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Statistical and Simulation Modeling of Brown Shrimp Population Dynamics in the Northern Gulf of Mexico.

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STATISTICAL AND SIMULATION MODELING
OF BROWN SHRIMP POPULATION DYNAMICS
IN THE NORTHERN GULF OF MEXICO

A Dissertation

Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
In partial fulfillment of the
Requirements for the degree of
Doctor of Philosophy

In

The Department of Oceanography and Coastal Sciences

by
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ABSTRACT

This dissertation used statistical and simulation modeling to examine population dynamics of brown shrimp, *Penaeus (Farfantepenaeus) aztecus*. Brown shrimp are ideal to use in examining recruitment because shrimp represent a common life history strategy, because they are commercially important, and because there are extensive data available. In the first section of this dissertation, I used long-term monitoring data to examine correlative relationships between annual, stage-specific abundance estimates and environmental factors. Criticisms of traditional correlative studies were addressed by using a spatially and temporally-extensive dataset, by comparing stepwise multiple regression to Bayesian model averaging, and by investigating nonlinear relationships with generalized additive models. Postlarval abundance was not well described by any statistical model. Juvenile abundance was partially described by environmental variables such as temperature, water clarity, and water level. Adult abundance was well described by early juvenile abundance, salinity, and temperature. These results suggested that juvenile abundance may be the critical component in determining the year-class strength of shrimp.

In the second section of this dissertation, a spatially-explicit, individual-based simulation model was developed to further investigate relationships between estuarine habitats and juvenile shrimp survival. The model simulated the movement, mortality, and growth of individual shrimp during their residence in estuarine marshes. Relationships between shrimp survival and marsh attributes (amount of vegetation and edge habitat) were examined by overlaying the simulation on 4 habitat maps created from aerial photographs. The model was corroborated with fine-scale density patterns observed in the northern Gulf of Mexico, and sensitivity analyses were performed.

Surviving shrimp grew faster, moved less, spent more time in vegetation, and experienced slightly higher local densities than shrimp that died during the simulation. Maps with more edge habitat supported higher simulated survival under baseline conditions, under high shrimp densities, under alternative rules about movement, and under realistic uncertainty in model inputs. The characteristics of surviving shrimp suggested that high-edge habitats increase survival by providing shrimp direct access to the benefits of vegetated marsh without the high-density cost that may be encountered in low-edge habitats. These results highlight the important role of marsh habitat in determining the recruitment of an estuarine-dependent species.

CHAPTER 1. INTRODUCTION

This dissertation used statistical and simulation modeling to examine population dynamics of the brown shrimp, *Penaeus (Farfantepenaeus) aztecus*. Brown shrimp represent a life history strategy that is common to many commercially-exploited fish and shellfish species. Therefore, all of the methods and some of the conclusions reached in this dissertation can be applied to other estuarine-dependent organisms. Given the current state of depressed fish populations worldwide and the unprecedented pressure on fish populations of harvesting beyond sustainable levels and habitat degradation, it is important to develop new methods for exploring and understanding the population dynamics of estuarine-dependent fish and shellfish.

Two new analytical approaches are presented in Chapter 2 and Chapter 3 of this dissertation. Chapter 2 used stepwise multiple regression, Bayesian model averaging, and generalized additive models to examine correlative relationships between annual, stage-specific, brown shrimp abundance estimates and environmental factors. Because the statistical analysis in Chapter 2 identified the importance of juvenile shrimp survival within the estuaries, Chapter 3 investigated the mechanisms underlying the relationship between estuarine habitat and shrimp survival. The analytical approach in Chapter 3 used a fine-scale geographic analysis and a spatially-explicit, individual-based simulation model to examine the relationship between juvenile shrimp survival and marsh characteristics (i.e., vegetation:water ratios and amount of edge habitat). A synthesis of the conclusions reached by combining the statistical and simulation models is presented in Chapter 4.

1.1 Study organism

Brown shrimp are an ideal species for examining recruitment dynamics because they represent a commercially-important life history strategy and have an essentially annual life cycle. Like other estuarine-dependent organisms, adult brown shrimp spawn offshore, the larvae are transported shoreward, and postlarvae settle in the estuaries. Juveniles grow within the estuary and then migrate offshore. Unlike long-lived, estuarine-dependent finfish, the brown shrimp population consists almost entirely of organisms less than one year old. The absence of multiple year classes in the shrimp population simplifies the analysis of recruitment processes.

The shrimp fishery is Louisiana's most valuable commercial fishery. Louisiana's shrimp landings account for approximately 40% of the Gulf of Mexico landings, and both absolute landings and the contribution of Louisiana landings to the Gulf of Mexico landings have increased since the early 1970's. The shrimp fishery consists of an inshore component (from the coastline toward the interior, including marshes, lakes, and canals) and an offshore component (from the coastline toward the Gulf of Mexico). The brown shrimp fishery is monitored by both fishery-independent and fishery-dependent methods.

The economic value of the Gulf of Mexico shrimp fishery has fueled over 50 years of research into the population dynamics of brown shrimp. Research goals include documenting interannual variation in commercial shrimp catch and identifying the environmental factors that influence shrimp production. Understanding the sources of variation in shrimp recruitment is especially important to Louisiana because Louisiana is losing coastal wetland habitats, several major freshwater and sediment diversions (which will affect marsh habitat) are being considered, and highly restrictive fishery regulations are presently

used to maintain a sustainable shrimp harvest. Additionally, there is an effort in the United States to examine the relationship between fishery resources and essential fish habitat.

State and federal monitoring programs made it possible to assemble a long-term dataset for use in this dissertation. The dataset included 28 years (1970-1997) of stage-specific brown shrimp abundance estimates and a suite of environmental variables. All of the data were specific to Louisiana, but were likely reflective of the northern Gulf of Mexico fishery because approximately 40% of the shrimp landings in the Gulf are landed in Louisiana. I used measures of catch-per-unit-of-effort (CPUE) as an index of abundance at four life stages: postlarvae (number of shrimp•m⁻²), early juveniles in the marshes (number of shrimp per 10 minute, 1.8 m otter trawl), late juveniles in bays (number of shrimp per 10 minute, 4.8 m otter trawl), and adults (pounds of commercial catch per standard day fished). I estimated annual indices of predator abundance and environmental factors including water temperature, salinity, water clarity, river flow, precipitation, acres of marsh > 10 ppt, water level, and atmospheric weather conditions. These data were statistically analyzed in Chapter 2, and portions of the assembled database were used to help configure the simulation model used in Chapter 3.

1.2 Statistical modeling

Chapter 2 of my dissertation used statistical modeling to examine correlative relationships between annual, stage-specific, brown shrimp abundance estimates and environmental factors. This section of my dissertation started with traditional correlative methods and incorporated two new statistical techniques that are only rarely applied to fishery issues: Bayesian model averaging and generalized additive models. The thoroughness of the statistical

approach and the extensive dataset increased our confidence in the biological conclusions reached in Chapter 2.

Correlation analysis is a common approach to analyzing long-term datasets of brown shrimp and other estuarine-dependent species. Correlative studies are useful because they can help identify influential life stages, critical time periods, and important environmental variables, all of which enable more informed management decisions. Correlative analyses, however, have received substantial criticism. The short-comings of simple correlative analysis include identifying spurious relationships, assembling a dataset with multicollinear predictor variables (which may produce arbitrarily selected prediction terms), mis-specifying nonlinear relationships between the response and predictor variables, and failing to provide a method to address model uncertainty.

The extensive brown shrimp dataset and the combination of stepwise multiple regression, Bayesian model averaging, and generalized additive models addressed several criticisms of simple correlative analysis. First, the likelihood of spurious relationships was decreased by using a spatially-extensive and temporally-extensive dataset that contained carefully chosen predictor variables. Second, model uncertainty was addressed by comparing the stepwise multiple regression models to models that were fit using Bayesian model averaging. Third, nonlinear relationships were investigated with generalized additive models.

Chapter 2 presents the results of the statistical analysis of the relationships among the 26 years of life-stage abundances and environmental variables. The analyses were designed to determine which life stages were important in determining annual recruitment,

and to quantify the dependence of each life stage abundance on previous life stage abundances and environmental conditions.

1.3 Simulation modeling

Chapter 3 used a fine-scale, geographic analysis and a spatially-explicit, individual-based simulation model to examine the relationship between juvenile shrimp survival and marsh characteristics (i.e., vegetation:water ratios and amount of edge habitat). The simulation model was developed as a way to examine, in greater detail, the juvenile life stage that the statistical analysis of Chapter 2 identified as important in determining recruitment. At current population levels in Louisiana, the year-class strength of brown shrimp is related to juvenile survival within the estuary; yet, environmental predictors described less than half of the interannual variation in juvenile shrimp abundance. Some of the unexplained variation in the statistical modeling can likely be explained by variation in habitat-related effects on growth and mortality. Hence, I used a spatially-explicit, individual-based model to examine how fine-scale habitat patterns affect juvenile survival.

Individual-based modeling offers a straight-forward way of combining spatial information with empirical field data in order to quantitatively explore the relationship between habitat and shrimp survival. Individual-based models (IBMs) simulate population-level behavior by representing the population as an assemblage of interacting individuals. The individual-based approach is appropriate for simulating brown shrimp because there is extensive empirical data and because fine-scale movement is easier to simulate in an IBM than in more aggregated modeling approaches. When simulating early life stages, it can be important to know the characteristics of surviving individuals because early life stages often have high mortality rates,

and the relatively few surviving individuals may be determined by a distinct set of characteristics. Individual-based modeling enables a direct comparison of the characteristics of survivors compared to those individuals that died.

In order to examine the effects of vegetation and edge habitat, the simulation model was overlaid on 4 habitat maps, which represented marshscapes with different amounts of vegetation and edge habitat. The habitat maps represented realistic marshscapes in southern Louisiana and were created by performing a vegetation-water classification of portions of the Cocodrie NE Digital Orthophoto Quarter Quadrangle (DOQQ). The DOQQ is an orthorectified digital image of an aerial photograph that was acquired in February 1998. Each unit (or pixel) in the image represented one square meter. To create the habitat maps, I chose four 100 m x 100 m subsets from the DOQQ and translated each square meter of the classified image into one cell of the habitat map.

The four habitat maps represented snapshots in a simplified continuum of marsh disintegration: low edge and high vegetation, high edge and high vegetation, high edge and low vegetation, and low edge and low vegetation. Habitat maps were categorized based on the percentage of edge and vegetation. Habitat maps with < 3% edge were considered low-edge marshscapes, and maps with about 6% edge were considered high-edge marshscapes. Habitat maps with 50% water were considered high-vegetation marshscapes, and maps with 70% water were considered low-vegetation marshscapes.

The model developed in Chapter 3 simulated the movement, mortality, and growth of individuals introduced in weekly shrimp cohorts. Shrimp location (cell), survival status, and length were updated during each of the four tidal stages (rising, high, falling,

low) simulated each day. Each simulation began on January 1 and ended on September 1 so that there were 245 days in each annual simulation. Individual characteristics (such as survival status, realized growth rates, and percentage of time in vegetation) were recorded for each shrimp. Model predictions for population statistics (e.g., mean percent survival, mean realized growth rates) were calculated for each habitat map.

Individual shrimp were tracked from the time they entered the marsh as postlarvae until they either died or reached 70mm, when juveniles typically begin to move offshore. The model did not attempt to simulate the transport of larvae or postlarvae into the estuaries; nor did it attempt to simulate the movement of sub-adults into large estuarine bays or into offshore waters. Rather, the focus of this analysis was on juvenile shrimp while they were associated with the marsh. This approach isolated and examined how ecological processes and spatial heterogeneity in estuarine habitats affect juvenile growth and survival.

The simulation contained both physical and biological components. The physical components included water temperature, tidal stage, and habitat patterns. The biological components included mortality, growth, and movement. Simulated predation mortality was influenced by shrimp size, movement, and habitat. Simulated shrimp growth was influenced by temperature, habitat, and local shrimp density. Simulated movement was influenced by tidal stage, habitat type, local density of other shrimp, and shrimp length.

Several techniques were used to examine the performance of the simulation. The model was corroborated by comparing the simulated density patterns with fine-scale density patterns observed in the northern Gulf of Mexico. Variation produced by stochastic elements in

the model were examined by comparing replicate simulations with different random number seeds. The effect of different movement rules was examined in three sets of simulations. The first varied the size-dependency of movement; the second varied the magnitude of movement; and the third made movement random. In order to examine the effect of input parameters on simulated shrimp survival, I performed two Monte Carlo analyses. The Monte Carlo sensitivity analysis varied input parameters slightly around their mean, and the Monte Carlo uncertainty analysis varied input parameters over a realistic range.

Chapter 3 presents the results of the individual-based modeling of shrimp survival for the four maps, and the results of the sensitivity analysis of movement rules and of parameter uncertainty. These analyses were designed to quantify and better understand how the spatial arrangement of marsh habitat affects juvenile shrimp growth and survival.

CHAPTER 2. ENVIRONMENTAL AND BIOLOGICAL FACTORS ASSOCIATED WITH STAGE-SPECIFIC ABUNDANCE ESTIMATES OF BROWN SHRIMP IN LOUISIANA: APPLYING A NEW COMBINATION OF STATISTICAL TECHNIQUES TO LONG-TERM MONITORING DATA

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2.1 Abstract

Several short-term and small-scale correlative studies have associated brown shrimp recruitment with high densities of sub-adults, high salinity, warm temperature, low riverflow, and low precipitation. In this paper we address criticisms of traditional correlative studies by using a spatially and temporally-extensive dataset, by comparing stepwise multiple regression (SMR) to Bayesian model averaging (BMA), and by investigating nonlinear relationships with generalized additive models (GAMs). We use this combination of statistical methods to examine relationships between annual, stage-specific abundance estimates and environmental factors. Bayesian model averaging (BMA) and SMR resulted in models with similar explanatory power, but BMA suggested fewer linear predictors. Generalized additive models (GAMs) did not suggest non-linear relationships among stage-specific abundance estimates. Postlarval abundance was not well described by any model. Juvenile abundance was partially described by environmental variables such as temperature, water clarity, and water level. Adult abundance was well described by early juvenile abundance, salinity, and temperature. These results suggest that juvenile abundance may be the critical component in determining year-class strength of brown shrimp. Identifying mechanisms that regulate

juvenile production within the estuary is a critical step in effectively managing Louisiana's brown shrimp resource.

2.2 Introduction

The shrimp fishery is Louisiana's most valuable commercial fishery. Louisiana's shrimp landings account for approximately 40% of the Gulf of Mexico landings, and both absolute landings and the contribution of Louisiana landings to the Gulf of Mexico landings have increased since the early 1970's. The shrimp fishery consists of an inshore component (from the coastline toward the interior, including marshes, lakes, and canals) and an offshore component (from the coastline toward the Gulf of Mexico). The fishery is monitored by both fishery-independent and fishery-dependent methods. Fishery-independent data are collected at several coastal locations by the Louisiana Department of Wildlife and Fisheries (LDWF, Figure 2.1).

The economic value of the Gulf of Mexico shrimp fishery has fueled over 50 years of research into the population dynamics of brown shrimp, *Penaeus (Farfantepenaeus) aztecus*. Research goals include documenting interannual variation in commercial shrimp catch and identifying the environmental factors that influence shrimp production. Understanding sources of variation in shrimp recruitment is especially important to Louisiana because Louisiana is losing coastal wetland habitats, because several major freshwater and sediment diversions are being considered, and because highly restrictive fishery regulations are presently used to maintain a sustainable shrimp harvest. Additionally, there is an effort in the United States to examine the relationship between fishery resources and essential fish habitat.

Brown shrimp are an ideal organism to use in examining recruitment dynamics of estuarine-dependent species because of the

extensive data available and because shrimp have an essentially annual life cycle. Like other estuarine-dependent organisms, adult brown shrimp spawn offshore, the larvae are transported shoreward, postlarvae settle in the estuaries, and juveniles undergo rapid growth within the estuary and then migrate offshore. Unlike long-lived estuarine-dependent finfish, the shrimp population consists almost entirely of organisms less than one year old (Caillouet et al. 1960). The absence of multiple year classes in the shrimp population simplifies the analysis of recruitment processes.

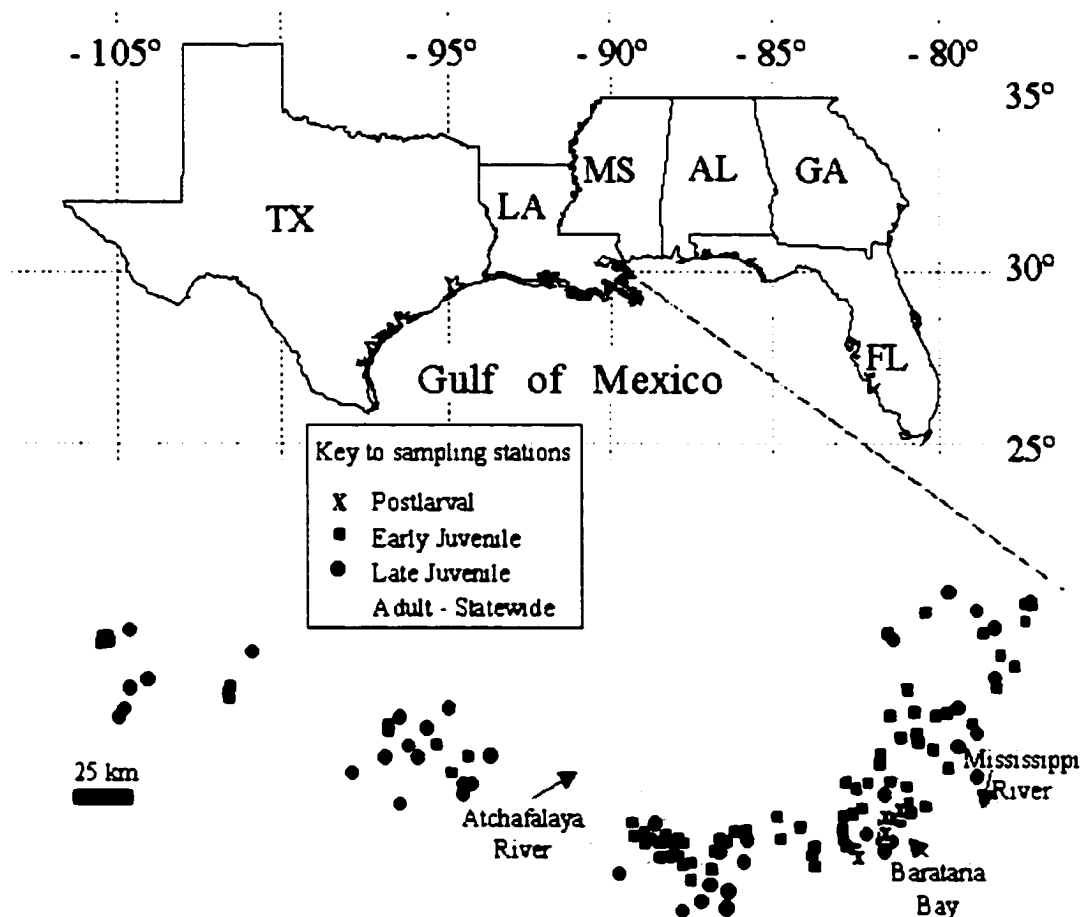


Figure 2.1. Map of the northern Gulf of Mexico and coastal Louisiana showing an example of Louisiana Department of Wildlife and Fisheries sampling stations for brown shrimp. Stations varied slightly from year to year, and the locations shown in this map represent a stations sampled in a typical year. Open water areas are shown in white. Postlarval sampling stations are indicated with an "x"; early juvenile sampling stations are indicated with a dark square; and late juvenile sampling stations are indicated with an open circle.

Correlation analysis is a common approach to analyzing long-term datasets of brown shrimp and other estuarine-dependent species. Correlative studies are useful because they can help identify influential life stages, critical time periods, and important environmental variables enabling more informed management decisions. Catch per unit effort (CPUE) is used extensively as an index of abundance, and there are many attempts to relate CPUE indices to environmental variables (e.g., Austin and Ingham 1979; Wyatt and Larreneta 1988). High brown shrimp harvests have been correlated with a high abundance of sub-adults, high salinity, warm temperature, low riverflow, and low precipitation (Caillouet and Baxter 1973; Barrett and Gillespie 1975; Barrett and Ralph 1977).

Correlative analyses, however, have received substantial criticism. The high risk of identifying spurious relationships is a major shortcoming of correlation studies (Walters and Collie 1988), and less complex datasets are more likely to identify spurious relationships (Tyler 1992). A second problem associated with correlative studies is the high probability of assembling a dataset that has multicollinear environmental predictor variables. If predictor variables are correlated, the results of regression analysis become less meaningful and possibly arbitrary. Classical multiple regression analysis selects a single model, even though there are often several plausible models that may include different combinations of predictor variables. Traditional multiple regression methods do not provide a way to address this uncertainty in model selection (Hoeting et al. 1999). A final criticism of simple correlative analysis is that it may fail to detect, or may mis-specify, nonlinear relationships between the response and predictor variables.

In this study, we modify the traditional correlative approach to address these common criticisms. We use stepwise multiple regression, Bayesian model averaging, and generalized additive models to examine relationships between annual, stage-specific abundance estimates of shrimp and environmental factors. First, we decrease the likelihood of spurious relationships by using a spatially-extensive and temporally-extensive dataset that contains carefully chosen predictor variables. Second, we address uncertainty in model selection by comparing the stepwise multiple regression (SMR) models to models we fit using Bayesian model averaging (BMA). Third, we investigate possible additive, nonlinear relationships by allowing spline functions within generalized additive models (GAMs). Our objective was to use this new combination of statistical tools to identify potentially influential environmental conditions and critical life stages within the brown shrimp life cycle. The thoroughness of our statistical techniques (especially in addressing model uncertainty and non-linearity) and our extensive dataset add to the confidence of our conclusions.

2.3 Methods

2.3.1 Data sources

We assembled a dataset that included 26 years (1970-1997) of stage-specific brown shrimp abundance estimates and a suite of environmental variables. All of the data were specific to Louisiana, but are likely reflective of the northern Gulf of Mexico fishery because approximately 40% of the shrimp landings in the Gulf are landed in Louisiana. We used measures of CPUE as an index of abundance at four life stages: postlarvae (number of shrimp•m⁻²), early juveniles in the marshes (number of shrimp per 10 minute, 1.8 m otter trawl), late juveniles in bays (number of shrimp per 10 minute, 4.8 m

otter trawl), and adults (pounds of commercial catch per standard day fished). We estimated annual indices of predator abundance and environmental factors including water temperature, salinity, water clarity, river flow, precipitation, acres of marsh with salinity > 10 ppt, water level, and atmospheric weather conditions.

The Louisiana Department of Wildlife and Fisheries (LDWF) provided the postlarval and juvenile abundance estimates. Although the data were collected by LDWF to make short-term management decisions, we are using the data to explore ecological relationships. A detailed description of the data collection procedures can be found in the Marine Fisheries Division Field Procedures Manual (LDWF 1996). Table 2.1 is a summary of the sampling procedures, and Figure 2.1 shows a map of sampling stations.

Table 2.1. Summary of Louisiana Department of Wildlife and Fisheries sampling protocols used to monitor postlarval and juvenile brown shrimp in southern Louisiana.

Stage	Sampling gear	Mesnsiz	Sampling location
Postlarval	0.5m plankton net	500.00 micron	Tidal passes
Early juvenile	1.8m (6') otter trawl	9.53 mm	Shallow marshes
Late juvenile	4.9m (16') otter trawl	19.05 mm	Bays, sounds, lakes

In general, the LDWF sampled weekly when the brown shrimp densities were historically high. Postlarval data were collected from four major tidal passes in Barataria Bay, which are assumed to function as a statewide index. We calculated weekly postlarval densities based on the catch per tow and flowmeter readings. Weekly estimates of juvenile abundance in Louisiana were obtained from 1.8 m and 4.9 m otter-trawl surveys from sampling stations throughout the Louisiana coast. Because of sample location and mesh size, the 1.8 m trawl selected smaller shrimp than the 4.9 m trawl (mean total length

of 60 mm versus 71 mm total length). Hence, we used the 1.8 m trawl data to estimate early-juvenile abundance in marshes and the 4.9 m trawl data to estimate late-juvenile abundance in bays.

We estimated adult abundance from monthly CPUE data (pounds of inshore and offshore Louisiana commercial landings per standard day fished). In preliminary analyses, we considered converting catch from pounds to numbers, as was done by DeLancey et al. (1994) in North Carolina. We decided to use pounds rather than numbers because CPUE in pounds and CPUE in numbers were well correlated, because using CPUE in numbers did not improve model fits, and because commercial landings in pounds are often used as an estimate of adult shrimp abundance (e.g., Barrett and Ralph 1977). Our adult estimates were calculated from National Marine Fisheries Service (NMFS) statistics for brown shrimp landed in Louisiana and from standardized effort data. Standardized fishing effort was derived from units of nominal effort (nets being pulled for a period of 24 hours). Standardized effort adjusts nominal effort according to the relative fishing power of each vessel in the Gulf of Mexico shrimp fleet relative to a standard vessel (Griffin et. al. 1997). Including relative fishing power in the calculation of standardized effort attempts to account for temporal changes in fishing efficiency.

We estimated predator abundance from the finfish caught in the LDWF's 4.9 m (16 foot) otter trawl surveys. Finfish are not the target species of this sampling program, and we did not expect the trawl catch to be an exact reflection of actual abundance. We did, however, expect the large sampling size (39,825 trawls over the 28 year period) to partially compensate for the non-targeted sampling design. Hence, these data should provide a rough index of predator abundance. We initially examined abundance data for *Lagodon rhomboides*

(pinfish), *Fundulus grandis* (gulf killifish), *Cynoscion nebulosus* (spotted seatrout), *Paralichthys lethostigma* (southern flounder), *Micropogonias undulatus* (Atlantic croaker), *Sciaenops ocellatus* (red drum), and *Leiostomus xanthurus* (spot), but only Atlantic croaker were ubiquitous enough to calculate an annual predatory index. We used only the longest 25% (> 7.5 cm total length) of the Atlantic croaker to calculate the predator index because analysis of juvenile croaker stomach contents show that shrimp are not a major dietary component (i.e., shrimp are < 10% of total dry weight) until croaker are longer than 7 cm (Sheridan 1979; Sheridan and Trimm 1983).

The first set of environmental data was acquired in conjunction with the biological sampling of the postlarval and juvenile abundances and included water temperature (°C), salinity (ppt), and water clarity (secchi depth recorded in feet and tenths). Due to the location of the plankton tows, salinity and temperature obtained in association with postlarval sampling represented environmental conditions in the tidal passes of Barataria Bay. Environmental parameters obtained in association with the 4.9 m trawls represented the general conditions in bays; whereas measurements obtained in association with the 1.8 m trawls represented environmental conditions in shallow marshes.

In cases where the LDWF sampled salinity and temperature at the surface and bottom of the water column, we used bottom samples whenever possible. To evaluate the relationship between surface and bottom conditions, we deleted any obvious outliers and used simple linear regression to compare the paired surface and bottom values. Bottom salinity explained > 90% of the variation in surface salinity, and the bottom temperature explained > 97% of the variation in surface temperature. The similarity between surface and bottom conditions was

expected because the water column in areas of data collection were generally shallow and well-mixed. Postlarval brown shrimp are primarily benthic, so we chose to use the bottom values for temperature and salinity. If bottom values were missing, we substituted surface values.

Because brown shrimp abundance may be influenced by acres of available nursery habitat, river flow, rainfall, marsh flooding, and onshore transport (Barrett and Gillespie 1975; Zimmerman et al. 1991; Childers et al. 1990), we assembled a second set of environmental data. Unlike the environmental data in the first set, this second set was collected independently of the biological sampling. The LDWF provided an annual estimate of the total number of marsh acres with a salinity > 10 ppt and also provided mean monthly Mississippi River flow (at Tarbert Landing, MS) and Atchafalaya River flow (at Simmesport, LA). The Louisiana Climate Center provided mean monthly precipitation in southern Louisiana and an index of synoptic weather conditions (see Muller and Willis 1983 for a description of the synoptic weather dataset). Frontal Gulf Return and Gulf Return weather conditions were extracted from the weather dataset and used as indices of onshore transport and marsh flooding events. Because water level data from coastal gauges represent marsh inundation (Childers et al. 1990), we used an index of water level from daily and monthly data reported for the United States Geological Survey tide gauge at Grande Isle, Barataria Bay, LA. The water-level data initially contained a strong linear trend component that represented long-term marsh subsidence, so we detrended the dataset by using the residuals from a linear regression of water level versus time (in months) for the period 1970-1997.

2.3.2 Annual indices

We chose to use annual indices because we were interested in the interannual variation in the fishery-dependent data, and because we were concerned about statistical problems associated with using monthly indices. During preliminary analyses (Haas et al. 1999), we built statistical models using annual indices for the stage-specific abundances and monthly indices for the environmental variables (e.g., April temperature, May salinity). Using monthly values for environmental variables caused us to consider too many predictor variables (over 60) relative to the 28 annual observations available. After carefully scrutinizing the preliminary models, we decided that using monthly indices could lead to a high probability of spurious correlations, unrealistically high correlation coefficients, and additional multicollinearity problems. Hence, for this analysis, we chose to create annual indices for all response and predictor variables.

We used seasonal subsets of data to represent critical biological and environmental time periods (Table 2.2). Biological data were chosen to include only the time periods of high shrimp abundance. Hence, low-catch samples did not dilute the signal contained within the high-catch samples, and yearly estimates represented the influence of the major brown shrimp spawning period. The environmental data were further narrowed to include only the time periods of peak shrimp abundance. The designated critical periods were generally narrower for the environmental variables than for the biological variables to minimize any dilution effects of averaging environmental conditions during periods with relatively low shrimp abundance.

Table 2.2. Summary of the months that were included in the critical biological and environmental periods for each life stage.

Index	Biological data	Environmental data
Postlarval	January - May	February - April
Juvenile	February - August	March - June
Adult	May - August	May - August

Annual averages of biological and environmental variables were calculated from data at the finest temporal scale available. Hence, the postlarval, early juvenile, and late juvenile indices were calculated from weekly data at multiple stations. Because some of the environmental data were only available on a monthly basis, several environmental indices (e.g., precipitation, river flow) were calculated from monthly data. The annual index of adult abundance was more complicated to calculate because the catch and effort data were reported separately. The adult index was calculated by dividing the monthly inshore catch by the monthly inshore effort; dividing the monthly offshore catch by the monthly offshore effort; calculating a mean monthly CPUE by averaging the monthly inshore CPUE and monthly offshore CPUE; then calculating a mean annual CPUE by averaging the monthly mean CPUE for May through August (Figure 2.2).

The annual average for each biological and environmental variable was calculated by using simple arithmetic means. We considered calculating averages using a general linear model approach to correct for slightly uneven spatial and temporal sampling from year to year. We chose, however, to calculate averages using the easily interpreted simple arithmetic means because means calculated from both methods were well correlated ($r^2 = 0.9181$ for postlarval data, $r^2 = 0.8844$ for early-juvenile data, $r^2 = 0.9268$ for late-juvenile data). We addressed multicollinearity concerns regarding the annual indices by averaging two salinity variables (salinity in bays and in marshes)

that were well-correlated ($r^2 = 0.8256$). We also omitted the variable for the number of marsh acres with salinity > 10 ppt because it was correlated with the new averaged estuarine salinity variable ($R^2 = 0.6626$). We filled in one missing value for water clarity in the marshes by predicting its value from the water clarity in the bays ($r^2 = 0.5575$), and we omitted 1970 from the postlarval analysis because we were missing values for turbidity in both the marshes and the bays.

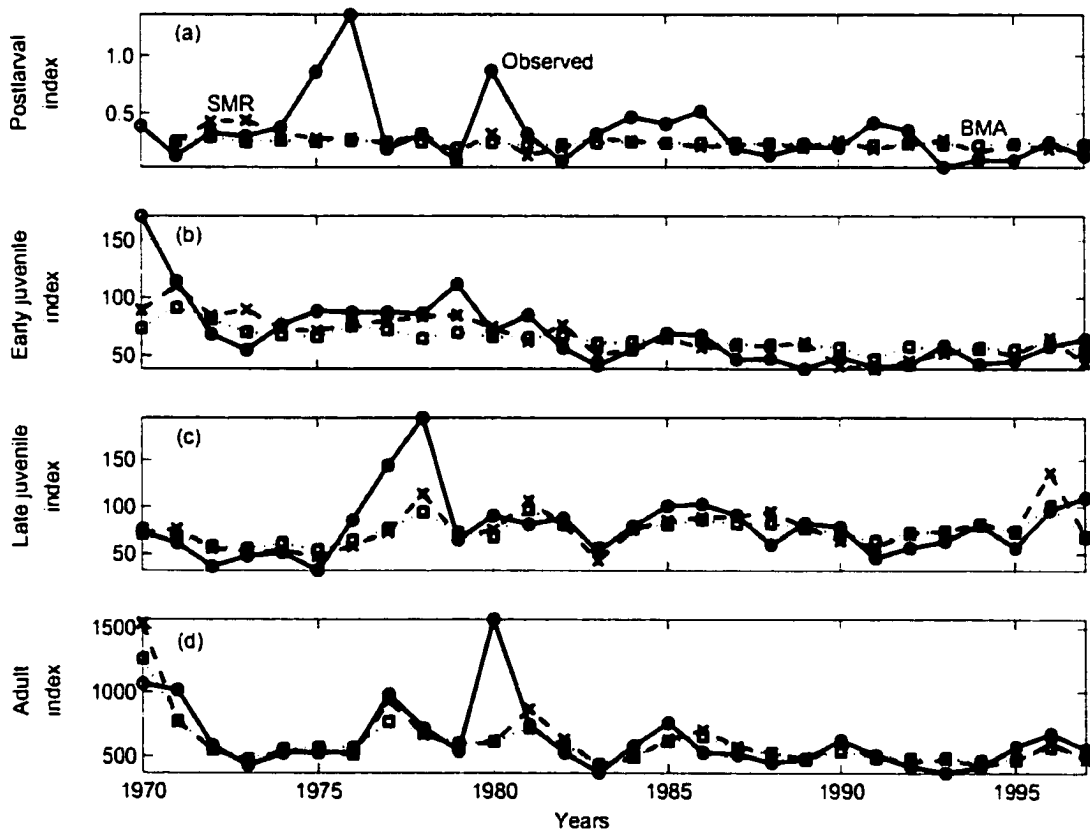


Figure 2.2. Predicted and observed brown shrimp abundance estimates for each life stage (a) postlarval, (b) early juvenile, (c) late juvenile, and (d) adult. Observed values are shown with a bold line and circular markers. Predicted values from the stepwise multiple regression analysis (SMR) are shown with a dashed line and X-markers. Predicted values from Bayesian model averaging (BMA) analysis are shown with a dotted line and square markers.

To create the annual indices used in the statistical analysis, we standardized predictor variables and transformed response variables. To enable direct comparison of regression parameters in SMR and BMA, we standardized the annual index for each predictor variable (including stage-specific abundance indices) by subtracting the mean from each annual value, and then dividing by its standard deviation. Figure 2.3 shows plots of the standardized indices for five predictor variables versus year. We corrected residual departures from normality by transforming the unstandardized abundance indices when we used them as response variables. We used a natural log transformation for the postlarval, early-juvenile, and late-juvenile indices; and we used a negative inverse transformation for the adult index.

2.3.3 Stepwise multiple regression (SMR)

We used regression analysis to explore the relationships among abundance estimates and environmental factors. Specifically, we fit four regression models to describe the interannual variation in the indices of adult, late-juvenile, early-juvenile, and postlarval abundance. In order to model shrimp abundance at each life stage, we used all available annual environmental indices plus all indices of preceding life-stage abundance estimates. Due to data limitations, some environmental indices (i.e., the predator index, salinity in tidal passes, and temperature in tidal passes) could not be calculated for the critical environmental period for each stage-specific model. Because adult abundance may be an indicator of spawning potential, we lagged the adult index for use as a possible predictor of postlarval abundance. We used the same list of predictor variables for the SMR and the BMA analysis (see Table 2.3).

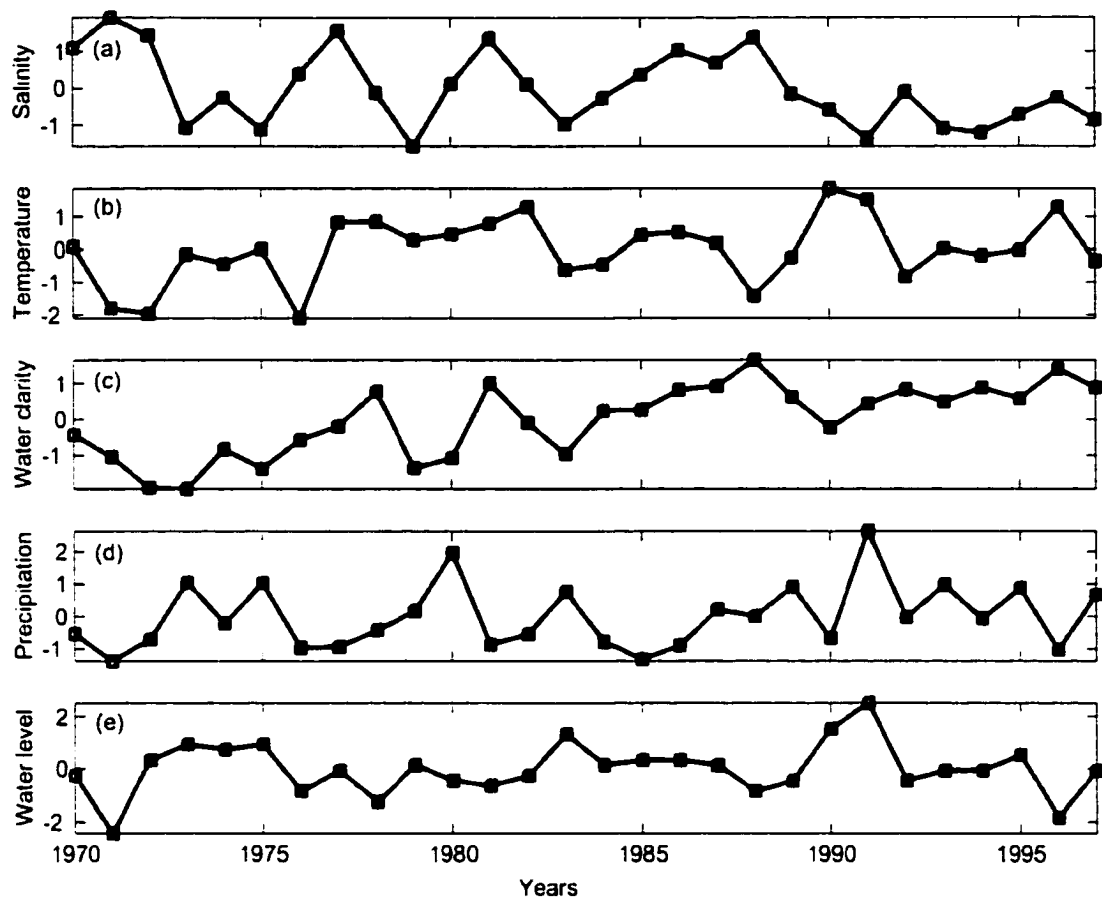


Figure 2.3. Examples of environmental indices plotted against the years included in the study period: (a) the estuarine salinity index for the adult models, (b) the marsh temperature index for the adult models, (c) the bay water clarity index for the juvenile models, (d) the precipitation index for the juvenile models, and (e) the water level index for the juvenile models.

The regression models were built using a forward stepwise regression procedure in SAS (selection = stepwise, SAS Institute 1990). The stepwise procedure started with a model with no predictor variables. If any F statistic (that reflected each variable's contribution to the model) was below the entry criteria ($p \leq 0.10$), the variable with the highest F statistic was added to the model. At each step, variables that were not significant at the 0.15 level were removed.

Table 2.3. The probability of a linear term in each Bayesian model describing stage-specific brown shrimp abundance estimates. Probabilities over 0.50 are in bold and have at least a 1:1 odds ratio of being included in the model. Dashes (-) indicate where environmental predictor variables were unavailable or where biological predictor variables were inappropriate for each stage-specific model.

	Post-larvae	Early juvenile	Late juvenile	Adult
Intercept	1.0000	1.0000	1.0000	1.0000
Lagged adult index	0.0355	-	-	-
Postlarval index	-	0.0715	0.0320	0.0580
Early juvenile index	-	-	0.0590	0.8740
Late juvenile index	-	-	-	0.1415
Frontal gulf return	0.0355	0.0385	0.0520	0.0375
Gulf return	0.0575	0.0395	0.0300	0.0270
Precipitation	0.0765	0.2390	0.1955	0.0420
Predator index	-	0.0850	0.0455	-
River flow rate	0.0570	0.0550	0.0540	0.2145
Salinity (estuary)	0.0465	0.1715	0.0745	0.4990
Salinity (passes)	0.0725	0.0395	0.0405	-
Temperature (bays)	0.0345	0.0560	0.2905	0.2165
Temperature (marshes)	0.0420	0.0780	0.1465	0.4320
Temperature (passes)	0.0250	0.1680	0.0340	-
Water Clarity (bays)	0.1355	0.5220	0.0720	0.0500
Water Clarity (marshes)	0.1195	0.0935	0.3375	0.0795
Water level	0.0385	0.3240	0.2735	0.0345

We examined the residuals from the SMR models for normality, homogeneity of variance, and non-independence of the error term. We used the Shapiro Wilks test to determine departures from normality, plotted residuals versus fitted values to identify possible non-heterogeneity of variance, and plotted residuals versus years to explore independence of the error terms. We also examined Cooks Distances to screen for influential observations. After transforming the biological response variables, we found no evidence against these basic regression assumptions and no evidence of highly influential observations in any of the final SMR models.

2.3.4 Bayesian model averaging (BMA)

Because we were concerned about uncertainty of model selection using the traditional regression techniques, we analyzed the same dataset using BMA. The traditional SMR built a single model for each

response variable by selecting a single subset of predictor variables. The BMA approach, on the other hand, examines a large sample of the possible models and averages the parameter estimates across the sample of possible models. The number of possible models equaled 2^P , where P equals the number of predictor variables (postlarval $P = 13$, early juvenile $P = 14$, late juvenile $P = 15$, adult $P = 13$). Thus, BMA calculated parameter estimates comparable to regression coefficients, but also estimated the probability of including each variable as a linear predictor.

We used BMA to calculate the mean of the posterior distribution of the coefficients for each predictor variable (see Lamon and Clyde 2000 for details). Although BMA allows different prior probabilities for each predictor variable, we gave each predictor variable the same prior probability in this analysis. Because we had many predictor variables, we used the Stochastic Search Variable Selection (SSVS) algorithm of George and McCulloch (1997) to traverse the model space. This Markov Chain Monte Carlo method was used to approximate BMA using a subset of all possible models. In SSVS, predictor variables were not removed from the model; instead, the coefficients of the predictor variables shrank toward zero when they were not included in many of the possible models visited by the SVSS algorithm. We calculated the probability of including each variable as a linear predictor by calculating the sum of the number of times the term was included in the sampled models and dividing by the total number of sampled models. When the probability of inclusion equaled 0.50, the term had a 1:1 odds ratio of being included. Variables with probabilities of inclusion < 0.50 were not considered likely predictor variables.

2.3.5 Comparison between stepwise multiple regression and Bayesian model averaging

We compared the results from SMR and BMA by examining the list of important predictor variables from each model and by comparing values of the coefficients for the important predictor variables. The SMR parameter estimates represent the direction and the slope of the relationship. In BMA, the sign of the parameter estimates still represents the direction of the relationship, but the magnitude of the coefficient is a function of the slope of the relationship and also of the likelihood of inclusion as a linear term. If a predictor was included in most of the possible models in the BMA, we expected the regression coefficients from both statistical methods to be similar. If, however, a predictor was not included in many of the possible models in BMA, we expected the coefficient calculated through BMA to shrink toward zero to represent uncertainty as to whether or not the predictor variable should be in the model.

The results of the SMR and BMA were further evaluated by comparing the predicted values and error terms from both models. We used the final equations from each SMR and BMA model to predict stage-specific abundance indices for each year in the study period, and we plotted the observed abundance estimates and the two sets of abundance predictions versus years.

2.3.6 Generalized additive models (GAMs)

We used GAMs (Hastie and Tibshirani 1990; Chambers and Hastie 1992) to explore the possibility of additive, non-linear relationships. GAMs have been used to relate fishery recruitment to stock size and environmental factors (Daskalov 1999) and are a flexible way to explore relationships that may be nonlinear. The response variable in GAMs is modeled by evaluating the function

corresponding to each predictor variable, then summing the values together with the intercept. We used GAMs as an exploratory method, rather than as our primary analysis tool, because the statistical parameters in GAMs can be difficult to interpret and GAMs use more degrees of freedom than do linear methods. Also, GAMs have shortcomings similar to those of the conventional linear regression models because they produce a single model in which the model uncertainty can not be directly assessed.

The GAM analysis was restricted to an exploration of the relationships between abundance indices and the environmental predictors that were identified by the SMR and BMA analysis. We restricted the analysis to a shortened list of predictor variables because the GAMs were over-parameterized if we included all the environmental predictors. We included all biological indices for previous life stages, all significant variables from the stepwise regression analysis, and all variables with greater than 0.50 probability of inclusion (i.e., linear relationship) as indicated by the BMA.

We used a stepwise model-fitting procedure in the S-PLUS software (step.gam, Statistical Sciences 1994) to iteratively evaluate the fit of the additive model. The initial full model consisted of an unspecified smooth function for each term. The final model was fit using an iterative technique called backfitting (Hastie and Tibshirani 1990). The model was reduced in a stepwise fashion using the Akaike Information Criterion (AIC, Akaike 1973) so that the final model was optimal in terms of AIC. The AIC uses a sum of squares criteria that includes a penalty for model complexity (number of parameters). In the reduced model, a predictor could remain included as a full smoothing spline term, could be reduced to a linear term, or could be

omitted from the model. We calculated an approximate R^2 value for each model by dividing the residual deviance by the null deviance, then subtracting that product from one.

We investigated the contribution of the postlarval term to the adult GAM because the relationship between postlarvae and adults appeared to be heavily influenced by a few outlying points, because the slope of the relationship was shallow, and because the postlarval term was not important in the SMR or BMA analysis. We evaluated the contribution of the postlarval term by specifying a reduced GAM model without the postlarval index and comparing it to the full GAM model with the postlarval term. We compared the R^2 values of the two models, and we used the ANOVA function in S-PLUS to produce a chi-square statistic that evaluated the difference in deviance between the full and reduced models.

2.4 Results

2.4.1 Stepwise multiple regression

Interannual variation in the index of postlarval abundance was not well described by the stepwise regression model (Table 2.4). Water clarity (in the bays) was the only predictor variable that entered the model (when the level of significance for entry was $\alpha = 0.10$). Only 10% of the variation in the index of postlarval abundance was explained by the model, and the overall regression model was not significant when evaluated at $\alpha = 0.05$. Because the lagged index of adult abundance was not a significant predictor variable, there was no direct evidence that postlarval recruitment was linearly related to spawning-stock size during the period of sampling.

Environmental predictors were important components in the models that described early juvenile abundance in the marshes and late

juvenile abundance in the bays (Table 2.4). Both regression models were significant when evaluated at $\alpha = 0.05$, and both models explained almost half of the variation in the indices of juvenile abundance. Indices of previous life stage abundances were not significant in either of the juvenile models. Temperature was the most important predictor of juvenile abundance, and it accounted for about 25% of the variability in the early and late juvenile models (partial $R^2 = 0.17 + 0.07$ for early juveniles and 0.25 for late juveniles). Water level and water clarity were the remaining predictors of juvenile abundances.

Table 2.4. Results of the stepwise multiple regression (SMR) analysis used to describe the stage-specific brown shrimp abundance indices. The order of the predictor variables represents the order in which they entered the model. A plus (+) or minus (-) in the second column indicates the slope of the regression coefficient.

Index	Significant terms (where alpha = 0.10)	Partial R^2	Model R^2	Model P-value
Postlarval	- Water clarity (bays)	0.1074	0.1074	0.0951
Early	- Temperature (passes)	0.1735	0.5180	0.0016
juvenile	- Water level	0.1025		
(marshes)	- Water clarity (bays)	0.1760		
	- Temperature (marshes)	0.0659		
Late	+ Temperature (bays)	0.2490	0.4399	0.0027
juvenile	+ Water clarity (bays)	0.1201		
(bays)	- Water level	0.0708		
Adult	- Early juveniles	0.3605	0.6195	0.0001
	- Salinity (estuary)	0.1115		
	- Temperature (marshes)	0.1475		

Although there were significant environmental predictors of the index of adult abundance, the index of early juvenile abundance was the most important predictor (Table 2.4). The model was highly significant ($p = 0.0001$) and explained over 60% of the variation in the index of adult abundance. The index of early-juvenile abundance accounted for over 36% of the variation in adult abundance. Salinity and temperature (in marshes) were significant predictors, and when

combined, they accounted for about 25% of the variation in the adult model.

2.4.2 Bayesian model averaging

The BMA results suggested that no predictor variables successfully modeled the interannual variation in the postlarval index (Table 2.3). None of the predictor variables had a high probability of inclusion as a linear term in the postlarval model, and the intercept was the only parameter that was included in more than 50% of the models. The two water clarity terms (in the bays and in the marshes) had the highest probabilities of inclusion, but the probabilities were low (i.e., each term was included in less than 15% of the models).

The BMA did not identify any of the indices of previous life stage abundance as likely predictors of either early or late juvenile abundances, and there was a low probability that environmental predictors were linearly related to either juvenile abundance index (Table 2.3). Water clarity in the bays was included as a linear term in approximately half (~ 1:1 odds ratio) of the early juvenile models. No other predictor was included in more than half of the models.

Bayesian model averaging identified both biological and environmental variables that were likely to have a linear relationship with the index of adult abundance (Table 2.3). The index of early juvenile abundance was included as a linear term in over 97% of the models. Salinity in the estuary and temperature in the marshes were included in slightly less than half of the sampled models.

2.4.3 Comparison between stepwise multiple regression and Bayesian model averaging

Stepwise multiple regression and BMA agreed on the sign of the regression coefficients for all of the most likely predictors (Table

2.5). The postlarval index was negatively related to water clarity (in bays). Both juvenile abundance indices were positively related to temperature and negatively related to water clarity (in bays), and water level. The index of adult abundance was positively related to the early juvenile index, salinity, and temperature (in marshes).

Table 2.5. Comparison of parameter estimates between the stage-specific models built via stepwise multiple regression (SMR) and Bayesian model averaging (BMA). Bold face in the third column indicates terms that are included in over 50% of the sample models, and bold face in the fourth column indicates significant terms in the stepwise multiple regression models. Bayesian parameter estimates are shrunk toward zero because they reflect the slope of the regression line and the probability of inclusion in the sampled models. A plus (+) or minus (-) in the third or fourth column indicates the slope of the regression coefficient.

Index	Most likely BMA terms	BMA estimate / P (inclusion)	SMR estimate
Postlarval	Water clarity (bays)	- 0.0395 / 0.1355	-0.2823
Early	Temperature (marshes)	+ 0.0068 / 0.0780	+ 0.1001
juvenile	Temperature (passes)	+ 0.0203 / 0.1680	+ 0.0926
(marshes)	Water clarity (bays)	- 0.0976 / 0.5220	- 0.2017
	Water level	- 0.0535 / 0.3240	- 0.1732
Late	Temperature (bays)	+ 0.0467 / 0.2905	+ 0.1339
juvenile	Water clarity (bays)	+ 0.0413 / 0.2720	+ 0.1187
(bays)	Water level	- 0.0415 / 0.2735	- 0.1084
Adult	Early juveniles	+ 0.000238 / 0.8740	+ 0.000237
	Salinity (estuary)	- 0.000112 / 0.4990	+ 0.000240
	Temperature (marshes)	- 0.000090 / 0.4320	+ 0.000203

The fit of both the SMR and the BMA models improved from the postlarval to adult stage. The error terms were similar using both methods (Table 2.6). Neither method adequately modeled the interannual variation in the postlarval index. Both juvenile SMR models ($R^2 \approx 0.45$) had better fits than the postlarval SMR model ($R^2 \approx 0.10$), but not as good as the adult SMR model ($R^2 = 0.62$). The predicted values calculated from the SMR and from the BMA tracked each other more closely than they tracked the observed values (Figure 2.2).

Several of the significant predictors in the SMR analysis had low probabilities of inclusion in the BMA (Table 2.5), which shrank the regression parameter estimates toward zero. Because terms with

less than 50% probability of inclusion are not considered likely predictors, the BMA identified fewer likely predictors than the SMR. Neither method identified likely predictors of postlarval abundance. The SMR identified four significant predictors of early juvenile abundance; whereas the BMA only identified one likely predictor. The late juvenile and adult SMR models had three significant predictors; whereas the BMA did not identify any likely predictors of the late juvenile stage and only one predictor of the adult stage.

Table 2.6. Comparison of the mean square error between the stage-specific models built via stepwise multiple regression (SMR) and Bayesian model averaging (BMA).

Response variable	SMR	BMA
Postlarval index	0.6896	0.6560
Early juvenile index (in the marshes)	0.0755	0.0780
Late juvenile index (in the bays)	0.0954	0.0862
Adult index ($\times 10^3$)	1.0874	0.9724

2.4.4 Generalized additive models

Generalized additive models did not identify any nonlinear relationships among the stage-specific abundance estimates, though the GAMs did suggest a possible nonlinear relationship with turbidity (Table 2.7). All but three of the spline terms were either omitted from the model or reduced to linear terms. In the early juvenile model, temperature was modeled with a nonlinear function. The shape of the curve, however, was not significantly different than linear (F-test, $p = 0.09$). In the late juvenile model, water clarity was modeled with a bell-shaped curve that was significantly different from linear (F-test, $p = 0.02$). In the adult model, salinity was modeled with a curved, but increasing function, that was only marginally different than linear (F-test, $p = 0.05$).

In general, the results of the GAM analysis were similar to those of the SMR. The higher R^2 values in the GAMs (Table 2.4 verses

Table 2.7) resulted partially from the addition of the spline terms and partially resulted from the difference in model building techniques. The SMR models were sampled according to *F* statistics, whereas the GAMs were selected based on maximizing AIC. With two exceptions, the GAMs included the same terms as in the SMR. In the first exception, the postlarval GAM did not include water clarity. This is not a meaningful departure from the SMR results because turbidity was only marginally significant in SMR model (Table 2.4, $p = 0.10$). In the second exception, the postlarval index was included in the adult GAM. The slope of the relationship with postlarvae was shallow and heavily weighted by a few outlying observations. The postlarval term contributed little to the adult model. The R^2 value for the full GAM model with the postlarval term was only slightly higher than the reduced GAM model without the postlarval term ($R^2_{\text{Full}} = 0.7681$; $R^2_{\text{Reduced}} = 0.7246$), and the reduced model was not significantly different than the full model (chi-square, $p = 0.9996$).

Table 2.7. Results from the stage-specific generalized additive models (GAMs) used to describe stage-specific brown shrimp abundance. A plus (+) or minus (-) before the name of the included term indicates the direction of the relationship, and an (S) indicates the variable was modeled with a smoothing spline term.

Index	R^2	Included terms	Omitted terms
Postlarval		none	Lagged adult index Water clarity (bays)
Early juvenile	0.6509	- Water level - Water clarity (marshes) (S) Temperature (marshes) + Temperature (passes)	Postlarval index
Late juvenile	0.6553	+ Temperature (bays) (S) Water clarity (bays) - Water Level	Postlarval index Early juvenile index
Adult	0.7681	+ Early juvenile index + Postlarval index (S) Salinity (estuary) + Temperature (marshes)	Late juvenile index

2.5 Discussion

The results presented in this study were fairly robust to slight changes in the way the data were assembled. During initial analyses, we considered deleting outlier values of the annual indices (particularly in the juvenile indices for 1970 and 1978). The SMR models built with and without the potential outliers were very similar, and we decided to include all values of annual indices. We also considered using the calendar year as a predictor variable. With the exception of the postlarval models (which show a time trend), the results from the SMR and BMA were similar in models with and without a year variable. We also examined the SMR and BMA results with log-transformed and untransformed response variables. The BMA produced very similar models with logged and untransformed response variables for each life stage, although the juvenile SMR models showed slight differences in the environmental variables included as significant predictors. For example, the early juvenile SMR model using the untransformed abundance index substituted salinity terms for the water clarity and water level terms included in the log-transformed abundance model that we described in this analysis. In preliminary analyses we also produced models for annual catch (as opposed to CPUE). We did not report these results because they were very similar to those of the CPUE models reported here when effort was included as a predictor variable in the catch model.

2.5.1 Comments on statistical methods

Bayesian model averaging and SMR methods resulted in models with similar explanatory power, but the BMA analysis suggested fewer linear predictor variables. Bayesian methods added to the analysis because they allowed us to quantify our confidence in the variable selection of the stepwise approach by examining the probabilities of inclusion

for each predictor variable. We might not expect similar performances from the BMA and SMR methods if we had more observations (when it would be more likely to find spurious significant relationships) or if we were using the model to make forecasts for observations that were not used in model fitting (Lamon and Clyde 2000).

We suggest using caution when evaluating models produced from SMR. In this analysis, the SMR produced models with possibly spurious correlations. For example, the late juvenile SMR model included temperature, water clarity, and water level; whereas the late juvenile BMA model did not identify any likely environmental predictor variables. Although it is possible for SMR to underparameterize a model by identifying only a single term from a suite of biologically-important multicollinear variables, comparison with BMA results suggest that our SMR models were probably over-parameterized. In either case, strict interpretation of SMR results, especially of predictor variables of moderate to low statistical importance, may produce misleading conclusions.

The GAMs were useful to this analysis for two reasons. First, they helped identify a possible non-linear relationship with turbidity. Second, the lack of spline terms in biological variables suggested we did not mis-specify non-linear relationships between successive life stages. This is an important consideration because relationships between successive life stages are often modeled with non-linear functions (e.g., classical spawner-recruit fisheries models). The GAMs are considered exploratory, and the final models should be interpreted with caution because we have the same concerns about multicollinearity and model uncertainty with the GAMs as we did with the SMRs. In future analyses we plan to more fully explore non-

linear relationships (both additive and non-additive) in this same dataset.

2.5.2 Environmental correlates

Temperature was positively correlated with shrimp abundance during all but the postlarval stage. The abundance indices for later life stages (early juvenile through adult) increased with increasing temperature. The positive relationship between temperature and shrimp production has been reported elsewhere (Barrett and Gillespie 1975; Barrett and Ralph 1977) and may result from increased growth at higher temperatures and a subsequent reduced period of vulnerability to sized-based predation mortality (Minello et al. 1989).

Increased salinity in the estuary was positively correlated with increased adult shrimp abundance. This salinity index was also correlated with the LDWF's annual estimate of the number of acres of marsh with salinity > 10 ppt, a metric that the LDWF has used to help evaluate the interannual variation in adult shrimp abundance.

Increased salinity has been historically associated with increased shrimp production (Barrett and Gillespie 1975; Barrett and Ralph 1977; Zimmerman et al. 1990a), but the association is not necessarily a direct result of a physiological preference of brown shrimp for high salinity. Rather, shrimp may be drawn to certain prey fields associated with high salinity (Zimmerman et al. 1990b), and fluctuations in salinity may represent fluctuations in the total acreage of appropriate nursery habitat (Barrett and Gillespie 1975).

The results of this study provided inconclusive evidence regarding the relationship between water clarity and shrimp abundance. The correlation between abundance and water clarity was negative for early juveniles, but positive or bell-shaped for the late juveniles. Negative correlations between water clarity and shrimp abundance may

be a product of increased shrimp production due to less predation pressure from visual predators (Minello et al. 1987). Negative correlations could also arise from differences related to catchability rather than production. High water clarity may decrease catches because shrimp in clear water may bury more in the substrate (Minello et al. 1987) or be better able to detect and avoid the sampling gear. Positive correlations between water clarity and shrimp abundance are possible if clear water supports high primary production and increases available food resources.

There are three possible reasons for the inconsistent relationships between water clarity and abundance. First, habitat differences (shallow marshes versus deeper bays) in the stage-specific sampling might account for different relationships between water clarity and catch. Second, if the relationship between water clarity and shrimp abundance is truly bell-shaped, linear methods may mis-model the relationship with a monotonically increasing or decreasing function. Third, it is possible that correlations between water clarity and abundance were caused by relationships between abundance and meteorological factors that influence water clarity levels.

Decreased water levels were associated with high indices of juvenile abundance. Water levels may effect sampling efficiency rather than the size of the population. Differences in catchability may explain why the correlation with water level is not carried into the adult life stage (when water level is not likely to affect sampling efficiency). When water level is low, shrimp lose access to the marsh and become concentrated in deeper channels where they are more susceptible to the sampling gear. The relationship between water level and shrimp production may be curvilinear. Childers et al. (1990) assert that there are low harvests in low-water years when

there is little marsh inundation and therefore minimal access to the marsh, and there are also low harvests when intense fresh-water input causes very high water levels and a reduced area of high-salinity shrimp habitat.

2.5.3 Importance of estuarine conditions

Three observations from this study suggest that estuarine conditions are critical in determining the year-class strength of brown shrimp. The first observation is the strong correlation between juveniles and adults. In this study, the variation in the early juvenile index explained more than half of the variation in adult abundance, and similar correlations between juvenile shrimp and commercial catch have been documented elsewhere (Klima et al. 1982, 1987). The second supporting observation is the lack of correlation between early life stages (i.e., postlarval and juvenile stages) and previous life-stage abundances. The third supporting observation is the important role of environmental parameters in explaining juvenile abundance. The regulatory role of processes occurring in the estuary has also been suggested in other studies (Barrett and Ralph 1977; Minello et al. 1989). These results combine to suggest that during the last 30 years, adult shrimp abundance was more influenced by estuarine conditions than by fluctuations in spawning-stock size.

One possible reason for undetected links between successive life stages could be insufficient abundance data. There are several factors that make it especially difficult to quantify stage-specific abundances of estuarine-dependent organisms: the ontogenetic shifts in habitat utilization, the effects of emigration and immigration, the influence of multiple environmental signals and their impact on catchability, the difficulty in using both fisheries-independent and fisheries-dependent estimates, and the time expenditure associated

with acquiring annual data. These same issues may have contributed to the lack of importance of the predatory index in this study.

Of all variables in our dataset, we believe the postlarval index was least likely to reflect actual abundances because the sampling effort was spatially-limited and because postlarvae are notoriously difficult to sample. Postlarval abundance is not historically well correlated with commercial catch (Sutter and Christmas 1983), and problems associated with postlarval data are well-documented (Christmas et al. 1966; Berry and Baxter 1969). Because postlarval recruitment is sporadic and patchy, it is questionable whether the current sampling protocol captures enough of the spatially and temporally-complex arrival patterns of postlarvae to be useful for long-term studies.

Because we lacked confidence in the postlarval index, we created an alternative model to explore the relationship between spawning-stock size and subsequent recruitment of their young. We represented the spawning stock with a one year lag of the adult index and the recruits with the late juvenile index. As in the initial postlarval model, the estimation of the spawning stock (lagged adult index) was not a significant predictor of recruitment to the late juvenile stage. Although the accuracy of the postlarval index needs to be resolved before we can make conclusive remarks regarding postlarval dynamics, the lack of a significant relationship between the lagged adult index and juveniles in the bays suggests that the undetected relationship between spawning-stock size and postlarval recruitment to the estuary was not merely caused by insufficient postlarval data.

During the period of study, spawning-stock size did not have a linear relationship with subsequent recruitment of young. Although both quasi-linear and Beverton Holt-type relationships between penaeid

stock and recruitment to various life stages have been proposed elsewhere, these models are highly controversial (Garcia 1983). In short-lived, highly-fecund species such as shrimp, a small spawning stock can support high recruitment to the fishery. Hence, brown shrimp recruitment may not be well-correlated with spawning stock (adults) under most conditions. Only when spawning stock falls below some critical level would recruitment be highly influenced by stock size.

Identifying mechanisms that regulate juvenile production within estuaries will be a critical step in the ongoing effort to effectively manage Louisiana's shrimp resource. Juvenile shrimp production may be the critical component in determining the year-class strength of brown shrimp in Louisiana, and estuarine conditions are likely to affect annual fishery recruitment. Although some estuarine conditions can not be managed (e.g., temperature, rainfall), there are several anthropogenic impacts that can be mitigated. We should further examine those estuarine processes that can be managed (e.g., fresh water diversions, wetland loss and fragmentation). We should also examine spatial components within the estuary. Environmental predictors described less than half of the interannual variation in juvenile shrimp abundance. Some of the unexplained variation in our statistical models can possibly be explained by small-scale spatial variation in habitat, which has not been traditionally included in correlative analysis. Because coastal Louisiana has undergone substantial wetland loss and fragmentation over the past 50 years, spatial analysis of the associations between estuarine habitat and shrimp growth and survival are particularly needed.

In this study, we have described a new combination of statistical tools that can be used to examine the dynamics of

estuarine-dependent fishery species. Our results have several important management implications. First, we believe that sustainable management practices can not be solely limited to regulating catch. At current stock levels, annual production appears to be more regulated by environmental conditions within the estuary rather than by postlarval arrival to the estuary. Second, we recommend focusing future investigations on processes that affect juvenile growth and survival in estuaries. A more thorough understanding of the interaction between estuarine dynamics and shrimp survival will not only help effectively manage the shrimp fishery, but may yield insights into the management of other commercially important estuarine-dependent species.

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CHAPTER 3. LINKING ESTUARINE HABITATS TO BROWN SHRIMP SURVIVAL: IMPLICATIONS OF A SPATIALLY-EXPLICIT, INDIVIDUAL-BASED SIMULATION MODEL.

3.1 Introduction

There is a growing awareness of the role of habitat in the production of fish and shellfish species. The passage of the Magnuson-Stevens Fishery Conservation and Management Act in 1996 has highlighted the importance of essential fish habitat, and habitat issues are beginning to be considered when evaluating fishery management plans. In many coastal areas, natural habitats are becoming fragmented and lost to encroaching human development. Understanding the spatial component of ecological processes is therefore critical, especially when attempting to manage exploited, estuarine-dependent species. Many recreationally and commercially important species utilize coastal marshes as nursery grounds (Minello 1999). Fortunately, our technical ability to represent spatially-complex habitats and the interactions between habitat and organisms is also increasing. Geographic information systems and spatially-explicit simulations allow us to quantitatively model how heterogeneous habitats affect aquatic biota.

Shrimp are an example of a commercially exploited species that may be highly affected by changes in marsh habitat. Like other estuarine-dependent species, adult brown shrimp spawn offshore, the larvae move shoreward, and postlarvae settle in the estuaries. Juveniles grow within the estuary and then migrate offshore. At current population levels in Louisiana, the year-class strength of brown shrimp appears to be related to juvenile survival within the estuary (Barrett and Ralph 1977, Minello et al. 1989b, Haas et al. In Press); yet, environmental predictors often describe less than half of the interannual variation in juvenile shrimp abundance (Haas et al. In

Press). Some of the unexplained variation in statistical models can possibly be explained by variation in habitat-related effects on growth and mortality, which have not been traditionally included in these correlative analyses.

Although the mechanisms are not well-understood, there is evidence to suggest that shrimp are influenced by marsh attributes (e.g., amount of vegetation, amount of edge habitat). On a system to system basis, shrimp harvests are correlated with wetland area (Turner 1977). More extensive wetland systems produce higher shrimp harvests. Because several processes occur as wetlands disintegrate, the relationship between habitat and shrimp production may involve habitat characteristics in addition to just total wetland area. As marshes disintegrate, two processes occur. Vegetation is converted into water; and the amount of edge habitat follows a dome-shaped curve, initially increasing, then peaking at intermediate levels of disintegration, and finally decreasing at high levels of disintegration (Browder et al. 1985). Changes in edge habitat are important to examine because juvenile brown shrimp are found associated with vegetated edge habitat (Minello 1999, Rozas and Zimmerman 2000). Brown shrimp rarely penetrate further than 3 m into the vegetation from the nearest water-vegetation interface (Peterson and Turner 1994). Given the high rate of coastal wetland loss in Louisiana (Britsch and Dunbar 1993) and the dome-shaped relationship between edge and marsh disintegration, it is critical to examine the relationship between wetland habitat and shrimp survival.

Individual-based modeling offers a straight-forward way of combining spatial information with empirical field data in order to quantitatively explore the relationship between habitat and shrimp survival. Individual-based models simulate population-level behavior

by representing the population as an assemblage of interacting individuals. The individual-based approach is appropriate for simulating brown shrimp because there is extensive empirical data and because fine-scale movement is easier to simulate in an IBM than in more aggregated modeling approaches. When simulating early life stages, it can be important to record the characteristics of surviving individuals because early life stages often have high mortality rates, and the relatively few surviving individuals may be determined by a distinct set of characteristics (Crowder et al 1992). Individual-based modeling enables the direct comparison of the characteristics of survivors compared to those that died.

This study used a spatially-explicit, individual-based simulation model to explore the role of marsh vegetation and edge habitat on shrimp survival. The model tracked the movement, mortality, and growth of individual shrimp during their residence in estuarine marshes. The relationship between shrimp survival and marsh attributes (amount of vegetation and edge habitat) were examined by overlaying the simulation model on various habitat maps that I created from aerial photographs. Biological parameters were derived from published estimates and from field data. I examined simulated shrimp survival across the four habitat maps which had different amounts of vegetation and edge habitat. I also performed a series of sensitivity analysis to investigate relationships between model input and predicted shrimp survival. Based on the results of simulation experiments and on the results of the sensitivity analyses, I offer suggestions for future research.

3.2 Methods

3.2.1 Model description

The model simulated the movement, mortality, and growth of individuals introduced as weekly shrimp cohorts. Shrimp location (cell), survival status, and length were updated during each of the four tidal stages (rising, high, falling, low) simulated each day. Each simulation began on January 1 and ended on September 1, so that there were 245 days in each annual simulation. Individual characteristics (such as survival status, realized growth rates, and percentage of time in vegetation) were recorded for each shrimp. Model predictions for population statistics (such as mean percent survival, mean realized growth rates) were calculated for each habitat map.

Individual shrimp were tracked from the time they entered the marsh as postlarvae until they either died or reached 70mm, when juveniles typically begin to move offshore. The year-class strength of brown shrimp appears to be established between postlarval entrance to the estuary and before migration offshore (Barrett and Ralph 1977, Minello et al. 1989b, Haas et al. In Press). Hence, the model did not attempt to simulate the transport of larvae or postlarvae into the estuaries; nor does it attempt to simulate the movement of sub-adults into large estuarine bays or into offshore waters. Rather, the focus of this analysis was on juvenile shrimp while they were associated with the marsh. This approach isolated and examined how ecological processes and spatial heterogeneity in estuarine habitats affect juvenile growth and survival.

3.2.1.1 Physical environment

The simulation model was overlaid on a physical environment that contained three components: water temperature, tidal inundation, and

habitat patterns. These three components were included because they are historically correlated with shrimp behavior and survival (Barrett and Gillespie 1973, Childers et al. 1990, Zimmerman et al. 1991, Turner 1977, Browder et al. 1989). Other physical parameters (such as salinity) were not included in this model because I considered them less likely to be influential on the small spatial scales used in these simulations.

Simulated daily water temperatures were derived from water temperature measurements recorded by the Louisiana Department of Wildlife and Fisheries (LDWF) in shallow marshes in coastal Louisiana (1970-1997). Water temperature in the marshes was regressed against a function of Julian day (JDAY). I used the resulting equation (Eqn. 1, $R^2=0.68$) to calculate the simulated daily water temperature (Figure 3.1).

$$\text{TEMP} = 23.157 - (2.459 \times \text{SIN}(\text{JDAY} \times 0.017)) - (7.161 \times \text{COS}(\text{JDAY} \times 0.017)) \quad \text{Eqn. 1}$$

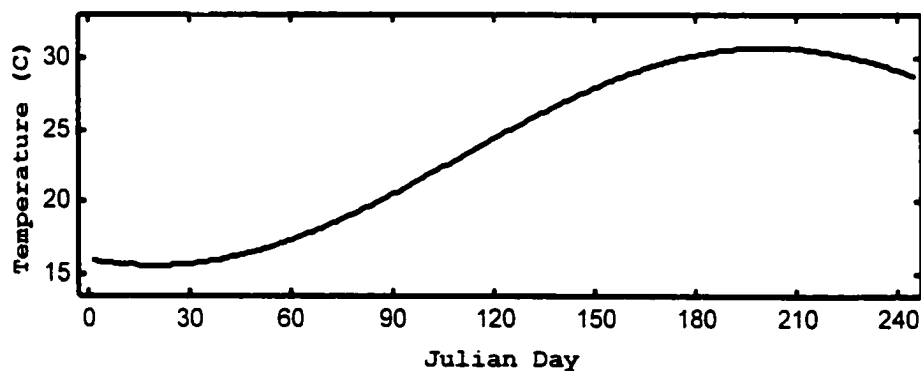


Figure 3.1. Daily water temperature (°C) used in model simulations. The temperature function used to calculate the simulated daily water temperature was derived from water temperatures in shallow Louisiana marshes.

The tidal stages were based on the probability of marsh inundation in coastal Louisiana marshes. I modeled tidal stages from observed marsh-inundation patterns rather than from astronomical conditions because access to vegetation within coastal Louisiana

marshes is often driven by meteorological events (wind events) rather than astronomical tides. I simulated a daily probability of flooding (P_{FLOOD}) by fitting a curve (Eqn. 2, Figure 3.2a) to the estimated marsh inundation in a hummocky southern Louisiana *Spartina* marsh over a 5 year period (Rozas and Reed, 1993).

$$P_{\text{FLOOD}} = (30.885 - 0.6732 \cdot \text{JDAY} + 0.0216 \cdot \text{JDAY}^2 - 0.000155 \cdot \text{JDAY}^3 + 0.000000336 \cdot \text{JDAY}^4) / 100 \quad \text{Eqn.2}$$

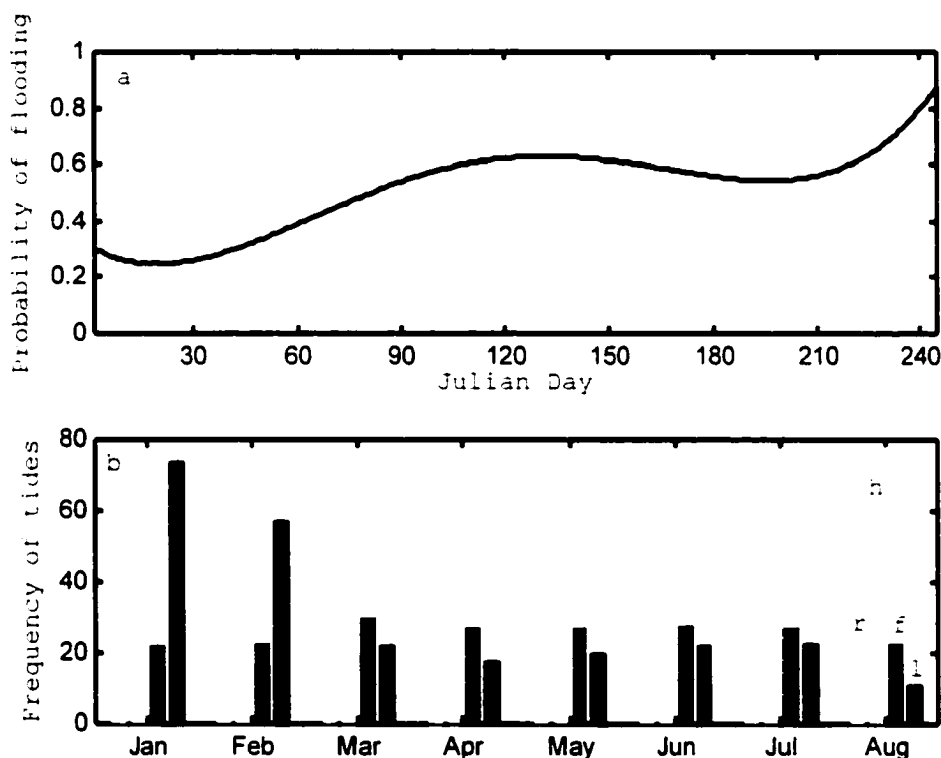


Figure 3.2. Seasonal changes in marsh inundation. a) Probability of flooding, based on published field observations, for each day in the simulation. b) Frequency of the simulated tidal stages in each month. White bars indicate rising (r) tides; light gray bars indicate high (h) tides; dark gray bars indicate falling (f) tides; and black bars indicate low (l) tides.

At the beginning of each 6-hour time-step, the tidal stage (i.e., rising, high, falling, or low) was assigned based on the probability of flooding and on the previous tidal stage. If a random number was less than the probability of flooding, the marsh was

assumed flooded. If the marsh was flooded and the previous tide was falling or low, then the current tidal stage was set to rising; if the marsh was flooded and the previous tide was rising or high, the current tidal stage was set to high. If the marsh was not flooded and the previous tide was falling or low, the current tidal stage was set to low; and if the marsh was not flooded and the previous tide was rising or high, the current tidal stage was set to falling. A representative series of resulting tides for one annual simulation is shown in Figure 3.2b.

In order to examine the individual and combined effects of vegetation and edge habitat, I created four habitat maps with different amounts of vegetation and edge habitat. The habitat maps represented realistic marshscapes in southern Louisiana and were created by performing a vegetation-water classification on portions of the Cocodrie NE Digital Orthophoto Quarter Quadrangle (DOQQ). The DOQQ is an orthorectified digital image of an aerial photograph that was acquired in February of 1998. Each unit (or pixel) in the image represented one square meter. To create the habitat maps, I chose four 100 m x 100 m subsets from the DOQQ and translated each square meter of the classified image into one cell of the habitat map (Figure 3.3).

To ensure that the habitat maps were large enough to capture marshscape patterns and to avoid being dominated by the borders of the map, I also created four 500 m x 500 m maps with edge and vegetation ratios similar to the 100 m x 100 m maps. The baseline simulation results from the larger maps were very similar to the baseline results from the smaller maps. Differences in survival were less than 2% on each of the maps. Hence, I used the 100 m x 100 m maps for all subsequent simulations.

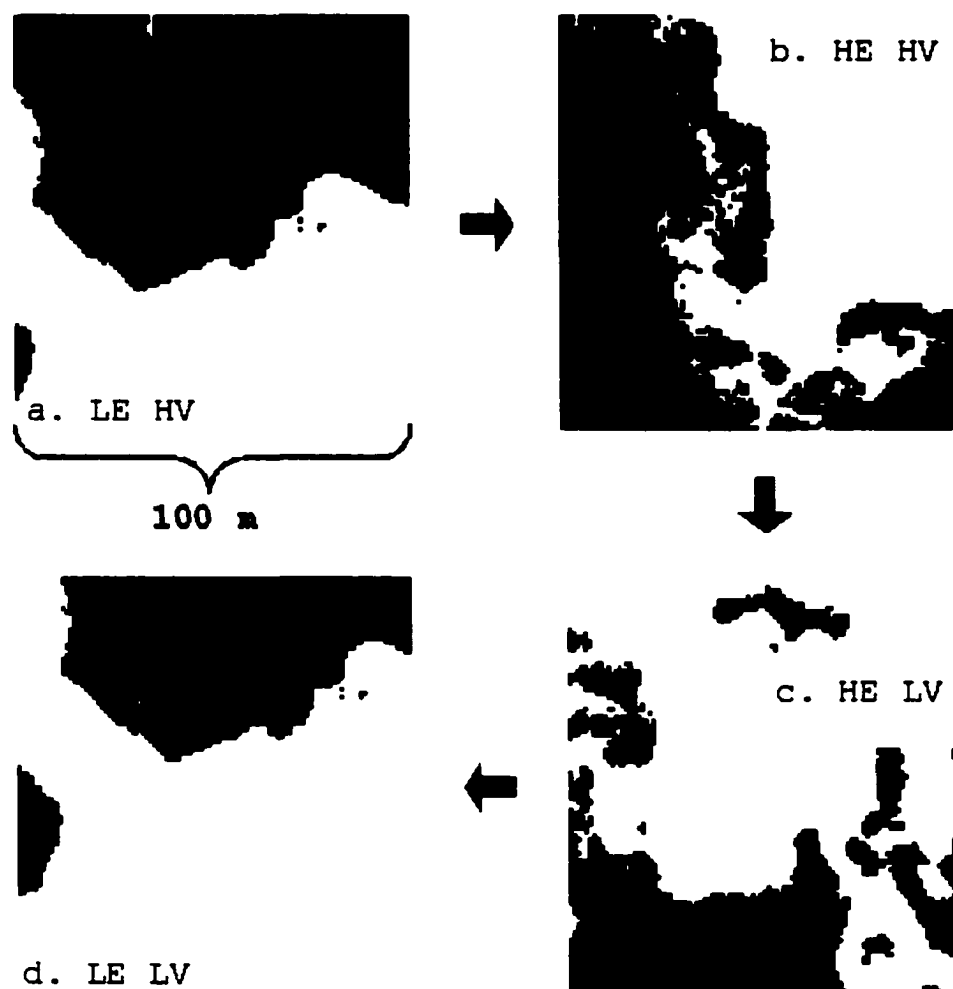


Figure 3.3. The 100 m x 100 m habitat maps were created by subsetting and classifying portions of the Cocodrie NE Digital Orthophoto Quadrangle (DOQQ). The gray represents water, and the black represents vegetated marshes. The four maps represent snapshots in a simplified continuum of marsh disintegration: a) Map LE HV - little edge and high amount of vegetation, b) Map HE HV - high edge and high amount of vegetation, c) Map HE LV - high edge and low amount of vegetation, and d) Map LE LV - less edge and low amount of vegetation.

I further classified the vegetation and water categories so that I could identify edge habitat. Water1 represented the edge of the water body. Cells that were in the water1 category included any water cells that shared a border or diagonal corner with a vegetated cell. Water2 represented water that shared a border or diagonal corner with a water1 cell. Hence, water2 cells were approximately 2 meters from vegetation. Water3 cells represented water adjacent to water2 and

were approximately 3 meters from vegetation. Water>3 represented all water cells not included in water1, water2, or water3. Water>3 cells were greater than 3 m from vegetation. Vegetated cells were similarly classified so that veg1 represented vegetated cells that shared a border or diagonal corner with a water cell; veg2 represented vegetation that was approximately 2m from water; veg3 represented vegetation approximately 3 m from water; and veg>3 represented interior vegetation that was greater than 3 m from water. The cells at the edges of the habitats maps were classified by considering the map a continuous unit that wrapped around from top to bottom and from side to side.

For clarity, I used the term "marsh" to refer to the complex of vegetation and water. The term "edge" refers to the interface between the vegetation and water (i.e., veg1 and water1 cells). The term "vegetated edge" refers to the vegetation directly adjacent to the vegetation-water interface (i.e., veg1).

The four habitat maps were categorized based on the percentage of edge and vegetation (Table 3.1). Habitats with < 3% edge were considered low-edge (LE) marshscapes, and those with >7% edge were considered high-edge (HE) marshscapes. Habitats with 50% vegetation were considered high-vegetation (HV) marshscapes, and those with 30% vegetation were considered (LV) marshscapes. The four habitat maps represented snapshots in a simplified continuum of marsh disintegration: low edge and high vegetation, high edge and high vegetation, high edge and low vegetation, and low edge and low vegetation.

3.2.1.2 Introduction of shrimp to estuarine marshes

Simulated shrimp entered the model in weekly cohorts. Cohort strength was derived from 28 years (1970-1997) of weekly postlarval

density data (number of postlarval shrimp per m^3) collected by the LDWF in four tidal passes in Barataria Bay, LA. Mean weekly postlarval densities were calculated from the field data.

Table 3.1. Percentage of vegetation and edge cells in each habitat map. Maps represented habitats with low edge (LE), high edge (HE), low vegetation:water ratios (LV), and high vegetation:water ratios (HV). Water1 represented water that was within 1 m of vegetation; water2 represented water 2m from vegetation; water3 represented water 3 m from vegetation; and water>3 represented water > 3m from vegetation. Veg1 represented vegetation within 1 m of water; veg2 represented vegetation 2m from water; veg3 represented vegetation 3 m from water; and veg>3 represents interior marsh vegetation > 3m from water.

	Habitat Maps			
	LE-HV	HE-HV	HE-LV	LE-LV
Water	49.93	50.23	69.96	69.83
water1	2.52	7.68	8.47	2.64
water2	1.80	3.26	5.61	1.94
water3	1.73	2.49	5.01	1.82
water>3	43.88	36.80	50.97	63.43
Vegetation	50.07	49.77	30.04	30.17
veg1	2.42	8.88	7.75	2.42
veg2	1.70	4.76	3.90	1.65
veg3	1.67	3.82	2.55	1.60
veg>3	44.28	32.31	15.84	24.50
Total	100.00	100.00	100.00	100.00

The postlarval density pattern was roughly bell-shaped and peaked in the second week of March (Figure 3.4). Because the inshore shrimp population consists almost entirely of organisms less than one year old (Caillouet et al. 1980), the weekly densities of postlarvae are assumed to represent all new individuals. Relative weekly cohort strength was computed from the field data as the weekly mean density divided by the sum of weekly mean densities. The number of shrimp in each simulated weekly cohort was calculated by multiplying the specified total number of postlarval shrimp in each annual simulation by the relative weekly cohort strength. The total number of postlarval shrimp in the baseline simulations was set at 100,000 postlarvae per year, so that simulated shrimp densities reflected natural field densities (see Corroboration section).

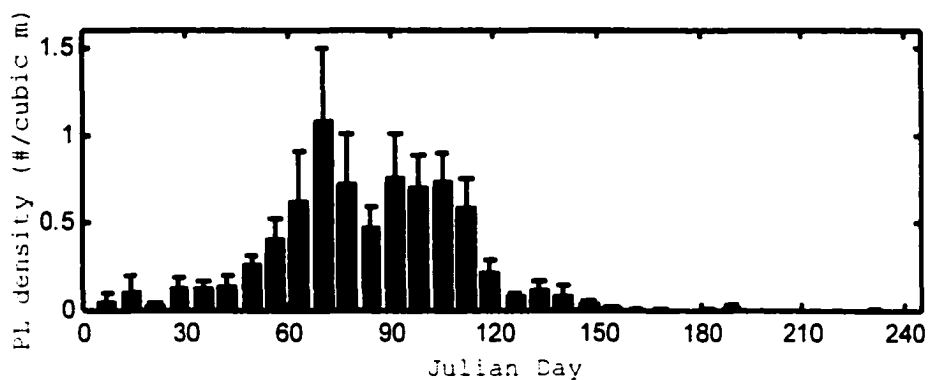


Figure 3.4. Postlarval data collected from 1970 to 1997 by the Louisiana Department of Wildlife and Fisheries from four tidal passes in Barataria Bay, LA. Error bars indicate ± 1 SE from the mean.

The weekly cohorts of shrimp entered the simulation at the beginning of a rising tide. Because the model began tracking shrimp when they recruit to vegetated habitat, shrimp were initially randomly distributed in water cells that were 2 meters or less from the edge (i.e., water1 or water2 cells). When postlarvae arrive in the estuarine nursery areas, they are generally 10 to 15 mm in total length (Baxter and Renfro 1967). Each simulated shrimp was randomly assigned an initial length from a normal distribution with mean = 15.0 mm, standard deviation = 2.5. Minimum and maximum values were specified (minimum = 5.0 , and maximum = 25.0) to eliminate unrealistically short or long lengths.

3.2.1.3 Movement

I used existing field data and observations to derive a set of movement rules that seemed to mimic shrimp movement patterns over tidal cycles and on meter space scales. Simulated shrimp movement depended on tidal stage, habitat type, local density of shrimp, and shrimp length. Figure 3.5 summarizes the movement rules. Because shrimp rarely penetrate further than 3 m into the vegetation (Peterson

and Turner 1994), I limited shrimp movement to vegetated cells that were within 3 meters of the water (i.e., veg1, veg2, veg3 cells).

Simulated shrimp could move farther as they grew longer and when they were in non-vegetated water. Motility (m) was used as an index of the potential distance a shrimp could move in one tidal stage. As shrimp grew longer, their motility increased ($m = 1$ for < 30 mm shrimp, $m = 2$ for $30 - 45$ mm shrimp, and $m = 3$ for > 45 mm shrimp). The neighborhood (n) of cells available for movement was a function of shrimp location and motility. During each tidal stage, shrimp could move n cells in any direction, including the diagonal directions. If shrimp were in vegetation (veg1, veg2, veg3), in water within 3 m of vegetation (water1, water2, water3), or moving to interior vegetation (veg2, veg3), the neighborhood of cells available for movement equaled their motility ($n = m$). Because shrimp can potentially move faster in water than in vegetation, if shrimp were in open water (water>3) and moving within the water (water1, water2, water3, water>3) or to the vegetated edge (veg1), the neighborhood expanded from $n = m$ to $n = m*3$.

Simulated shrimp moved according to the tides. During a rising or high tide, shrimp could move to any neighboring cell that was less than 4 m from the edge. During a falling tide, shrimp could move to water cells or to vegetated cells within m meters of the edge. The vegetated cells available during a falling tide were determined by the shrimp's motility. If $m = 1$, shrimp could move to water or veg1 cells; if $m = 2$, shrimp could move to water, veg1, or veg2 cells; and if $m = 3$ shrimp could move to water, veg1, veg2, or veg3 cells. During a low tide, shrimp could only move to water cells. If shrimp did not move to a water cell during low tide, they were considered stranded in the vegetation.

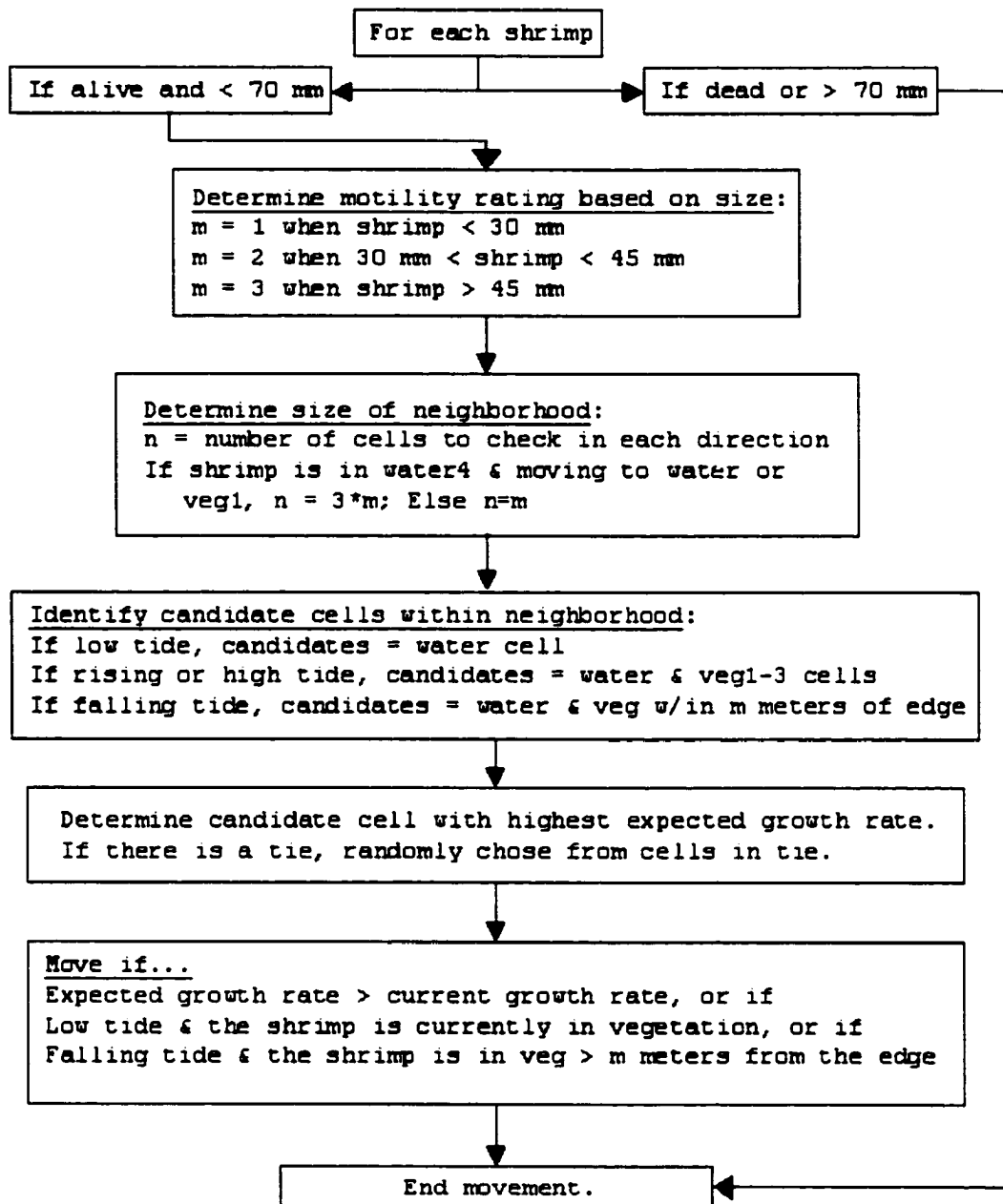


Figure 3.5. Flow Chart for movement subroutine.

Simulated shrimp selected for vegetated habitat. I constructed the movement rules so that simulated shrimp would mimic habitat-specific density patterns that are reported in field studies. Juvenile brown shrimp are found at higher densities in vegetated edges than in open water or in interior vegetation (Minello 1999, Rozas and Zimmerman 2000). The movement rules assumed that shrimp tend to move toward habitat than can support a higher growth rate (based on vegetation and local shrimp density). At each tidal stage, simulated shrimp moved to the neighboring cell which provided the best expected growth rate. Because growth was habitat and density-dependent (see Growth section), habitat and density also affected movement. If there was a tie for the best expected growth rate amongst the neighboring candidate cells, one cell was randomly chosen from the tied candidates. If none of the expected growth rates in the neighboring cells were higher than the current cell, the shrimp did not move.

In order to provide enough habitat for shrimp located near the sides of the habitat maps, shrimp were allowed to wrap around the sides of the habitat maps. When simulated shrimp reached the edge of the map, they continued around to the opposite edge of the map. Hence, a shrimp that reached the far right side of a map could potentially move to the far left of the map, and a shrimp in the uppermost right corner of the habitat map could potentially move to any other corner of the map.

3.2.1.4 Mortality

Two sources of mortality were simulated: stranding and predation. Stranding mortality affected shrimp that were stranded in a vegetated cell at low tide. Because stranded shrimp have an increased risk of physiological stresses resulting from possible salinity or temperature extremes and increased risk of predation on

the marsh surface, a 50% chance of death was imposed (see movement section) on stranded shrimp. The second source of mortality, predation mortality, was calculated (after movement and before growth) for each tidal stage.

Predation mortality was influenced by shrimp size, movement, and habitat. A baseline instantaneous mortality rate (BZMORT) of 0.005 per 6-hour tidal stage was derived from averaged size-specific estuarine mortality estimates for juvenile brown shrimp in the northern Gulf of Mexico. Estimates of mortality for 2-week periods for juvenile brown shrimp (12 mm to 30 mm) range from 23 to 61% (Minello et al. 1989b and references therein). The realized instantaneous mortality rate (RZMORT, Eqn. 3) was calculated by multiplying the baseline mortality rate by a size-based modifier (M_SZ), a habitat-based modifier (M_H), and a movement-based modifier (M_M). The size-based modifier decreased with increasing length, so that smaller shrimp had higher mortality rates (Eqn. 4, Figure 3.6a). The habitat-based modifier (M_H) was assigned 2.0 when shrimp were in water cells and 1.0 when shrimp were in vegetated cells. Because moving shrimp may be more vulnerable to predation, the movement-based modifier (M_M) increased with the number of cells moved in each tidal stage (NMOVED, Eqn. 5, Figure 3.6b). The probability of dying (PROBD) during a single tidal stage (6 hours) was calculated from the realized instantaneous mortality rate (Eqn. 6).

$$RZMORT = BZMORT * M_SZ * M_H * M_M \quad \text{Eqn. 3}$$

$$M_SZ = 53.092 * \text{shrimp_length}^{-1.0169} \quad \text{Eqn. 4}$$

$$M_M = (\text{nmoved} * .05) + .95 \quad \text{Eqn. 5}$$

$$PROBD = 1.0 - \text{EXP}^{-RZMORT} \quad \text{Eqn. 6}$$

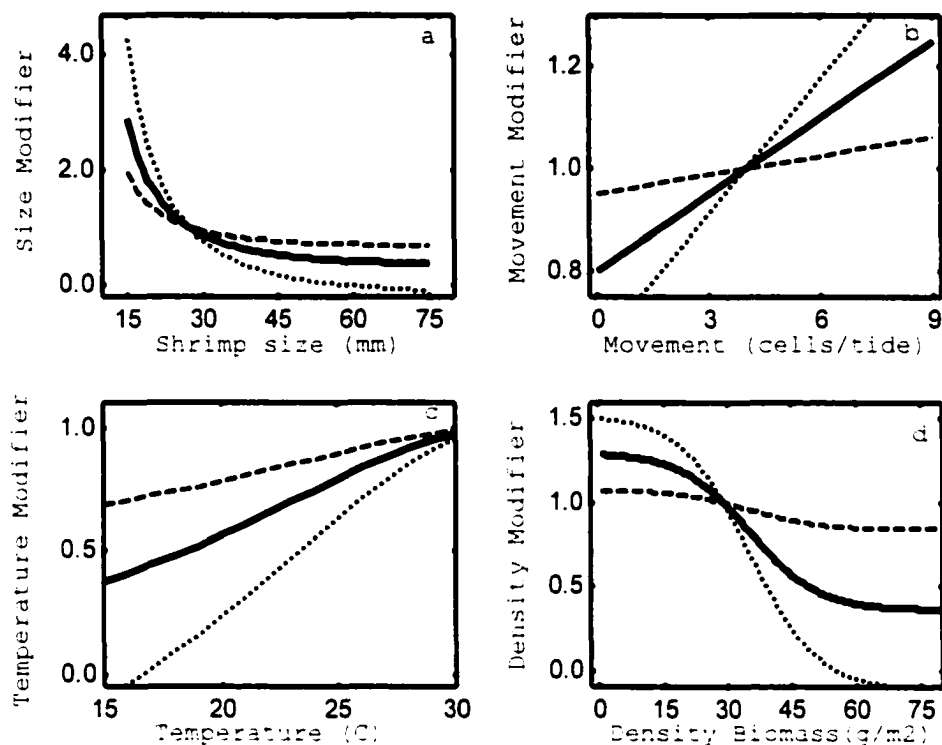


Figure 3.6. Mortality and growth and modifiers. a.) Size-dependent mortality modifiers. b.) Movement-dependent mortality modifiers. c.) Temperature-dependent growth modifiers. d.) Density-dependent growth modifiers. Solid lines represent baseline conditions (where the adjustment variable = 0). Dotted lines represent maximum sensitivity of shrimp to ecological process (where the adjustment variable = -0.75). Dashed lines represent minimum sensitivity of shrimp to ecological process (where the adjustment variable = 0.5 for temperature and size functions and 0.75 for the movement and density functions).

3.2.1.5 Growth

Simulated shrimp growth depended on temperature, habitat, and local shrimp density. Estimates for juvenile brown shrimp growth rates in the northern Gulf of Mexico vary from 0.1 to 3.3 mm / day (LDWF 1992 and references therein). Although shrimp growth varies according to habitat, local density, and shrimp size, most of the variation in growth is related to temperature. For this simulation, the average baseline growth rate (BGROW) was set to 1 mm / day. Each simulated shrimp was randomly assigned a baseline growth rate from a

normal distribution with mean = BGROW and standard deviation = $0.25 \cdot \text{BGROW}$. Minimum and maximum values were specified (minimum = 0.25, and maximum = 2.25) to eliminate unrealistically slow and fast growth rates. Shrimp maintained their baseline growth rate (BGROW) throughout the simulation. Realized growth rates (RGROW, Eqn. 7) varied throughout the simulation and were modified by a temperature-based modifier (G_T), a habitat-based modifier (G_H), and a density-based modifier (G_D).

$$\text{RGROW} = \text{BGROW} \cdot \text{G_T} \cdot \text{G_H} \cdot \text{G_D} \quad \text{Eqn. 7}$$

The growth modifiers (G_T, G_H, G_D) were derived from field and laboratory estimates of brown shrimp growth. Shrimp growth increases with temperature until maximum growth rates are achieved at optimal temperatures. For shrimp between 10 and 50 mm, growth rates are low (e.g., 0.08 - 0.46 mm / day) at 18°C and higher (e.g., 0.95 - 1.35 mm / day) at 32°C (Zein-Eldin and Aldrich 1965). The temperature modifier for growth was created from an equation used to describe temperature-dependent consumption for animals in warm water (Hewett and Johnson 1987, Eqn. 8, Figure 3.6c). Brown shrimp have slow growth

$$\text{G_T} = v^x \cdot e^{x \cdot (1.0 - v)} \quad \text{Eqn. 8}$$

Where

$$v = (T_M - \text{TEMP}) / (T_M - T_O)$$

$$T_M = \text{maximum temperature} = 40^\circ\text{C}$$

$$T_O = \text{optimal temperature} = 32^\circ\text{C}$$

$$\text{TEMP} = \text{simulated water temperature } (^\circ\text{C})$$

$$x = (w \cdot (1 + (1 + 4/y)^{-1})) / 400$$

$$w = \text{LN}(\text{THETA}) \cdot (T_M - T_O)$$

$$y = \text{LN}(\text{THETA}) \cdot (T_M - T_O + 2)$$

$$\text{THETA approximates a } Q_{10} \text{ function}$$

rates (0.77 mm/day) when in non-vegetated habitats with high shrimp densities; intermediate growth rates (0.95 mm/day and 1.03 mm/day) when in 50% *Spartina* with high shrimp densities or non-vegetated habitats with low shrimp densities, and fastest growth rates (1.41 mm/day) when in 50% *Spartina* with low shrimp densities (Minello and

Zimmerman 1991). From these estimates, the habitat modifier was assigned 2.0 for shrimp in vegetated cells and 1.0 for shrimp in water cells. The density modifier (G_D, Eqn. 9) was based on the above estimates and on an assumed relationship between growth rate and biomass density (Whaley 1997, Minello et al. 1989a, Figure 3.6d). Shrimp length was converted to mass before calculating biomass density within each cell (Eqn. 10). The relationship between mass and length was based on sex-specific weight-length relationships for brown shrimp (Parrack 1979). Biomass density for each cell was calculated by adding the mass of each shrimp located within the cell. Density was measured in biomass rather than individuals to account for the different competitive pressure exerted by a 15 mm shrimp verses a 70 mm shrimp.

$$G_D = 1.3 - 0.94 / (1 + e^{-(\text{biomass_density} - 1)}) \quad \text{Eqn. 9}$$

$$\text{shrimp_mass} = 0.0000037 * \text{shrimp_length}^3 \quad \text{Eqn. 10}$$

3.2.1.6 Corroboration

The density patterns of simulated shrimp were compared to density patterns measured in the field in order to corroborate the simulated movement behavior. The density patterns are an appropriate way to corroborate the model because simulated density patterns were not directly specified in the model. Rather, the density patterns emerged from combining movement rules with environmental input (such as temperature, tidal patterns, and habitat maps) and with biological inputs (such as growth rates, mortality rates, and biological rate modifiers).

3.2.1.7 Calculation of summary statistics

For each annual simulation, I calculated estuarine survival rates as the number of shrimp that survived to reach 70 mm. When shrimp exceed 70 mm, they generally begin offshore migrations by

moving through deeper channels and bays and into offshore water where they eventually become available to the fishery (Baxter et al. 1988, Fry et al. In Prep). Hence, the simulated estuarine survival rates reflect juvenile survival to the end of the estuarine-dependent life stage. Unless otherwise specified, recruitment refers to shrimp that survive to 70 mm.

Several statistics were calculated to describe the characteristics of shrimp that survived to 70 mm, and these statistics were contrasted with those of shrimp that did not survive. From data based on the surviving shrimp, I calculated the mean realized growth rate, the mean number of cells moved per tidal stage, and the mean percentage of time spent in vegetated cells. As a measure of local density, I also calculated the mean number of cellmates for all surviving shrimp. For comparison, I calculated these same statistics from data based on the non-surviving shrimp.

3.2.2 Effects of marshscape patterns

In order to examine the individual and combined effects of vegetation and edge on shrimp survival, I used a 2 x 2 factorial design with the simulation model. The amount of edge was the first factor, and the amount of vegetation was the second factor. I repeated this analysis under high density conditions where the initial number of postlarvae was increased from 100,000 to 300,000 and then to 600,000.

The same four categories that were used in the factorial design (i.e., low edge and high vegetation, high edge and high vegetation, high edge and low vegetation, and high edge and low vegetation) also represent snapshots in a simplified continuum of marsh disintegration. By evaluating the patterns of predicted survival along these four

habitat maps, hypotheses can be formed regarding the effect of marsh disintegration or restoration on juvenile brown shrimp survival.

3.2.3 Sensitivity analyses

3.2.3.1 Replicate simulations

I examined the variation produced by the stochastic elements in the simulation. In each annual simulation, there were several stochastic process. For example, the initial location of postlarvae, the probability of flooding, and the algorithm that randomly picked between tied cells with high expected growth rates were all random processes that varied with different random number seeds. In order to assess the variation created by these stochastic processes, I used five different random number seeds (-1111, -2222, -3333, -4444, and -5555) to create five replicates of the baseline conditions for each habitat map. I then compared means and coefficient of variation of the survival statistics.

3.2.3.2 Movement simulations

The formulation of movement in the model was likely important and highly uncertain. I therefore performed three additional simulations in which I modified the movement rules in order to assess their effect on the patterns of estuarine shrimp survival across the four habitat maps. In the first simulation, the movement rules were modified by omitting the size-dependency of movement. Motility (m) was set to 2 for all sizes of shrimp, which increased the distance evaluated by shrimp < 30 mm and decreased the distance evaluated by shrimp > 45 mm. In the second simulation, the movement rules were modified by doubling the size of the neighborhood ($n = 2 \cdot n$) of candidate cells available for movement. In the third simulation, the movement rules were modified by selecting a destination cell randomly rather than based on the best expected growth rate. I compared the

predicted survival across the four habitat maps for each of the three movement alternatives.

3.2.3.3 Monte Carlo simulations

In order to examine the effect of input parameters on simulated shrimp survival, I performed two Monte Carlo analyses. The Monte Carlo sensitivity analysis varied input parameters slightly around their mean, and the Monte Carlo uncertainty analysis varied input parameters over a realistic range. Both Monte Carlo analyses simultaneously varied input parameters in 100 repeated simulations. I used Latin hypercube sampling, a stratified random sampling technique, to ensure adequate representation of input probability distributions (Gardner et al. 1983, Rose et al. 1991).

I created four adjustment variables (MC_S, MC_M, MC_T, and MC_D) to use in the Monte Carlo analyses. These adjustment variables affected the strength of the rate modifiers (the size-based mortality modifier, the movement-based mortality modifier, the temperature-based growth modifier, and the density-based growth modifier, Figure 3.6). The rate modifiers were reset according to the value of the Monte Carlo adjustment variables (Eqns. 11 - 14). When the adjustment variable equaled zero, it had no effect on its respective rate modifier. As the value of the adjustment variable approached 1, the curve describing the relationship between the rate modifier and its predictor variable flattened, with a mean approaching 1. As the value of the adjustment variable approached -1, the curve became more steep. If a rate modifier became negative, it was reset to zero.

$$M_S = M_S + (MC_S * (1 - M_S)) \quad \text{Eqn. 11}$$

$$M_M = M_M + (MC_M * (1 - M_M)) \quad \text{Eqn. 12}$$

$$G_T = G_T + (MC_T * (1 - G_T)) \quad \text{Eqn. 13}$$

$$G_D = G_D + (MC_D * (1 - G_D)) \quad \text{Eqn. 14}$$

In both Monte Carlo analyses, 9 model inputs that affected mortality and growth rates were varied systematically. I varied the baseline mortality and growth rates (BZMORT, BGROW), the habitat-based rate modifiers (M_W, G_V), the Monte Carlo adjustment Variables (MC_S, MC_M, MC_T, MC_D), and the optimal temperature for shrimp growth (T_O, Eqn. 8). Within each annual simulation, the standard deviation of the baseline growth rates (BGROW) was set to $0.25 \cdot \text{BGROW}$.

The extent of variation in input parameters was different in Monte Carlo sensitivity and uncertainty analysis. In the sensitivity analysis, I set the coefficient of variation of the Monte Carlo Parameters to 5, and I specified the appropriate standard deviation for each variable ($\text{SD} = \text{CV} \cdot \text{mean} / 100$). Minimum and maximum values were set to $\pm 5 \cdot \text{SD}$ from the mean. The Monte Carlo sensitivity parameters were then selected from a normal distribution with specified mean and standard deviation (Table 3.2). In the uncertainty analysis, the bounds on the input parameters were chosen based on confidence in the accuracy of the estimates, rather than on a fixed departure from the mean. The Monte Carlo uncertainty parameters were then selected from a uniform distribution with specified means, minimums, and maximums (Table 3.3).

I used simple Pearson correlation coefficients between the input parameters and the percent recruitment to evaluate the sensitivity of the model to each input parameter. The greater the correlation between the parameter and percent recruitment, the more influence the parameter had in controlling the model behavior. Because I specified the inputs parameters to vary slightly around their mean, the results from the Monte Carlo sensitivity analysis showed the sensitivity of the model to input parameters regardless of the uncertainty about the

accuracy of the input parameter estimates. In the Monte Carlo uncertainty analysis, the input parameters varied according to the uncertainty in the estimates. Therefore, in the uncertainty analysis, the correlations between the parameters and percent recruitment suggested which portions of the model were most influenced by uncertainty in parameter estimates. The input parameters that were most closely correlated with survival should be more closely refined with additional information in subsequent studies.

Table 3.2. Description of parameter variation in the Monte Carlo Sensitivity Analysis. Input parameters varied slightly around their mean.

Variable	Monte Carlo Parameters		
	name	mean	St Dev
Baseline mortality rate	BZMORT	0.005	0.00025
Mortality modifier for water	M_W	2.000	0.10000
Strength of size-mortality function +1	M_S	1.000	0.05000
Strength of movement-mortality function +1	M_M	1.000	0.05000
Baseline growth rate	BGROW	1.000	0.05000
Growth modifier for vegetation	G_V	2.000	0.10000
Strength of density-growth function +1	G_D	1.000	0.05000
Strength of temperature-growth function +1	G_T	1.000	0.05000
Optimal temperature	T_O	32.000	1.60000

Table 3.3. Description of parameter variation in the Monte Carlo Uncertainty Analysis. Input parameters varied over a range that was determined by confidence in the accuracy of the estimates.

Variable		Monte Carlo Parameters		
		mean	min	max
Baseline mortality rate	BZMORT	0.005	0.003	0.007
Mortality modifier for water	M_W	2.000	1.000	3.000
Strength of size-mortality function	M_S	0.000	-0.750	0.500
Strength of movement-mortality function	M_M	0.000	-0.750	0.750
Baseline growth rate	BGROW	1.000	0.800	1.200
Growth modifier for vegetation	G_V	2.000	1.000	3.000
Strength of density-growth function	G_D	0.000	0.500	1.500
Strength of temperature-growth function	G_T	0.000	-0.750	0.750
Optimal temperature	T_O	32.00	28.000	36.000

3.3 Results

3.3.1 Corroboration

Published density estimates for estuarine brown shrimp show wide variation and are generally higher in early summer, higher in vegetation than water, and higher in edge than interior habitats. Mean brown shrimp densities can be as high as 28 shrimp per square meter of vegetation during May, and less than one shrimp per square meter of open water during summer or fall (Zimmerman et al. 1990). During peak densities in late spring, simulated shrimp were expected to be 10 times denser in vegetation than in water (Zimmerman et al. 1984). Brown shrimp densities in the northern Gulf of Mexico decline from the edge of the vegetation into the interior vegetation (Minello and Rozas, In press).

The simulated density patterns were similar to fine-scale density patterns observed in the northern Gulf of Mexico (Figure 3.7 and Figure 3.8). Simulated shrimp densities were higher in early spring than in summer (mean density at high tide for veg1 for Julian Day 90-120 = 15.93 shrimp/m² versus Julian Day 150-180 = 0.67 shrimp/m²); simulated densities were higher in vegetation than water (ratio of annual mean density during high tide in veg1, veg2, and veg3 versus wat1, wat2, wat3 = 9.66); and simulated densities were higher in edge than interior habitats (annual mean density during high tide in veg1 = 4.48 shrimp/m² versus veg3 = 1.61 shrimp/m²).

3.3.2 Characteristics of survivors

Surviving shrimp grew faster, moved less, spent more time in vegetation, and experienced slightly higher shrimp densities than shrimp that died during the simulation (Table 3.4). Surviving shrimp were defined as shrimp > 70 mm. Non-surviving shrimp were defined as shrimp that died during the simulation. Summary statistics were based

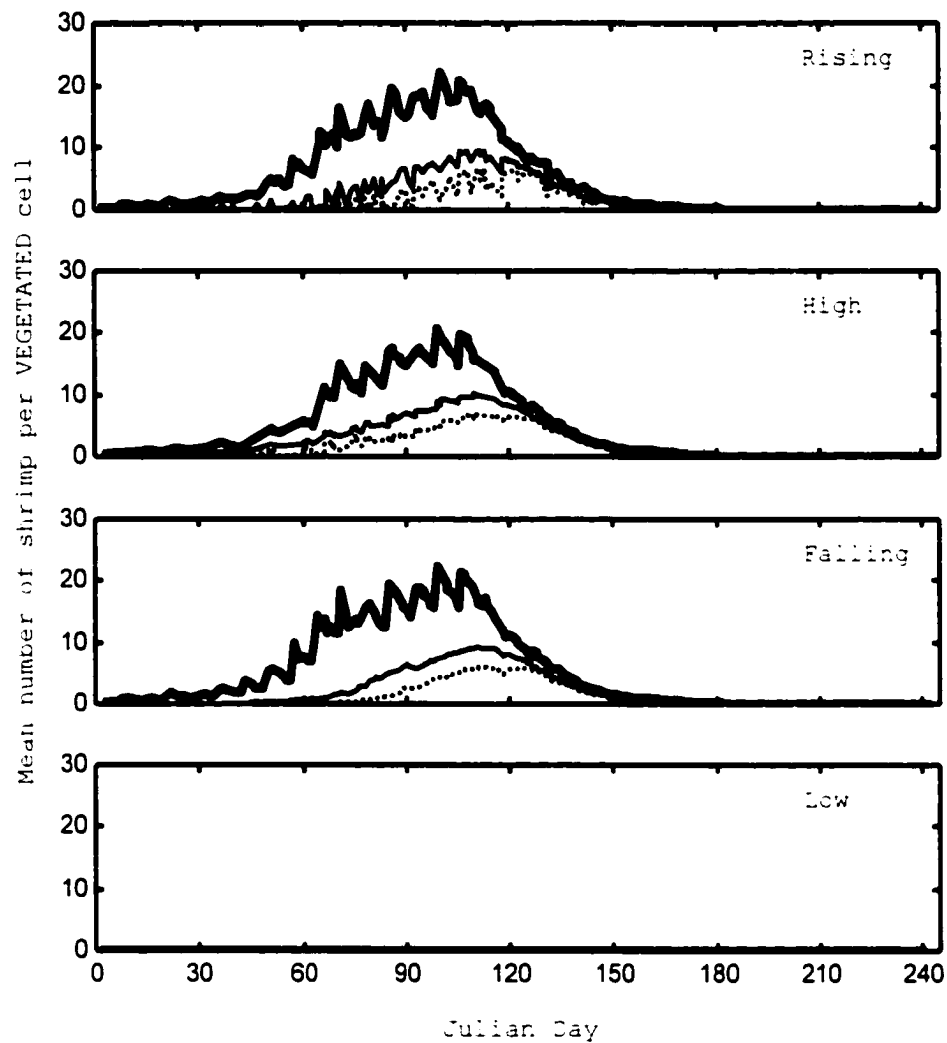


Figure 3.7. Average brown shrimp density in vegetated cells at each tidal stage for every day of the simulation. In general, heavier lines represent shrimp densities closer to the vegetation-water interface. Thick, solid lines represent shrimp densities in veg1 cells; thin, solid lines represent shrimp densities in veg2 cells; and dotted, solid lines represent shrimp densities in veg3 cells. These sample densities were obtained by running the model on the HE-HV map.

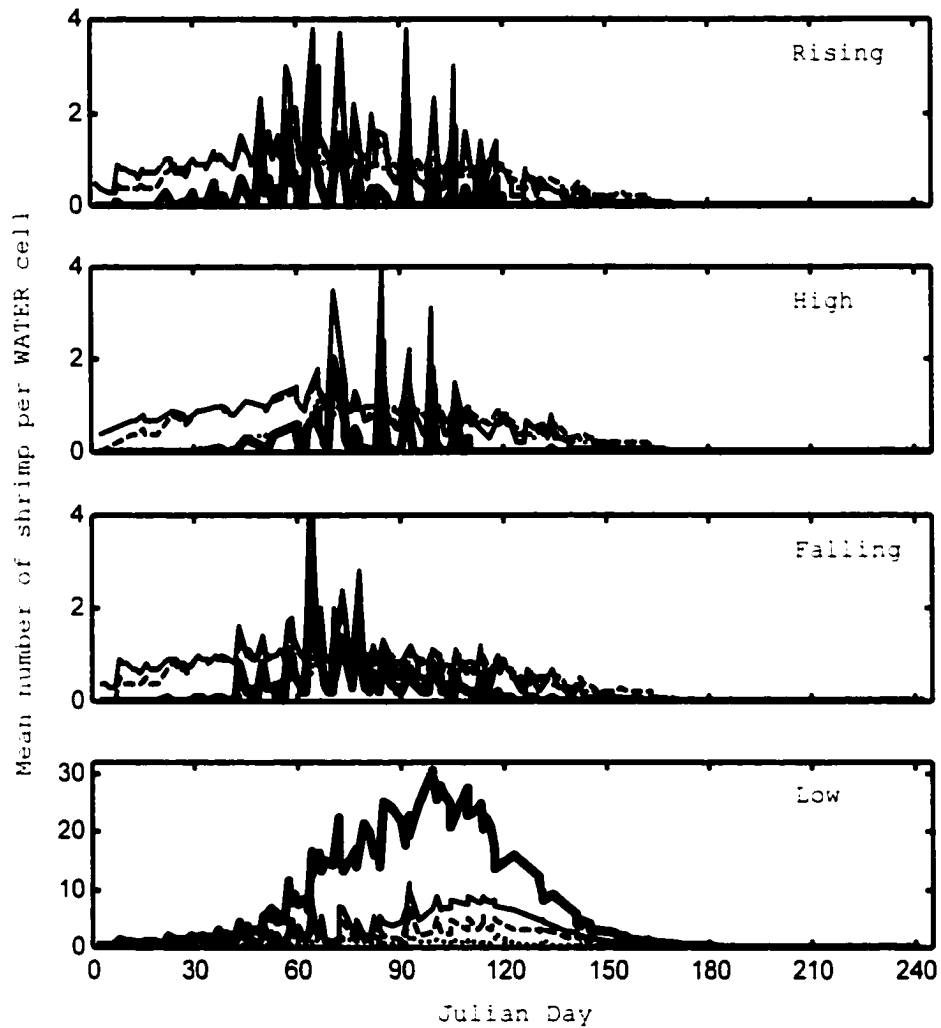


Figure 3.8. Average brown shrimp density in water cells at each tidal stage for every day of the simulation. In general, heavier lines represent shrimp densities closer to the vegetation-water interface. Thick, solid lines represent shrimp densities in water1 cells; thin, solid lines represent shrimp densities in water2 cells; thin, dashed lines represent shrimp densities in water3 cells; and thin, dotted lines represent shrimp densities in water>3 cells. These sample densities were obtained by running the model on the HE-HV map. Note change in Y axis in the Low tide figure.

on a simulation that was overlaid on the high edge and high vegetation map (HE-HV).

Table 3.4. Characteristics of surviving and non-surviving simulated brown shrimp. Statistics represents the results of a single simulation overlaid on the high edge, high vegetation habitat map.

	Survivors	Non-Survivors
Percent of total	30.22	69.78
Realized growth rate (mm / day)	1.35	0.71
Cells moved (per tide)	3.16	7.21
Time spent in vegetation (%)	73.21	46.88
Local density (shrimp / cell)	11.29	10.15

3.3.3 Marshscape patterns

Maps with more edge habitat supported higher shrimp survival to 70 mm (Table 3.5). Estuarine shrimp survival was higher in habitat maps with more edge habitat (roughly 30% survival in high-edge habitats versus roughly 23% survival in low edge habitats). The amount of vegetation affected simulated survival less than the amount of edge habitat. Habitat maps with more vegetation supported negligibly more survival (1 to 2% more) than did habitats with less vegetation. The high-edge habitat maps produced survivors that grew slightly faster, moved less, spent more time in the vegetation, and were in less dense configurations. If the habitat maps are viewed as a continuum of marsh disintegration, survival peaked in the intermediate levels of marsh disintegration when edge habitat was highest.

In most cases, high density conditions did not change the patterns of survival or patterns of survival characteristics documented in the four habitat maps under baseline densities (Table 3.5). Regardless of the initial postlarval density, high-edge habitat maps produced higher estuarine survival and shrimp that moved less and spent more time in vegetation. The baseline trend of high-edge maps producing higher realized growth rates and less dense assemblages of

shrimp became slightly diluted under the highest density conditions. Increasing density decreased survival, decreased growth rates, and slightly decreased time spent in vegetation. There was no clear trend between increasing density and the amount of shrimp movement.

Table 3.5. Summary statistics for simulations that explored the effects of marshscape patterns and stochastic variability on brown shrimp survival in habitats representing a continuum of marsh deterioration. Maps represent habitats with low edge (LE), high edge (HE), low vegetation:water ratios (LV), and high vegetation:water ratios (HV). Variability within each map represents stochastic processes in the model. The mean and covariance (shown in parenthesis) were produced by running the simulation 5 times with identical input parameters but with five different random number seeds. The statistics from the high density simulations were produced from a single run. The initial number of postlarvae in each annual simulation is shown in hundreds of thousands under the column marked "PLS".

	Habitat Maps				
	PLS	LE-HV	HE-HV	HE-LV	LE-LV
Survival (% of total)	1	23.52 (4.3)	31.04 (4.6)	28.82 (4.9)	22.81 (4.8)
	3	18.87	29.25	27.68	18.53
	6	15.81	23.09	21.66	15.03
Growth rate (mm/day)	1	1.33 (0.6)	1.37 (2.1)	1.34 (1.1)	1.33 (1.5)
	3	1.14	1.30	1.22	1.18
	6	0.97	1.08	1.00	1.00
Movement (cells/tide)	1	5.08 (9.1)	3.14 (5.1)	3.27 (6.0)	5.60 (9.0)
	3	6.65	3.56	3.56	6.38
	6	4.84	3.91	3.21	5.15
Time (hr) in vegetation	1	69.04 (3.3)	76.06 (5.0)	71.00 (4.5)	66.54 (5.1)
	3	68.12	76.45	74.62	67.46
	6	50.94	72.62	65.84	48.42
Density (shrimp/cell)	1	19.87 (4.1)	11.40 (3.5)	12.77 (6.2)	17.31 (7.3)
	3	51.90	33.87	36.68	43.02
	6	59.40	59.86	50.67	55.03

3.3.4 Sensitivity analyses

3.3.4.1 Replicate simulations

The stochastic processes in the model produced slight variation in the output variables (Table 3.5). The stochastic variation (produced by different random number seeds) was generally less than variation produced by different habitat maps. The coefficient of variation of all output was always less than 10. The most variable

prediction was the mean number of cells moved per tide (CV = 9.1 on LE-HV map), and the least variable prediction was the mean realized growth rate.

3.3.4.2 Movement simulations

Although altering the movement rules affected the magnitude of predicted survival, the pattern of the increased survival with increased amount of edge habitat was insensitive to changes in the movement rules (Table 3.6). Adjusting the movement rules so that movement was independent of size ($m = 2$ for all shrimp) did not change the trends in survival, but did disrupt the trend of high-edge maps producing survivors that spent more time in vegetation. Doubling the neighborhood ($n = 2 \cdot n$) of cells available for movement negligibly decreased the survival, but all trends that were described in the baseline scenario remained constant. Selecting a destination cell randomly rather than based on the best expected growth rate substantially decreased the survival in all 4 habitat maps. Random movement also disrupted the pattern of decreased densities in the high-edge habitats. Nevertheless, the high-edge maps invariably produced higher survival, with shrimp that moved less and had slightly higher growth rates.

3.3.4.3 Monte Carlo simulations

Both the Monte Carlo sensitivity analysis and the Monte Carlo uncertainty analysis showed that the model was most sensitive to temperature-related growth and to mortality rates (Table 3.7). Specifically, estuarine survival was higher in simulations with lower optimal temperatures for growth (T_O), higher sensitivity of growth rates to temperature (G_T), and lower baseline mortality rates (BZMORT). The consistency of the model results across the habitat maps suggests that the model was sensitive to the same parameters

regardless of habitat. The mean percent survival for the sensitivity and uncertainty analysis, for all combinations of input parameters, was higher on high-edge habitat maps.

Table 3.6. Summary statistics for simulations that explore the effect of movement rules on the patterns of estuarine shrimp survival in habitats representing a continuum of marsh deterioration. In the first simulation, movement rules were modified so that shrimp motility would remain constant regardless of shrimp size ($m = 2$). In the second simulation, the movement rules were modified by doubling ($n = 2 \cdot n$) the size of the neighborhood of cells available for movement. In the third simulation, the movement rules were modified by selecting a destination cell randomly rather than based on the best expected growth rate. Maps represent habitats with low edge (LE), high edge (HE), low vegetation:water ratios (LV), and high vegetation:water ratios (HV).

		Habitat Maps			
		LE-HV	HE-HV	HE-LV	LE-LV
Estuarine survival rate (% of total)	$m = 2$	24.75	29.67	27.44	22.21
	$n = n \cdot 2$	21.69	27.64	28.37	21.72
	random	9.43	15.19	12.37	9.53
Realized growth rate (mm/day)	$m = 2$	1.36	1.37	1.36	1.34
	$n = n \cdot 2$	1.37	1.42	1.39	1.37
	random	1.08	1.13	1.09	1.06
Movement (cells/tide)	$m = 2$	5.39	4.14	3.83	6.95
	$n = n \cdot 2$	9.19	5.09	5.78	8.18
	random	8.09	4.15	5.70	7.36
Time in vegetation (%)	$m = 2$	75.07	76.31	72.16	69.92
	$n = n \cdot 2$	74.14	76.25	76.62	70.43
	random	19.06	31.00	22.53	17.52
Local density (shrimp/cell)	$m = 2$	25.66	12.77	13.40	19.73
	$n = n \cdot 2$	21.62	9.58	11.51	17.32
	random	6.43	6.04	4.39	5.40

The correlations between input parameters and recruitment did not change dramatically between the sensitivity analysis and the uncertainty analysis. This suggests that our uncertainty in parameter estimates was not driving the model results. When I factored our uncertainty about parameter estimates into the Monte Carlo analysis, there were only slight departures from the sensitivity analysis: a small increase in the variation attributed to changes in the strength of the temperature-dependent growth modifier, and a small decrease in the variation attributed to changes in the optimal growth rate (Table 3.7).

Table 3.7. Pearson's correlation coefficients between the percent survival and input parameters and output variables from the Monte Carlo simulations in both the Sensitivity Analysis (S) and Uncertainty Analysis (U). Maps represent habitats with low edge (LE), high edge (HE), low vegetation:water ratios (LV), and high vegetation:water ratios (HV). Coefficients with absolute values greater than 0.50 are shown in bold. See Tables 3.2 and 3.3 for an explanation of the abbreviations used with the input parameters. The units for the output information are as follows: realized growth rate (mm/day), time in vegetation (d), local density (shrimp/cell), and movement (cells/tide).

	Habitat Maps							
	LE-HV		HE-HV		HE-LV		LE-LV	
	S	U	S	U	S	U	S	U
% Survival-Mean	23.51	21.62	30.26	26.76	28.71	25.60	22.70	21.36
% Survival-SD	4.87	12.72	5.18	14.13	5.16	13.92	5.02	12.92
BZMORT	-0.31	-0.35	-0.35	-0.38	-0.33	-0.37	-0.35	-0.34
M_W	-0.20	-0.31	-0.18	-0.28	-0.22	-0.31	-0.19	-0.33
M_S	-0.01	-0.12	-0.07	-0.11	-0.09	-0.08	-0.08	-0.14
M_M	0.07	0.16	0.06	0.07	0.06	0.05	0.13	0.14
BGROW	0.20	0.17	0.22	0.18	0.21	0.15	0.20	0.18
G_V	0.11	0.18	0.16	0.16	0.05	0.15	0.13	0.17
G_D	0.13	0.05	0.09	0.05	0.09	0.05	0.07	0.03
G_T	0.28	0.52	0.32	0.55	0.37	0.54	0.31	0.52
G_O	-0.85	-0.54	-0.81	-0.54	-0.81	-0.54	-0.81	-0.54
Growth rate	0.88	0.59	0.88	0.63	0.86	0.60	0.86	0.59
Time in vegetation	0.16	0.21	-0.08	-0.08	0.02	0.00	0.29	0.31
Local density	0.39	0.44	0.36	0.73	0.35	0.74	0.57	0.62
Movement	0.42	0.75	0.44	0.76	0.25	0.77	0.22	0.71

3.4 Discussion

3.4.1 Shrimp movement

Although movement rules were based on the results of field studies, they probably represent the most speculative aspect of the model. The general pattern of migration over a shrimp's entire life cycle is well-documented, but very little is known about how individual shrimp move on fine spatial and temporal scales. Part of the reason so little is known about small-scale movement patterns is that is difficult to track small, aquatic organisms that molt (and lose identification tags). There are tagging studies that examine shrimp movement (e.g., Sheridan et al. 1989, Clark et al. 1974), but

these generally track movement on a weekly or monthly basis and offer little insight into daily-scale movement patterns.

The magnitude of movement that resulted from these movement rules was consistent with the conclusions reached in a recent study that used size and density estimates along with an analysis of stable isotopes to explore brown shrimp movement and residency (Fry et al. In Prep). Fry et al. sampled shrimp 10 mm to 129 mm total length from a Louisiana salt marsh that neighbors the habitat maps, and they found strong differences in stable isotope signatures between geographically-close but ecologically-different habitats. This suggests that for juvenile brown shrimp within the estuary, there is only a small amount of movement between habitats. Shrimp in marsh ponds and shallow channels were largely resident. Average residence time in small marsh ponds was estimated at approximately 72d. Fry et al. speculate that small juvenile shrimp move more in sub-optimal habitats (deep channels and bays), but move less when they reach optimal habitat (marsh ponds and shallow channel margins).

The movement of shrimp in the simulation model was consistent with the speculations reached in Fry et al. (In Prep) about the movement of shrimp in Louisiana marshes. Simulated shrimp spent the majority of the time moving small distances near optimal edge habitats. When simulated shrimp encountered open water environments, they moved more quickly until they again reached vegetated edge habitat.

3.4.2 Edge habitat and predicted survival

The pattern of increasing shrimp survival with increasing edge habitat remained consistent through all simulations. High-edge habitats produced higher simulated survival under baseline conditions, under high (3x) and extremely high (6x) initial number of shrimp, when

movement was not related to size, when potential movement distance was doubled, and when movement was random. High-edge habitats also produced higher mean simulated survival in the uncertainly analysis, where input parameters were simultaneously varied across a range of likely values.

The simulated estuarine survival in this model was most highly correlated with temperature-related growth. Future studies that attempt to predict the magnitude of recruitment should incorporate accurate information about the relationships between growth and temperature. A more precise description of growth and temperature was not required in this study because I was interested in trends in recruitment patterns across different habitats, rather than in the sheer magnitude of recruitment. Even under extreme simulated conditions when growth was very sensitive to temperature ($G_T = 0.75$) and when the optimal temperature for growth was low ($T_O = 28^\circ\text{C}$), survival was still higher in maps with more edge habitat.

The pattern of increased shrimp survival with increased edge habitat is consistent with correlative studies and with other simulations at larger scales. Browder et. al. (1989) described a positive correlation between annual shrimp catch and an annual estimate of the amount of edge habitat. Faller (1979) described a correlation between shrimp harvest and the area of marsh that has a threshold amount of edge habitat. Minello and Rozas (In Press) used fine-scale density patterns to simulate the effect of adding creeks to solid vegetation, and they predicted that increasing the number of creeks would increase shrimp densities (until a maximum was reached).

The characteristics of surviving shrimp offer evidence of what may cause the patterns of shrimp survival documented in descriptive

and correlative studies. Field studies have suggested that shrimp are generally concentrated in edge habitat, but how this trend translated into higher survival rates was speculative. The model analysis showed that simulated shrimp which survived until 70 mm had higher growth rates, spent more time in vegetation, and moved less than shrimp that did not survive to 70 mm. The simulated survivors in high-edge habitats, as compared to low-edge habitats, moved less, spent more time in vegetation, and were in less dense configurations. This suggests that high-edge habitat increases survival by providing shrimp direct access to the benefits of vegetated marsh without encountering high local densities that may be common in low-edge habitats.

3.4.3 Management implications

Severe mortality rates in the early life stages of highly-fecund organisms limit the range of percent survival that can be triggered by environmental conditions. For example, if the biological rates for simulated shrimp in this model were set at the optimal conditions experienced in vegetation (high growth and low mortality rates) for 100% of the time, simulated shrimp survival increased to approximately 50%. If the biological rates were set to open water conditions (low growth and high mortality rates) for 100% of the time, simulated shrimp survival decreased to approximately 10%. Even under these unrealistically good and bad conditions, the maximum range in predicted survival was limited to 40%.

Small changes in the percent of estuarine survival can translate into significant changes in recruitment to the fishery. The spatial extent of this simulation was small (10,000 m²), but if allowed to represent average marsh conditions, very rough predictions can be made about changes in survival over larger spatial scales. For example, under baseline conditions, approximately 5,000 more shrimp survived in

high-edge habitats than in low-edge habitats. If this increase in survival is translated onto the scale of an estuary or bay system (200,000 ha) rather than a habitat patch (1 ha), the difference in survival between high-edge habitats and low-edge habitats may increase to 1 million shrimp.

Because brown shrimp survival appears to be related to edge habitat, the management of the species should be extended from protecting the spawning stock through catch regulations to also protecting the estuarine life stages through habitat conservation and restoration. The dome-shaped relationship between edge habitat and marsh disintegration (Browder et al. 1986) suggests the productive high-edge habitats will occur during intermediate levels of marsh disintegration. If marsh disintegration continues past intermediary levels, estuarine marshscapes may shift from predominantly high-edge habitats to low-edge habitats (Browder et al. 1989). The results of this study suggest such a shift would be accompanied by a decrease in the estuarine production of shrimp. The growing interest in defining essential fish habitat should be accompanied by continued analysis of spatially-explicit processes.

Given the potential importance of edge habitat to the survival of brown shrimp, it is important to examine the relationships between estuarine-dependent organisms and the quantity as well as quality of edge habitat. In this simulation model, edge habitat acted as a bridge between the vegetation and open water, yet in the northern Gulf of Mexico, the interface between vegetation and water often acts as a barrier rather than bridge. For example, natural marshscapes are often fragmented by dredged canals or pipelines (Tabberer et al. 1985). Elevated spoil banks, which are impenetrable by strictly aquatic organisms, often line these canals. Though a few studies

(e.g., Rozas and Reed 1994) have investigated relationships between estuarine organisms and landscapes impacted by artificial canals, the quality of habitat produced by different edge environments needs to be further explored.

The results of this study offer a rationale to preserve habitats with natural edge. Simulated brown shrimp survival was higher in habitats with high-edge than in habitats with low-edge. Preserving habitats with natural edge may benefit other fisheries because shrimp represent an estuarine-dependent life-history strategy that is common to many ecologically and commercially-important species (e.g., blue crabs, red drum). Many fish in the estuaries display similar density patterns to brown shrimp. The most common small estuarine fishes are found highly concentrated in marsh edges (Baltz et al. 1993). The marshscape patterns that influenced simulated shrimp survival may therefore also influence the survival of other estuarine-dependent species.

3.5 References

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CHAPTER 4. SUMMARY AND CONCLUSIONS

This dissertation used statistical and simulation modeling to examine brown shrimp population dynamics in the northern Gulf of Mexico. Brown shrimp were chosen as a study organism because they represent a life history strategy that is common to many ecologically-important and commercially-exploited species and because there is extensive data available. Two analytical approaches were used to examine brown shrimp population dynamics. Chapter 2 used three statistical techniques to examine correlative relationships between annual, stage-specific, brown shrimp abundance estimates and environmental factors. Chapter 3 combined a fine-scale geographic analysis with a spatially-explicit, individual-based simulation model to examine the relationship between juvenile shrimp survival and marsh characteristics (i.e., vegetation:water ratios and amount of edge habitat).

Chapter 2 used stepwise multiple regression, Bayesian model averaging, and generalized additive models to examine relationships between annual brown shrimp abundance and environmental factors. I analyzed a dataset that included 28 years (1970-1997) of stage-specific brown shrimp abundance estimates (postlarvae, early juveniles, late juveniles, and adults) and a suite of environmental variables (water temperature, salinity, water clarity, river flow, precipitation, acres of marsh > 10 ppt, water level, and atmospheric weather conditions).

Bayesian model averaging and stepwise multiple regression resulted in models with similar explanatory power, but Bayesian model averaging suggested fewer linear predictors. Generalized additive models did not suggest non-linear relationships among stage-specific abundance estimates. Interannual variation in postlarval abundance

was not well described by predictor variables in any of the statistical analyses. Variation in juvenile abundance was partially described by environmental variables such as temperature, water clarity, and water level. Annual variation in adult abundance was well described by early juvenile abundance, salinity, and temperature.

Environmental variables indicative of estuarine conditions were among the significant predictors of shrimp abundance at every life stage. Water temperature was positively correlated with shrimp abundance during all but the postlarval stage. Decreased water levels were associated with high juvenile shrimp abundance. Increased salinity was positively correlated with increased adult shrimp abundance.

Three observations from Chapter 2 suggested that estuarine conditions are critical in determining the year-class strength of brown shrimp. The first observation was the strong correlation between juveniles and adults. Variation in the early juvenile index explained more than half of the variation in adult abundance. The second supporting observation was the lack of correlation between early life stages (i.e., postlarval and juvenile stages) and previous life-stage abundances. The third supporting observation was the important role of environmental variables in explaining juvenile abundance. These results combine to suggest that, during the last 30 years, adult shrimp abundance was greatly influenced by estuarine conditions.

The results of Chapter 2 suggest that identifying mechanisms that regulate juvenile production within estuaries will be a critical step in the ongoing effort to effectively manage Louisiana's shrimp resource. Juvenile shrimp production may be the critical component in determining the year-class strength of brown shrimp in Louisiana, and

estuarine conditions are likely to affect annual fishery recruitment. Although some estuarine conditions can not be managed (e.g., temperature, rainfall), there are several anthropogenic impacts that can be mitigated. Those estuarine processes that can be managed (e.g., fresh water diversions, restoration of natural hydrology, wetland loss and fragmentation) should be further investigated.

The results of Chapter 2 also suggest that spatial components within the estuary should be examined. Environmental predictors alone described less than half of the interannual variation in juvenile shrimp abundance. Some of the unexplained variation in the statistical models can possibly be explained by small-scale spatial variation in habitat, which has not been traditionally included in correlative analysis. Because coastal Louisiana has undergone substantial wetland loss and fragmentation over the past 50 years, spatial analysis of the associations between estuarine habitat and shrimp growth and survival are particularly relevant.

The results in Chapter 2 have several important management implications. First, they suggest that sustainable management practices can not be solely limited to regulating catch. At current stock levels, annual production appears to be more regulated by environmental conditions within the estuary rather than by postlarval arrival to the estuary. Second, they suggest focusing future investigations on processes that affect juvenile growth and survival in estuaries. A more thorough understanding of the interaction between estuarine dynamics and shrimp survival will not only help effectively manage the shrimp fishery, but may yield insights into the management of other commercially-important, estuarine-dependent species.

Chapter 3 was designed to examine in greater detail the juvenile life stage and the spatial components of habitat that were recommended for further study based on the statistical analysis of Chapter 2. Specifically, Chapter 3 used a fine-scale, spatially-explicit, individual-based simulation model to examine the effects of vegetation and edge habitat on juvenile brown shrimp survival. The model was overlaid on four habitat maps which represented snapshots in a simplified continuum of marsh disintegration: low edge and high vegetation, high edge and high vegetation, high edge and low vegetation, and low edge and low vegetation.

The model developed in Chapter 3 simulated juvenile shrimp while they were associated with the marsh. Postlarval shrimp (approximately 15 mm total length) entered the simulation in weekly cohorts. Each annual simulation began on January 1 and ended on September 1. Individual shrimp were tracked from the time they entered the marsh as postlarvae until they either died or reached 70mm. The simulation contained both physical and biological components. The physical components included water temperature, tidal stage, and habitat patterns. The biological components included mortality, growth, and movement.

Simulated shrimp survival was compared across the four habitat maps. Individual characteristics (such as survival status, realized growth rates, and percentage of time in vegetation) were recorded for each shrimp. Model predictions for population statistics (such as mean percent survival, mean realized growth rates) were calculated under baseline and high shrimp densities for each habitat map.

The model was corroborated by comparing the simulated shrimp density patterns with fine-scale density patterns observed in estuaries of the northern Gulf of Mexico. Variation produced by

stochastic elements in the model was examined by comparing replicate simulations with different random number seeds. The sensitivity of the model to shrimp movement was examined by changing the movement rules and comparing simulated survival. In order to examine the effect of input parameters on simulated shrimp survival, I performed two Monte Carlo analyses. The Monte Carlo sensitivity analysis varied input parameters slightly around their mean, and the Monte Carlo uncertainty analysis varied input parameters over a realistic range.

The simulated density patterns were similar to fine-scale density patterns observed in the northern Gulf of Mexico. Surviving shrimp grew faster, moved less, spent more time in vegetation, and experienced slightly higher local densities than shrimp that died during the simulation. The pattern of increased shrimp survival with increased edge habitat predicted under baseline conditions was robust. While the absolute magnitude of survival differed, higher survival was always associated with higher edge under high shrimp densities, under alternative rules about movement, and under realistic uncertainty in model inputs.

Because the simulated estuarine survival in this model was most highly correlated with temperature-related growth, future studies that attempt to predict the magnitude of shrimp recruitment should incorporate accurate information about the relationships between growth and temperature. A more precise description of growth and temperature was not required in this study because I was interested in trends in recruitment patterns across different habitats, rather than in the sheer magnitude of recruitment. Even under extreme simulated conditions when growth was very sensitive to temperature and when the optimal temperature for growth was low, survival was still higher in maps with more edge habitat.

The characteristics of surviving shrimp offer mechanisms which may help explain the general pattern of increasing shrimp survival with increasing edge habitat that is documented in descriptive and correlative studies. Simulated shrimp that survived until 70 mm had higher growth rates, spent more time in vegetation, and moved less than shrimp that did not survive to 70 mm. The simulated survivors in high-edge habitats, as compared to low-edge habitats, moved less, spent more time in vegetation, and were in less dense configurations. This suggests that high-edge habitat increases survival by providing shrimp direct access to the benefits of vegetated marsh without encountering high local densities that may be common in low-edge habitats.

Because brown shrimp survival appears to be related to edge habitat, the management of brown shrimp should be extended from the current approach of protecting the spawning stock through catch regulations to also protecting the estuarine life stages through habitat conservation and restoration. Productive high-edge habitats occur during intermediate levels of marsh disintegration, and if marsh disintegration continues past intermediary levels, estuarine marshscapes may shift from predominantly high-edge habitats to low-edge habitats. The results of this study suggest such a shift would be accompanied by a decrease in the estuarine production of shrimp. The growing interest in defining essential fish habitat should be accompanied by continued analysis of spatially-explicit processes.

Given the potential importance of edge habitat to the survival of brown shrimp, further investigations are recommended to examine the relationships between estuarine-dependent organisms and the quantity as well as quality of edge. In the simulation model, edge habitat acted as a bridge between the vegetation and open water, yet in the

northern Gulf of Mexico, the interface between vegetation and water often acts as a barrier rather than bridge. For example, natural marshscapes are often fragmented by dredged canals or pipelines. Elevated spoil banks, which are impenetrable by strictly aquatic organisms, often line these canals. The quality of habitat produced by these different edge environments needs to be further explored.

The results of Chapter 3 offer rationale to preserve habitats with natural edge and to restore habitats without natural edge. Simulated brown shrimp survival was higher in habitats with high-edge than with low-edge. Preserving habitats with natural edge may benefit other fisheries because shrimp represent an estuarine-dependent life strategy that is common to many ecologically or commercially-important species. The marshscape patterns that influenced simulated shrimp survival may therefore also influence the survival of other estuarine-dependent species.

The statistical modeling in Chapter 2 and the simulation modeling in Chapter 3 offer a new perspective on brown shrimp population dynamics, as well as a new combination of quantitative tools for analyzing the population dynamics of estuarine-dependent organisms. Chapter 2 presented the statistical analysis of the relationships among life-stage abundances and environmental variables. These analyses identified the important role of estuarine conditions and juvenile abundance in determining annual brown shrimp recruitment to the fishery. Chapter 3 presented the results of the individual-based modeling of shrimp survival for the four habitat maps. These analyses quantified the relationship between the spatial arrangement of marsh habitat and juvenile brown shrimp growth and survival. These results highlight the important role of marsh habitat in determining the recruitment of an estuarine-dependent species.

APPENDIX: LETTER OF PERMISSSION

McClymont, Paul


To: Heather Lynn Haas
Cc: Heyman, Judy
Subject: RE: Manuscript J16250

Dear Heather

Permission is granted for use of the material, as stated below, provided that acknowledgement is given to the source. Since the manuscript has not yet been published, we request that your dissertation not be made generally available until publication of your manuscript has taken place.

A signed copy of this permission will also be sent.

Sincerely


Paul McClymont
Business Manager
NRC Research Press
paul.mcclymont@nrc.ca
Phone: 613-993-9093
Fax: 613-952-7656

-----Original Message-----

From: Heather Lynn Haas [mailto:hhaas@lsu.edu]
Sent: Monday, October 15, 2001 3:43 PM
To: McClymont, Paul
Subject: Re: Manuscript J16250

Dear Paul,

I am writing regarding 'Environmental and biological factors associated with stage-specific brown shrimp abundances in Louisiana: applying a new combination of statistical techniques to long-term monitoring data', written by Heather L. Haas, E. Conrad Lamon III, Kenneth A. Rose, and Richard P. Shaw. This manuscript (J16250) has been accepted for publication in the Canadian Journal of Fisheries and Aquatic Sciences.

I am writing to request a signed release from CJFAS so that I can use this manuscript in my dissertation.

Thank you.

Heather Haas
2240 Tulip Street
Baton Rouge, LA 70806
225-387-1319

At 11:31 AM 10/15/2001 -0400, you wrote:

>Hello Heather

>

>You need to get permission from us/me. Send me an E-mail with complete
>author and title information and stating that it has been accepted for
>publication in CJFAS and state the purpose of use. I will reply with
>permission for inclusion in your dissertation. If you require a signed copy,
>I will print out your E-mail and sign and mail back to you. This is the
>fastest method.

1

VITA

Heather Lynn Haas was born on December 4, 1968, in Schnecksville, Pennsylvania. Heather is the daughter of Sharon K. Haas and Harry W. Haas. After graduating from Parkland High School, Heather entered the Western College Program of Miami University, Oxford, Ohio. She graduated in 1992 with a bachelor of philosophy degree in Interdisciplinary Studies, with a focus in Biological and Cultural Diversity. Following graduation, Heather worked for three years as a science instructor at the Newfound Harbor Marine Institute, Big Pine Key, Florida. In 1995, Heather returned to school at the University of Massachusetts Dartmouth, where she earned a master of science degree in Marine Biology. Heather came to Louisiana State University during the summer of 1997, and in December 2001 she will receive the Doctor of Philosophy degree with a Major in Oceanography and Coastal Sciences and a minor in Applied Statistics.

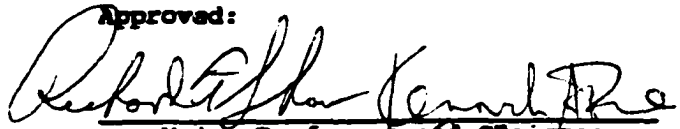
DOCTORAL EXAMINATION AND DISSERTATION REPORT

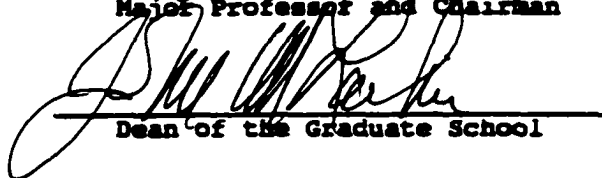
Candidate: Heather Lynn Haas

Major Field: Oceanography and Coastal Sciences


Title of Dissertation: Statistical and Simulation Modeling of Brown Shrimp Population Dynamics in the Northern Gulf of Mexico


Approved:



Major Professor and Chairman


Dean of the Graduate School

EXAMINING COMMITTEE:


R.E. Kline


William E. Kline


James P. Cleary (dissent)

Date of Examination:

November 2, 2001