

Abstract—A density prediction model for juvenile brown shrimp (*Farfantepenaeus aztecus*) was developed by using three bottom types, five salinity zones, and four seasons to quantify patterns of habitat use in Galveston Bay, Texas. Sixteen years of quantitative density data were used. Bottom types were vegetated marsh edge, submerged aquatic vegetation, and shallow non-vegetated bottom. Multiple regression was used to develop density estimates, and the resultant formula was then coupled with a geographical information system (GIS) to provide a spatial mosaic (map) of predicted habitat use. Results indicated that juvenile brown shrimp (<100 mm) selected vegetated habitats in salinities of 15–25 ppt and that seagrasses were selected over marsh edge where they co-occurred. Our results provide a spatially resolved estimate of high-density areas that will help designate essential fish habitat (EFH) in Galveston Bay. In addition, using this modeling technique, we were able to provide an estimate of the overall population of juvenile brown shrimp (<100 mm) in shallow water habitats within the bay of approximately 1.3 billion. Furthermore, the geographic range of the model was assessed by plotting observed (actual) versus expected (model) brown shrimp densities in three other Texas bays. Similar habitat-use patterns were observed in all three bays—each having a coefficient of determination >0.50. These results indicate that this model may have a broader geographic application and is a plausible approach in refining current EFH designations for all Gulf of Mexico estuaries with similar geomorphological and hydrological characteristics.

Manuscript approved for publication 22 December 2003 by Scientific Editor. Manuscript received 20 January 2004 at NMFS Scientific Publications Office. Fish. Bull. 102:264–277 (2004).

A habitat-use model to determine essential fish habitat for juvenile brown shrimp (*Farfantepenaeus aztecus*) in Galveston Bay, Texas

Randall D. Clark

John D. Christensen

Mark E. Monaco

Biogeography Program
Center for Coastal Monitoring and Assessment
National Center for Coastal Ocean Science
National Ocean Service, NOAA
Silver Spring, Maryland 20910
E-mail address (For R. D. Clark): Randy.Clark@noaa.gov

Philip A. Caldwell

Geoffrey A. Matthews

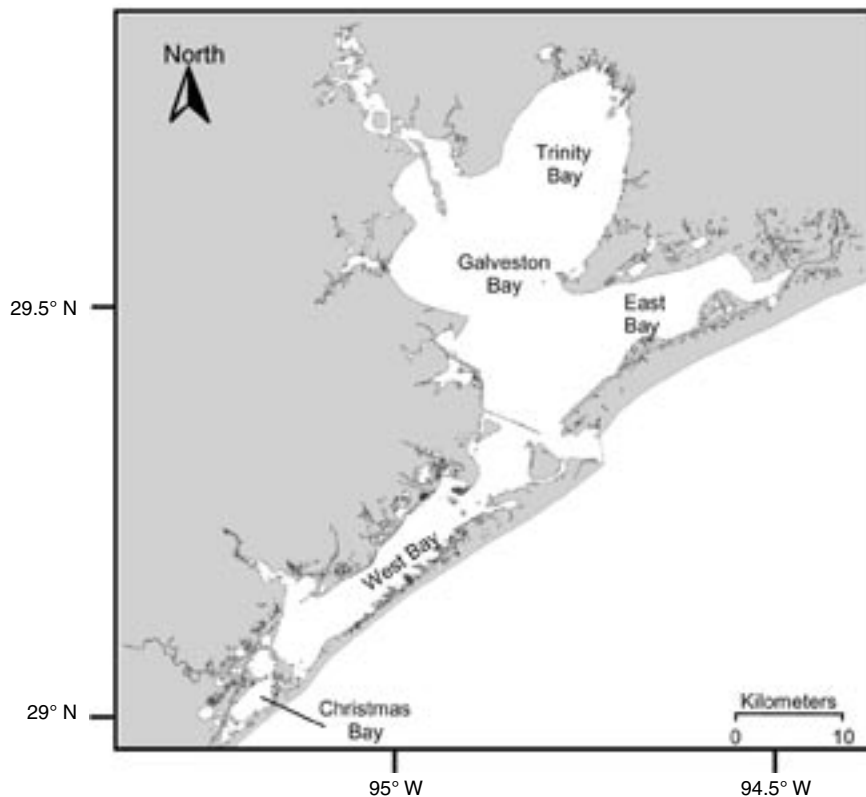
Thomas J. Minello

Fishery Ecology Branch
Galveston Southeast Fisheries Science Center Laboratory
National Marine Fisheries Service, NOAA
Galveston, Texas 77550

Shallow estuarine habitats, whose complexity promotes survival and growth, are used by many young fish and macro-invertebrate species (Boesch and Turner, 1984). A complete understanding of how these habitats sustain species productivity is unknown and has become a focal point of federal fishery management programs. The National Marine Fisheries Service (NMFS) has developed guidelines to identify essential fish habitat (EFH) for all federally managed species based on four levels of available information that encompass the ecological linkages between habitats and fishery production. Examination of habitat-use patterns (habitat-related densities) are needed to determine which habitats are likely to be most essential. These patterns are measurable and can be reasonable indicators of habitat value. Relative habitat values have been estimated by comparing animal densities under the assumption that high densities reflect greater habitat quality and preferred habitat (Percy and Myers, 1974; USFWS, 1981; Zimmerman and Minello, 1984; Sogard and Able, 1991; Baltz et al., 1993).

Considerable bottom-type variation exists in northern Gulf of Mexico estuaries, including intertidal marsh, submerged aquatic vegetation, oyster reef, mangroves, tidal mudflats, and subtidal bay bottom. Within each of these habitats, environmental and structural gradients may affect the functional role or importance of these habitats for particular species. To understand these relationships, fisheries independent monitoring (FIM) data are needed to determine species-habitat affinities that provide evidence that not all habitats are of equal importance for the maintenance of a population (Monaco et al., 1998; Minello 1999; Beck et al., 2001). Habitat affinities may change with spatial and temporal fluctuations of environmental variables, such as salinity and temperature (Copeland and Bechtel, 1974; Baltz et al., 1998).

In this study we developed predictive models that estimate brown shrimp (*Farfantepenaeus aztecus*, formerly *Penaeus aztecus* [see Perez-Farfante and Kensley, 1997]) habitat-use patterns and interactions as a function of density-independent processes in Galveston Bay, Texas. Previous com-

**Figure 1**

Map of Galveston Bay, Texas.

parisons of brown shrimp densities among different bottom types in Louisiana and Texas estuaries have been conducted within limited temporal and spatial scales (Peterson and Turner, 1994; Zimmerman et al., 1984; Zimmerman et al., 1990b; Rozas and Minello, 1998; Minello, 1999).

Our work expands upon these studies by developing a multivariate bottom-type use and environmental model incorporated into a geographic information system (GIS) that provides a spatial assessment of habitat use. In addition, the model is designed to be transferable to other northern Gulf of Mexico estuaries and thus would allow fishery managers to identify the relative importance of habitat types for population maintenance and recruitment into the fishery.

Materials and methods

Geographic setting

The Galveston Bay complex (Fig. 1) encompasses approximately 2020 km² and is one of the largest estuaries in the northern Gulf of Mexico (NOAA, 1989). Comprising several major embayments, including Trinity, Galveston, East, and West bays, the complex contains many smaller interconnecting subbays, rivers, streams, tidal creeks, wetlands, reefs, and tidal flats around its periphery.

The bay bottom is mostly flat and shallow (mean depth is approximately 2 m) and has slightly elevated oyster reefs, elevated dredge material areas, river channels, and deeper dredged navigation channels.

Data collection

Sixteen years (1982–97) of brown shrimp density data were analyzed to quantify areas of potential EFH. A total of 46,080 brown shrimp were captured during this time period with a mean total length of 27.5 mm (Fig. 2). Data from published studies by Czaplá (1991), Minello et al. (1991), Minello and Zimmerman (1992), Minello and Webb (1997), Rozas and Minello (1998), Zimmerman et al. (1984, 1989, 1990a, 1990b), Zimmerman and Minello (1984), and various unpublished sources from the Galveston Laboratory of the National Marine Fisheries Service were combined to comprise a comprehensive density database of associated bottom-type and environmental data that would support model development and GIS analyses. All samples were collected by using a drop trap sampler, described in Zimmerman et al. (1984), which employs large cylinders (1.0 or 2.6 m² area) released from a boom affixed to a boat to entrap organisms. This quantitative technique samples fishes and macro-invertebrates in highly structured shallow-water habitats such as salt marshes, seagrass beds, and oyster reefs where the efficiency of conventional trawl and bag-seine gear is diminished.

Habitat mapping

The underlying spatial framework for incorporating model predictions into the GIS consisted of six maps: four salinity periods, one bathymetric map, and one map defining bottom-type distribution. All GIS maps were developed in Universal Transverse Mercator projection, UTM, datum-1983, zone-15, using ArcView 3.1 (Redlands, CA) software. Each map consisted of 10×10 m grid cells where each cell contained pertinent salinity, depth, or bottom-type information.

Salinity maps were developed from depth-averaged salinity models by using historical Galveston Bay data collected during 1979–90 (Orlando et al., 1993). Four salinity periods were identified to represent typical salinity conditions under average seasonal freshwater inflow: low (March–June), increasing (July), high (August–October), and decreasing (November–February). Five isohalines were developed to display spatial salinity distribution (Christensen et al.¹): 0–0.5, 0.51–5, 5.1–15, 15.1–25, and >25 parts per thousand (ppt) (Fig. 3).

Bottom types from the drop sample database were divided into three categories:

Marsh edge (ME)	intertidal marsh within 5 meters of open water habitat. This category consisted primarily of saltmarsh cord grass (<i>Spartina alterniflora</i>), and smaller proportions of salt meadow-grass (<i>Spartina patens</i>), black needle-rush (<i>Juncus roemerianus</i>), salt grass (<i>Distichlis spicata</i>), bullrushes (<i>Scirpus</i> spp.), and cattails (<i>Typha</i> spp.);
Submerged aquatic vegetation (SAV)	consisted primarily of shoalgrass (<i>Halodule wrightii</i>), wigeongrass (<i>Ruppia maritima</i>), and a sporadic distribution of wild celery (<i>Vallisneria americana</i>);
Shallow non-vegetated bottom (SNB)	generally restricted to waters less than 1 meter deep, including creeks, ponds, shoreline, and open bay habitat.

Density data for other bottom types were limited and were not used in the analysis.

Wetland maps, used in the creation of the bottom type map in the GIS, were obtained from the U.S. Fish and Wildlife Service's national wetland inventory (NWI). The NWI maps were obtained as vector files, created by digitizing boundaries between wetland types from 1989 aerial photographs and classified by using the classification scheme of Cowardin et al. (1979). Regularly flooded emergent vegetation and submerged aquatic vegetation distributions from

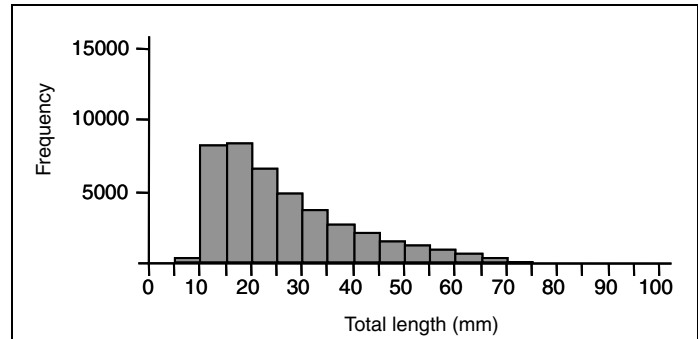


Figure 2

Total-length frequency distribution for juvenile brown shrimp captured in drop traps within Galveston Bay (1982–97).

the NWI maps of Galveston Bay were chosen to represent ME and SAV, respectively, from the drop sample database. Nonvegetated open water areas with depths greater than 1 m were eliminated throughout the bay to reflect depth range from the drop sample database. This elimination was done by plotting approximately 400,000 depth soundings obtained from the National Geophysical Data Center (NGDC), and a bathymetric grid map was developed in 1-m contours with ArcView 3.1 (6 nearest neighbors, power=2). The nonvegetated open water map from NWI was overlaid with the bathymetric map and only those areas within the 1-m contour were extracted and added to the bottom-type map (Fig. 4).

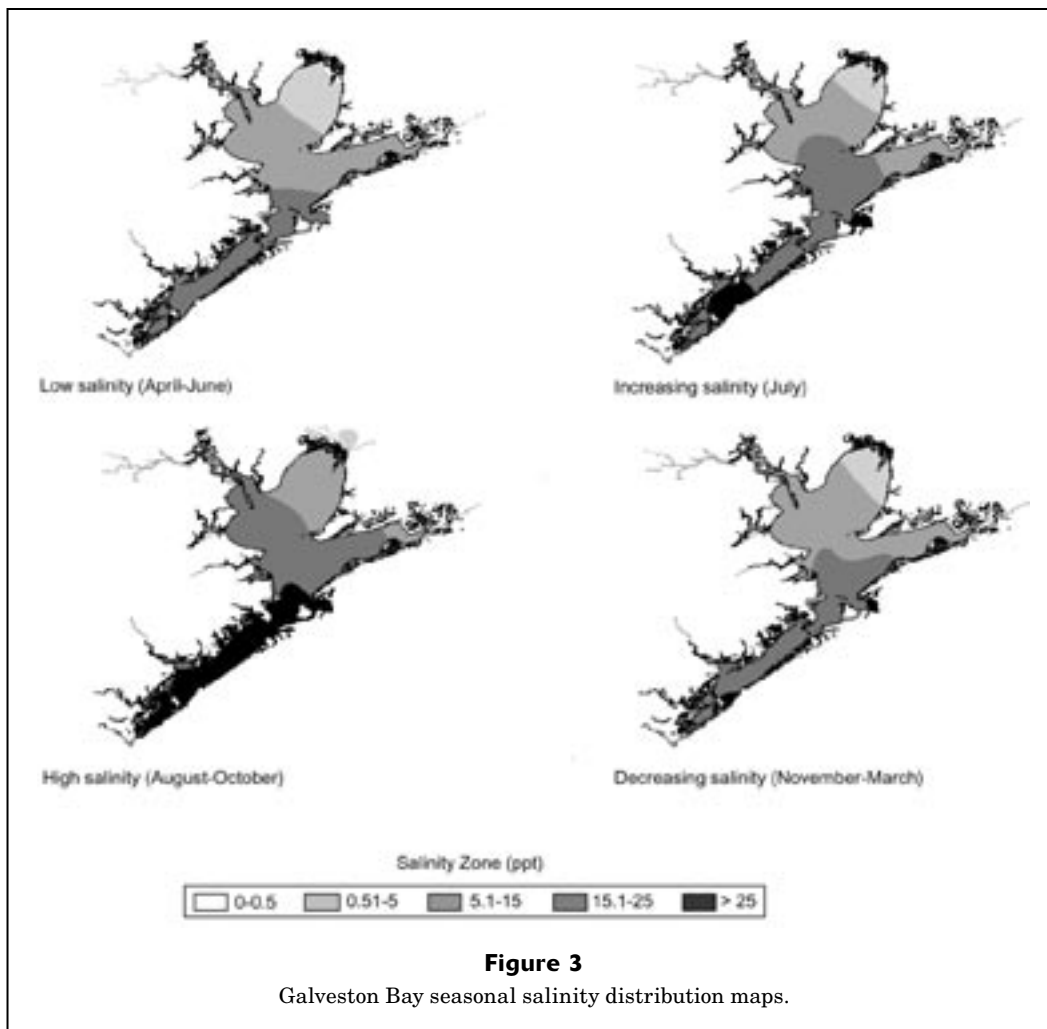
Two maps were used to plot (map) seasonal model predictions, bottom type, and the respective salinity period. The salinity maps did not completely correspond temporally with seasons defined by cluster analysis of *in situ* temperature recordings from the density database. Salinity periods were chosen to correlate with temporal seasons based on maximum monthly overlap to develop the seasonal prediction maps: low salinity (spring); increasing salinity (summer); high salinity (fall); and decreasing salinity (winter).

The total area of Galveston Bay (2020 km²) was determined by combining the total areas for regularly flooded emergent vegetation, irregularly flooded emergent vegetation, SAV, and open water classifications from NWI data. The bottom-type map reflects the study area and totaled 565.6 km² after excluding all areas >1 m in depth and with irregularly flooded emergent vegetation: SNB = 476.2 km², ME = 84.9 km², and SAV = 4.5 km². Initially, NWI's SAV classification totaled 5.7 km², but the final SAV coverage was reduced to 4.5 km² based on SAV mapping by White et al. (1993).

Regression modeling

ANOVA and Tukey-Kramer multiple means comparisons were used to determine if mean density varied significantly by bottom type, salinity zone, and season. Multiple regression with significant predictors was used to predict mean log density. The model was then applied to the GIS maps

¹ Christensen, J. D., T. A. Battista, M. E. Monaco, and C. J. Klein. 1997. Habitat suitability modeling and GIS technology to support habitat management: Pensacola Bay, Florida Case Study, 58 p. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, MD.



to spatially display model predictions in each 10×10 m cell. The resulting values for each cell (predicted mean log density) were converted to numbers/m² and reclassified into 5 percentiles based on their resultant distribution: 0–20%, 21–40%, 41–60%, 61–80%, and 81–100%. All statistical analyses were conducted with JMP statistical software (SAS Institute, Cary, NC).

Due to difficulties in creating continuous salinity and temperature contour maps in GIS, these variables were classified as follows: salinity was classified by one of the five isohaline zones described previously and analyzed as such to determine its influence on brown shrimp distribution; and water temperature was classified by season determined by cluster analysis and analyzed to examine possible temporal effects of brown shrimp distribution.

Spatial patterns were evaluated by comparing the predicted mean log density values with the observed mean log density values from Galveston Bay drop samples. Additionally, the model's predictive performance was assessed by comparing the predicted mean log density values with observed mean log density values from samples collected in Matagorda, Aransas, and San Antonio bays using the

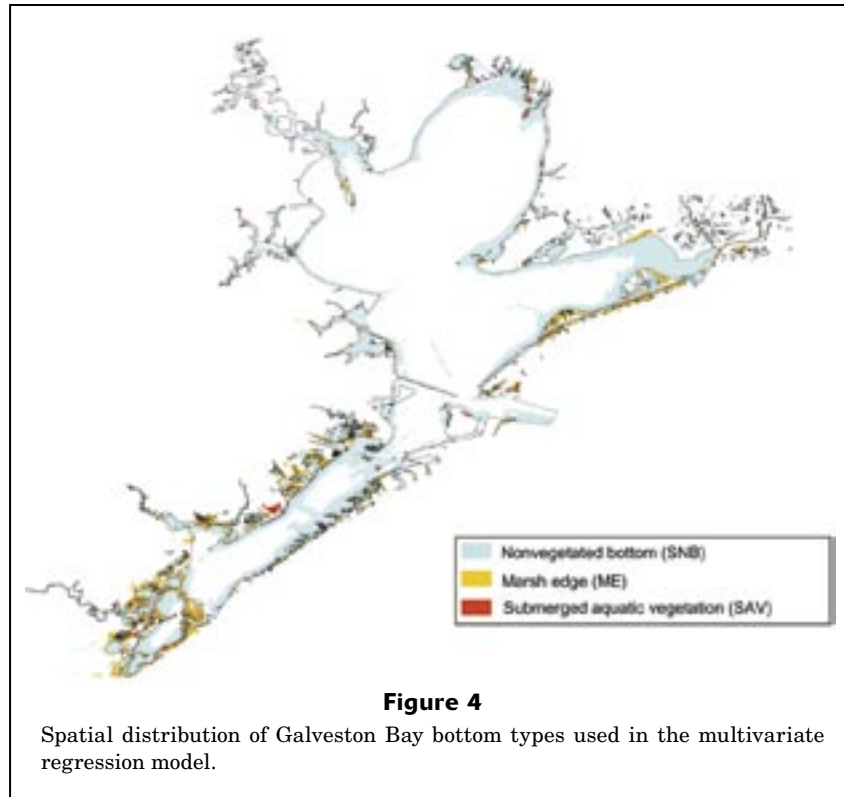
same collection method. With this approach, the assumption was made that brown shrimp modeled in Galveston Bay respond similarly to the range of biotic and abiotic factors in the other bay systems.

Drop sample data collected during July–September 1984 ($n=128$), and April–June 1985 ($n=144$) from West Bay (ME, SNB) and Christmas Bay (ME, SAV, and SNB) were used to examine bottom-type preference or selectivity. Tukey-Kramer multiple comparisons test was used to compare log density patterns in areas where ME and SAV occurred together and in areas where SAV was not present.

Results

Brown shrimp model

ANOVA and Tukey-Kramer pair-wise comparisons showed significant differences in brown shrimp log density between the three bottom types, five salinity zones, and four seasons (Fig. 5). Multiple regression models were run with these discrete variables (Mahon and Smith, 1989;

**Table 1**

Results of the least squares multiple regression model for predicting seasonal brown shrimp density in Galveston Bay, Texas.
* = significant at $P < 0.05$.

Model fit	r^2	Mean	Observations (n)	Mean square error	
	0.73	0.47	47	0.20	
ANOVA					
Source	df	Sum of squares	Mean square	F ratio	Prob > F
Model	17	5.74	0.33	8.43	
Error	29	1.61	0.04		
Total	46	6.90			<0.0001*
Effects					
Source	df	Sum of squares		F ratio	Prob > F
Season	3	1.85		15.43	<0.0001*
Bottom type	2	0.61		7.57	0.0023*
Salinity zone	4	3.15		19.68	<0.0001*
Bottom type × Salinity zone	8	0.86		2.69	0.0242*

Krumgalz et al., 1992; Garrison, 1999) and we tested for possible interactions between the variables. Only the interaction between bottom type and salinity zone yielded

statistically significant results. ANOVA results for the model including the bottom-type and salinity-zone interaction term (Table 1) and variable coefficients (Table 2) fitted

Table 2

Variable coefficients (log +1) derived from brown shrimp multivariate regression model. ME = marsh edge; SAV = submerged aquatic vegetation; SNB = shallow nonvegetated bottom.

y-intercept	Bottom type	Season	Salinity zone	Bottom type × salinity zone
0.335	0.113 (ME)	0.239 (spring)	-0.525 (0–0.5)	-0.104 (ME/0–0.5)
	0.043 (SAV)	0.165 (summer)	-0.147 (0.5–5)	-0.055 (SAV/0–0.5)
	-0.156 (SNB)	-0.045 (fall)	0.079 (5–15)	0.159 (SNB/0–0.5)
		-0.359 (winter)	0.286 (15–25)	0.273 (ME/0.5–5)
			0.307 (>25)	-0.396 (SAV/0.5–5)
				0.123 (SNB/0.5–5)
				-0.030 (ME/5–15)
				0.049 (SAV/5–15)
				-0.018 (SNB/5–15)
				-0.119 (ME/15–25)
				0.288 (SAV/15–25)
				-0.168 (SNB/15–25)
			-0.018 (ME/>25)	
			0.114 (SAV/>25)	
			-0.096 (SNB/>25)	

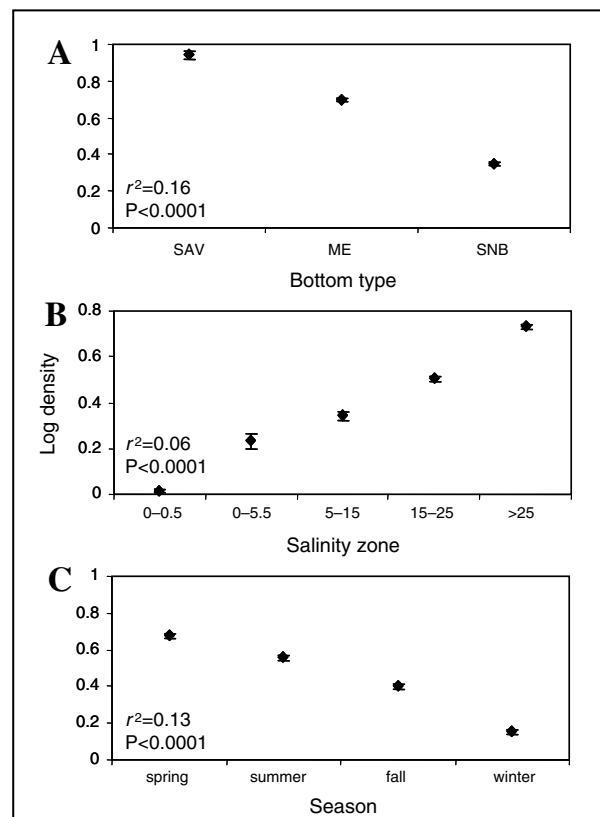
the data well ($r^2=0.73$, $n=47$). Overall, density predictions were highest in the spring, declined through summer and fall, and reached the lowest values during winter (Fig. 6). SNB density predictions were highest in the >25 ppt salinity zone and declined as salinity declined in the estuary. ME density predictions exhibited similar density prediction trends; however, a smaller peak was observed in the 0.5–5 ppt salinity zone. This result may be an artifact of two fall samples that exhibited high density within this salinity zone. Density predictions within SAV were near zero in the lower two salinity zones, peaked in the 15–25 ppt salinity zone, and slightly decreased in the >25 ppt salinity zone.

Model prediction maps

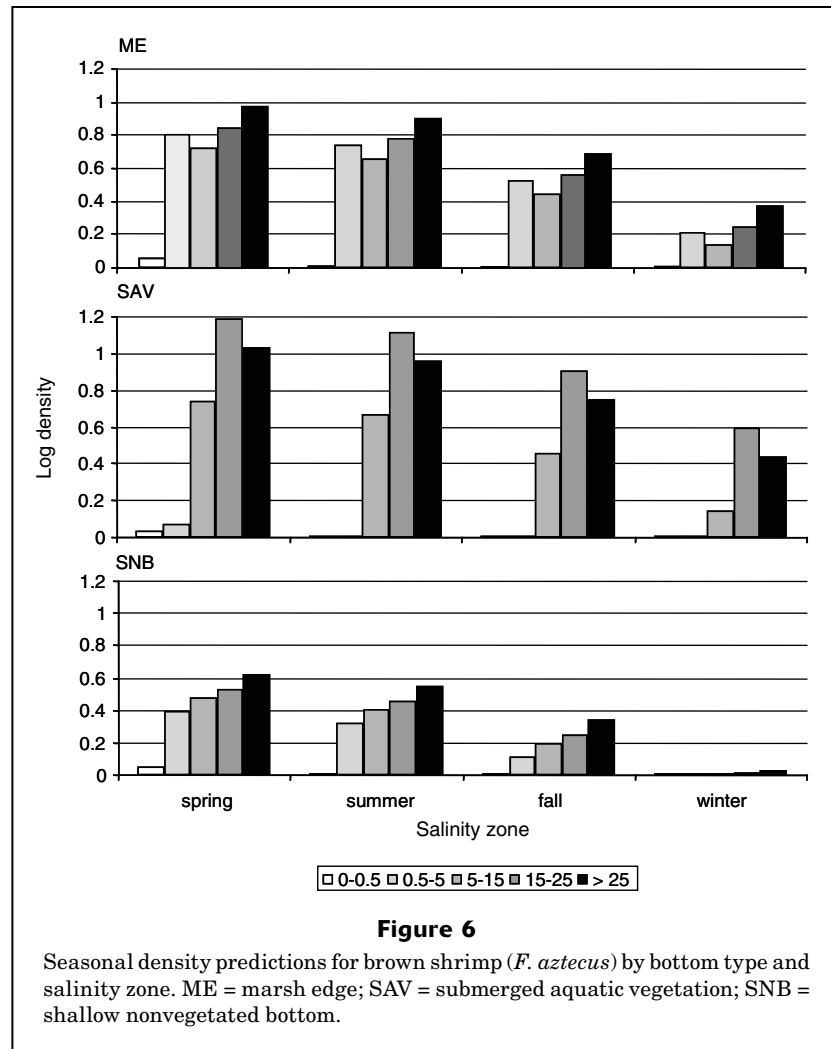
For all seasons, highest density predictions corresponded with ME and SAV bottom types within the region of the bay with highest salinity—Christmas and West bays (Fig. 7). Density predictions decreased within all bottom types as salinity declined in the middle and upper regions of the bay. Spring density predictions were the highest; maximum values were predicted within ME ($6.14/\text{m}^2$) and SAV ($14.49/\text{m}^2$) located in Christmas and West bays (Fig. 7). Density predictions steadily declined through the middle bay and declined to $1/\text{m}^2$ or less within SAV and SNB in the upper region of the bay (Trinity Bay) where salinities were less than 5 ppt. Density predictions during summer, fall, and winter were lower than those observed during the spring but exhibited similar spatial trends—higher predictions within the high salinity vegetated bottom types, and decreasing with decreasing salinity.

Model performance

Spatial patterns were assessed by plotting predicted mean density values from the model and observed mean density

**Figure 5**

Analysis of variance and Tukey–Kramer pair-wise comparisons of brown shrimp density between (A) bottom type, (B) salinity zone and, (C) season. Mean densities are represented by solid diamonds and lines determine standard error. SAV = submerged aquatic vegetation; ME = marsh edge; SNB = shallow non-vegetated bottom.



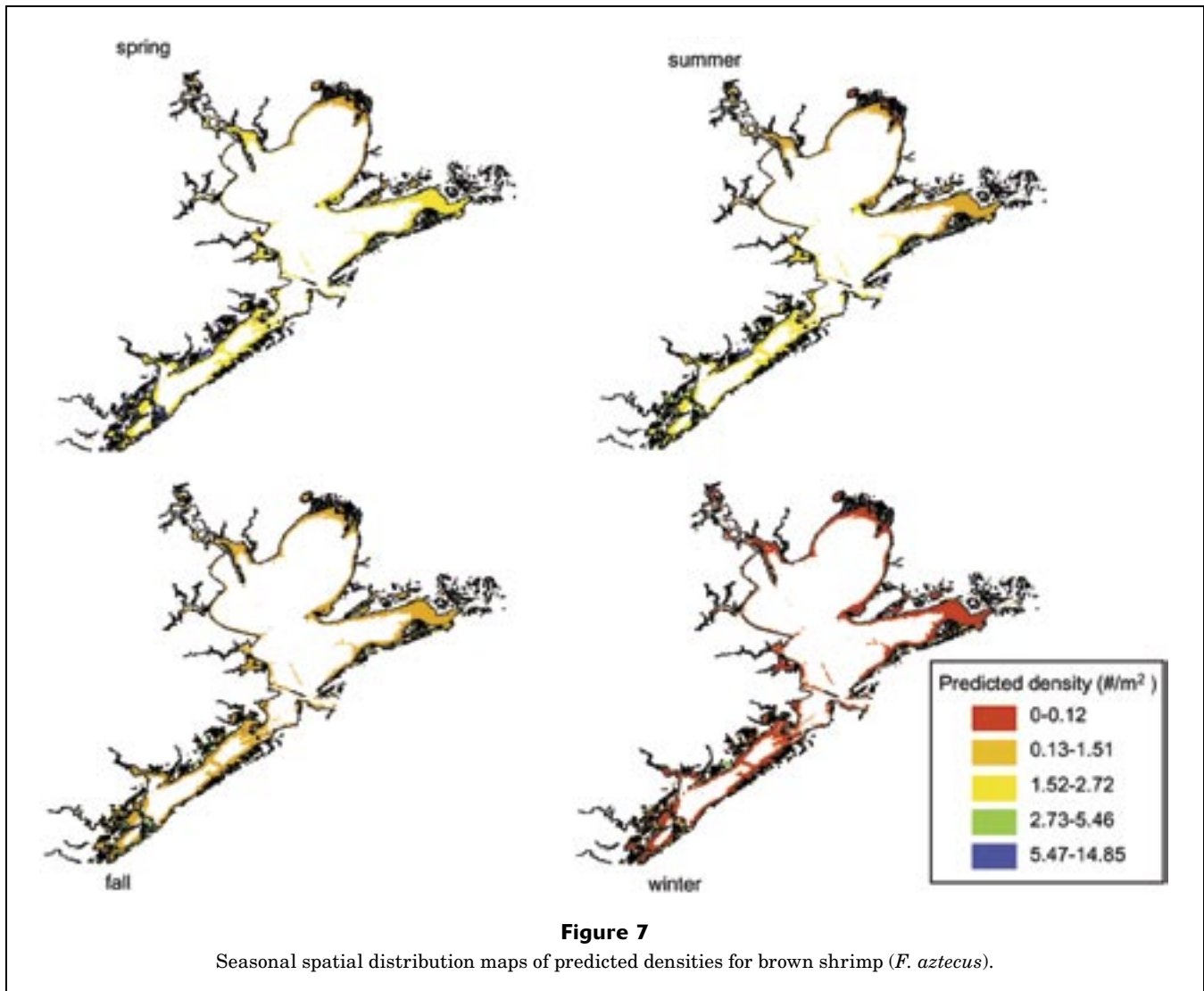
values from drop sample data collected in Galveston Bay. Regression analysis from this plot exhibited a strong positive relationship ($r^2=0.83$, $P<0.0001$) between predicted and observed density data (Fig. 8). This analysis was performed to verify how the model represented the observed density data.

Model performance and transferability were assessed by regressing predicted mean density values from the Galveston Bay model on observed mean density values from drop sample data collected in Matagorda, San Antonio, and Aransas bays (Fig. 9). Regression analysis produced a positive relationship for the entire drop sample data from these bays combined ($r^2=0.56$) and individually: Matagorda— $r^2=0.54$; San Antonio— $r^2=0.57$; and Aransas— $r^2=0.56$. In Aransas and San Antonio bays, brown shrimp densities were greatest during the spring within the SAV bottom type and within salinities >15 ppt. In Matagorda Bay, brown shrimp densities were greatest in the spring within ME bottom types in waters >15 ppt. No SAV samples were taken in this estuarine system.

Use of bottom types

Results from spring (1985) and fall (1984) drop samples within Christmas and West Bay (in lower Galveston Bay) bottom types revealed significantly greater brown shrimp densities in Christmas Bay SAV than adjacent ME and SNB ($P<0.0001$). Brown shrimp densities in West Bay ME were not significantly different from Christmas Bay SAV but were significantly greater than densities within adjacent SNB and Christmas Bay ME and SNB bottom types (Fig. 10).

The model results were also used to roughly estimate an overall population of approximately 1.3 billion juvenile brown shrimp in Galveston Bay during the spring season, by multiplying predicted densities by bottom-type area (Table 3). Total area of bottom types in Galveston Bay were as follows: 4.5 km² (SAV); 84.9 km² of marsh edge (ME); and 1627.2 km² of nonvegetated bottom (29% [476.2 km²] of the latter area was considered SNB). On the basis of predicted densities in different salinity regimes, we estimated that there would be 51.0 million shrimp



in SAV and 858.7 million shrimp in SNB. We used marsh edge densities to estimate 473.5 million shrimp in regularly flooded vegetation or about 55,700 shrimp per hectare of this habitat type.

Discussion

Various factors are considered important in defining nursery areas for juvenile estuarine-dependent organisms; however, the specific contributions of these factors are poorly understood (Beck et al., 2001). Specific combinations of physiochemical conditions and cyclic primary production that are related to food availability, growth, and sanctuary from predation often define optimal environments (Miller and Dunn, 1980). Barry et al. (1999) considered prey availability to be a necessary component defining the nursery function of estuarine habitats.

Shrimp and blue crab production has been correlated with the availability of wetland habitat in estuaries (Turner, 1977; Zimmerman et al., 2000). In the present study, brown shrimp were most abundant in the lower bay where vegetated habitats were most abundant. Zimmerman et al. (1990b) reported that benthic infauna are most abundant in vegetated habitats within lower Galveston Bay and are nutritionally important for penaeids (Zein-Eldin and Renaud, 1986; McTigue and Zimmerman, 1991, 1998). In addition, field and laboratory experiments have shown that brown shrimp growth is positively correlated with the abundance of marsh epiphytes and phytoplankton (Gleason and Zimmerman, 1984).

Most estuarine nekton are adaptable to the highly dynamic environmental conditions exhibited within estuaries (Gifford, 1962; Tagatz, 1971; Zimmerman et al., 1990b). These organisms are commonly found in a wide range of salinities and temperatures and are most affected by sudden changes in these environmental conditions

Table 3

Estimated area (km²) of each bottom type and salinity zone combination sampled during spring (March–May), and estimated brown shrimp population based on spring density predictions from the model. ME = marsh edge; SAV = submerged aquatic vegetation; SNB = shallow nonvegetated bottom.

Bottom type	Salinity zone (ppt)	Bottom type area (km ²)	Density estimate (number/m ²)	Population estimate (millions)	Shrimp/ha. (thousands)
ME	0–0.5	1.4	0.14	0.2	1428
	0.5–5	1.6	5.50	8.8	55,000
	5–15	22.4	4.44	99.4	44,375
	15–25	59.5	6.14	365.3	61,394
	>25	0	8.46	0	0
	Total	84.9		473.5	55,771
SAV	0–0.5	1.0	0.09	0.09	9000
	0.5–5	0.03	0.18	0.005	1667
	5–15	0.02	4.56	0.09	45,000
	15–25	3.5	14.52	50.8	145,142
	>25	0	9.91	0	0
	Total	4.5		51.0	114,680
SNB	0–0.5	29.6	0	0	0
	0.5–5	54.2	1.01	54.7	10,092
	5–15	183.6	1.61	295.6	16,100
	15–25	203.3	2.41	489.9	24,097
	>25	5.5	3.37	18.5	33,636
	Total	476.2		858.7	18,032
Total	565.6			1383.2	24,455

(Christensen et al., 1997). In laboratory experiments, Zein-Eldin and Aldrich (1965) concluded that higher salinities are more favorable for brown shrimp. Salinities of

20 ppt or greater were considered optimum in data from Louisiana (Barrett and Gillespie, 1973).

In the present study, brown shrimp were captured throughout Galveston Bay, but highest densities were observed in the lower bay where salinities were greater than 15 ppt. This spatial trend was further strengthened by greater abundance of vegetated bottom types in the lower portions of the bay, where nearly half of the total marsh edge and 90% of sea-grass beds are located (Fig. 4). These bottom types are regularly inundated and provide stable substrate for brown shrimp prey (epiphytic algae and infauna), whereas seasonal oligohaline marsh and SAV habitats in the upper bay may not promote favorable conditions for prey organisms (Zimmerman et al., 1990b). Therefore, salinity effects and the greater availability of vegetated habitats in the lower bay may work in a complementary manner to provide nursery areas for brown shrimp in Galveston Bay.

Previous attempts to examine spatial patterns of abundance and to determine linkages between organisms and habitat included the development of habitat suitability index (HSI) models. Early methods were derived by the U.S. Fish and Wildlife Service (USFWS) for freshwater species, where the HSI was defined as a numerical index that represented the capacity of a given habitat to support a selected species. The scale of HSI values (0–1.0) reflects a linear relationship between suitability and carrying capacity

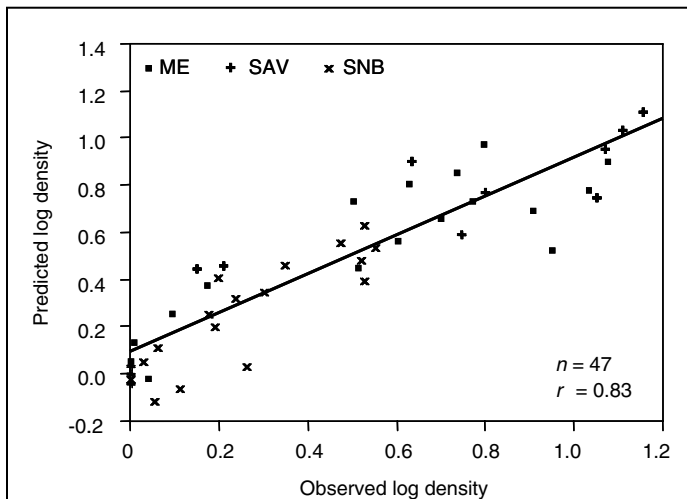
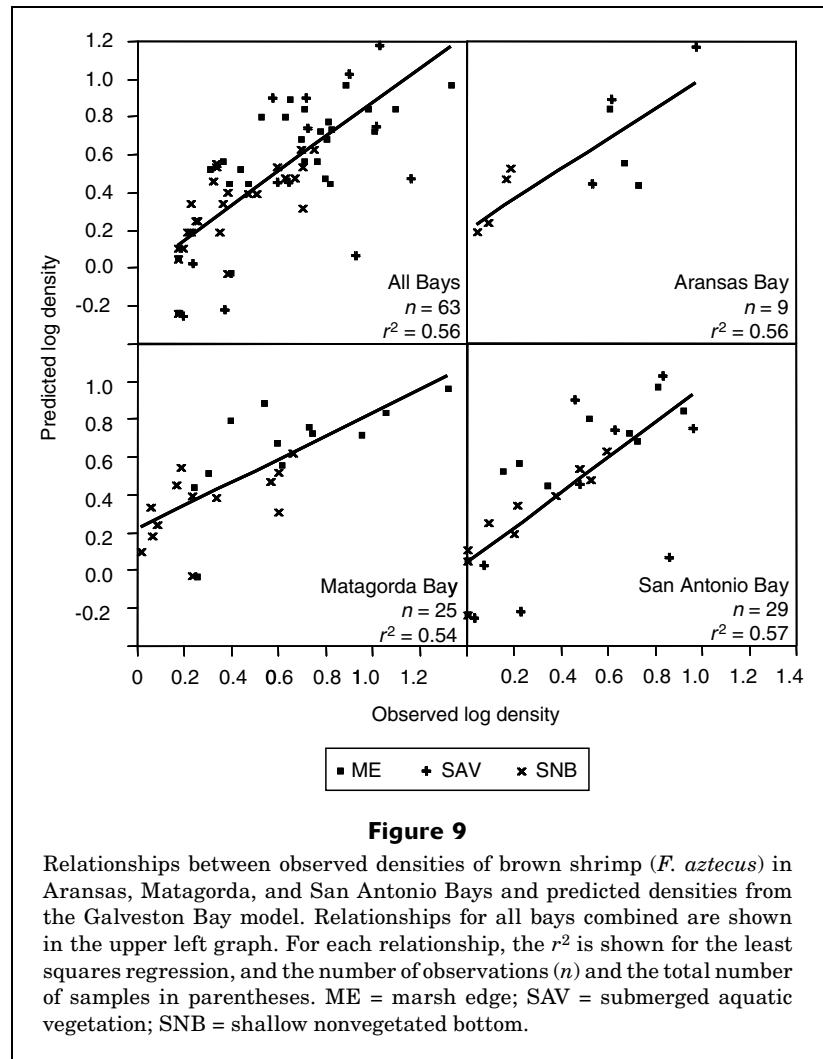


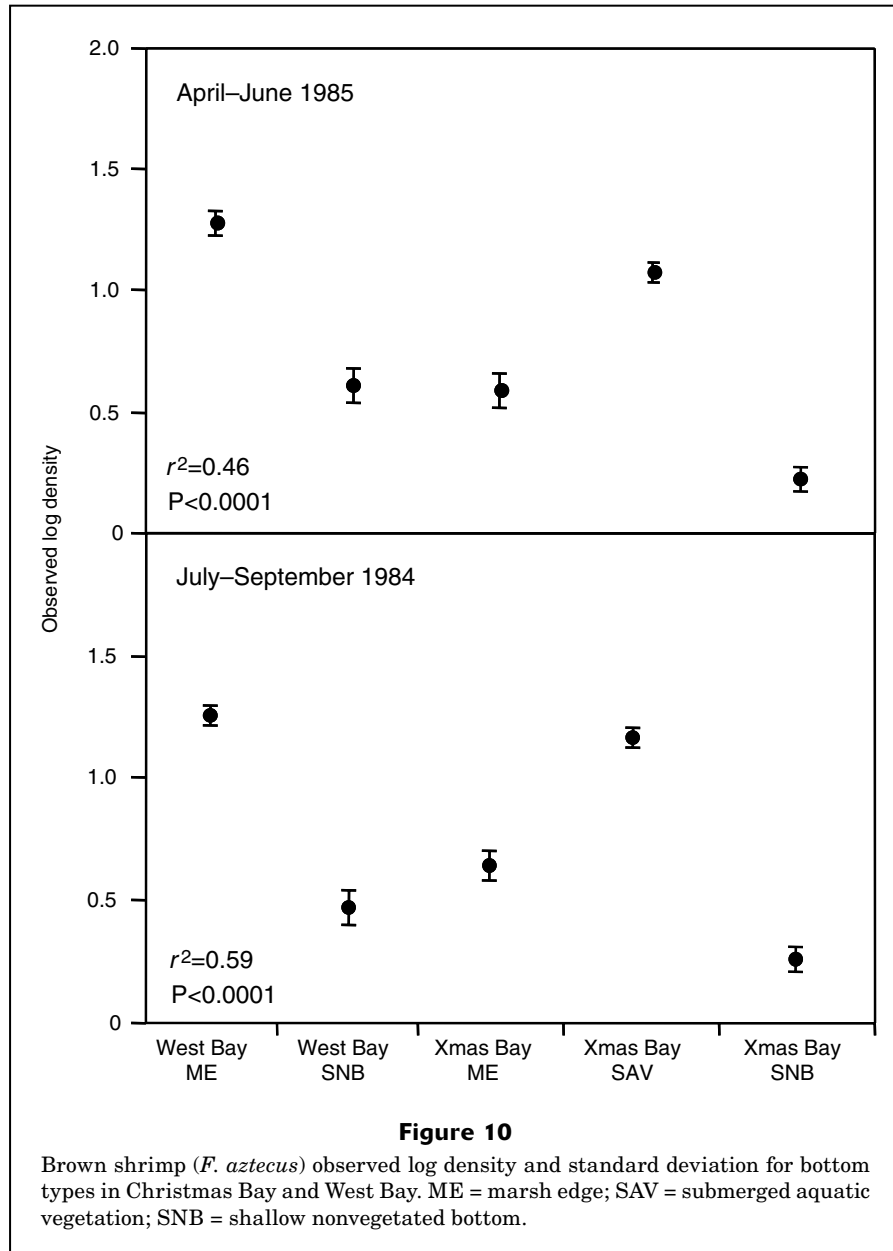
Figure 8

Relationship between predicted and observed densities of brown shrimp (*F. aztecus*) in Aransas, Matagorda and San Antonio bays and predicted densities from the Galveston Bay model. ME = marsh edge; SAV = submerged aquatic vegetation; SNB = shallow nonvegetated bottom.



(USFWS, 1981). Recently, Christensen et al.¹ and Brown et al., 2000, developed suitability indices, based on literature reviews and expert opinion, and raster-based GIS models that produce a spatial view of relative suitability. The Florida Fish and Wildlife Conservation Commission-Marine Research Institute (FMRI) and the National Ocean Service's Center for Coastal Monitoring and Assessment (NOS/CCMA) collaborated to develop a suite of quantitative HSI modeling approaches, using fisheries-independent monitoring catch-per-unit-of-effort (CPUE) data (Rubec et al., 1998, 1999, 2001). These studies used an unweighted geometric mean formula as part of the HSI models to assess overall suitability. This approach assigns equal weight to all factors by using scaled suitability indices as inputs to the model. The regression approach used in this study more appropriately weights density according to the factors in the model and allows a more robust technique to elucidate spatial patterns of habitat use by using actual CPUE data. In addition, the method described in our study can support more complex analyses, such as interaction effects or trophic relationships (or both).

Our ANOVA (Table 1) revealed that season, bottom type, salinity, and the interaction between salinity and bottom type are significant factors that influence the distribution of juvenile brown shrimp in Galveston Bay. The addition of the interaction effect to the model increases the coefficient of determination from 0.63 to 0.73. Without this term in the model, predicted values for brown shrimp density are overestimated compared to the observed density data. Seagrass beds in salinities greater than 15 ppt supported significantly greater densities of brown shrimp than did marsh edge. However, in locations with salinities less than 15 ppt, brown shrimp densities were not significantly different between the two bottom types. These results indicate significantly lower use among all the bottom types analyzed in the fresher portion of the estuary. It is likely that salinity and a combination of other environmental factors directly or indirectly (or directly and indirectly) affect abundance on bottom types and habitat quality in this region. The results indicate that SAV supports greater brown shrimp density than do ME and SNB; however, SAV accounts for less than 1% of the total bottom type within



Galveston Bay. Our data suggest that brown shrimp select SAV over ME when these habitats co-occur (Christmas Bay) and select ME when grassbeds are absent (West Bay) (Fig. 10). Habitat submergence time may explain high SAV use in Christmas Bay (Rozas and Minello, 1998). Subtidal grassbeds may provide more continuous refuge and food supply at both low and high tides than the marsh surface, which can be accessed only during high tides. Additionally, brown shrimp were significantly smaller in SAV ($\bar{x}=17$ mm) than in ME ($\bar{x}=25$ mm) (t -test, $P<0.001$), which may imply ontogenetic changes in habitat or trophic requirements (Conrow et al., 1990; Thomas et al., 1990; Rozas and Minello, 1999). Differences in the use of bottom types may correspond with the population's size distribution at the time of sampling. Additional research is needed to reveal

ontogenetic habitat shifts and relationships among shallow estuarine bottom types (McIvor and Rozas, 1996).

Assessment of the model performance was based on FWS HSI theory where there is a positive relationship between HSI value and the carrying capacity of the available habitat. In the present study, the relationship equates high brown shrimp densities with optimal habitat conditions that promote high carrying capacity. Therefore, low densities would reflect a low suitability or a low capacity to support the population. Comparisons of predicted density with that of observed values from Galveston Bay, and other Texas bays (Figs. 7 and 8) agree with FWS theory by exhibiting a strong relationship between density and suitable habitat as determined from the model. Model performance and transferability were examined by applying

the Galveston Bay model (with interaction term) to brown shrimp density data from Aransas, Matagorda, and San Antonio bays. The results indicated similar habitat-use patterns in Aransas and San Antonio bays; there were higher densities in high-salinity seagrass beds and a declining density as salinity decreased in these bay systems. No SAV samples were taken in Matagorda Bay; however, the model performed well in predicting greater brown shrimp density in higher-salinity marsh-edge habitats. Our analysis suggests that although the empirical model is complex, it is general enough to be applicable across a broader range of habitat types. The model results may, however, have some geographic limitations. For instance, the model may not perform well within the Laguna Madre in south Texas, where freshwater inflow is diminished and hypersaline conditions exist. This conclusion is consistent with Rubec et al. (1999), who used similar methods to demonstrate that HSI models are applicable across estuaries in central Florida. Our results are promising in view of previous efforts where predictions of nekton abundance with empirical models have proven difficult.

Currently, estuarine EFH for most federally managed species in the Gulf of Mexico exists as mapped estimates of relative abundance from NOS's estuarine living marine resources (ELMR) database (GMFMC, 1998; Nelson and Monaco, 2000). The entire Galveston Bay complex was considered EFH for brown shrimp based on ELMR relative abundance data. Our model, generated by using brown shrimp density data, provides a more spatially resolved delineation of EFH (in waters <1 m depth) for brown shrimp <100 mm.

The analyses described in the present study focused on bottom types in waters less than 1 m which comprise about 25% of the available habitat in Galveston Bay. Trawl CPUE data from Texas Parks and Wildlife Department (TPWD) were analyzed to compare abundance and distribution patterns in waters >1 m. These trawls (3.8-cm stretched mesh) do not capture small size classes (<50 mm TL) of brown shrimp efficiently; thus the trawl analysis provides information only on larger size classes (mean=89 mm). However, few individuals in smaller size classes of shrimp (<50 mm TL) are likely to inhabit deeper bay waters; density estimates of small nekton, including shrimp, decline rapidly with depth (Mock, 1966; Baltz et al., 1993; Rozas, 1993; Rozas and Zimmerman, 2000). In addition, these CPUE values are likely underestimates of brown shrimp density; catch efficiency for shrimp in trawls can be roughly estimated at 20% (Zimmerman et al., 1984; Rozas and Minello, 1997). Despite these problems, shrimp abundance estimates in water >1 m appear low; abundance estimates from TPWD trawl data in deep open-bay waters were almost two orders of magnitude lower than densities in shallow water habitats.

Brown shrimp population estimates from the present study (Table 3) were highest in the lower bay (224,568 per ha.). Seagrass beds accounted for more than 60% of the estimate (145,142 per ha.) and marsh edge and nonvegetated bottom types combined were estimated at approximately 79,000 per ha. As noted earlier, the NWI regularly flooded emergent vegetation classification is not all marsh edge but

is a complex of SNB, marsh edge, and inner marsh with different shrimp densities associated with each of these microhabitat types. Minello and Rozas (in press) modeled small-scale density patterns on the marsh surface in a 437-ha. salt marsh of lower Galveston Bay and applied these data to a GIS analysis of marsh landscape patterns. In this highly fragmented marsh complex that was 37% SNB and 63% marsh vegetation, they estimated brown shrimp populations at 37,000 per ha. We could not estimate brown shrimp populations in irregularly flooded emergent vegetation, although the areal coverage of this habitat type was large. Compared with the regularly flooded wetlands, overall densities of brown shrimp in these irregularly flooded systems should be relatively low because of higher marsh surface elevations (Rozas and Reed, 1993; Minello et al., 1994; Minello and Webb, 1997) and restricted tidal access (Rozas and Minello, 1999). We also were unable to assess the contribution of oyster reef as habitat for brown shrimp. Coen et al. (1999), however, reported brown shrimp on oyster reefs, and Powell (1993) estimated that there was 108 km² of this habitat in Galveston Bay.

Our modeling results provide evidence that estuarine habitat types are discriminately used by brown shrimp. The success of transferring our empirical model from Galveston Bay to adjacent bay systems in Texas suggests that the model has a broad application and can possibly be used to simulate patterns of habitat use in systems that lack sufficient density data. Continuing collections of density data in Gulf estuaries are necessary to make additional interestuary comparisons and to determine whether these habitat-use patterns differ throughout the distributional range of brown shrimp. The use of other habitat types also needs to be examined. For example, other available habitat types from Galveston Bay, such as oyster reef and inner marsh, and from other Gulf estuaries, such as mangrove, calcium carbonate rock formations, and sponge communities, may be important habitats for this federally managed species.

Acknowledgments

Funding and support for this work was provided by the Southeast Region of NOAA's National Marine Fisheries Service, The Southeast Fisheries Science Center, and the Biogeography Program of the National Ocean Service. We would like to thank Pete Sheridan, Lawrence Rozas, Ken Heck, and Roger Zimmerman for providing access to published and unpublished data sets. John Boyd helped with construction of the nekton density database.

Literature cited

- Baltz, D. M., J. W. Fleeger, C.F. Rakocinski, and J. N. McCall. 1998. Food, density, and microhabitat: factors affecting growth and recruitment potential of juvenile saltmarsh fishes. *Environ. Biol. Fish.* 53:89-103.
- Baltz, D. M., C. Rakocinski, and J. W. Fleeger. 1993. Microhabitat use by marsh-edge fishes in a Louisiana estuary. *Environ. Biol. Fish.* 36:109-126.

- Barret, B. B., and M. C. Gillespie.
1973. Primary factors which influence commercial shrimp production in coastal Louisiana. *La. Wild Life Fish. Comm., Tech. Bull.* 9, 28 p.
- Barry, J. P., M. M. Yoklavich, G. M. Cailliet, D. A. Ambrose, and B. S. Antrim.
1999. Trophic ecology of the dominant fishes in Elkhorn Slough, California, 1974–1980. *Estuaries* 19:115–138.
- Beck, M. W., K. L. Heck Jr., K. Able, D. Childers, D. Eggleston, B. M. Gillanders, B. Halpern, C. Hays, K. Hoshino, T. Minello, R. Orth, P. Sheridan, and M. Weinstein.
2001. The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates. *Bioscience* 51:633–641.
- Boesch, D. F., and R. E. Turner.
1984. Dependence of fishery species on salt marshes: The role of food and refuge. *Estuaries* 7:460–468.
- Brown, S. K., K. R. Buja, S. H. Jury, M. E. Monaco, and A. Banner.
2000. Habitat suitability index models for eight fish and invertebrate species in Casco and Sheepscot Bays, Maine. *N. Am. J. Fish. Manag.* 20:408–435.
- Christensen, J. D., M. E. Monaco, and T. A. Lowery.
1997. An index to assess the sensitivity of Gulf of Mexico species to changes in estuarine salinity regimes. *Gulf Res. Rep.* 9(4):219–229.
- Coen, L. D., M. W. Luckenbach, and D. L. Breitburg.
1999. The role of oyster reefs as essential fish habitat: a review of current knowledge and some new perspectives. *In Fish habitat: essential fish habitat and rehabilitation* (L. R. Benaka, ed.), p. 438–454. *Am. Fish. Soc., Symposium* 22, Bethesda, MD.
- Conrow, R. A., V. Zale, and R. W. Gregory.
1990. Distributions and abundances of early life stages of fishes in a Florida lake dominated by aquatic macrophytes. *Trans. Am. Fish. Soc.* 119:521–528.
- Copeland, B. J., and T. J. Bechtel.
1974. Some environmental limits of six gulf coast estuarine organisms. *Contrib. Mar. Sci.* 18:169–204.
- Cowardin, L. J., V. Carter, F. C. Golet, and E. T. Laroe.
1979. Classification of wetlands and deepwater habitats of the United States. *U.S. Fish Wildl. Serv. Biol. Serv. Program FWS/OBS-79/31*, 131 p.
- Czapla, T. E.
1991. Diets and prey selection of pinfish and southern flounder in a *Halodule wrightii* seagrass meadow. Ph.D. diss., 119 p. Texas A&M Univ., College Station, TX
- Garrison, L. P.
1999. Vertical migration behavior and larval transport in brachyuran crabs. *Mar. Ecol. Prog. Ser.* 176:103–113.
- Gifford, C. A.
1962. Some aspects of osmotic and ionic regulation in the blue crab, *Callinectes sapidus*, and the ghost crab, *Ocypode albicans*. *Publ. Inst. Mar. Sci.* 8:97–125.
- Gleason, D. F., and R. J. Zimmerman.
1984. Herbivory potential of postlarval brown shrimp associated with salt marshes. *J. Exp. Mar. Biol. Ecol.* 84:235–246.
- GMFMC (Gulf of Mexico Fishery Management Council).
1998. Generic amendment for addressing essential fish habitat requirements. Prepared by the GMFMC, October 1998, 34 p.
- Krumgalz, B. S., G. Fainshtein, and A. Cohen.
1992. Grain size effect on anthropogenic trace metal and organic matter distribution in marine sediments. *Sci. Total Environ.* 116(1–2):15–30.
- Mahon, R. and R. W. Smith.
1989. Comparison of species composition in a bottom trawl calibration experiment. *J. Northw. Atl. Fish. Sci.* 9:73–79.
- McIvor, C. C., and L. P. Rozas.
1996. Direct nekton use of intertidal saltmarsh habitat and linkage with adjacent habitats: a review from the south-eastern United States. *In Estuarine shores: evolution, environments and human alterations* (K. F. Nordstrom and C. T. Roman, eds.), p. 311–334. John Wiley and Sons, Ltd., Chichester, England.
- McTigue, T. A., and R. J. Zimmerman.
1991. Carnivory versus herbivory in juvenile *Penaeus setiferus* (Linnaeus) and *Penaeus aztecus* (Ives). *J. Exp. Mar. Biol. Ecol.* 15:1–16.
1998. The use of infauna by juvenile *Penaeus aztecus* (Ives) and *P. setiferus* (Linnaeus). *Estuaries* 21:160–175.
- Miller, J. M., and M. L. Dunn.
1980. Feeding strategies and patterns of movement in juvenile estuarine fishes. *In Estuarine perspectives* (V. S. Kennedy, ed.), p. 437–448. Academic Press, New York, NY.
- Minello, T. J.
1999. Nekton densities in shallow estuarine habitats of Texas and Louisiana and the identification of essential fish habitat. *In Fish habitat: essential fish habitat and rehabilitation* (L. Benaka, ed.), p. 43–75. *Am. Fish. Soc.*, Bethesda, MD.
- Minello, T. J., and L. P. Rozas.
In press. Nekton populations in Gulf Coast wetlands: fine-scale spatial distributions, landscape patterns, and restoration implications. *Ecol. Appl.*
- Minello, T. J., and J. W. Webb Jr.
1997. Use of natural and created *Spartina alterniflora* salt marshes by fishery species and other aquatic fauna in Galveston Bay, Texas, USA. *Mar. Ecol. Prog. Ser.* 151:165–179.
- Minello, T. J., J. W. Webb Jr., R. J. Zimmerman, R. B. Wooten, J. L. Martinez, T. J. Baumer, and M. C. Patillo.
1991. Habitat availability and utilization by benthos and nekton in Hall's Lake and West Galveston Bay. NOAA Tech. Memo. NMFS-SEFC-275, 37 p.
- Minello, T. J., and R. J. Zimmerman.
1992. Utilization of natural and transplanted Texas salt marshes by fish and decapod crustaceans. *Mar. Ecol. Prog. Ser.* 90:273–285.
- Minello, T. J., R. J. Zimmerman, and R. Medina.
1994. The importance of edge for natant macrofauna in a created salt marsh. *Wetlands* 14:184–198.
- Mock, C. R.
1966. Natural and altered estuarine habitats of penaeid shrimp. *Proceedings of the Gulf and Caribbean Fisheries Institute, 19th annual session*, p. 86–98. Gulf and Caribbean Fish. Inst., Fort Pierce, FL.
- Monaco, M. E., S. B. Weisberg, and T. A. Lowery.
1998. Summer habitat affinities of estuarine fish in US mid-Atlantic coastal systems. *Fish. Manag. Ecol.* 5:161–171.
- NOAA (National Oceanic and Atmospheric Administration).
1989. *Estuaries of the United States: vital statistics of a natural resource base*, 79 p. Strategic Environmental Assessments Division, National Ocean Service (NOS), NOAA, Rockville, MD.
- Nelson, D. M., and M. E. Monaco.
2000. National overview and evolution of NOAA's estuarine living marine resources (ELMR) Program. NOAA Tech. Memo. NOS NCCOS CCMA 144, 60 p. Center for

- Coastal Monitoring and Assessment, NOS, NOAA, Silver Spring, MD.
- Orlando, S. P. Jr., L. P. Rozas, G. H. Ward, and C. J. Klein.
1993. Salinity characteristics of Gulf of Mexico estuaries, 209 p. Office of Ocean Resources and Conservation and Assessment, NOAA, Silver Spring, MD.
- Pearcy, W. G., and S. S. Myers.
1974. Larval fishes of Yaquina Bay, Oregon: a nursery ground for marine fishes? *Fish. Bull.* 72:201–213.
- Perez-Farfante, I., and B. Kensley.
1997. Penaeoid and sergestoid shrimps and prawns of the world; keys and diagnoses for the families and genera. *Memoires du Muséum National d'Histoire Naturelle*, tome 175, 233 p.
- 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* 17:235–262.
- Powell, E. N.
1993. Status and trends analysis of oyster reef habitat in Galveston Bay. *In* Proceeding, second state of the bay symposium (R. W. Jensen et al., eds.), p. 207–209. Galveston Bay National Estuary Program, Houston, TX.
- Rozas, L. P.
1993. Nekton use of salt marshes of the southeast region of the United States. *In* Proc. 8th symp. coastal and ocean management (O. T. Magoon, W. S. Wilson, H. Converse, and L. T. Tobin, eds.), p. 528–537. Coastal Zone '93 Conference, Am. Soc. Civil Eng., New Orleans, LA.
- Rozas, L. P., and T. J. Minello.
1997. Estimating densities of small fishes and decapod crustaceans in shallow estuarine habitats: a review of sampling design with focus on gear selection. *Estuaries* 20: 199–213.
1998. Nekton use of salt marsh, seagrass, and nonvegetated habitats in a south Texas (USA) estuary. *Bull. Mar. Sci.* 63(3):481–501.
1999. Effects of structural marsh management on fishery species and other nekton before and during a spring drawdown. *Wetl. Ecol. Manag.* 7: 121–139.
- Rozas, L. P., and D. J. Reed.
1993. Nekton use of marsh-surface habitats in Louisiana (USA) deltaic salt marshes undergoing submergence. *Mar. Ecol. Prog. Ser.* 96:147–157.
- Rozas, L. P., and R. J. Zimmerman.
2000. Small-scale patterns of nekton use among marsh and adjacent shallow nonvegetated areas of the Galveston Bay estuary, Texas (USA). *Mar. Ecol. Prog. Ser.* 193:217–239.
- Rubec, P. J., M. S. Coyne, R. H. McMichael Jr., and M. E. Monaco.
1998. Spatial methods being developed in Florida to determine essential fish habitat. *Fisheries* 23(7):21–25.
- Rubec, P. J., J. C. W. Bexley, H. Norris, M. S. Coyne, M. E. Monaco, S. G. Smith, and J. S. Ault.
1999. Suitability modeling to delineate habitat essential to sustainable fisheries. *Am. Fish. Soc. Symp.* 22:108–133.
- Rubec, P. J., S. G. Smith, M. S. Coyne, M. White, A. Sullivan, T. MacDonald, R. H. McMichael Jr., M. E. Monaco, and J. S. Ault.
2001. Spatial modeling of fish habitat suitability in Florida estuaries. *In* Spatial processes and management of marine populations (G. H. Kruse, N. Bez, A. Booth, M. W. Dorn, S. Hills, R. N. Lipcus, D. Pelletier, C. Roy, S. J. Smith, and D. Witherell, eds.), p. 1–18. Sea Grant report AK-SG-01-02. Univ. Alaska, Fairbanks, AK.
- Sogard, S. M., and K. W. Able.
1991. A comparison of eelgrass, sea lettuce macroalgae, and marsh creeks as habitats for epibenthic fishes and decapods. *Estuar. Coast. Shelf Sci.* 33:501–519.
- Tagatz, M. E.
1971. Osmoregulatory ability of blue crabs in different temperature-salinity combinations. *Ches. Sci.* 12:14–17.
- Thomas, J. L., R. J. Zimmerman, and T. J. Minello.
1990. Abundance patterns of juvenile blue crabs (*Callinectes sapidus*) in nursery habitats of two Texas bays. *Bull. Mar. Sci.* 46:115–125.
- Turner, R. E.
1977. Intertidal vegetation and commercial yields of penaeid shrimp. *Trans. Am. Fish. Soc.* 106:411–416.
- USFWS (U.S. Fish and Wildlife Service).
1981. Standards for the development of habitat suitability index models for use with the habitat evaluation procedures. Report 103, ESM release 1-81, 66 p. Division of Ecological Services, USFWS, Washington, DC.
- White, W. A., T. A. Tremblay, E. G. Wermund Jr., and L. R. Handley.
1993. Trends and status of wetland and aquatic habitats in the Galveston Bay System, Texas, 225 p. Galveston Bay National Estuary Program, Galveston, TX.
- Zein-Eldin, Z. P., and D. V. Aldrich.
1965. Growth and survival of postlarval *Penaeus aztecus* under controlled conditions of temperature and salinity. *Biol. Bull. (Woods Hole)* 129:199–216.
- Zein-Eldin, Z. P., and M. L. Renaud.
1986. Inshore environmental effects on brown shrimp, *Penaeus aztecus*, and white shrimp, *P. setiferus*, populations in coastal waters, particularly Texas. *Mar. Fish. Rev.* 48:9–19.
- Zimmerman, R. J., and T. J. Minello.
1984. Densities of *Penaeus aztecus*, *P. setiferus* and other natant macrofauna in a Texas salt marsh. *Estuaries* 7: 421–433.
- Zimmerman, R. J., T. J. Minello, T. J. Baumer, and M. C. Castiglione.
1989. Oyster reef as habitat for estuarine macrofauna. NOAA Tech. Memo., NMFS-SEFC-249, 16 p.
- Zimmerman, R. J., T. J. Minello, M. C. Castiglione, and D. L. Smith.
1990a. The use of *Juncus* and *Spartina* marshes by fisheries species in Lavaca Bay, Texas, with reference to effects of floods. NOAA Tech. Memo., NMFS-SEFC-251, 40 p.
- 1990b. Utilization of marsh and associated habitats along a salinity gradient in Galveston Bay. NOAA Tech. Memo., NMFS-SEFC-250, 68 p.
- 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. *In* Concepts and controversies in tidal marsh ecology (M. P. Weinstein and D.A. Kreeger, eds.), p. 293–314. Kluwer Academic Publ., Dordrecht, The Netherlands.
- Zimmerman, R. J., T. J. Minello, and G. Zamora.
1984. Selection of vegetated habitat by *Penaeus aztecus* in a Galveston Bay salt marsh. *Fish. Bull.* 82:325–336.