

Small Spatial Scale Variation in Fish Assemblage Structure in the Vicinity of the Northwestern Gulf of Mexico Hypoxic Zone

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Abstract Seasonal hypoxia [dissolved oxygen (DO) ≤ 2 mg Γ^{-1}] occurs over large regions of the northwestern Gulf of Mexico continental shelf during the summer months (June–August) as a result of nutrient enrichment from the Mississippi–Atchafalaya River system. We characterized the community structure of mobile fishes and invertebrates (i.e., nekton) in and around the hypoxic zone using 3 years of bottom trawl and hydrographic data. Species richness and total abundance were lowest in anoxic waters (DO ≤ 1 mg Γ^{-1}) and increased at intermediate DO levels (2–4 mg Γ^{-1}). Species were primarily structured as a benthic assemblage dominated by Atlantic croaker (*Micropogonias undulatus*) and sand and silver seatrout (*Cynoscion* spp.), and a pelagic assemblage dominated by Atlantic bumper (*Chloroscombrus chrysurus*). Of the environmental variables examined, bottom DO and distance to the edge of the hypoxic zone were most strongly correlated with assemblage structure, while temperature and depth were important in some years. Hypoxia altered the spatial distribution of both assemblages, but these effects were more severe for the benthic assemblage than for the pelagic assemblage. Brown shrimp, the primary target of the commercial shrimp trawl fishery during the summer, occurred in both assemblages, but was more abundant within the benthic assemblage. Given the similarity of the demersal nekton community described here to that taken as bycatch in the shrimp fishery, our results suggest that hypoxia-induced changes in spatial dynamics have the potential to influence

harvest and bycatch interactions in and around the Gulf hypoxic zone.

Keywords Hypoxia · Assemblage structure · Gulf of Mexico · Spatial dynamics · Edge effects · Eutrophication · Bycatch · Community dynamics

Introduction

Understanding the spatial dynamics of marine fishes at a community level is a practical way to advance ecosystem-based fisheries management (Mangel and Levin 2005; Francis et al. 2007; Marasco et al. 2007). Changes in the spatial distributions of species can cause changes in spatial overlap of predators and prey, and of competitors, that alter trophic dynamics and ultimately influence productivity. Species assemblages can be important ecological units that interact trophically and respond similarly to environmental and habitat conditions. A spatial perspective of ecological communities can also help define how and where anthropogenic activities affect ecosystems, and help identify or evaluate spatially based management approaches and monitoring strategies. Ultimately, a better understanding of community dynamics across a range of spatial scales is needed for advancing ecosystem-based approaches to management.

At large spatial scales (1,000 km) in continental shelf ecosystems, fishes and macroinvertebrates (i.e., nekton) typically occur as species assemblages that are geographically structured along depth and environmental gradients (Bianchi 1992; Gomes et al. 2001; Fossheim et al. 2006; Tolimieri and Levin 2006). These spatial patterns often reflect variation among species in physiological tolerances or preferences for abiotic conditions (e.g., temperature, salinity, and dissolved oxygen (DO); Bianchi 1991; Jacob et al. 1998; Beentjes et al. 2002), though the availability of

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food resources and species interactions (e.g., competition and predation) can influence large-scale spatial patterns as well (Jacobson and Vetter 1996; Giberto et al. 2004; Rooper and Martin 2009). Assemblage structure can be highly persistent over years to decades (Gomes et al. 1995; Jay 1996; Francis et al. 2002; Sousa et al. 2005; James et al. 2008; Jaureguizar et al. 2006), with temporal shifts often associated with chronic overexploitation (Levin et al. 2005; González-Troncoso et al. 2006; DeMartini et al. 2008), habitat loss (Collie et al. 2005), or climate change (Attrill and Power 2002; Fock 2008; Tian et al. 2008). Within this large-scale geographic structure, “nested” assemblages that are more spatially and temporally dynamic and reflect processes operating at smaller spatial scales have sometimes been identified (Martino and Able 2003; Rueda and Defeo 2003; Henriques et al. 2007; Snickars et al. 2009; Baptista et al. 2010). At these smaller spatial scales, local bathymetry and substrate type, vegetation, and local hydrodynamics are often correlated with assemblage structure (Moranta et al. 2006; Menezes et al. 2006; Anderson and Yoklavich 2007). For example, seasonal low DO in estuaries alters the structure of estuarine fish communities at the local patch scale (meters to kilometers) but not at the larger scale of the estuary (100 km), where larval recruitment and seasonal migrations drive community dynamics (Eby and Crowder 2004). Little is known about the dynamics of fish communities at these smaller spatial scales in continental shelf ecosystems.

Hypoxia ($\text{DO} \leq 2.0 \text{ mg l}^{-1}$) can influence the structure of nekton communities by altering the spatial distributions and associations of species (Eby and Crowder 2004; Keller et al. 2010), as well as through direct and indirect effects on demographic rates that determine patterns in the relative abundance of species (Breitburg et al. 1999; Stierhoff et al. 2006; Thomas and Rahman 2012). In a broad comparative study across taxa, DO thresholds that induced lethal effects in fish and crustaceans ranged from 0.5 to 3.0 mg l^{-1} and those that induced sublethal effects ranged from 2.0 to 4.5 mg l^{-1} (Vaquer-Sunyer and Duarte 2008). This large variation among taxa in responses to hypoxia suggests the potential for DO to have strong effects on community dynamics. In contrast to sessile species where the primary effect of hypoxia exposure is a direct influence on demographic rates, mobile species typically respond behaviorally to low DO in ways that alter spatial distributions (Tyler and Targett 2007; Craig et al. 2010; Essington and Paulsen 2010). While avoidance of hypoxic bottom water has been documented in numerous lab and field studies (Wannamaker and Rice 2000; Bell and Eggleston 2005; Stierhoff et al. 2009; Craig 2012), little is known about how avoidance behavior influences the species composition and spatial distributions of mobile nekton communities. Such information is

needed to identify potential indirect effects associated with hypoxia avoidance as well as the spatial scale over which they occur.

The northwestern Gulf of Mexico continental shelf experiences one of the largest seasonal hypoxic zones known (Bianchi et al. 2010; Rabalais et al. 2010). During the summer months (June–August), freshwater and nutrient inputs from the Mississippi–Atchafalaya River system fuel the development of bottom water hypoxia on the stratified inner Louisiana shelf (5–30 m depth). Based on mapping surveys, the area of hypoxia can extend over $>22,000 \text{ km}^2$ in some years and has generally increased since the 1980s, though with considerable annual variability (Rabalais et al. 2002; Turner et al. 2008). Paleo-studies and hindcasting models indicate increasing oxygen stress since the early 1900s, with hypoxia becoming more severe beginning in the 1960s to 1970s (Justic 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 average area of hypoxic bottom water to about one-third (i.e., $5,000 \text{ km}^2$) of its recent historical average by the year 2015 (Rabalais et al. 2007b; EPA 2008).

Anecdotal descriptions from data collected aboard shrimp vessels suggest the demersal nekton community on the northwestern Gulf of Mexico shelf is structured primarily along depth gradients, with a nearshore assemblage (shore to 30-m depth; “white shrimp grounds”), a mid- to outer shelf assemblage (30–90 m, “brown shrimp grounds”), and a shelf break-slope assemblage ($>90 \text{ m}$; Chittenden and McEachran 1976; Chittenden and Moore 1977). These early studies suggested species diversity generally increased with depth, with the highest demersal biomass occurring close to shore on the western Louisiana shelf and dominated by estuarine-dependent species, in particular juvenile sciaenids (e.g., Atlantic croaker, *Micropogonias undulatus*; spot, *Leiostomus xanthurus*; silver and sand seatrout, *Cynoscion* spp.). These species were harvested as part of an industrial groundfish fishery from the 1950s to 1970s, but are now taken primarily as bycatch in the commercial shrimp trawl fishery (Gutherz et al. 1975; Gutherz 1976; Nance and Scott-Denton 1997). Efforts to reduce shrimp trawl bycatch in the Gulf have focused mostly on gear modifications and limited closed areas to reduce the harvest of high profile species such as sea turtles (Crowder et al. 1994) and red snapper (*Lutjanus campechanus*; Gallaway and Cole 1999). The possibility that hypoxia influences bycatch interactions with the broader nontarget nekton community has only recently been considered (Craig 2012). This issue is particularly relevant in the Gulf due to historically high shrimp trawl bycatch rates (Nance and Scott-Denton 1997; Ortiz et al. 2000) and because there is strong spatial and temporal

overlap between hypoxia and the shrimp fishery on the shelf (McDaniel et al. 2000; Macal 2002).

We used bottom trawl and hydrographic data collected in a region of the Louisiana shelf that typically experiences severe seasonal hypoxia to investigate the effects of bottom DO and other environmental factors (e.g., depth, temperature, and salinity) on the structure of mobile demersal fishes and invertebrates (including commercially harvested shrimp) in and around the hypoxic zone. First, we tested the hypothesis that nekton are structured as distinct assemblages that are persistent over time. While this is often the case at large spatial scales (>100 km) in continental shelf ecosystems, few studies have been conducted at small spatial scales or in highly disturbed habitats where assemblage structure may be less well defined. Second, we hypothesized that bottom DO is the primary environmental variable driving assemblage structure. On the inner Louisiana shelf, bottom DO exhibits nearly the full range of possible variability (anoxic, $\leq 1 \text{ mg l}^{-1}$ to saturated, $\geq 8 \text{ mg l}^{-1}$) while other environmental factors vary over a more narrow range, suggesting the effects of bottom DO may be particularly strong at the spatial scales considered here. Third, we hypothesized that species assemblages have different spatial distributions that reflect avoidance responses to hypoxic bottom water. Craig (2012) showed that avoidance thresholds of individual species in the Gulf range two-fold among species, with several species aggregating at relatively short distances (<5 km) from the inshore and offshore edges of the hypoxic zone. This suggests nekton communities may be structured by tolerance to low DO or in relation to distance from the hypoxic edge. Fourth, we hypothesized that brown shrimp, the primary target of the commercial shrimp trawl fishery during summer, are associated with particular assemblages more so than others. We quantified the abundance of brown shrimp within each identified assemblage as a measure of the strength of association with the nontarget nekton community, and used this measure of association to infer the potential implications of hypoxia for bycatch interactions in the vicinity of the Gulf hypoxic zone.

Methods

Study Sites

Two study sites ($\sim 4,000 \text{ km}^2$ each and $\sim 50 \text{ km}$ apart) were established within and near the larger hypoxic zone on the inner Louisiana shelf in water depths of 2 to 35 m and extending up to 75 km from shore (Fig. 1). These sites were within a region that is heavily influenced by the Mississippi–Atchafalaya River plume, which typically extends across the inner Louisiana shelf to the Texas border during late spring

and summer (Chen et al. 2000). This region has historically supported the highest nekton biomass in the northwestern Gulf (Moore et al. 1970), but currently experiences severe hypoxia during most of the summer months (June to August). The eastern site is strongly influenced by riverine inputs from the mainstem of the Mississippi River and has experienced bottom water hypoxia nearly every year since at least the early to mid 1980s (Craig et al. 2005; Rabalais et al. 2002). The western site is influenced by additional riverine inputs from the Atchafalaya River, which is currently regulated at about 30 % of the total flow of the Mississippi–Atchafalaya system, and has experienced hypoxia more intermittently over this period. Community composition and environmental conditions were sampled at 82 to 115 stations over a 1 to 2-week period during the end of July from 2002 to 2004, with the goal of sampling both in hypoxic waters as well as in oxygenated waters located immediately inshore and offshore of the hypoxic zone. The eastern site was sampled each year, but vessel problems limited sampling at the western site in 2002 (no sampling conducted) and 2003 (17 stations sampled).

Trawl and Hydrographic Surveys

Each station was sampled for nekton and environmental parameters using a two-stage, grid-based sampling design (Lohr 1999). First, a 10-km square grid was overlaid onto each study site and randomly sampled over several consecutive days to map the general distribution of hypoxia and demersal species. Second, each 10-km grid cell that encompassed an inshore or offshore edge of the hypoxic zone (defined as the 2.0 mg l^{-1} DO contour) based on this initial mapping was then split into 16 cells (2.5 km^2) and randomly re-sampled to better define the edge of the hypoxic zone and the associated distribution of nekton. The survey vessel was double-rigged with a 12.8-m mongoose trawl towed from the starboard outrigger and a 12.8-m flat (shrimp) trawl towed concurrently from the port outrigger. Depth recorders attached to the headrope of each trawl indicated the mongoose trawl extended over the bottom 3–4 m of the water column while the shrimp trawl extended over the bottom meter of the water column (Craig et al. 2010). The trawls were towed parallel to depth contours for 20 min at a vessel speed of 5 km h^{-1} (~ 3 knots). All fish and invertebrates were identified to species, measured (nearest millimeter), and counted. Most species sampled had mean lengths from 100 to 200 mm and unimodal size distributions (age-0 or age-1 fish). DO (milligrams per liter), temperature (degrees Celsius), salinity, and water depth (meter) were measured before and after each tow using a CTD profiler equipped with an SBE 43 DO sensor (SeaBird Electronics, Inc., Bellevue, WA, USA). See Craig et al. (2010) and Craig (2012) for additional details regarding the sampling design.

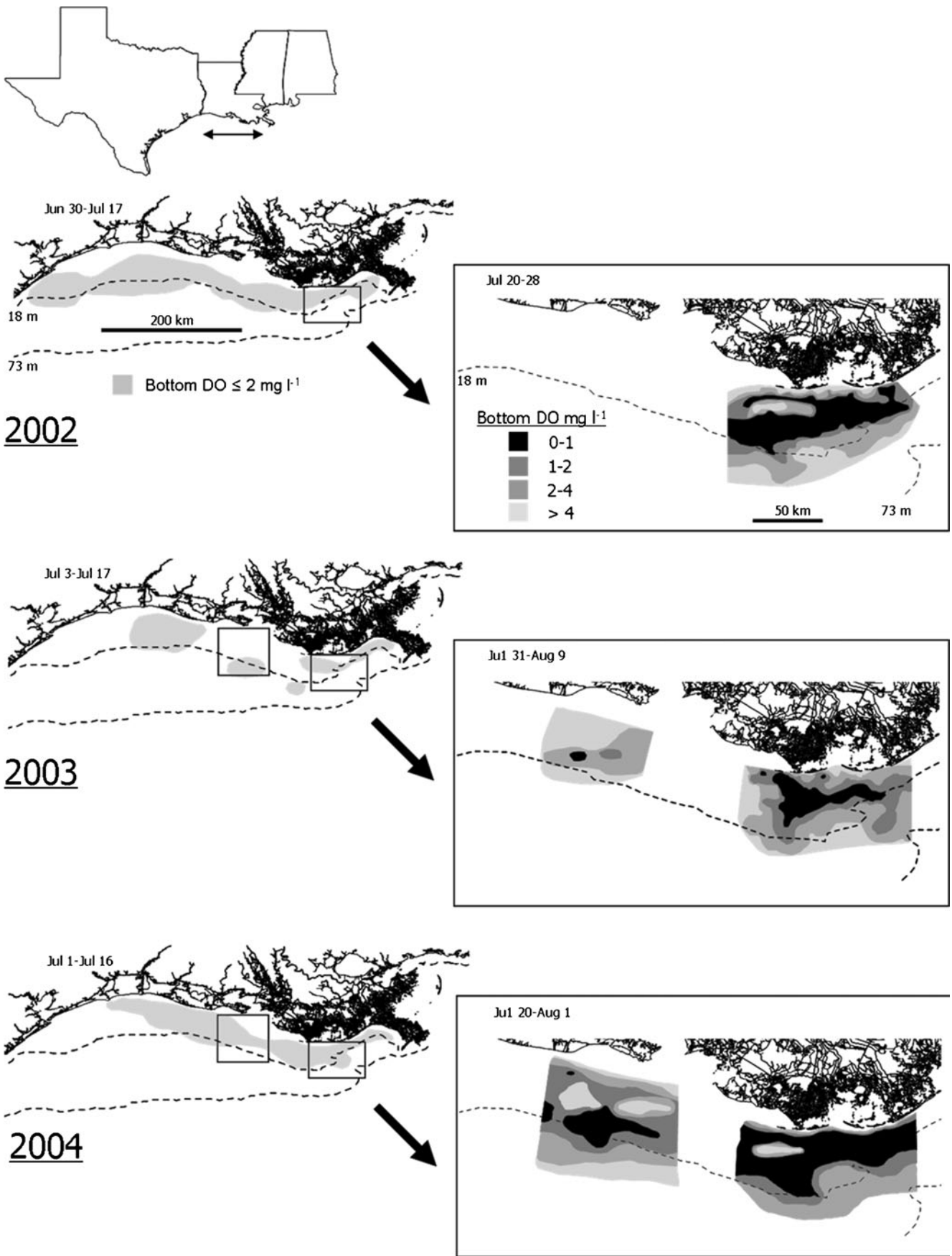


Fig. 1 Map of the study area in the northwestern Gulf of Mexico. *Gray areas* show the distribution of hypoxia ($\text{DO} \leq 2.0 \text{ mg l}^{-1}$) along the Louisiana and upper Texas coasts based on hydrographic measurements from the Southeast Area Monitoring and Assessment Program (SEAMAP) shipboard surveys. *Outsets with gray to black shading* are the interpolated distribution of bottom DO at the two study sites on the Louisiana inner continental shelf. *Dates above each map* are the sampling periods

Data Analysis

There were only minor differences in the catch composition of the two trawls towed concurrently at each station, therefore, data were combined (see Craig 2012). The combined catch at each station was standardized to a tow length of 1.85 km based on the distance between the beginning and ending location of the trawls. DO (milligrams per liter), temperature (degrees Celsius), salinity, and depth (meter) from the environmental profiles were averaged over the bottom meter of the water column, and between the beginning and ending CTD casts of each trawl tow to represent bottom conditions at each station. Given that several species aggregate at relatively short distances (<5 km) just beyond the margin of the hypoxic zone

(Craig 2012), we also considered distance to the hypoxic edge as an explanatory variable. Bottom DO was interpolated spatially for each study site using universal kriging with a quadratic drift component. The distance to the edge of the hypoxic zone was calculated as the minimum distance of each station from the 2.0 mg l^{-1} bottom DO contour estimated from the spatial interpolation of the CTD data. 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 the ending location of each tow.

Multivariate analyses were used to characterize assemblage structure and relationships to environmental variables using the Plymouth Routines in Multivariate Ecological Research software (PRIMER v6.1.11; Clarke and Warwick 2001; Clarke and Gorley 2006). The analysis was limited to 27 of the most common taxa that together accounted for 92.8 % to 93.7 % of the catch over the 3 years (Table 1). These species were chosen based on their ranked abundance within a year and consistency in relative abundance across the 3 years. Most taxa were considered at the species level, but three taxa

Table 1 List of taxa included in the multivariate analyses, including habitat type (*P* pelagic, *D* demersal), total estimated abundance (CPUE), percentage of total estimated abundance (%), and rank (R)

Scientific name	Common name	Habitat	CPUE	%	R
<i>Chloroscombrus chrysurus</i>	Atlantic bumper	P	203,573	39.48	1
<i>Peprilus burti</i>	Gulf butterfish	P	13,645	2.65	6
<i>Anchoa</i> spp.	Anchovies	P	13,169	2.55	7
<i>Opisthonema oglinum</i>	Atlantic threadfin herring	P	3,944	0.76	14
<i>Scomberomorus maculatus</i>	Spanish mackerel	P	1,615	0.31	19
<i>Peprilus alepidotus</i>	Harvestfish	P	1,173	0.23	20
<i>Rhinoptera bonasus</i>	Cownose ray	P	259	0.05	26
<i>Micropogonias undulatus</i>	Atlantic croaker	D	161,311	31.29	2
<i>Cynoscion</i> spp.	Seatrout	D	21,724	4.21	3
<i>Prionotus longispinosus</i>	Bigeye searobin	D	15,977	3.10	5
<i>Stenotomus caprinus</i>	Longspine porgy	D	11,555	2.24	8
<i>Leiostomus xanthurus</i>	Spot	D	10,537	2.04	9
<i>Trichiurus lepturus</i>	Atlantic cutlassfish	D	7,011	1.36	11
<i>Larimus fasciatus</i>	Banded drum	D	4,230	0.82	13
<i>Arius felis</i>	Hardhead catfish	D	2,402	0.47	16
<i>Synodus foetens</i>	Inshore lizardfish	D	726	0.14	21
<i>Saurida brasiliensis</i>	Large-scale lizardfish	D	529	0.10	22
<i>Etropus crossotus</i>	Fringed flounder	D	513	0.10	22
<i>Lutjanus campechanus</i>	Red snapper	D	340	0.07	24
<i>Prionotus tribulus</i>	Bighead searobin	D	276	0.05	26
<i>Farfantepenaeus aztecus</i>	Brown shrimp	D	20,203	3.92	4
<i>Loligo</i> and <i>Lolliguncula</i> spp.	Squid	P	7,531	1.46	10
<i>Squilla</i> spp.	Mantis shrimp	D	6,184	1.20	12
<i>Litopenaeus setiferus</i>	White shrimp	D	2,952	0.57	15
<i>Portunus gibbesii</i>	Iridescent swimming crab	P	2,076	0.40	17
<i>Callinectes similis</i>	Lesser blue crab	D	1,784	0.35	18
<i>Callinectes sapidus</i>	Blue crab	D	362	0.07	24
Species richness			27		
Total abundance			515,601	100.00	

consisted of multiple, closely related species. Silver seatrout (*Cynoscion nothus*), sand seatrout (*Cynoscion arenarius*), and unidentified seatrout were grouped as seatrout (*Cynoscion* spp.); bay anchovy (*Anchoa mitchilli*), dusky anchovy (*Anchoa lyolepis*), striped anchovy (*Anchoa hepsetus*), silver anchovy (*Engraulis eurystole*), and unidentified anchovies were grouped as anchovies (*Anchoa* spp.); and arrow squid (*Loligo pleii*), longfin squid (*Loligo pealeii*), and Atlantic brief squid (*Lolliguncula brevis*) were grouped as squid (*Loligo* and *Lolliguncula* spp.). These species were grouped because (1) abundance at the species level varied considerably across years for some species (e.g., *L. pleii* and *L. pealeii*), (2) some individuals could only be identified to genus at some of the stations (0–4.9 % of stations over the 3 years), and (3) preliminary analyses indicated similar responses to hypoxia within these taxonomically similar groups. Taxa were characterized as primarily pelagic or benthic based on their juvenile and adult life stage using references from a variety of sources (e.g., McEachran and Fechhelm 1998; Collette and Klein-MacPhee 2002; Froese and Pauly 2008). Catch-per-unit-effort (CPUE) for each species was $\ln(x+1)$ transformed to balance the contribution from abundant versus rare species. There was no difference in assemblage structure between the eastern and western sites in 2003 (ANOSIM, $R=-0.132$, $p=0.99$) or in 2004 (ANOSIM, $R=-0.002$, $p=0.44$; the western site was not sampled in 2002); therefore, data were pooled over the two sites for the community analysis. A station-by-station dissimilarity matrix was created for each year from the \ln -transformed CPUE data using the Bray–Curtis coefficient. Bray–Curtis dissimilarity matrices were then used to create dendrograms using the group-average linkage hierarchical agglomerative clustering technique, which groups stations based on similar species composition and abundance (Clarke and Warwick 2001).

A method similar to that used by Doyle et al. (2002), Duffy-Anderson et al. (2006), and Bosman et al. (2011) was used to determine the number of assemblages based on visual inspection of the dendrograms. First, a horizontal line was drawn across each dendrogram at a dissimilarity level that intersected the longest vertical lines emerging above groups of stations (assemblages). These assemblages were considered the most stable because the vertical lines that characterized them represent the greatest range in dissimilarity at which no stations were lost or gained. Two additional criteria used by Bosman et al. (2011) were also adopted. First, the horizontal line had to be drawn at a dissimilarity level ≥ 60 % to insure that the assemblages identified were more dissimilar than similar to each other. Second, the horizontal line had to intersect at least two assemblages, each containing greater than 10 % of the total number of stations sampled in order to avoid identifying an assemblage based on only a small number of stations. Once assemblages were identified from the dendrograms, the similarity profile permutation test

(SIMPROF) of PRIMER was used to determine if they were significantly different from one another (Clarke et al. 2008). The contribution of individual species to the average similarity within assemblages (“typifying species”) and the average dissimilarity among assemblages (“discriminating species”) was determined using the similarity percentage routine (SIMPER) (Clarke and Warwick 2001). ANOSIM was used to test for differences in assemblage structure across the 3 years. Species assemblages derived from the dendrograms were also cross-checked with non-metric multi-dimensional scaling (nMDS) ordinations by superimposing the assemblages onto the nMDS plots, also developed using the Bray–Curtis dissimilarity matrices (Clarke and Warwick 2001). The assemblages were then plotted on maps of the study area to determine if they were spatially coherent and persistent from year to year.

Environmental variables that were most strongly correlated with assemblage structure in each year were determined using the BIO-ENV routine of PRIMER (Clarke and Warwick 2001; Clarke and Gorley 2006). Depth, bottom temperature, bottom DO, bottom salinity, and distance to the edge of the hypoxic zone were included in the analysis. Preliminary analyses indicated that results were similar based only on data collected at site 1 (intensively sampled each year) to those based on data combined from site 1 and site 2. Because hypoxia was largely absent from the western site, distance to the edge of the hypoxic zone was not included in the BIO-ENV analysis for this year. Environmental variables were first normalized by subtracting the mean and dividing by the standard deviation to account for differences in measurement scale (Clarke and Gorley 2006). BIO-ENV creates a station-by-station dissimilarity matrix based on Euclidean distance for each environmental variable separately and for each possible combination of the five variables. Each environmental dissimilarity matrix was then ranked and compared to the ranked biological (fish and invertebrate data) dissimilarity matrix using the weighted Spearman rank correlation coefficient (ρ_w).

We tested for effects of bottom DO on species richness and total CPUE (pooled over all species) using ANOVA followed by Bonferoni-corrected multiple comparisons. We tested for differences in the geographic location (inshore vs. offshore of the hypoxic zone), DO levels occupied, and the occurrence and abundance of brown shrimp among the identified assemblages using generalized linear models (McCullagh and Nelder 1989). Models included terms for year, assemblage, and their interaction. Response variables were assumed to follow a binomial (geographic location and occurrence of brown shrimp), normal (DO), or Poisson (abundance) distribution. If interaction effects were significant, models were run separately within each year.

Results

Environmental Conditions on the Nearshore Gulf of Mexico Shelf

Hypoxia was present on the shelf in each of the 3 years but extended over a larger area in 2002 and 2004 compared to 2003 (Fig. 1). This is consistent with patterns based on shelf-wide mapping cruises, where hypoxia extended over ~22,000 km² in 2002, ~15,000 km² in 2004, but only ~8,500 km² in 2003 (Fig. 1; Turner et al. 2008). Hypoxia was widespread at the eastern site in each of the 3 years, extending over 42 % to 63 % of the study area. Hypoxia was mostly absent from the western site in 2003 (<5 % of the study area) but was severe at this site in 2004 (59 % of the study area). Bottom DO ranged from anoxic to saturated among stations (0.15 to 8.72 mg l⁻¹), and was typically higher in oxygenated waters inshore of the hypoxic zone (mean across years, 3.90–4.97 mg l⁻¹) compared to offshore of the hypoxic zone (mean across years, 2.98–3.55 mg l⁻¹), probably due to extensive wind and tidal mixing of shallow inshore waters. Several shallow, oxygenated shoals occurred within the interior of the hypoxic zone that were completely or partially surrounded by low DO water (Fig. 1). Bottom temperatures ranged from 19.4 °C to 31.9 °C and declined with increasing depth and distance from shore. Bottom salinities ranged from 20.5 to 36.5 but were mostly >30, with lower salinities occurring in limited areas close to shore. There was no difference in average temperature ($F_{1,206}=0.01$, $P=0.93$), salinity ($F_{1,206}=0.264$, $P=0.61$), or depths ($F_{1,206}=0.204$, $P=0.65$) sampled across the 3 years. Hypoxic bottom waters occurred at depths of 2.1 to 30.0 m, bottom temperatures of 22.1 °C to 29.6 °C, and bottom salinities of 29.3 to 36.3.

Species Richness and Total Abundance in and Around the Hypoxic Zone

A total of 164 fish and invertebrate taxa were sampled on the inner Louisiana shelf. Species richness was typically lowest in anoxic and hypoxic water (Fig. 2; 2002: $F_{3,88}=19.1$, $P<0.0001$; 2003: $F_{3,78}=4.37$, $P=0.007$; 2004: $F_{3,111}=8.74$, $P<0.0001$). In anoxic water, catches were comprised mostly of small numbers of pelagic or benthopelagic species, including jellyfish (*Phyllorhiza punctata* and *Aurelia aurita*), Atlantic bumper, Atlantic threadfin herring (*Opisthonema oglinum*), squid (*Loligo* and *Lolliguncula* spp.), and scaled sardine (*Harengula jaguana*). Species richness at DO levels from 1 to 2 mg l⁻¹ was two- to three-fold higher than that in anoxic waters, and leveled off at higher DO levels. Patterns in total CPUE (all species combined) were similar to those for species richness, with the lowest abundance in anoxic and

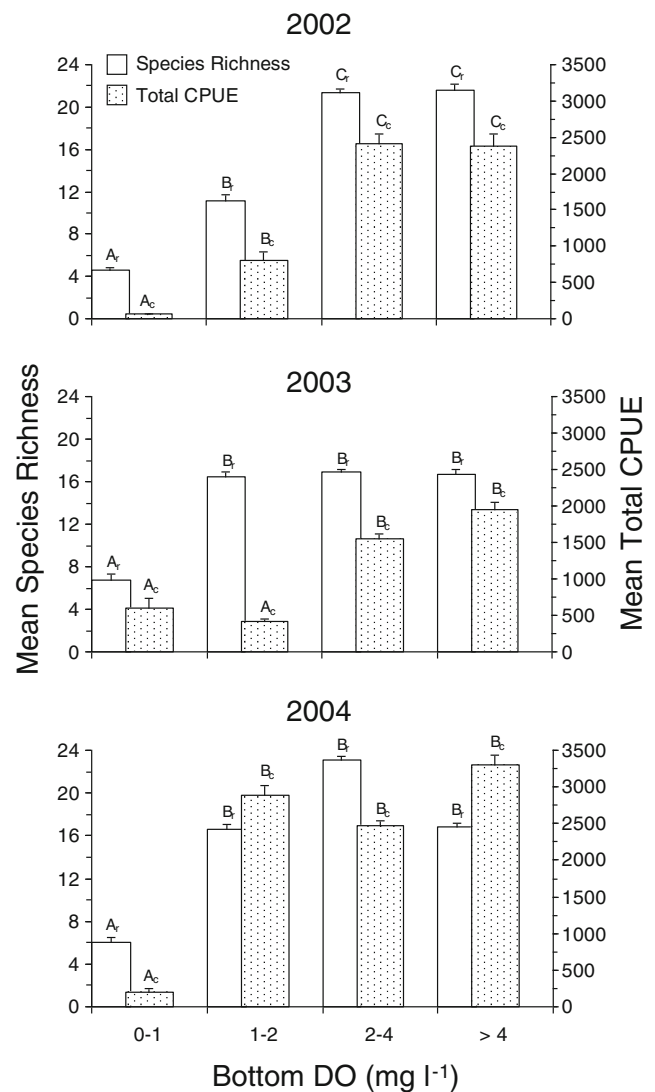


Fig. 2 Mean species richness and total catch-per-unit-effort (CPUE) as a function of bottom dissolved oxygen (DO) from trawl and hydrographic surveys on the inner Louisiana shelf (2002–2004). Subscripted letters indicate significant differences ($P\leq 0.05$) based on Bonferroni-corrected multiple comparisons. The 'r' subscript refers to species richness, and the 'c' subscript refers to total CPUE. Error bars are standard errors

hypoxic water and similar abundance across higher DO levels (2002: $F_{3,88}=27.9$, $P<0.0001$; 2003: $F_{3,78}=10.9$, $P<0.001$; 2004: $F_{3,111}=2.68$, $P=0.04$).

Multivariate Analyses of Community Structure

A total of 515,601 individuals from 20 fish and seven invertebrate taxa were included in the multivariate analysis (Table 1). Five demersal fish taxa (Atlantic croaker, seatrout, bigeye searobin, longspine porgy, and spot), three pelagic fish taxa (Atlantic bumper, Gulf butterflyfish, and anchovies), and one invertebrate species (brown shrimp) accounted for 87.6 % of the catch. These nine taxa were each captured in 27.4 % to

77.9 % of the tows conducted over the 3 years. Atlantic bumper and Atlantic croaker accounted for most of the catch (39.5 % and 31.3 %, respectively), while brown shrimp was the most abundant invertebrate species (3.9 % of the catch). No other species accounted for >5 % of the total catch in a given year.

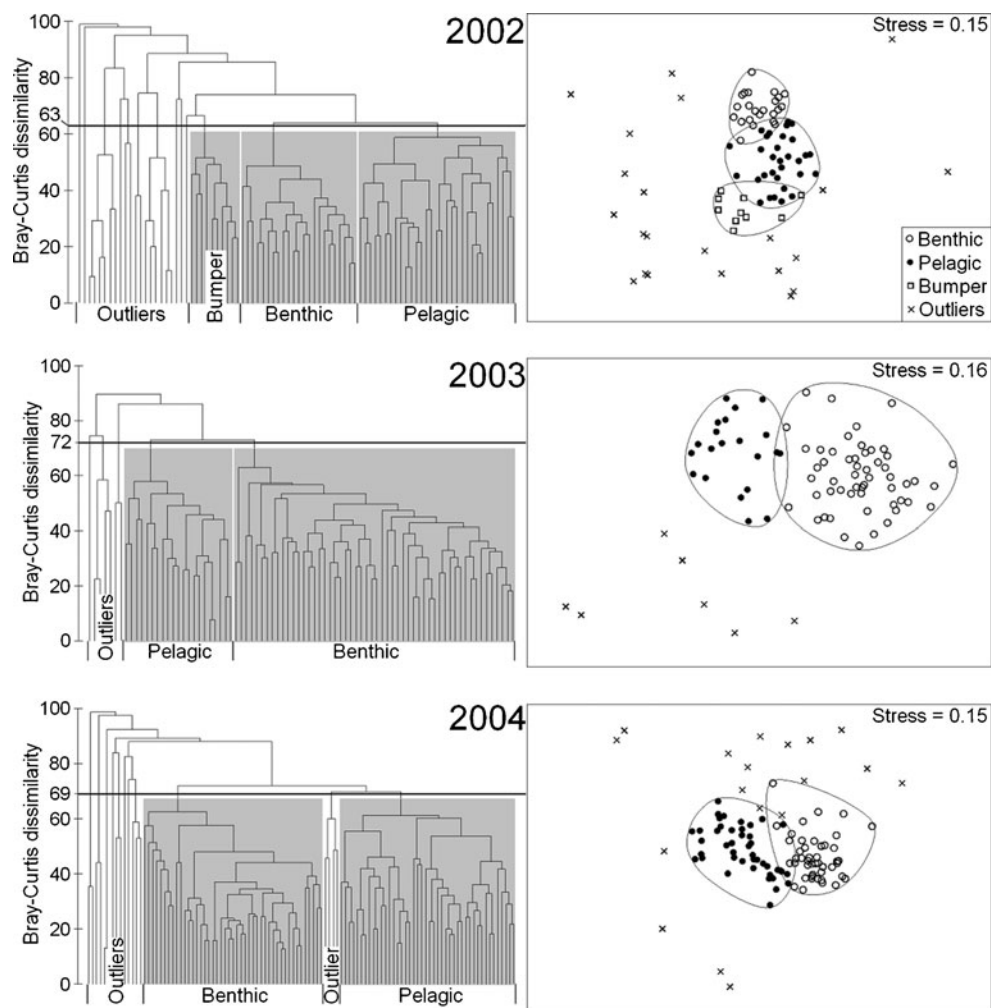
Assemblage Structure

Cluster analysis identified two to three major assemblages (i.e., assemblages containing greater than 10 % of the total number of stations in a given year) at dissimilarity levels ranging from 63 % to 72 % (Fig. 3). The remaining station clusters made up less than 0.2 % of the total catch (typically less than five species), contained from one to six stations each, and were peripheral to the major assemblages in nMDS plots. A “benthic assemblage” dominated by Atlantic croaker and seatrout was identified in each of the 3 years and contained 27 % to 66 % of the stations sampled; 54 % to 80 % of the catch in this assemblage was of species that are considered primarily benthic (Table 1). A “pelagic assemblage” dominated by Atlantic

bumper and squid was also identified in each year and contained 26–41 % of the stations sampled; 84–99 % of the catch in this assemblage was of species considered primarily pelagic. A third assemblage (“bumper assemblage”) dominated by small catches of Atlantic bumper (71 % of the assemblage), Atlantic threadfin herring (19 % of the assemblage), and other mostly pelagic species was identified only in 2002. Cownose rays were also present at 70 % of the stations within the bumper assemblage. This assemblage included a small percentage of the stations (12 %) and only 0.1 % of the total catch, and was not identified in 2003 or in 2004.

The three assemblages were also evident on two-dimensional nMDS plots (Fig. 3). Stress values, which indicate how accurately the nMDS plot displays the relationship among stations in low dimensional space, ranged from 0.15 to 0.16; stress values <0.20 indicate an interpretable two-dimensional plot (Clarke and Warwick 2001). The assemblages were significantly different from each other in each of the 3 years (SIMPROF, all $P < 0.05$), consistent with the visual patterns evident from the dendrograms and the

Fig. 3 Dendrograms (left panels) and nMDS plots (right panels) of major assemblages based on trawl data collected on the inner Louisiana shelf (2002–2004). The dark horizontal line on each dendrogram is the dissimilarity level at which assemblages were identified (see text for details). Major assemblages are highlighted in gray and encircled on the nMDS plots



nMDS plots, but were similar across the 3 years (ANOSIM, $R=0.012$, $P=0.096$).

Assemblage Composition

Atlantic croaker, seatrout, Atlantic bumper, and bigeye searobin typified the benthic assemblage in each of the 3 years; several additional species contributed smaller amounts to the similarity in particular years (Table 2). The pelagic assemblage was less diverse than the benthic assemblage and was typified by large catches of Atlantic bumper, while squid and Atlantic threadfin herring contributed in some years. Brown shrimp were present in both the benthic and the pelagic assemblage but made relatively small contributions (1–11 %) to the average similarity across the years.

Dissimilarity between the benthic and the pelagic assemblage ranged from 64 % to 73 % across years (Table 3). Species that consistently discriminated between the benthic and the pelagic assemblages were Atlantic croaker, seatrout, Atlantic bumper, and bigeye searobin. Gulf butterfish, spot, brown shrimp, white shrimp (*Litopenaeus setiferus*), and mantis shrimp (*Squilla* spp.), which were all more abundant in the benthic than in the pelagic assemblage, also contributed to the dissimilarity in some years. The primary difference between the two assemblages, however, was the high abundance of croaker in the benthic assemblage (39–59 % of the total catch) and the high abundance of bumper in the pelagic assemblage (73–97 % of the total catch). No species was unique to either assemblage over the 3 years.

Not surprisingly, the bumper assemblage identified only in 2002 was more similar to the pelagic assemblage than to the benthic assemblage (Tables 2 and 3). Cownose rays, a highly mobile, benthopelagic species, also contributed to the average similarity within the bumper assemblage. The

bumper assemblage was comprised of much smaller catches of Atlantic bumper than in the pelagic assemblage, and this difference accounted for most of the dissimilarity, while Atlantic croaker and seatrout contributed most to dissimilarity with the benthic assemblage.

Relationship Between Assemblage Structure and Environmental Variables

In analyses of single environmental variables, DO (2002 and 2003) and distance to the edge of the hypoxic zone (2004) were most strongly correlated with assemblage structure (Table 4). When environmental variables were considered in combination, DO and distance to the edge along with depth (2003 only) and temperature (2004 only) were most strongly correlated with assemblage structure. In 2002, the year when hypoxia was most severe, no combination of environmental variables led to a higher correlation coefficient than bottom DO alone. The total variation in community structure explained by the environmental variables never exceeded 21 %.

Geographic Location of Assemblages

The geographic distribution of the benthic and pelagic assemblages differed among years in relation to the severity of hypoxia (Fig. 4). The benthic assemblage occurred mostly offshore of the hypoxic zone in 2002 and 2004, the years when hypoxia was most severe, but occurred both inshore and offshore of the hypoxic zone in 2003 when hypoxia was much less severe. In addition, the benthic assemblage occurred across the full range of sampled depths at the western site in 2003 when very little hypoxia was present, indicating these patterns were the result of displacement inshore and

Table 2 Species contributing to the average percent similarity within the benthic, pelagic, and bumper (2002 only) assemblages based on the results of SIMPER

Benthic assemblage				Pelagic assemblage				Bumper assemblage	
Species	2002	2003	2004	Species	2002	2003	2004	Species	2002
Atlantic croaker	17.17	16.80	14.07	Atlantic bumper	41.64	83.13	48.87	Atlantic bumper	71.76
Seatrout	15.15	9.89	11.77	squid	14.08	4.81	11.26	Atlantic thread herring	10.35
Atlantic bumper	10.16	16.51	6.34	Atlantic thread herring	9.35	3.45	7.15	Cownose ray	9.26
Gulf butterfish	9.21	2.96	5.36	brown shrimp	8.23	1.19	3.59		
Bigeye searobin	8.61	5.59	7.94						
Brown shrimp	4.85	11.22	8.17						
Squid	3.24	6.20	7.35						
White shrimp	3.19	6.43	1.18						
Mantis shrimp	2.07	0.50	7.23						
Iridescent swimming crab	1.86	1.05	6.43						
Average similarity	59.36	50.36	52.02		47.15	49.89	45.47		54.17

Species contributing >5 % in any 1 year are shown. Percent contributions that were >5 % are in *bold*

Table 3 Species contributing to the average dissimilarity between the benthic and pelagic assemblage, the benthic and bumper (2002 only) assemblage, and the pelagic and bumper assemblage, and their mean CPUE within each assemblage based on the results of SIMPER

Species	Benthic vs. pelagic				Benthic vs. bumper				Pelagic vs. bumper								
	2002		2003		2004		2002		2002		2002						
	Benthic	Pelagic %	Benthic	Pelagic %	Benthic	Pelagic %	Benthic	Pelagic %	Benthic	Pelagic %	Benthic	Pelagic %					
Atlantic croaker	606.89	3.57	10.47	71.97	0.19	11.98	203.38	7.25	8.06	Atlantic croaker	606.89	0.00	13.00	Atlantic bumper	398.41	36.71	11.84
Seatrout	168.02	0.67	9.40	13.15	0.07	7.44	52.52	2.49	6.50	Seatrout	168.02	0.00	10.58	Squid	14.33	0.38	9.66
Gulf butterfish	46.94	0.57	7.01	3.53	0.03	4.16	17.17	0.11	5.00	Gulf butterfish	46.94	0.00	7.74	Brown shrimp	11.55	0.23	9.08
Bigeye searobin	35.23	2.00	5.75	6.17	0.12	5.70	27.50	0.30	5.90	Bigeye searobin	35.23	0.07	7.17	Atlantic thread herring	9.59	2.60	8.52
Spot	18.11	2.71	5.53	5.36	0.00	5.21	5.69	0.79	3.33	Spot	18.11	0.00	5.70	Anchovies	7.00	0.00	6.97
Atlantic bumper	69.81	398.41	5.10	65.02	349.72	8.56	16.99	491.75	7.86	Atlantic cutlassfish	17.92	0.00	5.59				
Brown shrimp	16.99	11.55	5.05	17.36	0.70	7.72	33.81	5.05	5.48								
White shrimp	4.99	1.56	3.58	6.39	0.31	5.72	1.97	2.32	2.68								
Mantis shrimp	4.00	0.13	3.42	0.51	0.00	1.25	19.70	0.22	5.93								
Average dissimilarity			63.95		72.99		71.83						84.30				66.50

Species contributing >5 % in any 1 year are shown. Percent contributions that were >5 % are in bold

offshore due to hypoxia. Even so, 26 % to 67 % of the stations in the benthic assemblage occurred in moderately hypoxic (1–2 mg l⁻¹) water mostly along the offshore edge of the hypoxic zone. In contrast, the pelagic assemblage occurred both inshore and offshore of the hypoxic zone in each year, but abundance was typically highest in shallow, well-oxygenated water close to shore. The pelagic assemblage was not found at the western site in 2003, despite the near absence of hypoxia. In contrast to the benthic assemblage, the pelagic assemblage was typically associated with high DO water, with 62 % to 82 % of the stations occurring in waters with DO ≥ 2 mg l⁻¹. Differences in the DO levels occupied by the benthic and pelagic assemblages were significant in 2002 ($F_{1,52}=5.31, P=0.025$) and 2004 ($F_{1,54}=23.5, P<0.0001$) but not in 2003 ($F_{1,57}=1.35, P=0.25$). Similarly, differences in the geographic distribution of the two assemblages were significant in 2002 ($F_{1,52}=37.4, P<0.0001$) and 2004 ($F_{1,54}=98.3, P<0.0001$), but not in 2003 ($F_{1,57}=0.718, P=0.40$).

Oxygenated Interior Shoals

The bumper assemblage identified only in 2002 occurred mostly on interior oxygenated shoals that were completely surrounded by hypoxic bottom water, and to some extent along the nearby inshore edge of the hypoxic zone (Fig. 4). Sampling was limited to the edges of the shoals due to depth limitations of the survey vessel. Species that were particularly abundant or frequent near shoals included Atlantic bumper, Atlantic threadfin herring, jellyfish (*Scyphozoa*), cownose rays, cobia (*Rachycentron canadum*), squid, Spanish mackerel, sharksucker (*Echeneis naucrates*), sharpnose sharks (*Rhizoprionodon terraenovae*), iridescent swimming crab (*Portunus gibbesii*), blue crabs (*Callinectes sapidus* and *Callinectes similis*), and red drum (*Sciaenops ocellatus*).

Association of Brown Shrimp with the Benthic and Pelagic Assemblages

The frequency of occurrence and the abundance of brown shrimp were typically higher in the benthic assemblage than in the pelagic assemblage (Fig. 5). Brown shrimp occurred at 78–89 % of the stations within the benthic assemblage but only 29–74 % of stations within the pelagic assemblage over the 3 years ($F_{1,212}=28.2, P<0.0001$). The occurrence of brown shrimp within the two assemblages differed among years, however (year × assemblage interaction: $F_{2,212}=3.93, P=0.021$). Differences among years were driven mostly by the pelagic assemblage, with brown shrimp occurring at 74 % of stations in the pelagic assemblage in 2002, similar to that in the benthic assemblage ($F_{1,52}=0.116, P=0.735$), but only 29 % and 52 % of stations within the benthic assemblage in 2003 ($F_{1,73}=23.4, P, 0.0001$) and 2004

Table 4 Single and multiple environmental variable correlations with assemblage structure as determined by the weighted Spearman rank correlation coefficient (ρ_w) using BIO-ENV

Year	<i>n</i>	<i>p</i>	Variables	ρ_w	Best variable combination	ρ_w
2002	86	0.002	DO	0.13	DO	0.13
			Distance to edge	0.10		
			Depth	0.02		
			Temperature	-0.02		
			Salinity	-0.10		
2003	82	0.002	DO	0.06	DO, depth	0.12
			Depth	0.03		
			Salinity	0.01		
			Temperature	-0.02		
			Distance to edge	0.17		
2004	107	<0.001	Distance to edge	0.17	Distance to edge, temperature	0.21
			Temperature	0.14		
			Depth	0.12		
			Salinity	0.05		
			DO	0.02		

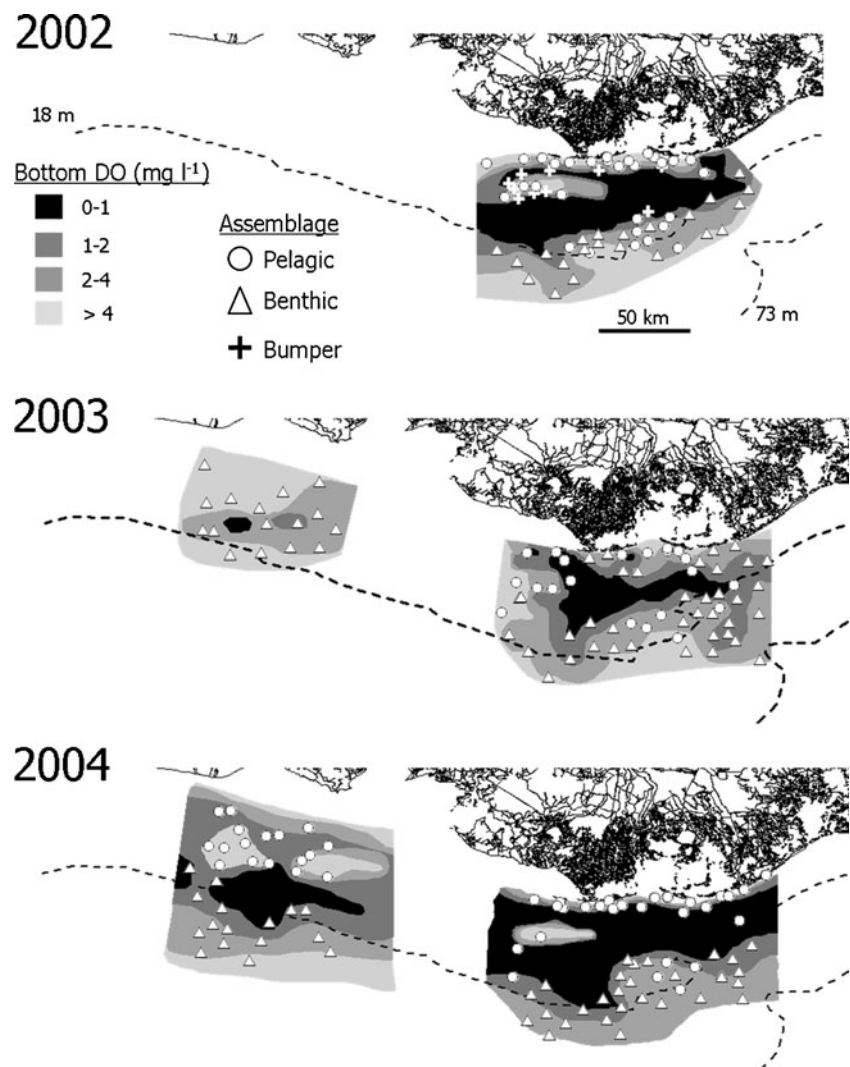
n is the number of stations included in the analysis each year, and *p* is the probability of obtaining ρ_w or greater by chance. Distance to the edge of the hypoxic zone was not included in the 2003 analysis (see text)

DO dissolved oxygen

($F_{1,87}=12.7$, $P=0.006$), respectively. Even so, average CPUE of brown shrimp was 2- to 25-fold higher in the benthic assemblage than in the pelagic assemblage,

and this difference was similar over the 3 years (Fig. 5; assemblage effect: $F_{1,212}=4.91$, $P=0.028$; year \times assemblage interaction: $F_{2,212}=1.04$, $P=0.36$).

Fig. 4 Spatial location of the benthic, pelagic, and bumper (2002 only) assemblages in relation to bottom dissolved oxygen (DO) on the inner Louisiana shelf (2002–2004)



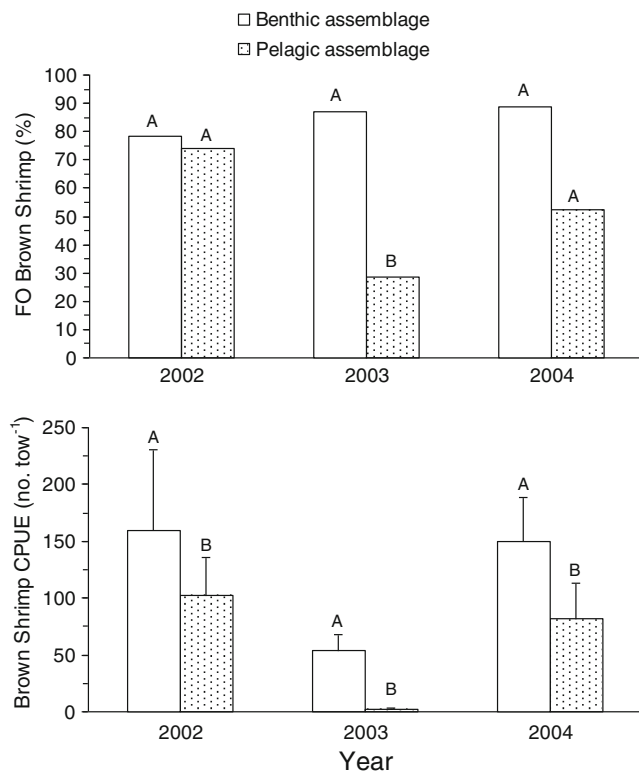


Fig. 5 Frequency of occurrence (*top panel*) and mean CPUE (*bottom panel*) of brown shrimp at stations within the benthic and pelagic assemblages (2002–2004). Error bars are standard errors. Letters denote significant differences in brown shrimp CPUE within years

Discussion

Abundance and species richness of mobile fishes and invertebrates declined in regions of the northwestern Gulf of Mexico shelf that experienced low DO. The greatest declines occurred at DO levels of 1–2 mg l⁻¹, which are near incipient lethal levels and similar to estimated avoidance thresholds for several individual species in the Gulf (Craig 2012). These results are consistent with prior studies that have shown similar declines in abundance and species richness in areas with low DO (Howell and Simpson 1994; Eby and Crowder 2004; Keller et al. 2010; Kodama et al. 2010). While direct mortality due to hypoxic bottom water has been reported for some species with low motility in the Gulf (Rabalais et al. 2001), these patterns are more likely the result of hypoxia avoidance behavior (Craig and Crowder 2005; Zhang et al. 2009; Craig 2012). The sharp declines at 1–2 mg l⁻¹ and the lack of DO effects at higher levels (i.e., >2 mg l⁻¹) suggest these spatial gradients can be characterized as a threshold response whereby species composition and abundance change rapidly over relatively short distances at low to moderate DO levels. Because the consequences of hypoxia for mobile species are mediated in large part by shifts in distribution, characterizing distribution shifts and associated changes in community composition is important for understanding the indirect effects of hypoxia.

In and around the hypoxic zone on the inner Louisiana shelf, mobile fishes and invertebrates were structured primarily as two assemblages, a relatively diverse benthic assemblage dominated by Atlantic croaker and seatrout (*Cynoscion* spp.) with smaller contributions from several other mostly benthic species, and a low diversity pelagic assemblage dominated by Atlantic bumper with smaller contributions from squid and Atlantic threadfin herring. The “benthic” and “pelagic” designation used here is a simplification, as many of the sampled species migrate in the water column to varying degrees and our trawls did not fully sample the pelagic habitat. In addition, none of the 27 species considered were unique to either assemblage, and Atlantic bumper, in particular, were ubiquitous in the study area and occurred in both assemblages. Nevertheless, dissimilarity values between the benthic and pelagic assemblages were relatively high, assemblage structure was persistent over the 3 years, and the assemblages tended to be spatially segregated, indicating they were distinct.

Most studies of fish assemblages in continental shelf ecosystems have been based on data from monitoring surveys with much greater spatial extent but much lower spatial resolution than reported here (Jay 1996; Gomes et al. 2001; Beentjes et al. 2002; Gaertner et al. 2005; Sousa et al. 2005; James et al. 2008). These studies have typically identified assemblages that are geographically structured across broad depth and environmental (e.g., temperature) gradients. Of the environmental variables examined here, bottom DO and distance to the edge of the hypoxic zone were most strongly correlated with assemblage structure. Correlations with temperature and depth, which are typically important at larger spatial scales in shelf ecosystems (Gomes et al. 2001; Jaureguizar et al. 2006; Tolimieri and Levin 2006), were significant in only one of the 3 years (in combination with DO), while salinity was not significant in any year. Craig (2012) found similar strong effects of DO and weak effects of other environmental factors in an analysis of individual species' distributions. The lack of correlation with other environmental factors may be related to the spatial and temporal scale of this study. Temperature typically has a strong effect on the seasonal structure of fish communities (Jaureguizar et al. 2004), while salinity is often important at spatial scales that span a low salinity to marine ecotone (Martino and Able 2003). Our study occurred during late July in a particular region of the shelf that is a transition zone from estuarine and riverine influenced nearshore waters to marine offshore waters. Bottom DO is the primary source of variability in abiotic conditions at this spatial scale, perhaps accounting for its importance in our analysis. In addition, hypoxia bifurcates the distribution of organisms, with some individuals moving to oxygenated waters inshore of the hypoxic zone while others move offshore of the hypoxic zone, possibly obscuring relationships with

environmental variables that vary monotonically across the shelf (e.g., temperature and salinity). Even so, the benthic and pelagic assemblages documented here do not represent groups of species organized based on similar tolerance to low DO, as originally hypothesized. For example, Atlantic croaker had the highest average DO avoidance threshold (1.99 mg l^{-1}), and sand seatrout had one of the lowest avoidance thresholds (1.1 mg l^{-1} ; Craig 2012), yet both species were important components of the benthic assemblage. Rather, the two assemblages appear to reflect localized groups of species with similar spatial distributions beyond the area of hypoxia. Further studies are needed to determine if these local assemblages are nested within a larger scale geographic structure related to variation in temperature, depth, and salinity across the shelf, as has been reported for fish communities in other shelf ecosystems (Moranta et al. 2006; Anderson and Yoklavich 2007; Snickars et al. 2009).

It is not surprising that hypoxia had particularly strong effects on the spatial distribution of the benthic assemblage, given that low DO is largely restricted to the bottom waters. The benthic assemblage was primarily distributed offshore of the hypoxic zone when hypoxia was severe (2002 and 2004) but occurred inshore and offshore when hypoxia was more moderate (2003 eastern site) and across the shelf when hypoxia was absent (2003 western site). Prior studies in the Gulf indicate that species evading hypoxia aggregate at relatively short distances (<5 km) just beyond the margins of the hypoxic zone (Craig and Crowder 2005; Craig 2012). These results are consistent with a number of studies indicating that organisms evading low DO often remain in close proximity to hypoxic bottom water and, in many cases, rapidly re-occupy previously hypoxic areas once hypoxia dissipates (Pihl et al. 1991; Eby and Crowder 2004; Tyler and Targett 2007; Kodama et al. 2010). Anecdotal descriptions from the 1960s prior to when hypoxia was severe indicate most of the species comprising the benthic assemblage are typically distributed from shore to the 20-m depth contour during summer (Darnell et al. 1983). The typical nearshore distribution of the benthic assemblage during summer is probably due to the warm temperatures and possibly higher food resources that characterize this region, as well as associations of many of these species with inshore estuarine waters. Shifts in distribution to deeper offshore waters suggest the benthic assemblage is displaced to regions of the shelf they otherwise would not inhabit. The consequences of these hypoxia-induced shifts in spatial distribution are not well known. Craig and Crowder (2005) showed that the temperature distributions of Atlantic croaker and brown shrimp offshore of the hypoxic zone were lower than those considered optimal for growth, suggesting possible bioenergetics implications associated with displacement to deeper offshore waters. However, Baustian et al. (2009) showed that densities of benthic infaunal prey

were higher offshore than inshore of the Gulf hypoxic zone, suggesting better foraging conditions offshore. The high densities of nekton near the edges of the Gulf hypoxic zone may also enhance intra- or inter-specific competition as well as predation mortality, particularly if predators are able to locate areas of high prey density near the hypoxic edge. The benthic assemblage may also experience a number of sublethal effects from exposure to moderately low DO water ($2\text{--}3 \text{ mg l}^{-1}$) offshore of the hypoxic zone. For example, Atlantic croaker, the dominant species within the benthic assemblage, experience reproductive impairment and masculinization due to exposure to sublethal DO levels (Thomas and Rahman 2012). The extent to which these and other sublethal effects extend to other species within the benthic assemblage are unknown.

The pelagic assemblage was much less diverse than the benthic assemblage and was dominated by Atlantic bumper, with smaller numbers of squid (*Loligo* spp. and *Lolliguncula* spp.) and Atlantic threadfin herring (*O. oglinum*). In contrast to the benthic assemblage, the pelagic assemblage occurred inshore and offshore of the hypoxic zone in each year, with the highest abundance in shallow, well-oxygenated inshore waters. Pelagic organisms can move both horizontally and vertically to avoid low bottom DO (Taylor et al. 2007; Zhang et al. 2009; Vanderploeg et al. 2009), and this additional behavioral flexibility may account for the generally weaker effects of annual differences in hypoxia severity on the distribution of the pelagic assemblage compared to the benthic assemblage. Even so, our bottom trawl gear did not sample the entire pelagic habitat. Hydroacoustic studies in the Gulf have identified pelagic fish biomass above the bottom hypoxic layer, though the species composition of the pelagic fish community in this region is not well known (Hazen et al. 2009; Zhang et al. 2009). Species comprising the pelagic assemblage described here, in particular Atlantic bumper, may be important components of the pelagic community above the bottom hypoxic layer. While Atlantic bumper also aggregate in bottom waters near the hypoxic edge, they have one of the lowest and most variable DO avoidance thresholds (Craig 2012), suggesting they may also move vertically in response to low bottom DO. Zhang et al. (2009) showed that spatial overlap between pelagic fish biomass and mesozooplankton prey in the Gulf declined when hypoxia was severe, suggesting hypoxia spatially segregates pelagic fishes from their food resources. Both spatial segregation (Taylor et al. 2007; Ludsins et al. 2009; Larsson and Lampert 2011) and compression (Keister et al. 2000; Vanderploeg et al. 2009) of pelagic fishes and zooplankton prey has been reported in other systems. Similarly, bottom water hypoxia can increase (Prince and Goodyear 2006; Costantini et al. 2008) or decrease (Neuenfeldt 2002) spatial overlap of planktivores and highly mobile piscivorous fishes. These hypoxia-induced shifts in spatial overlap can influence predation mortality rates and trophic transfer efficiency (Keister et al. 2000; Taylor et al.

2007) but are difficult to predict a priori, and likely depend on the particular nature of low DO and species interactions in hypoxic ecosystems.

The bumper assemblage identified in 2002 occurred almost exclusively in the vicinity of several shallow, oxygenated shoals within the interior of the hypoxic zone. Hypoxia was most severe and persistent in 2002, perhaps enhancing the use of these oxygenated shoal habitats as a spatial refuge for organisms evading hypoxia. Cownose rays, a benthopelagic species that is common on the Louisiana shelf during the summer, were also associated with the bumper assemblage. Cownose rays prefer areas of the shelf with hypoxic bottom water but use oxygenated pelagic habitats above the bottom hypoxic layer, probably to forage on hypoxia-stressed emergent benthos (Craig et al. 2010). Similar opportunistic foraging behavior has been documented in a number of systems (Rahel and Nutzman 1994; Nestlerode and Diaz 1998; Long and Seitz 2008; Neuenfeldt et al. 2009). These oxygenated interior shoals may be important refuge habitats for evading organisms, but may also act as traps where trophic interactions are intensified. The latter possibility is supported by the presence of a number of highly piscivorous species (e.g., sharks, cobia, and mackerels) near these shoals as well.

The juxtaposition of high fisheries productivity, high biomass of nontarget and mostly juvenile species, and seasonally severe hypoxia suggests low DO may play an important role in mediating the spatial dynamics of shrimp harvest and bycatch on the inner Louisiana shelf. The composition of the species assemblages described here is similar to that reported in prior bycatch characterization studies of the nearshore shrimp trawl fishery in the Gulf (Gunter 1936; Hildebrand 1954; Nance and Scott-Denton 1997), as well as that of the industrial groundfish fishery that operated from the 1950s to the 1970s (Gutherz et al. 1975; Gutherz 1976). For example, the top ten most abundant bycatch species from shelf-wide observer coverage of the shrimp trawl fishery were included in our study (Nance and Scott-Denton 1997), while about three quarters of the finfishes considered here were among the 20 most dominant species in the industrial groundfish fishery from the 1970s (Gutherz 1976). Shrimp bycatch rates used in a number of stock assessments for Gulf species are generated in part from fishery-independent surveys using the same gear and similar sampling procedures as in this study (Gallaway et al. 1998; Ortiz et al. 2000). While there are certainly differences between bottom trawl surveys and actual commercial shrimping operations, the species assemblages documented here probably reflect the general species composition and spatial distribution of the nontarget nekton community encountered by shrimpers in the vicinity of the Gulf hypoxic zone. The nearshore Louisiana shelf (<20 m depth) where this study was conducted has some of the highest reported bycatch rates in the Gulf (Ortiz et al. 2000; Nance and Scott-Denton 1997), which is not surprising given the

historically high biomass of demersal fish and crustaceans (Moore et al. 1970) and high levels of shrimping effort (McDaniel et al. 2000) in this region. Even so, estimated finfish bycatch in the Gulf shrimp fishery has declined in recent years (Ortiz et al. 2000; Cowan et al. 2008) due to a combination of requirements for bycatch reduction devices, gulf-wide declines in shrimping effort (Caillouet et al. 2008), and possibly the population effects of bycatch that have reduced the abundance of nontarget species (Diamond et al. 2000; Shepherd and Myers 2005; Jeffers et al. 2008). Not surprisingly, brown shrimp, which are closely associated with the seafloor, were more abundant within the benthic assemblage than the pelagic assemblage, though they occurred with relatively high frequency in both assemblages. If shrimpers target hypoxic edge habitats where both shrimp and finfish densities are high, then both harvest and bycatch rates may be elevated in the vicinity of the hypoxic zone, particularly for benthic species. Alternatively, because the benthic assemblage shifted to offshore habitats when hypoxia was severe, susceptibility to the fishery may decline if the fishery remains inshore during periods of severe hypoxia. This latter possibility is supported by analyses of commercial catch and effort data that suggest historical shrimping effort off Louisiana was concentrated close to shore and remains high in inshore waters when hypoxia is severe, possibly due to hypoxia-induced increases in catch rates associated with blocked migrations of shrimp emigrating from estuaries to the shelf (Zimmerman and Nance 2001). A better understanding of the emigration of estuarine-dependent species to the nearshore shelf, how shrimpers respond to hypoxia-induced shifts in the distribution of shrimp, and more direct information on harvest and bycatch rates is needed to address the effects of hypoxia on the shrimp trawl fishery.

Ecosystem-based approaches to management have emphasized the importance of a spatial perspective, consideration of anthropogenic activities that influence marine habitats, and accounting for species interactions in the management of marine resources (Mangel and Levin 2005; Marasco et al. 2007). We have shown that target and nontarget species of the commercial shrimp fishery on the inner Louisiana shelf are structured as distinct species assemblages in the vicinity of the Gulf hypoxic zone. These assemblages presumably reflect groups of species that interact trophically and respond in similar ways to hypoxia disturbance, hence, providing a basis for extending single species analyses to the community level. They may also serve as useful constructs to help understand potential interactions between hypoxia, shrimp harvest, and the bycatch of nontarget species, the minimization of which is an explicit goal of most ecosystem approaches to fisheries management.

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