



Coastal Protection and Restoration Authority  
150 Terrace Avenue, Baton Rouge, LA 70802 | [coastal@la.gov](mailto:coastal@la.gov) | [www.coastal.la.gov](http://www.coastal.la.gov)

## 2017 Coastal Master Plan

---

# Attachment C3-15: Gulf Menhaden, *Brevoortia patronus*, Habitat Suitability Index Model



Report: Final

Date: April 2017

Prepared By: Shaye E. Sable (Dynamic Solutions), Ann C. Hijuelos (The Water Institute of the Gulf), Ann M. O'Connell (University of New Orleans), and James P. Geaghan (Louisiana State University)

## Coastal Protection and Restoration Authority

This document was prepared in support of the 2017 Coastal Master Plan being prepared by the Coastal Protection and Restoration Authority (CPRA). CPRA was established by the Louisiana Legislature in response to Hurricanes Katrina and Rita through Act 8 of the First Extraordinary Session of 2005. Act 8 of the First Extraordinary Session of 2005 expanded the membership, duties and responsibilities of CPRA and charged the new authority to develop and implement a comprehensive coastal protection plan, consisting of a master plan (revised every five years) and annual plans. CPRA's mandate is to develop, implement and enforce a comprehensive coastal protection and restoration master plan.

### **Suggested Citation:**

Sable, S. E., Hijuelos, A. C., O'Connell, A. M., and Geaghan, J. P. (2017). *2017 Coastal Master Plan: Attachment C3-15: Gulf Menhaden, Brevoortia patronus, Habitat Suitability Index Models*. Version Final. (pp. 1-30). Baton Rouge, Louisiana: Coastal Protection and Restoration Authority.

## Acknowledgements

This document was developed as part of a broader Model Improvement Plan in support of the 2017 Coastal Master Plan under the guidance of the Modeling Decision Team (MDT):

- The Water Institute of the Gulf - Ehab Meselhe, Alaina Grace, and Denise Reed
- Coastal Protection and Restoration Authority (CPRA) of Louisiana – Mandy Green, Angelina Freeman, and David Lindquist

Buddy “Ellis” Clairain, Moffatt and Nichol, served as subtask leader on the effort, participated in coordination meetings, and provided comments on earlier versions of this report.

Leland Moss, Amanda Richey, and Camille Stelly assisted with preparing graphics and summaries of literature used in this report.

The Louisiana Department of Wildlife and Fisheries provided the data used in the analysis as well as input throughout the project. The following individuals from LDWF participated in coordination meetings, provided comments, and helped answer questions regarding the datasets used in the analysis:

- Harry Blanchet
- Michael Harden
- Rob Bourgeois
- Lisa Landry
- Brian Lezina
- Bobby Reed
- Dawn Davis
- Jason Adriance
- Glenn Thomas
- Patrick Banks

This effort was funded by the Coastal Protection and Restoration Authority (CPRA) of Louisiana under Cooperative Endeavor Agreement Number 2503-12-58, Task Order No. 03.

## Executive Summary

The 2012 Coastal Master Plan utilized Habitat Suitability Indices (HSIs) to evaluate potential project effects on fish and shellfish species. Even though HSIs quantify habitat condition, which may not directly correlate to species abundance, they remain a practical and tractable way to assess changes in habitat quality from various restoration actions. As part of the legislatively mandated five year update to the 2012 plan, the fish and shellfish habitat suitability indices were revised using existing field data, where available, to develop statistical models that relate fish and shellfish abundance to key environmental variables. The outcome of the analysis resulted in improved, or in some cases entirely new, suitability indices containing both data-derived and theoretically-derived relationships. This report describes the development of the habitat suitability indices for juvenile and adult Gulf menhaden, *Brevoortia patronus*, for use in the 2017 Coastal Master Plan modeling effort.

## Table of Contents

---

Acknowledgements .....	iii
Executive Summary .....	iv
List of Tables.....	vi
List of Figures.....	vi
List of Abbreviations .....	vii
1.0 Species Profile .....	1
2.0 Approach .....	4
2.1 Seines .....	5
2.2 Experimental Gill Nets.....	7
2.3 Statistical Analysis .....	9
3.0 Results .....	10
3.1 Seines .....	10
3.2 Experimental Gill Nets.....	11
4.0 Habitat Suitability Index Model for Juvenile Gulf Menhaden.....	13
4.1 Applicability of the model .....	13
4.2 Response and Input Variables .....	13
5.0 Habitat Suitability Index Model for Adult Gulf Menhaden .....	18
5.1 Applicability of the model .....	18
5.2 Response and Input Variables .....	18
6.0 Model Verification and Future Improvements.....	21
7.0 References.....	22

## List of Tables

---

Table 1: Habitat Requirements for Gulf Menhaden Life Stages.....	4
Table 2: List of Selected Effects with Parameter Estimates and their Level of Significance for the Resulting Polynomial Regression in Equation 1.....	10
Table 3: List of Selected Effects with Parameter Estimates and their Level of Significance for the Resulting Polynomial Regression in Equation 2.....	12

## List of Figures

---

Figure 1: Gulf Menhaden Life Cycle Diagram from Christmas et al. (1982). ....	2
Figure 2: Space-Time Plot by Life Stage for Gulf Menhaden Showing Relative Abundance in the Upper, Mid, and Lower Region of the Estuary and the Inner and Outer Shelf Regions by Month..	3
Figure 3: Length-Frequency Distribution of Gulf Menhaden Caught in the 50 Foot Seine Samples for Louisiana. ....	6
Figure 4: Mean CPUE of Gulf Menhaden by Month for Each Year in the 50 Foot Seine Samples. ....	7
Figure 5: Length-Frequency Distribution of Gulf Menhaden Caught in the Gill Net Samples for Louisiana. ....	8
Figure 6: Mean CPUE of Gulf Menhaden by Month for Each Year in the Gill Net Samples. ....	8
Figure 7: Surface Plot for the Polynomial Regression in Equation 1 over the Range of Salinity and Temperature Values and using a Mean Day of April 15 in the Equation.....	11
Figure 8: Plot for the Polynomial Regression in Equation 2 over the Range of Salinity and Temperature Values and using a Mean Day of June 29 (day 180) in the Equation. ....	12
Figure 9: Surface Plot Demonstrating the Predicted Suitability Index (0-1) for Juvenile Gulf Menhaden in Relation to Salinity and Temperature and Resulting from the Back-Transformation and Standardization of the Polynomial Regression in Equation 1. ....	14
Figure 10: The Suitability Index for Juvenile Gulf Menhaden in Relation to the Percent Emergent Vegetation (Percent Land = $V_2$ ). ....	15
Figure 11: Holling Type III Functional Response (Holling, 1959) Fit to Data Describing Juvenile Gulf Menhaden Ingestion Rate by <i>Chl a</i> Concentration (taken from Lynch, 2007). ....	16
Figure 12: The Resulting Suitability Index ( $SI_3$ ) for Juvenile Gulf Menhaden in Relation to <i>Chlorophyll a</i> Concentration in a 500 X 500 m Cell. ....	17
Figure 13: Surface Plot Demonstrating the Predicted Suitability Index (0-1) for Adult Gulf Menhaden in Relation to Salinity and Temperature and Resulting from the Back-Transformation and Standardization of the Polynomial Regression in Equation 2. ....	19
Figure 14: The Suitability Index for Adult Gulf Menhaden in Relation to the Percent Land = $V_2$ . ....	20

## List of Abbreviations

---

Chl <i>a</i>	Chlorophyll <i>a</i>
CPRA	Coastal Protection and Restoration Authority
CPUE	Catch per unit effort
DO	Dissolved oxygen
HSI	Habitat Suitability Index
ICM	Integrated Compartment Model
LDWF	Louisiana Department of Wildlife and Fisheries
SI	Suitability Index
SL	Standard length
SAS	Statistical Analysis Software
SAV	Submerged aquatic vegetation
TL	Total length
YOY	Young-of-year

## 1.0 Species Profile

Gulf menhaden are pelagic, schooling planktivores found primarily in the Gulf of Mexico, extending from southwestern Florida to the Yucatan Peninsula of Mexico. The species is most abundant from Apalachicola, Florida to Matagorda Bay Texas (Pattillo et al., 1997). Menhaden play a critical ecosystem role in that they are both primary consumers and generalist filter feeders (Ahrenholz, 1991; Deegan, 1986; Olsen et al., 2014) and prey to a wide spectrum of higher level predators (Vaughan et al., 2007).

There is an extensive commercial fishery for Gulf menhaden that dates back to the late 19<sup>th</sup> century (Nicholson, 1978). The fishery peaked at 982,800 tons during the 1984 fishing year, while the 2004 data had Louisiana landings at 468,736 tons, making up 11% of all commercial landings in the United States (Vaughan et al., 2007). The majority of the catch is caught in Louisiana waters in large part because purse seining is still legal in Louisiana unlike in Florida and Alabama (Vanderkooy & Smith, 2002). There is no recreational fishing for menhaden as an end catch, although it is very useful as a bait fish for some of the dominant recreational fishing (Pattillo et al., 1997).

Populations are influenced by hurricanes and the hypoxic “dead” zone in the northern Gulf of Mexico. Hurricanes Katrina and Rita affected the population both positively in that fishing effort decreased substantially and negatively in that many larval and juvenile habitats were destroyed (Vaughan et al., 2007). The “dead” zone likely does not directly cause large fish kills but rather causes Gulf menhaden schools to shift and concentrate in oxygenated areas which might make them more susceptible to fishing pressure (Smith, 2001). Hypoxic conditions only threaten Gulf menhaden populations if they occur in the estuaries or basins where higher dissolved oxygen (DO) waters are not easily accessible (Christmas et al., 1982).

Figure 1 is the conceptual life history model from Christmas et al. (1982) and demonstrates the life cycle for Gulf menhaden including the general movement and locations of the life stages on the continental shelf and within the estuary. Spawning occurs in the fall through early spring on the shelf. Eggs are buoyant and hatching occurs within 1-3 days (Lassuy, 1983 and references therein). Yolk-sac larvae are carried inshore and to the estuaries by currents (Figure 1). The feeding larval stage begins around 2.6 mm standard length (SL) and lasts three to five weeks (Christmas et al., 1982 and references therein). Feeding larvae continue to move further up the estuary into shallow bays and river tributaries (Figure 1). Metamorphosis to the juvenile stage occurs around 19 mm SL in the low salinity, nutrient-rich waters in the upper estuary and around river mouths (Christmas et al., 1982). Juveniles remain in the lower salinity regions of the upper estuary until they reach a size around 40 mm SL. Late juveniles (40 mm – 85 mm SL) move further down the estuary and into deeper waters (Figure 1). Sexual maturation occurs after two growing seasons. Adults typically range in size from 102-250 mm fork length with an average lifespan of 2-3 years (Pattillo et al., 1997 and references therein; Deegan, 1990). Adults move inshore and up into the estuary and rivers during spring and summer (Deegan, 1990) and then on to the shelf to spawn during the fall and winter (Figure 1) with very little alongshore (east/west) movement (Shaw et al., 1985).

The spatial and temporal distribution of Gulf menhaden life stages within the estuary is summarized by a space-time plot (Figure 2). The space-time plot indicates the relative abundance of each life stage throughout the year in each region: upper, mid, and lower estuary, and inner and outer shelf. The regions of the estuary are characterized by similar habitats and environmental conditions (Table 1). Generally, the upper estuary is primarily comprised of shallow creeks and ponds with the greatest freshwater input, lowest average



salinities, and densest fresh and intermediate marsh and submerged aquatic vegetation. The mid estuary is comprised of more fragmented intermediate and brackish marsh vegetation with salinities usually between 5 and 20 ppt. The lower estuary is comprised mainly of open water habitats with very little marsh, deeper channels and canals and barrier islands with salinities generally above 20 ppt. The inner and outer shelf regions are defined as the open marine waters divided by the 20 meter isobath.

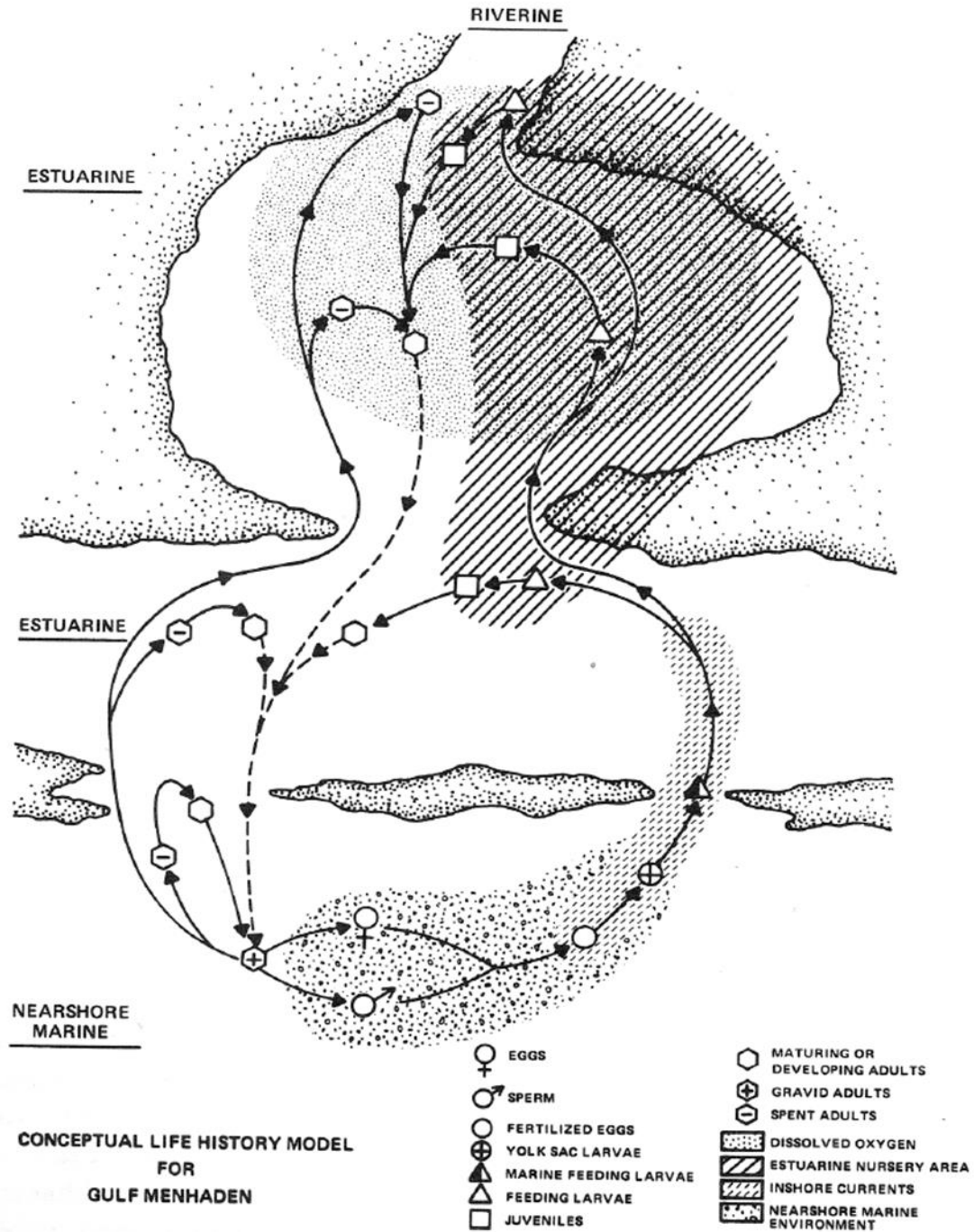


Figure 1: Gulf Menhaden Life Cycle Diagram from Christmas et al. (1982).

			J	F	M	A	M	J	J	A	S	O	N	D
Egg	Estuary	Upper												
		Mid												
		Lower												
	Shelf	Inner												
		Outer												
Larvae	Estuary	Upper												
		Mid												
		Lower												
	Shelf	Inner												
		Outer												
Juvenile	Estuary	Upper												
		Mid												
		Lower												
	Shelf	Inner												
		Outer												
Adult	Estuary	Upper												
		Mid												
		Lower												
	Shelf	Inner												
		Outer												

**Figure 2: Space-Time Plot by Life Stage for Gulf Menhaden Showing Relative Abundance in the Upper, Mid, and Lower Region of the Estuary and the Inner and Outer Shelf Regions by Month.** White cells indicate the life stage is not present, light grey cells indicate the life stage is at moderate abundance, dark grey cells indicate abundant, and black indicates highly abundant.

**Table 1: Habitat Requirements for Gulf Menhaden Life Stages.** Pattillo et al., (1997) was the primary source used to construct the table and the reader should refer to references therein.

Life Stage: Process	Salinity (ppt) Optimum (Range)	Temperature (°C) Optimum (Range)	Depth (m)	Preferred Substrate	DO (ppm)
Egg	>29	17-20	-	-	>3
Larvae	25-29 (2-30)	12-30 (2.5-35.5)	-	Soft mud for organic content	>3
Juveniles	5-10 (5-30)	-	-	-	>3
Adults: Foraging	20-29 (0-67)	-	Spring/ summer: 1.8-14.6 Fall/winter: 7.3-87.8	-	>3
Spawning	>29	-	<18 (2-128)	-	>3

## 2.0 Approach

The statistical analyses used the data collected by the Louisiana Department of Wildlife and Fisheries' (LDWF) long-term Fisheries-Independent Monitoring program conducted for coastal marine fish and shellfish species. The program employs a variety of gear types intended to target particular groups of fish and shellfish; although all species caught, regardless if they are targeted, are recorded in the database. Due to the variable catch efficiency of the gear types, catch per unit effort (CPUE) for Gulf menhaden was estimated as total catch per sample event for each gear type separately. The LDWF gears that caught consistent and relatively high abundances of the species of interest over time were used for the statistical analysis.

Data from the 50 ft seine and the 750 ft experimental gill net were evaluated for statistical relationships among the associated environmental data and Gulf menhaden CPUE. The 50 ft seines have historically been sampled once or twice per month at fixed stations within each coastal basin by LDWF to provide abundance indices and size distributions of the small fishes and invertebrates using the shallow shoreline habitats of the estuaries (LDWF, 2002). The seine is 6 ft in depth and has a 6 ft by 6 ft bag in the middle of the net and a mesh size of 1/4 in bar. The seines consistently sample high numbers of juvenile (i.e., young-of-year (YOY)) Gulf menhaden and the gear type is used for a juvenile recruitment index in Louisiana waters for the regional stock assessment on Gulf menhaden (SEDAR, 2013). The 750 ft experimental gill nets have historically been sampled once per month at fixed stations from October through March and twice per month from April through September to provide abundance indices and sizes for adult finfish such as spotted seatrout, Gulf menhaden and red drum. The experimental gill nets are 750 ft long, 8 ft deep, and comprised of five 150 ft panels of 1 in, 1-1/4 in, 1-1/2 in, 1-3/4 in, and 2 in bar mesh (LDWF, 2002). The experimental gill net samples conducted by LDWF are used as a fisheries-independent index for adult Gulf menhaden in the northern Gulf of Mexico stock

assessment (SEDAR, 2013) since the gear type consistently collects relatively high numbers of adult Gulf menhaden.

LDWF also measures temperature, conductivity, salinity, turbidity, DO and station depth in concurrence with the biological (catch) samples. Conductivity and salinity were highly correlated, so for this analysis only salinity was used. Station depth was not used in the analysis as it characterizes the station and is not measured to serve as an independent variable for CPUE. DO has only been measured consistently since 2010, so DO was not included in the analyses since the minimal sample size greatly limits the ability to statistically test for significant species-environment relationships. For the analyses, the associated turbidity, salinity, and temperature measurements were evaluated with the juvenile and adult CPUE from the seine and gill net station samples. Salinity and temperature are measured at the top and bottom of the water column and an average of their measurements were used for the analyses. Examination of the top and bottom measurements usually showed no or little difference between the two, and often only top or bottom salinity was collected such that the mean value was the result from the single measurement.

Other important variables such as prey concentration (using Chlorophyll concentration as a proxy; Friedland et al., 1996) and vegetated/non-vegetated habitat are not available from the LDWF datasets. However, a cursory examination of the catch and length data from the seines and gill nets was made to support the premise that smaller juveniles would be caught near the shallow vegetated habitats (Baltz & Jones, 2003). The primary focus of the statistical analysis was on the water quality data collected by LDWF, and then theoretical, literature-based relationships for prey concentration and wetland vegetation were incorporated.

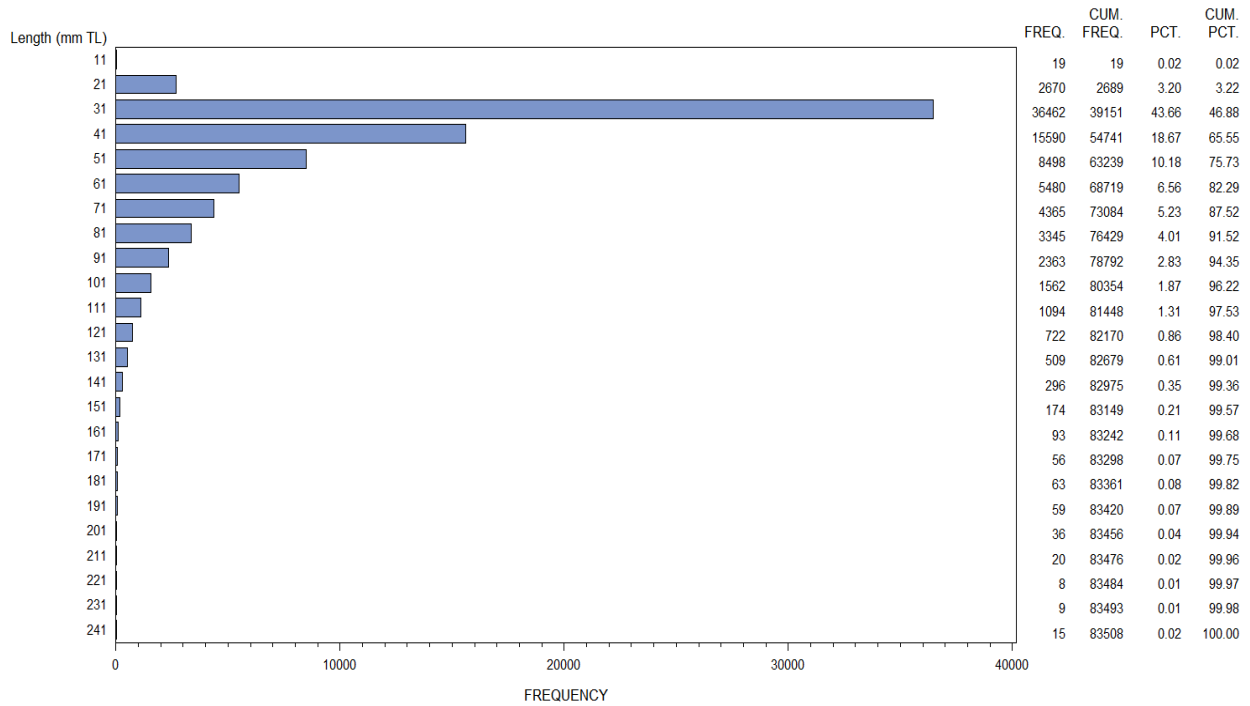
Length distributions of the species were plotted by each gear type to determine if the catch was comprised of primarily juveniles, adults, or a combination of the life stages. The mean monthly CPUE by year for the species in each gear was also estimated and then plotted to determine which months had the highest consistent catch over time and which months had variable and low or no catch over time. These plots allowed for subsetting of the data by the months of highest species catch in order to reduce the amount of zeroes in the dataset. In this way, the analysis was not focused on describing environmental effects on species catch when the species typically are not in the estuaries or else at very low numbers.

## 2.1 Seines

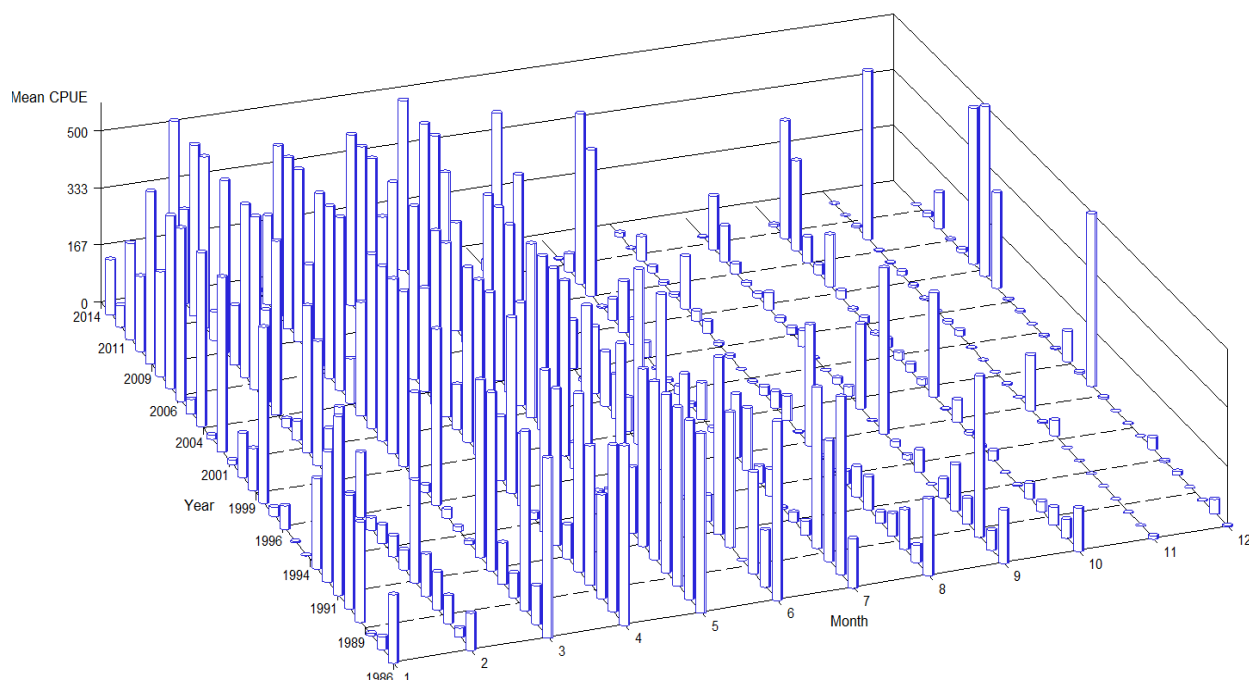
The length distribution of Gulf menhaden caught in the 50 ft seine samples indicated that nearly all were juveniles (i.e., YOY) less than 100 mm total length (TL; Figure 3). Gulf menhaden typically mature after two growing seasons, at lengths around 110-130 mm TL (Deegan, 1990). Sizes above 105 mm TL constituted less than 3% of the total Gulf menhaden catch in seines. Therefore, it was assumed that the estimated CPUE from the 50 ft seine samples were representative of juvenile Gulf menhaden.

The plot of mean CPUE by month for each year indicated juvenile Gulf menhaden catch in the 50 ft seines was consistently highest during January through July (Figure 4). This seasonality of juvenile Gulf menhaden catch in the seine samples coincides with their life history information of peak spawning on the shelf from about October through March with juveniles moving into and up the estuaries about 6 weeks after spawning (Ahrenholz, 1981). Therefore, the seine data from January through July were used for the statistical evaluation of the juvenile Gulf menhaden CPUE-environment relationships, and the months of August through December were dropped from the analysis as those months showed low and inconsistent catch of Gulf menhaden in the seines (Figure 4).

The seine data collected in January through July over all available years of record (1986-2013) across the Louisiana coastline were evaluated to determine if the averaged salinity, averaged water temperature, and/or turbidity data were related to the juvenile Gulf menhaden CPUE. Day of year and its squared term were also included in the model to account for the seasonal variation in juvenile Gulf menhaden abundance within the estuaries.



**Figure 3: Length-Frequency Distribution of Gulf Menhaden Caught in the 50 Foot Seine Samples for Louisiana.**



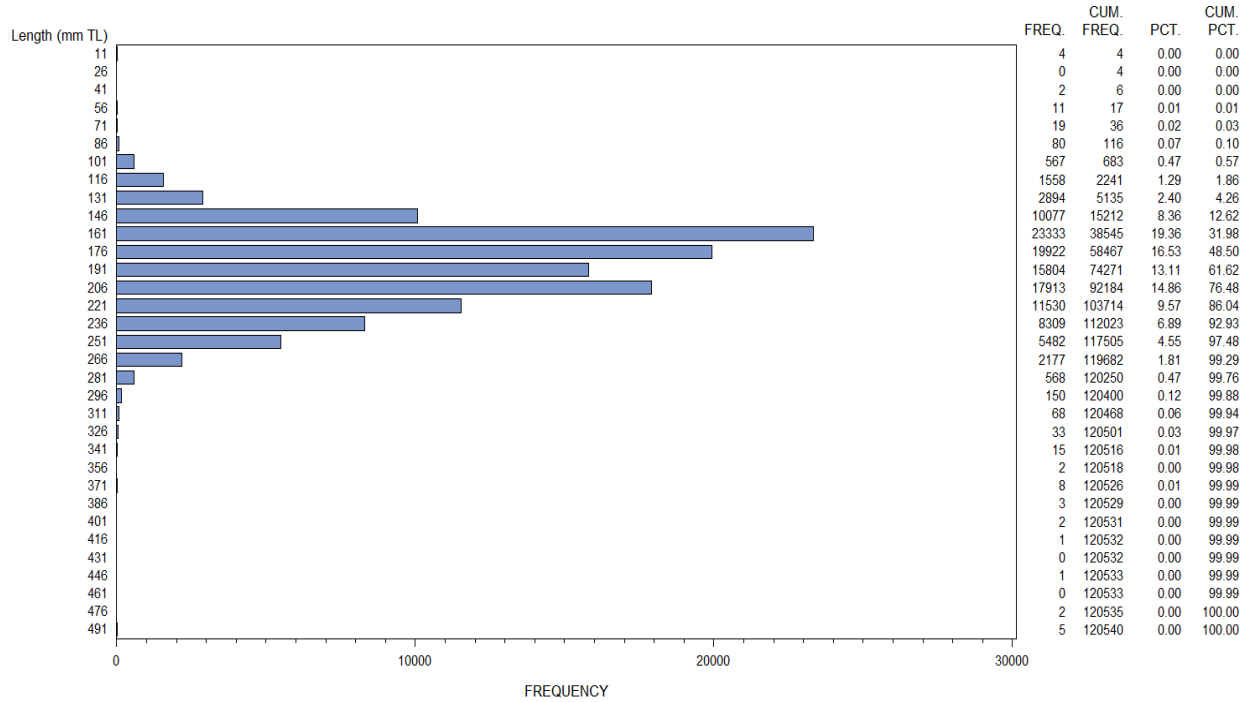
**Figure 4: Mean CPUE of Gulf Menhaden by Month for Each Year in the 50 Foot Seine Samples.**

## 2.2 Experimental Gill Nets

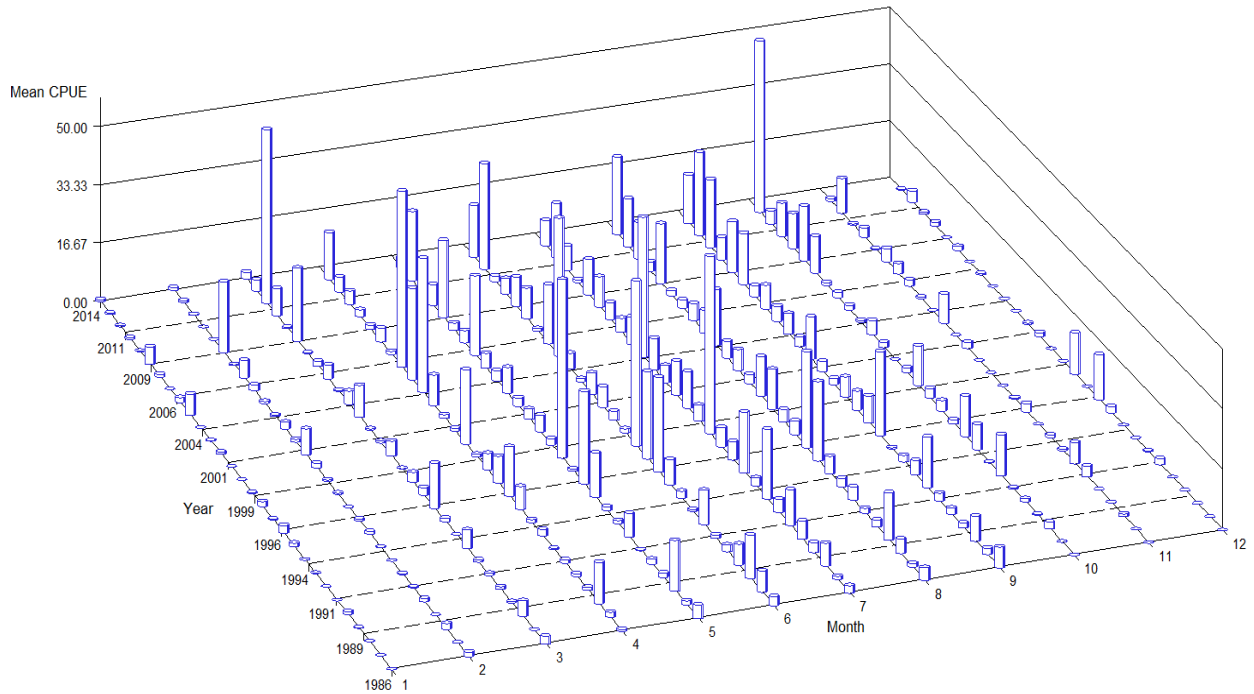
The length distribution of Gulf menhaden caught in the experimental gill net samples indicated that nearly all were adults (i.e., Age-1+, or past their first year) greater than 102 mm TL (Figure 5). Sizes below 102 mm TL constituted less than 2% of the total Gulf menhaden catch. Therefore, it was assumed that the estimated CPUE from the gill net samples were representative of adult Gulf menhaden.

The plot of mean CPUE by month for each year indicated adult Gulf menhaden catch in gill nets is most evident from March through October (Figure 6). This seasonality of adult Gulf menhaden catch in the gill nets coincides with their life history information of peak spawning on the shelf from about October through March (Ahrenholz, 1981). Therefore, the gill net data from March through October were used for the statistical evaluation of the adult Gulf menhaden CPUE-environment relationships.

The gill net data collected from March through October over all available years of record (1986-2013) across the Louisiana coastline were evaluated to determine if the averaged salinity, averaged water temperature, and/or turbidity data were related to the adult Gulf menhaden CPUE. Day of year and its squared term were also included in the model to account for the seasonal variation in Gulf menhaden abundance within the estuaries.



**Figure 5: Length-Frequency Distribution of Gulf Menhaden Caught in the Gill Net Samples for Louisiana.**



**Figure 6: Mean CPUE of Gulf Menhaden by Month for Each Year in the Gill Net Samples.**

## 2.3 Statistical Analysis

The statistical approach was developed to predict mean CPUE in response to environmental variables for multiple species of interest and was designed for systematic application across the coast. The methods described in detail below rely on the use of polynomial regressions and commonly-used Statistical Analysis Software (SAS) procedures that can be consistently and efficiently applied to fishery-independent count data for species with different life histories and environmental tolerances. As a result, the same statistical approach was used for each of the fish and shellfish species that are being modeled with HSI in the 2017 Coastal Master Plan.

The species CPUE data were transformed using  $\ln(\text{CPUE}+1)$ . Given that the sampling is standardized and CPUE represent discrete values (total catch per sample event),  $\ln(\text{CPUE}+1)$  transformation was appropriate for the analysis. Distributions that are reasonably symmetric often give satisfactory results in parametric analyses, due in part to the effectiveness of the Central Limit Theorem and in part to the robustness of regression analysis. Nevertheless, it is expedient to approximate normality as closely as possible prior to conducting statistical analyses. The negative binomial distribution is common for discrete distributions for samples consisting of counts of organisms when the variance is greater than the mean. In these cases, the natural logarithmic transformation is advantageous in de-emphasizing large values in the upper tail of the distribution. As a result, the data were natural log-transformed for the analysis. The transformation worked generally well in meeting the assumptions of the regression analysis.

Predictive models can often be improved by fitting some curvature to the variables by including polynomial terms. This allows the rate of a linear trend to diminish as the variable increases or decreases. Scientists have previously described relationships of estuarine species to factors like salinity and temperature as nonlinear, and it can be expected that the Gulf menhaden respond nonlinearly to environmental variables as well (i.e., they have optimal values for biological processes; Pérez-Castañeda & Defeo, 2005; Villarreal et al., 2003). Thus, polynomial regression was chosen for the analyses. Another consideration in modeling the abundance of biota is the consistency of the effect of individual variables across the level of other variables. The effect of temperature, for example, may not be consistent across all levels of salinity. These changes can be modeled by considering interaction terms among the independent variables in the polynomial regression equation.

Given the large number of potential variables and their interactions, it is prudent to use an objective approach, such as stepwise procedures (Murtaugh, 2009), to select the variables for inclusion in the development of the model. The SAS programming language has a relatively new procedure called PROC GLMSelect, which is capable of performing stepwise selection where at each step all variables are rechecked for significance and may be removed if no longer significant. However, there are a number of limitations to PROC GLMSelect. GLMSelect is intended primarily for parametric analysis where the assumption of a normal distribution is made. It does not differentially handle random variables, so modern statistical techniques involving random components, non-homogeneous variance and covariance structure cannot be used with this technique. As a result, PROC GLMSelect was used as a 'screening tool' to identify the key variables (linear, polynomial, and interactions), while the SAS procedure PROC MIXED was used to calculate parameter estimates and ultimately develop the model. PROC MIXED is intended primarily for parametric analyses, and can be used for regression analysis. Although it is capable of fitting analyses with non-homogenous variances and other covariance structures, the ultimate goal of the analysis was to predict mean CPUE, not hypothesis testing or for placing confidence intervals on the model estimates. The statistical significance levels for the resulting parameters were used to evaluate whether the parameters of the polynomial regression model adequately described the predicted mean ( $p < 0.05$ ).



## 3.0 Results

### 3.1 Seines

The regression analyses for the seines were initially run with salinity, temperature and turbidity as independent variables, but the range in turbidity values turned out to be very small with nearly all secchi depth measurements at the sampling stations being less than 2 ft. Including turbidity (secchi depth in feet) within the polynomial regression equation caused much more flipping (i.e., quickly changing direction) within the function and unrealistic predicted CPUE values. Therefore, turbidity was dropped as an independent variable and the statistical analysis of the seines was re-run with temperature, salinity, and day.

The resulting polynomial regression model from the seine analysis describes juvenile Gulf menhaden CPUE (natural log transformed) in terms of all significant effects from salinity and temperature, the squared terms and the interactions, and day of year (Equation 1; Table 2). Surface response plots are used to visually depict the relationships for the two interacting independent variables (x,y) and CPUE (z) with the day variable set to its mean value (Figure 7). The scatter plot overlaid on the surface response shows the LDWF data used to develop the polynomial regression (Figure 7).

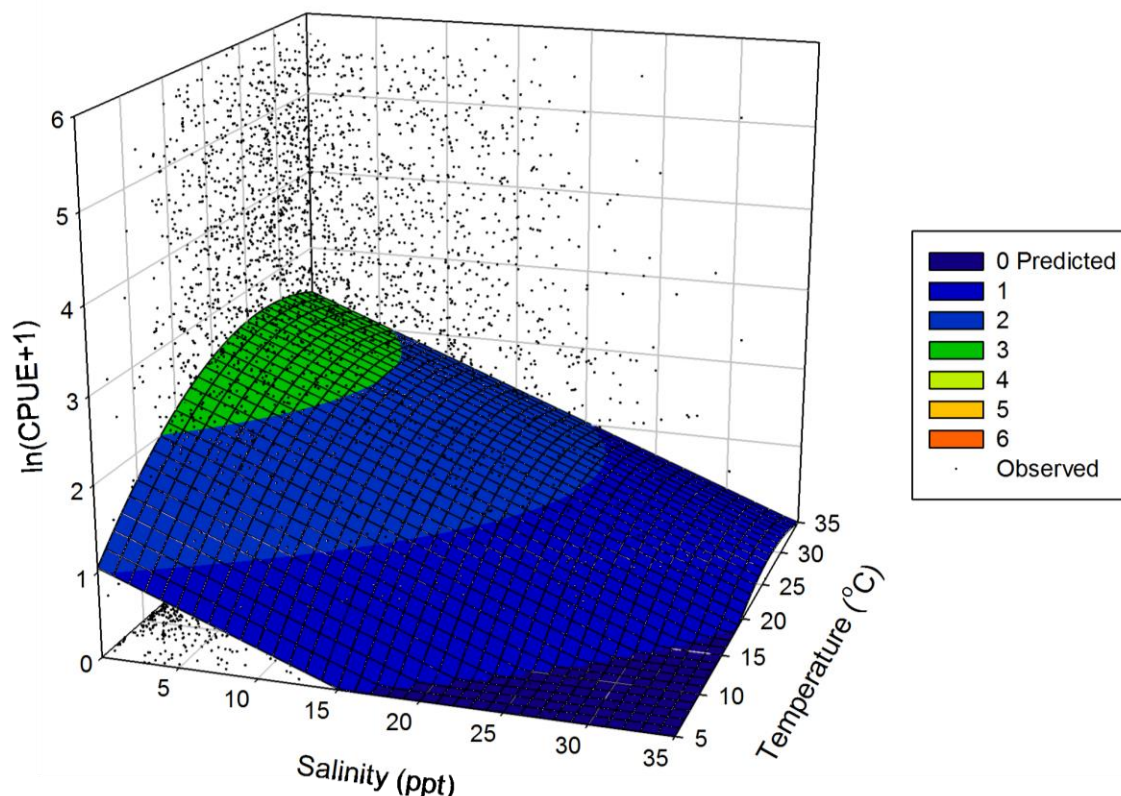
The surface response plot (Figure 7) shows that juvenile Gulf menhaden abundance [ $\ln(\text{CPUE}+1)$ ] is a peak function of temperature. Juvenile Gulf menhaden catch in the seines increases from low temperatures of about 5 °C, gradually peaks from about 20°C through 30°C and then decreases again at higher temperatures. Juvenile catch in seines increases linearly with decreasing salinities for all temperatures (Figure 7). This result agrees with the life history information (Figure 1 and Table 1) that juvenile Gulf menhaden move and stay in the upper, low-salinity regions of estuaries to feed and grow. The surface response equation is truncated to predict zero catch at salinities greater than 20 ppt when temperatures fall below 15 °C because there were no catch data for juvenile Gulf menhaden at these temperature and salinity combinations.

$$\ln(\text{CPUE} + 1) = -0.4572 + 2.6189(\text{Day}) - 1.3848(\text{Day}^2) - 0.06918(\text{Salinity}) + 0.1778(\text{Temperature}) - 0.00331(\text{Temperature}^2) \quad (1)$$

**Table 2: List of Selected Effects with Parameter Estimates and their Level of Significance for the Resulting Polynomial Regression in Equation 1.**

Selected Effects	Parameter Estimate <sup>1</sup>	p value
Intercept	-0.4572	0.1118
Day	2.6189	<.0001
Day <sup>2</sup>	-1.3848	<.0001
Salinity	-0.06918	<.0001
Temperature	0.1778	<.0001
Temperature <sup>2</sup>	- 0.00331	<.0001

<sup>1</sup> Significant figures may vary among parameters due to rounding or accuracy of higher order terms.



**Figure 7: Surface Plot for the Polynomial Regression in Equation 1 over the Range of Salinity and Temperature Values and using a Mean Day of April 15 in the Equation.** The scatter plot of salinity, temperature and juvenile Gulf menhaden CPUE data from the 50 ft seine station samples are overlaid on the plot.

## 3.2 Experimental Gill Nets

The regression analyses for the gill nets were also initially run with salinity, temperature and turbidity as independent variables. However, turbidity was dropped as an independent variable for the reasons previously stated in Section 3.1.

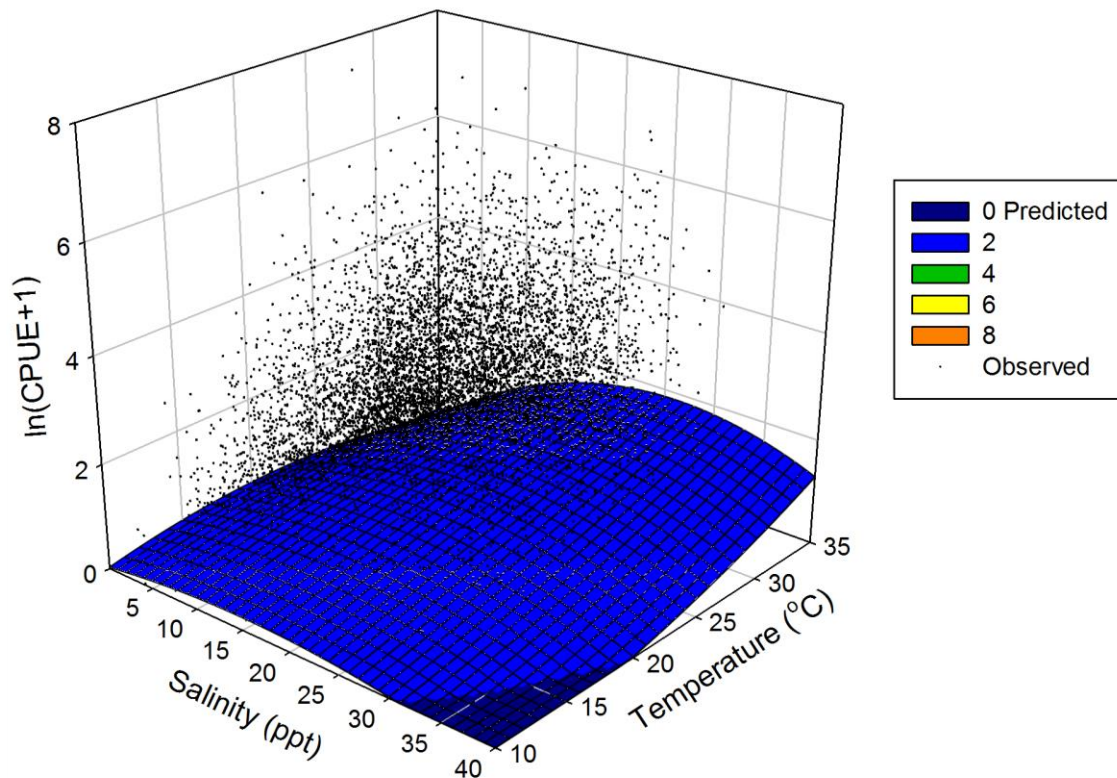
The resulting polynomial regression model (Equation 2) from the gill net analysis describes adult Gulf menhaden CPUE (natural log transformed) in terms of all significant effects from salinity and temperature, the squared terms and the interactions, and day of year. Table 3 lists the selected effects with the parameter estimates and their resulting level of significance for the polynomial regression. The surface response plot demonstrates the relationships for the two interacting independent variables (x,y) and CPUE (z) with the day variable set to its mean value (Figure 8). The scatter plot overlaid on the surface response shows the LDWF gill net data used to develop the polynomial regression.

The surface response plot in Figure 8 indicates that adult Gulf menhaden abundance [ $\ln(\text{CPUE}+1)$ ] increases with temperature primarily when salinities are greater than about 20 ppt. This result agrees with previous findings that peak concentrations of developing adult Gulf menhaden are found in the mid to lower regions of the estuary as they move towards the shelf during the summer months (Figure 1 and Figure 2; Pattillo et al., 1997 and references therein).

$$\ln(CPUE + 1) = -0.9567 + 0.3062(\text{Day}) - 0.1123(\text{Day}^2) + 0.01829(\text{Salinity}) + 0.1109(\text{Temperature}) - 0.00018(\text{Salinity}^2) - 0.00008(\text{Temperature} * \text{Salinity}^2) - 0.00263(\text{Temperature}^2) + 0.000112(\text{Salinity} * \text{Temperature}^2) \quad (2)$$

**Table 3: List of Selected Effects with Parameter Estimates and their Level of Significance for the Resulting Polynomial Regression in Equation 2.** Interactions between variables are denoted by \*.

Selected Effects	Parameter Estimate	p value
Intercept	-0.9567	0.0010
Day	0.3062	0.0830
Day <sup>2</sup>	-0.1123	0.0137
Salinity	0.01829	0.1510
Temperature	0.1109	<.0001
Salinity <sup>2</sup>	0.00018	0.8179
Temperature*Salinity <sup>2</sup>	-0.00008	0.0069
Temperature <sup>2</sup>	-0.00263	<.0001
Salinity*Temperature <sup>2</sup>	0.000112	<.0001



**Figure 8: Plot for the Polynomial Regression in Equation 2 over the Range of Salinity and Temperature Values and using a Mean Day of June 29 (day 180) in the Equation.** The scatter plot of salinity, temperature and adult Gulf menhaden CPUE data from the gill net station samples are overlaid on the plot.

## 4.0 Habitat Suitability Index Model for Juvenile Gulf Menhaden

Although the polynomial regression function in Equation 1 appears complex, the regression model is simply describing the relationship among juvenile Gulf menhaden catch in the seines and the salinity and temperature taken with the samples. In order to use the polynomial regression (Equation 1) within the juvenile Gulf menhaden HSI model, the equation was standardized to a 0-1 scale. Standardization of the equation was performed by first back-transforming the predicted CPUE  $[\ln(\text{CPUE}+1)]$  to untransformed CPUE values. The predicted untransformed CPUE values were then standardized by the maximum predicted (untransformed) CPUE value from the response function. Maximum CPUE was calculated by running the polynomial model through salinity and temperature combinations that fall within plausible ranges.

A predicted maximum juvenile Gulf menhaden  $\ln(\text{CPUE}+1)$  value of 3.156 was generated from the seine polynomial regression at a temperature of 27°C and salinity of 0 ppt. The back-transformed CPUE value (22.48) was used to standardize the other predicted untransformed CPUE values from the regression. The resulting standardized water quality suitability index (SI) was combined with standardized (0-1) indices for emergent vegetation and plankton prey concentration (as indicated by Chlorophyll *a* concentration) to produce the juvenile Gulf menhaden HSI model. All three components of the model are equally weighted and the geometric mean is used as all variables are considered essential to juvenile Gulf menhaden:

$$\text{HSI} = (\text{SI}_1 * \text{SI}_2 * \text{SI}_3)^{1/3}$$

Where:

SI<sub>1</sub> – Suitability index for juvenile Gulf menhaden in relation to salinity and temperature during the months of January through July (V<sub>1</sub>)

SI<sub>2</sub> – Suitability index for juvenile Gulf menhaden in relation to the percent of cell that is emergent vegetation (V<sub>2</sub>)

SI<sub>3</sub> – Suitability index for juvenile Gulf menhaden in relation to Chlorophyll *a* concentration in the cell (V<sub>3</sub>)

### 4.1 Applicability of the model

This model is applicable for calculating the habitat suitability index for YOY juvenile Gulf menhaden (median size about 35 mm TL from Figure 3) from January through July in coastal Louisiana marsh edge and shallow shoreline habitats of the estuaries.

### 4.2 Response and Input Variables

#### V<sub>1</sub>: Salinity and temperature during the months of January through July

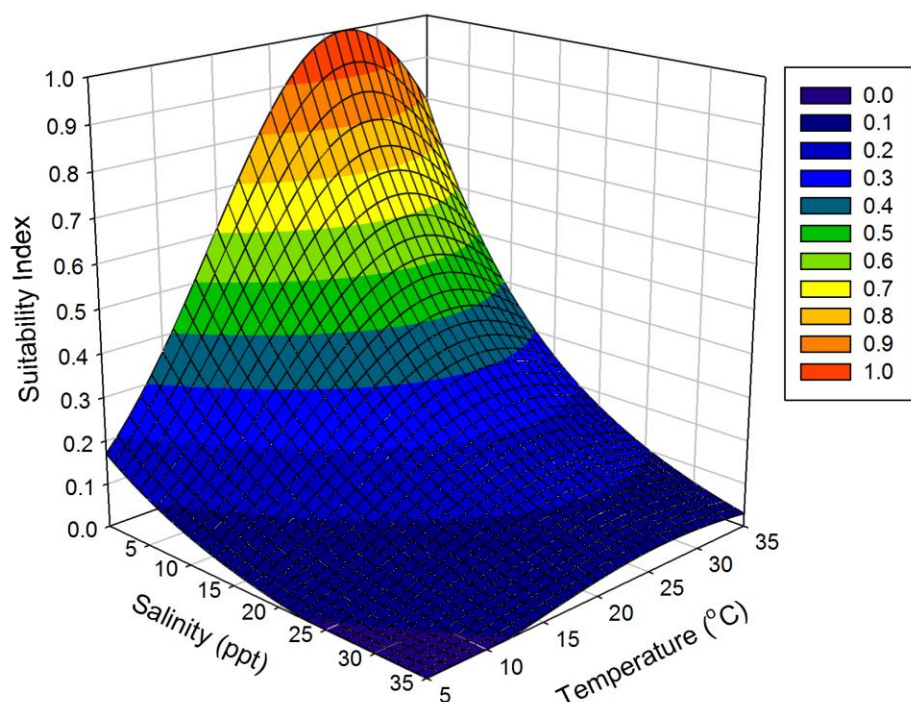
Calculate monthly averages of salinity (ppt) and temperature (°C) from January through July and substitute the averaged values into Equation 1 to estimate the juvenile Gulf menhaden CPUE (predicted as  $\ln(\text{CPUE}+1)$ ). The resulting suitability index (SI<sub>1</sub>) should then be calculated as:

$$SI_1 = \frac{e^{\ln(CPUE+1)} - 1}{22.48}$$

Where:

$$\ln(CPUE + 1) = -0.4572 + 2.6189(1.04) - 1.3848(1.04^2) - 0.06918(\text{Salinity}) + 0.1778(\text{Temperature}) - 0.00331(\text{Temperature}^2)$$

which includes the steps for back-transforming the predicted CPUE from Equation 1 and standardizing by the maximum predicted (untransformed) CPUE value equal to 22.48. The surface response for  $SI_1$  is demonstrated in Figure 9.



**Figure 9: Surface Plot Demonstrating the Predicted Suitability Index (0-1) for Juvenile Gulf Menhaden in Relation to Salinity and Temperature and Resulting from the Back-Transformation and Standardization of the Polynomial Regression in Equation 1.**

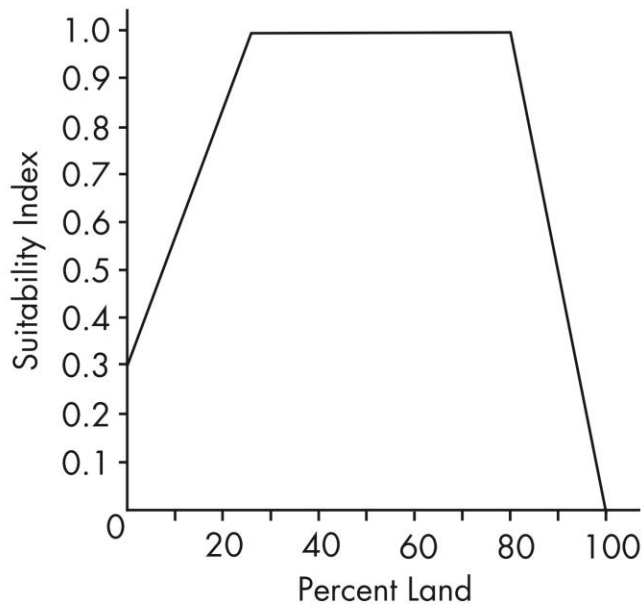
Rationale: Salinity and temperature are important abiotic factors that can influence the spatial and temporal distribution of juvenile Gulf menhaden in the estuaries within a year. The suitability index for juvenile Gulf menhaden resulted from the polynomial regression model that described the fit to the observed seine catch data in relation to the salinity and temperature measurements taken concurrent with the LDWF seine samples. The resulting suitability index predicts salinity and temperature ranges and optimums that agree well with the ranges and optimums previously described in the literature for juvenile Gulf menhaden (Table 1).

Limitations: The variable 'day' in Equation 1 has been replaced by a constant value equal to the mean day from the analysis (April 15).<sup>2</sup> Holding 'day' constant prevents the variable from contributing to the within- or among-year variation, so that only salinity and temperature can vary within and among years. Further, the optimal salinities and temperatures should not be interpreted as optimums for specific biological processes, such as growth or reproduction. Instead, the optimums represent the conditions in which juvenile Gulf menhaden most commonly occur, as dictated by physiological tolerances, prey availability, mortality, seasonal movements, and other factors.

**V<sub>2</sub>: Percent of cell that is covered by land and including all types of emergent vegetation**

Calculate the percent of the (500 X 500 m) cell that is wetland (covers all emergent wetland vegetation types) and substitute V<sub>2</sub> into the suitability index (SI<sub>2</sub>) for juvenile Gulf menhaden. The equation for SI<sub>2</sub> is plotted in Figure 10. The index is calculated as:

$$\begin{aligned}
 SI_2 &= 0.028 * V_2 + 0.3 && \text{for } V_2 < 25 \\
 1.0 &&& \text{for } 25 \leq V_2 \leq 80 \\
 5.0 - 0.05 * V_2 &&& \text{for } V_2 > 80
 \end{aligned}$$



**Figure 10: The Suitability Index for Juvenile Gulf Menhaden in Relation to the Percent Emergent Vegetation (Percent Land = V<sub>2</sub>).**

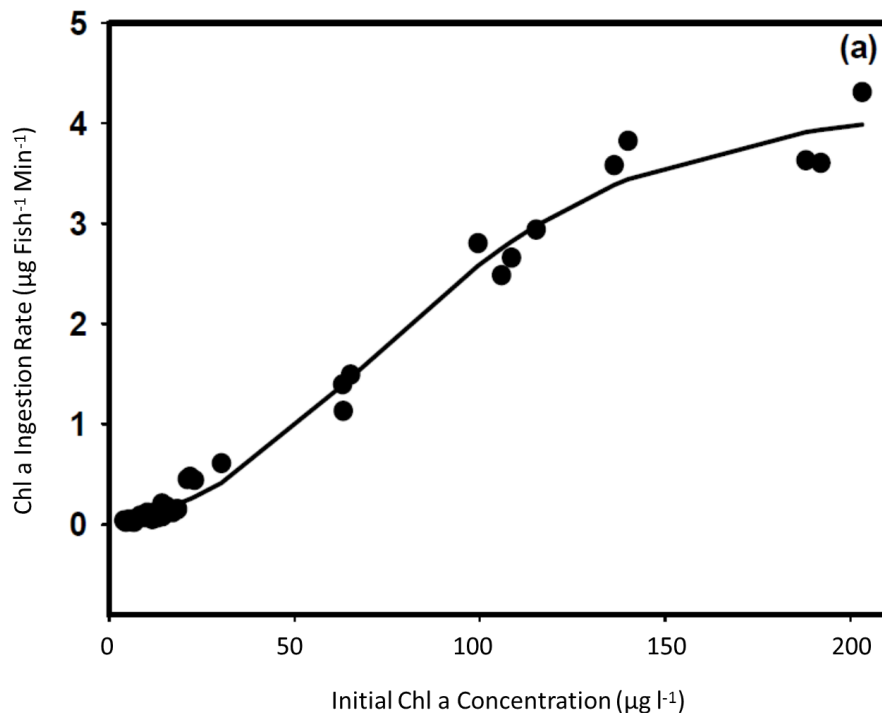
<sup>2</sup> Day of the year is scaled between 1 and 3.65 (i.e., 365/100) because the coefficients for higher power terms get exceedingly small and often do not have many significant digits. For example, a coefficient of 0.00004 may actually be 0.0000351 and that can make a big difference when multiplied by 365 raised to the power of 2. By using a smaller value, decimal precision is improved.

**Rationale:** The percent of wetland or total vegetated area within the cell is directly proportional to the marsh habitat's long-term carrying capacity for the juvenile Gulf menhaden. This relationship was initially defined by Minello and Rozas (2002) for juvenile brown shrimp, white shrimp and blue crab and subsequently incorporated into HSIs for the brown shrimp, white shrimp, and juvenile spotted seatrout in the 2012 Coastal Master Plan (CPRA, 2012) to represent these species dependence upon shallow marsh habitats for feeding and growth (Baltz & Jones, 2003). Marsh vegetation and shallow tidal marsh creeks and channels are equally important habitat to juvenile Gulf menhaden in their first year of life, providing increased plankton prey production and cover from predators (Deegan, 1990; Christmas et al., 1982). Thus, the optimum percent wetland SI for juvenile Gulf menhaden was set similar to that of the 2012 Coastal Master Plan HSIs (CPRA, 2012) at 25-80%. The SI for 0% wetland (or 100% open water) was set at 0.3 to reflect the lower protection from predation afforded by open water.

**Limitations:** The amount of marsh edge habitat is indirectly taken into account in the increased food/cover estimates of the percent wetland variable ( $V_2$ ). The open water proportion of the cell that includes submerged aquatic vegetation (SAV) is not included in the increased food/cover component of the model given that this species does not rely heavily on SAV.

### **V<sub>3</sub>: Chlorophyll *a* concentration in cell**

$V_3$  is the concentration of Chl *a* ( $\mu\text{g/l}$ ) for the 500 X 500 m cell. The suitability index describes juvenile Gulf menhaden feeding in response to Chl *a* concentration, as described by Lynch (2007; Figure 11).

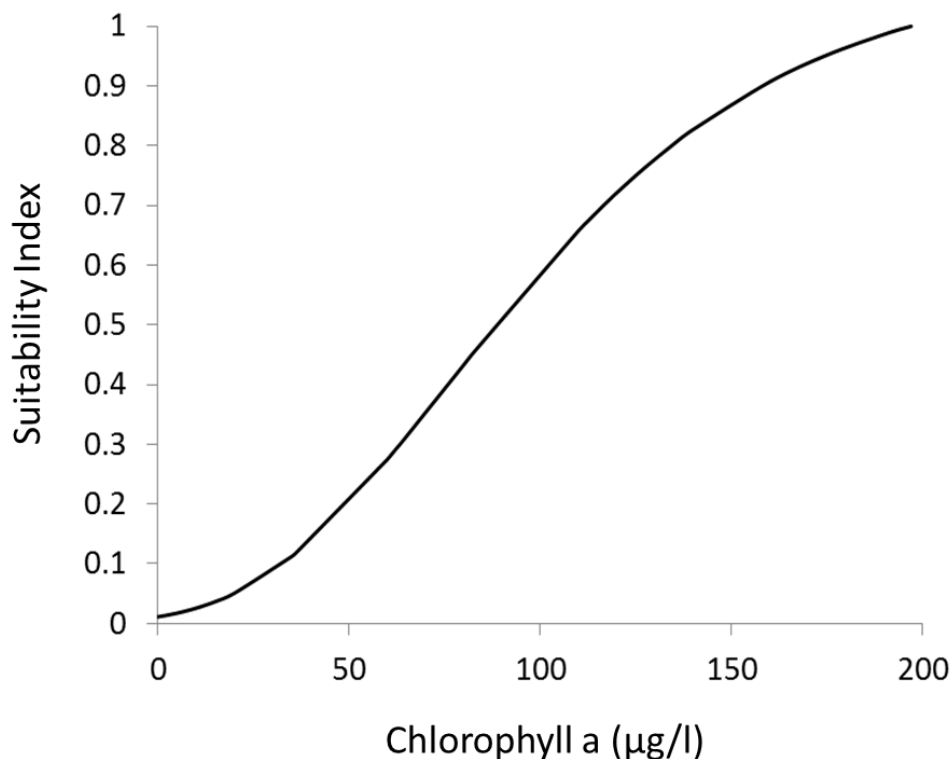


**Figure 11: Holling Type III Functional Response (Holling, 1959) Fit to Data Describing Juvenile Gulf Menhaden Ingestion Rate by Chl *a* Concentration (taken from Lynch, 2007).**



The resulting suitability index ( $SI_3$ ) demonstrated in Figure 12 is standardized by simply dividing the predicted ingestion rates from Lynch (2007) by the maximum predicted ingestion rate of  $3.82 \mu\text{g fish}^{-1} \text{min}^{-1}$  (Figure 11).

$$SI_3 = \frac{4.18e^{(-4.59e^{(-0.02 \cdot \text{Chl } a)})}}{3.82}$$



**Figure 12: The Resulting Suitability Index ( $SI_3$ ) for Juvenile Gulf Menhaden in Relation to Chlorophyll a Concentration in a 500 X 500 m Cell.**

**Rationale:** The Type III (sigmoidal) feeding response function best fit the Gulf menhaden ingestion rate data when compared to Holling Type I (linear) and Type II (asymptotic) feeding functions (Lynch, 2007). The sigmoidal response is often used to describe fish feeding in response to plankton prey concentration because ingestion rates are low at low plankton concentrations and rates increase with increases in prey but also as fish swimming speed increases (Durbin et al., 1981; Luo et al., 2001; Lynch, 2007). Previous studies in the Gulf of Mexico have stated that Gulf menhaden schooling and movement on the shelf and within the estuaries is determined by their prey concentrations (Shaw et al., 1985, Deegan, 1990, Pattillo et al., 1997), so the suitability index is appropriate to describe the dependence of Gulf menhaden juveniles on Chl a concentration and distribution within the estuaries.

**Limitations:** The relationship assumes that habitat suitability for juvenile Gulf menhaden is directly related to Chl a concentration, and that phytoplankton and zooplankton sizes and composition,



suspended detritus, and particulate organic carbon do not affect Gulf menhaden ingestion rates.

## 5.0 Habitat Suitability Index Model for Adult Gulf Menhaden

A predicted maximum adult Gulf menhaden  $\ln(\text{CPUE}+1)$  value of 1.918 was generated from the gill net polynomial regression at a temperature of 35°C and salinity of 26 ppt (see Section 4.0 for description of how the maximum value was generated). The back-transformed CPUE value (5.81) was used to standardize the other predicted untransformed CPUE values from the regression. The surface response that describes the standardized adult Gulf menhaden response (0-1) to salinity and temperature is shown in Figure 13. This predicted response surface is the resulting water quality suitability index to be used for the adult Gulf menhaden. The standardized water quality index was combined with standardized (0-1) indices for percent wetland (open water) habitat and plankton prey concentration (as indicated by Chlorophyll *a* concentration) to produce the adult Gulf menhaden HSI model. All three components of the model are equally weighted and the geometric mean is used as all variables are considered essential to adult Gulf menhaden:

$$\text{HSI} = (\text{SI}_1 * \text{SI}_2 * \text{SI}_3)^{1/3}$$

Where:

$\text{SI}_1$  – Suitability index for adult Gulf menhaden in relation to salinity and temperature during the months of March through October ( $V_1$ )

$\text{SI}_2$  – Suitability index for adult Gulf menhaden in relation to the percent of cell that is emergent vegetation ( $V_2$ )

$\text{SI}_3$  – Suitability index for adult Gulf menhaden in relation to Chlorophyll *a* concentration in the cell ( $V_3$ )

### 5.1 Applicability of the model

This model is applicable for calculating the habitat suitability index for adult Gulf menhaden (median size about 175 mm TL from Figure 5) from March through October in the open waters of Louisiana estuaries.

### 5.2 Response and Input Variables

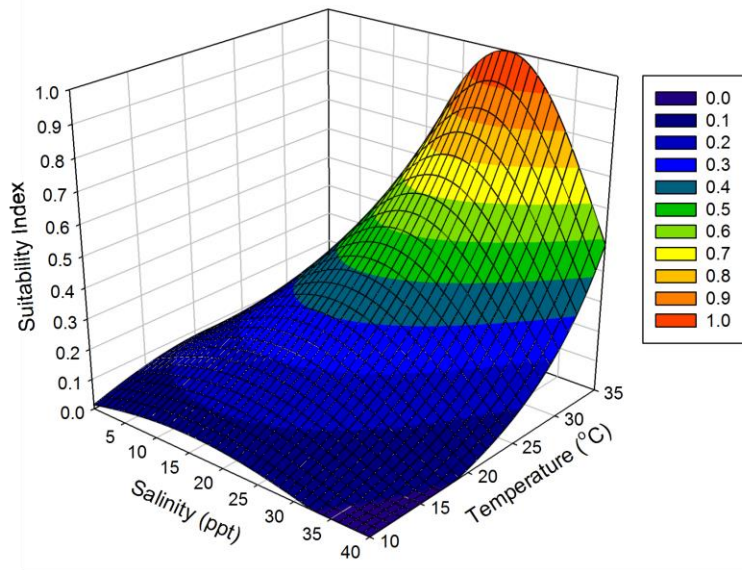
Calculate monthly averages of salinity (ppt) and temperature (°C) from March through October:

$$\begin{aligned} V_1 = & -0.9567 + 0.3062(1.8) - 0.1123(1.8^2) + 0.01829(\text{Salinity}) + 0.1109(\text{Temperature}) \\ & - 0.00018(\text{Salinity}^2) - 0.00008(\text{Temperature} * \text{Salinity}^2) - 0.00263(\text{Temperature}^2) \\ & + 0.000112(\text{Salinity} * \text{Temperature}^2) \end{aligned}$$

The resulting suitability index ( $\text{SI}_1$ ) should then be calculated as:

$$\text{SI}_1 = \frac{e^{V_1} - 1}{5.81}$$

which includes the steps for back-transforming the predicted CPUE from Equation 2 and standardizing by the maximum predicted (untransformed) CPUE value equal to 5.81. The surface response for  $SI_1$  is demonstrated in Figure 13.



**Figure 13: Surface Plot Demonstrating the Predicted Suitability Index (0-1) for Adult Gulf Menhaden in Relation to Salinity and Temperature and Resulting from the Back-Transformation and Standardization of the Polynomial Regression in Equation 2.**

*Rationale:* Salinity and temperature are important abiotic factors that can influence the spatial and temporal distribution of adult Gulf menhaden in the estuaries within a year. The suitability index for adult Gulf menhaden resulted from the polynomial regression model that described the fit to the observed gill net catch data in relation to the salinity and temperature measurements taken concurrent with the LDWF gill net samples. The resulting suitability index predicts salinity and temperature ranges and optimums that agree well with the ranges previously described in the literature for adult Gulf menhaden (Table 1).

*Limitations:* The variable 'day' in Equation 2 has been replaced by a constant value equal to the mean day from the analysis (June 29). Holding 'day' constant prevents the variable from contributing to the within- or among-year variation, so that only salinity and temperature can vary within and among years. Further, the optimal salinities and temperatures should not be interpreted as optimums for specific biological processes, such as growth or reproduction. Instead, the optimums represent the conditions in which the adult Gulf menhaden most commonly occur, as dictated by physiological tolerances, prey availability, mortality, seasonal movements, and other factors.

## **V<sub>2</sub>: Percent of cell that is covered by land**

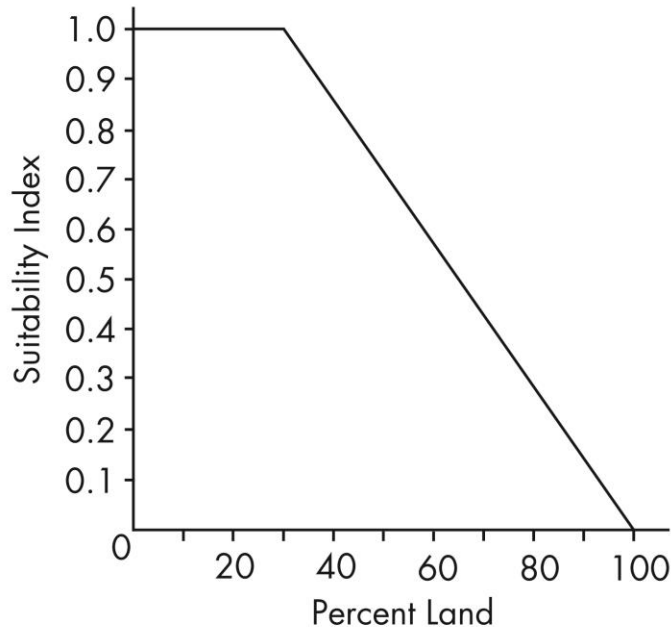
Calculate the percent of the (500 X 500 m) cell that is wetland (covers all emergent wetland vegetation types) and substitute  $V_2$  into the suitability index ( $SI_2$ ) for adult Gulf menhaden. The equation for  $SI_2$  is plotted in Figure 14. The index is calculated as:

$$SI_2 = 1.0 \quad \text{for } V_2 \leq 30$$

$$1.428 - 0.0143 * V_2 \quad \text{for } V_2 > 30$$

Rationale: Adult Gulf menhaden more commonly use the larger open water habitats presumably because their plankton prey are more abundant and concentrated in the open waters. The SI for adult menhaden was set to 1.0 when percent land within a cell is 0-30% (or open water at 100-70%) in order to place adult Gulf menhaden within the open water habitats of the estuaries. The suitability of a cell for supporting adult Gulf menhaden will then decrease as percent land increases beyond 30%, and the cell is not suitable for adult Gulf menhaden when percent land reaches 100%.

Limitations: None.



**Figure 14: The Suitability Index for Adult Gulf Menhaden in Relation to the Percent Land =  $V_2$ .**

### **$V_3$ : Chlorophyll $a$ concentration in cell**

$V_3$  is the concentration of Chl  $a$  ( $\mu\text{g/l}$ ) for the 500 X 500 m cell. The suitability index describes adult Gulf menhaden feeding in response to Chl  $a$  concentration, as described by Lynch (2007; Figure 11). Use the same relationship for adult Gulf menhaden with the same resulting suitability index ( $SI_3$ ) demonstrated in Figure 12.

Rationale: The Type III (sigmoidal) response is often used to describe fish feeding in response to plankton prey concentration because ingestion rates are low at low plankton concentrations and rates increase with increases in prey but also as fish swimming speed increases (Durbin et al., 1981; Luo et al., 2001; Lynch, 2007). Although this feeding response was found for juvenile Gulf menhaden and not for adults in the Lynch (2007) experiments, adult Gulf menhaden filter larger-sized phytoplankton that are a source of Chl  $a$ , as well as zooplankton which are often found in close association with phytoplankton (Chl  $a$ ) concentrations (Olsen et al., 2014). Therefore, the suitability index also should be appropriate to describe the dependence of adult Gulf menhaden on Chl  $a$  concentration and distribution within the estuaries.

Limitations: The suitability index assumes that the relationship found to exist between juvenile Gulf menhaden and Chl *a* concentration is the same for adults. Lynch (2007) failed to detect an ingestion response in adult Gulf menhaden to the Chl *a* concentrations using the same series of experiments, but noted that adults generally filter larger-sized phytoplankton and zooplankton than the phytoplankton used in his study.

## 6.0 Model Verification and Future Improvements

A verification exercise was conducted to ensure the distributions and patterns of HSI scores across the coast were realistic relative to current knowledge of the distribution of Gulf menhaden. In order to generate HSI scores across the coast, the HSI models were run using calibrated and validated Integrated Compartment Model (ICM) spin-up data to produce a single value per ICM grid cell. Given the natural interannual variation in salinity patterns across the coast, several years of model output were examined to evaluate the interannual variability in the HSI scores. An accurate representation of phytoplankton in the system was not available as input to generate a chlorophyll *a* suitability index score, and thus  $Sl_3$  was held constant at 1 for all model runs.

For the juvenile Gulf menhaden model, high scores were observed around fragmented marsh areas, such as those within Barataria, Breton, and Terrebonne basins. Scores were lowest in open water bodies closest to the Gulf of Mexico such as Chandeleur Sound, southern Barataria Bay, and Vermilion Bay. For adult Gulf menhaden, the reverse was observed. Highest scores were observed in lakes and bays closest to the Gulf, with HSI scores decreasing further inland into fresher areas. However, the majority of areas with high scores ranged from 0.6 to 0.8, with few areas exceeding 0.8. The lack of HSI scores greater than 0.8 is a result of the lower temperatures modeled across the coast relative to the optimum temperatures identified for adult Gulf menhaden in the polynomial regressions. Further, a limitation of the HSI models is that there are no geographic constraints that prevent the model from generating HSI scores in areas where the species are not likely to occur. For example, habitat in certain areas may be highly suitable but likely may never be occupied due to accessibility constraints (e.g., impounded wetlands) or perhaps because of the life cycle (e.g., larvae are not carried into the upper basins and therefore these areas may be under-utilized by juveniles). In both the juvenile and adult models, HSI scores greater than 0 were observed in isolated areas in the upper Atchafalaya Basin, where the species are not known to occur. In a survey of finfish fauna between Simmesport and Morgan City, Gulf menhaden were limited to the marine and estuarine areas of the Atchafalaya Basin (Lambou, 1990) and thus are not likely to occur in these most northern reaches. As a result, the areas of the northern Atchafalaya are being excluded from the HSI model domain. Overall, the results of the verification exercise were determined to be accurate representations of both juvenile and adult Gulf menhaden habitat distributions in coastal Louisiana.

Although the polynomial regression model used to fit the LDWF seine and gill net data produced functions relating Gulf menhaden catch to salinity and temperature that generally agreed with their life history information and distributions (Pattillo et al., 1997), polynomial models can predict unreasonable results outside of the modeled data range. Other statistical methods and modeling techniques exist for fitting nonlinear relationships among species catch and environmental data that could potentially improve the statistical inferences and model behavior outside of the available data. A review of other statistical modeling techniques could be conducted in order to determine their applicability in generating improved HSI models in the future.

## 7.0 References

- Ahrenholz, D. W. (1981). Recruitment and exploitation of Gulf menhaden, *Brevoortia patronus*. *Fishery Bulletin*, 79, 325–335.
- Ahrenholz, D. W. (1991). Population biology and life history of the North American menhadens, *Brevoortia* spp. *Marine Fish Review*, 53(4), 3–19.
- Baltz, D. M., and Jones, R. F. (2003). Temporal and spatial patterns of microhabitat use by fishes and decapod crustaceans in a Louisiana estuary. *Transactions of the American Fisheries Society*, 132, 662–678.
- Christmas, J. Y., McBee, J. T., Waller, R. S., and Sutter, F. C. (1982). Habitat Suitability Index Models: Gulf Menhaden. U.S. Department of the Interior Fish and Wildlife Service, FWS/OBS-82/10.23. (p. 31).
- Coastal Protection and Restoration Authority (CPRA). (2012). *Louisiana's Comprehensive Master Plan for a Sustainable Coast*. Baton Rouge, LA: CPRA. (p. 186).
- Deegan, L. A. (1986). Changes in body composition and morphology of young-of-the-year Gulf menhaden, *Brevoortia patronus* Goode, in Fourleague Bay, Louisiana. *Journal of Fish Biology*, 29(4), 403–415.
- Deegan, L. A. (1990). Effects of estuarine environmental conditions on population dynamics of young-of-the-year Gulf menhaden. *Marine Ecology Progress Series*, 68, 195–205.
- Durbin, A. G., Durbin, E. G., Verity, P. G., and Smayda, T. J. (1981). Voluntary swimming speeds and respiration rates of a filter-feeding planktivore, the Atlantic menhaden, *Brevoortia tyrannus*. *Fisheries Bulletin*, 78, 877–886.
- Friedland, K.D., Ahrenholz, D.W., and Guthrie, J.F. (1996). Formation and seasonal evolution of Atlantic menhaden juvenile nurseries in coastal estuaries. *Estuaries*, 19, 105–114.
- Holling, C.S. (1959). Some characteristics of simple types of predation and parasitism. *Canadian Entomology*, 91, 385–398.
- Lambou, V.W. (1990). *Importance of bottomland hardwood forest zones to fishes and fisheries: the Atchafalaya Basin, a case history*. Pages 125–193 in J. G. Gosselink, L. C. Lee, and T. A. Muir, editors. *Ecological processes and cumulative impacts: illustrated by bottomland hardwood wetland ecosystems*. Lewis Publishers, Inc., Chelsea, Michigan.
- Lassuy, D.R. (1983). *Species profiles: life histories and environmental requirements (Gulf of Mexico): Gulf menhaden*. U.S. Fish and Wildlife Service Biological Report FWS/OBS-82/11.2, 13 p.
- Louisiana Department of Wildlife and Fisheries. (2002). *Marine fisheries division field procedure manual*. Version 02-1.
- Luo, J., Hartman, K. J., Brandt, S. B., Cerco, C. F. (2001). A spatially-explicit approach for estimating carrying capacity: An application for the Atlantic menhaden (*Brevoortia tyrannus*) in Chesapeake Bay. *Estuaries*, 24, 545–556.

- Lynch, P. D. (2007). *Feeding ecology of Atlantic menhaden (Brevoortia tyrannus) in Chesapeake Bay*. M. S. Thesis, The College of William and Mary, Virginia.
- Minello, T. J., and Rozas, L. P. (2002). Nekton in Gulf coast wetlands: Fine-scale distributions, landscape patterns, and restoration implications. *Ecological Applications*, 12(2), 441–455.
- Murtaugh, P. A. (2009). Performance of several variable-selection methods applied to real ecological data. *Ecology Letters*, 12(10), 1061–1068.
- Nicholson, W. R. (1978). *Gulf menhaden (Brevoortia patronus) purse seine fishery: Catch, fishing activity, and age and size composition* (No. NMFS SSRF-722). U.S. Dept. of Commerce, National Oceanic and Atmospheric Administration, National Marine Fisheries Service.
- Olsen, Z., Fulford, R., Dillon, K., and Graham, W. (2014). Trophic role of gulf menhaden *Brevoortia patronus* examined with carbon and nitrogen stable isotope analysis. *Marine Ecology Progress Series*, 497, 215–227.
- Pattillo, M. E., Czaplá, T. E., Nelson, D. M., and Monaco, M. E. (1997). *Distribution and abundance of fishes and invertebrates in Gulf of Mexico estuaries, Volume II: Species life history summaries*. ELMR Rep. No. 11. NOAA/NOS Strategic Environmental Assessments Division, Silver Spring, MD. 377 p.
- Pérez-Castañeda, R., and Defeo, O. (2005). Growth and mortality of transient shrimp populations (*Farfantepenaeus* spp.) in a coastal lagoon of Mexico: role of the environment and density-dependence. *ICES Journal of Marine Science: Journal Du Conseil*, 62(1), 14–24. doi:10.1016/j.icesjms.2004.10.005
- SEDAR. (2013). *SEDAR 32A - Gulf of Mexico Menhaden Stock Assessment Report*. SEDAR, North Charleston, SC, 422 p.
- Shaw, R. F., Cowan, J. H., and Tillman, T. L. (1985). Distribution and density of *Brevoortia patronus* (Gulf menhaden) eggs and larvae in the continental shelf waters of western Louisiana. *Bulletin of Marine Science*, 36(1), 96–103.
- Smith, J. W. (2001). Distribution of catch in the Gulf menhaden, *Brevoortia patronus*, purse seine fishery in the northern Gulf of Mexico from logbook information: Are there relationships to the hypoxic zone? In Rabalais, N. and Turner, R. E. (Eds.) *Coastal Hypoxia: Consequences for Living Resources and Ecosystems*, Coastal and Estuarine Studies 58, Washington, D. C. pp. 311–20.
- Vanderkooy, S. J., and Smith, J. W. (2002). The menhaden fishery of the Gulf of Mexico, United States: A regional management plan (No. 99). Ocean Springs, MS: Gulf States Marine Fisheries Commission.
- Vaughan, D. S., Shertzer, K. W., and Smith, J. W. (2007). Gulf menhaden (*Brevoortia patronus*) in the U.S. Gulf of Mexico: Fishery characteristics and biological reference points for management. *Fisheries Research*, 83, 263–275.
- Villarreal, H., Hernandez-Llamas, A., and Hewitt, R. (2003). Effect of salinity on growth, survival and oxygen consumption of juvenile brown shrimp, *Farfantepenaeus californiensis* (Holmes). *Aquaculture Research*, 34(2), 187–193. doi:10.1046/j.1365-2109.2003.00808.x