

Parameterisation of oxygen dynamics in the bottom water of the Baltic Sea–North Sea transition zone

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ABSTRACT: An organic carbon budget for the Kattegat and Belt Seas in the North Sea–Baltic Sea transition zone was used to parameterise the pelagic and benthic respiration in a new oxygen model, OXYCON, which describes the influence of temperature-dependent pelagic and benthic respiration on bottom water oxygen conditions. The significance of respiration versus physical mixing and advection processes for the bottom water oxygen concentration was analysed through a sensitivity study where the OXYCON model was implemented in 2 transport models: a Lagrangian model of bottom water transport, based on an age-tracer of the bottom water transit-time through the area, and a 3-dimensional circulation model of the transition zone. The solutions of both models were in accordance with the observed spatial and temporal distribution of oxygen in the area during the period 2001 to 2003. In particular, the temporal and spatial dynamics of a severe hypoxic event in 2002 were well described. The inter-annual variability of hypoxia during this period could therefore be explained by changes in physical mixing and ventilation of the bottom layer with oxygen-rich surface water and by the bottom water temperature. Variability in the sources of organic material available for remineralisation in the bottom water seems to have less influence on the inter-annual variation in hypoxia but instead determines the background conditions and the long-term trend in oxygen dynamics.

KEY WORDS: Hypoxia · Carbon mineralisation · Respiration · Baltic Sea · Kattegat · Modelling

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INTRODUCTION

Hypoxia is a world-wide phenomenon that is found in many estuaries and coastal regions and causes negative effects on ecosystems and losses of benthic habitats (Diaz 2001, Diaz & Rosenberg 2008). The effects of hypoxia on benthic communities range from shifts in community structure and diversity (Conley et al. 2007) to a complete collapse of benthic faunal communities (Weigelt & Rumohr 1986, Diaz & Rosenberg 1995, Gray et al. 2002). Occasionally, the effect of hypoxia propagates to the pelagic ecosystem where fish mortality is caused by either hypoxia per se or by the associated release of toxic hydrogen sulphide from the sediment (Weigelt & Rumohr 1986, Christensen et al. 2004). Therefore, hypoxia

has been considered by some authors to be the most significant threat to benthic biodiversity (Gray et al. 2002).

From the few areas where historic data or long time series of oxygen conditions exist, such as in the Chesapeake Bay (Hagy et al. 2004) and the Baltic Sea–North Sea transition zone (Andersson & Rydberg 1988, Conley et al. 2007) or, in the case of the Gulf of Mexico, where historic oxygen conditions have been reconstructed from analyses of sediment cores (Rabalais et al. 2007), it is evident that hypoxia has generally become more widespread and frequent during recent decades due to increasing eutrophication during the late twentieth century (Diaz & Rosenberg 2008). However, it is the complex interaction between biological processes regulating the

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respiratory oxygen consumption and physical processes regulating the ventilation of the water column that eventually leads to hypoxic conditions. Several models have been developed for various marine systems to study the causes of hypoxia and the coupling of hypoxia to climate factors and eutrophication (for review see Peña et al. 2010).

The most vulnerable areas for developing hypoxia are generally characterised by high productivity, and thereby high respiratory oxygen demand and/or a stratified water column that reduces the ventilation of the bottom water. The Kattegat and the Belt Sea, which form the transition zone between the North Sea and the Baltic Sea, fit into this category (Bendtsen et al. 2009). This region is characterised by a persistent halocline through most of the year, separating an upper layer of well-oxygenated brackish water from the Baltic Sea from a bottom layer of high-saline Skagerrak water. The bottom water mass occasionally becomes hypoxic (Stigebrandt 2001, Conley et al. 2007). Every year in late summer and autumn patches of hypoxic bottom water are observed. The locations of these patches change over the season and from year to year, but they are generally much more frequent in the southern part of the area, closest to the Baltic Sea, where the bottom water mass has been isolated from the surface layer for the longest time. The dynamics of oxygen in the transition zone also affect the oxygen conditions in the deep basins of the central Baltic Sea where some of the inflowing water eventually ends up. In the long-term perspective, declining oxygen concentration during the late twentieth century has evolved in parallel with increasing eutrophication (Andersson & Rydberg 1988, Conley et al. 2007), which has caused a doubling of the primary productivity from the 1950s to the 1980s (Richardson & Heilmann 1995, Andersson 1996). During the last few decades, there have been certain years where prolonged periods of calm weather and high temperatures have caused hypoxia and even anoxia over large areas for weeks or months (Conley et al. 2007). The latest severe oxygen depletion event associated with extensive damage of the benthic fauna community was in 2002 (Hansen et al. 2004).

Observations from the area show inter-annual coupling between the oxygen conditions and weather conditions regulating the ventilation of bottom water (HELCOM 2003), but it is still unclear to what extent changes in the physical mixing and transportation versus variation in the respiratory oxygen consumption influence the inter-annual variations in oxygen concentration. There are indications that years of low

primary production coincide with relatively good oxygen conditions in the following autumn (Conley et al. 2007). However, during the last decade, nutrient levels have decreased again in the area (Carsensen et al. 2006, Rydberg et al. 2006); in spite of this, there has been no significant improvement of the oxygen conditions in the bottom water.

Even though hypoxia is caused by biological respiration, there are remarkably few direct observations on oxygen consumption in the bottom water and sediment in the literature from this area and none of them are based on recent data (Kannevorff & Christensen 1986, Rydberg et al. 1990, Graneli 1992, Kruse & Rasmussen 1995). In a study of the temperature dependency of benthic community respiration, Kannevorff & Christensen (1986) found that the respiration rate could be characterised by a Q_{10} value of 3.5 (Q_{10} represents the relative increase of the respiration rate due to a 10°C change in temperature). However, Q_{10} for pelagic respiration has not been studied in the area.

The objective of this study was to analyse the seasonal oxygen dynamics in the bottom water of the transition zone by quantifying the relative importance of advection, mixing, and pelagic and benthic sinks due to remineralisation of organic matter. A carbon budget for the area was constructed from previous studies and used to parameterise a model of the OXYgen CONsumption in the bottom water due to pelagic and benthic respiratory sinks (OXYCON). The relative role of pelagic and benthic respiration in the model was analysed. OXYCON has previously been successfully validated in a box model study (Jonasson et al. 2012) and in a study of the effect of global warming on hypoxia (Bendtsen & Hansen 2012). The present study focuses on processes and dynamics of benthic and pelagic remineralisation rates, and we discuss how the relatively simple parameterisation of OXYCON relates to the present knowledge in the literature of the carbon dynamics of the ecosystem. The OXYCON model was implemented in 2 model parts: a Lagrangian model of bottom water transport, based on a 'ventilation age' tracer of the bottom water transit-time through the area, and a nested 3-dimensional circulation model of the transition zone. The model results were validated against an extensive data set from the area, and the spatial and temporal variability in oxygen was analysed during the 3 yr period from 2001 to 2003. Finally, a sensitivity study of OXYCON implemented in the Lagrangian model to changes in temperature, export production, mixing and advection processes was analysed.

MODEL DESCRIPTION

Study area

This study considers the oxygen dynamics in the North Sea–Baltic Sea transition zone, covering the Kattegat, Belt Seas and western Baltic Sea. The mean conditions in the transition zone between the Baltic Sea and the North Sea (Fig. 1) can be characterised as a large-scale estuarine circulation with low-saline outflowing Baltic surface water and high-saline inflowing Skagerrak water (Fig. 2). The low Baltic Sea salinity is sustained by a relatively large mean runoff to the area of about $15\,000\text{ m}^3\text{ s}^{-1}$. On shorter time-scales, the dynamics are primarily influenced by barotropic in- and outflows to the Baltic Sea forced by wind-induced water level differences across the area. In particular, storm events may lead to large inflows from the Skagerrak to the deeper basins in the Baltic Sea, and during such events the entire volume of bottom water is renewed in the Kattegat and Belt Seas (Matthäus & Franck 1992).

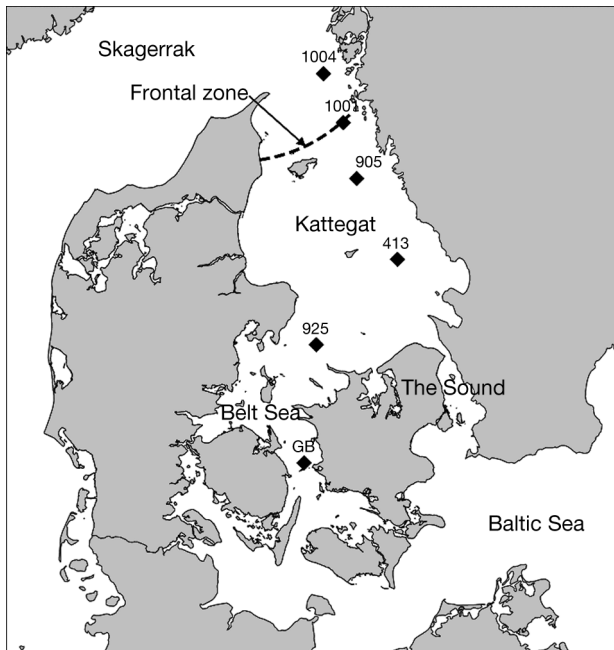


Fig. 1. The North Sea–Baltic Sea transition zone showing the average position of the Kattegat–Skagerrak front and positions of the monitoring stations in the northern (Stn 905; $57^{\circ}11.06'\text{ N}$, $11^{\circ}39.62'\text{ E}$), central (Stn 413; $56^{\circ}0.10'\text{ N}$, $12^{\circ}07.00'\text{ E}$), and southern Kattegat (Stn 925; $56^{\circ}07.86'\text{ N}$, $11^{\circ}09.47'\text{ E}$) and in the Great Belt (Stn GB; $55^{\circ}30.50'\text{ N}$, $10^{\circ}52.80'\text{ E}$) used to characterise temperature, oxygen and primary productivity in the study area. The monitoring stations 1004 and 1001 in the Skagerrak, outside the study area, were used to define the hydrography at the northern boundary of the models

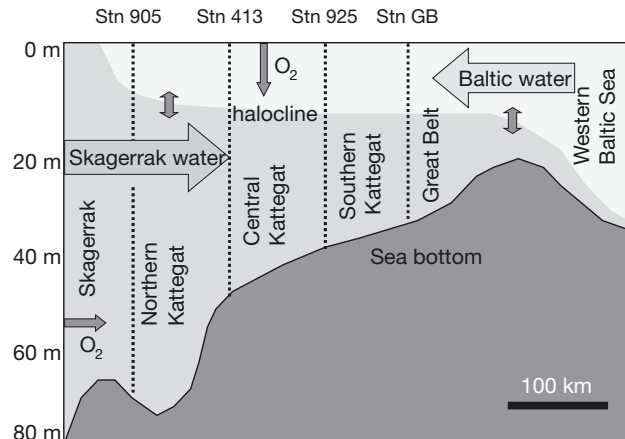


Fig. 2. Schematic illustration showing the hydrography in a transect from the Kattegat–Skagerrak frontal zone to the entrance of the Baltic Sea. Outflowing low-saline Baltic water and inflowing high-saline Skagerrak water are indicated, and the sources of bottom water oxygen are shown with arrows. The approximate positions of Stns 905, 413, 925 and GB are marked (cf. Fig. 1)

The area is relatively shallow, with an average water depth of about 18 m. Therefore, the residence time of the bottom water is only about 30 to 60 d in the Kattegat area (Bendtsen et al. 2009), but with large seasonal variations. The Kattegat–Skagerrak front separates the low-saline surface water in the Kattegat from the high-saline water in the Skagerrak. South of the front and throughout the transition zone there is a persistent halocline at a depth of about 15 m separating the bottom layer of Skagerrak water from the upper layer of Baltic Sea water (Fig. 2). The tide is relatively weak, and the tidal amplitude typically is $<40\text{ cm}$ in the inner Danish waters and decreases to $<10\text{ cm}$ in the western Baltic Sea. The stratification of the water column limits ventilation of the bottom water; therefore, the oxygen concentration is generally low in the southern part of the area from August to October. In years with calm weather conditions, severe hypoxia can prevail for weeks to months in these areas. The mean depth of the area with a bottom water layer (i.e. areas with a depth $>15\text{ m}$) is 27 m, and the mean thickness of the bottom layer below the halocline (i.e. below 15 m) is thereby about 12 m. Monitoring stations within the area have been sampled for oxygen and water chemistry during the last few decades (Fig. 1).

The depth at Stn 1004 (Fig. 1), located north of the Kattegat–Skagerrak front, is about 100 m, and the water column is generally well mixed and thereby differs markedly from the stratified conditions in the more shallow areas south of the front (Fig. 3). The seasonal temperature cycle and inter-annual differences

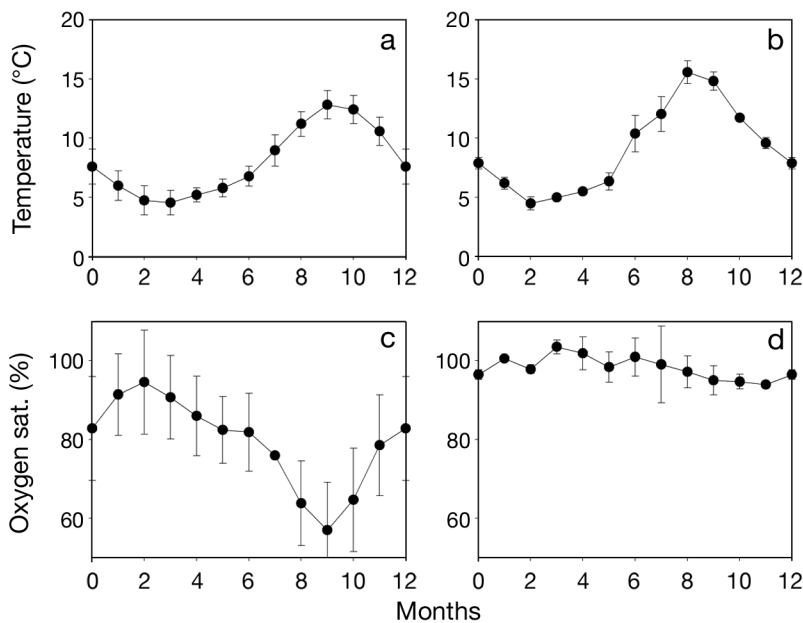


Fig. 3. Seasonal bottom water temperature and oxygen saturation (a,c) in the Kattegat and Belt Seas and (b,d) at the Kattegat–Skagerrak front. Data from the Kattegat and Belt Seas represent the mean values of Stns 413, 925 and GB over the period from 2000 to 2006, and data from Stns 1004 and 1007 from the same period represent the conditions at the Skagerrak–Kattegat front. Error bars = SD

generally follow the variability in air temperature. The temperature ranges from about 5°C throughout the water column in winter (average for 2000 to 2006) to a maximum of about 16°C in the upper 70 m and 11°C in the deepest 30 m of the water column in September (Fig. 3).

Parameterisation of the OXYCON model

A carbon budget of the area was constructed from earlier studies, and the corresponding respiratory processes were parameterised. The assumptions underpinning the parameterisation of the oxygen sinks are described below and subsequently discussed (see 'Discussion').

It is assumed that the annual remineralisation of organic matter in the bottom water and sediment almost balances the primary export production in the surface layer. The carbon budget (Fig. 4) assumes an annual primary production of 160 g C m⁻² yr⁻¹ and hereof 80 g C m⁻² yr⁻¹ is exported across the halocline as particulate organic carbon (POC). In the bottom layer, 45 g C m⁻² yr⁻¹ is remineralised while sinking through the bottom water layer and the rest is deposited on the sediment. If the remineralisation

rate increases in the bottom water, less material will reach and be deposited on the bottom. The organic material in the sediment is remineralised by macrofauna, with the microbial communities accounting for 20 and 13 g C m⁻² yr⁻¹, respectively. The remaining 2 g C m⁻² yr⁻¹ is assumed to be permanently buried in the sediment. Furthermore, the parameterisation of OXYCON implies that the overall mineralisation of the system is not affected by horizontal transport of dissolved organic matter (DOC) because the degradability of DOC is assumed to be very low. Horizontal transport of POC is also neglected because the residence time of POC in the water column is much less than the residence time of the bottom water in the area (see 'Discussion').

Measurements have shown that the molar ratio of carbon/nitrogen of the exported organic material is 9.9 (Olesen & Lundgaard 1995), which suggests a molar ratio of O₂ and C of 1.2.

However, ammonium released by ammonification below the halocline accumulates in the bottom layer during summer and some of it is returned by mixing to the surface layer instead of being oxidised in the bottom layer to nitrate. Therefore, the remineralisation ratio ranges between 1 and 1.2. In OXYCON it is assumed that half of the ammonium is returned to the surface layer; therefore, the ratio between oxygen and carbon is 1.1 for all respiratory processes. It is assumed that all respiratory processes in the sediment and the water column have the same temperature dependence $f(T)$ given by:

$$f(T) = Q_{10}^{\left(\frac{T-T_{\text{ref}}}{10}\right)} \quad (1)$$

with a Q_{10} value of 3 and a reference temperature of $T_{\text{ref}} = 4^\circ\text{C}$.

Three oxygen sinks (S) in the bottom water are considered: pelagic respiration (Pr), benthic macrofaunal respiration (Fr) and the diffusive oxygen uptake by the sediment due to aerobic microbial respiration and chemical oxidation of reduced substances referred to as microbial respiration (Mr) hereafter:

$$S = -Pr - Fr - Mr \quad (2)$$

The 2 benthic sink terms are scaled to the thickness of the bottom layer and describe the uptake per cubic

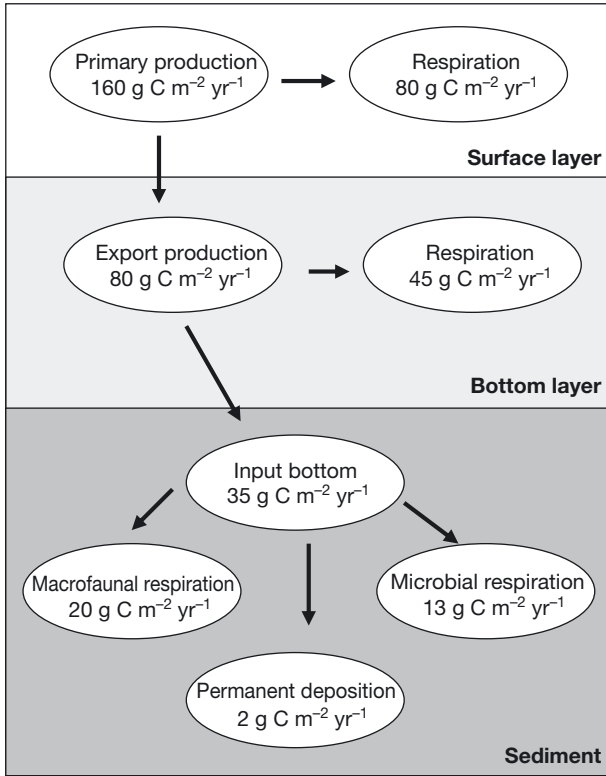


Fig. 4. Annual carbon budget of the Kattegat and Belt Seas, showing the assumed primary production and respiration in the surface water and the respiration rate in the bottom water and sediment, respectively

metre. The oxygen sinks depend to a varying extent on the oxygen concentration, and this is described by saturation kinetics with specific half-saturation constants for each of the sinks.

The pelagic respiration rate is assumed to be limited by temperature and the concentration of suspended POC and to be weakly dependent on the oxygen concentration. This is parameterised by saturation kinetics with a low half-saturation constant: $k_1 = 5 \mu\text{M O}_2$. The export of POC from the surface layer is assumed to sustain a constant bottom water concentration of POC throughout the season, so pelagic respiration is given by:

$$Pr = f(T)R_1 \left(\frac{O_2}{O_2 + k_1} \right) \quad (3)$$

where R_1 is a respiration constant ($\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$) to be determined.

The macrofauna includes predators and organisms feeding on various fractions of organic matter in the sediment or POC suspended near the bottom. Some macrofaunal species are regulators and can compensate for declining oxygen and maintain a constant

respiration rate within a range of oxygen concentrations, whereas others are conformers and their respiration declines with decreasing oxygen concentrations. However, it is assumed that the community consists of one group with the same respiratory performance and that there is no seasonal variation in food availability. Therefore, the respiration rate (R_2) of the community depends only on temperature and to a minor extent on oxygen availability. The effect of the ambient oxygen concentration is parameterised by saturation kinetics with a high half-saturation constant $k_2 = 60 \mu\text{M O}_2$. This value of k_2 is higher than the typical threshold concentration at which behavioural changes are observed in macrofaunal species (Diaz & Rosenberg 1995) and therefore are assumed to represent the respiratory performance of the whole macrofaunal community. Total benthic respiration becomes relatively more important for the oxygen concentration in places with a shallow layer of bottom water. The consumption rate of oxygen due to macrofaunal respiration on the whole bottom layer is thereby given by:

$$Fr = \frac{1}{\Delta z} f(T)R_2 \left(\frac{O_2}{O_2 + k_2} \right) \quad (4)$$

where Δz is the depth of the bottom layer and R_2 is the respiration rate (in $\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$) of the macrofaunal community.

Respiration of the microbial community is regulated by temperature and the availability of oxygen in the sediment. As the oxygen consumption in the sediment increases, the diffusive oxygen uptake through the benthic boundary layer also increases. The oxygen uptake thereby depends on the oxygen concentration gradient across the diffusive boundary layer; therefore, it is assumed that the microbial oxygen uptake scales with oxygen saturation in the bottom water. The microbial consumption rate can thereby be described as:

$$Mr = \frac{1}{\Delta z} f(T)R_3 \left(\frac{O_2}{O_2(\text{sat})} \right) \quad (5)$$

where $O_2(\text{sat})$ is the saturation concentration of oxygen depending on temperature and salinity and R_3 is the respiration rate constant ($\text{mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$). In Eq. (5) we normalise the oxygen dependence with the oxygen saturation to make the dimension of the microbial respiration rate (R_3) comparable to the macrofaunal respiration rate above. Oxygen saturation shows relatively little variation, within 80 and 60%, in the summer to fall period, with typical values around 300 μM .

Lagrangian model of the bottom water oxygen dynamics

We refer to the simple oxygen transport model below as the ‘Lagrangian’ model because the model solves the temporal changes of oxygen in a fixed volume of water during its passage through the model domain. This corresponds to the Lagrangian description of temporal changes in a fluid element in contrast to an Eulerian description in which temporal changes are considered at a fixed position in space (e.g. the 3-dimensional model below is based on an Eulerian description of model state variables). In the Lagrangian transport model, the bottom layer is assumed to be homogeneous and at a constant depth, so changes in oxygen concentration are simply described as:

$$\frac{dO_2}{dt} = S \quad (6)$$

where S is the heterotrophic sink term described in the OXYCON model (Eq. 2). Autotrophic oxygen production is neglected as it is assumed to play a minor role in the overall oxygen conditions in the bottom layer, because the euphotic zone is generally above the pycnocline depth (Lund-Hansen 2004). Thus, the sink term in the Lagrangian model is determined by the temperature of the inflowing bottom water and the varying oxygen concentrations in the bottom water during its passage through the area.

The bottom water that originates from the Skagerrak is well mixed, and it is assumed to be 100% saturated with oxygen. During the subsequent southward transport in the bottom layer, the initial oxygen content is both influenced by respiratory oxygen consumption and mixing with oxygen-rich water from the surface layer.

The simple oxygen model is based on the ‘ventilation age’ rather than the actual time elapsed during the transport of bottom water from the northern boundary toward the Baltic Sea. Bendtsen et al. (2009) defined the ‘ventilation age’ tracer such that the ventilation-age represented the time elapsed since the water was in contact with either the surface or the northern boundary towards the Skagerrak. The ventilation age is therefore shorter than the age itself of a water mass moving towards the Baltic Sea, because the ventilation age is constantly ‘refreshed’ by mixing with ‘younger’ water from the surface layer. Bendtsen et al. (2009) found that the ventilation age tracer correlated inversely with the bottom oxygen conditions in the area and in general described the combined effects from mixing and advection on the bottom water conditions. Daily oxygen

concentrations were simulated with the Lagrangian transport model for 4 monitoring stations covering the north–south gradient in the area: Stns 905, 413, 925 and GB (Fig. 1).

Calculation of the oxygen concentration in the Lagrangian model (Eq. 6) used the ventilation age (a) in a water mass to determine the integrated oxygen consumption, which is then subtracted from the initial oxygen content of the water entering the bottom layer in the Kattegat according to:

$$O_2(t = a) = O_2(t_0) - \int_{t_0}^a S dt \quad (7)$$

The initial oxygen concentration $O_2(t_0)$ is the saturation content determined from monthly mean temperatures and salinities in the depth interval between 15 and 45 m at the northern boundary (Stn 1004). The conditions at Stn 1004 are representative of the temperature, salinity and oxygen concentration of the bottom water subducted into the Kattegat area. Data show that the inflowing bottom water from the intermediate layer is close to 100% saturated with oxygen throughout the year (Fig. 3). Super-saturation of 110 to 115% oxygen saturation occurs only in the upper 15 m during the productive season (March to September), and values <85% are only observed at depths below 70 m. Due to the seasonal temperature cycle, the oxygen concentration in the inflowing water ranges between 335 μM in early spring and 246 μM during summer.

The ventilation age (a) was simulated by the 3-dimensional model for the period 2001 to 2003, according to the study of Bendtsen et al. (2009), and is also described further below.

The respiration rate constants R_1 , R_2 and R_3 in Eqs. (3) to (5) are determined for conditions representing the averaged seasonal cycle of temperature and oxygen in Kattegat bottom waters from 2000 to 2006 (Fig. 3). The oxygen consumption is continuously integrated for a water mass represented by the average seasonal ventilation age (a) according to Eq. (7) and the values R_1 , R_2 and R_3 are fitted to match a total remineralisation of 45, 20 and 13 $\text{g C m}^{-2} \text{yr}^{-1}$, respectively (Fig. 4), using a molar remineralisation ratio between carbon and oxygen of 1.1. The same procedure is used to find the values of R_1 , R_2 and R_3 in the sensitivity study of OXYCON.

High-resolution 3-dimensional model of the area

The 3-dimensional model was a nested high resolution circulation model of the area. The model was

based on the COHERENS model (Luyten et al. 1999), which is a primitive equation 3-dimensional circulation model. The model was formulated on a 2×2 nautical mile horizontal spherical grid (approximately 3700×3700 m), with 30 vertical sigma layers, and covered the region from the northern Kattegat to the Arkona Basin in the Baltic Sea. The vertical turbulent diffusion was based on a k - ϵ turbulent closure scheme (Luyten 1996, Luyten et al. 1999), and, in case of vertical instabilities, a convective adjustment scheme was applied, whereby all unstable grid cells were identified and subsequently mixed. Because of the relatively high horizontal resolution there was no explicit horizontal diffusion in the transport and momentum equations.

The basic model setup applied in this study was previously validated in the study of Bendtsen et al. (2009) in which the inter-annual variability of temperature and salinity during the period from 2001 to 2003 was analysed. The model was forced with meteorological fields from an operational atmospheric model (Brandt et al. 2001).

In addition to temperature and salinity, the model also solved transport equations for a conservative tracer (c), an age tracer (α) and oxygen (O_2). The transport equations were given by:

$$\begin{aligned} \frac{\partial c}{\partial t} + A(c) &= D(c) \\ \frac{\partial \alpha}{\partial t} + A(\alpha) &= D(\alpha) + c \\ \frac{\partial O_2}{\partial t} + A(O_2) &= D(O_2) + S \end{aligned} \quad (8)$$

where A and D represent the advective and turbulent diffusive operators, respectively, and S is the oxygen sink defined by OXYCON (Eq. 2). The conservative tracer ($0 \leq c \leq 1$) determines the spatial distribution of water advected from the Skagerrak or transported by mixing from the surface (determined by the boundary conditions given below), and the age concentration tracer shows the corresponding elapsed time since the water was ventilated from the source regions, i.e. the surface or the Skagerrak boundary (Bendtsen et al. 2009). The age of a water parcel reflects the time elapsed since the water parcel left a source region, and the age of a water volume reflects the corresponding mean age of all the ‘water parcels’ that constitute the volume. In general, only a fraction of all the water parcels in a given water volume have been in contact with the source boundaries, and this fraction is determined by the conservative tracer c . The corresponding mean age (a) of a water volume is therefore determined by $a = \alpha/c$ (Delhez et al. 1999,

Deleersnijder et al. 2001). The boundary conditions for the conservative tracer (c) are $c = 1$ at the surface and at the northern boundary, zero at the eastern boundary and a no flux condition at the bottom, and the initial concentration is zero. Thereby the conservative tracer quantifies the amount of water that originates from either the surface or from the northern Kattegat in relation to the water advected from the Baltic Sea. The boundary conditions for the age tracer (α) is zero at the surface and at the northern boundary, and a no flux condition is applied at the eastern boundary and at the bottom, corresponding to the ‘ventilation age’ tracer defined by Bendtsen et al. (2009). The initial concentration of the age tracer is obtained by first integrating the model 1 yr (in 2001) and then using the obtained age distribution as the initial concentration from 1 January 2001.

The northern open boundary conditions of oxygen were determined from the observed monthly averaged oxygen saturation profiles for the period from 1948 to 2006 recorded at Stn 1004 close to the Kattegat–Skagerrak front (ranging between 88 and 100%), a no flux boundary condition at the eastern boundary and at the bottom, and 100% saturation in the surface layer. Initial conditions of water level, temperature, salinity, age and oxygen are determined by integrating the model for the year 2001, and then using the obtained fields as initial values from the start of 2001. The model was then integrated continuously for the period from 2001 to 2003. The OXYCON model was implemented in the 3-dimensional model where pelagic respiration (Pr) and benthic respiration ($Fr + Mr$) were defined by Eqs. (3) to (5). The pelagic sink was applied to all grid cells in the model, while the benthic sink was only applied to the deepest grid cell in the model.

RESULTS

Respiration rates in OXYCON

In order to match an integrated annual remineralisation of $45 \text{ g C m}^{-2} \text{ yr}^{-1}$ in a 12 m deep water column, the pelagic respiration rate constant R_1 (Eq. 2) was found to be $0.6 \text{ mmol O}_2 \text{ m}^{-3} \text{ d}^{-1}$ (equivalent to $6.5 \text{ mg C m}^{-3} \text{ d}^{-1}$) at a reference temperature of 4°C . The microbial and macrofaunal respiration rates were assumed to represent about 60 and 40% of the total benthic respiration, respectively, and the corresponding representative values for the respiration rate constants for the benthic macrofauna (R_2) and the microbial community (R_3) were then found to be

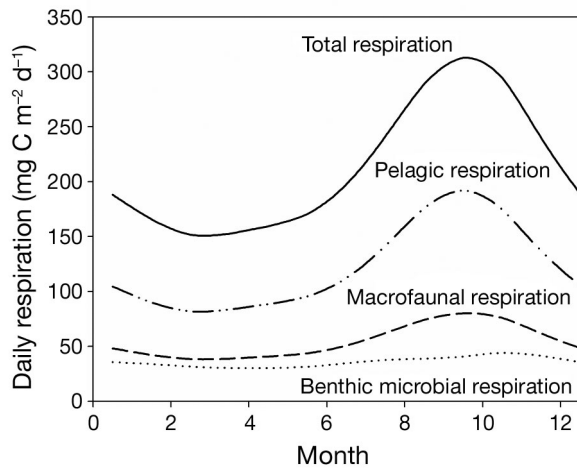


Fig. 5. Seasonal cycle of organic carbon remineralisation in the bottom water of the Kattegat–Belt Seas area (cf. Eqs. 3 to 5) of the benthic microbial community (dotted line), benthic macrofaunal community (dashed line), the pelagic respiration (dot-dash line) and the total remineralisation (solid line)

4.08 mmol O₂ m⁻² d⁻¹ (0.34 mmol O₂ m⁻³ d⁻¹) and 2.88 mmol O₂ m⁻² d⁻¹ (0.24 mmol O₂ m⁻³ d⁻¹), respectively.

The sum of the 3 respiration rate constants combined with the seasonal temperature and oxygen resulted in an annual respiratory oxygen consumption below the halocline of 229 g O₂ yr⁻¹ m⁻², corresponding to 78 g C m⁻² yr⁻¹ for the entire area. Due to the seasonal temperature variation, the total daily remineralisation ranged from 0.15 g C m⁻² d⁻¹ in March to 0.32 g C m⁻² d⁻¹ in September. These rates balanced the assumed flux of POC across the halocline (Fig. 5).

Simulations of the ventilation age

The distribution of the ventilation age tracer in the bottom water reaches a quasi-stationary state where the bottom water is relatively young close to the northern Kattegat boundary and in shallow regions where the bottom water is influenced by mixing with surface water (Fig. 6). The age distribution has a strong seasonal signal, where higher winds and cooling of surface water increase advection and mixing during winter time, whereas calm conditions and stronger stratification reduce mixing during the summer and early autumn period. This causes the ventilation age to increase from about 1 mo in the central Kattegat during winter to about 2 mo during late summer, and even larger seasonality is seen in the Great Belt region where the mean age in September

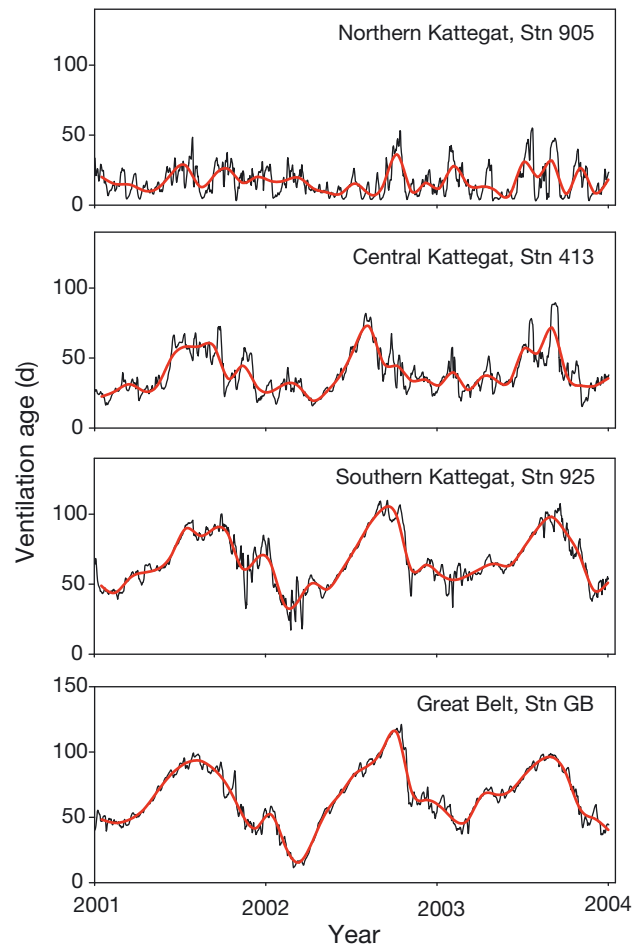


Fig. 6. Ventilation age at 30 m depth at (a) Stn 905, (b) Stn 413, (c) Stn 925 and (d) Stn GB from 2001 to 2003. The ventilation age is shown in units of days. The black line represents daily values, and the red line shows a 30 d running mean

is about 3 mo between 2001 and 2003 (Fig. 6). However, inter-annual variability in advection of bottom water from the Skagerrak and wind-induced mixing cause significant change in the age distributions. For example, during September 2002 the ventilation age is about 100 to 120 d in the southern Kattegat and in the Belt Sea, whereas it is only about 80 to 100 d in 2001 and 2003 (Fig. 6). The inter-annual variability in the ventilation age is largest during the late summer and early autumn period.

Results from modelling of oxygen

The simulated oxygen concentrations with the Lagrangian transport model, using daily values of the ventilation age tracer at each of the 4 stations (905,

413, 925, and GB), are in accordance with the observed temporal evolution of oxygen from 2001 to 2003 (Fig. 7). Also the spatial pattern of changes in oxygen across the transition zone is in good accordance with observations. In the northern Kattegat, where the ventilation age is relatively low, the oxygen content is mainly determined by the boundary conditions (i.e. $O_2(\text{sat})$), and the short-term variability reflect the day to day variations in current directions and mixing intensity which affect the ventilation age. Further south, in the area from Stn 413 to Stn GB, respiration processes become increasingly important and, consequently, the north–south gradient of declining oxygen concentration parallels the gradient of increasing ventilation age.

The spatial and temporal distributions of the 3-dimensional model solutions of oxygen in the

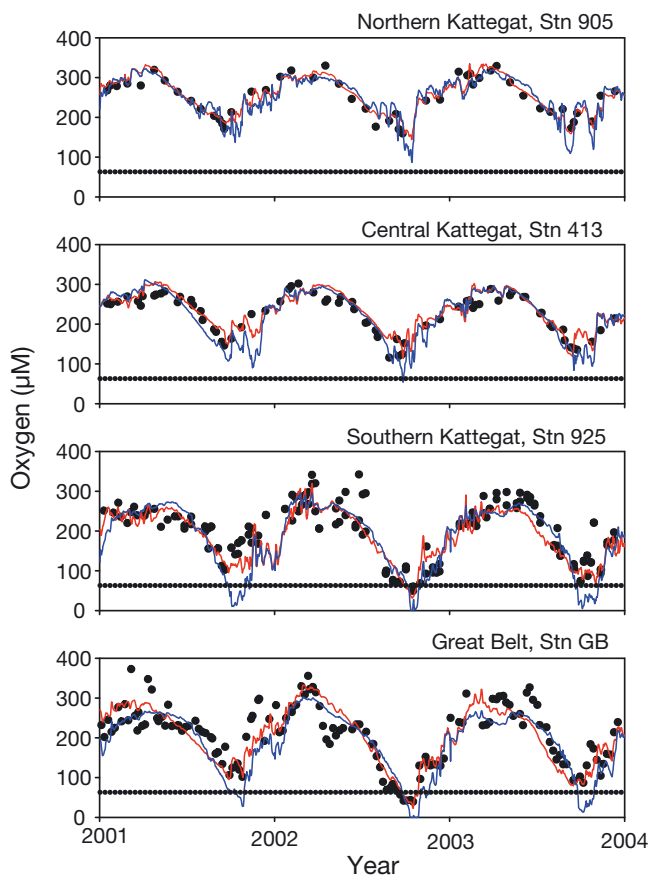


Fig. 7. Solutions of the Lagrangian transport model (blue line) and the 3-dimensional model of oxygen concentration (red line) at 30 m depth or at the model bottom when it is shallower than 30 m during the period from 2001 to 2003 at 4 stations. The corresponding observations (black dots) are shown at depth levels above the bottom identical to the difference between the 30 m depth level and the total model depth at each station

bottom water are also in accordance with the observations at the 4 monitoring stations. However, the inter-annual variability is better resolved in the 3-dimensional model than in the simpler Lagrangian transport model (Fig. 7), because internal mixing and effects from varying bottom depths in the model domain are considered explicitly in the 3-dimensional model but not in the idealised Lagrangian model. However, the 2 model solutions, in general, show good conformity with observations, because application of the age-tracer in the Lagrangian model implicitly takes some of these effects into account.

Thus, both model solutions resolve the observed oxygen concentration in space and time. In particular, the gradual decrease of bottom water oxygen from spring to autumn is well resolved in the 2 models; this supports the contention that the balance between mixing and respiration is well described in the models. However, both models seem to underestimate oxygen concentrations for the late autumn of 2001 in the southern Kattegat (Stn 925). At that time the observed values show that the bottom water is almost saturated with oxygen. This could be explained by an episodic advection of oxygen-rich bottom water which is not resolved in the 3-dimensional simulations in that particular case.

According to the simple transport model, hypoxic conditions prevail in the bottom water for 106 and 50 d at Stns 925 and GB, respectively, during the period from 2001 to 2003 (Table 1, Scenario 1). If the relative contribution of pelagic and benthic respiration changes, this will influence the oxygen conditions. In an extreme scenario, where no organic matter reaches the bottom due to low sedimentation rates or the absence of benthic respiration and all respiration occurs in the water column, the number of hypoxic days will increase by 60%, while, in the opposite case, where all the exported organic material is mineralised by the benthic macrofaunal and microbial communities, the number of hypoxic days will be reduced to only 30% of the present-day level (Scenarios 2 and 3). In a scenario with a 30% increase in the ventilation age, corresponding to reduced mixing of the water column prevailing under very calm weather conditions (Bendtsen et al. 2009), the number of hypoxic days increases by a factor of 2 to 3; this emphasises the sensitivity of the oxygen concentration to the ventilation of the bottom water in the area (Scenario 4).

The scenario with a 3°C higher temperature all year round shows the relatively large sensitivity of OXYCON to temperature, and the number of

Table 1. Number of hypoxic days ($<63 \mu\text{M O}_2$) simulated by the Lagrangian model at 30 m depth during the years 2001 to 2003 in the Great Belt (Stn GB), southern Kattegat (Stn 925), central Kattegat (Stn 413) and northern Kattegat (Stn 905) and the corresponding amount of organic carbon respiration below the halocline in the standard scenario (Scenario 1), which uses the parameterisation described in Eqs. (3) to (5) and the ventilation age calculated for 2001 to 2003. The sensitivity of the model is shown for scenarios where all respiration occurs either in the water column (Scenario 2) or in the sediment (Scenario 3) and in a scenario where the ventilation age tracer is 30 % older (Scenario 4). The warm scenarios (5 & 6) show the effect of a 3°C warmer water column with and without reduction of the benthic respiration (i.e. scaling Eqs. 4 & 5 with a factor of 0.55)

Scenario	Stn GB (d)	Stn 925 (d)	Stn 413 (d)	Stn 905 (d)	Total respiration (g C m ⁻² yr ⁻¹)
1. Standard	50	106	2	0	78
2. As standard, but all respiration in the water column	112	165	12	0	79
3. As standard, but all respiration at the bottom	15	27	0	0	78
4. As standard, but ventilation age increased 30 %	182	114	26	2	78
5. Warm scenario (+3°C)	217	261	114	29	104
6. Warm scenario, benthic respiration reduced 45 %	138	186	9	2	83

hypoxic days increases by a factor of 2 to 3 in the Belt Seas and the southern Kattegat (i.e. 261 and 217 d, at Stns 925 and GB, respectively). The central and northern Kattegat also experience hypoxia for 114 and 29 d, respectively (Scenario 5). However, in the warm scenarios the total remineralisation of organic carbon exceeds the assumed export production, and therefore the benthic sink would have to be reduced accordingly so the oxygen consumption would balance the annual export of 80 g C m⁻² yr⁻¹. A sensitivity study with the Lagrangian transport model shows that a reduction of the benthic respiration by 45 % compensates the increased respiration in a 3°C warmer water column (Scenario 6) such that the total respiration is in accordance with the present-day annual budget.

DISCUSSION

The modelling approach assumes that, at a regional scale, the system respiration below the halocline in the North Sea–Baltic Sea transition zone may be adequately described by simple parameterisation of the seasonal respiration, without considering short-term feedback mechanisms between organic carbon sources and respiration rates. Following this assumption, the overall eutrophication level is mainly relevant for the total remineralisation of organic matter on an annual or decadal time scale, as discussed below, whereas the short-term oxygen variations are primarily regulated through physical factors such as advection and mixing of the water (Bendtsen et al. 2009, Jonasson et al. 2012). Very calm weather conditions, corresponding to the sensitivity study with increased ventilation age, will reduce the oxygen content of the bottom water sig-

nificantly. Bendtsen et al. (2009) demonstrated that the ‘ventilation age tracer’ could be used to describe the influence from physical mixing and advection of water in the area. As the present model solutions are in good agreement with observations at the 4 stations during the 3 yr period, this verifies that the ventilation age tracer, used in the simple oxygen transport model, is a relevant proxy in which the influence from physical transports is considered implicitly. Assessments of the relative importance of physical mixing processes for the oxygen distribution can therefore be quantified from the spatial and temporal distributions of the ventilation age tracer as described by Bendtsen et al. (2009).

Estimates of primary production and export of POC

The good correspondence between model simulations and observations supports the assumptions behind the OXYCON description of the benthic and pelagic respiratory sinks, and that the applied annual remineralisation of organic matter below the halocline of 78 g C m⁻² yr⁻¹ is representative for the area; these assumptions are discussed further below.

There is no feedback between the pools of organic matter and oxygen consumption in the OXYCON model; therefore, the exact value of the mean annual export production is critical for the overall oxygen consumption. Based on relatively few studies in the literature from the open parts of the Kattegat and Belt Sea, we estimated that the input of organic material to the bottom layer was sustained by a total primary production of 160 g C m⁻² yr⁻¹. Previous studies include Richardson & Christoffersen (1991), who estimated the primary production to be 290 g C

$\text{m}^{-2} \text{yr}^{-1}$ in the southern Kattegat, and (Richardson & Heilmann 1995), who reported an average annual primary production in the Kattegat of about $200 \text{ g C m}^{-2} \text{yr}^{-1}$ in the period from 1984 to 1993. Rydberg et al. (2006) analysed 50 yr of primary production data and reported a mean primary production from 1990 to 2002 of 150 to $240 \text{ g C m}^{-2} \text{yr}^{-1}$ for the Belt Seas, $110 \text{ g C m}^{-2} \text{yr}^{-1}$ for the eastern Kattegat and 150 to $230 \text{ g C m}^{-2} \text{yr}^{-1}$ for the western Kattegat. Carstensen et al. (2003) estimated a much lower production in the Kattegat of only $116 \text{ g C m}^{-2} \text{yr}^{-1}$ between 1989 and 1997 using a semi-empirical model. However, they did not include primary production associated with the subsurface chlorophyll maximum, which was estimated to account for 30% of the annual production (Richardson & Christoffersen 1991). As primary productivity has probably declined due to declining nutrient levels during the last decades (Carstensen et al. 2006, Rydberg et al. 2006), the earlier primary production estimates may have been higher than those estimated for the period analysed in this study (i.e. 2001 to 2003). Therefore, the above numbers are generally consistent with the assumed primary production of $160 \text{ g C m}^{-2} \text{yr}^{-1}$. In fact, the Danish monitoring program encompasses direct measurements of the primary production in the study area of $159 \pm 15 \text{ g C m}^{-2} \text{yr}^{-1}$ as an average (\pm SD) for the period from 1998 to 2009 (Henriksen et al. 2011), and for the 3 yr of special interest, 2001, 2002 and 2003, the estimated annual production is fairly constant, with values of 152, 160 and $146 \text{ g C m}^{-2} \text{yr}^{-1}$, respectively. The same data show that the seasonal cycle in primary production ranges from about $205 \text{ mg C m}^{-2} \text{d}^{-1}$ in February to peak values of $756 \text{ mg C m}^{-2} \text{d}^{-1}$ in July, then declines to $224 \text{ mg C m}^{-2} \text{d}^{-1}$ in November and reaches minimum productivity during winter (December to February), with values $<100 \text{ mg C m}^{-2} \text{d}^{-1}$ as an average for 1998 to 2009. The OXYCON parameterisation assumed that about 50% of the primary production is exported below the halocline, and therefore these measurements are in accordance with the estimated seasonal range in export production in OXYCON of $150 \text{ mg C m}^{-2} \text{d}^{-1}$ in the winter season to $320 \text{ mg C m}^{-2} \text{d}^{-1}$ in the summer. However, estimates of the primary productivity from December to January suggest that the export is about $100 \text{ mg C m}^{-2} \text{d}^{-1}$ lower than assumed.

A previous study of the seasonal sedimentation with sediment traps estimated the flux to the bottom layer to be 63 g C m^{-2} during the productive season from March to October, and the export rates ranged from about $200 \text{ mg C m}^{-2} \text{d}^{-1}$ in

April, increasing to about $400 \text{ mg C m}^{-2} \text{d}^{-1}$ during the late summer (Olesen & Lundsgaard 1995). This is also in accordance with the applied range between 150 and $300 \text{ mg C m}^{-2} \text{d}^{-1}$ in OXYCON, except that these rates are about 25% higher. But, as discussed above, the difference can be explained by more eutrophic conditions in the 1990s than between 2001 and 2003. Graneli (1992) estimated the input to the bottom water layer to be $80 \text{ g C m}^{-2} \text{yr}^{-1}$ for an area in the southeastern Kattegat. This part of the area is more oligotrophic than the rest of the Kattegat and Belt Seas (Rydberg et al. 2006). Thus, this value also indicates that the export production was slightly lower from 2001 to 2003 than in the 1990s.

Bottom water POC concentration

OXYCON assumes that the concentration of POC in the bottom water is constant such that the seasonal variation in export of POC to the bottom layer is balanced by corresponding changes in the remineralisation of POC. This assumption may at first appear counter-intuitive because the seasonal cycle in sedimentation from the surface layer shows a distinct seasonal peak during a few weeks in the spring in conjunction with the diatom spring bloom (Olesen 1993, Olesen & Lundsgaard 1995) and this input contributes significantly to the total annual sedimentation (e.g. Smetacek 1985, Wassmann 1991). However, the spring bloom sinks fast through the water column (Olesen & Lundsgaard 1995), and the organic material contained herein appears relatively resistant to degradation once deposited on the bottom (Hansen & Josefson 2001, 2004, Josefson & Hansen 2003), with decay rates as low as 0.007 d^{-1} (Hansen & Josefson 2003); the corresponding oxygen consumption may therefore be considerably lower than suggested by the total amount of organic matter entering the bottom water. However, apart from the spring bloom peak, Olesen & Lundsgaard (1995) observed a relatively constant concentration of POC in both the surface and bottom layers of the Kattegat, with average concentrations of 27 and $15 \mu\text{M}$ POC, respectively.

An estimate of the residence time of POC in the bottom water can be calculated from the parameterisation of the pelagic sink of POC, as the total remineralisation of $Pr = 45 \text{ g C m}^{-2} \text{yr}^{-1}$ has to balance the flux of POC through the bottom water. In steady state the vertical balance between pelagic respiration and the export flux is given by:

$$w_s(\text{POC}(z = -H) - \text{POC}(z = -h_m)) = Pr \quad (9)$$

where the sinking velocity (w_s) is assumed to be constant in the bottom layer and h_m and H denote the depth of the mixed layer and the bottom depth, respectively. Using the above-mentioned values of 27 and 15 $\mu\text{M O}_2$ for the POC concentration in the surface and bottom layers, respectively, and assuming that the POC is homogeneously distributed in the 2 layers, the sinking velocity becomes 0.9 m d^{-1} . This gives a residence time of POC in the 12 m deep bottom layer of about 2 wk, which is much shorter than the average residence time of the bottom water of about 2 to 3 mo in the area (Bendtsen et al. 2009). This means that the oxygen concentration in a volume of water reflects the cumulated respiration that results from production regimes of different surface water masses on a time scale of months. Local plankton blooms may therefore have limited effect on the distribution of oxygen because the bottom layer is relatively well mixed and local and short-term variability in the respiration rates and ecological feedbacks on the oxygen sinks can be neglected while still getting a reliable description of the oxygen dynamics.

Distribution of benthic and pelagic respiration

Jørgensen & Revsbech (1989) concluded that 90% of the export of POC across the halocline in the Kattegat was respired in the bottom water and benthic communities and the rest was buried in the sediment. Graneli (1992) reported that benthic respiration contributed with a remineralisation of 28 $\text{g C m}^{-2} \text{ yr}^{-1}$. However, Kanneworff & Christensen (1986) found an annual benthic respiration corresponding to 44 $\text{g C m}^{-2} \text{ yr}^{-1}$ in a seasonal mesocosm study with benthic communities from the Sound (in the vicinity of the Kattegat). A higher respiration rate can be deduced from the results by Rysgaard et al. (2001) who measured oxygen uptake and the efflux of dissolved inorganic carbon (DIC) in the sediment. They found oxygen uptake rates ranging from 8.31 to 10.5 $\text{mmol O}_2 \text{ m}^{-2} \text{ d}^{-1}$ and efflux rates of 8.7 to 13 $\text{mmol DIC m}^{-2} \text{ d}^{-1}$ at 5.3°C in May, which equals 27 to 47 $\text{g C m}^{-2} \text{ yr}^{-1}$. However, the benthic respiration of that study may be even higher once adjusted for seasonal temperature cycles. The relative contribution of microbial and macrofaunal benthic respiration in OXYCON is in accordance with Jørgensen & Revsbech (1989) who reported that macrofaunal respiration contributed two-thirds of the total benthic respiration.

Correspondingly, Rysgaard et al. (2001) and Kanneworff & Christensen (1986) found that macrofaunal respiration could account for 0 to 65% and 30 to 40%, respectively, of the benthic respiration.

The sensitivity study showed that the relative contribution of benthic and pelagic respiration is important for oxygen dynamics. Pelagic respiration is comparatively more important than benthic respiration for creating hypoxia in areas where the bottom water layer is >12 m deep. Kemp et al. (1992) concluded that pelagic respiration in stratified estuaries was the most important oxygen sink, if the bottom water layer was 5 m or deeper. The shallower the bottom layer, the more significant the benthic respiration is and the faster the oxygen concentration declines.

The kinetics of the 2 oxygen sinks also differ, with implications for the oxygen dynamics. In accordance with Sampou & Kemp (1994), we assume that pelagic respiration is not limited by oxygen concentration and does not cease when oxygen declines; therefore, hypoxia can develop quickly due to pelagic respiration. In contrast, the sediment holds a large pool of organic carbon, while oxygen, in general, is only available in the upper few millimetres of the sediment. Therefore, the oxygen concentration in the bottom water becomes limiting for microbial remineralisation of organic matter in the sediment under hypoxic conditions (Rysgaard et al. 2001). The oxygen concentration is close to zero at the sediment-water interface during the hypoxic season so the uptake is regulated by the concentration in the bottom water. Therefore, as a rough simplification, OXYCON describes the benthic microbial oxygen uptake as a linear function of the oxygen concentration in the bottom water. The benthic macrofaunal respiration is less dependent on the flux of oxygen across the diffusive boundary layer because the most abundant species of macrofauna can actively ventilate their surroundings (Diaz & Rosenberg 1995) and to some extent compensate for declining oxygen concentrations. We argue that it is necessary to parameterise the 3 benthic and pelagic oxygen sinks separately in oxygen models because these differences have implications for the oxygen dynamics at low concentrations. For example, in the sensitivity experiments with the warm scenarios, where the total remineralisation was maintained by reducing benthic respiration, the higher temperatures caused increased oxygen uptake during the late summer. This result was primarily due to pelagic respiration which became relatively more important during the hypoxic season when pelagic uptake is less limited by low oxygen concentration than is benthic uptake.

At very low and ecologically critical oxygen levels, the simple oxygen model probably gives an unrealistic description of the oxygen dynamics because other feedback mechanisms come into play, such as changes in the redox profiles of the sediment, the introduction of hydrogen sulphide in the water column, or mass mortality of the benthic fauna, and this can completely change the functioning of the ecosystem as well as the biogeochemical processes at the sediment–water interface (Morse & Eldridge 2007, Eldridge & Morse 2008). Thus, the present parameterisation describes processes leading to hypoxia, while the dynamics of oxygen consumption during severe hypoxia and in the subsequent recovery phase of the ecosystem may be different than those described by the model.

Effect of temperature on the respiration rate

The Q_{10} value of 3, assumed for all respiratory processes in this study, is critical for the seasonal description of oxygen dynamics, and lower Q_{10} values or different Q_{10} values for benthic and pelagic respiration combined with a stronger seasonality in the export of POC could, in principle, provide an equally good correspondence with observed values. However, the assumed export rates are in accordance with the observations from the area. Furthermore, a Q_{10} value of 3 is in accordance with the values used by Rasmussen et al. (2003) and lies within the typical range of between 2 and 3.5 reported from other areas (Robinson & Williams 1993, Lefevre et al. 1994, Lomas et al. 2002). Kannevorff & Christensen (1986) reported a Q_{10} of 3.5 for benthic community respiration. The ability of OXYCON to reproduce seasonal and inter-annual oxygen dynamics indicates that the value of Q_{10} is close to 3; this temperature sensitivity, together with variations in the ventilation of the bottom water, are the most important factors regulating short-term oxygen dynamics in this area. The temperature dependence is also an important aspect of the potential increase of hypoxia in the area due to global warming (Bendtsen & Hansen 2012).

CONCLUSIONS

The total remineralisation in the OXYCON model was found to range between $0.15 \text{ g C m}^{-2} \text{ d}^{-1}$ in early spring and $0.32 \text{ g C m}^{-2} \text{ d}^{-1}$ in late summer for the North Sea–Baltic Sea transition zone, and this was

found to be in accordance with previous studies from the area. In total, the mean annual remineralisation below the halocline is estimated to be $78 \text{ g C m}^{-2} \text{ yr}^{-1}$. Implementation of the OXYCON model in both a simple Lagrangian transport model and a 3-dimensional model of the area were also consistent with the observed spatial and temporal distributions of oxygen from 2001 to 2003. By assuming that the concentration of organic material suspended in the water column and in the sediment is relatively constant during the seasons, changes in oxygen concentration in the bottom water can be explained by the seasonal range of bottom water temperatures from 5 to 16°C and a temperature dependency of the respiratory processes corresponding to a Q_{10} value of 3. Implementation of OXYCON in a Lagrangian transport model, where the influence from mixing and advection of water masses on oxygen concentrations was described by a ventilation age tracer, showed that it was possible to resolve the observed temporal and spatial distributions of oxygen in the bottom water during the period from 2001 to 2003. This demonstrated that a ‘ventilation age’ tracer is a relevant proxy for the influence from mixing and advection on oxygen conditions.

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