

Gulf of Mexico Science

Volume 18
Number 2 *Number 2*

Article 5

1999

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DOI: 10.18785/goms.1802.05

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Recommended Citation

Howe, J. C. and R. K. Wallace. 2000. Relative Abundance of Postlarval and Juvenile Penaeid Shrimps in Submerged Aquatic Vegetation and Emergent Marsh Habitats. *Gulf of Mexico Science* 18 (2). Retrieved from <https://aquila.usm.edu/goms/vol18/iss2/5>

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Relative Abundance of Postlarval and Juvenile Penaeid Shrimps in Submerged Aquatic Vegetation and Emergent Marsh Habitats

JEFFREY C. HOWE AND RICHARD K. WALLACE

Postlarval and juvenile densities of *Farfantepenaeus aztecus*, *Farfantepenaeus duorarum*, and *Litopenaeus setiferus* were compared among emergent marsh (*Spartina alterniflora*), submerged aquatic vegetation (*Ruppia maritima*), and adjacent unvegetated areas at the east end of Fowl River along Mobile Bay, AL. A total of 108 samples were collected between July 1994 and Nov. 1995, of which 76 samples contained at least one of the three penaeid species. Of the 507 penaeid shrimp collected, 303 (60%) were collected in the *R. maritima* beds, 152 (30%) in the *S. alterniflora*, and 52 (10%) in the sand/mud habitat. The mean densities of *F. aztecus*, *F. duorarum*, and all three penaeid species combined were significantly greater in the *R. maritima* beds compared with those in both the *S. alterniflora* and sand/mud habitats. Presence of vegetation appeared to have little effect on shrimp size because no significant difference in size of shrimp between habitats was recorded. Generally, there was little correlation between shrimp density and abiotic factors within the three habitats, but a significant negative correlation was found between *F. aztecus* density and *S. alterniflora* density. Results suggest that habitats with submerged aquatic vegetation, *R. maritima*, are utilized more by both *F. aztecus* and *F. duorarum* over those characterized by the emergent vegetation, *S. alterniflora*. Because shrimp densities did not exhibit any patterns in relation to a variety of hydrographic factors, additional field studies should focus on biotic parameters (i.e., predation, competition, food availability, habitat structure) to better determine the factors that affect penaeid shrimp abundance within estuarine habitats.

Estuarine habitats are used extensively by juvenile fishes and crustaceans as nurseries because of their high productivity and structural complexity. Although these habitats are variable, evidence clearly shows that many commercially important species depend on these habitats for food, growth, and protection (Turner, 1977; Minello and Zimmerman, 1983, 1991; Boesch and Turner, 1984; Minello et al., 1989; Peterson and Turner, 1994; Kneib, 1997). Vegetation, salinity, and temperature are the most important biotic and abiotic factors associated with estuarine habitats with respect to shrimp survival and growth (Zein-Eldin, 1963; Zein-Elden and Aldrich, 1965; Wiesepape et al., 1972; Zimmerman et al., 1984; Zein-Eldin and Renaud, 1986; Herke et al., 1987; Sheridan, 1992; Montague and Ley, 1993; Wenner and Beatty, 1993; DeLancey et al., 1994). Additional factors such as time of day, year, lunar phase, tide, marsh elevation, predation, and secondary production have also been shown to influence shrimp abundance (Hunter and Feller, 1987; Gleason and Wellington, 1988; Minello et al., 1989; Rogers et al., 1993; DeLancey et al., 1994; Kneib and Wagner, 1994; Minello and Webb, 1997).

Vegetation in tidal marsh habitats may pro-

vide food, protection, and substrate for postlarval and juvenile shrimp (Minello and Zimmerman, 1983; Zimmerman et al., 1984; Minello et al., 1989; Rozas and Reed, 1993; Kneib, 1997). Howe et al. (1999) documented significantly higher shrimp densities in emergent vegetated habitats compared with unvegetated in Mobile Bay, AL. Other studies have reported similar findings concerning shrimp densities in vegetated marsh habitats in Texas, Louisiana, and Florida (Zimmerman and Minello, 1984; Zimmerman et al., 1984; Minello and Zimmerman, 1985; Sheridan, 1992; Montague and Ley, 1993; Rozas and Reed, 1993). These studies stress the important role of marsh vegetation regarding juvenile penaeid (especially *Farfantepenaeus aztecus*) shrimp. Little information is available on the relative importance of submerged aquatic vegetation. However, in a study conducted by Loesch (1965) in Mobile Bay, an average of 33.8 shrimp per 3-min drag at a site containing submerged vegetation (*Ruppia maritima* and *Vallisneria*) compared with only 0.2–3.2 shrimp at all other sites void of submerged vegetation was recorded. Unfortunately, because drag-bar nets and minnow seines were used in this study, emergent vegetated sites were not sampled for comparison.

Although marsh vegetation appears important, other studies have shown that not all penaeid shrimp exhibit a strong affinity for vegetated habitats (Zimmerman and Minello, 1984; Minello and Zimmerman, 1985, 1991; Wenner and Beatty, 1993). Based on the lack of significant differences in the density of *Litopenaeus setiferus* between vegetated and nonvegetated habitats, Zimmerman and Minello (1984) suggested that *L. setiferus* might utilize vegetated and nonvegetated habitats on an equivalent basis and that they may respond to different factors compared with *F. aztecus*. In addition, Minello and Zimmerman (1985) demonstrated that *F. aztecus* select for vegetated habitats more often than *L. setiferus* in the field and hypothesized that an active habitat selection component was responsible on the basis of laboratory studies. Also, laboratory studies showed that other environmental variables (food availability, salinity, turbidity, and light) directly affected the distribution of *F. aztecus* in relation to vegetation, whereas these variables had little effect on the selection for vegetation by *L. setiferus* (Minello et al., 1990).

Because of the lack of information concerning the relative importance of submerged vegetation regarding shrimp densities, the objective of the present study was to compare the importance of three different habitats (marsh grass, *Spartina alterniflora*; submerged vegetation, *R. maritima*; sand/mud) in respect to naturally occurring densities of postlarval and juvenile *F. aztecus*, *F. duorarum*, and *L. setiferus* in a tidal estuary.

MATERIALS AND METHODS

The study site was near the mouth of east Fowl River along Mobile Bay, AL, where water depth was less than 1 m (Fig. 1). All samples were collected with a cylindrical aluminum drop sampler (1.40 m diameter \times 1.23 m) similar to that used in Howe et al. (1999).

Between July 1994 and Nov. 1994 and April 1995 and Nov. 1995, three random samples, each representing a 1.5-m² area, were collected monthly from each of three habitats (emergent salt marsh grass, submerged vegetation, sand/mud habitat). All samples were collected within a 100-m radius of each other. During 1994 and 1995, samples were not collected in Oct. and Aug., respectively, because of adverse weather. All sampling was scheduled during high tide when both vegetated and nonvegetated habitats were equally available. If a watertight seal was not possible at the selected sampling site because of topography, etc., a

new drop was made in an adjacent area. Water depth and sediment penetration were measured inside the cylinder. Although sediment composition was not analyzed, penetration depth was measured to examine shrimp distribution patterns in relation to soft and firm habitat bottom. At each sample, sediment penetration was measured three times with a graduated section of polyvinyl chloride pipe placed upon the sediment and releasing a 2.3-kg weight from a constant height (38 cm). The mean sediment penetration depth was used for statistical analysis as a single data value. Water temperature (C), dissolved oxygen (DO; ppm), and salinity (‰) were measured with a Hydrolab Surveyor II[®]. Occasional failures of the Hydrolab resulted in either missing data or water temperature and salinity being measured with a thermometer and refractometer.

At samples within the salt marsh areas, the *S. alterniflora* stems were counted, removed by clipping at the substrate, rinsed and shaken within the sampling cylinder, and bagged prior to collection of juvenile and postlarval shrimp. Similarly, at submerged vegetative sites, *R. maritima* was removed by clipping and bagged before shrimp were collected. Shrimp were collected from each drop sample by performing six complete sweeps within the drop cylinder with a 650- μ m-mesh dip net (28 cm \times 30 cm). On the basis of previous experience with drop sampling (Howe et al., 1999), six dip net sweeps were found to be more than adequate in collecting all shrimp present in the cylinder. Once collected, shrimp were bagged and placed on ice for future identification. In the laboratory, shrimp were preserved in 10% formalin for 48 hr, then rinsed in freshwater, and transferred to 50% isopropanol. Shrimp were then sorted, identified, and measured to the nearest 0.5 mm from rostral tip to end of telson. Plant material was examined for the presence of any remaining shrimp, weighed wet, dried for 48 hr at 100 C, and then weighed again.

Early postlarvae up to 12 mm total length (TL) were distinguished by rostral, antennal scale, and pereopod characteristics (Pearson, 1939; Williams, 1959). The presence of spines on the dorsal carina of the sixth abdominal segment differentiated postlarval (5–25 mm TL) *F. aztecus* and *F. duorarum* from postlarval *L. setiferus*, which lack these spines (Ringo and Zamora, 1968; Zamora and Trent, 1968). Rostral characteristics were used to distinguish juveniles of all three species between 17 mm and 47 mm TL (Williams, 1953, 1984). Adults (>50 mm TL) were differentiated by a series of mor-

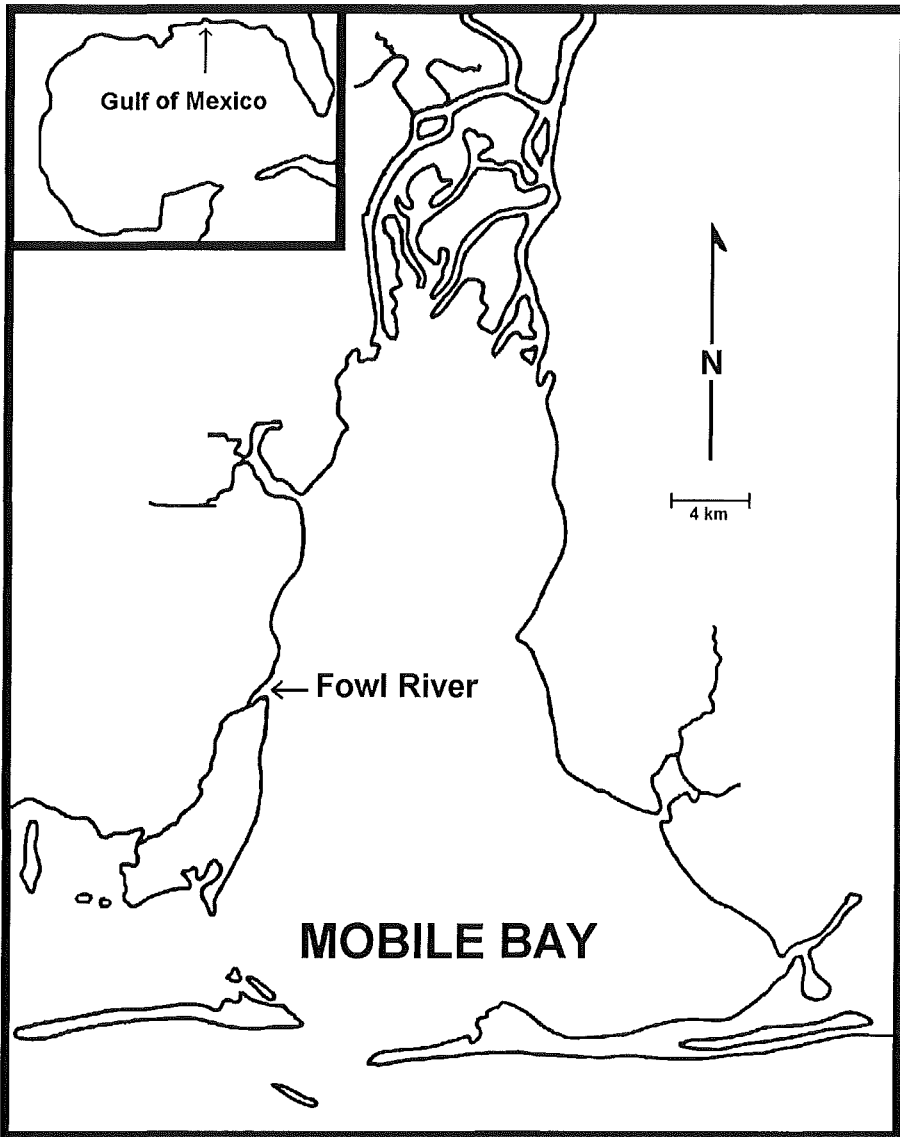


Fig. 1. Study site located at east end of Fowl River along Mobile Bay, AL.

phological (Farfante, 1988) and juvenile rostral characteristics (Williams, 1953). In addition, a representative sample of the collected shrimp was sent to the National Marine Fisheries Service, Galveston Laboratory, for identification and the specimens were used as references.

Statistical Analysis System (SAS) 6.04 was used for all statistical procedures (SAS Institute Inc., 1987). The Shapiro-Wilk statistic, *W*, was computed for shrimp densities and TLs to test for normality (Sokal and Rohlf, 1981). Normality was established for both shrimp densities and TL. In addition, the data were exam-

ined for homogeneity of population variances by Hartley's test (Sokal and Rohlf, 1981). Because homogeneity did not exist between population variances, the data were transformed ($\log y$) in order to stabilize the variances. Shrimp density and TL data for all 1994-95 samples were compared among habitats by an analysis of variance (ANOVA). In order to eliminate variation due to seasonal differences in species abundance, the variable "date" was included in all ANOVA analyses. If a significant ($P \leq 0.05$) difference in population means or TL was observed, a Tukey's honestly significant difference test was performed to differentiate

TABLE 1. Hydrographic and physical data by year for all drop samples taken in Fowl River, AL.

Year	Statistic	Dissolved oxygen (ppm)	Salinity (‰)	Temperature (C)	Substrate penetration (cm)	Water depth (cm)
1994	Mean	8.2	8.2	25.5	8.2	51.5
	n	36	45	45	44	44
	Range	6.4–11.5	3.3–10.0	21.2–28.0	1.0–21.0	34.0–91.0
	SD	2.0	2.6	2.5	5.0	13.3
1995	Mean	8.3	7.8	25.2	7.3	45.6
	n	36	63	63	63	63
	Range	6.5–9.7	4.0–12.4	16.0–30.8	2.3–18.7	22.0–85.0
	SD	1.3	3.3	5.1	3.3	13.3
1994–95 combined	Mean	8.3	8.0	25.3	7.7	48.0
	n	72	108	108	107	107
	Range	6.4–11.5	3.3–12.4	16.0–30.8	1.0–21.0	22.0–91.0
	SD	1.7	3.0	4.2	4.1	13.6

the population means. Pearson correlation analyses were performed to measure the intensity of association observed between shrimp abundance and the measured environmental parameters. Correlation analysis was performed rather than regression because in many instances variables were thought to be interdependent or covariant (e.g., temperature and oxygen concentration). Regression would have been inappropriate because it describes the dependence of one variable on another independent variable (Sokal and Rohlf, 1981).

RESULTS

A total of 108 samples were collected from vegetated and nonvegetated habitats at the east end of Fowl River. During the 11-mo study, a wide range of hydrographic and physical parameters were recorded (Table 1). Seventy-six samples contained at least one of the three penaeid species, with *F. duorarum* (47%) being the most abundant (Table 2). Of 507 penaeid shrimp collected at all three habitats, 303 (60%) were collected in *R. maritima* beds, 152 (30%) in *S. alterniflora*, and 52 (10%) in the

sand/mud habitat (Table 2). Presence of vegetation appeared to have little effect on shrimp size because no significant differences (*F. aztecus*, $P = 0.0877$; *F. duorarum*, $P = 0.3549$; *L. setiferus*, $P = 0.3688$) were observed among habitats (Table 2). Within the sand/mud habitat, *F. aztecus* was significantly ($P = 0.0263$) larger than *F. duorarum* (Table 2). Mean densities were significantly greater in the *R. maritima* beds than in the *S. alterniflora* and sand/mud habitats for both *F. aztecus* ($P = 0.0001$) and *F. duorarum* ($P = 0.0005$) as well as for all three penaeid species ($P = 0.0001$) combined (Fig. 2).

Correlation analyses of the hydrographic and biotic factors with shrimp density at each of the three habitats revealed no clear trend (Table 3). Positive correlations between shrimp density and water temperature, salinity, stem density, wet plant weight, and dry plant weight were expected; however, these relationships were not established (Table 3). Only *F. aztecus* exhibited a significant positive correlation with water temperature (*R. maritima* and *S. alterniflora* habitats) but a negative correlation with *S. alterniflora* stem density. *Farfantepen-*

TABLE 2. Total numbers, percentages, and mean total length (TL) of three penaeid species collected in three different habitats at the east end of Fowl River, AL between July 1994 and Nov. 1995.

Species	Habitat								
	<i>Ruppia maritima</i>			<i>Spartina alterniflora</i>			Sand/mud		
	n	%	TL (mm)	n	%	TL (mm)	n	%	TL (mm)
<i>Farfantepenaeus aztecus</i>	120	39.6	25.2	33	21.7	29.3	14	26.9	34.6 ^a
<i>Farfantepenaeus duorarum</i>	148	48.8	21.6	70	46.1	23.1	23	44.2	18.8 ^a
<i>Litopenaeus setiferus</i>	35	11.6	22.7	49	32.2	25.8	15	28.8	28.1
Total	303	100.0	23.1	152	100.0	25.3	52	100.0	25.7

^a Significant difference at $P \leq 0.05$ (Tukey's honestly significant difference test).

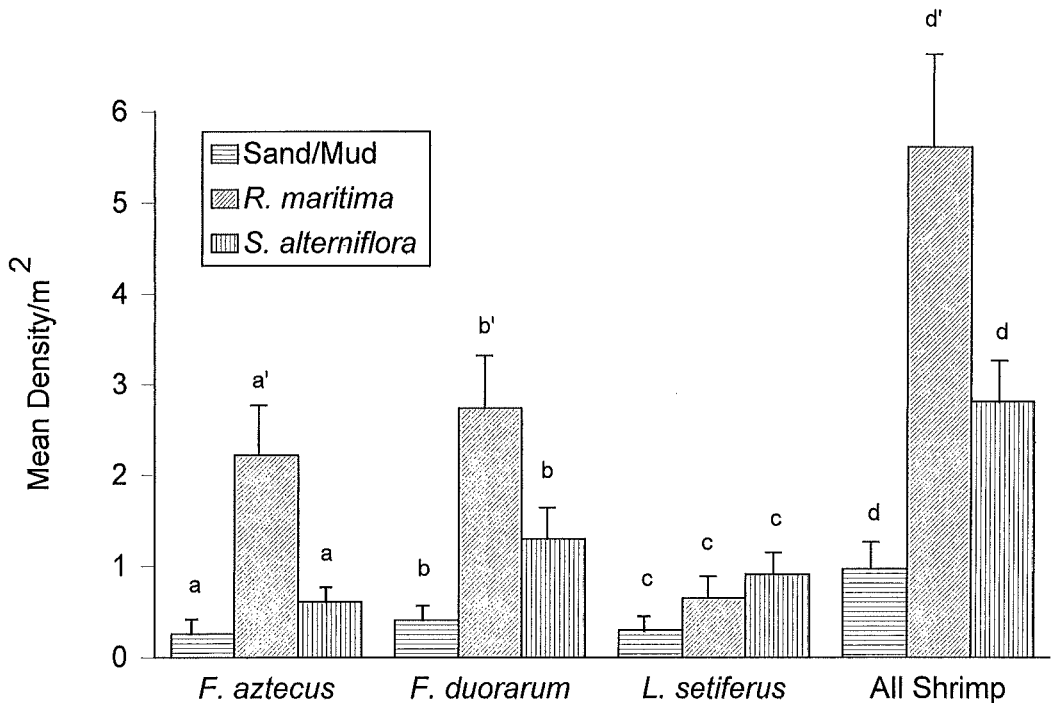


Fig. 2. Mean shrimp density per square meter (\pm SE) of each penaeid species collected at each habitat. Significant differences ($P \leq 0.05$) in mean shrimp density for each species are indicated by letter superscript within each species. Number of samples analyzed per habitat was 36.

aeus duorarum showed a significant negative correlation with salinity (*R. maritima* habitat), and the density of *F. setiferus* was negatively correlated with DO (*S. alterniflora* habitat) (Table 3). Correlation analyses conducted on all data regardless of habitat showed a significant positive correlation between the density of *F. aztecus* and the combined density of all three penaeids with water temperature ($r = 0.25$ and 0.20 , respectively). In addition, *L. setiferus* density exhibited a significant negative correlation ($r = -0.24$) with DO.

DISCUSSION

Previous studies by Zimmerman and Minello (1984), Zimmerman et al. (1984), Minello and Zimmerman (1985), Sheridan (1992), Montague and Ley (1993), Rozas and Reed (1993), and Howe et al. (1999) reported significantly greater shrimp densities in emergent vegetation compared with nonvegetated habitats. However, in the present study, shrimp densities were significantly greater only in the *R. maritima* beds compared with densities in both *S. alterniflora* and the sand/mud habitat. Similarly, Loesch (1965) reported that *F. aztecus* were concentrated in areas containing *R. maritima*

and *Vallisneria* sp. in Mobile Bay. Our results suggest that penaeids may prefer submerged vegetation such as *R. maritima* over an emergent vegetation. Hence, *R. maritima* beds may potentially be more important as a nursery ground than emergent marsh grass. However, other criteria may be involved in establishing these patterns of occurrence. Although all sampling was conducted during high tide, the fringing marsh *S. alterniflora* beds were affected more by tidal fluctuations than were the *R. maritima* beds and nonvegetated areas that were located farther away from the shoreline. Consequently, the distribution patterns of penaeid shrimp may depend on the migration of nekton, which may be affected by tidal fluctuations (Kneib, 1997). For example, the grass shrimp *Palaemonetes pugio*, which prefers submerged aquatic vegetation (Rozas and Odum, 1987), is an important prey item of *L. setiferus* (Kneib, 1997). In addition, subtle physical and chemical alterations to these environments may ultimately influence shrimp distribution and abundance.

The relative importance of salt marsh vegetation to shrimp may also be species specific. For example, Zimmerman and Minello (1984)

TABLE 3. Pearson correlation coefficients for parameters correlated with shrimp densities by habitat from July 1994 to Nov. 1995.

Parameter	Species			All species combined
	<i>Farfantepenaeus aztecus</i>	<i>Farfantepenaeus duorarum</i>	<i>Litopenaeus setiferus</i>	
<i>Ruppia maritima</i> beds				
Dissolved oxygen	0.00	0.12	-0.21	0.01
Dry plant weight	-0.06	-0.05	-0.23	-0.13
Salinity	-0.08	-0.33 ^a	0.04	-0.23
Secchi	0.16	0.14	-0.36	0.13
Substrate penetration	-0.04	0.29	-0.08	0.13
Water depth	-0.16	0.10	0.27	0.05
Water temperature	0.39 ^a	0.09	0.08	0.28
Wet plant weight	0.05	-0.10	-0.25	-0.10
Sand/mud				
Dissolved oxygen	0.22	0.31	-0.09	0.28
Salinity	-0.25	0.05	0.13	-0.01
Secchi	0.11	-0.08	-0.01	0.01
Substrate penetration	-0.05	0.27	-0.24	-0.02
Water depth	-0.17	0.20	0.03	0.05
Water temperature	0.06	0.09	0.25	0.24
<i>Spartina alterniflora</i>				
Dissolved oxygen	-0.05	-0.11	-0.43 ^a	-0.33
Dry plant weight	-0.16	-0.29	0.18	-0.16
Salinity	0.01	0.15	0.07	0.15
Secchi	0.08	-0.08	-0.22	-0.13
Substrate penetration	-0.07	0.31	0.14	0.28
Water depth	-0.05	0.08	0.14	0.13
Water temperature	0.40 ^a	0.04	0.11	0.19
Wet plant weight	-0.01	-0.30	0.00	-0.22
<i>Spartina</i> density (m ²)	-0.28 ^a	-0.23	0.23	-0.12

^a Significant correlation ($P \leq 0.05$).

indicated that for most of the spring, young *F. aztecus* selected estuarine vegetation. Only until mid-March was there selection for unvegetated bottom when few shrimp were present. In contrast, *L. setiferus* selected for vegetation only infrequently and regardless of season, which produces an overall inconsistent distribution for this species in relation to its density in vegetated habitats (Zimmerman and Minello, 1984). Moreover, penaeid shrimp distribution and the use of marsh vegetation or nonvegetated areas by shrimp may also be in response to competitive interactions between co-occurring species. For example, Giles and Zamora (1973) were able to demonstrate the displacement of *L. setiferus* from vegetative to nonvegetated habitat by *F. aztecus* in the laboratory.

Although the presence of vegetation may have a pronounced effect on shrimp density, it appears, on the basis of our results, to have little if any influence on shrimp size. These results are similar to a laboratory study conducted by Minello et al. (1990) that reported no significant effect on selection for habitat struc-

ture by either *L. setiferus* or *F. aztecus* within the size range of 35–84 mm TL.

Other studies indicate that there may be a nutritional advantage in habitat selection; therefore, the value of vegetation may be species specific (Minello and Zimmerman, 1991). Density patterns of *F. aztecus* in estuaries clearly demonstrate the importance of macrophytic vegetation. In a study conducted by Minello and Zimmerman (1991), *F. aztecus* enclosed in cages with access to *S. alterniflora* marsh surface grew faster compared with those in cages placed in nonvegetated bottom. On the other hand, the growth rates of *L. setiferus* did not differ significantly between both habitats. The fact that *L. setiferus* is not an efficient benthic feeder, and hence is unable to exploit a wide variety of plant and animal foods, may partly explain its low affinity for vegetated habitat (Minello and Zimmerman, 1991). A better understanding of the diet and distribution of food items of importance to *L. setiferus* is necessary in order to explain habitat use of this species.

The movement patterns of penaeid shrimp between intertidal marsh edge vegetation and vegetated or unvegetated subtidal bottoms need more study. In a field experiment, pinfish (*Lagodon rhomboides*) were more than twice as abundant in intertidal marshes adjacent to seagrass beds as in those adjacent to unvegetated intertidal bottom and were 90% heavier when allowed access to both habitats compared with those confined to one habitat (intertidal vegetation) or the other (unvegetated bottom) (Irlandi and Crawford, 1997). These findings along with our observations suggest that the combination of submerged aquatic vegetation with emergent marsh provides particularly good habitat for young penaeid shrimp and other estuarine nekton. Understanding interactions involving heterogeneous habitats is necessary if we are to explain density, distribution, movement, and growth of penaeid shrimp in these complex and dynamic estuarine environments.

ACKNOWLEDGMENTS

We thank M. Goodwin, M. McCrory, B. Page, and R. Shaneyfelt for their assistance in collecting and sorting samples. We thank J. Grover and especially T. Munroe for critical review of the manuscript. M. Maceina provided valuable statistical guidance.

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