

ORIGINAL RESEARCH ARTICLE

Dissolved oxygen variability in the southern Baltic Sea in 2013–2018

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Summary This paper discusses changes in the dissolved oxygen concentration (DOC) in the southern Baltic Sea. The oxygenation of the whole water column was estimated. Monthly mean DOCs, as well as a detailed description of the annual surface layer dissolved oxygen (DO) cycle, are presented. The DO cycle at the surface is characterized by two maxima in March/April and November, and by two minima in July/August and December. The DO decline time after the major Baltic inflow (MBI) in 2014 was estimated at about 10 months for the Bornholm Deep and Słupsk Furrow. Whereas the Bornholm Basin was relatively well oxygenated, low oxygen concentrations ($<4 \text{ mg l}^{-1}$) were measured in the deep layer of the Gdańsk Deep throughout the inflow period. In addition, the cod spermatozoa activation layer together with the neutral egg buoyancy layer for the Bornholm Basin and Słupsk Furrow are discussed on the basis of the measured DOCs and the variability in hydrographic conditions.

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1. Introduction

Dissolved oxygen concentration (DOC) is an important property of sea water, affecting the structure and intensity of marine life. In the surface layer, the primary source of dissolved oxygen is air-sea exchange: this leads to near saturation of this layer. Oxygen in the marine environment is also derived from photosynthesis – primary production depends strongly on light availability and water temperature (Woźniak et al., 1989). Whereas the water in the upper layer is well oxygenated, the instantaneous DOC is subject to seasonal fluctuations. This results from the different solubility of oxygen at different temperatures and the seasonal inten-

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sity of photosynthesis. One of the main processes responsible for the decline in the amount of oxygen is consumption by bacteria during the decomposition and mineralization of organic matter (Walker, 1980). In addition, oxygen is used by marine organisms during respiration, while chemical reactions involving oxygen, such as the oxidation of methane or ammonia, play an important role in its depletion.

The extent of oxygenation of sea water is also affected by its excessive eutrophication (Carlson, 1997). Enrichment of water with nutrients, especially phosphorus, nitrogen and carbon in the surface layer, results in elevated biological production (Jarvie et al., 2018). The very rapid growth of phytoplankton causes algal blooms and reduces water transparency. The accumulation of algae on such a massive scale increases the mortality not only of these organisms but of marine fauna as well. The descending transport of decomposing organic detritus to the sea bed increases oxygen consumption in the deep layers, and exhaustion of oxygen resources in the bottom layer leads to the disappearance of deep-sea fauna, including relict species. In addition, some fish cease spawning, as a result of which valuable species vanish.

The Baltic Sea is currently one of the largest dead zones in the world (Conley et al., 2009; Diaz and Rosenberg, 2008). Indeed, the extents of hypoxia and anoxia zones have been expanding in the Baltic Proper, the Gulf of Finland and the Gulf of Riga (Hansson and Andersson, 2016). The coverage of these zones increased from ca 5% between 1960 and 1995 up to ca 17% from 2000 to 2016. According to Meier et al. (2006), the decade-long stagnation periods without Major Baltic Inflows (MBIs), with decreasing oxygen and increasing hydrogen sulphide levels, may have been caused by large freshwater inputs and anomalously high zonal wind speeds. According to Mohrholz (2018), the main driver of the temporal and spatial spread of suboxic and anoxic conditions is most probably the increased eutrophication during the last century.

The varied bathymetry of the Baltic Sea severely hampers water exchange between its basins. Vertical water exchange is also limited: wind-driven and convective mixing are restricted by the pycnocline. The main processes ensuring water exchange in the deep layer of the Baltic Sea are the MBIs from the North Sea (Feistel et al., 2006; Fischer and Matthäus, 1996; Lass and Matthäus, 1996; Lehmann et al., 2004; Matthäus and Frank, 1992; Reissmann et al., 2009). Since 1983, an MBI has occurred once every 10 years (Dahlin et al., 1993; Jakobsen, 1995; Liljebldh and Stigebrandt, 1996; Matthäus and Lass, 1995; Mohrholz et al., 2015; Piechura and Beszczyńska-Möller, 2004; Rak, 2016). However, the only pathway along which inflowing highly saline and oxygen-rich water can enter the central and northern Baltic is the area of the Slupsk Furrow. Therefore, this region in the southern Baltic is extremely important as regards the hydrology and biology of the entire Baltic.

Depending on the type of forcing, one distinguishes between barotropic and baroclinic inflows. Barotropic inflows are forced by the difference in sea levels between the Baltic and the North Sea (Feistel et al., 2003; Fischer and Matthäus, 1996; Franck et al., 1987; Matthäus and Franck, 1992). One factor promoting the generation of major inflows is the decrease in river dis-

charges (Schinke and Matthäus, 1998). Appearing mainly in autumn and winter, waters from barotropic inflows are rich in oxygen and salt. The weaker, baroclinic inflows are forced by the baroclinic pressure gradient (Feistel et al., 2003; Fischer and Matthäus, 1996; Franck et al., 1987; Matthäus and Franck, 1992) and usually occur in late summer. Those waters are also rich in oxygen, though less so than waters from barotropic inflows. Winter and spring inflows increase salinity and oxygen content, while reducing temperature in the bottom layers. Summer and autumn inflows increase salinity and temperature, but oxygen levels are lower. The main inflows were characterized by Matthäus and Franck (1992), who pointed out that inflows of medium or greater intensity occur much less frequently than weak intensity inflows.

Forming at the base of the surface layer, the dicothermal layer is specific to the Baltic Sea and to other seasonally ice-covered seas. It appears in spring, when the surface layer is warmed from above while the temperature of the layer beneath is still near freezing. On the other hand, the deep, bottom layer remains at ca 3–6°C, but because of its higher salinity is much denser than the layer above it. The dicothermal layer persists throughout the summer, ultimately disappearing only as a result of autumn convection. Because of the nature of its formation, this layer is also known as ‘old winter water’ or the *Cold Intermediate Layer (CIL)*.

All the above factors influence the complex spatial structure of DO in the Baltic Sea, which has a marked effect on marine life. Oxygen loss is increasingly being recognized as a major threat to marine ecosystems, altering habitat conditions in many parts of the global ocean (Oschlies, 2018). Hypoxia with a combination of reduced prey availability along with increased parasite burdens have contributed to a worsening Baltic cod (*Gadus morhua*) population status (Casini et al., 2016; Eero et al., 2015). Cod in the Baltic are assessed and managed as two distinct stocks. The eastern cod stock lives to the east of the island of Bornholm while the western stock inhabits the area from west of Bornholm to the Sound and the Danish Belts (Bagge et al., 1994). The differences between the two populations have been established by tagging, phenotypic and genetic programmes (Berner and Borrmann, 1985; Müller, 2002; Nielsen et al., 2005; Nielsen et al., 2003; Otterlind, 1985). However, the tagging programme indicates that the eastern and western stocks co-occur in the Arkona Basin (Aro, 1989; Nielsen et al., 2013). The eastern Baltic stock is about five times larger than the western one (Eero et al., 2015). Identification of the cod’s spawning areas is based on ichthyoplankton surveys. However, two major problems crop up with this approach to identification. Firstly, the natural buoyancy layer may change as a result of salinity changes in the area. Quantitative sampling is therefore demanding, because it is impossible to sample close to the seabed, near the greatest concentration of eggs. Secondly, the distribution of eggs and early larvae can change or switch their spawning origin owing to the highly variable environmental conditions. Eastern Baltic cod utilize the deep basins (Bornholm Basin, Gdańsk Deep and Gotland Basin) as spawning habitats (Köster et al., 2001), but the most important spawning ground in the Baltic is in the Bornholm Basin (Bagge et al., 1994). Low salinity can

limit the fertilization of fish eggs by inhibiting the activation of spermatozoa (Hüssy, 2011). The minimum salinity required by Baltic cod differs between stocks, from $S \geq 11$ –12 PSU in the eastern Baltic to $S > 15$ –16 PSU in the western Baltic (Nissling et al., 1994; Nissling and Westin, 1997). At lower salinities, the eggs will sink and fail to hatch (Westernhagen, 1970). Because of the low oxygen content at the depth where the eggs sink, the cod cannot reproduce. Superimposed on this primary driver, oxygen content and temperature have a significant effect on egg/larva development and survival. The whole spawning season for all stocks lasts for 6–7 months. However, peak spawning is limited to no longer than two months, with a pronounced trend towards progressively later spawning along a gradient from north-west to east (Bleil et al., 2009; Vitale et al., 2008). The cod in the Kattegat are the first to start spawning, peaking in January/February (Vitale et al., 2005). In the Bornholm Basin, cod spawning peaks in July/August (Bleil et al., 2009; Wieland et al., 2000). Generally, small fish are rather stationary, whereas adult cod migrations are associated with spawning (Rose et al., 2018).

The aim of this study was to describe the recent variability of DO in southern Baltic sea water. The locations of the study area were chosen because of their significance for the hydrography of the entire Baltic, especially under the influence of MBIs. MBIs transport large amounts of DOC into the Baltic: as Mohrholz et al. (2015) pointed out, the total amount of oxygen transported into the Baltic during MBI 2014 was estimated at 2.04×10^6 t. It takes approximately 30 years for the Baltic Sea waters to be fully exchanged (Stigebrandt, 2001). However, no direct calculations about the time scale of the impact of MBI on DO have been performed to date. We therefore investigated this impact in the deepest regions of the Bornholm Basin, Stupsk Furrow and Gdańsk Deep. The two MBIs in 1976 were responsible for the greatest landings of cod ever recorded in the Baltic (Matthäus et al., 2008). Accordingly, the link between MBIs and cod reproduction is unquestionable. Therefore, based on the findings of this work as well as on the critical values of physicochemical parameters for cod egg fertilization and survival, we assessed the cod fertilization layer as well as the egg neutral buoyancy layer in the basins surveyed. Finally, we examined the changes in those layers under the influence of MBIs.

2. Methodology

2.1. Study area

With a total surface area of 420 000 km², the Baltic is one of the largest brackish water bodies in the world. However, this large sea is relatively isolated from the ocean. The only connection with the North Sea is through the Sound and the Belt Seas. Bringing oxygen and salt, saline waters enter the Baltic mainly during winter storms, thereby improving oxygen conditions in the Baltic deeps. The freshwater input to the Baltic from rivers corresponds to about one fortieth of the total water volume per year (Bergström et al., 2001). This complex hydrological situation creates a characteristic brackish water gradient: whereas the surface salinity is about 15–18 PSU in the Sound, it falls to 7–8 in the Baltic Proper and to 0–3 in the Gulf of Finland. The up-

per fresher and deep saline waters are separated by a halocline. Simultaneously, the strong halocline coincides with the pycnocline, which limits the vertical range of wind mixing and convection (Feistel et al., 2006; Lehmann et al., 2004; Matthäus and Franck, 1992; Matthäus and Lass, 1995; Reissmann et al., 2009).

This paper focuses on three areas in the southern Baltic Sea: the Bornholm Basin (BB), the Stupsk Furrow with the Stupsk Sill (SF), and the Gdańsk Deep (GD). These areas are distinguished by the 70 m isobath (Figure 1). They are also delimited by longitude: BB – 15° and 16.35°; SF – 16.76° and 17.95°; GD – 18.37° and 19.28°.

Situated to the north-east of the island of Bornholm, the Bornholm Basin is connected to the Arkona Basin via the Bornholm Gate. Oxygen-rich, inflowing waters can move through the Bornholm Gate towards the Bornholm Deep. The shallow Rønne, Odra and Orla banks restrict the advection of saline water on the southern side. On the eastern side, the route for MBIs flowing in from the Bornholm Basin is towards the Stupsk Furrow. These areas are separated by a 50 m deep threshold known as the Stupsk Sill.

An elongated, parallel-sided basin with an asymmetrical cross-sectional shape, the Stupsk Furrow has a total length of ca 115 km and a width of 25 km. The greatest depth of the furrow is about 90 m. The Stupsk Furrow is limited by two thresholds: the Western and Eastern Stupsk Sills. The Stupsk Furrow is a highly dynamic area and, because it provides a transit for inflow waters, is decisive for the hydrography of the entire Baltic Sea.

The Gulf of Gdańsk and the Gdańsk Deep form the Gdańsk Basin, the greatest depth of 115 m being in the central part. The Gdańsk Basin is separated from the Stupsk Furrow and Gotland Basin by an 85 m deep diagonal sill. Both models and measurements indicate that the Gdańsk Deep does not actively participate in the inflow of waters to the deep areas of the Baltic Sea, but acts as a buffer (Elken, 1996; Jankowski and Livingstone, 2003).

2.2. Field Data

The hydrographic data used in this paper were obtained by the Institute of Oceanology, Polish Academy of Sciences (IO PAN) and the Institute of Oceanology, P.P. Shirshov Russian Academy of Sciences (IO RAN).

IO PAN used towed CTD (Conductivity, Temperature, Depth) and Oxygen probes to acquire high-resolution transect records along the main profile in the southern Baltic (Rak and Wiczorek, 2012). This transect runs along the main axis of the deep basins in the southern Baltic, from the Bornholm Basin through the Stupsk Furrow to the Gdańsk Deep (Figure 1). The data were collected during regular cruises of *r/v Oceania* in 2013–2017 (Table 1). A total of 15 transects with over 12 000 casts were recorded. The spatial resolution of measurements was ca 200–500 m in the horizontal and 3 cm (30 measurements per metre) in the vertical.

IO RAN used a moored Aqualog System (Ostrovskii, 2013) located at 55°12.7'N 16°41.2'E to gather data on the eastern slope of the Stupsk Sill (Figure 1). The mooring was redeployed during three expeditions in order to maintain continuity of measurements. The record started on 12 May 2016 and ended on 13 May 2017. This long-term, continuous

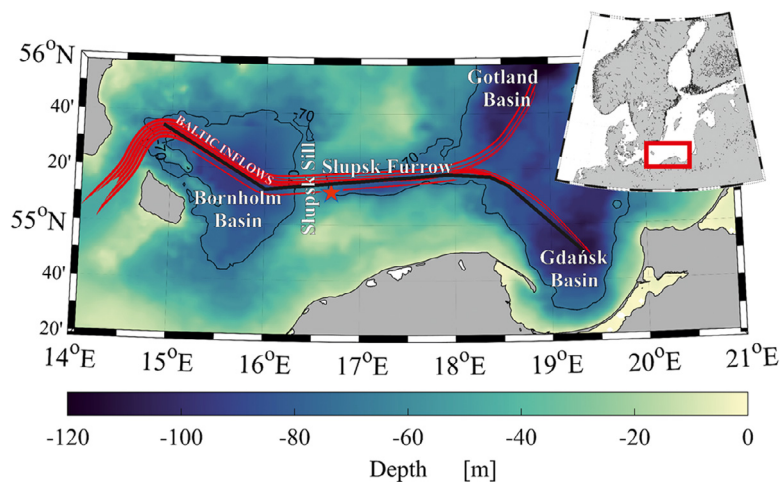


Figure 1 Location of measurements in the southern Baltic Sea. The solid black line represents the main course taken by *r/v Oceania*, and the star shows the position of the Aqualog. The red lines indicate the routes taken by MBIs.

Table 1 Specification of measurement methods.

Platform	Data measurement period (dd.mm.yyyy)	Sensors used		Data acquisition type
		CTD	DO	
<i>r/v Oceania</i>	03.04.2015, 02–03.01.2017; 24–26.02.2015; 01–03.03.2013; 22–26.04.2013; 22–24.05.2016, 11–14.05.2017; 12–13.09.2016; 09–13.10.2013, 09–12.10.2014, 01–04.10.2015; 26–29.11.2014, 26–27.11.2015, 22–25.11.2016; 09–12.12.2013;	SBE 49 FastCAT	JFE Advantech Rhinko probe	Towed probe
Argo float	06.02.2018–18.07.2018;	SBE 41	AANDERAA OPTODE 4330	Autonomous floats
Aqualog	12.05.2016–13.05.2017;	SBE 19plus	SBE 43F sensor	Moored system

vertical profiling system gathered hydrographic information about CTD and DO from the water column from 15 m below the sea surface to 68 m depth (3 m above the seabed). The temporal resolution of this system was about 2 hours, the time taken by Aqualog to move down to the end of the wire and back up to its original position.

The third type of data came from the autonomous profiling Argo float (Argo, 2018). This was set up by IO PAN in the Bornholm Basin on 6 February 2018. For the next five months, the float measured CTD and DO in the southern Baltic. The deployment position and trajectory are shown in Figure 2. The autonomous float spent most of the time drifting at the parking depth about 60 m. The float performed a full profile from bottom to surface every 2 days, while at the surface it transmitted data via satellites and determined the geographic position of the unit. The vertical resolution of the transmitted data was 1 m. The first measurements by the Argo floats in the Baltic were performed by Finnish oceanographers in the Bothnian Sea (Haavisto

et al., 2018) and in the Gotland Deep (Siiriä et al., 2019). The IO PAN experiments proved the usefulness of Argo floats for the monitoring in the Southern Baltic.

The raw data collected from *r/v Oceania* was averaged into 0.5 m vertical layers, the data collected from Aqualog into 1 m layers. For the analysis, the data was gridded in Matlab into fixed vertical and horizontal layers. Data averaged into 1 m layers were used for the seasonal analysis of the DO cycle. To study the variability of the CIL, the halocline and thermocline depths were determined by the maximum temperature and salinity gradient in the water column. The spermatozoa activation layer and natural buoyancy layers were determined on the basis of critical values for salinity and DO (Hüssy, 2011). The spermatozoa activation layer was established for salinities of 11 PSU or higher with a minimum DOC of 5 mg l⁻¹. The natural buoyancy layer was located for a salinity of 14.5+1.2 PSU and a DOC of 2 mg l⁻¹. The critical DOC for egg survival during incubation is 2 mg l⁻¹.

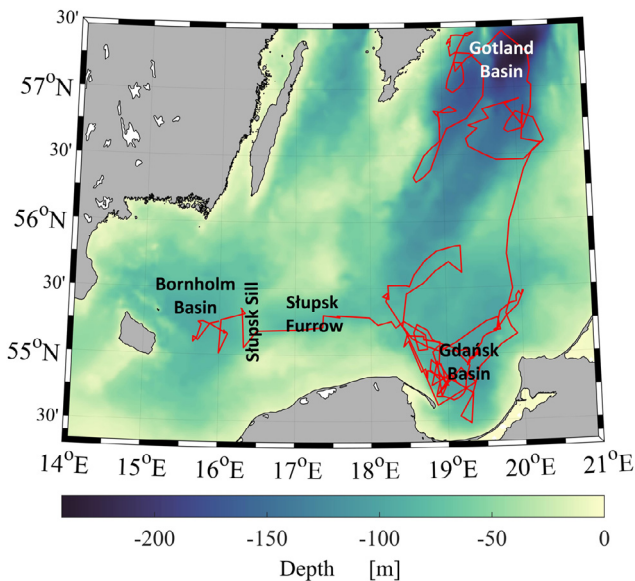


Figure 2 Deployment position and trajectory of the Argo float in the southern Baltic Sea. The float was launched in the Bornholm Basin in February 2018.

3. Results

3.1. Spatial variations in DO stratification

The highest DOCs in the Bornholm Basin, Słupsk Furrow and Gdansk Deep are found in the surface layer (Figure 3): they are no greater than 14.5 mg l^{-1} . The upper layer is relatively homogeneous with a standard deviation of DO up to 2 mg l^{-1} . DO variation in the upper layer (ca 55 m thick) is due to large fluctuations of water temperature, which affect oxygen solubility, and to the seasonality of oxygen production during photosynthesis. The oxygen content in the oxycline is ca 8 mg l^{-1} less, and the thickness of this layer is determined by the position of the upper boundary of the halocline with respect to the seabed. The range of changes as well as the content of dissolved oxygen in the deep waters of the Baltic Proper depend directly on the advection of dense, saline waters from the North Sea. Both the DOC in the bottom layer and its variability decrease with distance from the

Danish Straits. The oxygen content in the 25 m-thick deep layer of the Bornholm Basin is ca $4 \pm 3 \text{ mg l}^{-1}$ (Table 1); the oxygenation of this layer takes extreme values, from relatively well oxygenated to anoxic. The Słupsk Furrow is fairly well oxygenated for most of the time, but periodically, the less well oxygenated waters contain ca 2.6 mg l^{-1} of dissolved oxygen. In the Gdansk Deep, poor oxygenation ($< 4 \text{ mg l}^{-1}$) is the rule: there, the average oxygen content within the ca 20 m-thick bottom layer is $2 \pm 1 \text{ mg l}^{-1}$.

The annual changes in DOCs are presented as monthly averages along the main axis of the deep basins in the southern Baltic Sea (Figure 4). Because of the insufficient number of surveys, the transects from June to August are not shown. Generally, the vertical DO distribution reflects the salinity pattern (dashed blue line). Therefore, two layers of DO, separated by the steep oxycline, can normally be distinguished. In the upper layer, DO also seasonally reflects temperature changes (solid red line): owing to the greater impact of the CIL on the oxygen content, a three-layered structure of DO then becomes recognizable. From January to May there is almost homogeneous oxygenation of the upper layer. As the oxygen content decreases with increasing temperature, the lowest annual oxygen content in the measured time series was in September and October, as the summer months are missing from the dataset. Moreover, when oxygenation of the upper layer is at a minimum, greater vertical gradients of DO are noticeable at a depth of $50 \pm 10 \text{ m}$. The lower temperature of the diathermal layer in the surrounding water causes differences in the oxygen content. The least oxygenation of the CIL can be expected in the vicinity of the Danish Straits and increases with distance towards the deeps of the Baltic Sea. After November, with increasing DOC, the upper layer becomes homogeneous. The maximum oxygen concentration in the upper layer in March/April reaches ca 14 mg l^{-1} . Further oxygenation of the upper layer and the penetration of oxygen into the deeper layer closes the annual cycle.

The dense waters of the Baltic Sea below the halocline (50–60 m) are isolated from the sources of oxygen: therefore, anaerobic conditions often prevail in the deep basins. Only the advection of dense, well-oxygenated water can transport oxygen efficiently into the deepest basins. Some of the results presented here were obtained during the 2015 inflow, which affected the conditions in the deep layer of the Bornholm Basin. From January to March, DOC in this re-

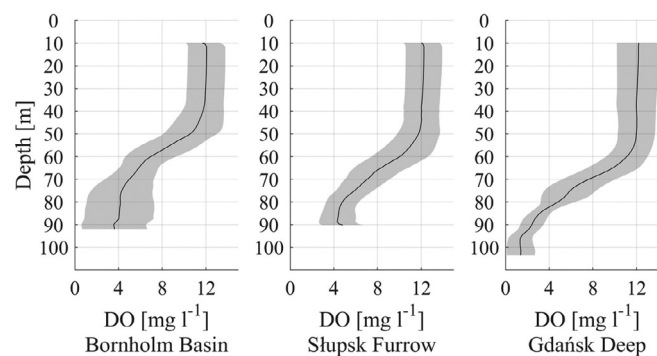


Figure 3 The average, long-term oxygen content with associated standard deviation in the Bornholm Basin, Słupsk Furrow and Gdansk Deep.

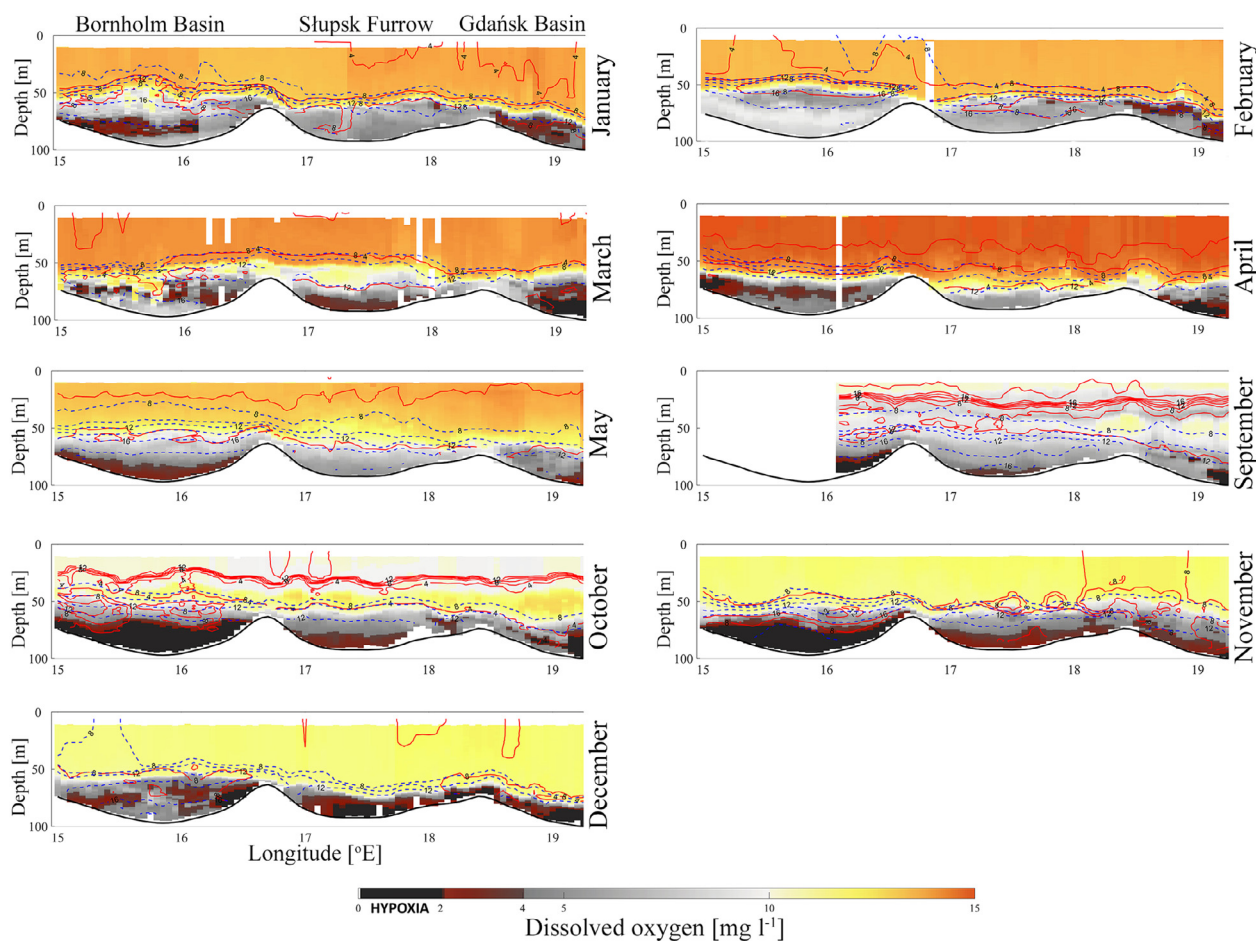


Figure 4 Monthly distributions of dissolved oxygen along the main transect in 2013–2017. Based on data from 2 cruises in January, 1 each in February, March and April, 2 in May, 1 in September, 3 in October, 3 in November and 1 in December. Temperature (solid red line), salinity (dashed blue line).

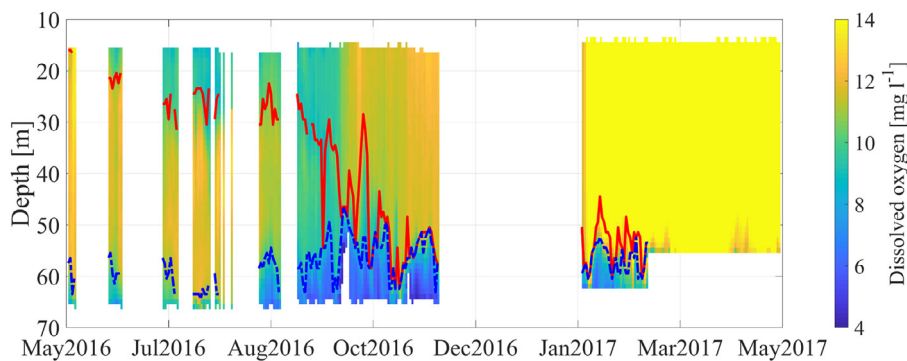


Figure 5 The Aqualog system measurements 12 May 2016–13 May 2017. Thermocline (red line), halocline (blue line).

gion was thus very high, $> 8 \text{ mg l}^{-1}$ (Figure 4). As shown in the previous section, the average for the Bornholm Basin is ca 5 mg l^{-1} .

3.2. DO and CIL transformation

The transformation of the CIL with respect to DOC in the southern Baltic is shown in Figures 5 and 6. Although the

CIL forms in winter, it is most noticeable in summer, when the remnants of cold winter water become covered by warmer surface water. The thermocline, the upper limit of the CIL, starts to form in May/June and persists until late November/December. The CIL slowly erodes by mixing with warmer, overlying waters. Therefore, the maximum value of the temperature gradient slowly falls at a rate of ca 10 m depth per month, reaching the halocline in winter. Winter storms align the temperature in the upper layer and thus

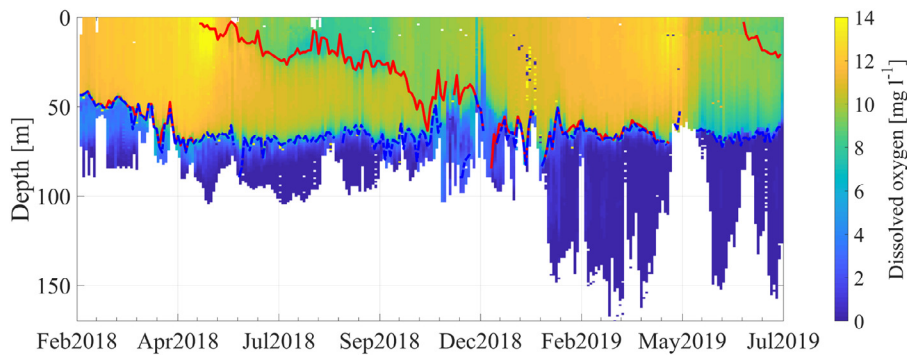


Figure 6 Argo float measurements from 6 February to 18 July 2018. Thermocline (red line), halocline (blue line).

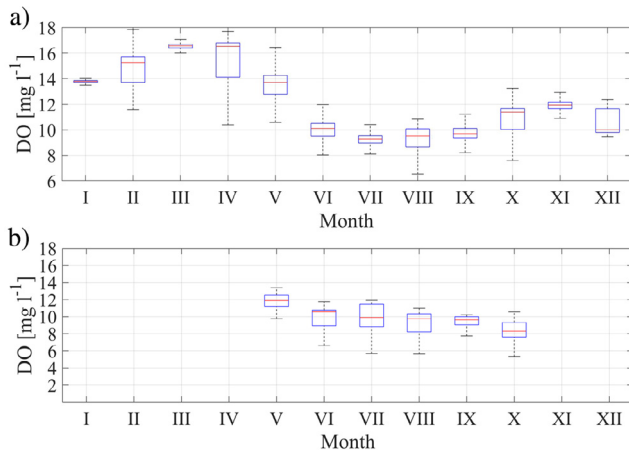


Figure 7 Seasonal DO in the 0–20 m layer (upper plot) and in the CIL (lower plot) in the southern Baltic Sea. The results for 2013–2018 were obtained during cruises of *r/v Oceania*, from the Aqualog mooring system and from Argo float data.

close the annual CIL cycle. The halocline, the lower limit of the CIL, lies at about 55 m depth. The upward and downward movement of the halocline is associated with near-bottom advection, so variation in the vertical can reach up to 15 m.

The seasonal changes in DO in the southern Baltic are presented as the average for the 0–20 m layer and for the CIL (Figure 7). Surface water oxygenation (upper plot) peaks in March/April. Having achieved this spring maximum, the oxygen in the water column is then systematically consumed until the first oxygenation minimum is reached in July. With falling temperatures, the oxygen content again rises continually to the second maximum in November, after which it again drops to a minimum in December, thus closing the annual DO cycle in the southern Baltic.

At the depth of the CIL (lower plot), the oxygen content differs from that in the surface layer. The differences arise during the warmest months, when the first minimum is reached at the surface. The difference in DOC between the surface layer and CIL can be as high as 4 mg l^{-1} in summer. In the CIL, moreover, there is a constant decrease in DOC with only one maximum (May) and minimum (October). As a result of mixing and diffusion at the upper and lower limits of the CIL, a decrease in DOC can be expected. DO is transported from the edge of the CIL (ca 10 m depth) to the

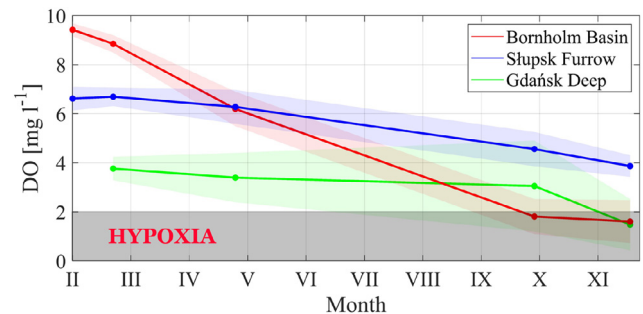


Figure 8 Dynamics of DO decline after MBI 2014, measured in 2015 (average DO below 70 m depth in the Bornholm Basin, Stupsk Furrow and Gdańsk Deep). The shaded areas indicate standard deviations.

upper and lower layers. The CIL thus acts as a reservoir of oxygen for the less oxygenated layers.

3.3. Influence of inflows on deep layer oxygenation

The average DOC and its standard deviation were calculated in order to estimate the changes in DO after MBI 2014. Figure 8 shows the temporal evolution of DO in the layer below 70 m depth for three areas in the Baltic Proper. The highest values (ca 9.5 mg l^{-1}) were recorded in January/February 2015 in the Bornholm Basin. The monthly DO decrease in this region was ca 1 mg l^{-1} . Thus, just 10 months from the beginning of the inflow, anoxic conditions returned to the layer below the halocline. In the Stupsk Furrow, the decrease in DO was slightly slower: this depletion took 11 months, and the lowest oxygen concentration in this region was ca 4 mg l^{-1} . However, during the entire inflow period, low DO water was not expelled from the deep layer of the Gdańsk Deep. In the intermediate layer (the upper value of STD in the figure), at a depth of ca 70 m, the oxygen content increased slightly to ca 4.8 mg l^{-1} .

Figure 9 compares the temperature and salinity of MBI 2014 (recorded in January and May 2015) with the corresponding values for the weak inflows in November 2014 and 2016. Overall, MBIs are characterized by a higher density and lower temperature than baroclinic inflows. However, the temperatures of the inflows depend on the season in which they occur. During MBIs, higher DOCs are measured

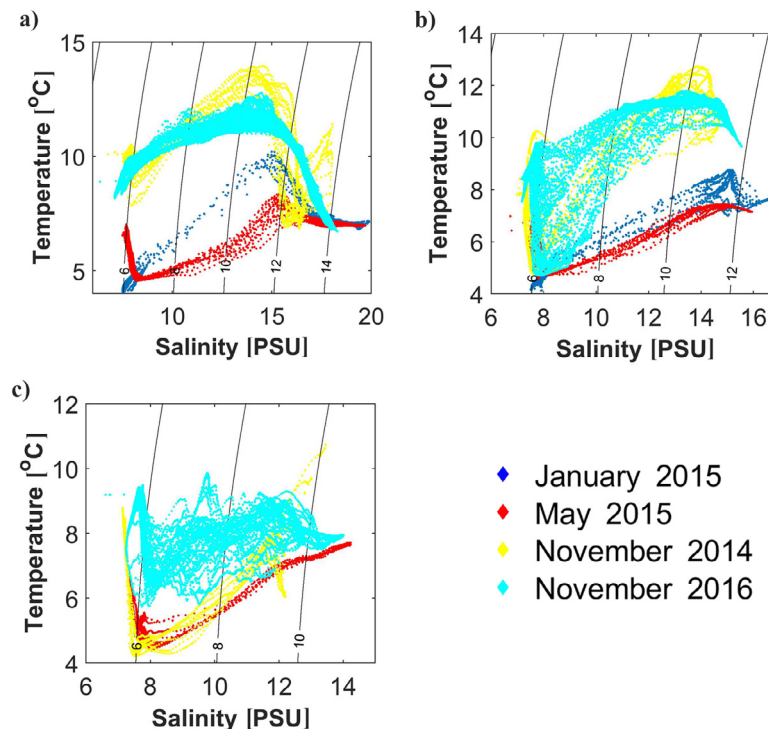


Figure 9 Comparison of the TS diagrams for MBI 2014 recorded in January and May 2015 with the weak inflows recorded in November 2014 and 2016. The figures represent the Bornholm Basin (a), Słupsk Furrow (b) and Gdańsk Deep (c).

in the deepest layers in Bornholm Deep and Słupsk Furrow (Figure 10).

During November 2014 and 2016, intrusions of warm waters below the halocline were recorded in the Bornholm Basin. Having passed the Słupsk Sill, they sank to the sea bed. The sinking was accompanied by increased mixing, so the lower limits of the transition layers (thermocline/oxycline) reached 75 m depth in the Słupsk Furrow (Figure 10). In the Gdańsk Deep the upper limit of the oxycline lay at 47–57 m, the lower one at 74–83 m.

3.4. Cod spermatozoa activation and natural buoyancy layers

A very interesting aspect is the possible effect of DO on the eggs of Baltic cod. Based on the mean salinity and mean DO data from 2013–2017 along the main axis in the southern Baltic, we were able to distinguish the Baltic cod's egg fertilization (Figure 11) and neutral egg buoyancy layers. The spermatozoa activation layer lay at 52–73 m depth in the Bornholm Basin and 62–81 m in the Słupsk Furrow. Conditions in the Gdańsk Deep were not appropriate for spermatozoa activation.

After fertilization, the egg enters the optimum depth determined by its neutral buoyancy. The neutral egg buoyancy layer in the Bornholm Basin lies within the range of the spermatozoa activation layer. However, in the Słupsk Furrow, a fertilized egg can sink to reach the optimum buoyancy depth.

The spermatozoa activation and neutral egg buoyancy layers overlap in the Bornholm Deep throughout the mea-

surement period (Figure 12). In the Słupsk Furrow, these layers are sometimes separated: eggs can be fertilized in the transition layer but will sink to the deeper layers. If the oxygen conditions are suitable, cod eggs will survive in the deep water of the Słupsk Furrow. For most of the time, however, conditions in the Gdańsk Deep do not ensure cod egg survival there. Stronger advection can bring saline, oxygenated waters to this region, which will guarantee the existence of the spermatozoa activation and neutral buoyancy layers. After MBI 2014, these layers were separated in the Gdańsk Deep.

4. Discussion

This paper characterizes oxygen variability in the three basins of the Baltic Proper: the Bornholm Basin, Słupsk Furrow and Gdańsk Deep. It describes the average DO in those basins and the monthly distributions of DOC along the main transect. This paper estimates the time scale of the DO change after an MBI. Finally, the spermatozoa activation layer as well as the natural buoyancy layer of the Baltic cod has been determined. The analysis is based on measurements of CTD and DO performed during regular cruises of *r/v Oceania* across the Baltic in 2013–2017, the moored Aqualog system (2016–2017) and the autonomous Argo float deployed in 2018. This is the first time that changes in DO have been estimated for an Baltic inflow period. This research is also the first attempt to estimate the depth that meets the conditions required for the survival of cod eggs in the early stages of their existence.

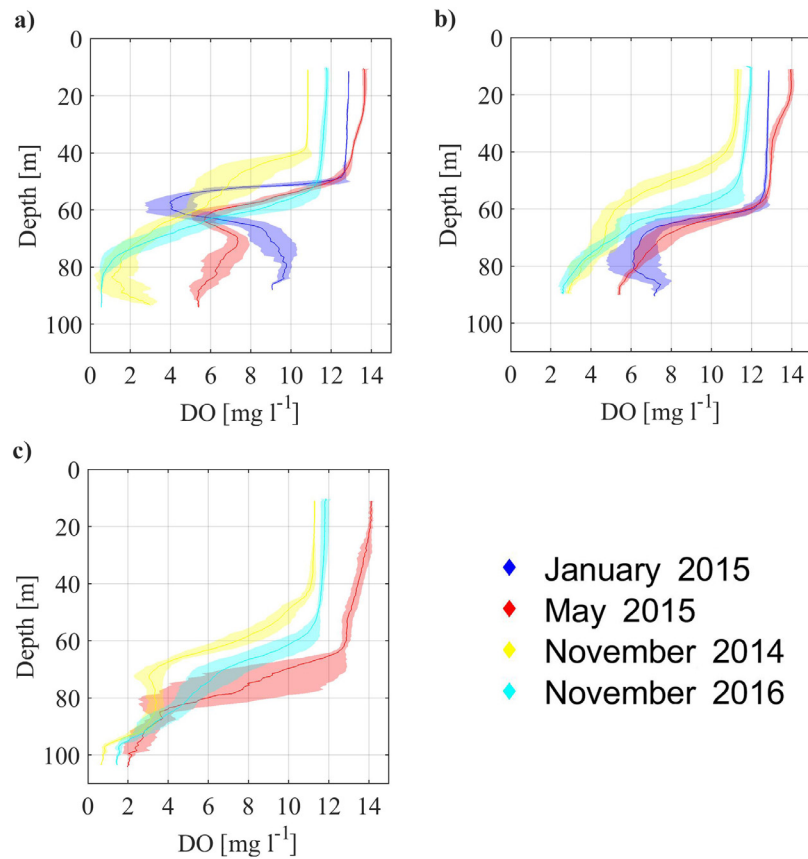


Figure 10 Comparison of DO during MBI 2014 recorded in January and May 2015 with the weak inflows recorded in November 2014 and 2016. The figures represent the Bornholm Basin (a), Słupsk Furrow (b) and Gdańsk Deep (c).

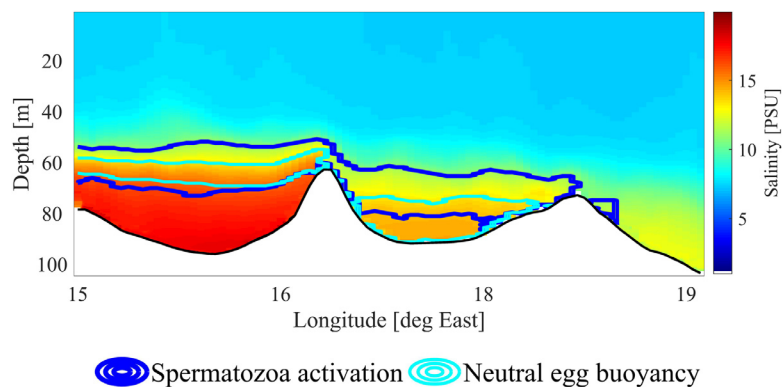


Figure 11 Cod spermatozoa activation layer (dark blue lines) and the neutral egg buoyancy layer (light blue lines) along the main axis in the southern Baltic Sea.

4.1. DO variability in the southern Baltic Sea

Steep spatial gradients and DO stratification occur in the deeper layers of the Baltic Sea. The stratification of DO in the southern Baltic reflects the salinity distribution. One can therefore recognize a two-layered structure: an upper (euphotic) zone and a lower one, separated by the oxycline. However, the DO distribution partly reflects the temperature pattern, just as it reflects the salinity field, so a seasonally three-layered DO structure occurs.

The highest oxygen content is in the layer in contact with the atmosphere, where photosynthesis also takes place. As this layer is relatively homogeneous to the depth of the oxycline, a seasonal DO cycle is distinguishable in the surface layer of the southern Baltic. This cycle has two maxima and two minima. The first DO maximum, occurring in spring, is related to the increased rate of photosynthesis at this time (Renk, 1974; Woźniak, 1989). There are variants when the first maximum appears in March or April. The second maximum falls in November. The first minimum falls in

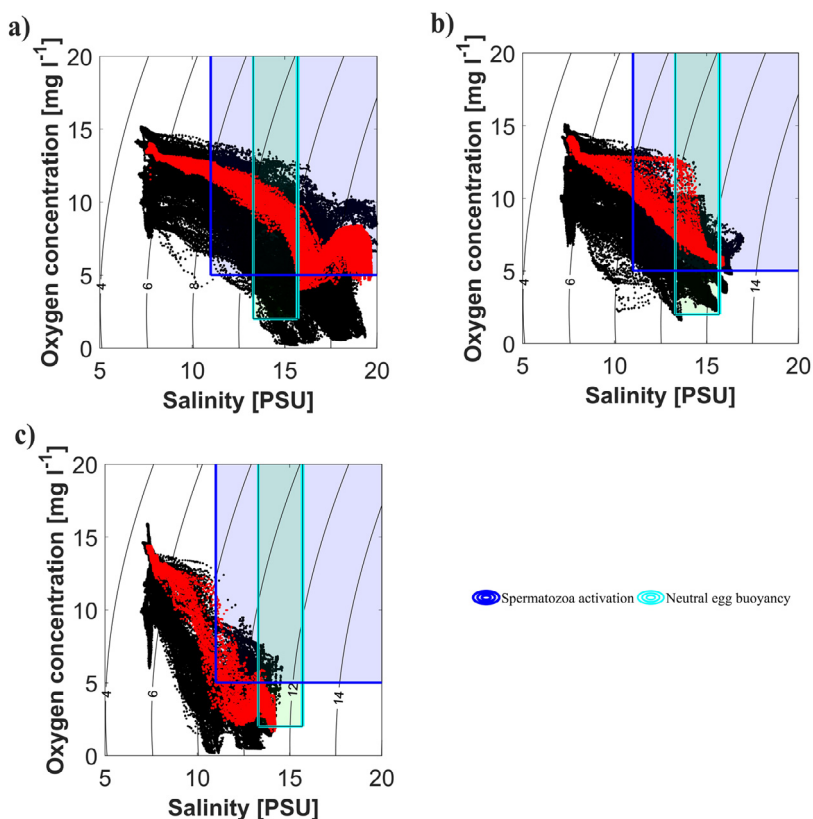


Figure 12 OS diagrams for the Bornholm Basin (a), Słupsk Furrow (b) and Gdańsk Deep (c). The red dots represent the MBI, May 2015.

July/August, and the second in December, closing the annual cycle of oxygenation changes of the surface layer.

The CIL has a great impact on the DO structure in the southern Baltic. Owing to the greater solubility of oxygen in colder waters, the CIL is a reservoir of oxygen for the less oxygenated upper and lower layers. Furthermore, steady decreases of oxygen are recorded in the CIL from May to October. The smallest thickness of the CIL can be expected in the vicinity of the Danish Straits. Moving from the Straits towards the deeps of the Baltic, the thickness of the CIL increases. Therefore, a greater DO content in this layer can be expected in the Gdańsk Basin than in the Bornholm Deep.

4.2. DO variability in the near-bottom layer

Below the halocline, where dense waters are separated from the direct source of oxygen, one of the main processes capable of transporting oxygen into the Baltic deep waters is advection. Therefore, one can expect the greatest oxygenation of the deep layer to be in the vicinity of the Danish Straits. The oxygenation of the near-bottom layer in the Bornholm Basin takes extreme values, from relatively well oxygenated during inflow periods to anaerobic during stagnation periods. Monitoring data (Mohrholz, 2018) indicate, however, that during stagnation periods before and after MBI 2014, oxygen in the Bornholm Deep increased several times. With increasing distance from the Straits, oxygenation of the deep waters decreases. In the Gdańsk

Deep, where advection is severely limited by the Słupsk Sill, oxygen-deficient conditions ($< 4 \text{ mg l}^{-1}$) are permanent.

4.3. Water oxygenation during inflows

The greatest volume of oxygen pushed into the Baltic's deepest basins originates from barotropic inflows. With a total saline water volume of 198 km^3 , MBI 2014 transported $2.04 \times 10^6 \text{ t}$ of oxygen into the Baltic (Mohrholz et al., 2015). Two months after the inflow, DOC in the Bornholm Basin was ca 9 mg l^{-1} , while in the Słupsk Furrow it was ca 7 mg l^{-1} . However, 9 months after the start of the inflow, anaerobic conditions (2 mg l^{-1}) returned to the deep layer of the Bornholm Basin and 10 months later to the Słupsk Furrow ($< 4 \text{ mg l}^{-1}$). Moreover, despite the large volume of MBI 2014, oxygen-deficient conditions persisted in the Gdańsk Deep.

The very high rate of oxygen consumption in the anaerobic layers in the Baltic Proper after MBI 2014 can be explained by biological production, which used up the newly supplied oxygen. Oxygen is also consumed during the decomposition of dead organisms. With declining oxygen, phosphorus is released from the sediments (Stigebrandt and Kalén, 2013) and transported to the upper layers (Viktorsson et al., 2012), thus stimulating biological production and consequently intensifying oxygen consumption in the bottom layer.

The advection of dense MBI waters in the Baltic propagates them over the seabed. The inflow volume of ca

198 km³ and mixing processes enhanced the oxygenation of the bottom layer. An exceptional feature of the last inflow was the mixing of three water masses in the Bornholm Basin: the MBI waters, the warm intrusion and the waters previously occupying the Bornholm Deep. The MBIs in December 2002 (Meier et al., 2004) and 2014 (Rak, 2016) were preconditioned by weaker inflows. Those inflows moved some way towards the Słupsk Sill and partially mixed with anoxic deep waters in the Bornholm Deep. The inflow in the Bornholm Deep therefore took the form of intrusions as a result of being pushed upwards by the MBI. Thus, in January and February 2015, a warm, poorly oxygenated layer was recorded above the deep, well-oxygenated water in the Bornholm Basin.

The advection of weaker inflows propagates in the form of an intrusion, raising the oxycline and halocline in the Bornholm Basin; the movement of inflow waters over the Słupsk Sill was thus possible. This warm, relatively well-oxygenated intrusion passed the Słupsk Sill and sank. The sinking was accompanied by increased mixing, so the lower limit of the transition layer (oxycline) extended to 75 m depth in the Słupsk Furrow.

Advection of DO during an MBI leads from the deep layer of the Bornholm Basin to the Słupsk Furrow. During weaker inflows, DO advection extends from the intermediate layer in the Bornholm Basin.

4.4. Baltic cod spermatozoa activation and natural buoyancy layers

Dissolved oxygen and the requisite salinity in the sea are important requirements for survival. For the Baltic cod, oxygen is necessary from the early stages of its life. In order to begin spawning, the physical properties of the water have to match the cod's requirements. In the Bornholm Basin the critical salinity for spermatozoa activation is $S > 11\text{--}12$ PSU (Nissling and Westin, 1997). Neutral egg buoyancy is maintained at ca 14.5 ± 1.2 PSU. During incubation, cod eggs can survive when $\text{DOC} > 2 \text{ mg l}^{-1}$ (Rohlf, 1999; Wieland et al., 1994). However, at $\text{DOC} < 5 \text{ mg l}^{-1}$ the cod stock begins to decline (Köster et al., 2005). In the Bornholm Basin the waters enabling spermatozoa activation lie in a 21 m-thick layer at an average depth of ca 62 m, while in the Słupsk Furrow they are in a 19 m-thick layer at an average depth of 71 m. The differences between the lower limit of the spermatozoa activation layer in the Bornholm Basin and the Słupsk Furrow results from the deep layer DO conditions. After fertilization, the egg enters the optimum depth determined by its neutral buoyancy. In the Bornholm Basin the neutral buoyancy layer (65 ± 5 m) lies within the spermatozoa activation layer. However, in the Słupsk Furrow, fertilized eggs can be found at depths from 75 m to the seabed, whereby only the upper limit is within the range of spermatozoa activation. Therefore, fertilized eggs can sink to reach the optimum depth. Based on average values of salinity and DO, no cod spermatozoa activation layer and no egg neutral buoyancy layer exist in the Gdańsk Deep. However, inflows from the North Sea can guarantee the existence of those layers.

Recapitulating, cod eggs can survive in the layer where they were fertilized in the Bornholm Basin. In the Słupsk

Furrow, the eggs can leave the fertilization layer and sink to the bottom, because the neutral buoyancy layer only partly overlaps the spermatozoa activation layer. After fertilization, eggs can survive in the bottom layer of the Słupsk Furrow. During stagnation, there are no conditions which can guarantee egg survival in the Gdańsk Deep. Only during inflow periods do the fertilization layer and neutral buoyancy layer reappear.

Fertilized eggs from the Bornholm Deep can be transported to the Słupsk Furrow by deep currents. Owing to the position of the neutral buoyancy layer at the intermediate layer depth, movement above the sill is limited by the upward movement of the halocline. One factor which can shift the halocline upwards is the strong advection of saline, well-oxygenated waters from the North Sea (Mohrholz et al., 2015). Unlike weak inflows, MBIs refresh the deep layer of the Bornholm Basin, allowing cod to fertilize their eggs in the whole water layer from the halocline to the seabed. On the other hand, weaker inflows increase the transition layer thickness and have a great impact on the upward movement of the halocline.

5. Conclusions

1. At the surface layer the DO seasonal cycle has two maxima and two minima. The first maximum appears in March or April, the second in November. The first minimum appears in July/August, the second in December.
2. The CIL is a reservoir of oxygen for the less oxygenated upper and lower layers. A steady decrease in DO can therefore be expected from May to October.
3. The DOC at the bottom of the Bornholm Basin varies between well oxygenated to anaerobic.
4. Oxygen deficient conditions with $\text{DO} < 4 \text{ mg l}^{-1}$ at the bottom of the Gdańsk Deep are permanent.
5. Nine months after MBI 2014, anaerobic conditions returned to the deep layer of the Bornholm Basin, but oxygen-deficient conditions persisted in the Gdańsk Deep.
6. Cod eggs can survive in the layer where they were fertilized in the Bornholm Basin. The eggs can leave the fertilization layer and sink to the bottom in the Słupsk Furrow. There are no conditions which can guarantee egg survival during the stagnation period in the Gdańsk Deep.
7. Only advection of water from the North Sea can guarantee the existence of the cod spermatozoa activation layer and the egg neutral buoyancy layer in the Gdańsk Deep.

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