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## **Influence of the marsh edge on the structure and trophic ecology of the fish and macroinvertebrate community in a Louisiana estuarine ecosystem**

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**INFLUENCE OF THE MARSH EDGE ON THE STRUCTURE AND TROPHIC  
ECOLOGY OF THE FISH AND MACROINVERTEBRATE COMMUNITY IN A  
LOUISIANA ESTUARINE ECOSYSTEM**

A Dissertation

Submitted to the Graduate Faculty of the  
Louisiana State University and  
Agricultural and Mechanical College  
in partial fulfillment of the  
requirements for the degree of  
Doctor of Philosophy

in

The Department of Oceanography and Coastal Sciences

by

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May, 2004

## **DEDICATION**

I would like to dedicate this dissertation to my daughters, Maria del Mar and Estefania Beatriz, who gave me the strength to continue with my dream of getting a doctoral degree, in spite of all the difficulties I had to sort through during these years in a foreign country and under the pressure that implies being a husband and a parent while in graduate school.

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## ABSTRACT

Habitat degradation of saltmarsh ecosystems reduces the suitability of the marsh as permanent environments for resident species and seasonal nursery grounds for transient fauna. This study was conducted in Terrebonne-Timbalier bays near Cocodrie, Louisiana. Fishes and macroinvertebrates were collected using a drop sampler in marsh-edge and open-water habitat types, in three locations (i.e., pond, channel, and bay), and four seasons (Fall of 2000, Winter of 2000-2001, and Spring and Summer of 2001). The specific objectives of this study were: (1) to determine the difference in composition and structure of fish and macroinvertebrate communities, (2) to establish the food habits of the fish community, and (3) to determine the dependence on *Spartina alterniflora* of fishes and macroinvertebrates through the use of stable isotope techniques. Densities of resident and transient species including darter goby, naked goby, and brown shrimp were detectably different among habitat types, seasons, and locations. The naked goby consumed higher abundances of harpacticoid copepods along the marsh edge than in the open water. Bay anchovy and naked goby had detectable differences in prey utilization among seasons and ingestion was associated with changes of environmental variables. Despite the presence of detritus in the stomachs of several fish species, it was relatively rare. Naked goby was the only species that had detectable differences in carbon stable isotopes between marsh-edge and open-water habitat types. Significant seasonal variations were identified in the carbon isotopic values of naked goby, daggerblade grass shrimp, and blue crab, and in the nitrogen isotopic values of brown shrimp. In the field experiments with naked goby, differences in prey utilization and in carbon or nitrogen isotope values were not detectable among habitat types. The marsh edge is essential for

food and refuge for estuarine nekton, but macroinvertebrates densities may be more sensitive to marsh loss than fish densities. Nevertheless, marsh loss may have an effect on the feeding ecology of juvenile fishes that rely primarily on benthic prey along the marsh edge. The relative contribution of *Spartina alterniflora* to support the nekton community was less than 35% in the study area.

## CHAPTER I.

### INTRODUCTION: MARSH EDGE LOSS AS A FACTOR INFLUENCING FISHERIES IN LOUISIANA ESTUARIES

Saltmarsh estuaries are highly productive ecosystems that are distributed in temperate coastal wetlands (Day *et al.* 1989). Saltmarsh production varies widely depending on the duration of tidal inundation, relief, age of the marsh, sedimentation, nutrients, and salinity among other factors (Knox 1986). In Louisiana, large areas of intertidal marshes are dominated by the smooth cordgrass, *Spartina alterniflora* (Pezeshki and DeLaune 1995), with productivity inversely related to distance from the marsh-water interface (Gallagher *et al.* 1980). Vertical accretion is important for marsh stability, but in Louisiana compaction and subsidence dominate over sedimentary accretion, and *Spartina* marshes are converted to open water (Nyman and DeLaune 1999).

Louisiana not only contains approximately 40% of the coastal wetlands of the continental United States (Emmer *et al.* 1992), but also has one of the highest rates of wetland loss (Coleman, *et al.* 1998). The total area of coastal salt marsh has decreased substantially over the last decades as wetlands have been filled for development, dredged for petroleum exploration, or converted to open water through subsidence (Mitsch and Gosselink 1986, Turner and Boesch 1987). From 1983 to 1990 land was converted to open water at an average rate of more than 50 km<sup>2</sup> yr<sup>-1</sup> in Louisiana's Mississippi River deltaic plain (Dunbar *et al.* 1992). Loss of marsh-edge habitat type may reduce the suitability of the marsh as permanent environments for resident species and seasonal nursery grounds for transient fauna (Hoss and Thayer 1993). The marsh edge is the



transitional band (*i.e.*, ecotone) at the interface of the marsh and open water (Rakocinski *et al.* 1992) and supports high densities of nekton compared to nearby habitats (Minello *et al.* 1994), which is known as the marsh-edge effect (Chadwick 1997). Thus, higher proportions of marsh edge compared to open water are of primary importance to fisheries in coastal Louisiana. The amount of marsh edge regulates habitat use for nekton (Baltz *et al.* 1993, Minello *et al.* 1994), and subsequently may influence fisheries production (Chesney *et al.* 2000).

It seems that Louisiana fisheries appear to be resilient because in spite of marsh loss, commercial species such as brown shrimp, white shrimp, and blue crab have not shown decreasing trends since 1972, and bay anchovy and Gulf menhaden show increasing trends over the same period (Chesney *et al.* 2000). Nevertheless, when marsh habitat is initially broken up, the amount of edge increases until a maximum is reached, but further deterioration leads to marsh-edge loss (Browder *et al.* 1989). Thus, fish production may not be negatively affected in the first stages of marsh loss, but eventually broken marsh becomes open water affecting fisheries (Browder *et al.* 1985). Deep water near the marsh edge allows larger predators more access to estuarine habitats affecting the function of the marsh as a refuge for small nekton (Deegan 2002). Estuarine nekton abundance declines when the marsh cover is less than 30% compared with the adjacent open water (Minello and Rozas 2002).

Marsh management and restoration projects are being conducted as a response to rapid loss of wetlands in coastal Louisiana (Peterson and Turner 1994). Pressures on marsh nursery habitats from coastal activities such as channelization, unplanned land use, dredging, erosion, industrial and waste water pollution, as well as natural phenomena

such as rising sea level (Wenner and Beatty 1993) may contribute to observed patterns of land loss. Given such widespread wetland loss, it is important to compare different habitats types at various scales within an estuarine system to identify the main factors that are influencing estuarine fisheries. The major goal of this study was to conduct seasonal comparisons of nekton densities and the trophic ecology between marsh-edge and open-water habitat types at different spatial scales (i.e., bay, channel, and pond). The study encompassed spatial and temporal scales characterized by seasonal sampling and different distances from the marsh edge across three locations that typified the landscape of the marsh ecosystem: a small pond, connecting channel, and an open bay. The specific objectives were: (1) to determine the difference in composition and structure of fishes and macroinvertebrates, (2) to establish the food habits of the fish community, and (3) to examine the trophic pathways from primary producers to fishes and macroinvertebrates.

Chapter two compares the ecology of nekton residing in the marsh-edge and adjacent open-water habitat types. In this chapter I compare the seasonal abundance of fishes and macroinvertebrates between the marsh-edge and the adjacent open-water habitat types at different spatial scales and identify environmental variables that contribute to observed distribution and abundance patterns. Chapter three examines the feeding ecology of fishes residing in the marsh-edge and adjacent open-water habitat types across a landscape scale. In this chapter I describe comprehensive information about the feeding of estuarine fishes by analyzing stomach contents to determine their trophic role in the community. I also test whether habitat type (marsh edge and open water) and environmental variability affects the structure of estuarine food webs. In Chapter four, I

estimate the contribution of primary producers to nekton residing in both the marsh-edge and adjacent open-water habitat types by stable carbon and nitrogen isotope analyses. I also test the importance of *Spartina alterniflora* as a food source for estuarine nekton. Field enclosure experiments with naked goby were also performed to compare food habits and relative food sources among habitat types such as marsh edge with vegetation, marsh edge without vegetation, and open water. Finally in Chapter five, I synthesize my main findings and discuss other factors not taken into account.

The major finding of this study is that the marsh edge is essential for food and refuge for estuarine nekton, but macroinvertebrates densities may be more sensitive to marsh loss than fish densities. Nevertheless, marsh loss may have an effect on the feeding ecology of juvenile fishes that rely primarily on benthic prey along the marsh edge. The relative contribution of *Spartina alterniflora* to support the nekton community was less than 35% in the study area. The marsh edge is important for providing food and refuge to estuarine fauna and conservation of marsh ecosystems will enhance the suitability of estuarine fisheries.

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## CHAPTER II.

### COMPARATIVE ECOLOGY OF NEKTON RESIDING IN MARSH-EDGE AND ADJACENT OPEN-WATER HABITAT TYPES IN A LOUISIANA ESTUARY

#### Introduction

In the Gulf of Mexico, several fishery species spawn in coastal waters and their larvae migrate into the estuary where they become juveniles using the marsh as nursery grounds (Minello 1999). Seasonal and spatial variations in recruitment, distribution, and survival of estuarine nekton are influenced by structural heterogeneity, physical factors, tidal regimes, predation, productivity, and food availability among other variables (Rakocinski *et al.* 1992, Baltz *et al.* 1993, Minello *et al.* 1994, Baltz *et al.* 1998, Rozas and Zimmerman 2000). Marsh flood frequency and flood duration control nekton access to marsh-surface habitats affecting survival and growth (Rozas 1995). Also, utility of habitat types is related to water-surface elevation and the substrate profiles crossing the ecotone in adjacent open water and the *Spartina* marsh (Deegan 2002). Nevertheless, the function and value of salt marshes for juvenile fishery species and other nekton are difficult to measure (Minello and Webb 1997).

I approached the question of habitat and prey use among small adult and juvenile fishes and macroinvertebrates by fine-scale studies of distribution and abundance at the microhabitat level (Baltz 1990). At the finest scale the microhabitat of an individual is the site that it occupies at a given point in time (Hurlbert 1981, Baltz *et al.* 1993). Presumably, fishes and macroinvertebrates select a site to occupy in response to variables that optimize their net energy gain while avoiding predators and competitors (Jones *et al.* 2002). Because similarly sized individuals of a species should select similar microhabitats, careful measurements of many individuals and associated physical,

chemical, and biological variables should define the response of the size class (Livingston 1988) or population (*i.e.*, its density pattern) to environmental gradients (Hurlbert 1981, Baltz 1990) and describe habitat use patterns from a fish's eye view. Biologists often identify habitat types, but most fishes and macroinvertebrates range more widely and their patterns of habitat use are not always well defined by study of a limited number of habitat types. Nevertheless, my focus on two habitat types is justified to address landscape changes as the abundance and influence of *Spartina* marsh decline in Louisiana coastal waters.

In the last century, the spatial extent of salt marshes has been reduced since they are highly vulnerable to anthropogenic influences (Thomas 1995). Large areas that were once vegetated intertidal habitat (salt marsh) have been converted into shallow open-water areas (Chesney *et al.* 2000). Specifically, *Spartina* salt marshes are being converted from tidally flooded marsh with associated marsh-edge habitats to open-water habitats (Zimmerman *et al.* 1991). Although the use of coastal salt marshes and adjacent open water by nekton is well studied, little is known about impact that marsh-edge loss might have on the abundance and distribution of ecologically and economically important nekton species.

The marsh edge is highly productive and provides food and refuge for both resident and transient organisms (Peterson and Turner 1994). Estuarine nekton, including economically important species (Zimmerman *et al.* 1991), depends on this ecotone (Minello *et al.* 1994). Differences in the density of estuarine fishes and macroinvertebrates between the marsh-edge and open-water habitat types should reflect particular habitat selection or dependency of these organisms (Zimmerman and Minello

1984). Thus, I tested whether estuarine nekton species select specific habitat types at different spatial scales. The specific objectives were to compare the seasonal variation of nekton along marsh-edge with adjacent open-water habitat types across a landscape gradient running from a small pond, through a channel, and a large bay and to associate their distributional patterns with variation of selected environmental attributes. I found that estuarine macroinvertebrates were more abundant along the marsh edge, whereas fishes were similar distributed in both marsh-edge and open-water habitat types.

## **Materials and Methods**

### **Study Area**

The study was conducted near Cocodrie, Louisiana in the Terrebonne-Timbalier bay system (Figure 2.1). The study area is now isolated largely from the influence of the Mississippi River by a levee system that permits only minimal sediment input (Delaune *et al.* 1987) and is characterized by shallow bays, channels, and small ponds, with fine sediments, turbid waters, and salinities typically ranging between 0 and 28 psu throughout the year (<http://weather.lumcon.edu/stationdata.asp>). Tides are predominantly diurnal with a mean range of approximately 0.4 m, and are often wind-dominated (Shirzad *et al.* 1989; <http://weather.lumcon.edu/stationdata.asp>). The study area is within the saline marsh category (Chabreck and Linscombe 1991) dominated by the smooth cordgrass, *Spartina alterniflora* (Fry *et al.* 2003, Baltz *et al.* in review). The marsh is now classified as coastal submergent, since transgression has been dominant (Stevenson *et al.* 1986), following active delta development that occurred between 800 and 1,200 years ago (Penland *et al.* 1987). The deltaic sediments are rapidly subsiding, and relative sea-level rise rates for the area are estimated at 1.1-1.3 cm yr<sup>-1</sup> (Penland *et al.* 1988).



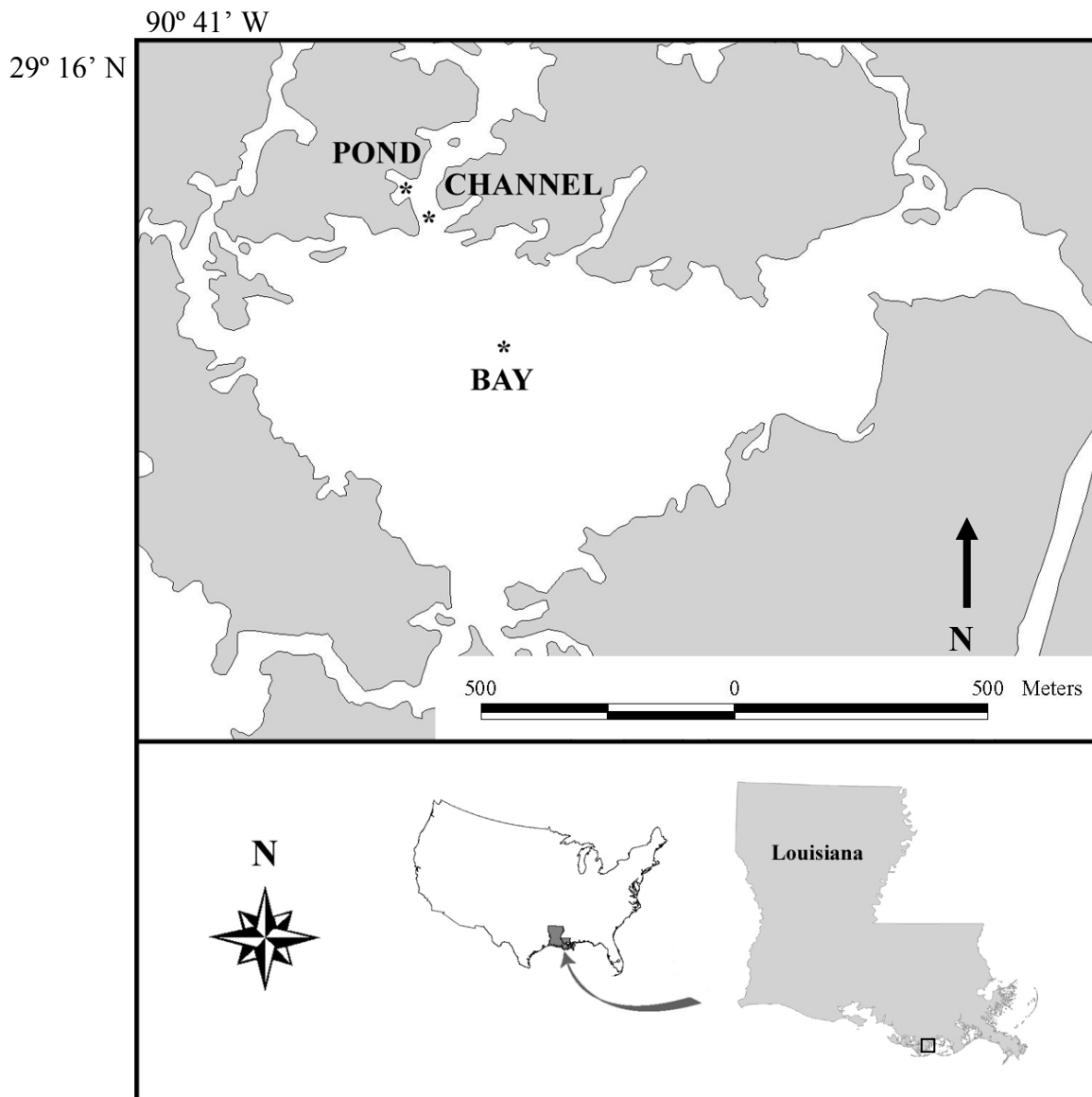


Figure 2.1. Study area indicating pond, channel, and shallow bay locations near the Louisiana Universities Marine Consortium (LUMCON) in Terrebone Bay, Louisiana.

### Sample Collection

Fishes and macroinvertebrates were collected using a drop sampler, a clear acrylic cylinder (1.2 m diameter and 1.2 m height) with a metal ring on the bottom. It was released from a boom attached to a small boat (Arrivillaga and Baltz 1999, Baltz *et al.* in review). Nekton were removed from the sampler by thoroughly sweeping the enclosed

volume with fine mesh nets (Cummings model 270-12, 5 mm mesh) repeatedly until three successive passes yielded no additional organisms (Duffy and Baltz 1998).

Sampling was stratified by habitat type, location, and season. Four samples were taken at the marsh edge (< 1 m from the edge) and four in open water (> 1 m from edge), in each location strata (i.e., bay, channel, and pond in Figure 2.1), and each season for a total of 96 samples. Seasonal sampling included Fall of 2000 (September-November), Winter of 2000-2001 (November-February), Spring of 2001 (March-May), and Summer of 2001 (June-August) collections. To ensure that all samples were independent, careful placement and collection avoided interference with subsequent samples. Samples were field sorted and transported on ice to the laboratory where they were frozen pending analyses.

A total of six environmental variables were examined at each sampling site including minimum and maximum depths (cm), salinity (psu), temperature (°C), dissolved oxygen (DO mg l<sup>-1</sup>), and distance from the marsh edge. Temperature, salinity, and dissolved oxygen were determined by using a Hydrolab model SRV2-SU meter. Median depth and substrate relief (i.e.,  $\Delta$  depth = max - min depths) were calculated using the minimum and maximum depth values. Water samples were collected to determine turbidity (NTU) and chlorophyll *a* (µg l<sup>-1</sup>) in the lab. These samples were maintained in cold storage until turbidity samples were read on a Hach 2100N turbidimeter and chlorophyll *a* values determined by acetone extraction. Fishes and macroinvertebrates were identified to species (Hoese and Moore 1977, Hopkins *et al.* 1989, Williams 1984), and were measured to the nearest millimeter standard length (SL) for fishes, total length (TL) for shrimp, and carapace width (CW) for crabs.

## Data Analysis

Differences in the environmental variables were assessed in a three-way multivariate analysis of variance (MANOVA), with season, location, and habitat type as main factors (using general linear model and least-square mean procedure, SAS Institute 1996). All the environmental variables were transformed using  $\log_{10}(x + 1)$  to improve the normality of the residuals (Green 1979) and residual plots and residual biplots were examined to confirm that the assumptions of normality and variance homogeneity of residuals were met after transformation. For further interpretation, the univariate analysis of variance of each environmental variable was checked. Differences in the environmental variables were examined using Tukey's adjustment for multiple pairwise comparisons.

Eight community descriptors, including total nekton (the sum of all fish and macroinvertebrate species), total fishes, pelagic fishes, demersal fishes, total macroinvertebrates, richness, evenness (Pielou's index, Pielou 1966), and diversity (Shannon-Weiner index, Magurran 1988), were analyzed in a three-way MANOVA with four seasons, three locations (i.e., pond, channel, and bay), and two habitat types (i.e., marsh edge and open water) as main factors as described above. Abundances were converted to density measurements (number of individuals  $\text{m}^{-2}$ ) by dividing the number of individuals observed in each sample by the basal area of the drop sampler (i.e.,  $1.18 \text{ m}^2$ ) and transformed using  $\log_{10}(x + 1)$ . To test the hypothesis that the densities of fish and invertebrate species varied among seasons, locations, and habitat types, a three-way MANOVA was performed using the density of the most abundant species (frequency of occurrence more than 10%, Table 2.1) as the dependent variables. Further patterns in the

variability in density of these species were explored by univariate analysis of variance and multiple pairwise comparisons as described above.

A multivariate multiple regression analysis was performed to determine which environmental variables were related to the community descriptors and the densities of the most abundant species. Collinearity between independent variables was assessed by examining variance inflation factors (VIF; Allison 1991). Variables were determined to be primarily independent if VIF values were close to 1, and no individual value was greater than 10. Variables included in the multiple regressions were selected by a stepwise approach. An entry and exit p-value of 0.15 was chosen to identify a suite of variables that were important in describing the given dependent variable. The highest F-value was used at each step to identify the variable that contributed the most to the overall  $R^2$  value. Subsequent variables were chosen in the same manner; however, after each new addition all included variables were reexamined to ensure that they met the criteria (i.e.,  $P > F$  is less than 0.15). If the variable was no longer significant, it was eliminated from the model.

Variation in microhabitat use was examined by principal component analysis (PCA) based on the correlation matrix (Baltz *et al.* 1993) of the environmental variables. The PCA was conducted using the Factor Procedure in SAS and rotating the first three factors using the varimax option (SAS Institute 1996). The PCA was used to resolve eight intercorrelated environmental variables into three orthogonal variables to facilitate visualization and simplify comparisons among species.

## Results

Environmental conditions in the study area such as median depth, temperature, salinity, turbidity, and distance from the edge changed seasonally across locations and between habitat types (MANOVA,  $F_{6,65} = 3.95$ ,  $p < 0.0001$ ). The three-way interaction of change in depth, dissolved oxygen, and chlorophyll *a* was not significant (Table 2.1, ANOVA,  $F_{6,72} \leq 1.51$ ,  $p \geq 0.1859$ ). Median depth was lowest in winter in the pond along the edge and highest in fall in the bay in open water (ANOVA,  $F_{6,72} = 7.31$ ,  $p < 0.0001$ ). Temperature was lowest in winter in the channel in open water and highest in summer in the bay in open water (ANOVA,  $F_{6,72} = 5.85$ ,  $p < 0.0001$ ). Salinity was lowest in winter in the pond in open water and highest in fall, also in the pond in open water (ANOVA,  $F_{6,72} = 7.73$ ,  $p < 0.0001$ ). Turbidity was lowest in summer in the pond in open water and highest in winter in the channel along the edge (ANOVA,  $F_{6,72} = 2.25$ ,  $p = 0.0475$ ). Distance to the marsh edge was lowest in winter in the channel and highest in fall in the bay in open water (ANOVA,  $F_{6,72} = 8.53$ ,  $p < 0.0001$ ).

Total nekton captures were different among habitat types, locations, and seasons. In 96 drop samples, 1002 individuals belonging to 19 fish and 6 macroinvertebrate species were identified (Table 2.2). In general, nekton abundance (individuals  $m^{-2}$ ) was higher along the marsh edge than in open water, since 57% of fishes and 68% of macroinvertebrates were found along the marsh edge. Fish abundance was higher in the channel (53%) than in the bay (43%) or the pond (4%) and so was macroinvertebrate abundance with 42%, 33%, and 25% of the individuals respectively. Fish abundance peaked in summer (41%) and declined through fall (37%), winter (16%), and spring (6%). Macroinvertebrate abundance was highest in winter (63%), dropped off in spring

Table 2.1. Means of the environmental variables by season, location, and habitat type, estimated by least square means ( $\pm$  SE). Pairwise comparisons (Tukey's adjustment) are represented by letters reading vertically for each environmental variable with a significant three-way interaction ( $p \leq 0.05$ ). Each mean is the average of 4 samples for a total of 96 samples.

Season	Location	Habitat	Median depth (cm)	$\Delta$ depth (cm)	Temperature ( $^{\circ}$ C)	Salinity (psu)	Dissolved Oxygen (ppm)	Turbidity (NTU)	Chlorophyll <i>a</i> ( $\mu$ g/l)	Distance to the marsh edge (m)	
Fall	Bay	Edge	37.7 $\pm$ 3.07 A	4.5 $\pm$ 0.87	26.2 $\pm$ 0.10 A	10.7 $\pm$ 0.33 AB	6.9 $\pm$ 0.29	22.0 $\pm$ 2.40 AB	31.2 $\pm$ 2.12	0.5 $\pm$ 0.16	A
		Open	80.0 $\pm$ 3.49 B	5.0 $\pm$ 1.47	31.4 $\pm$ 0.34 B	10.1 $\pm$ 0.44 AB	8.1 $\pm$ 0.36	9.5 $\pm$ 0.64 AC	33.7 $\pm$ 0.05	104.5 $\pm$ 18.80 B	
	Channel	Edge	36.5 $\pm$ 3.06 A	4.0 $\pm$ 1.22	28.3 $\pm$ 0.16 AB	10.7 $\pm$ 0.07 AB	7.5 $\pm$ 0.36	38.5 $\pm$ 3.50 AB	30.6 $\pm$ 4.36	0.58 $\pm$ 0.20	A
		Open	54.4 $\pm$ 6.92 AB	4.2 $\pm$ 0.75	24.1 $\pm$ 2.57 AD	19.6 $\pm$ 2.88 CB	7.2 $\pm$ 0.68	10.1 $\pm$ 3.09 AC	33.8 $\pm$ 0.05	17.0 $\pm$ 9.39	CD
	Pond	Edge	36.0 $\pm$ 3.36 A	5.5 $\pm$ 1.55	25.2 $\pm$ 1.43 AD	14.8 $\pm$ 3.29 B	6.8 $\pm$ 0.30	37.7 $\pm$ 16.17 AB	39.6 $\pm$ 3.50	0.5 $\pm$ 0.18	A
		Open	34.9 $\pm$ 2.69 A	3.7 $\pm$ 0.48	23.5 $\pm$ 1.34 AD	21.2 $\pm$ 0.06 C	6.9 $\pm$ 0.73	16.5 $\pm$ 3.20 A	33.9 $\pm$ 0.04	4.6 $\pm$ 1.27	E
Winter	Bay	Edge	14.7 $\pm$ 1.05 C	3.0 $\pm$ 1.68	25.3 $\pm$ 0.37 AD	9.8 $\pm$ 0.23 AB	7.4 $\pm$ 0.58	43.2 $\pm$ 3.75 AB	5.1 $\pm$ 0.07	0.6 $\pm$ 0.10	A
		Open	18.2 $\pm$ 1.66 CD	3.0 $\pm$ 0.91	15.0 $\pm$ 0.22 C	4.9 $\pm$ 1.18 DE	7.6 $\pm$ 0.06	15.7 $\pm$ 5.12 AC	5.6 $\pm$ 1.89	11.7 $\pm$ 6.29	DE
	Channel	Edge	17.0 $\pm$ 1.51 C	2.5 $\pm$ 0.64	21.8 $\pm$ 0.45 D	9.5 $\pm$ 0.06 AB	6.5 $\pm$ 0.20	54.7 $\pm$ 4.50 B	5.2 $\pm$ 0.13	0.2 $\pm$ 0.05	A
		Open	20.1 $\pm$ 0.99 CD	3.2 $\pm$ 0.63	12.7 $\pm$ 0.72 C	5.1 $\pm$ 0.08 DE	7.3 $\pm$ 0.14	22.2 $\pm$ 1.65 AB	4.3 $\pm$ 0.44	16.7 $\pm$ 1.38	CD
	Pond	Edge	10.6 $\pm$ 1.31 C	1.7 $\pm$ 0.25	25.6 $\pm$ 0.22 AD	8.6 $\pm$ 0.15 A	6.9 $\pm$ 0.13	30.5 $\pm$ 6.61 AB	5.0 $\pm$ 0.04	0.5 $\pm$ 0.05	A
		Open	21.5 $\pm$ 0.64 CD	2.7 $\pm$ 0.75	13.5 $\pm$ 0.20 C	3.3 $\pm$ 0.06 D	7.8 $\pm$ 0.06	16.5 $\pm$ 0.64 A	4.9 $\pm$ 0.06	8.2 $\pm$ 0.63	DE
Spring	Bay	Edge	44.6 $\pm$ 2.25 A	2.7 $\pm$ 0.75	22.8 $\pm$ 1.10 AD	7.0 $\pm$ 0.49 AE	7.5 $\pm$ 0.25	10.2 $\pm$ 2.89 AC	4.9 $\pm$ 0.81	0.6 $\pm$ 0.18	A
		Open	66.0 $\pm$ 3.96 B	2.5 $\pm$ 0.29	23.8 $\pm$ 0.60 AD	7.2 $\pm$ 0.32 AE	7.7 $\pm$ 0.15	10.9 $\pm$ 2.27 AC	5.0 $\pm$ 0.60	23.7 $\pm$ 2.39	C
	Channel	Edge	35.1 $\pm$ 0.55 A	1.7 $\pm$ 0.48	25.4 $\pm$ 0.06 AD	7.2 $\pm$ 0.06 AE	7.5 $\pm$ 0.26	7.1 $\pm$ 0.64 AC	8.2 $\pm$ 1.30	0.2 $\pm$ 0.09	A
		Open	35.5 $\pm$ 0.89 A	1.5 $\pm$ 0.29	21.4 $\pm$ 0.22 D	6.7 $\pm$ 0.09 AE	7.7 $\pm$ 0.17	21.7 $\pm$ 5.18 AB	11.6 $\pm$ 1.70	12.2 $\pm$ 1.25	DE
	Pond	Edge	29.2 $\pm$ 5.78 AD	2.0 $\pm$ 0.00	23.3 $\pm$ 0.38 AD	4.1 $\pm$ 0.12 DE	8.7 $\pm$ 0.38	38.6 $\pm$ 7.00 AB	6.0 $\pm$ 0.58	0.2 $\pm$ 0.04	A
		Open	52.9 $\pm$ 2.00 AB	2.7 $\pm$ 0.49	24.5 $\pm$ 0.06 AD	4.5 $\pm$ 1.15 DE	7.6 $\pm$ 0.36	42.7 $\pm$ 5.37 AB	5.7 $\pm$ 0.74	7.0 $\pm$ 0.41	DE
Summer	Bay	Edge	29.7 $\pm$ 2.56 AD	3.5 $\pm$ 1.5	32.2 $\pm$ 0.48 B	5.2 $\pm$ 0.13 E	5.7 $\pm$ 0.80	5.0 $\pm$ 5.86 C	6.8 $\pm$ 0.06	0.3 $\pm$ 0.08	A
		Open	57.6 $\pm$ 5.12 AB	4.7 $\pm$ 1.75	33.2 $\pm$ 0.06 B	8.0 $\pm$ 0.05 A	8.6 $\pm$ 0.30	2.2 $\pm$ 0.41 CD	6.8 $\pm$ 0.06	53.7 $\pm$ 15.73	BC
	Channel	Edge	37.4 $\pm$ 0.90 A	1.7 $\pm$ 0.25	30.4 $\pm$ 0.40 AB	8.5 $\pm$ 0.39 A	6.7 $\pm$ 0.71	6.4 $\pm$ 1.54 CA	6.8 $\pm$ 0.06	0.4 $\pm$ 0.08	A
		Open	41.0 $\pm$ 3.32 A	1.5 $\pm$ 0.29	33.0 $\pm$ 0.16 B	6.7 $\pm$ 0.43 AE	7.4 $\pm$ 0.17	1.6 $\pm$ 0.25 CD	6.8 $\pm$ 0.06	8.7 $\pm$ 0.48	DE
	Pond	Edge	43.4 $\pm$ 1.03 A	1.7 $\pm$ 0.25	28.3 $\pm$ 0.34 AB	4.8 $\pm$ 0.34 DE	4.5 $\pm$ 0.37	1.8 $\pm$ 0.40 CD	6.8 $\pm$ 0.06	0.6 $\pm$ 0.02	A
		Open	52.7 $\pm$ 2.06 AB	2.0 $\pm$ 0.00	29.3 $\pm$ 0.18 AB	6.6 $\pm$ 0.62 AD	5.4 $\pm$ 0.37	1.0 $\pm$ 0.13 D	7.0 $\pm$ 0.06	11.0 $\pm$ 1.29	DE

Table 2.2. Nekton abundance ranking, percentage frequency of occurrence (%F) in the experimental samples, size range (in mm, standard length for fishes, total length for shrimp and carapace width for crabs), and mean density (individuals m<sup>-2</sup>, mean of 96 samples) of the fishes and macroinvertebrates collected in the marsh-edge and open-water habitat types. Species selected for detailed statistical examination identified by an asterisk.

Species	Common name	N	%F	Size range	Mean density ( $\pm$ SE)		
					Marsh edge	Open water	Combined
<i>Palaemonetes pugio</i> *	Daggerblade grass shrimp	396	34.4	10-45	5.139 $\pm$ 0.232	1.736 $\pm$ 0.099	3.438 $\pm$ 0.091
<i>Anchoa mitchilli</i> *	Bay anchovy	217	31.2	11-54	2.726 $\pm$ 0.163	1.042 $\pm$ 0.051	1.884 $\pm$ 0.061
<i>Callinectes sapidus</i> *	Common blue crab	137	43.7	5-50	1.111 $\pm$ 0.051	1.267 $\pm$ 0.041	1.189 $\pm$ 0.023
<i>Farfantepenaeus aztecus</i> *	Brown shrimp	104	33.3	12-91	1.215 $\pm$ 0.056	0.590 $\pm$ 0.022	0.903 $\pm$ 0.021
<i>Gobiosoma bosc</i> *	Naked goby	42	20.8	12-43	0.191 $\pm$ 0.011	0.538 $\pm$ 0.027	0.365 $\pm$ 0.010
<i>Ctenogobius boleosoma</i> *	Darter goby	18	13.5	17-47	0.052 $\pm$ 0.004	0.260 $\pm$ 0.013	0.156 $\pm$ 0.005
<i>Pogonias cromis</i>	Black drum	18	1.0	19-33	0	0.313 $\pm$ 0.045	0.156 $\pm$ 0.016
<i>Cynoscion nebulosus</i>	Spotted seatrout	12	7.3	12-63	0.191 $\pm$ 0.011	0.017 $\pm$ 0.003	0.104 $\pm$ 0.004
<i>Rhithropanopeus harrissi</i>	Harris' mud crab	11	4.2	4-12	0.174 $\pm$ 0.016	0.017 $\pm$ 0.003	0.095 $\pm$ 0.006
<i>Micropogonias undulatus</i>	Atlantic croaker	8	2.1	22-38	0	0.139 $\pm$ 0.016	0.069 $\pm$ 0.006
<i>Fundulus heteroclitus heteroclitus</i>	Mummichog	5	2.1	45-65	0.069 $\pm$ 0.010	0.017 $\pm$ 0.003	0.043 $\pm$ 0.004
<i>Microgobius thalassinus</i>	Green goby	4	3.1	29-42	0.017 $\pm$ 0.003	0.052 $\pm$ 0.006	0.035 $\pm$ 0.002
<i>Membras martinica</i>	Rough silverside	4	3.1	47-71	0.069 $\pm$ 0.006	0	0.035 $\pm$ 0.002
<i>Panopeus herbstii</i>	Common mud crab	4	3.1	5-8	0.052 $\pm$ 0.006	0.017 $\pm$ 0.003	0.035 $\pm$ 0.002
<i>Cynoscion arenarius</i>	Sand seatrout	3	3.1	32-51	0.017 $\pm$ 0.003	0.035 $\pm$ 0.004	0.026 $\pm$ 0.002
<i>Leiostomus xanthurus</i>	Spot	3	3.1	28-83	0.035 $\pm$ 0.004	0.017 $\pm$ 0.003	0.026 $\pm$ 0.002
<i>Myrophis punctatus</i>	Speckled worm eel	3	3.1	52-115	0.017 $\pm$ 0.003	0.035 $\pm$ 0.004	0.026 $\pm$ 0.002
<i>Bairdiella chrysoura</i>	Silver perch	2	2.1	31-33	0.017 $\pm$ 0.003	0.017 $\pm$ 0.003	0.017 $\pm$ 0.001
<i>Symphurus plagiura</i>	Blackcheek tonguefish	2	2.1	12-51	0.017 $\pm$ 0.003	0.017 $\pm$ 0.003	0.017 $\pm$ 0.001
<i>Menidia beryllina</i>	Inland silverside	2	2.1	31-62	0.035 $\pm$ 0.004	0	0.017 $\pm$ 0.001
<i>Gobionellus oceanicus</i>	Highpin goby	2	2.1	43-178	0	0.035 $\pm$ 0.004	0.017 $\pm$ 0.001
<i>Litopenaeus setiferus</i>	White shrimp	2	2.1	28-35	0	0.035 $\pm$ 0.004	0.017 $\pm$ 0.001
<i>Brevoortia tyrannus</i>	Atlantic menhaden	1	1.0	33	0.017 $\pm$ 0.003	0	0.009 $\pm$ 0.001
<i>Stellifer lanceolatus</i>	Star drum	1	1.0	43	0	0.017 $\pm$ 0.003	0.009 $\pm$ 0.001
<i>Citharichthys spilopterus</i>	Bay whiff	1	1.0	14	0	0.017 $\pm$ 0.003	0.009 $\pm$ 0.001
Number of species					19	22	25

(8%) and summer (5%), and rose again in the fall (24%). Sixteen of 25 fish and macroinvertebrate species were found in both marsh edge and open-water habitat types (Table 2.2) and half of these species were more abundant along the marsh edge. Of the rest, three species were found exclusively along the marsh edge and six in open water.

Species richness, evenness, diversity and the abundance of assemblage groups varied throughout the year among habitat types and locations (MANOVA,  $F_{6, 65} = 1.98$ ,  $p = 0.0003$ ). However, univariate three-way interactions for the assemblage groups were not significantly different (ANOVA,  $F_{6, 72} \leq 2.08$ ,  $p \geq 0.0656$ ). Species richness and evenness were lowest in winter in the pond in open water and highest in fall in the bay in open water (Table 2.3, ANOVA,  $F_{6, 72} = 2.41$ ,  $p = 0.0356$  and  $F_{6, 72} = 2.33$ ,  $p = 0.0412$ , respectively). Diversity was also highest in fall in the bay in open water, but was lowest in summer in the channel along the edge (ANOVA,  $F_{6, 72} = 3.56$ ,  $p = 0.0038$ ). Most of the individuals captured were juveniles and their sizes were different among seasons, but were not different among habitat types and locations. More than half (52%) of captured bay anchovy were between 10 and 19 mm SL, 86% of naked goby were 10 to 29 SL, 56% of darter goby were 20 to 29 SL, 47% of brown shrimp were 10 to 29 TL, 62% of grass shrimp were 20 to 29 TL, and 55% of blue crab were 10-19 CW (Figure 2.2).

Mean densities of the most abundant species including naked goby, darter goby, and brown shrimp varied throughout the year among locations and habitat types (MANOVA,  $F_{6, 65} = 3.31$ ,  $p < 0.0001$ ). In the univariate analyses, the three-way interaction was not significant for bay anchovy, grass shrimp, and blue crab ( $F_{6, 72} \geq 1.79$ ,  $p \geq 0.1138$ ). Darter goby was present in some fall and winter samples, but was absent in spring and summer samples (Table 2.4). Darter goby density was equally low in fall in



Table 2.3. Mean densities of the assemblage groups, species richness, evenness, and diversity indices by season, location and habitat, estimated by least square means ( $\pm$  SE). Posterior pairwise comparisons (Tukey's adjustment) represented by letters reading vertically for each species with a significant three-way interaction ( $p \leq 0.05$ ). Each mean is the average of 4 samples for a total of 96 samples.

Season	Location	Habitat	Total fishes	Pelagic fishes	Demersal fishes	Total invertebrates	Total nekton	Richness	Evenness	Diversity
Fall	Bay	Edge	9.3 $\pm$ 5.48	7.6 $\pm$ 4.73	1.7 $\pm$ 1.04	5.1 $\pm$ 1.99	14.4 $\pm$ 5.01	3.0 $\pm$ 0.81 A	1.1 $\pm$ 0.30 A	0.7 $\pm$ 0.28 AB
		Open	11.6 $\pm$ 1.52	7.2 $\pm$ 1.64	4.5 $\pm$ 1.48	3.4 $\pm$ 0.91	15.0 $\pm$ 1.17	4.5 $\pm$ 0.72 A	1.6 $\pm$ 0.26 A	1.2 $\pm$ 0.16 A
	Channel	Edge	1.5 $\pm$ 0.72	0.4 $\pm$ 0.24	1.1 $\pm$ 0.64	9.7 $\pm$ 2.03	11.2 $\pm$ 1.84	1.9 $\pm$ 0.41 AB	0.7 $\pm$ 0.15 AB	0.4 $\pm$ 0.18 AB
		Open	3.8 $\pm$ 1.75	1.5 $\pm$ 1.48	2.3 $\pm$ 1.22	1.7 $\pm$ 0.35	5.5 $\pm$ 1.57	2.3 $\pm$ 0.41 AB	0.8 $\pm$ 0.15 AB	0.8 $\pm$ 0.16 AB
	Pond	Edge	0.2 $\pm$ 0.21		0.2 $\pm$ 0.21	8.0 $\pm$ 4.38	8.3 $\pm$ 4.30	1.5 $\pm$ 0.64 AB	0.5 $\pm$ 0.23 B	0.5 $\pm$ 0.27 AB
		Open	0.8 $\pm$ 0.35		0.8 $\pm$ 0.35	5.3 $\pm$ 0.80	6.1 $\pm$ 0.87	2.3 $\pm$ 0.40 AB	0.8 $\pm$ 0.15 AB	0.8 $\pm$ 0.18 AB
Winter	Bay	Edge	0.8 $\pm$ 0.35		0.8 $\pm$ 0.35	16.9 $\pm$ 6.81	17.8 $\pm$ 7.10	1.9 $\pm$ 0.63 AB	0.7 $\pm$ 0.23 AB	0.3 $\pm$ 0.16 AB
		Open	0.6 $\pm$ 0.41		0.6 $\pm$ 0.41	11.0 $\pm$ 5.10	11.6 $\pm$ 5.41	2.1 $\pm$ 0.55 AB	0.8 $\pm$ 0.20 AB	0.5 $\pm$ 0.21 AB
	Channel	Edge	1.7 $\pm$ 1.15		1.7 $\pm$ 1.15	25.2 $\pm$ 10.6	26.9 $\pm$ 11.63	2.3 $\pm$ 0.87 AB	0.8 $\pm$ 0.32 AB	0.5 $\pm$ 0.18 AB
		Open	8.9 $\pm$ 3.49		8.9 $\pm$ 3.49	16.1 $\pm$ 4.76	25.0 $\pm$ 8.15	3.6 $\pm$ 0.41 A	1.3 $\pm$ 0.15 A	1.2 $\pm$ 0.15 A
	Pond	Edge				16.3 $\pm$ 11.33	16.3 $\pm$ 11.33	0.8 $\pm$ 0.35 AB	0.3 $\pm$ 0.13 B	0.2 $\pm$ 0.16 B
		Open				1.3 $\pm$ 1.27	1.3 $\pm$ 1.27	0.4 $\pm$ 0.42 B	0.1 $\pm$ 0.15 B	0.2 $\pm$ 0.16 B
Spring	Bay	Edge	1.3 $\pm$ 1.55	1.1 $\pm$ 1.41	0.2 $\pm$ 0.21	2.1 $\pm$ 0.42	3.4 $\pm$ 0.60	1.7 $\pm$ 0.34 AB	0.6 $\pm$ 0.13 B	0.5 $\pm$ 0.21 AB
		Open	1.1 $\pm$ 0.63	1.1 $\pm$ 0.63		1.3 $\pm$ 1.73	2.3 $\pm$ 1.17	1.3 $\pm$ 0.55 AB	0.5 $\pm$ 0.20 B	0.4 $\pm$ 0.24 AB
	Channel	Edge	1.1 $\pm$ 0.21	1.1 $\pm$ 0.21		2.3 $\pm$ 0.53	3.4 $\pm$ 0.35	2.5 $\pm$ 0.00 A	0.9 $\pm$ 0.00 AB	1.0 $\pm$ 0.03 A
		Open	0.2 $\pm$ 0.21	0.2 $\pm$ 0.21		1.9 $\pm$ 0.72	2.1 $\pm$ 0.88	1.0 $\pm$ 0.53 AB	0.4 $\pm$ 0.19 B	0.3 $\pm$ 0.26 AB
	Pond	Edge	0.4 $\pm$ 0.42	0.4 $\pm$ 0.42		2.3 $\pm$ 0.41	2.7 $\pm$ 0.41	2.1 $\pm$ 0.42 AB	0.8 $\pm$ 0.15 AB	0.8 $\pm$ 0.19 AB
		Open	0.2 $\pm$ 0.21	0.2 $\pm$ 0.21		1.5 $\pm$ 0.41	1.7 $\pm$ 0.35	1.5 $\pm$ 0.21 AB	0.5 $\pm$ 0.08 B	0.5 $\pm$ 0.17 AB
Summer	Bay	Edge	4.2 $\pm$ 2.05	2.5 $\pm$ 2.54	1.7 $\pm$ 0.77	5.5 $\pm$ 2.80	9.7 $\pm$ 2.20	3.2 $\pm$ 0.21 A	1.2 $\pm$ 0.08 A	1.0 $\pm$ 0.12 A
		Open	2.7 $\pm$ 1.94	2.3 $\pm$ 1.81	0.4 $\pm$ 0.24	0.4 $\pm$ 0.24	3.2 $\pm$ 2.09	1.3 $\pm$ 0.55 AB	0.5 $\pm$ 0.20 B	0.3 $\pm$ 0.19 AB
	Channel	Edge	20.5 $\pm$ 9.31	20.3 $\pm$ 9.46	0.2 $\pm$ 0.21	0.2 $\pm$ 0.21	20.8 $\pm$ 9.43	1.1 $\pm$ 0.21 AB	0.4 $\pm$ 0.08 B	0.1 $\pm$ 0.03 B
		Open	1.3 $\pm$ 0.24	0.2 $\pm$ 0.21	1.1 $\pm$ 0.21	0.8 $\pm$ 0.60	2.1 $\pm$ 0.42	2.1 $\pm$ 0.42 AB	0.8 $\pm$ 0.15 AB	0.9 $\pm$ 0.17 AB
	Pond	Edge	1.3 $\pm$ 0.42	1.3 $\pm$ 0.42			1.3 $\pm$ 0.42	0.8 $\pm$ 0.00 B	0.3 $\pm$ 0.00 B	
		Open								

the bay in open water and in winter in the bay both along the edge and in open water. The highest density of this species was in winter in the channel in open water (ANOVA,  $F_{6, 72} = 2.41$ ,  $p = 0.0354$ ). Naked goby was absent in all spring samples and was present in just half of the samples taken in the other three seasons (Table 2.4). Naked goby density was lowest in summer in the channel along the edge and highest in fall in the bay in open water (ANOVA,  $F_{6, 72} = 2.89$ ,  $p = 0.0139$ ). Brown shrimp was absent in winter samples and was marginally captured in summer (Table 2.4). Brown shrimp density was lowest in spring in the pond in open water and highest in fall in the channel along the marsh edge (ANOVA,  $F_{6, 72} = 13.60$ ,  $p < 0.0001$ ).

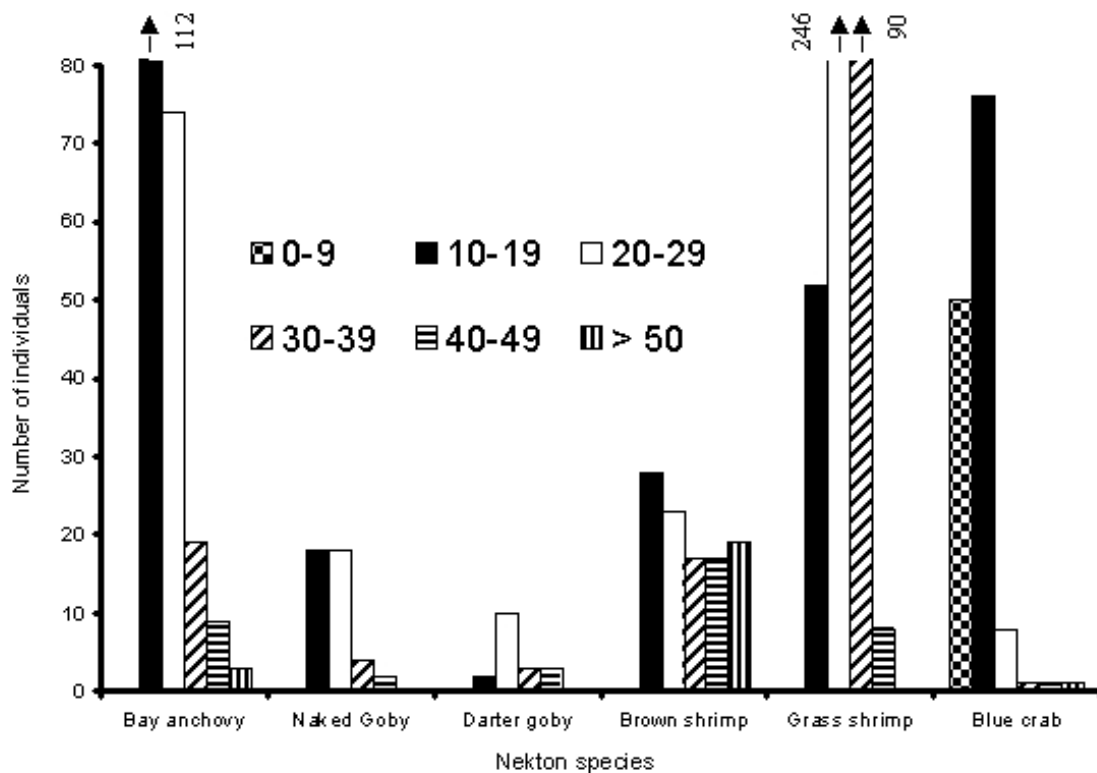


Figure 2.2. Size frequency distribution of the most abundant nekton species sampled in Terrebonne Bay, Louisiana. Nekton species were measured to the nearest mm of standard length for fishes, total length for shrimp, and carapace width for crabs.

Table 2.4. Mean densities of the most abundant species by season, location and habitat, estimated by least square means ( $\pm$  SE). Posterior pairwise comparisons (Tukey's adjustment) represented by letters reading vertically for each species with a significant three-way interaction ( $p \leq 0.05$ ). Each mean is the average of 4 samples for a total of 96 samples.

Season	Location	Habitat	Bay anchovy	Darter goby	Naked goby	Brown shrimp	Grass shrimp	Blue crab
Fall	Bay	Edge	7.6 $\pm$ 4.73		0.6 $\pm$ 0.64 A	0.8 $\pm$ 0.60 AB	2.5 $\pm$ 1.80	1.3 $\pm$ 1.01
		Open	7.2 $\pm$ 1.64	0.2 $\pm$ 0.21 A	3.0 $\pm$ 1.12 B	2.7 $\pm$ 0.72 BC	0.6 $\pm$ 0.41	
	Channel	Edge	0.2 $\pm$ 0.21			9.3 $\pm$ 1.66 D		0.4 $\pm$ 0.42
		Open	1.5 $\pm$ 1.48	0.4 $\pm$ 0.24 A	1.9 $\pm$ 1.36 AB		0.4 $\pm$ 0.42	1.3 $\pm$ 0.24
	Pond	Edge				0.8 $\pm$ 0.49 AB	3.4 $\pm$ 3.39	3.6 $\pm$ 2.41
		Open		0.4 $\pm$ 0.24 A		1.3 $\pm$ 0.55 AB		4.0 $\pm$ 1.22
Winter	Bay	Edge		0.2 $\pm$ 0.21 A	0.4 $\pm$ 0.24 A		16.1 $\pm$ 6.88	0.8 $\pm$ 0.60
		Open		0.2 $\pm$ 0.21 A	0.4 $\pm$ 0.42 A		7.8 $\pm$ 4.20	3.0 $\pm$ 1.00
	Channel	Edge		0.4 $\pm$ 0.24 A			19.7 $\pm$ 10.08	5.5 $\pm$ 2.46
		Open		1.9 $\pm$ 0.53 B	0.4 $\pm$ 0.42 A		11.2 $\pm$ 4.76	4.9 $\pm$ 1.17
	Pond	Edge					15.9 $\pm$ 11.51	0.4 $\pm$ 0.42
		Open					0.4 $\pm$ 0.42	0.8 $\pm$ 0.85
Spring	Bay	Edge	0.6 $\pm$ 0.41			2.1 $\pm$ 0.42 BC		
		Open	1.0 $\pm$ 0.64			0.8 $\pm$ 0.60 AB		0.4 $\pm$ 0.24
	Channel	Edge	0.85 $\pm$ 0.00			1.1 $\pm$ 0.41 AB	0.8 $\pm$ 0.60	0.4 $\pm$ 0.24
		Open	0.2 $\pm$ 0.21			1.5 $\pm$ 0.53 AB		0.4 $\pm$ 0.42
	Pond	Edge	0.2 $\pm$ 0.21			0.2 $\pm$ 0.21 A	1.5 $\pm$ 0.41	0.6 $\pm$ 0.21
		Open	0.2 $\pm$ 0.21			0.8 $\pm$ 0.35 AB	0.6 $\pm$ 0.21	
Summer	Bay	Edge	2.3 $\pm$ 2.33		1.1 $\pm$ 0.53 AB	0.4 $\pm$ 0.42 A	2.7 $\pm$ 2.45	0.2 $\pm$ 0.21
		Open	2.3 $\pm$ 1.81					0.4 $\pm$ 0.24
	Channel	Edge	20.3 $\pm$ 9.50		0.2 $\pm$ 0.21 A			0.2 $\pm$ 0.21
		Open	0.2 $\pm$ 0.21		0.8 $\pm$ 0.00 AB			0.2 $\pm$ 0.21
	Pond	Edge	1.1 $\pm$ 0.53					
		Open						

In the stepwise multiple regression analyses using eight environmental variables to predict the densities of assemblage groups, common species, and measures of diversity (Table 2.5), all 14 models were significant ( $F_{1,91} \leq 3.77$ ,  $P \leq 0.0490$ ). Although the best model explained 42 % of the variation, less than half of the models explained more than 20%. Many variables were included in the models, but the most notable had significant partial correlations (Table 2.5). The partial correlation of median depth was significant in all models except for richness, evenness, diversity, and the density of demersal fishes and darter goby. Most notably, according to the squared partial correlations, median depth explained 31% of daggerblade grass shrimp density variability, turbidity explained 24% of total macroinvertebrate density, and temperature explained 21% of blue crab density.

The common fish and macroinvertebrate species (i.e., with frequency of occurrence  $\geq 3\%$ , Table 2.1) used different resources (Figure 2.3a). The PCA of eight environmental variables identified only three factors with eigenvalues greater than one that collectively explained 67% of the variance (Table 2.6). Median depth and temperature loaded positively and turbidity loaded negatively on Factor 1, substrate relief ( $\Delta$  depth), salinity and chlorophyll *a* loaded positively on Factor 2, and dissolved oxygen and distance from the edge loaded positively on Factor 3. These three factors represented seasonal and spatial variations (Figure 2.3b). Darter goby, grass shrimp, and blue crab were found mostly in shallow, cool, turbid, and brackish waters (winter), whereas bay anchovy, naked goby, and brown shrimp were found in deeper, warmer, clearer, and more saline waters (spring and fall). Naked goby and darter goby were found in open water with relatively high oxygen levels, whereas bay anchovy, brown shrimp, and daggerblade grass shrimp were found nearer to the marsh edge.

Table 2.5 Stepwise multiple regression analyses of assemblage descriptors and considered species densities in relation to environmental variables. The variables are reported in the order they were entered by the model, which means that variable 1 has the highest overall F value ( $p \leq 0.05$ ). The nature of the relationship between the biological and environmental variables are represented by signs and the squared partial correlations are represented in parentheses. The significance level for variables retained in each model was  $P < 0.05$ , except for italicized variables ( $0.15 > P > 0.05$ ). High partial correlations indicated in bold print.

Season	R <sup>2</sup>	Variable 1	Variable 2	Variable 3	F value	P > F
Total nekton	0.16	+ Salinity (0.09)	- Median depth (0.07)		8.72	0.0003
Total fishes	0.07	+ Median depth (0.07)			7.46	0.0075
Pelagic fishes	0.19	+ Median depth (0.15)	+ Temperature (0.04)		11.26	< 0.0001
Demersal fishes	0.19	+ Distance (0.08)	+ $\Delta$ depth (0.05)		5.24	0.0008
Total macroinvertebrates	0.36	+ <b>Turbidity (0.24)</b>	- Median depth (0.06)	+ Salinity (0.06)	14.20	< 0.0001
Richness	0.08	+ <i>Dissolved oxygen (0.04)</i>	+ <i>Salinity (0.04)</i>		3.88	0.0240
Evenness	0.07	+ Dissolved oxygen (0.04)	+ <i>Salinity (0.03)</i>		3.77	0.0490
Diversity	0.06	+ Dissolved oxygen (0.06)			4.45	0.0142
Bay anchovy	0.18	+ Median depth (0.14)	+ Temperature (0.04)		10.52	< 0.0001
Darter goby	0.28	- Temperature (0.17)	+ Salinity (0.04)	+ Distance (0.04)	10.54	< 0.0001
Naked goby	0.13	+ Distance (0.09)	+ <i>Salinity (0.04)</i>		7.09	0.0014
Brown shrimp	0.29	+ Chlorophyll <i>a</i> (0.11)	+ Turbidity (0.06)	+ Median depth (0.12)	12.30	< 0.0001
Daggerblade grass shrimp	0.36	- <b>Median depth (0.31)</b>	+ <i>Chlorophyll a (0.03)</i>	+ <i>Turbidity (0.02)</i>	14.13	< 0.0001
Blue crab	0.42	- <b>Temperature (0.21)</b>	+ Salinity (0.18)		18.05	< 0.0001

Table 2.6. The rotated factors loadings from a principal component analysis for fishes and macroinvertebrates. Magnitude and signs of loadings indicate strength and direction of each variable's influence on a principal component. Loadings in bold were used to characterize factors.

Environmental variable	Principal component factors		
	1	2	3
Turbidity	<b>-0.85</b>	0.19	0.13
Median depth	<b>0.79</b>	0.25	0.31
Temperature	<b>0.62</b>	0.41	-0.30
Salinity	-0.02	<b>0.83</b>	-0.03
Chlorophyll <i>a</i>	0.37	<b>0.63</b>	-0.13
$\Delta$ depth	-0.12	<b>0.58</b>	0.43
Distance from edge	0.46	-0.12	<b>0.76</b>
Dissolved oxygen	-0.22	0.03	<b>0.74</b>
Variance explained	2.37	1.54	1.48
Proportion of variance explained	0.30	0.19	0.18
Cumulative proportion explained	0.30	0.49	0.67

## Discussion

For the community and its components, patterns of variation indicated differences among marsh edge and open water and seasons, and across a landscape gradient.

Densities of resident and transient species including darter goby, naked goby, and brown shrimp were significantly different among habitat types, seasons, and locations.

Macroinvertebrate densities were influenced mainly by turbidity, median depth and temperature. The marsh edge is essential for food and refuge for estuarine nekton, but macroinvertebrate species may be more sensitive to marsh loss than fish species.

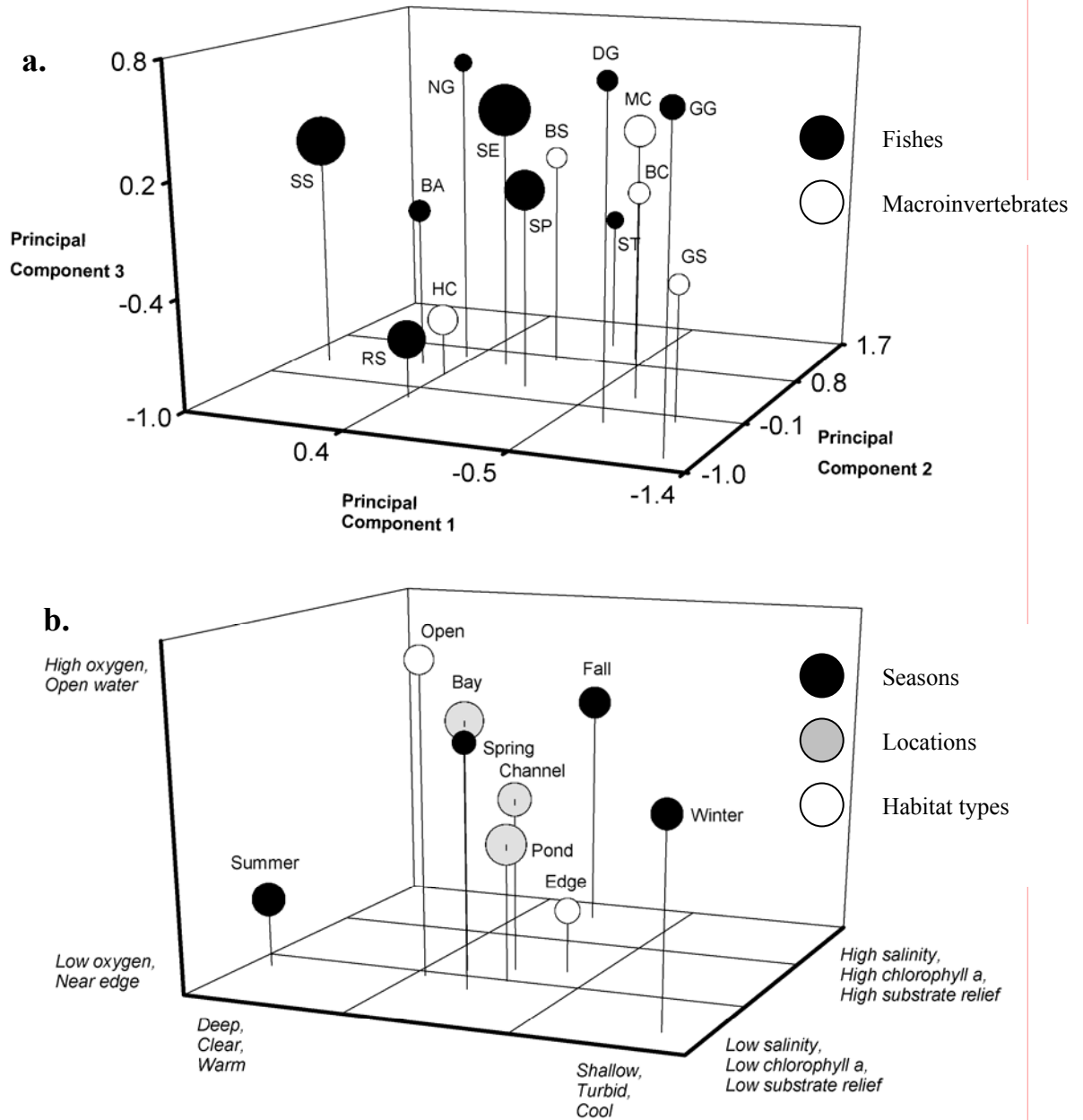


Figure 2.3. Resource use patterns of fishes and macroinvertebrates in Terrebonne Bay, Louisiana. (a) The location of centroids of each species are plotted in three-dimensional factor space with balloon radii representing one SE about the mean. Species codes are: BA = bay anchovy, BC = blue crab, BS = brown shrimp, DG = darter goby, HC = Harris' mud crab, GG = green goby, GS = daggerblade grass shrimp, MC = common mud crab, NG = naked goby, RS = rough silverside, SE = speckled worm eel, SP = spot, SS = sand seatrout, and ST = spotted seatrout. (b) Main factors are plotted to facilitate visualization of species resource use.

## Marsh Edge Versus Open Water

Estuarine residents such as darter goby and naked goby were more abundant in open water than along the marsh edge. In contrast, darter goby is more abundant in the marsh edge in Galveston, Texas (Rozas and Zimmerman 2000), more abundant in vegetated areas than in unvegetated areas in New Jersey estuaries (Sogard 1992), and is abundant in shallow waters in Louisiana (Baltz *et al.* 2003, Jones and Baltz 2002). Nevertheless, open water is important especially when marsh inundation is low (Childers *et al.* 1990). Minello *et al.* (1994) suggested that increasing the creek-marsh edge ratio results in an increase of fish densities, whereas invertebrate densities decrease. In contrast, a transient species such as bay anchovy was equally abundant along the marsh edge and in open water. Bay anchovy densities are generally higher in the open water (Minello *et al.* 1994, Rozas and Zimmerman 2000, Zimmerman *et al.* 1990), but Weinstein and Brooks (1983) suggested that bay anchovy is more abundant in the marsh edge when there is no submerged aquatic vegetation available.

A transient species such as brown shrimp was more abundant along the marsh edge. In other studies, brown shrimp are more abundant in the marsh edge than in the open areas as well (Minello *et al.* 1994, Zimmerman and Minello 1984). In contrast, Baltz *et al.* (in review), and Fry *et al.* (2003) did not detect abundance differences of this species between these two habitat types. A resident species such as daggerblade grass shrimp was not significantly more abundant in the marsh edge than in the open water, even in winter, when the marsh edge is subject to low flood duration (Shirzad *et al.* 1989), and larger nekton must retreat to subtidal areas (Kneib 1987). Daggerblade grass shrimp are more abundant along the marsh edge in small saltmarsh ponds in Louisiana



(Baltz *et al.* in review), in Galveston Bay (Minello *et al.* 1994, Rozas and Zimmerman 2000), and Lavaca Bays, Texas (Zimmerman *et al.* 1990), and in North Inlet, South Carolina (Porthouse 1996).

In general, species richness, evenness, and diversity were higher in open water than along the marsh edge. According with Minello and Webb (1997), fishes are more abundant in deep waters than macroinvertebrates. In contrast, in a salt marsh in Queensland, Australia, species richness and the density of common species is not different between vegetated and unvegetated habitats (Thomas and Connolly 2001). Although, Szedlmayer and Able (1996) suggested that species richness is positively related to habitat structural heterogeneity, results of this study do not support this pattern.

### **Seasonal Variation**

In this study, total fish and invertebrate densities were not different among seasons. However, only daggerblade grass shrimp and blue crab were captured throughout the year, whereas bay anchovy, naked goby, darter goby, and brown shrimp were absent in one or more seasons. In contrast Baltz and Jones (2003) and Jones *et al.* (2002) captured these species in all seasons in Barataria Bay and Vermilion-West Cote Blanche Bay, Louisiana, respectively. According with Minello (1999), macroinvertebrates are more abundant in estuaries, but fishes are more diverse. Species richness, evenness, and diversity were higher in fall, whereas Baltz *et al.* (1993) found higher fish densities in spring and summer declining in fall and winter.

Although naked goby and darter goby are considered estuarine residents (Baltz *et al.* 1993), these species were not sampled throughout the year in the present study. Darter goby was captured in fall and winter only and was more abundant in winter. In

winter, water levels are lowest when frontal passages of northerly winds push the shallow waters offshore (Chuang and Wiseman 1983). Peterson and Turner (1994) sampled monthly in a marsh close to my study area, and only found darter goby in fall and winter as well. In Barataria Bay, Louisiana, Jones *et al.* (2002) found high abundances of darter goby in winter also, but they found this species in summer in offshore samples. Rakocinski *et al.* (1992) sampled in spring and summer in the Barataria Basin and in both seasons, darter goby had the highest frequency of occurrence. Naked goby was abundant in fall and was absent in spring. In shallow habitat types, naked goby is the most abundant fish species in Texas and Louisiana (Minello 1999) and naked goby and darter goby are the most abundant fish species in Louisiana in spring (Baltz *et al.* 1993). Nevertheless, naked goby larvae are more abundant at the end of spring (Hendon *et al.* 2000, 2001), and mature adults may move to deeper waters within the estuary in this season, explaining the absence of this species in such as shallow water samples in spring.

Although bay anchovy was not present in winter samples, this species was similarly abundant the rest of the seasons. Jones *et al.* (2002) found higher abundances of bay anchovy in summer, whereas Baltz and Jones (2003) found higher abundances of bay anchovy in winter. Nevertheless, bay anchovy is a highly mobile and gregarious species (Blaxter and Hunter 1982), which may influence its capture densities between analogous studies. Larvae and juveniles of transient estuarine fishes and macroinvertebrates that spawn offshore such as bay anchovy and brown shrimp (Rozas and Minello 1997) eventually move into the estuary (Jones *et al.* 2002) resulting in highly seasonal fluctuations in abundance (Peterson and Turner 1994).

Brown shrimp were more abundant in fall (mainly adults) and were associated to chlorophyll *a*, turbidity, and median depth. Brown shrimp have also been found in higher abundances in fall and related to high turbidity levels (Minello and Webb 1997). Experiments with brown shrimp suggest that turbid water and a suitable substratum for burrowing reduces brown shrimp predation (Minello *et al.* 1987). In contrast, Jones *et al.* (2002) reported that brown shrimp are more abundant in spring and summer and are associated with depth and temperature, and Baltz and Jones (2003) found higher abundances of brown shrimp in summer and were associated with depth, salinity, and temperature. In general, brown shrimp are more abundant in spring and summer, since there is a higher abundance of juveniles (Minello 1999, Rozas 1992), and adults decline in fall due to fishing mortality (Jones *et al.* 2002). Nevertheless, predation is usually the main cause of brown shrimp mortality when there is limited access to intertidal vegetation (Minello *et al.* 1989).

Daggerblade grass shrimp was the most abundant species throughout the year and its abundance was related to shallow, turbid and cool waters. Also in Louisiana, daggerblade grass shrimp were associated with shallow water (Baltz *et al.* in review). Daggerblade grass shrimp is the most abundant nekton species in Texas and Louisiana estuaries and is associated with the marsh edge (Minello 1999). Nevertheless, daggerblade grass shrimp are found in low densities (Rozas and Minello 2001) or are smaller (Minello and Webb 1997) in marsh terraces (a wetland restoration tool) than in natural marshes. Zimmerman and Minello (1984) could not find any relationship between the abundances of daggerblade grass shrimp and environmental variables such as temperature, density, and water level. They attribute this to the broad tolerance range of

this species. The higher abundances of daggerblade grass shrimp in turbid and shallow waters in the present study (Figure 2.3) may be due to predation pressure (Ruiz *et al.* 1993).

Blue crab was similarly abundant in all seasons and was related with shallow, cool, and salty waters. Blue crab is more abundant in winter in Barataria Basin, Louisiana (Jones *et al.* 2002) and in Galveston Island, Texas (Zimmerman and Minello 1984) and these high abundances are related to shallow and cool waters in Louisiana and to changes in temperature, salinity, and water levels in Texas. Baltz and Jones (2003) found higher abundances of blue crab in winter, but in low salinities, since they sampled in the Atchafalaya Basin, Louisiana, an area with unusually high inputs of fresh water due to diversion in the Mississippi River flow (Baltz *et al.* 1993). Blue crab was also associated with shallow water in small ponds (Baltz *et al.* in review) and is the most abundant crustacean in shallow water, but mainly in fall in Louisiana and Texas (Minello 1999). Blue crab can tolerate desiccation and can move over dry marsh surfaces for short distances (Minello *et al.* 1994), which allows them to explore all marsh habitat types, including the marsh interior (Peterson and Turner 1994). Thomas *et al.* (1990) concluded that saltmarsh utilization by blue crab is favored by marsh edge, low tidal amplitudes, and long periods of tidal inundation.

### **Location Variation**

Darter goby and brown shrimp densities were highest in the channel, whereas naked goby densities were highest in the bay. In Galveston Bay, Texas Rozas and Zimmerman (2000) also found higher densities of darter goby in a channel, but naked goby densities were higher in a channel and brown shrimp in a shallow bay. Also in

Galveston Bay, naked goby and brown shrimp were more abundant in an experimental channel than in an adjacent bay (Minello *et al.* 1994). In Louisiana, brown shrimp < 40 mm and between 50-69 mm TL were more abundant in ponds, between 40-49 and 70-79 mm in a shallow channel, between 80-89 mm in a bay, and > 90 mm in a deep channel (Fry *et al.* 2003). The main difference between this study and other studies is that naked goby was more abundant in the bay than in the channel or the pond. Territorial behavior may be the factor influencing little movement of naked goby among locations (Dahlberg and Conyers 1973).

Understanding nekton abundance and distribution in various marsh habitat types is important to assess the value of the marsh for fisheries production (Hettler 1989). Although that density patterns may not conclusively determine whether a habitat type is essential for a species, habitats with high densities are more likely to be essential for that species (Minello 1999). Although the marsh edge is essential for several resident and transient species of commercial and ecological importance, the adjacent open water is also important for estuarine residents such as darter goby and naked goby. Louisiana fishery landings have not been reduced even with wetland loss, but fish production may have shifted from species requiring marsh edge to open water forms (Chesney *et al.* 2000). On the other hand, estuarine-dependent residents and transients move regularly between flooded *Spartina* and adjacent open-water habitats (Hettler 1989) and as fishes and macroinvertebrates increase in size, there is a habitat shift from the shallow marsh edge to deeper subtidal areas (Baltz *et al.* 1993).

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## CHAPTER III.

### FEEDING ECOLOGY OF FISHES RESIDING IN MARSH-EDGE AND ADJACENT OPEN-WATER HABITAT TYPES IN A LOUISIANA ESTUARY

#### Introduction

Estuarine-marsh ecosystems are essential not only for providing refuge to large numbers of juvenile fishes and invertebrates, but also as a food sources for resident and transient nekton species (Day *et al.* 1989). Estuarine fishes have broad trophic spectra (Darnell 1958, 1961), and food resources are patchily distributed (Lewis and Eby 2002, Whaley and Minello 2002). Meiofauna, specifically harpacticoid copepods, are the main prey items consumed by many benthic feeders and juvenile fishes (Alheit and Scheibel 1982). Harpacticoid copepods are aggregated in small patches within a habitat type (Sun and Fleeger 1991) due in part to their feeding behavior when seeking dense patches of diatoms (Decho and Fleeger 1988) and to hydrodynamic effects (Fleeger *et al.* 1995). Thus, determination of the availability of potential prey for estuarine fishes among habitat types is a compound problem.

Although several studies suggest that fishes are less effective predators in *Spartina* marshes (Minello and Zimmerman 1983, Stunz and Minello 2001), food resources for fishes are more abundant in vegetated habitat types (Whaley and Minello 2002). Estuarine fishes may utilize limited food resources more effectively in vegetated than in non-vegetated habitat types (Levin *et al.* 1997). Prey volumes of gulf killifish, *Fundulus grandis*, are significantly greater when they have access to the marsh surface in St. Louis Bay, Mississippi (Rozas and LaSalle 1990). Also, mummichog, *Fundulus heteroclitus*, growth rates are higher for individuals that have access to inundated marsh than for individuals that are restricted to the subtidal habitat types (Weisberg and Lotrich

1982). Moreover, fishes captured in areas with submerged aquatic vegetation have significantly more food in their stomachs than fishes captured in non-vegetated areas in northern Chesapeake Bay (Lubbers *et al.* 1990).

Specific prey distribution patterns may give some insights into the relative selection of food by estuarine fishes. In a South Carolina estuary, juvenile spot feed at high tide on the marsh surface as evidenced by stomach contents composed of two harpacticoid copepod species (*Mesochra mexicana* and *Quinquelaophonte capillata*) that reside only in this habitat type (Feller *et al.* 1990); spot also feed at low tide in subtidal habitat types consuming harpacticoid copepod species (*Pseudobrydia pulchella* and *Paronychocamptus wilsoni*) residing in this habitat type only (Feller *et al.* 1990). Thus, it is theoretically possible to identify differences in fish feeding behavior and to determine the role of food in different habitat types in estuaries including the marsh edge, flooded marsh, and open water. Nevertheless, in Louisiana, harpacticoid copepods are heterogeneously distributed and copepods that supposedly inhabit subtidal habitat types are found in intertidal habitat types as well (Phillips and Fleeger 1985), probably because of the restricted intertidal habitat associated with a low tidal amplitude.

The role of food for marsh-related fishes has been addressed before, but most studies have focused on the refuge role of marshes (Boesch and Turner 1984, McIvor and Odum 1988). A few studies have explored differential feeding habits among marsh habitat types for marsh-surface-dependent species (Rozas and LaSalle 1990, Weisberg and Lotrich 1982). Nevertheless, trophic interactions within fish communities associated with marsh edge and adjacent open water remains unclear. Community food webs are defined as the trophic interactions of species found in a particular habitat type (Briand

1983) and dietary studies provide information about linkages among species and their habitat types (Berg 1979). The objectives of this study were to obtain comprehensive information about the feeding of estuarine fishes and their role in the community and to test whether habitat type (marsh edge and open water) and environmental variability affect the structure of estuarine food webs. In general, fishes had higher abundances of prey in their stomachs along the marsh edge than in open water.

## **Materials and Methods**

### **Study Area**

The study was conducted near Cocodrie, Louisiana in the Terrebonne-Timbalier bay system (Figure 3.1). The study area is now isolated largely from the influence of the Mississippi River by a levee system that permits only minimal sediment input (Delaune *et al.* 1987) and is characterized by shallow bays, channels, and small ponds, with fine sediments, turbid waters, and salinities typically ranging between 0 and 28 psu throughout the year (<http://weather.lumcon.edu/stationdata.asp>). Tides are predominantly diurnal with a mean range of approximately 0.4 m, and are often wind-dominated (Shirzad *et al.* 1989; <http://weather.lumcon.edu/stationdata.asp>). The study area is within the saline marsh category (Chabreck and Linscombe 1991) dominated by the smooth cordgrass, *Spartina alterniflora* (Fry *et al.* 2003, Baltz *et al.* in review). The marsh is now classified as coastal submergent, since transgression has been dominant (Stevenson *et al.* 1986), following active delta development that occurred between 800 and 1,200 years ago (Penland *et al.* 1987). The deltaic sediments are rapidly subsiding, and relative sea-level rise rates for the area are estimated at 1.1-1.3 cm yr<sup>-1</sup> (Penland *et al.* 1988).

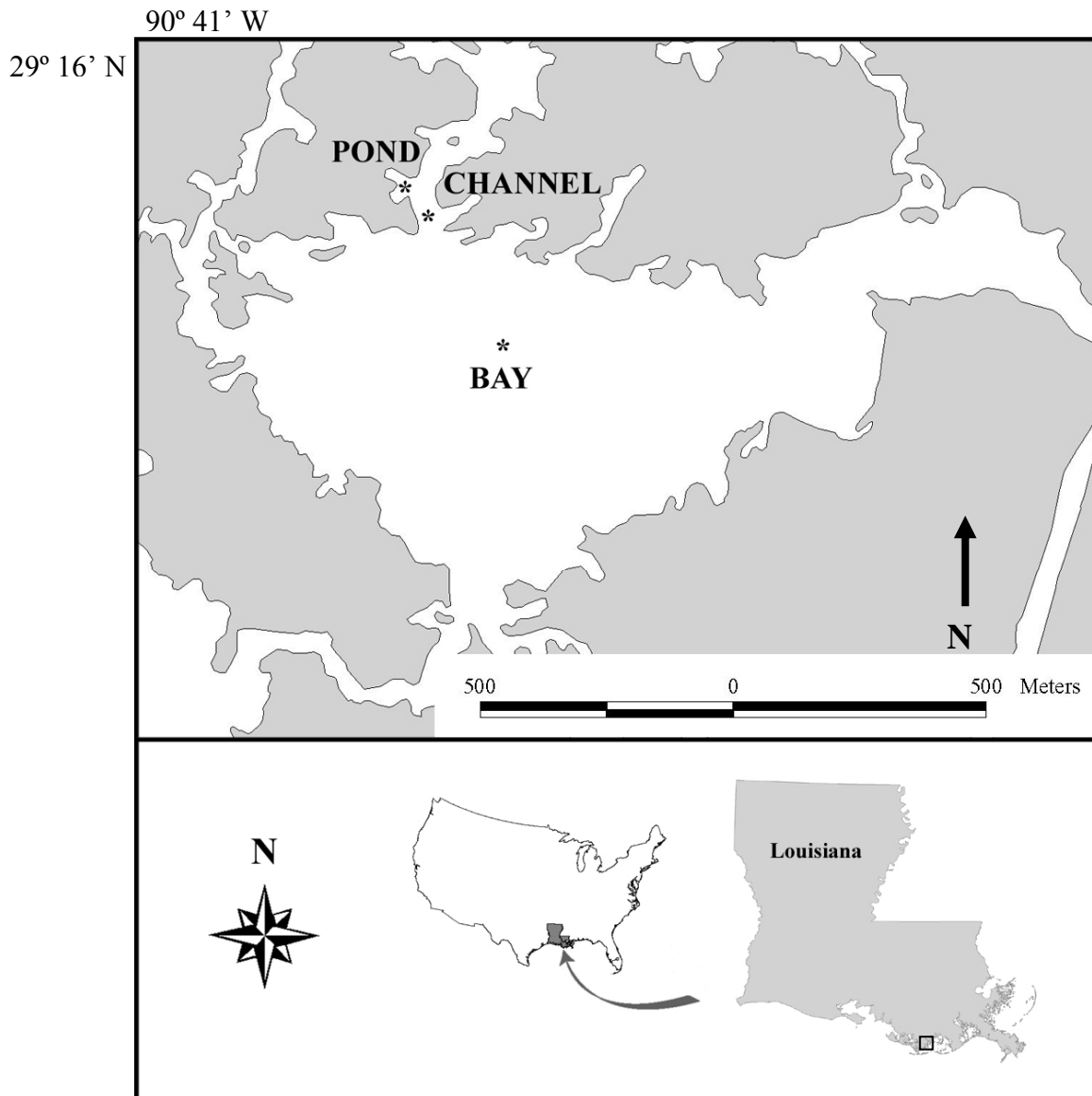


Figure 3.1. Study area indicating pond, channel, and shallow bay locations near the Louisiana Universities Marine Consortium (LUMCON) in Terrebone Bay, Louisiana.

### Sample Collection

Fishes were collected using a drop sampler, a clear acrylic cylinder (1.2 m diameter and 1.2 m height) with a metal ring on the bottom. It was released from a boom attached to a small boat (Arrivillaga and Baltz 1999, Baltz *et al.* in review). Fishes were removed from the sampler by thoroughly sweeping the enclosed volume with fine mesh nets (Cummings model 270-12, 5 mm mesh) repeatedly until three successive passes

yielded no additional organisms (Duffy and Baltz 1998). Sampling was stratified by habitat type, location, and season. Four samples were taken at the marsh edge (< 1 m from the edge) and four in open water (> 1 m from edge), in each location strata (i.e., bay, channel, and pond in Figure 3.1), and each season for a total of 96 samples. Seasonal sampling included Fall of 2000 (September-November), Winter of 2000-2001 (November-February), Spring of 2001 (March-May), and Summer of 2001 (June-August) collections. To ensure that all samples were independent, careful placement and collection avoided interference with subsequent samples. Samples were field sorted and then iced and transported to the laboratory where they were frozen pending analyses.

A total of six environmental variables were examined at each sampling site including minimum and maximum depths (cm), salinity (psu), temperature (°C), dissolved oxygen (DO mg l<sup>-1</sup>), and distance from the marsh edge. Temperature, salinity, and dissolved oxygen were determined by using a Hydrolab model SRV2-SU meter. Median depth and substrate relief (i.e.,  $\Delta$  depth = max - min depths) were calculated using the minimum and maximum depth values. Water samples were collected to determine turbidity (NTU) and chlorophyll *a* (µg l<sup>-1</sup>) in the lab. These samples were maintained in cold storage until turbidity samples were read on a Hach 2100N turbidimeter and chlorophyll *a* values determined by acetone extraction.

In the laboratory, fishes were identified to species (Hoese and Moore 1977) and measured to the nearest millimeter standard length (SL). After thawing, fish stomachs were removed and fixed in alcohol. The stomach contents were analyzed under a dissecting microscope, and prey items were enumerated and identified to the lowest

possible taxon. The percentage count of detritus was estimated visually and compared to the volume of prey items within each stomach.

Additionally, two field enclosure experiments were conducted in July and August of 2001 to test for differences in food consumption by naked goby among three habitat types: (1) marsh edge including *Spartina alterniflora* shoots, (2) marsh edge without *S. alterniflora* shoots, and (3) open water. The open-water enclosures were at least 3 m from the marsh edge. The marsh-edge enclosures were within 1 m from the marsh edge. Enclosures with vegetation overlapped the marsh-water interface with half including shoots of *S. alterniflora*. Cylindrical clear acrylic enclosures, approximately 0.75 m in diameter and 1.25 m in height, were placed 0.25 m deep into the mud. The enclosures had 10 cm diameter holes protected with a mesh (5 x 3.5 mm) to prevent escapement of fish while allowing water circulation. The top of the enclosures was above the water throughout the experiments and covered by a mesh (10 x 10 mm) to discourage avian predators. Four enclosures were placed in each of three habitat types for two weeks and this experiment was replicated in twelve different sites to avoid food resource depletion. Six fish were confined in each enclosure for a total of 144 individuals. This represents a density of 13.4 fish m<sup>-2</sup>, whereas natural abundance of naked goby in this study was 2.1 fish m<sup>-2</sup>. After two weeks, individuals were recovered and their stomach contents were analyzed as previously described.

### **Data Analysis**

Statistical analyses were applied to the most abundant species including bay anchovy, naked goby, and darter goby. Fish length and prey abundance data were transformed using  $\log_{10}(x + 1)$ , and subsequent examination of residuals and residual



plots and biplots indicated that assumptions of normality and variance homogeneity were met after transformation. Multivariate analysis of variance (MANOVA) and univariate analysis of variance (ANOVA) analyses were performed using the general linear model and the posterior pairwise comparisons were determined using the least-square mean procedure (Tukey's adjustment; SAS Institute 1996). For each selected predator, a ANOVA was performed to test whether fish length of the individuals with food in their stomachs varied among seasons, locations and habitat types. Fishes were grouped in size classes (every 10 mm) and prey use variations by fish size were tested in a one-way ANOVA. Then, prey abundance was divided by the predator's standard length to minimize the influence of fish size (large fish tend to eat more prey items than small fish). Differences in abundance of prey in the stomachs of the most abundant fishes (expressed as prey number/stomach) were assessed individually for each predator species in a three-way MANOVA with habitat type, season, and location as main factors. Species-specific differences in utilization of prey among factors were examined in univariate analysis (ANOVA). For the field experiments with naked goby, a two-way MANOVA was used to test differences in prey utilization among habitat types and replicate experiments. Prey utilization data of the experiments were standardized and transformed as mentioned above.

Differences in prey utilization were associated with each other and environmental variables by a canonical correlation (SAS institute 1996) for each species. Canonical correlation analyses were performed between the transformed environmental variables using  $\log_{10}(x + 1)$  and the transformed abundance of the prey items for the most abundant predators. These two groups of variables provided a series of canonical variates,

which are linear combinations of the original variables providing associations among all biological and environmental variables ( $> |0.31|$ ) (Geaghan and Huish 1980).

## **Results**

A total of 348 fishes belonging to 19 species were examined, but only 124 individuals had food in their stomachs. Harpacticoid copepods were the most abundant benthic prey for 10 species (Table 3.1a) and calanoid copepods the most abundant pelagic prey for four species (Table 3.1b). Detritus accounted for at least 50% of the food volume found in Atlantic menhaden and mummichog stomachs and less than 5% in the rest of the fishes. Most prey were more abundant in the stomachs of the individuals captured along the marsh edge (Figure 3.2). Nevertheless, detailed statistical analyses were limited to the most abundant fishes, bay anchovy, darter goby, and naked goby.

### **Bay Anchovy**

Bay anchovy ingested eight different prey categories and detritus in fall, spring, and summer, but were not captured in winter. The size of the individuals with food in their stomachs was significantly different among seasons (ANOVA,  $F_{2,27} = 9.15$ ,  $p = 0.0009$ ), but was not different among locations, habitat types, or interactions (ANOVA,  $F_{2,27} \leq 0.91$ ,  $p \geq 0.1451$ ). Individuals were significantly larger in spring ( $41.6 \pm 2.87$ ) than in summer ( $26.9 \pm 2.96$ ) and fall ( $30.9 \pm 1.54$ ). Almost 70% of bay anchovy individuals with food in their stomachs were juveniles between 19 to 38 mm SL, but prey utilization did not vary among size classes (ANOVA,  $F_{4,37} \leq 1.33$ ,  $p \geq 0.2781$ ). Prey utilization did vary seasonally (MANOVA,  $F_{16,14} = 6.87$ ,  $p = 0.0004$ ), but differences among locations, habitat types, the two-way interactions, and the three-way interaction were not significant (MANOVA,  $F_{24,21} \leq 1.19$ ,  $p \geq 0.3453$ ).

Table 3.1a. Mean annual abundances ( $\pm$  SE) of benthic prey consumed by fish species. Fishes with empty stomachs were excluded. The most abundant prey category for each species is in bold print. Species selected for detailed statistical examination were identified by an asterisk. HC = harpacticoid copepods, OS = ostracods, PO = polychaetes, NE = nematodes, JC = juvenile crab, SH = shrimp, and FI = fishes.

Species	Common name	N	Size range	Benthic prey						
				HC	OS	PO	NE	JC	SH	FI
<i>Anchoa mitchilli</i> *	Bay anchovy	42	11-54	2.6 ± 0.07						
<i>Gobiosoma bosc</i> *	Naked goby	28	12-43	<b>7.6 ± 0.24</b>	3.2 ± 0.12	1.3 ± 0.08		1.1 ± 0.06		1.1 ± 0.05
<i>Ctenogobius boleosoma</i> *	Darter goby	14	17-47	<b>11.6 ± 0.53</b>	4.3 ± 0.16	3.2 ± 0.18			3.7 ± 0.35	
<i>Cynoscion nebulosus</i>	Spotted seatrout	11	12-63	<b>4.7 ± 0.46</b>		0.7 ± 0.07			2.9 ± 0.88	0.2 ± 0.05
<i>Micropogonias undulatus</i>	Atlantic croaker	3	22-38	<b>6.3 ± 1.89</b>		5.3 ± 0.38	1.3 ± 0.14			0.7 ± 0.14
<i>Microgobius thalassinus</i>	Green goby	3	29-42	3.3 ± 1.39	3.0 ± 1.20	1.7 ± 0.38	1.0 ± 0.33			
<i>Menbras martinica</i>	Rough silverside	3	47-71		1.7 ± 0.96					
<i>Cynoscion arenarius</i>	Sand seatrout	3	32-51	1.0 ± 1.36					<b>2.3 ± 0.69</b>	
<i>Leiostomus xanthurus</i>	Spot	3	28-83	<b>40.0 ± 9.91</b>			2.0 ± 0.33	1.7 ± 0.96		1.3 ± 0.51
<i>Pogonias cromis</i>	Black drum	2	19-33	<b>4.0 ± 1.71</b>					0.5 ± 0.35	
<i>Fundulus heteroclitus heteroclitus</i>	Mummichog †	2	45-65	<b>5.5 ± 1.77</b>	3.5 ± 1.06	1.5 ± 0.35	0.5 ± 0.35		1.5 ± 0.35	
<i>Bairdiella chrysoura</i>	Silver perch	2	31-33	<b>19.0 ± 9.81</b>	2.5 ± 1.77					
<i>Gobionellus oceanicus</i>	Highpin goby	2	43-178	<b>37.5 ± 5.06</b>	0.5 ± 0.35		1.0 ± 0.71			
<i>Myrophis punctatus</i>	Speckled worm eel	1	52	<b>4.0</b>	3.0					
<i>Symphurus plagiura</i>	Blackcheek tonguefish	1	51	<b>5.0</b>	1.0	2.0				
<i>Menidia beryllina</i>	Inland silverside	1	31		3.0					
<i>Brevoortia tyrannus</i>	Atlantic menhaden †	1	33		3.0	1.0				
<i>Stellifer lanceolatus</i>	Star drum	1	43				1.0			
<i>Citharichthys spilopterus</i>	Bay whiff	1	14	2.0		1.0				

† At least 50% of detritus in stomachs

Table 3.1b. Mean annual abundances ( $\pm$  SE) of pelagic prey consumed by fish species. Fishes with empty stomachs were excluded. The most abundant prey category for each species is in bold print. Species selected for detailed statistical examination identified by an asterisk. DI = diatoms, CL = cladocerans, CN = copepod nauplii, CZ = crab zoea, CC = calanoid copepod, FE = fish eggs, and FL = fish larvae.

Species	Common name	N	Size range	Pelagic prey						
				DI	CL	CN	CZ	CC	FE	FL
<i>Anchoa mitchilli</i> *	Bay anchovy	42	11-54	2.6 $\pm$ 0.10	4.4 $\pm$ 0.13	10.8 $\pm$ 0.14	1.6 $\pm$ 0.05	<b>17.3 <math>\pm</math> 0.18</b>	0.8 $\pm$ 0.03	1.0 $\pm$ 0.04
<i>Gobiosoma bosc</i> *	Naked goby	28	12-43	2.0 $\pm$ 0.13					1.1 $\pm$ 0.05	
<i>Ctenogobius boleosoma</i> *	Darter goby	14	17-47	3.9 $\pm$ 0.21						
<i>Cynoscion nebulosus</i>	Spotted seatrout	11	12-63				0.8 $\pm$ 0.07	1.7 $\pm$ 0.12		0.5 $\pm$ 0.06
<i>Micropogonias undulatus</i>	Atlantic croaker	3	22-38					2.3 $\pm$ 0.38		
<i>Microgobius thalassinus</i>	Green goby	3	29-42	1.0 $\pm$ 0.58	<b>4.3 <math>\pm</math> 2.50</b>					
<i>Menbras martinica</i>	Rough silverside	3	47-71	21.3 $\pm$ 9.32	6.0 $\pm$ 3.46		5.3 $\pm$ 3.08	<b>34.3 <math>\pm</math> 9.41</b>		
<i>Cynoscion arenarius</i>	Sand seatrout	3	32-51					0.7 $\pm$ 0.38		0.7 $\pm$ 0.38
<i>Leiostomus xanthurus</i>	Spot	3	28-83		1.0 $\pm$ 0.58		0.7 $\pm$ 0.38			
<i>Pogonias cromis</i>	Black drum	2	19-33				0.5 $\pm$ 0.35	2.5 $\pm$ 0.35		
<i>Fundulus heteroclitus heteroclitus</i>	Mummichog †	2	45-65	4.0 $\pm$ 1.40					2.5 $\pm$ 1.06	
<i>Bairdiella chrysoura</i>	Silver perch	2	31-33	2.0 $\pm$ 1.41		1.5 $\pm$ 1.06		1.0 $\pm$ 0.71		0.5 $\pm$ 0.35
<i>Gobionellus oceanicus</i>	Highpin goby	2	43-178	6.0 $\pm$ 1.71					2.0 $\pm$ 1.41	
<i>Myrophis punctatus</i>	Speckled worm eel	1	52	2.0						
<i>Symphurus plagiura</i>	Blackcheek tonguefish	1	51					2.0		
<i>Menidia beryllina</i>	Inland silverside	1	31	5.0	3.0	1.0		<b>8.0</b>		
<i>Brevoortia tyrannus</i>	Atlantic menhaden †	1	33	<b>6.0</b>		1.0		3.0		
<i>Stellifer lanceolatus</i>	Star drum	1	43					<b>4.0</b>		
<i>Citharichthys spilopterus</i>	Bay whiff	1	14					<b>6.0</b>		

† At least 50% of detritus in stomachs

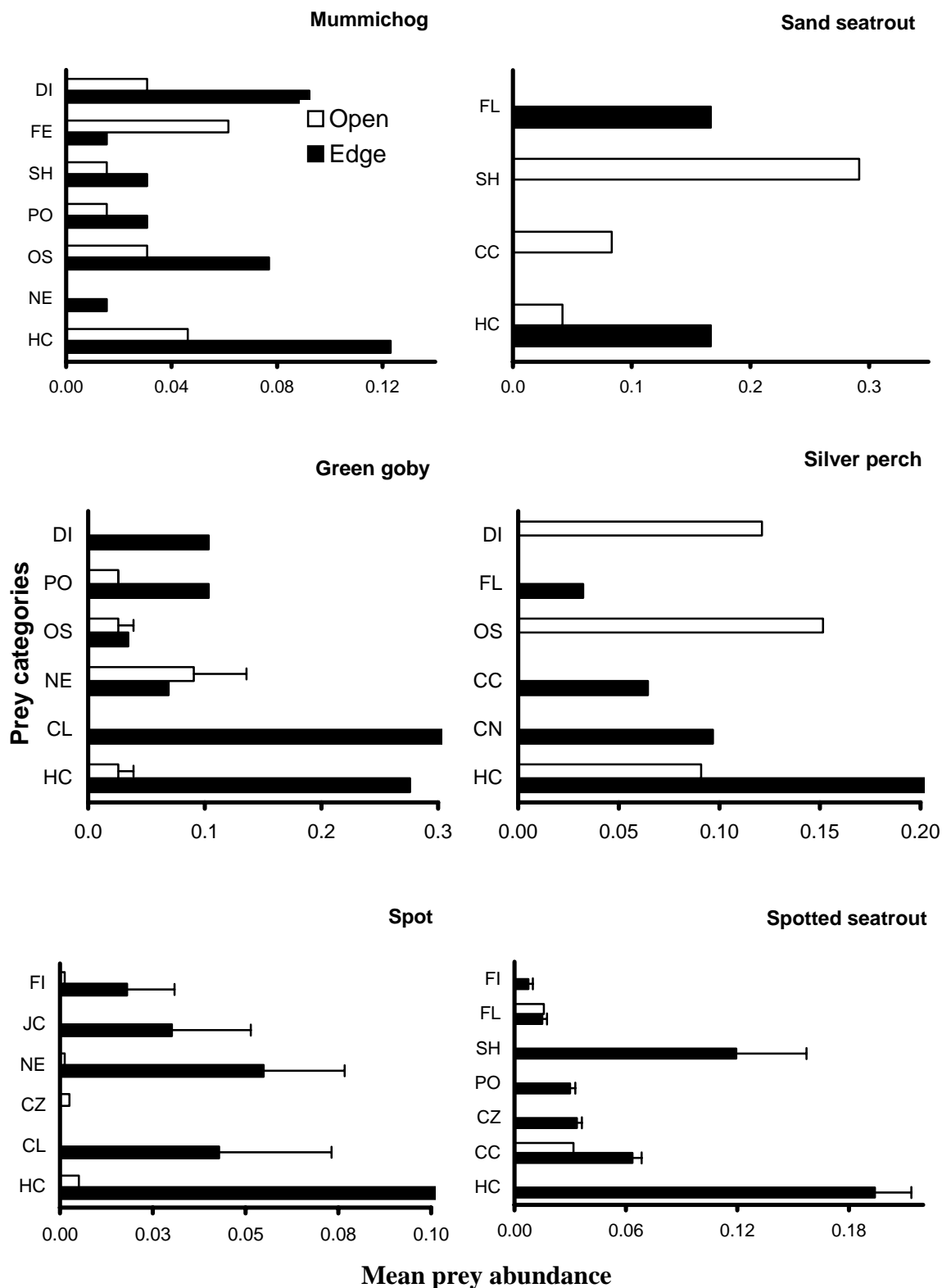


Figure 3.2. Mean abundance ( $\pm 1$ SE) of the prey categories ingested by the fish species with food in their stomachs in both marsh-edge and open-water habitat types. DI = diatoms, CL = cladocerans, CN = Copepod nauplii, HC = harpacticoid copepods, CL = calanoid copepods, CZ = crab zoea, NE = nematodes, OS = ostracods, PO = polychaetes, JC = juvenile crab, SH = shrimp, FE = fish eggs, FL = fish larvae, and FI = fishes.

Bay anchovy fed mainly on calanoid copepods (mostly *Acartia* spp.), copepod nauplii, and cladocerans (Table 3.1). Seasonal differences in abundance of prey items were detected for calanoid copepods, cladocerans, crab zoea, and diatoms (ANOVA,  $F_{2,14} \geq 9.32$ ,  $p \leq 0.0027$ ). All these prey categories were more abundant in summer (Figure 3.3). In general, most of the prey items were highly digested and further identification was not possible.

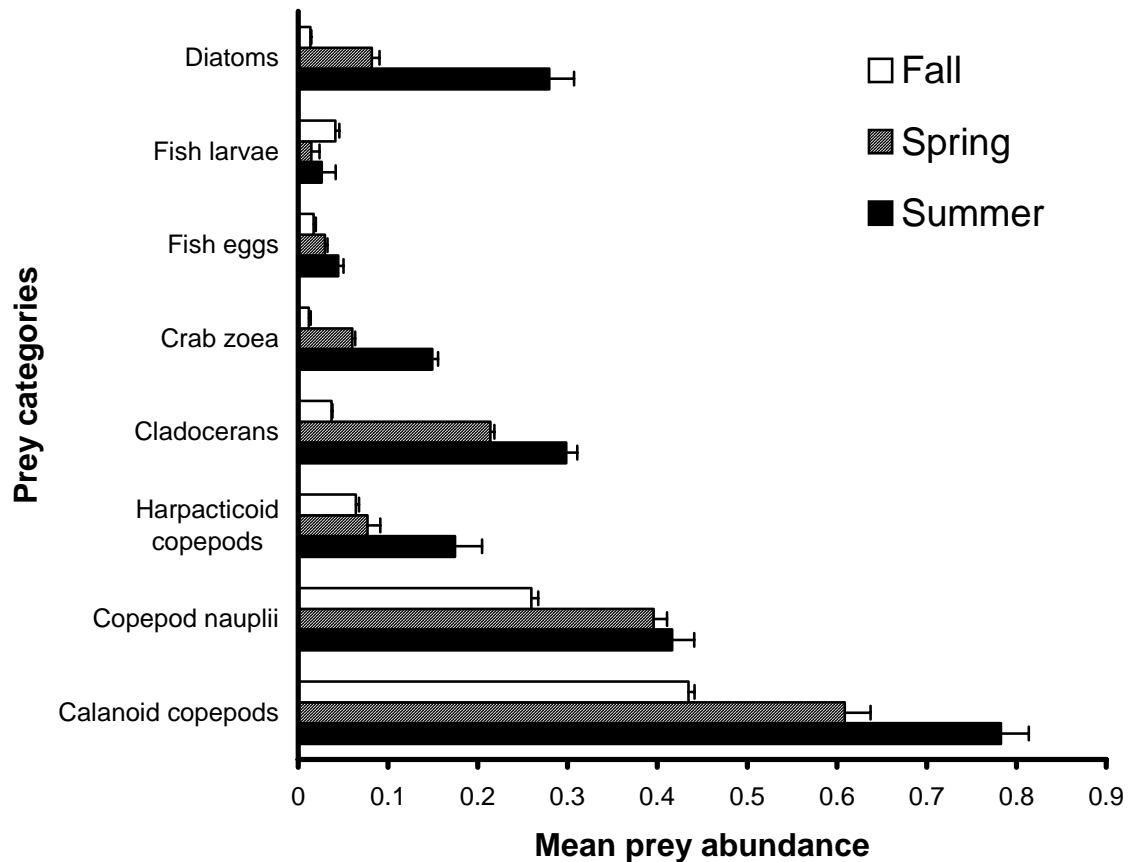


Figure 3.3. Mean abundance ( $\pm 1$ SE) of the prey categories ingested by bay anchovy among seasons.

In the canonical correlation analysis of bay anchovy, the first two canonical variates explained 78% of the variation of prey categories and environmental variables (Table 3.2). In the first canonical variate, crab zoea, diatoms, cladocerans, copepod

nauplii, and calanoid copepods were abundant in the stomachs of individuals captured in open, shallow, well oxygenated, clear, and cool waters. In the second canonical variate, fish larvae were abundant and harpacticoid copepods were rare in the individuals captured far from the edge in turbid, warm, brackish, and well oxygenated waters with low concentrations of chlorophyll *a*.

Table 3.2. Standardized canonical coefficients of the first two canonical variates with the prey categories consumed by bay anchovy and the environmental variables. Values > |0.31| in bold indicate strong loadings that explain more than 10% of variability.

<b>Prey categories</b>	<b>Canonical variate</b>	
	<b>1</b>	<b>2</b>
Crab zoea	<b>-0.60</b>	<b>-0.36</b>
Diatoms	<b>0.49</b>	<b>-0.48</b>
Cladocerans	<b>0.47</b>	-0.09
Copepod nauplii	<b>0.46</b>	<b>0.68</b>
Calanoid copepods	<b>0.35</b>	<b>0.36</b>
Harpacticoid copepods	-0.08	<b>-0.44</b>
Fish larvae	0.12	<b>0.36</b>
Fish eggs	0.17	-0.12
<b>Environmental variables</b>		
Median depth	<b>-0.95</b>	-0.23
Distance from edge	<b>0.89</b>	<b>0.58</b>
Turbidity	<b>-0.72</b>	<b>0.91</b>
Temperature	<b>-0.40</b>	<b>0.70</b>
Dissolved oxygen	<b>0.34</b>	<b>0.37</b>
Salinity	-0.02	<b>-0.63</b>
Chlorophyll <i>a</i>	-0.27	<b>-0.38</b>
$\Delta$ depth	0.09	0.05
Variance explained	1.64	0.83
Percentage variance explained	52	26
Cumulative percentage explained	52	78

### **Darter Goby**

Darter gobies ingested five different prey categories and detritus in fall and winter, but were not captured in spring and summer. The size of the individuals with

food in their stomachs was not significantly different among seasons, locations, habitat types, or interactions (ANOVA,  $F_{1,7} \leq 4.92$ ,  $p \geq 0.0620$ ). More than 73% of darter gobies with food in their stomachs were between 22-38 mm SL and the prey utilization did not vary among size classes (ANOVA,  $F_{3,11} \leq 2.68$ ,  $p \geq 0.0983$ ). Prey utilization did not vary among seasons, locations, habitat types or two-way interactions (MANOVA,  $F_{5,2} \leq 1.71$ ,  $p \geq 0.4088$ ). Insufficient degrees of freedom precluded a test of the three-way interaction. Darter goby fed mainly on harpacticoid copepods and grass shrimp (Table 3.1). Harpacticoid copepods were mostly unidentified (78%), but *Coullana* sp. (9%) and *Pseudostenhelia wellsi* were identified (13%).

In the canonical correlation analysis of darter goby, the first two canonical variates explained 95% of the variation (Table 3.3). Harpacticoid copepods were abundant and polychaetes were rare in individuals captured in open, shallow, saline, and clear waters with low substrate relief ( $\Delta$  depth) and low chlorophyll *a* levels. In the second canonical variate, grass shrimp were abundant and ostracods were rare in deep, saline, turbid, and cool waters with low chlorophyll *a* levels.

### **Naked Goby**

Naked gobies ingested seven different prey categories and detritus in fall, winter, and summer, but were not captured in spring. The size of the individuals with food in their stomachs was not significantly different among seasons, locations, habitat types, or interactions (ANOVA,  $F_{1,18} \leq 3.67$ ,  $p \geq 0.0714$ ). Almost 80% of all individuals with food in their stomachs were between 17-27 mm SL and the prey utilization did not vary among size classes (ANOVA,  $F_{3,24} \leq 1.28$ ,  $p \geq 0.3042$ ). Nevertheless, prey abundance in the stomachs of naked goby varied among habitat types (MANOVA,  $F_{7,5} = 7.77$ ,  $p =$



0.0191), seasons (MANOVA,  $F_{14, 10} = 5.30$ ,  $p = 0.0059$ ), and locations (MANOVA,  $F_{7, 5} = 5.18$ ,  $p = 0.0443$ ), whereas the two-way interactions were not significant (MANOVA,  $F_{7, 5} \leq 1.44$ ,  $p \geq 0.3558$ ). Insufficient degrees of freedom precluded a test of the three-way interaction.

Table 3.3. Standardized canonical coefficients of the first two canonical variates with the prey categories consumed by darter goby and the environmental variables. Values  $> |0.31|$  in bold indicate strong loadings that explain more than 10% of variability.

Prey categories	Canonical variate	
	1	2
Harpacticoid copepods	<b>0.95</b>	<b>0.98</b>
Polychaetes	<b>-0.52</b>	<b>-0.53</b>
Ostracods	0.30	<b>-0.80</b>
Grass shrimp	-0.21	<b>0.94</b>
Diatoms	0.07	-0.01
<b>Environmental variables</b>		
Salinity	<b>0.98</b>	<b>0.97</b>
Distance from edge	<b>0.93</b>	-0.14
Median depth	<b>-0.91</b>	<b>0.93</b>
Turbidity	<b>-0.78</b>	<b>0.87</b>
$\Delta$ depth	<b>-0.75</b>	-0.23
Chlorophyll <i>a</i>	<b>-0.63</b>	<b>-0.89</b>
Temperature	-0.05	<b>-0.55</b>
Dissolved oxygen	0.19	-0.02
Variance explained	2.09	0.95
Proportion of variance explained	82	13
Cumulative proportion explained	82	95

Naked goby fed mainly on harpacticoid copepods and ostracods (Table 3.1).

Habitat type differences in abundance of prey were detected for harpacticoid copepods and ostracods as well (ANOVA,  $F_{1, 11} \geq 10.33$ ,  $p \leq 0.0083$ ). These prey categories were more abundant in individuals captured along the marsh edge (Figure 3.4). Seasonal differences in abundance of prey were detected for harpacticoid copepods, ostracods,

juvenile crab, fish eggs, and fishes (ANOVA,  $F_{2, 11} \geq 6.91$ ,  $p \leq 0.0114$ ). All prey categories with significant differences by season were more abundant in individuals captured in winter (Figure 3.5). Location differences in abundance of prey were detected for harpacticoid copepods and ostracods (ANOVA,  $F_{1, 11} \geq 12.85$ ,  $p \leq 0.0043$ ). Both of these prey categories were more abundant in individuals captured in the channel (Figure 3.6). Some harpacticoid copepods were identified including *Coullana* sp. (17%) and *Pseudostenhelia wellsi* (14%), but most were highly digested and further identification was not possible (69%). Some of the fishes found in the stomachs of naked goby apparently were unidentified small gobies.

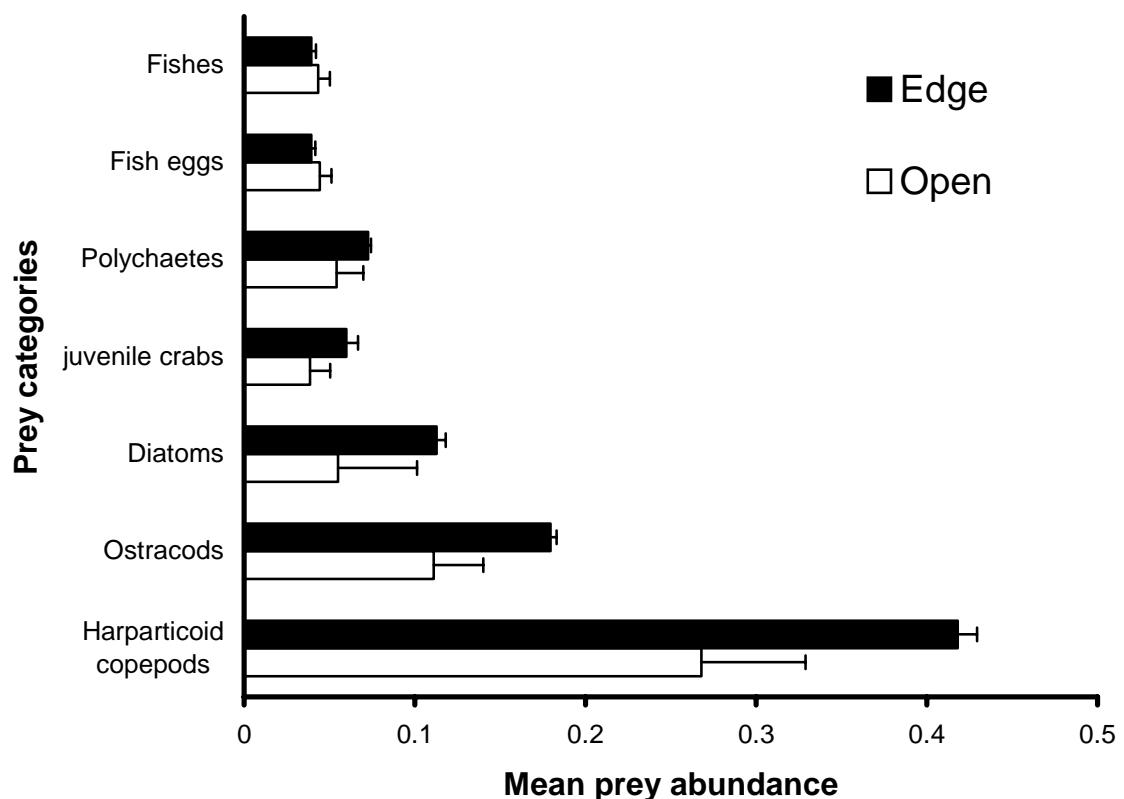


Figure 3.4. Mean abundance ( $\pm 1$ SE) of the prey categories ingested by naked goby among habitat types. Prey abundance was standardized by fish size (SL in mm).

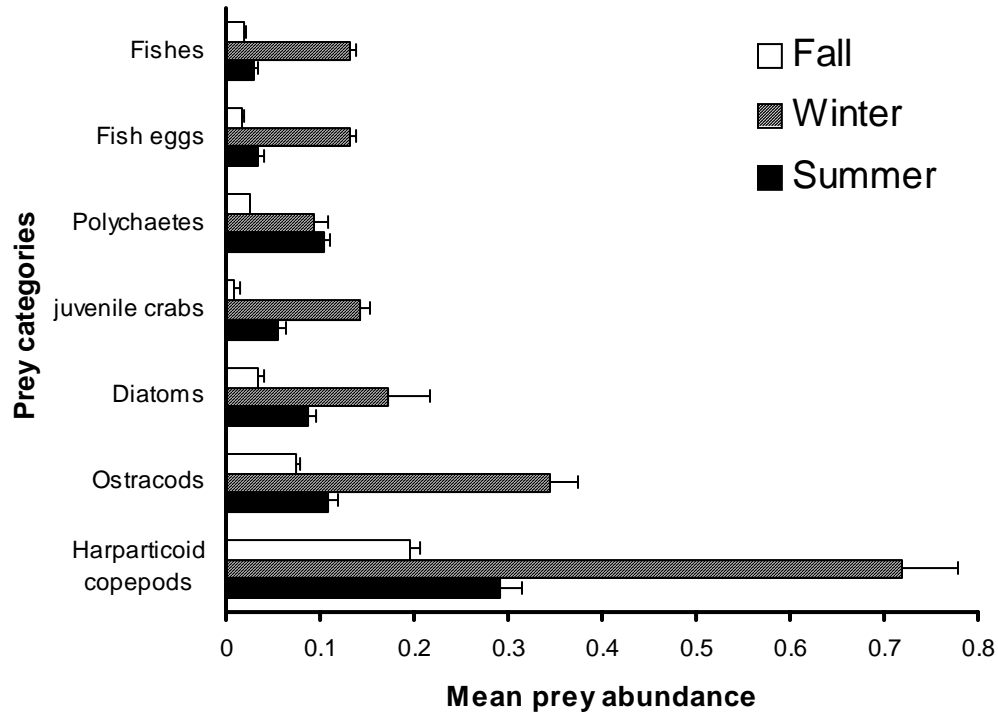


Figure 3.5. Mean abundance ( $\pm 1$ SE) of the prey categories ingested by naked goby among seasons. Prey abundance was standardized by fish size (SL in mm).

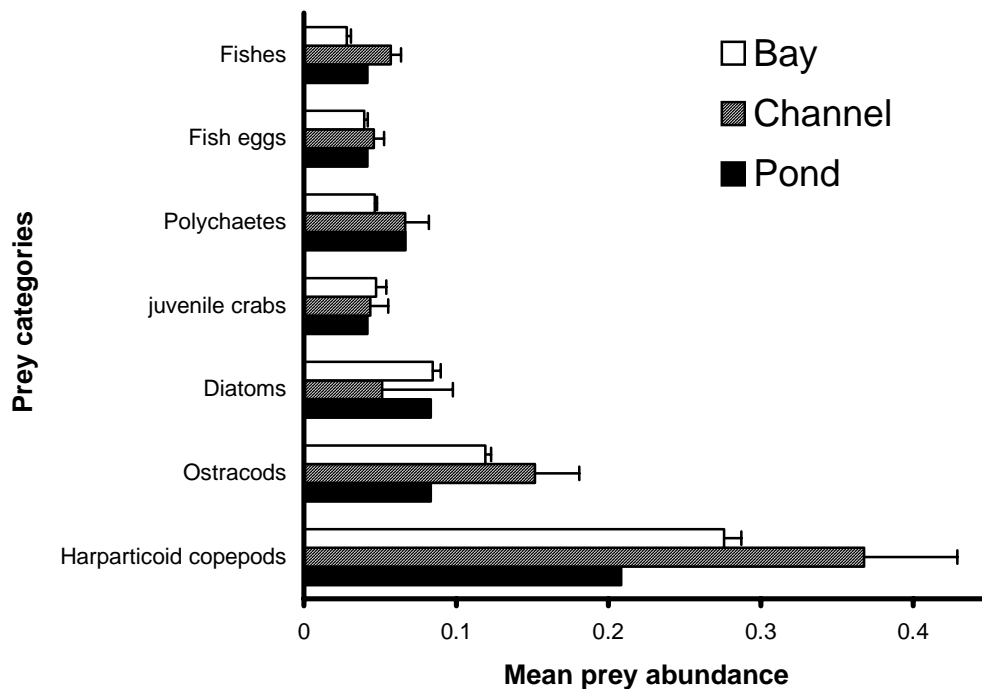


Figure 3.6. Mean abundance ( $\pm 1$ SE) of the prey categories ingested by naked goby among locations. Prey abundance was standardized by fish size (SL in mm).

In the canonical correlation analysis of naked goby the first two canonical variates explained 88% of the variation of prey categories and environmental variables (Table 3.4). In the first canonical variate, ostracods and fishes were abundant and harpacticoid copepods and polychaetes were rare in individuals captured in warm, clear, and saline waters with low chlorophyll *a* levels. In the second canonical variate, juvenile crabs and fish eggs were rare in individuals captured near the marsh edge, in deep and cold waters with high chlorophyll *a* levels and low substrate relief ( $\Delta$  depth).

Table 3.4. Standardized canonical coefficients of the first two canonical variates with the prey categories consumed by naked goby and the environmental variables. Values  $> |0.31|$  in bold indicate strong loadings that explain more than 10% of variability.

<b>Prey categories</b>	<b>Canonical variate</b>	
	<b>1</b>	<b>2</b>
Ostracods	<b>1.22</b>	<b>2.66</b>
Harpacticoid copepods	<b>-0.69</b>	<b>-1.08</b>
Polychaetes	<b>-0.34</b>	-0.14
Fishes	<b>0.33</b>	-0.17
Juvenile crabs	0.27	<b>-1.01</b>
Fish eggs	0.18	<b>-0.87</b>
Diatoms	0.28	0.40
<b>Environmental variables</b>		
Chlorophyll <i>a</i>	<b>-1.39</b>	<b>0.52</b>
Temperature	<b>0.49</b>	<b>-0.60</b>
Turbidity	<b>0.42</b>	0.58
Salinity	<b>0.41</b>	-0.01
Median depth	-0.01	<b>0.92</b>
Distance from edge	0.09	<b>-0.85</b>
$\Delta$ depth	0.03	<b>-0.65</b>
Dissolved oxygen	-0.10	0.16
Variance explained	1.21	0.97
Proportion of variance explained	76	12
Cumulative proportion explained	76	88

A total of 61 of 144 naked gobies were recaptured in the 24 enclosures (both experiments). These individuals were between 22-31 mm SL and had food in their stomachs including 10 prey categories and detritus (Figure 3.7). Abundance of prey in their stomachs did not vary among habitat types, experiments, or interaction (MANOVA,  $F_{10, 10} \leq 2.37$ ,  $p \geq 0.0953$ ).

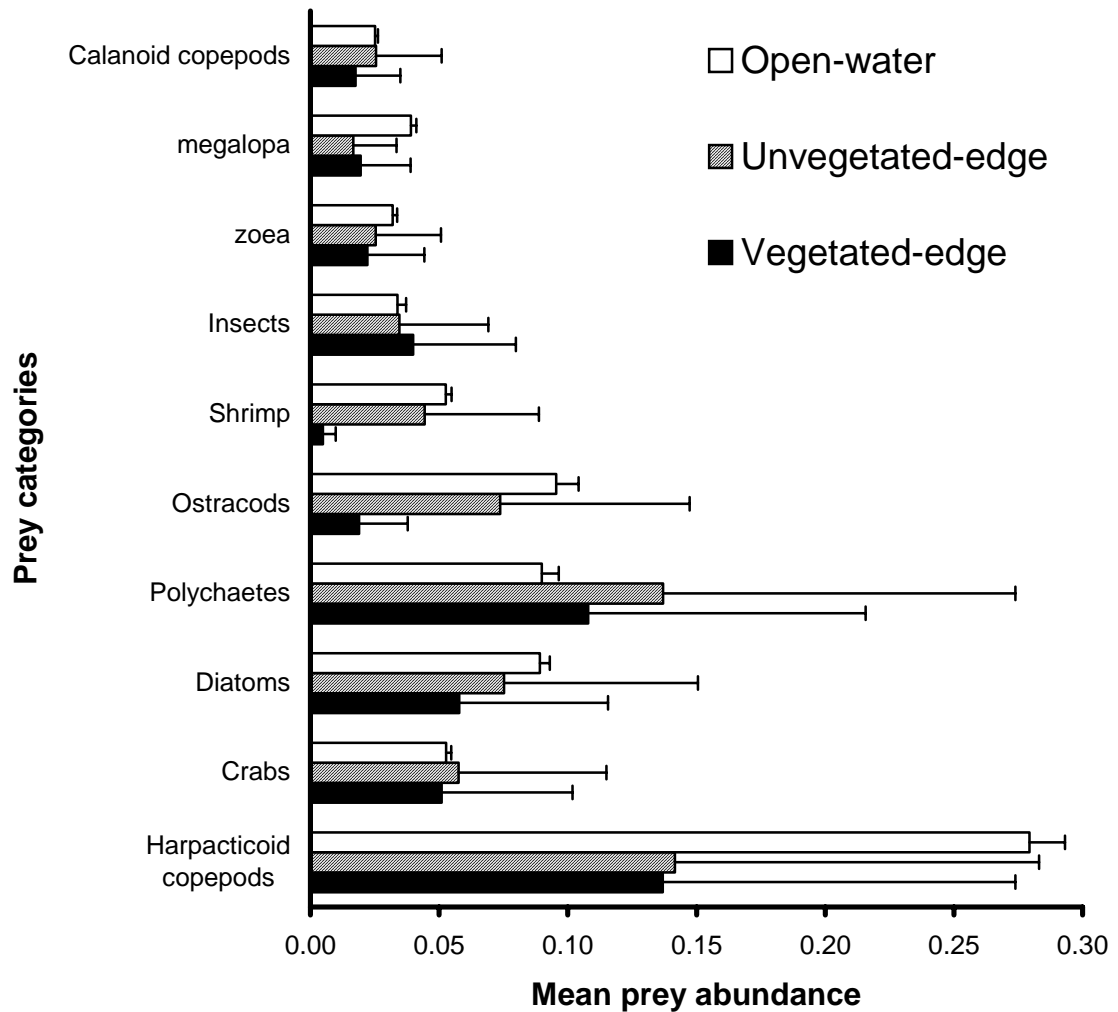


Figure 3.7. Mean abundance ( $\pm 1$ SE) of the prey categories ingested by naked goby among habitat types in the enclosure experiments. There were 4 experimental units in each habitat type in both experiments. Prey abundance was standardized by fish size (SL in mm).

## **Discussion**

Prey utilization differences were detected among habitat types, seasons, and locations for naked goby and bay anchovy. Naked goby consumed higher abundances of harpacticoid copepods along the marsh edge than in open water. In contrast, in the enclosure experiments, naked goby had no significant differences in the utilization of prey categories among habitat types. Bay anchovy and naked goby had significant differences in prey utilization among seasons and ingestion was associated with changes of environmental variables. Fishes ingested a variety of pelagic and benthic prey items, but most fish species fed primarily on harpacticoid copepods. Despite the presence of detritus in the stomachs of several fish species, it was relatively rare.

### **Marsh Edge Versus Open Water**

Prey utilized by naked goby varied between the marsh edge and open water throughout the year. Naked goby had higher amounts of harpacticoid copepods when captured along the marsh edge. In New Jersey estuaries, naked goby consume a higher proportion of harpacticoid copepods in vegetated than in unvegetated areas (Sogard 1992). Although harpacticoid copepods are fairly homogeneous in different marsh habitat types in Louisiana estuaries (Sun and Fleeger 1991), total meiofauna is more abundant in subtidal mudflats (Phillips and Fleeger 1985). In contrast, Sogard (1992) attributes higher growth rates of naked gobies in non-vegetated habitat types to higher prey availability, and suggests that individuals sacrifice growth in favor of increased refugia when occupying vegetated habitat types. The primary role of marsh-edge habitat type may yet prove to be refugia, although results of the current study indicate that feeding also plays an important part.

## Seasonal Variation

The most abundant estuarine fishes had seasonal diet shifts that may depend on prey abundance or predator selectivity. Bay anchovies ingested higher abundances of zooplankton in summer than in the other seasons in this study. Nevertheless, bay anchovies in summer were smaller and may select higher abundances of prey in seasons when this prey is available (Allen *et al.* 1995). Crab zoea were more abundant in the stomachs of bay anchovy in summer in this study and in Biloxi Bay, Mississippi (Din and Gunter 1986), which may be due to the smaller size of the individuals in this season. Although crab zoea were present, no crab megalops were found in stomachs of bay anchovy in this study or year around in Back Bay, Mississippi (Din and Gunter 1986). In contrast, crab megalops are the most abundant prey items in bay anchovy in summer in North Inlet estuary, South Carolina (Johnson *et al.* 1990). Although bay anchovy feeds on zooplankton populations, its impact in regulating zooplankton community structure is difficult to assess in estuaries (Johnson *et al.* 1990) and prey composition may change due to specific physico-chemical conditions in a given estuary.

Naked goby fed on meiofauna in higher proportions in winter than in other seasons in this study. Estuarine residents such as naked goby may take advantage of higher meiofauna abundances during winter months due to lower predation pressures by transient fishes (Whaley and Minello 2002). Shallow and clear waters were related with the highest abundance of the main prey categories consumed by bay anchovy and darter goby. In contrast, harpacticoid copepods abundance in the stomachs of naked goby was negatively associated to clear, warm, and saline waters. Nevertheless, these trends may change depending of the system and the species studied. For example, salinity is the

main environmental variable influencing the feeding of juvenile bay whiff in Barataria Bay, Louisiana, with optimum feeding in salinities between 16-18 psu (Toepper and Fleeger 1995a). Also, red drum and spotted seatrout juvenile growth rates are more influenced by physico-chemical variables than diet or extrinsic factors such as *Spartina alterniflora* stem density (Baltz *et al.* 1998).

### **Location Variation**

Differences in the abundance of prey categories in the stomachs of naked goby among locations may be due to limited movement in response to territorial behavior. Naked goby use depressions in the bottom and small patches of oysters as nests, and males guard their own eggs, but are cannibalistic on the eggs of other individuals (Dahlberg and Conyers 1973). Thus, naked gobies may reflect differences in prey availability among locations in saltmarsh estuaries with low tidal range. In macrotidal estuaries, juvenile spot feed on different harpacticoid copepod species that are spatially segregated by the wide tidal range (Feller *et al.* 1990). This behavior may suggest a feeding-related movement among locations by juvenile spot. In contrast, naked goby may not be moving among locations in Louisiana estuaries, but individuals residing in specific locations may use food resources differently.

### **Food Habits**

Except for three pelagic fish species, harpacticoid copepods were the most important prey for all fishes in this study. Naked goby and darter goby consumed harpacticoid copepods in high abundances. In New Jersey estuaries, naked goby consume harpacticoid copepods as well, and the fish growth rates are greatest with highest prey availability (Sogard 1992). Darter goby feed on meiofauna, mainly harpacticoid



copepods (Fitzhugh and Fleeger 1985, Gregg and Fleeger 1997, Toepfer and Fleeger 1995b), and may select harpacticoid copepods and ostracods over nematodes (Carle and Hastings 1982). Nevertheless, darter goby ingest meiofauna primarily by sediment feeding rather than active bottom picking (Gregg and Fleeger 1997). In this study, fairly equal abundances of harpacticoid copepods, *Coullana* sp. and *Pseudostenhelix wellsi*, were ingested by darter goby. In contrast, darter goby marginally ingest *Coullana* sp., whereas they consume high amounts of *P. wellsi* in Port Fourchon, Louisiana (Gregg and Fleeger 1997).

Bay anchovies primarily fed upon pelagic prey such as calanoid copepods, but ingested harpacticoid copepods as well. The rate of feeding of calanoid copepods may be dependent on the density of prey items in the sampling area (Din and Gunter 1986). In contrast, even though bay anchovy consumption patterns closely follow most prey availability changes in the surrounding water, this species actively selects some prey items, even when prey densities are low (Johnson *et al.* 1990). A related anchovy species, *Anchovia clupeioides*, actively selects calanoid copepods independently of this prey's abundance in the surrounding water (Duque and Acero 2003). In the present study, most of the calanoid copepods ingested by bay anchovy were identified as *Acartia* spp. In other studies, *Acartia tonsa* is the most abundant calanoid copepod species in the stomachs of bay anchovy (Sheridan 1978, Johnson *et al.* 1990). Nevertheless, when other prey items are readily available, the ingestion of calanoid copepods is reduced (Din and Gunter 1986). Bay anchovy not only feed on harpacticoid copepods (Allen *et al.* 1995), but also larvae and juvenile decapod and peracarid crustaceans (Johnson *et al.*

1990). Results of this study suggest that bay anchovy take advantage of suspended food linking benthic and pelagic food webs in marsh estuaries.

Although Darnell (1958, 1961) suggested that organic detritus is a key food item for most fishes and has an important role in estuarine food webs, detritus was relatively rare in the stomachs of most fishes in this study. Mummichog and Atlantic menhaden were the only species with relatively high percentages of detritus. Mummichog is an important link between the marsh surface and subtidal food webs (Valiela 1977).

However, detritus has a limited nutritional value to this species (Allen *et al.* 1994). It seems that in the study area, the benthic community contributes with most of the carbon to higher trophic levels. Relative importance of different prey categories may have been influenced by the use of abundance data only as opposed to gravimetric or volumetric methods (prey types differ in mass by at least two orders of magnitude). Nevertheless, the objective of this study was to detect differences in composition and utilization of prey among habitat types.

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## CHAPTER IV.

### CONTRIBUTION OF PRIMARY PRODUCERS TO NEKTON RESIDING IN MARSH-EDGE AND ADJACENT OPEN-WATER HABITAT TYPES IN A LOUISIANA ESTUARY

#### Introduction

Estuarine ecosystems have complex food webs that span terrestrial and aquatic environments and include fauna with a variety of feeding strategies (Day *et al.* 1989). Analyses of natural abundances of stable carbon and nitrogen isotopes have been employed in estuarine ecosystems to trace the flow of primary production through food webs (Fry and Sherr 1984). Analyses of multiple isotopes are useful for identification of trophic links and have shown that organic matter can be transported into distant environments (Valiela 1995). Generally carbon isotopes offer insights into how consumers obtain their energy and nutrients, and have been used to establish the sources of organic matter that support food webs (Marguillier *et al.* 1997, Peterson and Fry 1987), whereas nitrogen isotopes can indicate trophic levels (Peterson and Fry 1987). Feeding studies provide important quantitative information about food habits, food selectivity, and feeding rates, but these studies may be confounded by temporal variability in the availability of different prey species (Kaehler *et al.* 2000), whereas isotopic analyses estimate the relative contribution of food sources assimilated by organisms over a longer period of time (Currin *et al.* 1995).

A long standing paradigm credits detritus as the main food source supporting the high secondary production in estuaries. Dead organic material in form of detritus comes from many sources, but it is mainly *Spartina* spp. fragments in saltmarsh estuaries (Day *et al.* 1989, Odum and de la Cruz 1967). In an early study of saltmarsh estuaries in

Georgia, Teal (1962) found that 45% of the marsh production was exported by tides as detritus and likely supported a high estuarine secondary production. Teal's (1962) model was later termed the outwelling hypothesis, which is the detrital flux from marsh estuaries (Odum 1968). Other studies supported this view, resulting in the general conclusion that marsh detritus is responsible for high secondary production in estuarine ecosystems (Day *et al.* 1973, Odum *et al.* 1973, Odum 1980). In contrast, Nixon (1980) suggested that the export of detritus from tidal marshes may contribute to the standing crop of open-water primary producers, but may not result in greater fisheries production than is found in other coastal areas without saltmarsh organic supplements.

Studies with stable carbon isotopes have tested aspects of the outwelling hypothesis. In the same Georgia estuaries originally studied by Teal (1962), Haines (1976) found that fiddler crabs (*Uca pugnax*) feed mainly (57-83%) on algal carbon (benthic diatoms) instead of *Spartina alterniflora* carbon. Further Georgia studies indicated some distinctions in energy flows to different groups of consumers. Carbon isotopic values of marsh snails and insects were closer to those of *S. alterniflora*, but deposit feeding crabs, mud snails and filter-feeding bivalves were similar to those of benthic algae and phytoplankton in Georgia estuaries (Haines and Montague 1979). In another saltmarsh study at Carpinteria, California, macroinvertebrates had carbon isotopic values that were closer to algal values than to *Salicornia virginica* values (Page 1997); benthic microalgae had enriched  $\delta^{13}\text{C}$  values (approx. -16.5‰), whereas *S. virginica* values are depleted (approx. -27.5‰). If detritus from marsh plants were really important, fauna feeding on detritus in *S. virginica* marshes should strongly shift from enriched  $\delta^{13}\text{C}$  values to more negative values, but this was not observed in Carpinteria



salt marsh (Page 1997). In Georgia estuaries, Haines (1977) found that carbon isotopic values of organic seston did not match marsh detritus values, but resembled phytoplankton values. Also, in Barataria Bay, Louisiana, carbon isotopic values of juvenile brown shrimp were depleted in individuals collected near the marsh, suggesting low influence of *S. alterniflora* as a food source (Fry 1983). Thus, an alternative view is that algal production may contribute the majority of carbon cycling through estuarine fauna (Kneib *et al.* 1980, Currin *et al.* 1995). These findings support a shift from the outwelling paradigm suggesting that marsh detritus may not be the most important source sustaining the secondary production in estuaries.

Other studies using a combination of carbon, nitrogen, and sulfur stable isotopic analyses offer some support for both the outwelling and algal dominance views, indicating that *Spartina* and phytoplankton can have similar contributions as energy sources for estuarine food webs and benthic algae could have some importance as well (Peterson *et al.* 1985, 1986, Peterson and Howarth 1987). However, these authors were not able to determine benthic algae isotopic values and, interestingly, later studies showed that several consumers have values close to benthic algae (Currin *et al.* 1995).

Commercial and recreational fisheries are key components of Louisiana's economic resources (Chesney *et al.* 2000). Information needed for the stewardship of these fisheries and the food webs that support them is essential in the presence of environmental degradation, including wetland loss and nutrient over-enrichment. To this end, I used stable isotopes analyses: (1) to determine dependence on *S. alterniflora* by fishes and macroinvertebrates residing in Louisiana marsh estuaries, (2) to determine the dominant trophic pathway (detritus vs. algal) in these areas, and (3) to explore whether

differences in trophic pathways are influenced by proximity to marshes, especially to the marsh edge. This study tests the hypothesis that marsh detritus is the dominant food source in Louisiana estuaries.

This study used an unconventional interpretation of  $\delta^{13}\text{C}$  to estimate the relative importance of several primary producers to the diet of estuarine communities. This method estimates the minimum and maximum contribution of primary producers rather than a fixed average value. This min-max interpretation is necessary due to the structure of the data, where there are too many sources and not enough tracers (Phillips and Gregg 2003). No unique or average solution is possible in such cases, but it is still possible to determine minimum and maximum contributions, and this range constrains further interpretations. Min-max values come from pairwise comparisons using the  $\delta^{13}\text{C}$  values of three producers as end members and the  $\delta^{13}\text{C}$  value of a consumer after all possible combinations are explored (Figure 4.1a). Wide ranges in the results of mixing equations are not too informative, but small ranges are more useful (Figure 4.1b). The min and max relative contribution provided by the mixing model is calculated from the mean  $\delta^{13}\text{C}$  values of the consumer, which is the natural average of all sources taken by a given consumer. Nevertheless, there is some variability in these estimates, especially due to sampling variability associated with the consumer. Thus, since the mean value of the consumer has sampling variability, min and max  $\delta^{13}\text{C}$  values are provided with confidence limits that reflect the variability in the consumer's  $\delta^{13}\text{C}$  values. Variability associated with food source isotopic value is present also, but integrated average through trophic pathways using average values for food sources and letting consumers isotope values vary to obtain error estimates in this study provided minimum errors for these

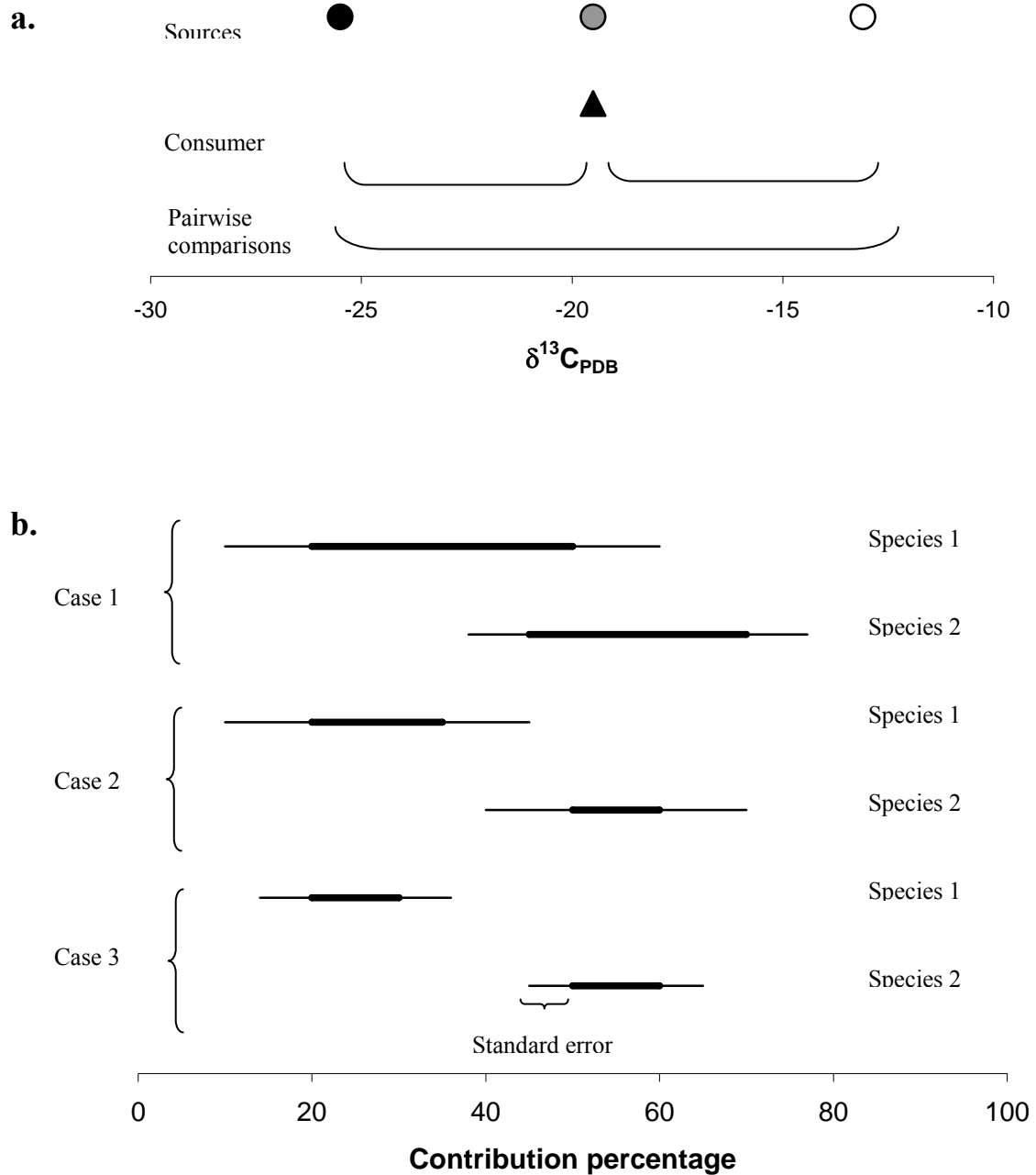


Figure 4.1. Relative contribution of primary producers to the diet of the estuarine community. (a) Minimum and maximum values come from pairwise comparisons of all possible contributions. (b) Min and max ranges are represented by thick lines and standard error by thin lines. Case 1 = species min and max overlap, case 2 = species standard error overlap, and case 3 = species do not overlap. Diet of species 1 and 2 are not considered significantly different for cases 1 and 2, but are different for case 3.

min-max models. This min-max method is most appropriate to disprove a food source as important for the diet of particular estuarine fauna species. Phytoplankton, benthic microalgae, and *Spartina alterniflora* values used in the model were taken from a previous study in nearby Louisiana marshes (Maddi 2003).

## **Materials and Methods**

### **Study Area**

The study was conducted near Cocodrie, Louisiana in the Terrebonne-Timbalier bay system (Figure 4.2). The study area is now isolated largely from the influence of the Mississippi River by a levee system that permits only minimal sediment input (Delaune *et al.* 1987) and is characterized by shallow bays, channels, and small ponds, with fine sediments, turbid waters, and salinities typically ranging between 0 and 28 psu throughout the year (<http://weather.lumcon.edu/stationdata.asp>). Tides are predominantly diurnal with a mean range of approximately 0.4 m, and are often wind-dominated (Shirzad *et al.* 1989; <http://weather.lumcon.edu/stationdata.asp>). The study area is within the saline marsh category (Chabreck and Linscombe 1991) dominated by the smooth cordgrass, *Spartina alterniflora* (Fry *et al.* 2003, Baltz *et al.* in review). The marsh is now classified as coastal submergent, since transgression has been dominant (Stevenson *et al.* 1986), following active delta development that occurred between 800 and 1,200 years ago (Penland *et al.* 1987). The deltaic sediments are rapidly subsiding, and relative sea-level rise rates for the area are estimated at 1.1-1.3 cm yr<sup>-1</sup> (Penland *et al.* 1988).

### **Sample Collection**

Fishes and macroinvertebrates were collected using a drop sampler, a clear acrylic cylinder (1.2 m diameter and 1.2 m height) with a metal ring on the bottom. It was

released from a boom attached to a small boat (Arrivillaga and Baltz 1999, Baltz *et al.* in review). Nekton were removed from the sampler by thoroughly sweeping the enclosed volume with fine mesh nets (Cummings model 270-12, 5 mm mesh) repeatedly until three successive passes yielded no additional organisms (Duffy and Baltz 1998).

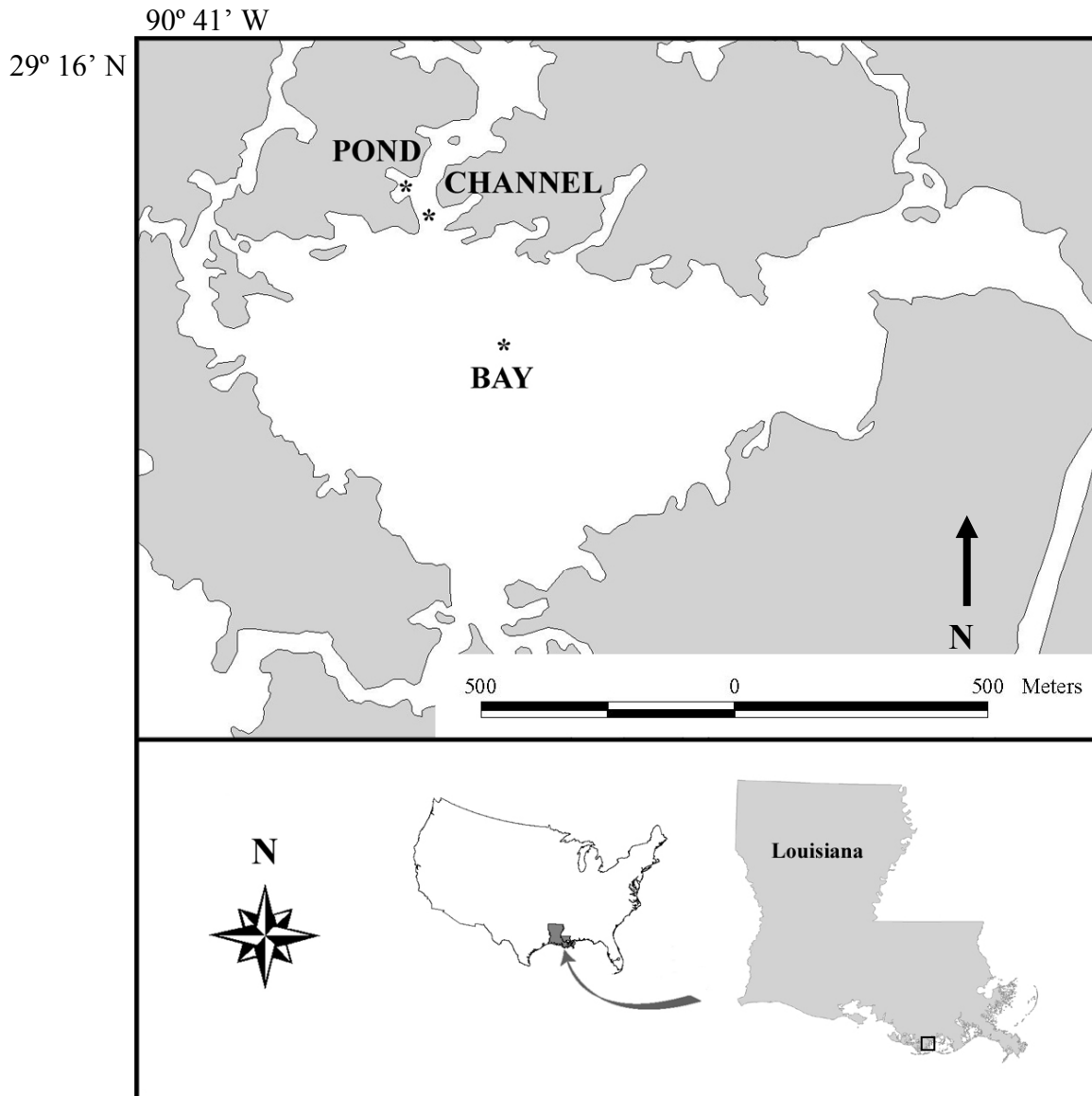


Figure 4.2. Study area indicating pond, channel, and shallow bay locations near the Louisiana Universities Marine Consortium (LUMCON) in Terrebone Bay, Louisiana.

Sampling was stratified by habitat type, location, and season. Four samples were taken at the marsh edge ( $< 1$  m from the edge) and four in open water ( $> 1$  m from edge), in each location strata (i.e., bay, channel, and pond in Figure 4.2), and each season for a total of 96 samples. Seasonal sampling included Fall of 2000 (September-November), Winter of 2000-2001 (November-February), Spring of 2001 (March-May), and Summer of 2001 (June- August) collections. To ensure that all samples were independent, careful placement and collection avoided interference with subsequent samples. Samples were field sorted and then iced and transported to the laboratory where they were frozen pending analyses.

A total of six environmental variables were examined at each sampling site including minimum and maximum depths (cm), salinity (psu), temperature ( $^{\circ}\text{C}$ ), dissolved oxygen ( $\text{DO mg l}^{-1}$ ), and distance from the marsh edge. Temperature, salinity, and dissolved oxygen were determined by using a Hydrolab model SRV2-SU meter. Median depth and substrate relief (i.e.,  $\Delta \text{ depth} = \text{max} - \text{min depths}$ ) were calculated using the minimum and maximum depth values. Water samples were collected to determine turbidity (NTU) and chlorophyll *a* ( $\mu\text{g l}^{-1}$ ) in the lab. These samples were maintained in cold storage until turbidity samples were read on a Hach 2100N turbidimeter and chlorophyll *a* values determined by acetone extraction. Fishes and macroinvertebrates were identified to species (Hoese and Moore 1977, Hopkins *et al.* 1989, Williams 1984) and measured to the nearest millimeter standard length (SL) for fish, total length (TL) for shrimp, and carapace width (CW) for crabs. Length for shrimp was measured from the tip of the rostrum to the tip of the telson.

After thawing, excised muscle tissue samples from individual organisms were dried at 60 °C for 48 hours. After grinding each sample, subsamples between 0.45 and 0.75 mg were weighed into small tin foil cups. These samples were used to determine the  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values using a Carlo Erba NA 1500 elemental analyzer linked to a Finnigan Delta Plus ratio mass spectrometer (Fry *et al.* 1992, 2003). Size-series of glycine (0.15-0.95 mg) and bovine liver (0.4-0.7 mg) were used for calibration and to correct for background blanks in the samples (Fry *et al.* 1992).

Additionally, a two-week field enclosure experiment was conducted in July of 2001 to test for differences in carbon and nitrogen isotopes of naked goby among three habitat types: (1) marsh edge including *Spartina alterniflora* shoots, (2) marsh edge without *S. alterniflora* shoots, and (3) open water. Twelve enclosures were used. A second identical experiment also with 12 enclosures was performed in the following month, August, at 12 different sites to avoid food resources depletion. The open-water enclosures were at least 3 m from the marsh edge. The marsh-edge enclosures were within 1 m from the marsh edge. Enclosures with vegetation overlapped the marsh-water interface with half including shoots of *S. alterniflora*. Cylindrical clear acrylic enclosures, approximately 0.75 m in diameter and 1.25 m in height, were placed 0.25 m deep into the mud. The enclosures had 14 holes of 10 cm diameter, protected with a mesh (5 x 3.5 mm) to prevent escapement of fish while allowing water circulation. The top of the enclosures was above the water throughout the experiments and covered by a mesh (10 x 10 mm) to discourage avian predators. Four enclosures were placed in each of three habitat types for two weeks. Six fish were confined in each enclosure for a total of 144 total individuals. This was a density of 13.4 fish m<sup>-2</sup>, whereas natural density of naked

goby in this study averaged 2.1 individuals m<sup>-2</sup>, but ranged up to 4 individuals m<sup>-2</sup>. After two weeks, individuals were recovered and stable carbon and nitrogen values were determined as previously described.

### Data Analysis

Nekton isotopic values were reported in the standard  $\delta$  notation representing the ratio of heavy to light isotopes as follows:

$$\delta X = [(R_{\text{sample}} - R_{\text{standard}}) / R_{\text{standard}}] * 1000$$

where X is <sup>13</sup>C or <sup>15</sup>N and R is <sup>13</sup>C/<sup>12</sup>C or <sup>15</sup>N/<sup>14</sup>N, respectively. Isotopic values are expressed as relative values on a per mil (‰) basis (Currin *et al.* 1995). Vienna Pee Dee Belemnite (VPDB) and atmospheric nitrogen (N<sub>2-air</sub>) were used, respectively as the C and N isotopic standards.

For comparisons of nekton isotopic values obtained in this study, carbon and nitrogen values of primary producers and meiofauna samples determined by Maddi (2003) were used; these samples were collected 2 m from the marsh edge in an intertidal mudflat near my study area in summer and fall of 2001 and winter and spring of 2002. Primary producers included particulate organic matter (POM) used as a proxy of phytoplankton, benthic microalgae (BMI), and standing *Spartina alterniflora*. Meiofauna included harpacticoid copepods such as *Coullana* sp., *Pseudostenhelia wellsi*, two species from the family Laophontidae (*Onychocamptus mohammed* and *Paronchocamptus huntsmani* in a proportion of 80-20%), nematodes, ostracods, and juvenile polychaetes, *Streblospio benedicti* (Maddi 2003).

Carbon and nitrogen isotopic values of the most abundant fishes and macroinvertebrates were plotted to explore possible variations among seasons, locations,



and habitat types. For abundant species, samples were grouped into 10 mm size classes and stable carbon and nitrogen values variations by size classes were tested by a one-way ANOVA. Since stable carbon and nitrogen values were not normally distributed, statistical analyses were performed with transformed stable carbon and nitrogen isotopic values using  $\log_{10}(x + 26)$  and  $\log_{10}(x + 1)$ , respectively. This methodology allowed all the carbon values to be positive since the most depleted carbon value for the most abundant species was  $> -26\text{‰}$ . Residuals and residual plots and biplots were examined to ensure that assumptions of normality and variance homogeneity of residuals were met after transformation.

Differences in carbon and nitrogen stable isotopic values were assessed for predator species in a three-way multivariate analysis of variance (MANOVA) by season, location, and habitat type as main factors (using general linear model and least-square mean procedure, SAS Institute 1996). Specific differences in stable carbon and nitrogen values among factors were examined in univariate analyses (ANOVA) and pairwise comparisons were conducted using Tukey's adjustment. For the field experiments with naked goby, a two-way MANOVA was used to test differences in stable carbon and nitrogen isotopic values among habitats types and replicate experiments. Data transformations were performed as mentioned above.

A multivariate multiple regression analysis was performed to determine which environmental variables were linearly related with the carbon and nitrogen values of the nekton. Stable carbon and nitrogen values were transformed as mentioned above and environmental variables were transformed using  $\log_{10}(x + 1)$ . Collinearity between independent variables was assessed by examining variance inflation factors (VIF; Allison

1991). Variables were determined to be primarily independent if VIF values were close to 1, and no individual value was greater than 10. Variables included in the multiple regressions were selected by using a stepwise approach. An entry and exit p-value of 0.15 was chosen to identify a suite of variables that were important in describing the given independent variable. The highest F-value was used at each step to identify the variable that contributed the most to the overall  $R^2$  value. Each variable was chosen in the same manner; however, after each addition all variables in the model were reexamined to ensure that they met the entry criterion (i.e.,  $p < 0.15$ ). Variables no longer meeting the criterion were eliminated from the model.

Relative contributions of primary producers to the diets of nekton species were estimated using a three-source mixing model that provided the range (min and max) of contributions after all possible combinations were explored as follows: the minimum and maximum solutions derive from two mixing equations:  $f_1 + f_2 + f_3 = 1$ , and  $\delta_1 f_1 + \delta_2 f_2 + \delta_3 f_3 = \delta C * 1$ , where  $f$  gives the fractional (proportion) contribution of each of the three sources denoted by subscripts 1-3, the second equation gives the weighted average mixing for the three sources with isotopic values of  $\delta_1$ ,  $\delta_2$ , and  $\delta_3$ , and  $\delta C$  is the isotopic composition of the consumer. Carbon isotopic values of phytoplankton, benthic microalgae, and *Spartina alterniflora* were used as possible sources for these analyses. With two equations and three unknown fractional contributions, there is no unique solution, but minimum and maximum estimates can still be obtained for each of the three primary producers in the following manner. Each of the fractions is sequentially set equal to zero to have two simpler equations that can be solved. For example, if  $f_1 = 0$ , then the equations are  $f_2 + f_3 = 1$ ,  $\delta_2 f_2 + \delta_3 f_3 = \delta C$ , and the solutions for  $f_3$  and  $f_2$  are  $f_3 =$

$(\delta C - \delta_2)/(\delta_3 - \delta_2)$  and  $f_2 = 1 - f_3$ . Doing the parallel exercises for  $f_2 = 0$  and then  $f_3 = 0$  yields three sets of solutions for  $f_1$ ,  $f_2$  and  $f_3$ , and minimum and maximum solutions can be obtained from examining the solution sets in which all three fractions are in the 0 to 1 range. With this model approach, the annual relative contributions of phytoplankton, benthic microalgae, and *S. alterniflora* were estimated for each nekton species. Also, seasonal contributions of *S. alterniflora* were estimated for the most abundant species. Finally, minimum and maximum relative contributions of *S. alterniflora* were estimated for the community after weighing by nekton densities (Chapter 2), and a biomass factor (1 for macroinvertebrates and 2 for fishes).

Due to a process known as fractionation (Fry 2003), consumers are usually 2.2‰ enriched in  $\delta^{15}\text{N}$  and 0.5‰ depleted in  $\delta^{13}\text{C}$  in comparison with their food source (McCutchan *et al.* 2003). Thus, values used in the mixing models were corrected for fractionation prior to analyses in four steps as follows:

1. The  $\delta^{15}\text{N}$  value of trophic level one was determined:

The consumers with the lowest  $\delta^{15}\text{N}$  values were identified and their mean was calculated. These consumers were three meiofauna species, *Coullana* sp., *Pseudostenhelia wellsi*, and ostracods taken by Maddi (2003), and the common mud crab of this study (Figure 4.3). The mean  $\delta^{15}\text{N}$  value for this trophic level was 7.7‰.

2. The  $\delta^{15}\text{N}$  value of the source was determined:

Trophic level zero representing the mean  $\delta^{15}\text{N}$  value of plants and detritus is 2.2‰ below trophic level one as follows:

$$\delta^{15}\text{N source} = (\delta^{15}\text{N trophic level one} - \delta^{15}\text{N fractionation})$$

thus:

$$5.5\text{‰} = (7.7\text{‰} - 2.2\text{‰})$$

3. The trophic level (TL) of each consumer was determined:

$$\text{TL consumer} = (\delta^{15}\text{N consumer} - \delta^{15}\text{N source}) / \delta^{15}\text{N fractionation}$$

for example, brown shrimp  $\delta^{15}\text{N}$  value was 10.1‰, then:

$$\text{TL}_{\text{consumer}} = 2.1 = (10.1\text{‰} - 5.5\text{‰}) / 2.2\text{‰}$$

4. Consumer  $\delta^{13}\text{C}$  value was corrected for fractionation:

$$\delta^{13}\text{C corrected} = \delta^{13}\text{C consumer} - (\text{TL consumer} * \delta^{13}\text{C fractionation})$$

the  $\delta^{13}\text{C}$  value of brown shrimp was -19.6, then:

$$-20.6\text{‰} = -19.6\text{‰} - (2.1 * 0.5)$$

Corrected  $\delta^{13}\text{C}$  values of consumers were used to estimate primary producers' relative contributions using the min-max model as described before.

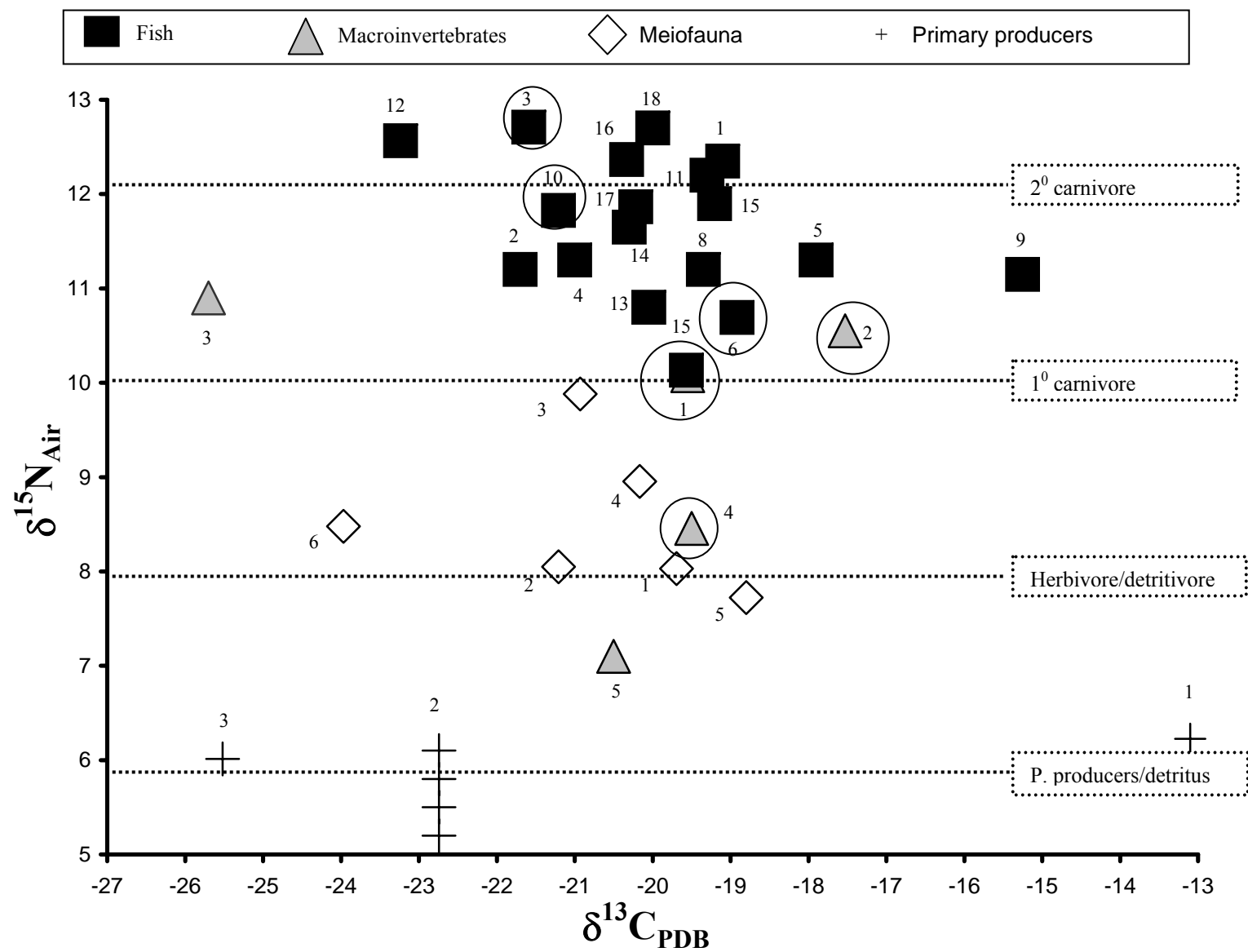
## Results

Nekton species used in isotopic analyses represented samples from four seasons, three locations, and two habitat types. A total of 153 individuals of 23 species were used for isotopic analysis where 60% of all individuals captured were fishes and 40% were macroinvertebrates. The 153 individuals represented 15% of the total number of organisms collected in this study. Fish and macroinvertebrate  $\delta^{13}\text{C}$  values had similar ranges of -25.4 to -14.7 ‰ and -26.2 to -14.5 ‰, respectively. The  $\delta^{15}\text{N}$  values ranged from 9.0 to 14.6 ‰ for fishes and 3.8 to 12.7 ‰ for macroinvertebrates (Figure 4.3). White shrimp had the most negative  $\delta^{13}\text{C}$  values closest to those of phytoplankton, whereas mummichogs had the least negative  $\delta^{13}\text{C}$  closest to those of *Spartina alterniflora*. Mud crabs had the lowest  $\delta^{15}\text{N}$  value of all fishes and macroinvertebrates sampled. The  $\delta^{15}\text{N}$  values indicated that most nekton species, primarily fishes, were

Primary producers	+ 1. <i>Spartina alterniflora</i> + 2. Benthic microalgae + 3. Phytoplankton
Meiofauna	◇ 1. <i>Pseudostenhelia wellsi</i> ◇ 2. <i>Coullana sp.</i> ◇ 3. Laophontids ◇ 4. Nematodes ◇ 5. Ostracods ◇ 6. <i>Streblospio benedicti</i>
Macroinvertebrates	△ 1. Brown shrimp △ 2. Grass shrimp △ 3. White shrimp △ 4. Blue crab △ 5. Mud crab
Fishes	■ 1. Atlantic croaker ■ 2. Atlantic menhaden ■ 3. Bay anchovy ■ 4. Blackcheek tongefish ■ 5. Black drum ■ 6. Darter goby ■ 7. Green goby ■ 8. Inland silverside ■ 9. Mummichog ■ 10. Naked goby ■ 11. Rough silverside ■ 12. Sand seatrout ■ 13. Highpin goby ■ 14. Silver perch ■ 15. Speckled worm eel ■ 16. Spot ■ 17. Spotted seatrout ■ 18. Star drum

Figure 4.3. Dual plot of annual mean carbon and nitrogen isotope values of primary producers (circles), meiofauna (diamonds), macroinvertebrates (triangles), and fish (squares). Primary producers and meiofauna mean values taken from Maddi (2003). Trophic levels determined by carbon isotopic values every 2.2 ‰ (dashed line; McCutchan et al. 2003). The most abundant nekton species are encircled. Benthic microalgae (BMI) nitrogen isotopic values were not determined.

(Figure con'd.)



separated from their potential food source (primary producers) by two or three trophic levels assuming a 2.2 ‰  $\delta^{15}\text{N}$  increase per trophic level (McCutchan *et al.* 2003). Generally  $\delta^{13}\text{C}$  values ( $\pm$  SE) for fishes and macroinvertebrates were intermediate between annual averages values of primary producers measured by Maddi (2003): phytoplankton ( $-25.5 \pm 0.1$  ‰), standing *Spartina alterniflora* ( $-13.1 \pm 0.01$  ‰), and microalgae values ( $-22.7 \pm 0.1$  ‰).

Univariate analyses of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values among size classes of the most abundant species indicated that there were only two species with size-specific changes in isotopic composition. Notably, carbon isotopic values were different between two size classes for blue crab (ANOVA,  $F_{1,12} \leq 12.29$ ,  $p \geq 0.0043$ ) and nitrogen isotopic values were significantly different for four size classes of darter goby (ANOVA,  $F_{3,9} \leq 9.85$ ,  $p \geq 0.0033$ ). Blue crabs between 11-19 mm CW had lower carbon isotopic values ( $-18.7 \pm 0.43$  ‰) than individuals between 20-29 mm ( $-22.3 \pm 2.2$  ‰). Larger individuals of darter goby (40-49 mm) had higher isotopic nitrogen values ( $12.2 \pm 0.35$  ‰) than individuals of the other three size classes (10-39 mm,  $10.23 \pm 0.08$  ‰). Carbon and nitrogen isotopic values did not vary among size classes for the remaining species ( $F_{7,12} \leq 2.82$ ,  $p \geq 0.0551$ ).

The stable carbon and nitrogen isotopic values of the most abundant species were significantly different among seasons and habitat types. Insufficient degrees of freedom precluded a test of the three-way interaction of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values in the three-way MANOVA. The two-way interactions (MANOVA,  $F_{4,26} \leq 2.45$ ,  $p \geq 0.0714$ ) and the location variation (MANOVA,  $F_{4,26} = 1.20$ ,  $p = 0.3357$ ) were not significant, but  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values varied among habitat types (MANOVA,  $F_{2,13} \geq 3.90$ ,  $p \leq 0.0249$ ) and

seasons (MANOVA,  $F_{4,26} \geq 6.47$ ,  $p \leq 0.0009$ ). Since interactions among main factors were not significant,  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values by habitat type, location, and season of six common species were examined in detail (Figures 4.4 to 4.9).

In univariate analyses of variance, one species had habitat type variation and four species had seasonal variations, but overall isotopes were uniform because of the limited number of samples analyzed (five significant differences of 84 possible). Bay anchovy carbon and nitrogen isotopic values were not different among habitat types or seasons (Table 4.1, Figure 4.4). Significant variation between habitat types was detected for darter goby  $\delta^{13}\text{C}$  values (ANOVA,  $F_{1,5} = 10.04$ ,  $p = 0.0248$ ) with enriched values along the marsh edge (Table 4.1, Figure 4.5a). The  $\delta^{13}\text{C}$  values of naked goby, daggerblade grass shrimp, and blue crab varied among seasons (ANOVA,  $F_{3,3} \geq 75.98$ ,  $p \leq 0.0025$ ). The  $\delta^{13}\text{C}$  values of naked goby were intermediate in fall, enriched in winter, and depleted in summer (Table 4.1, Figure 4.6c). The  $\delta^{13}\text{C}$  values of daggerblade grass shrimp were enriched in winter and spring and depleted in fall and summer (Table 4.1, Figure 4.7c). The  $\delta^{13}\text{C}$  values of blue crab were enriched in fall and depleted in other seasons with the lowest value in summer (Table 4.1, Figure 4.8c). However, these results may also reflect size difference since individuals of blue crab captured in fall and spring were smaller than in winter and summer. The  $\delta^{15}\text{N}$  values of brown shrimp varied among seasons (ANOVA,  $F_{2,8} = 11.63$ ,  $p = 0.0043$ ) with higher values in spring than summer and fall (Table 4.1, Figure 4.9c).

In the replicated field experiment, a total of 61 of 144 of naked gobies, between 22- 31 mm SL, were recovered from 24 enclosures. No significant differences in the stable carbon and nitrogen values were detected between experiments or among habitat



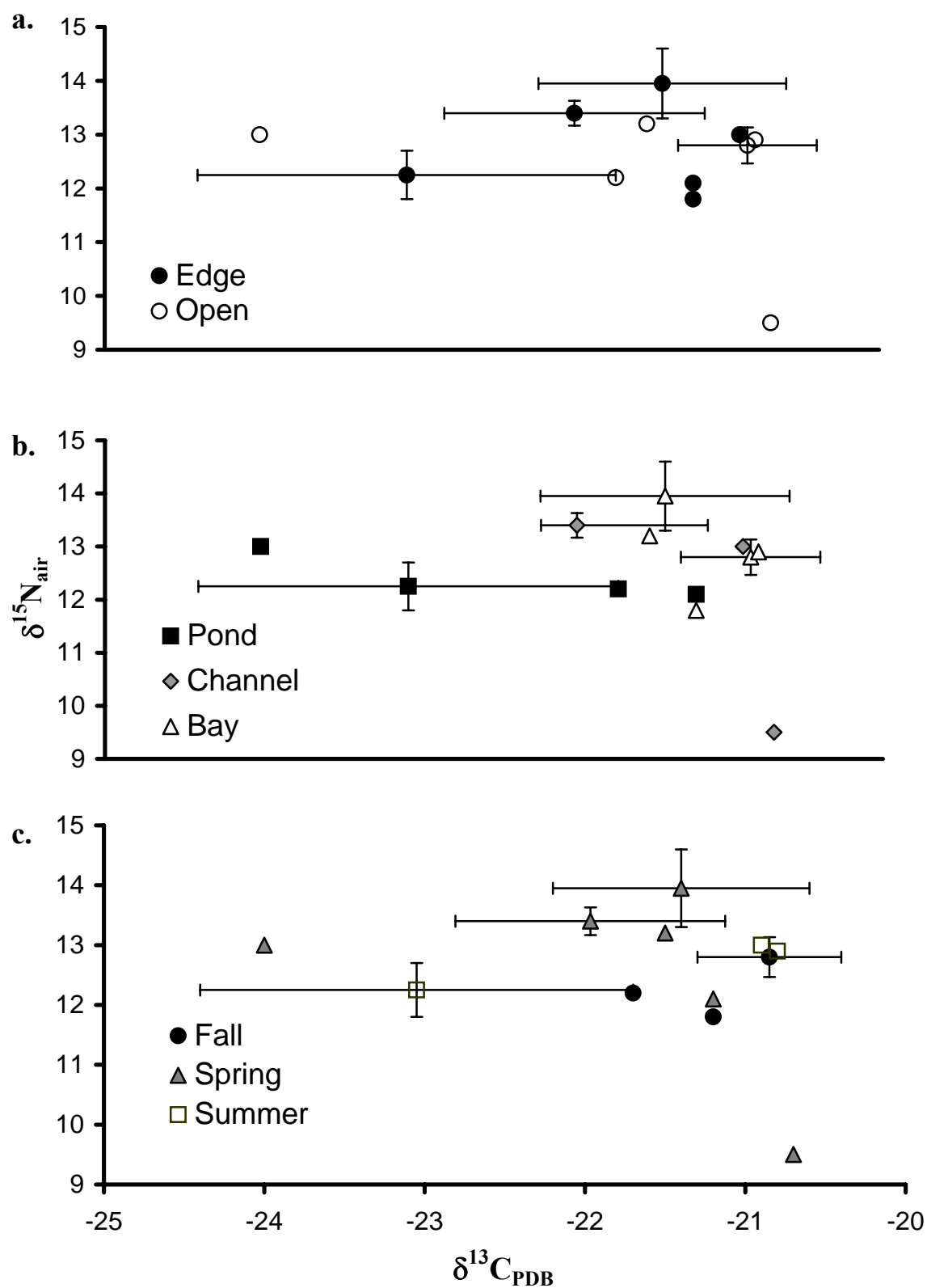


Figure 4.4. Dual plots of mean carbon and nitrogen isotope values of bay anchovy by (a) habitat types, (b) locations, and (c) seasons.

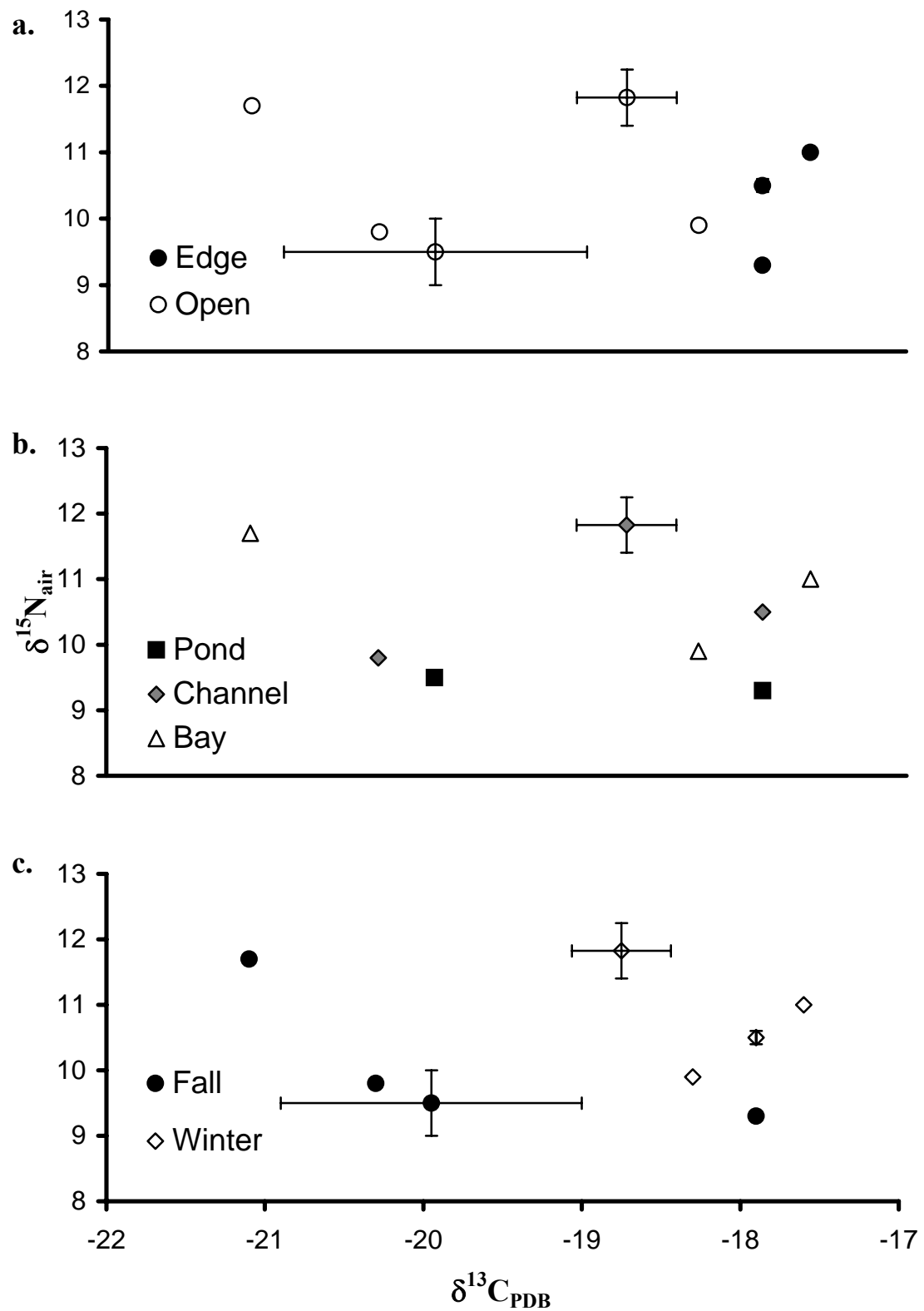


Figure 4.5. Dual plots of mean carbon and nitrogen isotope values of darter goby by (a) habitat types, (b) locations, and (c) seasons.

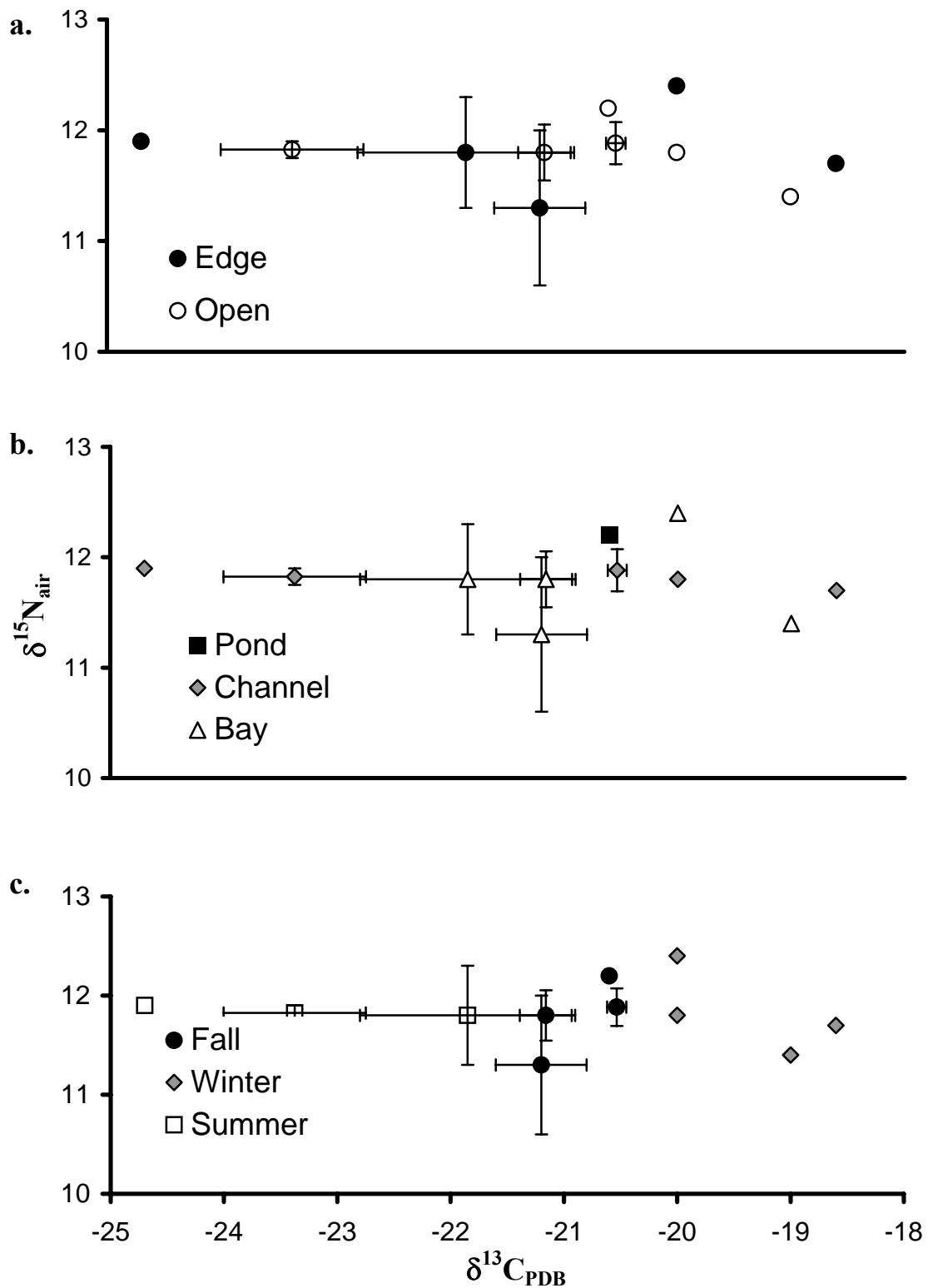


Figure 4.6. Dual plots of mean carbon and nitrogen isotope values of naked goby by (a) habitat types, (b) locations, and (c) seasons.

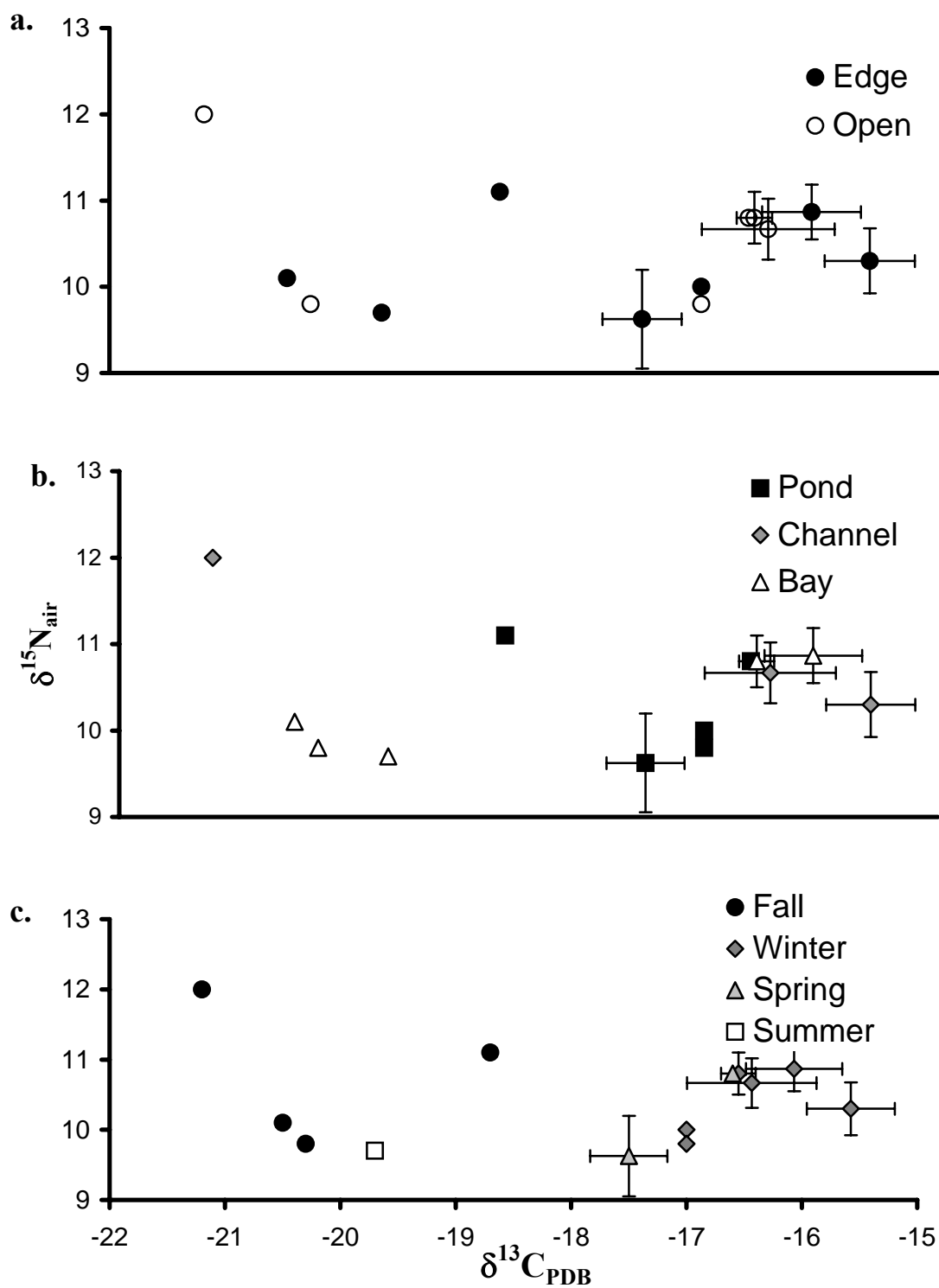


Figure 4.7. Dual plots of mean carbon and nitrogen isotope values of daggerblade grass shrimp by (a) habitat types, (b) locations, and (c) seasons.

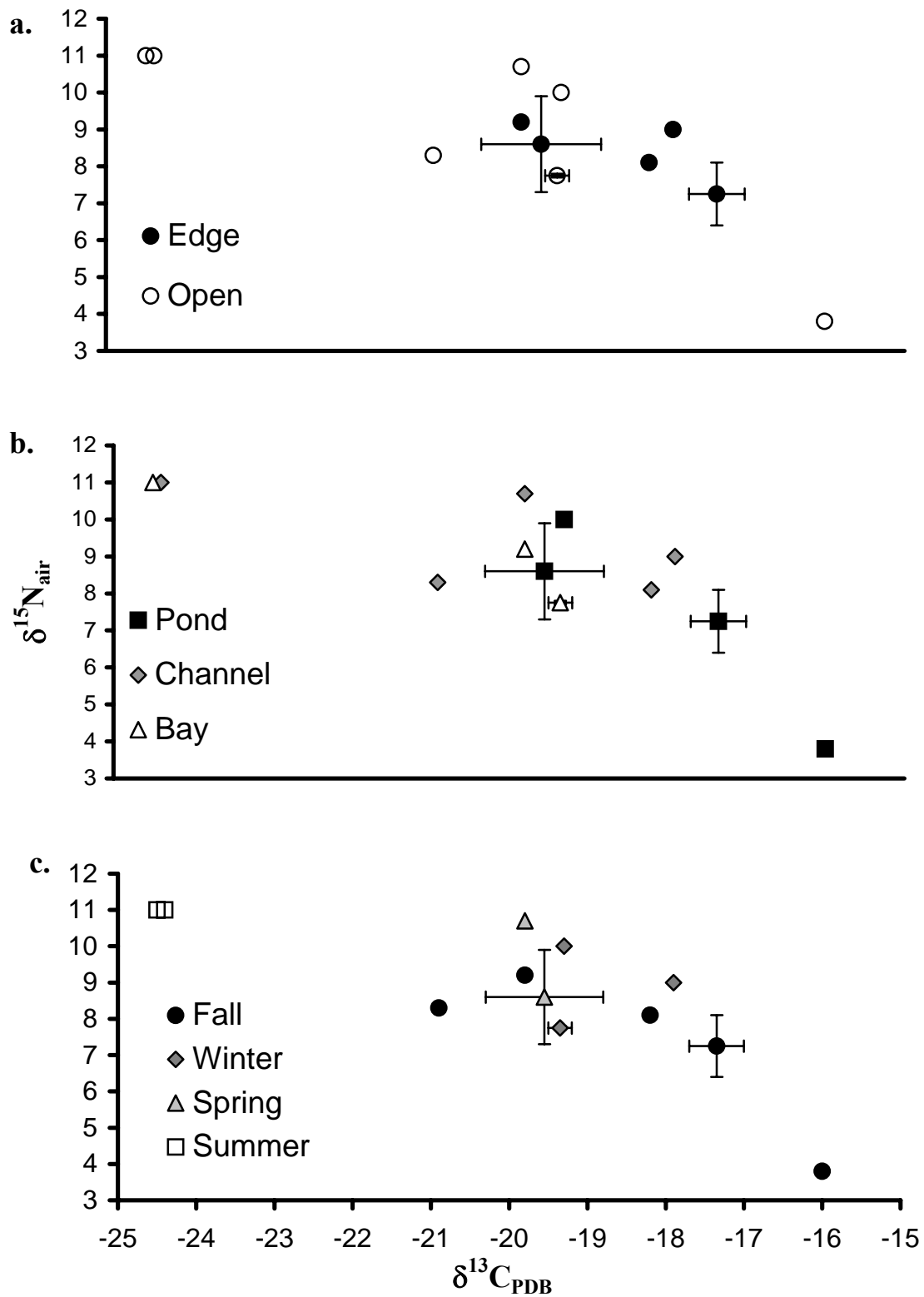


Figure 4.8. Dual plots of mean carbon and nitrogen isotope values of blue crab by (a) habitat types, (b) locations, and (c) seasons.

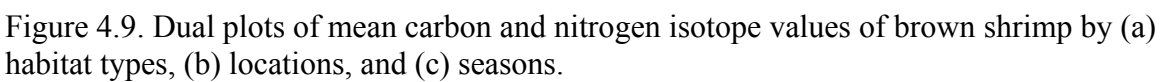


Table 4.1. Means of stable carbon and nitrogen isotopic values ( $\pm$  SE) for the most abundant fishes and invertebrates among seasons and habitats types calculated by least square means. Pairwise comparisons (Tukey's adjustment) are represented by letters reading vertically for each species ( $p \leq 0.05$ ). Stable carbon and nitrogen isotopic values with significant variations represented in bold print.

Season	Habitat	Bay anchovy			Darter goby†			Naked goby††		
		N	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	N	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	N	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Fall	Edge	1	-21.2	11.8	1	<b>-17.9 A</b>	9.3	2	<b>-20.5 <math>\pm</math> 0.25 AB</b>	11.5 $\pm$ 0.45
	Open	5	-21.0 $\pm$ 0.38	12.7 $\pm$ 0.28	4	<b>-20.3 <math>\pm</math> 0.47 B</b>	10.1 $\pm$ 0.57	12	<b>-20.8 <math>\pm</math> 0.13 A</b>	11.9 $\pm$ 0.14
Winter	Edge	0			3	<b>-17.8 <math>\pm</math> 0.10 A</b>	10.7 $\pm$ 0.17	2	<b>-19.3 <math>\pm</math> 0.70 AB</b>	12.0 $\pm$ 0.35
	Open	0			5	<b>-18.7 <math>\pm</math> 0.26 B</b>	11.4 $\pm$ 0.50	2	<b>-19.5 <math>\pm</math> 0.50 A</b>	11.6 $\pm$ 0.20
Spring	Edge	6	-21.6 $\pm$ 0.45	13.4 $\pm$ 0.34	0			0		
	Open	3	-22.1 $\pm$ 0.99	11.9 $\pm$ 1.20	0			0		
Summer	Edge	3	-22.3 $\pm$ 1.00	12.5 $\pm$ 0.36	0			3	<b>-22.8 <math>\pm</math> 1.09 B</b>	11.8 $\pm$ 0.29
	Open	1	-20.8	12.9	0			4	<b>-24.4 <math>\pm</math> 0.62 B</b>	11.8 $\pm$ 0.07
Total		19	-21.6 $\pm$ 0.28	12.7 $\pm$ 0.24	13	-18.9 $\pm$ 0.33	10.7 $\pm$ 0.31	25	-21.3 $\pm$ -0.31	11.8 $\pm$ 0.11
Season	Habitat	Blue crab††			Brown shrimp††			Daggerblade grass shrimp††		
		N	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$	N	$\delta^{13}\text{C}$	Nitrogen	N	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Fall	Edge	4	<b>-18.2 <math>\pm</math> 0.59 A</b>	7.95 $\pm$ 0.58	5	-19.4 $\pm$ 0.43	<b>9.3 <math>\pm</math> 0.38 A</b>	2	<b>-19.6 <math>\pm</math> 0.90 A</b>	10.6 $\pm$ 0.50
	Open	2	<b>-18.4 <math>\pm</math> 2.45 A</b>	6.0 $\pm$ 2.25	6	-18.9 $\pm$ 0.84	<b>9.4 <math>\pm</math> 0.034 A</b>	2	<b>-20.7 <math>\pm</math> 0.45 A</b>	10.9 $\pm$ 1.10
Winter	Edge	1	<b>-17.9 A</b>	9.0	0			8	<b>-15.9 <math>\pm</math> 0.28 BC</b>	10.5 $\pm$ 0.24
	Open	3	<b>-19.3 <math>\pm</math> 0.09 AB</b>	8.5 $\pm$ 0.75	0			6	<b>-16.6 <math>\pm</math> 0.27 BC</b>	10.6 $\pm$ 0.23
Spring	Edge	1	<b>-18.8</b>	7.3	3	-20.0 $\pm$ 0.71	<b>11.3 <math>\pm</math> 0.40 B</b>	4	<b>-17.5 <math>\pm</math> 0.33 AB</b>	9.6 $\pm$ 0.57
	Open	1	<b>-19.8 AB</b>	10.7	4	-19.7 $\pm$ 0.60	<b>11.3 <math>\pm</math> 0.61 B</b>	1	<b>-16.6 AC</b>	10.8
Summer	Edge	0			1	-21.4	<b>9.3 A</b>	1	<b>-19.7 A</b>	9.7
	Open	2	<b>-24.4 <math>\pm</math> 0.05 B</b>	11.0 $\pm$ 0.00	0			0		
Total		14	-19.6 $\pm$ 0.15	8.6 $\pm$ 0.13	19	-19.5 $\pm$ 0.09	10.1 $\pm$ 0.07	24	-17.2 $\pm$ 0.05	10.4 $\pm$ 0.04

† Habitat type variation

†† Seasonal variation

types (MANOVA,  $F_{2, 17} \leq 2.69$ ,  $p \geq 0.0969$ ). Nevertheless, fish in enclosures that included vegetation had carbon isotopic values depleted by approx 1.4 ‰ compared to individuals in the unvegetated marsh-edge and open-water enclosures (Table 4.2).

Table 4.2. Means of stable carbon and nitrogen isotopic values ( $\pm$  SE) of naked goby confined to enclosures in three habitat types. Four experimental units per habitat type and experiment were used in the analysis for a total of 24. In both experiments, 61 of 144 fishes were recaptured.

Stable isotope	Experiment	Vegetated-edge	Unvegetated-edge	Open-water
$\delta^{13}\text{C}$	1	$-19.62 \pm 0.30$	$-18.34 \pm 0.15$	$-18.91 \pm 0.65$
	2	$-19.59 \pm 0.87$	$-18.2 \pm 0.22$	$-18.84 \pm 0.21$
$\delta^{15}\text{N}$	1	$9.74 \pm 0.31$	$9.25 \pm 0.17$	$9.72 \pm 0.11$
	2	$9.53 \pm 0.47$	$9.04 \pm 0.11$	$9.15 \pm 0.07$

In the stepwise multiple regression analyses using environmental variables to predict carbon and nitrogen value changes of abundant species (Table 4.3), all six models for carbon ( $F_{1, 17} \geq 4.11$ ,  $P \leq 0.0587$ ) and all six for nitrogen ( $F_{1, 23} \geq 3.15$ ,  $P \leq 0.0893$ ) were significant. Carbon isotopic value variations were related mainly to salinity and turbidity for four species, distance from the edge and median depth for two species, and temperature for one species, substrate relief ( $\Delta$  depth), dissolved oxygen, and chlorophyll *a* were not related to isotopic values of any species. Nitrogen isotopic value variations were related mainly to salinity and temperature for three species, turbidity,  $\Delta$  depth, dissolved oxygen and chlorophyll *a* for one species, and median depth and distance from the edge were not related to any species. Carbon isotopic models for median depth explained 77% of variation for darter goby and 47% for daggerblade grass shrimp and turbidity explained 66% of the variation for blue crab and 40% for naked goby. Nitrogen isotopic models for salinity explained 54% of variation for darter goby.



Table 4.3. Stepwise multiple regression analyses of stable carbon and nitrogen isotopic values of selected species and environmental variables with overall model  $R^2$ . The variables are reported in the order they were entered by the model, which means that variable 1 has the highest overall F value ( $p \leq 0.05$ ). The nature of the relationship between the biological and environmental variables are represented by signs and the squared partial correlations are represented in parentheses. The significance level for variables retained in each model was  $P < 0.05$ , except for italicized variables ( $0.15 > P > 0.05$ ). High partial correlations indicated in bold print.

Species	Isotope	$R^2$	Variable 1	Variable 2	Variable 3	F	P > F
Bay anchovy	$\delta^{13}\text{C}$	0.19	+ Salinity (0.19)			4.11	0.0587
	$\delta^{15}\text{N}$	0.47	- Chlorophyll <i>a</i> (0.37)	+ Temperature (0.10)		9.95	0.0058
Naked goby	$\delta^{13}\text{C}$	0.50	+ <b>Turbidity (0.40)</b>	+ Distance (0.10)		10.99	0.0005
	$\delta^{15}\text{N}$	0.12	- <i><math>\Delta</math> depth (0.12)</i>			3.15	0.0893
Darter goby	$\delta^{13}\text{C}$	0.86	- <b>Median depth (0.77)</b>	- Distance (0.09)		31.80	< 0.0001
	$\delta^{15}\text{N}$	0.54	- <b>Salinity (0.54)</b>			13.06	0.0041
Brown shrimp	$\delta^{13}\text{C}$	0.51	+ Salinity (0.33)	+ Turbidity (0.18)		8.45	0.0031
	$\delta^{15}\text{N}$	0.57	- Salinity (0.33)	- Temperature (0.13)	- Turbidity (0.11)	8.99	0.0008
Daggerblade grass shrimp	$\delta^{13}\text{C}$	0.70	- <b>Median depth (0.47)</b>	+ Turbidity (0.12)	- Salinity (0.11)	15.58	< 0.0001
	$\delta^{15}\text{N}$	0.34	+ Salinity (0.17)	- Temperature (0.17)		5.33	0.0134
Blue crab	$\delta^{13}\text{C}$	0.74	+ <b>Turbidity (0.66)</b>	- Temperature (0.04)	+ Salinity (0.04)	30.16	< 0.0001
	$\delta^{15}\text{N}$	0.29	+ Dissolved oxygen (0.29)			5.23	0.0396

The two-source mixing model for carbon indicated that *S. alterniflora* made a relatively low contribution to the diet of most estuarine nekton species (Table 4.4, Figure 4.10). Annual relative contribution of *S. alterniflora* was highest for mummichog (66-73%), whereas phytoplankton contribution was highest for sand seatrout (76-95%). Contributions from benthic microalgae were generally inadequately constrained and showed wide ranges, (i.e., 0-98% for naked goby). Nevertheless, wide ranges were detected for phytoplankton and benthic microalgae, whereas narrow ranges were identified for *S. alterniflora* for the most abundant nekton species (Table 4.4, Figure 4.10). Since narrow ranges are more informative, further analyses of relative contributions of primary producers were focused on *S. alterniflora*.

The relative contribution of *S. alterniflora* was on average higher in spring (44%) and fall (38%) than in winter (36%) and summer (23%) for the most abundant nekton species (Table 4.5, Figure 4.11). Blue crabs were more influenced by *S. alterniflora* in fall and daggerblade grass shrimp in winter, spring, and summer (Table 4.5, Figure 4.11). Overall algae sources combined (phytoplankton + benthic algae) relatively contributed to the diet of the nekton community more than twice than *S. alterniflora* (Figure 4.12). The minimum and maximum contributions of *S. alterniflora* to the studied estuarine nekton community were 15 and 34%, respectively (Table 4.6, Figure 4.10). Nevertheless, contributions were 21 and 38%, respectively, when calculated using weighted contributions including nekton densities (Chapter 2) and a biomass factor (1 for macroinvertebrates and 2 for fishes).

Table 4.4. Annual relative contribution (%) of primary producers to the diet of estuarine nekton calculated with the mixing formula using annual mean  $\delta^{13}\text{C}$  values of phytoplankton ( $-25.52 \pm 0.40\text{‰}$ ), benthic microalgae ( $-22.74 \pm 0.40\text{‰}$ ), and *Spartina alterniflora* ( $-13.0 \pm 0.04\text{‰}$ ) as end members reported by Maddi (2003). Species are ranked according with the maximum relative influence of *S. alterniflora* to their diets. Species selected for detailed statistical examination identified by an asterisk. Trophic position: 1 = primary consumer, 2 = secondary consumer, and 3 = tertiary consumer.

Nekton species	Common name	N	Trophic Position	Size range (mm)	Phytoplankton		Benthic algae		<i>Spartina alterniflora</i>	
					Min	Max	Min	Max	Min	Max
<i>Fundulus heteroclitus</i>	Mummichog	2	2.5	53-65	0	27	0	34	66	73
<i>Palaemonetes pugio</i> *	Daggerblade grass shrimp	24	2.3	25-36	0	44	0	56	44	56
<i>Pogonias cromis</i>	Black drum	1	2.6	31	0	48	0	62	38	52
<i>Ctenogobius boleosoma</i> *	Darter goby	13	2.3	18-47	0	55	0	71	29	45
<i>Callinectes sapidus</i> *	Blue crab	14	1.3	12-22	0	56	0	72	28	44
<i>Farfantepenaeus aztecus</i> *	Brown shrimp	19	2.0	27-91	0	59	0	76	24	41
<i>Myrophis punctatus</i>	Speckled worm eel	3	2.1	52-115	0	59	0	77	23	41
<i>Microgobius thalassinus</i>	Green goby	4	2.9	29-42	0	60	0	77	23	40
<i>Micropogonias undulatus</i>	Atlantic croaker	2	3.1	30-38	0	60	0	77	23	40
<i>Menidia beryllina</i>	Inland silverside	2	2.5	31-62	0	60	0	77	23	40
<i>Membras martinica</i>	Rough silverside	3	3.0	47-71	0	61	0	79	21	39
<i>Panopeus herbstii</i>	Common mud crab	1	0.7	7	0	61	0	79	21	39
<i>Gobionellus oceanicus</i>	Highpin goby	2	2.4	43-178	0	65	0	83	17	35
<i>Stellifer lanceolatus</i>	Star drum	1	3.2	43	0	68	0	87	13	32
<i>Cynoscion nebulosus</i>	Spotted seatrout	6	2.8	17-63	0	68	0	87	13	32
<i>Bairdiella chrysoura</i>	Silver perch	2	2.8	31-33	0	68	0	88	12	32
<i>Leiostomus xanthurus</i>	Spot	3	3.1	28-83	0	70	0	90	10	30
<i>Brevoortia tyrannus</i>	Atlantic menhaden	1	2.6	33	0	73	0	94	6	27
<i>Gobiosoma bosc</i> *	Naked goby	25	2.8	19-43	0	76	0	98	2	24
<i>Symphurus plagiusa</i>	Blackcheek tonguefish	1	2.5	51	4	79	0	96	0	21
<i>Anchoa mitchilli</i> *	Bay anchovy	19	3.2	26-51	13	80	0	87	0	20
<i>Cynoscion arenarius</i>	Sand seatrout	3	3.2	32-51	76	95	0	24	0	5
<i>Litopenaeus setiferus</i>	White shrimp	2	2.4	28-35	2	0	2	0	2	0

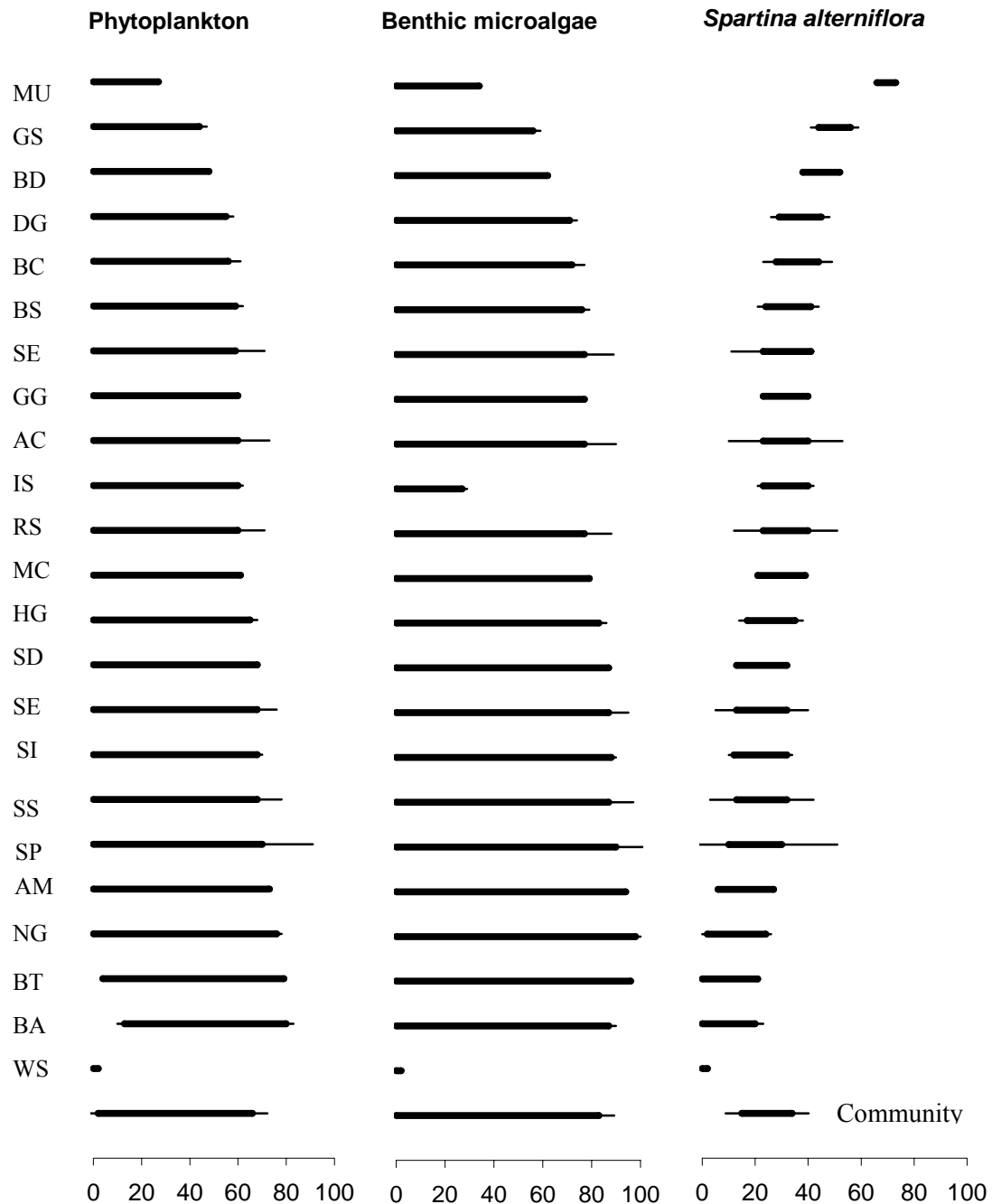


Figure 4.10. Annual relative contribution ( $\pm$ SE) of primary producers to the diet of nekton. MU = mummichog, GS = daggerblade grass shrimp, BD = black drum, DG = darter goby, BC = blue crab, BS = brown shrimp, SE = speckled worm eel, GG = green goby, AC = Atlantic croaker, IS = inland silverside, RS = rough silverside, MC = mud crab, HG = highfin goby, SD = star drum, SE = spotted seatrout, SI = silver perch, SS = sand seatrout, SP = spot, AM = Atlantic menhaden, NG = naked goby, BT = blackcheek tonguefish, BA = bay anchovy, WS = white shrimp.

Table 4.5. Relative contribution (%) of primary producers to the diet of estuarine nekton among seasons. Species are ranked according with the maximum relative influence of *Spartina alterniflora* in their diets. Fall ranking number is kept in the rest of the seasons for comparisons within species. Species absent in fall were not ranked. Only species captured in two or more seasons were included. Annual  $\delta^{13}\text{C}$  mean values of primary producers reported by Maddi (2003) were used in this analysis.

Season	Rank	Species	N	Size	Phyto-		Benthic		<i>Spartina</i>	
				range (mm)	Min	Max	Min	Max	Min	Max
Fall	1	Blue crab	6	10-19	0	45	0	56	44	55
	2	Brown shrimp	11	27-91	0	55	0	68	32	45
	3	Darter goby	5	23-43	0	61	0	77	23	39
	4	Daggerblade grass shrimp	4	25-44	0	65	0	82	18	35
	5	Naked goby	14	18-38	0	72	0	90	10	28
	6	Bay anchovy	6	26-45	0	75	0	94	6	25
		Average			0	62	0	68	22	38
Winter	4	Daggerblade grass shrimp	17	28-42	0	49	0	61	39	51
	3	Darter goby	8	18-47	0	65	0	80	20	35
	1	Blue crab	1	20-29	0	65	0	81	19	35
	5	Naked goby	4	22-43	0	77	0	95	5	23
		Average			0	64	0	79	21	36
Spring	4	Daggerblade grass shrimp	5	30-49	0	38	0	51	49	62
	1	Blue crab	2	10-19	0	51	0	69	31	49
	2	Brown shrimp	8	39-88	0	59	0	80	20	41
	6	Bay anchovy	9	34-54	7	76	0	93	0	24
		Average			0	56	0	76	24	44
Summer	4	Daggerblade grass shrimp	1	33	0	56	0	74	26	44
	2	Brown shrimp	1	59	0	69	0	90	10	31
	6	Bay anchovy	4	33-41	11	79	0	89	0	21
	5	Naked goby	7	17-42	43	87	0	57	0	13
	1	Blue crab	2	20-29	80	95	0	20	0	5
		Average			4	77	0	96	0	23

## Discussion

Some fishes and invertebrates had significant differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values among habitat types, seasons, and locations. Darter goby was the only species that had significant differences in carbon isotopic values between marsh-edge and open-water

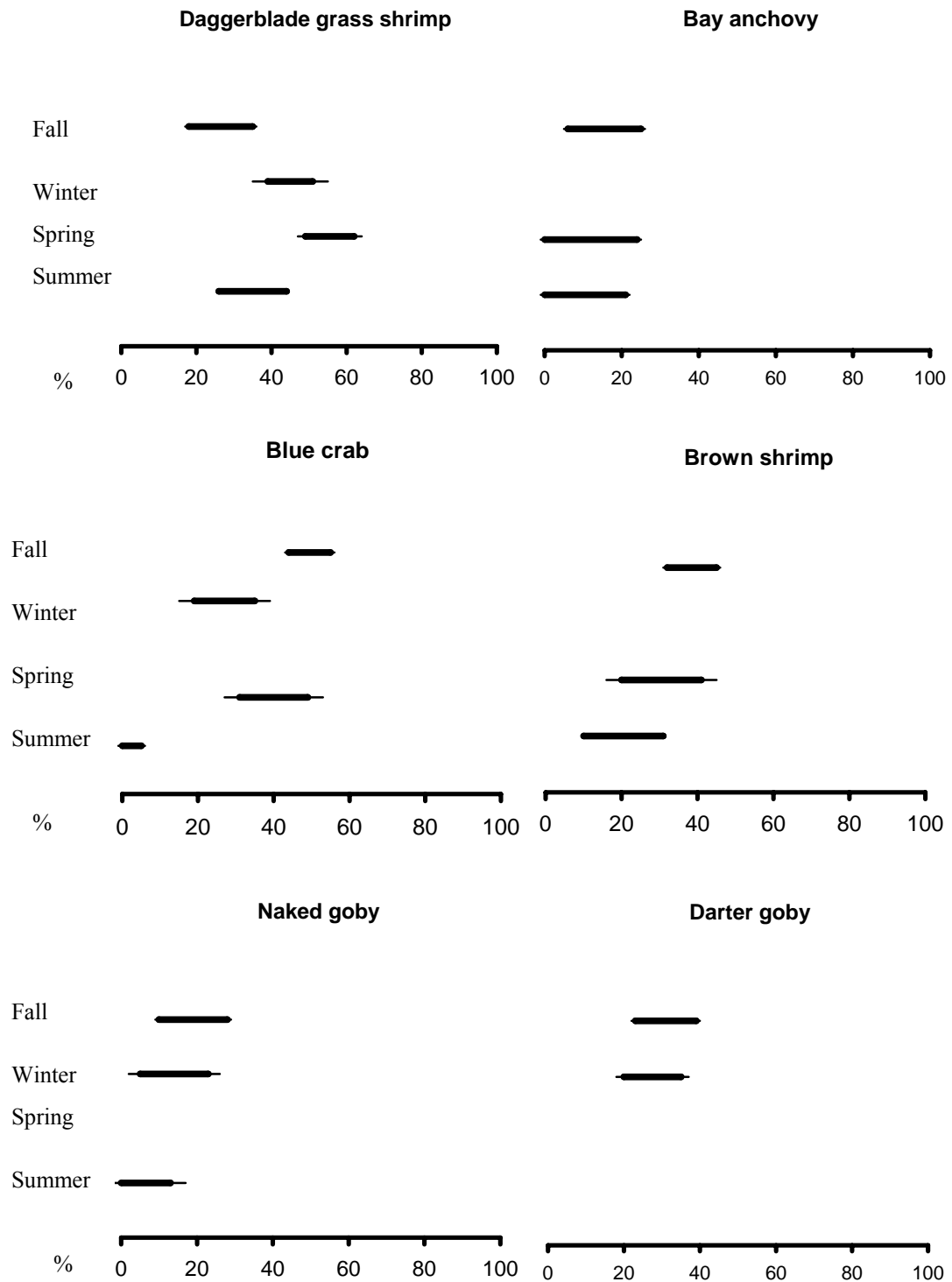


Figure 4.11. Relative contribution ( $\pm$  SE) of *Spartina alterniflora* to the diet of the most abundant nekton species by seasons.

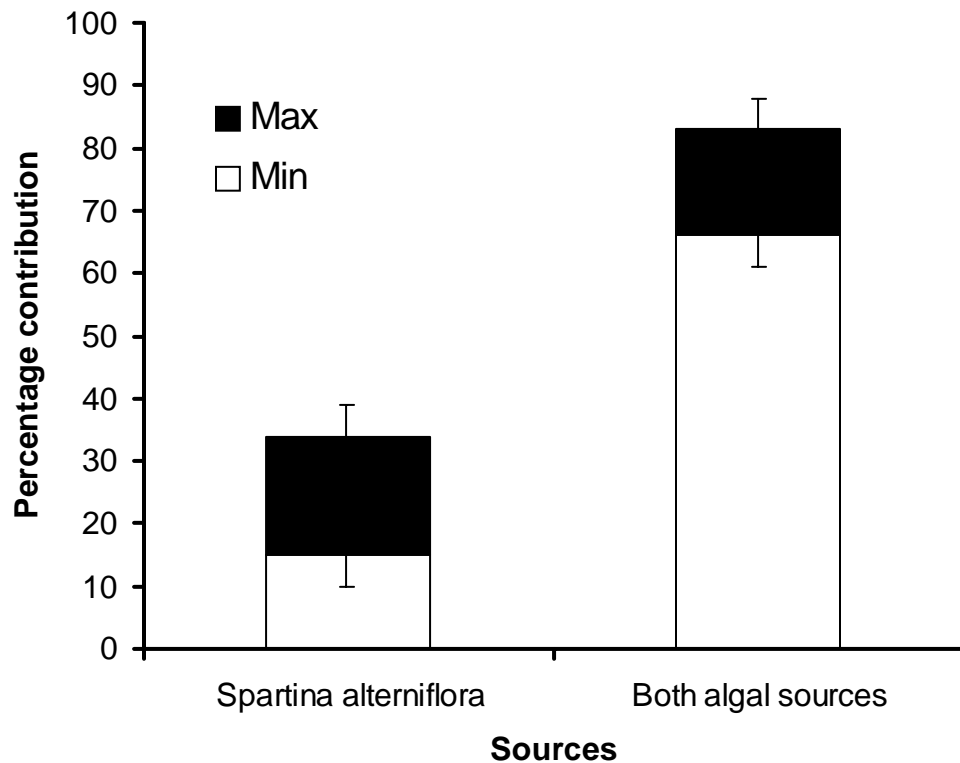


Figure 4.12. Maximum and minimum relative contribution of *Spartina alterniflora* and the combination of the algae sources (phytoplankton and benthic microalgae) to the diet of the nekton community in a Louisiana estuary.

habitat types. Significant seasonal variations were identified in the carbon isotopic values of naked goby, daggerblade grass shrimp, and blue crab, and in the nitrogen isotopic values of brown shrimp. Carbon isotopic values of blue crab and nitrogen isotopic values of darter goby varied between size classes. The influence of *Spartina alterniflora* was relatively minor in the diets of most juvenile fishes and macroinvertebrates with the lowest contribution in summer.

### **Marsh Edge Versus Open Water**

Darter goby relied on different food resources depending on habitat type suggesting mesoscale diet shifts in their diet. Specifically, carbon isotopic values were

Table 4.6. Estimated total contribution of *Spartina* spp. to the diet of the nekton community compared with other studies.

Source	Study area	Phyto-plankton	Benthic algae	<i>Spartina</i> spp.	Secondary consumer	$\delta^{13}\text{C}^a$	% Contribution	
							Min	Max
This study	Terrebone Bay, Cocodrie, LA	-25.5	-22.7	-13.1	Macroinvertebrates	-21.4	14	33
					Fishes	-21.3	15	34
					Total nekton	-21.3	15	34
Hughes and Sherr (1983)	Fox creek, Sapelo Island, GA	-24.7 <sup>b</sup>	-17.9 <sup>b</sup>	-13.6 <sup>b</sup>	Macroinvertebrates	-21.4	0	30
					Fishes	-22.0	0	24
					Total nekton	-21.7	0	27
	Crooked creek, Sapelo Island, GA	-24.7 <sup>b</sup>	-17.9 <sup>b</sup>	-13.6 <sup>b</sup>	Macroinvertebrates	-20.8	0	35
					Fishes	-22.1	0	23
					Total nekton	-21.4	0	30
	Duplin River, Sapelo Island, GA	-24.7 <sup>b</sup>	-17.9 <sup>b</sup>	-13.6 <sup>b</sup>	Macroinvertebrates	-18.8	0	53
					Fishes	-19.5	0	47
					Total nekton	-19.1	0	50
Deegan and Garritt (1997)	Upper estuary, Plum Island Sound, MA	-27.9	-18.0 <sup>c</sup>	-12.9	Macroinvertebrates	-24.7	0	21
					Fishes	-26.9	0	7
					Total nekton	-26.2	0	11
	Middle estuary I, Plum Island Sound, MA	-23.0	-18.0 <sup>c</sup>	-14.8	Macroinvertebrates	-17.3	22	70
					Fishes	-21.1	0	23
					Total nekton	-20.0	0	37
	Middle estuary II, Plum Island Sound, MA	-21.1	-18.0 <sup>c</sup>	-12.9	Macroinvertebrates	-16.8	24	52
					Fishes	-20.3	0	10
					Total nekton	-19.2	0	23
Kwak and Zedler (1997)	Tijuana estuary, CA	-20.8	-16.5	-15.1	Macroinvertebrates	-18.8	0	35
					Fishes	-17.9	0	51
					Total nekton	-18.4	0	42

<sup>a</sup>Values corrected for fractionation, macroinvertebrates = 0.5, fishes = 2, and total nekton = 1.5; <sup>b</sup>Maximum values in Table 1 of Haines and Montague (1979);

<sup>c</sup>Macroalgae value



more enriched in individuals collected along the marsh edge than in open water.

Nitrogen values of darter goby did not vary between habitat types at the species level, but did vary among size classes with higher values for larger individuals captured in open water. This may confirm a diet shift for larger individuals that move away from the marsh edge to adjacent open water. Nevertheless, some individuals within different marsh nekton species may specialize (Murdoch 1969) on few prey categories over a large area, whereas other individuals may have a broader diet explaining the relative high difference in isotopic values within the same species (Fry *et al.* 1999).

Although naked goby carbon and nitrogen isotopic values did not vary among habitat types in the field experiments, the slightly depleted values in individuals in the enclosures with vegetation might have been due to different food resource utilization than individuals in other enclosure treatments. When captured along the marsh edge, naked goby had higher numbers of harpacticoid copepods and ostracods in their diets (Chapter 3). In New Jersey estuaries, naked goby consume a higher proportion of harpacticoid copepods in vegetated than in unvegetated areas as well (Sogard 1992). Thus, naked goby may have relied on different food resources among habitat types. Nevertheless, it was not possible to determine if this differential food consumption was due to differential prey availability linked to different habitat types or predator selectivity when food availability is not a limiting factor.

### **Seasonal Variation**

Seasonal diet shifts were detected for naked goby, daggerblade grass shrimp, and blue crab. Naked goby individuals fed primarily on harpacticoid copepods and ostracods with higher abundances in winter than in other seasons (Chapter 3). Seasonal shifts in

carbon isotopic values of naked goby closely tracked the trends seen in harpacticoid copepods, ostracods, phytoplankton, and benthic algae reported by Maddi (2003), with enriched values in winter (Figure 4.13). Meiofauna, including harpacticoid copepods, are typically  $\delta^{13}\text{C}$  enriched in winter in Louisiana estuaries (Carman and Fry 2002). In contrast, carbon isotopic values of other resident species such as mummichog are more enriched in spring than in winter in Tar Landing Bay, North Carolina (Kneib *et al.* 1980).

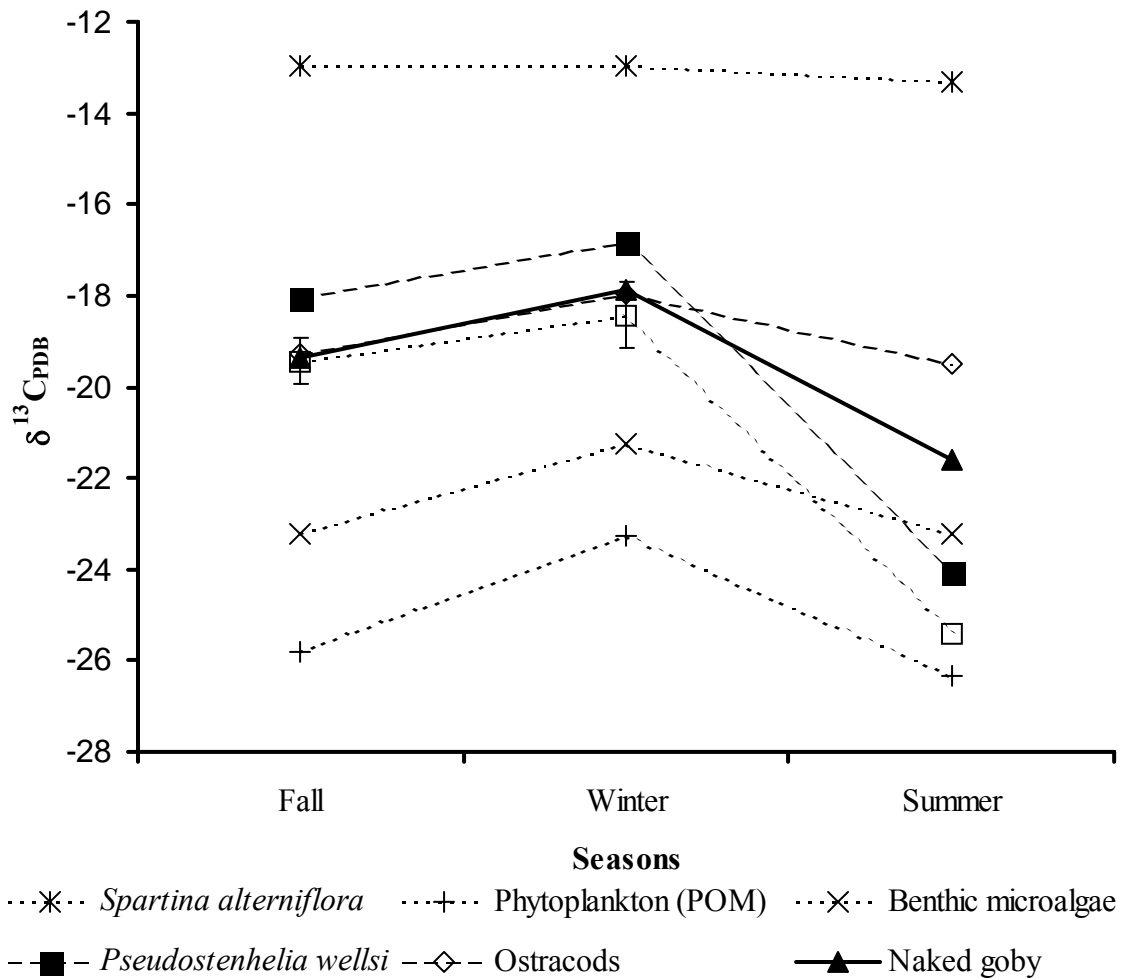


Figure 4.13. Single plot of the mean carbon values of naked goby compared to primary producers and meiofauna as potential food sources (chapter 3) by seasons. Primary producers and meiofauna mean values are from summer and fall 2001 and winter 2002 (Maddi 2003).

The carbon isotopic values of daggerblade grass shrimp were enriched in winter and depleted in spring, summer, and fall, following the benthic microalgae and phytoplankton trends (Maddi 2003; Figure 4.14). This species feeds mainly on microalgae and epiphytic algae on stems of *Spartina alterniflora* (Fleege *et al.* 1999). Nevertheless, benthic microalgae may be more important in food webs in spring, when macrophyte detritus is less available and marsh canopies are not fully developed, allowing greater light penetration to the sediment surface and potentially greater benthic microalgae production (Currin *et al.* 2003). Other shrimp species such as postlarval brown shrimp exhibit seasonal shifts in carbon isotopic values with growth as their diet change reflecting high turnover rates of carbon isotopic values in their tissue (Fry and Arnold 1982).

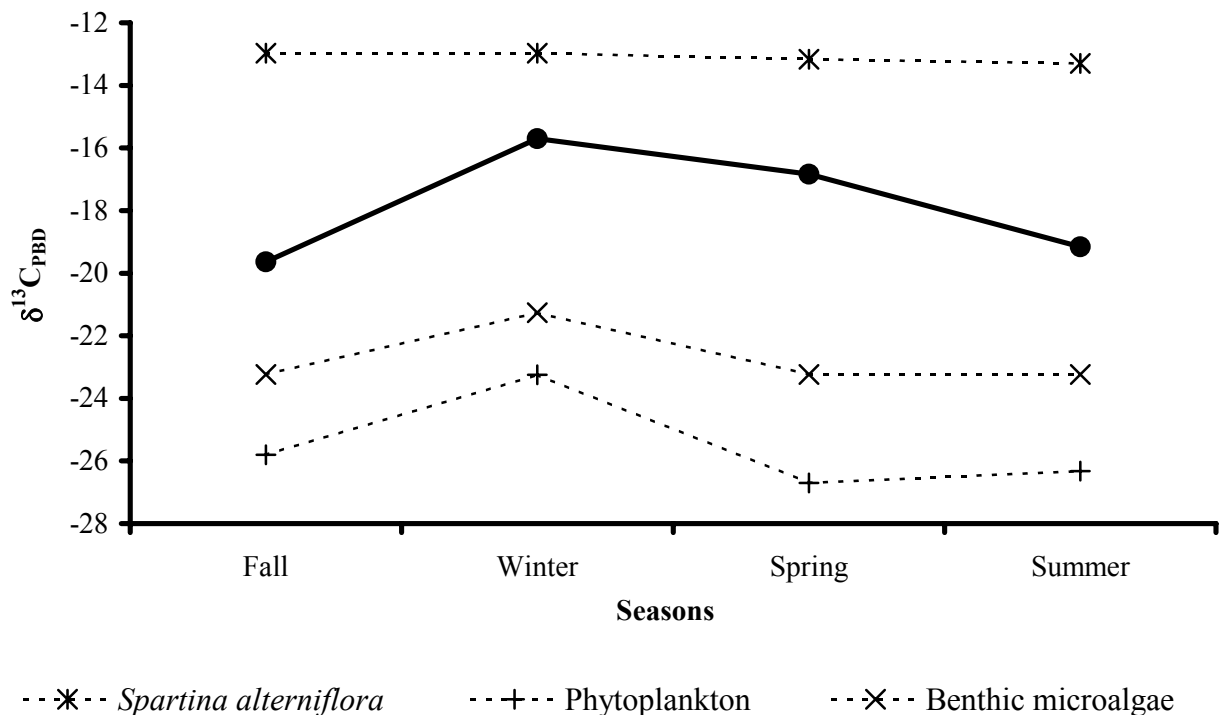


Figure 4.14. Single plot of the mean carbon values of daggerblade grass shrimp compared to primary producers by seasons. Primary producers and meiofauna mean values are from summer and fall 2001 and winter and spring 2002 (Maddi 2003).

The carbon isotopic values of blue crabs were enriched in fall and depleted in all other seasons with the lowest values in summer (Figure 4.8). In summer, the average size of blue crabs captured was larger, which may reflect both a size-related and a temporal diet shift to more depleted prey. Thus, the dependence of blue crabs on *Spartina alterniflora* as a potential food source may diminish as they grow (Figure 4.15). In Delaware Bay, carbon isotopic values of juvenile blue crabs living in open bays are similar to phytoplankton values, whereas larger individuals residing on the marsh utilize marsh-derived carbon (Dittel *et al.* 2000, Fantle *et al.* 1999). Nevertheless, growth experiments indicate that juvenile blue crabs feeding on detritus grow poorly, and amino acid analyses indicate that juveniles may feed on bacteria living on the detritus rather than directly on bulk detritus (Fantle *et al.* 1999). Also, stable isotope analyses indicate that juvenile horseshoe crabs shift from a diet based on phytoplankton to one supported by saltmarsh detritus as they grow in Nauset Beach, Massachusetts (Gaines *et al.* 2002). Interestingly, horseshoe crabs switch back to phytoplankton-base food webs as adults (Gaines *et al.* 2002).

Brown shrimp had higher nitrogen isotopic values in spring than summer and fall (Figure 4.9). Nevertheless, brown shrimp did not follow the  $\delta^{13}\text{C}$  values trends of primary producers and meiofauna (Maddi 2003) (Figure 4.16). Although harpacticoid copepods are the main prey of brown shrimp in the study area (Fry *et al.* 2003), phytoplankton and zooplankton represent important food resources for postlarval brown shrimp (abundant in early spring), whereas *Spartina alterniflora* detritus and epiphytes do not provide direct benefit in terms of metabolic maintenance (Gleason 1986, Gleason and Wellington 1988). Brown shrimp may feed on planktonic prey in spring when nitrogen

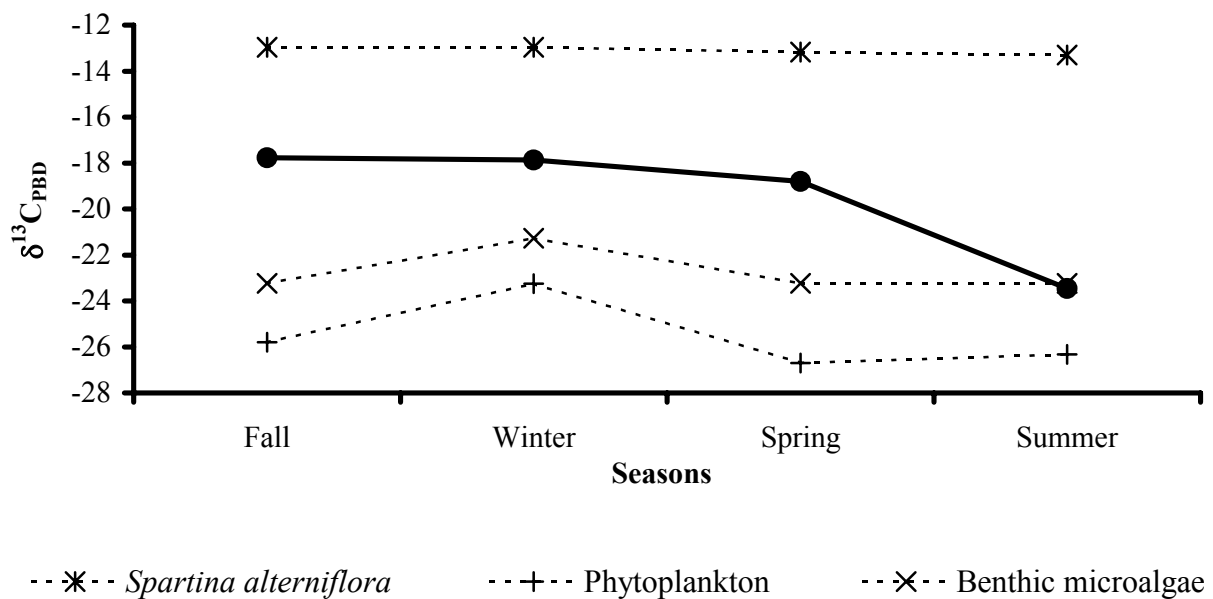


Figure 4.15. Single plot of the mean carbon values of blue crab compared to primary producers by seasons. Primary producers and meiofauna mean values are from summer and fall 2001 and winter and spring 2002 (Maddi 2003).

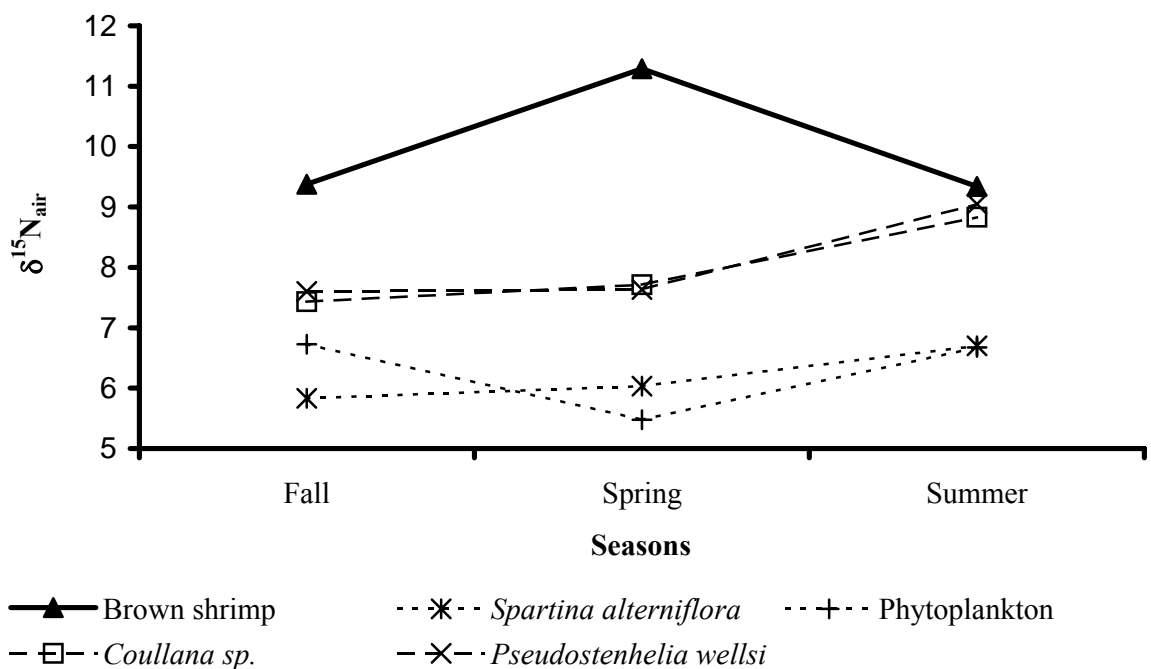


Figure 4.16. Single plot of the mean nitrogen values of brown shrimp compared to primary producers and harpacticoid copepods as potential food sources (Carman and Fry 2002) by seasons. Primary producers and meiofauna mean values are from summer and fall 2001 and winter 2002 (Maddi 2003).

isotopic values are further apart from meiofauna, but in fall and summer, when larger brown shrimp settle, they may feed mostly on benthic organisms with nitrogen isotopic values closer to meiofauna values.

### **Location Variation**

Brown shrimp had carbon isotopic value differences among locations as indicated by dual plots (Figure 4.9). Specifically, individuals captured in shallow bays ( $-20.6 \pm 0.09$  ‰) had relatively more depleted carbon isotopic values than individuals from channels ( $-18.9 \pm 0.15$  ‰) and ponds ( $-18.6 \pm 0.46$  ‰). Interestingly, Fry *et al.* (2003) found this trend for brown shrimp individuals captured in the same study area in spring of 2000. However, their results are somewhat different in the sense that they found more depleted values in individuals from shallow bays and channels than from ponds.

Fry *et al.* (2003) also found differences in nitrogen isotopic values in brown shrimp among locations with higher values in individuals from a channel than individuals from ponds. In this study, individuals from the shallow bay ( $10.3 \pm 0.29$  ‰) and the channel ( $10.5 \pm 0.30$  ‰) had slightly higher values than individuals from the pond ( $9.4 \pm 0.21$  ‰) as well. Fry *et al.* (2003) suggest that due to these isotopic differences among locations, brown shrimp limit their movement to small spatial scales ( $< 10$  m). Although in this study isotopic value differences were not statistically significant, visual analyses supported the idea of restricted movement of brown shrimp among adjacent locations.

Consumers tend to utilize sources of organic matter produced in the same region of the estuary in which they reside (Deegan and Garritt 1997). For example, in Tijuana Estuary and San Dieguito Lagoon, California, benthic microalgae of the vegetated salt marsh were considered the principal food resource of channel invertebrate populations

(Kwak and Zedler 1997), whereas in Carpinteria Salt Marsh, California, benthic microalgae sources used by channel consumers originate in the channel rather than the vegetated marsh (Page 1997). Marsh detritus is distributed along a declining gradient with maximum availability in the smallest marsh creeks to lower availability near the mouth of the estuary (Peterson *et al.* 1985). Isotopic compositions of bay anchovy vary among locations in Delaware Bay (Weinstein 2000); in the upper estuary, carbon values are similar to *Spartina alterniflora*, whereas closer to the mouth of the estuary carbon values are between *S. alterniflora* values and phytoplankton. Nevertheless, bay anchovy carbon isotopic values did not vary among locations in this study. Thus, it seems that the spatial scale in this microtidal study area was not large enough to detect similar trends in carbon isotopic values in bay anchovy.

### **Size Variation**

Carbon and nitrogen isotopic values of most of the abundant species did not change among size classes, except for carbon values of blue crab and nitrogen values of darter goby. The lack of variability in isotopic values among size classes might be due to the fact that most individuals collected were juveniles of restricted size range, which reflect recently acquired food resources (Deegan and Garritt 1997). Nevertheless, fishes and macroinvertebrates have isotopic compositions that change as they grow (Hesslein *et al.* 1993). The carbon isotopic values of early juvenile blue crab are close to phytoplankton values, whereas larger individuals utilize marsh-derived carbon (Dittel *et al.* 2000, Fantle *et al.* 1999). Darter goby may change their diet as they grow as indicated by their higher trophic level as adults. This pattern has been documented for other estuarine residents. For example, small mummichog has low nitrogen isotopic values,

whereas large individuals that begin feeding more heavily on harpacticoid copepods and polychaetes have enriched nitrogen values (Currin *et al.* 2003).

### **Primary Producer Pathways**

The three-source mixing model equation suggested that *Spartina alterniflora* may not be the most important energy source for nekton in Louisiana estuaries (Table 4.6). In general juvenile fishes did not consume high abundances of detritus in this study (Chapter 3), which supports this finding. In contrast to my general finding, detrital *Spartina* is the predominant source of carbon for harpacticoid copepods in North Inlet Estuary, South Carolina (Couch 1989). Two-and three-source mixing models identified *Spartina* as the major organic-matter source for fishes in Tijuana Estuary and San Dieguito Lagoon, California as well (Kwak and Zedler 1997). In Plum Island Sound Estuary, Massachusetts, *Spartina* or benthic microalgae are the most probable organic-matter sources for benthic feeders (Deegan and Garritt 1997).

Benthic feeders such as crabs, drums and croakers (family Sciaenidae), and gobies were relatively more connected to benthic microalgae pathways. Sediments of *Spartina* marshes support the highest benthic microalgae biomass and stable carbon isotopic values are more depleted than benthic microalgae from mudflats (Currin *et al.* 2003). Food webs are more dependent on benthic microalgae production in saltmarsh estuaries with low tidal range (Deegan and Garritt 1997). Benthic microalgae is a significant component of the food web supporting recently hatched mummichog in brackish marshes in New Jersey (Currin *et al.* 2003) and benthic microalgae and phytoplankton are the major food sources for the fauna in Graveline Bay Marsh, Mississippi (Sullivan and Moncreiff 1990).



Some pelagic species such as inland and rough silverside were relatively more influenced by benthic algae and *Spartina alterniflora* than phytoplankton. Thus, individual consumer species may use a mixture of food resources (Peterson *et al.* 1980, Peterson *et al.* 1986, Peterson and Howarth 1987) combining benthic and pelagic pathways (Deegan and Garritt 1997). For example, zooplankton may feed on resuspended benthic organisms that feed on detrital material (Couch 1989). In Plum Island Sound, Massachusetts, benthic consumers rely on *Spartina* and benthic microalgae, whereas the carbon values of pelagic consumers are closer to phytoplankton (Deegan and Garritt 1997). In Aiguillon Bay, France, *Spartina anglica* is not the main carbon source for invertebrates, which feed mainly on a mixture of benthic diatoms and phytoplankton in different proportions (Riera *et al.* 1999). *Spartina* is not always the most important food source for estuarine fishes, and benthic microalgae or phytoplankton may play a key role in estuarine food webs as well.

Other pelagic species such as Atlantic menhaden and bay anchovy were relatively more influenced by benthic microalgae and phytoplankton than *Spartina alterniflora* in this study. Phytoplankton carbon is more important as a food source for subtidal animals than for intertidal marsh fauna (Hughes and Sherr 1983). In contrast, in Louisiana, *Spartina*-derived detritus contributes at least 30% to the diet of juvenile Gulf menhaden (Deegan *et al.* 1990). In a New Jersey estuary, bay anchovies resemble the isotopic values of the benthic microalgae and *Spartina* salt marshes, even when captured several kilometers offshore, suggesting that phytoplankton is not as important for their diet (Weinstein *et al.* 2000). White shrimp had the closest carbon isotopic values to

phytoplankton in this study. Interestingly, white shrimp are omnivorous (McTigue and Zimmerman 1991), but can grow on a diatom diet (McTigue and Zimmerman 1998).

The mixing model is sensitive to other food sources such as sulfur oxidizing bacteria and these sources may influence the *Spartina alterniflora* contribution estimation. In the laboratory, bacteria that use the energy of reduced sulfur compounds to fix CO<sub>2</sub> from seawater may have  $\delta^{13}\text{C}$  values as low as -36‰ (Peterson *et al.* 1980). If this sulfur oxidizing bacteria value is used in the mixing equation, the minimum and maximum contributions of *S. alterniflora* would be higher (34 and 64%, respectively) for this study. However, carbon isotopic values of sulfur oxidizing bacteria in estuaries may be approximately -20‰ (Peterson *et al.* 1986). Thus, relative contribution of *S. alterniflora* would be little influenced by sulfur oxidizing bacteria (0 and 34%).

Ambiguities of stable isotope studies lie in the uncertainty in determining the actual food resource influencing predators when multiple end members are available (Currin *et al.* 2003, Phillips and Gregg 2003). Although for carbon values most nekton species were closer to benthic microalgae values in this study, mixing equations with three end members suggested that this primary producer contributed relatively little to their diets. Variability in carbon isotopic values among and within estuaries may affect the determination of food sources by using stable isotopes (Deegan and Garritt 1997). Thus, stable isotope techniques should be complemented with food habit studies to confirm these trends (Haines and Montague 1979). For example, in this study, mummichog was the nekton species with the carbon values closest to *Spartina alterniflora* values and was one of the two species in which detritus accounted for at least 50% of detritus in their stomachs (Chapter 3). Nevertheless, *Spartina* is not always the

dominant source of carbon for the *F. heteroclitus* food web (Currin *et al.* 2003), which confirms the dynamic complexity of estuarine food webs.

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## CHAPTER V.

### SUMMARY

This study focused entirely on unvegetated sites near the marsh edge and in increasingly more distant open water in pond, channel, and shallow bay habitat types. It also differed from other similar studies that focused on comparisons of flooded marsh and nearby unvegetated sites along the marsh edge (Zimmerman and Minello 1984, Minello *et al.* 1994, Rozas and Zimmerman 2000). It also encompassed spatial and temporal scales characterized by seasonal sampling at different distances from the marsh edge across three locations that typified a landscape change in Louisiana's marsh ecosystems: closed marshes converting to open marshes and eventually to open water as the areal coverage of *Spartina alterniflora* declines. Thus, this study is an effort to estimate the effect that marsh loss may have on estuarine food webs and changing patterns of species abundances as *Spartina* salt marsh is converted to open water.

The degradation of saltmarsh habitats reduces the suitability of salt marshes as permanent environments for resident species and as seasonal nurseries for transient fauna. The marsh edge and the adjacent open waters are important for fishes and macroinvertebrates that move between these habitat types. The marsh edge is essential for food and refuge for estuarine nekton, but macroinvertebrate species may be more sensitive to marsh loss than fish species. Nevertheless, marsh loss may have an effect on the feeding ecology of juvenile fishes that rely primarily on benthic prey along the marsh edge. Although the relative carbon contribution of *Spartina alterniflora* to support the nekton community was less than 35% in the study area, conservation of *Spartina* marsh ecosystems is important for maintaining and protecting estuarine fisheries.

Densities of estuarine fishes and macroinvertebrates varied according to distance from the edge with complex distribution patterns that depend on seasonal changes of one or more environmental variables. Densities of resident species including darter goby and naked goby were significantly different among habitat types, seasons, and across the landscape gradients with higher abundances in open water. In contrast, transient species such as brown shrimp were more abundant along the marsh edge. Nevertheless, some species were absent in the samples in one or two seasons. Median depth, temperature and turbidity influenced nekton abundance, specially abundance of macroinvertebrates.

Prey utilization differences were detected among habitat types, seasons, and locations for some fishes. Naked goby consumed higher abundances of harpacticoid copepods along the marsh edge than in the open water. In contrast, in the field enclosure experiments, no significant differences were detected in the utilization of prey categories by naked goby among habitat types. Bay anchovy and naked goby had significant differences in prey use among seasons and ingestion was associated with changes of environmental variables. Fishes ingested a variety of pelagic and benthic prey items, but most fish species fed primarily on harpacticoid copepods. Despite the presence of detritus in the stomachs of several fish species, it was relatively rare.

Some fishes and invertebrates had significant differences in  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  values among habitat types, seasons, and locations. Darter goby was the only species that had significant differences in carbon isotopic values between marsh-edge and open-water habitat types. In contrast, carbon and nitrogen isotopic value differences among habitat types were not detected for naked goby in the field enclosure experiments. Significant seasonal variations were identified in the carbon isotopic values of naked goby,

daggerblade grass shrimp, and blue crab, and nitrogen isotopic values of brown shrimp. Carbon isotopic values of blue crab and nitrogen isotopic values of darter goby varied between size classes. Carbon from *Spartina alterniflora* had a relatively low influence in the diet of most juvenile fishes and macroinvertebrates with the lowest contribution in summer.

This study highlights the importance of different habitat types in supporting the nekton community throughout coastal Louisiana. Although the marsh edge is essential for food and refuge for fishes, adjacent open-water habitats offer food resources that play an important role in estuarine food webs. While *Spartina alterniflora* made a relatively minor contribution of carbon moving through this estuarine food web, many nekton species appeared to rely on microalgal resources and benthic prey that are patchily distributed among habitat types.

I examined the ecological function of marsh-edge and adjacent open-water habitat types as suitable areas for food for estuarine nekton in a *Spartina alterniflora* dominated ecosystem. Nevertheless, marsh plants including *Spartina patens* and *Juncus* are also present in other estuaries. However, estuarine nekton species such as grass shrimp and blue crab select the *S. alterniflora* edge over *S. patens* and grass shrimp, brown shrimp, and blue crab select *S. alterniflora* over *Juncus* (Rozas and Zimmerman 2000). Marsh stem density is important for fauna structure as well, since low *S. alterniflora* stem quality have higher fauna abundances than dense *S. patens* and *Juncus* (West and Williams 1986). Both elevation and distance from the edge are important in determining saltmarsh use by brown shrimp and grass shrimp with highest densities of these species on the low-elevation flooded marsh surface (Minello *et al.* 1994). Additionally, higher

abundances of invertebrates are found in flooded marsh near to the edge than in the marsh interior (Rozas and Zimmerman 2000).

Despite the observation that the marsh edge supports the highest densities of estuarine fauna, other habitat types such as submerged aquatic vegetation (SAV) may be important for estuarine nekton. In Galveston Bay, Texas, juvenile red drum densities and growth are higher in SAV than along the marsh edge; however, the marsh edge may be the most important nursery habitat for this species in Texas, since the marsh cover is higher in estuaries (Stunz *et al.* 2002a, 2002b). In Terrebonne-Timbalier Basin of southeastern Louisiana, naked goby, grass shrimp and blue crab are most abundant in shallow canals when SAV is present (Rozas and Reed 1994). Also, in Back Sound, North Carolina, pinfish are most abundant in marsh-edge and the open-water habitat types when SAV is present (Irlandi and Crawford 1997), confirming the importance of the SAV for nekton survival.

Drop samplers and throw traps provide accurate density estimates for most nekton species (Zimmerman and Minello 1984, Sogard 1992) in habitat types with turbid waters or vegetation (Rakocinski *et al.* 1992). The drop sampling technique has been recommended for sampling quantitatively in marsh areas with shallow waters and muddy bottoms (Rozas and Minello 1997). Other fishing techniques such as beam trawls (Jones *et al.* 2002, Baltz and Jones 2003) are difficult to use near the marsh edge in muddy bottoms (Rozas and Minello 1997) and block nets (Hettler 1989) and flume nets (Milan 2003) are stationary requiring fixed samples sites (Rozas and Minello 1997). Although relatively few captures were typically obtained in this study (9 organisms m<sup>-2</sup> CPUE), drop sampling is the most appropriate technique to estimate nekton densities in shallow

estuaries. Proportionally, drop samplers capture more fishes than invertebrates in contrast to flume nets. Peterson and Turner (1994) caught 89% invertebrates and 11% fishes using flume nets, whereas in this study, the drop sampler caught 65% invertebrates and 35% fishes. Nevertheless, community structure variability occurs mainly due to seasonal and spatial fluctuations of biological factors such as food availability and to environmental variables such as temperature, salinity, turbidity, water depth, and flooding duration.

This study had some limitations due to small sample size and the number of habitat types covered. Specifically, two features seem worthy of comment for future research. First, sampling did not include all possible habitat types (*e.g.*, high intertidal pools in the marsh, flooded *Spartina*, and oyster reefs). Samples from a broader range of habitat types may have affected the results - *e.g.*, principal component analysis (Chapter 2) may have suggested that species respond to different factors than indicated in this study. Second, fish collections were often small, leading to a small sample size, which may contribute to low power to detect differences in the statistical tests. Food habits (Chapter 3) and stable isotopes (Chapter 4) studies may have also been sensitive to sample size. Thus, information about the use of the marsh-edge and open-water habitat types may also have been influenced by low sample sizes since some species were not sampled in all seasons. Nevertheless, quantitative conclusions of ecological processes in estuaries are complex since resource use of a given species may be broad and influenced by migratory and ontogenetic shifts in trophic interactions and habitat selection (Livingston 1988).

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**APPENDIX**  
**STABLE ISOTOPIC DATA**

Species	Season	Location	Habitat type	Size (mm)	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Atlantic croaker	Winter	Channel	Open	30	-20.8	12.8
				38	-17.4	11.9
Atlantic menhaden	Spring	Channel	Edge	33	-21.0	11.3
Bay anchovy	Fall	Bay	Edge	26	-21.2	11.8
				36	-22.1	11.9
				38	-20.0	13.4
				38	-20.8	12.7
				44	-20.5	13.2
				45	-21.7	12.2
	Spring	Bay	Edge	34	-22.2	13.3
				40	-20.6	14.6
				38	-21.5	13.2
		Channel	Edge	41	-23.5	13.8
				47	-21.8	13.0
				49	-20.6	13.4
	Summer	Pond	Open	50	-20.7	9.5
				51	-21.2	12.1
				54	-24.0	13.0
		Bay	Open	33	-20.8	12.9
				37	-20.9	13.0
				38	-21.7	12.7
Blackcheek tonguefish	Fall	Bay	Open	41	-24.4	11.8
				51	-21.7	11.2
Black drum	Winter	Channel	Open	11	-17.9	11.3
Blue crab	Fall	Bay	Edge	11	-19.8	9.2
				12	-18.2	8.1
				13	-20.9	8.3
				13	-17.7	6.4
				18	-17.0	8.1
				14	-16.0	3.8
	Winter	Bay	Open	17	-19.5	7.8
				19	-19.2	7.7
				28	-17.9	9.0
				13	-19.3	10.0
				18	-19.8	10.7
				21	-18.8	7.3
	Summer	Bay	Open	22	-24.5	11.0
				31	-24.4	11.0
Brown shrimp	Fall	Bay	Edge	27	-20.2	8.7
				41	-21.2	10.0

(Appendix con'd)



Species	Season	Location	Habitat type	Size (mm)	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$		
Darter goby	Spring	Channel	Edge	43	-20.0	10.2		
				44	-20.6	10.3		
			Edge	52	-18.5	8.9		
				57	-18.5	10.1		
		Pond	Edge	61	-20.6	8.6		
				63	-19.2	10.4		
			Open	72	-17.8	8.9		
				75	-17.8	8.8		
		Bay	Edge	91	-15.8	8.3		
				39	-22.0	11.8		
			Open	45	-18.7	10.9		
				48	-20.9	12.7		
		Summer	Channel	Edge	54	-20.6	11.8	
					62	-19.4	11.3	
	Open			77	-19.1	10.7		
				Pond	Edge	84	-20.3	9.9
	Open		88			-18.4	9.9	
	Bay		Edge		59	-21.4	9.3	
					Fall	Bay	Open	23
	Channel		Open	23				-20.3
	Pond		Edge	24		-17.9	9.3	
				Open		29	-20.9	10.0
	Winter		Bay	Edge	43	-19.0	9.0	
					18	-17.6	11.0	
				Open	22	-18.3	9.9	
					Channel	Edge	28	-17.9
			Open	31			-17.9	10.6
				37	-18.4	11.2		
		Grass shrimp	Fall	Bay	Edge	38	-18.1	11.1
						40	-19.5	12.9
47						-19.0	12.1	
25						-20.5	10.1	
25	-20.3					9.8		
28	-21.2					12.0		
Winter	Channel	Open	28	-18.7	11.1			
			44	-18.7	11.1			
		Edge	28	-16.9	11.5			
			Bay	Edge	28	-15.6	10.6	
	29	-15.7			10.5			
	Open	29		-16.7	11.1			
		31		-16.4	10.5			
	Channel	Edge	32	-15.7	10.5			
			33	-15.8	10.6			
			33	-14.5	10.9			
			33	-16.3	9.2			

(Appendix con'd)

Species	Season	Location	Habitat type	Size (mm)	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Green goby	Spring	Pond	Open	34	-15.6	10.8
				35	-17.5	11.2
				36	-16.2	10.0
			Edge	37	-17.0	10.0
			Open	38	-17.0	9.8
		Pond	Edge	38	-17.5	10.4
				40	-18.4	8.1
				42	-16.8	10.6
				30	-17.3	9.4
			Open	31	-16.6	10.8
	Summer	Bay	Edge	33	-19.7	9.7
	Winter	Channel	Edge	38	-19.2	11.6
			Open	39	-19.6	12.9
				33	-20.6	11.2
Inland silverside	Fall	Channel	Edge	62	-19.0	12.1
	Spring	Pond	Edge	31	-19.7	10.3
Mud crab	Fall	Pond	Edge	7	-20.5	7.1
Mummichog	Winter	Channel	Edge	53	-14.7	11.2
			Open	65	-15.8	11.1
Naked goby	Fall	Bay	Edge	18	-20.3	11.1
				18	-20.8	12.0
			Open	19	-21.3	11.2
				21	-21.4	11.2
				21	-20.8	12.2
				21	-21.8	12.0
				21	-20.5	12.4
		Channel	Open	22	-20.5	11.3
				22	-20.6	12.7
				23	-20.8	12.0
				24	-20.7	11.7
				24	-20.3	11.7
				25	-20.3	11.9
				38	-20.6	12.2
	Winter	Pond	Open	38	-20.6	12.2
			Edge	22	-20.0	12.4
			Open	24	-19.0	11.4
		Channel	Edge	34	-18.6	11.7
			Open	43	-20.0	11.8
	Summer	Bay	Edge	17	-22.8	11.3
				19	-20.9	12.3
				20	-24.7	11.9
		Channel	Edge	20	-24.7	11.9
			Open	24	-24.4	11.9
				33	-24.1	11.9
				36	-23.4	11.6
				42	-21.6	11.9

(Appendix con'd)

Species	Season	Location	Habitat type	Size (mm)	$\delta^{13}\text{C}$	$\delta^{15}\text{N}$
Rough silverside	Spring	Bay	Edge	71	-17.6	12.6
	Summer	Bay	Edge	47	-19.0	12.1
		Pond	Edge	48	-21.3	11.9
Sand seatrout	Fall	Bay	Open	32	-20.6	12.0
	Summer	Bay	Edge	44	-24.0	12.5
			Open	51	-25.1	13.2
Highfin goby	Fall	Bay	Open	178	-19.6	9.3
	Winter	Channel	Open	43	-20.5	12.3
Silver perch	Fall	Bay	Open	31	-20.5	11.7
		Pond	Edge	33	-20.1	11.6
Speckled worm eel	Fall	Pond	Open	35	-16.7	9.4
	Winter	Channel	Edge	83	-20.5	9.2
	Summer	Bay	Open	28	-21.5	11.8
Spot	Winter	Bay	Edge	17	-16.7	11.1
Spot	Spring	Bay	Edge	28	-18.9	13.1
Spot	Summer	Channel	Open	31	-25.4	12.9
Spotted seatrout	Fall	Bay	Edge	42	-20.1	12.1
				63	-19.9	12.6
				34	-19.0	10.7
				89	-18.4	11.1
	Summer	Pond	Open	52	-19.1	11.8
Star drum	Summer	Bay	Edge	115	-24.8	12.9
	Fall	Bay	Open	43	-20.0	12.7
White shrimp	Summer	Channel	Open	28	-25.2	10.9
				35	-26.2	10.9

## VITA

Guillermo Duque was born in Palmira, Colombia, in January 20, 1970. He is the son of Alberto Duque (deceased) and Dora Nivia, and the youngest brother of Fernando, Carmenza, Luisa Maria, Andres Alberto, and Maria del Rosario. He attended Gimnasio de Occidente High School in Cali, Colombia, graduating in 1986. He then served in the Colombian army for a year and entered college in fall of 1987. Guillermo graduated from Universidad del Valle (UV) in March of 1994 with a bachelor's degree in biology with emphasis in marine biology. The title of his B.S. thesis is: Trophic ecology and reproduction of *Oligoplites* (Pisces: Carangidae) species in the Ciénaga Grande de Santa Marta, Colombian Caribbean. In the UV, Guillermo was a teaching assistant for Vertebrate Zoology and Animal Physiology courses. Then, he entered a masters program in marine biology in the Universidad Nacional de Colombia (UNC) in January of 1994 and graduated in August of 1997. The title of his M.S. thesis is: Food habits and trophic relationships of *Anchovia clupeioides* (Pisces: Engraulidae) in the Ciénaga Grande de Santa Marta, Colombian Caribbean. At UNC he had the opportunity to be a teaching assistant in a course on Topics in Marine Science. Also, he was allowed to attend two international courses, one in summer of 1996 in Bermuda Biological Station for Research, Inc, Bermuda, titled: Biology of Fishes and another in May of 1997 in Harbor Branch Oceanography Institution, Fort Pierce, Florida, titled Ecology of Tropical Fishes. In 1997, he won a fellowship from the Colombian government agency, COLCIENCIAS (Instituto Colombiano para la Ciencia y la Tecnologia "Francisco Jose de Caldas"), to pursue doctoral studies in a foreign country. So, he entered the doctoral program in the Department of Oceanography and Coastal Sciences (DOCS) at the Louisiana State

University (LSU) in the fall of 1997 under the supervision of Dr. Donald M. Baltz. In this department, he chose to take coastal-related courses and minor courses in statistics and biology. He acquired teaching experience while at LSU as a teaching assistant in Introduction to Oceanography and as a laboratory instructor in Biology for Science Majors I in the Biology Department. Guillermo has five publications and two manuscripts in review and has presented his research work in 14 national and international meetings in five countries in both Spanish and English. He will earn his doctoral degree in Oceanography and Coastal Sciences in May of 2004. He then will go back to his home country, Colombia, to seek a job that will allow him to share his knowledge base in fish ecology and fisheries conservation to improve the living standards in his beloved Colombia.