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ARTICLE

Effect of Hypoxia on Diet of Atlantic Bumpers in the Northern Gulf of Mexico

Cassandra N. Glaspie*
Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, Oregon 97731, USA

Melissa A. Clouse
School of Pharmacy, Hampton University, Kittrell Hall, Hampton, Virginia 23668, USA

Aaron T. Adamack[1]
Department of Biology, Virginia Commonwealth University, Richmond, Virginia 23284, USA

YoonKyung Cha
School of Environmental Engineering, University of Seoul, Dongdaemun-gu, Seoul, South Korea

Stuart A. Ludsin
*Aquatic Ecology Laboratory, Department of Evolution, Ecology, and Organismal Biology, The Ohio State University,
1314 Kinnear Road, Columbus, Ohio 43212, USA*

Doran M. Mason
*National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory,
4840 South State Road, Ann Arbor, Michigan 48108, USA*

Michael R. Roman
*Horn Point Laboratory, University of Maryland Center for Environmental Science, Post Office Box 775, Cambridge,
Maryland 21613, USA*

Craig A. Stow
*National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory,
4840 South State Road, Ann Arbor, Michigan 48108, USA*

Stephen B. Brandt
Department of Fisheries and Wildlife, Oregon State University, 104 Nash Hall, Corvallis, Oregon 97731, USA

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*Corresponding author: cassandra.glaspie@gmail.com

[1] Present address: Fisheries and Oceans Canada, Northwest Atlantic Fisheries Centre, 80 East White Hills Road, Post Office Box 5667, St. John's, Newfoundland and Labrador A1C 5X1, Canada.

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Abstract

Cultural eutrophication is a global problem that often leads to hypoxic conditions in coastal systems. Although improving, our understanding of the impacts of hypoxia on trophic interactions in pelagic and benthopelagic food webs is limited. Toward this end, we evaluated diet composition of and mass-specific consumption by the Atlantic Bumper *Chloroscombrus chrysurus*, a numerically dominant planktivorous fish in the northern Gulf of Mexico, relative to dissolved oxygen concentration and fish size. Atlantic Bumper CPUE was similar in hypoxic and normoxic areas. Mean mass-specific consumption by small Atlantic Bumpers in hypoxic areas was greater than that of both small and large individuals in normoxic areas. The most commonly ingested prey type for both large and small Atlantic Bumpers was shrimp larvae. Large quantities of fish larvae were consumed by adult Atlantic Bumpers in hypoxic regions. These findings demonstrate that hypoxic conditions can alter feeding of dominant fishes in the northern Gulf of Mexico, which may influence energy flow in the region.

Hypoxia (dissolved oxygen [DO] ≤ 2 mg/L) is an environmental stressor that has grown in prominence in aquatic ecosystems worldwide (Rabalais et al. 2009). Hypoxia occurs naturally in many marine systems that are characterized by phenomena such as coastal upwelling, high productivity, and stratification (Rabalais et al. 2010). However, human activities, such as intensive agriculture practices and land use changes, have caused the magnitude and extent of hypoxia to increase (Turner et al. 2008; Bianchi et al. 2010). Within the United States, there are many systems that experience seasonal hypoxia, including Long Island Sound, Chesapeake Bay, and the northern Gulf of Mexico (NGOMEX; Anderson and Taylor 2001; Rabalais et al. 2001; Hagy et al. 2004).

The NGOMEX is the site of one of the world's largest human-caused coastal hypoxic zones, with an area exceeding 20,000 km^2 in some years (Rabalais et al. 2001; Turner et al. 2008; Bianchi et al. 2010). It also supports profitable commercial and recreational fisheries for the Spotted Seatrout *Cynoscion nebulosus*, Red Snapper *Lutjanus campechanus*, Red Drum *Sciaenops ocellatus*, King Mackerel *Scomberomorus cavalla*, Sheepshead *Archosargus probatocephalus*, Dolphinfish *Coryphaena hippurus*, and shrimp species, including white shrimp *Litopenaeus setiferus* and brown shrimp *Farfantepenaeus aztecus* (NMFS 2016). The effects of hypoxia on these commercial and recreational fisheries are of particular interest given recent evidence for hypoxia-related declines in productivity for brown shrimp (O'Connor and Whitall 2007; Huang et al. 2010).

Hypoxia holds great potential to alter food web interactions (Pihl et al. 1991; Diaz and Rosenberg 1995; O'Connor and Whitall 2007). Reduced oxygen levels, which typically form in the bottom layer of the water column (Diaz and Rosenberg 2008), have been shown to both increase (Pierson et al. 2009; Craig 2012; Roman et al. 2012) and decrease (Taylor and Rand 2003; Ludsin et al. 2009; Zhang et al. 2009) the spatial overlap between predators and prey. When prey habitat is compressed into the layer of water adjacent to the hypoxic zone, predators may be able to take advantage of dense prey resources, thus increasing trophic transfer (Prince and Goodyear 2006). However, several field studies have reported evidence that zooplankton use hypoxic bottom water as a refuge from predation (Vanderploeg et al. 2009; Zhang et al. 2009), which may interrupt trophic interactions. In addition, several studies have used information on species distribution shifts to measure the potential impact of hypoxia on fish growth (Costantini et al. 2008; Arend et al. 2011; Brandt et al. 2011; Zhang et al. 2014). Although these studies have no doubt improved our ability to assess the potential impact of hypoxia on food webs, few studies in the NGOMEX have actually quantified the impact of hypoxia on diet composition, especially for pelagic species (Rabotyagov et al. 2014).

We explored how hypoxia affects the diet of the Atlantic Bumper *Chloroscombrus chrysurus*, a numerically dominant pelagic species in the NGOMEX (Sánchez-Ramírez 2003; Lewis et al. 2007; Craig and Bosman 2013). The Atlantic Bumper is an important food source for a variety of commercially and recreationally important fishes (Shaw and Drullinger 1990; Leffler and Shaw 1992). Although the Atlantic Bumper is a common member of the NGOMEX pelagic community, little is known about its diet either in the presence or absence of hypoxia. Therefore, we also focused on quantifying differences in diet based on Atlantic Bumper size.

We hypothesized that consumption by Atlantic Bumpers is lower in hypoxic areas than in normoxic areas because fish experience a spatial mismatch with prey such as zooplankton and pelagic larvae, which exhibit vertical migration to avoid predators (Hopkins 1982; Nielson and Perry 1990) and can use the hypoxic zone as a refuge from predation (Breitburg et al. 1999; Ludsin et al. 2009). In addition, we expected diet composition to vary (1) between hypoxic and normoxic areas due to species-specific differences in zooplankton responses to hypoxia (Kimmel et al. 2009; Elliott et al. 2012; C. N. Glaspie and colleagues, unpublished manuscript) and (2) between small and large Atlantic Bumpers due to ontogenetic shifts in diet. Finally, we hypothesized that hypoxia negatively impacts Atlantic Bumper CPUE due to these changes in consumption. We conducted field surveys in hypoxic (≤2 mg/L DO) and normoxic (>2 mg/L DO) areas of the NGOMEX during summer in 2006–2008 to describe changes in catch, size, and diets of Atlantic Bumpers relative to DO availability.

METHODS

Field and laboratory procedures.— Atlantic Bumpers were collected in the NGOMEX (Figure 1) during August 4–13, 2006; July 30–August 7, 2007; and August 1–11, 2008, using the RV *Pelican* (Louisiana Universities Marine Consortium). Fish were captured with a bottom trawl (7.62-m headrope; 3.66-m mouth depth; 38-mm stretch mesh; 12-mm cod-end liner). Trawling occurred day and night in water depths between 7 and 42 m, and trawl duration (time for which the trawl was on the ocean bottom) varied between 10 and 60 min to ensure adequate collection of fish. After capture, Atlantic Bumpers were counted and frozen at −20°C. Fish CPUE was calculated as the number of fish caught per minute of trawling. Most trawls were between 10 and 30 min in length, and the only trawls longer than 30 min occurred in hypoxic zones (Supplementary Figure 1 available in the online version of this article); therefore, we omitted trawls with lengths longer than 30 min from analyses of CPUE to ensure that the distribution of trawl durations was similar between hypoxic and normoxic areas.

Before each trawl, a vertical conductivity–temperature–depth (Seabird SBE 9 with an SBE 43 DO probe) profile was taken to measure DO (nearest 0.01 mg/L) and temperature (nearest 0.1°C). Areas were considered hypoxic if at least half of the bottom third of the water column had a DO ≤ 2.0 mg/L (Figure 1). This definition of a hypoxic area was adopted because the trawl fished the bottom third of the water column.

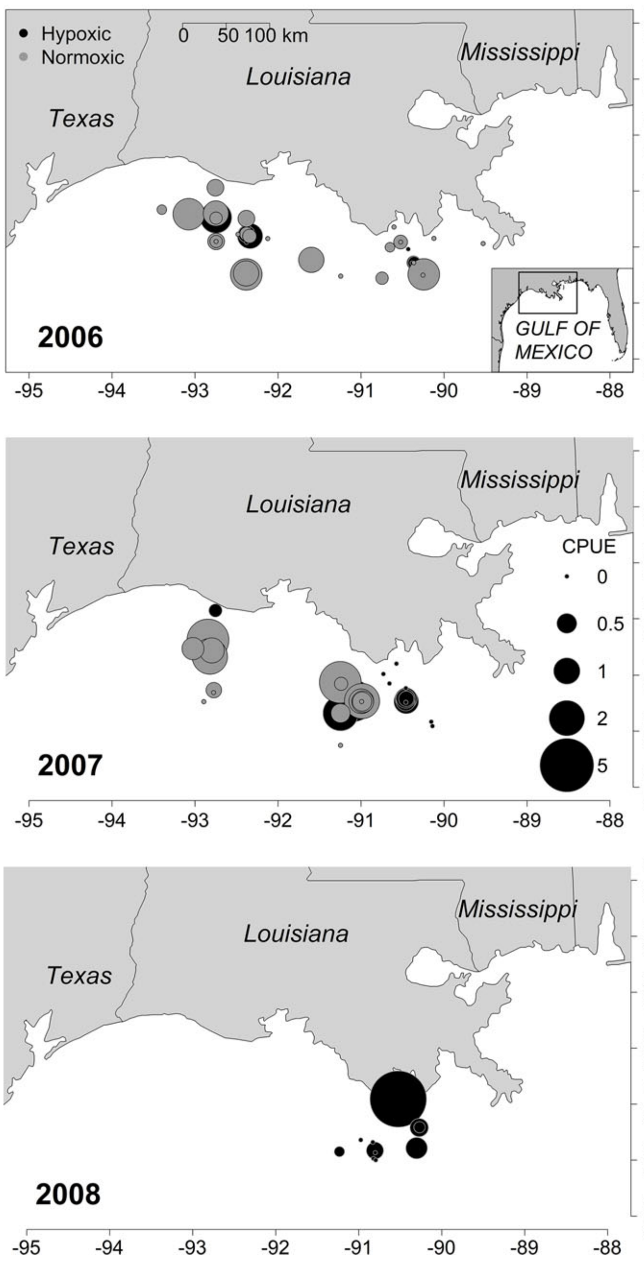

FIGURE 1. Map of the northern Gulf of Mexico study area and the locations of trawls conducted in 2006 (top), 2007 (middle), and 2008 (bottom). Symbol shading denotes bottom dissolved oxygen availability (hypoxic areas: ≤2 mg/L; normoxic areas: >2 mg/L). Symbol size indicates Atlantic Bumper CPUE (individuals caught per minute).

The stomach contents of Atlantic Bumpers were analyzed for each trawl to determine diet composition. In the laboratory, fish were thawed, and their TL (nearest 1 mm) and wet mass (nearest 0.1 g) were measured. Stomach contents were counted and identified to the lowest possible taxonomic unit by using a dissecting scope. Prey items (a minimum of 50 individuals) were measured to the nearest 0.01 mm with ImagePro Plus software (version 5.1.2.59; Media Cybernetics, Inc., Silver Spring, Maryland). Individual prey lengths were converted into dry mass (μg) by using length–mass relationships from the published literature (Fontaine and Neal 1971; Uye 1982; Cadman and Weinstein 1985; Chisholm and Roff 1990; Webber and Roff 1995; Hopcroft et al. 1998; Tita et al. 1999; Ara 2001; Remsen et al. 2004; Rose et al. 2004). Several common zooplankton species were analyzed as separate prey categories, including copepods *Acartia* sp., *Centropages* sp., *Corycaeus* sp., *Eucalanus* sp., *Oithona* sp., *Oncaea* sp., *Paracalanus* sp., and *Temora* sp. All other prey items were lumped into 1 of 11 prey categories: other calanoid copepods, such as *Clausocalanus* sp., *Labicera* sp., *Pseudodiaptomus* sp., *Undinula* sp., *Euchaeta* sp., and *Pontella* sp.; crab megalopae; crab zoeae; shrimp larvae; cyprid larvae;

fish larvae; crabs and shrimp; fish and squid; bivalves and gastropods; worms, such as polychaetes, oligochaetes, and nematodes; and other benthic organisms, including harpacticoid copepods, amphipods, tanaids, echinoderms, ostracods, cumaceans, and isopods. To calculate the total dry mass consumed for each taxon, the average dry mass per taxon was multiplied by the total number in the gut.

We calculated mass-specific consumption for each individual to examine differences in foraging potential in relation to oxygen availability. To do so, fish and their stomach contents were dried in a 70°C oven for 48 h. Mass-specific consumption was calculated as the total dry mass of the stomach contents (g) divided by the total dry mass of the fish (g) to account for differences in fish size and thus stomach capacity.

Statistical analysis.— To examine the effects of fish TL on diet, we assigned individual Atlantic Bumpers to a size-class based on the observed TL distribution of all Atlantic Bumpers caught (Figure 2). The length distribution was bimodal, suggesting two size-classes (small and large). Atlantic Bumpers with TLs less than 110 mm were classified as small, and Atlantic Bumpers with TLs of 110 mm or greater were classified as large.

Differences in Atlantic Bumper CPUE between hypoxic and normoxic areas were analyzed using ANOVA. Predictor variables included in the ANOVA models were DO (categorical; hypoxic or normoxic), time of day (categorical; day or night), and year (categorical; 2006, 2007, or 2008). Latitude and longitude (continuous) were included as covariates. Mass-specific consumption was also modeled using ANOVA, although we pooled fish by size category (small or large) for each trawl, including only trawls and size-classes with three or more fish (38 trawls; hypoxic/small, $n = 5$; normoxic/small, $n = 2$; hypoxic/large, $n = 9$; normoxic/large, $n = 22$). Predictor variables in the consumption model included DO (categorical; hypoxic or normoxic), fish size (categorical; small or large), time of day (categorical; day or night), year (categorical; 2006, 2007, or 2008), and latitude/longitude (continuous covariates). Tukey's honestly significant difference test was used for post hoc multiple comparisons. Assumptions of normality and homoscedasticity were assessed visually using quantile–quantile plots and residual plots. Catch per unit effort and consumption were log transformed to meet assumptions.

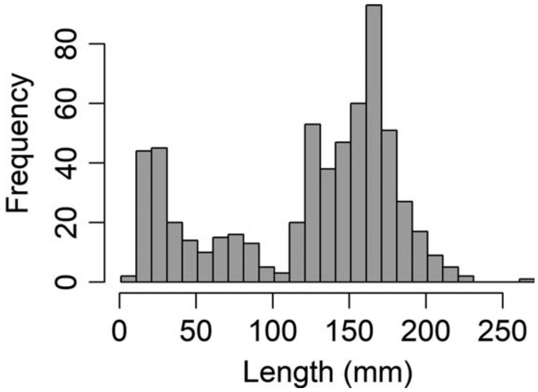

FIGURE 2. Length frequency (TL, mm) histograms describing Atlantic Bumpers that were captured in bottom trawls conducted in the northern Gulf of Mexico during summer 2006–2008.

We used multivariate ANOVA (MANOVA) to examine the effects of DO, fish size, time of day, and year on diet composition. The MANOVA was completed using Bray–Curtis dissimilarity matrices of average dry mass of prey categories pooled by fish size (small or large) for each trawl. The MANOVA was structured as a four-way design with the following factors: DO (normoxic or hypoxic), fish size (small or large), time of day the sample was collected (day or night), and year (2006, 2007, or 2008). Latitude and longitude were included as covariates to account for spatial autocorrelation, and model residuals plotted in space indicated no trends. An approximate MANOVA *F*-statistic was calculated on the Pillai's trace statistic (Hand and Taylor 1987). To better understand which species were responsible for MANOVA results, we performed a post hoc analysis by (1) running a similarity percentage (SIMPER) procedure (Clarke 1993) to determine specific prey categories/zooplankton taxa that contributed to differences in diet and (2) using univariate ANOVAs to further examine the top-two prey groups identified by SIMPER. All analyses were completed using R software (R Core Team 2017) and the "vegan" package (Oksanen et al. 2017).

RESULTS

The severity and extent of hypoxia differed throughout the duration of the study; 6.5% of sites were hypoxic in 2006, 61.1% were hypoxic in 2007, and 100.0% were hypoxic in 2008. In total, 97 trawls were conducted during summer in 2006–2008, with 563 Atlantic Bumpers captured. Atlantic Bumpers were found in 51% of trawls in hypoxic areas and 57% of trawls in normoxic areas. The mean CPUE (± 1 SD) of Atlantic Bumpers was 0.4 ± 0.6 fish/min in normoxic areas and 0.5 ± 1.0 fish/min in hypoxic areas. There was no effect of DO on Atlantic Bumper CPUE ($F_{1,\ 80} = 0.46$, $P = 0.50$; Supplementary Table 1). Mass-specific consumption was significantly greater in hypoxic areas than in normoxic areas, although this effect depended on fish size, evidenced by an interaction between DO and fish size (Table 1). Small fish in hypoxic areas had higher consumption than small fish in normoxic areas ($P = 0.01$; Figure 3A), large fish in hypoxic areas ($P < 1.0 \times 10^{-7}$), and large fish in normoxic areas ($P < 1.0 \times 10^{-7}$; Figure 3B). There was variability in consumption among years, with the highest

TABLE 1. Analysis of variance model results for Atlantic Bumper mass-specific consumption (dry mass of the stomach contents divided by the total dry mass of the fish) in the northern Gulf of Mexico, summer 2006–2008. Consumption was log transformed for analysis, and results are not back-transformed. Variables that were significant at $\alpha = 0.05$ are shown in bold italics.

Variable	df	Sum of squares	Mean square	*F*-value	*P*-value
Oxygen	***1***	***13.34***	***13.34***	***46.62***	$\boldsymbol{4.62 \times 10^{-7}}$
Time of day	1	0.59	0.59	2.07	0.16
Fish size	***1***	***37.94***	***37.94***	***132.64***	$\boldsymbol{2.91 \times 10^{-11}}$
Year	***2***	***2.94***	***1.47***	***5.14***	***0.01***
Latitude	1	0.13	0.13	0.46	0.50
Longitude	***1***	***3.77***	***3.77***	***13.18***	***0.001***
Oxygen × Time	1	0.07	0.07	0.26	0.61
Oxygen × Fish size	***1***	***5.31***	***5.31***	***18.55***	***0.0002***
Time × Fish size	1	0.33	0.33	1.14	0.30
Oxygen × Year	1	0.95	0.95	3.32	0.08
Time × Year	1	0.08	0.08	0.27	0.61
Latitude × Longitude	1	0.15	0.15	0.52	0.48
Residuals	24	6.86	0.29		

mass-specific consumption observed in 2006 and the lowest observed in 2007 ($P = 0.05$).

Across all trawls, 83% of the individuals collected had at least one prey item in their stomachs. The most commonly ingested prey type for both large and small Atlantic Bumpers (by frequency of occurrence) was shrimp larvae (Table 2). Shrimp larvae also dominated small Atlantic Bumpers' diets by mass (Table 2). However, large Atlantic Bumpers' diets (by mass) were primarily comprised of fish larvae, especially in hypoxic areas (Table 2). Zooplankton taxa commonly found in Atlantic Bumper diets were *Acartia* sp., *Centropages* sp., *Corycaeus* sp., *Eucalanus* sp., *Paracalanus* sp., and *Temora* sp. (Table 2).

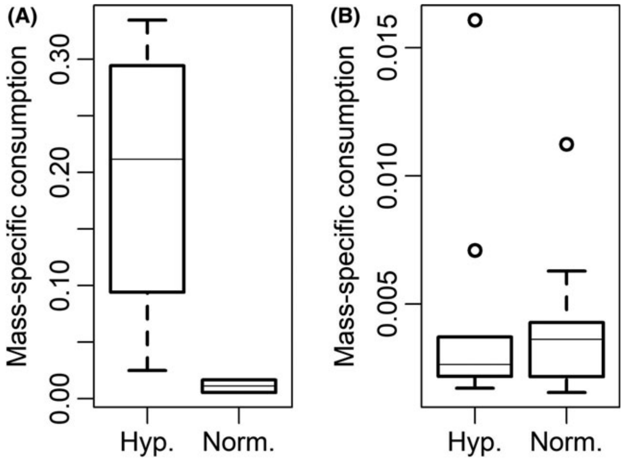

FIGURE 3. Mass-specific consumption (g prey/g fish; dry mass) by **(A)** small (<110 mm TL) Atlantic Bumpers and **(B)** large (≥110 mm TL) Atlantic Bumpers in hypoxic areas (Hyp.) and normoxic areas (Norm.) of the northern Gulf of Mexico, with boxes depicting the first to third quartiles and the horizontal line representing the median. Whiskers extend from the lowest data point that is still within 1.5 interquartile range (IQR) of the lower quartile to the highest data point that is still within 1.5 IQR of the upper quartile; data outside this range are denoted by circles.

Diet composition differed between hypoxic and normoxic areas, between large and small Atlantic Bumpers, and among years but did not differ by time of day; however, due to significant interactions between DO, fish size, time of day, and year, the main effects must be interpreted with caution (Table 3). The prey types that differed most between hypoxic and normoxic areas were shrimp larvae and fish larvae. The amount of shrimp larvae consumed was not significantly different between hypoxic (mean ± SD = 4,013 ± 10,373 μg) and normoxic (398 ± 1,617 μg) areas ($F_{1,\ 28} = 0.001$, $P = 0.96$). However, Atlantic Bumpers in hypoxic areas consumed significantly more fish larvae (mean ± SD = 1,101.54 ± 5,541.39 μg) than those in normoxic areas (83 ± 84 μg; $F_{1,\ 28} = 6.54$, $P = 0.02$). Although small Atlantic Bumpers rarely consumed fish larvae (Figure 4A), large Atlantic Bumpers in hypoxic regions almost exclusively consumed fish larvae (Figure 4B).

DISCUSSION

Atlantic Bumpers are a numerically dominant component of the NGOMEX pelagic fish assemblage (Craig and Bosman 2013), but there is little information on this species. The few studies that exist on Atlantic Bumpers have focused on the distribution, growth, and larval mortality (Tolley 1987; Shaw and Drullinger 1990; Leffler and Shaw 1992; Sánchez-Ramírez and Flores-Coto 1998; Comyns et al. 2003; Ditty et al. 2004). Particularly absent is knowledge on Atlantic Bumper diets, with one study on larvae from the southern Gulf of Mexico (Sánchez-Ramírez 2003) and several general diet studies from Brazil (Cunha et al. 2000; de Oliveira-Silva and Lopes 2002; Chaves and Umbria 2003). The present study indicates

TABLE 2. Diet composition by frequency of occurrence (freq; proportion of stomachs that contained the prey taxon) and sum of total dry mass (μg) found in all stomachs of small (<110 mm TL) and large (≥110 mm TL) Atlantic Bumpers for taxonomic prey groups in all years combined (*N* = total number of fish examined).

	Hypoxic areas				Normoxic areas			
Prey taxon	Freq small	Freq large	Mass small	Mass large	Freq small	Freq large	Mass small	Mass large
Acartia	0.00	0.03	0.0	2.4	0.29	0.07	47.6	19.3
Centropages	0.02	0.19	93.8	327.0	0.14	0.32	32.4	1,352.6
Corycaeus	0.10	0.39	5,120.5	115.7	0.04	0.57	0.7	1,066.5
Eucalanus	0.02	0.30	5,873.7	1,099.1	0.07	0.16	32.1	691.6
Oithona	0.12	0.01	1,720.1	0.1	0.00	0.02	0.0	1.0
Oncaea	0.01	0.05	1.4	1.9	0.00	0.16	0.0	55.2
Paracalanus	0.16	0.14	10,716.7	32.9	0.04	0.21	2.4	163.2
Temora	0.01	0.22	189.6	111.6	0.07	0.56	4.0	1,418.4
Other calanoids	0.08	0.03	584.2	7.2	0.00	0.13	0.0	305.7
Crab zoeae	0.01	0.13	114.2	3,227.2	0.14	0.11	8,649.9	8,250.3
Crab megalopae	0.01	0.07	515.3	2,174.9	0.11	0.12	2,503.6	35,370.7
Shrimp larvae	0.39	0.20	968,132.7	11,088.8	0.32	0.39	36,493.0	90,198.0
Cyprid larvae	0.00	0.04	0.0	54.5	0.07	0.21	16.2	1,185.5
Fish larvae	0.00	0.11	0.0	268,774.9	0.00	0.01	0.0	26,247.8
Fish and squid	0.00	0.03	0.0	1,462.9	0.00	0.01	0.0	6.8
Crabs and shrimp	0.01	0.02	1,373.1	3,392.1	0.00	0.02	0.0	22,116.6
Bivalves and gastropods	0.01	0.33	21.3	295.7	0.18	0.55	97.1	2,760.5
Worms	0.02	0.10	407.1	36.5	0.07	0.34	152.0	1,118.9
Other benthic	0.10	0.09	1,293.8	19.6	0.11	0.32	6.9	605.5
N			5	9			2	22

TABLE 3. Multivariate ANOVA results for the analysis of prey groups relative to Atlantic Bumper size-class (Fish size), dissolved oxygen (Oxygen), time of day (day/night), and year. The approximate *F*-statistic (Approx. *F*) was calculated on the Pillai's trace statistic. Variables that were significant at α = 0.05 are shown in bold italics.

Variable	df	Pillai's trace	Approx. *F*	*F* (df 1)	*F* (df 2)	*P*-value
Fish size	***1***	***0.91***	***5.6***	***19***	***10***	***0.004***
Oxygen	***1***	***0.95***	***10.68***	***19***	***10***	***0.0003***
Time of day	1	0.77	1.76	19	10	0.18
Year	***2***	***1.68***	***2.99***	***38***	***22***	***0.004***
Latitude	1	0.78	1.83	19	10	0.16
Longitude	***1***	***0.89***	***4.34***	***19***	***10***	***0.01***
Fish size × Oxygen	1	0.79	1.96	19	10	0.14
Fish size × Time	***1***	***0.89***	***4.14***	***19***	***10***	***0.01***
Oxygen × Time	***1***	***0.88***	***4.02***	***19***	***10***	***0.01***
Oxygen × Year	***1***	***0.84***	***2.82***	***19***	***10***	***0.05***
Time × Year	***2***	***1.56***	***2.05***	***38***	***22***	***0.04***
Latitude × Longitude	1	0.74	1.52	19	10	0.25
Residuals	28					

that Atlantic Bumpers in the NGOMEX mainly consume shrimp larvae and that their diet differs over ontogeny, with large individuals (≥110 mm) also consuming large quantities of fish larvae in hypoxic areas.

The results of this study did not support the hypothesis that hypoxia leads to a spatial mismatch between Atlantic Bumpers and prey such as zooplankton (Ludsin et al. 2009) or fish larvae (Breitburg et al. 1999). Instead, fish

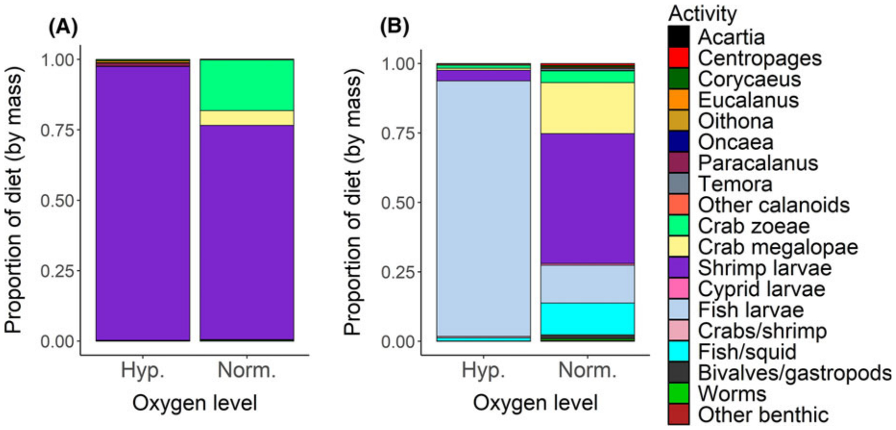

FIGURE 4. Taxonomic composition (proportion of the diet by mass) of stomach contents for **(A)** small (<110 mm TL) Atlantic Bumpers and **(B)** large (≥110 mm TL) Atlantic Bumpers caught in hypoxic areas (Hyp.) and normoxic areas (Norm.) of the northern Gulf of Mexico.

larvae were likely more susceptible to predation by large Atlantic Bumpers in hypoxic regions. Fish larvae in the NGOMEX may not use hypoxic areas as refuge; one field study in the region documented a complete absence of ichthyoplankton at DO levels less than 3.0 mg/L, suggesting that they exhibit avoidance behavior (Greer et al. 2016). In hypoxic areas, zooplankton aggregate above the hypoxic layer to avoid low-oxygen conditions (Pierson et al. 2009; Roman et al. 2012; Elliott et al. 2013; Möller et al. 2015). If zooplankton and fish larvae are prevented from normal vertical migration behavior and are confined to well-lit surface waters, they may be more available as prey for Atlantic Bumpers (Vanderploeg et al. 2009; Zhang et al. 2009).

Small Atlantic Bumpers also appeared to benefit from access to hypoxic areas, as bumpers in hypoxic areas consumed more prey—most of which was shrimp larvae—than individuals in normoxic areas. Shrimp larvae use low-oxygen water and congregate along the edges of hypoxic zones (Greer et al. 2016). If shrimp are easier to capture along hypoxic zone edges, these edge habitats may serve as hot spots for trophic transfer, similar to fronts and pycnoclines (Woodson and Litvin 2015). This could mean that more shrimp are incorporated into the pelagic food web and less shrimp are available for capture by fisheries.

Hypoxia did not reduce the catch of Atlantic Bumpers over the spatial and temporal scales examined in this study. Certain species and life stages are more tolerant of hypoxia than others (Rahel and Nutzman 1994; Burleson et al. 2001); Atlantic Bumpers may be tolerant of hypoxia (Craig 2012) and able to use hypoxic areas or margins as refuge from predators (Robb and Abrahams 2003; Vejřík et al. 2016) or for access to prey resources, as demonstrated by this study. Increased consumption in hypoxic areas may lead to increases in growth or condition, as was seen in billfishes in the Pacific (Prince and Goodyear 2006). Considering the relative abundance of Atlantic Bumpers in the forage fish community (Craig and Bosman 2013) and the value of forage fish as a prey resource for other commercially and recreationally important fish species (Engelhard et al. 2014; Pikitch et al. 2014), hypoxia may have consequences for energy flow in the NGOMEX food web.

Atlantic Bumper diets were affected by the presence of hypoxia during summer in the NGOMEX. Small individuals in hypoxic areas consumed more prey than their counterparts in normoxic areas. Although both small and large individuals consumed shrimp larvae throughout the NGOMEX, we also found that large individuals consumed fish larvae, especially in hypoxic areas. Our findings provide important basic knowledge on the diet of this numerically dominant species and can assist efforts to model energy flow and food web dynamics in relation to hypoxia.

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SUPPORTING INFORMATION

Additional supplemental material may be found online in the Supporting Information section at the end of the article.