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[Article]

Population and Production Estimates for Decapod Crustaceans in Wetlands of Galveston Bay, Texas

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Abstract.—The value of wetlands is reflected in the relative abundance and production of nekton, but these population variables have been difficult to estimate because of sampling problems, landscape complexity, tidal dynamics, and limited information on growth and mortality. We combined a landscape analysis of land–water patterns in regularly flooded wetlands of lower Galveston Bay, Texas, with data on small-scale (1–50-m) distribution patterns of nekton over the marsh surface to estimate population abundances of juvenile brown shrimp *Farfantepenaeus aztecus*, white shrimp *Litopenaeus setiferus*, and blue crab *Callinectes sapidus*. Using information on size frequencies, size–weight relationships, and growth rates, we estimated the wet biomass and production of these species from salt marshes and open-water habitats. In 17,673 ha of marsh complex (vegetation with a 150-m water buffer) in lower Galveston Bay, we estimated the standing crops (number/ha) at 19,382 for brown shrimp, 17,406 for white shrimp, and 16,726 for blue crabs, or 3.0, 2.2, and 4.2 times the standing crop estimates for shallow, open bay water. Annual production from the marsh complex was substantially higher than for open water and was estimated at 128 kg/ha for brown shrimp, 109 kg/ha for white shrimp, and 170 kg/ha for blue crabs.

Juvenile decapod crustaceans are common inhabitants of tidally flooded wetlands in the northwestern Gulf of Mexico. The value of these wetlands as nurseries (Beck et al. 2001) or as essential fish habitat (Schmitten 1999) is dependent upon their contribution to species productivity. Estimates of productivity generally require information on population size and biomass (Kneib 2003), but population estimates in these wetland complexes are difficult to obtain because vegetative structure makes sampling difficult, nekton are not evenly distributed across wetland landscapes, spatial distributions change with tidal inundation, and landscape topography can be highly complex (Kneib 2000; Minello and Rozas 2002; Minello et al. 2003). In this study, we continue our efforts to estimate nekton population sizes within shallow wetland habitats of the Galveston Bay system in Texas by combining regression models that describe fine-scale (1–50 m) density distributions with landscape analyses of land–water patterns.

Our study focuses on populations of juvenile brown shrimp *Farfantepenaeus aztecus*, white shrimp *Litopenaeus setiferus*, and blue crab *Callinectes sapidus* in polyhaline marshes of lower Galveston Bay. These species share a common life cycle; spawning generally occurs in coastal waters, and the young settle out of the plankton into estuarine habitats (Cook and Lindner 1970; Lindner and Cook 1970; Rabalais et al. 1995; Heck et al. 2001; Minello et al. 2003). Larval recruitment is temporally pulsed (Rogers and Herke 1985). Brown shrimp postlarvae arrive in early spring, whereas white shrimp arrive in late spring and early summer; larval recruitment of both species continues into fall (Baxter and Renfro 1967). After several months in shallow salt marsh habitats, subadult shrimp move into the open bay before migrating offshore (Trent 1967; Pullen and Trent 1969; Minello et al. 1989). Blue crab megalopae settle throughout the year, peaks occurring in late summer and fall (Rabalais et al. 1995; Morgan et al. 1996); this species remains in the estuary for most of its life cycle, except when adult females spawn in coastal waters (Williams 1984). Fishing pressure on adults of all three species is high, but these *r*-selected crustaceans show only weak spawner stock–recruitment relationships (Rothschild and Brunenmeister 1984; Nance and Nichols 1988; Rugolo et al. 1998).

We selected an 8-month period of the year (from April through November) to estimate population size and production in estuarine marshes of Galveston Bay. Juvenile abundances and water temperatures are generally high during this period (Rozas et al. 2007),

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and the vegetated marsh surface is usually inundated by seasonal high tides. During these months, the marsh edge in lower Galveston Bay is tidally inundated about 75% of the time (Minello and Webb 1997; Whaley and Minello 2002).

The marsh complex consists of vegetation interspersed with shallow open water, and the vegetation edge is important for decapod crustaceans. Spatial distributions in relation to this vegetation–water interface reflect many functional relationships with food, predators, and abiotic factors (Minello et al. 1994; Zimmerman et al. 2000). Minello and Rozas (2002) found that juvenile densities of penaeid shrimps and blue crabs were highest at the marsh edge and declined rapidly within marsh vegetation. They used this relationship along with mean densities in shallow, open water to estimate population sizes in a 437-ha marsh system of Galveston Bay. Our objectives in this study were to expand upon their approach by (1) refining the models to include the influence of the marsh edge on nearby nonvegetated bottom, (2) analyzing the land–water patterns in the approximately 20,000 ha of regularly flooded salt marshes present in Galveston Bay, and (3) incorporating length–weight relationships, length frequencies, and growth data in population analyses to provide estimates of biomass and productivity.

Methods

Density models.—In an earlier study, Minello and Rozas (2002) estimated fine-scale (1–10-m) nekton density patterns within marsh vegetation of lower Galveston Bay. To complement these data, we measured density patterns on nonvegetated bottom in relation to densities within marsh edge (marsh–water interface) vegetation. We collected nekton samples in edge vegetation and on shallow (<1 m depth) nonvegetated bottom near Gang's Bayou (Figure 1) in May, August, and November of 2000. We used a 2.6-m^2 area drop sampler (Zimmerman et al. 1984) and a stratified random sampling approach to collect a total of 91 samples when marsh vegetation was flooded. Approximately one-third of the samples were located in the marsh edge vegetation about 1 m (center of cylindrical sampler) shoreward of the marsh edge (Table 1); another third of the samples were located in shallow, open water between 1 and 10 m from the vegetated edge; and the remaining samples were located at distances from 11 to 227 m from the vegetation. We classified the nonvegetated samples into distance-classes of 1, 5, 15, 25, and 50 m from the marsh edge and calculated mean densities for these classes and for the vegetated marsh surface. We then standardized mean densities within sampling periods so that the vegetated-edge density was 1. We fit nonlinear regression models to the standardized mean densities for use in predicting the density of nekton on nonvegetated bottom at different distances from the marsh edge, based on a vegetated marsh edge density. Models to predict densities within marsh vegetation (also based on the marsh edge density) were modified slightly from those developed by Minello and Rozas (2002), by including additional standardized means from their validation data and by making them more robust. New density curves were based on the above relationships and the mean density (mean of monthly means from April to November) of these crustacean species in marsh edge habitat when the marsh surface is flooded. These edge densities were obtained from a large database of enclosure samples (1–2.6 m^2 area) collected in lower Galveston Bay on various projects beginning in 1982 (see Minello 1999).

To validate these density curves, we assembled all available data on densities at different distances from the marsh edge (collected by our laboratory from six Texas bays; for study descriptions see Zimmerman et al. 1990a, 1990b; Rozas and Minello 1998; Minello 1999; Rozas et al. 2000; Rozas and Zimmerman 2000; Rozas et al. 2007). About 90% of these samples came from Galveston Bay, but we excluded data used to build the models. Mean densities (mean of April to November monthly means) were calculated after classifying samples by month and distance from the marsh edge. Although limited to certain months and distances, this data set provided an independent test of the model's ability to predict average densities in salt marshes of Texas.

Landscape characteristics of Galveston Bay marshes.—We used 62 Digital Orthophoto Quarter Quadrangle (DOQQ) images made from 1995 color infrared (IR) aerial photographs in our analysis of marsh–land–water patterns (Texas Natural Resources Information System; www.tnris.state.tx.us); these images covered the entire estuarine shoreline of the Galveston Bay system (Figure 1). The DOQQs were subdivided into smaller images that overlaid the U.S. Fish and Wildlife Service national wetland inventory (NWI) digital map for regularly flooded salt marsh (estuarine, intertidal, emergent, persistent, and regularly flooded category [E2EM1N]).

We used ArcView 3.2 geographical information systems (GIS) software with its Image Analysis and Spatial Analyst extensions (ESRI, Redlands, California) to conduct landscape analyses of the regularly flooded salt marsh. Images were converted into 25 categories using the unsupervised iterative self organizing data clustering technique of Image Analysis. These 25 categories were then reduced to three classes:

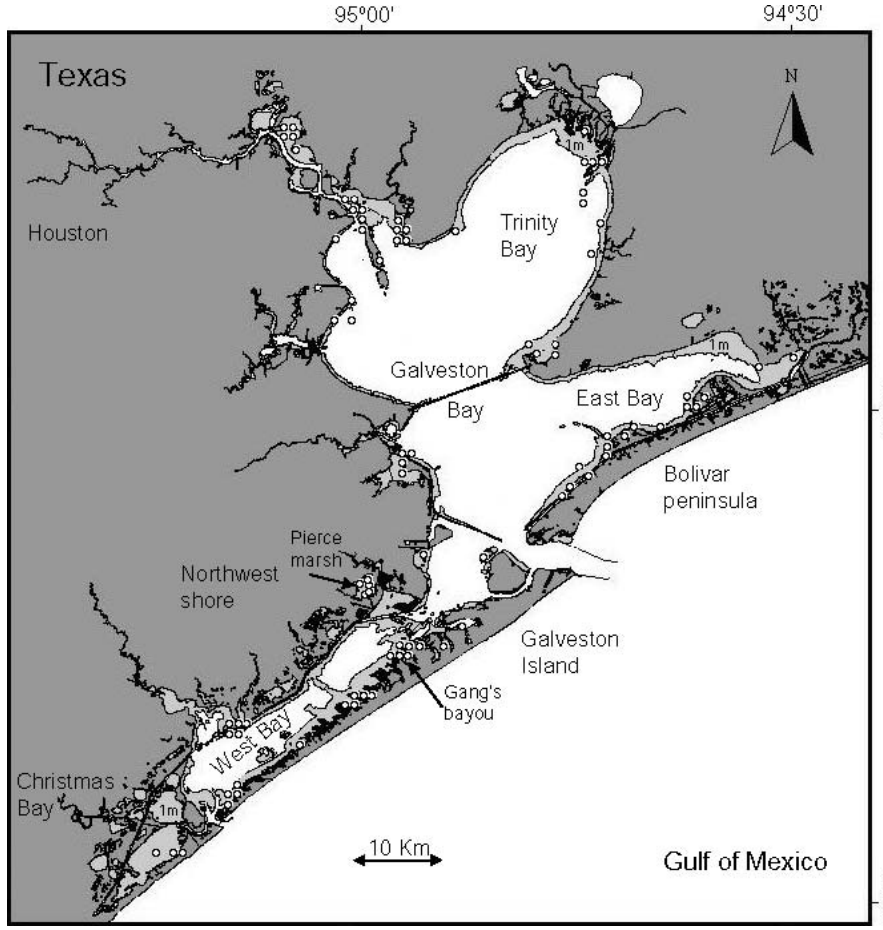

FIGURE 1.—Areas of Galveston Bay analyzed for wetland characteristics and nekton populations. A line indicates the boundary between the upper and lower bay; the circles indicate the locations where nekton samples were collected.

marsh vegetation, submerged nonvegetated bottom (water), and nonapplicable (everything else) and then converted from raster to vector format (i.e., from grid files to shape files). The classification of images was adjusted on the basis of the NWI information, inspection of the vegetation and water patterns in the original color IR image, input from experts familiar with the particular marsh area, and limited ground truth inspections (where necessary).

Distances from the vegetation–water interface were determined using Spatial Analyst. We classified the vegetation and water areas in each scene into different categories, based on distances (1-m increments) from the nearest marsh shoreline to a point 25 m beyond the vegetation–water interface. Areas farther than 25 m were consolidated into one category. We calculated the overall areal coverage of each of these distance categories within a marsh scene. To ensure that shallow ponds interspersed within marsh vegetation were not excluded in defining marsh boundaries, we included a buffer of 150 m of water from the vegetation–water interface. The area of marsh complex in our GIS analyses differs from the NWI estimates of regularly flooded estuarine marsh (E2EM1N) because our buffer incorporates an arbitrary amount of shallow water adjacent to marsh vegetation. To assess the impact of buffer size on nekton population estimates, we also present some estimates using a 25-m buffer. We used bathymetry data developed by the National Ocean Service (Clark et al. 1999) to estimate areas of shallow (<1 m) open water outside of the marsh complex.

Marsh and shallow-water population estimates.—The validated models for lower Galveston Bay provided estimates of nekton density at different

TABLE 1.—Mean densities (individuals/m^2) of brown shrimp, white shrimp, and blue crabs in vegetated marsh edge and at different distances from the edge in shallow open water of Galveston Bay. Standard errors are in parentheses; N = the number of samples.

		Open water				
Species and N	Marsh edge	1 m	5 m	15 m	25 m	50 m
		May 2000				
N	10	3	4	5	6	3
Brown shrimp	14.3 (3.2)	3.5 (0.6)	1.7 (0.3)	1.3 (0.4)	0.9 (0.3)	0.8 (0.2)
Blue crab	1.3 (0.2)	0.1 (0.1)	0.0 (0.0)	0.1 (0.1)	0.2 (0.1)	0.5 (0.5)
		August 2000				
N	11	4	5	2	2	6
Brown shrimp	3.8 (1.3)	0.5 (0.1)	0.6 (0.1)	0.0 (0.0)	0.2 (0.2)	0.1 (0.1)
White shrimp	5.4 (2.3)	2.4 (2.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)	0.0 (0.0)
Blue crab	1.9 (1.0)	1.1 (0.5)	0.6 (0.3)	0.4 (0.4)	0.0 (0.0)	0.0 (0.0)
		November 2000				
N	10	2	6	5	3	4
Brown shrimp	4.9 (1.7)	1.2 (0.8)	0.5 (0.2)	0.0 (0.0)	0.1 (0.1)	0.1 (0.1)
White shrimp	1.7 (0.8)	0.8 (0.8)	0.3 (0.1)	0.0 (0.0)	0.0 (0.0)	0.3 (0.1)
Blue crab	19.3 (5.2)	4.6 (0.8)	1.8 (0.7)	1.0 (0.3)	0.8 (0.8)	1.4 (0.5)

distances from the marsh edge. These data were combined with the GIS analysis to provide population abundance estimates. We assumed that modeled densities for shallow open water applied to areas up to 1 m in depth.

Biomass estimates were derived by multiplying the numerical data by a mean mass/individual (live or wet weight) that was determined by combining relative size-frequency data with size–weight relationships. Size-frequency data were obtained from the Galveston Bay enclosure database for all vegetated and nonvegetated samples in the lower bay. Only specimens 100 mm or less in size (total length [TL] for shrimp, carapace width [CW] for blue crabs) were included in the size frequency analysis, although nearly all (>99%) individuals caught were of qualifying size. Size-class intervals were 1 mm for shrimp and 5 mm for crabs. Kolmogorov–Smirnoff cumulative distribution tests were used to compare frequency distributions between vegetated and nonvegetated habitat types (Tate and Clelland 1957). Size–weight relationships were developed from measurements in our laboratory and from the literature. From 355 juvenile brown shrimp (23–68 mm TL), the relationship between total length (mm) and wet weight (g) was $W = 0.000006 \cdot \mathrm{TL}^{3.071}$ and R^2 was 0.96. For 198 white shrimp (25–71 mm TL), the regression was $W = 0.0000065 \cdot \mathrm{TL}^{2.998}$ and R^2 was 0.96. These relationships were similar to those developed by Fontaine and Neal (1971) and Mercer (1981) for different size ranges. We used the relationship between carapace width (mm) and wet weight (g) reported by Pullen and Trent (1970) for blue crabs (28–202 mm) because it was similar to one developed for small crabs (10–42 mm) in our samples.

Production was defined as the total expected increase in biomass over time for the population (Chapman 1978). The size frequency distributions used to represent populations were derived from a large number of individuals collected over different seasons, years, and locations (Figure 1); we assumed these distributions were stable over the periods analyzed and that mortality and emigration were integrated into the relationships. Estimated growth rates were used to calculate a projected daily increase in biomass for each size increment, and values for all size increments were then summed to calculate an average expected daily increase in individual wet weight in the population. This approach is comparable to Thompson and Bell's equilibrium yield calculations (Ricker 1975). For brown shrimp and white shrimp we used a fixed growth rate of 1 mm/d (Zein-Eldin and Aldrich 1965; Zein-Eldin and Griffith 1969; Knudsen et al. 1977; Minello et al. 1989; Minello and Zimmerman 1991). Although various growth models have been proposed for shrimp (Parrack 1979; Rothschild and Brunenmeister 1984), the length–age relationship appears to be linear for juveniles, and our unpublished laboratory and field experiments also suggest that growth of juveniles in length per day is unrelated to total length. For blue crabs (12–40 mm CW) we used a growth rate of 0.5 mm CW/d, based on data from our unpublished field and laboratory experiments and similar reported rates (Tagatz 1968; Leffler 1972; Chazaro-Olvera and Peterson 2004). The mean potential daily increase in mass per individual, calculated from these growth rates and size frequency distributions, was then multiplied by population abundance to estimate production.

Results

Density Models

The densities of shrimps and blue crabs measured at the Gang's Bayou study area generally showed a consistent decline from a peak in marsh edge vegetation (approximately 1 m shoreward of open water) to their low values in open water (Table 1). The regression models used to fit curves to the mean standardized densities on nonvegetated bottom (Figure 2) all had high R^2 values (>99%). The model fit within vegetation was more variable, and R^2 values ranged from 91% for brown shrimp to 44% for blue crabs (Figure 2).

We predicted nekton densities in a marsh complex at different distances from the vegetation edge by applying the standardized density models in Figure 2 to a mean observed density in vegetated marsh edge. These values were means of monthly mean densities and were based on 963 samples collected from April through November in lower Galveston Bay. Densities for the vegetated marsh edge were 13.4/m^2 (SE = 1.30) for brown shrimp, 8.9/m^2 (SE = 3.11) for white shrimp, and 8.1/m^2 (SE = 1.58) for blue crabs, and predicted density curves are shown in Figure 3.

The predicted and actual mean densities in vegetated marsh edge (see −1 m in Figure 3) differ slightly because the actual means include data from Texas marshes outside of Galveston Bay. Available validation data for different distances from the marsh edge were limited in their seasonal distribution (Table 2); for example, vegetated samples 5 m from the marsh edge were only available from May and September. The density model for brown shrimp, however, appeared to adequately represent average actual densities in polyhaline (annual salinity >15‰) marshes of Texas (Figure 3). The mean validation density for white shrimp at 5 m into the vegetation (based on 24 samples) was 11.5 shrimp/m^2 (SE = 11.5), until we removed an outlier from September 1994 that had 166 small (98% were <20 mm TL) white shrimp/m^2. The white shrimp model appeared to predict densities into open water up to 5 m from the vegetation, but it underestimated densities farther from the marsh edge. In the final model, we used a mean density of 0.8 shrimp/m^2 for distances farther than 5 m from the vegetation; this density was derived from a combination of model building and validation data (Figure 3). Blue crab densities were represented well by the initial model out to 10 m from the vegetation, but densities farther away from the marsh edge were overestimated by the initial model. In the final blue crab model, we used a mean density of 0.4 crabs/m^2 for distances farther than 10 m from the vegetation.

We did not estimate nekton populations in low-salinity (<15‰) marshes of Galveston Bay because the models were developed in polyhaline marshes and relatively little validation data were available (419 samples) for low-salinity marshes of Texas. A cursory comparison of modeled densities with these validation data suggested that the final white shrimp and blue crab models worked reasonably well, but mean brown shrimp densities within low-salinity marsh vegetation were substantially lower than modeled densities (see Minello 1999).

Landscape Characteristics of Galveston Bay Marshes

Most (90%) of the regularly flooded marshes of Galveston Bay are located in the lower bay (Figure 1; Table 3). Lower bay marshes were considered polyhaline, with average annual salinities generally greater than 15‰ (Clark et al. 1999). Figure 4 shows the typical pattern of vegetation with interspersed open water. We divided the lower bay into four regions, and the area of marsh complex in these regions ranged from 6,189 ha on the Northwest shore to 2,461 ha on Galveston Island (Table 3). Overall, 39% of the area in these lower bay marshes was vegetated (ranging from 22.9% on Galveston Island to 45.9% in Christmas Bay), and edge marsh (1 m shoreward of the marsh–water interface) averaged 9.7% (7.9–13.2%; Table 3). About 40% of the open water in these marshes was 25 m offshore of the edge marsh. The impact of selecting a 150-m buffer of open water can be seen here because the area of water 25–150 m from the vegetation edge (60% of open water) made up 36% of the combined marsh complex.

Marsh and Shallow-Water Population Estimates

Our nekton population estimates for all marshes in lower Galveston Bay were 342×10^6 brown shrimp, 308×10^6 white shrimp, and 296×10^6 blue crabs (Table 4). When standardized to 1 ha, the smallest populations were generally in West Bay; larger populations were in Christmas Bay and East Bay. Biomass and production patterns in different regions of the bay were similar to density patterns (Table 4); differences were due to significant variations in the size-frequency data between vegetated and nonvegetated areas of the marsh complexes (Table 5; Figure 5).

We also used our models to estimate nekton populations in shallow (<1 m deep) open-water areas of the bay system outside of the marsh complexes. Modeled densities for this open water were low at 0.64 brown shrimp/m^2, 0.80 white shrimp/m^2, and 0.40 blue crabs/m^2, but the area of this shallow, open water (28,971 ha) in the lower bay was larger than the total area of marsh complex analyzed (17,673 ha). Within

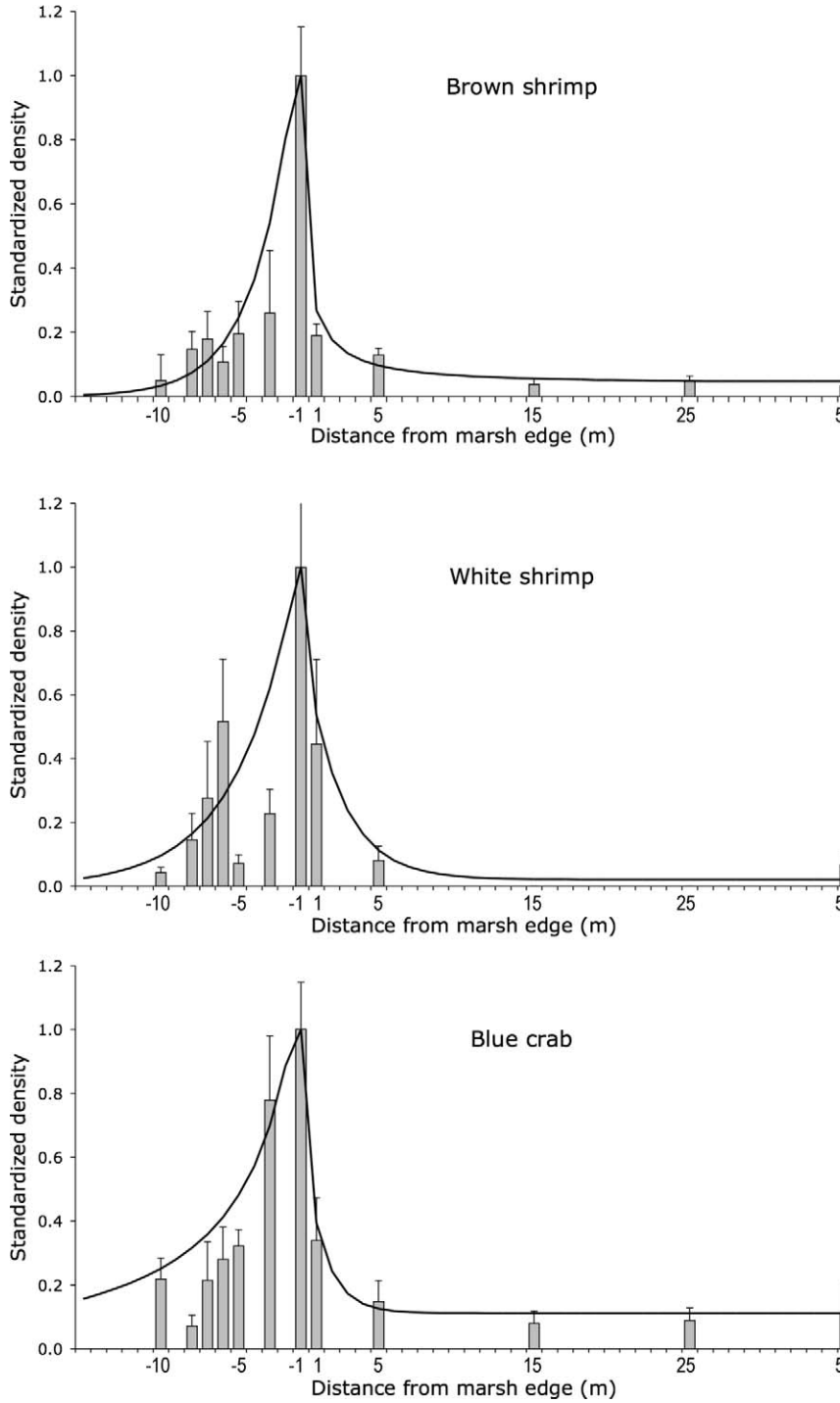

FIGURE 2.—Mean + SE standardized densities of brown shrimp, white shrimp, and blue crabs at different distances from the marsh edge used to develop the initial density models on vegetated (the negative portions of the *x*-axes) and nonvegetated (the positive portions) areas of Galveston Bay. Nonlinear regression was used to model densities (solid lines).

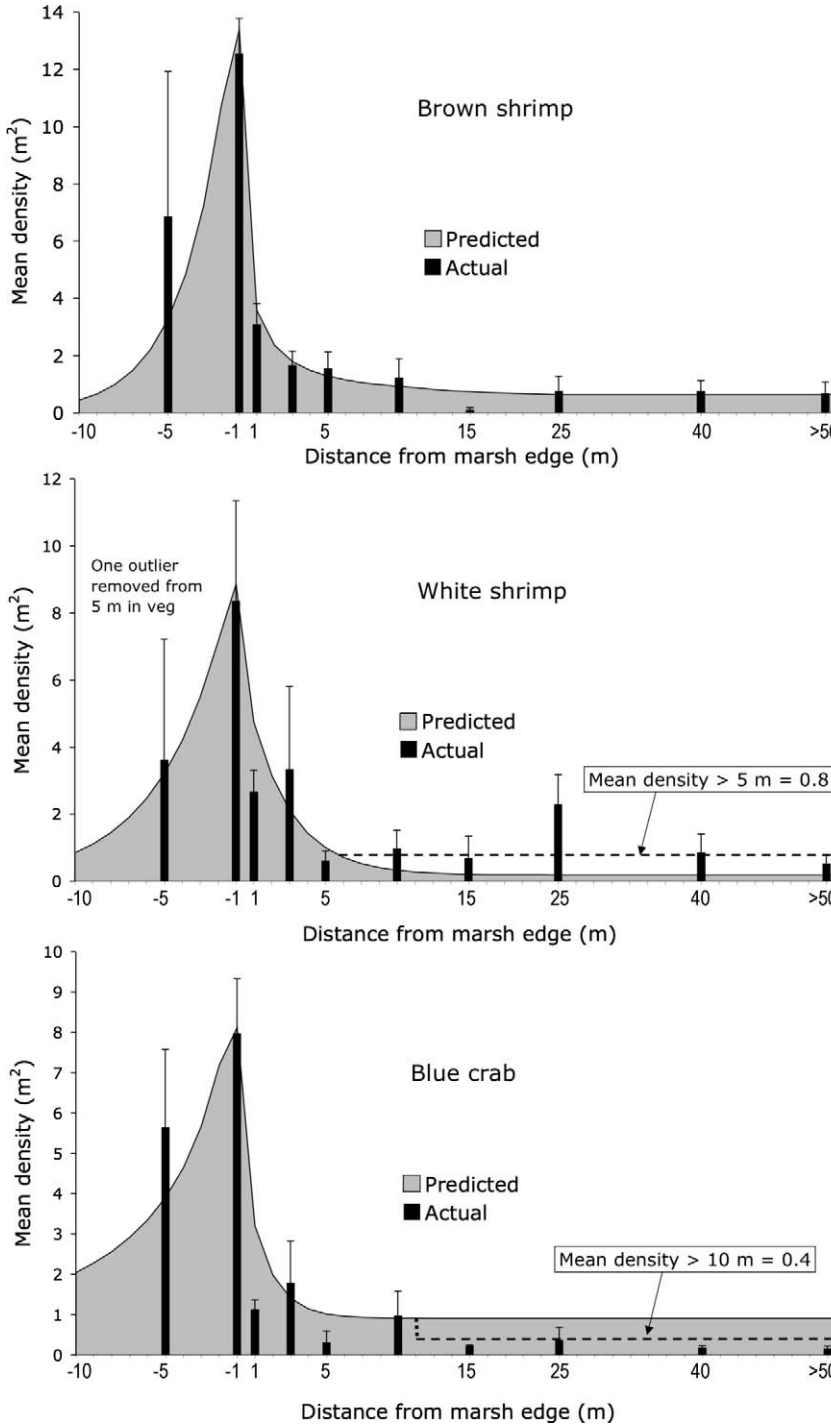

FIGURE 3.—Actual and predicted densities of brown shrimp, white shrimp, and blue crabs at different distances from the marsh edge. The actual values are means of monthly means (April–November) from high-salinity marshes (sample sizes are given in Table 2). The dashed lines for white shrimp and blue crabs represent the mean densities in open water that were used in the final models.

TABLE 2.—Seasonal and spatial distribution of the numbers of enclosure samples (from high-salinity [>15‰] areas of Texas bays, 1982 to 2002) used to validate nekton density models. Distances are either shoreward (vegetated; negative numbers) or offshore (open water; positive numbers) of the marsh edge.

Distance (m)	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Total
−5		14				10			24
−1	169	212	128	97	105	140	116	124	1,091
1	137	141	112	77	102	90	80	103	842
3		3		7	4		1	2	17
5		2			1			3	6
9		4				4	2		10
15		4			2				6
25		6			1	4	4		15
40		15			5	4	4		28
>50		18			1		11		30
Total									2,069

this shallow-water habitat (marsh complex plus open water less than 1 m deep) of lower Galveston Bay, the marsh complex supported 65% of the brown shrimp, 57% of the white shrimp, and 72% of the blue crabs by number (Table 6). Although marsh vegetation made up only 15% of this shallow-water habitat, it supported 45% of the brown shrimp, 34% of the white shrimp, and 53% of the blue crab populations.

Discussion

Population Size and Biomass

Our data support the conclusion that salt marshes are important for penaeid shrimps and blue crabs in the lower Galveston Bay ecosystem, not only from the standpoint of small-scale densities, as often reported in the literature, but also from a population point of view. Although the marsh complex (i.e., vegetated area and 150-m buffer of open water) made up about 38% of the shallow-water (<1-m) habitat in the lower bay, it supported 65% of the brown shrimp, 57% of the white shrimp, and 72% of the blue crab populations based on abundance. When standardized to 1 ha, the abundance of shrimps and crabs in the marsh complex was 2–4 times higher than in shallow, open water (Table 6). Relative marsh value increases if only vegetation is considered. That is, 1 ha of marsh vegetation supported 5.3 times more brown shrimp, 3.2 times more white shrimp, and 7.8 times more blue crabs (by number) than shallow open water outside of the marsh complex. Similarly, marsh vegetation supported 5 times more brown shrimp, 4 times more white shrimp, and 35 times more blue crab biomass than shallow, open water.

In a 437-ha marsh complex on Elmgrove Point in East Bay, Minello and Rozas (2002) estimated a per-hectare standing crops of 37,000 brown shrimp, 35,000 white shrimp, and 26,000 blue crabs. By comparison, the per-hectare standing crops in the 4,147-ha marsh complex we studied in East Bay was about 22,000 brown shrimp, 19,000 white shrimp, and 19,000 blue crabs. In addition to the variability associated with the larger area we analyzed, these smaller density estimates are primarily attributable to two changes in the modeling approach: (1) changing the definition of a marsh complex to include more open water (i.e., the 150-m buffer) and (2) refining the models to include a steep decline in open-water density with distance from the marsh edge.

Comparisons with other standing crop estimates are complicated by issues of gear efficiency (Kneib 1997; Rozas and Minello 1997; Connolly 1999), seasonality, and habitat definition and specificity (Minello et al. 2003). Relatively few population estimates have been attempted for large areas of estuarine wetlands. Sullivan et al. (1985), using a mark–recapture approach, estimated that there were 5,708–17,119/ha brown shrimp (>40 mm TL) in several estuarine ponds with fringing wetlands; they also estimated 8,242 brown shrimp/ha for all shrimp sizes based on an extrapolation of drop-sampler data. Clark et al. (2004) applied marsh edge densities to the entire marsh and estimated brown shrimp standing crops in high-salinity

TABLE 3.—Characterization of Galveston Bay regional marshes, where marsh vegetation is from areas of the bay classified as regularly flooded in the National Wetland Inventory. The marsh complex includes vegetated and open-water portions 150 m offshore of the vegetated marsh–open-water interface. The open water from edge (%) is the percentage of open water between 0–25 m and 25–100 m from the marsh edge. The marsh edge is the band of vegetation up to 1 m shoreward of the marsh–water interface.

	Marsh complex area (ha)			Open water from edge (%)		Marsh edge percent of	
Region	Open water	Vegetated	Total	≤25 m	>25 m	Vegetated area	Marsh complex
Lower bay, total	10,733	6,940	17,673	39.9	60.1	9.7	3.8
East Bay	2,315	1,833	4,147	39.1	60.9	10.4	4.6
Galveston Island	1,897	564	2,461	39.7	60.3	13.2	3.0
Northwest shore	3,883	2,306	6,189	38.8	61.2	7.9	2.9
Christmas Bay	2,638	2,237	4,875	42.5	57.5	10.1	4.6
Upper bay, total	1,429	534	1,963	25.1	74.9	8.2	2.2

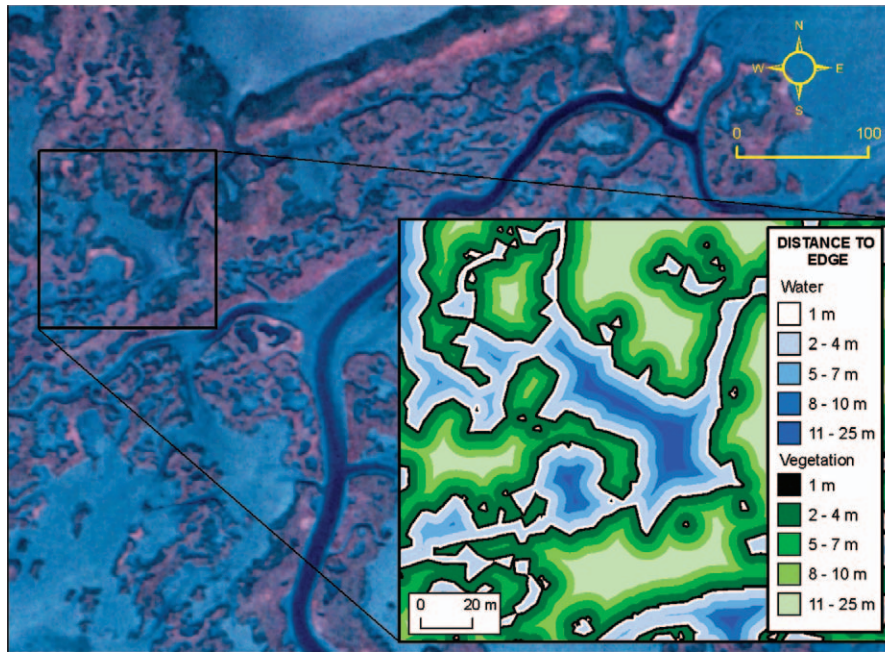

FIGURE 4.—Typical image of the marsh landscape, where the background is a Digital Orthophoto Quarter Quadrangle from Pierce Marsh (Figure 1) in lower Galveston Bay. The inset shows a classified image with a sample of some consolidated distance polygons.

marshes of Galveston Bay at 55,771–61,394/ha. Our analysis here, however, shows that 1-m-wide vegetated edge makes up only 9.7% of marsh vegetation or 3.8% of the marsh complex including the 150-m buffer. Our estimate for just the vegetated marsh area was 33,988 brown shrimp/ha. In Louisiana, Rozas and Minello (1999) used the average densities in different marsh habitats to estimate standing crops of 2,169–9,865/ha for brown shrimp and 2,444–4,007/ha for blue crabs. In another Louisiana marsh, Rozas and Minello (2001) made substantially higher standing crop estimates for these species, including a white shrimp estimate of about 75,000/ha. These extrapolations generally assumed that nekton were evenly distributed across the marsh surface, unlike the models we used.

For shallow, open water outside of the marsh complex, we estimated standing crops of about 6,400 brown shrimp/ha, 8,000 white shrimp/ha, and 4,000 blue crabs/ha. Martinez-Andrade et al. (2005) analyzed 27 years (1977–2003) of bag seine (13-mm mesh) data for shallow, open waters in Galveston Bay, and for all months of the year combined, their per-hectare estimates were 519 brown shrimp, 1,054 white shrimp, and 104 blue crabs. Even after adjustments for seasonality and gear efficiency, these values are considerably lower than our estimates. However, the mean lengths from their samples indicate that relatively few small crustaceans were collected. Trent et al. (1974) collected brown shrimp (as small as 8 mm TL) in lower Galveston Bay using trawls with a 2-mm mesh cover over the cod end. From 249 samples collected at seven stations from April to November (1965–1966), they reported catches equivalent to 6,100 brown shrimp/ha (using the area-swept method and a 35% catch efficiency).

We were also interested in comparing populations in marsh and shallow water with those potentially present in deeper (>1-m) bay water because there is a large amount of deeper water (about 57,000 ha) in lower Galveston Bay. We analyzed Galveston Bay trawl data (40–60 monthly samples in spring, summer, and fall from 1982 to 2004) provided by the Texas Parks and Wildlife Department Coastal Fisheries Branch (see Martinez-Andrade et al. 2005). These trawls had a 38-mm stretched mesh and mainly collected shrimp over 60 mm TL and crabs over 40 mm CW. Using a net catch efficiency of 35% (see Rozas and Minello 1997), we calculated mean standing crops of 39 brown shrimp/ha, 66 white shrimp/ha, and 24 blue crabs/ha. Trent et al. (1974), with their 2-mm trawl cover, however, showed that densities in the open bay can be much higher. Based on the same assumptions above for

TABLE 4.—Juvenile brown shrimp, white shrimp, and blue crab abundance, biomass, and production from lower Galveston Bay marshes. Total population values represent mean standing stocks from April to November (244 d); these values were also standardized per hectare of marsh present in each region (Table 3).

Region	Number		Biomass (kg)		Production (kg)	
	Total ($\times 10^6$)	Per hectare	Total	Per hectare	Per day	Per hectare per year
Brown shrimp						
East Bay	90.61	21,848	36,027	8.7	2,448	144
Galveston Island	41.60	16,902	16,719	6.8	1,120	111
Northwest Shore	102.99	16,640	41,188	6.7	2,776	109
Christmas Bay	107.34	22,018	42,656	8.7	2,900	145
Combined	342.54	19,382	136,590	7.7	9,244	128
White shrimp						
East Bay	79.78	19,237	33,584	8.1	2,058	121
Galveston Island	38.88	15,800	15,779	6.4	967	96
Northwest Shore	94.64	15,291	39,089	6.3	2,395	94
Christmas Bay	94.30	19,342	39,793	8.2	2,439	122
Combined	307.60	17,406	128,246	7.3	7,859	109
Blue crab						
East Bay	78.11	18,835	69,960	16.9	3,343	197
Galveston Island	33.35	13,553	25,325	10.3	1,267	126
Northwest Shore	90.50	14,623	76,185	12.3	3,701	146
Christmas Bay	93.63	19,206	84,607	17.4	4,033	202
Combined	295.60	16,726	256,077	14.5	12,344	170

their samples in shallow bay water, they recorded densities of 3,300 brown shrimp/ha at two stations in lower Galveston Bay. Additional studies are needed with quantitative sampling gear to address the value of deep, open bay habitats for juvenile crustaceans.

Nekton Production

We estimated the annual production (April–November) from the marsh complex in lower Galveston Bay to be 2.2×10^6 kg (128 kg/ha) for brown shrimp, 1.9×10^6 kg (109 kg/ha) for white shrimp, and 3.0×10^6 kg (170 kg/ha) for blue crabs. For blue crabs in particular, overwintering individuals may provide some additional productivity from December–March. However, reduced growth from burrowing in the substrate (Schaffner and Diaz 1988) and colder temperatures (Leffler 1972; Ju et al. 2001) probably minimizes this contribution. When standardized to 1 ha, production in the marsh complex was 3.1 (brown shrimp), 2.5 (white shrimp), and 8.8 (blue crab) times higher than in shallow, open (<1 m) water.

TABLE 5.—Brown shrimp, white shrimp, and blue crab biomass and daily production estimates per individual in different habitat types within Galveston Bay. The growth rates shown were used to calculate production from size-frequency data; growth is in total length for shrimp and carapace width for crabs. The marsh complex includes the vegetated area and the open-water band 150 m offshore of the vegetation–open-water interface.

Part of marsh complex	Biomass/ individual (g)	Daily growth (mm/d)	Individual production (g/d)
Brown shrimp			
Vegetated	0.39	1.0	0.027
Open water	0.42	1.0	0.027
White shrimp			
Vegetated	0.45	1.0	0.028
Open water	0.37	1.0	0.023
Blue crabs			
Vegetated	1.09	0.5	0.050
Open water	0.24	0.5	0.020

Our estimates of production are expected increases in the live- or wet-weight biomass that should be available to predators (including fishers and detritivores) or to exportation from the bay. Because there are various ways of measuring and expressing secondary productivity (Waters and Crawford 1973; Chapman 1978; Dolbeth et al. 2005), comparisons with values reported in the literature should be made with care. Kneib (2003) discussed the amount of secondary production that might reasonably be expected from salt marsh ecosystems, based on the amount of primary production available (Mendelssohn and Morris 2000; Sullivan and Currin 2000) and the ecological efficiencies involved in trophic transfers. However, the pathways and rates of biomass or energy flow from primary producers through an estuarine food web are complex (Nixon 1980; Fry et al. 1984; Dittel et al. 2000; Wainright et al. 2000). Shrimps and crabs are omnivorous (Laughlin 1982; Gleason and Zimmerman 1984; McTigue and Zimmerman 1991), albeit to different degrees, depending upon the species and size

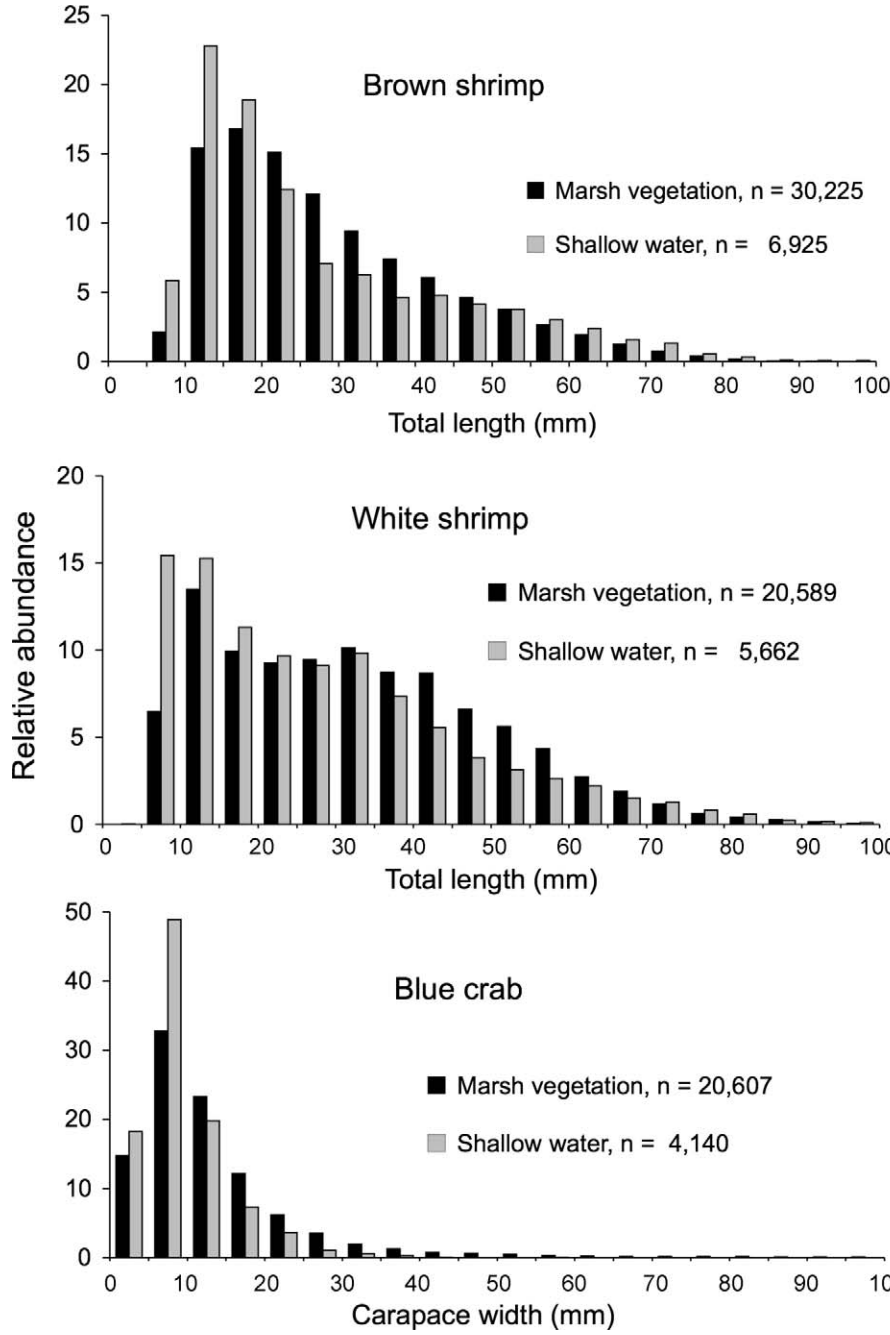

FIGURE 5.—Relative size-frequency data for brown shrimp, white shrimp, and blue crabs from enclosure samples collected in vegetated marsh areas and shallow, open waters (<1 m) of lower Galveston Bay. Shrimp lengths were recorded and analyzed in 1-mm increments but are displayed here in 5-mm intervals.

TABLE 6.—Brown shrimp, white shrimp, and blue crab population and production estimates for lower Galveston Bay marsh complexes, which include vegetated areas (6,940 ha) and open-water area partitioned into zones 0–25 m (4,287 ha) and 25–150 m (6,445 ha) offshore of the vegetation, and shallow bay waters (<1 m deep) outside the marsh complex (28,971 ha). Annual production values are from April to November.

Habitat	Total			Per hectare		
	Number (thousands)	Biomass (kg)	Production (kg/d)	Number	Biomass (kg)	Production (kg/year)
Brown shrimp						
Vegetation in marsh complex	235,878	92,138	6,409	33,988	13.3	225
Water in marsh complex 0–25 m from edge	65,513	27,304	1,742	15,281	6.4	99
Water in marsh complex 25–150 m from edge	41,201	17,172	1,095	6,392	2.7	41
Shallow bay water (<1 m)	185,191	77,183	4,923	6,392	2.7	41
Total	527,783	213,797	14,168	11,315	4.6	74
White shrimp						
Vegetation in marsh complex	180,502	81,531	4,998	26,009	11.7	176
Water in marsh complex 0–25 m from edge	75,608	27,789	1,702	17,635	6.5	97
Water in marsh complex 25–150 m from edge	51,563	18,951	1,160	8,000	2.9	44
Shallow bay water (<1 m)	231,767	85,184	5,216	8,000	2.9	44
Total	539,440	213,455	13,076	11,565	4.6	68
Blue crab						
Vegetation in marsh complex	217,138	237,099	10,792	31,288	34.2	379
Water in marsh complex 0–25 m from edge	52,718	12,751	1,043	12,296	3.0	59
Water in marsh complex 25–150 m from edge	25,781	6,236	510	4,000	1.0	19
Shallow bay water (<1 m)	115,883	28,028	2,292	4,000	1.0	19
Total	411,520	284,114	14,637	8,823	6.1	77

(Hunter and Feller 1987; Stoner and Buchanan 1990; Fantle et al. 1999). Food sources affect assimilation and trophic efficiency, and refractory marsh macrophytes probably pass through several detrital pathways to these consumers (Currin et al. 1995; Newell and Palm 1998; Newell and Porter 2000). Other sources of primary production and trophic pathways also may be important (Kreeger and Newell 2000; Fry et al. 2003); in particular, benthic microalgae probably contribute substantially to secondary production (Sullivan and Moncreiff 1990; Sullivan and Currin 2000). In addition, trophic efficiencies may be considerably higher than the commonly used 10% value. Trophic efficiency has two components; the fraction of the production from a lower trophic level that is consumed and the fraction of consumed production that results in production at the next trophic level (Royce 1972; Ricklefs 1973). This second component, assimilation efficiency, can be very high for penaeid shrimp (Condrey et al. 1972; Dall et al. 1990; Lawrence and Lee 1997).

Kneib (2003) used measures of nekton standing crop in Georgia salt marshes and production : biomass ratios gleaned from the literature to estimate both resident and transient nekton production. For transient species (including white shrimp and several fish species), he calculated an annual average standing crop of 0.49 individuals/m^2 (4,900/ha) and a dry-weight biomass of 0.17 g/m^2 (wet-weight equivalent, 7.6 kg/ha). He estimated annual dry-weight production of these transients to be 0.46 g/m^2 (wet-weight equivalent, 9.5 kg/ha). Our estimates of both nekton standing crop and production are much higher; for shrimp and crabs alone, we estimated average annual production at 407 kg/ha. These differences in measures of standing crop and production are related to (1) the difficulties involved in estimating nekton standing crops in salt marshes and the need to use a landscape approach (Zimmerman et al. 1986; Kneib 1997, 2000; Rozas and Minello 1997; Minello and Rozas 2002), (2) the dissimilarity in landscape structure, nekton use, tidal dynamics, and habitat value of salt marshes in the northwestern Gulf of Mexico compared with those on the southeastern U.S. coast (Wenner and Beatty 1993; Rozas 1995; McIvor and Rozas 1996; Zimmerman et al. 2000), and (3) the differences in production potential between most estuarine nekton and highly productive species that support large commercial fisheries.

If salt marshes are defined as vegetation and associated ponds and creeks (Deegan et al. 2000; Minello et al. 2003), other estimates of fishery production are comparable to those presented here for Galveston Bay. Herke et al. (1992) collected nekton emigrating from an unweired 35.2-ha marsh impoundment (that included 25% areal coverage of cordgrass *Spartina patens*) over 2 years in Louisiana and reported annual exported production (live weight) from the

impoundment of around 125 kg/ha for brown shrimp, white shrimp, and blue crabs combined. Restrictions to recruitment into ponds (all animals entered the impoundments through a 7.9-cm wide vertical slit) may have negatively affected their production estimates, and of course, production lost to mortality within the ponds is not included. In addition, these marsh ponds were located in irregularly flooded *S. patens* wetlands, where production may be relatively low compared with regularly flooded *S. alterniflora* marshes. In Chesapeake Bay, Cicchetti (1998) reported blue crab dry-weight production from the salt marsh edge to be 6 g/m^2 per 150-d period; Cicchetti and Diaz (2000) adjusted these values for the area of flooded marsh and calculated transient-nekton wet-weight production of 204 kg/ha. For comparison, blue crab dry-weight production in a seagrass bed was estimated by Fredette et al. (1990) at 7.7 g /m^2 (wet weight, about 346 kg/ha). Weinstein et al. (1984) reported dry-weight production of spot *Leiostomus xanthurus* from a marsh creek to be 4.6 g/m^2 (wet weight, about 207 kg/ha). Deegan (1993) estimated that Gulf menhaden *Brevoortia patronus* were annually exporting 38 g/m^2 of marsh on a dry-weight biomass (wet weight, about 1,710 kg/ha), or approximately 5–10% of primary production. Although not directly related to salt marshes, Deegan and Thompson (1985) calculated production of fishes in Louisiana estuaries and estimated annual values in wet weight of Atlantic croaker *Micropogonias undulatus* at 230 kg/ha and Gulf menhaden at 130 kg/ha.

We should expect high nekton production from salt marshes in the northwestern Gulf of Mexico if those marshes are supporting large crustacean fisheries. Shrimp are an annual crop, and we presume that the harvest in this fully exploited fishery is a minimal estimate of production derived from estuarine wetlands. Zimmerman et al. (2000) calculated that in 1996 there was about 74 kg of shrimp harvested for every hectare of salt marsh in the northwestern Gulf of Mexico. We estimate annual shrimp biomass production in lower Galveston Bay to be 236 kg/ha of salt marsh. Such comparisons with commercial harvests, however, are complicated by the definition and measurement of salt marsh areal extent, the contribution of other estuarine habitats, the impact of natural mortality, and the fishing exploitation rate.

The production potential of some transient fishery species is also evident in mariculture, where predators are controlled and natural mortality is minimized. Under intensive culture with supplemental food and high stocking levels (3.5–7.0 $\times$ 10^6 postlarvae/ha), white shrimp can produce between 10,000–31,000 kg/ha of live-weight biomass in less than 120 d (Samocha et al. 1998). In small fertilized ponds with no supplemental feeding, Wheeler (1969) stocked white shrimp postlarvae at 81,000/ha and harvested 659 kg/ha after 120 d (84% survival). Thus, production potential for these fishery species is high and depends upon recruitment of larvae, food availability, growth, and survival.

Assumptions and Error Analysis

Our analysis of shrimp and blue crab populations focused on regularly flooded salt marshes and shallow (<1 m), open-water habitats of lower Galveston Bay. Oligohaline marshes in the upper bay also support these species, but the areal extent of these marshes is limited. In addition, other habitat types such as deeper open bay water, irregularly flooded wetlands, seagrass beds, and oyster reefs probably contribute to the production of these nekton populations.

There are many causes of error in the population estimates derived from this modeling exercise. Some of these were discussed in Minello and Rozas (2002), such as the use of mean densities in vegetated edge habitat, effects of different salinity regimes, variations in marsh slope that may affect density patterns, lack of connectivity in some regularly flooded marshes, and GIS classification errors. By projecting these density relationships into shallow open water; comparing models with validation density data; and restricting our analyses to high salinity areas of the bay we have attempted to reduce some of this error. Our final density models appear consistent with general density patterns in high-salinity marshes of Texas, but additional validation data are needed to examine the efficacy of the models in lower-salinity marshes. These small-scale density patterns have not been extensively studied in other wetlands. Evidence for similar spatial patterns in Louisiana marshes is conflicting (Rozas and Reed 1993; Peterson and Turner 1994; Rozas and Minello 1999, 2001; Baltz and Jones 2003; Fry et al. 2003). Cicchetti and Diaz (2000), however, reported a similar density pattern for blue crabs in relation to depositional marsh edges in lower Chesapeake Bay.

In our production analysis we assumed that the recruitment of larvae into the bay is constant and that size-frequency distributions are stable, although all of these species enter estuaries and settle in waves or pulses (Baxter and Renfro 1967; Minello et al. 1989; Morgan et al. 1996; Rabalais et al. 1995; Heck et al. 2001). Stable size-frequency distributions can also provide mortality estimates, and we used a standard catch-curve analysis (Ricker 1975) to estimate mortality from the descending limb of the size-frequency distributions, after assigning ages to sizes from our growth estimates. Daily instantaneous mortality rates were 0.049 for brown shrimp (15–70 mm TL), 0.032

for white shrimp (10–70 mm TL), and 0.060 for blue crabs (5–40 mm CW). These mortality rates were generally comparable to other estimates for juvenile brown shrimp (McCoy 1972; Minello et al. 1989) and blue crabs (van Montfrans et al. 1991; Fitz and Wiegert 1992; E. G. Johnson, Smithsonian Environmental Research Center, personal communication) in Galveston Bay and other estuaries, and they supported the validity of our production estimates.

Conclusions

The contribution of salt marshes and other estuarine habitat types to the productivity of a species is of great interest and is the basis for determining whether habitats are essential (Minello 1999), whether they are nurseries (Beck et al. 2001), and whether we should rigorously protect them. Simply measuring standing crops of transient nekton in salt marshes has been difficult due to their structural complexity. Marsh vegetative structure makes it difficult to measure densities at the square-meter scale (Kneib 1997; Rozas and Minello 1997; Connolly 1999), and translating density measurements into population estimates is complicated by complexity at the landscape scale (Kneib 2000; Simenstad et al. 2000; Minello and Rozas 2002). Our modeling approach is an attempt to resolve these difficulties and is useful for making habitat comparisons because value for a species depends both on densities within habitat types (Beck et al. 2001) and on the areal extent of the habitat (Beck et al. 2003; Kraus and Secor 2005; Dahlgren et al. 2006). Once estimates of population abundance and standing crop biomass are obtained, a variety of techniques can be used to estimate production (Ricker 1975; Cicchetti and Diaz 2000; Kneib 2003; Dolbeth et al. 2005). Our approach is relatively crude, and we are developing models to incorporate variability in growth, mortality, and larval recruitment and to examine the effects of changing environmental conditions (Haas et al. 2004). Our production estimates for transient decapod crustaceans are relatively high compared with many estimates for marsh residents, transients in other marsh systems, and for freshwater fish. However, these species must be highly productive to support large fisheries. These results confirm that salt marshes in Galveston Bay are important in sustaining fishery production of penaeid shrimps and blue crabs. Although focusing on these species, we also recognize that productivity of other fishery species may depend on a variety of estuarine habitats.

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