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# Quantifying the heterogeneity of hypoxic and anoxic areas in the Baltic Sea by a simplified coupled hydrodynamic-oxygen consumption model approach



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## ABSTRACT

The Baltic Sea deep waters suffer from extended areas of hypoxia and anoxia. Their intra- and inter-annual variability is mainly determined by saline inflows which transport oxygenated water to deeper layers. During the last decades, oxygen conditions in the Baltic Sea have generally worsened and thus, the extent of hypoxic as well as anoxic bottom water has increased considerably. Climate change may further increase hypoxia due to changes in the atmospheric forcing conditions resulting in less deep water renewal Baltic inflows, decreased oxygen solubility and increased respiration rates. Feedback from climate change can amplify effects from eutrophication. A decline in oxygen conditions has generally a negative impact on marine life in the Baltic Sea. Thus, a detailed description of the evolution of oxygenated, hypoxic and anoxic areas is particularly required when studying oxygen-related processes such as habitat utilization of spawning fish, survival rates of their eggs as well as settlement probability of juveniles. One of today's major challenges is still the modeling of deep water dissolved oxygen, especially for the Baltic Sea with its seasonal and quasi-permanent extended areas of oxygen deficiency. The detailed spatial and temporal evolution of the oxygen concentrations in the entire Baltic Sea have been simulated for the period 1970–2010 by utilizing a hydrodynamic Baltic Sea model coupled to a simple pelagic and benthic oxygen consumption model. Model results are in very good agreement with CTD/O<sub>2</sub>-profiles taken in different areas of the Baltic Sea. The model proved to be a useful tool to describe the detailed evolution of oxygenated, hypoxic and anoxic areas in the entire Baltic Sea. Model results are further applied to determine frequencies of the occurrence of areas of oxygen deficiency and cod reproduction volumes.

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## 1. Introduction

The Baltic Sea (Fig. 1) is one of the largest brackish water ecosystems of the world that is characterized by strong variations in hypoxic and anoxic area extensions (e.g. Fonselius, 1981; Savchuk, 2010). Generally, hypoxia is often defined as O<sub>2</sub> < 2 ml l<sup>-1</sup> while anoxia is understood as the total lack of oxygen. The oxygen deficit develops from an imbalance between oxygen consumption and supply. The Baltic Sea is characterized by a north-eastward salinity gradient, and it is vertically stratified by a seasonal thermocline and a permanent halocline (Leppäranta and Myrberg, 2009). The related pycnoclines limit the transport of oxygen from the surface, and as a result oxygen in deeper layers can become depleted due to the breakdown of organic matter and direct respiration of species belonging to the entire range of trophic levels. Variations in

oxygen conditions are influenced by several mechanisms. The most crucial process for the renewal of oxygen-depleted water masses is the so-called major Baltic inflow, which transport highly saline and oxygenated water masses to the deep basins of the Baltic Sea (Schinke and Matthäus, 1998). The inflow of highly saline water in turn strengthens the stratification which leads to a decrease of vertical mixing; this potentially favors the development of hypoxia (Fonselius, 1981). Additionally, eutrophication intensifies both primary production of organic matter and oxygen consumption needed for its degradation (HELCOM, 2009). This is a major concern in the Baltic Sea where eutrophication is one of the key environmental problems. Furthermore, the ongoing climate warming affects large-scale oxygen conditions by decreased oxygen solubility and increased biogeochemical oxygen demand (Savchuk, 2010). Additionally, changes in the large-scale atmospheric forcing conditions as described by Lehmann et al. (2011) may have reduced the frequency of Baltic inflows and hence contribute to increased hypoxia. Due to these reasons, oxygen conditions in the Baltic Sea have generally worsened during the last decades and thus, the areal extension of hypoxia as well as anoxia has increased (Hansson et al., 2011).

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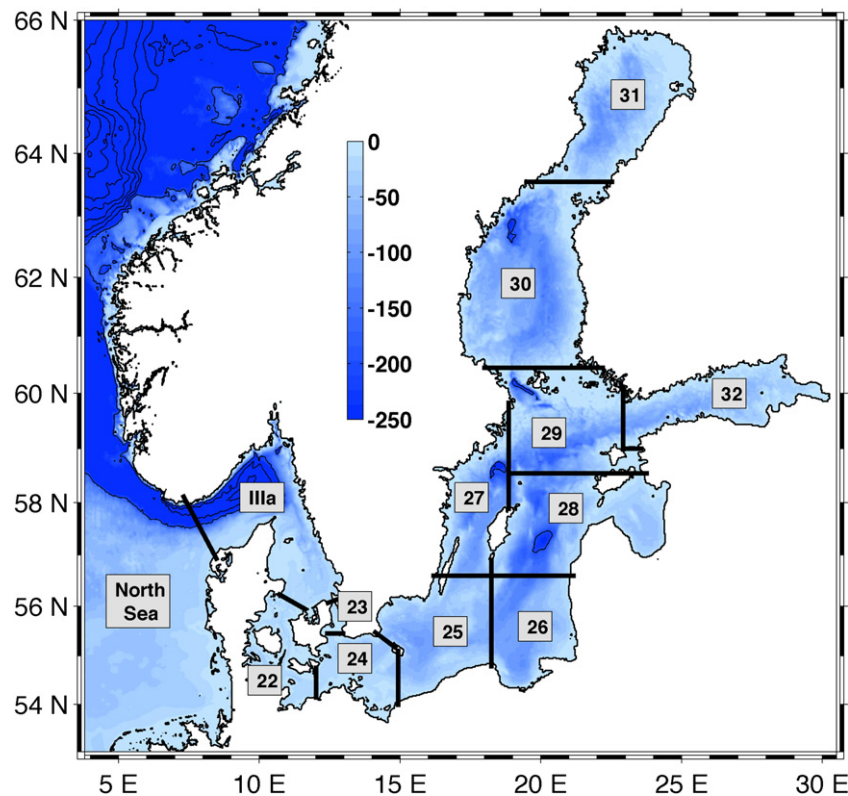


Fig. 1. Baltic Sea according to ICES sub-divisions.  
Based on <http://ices.dk/marine-data/maps/Pages/default.aspx>.

A decline in oxygen conditions has generally a negative impact on marine life in the Baltic Sea. Besides other abiotic parameters such as temperature and salinity, species distribution depends on the level of oxygen, which defines a major habitat requirement to which species' physiology is suited. Threshold levels of oxygen often form the physiological limits for the distribution of adult as well as of early life stages of several species (Hinrichsen et al., 2011). Thus, a detailed description of the evolution of oxygenated, hypoxic and anoxic areas is particularly required when studying oxygen-related processes such as habitat utilization of spawning fish, survival rates of their eggs as well as settlement probability of juveniles.

The main governing mechanisms of the occurrence of hypoxia are understood and can be described by physical–biogeochemical models (e.g. Eilola et al., 2009; Gustafsson, 2012; Neumann et al., 2012; Savchuk and Wulff, 2009). However, the single projection of marine biogeochemical cycles are of limited use because of uncertainties in the Baltic Sea models, the forcing functions and inaccurate nutrient inputs (Meier et al., 2011). Fully coupled biophysical models are a useful tool for understanding the processes related to inter-annual as well as to decadal variability in ecosystem dynamics. With those models it is possible to assess the relative importance of physical forcing independent of the impact of related external nutrient loads, and furthermore to analyze the possible effects of nutrient load reduction strategies (Gustafsson, 2012). However, profound uncertainties of the

biogeochemical cycles are due to unknown initial conditions, the bio-availability of nutrients in land runoff, the parameterization of sediment fluxes and the turnover of nutrients in the sediment (Daewel and Schrum, 2013; Eilola et al., 2011). The expansion of hypoxia reduces the DIN (dissolved inorganic nitrogen) pool by denitrification and the DIP (dissolved inorganic phosphorus) pool increases due to phosphate release from anoxic sediments, while in the shrinking phase the changes are opposite (e.g. Savchuk, 2010). These nutrient variations affect primary production of oxidizing organic matter both directly and through feedback generated by nitrogen fixation (Vahtera et al., 2007). Besides inaccuracies in the physical modeling of the state of the Baltic Sea, all these insufficiently quantified biogeochemical mechanisms additionally influence the oxygen dynamics and the description of hypoxic and anoxic conditions.

However, for the goal oriented studies of oxygen dynamics some aspects of the biogeochemical cycles might be neglected. Instead, for the detailed reproduction of the spatial and temporal evolution of oxygen concentration in the Baltic Sea, we applied a high resolution 3D-hydrodynamical model of the entire Baltic Sea (BSIOM, Lehmann and Hinrichsen, 2000) coupled with a simple pelagic and benthic oxygen consumption model (OXYCON, Bendtsen and Hansen, 2012) over the period 1970–2010. The complex biogeochemical cycle is parameterized by a simple empirical statistical relationship between primary production and oxygen consumption.

Data and model used in this study are described in the following Section. A detailed validation of the model is followed by its applications such as the calculation of the frequencies of occurrence of hypoxic and anoxic areas and cod reproduction volumes. The paper is finalized by a Discussion and conclusions Section.

## 2. Data and methods

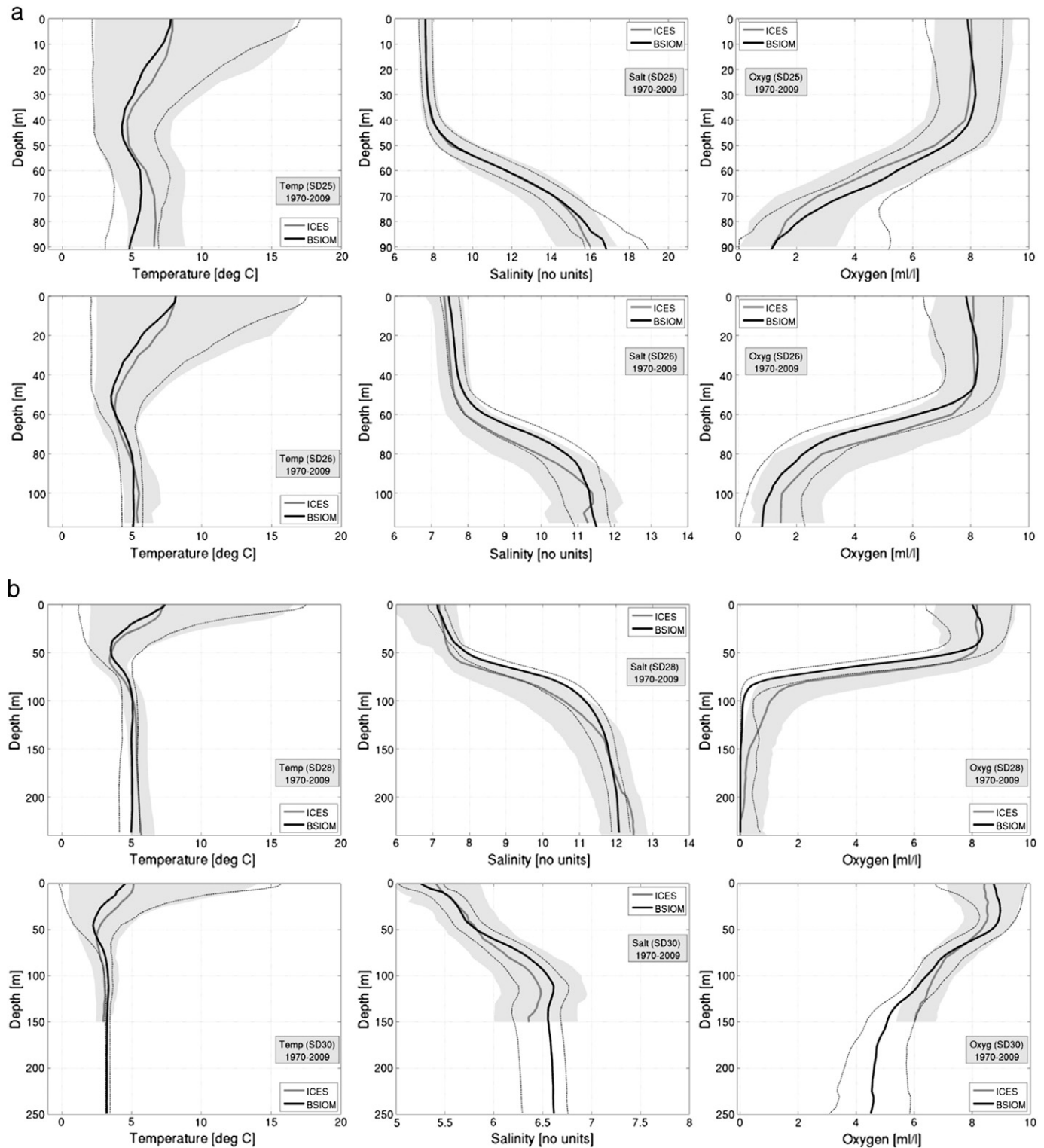
The numerical model used in this study is a three-dimensional coupled sea ice-ocean model of the Baltic Sea (BSIOM, Lehmann and

Table 1

Phytoplankton primary production in the different sea areas. Kat—Kattegat, BS—Belt Sea, BP—Baltic Proper, GoR—Gulf of Riga, GoF—Gulf of Finland, BoS—Bothnian Sea, BoB—Bay of Bothnia.

After Wasmund et al. (2001).

Region	Kat/BS	BP	GoR	GoF	BoS	BoB
Primary production ( $\text{gC m}^{-2} \text{yr}^{-1}$ )	190	200	261	82	52	17



**Fig. 2.** a. Quantiles (0.1, 0.5 and 0.9) of temperature, salinity and oxygen profiles for sub-divisions 25 and 26 for the period 1970–2009 based on ICES monthly database and BSIOM model output. b. Quantiles (0.1, 0.5 and 0.9) of temperature, salinity and oxygen profiles for sub-divisions 28 and 30 for the period 1970–2009 based on ICES monthly database and BSIOM model output.

Hinrichsen, 2000; Lehmann et al., 2002). The horizontal resolution of the coupled sea-ice ocean model is at present 2.5 km, and in the vertical 60 levels are specified, which enables the upper 100 m to be resolved into levels of 3 m thickness. The model domain comprises the Baltic Sea, including the Kattegat and the Skagerrak. At the western boundary, a simplified North Sea basin is connected to the Skagerrak to represent

characteristic North Sea water masses in terms of characteristic temperature and salinity profiles resulting from the different forcing conditions (Lehmann, 1995). Prescribed low frequency sea level variations in the North Sea/Skagerrak were calculated from the BSI (Baltic Sea Index, Lehmann et al., 2002; Novotny et al., 2006). The coupled sea ice-ocean model is forced by realistic atmospheric conditions taken from the



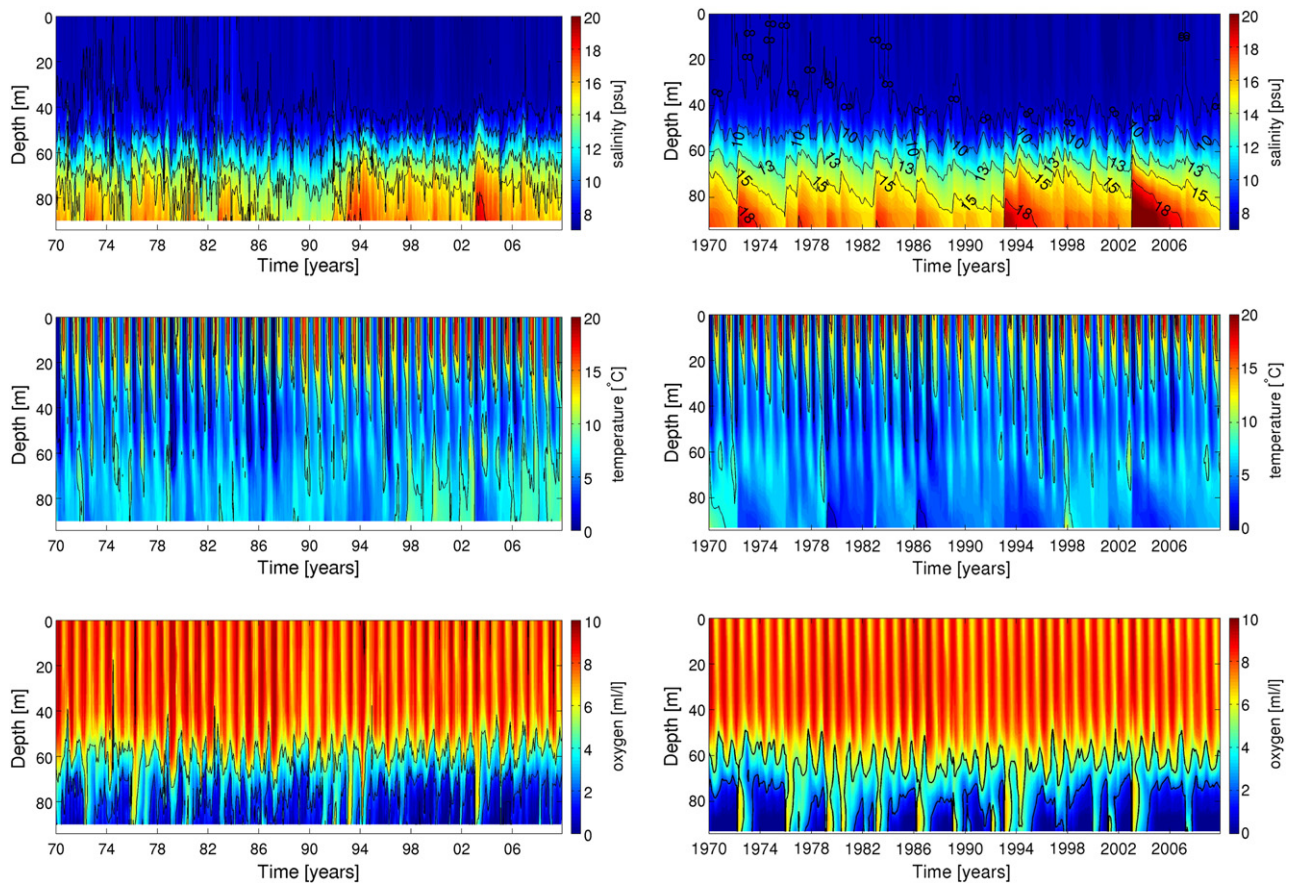


Fig. 3. Time series of salinity (top), temperature (middle) and oxygen (bottom) of ICES profiles of the ICES sub-division 25 (left) and BSIOM-OXYCON (right).

Swedish Meteorological and Hydrological Institute (SMHI Norrköping, Sweden) meteorological database (Lars Mueller, pers. comm.) which covers the whole Baltic drainage basin on a regular grid of  $1 \times 1^\circ$  with a temporal increment of 3 h. The database consists of synoptic measurements that were interpolated on the regular grid with a two-dimensional optimum interpolation scheme. This database, which for modeling purposes was further interpolated onto the model grid, includes surface pressure, precipitation, cloudiness, air temperature and water vapor mixing ratio at 2 m height and geostrophic wind. Wind speed and direction at 10 m height were calculated from geostrophic winds with respect to different degrees of roughness on the open sea and off the coast (Bumke et al., 1998). BSIOM forcing functions, such as wind stress, radiation and heat fluxes were calculated according to Rudolph and Lehmann (2006). Additionally, river runoff was prescribed from a monthly mean runoff data set (Kronsell and Andersson, 2012). The numerical model BSIOM has been run for the period 1970–2010.

The oxygen consumption model (OXYCON, Hansen and Bendtsen, 2013; Jonasson et al., 2012) describes one pelagic oxygen sink and two benthic sinks due to microbial and macrofaunal respiration. Pelagic and benthic oxygen consumption is modeled as a function of temperature and oxygen concentration. Originally, Bendtsen and Hansen (2012) developed OXYCON for the North Sea–Baltic Sea transition area including the Kattegat and the Belt Sea. They estimated an annual average of primary production to be  $160 \text{ gC m}^{-2}$  for this area (for details about the OXYCON model, see Bendtsen and Hansen, 2012). However, a constant rate of primary production is not suitable when simulating the entire Baltic Sea. Generally, primary production depends on available nutrients, light and stratification for the specific areas of the Baltic. Thus, the consumption rates were adjusted to the mean annual primary production of the different sub-basins of the

Baltic Sea (Table 1, Wasmund et al., 2001). The primary production of the Kattegat and Belt Sea was taken to be 100% and the primary production of the different basins was determined in relation to this production. At the sea surface, the oxygen flux is based on the oxygen saturation concentration determined from the modeled sea surface temperature and salinity values. It is clear that the phytoplankton primary production shows strong inter-annual variations and long-term trends (e.g. Rydberg et al., 2006), but in lack of sufficient data we applied this simple approach.

For model validation, we compiled oxygen data for the whole Baltic Sea (ICES sub-divisions: SD22–32; Fig. 1) from the ICES oceanographic database available from depth-specific CTD (conductivity, temperature, depth) and bottle measurements. From the database, all available oxygen values were selected between 1970 and 2010. Data were subsequently aggregated to obtain monthly means per year and per 5-m depth stratum. In a further step, data gaps were closed by linear vertical and temporal interpolation. For an even more detailed comparison of the model output a second data set was available comprising highly spatially resolved CTD data. This data set consists of observations based on routine research cruises in different parts of the western and central Baltic (SD22–SD28) between April 2002 and August 2010 carried out mainly by GEOMAR. The physical parameters (salinity, temperature, and oxygen) of the water column were obtained from a CTD/O<sub>2</sub> system. The most frequently observed area was the Bornholm Basin, with a horizontal resolution of the station grid of about 10 nm.

### 3. Results

Daily mean fields of temperature, salinity and oxygen have been extracted as model results for the period 1970–2010 for subsequent analysis. Fig. 2 shows the comparison of simulated and observed mean

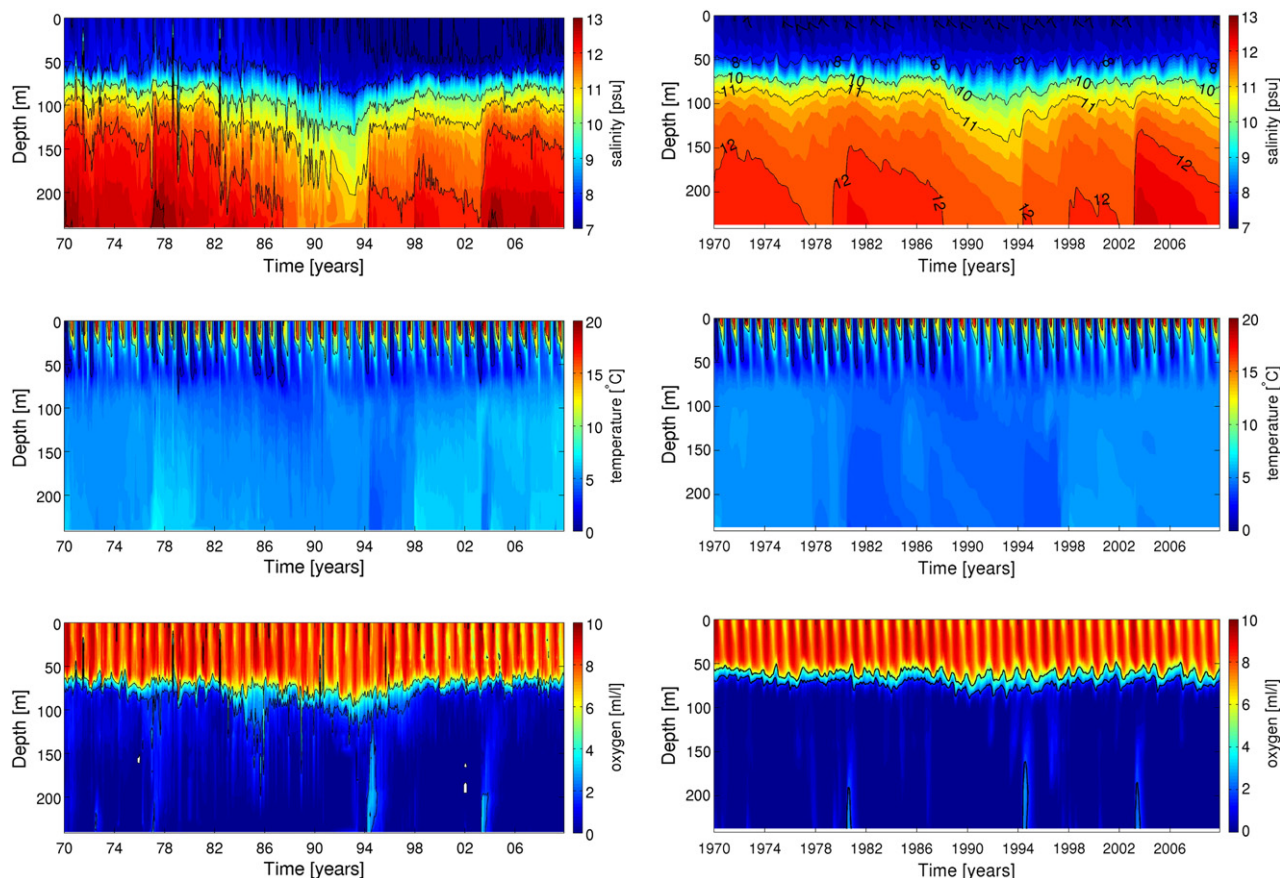


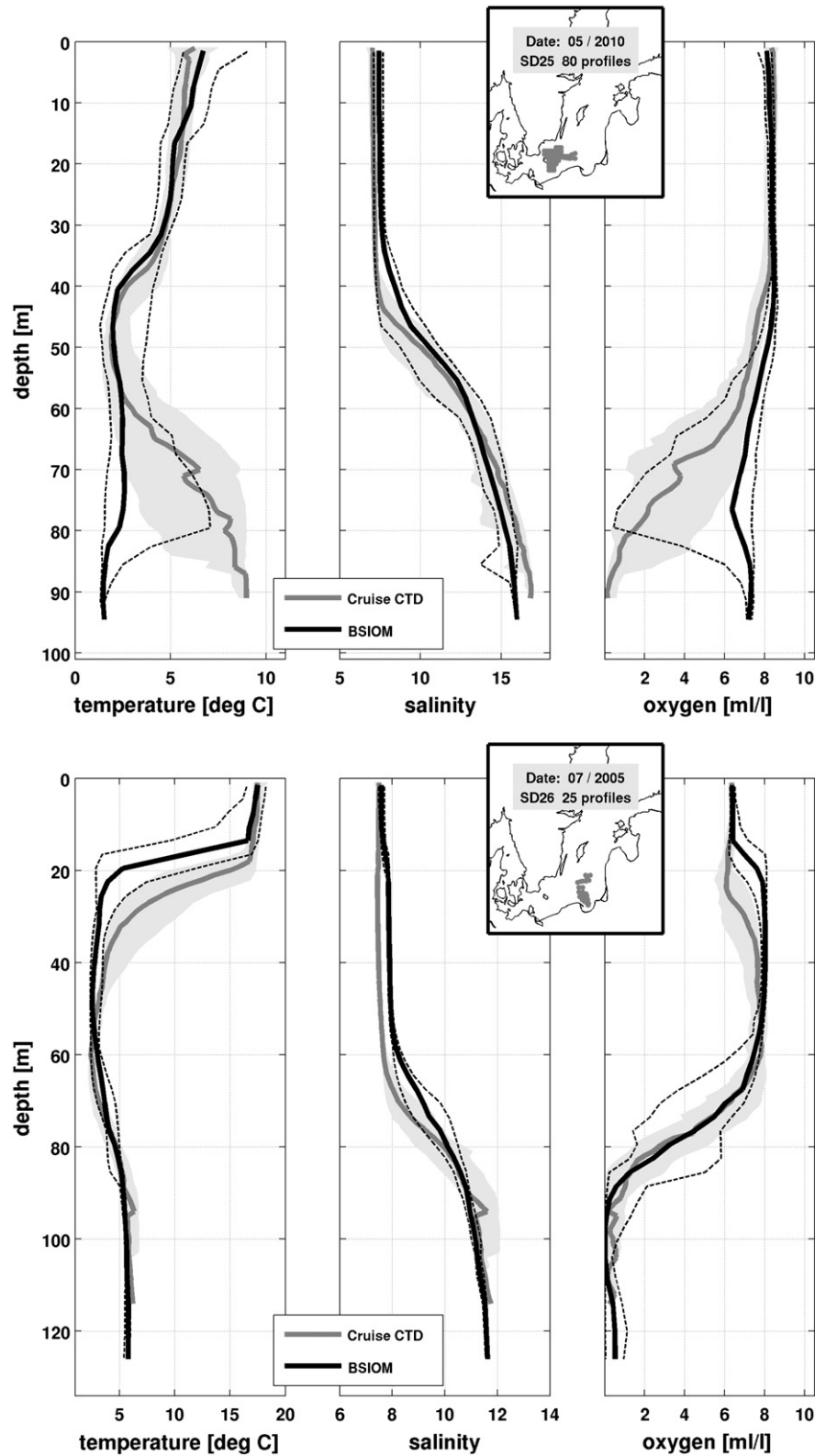
Fig. 4. Times series of salinity (top), temperature (middle) and oxygen (bottom) of ICES profiles ICES sub-division 28 (left) and BSIOM-OXYCON (right).

profiles of temperature, salinity and oxygen of the ICES sub-divisions 25, 26 and 28 (see Fig. 1 for reference), known as the present major spawning grounds of the eastern Baltic cod stock. Additionally, we made the same comparison for the ICES sub-division 30 (Bothnian Sea), to demonstrate that our model performed well in this specific area. In contrast, simulation results obtained from physical-biogeochemical models for this area revealed weaknesses in the simulation of oxygen consumption and nutrient dynamics (Daewel and Schrum, 2013; Eilola et al., 2011). The mean and natural variability range is well captured by BSIOM (Fig. 2). The quality of our results are similar to Gustafsson (2012), who used a state-of-the-art coupled physical-biogeochemical model with 13 pelagic state variables and four variables to describe the storage of organic and inorganic material in sediments. A comparison between observations and model results of the temporal development of temperature, salinity and oxygen profiles of the sub-division 25 and 28 is presented in Figs. 3 and 4. The overall evolution of temperature, salinity and oxygen as well as the varying depths of the halo-, thermo- and oxycline in both sub-divisions is well reproduced by the model. The combined impact on temperature, salinity and oxygen due to several inflows especially for the strong major Baltic inflows in 1973, 1976, 1993 and 2003 can be obtained from observations, but also from the simulation.

An even more comprehensive data validation of our model results is shown in Fig. 5 where CTD measurements of two hydrographic surveys (July 2005 and May 2010) are compared with model data. The comparison data set generated from the model simulation comprises the average of the surrounding  $3 \times 3$  profiles at the same location and date as the observations have been taken. The correspondence between the profiles is very high, deviations in oxygen profiles are mostly due to deviations in the description of the temperature profiles. In our simulation, in

May 2010 the deep water of the Bornholm Basin was ventilated by a cold deep water inflow which could not be observed from CTD-profiles (Fig. 5). However, the range of observed deep water temperatures is relatively broad. This implies a coexistence of water masses of different temperatures in the deep Bornholm Basin. Most probably this deviation is due to a temporal shift between real and simulated inflowing water masses. Also the volume of the inflow could be over- or underestimated. It should be noted that the initial conditions of BSIOM have been constructed from earlier model runs which most closely resembled hydrographic conditions of winter 1970. After initialization, no further adjustment has taken place. Thus, the simulation of hydrographic conditions in the Baltic Sea for over forty years has been driven only by the prescribed atmospheric forcing, runoff and the western boundary conditions, without any correction or data assimilation.

The cod reproduction volume (CRV) is an index for potential egg survival, i.e. the volume of water fulfilling minimum requirements for successful egg development (Plikshs et al., 1993). Egg survival is one of the key processes affecting Baltic cod recruitment variations (Köster et al., 2005). For example for the Bornholm Basin, the CRV can be calculated by horizontally integrating the spawning layer thickness defined by the vertical range of water masses with  $O_2 > 2$  ml/l,  $S > 11$  PSU and  $T > 1.5$  °C. Firstly, we calculated monthly mean CRVs from BSIOM based on profiles extracted at locations on the model grid with water depths larger than 69 m for the period 1970–2010. In lack of spatial resolved CTD station data for past decades, MacKenzie et al. (2000) proposed a method to determine the temporal development of the CRVs from only 4 central CTD stations in the Bornholm Basin. We followed the method proposed by MacKenzie et al. (2000) and calculated the monthly mean CRVs based on the ICES oceanographic data base for



**Fig. 5.** Quantiles (0.1, 0.5 and 0.9) of temperature, salinity and oxygen profiles for sub-division 25 in May 2010 (top) and 26 in July 2005 (bottom) based on GEOMAR CTD-measurements and BSIOM model output.

the same period. However, ICES oceanographic data are only available as monthly and over the sub-division averaged CTD-profiles. Thus, we adapted the method to be used with only one central station in the Bornholm Basin. Fig. 6 displays the CRVs calculated for May which

represents the peak of the eastern Baltic cod spawning period (Wieland et al., 2000). CRVs based on observations and model data are highly correlated ( $r = 0.71$ ), although the results are based on different spatial and temporal resolutions. For some years (1981–1983,



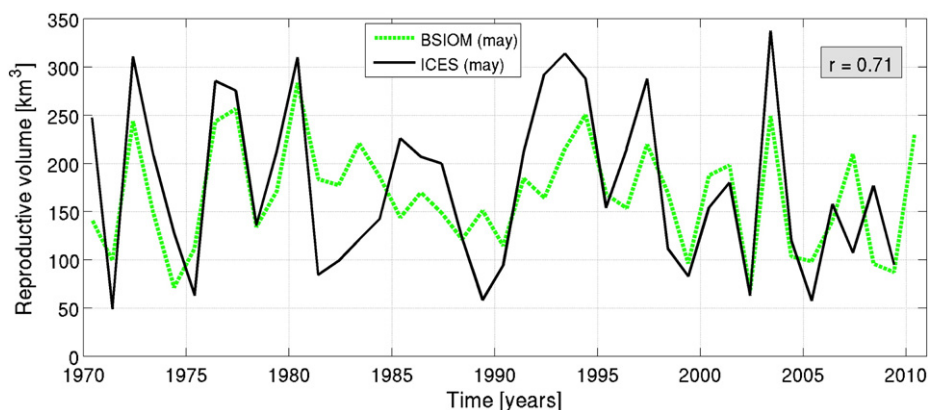


Fig. 6. Time series of the Baltic cod reproduction volumes in the Bornholm Basin based on observations (ICES) and hindcast model results (BSIOM, locations with water depths  $\geq 69$  m).

1992–1993) the agreement between the results is less satisfactory. This, in contrast to the model data resolution, might be due to the less regular nature of the non-synoptically resolved hydrographic data in space and time provided by the ICES oceanographic database.

From the BSIOM model simulation the maximum extent of hypoxic and anoxic conditions, including Baltic Proper, Gulf of Riga and Gulf of Finland has been calculated (Fig. 7). There is a high inter-annual variability with the smallest hypoxic area occurring in 1993 at the peak of the stagnation period when salt water intrusions were at their minimum. The smallest anoxic area can be found one year later in 1994 when the highly saline and oxygenated water of the major inflow in 1993 reached the eastern Gotland Basin. The inflow in 1993 strengthened the stratification and inhibited subsequent ventilation so that oxygen conditions quickly turned to even worse conditions as before 1993. Compared to observations, the determination of hypoxic and anoxic areas is based on daily mean values and the full model resolution (2.5 km). The results obtained from our model run agree with the area extents calculated from observations (Hansson et al., 2011; Savchuk, 2010). However, our estimates of the anoxic conditions for the period 1970–1980 are somewhat higher than the values obtained from observations. This could be due to the initial conditions of our model run or to an overestimation of the annual primary production rates which for our simulation are constant over the whole period 1970–2010 (Fig. 7). Primary production rates in the different basins of the Baltic Sea have changed over the past 40 years (e.g. Wasmund et al., 2001), which was also confirmed by the reduction in water transparency in most of the Baltic Sea sub-basins (Fleming-Lehtinen and Laamanen, 2012).

Fig. 8 depicts the mean spatial distribution of the occurrence frequencies of hypoxic conditions ( $O_2 \leq 2$  ml/l) within the entire Baltic Sea for the period 1970–2010. Here, the transition area between the North Sea restoring area and the Skagerrak with the extent of the deep Norwegian Trench are masked out, because oxygen conditions at the bottom of the model seem somewhat unrealistic. We find strong hypoxic conditions while observations, although sparsely available, do not seem to confirm this. A possible explanation could be a misrepresentation of the initial oxygen conditions in this area. Additionally, the deep water ventilation of the Skagerrak is happening in the North Sea, this process is not resolved by our western boundary condition. Furthermore, the applied oxygen depletion rates might differ from those in the Danish Straits and therefore lead to hypoxic or anoxic conditions at the bottom.

While high frequencies for hypoxia were found in the deep basin areas of the Bornholm Basin (40 to 70%), the Gdansk Deep (50 to 80%) and the Gotland Basin ( $>80\%$ ), anoxia ( $O_2 = 0$  ml/l) is mainly limited to the eastern and western Gotland Basin (90 to 100%). As the Bornholm Basin and the Gdansk Deep area are well known as major spawning grounds of eastern Baltic cod, the deep water oxygen conditions are essential for cod reproduction. The bottom oxygen frequently was found to be below the required level for cod egg survival, successful cod egg development was mainly only limited to the pelagic zones of the spawning areas. For the Belt Sea, hypoxic conditions occur up to 30% in the 41 year time range (Fig. 8). While in the Stolpe Channel only rarely low oxygen conditions occur, for the Gulf of Bothnia oxygen conditions are never below 2 ml/l. A detailed comparison for two

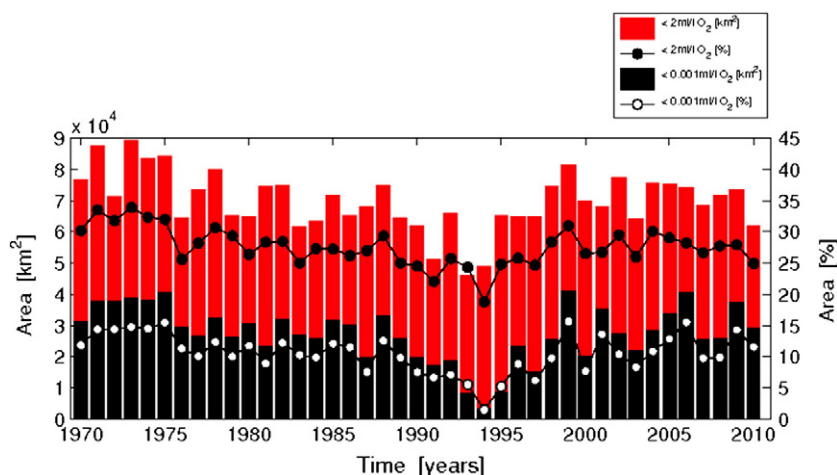


Fig. 7. Extent of hypoxic (red) and anoxic (black) bottom water in the Baltic Sea for the period 1970–2010.



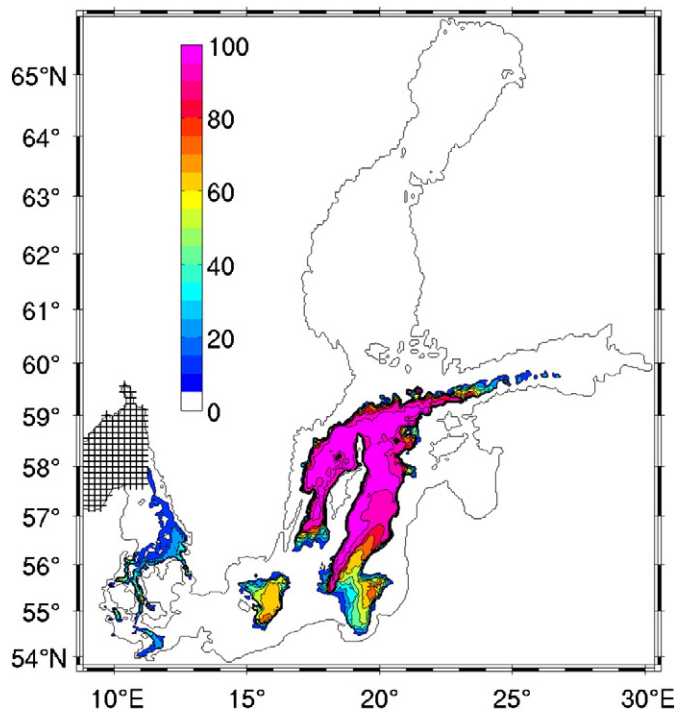


Fig. 8. Frequency of hypoxia ( $O_2 \leq 2$  ml/l) in the Baltic Sea for the period 1970–2010.

consecutive years, namely 2002 and 2003 (Fig. 9) shows the observed reduction of hypoxic and anoxic areas in the results of the model simulation. This reduction in hypoxic and anoxic areas is a consequence of the renewal of Baltic deep waters during spring 2003 (Feistel, 2003). This inflow event is considered as the most important one since 1993 and it transported well oxygenated water from the Kattegat to the deeper basins. These simulated specific oxygen conditions in different areas of the Baltic Sea are in good agreement with observations (e.g. Hansson et al., 2011).

#### 4. Discussion and conclusions

The Baltic Sea is subject to major temporal and spatial variability in important abiotic variables, e.g. temperature, salinity, oxygen concentration and nutrients, which drive bottom up and top down food web processes (e.g. Möllmann et al., 2009). However, many species are believed to exist at the limit of their physiological tolerance, in areas and habitats

that do not represent their marine or fresh water origin. Moreover, the spatial and temporal distributions of many marine and freshwater species change in fairly regular and cyclical patterns, because the adaptive value of their distributions are strongly coupled with the surrounding habitat. Besides the abiotic conditions the extent of species distributions is determined by the level of oxygen conditions, which define a major habitat requirement to which species' physiology is suited. Threshold levels of oxygen often form the physiological preferences for the distribution of adult as well as of early life stages of several species. Observation of in situ migration of individuals is difficult and usually constrained to only short periods. Thus, high resolution 3D circulation models of the Baltic Sea coupled to innovative oxygen sub-models (e.g. OXYCON) could be implemented to calculate highly resolved hydrographic property fields, which are needed to make the link to habitat estimation studies.

The modeling results of our study are based on relatively simple empirical derived respiratory relationships of oxygen consumption in the water column and a boundary condition of oxygen production at the sea surface. The complex biogeochemical cycle is not resolved, and thus process studies and budget calculations are not possible. There is no guaranty that outside the training range the used simple empirical relationship is valid. However, the close agreement of our model results with observations suggests the model's capability of simulating oxygen dynamics that can be used in detailed analyses of ecological and environmental interactions. Our modeling approach could for instance help to improve the understanding of the horizontal and temporal development of environmental variables functioning as boundaries for the distribution of many organisms living in the Baltic Sea.

It is evident that our modeling approach reach its limitation if the primary production, and hence the associated oxygen consumption, is changing due to eutrophication or other changes in nutrients cycling. Hind- and forecasts beyond available primary production data are difficult since the primary production does not only depend on external nutrient loads but also on internal feedback. However, the effect of interannual variability of primary production could be considered if better temporally and spatially resolved estimates of primary production could be utilized for instance from satellite data. Water transparency is dependent on the amount of particulate and dissolved material, such as phytoplankton biomass, humic substances and other organic as well as inorganic particles suspended in the water. Measurements of water transparency are available for the different sub-basins of the Baltic Sea since the beginning of the 19th century (HELCOM, 2009). However, a trend of Secchi depth increase/decrease is not necessarily related to an increase/decrease of phytoplankton biomass in the Baltic Sea (Fleming-Lehtinen and Laamanen, 2012).

Wasmund et al. (2001) compiled primary production data resolved for the different sub-basins of the Baltic Sea for at least two time periods, around 1970–80 and 1990–2000. Over the period of about 20 years

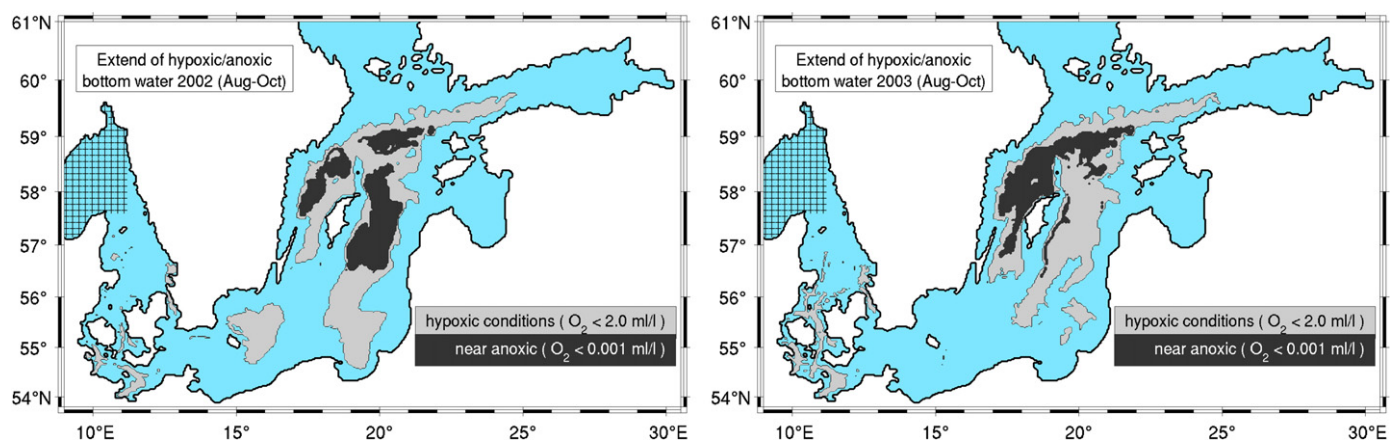


Fig. 9. Mean extent of hypoxic/anoxic bottom water for August–October 2002 and 2003.

primary production nearly doubled in almost all regions of the Baltic Sea. To test the model results with respect to varying primary production/oxygen consumption rates, we performed a sensitivity run of BSIOM-OXYCON varying oxygen consumption rates according to changes in the primary production (Wasmund et al., 2001), linearly increasing from 1970 until 1997, and afterwards constant rates as in the previous model run. The initial conditions were the same as for the previous run except, there were no anoxia close to the bottom and minimum oxygen values were set to  $> 2 \text{ ml l}^{-1}$ . The varied primary production and hence oxygen depletion rates resulted in significantly reduced extensions of hypoxic and anoxic areas before 1993 and similar results afterwards (for details s. Supplementary data). Thus, further improved model results could be achieved if better temporally and spatially resolved estimates of primary production could be utilized.

Furthermore, considering that the  $\text{CO}_2$  concentration in the atmosphere is continuously rising and therefore inducing changes in the carbonate system and the communities of primary producers, the biological processes of up- and degrading the oxygen content in the water column will become even more important for the Baltic Sea environment within this century. Thus, the implementation of the OXYCON sub-model into our modeling framework suggests its applicability for different purposes. Firstly, the model could be run to hind-cast and analyze the dynamics of highly spatio-temporally resolved hydrographical property fields including oxygen, to be used for example in models on habitat extension. This includes investigations on how the frequency and magnitude of deep water inflow events determine the volume and variance of deep-water oxygen levels below the halocline. To mitigate undesired effects on the Baltic Sea ecosystem, an effective marine management will also depend on the understanding of current anthropogenic drivers, i.e. human activities that precipitate pressures on the natural environment. Thus, the model is planned to be utilized for sensitivity analyses of oxygen-related spatial habitat distributions under multiple combinations of natural and anthropogenic drivers (climate change, eutrophication, primary production, new species introductions, food web changes) and might help to test hypotheses, providing results of fundamental importance to Baltic Sea ecosystem management.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <http://dx.doi.org/10.1016/j.jmarsys.2014.02.012>.

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