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Modeling dissolved oxygen dynamics and coastal hypoxia: a review

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Abstract

Hypoxia occurs in marine ecosystems throughout the world, influences biogeochemical cycles of elements and may have severe impacts on marine life. Hypoxia results from complex interactions between physical and biogeochemical processes, which can not be addressed by observations alone. In this paper, we review oxygen dynamical models that have been applied in studies of factors controlling coastal hypoxia and in predictions of future states. We also identify scientific issues that need further development and point out some of the major challenges. Over recent decades, substantial progress has been made in the development of oxygen dynamical models. Considerable progress has been made towards the parameterization of biogeochemical processes in the water column and sediments, such as the dynamic representation of nitrification-denitrification. Recent advances in three-dimensional coupled physical-ecological-biogeochemical models allow better representation of physical-biological interactions. Several types of modelling approaches, from simple to complex, have significantly contributed to improve our understanding of hypoxia. We discuss the applications of these models to the study of the effects of oxygen depletion on biogeochemical cycles, links between nutrient enrichment and hypoxia development, impacts of hypoxia on marine ecosystems and predictions of climate change responses. However, for some processes models are still crude. For example, current representations of organic matter transformations and remineralization are incomplete, as they are mostly based on empirical parameterizations at few locations. For most of these processes, the availability of validation data has been a limiting factor in model development. Another gap is that, in virtually all nutrient load models, efforts have focused on nutrient utilization and organic matter degradation, whereas three-dimensional mixing and advection have been less well represented. Explicit inclusion of physical and biogeochemical processes in models will help us answer several important questions, such as those about the causes of the observed worldwide increase in hypoxic conditions, and future changes in the intensity and spread of coastal hypoxia. At the same time, recent

quantitative model intercomparison studies suggest that the predictive ability of our models may be adversely affected by their increasing complexity, unless the models are properly constrained by observations.

1 Introduction

Low dissolved oxygen (DO) concentrations (hypoxia) influence biogeochemical cycles of elements and may have severe negative impacts on marine ecosystems, such as mortality of benthic fauna, fish kills, habitat loss, and physiological stress (Levin et al., 2009; Ekau et al., 2009). Hypoxia occurs in subsurface waters of a variety of coastal environments including fjords, eastern boundary upwelling regions, off large estuaries, and semi-enclosed seas. Coastal hypoxia can occur naturally in bottom waters of silled basins and fjords with restricted circulation (e.g. the Black Sea) and in coastal upwelling regions where oxygen-poor and nutrient-rich deep waters are transported onto continental shelves (e.g. eastern Pacific Ocean). It can also occur due to human-caused perturbations such as riverine nutrient fertilization of coastal waters and global warming, which will likely lead to reduced oxygen solubility, enhanced stratification and reduced winter ventilation. A recent study found that the number of dead zones in the coastal oceans has increased exponentially since the 1960s (Diaz and Rosenberg, 2008), in part due to the increase in coastal eutrophication fueled by riverine runoff of fertilizers. Nutrient loading enhances primary production, leading to higher sedimentation fluxes of organic matter and the increased bacterial consumption of oxygen below the pycnocline. At the same time, large volumes of fresh water increase the vertical density gradient, reducing the transfer of DO from the surface to deep water. Knowledge of the importance of changes and interactions among natural and human-induced drivers of the oxygen balance is limited. Improving our understanding and prediction of these drivers is of great importance, given their potential to significantly expand the occurrence and increase the frequency of coastal hypoxic events.

Hypoxia results from an imbalance between biological oxygen production and con-

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sumption, and oxygen fluxes due to physical transport processes. The resulting oxygen depletion can be persistent, periodic or episodic. Persistent hypoxic conditions are observed in numerous fjords and semi-enclosed seas with year-round density stratification and low flushing rates (e.g. Baltic Sea), over deep trenches (e.g. Cariaco Basin),

5 and in oxygen minimum zones (OMZ) where weak ocean ventilation in association with biogeochemical cycling of oxygen maintains low DO (e.g. eastern tropical Pacific Ocean). The strong vertical oxygen gradients in these regions exert a considerable influence on the biogeochemical properties and organism distributions. Permanent hypoxic regions play important roles in the global nitrogen cycle, being the main areas of

10 nitrogen loss (as N_2 and N_2O) to the atmosphere through denitrification and anammox processes (e.g. Codispoti et al., 2001; Kuypers et al., 2003). These regions are also involved in the production of important climatic gases such as N_2O (e.g. Bange et al., 1996), H_2S (e.g. Naqvi et al., 2000) and CH_4 (e.g. Cicerone and Oremland, 1988). Significant progress has been made to incorporate these complex biogeochemical cycles

15 in models of low-oxygen environments in semi-enclosed seas such as the Black Sea (Oguz et al., 2000; Konovalov et al., 2006; Yakushev et al., 2007; Grégoire et al., 2008), but not in other regions (e.g. OMZ). A time-series analysis of DO concentrations in the tropical ocean revealed vertical expansion of the OMZ in the eastern tropical Atlantic and the equatorial Pacific over the past 50 years (Stramma et al., 2008). This finding

20 supports climate model predictions of dissolved oxygen declines and expansion of the OMZ under global warming conditions (Matear and Hirst, 2003). Expansion of the OMZ could have significant environmental and ecological impacts and will inevitably alter the global nitrogen cycle and the distribution of marine organisms.

Periodic oxygen depletion has been observed in many systems and may occur more

25 often than seasonally, lasting from hours to weeks. Seasonal fluctuations in DO resulting in hypoxia are usually driven by summer stratification of the water column coupled with increased production of organic matter. The settling and subsequent decomposition of this organic matter promotes oxygen depletion in bottom waters as indicated by models of, for example, the inner continental shelf of the northern Gulf of Mexico

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(Hetland and DiMarco, 2007) and Chesapeake Bay (Xu and Hood, 2006). Large diurnal fluctuations of DO between nighttime hypoxia and daytime supersaturation have been observed in shallow tidal creeks, lagoons, and estuaries, (e.g. D'Avanzo and Kremer, 1994). In a coastal embayment of the Chesapeake Bay, model simulations indicate that high primary production during daytime results in supersaturated DO, while at night respiration overwhelms the DO supply, often leading to hypoxia (Shen et al., 2008). Infrequent episodic oxygen depletion with less than one event per year seems to be the first indication that a system has reached a critical point of eutrophication, which, in combination with physical processes that restrict water exchange, can tip the system into hypoxia (Diaz and Rosenberg, 2008). Fluctuations in the extent and duration of low oxygen events can lead to significant ecological and economic impacts.

In coastal regions, hypoxia results from complex interactions between climate, weather, basin morphology, circulation patterns, water retention times, freshwater inflows, stratification, mixing and nutrient loadings (Druon et al., 2004; Gilbert et al., 2005). Because of the numerous physical and biogeochemical processes involved, the development of numerical models that enable DO responses to the external/internal environment to be estimated is essential for understanding the dynamics of hypoxia. Models are useful tools in scientific research of coastal ecosystems and for site-specific scenario studies of management strategies; they are needed to provide advice to policy makers about the probable effectiveness of various remedial actions at affordable costs.

Biogeochemical models that include the oxygen cycle have contributed to improved understanding of diverse aspects of hypoxia, such as processes responsible for its development (Druon et al., 2004), controls on its extent and temporal variability (Sohma et al., 2008), its impact on biogeochemical cycles (Oguz et al., 2000), issues related to eutrophication (Grégoire et al., 2008), and effects of climate change on DO concentrations (Matear and Hirst, 2003). They have been also useful in planning and forecasting marine system responses to different management scenarios and in providing guidelines for setting goals of nutrient reductions (e.g. Cerco and Cole, 1993; Scavia and

Donnelly, 2007). Because hypoxia occurs in regions with different physical settings and biogeochemistry, it is difficult to use the same model everywhere. Estuarine and coastal regions pose a further challenge to modellers. Substantial river discharges and relatively shallow waters often result in large fluctuations and strong spatial gradients in

5 physical and biogeochemical variables that have proven difficult to replicate in models. How important it is for models to capture this variability when assessing the potential impacts of local management strategies or predicting impacts of future conditions on hypoxia remains unclear.

This review is a contribution to SCOR Working Group 128, which aims to synthesize

10 the state of the science for several aspects of coastal hypoxia (Zhang et al., 2009). Here, we provide an overview of the state of the art and major findings from recent efforts to model hypoxia, focusing primarily on mechanistic models. In the following two sections, we describe some of the approaches used to model DO dynamics in the water column (Sect. 2) and biogeochemical reactions that occur under low oxygen and

15 anoxic conditions in the water column and sediments (Sect. 3). Section 4 deals with nutrient enrichment and hypoxia prediction models, and Sect. 5 deals with modeling the impacts of hypoxia on marine ecosystems. In Sect. 6, attempts to predict the effects of climate change on hypoxia are described. Finally, we summarize our main findings, identify model components that require further development, and discuss possible fu-

20 ture research directions in modeling hypoxic conditions.

2 Approaches to modeling dissolved oxygen dynamics

The concentration of DO in the ocean is dependent on air-sea fluxes, physical transports, and biogeochemical processes where DO and organic matter are produced via photosynthesis and are consumed through the oxidation of organic matter in the water

25 column and in bottom sediments (Fig. 1). In biogeochemical models, DO is usually represented as a model compartment and is described by partial differential equations that satisfy mass conservation. Most models are developed for a specific region and,

depending on the application and available information, differ markedly in the level of complexity and temporal and spatial resolution. Simple models use empirical or semi-empirical functions to describe oxygen sources and sinks (e.g. Justić et al., 2002). More complex models couple mechanistic physical and biogeochemical modules that simulate detailed biophysical interactions and DO dynamics (e.g. Sohma et al., 2008). Biogeochemical models may use relatively simple (if any) model formulations for food web interactions and organisms other than phytoplankton. These formulations range from simple NPZD-type models (nutrient, phytoplankton, zooplankton, detritus) (e.g. Xu and Hood, 2006) to multi-nutrient, size-structured ecosystem models (e.g. Los et al., 2008). Models may include only biogeochemical processes in the water column (e.g. Yakushev et al., 2007) or take into account the interactions of water column and sediment processes (e.g. Sohma et al., 2008; Soetaert and Middelburg, 2009). In general, the importance of including benthic processes increases with decreasing water depth because greater proportions of sinking organic matter reaches the seafloor in shallow marine systems. Likewise, physical models can be simple box models (e.g. Justić et al., 2002), 1-D vertical models (Oguz et al., 2000) or fully 3-D hydrodynamic models (e.g. Grégoire and Lacroix, 2001). Each of these components is discussed in more detail below.

2.1 Air-sea exchange of oxygen

Oxygen fluxes across the sea surface result from the difference in partial pressure of the gas in the ocean surface layer and in the atmosphere. Following Wanninkhof (1992), the flux of oxygen across the air-sea interface, F_O, can be calculated as

$$F_O = K \left(O_2^{surf} - O_2^{sat} \right) ,$$ (1)

where O_2^{sat} is the saturation concentration which depends on sea-surface temperature and salinity (e.g. Garcia and Gordon, 1992), O_2^{surf} is the oxygen concentration in the

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surface mixed layer, and K is the transport velocity given by

$$K = a(u^2 + v)(ScO_2/660)^{-1/2} \, , \tag{2}$$

where coefficient $a=0.337\,\mathrm{cm\,s^2\,h^{-1}\,m^{-2}}$, ScO_2 is the Schmidt number for oxygen, which is temperature dependent (Keeling et al., 1998), u^2 is the square of the mean wind speed and v is the variance of the wind speed. An alternative formulation, which takes into account the effect of gas transfer due to bubbles, is described in Justić et al. (2002).

2.2 Production and consumption of oxygen in the water column

Oxygen is produced in the upper water column during photosynthetic production of particulate and dissolved organic matter and is consumed during respiration of living organisms, remineralization of organic matter (particulate and dissolved) and nitrification. Several models indicate that detritus remineralization is the main consumer of oxygen in sub-surface waters (Oguz et al., 2000; Grégoire and Lacroix, 2001; Xu and Hood, 2006). The remineralization of organic matter consumes DO both directly through oxic respiration and indirectly through oxidation of a variety of metabolites (e.g. Mn(II), Fe(II), S(-II)), predominantly by chemolitotrophic bacteria. The particulate organic matter not remineralized in the water column is deposited to the sediments. When organic matter production is high, the settling and subsequent decomposition of this organic matter may result in oxygen depletion in bottom waters.

In most models, DO is not represented in the modeled biological processes directly but is coupled to the food web production and consumption of organic matter. Because nitrogen is usually the main nutrient limiting phytoplankton production in the ocean, most biogeochemical models are expressed in nitrogen units (e.g. Peña, 2003). Thus, the rates of biological production and consumption of oxygen are calculated from the magnitude of the associated nitrogen flux and the stoichiometric coefficient of O_2:N of organic matter. Different processes may occur at different specified O_2:N ratios.

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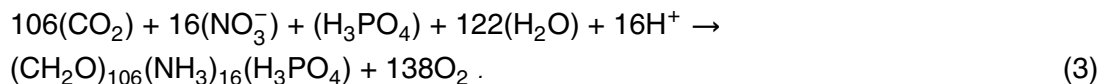Full Screen / Esc

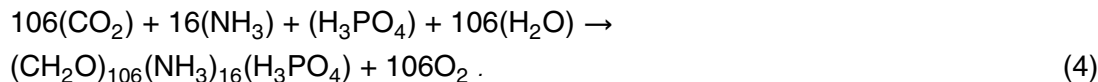Printer-friendly Version

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Alternatively, empirical or semi-empirical formulations might be used to compute primary productivity, net productivity (photosynthesis minus community respiration) and remineralization rates (e.g. Justić et al., 1996; Borsuk et al., 2001; Scavia et al., 2006).

Phytoplankton growth is co-limited by light and nutrient and is temperature dependent. Given its light dependency, photosynthesis mostly occurs in the upper water column, but it can also be of potential importance throughout the water column and on the sea floor when light levels are adequate (Rowe, 2001; Hagy and Murrel, 2007). Depending on the sources of fixed nitrogen (NO_3^- and NH_4^+) used by phytoplankton, primary production can be described in a simplified manner as:

Production using NO_3-N

$$106(CO_2) + 16(NO_3^-) + (H_3PO_4) + 122(H_2O) + 16H^+ \rightarrow$$
$$(CH_2O)_{106}(NH_3)_{16}(H_3PO_4) + 138O_2 \ . \tag{3}$$

Production using NH_4-N

$$106(CO_2) + 16(NH_3) + (H_3PO_4) + 106(H_2O) \rightarrow$$
$$(CH_2O)_{106}(NH_3)_{16}(H_3PO_4) + 106O_2 \ . \tag{4}$$

Thus, when nitrate fuels phytoplankton growth, the relation of oxygen production to nitrogen assimilated is $138/16=8.625$ whereas when ammonia fuels production the relation is $106/16=6.625$. This relationship assumes the average composition of the organic tissue of phytoplankton is carbohydrate, however, the subsequent formation of proteins and lipids involve the release of excess oxygen. Thus, the oxygen content of plankton is lower than those traditionally assumed in Eqs. (3) and (4) as indicated by actual observations of algal elemental ratios and metabolite composition and content (Anderson, 1995). In models where primary producers are divided into functional groups (e.g. diatoms, flagellates, blue green algae, etc), the proportion of production resulting from uptake of ammonia or nitrate might differ among these groups.

Phytoplankton cells are either transferred to the rest of marine food web where a portion of the organic matter is converted to detritus (cellular debris, zooplankton feces,

etc.) or they become senescent and sink by gravity into deep water. In models this organic matter is lumped into a detritus compartment or is divided according to its remineralization rate into fast-labile, slow-labile and refractory parts. The remineralization of this organic matter (detritus) by heterotrophic bacteria is controlled by the

5 concentration of oxygen. If DO is depleted, then nitrate is used to oxidize detritus and, if nitrate disappears, sulphate is reduced to hydrogen sulphide (see Subsect. 3.1). In oxygenated waters, detritus is remineralized at the expense of oxygen resulting in the production of ammonium and phosphate:

$$(CH_2O)_{106}(NH_3)_{16}(H_3PO_4) + 106O_2 \rightarrow 106CO_2 + 16NH_3 + H_3PO_4 + 106H_2O \, , \qquad (5)$$
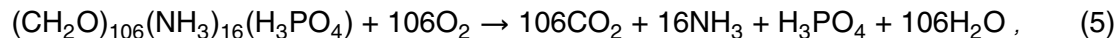
10 here the ratio of oxygen demand to recycled nitrogen equals the stoichiometric ratio of 6.625.

Remineralization of sinking organic matter within the oxygenated part of the water column may be parameterized as a first order decay relation of detritus available for decomposition (Justić et al., 2002) or be described using empirical formulations such

15 as an exponential decrease with water depth (Buesseler et al., 2007). In addition, remineralization can be modeled as a function of temperature and DO (e.g. Shen et al., 2008). The oxygen dependence can be modeled as a linear function (e.g. Yakushev and Neretin, 1997) or as a non-linear function, such as Michaelis-Menten type kinetics (e.g. Sohma et al., 2008). Many models simulate the remineralization of sinking organic

20 matter throughout the water column without explicitly including the organisms involved (e.g. Grégoire and Lacroix, 2001). Including the role of bacteria in models explicitly, such as in the Tuchkovenko and Lonin (2003) model, allows consideration of how non-uniform spatial distribution of bacterial biomass affects biogeochemical oxidation of organic matter, nutrient regeneration and oxygen consumption.

25 The respiration rates of living organisms are either modeled as a fraction of their biomass (e.g. Neumann, 2000) or as a fraction of their growth rate (e.g. Sohma et al., 2008). As in the case of detritus remineralization, respiration rates can also be modeled as a function of temperature and/or DO concentration. Moreover, depending

on the complexity of the ecosystem module, the number of species or functional groups considered varies and can include one or more types of phytoplankton, zooplankton, and/or bacteria.

Nitrification, the bacterial transformation of NH_4^+ to NO_2^- and NO_3^-, consumes oxygen according to:

$$NH_4^+ + 1.5O_2 \rightarrow NO_2^- + 2H^+ + H_2O \,, \tag{6}$$
$$NO_2^- + 0.5O_2 \rightarrow NO_3^- \,. \tag{7}$$

The depth distribution of nitrification is tied to the supply of ammonium from decomposition of organic matter and excretion by plankton groups, and is restricted to very low light regions due to light inhibition of nitrifying bacteria (Olson, 1981). In most models, the nitrification process is parameterized as a direct conversion of ammonium into nitrate without the intermediate step of nitrite formation (e.g. Grégoire and Lacroix, 2001). Nitrification can be modelled as a simple first order process and be expressed as a function of the oxygen concentration in the water column:

$$\text{Nitrification} = af(O_2)NH_4^+ \,, \tag{8}$$

where a is the maximum nitrification rate and $f(O_2)$ is a non-dimensional function of dissolved oxygen concentration representing the tolerance of nitrifying bacteria to oxygen and can be represented by Michaelis-Menten-Monod kinetics (Oguz et al., 2000; Yakushev and Neretin, 1997). Nitrification is the primary source mechanism for marine N_2O production (Yoshinari, 1976). However, an increase in the marine production of N_2O has been reported on the low-oxygen zones of the western Indian continental shelf probably caused by the addition of anthropogenic nitrate and its subsequent denitrification (Naqvi et al., 2000). N_2O is the third most important natural long-lived greenhouse gas after CO_2 and CH_4 and exerts a strong influence of climate and atmospheric chemistry. Suntharalingam et al. (2000) developed a simple source function which models N_2O production as a function of organic matter remineralization and oxygen concentration. Similarly, Nevison et al. (2003) derived a parameterization for the

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instantaneous production of N_2O per mole of O_2 consumed as a nonlinear function of O_2 and depth. The parameterization is based on laboratory and oceanic data and is designed for use in ocean biogeochemistry models.

2.3 Sediment oxygen demand

5   In shallow waters, consumption of oxygen in the sediments can greatly exceed its consumption in the water column, and the relative importance of sediment for the oxygen budgets increases with decreasing water depth (e.g. Eldridge and Morse, 2008; Sohma et al., 2008). Oxygen is transported into the sediments by a number of mechanisms, but mechanistic sediment models commonly consider two: molecular diffusion
10 and bioirrigation (Meile and Van Cappellen, 2003; Meysman et al., 2006). The rates of oxygen transfer by molecular diffusion, J_{dif}, can be calculated from Fick's law

$$J_{dif} = -\varphi D \frac{dO_2}{dz} ,$$ (9)

using the known porosity (φ), diffusion coefficients (D) corrected for sediment temperature and tortuosity (Boudreau, 1997) and the oxygen concentration gradients (dO_2/dz),
15 which may be measured, simulated, or even analytically derived (e.g. Cai and Sayles, 1996; Epping and Helder, 1997). Diffusive fluxes, however, usually fall short of the directly measured oxygen uptakes (e.g. Silverberg et al., 1987) because bioirrigation, which generally cannot be modelled as a diffusive process, accounts for 40–60% of the total oxygen flux into the sediment (Glud, 2008; Fig. 2). Bioirrigation is a three-
20 dimensional process, and oxygen supplied through animal burrows is with great probability (>90%) missed by one-dimensional measured profiles (Furukawa et al., 2000), making such profiles poorly suitable for the calibration of bioirrigation rates. Bioirrigation is typically modeled as a non-local exchange of porewater with the overlying water, which changes the concentration of sediment solutes at a rate $\alpha_{irr}(z)(C(z)-C_0)$, where
25 C and C_0 are the solute concentrations, respectively, at depth z within the sediment and in the overlying water, and α_{irr} is the bioirrigation coefficient, which generally de-

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pends on z. The values of bioirrigation coefficients and their depth dependences are poorly constrained, and their responses to oxygen depletion are more often guessed than measured (see below).

Spatially continuous sediment models often distinguish between oxygen consumption directly by benthic respiration and its consumption by the reduced chemical products of anaerobic metabolisms. In the upper oxidized layer of sediment, oxygen is consumed primarily by the direct respiration of benthic macro- and micro-fauna, which is described conventionally by Monod kinetics with a half-saturation constant between 1 and 8 $\mu mol\,O_2\,L^{-1}$ (e.g. Katsev et al., 2007). The model of Benoit et al. (2006), for example, considered this layer only, arguing that the reduced solutes, such as Fe^{2+} and HS^-, precipitate in the reduced sediment without contributing to the sediment oxygen demand (SOD). Most commonly, however, contributions of the secondary metabolic products, such as hydrogen sulfide, are taken into consideration. The reduced species are produced in the sediment below the depth of oxygen penetration (OPD), transported upwards by molecular diffusion and the actions of benthic organisms, become oxidized primarily around the OPD, and contribute between 30% and 80% of the total SOD (e.g. Soetaert et al., 1996). When detailed information about the anaerobic metabolic pathways is not required, the reduced solutes can be conveniently represented by their effective concentrations known as oxygen demand units (Soetaert and Middelburg, 2009; Sohma et al., 2008), which simplifies keeping track of oxygen budgets.

Ultimately, SOD is determined either by the rates at which oxygen can be transported into the sediment (transport) or the rates at which it can be consumed within the sediment (reaction). The transport rate depends on the oxygen concentration gradients near the sediment-water interface, and the consumption of oxygen relies predominantly on organic carbon as a terminal electron donor. It is therefore not surprising that reaction-transport diagenetic models indicate that the SOD is sensitive predominantly to the sedimentation flux of organic matter, the intensity of bioirrigation, and the oxygen concentration in the overlying water (Morse and Eldridge, 2007; Katsev et

al., 2007). Sediment temperature, which regulates the rates of microbial metabolisms, is another control factor (Rowe, 2001). Given the relatively small number of control parameters, statistical parameterizations of the SOD may be possible. Suggested parameterizations so far rarely included more than two variables. For example, Heip et

5 al. (1995) parameterized the SOD as an exponential function of water depth, assuming that the water depth is a sufficiently good predictor for the deposition flux of organic carbon. Such parameterizations, however, cannot account for the variations in bioirrigation rates. As a compromise between statistical empirical models and mechanistic, site-specific reaction-transport models, Borsuk et al. (2001) suggested a Bayesian ap-

10 proach that is based on a hierarchy of globally-common and site-specific parameters and could improve the accuracy of model predictions.

Statistical parameterizations generally cannot account for temporal variations; in such situations, simulations typically have to be tailored to a specific site. SOD can fluctuate diurnally, due to the production of oxygen by benthic photosynthesis (Sohma

15 et al., 2008; Rowe, 2001), seasonally, due to the depletion of oxygen and higher primary productivity in the water column (Morse and Eldridge, 2008), and interannually, in response to external nutrient inputs and other factors (Katsev et al., 2007). Bioirrigation rates can vary between the beginning, the peak, and the end of the hypoxic period (Morse and Eldridge, 2008). Spatial variations also affect the SOD. Using a spatially

20 explicit model for Tokyo Bay, Sohma et al. (2008) showed that the central bay and the tidal flats were connected in terms of the oxygen sinks and sources and interdependent. Because shallow and deep areas can differ substantially in terms of their benthic ecosystems, the study argued for considering such ecosystems separately.

2.4 Advective-dispersive transport processes

25 Doney et al. (2004) showed how critical it is to include realistic physics if one hopes to reproduce the biogeochemistry with any degree of reliability. Oxygen concentrations in the water column are affected by fluxes across the air-sea interface (Eq. 1) and across the sediment-water interface (Eq. 9). Within the water column itself, the oxygen budget

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can be expressed by the following oxygen balance equation:

$$\frac{\partial O_2}{\partial t} + u\frac{\partial O_2}{\partial x} + v\frac{\partial O_2}{\partial y} + w\frac{\partial O_2}{\partial z} - K_z\frac{\partial^2 O_2}{\partial z^2} - K_H\left(\frac{\partial^2 O_2}{\partial x^2} + \frac{\partial^2 O_2}{\partial y^2}\right) + nct = 0 \,, \qquad (10)$$

in which the first term represents the local rate of change of oxygen concentration with time. The second and third terms represents advection by currents in the east-west and north-south directions, respectively. In mass balance box models, flow data from field observations or from prognostic three-dimensional models of ocean circulation are required to represent advection (Cerco and Cole, 1993; Bierman et al., 1994). The fourth term represents vertical transport by upwelling or downwelling. The fifth term represents vertical mixing in which $K_z(x, y, z)$ is the vertical eddy diffusivity. The sixth term represents horizontal diffusion where $K_H(x, y, z)$ is the horizontal eddy diffusivity. Finally, the non-conservative terms (nct) represent processes such as photosynthesis, respiration and bacterial organic matter remineralization.

In fjords and semi-enclosed seas with shallow sills (e.g. Baltic Sea), between flushing events, the advection terms and horizontal diffusion are essentially equal to zero, so that waters beneath the pycnocline can only be oxygenated by vertical diffusion. Thus, such water bodies are often prone to develop hypoxic/anoxic conditions bellow sill depths (Eilola et al., 2009). Lack of ventilation at the sea surface is indeed one of the key factors driving hypoxia. Bendtsen et al. (2009) modeled the ventilation of bottom waters in the region of the Kattegat using a $k-c$ turbulence closure scheme. Their simulations suggest that bottom waters were less well ventilated in 2002 than in 2001 (about 20 days older in 2002) due to greater stratification in 2002. This led to an extreme hypoxic event in the autumn 2002 in the southern Kattegat. Similarly, in the open ocean, Karstensen et al. (2008) showed that OMZ are primarily a consequence of weak ocean ventilation. Oxygen supply to OMZ originates from a surface outcrop area and can also be approximated by the ratio of ocean volume to ventilating flux.

The vertical mixing term, $K_z\partial^2 O_2/\partial z^2$, plays a key role in the local oxygen balance (Eq. 10). Its magnitude depends on the value of vertical eddy diffusivity K_z, which

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is highly variable in both space and time as it depends on the gradient Richardson number Ri (MacKinnon and Gregg, 2005), defined by

$$\text{Ri} = \frac{N^2}{\left(\frac{\partial u}{\partial z}\right)^2 + \left(\frac{\partial v}{\partial z}\right)^2} = \frac{\left(\frac{-g}{\rho}\frac{\partial \rho}{\partial z}\right)}{\left(\frac{\partial V}{\partial z}\right)^2} \,, \tag{11}$$

where N is an index of stratification strength known as the buoyancy frequency, ρ is the
₅ water density, g is the gravitational acceleration and $\partial V/\partial z$ is the vertical shear of horizontal current. The gradient Richardson number, Ri, expresses the ratio of turbulence suppression by stratification (numerator) relative to vertical shear production of turbulence (denominator). When Ri>1/4, turbulence is suppressed, and vertical transport of oxygen from surface to bottom layers by turbulent mixing is unlikely to occur. Thus,
₁₀ strong vertical density gradients and/or weak current shears can suppress vertical mixing and be favorable to hypoxia. Key physical factors that produce stronger vertical density gradients ($\partial \rho/\partial z$) and thus reduce vertical mixing include freshwater inputs from rivers or precipitation, and warmer surface temperatures from absorption of solar radiation or sensible heat input. Factors responsible for producing enhanced vertical
₁₅ shear ($\partial V/\partial z$) and enhanced vertical mixing include tidal and wind-driven currents, inertial waves, internal tides, surface heat losses to the atmosphere, surface waves and Langmuir cells (Kantha and Clayson, 2000). Vertical overturns due to shear instability (Ri<1/4) generally occur at vertical scales that are smaller than the vertical grid spacing, and so must be parameterized in turbulence closure models (e.g. Mellor and
₂₀ Yamada, 1982).

In a one-dimensional model that couples water-column physics with pelagic biogeochemistry in a 50 m water column and with benthic biogeochemistry in a 60 cm sediment column, Soetaert and Middelburg (2009) show how stratification affects vertical mixing intensity and oxygen concentrations in the water column. Their model param-
₂₅ eterized vertical mixing by using the $k-\varepsilon$ turbulence closure scheme of Gaspar et al. (1990). In a study of the water column oxic/anoxic interface in the Black and Baltic
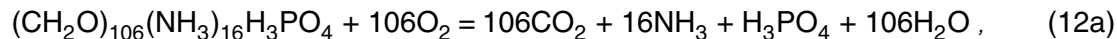
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Seas, Yakushev et al. (2007) used the General Ocean Turbulence Model (GOTM, Um-lauf et al., 2005), a one-dimensional model that offers the user the possibility of using several different statistical turbulence closure schemes.

Such one-dimensional models are useful for the insight that they can provide about the relative importance of processes that are usually too expensive to include in 2-D or 3-D models in terms of computing time. However, by design, they do not allow us to consider the role of wind-driven coastal upwelling or downwelling which sometimes play an important role in oxygen dynamics. For example, in Long Island Sound, Wilson et al. (2008) argue that changes in wind-driven upwelling are responsible for the continued increases of hypoxic conditions despite major reductions in organic matter load from New York City.

3 Modeling the effect of oxygen depletion on biogeochemical cycles

3.1 Processes in the water column

Nitrogen in organic and inorganic compounds has vital importance for regulating re-dox transformations of C, N, S, Mn and Fe within the water column. The discovery of new links and feedback mechanisms between these redox cycles has greatly improved general understanding of the role of nitrogen cycling in marine environments (Hulth et al., 2005). The emerging feature of nitrogen cycling is its involvement in a complex set of regulatory mechanisms, some of which are known to be mediated by a metabolically diverse range of microorganisms but, at the same time, our understanding of the sub-ject remains far from satisfactory. In this section, we focus on the most sophisticated models that include, in addition to the water-column biogeochemical processes related to oxygen consumption, the permanent or quasi-permanent suboxic–anoxic systems with redox reactions for sulfide, nitrate, ammonium together with manganese (Mn) and iron (Fe) cycling as observed in the Framvaren Fjord, Cariaco Trench, Baltic Sea and Black Sea.

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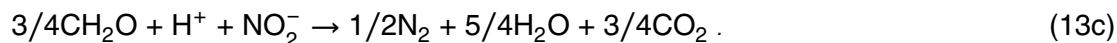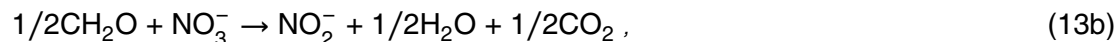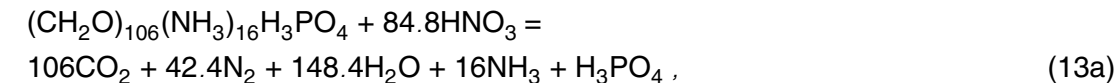
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Several models specifically deal with the dynamically-coupled oxic, suboxic and anoxic systems through such regulatory cycling mechanisms within different parts of the water column. For example, Yakushev et al. (2007) configured such a model for the Baltic and Black Seas whereas Oguz et al. (2000), Konovalov et al. (2006), and Grégoire et al. (2008) proposed similar models for the Black Sea interior basin with comparable biogeochemical complexity and processes that included the production and decay of organic matter, reduction and oxidation of nitrogen, sulfur, manganese, and iron species, and the transformation of phosphorus species. They simulated the annual structure of organic matter production explicitly with food web models and re-produced three dimensional spatial structure fairly realistically (e.g. Grégoire et al., 2008).
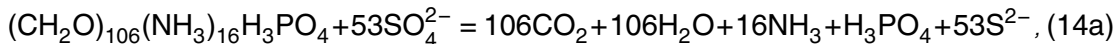
In the presence of oxygen, the redox reactions include oxidation of particulate organic matter, hydrogen sulfide, ammonium and dissolved manganese by dissolved oxygen. These reactions are

$$(CH_2O)_{106}(NH_3)_{16}H_3PO_4 + 106O_2 = 106CO_2 + 16NH_3 + H_3PO_4 + 106H_2O \, , \qquad (12a)$$

$$HS^- + 1/2O_2 + H^+ = S^0 + H_2O \, , \qquad (12b)$$

$$NH_4^+ + 2O_2 = NO_3^- + 2H^+ + H_2O \, , \qquad (12c)$$

$$2Mn^{2+} + O_2 + 2H_2O = 2MnO_2 + 4H^+ \, . \qquad (12d)$$

In the absence of oxygen, heterotrophic denitrification follows the reaction

$$(CH_2O)_{106}(NH_3)_{16}H_3PO_4 + 84.8HNO_3 =$$
$$106CO_2 + 42.4N_2 + 148.4H_2O + 16NH_3 + H_3PO_4 \, , \qquad (13a)$$

$$1/2CH_2O + NO_3^- \rightarrow NO_2^- + 1/2H_2O + 1/2CO_2 \, , \qquad (13b)$$

$$3/4CH_2O + H^+ + NO_2^- \rightarrow 1/2N_2 + 5/4H_2O + 3/4CO_2 \, . \qquad (13c)$$

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In oxygen depleted waters, the following oxidation-reduction reactions take place:
Sulfate reduction

$$(CH_2O)_{106}(NH_3)_{16}H_3PO_4 + 53SO_4^{2-} = 106CO_2 + 106H_2O + 16NH_3 + H_3PO_4 + 53S^{2-} , \quad (14a)$$

Anammox

$$NO_2^- + NH_4^+ \rightarrow N_2 + 2H_2O , \quad (14b)$$

Thiodenitrification

$$3H_2S + 4NO_3^- + 6OH^- \rightarrow 3SO_4^{2-} + 2N_2 + 6H_2O . \quad (14c)$$
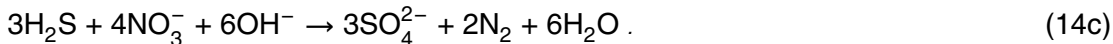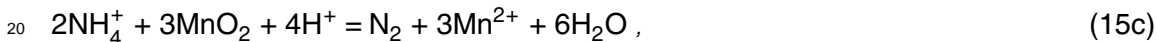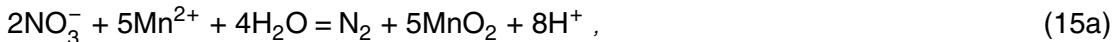
Regarding Mn oxidation and reduction, the reactions proposed to control manganese cycling include oxidation of dissolved manganese (Mn^{2+}) by nitrate in the suboxic layer to produce settling particulate manganese (MnO_2) and nitrogen gas (N_2) (Eq. 15a). HS^- and ammonium (NH_4^+) transported toward the oxic-anoxic interface from deeper levels are oxidized by MnO_2 to form elemental sulfur (S^0), N_2 and Mn^{2+} (Eqs. 15b and 15c). S^0 is reduced back to HS^- by bacteria and N_2 escapes to the atmosphere, whereas dissolved manganese produced locally is re-oxidized by nitrate. Dissolved manganese (Mn^{2+}) is formed via the reduction of Mn(IV) oxide by sulfide (Eqs. 15d and e). Similar oxidation-reduction reactions are described for iron cycling, but they are less efficient compared to manganese cycling.

$$2NO_3^- + 5Mn^{2+} + 4H_2O = N_2 + 5MnO_2 + 8H^+ , \quad (15a)$$

$$H_2S + MnO_2 \rightarrow S^0 + Mn^{2+} + 2OH^- , \quad (15b)$$

$$2NH_4^+ + 3MnO_2 + 4H^+ = N_2 + 3Mn^{2+} + 6H_2O , \quad (15c)$$

$$2Mn^{4+} + HS^- + OH^- \rightarrow 2Mn^{3+} + S^0 + H_2O , \quad (15d)$$

$$2Mn^{3+} + HS^- \rightarrow 2Mn^{2+} + S^0 + H^+ . \quad (15e)$$

These reactions form a coupled and highly interactive system that indicates a continuous loss of nitrogen in the form of N_2 gas to the atmosphere, and thus requires a continuous supply of NO_3^- into the redox layer to oxidize dissolved manganese diffusing from deeper levels. The necessary nitrate supply is provided continuously by its downward diffusion from the upper levels where the nitrification process produces nitrate.

The models correctly reproduce observed biogeochemical cycles when configured with appropriate initial and boundary conditions for particular basins. Organic matter, formed during phytoplankton bloom periods, determines water column biochemical structure depending on the competition between DO consumption for oxidation of organic matter in the euphotic layer and consumption for oxidation of reductants supplied from the anoxic deep water. As a result, ammonification, nitrification, denitrification and sulfate reduction dominate in the spring and summer, while the oxidation of reduced forms of metals and of hydrogen sulfide dominates in the winter. In the Black Sea, dissolved oxygen concentration varies from $450\,\mu mol\,O_2\,L^{-1}$ in winter months within the deep mixed layer to $250\,\mu mol\,O_2\,L^{-1}$ within the shallow summer mixed layer (Fig. 3). Below the mixed layer, oxygen concentration decreases linearly within the so-called oxycline. Its slope depends on the physical properties as well as amount of organic matter in the water column. Remineralization acts as a major sink of oxygen at these depth zones and exceeds the oxygen consumption in the nitrification process.

The oxycline zone typically coincides with the nitracline where nitrate concentration increases with depth to a maximum value, below which it decreases to zero at the anoxic interface (Fig. 3). The increasing concentrations with depth reflect building-up of nitrate as a consequence of the nitrification and nitrogen recycling. Its slope changes seasonally depending on the biological processes within the euphotic layer. Below the nitrate maximum, the decrease with depth is due to denitrification that takes place in two steps with an intermediate nitrite formation as shown in Fig. 3 in the region where nitrate goes to zero. According to the model, H_2S was present about 5–10 m below the depth of onset of the increase in NH_4^+, while maximum absolute values (1.5 µM) for S^0

occurred at the depth at which H_2S appeared. The S_2O_3 concentrations were uniform, with a small maximum of 0.2 µM at a depth slightly above the H_2S onset.

It is important to note that H_2S reduces to trace values at deeper levels than the depths at which DO concentration vanishes. Therefore oxidation of nitrate to dissolved
5 manganese takes place in the region near the anoxic interface, the resulting dissolved manganese diffuses upward from deeper levels to produce particulate manganese. The latter then oxidizes hydrogen sulphide and generates, as a by-product, dissolved manganese that further contributes to maintaining the redox processes in this zone. Elemental sulfur is also produced as a by-product in these processes. The sulfur peak
10 (S^0) shown in Fig. 3 thus identifies the vertical extent of these redox reactions.

3.2 Combined water column sediment models

Coupling between the model's sediment and water column compartments can be an important consideration that affects the simulated dynamics of nutrient and carbon cycling (Middelburg and Levin, 2009). The availability of fixed N, for example, is strongly
15 affected by sediment denitrification (Fennel et al., 2006) and primary production may be stimulated when increased sediment denitrification causes NO_3^- to be removed as NH_4^+ instead of N_2 (Kemp et al., 2005). Anoxic bottom waters may lead to the remobilization of sediment phosphorus, which, in turn, may foster eutrophic conditions and anoxia (Wallmann, 2003). Stand-alone diagenetic models often neglect such feed-
20 backs altogether by imposing the solute concentrations and sedimentation fluxes at the sediment water interface (Morse and Eldridge, 2007), or resort to using recycling coefficients that relate sediment nutrient effluxes to the sedimentation fluxes of organic carbon (Katsev et al., 2006a, 2007). Soetaert et al. (2000) suggested that the optimum approach is to include the evolution of sedimentary particulate matter in model solu-
25 tion and parameterize bottom fluxes of dissolved constituents based on mass budget considerations. Most coupled benthic-pelagic models now follow this approach (e.g. Luff and Moll, 2004). Some coupled models considered oxygen demand only in their lowermost compartment, i.e. either the sediment (Benoit et al., 2006) or a combined

bottom-water and sediment layer (Justić et al., 2002). This approach, however, is potentially misleading, as oxygen demand in the lower water column can be not only substantial but also out of phase with the oxygen demand in the sediment. In the Gulf of Mexico, for example, simulations suggest that the SOD contributes between 22%
5 and 73% of the total oxygen consumption in the lower water column (Bierman et al., 1994) and that, during seasonal hypoxia, the locus of oxygen consumption may shift from the sediment into the water column (Eldridge and Morse, 2008).

3.2.1 Phosphorus re-mobilization and burial efficiency

Phosphate binding to iron oxides makes phosphorus fluxes sensitive to redox con-
10 ditions and therefore responsive to carbon loadings and oxygen concentrations. In particular, the release of phosphorus from the sediments when bottom waters become hypoxic is one of the key feedback mechanisms responsible for delayed recoveries from hypoxia in several marine systems (Kemp et al., 2009). Remobilization of phosphorus during hypoxic events occurs in the near-surface sediment layers when iron
15 oxides become reduced and the released phosphate is transported into the overlying water by either molecular diffusion, sediment resuspension (Eilola et al., 2009), or bioirrigation, with the latter potentially accounting for up to half of the total phosphate efflux (Katsev et al., 2007). To reproduce these dynamics, models have to include a number of physical and biogeochemical sediment processes. Phosphate immobilization at the
20 surfaces of ferric iron and other particles is often assumed to be done by adsorption and is simulated as a fast (equilibrium) reversible process. Precipitation of phosphate with ferrous minerals in the reduced sediment and the dissolution of such minerals in the presence of hydrogen sulfide are simulated using effective mineral phases, such as vivianite or fluorapatite (Slomp et al., 1996). The quantitative characterization of such
25 reactions, however, is poorly known, and little kinetic information is available. Despite observations that C:P ratios typically increase with depth within the sediment, the organic P pool is often described in sediment models as a fixed fraction of the sediment organic matter (Morse and Eldridge, 2007; Savchuk and Wulff, 2007).

In the Baltic Sea, Eilola et al. (2009) parameterized the phosphorus release capacity as a function of oxygen concentration and salinity during hypoxic conditions, whereas under oxic conditions, organic carbon flux was suggested to be a better predictor. Sensitivity analyses from the more detailed reaction-transport models also indicate that P effluxes depend primarily on the sedimentation fluxes of organic matter and the concentrations of oxygen in the overlying water (e.g. Katsev et al., 2007). In brackish waters, P effluxes may also be affected by the concentration levels of dissolved sulfate relative to the concentrations of DO (e.g. Katsev et al., 2006a).

In seasonally anoxic areas, observations (e.g. see references in Kemp et al., 2005) and model simulations (Krom and Berner, 1981; Eilola et al., 2009) indicate that P mobilizations occur from the top few cm of the sediment and are controlled by the redox potential. In other instances, the dominant processes may be different. By characterizing P regeneration with a dimensionless Damköhler number, Van Raaphorst et al. (1988) concluded that, whereas high effluxes of P during the summer were controlled by the processes near the sediment-water interface, low winter fluxes depended more on processes in the anaerobic sediment. On longer time scales, the sediment Fe-oxide layer may become saturated with phosphate, making P effluxes insensitive to redox conditions (e.g. Eilola et al., 2009). For example, in the decadally hypoxic St. Lawrence Estuary, sediment incubations indicated significant P effluxes into the oxic waters, and simulations revealed that P effluxes were insensitive to oxygen concentrations (Katsev et al., 2007). Spatial variability can also be important. In the seasonally hypoxic Tokyo Bay, the model of Eilola et al. (2009) showed that, as the size of the hypoxic area fluctuated about its average value, the sediment switched between being a sink or a source of P.

3.2.2 Sediment denitrification and NH_4^+ release

The sediment nitrogen cycle reacts to oxygen depletion in a number of ways, with the magnitude and the direction of the net effect being dependent on the responses of the individual constituent pathways of the cycle. Similarly to the responses of the

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phosphorus cycle, the feedback mechanisms between water column hypoxia and the sediment N cycle can delay the recovery of marine systems from hypoxia (Kemp et al., 2009). Nitrogen is supplied into the sediment either as particulate N or dissolved nitrate, and particulate organic N is returned to the water column upon its mineralization as nitrate, ammonium, or N_2 (Middelburg et al., 1996). Sediment denitrification removes the produced nitrate, as well as the nitrate supplied from the overlying water column, and increases the porewater concentrations of ammonium. Because denitrification is energetically less favorable than aerobic mineralization, it is partially inhibited at oxygen concentrations $>0.1–10\,\mu mol\,O_2\,L^{-1}$. Below these levels, denitrification rates are typically described by Monod kinetics with a half-saturation constant in the range of $1–80\,\mu mol\,NO_3\,L^{-1}$ (e.g. Luff and Moll, 2004). Denitrification rates increase with the organic carbon flux but may increase or decrease with oxygen concentration in the bottom water (Middelburg et al., 1996; Morse and Eldridge, 2007; Katsev et al., 2007). Oxidation of ammonium to nitrate (nitrification) decreases when the oxygen levels are low, and hypoxia typically increases NH_4^+ effluxes from sediments (McCarthy et al., 2008). Whereas in oxic sediments oxidation of ammonium makes the sediment a source of nitrate to the overlying waters, hypoxic sediments are typically nitrate sinks (Middelburg et al., 1996).

Several statistical parameterizations for benthic denitrification rates have been suggested. Middelburg et al. (1996) derived a parameterization in terms of organic carbon fluxes and bottom water concentrations of O_2 and NO_3^-. Fennel et al. (2006) suggested a parameterization for estuarine, coastal, and continental shelf regions, linking denitrification to the SOD in oxic bottom waters. A subsequent study (Fennel et al., 2009) suggests that the relatively easily measured SOD is a better predictor of sediment denitrification than the sea water interface concentrations of oxygen and nitrate, and in shallow regions with strong sediment resuspension SOD is a better predictor than the flux of organic carbon. The study also concluded that, whereas in oxic waters denitrification is sufficiently well correlated with SOD, reproducing denitrification in hypoxic and anoxic waters requires a combination of mechanistic diagenetic models and

measurements.

3.2.3 Transient adjustment vs. steady state

Temporal responses of sediment geochemistry to hypoxia typically mimic the thermo-dynamic sequence of organic carbon mineralization (Middelburg and Levin, 2009). Ef-
fluxes of Mn and Fe increase (Pakhomova et al., 2007), and sulfides accumulate within the sediment. Denitrification rates vary insignificantly, and oxic respiration is replaced primarily by sulfate reduction (Middelburg et al., 1996; Katsev et al., 2007). Effluxes of sediment nutrients almost always lag behind changes in the water column conditions. For example, during seasonal hypoxia, the sediment effluxes of metabolites, such as
NH_4^+, lag behind their sediment production by several weeks (Eldridge and Morse, 2008). Lags can be also expected upon the restoration of oxic conditions: for exam-ple, recovery of nitrifying bacteria from anoxia can take weeks to months (Kemp et al., 2005). Katsev et al. (2007) found that sediments in the Lower St. Lawrence Estuary approached steady-state on a time scale of several centuries and, even on a decadal
time scale, sediment effluxes differed substantially from their steady-state values. Nev-ertheless, because of the lack of data, mechanistic diagenetic models frequently re-sort to calibrations at steady-state, after which transient behaviors are simulated using temporal variations in a few selected parameters, such as bottom water oxygen con-centrations or the sedimentation fluxes of organic carbon (Morse and Eldridge, 2008;
Katsev et al., 2007).

Internal (sediment-water) fluxes of nutrients that are high relative to the external (in and out of the water body) fluxes cause slower responses to changes in the external nutrient inputs or remediation (Kemp et al., 2009). For example, in shallow enclosed systems with high sedimentation and release fluxes of phosphorus, such as the Baltic
Sea, recovery after eutrophication can take hundreds of years (Savchuk and Wulff, 2007). At the onset of anoxia, oxygen can be consumed in the bulk sediment within several days, but re-oxygenation upon the restoration of oxic conditions takes longer, as oxygen supplied from the sediment surface is being consumed by the accumulated

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reduced substances (Katsev et al., 2006b), thus delaying recovery (Kemp et al., 2009).

4 Nutrient enrichment and hypoxia models

Rivers can have significant impacts on the hydrography and biogeochemistry of coastal regions. During the past 50 years, human activities have strongly impacted the river fluxes of nutrients (N and P) and organic carbon to the coastal ocean resulting in eutrophication in the shelf seas adjacent to the river influx enriched in nutrients. Eutrophication acts as an enhancing factor to hypoxia and anoxia and, when coupled with adverse physical conditions, can increase the frequency and severity of hypoxia. An increase in riverine fresh-water flux may also favor hypoxia, by enhancing the stratification of adjacent marine waters, which decreases the vertical mixing of oxygen (Eq. 10). Rabouille et al. (2001) evaluated the responses of the biogeochemical cycles of C, N and O in the global coastal ocean to human perturbations using a process-based model. Their model results show that over the past 50 years, primary production in the coastal ocean has doubled and has become more heterotrophic. Contrary to expectations, the denitrification efficiency decreases in their model suggesting that the role of the coastal ocean in regulating inorganic nitrogen discharge by the river is weak. Cotrim da Cunha et al. (2007) assessed the potential impact of changes in river nutrient supply on the global and coastal ocean biogeochemistry. They found that increasing river nutrient inputs enlarges the low oxygen areas under riverine influence in the eastern Tropical Pacific, Bay of Bengal, and especially in the coastal eastern tropical Atlantic under the influence of the Congo River.

Hypoxia has commonly been attributed to eutrophication caused by anthropogenic nutrient (N and P) enrichment, but eutrophication is only one of the risk factors associated with hypoxia in estuaries. Other factors, in particular those related to the physical processes, are known to be important as well. Several models have been developed to understand the mechanisms that link river discharge and nutrient concentration to hypoxia development and cessation (Bierman et al., 1994; Lowery, 1998; Justić et al.,

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2002; Shen et al., 2008). In the Mississippi River Plume/Inner Gulf of Mexico Shelf region, the model of Justić et al. (2002) suggests that a long-term increase in riverine nutrient fluxes has been responsible for the historical decrease in bottom layer oxygen concentrations in this region. Similarly, the Bierman et al. (1994) model indicates that chemical-biological processes appear to be relatively more important than advective-dispersive transport processes in controlling bottom-water dissolved-oxygen dynamics. In contrast, Hagy and Murrell (2007) found that the extent of hypoxia in Pensacola Bay, northern Gulf of Mexico, may be attributed largely to natural susceptibility to hypoxia resulting from high freshwater inflow and low amplitude diurnal tides rather than to eutrophication. Rowe (2001) used a mass balance model to quantify the degree to which oxygen consumption in deep water and in sediments exceeds net production and thus the time it takes to reach hypoxic conditions following the spring onset of stratification. The interaction between physical transport and hypoxia has not been examined in many estuaries.

The importance of developing predictive models of nutrients, primary production and DO has long been recognized for their utility in evaluation of the potential effectiveness of nutrient management strategies designed to reduce hypoxia. Several types of management models have been developed to assess the impact of riverine nutrient fluxes on coastal systems and to predict seasonal variability of hypoxia. Some models express biogeochemical processes through empirically derived parameterizations that link key nutrient load to hypoxia events (e.g. Lowery, 1998; Justić et al., 2002; Turner et al., 2006). Others have developed mechanistic physical-biogeochemical models to simulate detailed oxygen and nitrogen dynamics (Cerco and Cole, 1993; Los et al., 2008; Blauw et al., 2009). Both approaches are useful, yet both have limitations. Statistical approaches allow for estimates of predictive uncertainty to a greater extent than is possible with more complex models, but they are only correlative and do not represent biophysical processes. On the other hand, complex mechanistic models are more realistic, including non-linear interactions and feedbacks among processes and external stressors, but their utility in management applications is limited if they are not

well constrained and validated by observations. Several studies (e.g. Borsuk et al., 2001) have pointed to the need of developing models of intermediate complexity which balance the need of realism (i.e. complexity) against available data and understanding for environmental management and decision-making.

5   Variability in climate and ocean dynamics controls much of the interannual variability in hypoxia extent. For example, in the northern Gulf of Mexico, it was shown that the size of the hypoxic zone varies with precipitation (Justić et al., 1996) being significantly larger in wet years than in dry years. Scavia et al. (2003) use a biophysical model to explore the relative influence of nitrogen load and ocean variability on changes in
10 hypoxia. They find that year-to-year variability in oceanographic conditions can significantly mask, in the short term, the effect of reduced nitrogen loads on the size of the hypoxic zone. These model results stress the importance of setting management goals that take into account the long-term consequences of climate variability and change.

4.1 Northern Gulf of Mexico

15 The largest zone of oxygen–depleted coastal waters in the western Atlantic Ocean is in the Mississippi River discharge region of the northern Gulf of Mexico (NGOM). A range of modeling approaches, from simple to complex, have contributed to a better understanding of the factors influencing hypoxia in the Mississippi River plume region. Turner et al. (2006) used a purely empirical approach, fitting simple and multiple linear regres-
20 sion models of hypoxic bottom area against various nutrient loads from the combined Atchafalaya and Mississippi Rivers. They tested different nutrient loading lag times and found the best relationship (r^2=0.60 for total phosphorus) was obtained two months (May) prior to the maximum observed extent of hypoxia (July). By adding the variable "Year" in the multiple regression, they were able to explain even more of the variance
25 (r^2=0.82) by using the nitrite+nitrate loading from the month of May as a predictor of bottom hypoxic area in July. They justified the introduction of the "Year" term by arguing that the storage of organic carbon in the sediment increases with time, thus increasing sediment oxygen demand.

Neglecting cross-shelf exchange processes and assuming that the Mississippi-Atchafalaya freshwater plume can be represented as a river to a first approximation, Scavia et al. (2003) simulated hypoxia in the NGOM using a one-dimensional model that is used extensively in simulations of oxygen concentrations in rivers and estuaries (Chapra, 1997). This river model predicts oxygen concentration downstream from point sources of organic matter loads using mass balance equations for oxygen-consuming organic matter, in oxygen equivalents, and dissolved oxygen deficit. In that model the Mississippi and Atchafalaya Rivers are represented by distinct point sources of organic matter. This relatively simple, mechanistic model explained 45–55% of the variability in hypoxic bottom area. In follow-up studies, Donner and Scavia (2007) combined this hypoxia model with a watershed model to assess the impact of precipitation variability in the Mississippi-Atchafalaya River Basin (MARB) on NGOM hypoxia, and Scavia and Donnelly (2007) performed simulations with the goal of proposing N and P reduction targets in the MARB to bring back the size of the hypoxic zone to 5000 km^2 by 2015.

There have been several other models dealing with hypoxia in the NGOM. Justić et al. (1996, 2002) simulated oxygen dynamics at one location within the hypoxic zone, using a model that has two vertical layers and is forced by meteorological data and nitrogen loading from the Mississippi-Atchafalaya Rivers. Bierman et al. (1994) simulated the steady-state summertime conditions for the hypoxic area using a three-dimensional mass balance model that takes into account some of the interactions between food web processes, nutrients, and oxygen. Green et al. (2006) used a surface mixed layer model based on food web dynamics and relatively simple two-dimensional physics (no vertical dimensionality) of the Mississippi River plume. Their model predicts the relationship between carbon sources and bottom-water oxygen depletion, but does not include changes to either N or P inputs or dynamics.

Finally, fully prognostic, primitive equation, 3-dimensional models of ocean physics have recently been employed to gain further insight into the role of buoyancy forcing and stratification for the development of hypoxia in the NGOM. Hetland and DiMarco (2007) used the ROMS (Regional Ocean Modeling System) and simplified biogeo-

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chemistry. Their simulations show that the freshwater plumes from the Atchafalaya and Mississippi Rivers are often distinct from one another and that both contribute significantly to the development of hypoxia on the shelf through their influence on both stratification and nutrient delivery. Wang and Justić (2009) modeled the circulation and stratification of the Louisiana-Texas continental shelf using a different physics model, FVCOM (Finite Volume Coastal Ocean Model), as a preliminary step towards the development of a coupled three-dimensional model of physics and biogeochemistry for the Mississippi River Plume area. Hagy and Murrell (2007) examine the physical factors affecting development and maintenance of hypoxia in Pensacola Bay, a NGOM estuary, using box models to quantify the physical transport regime and net O_2 consumption rates for the lower water column and sediments. Their study suggests that the current extent of hypoxia in Pensacola Bay may be largely attributable to natural susceptibility to hypoxia resulting from physical factors. They point out that because high freshwater inflow and low-amplitude diurnal tides are characteristic of the entire NGOM coast, these physical factors are probably important regionally, not just in Pensacola Bay.

In the future, with the advent of Earth System models of ever increasing complexity, we may envisage a coupling of atmospheric models with watershed hydrology models, ocean models and sediment diagenesis models. Watershed models of nutrient origin, fate and transport play a key role in the assessment of the most effective remedial measures in order to reduce nitrate and phosphorus loads from rivers. These include the SPARROW (SPAtially Referenced Regression On Watershed attributes) model of Alexander et al. (2008) and the SWAT (Soil and Water Assessment Tool) model of Gassman et al. (2007).

4.2 Black Sea

Black Sea ecosystem-based modeling studies are described in Oguz et al. (2005), and the present study therefore provides complementary information in terms of nutrient enrichment studies. In general, the modeling studies focussed more closely on food web interactions rather than hypoxia within the shallow northwestern shelf. The exist-

ing modeling studies may be classified into three groups. The first group deals with the interior deep basin away from the direct effects of eutrophication. An early model of this kind was presented by Oguz et al. (2001). The objective was to come up with a model structure that had an optimum complexity and was able to describe the main features

5 of the food web structure and nutrient cycling for the eutrophic ecosystem period in the Black Sea (i.e. 1980s). It consisted of two groups of phytoplankton (small and large fractions), microzooplankton, mesozooplankton, bacterioplankton, three opportunistic species (*Noctiluca scintillans*, *Aurelia aurita*, *Mnemiopsis leidyi*), dissolved and particulate organic nitrogen, ammonium and nitrate compartments. Oguz et al. (2001) per-

10 formed simulations to explore characteristic features of the *Aurelia*- and *Mnemiopsis*-dominated ecosystems, respectively. The *Aurelia*-dominated ecosystem model configuration for the early 1980s was shown to realistically simulate the annual cycles of phytoplankton, mesozooplankton, *Noctiluca* and *Aurelia*, consistent with the observations. The top-down control exerted by *Mnemiopsis* was then examined to understand

15 how it alters the autotroph and heterotroph annual biomass structures.

Typically, models developed for specific regions perform well for the particular system for which they were developed, but when applied to other systems, their performance tends to be poor even after re-parameterization. However, the development of generic ecological models for estuaries that integrate biological and physical pro-

20 cesses in a simulation of basic ecosystem dynamics for generic application to coastal waters, such as the generic ecological model for estuaries (GEM) described by Blauw et al. (2009), allows for general application to different coastal and estuarine systems. This model has been applied successfully in a range of scenarios studies, which have formed the basis for several major policy and management decisions and infrastruc-

25 tural developments in coastal zones in the Netherlands and worldwide.

Grégoire et al. (2008) have developed a more sophisticated one-dimensional coupled physical–biogeochemical model. The biogeochemical model included 24 state variables, with three groups of phytoplankton: diatoms, small phototrophic flagellates and dinoflagellates, two zooplankton groups: micro- and mesozooplankton, two groups

of gelatinous zooplankton: the omnivorous and carnivorous forms, an explicit representation of the bacterial loop: bacteria, labile and semi-labile dissolved organic matter, and particulate organic matter. The model simulates oxygen, nitrogen, silicate and carbon cycling. It also explicitly represents the processes in the anoxic layer. The coupled model extends down to the sediments (~2000 m depth) and is forced at the air–sea interface by the 6 hourly ERA-40 reanalysis of ECMWF data. The model has been calibrated and validated using a large set of data available in the Black Sea TU Ocean Base. To calibrate the particle dynamics and export, the chemical model was run off-line with the particle and microbial loop model in order to check its capacity to simulate anoxic waters. In a 104 year run, the model simulated NH_4^+ and H_2S profiles similar to observations but steady state was not reached suggesting that the Black Sea deep waters are not at steady state. The fully coupled model was then used to simulate the period 1988–1992 of the Black Sea ecosystem.

The model solutions exhibited complex dynamics imparted by the explicit modeling of top predators. The integrated chlorophyll and phytoplankton biomasses, mesozooplankton biomass, depth of oxycline, primary production, bacterial production, surface concentrations of nutrients and plankton simulated by the model and obtained from available data analysis were compared and showed a satisfactory agreement. Also, as in the data, the model showed a continuous development of phytoplankton throughout the year, with an intense spring bloom dominated by diatoms and a fall bloom dominated by dinoflagellates. Dinoflagellates dominated from summer until late fall while small phototrophic flagellates were never dominant in terms of biomass, but were present almost throughout the year except in winter. The model simulated an intense silicate removal associated with increased diatoms blooms which were promoted by increased nutrient conditions, and by the presence of gelatinous zooplankton. This silicate pumping led to silicate limitation of diatom development in summer, allowing for the development of dinoflagellate populations.

The second group of models was specifically designed for the northwestern ecosystem that receives high nutrient load from the regional rivers (Danube, Dniepr, Dniestr,

Bug). They have mostly 1-D structures and are designed to explore roles of different processes and/or to test some hypotheses. For example, Lancelot et al. (2002) studied the role of nutrient enrichment on destabilization of the northwestern shelf ecosystem within the last three decades. Particular emphasis was given to establishing the

5   link between changes in nutrients, phytoplankton composition and food web structures during the course of ecosystem evolution. Their ecosystem model configuration is the most sophisticated one used in the Black Sea so far, and incorporates carbon, nitrogen, phosphorus and silicon cycling of both planktonic and benthic systems. Phytoplankton are represented by three different groups (diatoms, flagellates, opportunistic

10   species), microzooplankton, mesozooplankton, opportunistic herbivore *Noctiluca*, and gelatinous carnivore species *Aurelia*, *Mnemiopsis*, as well as two different biodegradability classes of particulate and dissolved organic matter. The simulations suggest that phosphorus is the major limiting nutrient for the northwestern shelf instead of nitrate or silicate. In the case of a well-balanced N:P:Si nutrient enrichment scenario, the

15   planktonic food web is characterized by a linear, diatom-copepod type food chain. The gelatinous carnivores are enhanced through their feeding on copepods. In the case of unbalanced nutrient inputs, such as nitrogen or phosphate deficiency, the food chain is dominated by microbial processes. Under these conditions, significant reduction in gelatinous organisms is predicted as observed in the 1990s. The major implication of

20   the latter simulations is to relate the observed positive sign of recovery in the ecosystem to the reduction in anthropogenic nutrient supply, in particular phosphate.

    In regard to the northwestern Black Sea shelf region, Grégoire and Friedrich (2004) employed a 3-D coupled biogeochemical-hydrodynamical model to assist the interpretation of benthic observations and to investigate sediment dynamics of the north-

25   western shelf. Measurements of benthic fluxes (oxygen, nutrients, redox compounds) with in situ flux chambers on the shelf were analyzed. Model results and in situ observations revealed intense benthic recycling and high benthic nutrient fluxes in the nearshore zone and in the northern part of the shelf. This region covers about 15% of the shelf area and is connected to the high productivity and high sedimentation caused

by riverine input of organic matter. On the outer shelf, covering about 85% of the shelf area, benthic nutrient regeneration is low due to low productivity. The organic matter is found to be decomposed by aerobic respiration. The sulfate reduction is the main anaerobic pathway in the coastal region, whereas denitrification is more important on the outer shelf. A small amount of organic matter is decomposed by methanogenesis. A mass balance study (Grégoire and Beckers, 2004) demonstrated that the NW shelf sediments are an efficient sink for riverine nitrogen, trapping about 50% of the annual river discharge in total inorganic N. The same model was also used to describe shelf-deep basin interactions, the export of organic matter towards the shelf sediments and into the anoxic deep waters of the open sea, and the loss of nitrogen gas to the atmosphere. The model estimated a vertically integrated gross annual primary production of $130\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ for the whole basin, $220\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ for the shelf and $40\,\mathrm{g\,C\,m^{-2}\,yr^{-1}}$ for the central basin. In agreement with sediment trap observations, model results indicated a rapid and efficient recycling of particulate organic matter in the sub-oxic portion of the water column (60–80 m) of the open sea. More than 95% of the PON produced in the euphotic layer was recycled in the upper 100 m of the water column, 87% in the upper 80 m and 67% in the euphotic layer. The model estimate that the annual export of POC towards the anoxic layer represents 2% of the annual primary production of the open sea.

4.3 Baltic Sea

The Baltic Sea is a semi-enclosed sea, consisting of several connected basins of different depths. The ecosystem of this region is controlled by physical processes and forced by external input of nutrients due to river loads and atmospheric deposition. Human activities have increased the loads of nutrients delivered to the Baltic Sea by river runoff and atmospheric input. Several models of different complexity have been developed to evaluate the ecosystem response to nutrient load reduction.

Carlsson et al. (1999) developed a simple semi-empirical management model to predict seasonal variability in near bottom oxygen concentration in Baltic archipelago

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areas. In the model, empirical variations in deep water oxygen concentrations were explained by variations in organic load and deep water turnover time. The model can be used to predict the lowest oxygen concentration during the year and to identify coastal areas where low concentrations are likely to appear.

5   Neumann (2000) used a coupled ecosystem and circulation model to simulate the nitrogen fluxes, both the propagation through the food web and the physical transport. The ecosystem model included: ammonium, nitrate, phosphate, diatoms, flagellates, blue-green algae, detritus, zooplankton, oxygen and sediment. The annual cycle of nitrogen was simulated with a high spatial resolution ($\sim$5.5 km). The model demon-

10 strated the importance of shallow coastal areas for the removal of river borne nitrogen. The fate of exported nitrogen was strongly connected to weather conditions, which determines where nitrogen is transported. In a subsequent study, Neumann et al. (2002) used the same ecosystem model and a full 3-D coupled circulation model to study the response of the model ecosystem to a 50% reduction of riverine nutrient loads. It

15 was found that the model food web reacts to the load reduction in a complex manner and that while the total biomass and nutrients inventories were reduced, there were significant regional differences. In particular, the biomass of diatoms, flagellates and zooplankton decreased while the biomass of cyanobacteria, which can fix atmospheric nitrogen, increased in response to the reduced loads.

20   Savchuk and Wulff (2007) developed a mechanistic model (SANBALTS) that coupled nitrogen and phosphorus cycles to evaluate management options for reducing Baltic Sea eutrophication. They found that contemporary nutrient cycles are primarily driven by internal biogeochemical processes and thus the entire sea and its sub-basins would react slowly to any external perturbations caused either by nutrient load or by climate

25 change. Also, because of the high interconnectivity of the Baltic Sea basins, the impact of local water protection measures would always be modified by long-range transports of nutrients entering the sea via other basins. These suggest slow and relatively weak response of the Baltic Sea trophic state to possible reductions of nutrient loads. Later, Savchuk et al. (2008) used SANBALTS to reconstruct nutrient conditions in the Baltic

Sea a century ago. They found that the "pre-industrial" trophic state could have been more phosphorus limited than today because simulated basin-wide annual averages of dissolved inorganic phosphorus concentrations were about 40–80% of their present day value, while dissolved inorganic concentrations were almost the same as today.

5   The biogeochemical mechanism causing this shift in the model combines higher N:P ratios of external nutrient inputs with feedbacks in the nutrient cycles. In contrast, improved oxygen conditions increased phosphorus removal from the water column and its retention in the sediments.

Recently, Eilola et al. (2009) developed a model SCOBI (Swedish Coastal and
10 Ocean Biogeochemical model) that includes oxygen and phosphorus to investigate the Baltic response to climate variations and anthropogenic activities on long time scales (100 years). The model contains inorganic nutrients, nitrate, ammonium and phosphate, three functional groups of phytoplankton (diatoms, flagellates and others and cyanobacteria), zooplankton and detritus. The sediments contain nutrients in the form
15 of benthic nitrogen and phosphorus. They show that the SCOBI model coupled to a circulation model is capable of reproducing the main features of phosphorus cycling in the Baltic Sea. The model, forced by naturally varying freshwater flow and climatological nutrient concentrations, simulates the observed increase and variability of hypoxic areas during the last 30 years (1969–1998) of the modeled period. The results
20 emphasize the importance of internal phosphorus and oxygen dynamics, the variability of physical conditions and the natural long-term variability of phosphorus supplies from land on the phosphorus content in the Baltic Sea water column.

5   Modeling the influence of hypoxia on ecosystems

5.1   Influence of hypoxia on food web interactions

25 Hypoxia may have profound impacts on trophic interactions through its direct mortality effect on mobile species and benthic organisms, or as a result of indirect effects such

as habitat loss and physiological stress that may alter prey-predator interactions. There are few models that specifically address the effect of hypoxia on a marine ecosystem. This is not surprising given the complexity of marine ecosystems and the major challenges that still remain to represent multiple trophic levels and functional groups in ecosystem models. Nevertheless, ecosystem models have been useful for quantifying the influence of hypoxia on food web dynamics, changes in nutrients composition and size of suitable habitat. One way to deal with the level of complexity is to identify key organisms and processes that need to be represented in the specific application, versus those that can be grouped or ignored.

Ecosystem models for Chesapeake Bay (Baird and Ulanowicz, 1989), the Kattegat (Pearson and Rosenberg, 1992) and the Neuse River estuary (Baird et al., 2004) show hypoxia-enhanced diversion of energy flows into microbial pathways to the detriment of higher trophic levels. In Chesapeake Bay, there is a predominance of planktonic components with most of the energy flow channelled through the meso-zooplankton (Baird and Ulanowicz, 1989). In the Kattegat, the analysis of Pearson and Rosenberg (1992) indicated that most of the energy flows through the benthic components in this system. Thus, intermittent summer hypoxia below the halocline has severe effects on the ecosystem leading to a reduction in macrobenthic organisms. Despite these differences, both modeled systems respond to hypoxia in a similar way by diverting the energy flow towards the microbial pathway.

Hypoxia can change the functional groups that dominate the phytoplankton community through its differential effect on the inventories of nitrate and phosphate. Anoxic conditions favor the benthic release of phosphate while suboxic sediments and oxygen-depleted waters remove nitrogen by denitrification. For example, a system lacking nitrogen could favor cyanobacteria, which can fix atmospheric nitrogen. Eilola et al. (2009) model oxygen dynamics, phosphorus cycling and the variability of cyanobacteria blooms in the Baltic Sea using the SCOBI model coupled to a circulation model. They find that a large fraction of the interannual variability of cyanobacteria abundance depends on the concentration of surface layer phosphorus in late winter. Their simu-

lation suggests that the sediments of the Baltic act as an internal phosphorus sink or source depending on whether the extension of anoxic bottom waters is smaller or larger than the long-period average anoxic area, and thus affect the occurrence of unwanted cyanobacteria blooms.

The spatial and temporal distribution and severity of hypoxia in a coastal system vary according to a combination of environmental factors and, thus, the impacts on living resources also vary. For example, the mortality of living resources is associated with the frequency of hypoxia and its duration, and the horizontal and vertical distributions of organisms depend on the distribution of hypoxic waters. Kremp et al. (2007) used a 3-D ecosystem model to simulate how the oxygen dynamics is affected by inflow events in the Baltic Sea, which occur at irregular intervals of one to ten years and renew the bottom waters of the central Baltic. They find that the extent of hypoxia and suitable habitat volume of calanoid copepods and optimal volume for the reproduction of cod could not be calculated with confidence because they all vary considerably in response to different meteorological data used to force the model. Karim et al. (2002) developed a probabilistic model to calculate the occurrence of oxygen-depleted water and applied this method to a eutrophicated shallow bay in western Japan to investigate the environmental impact of eutrophication on the living resources. They found that this method allowed them to evaluate the spatial and temporal pattern and severity of damage caused by hypoxia on living resources.

5.2 Influence of hypoxia on gelatinous zooplankton

Hypoxia may promote populations of low-oxygen-tolerant organisms, as in the case of jellyfish outbreaks in the Black Sea, Gulf of Mexico, southeast Asia, USA, etc., (Purcell et al., 2007; Richardson et al., 2009). The greater tolerance of polyps and medusae to low oxygen conditions ensures that jellyfish survive and even reproduce during hypoxic events, whereas fish are unable to do so. The ctenophore *Mnemiopsis leidyi* can have a better feeding success in low-oxygen environments because its prey (copepods), which are less-tolerant to low oxygen conditions, become more vulnerable to preda-

tion (Decker et al., 2004). Gelatinous species may generally inhabit regions of low oxygen that are avoided by zooplanktivorous fishes demanding relatively high oxygen concentration. This could lead to dominance of gelatinous predators over fish in areas affected by severe hypoxia and might alter energy pathways in these systems (Decker et al., 2004). Fishing activities that accompany eutrophication and hypoxia can further improve conditions for jellyfish dominance by removing their predator and competitor fish species. More enhanced gelatinous predation on zooplankton may, on the other hand, reduce zooplankton grazing on phytoplankton, which in turn may promote phytoplankton production that then reinforces hypoxia (Purcell et al., 2007). Such nonlinear internal feedback mechanisms lead to the development of a jelly-dominated food web structure that often replaces or dominates fish-dominated food web structure.

To our knowledge, there are few models that explicitly incorporate the effects of varying DO conditions on gelatinous zooplankton feeding and survival. Kolesar (2006) studied the effects of ctenophore (*M. leidyi*) predation and competition with fish (bay anchovy, *Anchoa mitchilli*) larvae at varying DO concentrations in the Chesapeake Bay system using an individual-based, spatially-explicit food web model of the ctenophore-fish larvae-copepod system. One major difficulty in such models is the lack of adequate observational knowledge to develop robust parameterizations for oxygen regulation of growth and survival characteristics. Nevertheless, the model simulations suggested that DO concentration alone does not have a significant effect on ingestion of fish larvae by ctenophores. But increased occurrence of low DO favored oxygen tolerant ctenophore predators, decreased vertical overlap between ctenophores and larval fish that together resulted in more larval fish predation (i.e. reduction in larval fish abundance) at the expense of their increased growth by 47–70% from first feeding to 15 mm. The high consumption rates of ctenophores coupled with their potential for rapid increase in biomass makes them voracious planktonic predators (e.g. Purcell and Decker, 2005). The model suggests that the ctenophore-larval fish-zooplankton interactions depend not only on the DO concentration but also on the way in which they are distributed vertically within the water column according to their DO requirements. For

example, the large degree of vertical overlap between ctenophores and larval fish in high DO food webs may result in lower densities and smaller size classes of copepod prey available to larval fish. However, a model of the lower trophic food web coupled to a bioenergetic-based anchovy population dynamics model (Oguz et al., 2008) indi-
5 cates that the level of nutrient enrichment may be more critical than the level of hypoxia for the development of the gelatinous species *Mnemiopsis leidyi* as observed in the Black Sea at the time of anchovy stock collapse during 1989–1990.

5.3 Effects on benthic organisms, bioturbation, and bioirrigation

Benthic responses to estuarine, enclosed sea, or open shelf hypoxia depend on the du-
10 ration, repeatability, and intensity of oxygen depletion, and on whether H_2S is formed (Levin et al., 2009). In environments such as the OMZ, benthic fauna can be adapted to DO levels as low as $0.1\,\text{ml}\,O_2\,L^{-1}$ (Diaz and Rosenberg, 2008), which indicates that low oxygen levels do not automatically result in low benthic activities. In recently hypoxic areas, however, dissolved oxygen concentrations below $0.5\,\text{ml}\,L^{-1}$ cause mass
15 mortality and cessation of bioturbation (Diaz and Rosenberg, 2008; Kemp et al., 2005). Production of HS^- in the reduced sediment tends to eliminate deeper-dwelling species (Aller, 1994), decreasing the depth of bioturbation. When oxygen levels recover, sediments become recolonized, but recolonization takes time and the temporal response of the benthic community exhibits a hysteresis (Diaz and Rosenberg, 2008). The early
20 colonists are typically smaller organisms which, because bioturbation scales with body size (Meysman et al., 2003), bioturbate to a shallower depth and with lower intensity than the pre-hypoxia macrofauna (Levin et al., 2009). Benthic responses may vary by species.

Relationships between macrofauna diversity and the sediment-water exchange
25 fluxes are highly complex (Middelburg and Levin, 2009) and understudied. Biological studies tend to focus on the effects of hypoxia on biological communities and such characteristics as diversity, biomass, and population densities. Geochemical studies, on the other hand, are concerned with the area-averaged chemical fluxes and there-

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fore rely on the effective parameterizations of bioturbation and bioirrigation rates. The distinction between the effects on communities and the effects on rates is important. So far, relatively few efforts have been expended on quantifying how oxygen depletion affects the rates of solute and solid phase transports by benthic organisms. Sediment

5 models have to rely on the assumed, rather than measured, relationships between the bioirrigation/bioturbation coefficients and the sediment water interface oxygen concentration. Parameterizations range from linear (Fossing et al., 2004; Morse and Eldridge, 2007) to strongly nonlinear (Ritter and Montagna, 1999), to threshold-type (Wallmann, 2003). Eldridge and Morse (2008) consider bioirrigation coefficients that scale lin-

10 early with O_2 concentrations recorded at 1 mm below the sediment surface, whereas Wallmann (2003) assumed that bioturbation decreases rapidly when the oxygen concentration drops below $20 \, \mu\text{mol} - O_2 \, L^{-1}$. Comparison of gradual vs. threshold-type responses (Katsev et al., 2007) reveals that the choice of this approximation is one of the most significant determining factors for the benthic fluxes predicted by the model. Be-

15 cause different types of organisms are affected by hypoxia in different ways, it appears advantageous to consider different organism groups separately. Archer et al. (2002) differentiate between the responses of bioturbators and bioirrigators: for bioturbation, they assumed a Monod-type decrease with half-saturation constant $20 \, \mu\text{mol} \, O_2 \, L^{-1}$, whereas the bioirrigation intensity, following the observations of Reimers et al. (1992),

20 is assumed to have a maximum at around $O_2 = 8 \, \mu\text{mol} \, O_2 \, L^{-1}$. Sohma et al. (2008) used a coupled diagenetic-ecological model and distinguished between suspension feeders and deposit feeders. The study parameterized bioturbation and bioirrigation coefficients as hyperbolic functions of the organism densities and treated the consumption and production of living organisms explicitly.

25 **6 Predicting the effect of climate change on hypoxia**

Global ocean circulation models predict that with increasing concentrations of atmospheric greenhouse gases due to human activities, the meridional overturning circula-

tion will become weaker (Lohmann et al., 2008). To our knowledge, the earliest attempt to look at the implications of changes in the global thermohaline circulation on oxygen dynamics was made by Sarmiento et al. (1998), who predicted that on average, O_2 will decrease by $8 \, \mu mol \, kg^{-1}$ from 1990 to 2065. This work was followed by studies by Matear et al. (2000), Bopp et al. (2002) and Matear and Hirst (2003) who made global predictions of oxygen decline of similar magnitude. In all of these studies, the predicted rate of oxygen outgassing from the global ocean (Fig. 4) is three to four times faster than one might have predicted from the temperature-dependence of oxygen solubility alone (Garcia and Gordon, 1992). This would lead to thicker OMZ (Oschlies, 2008). Early signs of this decrease in oxygen may have been detected by Stramma et al. (2008), but this needs to be confirmed by other studies. In fact, due to substantial interannual and interdecadal variability in the models and observations (Deutsch et al., 2005; Garcia et al., 2005; Frölisher et al., 2009), reliable detection of a negative, global, oxygen trend remains a challenge (Gilbert et al., 2009).

Moreover, general circulation models also predict that climate change will deplete oceanic oxygen by increasing stratification and warming as well as by causing large changes in rainfall patterns (IPCC, 2007). Hydrological changes may influence the delivery of nutrients and organic matter from land to coastal systems and thus modify the consumption of oxygen in coastal systems. The effects of increased precipitation, due to climate change, on seasonal oxygen cycling and hypoxia in the northern Gulf of Mexico was investigated by Justić et al. (1996) using a coupled physical-biological two-box model. Model simulations for a doubled CO_2 climate, which is likely to increase precipitation in the Mississippi River watershed by ~20%, predicts a 30–60% decrease in summertime subsurface oxygen content relative to a 1985–1992 average. This suggests that climate change in the northern Gulf of Mexico coastal region will likely have major impacts on benthic and epibenthic species diversity and community structure.

On much longer time scales, Schmittner et al. (2008) presented climate change projections for 2000 years into the future to a continuation of the present emission trends using a coupled, intermediate complexity global model of climate, ecosystems and

biogeochemical cycles. Model results show a decrease in subsurface oxygen concentration, tripling the volume of suboxic water and quadrupling the global water column denitrification. In the model, increasing temperatures lead to faster recycling rates in the marine ecosystem, and global primary production is boosted to almost double its
5   pre-industrial values. Warmer ocean temperatures lead to lower solubility of oxygen, which together with slower ventilation of the deep ocean lead to a ∼30% decrease of global mean oxygen concentration by year 3000. The oxygen changes are consistent with earlier 600-year model simulations using a simpler biogeochemical model (Matear and Hirst, 2003). Along the west coast of North America, the model predicts oxygen
10   reductions of 40–80%. Such strong reduction in oxygen concentrations will very likely increase the frequency of hypoxic events on the shelves. Likewise, using an Earth System model with simpler ocean physics but taking into account other biogeochemical processes such as the destabilization of methane hydrates with prolonged global warming, Shaffer et al. (2009) argue that the oxygen decrease will be substantial and
15   last for several thousands of years.

7   Summary and recommendations

Several types of modeling approaches, from simple to complex, have significantly improved our understanding of diverse aspects of hypoxia in many coastal regions. In particular, models have been valuable at determining the extent of hypoxia, identifying
20   ing factors affecting its development and maintenance, and predicting the responses of DO concentrations to changes in riverine nutrient loads. Surprisingly, little effort has been done to model OMZ and associated coastal upwelling regions even though hypoxia events have been reported in all major upwelling systems, especially associated with eastern boundary currents. Substantial progress has been made in the
25   last decade towards simulating biogeochemical processes in permanent or quasi-permanent suboxic-anoxic systems including redox cycles of C, N, S, Mn and Fe within the water column and sediments. However, published modeling efforts often do not ex-

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plicitly accounts for N_2O production/consumption in the anoxic breakdown of nitrite, a significant shortcoming given the role of N_2O as a long lived greenhouse gas. Mathematical models of biogeochemical redox transformations has been useful tools for filling knowledge gaps and directing further studies, such as those aimed at determin-
5 ing the effects of natural and anthropogenic forces.

Recent advances in 3-D coupled physical-chemical-biological models represent a step toward a quantitative understanding of the physical and biological processes contributing to hypoxia. Empirically, it is often difficult to distinguish between the effects of increased freshwater discharge (buoyancy forcing) and increased nutrient loading
10 from the watershed on the extent and duration of hypoxic conditions, as nutrient loading is generally positively correlated with river discharge. But model sensitivity analyses allow evaluating separately the roles of stratification and nutrient load on hypoxia development. Uncertainties still exist regarding the temporal and spatial resolution required to simulate possible impacts of future conditions, including local management sce-
15 narios. In shallow waters, the fluxes through the sediment-water interface are largely controlled by the dynamics of the bottom boundary layer, which can be described adequately only with a 3-D model approach. At present, most models are unable to represent details of coastal areas and circulation because of their coarse spatial resolution. Higher model resolution would improve the results from these simulations as
20 well as climate change predictions since most general circulation models applied at basin and global scales do not resolve the continental shelves adequately.

In contrast, modelling the response of marine ecosystems to hypoxia is still in its infancy, and many significant problems remain. Virtually all modelling efforts have focused on lower trophic levels, whereas higher trophic levels have been mostly ignored.
25 In some cases, incorporating higher trophic levels may be essential for modelling sinking particle fluxes. However, major challenges remain in terms of developing, parameterizing and validating complex biogeochemical/ecosystem models. Ecosystem processes are important determinants of the biogeochemistry of the ocean, and they can be profoundly affected by changes in climate. Ocean modelling is now at a stage

where increasingly complex hydrodynamical models are coupled to increasingly complex biological descriptions. However, decreases in predictive ability occur if models are not properly constrained with available data (Friederichs et al., 2007). Perhaps the most immediate need is for more rigorous validation of our models, using inde-
5 pendent datasets that quantitatively assess the predictive skill. Although empirical and semi-empirical models can be useful, an important role of biogeochemical modeling in hypoxic studies is to test and improve our knowledge of key processes, which is a priori eliminated by adopting an empirical approach. Certainly, mechanistic models developed to date have provided substantial insights into the relative contributions of
10 various processes; however, many limitations remain.

Most models describe biogeochemical cycles under the assumption of generally constant stoichiometric ratios. At this time, the stoichiometric relationship between oxygen, carbon and other macro- and micro-nutrients is uncertain, given the complex character of coastal hypoxia, such as different remineralization and burial efficiency of organic
15 carbon and nutrients. Differences between remineralization spatial and temporal scales of different elements result in decoupling of the cycles of these elements, changes in their ratios, and changes in apparent nutrient limitation. A quantitative understanding of the processes affecting detritus remineralization at depth is still lacking. Sediment trap experiments from relatively few locations have provided useful information on particu-
20 late organic fluxes as a function of depth. From these data, empirical relationships for the particulate organic matter remineralization with depth have been derived and used to model remineralization rates in diverse environments. Moreover, there is a need for more research and experimental data on the temperature dependency of biological rates such as microbial recycling and remineralization of particulate organic matter and
25 maximum growth rates given their tremendous importance for climate change simulations.

To improve model simulations of DO in shallow regions, more information is needed on what controls the lower-layer autotrophic and heterotrophic processes. Such improvements would lead to better understanding of how photosynthesis in this layer

responds to light, nutrients and autotrophic biomass. Likewise, for sediment-water-column models, better parameterizations are needed for phosphorus release capacity and burial, defined as functions of organic carbon fluxes, oxygen and sulfate concentrations in the overlying water, and Fe(III) availability. Short-term, e.g. seasonal, effects

5 need to be distinguished from long term effects. We need to improve characterizations of the bioturbation and bioirrigation responses to hypoxia and the associated changes in sediment geochemistry. Whereas much work focuses on characterizing the responses of benthic biological communities, fewer efforts have been dedicated to characterizing the associated changes in sediment mixing rates. For such characteri-

10 zations, a functional group approach could be promising.

The development of modeling techniques and skills will be supported by advanced observing systems that are in the planning stages for coastal areas as, for example, Global Ocean Observing System. There is a need for collaboration between observationalists and modelers to make the best use of advances in modeling techniques and

15 continuous automated observations of DO and other chemical parameters, as well as sensors of the biogeochemical and biological impacts of hypoxia. Recent technological developments have enabled scientists to routinely monitor oxygen concentrations remotely and transmit data in real-time, which offer opportunities to monitor changes in the ocean oxygen regime and to validate prediction of trend of oxygen in numeric mod-

20 els. It is timely to have a coordinated examination of the requirements for such observing systems and modeling facilities, in terms of detecting and modeling hypoxic events and their consequences. Guidelines are needed for determining the relevant temporal and spatial scales for the integrated observing and modeling activities in coastal areas affected by intermittent hypoxia events.

25 Overall, the research community recognizes the critical importance of models in studies of oceanic hypoxia. We can therefore expect further improvements in the development of models and in their ability to simulate and predict changes in the extent and intensity of hypoxia in both coastal regions and the global ocean. These improved models will help to improve our understanding of the impacts of hypoxia on marine

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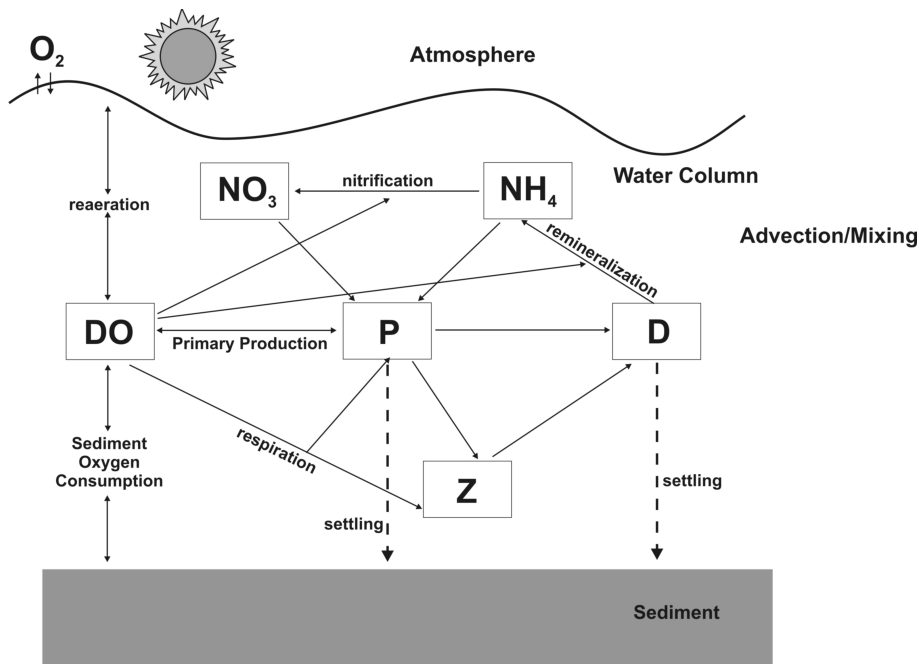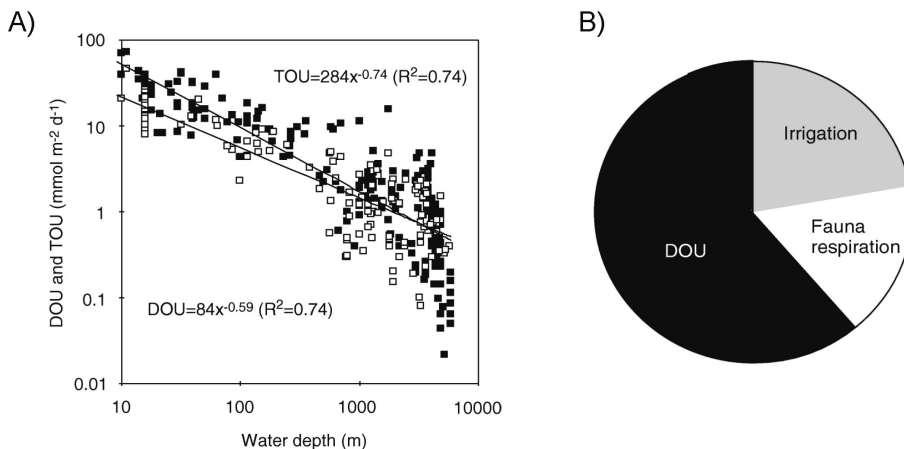
Fig. 1. Schematic representation of oxygen cycling in the water column where DO, P, D and Z represent dissolved oxygen, phytoplankton, detritus and zooplankton, respectively.

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Fig. 2. (A) The total oxygen uptake (TOU; closed symbols) and diffusive O_2 uptake (DOU; open symbols) as a function of water depth from several in situ studies, and **(B)** processes responsible for the O_2 consumption in Aahus Bay (after Glud, 2008).
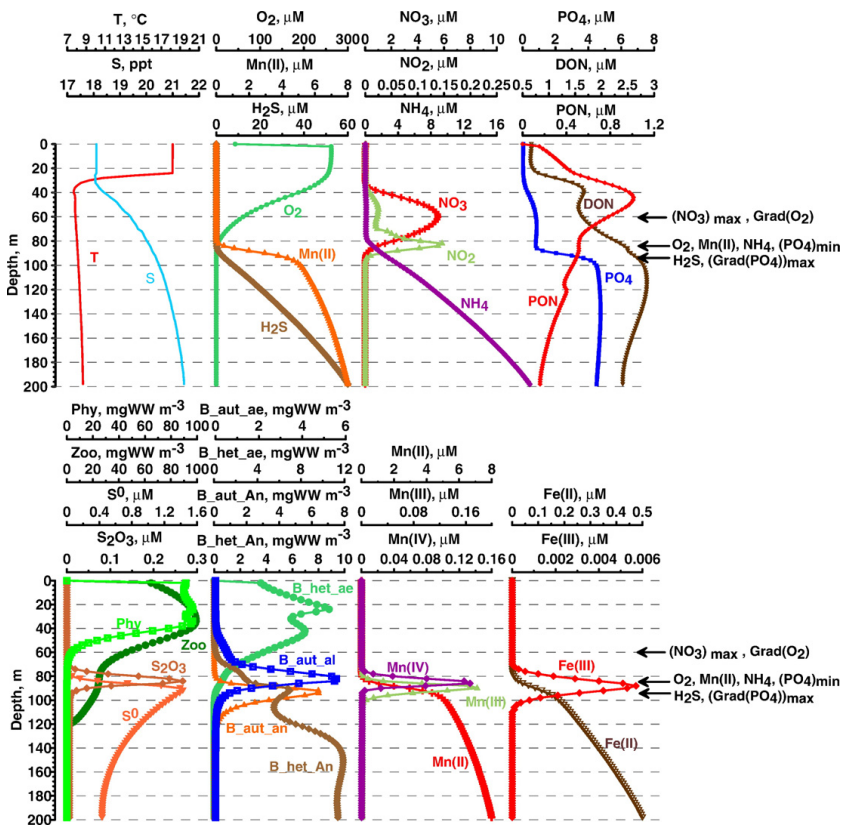
Fig. 3. The vertical distribution of various biogeochemical properties within the water column simulated by the model for summer conditions in the Black Sea (after Yakushev et al., 2007). DON=dissolved organic nitrogen; Phy=phytoplankton; Zoo=zooplankton, B_aut_ae=aerobic autotrophic bacteria; B_het_ae=aerobic heterotrophic bacteria; B_aut_An=anaerobic autotrophic bacteria; B_het_An=anaerobic heterotrophic bacteria; S^0=elemental sulfur.
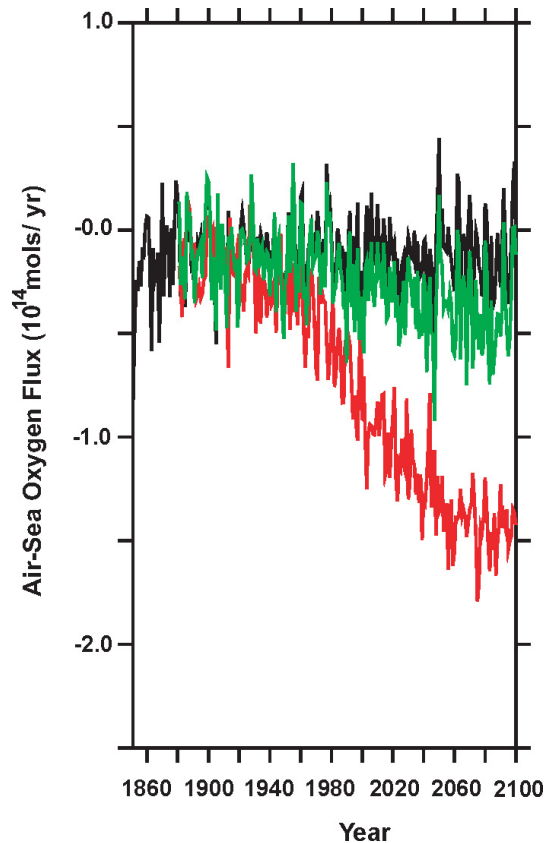
Fig. 4. Global averaged oceanic uptake of oxygen (10^{14} mols yr^{-1}). The black line denotes the control experiment with a constant atmospheric level of CO_2, the red line denotes the greenhouse forcing experiment using the IS92a radiative scenario, and the green line denotes the control experiment with the solubility of oxygen calculated using the sea surface temperature from the greenhouse gas forcing experiment. Adapted from Matear et al. (2000).