



# Broad-scale effects of hypoxia on benthic community structure in Chesapeake Bay, USA

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## ABSTRACT

Benthic communities provide secondary production for higher trophic levels, and changes in benthic community structure can be a harbinger for associated food web alterations. Benthic communities can be affected by variations in water quality, with low dissolved oxygen reducing benthic abundance and biomass. We quantified the effects of dissolved oxygen and other environmental factors upon changes in density, biomass, and diversity of the macrobenthic community from long-term data (1996–2004) from the Chesapeake Bay Program's benthic monitoring. Benthic density, biomass, and diversity were significantly and negatively correlated with water depth and positively correlated with the dissolved oxygen level. In an assessment of multiple models using Akaike's Information Criteria, oxygen was the single best predictor of summer benthic infaunal density by depth. Biomass was best predicted by depth, salinity, and dissolved oxygen together. Moreover, oxygen was among the important factors determining Shannon ( $H'$ ) diversity. Benthic diversity in Chesapeake Bay over 2001–2004 was historically low compared to that over the years 1996–2000 and was directly correlated with the severity of hypoxia. Hypoxia leads to mass mortality of benthos, which reduces the overall availability of secondary production to higher trophic levels and can affect overall productivity in Chesapeake Bay. Regions with low dissolved oxygen should be managed to minimize deleterious anthropogenic effects on benthos that may affect higher trophic levels.

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## 1. Introduction

### 1.1. Hypoxia in Chesapeake Bay

Hypoxia (here defined as dissolved oxygen  $<2$  mg  $L^{-1}$ ; Vaquer-Sunyer and Duarte, 2008) in Chesapeake Bay is a form of anthropogenic habitat degradation (Zimmerman and Canuel, 2000) that has been increasing through time (Hagy et al., 2004). In Chesapeake Bay, a system with deep channels and shallow shoals, hypoxia typically is a summer phenomenon that occurs due to nutrient runoff, sinking of algal blooms, high benthic respiration, and stratification of the water column (Haas, 1977; Officer et al., 1984; Seliger et al., 1985; Boynton and Kemp, 2000). In some Bay tributaries, such as the York River, hypoxia is short lived (i.e., days), with typically 2–3 hypoxic events each summer (Pihl et al., 1991); however, hypoxia may be more severe and long-lasting (i.e., months) in other areas of the Bay, such as the Rappahannock River (Llansó, 1992) and the Bay's mainstem in Maryland.

### 1.2. Faunal responses to low dissolved oxygen

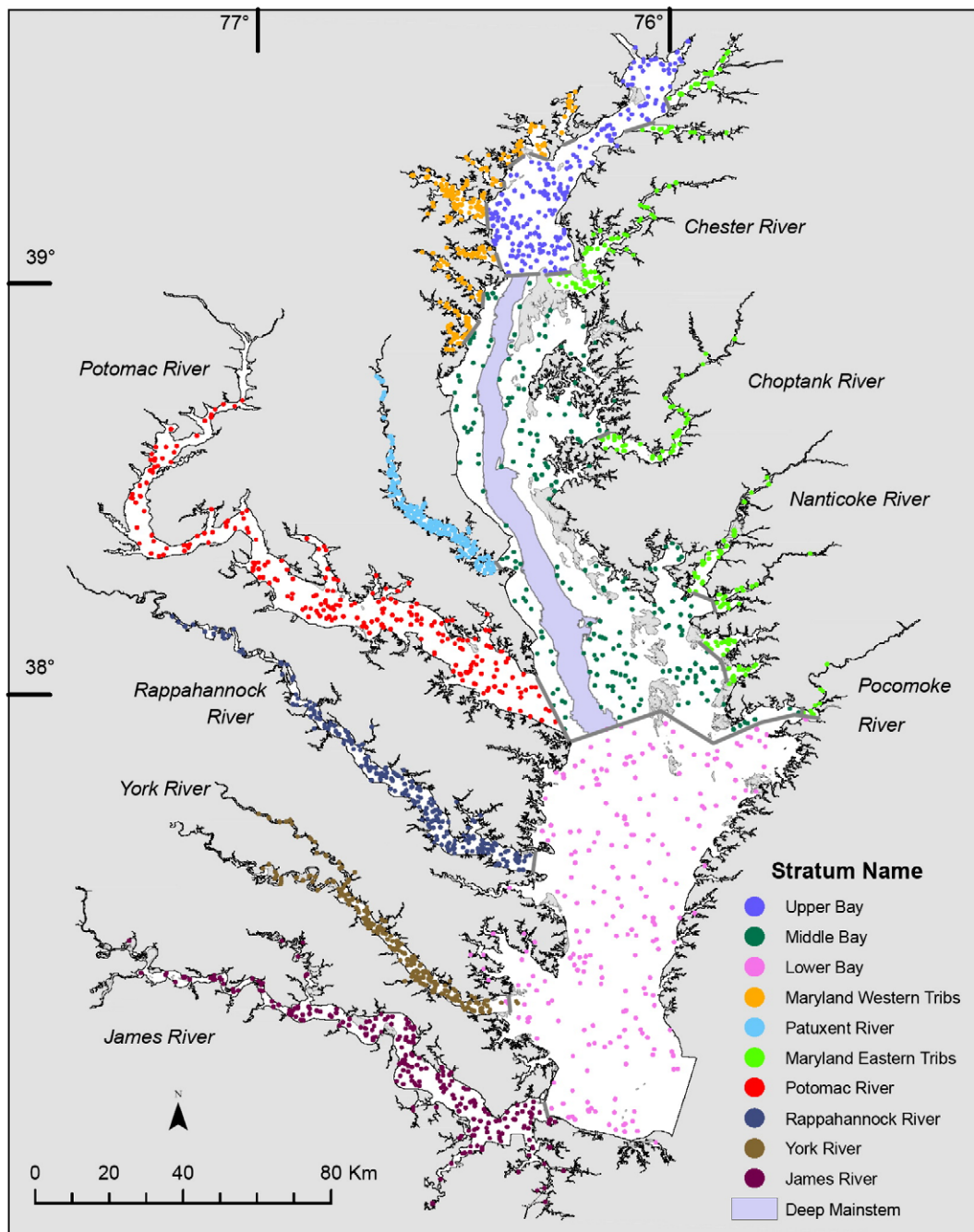
Hypoxia is generally thought to be detrimental because it is associated with reductions in benthic infauna (Holland et al., 1977; Stachowitsch, 1984; Diaz and Rosenberg, 2008) due to hypoxic stress. Hypoxic stress can occur at the physiological level (e.g., metabolic rate), individual level (e.g., growth, fecundity, or mortality), population level (e.g., immigration, emigration, or population abundance), or community level (e.g., alteration of species composition; see Holland et al., 1987; Breitburg, 1992; Dauer et al., 1992; Diaz et al., 1992; Breitburg et al., 1997; Taylor and Eggleston, 2000). At the community level, which we are examining, changes due to low oxygen effects are influenced in a multivariate manner by exposure to a combination of (1) critical oxygen levels, (2) the temporal duration of a given oxygen level, (3) the spatial extent of exposure, (4) species-specific tolerances, (5) intra-specific ontogenetic tolerances, and (6) other environmental conditions (e.g., temperature). Some benthic species (e.g., bivalves and polychaetes) are tolerant of short-lived hypoxic levels of  $<2$  mg  $L^{-1}$  (e.g., as seen in the York River; Pihl et al., 1991). Other species (e.g., crustaceans and echinoderms) may be killed by mild hypoxia (2–3 mg  $L^{-1}$ ) that lasts only hours (Vaquer-Sunyer and Duarte, 2008); however, most macrobenthic species show mortality within a short period (days) when oxygen levels approach or are

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below  $1 \text{ mg L}^{-1}$  (Hines and Comtois, 1985; Weigelt and Rumohr, 1986; Llansó, 1992; Diaz and Rosenberg, 1995, 2008). The migration of benthic infauna to shallow depths within the sediment in response to hypoxia (Rosenberg et al., 1991; Long et al., 2008) may render them more susceptible to predation (see *Behavioral responses that affect predation* section below; Pihl et al., 1992; Nestlerode and Diaz, 1998; Taylor and Eggleston, 2000), facilitating transfer of benthic production to higher trophic levels (Long and Seitz, 2008). Thus, relative to higher trophic levels, the overall effect of low dissolved oxygen on the benthos can be positive or negative depending on the areal extent, duration, and severity of the hypoxic event (Long, 2007).

Physical factors besides dissolved oxygen influence benthic density and biomass. Water depth is correlated with infaunal densities; shallow waters generally house much higher densities of organisms

(Hagy et al., 2004; Seitz et al., 2006), but this correlation is likely due to the effects of other factors that vary with depth (e.g., oxygen levels, food availability). Salinity is important as physiological tolerances of estuarine species, and consequently their abundances, vary greatly between species (Diaz and Schaffner, 1990). Sediment texture greatly affects benthic community composition, with benthic habitats with high silt–clay content characterized by reduced levels of density and biomass (Boesch, 1973, 1977; Ricciardi and Bourget, 1999; Seitz et al., 2006). Moreover, food availability (as indicated by sediment organic content) can affect density and biomass (Dauer et al., 1992; Rodil et al., 2008), as can extremes in temperature (Ankar and Jansson, 1973). Chesapeake Bay has overlapping gradients of these physical factors, making for complex patterns in spatial and temporal distributions of the benthic infaunal community. Previous studies typically have



**Fig. 1.** Chesapeake Bay with sampling points from the years 1996–2004 color-coded for strata in the Chesapeake Bay Program's benthic monitoring. Darker shading in the center of the "Middle Bay" section denotes an area that is eliminated from sampling.

addressed patterns in the benthos in relation to one or two physical factors; here we explicitly examine the relative influences of multiple factors (water depth, dissolved oxygen, salinity, temperature, total sediment organic carbon, and the sediment silt–clay content) on benthic community structure.

### 1.3. Behavioral responses that affect predation

Behavioral responses may increase the ability of benthic organisms to survive under hypoxia, but may increase susceptibility to predation. Mobile organisms can escape from affected areas (Pihl, 1989; Baden et al., 1990; Pihl et al., 1991; Lenihan et al., 2001). Sessile organisms may stretch bodies or body extensions (e.g., bivalve siphons) into the water column in an attempt to reach higher oxygen levels farther up in the water column (Jørgensen, 1980; Taylor and Eggleston, 2000; Seitz et al., 2003). This response may render the individual more vulnerable to predation (e.g., Long and Seitz, 2008). Species-specific tolerances to low oxygen levels potentially result in species-specific susceptibilities to predators, thus altering species composition of macrobenthic communities (Jørgensen, 1980; Breitburg, 1992; Pihl et al., 1992).

### 1.4. Ecosystem effects

From a fisheries perspective, the ecosystem-level effect of hypoxia might be positive if the transfer of production to higher trophic levels is increased or negative if resultant mortality shifts production to the microbial food web (Baird et al., 2004). Thus, the severity and duration of hypoxia may affect trophic transfer through food webs (Breitburg, 1992; Breitburg et al., 1997). Weakened and exposed infauna can be exploited successfully by predators when hypoxia is brief (Nestlerode and Diaz, 1998), whereas predators can be physiologically stressed and unable to exploit weakened infauna when hypoxia is severe (Holland et al., 1987). For example, in the York River, the exploitation of infauna by epibenthic predators may be common because of the moderate level of low dissolved oxygen ( $0.2\text{--}0.8\text{ mg L}^{-1}$ ), its short duration (usually  $<5$  days), and easy access to the hypoxic zone (depths  $>9$  m) from nearby normoxic areas

(Diaz and Rosenberg, 1995). Predators may enter the hypoxic areas and feed on dead and dying species on the sediment surface (Pihl et al., 1992). In areas where hypoxic stress results in mortality of both resident benthos and recent spring recruits and also prohibits predator intrusion, e.g. the deep trench region in the upper Chesapeake Bay (Holland et al., 1987), all secondary production enters the microbial food web (Baird et al., 2004).

The objectives of this study were to determine the importance of hypoxia and other physical variables in influencing benthic density, biomass, and diversity ( $H'$ ) throughout Chesapeake Bay. No previous studies on Chesapeake Bay benthic community structure have compared the relative roles of various environmental factors in driving benthic communities and also include bottom dissolved oxygen levels in a multivariate modeling approach.

## 2. Methods

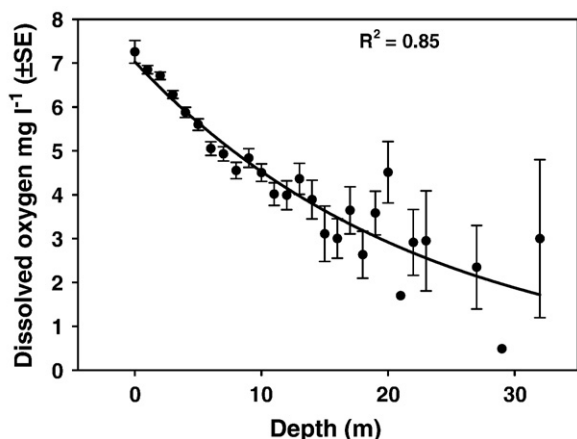
### 2.1. Long-term monitoring field methods

As part of the Chesapeake Bay Monitoring Program, the macrobenthos have been sampled since 1984 in Maryland and since 1985 in Virginia (Dauer et al., 2000; Llansó et al., 2003). Initially the benthic monitoring program consisted of fixed-point stations sampled throughout the year (in Maryland 10–11 times per year and in Virginia four times per year) that were used primarily to examine long-term trends in benthic communities (e.g., Dauer and Alden, 1995; Dauer, 1997). Stations are located from tidal freshwater regions through polyhaline regions of the major tributaries and the mainstem of the Bay. In 1996 a probability-based sampling program was added consisting of a stratified-random sampling design with 25 random sites in each of ten strata within Chesapeake Bay (Fig. 1) covering all tidal regions. All sampling occurs during a summer index period (July 15 to September 30) to allow the application of the Benthic Index of Biotic Integrity (Weisberg et al., 1997; Alden et al., 2002). The deep trench region of the mainstem of Chesapeake Bay was eliminated from sampling because previous sampling showed this region to be azoic

**Table 1**  
Mean values of physical factors and response variables by depth for 27 sampling depths within which 2250 data points fell.

Depth code (m)	Number of samples	Mean DO ( $\text{mg L}^{-1}$ )	Mean salinity (psu)	Mean temp ( $^{\circ}\text{C}$ )	% Silt clay	TOC %	Infaunal density ( $\text{ind. m}^{-2}$ )	Biomass ( $\text{g AFDW m}^{-2}$ )	Shannon diversity ( $H'$ )
0	31	7.26	10.32	26.30	41.90	3.53	5897.99	5.29	2.23
1	274	6.85	10.22	25.65	44.83	3.10	4715.08	9.39	2.33
2	377	6.71	10.46	25.16	46.82	2.39	6611.79	6.23	2.24
3	310	6.29	10.97	25.27	50.99	3.08	3874.09	5.78	2.28
4	215	5.88	10.96	25.44	56.85	2.87	4836.96	12.20	2.25
5	199	5.60	11.55	25.24	57.19	3.02	4033.05	9.80	2.30
6	164	5.05	12.25	25.39	60.05	3.16	3173.78	8.83	2.01
7	150	4.93	13.35	25.37	56.80	2.81	2445.71	4.64	2.11
8	114	4.55	13.81	25.40	60.14	2.61	2779.27	6.00	2.17
9	83	4.84	14.82	24.87	60.93	2.95	2700.57	5.10	2.08
10	80	4.50	15.86	25.15	58.80	2.74	2907.10	2.68	2.39
11	60	4.02	17.26	24.77	69.15	3.28	2433.69	0.90	1.89
12	39	3.99	17.19	25.08	65.48	2.65	1784.95	1.59	1.82
13	33	4.36	16.88	24.68	59.47	3.20	2806.38	1.10	2.27
14	25	3.89	17.39	24.75	63.74	2.89	4119.73	1.84	2.03
15	15	3.11	16.99	25.16	68.81	3.04	2085.25	16.43	1.48
16	21	3.00	15.66	25.70	74.91	3.92	1166.74	4.53	1.21
17	15	3.64	20.80	24.66	55.68	3.29	3101.47	4.74	2.34
18	11	2.63	15.61	26.08	70.15	3.66	1245.81	7.10	1.46
19	13	3.58	18.62	25.29	79.58	3.22	1192.30	2.72	2.07
20	6	4.51	13.10	24.19	54.83	3.32	2089.67	1.33	1.75
21	1	1.70	23.00	24.90	22.84	3.64	1383.48	0.41	3.23
22	3	2.91	17.70	25.58	67.46	4.28	211.91	0.07	1.81
23	4	2.95	21.88	24.73	29.20	4.18	3448.26	0.70	2.26
27	4	2.35	20.33	24.75	85.16	4.00	844.89	0.29	1.86
29	1	0.49	17.50	25.05	85.33	3.40	0.00	0.00	0.00
32	2	3.00	19.30	23.35	97.84	7.83	635.04	0.19	2.05

Depth code refers to the nominal meters in depth for values less than the next whole number (i.e., depth 1 includes 1.0 m–1.99 m). DO = dissolved oxygen, TOC = total organic carbon, AFDW = Ash-free dry weight.



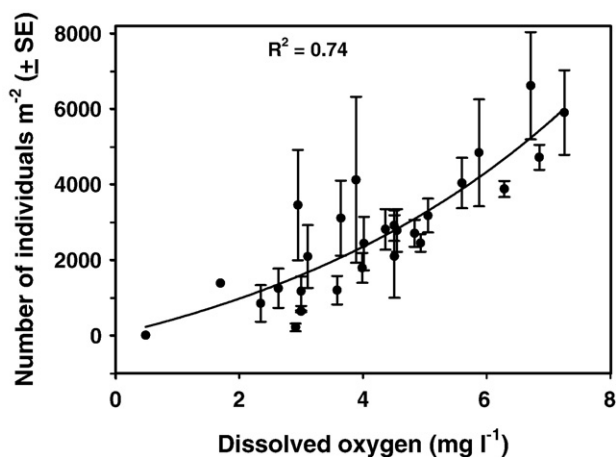
**Fig. 2.** Relationship of mean dissolved oxygen concentrations ( $\text{mg l}^{-1}$ ) within each depth interval ( $\pm \text{SE}$ ) from random sites for the Chesapeake Bay benthic monitoring in the summers of 1996–2004. Non-linear regression, single, exponential decay curve fit to data.

during the summer (Fig. 1; darker shading in “Deep Mainstem”). At all sites, the benthos was sampled with a Young grab, which samples an area of  $0.044 \text{ m}^2$  to a maximum depth of 10 cm. Sample volume and penetration depth were measured. Samples with a penetration depth of less than 7 cm were rejected and the site re-sampled. One sample was collected for benthic community analysis at each random site. Samples were sieved through a 0.5-mm screen using an elutriative process. Organisms and detritus retained on the screen were preserved in a 10% formaldehyde solution stained with Rose Bengal.

Two surface-sediment subsamples of approximately 120 ml each were collected for silt–clay and organic carbon and nitrogen analysis from an additional grab sample at each sampling location. All subsamples were frozen before processing in the laboratory. Dissolved oxygen (DO), salinity, conductivity, temperature, and pH were measured at each location at approximately 1 m from the bottom using a multi-parameter water quality sonde.

Benthic samples were processed to identify and enumerate each species present and to measure species-specific ash-free dry-weight biomass. Ash-free dry-weight (AFDW) biomass was measured for each species by drying the organisms to a constant weight at  $60^\circ \text{C}$  and ashed in a muffle furnace at  $500^\circ \text{C}$  for 4 h.

Sediment samples were analyzed for percent silt–clay content and carbon content. Sand was separated from mud by wet-sieving through a  $63\text{-}\mu\text{m}$  sieve, and the silt–clay fraction of the sediment was weighed (Folk,



**Fig. 3.** Relationship of mean density of benthic organisms ( $\text{individuals m}^{-2}$ ) within each depth interval ( $\pm \text{SE}$ ) compared to mean dissolved oxygen (within each depth interval) from random sites for the Chesapeake Bay benthic monitoring in the summers of 1996–2004. Non-linear regression, quadratic increase curve fit to data.

1966). The total organic carbon (TOC) of the sediment was measured in the Maryland samples with a carbon analyzer and in the Virginia samples as the total volatile solids by a loss-upon-ignition method.

## 2.2. Statistical analyses

We used random samples collected from 1996–2004, which resulted in 2250 samples. From those 2250 data points, samples from each 1-m depth interval were combined and averaged to assess patterns in the benthos by depth resulting in 27 points (depths) for each of the response variables and the independent variables (Table 1). Mean depth categories ranged from 0 m (0–0.99 m) to 32 m (32.0–32.99 m). The means for the response variables density ( $\text{individuals m}^{-2}$ ), biomass ( $\text{g AFDW m}^{-2}$ ), and Shannon diversity ( $H'$ ; in  $\log_2$ ) were compared to the means for the independent variables temperature, DO, salinity, TOC, sediment silt/clay fraction, and depth with least-squares regression models along with Akaike's Information Criterion (AIC) to examine driving forces producing patterns in the benthos. An information-theoretic approach was used for analyzing benthic community structure because these methods provide excellent means of determining the relative influence of many potential variables. We established multiple hypotheses, represented by generalized linear models and used each model's residual sum of squares with the AIC corrected for small sample size (AICc) to select the model(s) that optimized goodness-of-fit and parsimony (Burnham and Anderson, 2002; Anderson, 2008). Each model represented a different combination of variables that could describe differences observed in the response variables among the depth categories. In cases involving small sample sizes, a second-order AIC correction (AICc) is necessary and was calculated for each model as follows:

$$\text{AICc} = n \cdot \ln(\sigma^2) + 2k \left[ \frac{n}{n - k - 1} \right]$$

where  $\ln(\sigma^2)$  is the natural logarithm of the residual sum of squares divided by the sample size  $n$  (27 in this case), and  $k$  is the number of estimable parameters. To rank the different models,  $\Delta\text{AICc}$  was calculated as

$$\Delta\text{AICc} = \text{AICc}_i - \text{AICc}_{\min}$$

where  $\text{AICc}_i$  are the values for each of the  $i$  models and  $\text{AICc}_{\min}$  is the lowest AICc value of all the models. By definition, the best model has  $\Delta\text{AICc} = 0$ . We also calculated Akaike weights ( $w_i$ ) for each model to

**Table 2**

Akaike's Information Criterion (AICc) rank and weights of models ( $w_i$ ) for benthic density ( $\text{individuals m}^{-2}$ ) per depth interval versus physical variables derived from residual sums of squares from regression models.

Variables in models	K	AICc	$\Delta\text{AICc}$	$w_i$	Likelihood
<b>DO*</b>	<b>3</b>	<b>204.48</b>	<b>0.00*</b>	<b>0.366624</b>	<b>1.00</b>
<b>DO, depth</b>	<b>4</b>	<b>204.96</b>	<b>0.48</b>	<b>0.288171</b>	<b>0.79</b>
<b>DO, depth, salinity, silt/clay</b>	<b>6</b>	<b>206.51</b>	<b>2.03</b>	<b>0.132997</b>	<b>0.36</b>
<b>DO, depth, salinity</b>	<b>5</b>	<b>206.63</b>	<b>2.14</b>	<b>0.125282</b>	<b>0.34</b>
<b>Depth</b>	<b>3</b>	<b>207.52</b>	<b>3.04</b>	<b>0.080058</b>	<b>0.22</b>
Depth, DO, salinity, temp, TOC, silt/clay	8	214.29	9.81	0.002712	0.01
Depth, DO, salinity, temp, TOC	7	213.462	8.981	0.004107	0.01
Salinity	3	222.509	18.031	0.000045	0.00
Silt/clay	3	227.852	23.374	0.000003	0.00
Temp, TOC, silt/clay	5	230.842	26.364	0.000001	0.00
TOC	3	232.339	27.861	0.000000	0.00

Models are listed in order from best to worst. Variables made available to the model included depth, dissolved oxygen (DO), salinity, temperature (Temp), total organic carbon (TOC), and sediment silt/clay fraction.  $K$  = estimable number of parameters in the model. AICc is the AIC model with a correction factor for low sample size. Akaike weights ( $w_i$ ), or probabilities, and likelihood ( $w_i/w_{\max}$ ) are given for each model. Models with strong support ( $\Delta\text{AICc} < 4.0$ ) are shaded. \*Indicates the best model.



estimate the probability that a particular model is the best among the set of R models given the data:

$$w_i = \frac{e^{-\frac{1}{2}\Delta_i}}{\sum_{r=1}^R (e^{-\frac{1}{2}\Delta_r})}$$

where  $\Delta_i$  is  $\Delta AIC_c$ . The ratio of the  $w_i$  of the model of interest to the  $w_i$  of the best model in the set provided an additional measure of likelihood for each model. Models with  $\Delta AIC_c < 4.0$  and a probability  $\geq 0.10$  in a model set were considered likely models. If a parameter was included in more than one of the likely models, it was considered a good predictor for that response variable. To visualize the patterns of the three response variables with DO, and DO with depth, multiple curves were fit to the data and the one with the best fit (highest  $R^2$ ) is presented.

We conducted an additional analysis of temporal trends in Shannon diversity and DO by year and examined the severity of hypoxia in terms of the % of the DO readings  $< 2 \text{ mg L}^{-1}$  and the mean value for the DO readings  $< 2 \text{ mg L}^{-1}$  by year. We also examined the relationship between the hypoxic severity and mean Shannon diversity by year to investigate ramifications of low DO for diversity over time.

### 3. Results

#### 3.1. Physical variables

Mean summer bottom-water temperatures within each depth interval ranged from  $23.4^\circ \text{C}$  (at 32 m depth) to  $26.3^\circ \text{C}$  (at  $< 1 \text{ m}$ ), mean salinities ranged from 10.2 practical salinity units, psu (at 1 m) to 23.0 psu (at 21 m), mean sediment silt-clay fraction ranged from 22.8% (at 21 m) to 97.8% (at 32 m), mean TOC ranged from 2.39% (at

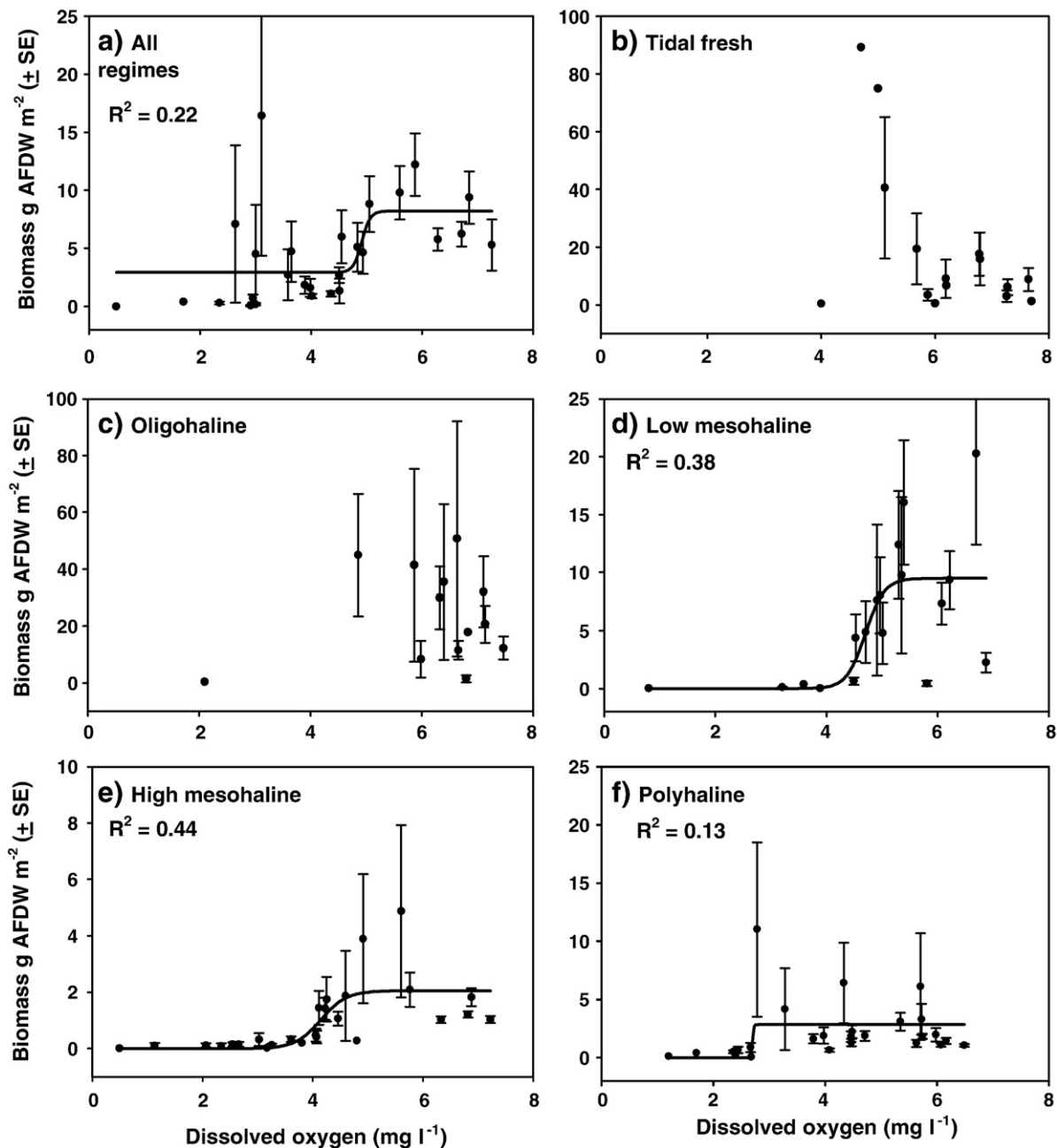


Fig. 4. Mean biomass per depth interval ( $\pm$  SE) compared to mean dissolved oxygen for (a) all salinity regimes combined, (b) tidal freshwater, (c) oligohaline, (d) low mesohaline, (e) high mesohaline, and (f) polyhaline salinity regimes. Non-linear regression, sigmoidal curve fit to data when possible. Note that y-axis scales change among panels.

**Table 3**

Akaike's Information Criterion (AICc) rank and weights of models ( $w_i$ ) for mean biomass (g AFDW  $m^{-2}$ ) per depth interval versus physical variables derived from residual sums of squares from regression models.

Variables in models	K	AICc	$\Delta$ AICc	$w_i$	Likelihood
<b>Depth*</b>	<b>3</b>	<b>52.799</b>	<b>0.000*</b>	<b>0.201473</b>	<b>1.000</b>
<b>Salinity</b>	<b>3</b>	<b>52.803</b>	<b>0.004</b>	<b>0.201117</b>	<b>0.998</b>
<b>DO</b>	<b>3</b>	<b>52.816</b>	<b>0.017</b>	<b>0.199756</b>	<b>0.991</b>
<b>TOC</b>	<b>3</b>	<b>52.831</b>	<b>0.032</b>	<b>0.198318</b>	<b>0.984</b>
<b>Silt/clay</b>	<b>3</b>	<b>52.845</b>	<b>0.046</b>	<b>0.196904</b>	<b>0.977</b>
Depth, DO	4	61.739	8.940	0.002306	0.010
Depth, DO, salinity	5	69.001	16.202	0.000061	0.000
Temp, TOC, silt/clay	5	69.015	16.216	0.000061	0.000
Depth, DO, salinity, silt/clay	6	75.231	22.432	0.000003	0.000
Depth, DO, salinity, temp, TOC, silt/clay	8	85.831	33.032	0.000000	0.000
Depth, DO, salinity, temp, TOC	7	80.771	27.972	0.000000	0.000

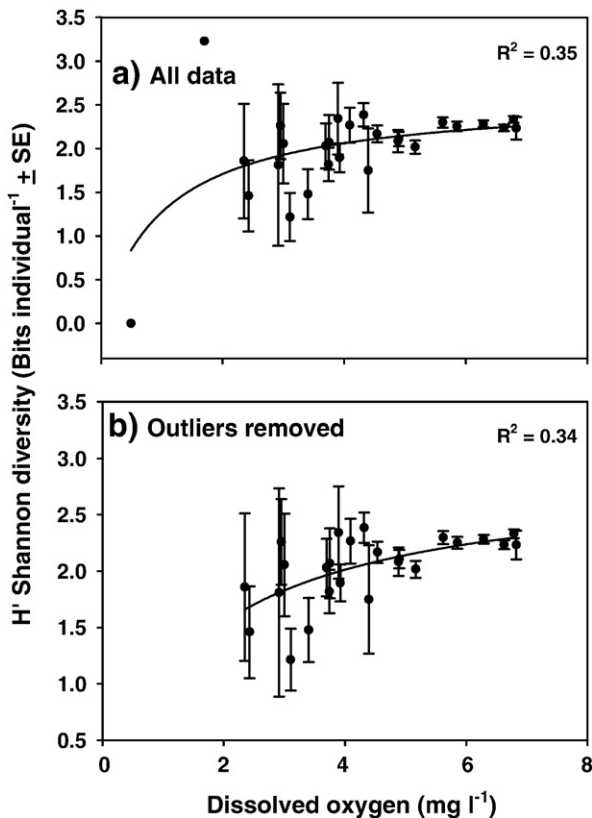
\* Indicates the best model.

See Table 2 for further explanation.

2 m) to 7.83% (at 32 m), and mean DO ranged from 0.49  $mg\ L^{-1}$  (at 29 m) to 7.26  $mg\ L^{-1}$  (at <1 m; Table 1). Dissolved oxygen was highly negatively correlated with depth (non-linear regression  $R^2 = 0.85$ ; Fig. 2). The variability in the DO values increased with depth due to a preponderance of hypoxic sites in the deep channels in Maryland, with fewer hypoxic sites throughout the Virginia deep channels.

### 3.2. Benthic community comparisons

The mean benthic density within each depth interval ranged from 0 to 6611 ind.  $m^{-2}$ , and benthic density dropped exponentially with



**Fig. 5.** (a) Mean Shannon diversity ( $H'$ ) per depth interval ( $\pm$ SE) compared to mean dissolved oxygen with non-linear regression line fit. Non-linear regression, hyperbolic curve fit to data. The lowest DO value at 0.49  $mg\ L^{-1}$  was from our 29 m depth interval where only one sample was taken and therefore had undue influence on the low end of the curve, and at the 21 m depth interval only one sample was taken also (data were then plotted without outliers); (b) linear regression without the two outliers that had only one data point each (DO = 0.49  $mg\ L^{-1}$  and DO = 1.7  $mg\ L^{-1}$ ) of mean Shannon diversity ( $H'$ ) per depth interval ( $\pm$ SE) compared to mean dissolved oxygen.

**Table 4**

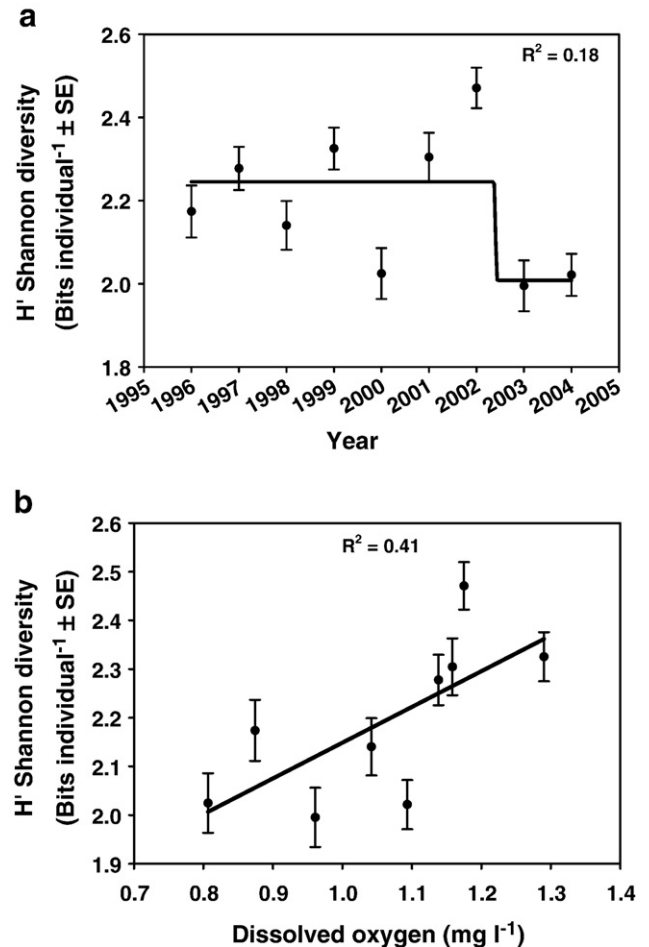
Akaike's Information Criterion (AICc) rank and weights of models ( $w_i$ ) for mean Shannon diversity ( $H'$ ) per depth interval versus physical variables derived from residual sums of squares from regression models.

Variables in models	K	AICc	$\Delta$ AICc	$w_i$	Likelihood
<b>Depth, DO, salinity*</b>	<b>5</b>	<b>-51.0259</b>	<b>0.0000*</b>	<b>0.525682</b>	<b>1.00</b>
<b>Depth, DO, salinity, temp, silt/clay</b>	<b>7</b>	<b>-50.2768</b>	<b>0.7491</b>	<b>0.361467</b>	<b>0.69</b>
<b>Depth, DO, salinity, temp</b>	<b>6</b>	<b>-47.8841</b>	<b>3.1418</b>	<b>0.109268</b>	<b>0.21</b>
Temp, silt/clay	4	-40.9893	10.0366	0.003478	0.01
DO	3	-32.9663	18.0596	0.000063	0.00
Depth	3	-30.8944	20.1315	0.000022	0.00
Depth, DO	4	-30.3164	20.7095	0.000017	0.00
Salinity	3	-26.5886	24.4373	0.000003	0.00
Silt/clay	3	-26.7657	24.2602	0.000003	0.00

\* Indicates the best model.

See Table 2 for further explanation.

decreases in oxygen (Fig. 3; non-linear regression  $R^2 = 0.74$ ). Densities in the hypoxic areas (<2.0  $mg\ L^{-1}$  oxygen) were below 2000 ind.  $m^{-2}$ , whereas they were nearly four times greater at the highest DO concentrations (>7  $mg\ L^{-1}$ ). Density also was low in deeper water, was low with higher salinity, and tended to be low when % silt-clay was high (though % silt-clay was correlated with depth). We identified five models with significant support ( $\Delta$ AICc < 4.0, and  $w_i > 0.10$ , as defined in Methods), which accounted for 99% of the Akaike weights (Table 2). The following five models, (1) model with DO alone, (2) model with depth and DO, (3) model with depth, DO, and salinity, (4) model with depth, DO, salinity, and sediment silt-clay fraction, and (5) model with depth alone, had strong support in the AIC analysis (Table 2). Note that



**Fig. 6.** Mean Shannon diversity ( $H'$ ) per year ( $\pm$ SE) averaged by depth (a) through time; non-linear regression, sigmoid curve fit to data; (b) compared to mean level of hypoxia at those sites where readings <2  $mg\ l^{-1}$  were recorded.

**Table 5**

Mean values of dissolved oxygen (DO) by year, percentage of DO readings (of 250 per year) that were  $<2$  mg L<sup>-1</sup>, mean DO of that fraction of readings, and corresponding annual Shannon diversity (H').

Variable/Year	Mean DO (mg L <sup>-1</sup> )	% of DO values $\leq 2$ mg L <sup>-1</sup>	Mean of DO $\leq 2$ mg L <sup>-1</sup>	Shannon diversity
1996	5.60	10.4	0.87	2.17
1997	5.73	4.8	1.14	2.28
1998	5.52	12.0	1.04	2.14
1999	6.46	1.2	1.29	2.33
2000	5.33	3.6	0.81	2.02
2001	5.37	9.2	1.16	2.30
2002	5.78	2.4	1.18	2.47
2003	5.45	8.4	0.96	2.00
2004	5.76	6.0	1.09	2.02

the top four models included DO, with the top model comprised of DO alone (Table 2). Oxygen was nearly three times more likely to explain the data than a combination of oxygen, depth, salinity, and sediment silt-clay fraction (Table 2, comparison of  $w_i$  values).

Biomass was low in oxygen conditions below  $\sim 4.0$  mg L<sup>-1</sup>, rising after  $4.5$  mg L<sup>-1</sup> (Fig. 4a, All regimes). General patterns for all salinity regimes combined appeared to be driven by patterns in low mesohaline, high mesohaline, and polyhaline salinity regimes, which typically experience summer hypoxia (Fig. 4). Extremely high biomass values at  $2.7$  and  $3.1$  mg L<sup>-1</sup> DO occurred due to samples comprised of large percentages of mollusks (93% and 95%, respectively). As with density, biomass was lower when depth was greater and salinity and % silt-clay were higher (Table 1). Mean depth was highly correlated with DO (linear least-squares regression  $R^2 = 0.80$ ), correlated with salinity (linear least-squares regression  $R^2 = 0.65$ ), correlated with TOC (linear least-squares regression  $R^2 = 0.39$ ), and correlated with the sediment silt-clay fraction (linear least-squares regression  $R^2 = 0.20$ ). Not surprisingly, models with depth alone, salinity alone, DO alone, TOC alone, and silt-clay fraction alone were all good predictors of biomass in the AIC analysis (Table 3).

Mean Shannon diversity (H') was high when DO was high (Fig. 5a; non-linear regression  $R^2 = 0.35$ ), and this relationship held without two extreme outliers (Fig. 5b; non-linear regression  $R^2 = 0.34$ ). In the AIC analysis, a model with the variables DO, depth, and salinity was the best predictor of H' diversity (i.e., had the highest probability; Table 4), but this was only 1.45 times more likely than the second best model. The second strongest model (probability  $\geq 0.10$ ) included the variables DO, depth, salinity, sediment silt/clay fraction, and temperature. The third model with strong support included all variables except sediment silt/clay fraction.

Mean Shannon diversity decreased in a step-wise fashion through time, with the lowest values during this study occurring in the last two years (2003 and 2004) (Fig. 6a; Table 5). Subsequent years had similarly low values, with mean Shannon diversity for 2005 ( $1.98 \pm 0.058$  SE), 2006 ( $1.96 \pm 0.060$  SE), and 2007 ( $1.96 \pm 0.062$  SE) the lowest in the Chesapeake Bay Program's monitoring record for random stations (D. Dauer and R. Llansó, unpublished data). Shannon diversity was positively correlated with oxygen level at hypoxic sites (mean of DO values at sites  $<2$  mg L<sup>-1</sup>; Fig. 6b); however, the extent of hypoxia (% of sites with DO  $<2$  mg L<sup>-1</sup>) did not increase over time (Table 5).

## 4. Discussion

### 4.1. Benthic community structure

For the bay-wide trends in the summer benthos, dissolved oxygen (DO) was an important predictor of benthic density, biomass, and diversity by depth. Though our model including oxygen, salinity, depth, and sediment silt/clay fraction received some support, our AIC analysis determined that oxygen was the variable with the greatest impact on benthic density by depth. Summer bottom oxygen was

highly correlated with depth, which is not surprising due to the typical development of stratification in deeper channels (Haas, 1977; Officer et al., 1984; Seliger et al., 1985). Though other physical variables (e.g., sediment type, salinity, depth) affect benthic density (Holland, 1985; Diaz and Schaffner, 1990; Diaz and Rosenberg, 1995; Diaz and Solow, 1999; Dauer et al., 2008), oxygen was the single best predictor for benthic density by depth in Chesapeake Bay in the summer. In earlier studies in the Bay, there was a significant hypoxia-related change in the benthic macroinfauna whereby estuarine and eurytolerant marine species (e.g., *Heteromastus filiformis*, *Macoma balthica*, *Mya arenaria*) responded to lower oxygen concentrations with long-term declines in abundance and biomass, whereas opportunistic species (e.g., *Streblospio benedicti*) responded with long-term increases in abundance over the years 1971–1984 (Holland et al., 1987). More recently, increases in nutrients have led to more severe hypoxia in Chesapeake Bay (Hagy et al., 2004).

The central channel of Chesapeake Bay is the area most severely affected by low DO, but many areas outside of that zone are also influenced by low DO (e.g., Rappahannock River; Dauer and Alden, 1995; Llansó et al., 2003). Though central Maryland channels  $>12$  m depth are purposely eliminated from the Chesapeake Bay Program's benthic monitoring (and this study) as potential sampling zones because of the lack of infauna, other areas among the remaining sampling locations outside of the central mainstem Bay (all sites included in this study), have reduced benthic densities where low DO has developed (Llansó, 1992; Long and Seitz, 2009). Though degradation of benthos in the Bay's tributaries (Llansó, 1992; Dauer et al., 2000), as well as in the mainstem Bay (Hagy, 2002) has been noted previously, the large-scale and long-term sampling incorporated in our study provides strong support for the importance of dissolved oxygen in driving broad-scale benthic community structure. Hypoxia was an important factor in determining benthic density along the depth axis.

Changes in biomass associated with low DO can have ramifications for higher trophic levels. Biomass of the benthic community was substantially higher at elevated oxygen levels, and a sigmoid curve best described the relationship. The inflection point on this curve suggests that there is a DO threshold value ( $\sim 4.5$  mg L<sup>-1</sup>) above which a high-biomass community can exist. At the low oxygen levels, mean biomass was extremely low ( $<3$  g AFDW m<sup>-2</sup>) implying that these areas would be poor foraging zones for epibenthic predators, such as the fish croaker (*Micropogonias undulatus*) and spot (*Leiostomus xanthurus*), as well as blue crabs (*Callinectes sapidus*) (Hines et al., 1990; Seitz et al., 2003, 2006). Above  $4.5$  mg L<sup>-1</sup>, biomass was up to four-fold higher, suggesting that those areas would provide substantially more food resources for the epibenthic predators. The biomass throughout normoxic areas in estuaries and coastal systems previously has been correlated with primary production (Herman et al., 1999), yet mid-Bay biomass does not conform to this pattern (Kemp et al., 2005), which suggests that mid-Bay benthos has been degraded by hypoxic conditions (Hagy, 2002).

In contrast to short-lived hypoxia (lasting days) where benthos exhibit behaviors that render them more susceptible to predation (Taylor and Eggleston, 2000; Long et al., 2008), it is likely that long-lasting hypoxia (weeks to months, typical in the Rappahannock River; Llansó, 1992) causes direct mortality of large expanses of benthos. The hypoxic zones that develop have large interior zones that are too far from normoxia for marauding predators to reach. Thus, the benthos likely die from stress and are incorporated into the microbial food web (Baird et al., 2004). In our examination of the Chesapeake Bay, high biomass and productivity (which can be estimated from biomass; Edgar, 1990) can only be maintained where oxygen levels are above  $\sim 4.5$  mg L<sup>-1</sup> in Chesapeake Bay. The lower levels of biomass below  $4.5$  mg L<sup>-1</sup> DO suggest that these lower-oxygen zones will reduce secondary production available to predators (Sturdivant, Diaz, Dauer, and Llansó, in prep.).

Diversity was also directly related to DO, and a model combining DO, depth, and salinity was the best in describing diversity differences. In homiohaline temperate estuaries, the well-known Remane Curve relationship between species richness and salinity is generally well supported (Remane and Schlieper, 1971; Wolff, 1983), and salinity generally increases with depth due to physical properties. Shallow water (<1.5 m depth) benthic community diversity has been reported to be higher than that in deeper communities, which was attributed to higher species richness stemming from superior habitat quality (Seitz et al., 2006). Thus, the influence of depth on diversity that we observed is anticipated.

A potential loss in benthic diversity is a severe consequence of the hypoxia-induced loss of habitat quality. In our study, benthic Shannon diversity from 1996–2004 in Chesapeake Bay has worsened and appears to be remaining at low levels through 2007. This is of concern given that previous studies of diversity showed increases in species richness in the lower Bay tributaries from 1985 to 1991 (Dauer and Alden, 1995); however, biomass of opportunists (an indication of deteriorating conditions) increased in the Bay's mainstem and Rappahannock River (Dauer et al., 1984; Dauer and Alden, 1995). It was suggested that these deteriorating conditions were due to low-DO events previously recorded in the mainstem (Dauer et al., 1992).

The increasing severity of hypoxia over time in Chesapeake Bay (Hagy et al., 2004) along with the positive relationship between DO and diversity (Fig. 5) raises concern about changes in diversity in the future. Habitat destruction is a major threat to marine biodiversity (Norse and Crowder, 2004) and can act synergistically with other stressors in the system to eliminate the species that could otherwise survive one stressor (Breitburg and Riedel, 2005). Given that other stressors to the benthic community, such as pollution, may be increasing concurrently, it is likely that diversity will continue to decrease. The impact of such reductions in diversity on other aspects of the food web are unknown, thus, actions must be taken to reverse the negative anthropogenic effects on the ecosystem.

#### 4.2. Conclusions

In Chesapeake Bay, the severity of hypoxia has been increasing temporally (Hagy et al., 2004) and we show that the benthic community suffers losses of density, biomass, and Shannon diversity ( $H'$ ) in association with low dissolved oxygen (DO). Although water depth, salinity, and sediment composition (% silt–clay) had some influence on benthic communities, DO was generally a better predictor of benthic density, biomass, and diversity patterns by depth. For example, DO was nearly three times more likely to explain changes in benthic density than was a combination of DO, depth, salinity, and % sediment silt/clay.

In previous manipulative experiments (Long and Seitz, 2008), low DO had a negative effect on infauna but increased trophic transfer of secondary production to predators in short-lived hypoxia (a few days) in the York River; however, trophic transfer has been reduced in zones that have prolonged severe hypoxia (Stachowitsch, 1984). This suggests that there is a trade-off between positive ecosystem effects when hypoxia is moderate (e.g., York River) and negative effects when hypoxia is severe (e.g., mainstem Chesapeake Bay). Thus, the overall effect of low DO on trophic transfer will depend on the severity and duration of hypoxia. If moderate levels of hypoxia increase trophic transfer and severe levels decrease it, then the overall level of trophic transfer over a gradient of hypoxia is hypothesized to have a unimodal pattern, similar to benthic patterns in the intermediate disturbance hypothesis (Grime, 1973; Connell, 1978; Wilkinson, 1999) and benthic responses to nutrient loading (Caddy, 1993).

In sum, for Chesapeake Bay benthos, there have been major changes in the ecosystem as a result of human activities (Zimmerman and Canuel, 2000). Moreover, the resilience of the system has been compromised due to anthropogenic activities such as loss and

fragmentation of forests, loss of wetlands and hardening of the shoreline (Seitz et al., 2006), and degradation of the benthic communities (Boesch, 2006). Though moderate levels of hypoxia (days to weeks) with a small spatial influence (square meters) may have positive effects on trophic transfer (Long and Seitz, 2008), severe hypoxia (weeks to months) over large spatial expanses (hectares) have negative effects on the benthos of the Chesapeake Bay in summer. Thus far, increasing negative effects of low DO in Chesapeake Bay have not led to fisheries losses (Kemp et al., 2005), likely due to increased trophic transfer under moderate hypoxia. However, further increases in hypoxia may push the system beyond its capacity to rebound (Long, 2007; Diaz and Rosenberg, 2008) thus exceeding a potential ecological threshold (Groffman et al., 2006), changing the ecosystem state, and requiring greater and/or different restoration actions in an adaptive management sense (Boesch, 2006). Additional increases in low DO may result in hypoxic zones of sufficiently large areal extent that reduce benthic biomass and density, which may ultimately reduce transfer of productivity to higher trophic levels. Our results highlight the necessity to decrease hypoxia and increase water quality in the Chesapeake Bay in an effort to ameliorate the deleterious effects of anthropogenic influences on the benthic communities before the resilience of the system is further compromised.

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