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Effect of Changes in Dissolved Oxygen Concentrations on the Spatial Dynamics of the Gulf Menhaden Fishery in the Northern Gulf of Mexico

Brian J. Langseth,*,[1] Kevin M. Purcell, J. Kevin Craig, Amy M. Schueller, Joseph W. Smith, and Kyle W. Shertzer

National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Science Center, Beaufort Laboratory, 101 Pivers Island Road, Beaufort, North Carolina 28516, USA

Sean Creekmore and Kenneth A. Rose

Department of Oceanography and Coastal Sciences, Louisiana State University, 2135 Energy, Coast, and Environment Building, Baton Rouge, Louisiana 70803, USA

Katja Fennel

Oceanography Department, Dalhousie University, 1355 Oxford Street, Halifax, Nova Scotia B3H 4R2, Canada

Abstract

Declines in dissolved oxygen (DO) concentrations in aquatic environments can lead to conditions of hypoxia (DO ≤ 2 mg/L), which can directly and indirectly affect aquatic organisms. Direct effects include changes in growth and mortality; indirect effects include changes in distribution, movement, and interactions with other species. For mobile species, such as the pelagic filter-feeding Gulf Menhaden *Brevoortia patronus*, indirect effects are more prevalent than direct effects. The northern Gulf of Mexico experiences one of the largest areas of seasonal hypoxia in the world; this area overlaps spatially and temporally with the Gulf Menhaden commercial purse-seine fishery, which is among the largest fisheries by weight in the United States. Harvest records from the Gulf Menhaden fishery in 2006–2009 and fine-scale spatial and temporal predictions from a physical–biogeochemical model were used with spatially varying regression models to examine the effects of bottom DO concentration, spatial location, depth, week, and year on four response variables: probability of fishing, total Gulf Menhaden catch, total fishery effort, and CPUE. We found nearshore shifts in the probability of fishing as DO concentration declined, and we detected a general westward shift in all response variables. We also found increases in CPUE as DO concentration declined in the Louisiana Bight, an area that experiences chronic, severe hypoxia. The overall effects of environmental conditions on fishing response variables appeared to be moderate. Nevertheless, movement of either Gulf Menhaden or the purse-seine fishery in response to environmental conditions could potentially affect the susceptibility of Gulf Menhaden to harvest and could therefore influence assessment of the stock and associated stock status indicators.

Declines in the concentration of dissolved oxygen (DO) in water can affect the magnitude of fishery landings in two fundamental ways. The first is through direct effects on processes that underlie biological production, such as changes in

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growth (McNatt and Rice 2004; Stierhoff et al. 2009), mortality (Shimps et al. 2005), and reproduction (Thomas and Rahman 2012), which can lead to changes in abundance. The second is through indirect effects on the spatial and temporal dynamics of the targeted resource, such as shifts in distribution, which can influence the interaction between the resource and the fishery, independent of the resource's abundance (Breitburg et al. 2009; Craig 2012; Stramma et al. 2012). Many studies have assessed the direct and indirect effects of low DO concentrations on aquatic organisms (Pollock et al. 2007). Although the relative magnitude of direct and indirect effects depends on the organism as well as on the DO concentration, there is growing evidence that for mobile species, indirect effects are more important than direct effects (Craig et al. 2001; Breitburg et al. 2009; Rose et al. 2009).

The northern Gulf of Mexico (GOM) experiences one of the largest areas of seasonal hypoxia (DO $\leq$ 2 mg/L) in the world (Rabalais et al. 2002). Riverine inputs from the Mississippi–Atchafalaya River system, which drains 41% of the contiguous United States, contribute large amounts of nutrients to nearshore coastal Louisiana waters. These nutrients stimulate high rates of primary production, which can lead to high rates of microbial respiration and ultimately reduce the concentration of DO in the water column (Rabalais et al. 2002; Bianchi et al. 2010). If stratification of the water column is strong enough that re-aeration of bottom waters is inhibited, then the DO concentration can decline sufficiently to cause widespread hypoxia. In the northern GOM, hypoxia typically peaks in summer (June–August), when the water column is strongly stratified and nutrient inputs from spring runoff have stimulated high levels of primary production (Rabalais et al. 2002; Bianchi et al. 2010). The spatial extent of seasonal hypoxia in the northern GOM can be extensive in some years, exceeding 20,000 km^2 and spreading westward from the outflow of the Mississippi River (i.e., the Mississippi Delta) to as far as the Louisiana–Texas border (Rabalais et al. 2007).

Similar to other highly productive systems that are susceptible to hypoxia, the northern GOM also supports highly productive fisheries (Breitburg et al. 2009). Landings of Gulf Menhaden *Brevoortia patronus* annually rank first among GOM fisheries landings and second among U.S. fisheries landings in terms of weight (NMFS 2012). Gulf Menhaden are small clupeid fish that form large, dense, near-surface schools during spring through fall in the northern GOM (Ahrenholz 1991). The schools are targeted by large purse-seine vessels, which are guided to the schools with the assistance of aerial spotter pilots. The fishery operates from mid-April through late October, and monthly landings usually peak between June and August. Fishing operations are coastal in nature, with about 90% of the catch occurring within 16.09 km (10 mi) of shore (Smith et al. 2002). Catches range from eastern Mississippi to eastern Texas, but most (up to 90%) of the harvest occurs off the coast of Louisiana (Smith et al. 2002). Hence, there is strong spatial and temporal overlap between the purse-seine fishery for Gulf Menhaden and seasonal hypoxia in the northern GOM.

Gulf Menhaden and other pelagic species are influenced by direct effects of exposure to low DO but are probably more susceptible to indirect effects associated with avoidance because they are highly mobile and mostly utilize the upper water column above the low-DO bottom layer. Among field studies in the northern GOM, pelagic fishes avoided areas of low bottom DO and aggregated both horizontally and vertically near the edges of the GOM hypoxic zone (Hazen et al. 2009; Zhang et al. 2009). Similar aggregations along the edges of hypoxic zones have been observed for shrimp in the GOM (Craig and Crowder 2005; Craig et al. 2005; Craig 2012), and aggregations above hypoxic zones have also been observed for pelagic species in the Laurentian Great Lakes (Vanderploeg et al. 2009), Chesapeake Bay (Ludsin et al. 2009), and the northeast Atlantic Ocean (Stramma et al. 2012). Comparisons of results from simulation models that integrated multiple direct and indirect effects of hypoxia also suggested that indirect effects due to altered spatial distributions or food web interactions had a greater effect on growth and survival than direct effects of exposure to low DO concentrations (Rose et al. 2009).

Despite evidence for direct and indirect effects of hypoxia on pelagic fish species as well as other marine organisms, there is limited evidence that hypoxia broadly affects fishery landings (Breitburg et al. 2009; Rose et al. 2009; Bianchi et al. 2010). However, Zimmerman and Nance (2001) and later O'Connor and Whitall (2007) found negative correlations between the area of hypoxia in the GOM and landings in the commercial shrimp fishery. Conceptually, distributional changes influenced by hypoxia have implications for commercial fisheries. Aggregation along the edge of hypoxic zones has the potential to enhance the catch rates of targeted species as well as affect the overlap between target species and bycatch species at small spatial scales (Craig 2012; Craig and Bosman 2013). Aggregation above hypoxic zones can similarly enhance catch rates by making pelagic species more susceptible to pelagic fishing gears (Ludsin et al. 2009; Vanderploeg et al. 2009; Zhang et al. 2009; Stramma et al. 2012).

Only one previous study has used commercial fishery data to assess the effects of hypoxia on the catch distribution in the northern GOM Gulf Menhaden fishery (Smith 2001). Smith (2001) divided Gulf Menhaden landings into a 10- × 10-min spatial grid for each of 3 months (June–August) during 3 years (1994–1996) and qualitatively compared landings patterns to the overall areal extent of hypoxia each year. He hypothesized that (1) Gulf Menhaden harvest would decline during extreme years of hypoxia, when low DO concentrations impinged along the shoreline; and (2) a continuous band of hypoxia along the northern GOM would concentrate Gulf Menhaden landings into normoxic waters off western Louisiana. There was some evidence of reduced catches offshore of Louisiana during years of severe hypoxia, but conclusions about finer-scale shifts in the spatial distribution of the fishery were not possible due to the limited spatial resolution of the data.

Comprehensive empirical information on the spatial and temporal dynamics of the GOM hypoxic zone is limited. The spatial extent of hypoxia in the GOM has been estimated since 1985 from an annual shelfwide survey conducted during late July (Rabalais et al. 2007; Obenour et al. 2013). Higher-resolution temporal data also exist from a mooring at a single location in the GOM (Rabalais et al. 2007). However, because DO concentrations are a function of numerous physical and biological processes and can vary in scale both spatially (meters to hundreds of kilometers) and temporally (minutes to months; Eldridge and Morse 2008), sampling over time in one location or over space during one time period is unable to capture the DO variability that actually exists.

Predictions of DO concentrations from combined physical–biogeochemical models are an alternative to empirical DO measurements. Several models have been constructed to predict DO dynamics in the northern GOM and can provide finer-resolution data from which to assess the effects of DO concentration on the distribution of fishery landings (Hetland and DiMarco 2008; Fennel et al. 2013; Justić and Wang 2014). Although uncertainties in model-derived DO estimates can be amplified by errors in observation and from the modeling process (Mattern et al. 2013), model-predicted estimates provide spatial and temporal resolution that is more closely related to the scales over which hypoxia occurs (Eldridge and Morse 2008). Given the amount of sampling effort that would be necessary to characterize the high-resolution spatial (meters) and temporal (days) dynamics of bottom-water DO concentrations in the northern GOM, it is likely that model-derived estimates will provide the best available information for the foreseeable future.

We used spatially explicit regression models (generalized additive models [GAMs]) to explore the localized effect of bottom DO concentration and other factors on the harvest of Gulf Menhaden in the northern GOM. Our objectives were to determine the extent to which changes in DO concentration influenced the spatial distribution of the fishery and the magnitude and rate of harvest. Based on prior studies with Gulf Menhaden and other pelagic species, we hypothesized that landings of Gulf Menhaden would be concentrated in locations surrounding areas of hypoxia and would be sparse in locations within areas of hypoxia. Output from a predictive physical–biogeochemical model that provided high-resolution spatial and temporal DO data was linked to records of individual purse-seine sets in the Gulf Menhaden fishery. We then assessed the spatial effect of DO on four attributes of the commercial fishery: the probability of fishing, total catch, total effort, and overall CPUE. The effects of DO on these attributes were examined on the scale of 5- × 5-min grid cells. We also evaluated the influence of other covariates (depth, geographic location, week, and year) on the spatial and temporal patterns of fishing within the Gulf Menhaden fishery. We conclude our analysis with a discussion of the potential application of our results to the stock assessment for Gulf Menhaden in the northern GOM.
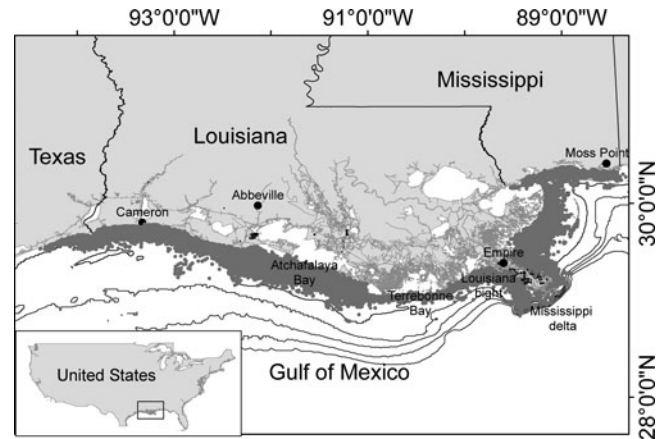

FIGURE 1. Map of fishing locations in the Gulf Menhaden fishery, northern Gulf of Mexico. Black circles represent cities that currently contain processing plants for Gulf Menhaden. Contour lines represent the 10-, 20-, 30-, 40-, and 50-m isobaths.

METHODS

Data.—Two data sets were used in our analysis: the first contained harvest records of individual purse-seine sets for the Gulf Menhaden fishery (Figure 1), and the second contained environmental covariates from a physical–biogeochemical model that were expected to influence harvest. Captains of vessels in the Gulf Menhaden fishery participate in a logbook program called the Captain's Daily Fishing Reports (CDFRs). Although participation is voluntary, compliance is believed to be 100% (Smith et al. 2002). During the fishing season, CDFRs are routinely sent to the National Marine Fisheries Service's Beaufort Laboratory, where they are digitized and stored electronically. The CDFRs summarize daily vessel activity, itemizing individual purse-seine sets with data including information on estimated catch, whether a spotter pilot was used to make the set, set location, the fishing plant where the vessel is based, estimated distance from shore, day of set, and weather conditions. Since 2000, Gulf Menhaden have been landed by about 35–40 vessels for processing at four fish factories located at Moss Point, Mississippi, and at Empire, Abbeville, and Cameron, Louisiana. Catches are reported in units of 1,000 standard fish (1 unit is ∼304 kg; Smith 1991). Fishing locations have been identified via Global Positioning System coordinates since 2005, which has greatly enhanced the spatial resolution of the data. Prior to 2005, fishing locations were based on proximity to known landmarks. In total, 75,132 CDFR records of purse-seine set locations and catches from 2006 to 2009 were available, but we used 70,570 records in our analysis. We excluded records where corresponding environmental covariates (see paragraph below) were unavailable, which was primarily in the northeastern range of the fishery along the Mississippi coast but also in intermittent locations along the shoreline.

The second data set contained predictions of bottom DO concentrations and associated depths, which were used as

environmental covariates in our analysis. Daily predictions of DO concentrations in the northern GOM over a three-dimensional irregular grid were available from simulations of a physical–biogeochemical model (Fennel et al. 2013). Based on this model, predicted DO concentrations and corresponding depth values taken at 1600 hours at the minimum of 100 m or the bottom depth were generated for approximately 1-km square grids each day from January 1, 2006, to December 29, 2009, between 87.78°W and 94.64°W and between 28.00°N and 30.21°N. The nearest estimates of DO and corresponding depth were assigned to each fishing record in the CDFR data set to form a combined data set.

Spatial and temporal aggregation of the combined data set was necessary to develop suitable response variables with which to measure effort in the fishery. Data were aggregated spatially into weekly 5- × 5-min grid cells. We chose to aggregate over 5-min grid cells because they provided a smaller spatial extent than the 10- × 10-min grids used by Smith (2001) but were still large enough to provide contrast in effort among grid cells. We chose to aggregate by week because the fishery operates on a weekly basis, setting nets primarily during Monday–Friday. A week was defined as Sunday–Saturday, starting with the third week in April (week 1; which corresponds to the start of the fishing season) and ending with the last week in October (week 29). The spatial location (longitude and latitude) for the centroid of each 5- × 5-min grid cell was used as the spatial identifier in the aggregated data set, and the nearest DO estimate and corresponding depth for each fishing record were averaged within each grid × week combination.

Four response variables were used to investigate the effect of environmental covariates on harvest in the Gulf Menhaden fishery. Three response variables were based on only positive fishing events (i.e., grid × week combinations in which a purse seine was set), whereas the fourth response variable was a binary response variable indicating whether a purse seine was set and was based on all possible grid × week combinations. Two of the response variables based on positive fishing events were total catch (in units of 1,000 standard fish) and total effort (in number of purse-seine sets), summed over all sets within a grid × week combination. The third response variable was the CPUE for each grid × week combination and was computed from the first two response variables as total catch divided by total effort. The fourth response variable measured the probability that fishing occurred in a grid cell. Grid cells where at least one set for Gulf Menhaden occurred during 2006–2009 were included in the sample space of total possible grids. Grid cells where fishing occurred within a week were assigned a value of 1, whereas grid cells where fishing did not occur within a week were assigned a value of zero. Given that grid × week combinations in which Gulf Menhaden sets did not occur were necessary when examining the probability of fishing, we changed the way DO concentrations and corresponding depths were aggregated when using the probability of fishing as the response variable.

Every DO value and corresponding depth record from the environmental data set within a 5- × 5-min grid cell (rather than the DO value and corresponding depth nearest to each fishing record) was averaged across the week. The final aggregated data set based on positive fishing events included 7,535 records for the three response variables (catch, effort, and CPUE), with longitude, latitude, week, DO, and depth as covariates. The final aggregated data set based on all possible fishing locations included 39,378 records for the binary response variable (probability of fishing), with longitude, latitude, week, DO, and depth as covariates.

Regression models.—We used GAMs to determine the effects of DO and other covariates on the two types of response variable: (1) measures of harvest where Gulf Menhaden were caught and (2) the probability of fishing for Gulf Menhaden at specific grid × week combinations (Hastie and Tibshirani 1986). A spatially varying component for DO was included in each GAM (Wood 2006) to determine the localized effect of DO (i.e., effect for each grid cell) on each response variable. We assumed that the effect of DO on each response variable was linear but that the magnitude and direction of the effect could differ by location. The interpretation of the spatially varying DO term is therefore the change in the response variable corresponding to a unit decrease in DO for each grid cell. We only considered effects in our analysis that were significantly different from zero at an α level of 0.05. Spatially varying GAMs have been used to assess the effects of environmental factors on spatial patterns in abundance (Bacheler et al. 2009; Bartolino et al. 2011; Ciannelli et al. 2012) and in commercial fishery landings (Bacheler et al. 2012; Bartolino et al. 2012).

Distributional assumptions are required when using GAMs. A negative binomial distribution was assumed for catch and effort (discrete response variables) within each grid × week combination. Alternative values for the dispersion parameter of the negative binomial were initially estimated but greatly increased the computation time. Values of the dispersion parameters that maximized model fit were estimated at very near to 1, so the value of 1 was used for the final models. A lognormal distribution was assumed for CPUE, which was continuous and nonnormal, and a binomial distribution was used to model the probability of fishing in a grid × week combination.

We used a similar set of covariates for models of each response variable. Covariates included (1) year, which was modeled as a factor and ranged from 2006 to 2009; (2) week, which was modeled as a continuous variable and ranged from 1 to 29; (3) depth, which was modeled as a continuous variable and ranged from 5 to 95 m; (4) spatial location (longitude and latitude); and (5) a spatially varying DO term, with DO values ranging from 0.01 to 10.0 mg/L. The significance of each term was determined by backward model selection based on Akaike's information criterion (AIC; Burnham and Anderson 2002) and generalized cross-validation (GCV; Wood 2006) scores. If the removal of any one term resulted in smaller AIC or GCV scores, then the term was removed from the final model. The full model

for each of the four response variables was

$$x_{\varphi,\lambda,t,y} = \alpha_y + s_1(\varphi_{t,y}, \lambda_{t,y}) + s_2(\varphi_{t,y}, \lambda_{t,y})D_{\varphi,\lambda,t,y}$$
$$+ g_1(t) + g_2(Z_{\varphi,\lambda,t,y}) + \varepsilon_{\varphi,\lambda,t,y}, \tag{1}$$

where $x_{\phi,\lambda,t,y}$ is the value of the response variable for each grid cell with longitude ϕ and latitude λ in week t and year y; α_y is the year-specific intercept; D is the model-predicted DO concentration for each grid $\times$ week combination; Z is the depth for each grid $\times$ week combination; s and g are two-dimensional and one-dimensional smooths, respectively (Wood 2006); and ε is the residual error term, which was modeled as $N(0, \sigma^2)$ when the response was $\log_e(CPUE)$. Diagnostics of model residuals from the full models showed some skewness in negative residuals for set number and CPUE. Other distributions and assumptions were explored, but our results were robust to these changes. We therefore considered our assumptions appropriate. All statistical modeling was performed by use of the mgcv package in R version 2.15.1 (Wood 2006; R Core Development Team 2012).

RESULTS

Data

Harvest of Gulf Menhaden in the northern GOM overlapped with locations that experienced low DO concentrations (Figures 2, 3). Fishery catches were greatest immediately east of the Mississippi Delta; immediately west of the Mississippi Delta (i.e., the Louisiana Bight); and west of Atchafalaya Bay, which is at the mouth of the Atchafalaya River, extending to the Texas border (Figure 2). The Louisiana Bight and the region west of Atchafalaya Bay also experienced the lowest concentrations of DO, whereas east of the Mississippi Delta, the DO concentrations were generally high (Figure 3). Output from GAMs was used to better determine the effects of DO concentration on Gulf Menhaden harvest.

Regression Models

All covariates considered in equation (1) were significant in explaining each of the four response variables and were included in all final models (Table 1). We sequentially removed each covariate from the final models to determine the importance of each in explaining model deviance. Depth and spatial location
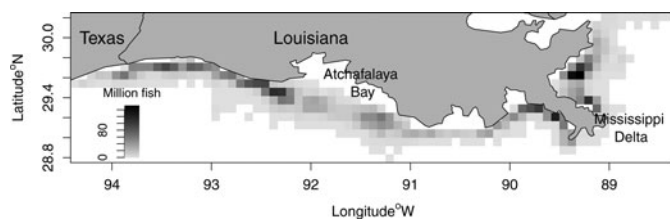

FIGURE 2. Locations of total Gulf Menhaden landings (millions of fish) at 5- × 5-min grid cells, summed over all fishing sets in the northern Gulf of Mexico during 2006–2009 (darker shading in cells = more fish caught; lighter shading in cells = fewer fish caught).
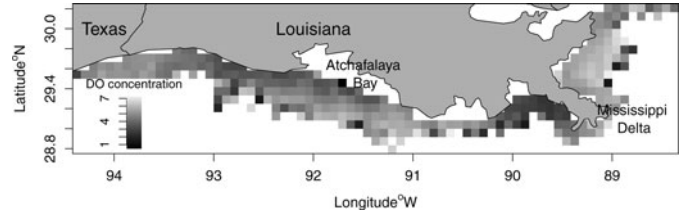

FIGURE 3. Dissolved oxygen (DO) concentrations (mg/L) at 5- × 5-min grid cells, averaged over all fishing sets in the northern Gulf of Mexico during 2006–2009 within each grid (darker shading in cells = lower DO concentration; lighter shading in cells = higher DO concentration).

(longitude and latitude) explained the most deviance in the probability of fishing, catch, and effort for each grid × week combination (Table 1). Lesser amounts of deviance were explained by spatially varying DO, week, and year. The covariates that explained the most deviance in CPUE were different than those explaining the most deviance for the other response variables. The greatest amount of deviance in CPUE was explained by week, followed by year, the two spatial terms, and lastly depth. The total percent deviance explained by the full models ranged between 10% and 22% depending on the response variable used (Table 1). The probability of fishing included information on fished locations as well as nonfished locations, and the amount of deviance explained by the full model was greater (22.4%) than that for other response variables (<14.0%).

We observed similar patterns in the estimated effects of each covariate across response variables. As depth increased from all but the shallowest of waters (5 m), the probability of fishing (Figure 4A), total catch (Figure 4B), and total effort (Figure 4C) all declined. The effect of depth on the probability of fishing (Figure 4A) showed some bimodality, with high values at the shallowest depths and intermediate (20–40-m) depths. Variation around the effect of depth was high at greater depths for all response variables due to fewer data points at those depths. The effect of depth on the probability of fishing was less variable than the effects on other response variables because a greater amount of deviance was explained by the model. Despite the general decline in catch and effort with increasing depth, CPUE was relatively constant across the depth range (Figure 4D). The effect of depth on CPUE barely differed from zero and was only weakly significant. Wood (2006) recommended caution with weakly significant terms, so although depth was significant, it did not appear to affect Gulf Menhaden CPUE.

The general effect of week on Gulf Menhaden harvest was also similar across all four response variables but was much smaller in magnitude than the effect of depth (Figure 4). Response variables increased from the beginning of the season to a first peak between week 8 and week 14 (early June to mid-July). After the initial peak, the response variables declined for a period of time before increasing to a second peak at week 20–25 (early August to mid-September). Week of the fishing season had the strongest effect on CPUE (Table 1), with a well-defined peak in mid-July (Figure 4H), whereas the other response variables

TABLE 1.   Generalized cross-validation (GCV) scores, differences in Akaike's information criterion (δAIC) from the full model, and the percentage of deviance explained by the full model and each corresponding submodel with one covariate removed for the four response variables (probability of fishing, total Gulf Menhaden catch, total effort, and CPUE; see Methods). The lowest values of GCV and δAIC for each response variable indicate the best model.

Model	GCV	δAIC	Deviance explained (%)
Probability of fishing			
Full model: year + location + (location × DO) + week + depth	−0.184	0	22.4
Year removed	−0.182	47	22.3
Week removed	−0.174	342	21.5
Location × DO removed	−0.171	450	21.1
Location removed	−0.152	1,092	19.3
Depth removed	−0.145	1,336	18.7
Total catch			
Full model: year + location + (location × DO) + week + depth	0.68	0	10.0
Year removed	0.683	22	9.7
Week removed	0.699	139	8.8
Location × DO removed	0.699	142	8.6
Location removed	0.701	158	8.4
Depth removed	0.712	241	8.1
Total effort			
Full model: year + location + (location × DO) + week + depth	−0.062	0	14.0
Year removed	−0.061	6.9	13.8
Week removed	−0.057	32	13.4
Location × DO removed	−0.054	56	12.7
Location removed	−0.050	88	12.3
Depth removed	−0.034	208	11.3
CPUE			
Full model: year + location + (location × DO) + week + depth	0.436	0	11.9
Depth removed	0.437	7.9	11.7
Location removed	0.441	73	10.3
Location × DO removed	0.441	80	10.3
Year removed	0.447	187	9.7
Week removed	0.450	235	8.9

plateaued between June and August (Figure 4E–G). Overall, the majority of Gulf Menhaden harvest occurred during June–August.

Relative to other covariates, year explained little of the variation in response variables except CPUE (Table 1). Consequently, the year effects for CPUE were the largest among the four response variables, and error bounds of ±2 SEs did not overlap zero. Year was modeled as a factor to avoid overparameterization, and year effects were estimated relative to a reference year, which was 2006. Year effects in 2008 were the most extreme among all years, reducing the probability of fishing by 0.22 and reducing effort by 0.12 relative to 2006 but increasing catch by 0.13 and increasing $\log_e$(CPUE) by 0.30 relative to 2006, all on the scale of the link functions. Despite 2008 having large effects, consistent patterns among years for each response variable were not predicted.

The effect of DO on each response variable varied spatially and was comparable in magnitude to the overall effects of week and year (Figure 5). Patterns in local DO effects were present in the western range of the fishery, the eastern range of the fishery north of the Mississippi Delta, and the region between Atchafalaya Bay and the Mississippi Delta. We present results for each of these regions, beginning with the western region.

There were significant increases in all response variables as DO concentration declined in the western range of the fishery (Figure 5). In this region, the effects of DO on the probability of fishing were greatest along the shore and extended from the Texas–Louisiana border to the western edge of Atchafalaya Bay, consistent with westward movement in the fishery as DO concentration declined (Figure 5A). Probabilities of fishing in this region were moderate (between 0.25 and 0.50 on the original scale), so DO affected locations that generally were fished. The effects of DO on catch (Figure 5B), effort (Figure 5C), and CPUE (Figure 5D) were greatest on the boundaries of the western region, near the Texas–Louisiana border, and offshore of Atchafalaya Bay (Figure 5B–D). Although the spatial effects of DO were greatest in these locations, these areas had small predicted values for the response variables, indicating that DO
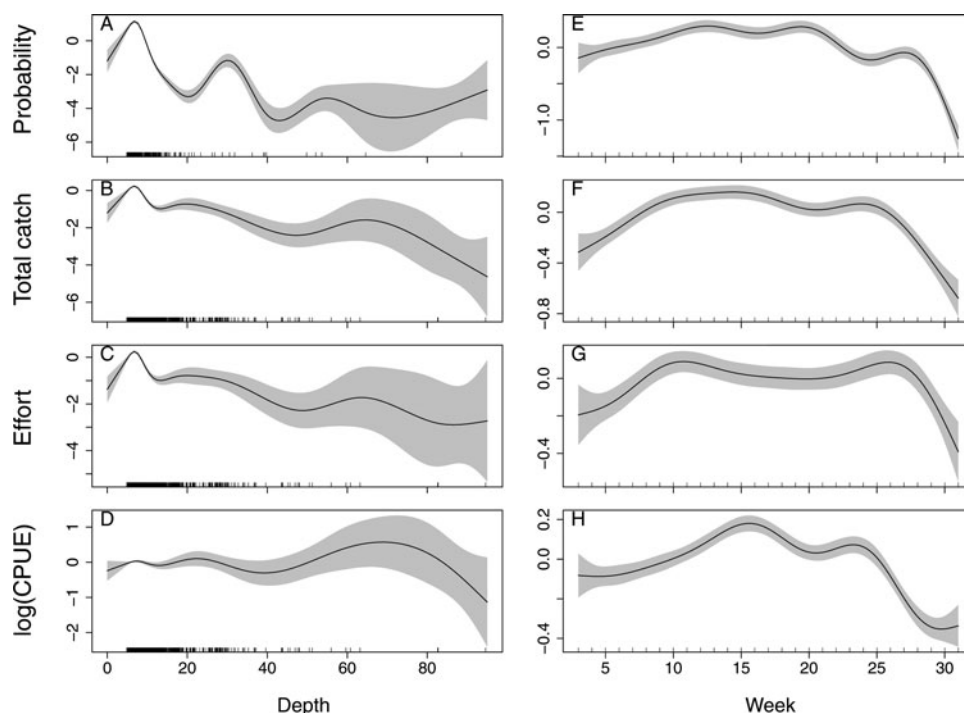
FIGURE 4. Partial effects (solid line) of depth and week on the response variables at the scale of the link function for each of four models: **(A)** effect of depth on the probability of fishing in each grid × week combination (on a logit scale), **(B)** effect of depth on total Gulf Menhaden catch (units = 1,000 standard fish, on a log scale), **(C)** effect of depth on total effort (number of sets, on a log scale), **(D)** effect of depth on $\log_e$(CPUE) within each grid × week combination, **(E)** effect of week on the probability of fishing, **(F)** effect of week on total catch, **(G)** effect of week on total effort, and **(H)** effect of week on log(CPUE). The shaded areas represent ± 2 SEs. Vertical lines along the x-axis represent the individual data values used in the model. A different data set was used for the probability model (see Methods).

had an effect on locations where catch and effort were typically low. Overall, the distribution of catch shifted westward to locations with lower levels of harvest when DO concentrations declined.

Increases in the response variables as DO concentration declined also occurred in the eastern range north of the Mississippi Delta. Similar to the results for the western range, as DO concentrations declined the probability of fishing increased along the shoreline, consistent with a nearshore shift in the fishery (Figure 5A). Predicted probabilities of fishing at particular locations in the eastern range were slightly higher than probabilities in the western range; therefore, declines in DO concentration also affected locations that experienced moderate to high harvest. In contrast to effects on the probability of fishing, the catch (Figure 5B), CPUE (Figure 5D), and (to a lesser extent) effort (Figure 5C) increased offshore as DO concentration declined. Therefore, despite an increased probability of fishing nearshore, declines in DO did not result in a greater catch in nearshore areas.

For the most part, decreases in the response variables with declines in DO concentration occurred only in the region between Atchafalaya Bay and the Mississippi Delta (Figure 5); this area is subject to severe and frequent hypoxia. Moderate declines in the probability of fishing extended across the entire region (Figure 5A). Declines in catch mostly occurred just east

of Atchafalaya Bay (Figure 5B), whereas declines in effort—although greatest just east of Atchafalaya Bay—also extended to the Mississippi Delta (Figure 5C). Declines in CPUE were compressed into a very small region just east of Atchafalaya Bay and off Terrebonne Bay, whereas in the region closer to the Mississippi Delta, CPUE increased with declining DO concentration (Figure 5D). Values for all response variables off Terrebonne Bay were low, as little fishing effort typically occurred there, so declines in the response variables were relatively modest on an absolute scale.

Within the region between Atchafalaya Bay and the Mississippi Delta, the Louisiana Bight was unique because there was no common pattern among all four response variables. As in other areas of the GOM, declines in DO concentration in the Louisiana Bight resulted in increased fishing probabilities at locations near shore (i.e., the western shore; Figure 5A). In addition, both the probability of fishing and the fishing effort (Figure 5C) declined offshore as DO concentration declined, suggesting that vessels made fewer trips into the Louisiana Bight as DO levels declined. The predicted probability of fishing and the total effort were highest in the Louisiana Bight (Figure 5A, C), so these spatial effects were relatively large on an absolute scale in comparison with other regions. Similar to patterns in the eastern range of the fishery, the CPUE increased throughout the
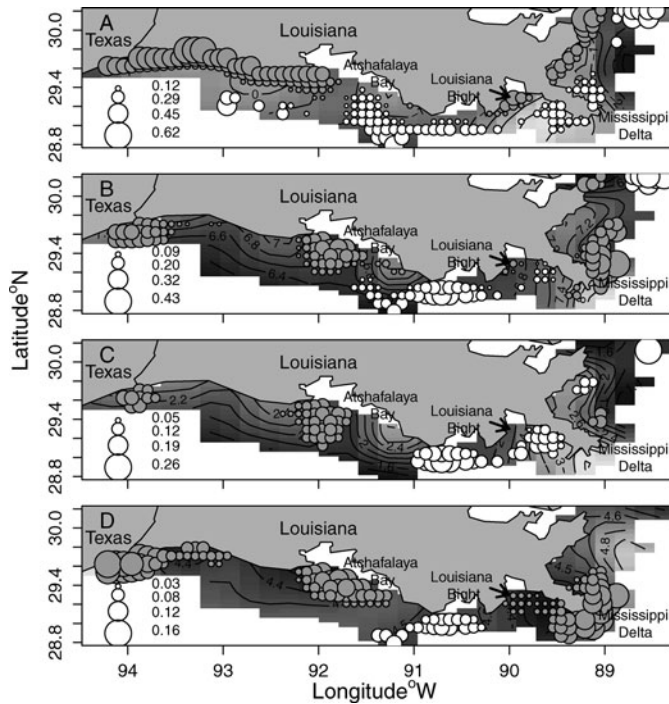
FIGURE 5. Spatially varying generalized additive model plots, showing the predicted values of four response variables for the Gulf Menhaden fishery at 5- × 5-min spatial grid cells, as well as the effect of changes in dissolved oxygen (DO) concentration on model predictions. Response variables include **(A)** the probability of fishing in a grid cell (on a logit scale), **(B)** total catch in a grid cell (units = 1,000 standard fish, on a log scale), **(C)** total effort in a grid cell (number of sets, on a log scale), and **(D)** $\log_e$(CPUE). Lighter shading indicates a higher predicted value of each response variable. Overlaid on the predictions are white and gray bubbles, which indicate the change in the response variable for a unit decrease in DO concentration for that grid (white bubbles = decreases in the response variable; gray bubbles = increases in the response variable). Circle size corresponds to the size of the DO effect on the response variable. Only locations where effects were significantly different from zero ($\alpha = 0.05$) are shown.

Louisiana Bight, albeit slightly, as DO concentration declined (Figure 5D). Predicted CPUE was already low in the Louisiana Bight, so declines in DO concentration reduced the CPUE values even more. Overall, spatially varying DO effects at locations within the Louisiana Bight supported the general results from other regions: the fishery shifted toward shore and the CPUE increased as the DO concentration declined. Contrary to results for other regions, fishing effort in the Louisiana Bight decreased in response to declining DO concentrations.

DISCUSSION

Smith (2001) hypothesized a link between hypoxia and Gulf Menhaden landings. Our study is the first to quantitatively test this link with detailed spatial data and to provide evidence supporting the hypothesis. We have demonstrated that declining concentrations of bottom DO can influence the spatial distribution of the catch, effort, CPUE, and probability of fishing in the Gulf Menhaden fishery of the northern GOM. Spatial

patterns in the effects of DO on response variables were consistent with a westward and nearshore shift in the fishery as bottom DO concentration declined. A nearshore shift in the fishery supported our hypothesis that Gulf Menhaden would be found along the edges of hypoxic areas, which are offshore and impinge along the shoreline during extreme years (Rabalais et al. 2007). A westward, nearshore shift in the fishery supported Smith's (2001) hypothesis that a near-continuous band of hypoxia along the coast would aggregate Gulf Menhaden into normoxic regions along western Louisiana. Additionally, we found evidence that CPUE increased as DO concentration declined in the Louisiana Bight, a region that typically experiences chronic, severe hypoxia. Such behavior could be explained by enhanced aggregation of Gulf Menhaden vertically above the low-DO bottom layer. Vertical aggregation in response to declines in DO concentration has been found for both pelagic and demersal species in the GOM (Hazen et al. 2009; Zhang et al. 2009) and other ecosystems (Stramma et al. 2012), although evidence against strong DO effects for the entire water column also exist (Zhang et al. 2014).

Patterns in the partial effects of depth and week in our analysis supported what is generally known about the Gulf Menhaden fishery. The partial effect of depth indicated a declining trend for all response variables except CPUE. Gulf Menhaden are common in nearshore, shallow waters during the fishing season (Ahrenholz 1991). The majority of landings occur within 16.09 km (10 mi) of shore (Smith et al. 2002), a region that is characterized by shallow (<20 m) and gradually changing isobaths except in the proximity of the Mississippi Delta. Therefore, catch, effort, and the probability of fishing were likely greatest in shallow waters as a consequence of greater Gulf Menhaden abundance and the reduced operating costs of fishing at short distances from home ports. Bimodality in the effect of depth on the probability of fishing at 5 and 30 m could result if Gulf Menhaden aggregate both inshore and offshore of the hypoxic zone, as has been shown for other species (Craig 2012; Craig and Bosman 2013). The depths of the two modes corresponded to the approximate inshore and offshore edges of the hypoxic zone (Rabalais and Turner 2001), suggesting some preference for fishing near the hypoxic zone; however, similar patterns were not observed for the effects of depth on catch, effort, or CPUE. Similarities in the effect of depth on CPUE across all depths could result if spatial patterns in fishing effort mirrored those in the spatial distribution of Gulf Menhaden, which is plausible given that the fishery employs spotter pilots to help direct boats on where to set.

The partial effect of week showed a similar trend among all response variables. The response variables increased during the beginning of the fishing season (April–May), plateaued or peaked during the middle of the season (June–August), and then declined towards the end of the season (September–November). Catch per unit effort exhibited the highest peak among all response variables during the summer (June–August), when hypoxia is typically most severe. A peak in CPUE during the

summer is consistent with enhanced susceptibility of Gulf Menhaden to the fishery, possibly due to hypoxia-induced shifts in spatial distributions; however, these effects were not particularly large, and other explanations are possible. Even so, high values for all response variables during the mid-summer hypoxia period suggest that the observed spatial patterns in DO effects were driven mostly by the time frame during which hypoxia was typically most severe within the fishing season.

Local effects of declines in DO concentration on response variables for the Gulf Menhaden fishery supported findings from previous studies about the effects of hypoxia on catches of pelagic and demersal species in the GOM. Craig (2012) reported that northern brown shrimp *Farfantepenaeus aztecus* and demersal finfishes aggregated within 1–3 km of the nearshore and offshore edges of the hypoxic zone and that spatial overlap among the species was strongest during years when hypoxia was most severe. Zhang et al. (2009) found similar patterns of horizontal aggregation along the offshore edge of the hypoxic zone for pelagic biomass in sub-pycnocline waters. The nearshore shifts in the probability of fishing with declining DO concentrations suggest that the Gulf Menhaden fishery responds to hypoxia-induced shifts in the horizontal distribution of their target species; however, fishery-independent information on the spatial distribution of Gulf Menhaden would be necessary to test this hypothesis. Zhang et al. (2009) also found that pelagic species moved vertically in the water column to avoid hypoxic conditions, which could explain the increased CPUE as DO concentrations declined in the Louisiana Bight. It was a bit surprising, however, that similar increases in CPUE did not occur elsewhere. However, hypoxia persistently develops in the Louisiana Bight (Rabalais et al. 2002), and when coupled with the strong environmental and depth gradients in the Louisiana Bight, this may enhance spatial aggregation more so than in other GOM regions where spatial gradients and hypoxic conditions are typically weaker.

Given the persistence of hypoxia in the Louisiana Bight, we were also surprised that localized effects of declines in DO were not stronger than effects in other locations. The size of the spatial grid used in our analysis may have influenced the ability of our model to capture DO effects in the Louisiana Bight. Depth contours are close together in the Louisiana Bight, so covariates are averaged over more dynamic conditions than in other areas of the GOM. In contrast, the western and eastern ranges of the fishery have very shallow bathymetry, and the fishery operates on a broader spatial scale. Consequently, differences in the variability of physical processes between the Louisiana Bight and other regions of the GOM may explain why the effects of changes in DO concentration were relatively large and similar across response variables in the western and eastern ranges but not in the Louisiana Bight.

The limitations of our study should be considered when interpreting the results. One primary limitation of our study was that we used predictive model output of bottom DO concentrations from a physical–biogeochemical model as input into our anal-

ysis (Fennel et al. 2013). Predictive physical–biogeochemical models are complex and explicitly account for many processes that influence hypoxia formation. Such processes are themselves uncertain, potentially compounding error in the final model output. Fennel et al. (2013) reduced the potential for error by validating model predictions of the area of hypoxia in July against yearly estimates of the total area of hypoxia in the northern GOM for 2004–2007 from annual shelfwide surveys (Rabalais et al. 2002). Comparison to the total area of hypoxic bottom water based on shelfwide surveys in late July provided a validation of the model, but the extent to which the model captured the exact locations of hypoxic bottom water and how the area of hypoxia in July compares with hypoxic areas present during other time periods remain unknown. Fennel et al. (2013) also warned about the sensitivity of their model predictions to assumptions about sediment oxygen consumption and the choice of physical horizontal boundaries. Uncertainties in the model used by Fennel et al. (2013) were assessed by Mattern et al. (2013), who found that 20% variation in initial physical parameters (e.g., wind and river inflow) could affect predictions of the total area of hypoxia by up to 40%.

We used fine-scale estimates of bottom DO concentration because part of the difficulty in determining the effects of hypoxia on fisheries is that DO dynamics operate on spatial and temporal scales that are much finer than the typical fishery range and season. It is unlikely that simple correlative analyses at aggregate spatial (e.g., entire fishing grounds) and temporal (e.g., annual) scales have sufficient statistical power to detect and isolate hypoxic (or other environmental) effects on aggregate fishery landings. The power of our approach was the ability to quantify the effects of low bottom DO on aspects of the Gulf Menhaden fishery at the localized scales at which these effects were most likely to occur. The immediate challenges for future work are to further confirm the fine-scale spatial and temporal variation in DO predicted by the physical–biogeochemical modeling and to determine whether and how localized DO effects on the fishery translate to larger scales. The most recent stock assessment of Gulf Menhaden showed declines in landings and in fishing effort since the mid-1980s, although total biomass and indices of abundance were relatively stable or slightly increasing in recent years (SEDAR 2013). Hence, despite the Gulf Menhaden fishery's inshore and westward shifts associated with low bottom DO concentrations, there is no evidence to date of large-scale effects on the Gulf Menhaden population or the fishery.

Another limitation of our study was that we only considered effects on fishery response variables due to changes in a few environmental covariates (i.e., DO, depth, and spatial location). Spatial distributions of Atlantic Menhaden *B. tyrannus* in estuaries are related to spatial gradients in phytoplankton biomass and possibly salinity and other environmental factors (Friedland et al. 1996), which may be correlated with bottom DO at particular spatial and temporal scales. Zhang et al. (2014) found that temperature and prey availability explained more variation in growth potential for Gulf Menhaden in the GOM

than did DO given that the extent of hypoxic conditions into the water column was relatively limited. Consequently, greater information on the vertical extent of DO would also improve our analysis. Inclusion of depth and spatial location as predictor variables accounts for some of the variation associated with potentially important environmental predictors (e.g., turbidity, salinity, and temperature) without the introduction of additional uncertainty associated with deriving these predictors from other data sources. Generating such environmental data on the scales of our analysis provides further challenges. In addition to factors that could affect Gulf Menhaden distribution, we also did not include factors that could potentially influence the distribution of the fishery. There is a growing body of literature showing the effect of fisher behavior on fleet dynamics; market prices, operation costs, recent catches, and historical fishing patterns have all been shown to affect the choice of fishing locations (van Putten et al. 2012). We investigated the distance to the home port in preliminary analyses, but our results were similar to the simpler approach presented herein, so we ultimately excluded that variable from our final analysis.

Our models captured a relatively small amount of the overall variability in the data, which may also be perceived as a limitation. Deviance explained by our models ranged from 10.0% to 22.4% depending on the response variable. Spatially varying GAMs used for studies in the Gulf of Alaska and eastern Bering Sea explained 47–83% of the deviance using only environmental variables, but these were based on fishery-independent surveys (Bacheler et al. 2009, 2010; Bartolino et al. 2011). Fishery-independent surveys smooth over temporal and spatial variability by standardizing the fishing process at specified dates and random locations. The amount of variability explained by our models was more comparable to the variability explained by models of fishery-dependent data in the eastern Bering Sea (Bacheler et al. 2012). For studies in the GOM, Craig and Crowder (2005) explained 20–35% of the deviance of presence/absence data in fishery-independent surveys for a demersal fish species. The ability of our models to explain variability in the data should also be considered in relation to the complexity of the process being modeled. Hypoxia in the GOM has been extensively studied and is affected by many interrelated factors (Bianchi et al. 2010). The fishing process is also highly complex and driven by numerous factors (van Putten et al. 2012). Consequently, although additional covariates related to the spatial distribution of fish and the location choices of fishers might have increased the amount of deviation explained by our model, the percent deviance explained could still remain low due to variability in fishery data and in the processes affecting DO concentration within the GOM.

Management Implications

We have demonstrated nearshore and westward movements in the distribution of the Gulf Menhaden fishery as bottom DO concentrations declined. One potential consequence of the fishery's shift in distribution would be a change in the effectiveness of fishing effort on harvesting fish—in other words, a change in Gulf Menhaden catchability to the fishery. Changes in a resource's catchability to its fishery have been investigated in relation to many factors, including technological changes in the fishery over time and distributional changes in the resource over time and space (Wilberg et al. 2010). Time-varying and spatially varying catchability has important management implications because most stock assessment models, including those used to support the management of Gulf Menhaden, assume constant catchability (Wilberg et al. 2010). If catchability is underestimated in these models, then biomass estimates are biased high and fishing mortality estimates are biased low, potentially leading to less-conservative management advice than intended (Wilberg et al. 2010). The movement of Gulf Menhaden into locations nearer to shore and to the western part of the fishery and the higher catch rates in the Louisiana Bight as DO concentrations decline could potentially affect catchability and could have consequences for the stock-wide assessment of Gulf Menhaden, but we do not know the magnitude of such effects. The consequences could be small given that (1) the current assessment of Gulf Menhaden is performed on an annual time step and over the entire range of the fishery and (2) the effects observed in our research were often in locations where moderate catch and effort occurred. More direct analysis of key stock assessment assumptions—particularly the assumption of constant catchability over time and space—is needed to determine the consequences for management and is the subject of ongoing investigation.

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