Effects of seasonal hypoxia on macrobenthic production and function in the Rappahannock River, Virginia, USA

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ABSTRACT: Since colonial times, anthropogenic effects have eroded Chesapeake Bay's health, resulting in an increase in the extent and severity of hypoxia (≤ 2 mg O_2 l^{-1}), adversely affecting community structure and secondary production of macrobenthos in the Bay and its tributaries. The influence of hypoxia on macrobenthic communities is well documented, but less well known is the regulatory effect of hypoxia on macrobenthic production. Changes in macrobenthic production were assessed in the lower Rappahannock River, a sub-estuary of Chesapeake Bay, in an area known to experience seasonal hypoxia. During the spring, summer, fall, and following spring of 2007 and 2008, 10 samples were collected each season for a total of 80 samples, and macrobenthic production was estimated using Edgar's allometric equation. Additionally, from early spring to late fall, dissolved oxygen concentrations were measured continuously at 2 of the 10 sites in 2007, and 2 of the 10 sites in 2008; in conjunction, the macrobenthic community was assessed through bi-weekly grab samples at these sites. Hypoxic sites had as much as 85% lower macrobenthic production compared to normoxic sites, and macrobenthic production at hypoxic sites was associated with primarily smaller, disturbance-related annelids. Macrobenthic production differed across seasons, and estimated sediment reworking rates were significantly higher during normoxia, indicating that the functional role of the macrobenthic community changed during hypoxia.

KEY WORDS: Oxygen depletion · Secondary production · Chesapeake Bay · Macrobenthos · Energy flow

INTRODUCTION

Oxygen, a key element in the metabolic processes of most metazoan organisms, is found in a dissolved form in aquatic environments as a result of primary production and atmospheric diffusion (Breitburg et al. 2003). In estuaries, once dissolved into surface waters, dissolved oxygen (DO) is normally mixed down into bottom waters by turbulence or gravitational circulation (Kuo & Neilson 1987, Burchard & Schuttelaars 2012). During the spring and summer months, a pycnocline develops as a result of the spring freshet and warmer surface waters (Taft et al. 1980). This stratification hampers the supply of DO to

bottom waters, and as the consumption rate exceeds resupply, DO concentrations decline, and the system can experience hypoxia (Kemp et al. 2005). We define hypoxia as DO concentrations of ≤ 2 mg O_2 l^{-1}, mild hypoxia as 2.1 to 2.8 mg O_2 l^{-1}, normoxia as >2.8 mg O_2 l^{-1}, and anoxia as the complete absence of oxygen (Tyson & Pearson 1991).

Hypoxia is closely associated with eutrophication arising from altered coastal nutrient budgets that can be linked to increased human population, whether through urbanization in coastal river drainages or through expanded agricultural activities (Diaz 2001). Though intermittent hypoxia in the Bay may have been a natural phenomenon, sediment cores indicate

that the frequency and extent of hypoxia increased with colonization and subsequent land cover changes (Cooper & Brush 1991, Cooper 1995, Hagy et al. 2004). Anthropogenic disturbance has resulted from activities that mobilize nitrogen and phosphorous compounds through land clearing, application of fertilizer, discharge of human waste, animal production, and combustion of fossil fuels (Cloern 2001). In Chesapeake Bay, runoff from agricultural practices is the main source of nutrient loading (Magnien et al. 1995).

Seasonal hypoxia occurs throughout Chesapeake Bay and some of its tributaries during the summer months, and was first detected in DO measurements in the Potomac (a tributary) in the 1910s (Sale & Skinner 1917), and in the main stem Chesapeake Bay in the early 1930s (Newcombe et al. 1939, Zimmerman & Canuel 2000). The most severe low-oxygen events, in terms of duration and DO concentration, occur in the main stem (Officer et al. 1984, Stow & Scavia 2009), and hypoxic conditions in the Bay last approximately 120 d (May to September; Murphy et al. 2011). From the 1950s through the 1990s, there has been a substantial increase in hypoxic/anoxic water in Chesapeake Bay, from ~3 km^3 in the 1950s, to ~10 km^3 in the 1990s (Hagy et al. 2004), with no decline in the 21st century (Murphy et al. 2011). The increase in the spatial extent of Chesapeake Bay hypoxia has consequences for the benthos (Riedel et al. 2008, Vaquer-Sunyer & Duarte 2008, Van Colen et al. 2010). While gravitational circulation drives hypoxia development in the Bay (Kuo & Neilson 1987), the outer edge of Chesapeake Bay's main stem hypoxic water may be advected into shallow areas, such as the Bay's tributaries, through horizontal transport (Breitburg 1990). In the Rappahannock River, our area of interest, a combination of tidal mixing and proximity to main-stem hypoxic waters controls the seasonal hypoxia, which lasts throughout most of the summer (Kuo & Neilson 1987, Kuo et al. 1991, Park et al. 1996).

The effects of hypoxia on benthic community structure are generally understood to include a series of predictable and graded responses (Rabalais et al. 2001). At the initial onset of hypoxia, organisms increase respiration (Wannamaker & 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 & Rosenberg 1995). Infauna migrate closer to the sediment surface as reduced compounds (e.g. H_2S) accumulate, and have been observed on or extending above the sediment surface in a moribund condition (Tyson & Pearson 1991, 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 species (Llansó 1992, Diaz & Rosenberg 1995, Levin et al. 2009). At the functional level, there is less understanding of how hypoxia interacts with macrobenthic production and the subsequent trophic transfer of energy (Baird et al. 2004, Long & Seitz 2008).

Productivity is an intriguing component of the energy budget in marine benthic habitats, as it provides an index of community processes proportional to total community respiration and consumption, and it integrates the influence of numerous biotic and environmental variables affecting individual growth and population mortality (Edgar & Barrett 2002, Cusson & Bourget 2005). Production can be defined as the quantity of matter or energy that is available for the next higher trophic level, and an estimate of productivity can be obtained by relating the calculated production to the biomass present (Dolbeth et al. 2012). Secondary production, or the heterotrophic production of organic matter, is viewed as an estimate of estuarine health (Diaz & Schaffner 1990, Dolbeth et al. 2005). The production of macrobenthos is important, as these fauna serve as a link in the energy transfer from primary consumers to higher trophic levels (Nilsen et al. 2006), and is a pathway by which organic carbon is recycled out of the sediment and eventually out of Chesapeake Bay system (Diaz & Schaffner 1990). Community production is rarely measured directly, due to methodological difficulties (Edgar 1990). While direct calculations of macrobenthic production are costly and time-consuming (Wilber & Clarke 1998), methods have been proposed for the indirect calculation of macrobenthic production based on biotic and abiotic variables (e.g. Robertson 1979, Banse & Mosher 1980, Schwinghamer et al. 1986, Plante & Downing 1989, Brey 1990, 2001, Edgar 1990, Morin & Bourassa 1992, Sprung 1993, Tumbiolo & Downing 1994); recent reviews by Cusson & Bourget (2005) and Dolbeth et al. (2005) evaluated a number of these models and concluded that they reliably estimate secondary production. Measuring or estimating production is useful as it express all the components of an ecosystem in common units, allowing the function of the system to be better understood (Lindeman 1942). With production, thermodynamics acts as the common denominator defining the manner of energy transformation and ecological usefulness of varying energy forms (Benke et al. 1988, Wiegert 1988). The error associated with these broad habitat predictions is 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 & Schaffner 1990).

Using production theory and empirical models developed to quantify macrobenthic production without the requirement of intense sampling, we aimed to relate patterns of macrobenthic production in the Rappahannock River estuary to DO concentrations. Specific objectives of our study were to (1) assess the relationship between macrobenthic production and the physical factors of DO concentration, salinity, and % silt and clay; (2) describe patterns of macrobenthic production temporally (across weeks and seasons); and (3) determine taxonomic associations between macrobenthic production and DO concentration.
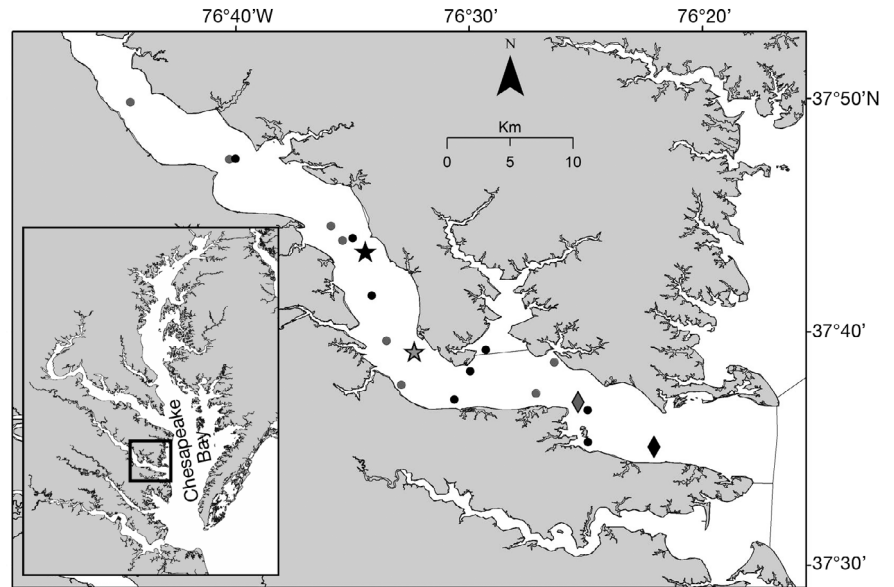

Fig. 1. Lower Rappahannock River depicting the spatial distribution of the 10 sites sampled in 2007 (gray symbols) and 2008 (black symbols), including special designation of the normoxic (diamond symbols) and hypoxic (star symbols) continuously monitored sites

MATERIALS AND METHODS

Study area

Of the 3 major tributaries of the lower Chesapeake Bay, the Rappahannock River is the only sub-estuary with the physical dynamics to allow sustained seasonal hypoxia (Kuo & Neilson 1987). In the lower Rappahannock, a combination of tidal mixing and to a lesser extent, proximity to main stem hypoxic waters, controls its seasonal hypoxia, which develops in late May and abates in early September (Kuo et al. 1991, Park et al. 1996).

Sampling design

The Chesapeake Bay Long-Term Benthic Monitoring Program (LTBMP) started annual random sampling of Chesapeake Bay and its tributaries in both Maryland and Virginia in 1996. The LTBMP divided the Bay into 10 sampling strata, with each having 25 random sampling sites per year; the Rappahannock River is one stratum within the LTBMP design. Sites were sampled by the LTBMP from late July to early September, with a new set of random sites selected each year (Dauer & Llansó 2003). Within the monitoring framework, we included 10 of the 25 randomly selected sites within the meso- and

polyhaline portions of the Rappahannock River estuary (Fig. 1). The meso- and polyhaline regions of the Rappahannock River were selected due to a history of sustained seasonal hypoxia during the summer months (Kuo & Neilson 1987, Park et al. 1996). In conjunction with the LTBMP summer sampling, all 10 sites were also sampled during the spring, and fall of 2007, and again in the spring of the following year (2008). This process was repeated with a new set of randomly selected sites in 2008, i.e. 10 sites sampled during the spring, summer, and fall of 2008, and they were sampled again in the spring of the following year (2009). Thus, our sample period covered the spring of 2007 through the spring of 2009. By randomly selecting sites during consecutive years, our results represent an unbiased spatial assessment of the meso- and polyhaline Rappahannock River, as opposed to looking at fixed sites that would be representative of only those specific locations. In this manuscript when discussing the seasonal sampling and results, '1st spring' will refer to the first time that samples were collected in the spring of the stated sampling year, and '2nd spring' will refer to samples collected in the spring of the following year to assess recovery (i.e. 2nd spring 2007 refers to samples collected in the spring of 2008 at the 2007 random sites, 2nd spring 2008 refers to samples collected in the spring of 2009 at the 2008 random sites).

Field methods

At each site, basic water quality parameters of DO concentration, salinity, and temperature were measured at the surface of the water column and approximately 0.5 m from the bottom using a YSI model 6600 datasonde. The mean depth of our seasonal sites in 2007 and 2008 was 6.4 (SD = 3.2) and 6.3 (SD = 3.4) m, respectively. Sediment grabs were collected for benthic community analysis using a Young grab (440 cm² to a depth of 10 cm). Samples were sieved *in situ* through a 0.5 mm screen using an elutriation process. Organisms and detritus retained on the screen were transferred into labeled jars and preserved in a 10% formaldehyde solution. They were later stained with Rose Bengal, a vital stain that aids in separating organisms from sediments and detritus. Two surface-sediment sub-samples of approximately 120 ml each were collected for grain-size analysis from an additional grab sample at each site.

Each year, 2 of the 10 sites were selected for continuous DO monitoring: in 2007, Sites 18 and 25, and in 2008, Sites 11 and 12. Site selection was based on DO concentration, with one site having a history of normoxia (Sites 25 and 12) and the other, hypoxia (Sites 18 and 11). Different sampling sites were selected each year, instead of a longer study of 2 sites, to ensure observed trends between sites were not anomalous, and due to the nominally normoxic site in 2007 experiencing hypoxia. Aside from DO and depth, the 2 sites chosen each year had similar physical parameters. At each location, a single tripod was deployed with a Hach DS500X water quality datasonde, positioned approximately 0.5 m above the sediment surface. DO concentration, salinity, and temperature measurements were recorded at 20 min increments for a 2 wk period. Every 2 wk, datasondes were collected for maintenance and data retrieval, and new datasondes were deployed. Occasionally the datasondes malfunctioned and did not record data; these are represented by gaps in the continuous

DO data, and are discussed further in the 'Results' section. Additional grab samples were collected at each site with a Young grab during the bi-weekly datasonde swap, and water quality control measurements were collected approximately 0.5 m from the bottom using a YSI model 6600 datasonde. The grab methodology described previously was implemented in the bi-weekly sampling.

Laboratory methods

All macrobenthic samples were processed to identify and enumerate each species present and to measure species-specific ash-free dry-weight (AFDW) biomass. Organisms were sorted from detritus under dissecting microscopes, identified to the lowest possible taxonomic unit, and counted. AFDW biomass was measured for each species by drying organisms to a constant weight at 60°C and ashing in a muffle furnace at 500°C for 4 h. Sediment samples were wet-sieved for % silt and clay content (Folk 1973).

Macrobenthic production

Edgar (1990) developed a general allometric equation ($p = 0.0049 \times B^{0.80} T^{0.89}$) from a meta-analysis of production estimates for benthic macrofaunal populations that relates daily macrobenthic production (P; µg C d^{-1}) to biomass (B; µg AFDW) and water temperature (T; °C) with $r^2 = 0.94$. 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, Cusson et al. 2006), and Edgar's (1990) equation was derived for estuarine macrobenthic species in temperate latitudes, similar to our study. Additionally, he also formulated specific allometric equations for various animal groups (crustaceans, molluscs, and polychaetes), which were used in this study to estimate production for each respective group; the general equation was used for animals that did not fall into one of the 3 aforementioned groups (Table 1). The only departure from Edgar's method, which used the mean AFDW of animals retained on a series of sieves of differing mesh sizes, was the usage of mean AFDW of each species by sample (Rakocinski & Zapfe 2005). Biomass measurements at the species level allowed for the examination of taxonomic and functional group associations between production and DO.

The theoretical basis for Edgar's (1990) equation is grounded in the metabolic theory of ecology that

Table 1. Equations relating daily macrobenthic production P (µg C d^{-1}) to faunal ash-free dry-weight B (µg) and water temperature T (°C) for different animal groups, where $p = x \times B^y \times T^z$. Data derived from Edgar (1990)

	x	y	z	Eq.
General	0.0049	0.8	0.89	1
Polychaeta	0.0035	0.79	1.05	5
Crustacea	0.0013	0.81	1.32	6
Mollusca	0.0066	0.87	0.46	7

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 (e.g. Arias & Drake 1994, Edgar et al. 1994, Wilber & Clarke 1998, Bologna & Heck 2002, Cowles et al. 2009, Douglass et al. 2010, Blake & 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 & Drake 1994, Wilber & 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 & Downing (1994) model, which predicts annual macrobenthic production from depth, annual mean biomass, and water temperature. Hagy (2002) found little to no difference between the 2 models. Further, Blumenshine & Kemp (2000) validated the accuracy of the Tumbiolo & Downing (1994) model against direct calculations of production in Chesapeake Bay (Holland et al. 1988). Given the close agreement between the Tumbiolo & Downing (1994) model and Edgar (1990) model, the Edgar (1990) model was selected based on its more appropriate time-step (e.g. seasonal production rather than annual mean production).

Data analysis

A repeated-measures ANOVA was conducted on the seasonal replicate data for 2007 and 2008 to determine the variance in production among 4 seasons (spring, summer, fall, and the following spring). The model included year as a factor with the randomly selected sites as the repeated measures, and the varying season as the treatment. The physical parameters DO concentration, salinity, and % silt/clay were covariates. Normality was checked with the Shapiro-Wilk test, and homogeneity of variance with Bartlett's test. Non-normal data was log transformed. Tukey's HSD test was used for multiple mean comparisons (Zar 1999).

In an information-theoretic approach, general linear models (GLM) were posed, using residual sums of squares (RSS) estimates to determine Akaike's information criterion (AIC) for our seasonal replicate data. AIC is a measure of the explanatory power of a statistical model that accounts for the number of parameters in the model. The RSS (derived from the re-

peated-measures analysis) of the estimated model parameter (θ) was determined given the data (Gotelli & Ellison 2004), and this approach determined the model that optimized goodness of fit and best reflected effects on macrobenthic production. When comparing among multiple models for the same phenomenon, the model with the lowest AIC value was considered to be the best model. For this study, corrected AIC (AIC_c), a second-order bias correction necessary for small samples (Burnham & Anderson 2002), was used to determine model strength. AIC_c values were then used to determine AIC differences (Δ_i), relative to the smallest AIC_c value in the set of tested models. Hence, Δ_i rescaled AIC_c values such that the model with the minimum AIC_c value had a $\Delta_i = 0$. Derived Δ_i values were used to determine Akaike weights (w_i). The w_i summed to 1, and were interpreted as the probability that model i was the expected best model for the sampling situation considered. If a 'best' model could not be determined, model averaging was conducted. Model-averaged estimates for the measured variables are derived from the sum of the β estimates multiplied by the w_i, for all models. Instead of using only those models with a lot of support, all models were used in model averaging to ensure the w_i summed to 1. This is an appropriate method of model averaging, as models with little or no support essentially get ignored in the calculation, i.e. they are weighted very little (Burnham & Anderson 2002). Sturdivant (2011) determined that DO concentration, salinity, and grain size had significant relationships with macrobenthic production in Chesapeake Bay; thus, the 7 models constructed in this paper used those parameters and were hierarchically based on those findings (Table 2).

For the continuous-monitoring data, paired t-tests were used to determine differences in macrobenthic

Table 2. Parameters for the general linear models (g_x), corresponding to the different hypotheses concerning the effects on macrobenthic production (response = macrobenthic production = θ). k = number of parameters, including σ^2 as a parameter. DO = dissolved oxygen

Model	k	α constant	x_1 DO	x_2 salinity	x_3 grain size
g_1	3	α	$\beta1$		
g_2	3	α		$\beta2$	
g_3	3	α			$\beta3$
g_4	4	α	$\beta1$	$\beta2$	
g_5	4	α	$\beta1$		$\beta3$
g_6	4	α		$\beta2$	$\beta3$
g_7	5	α	$\beta1$	$\beta2$	$\beta3$

production between sites for each year, and to validate differences (or the lack of) in the physical parameters at the hypoxic and normoxic sites. Regression analysis was conducted to determine correlations between DO concentration and macrobenthic production for the continuous-monitoring data. ANOVA was used to assess production differences between the functional groups mobility and feeding type due to >2 functional types for both the mobility and feeding type functional groups. Using taxonomic identification and biomass measurements from samples collected in 2007 and 2008, mean estimations of sediment reworking rates (SRR) were calculated from values reported in Diaz & Schaffner (1990). SRR is analogous to bioturbation, the biological reworking of sediments (Meysman et al. 2006). Mean estimations of SRR (in mg DW_{sed} ind.$^{-1}$ d^{-1}) were compared for normoxic and hypoxic sites in 2007 and 2008 using a paired t-test. All statistical analyses were conducted using R Statistical software; means are presented with standard deviations unless otherwise noted.

RESULTS

The RSS for each of the 7 models (Table 2) were used to generate the AIC_c results (Table 3). Based on the calculated Akaike weights, model g_1 (which included DO alone) had the highest w_i, while models g_2 (salinity), g_3 (% silt and clay), g_4 (DO and salinity), and g_7 (DO, salinity, and % silt and clay) were equally plausible (i.e. had a $w_i \geq 0.10$). However, overwhelming evidence for a single superior model, indicated by a $w_i \geq 0.90$ (Burnham & Anderson 2002), did not exist. To better clarify which variable (DO, salinity, or grain size) was most important to our esti-

mated parameter (macrobenthic production), for each variable the w_i were summed from each model containing one of the aforementioned variables. Summed w_i were as follows: DO = 0.72, salinity = 0.53, and % silt and clay = 0.32, indicating DO was the most important of the 3 measured variables, but strong evidence existed for the importance of salinity as well. Given the strong support for a number of models and the parity in importance between 2 of the 3 measured variables, model averaging was employed for all models. Based on model-averaged results (Table 4), DO concentration and salinity had the most impact on macrobenthic production during 2007 and 2008 in the lower Rappahannock River. For each 1 mg l^{-1} increase in DO concentration, the rate of macrobenthic production increased by 27.6 mg C m^{-2} d^{-1}, and it increased by 15.6 mg C m^{-2} d^{-1} per psu decrease of salinity. Percent silt and clay had a marginal effect on macrobenthic production, increasing the rate of production by 3.1 mg C m^{-2} d^{-1} per percentage point increase in % silt and clay. Mean salinity of all sampling sites over our study period was 14.3 ± 2.6 psu, indicating little variation in salinity, and mean % silt and clay across all samples during our study period was 61.2 ± 12.2%.

Macrobenthic production differed among seasons (Fig. 2), with the highest rate in the 1st spring (2007). Compared with 1st spring, the 2007 summer macrobenthic production was lower by ~90%, and overall, the lowest observed. In the fall, macrobenthic production was higher than the summer by ~70%. Macrobenthic production in the 2nd spring was approximately equal to the fall but did not parallel the 1st spring. A similar trend was observed in the 2008 sampling. The 1st spring was the highest overall and summer the lowest, ~80% lower than 1st spring. Fall macrobenthic production in 2008 was ~70% higher than summer, but not as high as 1st spring, and 2nd spring production was substantially lower than the 1st spring. In both years, there was high variability in the 1st spring and low variability in the summer.

Table 3. Constructed Akaike's information criterion (AIC) table displaying results of each model (models are defined in Table 2); k = the number of parameters with error as a parameter, RSS = residual sums of squares, AIC_c = corrected Akaike's information criterion, Δ_i = AIC differences relative to the smallest AIC_c value, w_i = Akaike weights

Model	k	RSS	AIC_c	Δ_i	w_i
g_1	3	35 950 168	244.8	0.00	0.30
g_2	3	40 128 749	246.7	1.91	0.11
g_3	3	39 611 986	246.5	1.69	0.13
g_4	4	31 561 010	245.0	0.21	0.27
g_5	4	39 258 209	248.8	4.01	0.04
g_6	4	39 349 502	248.9	4.05	0.04
g_7	5	29 958 470	246.7	1.93	0.11

Table 4. Model averaged estimates for the 3 measured variables including dissolved oxygen, salinity, % silt and clay. β_j denotes the estimator of β based on model g_i; SE denotes the standard error

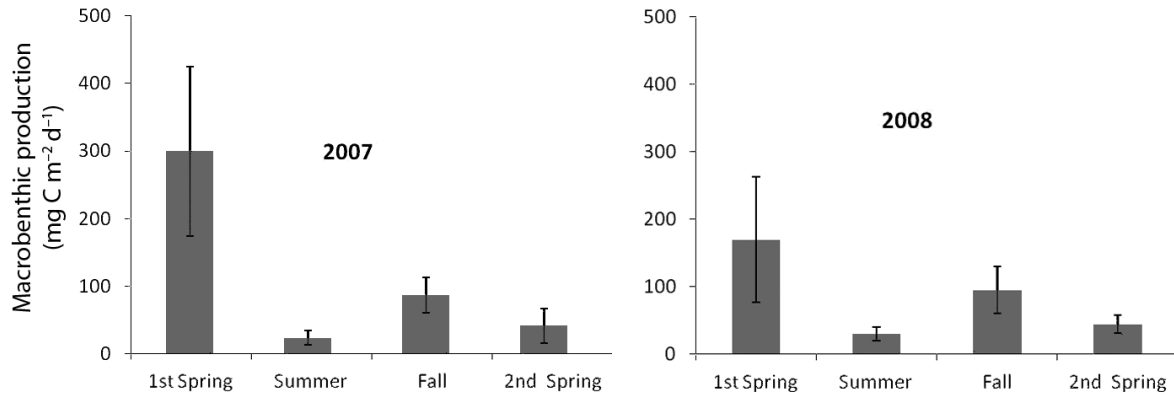| Variable	β_j	SE
Dissolved oxygen	27.6	22.9
Salinity	−15.6	16.8
% silt and clay	3.1	2.0

Fig. 2. Mean daily macrobenthic production by year and season. Samples were collected during the 1st spring, summer, fall, and 2nd spring between spring 2007 and spring 2009. Error bars represent ±1 SE; n = 10 for each season by year treatment (i.e. 1st spring n = 10) for a total N = 80

DO measurements collected by datasondes at each of the continuously monitored sites from 2007 (Sites 18 and 25) and 2008 (Sites 11 and 12) were compared to corresponding point measurements of DO using a paired t-test to validate the accuracy of datasonde readings (Fig. 3). There was no significant difference between corresponding datasonde readings and point DO measurements for any of the 4 sites, provid-

ing confidence in our DO concentration data. In 2007, 55% of the observed DO measurements at hypoxic Site 18 were hypoxic, compared to less than 20% at normoxic Site 25. Note that in 2007, the nominally normoxic Site 25 (Fig. 3A) was not a true normoxic site as it experienced short durations of hypoxia on several occasions; this assessment does not include the considerable data gap for the time when Site 25 was under hypoxic conditions, which would have increased the hypoxic percentage assessment for Site 25. In 2008, 45% of the observed DO measurements at hypoxic Site 11 were hypoxic with 15% of the observed DO at anoxic levels. At normoxic Site 12, less than 2% of DO measurements were hypoxic.

There was no significant difference in salinity, temperature, or % silt and clay between our continuously monitored normoxic and hypoxic sites in 2007 or 2008 (Table 5). Depth was significantly different between the normoxic and hypoxic sites in 2007 and 2008, however, depth, when factored in with salinity, % silt and clay, and temperature, had no significant effect on daily macrobenthic production in Chesapeake Bay or its tributaries (Sturdivant 2011). Therefore, with similar physical parameters between the normoxic and hypoxic sites for both years, macrobenthic production was regressed against only
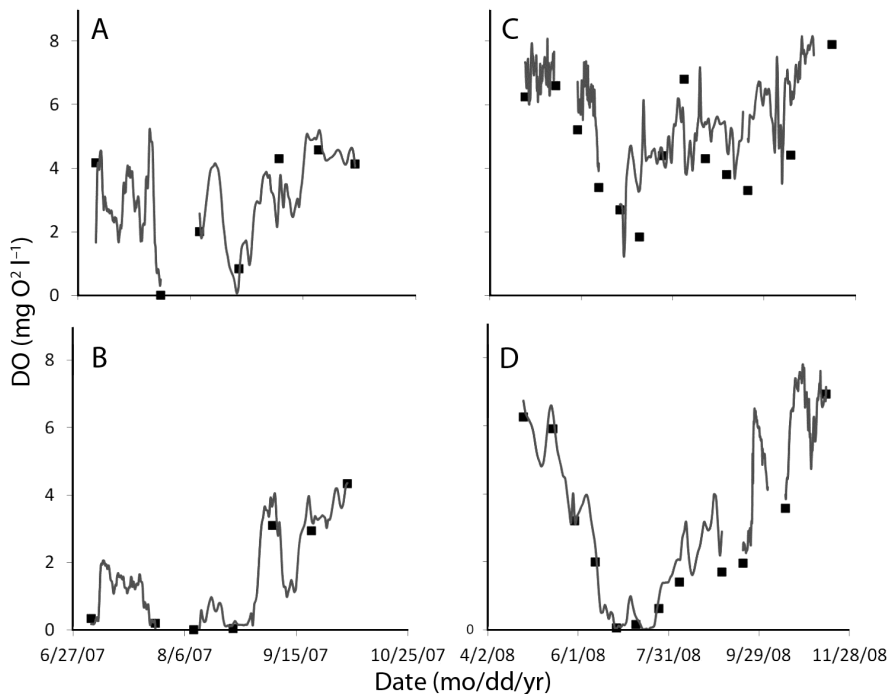

Fig. 3. Dissolved oxygen (DO) concentration data for each of the 4 continuously monitored sites (gray line), compared to corresponding point DO measurements (black squares). No significant differences between datasonde readings and corresponding point DO measurements for (A) the 2007 normoxic Site 25 (df = 6, T = −0.97, p = 0.377), (B) the 2007 hypoxic Site 18 (df = 6, T = 0.22, p = 0.834), (C) the 2008 normoxic Site 12 (df = 12, T = 0.51, p = 0.62) and (D) the 2008 hypoxic Site 11 (df = 12, T = 0.18, p = 0.89). Gaps in data represent time periods when data was not collected due to datasonde malfunction

Table 5. Statistical comparison, using paired *t*-tests, of physical data from the continuously monitored (A) 2007 sites, hypoxic Site 18 (Hyp) and normoxic Site 25 (Norm); and (B) 2008 sites, hypoxic Site 11 (Hyp) and normoxic Site 12 (Norm). Depth was the only physical parameter that was significantly different

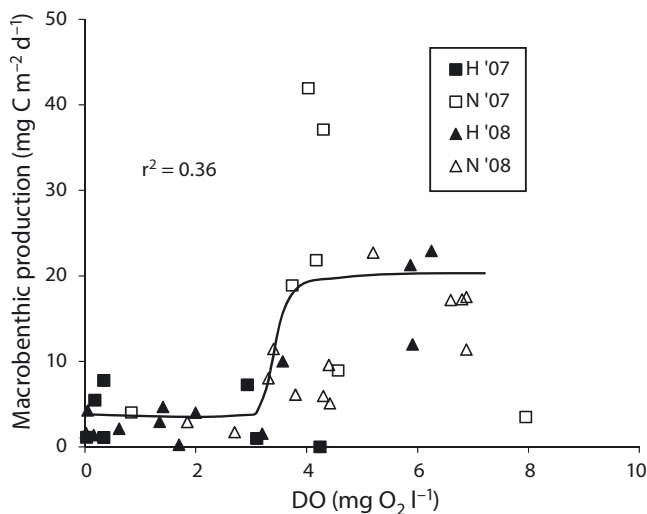| A) Parameter	Site 18 (hyp)	Site 25 (norm)	df	*T*	p
Temp (°C)	25.8	26.0	6	−0.6	0.54
Salinity (psu)	18.6	17.9	6	1.4	0.20
% silt and clay	89.8	90.0	6	−0.4	0.67
Depth (m)	10.6	9.6	6	11.1	<0.0005
B) Parameter	Site 11 (hyp)	Site 12 (norm)	df	*T*	p
Temp (°C)	21.8	22.2	12	−2.1	0.06
Salinity (psu)	14.5	14.8	12	−0.7	0.48
% silt and clay	98.4	94.2	12	1.8	0.05
Depth (m)	9.8	7.7	12	10.6	<0.0005

Fig. 4. Dissolved oxygen concentration and daily macrobenthic production for the continuously monitored hypoxic and normoxic sites in 2007 and 2008. There was a sigmoid relationship between DO and daily macrobenthic production (df = 39, *F* = 10.31, p = 0.0003). Squares represent 2007 data; triangles represent 2008 data. Solid symbols indicate the hypoxic (H) sites, and hollow symbols the normoxic (N) sites

DO concentration (Fig. 4). There was a sigmoid relationship between daily macrobenthic production and DO concentration; macrobenthic production was low in DO concentrations below ~3.0 mg O_2 l^{-1}, rising greater than an order of magnitude between 3.0 and 4.0 mg O_2 l^{-1}. Macrobenthic production was also more variable at higher DO concentrations; the standard error (SE) of mean macrobenthic production at

normoxic DO concentrations (>2.8 mg O_2 l^{-1}) was 2.2 mg C m^{-2} d^{-1}, compared to a SE of 0.5 mg C m^{-2} d^{-1} at DO concentrations ≤2.8 mg O_2 l^{-1}.

The bi-weekly macrobenthic production and community composition between the normoxic and hypoxic sites in 2007 (Sites 25 and 18, respectively) and 2008 (Sites 12 and 11) were compared. Species richness was ~30% lower at hypoxic Site 18 and ~40% lower at hypoxic Site 11 compared to normoxic Sites 25 and 12, respectively. In 2007, macrobenthic production at Site 18 was significantly lower than Site 25 (df = 6, *T* = −2.87, p = 0.029; Fig. 5A); the hypoxic site had on average 85% lower production than the normoxic site. Hypoxia-resistant species contributed to half of the macrobenthic production at Site 25, and ~85% of the macrobenthic production at Site 18 (Table 6). The hypoxia-resistant spionid *Paraprionospio pinnata* dominated macrobenthic production at Site 18, contributing to ~78% of the total macrobenthic production. In 2008, macrobenthic production was not significantly different between Sites 11 and 12, but a trend of higher production at normoxic Site 12 existed (Fig. 5B). Site 11 had on average 36% lower production than Site 12, but this assessment included early spring, a time period unaffected by hypoxia, and when macrobenthic production was approximately equal at both sites. Mean macrobenthic production at Sites 11 and 12 between 25 April 2008 and 12 November 2008 was not significantly different (df = 12, *T* = −2.11, p = 0.056), at approximately 6.8 and 10.5 mg C m^{-2} d^{-1}, respectively. When the difference in production between these 2 sites was assessed starting at the development of hypoxia and going through until it ended (29 May 2008 to 12 November 2008), the production between the 2 sites was significantly different (df = 10, *T* = 2.25, p = 0.049), with macrobenthic production ~50% lower at Site 11 compared to Site 12 during this time period. Mean production during this period was 4.7 and 8.9 mg C m^{-2} d^{-1} at Sites 11 and 12, respectively. Overall, *P. pinnata* contributed to more than half of the observed macrobenthic production at the hypoxic site compared to only ~30% of macrobenthic production at the normoxic site in 2008.

In 2007 and 2008, there were no significant differences in macrobenthic production when tested by the functional groups of mobility or feeding types (p > 0.05), due to large variances observed in these groups. There were significant differences in mean estimates of SRR by site (Fig. 6). In 2007, macrobenthos at the normoxic site reworked an estimated 19 600 mg DW$_{sed}$ ind.$^{-1}$ d^{-1}, which was significantly
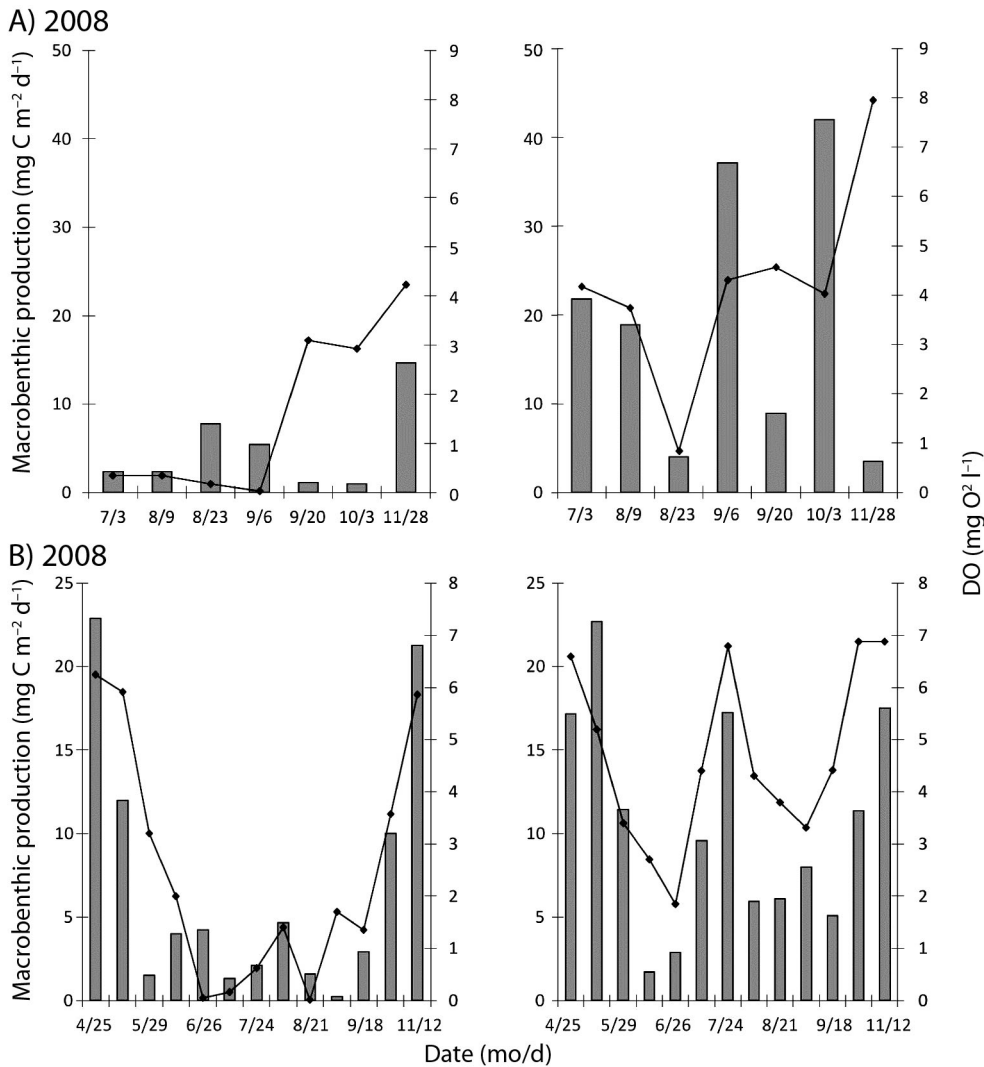
Fig. 5. Daily macrobenthic production (gray bars, left y-axis) and corresponding DO concentration (black line, right y-axis) for (A) hypoxic Site 18 and normoxic Site 25 in 2007; and (B) hypoxic Site 11 and normoxic Site 12 in 2008. In 2007, macrobenthic production was significantly different between Sites 18 and 25 (df = 6, $T = -2.87$, p = 0.029), and in 2008 macrobenthic production was not significantly different between Sites 11 and 12 (df = 12, $T = -2.11$, p = 0.056). Data was used to derive sigmoid relationship in Fig. 4. Note different scale between years

higher than SRR of 2200 mg DW_{sed} ind.$^{-1}$ d^{-1} estimated at the hypoxic site. A similar trend was observed in 2008: the normoxic site had significantly higher estimates of SRR at 5200 mg DW_{sed} ind.$^{-1}$ d^{-1}, compared to the estimates of 800 mg DW_{sed} ind.$^{-1}$ d^{-1} at the hypoxic site. The higher estimates of SRR at the normoxic sites were driven by the biomass of *Loimia medusa, Acteocina canaliculata,* and *Heteromastus filiformis* — species with high burrowing rates (Diaz & Schaffner 1990).

DISCUSSION

DO concentration had a measureable correlation with macrobenthic production in the Rappahannock River estuary; production was low below ~3 mg O_2 l^{-1}, and rose an order of magnitude between 3 and 4 mg O_2 l^{-1}. Seitz et al. (2009) documented similar results, finding sigmoid relationships between macrobenthic biomass and DO concentration in varying salinity regimes of Chesapeake Bay, with a threshold around 3 mg l^{-1} for polyhaline regions. The negative impacts of hypoxia on macrobenthic community structure are well documented (Diaz & Rosenberg 1995, Vaquer-Sunyer & Duarte 2008, Van Colen et al. 2010), and our results indicate hypoxia has equally negative effects on macrobenthic production. It is unclear whether the observed relationship between DO concentration and macrobenthic production is due to direct or indirect mechanisms. A lack of DO in bottom waters can cause direct mortality via asphyxiation (Diaz & Rosenberg 1995) and inhibit macrobenthic recruitment and growth, hampering production (Forbes & Lopez 1990, Powers et al. 2001); yet the impact of hypoxia on macrobenthos extends

Table 6. Compilation of the major hypoxia resistant species collected at the 4 continuously monitored sites: in 2007, hypoxic Site 18 (hyp) and normoxic Site 25 (norm); in 2008, hypoxic Site 11 (hyp) and normoxic Site 12 (norm). Values in the table represent the percentage of macrobenthic production contributed by each species by site; abundances are in parentheses and dash denotes no data. For taxon group: A = annelid, B = bivalve

| Taxon (group)	Hypoxia LT_{50} (h)	Site 18 (hyp)	Site 25 (norm)	Site 11 (hyp)	Site 12 (norm)	Source
Heteromastus filiformis (A)	168–312	–	0.1 (32)	3.3 (12)	0.1 (1)	Rosenberg (1972), Warren (1976), Kravitz (1983)
Loimia medusa (A)	72–113	0.8 (2)	1.8 (3)	–	1.2 (1)	Breitburg et al. (2003)
Macoma balthica (B)	212–1658	2.1 (2)	–	–	–	Aller et al. (1983), Brafield & Newell (1961), Hines & Comtois (1985)
Nereis succinea (A)	62–84	0.8 (1)	0.1 (1)	27.5 (20)	28.7 (17)	Fauchald & Jumars (1979), Kravitz (1983), Hines & Comtois (1985), Fong (1991), Sagasti et al. (2001)
Paraprionospio pinnata (A)	–	77.5 (48)	47 (79)	52.2 (52)	33.6 (50)	Dauer et al. (1981), Kravitz (1983), Schaffner (1987)
Streblospio benedicti (A)	43	1.3 (2)	1.4 (11)	3.6 (12)	3.5 (19)	Dauer et al. (1981), Hines & Comtois (1985), Kravitz (1983), Llansó (1991)
Tubificoides spp. (A)	720	1.3 (3)	–	–	0.3 (3)	Tevesz et al. (1980), Hines & Comtois (1985), Giere et al. (1999)
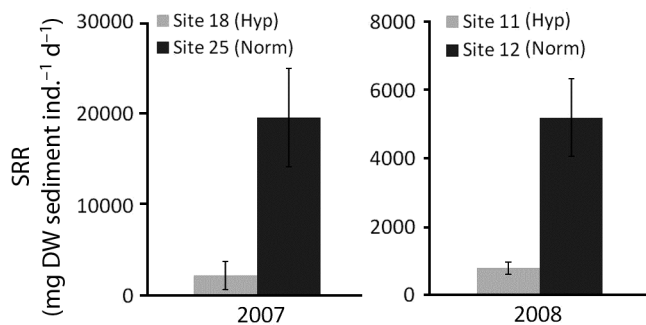
Fig. 6. Estimated sediment reworking rates (SRR, mg DW$_{sed}$ ind.$^{-1}$ d^{-1}) by sampling year and site. Normoxic sites in 2007 and 2008 had higher mean estimations of SRR when compared to hypoxic sites. In 2007, normoxic Site 25 and hypoxic Site 18 had significantly different mean estimations of SRR (df = 6, T = −3.90, p = 0.008). In 2008, normoxic Site 12 and hypoxic Site 11 had significantly different mean estimations of SRR (df = 12, T = −3.55, p = 0.004). Error bars represents ±1 SE

further. At the development of hypoxia, sessile organisms such as macrobenthos decrease feeding and movement (Riedel et al. 2008) in an attempt to depress their metabolism. If the organisms are able to avoid mortality via asphyxiation, such actions during prolonged hypoxic events could indirectly lead to starvation (Diaz & Rosenberg 1995). Additionally, during severe hypoxia and anoxia, sulfate (SO_4) is reduced to sulfide (H_2S), a toxic compound documented to contribute to macrobenthic mortality (Llansó 1991, Shumway et al. 1993, Vaquer-Sunyer & Duarte 2010) through inhibition of the electron transport chain in aerobic respiration (Torrans & Clemens 1982) by binding to cytochrome *c* oxidase resulting in chemical asphyxiation of cells (Bagarinao 1992, Collman et al. 2009). Predation is another factor possibly contributing to lowered production during hypoxia. Macrobenthos migrate upwards in the sediment during hypoxia to avoid low DO and sulfide toxicity (Sturdivant et al. 2012), and can breach and extend their bodies and appendages above the sediment surface, increasing susceptibility to predation (Pihl et al. 1992, Nestlerode & Diaz 1998, Long & Seitz 2008); though in some cases prey gain refuge from their less-tolerant predators under hypoxia due to predation inefficiency or predator exclusion (Brante & Hughes 2001, Altieri 2008).

Macrobenthic production in the lower Rappahannock River was variable between seasons in both 2007 and 2008. Spring is a productive time of year in coastal estuaries as nutrient input from spring freshets enriches shallow systems (Boynton et al. 1995, Magnien et al. 1995) concurrent with recruitment of many benthic organisms (Simon 1967, Sandifer 1972). The shallow nature of Chesapeake Bay fosters tight benthic-pelagic coupling, and water column productivity reaches the bottom through turbulent mixing and subsequent suspension feeding (Cloern 2001) or direct sedimentation (Davies & Payne 1984), thus fueling benthic production. Hypoxia is pervasive in Chesapeake Bay and its tributaries dur-

ing the summer months (Kuo et al. 1991, Hagy et al. 2004) and, as shown in this study, could account for the lower production observed during the summer via the direct or indirect mechanisms discussed in the preceding paragraph. Production only partially recovered in the fall, though this is not surprising. In the colder months, a lack of nutrient input that normally fuels spring production (Hagy et al. 2005), altered hydrography that mixes plankton below the critical depth (Jackson 2008), and lower temperatures reducing metabolism (Diaz & Schaffner 1990) all contribute to reduced productivity. However, the lack of recovery of macrobenthic production in the 2nd spring indicates a possibility of carry-over effects from the previous year. Lost production in hypoxic sites may negatively impact overall macrobenthic recruitment. Macrobenthos employ 2 nutritional recruitment strategies, planktotrophy and/or lecithotrophy (Levin et al. 1987), which have consequences for dispersal distance and population size (Thorson 1950, Kempf & Hadfield 1985). Planktotrophic development usually involves production of a larger number of smaller ova than lecithotrophic development, and because planktotrophic larvae are smaller and must feed in the water column, they spend more time in their larval phase before settlement, allowing for greater dispersal (Reed et al. 2000). Neither nutritional strategy guarantees increased settlement success (Levin & Huggett 1990); macrobenthic larval settlement is not purely random but selective (Watzin 1986). The dispersing larvae are responsible for recognizing the habitat that is optimal for survival and reproduction of the more sedentary adult forms (Chia & Rice 1978, Butman et al. 1988), and this process can be influenced by hydrodynamic processes, chemical induction, and suitability of respective substrate (Butman et al. 1988, Levin 2006, Koehl & Hadfield 2010). In addition, changes in macrobenthic community composition (discussed below) may affect larval recruitment, and subsequently production.

Macrobenthic production was as much as 85% lower at hypoxic sites, but the fate of the 'lost' production remains unknown. The simplest response is that it was never produced. Habitats that are exposed to extensive hypoxia and anoxia have low annual biomass and production (Rainer 1982, Levin 2003, Seitz et al. 2009). Macrobenthic production in areas that experience prolonged hypoxia is regulated by the amount of benthic recruitment and growth that occurs during periods of normoxia (Nichols 1977); therefore, the production at these sites is limited by productivity during normoxia. The lower production observed at hypoxic sites would thus not be a func-

tion of its removal, but rather that it was never created. Alternatively the 'lost' production could have been transferred to higher trophic levels, as hypoxia can enhance predation when predators capitalize on stressed prey (Seitz et al. 2003, Eggleston et al. 2005, Long & Seitz 2008), although severe hypoxia inhibits predation (Altieri 2008) and disrupts the normal energy flow to higher consumers (Baird et al. 2004). Moreover, severe prolonged hypoxia could alternatively allow for the microbial community, which can utilize other compounds as electron acceptors (NO_3^-, MnO_4, $FeOH$, SO_4^{2-}, and CO_2) when DO is absent, to process macrobenthic production through the microbial food web (Baird et al. 2004). A combination of these processes is likely responsible for the lowered production at hypoxic sites. During even short spells (on the order of a week) of hypoxia, the benthic environment of the Rappahannock River becomes microbially dominated (Sturdivant et al. 2012). Additionally, the relatively small spatial extent and lack of sustained severe hypoxia may allow for predators to capitalize on stressed macrobenthos (Llansó 1990, Pihl et al. 1992, Nestlerode & Diaz 1998.

Functionally, there were no significant differences in the production of feeding or mobility groups for macrobenthos at hypoxic vs. normoxic sites. This was driven by large variances in both types of groups, suggesting that hypoxia may affect the production of these functional groups equally; SRR were, however, significantly related to DO concentrations. Through the bioturbative process of sediment reworking, macrobenthos influence sediment geochemical and physical properties (Lohrer et al. 2004) increasing the quality of marine sediments. Hypoxia can negatively influence bioturbation (Sturdivant et al. 2012); the consequences of lowered rates of bioturbation include decreases in sediment permeability, remineralization, nutrient flux (Lohrer et al. 2004), and a shallower sediment oxic layer (Solan & Kennedy 2002). DO penetrates sediments by physical diffusion to only a few millimeters below the sediment surface (Revsbech et al. 1980), but bioturbation can distribute DO much deeper in the sediment (Aller 1982).

The spionid *Paraprionospio pinnata* dominated macrobenthic production at hypoxic sites in both years. *P. pinnata* is an opportunistic species that is morphologically adapted to tolerate a low oxygen environment, having elongated, proliferated, and numerous branchia (Dauer 1985, Lamont & Gage 2000). In addition to dominating production because of its stress tolerance, *P. pinnata* may have also benefited from less competition through reduction of other species during hypoxia (Seitz et al. 2009). In our study, species rich-

ness was 40% lower at hypoxic sites, potentially decreasing competitive pressure and allowing *P. pinnata* to capitalize on the organic-rich environment that generally accompanies eutrophication-induced coastal hypoxic areas (Pearson & Rosenberg 1978, Lu & Wu 1998). While hypoxic sites were dominated by *P. pinnata*, the production at normoxic sites was characterized by species with high SRR, such as *Loimia medusa*, *Acteocina canaliculata*, and *Heteromastus filiformis*. These species were notably absent at the hypoxic sites and contributed to the significant difference in SRR between normoxic and hypoxic sites. Species with life history traits that require high energy demands, such as burrowing to consume food or in search of prey, would be less adapted to an environment where metabolic depression is important to survival, such as in low oxygen environments (Levin 2003).

In our study, salinity and % silt and clay varied in their effects on macrobenthic production. In a previous study, there was a marginally significant positive relationship between macrobenthic production and % silt and clay and a significant negative relationship between macrobenthic production and salinity in Chesapeake Bay (Sturdivant 2011). Results from our study corroborated these findings; macrobenthic production increased 3.1 mg C m^{-2} d^{-1} per unit increase in % silt and clay, and increased 15.6 mg C m^{-2} d^{-1} per unit decrease in salinity. In estuaries worldwide, salinity is the major governing factor in organism distribution (Perkins 1974, Diaz & Schaffner 1990, Telesh & Khlebovich 2010). This study was designed to assess changes in macrobenthic production in a defined upper-mesohaline salinity range of the lower Rappahannock River, thus encompassing a small range of salinity with a mean salinity of 14.3 ± 2.6 psu. Had our study encompassed a larger salinity range, impacts on macrobenthic production may have been greater. On a total area basis, macrobenthic production 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 & Schaffner 1990). At moderate to high salinities, or when salinity is constant, patterns of benthic distribution are further correlated with sediment type (Dauer et al. 1984, Cooksey & Hyland 2007). However, % silt and clay had marginal impacts on macrobenthic production, and this is also likely due to the small spatial extent in which the study took place and the resultant small difference in % silt and clay among sites; mean % silt and clay was 61.2 ± 12.2%.

CONCLUSIONS AND IMPLICATIONS

Macrobenthic production was related to DO concentration, with macrobenthic production as much as 85% lower at hypoxic sites. The function of macrobenthic communities changed relative to DO concentration, with hypoxia-resistant spionids dominant during hypoxia and species with high SRR dominant during normoxia. Macrobenthic production differed across seasons, and 2nd spring macrobenthic production may have been impacted by the dynamics of the previous year. Salinity and sediment grain size had significant and marginally significant effects on macrobenthic production, respectively; but given the relatively small spatial extent of the study, DO concentration had the biggest impact on macrobenthic production. The consequences of observed hypoxia impacts on macrobenthic production are troublesome, as previous studies have documented negative cascading effects to higher trophic levels as a result of disturbance to macrobenthic communities (Powers et al. 2005).

There is a general understanding of the relationship between coastal eutrophication and hypoxia, and the consequences for marine fauna. The necessary action required to address the issue in the Bay and its tributaries is simple — reduce nutrient loading (Cloern 2001). Globally, a number of coastal systems that experienced anthropogenic-related hypoxia have shown that when nutrient loading is decreased, water quality increases, chronic hypoxia abates, and many of the associated problems discussed in this paper are mitigated (Kodama et al. 2002, Mee 2005, Diaz et al. 2008). While simple to acknowledge, the implementation of nutrient-reduction policies is far more complicated (Kemp et al. 2005). This is especially true in a system like Chesapeake Bay, where the watershed is impacted by multiple, separately governed states, and where 25% of the nitrogen input to the system comes from atmospheric deposition (Boynton et al. 1995, Magnien et al. 1995). Though a daunting task for managers, the framework for success in alleviating hypoxia through nutrient reduction is clear.

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