MODELLING ENVIRONMENTAL AND HABITAT EFFECTS ON YOUNG

BROWN SHRIMP PRODUCTION IN GALVESTON BAY, TEXAS, U.S.A

A Dissertation

by

JENNIFER PURVIANCE LEO

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Chair of Committee,	William E. Grant
Co-Chair of Committee	Thomas J. Minello
Committee Members,	Masami Fujiwara
	Russell A. Feagin
Head of Department,	Michael P. Masser

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ABSTRACT

Brown shrimp (*Farfantepenaeus aztecus*) support a commercially important fishery in the northern Gulf of Mexico, and juveniles use coastal estuaries as nurseries. Production of young shrimp from any given bay system, and hence commercial harvest of sub-adults and adults from the Gulf, is highly variable from year to year. We describe development of a spatially-explicit, individual-based model representing the cumulative effects of temperature, salinity, and access to emergent marsh vegetation on the growth and survival of young brown shrimp, and we use the model to simulate shrimp production from Galveston Bay, Texas, U.S.A. under environmental conditions representative of those observed from 1983 to 2012. We also describe a field growth study conducted from April 12 to June 9, 2011, designed to validate and improve the model.

The model reproduced biomass and size distribution patterns observed in field data. Although annual variability of modeled shrimp production did not correlate well ($R^2 = 0.005$) with fisheries independent trawl data from Galveston Bay, there was a significant correlation with similar trawl data collected in the northern Gulf of Mexico ($R^2 = 0.40$ p = 0.0005). Identifying and representing spatially variable factors such as annual recruitment timing and magnitude among bays, therefore, may be the key to understanding bay-specific contributions to the adult stock. In our field growth study, we used a mark-recapture approach to measure brown shrimp growth in three polyhaline marsh ponds over periods of two to four weeks. We recorded hourly temperature and

flooding data, and also measured biomass of infaunal food organisms. We

parameterized our production model with input from 2011 to compare modeled output to

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-1, 1.06 mm d-1, respectively),

however, growth rates differed significantly between marsh ponds. Data on infaunal

biomass suggest that spatial and temporal variability in available food organisms is

related to differences in growth, and the inclusion of such information may enhance the

model.

DEDICATION

To Dwight Augustus. Eternal fishing buddy, you almost got to see the end of the show.

ACKNOWLEDGEMENTS

CONTRIBUTORS AND FUNDING SOURCES

Contributors

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1. INTRODUCTION

Penaeid shrimps found in the northern Gulf of Mexico (GoM) include white shrimp, *Litopenaeus setiferus*, pink shrimp, *Farfantepenaeus duorarum*, and brown shrimp, *Farfantepenaeus aztecus* (Perez-Farfante and Kensley 1997). All of these are targeted by the commercial shrimping industry. United States landings in 2015 were estimated at 102 million kg (225 million pounds) valued at over 390 million dollars (National Marine Fishery Service, Fishery Statistics Division 2017). Over half of this catch was brown shrimp.

The brown shrimp life history has been studied extensively because of this important commercial fishery. The time from spawning until harvest for this species is usually less than 1 year (Cook and Lindner 1970). Adult brown shrimp spawn offshore with peak activity at depths of 27 to 46 m from October to December and March to May (Christmas and Etzold 1977; Renfro and Brusher 1982). Eggs hatch within 14-18 hours (Cook and Lindner 1970), and after passing through several larval stages (Lassuy 1983), postlarvae move into estuaries settling as juveniles in inshore bays (Dall *et al.* 1990; Fry 2008). Juveniles grow rapidly to sub-adult size then migrate offshore to complete their growth and spawn (Temple and Fischer 1967).

Recruitment of juveniles to the sub-adult (inshore) and adult (offshore) fishery appears dependent upon processes that take place during the estuarine phase of the shrimp's life history (Minello *et al.* 1989; Minello and Zimmerman 1991; Haas *et al.* 2001). There is little or no correlation demonstrated between number of spawners and

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number of recruits to the fishery (Neal 1975; Nance and Nichols 1988) or between

abundance of postlarvae entering bays and subsequent offshore landings (Berry and

Baxter 1969; Ford and St. Amant 1971; Baxter and Sullivan 1986). However, positive

correlations were found between abundance of juveniles and adults (Berry and Baxter

1969), and a strong correlation was identified between numbers of sub-adult/bait-sized

brown shrimp caught and annual offshore landings of adults (Baxter and Sullivan, 1986).

These relationships suggest that mortality is high and variable during the estuarine phase

of brown shrimp life history and that year-class strength is fixed before migration into

open bays (Minello *et al.* 1989).

Estuarine habitats in the northern GoM vary considerably and include intertidal

marsh, submerged aquatic vegetation, oyster reef, mangroves, tidal mudflats, and sub-

tidal bay bottom (Clark *et al.* 2004). Understanding the relative value of juvenile

habitats and potential nurseries is critical to the management of adult populations (Beck

et al. 2001; Adams *et al.* 2006). Beck *et al.* (2001) defined nurseries as juvenile habitats

whose "contribution per unit area to the production of individuals that recruit to adult

populations is greater, on average, than production from other habitats in which

juveniles occur." The contribution of a habitat is measured through a combination of

four factors: density, growth, survival of juveniles, and movement to adult habitats

(Beck *et al.* 2001).

Brown shrimp are present in several habitat and bottom types such as oyster reefs

(Stunz *et al.* 2010) and shallow open water (Minello 1999; Fry 2008;), but are found in

highest densities associated with seagrass and the emergent vegetation along the edge of

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salt marsh habitats (Zimmerman and Minello 1984; Minello and Rozas 2002; Minello *et al.* 2003). Since there is relatively little seagrass in Galveston Bay (Clark *et al.* 2004; King and Sheridan 2006), estuarine marshes have been considered important nursery areas, providing shrimp with favorable environmental conditions. Salt marshes provide refuge from predators (Minello and Zimmerman 1983; Minello *et al.* 1989, Minello 1993) and abundant food to support rapid growth (McTigue and Zimmerman 1991, 1998; Whaley and Minello 2002). Salt marshes contribute substantially to the productivity of brown shrimp (Minello *et al.* 2008) and are identified as Essential Fish Habitat (Minello 1999; NMFS 2010) as defined by the Magnuson-Stevens Fishery Conservation and Management Reauthorization Act (MSRA) of 2006.

The MSRA directs fishery management councils and the National Marine Fisheries Service (NMFS) to identify Essential Fish Habitat for all managed fishery species (Minello 1999). The NMFS Habitat Assessment Improvement Plan (HAIP) introduced in May of 2010 draws upon the mandates of the MSRA, calls for the improvement of fisheries management through the integration of habitat science, and emphasizes improving stock assessment models and their data input Yoklavich *et al.* (2010). The modeling approach proposed here is an attempt to quantify habitat effects on juvenile brown shrimp populations. Although several brown shrimp models are in the literature including a spatial density model (Minello *et al.* 2008), Individual Based Models (Haas *et al.* 2004; Roth *et al.* 2008), a bioenergetics model (Adamack *et al.* 2012), and various correlative models (Barrett and Gillespie 1973; Turner 1992; Haas *et al.* 2001) their output is not directly compatible with current stock assessment models.

Until recently, stock assessments for shrimp in the GoM have used Virtual

Population Analysis (VPA) developed by Nichols (1984). In 2009, an internal NMFS

panel reviewed the pink shrimp VPA and deemed its use inappropriate given that current

fishing effort is much lower than when the model was originally calibrated in 1994 (Hart

and Nance 2010; Hart, 2012). Hart and Nance (2010) suggested the adoption of Stock

Synthesis 3 (SS-3), a widely used and peer reviewed assessment model (Methot 2009;

Schirripa *et al.* 2009). Stock Synthesis 3 is accepted as a robust, reliable assessment

modeling software by the Alaska, Northwest, Northeast, Southeast, and Southwest

Fisheries Science Centers (and their respective Fisheries Management Councils) for

assessing other valuable fisheries (Hart and Nance 2010). In addition, SS-3 has the

capability to incorporate habitat and environmental information, but as of this writing

does not include inputs regarding juvenile habitat and environmental effects explicitly.

The economic value of the GoM shrimp fishery has fueled over 50 years of

research into population dynamics of brown shrimp (Haas *et al.* 2001) and mechanisms

through which habitats influence growth and survival (Minello and Zimmerman 1991).

Studies in Texas and Louisiana on juvenile brown shrimp have shown that growth and

survival in estuarine nurseries depend upon temperature, salinity, and access to emergent

marsh vegetation (Minello *et al.* 1989, 2008; Adamack *et al.* 2012). Modeling these

highly dynamic variables and their interactions is a cognitively and mathematically

complex task (Costanza *et al.* 1998; Grant and Swannack 2008). However, using a

holistic instead of reductionist approach is essential when modeling complex systems

(Costanza *et al.* 1993, 1998; Miller *et al.* 2000). Fortunately, model software

improvements include graphical programming languages and user-friendly interfaces specifically designed to facilitate modeling of nonlinear, dynamic systems (Costanza *et al.* 1998; Costanza and Gottleib 1998; Costanza *et al.* 2001; Ford 2010).

The development and analysis of a simulation model is beneficial at both predictive as well as conceptual levels (Carothers and Grant 1987). Building models that represent the assumed structure of a system requires the synthesis of existing data and theory and can help identify and fill knowledge gaps or identify areas in which conflicting hypotheses or parameter estimates are apparent (Carothers and Grant 1987; Costanza and Gottleib 1998).

My dissertation research has been divided into two separate but related manuscripts. Manuscript #1 describes the development of an individual-based model (IBM) that is an effort to estimate the annual influence of environmental conditions on juvenile brown shrimp production in GoM estuaries. Manuscript #2 discusses a field growth study we conducted in three Galveston Bay, Texas marsh ponds. We compared the data from the field study to simulations using the model described in Manuscript #1 in an effort to further evaluate the IBM, and identify factors that may improve model estimates.

2. SIMULATING ENVIRONMENTAL EFFECTS ON BROWN SHRIMP PRODUCTION IN THE NORTHERN GULF OF MEXICO[*]

2.1. Introduction

Brown shrimp (*Farfantepenaeus aztecus*) is a commercially important fishery species of the northern Gulf of Mexico, and landings generated over $245 million (US dollars) in 2013 (National Marine Fishery Service, Fishery Statistics Division 2015). The life history and population dynamics of brown shrimp have been studied extensively, and processes occurring during the juvenile phase in coastal estuaries appear to be important in determining population size (Zimmerman *et al.*, 2000). Brown shrimp usually spawn and are harvested within one year (Cook and Lindner, 1970). Adults spawn offshore with peak activity from October to December and March to May (Christmas and Etzold, 1977; Renfro and Brusher, 1982). Eggs hatch within 14-18 hours and pass through several larval stages (Cook and Lindner, 1970, Cook and Murphy, 1971) before moving into estuaries as postlarvae and settling as juveniles in inshore bays (Fry, 2008). Juveniles grow rapidly to sub-adult size and then migrate offshore to complete their growth to maturity (Trent, 1967). Young brown shrimp in the northern Gulf of Mexico utilize shallow estuarine habitats and grow from postlarvae (10-15 mm TL) to subadults (55-80 mm TL) within a few months (Cook and Lindner, 1970).

While brown shrimp juveniles occur in several habitat types including oyster reef (Stunz *et al.*, 2010) and shallow open water (Fry, 2008; Minello, 1999), highest densities are found in seagrass and salt marsh (Minello *et al.*, 2003; Stokes, 1974). Relatively little seagrass habitat exists in Galveston Bay or in many estuaries of the northwestern Gulf of Mexico (Handley *et al.*, 2007), and the majority of brown shrimp are found associated with emergent marsh vegetation (Minello and Rozas, 2002; Zimmerman *et al.*, 1984). Indeed, brown shrimp commercial yield has been correlated on a large scale with the presence of intertidal vegetation (Boesch and Turner, 1984; Turner, 1977).

The Galveston Bay system is the largest estuary in the state of Texas, U.S.A. (Figure 2.1) and the salt marshes and shallow water surrounding the bay are particularly important habitats for young shrimp (Minello *et al.* 2008). *Spartina alterniflora* is the dominant shoreline vegetation (Minello and Webb, 1997), and this intertidal habitat supports high densities of young brown shrimp when flooded (Zimmerman and Minello, 1984). Some mechanisms linking salt marsh habitats with brown shrimp production have been identified (Zimmerman *et al.*, 2000). Growth of juvenile shrimp is mainly a function of temperature and food availability (Zein-Eldin and Aldrich, 1965), with growth rates commonly reaching 1 mm day^{-1} (Knudsen *et al.*, 1977). Young brown shrimp feed on benthic invertebrates such as amphipods and polychaete worms (McTigue and Zimmerman, 1991, 1998), which often are most abundant within marsh vegetation (Whaley and Minello, 2002). These studies support the conclusion that growth rates should be highest when the vegetated marsh surface is available for foraging (Minello and Zimmerman, 1991). Shrimp access to the vegetated marsh
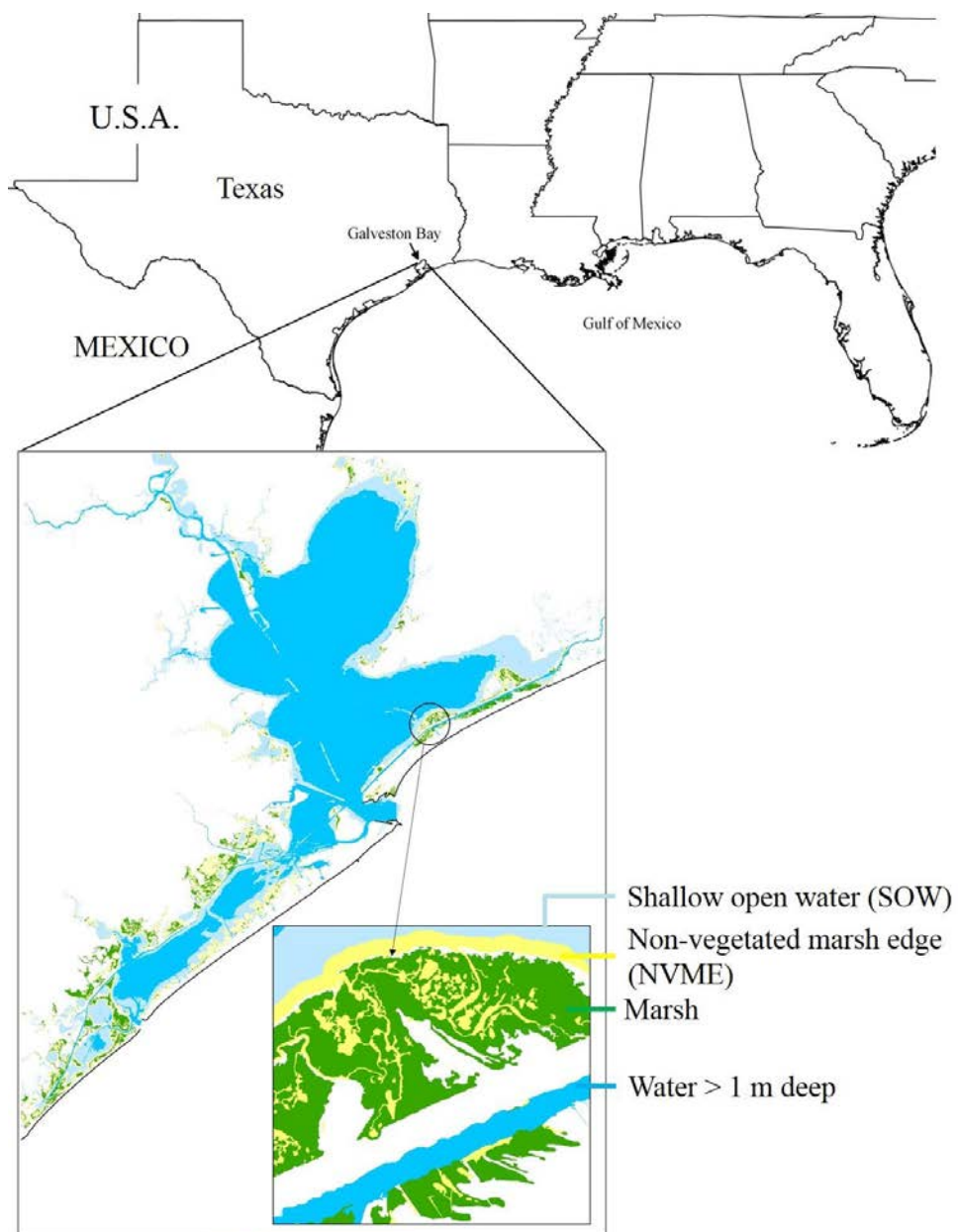
Figure 2.1 Map indicating the location of the Gulf of Mexico and Galveston Bay, Texas, U.S.A. Within Galveston Bay, approximate locations of areas of marsh (thin green line), non-vegetated marsh edge (NVME, thin yellow line), shallow open water (SOW, light blue area), and deeper (≥ 1 m deep) water (dark blue area) also are indicated.

surface is dependent upon tide height and marsh surface elevation (Childers *et al.*, 1990, Minello *et al.* 2012). In the northern Gulf of Mexico, tides are microtidal (<1 m), predominantly semi-diurnal, and strongly wind driven, resulting in water levels that regularly deviate from predicted tides (Minello *et al.* 2012; Rozas 1995). The increased growth rates associated with access to the vegetated marsh surface also may reduce the total time shrimp are available to predators (Rozas and Zimmerman, 2000), since mortality rates due to predation appear to decrease as shrimp grow (Minello *et al.*, 1989). Fish predation appears to be the primary source of mortality of young brown shrimp (Minello *et al.* 1989; Minello and Zimmerman, 1983), and vegetative structure also provides protection from such predation, likely resulting in greater survival when on the marsh surface (Kneib, 1995; Orth *et al.*, 1984; Minello *et al.*, 2003). Salinity effects on shrimp survival and growth are less clear. Laboratory experiments have shown little correlation between shrimp growth and salinity (Zein-Eldin, 1963, Zein-Eldin and Aldrich, 1965), but caging experiments along a salinity gradient in Barataria Bay, Louisiana suggest that low salinities result in slower growth rates in estuarine habitats (Rozas and Minello, 2011).

Brown shrimp production from the Galveston Bay system, or any given bay system in the northern Gulf of Mexico, is highly variable from year to year. Hence, it is difficult to predict annual commercial harvests from the Gulf or to assess the current status of brown shrimp stocks. The recent Habitat Assessment Improvement Plan (HAIP) of the NMFS calls for adjustments to the current stock assessment methodology, and the improvement of fisheries management through the integration of habitat science

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(Yoklavich *et al.*, 2010). Since recruitment of juveniles to the fishery appears dependent upon processes that take place during the estuarine phase of the shrimp life cycle, the incorporation of juvenile habitat effects on production should support a more complete stock assessment methodology.

Several recent models using a variety of approaches have focused on the production of juvenile brown shrimp. These have ranged in complexity from a relatively simple spatial density model estimating brown shrimp production from Galveston Bay marshes using an equilibrium yield approach (Minello *et al.*, 2008), to a bioenergetics model examining the potential impacts of freshwater diversions of the Mississippi River on the production of juvenile brown shrimp (Adamack *et al.*, 2012), to spatially-explicit individual-based models (IBMs) investigating the effects of habitat fragmentation and inundation on brown shrimp production (Haas *et al.*, 2004; Roth *et al.*, 2008). These IBMs simulate individual shrimp movements at a high spatial resolution (1 m^2 cell size) over relatively small areas (1 - 25 ha), and require long simulation times on relatively sophisticated computers.

In this paper, we present a spatially-explicit, individual-based model which simulates the cumulative effects of temperature, salinity, and access to emergent marsh vegetation on the growth and survival of young brown shrimp. We developed our model to estimate annual shrimp production from bay systems in the northern Gulf of Mexico and parameterized the model using 30 years of environmental data for Galveston Bay. We first describe model structure and function (Section 2), model calibration (Section 3), baseline simulations (Section 4), and sensitivity analyses (Section 5). We then use

the model to explore the uncertainty in estimations of shrimp production resulting from uncertainty in the timing of shrimp recruitment to the bay system (Section 6). Model production also was compared with abundance (CPUE) estimates from Galveston Bay and coastal Gulf waters as one means of assessing model performance (Section 7).

2.2. Model description

The model, which is spatially-explicit and individually-based, simulates the biomass production of brown shrimp in salt marsh habitats of the northern Gulf of Mexico and currently is parameterized to represent the environmental conditions and habitat characteristics of Galveston Bay. Three habitat types utilized by shrimp are included in the model: 1) **marsh** – regularly flooded intertidal salt marsh vegetation; 2) **non-vegetated marsh edge** (NVME)- water near (< 150 m from) the marsh vegetation; and 3) **shallow open water** (SOW) - relatively shallow (< 1m deep) non-vegetated water farther (> 150 m) from the marsh edge (Figure 2.1). These three habitat types comprise 17%, 28%, and 55%, respectively of the 63,500 ha of Galveston Bay shrimp habitat represented in the model. The 100 habitat cells (635 ha each) in the model also are identified by low (0-10 PSU), intermediate (10-20 PSU), and high (> 20 PSU) salinities, that change on a monthly basis (Figure 2.2). Salinity patterns in the bay were determined by the TxBLEND model (Guthrie *et al.* 2014). Postlarval shrimp (10 mm TL) are recruited into non-vegetated marsh edge and shallow open water on a daily basis; their distribution is based on relative densities observed in salinity-habitat combinations (Minello 1999). No shrimp are recruited directly into marsh habitat. A
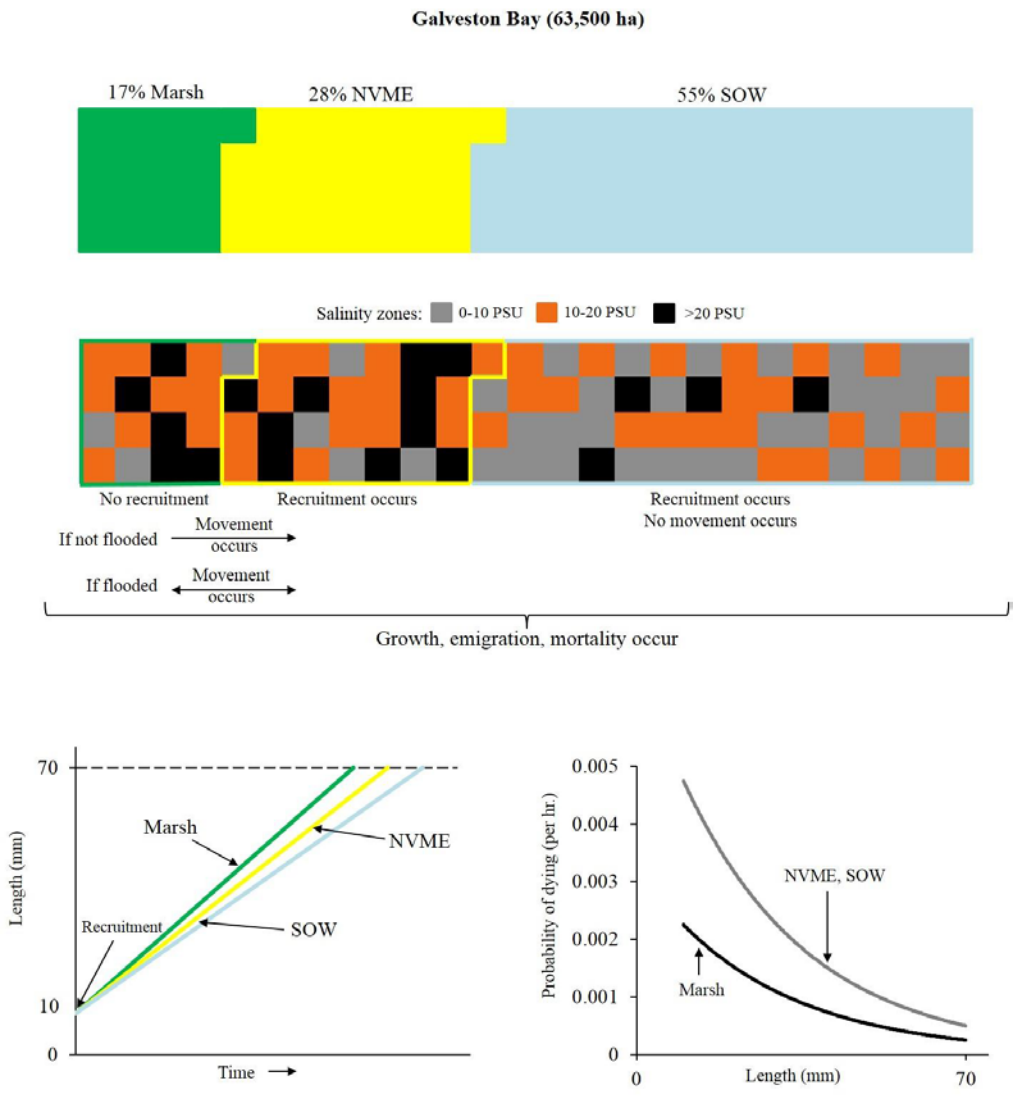
Figure 2.2 Schematic representation of the spatial relationships and dynamic processes included in the model. The top panel shows the relative abundance (fixed) of three habitats modeled in the bay. The second panel shows the distribution of salinities within these habitats; this distribution changes monthly. Location of daily recruitment and possible directions of shrimp movement is indicated below this. The graphs in the bottom panel depict the range of potential rates of growth and mortality encountered by the shrimp.

percentage of shrimp move into marsh habitat from the non-vegetated marsh edge when the marsh vegetation is flooded, and all shrimp move out of the marsh into the non-vegetated marsh edge when the marsh is no longer flooded. Shrimp in the shallow open water (> 150 m from marsh vegetation) do not leave that area. Shrimp growth, emigration, and mortality occur in all cells, with growth rates and mortality probabilities differing among cells (and also depending on temperature and salinity, see Figure 2.3).

Shrimp in the model recruit into the bay as postlarvae (10 mm TL), and they emigrate from nursery habitats to the open bay when they attain a length of 70 mm. The quantitative representations of movement, growth, mortality, and emigration of individual shrimp included in the model are summarized schematically in Figure 2.3. Rules representing the movement of individuals, described in the preceding paragraph, are probabilistic. Each hour when the marsh is flooded, each individual located in either the marsh or the non-vegetated marsh edge has a 69% probability of moving to a cell with the same salinity in the marsh vegetation and a 31% probability of moving to a cell with the same salinity in the non-vegetated marsh edge. If there is no cell with the same salinity, the individual moves into a cell with the salinity closest to the salinity of the cell from which it moved. Thus, any given individual may move back and forth between these two areas during periods of marsh flooding, but is likely to spend slightly more than twice as much of this time in the marsh vegetation. These values were based on relative densities in these habitats at flood tide reported by Minello *et al.* (2008).

Growth is a function of the water temperature, salinity, and habitat type (i.e., marsh, non-vegetated marsh edge, shallow open water) to which an individual is
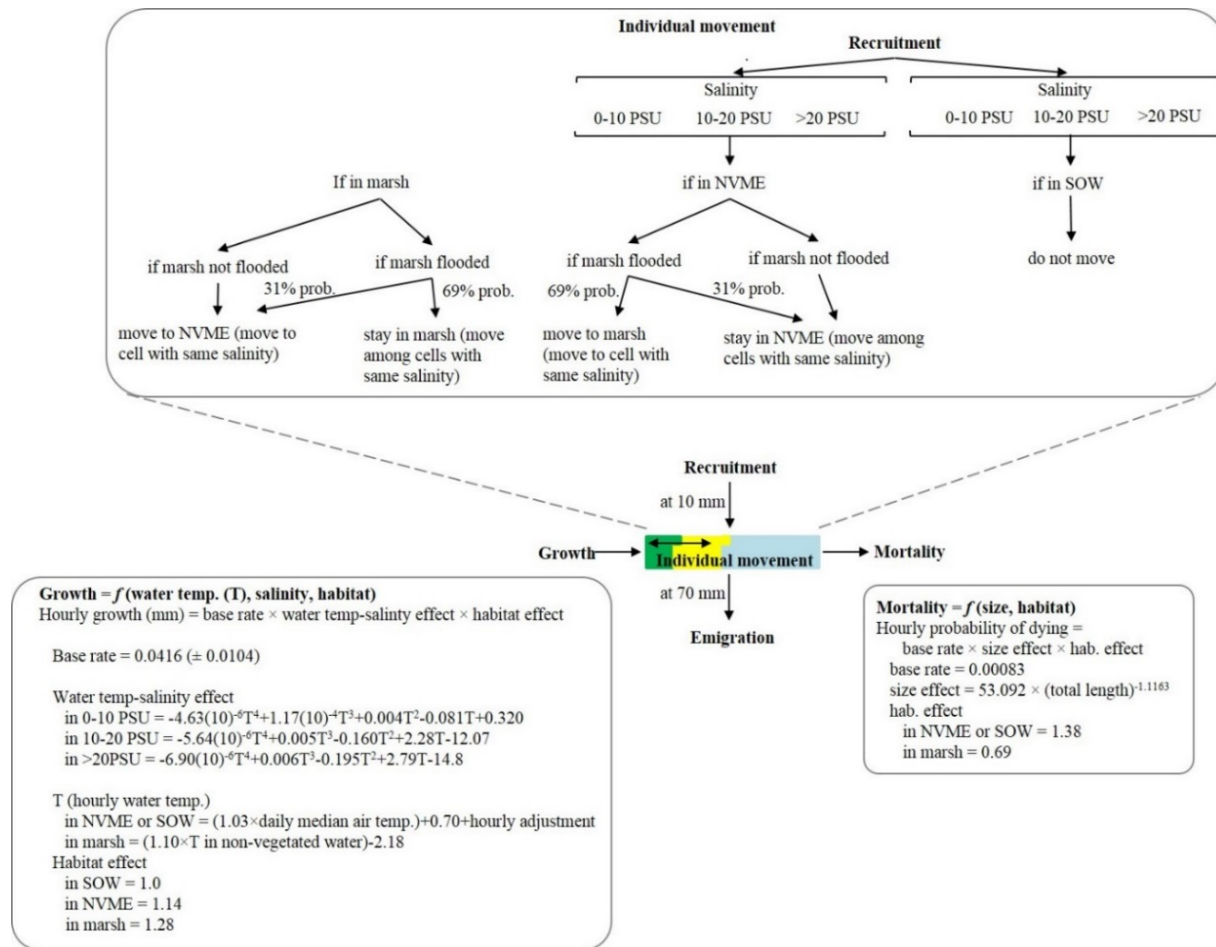
Figure 2.3 Schematic summary of the quantitative representations of the movement, growth, mortality, and emigration of individual shrimp included in the model. See text for details.

exposed (Figure 2.3). A probabilistic base growth rate (0.0416 ± 0.0104 mm hr^{-1}) is multiplied by two indexes representing 1) a water temperature-salinity effect and 2) a habitat effect. The water temperature-salinity effect is represented as a polynomial function of water temperature, which is different for each of the three salinity zones (Figure 2.4). Hourly water temperatures are calculated based on relationships between the median air temperature and measured water temperatures in marsh and non-vegetated marsh edge (see Appendix 1). The habitat effect is represented as a constant, which is different for each of the three habitats (1.28, 1.14, and 1.0 for marsh, non-vegetated marsh edge, and shallow open water, respectively). These values are based on based on experimental growth rates from field studies and infaunal prey distributions (Minello and Zimmerman, 1991; Rozas and Minello, 2011; Whaley and Minello, 2002)

Mortality (probability of dying) is a function of a base instantaneous rate (0.00083 hr^{-1}) multiplied by two indexes representing 1) a shrimp size effect and 2) a habitat effect (Figure 2.3). Mortality is reduced as shrimp grow, and the size effect is calculated as 53.092 * (total length in mm)$^{-1.1163}$. The habitat effect is represented as a constant, which is different for marsh vegetation (0.69) versus the two areas of non-vegetated water (1.38).

Input data required by the model for each calendar year being simulated include 1) current elevation of the marsh edge 2) hourly tide heights, 3) daily median air temperatures, and 4) monthly distribution of salinity zones among habitat types for the calendar year being simulated. The number of individual postlarval shrimp recruiting i

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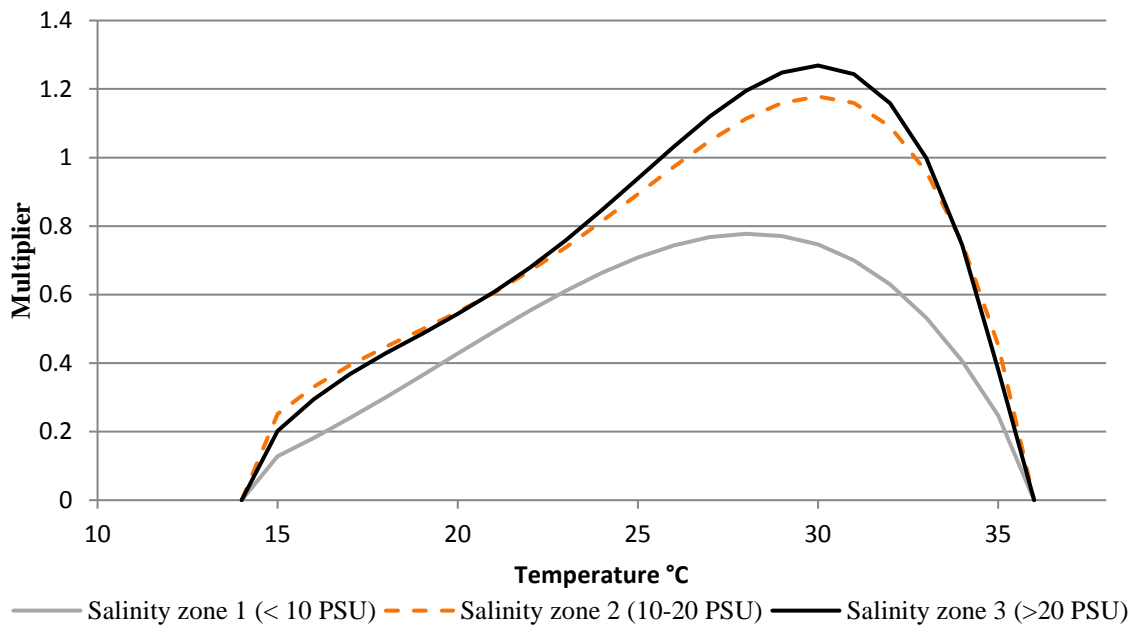
Figure 2.4 Plot of the effect of the interaction between temperature and salinity on growth.
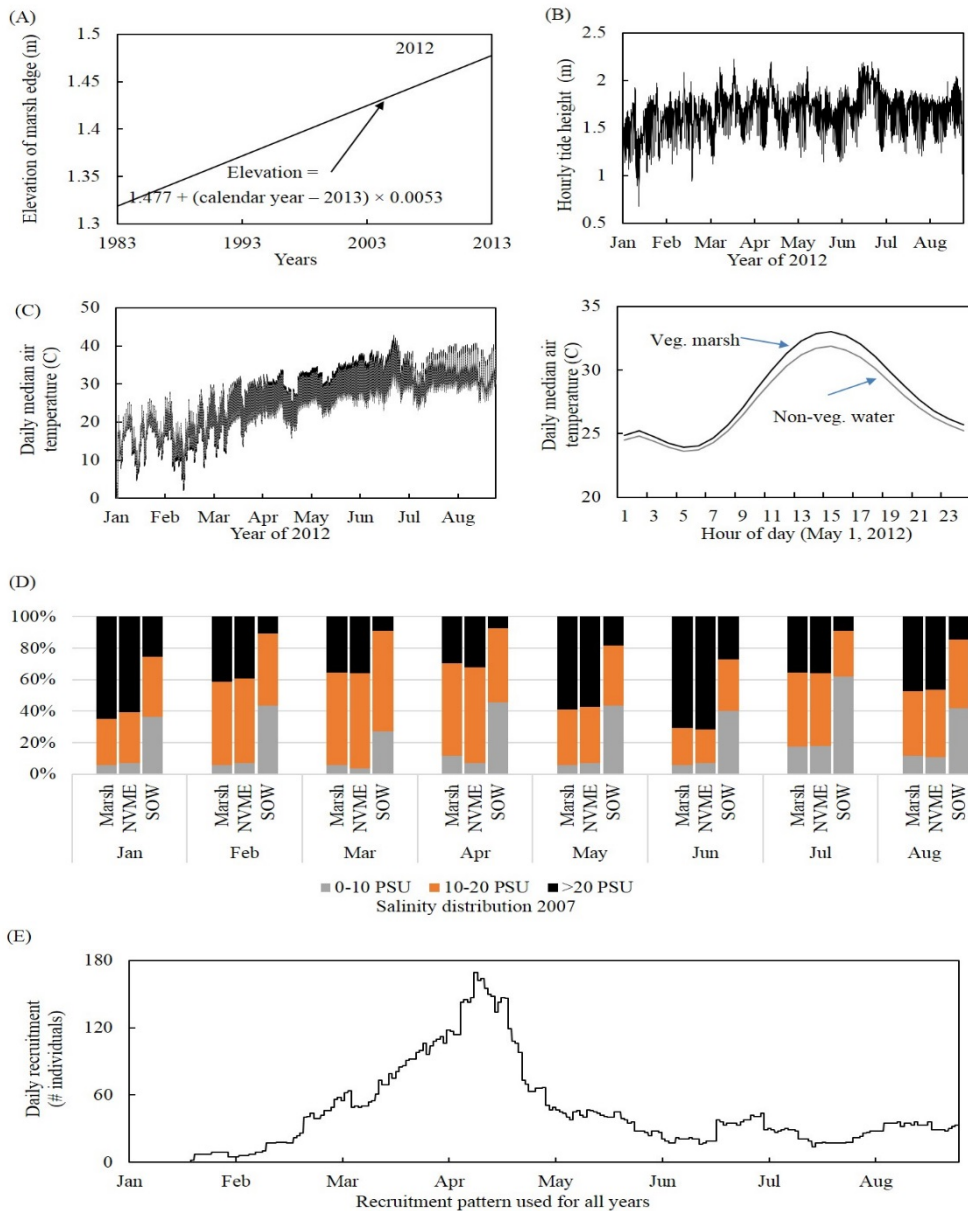
Figure 2.5 Examples input data required by the model, including (a) current (for the year being simulated) elevation of the marsh edge, (b) hourly tide heights, (c) daily median air temperatures, (d) proportion of habitats in each salinity zone, and (e) daily shrimp recruitment. Data presented are for January through August, in Galveston Bay, Texas, U.S.A.

nto the bay system each day during the simulation period is fixed. Graphs of input data

for January through August, 2012 are presented in Figure 2.5. Elevation of the marsh

edge is a function of the elevation measured in the baseline year of 2013 (1.477 m,

NOAA tide gauge 8771450, Galveston Pier 21, http://co-ops.nos.noaa.gov/) and relative

sea level rise over the years simulated (Figure 2.5a, see Appendix 1 for details). The

time series of environmental data representing hourly tide heights (Figure 2.5b), daily

median air temperatures (Figure 2.5c), and monthly salinities (Figure 2.5d) are based on

data from NOAA Tides and Currents

(https://tidesandcurrents.noaa.gov/waterlevels.html?id=8771450), NOAA National

Center for Environmental Information, (https://www.ncdc.noaa.gov/cdo-web/datatools),

and the Texas Water Development Board's TxBLEND model (Guthrie *et al.*, 2014),

respectively (see Appendix 1). The relative numbers of individual shrimp entering

Galveston Bay (Figure 2.5e) are based on data from collections of postlarvae in a

Galveston Bay tidal pass (Matthews, 2008) and abundance patterns observed in marsh

habitat (Rozas *et al.* 2007).

A detailed model description following the ODD (Overview, Design concepts,

Details) protocol for describing individual-based models as outlined by Grimm *et al.*

(2006) and Railsback and Grimm (2012) is presented in Appendix 1. In addition to the

equations and logical rules that constitute the model, which are summarized above,

Appendix 1 describes the rationale behind the model, model design concepts, key

assumptions, intermediate calculations linking information sources to the representation

of that information in the model, and the sequence of events and processes involved in the execution of the model.

2.3. Model calibration

We calibrated the model such that 1) simulated annual brown shrimp production was scaled to reasonable values, and 2) simulations could be run in a reasonable amount of time on available computing facilities. We accomplished 1) by assuming each simulated shrimp was a "super-individual" (Scheffer *et al.* 1995) representing 1 million "real" shrimp. This calibration resulted in simulated monthly and annual mean abundances and biomasses similar to those estimated based on field data from a polyhaline marsh complex in Galveston Bay spanning 11 years (Rozas *et al.*, 2007). We then accomplished 2) by multiplying the input data representing daily shrimp recruitment (Figure 2.5e) by 0.5. This kept the number of individuals being simulated during any given (simulated) hour under 2,000 and resulted in simulation times under 10 minutes on standard desktop computers. Since simulated shrimp behave independently of each other (i.e., there are no density-dependent relationships in the model), neither of these calibrations affect the interpretation of simulation results with regard to the relative influence of environmental factors on shrimp production (Figure 2.6).

2.4. Baseline simulations

We used a baseline version of the model, parameterized and calibrated as described above, to simulate annual brown shrimp production from Galveston Bay under environmental conditions representative of those observed from 1983 to 2012. We ran

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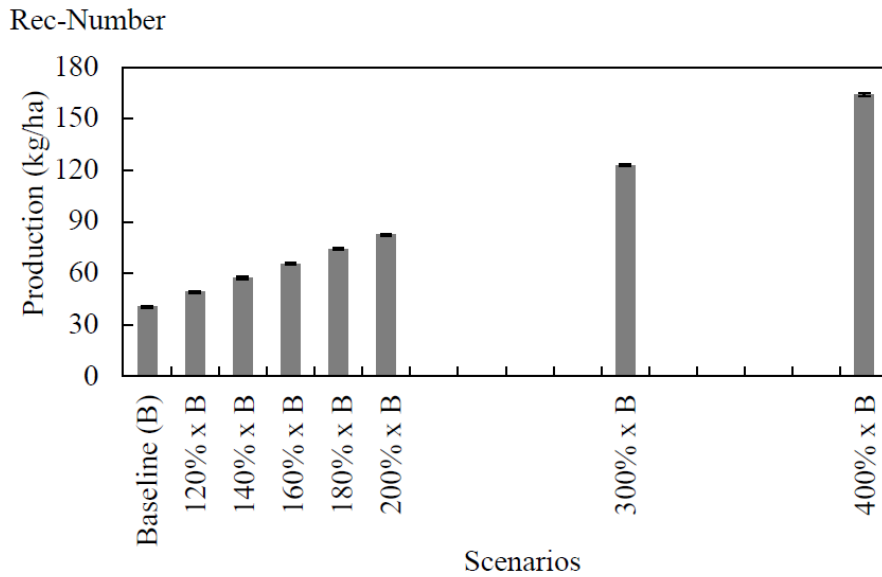
Figure 2.6 Sensitivity of model estimates of brown shrimp production (kg/ha) to changes relative to baseline in the number of "real" shrimp represented by each simulated shrimp. Mean (± SE, n = 10) production from January through August in Galveston Bay, Texas, U.S.A., is presented for simulations run with baseline parameter values and under environmental conditions representing the calendar year 2012 with the indicated changes in the number of "real" shrimp represented by each simulated shrimp
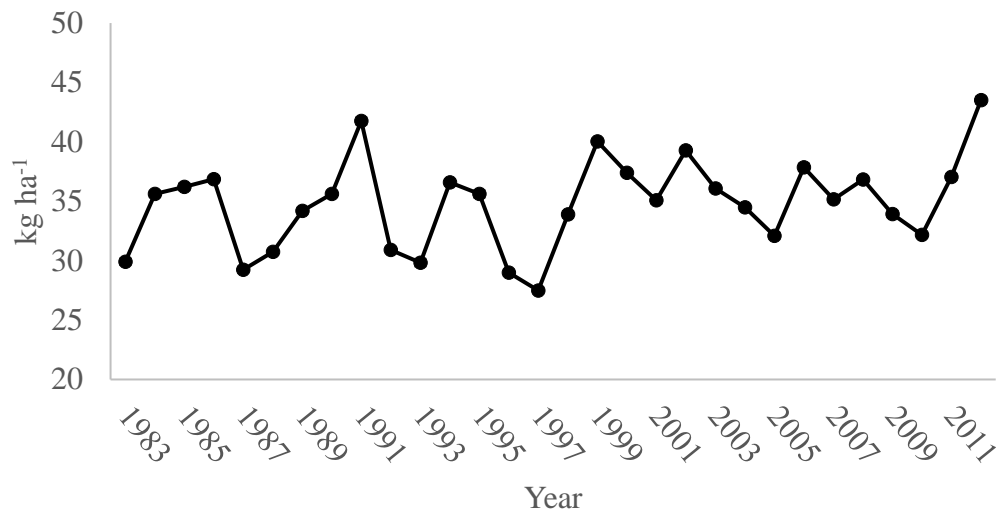
Figure 2.7 Mean (± SE, n = 10) production (kg/ha) of brown shrimp (*Farfantepenaeus aztecus*) from January through August in Galveston Bay, Texas, U.S.A., simulated under environmental conditions representing the indicated calendar years.

10 replicate stochastic (Monte Carlo) simulations representing each of these 30 years (i.e., using the tide, temperature, and salinity input data corresponding to each year). Mean annual (January through August) production ranged from 27.5 kg ha^{-1} in 1997 to 43.5 kg ha^{-1} in 2012, with an overall mean of 34.8 ($\pm$ 0.70 SE) kg ha^{-1} (Figure 2.7, see Figure A2.1, Appendix 2, for results of individual simulations).

2.5. Sensitivity analyses

We examined the sensitivity of model estimates of annual brown shrimp production to changes of $\pm10\%$ relative to baseline in values of key model parameters (growth rate, probability of mortality, and probability of moving into marsh vegetation of individual shrimp) and values of environmental input data (tide heights, median air temperatures). We also performed simulations in which the salinity of the entire bay was designated low (0-10 PSU), intermediate (10-20 PSU), or high (>20 PSU). For all analyses we ran 10 replicate stochastic simulations of each scenario for each year from 1983 through 2012 and compared the mean production of the treatment to the corresponding year's mean baseline value (Table 2.1). Increasing growth rates by 10% caused an overall 16% increase (annual range 13-20%) in production, whereas a 10% decrease resulted in an 18% decrease (annual range 16-21%) in production. A 10% increase in mortality probabilities resulted in a production decrease of 15% (annual range 11-16%) while a 10% decrease resulted in an 18% increase (annual range 14-21%) in production. When we increased the shrimp's probability of moving into the marsh by 10%, production increased 5% (annual range 3-8%) and conversely, decreased 5% (annual range 1-8%) with decreased probability of movement.

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Table 2.1 Results of sensitivity analysis showing the mean increase or decrease in shrimp production (kg ha^{-1}) associated with a 10% increase or decrease in each parameter. The salinity zone patterns differed among the 30 simulated years and so the delta value was variable by year as well.

Parameter	Δ	30 yr. mean % change from baseline	30 year range
Growth	+10%	+16%	+13 to +20%
	-10%	-18%	-16 to -21%
Mortality	+10%	-15%	-11 to -16%
	-10%	+18%	+14 to +21%
Movement	+10%	+5%	+3 to +8%
	-10%	-5%	-1 to -8%
Tide height	+10%	+11%	+5 to +21%
	-10%	-19%	-14 to -24%
Temperature	+10%	-2%	-12 to +8%
	-10%	-14%	-7 to -19%
Salinity			
0-10 PSU	Varied by	-55%	-49 to -59%
10-20 PSU	year	-7%	-12 to +9%
>20 PSU		±0%	-4 to +16%

We also conducted simulations by changing values of environmental input data by ±10%. Mean production estimates increased 11% (annual range 5-21%) in response to increasing tide heights (and thus, marsh habitat access) and decreased 19% (annual range 14-24%) with a decrease in tide height (and marsh access). The thirty year mean production was affected negatively by both decreasing and increasing air temperature. A 10% decrease in air temperature resulted in a 14% decrease (annual range 7-19%) in annual production. Increasing temperature 10% decreased production by a mean of 2%, with annual values ranging from a decrease of 12% to an increase of 8%. Although the overall mean change was negative, nine years of the 30 simulated saw an increase in production with an increase in temperature (Table 2.1, See Figure A2.2 and 2.3, Appendix 2, for results of example year, 2012). Simulations in which bay water salinities were entirely low (0-10 PSU), intermediate (10-20 PSU), or high (>20 PSU) resulted in mean production rates decreasing 55 (annual range 49-59%), 7 (annual range -12 to +9%), and 0% (annual range -4 to +16%), respectively, from the baseline mean.

2.6. Simulation of effects of timing of recruitment on brown shrimp production

To explore the uncertainty in estimations of shrimp production resulting from uncertainty in the timing of postlarval shrimp recruitment to the bay system, we ran simulations in which we shifted the time series of input data representing recruitment such that recruitment occurred 14, 21, and 28 days earlier than baseline, and 14, 21, 28, 35, and 42 days later than baseline. We did not change the relative shape of the recruitment curve (Figure 2.5e), but rather we shifted the entire curve earlier or later in the year. For each of these 9 scenarios (these 8 shifts plus a baseline scenario), we ran
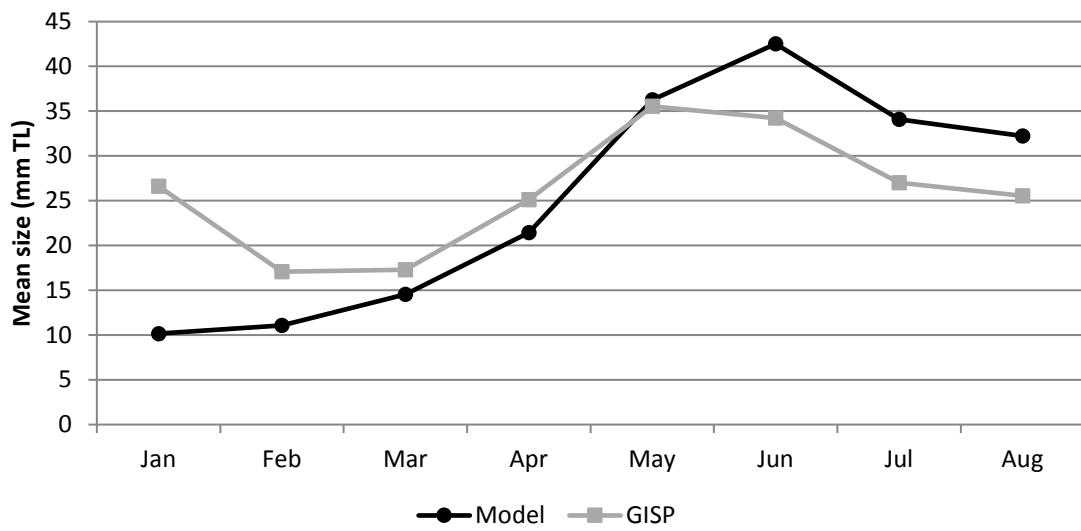
Figure 2.8 Comparison of shrimp mean size (mm TL) from model output and data from Galveston Island State Park (GISP)

10 replicate stochastic (Monte Carlo) simulations under environmental conditions representing each of the 30 years from 1983 to 2012 (i.e., using the tide, temperature, and salinity input data corresponding to each year) (a total of 9 x 10 x 30 = 2700 simulations). Mean production estimates decreased monotonically as recruitment occurred earlier than baseline under all environmental conditions simulated (Figure 2.8, see Figure A2.4, Appendix 2, for results of individual simulations). When recruitment occurred up to 21 days later than baseline, mean production estimates tended to increase or remain essentially unchanged under all environmental conditions. However, recruitment delays of 28 or more days affected mean production estimates differently under different environmental conditions, with estimates sometimes continuing to increase noticeably, sometimes decreasing noticeably, and often remaining relatively unchanged relative to shorter delays (e.g., under environmental conditions representative of 1987, 2012, and 1984, respectively).

2.7. Model evaluation

Patterns that emerged from our model included: seasonal trends in relative population size and structure, annual production variability, and inter-annual production variability. Seasonal trends in relative population size and structure were verified against field data collected in Galveston Bay at Galveston Island State Park (GISP) from 1982-1992 (Rozas *et al.*, 2007). We compared field data to our model output of the monthly mean size of shrimp, the size frequency distribution, the population size, and the standing biomass. Since the GISP data were used to derive some of our growth and mortality parameters (Minello *et al.*, 1989; Minello *et al.*, 2008; Roth *et al.* 2008; Rozas
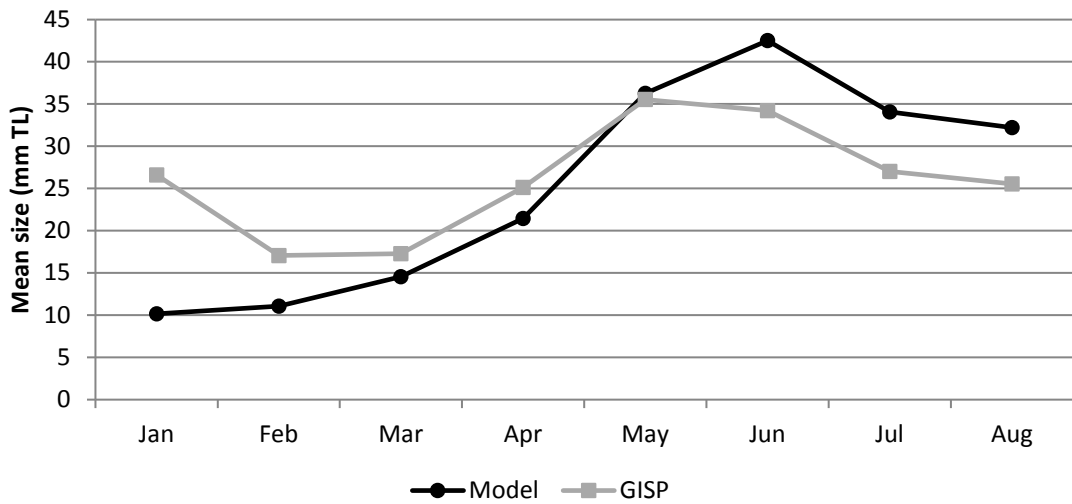
Figure 2.9 Comparison of shrimp mean size (mm TL) from model output and data from Galveston Island State Park (GISP)
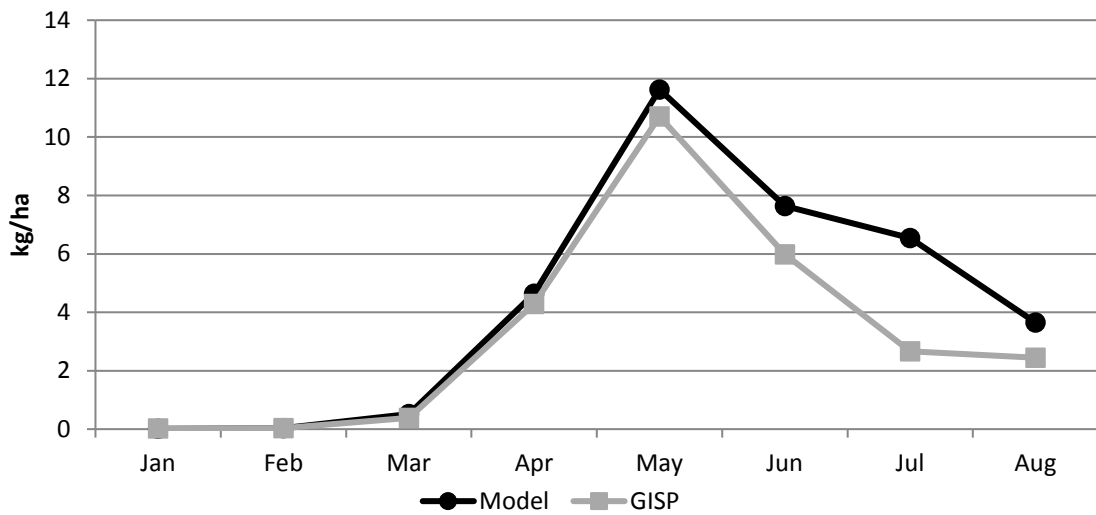
Figure 2.10 Comparison of shrimp standing biomass from model output and field data from Galveston Island State Park (GISP).

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et al., 2007), we used the comparisons as a method of verifying that the model processes were reproducing patterns that characterize the systems internal organization. The modeled monthly means for shrimp size, and standing biomass followed patterns similar to the GISP data set (Figures 2.9 and 2.10). Size distributions also were similar over time.

Minello *et al.* (2008) estimated a mean standing crop of 19,382 shrimp ha^{-1} in the polyhaline marsh complex over the period of April through November. Our model estimates a mean of 22,848 shrimp ha^{-1} in the polyhaline marsh (Zone 3) over the period of April through August for the years 1893 through 2012. We estimated that secondary production lost to predation (shrimp that die in the model) was a mean of 28% of the total production (kg ha^{-1}). This is less than the estimate from Roth *et al.* (2008) of 37%.

Several data sets estimating brown shrimp abundance were used to evaluate our model output. The Texas Parks and Wildlife Department collects shrimp using trawls at random locations in Galveston Bay every month (Brown *et al.*, 2013; Martinez-Andrade *et al.*, 2005), and monthly catch per unit effort (CPUE) data from 1982 through 2011 were available for model comparisons. Southeast Area Monitoring and Assessment Program (SEAMAP) summer trawl surveys provided another fishery independent source of abundance data (CPUE) available for most years of our simulations (1987-2012). We looked for general trends in inter-annual variability to facilitate comparison of our modeled production estimates (kg ha^{-1}) against catch data.

From 1982 through 2011, the mean size of shrimp caught by the TPWD trawls was 87.4 mm TL (Brown *et al.*, 2013), and we assumed that their samples represented
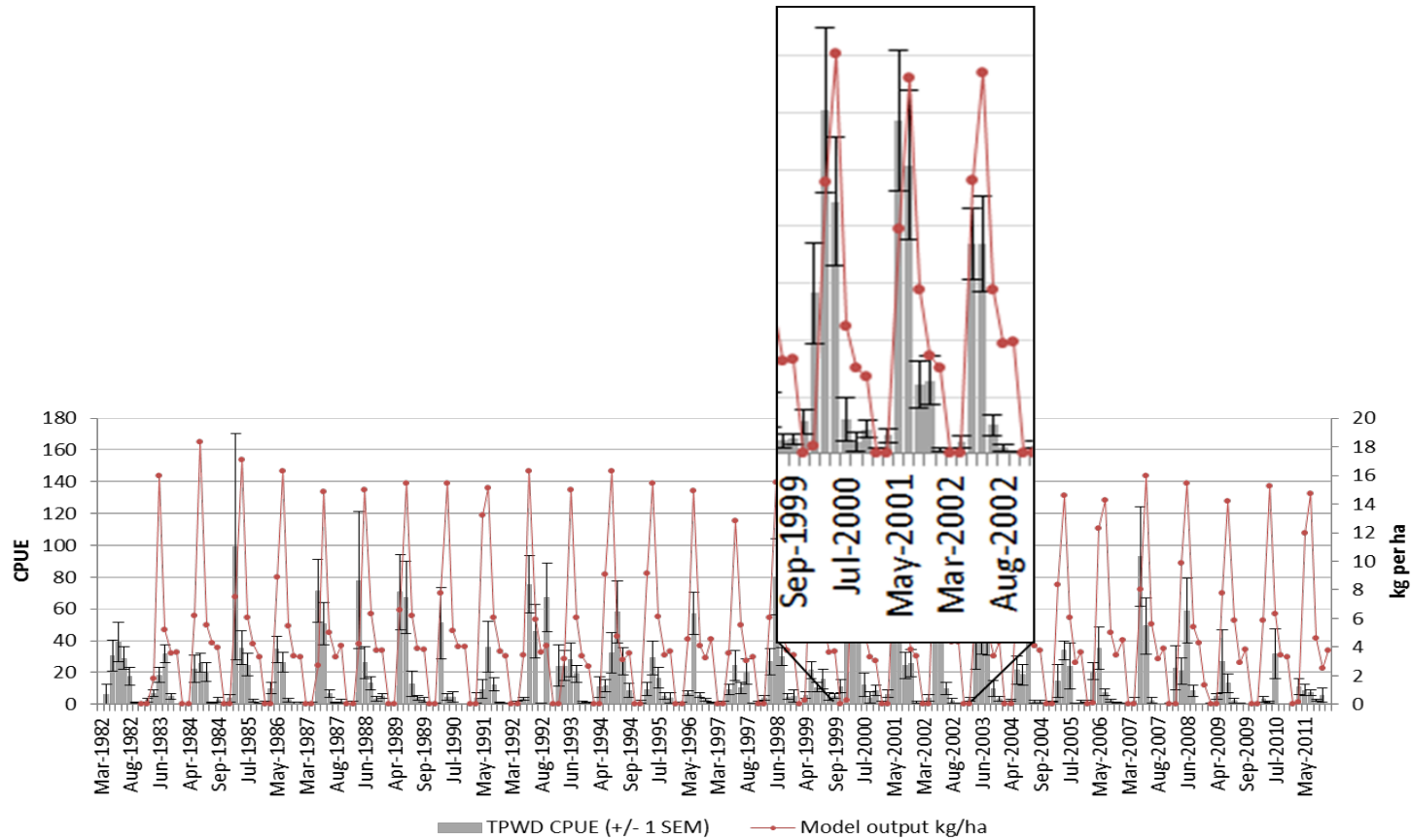
Figure 2.11 Seasonal pattern of production (March through August) from the model (kg/ha) and CPUE (number/per ha) from Texas Parks and Wildlife Department trawl sampling. Vertical bars represent +/- 1 standard deviation. Cutout shows detail.

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shrimp that had recently left the marsh complex and moved into open bay habitats. We compared TPWD CPUE from March through September with the modeled monthly production in kg ha^{-1} (Figure 2.11), and there are similarities in the seasonal pattern. Months of peak production in the model generally coincided with months of peak CPUE. Our estimates of annual production only include production through August, since TPWD data show that there are very few brown shrimp caught in the bay after this time. Annual variability in modeled production was lower than expected when compared to TPWD data, and there was a poor relationship between our annual model output and TPWD mean CPUE for each year. A linear regression was not significant with an R^2 value of only 0.005.

SEAMAP trawl surveys follow a stratified random sampling method and sample across the northwestern GoM from near shore out to the border of the United States Exclusive Economic Zone (EEZ). Linear regression analysis of SEAMAP summer survey CPUE with our model's annual output was significant (p = 0.0005) and had an R^2 of 0.40 (Figure 2.12). Since the SEAMAP summer survey is conducted in June and July, we also examined the relationship with our model output up until May of each year from 1987 through 2012. We expect shrimp that emigrated from the marsh complex in May would be available to the SEAMAP survey in June and July. The May model output has a mean production of 9.2 kg ha^{-1}, is more variable than the August production estimates, and ranges from 3.5 to 18.8 kg ha^{-1}. Regression analysis of the model's May production with the SEAMAP summer CPUE was significant (p = 0.002) and had an R^2 value of 0.45 (Figure 2.12).
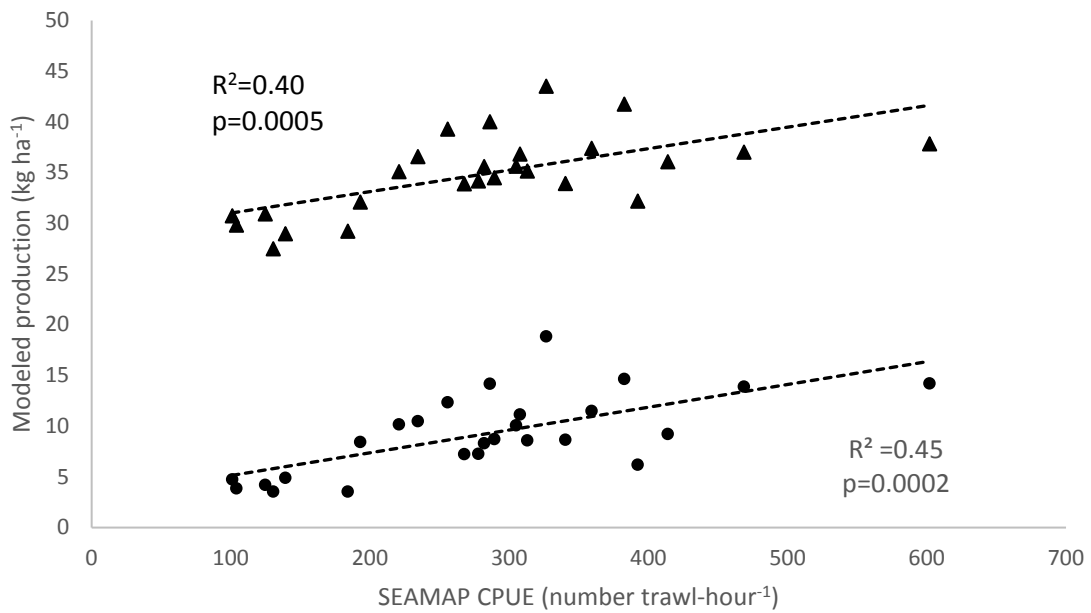
Figure 2.12 Regression of modeled production (kg ha^{-1}) through May (circles) and August (triangles) with SEAMAP Summer CPUE (number trawl-hour^{-1}) for years 1987 through 2012.

2.8. Discussion

Model estimates of annual brown shrimp production from Galveston Bay differed noticeably under different environmental conditions affecting the growth, mortality, and access to marsh vegetation of juvenile brown shrimp. The lowest production estimate generated under temperatures, salinities, and tides (marsh flooding events) representative of the years from 1983 to 2012 was approximately 63% of the highest estimate. By comparison, model sensitivity to the uncertainty associated with a 10% change in values of key parameters caused less than a 25% change in baseline production estimates under any given set of environmental conditions. Galveston Bay is typical of most bay estuarine systems of the northern Gulf of Mexico, and this variation in simulated production estimates is consistent with the year-to-year variability in estimates of brown shrimp catch per unit of effort (CPUE) in the northern Gulf of Mexico (Pollack and Ingram, 2012).

The importance of interaction between environmental conditions within and outside the bay system in generating this year-to-year variability in brown shrimp production was emphasized by simulations in which we shifted the seasonality of recruitment. Over the range of seasonal shifts simulated (from 28 days earlier to 42 days later in the year), the lowest production estimate was approximately 70 percent of the highest estimate. These simulations suggest that shifts in seasonality of recruitment caused by environmental conditions outside the bay may cause differences in production in any given year equal to those resulting from differences in environmental conditions within the bay. Furthermore, although earlier recruitment generally results in relatively

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lower production and later recruitment in relatively higher production (undoubtedly temperature-related), recruitment delayed beyond some threshold, which depends on conditions within the bay, may result in relatively lower production. In our simulations, this threshold ranged from a delay of 28 to 42 days (e.g., under bay conditions representative of the calendar years 2012 and 2007, respectively).

Various mechanisms that may cause variability in the timing of postlarval recruitment have been proposed. During winter and early spring, Arctic frontal passages are common and drive currents offshore, delaying postlarval emigration from Gulf waters (Benfield and Downer, 2001; Wenner *et al.*, 1998). Additionally, brown shrimp may actively delay their emigration from the Gulf to shallow water habitats in response to cold frontal passages via vertical migration (Rogers *et al.*, 1993). Hughes (1969) suggested that pink shrimp *Farfantepenaeus duorarum* sense changes in salinity and tide state as cues to enter estuaries, and Blanton *et al.* (1999) found evidence that white shrimp *Litopenaeus setiferous* likely utilize a set of cues that include tidal phase, water temperature, and wind. It also has been suggested that timing of recruitment may be affected by endogenous rhythms that control the swimming activity of postlarval penaeids (Ogburn *et al.*, 2013).

Superimposed on effects of timing of recruitment on shrimp production are effects of differences in magnitude of recruitment, which we held constant in all our simulations. This simplifying assumption facilitated identification of the relative effects on production of environmental conditions within the bay, in which we were most interested. This assumption could be relaxed in future work with the model. Data from

22 years of sampling postlarvae entering Galveston Bay (Matthews, 2008) suggest that annual peak abundances may be as much as 80 times the mean annual abundance, and peak annual population estimates of small shrimp (12-20 mm total length) based on data collected at the Galveston Island State Park over an 11-year sampling period differed by as much as five times (Rozas *et al.*, 2007). Our model calibration exercises suggested a linear relationship between model estimates of shrimp production and total number of shrimp recruited during a simulation. However, this linear relationship results from our representation of the growth, mortality, and movements of individual shrimp as being independent of shrimp population density. These also are simplifying assumptions that could be relaxed in future work with the model, perhaps drawing on some of the below-mentioned studies.

Brown shrimp appear to feed mainly on benthic infauna (McTigue and Zimmerman 1991) Laboratory and field caging studies have demonstrated that foraging by both brown shrimp and white shrimp *Litopenaeus setiferous* can reduce populations of benthic infauna (Beseres and Feller, 2007; Zimmerman *et al.*, 2000). Field caging experiments have shown some evidence of food limitation of growth (Rozas and Minello, 2009; Rozas *et al.,* 2014), and as shrimp population density increases, *per capita* availability of food will become limiting at some point. Documenting a density-dependent effect on shrimp growth, however, is difficult because brown shrimp may move to avoid areas of low prey density and may consume alternate food items such as benthic algae and phytoplankton during periods of low infaunal abundance (Gleason, 1986; Gleason and Wellington, 1988; Gleason and Zimmerman, 1984).

Brown shrimp mortality appears to result mainly from predation, and laboratory experiments do not suggest a strong relationship between brown shrimp density and mortality (Minello *et al.*, 1989). While the functional response of fish predators may be affected by shrimp density (Holling, 1959), it is likely that such a relationship is size-related, since smaller shrimp are found in higher densities than larger shrimp; our model includes a size-related mortality function. However, seasonal and annual changes in fish predator abundance (Minello and Zimmerman, 1983; Overstreet and Heard, 1978; Rooker *et al.*, 1998) likely change predation rates. The abundance and composition of brown shrimp predators also differs spatially within Galveston Bay, as well as among other bays of the northern Gulf of Mexico (Nelson *et al.*, 1992).

Primary assumptions in our model are that brown shrimp abundance and growth are higher in salt marsh vegetation than in shallow open water. High densities of brown shrimp on the marsh surface and particularly at the marsh edge have been consistently found in Galveston Bay and other Texas estuaries (Minello *et al.*, 2008, Zimmerman *et al.*, 1984), but this pattern may not occur in all estuarine systems and may be related to tidal flooding characteristics (Minello *et al.*, 2012; Rozas and Minello 2015). Information on habitat-related shrimp growth is limited, but there is some evidence from caging experiments that brown shrimp growth is increased in marsh vegetation (Minello and Zimmerman 1991, Rozas and Minello, 2009). Populations of benthic infaunal prey also are higher in marsh vegetation than adjacent open water and generally highest at the marsh edge (Whaley and Minello, 2002). This edge effect has not been incorporated into our model, and the model could perhaps be improved by separating marsh edge

habitat from the rest of the marsh. Delineation of the area of marsh edge habitat, as opposed to the area of marsh vegetation inundated at high tides, as currently represented in our model, would require finer-scale spatial resolution of habitat distribution in the bay. Such an approach would allow us to simulate the effect of changes in marsh edge on shrimp production, but the explicit inclusion of such fine spatial resolution also would result in longer simulation run times.

Future work with the model will be directed at potential incorporation of modeled environmental effects into the Gulf of Mexico brown shrimp stock assessment model (SS-3, Hart, 2012). We expect to explore the relative benefits of relaxing some current model assumptions and also re-parameterize the model to represent conditions in Barataria Bay, Louisiana. Linking living marine resources and their habitat is essential to fisheries stock management (Yoklavich *et al.*, 2010). Ultimately, we hope our model will provide a useful tool, both conceptually and quantitatively, for exploring the linkages between environmental conditions in estuarine nursery habitats in the northern Gulf of Mexico and the production of shrimp species utilizing these habitats (Beck *et al.* 2001; Boesch and Turner, 1984).

3. ASSESSING VARIABILITY IN JUVENILE BROWN SHRIMP GROWTH RATES

IN SMALL MARSH PONDS: AN EXERCISE IN MODEL EVALUATION AND

IMPROVEMENT

3.1 Introduction

The United States Gulf of Mexico (GoM) landings of penaeid shrimp in 2015

were valued at 340 million dollars, and brown shrimp (*Farfantepenaeus aztecus*)

comprised almost half of the catch (National Marine Fisheries Service, Fishery Statistics

Division, 2015). Brown shrimp have a largely annual life history (Fry, 2008; Minello *et*

al., 1989); adults spawn offshore and postlarvae are transported by currents to estuarine

habitats (Cook and Lindner, 1970; Temple and Fischer, 1967). 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 overall shrimp

production and fishery yield (Haas *et al.*, 2001; Minello *et al.*, 1989; Minello and

Zimmerman, 1991).

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 from the shallow waters of Galveston Bay, TX. 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, shrimp that

grow faster are more likely to survive. All of the environmental drivers in the model

affect growth, including temperature, salinity, and tidal access to salt marsh habitat. 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 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 increases in our IBM when shrimp are within vegetated habitat, 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 (Manino and Montagna, 1997; Whaley and Minello 2002), we identified infaunal distribution as a potential source of variability between modeled growth and observed growth in the field.

We conducted a mark-and-recapture study in three marsh ponds to estimate juvenile shrimp growth and further evaluate model performance. During the study period over several months in the spring/summer of 2011we recorded water temperatures and water levels at hourly intervals. Salinity was measured during each

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tagging interval, and we sampled benthic infauna at the beginning and end of the study.

We assessed how well the model estimates of water temperature and tidal flooding of the

marsh represented the observed data from the ponds. We compared shrimp growth

estimates from the study to estimates from the model and examined benthic infaunal

biomass distribution as a potential cause of variability.

3.2 Materials and methods

Site selection and characterization

We selected three marsh ponds for our growth study. These ponds were fringed

with *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), within the marsh complex

and along the bay side of Galveston Island (Figure 3.1). The park is located along the

shore of West Bay, a polyhaline 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). We selected the Moses Lake pond in an effort to include a mesohaline pond.

This pond is north of the Texas City Dike and closer to freshwater input from the Trinity

and San Jacinto rivers. Salinities during the duration of the study, however, were

consistently polyhaline in all three ponds.

Each pond has a nonvegetated mud bottom surrounded by intertidal vegetated

marsh dominated by *Spartina alterniflora*. We used GIS and Digital Orthophoto Quarter
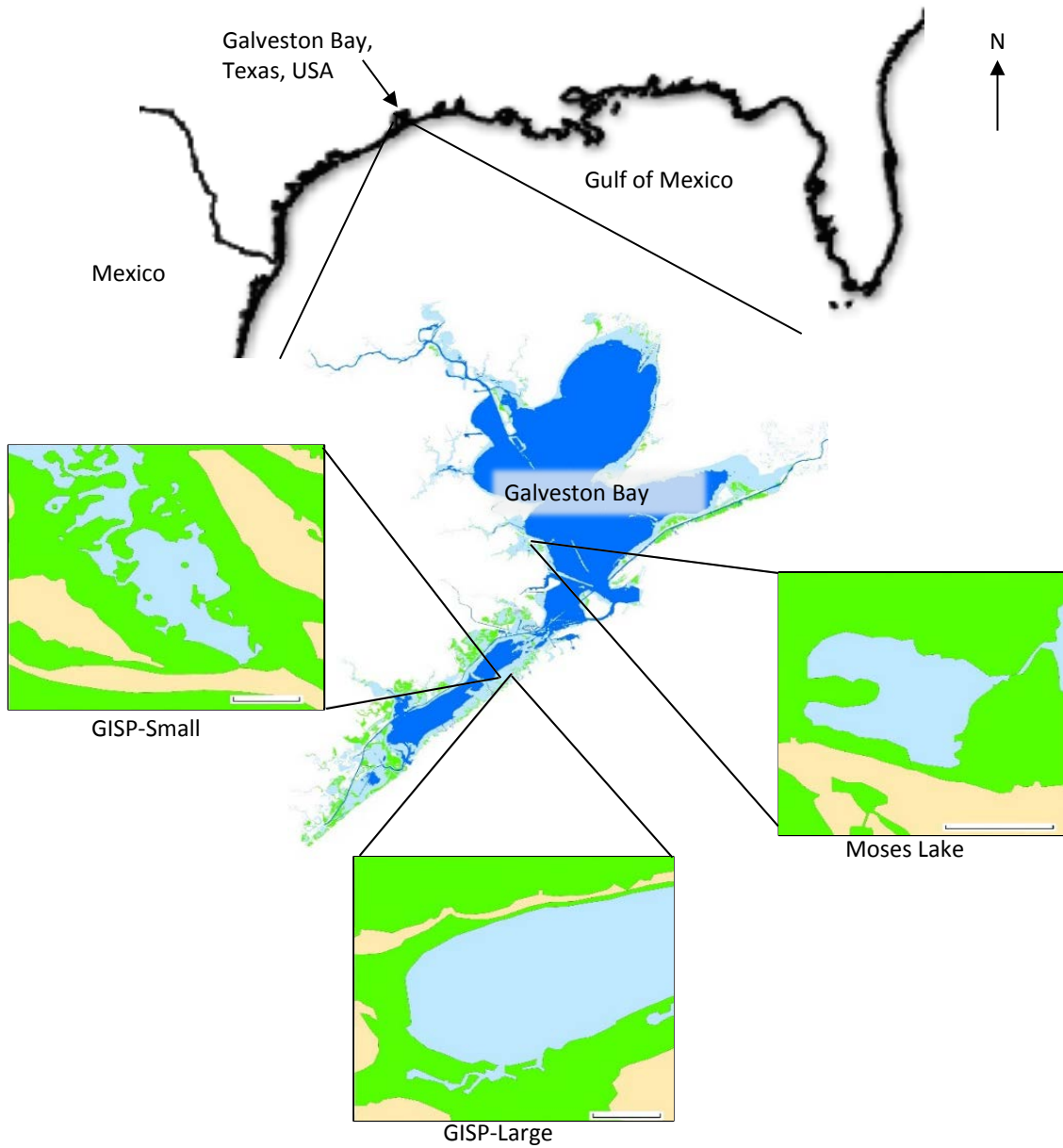
Figure 3.1 The three experimental ponds located within Galveston Bay, Texas. GISP-Small and GISP-Large are in West Bay inside the Galveston Island State Park. The Moses Lake pond is located 20 km to the north of the park and north of the Texas City Dyke. Green indicates the marsh vegetation and light blue indicates the non-vegetated shallow ponds. Dark blue indicates areas of water deeper than 1 m and were not included in the model estimates. Bar in lower, right corner of pond detail images represents 20 m.

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 also measured the marsh elevation profile in each pond based on five transects established perpendicular to the vegetated marsh edge. We estimated relative 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. We used these relative elevation data in conjunction with hourly monitoring of tide height to estimate marsh flooding frequency and duration in each pond. Data loggers (HOBO, Onset Corporation, Massachusetts) were used to record hourly water depth and temperature hourly. We assumed that the marsh was flooded when the water depth at the marsh edge reached 10 cm, the point in the model at which shrimp can access the marsh vegetation.

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 brown shrimp marsh residence. We collected benthic cores in each pond and measured infaunal abundance and biomass in relation to the distance from the marsh edge. We collected sediment cores at 10 sites 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 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 pooled core samples (10 replicates x 3 distances from

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edge x 3 ponds x 2 collection periods). Core collection and analysis followed methods

from Whaley and Minello (2002). In the lab, we sorted, counted, dried (at 100 °C for 24

hours), and weighed crustaceans and annelids sorted from the top 2.5 cm of each core.

We estimated prey biomass as a measure of the dry weight of annelids and crustaceans

in g m^{-2}.

Shrimp growth estimates

In each pond, we collected shrimp using a bag seine and sorted them into 2-mm

total length (TL) size classes between 30 and 50 mm. We selected two to four size

classes for tagging based on their abundance to maximize the number of tagged

individuals in as few size classes as possible. We attempted to tag at least 300 shrimp

during each sampling effort; however, during the earlier and later efforts, we were

limited by lower abundance of shrimp in the 30 to 50 mm size range (see Table 3.1).

We tagged shrimp using Visible Implant Elastomer (VIE, Northwest Marine

Technology, Inc., Shaw Island, WA, USA), a non-toxic compound that is injected as a

liquid and cures to a soft rubbery texture within a short period of time (< 24 hrs). We

tagged shrimp ventrally, in the muscle of the sixth abdominal segment. Each size class

had a unique tag color. At the initiation of the study, we placed a block net

(approximately 8 mm mesh) across the mouth of each pond to prevent shrimp from

moving out of the pond.

Tagging and recovery efforts occurred 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

(see Table 3.1). There were five visits to GISP-Small, and three each at GISP-Large and

Table 3.1 Sampling schedule for three growth study ponds, size of tagged shrimp, and the number of recaptured tagged shrimp. The total shrimp recaptured during each sampling date 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	4/12/2011	34	32	1	4/26/2011 (1)
		38	16	1	4/26/2011 (1)
		46	13	1	4/26/2011 (1)
	4/26/2011	32	78	6	5/10/2011 (4)
					5/24/2011 (2)
		36	213	9	5/10/2011 (8)
					5/24/2011 (1)
	5/10/2011	34	187	25	5/24/2011 (24)
					6/7/2011 (1)
		36	175	19	5/24/2011 (19)
	5/24/2011	36	167	5	6/7/2011 (5)
		38	157	1	6/7/2011 (1)
	6/7/2011	40	47	-	-
		42	37	-	-
		Total	1122	68 (6.1%)	
GISP-Large	4/21/2011	36	195	9	5/12/2011
		40	156	8	5/12/2011 (7)
					6/1/2011 (1)
	5/12/2011	32	89	9	6/1/2011
		36	117	5	6/1/2011
		40	120	8	6/1/2011
		Total	677	39 (5.8%)	
Moses Lake	4/20/2011	34	43	3	5/5/2011
		36	40	2	5/5/2011
		42	31	3	5/5/2011
		44	38	3	5/5/2011
	5/5/2011	36	162	4	6/2/2011
		40	138	2	6/2/2011
		Total	452	17 (3.8%)	
		Grand total	2251	124 (5.5%)	

Moses Lake. During this time, we tagged and released more than 2200 shrimp. Total length (mm TL) of recovered tagged shrimp was measured and their tag color was recorded. We calculated growth rate by subtracting the starting TL from the final TL and dividing by the number of days at large.

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 survival of young brown shrimp. The model is parameterized to represent the environmental conditions and habitat characteristics of Galveston Bay, Texas. Individual shrimp recruit to the system and may grow or die on an hourly time-step. Growth is driven by temperature, salinity, and habitat, while mortality is driven 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 growth rate increase, and mortality risk decrease.

All of the environmental drivers in the model affect growth including salinity, temperature, and tidal access to salt marsh habitat. Salinity input data in the model were developed from a salinity transport model (TxBLEND, Guthrie *et al.*, 2014) that provided monthly estimates of area in each of three salinity zones: zone 1 (0-10), zone 2 (10-20), and zone 3 (>20). While juvenile brown shrimp can tolerate a wide salinity range (Saoud and Davis, 2003; Simmons, 1957; Zein-Eldin and Aldrich, 1965; Zein-Eldin and Renaud, 1986), they are found at highest densities in mesohaline (zone 2) and polyhaline (zone 3) regions of estuaries (Haas *et al.*, 2001; Rozas and Minello, 2010;

Zimmerman *et al.*, 1990). For the purpose of comparing model output with our growth

study, in which all three ponds remained polyhaline, all cells in the model were

parameterized with zone 3 salinity.

In all salinity zones, growth rates increase with temperature, peak around 30°C,

and then slow substantially. Expected hourly water temperature values are determined

by the model 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.

Flooding of the marsh surface gives shrimp access to additional infaunal prey for

increased growth (Roth *et al.*, 2008; Whaley and Minello, 2002) and is a function of

both tidal dynamics and marsh topography (Minello *et al.*, 2012; Rozas, 1995). The

model determines expected marsh flooding 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 ID 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 ODD protocol.

Model evaluation

We ran 10 simulations of the Leo *et al.* (2016) model using temperature (median

air) and tide (Pier 21) data available for 2011. These inputs generated expected hourly

temperature and flooding in the model. We plotted the expected temperature values and

expected flooding for comparison with observed temperature and flooding values

recorded in each pond. We parsed the modeled hourly growth rate output into habitat

type, and examined only the output from the marsh complex habitat (marsh vegetation

and nonvegetated marsh edge). Then we calculated the mean modeled or expected daily

growth rate during the period specific to each pond (Table 3.2). We compared the

expected growth rate with the observed growth rate estimate from each pond. We then

re-parameterized the model three ways: 1) with observed temperature and flooding

inputs specific to each pond; 2) with expected temperatures and pond-specific observed

flooding; and 3) with pond-specific observed temperatures and expected flooding. We

ran 10 simulations under each of these sets of tide and temperature conditions, and

determined the pond-specific expected growth rates.

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 Analysis of

Variance (AOV) and Tukey's HSD to compare growth rates among ponds. We also used

a 2-way AOV to compare infaunal biomass among ponds and distances (1 m, -1 m, -5

m) from the pond edge. We conducted this analysis separately for the infaunal data

collected before and after the growth study. 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

Table 3.2 Pond-specific modeled growth rates (mm d^{-1} TL) under estimated (EST) and actual (ACT) values of temperature and flooding compared with pond-specific observed growth rates.

Location Dates	Conditions modeled		Modeled growth (SE)	Observed Growth (SE)
	Temperature	Flooding		
GISP-Small April 12 - June 7	EST$_T$	EST$_F$	1.13 (0.011)	1.02 (0.030)
	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 April 21 - June 1	EST$_T$	EST$_F$	1.15 (0.012)	1.03 (0.027)
	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 April 20 - June 2	EST$_T$	EST$_F$	1.15 (0.011)	1.26 (0.058)
	ACT$_T$	ACT$_F$	1.14 (0.010)	
	EST$_T$	ACT$_F$	1.13 (0.010)	
	ACT$_T$	EST$_F$	1.16 (0.011)	

regressions between field-recorded temperatures and those predicted by the temperature submodel and between actual marsh flooding and modeled flooding durations.

3.3 Results

Pond characteristics

The GISP-Small pond's nonvegetated area was 668 m² with 244 m of marsh edge-open water interface. The edge was highly reticulated and enclosed small islands of *S. alterniflora* within the pond. GISP-Large had 3299 m² of nonvegetated area and 268 m of marsh edge interface. The Moses Lake pond area was 471 m² with 132 m of marsh edge (Figure 3.1). 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 3.2). The three elevation profiles were similar to that reported in Minello *et al.* (2012) for Galveston Bay.

During the GISP-Small study period, marsh edge was observed flooded 75.4% of the time and observed water temperatures ranged from 14.6 to 33.3°C with a mean of 26.3°C. At GISP-Large, marsh edge was observed flooded 78.2% of the time, and observed water temperatures ranged from 14.6 to 34.8°C with a mean of 26.4°C. Moses Lake marsh edge was observed flooded 63.8% of the time, and observed water temperatures ranged from 13.6 to 37.7°C with a mean of 26.1°C. Salinity measured during each shrimp tagging/recapturing effort ranged from 24 to 29.

Infauna

Annelids made up the bulk of benthic infauna (Figure 3.3), with an average of 85% of the total biomass. At the initial sampling period in all ponds, biomass was
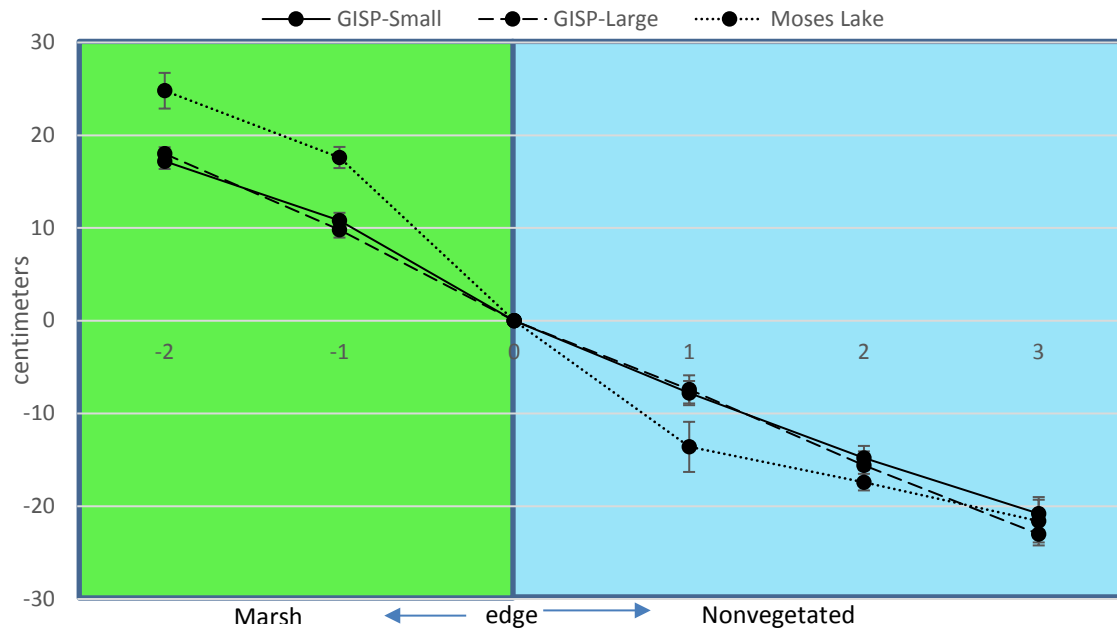
Figure 3.2 Elevation profiles of GISP-Small, GISP-Large, and Moses Lake ponds. Elevations are relative to the marsh vegetation-open water interface (at zero on the horizontal axis) with +/- 1 SE bars.
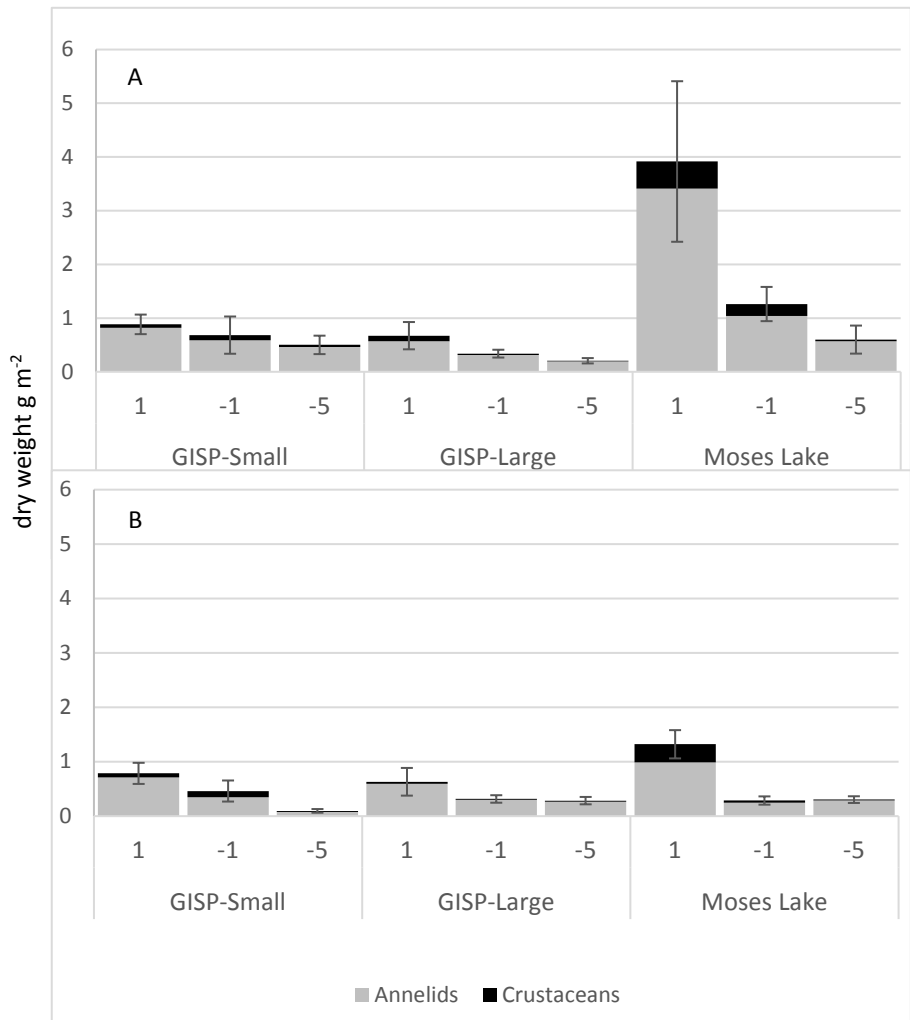
Figure 3.3 Grams m^{-2} dry weight of annelids and crustaceans at three distances from the marsh edge (1 m into the vegetation, -1 m and -5 m into the nonvegetated habitat). In each pond, samples were taken at the start (Initial, A) and end (Final, B) of the field project. Error bars represent +/- 1 SE.

significantly higher (AOV and Tukey's HSD, 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 (AOV and Tukey's HSD, p < 0.0021), with more than four times the biomass in the vegetated habitat samples than those in 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. However, biomass in the vegetation was significantly higher (p < 0.0001) than that in the nonvegetated samples in all ponds.

Shrimp growth

Between April 12 and June 7, 2011, we tagged 2251 shrimp in the three marsh ponds and recovered 5.5% of tagged shrimp (see Table 3.1). 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 day^{-1} TL, respectively (Table 3.2). The mean growth rate of all recaptured shrimp from all ponds was 1.06 mm day^{-1} TL (SE = 0.021, n = 124). Growth rate was significantly higher in Moses Lake than in either GISP pond (AOV and Tukey's HSD, p = 0.0004). During the periods between tagging efforts, the pond-specific mean growth rate estimates ranged from 0.92 to 1.50 mm day^{-1} TL (Figure 3.4). 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

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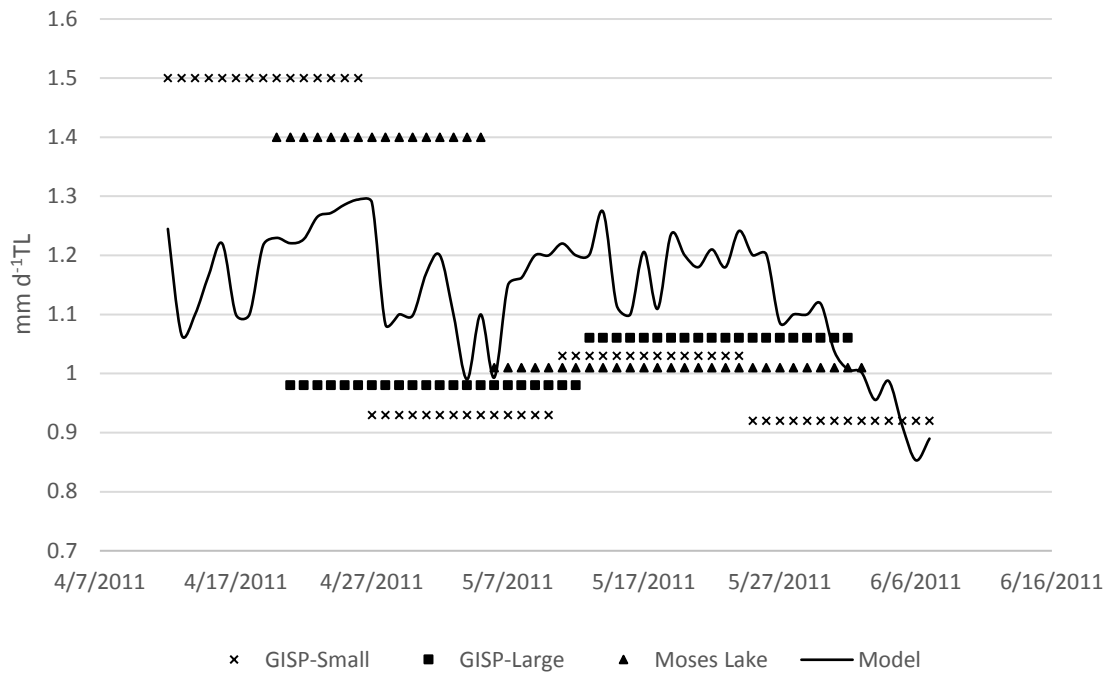
Figure 3.4 Markers represent mean daily growth rates from each pond site based on the mean estimate of growth rate during each elapsed time period between tagging efforts. The solid line represents the modeled mean daily growth rate for shrimp in the polyhaline marsh complex micro-habitats (marsh vegetation and nonvegetated marsh pond).

(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 shrimp size and growth rate (p = 0.006, R^2 = 0.060).

Model evaluation

The duration of the growth study at GISP-Small was from April 12 to June 7, 2011. Modeled shrimp growth averaged 1.13 mm d^{-1} TL (SE = 0.011) during that time. Estimated hourly water temperature ranged from 16.8 to 38.7°C with a mean of 27.6°C, which compared well with actual temperatures in GISP-Small (R^2 = 0.827, p < 0.0001, Figure 3.5, Table 3.2). The estimated marsh flooding occurred 77.1% of the time, compared to actual flooding 75.4% of the time at GISP-Small (Figure 3.6, Table 3.2).

Our growth study ran from April 21 to June 1 at GISP-Large. The mean modeled growth rate was 1.15 mm d^{-1} TL during that time (Table 3.2). Estimated temperatures ranged from 14.6 to 34.8°C with a mean of 27.1°C, again demonstrating a good relationship with actual temperatures from GISP-Large (Figure 3.5, R^2 = 0.826, p < 0.0001). Estimated marsh flooding occurred 77.4% of the time compared to actual flooding 78.2% (Figure 3.6). At both GISP sites, the model estimates of flooding matched actual flooding 90% of the time.

At Moses Lake, our growth study ran from April 20 to June 2. The mean modeled growth rate was 1.15 mm d^{-1} TL during that time (Table 3.2). Estimated temperatures ranged from 13.6 to 36.7°C with a mean of 27.0°C (Figure 3.5, R^2 = 0.772, p < 0.0001). Estimated flooding occurred 77.6% of the time compared to 63.8% actual
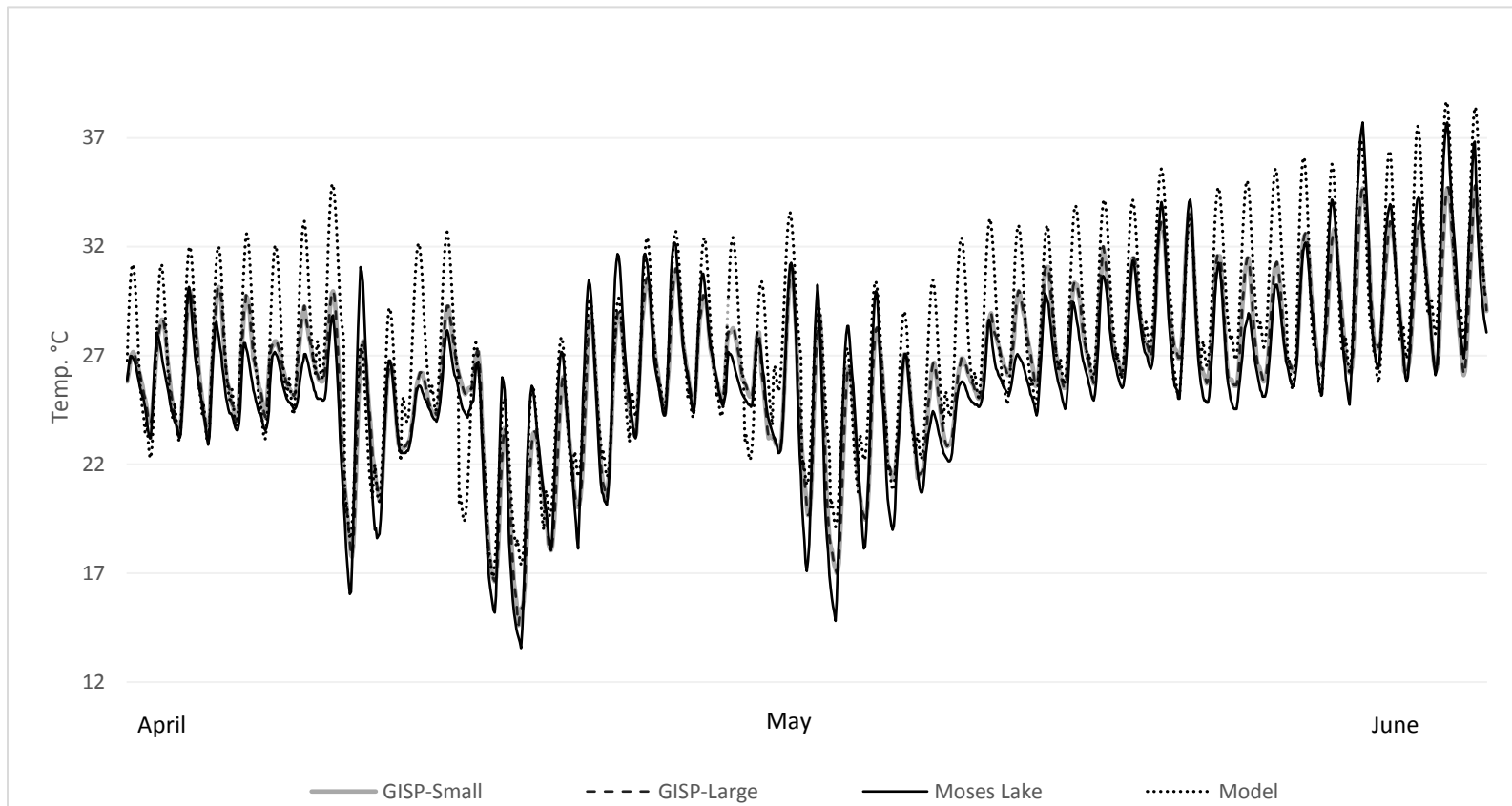
Figure 3.5 Model estimated temperatures plotted with actual temperatures in the GISP-Small, GISP-Large, and Moses Lake ponds. Regression analysis between estimated and actual pond temperature and were significant for all three ponds.
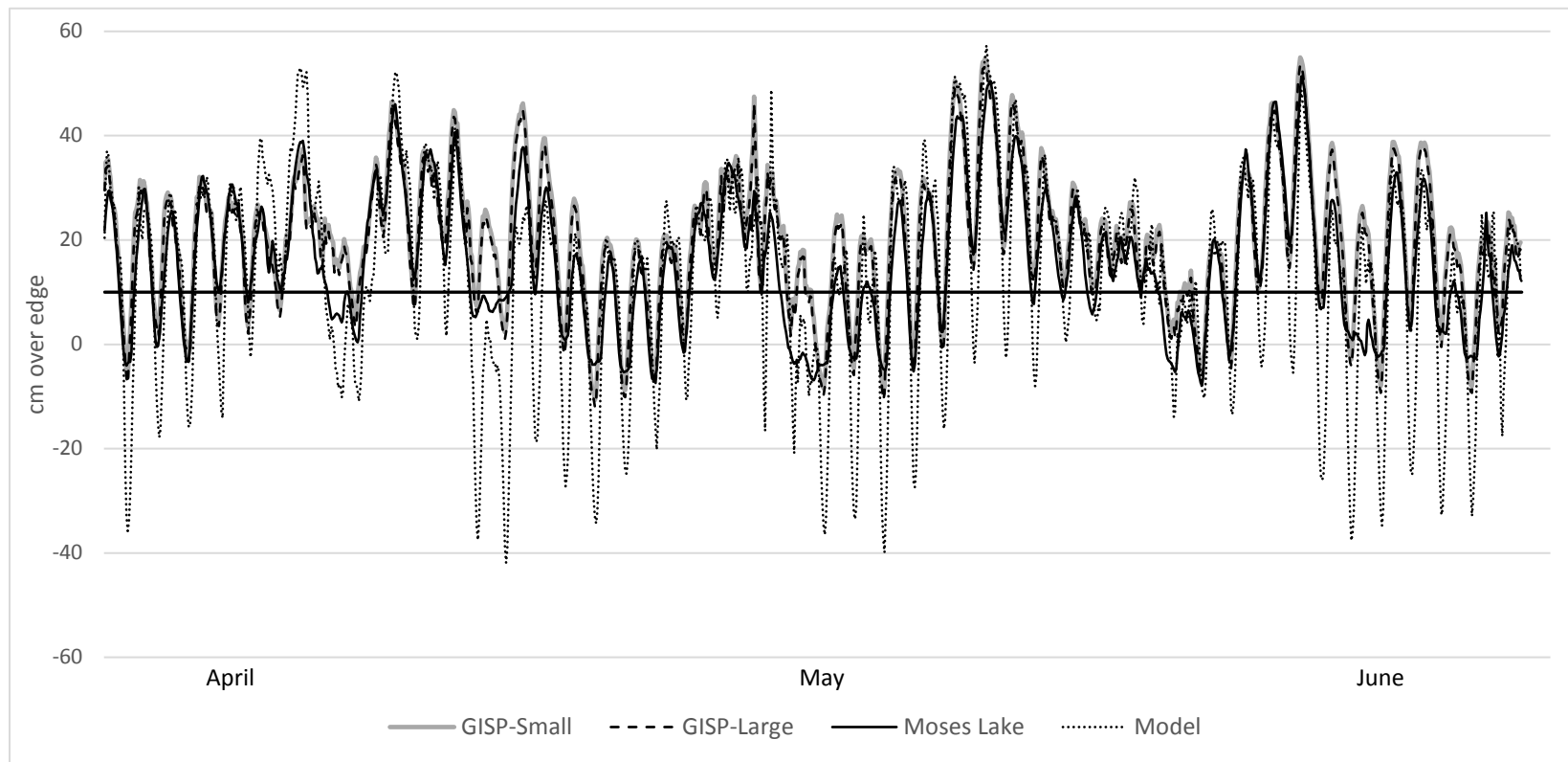
Figure 3.6 Model estimated flooding plotted with actual flooding in the GISP-Small, GISP-Large, and Moses Lake ponds. When the water depth reaches 10 cm over the marsh edge, shrimp in the model simulation can move into marsh vegetation. The model predicted marsh flooding correctly 90% of each study period at GISP-Small and GISP-Large, and 82% of the study period at Moses Lake.

flooding (Figure 3.6). In the Moses Lake pond, the model correctly predicted flooding 82% of the time.

When the model was re-parameterized to use pond-specific actual temperature and flooding values, modeled mean growth rates were 1.22, 1.23, and 1.14 mm d^{-1} TL for GISP-Small, GISP-Large, and Moses Lake, respectively (Table 3.2). In GISP ponds, simulated growth increased when actual data was used as model input. However, the mean modeled growth rate at Moses Lake was reduced. When we used a combination of estimated temperature and pond-specific actual flooding values, the modeled mean growth rates were 1.15, 1.17, and 1.13 mm d^{-1} TL for GISP-Small, GISP-Large, and Moses Lake, respectively. In both GISP pond simulations, this resulted in higher modeled growth rates than when we used exclusively estimated values, but slower growth rates than using exclusively actual values. The combination of estimated temperature and actual flooding values further depressed Moses Lake's modeled growth rates. When we used actual temperature values and estimated flooding, the mean modeled growth rates were 1.21, 1.20, and 1.16 mm d^{-1} TL for GISP-Small, GISP-Large, and Moses Lake, respectively (Table 3.2). Again, GISP pond modeled growth rates were higher than those in simulations using exclusively estimated values but not as high as when using exclusively actual data. Moses Lake modeled growth rates were highest using this combination of input data.

3.4 Discussion

We used field estimates of brown shrimp growth from three marsh ponds in Galveston Bay, Texas, to evaluate the performance of an individual-based model. The

model was constructed to estimate annual production of brown shrimp from intertidal and shallow water estuarine marsh habitat. The model's estimate of mean growth rates during the field study was similar to growth rates 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-and-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. Individual growth rate values observed from our recaptured shrimp however, were normally distributed and in a wide range (0.29 to 1.86 mm d^{-1}). Additionally, our mean estimates of growth rate are comparable 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 (Chavez, 1973; Knudson *et al.*, 1977; Rozas and Minello, 2011; Zein-Eldin, 1963).

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 with actual data from the individual ponds (R^2 = 0.827, 0.826, and 0.772 for GISP-Small, GISP-Large, and Moses Lake, respectively). In general, actual pond temperature maxima were cooler than estimated temperature maxima (Figure 3.5). The tide submodel determines when the marsh vegetation is flooded based on elevation data. Edge elevation profiles from all three ponds are well

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within the estimated mean edge elevations of *Spartina* marshes in Galveston Bay

(Minello *et al.*, 2012, 2015). We compared the estimated tidal pattern of marsh to actual

flooding in the individual ponds. The model predicted that marsh habitat would be

flooded 77.1% of the time. This is similar to the GISP-Small actual flooding 75.4% of

the time and GISP-Large flooding 78.2% of the time. Actual flooding at Moses Lake

however, was 63.8% of the time.

GISP-Small and GISP-Large modeled growth rates were over-estimated and

modeled growth rates at Moses Lake were underestimated when compared to observed

growth. The difference in actual versus estimated temperatures may explain the

relatively slower growth rate observed in shrimp recaptured from GISP ponds, but the

mean growth rate observed in Moses Lake was significantly higher than estimed by the

model while temperatures were similar among the three ponds. We did not find a

relationship between observed growth rates and actual water temperatures in the ponds.

This result is likely due to the small range of mean daily temperatures that occurred over

the period of the field study. When we used actual data in the model, the modeled

growth rates increased at both GISP ponds. Since actual temperatures were cooler than

estimated temperatures, modeled growth rates were probably higher due to the shrimp

spending more time at optimal temperatures and less time at temperatures above 30°C at

which point, growth slows considerably (see Leo *et al*., 2016). Simulations of Moses

Lake using actual data resulted in slightly slower modeled growth than when using

estimated values. This change was likely due to the decreased access to vegetated

habitat. We would expect to see a slower growth rate because of the slightly limited

marsh access, and when we parameterized the model with actual values, modeled Moses Lake growth rates were lower than those of either GISP pond. The observed mean growth rate at Moses Lake though, was significantly higher those observed at either the GISP pond, as well as the modeled mean growth rate.

Although the modeled growth rates were similar to the observed mean growth of all tagged and recaptured shrimp (1.06 mm d^{-1} TL), we did see variability between observed growth rates in the ponds we studied. This difference suggests that growth rate is not strictly predicted by temperature and flooding patterns. Although 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 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 growth rate at Moses Lake to be lower than that of either GISP pond. Still, the mean growth rate estimate at Moses Lake was significantly higher.

We recognize that brown shrimp growth rates are dependent upon more complex interactions than those of tide and temperature, but the discrepancy between our modeled growth and observed growth becomes more apparent when scaling down from the whole of Galveston Bay to a single marsh pond. The model does not include parameters describing infaunal biomass, the main food source of brown shrimp (McTigue and

Zimmerman, 1991). Whaley and Minello (2002) described a spatial pattern of benthic abundance at different distances from the marsh edge wherein abundance is highest in the first meter of vegetation. They also described a temporal pattern in which abundance is higher in spring and declines toward the end of summer (presumably the result of predation during the high tides of spring and summer). If infaunal prey availability is a primary driver of growth, then the significantly higher growth rate seen in Moses Lake shrimp could be explained by the significantly higher infaunal biomass sampled there. Although shrimp in Moses Lake experienced shorter periods of marsh vegetation flooding, the vegetated marsh sampled at Moses Lake had greater than three times the amount of annelid and crustacean biomass (Figure 3.3) than the vegetated marsh sampled at GISP ponds. This elevated infaunal biomass in the vegetated habitat may have been higher than the biomass on nonvegetated bottom as a result of a shorter period of flooding limiting shrimp access. However, the samples taken at 1 m and 5 m from the edge in the nonvegetated habitat also contained significantly more infaunal biomass than their counterparts in both GISP ponds. Therefore, it seems more likely that patterns of infaunal abundance vary among marsh locations within Galveston Bay and may significantly drive brown shrimp growth rates. Understanding what causes this variability, and to what extent it affects growth, has the potential to improve the quality of the brown shrimp production model.

4. CONCLUSIONS

The utility of ecological models is found in both the process of model development, as well as in the model itself (Grant and Swannack, 2008). While some ecological models have proven to be useful in predicting ecosystem changes, much of the discovery about system dynamics can be gleaned through the design and development of a model. The iterative progression in model development requires the designer to identify, examine, and quantify complex ecological linkages, and these are sometimes ephemeral and oftentimes unknown. Bounding the system of interest forces the designer to assess which cause-and-effect relationships are most influential to the question they are trying to answer, and what could be considered excessive detail. The resulting model is hopefully useful in its predictive capacity, but such models can be even more useful in their ability to identify knowledge gaps and potential leverage points as well as to compare conflicting hypotheses.

The Leo *et al.* (2016) brown shrimp model output resulted in highly variable estimates of annual sub-adult production from Galveston Bay. Production increases were associated with parameters that increased individual shrimp growth and reduced mortality rates. Estimated production from Galveston Bay was significantly related to estimates of offshore, adult shrimp population size and may represent generic production trends in bays of the northern Gulf of Mexico. Model output, however, did not compare well with trawl data estimating shrimp abundance from Galveston Bay. This discrepancy requires us to look for a potential explanation within the design of the

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model. The current relationships between drivers and vital rates reflect values found in

the published literature. There are, however, parameters that were excluded from the

model (e.g., density dependent growth and mortality, spatial and temporal distribution of

infauna) because there is a lack of data describing such linkages to brown shrimp vital

rates. This becomes an issue when the model is scaled down to a single marsh pond. At

that small relative scale, model estimates of growth rate were not similar to observed

growth rates in our study ponds. Furthermore, observed growth rates were not similar

among ponds (GISP v. Moses Lake). These differences indicate that some parameter,

functioning at the pond-specific scale, has not been accounted for in the model. My

results suggest that adding information on spatial and temporal variability in infaunal

populations would likely improve the model.

At the larger, bay scale, there is question as to the timing and magnitude of

recruitment. Drivers of these parameters are outside of the bounds of the currently

modeled system, however sensitivity analyses revealed that changes in either timing or

magnitude of recruitment have a substantial effect on annual production estimates.

Future research priorities designed to improve the model output might include

addressing the spatial and temporal distribution of benthic infauna, the abundance and

temporal variability of brown shrimp predators, and factors that affect the timing and

magnitude of larval shrimp recruitment to the bay.

Since stock assessment results provide the technical basis for setting acceptable

fishing pressure, it is necessary to use the highest quality and most complete input data

available (NMFS 2001), and it is imperative to incorporate the effects of habitat

characteristics on the overall productivity of managed fishery stocks. Simulation

modeling of system dynamics allows for these types of adjustments (Ford, 2010;

Meadows, 2008; Grant and Swannack, 2008). Ultimately, we hope that our simulation

results can be incorporated into the brown shrimp stock assessment.

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This appendix contains a description of the model following the ODD (Overview, Design concepts, Details) protocol for describing individual-based models as outlined by Grimm *et al.* (2006) and Railsback and Grimm (2012). The model is programmed in NetLogo® (Wilensky, 1999), which is freely downloadable and runs on most operating platforms. Note that some material included in this appendix, particularly related to the description of submodels, is also described in the text. This material is repeated here for sake of completeness with regard to the ODD protocol.

1. Overview

1.1 Purpose

The purpose of this model is to simulate the recruitment, growth, mortality, and biomass production of brown shrimp in salt marsh habitats of the northern Gulf of Mexico as a function of temperature, salinity, and access to the tidally inundated, vegetated marsh surface. The model currently is parameterized based on available literature describing relationships between brown shrimp and the environmental characteristics of Galveston Bay, Texas. However, the model could be re-parameterized to represent the environmental conditions in other northern Gulf of Mexico salt marshes, such as those found in Barataria Bay, Louisiana, and model production estiimates could

be used as input to the brown shrimp stock assessment model of the U.S. National

Marine Fisheries Service (SS-3).

1.2 Entities, state variables, and scales

State variables include (1) 100 habitat cells and (2) a variable number of

individual shrimp. Attributes of habitat cells include (1) location (x and y coordinates),

(2) habitat type, (3) salinity zone (low, 0-10 PSU; medium, 11-20 PSU; high, >20 PSU),

(3) current salinity (PSU), and (4) water temperature (°C). Attributes of individual

shrimp include (1) state (alive, dead, emigrated), (2) age (hours), (3) recruitment-day

(day-of-year), (4) death-day (day-of-year), (5) emigration-day (day-of-year), (6) size

(total length in mm), (7) in-marsh? (yes or no), (8) in-habitat (current habitat type), (9)

in-zone (current salinity zone), (10) prob-mort (current daily probability of dying), (11)

growth/hr (current hourly growth rate), and (12) growth/day (current daily growth rate).

Each simulated individual shrimp is a "super-individual" (Scheffer *et al.* 1995)

representing 1 million "real" shrimp.

The global environment is defined by (1) the 100 habitat cells, each representing

a 635-ha area of the 63,500 ha Galveston Bay system, including habitats of

intermittently flooded marsh vegetation (Marsh, 17 cells), non-vegetated marsh edge

(NVME, 28 cells), and shallow non-vegetated water (SOW, 55 cells), (2) height of the

marsh edge, and (3) time series of input data representing (a) tide heights, (b) median air

temperatures, (c) the distribution of salinity zones among habitat types, and (d) number

of newly-recruited shrimp. Each simulated time step represents one "real" hour, and

simulations are run for 5,832 hours, which represents the period from January 1 through

August 31st. This time span should be sufficient to represent environmental influences

affecting the annual production of brown shrimp, since few shrimp appear in the open

bay after the end of August (Brown *et al.,* 2013; Martinez-Andrade, 2005), and most

shrimp are spawned and harvested within a year.

1.3 Process overview and scheduling

An overview of the sequence of events and processes involved in the execution

of the model is provided in Figure A1.1. After values of model parameters are set,

spatial structure of the model is defined, and output files are initialized, time series of

values of input data for the year being simulated are read into the model. Then sub-

models are executed iteratively until the end of the 243-day (January through August)

simulation. Sub-models calculating (1) water temperatures in vegetated and non-

vegetated habitats, (2) tide height and marsh flooding, (3) shrimp movements, (4) shrimp

mortality, (5) shrimp emigration, and (6) shrimp growth, as well as sub-models (7)

summarizing attributes of the shrimp population and (8) writing simulation results to

output files, are executed each hour. Sub-models updating (1) shrimp recruitment, and

(2) median air temperature are executed at the beginning of each day. Sub-models

updating the distribution of salinity zones are executed at the beginning of each month.

2. Design concepts

2.1 Basic principles

Juvenile brown shrimp are present in several habitat and bottom types as well as

shallow open water (Fry, 2008; Minello, 1999; Stunz *et al.,* 2010), but they are found in

Initialization

Set parameter values (marsh edge elevation (m), probability of moving into marsh if marsh is flooded, size (mm) at which shrimp are recruited to marsh, size (mm) at which shrimp emigrate from marsh)

Create initial habitat types (marsh vegetation, non-vegetated water < 150m from marsh edge, non-vegetated water ≥ 150m from marsh edge) and salinity zones (low, medium, high)

Initialize output files

Input data

Hourly tide heights (m, 5834 values for the year being simulated)

Daily median air temperatures (C, 365 values for the year being simulated)

Daily shrimp recruitment (number of individuals, 365 values, the same for all years simulated)

Monthly salinities (PSU, 12 values for each of 3 salinity zones, the same for all years simulated)

Submodels

Monthly / Daily / Hourly

Update distribution of salinity zones (low, medium, high)

Update shrimp recruitment

Update median air temperature

Calculate water temperatures in vegetated and non-vegetated habitats

Calculate tide height and marsh flooding

Calculate shrimp movements

Calculate shrimp mortality

Calculate shrimp emigration

Calculate shrimp growth

Summarize attributes of shrimp population
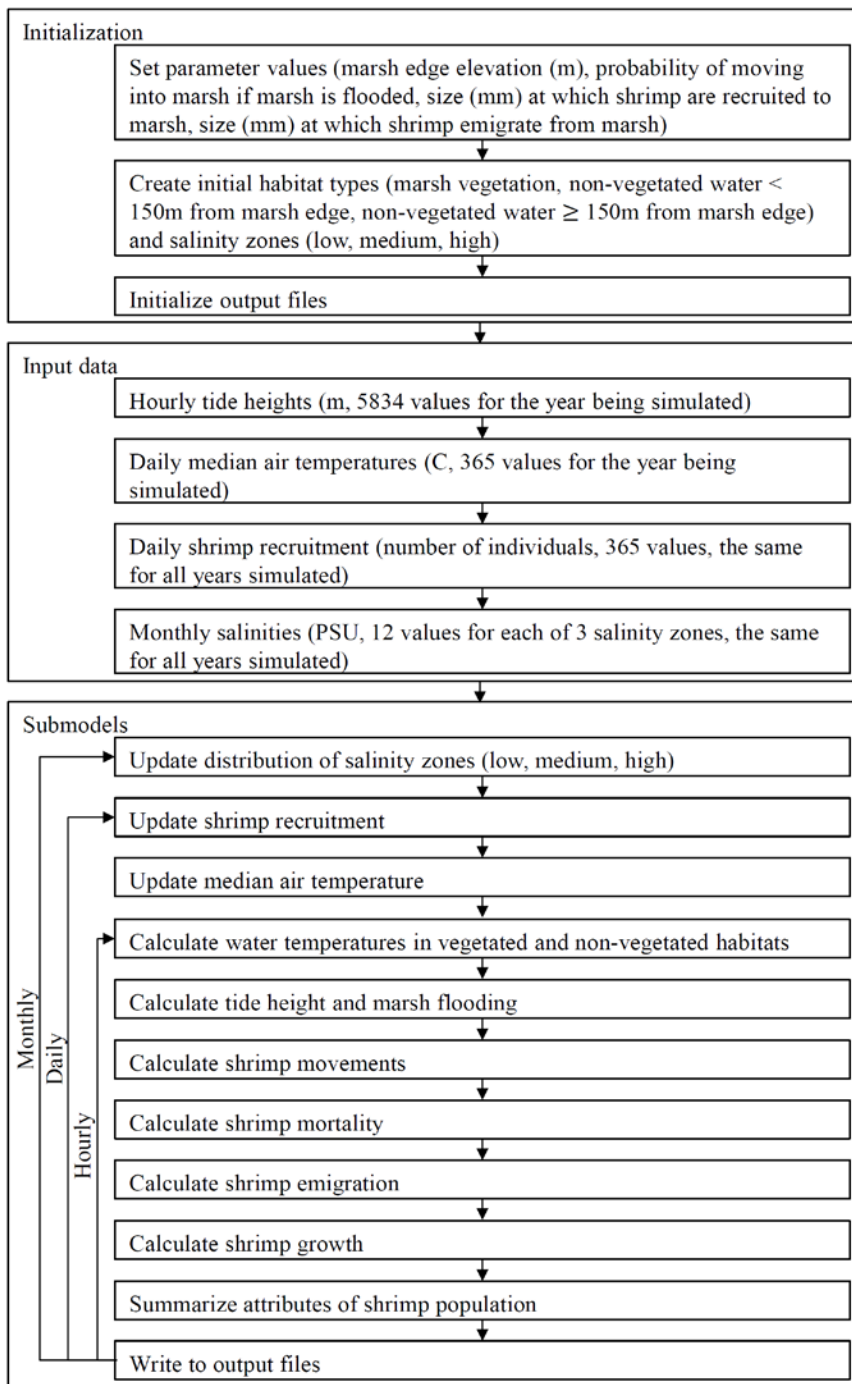
Write to output files

Figure A1.1. Overview of the sequence of events and processes

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highest densities associated with emergent vegetation along the edge of salt marsh habitats (Minello *et al.,* 2003; Minello and Rozas, 2002; Zimmerman and Minello, 1984). Understanding the relative value of juvenile habitats, potential nurseries, and essential fish habitat (EFH) is critical to the management of adult populations (Adams *et al.,* 2006; Beck *et al.,* 2001). In our model, we are examining the basic principles associated with the nursery role concept, specifically, how differences in habitat and environmental qualities affect the successful recruitment of sub-adult shrimp to the fishery. Linkages between environmental variables (e.g., salinity, temperature, access to emergent marsh vegetation) and brown shrimp vital rates have been identified (Barrett and Gillespie, 1973; Boesch and Turner, 1984; Turner, 1992; Zein-Eldin and Aldrich, 1965; Zimmerman *et al.,* 2000; many others). Salt marshes provide refuge from predators (Minello, 1993; Minello *et al.,* 1989; Minello and Zimmerman, 1983) and abundant food to support rapid growth (McTigue and Zimmerman, 1991, 1998; Whaley and Minello, 2002). Here, we model the cumulative effects of these linkages.

2.2 Emergence

Population size, standing biomass, and size structure emerge from the model processes controlling growth, mortality, and movement of individuals. Production from the marsh is driven by the effects of temperature, salinity, and tide height on the processes of growth, mortality, and movement.

2.3 Adaptation

Shrimp that recruit to the marsh complex have the ability to move between vegetated and non-vegetated habitats. During each time step in which the marsh surface

is flooded, each shrimp has a 0.69 probability of staying in or moving into marsh vegetation. This recreates in the model, abundance patterns that have been observed in the field (Minello *et al.*, 2008; Minello and Rozas, 2002), and is indirectly objective-seeking.

2.4 Sensing

Shrimp in the marsh complex (marsh vegetation plus marsh water) can sense when the vegetated marsh is flooded and is accessible. When a shrimp moves from one patch to another, it also can sense the salinity of other patches, which allows movement to a patch with the same salinity of the one it is leaving.

2.5 Stochasticity

During initialization, and subsequently when the number of cells representing each type of salinity zone changes, salinity zones are assigned to cells stochastically. During simulations, each hour, the order in which individual shrimp are chosen to execute their activities is randomized. Mortality of individuals is represented as a daily probability of dying, and movement of individuals between the vegetated marsh surface and the non-vegetated marsh is represented probabilistically.

2.6 Observation

The most important model output is an estimation of annual brown shrimp production from the shallow estuarine habitats of the bay. The total population of shrimp in the bay, the shrimp density within each habitat type and salinity zone, and the standing biomass can be observed from the model. The production of shrimp per hectare

of marsh complex and per hectare of shallow water also can be observed, as can the number of shrimp recruited to the open bay population.

3. Details

3.1 Initialization (Figure A1.1)

First, values are assigned the parameters representing (1) elevation (m) of the marsh edge for the year being simulated (= 1.477 + ((calendar-year – 2013) * 0.0053)), (2) probability of an individual moving into (staying in) marsh vegetation (= 0.69), (3) size (total length in mm) of shrimp at recruitment (=10), and (4) size of shrimp at emigration (=70). The estimate of the average elevation of the marsh edge in 2013 was based on tide gauge station data from measurements at 12 marshes in 2013 (http://co-ops.nos.noaa.gov/). This elevation is adjusted for the year being simulated based on estimated changes due to relative sea level rise (Figure 5a).

Next, habitat types (which do not change during the simulation) and salinity zone types (which do change during the simulation) are assigned to cells. Moving from left to right along a 25 x 4 cell lattice, 17 cells are defined as marsh, 28 cells are defined as non-vegetated marsh edge (NVME), and 55 cells are defined as shallow open water (SOW). The relationship of this spatial arrangement of habitat types to the geography of Galveston Bay is shown in Figures 2.1 and 2.2. The 100 habitat cells, each representing 1% of the total modeled area in Galveston Bay, were identified based on a GIS analysis of 2006 USFWS National Wetland Inventory (NWI) data and a bathymetry analysis for the bay. Habitat types from this analysis were classified as either marsh vegetation, or

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shallow water. Previous analyses in Galveston Bay estimated that the water (ponds and creeks) included within the marsh complex was 1.63 times the amount of vegetated area (Minello *et al.,* 2008). We used this multiplier to estimate the total amount of water associated with the marsh vegetation identified in the NWI for the bay. The marsh complex, therefore, consisted of 45 patches (17 patches of marsh and 28 patches of NVME), with the remaining 55 patches of SOW.

The appropriate number of cells in each habitat type is assigned to a particular salinity zone based on a GIS analysis of the TxBLEND model output for the month (see section on input data below).

3.2 Input data (Figure A1.1)

Hourly tide heights, daily median air temperatures, monthly distribution of salinity zones among habitat types, and daily recruitment numbers are read from external files. We developed these input data for Galveston Bay based on analyses of data collected over the 30-year period from 1983 to 2012. Hourly tide heights (Figure 2.5b) were based on tide data from the Pier 21 NOAA tide gauge (NOAA Tides and Currents https://tidesandcurrents.noaa.gov/waterlevels.html?id=8771450). Daily median air temperatures (Figure 2.5c) were obtained from the NOAA National Center for Environmental Information, (http://www.ncdc.noaa.gov/cdo-web/search). Monthly salinity values for each of the three salinity zones (Figure 2.5d), as well as the numbers of cells representing each salinity zone, were based on TxBLEND modeling of the Galveston Bay system (Guthrie *et al.*, 2014). Salinity zones were categorized as low (0-10 PSU), medium (10-20 PSU), or high (>20 PSU) and salinities within these zones, as

well as distribution cells representing these zones, were estimated monthly based on TxBLEND output. We assumed that daily salinities did not vary within months.

Daily recruitment numbers (Figure 2.5e) were based on several studies of the magnitude and timing of postlarval recruitment, as well as our unpublished data, which indicated that shrimp begin to move through the passes into the bays in mid-March with peak recruitment numbers occurring in April (Baxter and Renfro, 1967; Berry and Baxter, 1969; Matthews, 2008). Abundance patterns from drop sampler data recorded monthly and bi-monthly over 11 years in the marsh complex within Galveston Island State Park indicated that abundance of settlers appears to peak two weeks after the average peak of postlarvae entering the bay (Rozas *et al.*, 2007). We used the temporal pattern of recruitment from the passes with a delay of two weeks as a recruitment pattern for shrimp to the marsh. Since shrimp density in Galveston Bay differs depending on habitat type and salinity (Minello, 1999; Minello *et al.*, 2008), we distributed the recruited shrimp among habitat cells based on the current spatial distribution of habitat types and salinity zones using a standardized relative density matrix (described in Table A1.1).

3.3 Submodels (Figure A1.1)

3.3.1 Update salinity zones (low, medium, high)

The number of cells in each salinity zone in each habitat type is updated monthly based on input data, with each cell assigned a salinity zone probabilistically based on its habitat type and a salinity corresponding to its salinity zone (see data input section).

Table A1.1. Description of process flow for recruit distribution using the relative density matrix.

Relative densities observed in the field.

Salinity	Marsh Complex	Shallow water
0-10 PSU	14	5
10-20 PSU	18	6
> 20 PSU	43	14

The model calculates how many cells are in each habitat type/salinity zone combination and multiplies that number by its relative density value.
Example: number of cells in each habitat type and salinity for March of 2007.

Salinity	Marsh Complex	Shallow water
0-10 PSU	2	10
10-20 PSU	10	24
> 20 PSU	32	22

Product of the number of cells and the relative density value.

Salinity	Marsh Complex	Shallow water
0-10 PSU	28	50
10-20 PSU	180	144
> 20 PSU	1376	308
total		2086

Distribution of the sum of the recruits that enter the system on this day.

Salinity	Marsh Complex	Shallow water
0-10 PSU	1.4%	2.4%
10-20 PSU	8.6%	6.9%
> 20 PSU	66.0%	14.8%

3.3.2 Update shrimp recruitment

Shrimp recruitment (number of shrimp entering the system) is updated daily (shrimp are recruited into the system in a single cohort at midnight) based on input data (Figure 2.5e, see data input section).

3.3.3 Update median air temperature

Median air temperature is updated daily based on input data (Figure 2.5c, see data input section).

3.3.4 Calculate temperatures in vegetated and non-vegetated habitats

Hourly temperatures in marsh cells and the non-vegetated habitats (NVME and SOW) are based on daily median air temperature (Figure 2.5c) and hourly bottom water temperatures measured from March 16, 2006 through May 31, 2007 in a Galveston Bay marsh complex, both within the vegetation (5 m from the edge) and in shallow water (ranged between 0.5 and 1.5 m deep depending on tide) outside of the vegetation (unpublished data). We first calculated mean hourly deviations of field data from mean daily water temperatures by month. Next we developed monthly regressions between the non-vegetated water temperature and the median daily air temperature. We then estimated hourly non-vegetated water temperatures functions by month and hour. Finally, we estimated hourly vegetated water temperatures based on an empirical relationship between the vegetated water temperature data and non-vegetated water temperature data.

3.3.5 Update tide height and calculate marsh flooding

Hourly tide height (Figure 2.5b) is based on hourly tide station data (NOAA gauge 8771450, Galveston Pier 21) and is used to determine if the marsh surface is

flooded. In 2013, we measured flooding rates in twelve salt marshes of Galveston Bay, and related average water level at the marsh edge to an elevation of 1.477 m on the Pier 21 gauge (station datum). If the station datum was 10 cm higher than this marsh edge height in 2013, we considered the marsh to be flooded and accessible to brown shrimp. For other years, we adjusted this level on the Pier 21 gauge to account for relative sea level rise over the period of our model runs (Figure 2.5a). The bay experienced relatively high levels of subsidence over this period due to oil and groundwater extraction (Feagin *et al.*, 2005). We plotted mean sea level on the Pier 21 gauge from 1970-2014 and determined that relative sea level on the station datum increased 5.4 mm/year over that period. We therefore adjusted the elevation of the marsh edge in relation to the gauge by this amount each year. This adjustment assumes that the gauge and the marshes are sinking relative to sea level at the same rate, and that the vertical location of the marsh edge is mainly determined by an inability of *S. alterniflora* to withstand further tidal inundation (McKee and Patrick, 1988; Minello *et al.*, 2012; Tiner, 1993).

3.3.6 Calculate shrimp movements

Shrimp move between the NVME and marsh when the latter is flooded. Shrimp in the marsh move to the NVME when the former no longer is flooded. Shrimp in the SOW do not leave that area. Shrimp growth, emigration, and mortality occur in all areas, with growth rates and mortality probabilities differing among areas (and also depending on temperature and salinity, see Figure 2.3).

The quantitative representations of movement, growth, mortality, and emigration of individual shrimp included in the model are summarized schematically in Figure 2.3. Rules representing the movement of individuals, described in the preceding paragraph, are probabilistic. If the marsh is flooded, each hour each individual located in either the marsh or the NVME has a 69% probability of moving to a cell with the same salinity in the marsh and a 31% probability of moving to a cell with the same salinity in the NVME. If there is no cell with the same salinity, the individual moves into a cell with the salinity closest to the salinity of the cell from which it moved. Thus any given individual may move back and forth between these two areas during periods of marsh flooding, but is likely to spend slightly more than twice as much of this time in the marsh.

3.3.7 Calculate shrimp mortality

Mortality (probability of dying) is a function of a base rate (0.00083 / hr) multiplied by two indexes representing (1) a size (of the individual) effect and (2) a habitat effect (Figure 2.3). The size effect is based on total length ($53.092 * $ (total length in mm)$^{-1.1163}$). Thus mortality decreases exponentially as total length increases, following the pattern described by Roth *et al.* (2008) and supported by field data from Minello *et al.* (1989). The habitat effect is represented as a constant, which is different for marsh vegetation (0.69) versus the two areas of non-vegetated water (1.38). The presence of marsh vegetation reduces brown shrimp mortality (Minello 1993; Minello *et al.*, 1989). There also is some experimental evidence of temperature related mortality. Zein-Eldin and Alderich (1965) reported increased mortality at temperature extremes,

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especially for brown shrimp in low-salinity water (as high as 80% mortality in 11°C water that had less than 15 PSU). However, there is limited data on the behavior of shrimp under these conditions in the field, and potentially, they can avoid extreme temperatures through movement to deeper water or by burrowing in the substrate (Aldrich *et al.*, 1968). Thus, we chose not to include temperature-related mortality in the model.

3.3.8 Calculate shrimp emigration

Individuals emigrate when they attain a length of 70 mm (they are recruited at a length of 10 mm) (Cook and Lindner, 1970).

3.3.9 Calculate shrimp growth

Growth is a function of the water temperature, salinity, and habitat conditions (marsh, NVME, SOW) to which an individual is exposed (Figure 2.3). A probabilistic base growth rate (0.0416 ± 0.0104 mm hr^{-1}) is multiplied by two indexes representing (1) a water temperature-salinity effect and (2) a habitat effect. The water temperature-salinity effect is represented as a polynomial function of water temperature, which is different for each of the three salinity zones (Figure 2.4). Hourly water temperatures for NVME and SOW are calculated based on the median air temperature, and hourly water temperatures for the marsh is calculated based on a relationship between the water temperature in open water and that in the marsh. The habitat effect is represented as a constant, which is different for each of the three habitats (1.28, 1.14, and 1.0 for marsh, NVME, and SOW, respectively).

Brown shrimp grow ≈1 mm per day in total length (Knudsen *et al.,* 1977), and experience fastest growth at ≈30 °C, assuming access to plentiful food (Zein-Eldin and Aldrich, 1965). Salinity appears to affect growth both directly through osmoregulatory costs and indirectly by controlling the abundance of benthic infaunal prey (Adamack *et al.,* 2012; Rozas and Minello, 2011, 2015), with growth being lowest at salinities between 0-10 PSU. While it has been difficult to directly measure the effect of intertidal vegetation on shrimp growth due to potential experimental artifacts (Kellison *et al.,* 2003; Peterson and Black, 1994), there is some experimental evidence suggesting that growth rates of brown shrimp are increased in marsh habitat (Minello and Zimmerman, 1991, Rozas and Minello, 2009). Benthic infaunal food for shrimp also is found in higher abundance on the vegetated marsh surface, especially within the first meter from the edge (Whaley and Minello, 2002). Based on these data, we represented growth rate as being fastest when shrimp are in the marsh, and slowest when they are located in the SOW.

3.3.10 Summarize attributes of shrimp population

After each hour of simulated time, (1) standing biomass (kg / ha) of the shrimp population (calculated as $(0.000006 * (\text{mean-size-mm}^{3.071}) * \text{number of simulated shrimp} * \text{number of real shrimp per simulated shrimp}) / 63,500)$ and (2) shrimp biomass production (kg ha^{-1}) (calculated as $0.000006 * (70^{3.071}) * \text{number of emigrated shrimp}$) are calculated.

3.3.11 Write to output files

After each hour of simulated time, in addition to the current values of the

attributes of the shrimp population described in the previous section, the current values

of environmental conditions (tide height, median air temperature, water temperatures in

vegetated and non-vegetated habitats, salinities in low, medium, and high salinity zones)

and descriptors of current habitat conditions (number of cells in salinity zone in each

habitat type and whether or not the marsh is flooded) are written to Excel text files.

APPENDIX 2[*]

This appendix contains results of each of the replicate stochastic (Monte Carlo) simulations run under baseline conditions and as part of the various sensitivity analyses presented in the text. These include sensitivity of model estimates of brown shrimp (*Farfantepenaeus aztecus*) production (kg/ha) (1) to the 30 different sets of baseline environmental conditions (Figure A2.1), (2) to changes of ± 10% relative to baseline in parameter values representing individual growth rate, probability of mortality, and probability of moving into (staying in) the area of intermittently flooded marsh vegetation (Figure A2.2), (2) to changes of ± 10% relative to baseline values of the time series of input data representing tide heights and median air temperatures, (Figure A2.3), (4) to changes in the number of "real" shrimp represented by each simulated shrimp (Figure A2.4), and (5) to changes relative to baseline in the timing of shrimp recruitment (Figure A2.5).
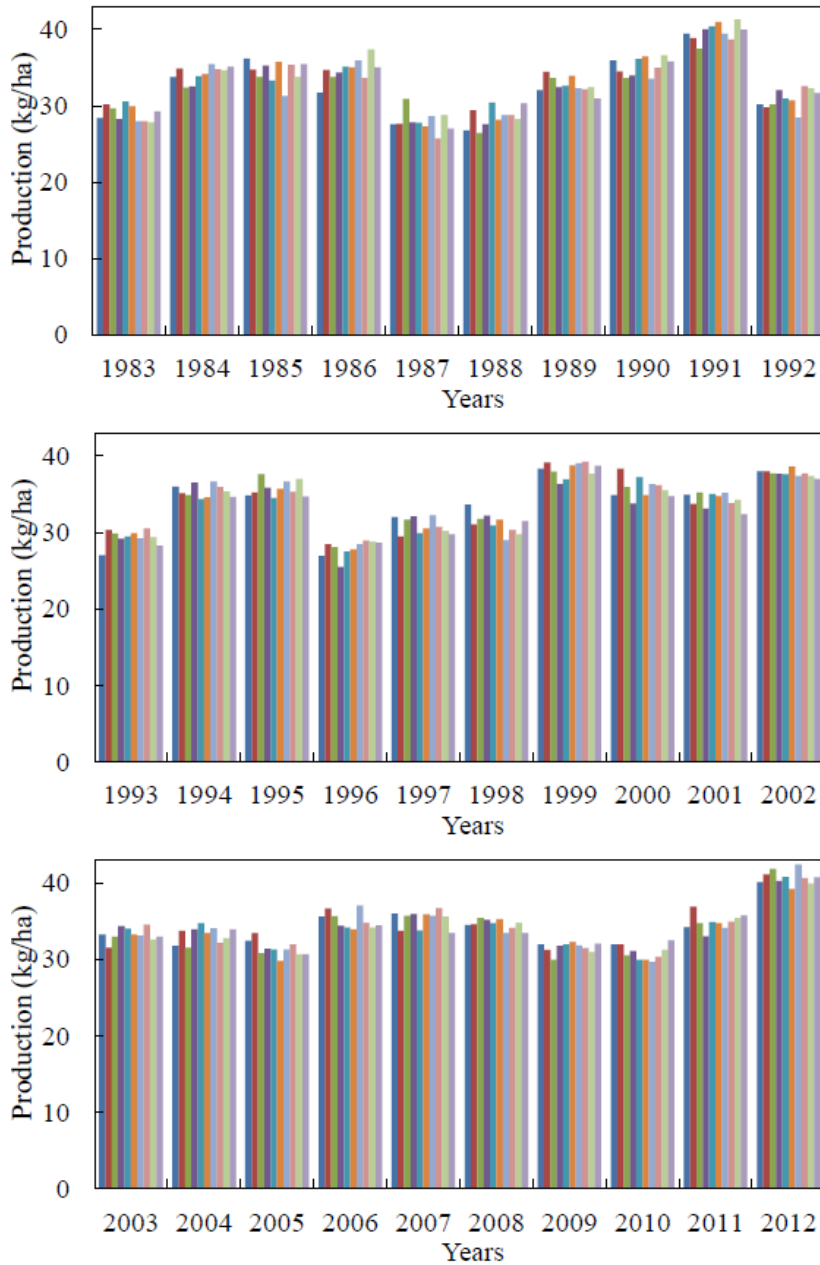
Figure A2.1. Production (kg/ha) of brown shrimp (*Farfantepenaeus aztecus*) from January through August in Galveston Bay, Texas, U.S.A., simulated under environmental conditions representing the indicated calendar years. Each bar represents one of 10 replicate stochastic (Monte Carlo) simulations.
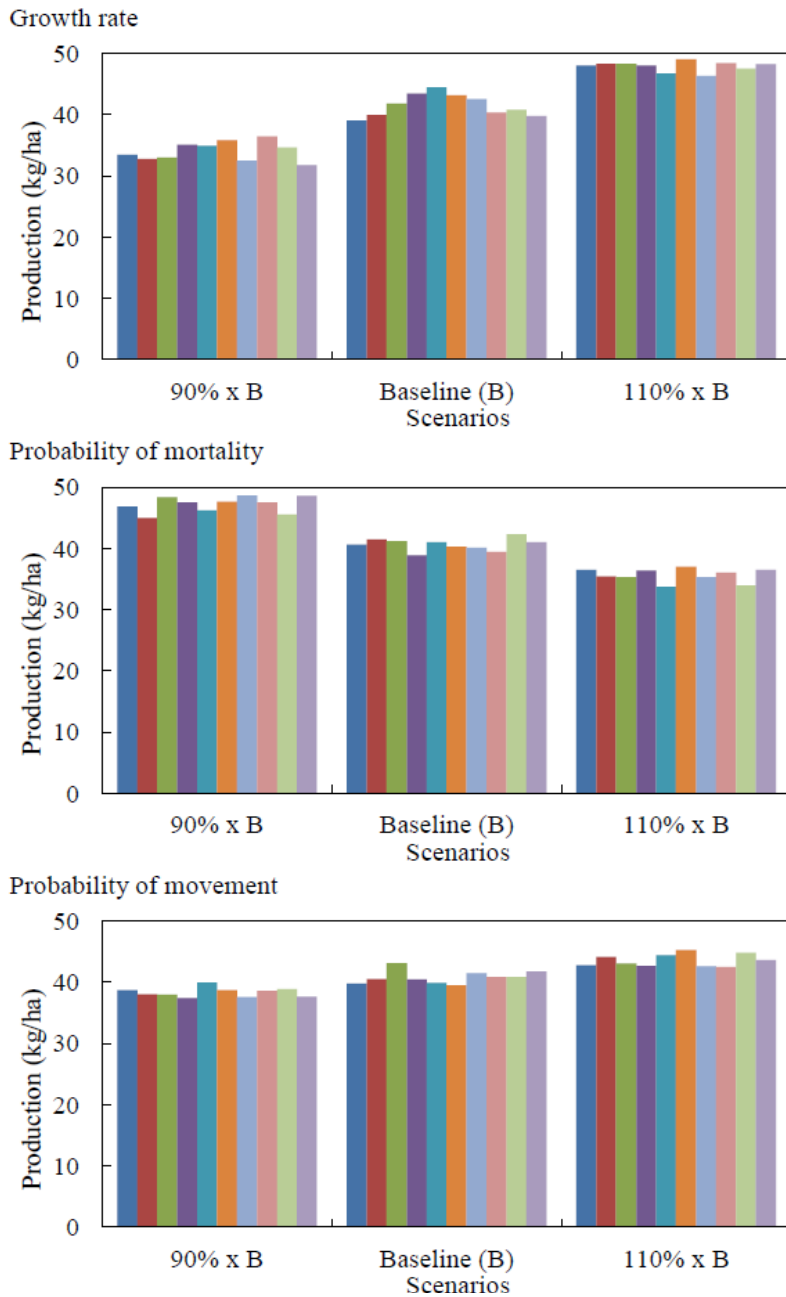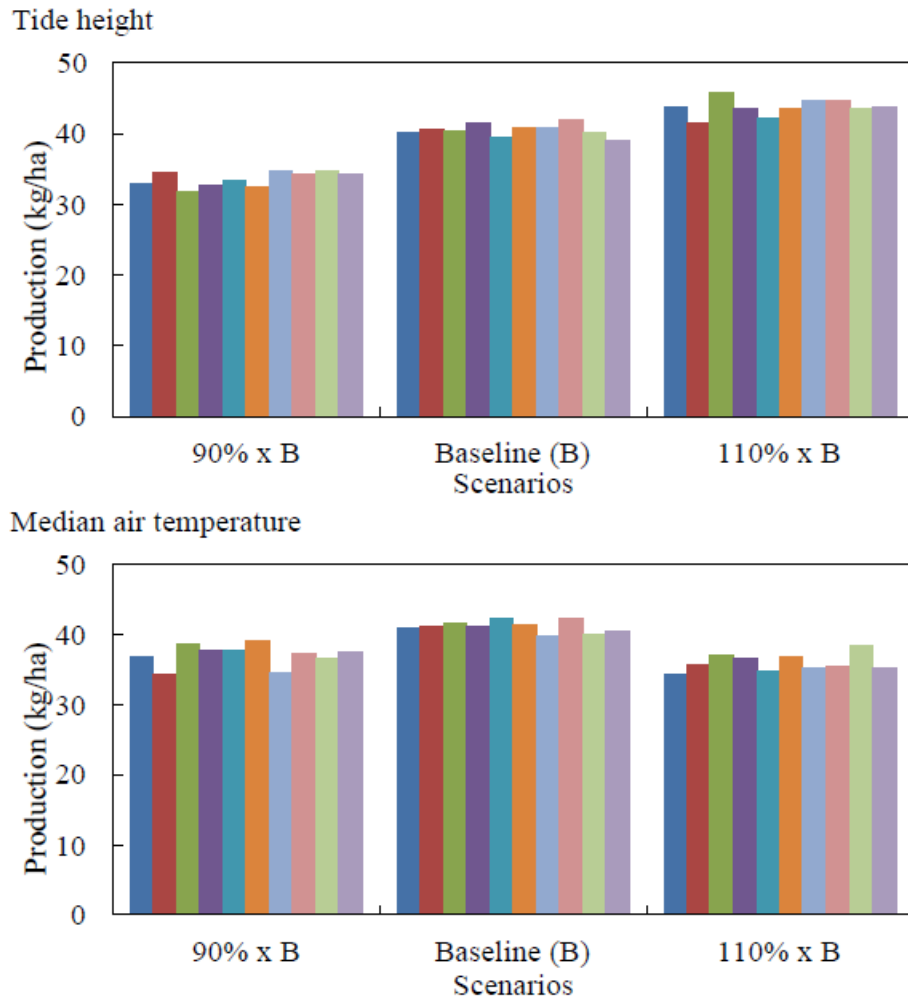
Figure A2.2. Sensitivity of model estimates of brown shrimp (*Farfantepenaeus aztecus*) production (kg/ha) to changes of ± 10% relative to baseline in parameter values representing individual growth rate, probability of mortality, and probability of moving into (staying in) the area of intermittently flooded marsh vegetation. Production from January through August in Galveston Bay, Texas, U.S.A., is presented for each of 10 replicate stochastic (Monte Carlo) simulations run under environmental conditions representing the calendar year 2012 and the indicated
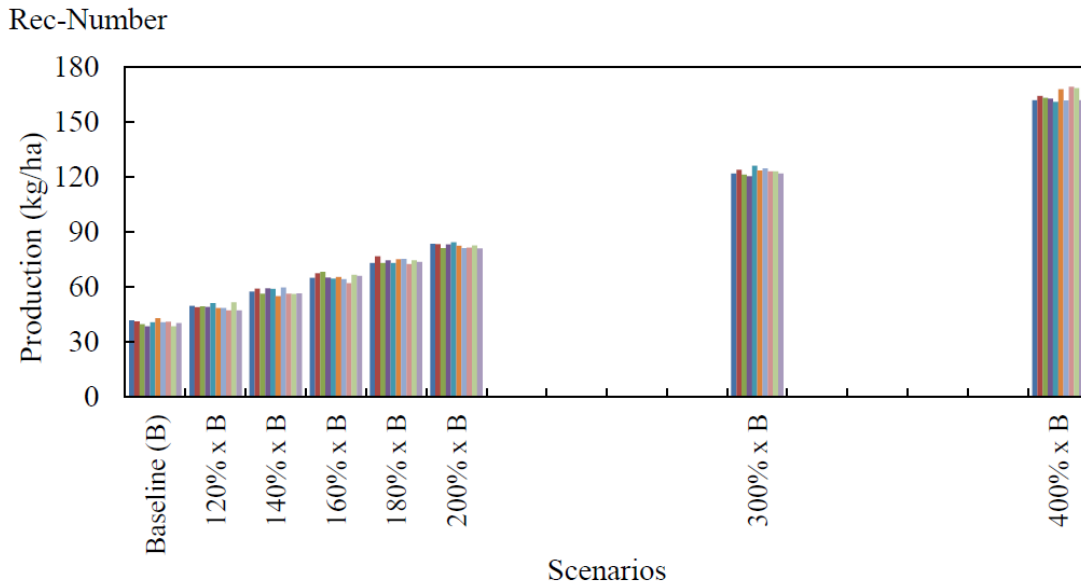
Figure A2.3. Sensitivity of model estimates of brown shrimp (*Farfantepenaeus aztecus*) production (kg/ha) to changes of ± 10% relative to baseline values of the time series of input data representing tide heights and median air temperatures. Production from January through August in Galveston Bay, Texas, U.S.A., is presented for each of 10 replicate stochastic (Monte Carlo) simulations run with baseline parameter values and under environmental conditions representing the calendar year 2012, except for the changes in the indicated time series of environmental driving variables.

Rec-Number

Figure A2.4. Sensitivity of model estimates of brown shrimp (*Farfantepenaeus aztecus*) production (kg/ha) to changes relative to baseline in the number of "real" shrimp represented by each simulated shrimp. Production from January through August in Galveston Bay, Texas, U.S.A., is presented for each of 10 replicate stochastic (Monte Carlo) simulations run with baseline parameter values and under environmental conditions representing the calendar year 2012 with the indicated changes in the number of "real" shrimp represented by each simulated shrimp.
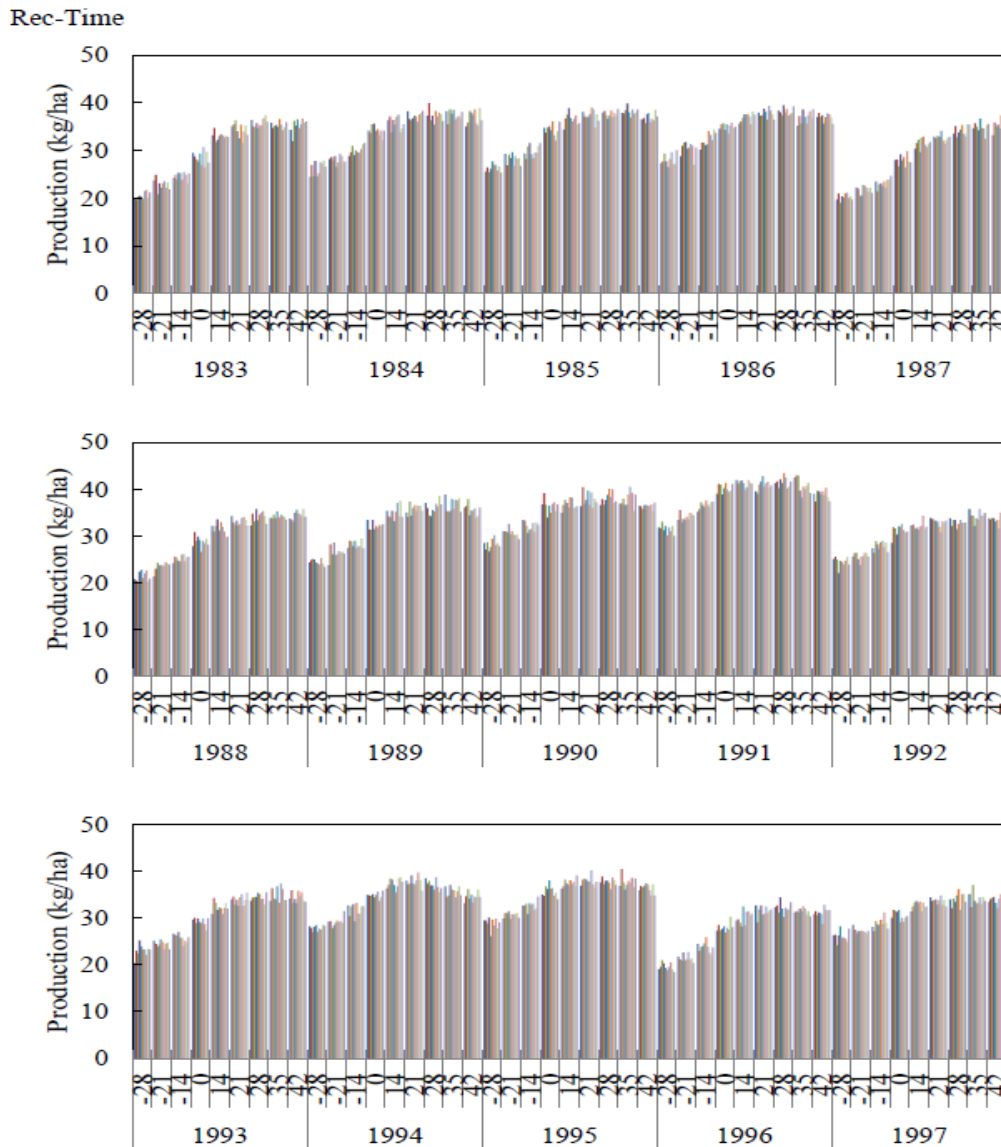
Figure A2.5. Sensitivity of model estimates of brown shrimp (*Farfantepenaeus aztecus*) production (kg/ha) to changes relative to baseline in the timing of shrimp recruitment. Production from January through August in Galveston Bay, Texas, U.S.A., is presented for each of 10 replicate stochastic (Monte Carlo) simulations run under environmental conditions representing the indicated calendar year with the indicated change in the timing of recruitment. Minus 14, -21, and -28 represent recruitment occurring 14, 21, and 28 days earlier than baseline, whereas 14, 21, 28, 35, and 42 represent recruitment occurring 14, 21, 28, 35, and 42 days later than baseline. The relative shape of the recruitment curve (Figure 5e) was not changed, the entire curve was shifted earlier or later in the year.
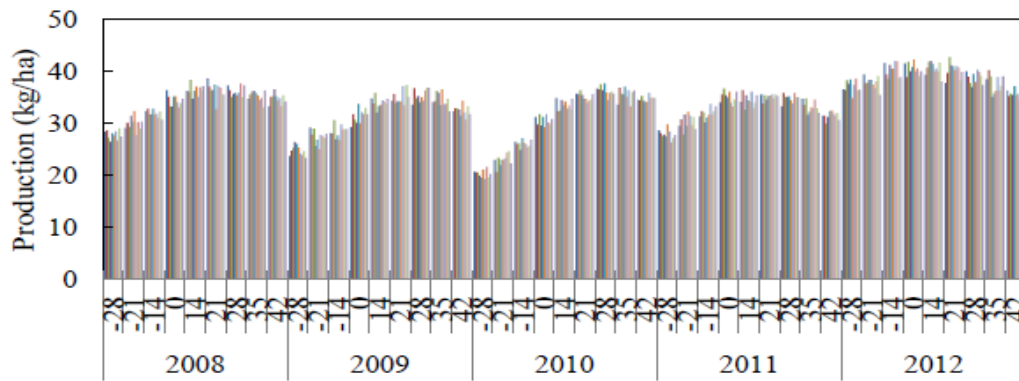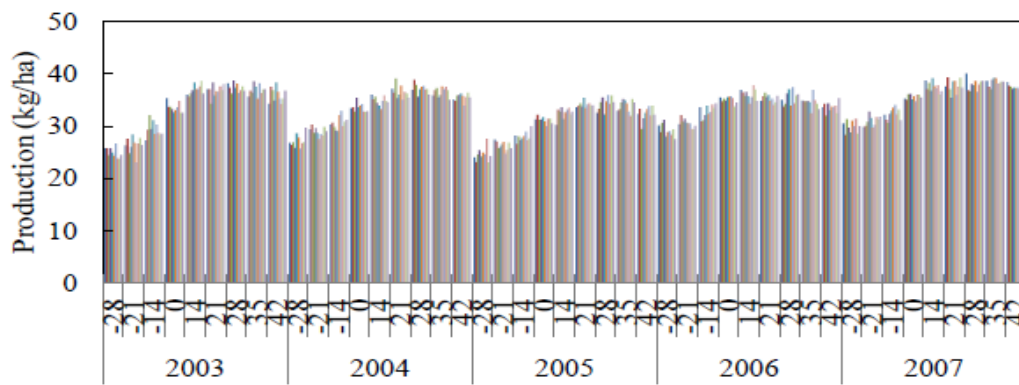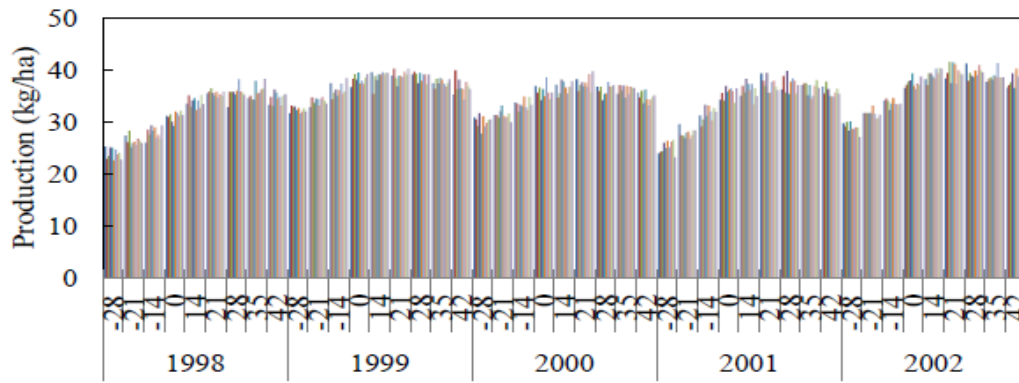
Figure A2.5. (Continued)