

Ecological Forecasting and the Science of Hypoxia in Chesapeake Bay

JEREMY M. TESTA, J. BLAKE CLARK, WILLIAM C. DENNISON, E. CAROLINE DONOVAN, ALEXANDER W. FISHER, WENFEI NI, MATTHEW PARKER, DONALD SCAVIA, SUZANNE E. SPITZER, ANTHONY M. WALDROP, VANESSA M.D. VARGAS, AND GREGORY ZIEGLER

Chronic seasonal low oxygen condition (hypoxia) occurs in the deep waters of Chesapeake Bay as a result of eutrophication-induced phytoplankton blooms and their subsequent decomposition. Summertime hypoxia has been observed in Chesapeake Bay for over 80 years, with scientific attention and understanding increasing substantially during the past several decades after rigorous and routine monitoring programs were put in place. More recently, annual forecasts of the severity of summer hypoxia and anoxia (no oxygen) from simple empirically derived nutrient load-response models have been made. A review of these models over the past decade indicates that they have been generally accurate, with the exception of a few summers when wind events or storms significantly disrupted the water column. Hypoxic and anoxic conditions, as well as their forecasts, have received increased media attention over the past 5 years, contributing to an ongoing public dialogue about Chesapeake Bay restoration progress.

Keywords: dead zone, anoxia, ecological forecast, eutrophication, hypoxia

Ecological forecasting in coastal ecosystems

In the face of changing natural and anthropogenic-driven drivers, predicting future ecosystem states continues to gain increased attention (Clark et al. 2001, Justic et al. 2007, Petchey et al. 2015). Forecasting is driven by a desire to anticipate future states and to inform users about potential ecological impacts of changes in key drivers. Ecological models that produce predictions, projections, or scenarios in lake, coastal, and estuarine systems range, for example, from nowcasts and short-term predictions (days) to mid- and long-term projections. Although the short-term forecasts (e.g., Brown et al. 2013, Wynne et al. 2013, Bertani et al. 2016) generate alerts for public use of waters for drinking, swimming, and shellfish harvesting and to determine sampling needs, they are the exception rather than the rule. They contrast, for example, with the need for scenarios that guide longer-term policy decisions in lakes (Jorgensen 2010) and oceans, including for fisheries (Costantini et al. 2008, Hare et al. 2010, Fulton et al. 2011, Link et al. 2011, Gårdmark et al. 2013, Nye et al. 2013); agriculture (e.g., Fraise et al. 2006); water quality (Komatsu et al. 2007, Scavia et al. 2016); responses to sea-level rise, warming temperatures, and elevated $p\text{CO}_2$ (e.g., Orr et al. 2005, Barange et al. 2014); and a wide range of population-level dynamics at a variety of scales

(McKee et al. 2004, Thuiller et al. 2006). These approaches are useful for making quantitative predictions that can guide water-quality management, conservation, and food security and should benefit from improved treatments of uncertainty and data availability (Clark et al. 2001, Petchey et al. 2015). Here, we focus on the ecological forecasts related to oxygen dynamics.

Beyond their heuristic value, these models are generally used in two modes: *forecast models* are forced by known drivers (e.g., measured nutrient loads or temperature) and used for short-term to seasonal forecasts, whereas *scenario models* are forced by hypothetical drivers (e.g., anticipated temperature or desired nutrient loads) and used for planning purposes. The former produce specific forecasts (e.g., hypoxic volume or species distributions), whereas the latter often produce response curves (e.g., hypoxia versus nutrient load or a distribution map of species). In many cases, the same model can be used in both modes, with routine forecasts providing skill assessments and measures of confidence useful for constraining scenario simulations. These models can also be developed in multiple ways and with varying complexities, including mechanistic, spatially resolved, dynamic biogeochemical models (e.g., Cerco 1995, Fennel et al. 2013, Testa et al. 2014); stochastic models based

on empirical correlations (e.g., Turner et al. 2006); simple biophysical models embedded within statistical frameworks (Evans and Scavia 2011, Obenour et al. 2012); and models that combine spatially resolved, biophysical dynamics and statistical formulations (Bocaniov and Scavia 2016).

Chesapeake Bay has a rich history of ecological modeling, motivated by the need to understand changes in water quality and hypoxia under different hypothetical nutrient-management scenarios. Complex biogeochemical models have played an important role in advising the public policy debate regarding the Bay's response to proposed load reductions and in providing insights into the dynamics behind hypoxia development (Boesch et al. 2001). These coupled hydrodynamic and biogeochemical models have also been used in scenario development (Cercio 1995, Testa et al. 2014) and are the basis of current total maximum daily load (TMDL) targets for nutrient loads to Chesapeake Bay (Wainger 2012). Statistical and hybrid models have also been used to provide ecological forecasts and scenarios (Evans and Scavia 2011) and are valuable because they avoid the complexity and computational requirements of three-dimensional simulations and are inherently constrained by prior long-term observations. Although these simple models provide limited insights into hypoxia dynamics, they are useful in assessing prediction uncertainty and can more readily be transitioned into operational forecasts to be used by management agencies.

Following a rich history of research into factors controlling the dynamics of dissolved oxygen (DO) in Chesapeake Bay, several statistical and hybrid models were developed to forecast summer volumes of hypoxia and anoxia. These models, used routinely since 2007, have supported improved decision-making, increased scientific understanding, and an expanded public awareness. In the pages that follow, we evaluate the performance of the forecasts over the years and associate the forecasts with developments in our understanding of oxygen dynamics, our ability to predict these dynamics in both the present and future, and their role in increasing public and policy awareness.

Chesapeake Bay and eutrophication-induced hypoxia

Chesapeake Bay and its watershed cover an area of approximately 11,000 square kilometers (km²) and 167,000 km², respectively (Kemp et al. 2005), containing parts of Delaware, Maryland, New York, Pennsylvania, Virginia, West Virginia, and the District of Columbia (figure 1). Land-based activities associated with the 18 million watershed residents are major drivers of nutrient input into the Bay, which influences processes within the Bay's deep channel (20–30 meters [m]) and broad, shallow shoals (mean depth of the Chesapeake is approximately 6.5 m). The majority of water and nutrients delivered to Chesapeake Bay derive from the Susquehanna and Potomac Rivers, and these inputs fuel the development of hypoxia every summer in the Bay's main stem and several tributaries. The traditional conceptual model for eutrophication-induced hypoxia involves the input of

nutrients during high winter–spring river flows that cause intense spring water-column algal production and biomass accumulation that sinks to deeper waters, fueling late-spring and summer heterotrophic mineralization of organic matter and associated oxygen depletion (figure 2; Hagy et al. 2004). Winter–spring river flows also increase surface buoyancy that causes water-column stratification in late spring and early summer, insulating bottom waters from oxygen introduced via atmospheric ventilation and phytoplankton production and resulting in strong vertical gradients in oxygen and temperature (figure 2). Thus, interannual variations in river flows and nutrient loads strongly control interannual variations in the severity of oxygen depletion over decadal timescales (Hagy et al. 2004, Li et al. 2016) and have led to hypoxic zones that range from 2.4 to 11.5 cubic kilometers (km³) in midsummer (figure 3), depending on the magnitude of freshwater inputs, nutrient inputs, and wind conditions that may support the physical replenishment of oxygen (figure 2). There are numerous biological and biogeochemical consequences of these depleted oxygen conditions. These include but are not limited to the exclusion of most living organisms from deep-water habitats because of depleted oxygen conditions (Díaz and Rosenberg 2008), altered food-web interactions (Decker et al. 2004), and the predominance of anaerobic respiratory processes in the water column and sediments that produce toxic substances (hydrogen sulfide; Marvin-DiPasquale and Capone 1998) and greenhouse gases (methane; Gelesh et al. 2016). Depleted oxygen conditions are also known to favor the recycling of nutrients that may support additional phytoplankton growth (figure 2; Howarth et al. 2011, Testa and Kemp 2012).

An ever-changing conceptual model

The first observations of Chesapeake Bay hypoxia were made in the lower reaches of the Potomac River 100 years ago (Sale and Skinner 1917) and 20 years later in the central channel of the main stem (Newcombe and Horne 1938). More recent paleoecological studies have revealed that low-oxygen conditions have been a feature of Chesapeake Bay for centuries (Zimmerman and Canuel 2000), dating back to alterations of the landscape by early European colonists. Although this early existence of hypoxia may be surprising to some, the bathymetry and circulation of Chesapeake Bay conspire to naturally encourage oxygen depletion, whereby up-estuary flowing water in the Bay's deep central channel is isolated from the atmosphere for long periods (more than 3 months). This landward-flowing bottom water is overlain by a seaward-flowing surface layer, and the extent to which these layers are separated (i.e., stratification) is enhanced by freshwater inputs, leading early investigators to associate interannual variations in hypoxia to the magnitude of flow from the Susquehanna River and associated reduction in bottom-water aeration (e.g., Taft et al. 1980).

However, after decades of oxygen and hydrographic measurements had accumulated by the mid-1980s, investigators

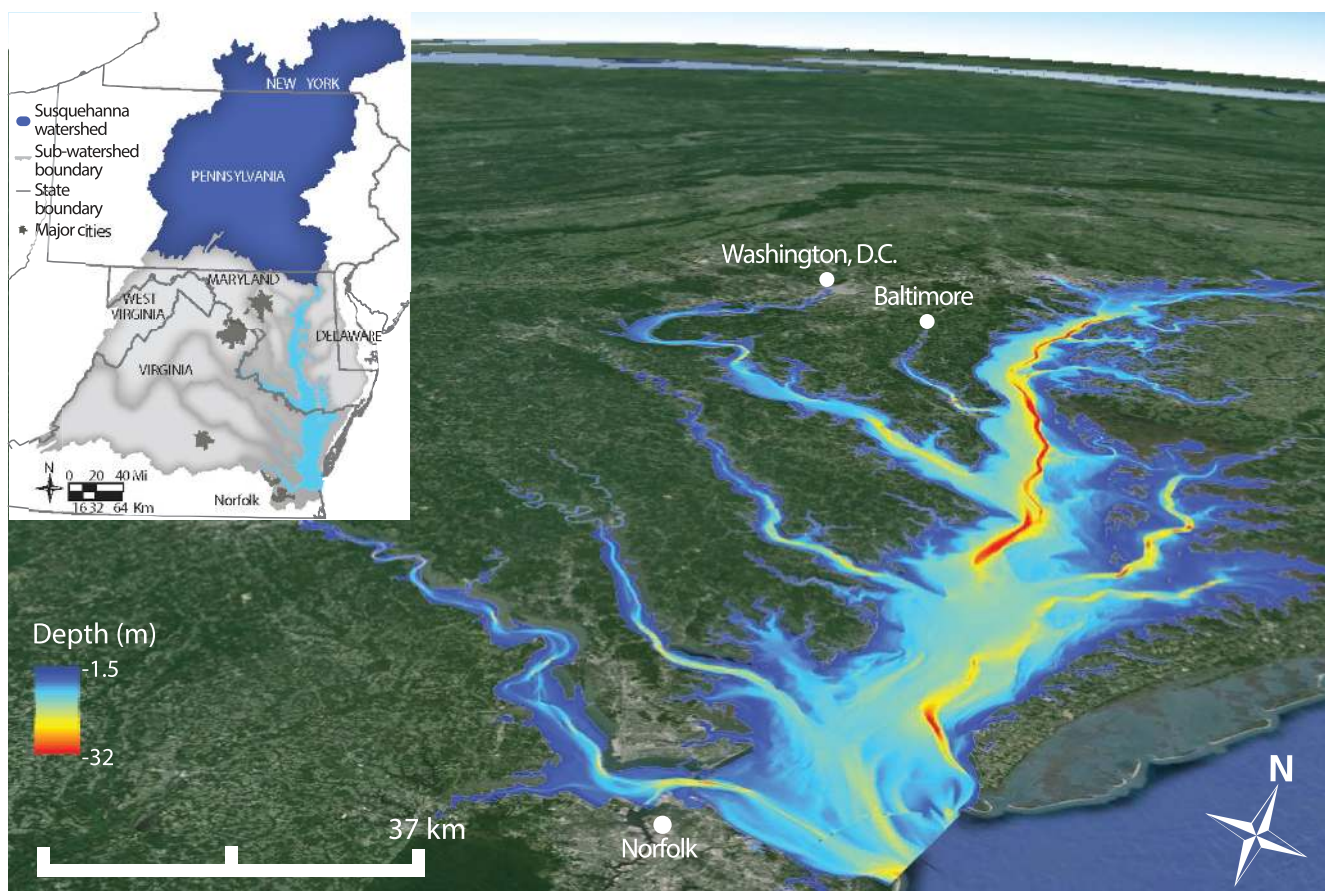


Figure 1. A map of Chesapeake Bay with colors indicating water depth. The inset map highlights the Susquehanna River watershed, which is the primary freshwater and nutrient source to the main stem of Chesapeake Bay. Sources: Satellite map from Google Earth and bathymetry from the National Oceanic and Atmospheric Administration.

began to identify that long-term increases in the extent and severity of low oxygen conditions could not be explained by the physical effects of riverine inputs alone. Nutrient inputs and associated phytoplankton production were identified as causative agents (Officer et al. 1984) at a time when the negative impacts of low-oxygen conditions on the overall function of Chesapeake Bay were being identified (Seliger et al. 1985), including the effects of low oxygen on many key components of the food web (e.g., figure 2; Llanso 1992). During this same period, literature activity related to Chesapeake Bay hypoxia began in earnest, which, interestingly if not coincidentally, corresponded to the expanding hypoxic volumes (figure 4). It was at this time that calls for the restoration of Chesapeake Bay gained steam (e.g., the 1983 Chesapeake Bay Agreement) and the establishment of a Bay monitoring program in 1984 led to the development of data sets that allowed for fortnightly to monthly estimates of Bay-wide hypoxia extent over several decades (1985 through the present). Once these data sets were available in later years, it became increasingly clear that Bay-wide volumes of low-oxygen water displayed the long-term increases associated with eutrophication (Hagy et al. 2004, Li et al. 2016),

despite the complicating effects of the high interannual variability associated with river flow and climatic conditions, such as wind speed and direction.

Increasing interest in the causes and consequences of Chesapeake Bay hypoxia in the ensuing decades led to expanded modeling, retrospective analyses, and further insights, as well as building more complexity into conceptual models of oxygen depletion. During the 1990s, many of the fundamental studies to understand the cycling and dynamics of oxygen and nutrients and their ecological effects took place (e.g., Boicourt 1992, Díaz et al. 1992, Kemp et al. 1992, Cowan and Boynton 1996), giving way to a rapid increase in literature activity and associated breakthroughs in our understanding of the scope of the phenomena (figure 4). Although the effects of wind stress on vertical mixing and oxygen replenishment during strong storms had long been recognized (Goodrich et al. 1987), retrospective analysis coupled with model simulations suggested that both wind speed and direction were important in controlling the magnitude of oxygen replenishment (Scully 2010b). It was also clear from these studies that long-term changes in hypoxia could result from large-scale changes in climate and wind

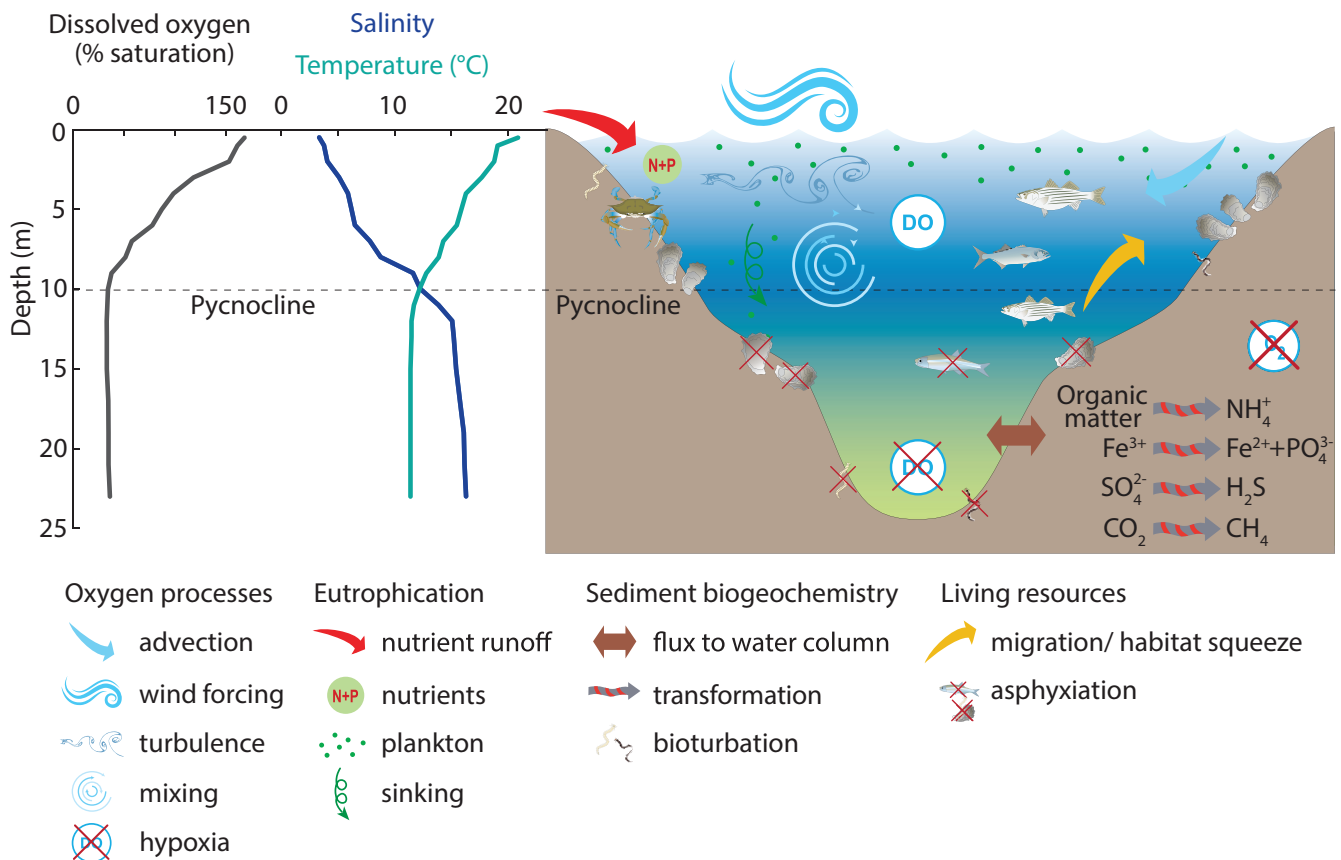


Figure 2. This conceptual diagram of hypoxia extent and ecosystem effects in Chesapeake Bay illustrates how hypoxia is driven by eutrophication and physical forcing while affecting sediment biogeochemistry and living resources. Nutrient runoff from the land leads to a surplus of nitrogen and phosphorus in the water column. Excess nutrients enhance phytoplankton production, which increase vertical carbon flux and associated bottom-water respiration. Advection and wind forcing generate turbulence and altered circulation that can result in elevated mixing of oxygen into deeper waters. Low dissolved oxygen below the pycnocline makes deeper waters unsuitable for many species in the Chesapeake Bay, leading to a habitat squeeze in the water column, where many species are forced to migrate upward (Schlenger et al. 2013). Anoxia also suffocates benthic communities, reducing bioturbation and contributing to a positive feedback loop in which nutrients recycled from organic matter are efficiently released back to the water column (NH_4^+ and PO_4^{3-}) and oxygen-consuming solutes (sulfide, methane) are generated by anaerobic reactions to further enhance anoxia in sediments and the water column. Symbols courtesy of the IAN symbol library (<http://ian.umces.edu/symbols>).

patterns, in addition to changes in nutrient inputs (figure 2; Scully 2010a).

Although much of the research community had quantified hypoxia as a midsummer average volume for decades, it recently became apparent that multidecadal changes in hypoxic volume during the early summer were different from those of later summer and that the primary controlling factors altered seasonally (Murphy et al. 2011, Zhou et al. 2014, Du and Shen 2015). Further examinations of feedback processes associated with oxygen depletion (Testa and Kemp 2012), diverse geochemical processes within anoxic zones (Lee et al. 2015), and fine spatial and temporal scale physical processes (Scully 2016a) brought increased attention to the truly complex nature of the hypoxia problem. Nonlinearities and covariability among the many drivers of

DO in Chesapeake Bay continue to challenge the scientific community to better understand oxygen dynamics.

With new breakthroughs in the mechanistic understanding of hypoxia in this most recent age of discovery, Chesapeake Bay hypoxia forecasts were initiated in 2007 as literature activity expanded after 2009 (figure 4). Accompanying these changes was a large increase in the use of three-dimensional models to analyze oxygen dynamics and biogeochemical process, which both resulted from and contributed to elevated literature activity (Xu and Hood 2006, Testa et al. 2014, Irby et al. 2016, Scully 2016b). Application of these models has led to the first attempts to quantitatively isolate the dominant spatial and temporal drivers of hypoxic volumes (Li et al. 2016, Scully 2016b) while setting the stage for ever-advanced forecasting tools in Chesapeake Bay.

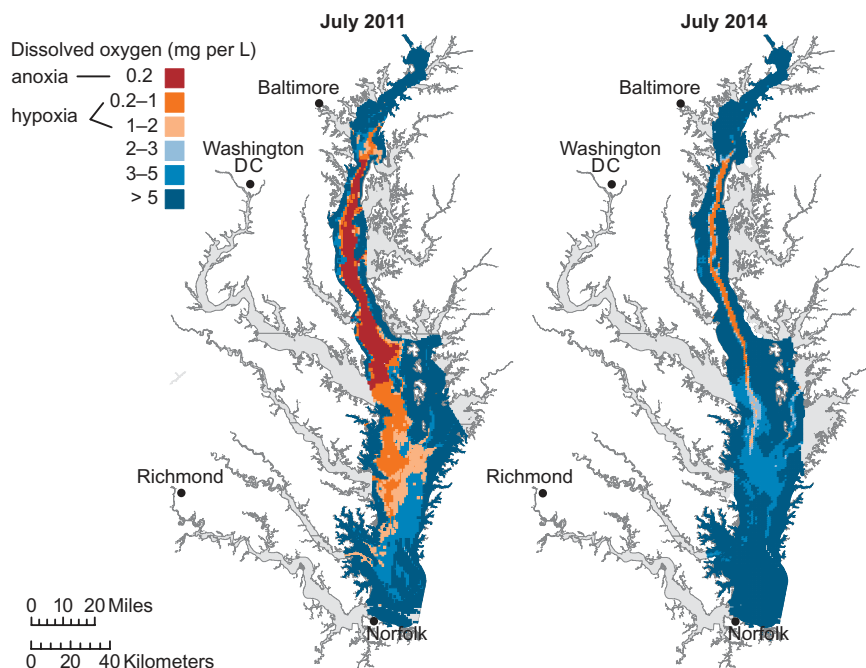


Figure 3. A map of bottom water oxygen concentrations in Chesapeake Bay for two contrasting years, including July 2011 (near-record high hypoxic volume) and July 2014 (near-record low hypoxic volume). The colors corresponding to the oxygen-concentration thresholds used in forecast models are indicated. Abbreviations: L, liters; mg, milligrams.

Forecasting hypoxia in Chesapeake Bay

Decades of monitoring DO and other key water properties resulted in data sets rich enough to develop and test annual forecast models for the volume of hypoxia and anoxia. These forecasts not only gave the public a glimpse into the factors relevant for oxygen dynamics but also established an annual effort whereby scientists could investigate the causes for a particular year's hypoxic volumes by examining forecast successes and failures. These forecasts also brought annual enhanced attention to Chesapeake Bay oxygen depletion, or "dead zone" formation, complementing forecasts in other large ecosystems in the United States (e.g., the Northern Gulf of Mexico and Lake Erie).

The forecasts required a metric representing oxygen conditions throughout a large portion of Chesapeake Bay. Therefore, we estimated a Chesapeake Bay-wide hypoxic and anoxic volume because these volumes integrate the ecosystem-scale extent of low oxygen conditions. Such estimates required interpolation of oxygen concentrations from 30–35 stations to represent the entire main stem of the Bay. Although multiple interpolation methods have been applied in Chesapeake Bay (Hagy et al. 2004, Murphy et al. 2011, Zhou et al. 2014), we interpolated to a two-dimensional length–depth grid using ordinary kriging (as has been described by Murphy et al. 2010, 2011) and calculated the volume of all cells with a DO concentration less than $62.5 \mu\text{M}$ (hypoxia) or less than $6.25 \mu\text{M}$ (anoxia). These volumes were collated with published hypoxic volumes for

Chesapeake Bay computed for a subset of years from 1950 to 1983 using historic cruise data (Hagy et al. 2004).

Three models were used to make predictions of summer hypoxic and anoxic volumes based on January to May nutrient loads and other physical conditions each year. The models were designed (a) to capture differences in the variability of moderately (hypoxia) versus severely (anoxic) oxygen-depleted conditions and (b) to forecast intraseasonal changes in low-oxygen volumes (early summer, midsummer, later summer). Intraseasonal predictions are valuable for understanding differences in hypoxia and anoxia extent in response to seasonally varying physical conditions, sensitivity to spring nutrient loads, alterations of organic matter production and deposition patterns, and long-term trends (Murphy et al. 2011, Lee et al. 2013).

The hypoxia model predicts mean July hypoxic volumes using January to May total nitrogen (TN) loads from the Susquehanna River and is based on an adaptation of the Streeter-Phelps oxygen sag model (Scavia et al. 2006), similar to

one developed for the Gulf of Mexico (Scavia et al. 2004). It simulates organic-matter decay, oxygen flux through the pycnocline, and subpycnocline up-estuary advection as a simple first-order processes. TN loading from the Susquehanna River is used as a surrogate for biological oxygen demand from the decay of phytoplankton biomass, consistent with studies that have shown the middle reaches of Chesapeake Bay are nitrogen limited (Fisher et al. 1992, Cerco 1995, Hagy et al. 2004) and that phytoplankton biomass in the mid-Bay accounts for as much as 90% of the annual organic matter budget of the estuary (Kemp et al. 1997). Using the Susquehanna River loads and the initial oxygen deficit estimated from oxygen measurements, the hypoxic volume forecasts, error bounds, and model coefficients were estimated using Bayesian inference (Stow and Scavia 2009, Evans and Scavia 2011, Liu et al. 2011) for 22 years of data.

The anoxic volume forecasts were based on two models: one that forecasts the June-to-mid-July volume ("early summer") and one that forecasts the mid-July-to-September volume ("late summer"). The models were based on analysis of anoxic volumes as were reported by Murphy and colleagues (2011). The "early summer" model was a multiple linear regression that included January to April Susquehanna and Potomac River TN loads, May Susquehanna River flow, the fraction of hours with southeast winds during March to May (which are a surrogate for May–June winds, because forecasts were typically made in early June), and the annual

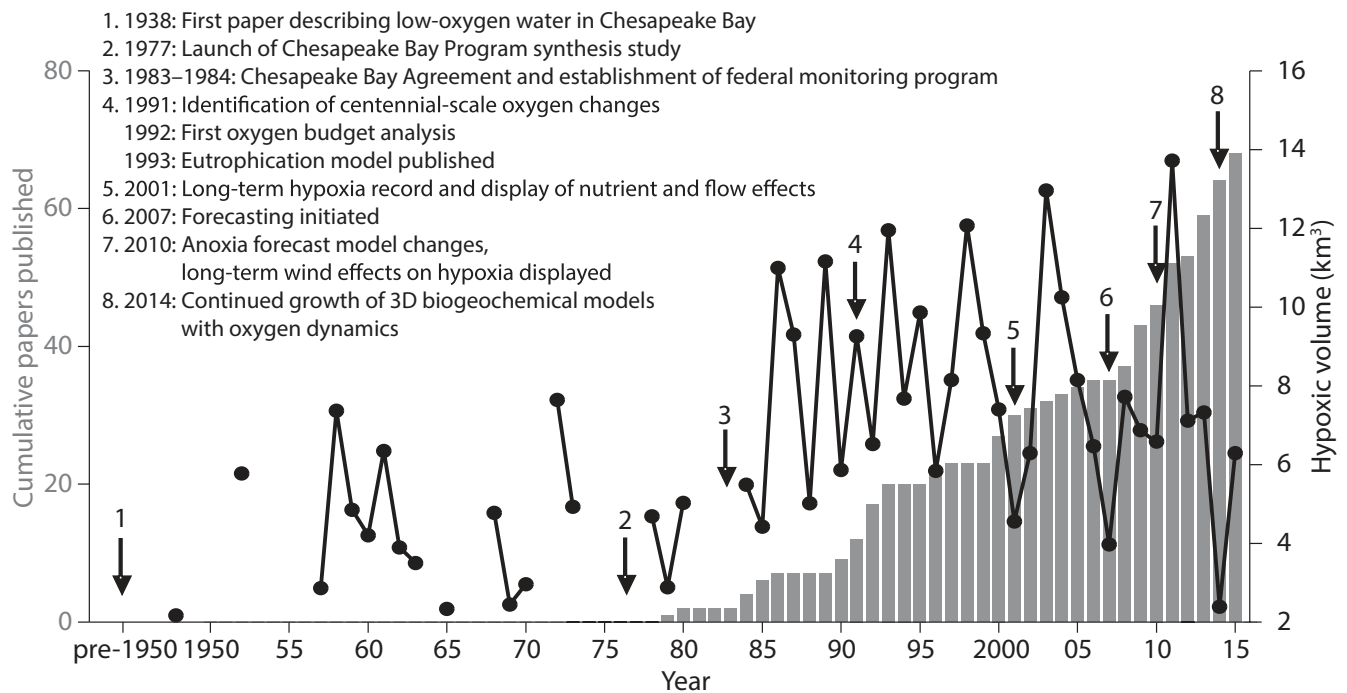


Figure 4. (a) Time series of the average July hypoxic (dissolved oxygen, DO, less than 2 milligrams per liter) volume in Chesapeake Bay (black lines and circles), (b) the cumulative number of peer-reviewed publications that focus on Chesapeake Bay DO and hypoxia (gray bars), and (c) key milestones for Chesapeake Bay watershed management and scientific discovery (list in upper left). The literature search, which included the range of years from 1950 to 2015 using “oxygen OR hypoxia OR anoxia” and the word “Chesapeake” in the title as keywords (Web of Science accessed 15 April 2016), produced 72 positive hits. We removed three references on the basis of a detailed review of the list. Abbreviation: km³, cubic kilometers.

average sea level during the prior year. The “late summer” model was a simple linear regression based on January to May TN loads. Details on these statistical models are available on the Chesapeake hypoxia forecast website (<http://tinyurl.com/zkt6gxz>; <http://ian.umces.edu/ecocheck/forecast/chesapeake-bay/2015>), and we present the regression equations for each forecast below:

$$\text{Anoxic Volume}_{\text{early summer}} = b_0 + b_1(\text{TN Load}_{\text{JA}}) + b_2(\text{RFlow}) + b_3(\text{MSL}) - b_4(\%SE \text{ wind})$$

$$\text{Anoxic Volume}_{\text{late summer}} = b_0 + b_1(\text{TN Load}_{\text{JM}})$$

where $\text{TN Load}_{\text{JA}}$ is the January to April total nitrogen load from the Susquehanna and Potomac Rivers; $\text{TN Load}_{\text{JM}}$ is the January to May total nitrogen load from the Susquehanna River; Rflow is the combined May Susquehanna and Potomac River freshwater flow (<http://waterdata.usgs.gov/md/nwis>); MSL is the mean sea level relative to mean low water measured at Baltimore, Annapolis, Kiptopeke (Virginia), and the Chesapeake Bay Bridge Tunnel (<http://tidesandcurrents.noaa.gov/stations.html?type=Historic+Water+Levels>); and $\%SE \text{ wind}$ is the percentage of winds during March to May that are from the southeast (measured at the Patuxent Naval Air Station; 38.2725°N, 76.4306°W).

Forecast skill assessment

We analyzed the performance of the three forecast models for main-stem predictions made between 2007 and 2015 (figure 5). Forecast performance was at times influenced by unpredictable aspects of summer climatic conditions, such as large precipitation or wind events. We also analyzed summer atmospheric conditions to quantify climatic conditions over the 10-year forecast period. Surface wind, temperature, and pressure measurements from Thomas Point lighthouse near the Chesapeake Bay Bridge were used to calculate 10-m neutral wind conditions following Fairall and colleagues (2003) and Scully (2016a). The adjustment to neutral conditions accounts for any biases in the averaging process that may stem from surface temperature gradients influencing the transfer of momentum from the atmosphere to the estuary. Wind conditions were observed for over 75% of the analysis period (May through July) for all years except 2010. For that year, we filled in data using the highly correlated nearby station (Tolchester Beach, Maryland). The average wind direction was calculated from vector components (east–west, north–south) of the 10-m neutral wind field.

Although hypoxia forecasts accurately captured the substantial year-to-year variability in observed hypoxic volumes (figure 5), overprediction in 2007 and 2014 appears related

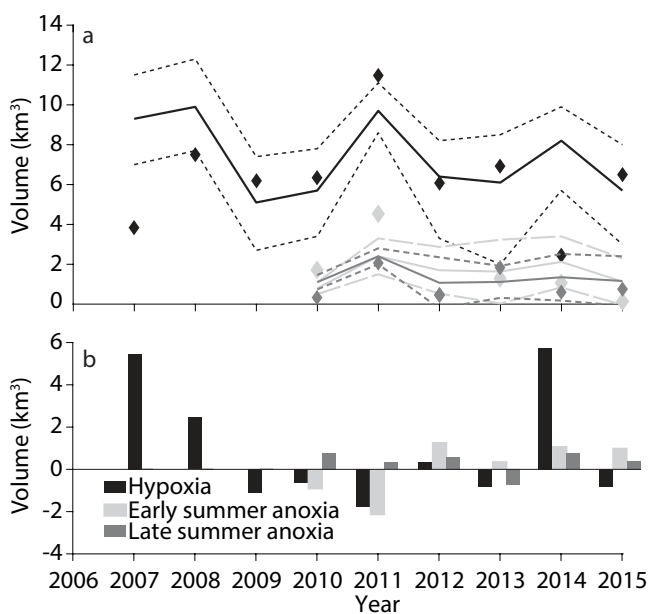


Figure 5. (a) Forecasts for Chesapeake Bay low-oxygen volumes and (b) the associated forecast residuals (modeled–observed). The solid lines represent the forecasted value, the dashed lines represent the 95% confidence interval for each forecast, and the diamonds signify the observed volume for each year. The black diamonds and bars represent July hypoxia, the light-gray diamonds and bars represent early summer anoxia, and the dark-gray diamonds and bars represent late summer anoxia. Abbreviation: km³, cubic kilometers.

to summer tropical storms that disrupted the hypoxic region prior to the measurement cruises. Therefore, 2007 and 2014 stand out from other years because their atypical strong July storms with higher-than-average frequencies of wind speeds above 4 m per second are sufficient to induce substantial vertical mixing. In 2014, Hurricane Arthur made landfall in North Carolina as a category-2 hurricane on 4 July, and strong, persistent winds over subsequent days mixed the water column well beyond that typical of tidal and synoptic wind-driven mixing, resulting in a very low July hypoxic volume (figure 3). In 2007, 15% of the July wind speeds were measured at more than 4 meters per second, which is higher than in any other year in which forecasts were done.

A comparison of hypoxia forecast volume residuals (without 2007 and 2014) with average wind direction observed between May and July shows that surface wind conditions explain a significant fraction of the observed hypoxic volume variance currently unaccounted for in the Scavia and colleagues (2006) model (figure 6). A linear regression explained 76% of the variation in forecast residuals, with southeasterly winds resulting in overpredictions and southwesterly winds resulting in underpredictions (figure 6). This is consistent with the wind-driven straining of the density field described by Scully (2010a). With improvements in extended weather forecasts and increases in the number

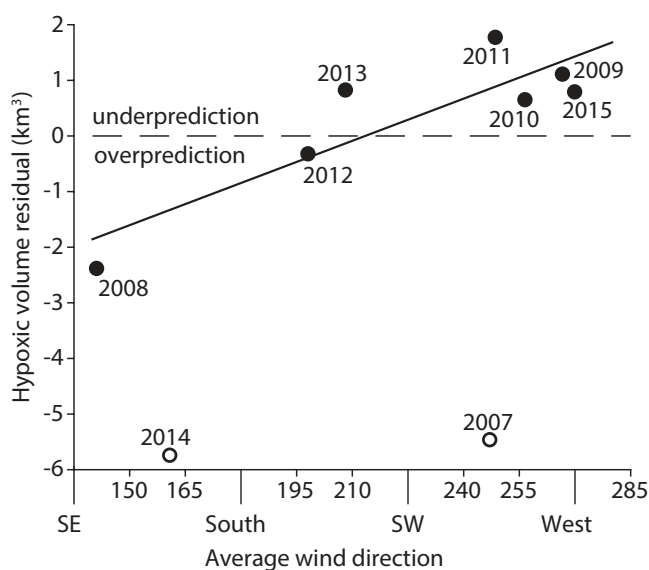


Figure 6. Observed minus forecasted hypoxic volume plotted as a function of the average wind direction observed between May and July (black dots). The black line represents a linear regression with an R^2 value of 0.76 ($p < .01$). Two years, 2007 and 2014 (white dots), were excluded from the analysis because of atypical early-summer conditions.

and types of data used to drive the models, we expect future model improvements by, for example, factoring in summer tropical storm forecasts (<http://tinyurl.com/hyvlsnz>).

The anoxia forecasts also captured much of the variability, although there was substantial overpredicting in some years (e.g., 2014; figure 5). Although the hypoxia forecast had a root mean squared deviation of 2.88 km³, the early summer and late summer anoxia forecasts had a root mean squared deviation of 0.91 and 0.46 km³, respectively, which is proportionately larger than that for hypoxia. Relatively larger errors in the early summer anoxia forecast compared with the late summer forecast are due to the largely missed prediction of the large anoxic volume observed in 2011, which underscores the difficulty in predicting a volume that varies substantially from year to year under the control of alternative causative forces. In contrast, the late summer anoxic volumes tended to be smaller than predicted in recent years (figure 5), which corresponds to a long-term decline in anoxic volume during this period of the summer (figure 7). Although this anoxia decline may be associated with modest reductions in winter–spring nutrient loading from the Susquehanna River, as have been recently observed (Harding et al. 2015), anoxic volumes appear to be declining faster than expected from nitrogen loading and therefore from the forecast models (figure 7), highlighting the need for new investigations to understand these long-term patterns and improve the summer anoxia forecasting tools.

Although current management recommendations for the Bay were put in place prior to the development of these

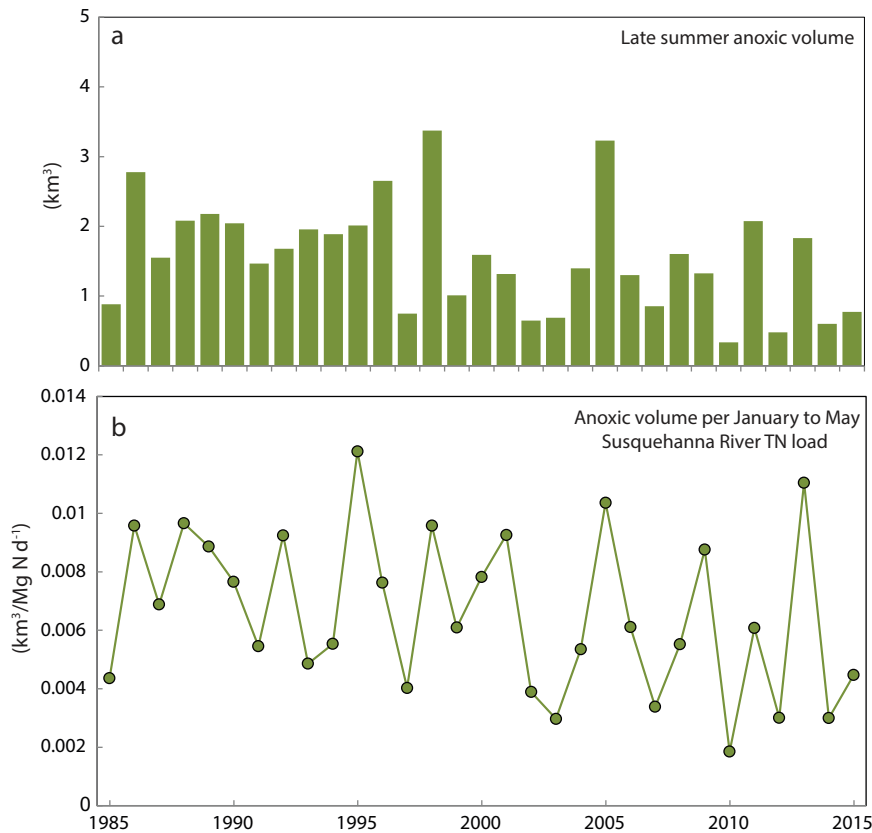


Figure 7. (a) Time series (1985–2015) of late summer (late July–September) anoxic volume in Chesapeake Bay. (b) Late summer anoxic volume generated per unit January to May Susquehanna River total nitrogen load to Chesapeake Bay. Abbreviations: km³, cubic kilometers; Mg, megagrams.

simple models, their use in future reassessments could be powerful. As such, the relative success of these annual forecasts (figure 6), perhaps with modest improvements (figure 5), builds confidence in their use in scenario mode to complement existing models used to generate nutrient loading targets for Chesapeake Bay (Cercio 1995). For some ecosystems, forecast models similar to those discussed here (simple to more complex) are indeed being used to help set nutrient-loading targets for the Northern Gulf of Mexico (Evans and Scavia 2011) and Lake Erie (Scavia et al. 2016). The disadvantages of using simple forecast models include the fact that they only represent a fraction of the known controlling variables for hypoxia, they are limited to prediction within the range of observed data, and they generate predictions for periods that are months into the future and therefore have unknown climatic conditions. However, the clear advantages of these models are that they accurately reproduce the features they were designed to address, are computationally inexpensive, are mathematically simple, and can leverage the wealth of long-term data that has been collected to better understand the controls on key ecological problems. In addition, because they show substantial skill in capturing the relatively large changes in annual low-oxygen conditions, they have increased public attention around the

hypoxia problem while providing new insights into the relative contribution of different external controls (e.g., wind and sea level).

Media coverage link to forecasts

Following the initiation of the Chesapeake Bay hypoxia forecasts, media activity related to hypoxia increased substantially (figure 8). Both Chesapeake Bay hypoxia online news articles and articles mentioning the forecasts increased substantially since the start of forecasting in 2007 (figure 8), with articles mentioning forecasts making up 43%, 41%, and 56% of all articles related to Chesapeake Bay hypoxia in 2013, 2014, and 2015, respectively. One of the goals of providing these annual forecasts, in addition to increasing scientific understanding and potential guidance, is to raise public and political awareness of the problem. These results indeed show a marked increase in visibility for the issue of Chesapeake Bay hypoxia and corresponding ecological forecasts. Although we cannot conclude that the forecasts were the primary driver of this increase in media attention (e.g., President Obama's 2009 executive order for Chesapeake Bay restoration), the contribution of these forecasts is clear, especially in the past few years given the increased number

of media articles that specifically mention the forecasts.

Another key value of forecasts is their ability to communicate the complex ecology of the Bay in a simplified way. Early printed newsletters to explain the forecasts evolved into accessible interactive websites and electronic communications that supplemented press releases from the participating state and federal agencies. Our hypoxic and anoxic volume forecasts were publicized in June of each year through press releases arranged by the US National Oceanic and Atmospheric Administration, the University of Michigan (U-M), and the University of Maryland Center for Environmental Science (UMCES). Press releases were supplemented by websites maintained by U-M and UMCES (<http://tinyurl.com/zkt6gxz>) that explained ecological issues associated with hypoxia and anoxia, described the forecast methodologies, and provided annual reviews to evaluate any unexpected factors causing the forecasts to deviate from the observed volumes. These annual updates provided platforms to discuss new discoveries related to controls on oxygen depletion (e.g., long-term decline in later summer anoxia) while allowing for continuous improvement of the forecast modeling tools.

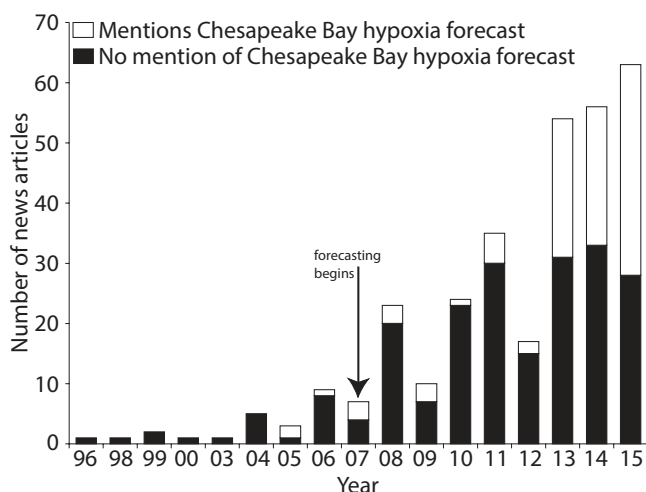


Figure 8. The number of online news articles published each year that mention Chesapeake Bay hypoxia. Each year is split into articles that mention Chesapeake Bay hypoxia forecasting (white) and articles that do not mention forecasting (black). Google News searches of articles published between 1 January 1950 and 31 December 2015 that included the phrase “Chesapeake Bay hypoxia” (or “dead zone” or “low-oxygen”) were performed and then augmented by Google searches on “Chesapeake Bay hypoxia news” to generate a time course of new articles after removing duplicates.

The challenges ahead for forecasting efforts

The enduring need for quantitative tools to predict future ecosystem states within highly complex and ever-changing natural systems challenges the scientific community to build ever-improving forecast models. Prospects of increasing anthropogenic pressures and a dynamic, altered global climate system underscore the difficulty in making such predictions. We do not propose that the future of forecasting is dire (rather the opposite), but we wish to highlight some particular challenges to the specific problem of forecasting hypoxia.

Weather and climate-change impacts. Local and regional weather influence the ability to make seasonal forecasts because once nutrient and freshwater inputs have established the potential for hypoxia and anoxia (which we forecast), subsequent wind stress can affect oxygen distributions and replenishment (figure 2). Although river-flow induced stratification and nutrient load are highly correlated with hypoxic volumes at decadal scales (Hagy et al. 2004) and serve as the basis for seasonal hypoxia forecasts, the wind speeds and directions during summer are key secondary variables explaining interannual variability in hypoxia and anoxic volumes (figure 6). Elevated wind speeds can replenish bottom-water oxygen through the turbulent downward vertical mixing of oxygen (Blumberg and Goodrich 1990); however, more subtle circulation responses to both wind speed and

direction can also either suppress or enhance the mixing of deep waters with oxygenated surface waters both vertically and laterally (Scully 2010b).

Although these weather dynamics could potentially be accommodated in future seasonal forecasts, their long-term trends are driven by climate change and are therefore likely to influence longer-term scenarios. Temperature increases, changes in precipitation patterns, altered wind conditions, and water-level changes are potential consequences of climate change for coastal and Great Lakes ecosystems (Johnson et al. 2016). These large-scale phenomena may contribute to changes in the availability of oxygen and biological oxygen consumption, which determine the occurrence and severity of hypoxia (Díaz and Rosenberg 2008). Climatic changes will affect scenarios by creating a new range of conditions that are outside the range of data used to create the models. Climate changes may also increase the importance of variables or processes that were previously unimportant (e.g., marsh erosion) or lead to long-term changes in conditions (e.g., winds) that cannot be accurately predicted by the forecast models. Given that geological analyses and more modern measurements have highlighted the role of climate in altering hypoxia via changes in sea level, temperature, freshwater inputs, and changes in wind (Justic et al. 1996, Grantham et al. 2004, Zillen et al. 2008), the potential for a changing climate to affect long-term forecasting of hypoxia and other ecosystem and food-web processes (Ihde et al. 2016) is high.

In Chesapeake Bay specifically, climatic changes present a challenge to forecasting given the system’s sensitivity to many biological and physical forces. Johnson and colleagues (2016) and Najjar and colleagues (2010) reviewed a range of model projections for future climates in Chesapeake Bay, which generally suggest increases in water temperature, precipitation, and sea level over the next century, although the magnitude and seasonality of these changes remain uncertain. Generally, warmer temperatures would reduce the oxygen concentration in the water, enhance the stratification in summer, and increase the metabolic rate of microbes and other living organisms. Sea-level rise will deepen the main channel, which may allow salt intrusion and stronger stratification but may also increase tidal mixing. All of these factors would lead to more severe summer hypoxia and anoxia in Chesapeake Bay than would otherwise be predicted. In recent decades, the unusual climate variability of the Chesapeake Bay watershed influenced the timing and amount of river inflow, which is a key determinant of the timing of hypoxia onset (Testa and Kemp 2014), suggesting that the seasonality of hypoxia might also be sensitive to climate. Many large-scale climatic cycles are associated with interannual changes in Chesapeake Bay hypoxia via their effects on precipitation and wind variability, including El Niño and the North Atlantic Oscillation (Muller and Muller 2015, Scully 2010a). The Chesapeake Bay ecosystem is physically and biologically complex; therefore, ecological responses to nutrient load and river runoff changes may

be nonlinear (Li et al. 2009, Testa et al. 2014). Nonlinear responses are difficult to predict, increasing the difficulty in producing accurate long-term forecasting of summer hypoxic volume in Chesapeake Bay, especially in the face of climate change.

Other nutrient sources. Although recent analyses have suggested a modest decline in nitrogen loads from the Susquehanna River (Murphy et al. 2011, Harding et al. 2015), there are other sources of nitrogen to Chesapeake Bay. Although these models are driven by loads from the Susquehanna and Potomac basins that represent approximately 70% of the total watershed TN load, loads from other tributaries and the atmosphere may be important (Eshleman et al. 2013, Zhou et al. 2014). The storage of legacy nutrients in groundwater will likely lead to delayed nutrient inputs to the estuary, although the duration of this delay (years to decades) is dependent on the local hydrology and land-use history (e.g., Sanford and Pope 2013). Internal recycling can also be a significant short-term nutrient source (Howarth et al. 2011). Sediments host a variety of microbial mediated redox reactions in anaerobic (anoxic) conditions that tend to enhance the production and release to the overlying water of ammonium (NH_4^+), hydrogen sulfide (H_2S), and phosphate (PO_4^{3-}), further exacerbating low oxygen both directly and indirectly (e.g., figure 2; Testa and Kemp 2012). One consequence of this is that the establishment of anoxia may lead to nutrient transformations that lead to the maintenance or expansion of anoxic or hypoxic conditions, with the most significant impact being delays in the response of the Bay to changes in external loads.

Conclusions

Chesapeake Bay has a long history of scientific research related to understanding the dynamics of low-oxygen conditions that has rapidly grown in scope and magnitude over the past several decades. The conceptual model of hypoxia and anoxia in Chesapeake Bay has grown in complexity during this time but has also been refined to reflect an ever-improving understanding of the various controls on and feedback loops associated with oxygen depletion. Forecasts of summer hypoxic and anoxic volumes were made possible by the understanding that was developed over past decades, and these forecasts have stimulated increased public attention toward the problem and will continue to instigate new research questions for decades to come.

It is interesting to note that significant advances in the understanding and modeling of hypoxia and its controls (highlighted by a rapid increase in the literature) appeared to occur decades after monitoring investments began. Whereas the Chesapeake Bay monitoring program was initiated in the mid-1980s, the scientific understanding and data to support the development of hypoxia forecast models did not accumulate until the mid-2000s. Indeed, the majority of insights related to controls on hypoxia and its biogeochemical effects

were made as a result of direct analysis of monitoring data (Hagy et al. 2004, Murphy et al. 2011, Testa and Kemp 2014) or via the application of models that relied heavily on monitoring data (Scully 2010a, Zhou et al. 2014, Li et al. 2016). In the modern era of stagnant or declining support for monitoring programs, these findings highlight the need for the maintenance of long-term monitoring programs and the fact that the large increases in publications, scientific understanding, and policy advice that occurred decades after the program began were only possible because of it. Similar themes have played out in other well-monitored systems worldwide (Wilson et al. 2008, Tucker et al. 2014, Riemann et al. 2015).

Because the primary goal of seasonal forecasts is to inform potential ecosystem users, the continual improvement of those forecasts is important. We envision that ecological forecasts will continue to embrace the “multiple-model” approach, which is already common in developing climate and hurricane projections and increasingly common in natural-resource issues (Bierman et al. 1980, Stow et al. 2003, Scavia et al. 2004, Weller et al. 2013, Scavia et al. 2016). The benefits, especially during the early stages of ecological forecast development, include viewing problems from different conceptual and operational perspectives, using common data sets in different ways, providing multiple lines of evidence, and reducing decision risk on the basis of a diversity of perspectives.

We have found that communicating forecasts in a clear and consistent manner using visualizations and narratives of forecasts has been especially valuable in drawing attention to the forecasts and gaining new scientific insights from forecast assessment. Finally, in the specific case of DO forecasts, we expect that the increasing use of three-dimensional hydrodynamic–biogeochemical models will allow for the development of shorter-term forecasts that will be of great use to end users because they provide spatially explicit maps of expected low DO conditions. Such forecasts would also allow for the forecasting of hypoxia associated with the rapid cycling of DO in shallow (less than 5 m) estuarine environments over timescales of hours or days (e.g., Tyler et al. 2009), which can have acute ecological effects in shallow coastal ecosystems (Luther et al. 2004). Current projects comparing multiple biogeochemical models are testing the best methodology for operational predictions (Irby et al. 2016), and a forecast product using some version of a mechanistic biogeochemical model is imminent.

Acknowledgments

We would like to recognize Rebecca Murphy for her contributions to the anoxia forecasting process included as part of this effort. We also thank the multiple federal and state agencies that have been instrumental in collecting the data, funding research, and supporting forecast efforts in the Chesapeake Bay. These agencies include the Maryland Department of Natural Resources, the US National Oceanic

and Atmospheric Administration, the US Environmental Protection Agency Chesapeake Bay Program, the United States Geological Survey, the National Science Foundation, and many others. All data presented in this manuscript are available on publically available websites managed by the representative agencies. We are grateful to Walter Boynton for providing insightful comments on an early version of this manuscript. This work was partially supported by grants from the US National Oceanic and Atmospheric Administration, including nos. NA12OAR4320071 and NA07NOS4780191 (CSCOR), the US National Science Foundation (no. CBET1360415), and the University of Michigan Graham Sustainability Institute. This paper was developed initially by a graduate class entitled “Ecological Forecasting in Practice” (MEES 708L) in the University of Maryland Marine–Estuarine Environmental Sciences Graduate Program. This is contribution no. 5319 to the University of Maryland Center for Environmental Sciences and CHRP publication no. 216.

References cited

- Barange M, Merino G, Blanchard JL, Scholtens J, Harle J, Allison EH, Allen JI, Holt J, Jennings S. 2014. Impacts of climate change on marine ecosystem production in societies dependent on fisheries. *Nature Climate Change* 4: 211–216.
- Bertani I, Obenour DR, Steger CE, Stow CA, Gronewold AD, Scavia D. 2016. Probabilistically assessing the role of nutrient loading in harmful algal bloom formation in western Lake Erie. *Journal of Great Lakes Research* 42: 1184–1192.
- Bierman VJ, Dolan DM, Stoermer EF, Gannon JE, Smith VE, Commission GLB. 1980. Development and Calibration of a Spatially Simplified Multi-Class Phytoplankton Model for Saginaw Bay, Lake Huron: Great Lakes Environmental Planning Study. Great Lakes Basin Commission.
- Blumberg AF, Goodrich DM. 1990. Modeling of wind-induced destratification in Chesapeake Bay. *Estuaries* 13: 236–249.
- Bocaniov SA, Scavia D. 2016. Temporal and spatial dynamics of large lake hypoxia: Integrating statistical and three-dimensional dynamic models to enhance lake management criteria. *Water Resources Research* 52: 4247–4263. doi:10.1002/2015WR018170
- Boesch DF, Brinsfield RB, Magnien RE. 2001. Chesapeake Bay eutrophication: Scientific understanding, ecosystem resotration, and challenges for agriculture. *Journal of Environmental Quality* 30: 303–320.
- Boicourt WC. 1992. Influences of circulation processes on dissolved oxygen in the Chesapeake Bay. Pages 7–59 in Smith DE, Leffler M, Mackiernan G, eds. *Oxygen Dynamics in the Chesapeake Bay: A Synthesis of Recent Research*. Maryland Sea Grant College.
- Brown CW, Hood RR, Long W, Jacobs J, Ramers DL, Wazniak C, Wiggert JD, Wood R, Xu J. 2013. Ecological forecasting in Chesapeake Bay: Using a mechanistic–empirical modeling approach. *Journal of Marine Systems* 125: 113–125.
- Cerco CF. 1995. Simulation of long-term trends in Chesapeake Bay eutrophication. *Journal of Environmental Engineering* 121: 298–310.
- Clark JS, et al. 2001. Ecological forecasts: An emerging imperative. *Science* 293: 657–660.
- Costantini M, Ludsins SA, Mason DM, Zhang X, Boicourt WC, Brandt SB. 2008. Effect of hypoxia on habitat quality of striped bass (*Morone saxatilis*) in Chesapeake Bay. *Canadian Journal of Fisheries and Aquatic Sciences* 65: 989–1002.
- Cowan JL, Boynton WR. 1996. Sediment–water oxygen and nutrient exchanges along the longitudinal axis of Chesapeake Bay: Seasonal patterns, controlling factors and ecological significance. *Estuaries* 19: 562–580.
- Decker MB, Breitbart DL, Purcell JE. 2004. Effects of low dissolved oxygen on zooplankton predation by the ctenophore *Mnemiopsis leidyi*. *Marine Ecology Progress Series* 280: 163–172.
- Díaz RJ, Rosenberg R. 2008. Spreading dead zones and consequences for marine ecosystems. *Science* 321: 926–929.
- Díaz RJ, Neubauer RJ, Schaffner LC, Pihl L, Baden SP. 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 Supplement* 1: 1055–1068.
- Du J, Shen J. 2015. Decoupling the influence of biological and physical processes on the dissolved oxygen in the Chesapeake Bay. *Journal of Geophysical Research: Oceans* 120: 78–93.
- Eshleman KN, Sabo RD, Kline KM. 2013. Surface water quality is improving due to declining atmospheric N deposition. *Environmental Science and Technology* 47: 12193–12200.
- Evans MA, Scavia D. 2011. Forecasting hypoxia in the Chesapeake Bay and Gulf of Mexico: Model accuracy, precision, and sensitivity to ecosystem change. *Environmental Research Letters* 6 (art. 015001).
- Fairall CW, Bradley EF, J.E.Hare, Grachev AA, Edson JB. 2003. Bulk parameterization of air–sea fluxes: Updates and verification for the COARE algorithm. *Journal of Climate* 16: 571–591.
- Fennel K, Hu J, Laurent A, Marta-Almeida M, Hetland R. 2013. Sensitivity of hypoxia predictions for the Northern Gulf of Mexico to sediment oxygen consumption and model nesting. *Journal of Geophysical Research: Oceans* 118: 990–1002.
- Fisher TR, Peele ER, Ammerman JW, L.W. Harding J. 1992. Nutrient limitation of phytoplankton in Chesapeake Bay. *Marine Ecology Progress Series* 82: 51–63.
- Fraisse CW, Breuer NE, Zierden D, Bellow JG, Paz J, Cabrera VE, Garcia y Garcia A, Ingram KT, Hatch U, Hoogenboom G. 2006. AgClimate: A climate forecast information system for agricultural risk management in the southeastern USA. *Computers and Electronics in Agriculture* 53: 13–27.
- Fulton EA, et al. 2011. Lessons in modelling and management of marine ecosystems: The Atlantis experience. *Fish and Fisheries* 12: 171–188.
- Gårdmark A, et al. 2013. Biological ensemble modeling to evaluate potential futures of living marine resources. *Ecological Applications* 23: 742–754.
- Gelesh L, Marshall K, Boicourt WC, Lapham L. 2016. Methane concentrations increase in bottom waters during summertime anoxia in the highly eutrophic estuary, Chesapeake Bay, USA. *Limnology and Oceanography* 61: S253–S266.
- Goodrich DM, Boicourt WC, Hamilton P, Pritchard DW. 1987. Wind-induced destratification in Chesapeake Bay. *Journal of Physical Oceanography* 17: 2232–2240.
- Grantham BA, Chan F, Nielsen KJ, Fox DS, Barth JA, Huyer A, Lubchenco J, Menge BA. 2004. Upwelling-driven nearshore hypoxia signals ecosystem and oceanographic changes in the northeast Pacific. *Nature* 429: 749–754.
- Hagy JD, Boynton WR, Keefe CW, Wood KV. 2004. Hypoxia in Chesapeake Bay, 1950–2001: Long-term change in relation to nutrient loading and river flow. *Estuaries* 27: 634–658.
- Harding LW, Gallegos CL, Perry ES, Miller WD, Adolf JE, Mallonee ME, Paerl HW. 2015. Long-term trends of nutrients and phytoplankton in Chesapeake Bay. *Estuaries and Coasts* 39: 664–681.
- Hare JA, Alexander MA, Fogarty MJ, Williams EH, Scott JD. 2010. Forecasting the dynamics of a coastal fishery species using a coupled climate–population model. *Ecological Applications* 20: 452–464.
- Howarth R, Chan F, Conley DJ, Garnier J, Doney SC, Marino R, Billen G. 2011. Coupled biogeochemical cycles: Eutrophication and hypoxia in temperate estuaries and coastal marine ecosystems. *Frontiers in Ecology and the Environment* 9: 18–26.
- Ihde TF, Kaplan IC, Fulton EA, Gray IA, Hasan M, Bruce D, Slacum W, Townsend HM. 2016. Design and Parameterization of the Chesapeake Bay Atlantis Model: A Spatially Explicit End-to-End Ecosystem Model. US Department of Commerce, National Oceanic and Atmospheric Administration. Technical Memorandum no. NMFS-F/SPO-166.

- Irby ID, et al. 2016. Challenges associated with modeling low-oxygen waters in Chesapeake Bay: A multiple model comparison. *Biogeosciences* 13: 2011–2028.
- Johnson Z, Bennett M, Linker L, Julius S, Najjar R, Mitchell M, Montali D, Dixon R. 2016. The Development of Climate Projections for Use in Chesapeake Bay Program Assessments. Scientific and Technical Advisory Committee (STAC), Chesapeake Bay Program. STAC Publication no. 16-006.
- Justic D, Rabalais NN, Turner RE. 1996. Effects of climate change on hypoxia in coastal waters: A doubled CO₂ scenario for the northern Gulf of Mexico. *Limnology and Oceanography* 41: 992–1003.
- Justic D, Bierman VJ, Scavia D, Hetland RD. 2007. Forecasting Gulf's hypoxia: The next 50 years? *Estuaries and Coasts* 30: 791–801.
- Kemp WM, Sampou PA, Garber J, Tuttle J, Boynton WR. 1992. Seasonal depletion of oxygen from bottom waters of Chesapeake Bay: Roles of benthic and planktonic respiration and physical exchange processes. *Marine Ecology Progress Series* 85: 137–152.
- Kemp WM, Smith EM, Marvin-DiPasquale M, Boynton WR. 1997. Organic carbon balance and net ecosystem metabolism in Chesapeake Bay. *Marine Ecology Progress Series* 150: 229–248.
- Kemp WM, et al. 2005. Eutrophication of Chesapeake Bay: Historical trends and ecological interactions. *Marine Ecology Progress Series* 303: 1–29.
- Komatsu E, Fukushima T, Harasawa H. 2007. A modeling approach to forecast the effect of long-term climate change on lake water quality. *Ecological Modelling* 209: 351–366.
- Lee DY, Owens MS, Doherty M, Eggleston EM, Hewson I, Crump BC, Cornwell JC. 2015. The effects of oxygen transition on community respiration and potential chemoautotrophic production in a seasonally stratified anoxic estuary. *Estuaries and Coasts* 38: 104–117.
- Lee YJ, Boynton WR, Li M, Li Y. 2013. Role of late winter–spring wind influencing summer hypoxia in Chesapeake Bay. *Estuaries and Coasts* 36: 683–696.
- Li M, Zhong L, Harding LW. 2009. Sensitivity of plankton biomass and productivity to variations in physical forcing and biological parameters in Chesapeake Bay. *Journal of Marine Research* 67: 667–700.
- Li M, Lee YJ, Testa JM, Li Y, Ni W, Kemp WM, Toro DMD. 2016. What drives interannual variability of estuarine hypoxia: Climate forcing versus nutrient loading? *Geophysical Research Letters* 43: 2127–2134.
- Link JS, Nye JA, Hare JA. 2011. Guidelines for incorporating fish distribution shifts into a fisheries management context. *Fish and Fisheries* 12: 461–469.
- Liu Y, Arhonditsis GB, Stow C, Scavia D. 2011. Comparing Chesapeake Bay hypoxic-volume and dissolved-oxygen profile predictions with a Bayesian Streeter-Phelps model. *Journal of the American Water Resources Association* 47: 1348–1363.
- Llanos RJ. 1992. Effects of hypoxia on estuarine benthos: The Lower Rappahannock River (Chesapeake Bay), a case study. *Estuarine, Coastal, and Shelf Science* 35: 491–515.
- Luther GW, Ma S, Trouwborst R, Glazer B, Blickley M, Scarborough RW, Mensinger MG. 2004. The roles of anoxia, H₂S, and storm events in fish kills of dead-end canals of Delaware inland bays. *Estuaries* 27: 551–560.
- Marvin-DiPasquale MC, Capone DG. 1998. Benthic sulfate reduction along the Chesapeake Bay central channel. I. Spatial trends and controls. *Marine Ecology Progress Series* 168: 213–228.
- McKee JK, Sciuilli PW, Focce CD, Waite TA. 2004. Forecasting global biodiversity threats associated with human population growth. *Biological Conservation* 115: 161–164.
- Muller AC, Muller DL. 2015. Forecasting future estuarine hypoxia using a wavelet based neural network model. *Ocean Modelling* 96: 314–323.
- Murphy RR, Curriero FC, Ball WP. 2010. Comparison of spatial interpolation methods for water quality evaluation in the Chesapeake Bay. *Journal of Environmental Engineering* 136: 160–171.
- Murphy RR, Kemp WM, Ball WP. 2011. Long-term trends in Chesapeake Bay seasonal hypoxia, stratification, and nutrient loading. *Estuaries and Coasts* 34: 1293–1309.
- Najjar RG, Pyke CR, Adams MB, Breitbart D, Hershner C, Kemp M, Howarth R, Mulholland MR, Paolisso M, Secor D. 2010. Potential climate-change impacts on the Chesapeake Bay. *Estuarine, Coastal and Shelf Science* 86: 1–20.
- Newcombe CL, Horne WA. 1938. Oxygen-poor waters of the Chesapeake Bay. *Science* 88: 80–81.
- Nye JA, Gamble RJ, Link JS. 2013. The relative impact of warming and removing top predators on the Northeast US large marine biotic community. *Ecological Modelling* 264: 157–168.
- Obenour DR, Michalak AM, Zhou Y, Scavia D. 2012. Quantifying the impacts of stratification and nutrient loading on hypoxia in the Northern Gulf of Mexico. *Environmental Science and Technology* 46: 5489–5496.
- Officer CB, Biggs RB, Taft JL, Cronin E, Tyler MA, Boynton WR. 1984. Chesapeake Bay anoxia: Origin, development and significance. *Science* 223: 22–27.
- Orr JC, et al. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437: 681–686.
- Petchey OL, et al. 2015. The ecological forecast horizon, and examples of its uses and determinants. *Ecology Letters* 18: 597–611.
- Riemann B, et al. 2015. Recovery of Danish coastal ecosystems after reductions in nutrient loading: A holistic ecosystem approach. *Estuaries and Coasts* 39: 82–97.
- Sale JW, Skinner WW. 1917. The vertical distribution of dissolved oxygen and the precipitation by salt water in certain tidal areas. *Journal of the Franklin Institute* 184: 837–848.
- Sanford WE, Pope JP. 2013. Quantifying groundwater's role in delaying improvements to Chesapeake Bay water quality. *Environmental Science and Technology* 47: 13330–13338.
- Scavia D, Justic D, Bierman VJ. 2004. Reducing hypoxia in the Gulf of Mexico: Advice from three models. *Estuaries and Coasts* 27: 419–425.
- Scavia D, Kelly ELA, Hagy JD. 2006. A simple model for forecasting the effects of nitrogen loads on Chesapeake Bay hypoxia. *Estuaries and Coasts* 29: 674–684.
- Scavia D, DePinto J, Bertani I. 2016. A multi-model approach to evaluating target phosphorus loads for Lake Erie. *Journal of Great Lakes Research* 42: 1139–1150. (12 April 2017; <http://dx.doi.org/10.1016/j.jglr.2016.1009.1007>)
- Schlenger AJ, North EW, Schlag Z, Li Y, Secor DH, Smith KA, Niklitschek EJ. 2013. Modeling the influence of hypoxia on the potential habitat of Atlantic sturgeon *Acipenser oxyrinchus*: A comparison of two methods. *Marine Ecology Progress Series* 483: 257–272.
- Scully ME. 2010a. The importance of climate variability to wind-driven modulation of hypoxia in Chesapeake Bay. *Journal of Physical Oceanography* 40: 1435–1440.
- . 2010b. Wind modulation of dissolved oxygen in Chesapeake Bay. *Estuaries and Coasts* 33: 1164–1175.
- . 2016a. Mixing of dissolved oxygen in Chesapeake Bay driven by the interaction between wind-driven circulation and estuarine bathymetry. *Journal of Geophysical Research: Oceans* 121: 5639–5654.
- . 2016b. The contribution of physical processes to inter-annual variations of hypoxia in Chesapeake Bay: A 30-yr modeling study. *Limnology and Oceanography* 61: 2243–2260. doi:10.1002/lno.10372
- Seliger HH, Boggs JA, Biggley WH. 1985. Catastrophic anoxia in the Chesapeake Bay in 1984. *Science* 228: 70–73.
- Stow CA, Scavia D. 2009. Modeling hypoxia in the Chesapeake Bay: Ensemble estimation using a Bayesian hierarchical model. *Journal of Marine Systems* 76: 244–250.
- Stow CA, Roessler C, Borsuk ME, Bowen JD, Reckhow KH. 2003. Comparison of estuarine water quality models for total maximum daily load development in Neuse River Estuary. *Journal of Water Resources Planning and Management* 129: 307–314.
- Taft JL, Taylor WR, Hartwig EO, Loftus R. 1980. Seasonal oxygen depletion in Chesapeake Bay. *Estuaries* 3: 242–247.
- Testa JM, Kemp WM. 2012. Hypoxia-induced shifts in nitrogen and phosphorus cycling in Chesapeake Bay. *Limnology and Oceanography* 57: 835–850.
- . 2014. Spatial and temporal patterns in winter–spring oxygen depletion in Chesapeake Bay bottom waters. *Estuaries and Coasts* 37: 1432–1448.

- Testa JM, Li Y, Lee YJ, Li M, Brady DC, Toro DMD, Kemp WM. 2014. Quantifying the effects of nutrient loading on dissolved O₂ cycling and hypoxia in Chesapeake Bay using a coupled hydrodynamic–biogeochemical model. *Journal of Marine Systems* 139: 139–158.
- Thuiller W, Lavorel S, Sykes MT, Araújo MB. 2006. Using niche-based modelling to assess the impact of climate change on tree functional diversity in Europe. *Diversity and Distributions* 12: 49–60.
- Tucker J, Giblin AE, Hopkinson CS, Kelsey SW, Howes BL. 2014. Response of benthic metabolism and nutrient cycling to reductions in wastewater loading to Boston Harbor, USA. *Estuarine, Coastal and Shelf Science* 151: 54–68.
- Turner RE, Rabalais NN, Justić D. 2006. Predicting summer hypoxia in the northern Gulf of Mexico: Riverine N, P and Si loading. *Marine Pollution Bulletin* 52: 139–148.
- Tyler RM, Brady DC, Targett T. 2009. Temporal and spatial dynamics of diel-cycling hypoxia in estuarine tributaries. *Estuaries and Coasts* 32: 123–145.
- Wainger LA. 2012. Opportunities for reducing total maximum daily load (TMDL) compliance costs: Lessons from the Chesapeake Bay. *Environmental Science and Technology* 46: 9256–9265.
- Weller DE, Benham B, Friedrichs M, Najjar R, Paolisso M, Pascual P, Shenk G, Sellner K. 2013. Multiple Models for Management in the Chesapeake Bay. Scientific and Technical Advisory Committee (STAC), Chesapeake Bay Program. STAC Publication no. 14-004.
- Wilson RE, Swanson RL, Crowley HA. 2008. Perspectives on long-term variations in hypoxia conditions in western Long Island Sound. *Journal of Geophysical Research* 113 (art. C12011).
- Wynne TT, Stumpf RP, Tomlinson MC, Fahnenstiel GL, Dyble J, Schwab DJ, Joshi SJ. 2013. Evolution of a cyanobacterial bloom forecast system in western Lake Erie: Development and initial evaluation. *Journal of Great Lakes Research* 39: 90–99.
- Xu J, Hood RR. 2006. Modeling biogeochemical cycles in Chesapeake Bay with a coupled physical–biological model. *Estuarine, Coastal and Shelf Science* 69: 19–46.
- Zhou Y, Scavia D, Michalak AM. 2014. Nutrient loading and meteorological conditions explain interannual variability of hypoxia in Chesapeake Bay. *Limnology and Oceanography* 59: 373–384.
- Zillen L, Conley DJ, Andren T, Andren E, Gjorck S. 2008. Past occurrences of hypoxia in the Baltic Sea and the role of climate variability, environmental change and human impact. *Earth-Science Reviews* 91: 77–92.
- Zimmerman AR, Canuel EA. 2000. A geochemical record of eutrophication and anoxia in Chesapeake Bay sediments: Anthropogenic influence on organic matter composition. *Marine Chemistry* 69: 117–137.

Jeremy M. Testa (jtesta@umces.edu) is an assistant professor at Chesapeake Biological Laboratory at the University of Maryland Center for Environmental Science, in Solomons. William C. Dennison is vice president for science application, E. Caroline Donovan is a program manager, and Suzanne E. Spitzer and Vanessa M. D. Vargas are graduate students at the Integration & Application Network at the University of Maryland Center for Environmental Science, in Cambridge and Annapolis. J. Blake Clark, Alexander W. Fisher, and Wenfei Ni are graduate students at Horn Point Laboratory at the University of Maryland Center for Environmental Science, in Cambridge. Matthew Parker is an aquaculture business specialist at the University of Maryland Extension, in Clinton. Donald Scavia is a professor of sustainability at the Graham Sustainability Institute at the University of Michigan, in Ann Arbor. Anthony Waldrop is a graduate student at the University of Maryland, in College Park. Gregory Ziegler is a senior faculty specialist at the Wye Research and Education Center, in Queenstown, Maryland.