Relative influence of habitat fragmentation and inundation on brown shrimp *Farfantepenaeus aztecus* production in northern Gulf of Mexico salt marshes

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ABSTRACT: We used a spatially explicit individual-based model to investigate the relative influences of inundation and habitat fragmentation on brown shrimp *Farfantepenaeus aztecus* production in northern Gulf of Mexico (NGOM) salt marshes. The model simulates the mortality, growth, and movement of a population of brown shrimp from their arrival in *Spartina* salt marsh as post-larvae in spring to their emigration as sub-adults in summer and fall. We quantified production in terms of sub-adult export, growth production (a measure of total shrimp growth), and trophic transfer (total shrimp mortality). We utilized a factorial design to simulate shrimp on all combinations of 4 maps that represented an idealized progression of habitat fragmentation and 4 inundation regimes from each of 2 locations in the NGOM (Louisiana and Texas). We also quantified the configuration of the marsh landscape to determine if specific metrics could be utilized as a proxy for shrimp production within a single inundation regime. Our results indicate that inundation is more important than habitat fragmentation for determining sub-adult export, growth production, and trophic transfer, but that marsh configuration has a strong influence on shrimp production within a single inundation regime. Inundation affected all 3 measures of shrimp production, primarily due to decreased mortality incurred when shrimp have access to vegetation through marsh flooding. We conclude that simple metrics of marsh configuration are capable of adequate predictions of shrimp production in static landscapes, but future research must consider the dynamic relationship between inundation and marsh fragmentation to fully assess how these forces affect shrimp production.

KEY WORDS: *Farfantepenaeus aztecus* · Fragmentation · Inundation · Production · *Spartina* · Salt marsh · Gulf of Mexico · Estuaries · Individual-based model

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INTRODUCTION

The persistence and productivity of many species worldwide is threatened by habitat loss and fragmentation, and there are few areas in the world where these problems are more apparent than in coastal areas of the northern Gulf of Mexico (NGOM) (Britsch & Dunbar 1993, White & Tremblay 1995). In Louisiana alone, >1000 km² of coastal land, mostly comprised of fresh, brackish, and salt marshes, could be lost by 2018 without human mitigation (Reyes et al. 2000). Factors leading to land loss are numerous, and include natural deltaic processes such as erosion and subsidence as well as human modification of natural hydrology through freshwater diversion and canal building (Deegan et al. 1984, Day et al. 2007). The loss and fragmentation of *Spartina* salt marshes are of particular concern because this habitat provides a nursery function for many recreationally and commercially important fish and shellfish species (Zimmerman & Minello 1993, Beck et al. 2001, 2003).

The productivity of many estuarine-dependent species is tied to the presence or abundance of intertidal vegetation, such as mangroves, seagrass, and salt

marsh. Several studies from the NGOM and elsewhere have documented a positive relationship between fishery landings and the extent of intertidal vegetation (Zimmerman et al. 2000, Jackson et al. 2001, Loneragan et al. 2005, Manson et al. 2005). Vegetation provides increased foraging opportunities and shelter from predators (Rozas & Zimmerman 2000, Beck et al. 2001, Kraus & Secor 2005). Thus, the productivity of many species is tied to their ability to access intertidal vegetation (Weinstein 1979, Zimmerman et al. 1991, Kneib 1997), that is, in turn, controlled by both the amount of edge habitat (intersection of vegetation and water) and the local pattern of inundation (Weinstein et al. 2000, Minello et al. 2003). Patterns of nekton use related to marsh edge (e.g. Minello et al. 1994, Peterson & Turner 1994, Minello & Rozas 2002) and the role of inundation on species productivity (Zimmerman et al. 1991, Rozas 1995, Minello et al. 2003) are well documented. The relative importance of marsh fragmentation (i.e. marsh edge) versus inundation for species productivity, however, has received less attention.

Using field data to systematically assess the relative influence of habitat fragmentation and inundation patterns on estuarine species productivity is difficult. Most field investigations sample on coarse spatial scales (stations or transects) on a weekly to monthly basis, and are often restricted to using nekton density or indices of relative abundance (rather than productivity) to infer the importance of a given habitat (Baltz et al. 1993, Peterson & Turner 1994, Bretsch & Allen 2006). Results from field studies have been extrapolated to estimate how marsh fragmentation or altered inundation patterns could influence a given species (Zimmerman et al. 2000, Minello & Rozas 2002, Rozas et al. 2005), but the validity of these studies is limited by the combination of marsh conditions and inundation present during sampling. Short-term tidal fluctuations and fine-scale habitat heterogeneity can be critical to general predictions of species productivity, and the magnitude and influence of these fluctuations and heterogeneity can vary among geographic areas (Baltz et al. 1993, Peterson & Turner 1994, Minello & Rozas 2002). General extrapolations of productivity to often unobserved combinations of conditions are highly uncertain. Simulation modeling offers a complementary approach to field studies by integrating information into a framework that allows researchers to systematically explore the effects of marsh fragmentation and inundation patterns on species productivity.

In the present paper, we use a spatially explicit, individual-based model (IBM) to investigate and quantify the relative influence of habitat fragmentation and inundation patterns on the production of brown shrimp *Farfantepenaeus aztecus* in NGOM salt marshes. Spatially explicit IBMs are able to include habitat hetero-

geneity, while allowing individuals (rather than entire populations) to respond to environmental stimuli that can vary across space or through time (DeAngelis & Gross 1992, Tyler & Rose 1994). The model follows individual shrimp introduced as weekly cohorts from their arrival in a *Spartina* salt marsh–water complex in the spring to their emigration to off-shore areas in the fall. The model utilizes physical and biological data from 2 important but disparate geographic regions in the NGOM to guide model creation and corroboration, namely from Louisiana (Caminada Bay) and Texas (Galveston Bay). These locations represent a contrast in terms of the geological processes that led to marsh formation (Blum et al. 2002) and their inundation patterns (Marmer 1954); together these influence marsh structure and shrimp utilization of available habitat. We implement the model within a factorial design, in which we simulated shrimp production on combinations of habitat and inundation patterns associated with the Louisiana and Texas locations. We also use the simulation results to relate productivity to easily measurable aspects of landscape configuration. We wanted to determine if landscape proxies for shrimp production were possible because of the practical difficulties in estimating production directly from field sampling. Our approach relating structure to function in a coastal ecosystem (sensu MacArthur & Wilson 1967), provides useful information on how marsh fragmentation and inundation can affect the productivity of a key marsh-associated species.

MATERIALS AND METHODS

Model description. The model simulated the hourly growth, mortality, and movement of a population of individual brown shrimp *Farfantepenaeus aztecus* on 500×500 m maps of 1 m² grid cells classified as either vegetation or water. We simulated inundation on each map by cross-referencing water levels taken from USGS tidal gages with marsh elevation profiles, such that water levels could be tied to marsh elevations. Water levels, combined with the assigned elevation of each cell, determined water depth on each cell. The elevation of each cell was assigned based on the distance of each cell to its nearest edge cell. Water depth, which varied hourly, controlled which cells were accessible to shrimp. Simplifications intended to ensure a fair comparison among simulations included utilizing a single elevation profile on each map to assign elevations to spatial cells and eliminating temperature variation within a map. Each model simulation was for 364 d starting on 1 January. For simplicity and convenience of presentation in this paper, we use the labels 'Louisiana' and 'Texas' to contrast the source

of different habitat maps, water level patterns, and marsh elevation profiles. We recognize that the Louisiana and Texas labels are not truly unique because similar maps, water levels, and marsh elevation profiles are likely to occur in both locations. Our use of both information sources ensures results that are generally representative of possible alternative configurations of micro-tidal marsh ecosystems found in the NGOM. Our model is a much expanded version of an earlier model described by Haas et al. (2001).

Physical environment. We simulated shrimp on 4 habitat maps that represented an idealized progression of fragmentation in 2 specific locations in the NGOM: Caminada Bay in Louisiana (USA) and Galveston Bay in Texas (USA). At each location, we selected 500 × 500 m areas from aerial orthophotos digitized with GIS at 1 m resolution that approximated stages of increasing marsh fragmentation (solid, coarse, fine, and open; Fig. 1). Each 1 m^2 cell in the orthophoto was classified as vegetation or water. The Louisiana and Texas solid stage maps were both about 75% vegetation, the coarse and fine stage maps were 42 to 50% vegetation, and the open stage maps were about 20% vegetation.

Each hour, the water depth on each cell was computed by combining the water level for that hour (Fig. 2a) with an elevation assigned from marsh elevation profiles (Fig. 2b). Water levels were defined as the vertical offset (in cm) relative to zero being located at the marsh edge. We used observed hourly water levels from permanent NOAA tide gages located at Grand Isle, LA (Station ID 8761724) and at Pier 21 in Galveston, TX (Station ID 8771450), and incorporated time lags into each time series to account for the distances between the maps and the gage locations (Fig. 2a). Water levels at the gages were shifted by several hours until they agreed with short-term water level recordings made on-site at the map locations. Marsh elevation profiles were the mean of repeated measurements on transects taken in the vicinity of the orthophoto locations. The Louisiana marsh elevation profile showed a rapid change in elevation over a relatively small distance near the edge, typical of a cut-bank marsh, while the Texas profile showed a more gradual and less overall change in elevation with distance from the edge (Fig. 2b). To avoid unrealistic stranding mortality (T. Minello unpubl. data), we truncated the lowest Texas water levels (Fig. 2a) so they never dropped >14 cm below the marsh edge. On all maps, areas in water >50 m from the marsh edge were considered deep-water refuge areas in order to prevent marsh
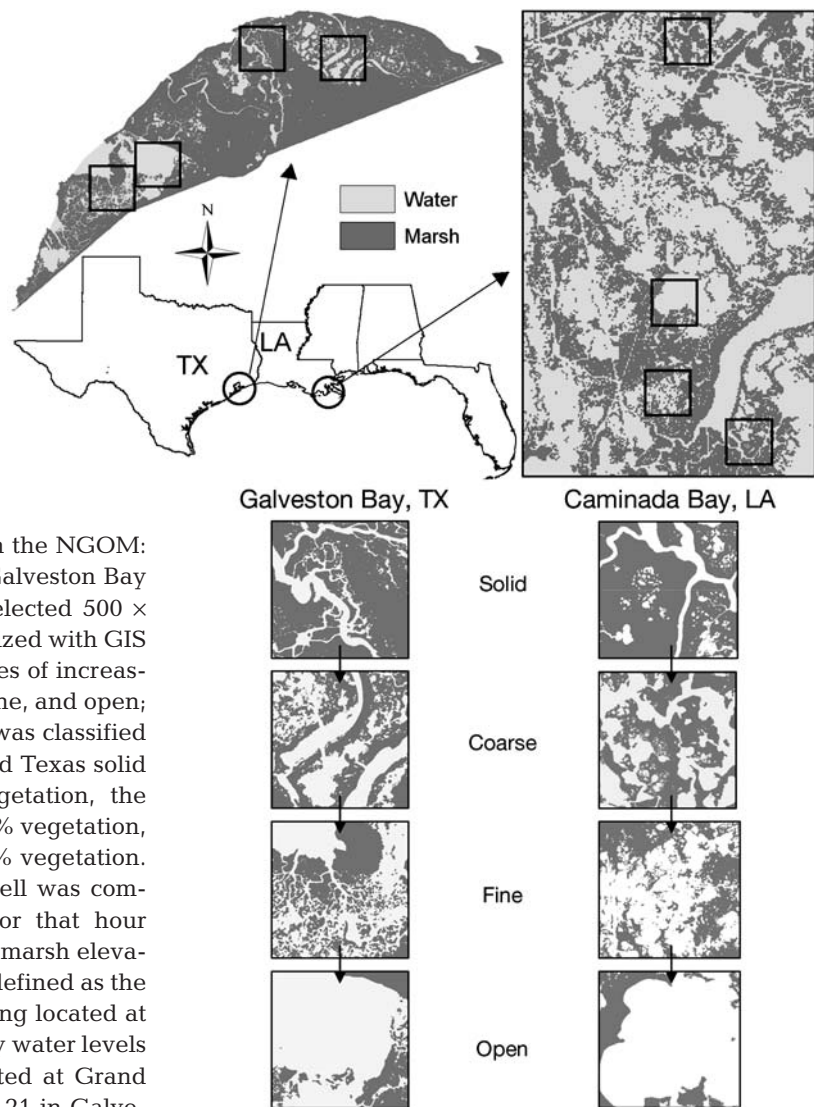

Fig. 1. Texas (Galveston Bay) and Louisiana (Caminada Bay) study areas and the solid, coarse, fine, and open stage map types extracted from the orthophotos. Darker areas indicate vegetation, while white areas indicate water

dewatering that would otherwise kill all shrimp in the simulation. However, all cells areas closer than 50 m to the marsh edge could drain during low-tide events.

Daily water temperature affected shrimp growth and was assumed constant over the spatial grid of cells and assumed the same for Texas and Louisiana (Fig. 2a). Comparison of water temperatures at the 2 permanent water level gages indicated daily water temperatures were more affected by season and regional metrological conditions than by specific map locations. In addition, using identical temperatures removed any Louisiana versus Texas temperature effect from our comparisons.

Post-larval introduction. Shrimp post-larvae were introduced into the model grid as weekly cohorts start-
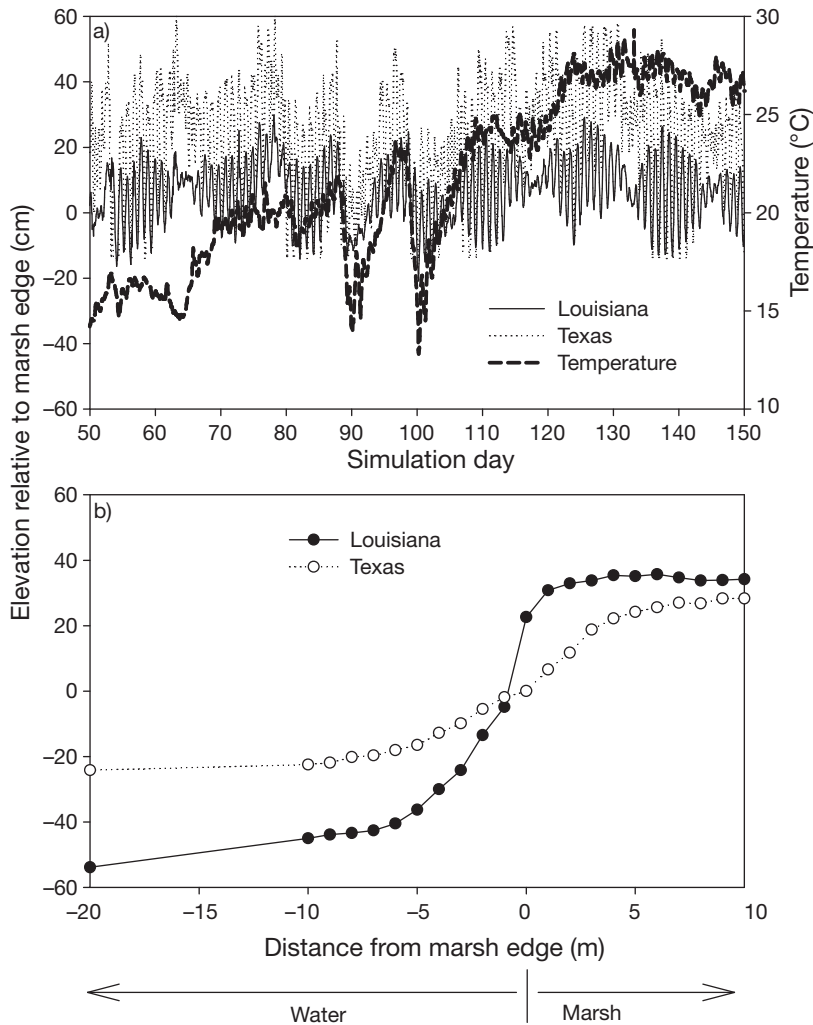
Fig. 2. (a) Water temperature and water levels for calendar Days 50 to 150 and (b) marsh elevation profiles used for simulations in Texas and Louisiana

ing in mid-February, peaking in mid-April (Rogers et al. 1993), and declining through the summer into the fall (Baxter & Renfro 1965) (Fig. 3). The summed number (total) of individuals introduced was 4×10^6 individuals and was used in all simulations. The log-normal-like pattern of cohort strengths was roughly based on the relative abundances of small shrimp (≤15 mm) in weekly field samples from Galveston Island State Park taken between 1982 and 1992 (Fig. 3); we assumed a single peak based on Baxter & Renfro (1965) and Rogers et al. (1993), although the integrated pattern from field data suggested either a broad single peak with high month-to-month variability or a bimodal distribution.

Growth, mortality, and movement. Each individual shrimp was assigned a baseline growth rate at the beginning of a simulation. The baseline growth rate was multiplied each hour by a water temperature effect, a food effect based on the shrimp's distance

from the marsh edge, and a density-dependent effect based on the standing stock (in grams) of all shrimp in the same cell (Table 1). The baseline growth rate (G_{BASE}) for each individual was initially selected from a normal distribution (mean = 1.0 mm d^{-1}, SD = 0.25 mm d^{-1}) (Lassuy 1983).

The temperature-based modifier (G_{TEMP}) followed the temperature-dependent respiration and consumption function from fish bioenergetics modeling (Hanson et al. 1997). The function rose slowly at a rate determined by θ (2.5), reached 1 at the assumed optimal temperature ($t_{opt} = 32°C$), and then declined to zero at the assumed maximum temperature ($t_{max} = 40°C$).

The distance-based growth modifier (G_{DIST}) was derived from the relationship between benthic infaunal abundance (preferred shrimp prey) and distance from the marsh-water edge (Rozas & Zimmerman 2000, Whaley & Minello 2002). These studies indicate that, throughout the summer, infaunal densities are higher in vegetated cells near the edge than in water cells near the edge, and densities decrease in both directions with increasing distance from the edge. Thus, G_{DIST} was assigned a value of 2 at the marsh edge and decreased monotonically inland, and was assigned a value of 1.64 at the water edge and a value of 1 in all water cells farther from the edge.

The density-dependent growth modifier (G_{DENS}) followed a logistic-shaped function. G_{DENS} reached a high asymptote of 1.04 at low shrimp standing stocks and a low asymptote value of 0.96 at high shrimp standing stocks (Haas et al. 2001). Shrimp standing stock was computed in a cell by summing the individual shrimp weights (wet weight, in grams), computed from their individual lengths (mm) using a total length–wet weight relationship (weight = 0.0000037 × length$^{3.16}$). The density-dependent effect on growth and movement (below) were the only situations when the absolute shrimp densities mattered in model simulations, as they determined the magnitude of the density-dependent effect. We specified the function G_{DENS} to have a value of 1 at a shrimp standing stock of ~8 g m^{-2}, which was consistent with high values that occurred in cells in model simulations with the introduction of 4×10^6 post-larvae.

The survival status of each shrimp was evaluated hourly. The overall mortality rate was computed by multiplying a baseline mortality rate ($Mort_{BASE}$) by functions related to shrimp size, habitat type, and

movement (Table 1). The baseline mortality rate of $0.00083 \ h^{-1}$ was consistent with field-derived mortality rate estimates averaged over many studies and environmental conditions (Minello et al. 1989). The size-based modifier ($Mort_{SIZE}$) declined exponentially with shrimp length, the habitat-based modifier ($Mort_{HAB}$) doubled the mortality rate when the shrimp was not in vegetation (Minello et al. 1989), and the movement-based modifier ($Mort_{MOV}$) increased linearly with distance traveled (number of cells moved) each hour (Table 1). A random number from a uniform 0 to 1 distribution was generated each hour, and if the drawn number was less than the probability of dying for the hour ($1 - e^{Mort_{BASE} \cdot Mort_{SIZE} \cdot Mort_{HAB} \cdot Mort_{MOV}}$), the individual shrimp was killed and removed from the simulation.

Individual shrimp moved hourly via either attraction-based or emergency-based movement algorithms. Shrimp utilized an attraction-based movement algorithm when an individual's current cell remained submerged (≥5 cm deep) for at least the next 3 h, and switched to the emergency-movement algorithm when water depth dropped below 5 cm within the next 3 h.
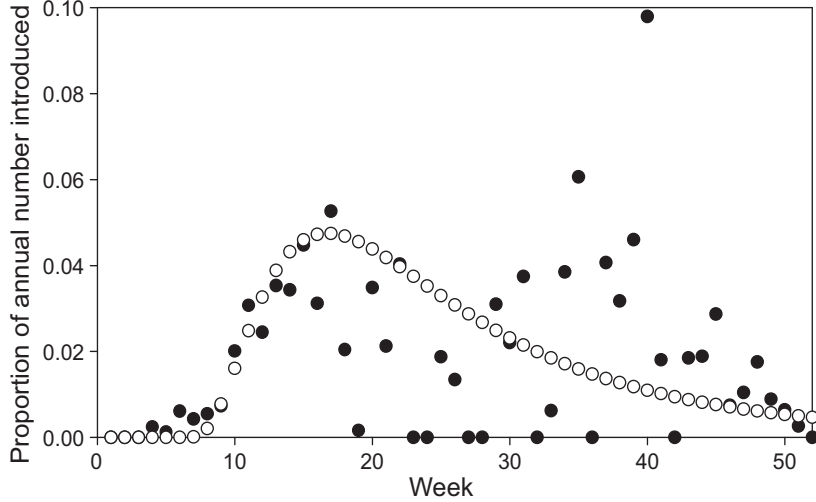

Fig. 3. *Farfantepenaeus aztecus.* Weekly proportional cohort strength of post-larval shrimp relative to the annual total in model simulations (O) and in empirical sampling (●). The total number of shrimp introduced in all simulations was 4.0×10^6, thus the total number of shrimp introduced each week was equal to the proportional cohort strength multiplied by 4.0×10^6

Table 1. Description and values of growth, mortality, and movement relationships in the individual-based model

Parameter	Description	Value/Function	Units
G_{BASE}	Baseline growth	$N(\mu,\sigma)$, where $\mu = 1$ and $\sigma = 0.25$	mm d^{-1}
G_{TEMP}	Temperature modifier	$v^x \exp[x(1 - v)]$, where $\quad w = \ln(\theta) \times (t_{max} - t_{opt})$ $y = \ln(\theta)(\ t_{max} - t_{opt} + 2)$ $x = \{w^2[1 + (1 + 40/y)^{0.5}]^2\}/400$ $v = (t_{max} - temp_t)/(t_{max} - t_{opt})$ $\theta = 2.5, \ t_{opt} = 32(°C), \ t_{max} = 40(°C)$	unitless unitless
G_{DIST}	Distance modifier	$1.69 \times (distance)^{-0.657}$ in marsh cells >1 m from edge 2 in marsh edge cells 1.64 in water edge cells 1 in all water cells >1 m from edge	unitless
G_{DENS}	Density-dependent modifier	$1.04 - 0.082/\{1 + \exp[-(cell \ biomass - 7.93)/2.0]\}$	unitless
$Mort_{BASE}$	Baseline mortality rate	0.00083	h^{-1}
$Mort_{SIZE}$	Size modifier	$53.092 \times length^{-1.1163}$	unitless
$Mort_{HAB}$	Habitat modifier	1 in marsh cells 2 in water cells	unitless
$Mort_{MOV}$	Movement modifier	(distance moved) $\times$ 0.0089 + 0.9556	unitless
Mot	Motility	1 for shrimp ≤30 mm, 2 for shrimp >30 and ≤45 mm 3 for shrimp >45 mm and then multiplied by 3 if in water cells	m h^{-1}
Mov_{DIST}	Attraction-based movement modifier	$1.69 \times (distance)^{-0.052}$ in marsh cells >1 m from edge 2 on marsh edge $1 + [0.2667\exp(0.2877 \times distance)]$ in all water cells	unitless
Mov_{DENS}	Density-dependent modifier	$1.04 - 0.082/\{1 + \exp[-(cell \ biomass - 7.93)/2.0]\}$	unitless
Mov_{RAND}	Random shock	$N(\mu,\sigma)$, where $\mu = 0$ and $\sigma = 2$	unitless

In attraction-based movement, shrimp evaluated the attractiveness of all cells within their neighborhood (following the 8-neighbor rule) and moved to the cell with the highest attractiveness index. The size of the neighborhood was defined by the motility (Mot) value that specified the number of cells to examine in all directions from an individual's current cell. Motility increased from 1 to 3 based on shrimp length, and was multiplied by 3 if the shrimp was located in a water cell. The attractiveness index was computed as a continuous value for each cell in the neighborhood as the product of a distance from edge function (Mov_{DIST}) and a density-dependent effect (Mov_{DENS}), plus a random component (Mov_{RAND}). The distance from edge multiplier (Mov_{DIST}) was derived to match field observations of shrimp densities relative to their distance from the marsh edge. Mov_{DIST} decreased more slowly from its peak value in marsh edge into vegetation than the distance effect for the growth rate (G_{DIST}), and continued to decrease below 1 with distance from edge into water cells. The density-dependent effect for movement (Mov_{DENS}) was the same function that was used for the density-dependent adjustment of the growth rate (G_{DENS}). A normal random deviate with mean zero and SD = 2.0 (Mov_{RAND}) was added to the attractiveness index of each cell in the neighborhood to simulate a variety of sources of uncertainty, such as our ignoring fine-scale heterogeneity in the marsh-elevation profiles and mistaken interpretation of environmental gradients by individual shrimp.

The emergency-movement algorithm was activated when the water depth dropped below 5 cm in an individual's current cell any time in the next 3 h. Emergency movement used water depths in cells, rather than the attractiveness index, to select destination cells. Emergency movement was used until the shrimp either died from stranding or reached a cell that had water deeper than 5 cm for the next 3 h, after which the attractiveness-based movement was resumed. Under emergency movement, shrimp expanded their motility (neighborhood) to 75 cells in all 8 directions and moved to the closest cell that would remain submerged for the next 3 h. Our selection of 3 h, while somewhat arbitrary, represents the least amount of time that was necessary to allow shrimp to respond to falling water levels and move to deeper areas. If no safe cells were available, the shrimp moved to the cell within the expanded neighborhood with the lowest elevation. If the shrimp had to settle for the lowest cell, then the algorithm was used again within the hour with the lowest elevation cell as the starting point. A shrimp either ended up in a cell that would remain submerged for the next 3 h or in the lowest elevation cell (after 2 tries) and emergency movement was applied again for the next hour. A shrimp was allowed to be in a dry cell for 5 consecutive hours, after which it was considered to have died from stranding. The emergency-movement algorithm is analogous to rheotactic movement, where a shrimp is able to sense outgoing water currents and retreats to a safe area if possible, but if not possible, then remains in small depressions or burrows into the sediments until desiccation, thermal stress, or anoxia leads to mortality after a few hours (Kneib 1997).

Production and landscape metrics. We quantified shrimp production on the habitat maps in 3 ways: growth production, sub-adult export, and trophic transfer. Growth production was defined as the sum of hourly weight changes over all live shrimp over all days in the simulation. Sub-adult export was computed as the total number of individual shrimp that reached a length of 70 mm during the simulation, which we assumed then emigrated from our simulated marsh and were no longer evaluated in the simulation. We considered shrimp mortality to be mostly predation and thus the biomass transferred to higher trophic levels (Haas et al. 2001). Trophic transfer was computed as the sum of the weights of all shrimp (determined from the lengths) at their death. Because growth of individuals is always positive, the sum of the biomass of sub-adult exports and trophic transfer equals total production. We include growth production as a separate measure because it provides additional information on how growth of individual shrimp, even those that eventually die, contributes to production.

We quantified the spatial configuration of water and vegetated cells on the habitat maps to determine if landscape configuration metrics can be used as a proxy for the 3 measures of shrimp production. We used the software program FRAGSTATS (McGarigal et al. 2002) to calculate metric values on all 8 maps. FRAGSTATS offers hundreds of landscape metrics that might be useful for our purpose; we selected a limited number that related to shrimp access to the marsh surface, which would likely thereby affect shrimp production (Zimmerman et al. 1991, 2000, Minello et al. 1994). The metrics used were measures of marsh abundance (percent of the landscape that is marsh), the amount of marsh-water edge (edge distance, in meters), landscape contiguity (clumpiness, unitless), and fractal dimension (unitless). Details on how these metrics are computed from habitat maps are provided by McGarigal et al. (2002). Clumpiness is computed from the proportion of the landscape that is marsh and the degree to which neighboring cells are alike in their habitat type. Clumpiness ranges from –1 when the vegetated cell patches are maximally disaggregated to a value of 1 when the vegetated cells are maximally clumped. Values of clumpiness less than zero indicate greater dispersion (or disaggregation) than expected under a spatially random distribution, and values greater than zero

indicate greater contagion. Fractal dimension combines information on the size and perimeter of vegetated cells into a single measure that indicates the shape complexity. Values of fractal dimension range between 1 and 2, with values near 1 implying the vegetated cells occur in simply shaped (e.g. circular, rectangular) patches, while values near 2 imply that the vegetated cells arranged in complex shapes. These metrics are not independent of one another, but offer alternative views of the landscape configuration. All of the metrics can be computed from spatial habitat maps showing vegetated and water cells. The utility and interpretation of the 4 metrics we selected, as well as other metrics, are discussed in more detail elsewhere (Griffith et al. 1986, Schumaker 1996, O'Neill et al. 1999).

Simulation corroboration. We corroborated the model by visually comparing simulated and observed shrimp densities and production based on data collected in Galveston Bay, Texas. Although the attraction-based movement algorithm was in part parameterized based on empirical data, we were unsure how shrimp distributions (both in space and time) would be influenced by the tandem of attraction-based and emergency-movement algorithms. We performed 2 graphical comparisons: mean monthly shrimp densities in vegetated edge cells averaged over the years from 1982 to 1992, and mean shrimp densities relative to the distance from the marsh edge for samples collected between April and September (Minello & Rozas 2002). The first comparison was to check how well the model captured the seasonal variation in shrimp densities, and the second comparison was to check how well the model captured habitat use by shrimp. We also compared overall averaged annual densities and annual total production between simulated and empirically derived values (Minello et al. 2008).

In both the seasonal variation and habitat use graphical comparisons, our emphasis was on pattern rather than the magnitude of the densities. We purposely introduced a fixed number of post-larval individuals in all simulations, and benchmarked density-dependent effects on growth and movement to the resulting standing stocks. We opted to standardize the post-larval introductions among simulations because our simulated peak densities in edge habitat were between 25 and 50% of the observed peak densities for studies in Galveston Bay. We opted for conservative densities because preliminary data collected from Louisiana suggested that shrimp densities there are lower than those observed in Texas. We therefore divided the data means and model-predicted means by their overall mean densities so the y-axis was in units of the multiplier of the overall mean. For the seasonal variation comparison, we divided each month's average value by the annual average value. For the habitat use comparison, we divided the average density in each meter-from-edge class by the average density in the edge habitat class. Model values were from simulations that utilized the 4 Texas maps, Texas water levels, and the Texas marsh elevation profile in order to maintain consistency with Galveston Bay where the empirical data were collected. To mimic the sampling methodology in the model, we computed mean densities only using hours when the entire marsh was inundated and only counting shrimp in vegetated edge cells for the seasonality check.

Effects of marsh configuration and inundation. We performed a $4 \times 4 \times 2$ factorial design (32 simulations) using the model to determine the relative influence of inundation regime, fragmentation stage (landscape configuration), and map location on shrimp production. The first factor of inundation regime (4 levels) was the combination of Louisiana or Texas water levels with Louisiana or Texas marsh elevation profiles. The second factor of fragmentation stage (4 levels) was whether the map was solid, fine, coarse, or open. The third factor of map location (2 levels) was whether the 4 maps came from the Louisiana orthophoto or from the Texas orthophoto.

We used fixed-effects ANOVA to partition the variability in the each production measure to the 3 factors. Caution is needed in interpreting the statistical significance of outputs from simulation models because one can control whether the differences in means are statistically significant by simply increasing the number of replicate model simulations, which determines the degrees of freedom of the tests. We also utilized Tukey's HSD (honestly significant differences) post hoc test to determine which combinations of factors and their levels were causing the main effects. All statistical tests used $\alpha = 0.05$.

Based on the ANOVA results showing the importance of inundation and fragmentation stage, we presented more detailed model output for 4 of the 32 simulations that used extreme combinations of inundation regime and fragmentation stages. The highest inundation occurred where Louisiana water levels were paired with the Texas marsh elevation profile (entire marsh was inundated 59% of the hours in the simulation), and the lowest inundation occurred where Texas water levels were paired with Louisiana marsh elevation profile (entire marsh was inundated 34% of the simulation). We used the highest and lowest inundation with the fine and open fragmentation stage maps for Texas, which differed greatly in their percent of open water and availability of high-quality edge cells. Similar results were obtained with the same conditions, but using the fine and open stage maps from Louisiana. We reported the percent of time spent in

vegetation cells, mean growth rate, and mean number of cellmates (shrimp in the same cell) for those individuals that ultimately survived to be exported. We also reported the averaged shrimp abundance by distance from edge for July, the cumulative number of shrimp that died, and their average weight at death. These more in-depth comparisons were designed to help us better understand why inundation regime and, to lesser extent, fragmentation stage were important determinants of shrimp production.

Relating landscape metrics to shrimp production. We used linear regression to relate the 4 landscape metrics to simulated shrimp production. We used the predicted production values from all 8 maps (4 from Louisiana and 4 from Texas), but under a single inundation regime (Texas water levels paired with the Texas marsh-elevation profile). We fit a quadratic regression model with the 8 production values as the response variable and 8 values of the landscape metrics as the explanatory variable. Separate regression models were fit to each of the 3 production variables (growth production, trophic transfer, and sub-adult export), with each of the 4 landscape metrics. We then evaluated the significance of each overall regression model and the significance of the squared landscape metric term. If the squared term was not significant, we reported the fit of the regression with the additive term only. The use of a quadratic equation for regression was to allow for dome-shaped relationships between shrimp production and marsh landscape features (Zimmerman et al. 1991, Peterson & Turner 1994, Minello & Rozas 2002).

RESULTS

Corroboration

The seasonality and habitat use of simulated shrimp *Farfantepenaeus aztecus* densities on Texas maps closely mimicked observed densities. Simulated and observed normalized shrimp densities rapidly increased during March, reached their maximum densities from April through July, and then declined at similar rates (Fig. 4). On the hourly time scale, simulated shrimp moved into vegetated edge and water edge cells whenever high water levels allowed access (Fig. 5). Habitat use, averaged over the months of high shrimp densities, showed that both sim-

ulated and observed shrimp utilized the edge cells and the adjacent vegetation cells (Fig. 6). In agreement with the observed data, peak shrimp densities were predicted in vegetated edge cells on all 4 stage maps, and were lower but still high in cells 1 and 2 m into vegetation. Although simulated and observed shrimp densities were lower in water cells near the edge than in vegetated cells near the edge, predicted densities in open water cells were higher than the observed densities. In particular, shrimp densities actually increased moving farther into water in the solid stage. This observation is a by-product of the emergency-movement algorithm, which forces shrimp to become densely aggregated in the few deep water refuges present on the solid stage map.

The annual averaged simulated densities and total production were lower but reasonable compared to measured densities and total production values reported by Minello et al. (2008) for 4 marshes in Galveston Bay. Recall that simulated densities in edge habitat were 25 to 50% of the observed values. However, higher simulated densities in open water cells compared to the observed data resulted in overall total production values that were more similar to empirical estimates. The average shrimp densities in model simulations, computed from April through November,
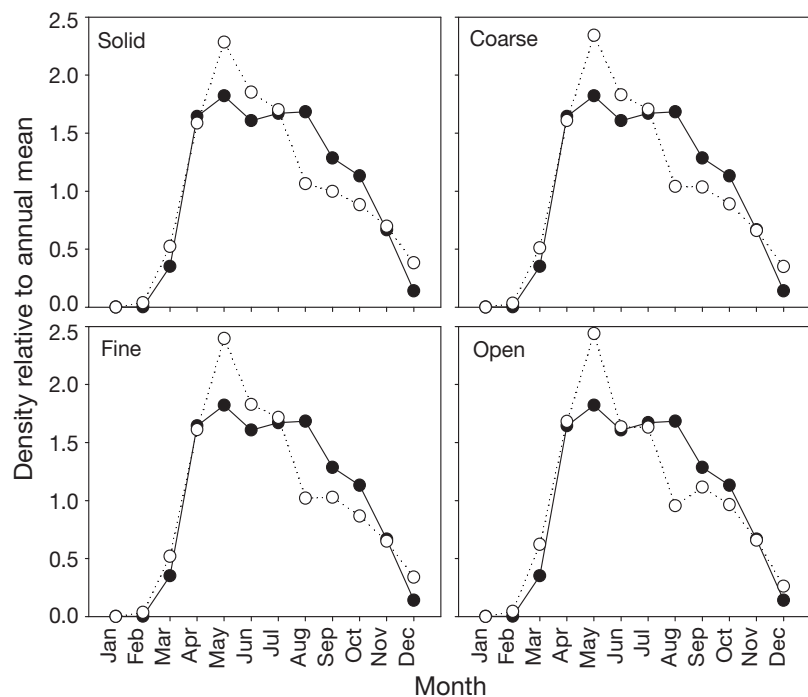
Fig. 4. *Farfantepenaeus aztecus.* Observed (●) and simulated (○) normalized mean shrimp densities by month for the solid, coarse, fine, and open fragmentation stage maps. Values are the mean density at the marsh edge in each month normalized to the mean shrimp density at the edge averaged over all months. Simulations on the 4 maps used Texas water levels paired with the Texas marsh elevation profile
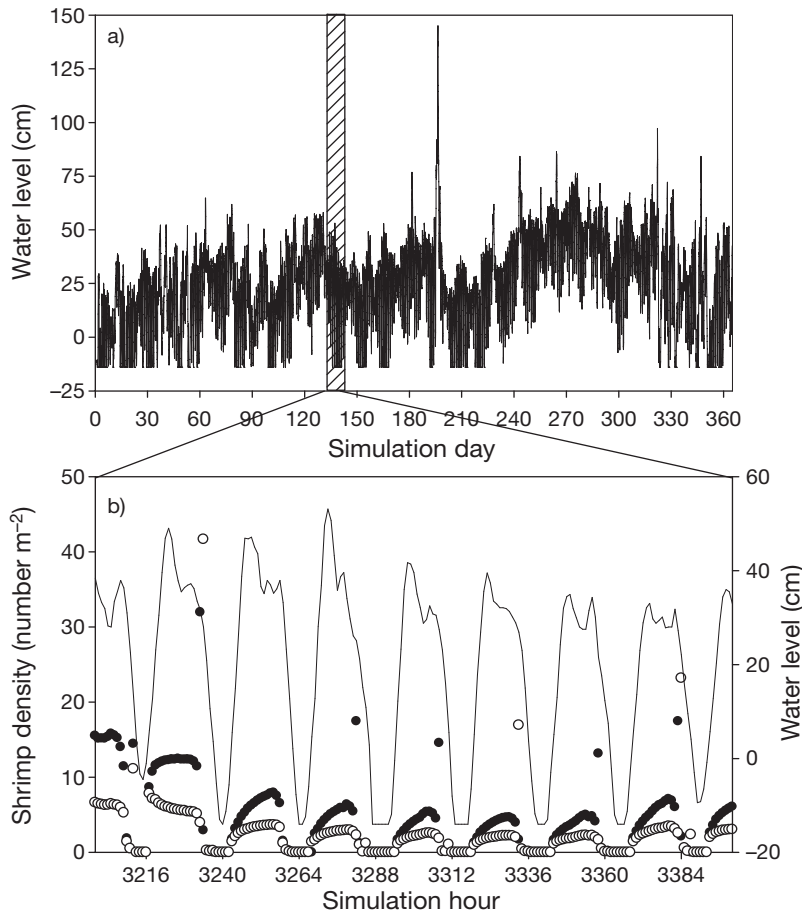
Fig. 5. (a) Water levels over the calendar year, and (b) a closer view of hourly water levels paired with hourly simulated shrimp mean densities in vegetated (●) and adjacent water (O) edge cells during a single week in May on the open stage map from Texas using Texas water levels paired with the Texas elevation profile

cant factor for determining growth production, trophic transfer, and sub-adult export (Table 2). Fragmentation stage was also a significant predictor of growth production and export, but less important (lower F-values) than inundation, and was not a significant predictor of trophic transfer. Map location (Louisiana or Texas ortho-photo) was not a significant predictor of any of the 3 measures of shrimp production.

Production was generally highest with the inundation regime that paired Louisiana water levels with the Texas marsh elevation profile, and lowest with Texas water levels paired with the Louisiana marsh elevation profile (Fig. 7). All pairwise comparisons of Louisiana or Texas water levels with Louisiana or Texas marsh elevation profiles were significantly different for all 3 production measures, except for the Louisiana water levels and Louisiana marsh elevation profile compared to the Texas water levels and Texas elevation profile for growth production and sub-adult export (Table 3). Predicted production for the 2 extreme combinations of Texas water levels paired with the Louisiana marsh profile and Louisiana water levels paired with the Texas marsh elevation profile

ranged from 11 500 ha^{-1} on the fine stage map to 12 700 ha^{-1} on the open stage map, which was lower than the reported average density of 19 382 ha^{-1} (low site: 16 640 ha^{-1}; high site: 21 848 ha^{-1}) in 4 locations in Galveston Bay. Similarly, total production (trophic transfer plus biomass of sub-adult exports) was 60 to 110 kg ha^{-1} yr^{-1} in simulations versus an average of 128 kg ha^{-1} yr^{-1} (low site: 109; high site: 145) in the 4 Galveston Bay marshes.

were 61 to 72 versus 87 to 107 kg ha^{-1} for growth production, 27.3 to 28.7 versus 32.3 to 33.3 kg ha^{-1} for trophic transfer, and 345 000 to 460 000 individuals versus 560 000 to 850 000 for sub-adult export (Fig. 7). Predicted production values for the other pairings of Louisiana water levels with Louisiana marsh profile and Texas water levels with Texas marsh profile were intermediate to these 2 extremes.

Effects of marsh configuration and inundation

Factorial simulation experiment

Inundation regime was more important than fragmentation stage or map location for determining all 3 measures of shrimp productivity. ANOVA results indicated that inundation was a signifi-

Table 2. ANOVA results of the $4 \times 2 \times 2$ simulation experiment showing the significance of the main effects involving the factors of inundation, fragmentation stage, and map location for each of 3 measures of production (growth production, sub-adult export, and trophic transfer)

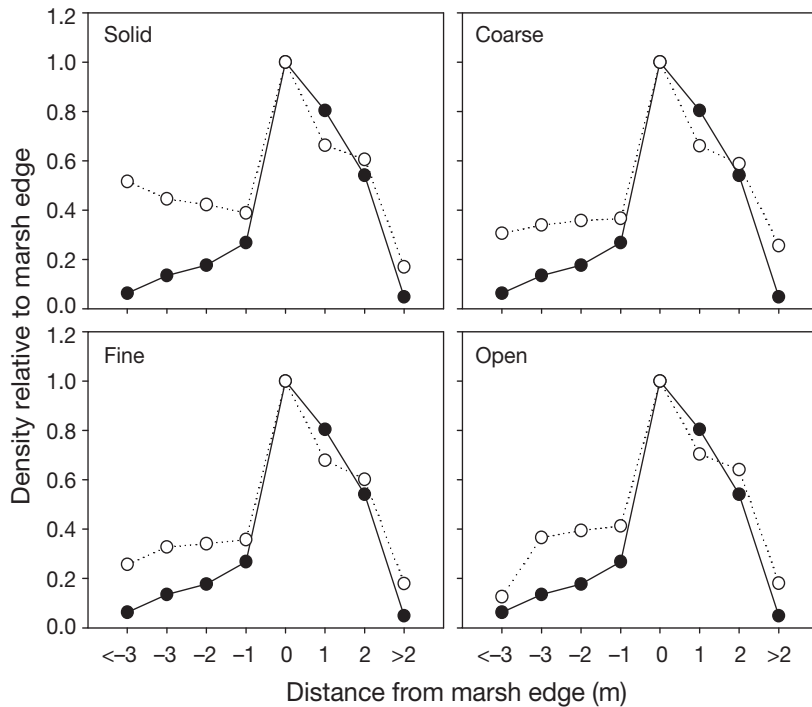| Factor	Growth production		Trophic transfer		Sub-adult export	
	F-value	p	F-value	p	F-value	p
Inundation	135.76	<0.001	217.89	<0.001	116.59	<0.001
Fragmentation stage	29.25	<0.001	1.25	0.3	36.69	<0.001
Map location	3.7	0.07	0.03	0.8	1.73	0.2

Fig. 6. *Farfantepenaeus aztecus.* Observed (●) and simulated (O) normalized mean shrimp densities plotted against distance from the marsh edge for the solid, coarse, fine, and open fragmentation stage maps. Values are the average mean density between April and September by meters from edge divided by the averaged shrimp density between April and September at the marsh edge. Simulations on the 4 maps used Texas water levels paired with the Texas marsh elevation profile

Detailed analysis of extreme condition simulations

Inundation regime, fragmentation stage, and movement rules together controlled how well the shrimp could access the marsh edge, where growth and survival were highest. Growth production and sub-adult export were higher with high inundation compared to low inundation, and within high or low inundation, were higher on the fine stage than on the open stage (Fig. 9a). The proportion of time shrimp spent in vegetated cells showed the same pattern as growth production and sub-adult export (Fig. 9b), which with the simple habitat effect on mortality (twice the rate in all water cells, Table 1), translated into increasing cumulative mortality with decreasing time spent in vegetation (bars in Fig. 9c).

Trophic transfer values were similar between high and low inundation and fine and open fragmentation stage maps (Fig. 9a). Trophic transfer was a trade-off between the number of shrimp that died and the average weight of individuals at their death.

The effect of fragmentation stage on growth production and sub-adult export values was statistically significant (Table 2), but smaller than the effect of inundation regime. Whereas open marsh stage maps had significantly lower growth production and sub-adult export values when compared against the other stage maps, the solid, coarse, and fine stage maps shared a significance grouping with at least one other stage (Fig. 8, Table 3). Mean growth production for the open stage was 72 versus 81.4, 83.8, and 88.4 kg ha^{-1} for the solid, coarse, and fine stage maps, respectively, and mean sub-adult export for the open stage was 442 000 versus 549 000, 560 000, and 604 000 individuals for the solid, coarse, and fine stage maps, respectively (Fig. 8). Trophic transfer values were similar across the 4 fragmentation stages (29.7 to 30.1 kg ha^{-1}) (Fig. 8, Table 3).

When predicted production values were combined over inundation regimes and fragmentation stages, there were no differences in production between the maps from the Louisiana versus Texas orthophotos (Table 3). Our selection of the solid, coarse, fine, and open stage maps from the 2 locations, while somewhat arbitrary, appeared to lead to similar production values between the 2 orthophotos.

Table 3. p-values of pairwise comparisons of growth production, sub-adult export, and trophic transfer conducted with Tukey's HSD (honestly significant differences) post hoc tests applied to the 4 × 2 × 2 factorial simulation experiment. The factors were fragmentation stage (solid, fine, coarse, open), inundation (Louisiana or Texas water levels combined with Louisiana or Texas marsh elevation profiles), and map location (source of the 4 fragmentation stages from Louisiana orthophoto or from Texas orthophoto)

| Comparison	Growth production	Export	Trophic transfer
Inundation (water levels/marsh elevation)			
LA/TX–LA/LA	<0.001	<0.001	<0.001
TX/LA–LA/LA	<0.001	<0.001	<0.001
TX/TX–LA/LA	0.602	0.988	0.007
TX/LA–LA/TX	<0.001	<0.001	<0.001
TX/TX–LA/TX	<0.001	<0.001	<0.001
TX/TX–TX/LA	<0.001	<0.001	<0.001
Fragmentation stage			
Fine–Coarse	0.078	0.054	0.660
Open–Coarse	<0.001	<0.001	0.261
Solid–Coarse	0.546	0.877	0.552
Open–Fine	<0.001	<0.001	0.884
Solid–Fine	0.004	0.010	0.998
Solid–Open	<0.001	<0.001	0.945
Location			
Texas–Louisiana	0.067	0.201	0.863
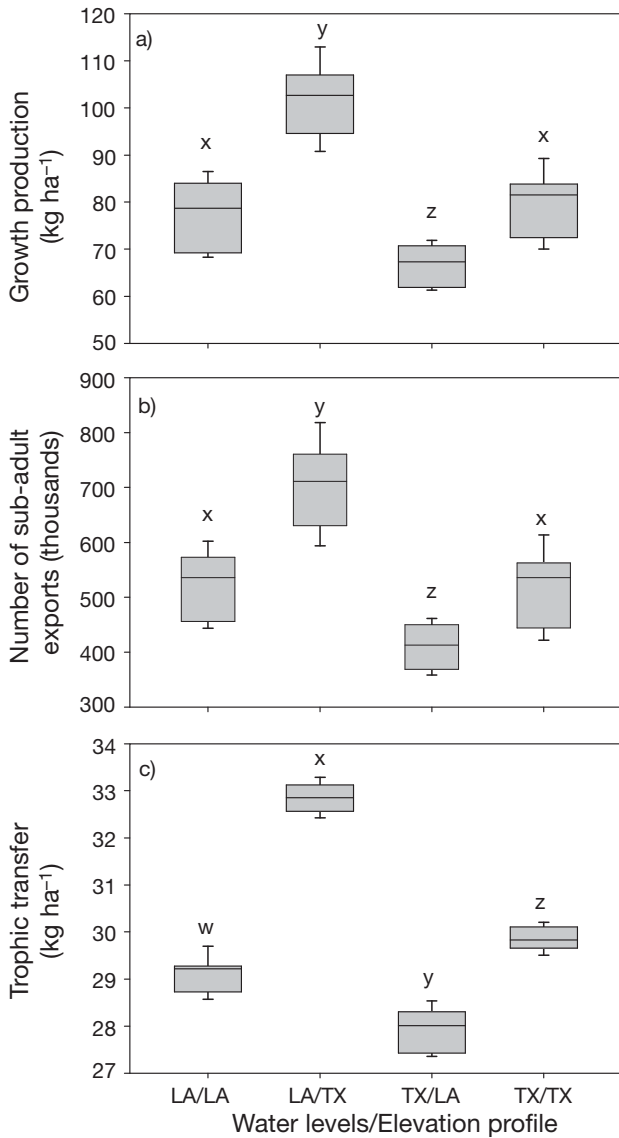
Fig. 7. Values of (a) growth production, (b) sub-adult export, and (c) trophic transfer for all simulations of the factorial experiment, grouped by the 4 combinations of water level (Texas or Louisiana) and marsh elevation profile (Texas or Louisiana). Boxplots show (from bottom up) the 25th, 50th, and 75th percentiles. Error bars are 99% confidence intervals. Letters above bars indicate significance groupings according to Tukey's honestly significant differences post hoc test (p-value < 0.05)
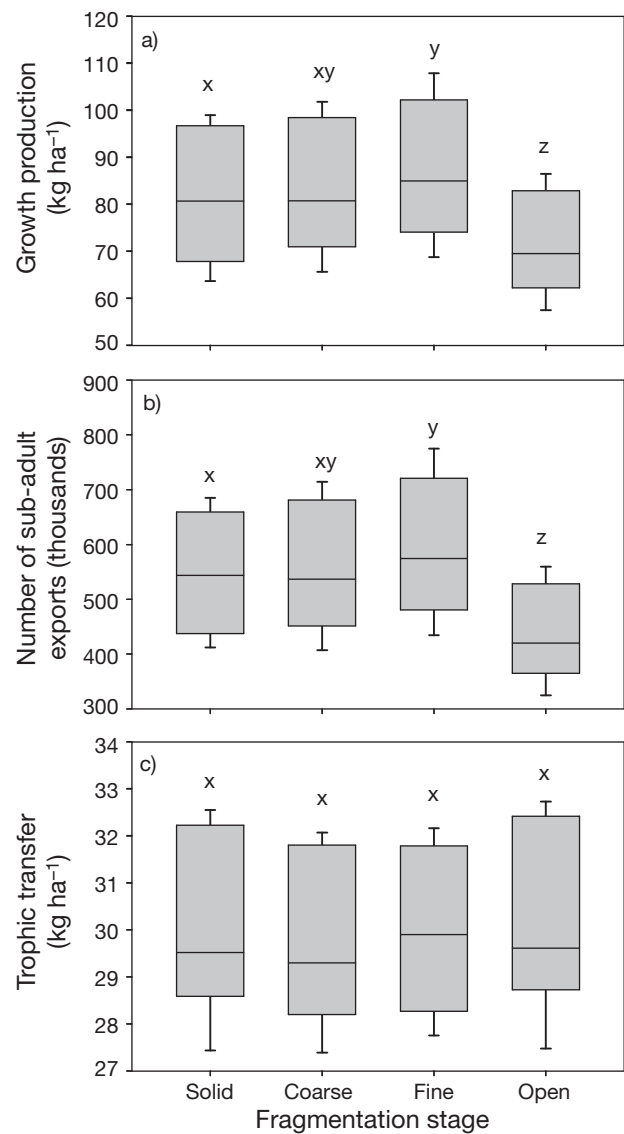
Fig. 8. Values of (a) growth production, (b) sub-adult export, and (c) trophic transfer for all simulations of the factorial experiment, grouped by the 4 fragmentation stages (solid, coarse, fine, and open). Boxplots show (from bottom up) the 25th, 50th, and 75th percentiles. Error bars are 99% confidence intervals. Letters above bars indicate significance groupings according to Tukey's honestly significant differences post hoc test (p-value < 0.05)

Whereas the average weight at death decreased, the number of dead shrimp increased across the 4 simulations (Fig. 9c). The greater number of individuals that died apparently offset the lower weights at death, and thus we predicted similar trophic transfer values across all simulations.

Mortality and growth rates both affected all 3 measures of production, and while the effect of inundation regime and fragmentation stage on mortality was clear, their effects on growth rate were more compli-

cated. Unlike cumulative mortality, the average growth rate of survivors did not simply increase with increasing time spent in vegetated cells. In general, the average growth rate attained by shrimp on the 2 open stage maps was lower relative to that obtained on the 2 fine stage maps (bars in Fig. 10a). Unlike the simple habitat effect on mortality, the habitat effect on growth rate was a gradient function that assigned different multipliers dependent on the distance from the edge (Table 1). High inundation on the fine stage
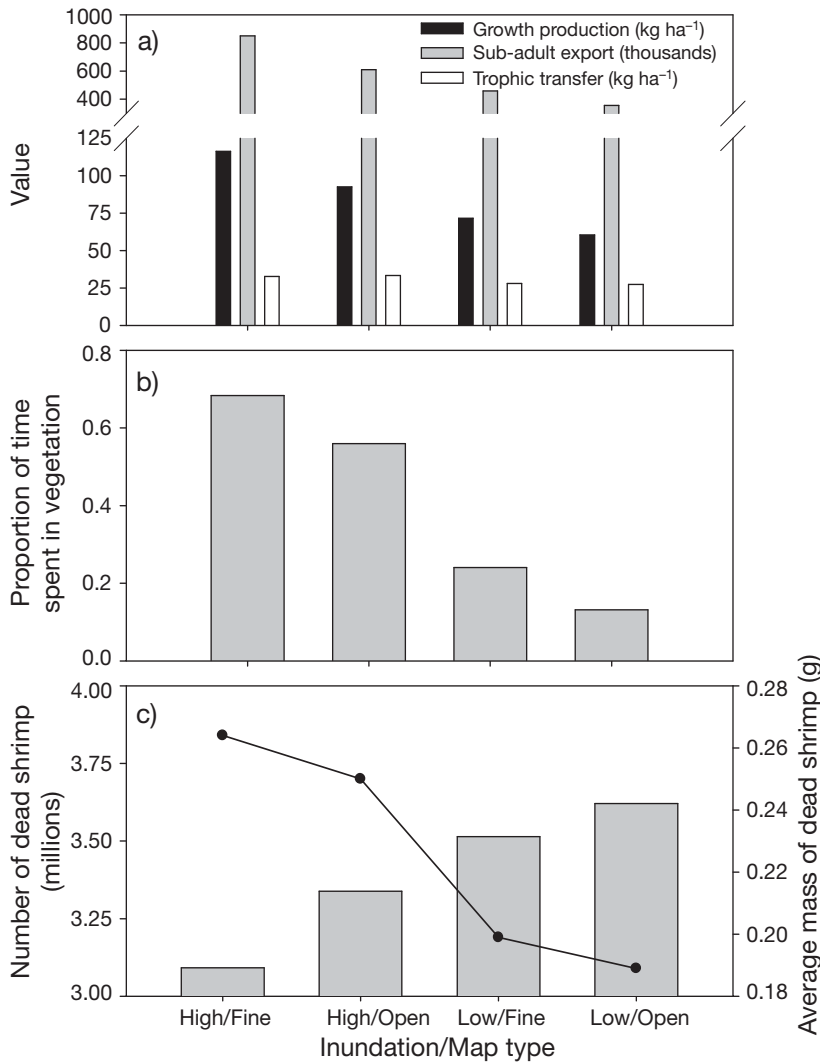
Fig. 9. Model results for the 4 extreme condition simulations of high or low inundation combined with the fine or open fragmentation stage maps. High inundation is Louisiana water levels paired with the Texas marsh elevation profile, and low inundation is Texas water levels paired with the Louisiana marsh elevation profile. Both the fine and open stage maps are from the Texas orthophoto: (a) growth production, sub-adult export, and trophic transfer; (b) average proportion of time (hours) that survivors spent in cells with vegetation; and (c) cumulative number of shrimp that died (bars) and their mean weight at death (●)

occupy either edge cells or a limited number of open water cells (closed circles in Fig. 10b). Fast growth rates occurred in this simulation despite sub-adult exports experiencing the highest number of cellmates (Fig. 10a). Rapid growth concurrent with many cellmates implies that the density-dependent effect on growth rate was much weaker than the habitat effect on growth rate. The 2 slowest growth rates were on the open stage under either inundation regime (Fig. 10a), reflecting the fact that the open stage had relatively few high-quality edge cells for shrimp to inhabit. Lower occupancy of edge cells on the open stage maps is evidenced by the high shrimp abundances found in open water cells relative to edge cells, even where inundation was high (open circle and triangle in Fig. 10b). The 2 open stage map simulations had intermediate values for the average number of cellmates (Fig. 10a).

Production and landscape metrics

When all 8 maps were compared under a single inundation regime, several landscape metrics provided adequate predictors of growth production and sub-adult export, but none were related to trophic transfer. Values of edge distance and percent marsh showed wide variation among the fragmentation stages (5 to 30 km; 20 to 80%, respectively), while the range of values of clumpiness and fractal dimension were narrow compared to their potential ranges. Clumpiness values were all between 0.86 and 0.98 (maximum range is -1 to 1), and fractal dimension values were between 1.15 and 1.21 (maximum range is 1 to 2). Edge distance, percent marsh, and clumpiness were all significant predictors of growth production (Fig. 11) and sub-adult export (Fig. 12), with R^2 values > 0.78. Growth production and sub-adult export were positively related to edge distance and percent marsh, except at the highest values along the x-axis, but they were negatively related to clumpiness. The quadratic term in each of the regressions involving edge distance and percent marsh was also significant, whereas only simple linear relationship was needed when clumpiness was the explanatory variable. The lack of differences in predicted trophic transfer among the fragmentation stages (Table 3, Fig. 8c) carried over into non-signifi-

resulted in many more shrimp being found in edge relative to open water (closed circle in Fig. 10b), because the entire stage was accessible and edge cells were abundant. The ability for shrimp to access abundant edge habitat resulted in survivors in this simulation spreading out on the map and experiencing the fewest cellmates (line in Fig. 10a). The second fastest growth rate of survivors was where low inundation was paired with the fine stage (Fig. 10a), for which access was limited but edge was abundant. In this case, limited access to abundant edge cells led many shrimp to
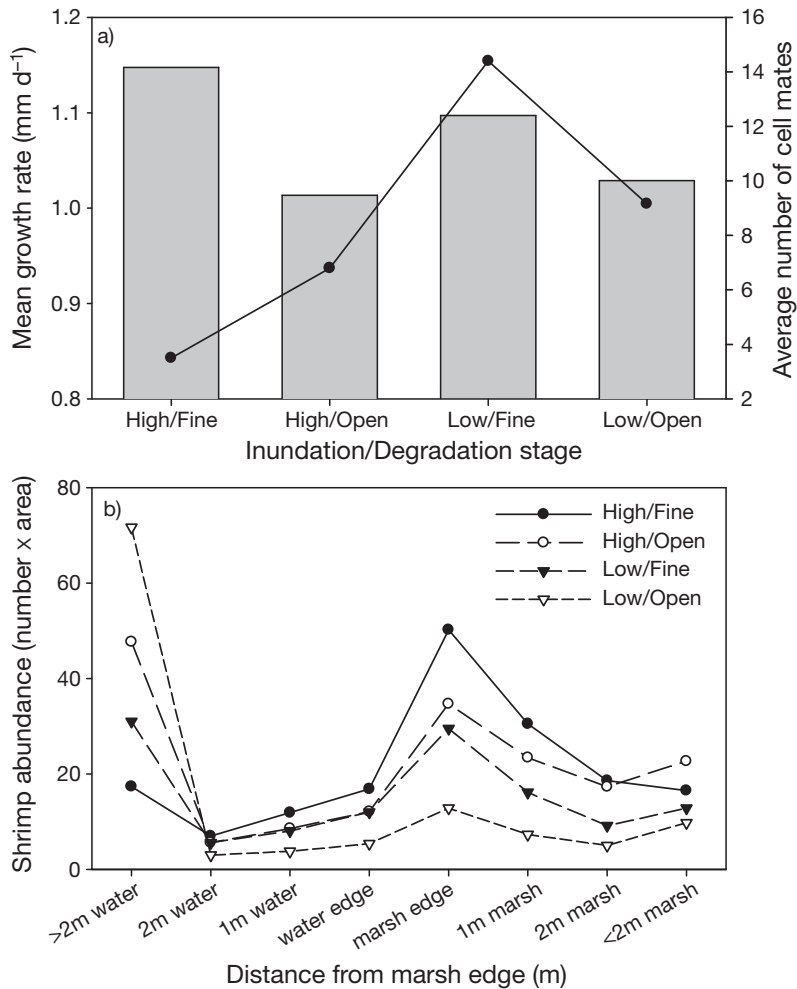
Fig. 10. Model results for the 4 extreme condition simulations of high or low inundation combined with the fine or open fragmentation stage maps. High inundation is Louisiana water levels paired with the Texas marsh elevation profile, and low inundation is Texas water levels paired with the Louisiana marsh elevation profile. Both the fine and open stage maps are from the Texas orthophoto: (a) average growth rate of the survivors (bars) and the average number of cellmates experienced by survivors (●), and (b) average shrimp abundance during July by distance from the edge. Average shrimp abundance was calculated as the mean shrimp density in July times the proportion of the map in each distance category

productivity of these species is linked to salt and brackish marsh habitat that is fragmenting and disappearing rapidly (Day et al. 2000). Understanding how inundation and marsh configuration interact to affect fish and shellfish production is critical to the early detection of reduced productivity and needed for effective and proactive management. Individual-based models that incorporate spatially explicit nekton density, growth, and survival provide a tractable method both for estimating nekton productivity and for comparing the habitat function of different estuarine landscapes.

We used the simulation model to systematically explore how contrasting inundation regimes and marsh fragmentation stages would affect 3 different measures of shrimp *Farfantepenaeus aztecus* production. Model corroboration focused on the seasonality and habitat use of normalized simulated shrimp densities on Texas maps that closely mimicked observed densities. Our factorial simulation experiment was based on observed water levels and marsh elevation profiles from Louisiana and Texas field data, and marsh configurations from orthophotos. Our approach was a trade-off between our analyses being grounded in realistic inundation patterns and marsh landscapes versus being generally applicable to the diversity of marshes that occur in the NGOM. A complete factorial design helped with generality by permitting us to predict production on all possible combinations of inundation regimes and fragmentation stages.

Our analysis indicated that shrimp production depended primarily on inundation and, to a lesser degree, on marsh configuration. In our simulations, inundation was more important than fragmentation stage or map location for determining all 3 measures of shrimp productivity (Table 2). The 4 combinations of inundation regime derived from the 2 (Louisiana and Texas) water levels and the 2 (Louisiana and Texas) marsh elevation profiles generated different estimates of growth production and sub-adult export, which generally increased with increasing marsh inundation (Fig. 7). Fragmentation stage had a smaller effect on production (Table 2), and was most apparent with the reduced growth production and sub-adult export observed on simulations that utilized open stage maps (Fig. 8). These results are

cant relationships between trophic transfer values and landscape metrics (Fig. 13). Fractal dimension was unrelated to growth production and sub-adult export, but showed the most promise of the landscape metrics for being a predictor of trophic transfer.

DISCUSSION

Coastal estuaries provide important nursery habitat for many commercially and recreationally important fish and shellfish species (Boesch & Turner 1984, Beck et al. 2001, Kraus & Secor 2005). In the NGOM, the
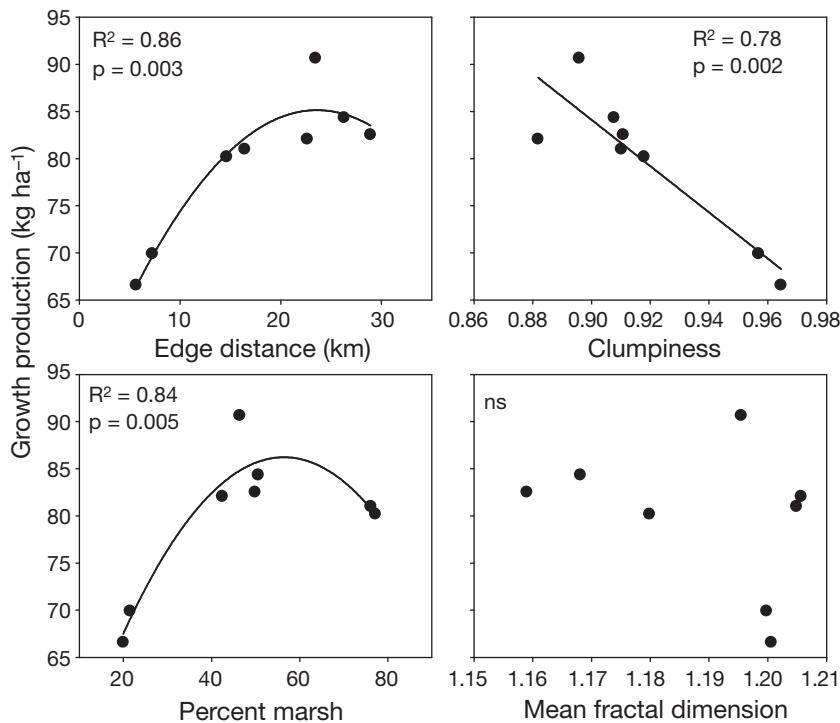
Fig. 11. Simulated values of growth production plotted against the landscape metrics of edge distance, percent marsh, clumpiness, and mean fractal dimension from simulations on all 8 maps (solid, coarse, fine, and open stage maps from Texas and from Louisiana) under the single inundation regime of Texas water levels paired with the Texas marsh elevation profile. The R^2 and p-values for the quadratic regression model fit are shown, except when the overall regression was not significant (denoted ns) or when the quadratic regression was significant but the squared term in the quadratic model was not significant. In this case, the purely linear regression model fit is shown

consistent with field studies of brown shrimp and other species in NGOM estuaries that show a strong relationship of nekton abundance and distribution with marsh flooding patterns and marsh-water interspersion (Zimmerman et al. 1991, Rozas & Reed 1993, Minello et al. 1994, Peterson & Turner 1994). In natural systems, inundation patterns regulate nekton access to the marsh surface (Rozas & Reed 1993, Kneib 1997, Minello et al. 2003), and nekton use of intertidal vegetation is positively related to the periodicity of inundation (Rozas 1995, Minello et al. 2003).

A more detailed examination of 4 extreme combinations of high versus low inundation with open versus fine stage maps showed that the higher growth production and sub-adult export under high inundation was due to the ability of shrimp to easily access edge habitat. Within high or low inundation simulations, higher production was the result of abundant edge on the fine stage map relative to that on the open stage map (Fig. 9). Inundation and edge availability together affected resultant shrimp habitat use, which in turn affected cumulative mortality in a straightforward way by regulating shrimp access to vegetated cells. In-

creased access to vegetation lowered shrimp mortality, which in turn allowed more shrimp to survive and contribute to both growth production and sub-adult export. Structure provided by marsh plants protects the young of estuarine fauna, including brown shrimp, from predators and increases their chance of survival (Minello et al. 1989, 2003, Shirley et al. 1990). In a meta-analysis of 11 controlled laboratory and field experiments comparing survival in treatments with or without vegetation (structure), survival rates of estuarine organisms were significantly higher in treatments with marsh vegetation when compared with nonvegetated treatments (Minello et al. 2003).

The same 4 extreme condition simulations showed that differences in inundation affected growth rate in a more complicated way than mortality rate. In particular, mean growth rates did not simply increase with increasing time spent in vegetated cells (Fig. 10). The ability for shrimp to attain high growth rates was an emergent function of the combined effects of inundation and the abundance of high-quality edge cells. Trophic transfer showed only small differences among inundation regimes and fragmentation stages in the extreme condition simulations. Trophic transfer was a trade-off between numbers dying and weight of individuals at their death, which responded oppositely to increases in inundation.

Across the range of habitat maps we simulated in our study, several metrics of landscape configuration had strong relationships with brown shrimp growth production and sub-adult export (Figs. 11 to 13). Percent marsh, edge distance, and clumpiness were all significant predictors of growth production and export, whereas fractal dimension was the best (but nonsignificant) predictor of trophic transfer. Edge distance and percent marsh are commonly used metrics to estimate shrimp and fish abundances at larger spatial scales (Baltz et al. 1993, Minello et al. 1994, Peterson & Turner 1994). There are many landscape metrics (Griffith et al. 1986, McGarigal et al. 2002), but they often exhibit relatively high collinearity. Given the ease of measuring and interpreting edge distance and percent marsh and their good fit to modeled production, we suggest the continued use of these 2 metrics for describing shrimp–habitat interactions within a given inundation regime. Fractal dimension offers some
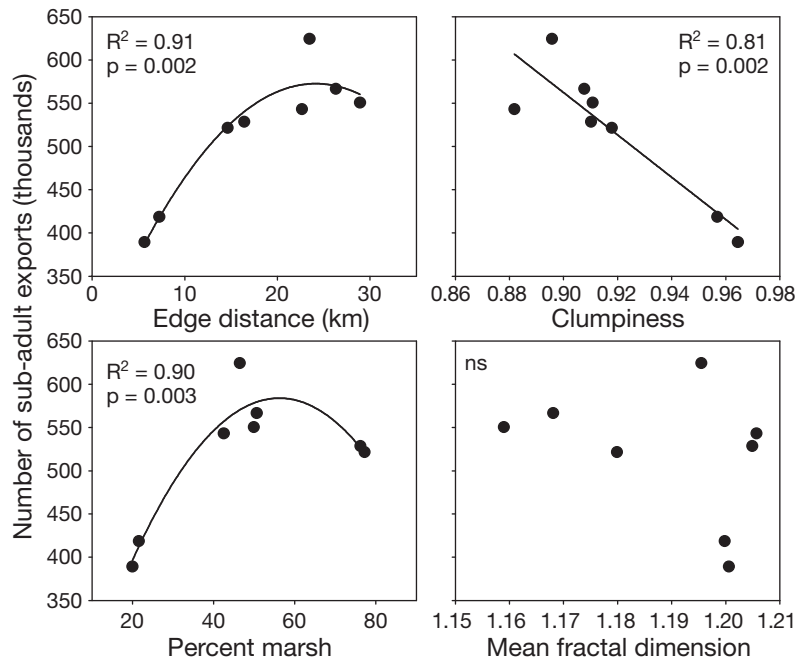
Fig. 12. Simulated values of sub-adult export plotted against the landscape metrics of edge distance, percent marsh, clumpiness, and mean fractal dimension from simulations on all 8 maps (solid, coarse, fine, and open stage maps from Texas and from Louisiana) under the single inundation regime of Texas water levels paired with the Texas marsh elevation profile. The R^2 and p-values for the quadratic regression model fit are shown, except when the overall regression was not significant (denoted ns) or when the quadratic regression was significant but the squared term in the quadratic model was not significant. In this case, the purely linear regression model fit is shown

promise for predicting shrimp trophic transfer (mortality), but further confirmation is needed on a wider range of simulated conditions.

Our model simulated shrimp movement and distribution on an hourly basis on a 1 m² spatial scale. Edge is highly scale dependent, as its linear length depends on the resolution of the spatial cells. Key trophic interactions may occur on a scale of minutes and centimeters, but little, if any, information is available on shrimp activity at these smaller scales (Main 1987). In fact, there is relatively little information available that is sufficiently detailed to validate our simulated individual shrimp movement in hourly steps on 1 m cells. Fine-scale data collection and modeling approaches are gaining popularity in aquatic population analyses (see, for example, Ault et al. 1999, 2003, Walters & Martell 2004). We decided that the 1 m² resolution in hourly increments was the best compromise between working on the ultra-fine centimeter-level scale of key shrimp–edge interactions and the broader scales of days and 10s of meters inherent in the available empirical information on shrimp growth, mortality, and movement. For example, we used marsh elevation profiles that only varied based on meters of distance from

the edge. Field data illustrate that marsh-water complexes typically have fine-scale variation in elevations that nekton utilize (Baltz et al. 1993, Kneib 1997).

We partially separated growth from movement in the model. Growth and movement shared some effects (distance from edge, density dependence), but we did not use identical functions for all of the shared effects (Table 1). We based our growth–distance relationship on field studies that documented the mean abundance of benthic infauna relative to the distance from the marsh edge, but we recognize that these patterns also change seasonally (Whaley & Minello 2002). Benthic infauna permit much higher growth rates than vegetation and detritus alone, and benthic infauna comprise a substantial portion of wild shrimp diets (McTigue & Zimmerman 1991, 1998). Shrimp movements may be greatly influenced by both dynamic and spatially varying growth rate potential and predation risk (Halpin 2000). Our representation of movement in the model is critical to predicting responses to changes in inundation and resultant habitat utilization, and we consider the movement aspects of our model to be only weakly corroborated.

A variety of approaches have been proposed for simulating the small-scale movement of aquatic organisms (see an early review in Tyler & Rose 1994). These approaches include using a collection of rules that evaluate the fitness (trade-off between growth and mortality) of cells within a local neighborhood (e.g. Railsback et al. 1999, Haas et al. 2001), using only the information in the current cell to influence the mix of random versus inertial movement (e.g. Humston et al. 2004), neural networks with training by genetic algorithms (Huse & Giske 1998), and game-theoretic approaches that use detection thresholds of environmental change (Anderson 2002, Goodwin et al. 2006).

Our approach is a relatively simple hybrid of the utility and fitness-based approaches. We force the utility approach by allowing the shrimp to switch from the attraction-based movement to emergency-based movement according to water level. We also greatly simplify the idea of fitness by using the value of the attractiveness index to evaluate neighboring cells. A more elaborate fitness-based approach would combine growth and mortality, and project fitness as the likelihood of reaching a desired size or time in the future (such as the end of the growing season or maturity).
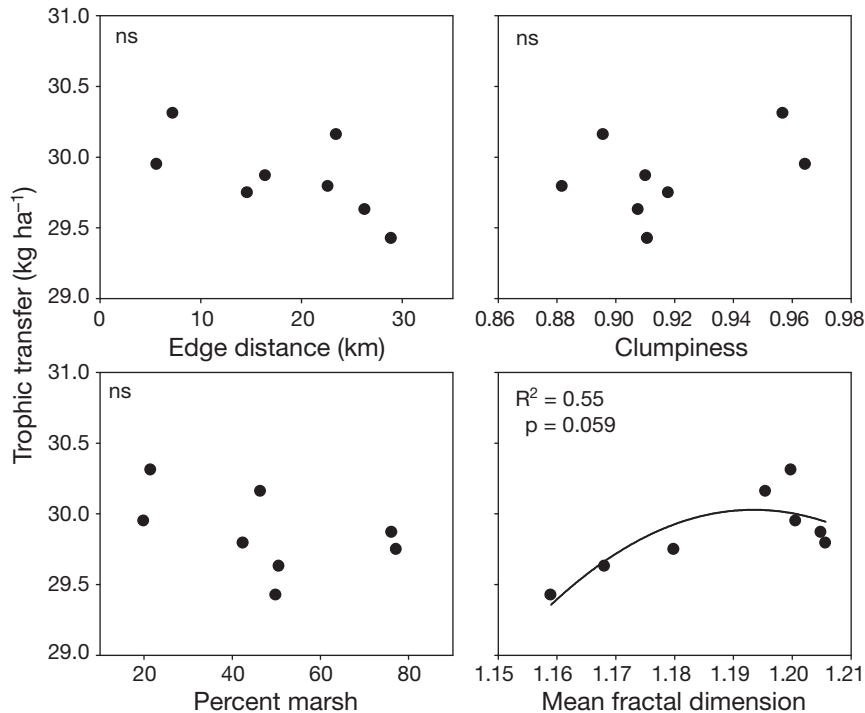
Fig. 13. Simulated values of trophic transfer plotted against the landscape metrics of edge distance, percent marsh, clumpiness, and mean fractal dimension from simulations on all 8 maps (solid, coarse, fine, and open stage maps from Texas and from Louisiana) under the single inundation regime of Texas water levels paired with the Texas marsh elevation profile. The R^2 and p-values for the quadratic regression model fit are shown, except when the overall regression was not significant (denoted ns)

The attractiveness index was derived by matching the patterns of shrimp densities relative to their distance from the edge in field studies (i.e. the pattern-matching discussed by Grimm et al. 2005). We simply used a shape for a function that results in realistic simulated shrimp usage of different cell habitat types. The rigidity in our movement approach (i.e. leaning towards empirical rather than mechanistic) can limit the types of questions that we can address with the individual-based model. Tagging and stable isotopes offer promising approaches to obtain sufficient individual movement tracks to relate to local environmental conditions (e.g. Haas et al. 2001, Webb & Kneib 2004, Kokko & Lopez-Sepulcre 2006). As field studies continue to progress towards measuring finer and finer scale movement and shrimp distributions, models such as the IBM used here will transition from pattern matching to approaches that are more mechanistic. Consequently, additional refinement of the model should focus on the movement algorithm.

The importance of inundation complicates forecasting of how future marsh fragmentation might affect shrimp production. Shrimp production showed a dome-shaped relationship with various measures of marsh condition, but simple measurement of marsh condition and production may not indicate how further marsh fragmentation will affect production. In many estuaries, current rates of relative sea level rise owing to global climate change and natural subsidence will increase inundation, but will also lead to increased marsh fragmentation. Increased inundation provides opportunities for erosion through wave action and the drowning of sediment-stabilizing plants (e.g. Chmura et al. 1992). Eventually, the marsh fragments to the point where it disappears or is completely submerged. How sea level rise and marsh erosion will affect the competing positive effects of shrimp access to vegetation versus the negative effects of marsh loss is neither simple nor straightforward, as our model analysis demonstrates. Additional analyses that explicitly couple inundation and marsh fragmentation should provide useful information to predict changes in shrimp production during the long-term marsh fragmentation process, and to compare alternative management scenarios for coastal restoration.

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