Effect of hypoxia on habitat quality of striped bass (*Morone saxatilis*) in Chesapeake Bay

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Abstract: Eutrophication-induced hypoxia may affect both benthic and pelagic organisms in coastal systems. To evaluate the effect of hypoxia on pelagic striped bass (*Morone saxatilis*), we quantified the growth rate potential (GRP) of age-2 and age-4 fish in Chesapeake Bay during 1996 and 2000 using observed temperature, dissolved oxygen, and prey abundance information in a spatially explicit bioenergetics modeling framework. Regions of the Bay with bottom hypoxia were generally areas with high quality habitat (i.e., GRP > 0 $g \cdot g^{-1} \cdot day^{-1}$), primarily because prey fish were forced into warm, oxygenated surface waters suitable for striped bass foraging and growth. In turn, by concentrating fish prey above the oxycline and removing bottom waters as a refuge, hypoxia likely enhanced striped bass predation efficiency and contributed to the recovery of striped bass during the mid-1990s, a time when the striped bass fishery also was closed. This short-term positive effect of hypoxia on striped bass, however, appears to have been counterbalanced by a long-term negative effect of hypoxia in recent years. Ultimately, hypoxia-enhanced predation efficiency, combined with an abundance of striped bass due to restricted harvest, appears to be causing overconsumption of prey fishes in Chesapeake Bay, thus helping to explain poor growth and health of striped bass in recent years.

Résumé : L'hypoxie produite par l'eutrophisation dans les systèmes côtiers peut affecter à la fois les organismes benthiques et pélagiques. Afin d'évaluer l'effet de l'hypoxie sur le bar d'Amérique, *Morone saxatilis*, une espèce pélagique, nous avons calculé le taux de croissance potentiel (GRP) des poissons d'âges 2 et 4 de la baie de Chesapeake en 1996 et en 2000 d'après les données d'observation de la température, de l'oxygène dissous et de l'abondance des proies dans un cadre de modélisation bioénergétique explicite en fonction de l'espace. Les régions de la baie qui connaissent une hypoxie en profondeur sont généralement des zones à habitat de haute qualité (c'est-à-dire, GRP > 0 $g \cdot g^{-1} \cdot jour^{-1}$) principalement parce que les poissons proies y sont repoussés vers les eaux superficielles chaudes et oxygénées qui sont idéales pour la recherche de nourriture et la croissance du bar. Ensuite, en rassemblant les poissons proies au-dessus de l'oxycline et en retirant les eaux du fond comme refuge, l'hypoxie a vraisemblablement amélioré l'efficacité de prédation du bar et contribué à la récupération du bar au milieu des années 1990, une période où la pêche au bar était aussi interdite. Cependant, cet effet positif à court terme de l'hypoxie sur le bar a été contrebalancé par une effet négatif à long terme de l'hypoxie au cours des années récentes. En dernière analyse, l'amélioration de l'efficacité de la prédation par l'hypoxie, combinée à une abondance de bars à cause de la pêche limitée, semble avoir provoqué une surconsommation des poissons proies dans la baie de Chesapeake, ce qui permet d'expliquer la croissance réduite et la mauvaise santé des bars ces dernières années.

[Traduit par la Rédaction]

Introduction

Hypoxia, brought about by cultural eutrophication, is a global threat to aquatic ecosystems (Caddy 1993; Carpenter et al. 1998; Cloern 2001). Cultural eutrophication exacerbates dissolved oxygen (DO) depletion by enhancing primary productivity and bacterial respiration (Caddy 1993; Diaz and Rosenberg 1995; Rabalais et al. 2002), resulting in hypoxia (DO < 4 $mg \cdot L^{-1}$), severe hypoxia (0.2 < DO < 2 $mg \cdot L^{-1}$), and anoxia (DO < 0.2 $mg \cdot L^{-1}$). In turn, hypoxia

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can affect zooplankton, benthic macroinvertebrates, and fishes directly through mortality (Roman et al. 1993; Diaz and Rosenberg 1995; Breitburg et al. 2001), as well as indirectly via sublethal effects that reduce growth rate, fecundity, access to refuge from predators, or general performance (Aku and Tonn 1999; Breitburg et al. 2001; Robb and Abrahams 2003).

Chesapeake Bay has experienced severe hypoxia since the 1950s (Hagy et al. 2004), owing primarily to anthropogenic eutrophication stemming from agricultural and urban development in a once largely forested watershed (Breitburg et al. 2001; Kemp et al. 2005). Hypoxia in Chesapeake Bay can occur from spring to fall, typically peaking during summer when severe hypoxia can occur in almost all of the sub-pycnocline waters in the central mesohaline section of the Bay (Hagy et al. 2004; Zhang et al. 2006). The large volumetric extent of hypoxic water may subsequently reduce the quantity of suitable habitat for pelagic fishes, especially for species that require use of subpycnocline waters for refuge, foraging, or growth. For example, Coutant (1985) hypothesized that bottom hypoxia could force subadult and adult striped bass (*Morone saxatilis*) to reside only in oxygenated surface waters where summertime temperatures might exceed optimal temperatures for growth (i.e., 15–18 °C; Hartman and Brandt 1995a). In turn, this temperature–oxygen "squeeze" could threaten striped bass in Chesapeake Bay by potentially reducing growth, fecundity, and survival (Coutant 1985). Moreover, hypoxia may reduce predator–prey encounter rates by providing a low DO refuge for smaller fish (i.e., prey), which can be more tolerant to hypoxia than their larger predators (Chapman et al. 1996a, 1996b; Robb and Abrahams 2003).

Our primary objective herein is to evaluate whether hypoxia can reduce striped bass habitat quality and quantity in Chesapeake Bay. We expected overall habitat quality and quantity to be lower during years with extensive hypoxia than in years with more normoxic conditions. We examined the potential effects of hypoxia on habitat quality for striped bass in Chesapeake Bay by modeling the spatially explicit bioenergetics-based growth rate potential (Brandt et al. 1992; Mason et al. 1995) of resident age-2 and age-4 striped bass (Mansueti 1961) during spring, summer, and fall of 1996 and 2000. Growth rate potential (hereafter GRP; $g\cdot g^{-1}\cdot day^{-1}$) is defined as the expected growth rate of an individual fish (of known size) in a volume of water with known habitat conditions (e.g., temperature, prey density, DO) and has been used as a quantitative index of habitat quality and quantity (Brandt et al. 1992; Mason et al. 1995). Assuming fish growth rates reflect habitat quality, positive GRP would reflect "high" habitat quality (Mason et al. 1995).

The years 1996 and 2000 were chosen from a larger data set collected during 1995–2000 because they demonstrate contrasting hypoxic conditions; there was higher precipitation, higher nutrient loading, and lower DO during 1996 than during 2000, a more typical year (Jung and Houde 2003; Roman et al. 2005; Zhang et al. 2006). Because bottom oxygen depletion was more severe in 1996 than in 2000 (Zhang et al. 2006), we also expected to find a greater temperature–oxygen squeeze on habitat quality during 1996 than during 2000. Ultimately, we discuss how hypoxia and availability of fish prey can affect habitat quality and quan-

tity for striped bass and, in turn, the striped bass population in Chesapeake Bay during recent decades.

Materials and methods

Study site

Chesapeake Bay, located along the mid-Atlantic coast of the US, is the largest of North America's 130 estuaries. The Bay is bordered by seven states and spans a latitudinal gradient of about 320 km (Fig. 1). The longitudinal gradient of the Bay ranges from ~4.5 km to ~48 km. The upper and lower regions of the Bay are relatively shallow (<20 m in depth), whereas the middle region has a deep channel (~40 m) running through its main stem. Chesapeake Bay drains a 167 000 km² watershed (Boesch et al. 2001), with nearly half of its fresh water entering via the Susquehanna River to the north. In turn, salinity tends to decrease from near fresh water (<0.5) in the upper region to near ocean concentrations (30–35) in the lower region (Roman et al. 2005; Zhang et al. 2006).

The deep, mesohaline channel in the middle region of the Bay historically became hypoxic, owing to density stratification, but certainly not anoxic (Officer et al. 1984; Hagy et al. 2004). More recently, the magnitude, extent, and duration of hypoxia has increased (Cooper and Brush 1991; Hagy et al. 2004) such that even shallow areas in the upper, middle, and lower regions can become periodically hypoxic (Zhang et al. 2006). Enhanced nitrogen inputs into the Bay from non-point (diffuse) sources are the primary cause of hypoxia in this system (Boynton et al. 1995; Boesch et al. 2001; Hagy et al. 2004).

Study species

Striped bass is a commercially, recreationally, and ecologically important estuarine-dependent species that inhabits the northeastern and central Atlantic coast of the US (Hartman and Margraf 2003). In Chesapeake Bay, commercial landings of striped bass have fluctuated widely. During the 1960s and 1970s, landings averaged over 3 million metric tons (t) per year, whereas during the early 1980s, harvest levels unexpectedly collapsed to <1 million t (Richards and Rago 1999). In 1985, the Atlantic States Marine Fisheries Commission (ASFMC) imposed a moratorium on commercial fishing for striped bass that lasted until 1995 (Richards and Rago 1999).

Striped bass use estuaries such as the Chesapeake Bay to spawn, and this is where they spend a significant component of their life. Premature striped bass remain in these estuaries, gradually shifting towards oceanic residence with maturation (age-5 to age-8). About 50%–75% of the males and 25%–50% of the females, however, ultimately remain resident in Chesapeake Bay during their entire lifetime (Secor and Piccoli 2007). Striped bass are tolerant of a large range of salinities and water temperatures; however, temperatures <6 °C and >28 °C can potentially have negative effects on growth (Hartman and Brandt 1995a).

Data collection

Inputs to our spatially explicit bioenergetics-based model included water temperature, prey fish density, and DO con-

Fig. 1. Transects sampled in Chesapeake Bay during 1996 and 2000. During summer 1996, data were collected along lateral transects 1, 3, and 6 (lower region) and 13, 15, and 17 (middle region); during summer 2000, data were collected along lateral transects 5, 8, and 10 (lower region) and 18, 20, and 22 (middle region).
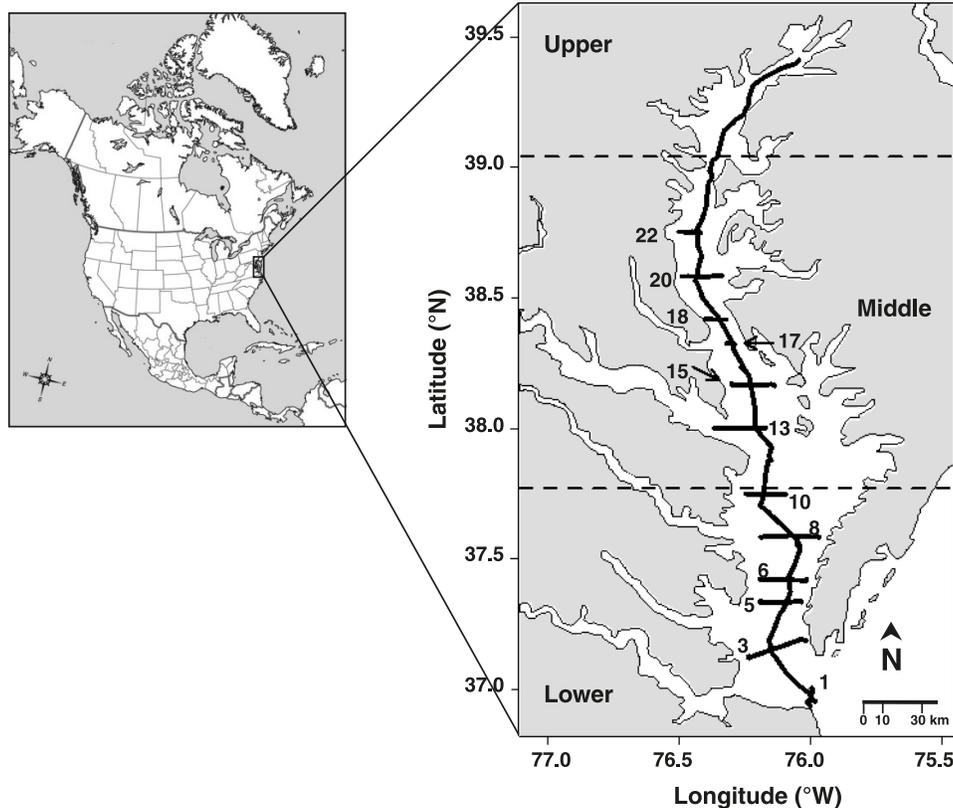
centrations, which were collected along axial (north–south) and lateral (east–west) transects in Chesapeake Bay (Fig. 1). Data were acquired during spring (25 April – 4 May), summer (12–26 July), and fall (22–31 October) of 1996 and during spring (29 April – 6 May), summer (26 July – 7 August), and fall (17–21 October) of 2000. These physical attributes (plus salinity and chlorophyll *a*) were collected along each transect with a ScanFish sensor package (model MK II; GMI, Denmark), whereas prey fish density was estimated using fishery acoustics. Both instruments were towed in tandem from the R/V *Cape Henlopen*, thus providing simultaneous measurements of these attributes through nearly the entire water column (see below).

Environmental data

The ScanFish was towed along a sinusoidal path throughout the water column at depths ranging from ~2 m above the bottom to ~2 m below the surface. On average, seven vertical profiles (3.5 undulations) were made per kilometre. Sensors recorded temperature, DO, and depth every 0.5 s, which were georeferenced using a global positioning system (GPS; model JRC-DGPS212W; Bethel Marine Electronics, Rockledge, Florida). The 320 km axial transect was sampled once per season per year, whereas the six lateral transects were surveyed during the summers of both years (Fig. 1). The axial transect was sampled continuously over 2–3 days (i.e., both day and night), whereas lateral transects were sampled during daytime (i.e., between dawn and dusk). During the summer of 1996, data were collected along lateral transects 1, 3, and 6

(lower region) and 13, 15, and 17 (middle region), whereas lateral transects 5, 8, and 10 (lower region) and 18, 20, and 22 (middle region) were sampled in the summer of 2000 (Fig. 1). These were the only daytime transects sampled during these years, with the sampling scheme being driven by a larger research program (Roman et al. 2005; Zhang et al. 2006). We focused our efforts on the daylight period because striped bass are considered a visual diurnal predator (Clark et al. 2003). Environmental data along transects were interpolated using the default kriging procedure (linear variogram algorithm, slope = 1, anisotropy = 0) in Surfer (version 8.0; Golden Software Inc., Golden, Colorado), and data along each transect were exported for modeling purposes as equal-sized cells (~1.1 km × 1 m along axial transects and ~50 m × 1 m depth interval along lateral transects), using the convert grid data function in Surfer.

Prey biomass density data

Acoustic estimates of striped bass prey fish (e.g., bay anchovy (*Anchoa mitchilli*), white perch (*Morone americana*)) biomass density were made with a surface-towed 120 kHz split-beam echosounder (3 pings per second, 0.4 ms pulse length, –66 dB re 1 µPa minimum acoustic backscatter threshold; model Simrad EY500; Kongsberg Maritime AS, Kongsberg, Norway). The transducer was mounted on a towed body, deployed alongside the research vessel at a depth of 1–2 m below the surface (dependent upon sea state), and towed at a speed of about 2 m·s^{-1}. Equipment performance was monitored in the field using the data acqui-

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Table 1. Model equations.

Equation	Description
$\mathrm{GRP} = \dfrac{K_{\mathrm{prey}}}{K_{\mathrm{pred}}}(C - (R + S + F + U))$	Growth rate potential (g·g^{-1}·day^{-1})
$C = \dfrac{C_{\max}B}{0.865 + B}$	Consumption (g·g^{-1}·day^{-1})
$C_{\max} = \mathrm{CA}\cdot M^{\mathrm{CB}}\cdot f_{\mathrm{C}}(T)\cdot f_{\mathrm{C}}(\mathrm{DO})$	Maximum consumption (g·g^{-1}·day^{-1})
$f_{\mathrm{C}}(T) = K_A\cdot K_B$	Temperature-dependent function (dimensionless)
$K_A = \dfrac{\mathrm{CK1}\cdot L1}{1 + \mathrm{CK1}\cdot(L1 - 1)}$	
$L1 = e^{G1\cdot(T - \mathrm{CQ})}$	
$G1 = [1/(\mathrm{CTO} - \mathrm{CQ}]\cdot \ln\left[\dfrac{0.98\cdot(1 - \mathrm{CK1})}{\mathrm{CK1}\cdot 0.02}\right]$	
$K_B = \dfrac{\mathrm{CK4}\cdot L2}{1 + \mathrm{CK4}\cdot(L2 - 1)}$	
$L2 = e^{G2\cdot(\mathrm{CTL} - T)}$	
$G2 = [1/(\mathrm{CTL} - \mathrm{CTM})]\cdot \ln\left[\dfrac{0.98\cdot(1 - \mathrm{CK4})}{\mathrm{CK4}\cdot 0.02}\right]$	
$f_{\mathrm{C}}(\mathrm{DO}) = -0.288 + 0.233(\%\mathrm{Sat}) - 0.000105(\%\mathrm{Sat})^2$	Dissolved oxygen dependent scale function (dimensionless)
$\%\mathrm{Sat} = 14.4 - 0.332T + 0.00342T^2$	Oxygen percent saturation
$R = \mathrm{RA}\cdot M^{\mathrm{RB}}\cdot f_{\mathrm{R}}(T)\cdot \mathrm{ACTIVITY}$	Respiration (g·g^{-1}·day^{-1})
$f_{\mathrm{R}}(T) = e^{\mathrm{RQ}\cdot T}$	Temperature-dependent function (dimensionless)
$\mathrm{ACTIVITY} = e^{\mathrm{RTO}}$	Activity multiplier (dimensionless)
$S = \mathrm{SDA}\cdot(C - F)$	Specific dynamic action (g·g^{-1}·day^{-1})
$F = \mathrm{FA}\cdot C$	Egestion (g·g^{-1}·day^{-1})
$U = \mathrm{UA}\cdot(C - F)$	Excretion (g·g^{-1}·day^{-1})

Note: Bioenergetics equations were from Hartman and Brandt (1995a); consumption equations were from Brandt et al. (2002); dissolved oxygen function (f_{C}(DO)) was from Brandt et al. (1998); and percent oxygen saturation of the water (%Sat) was from Wetzel (1983). See Table 2 for symbol definitions.

sition software distributed with the Simrad acoustical unit. Raw digitized acoustic signals were time-marked, geocoded using GPS, and saved to the hard drive for later processing. Calibrations of the Simrad EY500 were performed using a standard 38 mm tungsten carbide reference sphere during every cruise (Foote et al. 1987). Identification of acoustic targets was determined by aimed tows of a midwater trawl with a mouth opening of 18 m^2 (for sampling details, see Jung and Houde 2003).

Raw acoustic data were analyzed using Echoview 3.00 (SonarData Inc., Hobart, Tasmania, Australia) for standard echo integration and target strength (MacLennan and Simmonds 1992). The blanking distance was set at 1.5 m from the transducer and 0.5 m from the bottom, with surface noise being identified and omitted from the processing. Data were subdivided in cells (cell size of 50 m × 1 m depth) and echo-squared integration was performed in each cell. Echo-integration results were initially expressed as relative fish density units (S_{v}) and then scaled by mean backscatter cross section ($\overline{\sigma}_{\mathrm{bs}}$) to estimate fish density. Mean backscatter cross section was estimated using echoes from cells with $N_{\mathrm{v}} < 0.1$ (Rudstam et al. 2003), where $N_{\mathrm{v}} = c\,\tau\,\psi\,R^2 n_{\mathrm{EI}}$, c is the speed of sound (m·s^{-1}), τ is the transmit pulse duration (s), ψ is the equivalent beam angle in steradians, R is the target range

(m), and n_{EI} is the volumetric fish density (number·m^{-3}). Individual estimates of σ_{bs} were averaged within each cell to provide $\overline{\sigma}_{\mathrm{bs}}$. When estimates of σ_{bs} were unavailable in a cell because of the inability to differentiate individual fish targets ($N_{\mathrm{v}} > 0.1$), we calculated $\overline{\sigma}_{\mathrm{bs}}$ using adjacent cells. Number of fish per cubic meter (ρ) in each cell was then calculated as $\rho = S_{\mathrm{v}}/\overline{\sigma}_{\mathrm{bs}}$.

Fish biomass density per cell (g·m^{-3}) was determined by converting $\overline{\sigma}_{\mathrm{bs}}$ for each cell to target strength (TS) ($\sigma_{\mathrm{bs}} = 10^{(\mathrm{TS}/10)}$), and then converting TS to total length (TL) using TS–TL equations specific to the dominant prey species in the different regions of Chesapeake Bay (i.e., upper, middle, and lower; Fig. 1). Relationships used for the dominant species were as follows: bay anchovy TS = 17.9 log(TL) – 66.4 (S. Ludsin, unpublished data); white perch TS = 26.48 log(TL) – 69.45 (Hartman and Nagy 2005); and alosids (*Alosa* spp.) TS = 20 log(TL) –76 (Edwards and Armstrong 1984).

Taxa-specific TL was then converted to mass (*M*) using length–mass relationships derived from trawl catches: bay anchovy $M = -13.0956(\mathrm{TL})^{3.2714}$; white perch $M = -12.3718$ (TL)$^{3.2457}$; and alosids $M = -11.8614(\mathrm{TL})^{3.0318}$ (S. Jung, unpublished data; www.chesapeake.org/ties/mwt/SASSAMPL/L-W. htm). Mean mass was multiplied by acoustic-derived fish

Table 2. Parameters and variables used in our model equations (Table 1):

Symbol	Description	Value	Unit
Parameters			
K_{prey}	Energy density of prey (alosiids, bay anchovy, white perch)	5233, 5133, 6488	$J \cdot kg^{-1}$
K_{pred}	Energy density of predator (striped bass)	6488	$J \cdot kg^{-1}$
CA	Intercept for C_{max}	0.3021	$g \cdot g^{-1} \cdot day^{-1}$
CB	Exponent for C_{max}	–0.2523	Dimensionless
CK1	Proportion of C_{max} at CQ (age 2, age ≥ 3)	0.255, 0.323	Dimensionless
CTO	Optimal temperature at 0.98 of C_{max} (age 2, age ≥ 3)	18, 15	°C
CQ	Temperature for CK1 (age 2, age ≥ 3)	6.6, 7.4	°C
CK4	Proportion of C_{max} at CTL (age 2, age ≥ 3)	0.9, 0.85	Dimensionless
CTL	Temperature for CK4 (age 2, age ≥ 3)	32, 30	°C
CTM	Maximum temperature at 0.98 of C_{max} (age 2, age ≥ 3)	29, 28	°C
RA	Intercept for maximum standard respiration (age ≥ 1)	0.0028	$g \cdot g^{-1} \cdot day^{-1}$
RB	Exponent for maximum standard respiration (age ≥ 1)	–0.218	Dimensionless
RQ	Slope for temperature-dependent standard respiration (age ≥ 1)	0.076	Dimensionless
RTO	Coefficient for swimming speed dependence on metabolism (age ≥ 1)	0.5002	$s \cdot cm^{-1}$
SDA	Specific dynamic action coefficient	0.172	Dimensionless
FA	Proportion of consumed food egested	0.104	Dimensionless
UA	Proportion of assimilated food excreted	0.068	Dimensionless
Variables			
B	Prey fish biomass		$g \cdot m^{-3}$
DO	Dissolved oxygen concentration		$mg \cdot L^{-1}$
T	Water temperature		°C
M	Mass		g
%Sat	Percent oxygen saturation of water		Dimensionless

Note: Bioenergetics parameters were from Hartman and Brandt (1995*a*); prey energy densities were from Wang and Houde (1995), Hartman and Brandt (1995*a*), and Stewart and Binkowski (1986).

density in each cell to calculate prey fish biomass density ($g \cdot m^{-3}$). Data were then rescaled to conform to the environmental data collected by the ScanFish (i.e., to cell size of ~1.1 km × 1 m along axial transects and of ~50 m × 1 m depth along lateral transects), using identical procedures in Surfer, as described above. During the summer of 1996, prey fish biomass density along the axial transect was only measured in the southern part of the middle region and in the northern part of the lower region because of equipment problems, whereas environmental data were collected along then entire transect.

Modeling and data analysis

Growth rate potential was quantified along each transect using previously developed foraging and bioenergetics growth models for striped bass (Tables 1 and 2), assuming that (*i*) habitat conditions within a cell were constant for the entire day and were characteristic of the time period (e.g., season) and (*ii*) fish predation did not alter the prey biomass density (i.e., no density-dependent foraging or feedback mechanisms existed).

Foraging model

Consumption rate (C; $g \cdot g^{-1} \cdot day^{-1}$) of striped bass was modeled using a type II functional response model originally developed for lake trout by Eby et al. (1995) and later adapted to striped bass by Brandt et al. (2002) (Table 1). Consumption rate in each grid cell along a transect was assumed to be a function of striped bass mass, prey fish bio-

mass, water temperature, and DO concentrations by applying a DO-dependent scaling function as in Luo et al. (2001) and Brandt and Mason (2003) (Table 1). Our DO-dependent scaling function, $f_C(DO)$, was originally developed by Brandt et al. (1998) for striped bass by fitting experimental laboratory results to a quadratic model. To summarize, experiments were conducted using a 4 × 3 factorial design with four water temperature treatments (20, 23, 27, and 30 °C) and three DO treatments (100% saturation, 4 $mg \cdot L^{-1}$, and 2 $mg \cdot L^{-1}$). During each experiment, consumption was estimated by summing the mass of prey fish consumed. Growth was calculated as the difference between final weight and initial weight. The quadratic model provided a scalar value between 0 (no food consumption due to hypoxia) and 1.0 (food consumption occurs without any effect of DO), which was used as a multiplier ($f_C(DO)$) to the consumption model. Striped bass GRP was not affected by DO > 7 $mg \cdot L^{-1}$, but decreased by about 50% when DO = 5 $mg \cdot L^{-1}$. The minimum DO required for positive GRP varied with water temperature, as oxygen saturation concentration is a function of water temperature (Wetzel 1983). For temperatures in the range of 12–20 °C, the minimum DO for positive growth was ~2.5 $mg \cdot L^{-1}$. As temperature increased to 20–28 °C, the minimum DO for positive growth increased from 2.5 $mg \cdot L^{-1}$ to 4.5 $mg \cdot L^{-1}$. No consumption occurred at DO ≤ 1 $mg \cdot L^{-1}$ (i.e., $f_C(DO) = 0.0$).

Bioenergetics model

Growth rate potential ($g \cdot g^{-1} \cdot day^{-1}$) was calculated in each

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Fig. 2. Seasonal cumulative frequency distributions of (*a*) water temperature, (*b*) salinity, (*c*) dissolved oxygen, and (*d*) prey biomass density along the axial transect during 1996 (thin lines) and 2000 (thick lines). Because of equipment problems, prey biomass data along the axial transect in 1996 were only collected in the southern part of the middle region and in the northern part of the lower region.
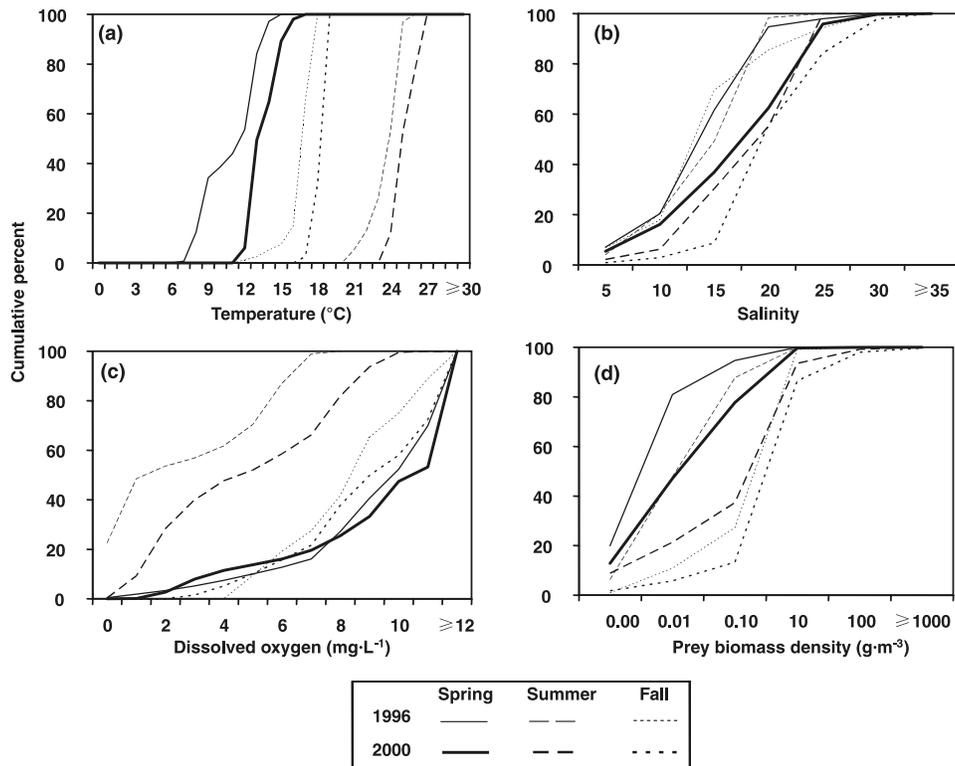
Table 3. Mean (±standard error, SE) temperature, dissolved oxygen, salinity, and prey biomass density per cell along the axial transect in Chesapeake Bay during 1996 and 2000.

Variable	1996			2000		
	Spring	Summer	Fall	Spring	Summer	Fall
Temperature (°C)	10.23±0.03	23.98±0.01	16.65±0.01	13.21±0.01	24.96±0.01	18.08±0.01
Salinity	14.33±0.06	15.55±0.08	14.28±0.08	17.12±0.08	17.93±0.07	20.14±0.07
Dissolved oxygen (mg·L^{-1})	8.99±0.05	2.50±0.07	8.40±0.03	10.83±0.06	4.50±0.04	8.67±0.04
Prey biomass (g·m^{-3})	0.03±0.001	0.09±0.02	0.72±0.05	0.42±0.07	6.47±0.67	29.9±2.60
No. of cells for environmental variables	4089	3762	5349	5062	4887	5103
No. of cells for prey biomass	2223	1205	2477	3028	3231	2349

Note: Environmental and prey biomass data collected along axial transect were subdivided into equal-sized cells; cell sizes were ~ 1.1 km × 1 m and 50 m × 1 m for environmental variables and prey biomass, respectively.

cell along transects using the Wisconsin bioenergetics model (Kitchell et al. 1977; Hanson et al. 1997; Table 1) as parameterized for striped bass (Hartman and Brandt 1995*a*; Table 2). Growth was scaled by the relative difference in energy density between prey and striped bass to account for differences in energy density between them (Table 2). We used prey-specific energy density values from the literature, with the exception of white perch where we used Hartman and Brandt's (1995*a*) striped bass energy density for white perch energy density.

We used mean (± standard error, SE) GRP per transect to compare overall potential growth between 1996 and 2000, using daytime lateral transect data. However, along the axial transect, we used both day and night data because axial sampling started at different hours of the day in the different years and so the diurnal sections of the axial transect were

not comparable among years and seasons. As such, comparisons of axial transect data across season and years should be viewed with some caution.

Effect of hypoxia on habitat quality

We used a two-step approach to evaluate the effect of hypoxia on availability of high quality habitat (HQH; i.e., the percentage of cells that support positive growth along a transect according to Mason et al. 1995). First, we ran the bioenergetics model with and without $f_C(DO)$ along each transect and compared the GRP values between the two runs using nonparametric Mann–Whitney U test on untransformed data, as all GRP data were highly non-normal ($P < 0.001$; Kolmogorov–Smirnov normality test). Second, for transects for which GRP values calculated with and without $f_C(DO)$ differed significantly ($P < 0.05$), we compared HQH obtained

Table 4. Mean (± standard error, SE) temperature, dissolved oxygen, salinity, and prey biomass density from pooled lateral transects in middle and lower regions of Chesapeake Bay during 1996 and 2000.

| | 1996 | | 2000 | |
| | Middle region | Lower region | Middle region | Lower region |
Variable				
Temperature (°C)	24.62±0.01	23.92±0.01	25.10±0.01	25.83±0.01
Salinity	12.15±0.02	20.33±0.04	16.92±0.05	18.92±0.02
Dissolved oxygen (mg·L^{-1})	4.88±0.02	5.50±0.01	8.66±0.05	7.70±0.02
Prey biomass (g·m^{-3})	0.09±0.001	0.01±0.001	16.92±0.02	0.11±0.02
No. of cells for environmental variables and prey biomass	11 248	7520	8561	11 406

Note: Environmental and prey biomass data collected along lateral transects were subdivided into equal-sized cells of 50 m longitude × 1 m depth.

Fig. 3. Maps of (*a*, *b*) temperature, (*c*, *d*) DO, and (*e*, *f*) prey biomass along the axial transect in 1996 and 2000. Because of equipment problems, prey biomass data along the axial transect in 1996 were only collected in the southern part of the middle region and in the northern part of the lower region.

Results

Environmental conditions

Temperature was cooler for all seasons in 1996 when compared with 2000 (Fig. 2*a*; Tables 3 and 4). Overall, average spring (± SE) temperatures were coldest (means 10.23 ± 0.03 °C and 13.21 ± 0.01 °C during 1996 and 2000, respectively) and summer temperatures were warmest (means 23.98 ± 0.01 °C and 24.96 ± 0.01 °C during 1996 and 2000,
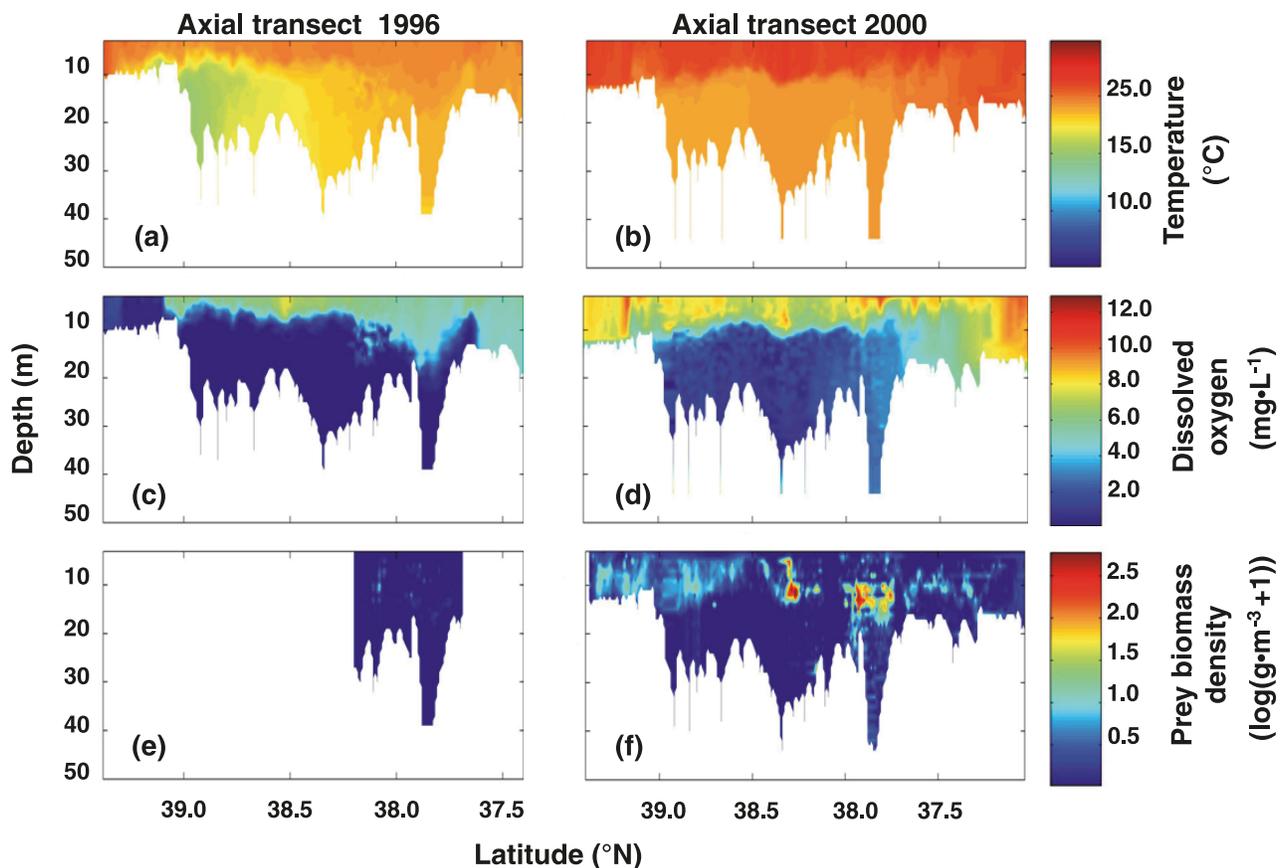
with f_C(DO) with HQH obtained without f_C(DO). In so doing, we assumed that the percentage decrease between these two HQH values represented the magnitude in the reduction of the striped bass habitat quality due to the oxygen effect.

respectively), with fall being intermediate (means 16.65 ± 0.01 °C and 18.08 ± 0.01 °C during 1996 and 2000, respectively). Optimal temperatures for age-2 and age-4 striped bass growth (i.e., 15–18 °C) were recorded only during fall, whereas temperatures that could potentially reduce growth (i.e., temperatures < 6 °C and temperatures > 28 °C) were not recorded in either year (Fig. 2*a*).

Hypoxia and anoxia were more prevalent during the summer of 1996 than during the summer of 2000. Mean (± SE) DO levels were 2.50 ± 0.07 mg·L^{-1} and 5.50 ± 0.01 mg·L^{-1} along the axial and lateral transects, respectively, during the summer of 1996, which were lower than levels along the axial (4.50 ± 0.04 mg·L^{-1}) and lateral (8.66 ± 0.05 mg·L^{-1}) during the summer of 2000, respectively (Tables 3, 4). Dur-

Table 5. Growth rate potential (mean ± standard error (SE) and median) and percentage of high quality habitat (HQH) for age-2 striped bass along the axial transect during spring, summer, and fall 1996 and 2000 and along lateral transects during summer 1996 and 2000.

| Years | Transect | GRP ($g \cdot g^{-1} \cdot day^{-1}$) | | | HQH | |
		Mean	SE	Median	%	N
1996	Axial					
	Spring	-7.96×10^{-4}	4.19×10^{-5}	-1.26×10^{-3}	9.0	2223
	Summer	-3.14×10^{-3}	7.12×10^{-5}	-3.81×10^{-3}	5.2	1205
	Fall	5.45×10^{-3}	1.80×10^{-4}	1.05×10^{-3}	56.4	2477
	Lateral summer					
	1	-2.60×10^{-3}	3.81×10^{-5}	-7.12×10^{-4}	7.6	1812
	3	-3.60×10^{-3}	1.93×10^{-5}	-3.81×10^{-3}	0.5	2335
	6	-3.98×10^{-3}	5.45×10^{-6}	-3.98×10^{-3}	0.0	3342
	13	-3.31×10^{-3}	3.10×10^{-5}	-3.85×10^{-3}	5.5	4268
	15	-2.35×10^{-3}	7.12×10^{-5}	-4.02×10^{-3}	14.9	3192
	17	-2.51×10^{-3}	5.87×10^{-5}	-3.65×10^{-3}	10.9	3367
2000	Axial					
	Spring	1.09×10^{-3}	1.01×10^{-4}	-1.26×10^{-3}	30.1	3023
	Summer	2.64×10^{-3}	1.59×10^{-4}	-1.76×10^{-3}	42.7	3231
	Fall	1.09×10^{-2}	2.68×10^{-4}	7.12×10^{-3}	58.0	2350
	Lateral summer					
	5	7.12×10^{-3}	1.89×10^{-4}	1.84×10^{-3}	62.3	3505
	8	1.63×10^{-3}	1.42×10^{-4}	-4.02×10^{-3}	33.0	4325
	10	5.45×10^{-3}	1.97×10^{-4}	-1.55×10^{-3}	46.3	3524
	18	-1.80×10^{-3}	1.09×10^{-4}	-3.98×10^{-3}	17.0	2447
	20	-1.55×10^{-3}	9.22×10^{-5}	-3.94×10^{-3}	18.8	3451
	22	4.19×10^{-4}	1.80×10^{-4}	-3.85×10^{-3}	28.0	1937

Note: N is number of cells.

ing summer, hypoxia encompassed 62% of the cells sampled during 1996, but only 48% of the cells sampled during 2000 (Fig. 2c). Hypoxia was less of an issue during spring in both years, occupying only 7.4% and 11.5% of the sampled water volume during 1996 and 2000, respectively (Fig. 2c). During fall 1996 and 2000, 0% and 5% of the sampled water volume was hypoxic, respectively (Fig. 2c). In spring, fall, and summer of 2000, anoxic waters occupied <0.3% of the sampled volume, whereas in the summer of 1996, anoxic waters occupied up to 22.5% of the sampled volume (Fig. 2c).

During spring of both years, hypoxia occurred near the bottom (below ~15 m depth) and was limited to the northern part of the middle region (also see Zhang et al. 2006). During summer 1996, hypoxia occupied nearly the entire upper region (Fig. 3b), all waters below 10 m depth in the middle region, and deeper waters of the more northerly part of the lower region (Fig. 3b). Similar to 1996, hypoxia was observed at depths below 10 m for the entire middle region (Fig. 3e) and in deeper portions of the lower region (Fig. 3e) during 2000; it did occur in the upper region, however. During fall of both years, the extent of hypoxia was similar to that in spring (Zhang et al. 2006).

Prey fish biomass and species composition

During 1996 and 2000, the dominant pelagic and bentho-pelagic fish, which constitute preferred prey of striped bass, were bay anchovy, white perch, blueback herring (*Alosa aestivalis*), Atlantic herring (*Clupea harengus*), and other alosids (Jung and Houde 2003). During all seasons, bay anchovy was the most abundant prey species in the middle and

lower regions (high salinity areas), whereas white perch was the most abundant in the upper region (low salinity areas) (Jung and Houde 2003).

During both years, overall prey fish biomass was lowest in spring and highest in fall, with summer being intermediate (Fig. 2d; Table 3). Overall prey biomass was lower in 1996 than in 2000 during all seasons (Fig. 2d; Tables 3 and 4). Summer mean (± SE) fish biomass along the lateral transects in the middle region was 0.09 ± 0.01 $g \cdot m^{-3}$ in 1996 compared with 16.92 ± 0.02 $g \cdot m^{-3}$ in 2000, whereas in the lower region, fish biomass was 0.01 ± 0.001 $g \cdot m^{-3}$ in 1996 compared with 0.11 ± 0.02 $g \cdot m^{-3}$ in 2000 (Table 4). Although prey abundance and species composition differed between years, nearly all fish prey (>80%) were located in oxygenated waters (DO > 4 $mg \cdot L^{-1}$) during all seasons (Figs. 3b–3f).

Growth rate potential (GRP) and high quality habitat (HQH)

Distributions of GRP, and hence HQH, were similar across the Bay during both years for age-2 and age-4 striped bass and closely resembled the pattern of prey–fish biomass. Thus, we have only presented model results for age-2 striped bass and refer the reader to Appendix A (Table A1) for a summary of age-4 results.

Growth rate potential and HQH values were generally lower in 1996 than in 2000 (Table 5). Mean GRP of age-2 striped bass per transect ranged from -7.9×10^{-4} to 5.45×10^{-3} $g \cdot g^{-1} \cdot day^{-1}$ (median GRP -7.12×10^{-3} to 1.05×10^{-3} $g \cdot g^{-1} \cdot day^{-1}$) in 1996 and from -1.80×10^{-3} to

1.09×10^{-2} g·g^{-1}·day^{-1} (median GRP -4.02×10^{-3} to 7.12×10^{-3} g·g^{-1}·day^{-1}) in 2000 (Table 5). Despite differences in GRP between years, HQH values were consistently lowest during spring, intermediate during summer, and highest during fall (Table 5).

During the spring of 1996, mean GRP was negative and only 9.0% of the sampled volume along the axial transect had the potential to support positive growth (Table 5). By contrast, during spring 2000, mean GRP was positive and 30.1% of the total volume had the potential to support positive striped bass growth (Table 5), likely owing to mean prey biomass density being 14-fold higher in 2000 than in 1996 (Table 3).

During the summer of 1996, mean GRP values were negative for the axial transect and all lateral transects (Table 5). Along the axial transect, 5.2% of the sampled volume had the potential to support positive growth, whereas along lateral transects, HQH ranged from 0.0% to 7.6% in the lower region and from 5.5% to 14.9% in the middle region. Summer 2000, however, provided a better potential growth environment for striped bass than summer 1996, owing to the combination of reduced hypoxia and a more than 70-fold greater availability of fish prey (Tables 3 and 4; Fig. 3). Average GRP values during 2000 were positive along both axial and all lateral transects, except for transects 18 and 20, where some fish prey occurred in hypoxic waters (2.5–3.5 mg·L^{-1}). During the summer of 2000, 42.7% of the axial transect cells were HQH cells, whereas the percentage of HQH cells ranged from 33.0% to 62.3% along lateral transects in the lower region and from 17.0% to 28.0% in the middle region (Table 5).

Fall of both years were periods of positive growth, owing in large part to high prey densities (Table 3). Mean GRP values were always positive during fall and higher than in both spring and summer (Table 5). Mean GRP values were lower in fall 1996 than in fall 2000; however, HQH values were similar between years, with 56.4% and 58% of the cells potentially supporting positive growth during 1996 and 2000, respectively (Table 5).

Hypoxia effects on GRP and HQH

The effect of f_C(DO) on GRP and HQH values varied seasonally. Our estimates of GRP along lateral transects were significantly lower ($P < 0.05$; Mann–Whitney U test; Table 6) when f_C(DO) was included in our model than without it. The only exception was transect 5 (lower region; Fig. 1) during summer 2000 (Table 6); hypoxia was absent along this transect. Likewise, along the axial transect, our index of HQH was always lower using the f_C(DO) than without it during summer and fall of both years (Fig. 4). By contrast, inclusion of the f_C(DO) did not cause significant differences in GRP during spring of both years (Table 6). The percent reductions in HQH owing to the inclusion of f_C(DO), however, were generally low, ranging from 1.29% to 6.06% in 1996 and from 0.47% to 8.81% in 2000 (Fig. 4).

The unexpectedly small reductions in HQH owing to inclusion of f_C(DO) in our model could be attributed to the lack of use of hypoxic waters by fish prey during both years (Figs. 3a–3f). When hypoxia was present along a transect (e.g., transect 17 during summer 1996 (Fig. 5d); transect 10 in summer 2000 (Fig. 5g)), positive GRP values occurred

Table 6. Mann–Whitney U test results from our comparison of GRP values calculated with and without f_C(DO) in our model.

Years	Transect	p
1996	Axial	
	Spring	0.431
	Summer	<0.0001
	Fall	0.012
	Lateral summer	
	1	0.001
	3	<0.0001
	6	<0.0001
	13	<0.0001
	15	0.013
	17	<0.0001
2000	Axial	
	Spring	0.052
	Summer	<0.0001
	Fall	<0.0001
	Lateral summer	
	5	0.056
	8	<0.0001
	10	<0.0001
	18	<0.0001
	20	<0.0001
	22	<0.0001

Note: Comparisons were made for the axial transect in spring, summer, and fall 1996 and 2000 and for each lateral transect sampled during summer 1996 and 2000. Where $p < 0.05$, GRP values are lower when f_C(DO) was included in the model than without it.

mainly above the hypoxic waters regardless of whether or not f_C(DO) was included in our model (Figs. 5e–5f, 5h–5i). There were instances in which some of the fish prey were found in hypoxic waters (e.g., transect 18 in summer 2000; Figs. 5l–5n). Although overall GRP values were lower in these cases, incorporation of f_C(DO) did not dramatically reduce GRP estimates and HQH values (~4.5% reduction; Fig. 4) because these fish were located in waters only just below the 4 mg·L^{-1} isopleth (Fig. 5g). When hypoxia was nearly absent (e.g., transect 1 during summer 1996; Figs. 5a–5c), positive, but low, GRP values were observed throughout the water column regardless of whether f_C(DO) was included in our model (Figs. 5a–5c).

Discussion

Temperature–oxygen squeeze hypothesis

Modeled estimates of GRP and our resultant index of HQH indicate that hypoxia can reduce habitat quality and quantity for striped bass in Chesapeake Bay, primarily during summer and fall. The observed reduction in HQH due to hypoxia, however, was unexpectedly minor, largely because (i) temperatures in oxygenated surface waters never exceeded levels that could reduce consumption and growth (i.e., 28 °C; Hartman and Brandt 1995a) and (ii) hypoxia did not limit access to available fish prey for striped bass. These findings only partly support Coutant's (1985) temperature–

Fig. 4. Estimates of high habitat quality (HQH) along our transects during (*a*) 1996 and (*b*) 2000 with (shaded bars) and without (open bars) f_C(DO) in our model.
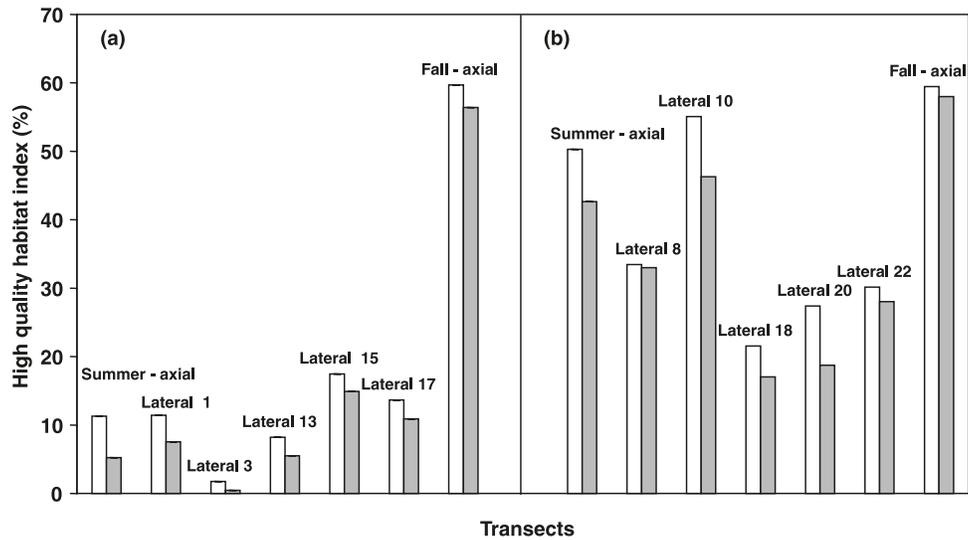
oxygen squeeze hypothesis; although we found an upward compression ("squeeze") of the habitat suitable for growth into surface waters above the hypoxic zone, we did not find a corresponding high-temperature squeeze from the top that could reduce consumption and ultimately growth.

This result counters previous research with Chesapeake Bay striped bass (Brandt and Kirsch 1993), which supported Coutant's (1985) temperature–oxygen squeeze hypothesis. The discrepancy between studies emanates primarily from different parameters used in the bioenergetics model to estimate GRP. Brandt and Kirsch (1993) used parameters from Moore (1988) developed for striped bass in Smith Mountain Lake (Virginia), whereas we used experimentally obtained parameters specific for Chesapeake Bay striped bass (Hartman and Brandt 1995*a*). In Brandt and Kirsch (1993), consumption (and consequently GRP) was modeled to decline dramatically at temperatures >21 °C and was zero at temperatures >25 °C, regardless of oxygen availability (Brandt et al. 1992). By contrast, striped bass in our model could grow in temperatures up to 28 °C (Hartman and Brandt 1995*a*), if suitable oxygen was available. Because temperatures >28 °C were not observed along transects, or along similar transects sampled in Chesapeake Bay during 1995–2000 (Zhang et al. 2006), and prey primarily occupied oxygenated waters above the hypoxic zone, there was no opportunity for a squeeze from the top to occur.

Cronin et al. (2003) reported that August mean temperatures in the top 10 m of the water column in Chesapeake Bay never exceeded 25 °C during 1949–2000. Thus, our conclusion of a lack of a temperature–oxygen squeeze appears robust, at least with respect to the past half of the 20th century. More recently, however, temperatures exceeding 28 °C have been observed in the upper 10 m of the water column in the main stem of the middle region during August and September 2005 (http://www.chesapeakebay.net/data/), a year in which the globally averaged annual mean surface temperature was the warmest recorded since 1880 (Shein 2006). Thus, although it is unlikely that striped bass in Chesapeake Bay experienced a temperature–oxygen squeeze

historically, if climate warming continues as expected (Shein 2006) and proposed management plans to mitigate bottom hypoxia are unsuccessful, then striped bass may begin to experience an annual summer temperature–oxygen squeeze that could potentially limit growth and perhaps production.

Hypoxia's effect on predator–prey interactions

We originally hypothesized that hypoxic conditions would provide a refuge from predation for smaller prey fishes (e.g., bay anchovy, Atlantic menhaden (*Brevoortia tyrannus*)), as tolerance to low DO concentrations appears to be negatively related to body size (Chapman et al. 1996*a*, 1996*b*; Robb and Abrahams 2003). Accordingly, we expected to find fish prey aggregated in areas where striped bass would likely be stressed by unsuitable DO concentrations. On the contrary, our acoustics surveys demonstrate that pelagic fish prey of striped bass generally do not use hypoxic waters in Chesapeake as a refuge. A similar avoidance of hypoxic waters in Chesapeake Bay by prey fishes was observed during 1997 and 1999 (S. Ludsin, unpublished data). Further, the small fraction of prey fish that we observed in hypoxic waters generally occupied DO concentrations believed to be tolerable by striped bass (3–4 mg·L^{-1}) (Chittenden 1971; Coutant 1985; Wannamaker and Rice 2000). Given the small vertical distance (metres) at which DO rapidly declines with depth, striped bass also could presumably make short temporal foraging bouts into the hypoxic waters (sensu Rahel and Nutzman 1994). Thus, we suggest that it is unlikely that hypoxia reduces access to fish prey in offshore pelagic waters of Chesapeake Bay.

In fact, our data suggest that hypoxia could actually enhance availability of fish prey to striped bass by "squeezing" prey into oxygenated surface waters. This phenomenon would be especially common during summer in the middle region and in the northern part of the lower region where hypoxia can occupy the bottom two-thirds of the water column. A similar finding has been observed in the Neuse River estuary, where hypoxia has been shown to force bay anchovy into surface waters at night (Taylor and Rand

Fig. 5. Maps of dissolved oxygen (DO) and growth rate potential (GRP) calculated during the day with and without f_C(DO) in our model. Representative lateral transect from both 1996 (*a–c*, lateral transect 1; *d–f*, lateral transect 17) and 2000 (*g–i*, lateral transect 10; *l–n*, lateral transect 18) are presented.
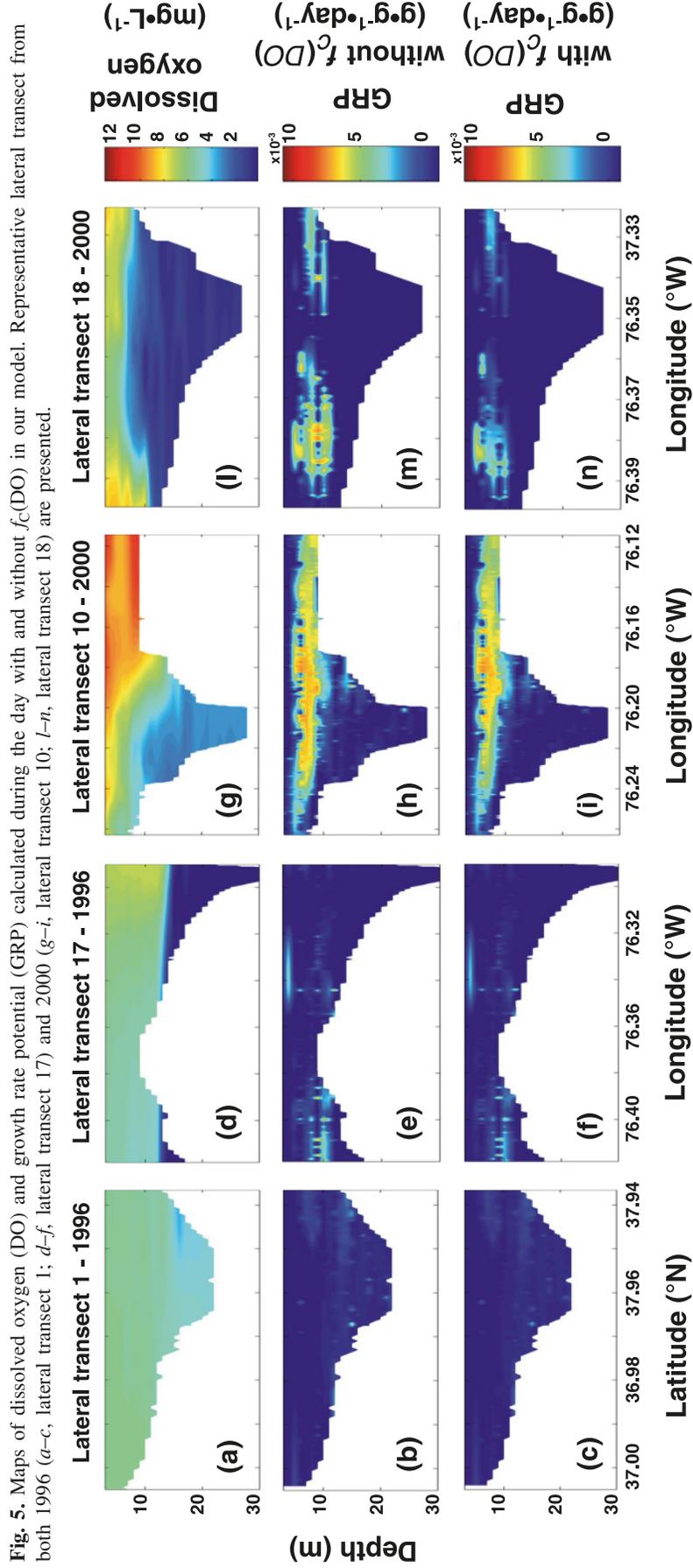
2003). Likewise, hypoxia has been shown to reduce the diurnal use of bottom waters by prey fish, resulting in fish being "squeezed" during both day and night into a narrow layer of water at or just above the oxycline, where they could be more vulnerable to striped bass predation (S. Ludsin, unpublished data).

This compression of prey into a small area during daylight hours may actually benefit visually feeding striped bass by enhancing predation efficiency and encounter rates with prey. Indeed, hypoxia has been shown to alter predator–prey interactions in other ecosystems. For example, Eby and Crowder (2002) demonstrated that hypoxia could increase overlap of croaker (*Micropogonias undulates*), spot (*Leiostomus xanthurus*), and blue crab (*Callinectes sapidus*) in the Neuse River estuary, potentially intensifying both competitive and predatory interactions. Eggleston et al. (2005) also indicated that juvenile blue crabs may experience increased cannibalism under in hypoxia-compressed conditions in the Neuse River estuary. Likewise, in Lake Hiidenvesi, Horppila et al. (2003) demonstrated that summer hypoxia and high temperatures in surface waters could squeeze both mysids (*Mysis relicta*) and smelt (*Osmerus eperlanus*) into a narrow layer, resulting in magnified smelt predation on mysids.

Overall, hypoxia could have opposing short-term effects on striped bass in Chesapeake Bay. In years in which surface temperatures exceed 28 °C, hypoxia could negatively affect striped bass by reducing quality and quantity of habitat through a temperature–oxygen squeeze. In cooler years, hypoxia may benefit striped bass by concentrating prey and increasing predator–prey encounter rates in oxygenated waters.

Effect of hypoxia on striped bass population

The recovery of striped bass in Chesapeake Bay occurred during years characterized by strong summertime hypoxia, consistent with levels observed during our study (Hagy et al. 2004). Thus, hypoxia may have played a role in the recovery by enhancing striped bass foraging efficiency through increased prey encounter rates. Given that hypoxia existed in Chesapeake Bay prior to the recovery, however, any short-term positive effect of hypoxia on striped bass foraging was likely secondary relative to reduced mortality experienced from a commercial fishing ban (Richards and Rago 1999).

More recently, however, hypoxia's elimination of bottom waters as a refuge for prey fish in much of the middle region during summer (S. Ludsin, unpublished data), which we contend benefited striped bass in the short-term through enhanced predation efficiency, may actually prove unfavorable for striped bass production in the long term. At present, a large striped bass population exists in Chesapeake Bay, primarily resulting from management actions that placed restrictions on harvest (Richards and Rago 1999). In turn, recent field and modeling studies suggest that striped bass predatory demand may be exceeding the capacity of the Bay to support the current striped bass population and that insufficient prey resources are likely responsible for recent (post-1995) reductions in striped bass growth and condition, as well as the increased prevalence of pathologies associated with malnutrition (Hartman and Brandt 1995*b*; Overton et al. 2003; Uphoff 2003). Indeed, Atlantic menhaden, which was historically the dominant prey of striped bass in Chesa-

peake Bay, is at very low levels, likely due to both overfishing and striped bass predation (Uphoff 2003). Likewise, bay anchovy recruitment is at record low levels (www.dnr.state.md.us/fisheries/juvindex/index.html#Indices), and consumption of bay anchovy by striped bass in recent years has increased relative to historical levels (Overton 2002; Griffin and Margraf 2003).

In summary, our results suggest that a temperature–oxygen squeeze historically has not limited growth of striped bass, but it may become important if climate warming in the region continues along its current trajectory (Shein 2006). Moreover, hypoxia may have indirectly benefited striped bass by increasing their foraging efficiency and, in this way, may have contributed to their recovery during the mid-1990s. However, although hypoxia may have benefited striped bass in the short term by providing access to more prey, the loss of bottom refugia for fish prey may ultimately lead to long-term negative consequences for the population by allowing the forage base to be overconsumed. Although more research is required to test the relevance of these hypotheses, our data clearly suggest that Chesapeake Bay agencies need to consider the effect of hypoxia when managing both striped bass and their prey.

Acknowledgments

References

Aku, P.M.K., and Tonn, W.M. 1999. Effects of hypolimnetic oxygenation on the food resources and feeding ecology of cisco in Amisk Lake, Alberta. Trans. Am. Fish. Soc. **128**: 17–30.

Boesch, D.F., Brinsfield, R.B., and Magnien, R.E. 2001. Chesapeake Bay eutrophication: scientific understanding, ecosystem restoration, and challenges for agriculture. J. Environ. Qual. **30**: 303–320.

Boynton, W.R., Garber, J.H., Summers, R., and Kemp, W.M. 1995. Inputs, transformations, and transport of nitrogen and phosphorus in Chesapeake Bay and selected tributaries. Estuaries, **18**: 285–314.

Brandt, S.B., and Kirsch, J. 1993. Spatially explicit models of striped bass growth potential in the Chesapeake Bay. Trans. Am. Fish. Soc. **122**: 845–869.

Brandt, S.B., and Mason, D.M. 2003. Effect of nutrient loading on Atlantic menhaden *Brevoortia tyrannus* growth rate potential in the Patuxent River. Estuaries, **26**: 298–309.

Brandt, S.B., Mason, D.M., and Patrick, E.V. 1992. Spatially-explicit models of fish growth rate. Fisheries, **17**: 23–35.

Brandt, S.B., Demers, E., Tyler, A.J., and Gerken, M.A. 1998. Fish bioenergetics modeling. Chesapeake Bay Ecosystem Modeling Program (1993–1998), Report to the Chesapeake Bay Program. US

Environmental Protection Agency, Chesapeake Bay Program Office, 410 Severn Avenue, Suite 109, Annapolis, MD 21403, USA.

Brandt, S.B., Mason, D.M., McCormick, M.J., Lofgren, B., Hunter, T.S., and Tyler, J.A. 2002. Climate change: implications for fish growth performance in the Great Lakes. Am. Fish. Soc. Symp. **32**: 61–76.

Breitburg, D.L., Pihl, L., and Kolesar, S.E. 2001. Effects of low dissolved oxygen on the behavior ecology and harvest of fishes: a comparison of the Chesapeake Bay and Baltic–Kattegat systems. *In* Coastal hypoxia: consequences for living resources and ecosystems. *Edited by* N.N. Rabalais and R.E. Turner. American Geophysical Union, Washington, D.C. pp. 241–268.

Caddy, J.F. 1993. Toward a comparative evaluation of human impacts on fishery ecosystems of enclosed and semi-enclosed seas. Rev. Fish. Sci. **1**: 57–95.

Carpenter, S.R., Caraco, N.F., Correll, D.L., Howarth, R.W., Sharpley, A.N., and Smith, V.H. 1998. Nonpoint pollution of surface waters with phosphorus and nitrogen. Ecol. Appl. **8**: 559–568.

Chapman, L.J., Chapmann, C.A., and Chandler, M. 1996*a*. Wetlands ecotones as refugia for endangered fishes. Biol. Conserv. **78**: 263–270.

Chapman, L.J., Chapmann, C.A., Ogutu-Ohwayo, R., Chandler, M., Kaufman L.S., and Keiter, A.E. 1996*b*. Refugia for endangered fishes from an introduced predator in Lake Nabugabo, Uganda. Conserv. Biol. **10**: 554–561.

Chittenden, M.E., Jr. 1971. Status of the striped bass *Morone saxatilis* in the Delaware River. Chesapeake Sci. **12**: 131 136.

Clark, K.L., Ruiz, G.M., and Hines, A.H. 2003. Diel variation in predator abundance predation risk and prey distribution in shallow-water estuarine habitats. J. Exp. Mar. Biol. Ecol. **287**: 37–55.

Cloern, J.E. 2001. Our evolving conceptual model of the coastal eutrophication problem. Mar. Ecol. Prog. Ser. **210**: 223–253.

Cooper, S.R., and Brush, G.S. 1991. Long-term history of Chesapeake Bay anoxia. Science (Washington, D.C.), **254**: 992–996.

Coutant, C.C. 1985. Striped bass temperature and dissolved oxygen: a speculative hypothesis for environmental risk. Trans. Am. Fish. Soc. **114**: 31–61

Cronin, T.M., Dwyer, G.S., Kamiya, T., Schwede, S., and Willard, D.A. 2003. Medieval Warm Period, Little Ice Age and 20th century temperature variability from Chesapeake Bay. Global Planet Change, **36**: 17–29.

Diaz, R.J., and Rosenberg, R. 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. Oceanogr. Mar. Biol. Annu. Rev. **33**: 245–303.

Eby, L.A., and Crowder, L.B. 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.

Eby, L.A., Rudstam, L.G., and Kitchell, J.F. 1995. Predator responses to prey population dynamics: an empirical analysis based on lake trout growth rates. Can. J. Fish. Aquat. Sci. **52**: 1564–1571.

Edwards, J.I., and Armstrong, F. 1984. Target strength experiments on caged fish. Scott. Fish. Bull. **48**: 12–20.

Eggleston, D.B., Bell, G.W., and Amavisca, A.D. 2005. Interactive effects of episodic hypoxia and cannibalism on juvenile blue crab mortality. J. Exp. Mar. Biol. Ecol. **325**: 18–26.

Foote, K.G., Knudsen, H.P., Vestnes, G., MacLennan, D.N., and Simmonds, E.J. 1987. Calibration of acoustic instruments for fish density estimation: a practical guide. ICES Coop. Res. **144**: 1–69.

Griffin, J.C., and Margraf, F.J. 2003. The diet of Chesapeake Bay striped bass in the late 1950s. Fish. Manag. Ecol. **10**: 323–328.

Hagy, J.D., Boynton, W.R., Keefe, C.W., and Wood, K.V. 2004. Hypoxia in Chesapeake Bay, 1950–2001: long-term change in relation to nutrient loading and river flow. Estuaries, **27**: 634–658.

Hanson, P.C., Johnson, T.B., Schindler, D.E., and Kitchell, J.F. 1997. Fish bioenergetics 3.0 for Windows. University of Wisconsin–Madison, Madison, Wis.

Hartman, K.J., and Brandt, S.B. 1995*a*. Comparative energetics and the development of bioenergetics models for sympatric estuarine piscivores. Can. J. Fish. Aquat. Sci. **52**: 1647–1666.

Hartman, K.J., and Brandt, S.B. 1995*b*. Predatory demand and impact of striped bass, bluefish, and weakfish in the Chesapeake Bay: applications of bioenergetics models. Can. J. Fish. Aquat. Sci. **52**: 1667–1687.

Hartman, K.J., and Margraf, F.J. 2003. US Atlantic coast striped bass: issues with a recovered population. Fish. Manag. Ecol. **10**: 309–312.

Hartman, K.J., and Nagy, B.W. 2005. A target strength and length relationship for striped bass and white perch. Trans. Am. Fish. Soc. **134**: 375–380.

Horppila, J., Liljendahl-Nurminen, A., Malinen, T., Salonen, M., Tuomaala, A., Uusitalo, L., and Vinni, M. 2003. *Mysis relicta* in a eutrophic lake: consequences of obligatory habitat shifts. Limnol. Oceanogr. **48**: 1214–1222.

Jung, S., and Houde, E.D. 2003. Spatial and temporal variability of pelagic fish community structure and distribution in Chesapeake Bay, USA. Est. Coast. Shelf. Sci. **58**: 335–351.

Kemp, W.M., Boynton, W.R., Adolf, J.E., Boesch, D.F., Boicourt, W.C., Brush, G., Cornwell, J.C., Fisher, T.R., Glibert, P.M., Hagy, J.D., Harding, L.W., Houde, E.D., Kimmel, D.G., Miller, W.D., Newell, R.I.E., Roman, M.R., Smith, E.M., and Stevenson, J.C. 2005. Eutrophication of Chesapeake Bay: historical trends and ecological interactions Mar. Ecol. Prog. Ser. **303**: 1–29.

Kitchell, J.F., Stewart, D.J., and Weininger, D. 1977. Applications of a bioenergetics model to yellow perch, *Perca flavescens*, and walleye, *Stizostedion vitreum vitreum*. J. Fish. Res. Board. Can. **34**: 1922–1935.

Luo, J., Hartman, K.J., Brandt, S.B., Cerco, C.F., and Rippetoe, T.H. 2001. A spatially-explicit approach for estimating carrying capacity: an application for the Atlantic menhaden *Brevoortia tyrannus* in Chesapeake Bay. Estuaries, **24**: 545–556.

MacLennan, D.N., and Simmonds, E.J. 1992. Fisheries acoustics. 1st ed. Chapman and Hall, London, UK.

Mansueti, R.J. 1961. Age, growth, and movements of the striped bass, *Rocco saxatilis*, taken in select fishing gear in Maryland. Chesapeake Sci. **2**: 9–36.

Mason, D.M., Goyke, A., and Brandt, S.B. 1995. A spatially explicit bioenergetics measure of habitat quality for adult salmonines — comparison between Lakes Michigan and Ontario. Can. J. Fish. Aquat. Sci. **52**: 1572–1583.

Moore, C.M. 1988. Food habits, population dynamics, and bioenergetics of four predator fish species in Smith Mountain Lake, Virginia. Ph. D. thesis, Virginia Polytechnical Institute and State University, Blacksburg, Virginia.

Officer, C.B., Biggs, R.B., Taft, J.L., Cronin, L.E., Tyler, M.A., and Boynton, W.R. 1984. Chesapeake Bay anoxia: origin, development, and significance. Science (Washington, D.C.), **223**: 22–26.

Overton, A.S. 2002. Striped bass predator–prey interactions in Chesapeake Bay and along the Atlantic Coast. Ph.D. dissertation, University of Maryland–Eastern Shore, Princess Anne, Maryland.

Overton, A.S., Margraf, F.J., Weedon, C.A., Pieper, L.H., and May, E.B. 2003. The prevalence of mycobacterial infections in striped bass in Chesapeake Bay. Fish. Manag. Ecol. **10**: 301–308.

Rabalais, N.N., Turner, R.E., Dortch, Q., Justic, D., Bierman, V.J., Jr., and Wiseman, W.J., Jr. 2002. Nutrient-enhanced productivity

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in the northern Gulf of Mexico: past, present and future. Hydrobiologia, **475**: 39–63.

Rahel, F.J., and Nutzman, J.W. 1994. Foraging in a lethal environment: fish predation in hypoxic waters of a stratified lake. Ecology, **75**: 1246–1253.

Richards, R.A., and Rago, P.J. 1999. A case history of effective fishery management: Chesapeake Bay striped bass. N. Am. J. Fish. Manag. **19**: 356–375.

Robb, T., and Abrahams, M.V. 2003. Variation in tolerance to hypoxia in a predator and prey species: an ecological advantage of being small? J. Fish Biol. **62**: 1067–1081.

Roman, M.R., Gauzens, A.L., Rhinehart, W.K., and White, J.R. 1993. Effects of low oxygen waters on Chesapeake Bay zooplankton. Limnol. Oceanogr. **38**: 1603–1614.

Roman, M.R., Zhang, X., McGilliard, C., and Boicourt, W.C. 2005. Seasonal and annual variability in the spatial patterns of plankton biomass in Chesapeake Bay. Limnol. Oceanogr. **50**: 480–492.

Rudstam, L.G., Parker, S.L., Einhouse, D.W., Witzel, L.D., Warner, D.M., Stritzel, J.L., Parrish, D.L., and Sullivan, P.J. 2003. Application of in situ target-strength estimations in lakes: examples from rainbow-smelt surveys in Lakes Erie and Champlain. ICES J. Mar. Sci. **60**: 500–507.

Secor, D.H., and Piccoli, P.M. 2007. Oceanic migration rates of upper Chesapeake Bay striped bass (*Morone saxatilis*), determined by otolith microchemical analysis. Fish. Bull. **105**: 62–73.

Shein, K.A. 2006. State of the climate in 2005. Bull. Am. Meteorol. Soc. **87**: 1–102.

Stewart, D.J., and Binkowski, F.P. 1986. Dynamics of consumption and food conversion by Lake Michigan alewives: an energetics-modeling synthesis. Trans. Am. Fish. Soc. **115**: 643–661.

Taylor, J.C., and Rand, P.S. 2003. Spatial overlap and distribution of anchovies (*Anchoa* spp.) and copepods in a shallow stratified estuary. Aquat. Living Resour. **16**: 191–196.

Uphoff, J.H. 2003. Predator–prey analysis of striped bass and Atlantic menhaden in upper Chesapeake Bay. Fish. Manag. Ecol. **10**: 313–322.

Wang, S.B., and Houde, E.D. 1995. Distribution, relative abundance, biomass and production of bay anchovy *Anchoa mitchilli* in the Chesapeake Bay. Mar. Ecol. Prog. Ser. **121**: 27–38.

Wannamaker, C.M., and Rice, J.A. 2000. Effects of hypoxia on movements and behavior of selected estuarine organisms from the south-eastern United States. J. Exp. Mar. Biol. Ecol. **249**: 145–163.

Wetzel, R.G. 1983. Limnology. 2nd ed. Saunders College Publishing, Toronto, Ontario, Canada.

Zhang, X., Roman, M., Kimmel, D., McGilliard, C., and Boicourt, W.C. 2006. Spatial variability in plankton biomass and hydrographic variables along an axial transect in Chesapeake Bay. J. Geophys. Res. Oceans, **111**: C05S11, doi:10.1029/2005JC003085.

Appendix A

Table A1. Growth rate potential (GRP; mean ± standard error (SE), median) and percentage of high quality habitat (HQH) for age-4 striped bass along the axial transect during spring, summer, and fall 1996 and 2000, and along lateral transects during summer 1996 and 2000.

| Years | Transect | GRP (g·g^{-1}·day^{-1}) | | | HQH | |
		Mean	SE	Median	%	N
1996	Axial					
	Spring	-5.03×10^{-4}	3.06×10^{-5}	-8.38×10^{-4}	9.0	2223
	Summer	-2.14×10^{-3}	4.61×10^{-5}	-2.56×10^{-3}	5.2	1205
	Fall	3.44×10^{-3}	1.17×10^{-4}	6.29×10^{-4}	56.4	2477
	Lateral summer					
	1	-1.80×10^{-3}	2.43×10^{-5}	-2.05×10^{-3}	7.6	1812
	3	-2.43×10^{-3}	1.22×10^{-5}	-2.60×10^{-3}	0.5	2335
	6	-2.68×10^{-3}	3.65×10^{-6}	-2.68×10^{-3}	0.0	3342
	13	-2.26×10^{-3}	1.97×10^{-5}	-2.60×10^{-3}	5.5	4268
	15	-1.68×10^{-3}	4.61×10^{-5}	-2.72×10^{-3}	14.9	3192
	17	-1.76×10^{-3}	3.73×10^{-5}	-2.43×10^{-3}	10.9	3367
2000	Axial					
	Spring	7.96×10^{-4}	6.70×10^{-5}	-8.38×10^{-4}	30.1	3023
	Summer	1.51×10^{-3}	1.01×10^{-4}	-1.30×10^{-3}	42.7	3231
	Fall	6.70×10^{-3}	1.72×10^{-4}	4.19×10^{-3}	58.0	2350
	Lateral summer					
	5	4.19×10^{-3}	1.22×10^{-4}	1.01×10^{-3}	62.3	3505
	8	8.80×10^{-4}	9.22×10^{-5}	-2.72×10^{-3}	33.0	4325
	10	3.27×10^{-3}	1.26×10^{-4}	-1.13×10^{-3}	46.3	3524
	18	-1.34×10^{-2}	7.12×10^{-5}	-2.68×10^{-3}	17.0	2447
	20	-1.01×10^{-3}	6.29×10^{-5}	-2.68×10^{-3}	18.8	3451
	22	1.05×10^{-4}	1.13×10^{-4}	-2.60×10^{-3}	28.0	1937

Note: N is number of cells.