the live oyster

resource and associated large-scale filtering ability, and 2) through reef fragmentation which increases the inclusion of mud substrate and associated organisms.

While not significantly different between harvest treatments, several species showed slightly higher abundances at harvested sites. Summerhayes et al. (2009) found a similar overall trend in elevated species abundances with increased small interstitial spaces associated with loose oyster shell (*Saccostrea glomerata*) in Australia; however, species richness increased with the number of live oysters in the field portion of their study, but decreased in the manipulative experiment. This led to their conclusion that field observations of richness were attributed to other estuarine environmental gradients and, similar to Tolley and Volety (2005), that the presence of live oysters did not play as important role contributing to species richness as structure alone. Summerhayes et al. (2009) did find differing assemblages with small changes in shell substrate, but similar to Tolley and Volety (2005), the manipulative experiment was likely too small-scale to capture how live oysters influence resident communities. The harvested reefs in the present study contained higher amounts of loose shell which could explain slightly higher abundances; however the strongest habitat associations observed for certain species were related to the presence of live oysters likely through the provision of preferred oyster veliger prey, or in their absence, the increase in primary production. As described below, oyster clusters and associated large interstitial spaces may also play a role in the population dynamics of resident species.

While differences in size frequency distributions and condition were not substantial between reef types, there is evidence the harvest activities may be having a subtle effect on populations of certain species. Gibson (1994) found that the most important habitat quality factors influencing juvenile flatfish were food abundance, predation pressure, and temperature,

but notes structure and quantity of habitat can drastically impact survivability. No differences in temperature were observed between harvest treatments, but differences in interstitial space size were observed (oyster clusters vs. loose shell), so condition of the species observed this study (also small, benthic species), are likely a function of food provision and refuge from predation. While no differences in the mean sizes of organisms were observed between harvest treatments, the size frequency distributions of *G. bosc, G. strumosus, H. ionthas* indicate that a higher percentage of individuals are reaching larger sizes at unharvested reef treatments. This could be attributed to the larger interstitial spaces found within oyster clusters providing more suitable refuge and/or possible abundant prey resources associated with live oysters described previously. Since there were no significant differences in the condition and abundance of *G. strumosus* and *H. ionthas* or the number of live oysters between harvest treatments, it is likely that size frequency distribution differences are caused by oyster clusters providing better refuge than shell for larger individuals.

For *G. bosc,* individual condition was greater at unharvested sites. In North Carolina, larval *G. bosc* are recruited to the population in late summer (Ross and Rhode 2004). The fact that northern Calcasieu Lake reefs apparently experienced a recent spawning event and southern Calcasieu Lake reefs did not, also suggest that individuals were in better condition on the unharvested reefs and/or these reefs provide better support than harvested reefs for post-larval gobies. Breitburg et al. (1995) reported that larval *G. bosc* aggregate on the downcurrent, low flow velocity sides of large structure (rocks) when compared smaller structure, independent of food density. Northern Calcasieu Lake reefs contained the largest oyster clusters observed in this study, providing seemingly optimal larval goby habitat, while southern Calcasieu Lake reef substrate consisted almost entirely of loose shell, offering little protection from currents. Larval

gobies also preferentially feed upon bivalve veligers (Harding 1999), and northern Calcasieu Lake contained more abundant mussels and live oysters than southern Calcasieu Lake, likely resulting in more frequently abundant veliger prey items. This refuge effect and possible increased abundance in preferred larval food was seemingly more important than the presence of box shells, the preferred spawning habitat of *G. bosc* (Crabtree and Middaugh 1982), which were more abundant in southern Calcasieu Lake.

Contradicting the elevated condition of *G. bosc* at unharvested reefs is the greater abundances observed at harvested reefs. No strong habitat preferences were found in the CCA which indicates that this species is an oyster reef generalist, enabling it to take advantage of diverse oyster reef conditions. Higher abundances at harvested reefs could be explained by increased refuge provision. While unharvested reefs may provide more abundant food sources, as evidenced by a greater weight per given length, the numerous, small interstitial spaces provided by the high quantities of loose shell on these reefs may provide better refuge for this small species than the fewer, larger spaces offered by oyster clusters.

Quantitatively sampling the resident oyster reef community is a difficult task given the complex, solid, and sharp nature of the habitat and cryptic nature these organisms; preventing effective use of trawls and seines. Several attempts have been made to discover the best sampling method for oyster reefs (Rozas and Minello 1997), and researchers often employ lift nets (Tolley and Volety 2005), drop samplers (Shervette and Gelwick 2008, Stunz et al. 2010), and benthic sleds (Robillard et al. 2010). However, it seems as though benthic trays offer the greatest versatility, being frequently used on oyster reef habitats throughout the southeastern United States (Lenihan et al. 2001, Lehnert and Allen 2002, Plunket and La Peyre 2005, Gregalis et al. 2009, Yeager and Layman 2011). The use of trays is not limited by water depth, as are lift

nets and drop samplers, and likely capture more cryptic organisms than benthic sleds that slide over the reef surface. The biggest drawback to using benthic trays is the potential for organisms to escape while the tray is brought to the surface. While catch efficiency in unknown, the behavior of the cryptic fauna of interest decreases the chances of escape, as the flight response of these organisms often involves retreating further into the tray substrate. However more mobile fish and shrimp likely do avoid capture, hence the importance of adding an enclosure device onto tray. The modified trays used in this study were developed to combine the versatility of benthic trays with the enclosure characteristics more typical of lift nets and throw traps in order to more efficiently sample oyster reef fauna.

While not directly comparable but most similar to the sampling method used in this study, Plunket and LaPeyre (2005) used open trays to sample harvested oyster leases in Barataria Bay, Louisiana, reporting lower densities of fish (13.9 per square meter) and invertebrates (168.4 per square meter) than the harvested reefs in this study (fish: 76.8, invertebrates: 230.0 per square meter). Other tray studies (Tolley and Volety 2005), and drop sampling studies (Shervette and Gelwick 2008, Stunz et al. 2010) on other oyster reefs in the northern Gulf of Mexico also report lower densities than those found in the present study. The greater densities reported in this study compared to other studies using trays could result from the addition of the net enclosure increasing CPUE, while the lower densities reported in drop-sampling studies could result from the fact that the sampled oyster reefs were very small, artificial structures surrounded by mud/sand bottom. Studies on coral reefs, however, show that this island effect should increase abundances, which was shown to be greater on small reef patches and be a function of perimeter to area ratios (Acosta and Robertson 2002).

Trophodynamics of the Resident Community:

Resident communities at both reef types appear to depend primarily on pelagic basal food sources (FPOM), evidence of the benthopelagic coupling services that oyster reefs provide. The community-wide increase in non-pelagic source fractions found at harvested reefs corresponds to the decrease in live oyster abundance and supports the role that oysters have in transferring carbon from the water column onto the benthos via filter-feeding activity. This study sought to differentiate the contributions of pelagic basal food sources and non-pelagic sources to oyster reef food webs, thus determining how the reduction of live oysters (and associated biodeposition activities) through harvest influences these contributions across the reef community. Benthic microalgae often contribute substantially to estuarine communities, and like marsh plants, often also have more enriched $\delta^{13}C$ values than FPOM. Differentiating source contributions of marsh plants and benthic microalgae would require inclusion of $\delta^{34}S$ levels into the mixing model. This is a difficult task in micro-tidal systems, not only to collect benthic microalgae which requires sampling mud flats exposed at low tide, but to cleanse the sample of abundant inorganic sulfur (Fry et al. 2008). It is not suspected that benthic microalgae substantially contribute to the sampled communities. In San Antonio Bay, Texas (also a shallow, turbid estuary), microphytobenthos contributed less than 2% of the primary production found in the water column (MacIntyre and Cullen 1996). Benthic macroalgae, seagrass epiphytes, and upstream terrestrial plant matter can also contribute to the basal food source pool, but these were not observed over the course of the study.

Elevation in the trophic position of organisms found at oyster reef vs. non-oyster reef habitats has been documented in Texas (Wrast 2008), Louisiana (Simonsen 2008), Florida (Abeels 2010), and China (Quan et al. 2011). The results of this study indicate that oyster

harvest increases the trophic position of resident organisms when compared to unharvested oyster reefs while maintaining trophic order. The mechanism for this trophic shift appears to be the increased phytoplankton abundance that occurs when fewer live oysters are present, as there is evidence that lower suspensivore abundance can increase zooplankton abundance (Lonsdale et al. 2009). Since CPOM samples were dominated by ctenophores, the CPOM trophic "jump" could represent the presence of several planktonic trophic transfers occurring at harvested reefs that are absent at unharvested reefs, or merely that ctenophores comprised a larger proportion of the CPOM samples collected at harvested sites. However, a definite explanation of elevated CPOM trophic positions would require thorough planktonic community analysis which was beyond the scope of this study.

Resident oyster reef species are benthically oriented, selectively feeding within the planktonic food web. At harvested reefs these species appear to prey upon plankton that have a higher trophic position than the same resident species at unharvested reefs, but also may also be consuming more infaunal organisms associated with the amounts of mud substrate at harvested reef. The slight increase in trophic positions of residents was too minor to suggest major dietary shifts. The maintenance of the trophic order between reef types, with the exception of CPOM, is an indication that resident nekton assemblages are fairly similar and that alterations to reef substrate are not substantially shifting feeding behaviors. This is supported by the lack of a harvest effect on bi-plot measures of niche breadth or community diversity (Layman et al. 2007). It appears that each species included in the stable isotope analysis has a well-defined trophic niche that is not altered by harvest and that while feeding behaviors may not change, the forage base may increase by the inclusion of mud bottom infauna, slightly elevating the trophic position of prey normally consumed.

CHAPTER 5: SUMMARY and CONCLUSIONS

While using dredges to harvest oysters is commonly viewed as a destructive activity due to frequent reef loss in other areas, in Louisiana oyster harvest has occurred in many areas for decades and reef habitats have been largely maintained (albeit through regular cultch supplementation). This allows one to argue that reefs in this area are currently experiencing moderate oyster harvest pressure, creating an intermediate level of disturbance on harvested reefs as opposed to the reef loss associated with overharvest. This disturbance directly effects reef structure through 1) the reduction of large oysters, 2) the reduction of oyster clusters/increase in loose oyster shell, and 3) reef fragmentation and the inclusion of mud into the reef substrate. The indirect effects of these reef structure alterations include 1) an increase in phytoplankton abundance resulting from reduced water column filtration, and 2) an increase in habitat heterogeneity. The decrease in benthopelagic coupling services increased resident community reliance on non-pelagic basal food sources, though pelagic food sources were still the dominant basal food source contributor. Elevated phytoplankton abundances and the presence of organisms associated with mud bottom likely increased basal consumer diversity which elevated the trophic positions of all sampled organisms. The increase in habitat heterogeneity at harvested sites occurred through the presence of more numerous, smaller interstitial spaces associated with oyster shell and the inclusion of another substrate type (mud) and associated infauna into the reef substrate.

The indirect effects of oyster harvest on resident community structure varied. Total abundance and the abundance of most species were not significantly affected by harvest disturbance, indicating maintenance of total refuge capacity. While the number of total species and fish species did not differ, the number of invertebrate species was greater at harvested reefs;

which is explained by the intermediate disturbance hypothesis. Strong oyster reef micro-habitat preferences were observed for *G. strumosus* and *H. ionthas* (live oysters), and *R. harrisii* and *Alpheus* sp. (phytoplankton abundance). Condition differences for *G.bosc* suggest preferred food items may be more abundant at unharvested reefs, and large oyster clusters may increase larval *G.bosc* survivability. Size frequency distributions indicate that all common fish species (*G. bosc, G. strumosus, H. ionthas* are reaching larger sizes at unharvested reefs likely due to the large interstitial spaces found among oyster clusters. Given the subtle differences in habitat complexity between harvest treatments, the abundance of live oysters appears to play a major role in determining the presence/absence of certain resident species. Abundant large, live oysters (aside from providing a shell source) and mussels can provide desirable veliger prey for fish species, where reduced bivalve abundance increases phytoplankton abundance which is exploited by other resident organisms. The largest impact of oyster harvest on the complexity of reef habitat is the increase in mixed shell/mud substrate, which likely contributes to an increased forage base for the same organisms that are associated with high phytoplankton abundances.

This is the first study known documenting the effects of oyster harvest on resident communities and reef structure on established oyster reefs, likely due to the scarcity of natural reef areas and sustainable oyster harvesting practices. Supplemental research could focus how oyster harvest effects the compositions of planktonic, infaunal, and secondary sessile communities, and whether resident communities are influenced by reef size and/or proximity to the edge of the oyster reef. This study reveals that both unharvested and harvested oyster reefs support resident communities in different ways and managers should strive towards maintaining both unharvested and sustainably harvested reef areas in order to maximize oyster reef diversity and associated ecosystem services.

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VITA

Steven Lee Beck was born in1984 and grew up on a small farm in Carlisle, Pennsylvania. Steve earned his Eagle Scout Award before graduating high school in 2002. In 2006 he received a Bachelor of Science in Biology from Juniata College in Huntingdon, Pennsylvania. He was a captain for the Juniata River Rats Men's Rugby Team. While at Juniata College, Steve worked in the specimen museum and at the Raystown Lake Field Station. He spent one summer working for the West Nile Virus Program at the Pennsylvania Department of Environmental Protection and the next summer he studied phytoplankton, blue crabs, and oysters in the Chesapeake Bay during an internship with the Morgan State University Estuarine Research Center. He studied abroad for a semester in southern India and this is where he met his future wife, Holly. After graduation, Steve served as a laboratory assistant for an ichthyology course at Shoals Marine Laboratory in the Gulf of Maine before heading to Wyoming as a seasonal fisheries technician. He then joined Holly in Wilmington, North Carolina and found work as a coastal wetland biologist at an environmental consulting firm for three years while she attended graduate school. He married Holly in Alaska in 2009. Also in 2009, he was accepted into Louisiana State University, School of Renewable Natural Resources to begin work on a Master of Science in Fisheries, which he will receive in May 2012. He is currently employed as a research associate for Louisiana State University working at the Estuarine Habitats and Coastal Fisheries Center in Lafayette, Louisiana.