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COLORADO RIVER FLOW RELATIONSHIPS TO BAY HEALTH: MODELING BENTHIC PRODUCTIVITY

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ABSTRACT

The Lavaca-Colorado Estuary is a major estuarine system along the Texas coast that provides major economic benefit to the region by supporting a variety of agricultural, residential, industrial, and recreational functions. The Matagorda Bay Health Evaluation (MBHE) component of the LCRA/SAWS Water Project (LSWP) Study Plan was created to assess the environmental effects that could result from further changes to inflow patterns in the Matagorda Bay system. To support this assessment, a bio-energetic model, calibrated using a long-term data set of benthic biomass, was run to relate macrobenthic biomass to salinity within the estuary. This model was applied to the current study to assess the role of freshwater inflow in controlling benthic productivity. Benthic productivity was calculated for two groups of macrobenthos, suspension feeders and deposit feeders; in two bays, Lavaca Bay and Matagorda Bay. Simulations of the Lavaca-Colorado Estuary, based on a calibration of data from 1991 - 1996, fit the observed data relatively well. However, following the year 2000, simulations predicted a much higher benthic biomass than in observed data. The increase in benthic biomass is likely explained by the decrease in predator populations, particularly blue crabs, which reduced loss to predation. Simulations on deposit and suspension feeder biomass exhibited responses due to natural and simulated salinity changes in both bay systems. As salinity increased, deposit feeding biomass increased while suspension feeding biomass decreased. Total biomass in Lavaca Bay was found to increase as salinity increased, which indicates that reduced inflow rates in this bay would not harm the benthic community. Total biomass concentration in Matagorda Bay decreased initially with increasing salinity but then gradually increased. Thus, reducing the freshwater inflow may cause the upper river communities to take on downstream community appearance. This effect is probably due to the benthic community acclimating to the elevated salinity or more salt tolerant species populating the area. It is concluded that freshwater inflow plays an important role in maintaining the observed character of estuarine productivity through the combined effects of the frequency, duration, timing, and magnitude of inflow, particularly during droughts or low-flow periods.

1. INTRODUCTION

1.1. Background

        The Lavaca-Colorado Estuary is a major estuarine system along the Texas coast that provides major economic benefit to the region by supporting a variety of agricultural, residential, industrial, and recreational functions. As a result of these human endeavors, the estuary has undergone dramatic changes in recent history (even resulting in a name change). Alterations in hydrology, circulation, and freshwater inflows have occurred due to anthropogenic activities, including human modifications of inflow to several major tributaries that supply the estuary, particularly the Lavaca River and the Colorado River. Prior to 1990, the name of the estuary was the Lavaca-Tres Palacios Estuary because the main supply of freshwater inflow came from the Lavaca and Tres Palacios rivers. After a diversion channel was completed in 1990 to redirect water from the Colorado River into Matagorda Bay, the Colorado River surpassed the Tres Palacios River as a major supply of freshwater to the system, and the name changed accordingly to the Lavaca-Colorado Estuary. This is just one example of the magnitude of change that has occurred with respect to inflow since 1990.

        Another change occurred in 1991 when the Colorado River was diverted into the eastern arm of Matagorda Bay via a flood diversion channel. In 1992, a dam was built in the river channel below the point of diversion. This project diverted Colorado River water that might have flowed into the Gulf of Mexico into the eastern arm of Matagorda Bay.

        The lower Colorado River basin supports a diverse ecological community that relies heavily on the quality and quantity of water moving through the system. The wide range of ecosystem components and ecological conditions associated with communities in the lower Colorado River and Matagorda Bay means that understanding its processes is quite challenging. The LCRA-SAWS Water Project (LSWP) has the potential to alter the flow regime for the lower Colorado River and, consequently, Matagorda Bay. The Matagorda Bay Health Evaluation (MBHE) has been established to assess the potential impact of these flow regime modifications. The present study is an integral part of the MBHE's objective to assess potential impacts/benefits on the aquatic resources of

Matagorda Bay with and without the project and also quantify the condition of the aquatic environment under different flow scenarios to satisfy federal and state permitting requirements and ensure that the environmental principles set forth for this project satisfied.

1.2. Benthic Studies

Historical studies have stressed the importance of freshwater inflow to estuarine system, and that inflow is a major factor driving estuary functioning and health (Chapman 1966, Kalke 1981). Inflows serve a variety of important functions in estuaries, including the creation and preservation of low-salinity nurseries, sediment and nutrient transport, allochthonous (outside) organic inputs, and movement and timing of critical estuarine species (Longley 1994). Benthic macrofauna (> 0.5 mm) are especially sensitive to changes in inflow, and can be useful in determining its effects on estuarine systems over time (Kalke and Montagna 1989).

Benthic macroinvertebrates are established indicators of water quality in both freshwater and marine systems, and can highlight different aspects of the environment, including pollutant levels, hypoxia/anoxia, turbidity, and salinity changes (Oglesby 1967, Merritt and Cummins 1984). Relatively sessile and long-lived, benthic macroinvertebrates can reveal temporal changes in the environment that simple hydrographic measurements and chemical analysis can either not determine, or are impractical to use because of sizeable monetary and time constraints. Ubiquitous and relatively inexpensive to collect and analyze, bnethic macrofauna are excellent tools in assessing both short- and long-term environmental conditions (Montagna and Kalke1992, 1995).

While many early studies in Texas estuaries focused on oyster reefs, recent benthic work has concentrated on the soft-bottom dwelling macrofauna and their relationship to several key environmental variables, including freshwater inflow, salinity, dissolved oxygen, depth, and sediment type (Kalke and Montagna 1991, Engle and Summers 2000). While grain size and type, as well as temperature, play significant roles in benthic macroinvertebrate community structure, freshwater inflow and corresponding changes in salinity are the primary factors controlling the distribution of marine and

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freshwater organisms within an estuary (Mannino and Montagna, 1994, Kalke and Montagna 1989, 1991, 1992, Attrill et al. 1996, Montagna et al. 2002). While sediment type and depth are important to benthic organisms, they are relatively minor factors controlling benthic community structure in most Gulf of Mexico estuaries when compared with salinity (Engle and Summers 2000). Depth, in particular, is rarely a key factor because most estuaries in Texas are relatively shallow (Baird et al. 1996, Engle and Summers 2000).

Benthic fauna are critical intermediaries in estuarine food webs and affect substrate structure, sediment, and water chemistry as well. Thus, a change in their community composition has the potential to affect many other biological and physical processes in estuarine habitats. Because freshwater inflow and salinity play such major roles in benthic community structure, it is important to understand the effects of inflow and other external factors to evaluate (and prescribe management options for) estuarine ecosystem health.

Using models to predict bay health is dependent upon knowing what is meant by "health." Ecological health can be defined as the determination that indicators of specific ecological conditions are in an acceptable range. Indicators are metrics for which sufficient information exists on the acceptable range of responses across broad spatial and temporal scales. For the current project, the metric being examined is benthic productivity responses to changes in freshwater inflow.

1.3. Ecosystem modeling

Ecosystem models are representations of underlying mechanistic relationships among ecological components and processes. Ideally, they reduce ambiguity and describe complexity with maximum parsimony. Models in ecology are useful because of the inherent complexity of ecological relationships, the characteristic variability in ecological systems, and the apparently unpredictable effects of deliberate modification of systems by man. It is difficult to understand benthic dynamics from empirical or static modeling analyses alone (e.g., multivariate statistical methods). The concept that benthos are an isolated subsystem, governed by internal interactions and "key species" is not sufficient to explain the heterogeneity of benthos community dynamics in closely

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related sites. However, a model can incorporate spatial variability to provide insights into the dynamics and interactions of benthic populations within an ecosystem, or to predict long-term effects of those interactions.

Modeling of an ecosystem can start from a qualitative conceptual model. The conceptual model is largely theoretical and heuristic. The purposes for modeling ecosystems can range from developing simple conceptual models to provide a general understanding of system behavior, to detailed realistic applications aimed at evaluating specific policy proposals. It is not possible to judge this whole range of models by the same criteria. At least three criteria are necessary: realism, precision, and generality. Unfortunately, no single model can maximize all three. The conceptual model has high generality for Texas estuarine systems, but low realism and low precision. A quantitative model, however, can provide the realism and precision, and test hypotheses drawn from the conceptual model.

A quantitative model requires a long-term data set to calibrate the model. In addition, independent data sets are also needed for model corroboration or validation before these models are used for extensive predictions. Long-term macrobenthos data for the Lavaca-Colorado Estuary was available, which made it possible to perform a modeling experiment on this system. A bioenergetic model was developed within and among four Texas estuaries (Lavaca-Colorado, Guadalupe, Nueces and Laguna Madre), which related macrobenthic productivity to salinity (Montagna and Li 1996). A five year data set from 1990-1995 of macrobenthic biomass was used to calibrate the model. The benthos were divided into two trophic groups: deposit feeders (that consume detritus or sediment organic matter) and suspension feeders (that filter phytoplankton or graze on benthic diatoms). Simulations for the eight Texas bays did fit the data well, indicating that the structure of Texas estuaries is strongly influenced by inflow and Gulf exchange. Within estuaries, the production to biomass ratio (P/B), with units of 1/year, increased with proximity to the freshwater inflow source. The P/B ratio for deposit feeders generally increased with water residence time, i.e., inflow volume adjusted by the estuary volume, but declined with water residence time for suspension feeders. This trend is consistent with the hypothesis that suspension feeders are good indicators of the importance of freshwater inflow on maintaining secondary production. Thus, regression

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coefficients determined from the earlier eight-bay study were used to compare the long-term data on benthic productivity within the Lavaca-Colorado Estuary.

1.4. Study Focus

Long-term macrobenthos data for the Lavaca-Colorado Estuary was used to perform a modeling experiment to determine the effects of alterations in freshwater inflow. The estuary is characterized by a primary and secondary bay, which experience a salinity gradient from sea to river because the primary bay is tidally influenced by connection to the Gulf of Mexico, and the secondary bay is connected to a freshwater source. Comparison of these bay types allows for an examination of effects over a large range salinity, which acts as a surrogate of freshwater inflow effects.

The goal of the present study was to characterize the salinity-benthos and salinity-ecological relationships within Lavaca Bay and Matagorda Bay to provide a means of assessing biological impacts or benefits of altering various flow regimes. Data generated from past studies and recently collected field data were used with the regression coefficients from an existing bioenergetics model (Montagna and Li 1996) to compare productivity over space and time. The model provides prediction capabilities necessary to evaluate the full range of potential flows from low to moderate to high on two ecological components of the lower Colorado River system throughout the annual hydrologic cycle.

2. MATERIALS AND METHODS

2.1. Study Sites

Six stations were chosen in the Lavaca-Colorado Estuary (Fig. 2.1 and Table 2.1). Two replicate stations (A and B) are in the secondary bay, where freshwater influences are greatest, and two other replicate stations (C and D) are in the primary bay, where marine influences are greatest. Using two stations in the freshwater-influenced zone and two stations in the marine-influenced zone replicates the effects at the treatment level and helps to avoid pseudoreplication. A diversion of the Lower Colorado River into the east arm of Matagorda Bay added two additional stations (E and F) in that lagoon. The data

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from Stations E and F were combined with data from Stations C and D to characterize the primary bay. Data from Stations A and B were pooled to characterize the secondary bay.
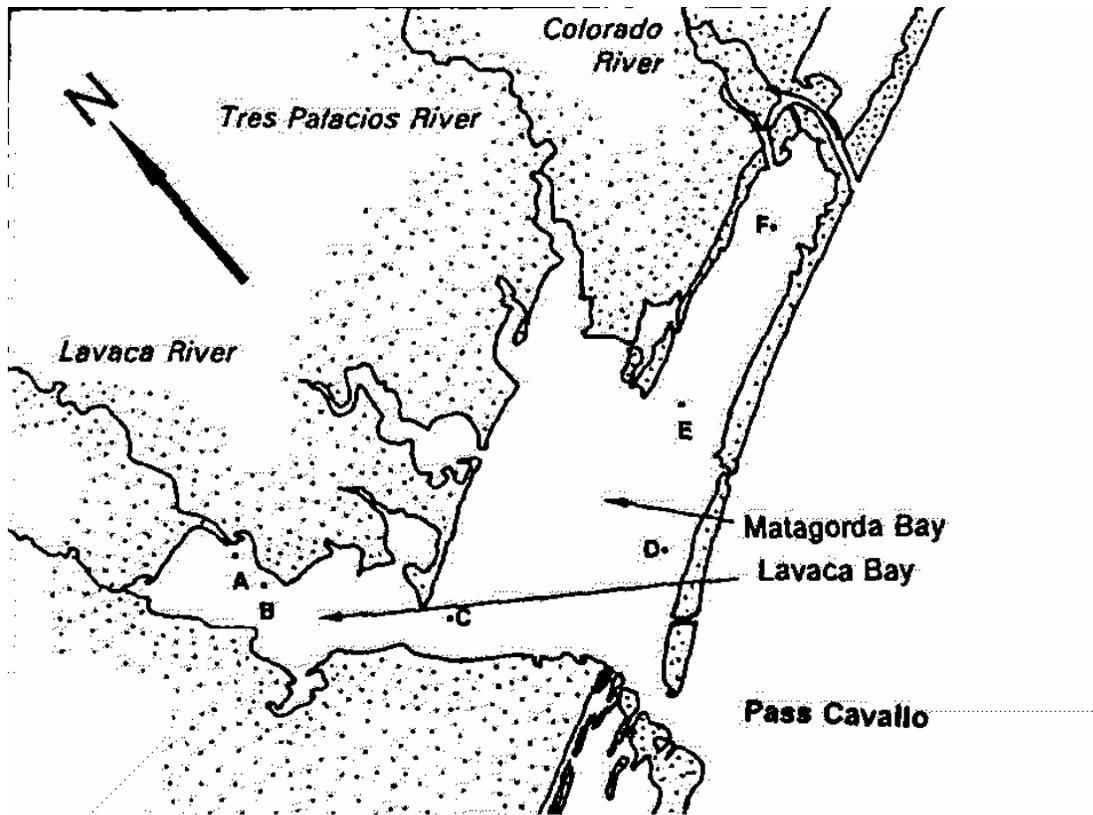
Figure 2.1. Study area and station locations.

Table 2.1. Sampling stations and sampling periods in the Lavaca-Colorado Estuary.

Stations	Bay Name	Bay Type	Sampling Period
A	Lavaca	Secondary	1984 - 2006
B	Lavaca	Secondary	1988 - 2006
C	Matagorda	Primary	1988 - 2006
D	Matagorda	Primary	1988 - 2006
E	East Matagorda	Lagoon	1993 - 1995 2004 - 2005
F	East Matagorda	Lagoon	1993 - 1995 2004 - 2005

2.2. Modeling Procedure

The model consisted of several mathematical equations that calculate the variation of benthos biomass in response to the variation in environmental data. The model's input was the observed long-term environmental data, and output was simulated benthos biomass over time. When the data input and benthos model input is fixed, simulation of observations can be improved by changing the mathematical equations. To model an ecosystem, several repeated cycles of structure, calibration, and simulation are required until the simulation of observations is satisfactory (Fig. 2.2). Each time, sensitivity analysis is performed before the calibration to determine if the output range of the simulation will cover the range of all observations. A parameter should be sensitive enough to change the model output, if not, then the parameter can be deleted. In the present study, the simulation of the observations is based on the previously calibrated parameters from Montagna and Li (1996).

For the current study, a database was assembled that includes data for salinity, benthos biomass, and other environmental variables. The data may be used as either observations for model calibration, input to the model, or as a forcing function to drive the model. Statistical analyses can be used to determine significant environmental factors or to simplify the model by reducing the unimportant variables in the model. The data collection is also used to set up initial parameter ranges. It is more efficient when the initial parameter ranges are as narrow as possible, because it reduces calibration effort and limits the possibility of a wrong calibration direction. When the ranges are unknown, the range of parameter values must be as large as possible to include all possibilities. Previous modeling studies are the best source of information for developing the model structure, calibration, and validation techniques.
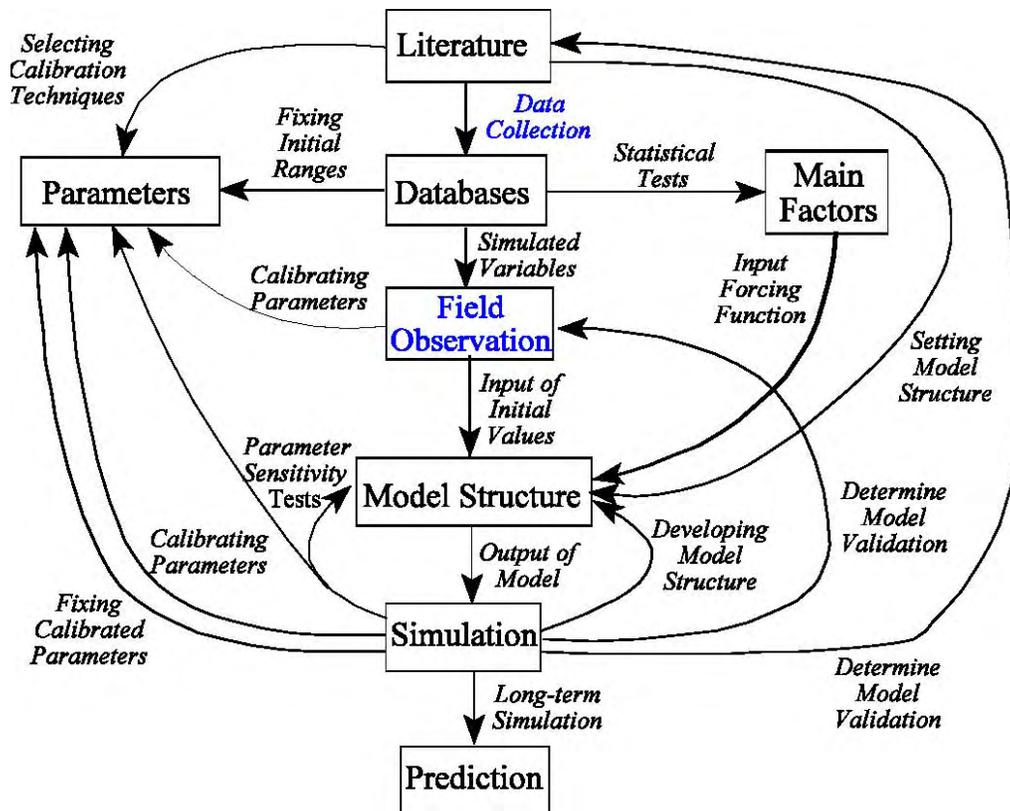
Figure 2.2. Flow diagram of the steps used to develop the model.

2.3. Databases

The availability of a database is the most important component for a modeling study, as it can determine the success of a modeling project. A good database provides a high number of observations, information from the literature, and low error rates due to high sample numbers. A good database can also provide independent data that can be used for model validation, a very crucial step in the modeling process. These characteristics of the database ensure the correct determination of parameters.

2.3.1. Benthic Macrofauna

Sampling of the Lavaca-Colorado Estuary began in November 1984 (Table 2.1). From previous studies, it was learned that long-term changes in benthos within these estuaries could be characterized by sampling on a quarterly basis (Kalke and Montagna

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1991). Starting in July 1988, a sampling program to compare the Lavaca-Colorado and Guadalupe Estuaries was initiated, which was funded by the Texas Water Development Board (TWDB). Since then, the program has been expanded to include the eastern arm of Matagorda Bay with funding from the Lower Colorado River Authority (LCRA). The goal for establishing these stations was to assess the effect of the Colorado River diversion on estuarine productivity. Funding for various other projects by the Coastal Bend Bays Foundation, Texas A&M Sea Grant Program, Corpus Christi Bay National Estuary Program, and the Texas Advancement Technology Program has contributed to the development of a long-term, coast-wide database on benthic biomass, abundance, and community structure.

During each sampling event, hydrographic measurements were also made, which included chlorophyll *a* nutrient concentrations, salinity, temperature, and water depth. Once each year (usually in October), sediment grain size, total nitrogen, and organic carbon content were also measured in sediments.

2.3.2. Predators

Fisheries data from 1988-present were obtained from Texas Park and Wildlife Department (TPWD) (Dailey et al. 1991). The Coastal Fisheries Division samples monthly in the Lavaca-Colorado Estuary using a shrimp trawl and bag seine. In a study of mercury bioaccumulation in different food chains, Montagna and Kathmann (in prep.) determined that black drum, red drum, and blue crab are the main predators on benthic infauna. Therefore, the average value for density of each of these three main predators was used.

2.3.3. Other Environmental Data

The salinity, temperature, and water depth data used in this study were also recorded by TPWD. The temperature simulation used in the model was taken from the previous study done by Montagna and Li (1996), and was compared to TPWD data (Figs. 2.3 and 2.4). Nutrient data for many of the same stations and periods are available (Whitledge 1989). There is not enough primary production data to form a time series, however, a range of values for primary production from previous studies

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is available (Table 2.2). Monthly day-length for the Texas coastal area was obtained from Tony Amos at UT Marine Science Institute. Table 2.3 summarizes the data available in the continuous long-term database assembled in order to model the Lavaca-Colorado Estuary.
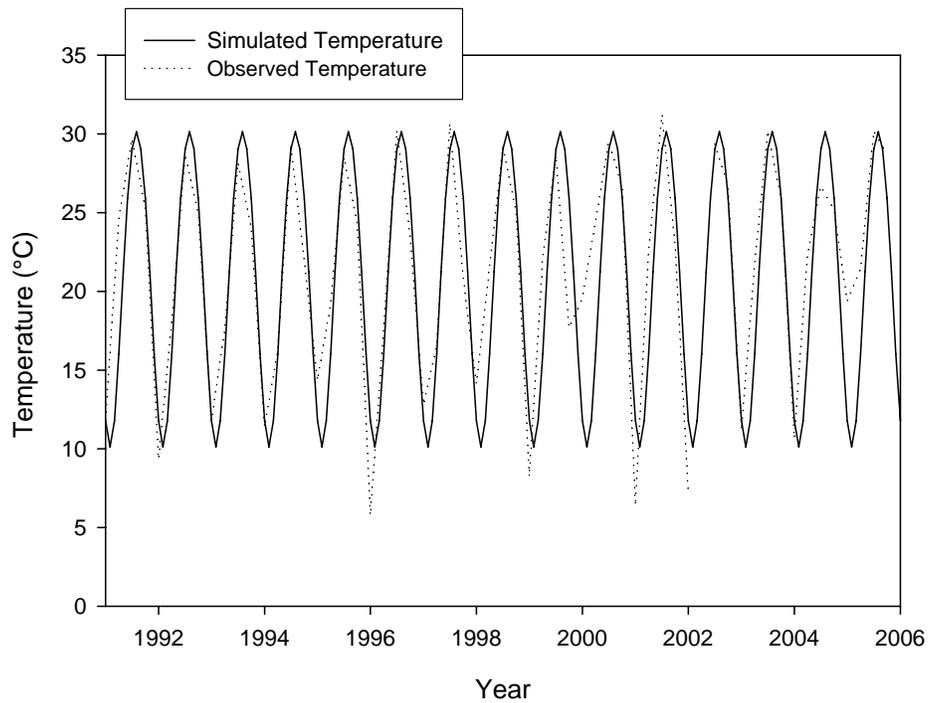
Figure 2.3. Temperature simulation vs. temperature collected by Texas Parks and Wildlife Department throughout Lavaca Bay.
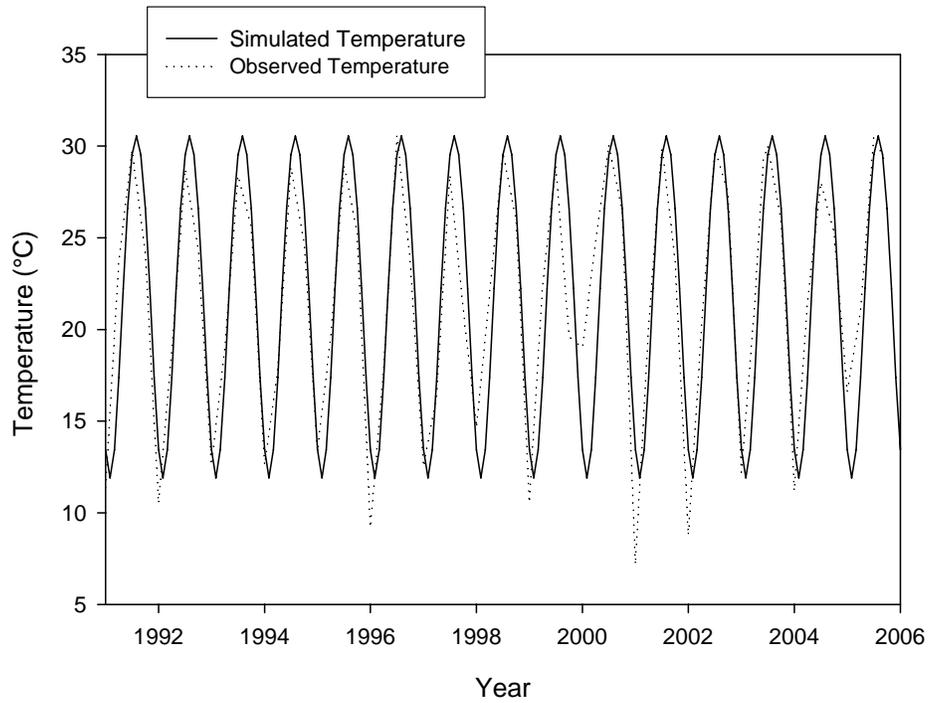
Figure 2.4. Temperature simulation vs. temperature collected by Texas Parks and Wildlife Department throughout Matagorda Bay.

Table 2.2. Available data for primary production from previous studies.

Bay	Previous record of primary production (g C $\cdot$ m^{-2} $\cdot$ d^{-1})	References
Lavaca	0.5 - 2.4	Brock (1994)
Matagorda	0.5 - 2.4	Brock (1994)

Table 2.3. Summary of data variables assembled for the continuous long-term database for modeling the Lavaca-Colorado Estuary. Period is given as the year and month for each estuary.

Variable	Dates (year/month)
Temperature	1988/04 - 2005/07
Salinity	1988/01 - 2005/07
Water Depth	1988/04 - 2005/07
Nutrients (N, P, Si)	1991/10 - 2005/04
Predator Density	1987/01 - 2005/07
Benthos Biomass	1988/04 - 2006/01

2.4. Model Structure

The long-term, benthic macrofaunal data set from the Lavaca-Colorado Estuary was used to calibrate the temporally dynamic model of biological processes. The two principle environmental factors associated with freshwater inflow are salinity and nutrient concentrations; therefore, the relationship between biomass of benthic macrofauna and these environmental factors was incorporated into the model. To test for inflow effects, the ideal input to the model would be freshwater inflow as the basic forcing function. However, inflow rates have variable effects depending on the hydrological and physiographic characteristics of each estuary. Therefore, a physical model that predicts salinity change under varying inflow scenarios would be needed to provide input to the biological model. To avoid this level of complexity, the empirical salinity values were used as input; thus, salinity was used as a surrogate for inflow. Salinity values represent the integration of all the physical characteristic of the estuary, e.g., size, inflow, outflow, tidal exchange, and climatic variability. Other inputs to the model included fish and crabs as predators, temperature, water depth, day length, and nutrient concentrations.

Odum (1971 and 1983) energy circuit language is used to present the model for simulating the Lavaca-Colorado benthic biomass (Fig.2.5). The current model includes four forcing functions: salinity, temperature, food sources, and predators. They drive the model mainly through four environmental limitations: salinity, temperature, food availability, and predation. Other forcing functions (e.g., nutrient

concentrations, day length, and water depth) drive the model through the estimation of food source availability by the calculation of primary production.

There are two main trophic guilds in benthic sediments: the grazing food-chain and the detrital food chain. Grazers utilize autotrophic production and detritivores utilize heterotrophic production. To simplify the model, all macrobenthic animals were separated into one of two groups: the suspension feeders and deposit feeders. Suspension feeders are defined as those who obtain their food sources through capturing suspended particles from the sediment surface or water column, filtering phytoplankton from the water column, or grazing benthic diatoms on the sediment surface. Suspension feeding taxa include the Mollusca, Crustacea, and Chironomid larvae. Deposit feeders are defined as those organisms that obtain their food through ingestion of the sediment, predation, or omnivory. The deposit feeders include the Hemicordata, Nemertinea, Ophiuroidea, Polychaeta, and Sipunculida. Many benthic organisms, e.g., mollusks and polychaetes, can alternate between being suspension feeding and deposit feeding. This simplification allows suspension feeders to be defined as organisms limited by autotrophic food sources, and deposit feeders as organisms limited by heterotrophic food sources.

Modeling benthic secondary production is not as simple as modeling primary production. The benthic food web is complex, and secondary production rates are not a function of physical-chemical variables. Primary producers, whose growth is based on irradiance and nutrient concentrations, are the main food source for suspension feeders. Therefore, it was necessary to predict the food sources for suspension feeders in the study model. Deposit feeders primarily consume particulate organic matter (POM), and this can be approximated by the concentration of total organic carbon (TOC) in sediments, which is empirically derived. The accumulation of POM, as well as the variation of nutrient concentrations and salinity due to temporal variations in freshwater inflows, were not simulated in this model. Instead, the measured concentration of nutrients and salinity were used as inputs. The mathematical formulae were based on known bioenergetic mechanisms of invertebrates.
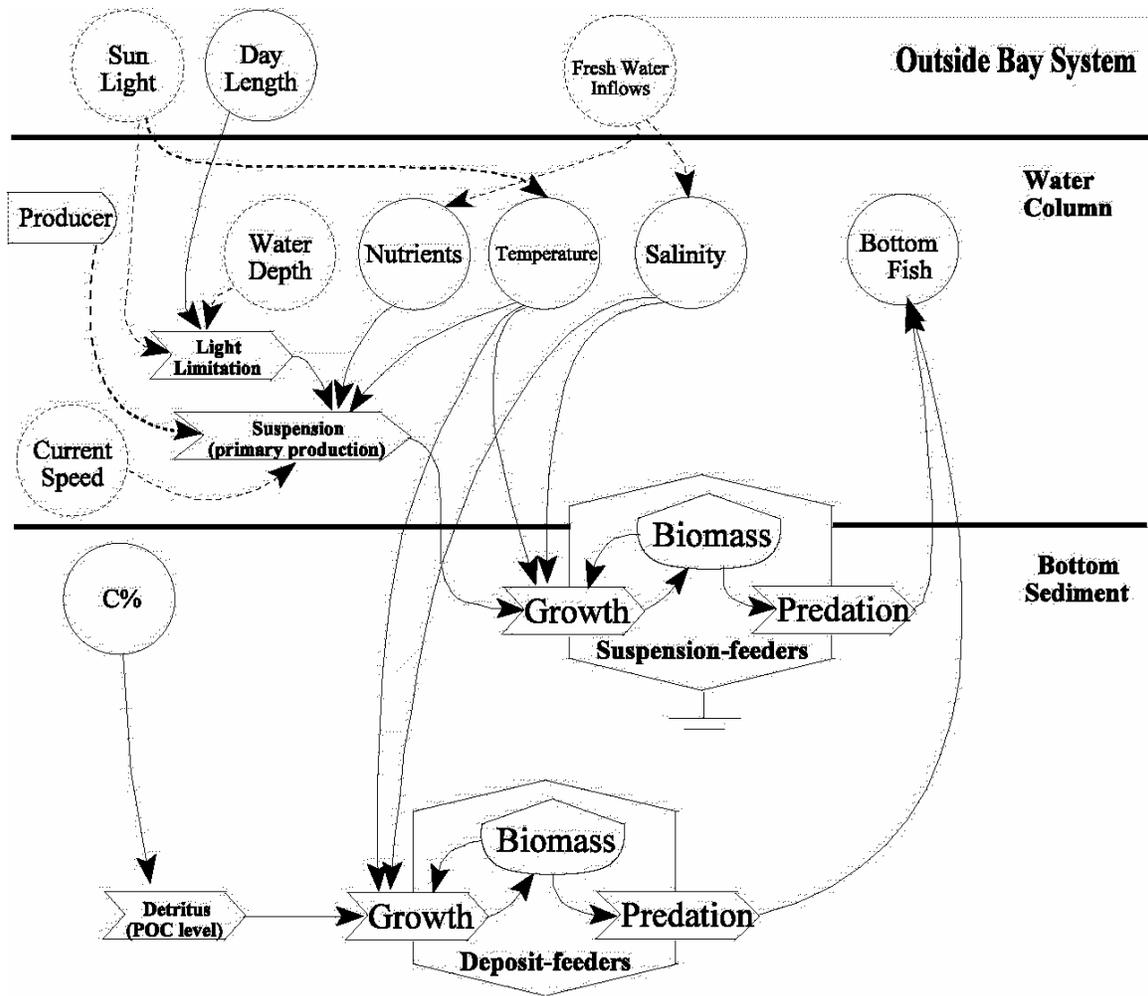
Figure 2.5. Energy circuit diagram for the structure of the benthic macrofauna biomass model. Dashed lines represent variables not included in the study model.

2.5. Development of Mathematical Formulae

The basic formula that describes the change of benthic biomass over time (Li et al. 1996) is based on the law of conservation of mass, and in the form:

$$\frac{d(B)}{d(t)} = I \cdot A - L - D \tag{1}$$

where B is the benthic biomass, t is time, I is the total intake of food by benthic infauna, A is average assimilation efficiency of benthic infauna, L is the total loss due to respiration, excretion and age-related mortality, D is total mortality caused by predators. Unfortunately, it is not possible to simulate B in terms of I and L, because available field

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data on food source standing stocks and respiration of benthic organisms are rare and incomplete in the study area. The approach used in this study replaces net growth rate in place of *I* and *L*.

2.5.1. Growth Rate of Benthic Biomass

The net growth rate is used in place of the intake rate, assimilation efficiency, respiration rate, aging mortality and excretion rate. The formula becomes a Lotka-Volterra growth rate model (Lotka 1925) in the form:

$$\frac{d(B)}{d(t)} = r \cdot B - g \cdot F \tag{2}$$

where *r* is the net growth rate without predation pressure. The predation loss is calculated by feeding rate of predators, *g*, and the density of predatory fish, *F*.

A logistic limitation term to growth rate is suggested by Brown and Rothery (1993), and takes the form:

$$\frac{d(B)}{d(t)} = r \cdot B \cdot \left(1 - \frac{B}{c}\right) - g \cdot F \tag{3}$$

where *c* is the biomass carrying capacity for a population that is limited by space. The *c* in equation (3) is only a limitation for the capacity of biomass. The limitation of a population and its biomass is also due to many other environmental effects. The study model is based on equation (3), and has been modified to include environmental limitation. The new equation contains a parameter to reduce the maximal growth rate (*r*) and maximal predation rate (*g*) by the effects of environmental limitation (*E*). The values of *E* are between 0 and 1. When *E* = 1, there is no environmental limitation, and the benthic population reaches maximal growth rate or the predators reach maximal feeding rate. When *E* = 0, environmental factors reach maximal limitation, benthic populations do not grow, or predators do not consume benthos. As there is more than one predator, the final equation for the model becomes:

$$\frac{d\left(B_{(i,j)}\right)}{d(t)} = \frac{r_{(i)}}{12} \cdot E_{ben(i,j)} \cdot B_{(i,j)} \cdot \left(1 - \frac{B_{(i,j)}}{c_{(i)}}\right) - 30 \cdot E_{fish(i,j)} \cdot \sum_k g_{(i,j,k)} \cdot F_{(j,k)} \qquad (4)$$

where i=1 or 2 for deposit feeders or suspension feeders; j=1-2 for the two bay systems; k=1-3 for three different predators: red drum, black drum and blue crab. The annual net growth rate is $r_{(i)}$, $E_{ben(i,j)}$ is the environmental limitation for benthic biomass growth, $c_{(i)}$ is the biomass carrying capacity levels for the two feeding groups, $g_{(i,j,k)}$ is the predation rate by fish k in bay j to prey benthos i, and $E_{fish(i,j)}$ is the environmental limitation for predation. There are two constants in equation 4. The parameter $r_{(i)}$ and is divided by 12 to convert annual growth to a monthly rate. The parameter $E_{fish(i,j)}$ is multiplied by 30 to convert daily densities to a monthly rate. The different benthic species have different biomasses in each bay, computed by their r, E, c and g. Predator abundances are also different in both bays. Benthic organisms should have the same r and c in each bay, however the dominant species in both the deposit-feeding group and suspension feeding group were different in each bay. For this research it was necessary to run the model separately for the different bay systems.

The term $E_{ben(i,j)}$ includes three effects: temperature limitation ($E_{tem(j)}$), salinity limitation ($E_{sal(i,j)}$), and food concentration limitation ($E_{food(i,j)}$):

$$E_{ben(i,j)} = E_{tem(j)} \cdot E_{sal(i,j)} \cdot E_{food(i,j)} \qquad (5)$$

2.5.2. Temperature Limitation

An exponential equation was used for the temperature effect (Carrada, 1983):

$$E_{tem(j)} = \frac{1}{e^{\frac{\left|T_{(j)} - T_{\max}\right|}{P_{(1)}}}} \qquad (6)$$

where $E_{tem(j)}$ is the temperature limitation, $T_{(j)}$ is the temperature, and T_{max} is the most suitable temperature, which is fixed at the highest temperature recorded at each location. When T is close to $p_{(1)}$, $E_{tem(j)}$ =1, and there is no temperature limitation. Therefore, $p_{(1)}$

is a parameter that describes the weighing due to temperature limitation. The higher $p_{(1)}$ is, the higher the sensitivity to temperature (Fig. 2.6).

2.5.3. Salinity Limitation

Salinity is one of the most influential environmental variables affecting benthic communities and is directly correlated with freshwater inflow. All invertebrates have optimal salinity ranges at which population growth is maximal, i.e., the highest metabolism rates (Wohlschlag et al. 1977). Because of these salinity effects, an exponential equation is used to model salinity limitation. The equation is similar in form to that used for temperature limitation:

$$E_{sal(i,j)} = \frac{1}{e^{\frac{|S_{(j)} - p_{(i,3)}|}{p_{(2)}}}} \tag{7}$$

where $E_{sal(i,j)}$ is the salinity limitation, $S_{(J)}$ is salinity, $p_{(i,3)}$ is the optimal salinity for a population, and $p_{(2)}$ is a parameter that describes the weight of the salinity limitation. There is no salinity effect when $p_{(2)} = \infty$. Salinity limitation has a centralized optimum, with greater effects at high and low salinities (Fig. 2.7). The greater the salinity tolerance range, the higher the $p_{(2)}$ value (Fig. 2.7).

T-Limitation = f(Temperature, $p_{(1)}$)
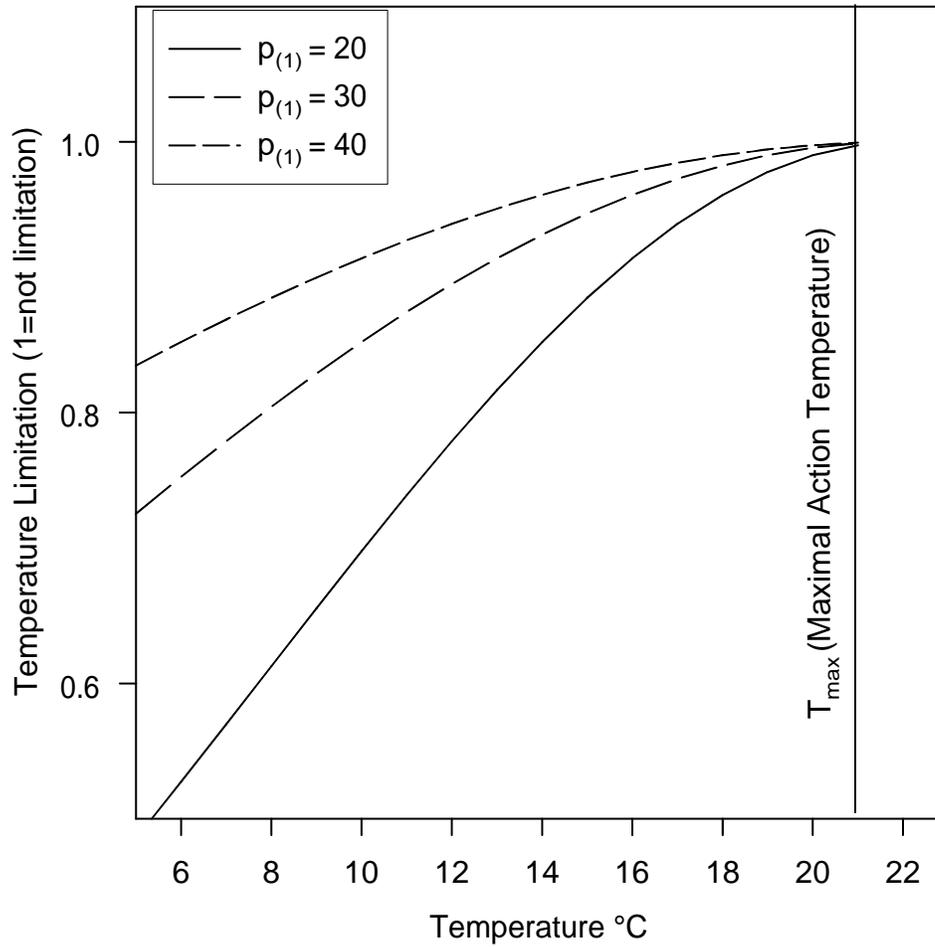
Figure 2.6. Effect of the weight of the parameter ($p_{(1)}$) on temperature limitation calculated via equation (6).
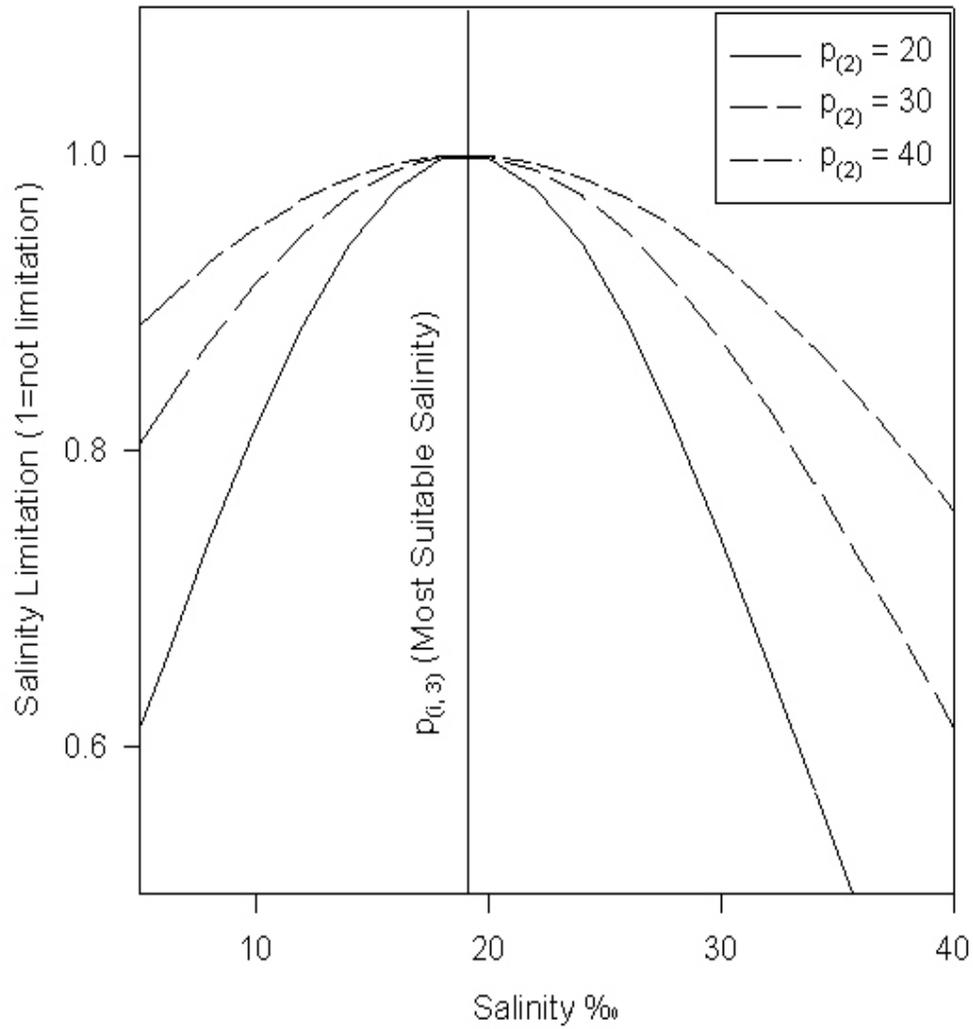
Figure 2.7. Effect of the weight of the parameter ($p_{(2)}$) on the salinity limitation calculated via equation (7).

2.5.4. Food Source Limitation

Michaelis-Menten kinetics is used to describe the food source limitation (Keen and Spain 1992):

$$E_{food(i,j)} = \frac{F_{(i,j)}}{F_{(i,j)} + p_{(i,4)}} \tag{8}$$

where $E_{food(i,j)}$ is the food limitation, $F_{(i,j)}$ is the concentration of the food source for benthic organisms (sedimentary POC for deposit feeders and primary production for suspension feeders), and $p_{(i,4)}$ is a parameter at which the food concentration is at half the maximum level of the population growth rate.

As two feeding groups were simulated in the model (deposit feeders and suspension feeders), there were two different food sources: detritus in sediment and organic matter in the water column. Sedimentary POM was used as a food source for deposit feeders, and expected primary production was used for suspension feeders. Increased consumer biomass ($B_{(i,j)}$) can increase food limitation, therefore, equation (8) transforms the ratio as a function of benthic biomass:

$$E_{food(i,j)} = \frac{\dfrac{F_{(i,j)}}{B_{(i,j)}}}{\dfrac{F_{(i,j)}}{B_{(i,j)}} + p_{(i,4)}} \tag{9}$$

2.5.5. Food Sources for Deposit Feeders

The sedimentary POM is expected to remain constant in each bay. Two parameters were used as POM levels, one specific to each bay. The POM levels were pre-calibrated by the observed carbon concentration ($C\%_{(j)}$) in the sediment (j=1-2 for two bays):

$$C\%_{(j)} = \frac{p_{pom(j)}}{p_{sed}} \cdot 100\% \tag{10}$$

where $p_{pom(j)}$ is the sedimentary POM level for each bay, and p_{sed} is a parameter for the average dry weight of the whole sediment. The POM levels for each bay represent the food sources for deposit-feeders ($F_{(i,j)}$) in each bay:

$$F_{(1,j)} = p_{pom(j)}$$
(11)

2.5.6. Food Sources for Suspension Feeders

Primary production is expected to be the most important food source for suspension feeders. Primary production is simulated as a function of day length, temperature, nutrient concentration and water depth. Primary production was pre-calibrated using data from previous studies (Stockwell 1989, Armstrong 1985) using the following formula:

$$F_{(2,j)} = D_{(j)} \cdot p_{mic(2)} \cdot \frac{1}{e^{\frac{|T_{(j)} - T_{max}|}{p_{mic(3)}}}} \cdot L_{(t)} \cdot E_{nut(j)}$$
(12)

where $F_{(2,j)}$ is the available food for suspension feeders, $D_{(j)}$ is the water depth adjustment described in equation (13), $p_{mic(2)}$ is the maximal monthly primary production rate, $p_{mic(3)}$ is the temperature limitation for primary production, $L_{(t)}$ is the day length that represents light limitation, and $E_{nut(j)}$ is the nutrient limitation for photosynthesis that includes concentrations of nitrogen (N), silica (Si), and phosphorus (P). Because suspension feeders only use the available food source 10 cm above the sediment surface, the following adjustment must be taken into consideration:

$$D_{(j)} = \frac{1000 \cdot 30}{0.42 \cdot 10 \cdot d_{(j)}}$$
(13)

where $d_{(j)}$ is the water depth and the final unit for suspension feeder food availability is measured in $\left(\frac{mg \cdot dw}{m^2 \cdot 10cm \cdot month} \right)$ where dw stands for dry weight. The constants are used to convert from 1000 µg to mg, 30 days per month, 42% Carbon content per dry weight, and 10 cm depth of sediment.

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2.5.7. Nutrient Limitation

Nutrient limitation ($E_{nut(j)}$) for photosynthesis was modeled according to the Redfield ratio of 106:16:15:1, which assumes that producers use carbon, N, Si, and P proportionally by weight (Redfield, 1934):

$$E_{nut(j)} = MIN\left(\frac{\frac{[N]_{(j)}}{[N]_{(j)} + p_{mic(1)}}}{16}, \frac{\frac{[P]_{(j)}}{[P]_{(j)} + p_{mic(1)}}}{1}, \frac{\frac{[Si]_{(j)}}{[Si]_{(j)} + p_{mic(1)}}}{15} \right) \quad (14)$$

where $[N]_{(j)}$, $[P]_{(j)}$, and $[Si]_{(j)}$ are concentrations of inorganic nitrogen, phosphorus and silica.

2.5.8. Day Length Limitation

Photosynthesis is limited by light, which varies seasonally. A sine function is used to simulate the seasonal cycle of day length:

$$L_{(t)} = p_{avg} + p_{amp} \cdot sin\left(\frac{2\pi \cdot (t)}{12} - p_{pha} \right) \quad (15)$$

where $L_{(t)}$ is day length at time t, p_{avg} is the average day length over a year, p_{amp} is the amplitude of the seasonal fluctuation, and p_{pha} is the correction factor for the beginning phase of the sine cycle at a given time.

2.5.9. Prey Density Limitation

Predation can be limited by temperature, salinity, benthic biomass, and predator density. In this study, we considered only the benthic prey biomass, because predation rates on benthic organisms are strongly related to benthic biomass. A complete ecosystem model would also include fish bioenergetics. Predator limitation, $E_{fish(i,j)}$, may be different for different predators, but in this study the same $E_{fish(i,j)}$ was used for all

predators, including black drum, red drum and blue crab. However, $E_{fish(i,j)}$ is different for deposit feeders and suspension feeders because of the different vertical distribution of these two groups within the soft-bottom habitat.

In addition to standing stock, a second characteristic of prey is its distribution. The feeding rate of predators is expected to increase exponentially when prey are aggregated in time or space. A logistics-type curve is used to simulate this effect (Montagna et al. 1993):

$$E_{fish(i,j)} = 1 - e^{-p_{(5)} \cdot B_{(i,j)}}$$

(16)

where $B_{(i,j)}$ is the biomass of the benthic prey (i = 1 or 2 for deposit feeders or suspension feeders, and j = 1-2 for both bays), and $p_{(5)}$ is a new parameter for the aggregation effect. When biomass ($B_{(i,j)}$) is at a very low level, the value of term $E_{fish(i,j)}$ is close to 0, and limitation due to the aggregation effect is nil. When the predator reaches its maximal grazing rate and $B_{(i,j)}$ is very high, the term $E_{fish(i,j)}$ is close to 1, and the limitation due to aggregation is at the maximal level.

2.6. Modeling Tool

The study model has been previously run and calibrated for the years between 1988 and 1996 (Montagna and Li 1996). This was done using the FORTRAN 77 language and facilitated by the PC software package SENECA (Simulation Environment for Ecological Application) (de Hoop et al. 1989).

2.7. Modeling Calibration

The Lavaca-Colorado Estuary was divided into two bays: the primary bay, Matagorda Bay, and the secondary bay, Lavaca Bay. The model was then calibrated individually for each of these bays (Montagna and Li 1996). Sampling of the Lavaca-Colorado Estuary began in November of 1984 (Kalke and Montagna 1991). The data set is incomplete, however, and periodically non-existent between 1984 and 1988 (Table 2.1). Sampling took place from 1988-1990, but less than four times per year. Unfortunately, there is a period from 1989 to 1990 when observations for nutrients are

missing. A five-year period, beginning in January 1991 and ending August 1995, is the best data series in terms of completeness, with four continuous observations for all variations per year in both bays. The calibration parameters from the five-year series were used in order to perform a more accurate prediction. Model parameters determined by Montagna and Li (1996) were used in order to simulate benthic macrofauna biomass in the Lavaca-Colorado Estuary from January 1991 to August 2005.

2.7.1. Day Length

Table 2.4 presents the results of calibration for Equation (15) that simulates the day length (Fig. 2.8), and were determined by Montagna and Li (1996). The day length simulation is very close to the observed data (Fig. 2.8). These results are used as the parameters in Equation (15) and became a forcing function for the main model.

Table 2.4. Calibration parameters for Equation (15) for the simulation of day length.

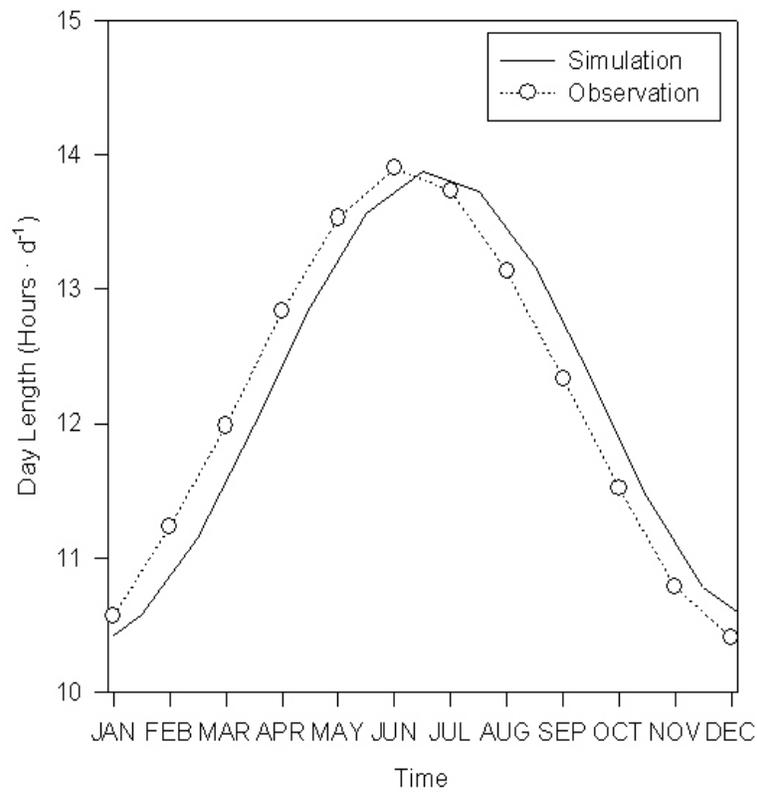| Parameter	Definition	Best Fit Value	Reduced Ranges		Initial Ranges	
			Minimum	Maximum	Minimum	Maximum
p_{avg}	Average value of the harmonic function	12.15849	12.15849	12.1585	11	13
p_{amp}	Amplitude of sinus function	1.755811	1.755809	1.755815	1	2
p_{pha}	Phase of sinus function at reference time	0.2244535	0.2244535	0.2244536	0	1

Figure 2.8. Simulation of day length over period of one year.

2.7.2. Primary Production

Table 2.5 presents results of the calibration of parameters for simulation of primary production that were formulated by equations (12) and (14) (Montagna and Li 1996).

Table 2.5. Calibration of parameters for primary production.

Parameter	Definition	Best Fit Value	Calibrated Ranges		Initial Ranges	
			Minimum	Maximum	Minimum	Maximum
$p_{mic(1)}$	Nutrient limitation	1.909248	1.856677	1.914145	0.5	2
$p_{mic(2)}$	Maximal primary production (g C • m • h)-2 -1	0.5093191	0.5076211	0.5105351	0.5	2
$p_{mic(3)}$	Temperature Limitation	11.39727	11.29732	11.39727	10	50

2.7.3. POM Level

To calibrate the POM level, p_{sed} was set at 18 (Li et al. 1996) in equation (10) and the carbon concentration was simulated (Montagna and Li 1996). The results of the calibration are listed in Table 2.6, which estimates the carbon concentration levels that were fit to the observations.

Table 2.6. Parameters for the calibration of POM levels (g dw • m^{-2} •10 cm^{-1}) for both bays.

Parameters	Definition	Best Fit Value	Calibrated Ranges		Initial Ranges	
			Minimum	Maximum	Minimum	Maximum
p_{sed}	Sediment Weight (g dw • m •10 cm)-2 -1	18[a]				
$p_{pom(1)}$	POM level for Lavaca Bay	10136.14	9973.851	10279.69	1000	30000
$p_{pom(2)}$	POM level for Matagorda Bay	10007.6	9589.807	10364.56	1000	30000

[a]Calibrated by Li et al.(1996)

2.7.4. Calibration of 1991-1995 Data Series

The model was calibrated individually for each bay system using the period from

January 1991 to August 1995. The initial ranges for the seventeen parameters were set within the same values for each bay. There were several thousand calibration runs, and all parameter ranges were reduced to less than 50% of the initial ranges. The results of the calibration are presented in the Table 2.7.

Table 2.7. Best fit parameter values from the calibration of the Lavaca-Colorado Estuary for the continuous five-year database: 1991 - 1995. Lavaca Bay did not have red drum and black drum observations, so the parameters $g_{(1, j, 1)}$ and $g_{(1, j, 2)}$ were not computed. The parameters are defined in equations (4-16).

Parameter	Best fit values for each estuary		Initial ranges
	Lavaca Bay	Matagorda Bay	
$p_{(1)}$	44.732329	42.42344	20, 45
$p_{(2)}$	19.66252	17.13879	20, 45
$p_{(1, 3)}$	34.88885	37.76986	20, 40
$p_{(1, 4)}$	96.10882	62.42303	0, 100
$g_{(1, j, 1)}$	-	0.5528514	0, 5
$g_{(1, j, 2)}$	-	3.470691	0, 5
$g_{(1, j, 3)}$	0.6814387	1.247655	0, 5
$p_{(5)}$	2.05926E-3	3.7239E-3	0.001, 0.01
$r_{(2)}$	5.80609	6.670129	5, 20
$c_{(1)}$	68.88308	30.30947	30, 70
$p_{(2, 3)}$	16.74664	5.10743	20, 40
$p_{(2, 4)}$	6.457159	15.1268	0, 100
$g_{(2, j, 1)}$	-	3.705585	0, 5
$g_{(2, j, 2)}$	-	0.4145367	0, 5
$g_{(2, j, 3)}$	0.9929386	1.195466	0, 5
$r_{(2)}$	5.343904	8.033044	5, 20
$c_{(2)}$	50.24743	99.65412	50, 100

3. RESULTS

The simulations of benthic biomass are based on the best fit parameters from the calibration of the period (1991 - 1995). All of the simulations were run from January 1991 until August 2005, and were compared to observed benthic macrofauna biomass data (Figs. 3.1 - 3.4).

3.1. Simulation of Benthos Biomass

The biomass variance was determined in Lavaca Bay and Matagorda Bay for deposit feeders and suspension feeders. Benthic biomass variance is defined as the average difference between observed and simulated biomass for a given time period (Table 3.1). The simulations for both bays and each feeding group fit the observed data relatively well during the calibration period, 1991 - 1995 (Figures 3.1 – 3.4). The most important part of the fit is that in general, the trends in the prediction over time fit the trends in the observed biomass over time. The worst fit was for deposit feeders in Lavaca Bay where the model predicts increasing biomass from 1991 to 1994 when the biomass actually decreased. Although the variance was high for Matagorda Bay deposit feeders also, the trends actually fit the data well. The high variance for Matagorda Bay is explained by the higher average biomass. As in most biological data, the variance increases with the mean.

Table 3.1. Biomass variance in the Lavaca-Colorado Estuary.

	Lavaca Bay		Matagorda Bay	
	Deposit Feeders	Suspension Feeders	Deposit Feeders	Suspension Feeders
1991 - 1995	4.497	1.871	5.255	0.617
1996 - 2000/07	-	-	5.488	1.552
1996 - 2001/04	1.512	0.583	-	-
1996 - 2006	7.879	2.036	8.993	6.814
2001/04 - 2006	14.56	3.57	-	-
2000/07 - 2006	-	-	13.322	13.063
1991 - 2006	6.692	1.978	7.552	4.561

Surprisingly, the validation biomass simulation for Lavaca Bay for the period from January 1996 through July 2000 seems to fit the observed data better than during

the calibration period for both deposit and suspension feeders. One exception is the Lavaca Bay suspension feeders, which had much higher biomass than predicted from 1997 through 2002 (Figure 3.2).

Unfortunately, three of the four simulations predict much higher biomass than those observed after the year 2000, and one predicts higher biomass after the year 2003. This increase in macrofauna biomass in the simulation is caused by a decrease in predator density (particularly blue crabs) in both bays at that time. There was a pronounced decrease in blue crab populations from 2000 to 2006 in Lavaca Bay (Figure 3.5) and Matagorda Bay (Figure 3.6).
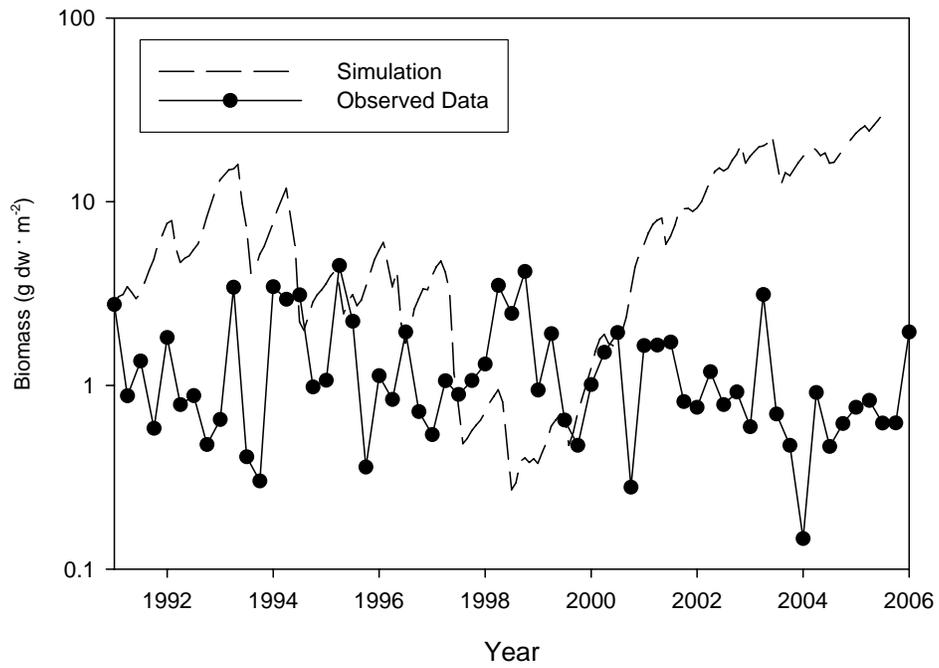
Figure 3.1. Simulation of deposit feeder biomass in Lavaca Bay for the period 1991 - 2006.
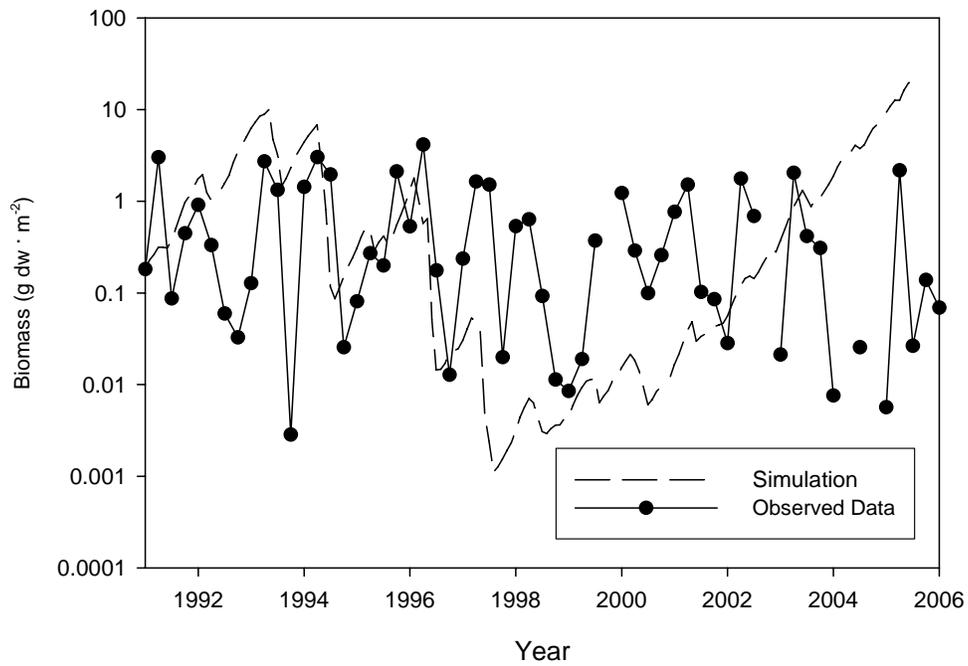

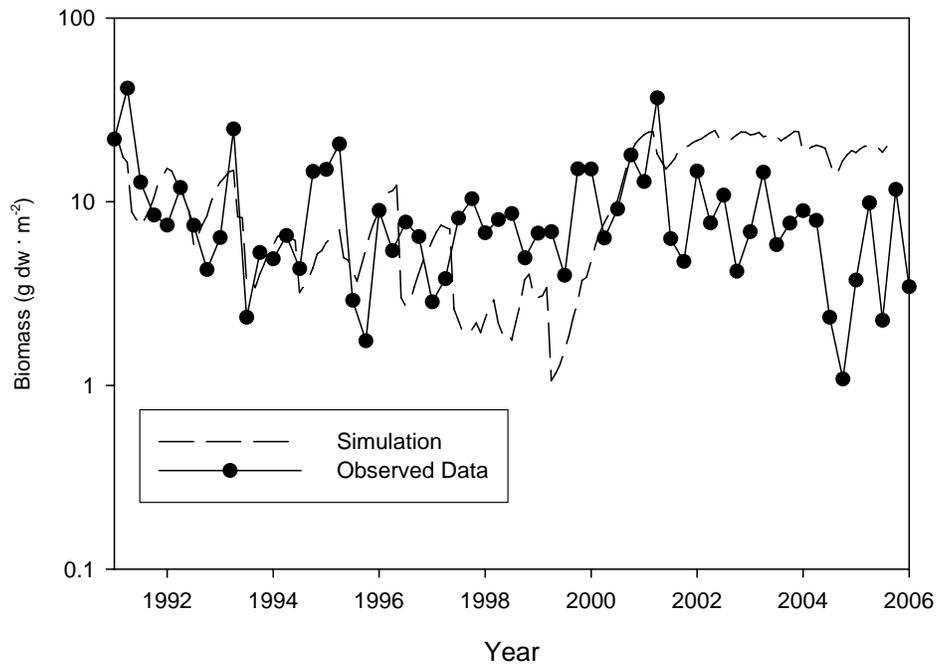Figure 3.2. Simulation of suspension feeder biomass in Lavaca Bay for the period 1991 - 2006.

Figure 3.3. Simulation of deposit feeder biomass in Matagorda Bay for the period 1991 - 2006.
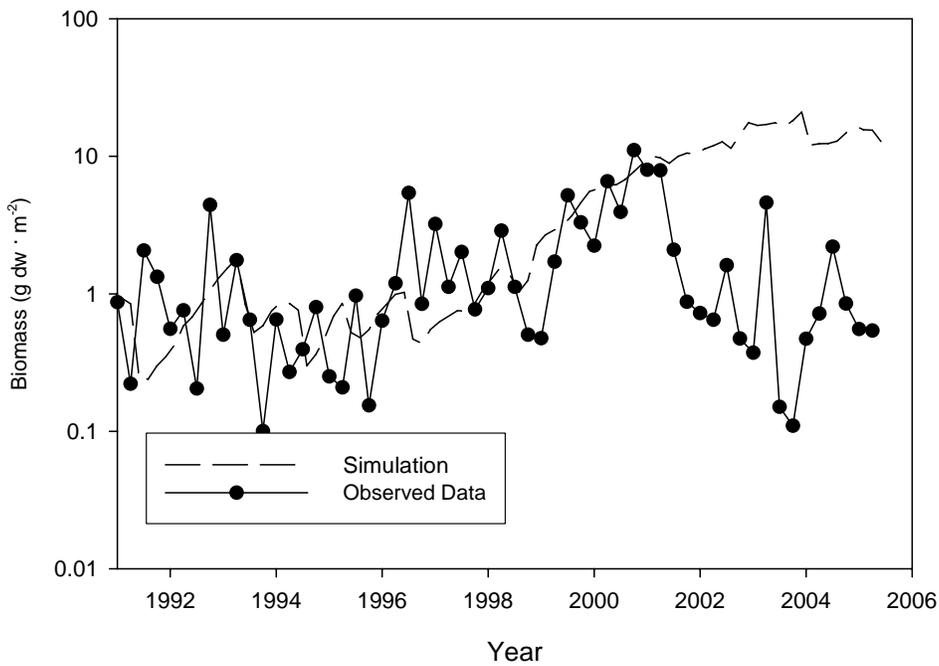

Figure 3.4. Simulation of suspension feeder biomass in Matagorda Bay for the period 1991 - 2006.
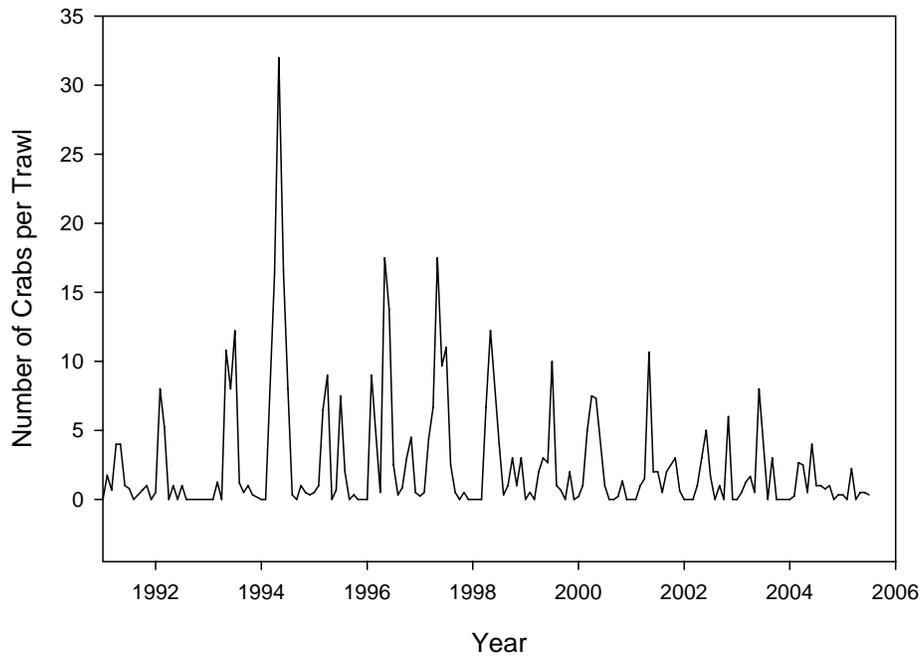
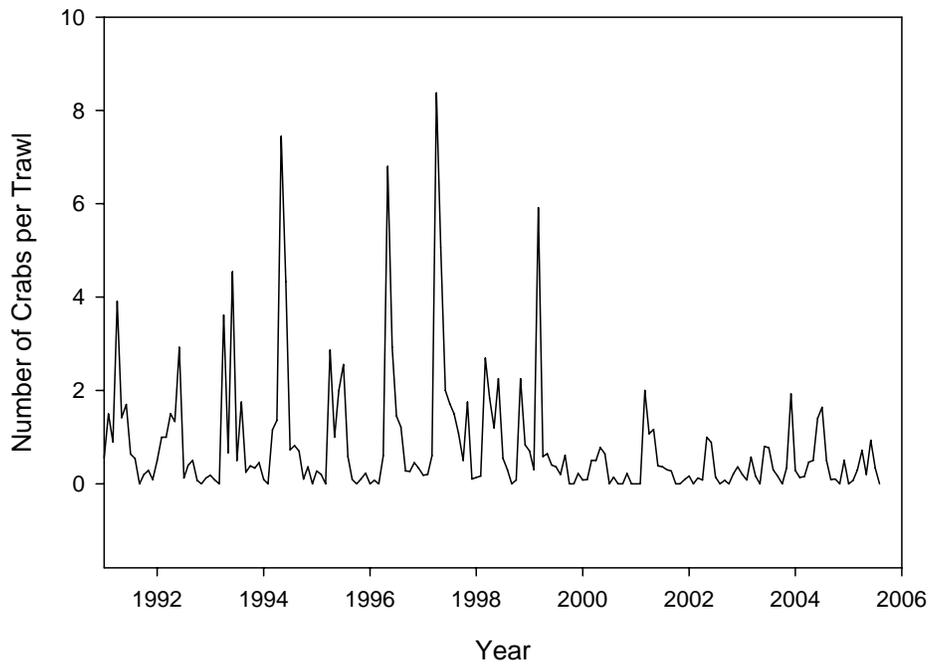Figure 3.5. Crab population in Lavaca Bay from 1991 - 2006 (TPWD data).

Figure 3.6. Crab population in Matagorda Bay from 1991 - 2006 (TPWD data).

3.2. Benthic Biomass Change Due to Salinity Increase

The deposit feeder and suspension feeder biomass were also simulated to reflect the response to a potential increase in salinity in both bays (Figs 3.7 - 3.14). These calculations were performed at 1% intervals up to a 30% increase from the original salinity observations. The simulations predict benthos biomass if the salinity had been higher than it was over the historical period. Simulations of deposit feeders followed a pattern of increasing gradually followed by a dramatic drop in biomass about once a year, with the lowest biomass concentration occurring in 1999 (Figures 3.7 and 3.11). After the year 2000, the biomass concentrations showed signs of slowly increasing and leveling off. Simulations of suspension feeders biomass followed the same pattern as the deposit feeders biomass, but did not have as many decreases in biomass prior to the year 1999, and had a trend of a slower increase in biomass after the year 2000 (Figs. 3.9 and 3.13).

As salinity increased, the model predicted an increase in deposit feeder biomass for both bays (Figs. 3.8 and 3.12). The scale of the increase was higher in Lavaca Bay (about 9 g dry weight m^{-2}) than in Matagorda Bay (about 5 g dry weight m^{-2}). However, as salinity increased, it was correlated to a decrease in suspension feeder biomass in both bays (Figs. 3.10 and 3.14). The scale of the decrease was very small in Lavaca Bay (about 1 g dry weight m^{-2}) compared to Matagorda Bay (about 5 g dry weight m^{-2}).

Total biomass concentration was calculated by addition of deposit and suspension feeder biomasses. Lavaca Bay total biomass increased with percent salinity increase (Fig. 3.15) because the decrease in suspension feeders was small compared to the increase in deposit feeders. In Matagorda Bay, biomass initially decreased, then gradually started to increase with increasing salinity because the increase in deposit feeders was similar to the decrease in suspension feeders biomass (Fig. 3.16).

Figure3.7. Simulations of deposit feeder biomass reflecting different salinity increases in Lavaca Bay.

Figure 3.8. Mean (± std error) biomass concentration of deposit feeders in Lavaca Bay in response to changes in salinity.

Figure 3.9. Simulations of suspension feeder biomass reflecting different salinity increases in Lavaca Bay.

Figure 3.10. Mean (± std error) biomass concentration of suspension feeders in Lavaca Bay in response to changes in salinity.
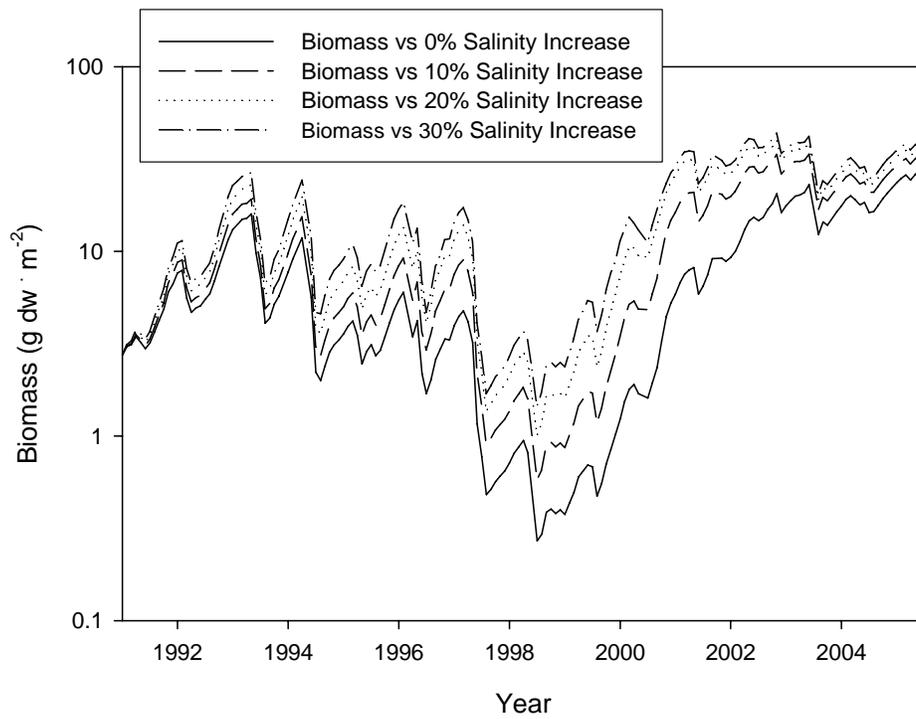
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Figure 3.11. Simulations of deposit feeder biomass reflecting different salinity increases in Matagorda Bay.
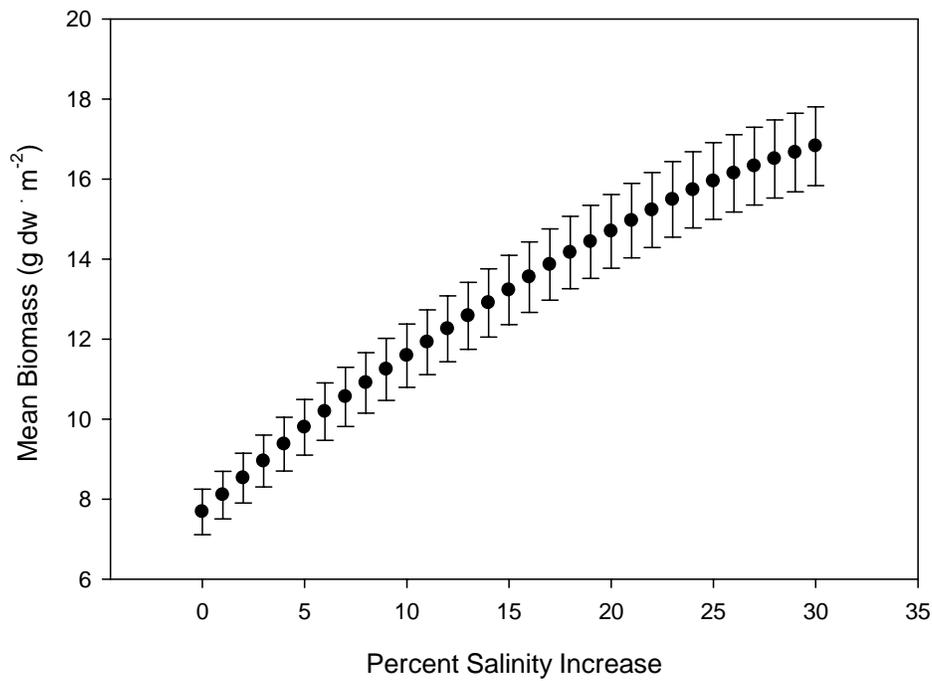

Figure 3.12. Mean (± std error) biomass concentration of deposit feeders in Matagorda Bay in response to changes in salinity.
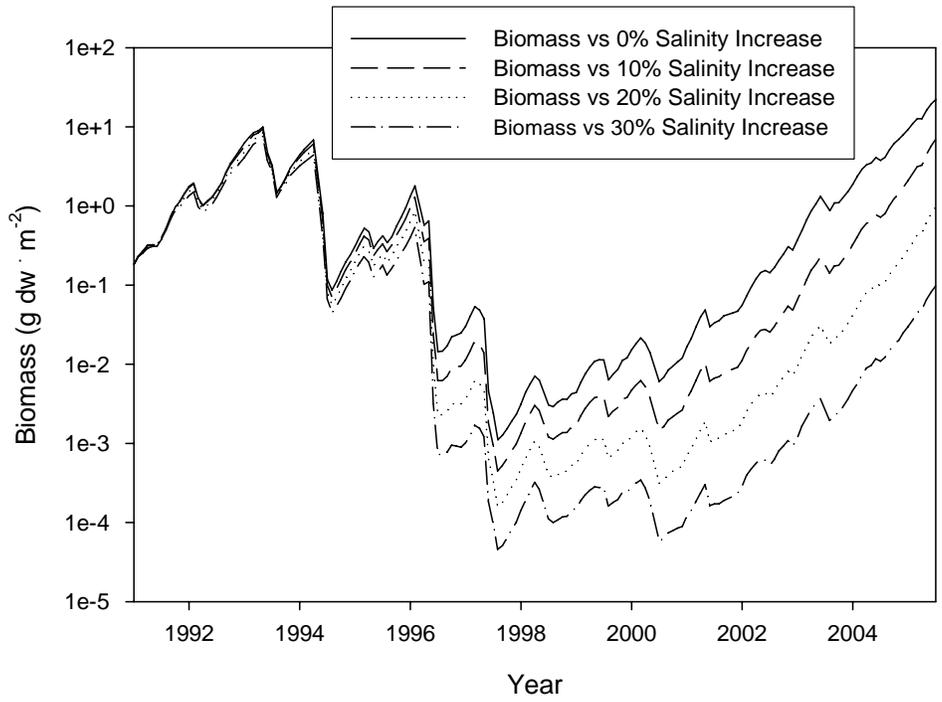
Figure 3.13. Simulations of suspension feeder biomass reflecting different salinity increases in Matagorda Bay.
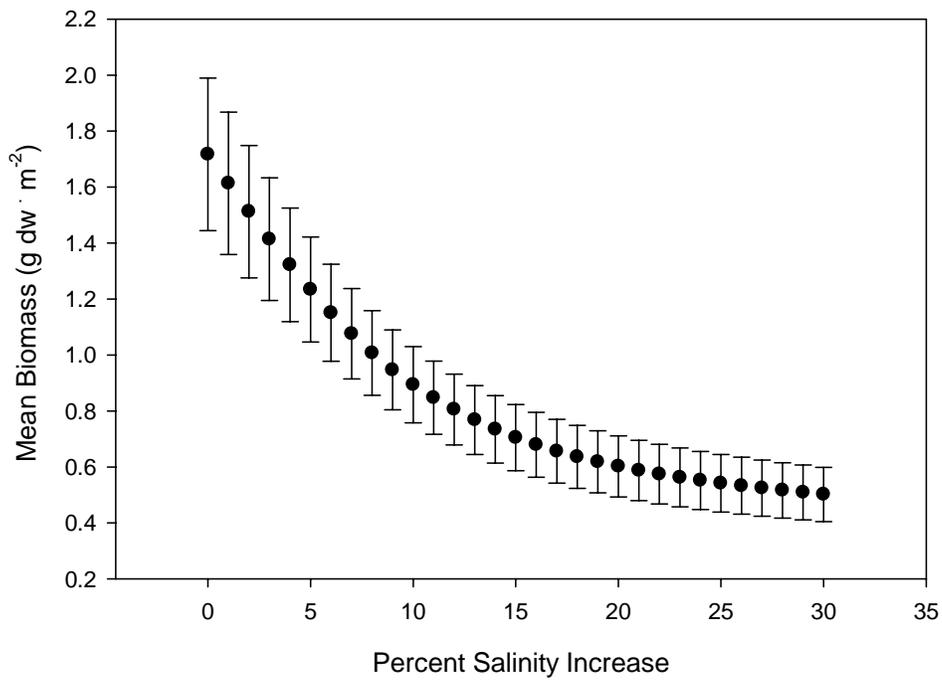

Figure 3.14. Mean (± std error) biomass concentration of suspension feeders in Matagorda Bay in response to changes in salinity.
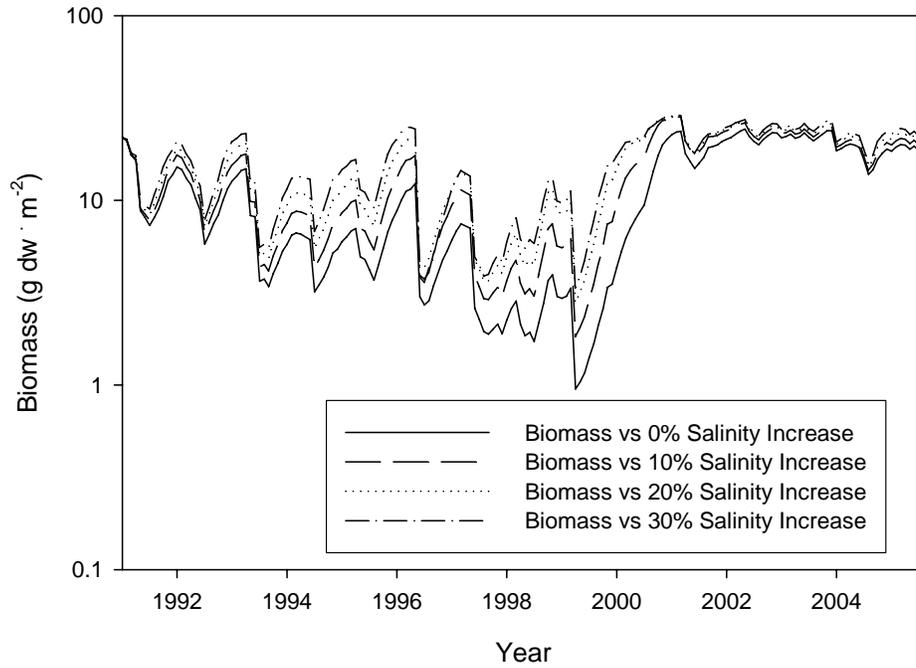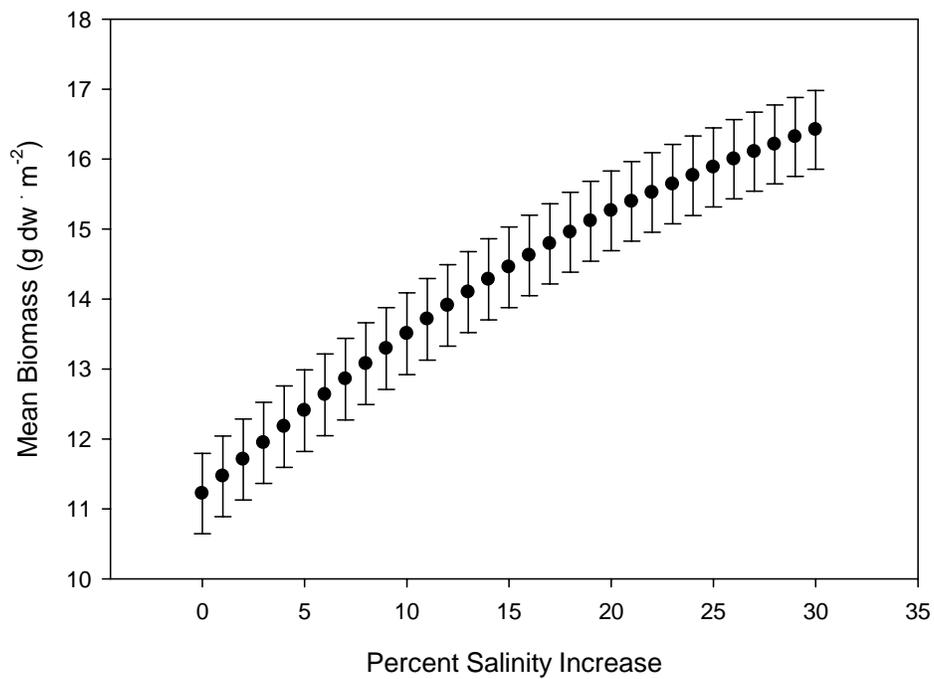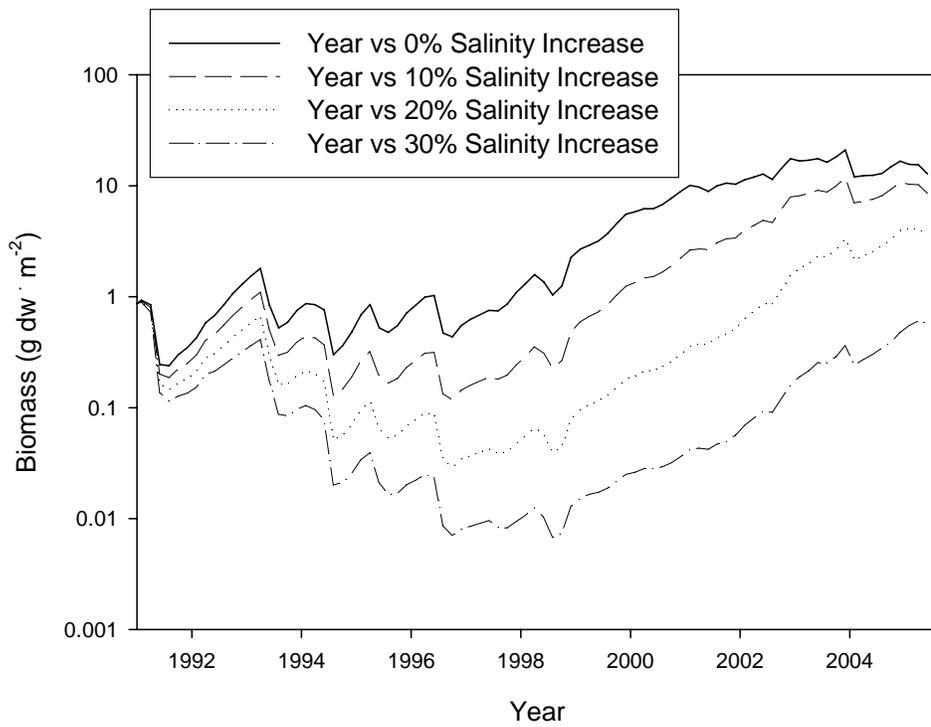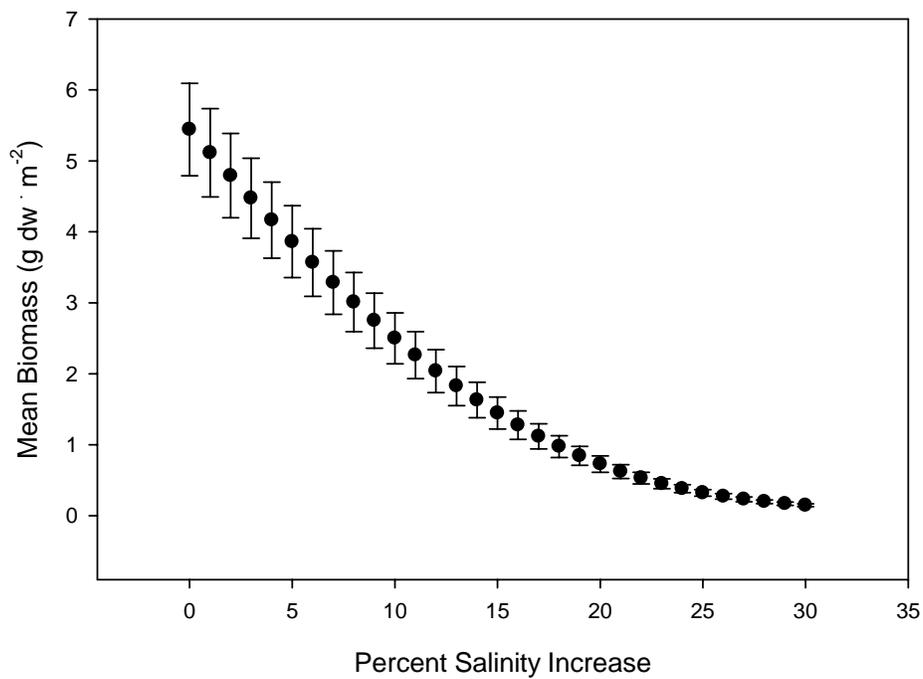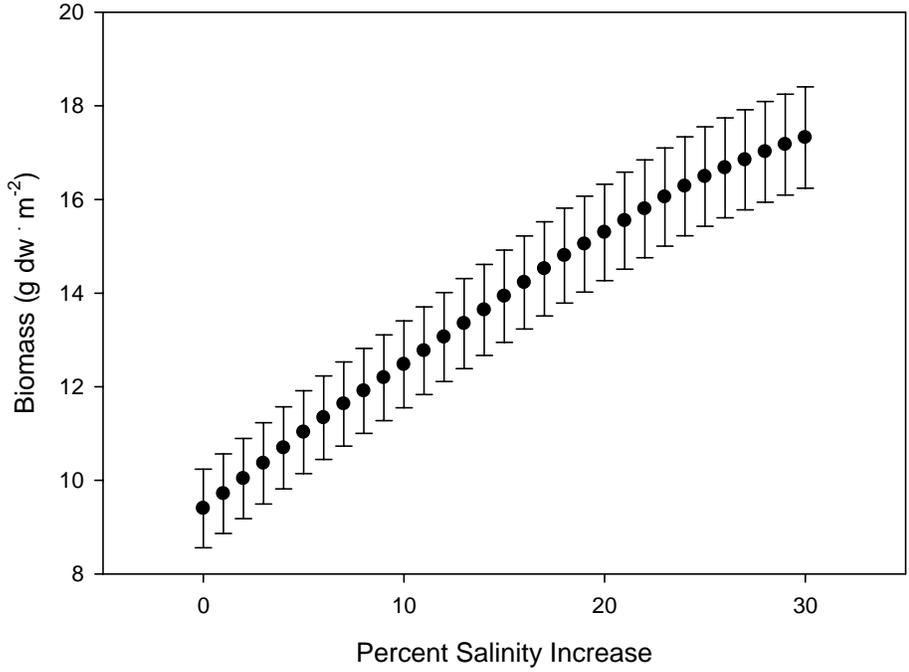
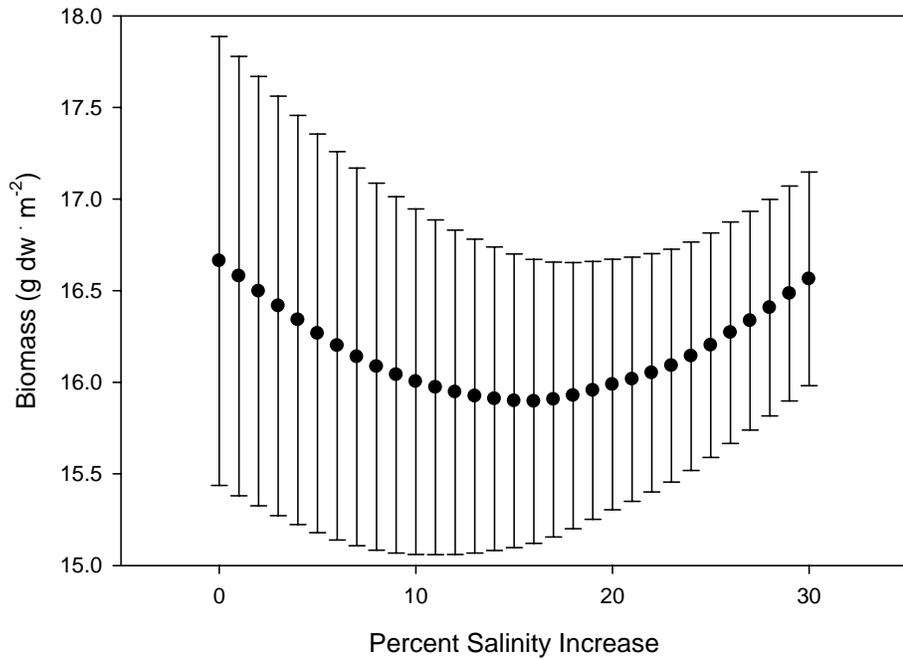Figure 3.15. Mean (± std error) total biomass concentration in Lavaca Bay in response to changes in salinity.

Figure 3.16. Mean (± std error) total biomass concentration in Matagorda Bay in response to changes in salinity.

4. DISCUSSION

4.1. Colorado River Diversion

A diversion channel from the Colorado River was built in 1991 to mitigate the effects of reduced freshwater inflow to Matagorda Bay from past water development projects. In 1992, a dam was added to divert the river into the channel. At that time, alterations in the exchange of seawater from the Gulf of Mexico also occurred, which included closure of Parker's Cut Dam near the mouth of the Colorado River to prevent saltwater from entering Matagorda Bay to help reduce the salinity.

A study following the alterations found diversity, abundance, and biomass to be higher in Matagorda Bay versus Lavaca Bay (Montagna 1994). It was indicated that as a result of the diversion project, Matagorda Bay became a healthier and more productive ecosystem than Lavaca Bay as indicated by increased diversity and biomass. This conclusion, however, is confounded by the much larger influence of human activities and development in Lavaca Bay, which should be taken into consideration when comparing the two ecosystems (Montagna 1994).

The Matagorda Bay Health Evaluation (MBHE) component of the LCRA/SAWS Water Project (LSWP) Study Plan was created to assess the environmental effects that could result from further changes to inflow patterns in the Matagorda Bay system.

A bio-energetic model, calibrated using a long-term data set on benthic biomass was developed that related macrobenthic biomass to salinity within the Lavaca-Colorado Estuary (Montagna and Li 1996). This model was applied to the current study to assess the role of freshwater inflow in controlling benthic productivity. The existing model was used to simulate what effects could occur due to the change in freshwater inflow, i.e. altering salinity in the model to observe how benthic productivity responds.

4.2. Modeling Benthic Biomass

Simulations of the Lavaca-Colorado Estuary from 1991-1996 fit the observed data relatively well, however, following the year 2000, simulations predicted a much higher biomass concentration than the observed data. The increase in benthic biomass can be explained by the decrease in predator populations, particularly blue crabs, which releases

predation pressure and could cause prey populations to increase. Numbers of blue crabs caught in the individual bays have been decreasing with a drop in numbers in the year 2000 (Figs. 3.5 and 3.6). In the model, predator density and benthic biomass are inversely correlated, which demonstrates that the model is incomplete and that another environmental factor is causing predator density to decrease and prey biomass to increase throughout the estuary.

4.3. Benthic Biomass Response to Salinity Changes

Simulations of deposit and suspension feeder biomass exhibited responses caused by changes in salinity in both bay systems (Figs. 3.7-3.14). In general, as salinity increased, deposit feeding biomass increased while suspension feeding biomass decreased.

Kalke and Montagna (1991) studied sites in the upper portion of Lavaca River and Bay from 1984 - 1986 to determine the effects of freshwater inflow on macrobenthos. A high freshwater inflow rate caused low salinity species to populate the area, and, therefore, it was determined that freshwater is necessary in the upper portion of the bay to induce recruitment of low salinity species. Following an inflow event, Chironomid larvae (suspension feeders) and *Hobsonia florida* (polychaete) increased in density, as both prefer lower salinity environments. In contrast, the mollusks, *Mulinia lateralis* and *Macoma mitchelli* (suspension feeders), and *Streblospio benedicti* and *Mediomastus californiensis* (deposit feeders) increased in benthic biomass during periods of low freshwater inflow (Kalke and Montagna 1991). These results support the findings of this study, which show that as percent salinity increases, deposit feeder biomass should increase while suspension feeding biomass should decrease.

It was also determined that chlorophyll *a* concentrations increased in the Lavaca River and Bay during high inflow rates, an indication that primary production is stimulated by freshwater (Kalke and Montagna 1991). As salinity increased during periods of low inflow, the chlorophyll *a* concentration decreased due to a growing population of mollusks (Kalke and Montagna 1991).

Rozas et al. (2005) investigated the effect of freshwater inflow in the Breton Sound Estuary, Louisiana, and found releases of freshwater from the Caernarvon

diversion structure lead to an increase in submerged aquatic vegetation (SAV) and dissolved oxygen concentrations. Macrofauna populations also increased in density and biomass with increasing inflow, which was probably due to the growing SAV coverage creating more habitat (Rozas et al. 2005).

Total biomass in Lavaca Bay was found to increase in concentration as salinity increased (Fig. 3.15), an indication that low inflow rates in this bay would be beneficial to the benthic community. Total biomass concentration in Matagorda Bay at first decreased with increasing salinity but then gradually increased (Fig. 3.16). Previous studies examined how benthic macrofaunal community structure varied over space and time in response to changes in inflow in Lavaca Bay and Matagorda Bay (Kinsey and Montagna 2005). The results found Matagorda Bay to be a healthier ecosystem in general compared to Lavaca Bay. There was also a direct relationship between freshwater inflow and salinity on benthic communities. Distinct station differences were found in community structure along salinity gradients, which implies that reduced flows will cause upstream communities to take on characteristics of downstream communities (Kinsey and Montagna 2005).

The ecology of south Texas estuaries has been studied for many years. Montagna and Kalke (1995) observed how freshwater inflow benefits estuaries in south Texas. *Mulina lateralis* was one of the dominant species found and is important as the predominant food source for black drum. This species was frequently found in secondary bays along the Texas coast where freshwater inflow has a large impact. It was concluded that recruitment events for *M. lateralis* are likely initiated by a significant change in salinity (Montagna and Kalke 1995). Freshwater inflow has obvious benefits to estuaries along the Texas coast. Only estuaries with high freshwater inflow rates support productive shellfish industries (Montagna and Kalke 1995).

4.4. Conclusions

This study used long-term data, and a model to predict how altering salinity in the Lavaca-Colorado Estuary might affect the productivity of the macrobenthos population. Based on observed patterns and model predictions, it appears that reducing the freshwater inflow may cause the upper river communities to take on downstream

community appearance, i.e. more salt tolerant species would dominant the community. The Lavaca Bay benthic community appears to benefit from reduced freshwater inflow by increasing in biomass. The macrobenthos in Matagorda Bay appear to decrease in biomass concentration at first, and then gradually start to increase in numbers. This effect is probably due to the benthic community acclimating to the higher salinity, or more salt tolerant species populating the area.

Freshwater inflow into an estuary has been recognized as an important factor in estuary productivity, affecting physical, chemical, and biological aspects of the system. Inflow results in increased circulation, salinity gradients, and sediment transport as well as enhancing the productivity of coastal fisheries (Powell et al. 2002). Nutrients from freshwater inflow become incorporated into the estuarine food web, and, along with an increase in vegetation, nutrients enhance the secondary production in the area (Rozas et al. 2002). It is clear that freshwater inflow is important in maintaining estuarine productivity. Management studies should consider not only the quantity of inflow required, but also seek to determine the regime of timing and magnitude of inflow that is needed to maintain functional, healthy ecosystems.

5. REFERENCES

Armstrong, N.E. 1985. The ecology of open-bay bottoms of Texas: a community profile. Fish and Wildlife Service, U.S. Department of the Interior, Biological Report, 85 (7.12), 105 pp.

Atrill, M.J., S.D. Rundle, and R.M. Thomas. 1996. The influence of drought-induced low freshwater flow on an upper-estuarine macroinvertebrate community. *Water Research* 30; 261-268.

Baird, C., M. Jennings, D. Ockerman, and T. Dybala. 1996. Characterization of nonpoint sources and loadings to Corpus Christi Bay National Estuary Program study area. EPA Report: CCBNEP-05. January 1996. 256 pp.

Brown D. and P. Rothery. 1993. Models in biology: mathematics, statistics and computing. John Wiley & Sons, 688 pp.

Carrada, G.C. 1983. Modeling of the Gulf of Naples, *In:* Quantitative analysis and simulation of Mediterranean coastal ecosystems: The Gulf of Naples, a case study (eds: G. Carrada, T. Hopkins, L. Jeftie and S. Morcos), *UNESCO Reports in Marine Science* 20: 80-153.

Chapman, E.R. 1966. The Texas basins project. In: R.F. Smith, A.H. Swartz, and W.H. Massmann (eds.), A symposium on estuarine fisheries. *American Fisheries Society* 95:83-92. Special Publ. No. 3. 154 pp.

Dailey, J.A., J.C. Kana, and L.W. McEachron. 1991. Trends in relative abundance and size of selected finfishes and shellfishes along the Texas coast: November 1975-December 1990. Texas Parks and Wildlife Department Management Data Series 74. Austin, Texas, 128 pp.

de Hoop, B.J., P.M.J. Herman, H. Scholten, and K. Soetaert. 1989. SENECA 1.5: A simulation environment for ecological application. Netherlands Institute of Ecology, center for Estuarine and Coastal Ecology, 180 pp.

Engle, V.D. and J.K. Summers. 2000. Biogeography of benthic macroinvertebrates in estuaries along the Gulf of Mexico and western Atlantic coasts. *Hydrobiologia.* 436:17-33.

Kalke, R.D. 1981. The effects of freshwater inflow on salinity and zooplankton populations at four stations in the Nueces-Corpus Christi and Copano-Aransas Bay systems, TX from October 1977-May 1975. *In:* R.D. Cross and D.L. Williams (eds.), Proceeding of the International Symposium on Freshwater Inflow to Estuaries. Washington, DC: U.S. Dept. Int. Fish & Wildlife, pp. 454-471.

Kalke, R.D. and P.A. Montagna. 1989. A Review: The effect of freshwater inflow on the benthos of three Texas estuaries, pp. 185-218. *In:* P.A. Montagna (principal investigator) Nitrogen Process Studies (NIPS): The Effect of Freshwater Inflow on Benthos Communities and Dynamics. University of Texas Technical Report No. TR/89-011. 370 pp.

Kalke, R.D. and P.A. Montagna. 1991. The effect of freshwater inflow on macrobenthos in the Lavaca River Delta and Upper Lavaca Bay, Texas. *Contributions in Marine Science.* 32: 49-71.

Keen, R.E. and J.D. Spain. 1992. Computer Simulation in Biology, a Basic Introduction. John Wiley and Sons, New York, 516 pp.

Kinsey, J. and P.A. Montagna. 2005. Response of benthic organisms to external conditions in Matagorda Bay. Annual Progress Report to the Lower Colorado River Authority. University of Texas, Marine Science Institute, Technical Report No. TR/05-004, Port Aransas, Texas, 41 pp.

Li, J., M. Vincx, and P.M.J. Hermen. 1996. A model for nematode dynamics in the Westerschelde Estuary. *Ecological Modeling*, 90: 271-284.

Longley, W.L. (ed.).1994. Freshwater inflows to Texas bays and estuaries: ecological relationships and methods for determination of needs Texas Water Development Board and Texas Parks and Wildlife Department, Austin, TX. 386 pp.

Lotka, A.J. 1925. Elements of physical biology. Williams & Wilkins, Baltimore, MD, 460 pp.

Mannino, B. A. and P. A. Montagna. 1994. Effects of freshwater inflow and sediment characteristics on small scale spatial variation of macrobenthic community structure in Nueces Bay. Thesis Report. 157 pp.

Merritt, R.W. and K.W. Cummins (eds). 1984. An Introduction to the Aquatic Insects of North America. Kendall/Hunt Publication Company, Dobuque, Iowa, 722 pp.

Montagna, P.A. 1994. Inflow needs assessment: Effect of the Colorado River diversion on benthic communities. The University of Texas Marine Science Institute Technical Report Number TR/94-001, Port Aransas, Texas, 63 pp.

Montagna, P.A. and J. Li. 1996. Modeling and monitoring long-term change in macrobenthos in Texas estuaries. Final Report to the Texas Water Development Board. University of Texas, Marine Science Institute, Technical Report No. TR/96-001, Port Aransas, Texas, 149 pp.

Montagna, P.A. and R.D. Kalke. 1992. The effect of freshwater inflow on meiofaunal and macrofaunal populations in the Guadalupe and Nueces estuaries, Texas. *Estuaries*, 15: 307-326.

Montagna, P.A. and R.D. Kalke. 1995. Ecology of infaunal Mollusca in south Texas estuaries. *American Malacolofical Bulletin*, 11: 163-175.

Montagna, P.A. and R.D. Kathmann. 2006. Bioaccumulation of mercury in Lavaca Bay, Texas assessed by using stable isotopes. In preparation.

Montagna, P.A., D.A. Stockwell, and R.D. Kalke. 1993. Dwarf surfclam *Mulina lateralis* (Say, 1822) populations and feeding during the Texas brown tide event. *Journal of Shellfish Research*, 12: 433-442.

Montagna, P.A., R.D. Kalke, and C. Ritter. 2002. Effect of restored freshwater inflow on macrofauna and meiofauna in Upper Rincon Bayou, Texas, USA. *Estuaries,* 25: 1436-1447.

Odum, H.T. 1971. Environment Power and Society. J. Wiley and Sons, New York.

Odum, H.T. 1983. Systems Ecology (reprinted as Ecological and General Systems). University Press of Colorado, Niwot, CO, 644 pp.

Oglesby, R.T. 1967. Biological and physiological basis of indicator organisms and communities: Section I – Biological basis, p. 267-269. In: T.A. Olson and F.J. Burgess (eds.), *Pollution and Marine Ecology.* Interscience Publishers, New York.

Powell, G.L., J. Matsumoto, and D.A. Brock. 2002. Methods for determining minimum freshwater inflow needs of Texas bays and estuaries. *Estuaries*, 25: 1262-1274.

Redfield, A.C. 1934. On the proportions of organic derivations in seawater and their relation to the composition of plankton. *In*: R.J. Daniel (ed) James Johnson Memorial Volume, University Press of Liverpool, 177-192 pp.

Rozas, L.P., T.J. Minello, I. Munuera-Fernandez, B. Fry, and B. Wissel. 2005. Macrofaunal distributions and habitat change following winter-spring releases of freshwater into the Breton Sound estuary, Louisiana (USA). *Estuarine Coastal and Shelf Science*, 65: 319-336.

Stockwell, D.A. 1989. Effects of freshwater inflow on the primary production of a Texas coastal bay system. Final Report, Data Synthesis Study (NIPS), The University of Texas Marine Science Institute, Technical Report No. TR/89-010, Port Aransas, Texas.

Whitledge, T.E. 1989. Nutrient distributions and dynamics in Lavaca, San Antonio and Nueces/Corpus Christi Bays in relation to freshwater inflow. Final Report, Data Synthesis Study (NIPS), The University of Texas Marine Science Institute, Technical Report No. TR/89-007, Port Aransas, Texas.

Wohlschlag, D.E., J.M. Wakeman, R. Vetter, and R.G. Ilg. 1977. Analysis of freshwater inflow effects on metabolic stresses of South Texas bay and estuarine fishes: continuation and extension. Report to Texas Department of Water Resources, by Marine Science Institute, University of Texas at Austin, Texas, 105 pp.