Sensitivity of the simulated Oxygen Minimum Zone to biogeochemical processes at an oligotrophic site in the Arabian Sea

Sankar S.[1,2], Polimene L.[2], Marin L.[2,3], Menon. N. N.[1], Samuelsen A.[4], Pastres R.[3], Ciavatta S.[2,5,*]

[1]Nansen Environmental Research Centre, India
[2]Plymouth Marine Laboratory, United Kingdom
[3]Ca' Foscari University of Venice, Italy
[4]Nansen Environmental Remote Sensing Center and Bjerknes Centre for Climate Research, Norway
[5]National Centre for Earth Observation, Plymouth Marine Laboratory, United Kingdom

* Corresponding author: Stefano Ciavatta, s.ciavatta@pml.ac.uk

Abstract

Oxygen minimum zones (OMZs) are large, low-oxygen areas in the global oceans. Although OMZs represent a serious threat to ecosystem functioning and services, our capability of modelling the main biogeochemical processes driving OMZ dynamic are still limited. Here we performed a full sensitivity analysis of a complex ecosystem model to rank the most important biogeochemical parameters influencing the simulation of the OMZ at an oligotrophic site in the open Arabian Sea. We applied a one-dimensional configuration of the European Regional Seas Ecosystem Model (ERSEM) - here advanced by including denitrification - coupled with the General Ocean Turbulence Model (GOTM). The coupled model was skilled in simulating the vertical gradients of climatological data of oxygen and nutrients. The sensitivity analysis of the model was carried out in two steps: *i)* a preliminary Morris screening analysis of 207 ERSEM parameters, which selected the three most influential groups of parameters; and *ii)* a subsequent Monte Carlo sampling-based analysis for ranking the importance of the 38 parameters within the three selected groups. Overall, the four most important parameters for the simulation of the minimum oxygen concentration were found to be: 1) the cubic half saturation constant for oxygenic control of denitrification; 2) the parameter regulating the fraction of ingested matter excreted by heterotrophic nanoflagellates; 3) the bacterial efficiency at low oxygen levels; and 4) the specific rate of bacterial release of capsular material. Based on these findings, and assuming that the ranking of the model parameters reflects the relevance of the process they characterize, we present a conceptual model describing the most important biogeochemical processes affecting the OMZ at the study site. Our results suggest that including bacteria explicitly in ecosystem models is useful to simulate and predict OMZs, provided that efforts are invested in estimating parameters characterizing the microbial loop in marine ecosystems.

Key words: marine ecosystem model; ERSEM; sensitivity analysis; oxygen minimum zone; bacteria; Arabian Sea

1. Introduction

Oxygen minimum zones (OMZs) are areas of the oceans characterized by low dissolved oxygen concentrations at intermediate depths (50-1000 m). Paulmier and Ruiz-Pino (2009) defined OMZs as regions where dissolved oxygen (DO) concentrations are less than 20 µmol L^{-1}, decreasing to 1 µmol L^{-1} in the core of the OMZ. In the present ocean, OMZs are expanding as a consequence of eutrophication and climate change, representing a serious threat for ecosystem functioning and services such as fisheries (Oschlies et al., 2008; Stramma et al., 2008; Diaz and Rosenberg, 2008; Gilbert et al., 2010; Rabalais et al., 2014; Duarte et al., 2015, Breitburg et al., 2018).

The formation, maintenance and intensification of the OMZs are governed by the interaction of physical processes (oxygen solubility driven by temperature and salinity, presence of regions of low ventilation and subsurface currents of poorly oxygenated water) with biological processes (primary production, heterotrophic activities, bacterial respiration and remineralization of organic matter).

Physical processes influencing OMZs are linked to global patterns of temperature, salinity and circulation. For example, Bopp et al. (2002) used a coupled climate-ocean biogeochemistry model to predict the decrease in DO with climate change and the net outgassing of DO from the ocean. They argued that the physical processes driving the reduction in DO were: *i)* changes in surface water solubility due to temperature increase; and *ii)* changes in the ocean circulation pattern. Matear and Hirst (2003) used a climate model coupled with an oceanic biogeochemical model to investigate the multi-century impact of protracted global warming on the ocean biogeochemical cycles. Their model predicted a decline in the DO concentration through most of the subsurface ocean in the future years.

Marine biogeochemical processes are also crucial drivers of OMZs, and OMZs strongly impact global biogeochemical cycles. As a basic conceptual scheme of biogeochemical drivers of OMZs (see, e.g., Sarmiento and Gruber, 2006), waters at intermediate depth receive organic matter produced and sinking from the upper euphotic layers; aerobic bacteria feeding on this organic matter and respiration by zooplankton consume oxygen and lower its concentration within the OMZ. Diaz and Rosenberg (2008) showed that hypoxic areas in the coastal oceans increased since the 1960s because of the increase in primary production fueled by riverine runoff and eutrophication. Oschlies et al. (2008) showed that OMZs are particularly sensitive to changes in the marine biology, by predicting a 50% increase in the global suboxic water volume by 2100 in response to the respiration of excess organic carbon formed at higher atmospheric CO_2 levels. Increase in primary production leads to increase in accumulation of particulate organic matter that, in turn, increases microbial activity and consumption of oxygen in the waters below. However, other processes complicate this basic scheme of OMZs, such as the possible switch of the microbial community towards anaerobic bacteria, which can reduce nitrates to N_2 gas through denitrification, and can reduce sulfate to hydrogen sulfide when the OMZ reaches anoxic conditions (Richards, 1965; Sarmiento and Gruber, 2006). Large amounts of biologically reactive nitrogen are removed from the oceans by anaerobic denitrifying bacteria in OMZs, with crucial impact on the global cycle of nitrogen (Paulmier and Ruiz-Pino, 2009). While the above-mentioned studies have identified the different biogeochemical processes influencing the OMZ, an understanding of their comparative impacts has not yet been achieved.

The overall objective of this study is to contribute to fill this gap, by ranking the importance of the biogeochemical processes which need to be carefully described to understand, simulate and predict OMZ formation and evolution in the oceans. This was done by ranking the importance of biogeochemical parameters of a complex marine ecosystem model. This model is the European Regional Seas Ecosystem Model (ERSEM) (Butenschön et al., 2016), which includes most of the biogeochemical processes driving OMZ dynamics. New for this study is that we included denitrification in ERSEM, since this process is relevant in OMZ systems, but it was not represented in the pelagic component of the model (Butenschön et al., 2016). We ranked the importance of ERSEM parameters for OMZ simulation, by using in sequence the Morris screening technique, followed by a Monte Carlo sampling-based ranking. These techniques are already proven to be useful with other marine biogeochemical models (Pastres and Ciavatta, 2005; Cossarini and Solidoro, 2008) and a marine food-web model (Morris et al., 2014). This is the first systematic sensitivity analysis of ERSEM.

In the present study, the analysis was performed using a one-dimensional (1-D) implementation of ERSEM for an oligotrophic site in the open Arabian Sea (Figure 1), advancing a comparable model configuration in this region by Blackford and Burkill (2002) and Blackford et al. (2004). The Arabian Sea is characterized by a vast OMZ with DO concentrations below 0.05 ml L^{-1}, at depths between 150 and 1250m (Van Bennekom and Hiehle, 1994), and it is one of the three major denitrification sites in world oceans (Codispoti, 1989; Naqvi et al.,

2005) with an annual denitrification rate of 10-30 Tg N yr^{-1} (Fauzi et al., 1993). At the present time, there is no consensus on which physical and biological processes maintain the spatial and seasonal pattern of the OMZ in the Arabian Sea (McReary et al., 2013; Roullier et al., 2014), and hypotheses include high respiration related to monsoon-driven primary productivity, slow advection of intermediate waters, and influx of low oxygen waters from the South Indian Ocean (Swallow, 1984; Naqvi, 1987; Jayakumar et al., 2004; Wiggert et al., 2005). Results from both a box model (Sarma et al., 2002) and an eddy-resolving model (Resplandy et al., 2012) showed that horizontal oxygen transport is important for maintaining the OMZ. At the same time, ecosystem models of varying complexity, including the seminal NPZD model of McCreary et al. (1996) and the model by Ryabchencnko et al. (1998) that resolved also the microbial-loop, were used to investigate the contribution of biological processes to the OMZ. The three-dimensional (3-D) coupled model by Anderson et al. (2007) confirmed the relevance of modelling bacteria to simulate the biogeochemical fluxes and demonstrated that vertical sinking of organic particles (in contrast to their horizontal transport) was a major driver of denitrification in the regional OMZ. For the first time, Blackford and Burkill (2002) and Blackford et al. (2004) applied the more complex ERSEM to this region, in a 1-D configuration with the physical model GOTM, and they found that vertical processes and microbial trophic dynamics were important drivers of biogeochemical variability in the Arabian Sea. This model added the representation of size classes of detritus and variable elemental ratios in the simulation of the Arabian Sea ecosystem – and these features were later recognized as essential ones to simulate OMZ in this region, as well as in the global ocean (Oschlies et al., 2008; McCreary et al., 2013).

However, the relative contribution of the different biogeochemical processes to the formation and evolution of the OMZ in the Arabian Sea remains uncertain, and further research has been invoked to improve their representation in mathematical models of this ecosystem (McCreary et al., 2013; Roullier et al., 2014). Therefore, we tested the sensitivity analysis methods in a case study that aims to rank the biogeochemical processes that determine the annual minimum value of oxygen concentration at the site in the open Arabian Sea in Figure (1). Here, spatial-temporal biogeochemical variability is lower, and the OMZ thinner, than in the Northern Arabian Sea (Kao et al., 2015), arguably making acceptable the application of a 1-D model configuration to study the formation of the and maintenance of the upper oxycline at the study site.

The paper is structured as follows. Section 2 describes the coupled physical-biogeochemical model, the sensitivity methods and the set-up of the analysis. In Section 3, the results are presented: first the skill of the OMZ simulation is evaluated by comparing the results to climatological data, and then the results of the screening and Monte Carlo-based sensitivity analyses are synthetized. In Section 4 we discuss the results by presenting a conceptual model of the OMZ formation, and concluding remarks are pointed out in Section 5.

2. Methods

2.1 Model description

The vertical dynamics of the water column were represented by coupling ERSEM with the 1-D hydrodynamic model GOTM (Figure 2) (Butenschön et al., 2016).

The general equation for the coupled GOTM-ERSEM model can be written as,

$$\frac{\partial c_i(\boldsymbol{c},\boldsymbol{p}_{bio},\boldsymbol{p}_{phys},t)}{\partial t} = \left.\frac{\partial c_i}{\partial t}\right|^{bio} + \left.\frac{\partial c_i}{\partial t}\right|^{phys} \qquad (1)$$

In equation (1) the first term on the right represents the biogeochemical equations of ERSEM and the second term represents the physical equations of GOTM; **c** represents the state vector collecting the model variables c_i, $\mathbf{p}_{bio}$ the vector collecting the parameters of ERSEM, and $\mathbf{p}_{phys}$ the vector of the parameters of GOTM.

The general equation of the scalar model output y can be written as,

$$y = g_i(\boldsymbol{c}, \boldsymbol{p}_{bio}, \boldsymbol{p}_{phys}, z, t) \quad (2)$$

Where g_i is a function of the model variables **c**, of the model parameters **p**, of the depth z in the water column, and of time t. We focused this work on the sensitivity of the annual average of the minimum value of dissolved oxygen simulated in the water column (c_i=O_2), with respect to the biogeochemical parameters of ERSEM ($\mathbf{p}_{bio}$):

$$y = \langle min_z[O_2(\boldsymbol{p}_{bio})] \rangle_a \quad (3)$$

Where min_z represents the minimum in the water column, and $\langle \quad \rangle_a$ the annual average. This minimum value was assumed to approximate the “intensity” of the OMZ (i.e. the degree of oxygen depletion, e.g. McCay et al., 2005) that is sensible to the biogeochemical processes investigated in this work.

2.1.1 The biogeochemical model ERSEM

ERSEM (Baretta et al., 1995; Blackford et al., 2004; Butenschön et al., 2016) is a biomass and functional group-based biogeochemical model describing the nutrient and carbon cycle within the low trophic levels of the marine ecosystem. Model state variables include living organisms, dissolved nutrients, organic detritus, oxygen and CO_2. Pelagic living organisms are subdivided in three functional groups describing the planktonic trophic chain: primary producers (phytoplankton), consumers (zooplankton) and decomposers (bacteria). Primary producers and consumers are subdivided into 4 and 3 size-based functional types, respectively. The phytoplankton community is composed of picophytoplankton, nanoflagellates, dinoflagellates and diatoms, while the zooplankton community is composed of mesozooplankton, microzooplankton and heterotrophic nanoflagellates (HNAN). Decomposers are modeled by one type of heterotrophic bacteria. Functional types belonging to the same group share common process descriptions but different parameterizations.

A key feature of ERSEM is the decoupling between carbon and nutrient dynamics allowing the simulation of variable stoichiometry within the modeled organisms. Chlorophyll is also treated as an independent state variable following the formulation by Geider et al. (1997). Consequently each plankton functional type is modeled with up to five state variables describing the cellular content of carbon, nitrogen, phosphorus, silicon, and chlorophyll-a. Dissolved organic matter (DOM) is produced by different processes involving phytoplankton, bacteria and zooplankton while its consumption is exclusively regulated by bacteria uptake. DOM is subdivided into labile, semi-labile and semi-refractory components (Polimene et al., 2006), in order to provide a representation of the range of organic compounds present in the marine DOM and their different levels of degradability. Particulate organic matter (POM) is produced by phytoplankton and zooplankton and it is divided into three size-based categories corresponding to different sedimentation rates. In this way it is possible to simulate the carbon export from the surface to the intermediate OMZ layers. In the version of ERSEM applied here, the decomposition of particulate organic matter is directly mediated by bacteria, and the partition between labile and semi-labile organic matter occurs in relation of the nutritional status of phytoplankton and bacteria (Polimene et al., 2006, 2007; Butenschön et al., 2016).

All the ERSEM equations are detailed in Butenschön et al. (2016) and we refer the reader to that paper for a comprehensive description of the mathematical formulations used in the model. Here we limit our description to the ERSEM representation of oxygen dynamics, which are the focus of the paper, and to the formulation describing denitrification, which was newly developed in this work. The pelagic net production of oxygen is modeled through the balance between gross primary production (gpp) and the whole community respiration (resp). The latter is computed as sum of the contributions of bacteria (carbon biomass B_C), of NZ=3 zooplankton groups (Z_C), and

NP=4 phytoplankton groups (P_C) (Butenschön et al., 2016):

$$\left.\frac{\partial O_2}{\partial t}\right|_{bgc} = -p_O^{resp}\left.\frac{\partial B_C}{\partial t}\right|_{resp} - p_O^{resp}\sum_{i=1}^{NZ}\left.\frac{\partial Z_C^i}{\partial t}\right|_{resp} - p_O^{resp}\sum_{i=1}^{NP}\left.\frac{\partial P_C^i}{\partial t}\right|_{resp} + p_O^{syn}\sum_{i=1}^{NP}\left.\frac{\partial P_C^i}{\partial t}\right|_{gpp} \quad (4)$$

Where p_O^{resp} is a stoichiometric factor converting the amount of carbon respired into oxygen consumption, and p_O^{syn} is a stoichiometric factor converting the amount of carbon assimilated through photosynthesis into oxygen production.

Denitrification was represented here by modifying the equation in Vichi et al (2007). This process was represented as the minimum of a potential denitrification ($Denit_{pot}$) and the bacterial nitrate demand (BND):

$$Denit = min\left(Denit_{pot}, BND\right) \qquad (5)$$

Where:

$$Denit_{pot} = Denix \cdot NO_3 \qquad (6)$$

And

$$BND = BOD \cdot \delta \cdot (1 - O2_{lim}) \qquad (7)$$

In equation (6), NO_3 is the available concentration of nitrate and *Denix* is the maximum specific denitrification rate. In equation (7), BOD is the bacterial oxygen demand, which is a function of the available organic carbon (POC+DOC), δ is a stoichiometric factor converting O_2 to NO_3, and $O2_{lim}$ is a cubic Michaelis-Menten function describing oxygen limitation (Vichi et al., 2007):

$$O2_{lim} = \frac{(O_2)^3}{(O_2)^3 + (chN3oX)^3} \qquad (8)$$

Where $chN3oX$ is the half-saturation constant for oxygenic control of nitrogen transformation.

Equations 7 and 8 imply that under well oxygenated conditions the BND is close to zero while it increases under low oxygen condition. If the environmental nitrate concentration is insufficient to satisfy the BND, then the production of reduction equivalents (HS) occurs. This latter process mimics the formation of reduced sulfur (HS^-) as observed when both oxygen and nitrate are depleted:

$$HS = BOD \cdot \delta' \cdot (1 - O2_{lim}) - Denit \cdot \varepsilon' \quad (9)$$

Where δ' and ε' are stoichiometric factors converting O_2 to HS^- and nitrate to HS^-, respectively.

The above equations 5-9 represent aerobic and anaerobic (e.g. denitrifying) bacteria through a single functional group. The model, in fact, describes a bulk bacteria biomass able to switch between different kinds of metabolism (aerobic, anaerobic) depending on environmental conditions, i.e., on O_2 and nitrate concentrations in the water column. We note that the model does not include chemolithotrophic bacteria, though they can be important for the nitrogen cycle within OMZs (Lam et al., 2009). However, Ward et al. (2009) found that heterotrophic denitrification is the main process responsible for N loss in the OMZ of the Arabian Sea, largely exceeding the chemolithotrophic anaerobic ammonia oxidation (anammox), making the absence of chemolithotrophy acceptable in our application.

2.1.2 The hydrodynamic model GOTM

GOTM (General Ocean Turbulence Model; Burchard et al., 1999) is a 1-D water column model used for the computation of hydrodynamic and thermodynamic processes related to vertical mixing. The model calculates velocities, turbulence, temperature and salinity, as well as heat, momentum and freshwater fluxes between the ocean and the atmosphere, when forced with local meteorological inputs. Routines for nudging observations also exist in GOTM and they were applied here for the relaxation of the model simulation towards salinity and water temperature profiles (see also the model set up in Section 2.4.1). Such relaxation has been widely used in previous GOTM-ERSEM applications in both shelf-sea and open ocean sites (e.g. Blackford et al., 2004; Torres et al., 2006; Polimene et al., 2012; 2014; 2015, Butenschön et al., 2016).

2.2. The screening Morris method

The GOTM-ERSEM model was subjected initially to a screening sensitivity analysis. This aimed to identify the subset of ERSEM parameters that are most important for the simulation of the minimum oxygen concentration at the study site. The screening sensitivity analysis used the Morris method, as proposed in Morris (1991), modified by Campolongo et al. (2007), and applied with marine models by Cossarini and Solidoro (2008) and Morris et al. (2014). The Morris technique, described thoroughly in Saltelli et al. (2008), is a qualitative sensitive analysis based on the concept of Elementary Effect (EE), which is an approximation of the first order partial derivative of the model output y with respect to an input factor X_i, i.e. a model parameter. If a model has k number of independent input factors X_i, where i=1, 2, ..., k, the elementary effect of the parameter X_i is given by:

$$EE_i^j = \frac{y\left(X_1^j, X_2^j, \ldots, X_{i-1}^j, X_i^j + \varDelta, X_{i+1}^j, \ldots, X_k^j\right) - y\left(X_i^j, X_2^j, \ldots, X_k^j\right)}{\varDelta} \qquad (10)$$

Where j represents an initial point in the space of the parameters, y represents the model output, and the increment $\Delta \in [0,1]$ is a pre-defined proportion of the range of variation of the parameters, which, being constant, allows the sensitivity index to account for the statistical distribution of the input factors (see the explicative example at page 120 in Saltelli et al., 2008). All the input parameters in (10) are incremented, in random order, leading the input vector X to cover a “trajectory” j in the space of the parameters. The trajectory has (k+1) nodes, that are sets of parameter values used to run the model (k+1) times and compute k elementary factors EE^j. A number j=1, …, r of trajectories is built by selecting randomly their j=1, …, r initial points in the space of the parameters. The initial points of the trajectories and the increments of the input factors are computed within ranges of variability that need to be defined.

Following Campolongo et al. (2007), we computed the sensitivity index for the input parameter X_i by averaging the absolute values of the elementary effects of that parameter across all the trajectories:

$$\mu_i^* = \frac{1}{r}\Sigma_{j=1}^{r}|EE_j^i| \quad (11)$$

The sensitivity index μ_i^* is computed by averaging $\left|EE_j^i\right|$ computed at points sampled within the whole space of the parameters. Therefore, this technique can be considered as a global screening technique, though each single elementary effect is a first order derivative, i.e. a local sensitivity (Campolongo et al., 2007). Importantly, the index μ* allows one to reduce the computational cost of the screening analysis by computing the sensitivity of input parameters pooled in groups. In fact, Campolongo et al., 2007 and Saltelli et al. (2008) showed that using the absolute values of the Elementary Effects preserves the reliability of the sensitivity index in eq. 11 also when the parameters within a group are changed by the same Δ proportion simultaneously, but in opposite direction (i.e. different signs of Δ). Exploiting this property, we subdivided the parameters of ERSEM into groups that refer to different ecosystem processes, and the sensitivity index μ* was calculated for each group (see Ciavatta et al., 2009 for an analogous approach). The drawback of grouping input factors is the loss of information regarding the relative importance of factors belonging to the same group. This was addressed by performing a Monte Carlo-based sensitivity analysis of the parameters within the groups.

2.3. Monte Carlo simulations and ranking method

A Monte Carlo sampling-based sensitivity analysis was applied to rank the importance of the *m* parameters $\mathbf{X}=(X_1, X_2, \ldots, X_i \ldots, X_m)$, i=1, 2, …, m, within the groups identified as most important in the Morris screening analysis (Saltelli et al., 2008). A crude Monte Carlo sampling scheme was used to generate a number n of realizations of the input factor vector **X**. These realizations were input to *n* model simulations that computed the target model output y in equation (3). The input-output relationship was represented by means of a multiple-regression model:

$$y = b_0 + \sum_{i=1}^{m} b_i X_i + residuals \tag{12}$$

and the standardized regression coefficients β_i were used as global sensitivity indices of the input factors (Saltelli et al., 2008):

$$\beta_i = \frac{b_i \sigma_{X_i}}{\sigma_y} \tag{13}$$

Where σ_{X_i} and σ_y are the standard deviations of the realizations of the input factor X_i and of the model output y, respectively. The regression coefficients in eq. (13) provide meaningful parameter rankings only when the linear regression explains a relatively large fraction of the model output variability (Saltelli et al., 2000). We assessed the linear regression by computing the fraction of explained variance (R^2), the regression significance (F-statistic of the null hypothesis of constant model, $p<0.01$), as well as the significance of the standardized regression coefficients (t-statistic, $p<0.05$).

2.4 Set up of the analysis

2.4.1 Set up of the model

The 1-D GOTM-ERSEM model was implemented for an oligotrophic site in the central Arabian Sea (65ºE, 13ºN), which falls within the OMZ in this region (Paulmier and Ruiz-Pino, 2009; Naqvi, 1991). The actual depth of the central Arabian Sea is close to 4500 m, but we have simulated the water column up to a depth of 500 m only, using 100 vertical levels. The selection of this maximum depth was based on previous studies, indicating that the upper 500 meters include the upper oxycline and the absolute minimum of oxygen (McCreary et al., 2013, Resplandy et al., 2012), as confirmed here by test simulations extending till the depth of 1500 meters (not shown). A deep-water remineralization closure scheme was applied to the lower boundary of the model (Figure 2). The closure describes the recycling of organic matter (producing inorganic nutrients and CO_2) as a linear function of the sinking biomass, at rates specified by the ERSEM remineralization parameters (Blackford et al., 2004; Butenschön et al., 2016).

In our application, GOTM simulation was relaxed to daily profiles of salinity and temperature derived from the output of the 3-D model HYCOM configured for the Indian Ocean (George et al., 2010). GOTM-ERSEM was forced with daily meteorological data and cloud cover data from NCEP/NCAR reanalysis (Kalnay et al., 1996) and precipitation data from GPCP (Adler et al., 2003). The profiles of the initial conditions of nutrients (nitrate, phosphate and silicate) were obtained from the World Ocean Atlas 2009 (Garcia et al., 2010a; Garcia et al., 2010b). The initial condition of oxygen was set equal to a constant value throughout the water column (20 mmol m^{-3}, consistent with climatological data at depth), to avoid pre-setting the position of the OMZ in the water column and letting the model simulation setting it. The model simulation was carried out for a period of four years (2002 to 2005) after a spin-up time of five years, which has been shown to be sufficient to achieve stable solutions of the 1D GOTM-ERSEM integration (e.g. Blackford et al

2004; Polimene et al., 2014) . The output of the four-year simulation was used to assess the skill of the model in simulating oxygen and nutrients (nitrate, phosphate and silicate), through comparison with World Ocean Atlas 2009 climatology (Garcia et al., 2010a; Garcia et al., 2010b), in the absence of in-situ observations of these variables at the study site. The sensitivity analysis and parameter ranking was carried out on the model output for the year 2002.

2.4.2 Set up of the Morris screening analysis

The configuration of ERSEM applied here has 342 pelagic parameters. However, parameters defining biogeochemical constants (e.g. the inverse of the Redfield ratio of phosphorous to carbon) were not object of this investigation, thus the number of parameters included in the screening analysis was 207. These parameters were categorized and divided into k=21 groups (Table 1). The increment of the input factors was set $\Delta=2/3$, following the recommendation in Saltelli et al., 2008.

Groups 1 to 7 comprised of parameters characterizing primary production, whereas groups 8 to 12 were bacteria-related parameters. The remaining groups included zooplankton parameters, food matrix parameters, deep-water remineralization closure parameters, sedimentation parameters and light extinction parameters.

The analysis was carried out with the range of variability of the uniform distribution of the parameters kept within -30% to +30% of the reference value of the parameters. The 30% variation with respect to the reference values of the parameters is often assumed in sensitivity analyses of environmental models when the real ranges are unknown (see, e.g., Ciavatta et al., 2009; Polimene et al., 2015; Pinna et al., 2015). In our application of the Morris method, we set a number r=10 trajectories for the k=21 groups of parameters. Thus the computational cost of the screening sensitivity analysis was $(k+1) \cdot r = 220$ model runs.

2.4.3 Set-up of the Monte Carlo sampling-based sensitivity analysis

The Monte Carlo sampling-based sensitivity analysis was performed by selecting n=1000 random values for each of the *m* independent input parameters found to be the most relevant in the screening analysis. In choosing this number *n* of model simulations, we considered the rule of thumb of at least 20 realizations for each input factor desirable for multiple regression analysis (Hair at al., 2006). As in the Morris application, we have used uniform distribution to generate random values within the range -30% to +30% of the reference value of the input parameters (see, e.g., Ciavatta et al., 2009; Polimene et al., 2015; Pinna et al., 2015). Each realization of the vector of input parameters was used to run a model simulation. The multiple regression analysis of the input-output relationship was performed using the software Origin, and the regression coefficients defining the sensitivity index for the parameter ranking were estimated using the least-squares method proposed by Draper and Smith (1981).

3 Results

3.1 Skill of the reference simulation

The model had significant skill in simulating the climatology of oxygen and nutrient observations at the study site. This is illustrated in Figures 3 and 4, which show comparable climatologies from the model output and the World Ocean Dataset 2009, and it is demonstrated quantitatively by the Taylor diagram in Figure 5, where all the variables are close to the optimal skill point.

The model represented the magnitude and range of all the variables, though it tended to underestimate nitrate and to overestimate phosphate (Figure 3). At surface, both the climatological data and the model confirm stable oligotrophic conditions, with nitrate concentrations < 2 mmol m^{-3} and phosphate < 0.5 mmol m^{-3} in all the months. The vertical gradients were reproduced adequately by the model: oxygen decreased from the aerated surface layer downwards, nutrients were higher in the ocean interior, and changes occurred more sharply between 50-200 m. In particular, in Figure 4, the model represented well the average vertical profile of oxygen ($\rho > 0.99$, $p < 0.01$, and RMSD=19 mmol m^{-3}), the depth of its absolute minimum (200 m in both the data and model climatologies), though the model tended to underestimate the oxygen climatological data on average (bias = -17 mmol m^{-3}).

The seasonal variability of the data is less well represented in the simulation. The model simulated the deepening of mixed layer and associated variability in DO concentration during the monsoon season from June to September (Figure 3). Some fluctuations of nutrient profiles are also reproduced in the monsoon season in the upper layer, but to a much lower extent. In particular, the simulation did not capture temporal variability below the oxycline and nutricline, such as the increase of silicate concentration at depth ~400 in May-June in the climatology dataset. Biases below the nutricline are likely due to the lack of lateral advection, as mentioned in Discussion.

The general good agreement between model and data is confirmed by the results in Figure 5, since the correlation coefficients are high ($\rho > 0.9$, $p < 0.01$), the variability of the climatology and the simulation are comparable ($\sigma/\sigma_o = 0.9$), and the biases are relatively low, with the exceptions of phosphate that was overestimated ($bias/\sigma_o = 0.4$) and nitrate that was underestimated ($bias/\sigma_o = -0.5$). High scores for the skill metrics are driven primarily by the model ability in simulating the average vertical gradients of the climatological data, rather than their seasonal variability.

3.2 Screening sensitivity analysis

The relevance of the groups of parameters resulting from the Morris analysis is shown in Figure 6. The 14th group (zooplankton loss parameters), 9th group (bacterial loss parameters) and 11th group (additional nutrient remineralization parameters) were found to be the three most relevant groups for the simulation of the OMZ, in order. The parameters included in the groups 14 and 9 characterize the biological processes of oxygen consumption by the zooplankton functional groups and by bacterial functional group, respectively. The parameters included in group 11 are associated to first order remineralization processes converting organic nutrients onto inorganic forms (phosphate and ammonium). These processes are assumed to complement the biologically mediated remineralization activity which is described in the model (Blackford et al., 2004; Butenschön et al., 2016). A complete list of the 38 parameters included in the three above groups is given in Table 2.

3.3 Ranking of the parameters

The 38 model parameters that emerged collectively as the most important in the screening analysis (Table 2) were the input factors to the Monte Carlo sampling-based sensitivity and ranking analysis. The results are presented in Table 3, which ranks the parameters in descending order of importance based on the magnitude of the standardized regression coefficient $|\beta|$ (eq. 13).

The four most important parameters, with $|\beta|$ higher than 0.3, were found to be: 1) the cubic half saturation constant for oxygenic control of denitrification (chN3oX); 2) the parameter regulating the fraction of ingested matter excreted (i.e. not assimilated) by the heterotrophic nanoflagellates (pu_eaZ6X); 3) the bacterial efficiency at low oxygen levels (puB1oX); and 4) the specific rate of bacterial release of capsular material (frB1R3). The first 21 parameters in Table 3 were associated to significant regression coefficients (t-test, $p<0.05$), while the remaining 17 parameters did not significantly influence the simulated minimum of oxygen. Importantly, the ranking provided by the sensitivity analysis was trustworthy, since the linear regression explained most of the model output variability ($R^2=0.94$), and it was highly significant (F-test, $p<0.01$) (see Table 3).

To assess further the robustness of the ranking, we performed a supplementary regression analysis including only the first eleven independent variables in Table 3 (i.e. those with $|\beta|>0.1$, arbitrarily); the results confirmed the overall dominance of those parameters in explaining the dissolved oxygen variability ($R^2=0.93$, F-test $p<0.01$), and reproduced their ranking in Table 3. This suggests that the results in Table 3 were not affected remarkably by redundancy among the many model parameters included in the analysis. We note also that the parameters object of the regression analysis were sampled randomly from independent uniform distributions, thus multicollinearity among regressors is not an issue in our application.

4. Discussion

The results indicated that model parameters regulating the metabolism of aerobic and anaerobic (denitrifying) bacteria and the loss terms of zooplankton (heterotrophic nanoflagellates, HNAN) play a prime role in our simulation of the OMZ at the study site. Assuming that the ranking of the model parameters reflects the relevance of the processes they characterize, we have inferred a conceptual model describing the most important biogeochemical processes affecting the OMZ in the oligotrophic site of the Arabian Sea area studied here (Figure 7).

At the surface, where light is sufficient to allow net growth of primary producers, oxygen is produced by phytoplankton and is consumed by both autotrophic and heterotrophic (zooplankton and bacteria) respiration, besides being exchanged with the atmosphere (Figure 7). Net photosynthesis fades at a depth of ~100 m marking the threshold between euphotic and twilight zone.

In the upper twilight zone (~100-200 m), heterotrophic prokaryotes are the most active organisms, while grazers' biomass (mesozooplankton) is close to zero because of the negligible concentration of phytoplankton. Here oxygen is consumed by remineralization of the sinking detritus and therefore DO decreases drastically. Anaerobic respiration of POC via denitrification becomes relevant, though the level of oxygen remains sufficient to also allow some aerobic respiration (Figure 7). As a consequence, the Michaelis-Menten constant "chN3oX" emerges as the most important parameter in our analysis, because it regulates the magnitude of denitrification and therefore the amount of organic matter which is respired without consuming oxygen ("chN3oX" in equation 8 has rank=1 in Table 3). In other words, this parameter impacts the OMZ simulation because it sets the threshold at which bacteria either do or do not consume oxygen. The efficiency of bacteria in using POC to grow is also crucial in determining the intensity of the OMZ, here approximated by the absolute minimum value of the oxygen profile. Low efficiency implies that a large portion of the carbon taken up by bacteria is respired, with a consequent high oxygen consumption (or nitrate consumption, in case of anaerobic metabolism) and low net bacterial production. On the contrary, high efficiency implies that a lower portion of carbon is respired, resulting in a higher bacteria biomass production. This explains the high rank scored by the bacteria efficiency parameter ("puB1oX" ranked 3rd in Table 3).

At ~200 m, both the simulation and the climatology show the absolute minimum of oxygen (Figure 4). Here there is a zone where the sinking detritus is still sufficient to allow some bacterial respiration. At this depth POC concentration is low and becomes a limiting factor for bacteria growth and respiration. This is illustrated in Figure 8, which shows that the simulated bacteria biomass follows (with a lag) the seasonal cycle of the detritus sinking from the euphotic zone. POC limitation implies that the oxygen minimum is linked to the ability of heterotrophs (bacteria and zooplankton predators) to survive in starvation conditions, i.e. it is linked to heterotrophs' "basal metabolism". This explains why parameters defining the basal metabolism of heterotrophs (i.e. bacteria rest respiration, and mortality of bacteria, HNAN and microzooplankton) are all within the ten most important parameters in Table 3. In other words, these parameters are important because they determine how much the heterotrophs are suited to survive and consume oxygen at the depth where POC is a limiting food.

Below the depth of 200 meters and till the depth of 500 m simulated here, oxygen increases slightly with depth because bacteria biomass is small (due to the reduced export of POC) and the consumption of oxygen is negligible. At that depth, the lack of heterotrophic biomass and low vertical transport maintain the DO concentration at ~5 mmol L^{-1}, which is a reminiscence of the initial condition, slightly lower than the climatological data at the study site (Figure 4).

The conceptual model in Figure 7 is consistent with previous experimental and modelling works, which showed that the dynamic POC-bacteria (both anaerobic and denitrifiers) is a relevant biological driver of the OMZ in the global oceans, as well as in the Arabian Sea (e.g. Ulloa et al., 2012; Roullier et al., 2014). Bacteria are the principal contributors of the community respiration in the pelagic ecosystems (Carlson et al., 2007, Cole. et al., 1988) and diverse microbial community act simultaneously both at the transition zones and within global OMZs (Beman and Carolan, 2013). This clearly holds for the Arabian Sea, where, for example, Gonsalves et al. (2011) observed aerobic and denitrifying bacteria coexisting in both a coastal site and an off-shore site, though denitrifiers were dominating the community at the coastal site. The importance of bacterial degradation of detritus, rather than dissolved organic carbon, was stressed also in previous modelling studies of the Arabian Sea (Anderson et al., 2007), and Roullier et al. (2014) argued that the anaerobic microbial respiration enhances production and accumulation of observed particles (of size < 100 μm) in the upper part of the OMZ in this region. Figure 8 shows that the absolute values of POC and bacteria biomass simulated by the model are low at the study site. This can be due to the oligotrophic nature of the central part of the Arabian Sea, which is a permanently stratified area and has lower biomass and bacterial activity with respect to the coastal regions. In fact, Gonsalves et al. (2011) measured lower concentrations of total organic carbon TOC in an offshore site with respect to a coastal one, and Campbell et al. (1998) reported lower bacteria and phytoplankton biomass in the central part of the basin than in in-shore waters.

Besides the POC-bacteria dynamics, the “complexity” of our ecosystem model pointed out the relevance of two processes less extensively investigated in previous modelling analysis of the OMZ in the Arabian Sea, i.e. the grazing on bacteria and the bacteria release of recalcitrant organic carbon (Figure 7).

In the simulated trophic web, bacterial biomass (thus its overall respiration and oxygen control) is top-down controlled by zooplankton grazing. Therefore, the parameter defining the efficiency of heterotrophic nanoflagellates (HNAN), which are the main grazers of bacteria, became an important factor for the formation of the OMZ, explaining rank=2 of “pu_eaZ6X” in Table 3. The primary role of HNAN in controlling bacterial biomass in the Arabian Sea was observed previously by Weisse (1999).

Our application suggested for the first time that bacteria production of recalcitrant organic carbon can have a relevant influence on the maintenance of an OMZ. The parameter regulating the release of capsular material by bacteria ranked in 4th position (frB1R3 in Table 3). This release produces recalcitrant dissolved organic carbon (RDOC), which is regarded as an important element for the global carbon cycle and potentially for climate regulation (Jiao et al., 2010; 2014). Our results suggest that the bacterially-mediated production of RDOC influences also the maintenance of the OMZs, because it reduces the bulk biomass of bacteria and therefore their oxygen consumption trough respiration.

The sensitivity analysis suggested that processes related to primary production have a less direct impact on the oxygen minimum at the site investigated here, though these processes are of importance in OMZ formation and evolution in general (Diaz and Rosenberg, 2008). In our study, the group of parameters related to primary production had relatively low importance and were not selected by the Morris screening analysis (groups 1-7 in Figure 6). This can be due to the fact that the model was implemented in a relatively oligotrophic area with a fully stratified water column (Figure 3) and relatively low primary production. Therefore, the mass of organic matter exported from the surface to the OMZ is low in absolute value (Figure 8). The weak connection between the euphotic (productive) zone and the twilight zone (where the OMZ is observed), makes the OMZ weakly dependent on primary production in our simulation.

Though our study site was chosen in a relatively stable oligotrophic area of the open Arabian Sea, where vertical 1-D processes were found to be dominant in driving both particle transport (Roullier et al., 2014) and denitrification (Anderson et al., 2007), the use of a 1-D model is certainly a limitation of our work. The assimilation of temperature and salinity profiles integrates the effects of 3-D hydrodynamics to a certain extent (Section 2.4.1), but lateral fluxes of oxygen and other biogeochemical components potentially relevant to the OMZ were not simulated. Therefore, we focused our simulation on the first 500 m of the water column, were the absolute minimum oxygen value is observed (Figure 4). This zone is above the deep oxycline at ~1000 m, typically observed in the Arabian Sea due to the influx of deep oxygen-rich waters (Swallow, 1984; Ulloa et al., 2012; Roullier et al., 2014) that clearly cannot be represented by a 1D model configuration. Furthermore, the model cannot account for the episodic intrusion of oxygen within the OMZ (Ulloa et al., 2012), which might contribute in sustaining aerobic activity. Our model does simulate aerobic activity within the OMZ (sustained by the residual initial conditions) however it does not reproduce the presence of mesozooplankton at depth, which are reported in previous works (e.g. Banse et al., 2014; Roullier et al., 2014). Similarly, the lack of lateral supply of POC might also contribute to the low concertation of detritus simulated at depth (Figure 8). Finally, the absence of lateral circulation might explain also the discrepancies between simulated and climatological seasonal cycles of nutrients and oxygen at depths below the absolute minimum (Figure 3). In particular, the model could not simulate the increase in silicate concentration observed typically in June at ~400 m, which extends upwards, and the decrease of nitrate concentration observed in June and October between 200 and 400 m. The relative increase of oxygen observed in climatological summer and autumn between 200 and 400m was not captured by the model either. However, the average annual vertical gradients were well represented by the model, as demonstrated by the skill metrics in Figure 5, and this supports further the use of the oxygen minimum value as target metric of the sensitivity analysis The choice of this OMZ indicator is coherent with the objective of this paper, which focuses on the effects of biogeochemical processes on the intensity of the minimum oxygen, rather than on the extension of the OMZ (e.g. water volume; Cabré et al., 2015), which cannot be represented by a one-dimensional model.

The 1-D ERSEM-GOTM applied here resulted adequate also in previous studies in the Arabian Sea (Blackford and Burkill, 2002; Blackford et al., 2004), as well as in other shelf and open ocean locations (e.g. Butenschön et al., 2016; Torres et al., 2006). We argue that our 1-D implementation in a relative stable OMZ site is particularly suitable for the objective of our biology-focused sensitivity analysis. On the one hand, a comprehensive sensitivity analysis can have a prohibitive computational cost with 3-D implementations of complex ecosystem models (Pastres and Ciavatta, 2005). On the other hand, the 1-D implementation allowed us to focus on the biogeochemical processes in "isolation", i.e. without the need to disentangle them from physical-driven mechanisms that could influence the simulation in 3-D implementations. In particular, the use of the ERSEM model (Butenschön et al., 2016) which embeds a fully resolved microbial loop (Polimene et al., 2006 and 2007) allowed us to focus on bacterial processes with a level of details not resolved in most of the marine ecosystem models applied previously (e.g. Anderson et al., 2007, Resplandy et al., 2012; McCreary et al., 2013), including previous versions of ERSEM as well (Blackford and Burkill, 2002; Blackford et al., 2004).

Finally, we recognize that our approach is based on the assumption that the ranking of the parameters reflects directly the ranking of the processes (i.e., if a parameter is important, the equation/process that includes that parameter is important) and that this assumption could not be always true. Indeed a parameter can result important (or not) because the equation/process in which is included is not well represented in the model. For example, a specific process could be poorly represented in the model even if it is crucial for the functioning of the real ecosystem, leading the parameter to be neglected by the sensitivity analysis. These weaknesses, which are implicit in any modelling study, need to be kept into account and inevitably add some degree of uncertainty to the results presented here.

5. Conclusions

This paper identifies the most relevant biogeochemical processes involved in the ERSEM simulation of the OMZ in a central oligotrophic site of the Arabian Sea. We found that processes related to both aerobic and denitrifying bacteria along with the loss term of bacteria and heterotrophic flagellates (HNAN) are the most important. This outcome also highlights the relevance of our new representation of denitrification in ERSEM. Other processes, like primary production, were found to be less relevant. These findings are consistent with previous studies, which suggested that the impact of bacteria on the OMZ is important in the Arabian Sea as well as in other parts of the global oceans (e.g. Ulloa et al., 2012; Roullier et al., 2014). Presently, only few marine ecosystem models include an explicit description of the microbial loop, but our study strongly indicates that OMZ models should explicitly include heterotrophic bacteria and their production of recalcitrant carbon.

Despite the clear limits of our 1-D model configuration, our application provided an objective list of the most important biogeochemical parameters that need to be quantified for future applications of a global configuration of ERSEM (Kwiatkowski et al., 2014) aiming to simulate the biogeochemical and physical dynamic underpinning OMZs and their predicted expansions. To this regard, we note that the sensitivity methods proposed here are in principle applicable to OMZ scalar metrics alternative to the absolute minimum applied here (e.g. OMZ area and volume below pre-set oxygen thresholds, Cabré et al., 2015) more suitable for three-dimensional applications accounting for horizontal transport processes.

Finally, we note that the analysis presented here is the first systematic sensitivity study of the ERSEM model with respect to its full set of parameters. The tools developed here are not limited to the study of the OMZs but can be applied straightforwardly to the study of different aspects of ocean biogeochemistry (e.g. carbon fluxes in the subtropical gyres), and to prioritize the parameters to be estimated in data assimilative simulations, as we are investigating in the framework of ongoing work.

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Table 1. List of the 21 groups of pelagic parameters investigated in the screening Morris analysis.

Group	Description	Number of parameters
1	Photosynthetic parameters	20
2	Metabolic carbon lost parameters (respiration)	5
3	Lost carbon by lysis parameters	4
4	Nutrient parameters	38
5	Q_{10} parameters : regulating temperature factors	4
6	Photosynthetically available fraction of irradiation	1
7	Other primary production parameters	17
8	Maximum specific gross uptake of bacteria	6
9	Bacterial loss parameters	6
10	Nutrient uptake / remineralization	4
11	Additional nutrient remineralization	11
12	Other bacteria parameters	2
13	Maximum zooplankton uptake	13
14	Zooplankton loss parameters	21
15	Q_{10} of zooplankton	7
16	Zooplankton nutrient quotas	6
17	Food matrix parameters	20
18	Deep-water remineralization closure parameters	4
19	Sedimentation parameters	7
20	Cellular structural parameters	4
21	Light extinction parameters	7

Table 2. Parameters included in the groups 9, 11 and 14 of the Morris screening analysis, which were investigated in the Monte Carlo-based sensitivity analysis.

No.	Notation	Description and units
Group 9: Bacterial loss parameters		
1	frB1R3	Fraction of activity respiration of bacterial uptake converted to semi-refractory DOC [unitl]
2	puB1oX	Bacterial growth efficiency at low oxygen levels [unitless]
3	puB1X	Bacterial growth efficiency at high oxygen levels [unitless]
4	sdB1X	Specific mortality of bacteria at reference temperature [day^{-1}]
5	srsB1X	Specific rest respiration at reference temperature [day^{-1}]
6	DeniX	Maximum specific denitrification rate [day^{-1}]
Group 11: Additional nutrient remineralization parameters		
7	chN3oX	Michaelis-Menten constant for oxygenic control of denitrification [mmol O$_2$ m^{-3}]
8	puR4_B1X	Fraction of small size POM available for bacteria uptake [unitless]
9	puR6_B1X	Fraction of medium size POM available for bacteria [unitless]
10	puR8_B1X	Fraction of large size POM available for bacteria [unitless]
11	redfieldX	Carbon to Nitrogen Redfield ratio [unitless]
12	rR2R1X	Specific rate for breakdown of semi-labile to labile DOC [unitless]
13	sN4N3X	Specific nitrification rate at reference temperature and silt concentration [day^{-1}]
14	sR1N1X	Specific dissolution of labile DOP to phosphate [day^{-1}]
15	sR1N4X	Specific dissolution of labile DON to ammonium [day^{-1}]
16	reoX	Specific reoxidation rate of reduction equivalents [day^{-1}]
17	R1R2X	Labile fraction of DOM production [unitless]
Group 14: Zooplankton loss parameters		
18	pe_R1Z4X	DOM-fraction of uptake excreted by mesozooplankton [unitless]
19	pu_eaRZ4X	Fraction of POM-uptake excreted by mesozooplankton [unitless]
20	pu_eaZ4X	Fraction of prey-uptake excreted by mesozooplankton [unitless]
21	puZ4X	Mesozooplankton assimilation efficiency [unitless]
22	sdZ4oX	Specific mortality of mesozooplankton due to oxygen limitation [day^{-1}]
23	sdZ4X	Specific basal mortality of mesozooplankton [day^{-1}]
24	srsZ4X	Specific rest respiration of mesozooplankton at reference temperature [day^{-1}]
25	Z4mortX	Specific overwintering mortality of mesozooplankton [day^{-1}]
26	Z4repwX	Specific overwintering respiration of mesozooplankton [day^{-1}]
27	pe_R1Z5X	DOM-fraction of uptake excreted by microzooplankton [unitless]
28	pu_eaZ5X	Fraction of prey-uptake excreted by microzooplankton [unitless]
29	puZ5X	Microplankton assimilation efficiency [unitless]
30	sdZ5oX	Specific mortality of microzooplantkon due to oxygen limitation [day^{-1}]
31	sdZ5X	Specific basal mortality of microzooplankton [day^{-1}]
32	srsZ5X	Specific rest respiration of microzooplankton at reference temperature [day^{-1}]
33	pe_R1Z6X	DOM-fraction of uptake excreted by heteroflagellates [unitless]
34	pu_eaZ6X	Fraction of prey-uptake excreted by heteroflagellates [unitless]
35	puZ6X	Heteroflagellates assimilation efficiency [unitless]
36	sdZ6oX	Specific mortality of heteroflagellates due to oxygen limitation [day^{-1}]
37	sdZ6X	Specific basal mortality of heteroflagellates [day^{-1}]
38	srsZ6X	Specific rest respiration of heteroflagellates at reference temperature [day^{-1}]

Table 3. Ranking of the parameters from the regression analysis of the output of the Monte Carlo simulations. | β | is the absolute value of the standardized regression coefficients, which are reported with their standard errors, and p-value is the level of significance of the t-test on the parameters. See Table 2 for description of the parameter notations. N.S. indicates model parameters that were not associated to significant regression coefficients (t-statistic).

Rank	Parameter	| β |	Standard error	p-value	Group
1	chN3oX	0.462	0.008	$p<0.05$	11
2	pu_eaZ6X	0.422	0.008	$p<0.05$	14
3	puB1oX	0.373	0.008	$p<0.05$	9
4	frB1R3	0.314	0.008	$p<0.05$	9
5	pu_eaZ5X	0.300	0.008	$p<0.05$	14
6	srsB1X	0.251	0.008	$p<0.05$	9
7	sdZ6oX	0.185	0.008	$p<0.05$	14
8	sdB1X	0.170	0.008	$p<0.05$	9
9	puZ5X	0.139	0.008	$p<0.05$	14
10	sdZ5oX	0.110	0.008	$p<0.05$	14
11	puZ6X	0.109	0.008	$p<0.05$	14
12	srsZ5X	0.080	0.008	$p<0.05$	14
13	puZ4X	0.044	0.008	$p<0.05$	14
14	srsZ6X	0.037	0.008	$p<0.05$	14
15	puB1X	0.036	0.008	$p<0.05$	9
16	sdZ6X	0.035	0.008	$p<0.05$	14
17	pe_R1Z4X	0.031	0.008	$p<0.05$	14
18	pu_eaZ4X	0.031	0.008	$p<0.05$	14
19	sdZ5X	0.021	0.008	$p<0.05$	14
20	srsZ4X	0.020	0.008	$p<0.05$	14
21	rR2R1X	0.018	0.008	$p<0.05$	11
22	sR1N1X	0.010	0.008	N.S.	11
23	DeniX	0.009	0.008	N.S.	9
24	Z4mortX	0.009	0.008	N.S.	14
25	pe_R1Z5X	0.008	0.008	N.S.	14
26	sdZ4X	0.008	0.008	N.S.	14
27	sR1N4X	0.006	0.008	N.S.	11
28	pe_R1Z6X	0.005	0.008	N.S.	14
29	redfieldX	0.005	0.008	N.S.	11
30	sdZ4oX	0.005	0.008	N.S.	14
31	puR4_B1X	0.004	0.008	N.S.	11
32	reoX	0.004	0.008	N.S.	11
33	Z4repwX	0.004	0.008	N.S.	14
34	sN4N3X	0.004	0.008	N.S.	11
35	R1R2X	0.003	0.008	N.S.	11
36	pu_eaRZ4X	0.002	0.008	N.S.	14
37	puR6_B1X	0.001	0.008	N.S.	11
38	puR8_B1X	0.001	0.008	N.S.	11

Regression statistics:
Number of cases = 1000; Coefficient of determination: $R^2=0.94$; F-value= 414.2

Figure Captions

Figure 1. Location of the study site in the Arabian Sea (65°E, 13°N).

Figure 2. Schematic of the coupled GOTM-ERSEM model configuration used in this study. ERSEM describes the biogeochemical and trophic processes that drive the evolution of inorganic and organic variables in the simulated pelagic environment, and the exchanges of oxygen and carbon dioxide with the atmosphere. Remineralization closure equations represent the fluxes at the deep water boundary. GOTM describes the physical vertical mixing in the water column, taking account of the meteorological forcing. The black arrows represent ecosystem processes described by Butenschön et al. (2016), and the white arrow represents denitrification, which was included in ERSEM in this work.

Figure 3. Model climatology computed from a simulation of years 2002-2005 (left), versus climatology data derived from the World Ocean Dataset 2009 (right), for oxygen and nutrients.

Figure 4. Annual average profile of oxygen in the climatologies derived from the model simulation of years 2002-2005 (“Model”) and from the World Ocean Dataset 2009 (“Data”).

Figure 5. Taylor diagram summarizing the model skill in reproducing the climatological data of oxygen (O2), nitrate (NO3), phosphate (PO4) and silicate (SiO). The diagram represents the Pearson correlation coefficient (ρ), the standard deviations of model and data (σ and σo, respectively) and the model bias. The optimal skill point is represented by the black dot with coordinates (1,0).

Figure 6. Result of the screening analysis based on the Morris method applied to 21 groups of

model parameters. The three most important groups (i.e. the ones with the highest values of the sensitivity index μ*) were, in order: I) group 14 (zooplankton loss parameters); II) group 9 (bacterial loss parameters); and III) group 11 (additional nutrient remineralization parameters).

Figure 7. Conceptual diagram of the most relevant biogeochemical processes driving the Oxygen Minimum Zone (OMZ) at the oligotrophic study site in the open Arabian Sea. At surface, oxygen (O2) is exchanged with the atmosphere, produced by phytoplankton, and consumed by both autotrophic and heterotrophic (zooplankton and bacteria) respiration. Net photosynthesis fades at the depth of ~100 m, which parts euphotic and twilight zone. Below this depth, bacteria remineralize aerobically the detritus sinking from the surface, thus consuming oxygen down to its lowest value at ~200 m. At low oxygen values, bacteria respire by reducing nitrate (NO3) via denitrification. We found that the release of recalcitrant dissolved organic carbon (RDOC) and grazing of heterotrophic nanoflagellates (HNAN) also contribute significantly to the formation of the OMZ, by reducing the bulk biomass of bacteria, hence their overall respiration.

Figure 8. Simulated annual evolution of particulate organic carbon (POC, continuous blue line) and bacteria biomass (dashed red line), at the depth of 200 m where the average annual minimum of dissolved oxygen occurs.