ASSESSMENT OF ESTUARINE HABITATS FOR RESIDENT AND ESTUARINE-DEPENDENT SPECIES: TOOLS FOR CONSERVATION AND MANAGEMENT

A Dissertation

by

VIRGINIA RHEA SHERVETTE

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

December 2006

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee, Frances Gelwick
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William Grant
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ABSTRACT

Assessment of Estuarine Habitats for Resident and Estuarine-dependent Species: Tools for Conservation and Management. (December 2006)

Virginia Rhea Shervette, B.A., Mercer University;

M.S., University of Southern Mississippi

Chair of Advisory Committee: Dr. Frances Gelwick

My research in coastal Ecuador and the northern Gulf of Mexico (GOM) elucidated differences in value of shallow estuarine habitats for fishes and invertebrates. I focused on mangrove and tidal river habitats in Ecuador, and oyster reef, vegetated marsh edge, and nonvegetated bottom habitats in the GOM.

Coastal Ecuador has lost 20-30% of mangrove wetlands over the past 30 years. Such habitat loss can impair the ecological functions of wetlands. In this study I identified the fish community of the remaining mangrove wetland in Rio Palmar, Ecuador. For comparison, an adjacent tidal river without mangroves, Rio Javita, was also sampled. I found that although Rios Palmar and Javita are characterized by relatively low fish-species richness compared to other tropical estuarine systems, they appear to provide important habitat for several economically- and ecologically-valued species.

In the GOM, I examined the fish and invertebrate communities of adjacent oyster reef (oyster), vegetated marsh edge (VME), and nonvegetated bottom (NVB) habitats. Three main relationships emerged: 1) Oyster and VME provide habitat for significantly

more species (as a measure of richness) relative to NVB; 2) Oyster and VME provide habitat for uncommon and rare species; and 3) Many of the species collected in multiple habitats occurred at higher abundances in oyster or VME habitat. Contrary to the current low value ranking of oyster habitat relative to other estuarine and salt marsh habitats, oyster provides high quality habitat for many species.

Understanding how key species utilize estuarine habitats is critical for future conservation and management efforts. My research indicated that VME habitat may provide better foraging options for juvenile pinfish (*Lagodon rhomboides*), and together with corroborating evidence from other studies, suggest that VME provides a critical nursery function for juvenile pinfish, especially in estuaries where seagrass habitat is sparse or nonexistent. Additionally, I documented that juvenile white shrimp (*Litopenaeus setiferus*) select for oyster habitat because of higher food availability and not because of refuge needs from predation by blue crabs. Oyster habitat appears to provide a nursery function for juvenile white shrimp. Overall, my research demonstrated that structurally complex habitats, such as mangroves, VME, and oyster provide essential habitat at the community, population, and individual levels.

DEDICATION

To my loving and supportive parents, my wonderful husband Stuart, my perfect son Ralston, my sweet James Kendall, Andrea, Robert, and Carolyn. In memory of my namesakes Virgie Mae McKinney and Evelyn Rhea Shervette, and their significant others Gram-pa and Grand-daddy.

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CHAPTER I

INTRODUCTION: ESTUARINE ECOLOGY, THE STUDY OF HABITAT-SPECIFIC NEKTON COMMUNITIES, AND DEFINING NURSERY HABITAT

Introduction

Estuaries provide essential natural resources and services for humans. Not only do they provide us with food in the form of fishes and invertebrates, estuaries transform our waste, accumulate mineral resources and provide us with countless other services. In spite of all this, humans all over the world continue to negatively impact estuarine ecosystems through activities such as alteration of habitat, pollution, and compromising freshwater input. In general, we recognize our actions as not always being in the best interest of the ecosystem and in many areas we have established management bodies that study, monitor, and regulate estuarine health and degradation. In protecting estuaries, scientists strive to understand them and provide resource managers with basic and applied information concerning all components of estuarine ecosystem function. One large avenue of research focuses on estuarine use by fishes, invertebrates, and other organisms.

From the perspective of fishes and invertebrates, estuaries consist of essential shallow habitats such as salt marshes, oyster reefs, mangrove forests, and seagrass beds. Species that spend their whole life cycle within an estuary are classified as estuarine

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This dissertation follows the style of Transactions of the American Fisheries Society.

residents. Those that rely on estuarine habitat during a particular life stage (usually as post-larvae and juveniles) are referred to as estuarine dependent or estuarine nursery species. These species can be freshwater or marine residents. Marine and freshwater fauna, whose existence does not depend on estuarine habitats, but use them opportunistically or serendipitously are categorized as marine transients or freshwater transients, respectively (Nordlie 2003). Often, these species groupings based on estuarine-use status are referred to as life history guilds or categories (Nordlie 2003). In order for estuarine management practices to be effective, resource managers must understand how and when species utilize estuarine habitats, which makes the study of estuarine habitat use by the different life history guilds imperative.

Habitat, habitat type, and microhabitat

Defining the concept of habitat within the context of estuarine ecology can be difficult due to an inconsistency of meaning within the literature. Some scientists use habitat to mean a location where an animal resides. In this context, habitat can be used interchangeably with the terms biotope (Whittaker et al. 1973), habitat type (Minello et al. 2003), and microhabitat (Baltz 1990). The boundaries of habitat in this sense are defined by the researcher instead of the organism and often are demarcated by some sort of structural component or lack of structure. Some examples of this usage are vegetated marsh edge habitat, mangrove creek habitat, and nonvegetated bottom habitat. Other scientists use the concept of habitat to mean the place where a particular population or life stage of the target species lives at any point in time (Baltz 1990). In this sense, habitat is defined by the species and encompasses all of that species habitat types during

any particular period. An example of this understanding is that white shrimp *Litopeneaus setiferus* has an adult habitat and a juvenile habitat both of which include multiple habitat types (Minello et al. 2003). In this dissertation, I use the concept of habitat within the confines of qualifying terminology. For example, mangrove creek habitat is the habitat within the creek channel from which organisms were collected. Vegetated marsh edge habitat means the habitat within 5 m of edge that is vegetated and where fauna reside.

Habitat structural complexity

Structural complexity may be one of the most important characteristics of estuarine habitats for associated fauna. Several studies have documented that macroinvertebrate densities (both epifauna and infauna) strongly correlate with increasing structural complexity of estuarine habitat (Diehl 1988; Zimmerman et al. 1989; Crowder and Cooper 1982; Grabowski and Powers 2004). This is because structure provides more substrate and surface area for food resources, such as epiphytic algae, to grow, which in turn, attracts associated epifauna, such as small invertebrates. In a literature review concerning the importance of seagrass habitat, Heck et al. (2003) concluded that structure, per se, rather than the type of structure, may be an important determinant of habitat value for estuarine-dependent nekton species. Experimental studies have found that enhanced structural complexity of habitat increases prey survival (Heck and Thoman 1981; Crowder and Cooper 1982; Grabowski 2002). Additionally, the availability of refuge within structurally complex habitats may constrain the spatial distribution and success of prey populations (Beck 1995; Beck 1997; Shervette et al.

2004). Structural complexity also provides an area of deposition for food resources and larval settlement (Summerson and Peterson 1984) which correlates with higher growth rate in structurally complex habitats (see reviews: Heck et al. 2003; Minello et al. 2003). Biogenic estuarine habitats such as mangrove wetlands, seagrass beds, oyster reefs, salt marshes, and coral reefs provide structurally complex habitat. Studies that examine the relative value of adjacent structurally complex habitats and habitats lacking structural complexity provide important information and understanding concerning habitat use by estuarine residents and estuarine-dependent species. Such information is essential for effective management practices.

Nekton communities of mangroves

Mangrove wetlands are essential ecosystems for countless reasons. Mangroves are a unique group of forested wetlands that dominate the land-sea interface between latitudes 25°N and 30°S (Lugo and Snedaker 1974). The Indo-West-Pacific region has 36 mangrove species while the New World has 10 mangrove species (Macnae 1963) and in both areas, mangrove wetlands support complex foodwebs and ecosystem dynamics (Lugo and Snedaker 1974). Mangroves occur in the intertidal zone of tropical and subtropical lagoons, estuarine coastal systems, and river deltas, providing structurally complex habitats for fauna. Twilley et al. (1996) described mangroves as the major form of vegetation that supports the biodiversity of tropical estuarine ecosystems. Because of their high primary productivity and export rates of organic matter, mangrove wetlands have been viewed as an important source of energy to higher trophic levels and

much effort has gone into understanding the faunal communities associated with mangrove habitats (Twilley et al. 1996).

Many unique characteristics of mangrove wetlands contribute to their utilization by small fishes and invertebrates. The high primary production provides food resources for primary consumers that attract and are eaten by secondary consumers (Odum and Heald 1972). Mangrove proproots and pneumatiphores provide structural complexity within the water column which serves as surface area for colonization of sessile flora and fauna and supplies refuge from predation for mobile fishes and invertebrates (Odum and Heald 1972; Robertson et al. 1992).

As with most estuarine ecosystems, mangrove wetlands are vanishing at an alarming rate due to anthropogenic destruction (Valiela et al. 2001). A need for information concerning nekton use of mangrove habitat exists all over the globe. Currently, the knowledge and understanding of nekton communities associated with mangroves is geographically biased. The majority of studies concerning faunal use of mangrove habitat have been conducted in the U.S.A., Australia, and New Zealand (Kathiresan and Binghan 2001; Sheridan and Hays 2003). Relatively few studies have examined nekton of mangroves in Central America, Africa, and south Asia. No studies have been published concerning the nekton communities of the western coast of South America, although a few studies have examined nekton communities of mangrove wetlands in Brazil (Barletta et al. 2003).

Salt marsh ecosystems in Gulf of Mexico

Salt marshes are also important estuarine ecosystems. Salt marsh ecosystems of the northern Gulf of Mexico cover nearly 2.1 million ha of coastline (Dardeau et al. 1992). Salt marsh productivity is the temperate equivalent of the productivity occurring in tropical mangroves. Additionally, salt marsh ecosystems support complex foodwebs and relatively high faunal diversity (Beck et al. 2001). Dominant salt marsh vegetation includes two main species, *Spartina alterniflora* and *Juncus roemerianus* (McIvor and Rozas 1996). Secondary production derived from Gulf of Mexico salt marshes and exemplified by large catches of fishery species such blue crab *Callinectes sapidus*, white shrimp *Litopenaeus setiferus*, and brown shrimp *Farfantapeneaus aztecus*, exceeds that of regions in other parts of the U.S. (Zimmerman et al. 1989; Orth and van Montfrans 1990).

Most studies concerning nekton use of GOM salt marshes focus on fishery species, although a few studies have examined nekton community dynamics. Salt marshes are composed of several habitat types. In a review of salt marsh habitat use by fishery species, Minello et al. (2003) categorized marsh habitat types into two broad groups: vegetated and nonvegetated. The vegetated group includes vegetated marsh edge habitat, vegetated inner marsh habitat, and seagrass habitat. The nonvegetated group includes intertidal and subtidal creeks, nonvegetated edge, pools and ponds, and oyster reefs. Minello et al. (2003) concluded in the review that vegetated marsh habitats appear to have a higher nursery value than nonvegetated marsh habitat, but that tidal dynamics and movement of nekton among habitats complicates the comparison.

Additionally, as a nonvegetated habitat, oyster reefs and oyster shell deposits are poorly understood in terms of their nursery value (Beck et al. 2001), nekton use, and associated nekton community composition (VRS, personal observation).

Nursery habitat hypothesis

In the Gulf of Mexico, many fishery species that live and spawn in coastal waters have juveniles that migrate into estuarine nursery grounds where they grow into subadults (Boesch and Turner 1984; Minello et al. 1994; Baltz et al. 1998; Zimmerman et al. 2000). Estuarine ecosystems have extremely high levels of primary production and are therefore likely to contribute substantially to the productivity of these fishery species (Kneib 1997). However, few studies have adequately defined species use of estuarine habitats and have yet to conclusively identify habitats that are essential in maintaining fishery production (Minello 1999). In spite of these deficiencies, numerous papers, books, and reports refer to estuarine habitats that contain juveniles of fishery species as nursery habitat. Beck et al. (2001), in agreement with Minello (1999), emphasized that the broadly accepted idea of estuarine habitats as having an essential nursery role in the life history of fishes is problematic. The nursery-role concept is rarely defined clearly in research and the resulting gap in knowledge hinders its effectiveness as a conceptual framework for research design as well as management plans in which the nursery-role ideas are considered. Although interest in the conservation and management of estuaries is intense and widespread, funds are limited and therefore should be targeted judiciously (Beck et al. 2001; Heck et al. 2003). The consistent identification of nursery-role habitat more effectively facilitates the use of limited funds.

The idea of "nursery habitat" has been in usage for nearly a century and basically applies to habitat used by juveniles of species that have some degree of spatial disconnect between juvenile and adult habitats (Beck et al. 2001). In the context of estuarine ecology, a fundamental premise of the nursery-role concept is that some estuarine juvenile habitats contribute disproportionately to the production of individuals recruiting to adult populations (Edgar and Shaw 1995). Beck et al. (2001) expounded on this assertion by developing a nursery-role hypothesis from which clear and testable predictions can be made. In their hypothesis they define a nursery habitat as one that contributes more individuals per unit area to the adult population than other habitats containing juveniles of the same species. Thus, a combination of density, growth, survival of juveniles within a delineated nursery habitat type, and the successful movement of juveniles from this nursery habitat to an adult habitat must be greater when compared to other juvenile habitat types.

Estuarine ecologists whose research focuses on identifying nursery habitats proffer two main reasons why a habitat provides a nursery function and thereby attracts nursery species (Minello 1999). Nursery habitats are thought to provide a setting for higher growth rates and lower predation rates (hence the emphasis on relative growth and survival). Variations in quantity and quality of food resources across potential nursery habitat affect the rate of development, which has consequences on survival. Likewise, different habitats offer varying degrees of complexity to shelter juveniles from predation (Van Dolah 1978; Minello et al. 1989). Studies concerning the identification of nursery habitat should address these functions (Beck et al. 2001). In addition, one

important function of habitat not considered in Beck et al. (2001), but identified in Heck et al. (2003) is the possible relationship between species diversity and the definition of nursery habitat. High species diversity within one habitat relative to surrounding habitats may play an important role in nursery function and potentially could serve as an additional metric for identifying nursery habitat (Heck et al. 2003).

Dissertation objectives

In this body of research, I examined habitat-specific nekton communities of estuaries within the context of habitat loss and habitat-specific nursery function. I targeted areas which previous research had not covered in the hopes that the result would fill in some knowledge gaps important for effective management of estuaries and estuarine function. Chapter II examined spatial and temporal variation in fish communities of a mangrove wetland in Ecuador that over the past 30 years has lost 90% of its forested area. For comparison, I also examined the fish community of a nearby tidal river. Chapter III documents spatial and temporal variation in habitat-specific nekton communities of adjacent vegetated marsh edge, oyster, and nonvegetated bottom habitats in a northern Gulf of Mexico estuary. In this chapter, I emphasize the importance of oyster as habitat within salt marshes and equate its importance to that of vegetated marsh edge habitat in providing food and shelter. Chapter IV explores the importance of vegetated marsh edge, oyster, and nonvegetated bottom habitats to seven species of invertebrates by examining habitat-specific abundances and size. Chapter V delves into the realistic applicability of the nursery-role hypothesis for pinfish *Lagodon rhomboides*, a common nursery dependent fish, by comparing habitat-specific growth in

the field and reviewing the peer-reviewed literature concerning habitat-specific density and survival. Chapter VI reports habitat-specific density, growth, and predation of juvenile white shrimp *L. setiferus*. I discuss my findings within the context of the nursery-role hypothesis and the current literature pertaining to nursery habitat of penaeids. Lastly, Chapter VII summarizes my findings and identifies some future research needs for estuarine ecology.

CHAPTER II

FISH COMMUNITIES OF A DISTURBED MANGROVE WETLAND AND AN ADJACENT TIDAL RIVER IN PALMAR, ECUADOR

Introduction

Mangroves are the dominant intertidal vegetation in subtropical and tropical estuarine systems (Chapman 1976; Duke 1992). Mangrove-dominated estuaries support essential ecological functions. Much like most estuarine ecosystems, mangrove wetlands intercept land-derived nutrients, pollutants, and suspended matter and act as a filtering system (Marshall 1994; Rivera-Monroy and Twilley 1996; Tam and Wong 1999; Valiela et al. 2001). Mangrove systems also export organic matter supporting near-shore food webs (Twilley 1988; Sasekumar et al. 1992; Twilley et al. 1997). Moreover, mangroves provide a direct benefit to humans through the provision of various extraction-based resources such as wood, lumber, honey, tannins, salt, and artisanal fisheries for mussels, crabs, and fish (Kathiresan and Bingham 2001; Alongi 2002).

Many studies have reported on the important role mangroves play in the life history of countless fish and invertebrate species (Chong et al. 1990; Robertson and Duke 1990; Yáñez-Arancibia et al. 1993; Ikejima et al. 2003). Mangrove wetlands provide estuarine residents and marine and freshwater transient species with essential food and shelter resources (Blaber 1986; Sheaves and Molony 2000; Laegdsgaard and Johnson 2001). However, unlike Florida, the Caribbean, Mexico, and Australia where

mangroves are often coupled with seagrasses and nekton assemblages are well documented (e.g., Yáñez-Arancibia et al. 1993; Laegsgaard and Johnson 1995; Nagelkerken et al. 2001; Poulakis et al. 2003), in South America, little information exists concerning the importance of mangroves to fishes and invertebrates. Basic information detailing fish community structure and species utilization of estuarine habitat in general, and mangrove habitat, in particular, is nonexistent for the tropical Pacific coast of South America.

In the past 30 years, coastal Ecuador has lost approximately 20 –30% of mangrove wetlands (Parks and Bonifaz 1994). Much of the loss of mangrove habitat in this region is primarily due to shrimp aquaculture (Olsen and Arriaga 1989; Twilley et al. 1993; Twilley et al. 1997). Such landscape modifications can impair the integrity of these wetlands and reduce their capacity to function as centers of biological diversity. Because subsistence fishing is a widespread method of provisioning families and fish production is likely mangrove-dependent, loss of these wetlands and their associated habitat also risks loss of a major source of livelihood and cultural tradition for people inhabiting coastal areas.

In order to assess environmental and ecological changes within a wetland, many studies have utilized fish community data (Whitfield and Elliott 2002). A suite of environmental variables drive the conditions available for fish (Blaber 1997; Lorenz 1999). Ecosystem level alterations of a mangrove wetland, including habitat loss and alteration, directly and indirectly affect biodiversity, including that of fish (Twilley et al. 1995). Characteristics of the fish communities within an estuarine ecosystem, such as a

mangrove wetland, including measures of diversity and richness, relative abundance, and trophic integrity can be useful in evaluating the relative health of an estuarine system (Whitfield and Elliot 2002; Harrison and Whitfield 2004). Eighty-nine percent of the total area of shrimp ponds constructed in intertidal zones in Ecuador occurs in the southern coastal region of Ecuador (Parks and Bonifaz 1994). Identifying the fish communities of mangrove wetlands in Ecuador is an important aspect in furthering the understanding of the ecological significance of mangrove habitat loss.

In Palmar, located in the Guayas province of southern Ecuador, a small stand of mangroves remains amid a mosaic of shrimp aquaculture ponds. My goal in this study was to document the remaining fish community of the heavily impacted mangrove wetland. Specifically I describe the fish assemblage across the two main seasons of coastal Ecuador (winter and summer) in the mangrove creeks of Palmar and compare my findings to those of the adjacent tidal river, Rio Javita, lacking mangroves. Less than 2 km separate the mouths of these two estuarine habitats.

Materials and Methods

Study area

Palmar, 95 km northwest of Guayaquil, Ecuador, is a small coastal town with approximately 4300 inhabitants, a large proportion of whom are dedicated to fishing (Solís-Coello and Mendívez 1999; Figure 2-1A). Annual temperature averages 23°C and the annual rainfall average is 250–300 mm (E. Blacio, unpublished data). Coastal Ecuador has two seasons, a dry season from December to May and a wet season from

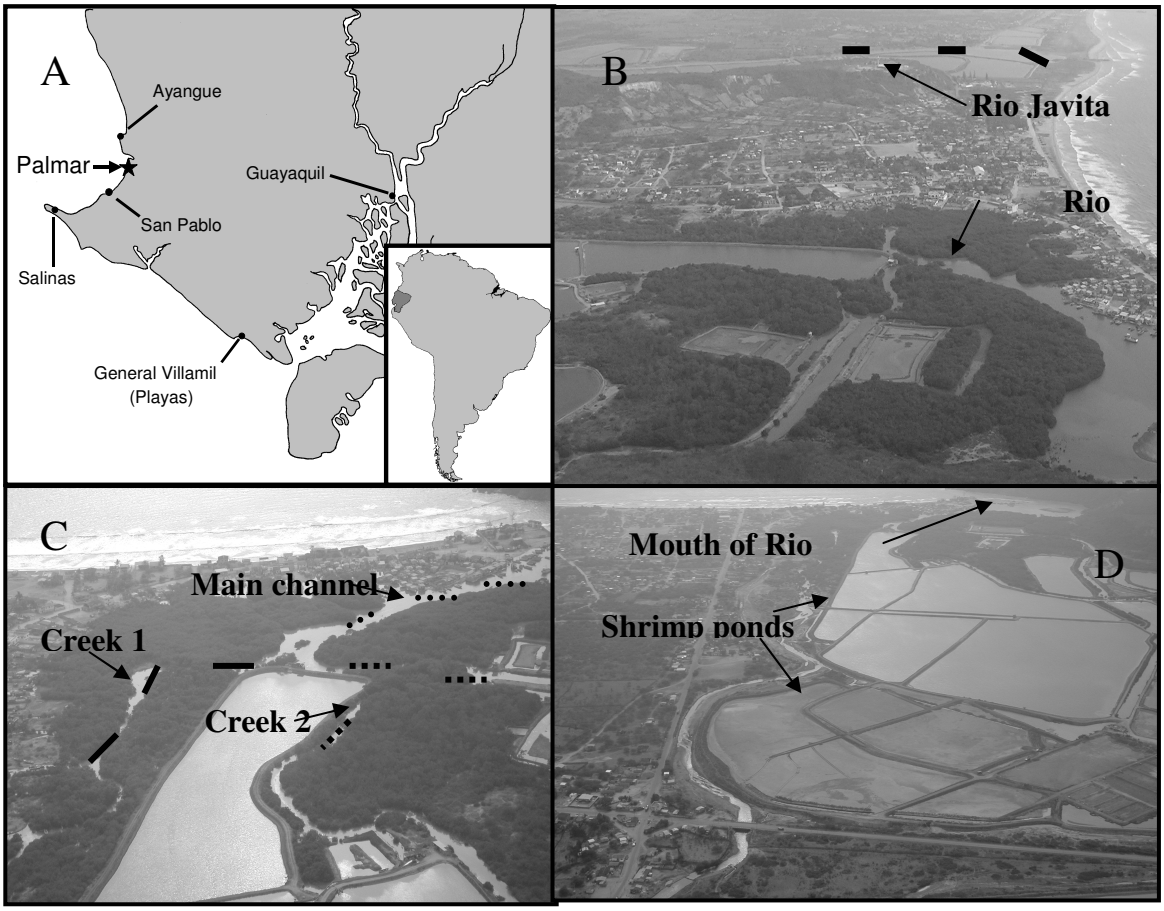

Figure 2-1. A) Location of Palmar on the coast of Ecuador. B) Rio Palmar relative to Rio Javita. Solid lines are general representation of three sites sampled along Rio Javita. C) The mangrove wetland of Palmar characterized by Main channel and Creeks 1 and 2. Circle-lines are general representation of three sites sampled along Main channel; Square-lines are general representation of three sites sampled along Creek 1; solid lines are general representation of three sites sampled along Creek 2. D) Picture illustrating some of the aquaculture ponds around and near Palmar mangrove wetland.

June to November. The mangrove wetland of Palmar (2°01' S and 80°44' W) is approximately 30 ha in size and comprised mainly of red mangrove *Rhizophora mangle* (Figure 2-1B, C). This wetland supports several subsistence fisheries including a mullet *Mugil* spp. fishery and two crab fisheries, a *Callinectes* sp. (Portunidae) and the red crab *Ucides occidentalis* (Ocypodidae). The small patch of mangroves near the mouth of Rio Palmar (Fig 2-1B, C, D) was much larger historically, and as recently as 25 years ago, may have been larger by an order of magnitude. Most of the original mangroves within the wetland were cleared for the construction of shrimp ponds (Figure 2-1C). The Palmar mangrove wetland is an isolated stand. Ecuador's primary mangrove area in the south is in the Gulf of Guayaquil and is the closest estuary with mangroves to Palmar. Rio Palmar consists of two small creeks upstream that meet and form the main channel which empties directly into the Pacific Ocean (Figure 2-1B, C). Rio Javita, a small coastal river lacking mangroves, is located approximately 2 km from the Palmar mangrove wetland (Fig 2-1A). Rio Javita is a shallow, turbid river under strong tidal influence, with a sandy bottom. Shrimp ponds surround both Rio Palmar and Javita.

Sampling design

I sampled the fish communities of the Palmar mangrove wetland and Rio Javita at the end of the coastal dry season in Oct/Nov 2003 and during the coastal wet season Mar/Apr 2004. A 7 m wide by 2 m high bag seine with 3 mm mesh was used to sample the fish community of Rio Palmar main channel, mangrove creeks, and Rio Javita during mid-tide. I refer to Rio Palmar Main channel, mangrove Creek 1, mangrove Creek 2, and Rio Javita as my four sampling areas. I sampled at three sites along each of the two

mangrove creeks and along the main channel of Rio Palmar (Figure 2-1). In Rio Javita, I sampled three sites along the river (Figure 2-1). I collected two samples for each of the six Creek sites on different dates each season. Rio Palmar Main channel and Rio Javita sites were sampled one time each season. A total of 36 samples was collected [2 seasons x (6 creek sites x 2 sampling periods + 3 main channel sites + 3 Javita sites)]. Within each sampling time period, I averaged data across total area sampled for each sampling area unless otherwise indicated. Sites are considered replicates within the four sampling areas.

For each sample, two people standing 6 m apart towed the bag seine for a series of measured distances in order to determine the catch per unit area. I determined the unit area sampled by assuming each seine tow covered a rectangular area and multiplied 6 m x total distance pulled (m). In order to determine the average depth of the creek or river site, I measured creek/river width at the beginning point, middle point, and end point of a seine tow then along each width, I measured depth at five equidistant points and calculated a mean depth from those measurements. I used a YSI-85 to measure salinity (PSU), dissolved oxygen concentration (DO; mg/l), and temperature (°C) for each sample. Additionally, I recorded percent mangrove cover as determined by the proportion of linear shoreline occupied by mangrove structure for each sample.

All fish collected were immediately preserved in 10% buffered formalin for 48 hrs, soaked and rinsed with water, sorted, and then stored in 70% ethanol or isopropanol. Fish were transported to Texas A&M University and identified to the lowest taxonomic

category (usually species), primarily according to Fischer et al. (1995), then measured (SL to 0.1 mm).

Statistical analyses

I calculated Shannon-Weaver's Index of Diversity (H^1), Jaccard's Index of Evenness (J), and species richness (number of species collected) for each of the four sampling areas, for the mangrove sites combined, and for each of the two sampling seasons. I used the following formula for diversity: $H^1 = -\Sigma (p_i/Q)*\ln(p_i/Q)$; where p_i is the proportion of the density comprised by the i^{th} taxon and Q is the total density of individuals collected. I used the following formula to calculate evenness: $J = H^1/\ln S$ where S is the total number of species collected.

For each sampling area, I calculated species densities and species relative abundances (density of one species/total density of all individuals collected for sample x 100). Total fish density data did not meet the assumption of normality. So, I tested for significant differences in total fish densities across sampling areas and between sampling seasons using a nonparametric Friedman Test. My null hypothesis was that no significant difference in median values of overall density existed among the four sampling areas and between the two sampling seasons. Four species of economic and/or ecological importance were selected for further analysis. Differences in size distributions of *Mugil curema*, *Ctenogobius sagitula*, *Lile stolifera,* and, *Atherinella serrivomer* were tested using Mann-Whitney U-test where individuals from Rio Palmar (mangroves present) and Rio Javita (no mangroves present) were aggregated across seasons for each species group.

Correspondence analysis (CA) of the species-by-replicate matrix was used to examine variation in species relative abundance among sampling area and season. Density data were log(x+1) transformed. Multi-response permutation procedures (MRPP) were used to test the null hypothesis of no difference in species relative abundance between the two seasons within and among the four sampling areas. MRPP is a non-parametric technique used to test the significance of a priori sample groupings when the data violate the assumptions of parametric procedures such as multivariate analysis of variance. When significant sample groupings were detected, pairwise comparisons were made using a Bonferroni corrected $\underline{\alpha}$ value.

Canonical correspondence analysis (CCA) was used to identify environmental gradients correlated with species' relative abundances. CCA is a weighted averaging method which directly relates community data to environmental variables by constraining species ordination patterns that correlate maximally with the environmental variables. Inter-set correlations between environmental variables (salinity, temperature, depth, and percent mangrove cover) were used to determine each variable's contribution. Monte Carlo permutation analysis simulation and forward selection were used to test the significance ($p < 0.05$) of the contribution of each variable to the CCA axes. All environmental variables were included in the CCA except DO because I did not have values for two sites in Rio Javita in the Mar/Apr samples due to equipment malfunction. Only significant, non-redundant variables were retained for interpretation. Both CA and CCA were performed using CANOCO (Version 4, Microcomputer Power) and MRPP was performed using PC-ORD version 4 (McCune and Mefford 1999).

Results

Environmental data

Temperature was higher in the Mar/Apr (30.6 °C) sampling period than the Oct/Nov sampling period (27. 0 °C; Table 2-1). Throughout both sampling periods, temperature, on average, was slightly lower at Rio Javita sites than at Rio Palmar sites (Table 2-1). Salinity appeared relatively stable across the two sampling periods (Table 2-1). The main channel appeared to have a lower salinity, on average, than the other sampling areas. Dissolved oxygen was relatively high during both sampling periods and at all sampling areas, although it was slightly lower during the Mar/Apr sampling period and in the Creeks 1 and 2 sampling areas. Depth was consistently shallow throughout sampling and at all sampling areas (Table 2-1). Percent mangrove cover was higher in Creeks 1 and 2 than in the main channel. No mangroves were present at Rio Javita (Table 2-1).

Species relative abundance and diversity

I collected a total of 12,231 individuals comprising 36 species (16 families) from Rio Palmar and Rio Javita. In terms of number of species per family, Gobiidae (7 species) was the most diverse for the mangrove sites followed by Gerreidae (5 species) and Engraulidae (4 species). For the tidal river sites, Carangidae (3 species) was the most diverse followed by Engraulidae and Gerreidae (2 species each). A total of 34 species were collected in the mangrove wetland, 21 of which were exclusive to the mangroves. A total of 14 species were collected in the tidal river, only 2 of which were

Table 2-1. Environmental variables collected for each sample. Mean values (standard error) for the two sampling periods and the four sampling areas are given.

Variable	Oct/Nov	Mar/Apr	Creek 1	Creek 2	Main	Javita
Temp (°C)	27.0 (0.77)	30.6 (0.42)	28.3 (0.60)	29.7 (0.94)	29.1 (1.89)	25.4 (0.74)
Salinity (ppt)	41.7 (1.08)	42.8 (2.11)	42.2 (1.89)	45.7 (1.71)	36.0 (1.84)	42.4 (0.54)
DO (mg l^{-1})	6.2 (0.39)	5.6 (0.37)	5.7 (0.69)	5.8 (0.36)	6.0 (0.43)	6.9 (0.35)
Depth (cm)	35 (3.4)	37 (3.6)	36 (5.8)	38 (3.9)	38 (3.2)	26 (3.0)
% mangrove	63 (7.7)	61 (7.6)	78 (3.7)	83 (1.4)	50 (7.3)	0 (0)

exclusive to the river. Seven species contributed 95% of the total density collected from Rio Palmar. These species included *Evorthodus minutus* (Gobiidae) with a relative abundance of 28.0%, *Ctenogobius sagittula* (Gobiidae) 24.4%, *Atherinella serrivomer* (Atherinidae) 21%, *Mugil curema* (Mugilidae) 18.2%, *Anchoa lucida* (Engraulidae) 1.4%, *Sphoeroides annulatus* (Tetraodontidae) 1.2%, and *Anchoa walkeri* (Engraulidae) 1.2% (Table 2-2). In contrast, Rio Javita had four species contributing 95% of the total density. These species included *M. curema* with a relative abundance of 48.7%, *A. serrivomer* 36.2%, *Lile stolifera* (Clupeidae) 6.9%, and *S. annulatus* 3.5% (Table 2-2).

Gobies dominated in samples collected from the mangrove sites in Oct/Nov. *Evorthodus minutus* comprised 34.1% of density collected from Rio Palmar and *C. sagittula* comprised 28.6%. *Atherinella serrivomer* was the third most abundant species in the Palmar Oct/Nov samples with a relative abundance of 27.5% followed by *A. lucida* and *A. walkeri* with relative abundances of 2.0 and 1.7%, respectively (Table 2-2; Figure 2-2). Rio Javita Nov/Oct samples were dominated by *A. serrivomer* (77.7% relative abundance) and *L. stolifera* (13.0% relative abundance). *Mugil curema* was the third most abundant species in Rio Javita Oct/Nov samples followed by *C. sagittula* and *S. annulatus* with relative abundances of 3.0%, 2.8%, and 2.3%, respectively (Table 2-2). Creek 1 deviated from the other three sampling areas in Oct/Nov in that *E. minutus* had the highest relative abundance and *C. sagittula* had the second highest. *Atherinella serrivomer* ranked highest in abundance for the other three sampling areas (Figure 2-2).

Mugil curema increased in abundance in the Mar/Apr samples for all Palmar sampling areas (58.23%) and the Javita sampling area (86.30%; Table 2-2, Figure 2-2).

Table 2-2. Species collected from Rios Palmar and Javita. The Resident/Diet column lists the known resident status for each species: ED is species that are estuarine dependent and utilize estuarine habitat as juveniles; MA is species that are marine species "accidentally" occurring in the estuary; ER is species that are estuarine residents. The diet status of each species is indicated as follows: GP is general predator; BC is benthic carnivore; O is omnivore; Z is zooplanktivore; P is planktivore; D is detritivore; and U indicates that diet for the species is unknown. Relative abundance (%) and density (number collected/100 m^2) in parentheses is listed for each fish species collected from Rio Palmar and Rio Javita between the two sampling seasons. Density data are combined for sites. CODE is the abbreviation for each species used in the CA and CCA. Overall Relative Abundance is combined for sites and seasons.

			Oct/Nov		Mar/Apr		Overall RA	
Fishes	CODE	Resident/ Diet[1]	Palmar	Javita	Palmar	Javita	Palmar	Javita
Elopidae								
Elops affinis	Elo aff	ED/GP	0 (0)	0 (0)	0.07 (0.05)	0 (0)	0.02	0
Albulidae								
Albula vulpes	Alb vul	ED/O	0 (0)	0.14 (0.04)	0 (0)	0 (0)	0	0.06
Clupeidae								
Lile stolifera	Lile sto	ED/Z	0.42 (0.68)	13.00 (3.97)	0 (0)	1.9 (0.72)	0.30	6.9
Engraulidae								
Anchoa exigua	Anc exi	MA/U-GP[2]	0.01 (0.02)	0 (0)	0 (0)	0 (0)	0.01	0
Anchoa lucida	Anc luc	ED/ U-GP[2]	1.99 (3.19)	0.42 (0.13)	0 (0)	0 (0)	1.40	0.19
Anchoa walkeri	Anc wal	ED/ U-GP[2]	1.70 (2.72)	0 (0)	0.09 (0.06)	0.41 (0.15)	1.22	0.23
Anchovia macrolepidota	Anc mac	ED/ P	0.01 (0.02)	0 (0)	0 (0)	0 (0)	0.01	0
Batrachoididae								
Daector dowi	Dae dow	ER/U-BC	0.98 (1.57)	0 (0)	0.28 (0.19)	0 (0)	0.77	0
Poeciliidae								
Poeciliopsis sp.	Poe sp	ER/U-D[3]	0.44 (0.71)	0 (0)	2.60 (1.75)	0 (0)	1.08	0
Atherinidae								
Atherinella serrivomer	Ath ser	ER/O[4]	27.48 (43.97)	77.73 (23.71)	4.10 (2.76)	2.21 (0.82)	20.56	36.18
Centropomidae								
Centropomus armatus	Cen arm	ED/U-O[5]	0.92 (1.47)	0 (0)	0.39 (0.26)	0 (0)	0.76	0
Centropomus robalito	Cen rob	ED/GP	0.01 (0.02)	0 (0)	0 (0)	0 (0)	0.01	0
Centropomus unionensis	Cen uni	ED/U-O[5]	0.09 (0.14)	0 (0)	0 (0)	0 (0)	0.06	0
Carangidae								
Caranx caninus	Car can	ED/U-GP[6]	0 (0)	0 (0)	0.21 (0.14)	0.14 (0.05)	0.06	0.08
Oligoplites sp.	Oli sp	ED/U-GP[6]	0.06 (0.09)	0 (0)	1.88 (1.26)	0.55 (0.21)	0.60	0.30
Selene brevoortii	Sel bre	ED/GP	0.02 (0.03)	0.14 (0.04)	0 (0)	0 (0)	0.01	0.06
Gerreidae								
Diapterus peruvianus	Dia per	ED/GP	0.28 (0.44)	0 (0)	0.45 (0.31)	0 (0)	0.33	0
Eucinostomus argenteus	Euc arg	ED/O	0.37 (0.59)	0 (0)	0 (0)	0 (0)	0.26	0

Table 2-2 continued.

Fishes	CODE	Resident/ Diet[1]	Oct/Nov		Mar/Apr		Overall RA	
			Palmar	Javita	Palmar	Javita	Palmar	Javita
Eucinostomus currani	Euc cur	ED/O	0.02 (0.04)	0.14 (0.04)	0 (0)	0 (0)	0.02	0.06
Gerreid sp.	Ger sp	ED/U-O[7]	0.20 (0.32)	0 (0)	0.17 (0.11)	0 (0)	0.19	0
Gerres cinereus	Ger cin	ED/O	0.05 (0.08)	0 (0)	0.05 (0.04)	0 (0)	0.05	0
Mugilidae								
Mugil cephalus	Mug cep	ED/D	0 (0)	0 (0)	0.06 (0.04)	0 (0)	0.02	0
Mugil curema	Mug cur	ED/D	1.35 (2.16)	2.97 (0.91)	58.23 (39.25)	86.30 (32.10)	18.22	48.68
Eleotridae								
Erotelis sp.	Ero sp	ER/U-O[8]	0.01 (0.02)	0 (0)	0.03 (0.02)	0 (0)	0.02	0
Gobiomorus sp.	Gob sp	ER/ U-O[8]	0.04 (0.06)	0 (0)	0 (0)	0 (0)	0.03	0
Gobiidae								
Bathygobius lineatus	Bat lin	ER/GP	0 (0)	0 (0)	0.02 (0.01)	0 (0)	0.01	0
Ctenogobius sagittula	Cte sag	ER/U-O[9]	28.62 (45.79)	2.83 (0.86)	14.26 (9.61)	4.00 (1.49)	24.37	3.47
Ctenogobius sp.	Cte sp	ER/U-O[9]	0.15 (0.24)	0 (0)	0 (0)	0 (0)	0.11	0
Evorthodus minutus	Evo min	ER/ U-O[9]	34.13 (54.60)	0 (0)	13.52 (9.12)	0 (0)	28.03	0
Gobionellus liolepis	Gob lio	ER/ U-O[9]	0.02 (0.04)	0 (0)	0.02 (0.01)	0 (0)	0.02	0
Gobionellus microdon	Gob mic	ER/ U-O[9]	0.04 (0.07)	0.14 (0.04)	0.14 (0.09)	0 (0)	0.07	0.06
Microgobius tabogensis	Mic tab	ER/ U-O[9]	0.01 (0.02)	0 (0)	0 (0)	0 (0)	0.01	0
Achiridae								
Achirus mazatlanus	Ach maz	ER/O	0 (0)	0 (0)	0 (0)	0.14 (0.05)	0	0.08
Paralichthyidae								
Citharichthys gilberti	Cit gil	ED/GP	0.06 (0.09)	0.28 (0.09)	0 (0)	0 (0)	0.04	0.13
Tetraodontidae								
Sphoeroides annulatus	Sph ann	ED/GP	0.34 (0.55)	2.26 (0.69)	3.36 (2.26)	4.55 (1.69)	1.24	3.51
Sphoeroides rosenblatti	Sph ros	ED/GP	0.13 (0.21)	0 (0)	0 (0)	0 (0)	0.09	0

[1] Diet information were obtained from the following sources: Odum and Heald 1972; Díaz Gonzáles and Soto 1988; Whitehead 1988; Allen and Robertson 1994; Bussing 1995; Fischer et al. 1995; Smith-Vaniz 1995; Whitehead and Rodriguez-Sánchez 1995; Teixeira and Helmer 1997; Bussing 1998; Crabtree et al. 1998; Lopez-Peralta and Arcila 2002; Sánchez Rueda 2002

[2] Speculative diets from Odum and Heald 1972: *A. mitchilli*

[3] Speculative diet from Gerking and Plantz 1980: *P. occidentalis*

[4] Shervette and Aguirre, unpublished data

[5] Speculative diets from McMichael et al. 1989: *C. undecimalis*; Díaz González and Soto 1988: *C. nigrescens, C. robalito*

[6] Speculative diets from Odum and Heald 1972: *O. saurus*; Blaber and Cyrus 1983: Three species of *Caranx*

[7] Speculative diet from Bussing 1995: *G. cinereus*

[8] Speculative diets from Nordlie 1981: *G. dormitor*, *E. amblyopsis*, and *E. pisonis*

[9] Speculative diets from Wyanski and Targett 1985: *E. lyricus*; Toepfer and Fleeger 1995: *C. boleosoma*

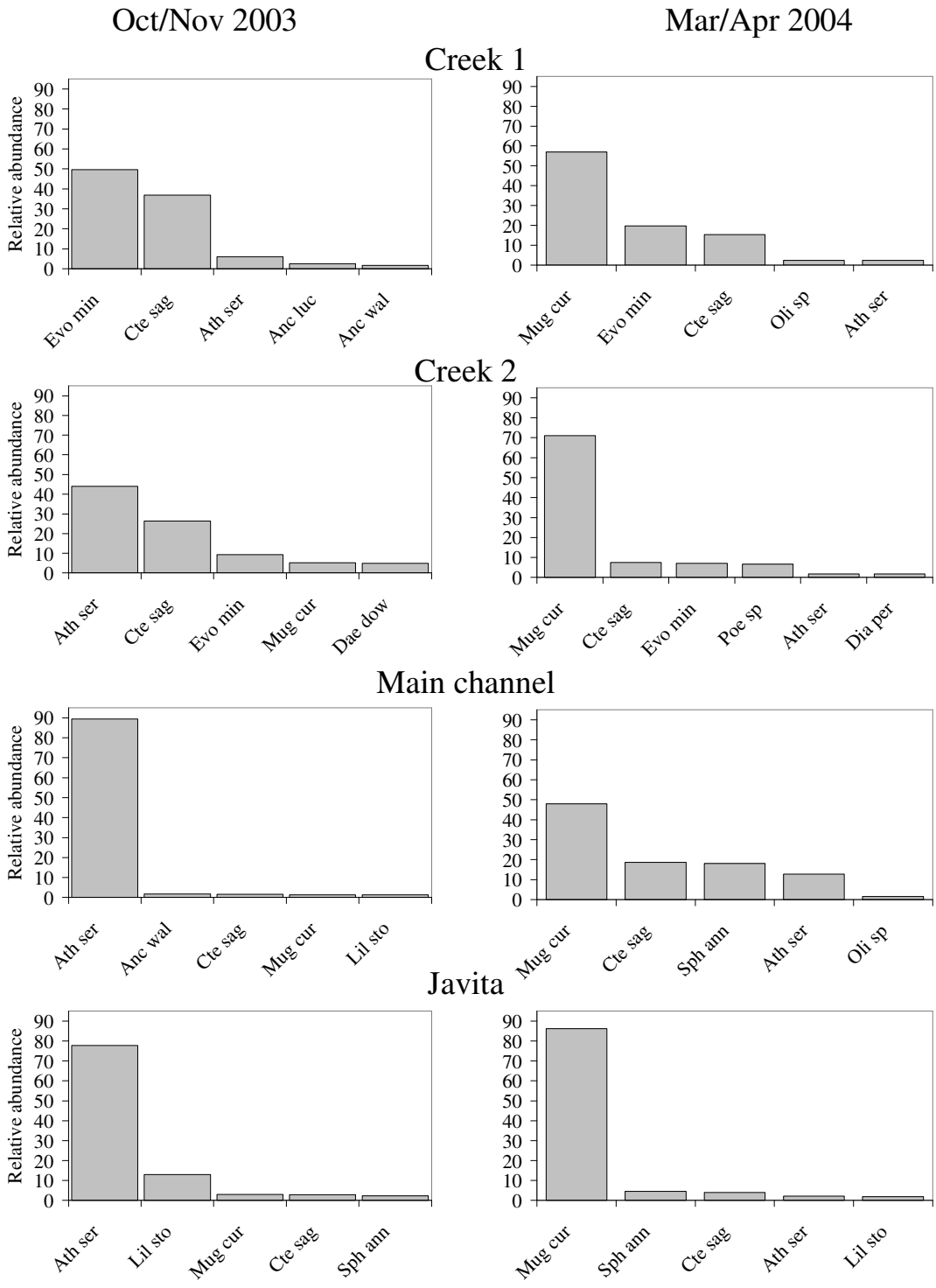

Figure 2-2. Overall relative abundance of the five most abundant species for each sampling area during the two sampling seasons. Species codes are indicated in Table 2-2. In Mar/Apr 2004 Creek 2 samples, *Atherinella serrivomer (Ath ser)* and *Diapterus peruvianus (Dia per)* tied for the fifth highest relative abundance.

Gobies continued to occur in high abundance in mangrove samples during Mar/Apr. *Ctenogobius sagittula* and *E. minutus* comprised 14.26 and 13.52% of fishes collected in mangroves (Table 2-2). *Atherinella serrivomer* abundance declined in Mar/Apr mangrove and Rio Javita samples (Figure 2-2).

Overall, diversity (H^1) was relatively low for all sampling areas and for both seasons (Table 2-3). More species were collected from the two creeks than the main channel or Rio Javita and species diversity followed the same trend (Table 2-3). Mangroves sites (Rio Palmar) had higher richness and diversity values compared to sites without mangroves (Rio Javita). More species were collected in the Oct/Nov sampling period than Mar/Apr and diversity was higher in Oct/Nov. Four and six species comprised 90% of the density from creeks 1 and 2, respectively. Evenness (J) was slightly lower in Creek 1 than Creek 2. Main channel and Rio Javita had 4 and 5 species, respectively, comprising 90% of the fish density collected in those sampling areas. Rio Palmar had 4 species comprising 90% of individuals and an evenness of 0.5, which was a little higher than Rio Palmar's evenness of 0.4. In both sampling periods, four species comprised 90% of the density of fishes collected and evenness was slightly greater in Oct/Nov than Mar/Apr because of overall differences in richness.

Fish density and size

Mean total fish density did not differ significantly among the four sampling areas (Friedmans: $\chi^2 = 5.4$, d.f. = 3, $p = 0.145$), but did differ between sampling seasons (Friedmans: $\chi^2 = 4.0$, d.f. = 1, $p = 0.046$; Figure 2-3). *Ctenogobius sagittula* collected from Rio Palmar were significantly smaller than those collected from Rio Javita (Mann-

Table 2-3. Shannon-Weaver Diversity Index (H^1), Pielou's Evenness Index (J), and species richness (number of species) by sampling area, rivers, and sampling seasons.

	Creek 1	Creek 2	Main Channel	Rio Palmar	Rio Javita	Oct/Nov 2003	Mar/Apr 2004
H^1	1.5	1.8	1.2	1.8	1.2	1.6	1.3
J	0.46	0.56	0.40	0.50	0.44	0.46	0.42
Number of species	26	26	20	34	16	31	23

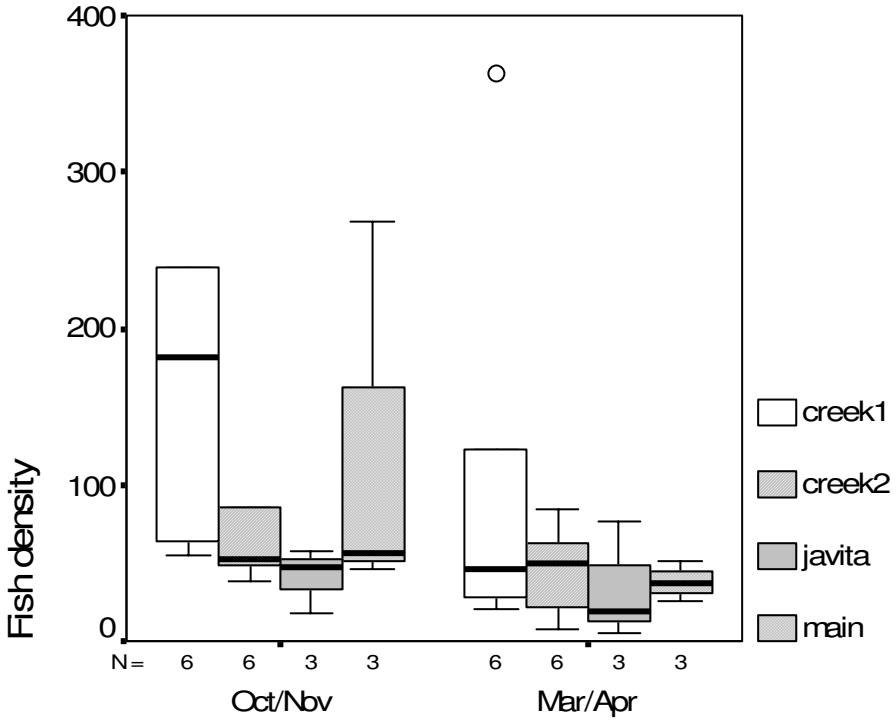

Figure 2-3. Boxplot of total fish density (number of fish collected/100 m^2) across the four sampling areas and between the two sampling seasons. The rectangular boxes represent the interquartile range which contains the 50% of values. The whiskers are lines that extend from the box to the highest and lowest values, excluding outliers. A line across the box indicates the median. The circle represents an outlier which is a data point whose value is between 1.5 and 3 box lengths from the upper edge of the box. Creek1 in Oct/Nov had one data point of fish density with a value of 1134 which has been excluded from this graph.

Whitney U-test: $p < 0.001$; Figure 2-4a). *Lile stolifera* collected from mangrove sites were also significantly smaller than those collected from Rio Javita (Mann-Whitney U-test: $p = 0.003$; Figure 2-4b). Size of *M. curema* did not vary significantly between Rio Palmar and Rio Javita (Mann-Whitney U-test: $p = 0.260$; Figure 2-4c). *Atherinella serrivomer* collected from mangrove sites were significantly smaller than those collected from sites without mangroves (Mann-Whitney U-test: $p < 0.001$; Figure 2-4d).

Fish communities

Differences in communities among sampling areas were significant both between and within seasons (Figure 2-5; Table 2-4). The CA produced two axes that explained 63.2% of the variation in species relative abundance. The CA indicated significant differences in fish community structure within and between seasons for the mangrove creeks relative to the main channel and Javita (Figure 2-5; Table 2-4). The main channel and Javita did not have significantly different communities overall or in either of the two sampling seasons (Figure 2-5; Table 2-4). Samples from the mangrove creeks generally had lower scores on Axis 2 associated with more *E. minutus*, *D. dowi*, *Centropomus* spp., and *A. lucida* relative to the main channel and Rio Javita (Figure 2-5). The main channel and Rio Javita had high scores on Axis 2 associated with *L. stolifera*, *M. curema*, and *S. annulatus* (Figure 2-5). In Oct/Nov samples, all sites had higher scores on Axis 1 associated with more *A. serrivomer, L. stolifera,* and *S. rosenblatti*. Mar/Apr samples had lower scores on Axis 1 associated with more *A. mazatlanus* (in Rio Javita), *E. affinis*, *Mugil* spp., and *Poeciliopsis* sp. (in mangrove creeks). The percent mangroves and mean depth were the only habitat variables significantly correlated with

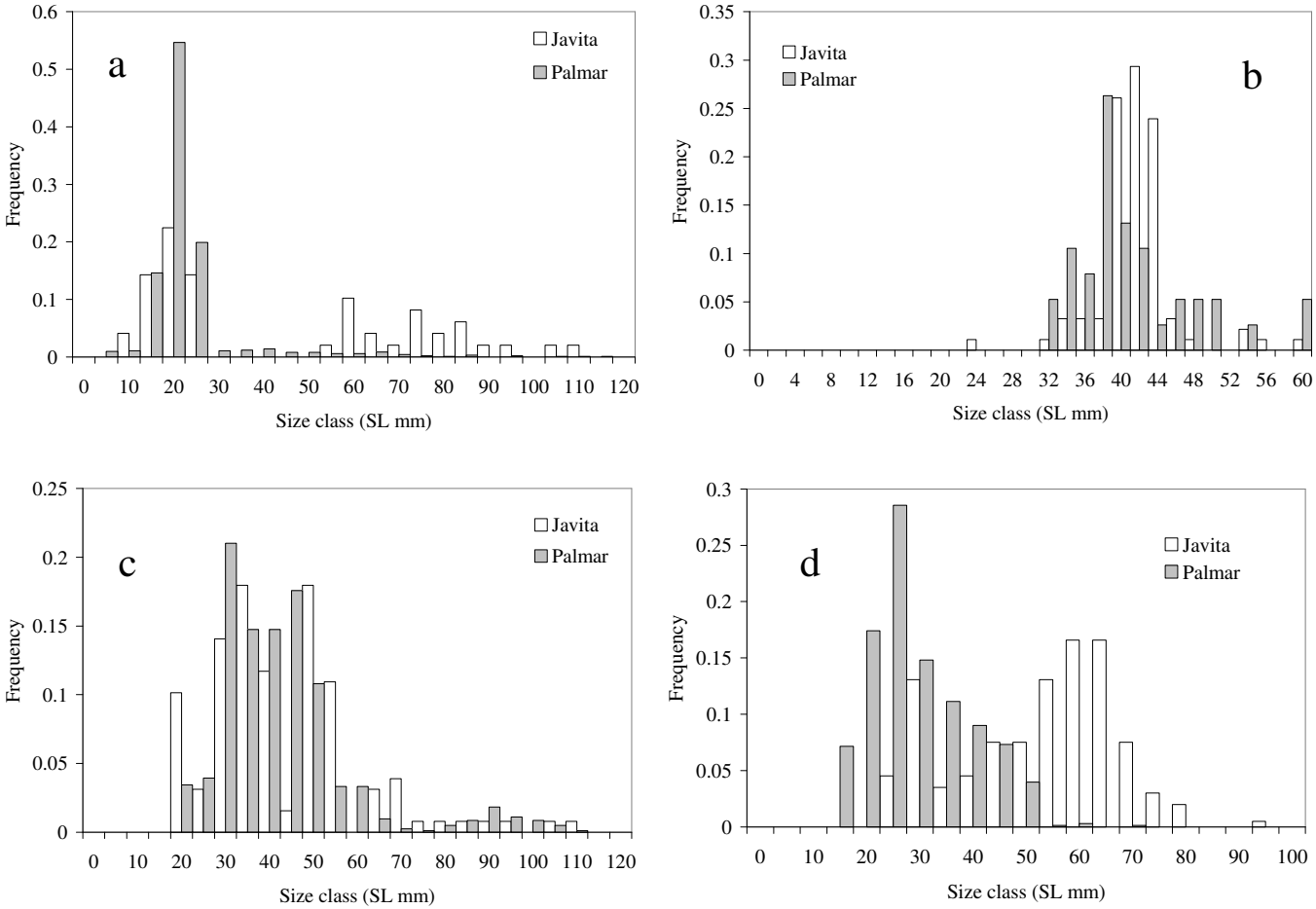

Figure 2-4. Size frequency distributions of (a) *C. sagittula*, (b) *L. stolifera*, (c) *M. curema*, and (d) *Atherinella serrivomer* collected from mangrove sites (Rio Palmar) and sites without mangroves (Rio Javita). Mean sizes of *C. sagittula* and *L. stolifera* collected from mangrove sites were significantly smaller than those collected from sites without mangroves.

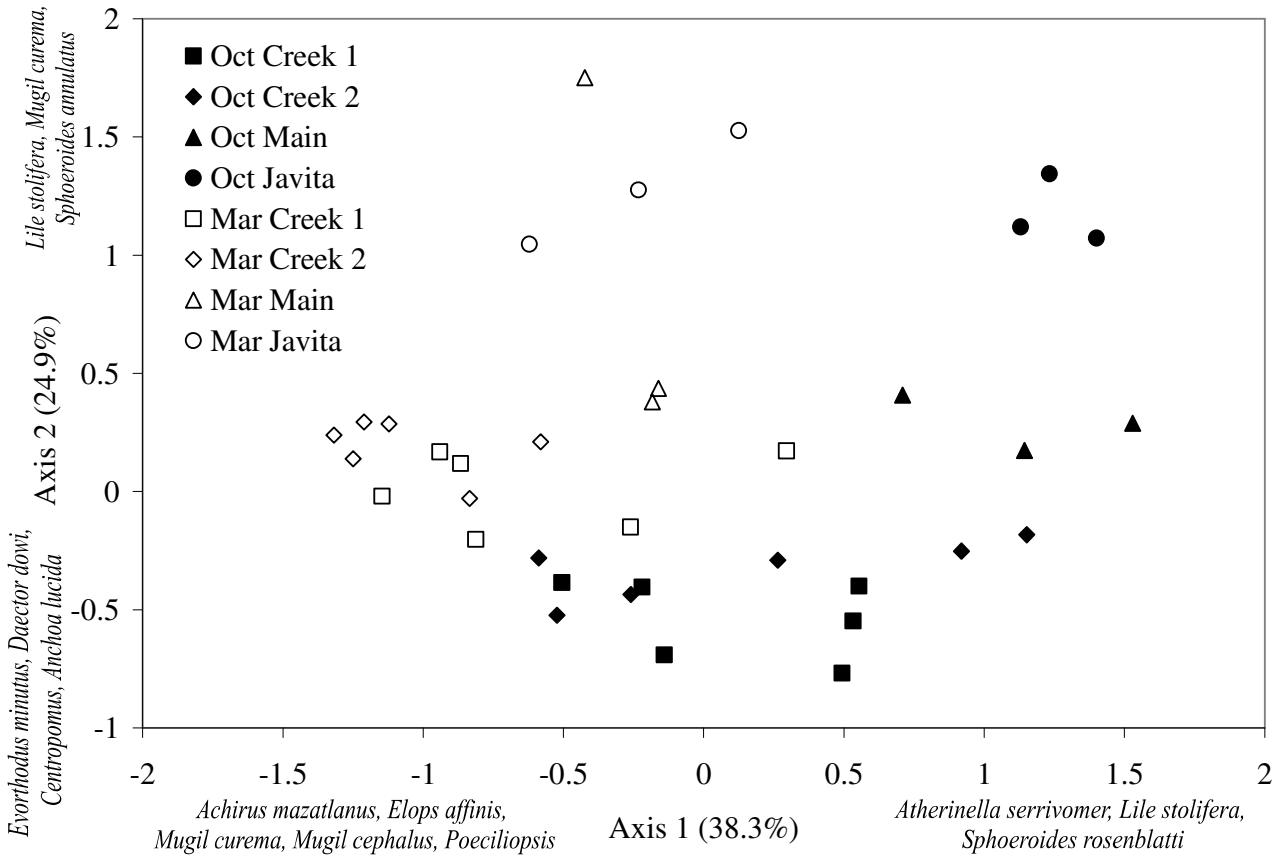

Figure 2-5. Plot of site scores for correspondence analysis (CA). The species associated with extreme scores are listed on each axis end. Creeks 1 and 2 communities were significantly different from Rio Javita during both sampling seasons.

Table 2-4. Effect size (A) and probability values for pairwise comparisons of sampling area groupings for seasons combined, Oct/Nov sampling, Mar/Apr sampling, and between the two sampling seasons. Significance was assessed at $\alpha = 0.003$ (Bonferroni correction).

Comparison	A	p
Seasons combined		
Creek 1 x Creek 2	0.001	0.342
Creeks x Main	0.072	0.007
Creeks x Javita	0.185	< 0.001
Main x Javita	0.007	0.346
Oct/Nov sampling		
Creek 1 x Creek 2	0.039	0.199
Creeks x Main	0.148	0.008
Creeks x Javita	0.397	< 0.001
Main x Javita	0.206	0.025
Mar/Apr sampling		
Creek 1 x Creek 2	0.049	0.128
Creeks x Main	0.127	0.004
Creeks x Javita	0.248	< 0.001
Main x Javita	0.084	0.688
Between seasons (Oct/Nov x Mar/Apr)		
Creek 1	0.239	0.005
Creek 2	0.238	0.005
Main	0.199	0.024
Javita	0.437	0.022

species relative abundances in CCA. Species that were strongly correlated with presence of mangroves on axis 1 and 2, such as *E. minutus, Poeciliopsis* sp., *Centropomus* spp., and *D. dowi*, were also associated with mangrove creeks in the CA ordination (Figure 2-5 and 6). *Albula vulpes* was strongly correlated with depth on Axis 1, but was only collected once (in Rio Javita Oct/Nov; Table 2-2; Figure 2-6). The species-environment relationship in my samples on Axis 1 and 2 of the CCA was relatively weak (eigenvalues of 0.165 and 0.150, respectively).

Discussion

Mangrove ecosystems support essential ecological functions acting as filters of land-derived materials, stabilizing shorelines, and providing nutrients to nearshore food webs (Twilley et al. 1996; Sasekumar et al. 1992; Twilley 1998). A significant loss of habitat within a mangrove wetland may potentially have important ecological consequences reflected in the fish community (Valiela et al. 2001; Whitfield and Elliott 2002). The goals of this study were to describe the fish community of the remaining mangrove wetland in Palmar, Ecuador, and to evaluate, to the extent possible, the relative ecological health of the fish community. Quantitatively assessing the relative ecological health of an estuarine system can be a difficult process, especially when no reference data exist. Harrison and Whitfield (2004) recognized four broad fish community attributes as key to assessing system health. These attributes include species diversity and composition, species relative abundance as it related to dominance by a few species, habitat nursery function as indicated by the occurrence of juveniles of

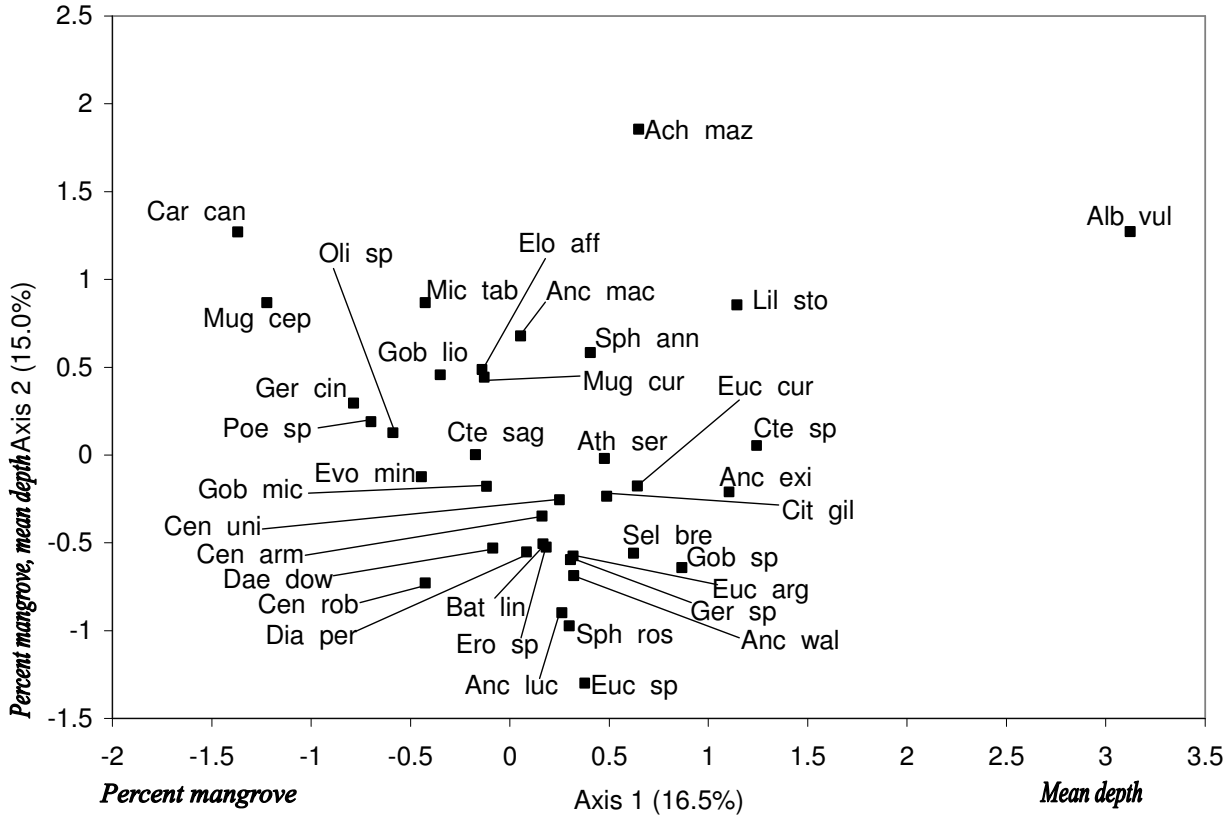

Figure 2-6. Plot of species score with the significant environmental variables in the first and second CCA axes. Species codes are given in Table 2-2. Percent of variation explained by the two CCA axes are given in parentheses.

estuarine-dependent marine species, and fish community trophic integrity. Mainly, species diversity tends to decline in communities exposed to biotic stress (Odum 1983) and stress may cause a shift in the relative abundance of a few species (Fausch et al. 1990). One measure of dominance by a few species under stressed conditions is the number of species comprising 90% of individuals collected (Harrison and Whitfield 2004). Environmental stress on an estuarine system may also alter its ability to provide the function of nursery for juveniles of marine species (Harrison and Whitfield 2004). Lastly, the trophic structure of a fish community can be altered under stress from environmental changes (Lorenz 1999; Khalaf and Kochzius 2002; Whitfield and Elliot 2002). In order to address the potential health of the fish community of Palmar, I discuss each of these issues.

Species diversity and community composition

When I compared the Palmar fish community with that of the tidal river, Rio Javita, I found that Palmar supported both a more diverse and significantly different fish community than Javita. Out of the 34 species collected in Rio Palmar, 21 were exclusive to the mangrove creeks and main channel and did not occur in Rio Javita, only 2 km away. No studies could be found in the peer reviewed literature concerning fish communities of tropical estuarine habitats along the Pacific coast of South America for comparisons. An Ecuadorian government report documenting the biodiversity of the Gulf of Guayaquil (GOG), a mangrove dominated estuary, sampled a total of 90 stations over a period of 4 months (June–September 1998) and documented a total of 50 fish species and species complexes (Yoong and Reinoso 1999). Of these, approximately 18

were also collected in my Rio Javita and Palmar samples. At least 19 of the species collected in Palmar and Javita were not documented in the Gulf of Guayaquil. One group of species collected frequently in GOG samples but absent from Palmar and Javita samples were members of the croaker/corvina family, Sciaenidae.

Upon initial examination, the fish communities of Palmar and Javita appeared lacking in species richness and diversity compared with other tropical and subtropical mangrove fish community studies that reported upwards of 80 species (Louis et al. 1995: 87 species; Chong et al. 1990: 119 species; Robertson and Duke 1990: 128 species; Tongnunui et al. 2002: 135 species). However, direct comparisons are difficult to make due to differences in overall area of wetlands and estuaries, experimental design, sampling effort, inclusion/exclusion of larval fishes, and length and frequency of sampling period (Rozas and Minello 1997). For my study, because I were targeting juvenile and small fishes of creek and tidal river habitats, I ultimately chose to use only one method for collecting fishes—seining which I acknowledge as having a suite of disadvantages associated with it (see review in Rozas and Minello 1997). Possibly, if I had used a difference sampling method, sampled more frequently and over a longer period of time, or included more sampling areas in my design, I may have collected additional species. Several other studies of mangrove fish communities have also employed tow nets, such as seines and trawls, as their collection method (Table 2-5). In order to account for some of the compounding factors limiting comparisons of my study with others, I have confined most of my comparisons to those studies employing similar sampling techniques (see citations in Table 2-5).

Table 2-5. Comparison of studies concerning fish communities of mangrove wetlands that utilized seining or trawling. Location and habitat indicates ocean connected to study wetland and main habitats sampled. Richness is the number of species collected. Shannon-Weaver Diversity Index (H^1) and Pielou's Evenness Index (J) were determined by the authors of this study from information given in cited text. H^1 and J were calculated using the equation listed in materials and methods of current study. Also, the number of species comprising 90% of individuals collect is listed for each study. The salinity range for each study is also listed. Data that were not available directly from the studies are listed as NA.

Location and habitat	Sampling gear and regime	Richness (H^1; J)	Spp. 90%	Fish density	Sal. range	Reference
Pacific, Palmar, Ecuador; Mangrove creeks at midtide	Seine (3 mm mesh) 1x ea season for two seasons	34 (1.8; 0.5)	4	1.3	28-55	This study
Indian, Negombo Estuary, Sri Lanka; Mangrove-lined shore	Drag and enclosure nets (9 mm mesh) monthly Sept 1986–Sept 1988 on new moon days high tide	56 (1.1; 0.3)	3	~ 0.05	1-33	Pinto and Punchihewa 1996
Pacific, Trang Province, Thailand; Mangrove creek	Seine (3 mm mesh) 1x ea. season in Mar, Aug/Sept, Nov/Dec from Aug 1996–Mar 1999 at midtide	58 (3.0; 0.8)	22	NA	20-35	Ikejima et al. 2003
Gulf of Mexico, Florida; Mangrove-line shore	Seine (3.2 mm mesh) monthly 1996–2000	81 (2.4; 0.5)	10	3.7	5-39	Poulakis et al. 2003
Caribbean, east coast Belize; Mangrove creeks	Otter trawl (48.3 mm mesh in wings and 15.2 mm mesh in cod end) 10-min tows 2x ea. month Feb 1985–April 1986	74 (2.7; 0.6)	21	NA	27-35	Sedberry and Carter 1993
Pacific, Australia; Mangrove-lined beach	Seine (12 mm mesh) monthly Jan 1990-Jan 1991	36 (1.4; 0.4)	6	NA	NA	Williamson et al. 1994
Pacific, Taiwan; Mangrove-lined river	Drift bagnets (1-110 mm mesh range) monthly Nov 1987–July 1990	105 (1.1; 0.2)	3	NA	4-33	Tzeng and Wang 1992

Out of seven studies of fish communities in mangroves that employed seining or trawling, this study had the lowest species richness, although by a small margin (Table 2-5). Williamson et al. (1994) examined the fish community of a mangrove-lined mudflat in Raby Bay located in the subtropical Moreton Bay, Queensland, Australia. Their study documented a total of 36 species and had a species diversity index (1.4) and an evenness index (0.4) lower than the current study ($H^1 = 1.8$; $J = 0.5$). Six species comprised 90% of individuals collected in Williamson et al. (1994) compared to the current study in which 4 species comprised 90% of individuals (Table 2-5). Pinto and Puchihewa (1996) collected a total of 56 species in their study of the fish community of a mangrove-lined shore in the tropical Negombo Estuary of Sri Lanka. They had a Shannon-Weaver diversity index of 1.1 and a Pielou's evenness index of 0.3 (Table 2-5). Even though Pinto and Punchihewa (1996) documented 22 more species than the current study, their diversity and evenness values appeared much lower indicating that, similar to my study, only a few species dominated their samples (3 species comprised 90% of individuals collected). In contrast, Ikejima et al. (2003) collected only two species more (total of 58 species of fish) from a mangrove creek in the tropical Trang Province of Thailand, but had a diversity index of 3.0, the highest of the 9 studies. A total of 22 species comprised 90% of individuals collected indicating that a relatively more equal amount of individuals were collected for each species.

In a Florida estuary with mangroves and seagrasses, Poulakis et al. (2003) documented 81 fish species of which 10 comprised 90% of total abundance. Sedberry and Carter (1993), sampled mangroves creeks of coastal Belize, collecting 74 fish

species. Twenty-one species comprised 90% of total abundance which helps to explain the relatively high fish diversity index of 2.7 from that study (Sedberry and Carter 1993; Table 2-5). The one study that collected more than 100 species had one of the lowest diversity index values (1.1) with an equally low evenness value (0.2; Tzeng and Wang 1992). Compared with these other studies, the fish community of Palmar appears to have a diverse fish community with lower species richness, overall.

Several global patterns in fish species richness exist (Alongi 2002) that may help in explaining why the Palmar mangrove wetland had fewer species. One potential factor contributing to the low species richness of Palmar is that the mangrove wetland is relatively small. Larger estuarine systems typically have more fish species than smaller ones (Alongi 2002; Blaber 2002; Raz-Guzman and Huidobro 2002). Additionally, habitat loss tends to result in lowering population densities and a loss of diversity and richness of most mangrove associated organisms (Alongi 2002). The mangrove wetland of Palmar may have once supported a larger number of fish species, but due to the reduction in total area of wetland, currently supports a smaller number. Another global pattern is that mangrove fish communities of the Indo-western Pacific are more speciose compared to Atlantic estuaries (Alongi 2002) and the same trend may apply to western Pacific estuaries. Moreover, connectivity between mangrove ecosystems and adjacent ecosystems such as coral reefs and seagrass beds may influence fish community composition (Robertson and Blaber 1992) and the mangrove wetland in this study does not appear to be in close proximity to other species-rich systems.

Another potential factor contributing to the low species richness of Palmar is the consistently higher salinity of the Palmar creeks and main channel compared to the other studies (Table 2-5). However, in a study on fish community structure in a coastal hypersaline lagoon lined with mangroves, Vega-Cendejas and Hernández de Santillana (2004) documented 81 species, most of which were collected in salinities greater than 38. Thirty-five of the 81 species were found in salinities greater than 60 (Vega-Cendejas and Hernández de Santillana 2004). Rios Palmar and Javita experienced low flow from freshwater sources during the wet season of my study. In fact, in the Oct/Nov collections, at the end of the coastal dry season, diversity and richness measures were higher compared to the Mar/Apr collections, during the coastal wet season. This is contrary to the increase in fish diversity and richness with the wet season that many other fish community studies of mangroves have documented (Flores-Verdugo et al. 1990, Laroche et al. 1997; Barletta et al. 2003). Both Palmar and Javita lose freshwater upstream to shrimp farming and irrigation. Moreover, both rivers receive effluents from the shrimp ponds and shrimp hatcheries located along their path. In spite of what appears to be a large amount of environmental stress, the mangrove creeks and main channel of Rio Palmar support a relatively diverse fish community especially for the overall small total area it covers.

Nursery function

Estuaries provide important habitat for larvae and juveniles of an assortment of marine organisms, many of which are economically-valued. Several studies have documented that mangrove habitats provide unique resources for juvenile fish when

compared with adjacent habitats such as seagrasses and mudflats (Laegdsgaard and Johnson 1995; Chong et al. 1990; Ikejima et al. 2003; Robertson and Duke 1987). Halliday and Young (1996) found that juveniles of economically important species contributed more than 76% of individuals collected from a subtropical mangrove forest in Tin Can Bay, Australia. Bell et al. (1984) documented 38% of the fish density in a temperate tidal mangrove creek in Botany Bay, New South Whales, were represented by juveniles of commercially important species. Morton (1990) documented 75% of the fish density in a subtropical mangrove area was comprised of economically important species. Little et al. (1988) also collected a high proportion of juvenile individuals (46%) in a mangrove creek on the coast of Kenya and noted a similar trend from other mangrove studies including Stoner (1986) with 55% of individuals collected being juveniles and Yanez-Arancibia et al. (1980) documenting 46% of individuals collected as juveniles.

In the present study, 21 species of the 36 collected from both rivers occurred as juveniles only. Species from families I collected, including Engraulidae, Gerreidae, Mugilidae, Centropomidae, and Carangidae, many of which are economically-valued, are known to use estuaries as juveniles (Robertson and Blaber 1992; Halliday and Young 1996; Blaber 1997; Ikejima et al. 2003). Therefore, the mangroves of Palmar and the tidal river habitat of Rio Javita, may provide an important nursery area for multiple economically-valued species. Moreover, the three centropomids, four of the five gerreid species, and two of the four engraulid species collected in the current study only occurred in the Palmar mangrove habitat, potentially indicating that even a mangrove

system as environmentally altered as Palmar provides unique habitat for juveniles of economically important species. In addition to the aforementioned families, I collected hundreds of leptocephalis larvae, belonging to the Albulidae and Elopidae families, in Rio Palmar and Rio Javita samples. This may indicate that both rivers provide habitat for larvae of these other two economically-valued groups (V. Shervette and W. Aguirre, unpublished data).

Trophic integrity

Mangroves function both structurally and ecologically in sustaining nearshore marine habitats and providing food and refuge for a myriad of organisms at different trophic levels (Odum and Heald 1972; Twilley 1988; Twilley et al. 1996). The complexity of food sources documented from mangroves illustrates changes in food diversity and fish preferences through fish ontogeny (Thayer et al. 1987; Robertson and Duke 1990; Twilley et al. 1996; Sheaves and Molony 2000). Diets of single species are often composed of 20 or more difference food categories. In fact, one characteristic of fish communities in mangrove wetlands is that the whole trophic structure is not comprised of definitive trophic levels, but rather, fish consume food resources from a diversity of sources (Twilley et al. 1996). The general characteristics of feeding relationships among fishes of mangrove habitats are characterized by five components (Twilley et al. 1996). First, feeding habitats are generally flexible in time and space in that fish consume what is available when it is available. Second, mangrove fishes share a common pool of the most abundant food resources. Third, most species take food from different levels of the food web. Fourth, fish diets tend to shift with growth, food

diversity, and locality within a mangrove estuary. Fifth, most fish use both pelagic and benthic trophic pathways.

Although I did not conduct diet analyses on the fishes I collected, I found no evidence that the trophic structure of the small and juveniles fish communities of Palmar and Javita were negatively impacted or altered compared to other estuarine fish communities from tropical, subtropical, and temperate studies (Sheaves and Molony 2000; Wilson and Sheaves 2001; Zetina-Rejón et al. 2003; Carrió et al. 2004). However, my sampling method limited us to small individuals and I cannot comment on the occurrence and trophic role of larger piscivorous predators, such as adult centropomids and carangids that often feed on smaller estuarine fishes.

Of the 36 species I collected in Rios Palmar and Javita, at least 20 species (or closely related species of those that no data have been collected concerning diet) are documented as consuming a combination of planktonic and benthic food sources (see Table 2-2 for trophic groups). No major trophic group appeared to be absent or represented in relatively low numbers (Table 2-2). I collected at least 13 species categorized as general predators or benthic carnivores and 17 species categorized as omnivores (Table 2-2).

The two species with the highest relative abundances in my study were juvenile mullet *M. curema* and tropical silverside *A. serrivomer*. As juveniles and adults *M. curema* and *M. cephalus*, often characterized as detritivores, consume benthic diatoms, foraminifers, nematodes, copepods, ostracods, amphipods, gastropods, and invertebrate and fish eggs, basically eating whatever is available (Sanchez Rueda 2002). Although

the diet of *A. serrivomer* is undocumented, other tropical and temperate silverside species (both Atherinopsidae and Atherinidae) consume plankton during the day and can shift to benthic food sources during the night (Odum and Heald 1972; Cassemiro et al. 2003; Logothetis et al. 2001). The same may be true for *A. serrivomer*.

One study in Australia examined the tropic fate of shrimp farm effluents in mangrove creeks (McKinnon et al. 2002). In their study they found that at least two fish species (both clupeids) fed directly on effluents suggesting the direct assimilation of particulates from the aquaculture ponds (McKinnon et al. 2002). Possibly, fish from Palmar and Javita utilize shrimp ponds effluents in a similar manner. Further dietary analysis of the fish communities in Rio Palmar and Javita would be useful in evaluating the trophic fate and impacts of shrimp pond effluents in those systems.

Conclusions

The mangrove wetland of Palmar appears to support a more diverse and species rich fish community than the nearby tidal river, Rio Javita. Palmar has lost approximately 90% of its wetland to shrimp farming and this habitat loss may partially explain the relatively low fish species richness found in the mangrove creeks and main channel compared to other mangrove fish communities. No other studies exist in the scientific peer-reviewed literature reporting the biodiversity of fishes in mangroves in the tropics along the eastern Pacific coast of South America which makes determining the potential level of the impact of habitat loss and alteration in Palmar difficult. However, other studies conducted in Central America and other tropical/subtropical mangrove systems have consistently documented fish communities with higher fish

species richness. Other potential reasons for the lower fish species richness in Palmar include the lack of connectivity to other ecosystems, elevated salinity, reduced freshwater input, and the potential contamination or pollution from shrimp farms. Study design and sampling methods could have contributed to my findings of low species richness, as well. Regardless of the comparatively low richness, the mangrove habitat of Palmar contained juveniles of several economically important species in the snook family (Centropomidae), which were not present in Rio Javita, a less structurally complex area. Both areas contained relatively high densities of juvenile mullet (*Mugil* spp.), a popular food fish, as well as large populations of *Atherinella* species, commonly found in fish and wading bird diets and often utilized as fish meal. Both Javita and Palmar appear to provide important habitat for ecologically and economically important fishes. Although further analysis of trophic integrity is needed, the Palmar mangrove wetland appears to support a complex trophic structure and does not appear to deviate in an obvious manner from the general characteristics of feeding relationships among fishes of mangrove habitats.

CHAPTER III

SEASONAL AND SPATIAL VARIATION IN NEKTON COMMUNITIES OF OYSTER AND ADJACENT HABITATS IN A MISSISSIPPI ESTUARY

Introduction

Estuaries along the Gulf of Mexico are characterized by a mosaic of shallow water habitats. Estuarine residents, such as grass shrimp (Family Palaemonidae), mud crabs (Family Xanthidae), gobies (Family Gobiidae), and toadfish (*Opsanus* spp.) depend on these shallow estuarine areas for food resources, refuge from predation, and sites for settlement and reproduction (Breitburg et al. 1995; Kneib 1997; Shervette et al. 2004). Estuarine-dependent marine residents, including several of economic importance, such as blue crabs *Callinectes sapidus*, white shrimp *Litopenaeus setiferus*, brown shrimp *Farfantapeneaus aztecus*, and spot *Leiostomus xanthurus* also utilize these habitats for food and refuge (Boesch and Turner 1984; Baltz et al. 1993; Howe and Wallace 2000; Harding and Mann 2001).

Common estuarine habitats, such as vegetated marsh, oyster reefs, and nonvegetated bottom, are considered essential for many fishes and invertebrates of economic and ecological interest. Several studies have documented the importance of vegetated marsh to fishes and invertebrates (see review Minello et al. 2003). Juveniles of several commercially-valued species depend on vegetated marsh habitats as evidenced by studies reporting higher growth rates in *Spartina* marsh edge habitat when compared to adjacent habitats (Minello et al. 1989; Stunz et al. 2001). Other studies

have demonstrated high survival rates of juveniles in salt marsh habitats (Minello and Zimmerman 1983, 1985; Minello et al. 1989). Not as much literature substantiates the importance of oyster habitat (see review: Peterson et al. 2003) relative to adjacent habitats. Glancy et al. (2003) found that oyster reefs support distinct assemblages of decapod crustaceans and represent an important ecological component of estuarine habitats. Glancy et al. (2003) speculated that the mechanisms underlying the importance of oyster habitat may include increased survival or greater forage availability for decapods. Nonvegetated bottom habitat, usually adjacent to vegetated marsh edge and oyster reefs, also supports many estuarine species (Zimmerman et al. 1990; Zimmerman et al. 1994; Rozas and Minello 1998; Castellanos and Rozas 2001). In fact, some species may select for open water habitat (including nonvegetated bottom areas) over vegetated marsh (Minello et al. 2003).

Several studies have characterized the inhabitants of oyster reef habitats along coastal Gulf of Mexico and Atlantic Ocean through various sampling strategies (Zimmerman et al. 1989; Larsen et al. 2001; Perry et al. 2001; Grabowski 2002; Glancy et al. 2003). Many of these studies examined nekton communities, abundances, and diversity between shallow vegetated and unvegetated habitats. However, few published studies have compared nekton communities, species abundances, and species richness between oyster and adjacent vegetated and unvegetated habitats (Zimmerman et al. 1989; Glancy et al. 2003). Such comparisons are essential in determining relative habitat value and targeting conservation efforts within estuaries (Beck et al. 2001). The goal of my study was to evaluate the relationship between habitat and nekton community

structure. In general, I investigated relationships among physical variables, habitats, and spatiotemporal variation in nekton community structure in a Mississippi estuary. Specifically, I characterized species composition, relative abundance, and richness of fishes and invertebrates occupying oyster, vegetated marsh edge, and nonvegetated bottom habitats in Grand Bay National Estuarine Research Reserve (GBNERR). In order to address the current lack of quantitative studies comparing oyster and adjacent habitats I designed my study to determine if oyster, vegetated marsh edge, and nonvegetated bottom habitats supported distinct nekton communities and if observed patterns varied seasonally and spatially within GBNERR.

Some of the habitat-related terminology in estuarine ecology is loosely defined. In an effort to avoid any confusion, I provide clarification of several terms used throughout this paper. I use the term "habitat" to mean any particular area that an organism occupies. In this paper, habitat designations derive their distinctions from a structural standpoint. I define "nekton" as organisms that are free-swimming during some time of their life cycle, which is similar to the usage in Minello et al. (2003) and specifically includes fishes and macroinvertebrates (both decapods and gastropods). The phrase "marsh complex" is used to indicate an area within an estuary that is contiguously connected and includes, but is not limited to, habitats such as inner marsh, marsh edge, nonvegetated bottom, seagrass beds, oyster reefs, and tidal creeks.

Materials and Methods

Study areas

Grand Bay National Estuarine Research Reserve is located on the Mississippi coast in the north central Gulf of Mexico (Figure 3-1). GBNERR is a productive and diverse estuary occupying a total area of 74.5 km^2 and is bordered on the west by the heavily industrialized Pascagoula Estuary and on the east by another heavily industrialized estuary, Mobile Bay. The Grand Bay Estuary is microtidal with a typical tidal range of 30–60 cm. For this study, I focused sampling in two main marsh complexes within GBNERR: Bayou Heron and Crooked Bayou. Bayou Heron is located in the upper zone of the estuary and is characterized by oligohaline salinities. Common shallow habitats included vegetated *Spartina alterniflora* marsh edge and inner marsh, *Crassostrea virginica* oyster reefs and oyster midden deposits, and shallow nonvegetated bottom. Additionally, Bayou Heron had small amounts of subtidal *Ruppia* that occurred in small, patchy beds. Crooked Bayou, located closer to the outer zone of the estuary, is approximately 6 km southwest of Bayou Heron. Crooked Bayou is characterized by polyhaline salinities, and is connected directly with Mississippi Sound. Common shallow habitats in the Crooked Bayou marsh complex included vegetated *Spartina alterniflora* marsh edge and inner marsh, *C. virginica* oyster reefs and oyster midden deposits, and shallow nonvegetated bottom. No subtidal seagrasses were observed in Crooked Bayou.

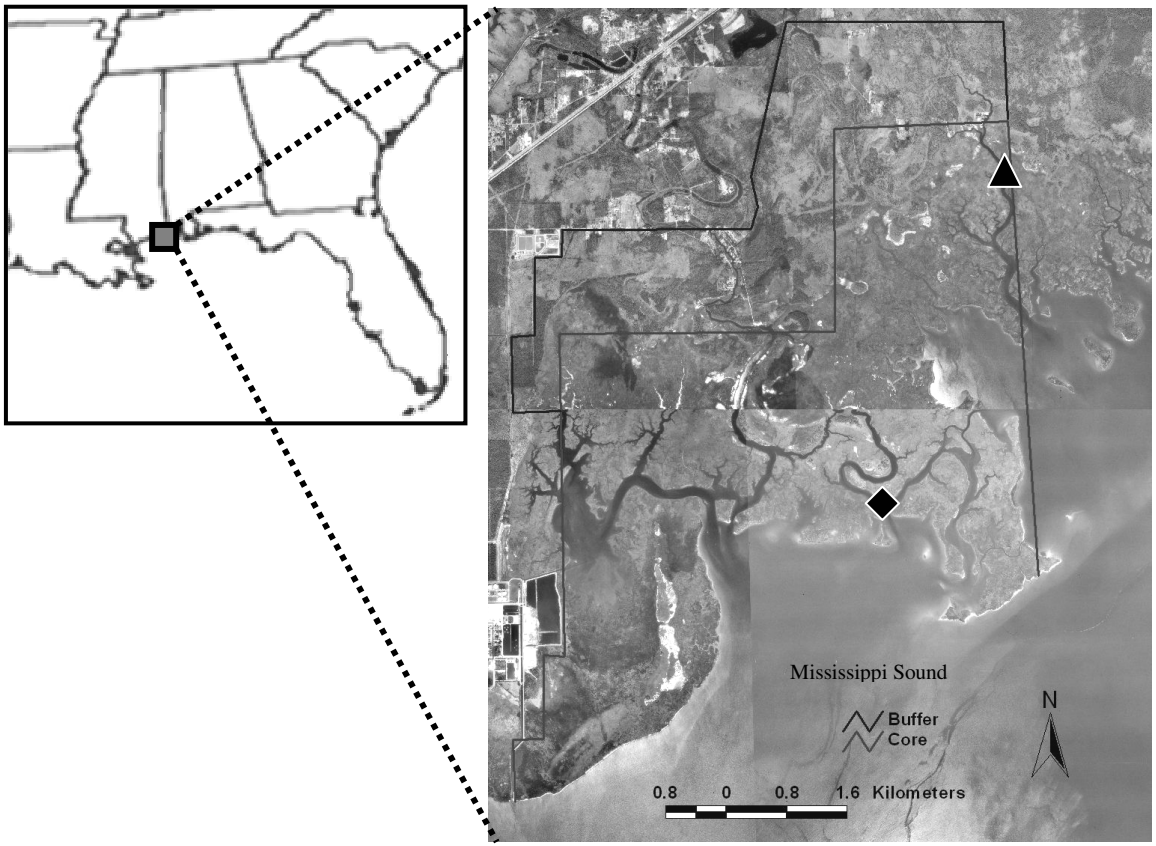

Figure 3-1. Map of Grand Bay National Estuarine Research Reserve, MS, where density and growth experiments were conducted. Triangle represents Bayou Heron site and diamond represents Crooked Bayou site. Note the proximity of the Crooked Bayou site to the Mississippi Sound.

Quantitative nekton sampling

In determining nekton community composition of vegetated marsh edge (VME), oyster, and nonvegetated bottom (NVB) habitats of GBNERR, I sampled in two marsh complexes that had all three of these habitats. For both sampling areas, sampling occurred in Fall 2003 (4-10 October), Spring 2004 (13-20 May), and Summer 2004 (16-28 July) within two hours of high tide when all target habitats were completely inundated. In order to determine where to sample within each habitat, I created a rough map of each sampling area on a numbered grid. I used a random numbers table with the map to determine where in each habitat to sample each replicate. I repeated this procedure each season for both sampling areas.

I chose drop sampling for assessing nekton communities of the three habitats because the catch efficiency does not appear to vary significantly with habitat characteristics (Rozas and Minello, 1997). I randomly collected four replicates in each of the three habitats present at the two sampling areas with a 1.17 m^2 drop sampler according to the procedures of Zimmerman et al. (1984). A total of 72 drop samples (2 sampling areas x 3 habitats x 4 replicates x 3 seasons) were collected by dropping a 1.4 m diameter x 1.5 m tall cylinder from a boom mounted on the bow of a skiff. Two people positioned the cylinder over the randomly selected site by slowly pushing the skiff by the stern. Once the cylinder was in place it was released from the boom and it rapidly enclosed a 1.17 m^2 area.

In each drop sample I measured temperature (°C), salinity (PSU), and dissolved oxygen (mg/L) using a YSI 85 meter and water depth (cm) using measuring tape. After

collecting these data I used a water pump and hose with plastic mesh (1 mm) fixed to the intake nozzle to pump out water from within the sampler. In VME habitat, I removed marsh vegetation from the sampler and recorded the number of stems present. In oyster habitat, percent oyster cover was recorded after water was removed. Then, all oyster was removed from sampler and washed over 3 mm plastic mesh netting and organisms present were collected. If any oyster was found in VME or nonvegetated bottom samples, percent oyster was recorded and oyster was processed as described previously. I collected nekton from the drop sampler with dipnets (3.2 mm mesh) until each of the two dipnetters had five consecutive no catches. Additionally, I inspected the bottom of the sampled area for organisms missed by nets after water was pumped out. All organisms collected were euthanized with high doses of MS-222 and then preserved in 10% buffered formalin for at least 4 d then transferred and stored in 70% ethanol. Fish and invertebrates were identified to species and measured: fish were measured to 0.1 mm standard length (SL), crabs to 0.1 mm carapace length (CL), and shrimp 0.1 mm total length (TL).

Additional collection of organisms

In order to obtain a qualitative assessment of the catch efficiency for my sampling method, I collected multiple seine samples in each of the three habitats at both sites during the Spring 2004 sampling. For each habitat, three seine hauls were made with a bag seine (7 m wide x 2 m high bag seine with 3 mm mesh). Distances for individual seine hauls were measured and total area seined within a habitat was determined by assuming seine area to be a rectangle and multiplying length of total haul

by 6 m (which was the distance apart between the two people pulling the seine). Marsh edge habitat and was sampled by one person standing approximately 2 m into marsh grass from marsh edge and kicking at grass while pulling the seine. Nonvegetated bottom habitat was sampled by seining parallel to marsh edge at least 2 m from edge. In the end, samples from VME and NVB habitats were combined and reported as marsh/NVB. Oyster midden habitat was sampled by towing the seine parallel to shore directly over submerged oyster rubble. Fishes and invertebrates from seine samples were humanely euthanized and then preserved, identified, and measured as described for drop samples.

Statistical analyses

Seasonal data were analyzed separately, unless otherwise indicated, because many species occurred during one season only. I calculated Shannon-Weaver's Index of Diversity (H^1), Jaccard's Index of Evenness (J), and species richness (number of species collected) for each habitat, season, and the two sampling areas . I used the following formula for diversity: $H^1 = -\Sigma\, p_i * \ln(p_i)$; where p_i is the proportion of the density comprised by the i^{th} taxa. I used the following formula to calculate evenness: $J = H^1/\ln S$ where S is the total number of species collected.

I used randomized block ANOVA to test for significant differences in total density (fish and macroinvertebrates combined) among habitats. Density data were log(x+1) transformed to meet assumptions of statistical analysis. Density was the dependent factor, habitat was the independent factor, and site was the blocking factor. I conducted additional separate randomized block ANOVA to determine significant

differences among habitats and between sites for the following dependent parameters: salinity, temperature, DO, depth, and species richness. If needed, data were log(x+1) or square-root transformed to mean assumptions of tests.

Correspondence analysis (CA) of the species-by-replicate matrix was used to examine variation in species relative abundance among habitats and seasons and between sites. Density data were log(x+1) transformed. Multi-response permutation procedures (MRPP) were performed to test the null hypothesis of no difference in species relative abundance among the three seasons within and among the two sites and three habitats. MRPP is a non-parametric technique used to test the significance of a priori sample groupings when the data violate the assumptions of parametric procedures such as multivariate analysis of variance. When significant sample groupings were detected, comparisons were made using Bonferroni corrected *p* values.

Canonical correspondence analysis (CCA) was used to identify environmental gradients correlated with species relative abundance. CCA is a weighted averaging method which directly relates community data to environmental variables by constraining species ordination patterns that correlate maximally with the environmental variables. Inter-set correlations between environmental variables (salinity, temperature, depth, stem density, and percent oyster) were used to determine each variable's contribution. Monte Carlo permutation analysis simulation and forward selection were used to test the significance ($p = 0.05$) of the contribution of each variable to the CCA axes. Only significant, non-redundant variables were retained for interpretation. Both

CA and CCA were performed using CANOCO (Version 4, Microcomputer Power) and MRPP was performed using PC-ORD version 4 (McCune and Mefford 1999).

Results

Environmental data

Although salinity was analyzed separately for each sampling period, results were similar: salinity did not vary significantly across habitats (randomized block ANOVA: $p > 0.05$; Table 3-1), but was consistently significantly higher at Crooked Bayou than at Bayou Heron (for all three seasons randomized block ANOVA: $p < 0.001$). Mean temperature increased with seasons (Table 3-1). Consistent for the three sampling periods, temperature did not vary significantly among habitats or between sites (randomized block ANOVA: $p > 0.05$). Depth was consistently significantly less in intertidal VME habitat relative to the other two habitats during the 3 sampling periods at both sampling areas (Table 3-1).

Community composition and dominance

A total of 633 individual fish representing 41 taxa in 22 families was collected with the drop sampler (Table 3-2). Twenty-eight species were collected in VME, 13 exclusively. Thirteen species were collected from NVB, none exclusively. Twenty-seven species were collected in oyster, 9 exclusively. In Fall03, Spring04, and Summer04, I collected 27, 17, and 25 fish species, respectively. Ten species were collected exclusively in Fall03, 4 species were collected exclusively in Spring04, and 5 species were collected exclusively in Summer04.

Table 3-1. Environmental variables collected each season. Values listed are means (standard error) for samples from each habitat at both sampling areas.

	Bayou Heron			Crooked Bayou		
	marsh	NVB	oyster	marsh	NVB	oyster
October 2003						
Salinity (PSU)	19.4 (0.09)	19.4 (0.13)	19.5 (0.16)	23.1 (0.06)	22.8 (0.19)	22.6 (0.10)
DO (mg/L)	6.85 (0.119)	6.83 (0.209)	6.56 (0.095)	7.04 (0.347)	6.43 (0.415)	6.34 (0.146)
Temperature (°C)	26.2 (0.51)	25.1 (0.75)	26.3 (0.46)	27.3 (0.72)	25.8 (0.48)	25.4 (0.35)
Depth (cm)	37 (4.7)	72 (9.9)	39 (5.6)	47 (4.3)	52 (9.6)	52 (5.4)
Stem density/m^2	92 (14.0)	–	2 (1.5)	143 (26.6)	–	–
Percent oyster	–	3 (2.5)	75 (5.0)	44 (10.7)	14 (8.0)	93 (2.5)
May 2004						
Salinity (PSU)	11.7 (0.96)	12.0 (1.41)	14.1 (0.72)	20.7 (0.19)	21.3 (0.41)	21.4 (0.09)
DO (mg/L)	5.63 (0.405)	5.55 (0.367)	5.88 (0.157)	6.42 (0.495)	6.04 (0.274)	6.30 (0.203)
Temperature (°C)	28.3 (0.43)	28.0 (0.34)	26.8 (0.35)	28.8 (0.82)	29.8 (0.70)	28.8 (0.91)
Depth (cm)	47 (7.2)	50 (10.7)	57 (3.9)	43 (4.9)	61 (8.1)	51 (4.7)
Stem density/m^2	190 (21.9)	1 (1.0)	–	175 (46.1)	–	–
Percent oyster	9 (1.3)	–	50 (12.4)	16 (5.9)	3 (1.4)	61 (13.0)
July 2004						
Salinity (PSU)	10.6 (0.53)	9.9 (1.03)	9.3 (1.08)	19.1 (0.44)	20.8 (0.03)	19.4 (0.74)
DO (mg/L)	4.72 (0.266)	5.01 (0.313)	4.82 (0.435)	5.62 (0.198)	6.32 (0.038)	5.19 (0.301)
Temperature (°C)	33.1 (0.15)	31.7 (0.49)	32.2 (0.73)	32.3 (0.13)	32.8 (0.09)	31.5 (0.46)
Depth (cm)	16 (1.4)	40 (18.5)	51 (18.4)	28 (5.3)	45 (1.7)	32 (6.4)
Stem density/m^2	137 (15.5)	–	–	93 (34.1)	–	–
Percent oyster	–	3 (2.5)	49 (9.2)	38 (16.1)	5 (5.0)	76 (13.8)

Table 3-2. Fishes and macroinvertebrates relative abundances (total number collected) from drop sampling. Relative abundances were calculated for the following subgroups: Fish, Shrimp, Crab, Gastropod. Species codes are listed for referencing. Habitat-specific relative abundances are given by habitat with data for sampling areas and seasons combined. Seasonal relative abundances are given with data for sites and habitats combined.

		Habitat			Season		
Species	Code	marsh	NVB	oyster	Fall	Spring	Summer
FISHES							
Ophichthidae							
Myrophis punctatus	Myr pun	3.6 (8)	3.0 (2)	0.6 (2)	1.5 (5)	3.4 (4)	1.6 (3)
Ophichthus gomesi	Oph gom	0.5 (1)	-	-	0.3 (1)	-	-
Engraulidae							
Anchoa mitchtchelli	Anc mit	-	4.6 (3)	1.5 (5)	0.9 (3)	4.3 (5)	-
Anchoa sp.	Anc sp	-	1.5 (1)	0.3 (1)	-	-	1.1 (2)
Synodontidae							
Synodus foetens	Sun foe	-	1.5 (1)	0.3 (1)	-	1.7 (2)	-
Batrachoididae							
Opsanus beta	Ops bet	1.4 (3)	-	-	0.6 (2)	0.9 (1)	-
Gobiesocidae							
Gobiesox stromosus	Gob str	2.7 (6)	-	3.8 (13)	1.2 (4)	8.6 (10)	2.6 (5)
Atherinidae							
Menidia berrylina	Men ber	6.8 (15)	-	2.9 (10)	2.2 (7)	8.6 (10)	4.2 (8)
Fundulidae							
Fundulus grandis	Fun gra	9.0 (20)	3.0 (2)	1.7 (6)	0.6 (2)	-	13.7 (26)
Fundulus jenkinsi	Fun jen	6.3 (14)	-	-	-	-	7.4 (14)
Poeciliidae							
Adenia xenica	Ade xen	0.5 (1)	-	-	-	-	0.5 (1)
Gambusia affinis	Gam aff	-	-	0.3 (1)	0.3 (1)	-	-
Heterandria formosa	Het for	0.5 (1)	-	-	-	0.9 (1)	-
Cyprinodontidae							
Cyprinodon variegatus	Cyp var	3.6 (8)	-	2.6 (9)	-	5.1 (6)	5.8 (11)
Syngnathidae							
Syngnathus floridae	Syn flo	0.9 (2)	-	-	0.3 (1)		0.5 (1)
Syngnathus louisianae	Syn lou	0.5 (1)	-	-	-	-	0.5 (1)
Triglidae							
Prionotus longispinosus	Pri lon	-	-	0.3 (1)	0.3 (1)	-	-
Lutjanidae							
Lutjanus griseus	Lut gri	0.5 (1)	-	-	-	-	0.5 (1)
Gerreidae							

Table 3-2 continued.

Species	Code	Habitat			Season		
		marsh	NVB	oyster	Fall	Spring	Summer
Eucinostomus argenteus	Euc arg	0.9 (2)	-	-	0.6 (2)	-	-
Eucinostomus melanopterus	Euc mel	3.6 (8)	-	2.6 (9)	5.2 (17)	-	-
Haemulidae							
Orthopristis chrysoptera	Ort chr	2.3 (5)	.	0.6 (2)	2.2 (7)	-	-
Sparidae							
Archosargus probatocephalus	Arc pro	0.9 (2)	-	-	0.3 (1)	-	0.5 (1)
Lagodon rhomboides	Lag rho	2.7 (6)	1.5 (1)	1.2 (4)	0.6 (2)	6.0 (7)	1.1 (2)
Sciaenidae							
Cynoscion nebulosus	Cyn neb	0.5 (1)	-	-	0.3 (1)	-	-
Leiostomus xanthurus	Lei xan	1.8 (4)	18.2 (12)	9.3 (32)	-	38.5 (45)	1.6 (3)
Mugilidae							
Mugil cephalus	Mug cep	-	-	0.3 (1)	-	-	0.5 (1)
Blennidae							
Chasmodes bosquianus	Cha bos	0.5 (1)	-	0.6 (2)	0.3 (1)	-	1.1 (2)
Hypsoblennius hentzi	Hyp hen	-	-	0.6 (2)	-	-	1.1 (2)
Hypsoblennius ionthas	Hyp ion	-	-	1.5 (5)	0.3 (1)	-	2.1 (4)
Gobiidae							
Ctenogobius boleosoma	Cte bol	14.4 (32)	25.8 (17)	6.1 (21)	11.7 (38)	7.7 (9)	12.1 (23)
Ctenogobius shufeldti	Cte shu	-	-	0.9 (3)	0.9 (3)	-	-
Evorthodus lyricus	Evo lyr	1.8 (4)	-	-	1.2 (4)	-	-
Gobionellus hastatus	Gob has	-	-	0.3 (1)	-	-	0.5 (1)
Gobiosoma bosc	Gob bos	30.6 (68)	25.8 (17)	56.2 (194)	62.6 (204)	4.3 (5)	36.8 (70)
Gobiosoma robustum	Gob rob	1.4 (3)	-	-	0.9 (3)	-	-
Microgobius gulosus	Mic gul	0.5 (1)	1.5 (1)	-	-	1.7 (2)	-
Paralichthyidae							
Citharichthys spilopterus	Cit spi	0.5 (1)	4.6 (3)	0.6 (2)	0.9 (3)	1.7 (2)	0.5 (1)
Paralichthys lethostigma	Par let	-	-	0.3 (1)	-	0.9 (1)	-
Cynoglossidae							
Symphurus diomedianus	Sym dio	-	1.5 (1)	0.6 (2)	0.3 (1)	0.9 (1)	0.5 (1)
Symphurus plagiusa	Sym pla	1.4 (3)	7.6 (5)	3.2 (11)	3.1 (10)	5.1 (6)	1.6 (3)
Tetrodontidae							
Sphoeroides parvus	Sph par	-	-	1.2 (4)	0.3 (1)	-	1.6 (3)
INVERTEBRATES-SHRIMP							
Penaidae							
Farfantapenaeus aztecus	Far azt	5.4 (53)	34.6 (9)	9.0 (47)	1.2 (8)	51.8 (100)	0.2 (1)
Farfantapenaeus duroram	Far dur	0.1 (1)	3.8 (1)	-	0.3 (2)	-	-
Litopenaeus setiferus	Lit set	19.8 (193)	61.5 (16)	70.6 (368)	56.2 (371)	3.1 (6)	29.9 (200)

Table 3-2 continued.

Species	Code	Habitat			Season		
		marsh	NVB	oyster	Fall	Spring	Summer
Palaemonidae							
Macrobrachium ohione	Mac ohi	-	-	0.2 (1)	-	0.5 (1)	-
Palaemonetes intermedius	Pal int	0.4 (4)	-	-	-	-	0.6 (4)
Palaemonetes pugio	Pal pug	68.2 (664)	-	13.4 (70)	30.9 (204)	44.6 (66)	66.5 (444)
Palaemonetes vulgaris	Pal vul	1.4 (14)	-	0.2 (1)	0.5 (3)	-	1.8 (12)
Palaemonetes sp.	Pal sp	2.2 (24)	-	-	3.2 (21)	-	-
Alpheidae							
Alpheus sp.	Alp sp	2.5 (24)	-	6.5 (34)	7.7 (51)	-	1.0 (7)
INVERTEBRATES-CRABS							
Paguridae							
Clibanarius vittatus	Cli vit	14.5 (59)	5.0 (3)	2.5 (16)	12.6 (58)	5.9 (11)	1.9 (9)
Portunidae							
Callinectes sapidus	Cal sap	20.2 (82)	23.3 (14)	9.1 (59)	13.6 (63)	20.4 (38)	11.7 (54)
Callinectes similis	Cal sim	0.5 (2)	1.7 (1)	0.2 (1)	0.2 (1)	1.6 (3)	-
Xanthidae							
Eurypanopeus depressus	Eur dep	41.1 (167)	16.7 (10)	45.4 (293)	52.0 (240)	27.4 (51)	38.7 (179)
Eurytium limosum	Eur lim	0.5 (2)	-	0.9 (6)	-	4.3 (8)	-
Menippe adina	Men adi	1.0 (4)	-	0.3 (2)	-	-	1.3 (6)
Panopeus obessa	Pan obe	0.7 (3)	-	6.8 (44)	-	5.4 (10)	8.0 (37)
Panopeus simpsoni	Pan sim	10.1 (41)	10.0 (6)	14.7 (95)	16.0 (74)	11.3 (21	26.4 (122)
Rithropanopeus harrisii	Rit har	8.9 (36)	33.3 (20)	18.5 (119)	5.4 (25)	15.1 (28)	26.4 (122)
Unidentified xanthid	Xan sp	2.0 (8)	10.0 (6)	1.4 (9)	0.2 (1)	8.6 (16)	1.3 (6)
Grapsidae							
Sesarma reticulatum	Ses ret	0.5 (2)	-	-	-	-	0.4 (2)
Porcelanidae (unidentified)	Por sp	-	-	0.2 (1)	-	-	0.2 (1)
INVERTEBRATES-GASTROPODS							
Littorinidae							
Littorina irrorata	Lit irr	33.8 (22)	-	5.7 (2)	2.9 (1)	43.1 (22)	7.1 (1)
Muricidae							
Stramonita (Thais) haemastoma	Tha hae	21.5 (14)	-	37.1 (13)	34.3 (12)	7.8 (4)	78.6 (11)
Neritidae							
Neritina usnea	Ner usn	44.6 (29)	-	57.1 (20)	62.9 (22)	49.0 (25)	14.3 (2)

VME habitat was dominated by *Gobiosoma bosc* (30.6% of total fish collected in VME), *Ctenogobius boleosoma* (14.4%) and *Fundulus grandis* (9.0%). NVB was dominated by *C. boleosoma* (25.8%), *G. bosc* (25.8%), and *Leiostomus xanthurus* (18.2%). The most abundant fishes collected in oyster were *G. bosc* (56.2%), *L. xanthurus* (9.3%), and *C. boleosoma* (6.1%).

In Fall 2003, fish samples were dominated by *G. bosc* (62.6%), *C. boleosoma* (11.7%), and *Eucinostomus melanopterus* (5.2%). In Spring04, *L. xanthurus* (38.5%) had the highest abundance followed by *G. stromosus* (8.6%), and *M. berrylina* (8.6%). In Summer2004, dominate fish species included *G. bosc* (36.8%), *F. grandis* (13.7%), and *C. boleosoma* (12.1%).

A total of 2734 individual invertebrates representing 24 taxa in 11 families was collected with the drop sampler. Twenty-two species were collected in VME habitat with three species exclusively. Ten species were collected in NVB habitat with none exclusively. Twenty species were collected in oyster, two species exclusively. Fall 2003 samples had 17 species of invertebrates with one species collected exclusively during that season. Spring04 samples had 16 species of invertebrates with 2 species exclusively. Summer04 samples had 19 species of invertebrates with 4 exclusively (Table 3-2).

Out of the 8 species of shrimp collected in VME habitat, *Palaemonetes pugio* (68.2% of total shrimp collected in VME), *Litopenaeus setiferus* (19.8%), and *Farfantapenaeus aztecus* (5.4%) were the most abundant. Eleven species of crab were collected in VME and the most abundant species included *Eurypanopeus depressus*

(41.1% of total crabs collected in VME), *Callinectes sapidus* (20.2%), and *Clibanarius vittatus* (14.1%). Three gastropods species were collected in VME: *Neritina usnea* (44.6% of gastropods from VME), *Littorina irrorata* (33.8%), and *Stramonita haemastoma* (21.5%).

NVB habitat had 3 species of shrimp and 7 species of crabs. Shrimp species included *L. setiferus* (61.5%), *F. aztecus* (31.6%), and *Farfantapenaeus duroram* (3.8%). The dominate crabs in NVB were *Rithropanopeus harrisii* (33.3%), *C. sapidus* (23.3%), and *E. depressus* (16.7%). Oyster habitat had 6 species of shrimp, 11 species of crabs, and 3 species of gastropods.

The most abundant shrimp species in oyster were *L. setiferus* (70.6%), *P. pugio* (13.4%), and *F. aztecus* (9.0%). The most abundant crabs in oyster were *E. depressus* (45.4%), *R. harrisii* (18.5%), and *P. simpsoni* (14.7%). *Neritina usnea* (57.1%) was the dominate gastropod in oyster followed by *S. haemastoma* (37.1%).

In Fall 2003 samples, I collected 7 species of shrimp; the most abundant species were *L.setiferus* (56.2%), *P. pugio* (30.9%), and *Alpheus sp*. (6.5%). I also collected 7 species of crabs and three species of gastropods during this season. Dominant crab species included *E. depressus* (52.0%), *P. simpsoni* (16.0%), and *C. sapidus* (13.6%). *Neritina usnea* (62.9%), *S. haemastoma* (34.3%), and *L. irrorata* (2.9%) also were collected in Fall03. During Spring04, I collected 4 species of shrimp, 9 species of crabs, and 3 species of gastropods. Dominant shrimp included *F. aztecus* (51.8%), *P. pugio* (44.6%), and *L. setiferus* (3.1%). The most abundant crab species during Spring 2004 were *E. depressus* (27.4%), *C. sapidus* (20.4%), and *R. harrisii* (15.1%). For the

gatropods, *N. usnea* (49.0%) continued to dominate samples in Spring04 followed by *L. irrorata* (43.1%) and *S. haemastoma* (7.8%). Summer04 samples had 7 species of shrimp, 10 species of crabs, and 3 species of gastropods. Dominate shrimp species included *P. pugio* (66.5 %), *L. setiferus* (29.929.9), and *P. vulgaris* (1.8 %). The most abundant crab species were *E. depressus* (38.7 %), *P. simpsoni* (26.4 %), and *P. obesa* (26.4 %). Gastropods collected during Summer04 included *S. haemastoma* (78.6 %), *N. usnea* (14.3 %), and *L. irrorata* (7.1 %).

Multivariate community analyses

Community structure differed significantly among the three seasons and between the two sites (Figure 3-2; Table 3-3). The CA produced two axes that explained 84% of the variation in species relative abundances. Samples collected in Spring 2004 generally had higher scores on Axis 1 associated with more *C. similis*, *L. xanthurus*, and *F. aztecus*. Fall and Summer samples generally had lower scores on Axis 1 associated with more *Alpheus sp*., *E. melanopterus*, and *Orthopristis chrysoura*. Spring VME and most of summer VME samples had higher scores on Axis 2 associated with more *F. grandis*, *C. variegates*, and *M. berrylina*.

Within Fall 2003 sampling season, community structure differed significantly between sites and among the site-habitat combinations (Figure 3-3a; Table 3-3). The CA produced two axes that explained 61% of the variation in species relative abundances. Bayou Heron samples generally had positive values on Axis 1 associate with the presence of *P. pugio*, *M. berrylina*, and *Evorthodus minutus*. Crooked Bayou

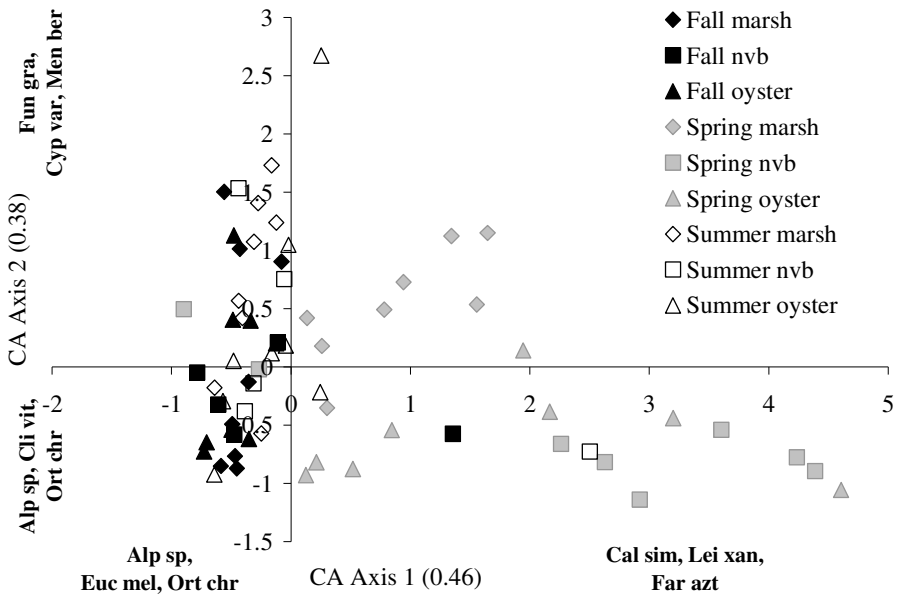

Figure 3-2. First two axes of CA for GBNERR samples from each habitat by season (data combined over sampling areas). Eigenvalues are given in parentheses. Species with highest loading scores on the ends of each axis are listed.

Table 3-3. Effect size (A) and probability values for comparisons of sampling groupings. For Season, I tested for significant differences among the three seasons (with all data within each season combined in three groups representing data for season), significant differences between sites (with all season and habitat data from each site combined representing data for sites), and significant differences among habitats (with all data from each season and site combined representing data for habitats). For each individual season I tested for significant differences between sites (habitat data combined), among habitats (site data combined), just habitats for each site individual, and among all six site/habitat combinations. Asterisk indicates significance after Bonferroni correction.

Comparison	A	p
Season		
All	0.171	<0.0001*
Site	0.063	0.0001*
Habitat	0.033	0.0154
October 2003		
Site	0.193	<0.0001*
Habitat	-0.019	0.6746
Heron habitat	-0.023	0.6183
Crooked habitat	0.225	0.0332
Site-habitat combinations	0.213	0.0017*
May 2004		
Site	0.110	0.0007*
Habitat	0.099	0.0058*
Heron habitat	0.0762	0.132
Crooked habitat	0.400	0.0001*
Site-habitat combinations	0.300	<0.0001*
July 2004		
Site	0.154	0.0001*
Habitat	0.148	0.0013*
Heron habitat	0.206	0.0016*
Crooked habitat	0.070	0.1086
Site-habitat combinations	0.317	<0.0001*

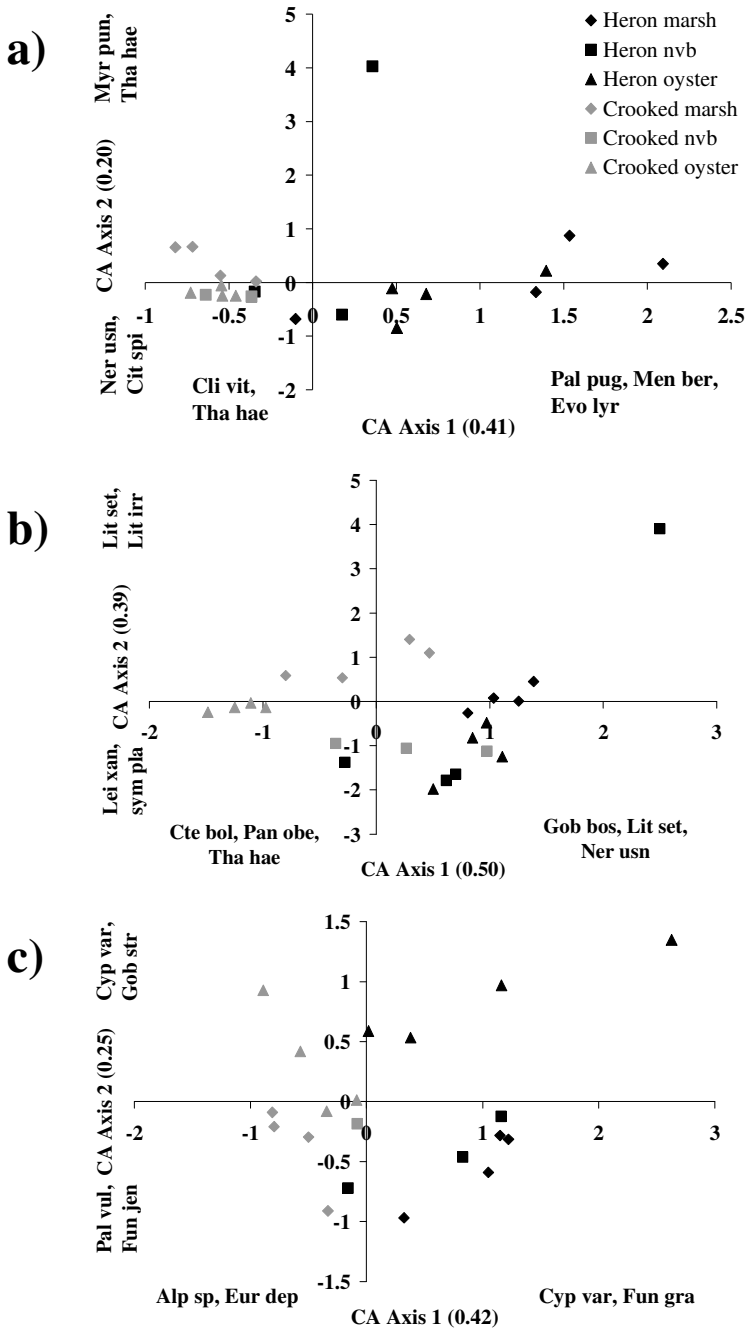

Figure 3-3. First two axes for CA analyses plotted for a) Oct 2003, b) May 2004, and c) July 2004. Eigenvalues are given in parentheses. Species with highest loading scores on the ends of each axis are listed.

samples generally had negative values on Axis 1 associated with the presence of two of the gastropod species *C. vittatus* and *S. haemastoma*.

Community structure during Spring 2004 sampling differed significantly between sites, among habitats, among habitats within Crooked Bayou, and among site-habitat combinations (Figure 3-3b; Table 3-3). The CA produced two axes that explained 89% of the variation in species assemblages. Crooked Bayou samples generally had more positive values on Axis 1 and were characterized by higher abundances of *C. bolesoma*, *P. obessa*, and *S. haemastoma*. Bayou Heron samples were characterized by higher abundances of *G. bosc*, *L. setiferus*, and *N. usnea*. During this season, major habitat differences were characterized by higher abundances of *L. irrorata* and *L. setiferus* in VME and *L. xanthurus* and *S. plagiusa* in NVB (Figure 3-3b).

Community structure during Summer sampling (July 2004) differed significantly between sites, among habitats, among habitats within Bayou Heron, and among site-habitat combinations (Figure 3-3c; Table 3-3). The CA produced two axes that explained 67% of the variation in species assemblages. Along Axis 1, Bayou Heron samples were characterized by higher abundances of *C. variegates* and *F. grandis* while Crooked Bayou samples were characterized by higher abundances of *Alpheus* sp. and *E. depressus*. Along Axis 2, oyster habitat was characterized by higher abundances of *G. stromosus* and *C. variegates*.

Canonical Correspondence Analysis (CCA) resulted in a total model inertia of 3.35. Eigenvalues, which indicate strength of the model, for the first four multivariate axes were 0.306 for CCA axis 1, 0.143 for CCA axis 2, 0.105 for CCA axis 3, and 0.078

for CCA axis 4. Cummulative percent variance of species-environmental relationship for all four CCA axes was 91.5%. Correlations between five of the six environmental variable and the first four axes were statistically significant ($p < 0.03$ for percent oyster, salinity, depth, marsh stem density, and temperature). All environmental variables were retained except for DO (Figure 3-4). Salinity, percent oyster, and depth were strongly correlated with Axis 1 (Figure 3-4). Axis 1 explained 44.2% of the species environmental relationship. Depth, marsh stem density, and temperature were strongly correlated with Axis 2 which explained 20.7% of the species-environmental relationship. Axis 1 models a salinity-oyster gradient that distinguishes species associated with the higher salinities of Crooked Bayou and some of the oyster associated species. The second axis represents a more seasonal gradient with species collected mainly in Spring 2004 (high scores) separated from species collected through the study (scores close to the origin) and species collected in seasons other than Spring 2004 (low scores).

Some of the more notable species environmental relationships include: 1) *Alpheus* sp., *P. simpsoni*, *P. obessa*, and *E. depressus* which are strongly associated with samples in which oyster was present, 2) *Clibanarius vittatus* and *S. haemostroma* are associated with higher salinities, and 3) *Palaemonetes pugio* was correlated with stem density (Figure 3-4).

Diversity, evenness, richness, and density

NVB habitat had the highest overall diversity and evenness compared to the other two habitats, but only 24 species were collected in NVB (Table 3-4). Oyster habitat had the seconded highest diversity, evenness, and a total of 49 species. VME

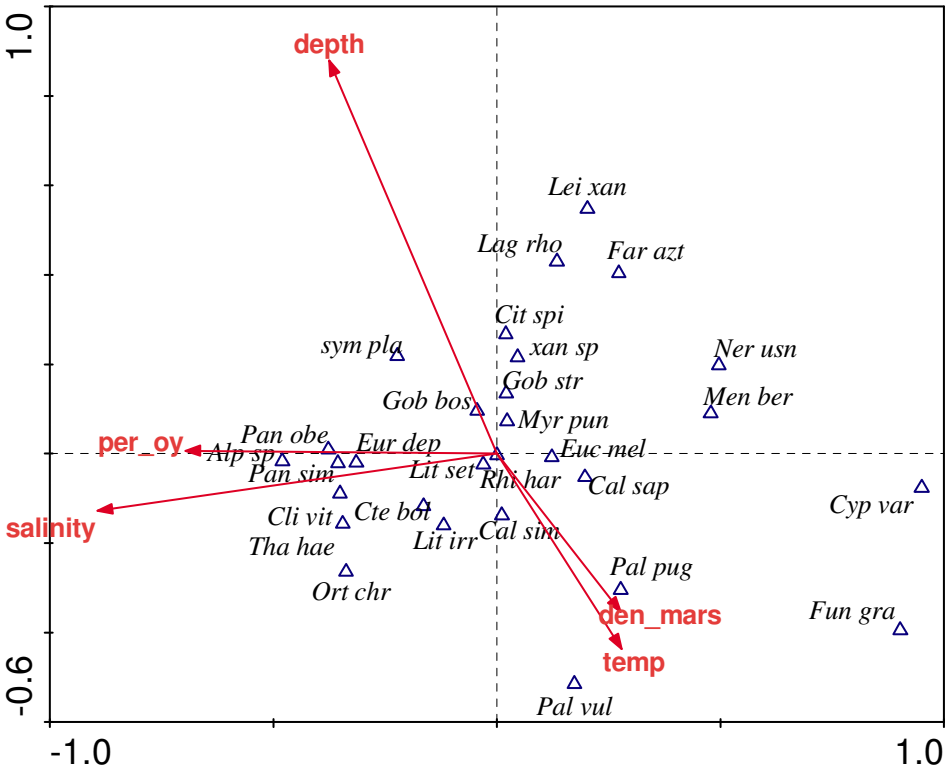

Figure 3-4. Plot of species scores on the first two axes from CCA with environmental data. Triangles plot the scores for species and vectors represent stem density (den_mars), temperature (temp), salinity, percent oyster (per_oy), and depth.

Table 3-4. Overall values for diversity, evenness, and richness for each habitat (with season and sampling area data aggregated), each season (with habitat and sampling area data aggregated), each sampling area (with season and habitat data aggregated).

	Habitat			Season			Sampling Area	
	marsh	NVB	oyster	Oct	May	Jul	Heron	Crooked
Diversity	2.42	2.71	2.57	2.43	2.80	2.33	2.42	2.61
Evenness	0.61	0.85	0.66	0.63	0.79	0.61	0.64	0.67
Richness	52	24	49	46	34	46	45	48

habitat had the highest number of species overall (52), but the lowest diversity and evenness. For seasons, Spring 2004 had the lowest overall species richness (34 species collected), but the highest diversity and evenness. Fall 2003 had the second highest diversity and evenness. Both Fall03 and Summer04 had a species richness of 46. Suumer 2004 had the lowest diversity and evenness. Bayou Heron had lower diversity, evenness, and richness than Crooked Bayou (Table 3-4).

For each of the 3 sampling periods, mean total richness among habitats was significantly different (Figure 3-5a). Within each season, mean total richness was significantly greater in VME and oyster habitat relative to nonvegetated habitat (Bonferroni post hoc comparisons $p < 0.005$; Figure 3-5a).

In Fall 2003, mean total density was significantly different among habitats (randomized block ANOVA: $F_{4,2} = 20.8$, $p < 0.001$) and not significantly different between sites ($F_{0.2,1} = 0.9$, $p = 0.4$). Bonferroni post-hoc tests indicated the following relationship for mean total density among the habitats (when significant $p < 0.001$): VME = oyster < NVB (Fig 3-5b). In Spring 2004 sampling, mean total density was significantly different among habitats ($F_{1.7, 2} = 48.3$, $p < 0.001$) and between sites ($F_{11, 1} = 6.1$, $p = 0.02$) with Crooked Bayou having the higher mean density. Post hoc tests indicated the following relationships among habitats for mean density: VME > oyster > NVB ($p < 0.03$). Mean densities in Summer 2004 sampling differed significantly among habitats ($F_{4.1, 2} = 25.3$, $p < 0.001$) and did not differ significantly between sites ($F_{0.3, 1} = 1.8$, $p = 0.2$). Post hoc tests indicated the following relationship among habitats for mean density: VME = oyster > NVB ($p < 0.001$).

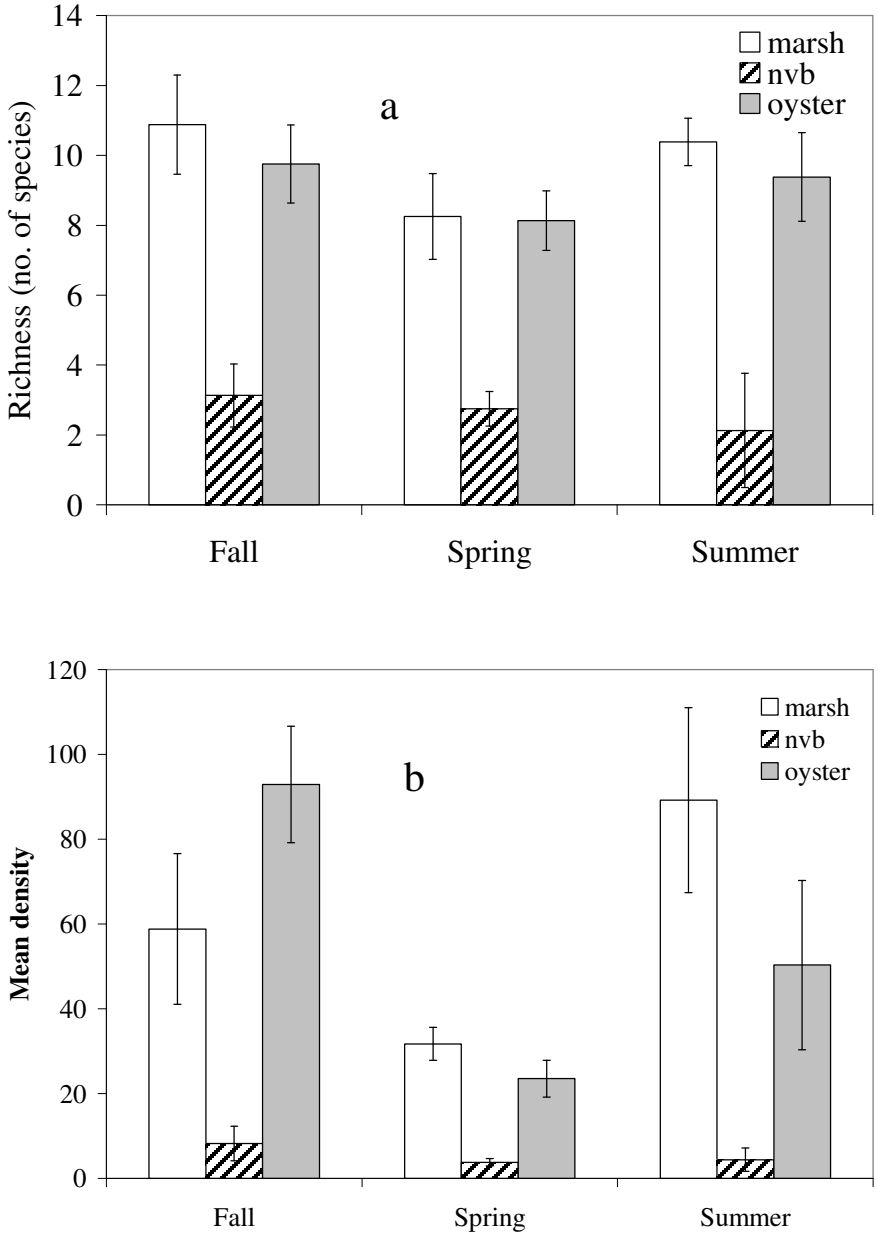

Figure 3-5. Mean species richness (a) and organism abundance (b) for each habitat during the three seasons of collection: Fall (Oct 2003), Spring (May 2004), and Summer (July 2004). Standard error is represented by the vertical bars.

Seine collections

Seining occurred only in the Spring 2004. In the seine samples I collected 9 fish species and 6 invertebrate species between the two sampling areas and among the three habitats (Table 3-5). Overall, fewer species were collected in seine samples and individuals tended to be larger relative to those collected in drop samples (Table 3-5).

At Bayou Heron, I collected two species, *L. setiferus* and *F. grandis*, that were not collected in drop sampling from any of the habitats. Additionally, Bayou Heron seine samples from marsh and NVB habitats combined I collected *L. rhomboides* and *Symphurus plagiusa* which were not collected in any of the drop samples from those habitats. In Crooked Bayou seine samples, I collected 6 species, *Anchoa hepsetus*, *Anchoa mitchelli*, *Brevoortia patronus*, *Menidia berrylina*, *Mugil cephalus*, and *Sesarma reticulum* that were not collected in drop samples in any of the habitats (Table 3-5). For both sampling areas, a smaller size range and mean size for blue crabs *C. sapidus* were collected by drop sampling compared to seining.

Several species were collected by both sampling methods including *C. sapidus*, *F. aztecus*, *L. rhomboides*, *L. xanthurus*, *M. berrylina*, and *P. pugio*. In general, larger blue crabs and brown shrimp were collected in seine samples. Similar-sized *L. xanthurus* and *P. pugio* were collected with both methods (Table 3-5).

Table 3-5. Species collected by seine in Spring (May 2004) are listed with corresponding data from drop samples for each seine species. Drop sample data are given for comparative purposes. I divided the species data by sampling area (Heron and Crooked) and habitats that were seined (oyster and marsh/NVB). Values for each species are listed as RA (Relative abundance), no. (total number in sample), mean size for individual species, and size range for species. An asterisk (*) indicates that a species was not collected by drop sampling in that habitat. A dash (-) indicates that no values were collected for size.

	Seine collections			Drop samples		
Species	**RA (no.)**	**Mean size**	**Size range**	**RA (no.)**	**Mean size**	**Size range**
Heron- oyster						
Callinectes sapidus	4.4 (21)	43	10-340	2.6 (2)	20	17-22
Farfantapenaeus aztecus	72.8 (350)	68	22-100	51.3 (39)	59	32-87
Fundulus grandis	0.2 (1)	60	60.1	*	*	*
Lagodon rhomboides	1.0 (5)	39	35-521	1.3 (1)	50	50
Leiostomus xanthurus	8.7 (42)	40	35-47	26.3 (20)	40	35-43
Litopenaeus setiferus	0.2 (1)	34	34	*	*	*
Menidia berrylina	12.7 (61)	52	42-64	2.6 (2)	25	25-26
Heron- marsh/NVB						
Farfantapenaeus aztecus	22.2 (2)	38	36-39	26.4 (32) / 30.8 (4)	45	22-70
Lagodon rhombiodes	33.3 (3)	38	34-44	*	*	*
Leistomus xanthurus	33.3 (3)	43	39-48	3.3 (4) / 46.2 (6)	39	35-44
Symphurus plagiusa	11.1 (1)	72	72	*	*	*
Crooked- oyster						
Callinectes sapidus	31.1 (14)	63	20-210	4.2 (6)	11	9-12
Farfantapenaeus aztecus	46.7 (21)	51	24-100	3.5 (5)	41	14-63
Mugil cephalus	22.2 (10)	91	75-110	*	*	*
Crooked- marsh/NVB						
Anchoa hepsetus	1.6 (2)	40	31-48	*	*	*
Anchoa mitchilli	2.4 (3)	46	44-51	*	*	*
Breevortia patronus	2.4 (3)	36	35-39	*	*	*
Callinectes sapidus	0.8 (1)	21	21	10.4 (18) / 4.5 (1)	20	4-78
Farfantapenaeus aztecus	3.2 (4)	60	48-100	9.2 (16) / 18.2 (4)	35	16-56
Lagodon rhombiodes	0.8 (1)	51	51	1.2 (2) / 4.5 (1)	53	46-61
Leistomus xanthurus	8.9 (11)	47	42-54	0 / 27.3 (6)	46	40-50
Littorina irrorata	5.6 (7)	-	-	11.6 (20) / 0	-	-
Menidia berrylina	4.0 (5)	65	26-84	*	*	*
Mugil cephalus	6.5 (8)	270	170-340	*	*	*
Palaemonetes pugio	62.9 (78)	25	16-35	42.8 (74) / 0	25	8-35
Sesarma reticulum	0.8 (1)	11	11	*	*	*

Discussion

Habitat-specific trends in nekton abundances and communities

When I examined nekton abundances, oyster habitat, both spatially and temporally, supported similarly high densities of nekton as VME habitat. Also, oyster habitat consistently equated VME habitat in species richness. Both oyster and VME supported significantly higher densities and species richness when compared with adjacent NVB. Several studies have documented higher animal abundances and densities in structured habitats, such as marsh or oyster, relative to unstructured habitat (Zimmerman et al. 1989; Lehnert and Allen 2002; Glancy et al. 2003; Heck et al. 2003). Additionally, some research has demonstrated higher species richness in structured habitats (Rozas and Zimmerman 2000; Leinhert and Allen 2002; Heck et al. 2003). My study supports the idea that oyster habitat, when compared with adjacent VME and NVB is occupied by a distinct community of fishes and invertebrates and supports high densities of these residents.

Direct comparisons of fish and invertebrate communities between adjacent VME and oyster habitats are lacking in current literature. To my knowledge, mine is the first peer-reviewed study to directly compare communities of adjacent oyster, VME, and NVB habitats. One study, Glancy et al. (2003) examined the invertebrate communities of adjacent seagrass, nonvegetated marsh edge, and oyster habitats and documented habitat-specific communities. Many studies have examined fish and invertebrate use of oyster habitat in general (Coen et al. 1999; Harding and Mann 1999, 2001; Glancy et al. 2003) and these studies have contributed greatly to the current understanding of oyster

habitat. However, few studies that utilized enclosure sampling included oyster in habitat comparisons (but see Zimmerman et al. 1989; Glancy et al. 2003; Minello et al. 2003). This deficit has resulted in the low value ranking of oyster habitat compared to other salt marsh estuarine habitats (Minello et al. 2003). In a meta-analysis aimed at examining the nursery role of salt marsh habitat types, Minello et al. (2003) determined the following ranking according to density patterns for fishes and invertebrates combined: seagrass > VME > nonvegetated marsh, open water, macroalgae > vegetated inner marsh > oyster. My study and Glancy et al. (2003) do not support such findings. Both studies clearly demonstrate that oyster supports higher nekton abundances relative to other shallow estuarine habitats.

The occurrence and prevalence of several species appeared related to the presence of live oyster clumps and oyster shell within the three habitats in my study. A similar relationship was documented in a Texas estuary (Zeug et al. in press). In my study, sampling was conducted in a random design within a turbid environment and on several occasions small clumps of oyster were discovered in and collected from VME and NVB habitats (Table 3-1). Mud crabs (*P. obessa*, *P. simpsoni*, *E. depressus*) and snapping shrimp (*Alpheus* sp.) were highly correlated with percent oyster present in samples according to CCA results (Figure 3-3). These species were collected in the non-oyster habitats, but only when oyster was also collected in the samples. *Eurypanopeus depressus* and *Panopeus* spp. are common oyster reef residents (Shervette et al. 2004, Glancy et al. 2003) and *Alpheus* spp. have also been collected in habitats where oyster was present (Zimmerman et al. 1989; Leinhert and Allen 2002; Glancy et al. 2003;

Shervette et al. 2004; Zeug et al, in press). Differences in habitat-specific communities in my study were not always strong because many species occurred in multiple habitats. If I had sampled exclusive NVB and VME habitats, I may have documented stronger differences in communities among habitats (Rozas and Minello 1997).

Oyster and VME may provide habitats for relatively rare species. Nine fish species and 2 invertebrate species were collected exclusively in oyster. Similarly for VME habitat, 13 fish species and 3 invertebrate species were collected exclusively in VME. None of these species occurred at high densities and one explanation for these findings is that my replication was too low and if I had collected more replicate samples in each habitat then my results may have differed. At least two of the fish species collected exclusively in oyster samples have been documented across multiple habitats in seine results and in other studies. Striped mullet *Mugil cephalus* juveniles and adults have been documented in VME and NVB habitats (Zimmerman et al. 1990a, b). Also, I collected stripe mullet in NVB/VME habitats in Spring 2004 seine samples. Southern flounder *P. lethostigma* has also been documented in other habitats (Zimmerman et al. 1989).

Of the 13 species exclusively caught in VME, grey snapper *Lutjanus griseus* and code goby *Gobiosoma robustum*, have also been documented in other habitats (Zimmerman et al. 1989; Shervette et al. 2004). However, evidence exists that at least some of the species I collected exclusively in one of my habitats may prefer that habitat and occur naturally in relatively low abundances, especially outside of peak recruitment periods. *Fundulus jenkinsi* was collected exclusively in summer VME and is considered

a rare species in GBNERR (M. Woodrey, research coordinator, GBNERR, personal communication). The two *Sygnathus* spp. were collected exclusively in VME in the current study and in a similar unpublished study (Zimmerman et al 1989). The lyre goby *Evorthodus lyricus* also appears to prefer VME habitat and occurs in relatively low abundances than other estuarine gobies (V. Shervette, unpublished data). The two blenny species collected exclusively in oyster habitat (*Hypsoblennius hentzi* and *H. ionthas*) are commonly associated with oyster reefs (Coen et al. 1999). Additionally, toadfish *O. beta*, an oyster-associated fish (Coen et al. 1999), was collected exclusively in marsh habitat, but only in samples with oyster. So, oyster and VME may provide important habitat for some of the less abundant fish species.

Many fish and invertebrate species found in two or more habitats occurred at higher densities in one specific habitat, either oyster or VME. For example, *F. grandis* was collected in all three habitats, but occurred at higher abundances in marsh samples. The goby *G. bosc* was also collected in all three habitats, but more was collected in marsh samples. For the invertebrates, white shrimp *L. setiferus*, the mud crabs *P. simpsoni*, *P. obessa*, and *E. depressus*, and *R. harrisoni*, were collected in multiple habitats, but consistently occurred in higher abundances in oyster. The grass shrimp *P. pugio* occurred in VME and oyster habitats, but more were consistently collected in VME. Other studies have found similar relationships with one or more of these species. During fall sampling, Minello and Webb (1997) collected a higher mean density of *G. bolesoma* in natural VME (3.3 individuals per 2.6 m^2) relative to NVB (0.9 individuals per 2.6 m2). That study also documented a higher mean density of *P. pugio* in VME

(234.5 individuals per 2.6 m^2) relative to NVB (0.6 individuals per 2.6 m^2) for the same season. Rozas and Reed (1993) found that *F. grandis* used structured habitat over non-structured habitat.

In summary, three trends emerged from my habitat-specific community comparisons: 1) Oyster and VME provide habitat for numerous species relative to NVB; 2) Oyster and VME provide habitat for some relatively rare species; and 3) Many species collected across multiple habitats occurred at higher abundances in oyster or VME habitat. These trends stress the importance of oyster and VME habitats, in general. Additionally, in GBNERR within the two marsh complexes sampled, NVB comprises roughly 75% of available shallow habitat while VME and oyster habitats comprise roughly 20 and 5% of available shallow habitat (V. Shervette, personal observation). This disproportionate ratio of available shallow habitats stresses even more the importance of VME and oyster as habitats within the marsh complexes of GBNERR.

Temporal and spatial trends in nekton abundances and communities

Differences in fish and invertebrate abundances and community structure may be related to observed differences in environmental variables. Many studies have observed a relationship between temporal and spatial shifts in community structure and changes in environmental factors such as temperature, salinity, and DO (Rakocinski et al. 1996; Gelwick et al. 2001; Akin et al. 2003). In the current study I found that salinity, temperature, and depth were associated with seasonal and spatial shifts in nekton communities. CA and MRPP results demonstrated that with each season and over the

course of the whole study the fish and invertebrate community of Crooked Bayou differed from that of Bayou Heron (Table 3-4). I also found that salinity varied temporally and was consistently higher in Crooked Bayou. Temperature also increased temporally, but did not vary between the areas sampled. Salinity is often cited as important in the organization of estuarine communities (Rakocinski et al. 1992; Baltz et al. 1998; Gelwick et al 2001; Kupschus and Tremain 2001; Akin et al 2003). In fact, salinity zones are commonly identified within an estuary and utilized in long-term monitoring of community dynamics as a measure of ecosystem health (Bulger et al. 1993). In my study, species such as the hermit crab *C. vittatus* and the oyster drill, *S. haemastroma*, common polyhaline species (V. Shervette, unpublished data), occurred only in samples from Crooked Bayou, where salinity was within the polyhaline range. Results from the CCA confirmed the strong relationship between the abundances of many of the species I collected and salinity.

The relative location of the two marsh complexes within the context of the whole estuary may also explain, in part, temporal and spatial differences in communities. Location also explains differences in salinities between the two areas. Bayou Heron is situated in the upper zone of GBNERR within 1 km of an underground freshwater source. Crooked Bayou, although receiving some freshwater from rain events, is located in a lower zone of the estuary and is directly connected to Mississippi Sound (Figure 3-1). These different locations may vary in their proximity to marine larval and freshwater larval supplies. Proximity to larval sources has been documented as an important factor in determining community composition and organismal abundances (Heck and Thoman

1984). Timing of larval recruitment also plays a role in temporal fish and invertebrate community composition and abundance patterns (Akin et al. 2003) and my study illustrated how temporal recruitment affects nektonic communities through the seasonal occurrence of several species such as white shrimp, brown shrimp, and spot.

Relative habitat value and nursery habitat implications

One important indicator of habitat value, in general, and nursery habitat value in particular, is the relative abundance of targeted species (Boesch and Turner 1984; Baltz et al. 1998; Minello 1999). Many studies evaluating habitat value assume that fishes and invertebrates select habitats with varying degrees of qualities and that higher abundances indicate higher quality habitat (McIvor and Odum 1988; Minello 1999). Value and quality are relative concepts within the context of individual studies, therefore generalizations of habitat value should be interpreted cautiously (Halpin 2000; Glancy et al. 2003). Estuarine and estuarine-dependent marine residents may select for or occur at higher abundances in specific estuarine habitats because they provide important food resources, refuge from predation, or both (Boesch and Turner 1984). Estuarine residents may also utilize a particular habitat over others because of habitat-specific reproductive-related reasons such as increased survival and growth of eggs, larvae, or juveniles (see review: Coen et al. 1999 and references therein).

Higher growth rates associated with certain estuarine habitats have been attributed to higher abundances of food resources (Summerson and Peterson 1984; Sogard 1992; Levin et al. 1997; Stunz et al. 2002a). Infauna and epifauna are common prey items for many of the species I collected and occur at higher abundances in

structured habitats (Zimmerman et al. 1989; McTigue and Zimmerman 1998). In fact, at least one study has documented that benthic organisms such as amphipods, annelid worms, and chironomid larvae that feed on detritus and living vegetal materials are some of the most important foods of primary and secondary estuarine consumers (Akin and Winemiller 2006). Also, many of the species I collected at higher abundances in VME and oyster, such as mud crabs, juvenile blue crabs, and grass shrimp, are preyed on by other species I collected like toadfish, pinfish, and spot.

Significant differences in habitat-specific growth rates have been documented for several estuarine species. White shrimp with access to VME grow significantly faster than those without access (Zimmerman et al. 1983). Brown shrimp grow faster in marsh than NVB (Minello et al. 1984). During the summer, mummichog, *Fundulus heteroclitus*, a closely related species to *Fundulus grandis*, experience higher growth rates in marsh habitat (Haplin 2000). Juvenile red drum grow faster in vegetated habitats (marsh and seagrass) compared to nonvegetated habitats (Stunz et al. 2002a). For all of these species, evidence exists that densities are higher in the habitats where growth was highest (Halpin 2000; Stunz et al. 2002b; Minello et al 2003) supporting a connection between higher growth rates and higher abundances within the same habitat.

Refuge from predation is another important function of oyster and VME habitats that may contribute to the higher habitat-specific densities I observed. Minello et al. (2003) asserted that habitat-specific survival estimates are an important way of measuring habitat quality for fishes and invertebrates. For example, evidence exists that VME relative to some other estuarine habitats provides higher survival rates for species

such as blue crabs, brown shrimp (Minello 1993), and red drum (Stunz and Minello 2001). In fact, in a review of pertinent literature, Heck et al. (2003) found that few differences existed in abundance, growth, or survival of nekton in seagrass habitat compared to other structured estuarine habitats. The review concluded that structure, in itself, rather than the type of structure, appeared to be an important determinant of a habitat's nursery value (Heck et al. 2003). This conclusion supports the similarly high nekton abundances I observed in oyster and VME habitats.

Habitat-related differences in depth may contribute to habitat-related differences in predation risk. In my study, VME samples were significantly shallower within each season relative to NVB and oyster. The combination of structure and water depth may influence habitat use by small fishes and invertebrates because predation risk may be greater in deeper NVB areas (Baltz et al. 1993; Ruiz et al. 1993; Heck and Coen 1995). Water depth, per se, is an important factor in determining predation risk (Ruiz et al. 1993). Predators of small fishes and invertebrates such as piscivorous fishes and blue crabs occupy areas of water > 70 m depth in higher abundances than shallower areas (Ruiz et al. 1993, V. Shervette, unpublished data from GBNERR). Additionally, Ruiz et al. (1993) documented that mortality rates from predation of several common estuarine and estuarine-dependent species increased with depth. Nekton densities were always higher in VME and oyster habitats relative to NVB habitat in my study and these densities, collected during high tide, may reflect the greater predation risk in the deeper, unstructured NVB habitat.

Oyster habitat provides an essential function for several of the resident species I collected. In addition to refuge from predation, clingfish *Gobiesox strumosus*, the two blenny species, naked goby *G. bosc*, and toadfish *O. beta* use oyster habitat for breeding and nesting. Male toadfish find nesting sites underneath oyster shells and call for females to deposit eggs there. Then the male remains in the nest, maintaining and guarding eggs (V. Shervette, personal observation). Gobies, blennies, and clingfish lay eggs on the inside of recently dead shells and also exhibit egg guarding behavior (Breitburg et al. 2000). Oyster habitat in Grand Bay may provide an essential function in the reproduction success for the goby, blenny, and toadfish species I collected.

Conclusions

The goal of my study was to determine the relationship between three common shallow estuarine habitats (oyster, VME, and NVB) and nekton community structure in order to address the dearth in research comparing oyster with adjacent habitats. In obtaining that goal, I documented three basic trends related to the importance of oyster and VME habitats: 1) Oyster and VME provide habitat for significantly more species relative to NVB; 2) Oyster and VME provide habitat for uncommon and rare species; and 3) Several species collected across multiple habitats occurred at higher abundances in oyster or VME habitat. I also found that contrary to the current low value ranking of oyster habitat relative to other estuarine habitats (Minello et al. 2003), oyster provides higher quality habitat for many species. As a structured habitat, oyster, similar to VME and submerged aquatic vegetation, may provide higher growth rates for some species and refuge from predation for others. As documented in studies concerning other

habitats, high abundances of certain species in oyster may be indicative of higher growth rates in oyster, greater refuge from predation in oyster, or both. Further research comparing habitat-specific growth and survival is essential in verifying the overall importance of oyster habitat for resident and nursery species. Oyster appears to support a temporally diverse and spatially distinct nekton community and deserves further attention in research and conservation.

CHAPTER IV

DECAPOD UTILIZATION OF ADJACENT OYSTER, VEGETATED MARSH, AND NONVEGETATED BOTTOM HABITATS IN A GULF OF MEXICO ESTUARY

Introduction

Crassostrea virginica oyster reefs and oyster shell deposits provide essential functions in estuarine ecosystems. As individual living organisms, oysters act as filters pulling particulate matter from the water column (Newell 1988). As three-dimensional conglomerate structures, oyster reefs interrupt water flow and serve as sites for suspended matter to settle (Dame et al. 1984). Oyster reefs and low profile accumulations of oyster shell provide complex structural matrices in which numerous sessile and mobile fauna seek refuge from physical disturbance, physiological stress, and predation (Coen et al. 1999). Oyster habitat also provides a site of concentrated food resources for a variety of species (Zimmerman et al. 1989).

Information concerning relative habitat value is essential in light of the current legal mandates concerning coastal habitat conservation and restoration (Coen et al. 1999). However, the current understanding of oyster as faunal habitat is limited by a lack of quantitative comparative studies with other habitats. Vegetated marsh and submerged aquatic vegetation habitats have been studied more extensively and are thought to rate relatively high in habitat function and value, especially when compared to adjacent nonvegetated bottom (Heck et al. 2003; Minello et al. 2003). Much research supports the notion that these vegetated habitats and their associated structural

complexity provide excellent refuge and food resources for estuarine residents and juveniles of estuarine-dependent species. Oyster habitat is also structurally complex and may provide similar functions as the vegetated habitats.

All structured habitats vary in the quality and quantity of refugia they provide and this variation may be reflected in the species utilizing these habitats. Juveniles of Gulf stone crab *Menippe adina* depend on habitat structural complexity for refuge from predation and their habitat needs shift with ontogeny (Shervette et al. 2004). Other species of invertebrates may have similar needs. Additionally, some invertebrates may chose certain habitats for associated food resources and are not as directly limited by the mosaic of refuges a habitat provides.

In order to add to the current understanding of oyster as an important estuarine habitat, I examined spatial and temporal trends in abundance and size of seven common decapod species across oyster and adjacent shallow habitats common to Mississippi estuaries. Of the seven species, four were estuarine residents of ecological importance: mud crab *Eurypanopeus depressus*, mud crab *Panopeus simpsoni*, mud crab *Rhitropanopeus harrisi*, and grass shrimp *Paleomonetes pugio*. The other three species were estuarine-dependent marine residents of ecological and economic importance: blue crab *Callinectes sapidus*; brown shrimp *Farfantapenaeus aztecus*, and white shrimp *Litopenaeus setiferus*. The three habitats examined were *Spartina alterniflora* vegetated marsh edge (VME), oyster reef and shell, and nonvegetated bottom (NVB).

Materials and Methods

Invertebrate sampling

I collected invertebrates in VME, oyster, and NVB habitats using a 1.17 m^2 drop sampler according to the procedures of Zimmerman et al. (1984). I utilized drop sampling in the three habitats because the catch efficiency does not vary significantly with habitat characteristics (Rozas and Minello 1997). I selected two marsh complexes in Grand Bay NERR (GBNERR), approximately 6 km apart, that had all three habitats. Sites of collection within habitats were selected randomly. I collected four replicate samples within each habitat at each sampling area. Sampling occurred in Fall 2003 (4-10 October), Spring 2004 (13-20 May), and Summer 2004 (16-28 July) within two hours of high tide when all habitats were completely inundated. I collected a total of 72 drop samples (4 replicates x 3 habitats x 2 sampling areas x 3 seasons).

I measured temperature (°C), salinity (PSU), and dissolved oxygen (mg/L) using a YSI 85 meter and water depth (cm) using a measuring tape for each drop sample. After collecting this data I used a hose with plastic mesh (1 mm) fixed to the intake nozzle to pump out water from within the sampler. In VME habitat, I removed marsh vegetation from the sampler and recorded the number of stems present. In oyster habitat, percent oyster cover was recorded after water was removed. Then all oyster was removed from sampler and washed over 3 mm plastic mesh netting and organisms present were collected. If any oyster was found in VME or nonvegetated bottom samples, percent oyster was recorded and oyster was processed as described previously.

Invertebrates were identified to species and measured: crabs to 0.1 mm carapace length (CL) and shrimp 0.1 mm total length (TL).

Statistical analyses

I chose nonparametric statistics because abundance and size data violated the normality assumption of parametric statistics. I used Kruskal-Wallis test, the nonparametric equivalent of a one factor ANOVA, to test for significant differences in abundance among habitats and among seasons for each species. If a significant difference in abundance among habitats occurred, I used a Mann Whitney U test, the nonparametric equivalent of a Student t-test, to test for pairwise comparisons for habitats and for seasons. If a species did not occur in all three habitats or all three seasons, then I used a Mann Whitney U test to test for significant differences between the two habitats or two seasons in which the species did occur. I also used Mann Whitney U to test for significant differences in abundance for each species between sampling areas. Because so many tests were conducted for abundance, I lowered the acceptance level for significance from the usual 0.05 to 0.01. I also used Kruskal-Wallis for size comparisons among habitats and among seasons for each species. For pairwise comparisons with size, I used Kolmogorov-Smirnov Z. Because so many tests were conducted for size, I lowered the acceptance level for significance from the usual 0.05 to 0.01.

Results

Abundance

Blue crab abundance varied significantly among the three habitats (Table 4-1). More blue crabs were collected in VME and oyster habitats relative to NVB habitats (Figure 4-1; Table 4-1). No significant difference in abundance was detected between VME and oyster (Table 4-1). No significant differences were detected in blue crab abundance among seasons or between sampling areas.

Brown shrimp were collected mainly during spring (Figure 4-1). No significant difference in abundance was detected for brown shrimp among habitats (Table 4-1), although total abundances in VME and oyster were high relative to NVB (Figure 4-1). No significant difference in abundance was detected between sampling areas.

White shrimp abundance varied significantly among habitats (Table 4-1). Significantly more white shrimp were collected in oyster habitat relative to NVB. No significant differences were detected in abundance between VME and NVB or between VME and oyster (Table 4-1). White shrimp were collected mainly in fall and summer with relatively few individuals found in spring (Figure 4-1). No significant differences in abundance were detected between fall and summer or between the two sampling areas (Table 4-1).

Grass shrimp were only collected in VME and oyster habitats (Figure 4-2) with significantly more found in VME (Table 4-1). No significant differences in abundance were detected among seasons or between sampling areas (Table 4-1).

Table 4-1. This table lists the results of the statistical comparisons for abundance. If a comparison among the three habitats or the three seasons was significant, then the pair-wise comparisons were also tested. A test was deemed significant at an alpha of 0.01.

Abundance comparisons	Test statistic	Significance
Blue crab		
Habitat	$\chi^2 = 20.99$	< 0.001
NVB x VME	U = 85.00	< 0.001
NVB x oyster	U = 136.50	0.001
VME x oyster	U = 212.50	0.115
Season	$\chi^2 = 3.59$	0.166
Site	U = 584.50	0.462
Brown shrimp		
Habitat	$\chi^2 = 4.32$	0.115
Site	U = 41.50	0.078
White shrimp		
Habitat	$\chi^2 = 13.19$	0.001
NVB x VME	U = 64.50	0.015
NVB x oyster	U = 40.50	0.001
VME x oyster	U = 95.50	0.224
Season	U = 217.00	0.128
Site	U = 278.00	0.830
Grass shrimp		
Habitat	U = 113.00	< 0.001
Season	$\chi^2 = 3.27$	0.195
Site	U = 643.50	0.959
E. depressus		
Habitat	$\chi^2 = 13.38$	0.001
NVB x VME	U = 170.50	0.003
NVB x oyster	U = 141.50	< 0.001
VME x oyster	U = 247.00	0.374
Season	$\chi^2 = 9.57$	0.008
fall x spring	U = 163.00	0.005
spring x summer	U = 286.00	0.958
fall x summer	U = 183.50	0.019
Site	U = 353.00	< 0.001
P. simpsoni		
Habitat	$\chi^2 = 10.45$	0.003
NVB x VME	U = 182.00	0.003
NVB x oyster	U = 179.00	0.002
VME x oyster	U = 262.50	0.557
Season	$\chi^2 = 13.38$	0.322
Site	U = 304.50	< 0.001
R. harrisii		
Habitat	$\chi^2 = 8.95$	0.011
NVB x VME	U = 221.00	0.069
NVB x oyster	U = 168.50	0.003
VME x oyster	U = 225.50	0.159
Season	$\chi^2 = 7.29$	0.026
Site	U = 483.00	0.029

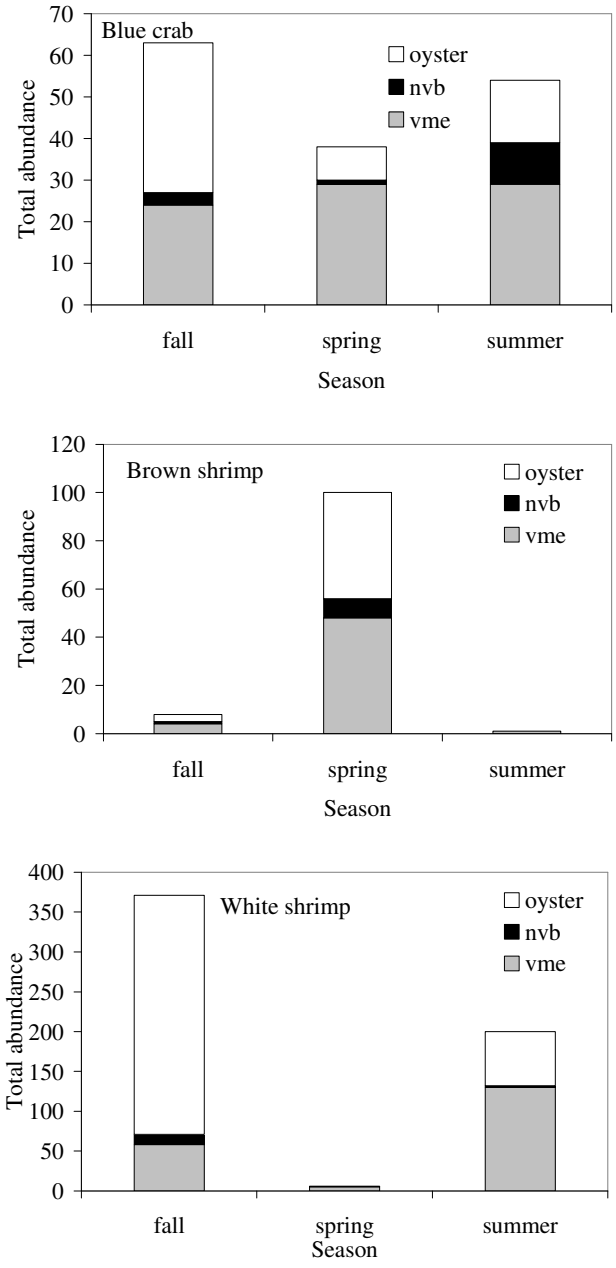

Figure 4-1. Total abundance values for each of the three estuarine dependent species for each season sampled. Total abundance is divided into the number of individuals collected from each habitat.

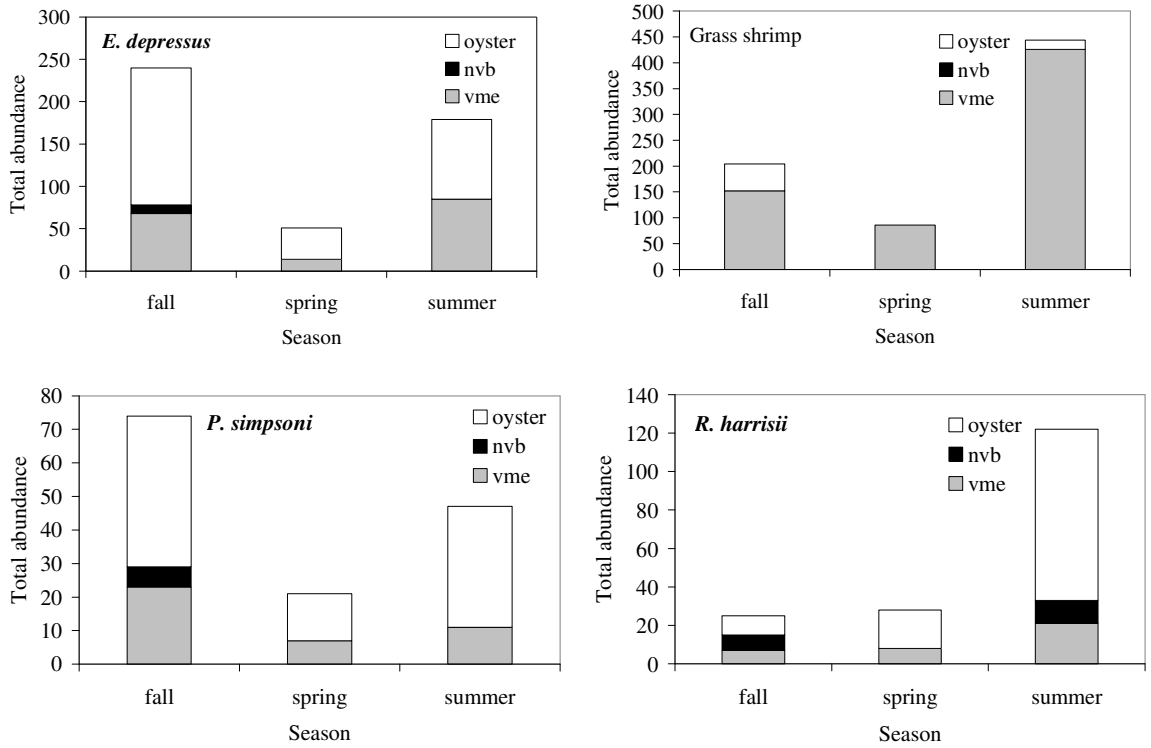

Figure 4-2. Total abundance values for each of the three estuarine resident species for each season sampled. Total abundance is divided into the number of individuals collected from each habitat.

Eurypanopeus depressus abundance varied significantly among habitats with significantly more occurring in oyster and VME relative to NVB (Table 4-1). Nearly twice as many *E. depressus* were collected in oyster than VME (Figure 4-2), but no significant difference in abundance was detected between those habitats. Seasonal abundance varied significantly with more *E. depressus* collected in fall than in summer or spring. Additionally, significantly more were collected at Crooked Bayou than Bayou Heron (Table 4-1).

Panopeus simpsoni abundance varied significantly among habitats with significantly more collected in VME and oyster than NVB. No difference in abundance was detected between VME and oyster. No significant difference in abundance occurred among season. Significantly more *P. simpsoni* were collected at Crooked Bayou than at Bayou Heron (Figure 4-2; Table 4-1).

Rhithropanopeus harrisii abundance was significantly higher in oyster relative to NVB (Table 4-1; Figure 4-2). No significant difference in abundance was detected among seasons or between sampling areas.

Size distributions

Oyster provided habitat for significantly smaller blue crabs than did marsh habitat. No significant difference in size was detected between NVB and oyster or NVB and marsh. Size did not vary significantly among seasons or between sampling areas (Tables 4-2 and 4-3).

VME provided habitat for significantly smaller brown shrimp than oyster. No significant difference in size was detected between oyster and NVB or NVB and VME

Table 4-2. This table lists the mean sizes (mm TL for shrimp and mm CW for crabs) for each species. Values were calculated for each habitat (season and sampling areas data aggregated), season (habitat and sampling area data aggregated), and sampling area (habitat and season data aggregated). Standard deviations are given in parentheses.

	Habitat			Season			Site	
	vme	oyster	nvb	fall	spring	summer	Heron	Crooked
Blue crab	24.8 (16.87)	16.2 (14.19)	20.7 (15.69)	21.0 (14.37)	20.8 (14.37)	19.9 (13.96)	22.4 (16.11)	18.5 (15.85)
Brown shrimp	40.7 (15.64)	56.4 (17.02)	43.3 (14.63)	-	48.5 (17.28)	-	52.6 (16.59)	34.3 (14.15)
White shrimp	45.0 (8.16)	47.9 (8.48)	55.7 (2.43)	47.4 (8.88)	-	48.0 (6.91)	45.3 (9.40)	49.4 (7.29)
Grass shrimp	22.2 (5.95)	*	20.4 (4.91)	18.3 (4.36)	24.7 (6.07)	23.6 (4.56)	19.3 (5.17)	24.0 (5.44)
E. depressus	8.0 (2.65)	7.4 (1.77)	6.9 (1.98)	6.9 (1.91)	9.2 (2.54)	7.7 (2.86)	7.4 (1.73)	7.3 (2.41)
P. simpsoni	10.8 (4.72)	8.0 (4.72)	10.1 (2.98)	10.9 (3.92)	9.5 (2.37)	8.0 (3.14)	7.8 (1.36)	10.3 (3.71)
R. harrisi	7.4 (2.68)	6.6 (2.05)	7.4 (2.16)	8.8 (2.58)	6.7 (3.33)	6.3 (1.82)	6.5 (2.19)	7.1 (2.27)

Table 4-3. This table lists the results of the statistical comparisons for size. If a comparison among the three habitats or the three seasons was significant, then the pair-wise comparisons were also tested. A test was deemed significant at an alpha of 0.01.

Size comparisons	Test statistic	Significance
Blue crab		
Habitat	$\chi^2 = 17.65$	< 0.001
nvb x vme	Z = 0.99	0.285
nvb x oyster	Z = 0.93	0.356
vme x oyster	Z = 2.80	< 0.001
Season	$\chi^2 = 0.39$	0.823
Site	Z = 1.23	0.095
Brown shrimp		
Habitat	$\chi^2 = 18.54$	< 0.001
nvb x vme	Z = 0.66	0.782
nvb x oyster	Z = 1.18	0.124
vme x oyster	Z = 2.10	< 0.001
Site	Z = 2.22	< 0.001
White shrimp		
Habitat	$\chi^2 = 29.16$	< 0.001
nvb x vme	Z = 2.56	< 0.001
nvb x oyster	Z = 1.98	0.001
vme x oyster	Z = 2.02	0.001
Season	Z = 1.48	0.025
Site	Z = 2.75	< 0.001
Grass shrimp		
Habitat	Z = 1.34	0.054
Season	$\chi^2 = 74.13$	< 0.001
fall x spring	Z = 4.17	< 0.001
fall x summer	Z = 2.03	0.001
spring x summer	Z = 3.77	< 0.001
Site	Z = 3.77	< 0.001
E. depressus		
Habitat	$\chi^2 = 20.98$	< 0.001
nvb x vme	Z = 0.72	0.681
nvb x oyster	Z = 0.82	0.516
vme x oyster	Z = 2.14	< 0.001
Season	$\chi^2 = 37.01$	< 0.001
fall x spring	Z = 3.29	< 0.001
fall x summer	Z = 1.21	0.106
spring x summer	Z = 2.19	< 0.001
Site	Z = 1.46	0.027
P. simpsoni		
Habitat	$\chi^2 = 3.90$	0.142
Season	$\chi^2 = 8.81$	0.012
fall x spring	Z = 0.97	0.301
fall x summer	Z = 1.69	0.007
spring x summer	Z = 1.24	0.091
Site	Z = 1.08	0.195
R. harrisii		
Habitat	$\chi^2 = 2.80$	0.247
Season	$\chi^2 = 17.85$	< 0.001
fall x spring	Z = 1.77	0.004
fall x summer	Z = 2.03	0.001
spring x summer	Z = 0.99	0.285
Site	Z = 0.87	0.434

(Tables 4-2 and 4-3). Brown shrimp collected in Bayou Heron were significantly larger than those collected in Crooked Bayou (Tables 4-2 and 4-3).

White shrimp collected in NVB were significantly larger than those collected in oyster. Additionally, those collected in oyster were significantly larger than shrimp collected in VME (Tables 4-2 and 4-3). No significant difference in size was detected between the two seasons tested (fall and summer). White shrimp from Crooked Bayou were significantly larger than those collected in Bayou Heron (Tables 4-2 and 4-3).

Grass shrimp size did not vary significantly among the two habitats in which it occupied. Grass shrimp size varied significantly among the three seasons, exhibiting the following relationship: spring > summer > fall (Tables 4-2 and 4-3). Grass shrimp size also varied significantly between sampling areas with individuals collected at Crooked Bayou significantly larger than those from Bayou Heron.

Size of *E. depressus* varied significantly among habitats with oyster providing habitat for significantly smaller crabs relative to VME. No differences in size were detected between oyster and NVB or VME and NVB. Size also differed significantly among seasons in the following manner: spring > fall = summer (Tables 4-2 and 4-3).

No significant differences in size among habitats were detected for *P. simpsoni* or *R. harrisii*. Seasonally, *P. simpsoni* collected in fall were significantly smaller than those collected in summer. No significant differences in size were detected for *P. simpsoni* between fall and spring or between spring and summer. *Rithropanopeus harrisii* size varied significantly among seasons, exhibiting the following relationship:

fall > spring = summer. Neither of these two species varied in size between sampling areas (Tables 4-2 and 4-3).

Discussion

Abundances of 6 out of the 7 species varied among the habitats I examined in Grand Bay. Oyster and VME provided unique habitats for most of those species. Oyster supported significantly higher abundances compared to adjacent NVB for 5 of the 7 species. Marsh habitat supported significantly higher abundances relative to adjacent NVB for 3 of the 7 species. VME also supported significantly higher abundances of grass shrimp than oyster. The species abundance patterns in this study reflect a combination of habitat selection and differential mortality associated with these habitats (Zimmerman et al. 1989).

I collected juvenile blue crabs in all three habitats and throughout my study period. Blue crab recruits into GOM estuaries as megalopae (Perry 1975) and juveniles occur in estuarine habitats throughout the year (Perry and Stuck 1982). In my study, blue crabs appeared to select for oyster and VME over NVB which may, in part, be related to habitat-specific availability of food resources. The diet of juvenile blue crab is broad. They are omnivores and feed on various crustaceans, mollusks, fishes, and detritus (Perry and McIlwain 1986). Common prey items for juvenile blue crab include many epifaunal and infaunal species frequenting oyster and VME habitats (Perry and McIlwain 1986; Zimmerman et al. 1989). A study from another Mississippi estuary also found a higher abundance of juvenile blue crab in VME than NVB (Rakocinski and

McCall 2004). Another reason for higher abundances of blue crab in oyster and VME is the need for refuge. The quality of habitat-specific refugia is an important factor regulating crab populations for many species (Beck 1995; Shervette et al. 2004). Significantly smaller blue crabs occupied oyster habitat relative to VME. Oyster may provide smaller spaces in which juvenile blue crabs can seek refuge compared to VME. Juveniles of another estuarine-dependent crab species, stone crab *Menippe adina*, utilize subtidal/intertidal oyster reef and oyster shell deposits at a small size in high abundance for refuge from predation (Shervette et al. 2004). Juvenile blue crabs may exhibit a similar need for refuge, because several predatory fish species that eat crabs are common to my sampling areas.

I did not detect a difference in habitat-specific occupancy for brown shrimp and I only collected brown shrimp at high abundance in spring samples. The seasonal abundance pattern I observed was supported by Howe and Wallace (2000) who also documented a peek recruitment period during spring for this species. Although I did not find a significant difference in abundance among the three habitat (which may have been due to high variability in samples), I collected 6 times more shrimp in VME and 5 times more shrimp in oyster relative to NVB (Figure 4-1). These total abundance comparisons may better reflect the relationship between brown shrimp abundance and habitat. The fact that brown shrimp select for VME over NVB is well established (see review in Zimmerman et al. 2000). Heck et al. (2003) asserted that for many nursery species, habitat selection is related to presence of structure, and not necessarily to what is providing the structure. Furthermore, brown shrimp abundance in VME is not correlated

with VME stem density (Zimmerman et al. 1984). This may explain why in my study brown shrimp occurred at similarly high abundances in the two structured habitats relative to NVB.

Larger juvenile brown shrimp occupied oyster habitat relative to VME and this may be related to habitat-specific availability of food, habitat-specific predation, or a combination of both. As brown shrimp grow during their time in estuarine waters, their specific habitat needs may also change. Further study is required to better understand these habitat-specific size differences.

The seasonal abundance and size patterns I observed for white shrimp were consistent with their recruitment into estuarine habitats (Muncy 1984). Juvenile white shrimp abundances in estuaries peak in summer and fall (Muncy 1984). White shrimp abundance in oyster was significantly higher relative to NVB. I discuss my findings concerning the habitat-specific abundance and size patterns I observed for this species in Chapter VI. Briefly, white shrimp grow faster in oyster relative to VME and NVB which may indicate more or better food resources in that habitat. Higher abundances of several estuarine and marine species in a particular habitat has been attributed to higher growth rates or increased food resources. See Chapter VI for references and an extensive discussion concerning this species.

In my study, grass shrimp clearly selected for VME over oyster and NVB. Other studies have also documented higher densities of this species in vegetated habitats relative to nonvegetated habitats (Zimmerman et al. 1989; Zimmerman et al. 1990; Minello et al. 1994; Rozas and Minello 1998). In addition, grass shrimp in my study and

in Zimmerman et al. (1989) occupied VME in higher abundances than oyster. Grass shrimp are often cited as major primary and detrital consumers in salt marshes (see Anderson 1985 and references therein). Grass shrimp *P. pugio* feeding habits are strongly tied to vegetated marsh resources, consuming vast quantities of marsh detritus, epiphytic microalgae that coat marsh stems, and associated epi- and infauna (see Anderson 1985 and references therein). Additionally, evidence exists that vegetated marsh may reduce predation rates on grass shrimp (Shervette, unpublished data). Grass shrimp are common items in the diets of a suite of predators (Anderson 1985), further necessitating their reliance on VME habitat.

The three mud crab species clearly selected for oyster habitat, especially when considered as an aggregate group. Individually, each species had higher abundances in oyster relative to NVB. Mud crabs were always collected in samples that contained oyster, including VME and NVB samples where a small amount of oyster was present. These species are considered oyster reef residents (Coen et al. 1999) and may compete among each other for refuge and for food resources within oyster habitat (Perry et al. 2000; Shervette et. al 2004). In another study concerning habitat use by xanthid crabs in Mississippi Sound, Shervette et al. (2004) found that juvenile stone crabs, *E.depressus*, and *P. simpsoni*, occupying oyster habitat, overlapped in size distributions. In that study they concluded that competition among crabs was necessitated by the presence of toadfish *Opsanus beta*, a common predator of xanthid crabs.

I did not detect significant differences in size among habitats for *P. simpsoni* or *R. harrisii*. Larger *E. depressus* were found associated with oyster in marsh samples.

This difference in size may related to differential survival rates of larger crabs in a less protective habitat (Shervette 2000). However, further research is needed to verify size selective predation in mud crabs.

Conclusions

In order to better understand the species-specific use of habitats within marshes of GBNERR, I examined the abundance patterns and size distributions of seven common invertebrate species among the three habitats. Three main trends emerged concerning habitat use. First, I observed that the four crab species (juvenile blue crab, *E. depressus*, *P. simpsoni*, and *R. harrisii*) occupied oyster and VME habitats in higher abundances relative to NVB with minor to moderate fluctuations in seasonal abundance. Smaller crabs tended to use oyster habitat (although differences were not significant for all four species) and this may be related to the higher abundance of smaller refuges in oyster habitat. The second trend, occurring for one species (grass shrimp), was the occupation of VME in significantly higher abundance than the other habitats. This may be related to grass shrimp reliance on VME stems, and associated flora and fauna, for refuge and food. The last trend observed was the relatively equal use of VME and oyster by the estuarine-dependent species brown shrimp and white shrimp. Both species selected for structured habitat over NVB and both species were significantly larger in oyster habitat. Additionally, the seasonal trends I observed were mainly related to reproductive cycles and seasonal recruitment patterns. Blue crabs and grass shrimp were relatively abundance throughout the three seasons examined. At least two of the mud crabs experienced peaks in abundance tied to their reproductive cycles. White and brown

shrimp also demonstrated peak abundances that were related to the influx of postlarval and juvenile penaeids into the estuary.

CHAPTER V

APPLICABILITY OF THE NURSERY HABITAT HYPOTHESIS THROUGH LITERATURE EVALUATION AND FIELD EXPERIMENTATION USING A COMMON ESTUARINE-DEPENDENT FISH

Introduction

Understanding the importance of estuarine habitat is a central theme in estuarine ecology. Various estuarine habitats repeatedly have been considered nurseries for many fish and invertebrate species, although the nursery concept remained largely undefined until recently (Beck et al. 2001). Currently, the accepted definition of nursery habitat for an individual species is a juvenile habitat that provides a greater proportion of individuals that recruit successfully to adult populations relative to other juvenile habitats on a per unit area basis (Beck et al. 2001; Minello et al. 2001; Heck et al. 2003; Peterson et al. 2003; Sheridan and Hays 2003). Within the context of this definition, the amount of habitat-specific secondary production (i.e. juveniles surviving to adulthood) that reaches adult populations depends on a combination of four factors: 1) density, 2) growth, 3) survival of juveniles, and 4) movement to adult habitat (Beck et al. 2001).

Initially, habitats were referred to as nurseries whenever they contained high densities of juveniles. Many studies concerning estuarine ecology include extensive data on habitat-specific abundances for species of interest (see habitat-specific reviews: Minello et al. 2001; Heck et al. 2003; Peterson et al. 2003; Sheridan and Hays 2003). Within this body of research, several studies have examined density and biomass across

seasons and a few studies have encompassed multiple years of data reporting additional information concerning temporal variation in habitat use. Although densities do not solely determine a habitat's nursery value, such data can corroborate conclusions based on additional evidence from studies of growth, survival, and movement of target species.

Pinfish *Lagodon rhomboides* Linnaeus is a numerically dominant estuarine transient species (Muncy 1984). Juveniles are found across a variety of estuarine habitats including marsh edge, oyster reef, and nonvegetated bottom making pinfish an ideal species for exploring the nursery role concept. The geographical range of pinfish spans both the Atlantic and Gulf coasts from Massachusetts to Texas and into Mexico. During fall and winter, adult pinfish aggregate in offshore waters to spawn (Muncy 1984). In spring and summer, juveniles (15 –100 mm) are abundant in estuarine waters. They are often associated with vegetated habitats such as *Spartina* marsh and seagrasses (Muncy 1984) and also occur in oyster habitat (Coen et al. 1999) and over nonvegetated bottom (Stoner 1979). Juvenile pinfish are ecologically important residents of estuarine habitats (Young and Young 1978). They are voracious predators (Darcy 1985, Stoner 1980), and potentially compete with other estuarine nekton for food resources and space. Small juveniles (16 –35 mm standard length; SL) are mainly carnivorous. As juveniles grow their diets become more omnivorous; they consume an increasing amount of algae and other plant materials (Stoner 1980).

In this study, I sought to understand the relative values of marsh, oyster, and nonvegetated bottom habitats for growth of juvenile pinfish in Grand Bay, MS. My specific objectives were 1) to determine the relative growth of juvenile pinfish in marsh,

oyster, and nonvegetated bottom habitats and 2) to determine if growth of pinfish varied between years. In addition, I examined information from the scientific literature concerning habitat-specific juvenile density and predation on juveniles in order to discuss the overall potential of these habitats to function as nurseries for pinfish.

Materials and Methods

Study area

Grand Bay National Estuarine Research Reserve (NERR) is a productive and diverse estuary occupying 74.5 km^2. Habitats such as *Spartina alterniflora* marsh edge and inner marsh, oyster reefs and oyster midden deposits, and shallow nonvegetated bottom are all common throughout Grand Bay. In addition, small beds of *Ruppia* and *Halodule* are sometimes present in parts of the Reserve. Grand Bay tides are diurnal, like much of the north Gulf of Mexico, and the tidal range is small; mean tidal range is approximately 40 cm. Grand Bay is bordered by two heavily industrialized areas, Pascagoula estuary on the west, and Mobile Bay on the east. The site of my growth experiment is located at the mouth of Crooked Bayou, which has a direct connection with Mississippi Sound (Figure 5-1).

Experimental design

To quantify growth of juvenile pinfish within each habitat type, we used field enclosures that restricted fish to a single habitat type and excluded predators, but allowed access to the bottom substrate for foraging. Enclosures have been used successfully to measure fish growth rates in a variety of habitats with a variety of fish

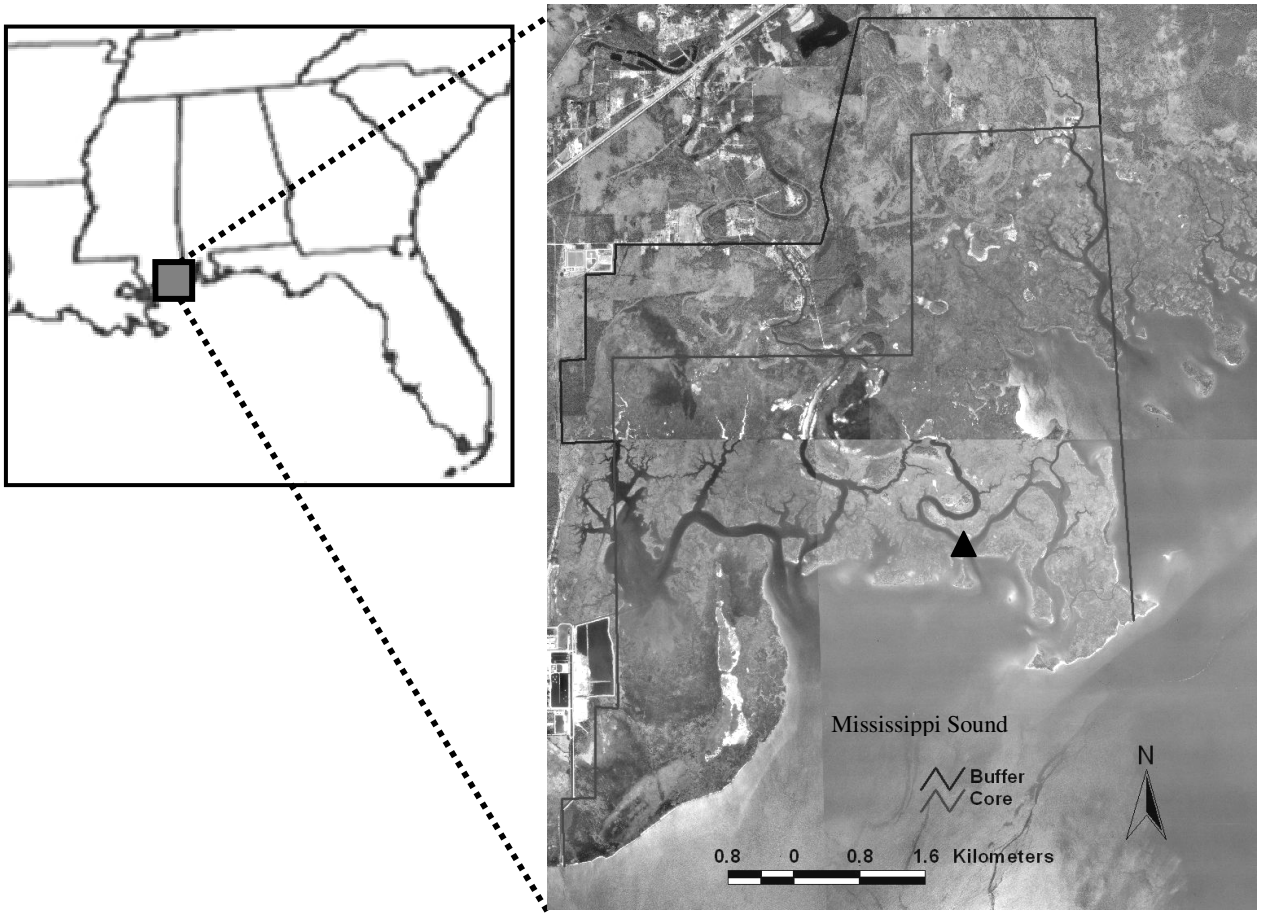

Figure 5-1. Map represents portion of Grand Bay National Estuarine Research Reserve, MS, where pinfish growth experiments were conducted. The black triangle is positioned close to the mouth of Crooked Bayou where Growth Samplers were placed for experiment.

species (de Lafontaine and Leggett 1987; Cowan and Houde 1990; Sogard 1992; Able et al. 1999; Haplin 2000; Phelan et al. 2000; Dahlgren and Eggleston 2002; Manderson et al. 2002). I used circular enclosures, 0.6 m radius and 1.0 m tall (0.283 m^2), constructed from polypropelene barrels with the bottom and top removed, and windows cut out and covered with 3-mm mesh nylon netting on top and sides (Figure 5-2). Windows allowed for water exchange and movement of prey organisms. Enclosures were pushed into the sediment at least 15 cm and a 20 cm lip extended from the ground to the bottom edge of the windows, allowing water to collect at low tide and maintain fish. Enclosures were anchored from the outside with metal stakes. When deployed, enclosures were swept repeatedly with dipnets in order to remove potential competitors and predators. Daily temperature, salinity, and dissolved oxygen were measured for each enclosure using a YSI-85 meter. I conducted this experiment once during July 2003 and once during July 2004.

Fish used in enclosures were seined from the area where I conducted the experiment (Figure 5-1). Captured juvenile pinfish were placed in aerated coolers filled with ambient water. Fish were randomly assigned to growth barrels. To follow the growth of individuals, I marked each with a distinctive anal fin clip. Pinfish were then held temporarily in a small, clear, plastic bag in order to limit their movement as I measured standard length (SL) to the 0.1 mm immediately before allowing the fish to swim out of the bag and into the growth barrel. Fish were monitored for 30 minutes for unusual behavior resulting from the stress of being handled, and individuals that appeared stressed were replaced. Each barrel contained 3 juvenile pinfish, and stocking

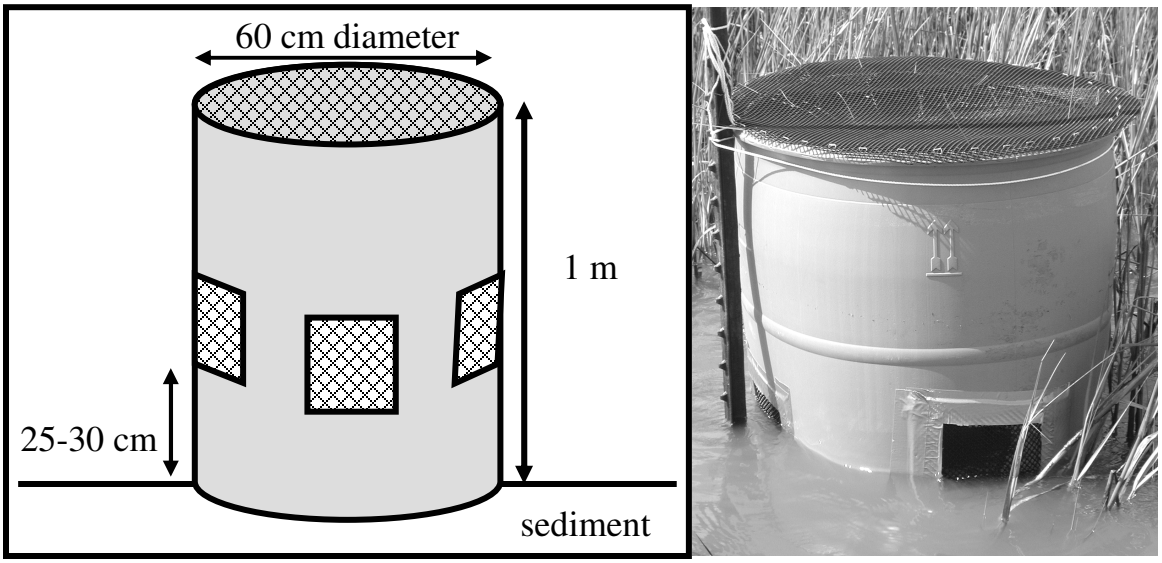

Figure 5-2. Schematic diagram of Growth Sampler and actual photo of sampler used in field experiment. A Growth Sampler consisted of a circular enclosure, 0.6 m radius and 1.0 m tall (0.283 m^2), constructed from polypropylene barrels with the bottom and top removed, and 4 windows cut out of sides. Nylon netting (3-mm mesh) covered top and sides of sampler.

density (10.6 fish/m^2) was within the range of values reported for total number of carnivorous fishes in estuarine habitats (Sogard et al. 1987). Each of the three habitat types (*Spartina* edge, oyster midden, and nonvegetated bottom) had four replicate growth enclosures.

Enclosures were monitored daily for 10 days and dead fish were removed when detected. At the end of each growth period, I netted fish from enclosures and anesthetized them with MS-222. Individuals were identified, measured, and then preserved in 10% buffered formalin, and later transferred to 70% ethanol for storage. I calculated daily growth rate of individuals as initial minus final SL and divided the difference by 10 days. I then calculated an average daily growth rate for each enclosure. I also calculated an overall percent recovery of pinfish for each habitat type and for each sampling period.

Statistical analyses

In order to determine if juvenile pinfish growth rate differed among habitats and between years, I tested the following null hypothesis: No difference in mean growth rate existed for pinfish among habitat types and between years. I used a two factor ANCOVA with year and habitat type as my independent factors, mean initial size as my covariate, and mean daily growth as my response variable. I used Bonferroni post hoc comparisons to test for differences in growth rate between habitats. Data met assumptions of tests and were left untransformed. I also tested for significant differences among habitats and between years for each of the three environmental measurements: salinity, temperature, and dissolved oxygen. I used individual two-factor

ANOVAs with the value of the environmental measurement as the response variable, and habitat and year as the two independent factors. Because I conducted multiple ANOVAs, I adjusted my acceptance level using a Bonferroni corrected alpha = 0.017. In order to address the possibility that survival (recovery) density of pinfish affected growth rates I used linear regression with habitat-specific percent recovery as the independent variable and growth rate as the dependent variable.

For experiments conducted within enclosures, as long as the effects of the enclosures are kept constant across all experimental treatments, then the effects of artifacts are also held constant (Peterson and Black 1994). Therefore, the results from the growth enclosure experiment apply to conclusions about the potential growth and comparative habitat value of the three habitat types. I did not assess absolute growth of pinfish within the different habitat types, but assessed relative growth in identical enclosures and duration within each habitat type, so artifacts of sampling design should not influence my assessment.

Results

Throughout the two 10-day growth periods, temperature ranged from 28.0 to 33.5^{o}C, salinity ranged from 10.7 to 18.2 ppt, and dissolved oxygen ranged from 4.80 to 6.82 mg/l (Table 5-1). I found no significant differences in temperature, salinity, or dissolved oxygen among the three habitat types (Table 5-2). Mean temperature was significantly higher in 2004 than 2003. Mean salinity was also higher in 2004 than 2003. No significant difference was detected for dissolved oxygen between years. I did

Table 5-1. Mean values for the three environmental variables and juvenile pinfish growth rate for each year and habitat type. Values in parentheses represent standard error of the mean.

Parameter	2003	2004	Marsh	NVB	Oyster
Salinity (ppt)	10.9 (0.03)	18.0 (0.02)	14.5 (1.36)	14.4 (1.36)	14.4 (1.36)
Temp (°C)	29.4 (0.26)	33.2 (0.05)	31.2 (0.78)	31.5 (0.62)	31.1(0.83)
DO (mg/L)	6.0 (0.08)	5.8 (0.13)	6.0 (0.11)	6.0 (0.12)	5.7 (0.18)
Growth rate (mm/day)	0.30 (0.067)	0.12 (0.036)	0.39 (0.071)	0.04 (0.014)	0.20 (0.051)

Table 5-2. Table of ANOVA results for salinity, temperature, and DO analyses and ANCOVA results for pinfish growth rate analysis.

Analysis	df	SS	F	p
ANOVA-Salinity				
Habitat	2	0.006	0.25	0.781
Year	1	309.602	26537.29	< 0.001
Habitat x year	2	0.001	0.04	0.965
ANOVA- Temperature				
Habitat	2	0.491	0.62	0.549
Year	1	85.504	215.78	<0.001
Habitat x year	2	1.473	1.86	0.185
ANOVA- DO				
Habitat	2	0.321	1.06	0.366
Year	1	0.373	2.47	0.133
Habitat x year	2	0.095	0.31	0.735
ANCOVA- growth rate				
Initial size	1	0.001	0.006	0.938
Habitat	2	0.438	22.761	< 0.001
Year	1	0.007	0.683	0.420
Habitat x year	2	0.015	0.770	0.478

not find significant interactions between habitat and year for any of the three environmental variables (Table 5-2).

Initial sizes of juvenile pinfish used in this study ranged from 40.7 to 79.5 mm SL. Pinfish recovery rates in July 2003 were 58% (marsh), 50% (nonvegetated bottom), and 67% (oyster), and in July 2004 were 50%, 75%, and 42% (respectively). Mean growth rates differed significantly among the three habitats, but not between years. I did not find a significant interaction for habitat and year. The covariate, initial size of pinfish, was also not significant (Table 5-2). Pinfish growth rate was significantly higher in marsh relative to oyster and nonvegetated bottom (Bonferroni post hoc: $p < 0.01$) and growth rate in oyster was significantly higher than nonvegetated bottom ($p < 0.05$). Mean growth in marsh was 0.37 mm/day +/- 0.073 SE in 2003 and 0.38 mm/day +/- 0.073 SE in 2004 (Figure 5-3). Mean growth in oyster habitat was 0.22 mm/day +/- 0.04 SE in 2003 and 0.12 mm/day +/- 0.033 SE in 2004 (Figure 5-3). Mean growth was 0.04 mm/day +/- 0.018 SE in 2003 and 0.02 mm/day +/- 0.006 SE in 2004 (Figure 5-3). Mean growth rates were 0.21 mm/day +/- 0.047 SE in 2003 and 0.18 mm/day +/- 0.052 SE in 2004. In addition, linear regression analysis of the dependent variable pinfish mean growth and the independent variable percent recovery did not detect a significant linear relationship between the two variables ($n = 6$, $R^2 < 0.01$, $p = 0.93$; Figure 5-4).

Discussion

This research was part of a larger project to assess the nursery value of several estuarine habitats for commonly occurring species such as pinfish that are frequently

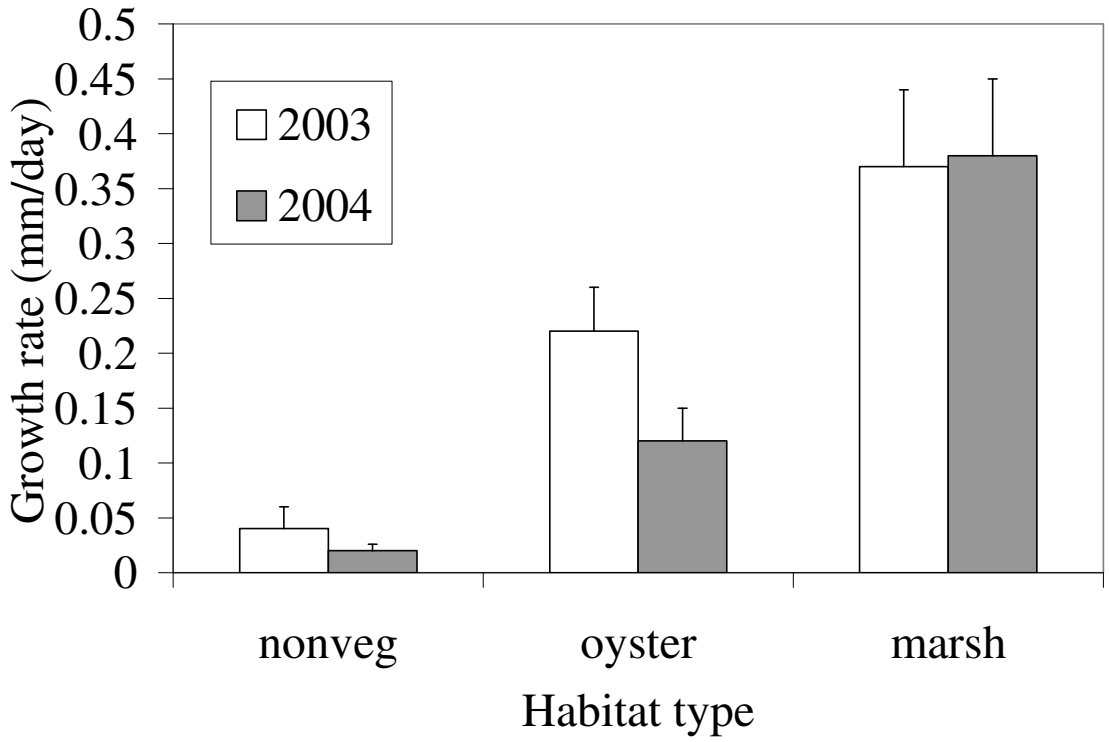

Figure 5-3. Mean growth rates of juvenile pinfish from Growth Samplers in nonvegetated bottom, marsh edge, and oyster habitats for July 2003 and July 2004. Error bars represent standard error. Growth order according to the results of Bonferroni post hoc comparisons was as follows: marsh > oyster > nonvegetated bottom.

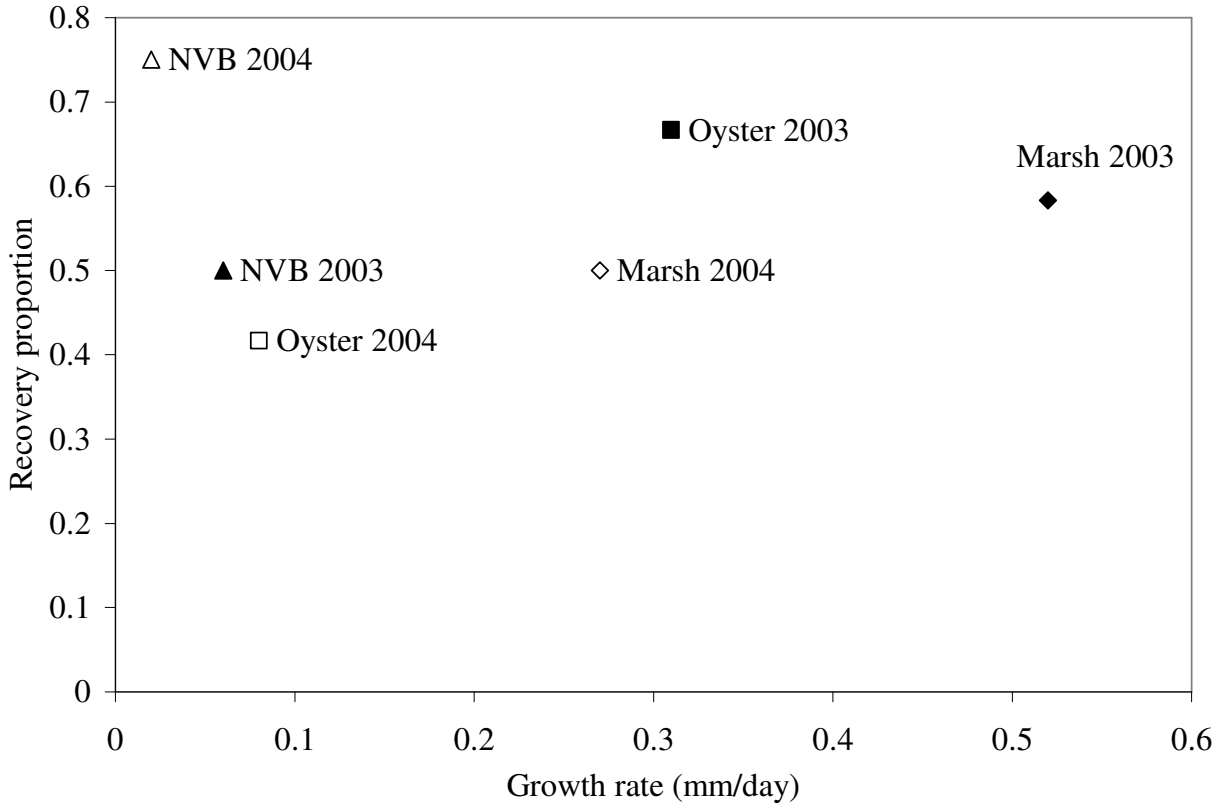

Figure 5-4. Relationship between mean growth rate (mm/day) of juvenile pinfish in each habitat for 2003 and 2004 and overall proportion of individuals recovered from habitats for both years. Habitats were nonvegetated bottom (NVB), marsh edge (marsh), and oyster midden (oyster).

found in multiple habitats. Some juvenile habitats contribute a greater proportion of individual juveniles recruiting to adult habitats (Beck et al. 2001). Through research comparing density, growth, survival, and movement to adult habitat, estuarine ecologists can obtain a better understanding of a habitat's nursery value relative to other habitats.

In this study, juvenile pinfish growth was significantly greater in marsh habitat than in adjacent oyster and nonvegetated bottom habitats. Additionally, pinfish growth in oyster habitat was significantly greater than in nonvegetated bottom and these findings were consistent through time. Rapid growth of juvenile fish may impart ecological advantages and enhance survivorship (Sogard 1997). A myriad of fish species utilize estuarine habitats as juveniles in order to exploit abundant food resources crucial for maintaining rapid growth (Boesch and Turner 1984; Heck and Thoman 1984; Kneib 1993). Fish with higher growth rates potentially move more quickly out of smaller size classes that are vulnerable to predation and into larger prey size refugia (Chase 1999). Other advantages of rapid growth during the juvenile period of development that influence successful recruitment to adult populations include enhanced swimming speed (Webb and Corolla 1981), increased ability to detect and escape predation (Fuiman 1994), and increased survival during winter months (Henderson et al. 1988; Post and Evans 1989). My results indicate that marsh habitat is important for juvenile pinfish because it may provide higher quality habitat for this species. Pinfish that utilize marsh habitat experience enhanced growth and thus potentially benefit from the associated advantages mentioned above.

In general, juvenile pinfish appear to select for vegetated and vegetated-like habitats (Stoner 1980; Jordan et al. 1996; Irlandi and Crawford 1997). Using meta-analysis, Minello et al. (2003) examined the nursery role of salt marshes and found that pinfish densities were significantly higher in vegetated marsh than nonvegetated marsh edge. In addition, they found densities of pinfish were similar in vegetated marsh and seagrass habitats. Similar conclusions were reported for studies across the northern Gulf of Mexico. In East Lagoon, Galveston Island, Texas (Levin et al. 1997) small juvenile pinfish (13–25 mm SL) were present in higher numbers in artificial seagrass plots as compared with nonvegetated sand plots, although large numbers also were documented for sand habitat. In West Bay and Galveston Bay (Minello and Webb 1997), higher densities of juvenile pinfish occurred in vegetated marsh edge than nonvegetated habitats. Nekton communities in marsh, seagrass, and nonvegetated habitats in Aransas National Wildlife Refuge, TX sampled in May 1994 contained higher densities of pinfish in vegetated habitats (marsh and seagrass combined) than adjacent nonvegetated bottom habitat (Rozas and Minello 1998). In a Florida estuary, abundances of pinfish were higher in seagrass beds than nearby sand flats (Jordan et al. 1996). These studies suggest that pinfish may actively select vegetated habitats because of food resource utilization (Irlandi and Crawford 1997; Levin et al. 1997) and refuge from predation (Jordan et al. 1996).

High growth rates of estuarine inhabitants appear to be related to increased food resources (Summerson and Peterson 1984; Sogard 1992; Levin et al. 1997), which are often habitat-specific (Zimmerman et al. 1989). In particular, exploitation of marsh

habitat appeared to increase growth rates in red drum *Sciaenops ocellatus* (Baltz et al. 1998; Stunz et al. 2002a) and decapod crustaceans (Zimmerman et al. 2000). Juvenile pinfish may also benefit from habitat-specific food resources. Pinfish in the size range used in my study (40–80 mm SL) are omnivores. In Apalachee Bay, FL (Stoner 1980), diet of pinfish 36-80 mm TL contained 30% plant material (mostly microepiphytes) and 70% macrobenthic fauna, including amphipods, small shrimp, harpacticoid copepods, polychaetes, calanoid copepods, bivalves, and invertebrate eggs. Potthoff and Allen (2003) examined diet of juvenile pinfish (64–-95mm SL) collected from flooded intertidal creeks that drain *Spartina* marsh during high tide and adjacent subtidal habitat during low tide. They found that the mean total volume of stomach contents was significantly higher in fishes from the intertidal habitat relative to subtidal habitat. Shrimp and fish comprised the majority of the intertidal fish diet (91% by volume) although plant material was also present (5% of diet by volume). In contrast, plant material comprised 53% of stomach contents of pinfish collected from the subtidal habitat.

Information concerning habitat-related abundances of epifauna and infauna (macrofauna) allows us to speculate on the availability of potential habitat-specific food items within the context of my results. However, because macrofaunal communities also are affected by elevation and hydroperiod (see review in Rozas 1995), I have limited my sources concerning macrofaunal communities to studies from Galveston Bay, TX, which is characterized by low to medium elevation gradients and regular tides with relatively low tidal amplitude (~30 cm; Hicks et al. 1983), and similar to conditions in

my study sites in Grand Bay, MS. Some studies did not find significantly different densities of infauna (including annelids, small crustaceans, and mollusks) between vegetated and nonvegetated habitats (Zimmerman et al. 1990a; Minello and Webb 1997; Table 5-3), whereas others found significant differences in densities for specific faunal groups (Zimmerman et al. 1989; Whaley 1997; Rozas and Zimmerman 2000; Table 5-3). In general comparisons between vegetated marsh habitats (edge and inner marsh consisting of mixed vegetation) and nonvegetated habitats (including pond, channel, cove, and shallow bay habitats), densities of polychaetes were consistently higher in nonvegetated habitat (Rozas and Zimmerman 2000; Table 5-3). When only vegetated marsh edge and nonvegetated marsh edge habitats were compared, polychaete densities were similar (Whaley 1997; Table 5-3). Oligochaete densities tended to be significantly higher from combined vegetated habitats than nonvegetated habitats (Whaley 1997; Rozas and Zimmerman 2000; Table 5-3). Annelid densities in a study comparing infaunal and epifaunal abundances across marsh, oyster, and nonvegetated bottom habitat (Zimmerman et al. 1989) were higher in oyster habitat as compared with nonvegetated bottom, but not when compared with marsh, and peracarid crustacean (amphipod, tanaid, and mysid) abundance was higher in oyster than either marsh or nonvegetated bottom (Table 5-3). Whaley (1997) found significantly higher densities of small crustaceans in vegetated marsh edge than in nonvegetated marsh edge in July 1995 samples (Table 5-3). In general, potential prey items such as amphipods and other small crustaceans and invertebrates) for juvenile pinfish appear to occur in greater densities in structured habitats than adjacent nonvegetated habitats.

Table 5-3. Table summarizes habitat-specific abundances of various infauna and epifauna groups that are potential prey items for pinfish juveniles. Study column identifies citation of research and dates of sampling. Potential prey column identifies study-specific organism groups. Vegetated habitats include marsh and marsh edge. Nonvegetated (NV) habitats include those listed. Significant difference (SD) and no significant difference (NSD) are indicated for groupings as denoted by individual studies.

Study	Potential prey group	Habitats and Significance of comparisons
Rozas and Zimmerman 2000		Marsh (mixed species edge and inner) v. NV (pond, channel, cove, shallow bay)
May 1993	Polychaetes	SD: NV > marsh
	Oligochaetes; Mollusks	NSD: NV = marsh
October 1993	Polychaetes	SD: NV > marsh
April 1994	Polychaetes; Mollusks; Crustaceans (amphipods, isopods)	SD: NV > marsh
	Oligochaetes	SD: marsh > NV
September 1994	Polychaetes; Crustaceans (amphipods, isopods)	SD: NV > marsh
	Oligochaetes	SD: marsh > NV
Minello and Webb 1997		Natural vegetated edge (marsh) v. natural NV edge
Fall 1990 and Spring 1991	Infauna (annelids and small crustaceans)	NSD: marsh = NV edge
Whaley 1997		Vegetated edge (marsh) v. NV edge
February 1995	Polychaetes; Oligochaetes; Crustacean density; Annelid biomass; Crustacean biomass	NSD: marsh = NV edge
April 1995	Polychaetes; Crustacean density; Annelid biomass; Crustacean biomass	NSD: marsh = NV edge
	Oligochaetes	SD: marsh > NV edge
May 1995	Polychaetes; Annelid biomass; Crustacean biomass	NSD: marsh = NV edge
	Oligochaetes; Crustacean density	SD: marsh > NV edge
July 1995	Polychaetes; Annelid biomass; Crustacean biomass	NSD: marsh = NV edge
	Oligochaetes; Crustacean density	SD: marsh > NV edge
August 1995	Polychaetes; Crustacean biomass	NSD: marsh = NV edge
	Oligochaetes; Crustacean density	SD: marsh > NV edge
	Annelid biomass	SD: NV edge > marsh
October and November 1995	Polychaetes; Oligochaetes; Crustacean density; Annelid biomass; Crustacean biomass	NSD: marsh = NV edge
Zimmerman et al. 1990		Vegetated edge (marsh) v. NV edge
Spring, summer, fall 1987 combined	All infauna combined (annelids, amphipods, mollusks)	NSD: marsh = NV edge
Zimmerman et al. 1989		Vegetated edge (marsh) v. NV edge v. oyster reef
Winter and summer 1988 combined	Annelids	SD: oyster > NV edge, oyster = marsh, marsh = NV edge
	Peracarid crustaceans (amphipods, small crustaceans, mysids)	SD: oyster > marsh > NV edge
	Mollusks	SD: oyster > marsh = NV edge

Because of their omnivorous diet, habitat-specific growth of pinfish could also be influenced by a habitat's potential for algal colonization. In addition to supporting higher densities of invertebrate prey, marsh and oyster habitats, as compared to nonvegetated bottom habitat, contain greater overall surface area for colonization by algae. In the marsh habitat where I conducted my growth experiment, mean *Spartina* stem density was 10 stems per barrel or approximately 36 stems/m^2. Each oyster replicate barrel contained approximately 12 L of a combination of ambient live oyster and oyster shell. The combination of greater potential prey densities (both infaunal and epifaunal) and greater overall surface area available for algal colonization, probably provides more food resources for juvenile pinfish in marsh and oyster habitat than over unvegetated bottom.

In addition to providing higher growth rates for juvenile pinfish, structured habitats, such as marsh edge and oyster reef, might provide juvenile pinfish with refuge from predation, both by decreasing predation and by promoting faster growth. In a laboratory mesocosm study that evaluated habitat-specific predation, survival of juvenile red drum was significantly higher across structured habitats relative to nonvegetated habitat (Stunz and Minello 2001). Predation rates on tethered brown shrimp were significantly lower in seagrass and marsh habitat than nonvegetated bottom (Minello 1993). This also may be true for predation on juvenile pinfish in structured versus unstructured habitats. Jordan et al. (1996) examined juvenile pinfish habitat selection between structured and unstructured habitats. They found that pinfish exhibited predator-mediated habitat selection. When a predator was present juvenile pinfish

selected for structured habitat (seagrass-like plastic strips) instead of unstructured habitat (sand bottom). In addition, Levin et al. (1997) documented that juvenile pinfish in plots open to predators were significantly larger than juvenile pinfish in predator exclusion plots indicating that predation on juvenile pinfish is likely size-dependent. Higher growth rates in structured habitats may enable juvenile pinfish to move out of size classes that are more susceptible to predation.

Growth results from enclosure experiments can provide important information concerning relative habitat value, but should be evaluated carefully. Results can vary among estuaries and across years (Phelan et al. 2000). Additionally, enclosures prevent movement of fish to other areas in which environmental conditions and food availability may be better. In order to insure that my juvenile pinfish did not deplete potential prey resources, I stocked each growth sampler with only 3 pinfish (10.6/m^2). I also fitted samplers with four windows covered with 3-mm mesh to allow for the recruitment of additional prey fauna. During my study, water quality measurements did not indicate the occurrence of low oxygen or extreme variation in salinity or temperature. My aim was to understand and compare the potential value of the predominate habitats for juvenile pinfish in Grand Bay, NERR. Growth rates calculated in my enclosures were similar to growth rates reported for juvenile pinfish in other studies (Levin et al. 1997; Spitzer et al. 2001). In addition, I repeated my study in two years and my growth results were consistent through time. Thus, I accounted for the potential variation that often goes unmeasured in growth enclosure experiments. My results provide a useful measure of

the relative differences in growth of juvenile pinfish that can be expected across marsh, oyster, and adjacent nonvegetated bottom in Grand Bay, MS.

In conclusion, my results suggest that marsh habitat provides an important nursery function for juvenile pinfish in Grand Bay NERR. By definition, nursery habitat recruits more individuals per unit area to the adult population relative to other juvenile habitats (Beck et al. 2001). A combination of density, growth, and survival of juveniles within a nursery habitat must be greater than in other juvenile habitats (Beck et al. 2001). Many studies have documented that juvenile pinfish densities, abundances, and recruitment are greater in vegetated habitats (Jordan et al. 1996; Levin et al. 1997; Minello and Webb 1997; Rozas and Minello 1998). My study demonstrated that growth of juvenile pinfish is significantly higher in marsh habitat compared to oyster and nonvegetated bottom. Higher habitat-specific growth of juvenile pinfish may be related to higher abundances of food resources in marsh habitat that have been documented in other studies. Lastly, indirect evidence and observations from several studies suggest that predation-related mortality of juvenile pinfish may be lower in structured habitat such as marsh and oyster relative to nonvegetated bottom, although this hypothesis has not been tested experimentally for pinfish. Therefore, marsh provides an important habitat for juvenile pinfish and may provide a nursery function.

CHAPTER VI

ASSESSMENT OF ESSENTIAL FISH HABITAT AS NURSERIES FOR JUVENILE WHITE SHRIMP *LITOPENAEUS SETIFERUS*

Introduction

As a result of the use of estuaries by juveniles of economically important species, many estuarine habitats have been coined nursery habitats (Boesch and Turner 1984; Minello et al. 1994). However, few studies have adequately defined species use of many of these habitats and conclusive evidence identifying essential habitats used for the recruitment of individuals to the adult population is still lacking (Rozas and Minello 1998; Minello 1999; Beck et al. 2001). A fundamental premise of the nursery-role concept is that some estuarine juvenile habitats contribute disproportionately to the production of individuals recruiting to adult populations (Edgar and Shaw 1995). Beck et al. (2001) expounded on this assertion by developing a nursery-role hypothesis from which clear and testable predictions can be made. They define a nursery habitat as one that recruits more individuals per unit area to the adult population than other habitats containing juveniles of the same species. According to this hypothesis, a combination of density, growth, survival of juveniles within a delineated nursery habitat, and the successful movement of juveniles from this nursery habitat to an adult habitat must be greater when compared to other juvenile habitats. Different habitats offer varying degrees of complexity to shelter juveniles from predation (Minello et al. 1989).

Likewise, variations in quantity and quality of food resources across habitats affect the rate of development, which has consequences on survival.

Much documentation exists concerning the importance of salt marsh habitat to fishes and invertebrates (see review Minello et al. 2003). Many natant macrofauna are dependent on vegetated habitat within marshes and several studies have reported higher growth rates of estuarine species in *Spartina* marsh edge habitat when compared to adjacent habitats (Minello et al. 1989; Stunz et al. 2002b). Other studies have demonstrated high survival rates in salt marsh habitats (Minello and Zimmerman 1983, 1985; Minello et al. 1989). Not as much literature substantiates the importance of oyster habitat (see review: Peterson et al. 2003) relative to adjacent habitats. Glancy et al. (2003) documented that oyster reefs support distinct assemblages of decapod crustaceans and represent an important ecological component of estuarine habitats. They go on to speculate that the mechanisms underlying the importance of oyster habitat may include increased survival or greater forage availability for decapods. Nonvegetated bottom habitat, usually adjacent to marsh edge, also supports many estuarine species, although overall nekton densities appear to be higher in vegetated marsh edge than nonvegetated areas (Minello et al. 2003). Fish species such as spot *Leiostomus xanthurus* and croaker *Micropogonias undulatus* appear to select for open water habitat (including nonvegetated bottom areas) over vegetated marsh (Minello et al. 2003).

White shrimp *Litopenaeus setiferus* are economically important for their commercial and recreational value as food and bait. They spawn in coastal waters; then, tides and currents transport larvae and early postlarvae to inshore waters (Perez-Farfante

1969). Tides facilitate their movement into estuarine habitats where food is abundant and predation levels are potentially lower for juveniles. Periods of peak abundance of juvenile white shrimp in estuaries in the Gulf of Mexico occur May to July and again in September to October (St. Amant and Lindner 1966). Peak recruitment of white shrimp juveniles into Texas estuaries occurs in June and September (Klima et al. 1982). Juvenile white shrimp remain in estuaries until they reach approximate sizes of 120-160 mm total length (TL) at which point they begin migrating offshore. Within estuaries, as juveniles grow, they migrate from shallow to deeper areas (Anderson 1966).

Juvenile white shrimp are found across simple and complex habitats including marsh edge, oyster reefs, and soft bottom making them model organisms for the study of the nursery role hypothesis through density, growth, and survival in Grand Bay and Weeks Bay National Estuarine Research Reserves. The goal of my study was to evaluate the role of marsh, oyster, and nonvegetated bottom in providing nursery habitat for this species. I specifically examined: 1) White shrimp density across the three habitats; 2) Juvenile white shrimp growth in the three habitats; and 3) Juvenile white shrimp survival under predation by blue crabs in the three habitats.

Materials and Methods

Study areas

Our two study areas are located in the north central Gulf of Mexico (Figure 6-1). Grand Bay NERR is a productive and diverse estuary occupying 74.5 km^2. Habitats such as *Spartina alterniflora* marsh edge and inner marsh, oyster reefs and oyster

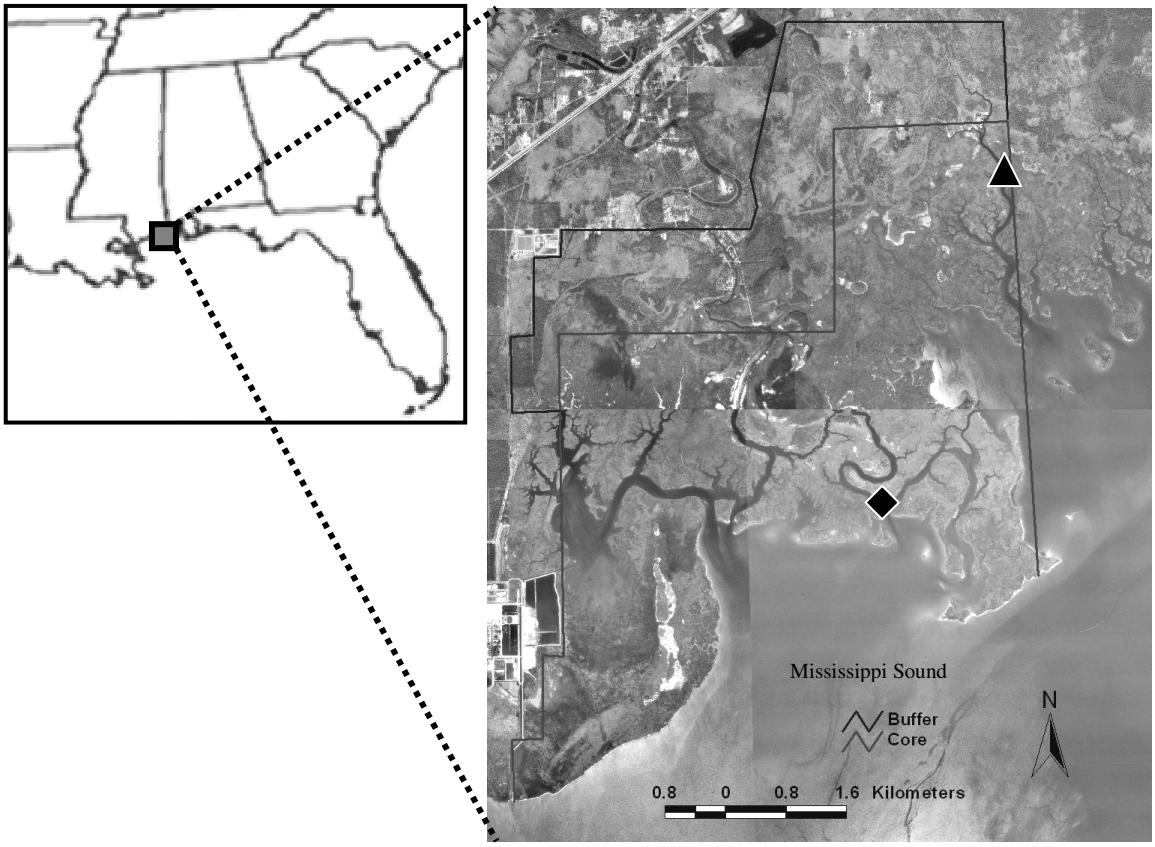

Figure 6-1. Map of Grand Bay National Estuarine Research Reserve, MS, where density and growth experiments were conducted. Triangle represents Bayou Heron site and diamond represents Crooked Bayou site. Note the proximity of the Crooked Bayou site to the Mississippi Sound.

midden deposits, and shallow nonvegetated bottom (soft-bottom) are all common throughout Grand Bay. The Reserve is bordered on the west by the heavily industrialized Pascagoula estuary and on the east by another heavily industrialized estuary, Mobile Bay. Weeks Bay NERR is a small, sub-bay of Mobile Bay occupying 8 km^2. Estuarine habitats present in Weeks Bay include *Spartina/Juncus* fringe marsh and shallow non-vegetated bottom. Weeks Bay supports relatively high densities of juveniles from many economically valued species such as brown shrimp (*Farfantapenaeus aztecus*), white shrimp, speckled seatrout (*Cynoscion nebulosus*), and blue crabs (McClintock et al. 1993; Shervette, personal observation).

Density experiment

In October 2003, at high tide when habitats were completely inundated, I collected four replicates in each of the three habitats present (marsh, oyster, and nonvegetated bottom) at two sites in Grand Bay NERR (Bayou Heron and Crooked Bayou; Figure 6-1) by sampling with a 1.17 m^2 drop sampler according to the procedures of Zimmerman et al. (1984). A total of 24 drop samples (2 sites x 3 habitats x 4 replicates) were collected by dropping a 1.4 m diameter x 1.5 m tall cylinder from a boom mounted on the bow of a skiff. Two people positioned the cylinder over a sample area by slowly pushing the skiff by the stern. Once the cylinder was in place it was released from the boom and it rapidly enclosed a 1.17 m^2 area. I chose the drop sampler for assessing shrimp densities over multiple habitats because the catch efficiency does not appear to vary significantly with habitat characteristics (Rozas and Minello 1997). In each drop sample I measured temperature, salinity, and dissolved oxygen using a YSI 85 meter and

water depth with a fixed gage. While pumping out water from the sampler through a plankton net, I collected all of the white shrimp and other nekton present with dipnets. Shrimp were preserved in 10% buffered Formalin for at least 4 d and then transferred to 70% ethanol for storage. I measured shrimp total length (TL: tip of rostrum to the end of the telson) to the nearest 0.1 mm. To determine white shrimp density within each replicate, I counted the number of individuals and divided by the area of bottom sampled. For oyster habitat, I estimated the percent cover of bottom by oyster for each replicate. For the marsh habitat, I removed and counted the number of *Spartina alterniflora* stems within each replicate and documented percent cover of live oysters if any were present.

To test the hypothesis that no difference in white shrimp density existed across habitats I used a block ANOVA with density as my dependent variable, site as my blocking factor, and habitat as my independent factor. Data were log transformed to meet assumptions of normality and homogeneity of variance. To test the hypothesis that no difference in shrimp size existed across the three habitats I used another block ANOVA with TL as my dependent variable, site as my blocking factor, and habitat as my independent factor. In this test the TL data met the assumptions of ANOVA and did not need transformation.

Growth experiment

In September 2003, I quantified growth of juvenile white shrimp within each habitat present at the Bayou Heron site in Grand Bay NERR using field enclosures (Growth Samplers; Figure 6-2) consisting of 0.28 m^2 by 1.0 m tall plastic barrel with

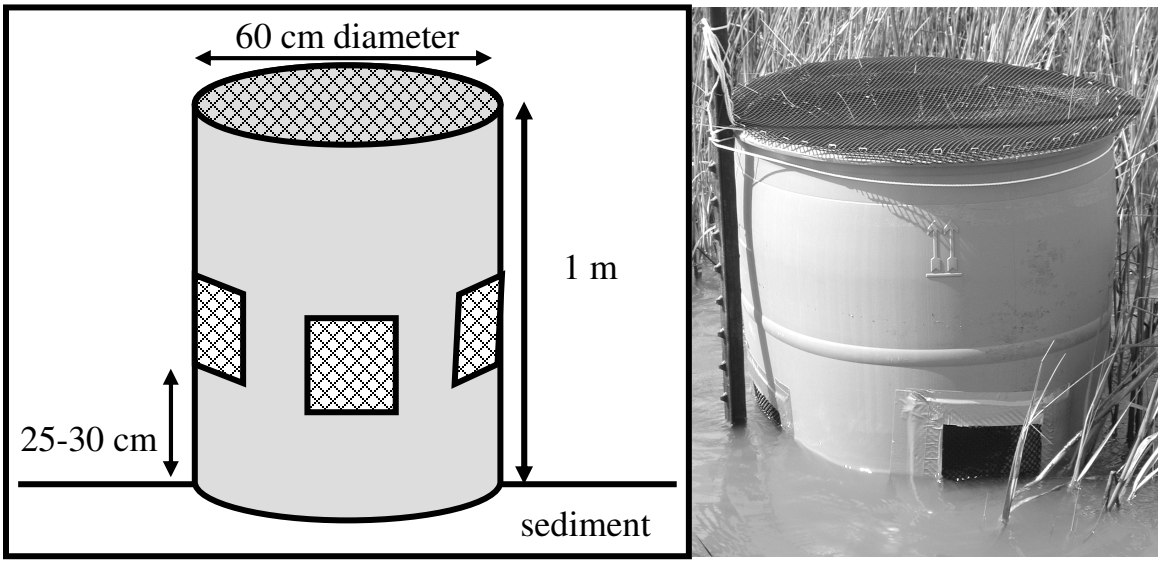

Figure 6-2. Schematic drawing and photograph of Growth Samplers used in the growth experiment.

four windows cut out and covered with 3 mm vexar plastic mesh which allowed for water exchange and prey organism recruitment into barrels. The barrels were pushed into sediment at least 15 cm and a 20 cm lip extending from the ground to the bottom edge of the windows allowed water to collect during lowtide to maintain shrimp. Each of the three habitats present (marsh, oyster, and nonvegetated bottom) had four replicate Growth Samplers. Each Sampler was stocked with four white shrimp measuring 40 mm total length (TL) collected from Bayou Heron by seine. Within each Sampler I measured daily salinity, temperature, and dissolved oxygen over the 16 day growth period. At the end of the experiment all shrimp were collected from Growth Samplers and final TL was measured and recorded for each shrimp. In order to calculate daily growth of shrimp I subtracted initial TL from final TL and divided by 16 days. I used a one factor ANOVA to test the null hypothesis that no difference in daily growth existed across the three habitats. I used mean growth from individual barrels as my dependent factor and habitat as my independent factor. Growth data did not violate assumptions of ANOVA and were left untransformed.

For experiments conducted within enclosures, as long as the effects of the enclosures are kept constant across all experimental treatments then the effects of artifacts are also held constant (Peterson and Black 1994). The results from my "Growth Sampler" experiment addressed the potential growth and comparative habitat value of the habitats. Because I were not trying to assess absolute growth of juvenile white shrimp within the different habitats, and only assess relative growth and the enclosures I

used within each habitat were the same size, composition, and duration, artifacts of sampling design should not be a problem.

Predation experiment

We conducted the predation portion of my study at Weeks Bay NERR, AL. In October 2004 and August 2005, I examined habitat-related predation on juvenile white shrimp using experimental mesocosms consisting of 1.2 m^2 circular plastic pools surrounded by plastic mesh 1.2 m in height which prevented shrimp from jumping out of pools. Pools were set outside in shaded areas next to Weeks Bay. In order to minimize potential effects of alternative food sources on predation rates, I simulated only the structural component of the three habitats: marsh, oyster, and nonvegetated bottom, in the mesocosms. Nonvegetated bottom habitat consisted of a depth of 5 cm of washed beach sand evenly spread on the bottom. I used sun-dried *Spartina alterniflora* stems planted in 5 cm of sand for the marsh habitat. The mean density of stems for the four replicates was 50 stems m^{-2} (+/- 14.5 SE), similar to stem densities measured from drop sampling. I simulated oyster habitat by scattering 75 L of oyster shells (which were sun-dried and washed) over 5 cm of sand. Oysters were scattered so that a portion of them created a pile extending as high as 30 cm. For all three treatments water depth was approximately 35 cm. At the beginning and end of each experimental run I measured salinity, dissolved oxygen, and temperature in each pool.

Ten juvenile white shrimp (size range 40 –75 mm TL), collected from Weeks Bay, were randomly assigned to each pool (8.3 shrimp m^{-2}). Two blue crabs, collected from Weeks Bay, were used in each pool as predators (1.7 blue crabs m^{-2} is similar to

blue crab densities observed in drop sampler data over oyster habitat from Grand Bay NERR). Only male blue crabs were used in order to prevent potential problems with mate guarding behavior. Blue crabs of similar sizes were paired in order to reduce cannibalism and pairs were randomly assigned to pools. Blue crabs, individually contained in plastic containers with multiple holes, were introduced into the pools stocked with shrimp. After a 2 hour acclimation period, blue crabs were released from containers and allowed to interact with shrimp. I allowed predators and prey to interact for 6 hours at the end of which I removed predators and counted the total number of white shrimp remaining. To test the hypothesis that no difference in predation-related mortality existed among the three treatments and between the two years, I used a two factor ANOVA with the proportion of shrimp surviving as the response variable, habitat and year as the two factors. Data did not violate assumptions of the test and were left untransformed.

A control run of the predation experiment was conducted in September 2004 to determine recovery rates and natural mortality of shrimp in the absence of predators. The protocol was identical to the predation experiment except that I did not introduce crabs into mesocosms. Ten shrimp were introduced into each of the four replicates of the three treatments and allowed to move about pools for eight hours total. Then shrimp were collected, water was drained from pools, and pools were carefully inspected for remaining shrimp. I used a one factor ANOVA to test for significant differences in survival/recovery of white shrimp from the control run with proportion of shrimp collected as the response variable and habitat as the main factor.

Results

Density and habitat-specific size

Bayou Heron had significantly lower salinity than Crooked Bayou (randomized block ANOVA: $F = 1035$, $p < 0.001$; Table 6-1). Dissolved oxygen, temperature, and depth did not differ significantly between the two sites. Depth varied significantly among habitats (randomized block ANOVA: $F = 4.8$, $p = 0.02$; Table 6-1). Mean depth in soft-bottom samples was significantly greater than mean depth in marsh samples (Bonferroni post hoc: $p = 0.03$). Salinity, DO, and temperature did not differ significantly among the three habitats.

A significant difference in juvenile white shrimp density occurred among the three habitats (randomized bock ANOVA: $F= 14.03$, $p < 0.001$; Figure 6-3). No significant difference occurred between the two sites (randomized block ANOVA: $F = 2.40$, $p = 0.13$; Figure 6-3). Mean shrimp densities over marsh, nonvegetated bottom, and oyster were 5.9 shrimp m^{-2} (2.8 SE), 1.4 shrimp m^{-2} (0.9 SE), and 32.1 shrimp m^{-2} (10.2 SE), respectively. Post hoc tests indicated that mean shrimp density over oyster was significantly higher than either marsh (Dunnett T3: $p = 0.02$) or nonvegetated bottom ($p = 0.002$). Marsh and nonvegetated bottom densities did not differ significantly ($p = 0.53$).

White shrimp size ranges from marsh, nonvegetated bottom, and oyster habitat were 19.9 –71.3 mm TL, 46.5 –67.6 mm TL, and 11.3 –67.5 mm TL, respectively. White shrimp size ranges from Bayou Heron and Crooked Bayou were 11.3 –71.3 mm TL and 19.9 –67.5 mm TL, respectively. A significant difference in mean shrimp TL

Table 6-1. Mean (Standard Error) values for environmental variables measured during density study for each habitat type (sites pooled) and for each site (habitats pooled).

	Sampling areas		Habitats		
Parameter	Bayou Herron	Crooked Bayou	Marsh	Nonveg	Oyster
Salinity (ppt)	19.4 (0.01)	22.8 (0.01)	21.3 (0.69)	21.1 (0.67)	21.0 (0.61)
DO (mg l^{-1})	6.7 (0.09)	6.6 (0.19)	6.9 (0.17)	6.6 (0.02)	6.4 (0.09)
Temp (^{o}C)	25.8 (0.35)	26.2 (0.37)	26.7 (0.45)	25.5 (0.43)	25.9 (0.32)
Depth (cm)	49 (6.1)	50 (3.7)	42 (3.5)	62 (7.4)	45 (4.4)

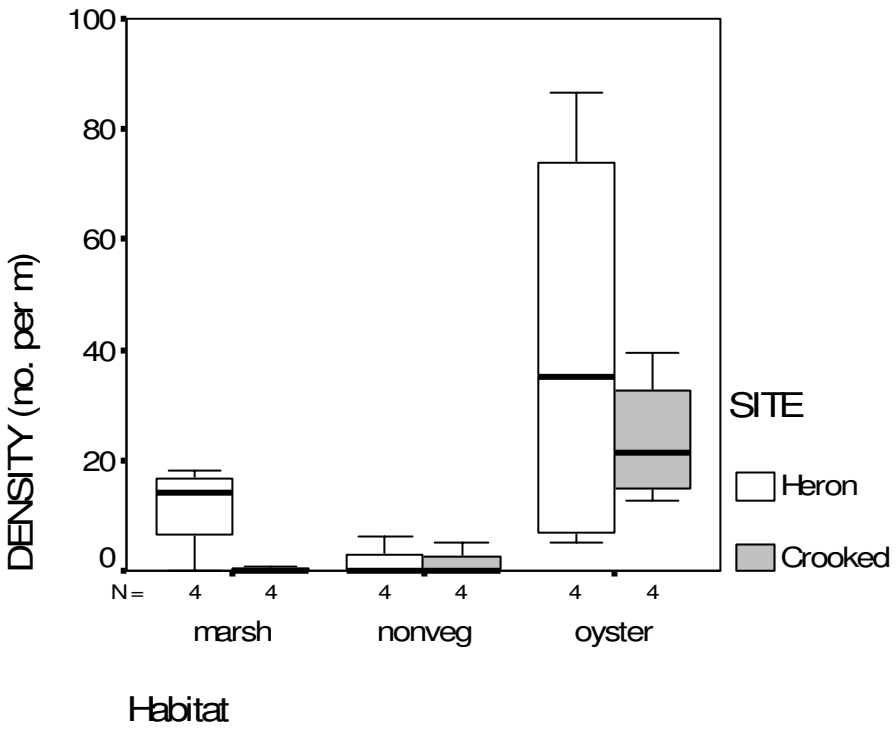

Figure 6-3. Boxplot of white shrimp density for each habitat at the two sites. Rectangles represent the middle half of the sample with an end at each quartile. The horizontal line inside the rectangle represents the median. Vertical lines with horizontal line attached at extremes represent the range of data excluding outliers.

occurred across the three habitats (randomized block ANOVA: $F = 11.8$, $p < 0.001$; Figure 6-4) and for the blocking factor of site ($F = 19.5$, $p < 0.001$). Shrimp mean TL was 43.2 mm +/- 9.34 SD for marsh, 57.9 mm +/- 5.82 SD for nonvegetated bottom, and 47.8 +/- 8.45 SD for oyster. Shrimp collected in Bayou Heron and Crooked Bayou had TL means of 45.5 mm +/- 9.00 SD and 50.7 mm +/- 7.74 SD, respectively. Post hoc tests indicated that shrimp collected from nonvegetated bottom were significantly larger than shrimp collected from oyster and marsh (Bonferroni: $p < 0.001$ for both comparisons). Shrimp collected from oyster were significantly larger than shrimp collected from marsh ($p < 0.001$).

Growth

Throughout the 16 day growth period temperature ranged from 25.0 to 27.2^{o}C, salinity ranged from 8.1 to 10.7 ppt, and dissolved oxygen ranged from 6.14 to 7.73 mg/L. Measured water quality parameters did not vary significantly across the three habitats. Shrimp recovery rates for marsh, nonvegetated bottom, and oyster were 44, 88, and 56%, respectively. Mean growth rates for shrimp differed significantly across the 3 habitats (ANOVA: $F = 13.3$, $p = 0.002$; Figure 6-5). Mean growth over oyster was 0.7 mm/day +/- 0.11 SE which was significantly higher than mean growth over marsh (0.2 mm/day +/- 0.04 SE; Bonferroni post hoc $p = 0.003$) and nonvegetated bottom (0.3 mm/day +/- 0.03 SE; Bonferroni post hoc $p = 0.009$). No significant difference in growth occurred between marsh and nonvegetated bottom habitats (Bonferroni post hoc: $p = 1.00$).

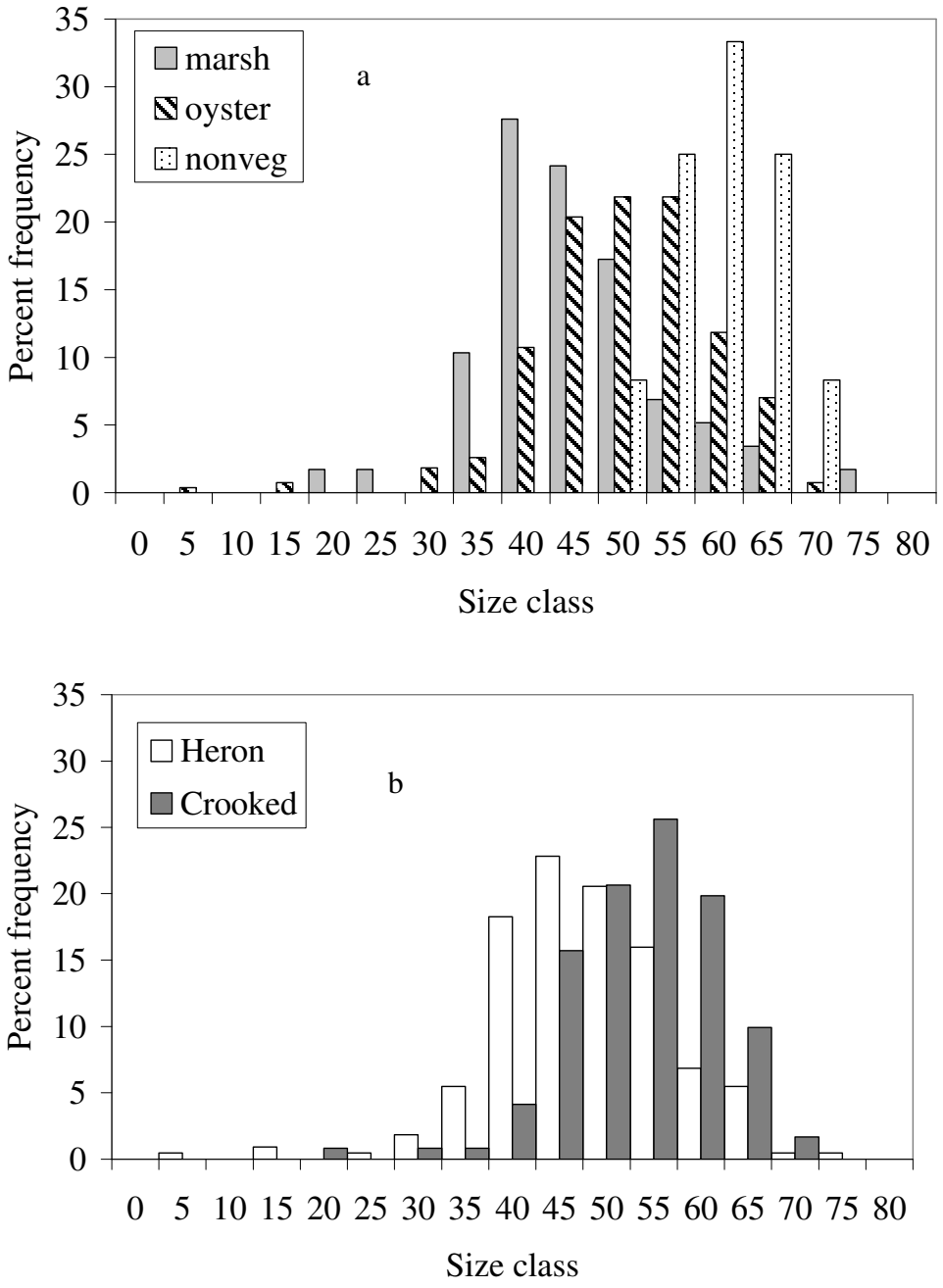

Figure 6-4. Percent frequency distribution of white shrimp size classes by a) habitat and b) site for individuals collected in density experiment.

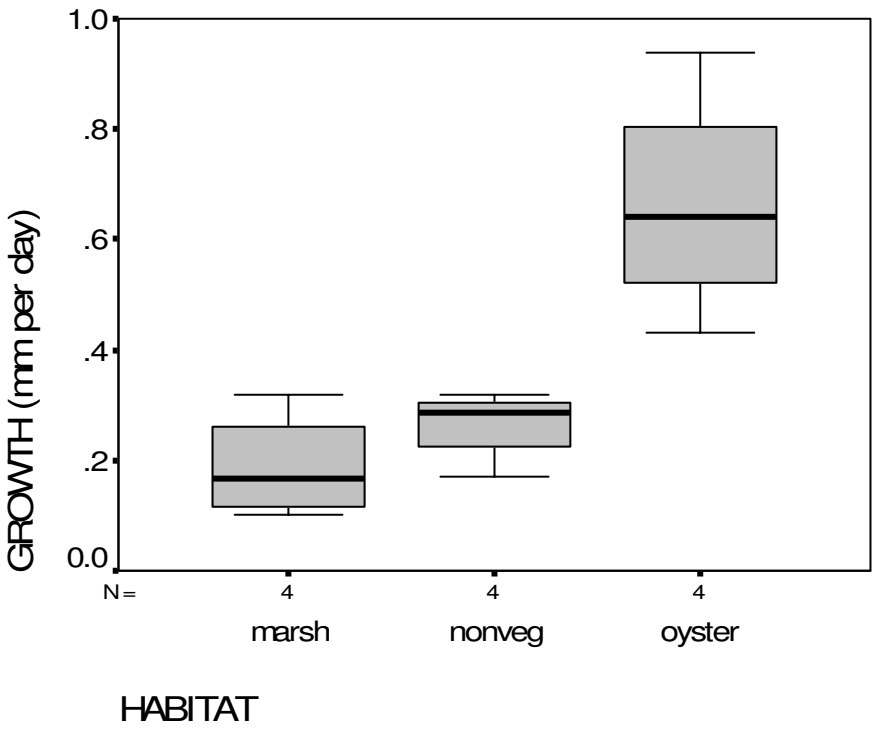

Figure 6-5. Boxplot of juvenile white shrimp growth rate for each habitat at Bayou Heron. Numbers (N) represent number of replicates (growth barrels) in the analysis for each habitat. The horizontal line inside the rectangle represents the median. Vertical lines with horizontal line attached at extremes represent the range of data excluding outliers.

Predation

Mean salinity (Table 6-2) was significantly different among treatments (randomized block ANOVA: $F = 4.7$, $p = 0.02$) and between years ($F = 251.1$, $p < 0.001$). Mean salinity in marsh treatment was significantly lower than oyster (Bonferroni post hoc: $p = 0.03$). Mean dissolved oxygen (Table 6-2) was significantly higher in October 2004 than in August 2005 (randomized block ANOVA: Blocking factor $F = 35.3$, $p < 0.001$). Mean temperature (Table 6-2) was significantly lower in October 2004 than in August 2005 (block ANOVA: Blocking factor $F = 582.6$, $p < 0.001$).

Size of crabs used in this experiment ranged from 120 to 160 mm CW with no significant difference in crab size across habitat treatments. Percent survival of juvenile white shrimp differed significantly among the three habitats (two factor ANOVA: $F = 8.0$, $p = 0.003$) and between the two years ($F = 86.9$, $p < 0.001$; Figure 6-6). No interaction was detected ($F = 1.8$, $p = 0.19$). Percent survival of juvenile shrimp in oyster, marsh, and nonvegetated bottom was 23.8 % +/- 8.00 SE, 46.3 % +/- 11.94 SE, and 48.7% +/- 12.74 SE, respectively). Survival in oyster was significantly lower than survival in marsh (Bonferroni post hoc $p = 0.016$) or sand (Bonferroni post hoc $p = 0.007$). Mean percent survival for October 2004 and August 2005 was 65.8 % +/- 6.45 SE and 13.3 % +/- 3.55 SE, respectively. In the control run I collected 100% of shrimp from sand, 97.5% from oyster, and 95.0% from marsh. I did not detect a significant difference in survival/recovery of white shrimp in the control experiment (ANOVA: $F = 0.6$, $p = 0.57$).

Table 6-2. Mean (Standard Error) values for environmental variables measured during predation study for each habitat type (dates pooled) and for each date (habitats pooled).

	Year		Habitats		
Parameter	October 2004	August 2005	Marsh	Nonveg	Oyster
Salinity (ppt)	4.8 (0.02)	3.4 (0.10)	4.0 (0.32)	4.0 (0.31)	4.3 (0.20)
DO (mg l^{-1})	6.1 (0.06)	5.2 (0.14)	5.6 (0.20)	5.8 (0.18)	5.5 (0.24)
Temp (^{o}C)	24.4 (0.11)	29.3 (0.16)	26.8 (0.90)	26.8 (0.87)	27.0 (1.01)

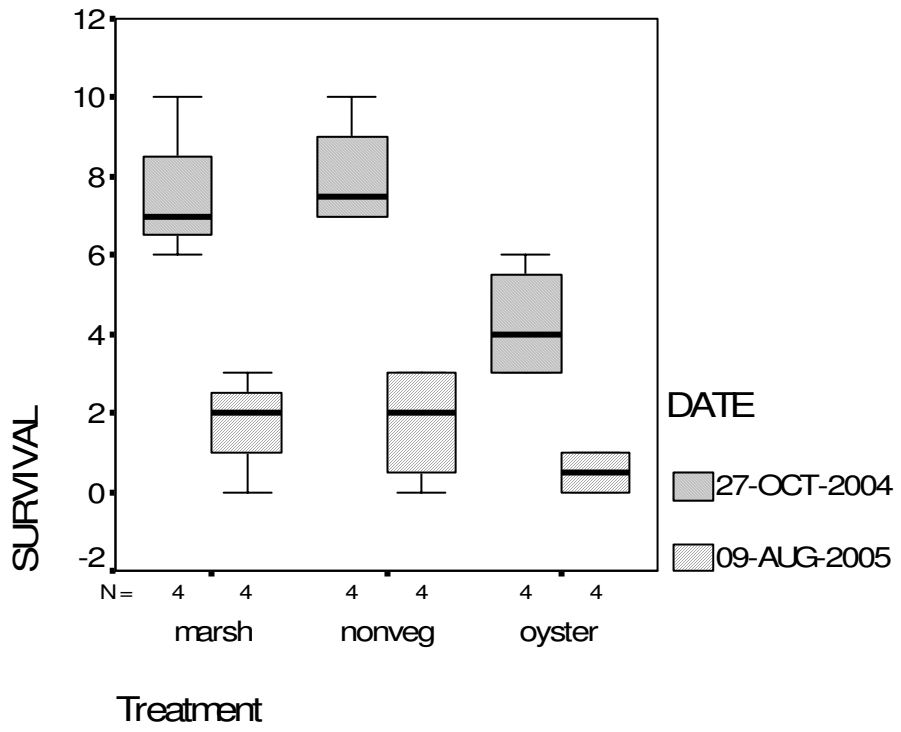

Figure 6-6. Boxplot for the number of juvenile white shrimp remaining after 6 hr interaction period with blue crabs for each habitat treatment. N is the number of replicate mesocosms used for each treatment on the two dates. The horizontal line inside the rectangle represents the median. Vertical lines with horizontal line attached at extremes represent the range of data excluding outliers.

Discussion

Density and habitat-specific size

The oyster habitat in my study area supported a significantly higher density of white shrimp than adjacent marsh and nonvegetated bottom habitats. Although, much research exists in the published literature comparing habitat-related densities of nekton in estuaries (Zimmerman et al. 2000; Heck et al. 2003; Minello et al. 2003; Peterson et al. 2003), very few studies have included oyster habitat in their sampling design (but see Glancy et al. 2003). White shrimp densities reported in this study for marsh and nonvegetated habitat are well within the range of white shrimp densities from comparable habitats in Texas, Louisiana, and Alabama estuaries during similar times of the year (Table 6-3). Studies in Texas estuaries reported mean densities ranging from 0.6 –26.7 m^{-2} in marsh habitat and 0.0–11.7 m^{-2} in nonvegetated bottom habitat (Zimmerman and Minello 1984; Minello and Zimmerman 1985; Zimmerman et al. 1990a; Zimmerman et al. 1990b; Minello and Webb 1997; Rozas and Minello 1998; Rozas and Zimmerman 2000). Studies in a Louisiana estuary found mean densities ranging from 0.0–3.4 m^{-2} in marsh habitat (Rozas 1992; Rozas and Reed 1993). In Mobile Bay, AL, Howe and Wallace (2000) and Howe et al. (1999) found white shrimp densities of approximately 0.0–6.0 m^{-2} in vegetated habitat and 0.0–0.7 m^{-2} in nonvegetated habitat.

In addition to my study, one other study from north GOM sampled oyster habitat in comparing nekton densities across multiple habitats. Zimmerman et al. (1989) focused on assessing an oyster reef as nursery habitat for juveniles of several

Table 6-3. List of studies and the reported densities for white shrimp in specific habitat types. For each study, I identified the habitat type(s) each paper examined as specifically as the paper identified them: Marsh edge (ME), *S. alterniflora* marsh edge (MESA), *S. alterniflora* marsh (M SA), nonvegetated (NV), and nonvegetated bottom (NVB). I also listed time of year and location for each study. In addition, I list if significant difference occurred in white shrimp densities between habitats: Vegetated habitats (VEG) and unvegetated habitats (NV). Not all studies made statistical comparisons (NA).

Habitat studied	Reported densities (m^{-2})	Time of year	Location of study	Statistical evidence	Source
MESA/ NV pond	13.5/6.0	Oct 1993	Galveston Bay, TX	No significant difference for VEG v. NV	Rozas and Zimmerman 2000
M SA/ Seagrass/ NVB	4.2/1.9/0.0	Sept 1993	Aransas NWR, TX	Significant difference for VEG v NV	Rozas and Minello 1998
Natural MESA/ NVB Created MESA/ NVB	30.4/6.0 19.8/6.3	Fall 1990	Galveston Bay, TX	No significant difference for MESA v. NV (Natural and Created)	Minello and Webb 1997
MESA (Hummocky Spartina)	2.0	Oct 1991	Terrebonne-Timbalier Estuary, LA	NA	Rozas and Reed 1993
M SA	0.8	Aug-Oct 1991	Terrebonne-Timbalier Estuary, LA	NA	Rozas 1992
ME (Delta: Juncus and Spartina mix)/ NVB	3.5/1.0[a]	Oct 1985	Lavaca Bay, TX	Significant difference VEG vs. NVB	Zimmerman et al. 1990a
ME SA/NVB	26.3/11.7[c]	Summer and Fall	Near Galveston, Island, TX	Significant difference VEG vs. NV	Zimmerman and Minello 1984

[a] Densities are approximate estimates derived from graph in text.

[b] Significance was calculated for coastal and delta sites samples across the three seasons sampled.

[c] These are the densities from Zimmerman and Minello (1984) as reported in Zimmerman et al. (2000).

economically valued species including penaeid shrimp, but did not find white shrimp in oyster habitat. Their study also used drop sampling as a means of collecting macrofauna over marsh, oyster reef, and nonvegetated bottom. Three important differences exist between my study and Zimmerman et al. (1989) that may explain the different results. First, I sampled white shrimp in Mississippi. Their study was in Galveston, TX. Possibly, white shrimp in Mississippi use oyster habitat and white shrimp in Texas do not. Second, the oyster habitat I sampled was oyster midden which was a combination of oyster rubble remaining from historical Native American consumption and live oyster. Zimmerman et al. (1989) sampled a well established oyster reef. Oyster rubble may offer different opportunities for foraging or protection than oyster reef habitat. Third, I sampled during a different season than their study. Zimmerman et al. (1989) had two sampling periods: winter (December 1988) and summer (July 1989). I sampled during the fall (October 2003). In December 1988, Zimmerman et al. (1989) collected mean white shrimp densities in marsh and nonvegetated bottom of 0.1 and 0.5 shrimp m^{-1}, respectively. Although they sampled oyster reef habitat, they did not find any white shrimp there. In July 1989, they collected mean white shrimp densities in marsh and nonvegetated bottom of 11.0 and 0.9 shrimp m^{-2}, respectively. Again, they did not find any white shrimp in their oyster habitat samples. Both of the sampling periods in Zimmerman et al (1989) are outside of peek juvenile white shrimp recruitment periods into estuaries (Muncy 1984). In my study, I also sampled marsh, oyster, and nonvegetated bottom. However, when I sampled in October 2003, not only did I collect white shrimp over oyster habitat, I found significantly higher densities over oyster

compared with marsh and nonvegetated bottom. I did not find a significant difference in white shrimp density between vegetated and nonvegetated bottom in Grand Bay, MS.

A general consensus does not exist in the current literature concerning significant differences in white shrimp densities between vegetated and nonvegetated habitat (Table 6-3). Some researchers have reported significant differences in mean density of white shrimp collected from vegetated versus nonvegetated habitat (Zimmerman et al. 1990a; Rozas and Minello 1998; Howe et al. 1999; Zimmerman et al. 2000) whereas other studies have not (Zimmerman et al. 1990b; Minello and Webb 1997; Rozas and Zimmerman 2000). And a few studies reported significant differences between these habitats for white shrimp densities in some sampling periods and no significant differences in other sampling periods (Zimmerman and Minello 1984; Minello and Zimmerman 1985).

One study examined selection for vegetated structure by brown shrimp *Farfantapenaeus aztecus* and white shrimp juveniles in partially vegetated enclosures with and without predators (Minello and Zimmerman 1985). The vegetated structure consisted of green straw that was similar to the structure of *Spartina* habitat. In the predator-free experiments, when species were examined separately, white shrimp did not select for vegetated or nonvegetated habitat during the day and selected for nonvegetated habitat during the night. In the presence of non-feeding predators (which were *Micropogonias undulatus* with mouths surgically sewn closed) juvenile white shrimp did not appear to alter their selection behavior. The results of the habitat selection study

suggest that white shrimp do not actively select for marsh structure, per se, even when a potential predator is present.

Depth was the only physical characteristic I measured for which I found a significant difference across habitats. The reason I found this difference is because all of my nonvegetated bottom habitat samples were in a more subtidal zone than marsh habitat which was more intertidal. Oyster midden habitat spanned across intertidal and subtidal zones. Other studies addressing habitat-associated densities of estuarine/marine organisms have also reported significant difference in depth or submergence time in vegetated versus adjacent or nearby nonvegetated habitats (Zimmerman and Minello 1984; Zimmerman et al. 1989; Rozas and Zimmerman 2000). However, in my study, differences in depth did not appear to influence differences in shrimp densities across habitats because depth was significantly different between marsh and nonvegetated bottom samples while shrimp density was significantly different between oyster and marsh samples and between oyster and nonvegetated bottom samples.

I did find significant differences in sizes of white shrimp collected from the two sites and from the three habitats. White shrimp were significantly smaller in Bayou Heron where salinity was significantly lower than Crooked Bayou. Bayou Heron is located in a more backwater area of Grand Bay (Figure 6-1) than Crooked Bayou which is nearer to MS barrier islands and open water connected with the Gulf of Mexico. According to Anderson (1966) juvenile white shrimp move from the upper reaches of estuaries to deeper, more open areas as they grow. In Grand Bay, significantly larger shrimp were also collected over the deeper, nonvegetated bottom habitat than the oyster

or marsh habitat. Intermediate sized juvenile shrimp were collected over oyster habitat and significantly smaller shrimp were collected from marsh habitat. As white shrimp grow during their time in estuarine waters, their specific habitat needs may change. The differences I observed in mean TL of white shrimp among the three habitats suggest that larger individuals may migrate to deeper areas.

Growth

In my study, juvenile white shrimp growth was significantly greater in oyster habitat than in marsh or nonvegetated bottom habitat. My growth experiment was small in scale (only one site and one season) and had only four replicates per habitat. Although I documented significantly higher growth in oyster habitat, I acknowledge that generalizations concerning habitat related growth of juvenile white shrimp should be tested further.

Increased food resources may be associated with high growth rates in various habitats (Summerson and Peterson 1984; Sogard 1992; Levin et al. 1997). In an unpublished study, Zimmerman et al. (1983) examined the relationships between food abundance, habitat value, and panaeid shrimp growth in the field and laboratory for vegetated and nonvegetated habitat. They found that growth rates of juvenile white shrimp enclosed in cages with access to *Spartina alterniflora* marsh versus cages restricting shrimp to nonvegetated bottom were not significantly different. They reported growth rates of 1.04 and 1.05 mm day^{-1} for white shrimp in vegetated and nonvegetated habitats, respectively. In my growth experiment, I also found that juvenile white shrimp growth in vegetated and nonvegetated habitat was not significantly

different. Although, the growth rates I report, 0.2 mm/day for vegetated and 0.3 mm/day for nonvegetated, are lower than Zimmerman et al. (1983). The main explanation for the discrepancy in growth rates between the two studies is that enclosure studies are used for determining relative growth rates and not absolute growth rates (Peterson and Black 1994). The actual values found for growth in the two experiments, although important, are not as relevant as the relationship between the values for vegetated and nonvegetated habitats within each study.

The feeding habits and diet of juvenile white shrimp in GOM estuaries have been elusive, but remains an essential component in assessing habitat value for this species. Food is potentially the principle attractant for white shrimp in habitat selection (Kneib 1984; Boesch and Turner 1984; McTigue and Zimmerman 1991). In general, penaeid shrimp walk along the benthic surfaces, probing and handling items they encounter (Dall et al. 1990). White shrimp are often observed hovering in the water column and may also capture food there (McTigue and Zimmerman 1998). One reason penaeid shrimp feeding habits, in general, are difficult to determine is because digestive processes impede gut content material identification (McTigue and Zimmerman 1991). Shrimp use mouthparts and a gastric mill to grind and shred food which renders the contents of their guts unidentifiable mush that is partially digested material with some isolated hard parts. As a result, much of the literature identifies juvenile and adult white shrimp as opportunistic omnivores (Muncy 1984; McTigue and Zimmerman 1991). Diet analyses have identified an array of items in white shrimp guts including: annelid/polychaete parts, copepods, tanaids, foramnifers, ostracods, gastropods, fish parts, bryozoans,

sponges, corals, algal filaments, and plant stems and roots (Williams 1955; Christmas and Etzold 1977; Mayer 1985). Perez-Farfante (1969) documented cannibalism in white shrimp. Although, Bardach et al. (1972) asserted that cannibalism leads to inefficient food conversion and may not be common in penaeids. McTigue and Zimmerman (1991) verified experimentally that the consumption of animal proteins by juvenile white shrimp supported growth in the laboratory while a diet of plant material only resulted in little growth and high mortality.

One potential food source for white shrimp in estuarine habitat is infauna and epifauna. McTigue and Zimmerman (1998) examined the use of infauna by juvenile brown shrimp and white shrimp. They found that the juvenile white shrimp did not remove infauna from sediment cores during the experiment nor did white shrimp grow to a significant degree when provided polychaetes or amphipods as food. McTigue and Zimmerman (1998) concluded that juvenile white shrimp do not rely on infaunal material for their main source of nutrition and speculate that the shrimp potentially feed on estuarine mysids and/or zooplankton (copepods). Kneib (1997) and Kneib and Knowlton (1995) found evidence that white shrimp feed on early life history stages of grass shrimp.

McTigue (1993) recognized that juvenile white shrimp depend on plant resources to a greater extent than do brown shrimp. Therefore, other potential food sources for white shrimp include microalgae and vascular plants and their detritus. Microalgae (including diatoms) are available suspended in the water column, settled on the sediment, growing edaphically on the sediment surface, and growing epiphytically on

Spartina stems. Plant detritus consists of mostly decomposing *Spartina* parts and includes the associated microbial community in addition to the plant material and may also provide a potential source of nutrients.

Within the context of my results, I can speculate as to the availability of potential habitat-specific food items for juvenile white shrimp. Several studies have compared the infaunal and epifaunal communities of vegetated and adjacent nonvegetated habitats (Zimmerman et al. 1990a; Minello and Webb 1997; Whaley 1997; Rozas and Zimmerman 2000) and one study compared infauna in adjacent marsh, oyster, and nonvegetated bottom (Zimmerman et al. 1989). Rozas and Zimmerman (2000) reported no significant differences for polychaete densities between vegetated and nonvegetated habitats for October 1993 samples. Minello and Webb (1997) did not find significant differences in infaunal densities between vegetated and nonvegetated habitats for their fall 1990 and spring 1991 samples, either. Whaley (1997) did not find significant differences in overall infaunal densities or epifaunal crustacean biomass between vegetated marsh edge and unvegetated marsh edge during the August or October 1995. Zimmerman et al. (1990) did not find significant differences for "forage animals" (which were the epifauna and infauna combined that they considered potential prey organisms for fishes and decapod crustaceans) between marsh and nonvegetated bottom habitats. In a study comparing infaunal and epifaunal abundances across marsh, oyster, and nonvegetated bottom habitat, Zimmerman et al. (1989) found significantly higher annelid densities in oyster habitat when compared with nonvegetated bottom, but not when compared with marsh. They also found significantly higher peracarid crustacean

(amphipod, tanaid, mysid) abundances in oyster than either marsh or nonvegetated bottom. From these studies, infaunal densities do not appear to differ between vegetated and unvegetated habitats, at least for the periods sampled. However, in the one study where oyster habitat was included, oyster habitat appeared to support higher densities of potential prey items for white shrimp.

In addition to possibly supporting higher densities of invertebrate prey, oyster habitat may have greater overall surface area for colonization of algae than vegetated and nonvegetated habitats. In the marsh habitat where I conducted my growth experiment, mean *Spartina* stem density was 10 stems per barrel or approximately 36 stems m^{-2}. Each oyster replicate barrel contained approximately 12 L of a combination of ambient live oyster and oyster shell. Intuitively, 13 L of oyster has an overall greater surface area than 10 stems of *Spartina*, although I did not actually measure surface area. I speculate that because of the combination of greater potential prey densities (both infaunal and epifaunal) and greater overall surface area available for algal colonization, oyster habitat may provide more food resources for juvenile white shrimp.

Predation

Survival of juvenile white shrimp was significantly lower in the oyster habitat when compared with both marsh and nonvegetated habitat. My study did not necessarily provide evidence that habitat structure is an important requirement for reducing mortality of an estuarine transient as other studies have shown (Minello and Zimmerman 1983, 1985; Minello et al. 1989; Rooker et al. 1998; Stunz and Minello 2001). Rather, my study indicates that the increased habitat structure in oyster shell may increase

predator feeding efficiency (Grabowski and Powers 2004) for blue crabs, which I characterize as intermediate predators. However, I found no previous study that examined natural blue crabs predation on white shrimp in the field (but see Mascaro et al. 2003). Minello et al. (1989) determined that the dominate fish predators of penaeids were southern flounder *Paralichthys lethostigma*, gulf killifish *Fundulus grandis*, pinfish *Lagodon rhomboides*, spot, speckled seatrout *Cynoscion nebulosus*, and red drum. Lab studies comparing predation rates on brown shrimp by estuarine fishes found that more brown shrimp survived in habitats with vegetated structure than in habitats without vegetated structure (Minello and Zimmerman 1983, 1985, Minello et al. 1989). I may have observed different results in my predation study if I had used fish as predators or if my crab predator density had been lower.

When I was initially designing the experiment for the predation component of this study, I used experimental gillnets in the areas where I was drop sampling in order to assess presence and activity of potential predators. I found that on average for every individual predatory fish I collected in my nets, I collected six adult blue crabs (Shervette, unpublished data). In addition, the fact that passive gillnetting is not an effective sampling technique for estimating blue crab densities (it tends to underestimate crab densities when compared to trawling and seining data; Shervette, personal observation), led me to conclude that blue crabs were the most abundant potential predator in my sampling area. Moreover, blue crabs have been observed to prey on penaeid shrimp (Lee and Wickins 1992; Stoner and Buchanan 1990), so I used them as my predator instead of predatory fish species used in other laboratory mesocosm

predation studies (Minello and Zimmerman 1983, 1985; Minello et al. 1989; Rooker et al. 1998; Stunz and Minello 2001).

Adult blue crab are highly agonistic (Jachowski 1974; Clark et al. 1999) and I attempted to account for their aggressive behavior in my experimental design by only using males in intermolt and pairing similar sized crabs in each experimental pool. The density of crabs I used was high, but consistent with ambient densities collected from oyster habitat in Grand Bay, MS (Shervette, unpublished data). Structurally complex habitats, such as oyster and marsh, are often characterized by high densities of intermediate predator and prey species (Grabowski 2002). In my study, blue crabs buried themselves in the sand in nonvegetated treatment and captured shrimp when they came within reach. I speculate that crabs exhibited this burrowing behavior in order to avoid each other. However, while in the marsh and oyster habitats, blue crabs appeared minimally hindered and actively foraged, reaching into stem clumps when possible and probing through oyster shells, manipulating and actually moving the oysters with their legs and claws.

Grabowski and Powers (2004) examined the role of habitat complexity on predation rates of juvenile hard clams by mud crabs in structurally simple (< 5 cm vertical relief of shells) and complex (> 10 cm vertical relief of shells) habitat. They found that at low and intermediate densities, mud crabs foraged at similar rates in simple and complex habitat. However, at high crab densities, foraging rates were highest in the more complex habitat. They concluded that structurally complex habitat provides refuge

to intermediate predators and their prey and appears to enhance a predators foraging efficiency by reducing the interference competition among predators.

My predation results for the oyster habitat support Grabowski and Powers (2004). In observing blue crabs and white shrimp during my experiment, I noticed that white shrimp, no matter the habitat, foraged wherever they could walk without moving into a clump of oyster or *Spartina* stems when a blue crab was near. The only time white shrimp reacted to blue crab presence was when crabs actively attempted to catch them. Minello and Zimmerman (1985) reported similar behaviors by white shrimp, which did not appear to select for marsh structure, per se, even when a potential predator (with mouth surgically sewn closed) was present. Therefore, if I categorized marsh habitat as providing more of an intermediate level of complexity, if I categorize oyster habitat as providing a higher level of complexity, and if I consider the crab density I used as an example of "high predator density" then my results are consistent with the "Complex Habitat" hypothesis examined in Grabowski and Powers (2004).

Laboratory predator experiments can be useful in comparing short-term prey survival among habitat structure. However, extrapolation of results to field conditions can be difficult (Stunz and Minello 2001). Factors such as trophic interactions, depth, salinity, and temperature may contribute to natural predation-related mortality of shrimp and I did not evaluate all of these possibilities. The water depth in my predation experiment was similar to that of GOM intertidal zone during high tide. My experiment also exhibited significant seasonal variation in salinity, temperature, and DO. Regardless of the environmental variability, my results were consistent: oyster habitat

yielded the lowest survival rates of white shrimp juveniles. Thus, I conclude that oyster habitat provides white shrimp with less refuge from crab predation compared to marsh and nonvegetated bottom habitats when blue crab density is high.

Conclusions

Human-induced modifications within estuarine ecosystems are inevitable. This is why information concerning the functional significance of EFHs for target species can be useful in the management and protection of those habitats. Oyster habitat in Grand Bay, MS, appears to play a significant role as a nursery area for white shrimp juveniles. Oyster supported the greatest densities of juvenile white shrimp during my sampling period. Oyster also supported the highest growth rates of juvenile white shrimp. Therefore, the high densities in oyster habitat are potentially related to greater food availability. My predation experiment demonstrated that predation on white shrimp by blue crabs, an intermediate predator, was highest in oyster habitat. If predation threat produced a greater density of white shrimp in oyster habitat then one would predict a greater effect of predators in other habitats. However, this was not what I observed. The much higher density of shrimp in oyster habitat combined with the higher predation rates in oyster suggest that habitat selection for food resources rather than predation was responsible for the density patterns I observed. My experiments were short-term and I acknowledge the possibility that important patterns may not have had sufficient time to emerge during my experiments. Insofar as my results indicate, oyster habitat provides an important function in the juvenile stages of white shrimp and should be consider as nursery habitat.

CHAPTER VII

CONCLUSIONS

Estuaries provide essential shallow water habitats such as salt marshes, oyster reefs, mangrove forests, and seagrass beds for many fishes and invertebrates. Both estuarine resident species and marine species whose juveniles reside in estuaries rely on estuarine habitats for food resources and refuge from predation. In order for estuarine management practices to be effective, resource managers must understand how and when species utilize estuarine. My dissertation research, as a whole, demonstrated that structural complexity is one of the most important characteristics of estuarine habitats for associated fauna.

The Palmar mangrove wetland supported a more diverse and species rich fish community than the nearby tidal river, Rio Javita. Palmar has lost approximately 90% of its wetland to shrimp farming and this habitat loss may partially explain the relatively low fish species richness found in the mangrove creeks and main channel compared to other mangrove fish communities. No other studies exist in the scientific peer-reviewed literature reporting the biodiversity of fishes in mangroves in the tropics along the eastern Pacific coast of South America, which makes determining the potential level of the impact of habitat loss and alteration in Palmar difficult. However, other studies conducted in Central America and other tropical/subtropical mangrove systems have consistently documented fish communities with higher fish species richness. Regardless of the comparatively low richness, the mangrove habitat of Palmar contained juveniles

of several economically important species in the snook family (Centropomidae), which were not present in Rio Javita, a less structurally complex area. Both areas contained relatively high densities of juvenile mullet (*Mugil* spp), a popular food fish, as well as large populations of *Atherinella* species, commonly found in fish and wading bird diets and often utilized as fish-meal. Both Javita and Palmar appear to provide important habitat for ecologically and economically important fishes. Although further analysis of trophic integrity is needed, the Palmar mangrove wetland appears to support a complex trophic structure and does not appear to deviate in an obvious manner from the general characteristics of feeding relationships among fishes of mangrove habitats.

The goal of my work in GBNERR was to determine the relationship between three common shallow estuarine habitats (oyster, VME, and NVB) and nekton community structure in order to address the dearth in research comparing oyster with adjacent habitats. In obtaining that goal, I documented three basic trends related to the importance of oyster and VME habitats: 1) Oyster and VME provide habitat for significantly more species relative to NVB; 2) Oyster and VME provide habitat for uncommon and rare species; and 3) Several species collected across multiple habitats occurred at higher abundances in oyster or VME habitat. I also found that contrary to the current low valuation of oyster habitat relative to other estuarine habitats, oyster provides higher quality habitat for many species. As a structured habitat, oyster, similar to VME and submerged aquatic vegetation, provides higher growth rates for some species and refuge from predation for others. As documented in studies concerning other habitats, high abundances of certain species in oyster may be indicative of higher

growth rates in oyster, greater refuge from predation in oyster, or both. Further research comparing habitat-specific growth and survival is essential in verifying the overall importance of oyster habitat for resident and nursery species. Oyster appears to support a temporally diverse and spatially distinct nekton community and deserves further attention in research and conservation.

In order to obtain a better understanding of species-specific use of habitats within marshes of GBNERR, I examined the abundance patterns and size distributions of seven common invertebrate species among the three habitats and documented three main trends. First, I observed that some species (juvenile blue crab, *E. depressus*, *P. simpsoni*, and *R. harrisii*) occupied oyster and VME habitats in higher abundances relative to NVB with minor to moderate fluctuations in seasonal abundance. Smaller crabs tended to use oyster habitat (although differences were not significant for all four species) and this may be related to the higher abundance of smaller refuges in oyster habitat. The second trend, occurring for one species (grass shrimp), was the occupation of VME in significantly higher abundance than the other habitats. This may be related to grass shrimp reliance on VME stems, and associated flora and fauna, for refuge and food. The last trend observed was the relatively equal use of VME and oyster by the estuarine-dependent species brown shrimp and white shrimp. Both species selected for structured habitat over NVB and both species were significantly larger in oyster habitat.

Human-induced modifications within estuarine ecosystems are inevitable. This is why information concerning the functional significance of estuarine habitats for target species can be useful in the management and protection of those habitats. In examining

juvenile pinfish use of estuarine habitats, I found that marsh habitat provides an important nursery function. By definition, nursery habitat recruits more individuals per unit area to the adult population relative to other juvenile habitats. A combination of density, growth, and survival of juveniles within a nursery habitat must be greater than in other juvenile habitats. Many studies have documented that juvenile pinfish densities, abundances, and recruitment are greater in vegetated habitats. My study demonstrated that growth of juvenile pinfish is significantly higher in VME habitat compared to oyster and NVB. Higher habitat-specific growth of juvenile pinfish may be related to higher abundances of food resources in marsh habitat that have been documented in other studies. Lastly, indirect evidence and observations from several studies suggest that predation-related mortality of juvenile pinfish may be lower in structured habitat such as VME and oyster relative to NVB. Therefore, VME provides an important habitat for juvenile pinfish and may provide a nursery function.

Lastly, my research demonstrated that oyster habitat played a significant role as a nursery area for white shrimp juveniles. Oyster supported the greatest densities and the highest growth rates for juvenile white shrimp. Therefore, the high densities in oyster habitat are potentially related to greater food availability. I also found that predation was highest in oyster habitat. The much higher density of shrimp in oyster habitat combined with the higher predation rates in oyster suggest that habitat selection for food resources rather than predation was responsible for the density patterns observed. Insofar as my results indicated, oyster habitat provides an important function in the juvenile stages of white shrimp and should be consider as nursery habitat.

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VITA

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