

Effects of hypoxia on habitat quality of pelagic planktivorous fishes in the northern Gulf of Mexico

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ABSTRACT: To evaluate the impact of hypoxia ($<2 \text{ mg O}_2 \text{ l}^{-1}$) on habitat quality of pelagic prey fishes in the northern Gulf of Mexico, we used a spatially explicit, bioenergetics-based growth rate potential (GRP) model to develop indices of habitat quality. Our focus was on the pelagic bay anchovy *Anchoa mitchilli* and Gulf menhaden *Brevoortia patronus*. Positive GRP was considered high-quality habitat (HQH) and negative GRP was considered low-quality habitat (LQH). Models used water temperature, dissolved oxygen (DO), zooplankton biomass, and phytoplankton concentration collected during the peak periods of hypoxia in 2003, 2004, and 2006 to estimate fish GRP. Results showed that hypoxic areas were always LQH. However, with respect to the entire water column, hypoxia had only a minor impact on overall habitat quality, with habitat quality being driven primarily by prey availability followed by water temperature. These results are in contrast to other ecosystems, such as the Chesapeake Bay, where hypoxia affects a larger fraction of the water column than in the Gulf of Mexico and has a significant impact on overall habitat quality. Differences in the effect of hypoxia on habitat quality between these 2 ecosystems suggest that the vertical extent of hypoxia relative to water column depth (i.e. hypoxic volume) is a fundamental consideration when evaluating the impacts of hypoxia on pelagic fish production.

KEY WORDS: Dead zone · Habitat suitability · Eutrophication · Food web · Non-point source pollution

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INTRODUCTION

The northern Gulf of Mexico has one of the world's largest anthropogenically-driven, seasonal hypoxic areas (Rabalais & Turner 2001, Turner et al. 2012). Massive deaths of sessile organisms and large decreases in benthic fish production during hypoxia

seasons are frequently reported (Petersen & Pihl 1995, Chan et al. 2008, Levin et al. 2009, Montagna & Froeschke 2009, Switzer et al. 2009, Thomas & Rahman 2012), while the impacts of hypoxia on mobile pelagic fish have only recently come into focus (Ekau et al. 2010). Hypoxia can subject pelagic fish to a sub-optimal physical environment, insufficient food re-

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sources, and enhanced encounter rates with predators or fishers (Eby & Crowder 2002, Stanley & Wilson 2004, Breitburg et al. 2009, Ludsin et al. 2009, Roberts et al. 2009). Assessing the impacts of hypoxia on pelagic fish is especially complicated because fish redistributions are involved. Impacts can differ across species and temporal and spatial scales. For example, in Chesapeake Bay and Lake Erie (USA), pelagic prey fish lose refuge habitats near the bottom due to hypoxia, which may force them higher into the water column and expose them to potentially higher predation mortality. Additionally, pelagic fish may experience lower prey availability, as some zooplankton can tolerate lower dissolved oxygen concentrations and use hypoxic zones as a refuge (Marcus 2001, Marcus et al. 2004, Ludsin et al. 2009, Roberts et al. 2009, Arend et al. 2011). Zooplanktivorous fish may also aggregate along the edge of the hypoxic zones in order to access the aggregations of zooplankton (Ludsin et al. 2009, Zhang et al. 2009). Predatory fish may temporarily benefit from hypoxia through increased encounter rates with forage fish that also aggregate along the edges of hypoxic areas or in warmer oxygenated surface areas (Costantini et al. 2008).

Although hypoxia-induced fish displacement in the northern Gulf of Mexico has been documented using trawl (Craig & Crowder 2005, Tyler & Targett 2007) and acoustics (Hazen et al. 2009, Zhang et al. 2009) sampling, the importance of hypoxia in this displacement relative to other habitat factors (e.g. temperature and prey availability) has not been fully evaluated, particularly for pelagic planktivores. Spatially-explicit, bioenergetics-based growth rate potential (GRP) modeling (Brandt & Kirsch 1993) offers a measure of fish habitat quality that accounts for the spatial arrangement of environmental factors (e.g. water temperature, dissolved oxygen concentration, prey density), fish physiological attributes, and fish foraging behavior to provide a spatial map of habitat quality. Many studies have demonstrated the positive relationship between GRP and habitat quality (Goyke & Brandt 1993, Nislow et al. 2000, Niklitschek & Secor 2005).

Here, our overall objective was to quantify the effect of hypoxia on species-specific habitat quality for 2 common species of pelagic planktivorous fishes in the northern Gulf of Mexico using spatially-explicit GRP models (Brandt et al. 1992). We selected age-0 Gulf menhaden *Brevoortia patronus* and age-1 bay anchovy *Anchoa mitchilli* because (1) both species are common pelagic fishes along the coasts of the Atlantic Ocean and Gulf of Mexico in the US (Sheridan 1978, McEachran & Fechhelm 1998, Smith

2001, Vaughan et al. 2007); (2) they represent different feeding guilds, with Gulf menhaden being phytoplanktivorous and bay anchovy being zooplanktivorous (McEachran & Fechhelm 1998); (3) bioenergetics parameters for both species and/or their congeners have been well documented (e.g. Luo & Brandt 1993, Luo et al. 2001); and (4) this choice provided an opportunity to directly compare the impact of hypoxia in the northern Gulf of Mexico to prior results from Chesapeake Bay using age-0 Atlantic menhaden *B. tyrannus* and age-1 bay anchovy (Luo & Brandt 1993, Luo et al. 2001, Adamack 2007, Adamack et al. 2012).

We hypothesized that bottom hypoxia would reduce habitat quality for bay anchovy during the peak hypoxic periods by reducing access to zooplankton prey as observed in Chesapeake Bay (Ludsin et al. 2009), but will have less effect on menhaden habitat quality, as Gulf menhaden mainly use the surface layer of the water column and phytoplankton are not affected by bottom layer hypoxia.

MATERIALS AND METHODS

We developed spatially-explicit GRP models for age-1 bay anchovy and age-0 Gulf menhaden. The overall model is a combined foraging model and bioenergetics model that requires spatial measures of prey density (zooplankton and phytoplankton), water temperature, and dissolved oxygen (DO). The foraging model estimates consumption as a function of water temperature, prey biomass, and DO, while the bioenergetics model uses the consumption estimates to provide an estimate of habitat quality in units of $\text{g g}^{-1} \text{ d}^{-1}$. Although GRP ($\text{g g}^{-1} \text{ d}^{-1}$) is the expected growth rate for an individual fish of a particular size in a volume of water with known habitat conditions (e.g. temperature, prey biomass, and DO), it is not necessarily a predictor of realized growth rates (Tyler & Brandt 2001) or fish distribution (Brandt et al. 1992, Mason et al. 1995, Höök et al. 2004, but see Nislow et al. 2000).

Data collection

Sampling locations. Field data were collected during 3 research cruises conducted between late July and early August in 2003, 2004, and 2006 (Fig. 1). In each year, cross-shelf (north-south) transects were sampled between the mouth of the Mississippi River and the Louisiana-Texas border. We chose transects

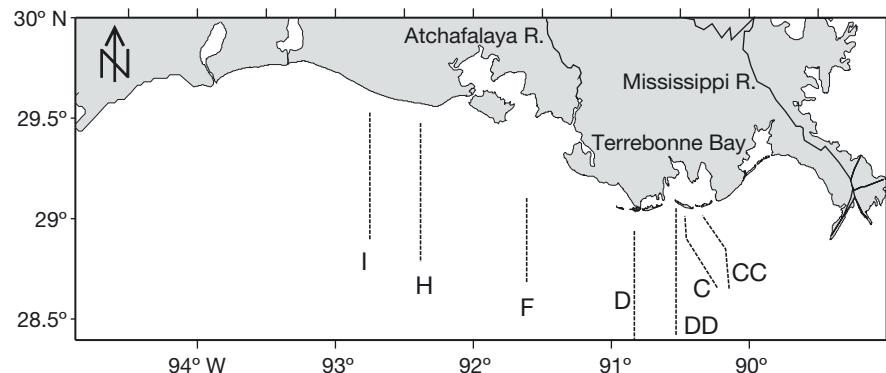


Fig. 1. Sampling transects in the northern Gulf of Mexico during 2003, 2004, and 2006. Letters indicate transects: CC, DD, D, and F in 2003; C, F, H, and I in 2004; and C and H in 2006

from each year that represented a range of DO conditions and those that had the most complete datasets. Specifically, we chose daytime Transects CC and DD, and nighttime Transects D and F from 2003, daytime Transects F and H, and nighttime Transects C and I from 2004, and Transects C and H from 2006 (Fig. 1). During 2006, Transects C and H were sampled twice, once during daytime (hereafter, C_{day} and H_{day}) and once during nighttime (hereafter, C_{night} and H_{night}). All daytime transects were surveyed from about 1 h after sunrise to about 1 h before sunset, whereas nighttime transects were surveyed from about 1 h after sunset to about 1 h before sunrise.

Biological and environmental data. For each transect, an undulating vehicle (Scanfish; GMI) equipped with a CTD (SeaBird 911), an optical DO sensor (Sea Bird SBE43), a fluorometer (Wetstar), and an optical plankton counter (OPC-1T, Focal Technologies), was towed from the RV 'Pelican' at a speed of $\sim 2 \text{ m s}^{-1}$, providing continuous measurements of water depth (m), salinity, temperature ($T, ^\circ\text{C}$), DO (mg l^{-1}), fluorescence, and zooplankton. Scanfish data were corrected for hysteresis. The DO sensor was calibrated against Winkler titration determinations of DO at fixed locations at the beginning and end of transects. Fluorescence readings were converted to chlorophyll (chl) a (CHL, $\mu\text{g l}^{-1}$) by collecting water samples for chl a determination and regressing the 2 variables (Roman et al. 2012). We followed the method of Zhang et al. (2000) using an OPC to estimate zooplankton biomass ($ZP, \text{mg l}^{-1}$). The Scanfish was undulated through the water column from about 2 m below the surface to about 2 m above the bottom, with a climb and dive speed of 0.3 m s^{-1} . The average horizontal resolution of the Scanfish was $3.5 \text{ undulations km}^{-1}$, with more undulations occurring in shallow water than in deep water. Observations were geo-referenced using a global positioning system. Data collected along each transect were interpolated using the default kriging procedure in Surfer® (v8, Golden Software), which

consisted of a linear variogram model with an anisotropy ratio of 1, anisotropy angle of 0, and a quadrant search type), and then binned ($50 \text{ m horizontal} \times 1 \text{ m vertical cells}$). Further details of our environmental data collection can be found in Roman et al. (2005), Kimmel et al. (2006, 2009), and Zhang et al. (2006).

Averages and ranges of physical and biological data were summarized for each transect across the entire water column and for the hypoxic portion of the water column only. To compare general differences in the means of measurements between the water column and hypoxic area, and differences in variables among years, we used 1-way ANOVA. The differences were considered statistically significant at $p < 0.05$.

Hypoxic areas. Hypoxic areas were defined as that part of the water column where DO was less than 2.0 mg l^{-1} from the interpolated $50 \text{ m horizontal} \times 1 \text{ m grid}$. The total hypoxic area for each transect was calculated by multiplying the total number of hypoxic cells by 50 m^2 and the percentage of the entire water column that was hypoxic (F_{hypoxia}), i.e. the percentage of the total number of cells for each transect with $\text{DO} < 2 \text{ mg l}^{-1}$.

GRP models

The GRP model combines a foraging function with a bioenergetics model (see Tables A1–A3 in the Appendix for model equations and parameters) for each fish species. The average size of age-1 bay anchovy was assumed to be 45 mm in total length and 0.7 g wet mass based on bottom trawls taken during 2006 (D. M. Mason unpubl. data). Age-0 Gulf menhaden were assumed to be 50 mm total length and 1.0 g wet mass (as per Brandt & Mason 2003). We ran GRP models in each $50 \text{ m horizontal} \times 1 \text{ m vertical cell}$, and assumed that no density-dependent foraging or feedback mechanisms existed (e.g. predation did not alter

prey biomass). For bay anchovy, the proportion of maximum consumption (P) in each cell was determined as a function of prey biomass using a Type II foraging function (Costantini et al. 2008) (Table A1). For Gulf menhaden, consumption was modeled as the volume of water filtered and was a function of phytoplankton density, gape size, swimming speed, and filtration retention efficiency (Table A2). If the menhaden consumption calculated from the volume filtered was greater than the temperature-dependent maximum consumption (C_{\max} , Table A2), consumption was set to C_{\max} and P was equal to 1.

For both species, we incorporated the effects of DO by adopting the DO function for Atlantic menhaden (Luo et al. 2001), which has also been used for other pelagic species in other ecosystems (e.g. Adamack 2007, Brandt et al. 2011). The function is a generic sigmoid relationship that takes a value between 0 and 1, and is used to scale fish consumption rates (Tables A1 & A2). We assumed that $\text{DO} < 2 \text{ mg l}^{-1}$ (hypoxia) had strong negative impacts on consumption rates, whereas $\text{DO} > 4 \text{ mg l}^{-1}$ had a minor effect, and that the half-saturation coefficient of DO for consumption was $3 \text{ mg O}_2 \text{ l}^{-1}$ (Luo et al. 2001, Brandt et al. 2011). These assumptions reflect observations that fish begin to show stress due to hypoxia when DO is $< 4 \text{ mg l}^{-1}$ (this DO level is sometimes referred to as moderate hypoxia; Stierhoff et al. 2006, Brandt et al. 2009), and often avoid hypoxic water ($< 2 \text{ mg O}_2 \text{ l}^{-1}$). Thus, the GRP was a function of fish size, temperature, food availability, and DO. We assumed that cells with $\text{GRP} > 0$ were high-quality habitat (HQH) and cells with $\text{GRP} < 0$ were low-quality habitat (LQH; Mason et al. 1995, Brandt et al. 2011).

The fraction of habitat that was LQH in each transect ($F_{-\text{GRP}}$) was calculated and compared to the fraction of habitat that was LQH in non-hypoxic water ($F_{(-\text{GRP},>2)}$) to examine the relative importance of hypoxia in determining overall habitat quality. We compared the proportion of the water with low habitat quality against the hypoxia area to see whether hypoxia was responsible for poor habitat conditions. To further evaluate the effects of DO on habitat quality, we ran both GRP models with and without the DO function and then compared the differences in average GRP and percentage of HQH and LQH between the whole transect and the hypoxic zone only.

Drivers of habitat quality

To assess the independent influence of each environmental variable on habitat quality, we ran each

GRP model using combinations of different levels of temperature, prey availability (ZP for bay anchovy and CHL for Gulf menhaden), and DO. Levels of each variable were set to values within the range of observed values (Table 1). Specifically, we used 8 DO levels (from 0.5 to 4.0 mg l^{-1} at 0.5 mg l^{-1} intervals); 31 zooplankton biomass levels (from 0 to 15 mg l^{-1} at 0.5 mg l^{-1} intervals); 31 chl *a* levels (from 0 to $15 \mu\text{g l}^{-1}$ at $0.5 \mu\text{g l}^{-1}$ intervals); and 13 temperature levels (from 20 to 32°C at 1°C intervals). We then displayed contours of GRP in the temperature versus prey parameter space for each DO level. We observed higher DO, ZP, and CHL concentrations in the field than we used in this analysis. Combined high DO and high prey concentration consistently resulted in positive GRP or HQH. By excluding these high values, we could more clearly show how GRP varies at lower levels of DO and prey concentrations.

RESULTS

Environmental conditions

Temperature. The highest temperature observed was 32.0°C in Transect H during 2004, and the lowest was 20.7°C in Transect CC during 2003 (Table 1). Average water-column temperatures differed slightly across years, ranging from 28.0°C in 2003 to 29.2°C in 2006 (Table 1). Average temperatures for all 3 years were near optimal for bay anchovy (27°C ; see Appendix 1) and Gulf menhaden (28 – 29°C ; see Appendix 2) prey consumption rates. With the exception of Transect I in 2004, for which the hypoxic area had approximately the same average temperature as the entire water column, the average temperatures for hypoxic areas in each year were colder than the averages for the entire water column (Tables 1 & 2). Despite this, average water temperatures in the hypoxic zone were near optimal for both anchovy and menhaden consumption during 2006, and only slightly lower than optimal during 2003 and 2004 (with the exception of Transect I during 2004).

Dissolved oxygen. Based on the fraction of the water column that was hypoxic (F_{hypoxia}), 2003 (0.03–0.07) and 2004 (0.04–0.15) appeared to be mildly to moderately hypoxic years, while 2006 (0.15–0.26) was a strongly hypoxic year (Table 2, Figs. 2–4). During 2006, as much as 26% of the water column was hypoxic along some transects, with an average of 19% (Table 2, Fig. 4), whereas no more than 7% of the water column was hypoxic along transects during 2003, with an average of 5% (Table 2, Fig. 2),

Table 1. Mean \pm SD (range in parentheses) of each environmental variable observed during sampling seasons across the entire water column of each transect in the northern Gulf of Mexico. 'Duration' shows the hours that Scanfish was underwater. 'Length' is the length of each transect. 'Average' rows are the averages of the means of environmental variables of transects during a sampling year. DO: dissolved oxygen; CHL: chlorophyll *a*; ZP: zooplankton biomass

Year	Transect	Duration (h)	Length (km)	Temperature (°C)	DO (mg l ⁻¹)	CHL (μg l ⁻¹)	ZP (mg l ⁻¹)
2003	Average			28.0 \pm 0.5	5.4 \pm 0.2	5.3 \pm 0.9	2.3 \pm 0.5
	C	3.4	36	27.2 \pm 2.5 (20.7–29.9)	5.2 \pm 1.7 (1.5–7.3)	4.2 \pm 1.3 (1.9–10.2)	1.5 \pm 1.2 (0.1–12.0)
	DD	3.0	32	28.4 \pm 1.5 (24.4–30.2)	5.7 \pm 1.7 (0.3–7.7)	6.3 \pm 3.1 (2.6–20.6)	2.7 \pm 1.6 (0.6–13.4)
	D	2.9	31	28.0 \pm 1.6 (23.9–30.6)	5.3 \pm 1.8 (0.8–8.1)	5.6 \pm 2.7 (1.9 \pm 25.5)	2.3 \pm 1.7 (0.2–11.9)
	F	2.6	28	28.2 \pm 1.6 (24.9–30.2)	5.4 \pm 1.6 (0.9–8.0)	5.1 \pm 2.2 (1.4–12.5)	2.6 \pm 1.2 (0.4–9.5)
2004	Average			28.7 \pm 0.8	4.8 \pm 0.4	4.6 \pm 1.4	1.6 \pm 0.4
	C	3.9	37	27.7 \pm 2.6 (22.4–31.3)	4.2 \pm 1.5 (1.1–6.6)	2.6 \pm 0.7 (1.0–6.4)	1.0 \pm 0.8 (<0.1–6.7)
	F	2.6	26	28.7 \pm 2.1 (24.6–31.6)	5.0 \pm 1.7 (1.6–7.1)	5.1 \pm 1.1 (2.1–8.7)	1.4 \pm 0.7 (0.2–6.0)
	H	2.4	22	28.9 \pm 2.2 (24.6–32.0)	5.0 \pm 2.0 (1.3–8.1)	5.2 \pm 3.0 (1.6–23.0)	1.9 \pm 1.0 (0.2–8.9)
	I	3.7	36	29.6 \pm 0.5 (28.4–30.7)	4.8 \pm 2.0 (1.3–7.2)	5.6 \pm 1.8 (1.6–14.0)	1.9 \pm 0.7 (0.5–8.8)
2006	Average			29.2 \pm 0.2	4.5 \pm 0.4	3.1 \pm 0.8	2.3 \pm 0.8
	C _{day}	5.6	38	29.3 \pm 1.2 (25.4–31.2)	4.0 \pm 2.1 (0.7–6.6)	4.2 \pm 2.1 (1.2–19.2)	3.4 \pm 1.9 (0.3–15.6)
	C _{night}	4.4	38	29.4 \pm 1.1 (25.6–30.8)	4.4 \pm 1.8 (0.6–6.3)	3.0 \pm 1.5 (1.0–8.7)	2.5 \pm 1.4 (0.1–8.9)
	H _{day}	1.4	14	29.0 \pm 1.3 (25.5–30.5)	5.0 \pm 1.9 (0.1–6.6)	2.4 \pm 0.8 (0.4–5.7)	1.5 \pm 1.1 (0–5.2)
	H _{night}	5.5	55	29.2 \pm 1.4 (25.9–30.5)	4.6 \pm 1.9 (0.2–6.4)	2.8 \pm 1.1 (1.4–6.9)	1.9 \pm 1.1 (0.3–9.6)

Table 2. Mean \pm SD (range in parentheses) of each environmental variable observed during sampling seasons in the hypoxic areas (water with dissolved oxygen, DO < 2 mg l⁻¹). 'F_{hypoxia}' indicates the spatial fraction of the water column that was hypoxic. The 'Average' rows are the average of the mean environmental variables of transects during a sampling year. CHL: chlorophyll *a*; ZP: zooplankton biomass

Year	Transect	Temperature (°C)	DO (mg l ⁻¹)	CHL (μg l ⁻¹)	ZP (mg l ⁻¹)	F _{hypoxia}
2003	Average	25.1 \pm 1.2 (23.3–25.8)	1.4 \pm 0.3 (1.0–1.8)	5.0 \pm 2.2 (3.1–8.1)	1.8 \pm 1.0 (1.0–3.3)	0.05 \pm 0.02
	C	23.3 \pm 2.4 (21.1–27.3)	1.8 \pm 0.1 (1.5–2.0)	3.1 \pm 0.8 (2.2–4.5)	1.0 \pm 0.4 (0.4–2.9)	0.03
	DD	25.7 \pm 0.3 (25.3–26.6)	1.0 \pm 0.5 (0.3–2.0)	4.5 \pm 0.4 (3.4–5.6)	1.8 \pm 0.7 (0.6–3.0)	0.06
	D	25.8 \pm 0.3 (25.6–26.5)	1.4 \pm 0.3 (0.8–2.0)	4.1 \pm 0.3 (3.6–5.0)	1.2 \pm 0.4 (0.5–2.0)	0.07
	F	25.6 \pm 0.3 (25.1–26.3)	1.5 \pm 0.3 (0.9–2.0)	8.1 \pm 0.8 (6.5–9.3)	3.3 \pm 0.5 (2.6–4.4)	0.04
2004	Average	26.7 \pm 2.0 (25.5–29.7)	1.7 \pm 0.2 (1.5–1.8)	4.8 \pm 2.2 (1.6–6.4)	1.3 \pm 0.4 (0.8–1.6)	0.10 \pm 0.05
	C	25.5 \pm 0.8 (24.0–27.8)	1.5 \pm 0.3 (1.1–2.0)	1.6 \pm 0.4 (1.2–2.7)	0.8 \pm 0.4 (0.3–1.6)	0.10
	F	25.7 \pm 0.2 (25.2–26.3)	1.8 \pm 0.1 (1.6–2.0)	5.9 \pm 0.7 (4.0–6.8)	1.0 \pm 0.4 (0.4–2.1)	0.04
	H	26.0 \pm 0.5 (25.2–27.6)	1.7 \pm 0.2 (1.3–2.0)	5.2 \pm 0.5 (3.8–6.4)	1.6 \pm 0.6 (0.5–2.9)	0.10
	I	29.7 \pm 0.3 (29.3–30.4)	1.7 \pm 0.2 (1.3–2.0)	6.4 \pm 1.3 (4.4–10.5)	1.6 \pm 0.6 (0.6–4.2)	0.15
2006	Average	27.7 \pm 0.4 (27.3–28.1)	1.3 \pm 0.0 (1.3–1.3)	4.1 \pm 0.6 (3.8–4.9)	2.9 \pm 1.3 (1.7–4.6)	0.19 \pm 0.05
	C _{day}	28.1 \pm 0.6 (27.0–29.4)	1.3 \pm 0.3 (0.7–2.0)	4.9 \pm 2.8 (2.1–19.2)	4.6 \pm 2.2 (0.4–15)	0.26
	C _{night}	27.9 \pm 0.6 (26.7–29.1)	1.3 \pm 0.3 (0.6–2.0)	3.8 \pm 1.5 (2.1–8.7)	3.1 \pm 2.1 (0.1–8.9)	0.16
	H _{day}	27.3 \pm 0.7 (26.1–28.5)	1.3 \pm 0.4 (0.1–2.0)	3.8 \pm 0.4 (2.3–4.6)	1.7 \pm 1.3 (0.1–5.2)	0.15
	H _{night}	27.3 \pm 0.7 (26.0–29.1)	1.3 \pm 0.4 (0.2–2.0)	3.8 \pm 0.7 (2.4–6.1)	2.1 \pm 0.8 (0.5–5.4)	0.17

and 15% during 2004, with an average of 10% (Table 2, Fig. 3). This reflects the broader spatial-temporal patterns in hypoxia observed by Rabalais et al. (2007). Average water-column DO for all transects and years was above 4 mg l⁻¹, with the lowest average DO (4.0 mg l⁻¹) observed during 2006 (Table 1). The average DO concentrations for the hypoxic areas each year were >1.0 mg l⁻¹ (Table 2).

Chlorophyll *a*. CHL distributions were patchy, ranging from 1 to >10 μg l⁻¹ within a single transect (Table 1, Figs. 2–4). Water-column average CHL varied across years and ranged from 3.1 μg l⁻¹ in 2006 to 5.3 μg l⁻¹ in 2003 (Table 1). Average CHL in 2006 was significantly lower than in 2003, but not significantly lower ($p = 0.1$) than that observed in 2004. The average CHL concentrations in the hypoxic areas were

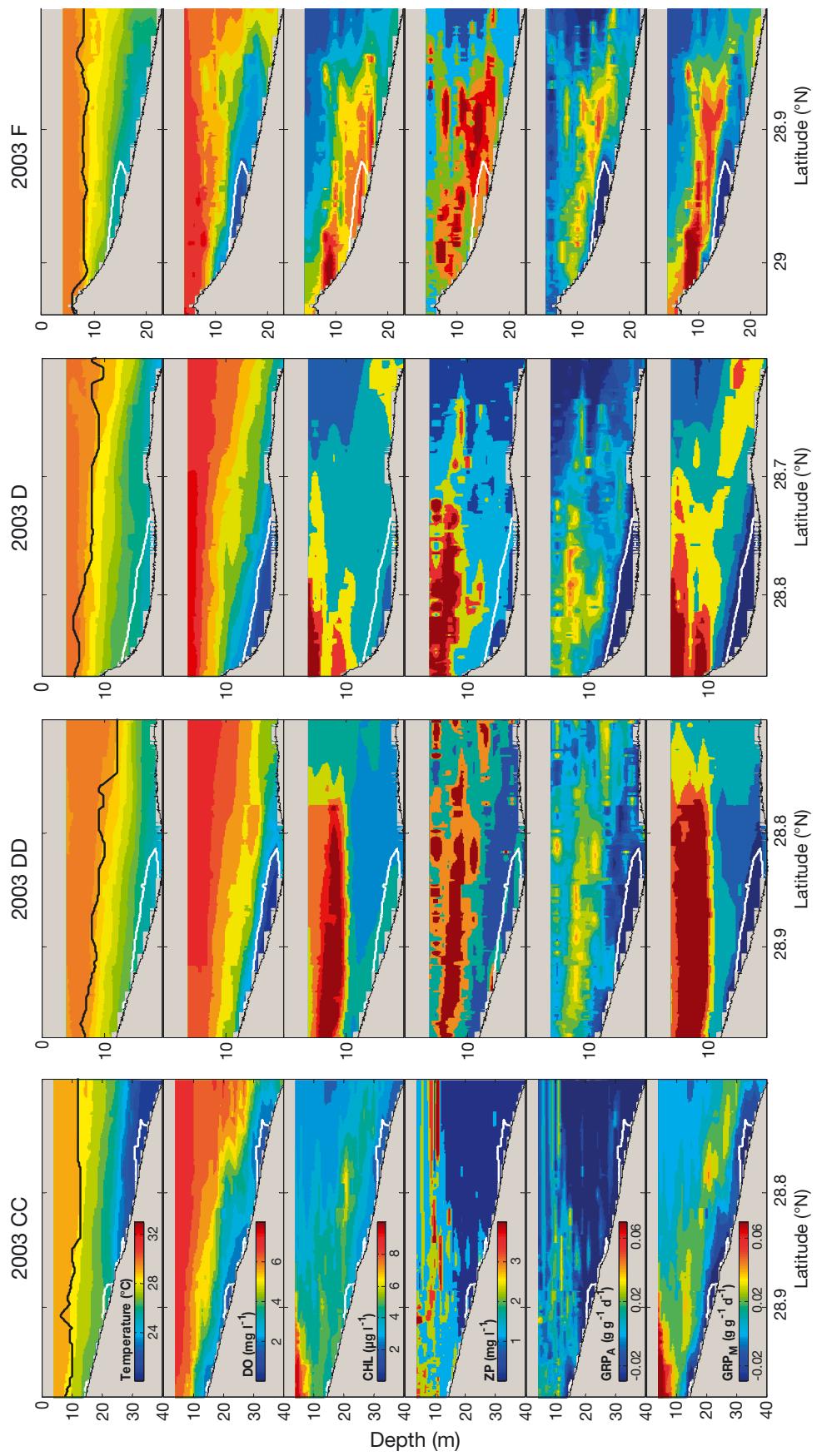


Fig. 2. Spatial distribution of water temperature ($^{\circ}\text{C}$), dissolved oxygen ($\text{DO}; \text{mg l}^{-1}$), chlorophyll *a* concentration ($\text{CHL}; \mu\text{g l}^{-1}$), total zooplankton biomass ($\text{ZP}; \text{mg l}^{-1}$), and growth rate potential of bay anchovy ($\text{GRP}_{\text{Ai}}; \text{g g}^{-1} \text{d}^{-1}$) and Gulf menhaden ($\text{GRP}_{\text{M}}; \text{g g}^{-1} \text{d}^{-1}$) for Transects CC, DD, D, and F in 2003. Black line in upper panels indicates the pycnocline; white line indicates the oxycline (2 mg $\text{O}_2 \text{l}^{-1}$). Note the different scales on the y-axes, with water surface (0 m) at the top

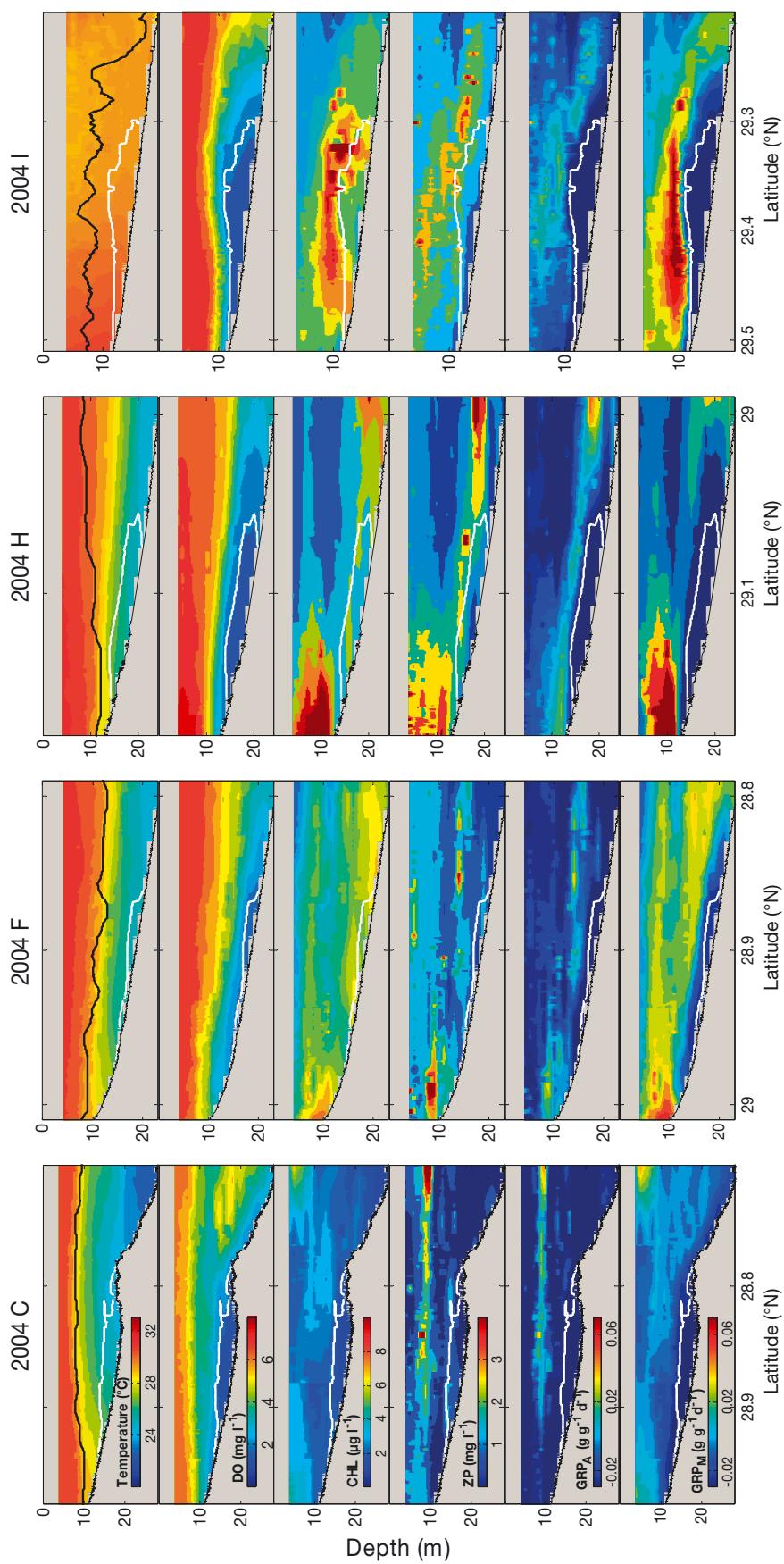


Fig. 3. Spatial distributions of water temperature ($^{\circ}\text{C}$), dissolved oxygen ($\text{DO}; \text{mg l}^{-1}$), chlorophyll *a* concentration ($\text{CHL}; \mu\text{g l}^{-1}$), total zooplankton biomass ($\text{ZP}; \text{mg l}^{-1}$), and growth rate potential of bay anchovy ($\text{GRPA}; \text{g g}^{-1} \text{d}^{-1}$) and Gulf menhaden ($\text{GRPM}; \text{g g}^{-1} \text{d}^{-1}$) for Transects C, F, H, and I in 2004. Black line in upper panels indicates the pycnocline; white line indicates the oxycline (2 $\text{mg O}_2 \text{l}^{-1}$). Note the different scales on the y-axes, with water surface (0 m) at the top

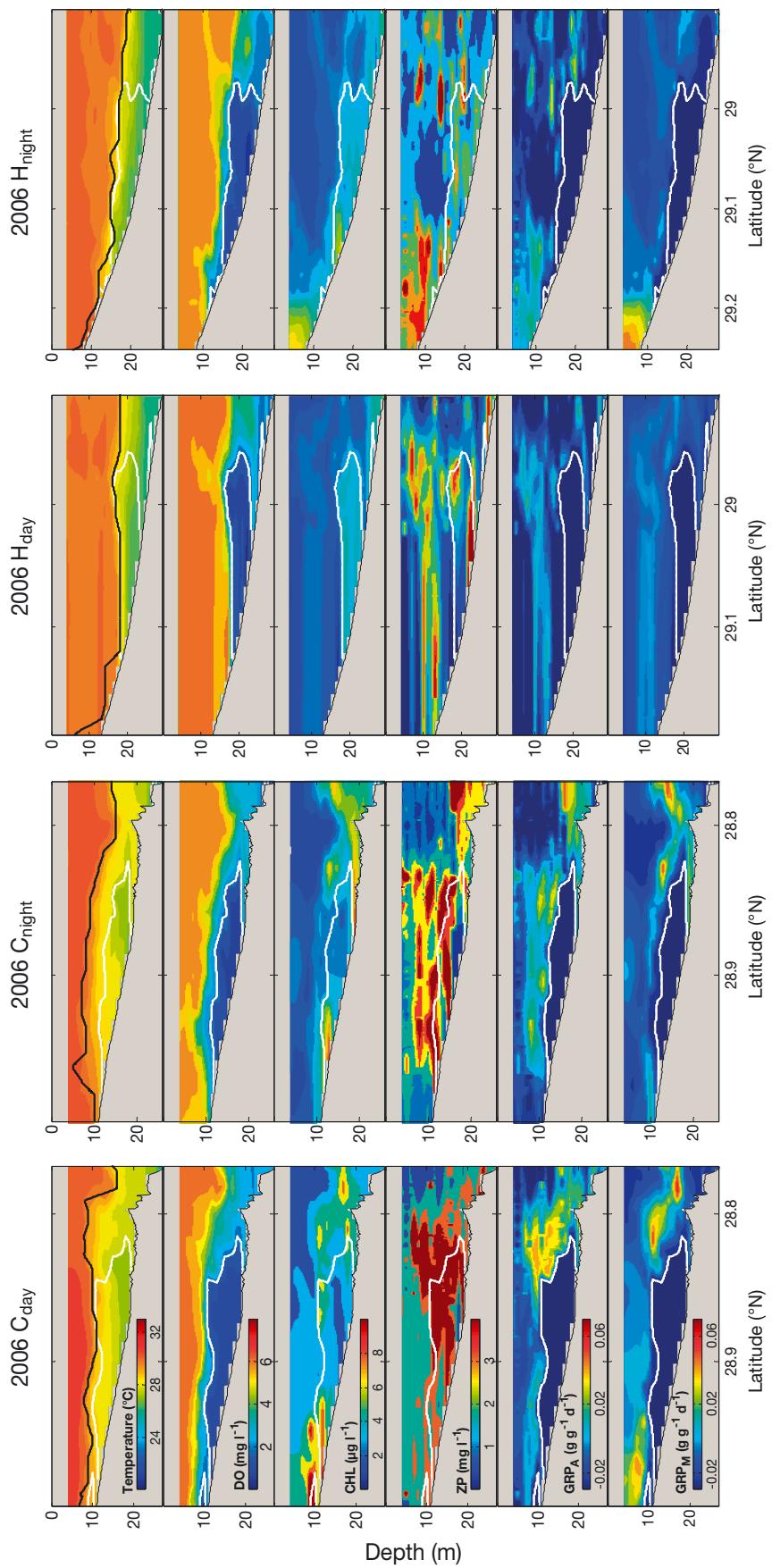


Fig. 4. Spatial distributions of water temperature (°C), dissolved oxygen (DO; mg l⁻¹), chlorophyll *a* concentration (CHL; µg l⁻¹), total zooplankton biomass (ZP; mg l⁻¹), and growth rate potential of bay anchovy (GRP_{Ai}; g g⁻¹ d⁻¹) and Gulf menhaden (GRP_M; g g⁻¹ d⁻¹) for Transects C and H in 2006. Black line in upper panels indicates the pycnocline; white line indicates the oxycline (2 mg O₂ l⁻¹). Note the different scales on the y-axes, with water surface (0 m) at the top

not significantly different from those across the entire water column, which indicated that hypoxic areas had approximately the same food concentrations as the whole water column for Gulf menhadens.

Zooplankton. Spatial variability in ZP biomass was evident across our transects, with biomass ranging from $<0.1 \text{ mg l}^{-1}$ (2004 C) to 15.6 mg l^{-1} (2006 C_{day}). Average ZP biomass across transects was 2.3 mg l^{-1} during 2003 and 2006, and 1.6 mg l^{-1} during 2004. During 2003 and 2004, average ZP biomass was significantly lower in the hypoxic areas than across the entire water column for all transects except Transect F in 2003. In contrast, all 4 transects in 2006 had higher (albeit non-significant, $p = 0.10$) average ZP biomass in the hypoxic area than across the entire transect (Tables 1 & 2, Fig. 4). The data indicated that food availability for bay anchovy was poorer in the hypoxic areas during the mildly hypoxic years 2003 and 2004 than in the whole water column, but was better in the hypoxic areas than in the whole water column during the strongly hypoxic year 2006.

Fish habitat quality

Hypoxic areas. Hypoxic areas were always low-quality habitats (i.e. negative GRP values) for bay

anchovy and menhadens (Figs. 2–5), even though portions of these areas had high prey concentrations and suitable temperatures (Table 2). In fact, the percentage of HQH in the hypoxic areas was 0 for both species (Fig. 6). Without hypoxia (DO function removed from the model), the average GRP and HQH within the hypoxic areas for both menhadens and anchovy (Figs. 5 & 6) increased. The percentage of HQH in the hypoxic areas, without the DO function being included in the model, was often close to or equal to 100% for menhadens, except along Transect C in 2004 due to low food concentrations. For anchovy, the HQH in hypoxic zones without the DO function ranged from 7% (2004 C) to 100% (2003 F) and on average was highest during 2006 (73%).

Water column. For bay anchovy, the average GRP for each transect was generally low across years and transects (Fig. 7). Without hypoxia, the water-column average GRP increased 20 to 335% during 2003 (note that Transect D transitioned from a negative to a positive average GRP), 17 to 73% during 2004, and 37 to 182% during 2006 (note GRP along Transects C_{day} and C_{night} became positive) compared to simulations that included the DO function (Fig. 7).

For Gulf menhadens, the average GRP was generally positive in 2003 and 2004 (except Transect C in 2004) but was negative during 2006 (Fig. 7). Without hypoxia, the water-column average GRP increased

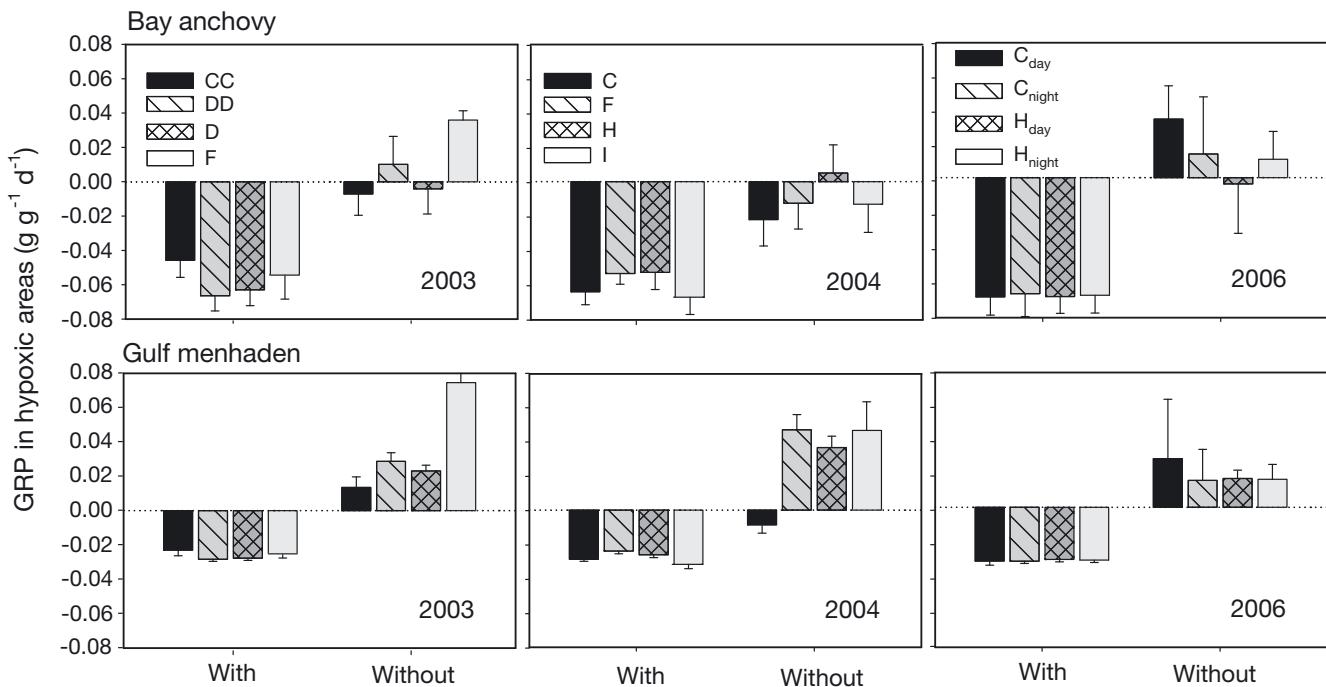


Fig. 5. *Anchoa mitchilli* and *Brevoortia patronus*. Mean \pm SD growth rate potential (GRP) in the hypoxic area (dissolved oxygen, DO $< 2 \text{ mg l}^{-1}$) with and without the DO function in the model for 3 years (2003, 2004, and 2006) for bay anchovy and Gulf menhadens

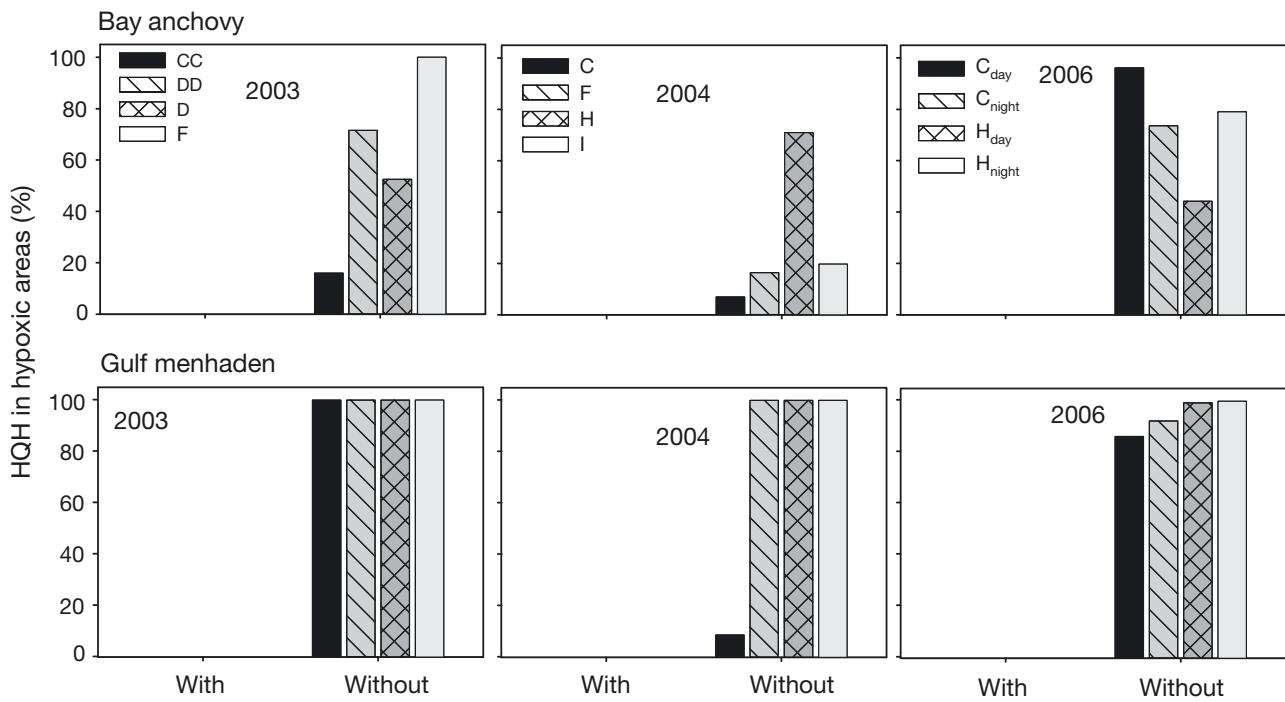


Fig. 6. *Anchoa mitchilli* and *Brevoortia patronus*. Percentage of cells that are high-quality habitat (HQH; GRP > 0) in the hypoxic areas (dissolved oxygen, DO < 2 mg l⁻¹) with and without the DO function in the model and for 3 years (2003, 2004, and 2006) for bay anchovy and Gulf menhaden. Note that values are 0 with the DO function in the model

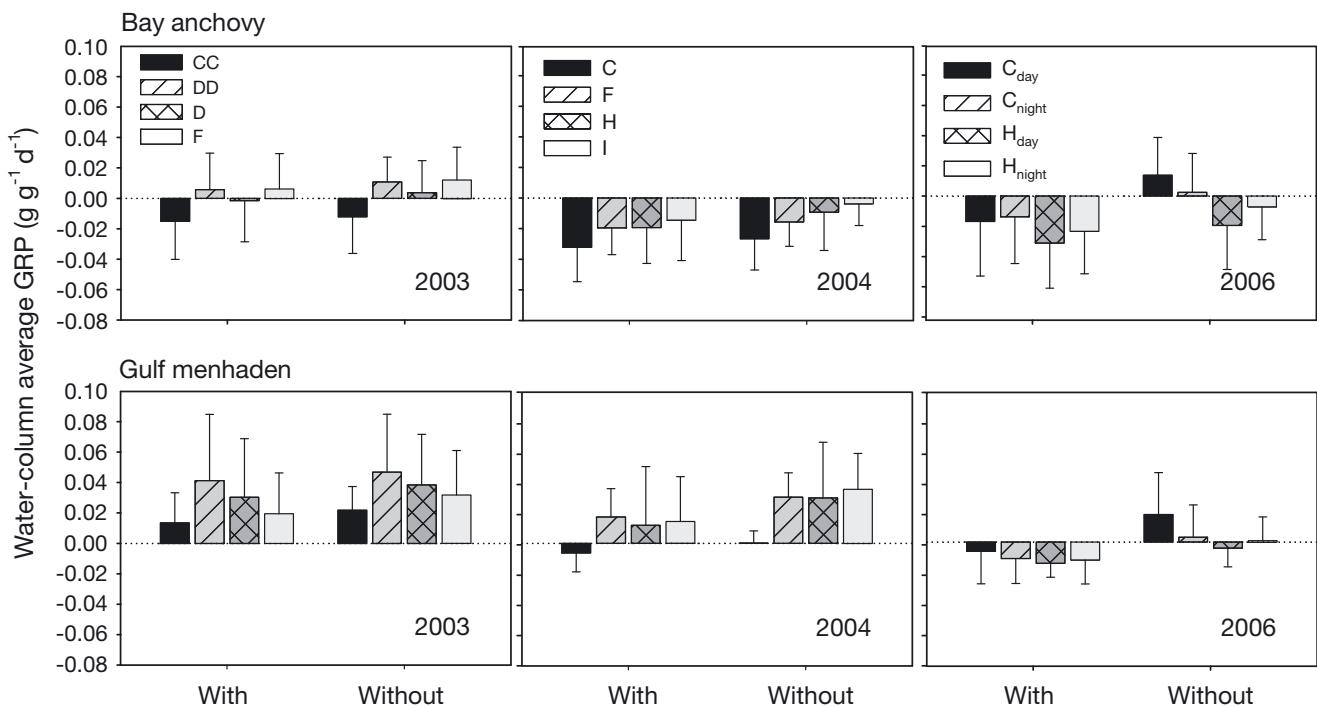


Fig. 7. *Anchoa mitchilli* and *Brevoortia patronus*. Mean ± SD growth rate potential (GRP) in the water column (the entire transect) with and without the dissolved oxygen (DO) function in the model for 3 years (2003, 2004, and 2006) for bay anchovy and Gulf menhaden

11 to 51% during 2003, 60 to 127% during 2004, and 62 to 346% during 2006 (note that Transects C_{day} and C_{night} transitioned from negative to positive GRP) compared to simulations without the DO function.

In general, the percentage of HQH in the water column was lower for bay anchovy than Gulf menhaden during 2003 and 2004 (Fig. 8). For anchovy, the percentage of HQH ranged from 31 to 68% during 2003 and 9 to 31% during 2004. In contrast, the percentage of HQH ranged from 72 to 89% during 2003 and from 30 to 82% during 2004 for Gulf menhaden. In 2006, the percentage of HQH for both species was similarly low (up to 38% for bay anchovy and 39% for Gulf menhaden). Without hypoxia in the model, the percentage of HQH increased by 8 to 15% during 2003, 18 to 61% during 2004, and 41 to 83% during 2006 for bay anchovy, and by 12 to 21% during 2003, 17 to 61% during 2004, and 96 to >100% (note the extremely low HQH for H_{day}) during 2006 for Gulf menhaden (Fig. 8).

Across years and transects, the average fraction of the water column that was hypoxic (F_{hypoxia}) was 0.12 (Table 2), whereas the average fraction of the water column that was considered LQH (F_{-GRP}) for bay anchovy and Gulf menhaden was 0.55 (Table 3). Generally, the LQH fractions of the oxygenated water column (>2 mg O₂ l⁻¹; F_(-GRP,>2)) were not much

different from the fraction for the entire water column and was less than 0.05 on average. Even in the most extreme situation, when 26% of the water column was hypoxic (2006 C_{day}), the percentage of the oxygenated water column that was LQH (47%) was only modestly lower than that of the entire water column (61%). The small differences between F_{-GRP} and F_(-GRP,>2) indicated that DO had little effect on the overall habitat quality. The regressions between Diff and F_{hypoxia} (Table 3) showed strong positive relationship between the impacts of hypoxia on the habitat quality and the sizes of hypoxic areas. For bay anchovy, the R² values for the regression were 0.82, 0.80, 0.81, and 0.71 for 2003, 2004, 2006, and the 3 years combined, respectively (Table 3). For Gulf menhaden, the R² of the regressions were 1.00, 0.71, 0.95, and 0.35 for 2003, 2004, 2006, and the 3 years combined, respectively (Table 3). The positive relationship indicated that the larger the hypoxic area was, the more hypoxia contributed to the overall water-column LQH.

Drivers of habitat quality (GRP)

For both fish species, when DO was <1.5 mg l⁻¹, temperature appeared to be slightly more important

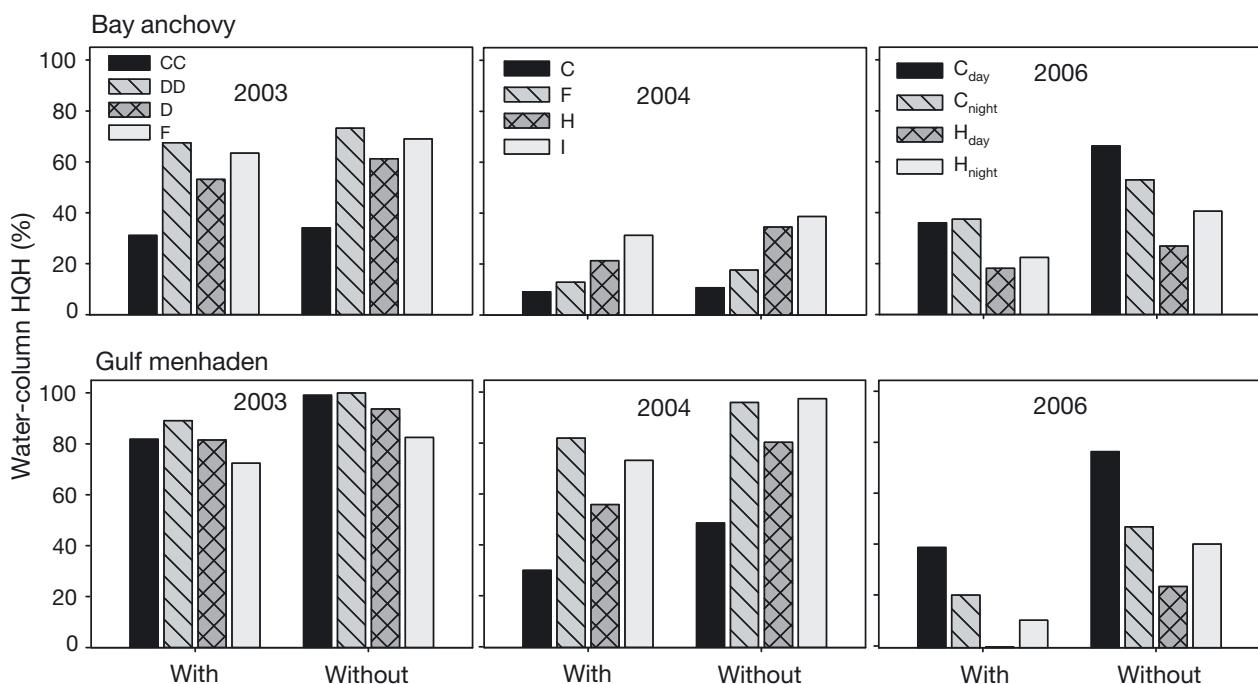


Fig. 8. *Anchoa mitchilli* and *Brevoortia patronus*. Percentage of cells that are high-quality habitat (HQH; GRP > 0) in the whole water column (the entire transect) with and without the dissolved oxygen (DO) function in the model and for 3 years (2003, 2004, and 2006) for bay anchovy and Gulf menhaden

than prey concentration in determining GRP, with lower water temperatures resulting in higher GRP. When DO was 2.0 mg l^{-1} , prey concentrations more strongly affected GRP. The combination of high prey concentrations and low temperatures led to the highest GRP predictions; however, all of the GRP predictions were negative; indicating that the habitat quality was poor and DO was the major controlling factor.

For bay anchovy, when DO was 2.5 mg l^{-1} or greater, GRP became positive (Fig. 9) for most combinations of temperature and ZP. GRP increased with increases in prey concentrations and was less affected by water temperature until temperature exceeded 30°C . When DO was $\geq 3.0 \text{ mg l}^{-1}$, higher ZP resulted in higher GRP under the same water temperatures; highest GRPs were for water temperatures that ranged between 23 and 28°C . ZP concentrations as low as 1.1 mg l^{-1} resulted in positive GRP at 20°C . GRP (or habitat

Table 3. Comparison of the amounts of low-quality habitat (LQH, where growth rate potential, GRP < 0) in hypoxic areas and the whole water columns. $F_{-\text{GRP}}$: spatial fraction of the water column with a negative GRP; $F_{(-\text{GRP},>2)}$: spatial fraction of oxygenated water column ($> 2 \text{ mg O}_2 \text{ l}^{-1}$) with a negative GRP; Diff: difference between $F_{-\text{GRP}}$ and $F_{(-\text{GRP},>2)}$; F_{hypoxia} : spatial fraction of the water column having hypoxia for each transect. * and ** indicate the r^2 values of the linear regression between Diff and F_{hypoxia} for individual years and for 2003 and 2006 combined, respectively

Year	Transect	$F_{-\text{GRP}}$	$F_{(-\text{GRP},>2)}$	Diff	F_{hypoxia}	r^2
Bay anchovy						
2003	C	0.69	0.68	0.01	0.03	0.7359**
	DD	0.32	0.28	0.04	0.06	
	D	0.47	0.43	0.04	0.07	
	F	0.37	0.34	0.03	0.04	
	Mean	0.46	0.43	0.03	0.05	0.8167*
2006	C_{day}	0.64	0.51	0.13	0.26	
	C_{night}	0.63	0.55	0.08	0.16	
	H_{day}	0.82	0.79	0.03	0.15	
	H_{night}	0.78	0.73	0.05	0.17	
	Mean	0.72	0.65	0.07	0.19	0.8102*
Gulf menhaden						
2003	C	0.18	0.16	0.02	0.03	0.3839**
	DD	0.11	0.06	0.05	0.06	
	D	0.18	0.12	0.06	0.07	
	F	0.28	0.25	0.03	0.04	
	Mean	0.19	0.15	0.04	0.05	1.0*
2006	C_{day}	0.61	0.47	0.14	0.26	
	C_{night}	0.79	0.75	0.04	0.16	
	H_{day}	1.00	1.00	0.00	0.15	
	H_{night}	0.89	0.87	0.02	0.17	
	Mean	0.82	0.77	0.05	0.19	0.9492*
Overall mean		0.55	0.50	0.05	0.12	

quality) decreased sharply at temperatures above 30°C , and became negative at temperatures above 32°C regardless of prey and DO concentrations.

For Gulf menhaden, positive GRP first occurred when DO was 2.5 mg l^{-1} and CHL was above $6.5 \mu\text{g l}^{-1}$ (Fig. 10). GRP increased with increases in prey availability and water temperature. When DO was greater than 3.0 mg l^{-1} , CHL was the dominant controlling factor within a range of CHL (1.8 – $15 \mu\text{g l}^{-1}$), resulting in positive and high GRP (or HQH) until water temperature exceeded 31°C . GRP (or habitat quality) decreased sharply at temperatures above 31°C , and became negative at temperatures above 32°C , regardless of food concentrations and DO conditions.

DISCUSSION

We hypothesized that hypoxia in the northern Gulf of Mexico negatively impacts habitat quality for bay anchovy but would only have a minimal impact for Gulf menhaden. In general, hypoxia resulted in the bottom being LQH for both species; however, on average, hypoxic areas account for 11% of the total habitat area, and 83% (for bay anchovy) and 72% (for menhaden) of the LQH was found in the oxygenated portion of the water column. From the perspective of the entire water column, hypoxic areas had only a small effect on overall habitat quality, suggesting that other factors, such as prey availability and water temperature, played a more important role in determining habitat quality for bay anchovy and Gulf menhaden in the northern Gulf of Mexico. For example, high CHL caused average GRP to be highly positive transect-wide for menhaden during 2003 and 2004, resulting in a high percentage of HQH across transects. Low CHL in transect C in 2004 resulted in the average GRP being negative and resulted in a low percentage of HQH across the transect. Low CHL during 2006 also resulted in low transect-wide average GRP and low percentage of HQH for Gulf menhaden across all transects. Although water-column average ZP and CHL were high enough to support positive growth and the water temperature was optimal for prey consumption during 2006, transect-wide average GRPs were often negative and the percentage of HQH was low. The reason was that phytoplankton and zooplankton distributions were very patchy, resulting in a small percentage of the water column being HQH and a much larger percentage being LQH. Other studies also observed this patchy distribution of food that resulted

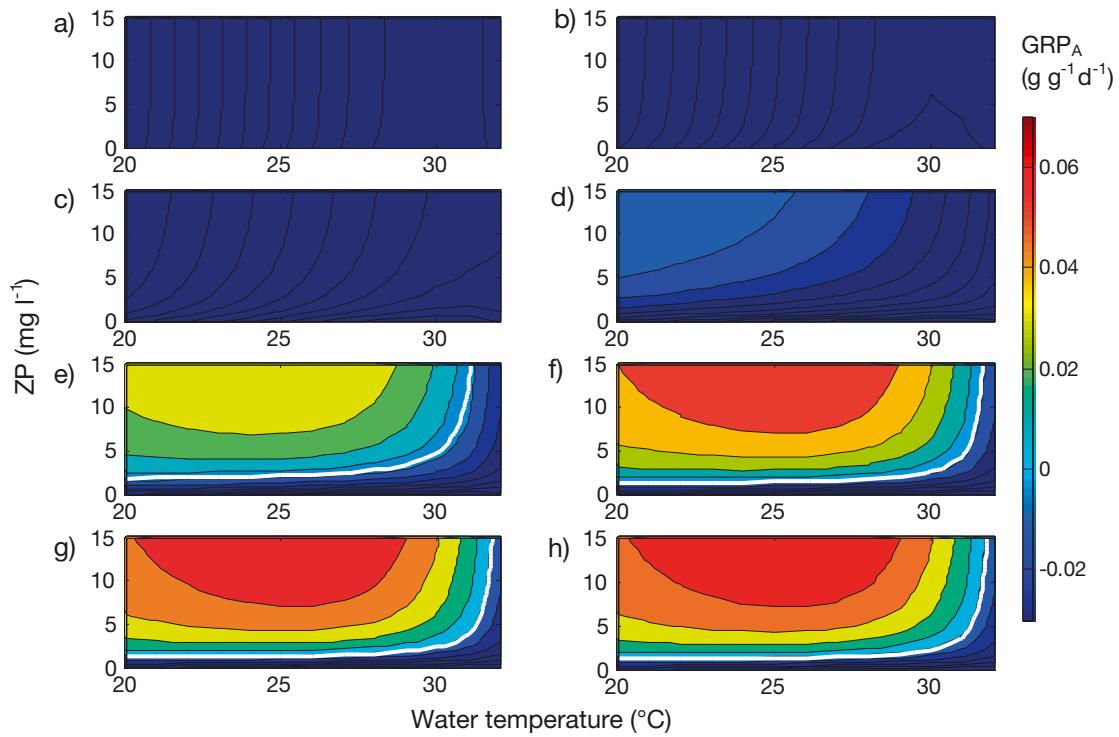


Fig. 9. *Anchoa mitchilli*. Effect of water temperature, zooplankton biomass (ZP), and dissolved oxygen (DO) on bay anchovy growth rate potential (GRP_A , $\text{g g}^{-1} \text{d}^{-1}$). DO concentration (mg l^{-1}) incremented by 0.5 mg l^{-1} from (a) 0.5 mg l^{-1} to (h) 4.0 mg l^{-1} . Thick white lines indicate the contour lines of $\text{GRP} = 0 \text{ g g}^{-1} \text{d}^{-1}$

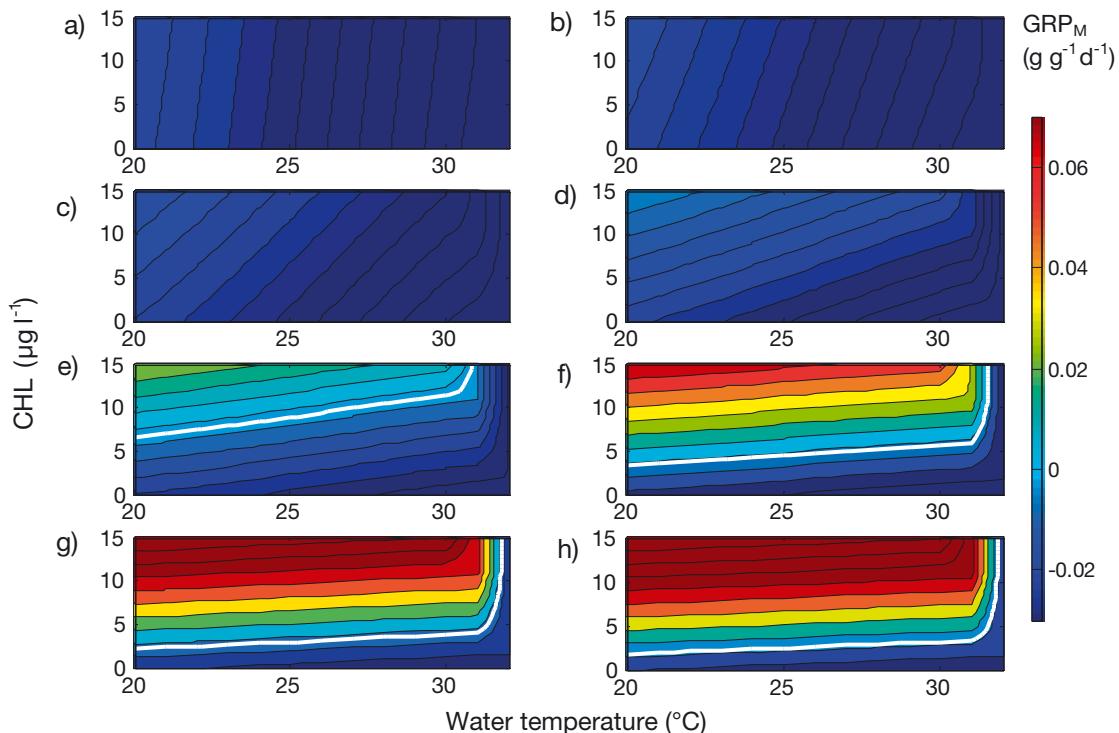


Fig. 10. *Brevoortia patronus*. Effect of water temperature, chlorophyll (CHL), and dissolved oxygen (DO) on Gulf menhaden growth rate potential (GRP_M , $\text{g g}^{-1} \text{d}^{-1}$). DO concentration (mg l^{-1}) incremented by 0.5 mg l^{-1} from (a) 0.5 mg l^{-1} to (h) 4.0 mg l^{-1} in (h). Thick white lines indicate the contour lines of $\text{GRP} = 0 \text{ g g}^{-1} \text{d}^{-1}$

in large percentage of LQH in the water (e.g. Brandt et al. 2011). Hypoxia may enhance this patchy distribution. Roman et al. (2012) suggested that bottom water hypoxia does not affect the amount of zooplankton in the total water column of the Gulf of Mexico or the areal integration of zooplankton standing stock, but shifts their vertical distribution up in the water column during the day. Unfortunately, we were not able to include this hypoxia effect on fish habitat quality by redistributing zooplankton. The distributions of zooplankton were the same with and without hypoxia scenarios in our simulation.

Observed water temperatures along transects were close to the optimal temperatures, 27°C for bay anchovy and 28–29°C for Gulf menhaden. However, the highest water temperatures (>32°C) observed are close to temperatures that could restrict fish growth regardless of prey and DO concentrations. The highest water temperatures tended to be in the nearshore area and near the surface of the water column. During warm years, menhaden may be pushed away from coastal areas and 'squeezed' into the middle portion of the water column (where phytoplankton concentrations are often low) by the 'hot' water nearshore and near the surface of the water column and by hypoxia in the lower water column. This type of 'squeeze' was originally reported by Coutant (1985) for striped bass in a reservoir and has also been documented for rainbow smelt *Osmerus mordax* in Lake Erie (Arend et al. 2011, Brandt et al. 2011). Moreover, warm temperatures likely increase the low-DO tolerance threshold (Vaquer-Sunyer & Duarte 2011). Water temperatures near 32°C could worsen thermal conditions and further reduce fish habitat in this region.

The GRP model represents an instantaneous snapshot of habitat quality and therefore does not consider competition for food or predation-induced local prey depletions. Mortality (predation or fishing) and competition for food are known to be influenced by hypoxia. For example, hypoxia may enhance jellyfish abundance in the northern Gulf of Mexico, as jellyfish are often more tolerant of low dissolved oxygen than fish and are able to consume large amounts of zooplankton that are potentially inaccessible to fish due to hypoxia (Keister et al. 2000, Purcell et al. 2001, Miller & Graham 2012). Aggregation of prey fish along the edge of hypoxic zones or patchy HQH may also lead to higher predation or fishing mortality (Smith 2001). In addition, our assessed impacts of hypoxia on habitat quality were highly fish-growth related. In Chesapeake Bay, GRP modeling studies used to quantify the effects of hypoxia on pelagic habitat quality for Atlantic menhaden *Brevoortia*

tyrannus (a phytoplanktivore) showed similar results, in that changes in DO concentrations had relatively little effect on habitat quality and growth rates of juvenile Atlantic menhaden in the Patuxent River (Luo et al. 2001, Brandt & Mason 2003). Rather, habitat quality and growth rate were related to nutrient loading, phytoplankton production, and season. Luo et al. (2001) found that the carrying capacity of Atlantic menhaden in Chesapeake Bay was dependent on season, with bottlenecks occurring in early June and during the fall. They explained that these temporal bottlenecks are a natural seasonal progression of the ecosystem as menhaden grow and develop in their first year of life. Our results with Gulf menhaden are consistent with the results observed for Atlantic menhaden in Chesapeake Bay, i.e. habitat quality was a function of phytoplankton concentrations, and hypoxia had only a small effect.

For bay anchovy in Chesapeake Bay, the effects of hypoxia were more complicated. A pair of individual-based modeling studies (Adamack 2007, Adamack et al. 2012) that examined the effects of hypoxia on bay anchovy eggs, larvae, juveniles, and adults in Chesapeake Bay and the Patuxent River showed that the effects of hypoxia differed by life stage. The direct effects of hypoxia (e.g. mortality due to asphyxiation) could cause mortality rates of 60% d⁻¹ for anchovy eggs. Hypoxia indirectly affected anchovy larvae through changes in their spatial overlap with their prey and predators. For anchovy larvae, the changes in spatial distribution were found to be beneficial, with anchovy larvae having lower overlap with their predators at moderate (1–3 mg l⁻¹) levels of bottom layer hypoxia (Breitburg et al. 1999, Adamack et al. 2012) while bay-wide simulations of juvenile and adult anchovy suggested that enhanced zooplankton production due to high nutrient loadings could enhance the production of adult anchovies (Adamack 2007). Ludsin et al. (2009) found that hypoxia induced changes in spatial distribution which negatively affected bay anchovy by separating them spatially from their zooplankton prey and concentrating them in a narrower habitat space (e.g. the portion of the water column above hypoxia), which in turn increased their vulnerability to predation by striped bass (Costantini et al. 2008). Similar observations have been made in Lake Erie for zooplanktivorous fish (rainbow smelt *Osmerus mordax*, yellow perch *Perca flavescens*) which were found to have limited access to prey and were concentrated at the thermocline where they were more vulnerable to predators including walleye *Sander vitreus* (Roberts et al. 2009, Vanderploeg et al. 2009, Brandt et al. 2011). Thus, the indirect interaction

of hypoxia and food web dynamics can simultaneously negatively and positively affect intermediate consumers (e.g. zooplanktivores) by decreasing their access to prey resources and increasing their vulnerability to predators but enhance overall prey availability and provide spatial refuges from some predators. Additionally, the effects of hypoxia have been shown to vary from negative to positive by life stage.

Hypoxia impacts on bay anchovy were also evident in the northern Gulf of Mexico in our results by the increased percentage of HQH in the absence of hypoxia. However, our results showed that much of the oxic water column is already LQH, and eliminating hypoxia would only slightly decrease the percentage of LQH across transects. In contrast to results for Chesapeake Bay, habitat quality for bay anchovy in the northern Gulf of Mexico was strongly influenced by zooplankton concentration and only minimally affected by hypoxia. Moreover, our results showed that the impacts of hypoxia on habitat quality increased with the increases in the sizes of hypoxic areas. Thus, the discrepancy between ecosystems is likely due to the vertical extent of hypoxia in the northern Gulf of Mexico compared to Chesapeake Bay. In Chesapeake Bay, hypoxia may extend up to 30 m from the bottom in a 40 m water column, whereas in our study, hypoxia typically extended <10 m in a 30 m water column (Kimmel et al. 2009, Ludsin et al. 2009, Zhang et al. 2009). Thus, zooplanktivorous fish appear to be sensitive to hypoxia, in how it modifies trophic interactions through differential changes in spatial distributions and the vertical extent of hypoxia.

Hypoxia can have numerous effects on pelagic species dependent on the life stage, trophic level, the vertical extent of hypoxia, and the temporal scale of the analyses. Quantifying the impacts of hypoxia on fish populations is not an easy task given the complex interactions among co-occurring factors. Our study showed that current hypoxia at the northern Gulf of Mexico has minor negative impacts on overall habitat quality of 2 pelagic planktivorous fish species.

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Appendix. Growth rate potential (GRP) model equations and parameters

Table A1. Bioenergetics model equations for bay anchovy from Luo & Brandt (1993) with other sources as indicated. See Table A3 for parameter definitions and values. DO: dissolved oxygen

Equation	Description	Equation	Description
$GRP = [C - (R + F + U)] \cdot ED_{\text{prey}}/ED_{\text{fish}}$	Growth rate potential (g g ⁻¹ d ⁻¹)	$f_c(ZP) = ZP/(K_s + ZP)$	Zooplankton-dependent foraging scale function (dimensionless); S. A. Ludsin (unpubl. data)
$C = C_{\max} \cdot P$	Adjusted consumption (g g ⁻¹ d ⁻¹)	$R = R_{\text{std}} \cdot ACT \cdot \frac{OC}{ED_{\text{prey}}} + S$	Adjusted standard respiration (g g ⁻¹ d ⁻¹)
$C_{\max} = a_c \cdot W^{b_c} \cdot f_c(T) \cdot f_c(DO)$	Mass- and temperature-specific maximum consumption (g g ⁻¹ d ⁻¹)	$R_{\text{std}} = a_r \cdot W^{b_r} \cdot f_r(T)$	(Mass- and temperature-specific standard respiration (g O ₂ g ⁻¹ d ⁻¹)
$f_c(T) = V^X \cdot e^{X \cdot (1-V)}$	Temperature-dependent function (dimensionless)	$f_r(T) = V^X \cdot e^{X \cdot (1-V)}$	Temperature-dependent function (dimensionless)
$V = (C_{TM} - T)/(C_{TM} - C_{TO})$		$V = (R_{TM} - T)/(R_{TM} - R_{TO})$	
$X = \{Z^2 \cdot [1 + (1 + 40/Y)^{0.5}]^2\}/400$		$X = \{Z^2 \cdot [1 + (1 + 40/Y)^{0.5}]^2\}/400$	
$Y = \log_{10}(C_Q) \cdot (C_{TM} - C_{TO} + 2)$		$Y = \log_{10}(R_Q) \cdot (R_{TM} - R_{TO} + 2)$	
$Z = \log_{10}(C_Q) \cdot (C_{TM} - C_{TO})$		$Z = \log_{10}(R_Q) \cdot (R_{TM} - R_{TO})$	
$f_c(DO) = 1/(1 + e^{-(DO - I_p)/0.455})$	DO-dependent foraging scale function (dimensionless); modified from Luo et al. (2001)	$S = SDA \cdot (C - F)$	Specific dynamic action (g g ⁻¹ d ⁻¹)
$P = f_c(ZP)$	Proportion of maximum consumption (dimensionless)	$F = a_F \cdot T^{b_F} \cdot C$	Egestion (g g ⁻¹ d ⁻¹)
		$U = a_U \cdot (C - F)$	Excretion (g g ⁻¹ d ⁻¹)

Table A2. Bioenergetics model equations for Gulf menhaden from Luo et al. (2001) and Brandt & Mason (2003). See Table A3 for parameter definitions and values. DO: dissolved oxygen

Equation	Description	Equation	Description
$GRP = [C - (R + F + U)] \cdot ED_{\text{prey}} / ED_{\text{fish}}$	Growth rate potential (g g ⁻¹ d ⁻¹)	$y_1 = \frac{1}{T_2 - T_1} \ln \left[\frac{K_2(1 - K_1)}{K_1(1 - K_2)} \right]$	
$\frac{Cons}{wt} = phy \cdot gap \cdot u \cdot eff \cdot f(DO)$	Consumption (g g ⁻¹ d ⁻¹)	$K_B = \frac{K_4 e^{y_2(T_4 - T)}}{1 + K_4(e^{y_2(T_4 - T)} - 1)}$	
$phy = CHL \cdot 65 / 0.1 / 1000$	Phytoplankton concentration (g ww m ⁻³)	$y_2 = \frac{1}{T_4 - T_3} \ln \left[\frac{K_3(1 - K_4)}{K_4(1 - K_3)} \right]$	
$gap = 2.586 \cdot 10^{-8} TL^{1.798}$	Mouth open area (m ²)	$C = \min \left\{ \frac{Cons}{W}, C_{\max} \right\}$	Adjusted consumption (g g ⁻¹ d ⁻¹)
$u = \frac{216 \cdot TL}{1 + e^{-0.798T + 6.378}}$	Swimming velocity (m d ⁻¹)	$R = R_{\text{std}} \cdot ACT \cdot \frac{OC}{ED_{\text{prey}}} + S$	Respiration (g g ⁻¹ d ⁻¹)
$eff = \frac{0.5}{1 + e^{-0.0528TL + 2.97}}$	Filtration retention efficiency (dimensionless)	$R_{\text{std}} = a_r \cdot W^{b_r} \cdot f_r(T)$	Mass- and temperature-specific standard respiration (g O ₂ g ⁻¹ d ⁻¹)
$f(DO) = 1 / (1 + e^{-(DO - I_p) / 0.455})$	DO-dependent foraging scale function (dimensionless)	$ACT = 1 + \left(\frac{2.5}{1 + e^{-0.798T + 6.378}} \right)$	Temperature dependence of activity multiplier (dimensionless)
$C_{\max} = a_c \cdot W^{b_c} \cdot f_c(T)$	Maximum consumption (g g ⁻¹ d ⁻¹)	$S = SDA \cdot (C - F)$	Specific dynamic action (g g ⁻¹ d ⁻¹)
$f_c(T) = K_A K_B$	Temperature-dependent function (dimensionless)	$F = a_F C$	Egestion (g g ⁻¹ d ⁻¹)
$K_A = \frac{K_1 e^{y_1(T - T_1)}}{1 + K_1(e^{y_1(T - T_1)} - 1)}$		$U = a_U(C - F)$	Excretion (g g ⁻¹ d ⁻¹)

Table A3. Definitions and values of parameters used in the growth rate potential (GRP) models. Most of the values are from Luo & Brandt (1993) and Luo et al. (2001). Other sources are indicated by superscripts. DO: dissolved oxygen

Parameter	Parameter description	Menhaden	Anchovy
<i>Consumption (C)</i>			
ED_{prey}	Energy density of prey (J g ⁻¹)	1877 ^a	2551
ED_{fish}	Energy density of fish (J g ⁻¹)	3937.6 ^a	4182
a_c	Intercept for C_{\max} (g g ⁻¹ d ⁻¹)	1.294	0.41
b_c	Exponent for C_{\max}	-0.312	-0.33
C_Q	Slope for temperature dependence of standard consumption	—	2.22
C_{TM}	Maximum temperature for consumption (°C)	—	33
C_{TO}	Optimal temperature for consumption (°C)	—	27
K_1, K_2, K_3, K_4	Proportion of C_{\max} at T_1, T_2, T_3, T_4	0.525, 0.98, 0.98, 0.81	—
T_1, T_2, T_3, T_4	Temperature for K_1, K_2, K_3, K_4 (°C)	18.2, 28, 29, 30.1	—
W	Fish biomass (g)	1	0.708
TL	Total length (mm)	50	45
I_p	Inflection point for DO-dependency function	3	3
K_s	Half-saturation point	—	1.6255
<i>Respiration (R)</i>			
a_r	Intercept for R_{std} (g O ₂ g ⁻¹ d ⁻¹)	0.003301	0.0115
b_r	Exponent for maximum standard respiration	-0.2246	-0.346
OC	Oxycalorific coefficient (J g ⁻¹ O ₂)	13382 ^b	13560 ^c
R_Q	Slope for temperature dependence of standard respiration	2.07	2.25
R_{TM}	Maximum temperature for R_{std} (°C)	36	36
R_{TO}	Optimal temperature for R_{std} (°C)	33	30
SDA	Specific dynamic action coefficient	0.172	0.10
ACT	Activity multiplier	—	2.0
<i>Egestion (F) and excretion (U)</i>			
a_F	Intercept for temperature dependence of egestion	0.14	0.77
b_F	Exponent for temperature dependence of egestion	—	-0.40
a_U	Proportion of assimilated food excreted	0.1	0.15

^aRippey (1993); ^bDurbin & Durbin (1983); ^cArend et al. (2011)