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Environmental determinants of Gulf Menhaden (*Brevoortia patronus*) oil content in the northern Gulf of Mexico

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ABSTRACT

Gulf Menhaden (*Brevoortia patronus*) are a species of commercial and ecological importance in the northern Gulf of Mexico, provisioning the second largest fishery by weight, in the United States, and providing critical ecosystem services in the coastal region. The recruitment and productivity dynamics of the stock are influenced by a suite of environmental factors but an understanding of the factors that determine individual variation in oil content (an indicator of an individual's commercial value to the fishery and its dietary value to predators) has not been well described. In this work I describe the temporal dynamics of oil content and determine the demographic characteristics that provide predictive power to describe annual contrasts. I relate the predicted patterns in oil yield to a suite of seasonal environmental data series including: the magnitude of spring Mississippi River discharge, spring wind vectors, and the preceding winter El Nino conditions. Two uncorrelated ($r = 0.06$, $p = 0.81$) population-level predictor variables were identified that have explanatory power to describe temporal patterns in oil content ($L\,kg^{-1}$); a weight-at-length power function parameter (a) and the von Bertalanffy asymptotic fork length (L_∞, mm FL): $L\,kg^{-1} = -0.158 - 0.026{*}a - 0.00163{*}L_\infty$ ($p < 0.05$, $R^2 = 0.42$). Analysis of the impacts of environmental variables on the oil content of Gulf Menhaden was evaluated comprehensively in a Bayesian framework by transforming the observed oil content information from two sources to a common scale. Parameters relating oil content to spring Mississippi River discharge and the preceding winter (December–February) El Nino Southern Oscillation index resulted in sample distributions from the posterior where zero was outside the 95% credible interval. This work contributes to the understanding of Gulf Menhaden as a prey species in the Gulf of Mexico and indicates that the value of the species to both the fishery and predators exhibits relatively large inter-annual variability controlled, in part, by seasonal environmental conditions.

1. Introduction

Gulf Menhaden, *Brevoortia patronus*, are considered a critical prey source for higher trophic levels in the Gulf of Mexico (Sagarese et al., 2016) and their role in the ecosystem has received attention recently (Geers et al., 2014). Gulf Menhaden, like other species in the families' Clupeidae and Engrualidae have been termed “wasp-waist” species or “forage fishes” because they provide a direct energy pathway to higher level consumers from primary and secondary sources (Fauchald et al., 2011). For example, Juvenile (age-0) Atlantic Menhaden in North Carolina (*B. tyrannus*), like their congeners in the northern GOM, live in salt marshes and estuaries where they feed on phytoplankton. Gulf Menhaden adults (age − 1 +) feed on zooplankton (diet composition 63.0–77.6%) and phytoplankton (diet composition 21.7–36.3%, Olsen et al., 2014). The accumulation in body mass, derived from these sources, is exported to coastal and pelagic marine food webs by the seasonal migration of this species (Mieczan et al., 2013).

In addition to their role as energy converters in the trophic web, Gulf Menhaden support a major commercial fishery, the second largest, by biomass, in the United States (Vaughan et al., 2011). The product of the fishery includes fish meal, fish oil, and fish solubles (Smith 1991). These products are used in a variety of applications including food for aquaculture and agricultural stocks and as pet food (Smith 1991). Fish oil is a high value product used as a nutritional supplement for human, agriculture, and aquaculture applications. Indeed, the lack of alternatives to fish oil remains a challenge to the aquaculture industry (De Silva et al., 2011). Because of its value to humans and the ecosystem, understanding inter-annual and intra-annual variations in condition and oil content is a focus for research (Deegan 1986).

Because of their role, a better understanding of the environmental factors that determine variation oil content is critical because of the importance of lipid content in the diet of prey species. Additionally, the identification of leading indicators of oil content would allow ecological and economic forecasting for resource management and fishing

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industry planning. Previous work has shown that Gulf Menhaden oil content is contingent on water temperature, salinity, and rainfall (Guillory 1986). Guillory (1986) documented that the annual oil content of Gulf Menhaden varies considerably. Such variation directly impacts the economics of the commercial reduction fishery in the northern GOM. Variations in individual oil content will have consequences for the numerous consumer species, also targeted by fisheries, which use menhaden as prey.

In this work I describe how oil content of Gulf Menhaden varies inter-annually and describe the demographic characteristics of the stock that can be used to predict it. I derive an index of ecosystem productivity based on the estimated oil content of the Gulf Menhaden stock and, given estimates of biomass removal by the commercial fishery, I estimate the temporal pattern of oil removal from the ecosystem. Finally, I examine if the seasonal magnitude of spring Mississippi River discharge, spring regional wind vectors, and the status of El Niño Southern Oscillation (ENSO) in the preceding winter have explanatory power to predict inter-annual variation in oil content.

2. Methods

To describe the dynamics of oil content and determine the environmental characteristics that provide predictive power to describe annual contrasts, I used data of the estimated magnitude of oil content ($L\,kg^{-1}$ wet weight) of Gulf Menhaden for the years 1963–1979 (n = 17), presented by Guillory (1986). These data were obtained by the National Marine Fisheries Service and provided to Guillory. To my knowledge these are the only publicly available annual estimates of oil density from the commercial reduction fishery in the northern Gulf of Mexico.

I evaluated the response of oil content to population characteristics. Individual growth, condition, and population size, are reported in the recent federal stock assessment of Gulf Menhaden, SEDAR 32 (SEDAR 2013) and are used here as candidate predictor variables. The stock assessment includes mean annual estimates of the von Bertalanffy growth function (VBGF) parameters (k, L_∞, and t_0) used to describe length-at-age and mean annual estimates of power function parameters (a and b) used to describe weight-at-length (1964–2011). The VBGF is widely used to predict fish length and is a non-linear asymptotic function:

$$L_t = L_\infty\left(1 - e^{-k(t-t_0)}\right).$$

L_t (FL, mm) is the expected length at age t (y) and the model has three parameters: L_∞ (mm) is the average maximum fork length (FL), k (y^{-1}) is the growth rate coefficient, and t_0 (y) is the hypothetical age of the species at length zero. In the assessment, estimated mean weight-at-length is determined using a power function:

$$W_L = aL^b,$$

W_L represents wet weight (g), L represents FL (mm), a is a coefficient term and b is an exponent describing change in length relative to weight. Estimates of age-specific and total population biomass are initiated at 1977 in the stock assessment model. Because of the limited overlap in these data (1977–1979) and oil content data reported by Guillory (1986), the oil content reconstruction was made using only VBGF and power function parameters.

I used multiple linear regression to determine if oil content ($L\,kg^{-1}$) can be predicted from the five population-level parameters reported in the stock assessment (a, b, k, L_∞, and t_0). Because the VBGF and power function parameters exhibit inter and intra-model correlation, a first step was to identify a parsimonious set of predictor variables that were not correlated. The estimated regression coefficients of the best fit model were used to extrapolate the mean and 95% prediction intervals of oil content from 1964 to 2011 to derive an index of ecosystem productivity. Given the estimates derived from the multiple linear regression the biomass of harvest was multiplied by the oil content to determine the mean annual extraction of oil (L) from the Northern Gulf of Mexico ecosystem.

To determine the environmental drivers that influence Gulf Menhaden oil content in the Gulf of Mexico I used the data reported from Guillory (1986) and an additional, confidential annual estimate of oil content (1995–2015, n = 21) provided by one of the two active reduction companies currently operating in the region, Daybrook Holdings, Inc. These data are reported in measurements of mass of oil relative to total biomass (%). To ensure confidentiality of the data and allow the oil content data from each of the two data sets to be analyzed together, each measure was transformed to a binary index [0,1]. The median value of each data set was determined and a one was assigned if the value was greater or equal to the value of the set-specific median value and a zero was assigned if the value was less than the value of the set-specific median value. Annual oil content data from both data sets (n = 38) used in this study are reported annually for the entire Gulf of Mexico stock, thus it was not possible to examine oil content at a finer temporal or spatial scale.

The binary index of oil content was evaluated in the context of a suite of environmental indices that included the magnitude of spring (March to May) Mississippi River discharge, spring zonal wind velocity (U-vector, easterly) and (V-vector, northerly), and the preceding winter (December to February) El Niño Southern Oscillation (ENSO) index conditions. Seasonal river discharge dynamics were investigated using the scaled mean spring (March–May, 1963–2015) Mississippi River discharge ($m^3\,s^{-1}$) from the U.S. Army Corps of Engineers (USACE) monitoring station (available at www.mvn.usace.army.mil) at River Mile 306.3 (31° 00′ 30′′ N, 91° 37′ 25′′ W). The two spring components of wind, U and V, were determined from March to May. Modeled data are available from NOAA's Earth Systems Research Laboratory, www.esrl.noaa.gov and reported at 2.5° × 2.5° resolution. The value for the scaled seasonal wind component was determined as the mean of the cells in the northern Gulf of Mexico bounded by latitude 27.67° to 30.68° N and longitude 86.50°–96.50° E. This spatial extent which coincides with the spatial extent of the Gulf Menhaden Stock in the northern Gulf of Mexico (Geers, 2014). Winter values of the ENSO index were obtained from the scaled mean of December to February. Data were obtained from NOAA's Earth Systems Research Laboratory.

The analysis of the impacts of environmental variables on the value of the oil content of Gulf Menhaden was evaluated in a Bayesian framework. The dichotomous response variable of oil content (y) was modeled with a Bernoulli distribution:

$$y \sim Bernoulli(\mu),$$

where μ is a linear combination of predictors:

$$\mu = logistic\left(\beta_0 + \sum_j B_j x_{i,j}\right).$$

The input variables in the linear model (X_j) are the seasonal (i) estimates of the river, wind vectors U and V, and ENSO indices described above. Each of the linear model coefficients, β, were specified to have non-informative priors:

$$\beta \sim Normal(0,0.001).$$

The program JAGS (Plummer, 2003) was used to fit the model to the data. 50,000 samples were taken from the posterior density of each parameter derived from Markov Chain Monte Carlo simulation.

3. Results

The stepwise AIC procedure enabled the identification of two predictor variables that have explanatory power to describe temporal patterns in oil content; the coefficient of the weight-at-length power function (a) and the von Bertalanffy asymptotic length parameter (L_∞,

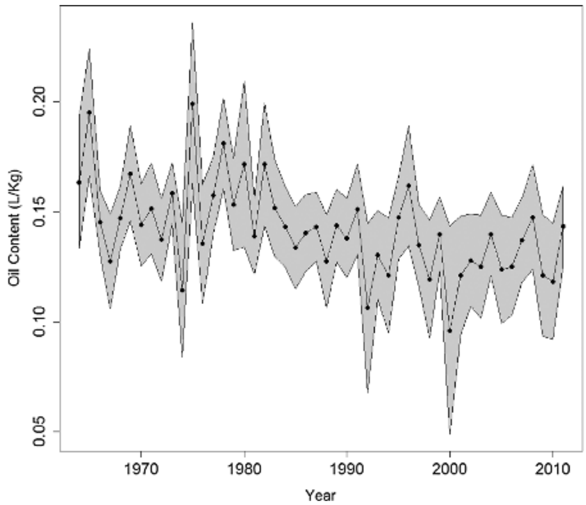

Fig. 1. Predicted mean and 95% Prediction Intervals of annual oil content (L kg^{-1}, closed points and line) from the multiple linear regression of Gulf Menhaden demographic parameters; the exponent of the weight-at-length power function (b) and the von Bertalanffy growth rate coefficient (k y^{-1}).

Table 1
Mean and 95% Confidence intervals of the multiple linear regression parameters that were used to derive mean values of Gulf Menhaden oil content (L kg^{-1}).

Model Parameter	Mean Estimate	95% Confidence Interval	*p*-value
Intercept	−196.8	−501.4 to 107.9	0.19
Power function parameter, *a*	−24.7	−50.2 to 0.72	0.056
von Bertalanffy parameter, L_∞	0.056	0.056–0.33	0.009

mm). The reconstruction of the time-series of oil content, although exhibiting some inter-annual variation (Fig. 1), was generally consistent throughout the time series (mean oil content 0.142 L/Kg, CV = 14.6%). The predicted annual mean oil content is: L kg^{-1} = $-0.158–0.026*a - 0.00163*L_\infty$ ($p < 0.05$, $R^2 = 0.42$, Table 1). The independent variables a and L_∞ are not significantly correlated (pairwise Pearson product-moment correlation r = 0.06, $p = 0.81$).

The scaled magnitude of spring river discharge, spring meridional (V) and zonal (U) components, and the winter ENSO all exhibited temporally variable patterns (Fig. 2). The winter El Niño Southern Oscillation index exhibited temporal variability for the time-series with minimum winter phases observed in 1998, 1978, 2005, and 2010. Positive conditions of large magnitude were observed in 2011, 1974, 2008, 1976. Similarly, spring Mississippi River discharge exhibits pronounced inter-annual variation in the magnitude and direction of deviations with the greatest observed positive deviations in total annual river discharge occurring in 1997, 1979, 1973, and 2008. Years of least total spring discharge were 1967, 2000, 1963, and 1977. Annual variations in Zonal wind (U-vector) magnitude is variable, exhibiting both westerly (negative) and easterly (positive) values. Strong spring westerly winds were observed in 1995, 2004, 1997, and 2001 and strong easterly winds were observed in 1978, 2010, 1996, and 1974. The spring magnitude of the meridional wind (V-vector) had strong negative values (north to south) in 1969, 1978, 2010, and 2002. Positive magnitude meridional wind vectors were observed in 1976, 2011, 1974, and 1967. The analysis of pairwise correlation of the candidate predictor variables indicated that there was a positive and strong correlation (Pearson product-moment correlation, $r = 0.632$) of spring meridional wind and winter ENSO values (Table 2). The pairwise correlation of the other candidate predictors ranged from $r = -0.173$ to 0.065.

The determination of the candidate environmental indicators to predict if oil content is greater than the median, was determined by evaluating the posterior distribution of the linear parameters derived from the Bayesian analysis (Fig. 3). This results of this analysis indicated that winter ENSO phase (median $\beta = -1.17$) and spring Mississippi River discharge (median $\beta = 0.97$) had predictive power to describe the probability of oil content being greater than the median. The 95% credible interval of samples of the parameter to describe the relationship of these variables from the posterior distribution were outside the value of zero (Fig. 3, Table 3). Similarly, 80% of the sampled posterior values of the parameter that relate oil content with meridional wind vector did not include zero (Fig. 3, Table 3). The probability that oil content of Gulf Menhaden, harvested during the fishing season, having greater than the median oil content is positively correlated with scaled spring Mississippi River discharge and negatively correlated with the scaled winter ENSO index (Fig. 4).

Because the consistency in the predicted mean estimate of oil content, annual extraction volume generally follows the magnitude of harvest biomass (Fig. 5). The magnitude of harvest of Gulf Menhaden exhibited peaks in the 1980′s and early 1990′s. At the end of the time series (2007–2011) the mean volume of oil extracted and mean magnitude of landings were relatively low, 466,000 mt and 62.7 million L, respectively.

4. Discussion

The characteristics of living resources at the individual level (e.g. length-at-age, condition, and fecundity) are determined by evolutionary, ecological, and environmental factors. Many harvested marine stocks (fishes and invertebrates) are subject to considerable inter-annual variability in oceanographic conditions that influence, in part, individual- and population-level characteristics. In this work I construct an extended time-series of oil content of Gulf Menhaden derived from demographic information and find that the probability of oil content, measured from the fishery, is correlated to a suite of seasonal and monthly environmental conditions in the NGOME. Similar to the work by Guillory (1986), this study highlights the importance of spring river discharge as an ecosystem indicator of productivity in the north central GOM. I document the utility of seasonal (winter) ENSO as a leading indicator of oil content for the Gulf Menhaden stock. Additionally, I find that the spring meridional wind component may also be a factor to describe the contrast in annual oil content. This work contributes to the understanding of Gulf Menhaden as a prey species in the Gulf of Mexico and indicates that the value (in caloric terms) of individuals of this species to both the fishery and predators exhibits predictable, at least in the short term, inter-annual variability.

The predicted annual oil content value was determined using annual values of population demographic parameters. In the multiple linear regression, I found that the coefficient of the weight-at-length power function (a) parameter and the von Bertalanffy asymptotic length parameter (L_∞, mm) are both negatively correlated to oil content. Thus, oil content is maximized when Gulf Menhaden have a greater weight-at-length and length-at-age during the fishing season. It is probable that variations in the spawning season may contribute to this variability: Females in spawning condition occur from September to April (Coombs 1969; Lewis and Roithmayr 1981). It is probable that the timing of spawning and recruitment may contribute to the variability in oil content. Environmental conditions that promote an individual's addition of biomass lead to fish of greater oil content. The menhaden fishery does not fish uniformly throughout the season and intra-annual patterns in the spatial distribution of harvest may also exist. Spatial and temporal variation in harvest may influence estimates of annual oil density, however a description of this was not possible because of the structure (annual and Gulf-wide temporal and spatial resolution) of the oil content data.

The ecological value of Gulf Menhaden in the trophic dynamics of the northern Gulf of Mexico has received much attention recently

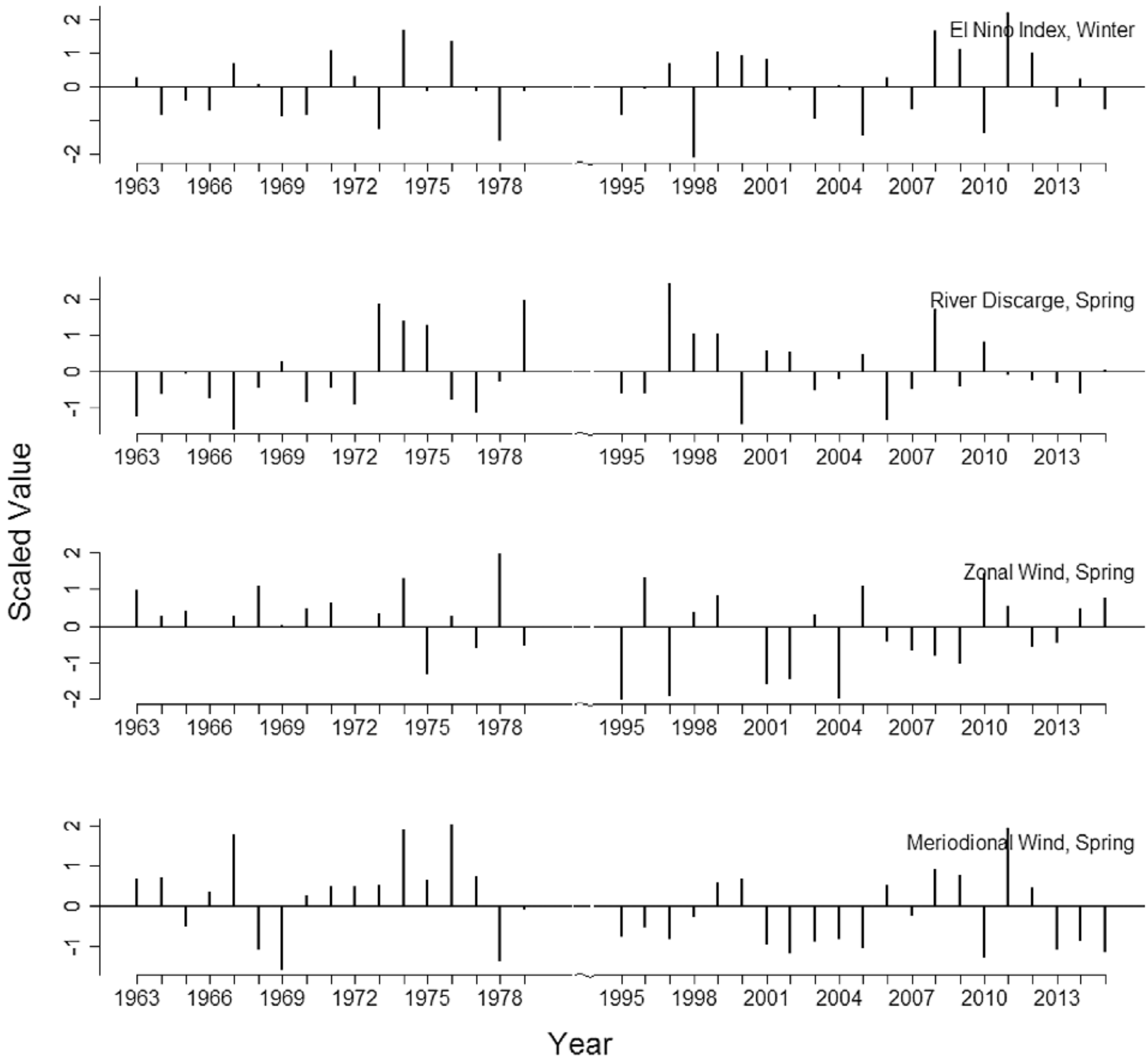

Fig. 2. Time series of scaled value of spring (March to May) Mississippi River discharge ($m^3 s^{-1}$), wind components for zonal (U-vector, m $second^{-1}$) and meridional (V-vector, m $second^{-1}$), and El Nino Southern Oscillation index values.

Table 2
Pearson-product moment correlation coefficients among environmental indices used in the linear formulation Bernoulli parameter.

Environmental Index	El Nino, Winter	River Discharge, Spring	Zonal Wind, Spring	Meridional Wind, Spring
El Nino, Winter	1.0	−0.018	−0.173	0.632
River Discharge, Spring	−0.018	1.0	−0.163	−0.149
Zonal Wind, Spring	−0.173	−0.163	1.0	0.065
Meridional Wind, Spring	0.632	−0.149	0.065	1.0

(Geers et al., 2016; Sagarese et al., 2016). These workers found, using modeling approaches based on an extensive literature data base, that Gulf Menhaden are a prey item for a wide variety of taxa. Red Drum and Speckled Seatrout in particular are major predators on the species (gomexsi.tamucc.edu) as are King and Spanish Mackerel, and Blacktip Shark (Sagarese et al., 2016). Using literature- and database-derived information about predator diets, model simulations suggest that Gulf Menhaden are a critical component of the ecosystem (Geers et al., 2016). Geers et al. (2016) predicted that when commercial harvest on Gulf Menhaden increased there was a decrease in biomass of predator species. They concluded that Gulf Menhaden is a critical trophic linkage. The observed variations in Gulf Menhaden oil content reported by Guillory (1986), and extended here, is relevant to the study of trophic linkages in the northern Gulf of Mexico. My documentation that oil content (and hence caloric value) of Gulf Menhaden varies inter-annually, indicates that the “importance” of Gulf Menhaden as a prey item will likely vary temporally. It is probable that when Gulf Menhaden are either very abundant or of high caloric value they will be an important part of the predator diets. Their relative importance can be evaluated as the impact that they have on the anabolic process of predators. To date, many modeling and ecosystem prediction efforts must necessarily focus on static diet metrics (e.g. mean percent weight or mean percent frequency of occurrence) and do not capture the temporal variability of caloric value. Understanding the temporal dynamics of oil content (as a proxy for calories removed by fishing) provides a tractable index of the impacts of the Gulf Menhaden purse seine fishery on the northern Gulf of Mexico ecosystem beyond measures of biomass or number of individual fish harvested.

The variability of Gulf Menhaden oil content illustrates the pronounced variation in ecosystem conditions in the northern Gulf of Mexico. Because Gulf Menhaden are primary and secondary consumers

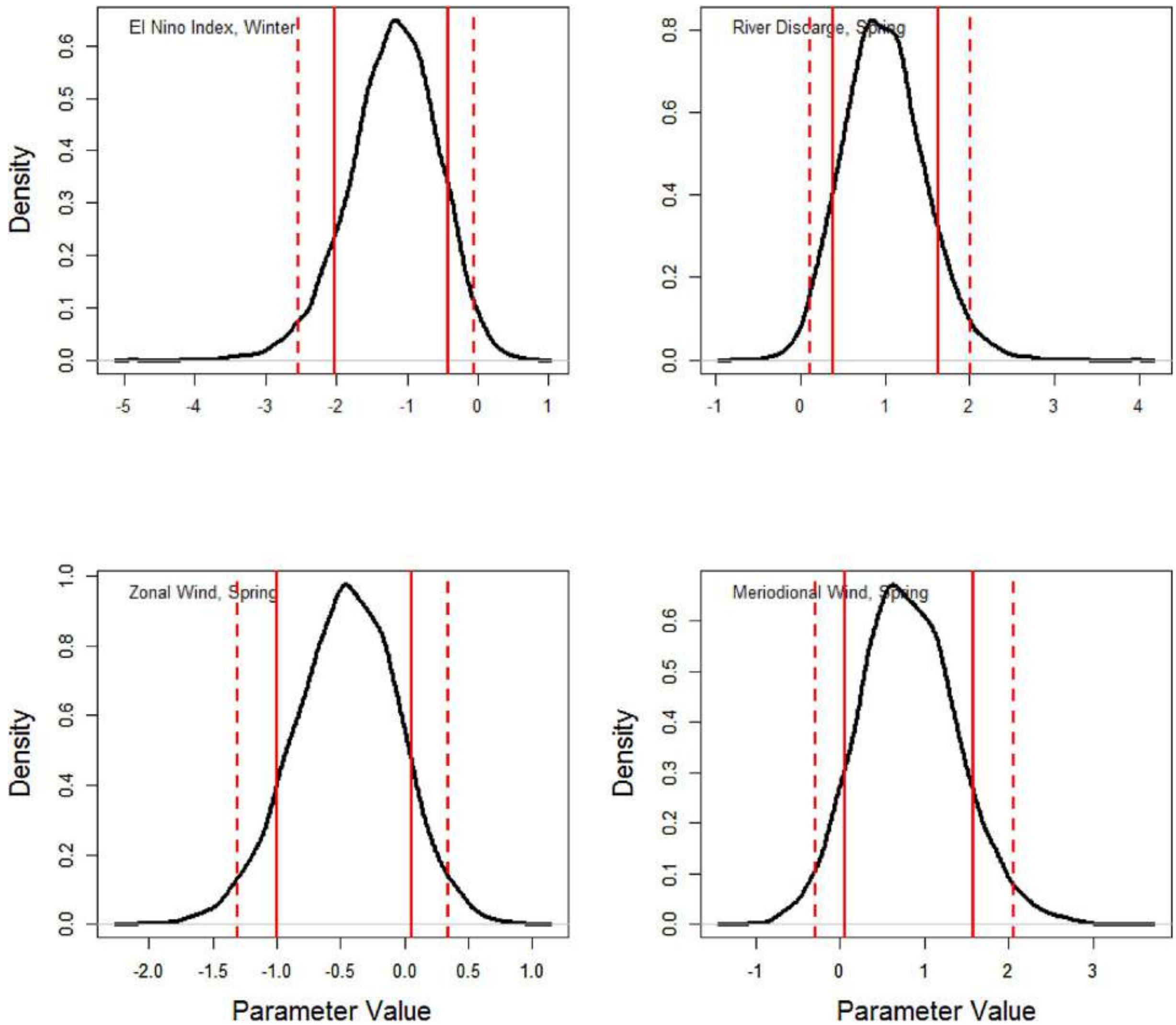

Fig. 3. Posterior density distribution of parameters used in linear component of the prediction model to relate oil content to spring (March to May) Mississippi River discharge ($m^3 s^{-1}$), wind components for zonal (U-vector, m second^{-1}) and meridional (V-vector, m second^{-1}), and El Nino Southern Oscillation index values.

Table 3
Quantiles of samples of linear parameters relating probability of oil content greater than the median and the associated environmental predictor.

	Quantiles of Samples from the Posterior Distribution				
Environmental Predictor	2.5%	10%	50%	80%	97.5%
Intercept	−0.80	−0.54	−0.04	0.46	0.73
El Nino, Winter	−2.53	−2.02	−1.17	−0.41	−0.07
River Discharge, Spring	0.13	0.39	0.97	1.62	2.01
Zonal Wind, Spring	−1.31	−0.99	−0.45	0.05	0.33
Meridional Wind, Spring	−0.29	0.08	0.79	1.58	2.06

(Olsen et al., 2014) I hypothesize that they are sensitive to variations in primary and secondary ecosystem productivity. I document inter-annual variations in the discharge of the Mississippi Rivers, the magnitude of and direction of wind, and seasonal El Nino Southern Oscillation index. The analysis indicates that Gulf Menhaden oil content is positively correlated to spring river discharge and negatively correlated to winter ENSO. Previous work has documented that nutrient flow export via freshwater discharge into the northern Gulf of Mexico serves to enhance fishery production (Grimes, 2001). The positive relationship of freshwater flow and fishery production of estuarine-dependent living marine resources has been observed worldwide (Gillson, 2011). Govoni (1997) and Vaughan et al. (2011) speculated that Mississippi-Atchafalaya freshwater discharge determines the size of the resulting freshwater and nutrient-laden (Lohrenz et al., 1997) plume front. They speculated that the freshwater plume serves to aggregate prey (Govoni and Grimes, 1992; Govoni et al., 1989) and provides increased feeding opportunities for predators. The plume boundary is an area of converging water masses that serves to concentrate organisms (Grimes, 2001). However, the mechanism of how increased oil content is realized under high flow conditions remains speculative. The result that winds from the south, in the spring, are positively associated with oil content in the summer may indicate that this forcing either changes the distribution of the river plume water or serves to reinforce the density gradient at the river plume front. Walker (1996) reported that the variability in the Mississippi river plume area is determined by both river discharge and wind direction and magnitude.

A fundamental principle of ecosystem-based fishery management and an outstanding research need for its successful implementation is understanding how temporally dynamic ecosystem conditions effect harvested stocks (O'Boyle et al., 2008). In this work I show, as Guillory (1986) did, that river discharge in the spring months provides a leading index of oil content for Gulf Menhaden and describe how winter ENSO conditions can provide a leading indicator of Gulf of Menhaden oil

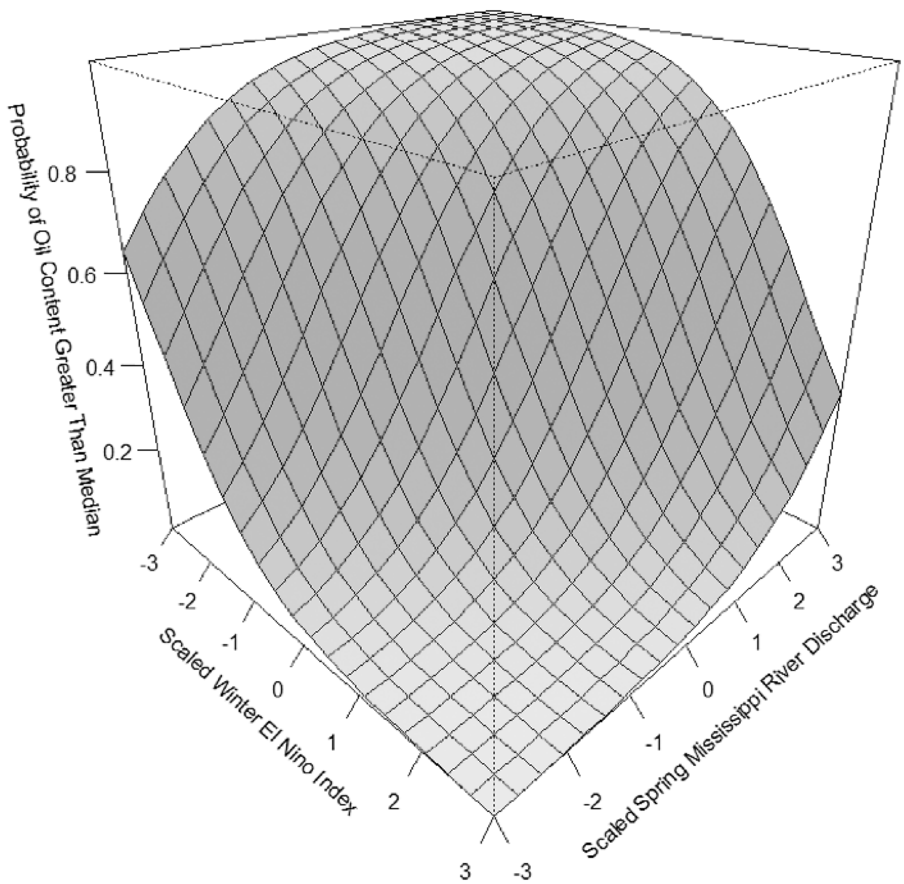

Fig. 4. Relationship of the probability of oil content greater than median value as a function of the median estimates of the linear parameters for the scaled variables spring (March to May) Mississippi River discharge ($m^3 s^{-1}$) and El Nino Southern Oscillation index values.

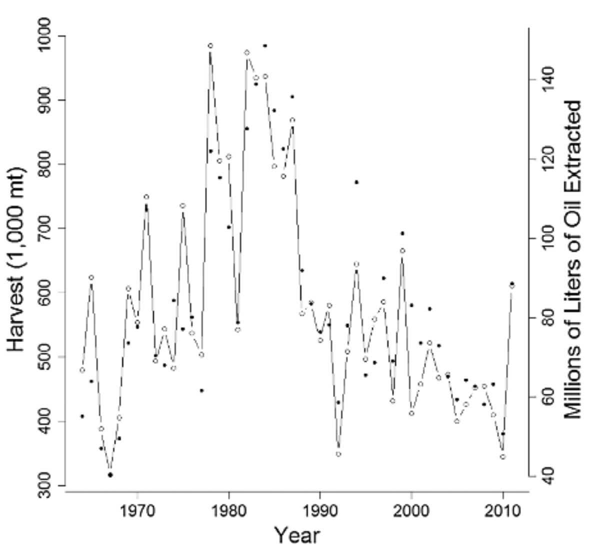

Fig. 5. Annual patterns of total landings in 1000 mt (closed circles) and associated predicted millions of liters of oil (gray line, open circles).

content. I acknowledge that more work needs to be done to determine, unambiguously, the causal mechanisms that impact oil content beyond the ecosystem indicators I examine here. The dynamics of the density gradient at the plume front, and the subsequent increases in primary and secondary production, occur at small spatial scales and these must be investigated. Directed effort on the biological dynamics that occur at the front are needed and these should be done with in situ sampling of the plume boundary.

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