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ARTICLE

Assessing Variability in Juvenile Brown Shrimp Growth Rates in Small Marsh Ponds: An Exercise in Model Evaluation and Improvement

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Abstract
Brown shrimp *Farfantepenaeus aztecus* support a commercially important fishery in the northern Gulf of Mexico, and the juvenile shrimp use coastal estuaries as nurseries. Production of young shrimp from these nurseries, and hence commercial harvest of adults from the Gulf, is highly variable from year to year. Our recently published, individual-based model attempted to explain this variability as a function of habitat and the environmental factors such as temperature, salinity, and access to intertidal marsh habitat. We conducted a mark–recapture field study between April 12 and June 9, 2011, to provide growth rate data for model testing, as well as to further examine factors that affect growth, including available food biomass. Brown shrimp growth rates were measured in three polyhaline marsh ponds over periods of 2 to 4 weeks. We recorded hourly temperature and flooding data and measured biomass of infaunal food organisms. We parameterized our production model with input from 2011 to compare modeled output with observed data. Mean growth rate estimates from the model were similar to the estimated mean growth rate observed in the field (1.13 mm/d and 1.06 mm/d, respectively); however, field growth rates differed significantly among three marsh ponds (1.02, 1.03, and 1.26 mm/d). Data on infaunal biomass suggest that spatial and temporal variability in available food organisms is related to differences in shrimp growth, and the inclusion of such information may enhance the model.

The U.S. Gulf of Mexico (GoM) landings of penaeid shrimp are valued at over US$300 million annually, and brown shrimp *Farfantepenaeus aztecus* comprise about half of the catch (NMFS Fishery Statistics Division 2015). Brown shrimp have a largely annual life history (Minello et al. 1989; Fry 2008); adults spawn offshore and postlarvae are transported by currents to estuarine habitats (Temple and Fischer 1967; Cook and Lindner 1970).

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Juveniles grow rapidly for several months in estuaries before they emigrate offshore as subadults (Christmas and Etzold 1977; Renfro and Brusher 1982). The inshore, estuarine-dependent phase is a period of high and variable growth rates and likely determines the overall production of young shrimp and resultant fishery yield (Minello et al. 1989; Minello and Zimmerman 1991; Haas et al. 2001).

In Leo et al. (2016) we described an individual-based model (IBM) that uses temperature, salinity, and access to estuarine salt marsh habitat to estimate brown shrimp production (in 70-mm individuals per hectare) from the shallow waters of Galveston Bay, Texas. The growth rate of shrimp at an hourly time step is an important aspect of the model and has a large influence on production estimates. Additionally, since mortality rates are size dependent (Minello et al. 1989), shrimp that grow faster are more likely to survive. The model has reproduced biomass and size distribution patterns observed in data from Galveston Bay from 1983 to 2012, and the annual production estimates correlate with fishery-independent estimates of abundance from offshore northern GoM trawls. There was no correlation, however, between model production estimates and trawl data collected in Galveston Bay. These comparisons between the model output and field studies suggest that, although temperature, salinity, and flooding patterns may influence production generally from estuaries along the northern GoM, there are other factors affecting production that are spatially and temporally variable within individual bays.

Juvenile shrimp are known to feed on benthic infauna, mainly crustaceans and annelids, from marsh sediments (McTigue and Zimmerman 1991, 1998), and the abundance and biomass of infauna are highest within the marsh vegetation (Whaley and Minello 2002). Although growth of brown shrimp increases in our IBM when they are within marsh vegetation, there is no explicit relationship between infaunal biomass and shrimp growth (Leo et al. 2016). Since infaunal abundance, composition, and biomass can be both spatially and temporally variable (Mannino and Montagna 1997; Whaley and Minello 2002), we identified infaunal distribution as a potential source of variation between modeled growth and observed growth in the field.

We conducted a mark–recapture field study of juvenile brown shrimp from April to June of 2011 to estimate growth rates and variability of the shrimp among small marsh ponds in Galveston Bay and to compare these with the growth rate estimates predicted by an IBM for brown shrimp production by Leo et al. (2016). Additionally, we examined benthic infaunal abundance as a potential factor in variability of growth rates. We also assessed how well the modeled estimates of water temperature and tidal flooding of the marsh vegetation represented observed data from the ponds.

METHODS

Site selection and characterization.— We selected three marsh ponds for our growth study that were generally representative of the marsh habitat in Galveston Bay. These ponds were fringed with saltmarsh cordgrass *Spartina alterniflora* and were connected to the bay by relatively narrow channels, which could be blocked by nets. Two sites were located within Texas Parks and Wildlife Department's Galveston Island State Park (GISP) along the bay side of Galveston Island (Figure 1). The park is located along the shore of West Bay, a polyhaline (salinity of 18‰ to 30‰) water body of the Galveston Bay estuary (Rozas and Minello 2009), and we designated the study ponds as GISP-Small and GISP-Large based on their relative sizes. The third pond was located 20 km away in Galveston Bay on the edge of the Nature Conservancy Prairie Preserve on Moses Lake (Moses Lake pond). This pond is north of the Texas City Dike and closer than either of the GISP ponds to freshwater input from the Trinity and San Jacinto rivers and was selected in an effort to include a mesohaline (salinity of 5‰ to 18‰) pond. Salinities during the duration of the study, however, were consistently polyhaline in all three ponds.

Each pond has a nonvegetated mud bottom. We used GIS and digital orthophoto quarter quadrangle (DOQQ) images made from color infrared aerial photographs to estimate the linear distance of marsh edge and the nonvegetated area in each pond. We estimated the marsh elevation profile in each pond by establishing five transects perpendicular to the vegetated marsh edge (Minello et al. 2012). Along each transect, we estimated elevation by measuring water depth at the marsh edge and at 1, 2, and 3 m into the nonvegetated water and 1 and 2 m into the vegetation (Figure 2). We used these relative elevation data in conjunction with hourly monitoring of tide height to estimate frequency and duration of marsh flooding in each pond. Data loggers (HOBO, Onset Corporation, Bourne, Massachusetts) were used to record hourly water depth and temperature and were placed near the center of the ponds at an elevation approximately 1 m lower than the edge to ensure submersion throughout the study period. We assumed that the marsh was flooded when the water depth at the marsh edge reached 10 cm, the point in our IBM at which shrimp can access the marsh vegetation.

Brown shrimp growth estimates.— We conducted mark–recapture studies in each experimental pond. We collected brown shrimp in each pond using a bag seine and sorted them into 2-mm-TL size-classes between 30 and 50 mm. We selected two to four size-classes for tagging based on the size-classes that were most abundant. We attempted to tag at least 300 shrimp during each sampling effort; however, the number of shrimp tagged varied over the study period due to shrimp availability (Table 1). We tagged shrimp

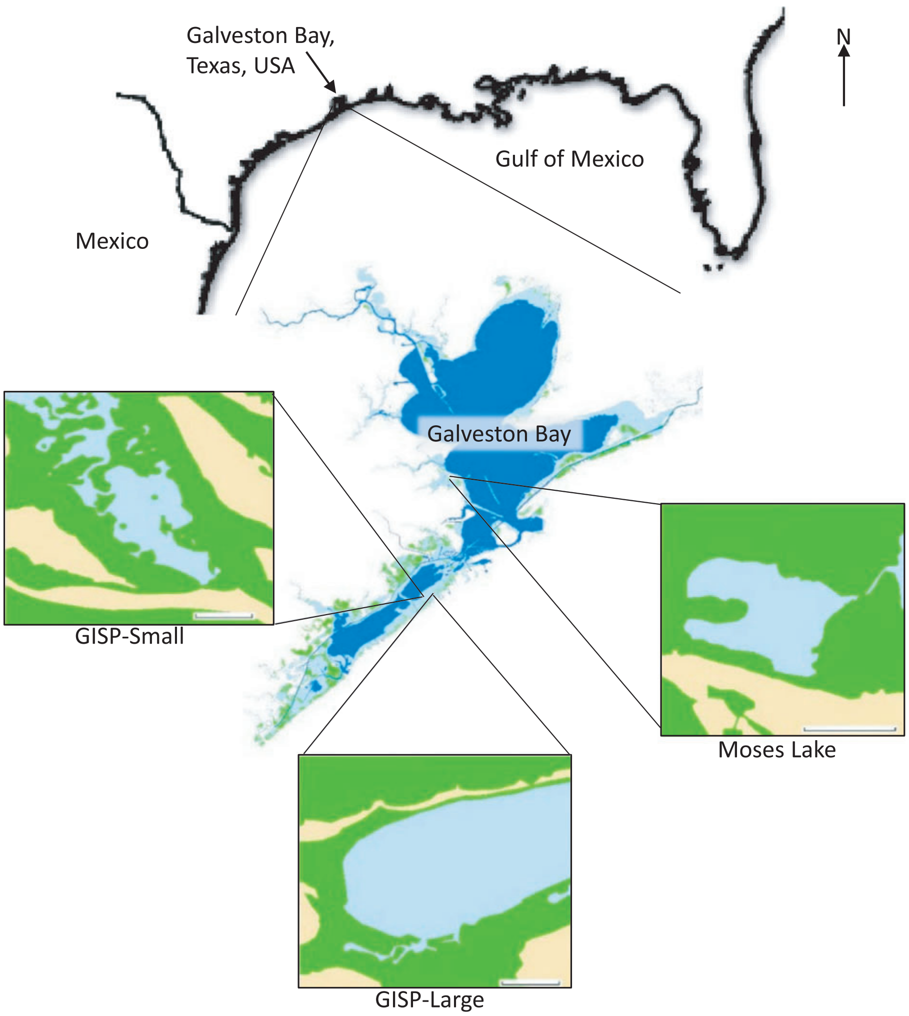

FIGURE 1. The three experimental ponds located within Galveston Bay, Texas, used in the mark–recapture growth study of brown shrimp. GISP-Small and GISP-Large ponds are in West Bay inside the Galveston Island State Park. The Moses Lake pond is located 20 km to the north of the park and north of the Texas City Dike. Green indicates the marsh vegetation and light blue indicates the nonvegetated shallow ponds. Dark blue indicates areas of water deeper than 1 m and were not included in the model estimates. The scale bar in the detailed images of ponds represents 20 m.

ventrally in the muscle of the sixth abdominal segment using Visible Implant Elastomer (VIE; Northwest Marine Technology, Shaw Island, Washington). Tagging has shown no effect on growth in lab studies (Baker and Minello 2010). Each size-class had a unique tag color. Tag colors were not duplicated in the same pond during the length of the study.

Tagging and recovery efforts occurred in all three ponds between April and June 2011 (Table 1). There were five visits to GISP-Small ponds and three each at GISP-Large ponds and Moses Lake. During this time, we tagged and released 2,251 shrimp. Total length (mm) of recovered tagged shrimp was measured, and their tag color was recorded. Growth rate was calculated for recovered, tagged shrimp color groups by subtracting the initial mean TL from the mean final TL and dividing by the number of days at large.

Mortality is closely linked to brown shrimp size and therefore growth, because mortality rates are size dependent. Our original methodology included data collection for mortality estimates. Complications in the field violated assumptions of our mortality estimate methodology, rendering them invalid. In the Discussion, we describe how the lack of mortality estimates from the field project could cause errors when comparing modeled output with field observations.

Brown shrimp production model overview.— The Leo et al. (2016) model is a spatially explicit IBM that simulates the cumulative effects of temperature, salinity, and access to emergent marsh vegetation on the growth and

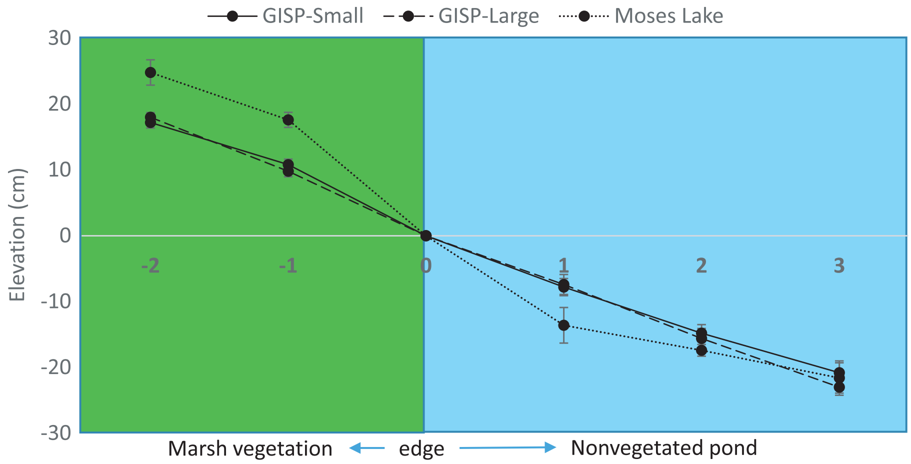

FIGURE 2. Elevation profiles of GISP-Small, GISP-Large, and Moses Lake ponds. Elevations are relative to the marsh vegetation–open water interface (at zero on the horizontal axis); error bars represent ±1 SE.

TABLE 1. Sampling schedule in 2011 for three growth study ponds, size of tagged brown shrimp, and the number of recaptured tagged shrimp. The total number of shrimp recaptured during each date of recapture is given in parentheses. We recaptured 5.5% of tagged individuals, overall.

Site	Tagging date	Size-class (mm TL)	Tagged shrimp	Recaptured shrimp	Dates of recapture
GISP-Small	Apr 12	34	32	1	Apr 26 (1)
		38	16	1	Apr 26 (1)
		46	13	1	Apr 26 (1)
	Apr 26	32	78	6	May 10 (4)
					May 24 (2)
		36	213	9	May 10 (8)
					May 24 (1)
	May 10	34	187	25	May 24 (24)
					Jun 7 (1)
		36	175	19	May 24 (19)
	May 24	36	167	5	Jun 7 (5)
		38	157	1	Jun 7 (1)
	Jun 7	40	47		
		42	37		
	Total		1,122	68 (6.1%)	
GISP-Large	Apr 21	36	195	9	May 12
		40	156	8	May 12 (7)
					Jun 1 (1)
	May 12	32	89	9	Jun 1
		36	117	5	Jun 1
		40	120	8	Jun 1
	Total		677	39 (5.8%)	
Moses Lake	Apr 20	34	43	3	May 5
		36	40	2	May 5
		42	31	3	May 5
		44	38	3	May 5
	May 5	36	162	4	Jun 2
		40	138	2	Jun 2
	Total		452	17 (3.8%)	
Grand total			2,251	124 (5.5%)	

survival of young brown shrimp. The model is parameterized to represent the environmental conditions and habitat characteristics of Galveston Bay. Individual shrimp recruit to the system and may grow or die on an hourly time step. Growth has a base value that is modified by temperature, salinity, and habitat (vegetated or nonvegetated). Mortality also has a base value that is modified by size (mm TL) and habitat. Depending on the tide height, shrimp may move between vegetated and nonvegetated habitats at each time step. Shrimp that move into vegetated habitat benefit from a slight increase in growth rate and a decrease in mortality risk.

To compare model output with our field growth study, in which all three ponds remained polyhaline, all cells in the model were parameterized with zone 3 salinity (≥20‰). In all salinity zones, modeled growth rates increase with temperature, peak around 30°C, and then slow substantially. Expected hourly water temperature values (EXP_T) in nonvegetated habitat are determined in the model by using the median daily air temperature (https://www.ncdc.noaa.gov/cdo-web/datatools) and relationships developed with daily median water temperature and a diel pattern of deviation from that median. From this, the model calculates water temperature in vegetated habitat based on an empirical relationship developed from unpublished data comparing water temperatures in vegetated and nonvegetated habitat.

Flooding of the marsh surface gives shrimp access to additional infaunal prey for increased growth (Whaley and Minello 2002; Roth et al. 2008) and is a function of both tidal dynamics and marsh topography (Rozas 1995; Minello et al. 2012). The model determines expected marsh flooding (EXP_F) by comparing the elevation of marsh edge in Galveston Bay with hourly water level data from the NOAA tide gauge located at Pier 21 in the Galveston ship channel (station number 8771450; https://tidesandcurrents.noaa.gov/waterlevels.html?id=8771450). When the tide gauge reads 10 cm higher than the marsh edge elevation, the vegetated marsh habitat cells become accessible to the modeled shrimp. The tide–elevation relationship is adjusted annually in the model for the effects of relative sea level rise. Appendix 1 in Leo et al. (2016) provides a complete model description in overview, design concepts, and details (ODD) protocol as outlined by Railsback and Grimm (2012).

Model evaluation.— We ran 10 simulations of the Leo et al. (2016) model using temperature and tide data available for 2011. Previous modelling showed that 10 replicates were sufficient to capture variability between model runs. These inputs generated hourly EXP_T and EXP_F values in the model, which we compared with actual temperature (ACT_T) and flooding (ACT_F) values recorded in each pond. Then we calculated the mean modeled daily growth rate (±SE) during the period specific to each pond (Table 2). We compared the modeled growth rate with the actual growth rate estimate from each pond. Then we parameterized the model with the pond-specific ACT_T and ACT_F values to see whether differences between modeled growth rates and actual growth rates could be caused by differences between actual and modeled tide and temperature values. To identify which parameters might drive differences between modeled and actual growth rates, we reparameterized the model twice more with (1) model-estimated temperatures and pond-specific actual flooding (EST_T, ACT_F) and (2) pond-specific actual temperatures and model-estimated flooding (ACT_T, EST_F). We ran 10 simulations under each scenario and determined the pond-specific modeled growth rates.

Infauna.— We examined the availability of infaunal food organisms by sampling benthic infauna at the beginning and end of the growth study to estimate abundance before and after peak marsh residence of brown shrimp. Benthic collections were performed in 2011 between April 12 and June 7 at GISP-Small, April 21 and June 1 at GISP-Large, and April 20 and June 2 at Moses Lake. We collected benthic cores in each pond and measured infaunal abundance and biomass in relation to the distance from the marsh edge. Ten replicate cores were collected at each of three distances from the marsh edge: 1 m into the vegetation, 1 m into the nonvegetated pond, and 5 m into the nonvegetated pond. We selected these collection sites randomly along the length of the marsh edge interface. At

TABLE 2. Comparison of modeled and actual temperature, flooding, and growth rate of brown shrimp, by pond.

	GISP-Small		GISP-Large		Moses Lake	
Variable	Actual	Modeled	Actual	Modeled	Actual	Modeled
Mean water temperature (range) (°C)	26.3 (14.6–33.3)	27.6 (16.8–38.7)	26.4 (14.6–34.8)	27.1 (14.6–34.8)	26.1 (13.6–37.7)	27.0 (13.6–36.7)
% time flooded	75.4	77.1	78.2	77.4	63.8	77.6
Growth rate (SE) (mm/d)	1.02 (0.030)	1.13 (0.011)	1.03 (0.027)	1.15 (0.012)	1.26 (0.058)	1.15 (0.011)

each site, we randomly collected three 5-cm-diameter sediment cores from within a 1-m^2 quadrat and then pooled the three cores for further analysis. This approach resulted in 180 core samples (10 replicates × 3 distances from edge × 3 ponds × 2 collection periods), each representing an area of 58.9 cm^2. In the lab, we counted, dried (at 100°C for 24 h), and weighed crustaceans and annelids as the main food sources for brown shrimp (Whaley and Minello 2002). We estimated prey biomass per square meter as the mean sum of the dry weight of annelids and crustaceans (g/m^2) at three distances from the marsh edge.

Data analysis.— We calculated mean growth rates for recovered shrimp in each of the three ponds. After testing for homogeneity of variance (F-max test), we used an ANOVA and Tukey's honest significant difference (HSD) test to compare growth rates among ponds. We used regression analysis to examine effects of size, temperature, and flooding duration on shrimp growth and to examine the relationships between measured growth and modeled growth. We also calculated regressions between ACT_T and the EXP_T. We evaluated the flooding submodel by comparing hourly the ACT_F (where "flooded" = 10 cm or greater water over the edge elevation) to the EXP_F. We used an ANOVA and Tukey's HSD test to compare growth rates between tide and temperature scenarios within each pond. Finally, we used a two-way ANOVA to compare infaunal biomass among ponds and distances (1 m, −1 m, −5 m) from the marsh edge. We conducted this analysis separately for the infaunal data collected before and after the growth study.

RESULTS

Pond Characteristics

Based on our analyses of infrared aerial photographs, we estimated that the GISP-Small pond's nonvegetated area was 668 m^2 and had 244 m of marsh edge–open water interface. The edge was highly reticulated and enclosed small islands of saltmarsh cordgrass within the pond. GISP-Large pond had 3,299 m^2 of nonvegetated area and 268 m of marsh edge interface. The Moses Lake pond area was 471 m^2 and had 132 m of marsh edge (Figure 1). A comparison of elevation profiles between ponds showed that the Moses Lake profile was slightly steeper than those in GISP, and that both ponds within GISP had similar profiles (Figure 2).

During the GISP-Small study period, the marsh edge was observed flooded (greater than 10 cm of water depth over the edge elevation) 75.4% of the time (Figure 3), and hourly observed water temperatures ranged from 14.6°C to 33.3°C (Figure 4) with a mean of 26.3°C. At GISP-Large, marsh edge was observed flooded 78.2% of the time (Figure 3), and observed water temperatures ranged from 14.6°C to 34.8°C (Figure 4) with a mean of 26.4°C. Moses Lake marsh edge was observed flooded 63.8% of the time (Figure 3), and observed water temperatures ranged from 13.6°C to 37.7°C (Figure 4) with a mean of 26.1°C. Salinity in each of the three ponds measured during each shrimp tagging–recapturing effort ranged from 24‰ to 29‰.

Brown Shrimp Growth

Over the course of the study, we recovered 5.5% of the 2,251 tagged brown shrimp from all three marsh ponds (Table 1). The mean growth rate of recaptured shrimp in GISP-Small, GISP-Large, and Moses Lake was 1.02 (SE = 0.030, n = 68), 1.03 (SE = 0.027, n = 39), and 1.26 (SE = 0.058, n = 17) mm TL/d TL, respectively (Table 2). The mean growth rate of all recaptured shrimp from all ponds was 1.06 mm TL/d (SE = 0.021, n = 124). Growth rate was significantly higher in Moses Lake than in either GISP pond (ANOVA and Tukey's HSD test: P = 0.0004). During the periods between tagging efforts, the pond-

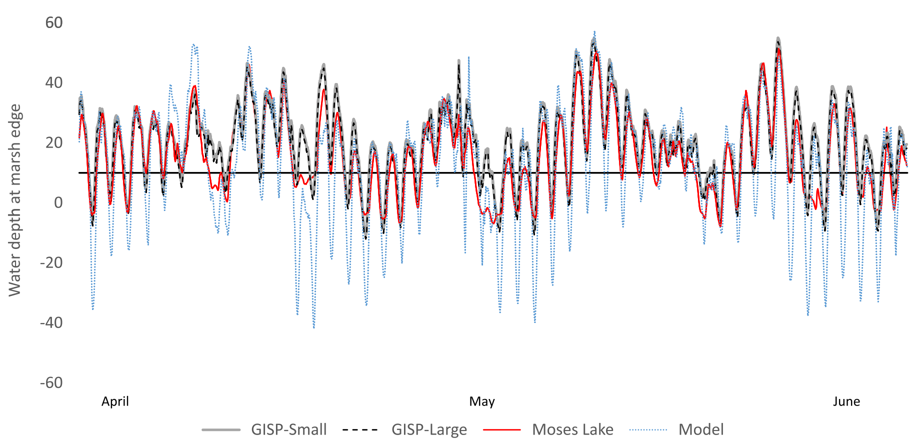

FIGURE 3. Model-estimated flooding plotted with actual flooding in the GISP-Small, GISP-Large, and Moses Lake ponds. When the water depth reaches 10 cm over the marsh edge (horizontal line), brown shrimp in the model simulation can move into marsh vegetation.

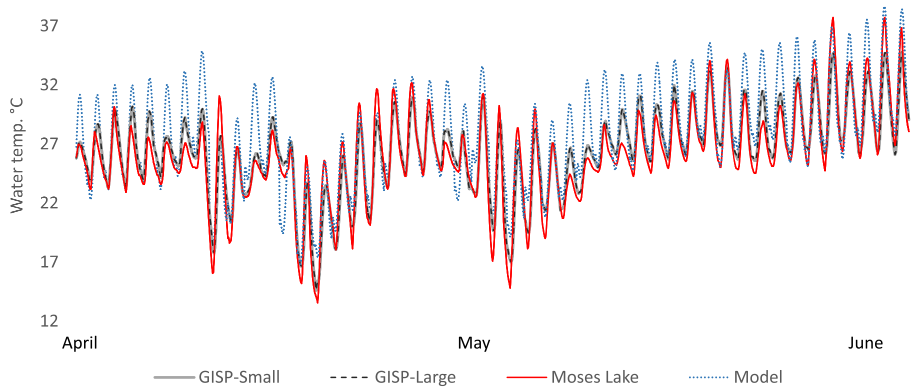

FIGURE 4. Model-estimated temperatures plotted with actual temperatures in the GISP-Small, GISP-Large, and Moses Lake ponds.

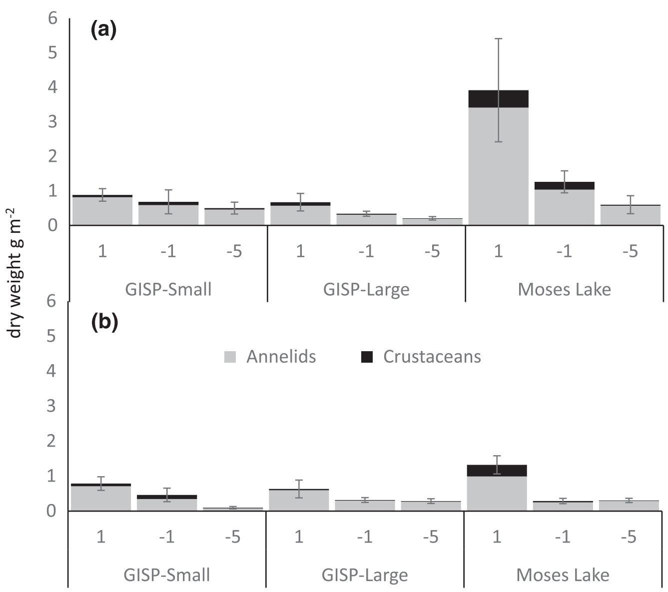

FIGURE 5. Average biomass (g/m^2 dry weight) of annelids and crustaceans at three distances from the marsh edge (1 m into the vegetation, −1 m and −5 m into the nonvegetated habitat). In each pond, samples were taken at the **(A)** start (initial samples) and **(B)** end (final samples) of the field project. Error bars represent ±1 SE. Initial samples were taken on April 12, 21, and 20, 2011, for GISP-Small, GISP-Large, and Moses Lake, respectively. Final samples were taken on June 7, 1, and 2, 2011, for GISP-Small, GISP-Large, and Moses Lake, respectively.

specific mean growth rate estimates ranged from 0.92 to 1.50 mm TL/d. There was no significant relationship between mean daily temperature and these growth rates (P = 0.223, R^2 = 0.012). In addition, there was no significant relationship between flooding duration and growth rate (P = 0.072, R^2 = 0.027). This lack of a relationship was likely due to the small range in mean values over those periods (mean daily temperature range: 24.2–29.1°C, flooding duration range: 71–82%). There was a weak but significant positive relationship between initial size group and growth rate (P = 0.006, R^2 = 0.060).

Model Evaluation

Modeled brown shrimp growth at GISP-Small averaged 1.13 mm TL/d (SE = 0.011). Estimated hourly water temperature ranged from 16.8°C to 38.7°C, with a mean of 27.6°C (Figure 4). A regression of modeled versus actual temperatures gave an R^2 value of 0.827 (P < 0.0001). Modelled marsh flooding occurred 77.1% of the time, correctly predicting actual flooding occurred 90% of the time (Figure 3). Actual and modeled growth, temperature, and flooding values for each pond are given in Table 2. When the model was reparameterized, growth rate was 1.22 mm TL/d when pond-specific actual temperature and flooding values (ACT_T, ACT_F) were used, 1.15 mm/d when estimated temperature and pond-specific actual flooding values (EST_T, ACT_F) were used, and 1.21 mm/d when actual temperature and estimated flooding values (ACT_T, EST_F) were used. Modelled growth rate was significantly lower when EST_T (P = 0.0019) was used.

At GISP-Large, the mean modeled growth rate was 1.15 mm TL/d. Estimated water temperatures ranged from 14.6°C to 34.8°C with a mean of 27.1°C (Figure 4). A regression of modeled versus actual temperatures gave an R^2 value of 0.826 (P < 0.0001). Modelled marsh flooding occurred 77.4% of the time and correctly predicted actual flooding occurred 90% of the time (Figure 3). When the model was reparameterized, growth rate was 1.23 mm TL/d when pond-specific actual temperature and flooding values (ACT_T, ACT_F) were used, 1.17 mm/d when estimated temperature and pond-specific actual flooding values (EST_T, ACT_F) were used, and 1.20 mm/d when actual temperature and estimated flooding values (ACT_T, EST_F) were used. Again, modelled growth rate was significantly lower when EST_T (P = 0.0020) was used.

At Moses Lake, the mean modeled growth rate was 1.15 mm TL/d. Estimated temperatures ranged from

13.6°C to 36.7°C with a mean of 27.0°C (Figure 4). A regression of modelled versus actual temperatures showed an R^2 value of 0.772 ($P < 0.0001$). Modelled flooding occurred 77.6% of the time and correctly predicted actual flooding occurred 82% of the time (Figure 3). When the model was reparameterized, growth rate was 1.14 mm TL/d when pond-specific actual temperature and flooding values (ACT_T, ACT_F) were used, 1.13 mm/d when estimated temperature and pond-specific actual flooding values (EST_T, ACT_F) were used, and 1.16 mm/d when actual temperature and estimated flooding values (ACT_T, EST_F) were used. These values were not significantly different among scenarios ($P = 0.0801$).

Infauna

Annelids made up the bulk of benthic infauna (Figure 3) and comprised an average of 85% of the total biomass. At the initial sampling period in all ponds, biomass was significantly higher (ANOVA and Tukey's HSD test: $P = 0.0065$) in the vegetated samples than in the nonvegetated samples. Mean biomass tended to be lowest in the samples collected in the nonvegetated locations 5 m away from the edge, but overall the nonvegetated biomass was not significantly different between the two distances. Moses Lake had significantly greater annelid and crustacean biomass (ANOVA and Tukey's HSD test: $P < 0.0021$), and more than four times the biomass occurred in the vegetated habitat samples than in those from either GISP pond. There was a significant interaction between pond and sample location ($P = 0.0365$). At the conclusion of the study, there was no difference in biomass between the ponds. Biomass in the vegetation, however, was significantly higher ($P < 0.0001$) than that in the nonvegetated samples in all ponds.

DISCUSSION

We used field estimates of brown shrimp growth from three marsh ponds in Galveston Bay to evaluate the performance of an individual-based model. The model's estimate of mean daily growth rate of shrimp during the field study was within 0.07–0.09 mm/d of the mean daily growth rate observed in the field demonstrating that the model is useful in predicting growth of brown shrimp at least within the tide and temperature parameters observed within the field study period. The mark–recapture approach to measuring shrimp growth in the field has the potential to overestimate growth through the selection of faster-growing animals for recapture since survival rates are size dependent, and slower-growing shrimp may experience higher mortality than relatively faster-growing shrimp. Growth rate values observed from our recaptured brown shrimp, however, were normally distributed and in a wide range (0.29–1.86 mm/d). Additionally, our mean estimates of growth rate are comparable (0.52–1.90 mm/d) to the results of brown shrimp growth experiments using a variety of methodologies: field caging, laboratory growth experiments, von Bertalanffy growth curve construction, and other methods of mark–recapture, which are not subject to the same artifacts (Zein-Eldin 1963; Chávez 1973; Knudsen et al. 1977; Rozas and Minello 2011). We were unable to account for mortality rates in our field study. If we make the assumption that the shrimp tagged in each size-class have growth rates normally distributed around some mean, and if mortality rates are higher for slower-growing individuals in the tagged group, then it is possible that the majority of recaptured shrimp are on the faster-growing end of that normal distribution, which would thus skew the growth rate estimates. However, if faster- and slower-growing shrimp are normally distributed among the marsh pond locations, we should still be able to detect relative differences in growth rates among the ponds in the study.

In the model, growth is driven by temperature and marsh flooding. The temperature submodel based on median air temperature performed well when we compared estimated temperature values EXP_T with actual data ACT_T from the individual ponds ($R^2 = 0.827$, 0.826, and 0.772 for GISP-Small, GISP-Large, and Moses Lake, respectively). In general, ACT_T temperature maxima were cooler than EXP_T temperature maxima. The EXP_F submodel determines when the marsh vegetation is flooded based on elevation data. Edge elevation profiles from all three ponds are well within the estimated mean edge elevations of *Spartina* marshes in Galveston Bay (Minello et al. 2012, 2015). The model predicted that marsh habitat would be flooded 77.1% of the time. This is within 2% of the ACT_F frequency of both the GISP-Small and GISP-Large ponds' actual flooding. The slightly steeper slope located at Moses Lake resulted in flooding almost 15% less frequently.

The EXP_T submodel predicted similar temperatures for all three ponds. The EXP_F was also similar for the three ponds. Since salinity did not change in the model, temperature and flooding were the only drivers of growth. These conditions resulted in similar growth rates among the three ponds. The ACT_T was also similar among ponds, but ACT_F was significantly lower at Moses Lake than at the GISP ponds. When ACT_T and ACT_F were used as model inputs, growth rates of shrimp in GISP-Small and GISP-Large ponds were slightly higher than in Moses Lake. These results were not consistent with our field study observations, suggesting that growth rate is not strictly predicted by temperature and flooding patterns.

Although brown shrimp in Moses Lake were exposed to lower temperatures than predicted by the model, as well as fewer opportunities to enter the marsh, they grew at a significantly higher rate than those in the model

TABLE 3. Pond-specific modeled growth rates (mm/d TL) for brown shrimp under estimated (EST) and actual (ACT) values of temperature ($_T$) and flooding ($_F$) compared with pond-specific actual growth rates.

	Conditions modeled			
Pond location and dates	Temperature	Flooding	Expected growth rate (SE)	Actual growth rate (SE)
GISP-Small	EST_T	EST_F	1.13 (0.011)	1.02 (0.030)
Apr 12–Jun 7	ACT_T	ACT_F	1.22 (0.010)	
	EST_T	ACT_F	1.15 (0.011)	
	ACT_T	EST_F	1.21 (0.010)	
GISP-Large	EST_T	EST_F	1.15 (0.012)	1.03 (0.027)
Apr 21–Jun 1	ACT_T	ACT_F	1.23 (0.010)	
	EST_T	ACT_F	1.17 (0.011)	
	ACT_T	EST_F	1.20 (0.011)	
Moses Lake	EST_T	EST_F	1.15 (0.011)	1.26 (0.058)
Apr 20–Jun 2	ACT_T	ACT_F	1.14 (0.010)	
	EST_T	ACT_F	1.13 (0.010)	
	ACT_T	EST_F	1.16 (0.011)	

simulations. Additionally, there was very little hourly difference between temperatures observed in GISP ponds and those in Moses Lake. Not only did the GISP ponds have a similar temperature pattern (on average, 0.33°C warmer), but the lower mean edge elevation resulted in longer and more frequent marsh vegetation flooding. Given those parameters only, one would expect estimates of shrimp growth rate at Moses Lake to be lower than that in either of the GISP ponds. Still, the mean growth rate estimate at Moses Lake was significantly higher.

Benthic infauna are an important food source for juvenile brown shrimp (McTigue and Zimmerman 1991). We observed significantly higher growth rates of shrimp in Moses Lake, the location with the highest infaunal abundance. We observed temporal patterns of higher infaunal abundance in spring and lower abundance in late summer. We also saw spatial patterns of abundance in which infauna were concentrated in vegetated edge habitat and less so in the shallow pond. These observations are consistent with Whaley and Minello (2002), in which they described a spatial pattern of benthic infaunal abundance at different distances from the marsh edge. Benthic infaunal abundance and biomass are highest in the first meter of vegetation, where shrimp access is limited by the tide. They also described a temporal pattern in which infaunal abundance is higher in spring and declines toward the end of summer, presumably the result of predation during the high tides of spring and early summer.

Based on these observations, the inclusion of benthic infauna data in our model may help resolve some of the differences between modeled and observed growth rates. However, the development and addition of these data may add an unnecessary layer of complexity to the model. The mean modeled growth rate under the conditions of 2011 was 1.13 to 1.15 mm/d (Table 3) but the actual growth rates were 1.02 to 1.26 mm/d. A 30-mm-TL brown shrimp growing at 1.02 mm/d would reach 70 mm TL (size at emigration) in 39 d, whereas one growing 1.26 mm/d would reach 70 mm TL in 31 d. The modeled shrimp growing 1.15 mm/d would reach 70 mm TL in 35 d. The benefit of slightly increasing the accuracy of modeled growth rates may not be worth the cost of developing the infaunal distribution data set and at the very least would depend on the spatial and temporal variability of the benthic infaunal distribution within Galveston Bay.

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REFERENCES

Baker, R., and T. J. Minello. 2010. Growth and mortality of juvenile white shrimp *Litopenaeus setiferous* in a marsh pond. Marine Ecology Progress Series 413:95–104.

Chávez, E. A. 1973. A study on the growth rate of brown shrimp (*Penaeus aztecus* Ives, 1891) from the coasts of Veracruz and Tamaulipas, Mexico. Gulf Research Reports 4:278–299.

Christmas, J. Y., and D. J. Etzold, editors. 1977. The shrimp fishery of the Gulf of Mexico United States: a regional management plan. Gulf Coast Research Laboratory, Ocean Springs, Mississippi.

Cook, H. L., and M. J. Linder. 1970. Synopsis of the biological data on the brown shrimp *Penaeus aztecus aztecus*, Ives, 1891. FAO (Food and Agriculture Organization of the United Nations) Fisheries Reports 57:1471–1497.

Fry, B. 2008. Open bays as nurseries for Louisiana brown shrimp. Estuaries and Coasts 31:776–789.

Haas, H. L., E. C. Lamon III, K. A. Rose, and R. F. Shaw. 2001. Environmental and biological factors associated with stage-specific abundance of brown shrimp (*Penaeus aztecus*) in Louisiana: applying a new combination of statistical techniques to long-term monitoring data. Canadian Journal of Fisheries and Aquatic Sciences 58:2258–2270.

Knudsen, E. E., W. H. Herke, and J. M. Mackler. 1977. The growth rate of marked juvenile brown shrimp, *Penaeus aztecus*, in a semi-impounded Louisiana coastal marsh. Proceedings of the Gulf and Caribbean Fisheries Institute 29:144–159.

Leo, J. P., T. J. Minello, W. E. Grant, and H.-H. Wang. 2016. Simulating environmental effects on brown shrimp production in the northern Gulf of Mexico. Ecological Modelling 330:24–40.

Mannino, A., and P. A. Montagna. 1997. Small-scale spatial variation of macrobenthic community structure. Estuaries 20:159–173.

McTigue, T. A., and R. J. Zimmerman. 1991. Carnivory versus herbivory in juvenile *Penaeus setiferus* (Linnaeus) and *Penaeus aztecus* Ives. Journal of Experimental Marine Biology and Ecology 151:1–16.

McTigue, T. A., and R. J. Zimmerman. 1998. The use of infauna by juvenile *Penaeus aztecus* Ives and *Penaeus setiferus* (Linnaeus). Estuaries 21:160–175.

Minello, T. J., L. P. Rozas, and R. Baker. 2012. Geographic variability in salt marsh flooding patterns may affect nursery value for fishery species. Estuaries and Coasts 35:501–514.

Minello, T. J., L. P. Rozas, S. P. Hillen, and J. A. Salas. 2015. Variability in salt marsh flooding patterns in Galveston Bay, Texas. NOAA Technical Memorandum NMFS-SEFSC-678.

Minello, T. J., and R. J. Zimmerman 1991. The role of estuarine habitats in regulating growth and survival of juvenile penaeid shrimp. Pages 1–16 *in* P. DeLoach, W. J. Dougherty, and M. A. Davidson, editors. Frontiers in shrimp research. Elsevier Scientific Publications, Amsterdam.

Minello, T. J., R. J. Zimmerman, and E. X. Martinez. 1989. Mortality of young brown shrimp *Penaeus aztecus* in estuarine nurseries. Transactions of the American Fisheries Society 118:693–708.

NMFS (National Marine Fisheries Service) Fishery Statistics Division. 2015. Available: https://www.st.nmfs.noaa.gov/commercial-fisheries/commercial-landings/annual-landings/index. (January 2017).

Railsback, S. F., and V. Grimm. 2012. Agent-based and individual-based modeling: a practical introduction. Princeton University Press, Princeton, New Jersey.

Renfro, W. C., and H. A. Brusher. 1982. Seasonal abundance, size distribution, and spawning of three shrimps (*Penaeus aztecus*, *P. setiferus*, and *P. duorarum*) in the northwestern Gulf of Mexico, 1961–1962. NOAA Technical Memorandum NMFS-SEFC-94.

Roth, B. M., K. A. Rose, L. P. Rozas, and T. J. Minello. 2008. Relative influence of habitat fragmentation and inundation on brown shrimp *Farfantepenaeus aztecus* production in northern Gulf of Mexico salt marshes. Marine Ecology Progress Series 359:185–202.

Rozas, L. P. 1995. Hydroperiod and its influence on nekton use of the salt marsh: a pulsing ecosystem. Estuaries 18:579–590.

Rozas, L. P., and T. J. Minello. 2009. Using nekton growth as a metric for assessing habitat restoration by marsh terracing. Marine Ecology Progress Series 394:179–193.

Rozas, L. P., and T. J. Minello. 2011. Variation in penaeid shrimp growth rates along an estuarine gradient: implications for managing river diversions. Journal of Experimental Marine Biology and Ecology 397:196–207.

Temple, R. F., and C. C. Fischer. 1967. Seasonal distribution and relative abundance of planktonic-stage shrimp (*Penaeus* spp.) in the northwestern Gulf of Mexico, 1961. U.S. National Marine Fisheries Service Fishery Bulletin 66:323–334.

Whaley, S. D., and T. J. Minello. 2002. The distribution of benthic infauna of a Texas salt marsh in relation to the marsh edge. Wetlands 22:753–766.

Zein-Eldin, Z. P. 1963. Effect of salinity on growth of postlarval penaeid shrimp. Biological Bulletin 125:188–196.