Analysis of the Chesapeake Bay Hypoxia Regime Shift: Insights from Two Simple Mechanistic Models

Yong Liu · Donald Scavia

Abstract Recent studies of Chesapeake Bay hypoxia suggest higher susceptibility to hypoxia in years after the 1980s. We used two simple mechanistic models and Bayesian estimation of their parameters and prediction uncertainty to explore the nature of this regime shift. Model estimates show increasing nutrient conversion efficiency since the 1980s, with lower DO concentrations and large hypoxic volumes as a result. In earlier work, we suggested a 35% reduction from the average 1980–1990 total nitrogen load would restore the Bay to hypoxic volumes of the 1950s–1970s. With Bayesian inference, our model indicates that, if the physical and biogeochemical processes prior to the 1980s resume, the 35% reduction would result in hypoxic volume averaging 2.7 km^3 in a typical year, below the average hypoxic volume of 1950s–1970s. However, if the post-1980 processes persist the 35% reduction would result in much higher hypoxic volume averaging 6.0 km^3. Load reductions recommended in the 2003 agreement will likely meet dissolved oxygen attainment goals if the Bay functions as it did prior to the 1980s; however, it may not reach those goals if current processes prevail.

Keywords Hypoxia · Regime shift · Mechanistic model · Chesapeake Bay · Conversion efficiency

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Introduction

Coastal hypoxia (dissolved oxygen ≤2 mg L^{-1}) has spread worldwide since the 1960s (Diaz and Rosenberg 2008), and has received considerable scientific and policy attention (e.g., NRC 2000; Bricker et al. 2007), as well as mounting documentation of its consequences (NRC 2000; Kemp et al. 2005; Turner et al. 2008). Chesapeake Bay is a large US estuary showing increased stress from nutrient over enrichment (Hagy et al. 2004), with low bottom-water oxygen concentrations first reported in the 1930s and significant increases in both severity and spatial extent since the 1950s (Newcombe and Horne 1938; Officer et al. 1984; Cooper and Brush 1991; Boesch et al. 2001). Boesch et al. (2001) found that, for a given freshwater discharge rate, the observed 1982–1992 hypoxic volume in Chesapeake Bay was two or more times larger than that of 1949–1984, suggesting that a threshold of nutrient loading or ecosystem response was reached. Hagy et al. (2004) showed that the estuary was less susceptible to hypoxia during 1950–1979 than in more recent years. Kemp et al. (2005) suggested that loss of benthic plant biomass and increased efficiency of nitrogen (N) and phosphorus (P) recycling may contribute to the changes in the Bay's ability to assimilate those inputs. Kemp and Goldman (2008) summarize the current state of the science related to thresholds in the Chesapeake Bay and similar ecosystems. This loss of assimilative capacity may indicate a state change (or regime shift) implying that disproportionately large nutrient load reductions may be required to bring hypoxia under control (Boesch et al. 2001). Such shifts have been observed in other estuaries and ecosystems (Scheffer and Carpenter 2003; Kemp and Goldman 2008), such as the Gulf of Mexico (Turner et al. 2008), and Ringkøbing Fjord, Denmark (Petersen et al. 2008).

As has been done for analysis of regime shifts in other ecosystems (Scheffer and Carpenter 2003; Solow and

Beet 2005; Genkai-Kato 2007; Savenkoff et al. 2007), we use models to help frame the analysis in the Chesapeake Bay. In regime shift modeling, one needs to consider the ability of the model structure to reflect the fundamental ecological processes, the method for estimating parameter values, and model uncertainties assessment. Several models have been developed for the Chesapeake Bay, ranging from complex mechanistic models (e.g., Cerco and Cole 1993; Cerco and Noel 2004) to simple statistical ones (Hagy et al. 2004). Complex mechanistic models can resolve important ecosystem processes; however, they are often over-determined (i.e., more coefficients than state variables and data) and require use of literature values and expert-judgment to select key parameter values. Statistical models are computationally more efficient and robust, but generally do not resolve physical, ecological, and biogeochemical processes. Simpler mechanistic models, combined with statistical methods for parameter estimation and analysis of uncertainties, offer an efficient path for regime shift analysis. A rather simple model, based on the one-dimensional Streeter-Phelps (SP) dissolved oxygen model, has been used successfully to model Chesapeake Bay hypoxic volumes (Scavia et al. 2006) and dissolved oxygen concentrations (Stow and Scavia 2008), and Gulf of Mexico hypoxic area (Scavia et al. 2003, 2004; Scavia and Donnelly 2007). We use that formulation in the present analysis, along with a surface-layer nutrient-driven phytoplankton model that has been used to explore estuarine susceptibility in general (Scavia and Liu 2009). We use these two simple mechanistic models with Bayesian estimation of parameters and prediction uncertainty to explore the nature of the regime shift in the Chesapeake Bay and to revise our forecasts of future hypoxia under different loading scenarios.

Ecological models are calibrated traditionally through trial-and-error, which is subject to drawbacks such as inefficiency, subjectivity, and unreliability (Zou et al. 2007). More recently, Bayesian inference has been used in environmental and ecological modeling (Malve and Qian 2006) because it provides a convenient way to combine existing information/past experience (priors) with models and current observations (likelihood) for projecting future ecosystem response (posterior). Thus, Bayesian methods can be more informative than conventional model calibration and they can be used to refine our knowledge of model inputs and to obtain prediction uncertainty bounds (Qian et al. 2003). This approach has several additional advantages, including expressing model outputs as probability distributions to better quantify uncertainties, rigorous assessment of expected consequences of different management actions, optimizing monitoring sampling design, and alignment with adaptive management (Reckhow 1994; Arhonditsis et al. 2007).

Methods

Data

We use January–May average daily TN loads from the Susquehanna River as the primary driver for predicting July surface-layer chlorophyll concentrations and hypoxic volumes in the mid-bay region of the Chesapeake Bay main stem, defined as in Fig. 1 of Scavia et al. (2006). Loads for 1945–1978 from the Susquehanna River were computed using empirical relationships from corresponding nitrate loads at Harrisburg, Pennsylvania (Hagy et al. 2004). Loads for 1979–2004 were from USGS, based on frequent measurements of Susquehanna River TN concentrations at Conowingo, Maryland and derived from the 7-parameter log-linear regression model described by Cohn et al. (1989). Because Susquehanna River loads are a major contributor to main-stem hypoxia, we use them as a surrogate for the entire Bay.

Dissolved oxygen data are those reported in Scavia et al. (2006) for the main stem Chesapeake Bay for 36 years from 1950–2003. The 137 sub-pycnocline average values reported for DO profiles for each of the 36 years were computed by interpolating observations to populate a regular grid with dimensions, first at 1-m resolution in the vertical and then at 1-km in the horizontal across constant depths (Hagy et al. 2004). Average July main stem Chlorophyll a concentrations are from Harding and Perry (1997) for 1950–1980 and from the Water Quality Database of Chesapeake Bay Program Office (http://www.chesapeakebay.net) for 1984–2003.

Streeter-Phelps (SP) Hypoxic Volume Model

This model was first applied to estimate hypoxic volumes in the Chesapeake Bay by Scavia et al. (2006). Subsequently, Stow and Scavia (2008) and Liu et al. (in review) used Bayesian configurations of this model to estimate and compare DO profile and hypoxic volume predictions under uncertainty. The model is an adaptation of the SP river model that predicts oxygen concentrations downstream of point sources of organic matter loads (Chapra 1997). Chesapeake Bay is stratified vertically in summer, with surface waters flowing seaward and bottom waters flowing landward. As such, a key assumption for this application was that Susquehanna River nutrient loads approximate a point source of organic matter (BOD) deposited to subpycnocline depths at the southern end of the mid-Bay region (220 km from the Susquehanna River mouth), and that this organic matter decays as it is transported up estuary below the pycnocline. The steady-state solution of Streeter-Phelps equation can be written as:

$$\text{DO} = \text{DO}_S - \frac{k_\text{d}\text{BOD}_u(F)}{k_r - k_\text{d}}\left(e^{-k_\text{d}\frac{x}{v}} - e^{-k_r\frac{x}{v}}\right) - D_i e^{-k_r\frac{x}{v}} \quad (1)$$

where DO = the dissolved oxygen concentration (mg L^{-1}), DO_s = the saturation oxygen concentration (mg L^{-1}), k_d = the BOD decay coefficient (per day), k_r = reaeration coefficient (per day), BOD_u = the ultimate BOD (mg L^{-1}), x = downstream distance from point source (kilometer), D_i = the DO deficit at the point source (mg L^{-1}), and v = net advection (km day^{-1}).

For our application to the Chesapeake Bay, k_r represents DO flux across the pycnocline and BOD_u is approximated by the nitrogen load times the C/N (5.67 g C per g N) and O_2/C (2.4 gO_2 per g C) ratios, divided by the up-estuary water flux, which was calculated as X-section area (600 km^2) multiply by the advection velocity (3.14 km per day). The details can be found in Scavia et al. (2006). In the original Streeter-Phelps formulation, v represents net advection. However, in this application it also represents all un-modeled process and associated uncertainties (e.g., movement of organic material through the upper food web, conversions between dissolved and particulate forms of organic carbon, sediment-water exchange processes, benthic respiration and mineralization, burial). F represents the combined effects of the fraction of net surface organic matter production that settles below the pycnocline and the extent of nitrogen recycling. This model predicts average concentration of dissolved oxygen below the pycnocline as a function of distance from the point source. Predicted hypoxic volume, V (km^3), is then estimated from the predicted length L (km) of the profile with concentrations below 2 mg L^{-1} and a regression equation determined from observations: $V = 0.00391L^2$ (Scavia et al. 2006).

Nutrient-Driven Phytoplankton Model

A simple, nutrient-driven phytoplankton model, based on previous studies on lakes and estuaries (Scavia 1980; Jørgensen 1994; Humborg et al. 2000; Tett et al. 2003; Fennel 2004; Painting and Devlin 2007; Swaney et al. 2008), was developed by Scavia and Liu (2009) to explore estuarine nutrient susceptibility. It is a simple surface-layer model with inputs and losses of biomass that allow a focus on key biogeochemical reactions (Kimmerer et al. 1993; Murray and Parslow 1999). Rather than model detailed nitrogen dynamics (including phytoplankton uptake and the many process involved in biogeochemical cycling), phytoplankton production is modeled as proportional to total nitrogen (TN) load times α, similar to the SP model application here and in earlier work for the Gulf of Mexico and the Chesapeake Bay (Scavia et al. 2003, 2006; Scavia and Donnelly 2007). Following Scavia and Liu (2009), Susquehanna River nitrogen load was converted to phytoplankton carbon production by multiplying the load by a factor α that encompasses the C/N ratio for nitrogen-limited

production and an "estuarine conversion efficiency factor" intended to capture the myriad processes involved in converting the nitrogen load to algal production. Phytoplankton sinking is modeled as a first-order loss rate and zooplankton grazing is modeled as a quadratic term in phytoplankton biomass similar to approaches for zooplankton mortality (Edwards and Yool 2000; Cerco and Noel 2004; Cranford et al. 2007) under the assumption that zooplankton grazer abundance will vary with phytoplankton abundance. The rate of change of surface mixed-layer phytoplankton carbon (B) is:

$$\frac{dB}{dt} = I_n - \frac{Q_{out}B}{V_1} - v'_{s1}B - LB^2 \tag{2}$$

$$I_n = \frac{TN_L}{V_1}\alpha = \frac{TN_R + TN_O}{V_1}\alpha = \frac{TN_R + Q_{in} \cdot N_O}{V_1}\alpha \tag{3}$$

$$V_1 = fz \cdot V, \quad v'_{s1} = \frac{v_s}{z_1} = \frac{v_s}{fz \cdot z}, \quad Q_{out} = \frac{V}{WRT} \tag{4}$$

where, B is phytoplankton biomass (g C m^{-3}); I_n is phytoplankton production (g C m^{-3} day^{-1}) derived from spring nutrient load (TN_L, g N per day) and the conversion factor (α, g C per g N); Q_{out} is the outflow to the ocean (m^3 per day); Q is the river freshwater discharge (1.13×10^8 m^3 per day, from NOAA NEEA dataset, http://ian.umces.edu/neea); Q_{in} is ocean inflow (Q_{out}-Q, m^3 per day); WRT is the salinity-based residence time (231 days, from NOAA NEEA dataset); v'_{s1} is the sinking rate (per day); v_s is the sinking velocity (meter per day); z_1 is the mixed layer depth (m); z is the estuary average depth (m); fz is the ratio of surface layer depth to the total depth (0.43, based on monitoring data analysis); L is the rate of loss to grazing by zooplankton (m^3 g C^{-1} per day); TN_L is the sum of TN_R (spring riverine TN load, g N per day) and TN_0 (ocean nitrogen influx, g N per day); N_0 is the ocean nitrogen concentration (0.016 mg L^{-1}, from NOAA NEEA dataset); V_1 is the mixed layer volume (m^3); and V is the estuary volume (m^3).

To explore the model's ability to reproduce summer conditions, we solved Eq. 2 analytically at steady state assuming this provides analytical power and adequate distinctions among years (Armstrong 1994; Fennel and Boss 2003). The steady state solution for surface-layer phytoplankton carbon (B) is:

$$B = \frac{-(Q_{out} + V_1v'_{s1}) + \sqrt{(Q_{out} + V_1v'_{s1})^2 + 4I_nLV_1^2}}{2LV_1}$$

$$\tag{5}$$

Parameter Estimation

In Bayesian analysis, all unknown parameters are treated as random variables and their distributions are derived from known information (Borsuk et al. 2001), thus providing a rigorous method for uncertainty analysis and presenting key information for analysis and management decision making (Reckhow 1994). Bayesian inference is based on Bayes' Theorem (Gill 2002):

$$p(\theta|y) = \frac{p(\theta)p(y|\theta)}{p(y)} = \frac{p(\theta)p(y|\theta)}{\int_\theta p(\theta)p(y|\theta)d\theta} \propto p(\theta)p(y|\theta) \qquad (6)$$

where $p(\theta|y)$ is the posterior probability of θ, which is the conditional distribution of the parameters after observation of the data; θ is the parameter to be estimated; $p(\theta)$ is the prior probability of θ (i.e., its assumed probability distribution before observation of data); $p(y|\theta)$ is the likelihood function, which represents the probability of the occurrence of the observations y given different realizations of the postulated mechanistic relationship between the response and predictor variables (e.g., Eq. 1).

Practical implementation of Bayesian approach had been limited because most non-linear models have mathematical forms that are analytically intractable when incorporated into Bayes theorem; it is impossible to obtain the analytically summarizing posterior distributions; and extensive computer time was needed to obtain numerical estimation (Stow and Scavia 2008). More recently, however, the Markov Chain Monte Carlo (MCMC) algorithm has been applied to obtain the numerical summarization of parameters (Qian et al. 2003). In MCMC algorithms, the posterior distribution is determined after the user-provided start values for targeted parameters and a sufficient "burn in" period for the model to converge. Then the converged model can effectively provide a representative, proportional, random sample from the posterior distribution. There are three steps in the Bayesian approach using MCMC sampling (Malve and Qian 2006): identifying the prior probability distributions, determining the likelihood function, and MCMC sampling. After sufficient "burn-in", results are saved for the statistical inferences (Malve and Qian 2006).

We implemented MCMC with Gibbs sampling with WinBUGS (version 1.4.3; Lunn et al. 2000), called from R (version 2.6.0; R2WinBUGS (version 2.1-8; Gelman and Hill 2007). The MCMC sampling was carried out using four chains, each with 20,000 iterations (first 10,000 discarded after model convergence); and samples for each unknown quantity was taken from the next 10,000 iterations using a thin (MCMC sampling interval) equal to 40 to reduce serial correlation. Statistical inference was based on the resulting 1,000 MCMC samples. A potential scale reduction factor, $Rhat$, was produced in R2WinBUGS to determine model convergence (at convergence, $Rhat=$ 1.0). $Rhat$ is approximately the square root of the variance of the mixture of all the chains divided by the average within-chain variance; if it is greater than 1.0, the chains have not mixed well (Gelman and Hill 2007). Standard error and the coefficient of determination (R^2) between observed and predicted values were used to test model results: (Gelman and Hill 2007).

Bayesian Framework the SP model For the SP model, transferring Eq. 1 into Bayes' theorem, the error term was assumed to be normally distributed with zero mean and variance. The likelihood function for hypoxic volume, with the error term assumed to be normally distributed with zero mean and variance of σ_V^2 is:

$$\prod_{i=1}^{36} \frac{1}{\sqrt{2\pi\sigma_V^2}} \exp\left[\frac{\left(V_i^O - 0.00391L_i^2\right)^2}{-2\sigma_V^2}\right] \qquad (7)$$

where i means the years; V_i^0 is the observed hypoxic volume for year i.

Bayesian Framework the phytoplankton model For the phytoplankton model, we have the following results:

$$\mathrm{Chl}a_i^m = \frac{1,000}{\gamma} \cdot \frac{-(Q_{out} + V_1 v'_{s1}) + \sqrt{(Q_{out} + V_1 v'_{s1})^2 + 4I_{ni}LV_1^2}}{2LV_1} + e_C \qquad (8)$$

where γ is the C/Chl a ratio, and e_C is the model error, assumed to be normally distributed with zero mean and variance of σ_C^2. The likelihood function can be described as:

$$\prod_{i=1}^{36} \frac{1}{\sqrt{2\pi\sigma_C^2}} \exp\left[\frac{\left(\mathrm{Chl}a_i^0 - \frac{1,000}{\gamma} \cdot \frac{-(Q_{out} + V_1 v'_{s1}) + \sqrt{(Q_{out} + V_1 v'_{s1})^2 + 4I_{ni}LV_1^2}}{2LV_1}\right)^2}{-2\sigma_C^2}\right] \qquad (9)$$

where $\mathrm{Chl}a_i^0$ is the observed Chl a value ($\mu g\ L^{-1}$).

Parameters estimation of SP Model There are five parameters in the SP model—D_i, v, K, k_d, and F. D_i represent upstream deficits, so we assumed annual D_i follow normal distributions with means equal to observations with small error based on the observations. We estimated constant values for v, K and k_d across all years, and individual values of F for each year to enable comparisons with α from the phytoplankton model. F was allowed to vary across years using a hierarchical structure such that F is normally distributed with mean 0.75, standard deviation 0.13, and restricted between 0 and 1 (e.g., N(0.75,0.13)I[0,1]), based on the assumption that the year-specific estimates arise from a common normal distribution (Stow and Scavia 2008). The following informative normal priors were used based our previous studies (Liu et al. in review): $K \sim$ N(0.60,0.20)I[0,1]; $k_d \sim$ N(0.11,0.05)I[0,]; and $v \sim$ N(2.5, 0.77)I[0,], where '(~)' denotes censoring to either eliminate negative values (I[0,]) or to restrict values between 0 and 1 (I[0,1]).

Parameters estimation of Phytoplankton Model There are four parameters in the phytoplankton model—α, L, γ, and v_s. We estimated constant values for L, γ, and v_s across all years, and individual values of α for each year to enable further exploration of the internal nutrient processes in the Bay and comparisons with F estimates in SP model.

Results

SP Model Allowing F to vary among years, while estimating fixed values for v, K, k_d, resulted in very good fit to hypoxic volume measurements (Fig. 1a; $R^2 = 0.99$). The corresponding R^2 for the measured vs. predicted oxygen concentration profiles is 0.80. Table 1 provides the posterior distributions of parameters, including the mean, sample standard deviation (SD), and five credible intervals (CI), as well as the values used in the more traditional calibration approach (Scavia et al. 2006). Our estimate for k_d is larger and K is smaller than those used by Scavia et al. (2006), but their 95% probability ranges include both values. The parameter v in Scavia et al. (2006) was varied yearly while here we estimated it as constant. The parameter F (Fig. 1b), representing the extent to which the TN load can produce oxygen-consuming bottom-water organic material, decreased between 1950 and 1980 and increased after 1980, consistent with the timing of the reported regime shift (Hagy et al. 2004, Kemp et al. 2005).

Phytoplankton Model Allowing α to vary among years, while estimating fixed values for L, γ, and v_s resulted good fit to Chl *a* measurements ($R^2 = 0.96$; $\sigma = 0.47$) (Fig. 2). The

posterior distributions of parameters are in Table 2. Our parameter estimates are consistent with typical literature values and with those determined for the Chesapeake Bay. For example, Cerco and Noel (2004) estimated L to be in the range of 0.10 to 2.0 for the Chesapeake Bay compared with our estimated mean (95% probability range) of 0.35 (0.20–0.59). Chesapeake Bay summer minimum C/Chl ratio (γ) is 30, with the maximum ranging between 150~200 and overall mean between 50 and 100 (Cerco and Noel 2004). Our estimated γ value is 81.8. Phytoplankton sinking rates generally range between 0.1 and 2.0 m per day (Chapra 1997) and Cerco and Noel (2004) found 0.10 m per day worked best in their Chesapeake Bay model. Our estimate was 0.49 m/day.

The parameters in the above paragraph were estimated as constants across all years; whereas we allowed the conversion factor, α, to vary for each year. That factor is composed of two terms: the C/N ratio for production and the estuarine efficiency factor (ε; Scavia and Liu 2009). By
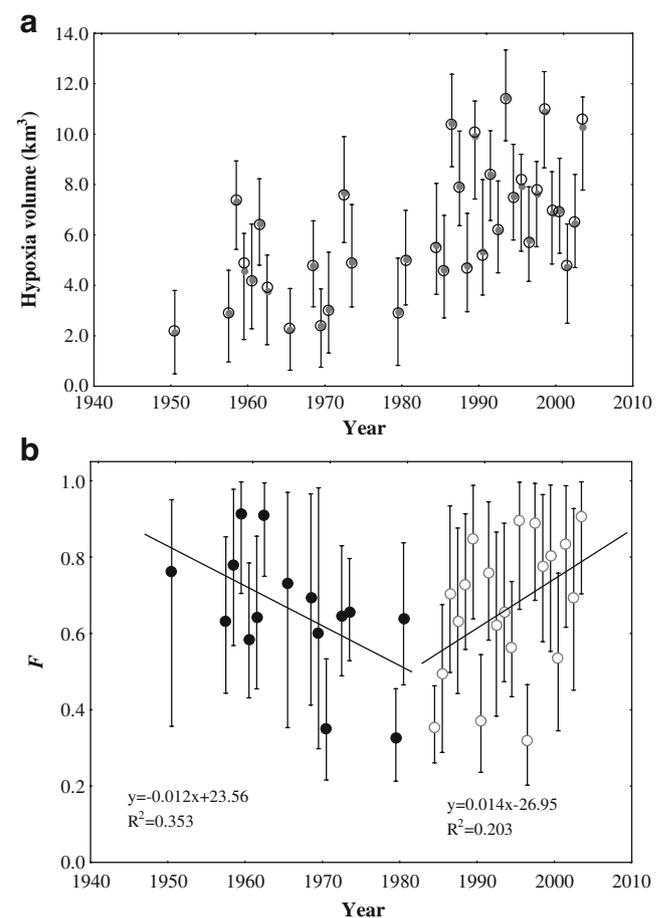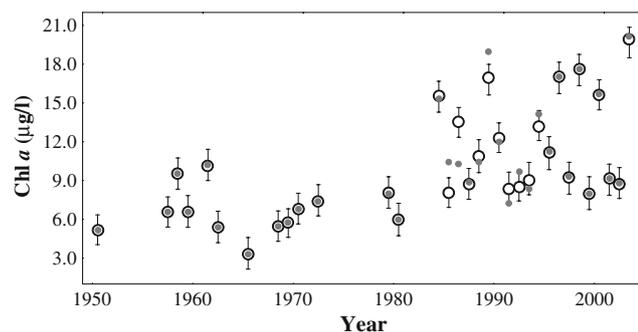

Fig. 1 (**a** *top*) Modeled hypoxic volume (*open circles*) and observations (*closed circles*); (**b** *bottom*) estimated F values (*closed circles* for those before 1980s and *open circles* for those after 1980s). *Error bars* represent the 95% CI of the estimates

Table 1 The Bayesian estimated parameters values in SP model

Parameters	Mean	SD	2.50%	25%	50%	75%	97.50%	Scavia et al. (2006)
k_d	0.16	0.04	0.09	0.13	0.16	0.19	0.24	0.09
v	2.11	0.69	1.06	1.59	2.10	2.57	3.59	Varied by year, with mean 2.4 and SD 0.8
K	0.35	0.12	0.17	0.26	0.34	0.45	0.61	0.60
σ_V	0.422	0.462	0.048	0.101	0.220	0.577	1.708	–

factoring out a constant C/N ratio of 5.67 g C per g N, ε varies between 2 and 20 with trends consistent with the reported regime shift around 1980 (Fig. 3). However, while as with F, it increased after 1980, it was rather constant before 1980. In an earlier cross-system application of this phytoplankton model for 75 estuaries, Scavia and Liu (2009) demonstrated that estuaries with river inflow divided by volume (Q/V) between 0.3 and 2.0 year^{-1} had ε values between 1.0 and 3.0 and were moderately susceptible to nutrient loads. Estuaries with Q/V greater than two were highly susceptible to nutrient loading. The ratio of river discharge to bay volume for the Chesapeake Bay is 0.75 year^{-1}, and using the same C/N ratio as in Scavia and Liu (2009), the estimated ε was 2.9±1.5, consistent with the transition from a moderate to highly susceptible system. Before discussing these trends in detail we compare model and observed process rates.

Modeled Rate Processes Before using models for either prediction or diagnosis, it is important to ensure the internal processes, in addition to the state variables, are consistent with observations, because it is possible to match state variables but have internal processes incorrect and compensating. This is particularly true for non-linear models. Estimates of summer primary production from the phytoplankton model ranged between 0.22 and 3.62 g C m^{-2} per day, with a mean value of 1.22±0.84 g C m^{-2} per day (mean value±one standard deviation), comparing favorably

Fig. 2 Nutrient-driven phytoplankton model results. Model estimates (*open circles*) with estimated 95% CI; observations in *closed circles*

to observations in the Chesapeake Bay (1.38±1.07 g C m^{-2} per day, Cerco and Noel 2004; 1.85 g C m^{-2} per day, Kemp et al. 1992).

Grazing and sedimentation losses in the phytoplankton model, expressed as a percent of total primary production, were 61.6±10.1% and 36.6±8.9%, respectively. McManus and Ederington-Cantrell (1992) reported that microzooplankton grazing consumed about 50–60% of the phytoplankton production in the Bay. Our results also suggest that grazing was more important than sedimentation in controlling phytoplankton biomass, similar to conclusions drawn by Malone (1992) and Cerco and Noel (2004) for the Chesapeake Bay.

Observed spring (March–April) sedimentation in the Chesapeake Bay has been reported to be 0.70 g C m^{-2} per day (Boynton et al. 1993) and 0.50 g C m^{-2} per day (Hagy et al. 2005). Our summer estimates from the phytoplankton model are in the range but, as expected for summer vs. spring, somewhat lower (0.39±0.16 g C m^{-2} per day). Our estimates of F in SP model range between 0.32 and 0.91, with mean of 0.67. These values are a bit lower than the 0.80–1.2 summarized from the literature and the 0.85 used in earlier models (Scavia et al. 2006).

Bottom layer respiration from the SP model is 0.093 g O$_2$ m^{-3} per day (95% probability interval: 0.048–0.156). An independent estimate of bottom-layer oxygen consumption based on mass-balances yielded 0.12±0.06, 0.20±0.08, and 0.42±0.15 mg O$_2$ L^{-1} per day for the upper, middle, and lower reaches of the mid-Bay region (Hagy et al. 2004; Scavia et al. 2006). Kemp et al. (1997) reported sediment and lower water column oxygen consumption rates (including sulfate reduction expressed in O$_2$ equivalents) for the mid-Bay region in 1990–1992. Combining the reported bottom water plankton respiration rates (Kemp et al.'s Fig. 4b) with sediment O$_2$ consumption rates converted to volumetric rates, assuming an average 6.5-m sub-pycnocline depth, we calculate a total metabolic rate between 0.08 and 0.5 g O$_2$ m^{-3} per day.

Average cross-pycnocline flux in the mid-Bay region from the SP model was 0.14 g m^{-3} per day (95% probability interval: 0.12–0.16). These are consistent with independent flux estimates based on mass-balances: 0.10±0.02, 0.10± 0.02, and 0.09±0.02 mg O$_2$ L^{-1} per day for the upper,

Table 2 The Bayesian estimated parameters values in phytoplankton model

Parameters	Mean	SD	2.50%	25%	50%	75%	97.50%
Sinking rate of phytoplankton (v_s, m per day)							
v_s	0.485	0.067	0.361	0.441	0.481	0.530	0.619
Loss rate to grazing (L, m^3 g C^{-1} per day)							
L	0.353	0.102	0.201	0.276	0.342	0.417	0.590
Carbon: Chl a ratio (γ)							
γ	81.8	11.5	60.7	73.1	80.7	91.0	102.8
Model standard error (σ_C)							
σ_C	0.47	0.29	0.03	0.20	0.47	0.71	0.96

middle, and lower reaches of the mid-Bay region (Hagy et al. 2004; Scavia et al. 2006).

Discussion

In earlier studies, Boesch et al. (2001), Hagy et al. (2004), Kemp et al. (2005), and Kemp and Goldman (2008) discussed a threshold change in the Chesapeake Bay hypoxia in the 1980s, when the Bay became more susceptible to nutrient loads. This is seen in both the plot of observed and modeled surface Chl a versus TN load (Fig. 4) and hypoxic volume versus TN load (Fig. 6).

Comparisons of F and ε The parameter F in the SP model and the efficiency factor ε in the phytoplankton model share similar constructs relating nutrient loads to plankton production. F parameterizes the relationship between nutrient load and phytoplankton production (a form of recycling efficiency) and the fraction of that production that settles into the bottom layer; whereas ε represents only the efficiency with which nutrient load is converted to surface production. While estimates of both parameters appear to have inflection points around 1980, F decreases signifi-

cantly before increasing, whereas ε is rather constant before increasing around 1980 (Figs. 1b and 3). A possible explanation for why F decreased but ε did not, is that during the earlier period, increased surface production was actually moving down estuary past the boundary of the SP model and outside of the mesohaline region that influences hypoxia. This is consistent with conclusions made by Harding and Perry (1997) who showed Chl a concentrations in the mesohaline portion of the Bay (inside the boundary of our model) remaining relatively constant after the 1950s, while concentrations in the polyhaline region (outside the boundary of the model) increased, presumably in response to increasing loads (see Figs. 1 and 2 of Harding and Perry 1997). Thus, to compensate for that change, the Bayesian estimator provided decreasing values of F (Fig. 1b). The rather constant conversion efficiency (ε) from the phytoplankton model suggests that it was only this translocation of surface production, not a regime shift that produced the decrease in percent of surface production influencing hypoxia (F).
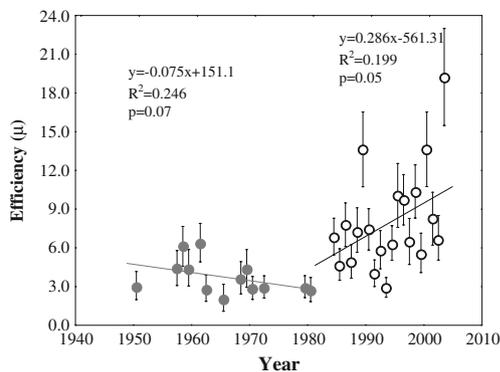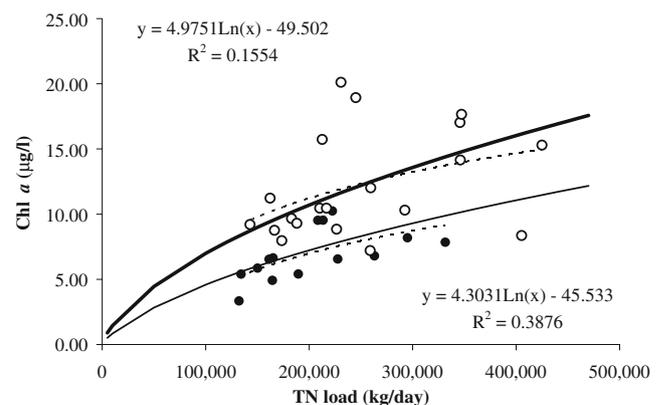
Fig. 3 Estimated Efficiency Factor (ε). *Error bars* represent the 95% CI of the estimates. *Closed circles* for those before 1980s and *open circles* for those after 1980s

Fig. 4 Chl a vs. TN load. Solid lines represent the results using phytoplankton model with ε values averaged for the period before 1980 (*thin*) and after 1980 (*bold*). The coefficient of determination (R^2) of Chl a are 0.37 and 0.28 for the period before 1980 and after 1980. Closed circles are observed Chl a before 1980 and open circles are for after 1980s. *Dotted lines* are regression results, with regression equations

Estuarine efficiency, Nitrogen recycling, and Bottom-water oxygen In contrast to the earlier period, both ε and F increase after 1980, suggesting the conversion efficiency has been increasing since then. Under reducing conditions, nitrification and thus denitrification is reduced such that NH_4 and NO_3 are recycled and made ultimately available for increased algal production (Diaz and Rosenberg 2008). Kemp et al. (2005) showed in the Chesapeake Bay that the fraction of NH_4 recycled from sediments is inversely related to bottom DO concentrations. Our estimates of recycling ε are consistent with that observation (Fig. 5a). We also find a similar, *albeit* opposite and less strong relationship between F and hypoxic volume after 1980 (Fig. 5b). Decreasing average DO concentrations would be consistent with increasing hypoxic volumes. Consistent with our earlier discussion, there is no direct relationship between hypoxic volume and F before 1980. These result show continuous increases in efficiency with decreasing subpycnocline oxygen concentrations (Fig. 5), suggesting a gradual transition to higher efficiency as opposed to an abrupt regime shift.

Forecasts and policy implication A version of the SP model has been used previously to evaluate the impacts of nutrient load scenarios in the Chesapeake Bay (Scavia et al. 2006). In that application, the model was calibrated to the full data set, irrespective of a regime shift. Here we exposed variations in parameters of the SP and phytoplankton models that are consistent with two important processes controlling the relationship between nutrient load and hypoxia development. The first process appears to be the extent to which surface production has an opportunity to develop and settle below the pycnocline before it moves down-estuary and outside the region physically susceptible to hypoxia formation. This feature was captured in decreasing values of F prior to 1980 in the SP model, consistent with findings reported in Harding and Perry (1997). The second process is the apparent increase in the ability of the estuary to recycling nitrogen and become more efficient in its conversion to algal biomass and hypoxia development. This positive feed-back between development of low oxygen conditions and increased recycle was captured by increases in both F in the SP model and ε in the phytoplankton model after 1980, consistent with Kemp et al (2005).

The phytoplankton model was useful for simulating surface chlorophyll, and for exploring the basis for increased hypoxia susceptibility after 1980. However, because the primary property of policy interest is the extent of hypoxic volume, we revise our previously published SP scenarios with new prior information available from this analysis. We again assumed v, K, and k_d were invariant across time, but allowed F and D_i to take on
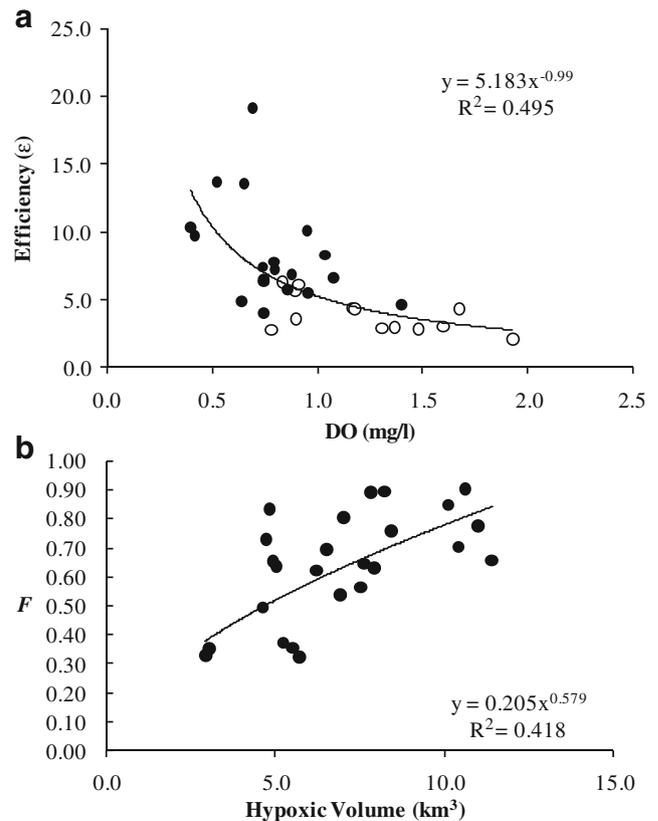

Fig. 5 (**a** *top*) Conversion Efficiency vs. observed bottom DO. *Closed circles* represent conditions after 1980 and open circles before 1980. (**b** *bottom*) F vs. Observed hypoxic volume (km^3) after 1980

different but constant mean values before and after 1980, as opposed to different values for each year. This allows us to develop scenarios for future nutrient loads under assumptions that the Bay remains at this heightened susceptibility or that reduced loads eventually returns the Bay's internal processes to those prior to the shift. We used pre- and post-1980s means for D_i and assumed F comes from a normal distribution with mean posterior distributions from Eq. 1 for years prior to and after the 1980s.

Recall that our models are driven by the Susquehanna River load, not total load for the Bay. In our earlier work, we suggested that a 35% reduction of total nitrogen load from the 1980–1990 Susquehanna River average (262,881 kg/day) would return the main-stem hypoxic volume to the levels observed in the 1950s–1970s (Scavia et al. 2006). Our current results (Fig. 6) indicated that, if the physical and biogeochemical processes of the period before the regime shift were controlling, that reduction would result in hypoxic volume averaging 2.7 km^3 in a typical year, below the average 4.2 km^3 hypoxic volume of 1950s–1970s. However, if the new conditions persist and the Bay remains more susceptible
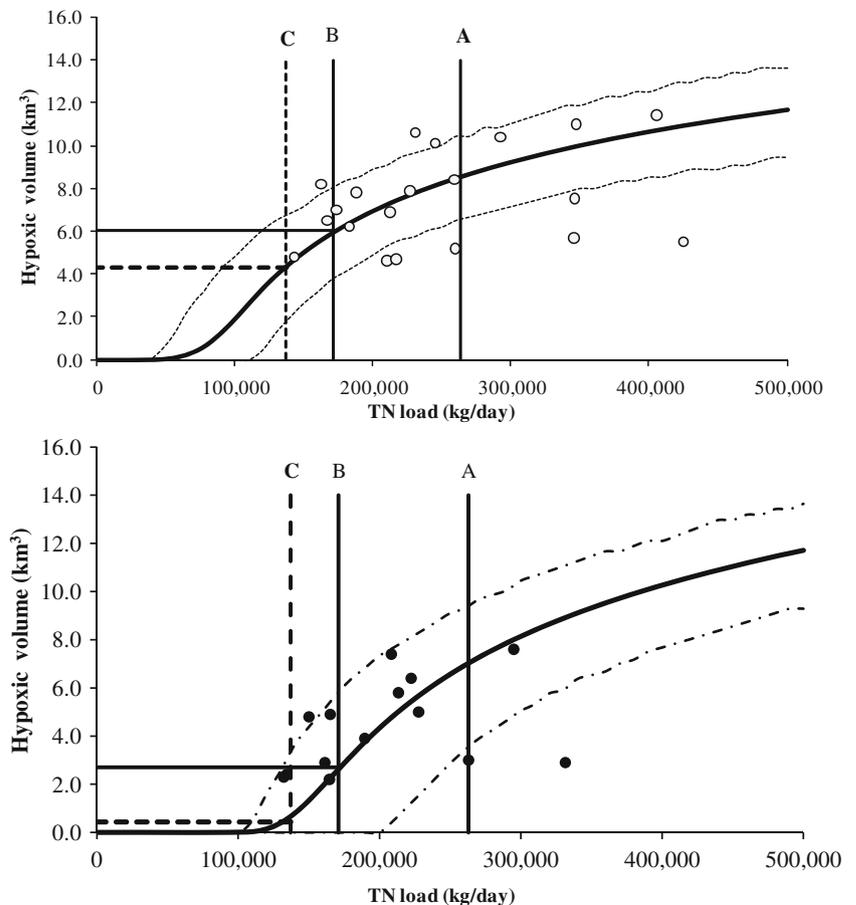
to nutrient loads, the 35% reduction would result in hypoxic volume averaging 6.0 km^3, higher than the target years.

In the Chesapeake Bay Program nutrient load setting process (Koroncai et al. 2003) load reduction level Option 2 was highlighted based on results from models with much more detailed ecological and spatial resolution (Cerco 1995a, b, Linker et al. 2002). This option was projected to reduce the area of bottom water with dissolved oxygen concentrations below 1 mg/L to less than 4% and the volume of water not reaching that attainment goal to less that 7%. These criteria are somewhat different from those used in the present study, but we can compare this scenario with our results. Option 2 includes a total nitrogen load from the Susquehanna River of 75.9 million pounds per year. Approximately 62% of the annual load from the Susquehanna comes in Jan–May, corresponding to 137,115 kg/day, or a 48% reduction from the 1980–1990 average. With this Jan–May load, our model suggests that hypoxic volume (concentrations less than 2 mg/L) would reach 4.3 km^3 under the new regime or 0.4 km^3 under the previous regime. Direct comparisons between our scenarios and those of the more detailed model are complicated by

the fact that theirs was based on 1 mg/L and ours are based on 2 mg/L; however, our projections with a pre-1980 calibration are consistent with those made with the detailed models—virtual elimination of hypoxia. However, our projections using the post-1980 calibration suggest further reductions may be needed to reach Bay goals. It is also worth noting that both measures of efficiency, F and ε, show increasing trends after 1980 (Figs. 1 and 3), and if those trends continue, even further nutrient reductions may be necessary unless action is taken soon. As have been discussed elsewhere (e.g., Scheffer and Carpenter 2003, Kemp and Goldman 2008), hysteresis effects may prevent a return to pre-shift conditions from following a smooth path back through time. Nutrient reductions below those of the past may be required to reset the stage.

Fig. 6 Hypoxic volume vs. Susquehanna River TN load for post-1980s (*top*) and pre-1980s (*bottom*). *Solid curves* represent the predicted means with upper panel for after 1980 and lower for before 1980. *Dashed lines* represent the 95% CI. Open circles represent values after 1980s and solid circle before 1980s. *Vertical solid lines* represent the average river nitrogen load (*Line A*) from 1980 to 1990 (262,881 kg/day) and the 35% reduction (*Line B*). *Line C* represents Option 2 in Koroncai et al. (2003). *Horizontal lines* represent the hypoxic volume corresponding to the reduction

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