Estuaries and Coasts
DOI 10.1007/s12237-013-9763-4

Relationship between Hypoxia and Macrobenthic Production in Chesapeake Bay

S. Kersey Sturdivant · Robert J. Díaz · Roberto Llansó · Daniel M. Dauer

Received: 23 July 2013 / Revised: 10 December 2013 / Accepted: 20 December 2013

Abstract Human development has degraded Chesapeake Bay's health, resulting in an increase in the extent and severity of hypoxia (≤ 2 mg O_2 l^{-1}). The Bay's hypoxic zones have an adverse effect on both community structure and secondary production of macrobenthos. From 1996 to 2004, the effect of hypoxia on macrobenthic production was assessed in Chesapeake Bay and its three main tributaries (Potomac, Rappahannock, and York Rivers). Each year, in the summer (late July−early September), 25 random samples of the benthic macrofauna were collected from each system, and macrobenthic production in the polyhaline and mesohaline regions was estimated using Edgar's allometric equation. Fluctuations in macrobenthic production were significantly correlated with dissolved oxygen. Macrobenthic production was 90 % lower during hypoxia relative to normoxia. As a result, there was a biomass loss of ~7,320–13,200 metric tons C over an area of 7,720 km^2, which is estimated to equate to a 20 % to 35 % displacement of the Bay's macrobenthic productivity during the summer. While higher consumers may benefit from easy access to stressed prey in some areas, the large spatial and temporal extent of seasonal hypoxia limits higher trophic level transfer, via the inhibition of macrobenthic production. Such a massive loss of macrobenthic production would be detrimental to the overall health of the Bay, as it comes at a time when epibenthic and demersal predators have high-energy demands.

Keywords Estuary · Energy flow · Benthos · Oxygen depletion · Secondary production

Introduction

Eutrophication, an increase in the supply and accumulation of organic matter to a system (Nixon 1995; Rabalais 2004), is pervasive and has led to a series of counteracting community impacts (Nixon 1995; Kemp et al. 2005); reductions in benthic species richness and increases in abundance and biomass are the most obvious (Pearson and Rosenberg 1978; Rabalais 2004). In addition, dissolved oxygen (DO), which is essential in the metabolism of most microbes and metazoans (Danovaro et al. 2010), has declined in many systems experiencing eutrophication and given rise to hypoxia and anoxia (Diaz and Rosenberg 2008). Hypoxia, a shortage in DO, is difficult to define, as different taxonomic groups, body sizes, and skeletal types have varying oxygen tolerances and thresholds (Diaz and Rosenberg 1995; Vaquer-Sunyer and Duarte 2008). A number of behavioral and sublethal effects are elicited in benthic invertebrates at DO concentrations between 2.8 and 2.0 mg O_2 l^{-1} (Tyson and Pearson 1991; Vaquer-Sunyer and Duarte 2008). As such, we define normoxia as DO concentrations >2.8 mg O_2 l^{-1} and divide low DO into two categories: as mild hypoxia 2.8–2.1 mg O_2 l^{-1}, and hypoxia ≤ 2 mg O_2 l^{-1} (Tyson and Pearson 1991).

Seasonal hypoxia occurs throughout Chesapeake Bay and some of its tributaries during the spring and summer months

Communicated by Judy Grassle

S. K. Sturdivant (✉)
Division of Marine Science and Conservation, Nicholas School of the Environment, Duke University, 135 Duke Marine Lab Rd., Beaufort, NC 28516, USA
e-mail: kersey.sturdivant@duke.edu

R. J. Díaz
Virginia Institute of Marine Science, College of William and Mary, Route 1208 Greate Road, Gloucester Pt., VA 23062, USA

R. Llansó
Versar, 9200 Rumsey Rd, Columbia, MD 21045, USA

D. M. Dauer
Department of Biological Sciences, Old Dominion University, Norfolk, VA 23529, USA

(Murphy et al. 2011) and was first detected in DO measurements in mainstem Chesapeake Bay in the early 1930s (Newcombe et al. 1939; Zimmerman and Canuel 2000) and in the Potomac, a tributary, in the 1910s (Sale and Skinner 1917). The most severe low oxygen events occur in the mainstem (Officer et al. 1984; Stow and Scavia 2009), and low oxygen conditions in the Bay last approximately 120 days from May to September (Murphy et al. 2011). While gravitational circulation drives hypoxia development in the Bay (Kuo and Neilson 1987), the outer edges of Chesapeake Bay mainstem hypoxic water may be advected into shallow areas, such as the Bay's tributaries, through horizontal transport (Breitburg 1990). From the 1950s through the 1990s, there has been a substantial increase in hypoxic/anoxic water in Chesapeake Bay: from approximately 3 km^3 in the 1950s, to approximately 10 km^3 in the 1990s (Hagy et al. 2004), and this trend continues into the 21st century (Murphy et al. 2011). The increase in the spatial extent of Chesapeake Bay hypoxia has consequences for the benthos (Vaquer-Sunyer and Duarte 2008; Seitz et al. 2009; van Colen et al. 2010). The ecological consequences of periodic and seasonal hypoxia vary and are hypothesized to regulate benthic populations (Diaz and Rosenberg 2008; Turner et al. 2012).

At the community structure level, hypoxic systems exhibit a predictable and graded series of responses to oxygen depletion, ranging from no obvious change, to mass mortality of bottom fauna (Diaz and Rosenberg 1995). At the initial onset of hypoxia, organisms increase respiration (Wannamaker and Rice 2000) and mobile fauna migrate from the area (Ludsin et al. 2009; Seitz et al. 2009). As DO further declines, sessile fauna cease feeding and decrease activities not related to respiration (Diaz and Rosenberg 1995). Infauna migrate closer to the sediment surface as reduced compounds accumulate and have been observed on or extending above the sediment surface in a moribund condition (Long et al. 2008; Sturdivant et al. 2012). Finally, if the duration of hypoxia is sustained, mass mortality occurs in all but the most tolerant of species (Diaz and Rosenberg 1995; Levin et al. 2009). The time period at which these observations occur varies based on the severity of hypoxia and can range from days to weeks (Diaz and Rosenberg 1995). At the functional level, there is less of an understanding of how low DO concentrations interact with macrobenthic production and subsequent trophic transfer of energy (Baird et al. 2004; Long et al. 2008).

Productivity provides an index of community processes proportional to total community respiration and consumption and integrates the influence of biotic variables and environmental conditions affecting individual growth and population mortality (Edgar and Barrett 2002; Cusson and Bourget 2005). Secondary production, or the heterotrophic production of organic matter, is viewed as an estimate of estuarine health (Diaz and Schaffner 1990; Dolbeth et al. 2005). The production of macrobenthic invertebrates is important as these fauna serve as a link in the energy transfer from primary consumers to higher trophic levels (Nilsen et al. 2006). It is estimated that approximately 20–50 % of benthic secondary production within the Bay is carried over from year to year as standing stock biomass (Baird and Milne 1981; Holland et al. 1988), and approximately 21,400–27,500 t C of benthic organisms are needed to support the Bay's demersal fishery yields (Diaz and Schaffner 1990).

Direct calculations of macrobenthic production are costly and time-consuming (Wilber and Clarke 1998), but methods have been proposed for the indirect calculation of production based on biotic and abiotic variables (Robertson 1979; Banse and Mosher 1980; Schwinghammer and Hargrave 1986; Plante and Downing 1989; Brey 1990, 2001; Edgar 1990; Morin and Bourassa 1992; Sprung 1993; Tumbiolo and Downing 1994); recent reviews by Cusson and Bourget (2005) and Dolbeth et al. (2005) evaluated a number of these models and concluded that they reliably estimate secondary production. Measuring production is useful as it expresses all the components of an ecosystem in common units, allowing the function of the system to be better understood (Lindeman 1942). Benthic abundance and biomass can supply basic information on potential energy available to higher consumers, but estimates of secondary production provide crucial information on trophic dynamics, and quantitative approximations of energy available to higher trophic levels (Wilber and Clarke 1998). The derived quantitative production measurements can then be used to make inferences about trophic transfer of energy (Dolbeth et al. 2012). The error associated with these broad habitat predictions can be large, but the value in the prediction is the ability to provide a relative starting point for assessing the magnitude of energy flow through the macrobenthos (Diaz and Schaffner 1990) and, specifically in this study, how that energy flow might be perturbed.

Using production theory and empirical models developed to quantify macrobenthic production without the requirement of intense sampling, we related patterns of macrobenthic production in Chesapeake Bay and its tributaries to DO concentrations. Specific objectives of our study were: (1) to describe patterns of macrobenthic production spatially (among systems) and temporally (by year); (2) to assess the relationship of macrobenthic production with the physical factors of DO concentration, salinity, and % silt/clay; and (3) to determine taxonomic associations between macrobenthic production and DO concentration.

Methods

Sampling Design

The Chesapeake Bay Long-Term Benthic Monitoring Program started a probability-based, stratified-random sampling of Chesapeake Bay and its tributaries in 1996, with 25 random sites in each of ten strata within the Bay (upper, middle, and lower Bay, Maryland western tribs, Maryland eastern tribs, Patuxent, Potomac, Rappahannock, York, and James River). All sampling occurred during a summer index period (late July to early September) to allow the application of the Benthic Index of Biotic Integrity (Weisberg et al. 1997; Alden III et al. 2002; Dauer and Llansó 2003). Within the monitoring framework, we included stations from all habitats within the mesohaline and polyhaline Chesapeake upper and lower Bay (referred to singularly in this study as the mainstem), Potomac, Rappahannock, and York Rivers, from 1996 to 2004 (Fig. 1). These are the main areas within the Chesapeake system that experience hypoxia (Park et al. 1996; Hagy et al. 2004; Murphy et al. 2011). The mainstem, Potomac River, and Rappahannock River all experience sustained seasonal hypoxia (Kuo and Neilson 1987; Stow and Scavia 2009; Murphy et al. 2011), with periodic hypoxia documented in the York River (Kuo and Neilson 1987).

Samples were collected with a Young grab (440 cm^2 to a depth of 10 cm) and sieved in the field through a 0.5-mm screen. Organisms, detritus, and sediment retained on the screen were transferred to labeled jars for preservation. At each station DO, salinity, and temperature were measured approximately 0.5 m from the bottom using a YSI model 6600 sonde. Samples were processed to identify and enumerate each species present as described by Dauer and Llansó (2003). Ash-free dry weight biomass was measured for each species by drying to a constant weight at 60 °C and ashing in a muffle furnace at 500 °C for 4 h. Sediment samples were wet-sieve analyzed for percent silt-clay content (Folk 1973).

Secondary Production

Prior to estimation of production, data from large epifaunal and infaunal species known to be over-dispersed and not adequately sampled by the Young grab were removed. These included the bivalves *Crassostrea virginica*, *Mercenaria mercenaria*, and *Geukensia demissa.*

Daily production was computed for each taxon in each sediment grab using the empirical model of Edgar (1990) ($P=0.0049B^{0.80}T^{0.89}$), which was derived from a meta-analysis of production estimates for benthic macrofaunal populations. This model relates daily production (P, ug day^{-1}) for a single macrobenthic invertebrate to body size (B, ug AFDW) and water temperature (T, °C) with $r^2=0.94$ (Edgar 1990). Indirect models for estimating secondary production are more accurate when applied to situations similar to those in which the model was derived (Dolbeth et al. 2005), and Edgar's (1990) equation was derived for estuarine species in temperate latitudes, similar to our study. Edgar (1990) formulated different models for different taxonomic groups (e.g., bivalves, crustaceans, polychaetes) but found them to be indistinguishable from the general model; therefore, this study used only the general model to estimate macrobenthic production. The only departure from Edgar's (1990) method, which uses the mean AFDW of invertebrates retained on a series of sieves of differing mesh size, was the usage of mean AFDW of each species by sample (Hagy 2002). Body size was computed by dividing the total biomass of each taxon by the reported abundance. Because the effect of body size is nonlinear (see equation above), community production was computed as the sum of production for each taxon, rather than as the production for the average size organism in the community (Hagy 2002). Biomass measurements at the species level allowed us to examine taxonomic and functional group associations between production and DO, and this method of production assessment was validated by Hagy (2002).

The theoretical basis for Edgar's (1990) equation is grounded in the metabolic theory of ecology, which shows, among other things, that a constant fraction of metabolism tends to be allocated to production across taxa (Brown et al. 2004). Edgar's (1990) equation has been used extensively to estimate secondary production of macrobenthos in temperate estuarine environments (Arias and Drake 1994; Edgar et al. 1994; Wilber and Clarke 1998; Bologna and Heck 2002; Cowles et al. 2009; Douglass et al. 2010; Blake and Duffy 2012; Rakocinski 2012), and it has been validated to produce similar production estimates when compared with other indirect methods of estimation or direct production measurements (Arias and Drake 1994; Wilber and Clarke 1998; Cowles et al. 2009). To verify the production estimates using Edgar's (1990) allometric equation in Chesapeake Bay, Hagy (2002) compared the structure and prediction of the Edgar (1990) model to the Tumbiolo and Downing (1994) model, which predicts annual macrobenthic production from depth and annual mean biomass and water temperature. Hagy (2002) found little to no difference between the two models. Further, Blumenshine and Kemp (2000) validated the accuracy of the Tumbiolo and Downing (1994) model against direct calculations of production in Chesapeake Bay (Holland et al. 1988). Given the close agreement between the Tumbiolo and Downing (1994) model and Edgar (1990) model, the Edgar (1990) model was selected based on its more appropriate time step (i.e., daily production rather than annual mean production, as this study estimated summer production) to allow for the estimation of seasonal production.

Analysis Strategy

Given the random selection of stations through time and the possibility that there might be a serial dependence between DO and habitat with time (year), a mixed-effect longitudinal design was used to analyze patterns in the data. Generalized estimating equations (GEEs) were applied with the normal distribution, identity link, and cross-year correlations within

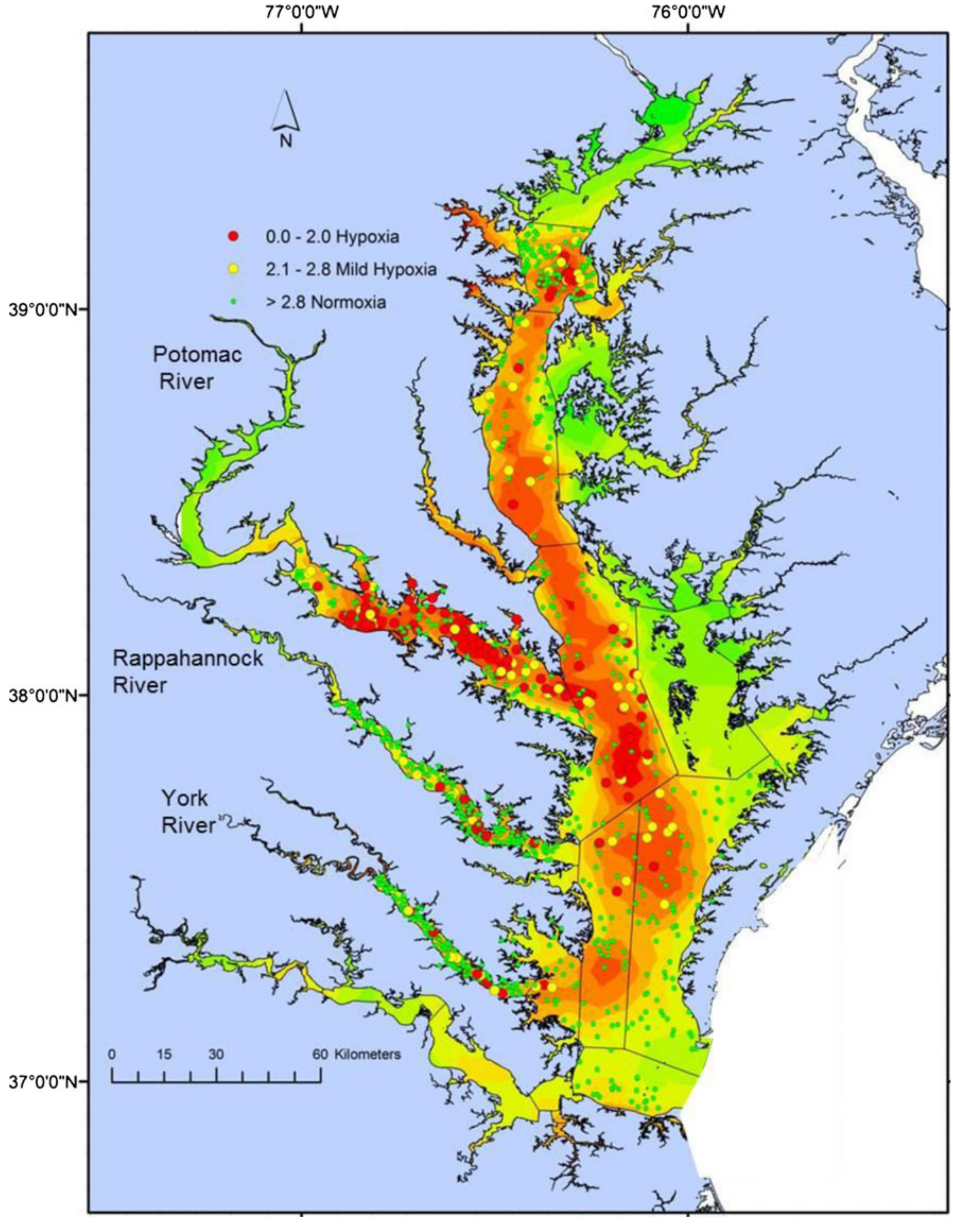

Fig. 1 Composite Chesapeake Bay summer dissolved oxygen (DO) concentrations from 1996 to 2004. *Circles* represent the sample sites from the five strata used in this study (middle Bay, lower Bay, Potomac River, Rappahannock River, and York River). *Shading* and *circle color* denotes DO concentration as stated in figure key. *Shading* is a graded interpolation of the DO concentrations represented by the *circles*

areas assumed to be equal (Zeger et al. 1988). Explanatory factors considered to be random were salinity, percent silt-clay, depth, and DO; this follows from stations being selected at random. Daily production was the dependent factor. Year and area (Mainstem, Potomac, Rappahannock, and York) were fixed, and interactions were not considered in our GEE model. To compare subregions of Chesapeake Bay, analysis of variance (ANOVA) was also used to test for differences between (spatially) and within (temporally) areas for quantitative parameters, and Tukey's HSD test was used for multiple mean comparisons. Normality was checked with the Shapiro–Wilk test and homogeneity of variance with Bartlett's test. If variance was not homogeneous, Welch ANOVA, which allows standard deviations to be unequal, was used in testing for mean differences (Zar 1999). All statistical tests were conducted using SAS® (SAS Institute 1989).

Results

The total area of Chesapeake Bay and its tributaries is approximately 12,000 km^2. The area of the mesohaline and polyhaline mainstem, Potomac, Rappahannock, and York Rivers covered by our study is approximately 7,720 km^2. Therefore, we estimated trends in summer daily macrobenthic production for approximately 65 % of Chesapeake Bay. Mean hypoxic volume from the mid-1980s to 2006 was 10.7×10^9 m^{-3} (SD 4.0×10^9); yearly hypoxic volumes for our observation period were compared as either being higher or lower than this mean (Hagy et al. 2004). Estimated summer daily macrobenthic production in Chesapeake Bay from 1996 to 2004 was significantly variable from year to year (Table 1, Fig. 2). Total macrobenthic production was significantly higher from 1999 to 2001, years with below average hypoxic volume, and lower in 2003 and 2004, years with above average hypoxic volume. Production remained relatively constant from 1996 to 1998 despite a greater than twofold increase in hypoxic volume.

Daily macrobenthic production was significantly related to DO concentration with higher production at sites with normoxia as opposed to hypoxia (Table 2, Fig. 3). From 1996 through 2004, mean production in Chesapeake Bay at normoxic sites was 39 mg C m^{-2} day^{-1}, which was significantly higher than the 4 mg C m^{-2} day^{-1} mean during hypoxia. The mean daily production of normoxic sites was not significantly different from the 11 mg C m^{-2} day^{-1} at mildly hypoxic sites. Overall, hypoxic sites had 90 % less production than normoxic sites (Fig. 3). Salinity also had a significant effect on macrobenthic production with higher production at lower salinities. The effect of grain size on macrobenthic production was marginally significant and depth had no effect (Table 2). Most of the variability in daily macrobenthic production was associated with DO concentration and salinity.

Table 1 Daily macrobenthic production (mg C m^{-2} day^{-1}) averaged by dissolved oxygen category for year and tributary

	Normoxia: >2.8 (mg l^{-1})			Mild Hypoxia: 2.8-2.0 (mg l^{-1})			Hypoxia: <2.0 (mg l^{-1})		
	Mean	SD	*n*	Mean	SD	*n*	Mean	SD	*n*
1996	36.3	73.9	80	4.2		1	1.3	2.7	21
Mainstem	45.7	91.2	45			0	1.6	3.0	7
Rappahannock	21.9	25.9	14			0	1.4	2.3	5
Potomac	61.5	92.0	4	4.2		1	1.0	3.0	9
York	17.5	32.0	17						
1997	34.5	78.8	83	9.5	18.6	16	3.2	1.6	7
Mainstem	49.1	88.8	33	14.0	14.8	12	5.5	0.2	2
Rappahannock	26.3	73.3	21	4.4	2.7	2			
Potomac	58.7	133.2	8	3.5	3.1	5	2.3	0.1	5
York	10.7	3.6	21						
1998	34.4	77.8	85	5.3	5.6	6	3.8	5.3	22
Mainstem	47.9	102.4	41	5.8	8.3	3	4.8	4.9	6
Rappahannock	17.3	11.2	15			0	10.1	6.1	5
Potomac	35.7	82.1	11	4.8	3.2	3	0.5	0.4	11
York	16.9	13.5	18						
1999	55.6	167.1	109	13.5	11.7	2	11.0		1
Mainstem	107.6	237.3	50	13.5	11.7	2			
Rappahannock	14.7	12.1	19				11.0		1
Potomac	7.4	12.4	20						
York	12.8	8.9	20						
2000	56.8	142.5	88	35.6	65.9	7	4.1	5.9	5
Mainstem	101.8	206.6	38	70.6	98.2	3	10.3	3.4	2
Rappahannock	16.6	28.3	18	0.0	0.0	2			
Potomac	26.6	43.6	16	18.7	5.0	2	0.0	0.1	3
York	25.5	24.1	16						
2001	55.2	144.1	88	12.8	12.0	7	1.6	4.4	10
Mainstem	82.7	184.5	51	11.9		1	0.0		1
Rappahannock	16.1	7.5	14	9.9		1			
Potomac	10.5	11.7	6	15.6	20.0	3	0.2	0.4	8
York	20.6	24.4	17	10.4	3.9	2	14.1		1
2002	44.4	93.9	106	4.5	4.5	2	5.1	4.2	2
Mainstem	79.3	130.3	45	7.7		1	5.1	4.2	2
Rappahannock	16.7	19.6	22						
Potomac	20.6	59.2	22	1.3		1			
York	19.1	10.4	17						
2003	15.7	16.4	76	6.9	7.0	10	5.6	7.0	21
Mainstem	19.0	21.5	33	8.5	7.9	6	11.0	3.8	6
Rappahannock	8.4	7.9	19			0			
Potomac	10.1	11.9	4	2.2	3.7	3	0.3	0.8	12
York	19.8	10.1	18	11.0		1	16.0	5.4	3
2004	20.3	24.0	60	8.1	6.9	12	2.2	3.0	0
Mainstem	23.6	31.2	27	8.8	8.5	5	1.8	1.9	5
Rappahannock	26.0	14.5	11	11.2	6.5	2	1.8	1.8	3
Potomac	2.3	4.3	10	0.0	0.0	2	0.0	0.0	2
York	22.5	14.8	12	10.4		3	9.9		1

Blank spaces represent no data. The table is used to generate Fig. 4

Production loss relative to hypoxia was analyzed in our study area for years 1998 and 2001; these years represent maximum and minimum volumes of hypoxia for our 9-year study, respectively (Hagy et al. 2004). In 2001, summer macrobenthic production averaged approximately 70 mg C m^{-2} day^{-1} within the Bay, which is equivalent to 0.07 t C km^{-2} day^{-1}. Hypoxic volume in Chesapeake Bay in 2001 was 6 km^3, covering approximately 960 km^2 (Hagy et al. 2004). Using the previous values, and operating under the assumption that hypoxic areas equal normoxic production when not hypoxic, production for the area affected by hypoxia should

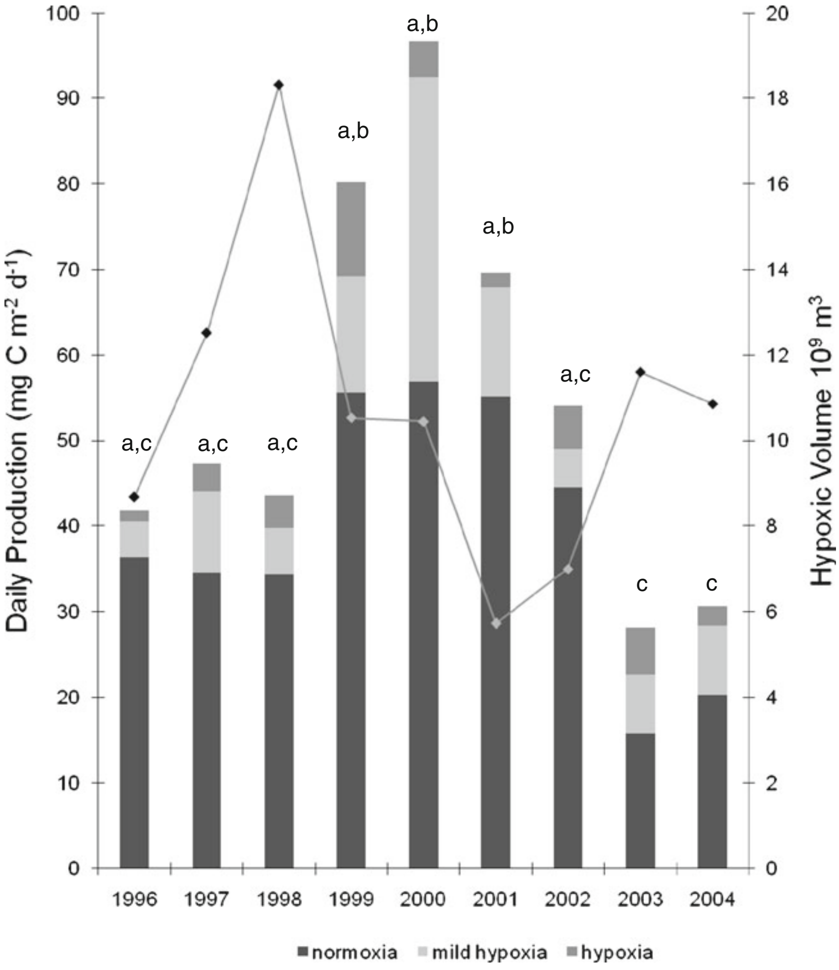

Fig. 2 Comparison of mean summer daily macrobenthic production (*bars*) by varying oxygen condition (*i.e. normoxia, mild hypoxia, hypoxia*) in Chesapeake Bay from 1996 to 2004. Total macrobenthic production was significantly different over time (df=8, F=2.43, p=0.013). Hypoxic volume (*line*) adapted from Hagy et al. 2004. Letter differences denote significance

have been 67 t C day^{-1}. Factoring in a 90 % reduction for the effect of hypoxia (Fig. 3), approximately 61 t C day^{-1} of biomass, was lost in 2001. This same calculation was conducted for 1998 when mean macrobenthic production was approximately 44 mg C m^{-2} day^{-1}, this is equivalent to 0.04 t C km^{-2} day^{-1}. Hypoxic volume in 1998 was 18 km^3 covering approximately 3,000 km^2, thus approximately 110 t C day^{-1} of biomass was lost in 1998. When 61 and 110 t C day^{-1} are scaled by 120 days, the average duration of hypoxia in the Bay (Murphy et al. 2011), the loss in biomass in hypoxic areas ranged from 7,320 to 13,200 t C. The habitat-weighted estimate of macrobenthic production for the entire Chesapeake Bay is 17 g C m^{-2} year^{-1} (Diaz and Schaffner 1990) that equates to 114,600 t C annually. Thus, from 6 % to 12 % of the Bay's macrobenthic productivity is either displaced to periods of normoxia or lost to the system every year due to hypoxia during the summer months.

When partitioned by production per unit area, mainstem Chesapeake Bay was the major contributor to summer daily macrobenthic production. Macrobenthic production in the mainstem Bay was significantly higher (df=3, F=14.23, p<0.0005) than production in the Potomac, Rappahannock, and York Rivers. Normoxic sites accounted for the majority of mainstem production; a similar pattern was observed in the tributaries (Table 1, Fig. 4). Macrobenthic production trends over time (year) were significantly different for sites that experienced normoxia and hypoxia in the mainstem (df=8, t=4.92, p=0.002) and Potomac River (df=8, t=3.28,

Table 2 Effect of salinity, percent silt+clay, depth, and DO on daily macrobenthic production

Parameter	*df*	Estimate	SE	Wald 95 % CI		Chi-square	Pr>Chi-square
Intercept	1	29.05	17.95	-6.13	64.22	2.6	0.106
Salinity	1	-3.12	0.71	-4.52	-1.73	19.2	<0.001
Silt+Clay	1	0.19	0.10	0.001	0.38	3.9	0.049
Depth	1	-0.004	0.83	-1.64	1.63	0.0	0.996
DO	1	8.92	1.81	5.37	12.47	24.3	<0.001

Based on maximum likelihood GEE model with data clustered by year within area (Mainstem, Potomac, Rappahannock, and York) p=0.017). Over the observed period, daily macrobenthic production in the Rappahannock was not significantly different between normoxia and hypoxia (*df*=8, *t*=2.78, *p*<0.06). This finding was likely influenced by the high amount of macrobenthic production observed at hypoxic sites for years 1998 and 1999 (Fig. 4). Mean hypoxic production in the Rappahannock during our observation period was 6.1 mg C m^{-2} day^{-1}. When 1998 and 1999 are excluded from the calculation, mean production at hypoxic sites was 0.5 mg C m^{-2} day^{-1}, illustrating the influence these 2 years had on overall mean hypoxic production. In the York River, samples were only collected in hypoxic areas in 2001, 2003, and 2004 (Fig. 4), due to the random sampling design and short-term periodic hypoxia in the system (Diaz et al. 1992). Production at hypoxic sites was compared between the four systems, and the mainstem and Potomac River had significantly lower (*df*=3, *F*=9.67, *p*=0.001) production during hypoxia than the York River; the Rappahannock was not significantly different from any system with relatively intermediate macrobenthic production during hypoxia.

Molluscs, annelids, and arthropods accounted for>98 % of production (Table 3). For all oxygen levels, daily mollusc production (35.2 mg C m^{-2} day^{-1}) was significantly higher (*df*=8, *F*=83.70, *p*<0.0005) than annelid production (8.6 mg C m^{-2} day^{-1}), which was significantly higher than arthropod production (3.8 mg C m^{-2} day^{-1}). The production was significantly different between normoxic and hypoxic sites for mollusc, annelids, and arthropods. Hypoxic sites had 95 % lower mean bivalve and gastropod production; this reduction was only significant (*p*=0.003) for bivalves due to the high variance in gastropod production. Mean polychaete (*p*<0.0005) and oligochaete (*p*=0.027) production was also significantly lower at hypoxic sites by 70 % and 95 %, respectively. Amphipods (*p*=0.013) and isopods (*p*<0.0005) had significantly lower mean production at hypoxic sites, 95 % for amphipods, and approximately 99 % for isopods.

Over the 9-year observation time, bivalve (*df*=8, *F*=2.70 *p*=0.006), annelid (*df*=8, *F*=4.41 *p*<0.0005), and arthropod (*df*=8, *F*=2.59, *p*=0.008) production were each analyzed separately and found to be significantly different among years. Tukey's multiple mean comparison was used to determine significant differences between years, and the maximum and minimum years of hypoxic volume were assessed for each group. For the maximum hypoxic year of 1998, bivalves, annelids, and arthropods had 90 %, 45 %, and 50 %, less production compared to 2001, the minimum hypoxia year

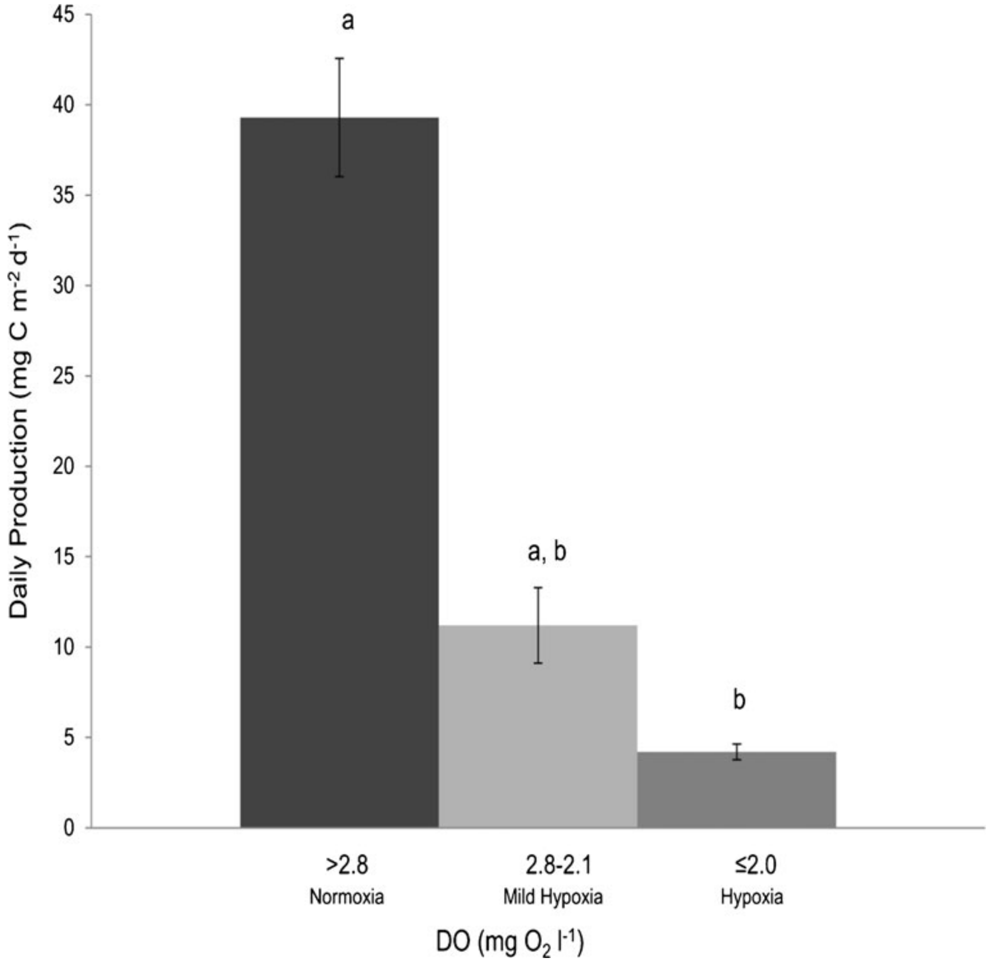

Fig. 3 Relationship between mean daily macrobenthic production and dissolved oxygen concentration in Chesapeake Bay. Letter differences represent significance (*df*=26, *F*=27.97, *p*<0.0005). Normoxic areas have significantly higher daily macrobenthic production than hypoxic areas. Error bars represent ±1 SE

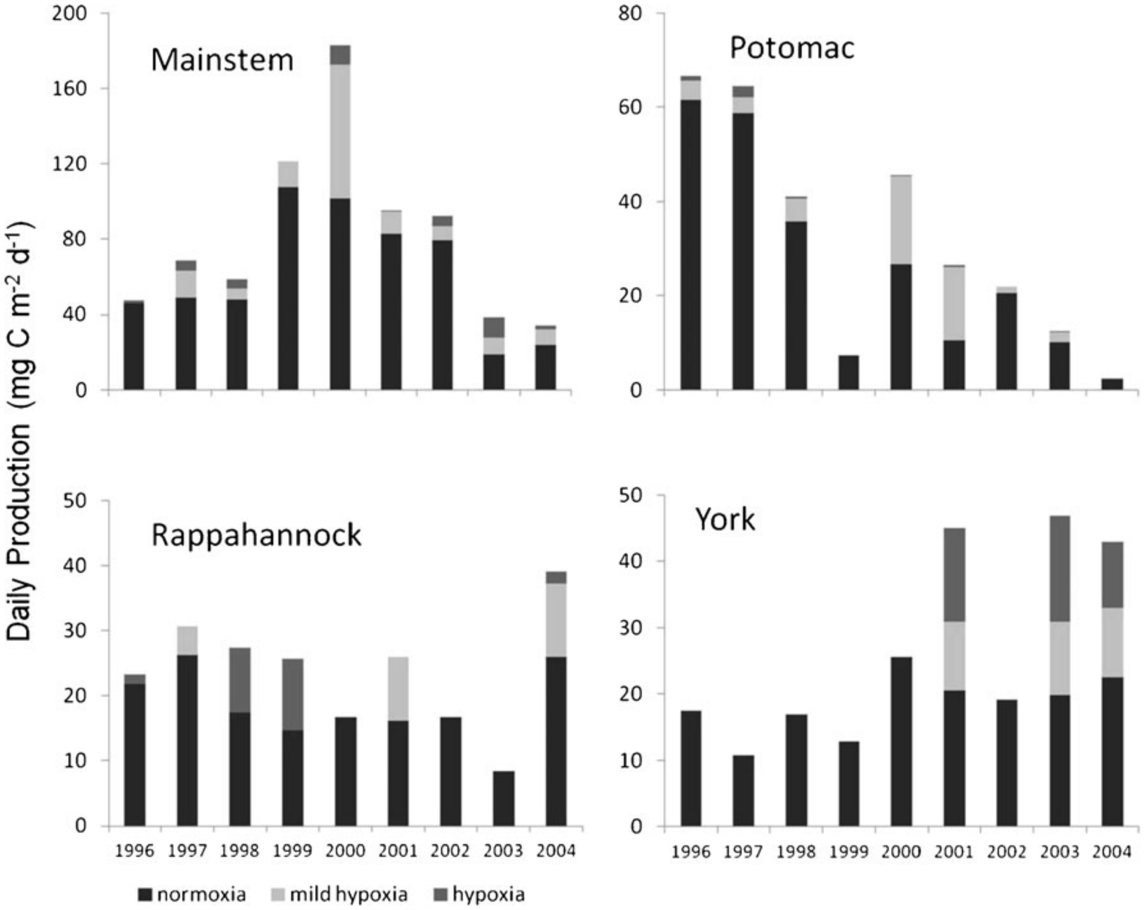

Fig. 4 Comparison of mean summer daily macrobenthic production (*bars*) by systems from 1996 to 2004. Temporal macrobenthic production was variable between systems. Note difference in *y* axis scale by system

during our study. These production differences between 1998 and 2001 were significant for molluscs and arthropods and trended in that direction for annelids. Spatially, there were significant differences between study areas in production by major taxon (Table 4). Mean daily mollusc and arthropod production was significantly higher in the mainstem and Potomac River, driven largely by bivalve and amphipod production, respectively. Annelid production in the mainstem and York River was significantly higher than Potomac production, with Rappahannock production not significantly different from either system. Differences in annelid production were driven by polychaete production.

Table 3 Comparison of oxygen condition and mean daily macrobenthic production

(*a*) *By phylum* (±*1SE*)

	n	Mollusca	Annelida	Arthropoda
		$p=0.002$	$p<0.0005$	$p<0.0005$
Normoxia	924	40.8 (4.4) a	9.6 (0.4) a	3.2 (0.3) a
Mild hypoxia	64	6.5 (3.1) a,b	3.7 (0.4) b	0.7 (0.2) b
Hypoxia	101	3.0 (2.5) b	2.5 (0.4) b	0.2 (0.1) b

(*b*) *By class* (±*1SE*)

	n	Bivalvia	Gastropoda	Polychaetea	Oligochaetea	Amphipoda	Isopoda
		$p=0.003$	ns	$p<0.0005$	$p=0.027$	$p=0.013$	$p<0.0005$
Normoxia	924	39.9 (4.4) a	0.8 (0.3)	7.7 (0.3) a	1.8 (0.3) a	1.5 (0.2) a	0.5 (0.1)
Mild hypoxia	64	6.2 (3.1) a,b	0.3 (0.1)	3.4 (0.4) b	0.3 (0.1) a,b	0.5 (0.2) a,b	0.1 (0.0)
Hypoxia	101	2.9 (2.5) b	0.1 (0.0)	2.4 (0.4) b	0.1 (0.0) b	0.1 (0.0) b	0.0 (0.0)

Letter differences denote significance

Table 4 Comparison of area and mean daily macrobenthic production

(*a*) *By phylum* (±*1SE*)

	n	Mollusca	Annelida	Arthropoda
		$p<0.0005$	$p<0.0005$	$p<0.0005$
Main Bay	486	52.1 (6.9) b	9.7 0.6) a	2.2 (0.2) a
Potomac	224	51.8 (9.9) a	5.7 (0.8) b	1.8 (0.3) a
Rappahannock	210	5.1 (1.7) b	7.5 (0.6) a,b	4.1 (0.6) b
York	169	2.1 (0.2) b	10.3 (0.7) a	4.4 (1.0) b

(*b*) *By class* (±*1SE*)

	n	Bivalvia	Gastropoda	Polychaeta	Oligochaeta	Amphipoda	Isopoda
		$p<0.0005$	ns	$p<0.0005$	ns	$p<0.0005$	$p=0.008$
Main	486	46.8 (6.8) a	0.6 (0.2)	8.6 (0.5) a	2.0 (0.4)	0.7 (0.1) a	0.7 (0.1) a
Poto	224	50.1 (9.7) a	1.7 (1.1)	3.0 (0.4) b	2.6 (0.7)	0.7 (0.2) a	0.4 (0.1) b
Rapp	210	4.8 (1.7) b	0.3 (0.0)	6.2 (0.6) e	1.3 (0.2)	2.0 (0.3) b	0.3 (0.1) b
York	169	1.9 (0.6) b	0.2 (0.1)	9.5 (0.7) a	0.8 (0.1)	3.1 (0.9) b	0.4 (0.1) b

Letter differences denote significance

Discussion

Daily macrobenthic production in Chesapeake Bay was significantly related to DO, with overall macrobenthic production at hypoxic sites < 90 % of normoxic values. For many major taxonomic groups, production decreases of 95 % or greater occurred. This drastic decrease in macrobenthic production would have negative consequences for Chesapeake Bay, as macrobenthic invertebrates link energy transfer from primary producers to economically important higher consumers (Möller et al. 1985; Brey 2001). Additionally, a loss in macrobenthic biomass of 7,320–13,200 t C was estimated to occur during the summer, reducing the yearly productive capacity of the Bay benthos by 6–12 %; energy demands of epibenthos and demersal fish, predators of benthic organisms, are at their highest during the summer months when these reductions occur. At face value, a 6–12 % loss in production may not appear damaging, but this should be viewed in the context of the annual habitat-weighted estimate. The focus of this study was to estimate production during the summer months, when hypoxia occurs. In Chesapeake Bay, there is no seasonal hypoxia in early spring, fall, and winter (Kemp et al. 2005); therefore, the importance of losses in summer production are more appropriately understood when assessed from a more limited seasonal scope. Production is not homogenous throughout the year (i.e., production varies by season) given the influence of temperature on metabolism and nutritional availability. However, using the data available, if the annual production estimate of Diaz and Schaffner (1990) is scaled to 120 days (the duration period of hypoxia in the Bay), 37,676 t C would be the seasonal summer estimate of production in the Bay. When the summer seasonal biomass loss of 7,320–13,200 t C is assessed against the summer seasonal estimate of production, as much as 20–35 % of macrobenthic production is displaced during the summer months when hypoxia occurs, an enormous loss in production.

Daily macrobenthic production in Chesapeake Bay fluctuated from year to year (Fig. 2). When production was compared to hypoxic volume for corresponding years (Hagy et al. 2004), there was a noticeable trend of lower macrobenthic production during years of above average hypoxic volume, and higher macrobenthic production during years of below average hypoxic volume. However, production also remained relatively constant from 1996 to 1998 during a greater than twofold increase in hypoxic volume. This observation could be explained by resource compensation in the presence of a deleterious condition. Concentrations of organic matter were not assessed in this study, so the available organic concentrations for macrobenthos were unknown. However, hypoxic volumes in coastal systems are correlated with eutrophication and the subsequent primary productivity generated (Lohrenz et al. 1990); greater primary productivity, greater hypoxic volume to the extent allowable by hydrography (Diaz 2001). Hypoxic volumes from 1996 to 1998 were some of the highest observed during our observation period and would have been correlated with above average primary productivity. The organic content of these blooms would eventually reach the macrobenthos in a relatively shallow system, such as Chesapeake Bay, and the organic rich environment fostered by the bloom would be of benefit to macrobenthos adapted to survive in hypoxia. While the increased hypoxic volume may have reduced macrobenthic production of hypoxia-sensitive taxa, the parallel organic rich environment may also have increased macrobenthic production of hypoxia-resistant taxa, explaining the relatively constant production over time (year).

It is also important to note that the sampling design may have affected observed trends. Sediment grabs and DO concentrations were point measurements collected during the daytime, every year in the summer. The limitation of point measurements is the snapshot view they provide, with little inference as to what occurs between data collection. It is very likely that some sites classified as normoxic when sampled experienced hypoxia at some point or multiple times throughout the season. This hypothesis was substantiated from an observational field experiment conducted during the summer of 2007 (Sturdivant et al. 2013). While the sites may not have experienced sustained hypoxia, periodic hypoxic events stress benthic organisms, causing direct mortality via asphyxiation, indirect mortality through predation, or impede growth (Pihl et al. 1991; Dauer et al. 1992; Llansó 1992). Another explanation for the observed trends could be predation pressure. If epibenthic predators and demersal fish are displaced from hypoxic zones, their presence in adjacent normoxic areas could increase the rate of predation and reduce overall macrobenthic production at these sites. This type of hypoxia-driven concentration of predators has been documented in Chesapeake Bay (Breitburg 2002) and the northern Gulf of Mexico (Craig and Crowder 2005).

The relatively constant levels of macrobenthic production from 1996 to 1998, despite the large increase in hypoxic volume, could also be explained by the correlation of macrobenthic production with other water quality variables. In estuaries worldwide, salinity is the major governing factor in organism distribution (Perkins 1974; Diaz and Schaffner 1990; Telesh and Khlebovich 2010). While this study focused on areas with salinity equal to or higher than mesohaline values, salinity in our study still ranged from the mesohaline to euhaline. On a total area basis, macrobenthic production in Chesapeake Bay is highest in polyhaline habitats and lowest in the euhaline habitats, with the majority of the Bay's macrobenthic production (~70 %) occurring in high mesohaline and polyhaline habitats (Diaz and Schaffner 1990). At moderate to high salinities, macrobenthic patterns are further correlated with sediment type (Boesch 1973; Cooksey and Hyland 2007), but in our study, percent silt/clay was only marginally correlated with macrobenthic production. When assessed over a large spatial scale, as was done in this study, the variability in macrobenthic production was related to a number of water quality parameters. Of the water quality parameters that this study assessed, DO concentration was the only one that had anthropogenic influence (Diaz and Rosenberg 1995).

While macrobenthic production was linked to DO concentration, the direct role hypoxia plays on the subsequent loss or recovery of macrobenthic production within the ecosystem is not known. The most obvious cause of death from lack of oxygen is asphyxiation (Diaz and Rosenberg 1995), although hydrogen sulfide toxicity, which is produced during the reduction of sulfate during severe hypoxia and anoxia (Torrans and Clemens 1982), also contributes to mortality through inhibition of the electron transport chain in aerobic respiration (Vaquer-Sunyer and Duarte 2010). In Chesapeake Bay regions experiencing hypoxia and anoxia, both processes likely contribute to the loss of macrobenthic production (Vissman 1990). Additionally, epibenthic predators and demersal fish can at times capitalize on stressed benthos during mild hypoxic events (Nestlerode and Diaz 1998; Seitz et al. 2003), although severe hypoxia inhibits predation (Altieri 2008) and disrupts the normal energy flow to higher consumers, allowing the microbial community to process macrobenthic production (Baird et al. 2004). Alternatively, it is also plausible that lower production at hypoxic sites, compared to normoxic sites, was not a result of mass mortality due to asphyxiation, sulfide toxicity, or predation, but simply that the production was never produced. Macrobenthic production at hypoxic sites is regulated by growth and recruitment during periods of normoxia (Nichols 1977); therefore, any lower production may have been a consequence of that production never having been created. Even more plausible is that, to varying degrees, all of these factors contribute to less production at hypoxic sites.

Of the four areas examined (Mainstem, Potomac, Rappahannock, and York), the York River experiences only periodic hypoxia, making hypoxia-mediated, macrobenthic production transfer to epibenthic/demersal predation likely. Strong gravitational circulation in the York River results in hypoxia covering a relatively small area for a short time (Kuo and Neilson 1987), with no apparent difference between hypoxic and normoxic production. Hypoxia in the York may be enough to stress the benthos, but not to cause direct mortality or inhibition of macrobenthic production. This would allow opportunistic epibenthic invertebrates and demersal fish species to take advantage of stressed benthic infauna that extend their appendages and bodies into the water column, in an attempt to escape dire conditions below the sediment–water interface (Pihl et al. 1992). Areas with periodic hypoxia, such as the York, likely facilitate trophic transfer of energy to epibenthic and demersal predators. The area of the York River assessed in this study accounted for only 1 % of the area of Chesapeake Bay, and 2 % of the observed hypoxic area.

The Rappahannock experiences both periodic and sustained hypoxia (Kuo et al. 1991) with daily macrobenthic production related to the duration and extent of hypoxia. In 1998 and 1999, macrobenthic production during hypoxia was similar to normoxia, but in 1996 and 2004, hypoxia production was significantly less than normoxia. In areas of the Rappahannock where periodic hypoxia occurs, daily macrobenthic production could be transferred to epibenthic and demersal predators. In locations where hypoxia is relatively sustained throughout the summer, daily macrobenthic production is virtually eliminated and microbial biomass flourishes (Sturdivant et al. 2012).

The Potomac and mainstem both experience severe seasonal hypoxia with >95 % reductions in macrobenthic production.

Periodic and seasonal hypoxia alters energy flow to epibenthic predators and demersal fish, with the latter shifting energy to the microbial community (Baird et al. 2004). Many epibenthic and demersal predators of macrobenthos already experience multiple stressors (i.e., HABs, chemical contaminants, disease) given the current health of the Bay (Boesch 2000; Breitburg et al. 2003). For predators, hypoxia couples these factors with a loss in potential prey energy, loss of habitat, and increased energy expenditure searching for suitable habitat and food.

At the taxonomic level, during hypoxia, there was significantly less macrobenthic production for the major phyla. Overall, bivalve production dominated during normoxia, particularly, in the mainstem and Potomac River; however, bivalve production was significantly less during hypoxia by 95 %. Vaquer-Sunyer and Duarte's (2008) synopsis of species resistant to hypoxia, found that bivalves fared better than any other groups based on LC_{50} and LT_{50}. The bivalves in common between our study and Vaquer-Sunyer and Duarte's (2008) synopsis, *Macoma balthica* and *Mulinia lateralisi*, had mean LT_{50s} of 529 and 159 h, respectively, at a DO concentration of 2 mg O_2 l^{-1}. However, these species accounted for only 15 % of total bivalve production in the present study and were rarely collected at hypoxic sites. Though some bivalves can survive for long periods of hypoxia in the laboratory, in situ there was a trend toward less bivalve production during hypoxia. Polychaete production during hypoxia was significantly less by 65 % (Table 3), one of the smallest observed decreases. Tolerances and behavioral strategies of polychaetes appeared to allow for more efficient survival and less loss in available production during hypoxia. Capitellids and spionids accounted for 50 % of polychaete abundance, and polychaetes in these families have been observed to survive for quite long times under low DO concentrations, with LT_{50s} of 312 h (Rosenberg 1972) and 43 h (Llansó 1991), respectively, at a DO concentration of 2 mg O_2 l^{-1}. Many capitellids and spionids have been observed living in DO conditions around 1 mg l^{-1}, although cessation of feeding and burrowing generally occurs (Warren 1977; Llansó 1991). Spionids, such as *Paraprionospio pinnata*, were observed swimming in the water column during low oxygen, and capitellids were seen lying on the sediment surface as strategies to reach more oxygenated water above the sediment–water interface (Diaz et al. 1992). The dominance of polychaete production during hypoxia appears to be a direct result of their morphology and life history strategies, making them more adaptable to changing DO conditions (Vaquer-Sunyer and Duarte 2008). Arthropod production was also significantly less by 95 % during hypoxia, and species in this class are known to adapt poorly to low DO concentrations (Winn and Knott 1992). Hoback and Barnhart (1996) found that gammarid amphipods have an LC_{50} of ~2.0 mg O_2 l^{-1}. Similar studies have shown amphipods from the same family experience an LT_{50} of 7–15 h at DO of 2.0 mg l^{-1} (Theede et al. 1969; Agnew and Jones 1986). Our study showed a 95 % loss of available amphipod production at this same DO threshold, indicating that while 50 % of the amphipods may still be present at 2.0 mg l^{-1}, their overall production is drastically diminished, reducing the potential transfer of energy.

The relative uniformity in the loss in production by class, during hypoxia was interesting. Previous work has shown that species perform differently in their physiological response to hypoxia (summarized in Vaquer-Sunyer and Duarte 2008). Despite differences among species in hypoxia sensitivity, we found large losses in daily production at each of the assessed higher taxonomic levels, which underlines the ubiquity of the effects of hypoxia on benthic production. Decreased daily benthic secondary production across taxa also translates to decreased trophic transfer potential to higher consumers that prey upon macrobenthic infauna.

Acknowledgments We thank the staff at Versar and the Old Dominion University for data from the Chesapeake Bay Program's Long-Term Benthic Monitoring Program. Maryland Department of Natural Resources and Virginia DEQ funded the benthic monitoring program. This study was supported in part by NOAA grant NA05NOS4781202 to R.J.D.

References

Agnew, D.J., and M.B. Jones. 1986. Metabolic adaptations of *Gammarus duebeni* Liljeborg (crustacean, amphipoda) to hypoxia in a sewage-treatment plant. *Comparative Biochemistry Physiology A* 84: 475–478.

Alden III, R.W., D.M. Dauer, J.A. Ranasinghe, L.C. Scott, and R.J. Llansó. 2002. Statistical verification of the Chesapeake Bay benthic index of biotic integrity. *Environmetrics* 13: 473–498.

Altieri, A.H. 2008. Dead zone enhance key fisheries species by providing predation refuge. *Ecology* 89: 2808–2818.

Arias, A.M., and P. Drake. 1994. Structure and production of the benthic macroinvertebrate community in a shallow lagoon in the Bay of Cadiz. *Marine Ecology Progress Series* 115: 151–167.

Baird, D., and H. Milne. 1981. Energy flow in the Ythan Estuary, Aberdeenshine, Scotland. *Estuarine and Coastal Shelf Science* 12: 455–472.

Baird, D., R.R. Christian, C.H. Peterson, and G.A. Johnson. 2004. Consequences of hypoxia on estuarine ecosystems function: energy diversion from consumers to microbes. *Ecological Applications* 14: 805–822.

Banse, K., and S. Mosher. 1980. Adult body mass and annual production/biomass relationships of field populations. *Ecological Monographs* 50: 353–379.

Blake, R.E., and J.E. Duffy. 2012. Changes in biodiversity and environmental stressors influence community structure of an experimental eelgrass *Zostera marina* system. *Marine Ecology Progress Series* 470: 41–54.

Blumenshine, S.C., and W.M. Kemp. 2000. Food versus habitat and limitation for benthic macrofauna in mesohaline regions of Chesapeake Bay. Ecosystem models of the Chesapeake Bay relating nutrient loadings, environmental conditions, and living resources. Final Report 1998–1999, Chapter I; University of Maryland Center for Environmental Science, Maryland. http://www.chesapeakebay.net/content/publications/cbp_13028.pdf

Boesch, D.F. 1973. Classification and community structure of macrobenthos in the Hampton Roads area, Virginia. *Marine Biology* 21: 226–244.

Boesch, D.F. 2000. Measuring the health of the Chesapeake Bay: Toward integration and prediction. *Environmental Research Section A* 82: 134–142.

Bologna, P.A., and K. Heck Jr. 2002. Impact of habitat edges on density and secondary production of seagrass-associated fauna. *Estuaries* 25: 1033–1044.

Breitburg, D.L. 1990. Near-shore hypoxia in the Chesapeake Bay: patterns and relationships among physical factors. *Estuarine, Coastal and Shelf Science* 30: 593–609.

Breitburg, D.L. 2002. Effects of hypoxia, and the balance between hypoxia and enrichment, on coastal fishes and fisheries. *Estuaries* 25: 767–781.

Breitburg, D.L., A. Adamack, K.A. Rose, S.E. Kolesar, M.B. Decker, J.E. Purcell, J.E. Keister, and J.H. Cowan Jr. 2003. The pattern and influence of low dissolved oxygen in the Patuxent River, a seasonally hypoxic estuary. *Estuaries* 26: 280–297.

Brey, T. 1990. Estimating productivity of macroinvertebrates from biomass and mean individual weight. *Meeresforschung* 32: 329–343.

Brey, T. 2001. Population dynamics in benthic invertebrates. A virtual handbook. Version 01.2 http://www.awibremerhaven.de/Benthic/Ecosystem/FoodWeb/Handbook/main.html. Alfred Wegener Institute for Polar and Marine Research, Germany.

Brown, J.H., J.F. Gillooly, A.P. Allen, V.M. Savage, and G.B. West. 2004. Toward a metabolic theory of ecology. *Ecology* 85: 1771–1789.

Cooksey, C., and J. Hyland. 2007. Sediment quality of the Lower St. Johns River, Florida: an integrative assessment of benthic fauna, sediment-associated stressors, and general habitat characteristics. *Marine Pollution Bulletin* 54: 9–21.

Cowles, A., J.E. Hewitt, and R.B. Taylor. 2009. Density, biomass and productivity of small mobile invertebrates in a wide range of coastal habitats. *Marine Ecology Progress Series* 384: 175–185.

Craig, J.K., and L.B. Crowder. 2005. Hypoxia-induced habitat shifts and energetic consequences in Atlantic croaker and brown shrimp on the Gulf of Mexico shelf. *Marine Ecology Progress Series* 294: 79–94.

Cusson, M., and E. Bourget. 2005. Global patterns of macroinvertebrate production in marine benthic habitats. *Marine Ecology Progress Series* 297: 1–14.

Danovaro, R., A. Dell'Anno, A. Pusceddu, C. Gambi, I. Heiner, et al. 2010. The first metazoa living in permanently anoxic conditions. *BioMedical Central Biology* 8: 1–30.

Dauer, D.M., and R.J. Llansó. 2003. Spatial scales and probability based sampling in determining levels of benthic community degradation in the Chesapeake Bay. *Environmental Monitoring and Assessment* 81: 175–186.

Dauer, D.M., A.J. Rodi Jr., and J.A. Ranasinghe. 1992. Effects of low dissolved oxygen events on the macrobenthos of the lower Chesapeake Bay. *Estuaries* 15: 384–391.

Diaz, R.J. 2001. Overview of hypoxia around the world. *Journal of Environmental Quality* 30: 275–281.

Diaz, R.J., and R. Rosenberg. 1995. Marine benthic hypoxia: a review of its ecological effects and the behavioural responses of benthic macrofauna. *Oceanography and Marine Biology an Annual Review* 33: 245–303.

Diaz, R.J., and R. Rosenberg. 2008. Spreading dead zones and consequences for marine ecosystems. *Science* 321: 926–929.

Diaz, R.J., and L.C. Schaffner. 1990. The functional role of estuarine benthos. In *Perspectives on the Chesapeake Bay: Advances in estuarine sciences*, ed. M. Haire and E.C. Krome, 25–56. Virginia: Chesapeake Research Consortium.

Diaz, R.J., R.J. Neubauer, L.C. Schaffner, L. Pihl, and S.P. Baden. 1992. Continuous monitoring of dissolved oxygen in an estuary experiencing periodic hypoxia and the effect of hypoxia on macrobenthos and fish. *Science of the Total Environment* 1: 1055–1068.

Dolbeth, M., A.I. Lillebo, P.G. Cardoso, S.M. Ferreira, and M.A. Pardal. 2005. Annual production of estuarine fauna in different environmental conditions: an evaluation of the estimation methods. *Journal of Experimental Marine Biology Ecology* 326: 115–127.

Dolbeth, M., M. Cusson, R. Sousa, and M.A. Pardal. 2012. Secondary production as a tool for better understanding of aquatic ecosystems. *Canadian Journal of Fisheries and Aquatic Sciences* 69: 1230–1253.

Douglass, J.G., K.E. France, J.P. Richardson, and J.E. Duffy. 2010. Seasonal and interannual change in a Chesapeake Bay eelgrass community: insights into biotic and abiotic control of community structure. *Limnology Oceanography* 55: 1499–1520.

Edgar, G.J. 1990. The use of the size structure of benthic macrofaunal communities to estimate faunal biomass and secondary production. *Journal of Experimental Marine Biology Ecology* 137: 195–214.

Edgar, G.J., and N.S. Barrett. 2002. Benthic macrofauna in Tasmanian estuaries: scales of distribution and relationships with environmental variables. *Journal of Experimental Marine Biology Ecology* 270: 1–24.

Edgar, G.J., C. Shaw, G.F. Watson, and L.S. Hammond. 1994. Comparisons of species richness, size-structure and production of benthos in vegetated and unvegetated habitats in Western Port, Victoria. *Journal of Experimental Marine Biology and Ecology* 176: 201–226.

Folk, R.L. 1973. Carbonate petrography in the post-Sorbian age. In *Evolving concepts in sedimentology*, ed. R.N. Ginsburg, 1–40. Maryland: Johns Hopkins University Press.

Hagy, J.D. 2002. Eutrophication, hypoxia, and trophic transfer efficiency in Chesapeake Bay. Ph.D. dissertation, University of Maryland, College Park, MD

Hagy, J.D., W.R. Boynton, C.W. Keefe, and K.V. Wood. 2004. Hypoxia in Chesapeake Bay, 1950–2001: Long-term change in relation to nutrient loading and river flow. *Estuaries* 37: 634–658.

Hoback, W.W., and M.C. Barnhart. 1996. Lethal limits and sublethal effects of hypoxia on the amphipod *Gammarus pseudolimnaeus. Journal of North American Benthological Society* 15: 117–126.

Holland, A.F., A.T. Shaughnessy, L.C. Scott, V.A. Dickens, J. Gerritsen, and J.A. Ranainghe. 1988. *Long-term benthic monitoring and assessment program for the Maryland portion of Chesapeake Bay: Interpretive report.* Maryland Department of Natural Resources: Power Plant Research Program.

Kemp, W.M., W.R. Boynton, J.E. Adolf, D.F. Boesch, W.C. Boicourt, et al. 2005. Eutrophication of Chesapeake Bay: Historical trends and ecological interactions. *Marine Ecology Progress Series* 303: 1–29.

Kuo, A.Y., and B.J. Neilson. 1987. Hypoxia and salinity in Virginia estuaries. *Estuaries* 10: 277–283.

Kuo, A.Y., K. Park, and M.Z. Moustafa. 1991. Spatial and temporal variabilities of hypoxia in the Rappahannock River, Virginia. *Estuaries* 14: 113–121.

Levin, L.A., W. Ekau, A.J. Gooday, F. Jorissen, J.J. Middelburg, et al. 2009. Effects of natural and human-induced hypoxia on coastal benthos. *Biogeosciences* 6: 2063–2098.

Lindeman, R.L. 1942. The trophic-dynamic aspect of ecology. *Ecology* 23: 399–418.

Llansó, R.J. 1991. Tolerance of low dissolved oxygen and hydrogen sulfide by the polychaete *Steblospio benedicti* (Webster). *Journal of Experimental Marine Biology Ecology* 153: 165–178.

Llansó, R.J. 1992. Effects of hypoxia on estuarine benthos: the lower Rappahannock River (Chesapeake Bay), a case study. *Estuarine and Coastal Shelf Science* 35: 491–515.

Lohrenz, M.E., M.J. Dag, and T.E. Whitledge. 1990. Enhanced primary production at the plume/oceanic interface of the Mississippi River. *Continental Shelf Research* 10: 639–664.

Long, W.C., B.J. Brylawski, and R.D. Seitz. 2008. Behavioral effects of low dissolved oxygen on the bivalve *Macoma balthica. Journal of Experimental Marine Biology Ecology* 359: 34–39.

Ludsin, S.A., X. Zhang, S.B. Brandt, M.R. Roman, W.C. Boucourt, et al. 2009. Hypoxia-avoidance by planktivorous fish in Chesapeake Bay: Implication for food web interaction and fish recruitment. *Journal of Experimental Marine Biology Ecology* 381: 121–131.

Möller, P., L. Pihl, and R. Rosenberg. 1985. Benthic faunal energy flow and biological interaction in some shallow marine soft bottom habitats. *Marine Ecology Progress Series* 27: 109–121.

Morin, A., and N. Bourassa. 1992. Modèles empiriques de la production annuelle et du rapport P/B d'inverteébrés benthiques d'eau courantes. *Canadian Journal of Fisheries and Aquatic Sciences* 49: 532–539.

Murphy, R.R., W.M. Kemp, and W.P. Ball. 2011. Long-term trends in Chesapeake Bay seasonal hypoxia, stratification, and nutrient loading. *Estuaries and Coasts* 34: 1293–1309.

Nestlerode, J.A., and R.J. Diaz. 1998. Effects of periodic environmental hypoxia on predation of a tethered polychaete, *Glycera americana*: implication for trophic dynamics. *Marine Ecology Progress Series* 172: 185–195.

Newcombe, C.L., W.A. Horne, and B.B. Shepherd. 1939. Studies on the physics and chemistry of estuarine waters in Chesapeake Bay. *Journal of Marine Research* 2: 87–116.

Nichols, F.H. 1977. Dynamics and production of *Pectinaria koreni* (Malmgren) in Kiel Bay, West Germany. In *Biology of benthic organisms*, ed. B.F. Keegan, P.O. Ceidigh, and P.J.S. Boaden, 453–463. Oxford: Pergamon Press.

Nilsen, M., T. Pedersen, and E.M. Nilssen. 2006. Macrobenthic biomass, productivity (P/B) and production in a high-latitude ecosystem, North Norway. *Marine Ecology Progress Series* 321: 67–77.

Nixon, S.W. 1995. Coastal marine eutrophication: A definition, social causes, and future concerns. *Ophelia* 41: 199–219.

Officer, C.B., R.B. Biggs, J.L. Taft, L.E. Cronin, M.A. Tyler, and W.R. Boynton. 1984. Chesapeake Bay anoxia: origin, development, and significance. *Science* 223: 22–27.

Park, K., A.Y. Kuo, and J. Neilson. 1996. A numerical model study of hypoxia in the tidal Rappahannock River of Chesapeake Bay. *Estuarine Coastal Shelf Science* 42: 563–581.

Pearson, T.H., and R. Rosenberg. 1978. Macrobenthic succession in relation to organic enrichment and pollution of the marine environment. *Oceanography and Marine Biology, an Annual Review* 16: 229–311.

Perkins, E.J. 1974. *The biology of estuaries and coastal waters.* London: Academic.

Pihl, L., S.P. Baden, and R.J. Diaz. 1991. Effects of periodic hypoxia on distribution of demersal fish and crustaceans. *Marine Biology* 108: 349–360.

Pihl, L., S.P. Baden, R.J. Diaz, and L.C. Schaffner. 1992. Hypoxia-induced structural changes in the diet of bottom feeding fish and crustacea. *Marine Biology* 112: 349–361.

Plante, C., and J.A. Downing. 1989. Production of freshwater invertebrate populations in lakes. *Canadian Journal of Fisheries and Aquatic Sciences* 46: 1489–1498.

Rabalais, N.N. 2004. Eutrophication. In *The Global Coastal Ocean Multiscale Interdisciplinary Processes, The Sea*, vol. 13, ed. A.R. Robinson, J. McCarthy, and B.J. Rothschild, 1–46. Boston: Harvard University Press.

Rakocinski, C.F. 2012. Evaluating macrobenthic process indicators in relation to organic enrichment and hypoxia. *Ecological Indicators* 13: 1–12.

Robertson, A.I. 1979. The relationship between annual production: biomass ratios and lifespans for marine macrobenthos. *Oecologia* 38: 193–202.

Rosenberg, R. 1972. Benthic faunal recovery in a Swedish fjord following the closure of a sulphite pulp mill. *Oikos* 23: 92–108.

Sale, J.W., and W.W. Skinner. 1917. The vertical distribution of dissolved oxygen and the precipitation of salt water in certain tidal areas. *Franklin Institute Journal* 184: 837–848.

SAS Institute. 1989. *SAS/STAT® User's Guide, Version 6. 4th edn, Oxford Oxford, Vol. 2.* Cary: SAS Institute.

Schwinghammer, P., and B. Hargrave. 1986. Partitioning of production and respiration among size groups of organisms in an intertidal benthic community. *Marine Ecology Progress Series* 31: 131–142.

Seitz, R.D., L.S. Marshall Jr., A.H. Hines, and K.L. Clark. 2003. Effects of hypoxia on predator-prey dynamics of the blue crab *Callinectes sapidus* and the Baltic clam *Macoma balthica* in Chesapeake Bay. *Marine Ecology Progress Series* 257: 179–188.

Seitz, R.D., D.M. Dauer, R.M. Llansó, and W.C. Long. 2009. Broad-scale effects of hypoxia on benthic community structure in Chesapeake Bay, USA. *Journal of Experimental Marine Biology Ecology* 381: 4–12.

Sprung, M. 1993. Estimating macrobenthic secondary production from body weight and biomass: a field test in a non-boreal intertidal habitat. *Marine Ecology Progress Series* 100: 103–109.

Stow, C.A., and D. Scavia. 2009. Modeling hypoxia in the Chesapeake Bay: Ensemble estimation using a Bayesian hierarchical model. *Journal of Marine Systems* 76: 244–250.

Sturdivant, S.K., R.J. Diaz, and G.R. Cutter. 2012. Bioturbation in a declining oxygen environment, *in situ* observations from Wormcam. *Public Library of Science ONE* 7(4): e34539. doi:10.1371/e34539.

Sturdivant, S.K., R.D. Seitz, and R.J. Diaz. 2013. Effects of seasonal hypoxia on macrobenthic production and function in the Rappahannock River, Virginia, USA. *Marine Ecology Progress Series* 490: 53–68.

Telesh, I.V., and V.V. Khlebovich. 2010. Principal processes within estuarine salinity gradient: A review. *Marine Pollution Bulletin* 61: 149–155.

Theede, H., A. Ponat, K. Hiroki, and C. Schliper. 1969. Studies on the resistance of marine bottom invertebrates to oxygen-deficiency and hydrogen sulphide. *Marine Biology* 2: 325–337.

Torrans, E.L., and H.P. Clemens. 1982. Physiological and biochemical effects of acute exposure of fish to hydrogen sulfide. *Comparative Biochemistry Physiology* 71: 183–190.

Tumbiolo, M.L., and J.A. Downing. 1994. An empirical model for the prediction of secondary production in marine benthic invertebrate populations. *Marine Ecology Progress Series* 114: 165–174.

Turner, R.E., N.N. Rabalais, and D. Justic. 2012. Predicting summer hypoxia in the northern Gulf of Mexico: Riverine N, P, and Si loading. *Marine Pollution Bulletin* 64: 319–324.

Tyson, R.V., and T.H. Pearson. 1991. Modern and ancient continental shelf anoxia: an overview. *Geological Society Special Publication* 55: 1–24.

van Colen, C., F. Montserrat, M. Vincx, P.M.J. Herman, T. Ysebaert, and S. Degraer. 2010. Long-term divergent tidal flat benthic community recovery following hypoxia-induced mortality. *Marine Pollution Bulletin* 60: 178–186.

Vaquer-Sunyer, R., and C.M. Duarte. 2008. Thresholds of hypoxia for marine biodiversity. *Proceedings of the National Academy of Sciences* 105: 15452–15457.

Vaquer-Sunyer, R., and C.M. Duarte. 2010. Sulfide exposure accelerates hypoxia-driven mortality. *Limnology and Oceanography* 55: 1075–1082.

Vissman, B. 1990. Sulfide detoxification and tolerance in *Nereis* (*Hediste*) *diversicolor* and *Nereis* (*Neanthes*) *virens* (Annelida: Polychaeta). *Marine Ecology Progress Series* 59: 229–238.

Wannamaker, C.M., and J.A. Rice. 2000. Effects of hypoxia on movements and behavior of selected estuarine organisms from the southeastern United States. *Journal of Experimental Marine Biology Ecology* 249: 145–163.

Warren, L.M. 1977. The ecology of *Capitella capitata* in British water. *Journal of Marine Biological Assessment UK* 57: 151–159.

Weisberg, S.B., J.A. Ranasinghe, D.M. Dauer, L.C. Schaffner, R.J. Diaz, and J.B. Frithsen. 1997. An estuarine benthic index of biotic integrity (B-IBI) for Chesapeake Bay. *Estuaries* 20: 149–158.

Wilber, D.H., and D.G. Clarke. 1998. Estimating secondary production and benthic consumption in monitoring studies: a case study of the impacts of dredged material disposal in Galveston Bay, Texas. *Estuaries* 21: 230–245.

Winn, R.N., and D.M. Knott. 1992. An evaluation of the survival of experimental populations exposed to hypoxia in the Savannah River estuary. *Marine Ecology Progress Series* 88: 161–179.

Zar, J.H. 1999. *Biostatistical Analysis*, 4th ed. New Jersey: Prentice Hall.

Zeger, S.L., K.Y. Liang, and P.S. Albert. 1988. Models for longitudinal data: A generalized estimation equation approach. *Biometrics* 44: 1049–1060.

Zimmerman, A.R., and E.A. Canuel. 2000. A geochemical record of eutrophication and anoxia in Chesapeake Bay sediments: anthropogenic influence on organic matter composition. *Marine Chemistry* 69: 117–137.