

2005

Nekton utilization of black mangrove (*Avicennia germinans*) and smooth cordgrass (*Spartina alterniflora*) sites in southwestern Caminada Bay, Louisiana

Melanie Christine Caudill

Louisiana State University and Agricultural and Mechanical College

Follow this and additional works at: https://digitalcommons.lsu.edu/gradschool_theses



Part of the [Oceanography and Atmospheric Sciences and Meteorology Commons](#)

Recommended Citation

Caudill, Melanie Christine, "Nekton utilization of black mangrove (*Avicennia germinans*) and smooth cordgrass (*Spartina alterniflora*) sites in southwestern Caminada Bay, Louisiana" (2005). *LSU Master's Theses*. 273.

https://digitalcommons.lsu.edu/gradschool_theses/273

This Thesis is brought to you for free and open access by the Graduate School at LSU Digital Commons. It has been accepted for inclusion in LSU Master's Theses by an authorized graduate school editor of LSU Digital Commons. For more information, please contact gradetd@lsu.edu.

NEKTON UTILIZATION OF BLACK MANGROVE (*AVICENNIA GERMINANS*)
AND SMOOTH CORDGRASS (*SPARTINA ALTERNIFLORA*) SITES
IN SOUTHWESTERN CAMINADA BAY, LOUISIANA

A Thesis

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
Master of Science

in

The Department of Oceanography and Coastal Sciences

by
Melanie Christine Caudill
B.S., University of Florida, 1999
December, 2005

ACKNOWLEDGEMENTS

I would like to acknowledge the faculty, staff, and graduate students of the Coastal Fisheries Institute and the Department of Oceanography and Coastal Sciences at Louisiana State University for contributing to the success of this project. I especially thank Dr. Richard F. Shaw, my major professor, for his patience, encouragement, and support and my committee members, Dr. Lawrence P. Rozas, Dr. Donald M. Baltz, and Dr. Irving A. Mendelssohn, for their guidance.

I would like to especially thank David Lindquist, whose help was invaluable from the beginning, building lift nets and boardwalks, through to the last sampling trip and Brian Milan for generously sharing his time and marsh expertise during the formative stages of this project. I also thank Carey Gelpi, Stan Howarter, Sean Keenan, Kari Malen, Michael McDonough, and Robin Weissert for their enthusiastic help in the field.

I would like to acknowledge several people who provided advice and resources that improved different aspects of this project: Dr. Kevin Carman and Carey Gelpi (meiofauna), Erick Swenson (water level), Wilton Delaune, Dr. James P. Geaghan (statistics), Dr. E. Barry Moser (statistics), and Pamela MacRae (statistics). I am grateful to Louisiana Universities Marine Consortium for providing funding support with a grant to study “Impacts of Climate Change on Coastal Louisiana” through their Graduate Student Research Program and to the Wisner Foundation for allowing me to conduct this study on their land.

Very special thanks are due to my parents, Ray and Ruth Caudill, my sisters, Brooke and Emily, Stanley Howarter, and all my family and friends for their unconditional love and support.

TABLE OF CONTENTS

ACKNOWLEDGEMENTS.....	ii
LIST OF TABLES.....	v
LIST OF FIGURES.....	vii
ABSTRACT.....	x
INTRODUCTION.....	1
METHODS.....	6
Study Area.....	6
Study Design.....	6
Habitat Measurements.....	9
Vegetation.....	9
Surface Elevation and Hydroperiod.....	10
Physicochemical Variables and Substrate Characteristics.....	11
Meiofauna Sampling.....	11
Fish and Decapod Crustacean Sampling.....	12
Lift Net Efficiency Experiment.....	12
Statistical Analyses.....	13
RESULTS.....	15
Habitat Characteristics.....	15
Vegetation.....	15
Surface Elevation and Hydroperiod.....	16
Physicochemical Variables and Substrate Characteristics.....	22
Meiofauna.....	24
Fish and Crustacean Habitat Use.....	26
Species Composition, Diversity and Richness.....	26
Abundance.....	32
Density.....	33
Biomass.....	37
Length.....	41
Fish and Crustacean Density - Habitat Associations.....	41
Lift Net Efficiency Experiment.....	43
DISCUSSION.....	53
Habitat.....	53
Fish and Crustacean Habitat Use.....	55
Conclusions.....	60
Implications.....	61
Black Mangrove and Transition Habitat Types as EFH.....	61

LITERATURE CITED.....	63
VITA.....	71

LIST OF TABLES

Table 1. Research comparing fish/invertebrate use of mangroves and adjacent habitat types.....	5
Table 2. Mean percent cover \pm 1 standard deviation at <i>Spartina</i> (<i>Spartina alterniflora</i>), mangrove (<i>Avicennia germinans</i>), and transition sites during fall (August to October 2003; N=5) and spring (March to June 2004; N=2) seasons. Percent cover was estimated within each 4 m ² lift net.....	15
Table 3. Physicochemical, vegetation, surface elevation, and hydroperiod characteristics at the <i>Spartina</i> , mangrove, and transition sites. Fall (August to October 2003) and spring (March to June 2004) means \pm 1 standard deviation (calculated from N samples) are presented. Areal stem cover is the product of mean stem area and stem density (no. stems 0.25 m ⁻²). ASC is presented as the percentage of stems 4 m ⁻² . Lift net surface elevations (cm) are the average of four lift net elevations taken per habitat type in December 2004. Maximum flooding depth (cm) is the value recorded with float and magnet at each lift net per sampling date. Flooding duration (%) is (the total hours marsh inundated / total hours in month) x 100. Flooding frequency is the average monthly percentage of high tide events that flooded the marsh/mangal surface.....	17
Table 4. Results of ANOVA tests for physicochemical, vegetation, surface elevation, and hydroperiod differences among <i>Spartina</i> , mangrove, and transition habitat types (H), between fall (August to October 2003) and spring (March to June 2004) seasons (S), and by habitat type and season interaction (H*S). Significant results are indicated with *(0.05 \geq p>0.01) and highly significant results with **(p \leq 0.01).....	18
Table 5. Percent of sediment from <i>Spartina</i> , mangrove, and transition cores (7.5 cm diameter x 7.5 cm long) retained on 2 mm, 500 μ m, 150 μ m, 63 μ m, and <63 μ m sieves.....	23
Table 6. Mean individuals core ⁻¹ \pm 1 standard deviation (SD), abundance, and percent abundance of meiofauna collected from the top two cm of 3.7 cm diameter x 12.5 cm long sediment cores (N=number of cores) collected within <i>Spartina</i> and mangrove lift nets during August and October (2003) and March and June (2004).....	25
Table 7. Results of ANOVA tests for differences in meiofauna taxa abundances between <i>Spartina</i> and mangrove habitat types (H), among August and October (2003) and March and June (2004) months (M), and by habitat type and month interaction (H*M). Significant results are indicated with *(0.05 \geq p>0.01) and highly significant results with **(p \leq 0.01).....	26
Table 8. Abundance, percent abundance, biomass (g), and percent biomass of fishes and crustaceans collected at <i>Spartina</i> , mangrove, and transition sites from August to October 2003 and March to June 2004. N=total lift net samples.....	28
Table 9. Mean densities (no. individuals m ⁻²) \pm 1 standard deviation of numerically abundant species collected at <i>Spartina</i> , mangrove, and transition sites during fall (August to October 2003) and spring (March to June 2004). N=total lift net samples.....	35

Table 10. Mean lengths (mm) \pm 1 standard deviation (calculated from N samples) of numerically abundant species collected at <i>Spartina</i> , mangrove, and transition sites during fall (August to October 2003) and spring (March to June 2004). Fish, shrimp, and crab lengths were measured as standard lengths (SL), rostrum lengths (RL), and carapace widths (CW), respectively. White shrimp and tidewater silversides were not collected during the spring season.....	44
Table 11. Results from the significant Canonical Correspondence Analysis (CCA; $p=0.002$) showing the weighted correlation matrix of habitat/environmental variables with the canonical axes. Axes 1 and 2 explained 52.5% and 21.2% of the variability, respectively, in fish and crustacean species densities.....	46
Table 12. Results from lift net efficiency experiment. Size range (mm), mean length (mm; fish, SL and shrimp, RL), number of organisms recovered (out of 40), and mean recovery (%) \pm 1 standard deviation are given for gulf killifish (<i>Fundulus grandis</i>) and grass shrimp (<i>Palaemonetes spp.</i>). Mean recovery estimates are the average of four tests per habitat type (<i>Spartina</i> , mangrove, and transition).....	52

LIST OF FIGURES

Figure 1. Study area in southwestern Caminada Bay, Louisiana, USA. Black mangrove (M), <i>Spartina</i> (S), and transition (T) sampling sites are shown.....	7
Figure 2. (a) <i>Avicennia germinans</i> (black mangrove), (b) <i>Spartina alterniflora</i> (smooth cordgrass), and (c) transition habitat types in southwestern Caminada Bay, Louisiana.....	8
Figure 3. (a) Mean stem densities (no. stems 0.25 m ⁻²) and (b) mean areal stem cover (% stems 4 m ⁻²) at <i>Spartina</i> , mangrove, and transition sites during August-October (2003), and March and June (2004). Error bars are equal to one standard deviation (N=4).....	19
Figure 4. Water level sensor data from <i>Spartina</i> , mangrove, and transition sites (a) 9/19/03 and (b) 10/16/03.....	20
Figure 5. Maximum flooding depths (cm) at <i>Spartina</i> , mangrove, and transition sites, 8 August 2003 to 29 June 2004. Error bars are equal to one standard deviation (N=4).....	21
Figure 6. Flooding durations (%) at <i>Spartina</i> , mangrove, and transition sites during fall (August to October 2003) and spring (March to June 2004). Flooding duration=[(hours marsh inundated)/(total hours in month) x 100]. Error bars are equal to one standard deviation (N≈30).....	21
Figure 7. Mean dissolved oxygen (mg L ⁻¹) at <i>Spartina</i> , mangrove, and transition sites, 8 August 2003 to 29 June 2004. Error bars are equal to one standard deviation (N=4).....	23
Figure 8. Mean abundances (no. individuals in top 2 cm of 3.5 cm diameter x 12.5 cm long meiofauna cores) of (a) nematodes, (b) crustacean nauplii, (c) kinorhynchans, (d) ostracods, and (e) copepods collected at <i>Spartina</i> (N=16) and mangrove (N=16) sites in August and October (2003) and March and June (2004). Error bars are equal to one standard deviation.....	27
Figure 9. Correspondence analysis showing (a) associations among <i>Spartina</i> (S), mangrove (M), and transition (T) sites and (b) associations between fish and crustacean species presence-absence data and sites.....	30
Figure 10. Contribution of fishes versus crustaceans to total catch at <i>Spartina</i> , mangrove, and transition sites.....	32
Figure 11. Mean (a) fish densities and (b) crustacean densities at <i>Spartina</i> (fall, N=24; spring, N=24), mangrove (fall, N=24; spring, N=22), and transition sites (fall, N=23; spring, N=23) during fall (August to October 2003) and spring (March to June 2004). Error bars are equal to one standard deviation.....	34

Figure 12. Mean densities (no. individuals m^{-2}) of (a) gulf killifish, (b) darter goby, (c) tidewater silverside, (d) grass shrimp, (e) white shrimp, (f) brown shrimp, (g) blue crab, and (h) gulf stone crab at <i>Spartina</i> , mangrove, and transition sites from 8 August 2003 to 29 June 2004. Error bars are equal to one standard deviation (N=4). P-values are significant habitat/seasonal differences.....	36
Figure 13. Contribution of fishes versus crustaceans to total biomass (g) at <i>Spartina</i> , mangrove, and transition sites.....	38
Figure 14. Mean (a) fish and (b) crustacean biomass (g) at <i>Spartina</i> (fall, N=24; spring, N=24), mangrove (fall, N=24; spring, N=22), and transition sites (fall, N=23; spring, N=23) during fall (August to October 2003) and spring (March to June 2004). Error bars are equal to one standard deviation.....	39
Figure 15. Mean biomass (g) of (a) gulf killifish, (b) darter goby, (c) striped mullet, (d) white shrimp, (e) blue crab, and (f) gulf stone crab at <i>Spartina</i> , mangrove, and transition sites from 8 August 2003 to 29 June 2004. Error bars are equal to one standard deviation (N=4). P-values are significant habitat/seasonal differences.....	40
Figure 16. Length-frequency graphs for (a) gulf killifish (SL), (b) darter goby (SL), (c) white shrimp (RL), and (d) blue crab (CW) collected at <i>Spartina</i> , mangrove, and transition sites, 8 August 2003 to 29 June 2004. P-values are significant habitat type differences.....	45
Figure 17. Results from CCA showing associations between fish and crustacean species densities (BC=blue crab, BS=brown shrimp, DG=darter goby, FC=fiddler crab, GK=gulf killifish, GS=grass shrimp, GSC=gulf stone crab, SMU=striped mullet, TS=tidewater silverside, WS=white shrimp) and habitat/environmental variables. Numeric habitat codes were assigned to <i>Spartina</i> (1), transition (2), and black mangrove (3) habitat types.....	46
Figure 18. Plots of (a) fish and (b) crustacean densities (no. individuals m^{-2} ; $\log_{10}(x+1)$ transformed) relative to salinity (ppt) at the <i>Spartina</i> , mangrove, and transition sites. Each point is the mean density of four lift net samples. Sampling occurred from 8 August 2003 to 29 June 2004.....	47
Figure 19. Plots of (a) fish and (b) crustacean densities (no. individuals m^{-2} ; $\log_{10}(x+1)$ transformed) relative to water temperature ($^{\circ}C$) at the <i>Spartina</i> , mangrove, and transition sites. Each point is the mean density of four lift net samples. Sampling occurred from 8 August 2003 to 29 June 2004.....	48
Figure 20. Plots of (a) fish and (b) crustacean densities (no. individuals $4 m^{-2}$; $\log_{10}(x+1)$ transformed) relative to stem density (no. stems $4 m^{-2}$) at the <i>Spartina</i> , mangrove, and transition sites. Each point is the mean density of four lift net samples, which were sampled concurrent with vegetation sampling over 5 dates from 8 August 2003 to 29 June 2004.....	49

Figure 21. Plots showing significant linear relationships between fish/crustacean densities (no. individuals m^{-2} ; $\log_{10}(x+1)$ transformed) and flooding duration (h tidal cycle $^{-1}$) at (a, b) mangrove and (c) transition sites. Regression line is indicated by a solid line.....50

Figure 22. Plots of (a) fish and (b) crustacean densities (no. individuals m^{-2} ; $\log_{10}(x+1)$ transformed) relative to maximum flooding depth (cm) at the *Spartina*, mangrove, and transition sites. Each point is the mean density of four lift net samples. Sampling occurred from 8 August 2003 to 29 June 2004.....51

ABSTRACT

This is the first study to compare nekton use and habitat value among *Spartina alterniflora* (*Spartina*), *Avicennia germinans* (black mangrove), and transition (*S. alterniflora* and *A. germinans*) sites within Louisiana's salt marsh-mangrove ecotone. Fishes and crustaceans were collected in Caminada Bay during fall 2003 and spring 2004 using 4 m², bottomless lift nets. Although analyses were unable to demonstrate significant differences in fish ($p=0.0753$) and crustacean ($p=0.1457$) densities and species composition ($p=0.8801$) across sites, habitat-specific trends in nekton use were evident. Fishes, including gulf killifish and sheepshead minnows, showed affinities for the *Spartina* site, while crustaceans, especially white shrimp, were more associated with the mangrove site. Total fish biomass ($p=0.0396$) and gulf killifish biomass ($p=0.0223$) and densities ($p=0.0543$) were significantly greater at *Spartina* than mangrove sites. White shrimp biomass was significantly greater at mangrove than *Spartina* ($p=0.0062$) and transition sites ($p=0.0143$) and gulf stone crab densities were also higher at mangrove than transition sites ($p=0.0061$). Habitat type, areal stem cover (ASC), turbidity, and temperature explained 52% of the variability in nekton densities. Greater structural complexity (ASC, $p<0.0001$) at the mangrove site may increase refuge value for crustaceans given that (1) most were juveniles, including white shrimp, brown shrimp, blue crabs, and gulf stone crabs, and (2) white shrimp and brown shrimp were positively associated with ASC. Lower ASC and greater flooding depths ($p=0.0318$) and durations ($p=0.0065$) at *Spartina* than at the higher elevation mangrove site may benefit larger nekton by increasing access to the flooded marsh. The transition site had similar vegetation characteristics as the *Spartina* site, but flooding depths and durations resembled the mangrove site. Nekton densities were positively related to flooding duration at mangrove (fish, $p=0.0031$; crustacean, $p=0.0040$) and transition sites (fish,

$p=0.0018$). Low fish use at mangrove and transition sites during spring 2004 suggests that (1) reduced hydroperiod negatively affects fishes, and (2) *Spartina* marshes may become especially important when meteorological events reduce access to mangrove and transition habitat types. More research is necessary to determine if these findings are representative of Louisiana's salt marsh-mangrove ecotone statewide, and to understand the fisheries implications of continued mangrove expansions.

INTRODUCTION

Mangroves replace salt marshes as the dominant coastal wetlands at subtropical and tropical latitudes (Mendelssohn & McKee 2000, Mitsch & Gosselink 2000). At 29°N latitude, coastal Louisiana is at the northernmost extent of the mangrove range in North America (Sherrod & McMillan 1985). In Louisiana, *Avicennia germinans* (black mangroves) and *Spartina alterniflora* (smooth cordgrass) form a salt marsh-mangrove ecotone. Within this landscape, black mangroves occupy higher elevations, on the fringe of bays and creekbanks, and smooth cordgrass salt marshes dominate lower elevations and interior marshes (Patterson & Mendelssohn 1991, Patterson et al. 1997). A transition zone occurs at intermediate elevations where *A. germinans* and *S. alterniflora* coexist (Patterson et al. 1997).

Black mangroves have been sporadically reported in Louisiana since the 1700's (Sherrod & McMillan 1985) and are currently most prevalent in the southcentral part of the state, around Port Fourchon and Grand Isle. Historically, periodic freeze events and resultant diebacks have controlled the distribution and abundance of black mangroves in the northern Gulf of Mexico (Sherrod & McMillan 1985). In fact, several days of severe freezing temperatures during the winters of 1983 and 1985 killed all above-ground black mangrove biomass at a study site near Port Fourchon (Patterson & Mendelssohn 1991). Mild temperatures since the last hard freeze, during the winter of 1989-90, have facilitated an expansion of black mangroves in Louisiana.

Global climate change models predict increases in air temperature of 1.4-5.8°C by 2100 (USGCRP 2002) that may enable mangroves to expand beyond their current range. However, sea level rise and local sediment availability will be the primary factors affecting future mangrove distributions (Field 1995). Predicting future changes to Louisiana's salt marshes and mangroves is confounded by natural and anthropogenic factors that have reduced sediment input

and accelerated local subsidence rates (Penland & Ramsey 1990, Turner 1990, Britsch & Dunbar 1993). Global climate change may facilitate vegetation shifts in coastal Louisiana, such as (1) widespread and permanent black mangrove expansion in the region and/or (2) the appearance and survival of less cold tolerant mangrove species (e.g., *Rhizophora mangle*) in the northern Gulf of Mexico (Gulf). Whether the current black mangrove expansion is a periodic phenomenon or a permanent vegetation shift linked to global warming, it is important to understand how black mangroves affect the fish and crustacean communities that rely on Louisiana's coastal wetlands.

Many studies have examined fish and crustacean use of Louisiana's salt marshes (Rakocinski et al. 1992, Baltz et al. 1993, Rozas & Reed 1993, Peterson & Turner 1994, Minello & Rozas 2002), yet none have compared their use among black mangrove, salt marsh, and transition habitat types. Congress reauthorized the Magnuson-Stevens Fishery Conservation and Management Act through the Sustainable Fisheries Act in 1996 to ensure that "essential fish habitat" (EFH) be designated for every species federally managed under fishery management plans. As such, EFH is defined as "those waters and substrate necessary to fish for spawning, breeding, feeding, and/or growth to maturity" (NOAA 1996). Currently, the role of black mangrove and transition habitat types as EFH in Louisiana is unknown.

The high fisheries production characteristic of the Gulf coast has often been attributed to the immense area and quality of these coastal habitats (Turner 1977, Zimmerman et al. 2000). Extensive coastal marshes across Louisiana and the northern Gulf account for 55% of the total wetlands in the United States (Mendelssohn & McKee 2000). These marshes support productive penaeid shrimp (*Litopenaeus setiferus*, *Farfantepenaeus aztecus*, *F. duorarum*) and blue crab (*Callinectes sapidus*) fisheries that constitute 66% and 25% of their respective national fisheries'

production (Zimmerman et al. 2000). In addition, Louisiana's commercial fish catch is second only to Alaska (Chesney et al. 2000).

It is a commonly held belief among fisheries scientists and managers that coastal wetlands provide important food and refuge resources for nekton (Boesch & Turner 1984, Rozas & Odum 1988). Epifaunal and infaunal organisms are an abundant, high quality food resource for fishes and crustaceans in both salt marshes (Rozas & LaSalle 1990, Minello & Zimmerman 1991, Gregg & Fleeger 1997, Gregg & Fleeger 1998, Smith et al. 2000, Whaley & Minello 2002) and mangroves (Stoner & Zimmerman 1988, Sasekumar et al. 1992, Ley et al. 1994, Sheridan 1997). In addition, these vegetated habitat types offer structurally complex refuge that may reduce predation pressure on small nekton and increase their growth and survival (Minello & Zimmerman 1983, Minello et al. 1989, Wilson 1989, Rozas & Minello 1998, Laegdsgaard & Johnson 2001, Sheridan & Hays 2003, Minello et al. 2003).

Salt marshes and mangroves are intertidal habitat types that are only accessible to fishes and crustaceans when inundated (Kneib & Wagner 1994, Rozas 1995). Consequently, hydroperiod, the frequency and duration of inundation, is the primary factor affecting nekton access to salt marshes and mangroves both temporally and spatially (Rozas 1995). Several factors affect hydroperiod, such as astronomical tides, meteorological/climatological effects, vertical movement of land surfaces, and coastal geomorphology (Rozas 1995). Hydrological conditions also affect the development of the physicochemical environment within the marsh and the biota that are found there (Mitsch and Gosselink 2000). Fish and crustacean metabolic processes, for example, are directly affected by salinity, temperature, and dissolved oxygen and indirectly by water depth, turbidity, light, and sediment type (Craig & Crowder 2000).

Fish and crustacean habitat selection integrates a combination of factors, including abiotic conditions, food resources, bioenergetics, competition, and predation (Craig & Crowder 2000). These factors are directly and indirectly affected by habitat structure (e.g., vegetation type), substrate (e.g., sediment grain size), hydrodynamics (e.g., currents, hydroperiod), and general hydrology (e.g., depth, temperature, salinity, turbidity; Minello 1999). Consequently, differences among Louisiana's salt marsh, black mangrove, and transition habitat characteristics may affect the availability and extent to which fishes and crustaceans select and use these habitat types.

Researchers often compare nekton use of two or more adjacent habitat types to gauge their relative habitat value. The latitudinal separation of salt marshes and mangroves limits direct comparative studies of habitat use to a few locations with salt marsh–mangrove ecotones. The majority of fish and crustacean research in mangroves has come from the tropics or Australia (Table 1), where differences in mangrove species, salt marsh species, associated biota, adjacent habitat types, geomorphology, hydroperiod, and climate make direct comparisons to Louisiana's salt marsh-mangrove ecotone difficult.

This is the first study to examine fish and decapod crustacean use of *Spartina alterniflora* (*Spartina*), *Avicennia germinans* (black mangrove), and transition (*S. alterniflora* and *A. germinans*) habitat types within Louisiana's salt marsh-mangrove ecotone. The research goals were as follows: (1) identify and compare *Spartina*, black mangrove, and transition habitat characteristics; (2) compare fish and decapod crustacean use among the three habitat types; and (3) discern the relative importance of different habitat characteristics on fish and crustacean use of *Spartina*, mangrove, and transition habitat types. Habitat use was evaluated by comparing fish and crustacean species diversity and richness, abundance, density, biomass, and size

(length). Habitat value was assessed by comparing the following characteristics: vegetation percent cover, stem density, areal stem cover, surface elevation, water depth, flooding frequency and duration, water temperature, salinity, dissolved oxygen, turbidity, sediment grain size, and benthic meiofauna composition and abundance. This research tested the null hypotheses that fish and crustacean use and habitat value did not differ among *Spartina*, mangrove, and transition sites or between fall and spring seasons.

Table 1. Research comparing fish/invertebrate use of mangroves and adjacent habitat types.

Study	Location	Study Animals	Habitat Type(s)
Acosta 1997	Puerto Rico	fish	mangroves, coral reef
Bell et al. 1984	Australia	fish	mangrove creek
Blaber et al. 1989	Australia	fish	mangrove, seagrass, open water, sand, mud
Bloomfield & Gillanders 2005	Australia	fish and invertebrates	mangrove, seagrass, marsh, nonvegetated
Chong et al. 1990	Malaysia	fish and shrimp	mangrove, mudflat, near /far inshore
Cocheret de la Morinière et al. 2004	Caribbean	fish	mangrove, seagrass
Ellis & Bell 2004	Florida (USA)	fish	intertidal mangrove forest
Halpern 2004	Caribbean	fish	mangroves
Hindell & Jenkins 2004	Australia	fish	mangrove, mudflat
Kuo et al. 1999	China	fish	mangrove creeks
Laegdsgaard & Johnson 2001	Australia	juvenile fish	mangroves
Laroche et al. 1997	Madagascar	fish	mangrove creeks
Ley et al. 1994	Florida (USA)	fish	mangroves
Ley et al. 1999	Florida (USA)	fish	mangrove prop roots
Lin & Shao 1999	China	fish	mangrove creek
Louis et al. 1995	Caribbean	fish	mangrove forests
McIvor & Smith 1995	Florida (USA) and Australia	crabs	intertidal mangrove forests
Mohan et al. 1997	India	shrimp	mangrove forest
Nagelkerken et al. 2000	Caribbean	fish	mangroves, seagrass, coral reef
Nagelkerken et al. 2002	Caribbean	fish	mangroves, seagrass, coral reef
Nagelkerken & van der Velde 2004	Caribbean	fish	mangrove, seagrass
Odum & Heald 1972	Florida (USA)	fish and invertebrates	mangrove
Pinto & Punchihewa 1996	Sri Lanka	fish	mangrove, seagrass
Rönnbäck et al. 1999	Phillipines	fish and shrimp	different mangrove species
Rooker & Dennis 1991	Puerto Rico	fish	mangrove prop roots
Sasekumar et al. 1992	Malaysia	fish and shrimp	mangrove inlets and creeks
Sheaves & Molony 2000	Australia	fish and crabs	intertidal mangrove forests
Sheridan 1992	Florida (USA)	fish and crabs	mangrove, seagrass, open water
Sheridan & Hays 2003	review paper	fish and crustaceans	mangrove, seagrass, reef, marsh, sand, mud
Wilson 1989	Florida (USA)	crabs	mangrove (prop roots, pneumatophores)

METHODS

Study Area

This study was conducted in southwestern Caminada Bay, Louisiana (29°13'N, 90°06'W) within the Wisner Wildlife Management Area (Figure 1). Caminada Bay (5,663 ha) is a shallow bay (≤ 2 meters) in southcentral Louisiana that connects with Barataria Bay to the east, Timbalier Bay to the west, and Grand Isle and the Gulf of Mexico to the south. Caminada Bay is within the Barataria Basin, which extends 110 km inland from the Gulf and consists of 145,000 ha of productive salt marsh (Baltz et al. 1993). Salinities within the salt marshes of the Barataria Basin range from 6-22 ppt and freshwater input to the system comes primarily from precipitation, which averages 160 cm year⁻¹ (Baltz et al. 1993). Coastal Louisiana is microtidal, with predominantly diurnal tides that average 0.32 m in range (Zetler & Hansen 1972). Louisiana's tidal regime is sensitive to meteorological forcing events (in particular winter/spring atmospheric cold front passages) that effectively override astronomical tides and prevent or enhance marsh flooding or draining depending on wind speed and direction (Rogers et al. 1993, Rozas 1995, Minello 1999). The close proximity of *Avicennia germinans*, *Spartina alterniflora*, and transition sites (Figure 2) within southwestern Caminada Bay allowed simultaneous sampling of the three habitat types, which minimized temporal and tidal variability.

Study Design

Bottomless lift nets (Rozas 1992), a type of enclosure sampling gear, were used to quantify fish and decapod crustacean densities and biomass at *Spartina*, black mangrove, and transition sites. Four, replicate, 4 m² lift nets were constructed one meter in from the vegetation-water interface at each of the three habitat types for a total of 12 lift nets. Lift nets were 2 m x 2 m x 1 m nets (1/8 inch mesh) attached to 4 m² wooden frames that were permanently inserted

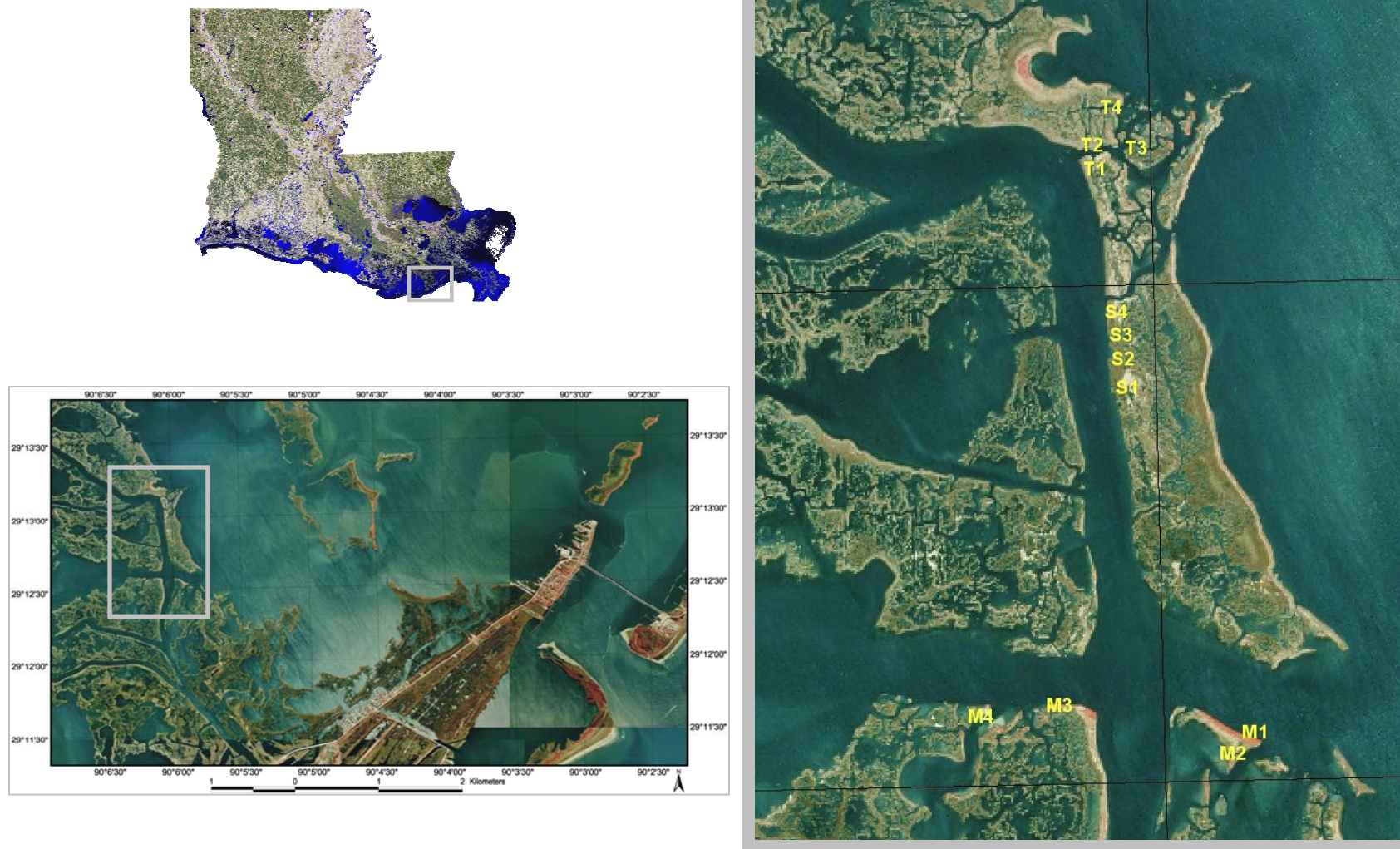


Figure 1. Study area in southwestern Caminada Bay, Louisiana, USA. Black mangrove (M), *Spartina* (S), and transition (T) sampling sites are shown.

a.) *Avicennia germinans*



b.) *Spartina alterniflora*



c.) Transition



Figure 2. (a) *Avicennia germinans* (black mangrove), (b) *Spartina alterniflora* (smooth cordgrass), and (c) transition habitat types in southwestern Caminada Bay, Louisiana.

into a narrow trench dug into the marsh floor. The nets collapsed flush with the marsh surface when they were not fishing. Ropes were tied to the four corners of the net and threaded through four corner guideposts. At slack high tide, two people remotely lifted each net with one swift pulling motion on the ropes. As the marsh drained, fishes and crustaceans were concentrated into a pit trap which was buried flush with the marsh surface at the lowest elevation within the

net. Temporary boardwalks surrounded each lift net and were used during net maintenance and removal of the catch to minimize disturbance to the vegetation and the marsh/mangal surface.

Lift nets must flood and drain completely to work effectively. Therefore, the 12 sampling dates were chosen to coincide with the highest tidal ranges each month. Fall and spring seasons were chosen because these are periods of high nekton abundances and high water levels in the marsh (Rozas 1995). Fall sampling occurred twice monthly from August to October 2003 for a total of six fall sampling trips. Spring sampling began in late March 2004, was suspended in April because of insufficient marsh flooding due to meteorological conditions, and resumed in May and June for a total of six spring sampling trips.

Habitat Measurements

Vegetation

Percent cover was visually estimated for each plant species present within *Spartina*, black mangrove, and transition lift nets. Percent cover was recorded five times during fall and at the beginning and end of the spring season. *Avicennia germinans* cover was specified as canopy or pneumatophores.

Stem densities, diameters, and heights were measured three times in fall and twice in spring using 0.25 m² quadrates. One quadrate was randomly placed in the front of the lift net (i.e., closest to the vegetation-water interface) and a second quadrate was randomly placed in the back of the lift net. Stem densities from the front and back quadrates were then averaged to calculate a mean stem density (no. stems 0.25 m⁻²) per lift net. Mangrove pneumatophores were measured as stems, in addition to the actual mangrove tree stems. Stem diameters (mm) and heights (cm) were measured for 20% of the total number of stems per quadrate. Stem diameters were measured to the nearest 0.1 mm using vernier calipers. Areal stem cover (ASC) was

calculated for each quadrat (2 per net) by multiplying the mean stem area by the number of stems (modified from Meyer et al. 2001). Mean ASC for each lift net was calculated by averaging ASC values from the front and back quadrats.

Surface Elevation and Hydroperiod

Surface elevation (cm) of the substrate at the marsh edge was estimated by measuring the vertical distance from the beam of a laser level set at the vegetation-water interface to the level water surface at low tide. Lift net surface elevations (cm) were similarly measured as the vertical difference from the beam of the laser level set at the vegetation-water interface to the middle of the lift net marsh floor. For both measurements, the laser level was placed atop a one meter, 7.5 cm diameter PVC pipe at the vegetation-water interface; this difference was subtracted from both marsh edge and lift net surface elevation calculations. Time was recorded concurrent with each elevation measurement to determine tide level from a nearby U.S. Geological Survey (USGS) water level sensor in Barataria Bay (USGS 73802515). Depth of inundation was calculated by subtracting lift net surface elevation from tidal level.

An Infinities Pressure Water Level Datalogger, which continuously recorded water level measurements every 15 minutes, was centrally located within each of the three habitat types. Water level sensors were not installed until September 2003; therefore, August water level values were estimated using lift net elevation data and water level data from the USGS sensor. Because the mangrove sensor malfunctioned for much of the spring season, mangrove water levels were estimated from the *Spartina* sensor after correcting for among-site elevation differences.

Maximum flooding depth (cm) was gauged at each lift net using a metal rod, disc-shaped float, and magnet. The magnet was pushed up the rod by the float with the rising tide. When the

tide receded, the magnet stayed in place and the float dropped with water level. Maximum flooding depth was then recorded as the distance from the bottom of the magnet to the marsh sediment. These water level gauges were located adjacent to a front corner of each lift net, one meter in from the vegetation-water interface.

Flooding frequency (%) is defined as the percentage of total tidal cycles that flooded the marsh/mangal surface each month. Flooding duration (%) is defined as the percentage of the total hours per month that the marsh/mangal surface was flooded. Flooding frequency and duration were estimated for each habitat type using on-site water level sensor data.

Physicochemical Variables and Substrate Characteristics

Salinity (ppt), water temperature ($^{\circ}\text{C}$), and dissolved oxygen (mg L^{-1}) were recorded at high tide at each lift net using a YSI Model 85 Water Quality Monitor. Water samples were taken at high tide on the marsh (two per site) and then filtered through pre-weighed 47 mm glass microfibre filters, dried in an oven for 24 hours at 60°C , and re-weighed to measure suspended solids/turbidity (mg L^{-1}). A total of three sediment cores (7.5 cm diameter x 7.5 cm long) were randomly taken within each lift net and combined to account for heterogeneity. A sediment core from one lift net per habitat type was randomly selected and sieved for grain size analysis. Sediment cores were dried in a 60°C oven for three days, soaked in detergent to soften sediment, wet sieved through no. 10 (2.00 mm), no. 35 (500 μm), no. 100 (150 μm), and no. 230 (63 μm) sieves, dried for three days in a 60°C oven, and weighed (g). The percentage of sediment retained on each sieve was calculated for each habitat type.

Meiofauna Sampling

The meiofauna component of this study was done in collaboration with Dr. Kevin Carman and Mr. Carey Gelpi (Department of Biological Sciences, Louisiana State University,

Baton Rouge) who were responsible for developing the sampling methodology and sorting and identifying the samples. Three meiofauna cores (3.5 cm diameter x 12.5 cm long) were taken within each lift net at low tide, concurrent with fish and crustacean sampling. The top two cm of each meiofauna core was extruded and preserved in formaldehyde (10% of stock solution) for sorting. A subsample of meiofauna cores from the mangrove (N=16 cores) and *Spartina* (N=16 cores) sites for the months of August and October (2003) and March and June (2004) were randomly selected for sorting. In the lab, Mr. Gelpi processed the meiofauna cores through 63 and 32 μm sieves to allow for better separation of sediment, stained the samples with a rose bengal and formaldehyde mixture, and then sorted, identified, counted, and recorded major taxa.

Fish and Decapod Crustacean Sampling

Fishes and crustaceans entrapped within lift nets at slack high tide were retrieved at low tide from each pit trap, sealed in plastic bags, and immediately put on ice. In the lab, each animal was identified to either the species level or the lowest practical taxonomic level. Fish and crustacean species diversity was calculated for each lift net sample using the Shannon-Weiner Diversity Index, $H' = -\sum (p_i)(\log^2 p_i)$ (Krebs 1989). Richness was expressed as the number of species/taxa per lift net sample. Fish and crustacean density estimates were reported as the number of individuals m^{-2} . Biomass (g) was recorded for each species/taxa per lift net sample. Standard length (SL), carapace width (CW) or rostrum length (RL) was recorded for each fish, crab, or shrimp, respectively. Grass shrimp (*Palaemonetes spp.*) lengths were not recorded. Mean lengths were calculated for each species/taxa per lift net sample.

Lift Net Efficiency Experiment

A lift net efficiency experiment was conducted in December 2004 to (1) estimate sample recovery for gulf killifish (*Fundulus grandis*) and grass shrimp and (2) to see if vegetation type

affected lift net recovery rates. Prior to the experiment, gulf killifish and grass shrimp were measured (SL and RL, respectively) and tagged (fin and uropod clipped, respectively). In addition, lift nets were repaired, cleared, and lifted at low tide. At high tide, ten grass shrimp and ten gulf killifish were released into each lift net. Grass shrimp were introduced first and given a couple minutes to hide before the gulf killifish were released. At low tide, the animals were collected from the pit traps and the percent of grass shrimp and gulf killifish recovered was calculated.

Statistical Analyses

The statistical design for this study was a split-plot design with sampling. Four, 4 m² lift nets were nested within each habitat type (*Spartina*, mangrove, transition). The whole plot was habitat type (H), with a whole plot error of net nested in habitat type (N(H)). The split plot was season (S) and habitat type by season interaction (H*S), with season by net nested in habitat type interaction (S*N(H)) as the error term. Habitat type and season were fixed effects and nets were random effects. This research tested the null hypotheses that fish and crustacean use and habitat characteristics did not significantly differ among the three habitat types, between seasons/among months, and by habitat type and month/season interaction.

Analysis of variance (ANOVA) with *a posteriori* Tukey tests was used to analyze stem density, ASC, surface elevation, maximum flooding depth, flooding frequency, flooding duration, water temperature, salinity, dissolved oxygen, turbidity, lift net sample recovery, fish and crustacean species diversity and richness, and dominant taxa density, biomass, and length data. Multivariate analysis of variance (MANOVA) was used to analyze meiofauna taxa abundance data and fish density, crustacean density, fish biomass, and crustacean biomass data.

Individual ANOVAs with *a posteriori* Tukey tests were used to investigate significant MANOVA results.

Correspondence analysis (CA) was used to generate spatial representations of species-site associations. Canonical correspondence analysis (CCA) was used to compare fish and crustacean densities with habitat characteristics (ter Braak 1986). Regression analyses were used to test for relationships between fish and crustacean densities and stem density, maximum flooding depth, and flooding duration.

Stem density, ASC, water temperature, turbidity, meiofauna abundance, species diversity, and fish and crustacean density, biomass, and length data were $\log_{10}(x+1)$ transformed prior to statistical analyses to satisfy or better meet assumptions of normality and homogeneous variance. The SAS Version 8.0 statistical software package was used for all analyses, except the CCA, which was analyzed using CANOCO Version 4.53. P-values ≤ 0.05 were considered significant for all statistical tests.

RESULTS

Habitat Characteristics

Vegetation

Vegetative cover within black mangrove lift nets was characterized by *Avicennia germinans* canopy (~70%), *A. germinans* pneumatophores and mud (~25%), and *Salicornia spp.* (Table 2). *Spartina alterniflora* stems accounted for about 90% of the cover within *Spartina* nets and non-vegetated mud made up the remaining area. *S. alterniflora* stems were also the majority of the vegetative cover (~70%) within transition nets, followed by *A. germinans* canopy (~20%), pneumatophores, non-vegetated mud (~7%), and *Salicornia spp.* (1%; Table 2).

Table 2. Mean percent cover \pm 1 standard deviation at *Spartina* (*Spartina alterniflora*), mangrove (*Avicennia germinans*), and transition sites during fall (August to October 2003; N=5) and spring (March to June 2004; N=2) seasons. Percent cover was estimated within each 4 m² lift net.

Habitat Type	Plant Species	Cover	Mean Percent Cover (% \pm 1 SD)	
			Fall (N=5)	Spring (N=2)
<i>Spartina</i>	<i>S. alterniflora</i>	stems	93.2 \pm 5.06	88.1 \pm 4.58
	non-vegetated	mud	6.9 \pm 5.06	11.9 \pm 4.58
Mangrove	<i>A. germinans</i>	canopy	72.2 \pm 12.97	69.1 \pm 8.89
	<i>A. germinans</i>	pneumatophores and mud	24.6 \pm 15.90	25.0 \pm 13.09
	<i>Salicornia spp.</i>	stems	8.1 \pm 7.54	15.7 \pm 8.14
Transition	<i>S. alterniflora</i>	stems	71.6 \pm 4.57	68.6 \pm 2.26
	<i>A. germinans</i>	canopy	20.5 \pm 4.26	23.8 \pm 3.54
	<i>A. germinans</i>	pneumatophores	12.5 \pm 2.89	0
	non-vegetated	mud	6.8 \pm 3.95	7.5 \pm 2.67
	<i>Salicornia spp.</i>	stems	1	1

Stem densities (no. stems 0.25 m⁻²) and areal stem cover (i.e., the product of mean stem area and stem density) were examined as a proxy for structural complexity. Stem densities were highest at the black mangrove site (fall, 159.2 \pm 47.1; spring, 150.3 \pm 22.0) and similar at *Spartina* (fall, 82.0 \pm 12.7; spring, 74.9 \pm 6.9) and transition sites (fall, 82.3 \pm 30.4; spring, 65.8 \pm 8.4; Table 3). Stem densities significantly differed among habitat types ($p < 0.0001$; Table 4),

with higher densities at the mangrove site than at both *Spartina* ($p < 0.0001$) and transition sites ($p < 0.0001$); however, *Spartina* and transition sites did not differ ($p = 0.6140$; Figure 3a).

Areal stem cover also significantly differed among habitat types ($p < 0.0001$; Tables 3 and 4), with higher ASC at the black mangrove site than at both *Spartina* ($p < 0.0001$) and transition ($p = 0.0002$) sites, but *Spartina* and transition sites did not differ ($p = 0.4834$; Figure 3b). Both stem densities and ASC did not differ seasonally ($p > 0.05$) or by habitat type and season interaction ($p > 0.05$).

Surface Elevation and Hydroperiod

Lift net surface elevations significantly differed among habitat types ($p = 0.0026$; Table 4). The mangrove site had significantly higher mean surface elevation (23.0 ± 4.03 cm) than transition (13.1 ± 5.39 cm; $p = 0.0510$) and *Spartina* sites (5.2 ± 5.67 cm; $p = 0.0020$; Table 3); however, transition and *Spartina* sites did not differ ($p = 0.1272$). Water level data from on-site sensors reflected these elevation differences (Figure 4).

Maximum flooding depths significantly differed among sites ($p = 0.0318$) and between seasons ($p = 0.0011$; Table 4 and Figure 5). Flooding depths were higher at the *Spartina* site (fall, 31.0 ± 9.67 cm; spring, 23.3 ± 11.62 cm) than at both mangrove (fall, 21.7 ± 7.88 ; spring, 17.2 ± 9.47 ; $p = 0.0446$) and transition sites (fall, 22.3 ± 6.31 ; spring, 17.0 ± 8.61 ; $p = 0.0457$; Table 3); however, mangrove and transition sites did not differ ($p = 0.9878$). Seasonally, water depths were higher during fall (24.7 ± 8.85 cm) than spring (18.4 ± 9.74 cm; $p = 0.0011$).

During fall, *Spartina* and transition sites flooded on 100% of possible tidal cycles and the mangrove site had a mean flooding frequency of $98.8 \pm 2.14\%$ (Table 3). During spring, mean flooding frequency was highest at *Spartina* ($86.0 \pm 21.50\%$) and transition sites ($83.0 \pm 18.70\%$) and lowest at the mangrove site ($51.0 \pm 22.70\%$; Table 3). This study was unable to find

Table 3. Physicochemical, vegetation, surface elevation, and hydroperiod characteristics at the *Spartina*, mangrove, and transition sites. Fall (August to October 2003) and spring (March to June 2004) means \pm 1 standard deviation (calculated from N samples) are presented. Areal stem cover is the product of mean stem area and stem density (no. stems 0.25 m^{-2}). ASC is presented as the percentage of stems 4 m^{-2} . Lift net surface elevations (cm) are the average of four lift net elevations taken per habitat type in December 2004. Maximum flooding depth (cm) is the value recorded with float and magnet at each lift net per sampling date. Flooding duration (%) is (the total hours marsh inundated / total hours in month) x 100. Flooding frequency is the average monthly percentage of high tide events that flooded the marsh/mangal surface.

	<i>Spartina</i>		Mangrove		Transition	
	Fall (2003)	Spring (2004)	Fall (2003)	Spring (2004)	Fall (2003)	Spring (2004)
Physicochemical Variables						
Water temperature ($^{\circ}\text{C}$)	26.2 \pm 4.25 (N=24)	28.4 \pm 2.23 (N=24)	26.6 \pm 3.99 (N=24)	27.8 \pm 2.16 (N=22)	26.6 \pm 3.91 (N=23)	28.3 \pm 2.23 (N=23)
Salinity (ppt)	21.1 \pm 2.35 (N=24)	18.5 \pm 1.36 (N=24)	21.9 \pm 3.84 (N=24)	18.7 \pm 3.26 (N=22)	21.8 \pm 3.48 (N=23)	18.2 \pm 1.76 (N=23)
Dissolved oxygen (mg L^{-1})	3.7 \pm 0.71 (N=24)	4.5 \pm 1.22 (N=24)	4.3 \pm 1.03 (N=24)	6.1 \pm 1.11 (N=22)	4.5 \pm 0.68 (N=23)	5.4 \pm 1.24 (N=23)
Turbidity (mg L^{-1})	58.1 \pm 48.50 (N=12)	89.6 \pm 127.2 (N=12)	55.2 \pm 34.60 (N=12)	64.8 \pm 49.40 (N=12)	56.1 \pm 34.20 (N=12)	62.3 \pm 21.10 (N=12)
Vegetation						
Stem Density (no. stems 0.25 m^{-2})	82.0 \pm 12.7 (N=12)	74.9 \pm 6.9 (N=8)	159.2 \pm 47.1 (N=12)	150.3 \pm 22.0 (N=6)	82.3 \pm 30.4 (N=12)	65.8 \pm 8.4 (N=8)
Areal Stem Cover (% stems 4 m^{-2})	1.4 \pm 0.2 (N=12)	1.4 \pm 0.3 (N=8)	3.7 \pm 1.2 (N=12)	3.7 \pm 1.7 (N=6)	1.7 \pm 0.4 (N=12)	1.4 \pm 0.3 (N=8)
Surface Elevation and Hydroperiod						
Mean Lift Net Surface Elevation (cm)		5.2 \pm 5.67 (N=4)		23.0 \pm 4.03 (N=4)		13.1 \pm 5.39 (N=4)
Maximum Flooding Depth (cm)	31.0 \pm 9.67 (N=17)	23.3 \pm 11.62 (N=11)	21.7 \pm 7.88 (N=18)	17.2 \pm 9.47 (N=17)	22.3 \pm 6.31 (N=21)	17.0 \pm 8.61 (N=24)
Flooding Frequency (%)	100 (N=3)	86.0 \pm 21.50 (N=3)	98.8 \pm 2.14 (N=3)	51.0 \pm 22.70 (N=3)	100 (N=3)	83.0 \pm 18.70 (N=3)
Flooding Duration (%)	95.9 \pm 6.62 (N=3)	75.0 \pm 28.82 (N=3)	89.5 \pm 9.34 (N=3)	13.2 \pm 10.31 (N=3)	91.4 \pm 10.79 (N=3)	40.4 \pm 12.42 (N=3)

Table 4. Results of ANOVA tests for physicochemical, vegetation, surface elevation, and hydroperiod differences among *Spartina*, mangrove, and transition habitat types (H), between fall (August to October 2003) and spring (March to June 2004) seasons (S), and by habitat type and season interaction (H*S). Significant results are indicated with *($0.05 \geq p > 0.01$) and highly significant results with **($p \leq 0.01$).

Habitat Characteristic	Source	df	F	Sig. of F
Water temperature (°C)	H	2, 134	0.06	0.9427
	S	1, 134	11.14	0.0011**
	H*S	2, 134	0.26	0.7707
Salinity (ppt)	H	2, 134	0.38	0.6879
	S	1, 134	42.88	<0.0001**
	H*S	2, 134	0.45	0.6400
Dissolved oxygen (mg L ⁻¹)	H	2, 134	15.07	<0.0001**
	S	1, 134	47.20	<0.0001**
	H*S	2, 134	3.12	0.0476*
Turbidity (mg L ⁻¹)	H	2, 6	0.30	0.7529
	S	1, 6	0.89	0.3823
	H*S	2, 6	0.06	0.9446
Stem Density (no. stems 0.25 m ⁻²)	H	2, 10	40.90	<0.0001**
	S	1, 43	3.23	0.0793
	H*S	2, 43	0.54	0.5868
Areal Stem Cover (% stems 4m ⁻²)	H	2, 8	39.34	<0.0001**
	S	1, 42	0.93	0.3397
	H*S	2, 42	0.83	0.4450
Lift Net Surface Elevation (cm)	H	2, 9	12.39	0.0026**
Maximum Flooding Depth (cm)	H	2, 9	5.14	0.0318*
	S	1, 103	11.34	0.0011**
	H*S	2, 101	0.22	0.8014
Flooding Duration (%)	H	2, 12	7.88	0.0065**
	S	1, 12	49.22	<0.0001**
	H*S	2, 12	5.16	0.0241*
Flooding Frequency (%)	H	2, 12	2.71	0.1068
	S	1, 12	14.15	0.0027**
	H*S	2, 12	2.34	0.1386

significant site-related differences in flooding frequency ($p=0.1068$); however, flooding frequency was significantly higher during fall ($99.6 \pm 1.23\%$) than spring ($73.2 \pm 24.72\%$; $p=0.0027$; Table 4).

Flooding durations (% of month that marsh/mangal surfaces flooded) significantly differed among habitat types ($p=0.0065$), between seasons ($p<0.0001$), and by habitat type and season interaction ($p=0.0241$; Table 4 and Figure 6). Flooding durations were significantly higher at the *Spartina* site (fall, $95.9 \pm 6.62\%$; spring, $75.0 \pm 28.82\%$) than at the mangrove site (fall, $89.5 \pm 9.34\%$; spring, $13.2 \pm 10.31\%$; $p=0.005$); however, flooding durations at the

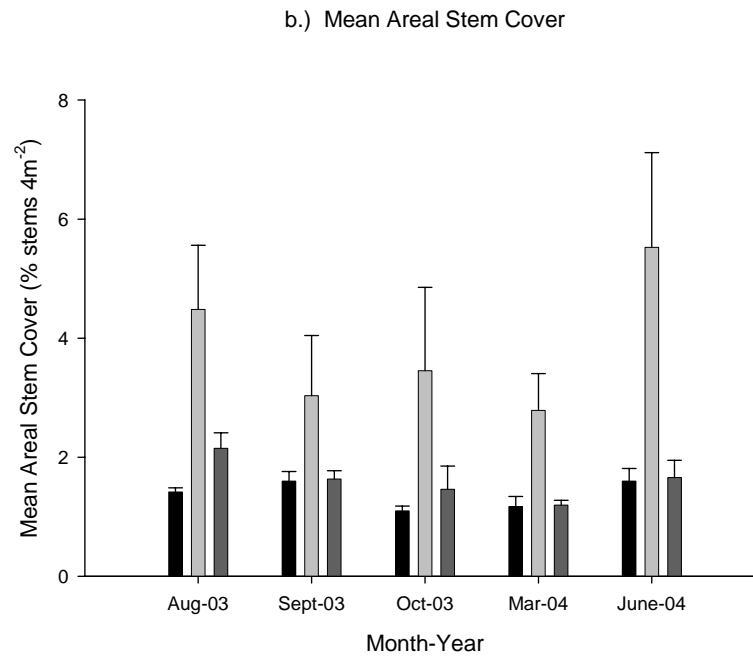
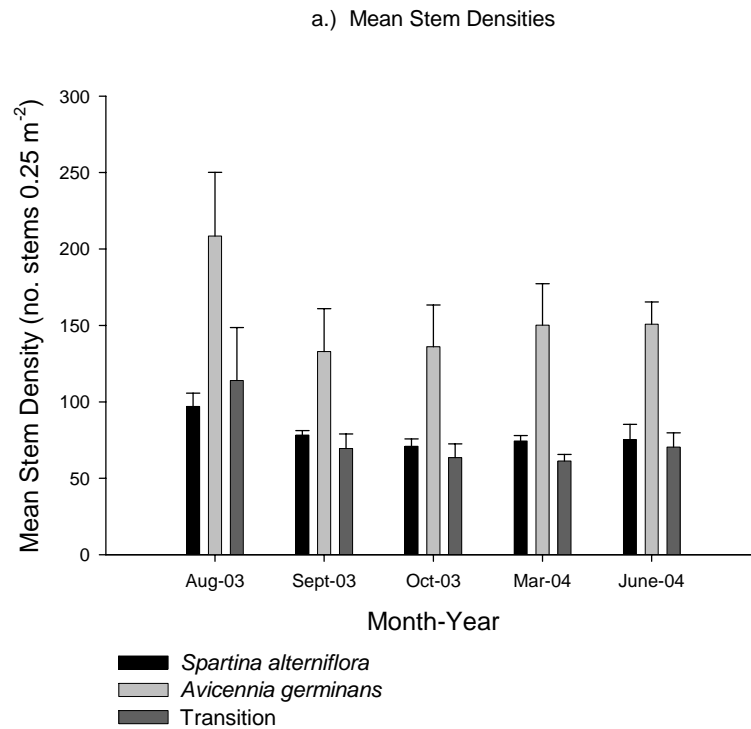


Figure 3. (a) Mean stem densities (no. stems 0.25 m⁻²) and (b) mean areal stem cover (% stems 4 m⁻²) at *Spartina*, mangrove, and transition sites during August-October (2003), and March and June (2004). Error bars are equal to one standard deviation (N=4).

transition site (fall, $91.4 \pm 10.79\%$; spring $40.4 \pm 12.42\%$) did not differ from mangrove ($p=0.2501$) or *Spartina* sites ($p=0.0994$; Table 3). Flooding durations were significantly greater during fall ($92.3 \pm 8.37\%$) than spring ($42.9 \pm 31.49\%$; $p<0.0001$).

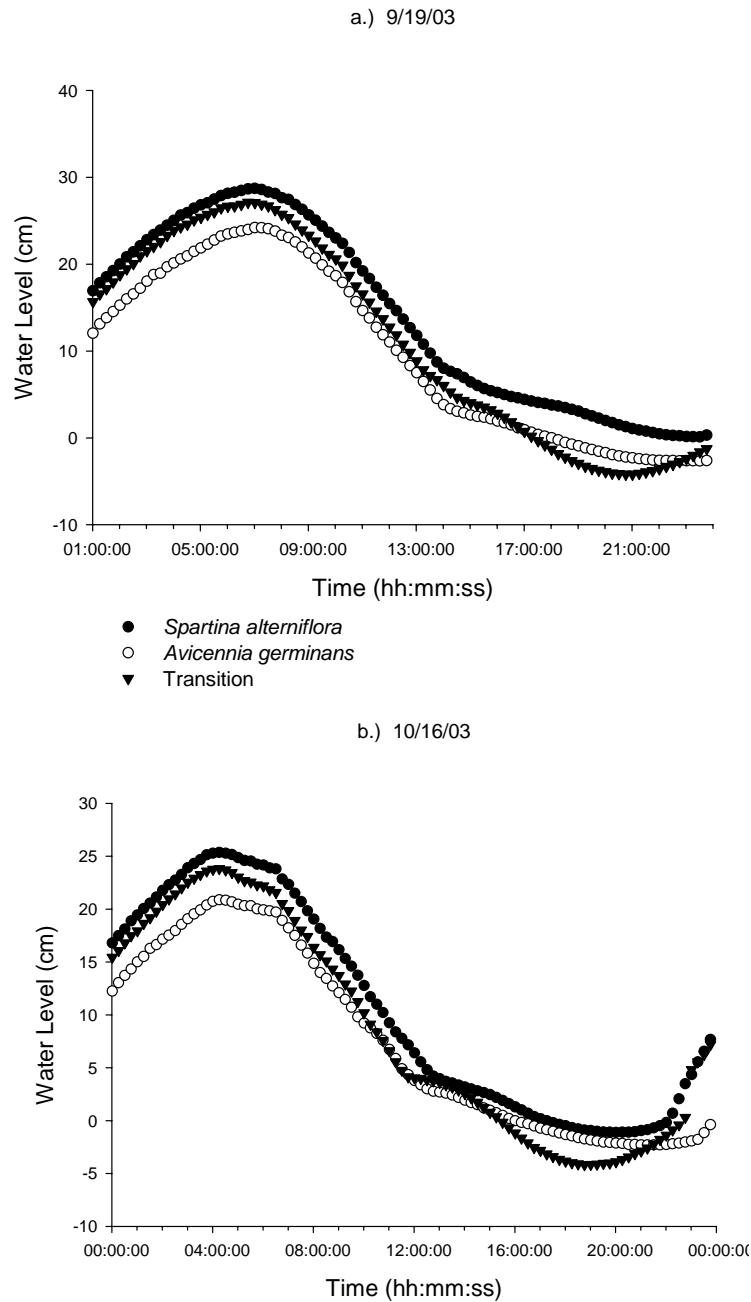


Figure 4. Water level sensor data from *Spartina*, mangrove, and transition sites (a) 9/19/03 and (b) 10/16/03.

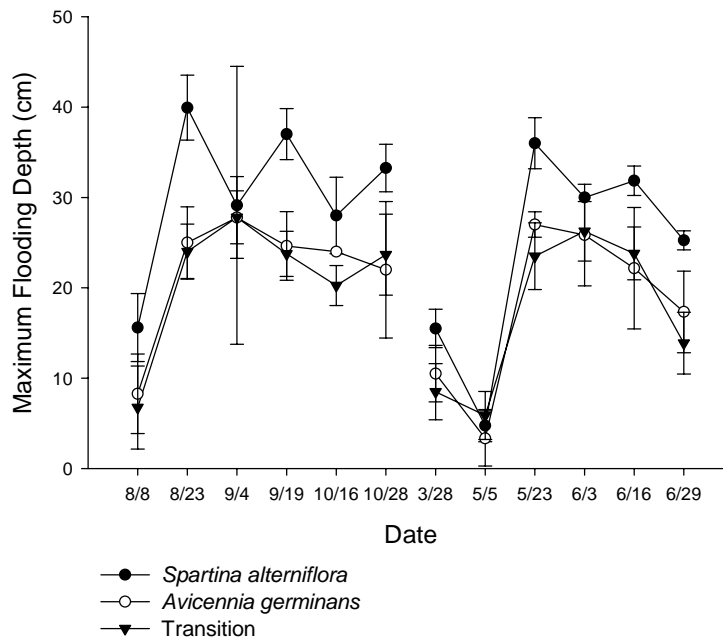


Figure 5. Maximum flooding depths (cm) at *Spartina*, mangrove, and transition sites, 8 August 2003 to 29 June 2004. Error bars are equal to one standard deviation (N=4).

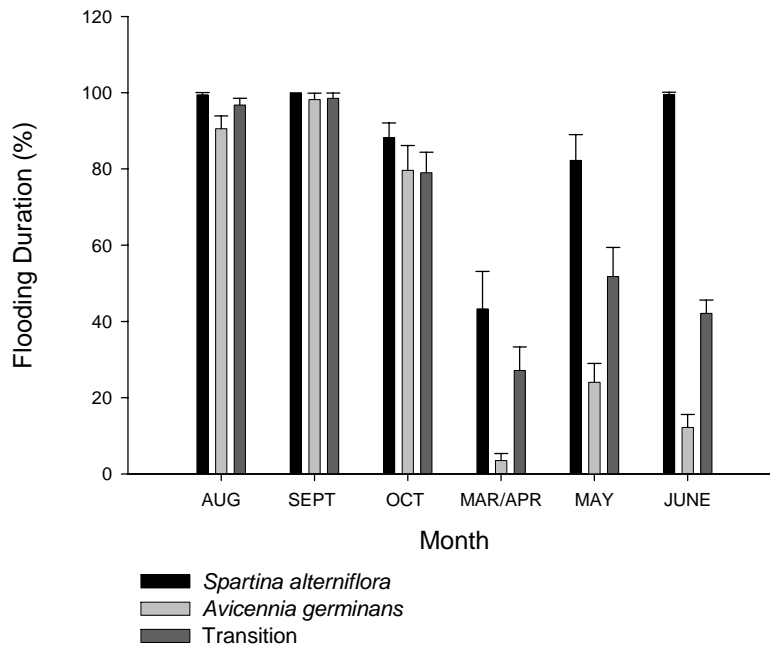


Figure 6. Flooding durations (%) at *Spartina*, mangrove, and transition sites during fall (August to October 2003) and spring (March to June 2004). Flooding duration=[(hours marsh inundated)/(total hours in month) x 100]. Error bars are equal to one standard deviation (N≈30).

Physicochemical Variables and Substrate Characteristics

Water temperatures ranged from 19.7 (October) to 30°C (August) in fall and from 24.3 (March) to 31.2°C (May) in spring. Water temperatures at *Spartina*, mangrove, and transition sites were not significantly different ($p=0.9427$; Tables 3 and 4); however, temperatures were significantly higher during spring ($28.2 \pm 2.19^{\circ}\text{C}$) than fall ($26.5 \pm 4.00^{\circ}\text{C}$; $p=0.0011$; Table 4).

Salinities ranged from 17.1 (September) to 27.6 ppt (October) in fall and from 11.6 (June) to 22.9 ppt (June) in spring. Salinities were not significantly different among the three habitat types ($p=0.6879$; Tables 3 and 4). However, salinities were significantly higher in fall (21.6 ± 3.26 ppt) than spring (18.5 ± 2.22 ppt; $p<0.0001$; Table 4).

Dissolved oxygen values ranged from 2.5 (September) to 6.8 mg L⁻¹ (October) in fall and from 2.6 (June) to 8.2 mg L⁻¹ (March) in spring. Dissolved oxygen significantly differed among habitat types ($p<0.0001$), between seasons ($p<0.0001$), and by habitat type and season interaction ($p=0.0476$; Table 4 and Figure 7). Dissolved oxygen values were significantly lower at the *Spartina* site (fall, 3.7 ± 0.71 mg L⁻¹; spring, 4.5 ± 1.22 mg L⁻¹) than at mangrove (fall, 4.3 ± 1.03 ; spring 6.1 ± 1.11 ; $p\leq 0.0001$) and transition sites (fall, 4.5 ± 0.68 ; spring, 5.4 ± 1.24 ; $p<0.0005$); however, mangrove and transition sites did not differ ($p=0.3320$; Table 3). Seasonally, dissolved oxygen was higher in spring (5.3 ± 1.35) than fall (4.2 ± 0.88).

Turbidity values ranged from 4.69 (August) to 139.86 mg L⁻¹ (October) in fall and from 6.37 (May) to 468.42 (March) in spring. Turbidities were not significantly different among habitat types ($p=0.7529$), between seasons ($p=0.3823$), or by habitat type and season interaction ($p=0.9446$; Tables 3 and 4).

In general, sediment grain sizes were similar among *Spartina*, mangrove, and transition sites. Silt and clay accounted for approximately 80-91% of the sediment collected at the three

habitat types (Table 5). However, there was a higher percentage of coarse plant material (>2 mm; 4.99%) at the *Spartina* site than at mangrove (1.01%) and transition sites (1.52%). Also, the mangrove site had a higher percentage of very fine sand (63µm; 16.91%) than both *Spartina* (1.39%) and transition sites (5.46%; Table 5).

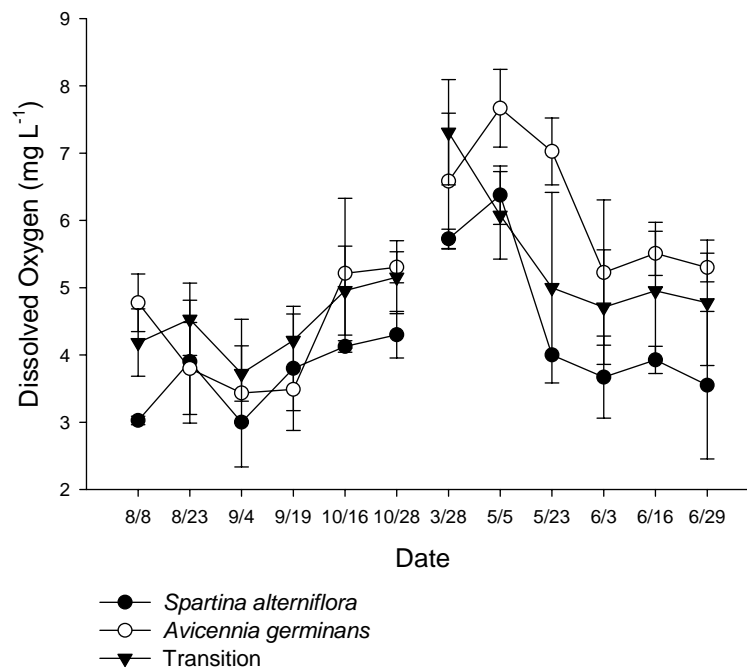


Figure 7. Mean dissolved oxygen (mg L^{-1}) at *Spartina*, mangrove, and transition sites, 8 August 2003 to 29 June 2004. Error bars are equal to one standard deviation (N=4).

Table 5. Percent of sediment from *Spartina*, mangrove, and transition cores (7.5 cm diameter x 7.5 cm long) retained on 2 mm, 500 µm, 150 µm, 63 µm, and <63 µm sieves.

Sieve Mesh Size	Grade	% Sediment retained per sieve		
		<i>Spartina</i>	Mangrove	Transition
2 mm	gravel and/or plant material	4.99	1.01	1.52
500 µm	coarse sand	1.28	0.19	0.90
150 µm	fine sand	0.92	1.10	1.44
63 µm	very fine sand	1.39	16.91	5.46
<63 µm	silt and/or clay	91.40	80.79	90.68

Meiofauna

A total of 26,811 and 22,449 meiofauna were collected from 16 *Spartina* and 16 black mangrove sediment cores, respectively, during August and October (2003) and March and June (2004; Table 6). Nematodes were the most abundant taxa collected and accounted for about 70% of total meiofauna abundance at both sites (Table 6). Crustacean nauplii, copepods, polychaetes, oligochaetes, kinorhynchs, and ostracods were also present in similar proportions at both habitat types (Table 6). Chironomids were only collected at the *Spartina* site and were too rare to include in statistical analyses.

Meiofauna taxa abundances differed significantly between *Spartina* and black mangrove habitat types (Wilks' $\lambda=0.430$, $F_{7, 18}=3.41$; $p=0.0169$), among months (August 2003, October 2003, March 2004, June 2004; Wilks' $\lambda=0.105$, $F_{21, 52}=2.96$; $p=0.0008$), and by habitat type and month interaction (Wilks' $\lambda=0.182$, $F_{21, 52}=2.01$; $p=0.0209$). Significant site differences, however, were the result of a single group, kinorhyncha, which was significantly more abundant at the mangrove site than at the *Spartina* site ($p=0.0154$; Table 7).

Nematode ($p=0.0071$), nauplii ($p=0.0094$), kinorhynch ($p=0.0001$), and ostracod ($p=0.0262$) abundances significantly differed among months (Table 7 and Figure 8). Nematode, nauplii, and kinorhynch abundances were highest in March/June 2004 and lowest in August 2003. Ostracod abundances were highest in June and lowest in March and August. Copepod abundances exhibited a significant habitat type and month interaction ($p=0.0021$; Table 7). In August, copepod abundances were high at the *Spartina* site and low at the mangrove site (Figure 8). The opposite trend occurred in March, when copepod abundances were lowest at the *Spartina* site and highest at the mangrove site.

Table 6. Mean individuals core⁻¹ ± 1 standard deviation (SD), abundance, and percent abundance of meiofauna collected from the top two cm of 3.7 cm diameter x 12.5 cm long sediment cores (N=number of cores) collected within *Spartina* and mangrove lift nets during August and October (2003) and March and June (2004).

Phylum	Subphylum	Group	Class	<i>Spartina</i> (N=16)			<i>Mangrove</i> (N=16)		
				Mean Individuals core ⁻¹ (± 1 SD)	Abundance	% of Total	Mean Individuals core ⁻¹ (± 1 SD)	Abundance	% of Total
Nematoda				1208.7 ± 842.4	19339	72.13	982.9 ± 827.2	15727	70.06
Arthropoda	Crustacea	Nauplii		173.3 ± 180.7	2772	10.34	122.3 ± 157.5	1956	8.71
Arthropoda	Crustacea	Copepoda		157.6 ± 95.35	2521	9.40	148.0 ± 135.1	2368	10.55
Annelida		Polychaeta		93.9 ± 156.6	1503	5.61	86.7 ± 132.4	1387	6.18
Annelida		Oligochaeta		29.5 ± 27.48	472	1.76	42.0 ± 29.85	672	2.99
Kinorhyncha				9.3 ± 22.85	148	0.55	11.9 ± 17.00	190	0.85
Arthropoda	Crustacea	Ostracoda		3.3 ± 3.96	52	0.19	9.3 ± 17.21	149	0.66
Arthropoda	Insecta		Chironomidae	0.3 ± 0.58	4	0.01	0.0 ± 0.00	0	0.00
Total					26811		Total	22449	

Table 7. Results of ANOVA tests for differences in meiofauna taxa abundances between *Spartina* and mangrove habitat types (H), among August and October (2003) and March and June (2004) months (M), and by habitat type and month interaction (H*M). Significant results are indicated with *($0.05 \geq p > 0.01$) and highly significant results with **($p \leq 0.01$).

Taxa	Source	df	F	Sig. of F
Nematodes	H	1, 24	0.95	0.3384
	M	3, 24	5.10	0.0071**
	H*M	3, 24	0.91	0.4486
Nauplii	H	1, 24	1.01	0.3249
	M	3, 24	4.79	0.0094**
	H*M	3, 24	1.15	0.3486
Copepods	H	1, 24	0.09	0.7716
	M	3, 24	1.52	0.2343
	H*M	3, 24	6.58	0.0021**
Polychaetes	H	1, 24	0.00	0.9606
	M	3, 24	1.10	0.3699
	H*M	3, 24	0.31	0.8199
Oligochaetes	H	1, 24	1.52	0.2302
	M	3, 24	1.12	0.3589
	H*M	3, 24	0.85	0.4779
Kinorhynchs	H	1, 24	6.81	0.0154*
	M	3, 24	10.65	0.0001**
	H*M	3, 24	0.69	0.5653
Ostracods	H	1, 24	1.69	0.2064
	M	3, 24	3.67	0.0262*
	H*M	3, 24	1.20	0.3305

Fish and Crustacean Habitat Use

Species Composition, Diversity and Richness

A total of 1738 fishes (18 species) and decapod crustaceans (6 taxa) were collected from 140 lift net samples at *Spartina*, black mangrove, and transition sites during August-October 2003 and March-June 2004 (Table 8). More species were collected at the transition site (21) than at *Spartina* (17) and mangrove sites (16; Table 8). Grass shrimp, darter gobies (*Gobionellus boleosoma*), blue crabs, white shrimp (*L. setiferus*), brown shrimp (*F. aztecus*), fiddler crabs (*Uca spp.*), gulf killifish, gulf stone crabs (*Menippe adina*), sheepshead minnows (*Cyprinodon variegatus*), tidewater silversides (*Menidia beryllina*), and striped mullet (*Mugil cephalus*) were collected at all three habitat types (Table 8).

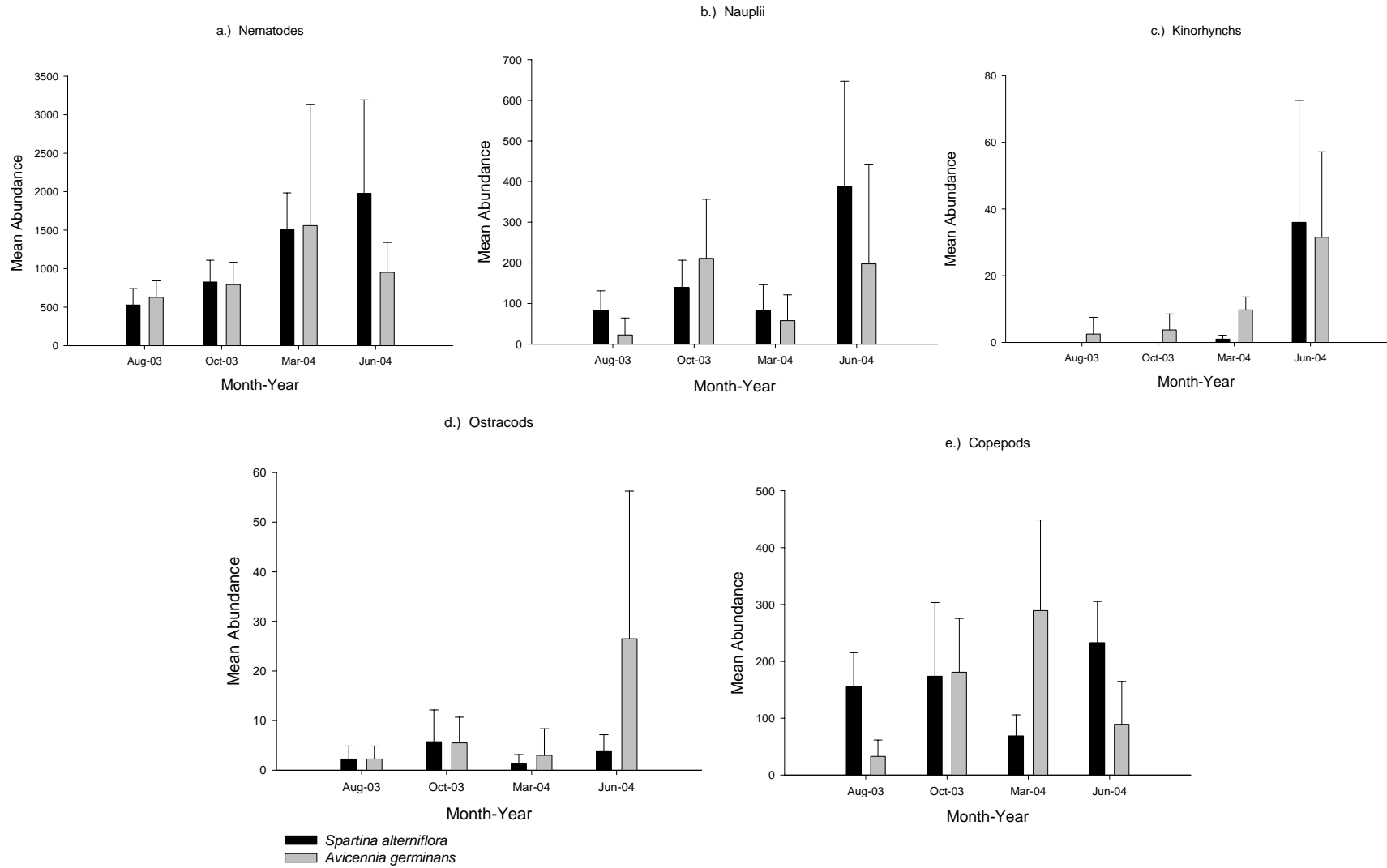


Figure 8. Mean abundances (no. individuals in top 2 cm of 3.5 cm diameter x 12.5 cm long meiofauna cores) of (a) nematodes, (b) crustacean nauplii, (c) kinorhynchids, (d) ostracods, and (e) copepods collected at *Spartina* (N=16) and mangrove (N=16) sites in August and October (2003) and March and June (2004). Error bars are equal to one standard deviation.

Table 8. Abundance, percent abundance, biomass (g), and percent biomass of fishes and crustaceans collected at *Spartina*, mangrove, and transition sites from August to October 2003 and March to June 2004. N=total lift net samples.

Taxa	Common Name	Abundance	% Abundance	Biomass (g)	% Biomass
<i>Spartina</i> (N=48)					
<i>Palaemonetes</i> spp.	grass shrimp	110	25.29	22.5	1.02
<i>Fundulus grandis</i>	gulf killifish	90	20.69	837.1	37.99
<i>Gobionellus boleosoma</i>	darter goby	45	10.34	14.5	0.66
<i>Callinectes sapidus</i>	blue crab	44	10.11	616.8	27.99
<i>Litopenaeus setiferus</i>	white shrimp	34	7.81	14.1	0.64
<i>Cyprinodon variegatus</i>	sheepshead minnow	28	6.44	47.3	2.15
<i>Menippe adina</i>	gulf stone crab	28	6.44	402.7	18.27
<i>Uca</i> spp.	fiddler crab	22	5.06	14.2	0.64
<i>Farfantepenaeus aztecus</i>	brown shrimp	10	2.30	12.6	0.57
<i>Bairdiella chrysoura</i>	silver perch	7	1.61	21.6	0.98
<i>Menidia beryllina</i>	tidewater silverside	4	0.92	4.2	0.19
<i>Adinia xenica</i>	diamond killifish	3	0.69	2.6	0.12
<i>Mugil cephalus</i>	striped mullet	3	0.69	101.8	4.62
<i>Fundulus similis</i>	longnose killifish	3	0.69	21.2	0.96
<i>Cynoscion nebulosus</i>	spotted seatrout	2	0.46	11.3	0.51
<i>Lagodon rhomboides</i>	pinfish	1	0.23	50.3	2.28
<i>Myrophis punctatus</i>	speckled worm eel	1	0.23	8.9	0.40
		Total 435		Total 2203.7	
Mangrove (N=46)					
<i>Palaemonetes</i> spp.	grass shrimp	394	53.46	53.8	3.86
<i>Litopenaeus setiferus</i>	white shrimp	105	14.25	95.0	6.82
<i>Callinectes sapidus</i>	blue crab	72	9.77	483.4	34.69
<i>Gobionellus boleosoma</i>	darter goby	44	5.97	8.0	0.57
<i>Menippe adina</i>	gulf stone crab	34	4.61	288.1	20.68
<i>Uca</i> spp.	fiddler crab	20	2.71	5.6	0.40
<i>Farfantepenaeus aztecus</i>	brown shrimp	20	2.71	32.2	2.31
<i>Menidia beryllina</i>	tidewater silverside	19	2.58	22.8	1.64
<i>Fundulus grandis</i>	gulf killifish	13	1.76	53.5	3.84
<i>Mugil cephalus</i>	striped mullet	9	1.22	278.2	19.97
<i>Citharichthys spilopterus</i>	bay whiff	2	0.27	16.8	1.21
<i>Cyprinodon variegatus</i>	sheepshead minnow	1	0.14	1.1	0.08
<i>Lobotes surinamensis</i>	triple tail	1	0.14	0.2	0.01
<i>Lagodon rhomboides</i>	pinfish	1	0.14	32.1	2.30
<i>Lutjanus griseus</i>	gray snapper	1	0.14	21.2	1.52
<i>Evorthodus lyricus</i>	lyre goby	1	0.14	1.3	0.09
		Total 737		Total 1393.3	
Transition (N=46)					
<i>Palaemonetes</i> spp.	grass shrimp	226	39.93	35.0	3.38
<i>Gobionellus boleosoma</i>	darter goby	90	15.90	11.3	1.09
<i>Callinectes sapidus</i>	blue crab	52	9.19	517.9	49.97
<i>Litopenaeus setiferus</i>	white shrimp	49	8.66	27.9	2.69
<i>Fundulus grandis</i>	gulf killifish	42	7.42	140.6	13.56
<i>Uca</i> spp.	fiddler crab	40	7.07	7.2	0.69
<i>Farfantepenaeus aztecus</i>	brown shrimp	16	2.83	20.8	2.01
<i>Menidia beryllina</i>	tidewater silverside	15	2.65	22.4	2.16
<i>Menippe adina</i>	gulf stone crab	9	1.59	114.8	11.08
<i>Mugil cephalus</i>	striped mullet	8	1.41	53.0	5.11
<i>Evorthodus lyricus</i>	lyre goby	4	0.71	1.9	0.18
<i>Cyprinodon variegatus</i>	sheepshead minnow	3	0.53	3.7	0.36
<i>Gobiosoma bosc</i>	naked goby	3	0.53	0.5	0.05
<i>Cynoscion nebulosus</i>	spotted seatrout	2	0.35	8.3	0.80
<i>Adinia xenica</i>	diamond killifish	1	0.18	0.5	0.05
<i>Bairdiella chrysoura</i>	silver perch	1	0.18	0.3	0.03
<i>Citharichthys spilopterus</i>	bay whiff	1	0.18	1.7	0.16
<i>Symphurus plagiusa</i>	blackcheek tonguefish	1	0.18	0.1	0.01
<i>Fundulus similis</i>	longnose killifish	1	0.18	1.3	0.13
<i>Lutjanus griseus</i>	gray snapper	1	0.18	0.3	0.03
<i>Opsanus beta</i>	gulf toadfish	1	0.18	67.0	6.46
		Total 566		Total 1036.5	

The following species were collected infrequently at only one of the three habitat types: speckled worm eels, *Myrophis punctatus* (*Spartina*); tripletails, *Lobotes surinamensis* (mangrove); naked gobies, *Gobiosoma bosc*, and gulf toadfish, *Opsanus beta* (transition; Table 8). Silver perch (*Bairdiella chrysoura*), diamond killifish (*Adinia xenica*), longnose killifish (*F. similis*), and spotted seatrout (*Cynoscion nebulosus*) were collected only at *Spartina* and transition sites. Bay whiff (*Citharichthys spilopterus*), gray snapper (*Lutjanus griseus*), and lyre gobies (*Evorthodus lyricus*) were collected at mangrove and transition sites. Pinfish (*Lagodon rhomboides*) were collected only at *Spartina* and mangrove sites.

Despite these individual species differences, species diversity was not significantly different among the three habitats types ($p=0.8801$), between seasons ($p=0.2243$), or by habitat type and season interaction ($p=0.6143$). Richness was significantly higher in fall (23 taxa) than spring (15 taxa, $p=0.0005$), but did not differ among habitat types ($p=0.5368$) or by habitat type and season interaction ($p=0.6691$).

The Correspondence analysis (CA) revealed site and species-site associations. The CA showed distinct separation of *Spartina* and black mangrove sites along Axis I (Figure 9a). Although transition sites were intermediate between mangrove and *Spartina* sites, they were more closely associated with mangrove sites (Figure 9a). The CA also showed species-site associations between sheepshead minnows, silver perch, gulf stone crabs, fiddler crabs, and diamond killifish and the *Spartina* and transition sites (Figure 9b). However, darter gobies, lyre gobies, blue crabs, tidewater silversides, brown shrimp, and striped mullet were more closely associated with mangrove and transition sites. Other taxa, such as gulf killifish and grass shrimp, showed common associations with all three habitat types.

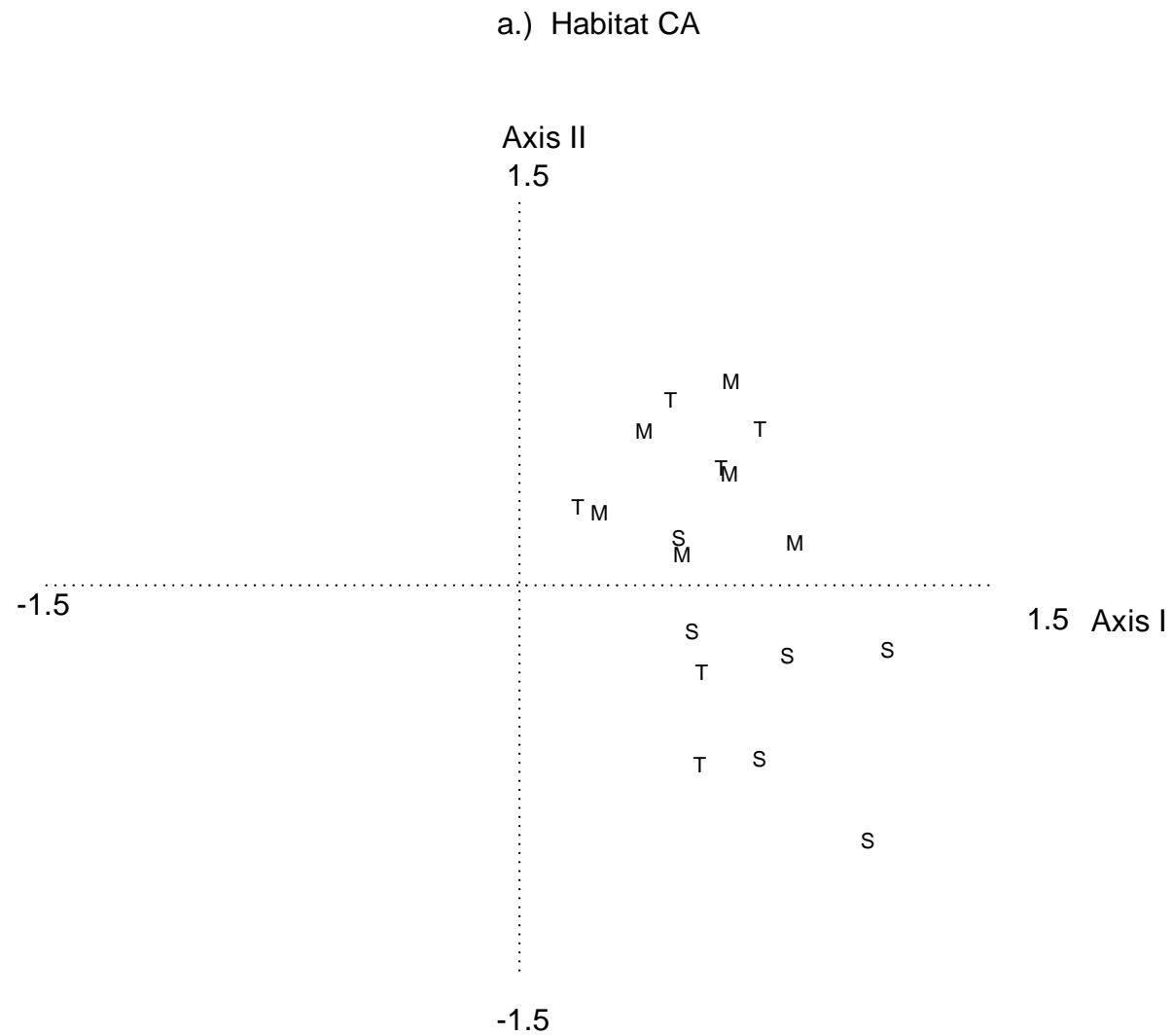


Figure 9. Correspondence analysis showing (a) associations among *Spartina* (S), mangrove (M), and transition (T) sites and (b) associations between fish and crustacean species presence-absence data and sites.

b.) Species and Habitat CA

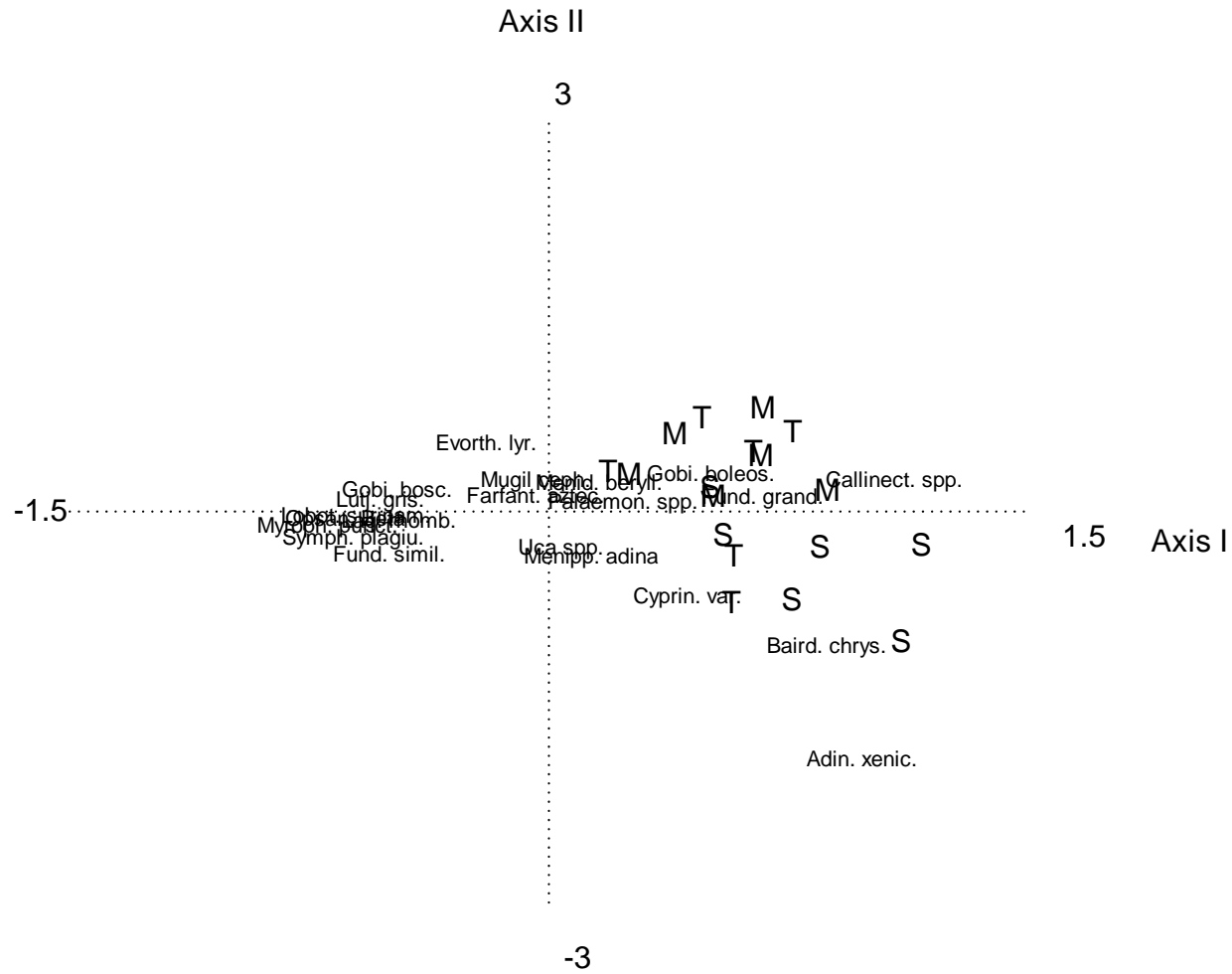


Figure 9 continued.

Abundance

Fish and crustacean total abundances were highest at the mangrove site (737), intermediate at transition (566), and lowest at the *Spartina* site (435; Table 8). Decapod crustaceans, specifically grass shrimp, dominated the catch at all three habitat types (Table 8 and Figure 10). At the mangrove site, in particular, crustaceans accounted for 88% of total catch (Figure 10). In addition, grass shrimp, white shrimp, brown shrimp, blue crabs, and gulf stone crabs were collected in higher abundances at the mangrove site than at *Spartina* and transition sites (Table 8).

Fishes, however, were generally more abundant at *Spartina* and transition sites than at the mangrove site, where fishes were only 12% of total catch (Figure 10). Gulf killifish and sheepshead minnows were most abundant at the *Spartina* site. Tidewater silversides, however, were generally more abundant at mangrove and transition sites (Table 8). Overall, darter gobies were one of the most abundant fishes collected at all three habitat types (Table 8).

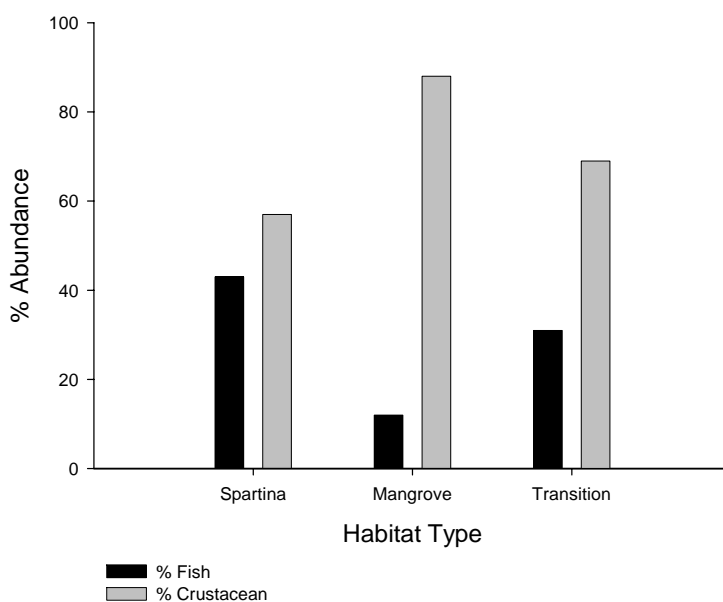


Figure 10. Contribution of fishes versus crustaceans to total catch at *Spartina*, mangrove, and transition sites.

Density

My study was unable to find significant site-related differences in fish and crustacean densities (fish, $p=0.0753$; crustaceans, $p=0.1457$); however, fish densities were generally higher at *Spartina* (fall, $1.05 \pm 0.84 \text{ m}^{-2}$; spring, $0.90 \pm 1.64 \text{ m}^{-2}$) and transition sites (fall, $1.59 \pm 1.44 \text{ m}^{-2}$; spring, $0.32 \pm 0.45 \text{ m}^{-2}$) and consistently lower at the mangrove site (fall, $0.79 \pm 0.82 \text{ m}^{-2}$; spring, $0.18 \pm 0.36 \text{ m}^{-2}$; Figure 11a). Of the fish species compared, only gulf killifish densities significantly differed among sites, with higher densities at the *Spartina* site than at the mangrove site ($p=0.0543$; Table 9 and Figure 12a).

Crustacean densities were typically highest at the mangrove site (fall, $5.09 \pm 6.83 \text{ m}^{-2}$; spring, $1.77 \pm 1.70 \text{ m}^{-2}$), intermediate at transition (fall, $3.15 \pm 2.87 \text{ m}^{-2}$; spring $1.11 \pm 0.87 \text{ m}^{-2}$), and lowest at the *Spartina* site (fall, $1.63 \pm 1.51 \text{ m}^{-2}$; spring $0.96 \pm 0.99 \text{ m}^{-2}$; Figure 11b). Of the decapod crustaceans compared, only gulf stone crabs exhibited significant site-related differences. Gulf stone crab densities were significantly higher at the mangrove site than at the transition site ($p=0.0061$), with no difference between *Spartina* and mangrove ($p=0.5868$) or *Spartina* and transition sites ($p=0.0797$; Table 9 and Figure 12h). White shrimp were only collected in the fall and, although densities were consistently higher at the mangrove site, site-related density differences were not significant ($p=0.1478$; Table 9 and Figure 12e).

Fish and crustacean densities were significantly higher during fall than spring (fish, $p=0.0002$; crustaceans, $p<0.0001$; Figure 11) and the densities of most taxa were more affected by season than habitat type. Tidewater silverside ($p=0.0027$), grass shrimp ($p=0.0007$), darter goby ($p=0.0009$), and brown shrimp ($p=0.0072$) densities were significantly higher during fall than spring (Table 9 and Figure 12). Blue crab and fiddler crab densities, however, did not differ among sites or seasonally ($p>0.05$; Table 9 and Figure 12).

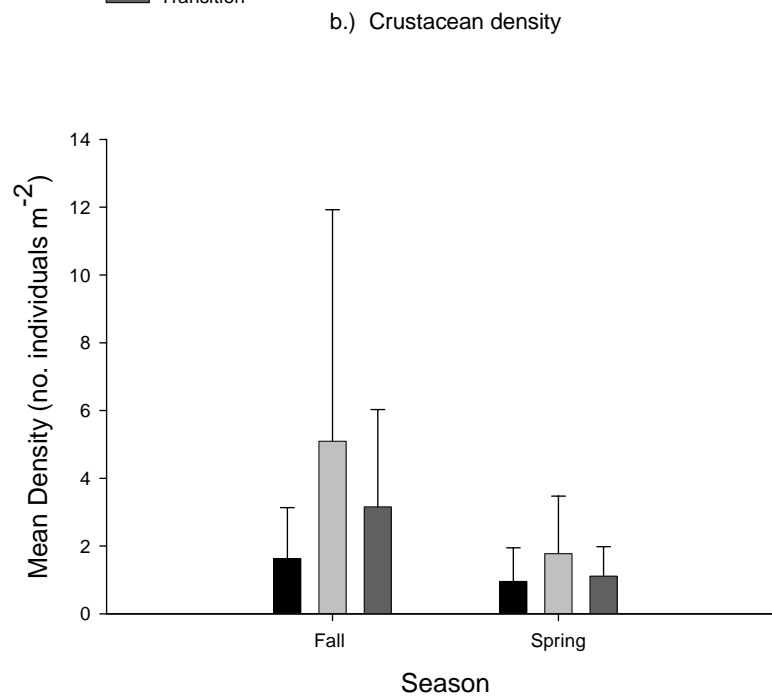
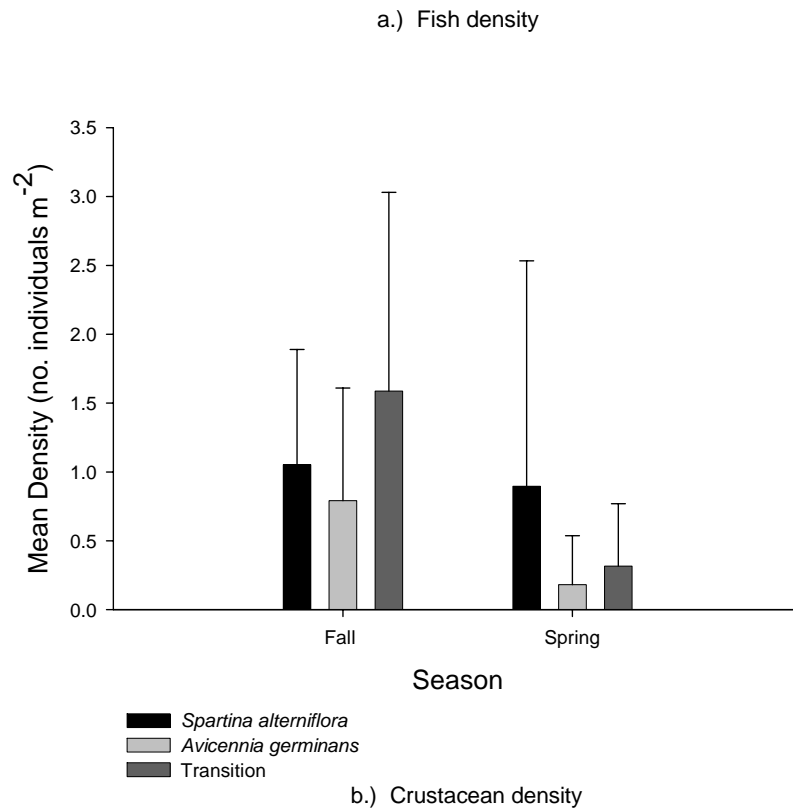


Figure 11. Mean (a) fish densities and (b) crustacean densities at *Spartina* (fall, N=24; spring, N=24), mangrove (fall, N=24; spring, N=22), and transition sites (fall, N=23; spring, N=23) during fall (August to October 2003) and spring (March to June 2004). Error bars are equal to one standard deviation.

Table 9. Mean densities (no. individuals m⁻²) \pm 1 standard deviation of numerically abundant species collected at *Spartina*, mangrove, and transition sites during fall (August to October 2003) and spring (March to June 2004). N=total lift net samples.

Scientific and Common Name	Mean Density (N=140)	Mean Densities (no. individuals m ⁻²)					
		<i>Spartina</i>		Mangrove		Transition	
		Fall (N=24)	Spring (N=24)	Fall (N=24)	Spring (N=22)	Fall (N=23)	Spring (N=23)
<i>Palaemonetes spp.</i> grass shrimp	1.30 \pm 2.867	0.69 \pm 1.056	0.46 \pm 0.761	3.16 \pm 5.946	1.03 \pm 1.466	1.98 \pm 2.139	0.48 \pm 0.617
<i>Litopenaeus setiferus</i> white shrimp	0.66 \pm 1.305	0.35 \pm 0.837	0	1.09 \pm 1.856	0	0.53 \pm 0.874	0
<i>Gobionellus boleosoma</i> darter goby	0.32 \pm 0.718	0.26 \pm 0.334	0.21 \pm 0.530	0.38 \pm 0.692	0.09 \pm 0.197	0.85 \pm 1.365	0.13 \pm 0.211
<i>Callinectes sapidus</i> blue crab	0.30 \pm 0.366	0.17 \pm 0.229	0.29 \pm 0.470	0.45 \pm 0.410	0.33 \pm 0.452	0.28 \pm 0.275	0.28 \pm 0.264
<i>Fundulus grandis</i> gulf killifish	0.26 \pm 0.672	0.45 \pm 0.699	0.49 \pm 1.303	0.09 \pm 0.231	0.05 \pm 0.166	0.33 \pm 0.388	0.13 \pm 0.376
<i>Uca spp.</i> fiddler crab	0.15 \pm 0.394	0.18 \pm 0.250	0.05 \pm 0.104	0.06 \pm 0.258	0.16 \pm 0.643	0.19 \pm 0.304	0.25 \pm 0.564
<i>Menippe adina</i> gulf stone crab	0.13 \pm 0.239	0.18 \pm 0.372	0.12 \pm 0.147	0.15 \pm 0.275	0.23 \pm 0.230	0.05 \pm 0.168	0.04 \pm 0.097
<i>Farfantepenaeus aztecus</i> brown shrimp	0.08 \pm 0.198	0.06 \pm 0.133	0.04 \pm 0.120	0.19 \pm 0.288	0.02 \pm 0.074	0.12 \pm 0.291	0.05 \pm 0.130
<i>Menidia beryllina</i> tidewater silverside	0.07 \pm 0.220	0.03 \pm 0.084	0.01 \pm 0.051	0.20 \pm 0.410	0	0.16 \pm 0.278	0
<i>Cyprinodon variegatus</i> sheepshead minnow	0.06 \pm 0.252	0.17 \pm 0.359	0.13 \pm 0.460	0	0.01 \pm 0.053	0.03 \pm 0.114	0
<i>Mugil cephalus</i> striped mullet	0.04 \pm 0.123	0.03 \pm 0.112	0	0.07 \pm 0.188	0.02 \pm 0.107	0.07 \pm 0.155	0.03 \pm 0.086

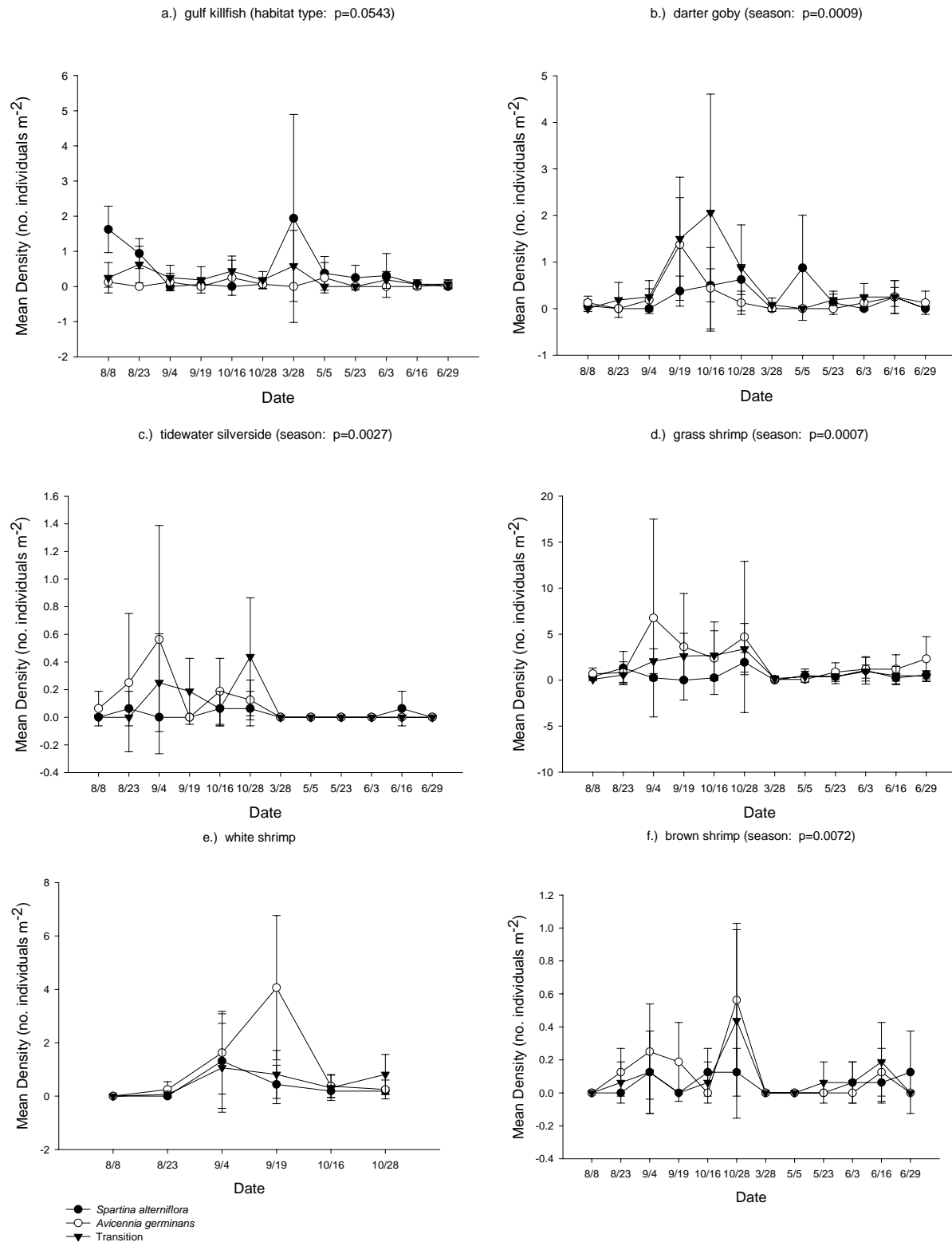


Figure 12. Mean densities (no. individuals m^{-2}) of (a) gulf killfish, (b) darter goby, (c) tidewater silverside, (d) grass shrimp, (e) white shrimp, (f) brown shrimp, (g) blue crab, and (h) gulf stone crab at *Spartina*, mangrove, and transition sites from 8 August 2003 to 29 June 2004. Error bars are equal to one standard deviation ($N=4$). P-values are significant habitat/seasonal differences.

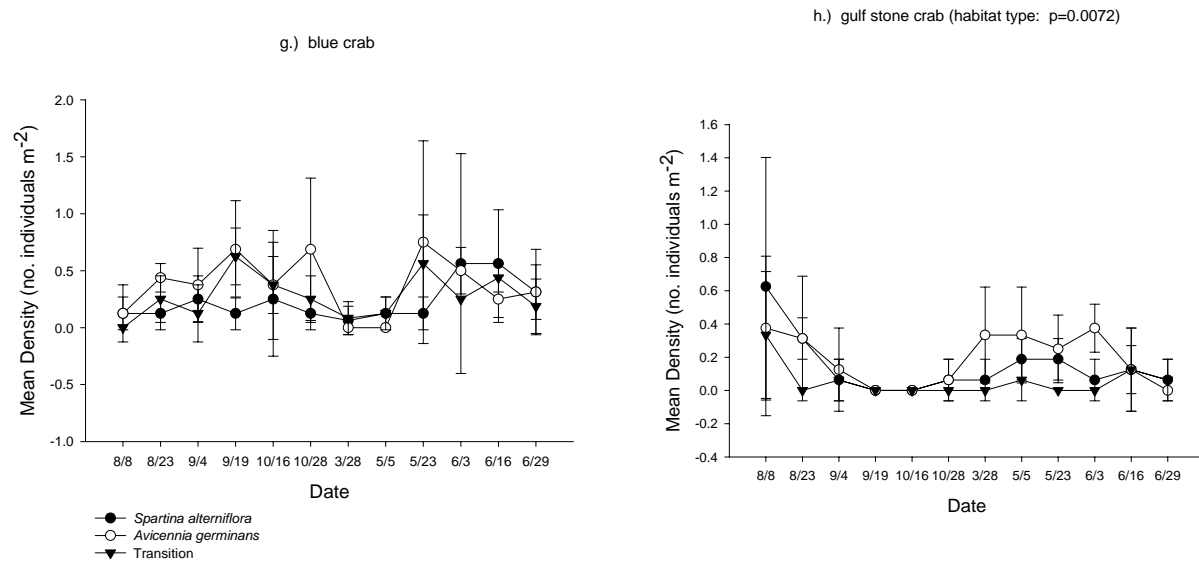


Figure 12 continued.

Biomass

Total biomass was highest at the *Spartina* site (2204 g) and similar at transition (1037 g) and mangrove sites (1393 g; Table 8). At the *Spartina* site, 51% of total biomass was from fishes and 49% from crustaceans (Figure 13). However, crustaceans accounted for the majority of total biomass (70%) at mangrove and transition sites (Figure 13). Examined together, fish densities, crustacean densities, fish biomass, and crustacean biomass significantly differed among habitat types (Wilks' $\lambda=0.067$, $F_{8, 12}=4.32$; $p=0.0117$), but not seasonally ($p=0.1408$) or by habitat type and season interaction ($p=0.2159$).

Fish biomass was responsible for these significant site-related differences ($p=0.0481$; Figure 14a) and was significantly greater at the *Spartina* site (fall, 23.5 ± 24.48 g; spring, 23.2 ± 74.39 g) than at mangrove (fall, 17.44 ± 45.60 g; spring, 0.8 ± 2.52 g; $p=0.0396$) and transition sites (fall, 12.0 ± 15.69 g; spring, 1.63 ± 4.65 g; $p=0.0299$). Seasonally, fish biomass was significantly higher during fall than spring ($p=0.0070$). Crustacean biomass was highest at *Spartina* (fall, 29.2 ± 46.38 g; spring, 15.97 ± 27.01 g) and mangrove sites (fall, 20.36 ± 21.86 g;

spring, 21.3 ± 26.06 g) and lowest at the transition site (fall, 17.2 ± 24.62 ; spring, 14.22 ± 19.19 ; Figure 14b), but did not differ among sites ($p=0.6050$) or between seasons ($p=0.2502$).

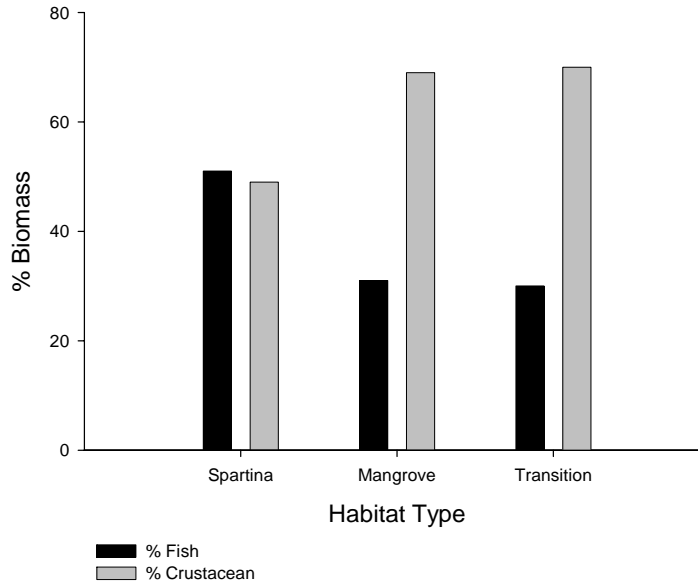


Figure 13. Contribution of fishes versus crustaceans to total biomass (g) at *Spartina*, mangrove, and transition sites.

Gulf killifish and striped mullet represented the majority of fish biomass at all three sites (Table 8). Gulf killifish contributed the most total biomass (837 g; 38%) at the *Spartina* site and accounted for the most fish biomass (141 g) and 14% of the total biomass at the transition site (Table 8). In addition, gulf killifish biomass was significantly greater at the *Spartina* site than at mangrove ($p=0.0223$) and transition sites ($p=0.0040$; Figure 15a). At the mangrove site, however, striped mullet represented the most fish biomass (278 g) and 20% of the total biomass (Table 8 and Figure 15c).

Blue crabs and gulf stone crabs contributed the majority of crustacean biomass at *Spartina* (1020 g), mangrove (772 g), and transition sites (633 g; Table 8). Although blue crab biomass was significantly higher during spring ($p=0.0354$), neither blue crab nor gulf stone crab

densities differed among habitat types ($p>0.05$; Figure 15e, f). White shrimp biomass, however, was significantly greater at the mangrove site (95 g) than at *Spartina* (14 g; $p=0.0062$) and transition sites (28 g; $p=0.0143$), but did not differ between *Spartina* and transition sites ($p=0.8856$; Table 8 and Figure 15d).

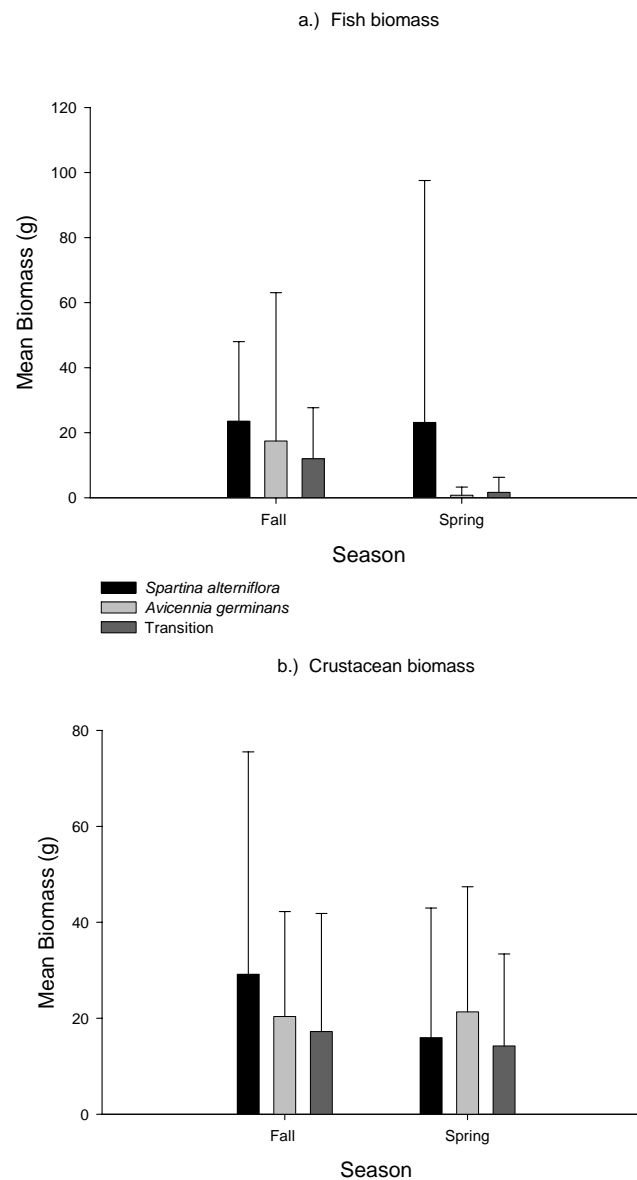


Figure 14. Mean (a) fish and (b) crustacean biomass (g) at *Spartina* (fall, N=24; spring, N=24), mangrove (fall, N=24; spring, N=22), and transition sites (fall, N=23; spring, N=23) during fall (August to October 2003) and spring (March to June 2004). Error bars are equal to one standard deviation.

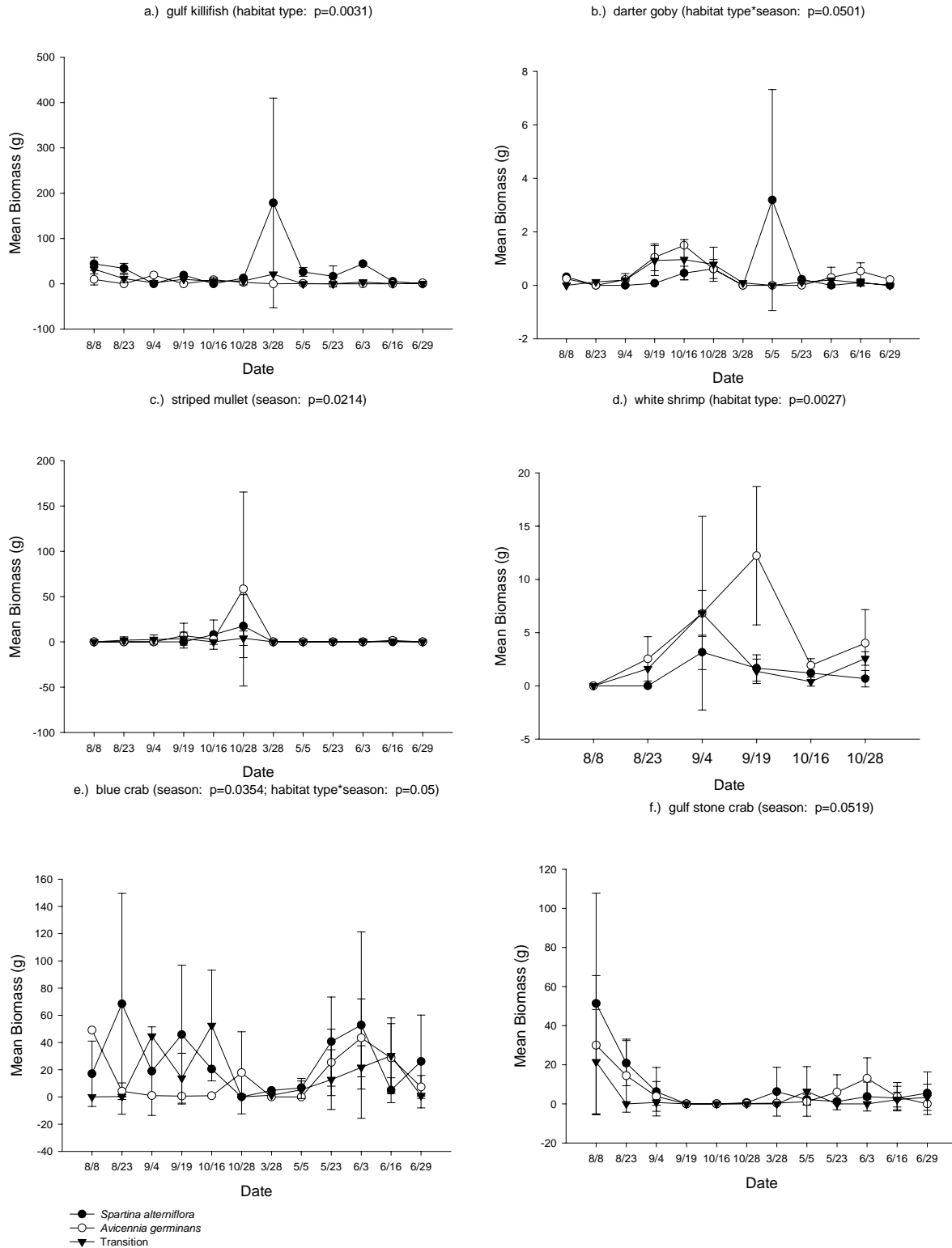


Figure 15. Mean biomass (g) of (a) gulf killifish, (b) darter goby, (c) striped mullet, (d) white shrimp, (e) blue crab, and (f) gulf stone crab at *Spartina*, mangrove, and transition sites from 8 August 2003 to 29 June 2004. Error bars are equal to one standard deviation (N=4). P-values are significant habitat/seasonal differences.

Length

A few taxa exhibited significant length differences among sites and/or seasons. Gulf killifish were significantly larger at the *Spartina* site than at the transition site ($p=0.0082$); however, gulf killifish lengths at the mangrove site did not differ from transition ($p=0.9136$) or *Spartina* sites ($p=0.1414$; Table 10 and Figure 16a). White shrimp rostrum lengths also significantly differed among habitat types ($p=0.0002$), with larger white shrimp at the mangrove site than at *Spartina* ($p=0.0017$) and transition sites ($p=0.0002$), but no difference between *Spartina* and transition sites ($p=0.5074$; Table 10 and Figure 16c). Seasonally, blue crabs were significantly larger during spring ($p=0.0407$; Table 10) and fiddler crabs were significantly larger during fall ($p=0.0387$).

Fish and Crustacean Density - Habitat Associations

Canonical correspondence analysis (CCA) revealed a statistically significant relationship between the two canonical axes representing fish/crustacean densities and habitat/environmental variables ($p=0.002$). Habitat (*Spartina*, mangrove, transition), areal stem cover, turbidity, and water temperature explained 52.5% of the variability in fish and crustacean densities on Axis 1 and dissolved oxygen, on Axis 2, explained an additional 21.2% of the variability (Table 11 and Figure 17). Salinity (Axis 3) and water depth (Axis 4) were the least important factors affecting nekton densities (Table 11 and Figure 17).

The CCA corroborated the ASC gradient observed among *Spartina*, black mangrove, and transition sites and identified certain taxa that may have affinities for specific habitat types and/or ASC. The black mangrove site was positively associated with ASC and the *Spartina* site was negatively associated with ASC (Figure 17). White shrimp, brown shrimp, and tidewater silverside densities were positively associated with the mangrove site and higher ASC; however,

gulf killifish were more closely associated with lower ASC characteristic of the *Spartina* site (Figure 17).

According to the CCA, densities of certain taxa were more influenced by environmental and/or hydrological conditions than by vegetation or habitat type. Blue crab densities were positively associated with salinity. Darter gobies, striped mullet, and grass shrimp densities reflected affinities for higher turbidity and greater flooding depths. Fiddler crab and gulf stone crab densities were associated with lower turbidity and warmer water temperatures (Figure 17).

Scatterplots of fish and crustacean densities and salinity showed highest densities between 16-23 ppt (Figure 18). Fish densities increased with salinity from 12 to about 23 ppt and then declined, whereas crustacean densities declined with salinity from 12 to about 23 ppt and then increased with salinity thereafter (Figure 18). Similar plots of nekton densities relative to water temperature showed no discernable trends (Figure 19).

Fish and crustacean densities did not exhibit significant linear relationships with stem density, nor were there any discernable site-related trends. However, fish densities were generally higher at *Spartina* and transition sites, where stem densities and ASC were lower than at the mangrove site (Figure 20). In contrast, higher crustacean densities were generally associated with the high pneumatophore densities characteristic of the mangrove site.

Multiple linear regression analyses revealed significant, positive relationships between fish/crustacean densities and flooding duration at mangrove (for fish, $r^2=0.21$, $p=0.0031$, fish density = $0.088 - 0.003$ flooding depth + 0.009 flood duration; for crustaceans, $r^2=0.21$, $p=0.0040$, crustacean density = $0.358 - 0.003$ flooding depth + 0.017 flood duration; Figure 21a,b) and transition sites (for fish, $r^2=0.32$, $p=0.0018$, fish density = $-0.118 + 0.002$ flooding depth + 0.019 flood duration; Figure 21c), but not at the *Spartina* site. Although there were no significant

relationships between fish and crustacean densities and flooding depth, fish and crustacean densities generally increased with water depth to about 20 and 25 cm at *Spartina* and transition sites, respectively. At the mangrove site, fish densities reached optima at a slightly deeper 30 cm and then declined thereafter (Figure 22).

Lift Net Efficiency Experiment

Lift net recovery estimates for gulf killifish ($p=0.6482$) and grass shrimp ($p=0.6426$) were not significantly different among *Spartina*, black mangrove, and transition habitat types. Lift net recovery estimates for gulf killifish were highest at the *Spartina* site ($92.5 \pm 9.57\%$) and lowest at the mangrove site ($77.5 \pm 32.0\%$; Table 12). However, recovery estimates for grass shrimp were highest at the mangrove site ($47.5 \pm 44.30\%$) and lowest at the *Spartina* site ($22.5 \pm 28.70\%$; Table 12).

Table 10. Mean lengths (mm) \pm 1 standard deviation (calculated from N samples) of numerically abundant species collected at *Spartina*, mangrove, and transition sites during fall (August to October 2003) and spring (March to June 2004). Fish, shrimp, and crab lengths were measured as standard lengths (SL), rostrum lengths (RL), and carapace widths (CW), respectively. White shrimp and tidewater silversides were not collected during the spring season.

Scientific and Common Name	Mean Lengths (mm)					
	<i>Spartina</i>		Mangrove		Transition	
	Fall	Spring	Fall	Spring	Fall	Spring
<i>Fundulus grandis</i> gulf killifish	66.8 \pm 15.49 (N=10)	59.1 \pm 19.25 (N=8)	57.7 \pm 20.84 (N=5)	32.4 \pm 14.97 (N=2)	42.5 \pm 16.54 (N=12)	38.3 \pm 11.31 (N=5)
<i>Gobionellus boleosoma</i> darter goby	22.0 \pm 4.60 (N=10)	23.4 \pm 9.40 (N=7)	24.5 \pm 2.34 (N=9)	22.0 \pm 7.63 (N=4)	22.1 \pm 3.80 (N=14)	17.4 \pm 3.39 (N=7)
<i>Menidia beryllina</i> tidewater silverside	47.7 \pm 6.43 (N=3)	.	45.8 \pm 7.01 (N=8)	.	49.2 \pm 7.88 (N=8)	.
<i>Litopenaeus setiferus</i> white shrimp	15.2 \pm 3.94 (N=9)	.	22.2 \pm 5.42 (N=15)	.	13.9 \pm 3.37 (N=10)	.
<i>Farfantepenaeus aztecus</i> brown shrimp	19.4 \pm 3.36 (N=5)	21.2 \pm 0.76 (N=3)	20.8 \pm 6.19 (N=9)	22.3 \pm 6.72 (N=2)	17.8 \pm 5.84 (N=5)	21.0 \pm 3.29 (N=4)
<i>Callinectes sapidus</i> blue crab	46.8 \pm 40.55 (N=11)	37.4 \pm 25.95 (N=13)	20.1 \pm 14.34 (N=17)	48.0 \pm 27.82 (N=13)	25.8 \pm 20.66 (N=13)	35.7 \pm 25.56 (N=16)
<i>Menippe adina</i> gulf stone crab	36.8 \pm 9.20 (N=9)	24.3 \pm 11.30 (N=10)	30.5 \pm 9.99 (N=6)	17.8 \pm 11.77 (N=12)	30.4 \pm 9.20 (N=3)	29.5 \pm 12.61 (N=4)
<i>Uca spp.</i> fiddler crab	11.2 \pm 5.05 (N=10)	10.3 \pm 5.11 (N=4)	9.0 \pm 3.46 (N=2)	4.3 \pm 0.35 (N=2)	8.7 \pm 3.29 (N=9)	5.3 \pm 2.19 (N=7)

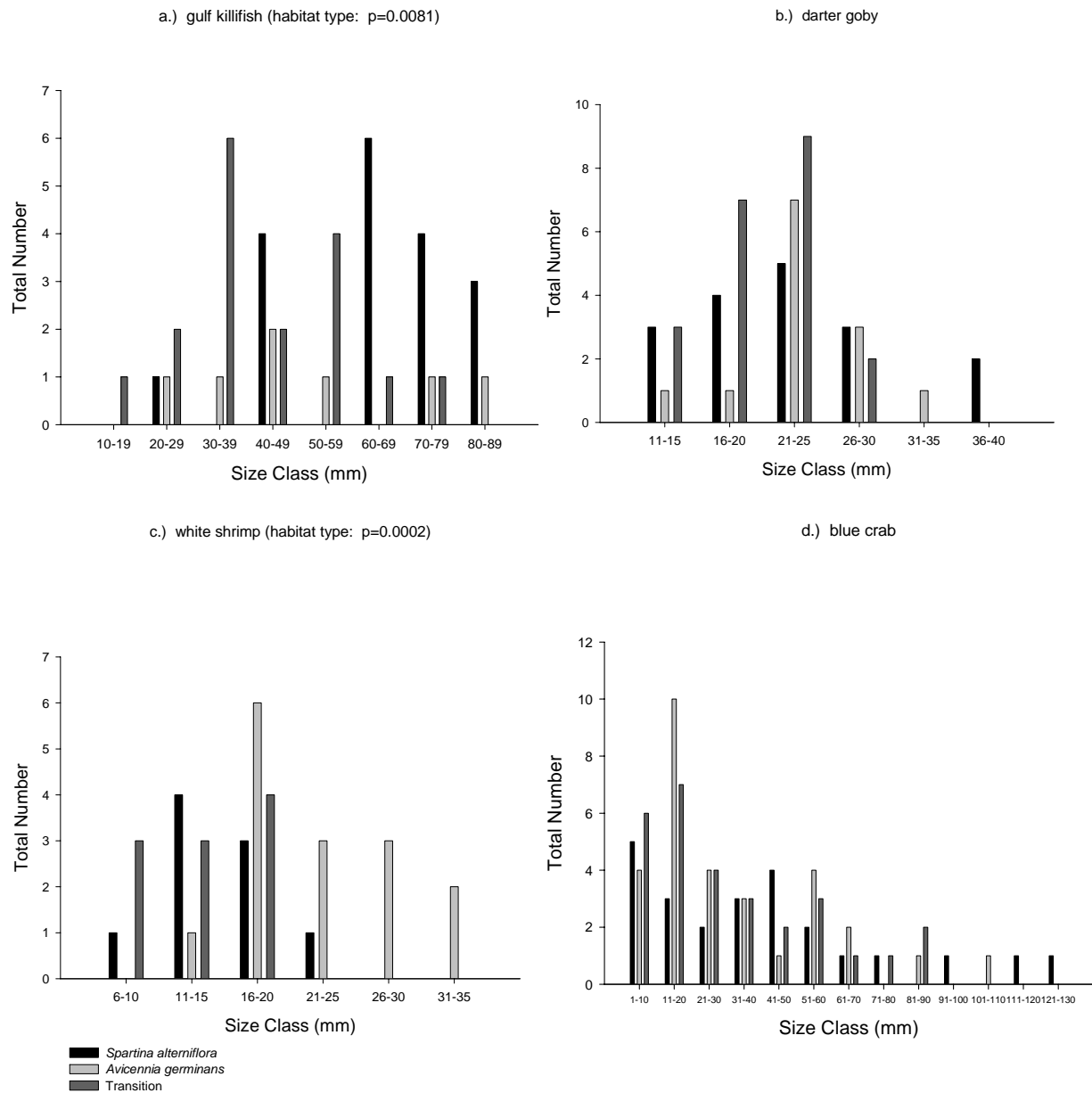


Figure 16. Length-frequency graphs for (a) gulf killifish (SL), (b) darter goby (SL), (c) white shrimp (RL), and (d) blue crab (CW) collected at *Spartina*, mangrove, and transition sites, 8 August 2003 to 29 June 2004. P-values are significant habitat type differences.

Table 11. Results from the significant Canonical Correspondence Analysis (CCA; $p=0.002$) showing the weighted correlation matrix of habitat/environmental variables with the canonical axes. Axes 1 and 2 explained 52.5% and 21.2% of the variability, respectively, in fish and crustacean species densities.

Variable	Axis 1	Axis 2	Axis 3	Axis 4
Habitat	-0.318	0.121	0.282	0.031
Water Depth	0.017	-0.158	0.166	0.072
Salinity	0.042	0.001	0.004	-0.289
Temperature	0.230	0.267	0.094	0.181
Turbidity	-0.231	-0.134	0.065	-0.017
Dissolved Oxygen	0.160	-0.254	0.186	-0.014
Areal Stem Cover	-0.239	0.189	0.237	-0.017

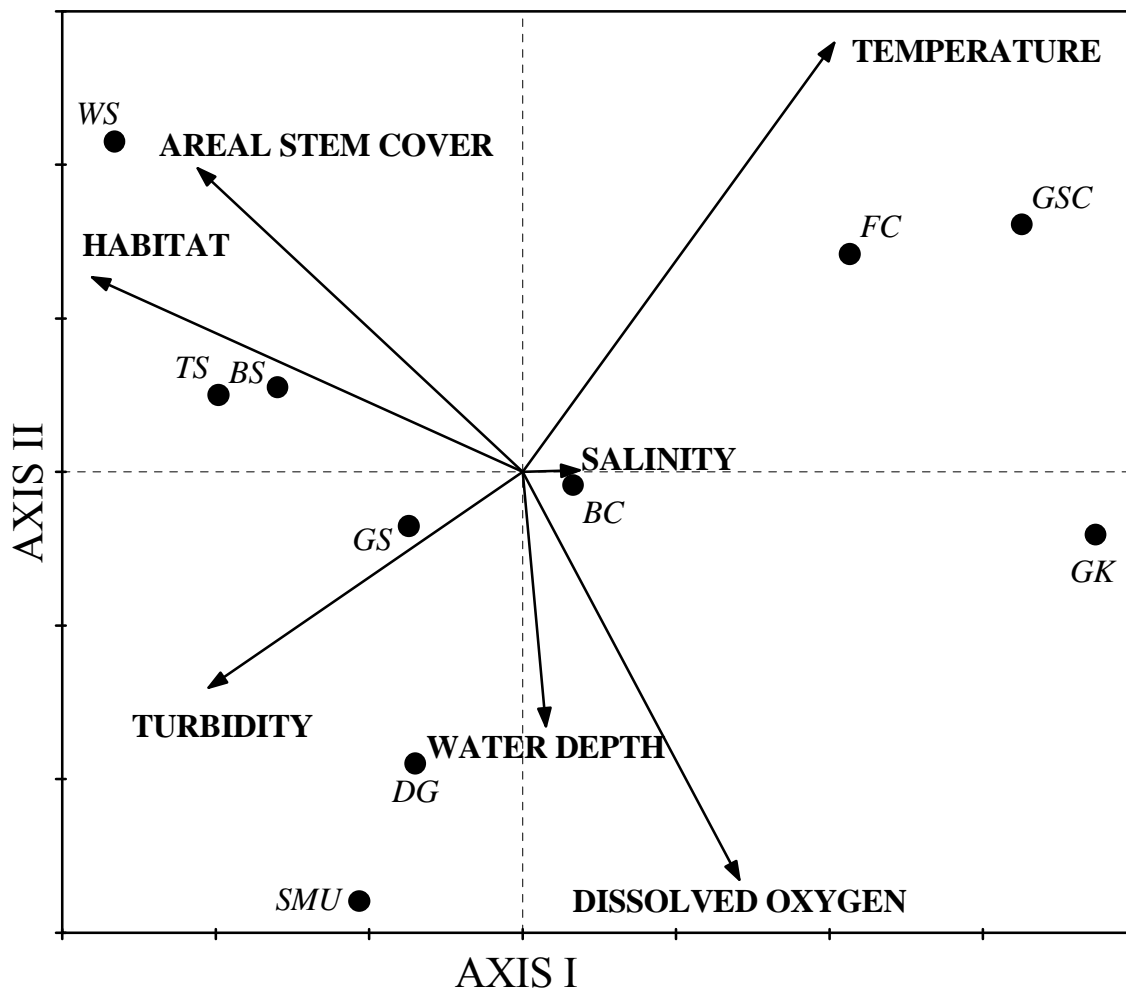


Figure 17. Results from CCA showing associations between fish and crustacean species densities (BC=blue crab, BS=brown shrimp, DG=darter goby, FC=fiddler crab, GK=gulf killifish, GS=grass shrimp, GSC=gulf stone crab, SMU=striped mullet, TS=tidewater silverside, WS=white shrimp) and habitat/environmental variables. Numeric habitat codes were assigned to *Spartina* (1), transition (2), and black mangrove (3) habitat types.

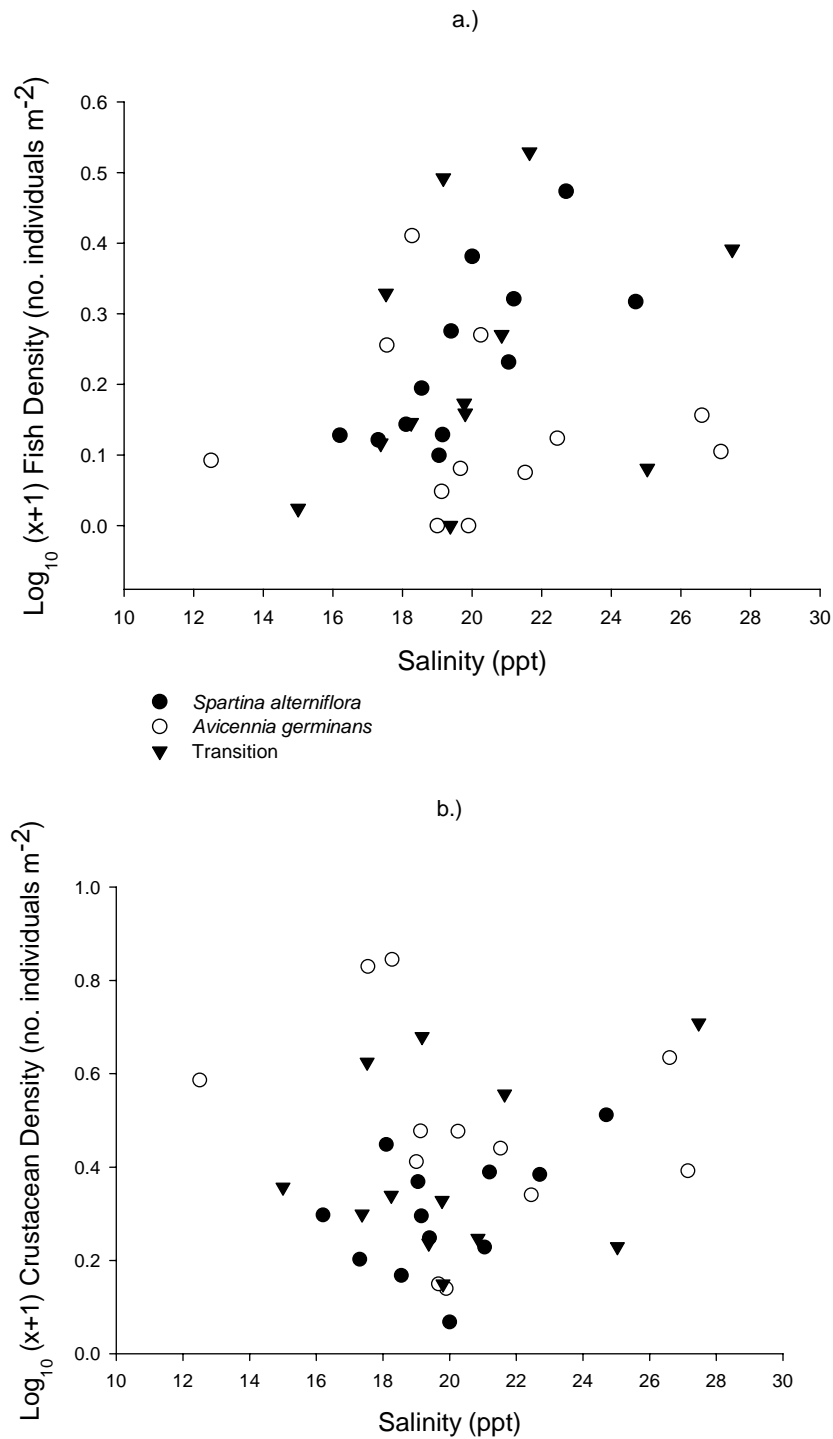


Figure 18. Plots of (a) fish and (b) crustacean densities (no. individuals m⁻²; log₁₀ (x+1) transformed) relative to salinity (ppt) at the *Spartina*, mangrove, and transition sites. Each point is the mean density of four lift net samples. Sampling occurred from 8 August 2003 to 29 June 2004.

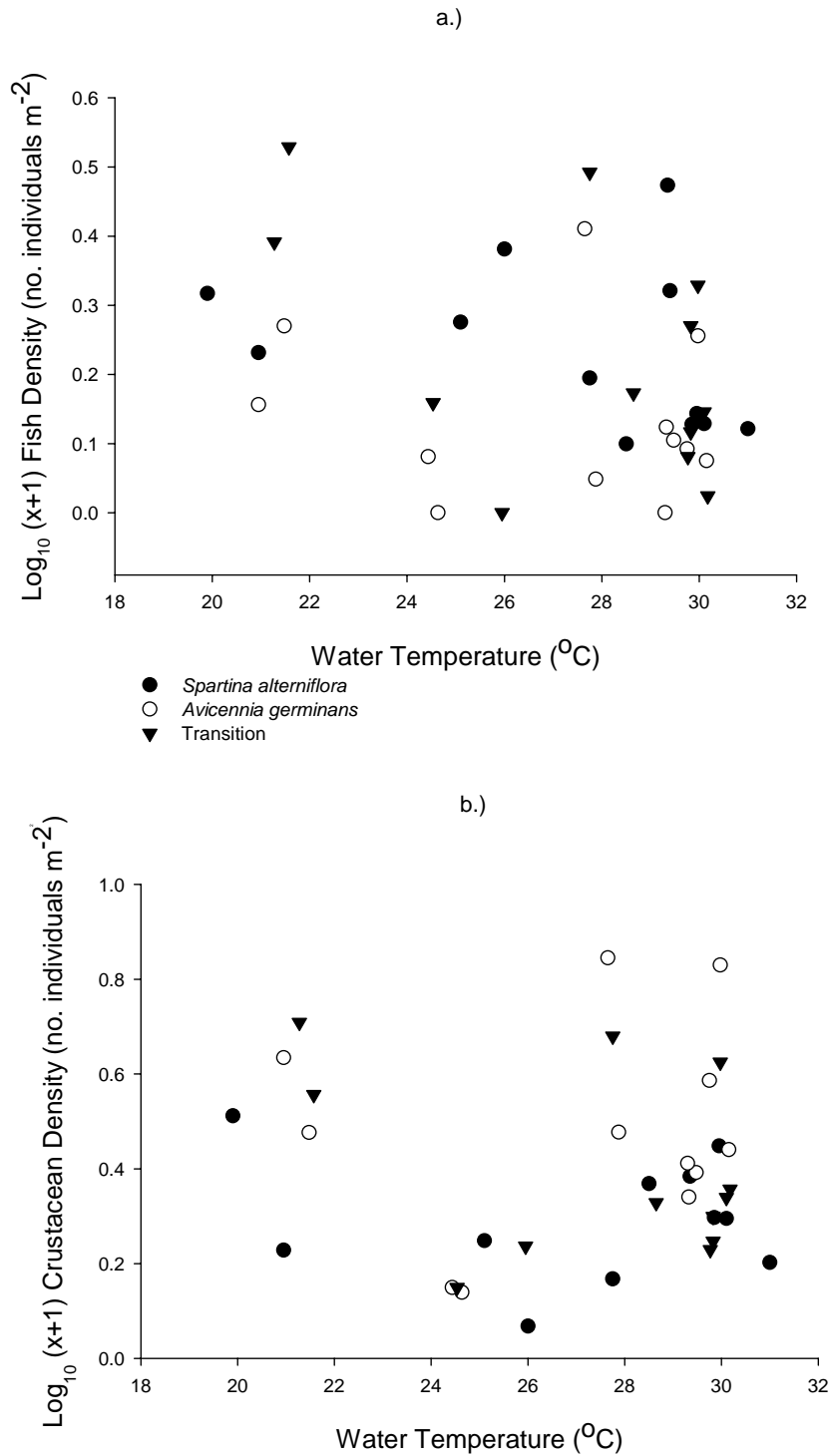


Figure 19. Plots of (a) fish and (b) crustacean densities (no. individuals m⁻²; log₁₀ (x+1) transformed) relative to water temperature (°C) at the *Spartina*, mangrove, and transition sites. Each point is the mean density of four lift net samples. Sampling occurred from 8 August 2003 to 29 June 2004.

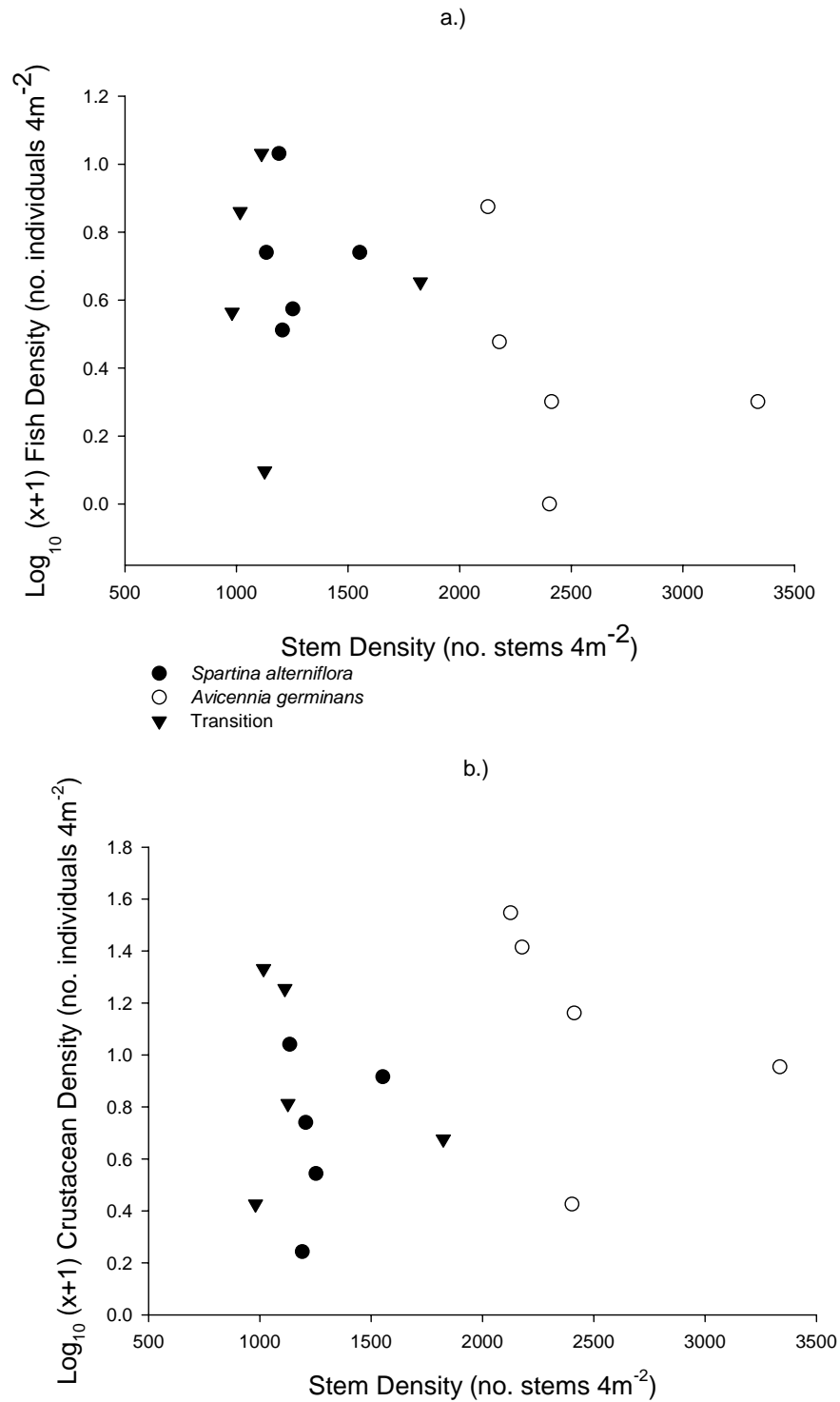


Figure 20. Plots of (a) fish and (b) crustacean densities (no. individuals 4 m⁻²; log₁₀ (x+1) transformed) relative to stem density (no. stems 4 m⁻²) at the *Spartina*, mangrove, and transition sites. Each point is the mean density of four lift net samples, which were sampled concurrent with vegetation sampling over 5 dates from 8 August 2003 to 29 June 2004.

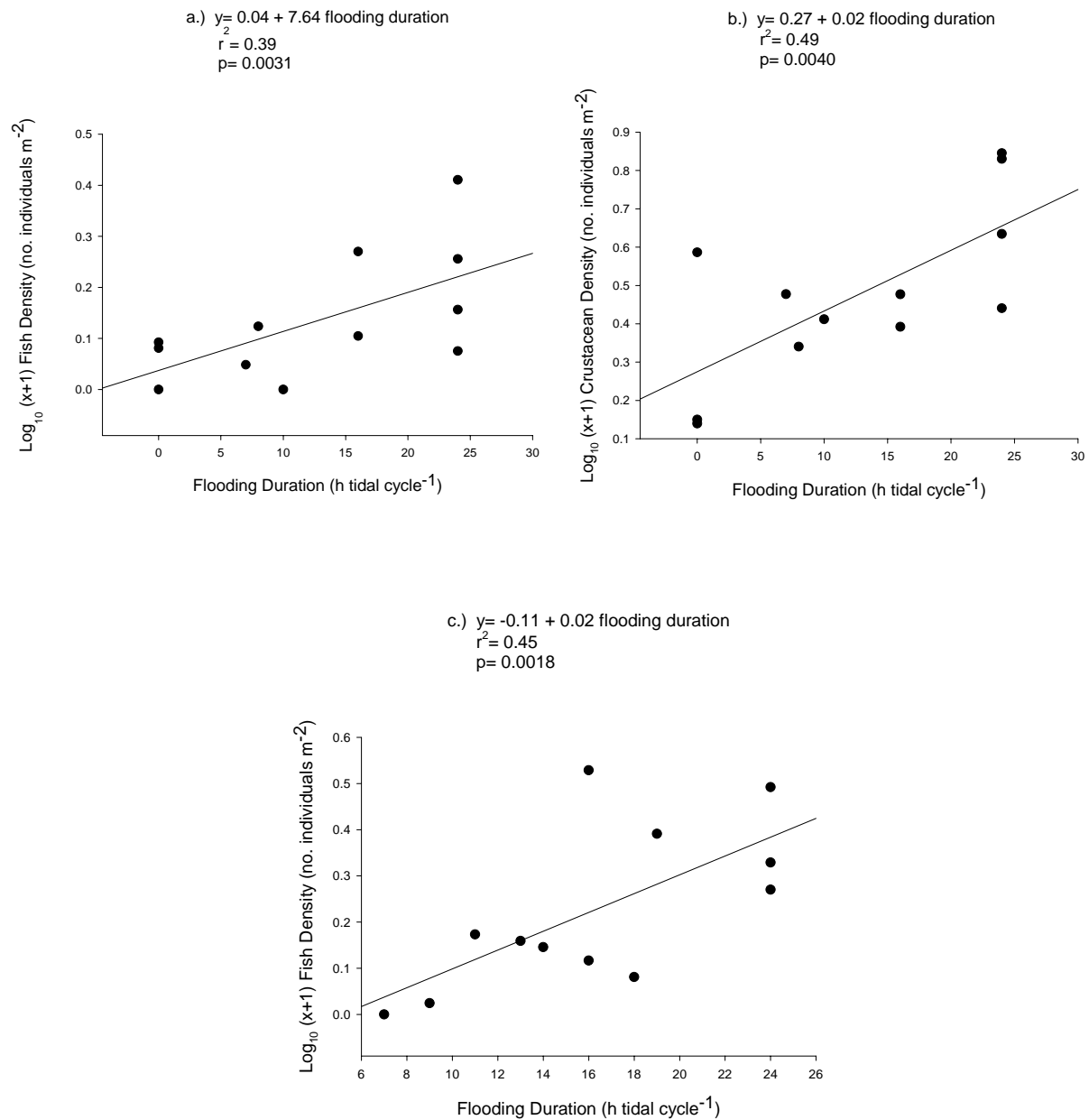


Figure 21. Plots showing significant linear relationships between fish/crustacean densities (no. individuals m^{-2} ; $\log_{10}(x+1)$ transformed) and flooding duration (h tidal cycle $^{-1}$) at (a, b) mangrove and (c) transition sites. Regression line is indicated by a solid line.

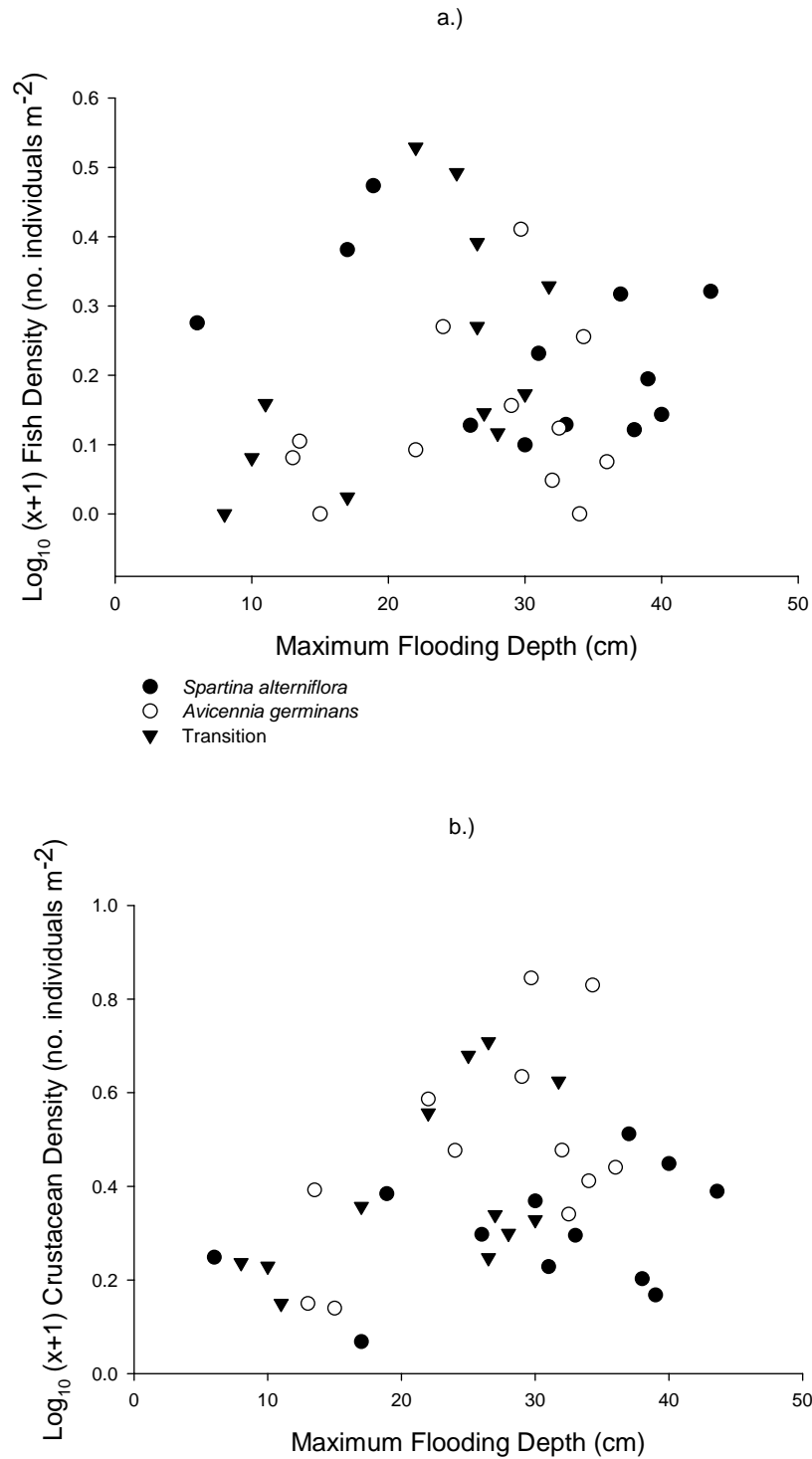


Figure 22. Plots of (a) fish and (b) crustacean densities (no. individuals m⁻²; log₁₀ (x+1) transformed) relative to maximum flooding depth (cm) at the *Spartina*, mangrove, and transition sites. Each point is the mean density of four lift net samples. Sampling occurred from 8 August 2003 to 29 June 2004.

Table 12. Results from lift net efficiency experiment. Size range (mm), mean length (mm; fish, SL and shrimp, RL), number of organisms recovered (out of 40), and mean recovery (%) \pm 1 standard deviation are given for gulf killifish (*Fundulus grandis*) and grass shrimp (*Palaemonetes spp.*). Mean recovery estimates are the average of four tests per habitat type (*Spartina*, mangrove, and transition).

Scientific and Common Name	Habitat Type	Size range, mm (mean)	No. recovered	Mean recovery (%) \pm 1 SD
<i>Fundulus grandis</i> gulf killifish	<i>Spartina</i>	50-75 (61.3)	37	92.5 \pm 9.57
	Mangrove	50-100 (62.5)	31	77.5 \pm 32.00
	Transition	43-88 (61.3)	34	85.0 \pm 19.10
<i>Palaemonetes spp.</i> grass shrimp	<i>Spartina</i>	9-16 (12.8)	9	22.5 \pm 28.70
	Mangrove	10-14 (12.3)	19	47.5 \pm 44.30
	Transition	10-15 (12.1)	12	30.0 \pm 38.30

DISCUSSION

Habitat

The significant vegetation and hydroperiod differences observed among *Spartina*, black mangrove, and transition sites may affect the accessibility and use of these habitat types by fishes and crustaceans. Black mangroves, for example, were the most structurally complex of the three habitat types and their dense pneumatophores may provide the greatest refuge benefits for small nekton. Similar stem densities at *Spartina* and transition sites (Figure 3a) may be because (1) *Spartina alterniflora* was the dominant vegetation type within the transition zone and (2) black mangroves growing there lacked the dense pneumatophores characteristic of monotypic black mangrove stands (Table 2).

Turbidity (Minello et al. 1987, Sasekumar et al. 1992, Benfield & Minello 1996), shading (Ellis & Bell 2004), and substrate conditions (Minello et al. 1987) confer refuge benefits for small nekton by reducing the effectiveness of visual predators. Although light levels were not measured, high turbidities across my study area (Table 3) may have minimized beneficial shade effects from the mangrove canopy for nekton (Benfield & Minello 1996). Higher sand content observed at the mangrove site (Table 5) may provide more favorable substrate for brown shrimp and other taxa that burrow to escape predation (Minello et al. 1987).

Surface elevations, highest at the mangrove site, intermediate at the transition site, and lowest at the *Spartina* site (Table 3), were consistent with the elevation gradient previously reported for the salt marsh-mangrove ecotone in Louisiana (Patterson & Mendelssohn 1991, Patterson et al. 1997). This elevation gradient is reversed in Australia, however, where salt marsh species (e.g., *Sporobolus virginicus*, *Samolus repens*, *Juncus krausii*, and *Sarcocornia quinqueflora*) occur at higher elevations than mangrove species (e.g., *A. marina*, *Aegiceras*

corniculatum; Saintilan & Williams 1999, Bloomfield & Gillanders 2005). Such elevation, hydroperiod, and plant species differences should be considered when comparing nekton use of salt marsh-mangrove ecotones in Louisiana versus Australia.

Greater flooding depths and durations made the *Spartina* site more accessible to nekton than the mangrove site (Figures 5 and 6). The transition site exhibited intermediate flooding durations, but low water levels resembled those at the mangrove site (Figures 5 and 6). Transition zones, in Louisiana, generally develop in higher elevation salt marshes where increased propagule retention and reduced propagule decay support mangrove survival (Patterson et al. 1997). Higher dissolved oxygen at mangrove and transition sites (Tables 3 and 4; Figure 7) may also be due to better-drained and more oxidized soils at these higher elevation sites (Patterson & Mendelsohn 1991).

A series of atmospheric cold fronts in early spring 2004 reduced water depths and hydroperiod at all three habitat types, but especially at the higher elevation mangrove and transition sites (Figures 5 and 6). Marsh flooding durations in the northern Gulf are generally greatest in fall and spring and lowest in summer and winter (Rozas 1995, Minello 1999); however, flooding durations during spring 2004 were low by comparison. In fact, spring water levels did not increase to average levels until late May and flooding durations remained low at mangrove and transition sites through late June (Figures 5 and 6). Therefore, *Spartina* marshes may become especially important for fishes and crustaceans when seasonal meteorological events reduce or prevent access to black mangrove and transition habitat types.

Benthic meiofauna composition and abundance were similar between *Spartina* and black mangroves sites (Tables 6 and 7) and were comparable to other salt marshes in Louisiana (Rutledge & Fleeger 1993) and Texas (Wardle et al. 2001, Whaley & Minello 2002). Meiofauna

abundances were lower in August when nekton abundances were high and higher in spring when nekton abundances were low (Figure 8), similar to patterns reported for benthic infaunal densities in a Texas salt marsh (Whaley & Minello 2002). Observed fluctuations in copepod abundances (Figure 8e) may also reflect changes in predation pressure related to site and seasonal differences in hydroperiod and nekton accessibility, since meiofauna composition and distribution are often affected by a combination of abiotic and biotic factors (Kneib 1984).

Several potential differences in food resources, however, were not investigated in my study, including meiofauna that dwell on smooth cordgrass stems (Rutledge & Fleeger 1993, Gregg & Fleeger 1998, Wardle et al. 2001) versus mangrove pneumatophores (Laegdsgaard & Johnson 2001) and differences in the plant material itself. Gobies and killifish, for example, often forage on plants when preferred benthic prey are unavailable (Rozas & Odum 1988). Stem densities can also affect the spatial distribution of food resources, with more concentrated food items among pneumatophores than less dense prop roots (Rönnbäck et al. 1999, Laegdsgaard & Johnson 2001). Benthic algal production, which may be more important than detritus in mangrove food webs (Stoner & Zimmerman 1988, Sheridan & Hays 2003), may also differ if light levels vary among *Spartina*, mangrove, and transition habitat types.

Fish and Crustacean Habitat Use

My study was unable to find significant differences in fish and crustacean densities among *Spartina*, black mangrove, and transition sites, possibly because sample sizes were low. However, site-related trends in nekton use were evident. Specifically, fishes showed affinities for the *Spartina* site and decapod crustaceans were more closely associated with the mangrove site. Fish and crustacean use at the transition site resembled patterns observed at both *Spartina*

and mangrove sites. Nekton densities appeared to be most affected by habitat type, areal stem cover, turbidity, and water temperature (Table 11).

The similar densities and species of fishes and crustaceans collected across sites indicate that nekton can and do use *Spartina*, mangrove, and transition habitat types. These similarities may be due to the close proximity of the three sites in the study area or because mangrove and transition habitat types account for a relatively small area within the salt marsh-dominated landscape. Black mangroves have co-existed with salt marshes in Louisiana since at least the 1700's; therefore, it is reasonable that fishes and crustaceans have adapted to use mangrove and transition habitat types. In fact, nekton often use a mosaic of habitat types, including several (e.g., oyster reef, seagrass beds, shallow nonvegetated bottom) not included for comparative purposes in this study.

Crustaceans may have a stronger affinity for vegetation than fishes because their densities are often higher than fish densities in vegetated habitat types (Minello et al. 2003). During my study, crustacean densities were consistently higher at the mangrove site (Figure 11b) and white shrimp and brown shrimp densities were also positively associated with higher ASC at the mangrove site (Figure 17). Structurally complex, vegetated habitats often support high shrimp densities, but lower densities and biomass of fish species (seagrass, Sheridan 1992; mangroves, Rönnbäck et al. 1999). Preferences may be species-specific, however, because densities of certain fish species have been positively related to structural complexity and/or shade in Caribbean mangroves (Cocheret de la Morinière et al. 2004).

Site-related differences in structural complexity and nekton size observed during my study may affect ontogenetic shifts in nekton use. Most of the crustaceans collected during my study were either small grass shrimp or juveniles, including white shrimp, brown shrimp (<25

mm RL), blue crabs, and gulf stone crabs (<50 mm CW; Table 10), that may have benefited from greater refuge from predation at the structurally complex mangrove site. Juvenile fish may also use mangroves if predators are present or food resources are associated with the structure (Laegdsgaard & Johnson 2001, Ellis & Bell 2004). Habitat needs often shift as nekton grow from protective habitats (e.g., mangrove or seagrass beds) to those with abundant food resources (e.g., mudflats or salt marshes; Rozas & Minello 1998, Craig & Crowder 2000, Laegdsgaard & Johnson 2001).

In general, larger nekton were collected at the *Spartina* site (fish, 50.9 ± 28.0 mm; crustacean, 24.6 ± 22.0 mm) than at the mangrove site (fish, 41.3 ± 28.5 mm; crustacean, 20.3 ± 16.5 mm). Lower stem densities at the *Spartina* site may benefit larger nekton, especially fishes, by increasing accessibility and maneuverability within the flooded marsh. Fish biomass was significantly greater at the *Spartina* site (Figure 14a) and gulf killifish were associated with lower ASC at the *Spartina* site (Figure 17). In general, the mangrove site supported higher crustacean densities, but lower fish biomass, than the *Spartina* site (Figures 11 and 14). Observed, site-related differences in structural complexity may affect size-dependent foraging and predation interactions on the flooded marsh/mangal surface (Heck & Crowder 1991).

A decline in fish use at higher elevation mangrove and transition sites during spring 2004 (Figures 11a and 14a), but not at the lower elevation *Spartina* site, suggests that low flooding depths and durations negatively affected fish use of these intertidal habitat types. Darter gobies and striped mullet were positively associated with flooding depth (Figure 17), perhaps because sufficient inundation is necessary to utilize their preferred marsh edge habitat types (Peterson & Turner 1994). Other estuarine-dependent nekton, such as postlarval brown shrimp and white shrimp that immigrate to Gulf coast estuaries in the spring and summer, respectively, may also

be affected by site-related and seasonal differences in accessibility. Water depth has been shown to be a primary factor affecting seasonal variability in brown shrimp densities (Zimmerman & Minello 1984).

My study found positive relationships between nekton densities and flooding duration at mangrove and transition sites (Figure 21), however, which suggest that nekton habitat use may be more affected by flooding duration than water depth. Increased submergence of low-elevation salt marshes in Louisiana may benefit brown shrimp by increasing the amount of time marsh resources are available (Rozas & Reed 1993). Osgood et al. (2003) reported positive relationships between fish densities and flooding duration at their lower elevation salt marshes, but found no clear relationship between fish densities and water depth at their higher elevation marshes. Although my study did not find significant relationships between nekton densities and flooding depth (Figure 22), positive correlations have been reported in salt marshes elsewhere (Yozzo & Smith 1998).

Abiotic conditions also contributed to variable fish and crustacean densities in this study. In fact, the physicochemical environment is often an important determinant of nekton distributions in salt marshes and mangroves (Rakocinski et al. 1992, Baltz et al. 1993, Pinto & Punchihewa 1996, Ley et al. 1999, Lin & Shao 1999, Able et al. 2001, Gelwick et al. 2001). My study found that grass shrimp and darter goby densities were positively associated with turbidity (Figure 17), perhaps because turbidity provides refuge benefits for small nekton in these marshes. In addition, a positive association between blue crab densities and salinity (Figure 17) may be linked to the migration of female blue crabs to higher salinity regions of the estuary to reproduce (Kneib 1997).

Although subtidal geomorphology was not quantified at *Spartina*, mangrove, and transition habitat types, site-related differences were apparent. In fact, the gently sloping, depositional *Spartina* edge may increase fish access to the flooded marsh compared to the steep, cut-bank mangrove edge (McIvor & Odum 1988). Fish and crustacean affinities for edge morphology, however, may be species-specific. Gulf killifish, which were positively associated with the *Spartina* site during my study (Figure 17), often select gently sloping, depositional marsh edge over cut-bank sites (Birdsong 2004). Tidewater silversides, however, were closely associated with the mangrove site (Figure 17) and their abundances have been positively correlated with the height of the emergent marsh bank (Birdsong 2004).

Mean nekton densities at *Spartina* (fish, $0.97 \pm 1.29 \text{ m}^{-2}$; crustacean, $0.94 \pm 1.10 \text{ m}^{-2}$), mangrove (fish, $0.50 \pm 0.70 \text{ m}^{-2}$; crustacean, $1.94 \pm 2.05 \text{ m}^{-2}$), and transition sites (fish, $0.95 \pm 1.24 \text{ m}^{-2}$; crustacean, $1.17 \pm 0.99 \text{ m}^{-2}$) were lower than estimates from studies using similar enclosure sampling techniques in salt marshes across Louisiana and Texas (fish, $7.71 \pm 0.81 \text{ m}^{-2}$; crustacean, $83.54 \pm 6.5 \text{ m}^{-2}$; Minello 1999). Fish densities at my mangrove site were lower than reports from mangroves in Florida (Thayer et al. 1987, Sheridan 1992) and the Philippines (Rönnbäck et al. 1999), but similar to densities in Australia (Morton 1990, Halliday & Young 1996, Vance et al. 1996). Low nekton densities may, in fact, be typical of mangroves when compared to marsh, seagrass, nonvegetated, and coral reef habitat types (Sheridan & Hays 2003, Bloomfield & Gillanders 2005).

The low nekton densities reported in my study may be due to: (1) differences in sampling location and methodology; (2) low water levels that reduced nekton access to sites during spring 2004; (3) nekton avoidance or escape from lift nets; and/or (4) predation within lift nets by larger nekton and birds. My lift nets sampled the flooded marsh surface within one

to three meters of the vegetation-water interface. Higher densities may be reported, however, if sampling occurs within the subtidal, nonvegetated edge where nekton aggregate, especially at low tide. These studies (Baltz et al. 1993) also report more pelagic species (i.e., gulf menhaden, bay anchovy) and fewer resident marsh nekton (i.e., gulf killifish, sheepshead minnows) than studies sampling flooded marsh surfaces (Rozas & Reed 1993). Although nekton avoidance of lift nets was possible, escape was unlikely because nets were repaired prior to each sampling event and recovery estimates (Table 12) were consistent with Rozas (1992). Predation within lift nets is assumed to be negligible (Rozas 1992); however, higher recoveries of grass shrimp from the more structurally complex mangrove site (Table 12) may reflect lower predation rates. If true, nekton densities reported in this study underestimate actual values and may be skewed given site-related differences in structural complexity.

Conclusions

In conclusion, the significant vegetation and hydroperiod differences observed among *Spartina*, black mangrove, and transition sites in southwestern Caminada Bay may affect the accessibility and use of these habitat types by nekton. Although similar taxa and densities of fishes and crustaceans were often collected across the three habitat types, site-related trends in nekton use were evident. In general, fishes, including gulf killifish and sheepshead minnows, showed affinities for the *Spartina* site and decapod crustaceans, especially white shrimp and brown shrimp, were more associated with the mangrove site. Habitat type, areal stem cover, turbidity, and water temperature were the primary factors affecting fish and crustacean densities. Greater structural complexity at the mangrove site may increase its refuge value for nekton since (1) many of the crustaceans collected were juveniles, including white shrimp, brown shrimp, blue crabs, and gulf stone crabs, and (2) white shrimp and brown shrimp were associated with

higher ASC. Lower ASC and significantly greater flooding depths and durations at the *Spartina* site than at the higher elevation black mangrove site may benefit larger nekton by increasing accessibility and maneuverability within the marsh. The transition site shared similar vegetation characteristics with the *Spartina* site, but more closely resembled flooding depths and durations observed at the mangrove site. Nekton densities were positively related to flooding duration at mangrove and transition sites. Reduced fish use at mangrove and transition sites during the spring suggests that *Spartina* marshes may become especially important for nekton when seasonal meteorological events minimize or prevent access to mangrove and transition habitat types.

Implications

Mild winters since 1989-90 have facilitated an expansion of black mangroves in coastal Louisiana. Mangroves are also increasingly planted for shoreline stabilization and habitat mitigation projects. More research is necessary to determine if my findings from southwestern Caminada Bay are representative of nekton use across Louisiana's salt marsh-mangrove ecotone. If they are representative, then as black mangroves move into higher elevation salt marshes, creating transition zones, there would likely be no effect or a temporary positive effect on fish and crustacean use. As transition zones become monotypic black mangrove stands, however, use by some fish species, particularly larger species or individuals, may decline. Decapod crustaceans, especially juveniles, are most likely to benefit from a continued expansion of black mangroves in coastal Louisiana.

Black Mangrove and Transition Habitat Types as EFH

My study addressed levels 1 (species distribution, range) and 2 (quantitative data) of the guidelines for identifying EFH (NMFS 1997). Several federally managed species, including

brown shrimp, white shrimp, gulf stone crab, and gray snapper, were collected at black mangrove and transition sites in southwestern Caminada Bay, Louisiana. In fact, white shrimp, brown shrimp, and gulf stone crabs were collected in their highest numbers, densities, and biomass at the mangrove site. In addition, white shrimp and brown shrimp densities were positively associated with the structurally complex mangrove site. My findings, if representative of Louisiana's salt marsh-ecotone, suggest that mangrove and transition habitat types support commercially-important decapod crustaceans. Before specific recommendations for EFH designations are made, however, more research is needed to (1) examine levels 3 (growth, reproduction, survival) and 4 (disproportional production) of the guidelines for identifying EFH (NMFS 1997); (2) test the mechanisms by which observed differences in structural complexity and hydroperiod affect nekton selection and use of *Spartina*, mangrove, and transition habitat types; (3) compare nekton use at additional sites across Louisiana's salt marsh-mangrove ecotone; and (4) determine the areal extent of black mangrove and transition habitat types across south Louisiana. If black mangroves continue to account for only a small percentage of the total area of coastal wetlands in Louisiana, then their actual contribution to EFH and overall fisheries production may not be significant.

LITERATURE CITED

- Able, K.W., D.M. Nemerson, R. Bush, and P. Light. 2001. Spatial variation in Delaware Bay (U.S.A.) marsh creek fish assemblages. *Estuaries* 24(3):441-452.
- Acosta, A. 1997. Use of multi-mesh gillnets and trammel nets to estimate fish species composition in coral reef and mangroves in the southwest coast of Puerto Rico. *Caribbean Journal of Science* 33:45-57.
- Bell, J.D., D.A. Pollard, J.J. Burchmore, B.C. Pease, and M.J. Middleton. 1984. Structure of a fish community in a temperate tidal mangrove creek in Botany Bay, New South Wales. *Australian Journal of Marine and Freshwater Research* 35:33-46.
- Baltz, D.M., C. Rakocinski, and J.W. Fleeger. 1993. Microhabitat use by marsh-edge fishes in a Louisiana estuary. *Environmental Biology of Fishes* 36:109-126.
- Benfield, M.C. and T.J. Minello. 1996. Relative effects of turbidity and light intensity on reactive distance and feeding of an estuarine fish. *Environmental Biology of Fishes* 46:211-216.
- Birdsong, T.W. 2004. Complexity and nekton use of marsh edge habitats in Barataria Bay, Louisiana. Master's thesis. Louisiana State University, Baton Rouge. 50pp.
- Blaber, S.J.M., D.T. Brewer, and J.P. Salini. 1989. Species composition and biomasses of fishes in different habitats of a tropical northern Australia estuary: their occurrence in the adjoining sea and estuarine dependence. *Estuarine Coastal and Shelf Science* 29:509-531.
- Bloomfield, A.L. and B.M. Gillanders. 2005. Fish and invertebrate assemblages in seagrass, mangrove, saltmarsh, and nonvegetated habitats. *Estuaries* 28(1):63-77.
- Boesch, D.F. and R.E. Turner. 1984. Dependence of fishery species on salt marshes: the role of food and refuge. *Estuaries* 7(4A):460-468.
- Britsch, L.D. and J.B. Dunbar. 1993. Land loss rates: Louisiana coastal plain. *Journal of Coastal Research* 9:324-338.
- Chesney, E.J., D.M. Baltz, and R.G. Thomas. 2000. Louisiana estuarine and coastal fisheries habitats: perspectives from a fish's eye view. *Ecological Applications* 10(2): 350-366.
- Chong, V.C., A. Sasekumar, M.U.C. Leh, and R. D'Cruz. 1990. The fish and prawn communities of a Malaysian coastal mangrove system, with comparisons to adjacent mud flats and inshore waters. *Estuarine and Coastal Shelf Science* 31:703-722.
- Cocheret de la Morinière, E., I. Nagelkerken, H. van der Meij, and G. van der Velde. 2004. What attracts juvenile coral reef fish to mangroves: habitat complexity or shade? *Marine Biology* 144:139-145.

- Craig, J.K. and L.B. Crowder. 2000. Factors influencing habitat selection in fishes with a review of marsh ecosystems. P. 241-261: In Weinstein, M.P. and D.A. Kreeger (eds.) Concepts and controversies in tidal marsh ecology: Kluwer Academic Publishers. Dordrecht, Netherlands.
- Ellis, W.L. and S.S. Bell. 2004. Conditional use of mangrove habitats by fishes: depth as a cue to avoid predators. *Estuaries* 27(6):966-976.
- Field, C.D. 1995. Impact of expected climate change on mangroves. *Hydrobiologia* 295:75-81.
- Gelwick, F.P., S. Akin, D.A. Arrington, and K.O. Winemiller. 2001. Fish assemblage structure in relation to environmental variation in a Texas Gulf coastal wetland. *Estuaries* 24(2):285-296.
- Gregg, C.S. and J.W. Fleeger. 1998. Grass shrimp *Palaemonetes pugio* predation on sediment- and stem-dwelling meiofauna: field and laboratory experiments. *Marine Ecology Progress Series* 175:77-86.
- Gregg, J.C. and J.W. Fleeger, Jr. 1997. Importance of emerged and suspended meiofauna to the diet of the darter goby (*Gobionellus boleosoma* Jordan and Gilbert). *Journal of Experimental Marine Biology and Ecology* 209:123-142.
- Halliday, I.A. and W.R. Young. 1996. Density, biomass and species composition of fish in a subtropical *Rhizophora stylosa* mangrove forest. *Marine and Freshwater Research* 47:609-615.
- Halpern, B.S. 2004. Are mangroves a limiting resource for two coral reef fishes? *Marine Ecology Progress Series* 272:93-98.
- Heck, K.L. Jr, and L.B. Crowder. 1991. Habitat structure and predator-prey interactions in vegetated aquatic systems. P. 281-295: In Bell, S.S., E.D. McCoy, and H.R. Hushinsky (eds.) *Habitat structure: the physical arrangement of objects in space*: Chapman and Hall. New York.
- Hindell, J.S. and G.P. Jenkins. 2004. Spatial and temporal variability in the assemblage structure of fishes associated with mangroves (*Avicennia marina*) and intertidal mudflats in temperate Australian embayments. *Marine Biology* 144:385-395.
- Kneib, R.T. 1984. Patterns of invertebrate distribution and abundance in the intertidal salt marsh: causes and questions. *Estuaries* 7(4A):392-412.
- Kneib, R.T. 1997. The role of tidal marshes in the ecology of estuarine nekton, P. 163-220: In Ansell, A.D., R.N. Gibson, and M. Barnes (eds.) *Oceanography and Marine Biology: An Annual Review*. UCL Press, London, U.K.

- Kneib, R.T. and S.L. Wagner. 1994. Nekton use of vegetated marsh habitats at different stages of tidal inundation. *Marine Ecology Progress Series* 106:227-238.
- Krebs, C.J. 1989. Species diversity measures. P. 328-368: In Wilson, C.M. and S. Pisano (eds.) *Ecological methodology*: HarperCollinsPublishers. New York.
- Kuo, S.-R., H.-J. Lin, and K.-T. Shao. 1999. Fish assemblages in the mangrove creeks of northern and southern Taiwan. *Estuaries* 22(4):1004-1015.
- Laegdsgaard, P. and C. Johnson. 2001. Why do juvenile fish utilise mangrove habitats? *Journal of Experimental Marine Biology and Ecology* 257:229-253.
- Laroche, J., E. Baran, and N.B. Rasoanandrasana. 1997. Temporal patterns in a fish assemblage of a semiarid mangrove zone in Madagascar. *Journal of Fish Biology* 51:3-20.
- Ley, J.A., C.C. McIvor, and C.L. Montague. 1999. Fishes in mangrove prop-root habitats of northeastern Florida Bay: distinct assemblages across an estuarine gradient. *Estuarine, Coastal and Shelf Science* 48:701-723.
- Ley, J.A., C.L. Montague, and C.C. McIvor. 1994. Food habits of mangrove fishes: a comparison along estuarine gradients in northeastern Florida Bay. *Bulletin of Marine Science* 54(3):881-899.
- Lin, H.-J. and K.-T. Shao. 1999. Seasonal and diel changes in a subtropical mangrove fish assemblage. *Bulletin of Marine Science* 65:775-794.
- Louis, M., C. Bouchon, and Y. Bouchon-Navaro. 1995. Spatial and temporal variations of mangrove fish assemblages in Martinique (French West Indies). *Hydrobiologia* 295:275-284.
- McIvor, C.C. and W.E. Odum. 1988. Food, predation risk, and microhabitat selection in a marsh fish assemblage. *Ecology* 69(5):1341-1351.
- McIvor, C.C. and T.J. Smith, III. 1995. Differences in the crab fauna of mangrove areas at a southwest Florida and a northeast Australia location: implications for leaf litter processing. *Estuaries* 18:591-597.
- Mendelssohn, I.A. and K.L. McKee. 2000. Saltmarshes and Mangroves. P. 501-536: In Barbour, M.G. and W.D. Billings (eds.) *North American vegetation*: Cambridge University Press. New York.
- Meyer, D.L., J.M. Johnson, and J.W. Gill. 2001. Comparison of nekton use of *Phragmites australis* and *Spartina alterniflora* marshes in the Chesapeake Bay, USA. *Marine Ecology Progress Series* 209:71-84.

- Minello, T.J. 1999. Nekton densities in shallow estuarine habitats of Texas and Louisiana and the identification of essential fish habitat. In: Benaka, L.R. (ed) Fish habitat: essential fish habitat and rehabilitation. American Fisheries Society Symposium 22:43-75.
- Minello, T.J. and L.P. Rozas. 2002. Nekton in Gulf Coast wetlands: fine-scale distributions, landscape patterns, and restoration implications. *Ecological Applications* 12(2):441-455.
- Minello, T.J. and R.J. Zimmerman. 1983. Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: the effect of simulated *Spartina* structure on predation rates. *Journal of Experimental Marine Biology and Ecology* 72:211-231.
- Minello, T.J. and R.J. Zimmerman. 1991. The role of estuarine habitats in regulating growth and survival of juvenile penaeid shrimp. P. 1-16: In DeLoach, P, W.J. Dougherty, and M.A. Davidson (eds.) *Frontiers in shrimp research*: Elsevier. Amsterdam, Netherlands.
- Minello, T.J., R.J. Zimmerman, and E.X. Martinez. 1987. Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: effects of turbidity and substratum on predation rates. *Fishery Bulletin* 85(1):59-70.
- Minello, T.J., R.J. Zimmerman, and E.X. Martinez. 1989. Mortality of young brown shrimp *Penaeus aztecus* in estuarine nurseries. *Transactions of the American Fisheries Society* 118:693-708.
- Minello, T.J., K.W. Able, M.P. Weinstein, and C.G. Hays. 2003. Salt marshes as nurseries for nekton: testing hypotheses on density, growth and survival through meta-analysis. *Marine Ecology Progress Series* 246:39-59.
- Mitsch, W.J. and J.G. Gosselink. 2000. *Wetlands*. Third edition. John Wiley & Sons, Inc. New York. 920pp.
- Mohan, P.C., R.G. Rao, and F. Dehairs. 1997. Role of Godavari mangroves (India) in the production and survival of prawn larvae. *Hydrobiologia* 358:317-320.
- Morton, R.M. 1990. Community structure, density and standing crop of fishes in a subtropical Australian mangrove area. *Marine Biology* 105:385-394.
- Nagelkerken, I. and G. van der Velde. 2004. Relative importance of interlinked mangroves and seagrass beds as feeding habitats for juvenile reef fish on a Caribbean island. *Marine Ecology Progress Series* 274:153-159.
- Nagelkerken, I., G. van der Velde, M.W. Gorissen, G.J. Meijer, T. van't Hof, and C. den Hartog. 2000. Importance of mangroves, seagrass beds and the shallow coral reef as a nursery for important coral reef fishes, using a visual census technique. *Estuarine, Coastal and Shelf Science* 51:31-44.

- Nagelkerken, I., C.M. Roberts, G. van der Velde, M. Dorenbosch, M.C. van Riel, E. Cocheret de La Morinière, and P.H. Nienhuis. 2002. How important are mangroves and seagrass beds for coral-reef fish? The nursery hypothesis tested on an island scale. *Marine Ecology Progress Series* 244:299-305.
- NMFS (National Marine Fisheries Service). 1997. Magnuson-Stevens Act provisions: essential fish habitat: interim final rule and request for comments. Federal Register (Docket 961030300-7238-04; I.D. 120996A): 66531-66559.
- NOAA (National Oceanic and Atmospheric Administration). 1996. Magnuson-Stevens Fishery Conservation and Management Act amended through 11 October 1996. National Marine Fisheries Service, National Oceanic and Atmospheric Administration Technical Memorandum NMFS-F/SPO-23. U.S. Department of Commerce, Washington, D.C.
- Odum, W.E. and E.J. Heald. 1972. The detritus-based food web of an estuarine mangrove community. P. 265-286: In L.E. Cronin (ed.) *Estuarine research*: Academic Press. New York.
- Osgood, D.T., D.J. Yozzo, R.M. Chambers, D. Jacobson, T. Hoffman, and J. Wnek. 2003. Tidal hydrology and habitat utilization by resident nekton in *Phragmites* and non-*Phragmites* marshes. *Estuaries* 26(2B):522-533.
- Patterson, C.S. and I.A. Mendelssohn. 1991. A comparison of physicochemical variables across plant zones in a mangal/salt marsh community in Louisiana. *Wetlands* 11:139-161.
- Patterson, S., K.L. McKee, and I.A. Mendelssohn. 1997. Effects of tidal inundation and predation on *Avicennia germinans* seedling establishment and survival in a sub-tropical mangal/salt marsh community. *Mangroves and Salt Marshes* 1:103-111.
- Penland, S. and K.E. Ramsey. 1990. Relative sea-level rise in Louisiana and the Gulf of Mexico: 1908-1988. *Journal of Coastal Research* 6(2):323-342.
- Peterson, G.W. and R.E. Turner. 1994. The value of salt marsh edge vs interior as a habitat for fish and decapod crustaceans in a Louisiana tidal marsh. *Estuaries* 17(1B):235-262.
- Pinto, L. and N.N. Punchihewa. 1996. Utilisation of mangroves and seagrasses by fishes in the Negombo Estuary, Sri Lanka. *Marine Biology* 126:333-345.
- Rakocinski, C.F., D.M. Baltz, and J.W. Fleeger. 1992. Correspondence between environmental gradients and the community structure of marsh-edge fishes in a Louisiana estuary. *Marine Ecology Progress Series* 80:135-148.
- Rogers, B.D., R.F. Shaw, W.H. Herke and R.H. Blanchet. 1993. Recruitment of postlarval and juvenile brown shrimp (*Penaeus aztecus* Ives) from offshore to estuarine waters of the northwestern Gulf of Mexico. *Estuarine, Coastal and Shelf Science* 36:377-394.

- Rönnbäck, P., M. Troell, N. Kautsky, and J.H. Primavera. 1999. Distribution pattern of shrimps and fish among *Avicennia* and *Rhizophora* microhabitats in the Pagbilao mangroves, Phillipines. *Estuarine, Coastal and Shelf Science* 48:223-234.
- Rooker, J.R. and G.D. Dennis. 1991. Diel, lunar and seasonal changes in a mangrove fish assemblage off southwestern Puerto Rico. *Bulletin of Marine Science* 49:684-698.
- Rozas, L.P. 1992. Bottomless lift net for quantitatively sampling nekton on intertidal marshes. *Marine Ecology Progress Series* 89:287-292.
- Rozas, L.P. 1995. Hydroperiod and its influence on nekton use of the salt marsh: a pulsing ecosystem. *Estuaries* 18:579-590.
- Rozas, L.P. and M.W. LaSalle. 1990. A comparison of the diets of gulf killifish, *Fundulus grandis* Baird and Girard, entering and leaving a Mississippi brackish marsh. *Estuaries* 13(3):332-336.
- Rozas, L.P. and T.J. Minello. 1998. Nekton use of salt marsh, seagrass, and nonvegetated habitats in a south Texas (USA) estuary. *Bulletin of Marine Science* 63(3):481-501.
- Rozas, L.P. and W.E. Odum. 1988. Occupation of submerged aquatic vegetation by fishes: testing the roles of food and refuge. *Oecologia* 77:101-106.
- Rozas, L.P. and D.J. Reed. 1993. Comparing nekton assemblages of subtidal habitats in pipeline canals traversing brackish and saline marshes in coastal Louisiana. *Wetlands* 14(4):262-275.
- Rutledge, P.A. and J.W. Fleeger. 1993. Abundance and seasonality of meiofauna, including harpacticoid copepod species, associated with stems of the salt-marsh cord grass, *Spartina alterniflora*. *Estuaries* 16(4):760-768.
- Saintilan, N. and R.J. Williams. 1999. Mangrove transgression into saltmarsh environments in south-east Australia. *Global Ecology and Biogeography* 8:117-124.
- Sasekumar, A., V.C. Chong, M.U. Leh, and R. D'Cruz. 1992. Mangroves as a habitat for fish and prawns. *Hydrobiologia* 247:195-207.
- Sheaves, M. and B. Molony. 2000. Short-circuit in the mangrove food chain. *Marine Ecology Progress Series* 199:97-109.
- Sheridan, P.F. 1992. Comparative habitat utilization by estuarine macrofauna within the mangrove ecosystem of Rookery Bay, Florida. *Bulletin of Marine Science* 50:21-39.
- Sheridan, P. 1997. Benthos of adjacent mangrove, seagrass, and non-vegetated habitats in Rookery Bay, Florida, USA. *Estuarine, Coastal and Shelf Science* 44:455-469.

- Sheridan, P. and C. Hays. 2003. Are mangroves nursery habitat for transient fishes and decapods? *Wetlands* 23(2):449-458.
- Sherrod, C.L. and C. McMillan. 1985. The distributional history and ecology of mangrove vegetation along the northern Gulf of Mexico coastal region. *Contributions in Marine Science* 28:129-140.
- Smith, K.J., G. Taghon, and K.W. Able. 2000. Trophic linkages in marshes: ontogenetic changes in diet for young-of-the-year mummichog, *Fundulus heteroclitus*. P. 221-237. In Weinstein, M.P. and D.A. Kreeger (eds.) *Concepts and controversies in tidal marsh ecology*: Kluwer Academic Publishers. Dordrecht, Netherlands.
- Stoner, A.W. and R.J. Zimmerman. 1988. Food pathways associated with penaeid shrimps in a mangrove-fringed estuary. *Fishery Bulletin* 86(3):543-551.
- ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology* 67:1167-1179.
- Thayer, G.W., D.R. Colby, and W.F. Hettler, Jr. 1987. Utilization of the red mangrove prop root habitat by fishes in South Florida. *Marine Ecology Progress Series* 35:25-38.
- Turner, R.E. 1977. Intertidal vegetation and commercial yields of penaeid shrimp. *Transactions of the American Fisheries Society* 106:411-416.
- Turner, R.E. 1990. Landscape development and coastal wetland losses in the northern Gulf of Mexico. *American Zoologist* 30:89-105.
- USGCRP (U.S. Global Change Research Program). 2002. *Our Changing Planet: The FY2002 U.S. Global Change Research Program*. Subcommittee on Global Change Research. Committee on Environmental and Natural Resources of the National Science and Technological Council. A Supplement to the President's Fiscal Year 2002 Budget. 74pp.
- Vance, D.J., M.D.E. Haywood, D.S. Heales, R.A. Kenyon, N.R. Loneragan, and R.C. Pendrey. 1996. How far do prawns and fish move into mangroves? Distribution of juvenile banana prawns *Penaeus merguensis* and fish in a tropical mangrove forest in northern Australia. *Marine Ecology Progress Series* 131:115-124.
- Wardle, W.J., T.J. Minello, J.W. Webb, T.-H. Wu, and J. Jewett-Smith. 2001. Algal pigments, meiofauna, and macrofauna from two edaphic salt marsh microhabitats in Galveston Bay, Texas, USA. *Wetlands* 21(4):474-483.
- Whaley, S.D. and T.J. Minello. 2002. The distribution of benthic infauna of a Texas salt marsh in relation to the marsh edge. *Wetlands* 22(4):753-766.

- Wilson, K.A. 1989. Ecology of mangrove crabs: predation, physical factors and refuges. *Bulletin of Marine Science* 44:263-273.
- Yozzo, D.J. and D.E. Smith. 1998. Composition and abundance of resident marsh-surface nekton: comparison between tidal freshwater and salt marshes in Virginia, USA. *Hydrobiologia* 362:9-19.
- Zetler, B.D. and D.V. Hansen. 1972. Tides in the Gulf of Mexico. In L. Cappuro and J.L. Reid (eds.) *Contributions on the physical oceanography of the Gulf of Mexico*: Gulf Publishing Co. 255pp.
- Zimmerman, R.J. and T.J. Minello. 1984. Densities of *Penaeus aztecus*, *Penaeus setiferus*, and other natant macrofauna in a Texas salt marsh. *Estuaries* 7(4A):421-433.
- Zimmerman, R.J., T.J. Minello, and L.P. Rozas. 2000. Salt marsh linkages to productivity of penaeid shrimps and blue crabs in the northern Gulf of Mexico. P. 293-314: In Weinstein, M.P. and D.A. Kreeger (eds.) *Concepts and controversies in tidal marsh ecology*: Kluwer Academic Publishers. Dordrecht, Netherlands.

VITA

Melanie Christine Caudill was born on January 19, 1977, in Hamilton, Ohio. She is the daughter of Raymond and Ruth Caudill and the sister of Brooke and Emily Caudill. Melanie graduated from Peters Township High School in McMurray, Pennsylvania, in 1995. She then moved to Gainesville, Florida, and earned a Bachelor of Science degree in wildlife ecology and conservation from the University of Florida (UF) in 1999. During college, she worked for Florida Lakewatch, a water-monitoring program affiliated with the Department of Fisheries and Aquatic Sciences at UF, sampling aquatic macrophytes and producing bathymetric maps for over 100 Florida lakes. Melanie then worked as a wildlife technician with the Florida Cooperative Fish and Wildlife Research Unit inventorying amphibians at Everglades National Park and the U.S. Virgin Islands. In 2002, Melanie began her graduate studies with Dr. Richard F. Shaw in the Department of Oceanography and Coastal Sciences at Louisiana State University. Her master's research was the first comparative study of fish and crustacean use of salt marsh, black mangrove, and transition habitat types in Louisiana.