

Climate-driven long-term trends in Baltic Sea oxygen concentrations and the potential consequences for eastern Baltic cod (*Gadus morhua*)

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Variations in oxygen conditions in the Baltic are influenced by several mechanisms. Generally, the frequency and magnitude of major inflows have been identified as the most crucial process for the renewal of oxygen-depleted water masses in the Baltic Sea. Furthermore, enhanced degradation of suspended organic matter by bacteria over the past few decades has increased oxygen consumption. Finally, the effects of large-scale climate warming are causing long-term variations in oxygen content and saturation as an observed increase in temperature has led to a general decrease in oxygen solubility of water masses. Oxygen-dependent relationships based on field data and laboratory experiments were used to analyse the impact of the observed decrease in oxygen content on eastern Baltic cod (*Gadus morhua*) stock-specific processes (e.g. survival rates of eggs, settlement probability of juveniles, habitat utilization of spawning fish, age structure of successful spawners, food consumption rates of adult fish). The observed long-term decline in oxygen conditions in the Baltic Sea has had a seemingly generally negative impact on oxygen-related processes for the different life stages of eastern Baltic cod. Experimentally derived results of oxygen-driven processes were validated by field data.

Keywords: Baltic cod environment, climate change, condition factor, egg survival, gut evacuation, habitat utilization, juvenile settlement probability, oxygen deficiency, warming.

Introduction

Apart from fishing pressure, several factors affecting the survival of eggs have been identified as major influences on recruitment processes and the subsequent stock abundance of eastern Baltic cod (*Gadus morhua*; hereafter referred to as Baltic cod) throughout the 20th century (Köster *et al.*, 2005). These factors, including direct predation on cod eggs, eutrophication (impacting oxygen levels necessary for egg survival), and climate-driven change in salinity (impacting egg buoyancy), are considered to be crucial in shaping the resource dynamics in future (Brander, 2010; Lindegren *et al.*, 2010). Eastern Baltic cod utilize the deep basins (Figure 1; Bornholm Basin ICES Subdivision 25, Gdańsk Deep Subdivision 26, Gotland Basin Subdivision 28) as spawning habitats (Köster *et al.*, 2001). However, the level of dissolved oxygen in these areas fluctuates widely and acute hypoxia is common. Successful cod spawning in the central Baltic Sea is restricted to areas with salinities varying between 11 and 20 psu. Cod eggs do not float in surface waters because of the low salinity in the

upper waters of the highly stratified central Baltic, but concentrate in a narrow depth range within and below the permanent halocline (Wieland and Jarre-Teichmann, 1997). Because of the commonly prevailing oxygen depletion at those depths, neutral egg buoyancy at depths above water layers with critical oxygen levels is hugely important for the survival of eggs and larvae (Vallin and Nissling, 2000).

Other factors that are more indirectly related to oxygen levels could be additional sources of early life-stage mortality. For example, low oxygen at the seabed may force larger juveniles to stay in the pelagic zone, where they may not be able to cover their energy demands because they will only be able to feed on small zooplankton organisms. Without finding a suitable settling habitat in an appropriate time-frame, which would allow them to feed on larger benthic organisms, juvenile cod might face starvation and possibly death during winter (Hüssy *et al.*, 1997). Sufficiently available benthic prey items are only found in regions with a relatively high concentration of oxygen at the

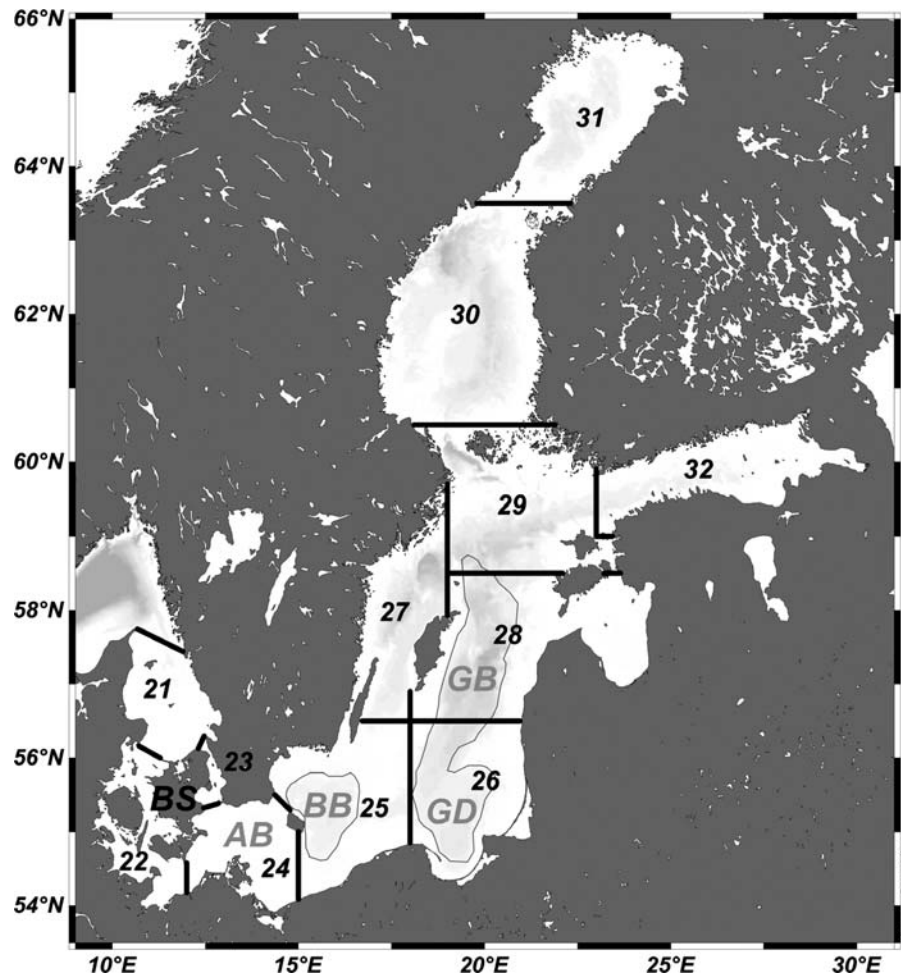


Figure 1. ICES Subdivisions (numbers) in the Baltic Sea and Baltic cod spawning areas: BS, Belt Sea; AB, Arkona Basin; BB, Bornholm Basin; GD, Gdańsk Deep; GB, Gotland Basin.

seabed. Hence, the spatial and temporal variability of oxygen concentration in bottom layers might affect the benthic food supply for demersal juvenile cod.

From laboratory experiments, it has been concluded that cod settling habitat requires a minimum oxygen saturation of 40% (Chabot and Dutil, 1999). Data storage tag (DST) recordings obtained from adult cod revealed that, for feeding purposes, cod can only stay in less-oxygenated water masses for some 10% of the time (Neuenfeldt *et al.*, 2009).

Adverse oxygen conditions result in behavioural and physiological stress. Several studies have revealed the multiple effects of adverse oxygen conditions on cod: (i) overall hypoxia tolerance (Plante *et al.*, 1998); (ii) physiological stress (Herbert and Steffensen, 2005; Johansen *et al.*, 2006); (iii) effects on metabolism (Schurmann and Steffensen, 1997; Claireaux *et al.*, 2000; Chabot and Claireaux, 2008; Petersen and Gamperl, 2010); (iv) reduced growth (Chabot and Dutil, 1999); and (v) reduced swimming performance (Herbert and Steffensen, 2005; Johansen *et al.*, 2006; Petersen and Gamperl, 2010).

The principal mechanisms influencing the replenishment of oxygen in the deep basins of the Baltic Sea are inflows of highly saline, oxygen-rich water from the North Sea. These water masses enter the central Baltic through the Belt Sea (Figure 1). Inflow

statistics based on long time-series of relevant parameters for the Baltic Sea (i.e. salinity, sea level, river run-off, precipitation, and air temperature), and for the North Atlantic and Europe (sea-level pressure), compiled by Schinke and Matthäus (1998) identified the main driving forces of major Baltic inflow. Recorded major Baltic inflow events were relatively frequent until the mid-1970s, but less frequent thereafter (Figure 2). As shown by MacKenzie *et al.* (2000) and Hinrichsen *et al.* (2002), most inflow events comprise relatively small volumes of highly saline water that does not substantially influence the vertical salinity distribution. However, especially since the start of the 1980s, the oxygen conditions in the deep basins have varied considerably, independent of major Baltic inflows. Several processes have been identified as influencing oxygen levels in the halocline and deep layers of the Baltic Sea: (i) lateral advection, which entails the inflow of water originating from the western Baltic and the Arkona Basin (Stigebrandt, 1987), (ii) river run-off, which has an effect on the volume and property exchange of the Baltic Sea (Lehmann and Hinrichsen, 2000) as well as on the effectiveness of penetration of inflows into the Baltic (Matthäus and Schinke, 1999), and (iii) variation in sea surface temperature in the western Baltic Sea, which results in differences in oxygen concentration at the sea surface and subsequent water mass transport towards the east.

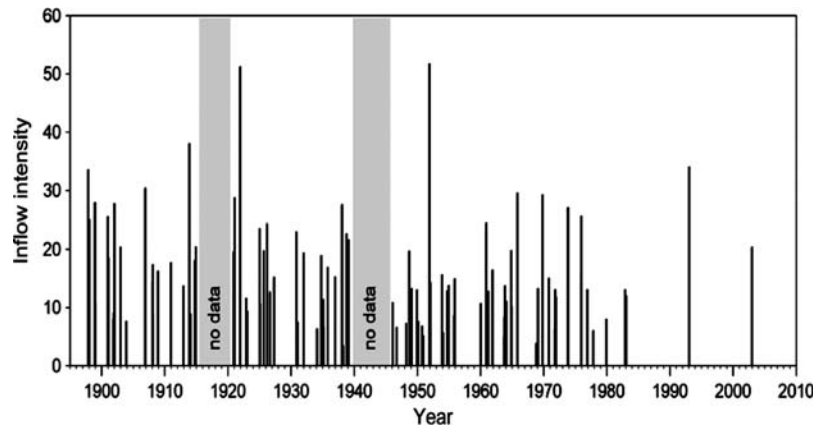


Figure 2. Time-series of major Baltic inflows and their intensity (data from Matthäus, 2006; Feistel *et al.*, 2008).

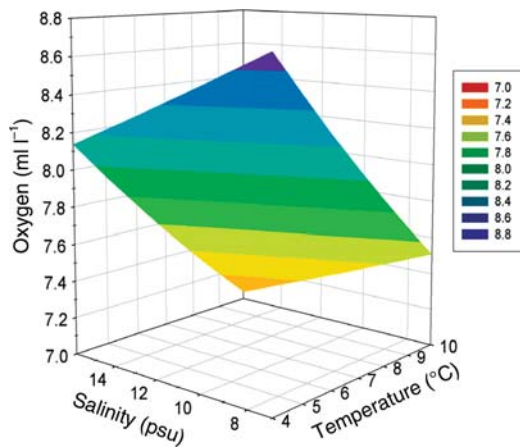


Figure 3. Temperature- and salinity-dependent oxygen solubility.

Dissolved oxygen concentration at the sea surface is a function of temperature and salinity, with saturation typically reaching 100% or more (Figure 3). However, such high levels of saturation below the halocline of the deep basins of the eastern Baltic can only be coupled to advective transport, because only advective transport can force vertical redistribution of temperature and oxygen within the deep basins of the Baltic Sea. Enhanced degradation of suspended organic matter by bacteria over recent decades has increased the oxygen consumption. Moreover, the effects of large-scale climate warming cause long-term variations in oxygen content and saturation as the observed increase in temperature leads to a general decrease in the oxygen solubility of water (Hinrichsen *et al.*, 2002).

The main objective of this study was to assess whether the observed long-term trends of declining oxygen concentration and saturation in the Baltic Sea have implications for process variations acting during the entire life cycle of Baltic cod. Further, we examined field data to evaluate the validity of the relationships derived experimentally.

Material and methods

Oxygen data for the Bornholm Basin, Baltic Sea (Figure 1), were compiled from the ICES oceanographic database of depth-specific CTD (conductivity, temperature, depth) and bottle measurements. From the database, all available oxygen values were selected

between 1951 and 2007. Data were subsequently aggregated to obtain monthly means per year and per 5-m depth stratum down to 100 m.

Spawning of eastern Baltic cod

Compared with other stocks in the North Atlantic, the eastern Baltic cod stock has an extended spawning period (ICES, 2005). During the first part of the time-series, the time of peak spawning identified based on estimated egg abundance in the Bornholm Basin was between the end of April and mid-June, but from the early 1990s on, the time of greatest egg production changed gradually to later in summer (Wieland *et al.*, 2000). Possible explanations for the shift in spawning time are large proportions of first-time spawners and decreasing water temperature (Wieland *et al.*, 2000), as well as limits on the essential fatty acids in Baltic cod diet attributable to climate-driven changes in the Baltic Sea foodweb (Tomkiewicz *et al.*, 2009). However, there have been indications of a slight reversal to earlier peak spawning during recent years (Schaber *et al.*, 2011), so we decided to analyse oxygen-related processes acting only during the egg and larval phases in May and August.

Eggs

To obtain an index of potential egg survival, Plikshs *et al.* (1993) defined a “reproduction volume” (RV), the volume of water fulfilling the minimum requirements for successful egg development (see also MacKenzie *et al.*, 2000). Salinities of ≥ 11 psu, a temperature of $>1.5^\circ\text{C}$, and an oxygen concentration of no less than 2 ml l^{-1} are considered necessary for successful Baltic cod fertilization and egg development (Westin and Nissling, 1991; Nissling *et al.*, 1994; Wieland *et al.*, 1994). However, because this index does not necessarily consider the actual oxygen conditions inside the RV, Rohlf (1999) developed a laboratory-based, oxygen-related egg survival (OES) index based on the fraction of the egg production expected to survive each year:

$$\text{OES} = (1 - e^{(0.71 \text{O}_2)})^{11.63}, \quad (1)$$

where O_2 (in ml l^{-1}) represents the ambient oxygen concentration.

Larvae

Newly hatched larvae and late-stage eggs of Baltic cod are buoyant at the same depths, so in accord with the vertical distribution of

eggs, yolk-sac larvae in the central Baltic are restricted to depths >50 m (Wieland, 1995). After depletion of yolk reserves, larvae have to migrate into the upper water layers to initiate feeding in a more-favourable habitat. The ability to perform those upward migrations depends mainly on the oxygen saturation level at the depths where the yolk-sac larvae reside. Based on laboratory experiments, Rohlf (1999) developed an index (larval vertical migration activity, LVMA) that represents the level of vertical migration activity at a given oxygen saturation:

$$\text{LVMA} = -28 + 2.3979 \text{O}_{\text{sat}} - 0.0141 \text{O}_{\text{sat}}^2, \quad (2)$$

where O_{sat} (%) represents the oxygen saturation. Both OES and LVMA (\pm s.d.) were calculated at three different density levels (isopycnals), representing the mean vertical location of peak egg abundance (1010.40, 1011.33, and 1012.26 kg m⁻³; Nissling et al., 1994).

Juveniles

As there is no specific information on oxygen tolerance or the preference of juvenile eastern Baltic cod at settlement, it was assumed that the same threshold of oxygen saturation for adult cod described by Chabot and Dutil (1999) can be applied. Typically, adult cod have a minimum requirement of ~40% oxygen saturation for survival, although short excursions into less-saturated water masses are possible (see below). To obtain a proxy for the settlement habitat size of juvenile cod in the Bornholm Basin (Figure 1), we selected all available depth values accounting for the minimum oxygen requirements of Baltic cod juveniles between 1951 and 2007 from the ICES oceanographic database. These depth values were converted into potential juvenile habitat size by calculating the size of the area in the Bornholm Basin that had near-seabed oxygen saturation >40%. Area sizes of suitable juvenile cod habitat were obtained from a hypsographic curve (Kossinna, 1921), which shows the bottom depth distribution of the Baltic Sea below the sea surface. The calculation of this hypsographic curve was based on data provided by Seifert and Kayser (1995).

Adults

According to the laboratory data of Claireaux et al. (1995) and Plante et al. (1998), cod can enter hypoxic conditions for a limited period. From DST data (Neuenfeldt et al., 2007) and *in situ* hydroacoustic measurements (Schaber et al., 2009), cod in the vertically stratified Baltic Sea actively and frequently descend into hypoxic waters, although the mean vertical distribution of pelagic cod decreases with progressing oxygen depletion in deeper layers (Schaber et al., 2009). The maximum residence time in hypoxic water increases with oxygen saturation to a constant level at oxygen conditions that are non-restrictive for cod activity (Neuenfeldt et al., 2009). Observations of sprat (*Sprattus sprattus*) concentrations at very low levels of oxygen levels, down to ca. 10% saturation (Stepputtis, 2006; Schaber et al., 2009), indicate that cod probably dive into hypoxic water to forage on sprat. To provide an estimate of the long-term trend in this vertical feeding migration of Baltic cod, we calculated the long-term evolution of the vertical extent of oxygen saturation levels between 15 and 40%.

Gastric evacuation rates (GERs) of adult Baltic cod, here considered to be a representative measure of the growth potential of the species, were calculated based on a model initially developed

by Temming and Andersen (1994). As hypoxia is frequent in the Baltic Sea, Teschner et al. (2010) modified that model to account for a slower rate of stomach evacuation under reduced oxygen saturation levels, as obtained from laboratory studies performed by Brach (1999):

$$\begin{aligned} \text{GER} \geq 65\% &= 1 - 0.0017(100 - \text{O}_{\text{sat}}) \\ \text{GER} < 65\% &= 1.4325 - 0.0141(100 - \text{O}_{\text{sat}}), \end{aligned} \quad (3)$$

where O_{sat} represents the oxygen saturation.

The GER was calculated at three different levels, chosen approximately according to the mean \pm s.d. ambient salinity levels derived for hydroacoustically identified individual cod in the Bornholm Basin in the years 2006–2009. Overall, the mean \pm s.d. ambient environmental salinity for a total of 13 745 cod was 14.5 ± 1.5 psu. For a detailed description of the methods employed to identify vertical distribution patterns of adult cod as well as for the allocation of ambient environmental parameters to each cod, the reader is referred to Schaber et al. (2009).

Fulton's K condition factor was used as the main indicator of the overall condition of adult cod. In all, annual mean values of K (\pm s.d.) were calculated for 5267 male and female cod (maturity stage 5, initiation of spawning; Tomkiewicz et al., 2002) sampled during trawl surveys in the Bornholm Basin in July and August from 1994 to 2009. The minimum catch number for K to be considered representative for a year was set to $n \geq 10$. Hence,

$$K = 100(WL^{-3}), \quad (4)$$

where W represents the weight (g) and L the total length (cm).

Results

Hydrography

Assessment of the long-term development of Baltic Sea oxygen concentration and of oxygen saturation reveals significant negative trends (Figure 4). The results of the oxygen-related processes affecting the different life stages of Baltic cod are summarized in Table 1. The minimum threshold value for OES ($\text{O}_2 \geq 2$ ml l⁻¹) was observed increasingly shallower over recent decades (ca. 2.5 m decade⁻¹; Table 1). The long-term trend in oxygen concentration ($\text{O}_2 > 2$ ml l⁻¹) indicates oxygen-related successful egg development survival in depths >90 m at the beginning of the time-series (1951), but only to ~80 m in 2007 (Table 1). The oxygen saturation level of 40% changed from 80 m deep at the start of the time-series to around ~65 m deep at the end of the 2000s (Figure 4).

Eggs

Oxygen data collected in May and August illustrate the effect oxygen consumption could have on the seasonal development of RV and OES. The data indicate that RV and consequently OES below the halocline decreased quickly between May and August (Table 1). On average, the vertical extension of RV is ~5 m larger in May than in August, but for both months, there was an overall decreasing trend in RV and OES, with a decadal loss of 2–2.5 m and 0.7–1.7%, respectively (Table 1, Figure 5a). Oxygen concentrations in the range where cod eggs are usually buoyant show a decreasing trend, indicating a relatively high OES (64.3%) in May 1951 for eggs with high buoyancy, but

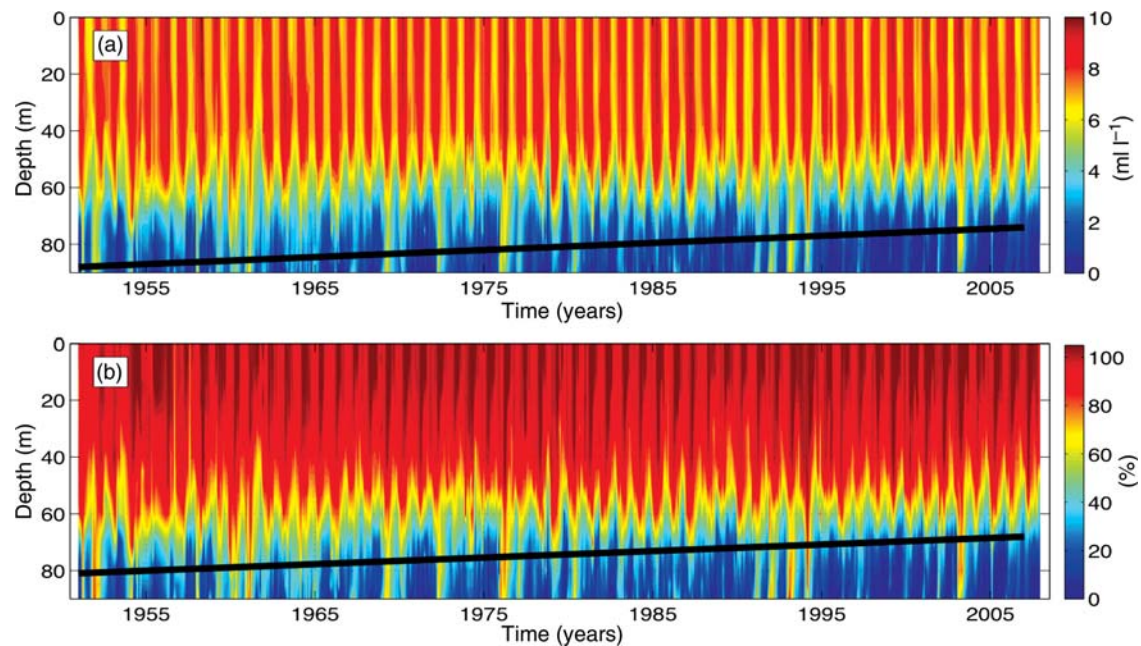


Figure 4. Long-term development of Baltic Sea oxygen (a) concentration and (b) saturation in the Bornholm Basin (from the ICES oceanographic database). Heavy black lines represent temporal development of isolines for 2 ml l^{-1} oxygen content and 40% oxygen saturation in (a) and (b), respectively, derived from linear regressions for the whole time-series (1951–2007).

close to zero (i.e. 1.7%) OES for eggs with low buoyancy in August 2007.

Yolk-sac and first-feeding larvae

The LVMA shows a similar long-term trend as RV and OES (Figure 5b). The ability to perform ontogenetic vertical migration during the early larval phase was only slightly influenced by oxygen concentration at high levels of egg buoyancy in May, but the effect of decreasing oxygen was amplified for less-buoyant eggs throughout the time-series (Table 1). Compared with the egg phase, the LVMA in August decreased at all buoyancy levels. At the end of the time-series, larvae that hatched from eggs of low buoyancy during the late spawning season showed a value of LVMA of 0% (Table 1), meaning that they could not complete the vertical migration to shallower layers of the water column needed to initiate first feeding. Hence, they probably failed to survive to more-advanced developmental stages.

Juveniles

The area providing favourable settling conditions for juvenile cod decreased by 900 km^2 per decade (Figure 5c). Compared with 1951, the area at the end of the time-series (2007) was reduced by >25%. Moreover, the areas hosting juveniles up to the age of 2 years were the same as those inhabited by adult cod, on their overwintering or feeding grounds (Aro, 1989; Hinrichsen *et al.*, 2009).

Adults

Predation of adult cod on clupeids might also be affected by the long-term development of oxygen conditions in the Bornholm Basin, because this parameter determines the lower distribution boundary and hence the extent of potential spatial overlap of predator (cod) and prey (clupeids). The observed depth range (15–40% oxygen saturation) that adult cod occupy for feeding purposes during their spawning season showed an increasing

vertical extension in May (8.7–12.5 m), but a negative trend (16.5–11.6 m) for August, when vertical swimming activity decreased. The latter could be due to greater frequencies of smaller so-called summer-inflows in recent years that led to an improvement in oxygen conditions in halocline waters during the late spawning season (Mohrholz *et al.*, 2006).

The GERs of adult cod decreased gradually with time (Figure 5d). The vertical range preferred by adult cod (Schaber *et al.*, 2009) had relatively large differences in evacuation rates. Cod residing deeper, i.e. in higher ambient salinity, showed a constant and relatively high level of gastric evacuation over the whole time-series, whereas the GER was more strongly affected by temporal changes in oxygen development deeper in the water column. This effect was more pronounced for all vertical levels later in the spawning season.

Overall results

As a major validation step for the model results, field data were obtained for various stages of Baltic cod during a long-term field programme in the Bornholm Basin and evaluated by relating observations to simulated oxygen-related trends in a qualitative manner.

Measurements of egg size performed for Baltic cod in the Bornholm Basin since the early 1970s revealed an increasing tendency for survival of larger, more-buoyant eggs than for smaller, less-buoyant eggs (Figure 6). To obtain an index of selective survival, differences in mean diameter of the eggs in developmental stages III and I were determined. A higher index, i.e. a higher diameter in late eggs, corresponds to relatively greater survival of larger eggs. In the Bornholm Basin, there was an indication of better survival of larger eggs from the late 1980s, decreasing after the inflow in 1993, but increasing again from 1993 to 2003. A strong year class in 1976 can be related to high overall oxygen concentration in the deep Bornholm Basin despite an apparently low

Table 1. Characteristic oxygen-related hydrography, regression parameters, and processes acting on eastern Baltic cod (*Gadus morhua*) during its life cycle.

Parameter	May				August				Reference
	Decadal change	Regression	Start 1951	End 2007	Decadal change	Regression	Start 1951	End 2007	
<i>Hydrography</i>									
Depth of O ₂ 2 ml l ⁻¹ (m)	-2.32	-0.3978	91.4	78.4	-2.69	-0.4542	87.8	72.7	Plikshs <i>et al.</i> (1993)
Depth of 40% O ₂ saturation (m)	-2.58	-0.3954	86.3	71.9	-1.87	-0.4208	77.6	67.2	Chabot and Dutil (1999)
<i>Cod life cycle</i>									
<i>Egg phase</i>									
Vertical extension of RV (m)	-2	-0.2688	30.5	19.3	-2.64	-0.3646	28.2	13.4	Plikshs <i>et al.</i> (1993)
OES in RV (%)	-0.7	-0.0676	50	45.8	-1.7	-0.2513	41.1	31.3	Rohlf (1999)
O ₂ (ml l ⁻¹) on 10.4 σ _t	-0.17	-0.1741	5.01	4.05	-0.28	-0.3517	4.21	2.64	-
O ₂ (ml l ⁻¹) on 11.3 σ _t	-0.23	-0.2085	4.09	2.82	-0.33	-0.3979	3.43	1.57	-
O ₂ (ml l ⁻¹) on 12.26 σ _t	-0.24	-0.2153	3.25	1.89	-0.31	-0.3804	2.59	0.87	-
OES (%) on 10.4 σ _t	-2.9	-0.1599	64.3	48.1	-5.6	-0.3768	52.3	20.8	-
OES (%) on 11.3 σ _t	-4.8	-0.256	50.7	23.8	-5.7	-0.4084	36.1	4.4	-
OES (%) on 12.26 σ _t	-3.8	-0.20663	34.6	13.4	-3.5	-0.3086	21.1	1.7	-
<i>Larval phase</i>									
LVMA (%) on 10.4 σ _t	-0.62	-0.0562	58	54.5	-3.18	-0.2566	54.4	36.6	Rohlf (1999)
LVMA (%) on 11.3 σ _t	-2.23	-0.1462	48.7	36.2	-5.0	-0.3562	44.7	15.0	Rohlf (1999)
LVMA (%) on 12.26 σ _t	-4.53	-0.2486	40.1	14.7	-6.0	-0.3913	32.4	0.0	Rohlf (1999)
<i>Juvenile phase</i>									
Settlement area in October (km ²)	-900	-0.5282	23 486	18 578	-	-	-	-	Hinrichsen <i>et al.</i> (2009)
<i>Adult phase</i>									
Distribution depth (m) at 15% saturation	-1.88	-0.3997	95	84.5	-2.76	-0.5002	94.1	78.7	Schaber <i>et al.</i> (2009) and Neuenfeldt <i>et al.</i> (2009)
Adult range (m)	0.7	0.1695	8.7	12.5	-0.89	-0.2095	16.5	11.6	
<i>Physiology</i>									
<i>GER</i>									
13.0 psu	-0.008	-0.063	0.79	0.75	-0.035	-0.2672	0.75	0.55	Brach (1999)
14.5 psu	-0.027	-0.1719	0.66	0.51	-0.052	-0.3658	0.59	0.30	Brach (1999)
16.0 psu	-0.042	-0.2279	0.54	0.31	-0.047	-0.341	0.42	0.16	Brach (1999)

For definition of RV, calculations of OES, index of LVMA, juvenile settlement area, and gut evacuation rate (GER), see text. The three density levels (σ_t) applied represent the mean vertical level of egg abundance ± s.d. (Nissling *et al.*, 1994). Salinity levels applied for the GER calculations were derived from mean ± s.d. vertical level of cod abundance (Schaber *et al.*, 2009).

egg buoyancy (Figure 4). This result is in accord with observations of cod egg development in incubation experiments. Wieland and Köster (1996) reported that the mean diameter of cod eggs had decreased from stage IA to stage IV by 6.9%.

Reduced oxygen-related consumption rates as well as Fulton's *K* condition factor of adult male and female cod at maturity stage 5 show similar trends (Figure 7). The time-series (1994–2009) showed that an increase in adult Baltic cod nutritional condition could be expected after an improvement in habitat suitability based on oxygen concentration, e.g. after the major Baltic inflows in 1993 and 2003. Generally, however, the overall condition factor decreased continuously through the time-series (female $r^2 = 0.67$, male $r^2 = 0.70$).

Discussion

The results of the analyses revealed that basin-wide, vertically resolved, monthly mean data can represent oxygen conditions for long periods, at least to following their influence on processes acting during the different life stages of Baltic cod. Correlations among long-term data suggest that oxygen-related processes in cod life stages appear to be coupled to the temporal oxygen

development in the inner deep basins of the Baltic Sea. Understanding of this linkage between physical processes and biological parameters of marine ecosystems has appeared as a consequence of the emergence of various methodologies, including laboratory experiments, field measurements, modelling, and data synthesis. In our case, oxygen as a measured physical ocean parameter was identified to permit short- to medium-term ecologically based process predictions. These predictions were possible because the process parameters were consistent over a long period.

Eggs of eastern Baltic cod need a minimum salinity of 11 psu for buoyancy (Wieland *et al.*, 1994), and that level usually prevails in and below the halocline of the deep Baltic Sea basins. Because of the observed decrease in oxygen concentration at high density (salinity) levels in the past, and an anticipated continuing trend in future (BACC Author Team, 2008), cod eggs were and potentially will continue to be frequently exposed to lethal concentrations of oxygen in the layer where they are neutrally buoyant.

The buoyancy of cod eggs varies with egg size and lipid content, both of which are related to the size and condition of females as well as to batch size (Kjesbu *et al.*, 1992; Nissling and Vallin, 1996), because eggs from large batches are generally smaller and

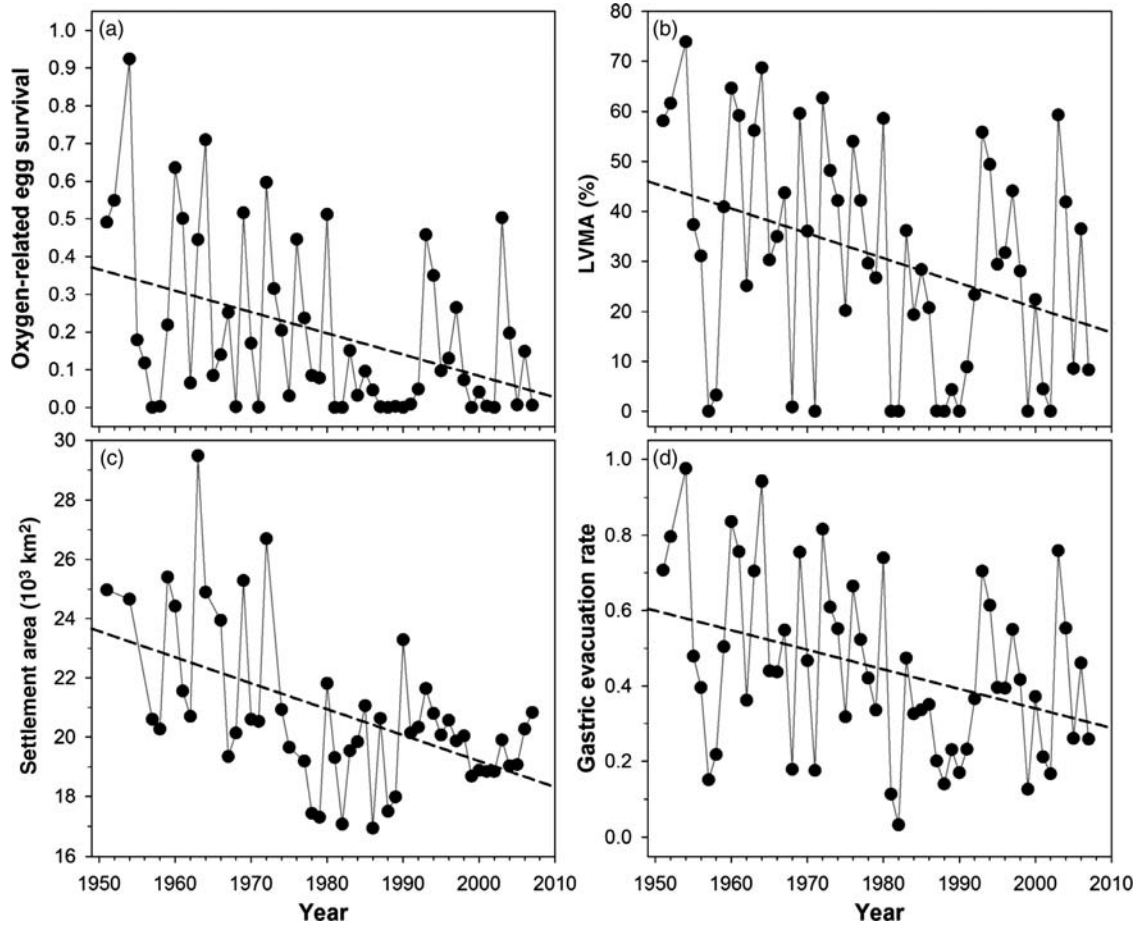


Figure 5. Long-term development of (a) oxygen-related Baltic cod egg survival (OES), (b) oxygen-related vertical swimming activity of larval cod (LVMA), (c) size of juvenile cod settlement areas, and (d) oxygen-related GERs of adult Baltic cod.

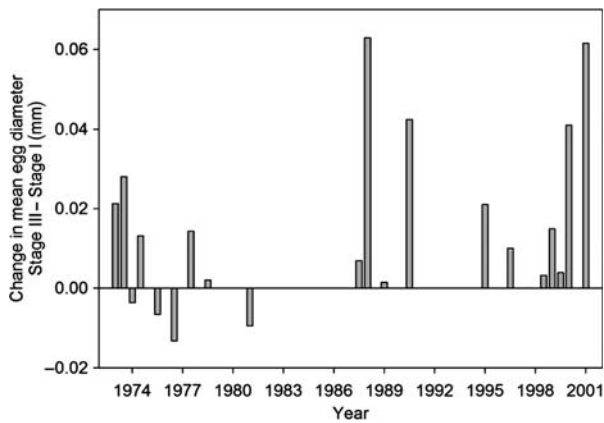


Figure 6. Time-series of the difference between stage I and stage III Baltic cod mean egg diameters in the Bornholm Basin.

have less lipid content than those from smaller batches. Larger females produce eggs with higher lipid content that are generally more buoyant than those produced by smaller cod (Nissling and Vallin, 1996), so it is highly likely that larger females produce eggs and larvae with a higher probability of survival in the marginal oxygen conditions in the Baltic Sea. Large females might

have a considerable impact on the production of eggs developing at lower density (salinity) and hence in more-clement oxygen concentrations. This also suggests an increase in the relative impact of female size with deteriorating spawning conditions, i.e. when the oxygen content in the RV decreases.

The OES relationship applied to oxygen concentration at various buoyancy levels revealed a notable decrease in OES during recent decades. Although environmentally driven rate processes cannot easily and directly be transferred from the laboratory to wild fish, the application of RV and OES to the model results on female size-specific egg production, egg size, and egg buoyancy would most likely result in declining egg survival related to female size. Therefore, the number of cod that could contribute successfully to egg development and survival has probably declined as a consequence of the general increase in oxygen depletion at the egg buoyancy levels needed by Baltic cod. This trend appears to be diametrically opposed to the situation in which larger, older cod are more influenced by fishing pressure. Currently, admissible mesh sizes for the Baltic cod fishery will only protect smaller females from capture, but these smaller females will likely not contribute significantly to egg production because of the ambient low oxygen concentrations at corresponding size-specific levels of egg buoyancy. Hence, there is a clear need to account for changing climate conditions in stock assessments and management advice. As an effective management tool,

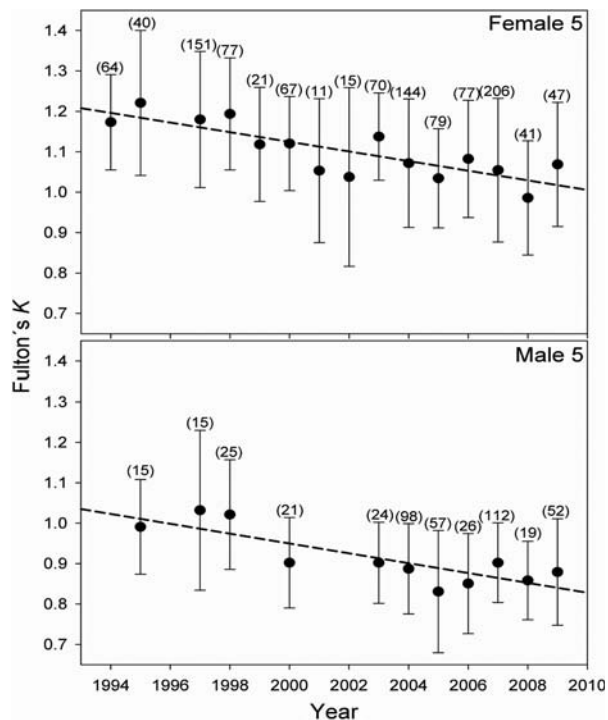


Figure 7. Mean annual condition factor K (Fulton) of adult male and female cod (ungutted weight, maturity stage V; initiation of spawning) from annual trawl samples collected between 1994 and 2009. Only annual catches of $n \geq 10$ fish of the appropriate sex/maturity stage were included.

regulations on mesh sizes in trawl fisheries or a complete change from trawl to trap and/or gillnet fisheries could lead to more size-selective fishing, but the performance of these regulations still needs to be evaluated relative to the changing oxygen environment of Baltic cod.

Density-dependent processes operating after the onset of larval and juvenile settlement may be of substantially greater importance if the spatial extent of the habitat for Baltic cod juveniles decreases as a result of deteriorating oxygen concentrations. Such trends will probably continue, because general improvements in the environmental conditions necessary for successful cod spawning (increases in salinity and oxygen content) and a growing juvenile habitat area are not to be expected in the 21st century (BACC Author Team, 2008). The output from climate-change scenarios predicts an overall increase in precipitation in the Baltic Sea catchment which could result in reduced inflow intensity of saline, well-oxygenated water masses into the Sea (Lehmann and Hinrichsen, 2000).

During recent decades, hydrographic conditions in the central Baltic have been influenced by large-scale climate conditions that have resulted in above-average temperature throughout the water column, as well as declining salinity and oxygen concentrations below the halocline. These changes have negatively impacted the reproductive success of cod and, combined with high fishing pressure, resulted in a decline in the cod stock to the lowest level on record by the early 1990s (Köster et al., 2005).

An increase in precipitation in the Baltic Sea catchment along with a resulting increase in river run-off had, as a result of

reduced frequency or less intense inflow (Lehmann and Hinrichsen, 2000), an impact on the volume and property exchange of the Baltic Sea with the North Sea, and hence on the three-dimensional salinity and oxygen distribution in the Baltic. This trend accelerated the detrimental effects of decreasing oxygen concentration in the deep basins for the entire life cycle of cod, and this situation can be expected to continue in future. However, with a predicted decrease in salinity during the 21st century (BACC Author Team, 2008), the Baltic Sea is likely to confront a reversed situation compared with past decades. As long as salinity in the deep basins of the Baltic Sea remains high, the depth range below the halocline suffers from frequent anoxia. However, when salinity below the halocline is low and when the vertical position of the halocline is deep, oxygen concentrations in deep layers are more favourable and allow recolonization by macrofauna (Gerlach, 1994). Unfortunately, this improvement of habitat for many macrofauna species has a detrimental effect on the survival of cod eggs. During periods of low salinity below the halocline, only eggs spawned by large, older females have a higher probability of survival, because only those eggs will be exposed to the optimal oxygen concentrations for their development.

Besides the negative impact of oxygen content on GER during recent decades, a decreasing oxygen content might also limit anabolism and hence the growth of Baltic cod, as indicated by the concomitant decreasing overall condition of adult cod. Gills, as the respiratory area of fish, cannot grow fast enough to compensate for increasing body weight and hence oxygen demand, so limiting overall growth performance (Pauly, 1981). If the past trend of decreasing oxygen concentration and saturation in the deep basins of the Baltic Sea continues, it is highly likely that the effective population size of Baltic cod will drop in terms of spawning-stock biomass (SSB). This almost certainly would result in a negative impact on fisheries that generally select for the most valuable traits, i.e. in selecting larger fish.

An increase in cod SSB has been observed recently. This was predicted in short-term forecasts (ICES, 2010) and was mostly related to a reduction in fishing mortality combined with improved abiotic conditions after inflow events from the North Sea (Lindegren et al., 2010). Recently, there have been indications of a slight reversal of the spawning season to earlier in the year (Schaber et al., 2011), so considering that the results here have revealed that conditions for all the processes analysed were generally better in May than in August, this may be an additional explanation for the improved recruitment and SSB recently (ICES, 2010). However, irrespective of any reduction in fishing pressure and potential changes in the spawning season, there remains a risk of long-term depression of the eastern Baltic cod stock with progressive climate change through both direct and indirect effects of changes in temperature, salinity, and oxygen concentration on early life stages. Additionally, progressive oxygen depletion will severely affect all life stages of Baltic cod.

Generally, the trends for the different oxygen-related processes acting on various different life stages are negative. However, it is impossible to rank their relative contributions to recruitment success. Currently, stock–recruitment relationships for Baltic cod do not consider life stages later than the egg, so future investigations need also evaluate the relative importance of later stages for recruitment success by combining the relationships used in this study with those already in existence. The metrics can be used as predictors in statistical stock–recruitment (Köster et al., 2001) or general additive models (Cardinale et al., 2009). Good

recruitment of cod in the late 1970s is partly considered to have been attributable to the massive expansion of suitable spawning and feeding habitat in areas next to the Bornholm Basin (Bagge *et al.*, 1994), so it would be revealing to establish and analyse the oxygen-related relationships also for those areas in future.

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