

Aggregation on the edge: effects of hypoxia avoidance on the spatial distribution of brown shrimp and demersal fishes in the Northern Gulf of Mexico

J. Kevin Craig*

Florida State University Coastal and Marine Laboratory, 3618 Highway 98, St. Teresa, Florida 32358-2702, USA

Present address: Southeast Fisheries Science Center, NOAA National Marine Fisheries Service, 101 Pivers Island Road, Beaufort, North Carolina 28516-9722, USA

ABSTRACT: The northwestern Gulf of Mexico shelf experiences the largest seasonal hypoxic (dissolved oxygen, $DO \leq 2.0 \text{ mg l}^{-1}$) zone in the western hemisphere. This study uses bottom trawl and hydrographic surveys over 3 yr to quantify low DO avoidance thresholds, patterns of aggregation in nearby oxygenated refuge habitats, and spatial overlap of brown shrimp *Farfantepenaeus aztecus* and several finfishes on the nearshore Louisiana shelf. On average, DO avoidance thresholds were low ($1 \text{ to } 3 \text{ mg l}^{-1}$) and near incipient lethal levels for similar species, suggesting organisms avoid the lowest, lethal DO levels on the shelf. Avoidance thresholds varied both within and among years, indicating that behavioral responses to low DO are context-dependent and vary in relation to the severity of hypoxia and possibly other factors. Despite the absence of physical barriers to movement, evading organisms aggregated at short distances (1 to 3 km) just beyond the margins of the hypoxic zone, indicating that sublethal and indirect effects of hypoxia are probably most intense within a relatively narrow region along the hypoxic edge. DO avoidance thresholds and patterns of aggregation were similar between brown shrimp, the primary target of the commercial shrimp trawl fishery, and several juvenile and small adult finfishes that comprise most of the bycatch. In addition, spatial overlap between brown shrimp and finfishes was highest in the years when hypoxia was most severe, and this effect was stronger for benthic fishes than for pelagic fishes. These results suggest the potential for enhanced harvest and bycatch interactions along the margins of the hypoxic zone as an indirect effect of hypoxia-induced shifts in spatial patterns. Such spatially mediated indirect effects are an important means by which hypoxia influences mobile species in the Gulf.

KEY WORDS: Eutrophication · Spatial statistics · Avoidance behavior · Bycatch · Catchability · Fishery interactions · Dead zone · *Farfantepenaeus aztecus* · Mississippi River plume

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INTRODUCTION

Cross-system comparisons of both freshwater and marine ecosystems have revealed a positive relationship between nutrient concentrations and fish biomass, reflecting the fundamental limits that nutrients impose on the productivity of upper trophic levels

(Ney 1996, Nixon & Buckley 2002). However, nutrient over-enrichment, or the stimulation of primary productivity to harmful levels by the anthropogenic addition of nutrients (NRC 2000), often leads to low dissolved oxygen (DO) or hypoxia ($DO \leq 2.0 \text{ mg l}^{-1}$). Direct exposure to hypoxic water impairs the growth (Stierhoff et al. 2006), reproduction (Thomas et al.

*Email: kevin.craig@noaa.gov

2007), and survival (Goodman & Campbell 2007) of organisms; however mobile species are typically able to avoid the lowest DO levels so that direct exposure to lethal conditions is often limited or ephemeral in the field (Eby & Crowder 2002, Craig & Crowder 2005, Tyler & Targett 2007). This suggests that hypoxia has mostly sublethal and indirect effects on mobile species that are mediated by behavioral avoidance and associated shifts in spatial distribution (Craig et al. 2001, Breitburg 2002, Rose et al. 2009). While the sublethal effects of exposure to low DO have received attention (e.g. Stierhoff et al. 2006, Thomas et al. 2007), indirect effects associated with hypoxia-induced changes in spatial distribution are less well known. Potential indirect effects of hypoxia avoidance include changes in the abiotic conditions (e.g. temperature) and the availability of food resources that influence the growth of organisms (Craig & Crowder 2005, Neuenfeldt & Beyer 2006), as well as changes in exposure to both natural predators and fisheries that influence mortality (Breitburg et al. 1999, Prince et al. 2010). Elucidating the linkages between behavioral avoidance of low DO, associated shifts in spatial distribution, and the attendant consequences for population vital rates (e.g. growth, mortality, reproduction) is important for determining the nature and magnitude of population level effects of hypoxia on mobile species (Breitburg et al. 2009a,b).

Quantifying the particular level of DO that induces avoidance behavior and the spatial scale over which evading organisms move is important for understanding the sublethal and indirect effects of hypoxia. Avoidance behavior is often characterized as a threshold response whereby organisms are rare or absent below a particular level of DO, but abundance is not strongly related to DO above the threshold (Howell & Simpson 1994, Eby & Crowder 2002, Vaquer-Sunyer & Duarte 2008). However, organisms may not avoid a single, fixed level of DO because avoidance behavior has been shown to depend on a number of factors, including other abiotic conditions (Skjæraasen et al. 2008), the nutritional state of organisms (Bernatis et al. 2007), physiological and behavioral adaptations (Brady et al. 2009), predation risk (Robb & Abrahams 2002), and even the spatial and temporal scale of observation (Bell & Eggleston 2005). While accounting for the numerous factors that can influence hypoxia avoidance in the field is difficult, some variability in behavioral responses to low DO and therefore variability in estimated avoidance thresholds should be expected. In a recent synthesis of low DO thresholds in marine metazoans, lethal and sublethal DO concentrations varied by 76

to 78% of the median across taxa (Vauquer-Sunyer & Duarte 2008). Field estimates of variability in response to low DO within particular species have not been reported.

Despite numerous field studies that report avoidance of low DO, surprisingly little is known about the spatial distributions of organisms beyond the area of hypoxia. In estuaries and tidal creeks where most studies have been conducted, fish evading low DO appear to move limited distances (meters to kilometers) and often return to previously hypoxic areas within a short time (hours to days) once conditions improve (Pihl et al. 1991, Eby & Crowder 2002, Tyler & Targett 2007). Anecdotal observations indicate that hypoxia can induce aggregations (i.e. 'jubilees') of evading organisms in oxygenated refuge habitats, particularly where the shoreline provides a constraint to movement (Loesch 1960). Based on shelf-wide, fishery-independent trawl surveys in the northwestern Gulf of Mexico, Craig & Crowder (2005) showed that brown shrimp *Farfantepenaeus aztecus* and Atlantic croaker *Micropogonias undulatus* aggregated at distances from 5 to 20 km beyond the offshore edge (2.0 mg l⁻¹ DO contour) of the hypoxic zone. These hypoxia-induced shifts in spatial distribution altered the temperatures that brown shrimp and croaker experienced and may have intensified trophic and fishery interactions in nearby oxygenated edge habitats. Such indirect effects of avoidance behavior were demonstrated at smaller spatial scales by Lenihan et al. (2001), who reported predatory fish declines in oyster reef habitat inundated with hypoxia, predator increases in nearby oxygenated refuge habitats, and prey declines in the refuge habitat, indicative of a cascading effect that extended beyond the hypoxic area.

The northwestern Gulf of Mexico shelf currently experiences the largest seasonal hypoxic zone in the western hemisphere (Rabalais et al. 2002, Turner et al. 2008). The shelf is located at the terminus of the Mississippi–Atchafalaya river system that drains 41% of the continental United States, making it the largest watershed in North America and the third largest watershed in the world (van der Leeden et al. 1990). Hypoxia occurs primarily in bottom waters during the summer (May to September) on the inner Louisiana shelf (<30 m depth), sometimes stretching to the north Texas shelf (see Fig. 1). Based on mapping surveys since the mid-1980s, the area of hypoxia has varied from <100 km² to >22 000 km² and has generally increased from the 1980s to the 1990s and 2000s, though with considerable annual variability (Rabalais et al. 2002, Turner et al. 2008). Evidence from paleo-

studies and hindcasting models indicate increasing oxygen stress since the early 1900s, with hypoxia becoming more severe beginning in the 1960s to 1970s (Justić et al. 2007, Rabalais et al. 2007a). Current efforts to manage the Gulf hypoxic zone have focused on voluntary and incentive-based nutrient reduction strategies within the watershed, with the goal of reducing the area of hypoxic bottom water to about one-third (i.e. 5000 km²) of its recent historical average (Rabalais et al. 2007b, Mississippi River/Gulf of Mexico Watershed Nutrient Task Force 2008).

The area of the Louisiana shelf that currently experiences hypoxia is within a region of high fishery productivity that has historically supported the highest biomass of demersal fish and crustaceans in the northwestern Gulf (i.e. 'the fertile fishery crescent'; Gunter 1963, Moore et al. 1970). The high productivity of this region is driven by nutrient inputs from the Mississippi–Atchafalaya River system and relatively open connections to productive, marsh-dominated estuaries (Grimes 2001, Cowan et al. 2008). The commercial shrimp trawl fishery is historically the highest-valued fishery in the Gulf with shrimping effort in coastal Louisiana peaking during the summer months when hypoxia is typically most severe (Zimmerman & Nance 2001). Analysis of landings data indicates that both shrimp catch and effort are low in areas of the shelf with hypoxic bottom water (Zimmerman & Nance 2001). Hypoxia may also block the offshore migration of brown shrimp to deeper shelf waters and induce alongshore migrations to Texas waters, where hypoxia is typically less severe (Zimmerman & Nance 2001). Brown shrimp, the primary target of the fishery during the summer, were considered fully exploited during the 1980s and 1990s with some evidence of growth overfishing in the early 1990s (Caillouet et al. 2008). While there is concern about the potential effects of hypoxia on the Gulf shrimp fishery, there has been little discernable pattern in regional or gulf-wide abundance indices that can be attributed to hypoxia or other single stressors, though the power to detect such effects with aggregate monitoring data is undoubtedly low (Diaz & Solow 1999, Chesney et al. 2000, Craig et al. 2005, Cowan et al. 2008). Any effects of hypoxia on the fishery are also embedded within larger economic considerations that influence harvest, including imports of farm-raised shrimp, high fuel prices, and several recent hurricanes (Caillouet et al. 2008).

The inner Louisiana shelf is also habitat for a diverse fauna of demersal fishes and invertebrates (Moore et al. 1970, Darnell et al. 1983). Many of these species were harvested as part of an industrial and

foodfish fishery from the 1950s to 1970s (Gutherz et al. 1975) but are now taken primarily as bycatch in the commercial shrimp trawl fishery (Nance & Scott-Denton 1997). Finfish bycatch typically exceeds the directed harvest in most shrimp trawl fisheries, and the Gulf fishery ranks among the highest in the amount of bycatch generated (Harrington et al. 2005). Efforts to manage bycatch have mostly focused on gear modifications and limited closed areas to reduce the bycatch of particular high profile species (sea turtles, Crowder et al. 1994; red snapper, Gallaway & Cole 1999). Less attention has been given to the broader fish community that comprises most of the bycatch (70% by weight, Nance & Scott-Denton 1997) or to how environmental factors, such as hypoxia, may affect bycatch interactions.

In this paper, I investigate the hypoxia avoidance and associated shifts in spatial distribution of brown shrimp and several juvenile and small adult finfishes on the inner Louisiana shelf using trawl and hydrographic data collected in and around the hypoxic zone. Given that DO is considered a limiting factor (*sensu* Fry 1971) with typically strong effects on the distribution of organisms, I hypothesized that the spatial distributions of demersal species would be more strongly related to DO than to other environmental factors (e.g. temperature, salinity, depth). Based on prior studies emphasizing species-specific variation in DO avoidance behavior (Eby & Crowder 2002, Bell & Eggleston 2005), I hypothesized that avoidance thresholds would vary among the most common demersal species in the Gulf, and I used a new analytical approach to estimate both the mean and the variance in species-specific DO avoidance thresholds over 3 yr. Further, I hypothesized that hypoxia-induced aggregations near the edge of the hypoxic zone were much stronger at the smaller spatial scales studied here than shown for brown shrimp and Atlantic croaker based on large-scale, aggregate monitoring data (Craig & Crowder 2005) and that aggregation in nearby oxygenated refuges extended to other species within the demersal fish community. While hypoxia can alter the spatial overlap between predators and prey, potentially influencing predation mortality rates (Ludsin et al. 2009, Neuenfeldt & Beyer 2006, Prince et al. 2010), few studies have addressed hypoxia effects on interactions between harvested species and commercial fisheries. I hypothesized that spatial overlap between target (brown shrimp) and nontarget (juvenile finfishes) species of the shrimp trawl fishery and, hence, the potential for enhanced harvest and bycatch interactions, was greater in years of more severe hypoxia.

MATERIALS AND METHODS

Trawl and hydrographic surveys

Two sampling sites (4000 to 5000 km² each) were established on the inner Louisiana shelf within the current shrimping and historical groundfish grounds (Fig. 1). The easternmost site was sampled in each of 3 yr (2002 to 2004) and has experienced bottom-water hypoxia nearly every year since the early 1980s (Rabalais et al. 2002, Craig et al. 2005). During 2003 and 2004 a second site further west that has experienced hypoxia intermittently over this period was also sampled. Stations were chosen based on a 2-stage sampling design (Lohr 1999). First, a 10 km square grid was overlaid onto each site and randomly sampled (1 station per grid cell) to map the general distribution of hypoxia and demersal species. Each 10 km grid cell that encompassed an inshore or offshore edge of the hypoxic zone was then randomly re-sampled (1 to 3 stations per grid cell) to better define the edge of the hypoxic zone and the associated distribution of demersal species. The sampling intensity (number of stations per unit area) of this design was about an order of magnitude greater than that of an ongoing shelf-wide, fishery-independent survey in the region (Fig. 1; Eldridge 1988, Craig et al. 2005).

Bottom trawl and hydrographic surveys were conducted from July 20 to 28, 2002, July 31 to August 9, 2003, and July 20 to August 1, 2004. Surveys were conducted aboard the RV 'Tommy Munro' (30 m vessel length) in 2002 and 2004 and the RV 'Longhorn' (32 m vessel length) in 2003. In each year, the vessels were rigged with a 12.8 m mongoose trawl (5.1 cm webbing in the body and 4.1 cm webbing in the cod end) with mud rollers, 2.4 × 1 m wooden chained doors, and tickler chain towed from the starboard outrigger. The mongoose trawl had a center bib attached to a third bridle cable that allowed the trawl to sample the bottom 4 to 5 m of the water column. During 2002 and 2004 the mongoose trawl was towed in tandem with a 12.8 m flat (shrimp) trawl attached to the port outrigger. The shrimp trawl was identical to the mongoose trawl except that it lacked a center bib so that the height of the headrope was limited to about 1 m above the bottom by the height of the doors. Depth recorders were attached to the bib of the mongoose trawl and the headrope of the shrimp trawl to monitor the thickness of the bottom layer sampled by each trawl. Trawls were conducted parallel to depth contours for 20 min at a speed of ~0.5 m s⁻¹. Exploratory analyses and prior studies with similar gear indicated

no difference in catch rates between single- and double-rigged vessels (Pellegrin 2004). Therefore, each trawl catch during 2003 when only 1 net was used was multiplied by a species-specific correction factor derived from the ratio of abundances in the shrimp and mongoose trawls in the other 2 yr. Catch per unit effort (CPUE) was calculated by adjusting the catches to a standard tow length of 1.85 km based on the distance between the beginning and ending trawl locations.

A conductivity, temperature, depth (CTD) probe (SeaBird Electronics) was used to profile physical characteristics of the water column at the beginning and ending location of each trawl. The CTD was equipped with an SBE 43 DO sensor (<0.5% drift over 1 to 2 mo). All sensors were calibrated immediately prior to and following the cruise; no post-calibration adjustments were necessary. Because trawling was along (rather than across) depth contours, the possibility that strong gradients in bottom DO were crossed over the course of a tow were minimized. This was verified by comparing the CTD profiles at the beginning and ending location of each tow. Average values of DO (mg l⁻¹), temperature (°C), and salinity over the bottom meter of the water column were used to represent bottom conditions. The thickness of the bottom hypoxic layer at each station was estimated as the distance from the seafloor to the 2.0 mg l⁻¹ oxycline, averaged between the beginning and ending CTD profiles. Bottom DO was interpolated separately for each study site using universal kriging with a quadratic drift component as in Craig & Crowder (2005) and Craig et al. (2010).

Statistical analysis

Effects of environmental factors

Partial mantel regressions were used to investigate the effects of environmental factors on the spatial distributions of the 10 most abundant demersal species in the trawl sampling (Mantel 1967). These species were primarily age-0 and age-1 fish (see Table 1 for average lengths) and were among the most common harvested in the historical groundfish fishery and as bycatch in the shrimp trawl fishery (Gutherz et al. 1975, Nance & Scott-Denton 1997, Diamond et al. 2000). Variables included in the model were bottom DO, salinity, temperature, depth, distance to shore, and space (latitude, longitude). Distance to shore was calculated as the shortest distance from each station to a continuous line overlaying the coastline and

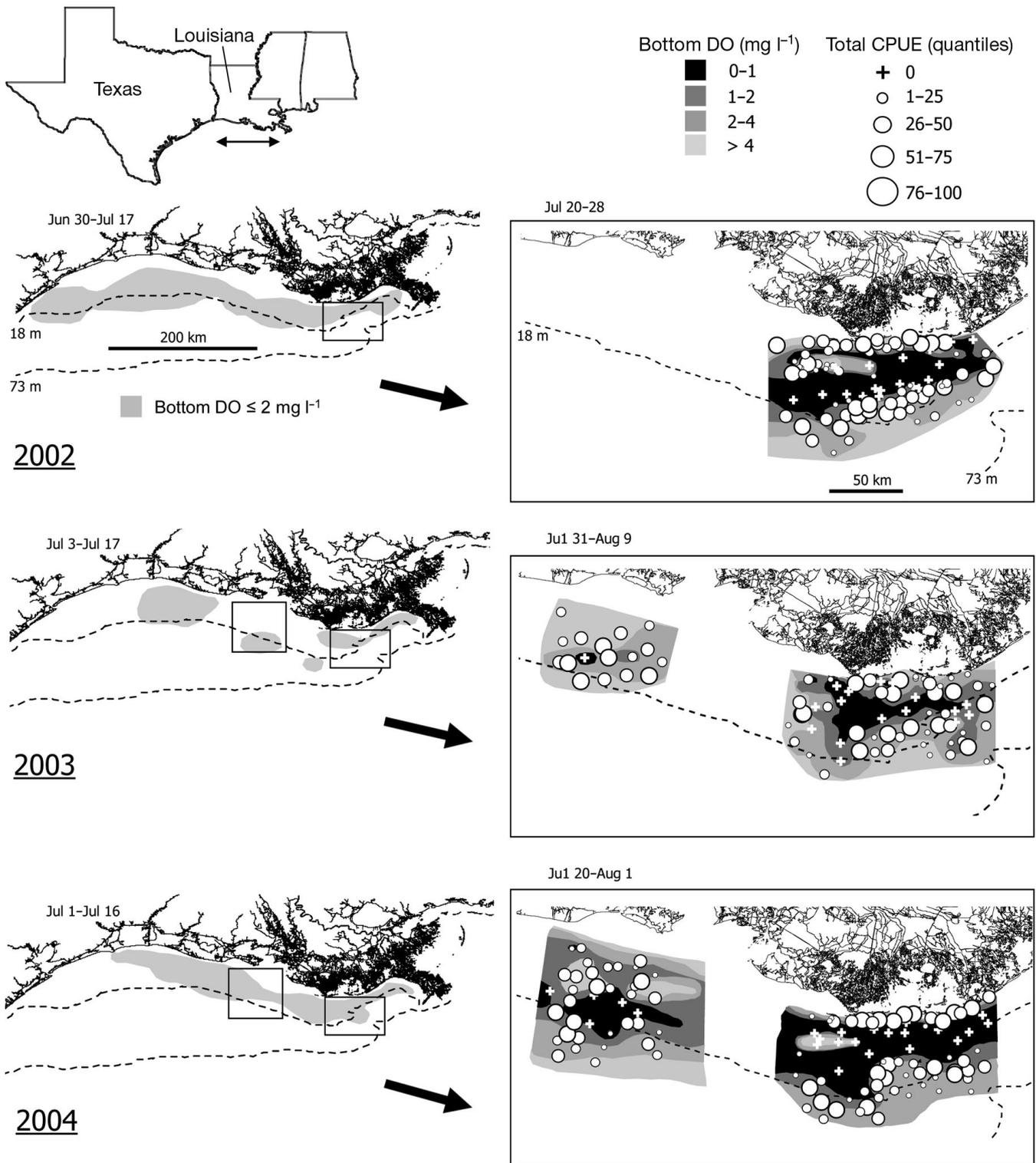


Fig. 1. Distribution of bottom dissolved oxygen (DO) at 2 spatial scales in the northwestern Gulf of Mexico over 3 yr. Gray areas along the Louisiana and upper Texas coasts are regions of bottom water hypoxia ($\text{DO} \leq 2.0 \text{ mg l}^{-1}$) from hydrographic measurements taken as part of the Southeast Area Monitoring and Assessment Program's (SEAMAP) fishery-independent surveys. Outsets with gray to black shading are the interpolated distributions of bottom DO from higher resolution surveys in particular regions of the larger hypoxic zone. Symbols are locations of trawl stations with larger symbols indicating higher abundance. Dates above each map are the sampling period

spanning the mouths of major estuaries. Separate models were run for each year (2002 to 2004) and species (presence or absence).

Mantel regressions are interpreted similarly to parametric partial regression models. Partial Mantel correlation coefficients indicate the amount of variation explained by a particular predictor variable after accounting for spatial autocorrelation within each predictor variable, intercorrelations among predictor variables, and spatial autocorrelation in the response variable. Mantel correlation coefficients are typically small, with coefficients <0.2 often being biologically significant. Significance tests were based on 10 000 permutations of the distance matrices, with the p-value calculated as the proportion of permutations for which the Mantel test statistic was greater than that observed (Manly 1997). Interactions among environmental factors were not investigated because of the relatively narrow range observed for most environmental variables (with the exception of DO) and because of low statistical power to detect interaction effects. Additional examples of Mantel regression can be found in Craig & Crowder (2005) and Zhang et al. (2009). Regressions were conducted with the 'ecodist' package in S-Plus version 7.0 (Goslee & Urban 2007).

DO avoidance thresholds

Scatterplots of CPUE versus bottom DO indicated a lower level of DO (a threshold) below which CPUE declined sharply, often to 0, with no apparent relationship between CPUE and DO above the threshold (see Fig. 3, 'Results'). Prior approaches to estimating DO thresholds from similar field data have either used nonparametric methods that specify a single 'cutoff' with no estimate of variance (e.g. categorical and regression trees; Eby & Crowder 2002) or have assumed a particular parametric model (e.g. logistic; Bell & Eggleston 2005), the functional form of which may influence the estimate of the low DO threshold. I modified a semi-parametric modeling approach originally developed by Welch et al. (1995) to estimate a mean DO avoidance threshold and associated variance separately for the 10 most abundant species in the trawl sampling (see also Craig et al. 2010). This approach assumes only that a low DO avoidance threshold with a mean and variance from a particular distribution exists. The functional form of the model was:

$$n(\text{DO}_i) = \bar{\mu} [\phi(\text{DO}_i | \text{DO}_{\text{threshold}}, \sigma_{\text{DO}}) - 1] \quad (1)$$

where $n(\text{DO}_i)$ is the observed CPUE of a particular species at station i with bottom dissolved oxygen DO_i , $\phi(\text{DO}_i | \text{DO}_{\text{threshold}}, \sigma_{\text{DO}})$ is the value of the cumulative normal probability distribution for CPUE at DO level DO_i , $\text{DO}_{\text{threshold}}$ is the mean DO threshold and σ_{DO} is the variance around this mean that together define the probability distribution, and $\bar{\mu}$ is a nuisance parameter that describes the mean CPUE at DO levels well above the threshold.

The mean threshold ($\text{DO}_{\text{threshold}}$) is the value of DO at which CPUE declines most rapidly and σ_{DO} reflects the rate of decline in CPUE near $\text{DO}_{\text{threshold}}$ (Fig. 2). A small σ_{DO} indicates a very rapid decline in abundance near the threshold consistent with a strong behavioral avoidance response to low DO, while a large σ_{DO} indicates a gradual decline in abundance near the threshold consistent with a relatively weak behavioral response to low DO. Hence, the variance about the mean threshold provides information on the strength of the avoidance response to low DO.

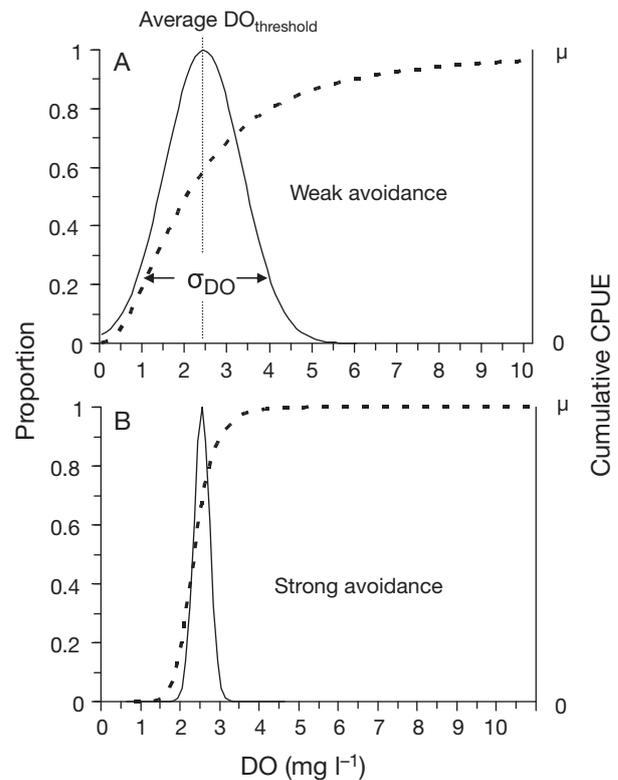


Fig. 2. Conceptual approach for modeling the mean and variance in dissolved oxygen (DO) avoidance thresholds at (A) weak and (B) strong avoidance responses. Dotted line represents the cumulative catch per unit effort (CPUE) over DO (μ). Solid curve represents the mean and the standard deviation of the DO avoidance threshold (σ_{DO}). A large variance indicates a gradual change in CPUE with decreasing DO and a weak avoidance response. A small variance indicates a rapid change in CPUE with decreasing DO and a strong avoidance response (after Welch et al. 1995)

I assumed a normal distribution for the avoidance threshold but also considered a lognormal distribution because catches showed some positive skew near the edge of the hypoxic zone (see Fig. 4). Exploratory analyses indicated little difference between the normal and lognormal models, with the estimated thresholds differing by $<0.25 \text{ mg l}^{-1}$; therefore, only the mean and variance from the normally distributed threshold model are reported. Additional details regarding the threshold model can be found in Welch et al. (1995) and Craig et al. (2010). The threshold model was also compared to a null (intercept-only) model and a linear model using Akaike's information criterion (AIC; Akaike 1973). Pseudo- R^2 values were calculated for the threshold and linear models as $1 - \ln(L_{\text{full}})/\ln(L_{\text{int}})$ where L_{full} is the likelihood of the full model (threshold or linear) and L_{int} is the likelihood of the intercept-only model. Estimates of the model parameters were obtained by maximum likelihood assuming uncertainty in individual trawl CPUEs were described by a negative binomial distribution. A negative binomial distribution was chosen because the distribution of CPUE was typically highly skewed with numerous small catches and a few very large catches, as is typical with trawl survey data (Power & Moser 1999). For display purposes, CPUE was $\log(x + 1)$ transformed and standardized for differences in abundance among years by dividing by $\bar{\mu}$.

Aggregation near the hypoxic edge

The threshold model described above estimates the mean and variance in species-specific DO levels that organisms avoid but does not address the consequences of this avoidance behavior for the spatial distribution of evading organisms beyond the hypoxic area. To investigate relationships between the abundance of organisms and the edge of the hypoxic zone, an exponential model and a non-monotonic (peaked) model were fit to the trawl data described above:

$$y = \beta_0 X^{\beta_1} \varepsilon \text{ (exponential)} \quad (2)$$

$$y = \beta_0 X^{\beta_1} e^{\beta_2 X} \varepsilon \text{ (non-monotonic)} \quad (3)$$

where y is CPUE, X is distance from the hypoxic edge, β_0 , β_1 and β_2 are parameters, and ε is a random error term. The exponential model (Eq. 2) represents an exponential decline in CPUE with increasing distance from the edge as reported in Craig & Crowder (2005) at a much larger spatial scale. The non-monotonic model (Eq. 3) is a modified Ricker function

where CPUE increases up to some distance from the hypoxic edge followed by a decline with increasing distance (determined by β_2). I estimated the distance to the edge of the hypoxic zone as the minimum distance of each station from the 2.0 mg l^{-1} bottom DO contour from the interpolation of the CTD data. Because some individuals were sampled in water with DO less than 2.0 mg l^{-1} , negative distances were assigned to stations toward the interior of the hypoxic zone from the 2.0 mg l^{-1} contour line and positive distances were assigned to stations outward from the 2.0 mg l^{-1} contour line. The 2 models above were fit separately to trawl CPUE for 5 species (brown shrimp, Atlantic croaker, Atlantic bumper *Chloroscombrus chrysurus*, spot *Leiostomus xanthurus*, sand seatrout *Cynoscion arenarius* and total CPUE (pooled over all species) using quantile regression (Cade & Noon 2003). I limited the statistical analysis to those species that were present at $\sim 50\%$ or more of the stations sampled in a given year to insure adequate sample sizes. Each model was fit to the linearized form ($\ln(y + 1)$) of Eqs. (2) & (3), and parameter estimates were recovered by back-transformation to the original scale (Koenker & Machado 1999). Ninety-five percent confidence intervals (CIs) were constructed for each parameter by iteratively inverting a rank score test with reference to a standard normal distribution as described in Cade et al. (1999). Models were fit to the upper 75th, 90th, and 95th quantiles to insure patterns were consistent across the upper percentiles of the CPUE distribution. The 2 models were compared for each quantile using AIC, akaike weights, and evidence ratios (Burnham & Anderson (2002).

Spatial overlap of target and nontarget species

To test the hypothesis that avoidance of low DO water and aggregation near the hypoxic edge enhances the potential for bycatch interactions, I calculated spatial overlap between brown shrimp, the primary target of the shrimp trawl fishery, and each of the 10 most abundant finfishes that comprise most of the bycatch. An index of spatial overlap that is relevant to potential bycatch is the proportion of a nontarget species that occurs in association with a target species. I calculated the proportion of each of 10 finfish species that occurred at stations with positive catches of brown shrimp and compared this index of spatial overlap across the 3 yr differing in the severity of hypoxia. I predicted that spatial overlap would be lowest in 2003, the year of least severe hypoxia, greatest in 2002, the year of most severe hypoxia,

and intermediate in 2004. I calculated bootstrapped CIs on the overlap values and tested for differences in spatial overlap across the 3 yr using random permutation tests as above (Manly 1997).

Vertical avoidance of bottom water hypoxia

Hydroacoustic sampling at a subset of stations in 2004 indicated fish-sized biomass in the water column above the bottom hypoxic layer, raising the possibility that organisms may also avoid bottom water hypoxia by moving vertically in the water column (Hazen et al. 2009). Another hydroacoustic study on the Louisiana shelf also reported pelagic, fish-sized biomass in the water column above the hypoxic zone (Zhang et al. 2009). Neither study identified the species composition of the pelagic fish community above the bottom hypoxic layer. The paired mongoose and shrimp trawls used here do not sample the entire water column and, therefore, are of limited use for identifying the species composition of pelagic and vertically migrating fishes, but each trawl does sample different portions of the bottom water column. If a particular species avoids hypoxia by moving vertically, then CPUE should be higher in the mongoose trawl because it samples a larger portion of the bottom water column, including oxygenated water above the bottom hypoxic layer, than in the shrimp trawl, which samples almost entirely within the bottom hypoxic layer (see 'Results'). To test the hypothesis of vertical avoidance using data from the 2 bottom trawls, I compared the CPUE of the 5 most abundant species between paired mongoose and shrimp trawls during 2002 and 2004 when the 2 trawls were towed in tandem at each station. The following generalized linear model was fit to the CPUE data for each species:

$$\text{DIF}_i = \beta_0 + \beta_1 \text{DO}_i + \beta_2 \text{Depth}_i + \beta_3 \text{DO}_i \times \text{Depth}_i + \beta_4 \text{Time}_i + \beta_5 \text{Year}_j \quad (4)$$

where DIF_i is the difference in CPUE between mongoose and shrimp trawls (mongoose CPUE – shrimp CPUE), DO_i is bottom DO at station i , and j is the year. If organisms vertically avoid low bottom DO, then the difference in CPUE between the paired mongoose and shrimp trawls should increase as bottom DO decreases. This prediction is based on the assumption that vertically evading organisms become more available to the higher-opening mongoose trawl and less available to the lower-opening shrimp trawl. If so, then the coefficient for the DO effect (β_1) in the above model should be negative. Water depth (β_2) and time

of day (β_4) were included as covariates and year (β_5) was included as a categorical term to account for annual effects. Because the vertical movement of organisms in response to low bottom DO may depend on the amount of overlying water column available, an interaction term between water depth and DO (β_3) was also included. Stations with no catch were excluded and a Gaussian distribution was assumed for the error term with an identity link function.

RESULTS

General description

Hypoxia was widespread at the eastern site in each of the 3 yr (Fig. 1). Hypoxia was mostly absent from the western site in 2003 (<5% of the study area) but was severe at this site in 2004 (the western site was not sampled in 2002). While the general distribution of hypoxia was similar to that based on lower resolution, shelf-wide sampling 2 to 3 wk earlier, considerable spatial structure in bottom DO was evident at the higher spatial resolution (Fig. 1). Strong gradients from anoxic ($\leq 1.0 \text{ mg l}^{-1}$) to normoxic ($> 2.0 \text{ mg l}^{-1}$) bottom water occurred over relatively short distances (1 to 5 km), and several oxygenated regions were found over shallow, wind-swept shoals that were completely or partially surrounded by water with low bottom DO. Hypoxia was most severe in 2002 (hypoxic area = 65.8%, median thickness = 2.9 m), least severe in 2003 (area = 41.5%, median thickness = 1.7 m), and intermediate in 2004 (area = 53.3%, median thickness = 2.5 m).

The distribution of demersal species was bifurcated by hypoxia, with high abundances both inshore and offshore of the hypoxic zone, some organisms occupying interior oxygenated shoal habitats, and very few organisms within the area of low bottom DO (Fig. 1). Atlantic bumper, Atlantic croaker, brown shrimp, spot, and sand seatrout accounted for 72 to 84% of the catch over the 3 yr. Of these 5 species, bumper and croaker were the most abundant, accounting for 36 to 49% and 28 to 38% of the catch, respectively. Mean lengths among species varied within a fairly narrow range (mostly 100 to 200 mm, Table 1) and were similar across years (all coefficients of variation among years <7%).

Mantel regressions

Of the 5 environmental variables, only bottom DO was significant for all species in each of the 3 yr

Table 1. Mean body size (\pm SD) and mantel regression results for the presence vs. absence of demersal species as a function of environmental variables on the nearshore Louisiana shelf. Mantel partial correlation coefficients (r) from separate regressions for each species and year are shown. Significant values in **bold** ($p \leq 0.05$) based on 10 000 permutations of the distance matrices. Body sizes were determined from forklength unless otherwise noted

Species	Body size (mm)	Oxygen			Salinity			Temperature			Depth			Distance to shore			Space		
		2002	2003	2004	2002	2003	2004	2002	2003	2004	2002	2003	2004	2002	2003	2004	2002	2003	2004
Atlantic bumper	129 \pm 29	0.25	0.15	0.14	0.15	0.09	0.09	0.08	0.12	0.03	0.02	0.02	0.06	0.03	0.09	0.06	0.01	0.02	0.03
<i>Chloroscombrus chrysurus</i>																			
Atlantic croaker	152 \pm 21 ^a	0.17	0.10	0.09	0.03	0.05	0.05	0.15	0.06	0.07	0.11	0.05	0.04	0.15	0.11	0.04	0.06	0.03	0.03
<i>Micropogonias undulatus</i>																			
Brown shrimp	113 \pm 20 ^a	0.19	0.06	0.07	0.04	0.06	0.05	0.04	0.05	0.02	0.03	0.03	0.03	0.02	0.02	0.04	0.13	0.05	0.01
<i>Farfantepenaeus aztecus</i>																			
Spot	161 \pm 28 ^a	0.13	0.06	0.07	0.02	0.03	0.05	0.10	0.01	0.06	0.11	0.01	0.04	0.11	0.03	0.04	0.05	0.03	0.01
Sand seatrout	195 \pm 57 ^a	0.19	0.04	0.10	0.03	0.07	0.04	0.12	0.05	0.05	0.15	0.03	0.05	0.06	0.08	0.09	0.06	0.01	0.01
<i>Cynoscion arenarius</i>																			
Longspine porgy	70 \pm 16	0.12	0.09	0.14	0.20	0.14	0.17	0.11	0.16	0.12	0.27	0.04	0.19	0.16	0.03	0.20	0.05	0.06	0.01
<i>Stenotomus caprinus</i>																			
Bigeye searobin	104 \pm 20 ^a	0.14	0.09	0.07	0.04	0.03	0.06	0.11	0.06	0.05	0.11	0.12	0.02	0.03	0.13	0.17	0.04	0.01	0.04
<i>Pristigaster longispinosus</i>																			
Gulf butterfish	125 \pm 18	0.12	0.06	0.09	0.11	0.02	0.11	0.18	0.05	0.02	0.26	0.00	0.13	0.24	0.12	0.16	0.03	0.05	0.03
Atlantic cutlassfish	134 \pm 44 ^b	0.13	0.03	0.07	0.12	0.03	0.06	0.17	0.05	0.01	0.25	0.10	0.06	0.17	0.01	0.06	0.03	0.05	0.00
<i>Trichiurus lepturus</i>																			
Inshore lizardfish	171 \pm 37	0.19	0.04	0.06	0.16	0.17	0.08	0.07	0.21	0.05	0.18	0.04	0.15	0.03	0.12	0.16	0.15	0.07	0.01
<i>Synodus foetens</i>																			

^aDetermined from total length. ^bDetermined from snout to vent length

(Table 1). In 2002, the year when hypoxia was most severe, correlations were highest between CPUE and DO, with DO explaining 39 to 71% more of the variation in spatial distributions than each of the other environmental variables. In 2003 and 2004 when hypoxia was less severe, the magnitude of the correlations with CPUE was more similar among the environmental variables, indicating somewhat weaker DO effects in these years. Salinity, temperature, depth, and distance to shore each had significant partial effects for some species in some years, but these effects were rarely as consistent or of the same magnitude as the DO effect. Residual spatial autocorrelation, reflecting spatial patterns in CPUE not accounted for by the environmental variables, was rarely significant, indicating that other unmeasured but spatially structured factors are unlikely to account for much additional variation at this spatial scale.

DO avoidance thresholds

For each species and year, the threshold model had a lower AIC than both the null (intercept-only) model and the linear model, supporting the existence of a lower DO threshold below which CPUE declined rapidly (Table 2). Akaike weights (not shown) in support of the threshold model exceeded 0.97 for all species and years. Even so, the threshold model explained a relatively small portion of the overall variation in CPUE (4 to 36% across species and years). The amount of variation explained was greater in 2002, the more severe hypoxic year (average R^2 across species = 21.8%), compared to 2003 and 2004 (average R^2 across species = 11.8% and 13.4%, respectively).

DO avoidance thresholds were relatively low, ranging from 0.88 to 2.73 mg l⁻¹ across the 10 species and 3 yr (Table 3, Fig. 3). When averaged over the 3 yr, all species had DO thresholds less than 2.0 mg l⁻¹ (range: 1.06 to 1.99 mg l⁻¹). Sand seatrout and Atlantic bumper had particularly low avoidance thresholds (range of means across years: 1.06 to 1.16 mg l⁻¹), while Atlantic croaker, spot, and Atlantic cutlassfish had the highest thresholds (range of means

Table 2. Difference in Akaike's information criterion (ΔAIC) for threshold (Thresh), linear, and intercept-only (Inter) models of catch per unit effort (CPUE) versus dissolved oxygen (DO) for 10 species on the Louisiana shelf. The threshold model had the lowest AIC for each species and year (indicated by '0'). See Table 1 for full species names

	2002			2003			2004		
	Thresh	Linear	Inter	Thresh	Linear	Inter	Thresh	Linear	Inter
Shrimp	0 (0.11)	34.5 (0.07)	109.5	0 (0.06)	49.8 (0)	51.8	0 (0.06)	42 (0.03)	81.8
Croaker	0 (0.24)	244.9 (0.06)	333.1	0 (0.14)	89.2 (0.06)	155.8	0 (0.09)	146.4 (0)	148.4
Spot	0 (0.31)	157 (0.14)	285.3	0 (0.13)	22.5 (0.1)	97.6	0 (0.18)	178.2 (0)	180.2
Seatrout	0 (0.15)	71 (0.07)	138.3	0 (0.12)	7.28 (0.12)	87.8	0 (0.06)	73.8 (0)	75.8
Bumper	0 (0.07)	125.4 (0.05)	91.8	0 (0.04)	15.9 (0.03)	57.1	0 (0.08)	74.3 (0.04)	156.2
Porgy	0 (0.31)	63.2 (0.14)	118.2	0 (0.19)	113.2 (0.04)	142.6	0 (0.14)	179.9 (0)	181.9
Butterfish	0 (0.27)	152.8 (0.09)	234.1	0 (0.1)	32.8 (0.05)	67	0 (0.18)	225 (0)	227
Cutlassfish	0 (0.36)	203.1 (0.13)	325.5	0 (0.08)	34.5 (0.03)	52.5	0 (0.12)	74.4 (0.02)	93.8
Bigeye	0 (0.12)	83.6 (0.07)	144.2	0 (0.18)	40.2 (0.02)	56.5	0 (0.09)	73.5 (0)	75.2
Lizardfish	0 (0.24)	36.6 (0.12)	75.9	0 (0.14)	8.5 (0.11)	28.3	0 (0.34)	184 (0.05)	214.3

Table 3. Maximum likelihood parameter estimates for the mean ($DO_{\text{threshold}}$) and standard deviation (σ_{DO}) of the dissolved oxygen avoidance threshold for 10 species on the Louisiana shelf. 95% CIs for each parameter are given in parentheses. See Table 1 for full species names

	2002		2003		2004	
	$DO_{\text{threshold}}$	σ_{DO}	$DO_{\text{threshold}}$	σ_{DO}	$DO_{\text{threshold}}$	σ_{DO}
Shrimp	1.57 (1.46–1.68)	0.112 (0.085–1.38)	1.07 (1.00–1.15)	0.108 (0.027–0.189)	1.28 (1.23–1.33)	0.091 (0.078–0.104)
Croaker	2.04 (1.98–2.11)	0.383 (0.378–0.388)	2.68 (2.58–2.78)	0.746 (0.728–0.774)	1.24 (1.19–1.29)	0.151 (0.150–0.152)
Spot	2.46 (2.38–2.53)	0.457 (0.453–0.461)	1.27 (1.24–1.30)	0.054 (0.053–0.055)	1.79 (1.74–1.84)	0.21 (0.179–0.242)
Seatrout	0.95 (0.89–0.99)	0.185 (0.163–0.207)	0.88 (0.43–1.34)	0.003 (0–0.009)	1.34 (1.26–1.44)	0.256 (0.241–0.280)
Bumper	1.5 (1.40–1.61)	0.619 (0.590–0.647)	0.66 (0.62–0.70)	0.272 (0.237–0.307)	1.31 (1.29–1.32)	0.196 (0.167–0.224)
Porgy	2.28 (2.08–2.49)	0.097 (0–0.233)	1.43 (0.88–1.99)	0.007 (0–0.025)	1.27 (1.24–1.31)	0.022 (0.007–0.037)
Butterfish	1.78 (1.71–1.85)	0.212 (0.182–0.242)	1.26 (1.18–1.33)	0.128 (0.064–0.191)	1.22 (1.19–1.24)	0.069 (0.054–0.084)
Cutlassfish	2.73 (2.63–2.83)	0.405 (0.348–0.462)	1.38 (1.20–1.56)	0.41 (0.296–0.523)	1.54 (1.44–1.64)	0.274 (0.196–0.352)
Bigeye	1.39 (1.31–1.46)	0.325 (0.290–0.359)	1.49 (1.33–1.65)	0.347 (0.176–0.519)	1.22 (1.15–1.30)	0.274 (0.206–0.342)
Lizardfish	1.77 (1.67–1.87)	0.002 (0–0.007)	1.69 (1.57–1.81)	0.017 (0–0.189)	1.68 (1.58–1.78)	0.254 (0.200–0.309)

across years: 1.84 to 1.99 mg l⁻¹). Differences in DO thresholds among species with different life history types were not particularly strong. For example, the range of thresholds among demersal sciaenids (croaker, spot, sand seatrout; 1.06 to 1.99 mg l⁻¹) spanned the full range of thresholds for all 10 species. Similarly, average thresholds for longspine porgy and Gulf butterfish (1.66 and 1.42 mg l⁻¹), 2 semi-pelagic species, were similar to those for inshore lizardfish and bigeye searobin (1.71 and 1.37 mg l⁻¹), 2 highly benthic species. Eight of the 10 species had higher DO avoidance thresholds in 2002, the more severe hypoxic year, compared to 2003 and 2004.

The variance in the mean avoidance threshold (σ_{DO}) ranged 4-fold across species (Table 3, Fig. 3). Some species showed little variation in avoidance and relatively rapid declines in abundance (small σ_{DO}) near the threshold, suggesting a strong avoidance response (brown shrimp, longspine porgy, inshore lizardfish), while others showed more gradual declines in abundance (large σ_{DO}) near the threshold, suggesting a weaker avoidance response (croaker, bumper, cutlassfish). Atlantic bumper, a vertically migrating species, had the highest variance, perhaps reflecting its ability to move both vertically and horizontally to avoid low bottom DO. For some species, the DO avoidance threshold varied little across the 3 yr (e.g. inshore lizardfish, 1.68 to 1.77 mg l⁻¹), while thresholds for other species varied 2- to 3-fold over the 3 yr (e.g. Atlantic croaker, 1.24 to 2.04 mg l⁻¹; Atlantic bumper, 0.66 to 1.50 mg l⁻¹).

All 10 species had average avoidance thresholds near or above 1 mg l⁻¹, which corresponds to habitat loss of 18 to 32% of the study area across the 3 yr. To link variation in avoidance thresholds among species and years to the amount of habitat loss, I estimated the additional reduction in available habitat that would occur for an increase in avoidance thresholds from 1 mg l⁻¹ (the level that was almost always avoided) to 2 mg l⁻¹ by estimating the amount of area between the 1 and 2 mg l⁻¹ contour lines for each of the 3 yr. I chose the range from 1 to 2 mg l⁻¹ because, on average, avoidance thresholds differed by 1.1 mg l⁻¹ across species (averaged across years) and differed by 0.83 mg l⁻¹ across years (averaged across species). In 2002 and 2004 when hypoxia was most severe, an increase in avoidance thresholds from 1 to 2 mg l⁻¹ would result in an additional 15 to 16% decline in available habitat within the study area. In 2003 when hypoxia was least severe, the same increase in avoidance thresholds would result in an additional 25% decline in available habitat.

Aggregation near the hypoxic edge

Organisms avoiding hypoxia aggregated at short distances just beyond the edge (2.0 mg l⁻¹ contour) of the hypoxic zone (Fig. 4). Average CPUE within a distance of 0 to 4 km from the hypoxic edge was 3- to 5-fold greater than at distances of 8 to 16 km from the edge (the maximum distances sampled). For each species, peaks in abundance occurred at shorter distances for higher quantiles of CPUE, indicating that the largest aggregations occurred closest to the edge. Atlantic bumper and croaker were most strongly associated with the hypoxic edge, with peaks in CPUE at distances of only 1 to 2 km away. Aggregation at these short distances was general, with peaks in CPUE at distances from 0 to 3.5 km from the edge for the other species, as well for total abundance pooled over species.

There was generally more statistical support for the Ricker model reflecting a peak in abundance at some distance from the hypoxic edge than for the model of exponential decline with increasing distance (Table 4). The Ricker model was the best approximating model for all species and quantiles, except for the 75th quantiles for Atlantic croaker and sand seatrout. Evidence ratios in support of the Ricker model typically increased at higher quantiles, consistent with the highest CPUE occurring nearest to the hypoxic edge. For example, the Ricker model approximating the 95th quantile of total abundance was 103 times more likely than the exponential model, reflecting a strong peak in total CPUE at a distance of about 1 km from the hypoxic edge (Fig. 4).

Spatial overlap of target and nontarget species

Spatial overlap between brown shrimp and nontarget finfishes varied widely among species and among years (29 to 100%). On average the range of overlap values was similar for benthic (63 to 95%) and pelagic (41 to 91%) species, with the exception of Atlantic bumper which had the lowest overlap (35 to 52%). Differences in spatial overlap among the 3 yr were significant for most of the benthic species (Atlantic croaker, spot, sand seatrout, and inshore lizardfish) but not for the more pelagic species (Atlantic bumper, longspine porgy, and Gulf butterfish) (Fig. 5). The exceptions were Atlantic cutlassfish and bigeye searobin, 2 highly benthic species, though differences were only marginally not significant ($p = 0.06$ and $p = 0.08$, respectively). Differences in overlap among years were marginally not signifi-

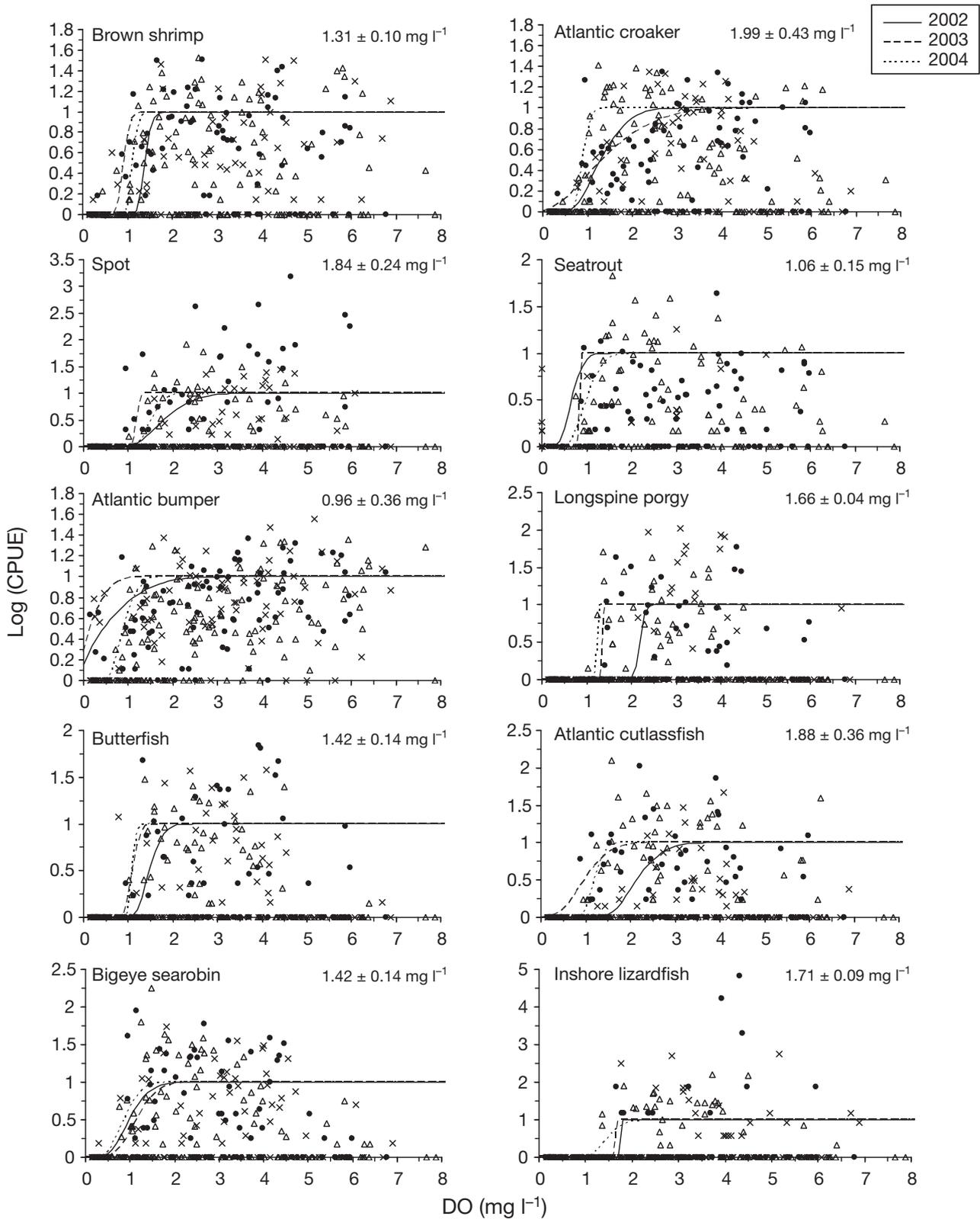


Fig. 3. Relationship between catch per unit effort (CPUE) and bottom dissolved oxygen (DO) for 10 species collected on the Louisiana shelf in (x) 2002, (●) 2003 and (Δ) 2004. Lines show the predicted CPUE as a function of DO based on the threshold model for each of the 3 yr. The mean and variance in the DO threshold over the 3 yr is given in the upper right corner of each panel

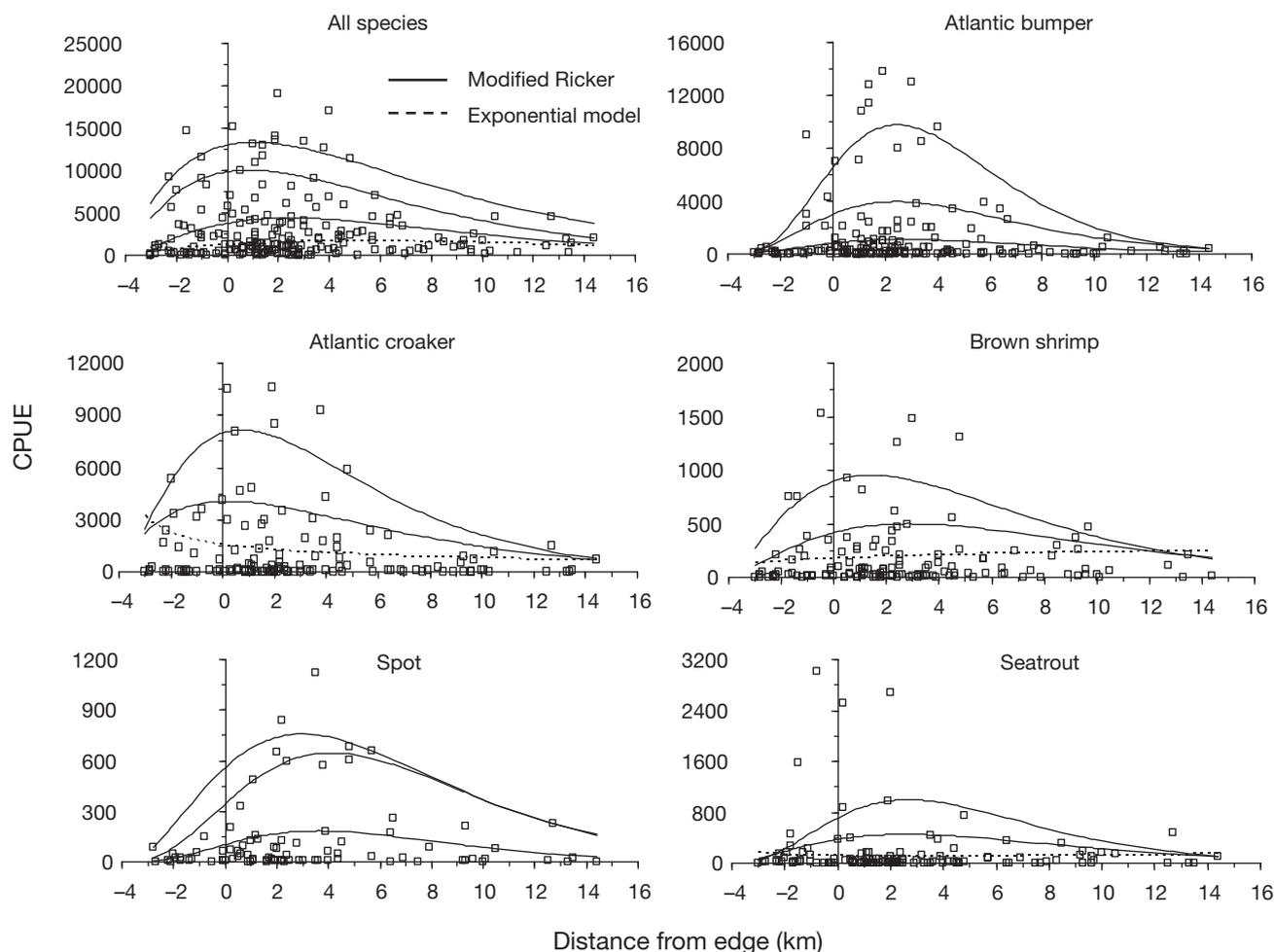


Fig. 4. Quantile regression plots of catch per unit effort (CPUE) as a function of distance from the edge of the hypoxic zone defined as the 2.0 mg l^{-1} dissolved oxygen (DO) contour. Negative distances are from the edge toward the interior of the hypoxic zone and positive distances are from the edge outward from the hypoxic zone. Lines show the predicted abundance for the best approximating model (modified Ricker or exponential) fit to the 95th (upper line), 90th (middle line), and 75th (lower line) quantiles of the CPUE distribution

cant ($p = 0.1$) for total abundance as well, probably due to the high abundance of Atlantic bumper, which showed little annual variation in spatial overlap with brown shrimp. For most species, overlap was lowest in 2003, the year of least severe hypoxia, compared to 2002 and 2004 when hypoxia was more severe. In contrast to the original hypothesis, spatial overlap was typically higher in 2004, the intermediate year in terms of hypoxia severity, compared to 2002, the most severe year.

Vertical avoidance of bottom water hypoxia

In 2002 and 2004 when the mongoose and the shrimp trawl were towed in tandem at each station, the mongoose trawl extended vertically over

an average distance of 4.0 to 4.3 m of the bottom water column at hypoxic stations (Fig. 6). The top of the mongoose trawl extended above the 2.0 mg l^{-1} oxycline at 80% of the stations by an average distance of 2.2 m. In contrast, the paired shrimp trawl extended vertically over an average distance of 1.3 m of the bottom water column and was below the 2.0 mg l^{-1} oxycline at 84% of the stations by an average distance of 3.2 m. The coefficient for the effect of bottom DO on the difference in CPUE (mongoose versus shrimp) between paired trawls was negative and highly significant for Atlantic bumper, consistent with some degree of vertical avoidance. In contrast, the DO coefficient was not significant for the other 4 species and in the opposite direction (positive) for 3 of these species (Table 5).

Table 4. Quantile regression results for trawl catch per unit effort (CPUE) as a function of distance from the edge of the hypoxic zone. β_0 , β_1 , and β_2 are the parameter estimates for the best approximating model. 95% CIs are given in parentheses. Quantiles for which the exponential model provided the best fit are shown in **bold**. Otherwise, the non-monotonic, peaked model provided the best fit (see text and Eqs 2 & 3 for details). The difference in Akaike's information criterion (ΔAIC) was determined between the best approximating model and the alternative model (exponential or non-monotonic). w_{best} is the Akaike weight, indicating the weight of evidence in support of the best approximating model compared to the alternative (0 to 1 scale). w_{best}/w_{alt} is the evidence ratio (i.e. Akaike weight of the best approximating model relative to that of the alternative, w_{alt}). Evidence ratios from 0 to 2 indicate substantial support, 4 to 7 indicate considerably less support, and >10 indicate essentially no support for the alternative model (Burnham & Anderson 2002). na: not applicable

Species	Quantile	β_0	β_1	β_2	AIC	ΔAIC	w_{best}	w_{best}/w_{alt}
All (n = 204)	75th	1203.7 (369.5, 2037.9)	1.49 (0.965, 2.02)	-0.229 (-0.288, -0.169)	146.9	11.7	0.997	344
	90th	5402.6 (2220.5, 8584.7)	1.08 (0.647, 1.51)	-0.223 (-0.317, -0.129)	188.7	3.5	0.849	5.6
	95th	7421.9 (4683.2, 14375.6)	0.945 (0.435, 1.45)	-0.187 (-0.322, -0.052)	203.6	9.3	0.99	103
Bumper (n = 176)	75th	107.2 (23.2, 191.2)	2.58 (1.88, 3.28)	-0.384 (-0.490, -0.278)	148.6	3.33	0.841	5.3
	90th	333.9 (103.5, 564.3)	2.88 (1.67, 4.09)	-0.448 (-0.538, -0.359)	193.5	3.52	0.853	5.82
	95th	296.6 (97.0, 496.2)	4.03 (3.11, 4.95)	-0.624 (-0.786, -0.462)	219.5	11.32	0.997	287
Croaker (n = 131)	75th	3211.8 (1666.9, 4756.7)	-0.521 (-1.04, 0.005)	na	140.5	4.35	0.898	8.81
	90th	2755.3 (1474.1, 4229.4)	0.907 (0.423, 1.33)	-0.217 (-0.333, -0.101)	161.5	0.971	0.619	1.62
	95th	3445.7 (1719.4, 5172.0)	1.55 (0.892, 2.21)	-0.328 (-0.515, -0.140)	174.7	0.708	0.588	1.42
Shrimp (n = 137)	75th	35.9 (14.0, 57.8)	1.89 (0.981, 2.87)	-0.245 (-0.318, -0.172)	101.5	0.171	0.521	1.09
	90th	132.3 (67.5, 199.8)	1.44 (0.620, 2.26)	-0.211 (-0.306, -0.116)	127.9	1.4	0.668	2.01
	95th	354 (211.0, 497)	1.44 (0.010, 2.88)	-0.267 (-0.321, -0.214)	148.4	6.03	0.953	20.4
Spot (n = 88)	75th	5.6 (2.2, 9.0)	3.4 (1.90, 4.90)	-0.446 (-0.603, -0.288)	62.4	0.97	0.619	1.62
	90th	21.7 (4.6, 38.8)	3.11 (0.916, 5.30)	-0.383 (-0.731, -0.034)	90.7	1.85	0.716	2.52
	95th	85.4 (63.6, 107.2)	2.32 (0.012, 4.62)	-0.332 (-0.496, -0.168)	96.9	2.18	0.749	2.98
Seatrout (n = 124)	75th	120.3 (4.7, 238.6)	-0.025 (-0.042, -0.001)	na	92.4	2.23	0.742	3.06
	90th	92.7 (33.8, 151.6)	1.8 (1.30, 2.31)	-0.275 (-0.399, -0.151)	130.8	0.001	0.5	1.05
	95th	69.1 (39.7, 98.5)	2.96 (1.85, 4.08)	-0.443 (-0.786, -0.100)	159.3	3.19	0.831	5.85

DISCUSSION

DO avoidance thresholds for 10 species on the inner Louisiana shelf that spanned a range of life history types and body morphologies were surprisingly similar and often ≤ 2.0 mg l⁻¹, consistent with a community that is relatively tolerant to low DO. Thresholds for brown shrimp, spot, and croaker over the 3 yr (1.1 to 2.7 mg l⁻¹) were similar to those reported in diverse prior laboratory and field studies with the same species (1.0 to 2.3 mg l⁻¹; Renaud 1986, Pihl et

al. 1991, Wannamaker & Rice 2000, Eby & Crowder 2002). Avoidance thresholds for the remaining 7 species (1.0 to 1.88 mg l⁻¹) were within this same general range. These avoidance thresholds are near laboratory estimates of incipient lethal levels for similar species, suggesting that organisms avoid only the lowest, lethal DO levels on the shelf. For example, the mean LC₅₀ (lethal concentration value at which 50% mortality occurs) in laboratory studies of several juvenile and small adult gulf coast species was 1.51 mg l⁻¹ (Goodman & Campbell 2007) and the

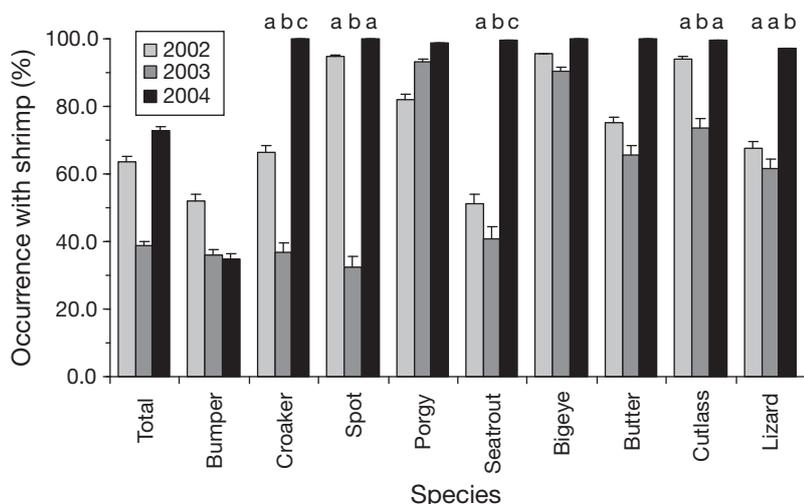


Fig. 5. Mean (+ SE) occurrence (%) of each of 9 finfish species (and total finfish catch) at stations with positive catches of brown shrimp (spatial overlap) on the Louisiana shelf in each year. Standard errors were based on 10 000 bootstrapped estimates of the mean. Different letters denote significant differences among years ($p \leq 0.05$) within a given species based on a random permutation test

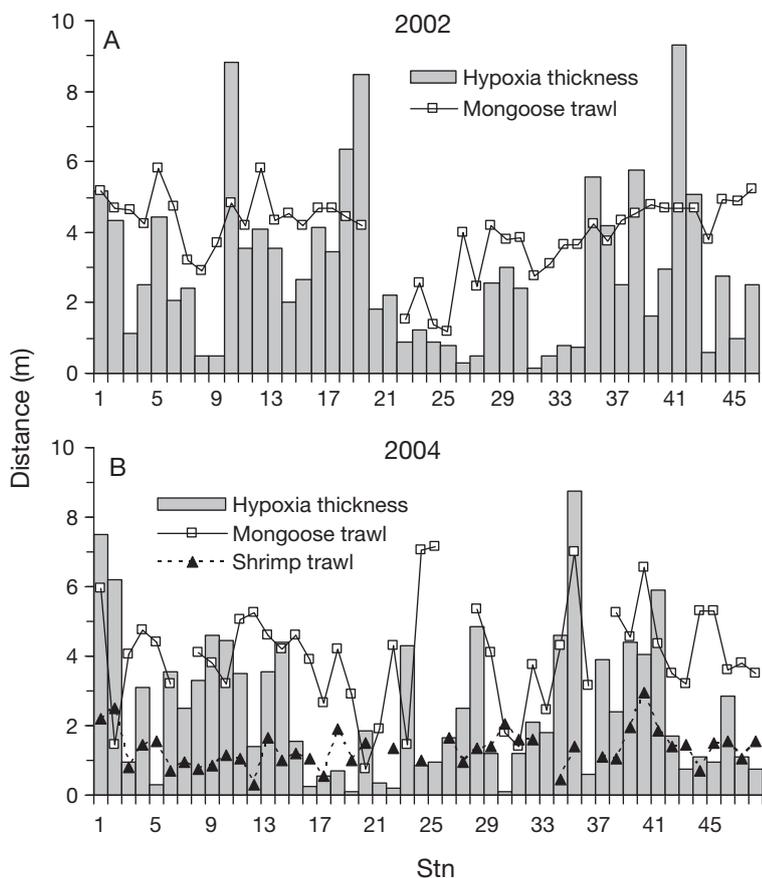


Fig. 6. Thickness of the bottom hypoxic layer and the height of the bottom water column sampled by paired mongoose and shrimp trawls at stations with bottom dissolved oxygen (DO) $\leq 2.0 \text{ mg l}^{-1}$ in (A) 2002 and (B) 2004. A depth sensor was not attached to the shrimp trawl in 2002. Distances refer to distance above the bottom

median lethal DO level reported from a synthesis of marine metazoans was 1.6 mg l^{-1} (Vaquer-Sunyer & Duarte 2008), values very similar to the average avoidance threshold of the 10 species studied here (1.52 mg l^{-1}). Similarly, the median LC_{50} for juveniles of several mid-Atlantic species was 0.5 to 1.6 mg l^{-1} (Miller et al. 2002), which is only slightly lower than the range of avoidance thresholds reported here (1.0 to 1.99 mg l^{-1}). The mean avoidance threshold for brown shrimp (1.30 mg l^{-1}) was similar to the LC_{50} for congeneric pink shrimp *Farfantepenaeus duorarum* determined in laboratory experiments (1.36 mg l^{-1} ; Goodman & Campbell 2007). Several flatfish species in the Gulf also appear relatively tolerant of low DO, occupying levels from 1 to 2 mg l^{-1} (Switzer et al. 2009). While these low avoidance thresholds indicate some tolerance to low DO, they also suggest that many organisms in the Gulf may be near a physiological threshold, whereby they avoid the direct lethal effects of low DO but experience both sublethal effects of occupying moderately low DO and indirect effects associated with altered spatial distributions.

Exposure to moderately low DO probably has sublethal effects on the growth and reproduction of several demersal species in the Gulf. For example, avoidance thresholds for Atlantic croaker over the 3 yr (1.2 to 2.7 mg l^{-1}) were consistently at or below levels where croaker in laboratory studies and in northeastern Gulf coast estuaries experience endocrine disruption and reproductive impairment ($\leq 2.7 \text{ mg l}^{-1}$; Thomas et al. 2007). Recent field studies have shown similar reproductive impairment in the same region of the Gulf studied here and indicate that croaker are exposed to DO levels during the summer (June to August) that are sufficiently low to impair reproduction during the subsequent fall (October to November) (Thomas & Rahman 2009). The importance and severity of these and other

Table 5. Parameter estimates for generalized linear models of the difference in catch per unit effort (CPUE) between paired mungoose and shrimp trawls towed in tandem during 2002 and 2004. Models were run separately for each species and are specified by Eq. (4) in the text. Standard errors are given in parentheses. DO: dissolved oxygen. *** $p < 0.001$, ** $p < 0.05$, * $p < 0.1$, ns = non-significant

Parameter	Atlantic bumper $R^2 = 0.77$	Atlantic croaker $R^2 = 0.85$	Brown shrimp $R^2 = 0.30$	Spot $R^2 = 0.59$	Sand seatrout $R^2 = 0.85$
Intercept	254.2 (32.3)	226.5 (38.7)	15436 (7.41)	11.84 (4.88)	34.4 (6.89)
DO	-20.93*** (7.06)	5.21 ns (8.11)	-0.649 ns (1.61)	0.486 ns (1.06)	1.03 ns (1.56)
Depth	-5.45* (2.26)	0.237 ns (2.22)	-0.208** (0.486)	-0.0387 ns (0.304)	0.151 ns (0.426)
DO × Depth	1.25* (0.672)	-0.158 ns (0.791)	-0.048 ns (0.135)	-0.0231 ns (0.085)	-0.011 ns (0.131)
Time	-0.00108 ns (0.00841)	-0.000608 ns (0.00762)	-0.00116 ns (0.00184)	-0.000302 ns (0.000920)	0.00011 ns (0.00139)
Year	123.9*** (6.22)	727.6*** (6.18)	-7.67*** (1.45)	-5.98*** (0.867)	24.14 ns (1.25)

sublethal effects probably varies among species and among years. For example, avoidance thresholds for juvenile spot over the 3 yr (1.3 to 2.5 mg l⁻¹) were consistently above levels where lab studies indicate increased mortality (1.2 mg l⁻¹, Shimps et al. 2005), consistent with avoidance of DO levels with direct lethal effects. However, thresholds were below levels where sublethal effects on growth of spot have been observed (1.5 mg l⁻¹, McNatt & Rice 2004) in 2003 but not in 2002 and 2004, suggesting spot may experience sublethal effects on growth only in some years. Whether sublethal effects of low DO are important for other species in the Gulf is uncertain because the DO levels that induce these effects are not known for most species. In other marine systems, different species occupying the same habitat can experience very different sublethal effects of low DO. For example, in estuarine tidal creeks comparative studies indicate that growth of juvenile summer and winter flounder is impaired by exposure to low DO (Stierhoff et al. 2006), but growth of juvenile weakfish from the same habitat is not (Stierhoff et al. 2009). A broad comparative analysis reported that the median DO threshold where sublethal effects have been observed was 4 mg l⁻¹ for fishes (range: 2.5 to 5.5 mg l⁻¹) and 3.5 mg l⁻¹ for crustaceans (range: 2 to 4.5 mg l⁻¹) (Vaquer-Sunyer & Duarte 2008). These values are well above most of the avoidance thresholds reported here, suggesting that sublethal effects of low DO exposure may be widespread among demersal fish and crustaceans in the Gulf.

The threshold modeling approach used here is novel in that it provides a means to quantify both the average level of DO that an organism avoids and the

variance in field-estimated avoidance thresholds with minimal assumptions. The variance about the mean threshold can be interpreted as a measure of the strength of low DO avoidance behavior, with a low variance indicating a strong avoidance response while a high variance indicates a weak avoidance response. The threshold modeling approach was originally developed to quantify the oceanic distribution of salmon in relation to temperature (Welch et al. 1995) but is particularly applicable to DO, which is generally thought to operate in a threshold manner, imposing a limit on the spatial distribution of organisms (Fry 1971). Advantages of this approach are that it is based on commonly collected field data (point estimates of CPUE and DO from a survey) and does not require assumptions about the functional form of the relationship between abundance and DO, as do parametric modeling approaches. The primary assumption is that the avoidance threshold can be characterized by a mean and a variance from a particular distribution (e.g. normal, lognormal).

The typically higher avoidance thresholds in 2002, when hypoxia extended over a larger area and a greater portion of the water column compared to 2003 and 2004, suggest that avoidance thresholds vary in relation to the annual severity of hypoxia. The greater severity of hypoxia in 2002 is supported by annual hypoxia mapping surveys (Turner et al. 2008) and fishery-independent trawl and hydrographic surveys in the region (Fig. 1). In contrast, repeated sampling during 2003 indicated that several storms mixed the water column during June and July prior to hypoxia re-forming on the inner Louisiana shelf in late July and early August (Baustian et al. 2009). Per-

haps the relatively thin and recently formed bottom hypoxic layer in 2003 still allowed organisms to access benthic habitats and associated food resources, such that they tolerated lower DO conditions. Supporting this possibility, sediment cores taken in 2003 indicated that infaunal prey were moderately abundant at hypoxic sites, with the highest prey densities within the upper 1 to 2 cm layer of the sediment (Baustian et al. 2009). Numerous studies have demonstrated that mobile organisms will tolerate short-term exposure to low DO in order to access hypoxic habitats that harbor food resources (Rahel & Nutzman 1994, Nestlerode & Diaz 1998, Taylor et al. 2007, Long & Seitz 2008, Craig et al. 2010). Such behavior probably induces a tradeoff between foraging and physiological stress that may lead to enhanced prey consumption in the short term. However, hypoxia-induced increases in short-term foraging may also lead to negative effects in the long term such as prey depletion, a less resilient prey community, and cumulative effects of physiological stress (Wu 2002, Costantini et al. 2008, Long & Seitz 2008).

The higher avoidance thresholds under more severe hypoxia documented here suggest that hypoxia avoidance is context-dependent, as has been shown in other systems (Bell & Eggleston 2005, Pierson et al. 2009). In estuarine systems, however, avoidance thresholds decreased under severe hypoxia, presumably because fish were forced to occupy lower DO levels due to habitat constriction between deeper hypoxic waters and the shoreline (Eby & Crowder 2002). In open continental shelf systems such as the northwestern Gulf, shoreline constraints to movement are probably less important. The higher avoidance thresholds under more severe hypoxia in 2002 may have been the result of more severe hypoxia-induced benthic mortality, such that a tradeoff between enhanced foraging on hypoxia-stressed benthos and the physiological costs of exposure to low DO did not exist. Hypoxia was more sustained prior to our sampling in 2002 compared to 2003 and 2004 supporting this possibility (Baustian & Rabalais 2009, Baustian et al. 2009). Alternatively, DO avoidance may be sensitive not only to the severity of hypoxia but to the spatial distribution of available habitat beyond the hypoxic area. When hypoxia is severe, as in 2002, most of the hypoxic zone is actually anoxic, and spatial gradients from anoxic to normoxic bottom waters are particularly strong near the edges of the hypoxic zone. Hence, the higher avoidance thresholds in 2002 may have been due to the limited availability of waters with moderately low but tolerable DO. Under these conditions, the variation in avoid-

ance thresholds among species and years documented here ($\sim 1 \text{ mg l}^{-1}$) may have only modest consequences for the actual amount of habitat loss ($\pm 15\%$) because bottom DO changes rapidly over short distances. In contrast, when hypoxia is moderate, as in 2003, bottom DO varies more gradually across the shelf such that a considerable amount of habitat within the range of documented avoidance thresholds is available. In this case, a difference in avoidance thresholds of 1 mg l^{-1} may have greater consequences for habitat loss ($\pm 25\%$) because spatial gradients in bottom DO are more gradual. In an experimental study, Herbert et al. (2011) showed that Atlantic cod *Gadus morhua* were more willing to enter hypoxic water when a well-oxygenated refuge was available nearby, supporting the possibility that avoidance thresholds are sensitive to the spatial arrangement of DO conditions beyond the hypoxic area. Similar context-dependency of DO avoidance behavior has been increasingly noted in a number of studies (Eby & Crowder 2002, Bernatis et al. 2007, Skjæraasen et al. 2008, Zhang et al. 2009).

Two recent hydroacoustic studies reported pelagic fish biomass overlying the bottom hypoxic layer, suggesting that low bottom DO may have indirect effects on processes in the upper water column (Hazen et al. 2009, Zhang et al. 2009); however neither study identified the species composition of the pelagic fish community above the hypoxic layer. Analysis of paired mongoose and shrimp trawls, which sampled different portions of the bottom water column, suggests that these pelagic fish may have been mostly Atlantic bumper. Other species that were common in the trawl survey and may be important components of the pelagic fish community include Atlantic threadfin herring *Opisthonema oglinum*, several anchovy species *Anchoa* spp., and squid (*Loligo* spp. and *Lolliguncula* spp.). Of the 5 most abundant species in the trawls, only bumper showed a vertical shift in distribution (higher catch rates in the mongoose trawl) as bottom DO declined. Bumper were also the most abundant species sampled and had one of the lowest but most variable DO avoidance thresholds, consistent with a species that has behavioral flexibility in avoiding hypoxic bottom waters. However, Bumper also showed the strongest aggregation near the horizontal edge of the hypoxic zone, suggesting they may use a combination of vertical and horizontal avoidance behavior to avoid low bottom DO. Craig et al. (2010) showed that cownose rays *Rhinoptera bonasus*, a highly mobile benthopelagic species, preferentially use regions of the shelf with hypoxic bottom water but occupy only the oxygenated habitats above

the bottom hypoxic layer, presumably to feed on hypoxia-stressed benthic invertebrates. In contrast, bumper is considered a pelagic planktivore, so that altered patterns of diel vertical migration and overlap with pelagic zooplankton prey may be more important than direct access to the bottom. Zhang et al. (2009) reported that overlap between acoustically-detected pelagic fish and zooplankton biomass decreased under severely hypoxic conditions in the Gulf, implying that low bottom DO leads to a decoupling of predators and prey in the water column. Similar studies in other systems have shown both increases (Keister et al. 2000, Vanderploeg et al. 2009) and decreases (Taylor et al. 2007, Ludsins et al. 2009) in spatial overlap of pelagic species in systems with low DO bottom water. Pierson et al. (2009) suggested that a threshold amount of bottom water hypoxia was needed to alter diel patterns of vertical migration, consistent with the notion that low DO effects on avoidance behavior and associated trophic interactions in the upper water column can depend strongly on the particular context in which they occur.

While numerous field studies have demonstrated that mobile organisms avoid low DO water (Howell & Simpson 1994, Eby & Crowder 2002, Tyler & Targett 2007), few have documented where evading organisms move and how spatial patterns in abundance change beyond the hypoxic area. The strength and generality of the aggregative response near the edge of the hypoxic zone was surprising, with strong peaks in abundance at distances less than 3 km from the hypoxic edge. This indicates much stronger aggregation near the hypoxic edge than previously thought. For example, using comparatively low resolution, shelf-wide trawl surveys, Craig & Crowder (2005) showed that brown shrimp and Atlantic croaker aggregated within 5 to 20 km of the offshore edge of the hypoxic zone. Similarly, Zhang et al. (2009) reported that 61 to 80% of pelagic fish biomass that occurred below the pycnocline was within 3 to 16 km of the offshore edge of the hypoxic zone. Hypoxia-induced aggregations, known as jubilees, have been documented at small spatial scales in response to the rapid advection of low DO water near shoreline habitats (e.g. Loesch 1960) but have not been reported at large spatial scales in open continental shelf systems where no obvious barrier to movement exists. These results indicate that despite the large area of hypoxia ($\geq 20\,000\text{ km}^2$), extending over nearly one-third of the western Louisiana shelf in some years, the spatial scale over which organisms are displaced is limited to relatively short distances (<5 km) from the edge of the hypoxic zone. Indirect and sublethal effects asso-

ciated with the avoidance of low DO are probably most pronounced within this relatively narrow 'halo' surrounding the hypoxic zone.

Several lines of evidence indicate that avoidance of low DO and aggregation near the edge of the hypoxic zone may enhance the susceptibility of brown shrimp and nontarget finfishes to the commercial shrimp trawl fishery. In general, contractions in the spatial distribution of fish populations and increases in aggregation can enhance catchability, or the proportion of the population captured by a given unit of fishing effort (Paloheimo & Dickie 1964, Winters & Wheeler 1985, Arreguín-Sánchez 1996). In addition to the strong aggregation of several species near the edge of the hypoxic zone documented here, the geographic range of brown shrimp over the larger western Louisiana shelf declined by about 25% from the mid-1980s to the 2000s concurrent with about a 3-fold increase in the area of hypoxic bottom water (Craig et al. 2005). This implies an increase in catchability to the shrimp fishery at both local and shelf-wide spatial scales. Shrimping effort on the shelf is typically highest in the nearshore region off of western Louisiana (where this study was conducted) and peaks in July when hypoxia is most severe (McDaniel et al. 2000, Macal 2002). Hence, there is strong spatial and temporal overlap between the commercial shrimp fishery and hypoxia. Brown shrimp were intermediate to the most common demersal fishes on the shelf in terms of their DO avoidance threshold and pattern of aggregation near the edge of the hypoxic zone, indicating target and nontarget species of the fishery do not segregate based on behavioral responses to low DO. In addition, spatial overlap between brown shrimp and nontarget finfishes was higher in years when hypoxia was more severe. Enhanced spatial overlap during years of more severe hypoxia was particularly evident for benthic species, though patterns were similar for most pelagic species as well. While overlap was generally high for all species (except for Atlantic bumper), the greater differences in overlap with benthic species among years differing in hypoxia severity suggests that hypoxia may have particularly important effects on bycatch of benthic fishes. These results suggest that if shrimpers respond to the marked changes in the distribution of shrimp and, in particular, focus effort near the edges of the hypoxic zone, then shrimp harvest and finfish bycatch may be enhanced as an indirect consequence of hypoxia-induced shifts in spatial patterns.

The effect of hypoxia-induced shifts in spatial distribution on susceptibility to fishing mortality war-

rants further investigation, particularly because the potential increases in catchability suggested here would tend to bias most models commonly used to assess harvested populations toward overestimation of abundance and underestimation of fishing mortality (Harley et al. 2001). In addition, presumed decreases in finfish bycatch brought about by increasingly stringent gear regulations over the last 2 decades may be offset to some extent by environmentally-driven increases in spatial overlap between brown shrimp and nontarget species. As a result, management advice regarding the status of the brown shrimp population, sustainable fishing mortality rates, and the efficacy of bycatch reduction efforts may be less conservative than intended. Consideration of these indirect effects of hypoxia on fishery interactions is particularly important for the northwestern Gulf because a large portion of the primary fishing grounds are now subject to seasonally and annually varying hypoxia. More generally, understanding the linkages between habitat alterations arising from processes occurring in coastal watersheds and fishery interactions in downstream marine systems is important for developing more ecosystem-based approaches to managing fisheries.

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