

Habitat suitability for oil and gas platform-associated fishes in Louisiana's nearshore waters

Ryan T. Munnelly^{1,4,*}, David B. Reeves¹, Edward J. Chesney², Donald M. Baltz¹,
Brian D. Marx³

¹Department of Oceanography and Coastal Sciences, Louisiana State University, Energy, Coast & Environment Building, Baton Rouge, Louisiana 70803, USA

²Louisiana Universities Marine Consortium, 8124 Hwy 56, Chauvin, Louisiana 70344, USA

³Department of Experimental Statistics, Louisiana State University, M.D. Woodin Hall, Baton Rouge, Louisiana 70803, USA

⁴*Present address:* Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, 100 8th Avenue Southeast, St. Petersburg, Florida 33701, USA

ABSTRACT: River discharge and seasonal, eutrophication-driven hypoxia within coastal waters of the northern Gulf of Mexico create a wide range of environmental conditions for fishes. Environmental conditions are most dynamic on the Louisiana shelf, a region in which oil and gas platforms (hereafter platforms) are abundant and serve as artificial reefs. Platforms provide a unique, vertically oriented substrate for fouling organisms and nekton throughout the water column and often span substantial gradients of salinity, temperature, dissolved oxygen (DO), and water clarity. During the summers of 2013 and 2014, we used paired video and hydrographic samples taken at 150 small platforms sited in nearshore waters (3.7–18.0 m water depth) to document the responses of platform-associated fishes to coastal water quality. Responses of the 26 analyzed fish species included substantial changes in habitat selection coupled with vertical habitat compression. The vertical extent of the water column suitable for fishes was compressed due to avoidance of hypoxic bottom water (DO <50 % saturation) and apparent avoidance of eutrophic surface strata with supersaturated oxygen conditions (140.7 ± 7.0 % saturation [95 % CI]). Generalized linear mixed models, habitat suitability indices, and factor analysis suggested that fish habitat-selection patterns varied significantly in the presence of hypoxia by up to 10 salinity units, 10°C, 30 % DO saturation, 6 m water depth, and 4.5 m Secchi depth. The differences in intraspecific distributions occurring in the presence and absence of hypoxia were often greater than interspecies separations within comparisons. These findings demonstrate an important indirect effect of eutrophication-driven hypoxia on fishes.

KEY WORDS: Hypoxia · Habitat compression · Eutrophication · River-influenced ocean margins · Physicochemical fish responses · Artificial reefs

Resale or republication not permitted without written consent of the publisher

1. INTRODUCTION

Eutrophication has been linked to the formation of extensive areas of recurring depleted bottom dissolved oxygen (DO) in a variety of aquatic habitats across the globe (Diaz & Rosenberg 2008). In general, systems that are eutrophic are highly productive aquatic ecosystems. However, excessive productivity

coupled with stratification can cause bottom oxygen to be reduced to levels that lower habitat quality for marine life (hypoxia). When DO is reduced below the tolerance level of an organism, the organism must move or perish (Rabalais et al. 1991). The cumulative effects of eutrophication and hypoxia are, therefore, difficult to decipher. For example, although enhanced productivity in the surface waters of hypoxic

*Corresponding author: ryan.munnelly@myfwc.com

zones ($\text{DO} < 2.0 \text{ mg l}^{-1}$) may lead to long-term increases in some pelagic fishes (Adamack et al. 2017, Glaspie et al. 2018), hypoxic bottom waters may also lead to long-term declines in some demersal fishes (Hondorp et al. 2010, Rose et al. 2018a,b).

Most of the world's largest hypoxic zones occur in enclosed and semi-enclosed basins (Diaz & Rosenberg 2008). Some of these systems are plagued by persistent anoxia and hypoxia, such as the Baltic and Black Seas, while extensive hypoxia in other systems is seasonal and transient, such as Lake Erie, Chesapeake Bay, the Seto Inland Sea, the East China Sea, and the northern Gulf of Mexico (nGOM). Consequently, not all systems and their fauna respond to hypoxia in the same way at both the population and ecosystem level. Many of the systems affected by hypoxia, such as the Baltic Sea and Chesapeake Bay, have experienced dramatic changes in their demersal and pelagic fishes while other systems, such as the nGOM, have not shown significant declines in fisheries landings over recent decades (Chesney & Baltz 2001, Hondorp et al. 2010). Despite the different responses among these systems to eutrophication, effects on fishes and invertebrates are evident in all systems at some level. For example, hypoxia has been shown to affect the spatial distribution of fish and invertebrate populations (Craig & Crowder 2005, Langseth et al. 2014, Kraus et al. 2015) and this redistribution can make them more vulnerable to fishing gear (Kraus et al. 2015, Purcell et al. 2017). Spatial redistribution has the potential to indirectly affect organisms by increasing densities along hypoxic margins (Craig 2012, Craig & Bosman 2013, Kraus et al. 2015), by changing the community structure of fishes and invertebrates (Craig & Bosman 2013), by altering predator–prey dynamics (Taylor & Rand 2003, Costantini et al. 2008, Webster et al. 2015) and by altering the quality of habitat selected by marine organisms (Eby 2001, Craig & Crowder 2005, Zhang et al. 2014). Increased use of suboptimal environmental conditions for variables such as salinity, temperature, water depth, and DO can affect metabolism, growth or reproduction (Thomas et al. 2006) and might lead to population bottlenecks if access to suitable habitat is insufficient (Coutant 1985, Dieterich & Fulford 2012). Spatially explicit population studies coupled with water quality models have been used to better understand the complicated effects of eutrophication and hypoxia (Adamack et al. 2017). Increased understanding of the complex interactions involved in these types of models is important for integration of an ecosystem approach to fisheries management within eutrophic systems.

While systems around the world that are affected by low oxygen have many similarities, the nGOM has several attributes that stand out as unique. It is the world's only open-shelf system affected by eutrophication and hypoxia in a subtropical environment (Chesney & Baltz 2001). Coastal Louisiana is a deltaic landscape at the terminal drainage of the third largest watershed on Earth (Milliman & Meade 1983). Consequently, a mean annual discharge of 580 km^3 (Milliman & Meade 1983) of fresh water drains into the nearshore waters off Louisiana's coast, resulting in estuarine conditions in the nearshore zone. Within the nearshore waters off Louisiana, salinity, temperature, turbidity, and nutrient distributions fluctuate in response to river discharge (Pokryfki & Randall 1987), winds (Rabalais et al. 1991), and currents (Wiseman et al. 1975, 1997) that influence the Mississippi and Atchafalaya river plumes, and their interactions with marine waters and bottom bathymetry (Hetland & Di-Marco 2008). River discharge typically peaks in early April (Turner & Rabalais 1991), and the inundation of nutrient-rich waters fuels intense phytoplankton blooms that co-occur with seasonal stratification of the water column and reduced shelf turnover (Cochrane & Kelly 1986). This stratification adds a vertical dimension to the existing lateral environmental gradients emanating from the river mouths. The water column can be dynamic, ranging from nearly fresh to fully marine, with temperature differences of several degrees (Wiseman et al. 1997), representing a substantial range of different habitat conditions for aquatic organisms like fishes.

The stratified, eutrophic conditions can cause depletion of DO in the lower water column during summer (Turner & Rabalais 1991, Justić et al. 1993, Rabalais et al. 2007). As a result, the seasonally recurring hypoxic zone of the nGOM is second in size only to the hypoxic zone of the Baltic Sea (Rabalais et al. 2002), with peak hypoxia typically forming by June and persisting through mid-September (Rabalais et al. 1991). Over several decades, the size of the hypoxic zone has grown in both area and total volume (Rabalais et al. 2002, Obenour et al. 2013) to a mean area of $16\,600 \text{ km}^2$ in recent years, with peaks $> 22\,000 \text{ km}^2$, and a 27 yr mean vertical extent of 3.9 m, with annual means as high as 6.2 and 6.3 m occurring in 2008 and 2009, respectively (Obenour et al. 2013). It is important to understand how hypoxia impacts fishes on the nearshore Louisiana shelf because coastal Louisiana supports many of the most highly productive US fisheries (Chesney et al. 2000), and eutrophication-driven hypoxia is increasing globally (Diaz & Rosenberg 2008, Breitburg et al. 2018).

Another distinctive feature of the Louisiana coastline is the multitude of oil and gas platforms (hereafter platforms) which extend from the bays and marshes seaward beyond the continental shelf. Platforms offer a unique opportunity to study the effects of hypoxia and how other physicochemical variables interact to influence fishes. In 2013 there were >2600 federally listed platforms in federal waters off Louisiana (BOEM 2018), as well as thousands of additional structures in state waters (Liu et al. 2018). These federal and state-regulated platforms are 'de facto artificial reefs' that provide hard substrate in a region that is otherwise dominated by soft sediments (Parker et al. 1983). Furthermore, many of these platforms are in areas where benthic hypoxia forms. A unique ecological service that platforms provide is vertical hard substrate that extends from the seafloor to above the sea surface. Platforms therefore serve as complementary features by providing vertical relief that extends into well-oxygenated waters in a region where natural reefs are rare, and relief is low (Gallaway & Cole 1998).

While coastal migration to more suitably oxygenated waters is the only option for some fishes responding to hypoxia (Switzer et al. 2006, 2009, Keller et al. 2010), many demersal and pelagic species first move up in the water column where more suitable DO conditions exist (Rabalais et al. 2001, Stanley & Wilson 2004, Reeves et al. 2018b). Suitable conditions for platform-associated species can thus be found around platforms in areas that might be less suitable given inadequate vertical relief (Stanley & Wilson 2004, Reeves et al. 2017). Although many aspects of hypoxia have been well studied, coincident responses of fishes throughout the water column have received relatively little attention (Stanley & Wilson 2004, Ludsins et al. 2009, Vanderploeg et al. 2009, Reeves et al. 2018b). Impacts of hypoxia on pelagic species have also been understudied (Prince & Goodyear 2006, Vanderploeg et al. 2009, Zhang et al. 2009, 2014, Glaspie et al. 2018). More generally, fish responses to environmental variation in stratified waters have not been investigated outside of model simulations (Breitburg et al. 1999, Zhang et al. 2014). Given the dominant influence that physicochemical properties can play in driving estuarine fish distributions (Baltz et al. 1998), these are important considerations within dynamic aquatic environments like estuaries, enclosed and semi-enclosed seas, and river-influenced ocean margins, such as nearshore Louisiana. Assemblage compositions in these settings are likely to reflect interwoven distributions of individual species (Remmert 1983) or life stage tolerances to many variables within a complex environ-

ment (Livingston 1988, Baltz & Jones 2003). A compelling example of one such environment, the Gulf of Bothnia in the Baltic Sea, is described by Kautsky & Kautsky (2000, p.8), who write: 'A mix of freshwater and marine fish species such as perch, pike, cod and flounder can often be caught in the same net'. Lateral and vertical movement in aquatic settings like these in response to an environmental variable or prey distribution might result in a trade off by requiring a fish to accept less favorable conditions of other variables (Eby & Crowder 2002, Craig & Crowder 2005, Prince & Goodyear 2006). For example, a fish moving up in response to hypoxia, or displaced prey might find itself in significantly warmer waters than it would otherwise select (Prince & Goodyear 2006, Costantini et al. 2008, Zhang et al. 2014). Such an interaction could result in eventual movement away from the platform in search of more suitable habitat, or fishes may tolerate less favorable physical conditions and remain associated with the platform if other needs can be met.

The goal of this study was to examine the habitat-selection patterns of platform-associated fishes for salinity, temperature, DO, water depth, and Secchi depth, and to compare patterns at platforms throughout the nearshore zone off coastal Louisiana. The regular presence of bottom-water hypoxia (DO <50% saturation or ~3.0–3.5 mg l⁻¹ across a wide range of observed salinities, temperatures, and pressures) throughout the study area presented a unique opportunity to evaluate the interactive effects of the vertical displacement of fishes in response to hypoxia, and habitat selection of other environmental variables. To our knowledge, this is the first study to evaluate habitat selection of fishes using a 3-dimensional approach that accounts for the vertical distributions of species occurring across the wide range of environmental variation associated with a stratified water column.

2. MATERIALS AND METHODS

2.1. Field sampling

Platforms were sampled along Louisiana's coast from Mississippi to Texas in waters 3.7–18 m deep using a modified-random strategy (Fig. 1). Platforms were selected using the Bureau of Ocean Energy Management (BOEM) platform information and United States Geological Survey (USGS) datasets to sample evenly across known sources of variability (distance to shore, depth, dominant sediment type, platform complexity, date of deployment, and prox-

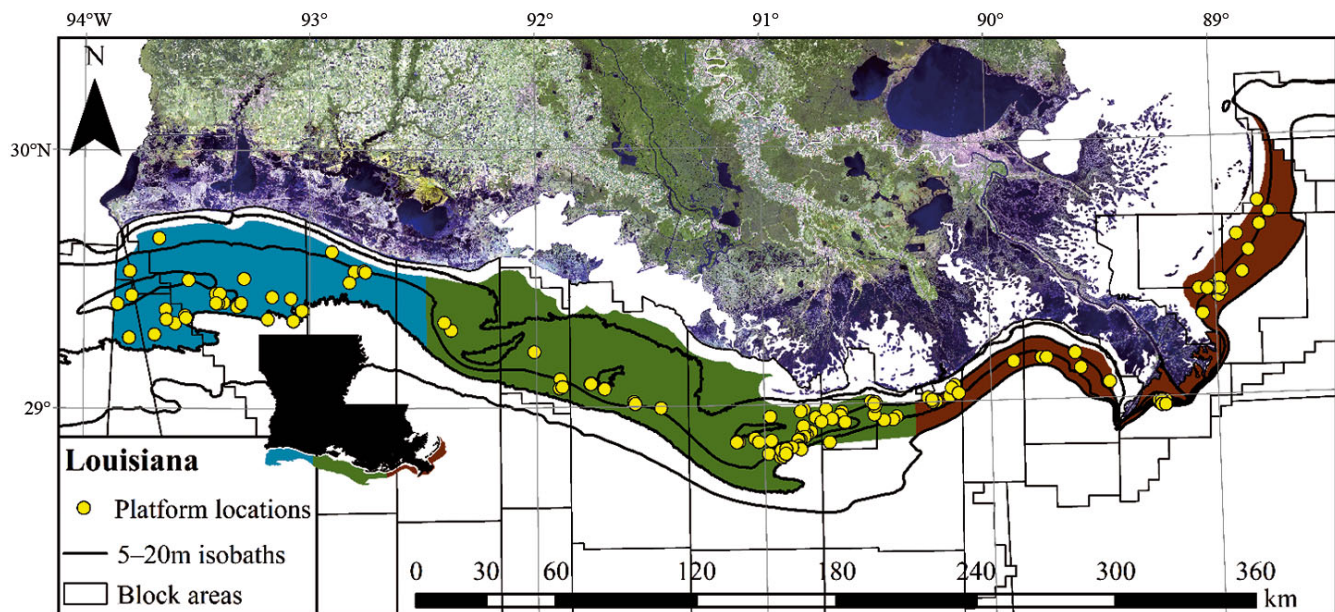


Fig. 1. Chart of the coastal zone off Louisiana. Yellow circles show the locations of all small platforms included in analyses ($n = 150$). The brown, green, and blue areas show the extent of the East, Central, and West regions referenced in the text

imity to other platforms). Sampling occurred during day trips aboard a small vessel and included 14 trips between 12 July and 6 September of 2013 and 14 trips from 2 July to 12 September of 2014.

The camera array consisted of a triangular-shaped aluminum frame with 3 outward-facing and 1 downward-facing synchronized GoPro Hero 3 cameras mounted to the underside of a PVC plate attached to the upper part of the frame. The array was lowered vertically (mean rate of $0.23 \pm 0.02 \text{ m s}^{-1}$ [95% CI]) on the down-current side near each platform and left on the bottom for 90 s. The array was not baited and had no supplemental lighting. The 3 outward-facing cameras were mounted at 120° from one another to provide a circular and non-overlapping field of view. Two forward-facing lasers spaced 10 cm apart were mounted on either side of the camera that was oriented toward the platform. The downward-facing camera was centrally mounted and used to record fishes swimming under the array, to record a depth gauge, and to provide benthic substrate images. Each camera had a 62° (horizontal) \times 36° (vertical) field of view, and recorded images at 30 frames s^{-1} . Following array retrieval, salinity, temperature, depth, DO, turbidity, and Secchi depth were collected using a YSI model 6820 V2 water quality sonde (hereafter YSI) and a 20 cm Secchi disk. YSI measurements were taken every 2 s, within $\sim 0.2 \text{ m}$ of the surface and the bottom.

2.2. Video processing

Videos of the fish assemblages were determined to be adequate for analyses if the submerged platform structure (the 'jacket') was in view (mean distance of $3.0 \pm 0.2 \text{ m}$ [95% CI]). This standard was adequate for the purposes of this study due to the strong association of most fishes with the platforms, and the small footprint of the platforms we targeted. The fish assemblages were concentrated around the small nearshore platforms, and were more conducive to video-based sampling than prior studies on larger structures reported (Scarborough Bull & Kendell 1994). Video and water quality data from 150 unique platform locations were used for analyzing fish assemblages. Of these 150 samples, 65 were obtained in 2013, and 85 were obtained in 2014. Furthermore, 84 of these samples were recorded in the absence of hypoxia while 66 were recorded in the presence of hypoxia (bottom DO $< 50\%$ saturation).

Videos were analyzed to estimate the minimum number of individuals present for each species (MAXNO) and to generate relative abundance estimates for the assemblages at each platform (Ellis & DeMartini 1995). This approach precluded double counting by using the maximum number of each species simultaneously recorded on video as an index of abundance (Priede et al. 1994, Willis & Babcock 2000, Wells & Cowan 2007). Since there was potential for

overlapping fields of view of the downward-facing camera with the outward-facing cameras, MAXNOs were compiled separately, and the higher of the 2 estimates for each species were used.

Of the 150 platforms analyzed, 37 were recorded with a single outward-facing camera and a synchronized downward-facing camera rather than the full array of 4 cameras. In these videos, the outward-facing camera maintained a view of the submerged structure. Disparities in water volume sampled occurring between camera array configurations, as well as due to variation in water clarity, were accounted for with a covariate (effort). Midwater turbidity was multiplied by the number of outward-facing cameras and standardized relative to the lowest value encountered, effectively down-weighting counts at platforms that sampled a larger volume of water. Estimates of species richness, Shannon-Wiener diversity, and assemblage composition did not significantly differ between the 2 camera array configurations when effort was accounted for (Munnelly 2016).

2.3. Habitat suitability analyses

Habitat suitability reflects habitat use relative to habitat availability (Bovee 1982). This information can be used to characterize patterns of habitat selection, or resource use, and species-specific environmental responses (Baltz 1990, Switzer et al. 2009). Additionally, this information can be used to evaluate potential shifts in patterns of habitat use by fishes in response to physicochemical variables, including DO (i.e. hypoxia; Switzer et al. 2009, 2015). We chose a 50% DO saturation level instead of the 2.0 mg l⁻¹ threshold typically used when defining hypoxia in aquatic environments (Breitburg 2002, Eby & Crowder 2002, Vaquer-Sunyer & Duarte 2008). We chose this standard because many fishes exhibit sub-lethal reactions, such as increased ventilation rates and decreased growth around 50% DO saturation (Breitburg 2002 and references therein), and avoid these conditions when possible (Howell & Simpson 1994, Eby & Crowder 2002, Vanderploeg et al. 2009).

Because of the complex structure of the water column around platforms, salinity, temperature, and DO were plotted by depth for all hydrographic profiles, and all major and minor haloclines, thermoclines, and oxyclines were identified (Fig. 2). This approach partitioned the water column into 2 to 8 distinct layers of varying vertical extent (strata) at each platform for 684 total strata among the 150 platforms analyzed. Environmental variation within each stratum

was minimal and so a single point was used to characterize the conditions occurring throughout its vertical extent. Frequency distributions of the summed extent of all water-column strata (in vertical meters) falling within the assigned ranges were created for salinity, temperature, DO, water depth, and Secchi depth to account for both lateral and vertical gradients and represent the habitat availability associated with each variable in 3 dimensions.

At platforms, species distributions often occurred across multiple vertical strata. In order to account for this and to determine how fishes were distributed over the larger environmental gradients occurring across all 684 strata, patterns of habitat use were described by weighted occurrences based on the relative abundance estimates of fishes at each platform (MAXNOs). Since MAXNO estimates could not be made for each individual stratum without potentially double counting individuals, proportional use was assumed for all strata in a water column, excluding strata that were clearly being avoided. Proportional MAXNOs were calculated by multiplying the MAXNOs by the fraction of the water column represented by each stratum not being avoided. Species-specific habitat use for each variable was represented by frequency distributions of the summed extent of all occupied strata (m). This approach provided a conservative microhabitat description (Baltz et al. 1993, Hurlbert 1981) of species-specific habitat suitability within a compressed water column that reflected weighted use patterns and described species responses along each environmental gradient.

This information was incorporated into a community microhabitat analysis evaluating the responses of the 26 species that were reliably detected and identified on video (all species with >10 observations and occurring at >5 platforms, see Supplement 1 at www.int-res.com/articles/suppl/m608p199_supp/). Factor analysis was used to resolve 6 variables into 4 factors. The variables included in the analysis were: salinity, temperature, DO, Secchi depth, water depth, and the extent of habitat compression (based on the number of vertical meters of the water column that fishes were not avoiding). A varimax rotation was used to scale orthogonal, multivariate factors relative to one another and to create a 3-dimensional environmental space useful for comparing patterns in the species-specific distributions relative to water quality. Factor centroids were weighted by abundances for 26 species each in the presence and absence of hypoxia. Centroids were plotted as bubbles representing 2 SE radii around the centroid means. Non-overlapping error bubbles suggested significant differences in habitat selection

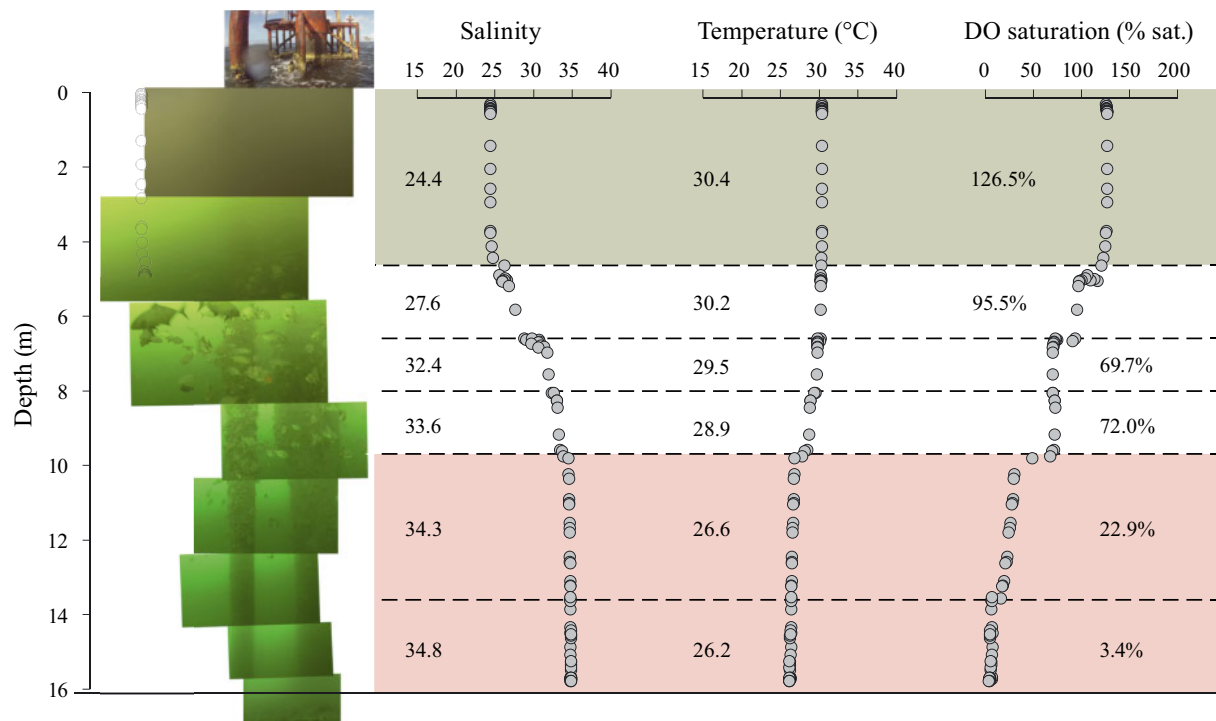


Fig. 2. Scaled photo-collage reconstruction of the submerged structure of platform ST 21-GC, recorded 20 August 2014. Plotted to the right are continuous salinity, temperature and DO profiles by depth relative to vertical fish distributions. Grey circles show individual YSI water quality sonde readings. Dashed lines indicate partitioned layers of the water column within which environmental readings were assumed constant in the analyses. Pink and green shading indicate layers of avoidance, while unshaded layers were used by fishes. Note: fishes present in images within the shaded layers were following the camera array. See Video S1 in Supplement 2 at www.int-res.com/articles/suppl/m608p199_supp/

among fishes in the presence and absence of hypoxia. In addition, the position of the weighted centroid means indicated the ways in which fish distributions varied with regard to the 6 physicochemical variables included in the 4 factors.

Habitat suitability indices (HSIs) were plotted for the 11 species that together composed >96% of the total number of fishes observed: Atlantic bumper *Chloroscombrus chrysurus* (~56%), Atlantic spadefish *Chaetodipterus faber* (~18%), blue runner *Caranx crysos* (~9%), bluefish *Pomatomus saltatrix* (~4%), sheepshead *Archosargus probatocephalus* (~3%), gray snapper *Lutjanus griseus* (~2%), sergeant major *Abudefduf saxatilis* (~1%), Bermuda chub *Kyphosus sectatrix* (<1%), young-of-the-year (YOY) greater amberjack *Seriola dumerili* (<1%), gray triggerfish *Balistes capricus* (<1%), and adult red snapper *Lutjanus campechanus* (<1%). Suitability plots were constructed for each of 5 environmental gradients (salinity, temperature, DO, Secchi depth, and water depth) in the presence and absence of hypoxia. Also indicated within each plot is the overall suitability calculated for fishes in the presence and absence of hypoxia. Habitat suitability (S) was calculated within

each interval of the smoothest possible habitat availability frequency curve following: $S = P(E | F) / P(E)$. P is the probability of a value of an environmental variable, E , given the presence of fish, F , in that interval, and $P(E)$ is the probability of a value of an environmental variable in that interval regardless of the presence of fish. The terms $P(E | F)$ and $P(E)$ represent the relative frequency distributions of fish occurrence and of environmental conditions for all samples, respectively (Baltz 1990). Raw suitability was normalized to 1 by dividing each interval value by the greatest suitability value for a given distribution.

2.4. Statistical models

We tested for significant shifts ($\alpha = 0.10$) in habitat suitability during the presence and absence of hypoxia using generalized linear mixed models (GLMMs) following Switzer et al. (2015). Combining GLMMs and HSI provides an analysis that indicates environmental drivers of fish habitat selection and describes the magnitude of variation between habitat selection comparisons. The response variable was the

MAXNO-derived relative abundance of each species, fit as lognormal distributions. Explanatory variables were fixed effects for hypoxia (presence vs. absence) and year (2013 vs. 2014), and continuous variables for salinity, temperature, DO, depth, and Secchi depth, and first-order interactions among all the continuous environmental variables and the presence of hypoxia. We also used a covariate to adjust for effort (SAS 9.4 Proc GLIMMIX). Sites were designated as repeated measures subjects to account for the clustered structure of the data (Breslow & Day 1980) and to preclude pseudo-replication (Hurlbert 1984). Additionally, denominator degrees of freedom were conservatively downscaled by fixing them at 126 for each term in the model, despite the repeated blocking structure. All other assumptions were met, and there was no indication of multicollinearity among environmental variables.

The extent of habitat compression from avoidance of the bottom-water hypoxic and surface strata was evaluated regionally at all hypoxic sites, including sites where videos were not used in analyses due to inadequate visibility ($n = 131$ of 343 water quality profiles) across the entire Louisiana coast for areas designated as East, Central, and West nearshore regions (Fig. 1), by dominant sediment types of sand (majority composition $\geq 63 \mu\text{m}$) or mud (majority composition $< 63 \mu\text{m}$), and by year (2013 and 2014). Regional and sediment type comparisons were based on Munnelly (2016), and sediment composition data was from IN-STAAR (2011). A 3-way ANCOVA compared region, dominant sediment type, and year ($\alpha = 0.05$), and included first-order interactions, and a covariate for depth, fit as a negative binomial distribution (SAS 9.4 Proc GLIMMIX). Tukey-Kramer post hoc adjustments were used for comparing significant interactions.

3. RESULTS

3.1. Observations

Video and diver observations suggested that fishes avoided water with low and high DO concentrations. All fishes observed near small platforms in nearshore Louisiana waters generally avoided strata with DO $< 50\%$

saturation, which occurred at 64 platforms. Included among these fishes were the small, cryptic species or early life stages that we regularly observed while diving (see Munnelly 2016 for a complete list). Additionally, fishes avoided surface strata ($3.5 \pm 0.3 \text{ m}$ thickness; means $\pm 95\%$ CI) of 46 of the platforms that were often turbid ($1.6 \pm 0.2 \text{ m}$ Secchi depth) and DO supersaturated, or hyperoxic ($140.7 \pm 7.0\%$ saturation). Fish distributions were, therefore, often compressed into midwater strata. Under low-DO conditions, YOY lane snapper *Lutjanus synagris* and *L. campechanus* were regularly displaced from their strong association with the bottom to a strong association with the platform jacket higher in the water column (Fig. 3D, Video S2). Similarly, southern stingray *Dasyatis americana*, red drum *Sciaenops ocellatus*, and black drum *Pogonias cromis* were observed as high as 4.7, 3.7, and 3.7 m, respectively, off the bottom and into waters $\geq 50\%$ DO saturation when low-DO bottom conditions were present. Conversely, species with strong associations with the more structurally complex platform features near the surface, including *Kyphosus sectatrix* and *Abudefduf saxatilis*, also moved down in the water column to depths immediately underlying surface strata. Fishes, in-

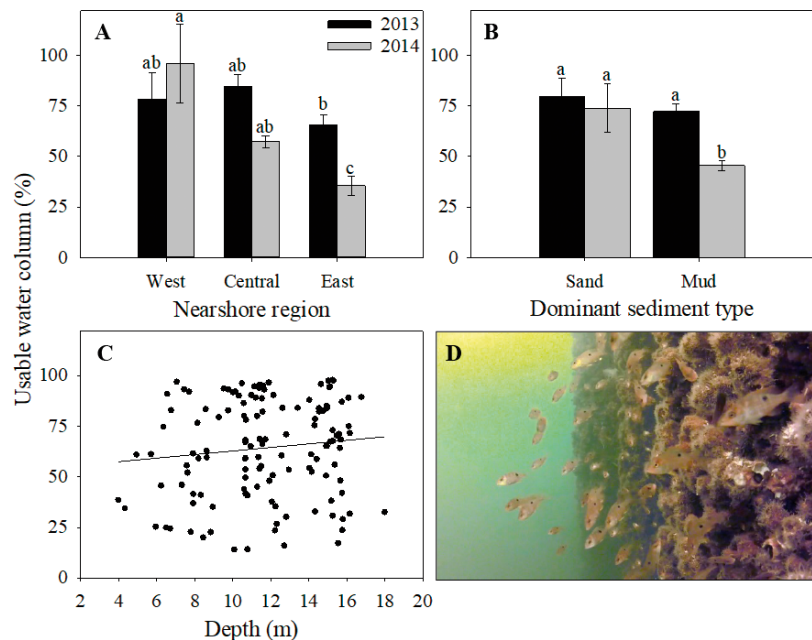


Fig. 3. Comparisons of the vertical extent of the fraction of the nearshore water column used by fishes for (A) all hypoxic sites ($n = 131$). Comparisons across nearshore Louisiana included significant effects of region (West, Central, and East); (B) dominant sediment type (sand or mud), year (2013 and 2014; A,B); and (C) depth. Bars represent 1 SE, and significant differences occurred between groups not sharing a letter. (D) Video frame showing young-of-the-year red and lane snapper up in the water column at nearshore platform SS 93-66 in response to hypoxic bottom conditions on August 21, 2014. The snapper were feeding in the current. See Video S2 in Supplement 2

cluding *Archosargus probatocephalus* and *L. griseus*, were occasionally observed entering strata with <50% saturation but these fishes were usually alone and MAXNOs were never obtained from strata with DO <50% saturation.

3.2. Habitat compression

The extent of habitat compression associated with the avoidance of hypoxia and surface strata varied significantly across nearshore Louisiana by region ($F_{2,122} = 6.64$, $p = 0.002$), dominant sediment type ($F_{1,122} = 5.01$, $p = 0.027$), year ($F_{1,122} = 12.15$, $p < 0.001$), and depth ($F_{1,122} = 27.37$, $p < 0.001$), and there was a significant region \times year interaction ($F_{2,122} = 9.47$, $p < 0.001$), and a significant dominant sediment type \times year interaction ($F_{1,122} = 6.21$, $p = 0.014$). Habitat compression was greater in 2014 than 2013, particularly in the East region (Fig. 3A; see Fig. 1 for regional boundaries), and greater over muddy sediments than over sand (Fig. 3B). In both years, there was a trend of decreasing habitat compression from east to west (Fig. 3A) and as water depth increased (Fig. 3C).

When habitat use was restricted due to avoidance of surface strata and DO-depleted bottom waters, GLMMs identified the physicochemical variables that fishes responded to, after accounting for year and effort (Table 1). Significant interaction terms involving hypoxia and other environmental variables indicated shifts in habitat use in the presence of hypoxia. Interactions between hypoxia and at least 1 other environmental variable significantly influenced the distributions of the 11 most abundant species.

3.3. Microhabitat factor analysis and habitat suitability indices

The factor analysis resolved 6 variables into 4 factors that together explained 90.72% of the environmental variation (Table 2). Factor 1 included increasing DO and decreasing salinity, which typified the upper water column strata. Factor 2 included increasing Secchi depth and increasing temperature, which most often reflected increasing distance from the Mississippi and Atchafalaya river deltas. Factor 3 was simply increasing depth, and Factor 4 was simply increasing habitat compression due to bottom-hypoxia and surface-strata avoidance. Factors 3 and 4 had identical eigenvalues and are interchangeable for interpretations when plotted against Factors 1 and 2 in 3 dimensions, explaining a cumulative 72.72% of the

Table 1. Generalized linear mixed model results for the physicochemical responses of the 11 dominant species comprising the nearshore Louisiana platform fish assemblage (n in parentheses). See Supplement 1 for full species names. Analyses were based on 684 water column layers at 150 platforms. Hypoxia is defined as bottom dissolved oxygen (DO) <50% saturation (n = 64). Denominator degrees of freedom were fixed at 126 for all analyses. * indicates significance of F-ratios at $\alpha = 0.10$ for variable \times hypoxia interactions. Temp = temperature

Environmental variable	<i>C. chrysurus</i> (17 261)	<i>C. faber</i> (5418)	<i>C. crysos</i> (2605)	<i>P. saltatrix</i> (1240)	<i>A. probatocephalus</i> (840)	<i>L. griseus</i> (708)	<i>A. saxatilis</i> (414)	<i>K. sectatrix</i> (295)	<i>S. dumerili</i> (263)	<i>B. capricornis</i> (254)	<i>L. campechanus</i> (252)
Salinity	F 0.02 p 0.881	8.78 0.004	0.00 0.956	2.00 0.160	4.23 0.042	0.48 0.492	8.78 0.004	04.02 0.047	0.81 0.371	0.25 0.620	0.31 0.580
Temp	F 1.09 p 0.299	3.26 0.074	0.01 0.907	1.50 0.222	03.01 0.085	0.02 0.876	3.26 0.074	1.53 0.219	0.31 0.576	2.19 0.141	0.32 0.575
DO	F 0.02 p 0.875	1.13 0.074	0.02 0.875	0.00 0.972	0.23 0.635	0.72 0.398	1.13 0.290	0.13 0.721	0.00 0.982	0.86 0.356	0.91 0.342
Depth	F 8.43 p 0.004	3.88 0.290	0.26 0.614	1.73 0.191	8.39 0.005	1.13 0.290	3.88 0.051	1.64 0.203	14.85 <0.001	4.01 0.048	0.00 0.980
Secchi	F 7.16 p 0.008	3.41 0.067	0.12 0.727	0.06 0.810	0.00 0.981	0.49 0.486	3.41 0.067	0.37 0.542	1.31 0.254	0.70 0.406	16.71 <0.001
Hypoxia	F 12.42 p 0.001	0.00 0.981	0.55 0.461	0.13 0.718	0.92 0.339	5.67 0.019	0.00 0.981	0.82 0.367	5.60 0.020	0.24 0.626	3.87 0.051

Table 1 continued on next page

Table 1 (continued)

Environmental variable	<i>C. chrysurus</i> (17 261)	<i>C. faber</i> (5418)	<i>C. crysos</i> (2605)	<i>P. saltatrix</i> (1240)	<i>A. probatocephalus</i> (840)	<i>L. griseus</i> (708)	<i>A. saxatilis</i> (414)	<i>K. sectatrix</i> (295)	<i>S. dumerili</i> (263)	<i>B. capricus</i> (254)	<i>L. campechanus</i> (252)
Year	<i>F</i> 33.33 <i>p</i> <0.001	16.11 <0.001	2.98 0.087	1.14 0.288	27.28 <0.001	25.28 <0.001	16.11 <0.001	12.07 0.001	2.25 0.136	6.22 0.014	3.42 0.067
Effort	<i>F</i> 0.98 <i>p</i> 0.324	0.09 0.762	1.25 0.266	0.79 0.376	3.94 0.049	8.46 0.004	0.09 0.762	0.03 0.856	2.08 0.152	0.09 0.770	7.49 0.007
Salinity × Temp	<i>F</i> 0.28 <i>p</i> 0.599	5.18 0.025	0.05 0.829	0.112 0.292	1.32 0.253	0.38 0.539	5.18 0.025	5.63 0.019	2.28 0.134	0.17 0.683	0.36 0.548
Salinity × DO	<i>F</i> 0.08 <i>p</i> 0.775	1.60 0.208	0.75 0.387	0.02 0.901	0.11 0.739	0.112 0.291	1.60 0.208	0.05 0.823	0.34 0.560	0.06 0.813	0.16 0.693
Salinity × Depth	<i>F</i> 0.58 <i>p</i> 0.446	14.50 <0.001	0.28 0.595	1.12 0.291	9.40 0.003	0.57 0.452	14.50 <0.001	2.30 0.132	15.23 <0.001	0.04 0.837	0.23 0.635
Salinity × Secchi	<i>F</i> 4.09 <i>p</i> 0.045	9.81 0.002	0.82 0.367	5.69 0.019	4.43 0.037	0.38 0.536	9.81 0.002	0.05 0.826	0.05 0.825	0.74 0.392	0.03 0.863
Temp × DO	<i>F</i> 0.16 <i>p</i> 0.693	1.43 0.235	0.01 0.940	0.06 0.807	0.16 0.685	1.54 0.217	1.43 0.235	0.00 0.959	0.07 0.790	0.59 0.443	0.54 0.465
Temp × Depth	<i>F</i> 11.25 <i>p</i> 0.001	0.45 0.503	0.36 0.549	1.64 0.203	4.92 0.028	0.65 0.421	0.45 0.503	0.50 0.480	9.91 0.002	8.22 0.005	0.42 0.519
Temp × Secchi	<i>F</i> 9.41 <i>p</i> 0.003	0.05 0.818	0.23 0.633	0.11 0.741	4.44 0.037	0.68 0.411	0.05 0.818	1.10 0.295	2.02 0.158	7.00 0.009	25.70 <0.001
DO × Depth	<i>F</i> 0.06 <i>p</i> 0.807	9.59 0.002	0.87 0.353	0.51 0.476	0.89 0.347	2.45 0.120	9.59 0.002	2.19 0.142	0.16 0.694	0.73 0.395	0.09 0.767
DO × Secchi	<i>F</i> 2.42 <i>p</i> 0.122	15.93 <0.001	0.71 0.400	1.75 0.188	15.65 <0.001	0.25 0.615	15.93 <0.001	0.07 0.786	1.54 0.216	7.27 0.008	6.78 0.010
Depth × Secchi	<i>F</i> 19.90 <i>p</i> <0.001	1.66 0.200	0.96 0.330	10.16 0.002	5.98 0.016	3.84 0.052	1.66 0.200	0.27 0.608	0.13 0.723	2.80 0.097	3.90 0.051
Salinity × Hypoxia	<i>F</i> 0.77 <i>p</i> 0.382	0.99 0.323	0.15 0.701	0.30 0.585	1.85 0.177	2.25 0.136	0.99 0.323	1.07 0.303	7.70* 0.006	3.90* 0.051	3.43* 0.067
Temp × Hypoxia	<i>F</i> 25.89* <i>p</i> <0.001	1.57 0.212	0.23 0.635	0.96 0.328	0.08 0.779	9.09* 0.003	1.57 0.212	0.36 0.550	3.74* 0.055	0.76 0.385	0.80 0.373
DO × Hypoxia	<i>F</i> 8.05* <i>p</i> 0.005	4.34* 0.039	0.03 0.861	0.31 0.577	2.48 0.118	1.77 0.185	4.34* 0.039	1.77 0.186	1.92 0.168	7.70* 0.006	4.31* 0.040
Depth × Hypoxia	<i>F</i> 0.56 <i>p</i> 0.455	0.06 0.808	11.39* 0.001	0.36 0.552	4.70* 0.032	0.07 0.787	0.06 0.808	4.04* 0.047	2.00 0.160	2.44 0.121	3.43* 0.067
Secchi × Hypoxia	<i>F</i> 9.26* <i>p</i> 0.003	6.44* 0.012	4.35* 0.039	8.38* 0.005	0.65 0.423	25.14* <0.001	6.44* 0.012	0.17 0.680	1.05 0.307	4.15* 0.044	6.58* 0.012

Table 2. Rotated factor loadings of 6 variables. The sign of each loading indicates whether variables are increasing or decreasing, while the magnitude indicates the strength of contribution to each factor. Underlines indicate the loadings used to guide interpretations about the system as described by these variables. var. expl.: variance explained

Environmental variable	Factor 1	Factor 2	Factor 3	Factor 4
DO	<u>0.91</u>	-0.06	0.07	-0.26
Salinity	<u>-0.87</u>	-0.11	0.21	-0.22
Secchi	-0.22	<u>0.86</u>	0.06	-0.34
Temperature	0.48	<u>0.78</u>	-0.23	0.05
Depth	-0.08	-0.06	<u>0.94</u>	0.25
Compression	-0.04	-0.21	0.30	<u>0.89</u>
Eigenvalue	1.86	1.42	1.08	1.08
Percent of var. expl.	31.05	23.67	18.00	18.00
Cumulative var. expl.	31.05	54.72	72.72	90.72

total variance (Fig. 4). Most species distributions occurred in significantly different physicochemical conditions when compared at platforms in waters above and below 50% DO saturation. For many fishes, habitat shifts due to hypoxia were greater within species than were interspecific differences at platforms in waters above or below 50% DO saturation. The gen-

eral trend for most species was an increased loading on factors 1, 3, and 4 in the presence of hypoxia. Thus, in general, the fish assemblages selected fresher, more highly oxygenated waters, in addition to occupying waters with a greater water depth as habitat compression increased. These shifts were, however, species specific, and the change in the centers of abundance relative to one another suggested that assemblage-level shifts in community structure occurred between comparisons.

Finally, the HSI plots show the magnitude of change in habitat selection in the presence and absence of hypoxia occurring within the near-shore part of the hypoxic zone without modeling other effects. Availability is expressed in meters (m) and reflects the cumulative vertical extent of all 684 layers as if stacked atop one another. In many cases, HSI plots in the presence and absence of hypoxia differed substantially; however, the range of tolerance for every species was wide (Figs. 5–9).

Results from the HSI analysis are best interpreted when compared with the significant interaction terms (p-values <0.10) between hypoxia and other environmental variables from the GLMMs. These significant

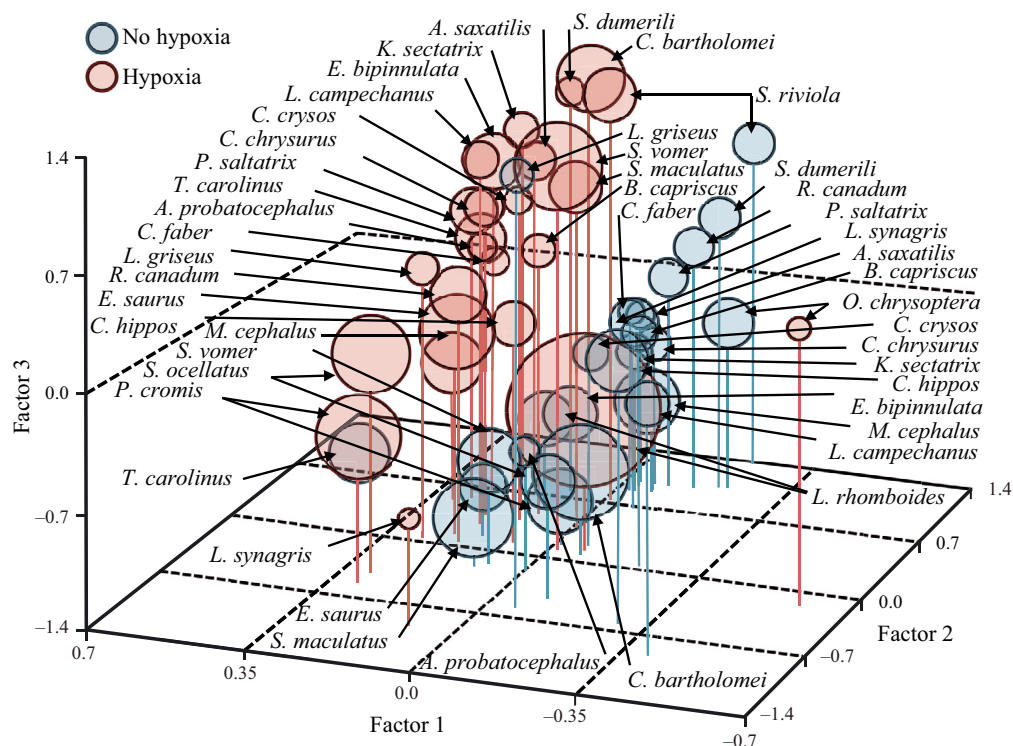


Fig. 4. Microhabitat plot describing the environmental use patterns of 26 species with respect to 3 principal component factors for (red) hypoxic (DO <50% saturation) and (blue) non-hypoxic water columns. Bubbles represent 2 SE around the centroid means for each species. See Supplement 1 for full species names

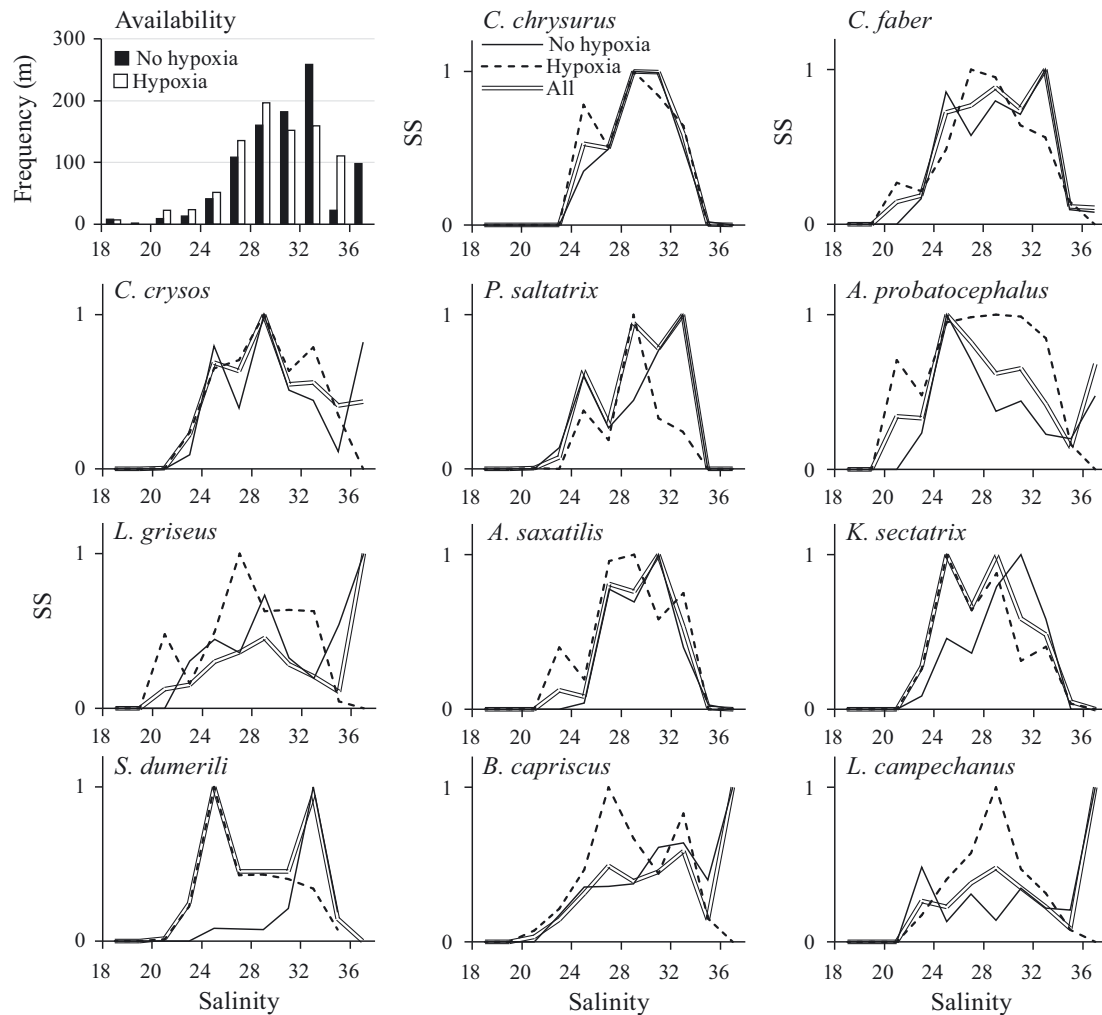


Fig. 5. Standardized suitability (SS) of 11 species responses to salinity. See Supplement 1 for full species names. Overall suitability is described by solid double-lines, while solid single-lines reflect responses at non-hypoxic sites, and broken lines reflect responses at hypoxic sites. Availability (top left panel) is shown as a frequency distribution of the summed extent of water column strata (m) within each salinity interval

interactions indicate that the effects of hypoxia and those of the additional variable were not independent. For example, there were significant shifts in salinity selection in the presence of hypoxia. Based on the significant salinity \times hypoxia interactions (Table 1), the -10 salinity unit shift in the peak frequency of the salinity selected by *Balistes capricus* (Fig. 5) likely reflected the significantly different habitat selection of salinity in the presence of hypoxia ($p = 0.051$). Similarly, there was a -8 salinity unit shift in the salinity selected by *Seriola dumerili* and *L. campechanus* ($p = 0.006$ and 0.067 , respectively).

There were significant shifts in temperature selection in the presence of hypoxia. Significant temperature \times hypoxia interactions (Table 1) helped explain a $+10^{\circ}\text{C}$ shift in the peak frequency of the temperature selected by *L. griseus* ($p = 0.003$; Fig. 6). Similarly,

there was a -5°C shift in the temperature selected by *Chloroscombrus chrysurus* ($p < 0.001$). Finally, there was a -4°C shift in the temperature range selected by *S. dumerili* ($p = 0.055$).

There were significant shifts in DO selection in the presence of hypoxia. Significant DO \times hypoxia interactions (Table 1) helped explain a -30% shift in the peak frequency of the DO selected by *Chaetodipterus faber* and *B. capricus* ($p = 0.039$ and 0.006 , respectively; Fig. 7). Similarly, there was a $+15\%$ shift in the DO selected by *A. saxatilis* and *L. campechanus* ($p = 0.039$ and 0.040 , respectively). The significant DO \times hypoxia interactions for *C. chrysurus* ($p = 0.005$) did not lead to apparent shifts in DO selection.

There were significant shifts in water depth selection in the presence of hypoxia. Significant water

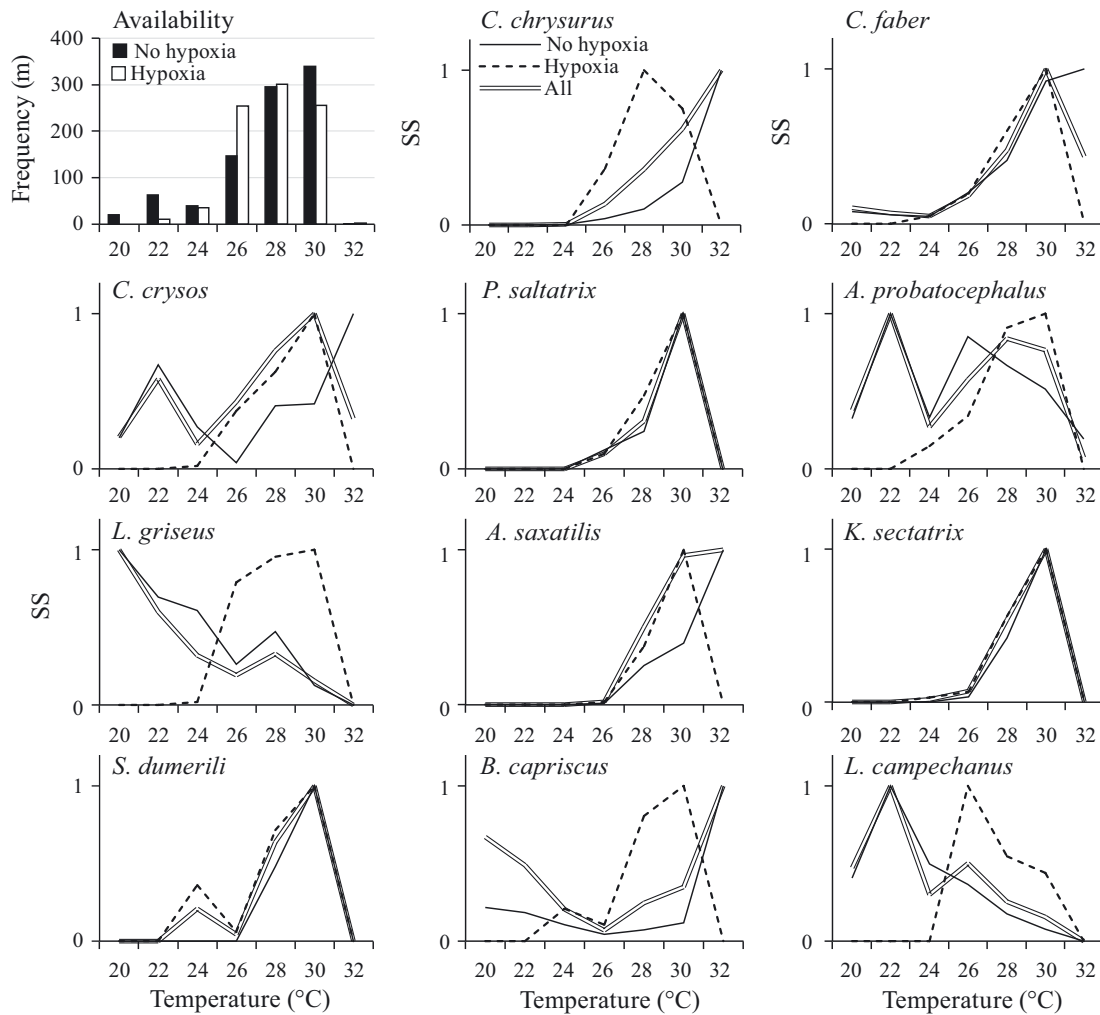


Fig. 6. Same as Fig. 5, but for temperature

depth \times hypoxia interactions (Table 1) helped explain +6 m and +2 m shifts in the peak frequency and range of water depth selection by *K. sectatrix* ($p = 0.047$; Fig. 8). Similarly, there were +2 m shifts in water depth selection by *L. campechanus* ($p = 0.067$). We also observed a –2 m shift in the peak frequency of water depth selected by *A. probatocephalus* ($p = 0.032$). Finally, there was a +4 m shift in the water depth range selected by *Caranx crysos* ($p = 0.001$).

There were significant shifts in surface-water clarity selection in the presence of hypoxia. Significant Secchi depth \times hypoxia interactions (Table 1) helped explain +1.5 m and –1.5 m shifts in the peak frequency and range of surface-water clarity selection by *Pomatomus saltatrix* ($p = 0.005$; Fig. 9). Similarly, there were +4.5 m and +1.5 m shifts in surface-water clarity selection by *L. campechanus* ($p = 0.005$). Also, a –1.5 m shift in the peak frequency of surface-water clarity selected by the planktivorous *C. chrysurus*

and *C. crysos* occurred ($p = 0.003$ and 0.039 , respectively). Although the peak frequency of surface-water clarity selected by *C. faber* remained consistent, waters with lower surface-water clarity were selected with greater frequency ($p = 0.012$). The significant Secchi depth \times hypoxia interactions for *L. griseus* ($p < 0.001$), *A. saxatilis* ($p = 0.012$), and *B. capricus* ($p = 0.044$) did not lead to apparent shifts in surface-water clarity selection.

4. DISCUSSION

Patterns of habitat selection by fishes that aggregate around small nearshore platforms in the nGOM are complex, especially because of the river discharges and the added effects of eutrophication and seasonal hypoxia. Eutrophication and hypoxia exert an influence on fishes throughout the water column,

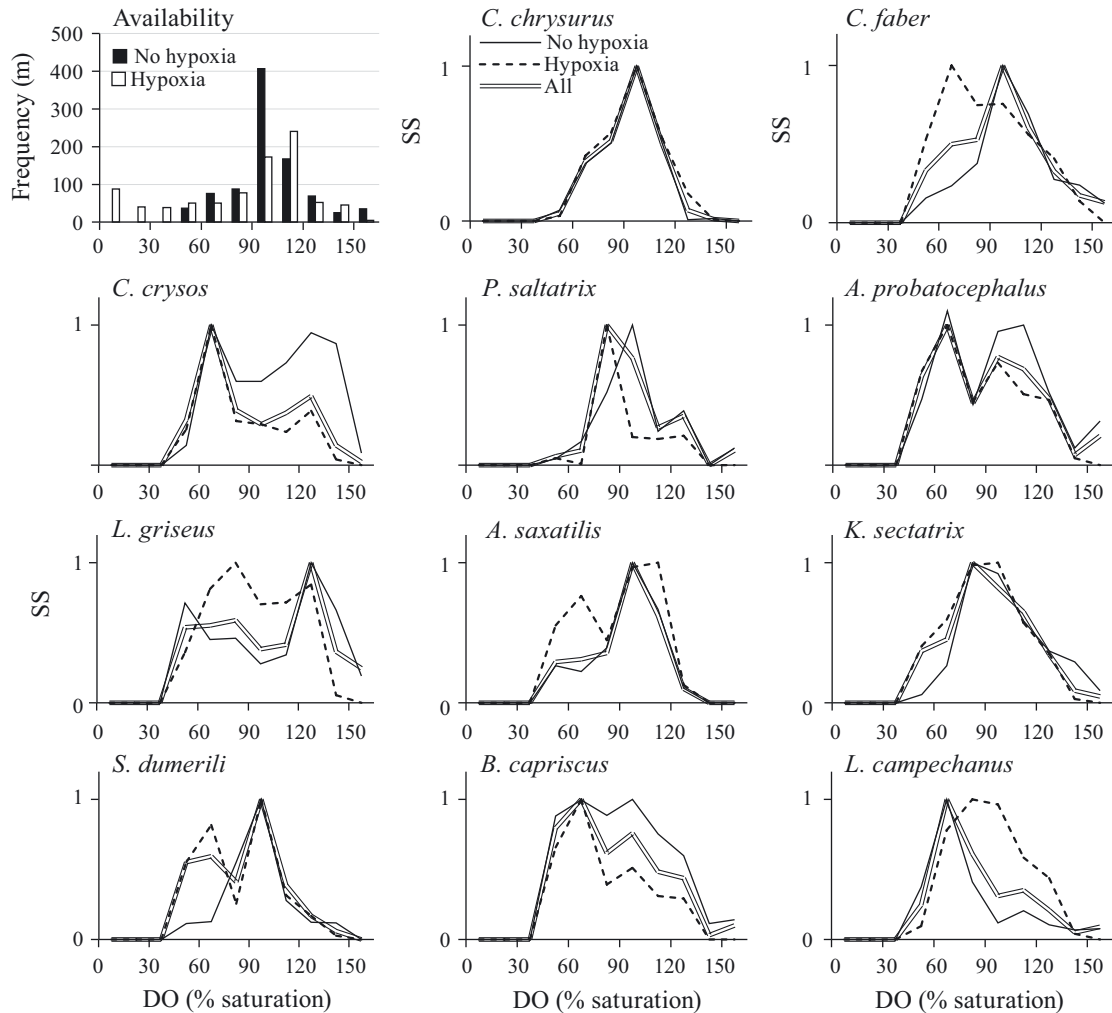


Fig. 7. Same as Fig. 5, but for dissolved oxygen (DO)

leading to habitat compression that limits access to the entire water column. During this study, DO reached concentrations where species-specific or life-history-stage tolerances were probably exceeded at high, as well as low tolerance levels. Habitat compression associated with the avoidance of hypoxic lower-water column strata and unsuitable surface strata significantly altered habitat selection for the most common fishes associated with near-shore platforms. Habitat compression also significantly shifted the assemblage structure of the fish community as a whole. This is an important finding given that physicochemical conditions and prey distributions are the primary factors determining species or life-stage distributions of fishes in dynamic estuarine environments (Remmert 1983, Baltz et al. 1993, 1998). Among the most important physicochemical variables structuring fish communities across marine–estuarine gradients are salinity (Gun-

ter 1961, Rakocinski et al. 1992), temperature (Rakocinski et al. 1992, Szedlmayer & Able 1996), DO (Rakocinski et al. 1992), water depth (Rakocinski et al. 1992), and water clarity (Blaber & Blaber 1980, Cyrus & Blaber 1992). At small nearshore platforms, shifts in habitat-selection patterns of up to 10 salinity units, 10°C, 30% DO saturation, 6 m water depth, and 4.5 m Secchi depth were observed when fishes were forced into midwater strata because of the need to avoid hypoxic lower water-column strata and unsuitable surface strata. On a community level intraspecific shifts in habitat selection in the presence of hypoxia were, in many cases, greater than those between species distributions, given the same habitat availability.

During the 2 yr that we observed fishes around platforms, we never saw any evidence of direct lethal effects of coastal hypoxia on fishes. However, the distributional responses of fishes within this DO-

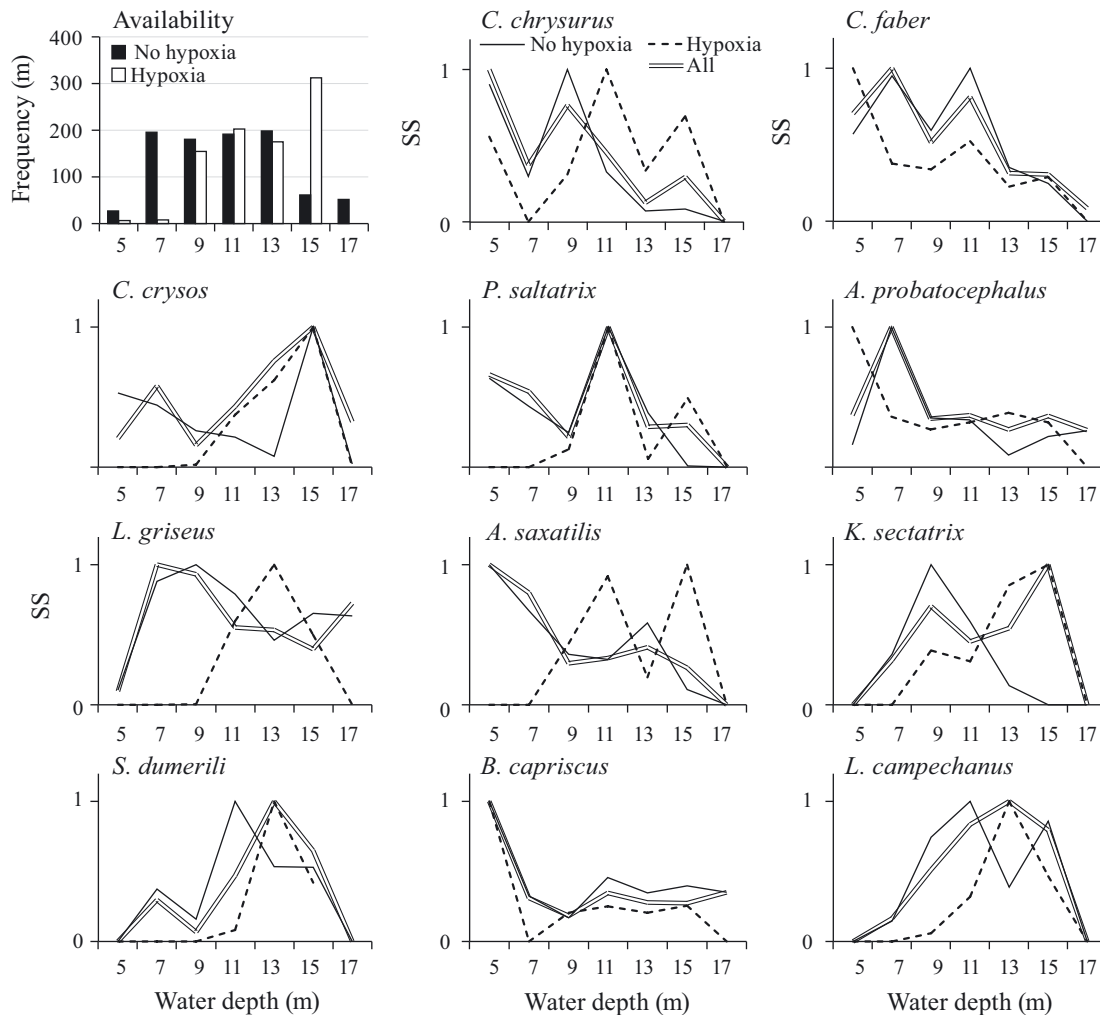


Fig. 8. Same as Fig. 5, but for depth

stressed environment demonstrated that sub-lethal effects of eutrophication might have important consequences. Several studies reported altered metabolic and growth rates associated with salinity (Lankford & Targett 1994, Bœuf & Payan 2001, Sampio & Bianchini 2002) and temperature variation (Wuenschel et al. 2004, Craig & Crowder 2005) within the range of environmental conditions that platform-associated fishes experienced when forced to avoid hypoxic lower water-column strata and surface strata. Altered reproductive potential within the nGOM hypoxic zone has also been documented (Thomas & Rahman 2010, 2012), and models have shown that the combined effects of temperature and reduced reproductive potential can have substantial negative effects on the long-term stability of displaced fish populations (Rose et al. 2018a,b).

Displacement of fishes or their prey due to environmental factors can also alter direct and indirect

trophic interactions (Keister et al. 2000, Webster et al. 2015). Distributions of prey are greatly influenced by eutrophication (Dagg & Breed 2003) and hypoxia (Pihl 1994, Briggs et al. 2017). Fishes might remain in areas they would otherwise leave in order to exploit emerging benthic prey or leave areas they might otherwise occupy due to depletion of prey during a persistent event (Pihl et al. 1991, Rahel & Nutzman 1994). Pelagic and planktivorous fishes within the hypoxic zone might benefit from the concentration of zooplankton biomass (Dagg & Breed 2003, Glaspie et al. 2018) and increased predator-prey interactions that occur when water column habitats are compressed by hypoxia (Prince & Goodyear 2006, Costantini et al. 2008, Roman et al. 2012). There is also evidence that areas fishes avoid can serve as a refuge for prey (Zhang et al. 2009, Kimmel et al. 2010, Webster et al. 2015), resulting in predator and prey spatial disconnects (Taylor & Rand 2003, Ludsin et al. 2009,

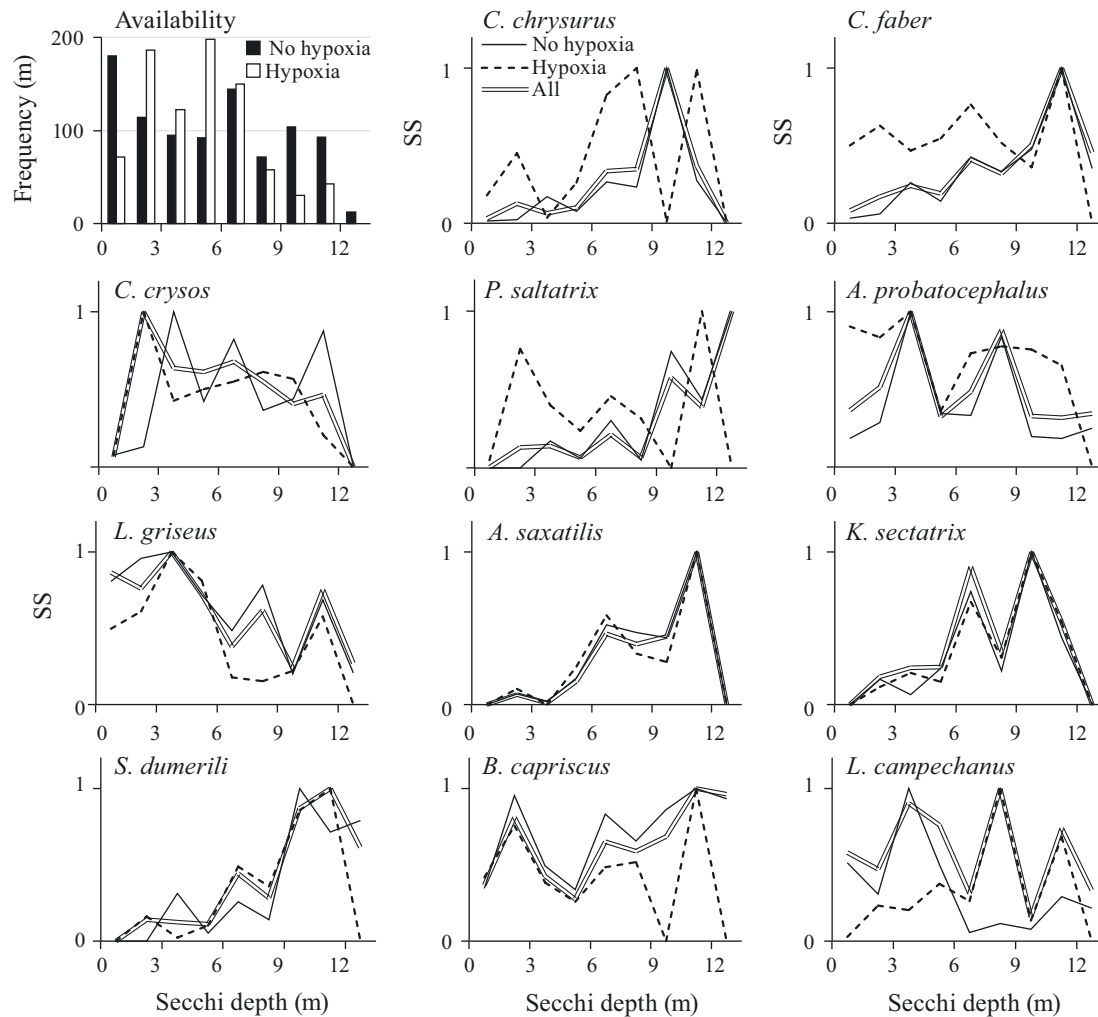


Fig. 9. Same as Fig. 5, but for Secchi depth

Vanderploeg et al. 2009). Habitat compression may also increase interspecific and intraspecific interactions when high densities of fishes become restricted by physiological demands (Coutant 1985, Eby & Crowder 2002, Dieterich & Fulford 2012). Further, displacement of fishes can alter fishing effort, and therefore impact fisheries, and management decisions (Craig & Crowder 2005, Langseth et al. 2014, Kraus et al. 2015).

Because of the large-scale perturbations that occur when bottom-water hypoxia forms in the nGOM, habitat selection in the absence of hypoxia might not mirror behavior patterns of the same fishes outside of the hypoxic zone. The overall suitability for each species (Figs. 5–9) describes habitat selection occurring within the hypoxic zone during the hypoxic season. These patterns might be useful for comparing selection from the same area pre- and or post-hypoxia, among years of varying hypoxia severity, or those

generated from other areas not influenced by a large region of depressed-DO concentrations. Also, if the avoidance of surface strata was caused by supersaturated DO, this restriction might be limited to part of the day when oxygen production was excessive.

When evaluating the effects of hypoxia on aquatic organisms, the threshold used to define hypoxia should carefully reflect the study objectives. We selected 50% DO saturation as the break point for our analyses because fishes were observed to avoid waters with <50% DO saturation, and a primary objective was to evaluate some of the effects of displacement by fishes capable of moving up in the water column. In a 3-dimensional environmental space as dynamic as nearshore Louisiana, this definition of hypoxia for fishes provides important habitat-selection information that would be lost if the 2.0 mg l⁻¹ standard had been used. Although some fishes were occasionally observed in waters <50% DO sat-

uration (and $<2.0 \text{ mg l}^{-1}$), they did not remain there for long, and MAXNOs for all species were always obtained in DO saturations $\geq 50\%$. *Archosargus probatocephalus* and *Lutjanus griseus* were regularly observed entering waters $<50\%$ saturation, a behavior consistent with previously observed forays into hypoxic water (Pihl et al. 1991, Rahel and Nutzman 1994, Webster et al. 2015). This behavior may also reflect physiologies of these species that make them more tolerant of low DO, but oxygen tolerances have not been established for these species.

Avoidance of surface strata was an unexpected finding which we cannot attribute to any one variable with absolute certainty. However, fishes often avoided surface strata despite otherwise suitable salinities, temperatures, and water clarity. The avoidance might have been caused by complex interactions among these and other abiotic or biotic factors which we did not measure, such as light availability, or predator–prey dynamics. However, the presence of supersaturated DO conditions (hyperoxia) was a variable observed at all sites where fishes avoided the surface-strata (mean DO of $140.7 \pm 7.0\%$ saturation [95 % CI]). Consequently, the scarcity of fishes in waters of DO $>125\%$, and the lack of any fishes detected in waters of DO $>140\%$ saturation, strongly suggest that DO supersaturation was the factor driving the observed avoidance behavior.

Although it is rarely documented in natural systems, supersaturation of atmospheric gases (nitrogen and oxygen) can cause gas bubble disease in fish (Gorham 1899, Marsh & Gorham 1905). Gas-supersaturated environments can cause diffusion of gases into body tissues, which can cause internal and external lesions, disrupt buoyancy control, and, if persistent, can fatally reduce circulation. Nitrogen has a more potent effect than oxygen supersaturation (Nebeker et al. 1978), while total gas pressure is the most important factor controlling gas bubble disease (Colt 1983).

Many aquatic organisms respond negatively to oxygen supersaturation (Nebeker et al. 1978). In tropical and subtropical marine environments surface waters are naturally slightly supersaturated with nitrogen (Emerson et al. 1995). Consequently, the total gas pressure found there is often high, a situation that could amplify the effects of photosynthetically derived oxygen supersaturation (Crunkilton et al. 1980). However, dissolved nitrogen was not measured during this study, and variation in total gas pressure throughout surface waters of the nGOM has not been documented.

Nevertheless, avoidance of supersaturated waters has been previously documented at levels of $\sim 125\%$

gas saturation, so exclusion from the surface waters in the nGOM related to supersaturation of gases is a feasible explanation for the avoidance of surface strata (Gray & Haynes 1977, Nebeker et al. 1978, Chamberlain et al. 1980, Parker et al. 1984). Mortality is only a risk where fishes cannot avoid gas-supersaturated environments such as in aquaculture settings or below dams, where bubble injection or heating of water supersaturates waters with dissolved gases. Renfro (1963) reported a fish kill in Galveston Bay during 1959 of more than 300 adult spotted seatrout *Cynoscion nebulosus*, many Atlantic croaker *Micropogonias undulatus*, various eels, and other fishes. He attributed the kill to photosynthetically derived oxygen supersaturation of 250 % in shallow waters where fishes could not avoid these conditions. In our study, a total of 109 of the 343 water quality samples (including the 150 paired with video data) had surface strata with DO saturation $>125\%$, and, while uncommon, DO values upward of 295 % were recorded in near-shore waters of coastal Louisiana. However, in open-water environments such as nearshore Louisiana, these conditions are easily avoided by fishes, as was observed at 46 of the 150 platforms included in the analyses. As with hypoxia, the indirect effects of displacement, rather than direct mortality, have greater overall impact on mobile organisms like fishes because they can affect every fish that remains in the area of the hypoxic zone.

Video-based sampling provided information on the distribution and behavior of fishes at a scale not obtainable with other methods. While trawling studies have attempted to evaluate habitat compression due to hypoxia and the effects of displacement of fishes within the water column (Hazen et al. 2009), video provided the finer spatial resolution needed in near-shore Louisiana waters. Our sampling was based on discrete points with paired video and continuous water quality profiles with a mean reading every $0.08 \pm 0.0074 \text{ m}$ (95 % CI), allowing us to characterize species-specific selection patterns. Despite their advantages, even unbaited and unlighted video arrays can alter fish behavior, with some species being attracted and others repelled. Video methods are also vulnerable to poor visibility and large schools of fish, for which MAXNO-derived relative abundance estimates become non-linear relative to actual abundance (Schobernd et al. 2014, Campbell et al. 2015), and post processing of the data becomes labor intensive. Hydroacoustic methods are less intrusive than video cameras and complement visual studies because they can greatly expand the sampling area beyond the limitations of visibility and camera fields of

view (Stanley and Wilson 2004, Zenone et al. 2017, Reynolds et al. 2018). However, standard hydro-acoustic methods also have limitations, such as difficulty monitoring fish very close to boundaries (near bottom, hard objects or the water surface) plus the inability to definitively or reliably identify species directly. Future studies of biotic and environmental interactions in complex settings such as nearshore Louisiana and other river-influenced ocean margins could benefit from a combined video-hydroacoustic sampling approach that accounts for the high variation in water quality.

Unbaited remote video systems did allow the observation of some behaviors in a minimally invasive way and without the chaotic behavior that bait can cause. In 1 interesting video, habitat compression by surface strata with supersaturated DO of 172% restricted Spanish mackerel *Scomberomorus maculatus*, *Caranx crysos*, *Chloroscombrus chrysurus*, cobia *Rachycentron canadum*, red drum *Sciaenops ocellatus*, black drum *Pogonias cromis*, and age 1–2 juvenile *Lutjanus campechanus* to within 3.5 m of the well-oxygenated seafloor in a 9 m water column. The pelagic species appeared to be feeding at the lower edge of a phytoplankton bloom within the surface strata (a commonly observed behavior) and a school of *S. ocellatus* was observed in apparent pursuit of the vertically compressed, and exploitable school of *C. chrysurus*.

In the example illustrated in Fig. 2 (see Video S1 in Supplement 2), 10 species of pelagic and demersal fishes in a 15.9 m water column were restricted to 4.7 m at midwater. Fishes were compressed into ~30% of the entire water column by DO levels <23% saturation (1.5 mg l^{-1}) below and >126% saturation (8.3 mg l^{-1}) above. In another instance of more extreme compression, the fish assemblage was restricted within a 1.4 m layer of a 14.3 m water column, constrained by waters containing <32% DO saturation (2.5 mg l^{-1}) below and 204% DO saturation (15.2 mg l^{-1}) above. This assemblage consisted of high abundances of densely packed *Chaetodipterus faber*, *C. crysos*, *L. griseus*, and *A. probatocephalus* (73 total fishes). In the latter case, the salinity and temperature within the usable part of the water column, 23.1 salinity units and 31°C, were near or beyond the tolerance levels of many species in this study (Figs. 5 & 6).

Many fishes do not readily leave nearshore platforms in the face of extreme environmental change but continue their strong association with them (Reeves et al. 2018b). Such fidelity often comes at the cost of reduced habitat suitability. Reasons to stay may accrue from reduced predation risk (Rountree

1989), greater prey availability on the platform itself (Beaver 2002, Reeves et al. 2018a, Reeves et al. in press a,b), or in surrounding waters (Keenan et al. 2003), or the use of platforms as current breaks that allow fishes to remain in an area where they would otherwise struggle to maintain position. This observation supports the hypothesis that use of suboptimal habitat generally increases as availability of optimal habitat is decreased by DO restrictions (Eby 2001, Zhang et al. 2014). This pattern of behavior is consistent with optimization theory (Kramer 1987) which predicts that fishes will minimize energetic costs and risks of predation in order to select an adequate if suboptimal set of environmental conditions. Prince & Goodyear (2006) noted such a response in the form of an interplay of DO, temperature, depth, and predator–prey dynamics in Pacific pelagic fishes. Elliott et al. (2012) found a similar interaction in the responses of zooplankton to salinity and temperature in the presence of hypoxia.

A benefit of platforms is that their fish aggregating device effects facilitate study of detailed responses to extremes of hydrographic conditions that sometimes approach or exceed the tolerances of fishes when habitat compression creates ephemeral habitat bottlenecks. These responses would be far more difficult to document elsewhere within the hypoxic region where fish densities are low or unaggregated. At the current rate of platform removal from nearshore Louisiana (~180 platforms yr^{-1} net loss from 2008–2017; BOEM 2018), soon few will remain to serve this purpose and they may be gone before their ecological role is fully understood. The apparent absence of negative population-level effects on fishery landings within the hypoxic region of the nGOM suggests that degradation of suitable fish habitat has not been severe enough to limit populations of most species (Chesney & Baltz 2001, Cowan et al. 2008, Breitburg et al. 2009). Even the most severely restricted waters sampled during this study (that had acceptable visibility) were being used by fishes. Nevertheless, avoidance of hypoxic bottom waters and surface strata significantly influenced habitat-selection patterns and probably influenced the spatial distributions for the most common fishes. Habitat compression reduced the volume and quality of suitable habitat, where tolerances to some physicochemical variables were exceeded or suboptimal conditions were tolerated. Ultimately, the perturbed physicochemical conditions and the amplified inter- and intraspecific interactions strongly influence species and life-history stage distributions at shallow-water nearshore platforms throughout the hypoxic zone

during the summer season. Although complex, new tools and approaches are helping to understand the overall impact these interactions have on fishes of the region (Chesney & Baltz 2001).

Acknowledgements. This project was funded by the Bureau of Ocean Energy Management (N12AC00015) and supported by a match from the Louisiana Department of Wildlife and Fisheries for a companion project. The research took place at the Louisiana Universities Marine Consortium and Louisiana State University. We thank Bill Childress for his field assistance. Opinions, findings, conclusions, or recommendations expressed in this report are those of the authors and do not reflect the views of the State of Florida.

LITERATURE CITED

- Adamack AT, Rose KA, Cerco CF (2017) Simulating the effects of nutrient loading rates and hypoxia on bay anchovy in Chesapeake Bay using coupled hydrodynamic, water quality, and individual-based fish models. In: Justić D, Rose K, Hetland R, Fennel K (eds) Modeling coastal hypoxia. Springer, Cham, p 319–357
- Baltz DM (1990) Autecology. In: Schreck CB, Moyle PB (eds) Methods for fish biology. American Fisheries Society, Bethesda, MD, p 585–607
- ✦ Baltz DM, Jones RF (2003) Temporal and spatial patterns of microhabitat use by fishes and decapod crustaceans in a Louisiana estuary. *Trans Am Fish Soc* 132:662–678
- ✦ Baltz DM, Rakocinski C, Fleeger JW (1993) Microhabitat use by marsh-edge fishes in a Louisiana estuary. *Environ Biol Fishes* 36:109–126
- ✦ Baltz DM, Fleeger JW, Rakocinski C, McCall JN (1998) Food, density, and microhabitat: factors affecting growth and recruitment potential of juvenile saltmarsh fishes. *Environ Biol Fishes* 53:89–103
- Beaver CR (2002) Fishery productivity and trophodynamics of platform artificial reefs in the northwestern Gulf of Mexico. PhD dissertation, Texas A&M University, TX
- ✦ Blaber SJM, Blaber TG (1980) Factors affecting the distribution of juvenile estuarine and inshore fish. *J Fish Biol* 17: 143–162
- ✦ BOEM (Bureau of Ocean Energy Management) (2018) Platform structures online query. www.data.boem.gov/Main/Default.aspx (accessed 9 November 2015)
- ✦ Bøeuf G, Payan P (2001) How should salinity influence fish growth? *Comp Biochem Physiol C Toxicol Pharmacol* 130:411–423
- Bovee KD (1982) A guide to stream habitat analysis using the Instream Flow Incremental Methodology. IFIP No. 12 (FWS/OBS No. 82/26). US Fish and Wildlife Service, Washington, DC
- ✦ Breitburg D (2002) Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. *Estuaries* 25:767–781
- ✦ Breitburg DL, Rose KA, Cowan JH Jr (1999) Linking water quality to larval survival: predation mortality of fish larvae in an oxygen-stratified water column. *Mar Ecol Prog Ser* 178:39–54
- ✦ Breitburg DL, Craig JK, Fulford RS, Rose KA and others (2009) Nutrient enrichment and fisheries exploitation: interactive effects on estuarine living resources and their management. *Hydrobiologia* 629:31–47
- ✦ Breitburg DL, Levin A, Oschlies A, Grégoire M and others (2018) Declining oxygen in the global ocean and coastal waters. *Science* 359:eaam7240
- Breslow NE, Day NE (1980) Statistical methods in cancer research. I. Analysis of case control studies international agency for research in cancer. WHO for IARC, Geneva
- ✦ Briggs KB, Craig JK, Shivarudrappa S, Richards TM (2017) Macrobenthos and megabenthos responses to long-term, large-scale hypoxia on the Louisiana continental shelf. *Mar Environ Res* 123:38–52
- ✦ Campbell MD, Pollack AG, Gledhill CT, Switzer TS, DeVries DA (2015) Comparison of relative abundance indices calculated from two methods of generating video count data. *Fish Res* 170:125–133
- ✦ Chamberlain GW, Neill WH, Romanowsky PA, Strawn K (1980) Vertical responses of Atlantic croaker to gas supersaturation and temperature change. *Trans Am Fish Soc* 109:737–750
- Chesney EJ, Baltz DM (2001) The effects of hypoxia on coastal ecosystems. In: Rabalais NN, Turner RE (eds) Coastal hypoxia: consequences for living resources and ecosystems. Coastal and Estuarine Studies, Vol 58. American Geophysical Union, Washington, DC, p 321–354
- ✦ Chesney EJ, Baltz DM, Thomas RG (2000) Louisiana estuarine and coastal fisheries and habitats: perspectives from a fish's eye view. *Ecol Appl* 10:350–366
- ✦ Cochrane JD, Kelly FJ (1986) Low-frequency circulation on the Texas-Louisiana continental shelf. *J Geophys Res* 91: 10645–10659
- ✦ Colt JE (1983) The computation and reporting of dissolved gas levels. *Water Res* 17:841–849
- ✦ Costantini M, Ludsins SA, Mason DM, Zhang X, Boicourt WC, Brandt SB (2008) Effect of hypoxia on habitat quality of striped bass (*Morone saxatilis*) in Chesapeake Bay. *Can J Fish Aquat Sci* 65:989–1002
- ✦ Coutant CC (1985) Striped bass, temperature, and dissolved oxygen: a speculative hypothesis for environmental risk. *Trans Am Fish Soc* 114:31–61
- Cowan JH Jr, Grimes CB, Shaw RF (2008) Life history, history, hysteresis, and habitat changes in Louisiana's coastal ecosystem. *Bull Mar Sci* 83:197–215
- ✦ Craig JK (2012) Aggregation on the edge: effects of hypoxia avoidance on the spatial distribution of brown shrimp and demersal fishes in the Northern Gulf of Mexico. *Mar Ecol Prog Ser* 445:75–95
- ✦ Craig JK, Bosman SH (2013) Small spatial scale variation in fish assemblage structure in the vicinity of the northwestern Gulf of Mexico hypoxic zone. *Estuaries Coasts* 36:268–285
- ✦ Craig JK, Crowder LB (2005) Hypoxia-induced habitat shifts and energetic consequences in Atlantic croaker and brown shrimp on the Gulf of Mexico shelf. *Mar Ecol Prog Ser* 294:79–94
- ✦ Crunkilton RL, Czarnecki JM, Trial L (1980) Severe gas bubble disease in a warm water fishery in the midwestern United States. *Trans Am Fish Soc* 109:725–733
- ✦ Cyrus DP, Blaber SJM (1992) Turbidity and salinity in a tropical northern Australian estuary and their influence on fish distribution. *Estuar Coast Shelf Sci* 35:545–563
- ✦ Dagg MJ, Breed GA (2003) Biological effects of Mississippi River nitrogen on the northern Gulf of Mexico—a review and synthesis. *J Mar Syst* 43:133–152
- ✦ Diaz RJ, Rosenberg R (2008) Spreading dead zones and consequences for marine ecosystems. *Science* 321:926–929

- Dieterich JW, Fulford RS (2012) Habitat suitability modeling to evaluate conservation and enhancement efforts for Gulf-strain striped bass in Mississippi coastal rivers. *Trans Am Fish Soc* 141:731–746
- Eby LA (2001) Response of a fish community to frequent and infrequent disturbances in estuarine ecosystems. PhD dissertation, Duke University, Durham, NC
- Eby LA, Crowder LB (2002) Hypoxia-based habitat compression in the Neuse River estuary: context-dependent shifts in behavioral avoidance thresholds. *Can J Fish Aquat Sci* 59:952–965
- Elliott DT, Pierson JJ, Roman MR (2012) Relationship between environmental conditions and zooplankton community structure during summer hypoxia in the northern Gulf of Mexico. *J Plankton Res* 34:602–613
- Ellis DM, DeMartini ED (1995) Evaluation of a video camera technique for indexing abundances of juvenile pink snapper, *Pristipomoides filamentosus*, and other Hawaiian insular shelf fishes. *Fish Bull* 93:67–77
- Emerson S, Quay PD, Stump C, Wilbur D, Schudlich R (1995) Chemical tracers of productivity and respiration in the subtropical Pacific Ocean. *J Geophys Res* 100:15873–15887
- Gallaway BJ, Cole JG (1998) Cumulative ecological significance of oil and gas structures in the Gulf of Mexico: a Gulf of Mexico fisheries habitat suitability model. Phase 2 model description. No. PB-98-141443/XAB. LGL Ecological Research Associates, Bryan, TX
- Glaspie CN, Clouse MA, Adamack AT, Cha Y and others (2018) Effect of hypoxia on diet of Atlantic bumpers in the northern Gulf of Mexico. *Trans Am Fish Soc* 147:740–748
- Gray RH, Haynes JM (1977) Depth distribution of adult chinook salmon (*Oncorhynchus tshawytscha*) in relation to season and gas-supersaturated water. *Trans Am Fish Soc* 106:617–620
- Gunter G (1961) Some relations of estuarine organisms to salinity. *Limnol Oceanogr* 6:182–190
- Hazen EL, Craig JK, Good CP, Crowder LB (2009) Vertical distribution of fish biomass in hypoxic waters on the Gulf of Mexico shelf. *Mar Ecol Prog Ser* 375:195–207
- Hetland RD, DiMarco SF (2008) How does the character of oxygen demand control the structure of hypoxia on the Texas-Louisiana continental shelf? *J Mar Syst* 70:49–62
- Hondorp DW, Breitburg DL, Davies LA (2010) Eutrophication and fisheries: separating the effects of nitrogen loads and hypoxia on the pelagic-to-demersal ratio and other measures of landings composition. *Mar Coast Fish* 2:339–361
- Howell P, Simpson D (1994) Abundance of marine resources in relation to dissolved oxygen in Long Island Sound. *Estuaries* 17:394–402
- Hurlbert SH (1981) A gentle depilation of the niche: Dicean resource sets in resource hyperspace. *Evol Theory* 5:177–184
- Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecol Monogr* 54:187–211
- INSTAAR (Institute of Arctic and Alpine Research) (2011). Seafloor substrates griddings, Gulf of Mexico. University of Colorado, Boulder, CO
- Justić D, Rabalais NN, Turner RE, Wiseman WJ (1993) Seasonal coupling between riverborne nutrients, net productivity and hypoxia. *Mar Pollut Bull* 26:184–189
- Kautsky L, Kautsky N (2000) The Baltic Sea, including Bothnian Sea and Bothnian Bay. In: Sheppard CRC (ed) *Seas at the millennium: an environmental evaluation*, Vol 41. Elsevier Science, Amsterdam, p 1–14
- Keenan SF, Benfield MC, Shaw RF (2003) Zooplanktivory by blue runner *Caranx crysos*: a potential energetic subsidy to Gulf of Mexico fish populations at petroleum platforms. In: Stanley DR, Scarborough-Bull A (eds) *Fisheries, reefs, and offshore development symposium*. American Fisheries Society, Bethesda, MD, p 167–180
- Keister JE, Houde ED, Breitburg DL (2000) Effects of bottom-layer hypoxia on abundances and depth distributions of organisms in Patuxent River, Chesapeake Bay. *Mar Ecol Prog Ser* 205:43–59
- Keller AA, Simon V, Chan F, Wakefield WW and others (2010) Demersal fish and invertebrate biomass in relation to an offshore hypoxic zone along the US West Coast. *Fish Oceanogr* 19:76–87
- Kimmel DG, Boicourt WC, Pierson JJ, Roman MR, Zhang X (2010) The vertical distribution and diel variability of mesozooplankton biomass, abundance and size in response to hypoxia in the northern Gulf of Mexico USA. *J Plankton Res* 32:1185–1202
- Kramer DL (1987) Dissolved oxygen and fish behavior. *Environ Biol Fishes* 18:81–92
- Kraus RT, Knight CT, Farmer TM, Gorman AM and others (2015) Dynamic hypoxic zones in Lake Erie compress fish habitat, altering vulnerability to fishing gears. *Can J Fish Aquat Sci* 72:797–806
- Langseth BJ, Purcell KM, Craig JK, Schueller AM and others (2014) Effect of changes in dissolved oxygen concentrations on the spatial dynamics of the Gulf menhaden fishery in the northern Gulf of Mexico. *Mar Coast Fish* 6:223–234
- Lankford TE, Targett TE (1994) Suitability of estuarine nursery zones for juvenile weakfish (*Cynoscion regalis*): effects of temperature and salinity on feeding, growth and survival. *Mar Biol* 119:611–620
- Liu Y, Hu C, Sun C, Zhan W, Sun S, Xu B, Dong Y (2018) Assessment of offshore oil/gas platform status in the northern Gulf of Mexico using multi-source satellite time-series images. *Remote Sens Environ* 208:63–81
- Livingston RJ (1988) Inadequacy of species-level designations for ecological studies of coastal migratory fishes. *Environ Biol Fishes* 22:225–234
- Ludsin SA, Zhang X, Brandt SB, Roman MR, Boicourt WC, Mason DM, Costantini M (2009) Hypoxia-avoidance by planktivorous fish in Chesapeake Bay: implications for food web interactions and fish recruitment. *J Exp Mar Biol Ecol* 381 (Suppl 1):S121–S131
- Marsh MC, Gorham FP (1905) The gas disease in fishes. Report of the Bureau of Fisheries 1904. Department of Commerce, Washington, DC, p 343–376
- Milliman JD, Meade RH (1983) World-wide delivery of river sediment to the oceans. *J Geol* 91:1–21
- Munnelly RT (2016) Fishes associated with oil and gas platforms in Louisiana's river-influenced nearshore waters. MSc thesis, Louisiana State University, LA
- Nebecker AV, Andros JD, McCrady JK, Stevens DG (1978) Survival of steelhead trout (*Salmo gairdneri*) eggs, embryos, and fry in air-supersaturated water. *J Fish Board Can* 35:261–264
- Obenour DR, Scavia D, Rabalais NN, Turner RE, Michalak AM (2013) Retrospective analysis of midsummer hypoxic area and volume in the northern Gulf of Mexico, 1985–2011. *Environ Sci Technol* 47:9808–9815
- Parker RO Jr, Colby DR, Willis TD (1983) Estimated amount of reef habitat on a portion of the US South Atlantic and

- Gulf of Mexico continental shelf. *Bull Mar Sci* 33:935–940
- ✦ Parker NC, Suttle MA, Fitzmayer K (1984) Total gas pressure and oxygen and nitrogen saturation in warm water ponds aerated with airlift pumps. *Aquacult Eng* 3:91–102
- ✦ Pihl L (1994) Changes in the diet of demersal fish due to eutrophication-induced hypoxia in the Kattegat, Sweden. *Can J Fish Aquat Sci* 51:321–336
- ✦ Pihl L, Baden SP, Diaz RJ (1991) Effects of periodic hypoxia on distribution of demersal fish and crustaceans. *Mar Biol* 108:349–360
- ✦ Pokryfki L, Randall RE (1987) Nearshore hypoxia in the bottom water of the northwestern Gulf of Mexico from 1981 to 1984. *Mar Environ Res* 22:75–90
- ✦ Priede IG, Bagley PM, Smith A, Creasey S, Merrett NR (1994) Scavenging deep demersal fishes of the Porcupine Seabight, north-east Atlantic: observations by baited camera, trap and trawl. *J Mar Biol* 74:481–498
- ✦ Prince ED, Goodyear CP (2006) Hypoxia-based habitat compression of tropical pelagic fishes. *Fish Oceanogr* 15: 451–464
- ✦ Purcell KM, Craig JK, Nance JM, Smith MD, Benneer LS (2017) Fleet behavior is responsive to a large-scale environmental disturbance: hypoxia effects on the spatial dynamics of the northern Gulf of Mexico shrimp fishery. *PLOS ONE* 12:e0183032
- Rabalais NN, Harper DE, Turner RE (2001) Responses of nekton and demersal and benthic fauna to decreasing oxygen concentrations. In: Rabalais NN, Turner RE (eds) *Coastal hypoxia: consequences for living resources and ecosystems*. Coastal and Estuarine Studies, Vol 58. American Geophysical Union, Washington, DC, p 115–128
- Rabalais NN, Turner RE, Wiseman WJ Jr (2002) Gulf of Mexico hypoxia, a.k.a. 'the dead zone'. *Annu Rev Ecol Syst* 33: 235–263
- Rabalais NN, Turner RE, Wiseman WJ Jr, Boesch DF (1991) A brief summary of hypoxia on the northern Gulf of Mexico continental shelf: 1985–1988. In: Tyson RV, Pearson TH (eds) *Modern and ancient continental shelf anoxia*. Geol Soc Lond Spec Publ, Vol 58. The Geological Society, London, p 35–46
- ✦ Rabalais NN, Turner RE, Sen Gupta BK, Boesch DF, Chapman P, Murrell MC (2007) Hypoxia in the northern Gulf of Mexico: Does the science support the plan to reduce, mitigate, and control hypoxia? *Estuaries Coasts* 30:753–772
- ✦ Rahel FJ, Nutzman JW (1994) Foraging in a lethal environment: fish predation in hypoxic waters of a stratified lake. *Ecology* 75:1246–1253
- ✦ Rakocinski CF, Baltz DM, Fleeger JW (1992) Correspondence between environmental gradients and the community structure of marsh-edge fishes in a Louisiana estuary. *Mar Ecol Prog Ser* 80:135–148
- ✦ Reeves DB, Munnelly RT, Chesney EJ, Baltz DM, Marx BD (2017) Stone crab *Menippe* spp. populations on Louisiana's nearshore oil and gas platforms: higher density and size at maturity on a sand shoal. *Trans Am Fish Soc* 146:371–383
- ✦ Reeves DB, Chesney EJ, Munnelly RT, Baltz DM (2018a) Barnacle settlement and growth at oil and gas platforms in the northern Gulf of Mexico. *Mar Ecol Prog Ser* 590: 131–143
- ✦ Reeves DB, Chesney EJ, Munnelly RT, Baltz DM, Marx BD (2018b) Abundance and distribution of platform-associated fishes around small oil and gas platforms in the northern Gulf of Mexico's hypoxic zone. *Estuar Coasts* 41:1835–1847
- ✦ Reeves DB, Chesney EJ, Munnelly RT, Baltz DM (in press a) Sheepshead *Archosargus probatocephalus* foraging patterns at oil and gas platforms in the northern Gulf of Mexico. *N Am J Fish Manage*, doi:10.1002/nafm.10229
- ✦ Reeves DB, Chesney EJ, Munnelly RT, Baltz DM, Maiti K (in press b) Trophic ecology of sheepshead and stone crabs at oil and gas platforms in the northern Gulf of Mexico's hypoxic zone. *Trans Am Fish Soc*, doi.org/10.1002/tafs. 10135
- Remmert H (1983) Studies and thoughts about the zonation along the rocky shores of the Baltic. *Aquilo Ser Zoologica* 22:121–125
- ✦ Renfro WC (1963) Gas-bubble mortality of fishes in Galveston Bay, Texas. *Trans Am Fish Soc* 92:320–322
- ✦ Reynolds EM, Cowan JH Jr, Lewis KA, Simonsen KA (2018) Method for estimating relative abundance and species composition around oil and gas platforms in the northern Gulf of Mexico, USA. *Fish Res* 201:44–55
- ✦ Roman MR, Pierson JJ, Kimmel DG, Boicourt WC, Zhang X (2012) Impacts of hypoxia on zooplankton spatial distributions in the northern Gulf of Mexico. *Estuar Coasts* 35: 1261–1269
- ✦ Rose KA, Creekmore S, Thomas P, Craig JK, Rahman MS, Miller Neilan R (2018a) Modeling the population effects of hypoxia on Atlantic croaker (*Micropogonias undulatus*) in the northwestern Gulf of Mexico. I. Model description and idealized hypoxia. *Estuar Coasts* 41: 233–254
- ✦ Rose KA, Creekmore S, Justić D, Thomas P and others (2018b) Modeling the population effects of hypoxia on Atlantic croaker (*Micropogonias undulatus*) in the northwestern Gulf of Mexico. II. Realistic hypoxia and eutrophication. *Estuar Coasts* 41:255–279
- Rountree RA (1989) Association of fishes with fish aggregation devices: effects of structure size on fish abundance. *Bull Mar Sci* 44:960–972
- Sampaio LA, Bianchini A (2002) Salinity effects on osmoregulation and growth of the euryhaline flounder *Paralichthys orbignyanus*. *J Exp Mar Biol Ecol* 269:187–196
- Scarborough Bull A, Kendall JJ Jr (1994) An indication of the process: offshore platforms as artificial reefs in the Gulf of Mexico. *Bull Mar Sci* 55:1086–1098
- ✦ Schobernd ZH, Bacheler NM, Conn PB (2014) Examining the utility of alternative video monitoring metrics for indexing reef fish abundance. *Can J Fish Aquat Sci* 71: 464–471
- ✦ Stanley DR, Wilson CA (2004) Effect of hypoxia on the distribution of fishes associated with a petroleum platform off coastal Louisiana. *N Am J Fish Manage* 24:662–671
- Switzer TS, Chesney EJ, Baltz DM (2006) Exploring temporal and spatial variability in nekton community structure in the northern Gulf of Mexico: unravelling the potential influence of hypoxia. *Proc Gulf Caribb Fish Inst* 57: 699–716
- ✦ Switzer TS, Chesney EJ, Baltz DM (2009) Habitat selection by flatfishes in the northern Gulf of Mexico: implications for susceptibility to hypoxia. *J Exp Mar Biol Ecol* 381:S51–S64
- ✦ Switzer TS, Chesney EJ, Baltz DM (2015) Habitat use by juvenile red snapper in the northern Gulf of Mexico: ontogeny, seasonality, and the effects of hypoxia. *Trans Am Fish Soc* 144:300–314
- ✦ Szedlmayer ST, Able KW (1996) Patterns of seasonal availability and habitat use by fishes and decapod crustaceans in a southern New Jersey estuary. *Estuaries Coasts* 19:697–709

- ✦ Taylor JC, Rand PS (2003) Spatial overlap and distribution of anchovies (*Anchoa* spp.) and copepods in a shallow stratified estuary. *Aquat Living Resour* 16:191–196
- ✦ Thomas P, Rahman MS (2010) Region-wide impairment of Atlantic croaker testicular development and sperm production in the northern Gulf of Mexico hypoxic dead zone. *Mar Environ Res* 69 (Suppl 1):S59–S62
- Thomas P, Rahman MS (2012) Extensive reproductive disruption, ovarian masculinization and aromatase suppression in Atlantic croaker in the northern Gulf of Mexico hypoxic zone. *Proc R Soc B* 279:19–27
- ✦ Thomas P, Rahman MS, Kummer JA, Lawson S (2006) Reproductive endocrine dysfunction in Atlantic croaker exposed to hypoxia. *Mar Environ Res* 62:S249–S252
- ✦ Turner RE, Rabalais NN (1991) Changes in the Mississippi River water quality this century: implications for coastal food webs. *Bioscience* 41:140–147
- ✦ Vanderploeg HA, Ludsin SA, Ruberg SA, Höök TO and others (2009) Hypoxia affects spatial distributions and overlap of pelagic fish, zooplankton, and phytoplankton in Lake Erie. *J Exp Mar Biol Ecol* 381 (Suppl 1): S92–S107
- ✦ Vaquer-Sunyer R, Duarte CM (2008) Thresholds of hypoxia for marine biodiversity. *Proc Natl Acad Sci USA* 105: 15452–15457
- ✦ Webster CN, Hansson S, Didrikas T, Gorokhova E, Peltonen H, Brierley AS, Lehtiniemi M (2015) Stuck between a rock and a hard place: zooplankton vertical distribution and hypoxia in the Gulf of Finland, Baltic Sea. *Mar Biol* 162:1429–1440
- Wells DRJ, Cowan JH Jr (2007) Video estimates of red snapper and associated fish assemblages on sand, shell, and natural reef habitats in the north-central Gulf of Mexico. In: Patterson WF III, Cowan J Jr, Fitzhugh GR, Nieland DL (eds) *Am Fish Soc Symp*, Vol 60. American Fisheries Society, Bethesda, MD, p 39–57
- ✦ Willis TJ, Babcock RC (2000) A baited underwater video system for the determination of relative density of carnivorous reef fish. *Mar Freshw Res* 51:755–763
- Wiseman WJ, Bane JM, Murray SP, Tubman MW (1975) Small scale temperature and salinity structure over the inner shelf west of the Mississippi River delta. *Mem R Soc Sci Liege* 10:277–286
- ✦ Wiseman WJ, Rabalais NN, Turner RE, Dinnel SP, MacNaughton A (1997) Seasonal and interannual variability within the Louisiana coastal current: stratification and hypoxia. *J Mar Syst* 12:237–248
- ✦ Wuenschel MJ, Jugovich AR, Hare JA (2004) Effect of temperature and salinity on the energetics of juvenile gray snapper (*Lutjanus griseus*): implications for nursery habitat value. *J Exp Mar Biol Ecol* 312:333–347
- ✦ Zenone AM, Burkepille DE, Boswell KM (2017) A comparison of diver vs. acoustic methodologies for surveying fishes in a shallow water coral reef ecosystem. *Fish Res* 189:62–66
- ✦ Zhang H, Ludsin SA, Mason DM, Adamack AT and others (2009) Hypoxia-driven changes in the behavior and spatial distribution of pelagic fish and mesozooplankton in the northern Gulf of Mexico. *J Exp Mar Biol Ecol* 381: S80–S91
- ✦ Zhang H, Mason DM, Stow CA, Adamack AT and others (2014) Effects of hypoxia on habitat quality of pelagic planktivorous fishes in the northern Gulf of Mexico. *Mar Ecol Prog Ser* 505:209–226

Editorial responsibility: Romuald Lipcius,
Gloucester Point, Virginia, USA

Submitted: February 26, 2018; Accepted: October 2, 2018
Proofs received from author(s): December 7, 2018