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Re-thinking the “ecological envelope” of Eastern Baltic cod (*Gadus morhua*): conditions for productivity, reproduction, and feeding over time

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Hypoxia is presently seen as the principal driver behind the decline of the former dominating Eastern Baltic cod stock (EBC; *Gadus morhua*). It has been proposed that both worsening conditions for reproduction and lower individual growth, condition, and survival are linked to hypoxia. Here, we elucidate the ecological envelope of EBC in terms of salinity stratification, oxygen content, and benthic animal biomasses, and how it has affected EBC productivity over time. The spawning conditions started deteriorating in the Gotland Deep in the 1950s due to oxygen depletion. In contrast, in the Bornholm Basin, hydrographic conditions have remained unchanged over the last 60 years. Indeed, the current extent of both well-oxygenated areas and the frequency of hypoxia events do not differ substantially from periods with high EBC productivity in the 1970s–1980s. Furthermore, oxygenated and therefore potentially suitable feeding areas are abundant in all parts of the Baltic Sea, and our novel analysis provides no evidence of a reduction in benthic food sources for EBC over the last 30 years. We find that while reproduction failure is intricately linked to hydrographic dynamics, a relationship between the spread of hypoxia and the decline in EBC productivity during the last decades cannot be substantiated.

Keywords: benthic biomass, Eastern Baltic cod, hypoxia, productivity, reproduction volume, spatial scales.

Introduction

Relating the effects of fishing on other variables affecting fish stock productivity (net population increase) is vital for fishery biology (Smith, 2007). Recent advances have put special attention on collapsed or on the verge of collapsing fish stocks (e.g. Murawski, 2010; Vert-pre *et al.*, 2013) since they can lead to regime shifts that may have long-lasting effects on ecosystem structure (Lindgren *et al.*, 2010; Möllmann *et al.*, 2015; Tomczak *et al.*, 2021). Regime shifts may impede the recovery of fish stock productivity despite drastic reductions in fishing effort (Swain and Chouinard, 2008), or even decoupling recovery from increased abundance (Vert-pre *et al.*, 2013).

Such changes have been observed for the Eastern Baltic cod (*Gadus morhua*; EBC), which, until the 2000s, was a major commercial fish stock and a vital part of the Baltic fish fauna (Hammer *et al.*, 2008; ICES, 2021; Figures 1 and 2). Here, we argue that the present low productivity of EBC, and its demise as a fishing object altogether in recent years, is an unprecedented phenomenon. However, the reasons for this recent deterioration of the stock status have remained unsettled (Eero *et al.*, 2015; ICES, 2019; Brander, 2020; Neuenfeldt *et al.*, 2020; Svedäng *et al.*, 2020; Casini *et al.*, 2021). Thus, it remains to clarify the different phases of its decline and the likelihood for various suggested drivers behind the development.

The stock was fished in the entire Baltic Proper (BP) and in the Bothnian Sea right up to latitude 63° N (Hessle, 1947). The productivity of EBC may have initially benefitted from

eutrophication of the Baltic Sea during the 20th century (Eero *et al.*, 2011), which increased the abundance of the prime prey fishes, herring (*Clupea harengus*) and, in particular, sprat (*Sprattus sprattus*, Eero, 2012), as well as the biomass of benthic fauna above the halocline (Ehrsten *et al.*, 2020).

Spawning stock biomass (SSB), landings and total stock biomass for fish above 35 cm in length ($TSB_{\geq 35}$) culminated in the middle of the 1980s, and the subsequent sharp decrease indicates a significant weakening of EBC thereafter (Hammer *et al.*, 2008; ICES, 2021; Figure 2a). The reductions in landings were more pronounced in the central and south-eastern Baltic Sea (ICES subdivision (SD) 26–29) than in the Bornholm Basin (SD 25; Figure 1; Eero *et al.*, 2007). The stock depletion coincided with intense fishing and reproduction failures in the Gotland Deep and Gdansk Deep, i.e. at two out of three major EBC spawning localities (Bagge *et al.*, 1994), which constituted the formerly dominant spawning units/subpopulations of EBC (Eero *et al.*, 2007). Since the late 1980s, reproduction occurs mainly in the Bornholm Basin (Köster *et al.*, 2005; 2017). This decline in reproduction has been linked to hydrographic changes, creating unsuitable egg development conditions (MacKenzie *et al.*, 2000).

In the Gdansk Deep, conditions for reproduction reappeared at the beginning of the 1990s, however, the subpopulation seems to have vanished at the time (Köster *et al.*, 2009). The loss of spawning sites reduced the distribution of recruits (Hinrichsen *et al.*, 2009) thereby contracted EBC and the

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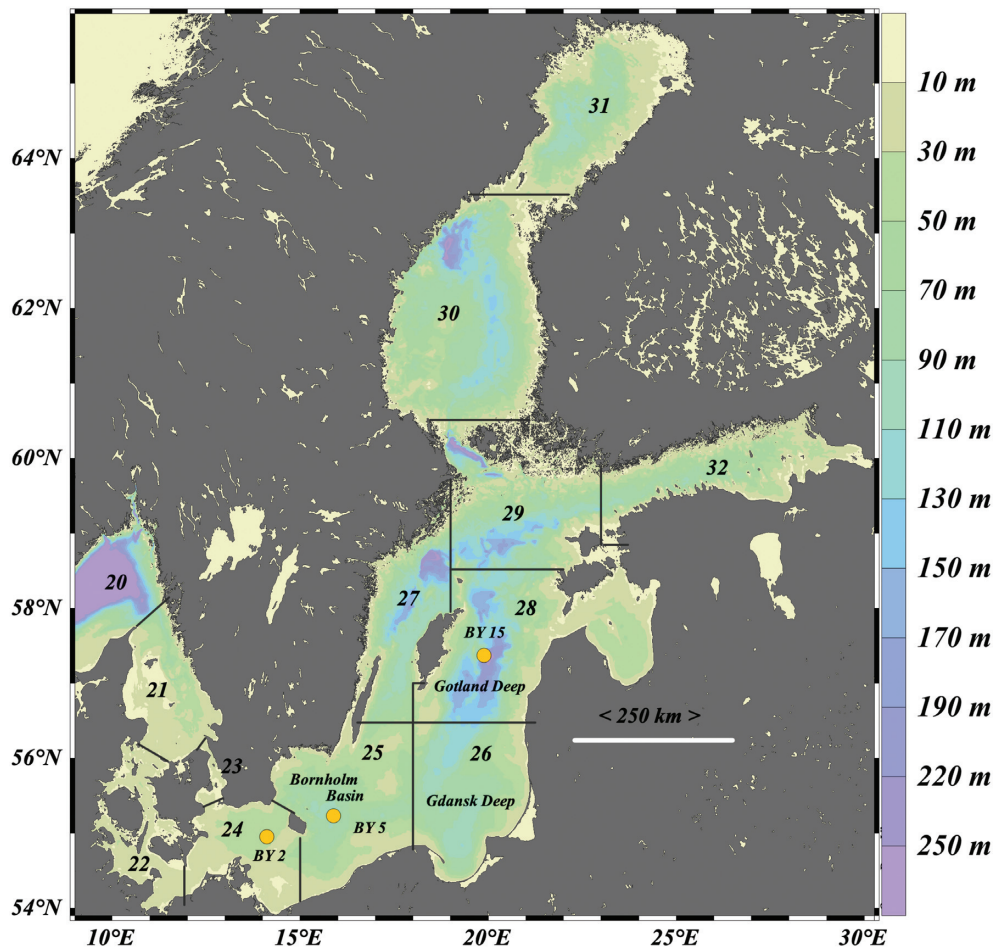


Figure 1. The Baltic Sea with the borders and numbers of the ICES subdivisions (SD) (www.ices.dk). EBC reproduction takes place in the Arkona basin west of Bornholm Island, in the Bornholm Basin, the Gdansk Deep, and Gotland Deep. The location of the hydrographic stations BY2, BY5, and BY15 are shown.

fishery to the southern part of the Baltic Sea, i.e. SD 24–26 (Eero *et al.*, 2012; ICES, 2019; McQueen *et al.*, 2020). This contraction of the population distribution has thoroughly changed the environmental constraints at play that may have restricted production levels since the 1990s.

Furthermore, since the late 2000s, in addition to the reproductive failure, the productivity of EBC is constrained either by factors related to individual growth (Eero *et al.*, 2012; Svedäng and Hornborg, 2014; McQueen *et al.*, 2020; Mion *et al.*, 2020) or increases in natural mortality (Eero *et al.*, 2015; Neuenfeldt *et al.*, 2020). While improved recruitment in the late 2000s in the Bornholm Basin and lower fishing pressure resulted in increased EBC abundance (e.g. ICES, 2011; Köster *et al.*, 2017), biomasses and catches continued to decline, contrary to what was anticipated (ICES, 2013). This enfeebled status of EBC manifests as increasingly truncated size distributions (Eero *et al.*, 2012; Svedäng and Hornborg, 2014; 2017; ICES, 2021), declining body condition (Casini *et al.*, 2016; 2021; ICES, 2021) as well as a weakening health status (SVA, 2016). It is noteworthy that, according to the latest analytical assessment (ICES, 2021), SSB has remained at similar levels since the 1990s (Figure 2a), while EBC landings have continuously declined even though catch quotas (TAC) in most years have not been limiting (Figure 2b). The reason for this discrepancy is the truncation of the size distribution (e.g. Svedäng and Hornborg, 2017), which means that a large part of the EBC

biomass has been too small to be targeted (below 35 cm in length). This is corroborated by the fact that $TSB_{\geq 35}$ is lower than SSB since about 2000 (ICES, 2021). As a result, the productivity, measured as landings per recruit (LPR), has declined (Figure 2c).

Feeding conditions are essential then analysing growth constraints. Benthic organisms, especially polychaetes and mysids, are important food items for all size groups of cod (e.g. Bagge *et al.*, 1994 and the references therein). Kulatska *et al.* (2019) observed that sprat, herring, the polychaete *Saduria enthomon* and mysids (mainly *Mysis mixta*) comprised most (about 80%) of EBC feed. However, EBC feeding opportunities on herring and sprat have been fundamentally altered over the past 50 years. Baltic herring stocks show long-term declines by 80%, central Baltic herring since the mid-1970s and western Baltic herring since the beginning of 1990s (ICES, 2021), while Baltic sprat demonstrates a tremendous increase in biomass since the 1950s–1960s in the southern parts of the Baltic Sea (Eero, 2012).

The hydrographic dynamics of the Baltic Sea and its constraints on cod reproduction

The hydrographic constraints on EBC reproduction over time, in different basins, is a matter of bathymetry, frequency and strength of inflows, climate and degree of eutrophication (e.g.

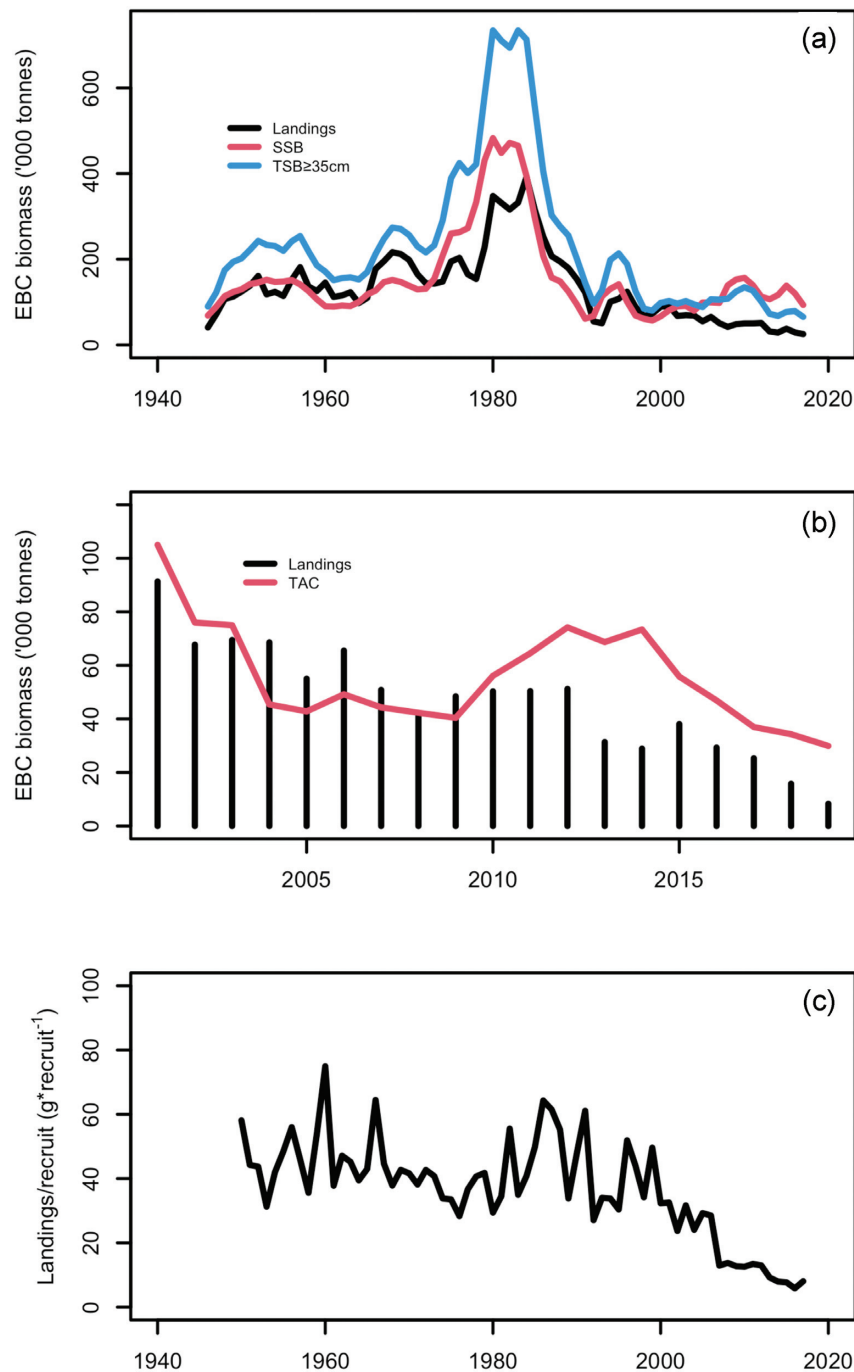


Figure 2. Productivity metrics of the EBC (ICES, 2021): (a) the reported landings of Baltic cod in ICES *SD* 24–32 (black line), 1946–2020 and estimated SSB (red line), 1946–2020 and estimated total biomass for fish >35 cm in length ($TSB_{\geq 35}$) (blue line) 1946–2020; (b) reported landings and total allowable catch (TAC) 2001–2019; (c) landings divided by estimated number of age zero recruits forwarded four years ($g * \text{recruit}^{-1}$).

MacKenzie *et al.*, 2000). According to experimental studies, the hydrographic boundaries for successful reproduction are defined by salinity ≥ 11 and oxygen content > 2 ml O_2/l (Westin and Nissling, 1991; Vallin *et al.*, 1999 and the references therein). Plikshs *et al.* (1993) described such water masses, which fulfilled the requirements necessary for successful fertilization and egg development of EBC, as the “reproduction volume” (RV). However, EBC cod eggs are rarely found at salinity > 14.5 (Nissling *et al.*, 1994), so including volumes with salinity > 14.5 introduces variability of no significance for reproduction.

To facilitate the understanding of RV dynamics, we, therefore, also present variations of the total volume of water between isohalines of 11 and 14.5 PSU ($WV_{11-14.5}$), i.e. irrespectively of oxygen content. We used estimates of $WV_{11-14.5}$ as an indicator of the stability of the vertical stratification of the water column and whether the level of salinity fulfilled the condition for successful reproduction or not.

The dynamics controlling the temporal variation of the RV differ between the basins. The Arkona Basin (*SD* 24) is the direct recipient of saline water from the Baltic entrance area (Figure 1). Stratification is almost permanently present since

minor inflows contribute to the pool of saline water buffered in the basin (e.g. Liljebldh and Stigebrandt, 1996; Gustafsson, 2001). The residence time of the deepwater of the Arkona basin is only a few months (Reed *et al.*, 2011). Recurrent inflows through the straits create fluctuating conditions, while the flow of deepwater further to the Bornholm Basin shows long-term variation. Gustafsson (2001) estimated that the average flow of saline water from the Arkona to Bornholm Basins was about 40% smaller in the 1980s than in the 1970s.

Contrary to the Arkona Basin, in the Bornholm Basin, as being significantly deeper than the sill of the outlet to Stolpe Channel (or Słupsk Furrow) (of about 59 m, Stigebrandt, 2017), the residence time of the deepest basin water is substantially longer (Figure S1). Only well below sill depth, the inter-annual variability is more prominent than seasonal or shorter variability (Stigebrandt, 2017). Deepwater salinities are consistently well above 11, and the deepest water is replenished as the salinity in the deep sinks below about 15 (Schmidt *et al.*, 2021). Long-term variations in oxygen depletion follow the general eutrophication trend, with gradually increasing hypoxia from the 1950s to 1980s and thereafter varying at a similar level (Carstensen *et al.*, 2014). The near-bottom water in the Stolpe Channel has an average salinity of about 13 and most often oxygen above 2 ml/l (Schmidt *et al.*, 2021).

The Gdansk Basin is connected to the Eastern Gotland Basin with a sill depth of about 100 m and the maximum depth is about 115 m (Leppäranta and Myrberg, 2009). Due to the sill depth, saline and oxygenated water masses are temporarily accumulated in the Gdansk Basin after inflows (Figure S2). Eventually, the water above 100 m will either be mixed into surface waters or be advected further to the north, and the halocline properties will be equilibrated with the much larger Eastern Gotland Basin. The more saline deepwater will remain in the Gdansk Basin until either mixed or replaced. This deepwater has higher salinity (approximately 12, Schmidt *et al.*, 2021) than at corresponding depths in the Eastern Gotland Basin and has, in general, been hypoxic since the 1950s (Schmidt *et al.*, 2021).

In the Eastern Gotland Basin, the deepwater can be subdivided into two parts (Figure S3), where the upper part of the halocline is relatively well ventilated by the continuous supply of intermediate salinity water (e.g. Stigebrandt, 1987; Holtermann *et al.*, 2020), while the deeper parts are subject to extended stagnation (e.g. Fonselius, 1969; Meier, 2005; Gustafsson and Stigebrandt, 2007). The extension of the well-ventilated layer seems to be limited by the salinity of the inflowing water in-between the very large Major Baltic Inflows (MBIs, Matthäus *et al.*, 2008), so in periods of weak stratification (lower deepwater salinities), ventilation extends deeper and hence reducing the extent of hypoxic area (Gerlach, 1994; Conley *et al.*, 2009). Since 1950, the hypoxic limit coincides reasonably well with the depth of salinity of about ten, although the hypoxic limit has somewhat shifted towards even lower salinities (Conley *et al.*, 2009) as the oxygen consumption has continued to increase (e.g. Carstensen *et al.*, 2014).

Are individual constraints on Baltic cod productivity linked to hypoxia?

It is suggested that increased hypoxia in the Baltic Sea may reduce the feeding opportunities for the EBC, thereby

constraining EBC productivity (Eero *et al.*, 2015). Hypoxia at the seafloor may disturb or obliterate the benthic animal production as well as trivialise the benthic community to a composition of small, short-lived species (Karlsson *et al.*, 2002; Norkko *et al.*, 2015; Gogina *et al.*, 2016). The lower abundance of larger benthic animals may lead to fewer feeding opportunities for medium-sized cod and impede shifts in feeding on benthic animals to forage fish (Karlsson *et al.*, 2019; Kulatska *et al.*, 2019; Niiranen *et al.*, 2019). Such structural changes could augment competition with other fishes, such as flounder (*Platyichthus flexus*; Orio *et al.*, 2019). However, Svedäng *et al.* (2020) recently found that the protein content in EBC otoliths [earstones] has increased since around 2005, implying recent increases in feeding rate, refuting the hypothesis that the decline in EBC productivity is due to lower feeding rates. It has also been suggested that hypoxia may act as a direct constraint on productivity by interacting with cod metabolism (Chabot and Dutil, 1999; Vaquer-Sunyer and Duarte, 2008), and thereby affecting health and growth (e.g. Limburg and Casini, 2018; 2019; Brander, 2020; Casini *et al.*, 2021).

Furthermore, inference on hypoxia effects on cod growth and survival have focused on the recent transition from the stagnation period around 1990 to the subsequent period with more stratified conditions. We suggest that understanding the coupling between reproduction, growth, and survival in EBC and hydrographic dynamics could be improved by exploring a longer-term development featuring more variation in Baltic Sea conditions. Since the distribution of EBC has contracted towards *SD 25* and that the spatial differences in the extent of hypoxia between different parts of the Baltic Sea have been overlooked in several previous studies, we pay special attention to the hydrographic dynamics and development in this area.

In addition, long-term studies regarding the Baltic benthic community on a sub-basin level above the halocline are lacking. While eutrophication is detrimental to benthic animal production due to increases in the expansion of hypoxic waters in deeper areas below the halocline (e.g. Villnäs and Norkko, 2011), higher primary production will also sustain higher biomasses of benthic animals in well-oxygenated areas above the halocline (Ehrnsten *et al.*, 2020). Therefore, analyses of changes in the benthic community must correspond to spatiotemporal scales relevant to EBC feeding.

Study objectives

Here, we investigate the contribution of variation in salinity and oxygen concentrations, driven by cyclic changes in the inflows of saline, Atlantic water masses, as well as by eutrophication of the Baltic Sea, to the “ecological envelope” of EBC over the last century. We also describe the successive variation in biomass of benthic fauna during the previous three decades to evaluate the indirect effect of oxygen conditions through effects on important prey. We thereby strive to clarify the following issues:

- a) the centurial development of RVs in relation to existing hydrographic conditions.
- b) the decline in growth/survivorship since the mid-1990s in relation to the centurial development of hypoxia and trends in biomass of benthic prey species since the year 1990.

Material and methods

Hydrographic data

We retrieved salinity and oxygen data for over a century of observations from the Baltic Environmental Database BED (<http://nest.su.se/bed>) and distributed databases hosted by Finland, Germany, Denmark, and Sweden (<http://nest.su.se/dataPorta1>). Naturally, data availability and coverage are not statistically homogeneous in time and space. The number of oceanographic stations performed during a year has increased over time from a few dozens in the early 1900s to several thousand nowadays (http://nest.su.se/bed/BED_samplings.shtml). Their spatial distribution has varied from year to year due to changing national and international monitoring guidelines and evolving goals and locations of irregular oceanographic surveys supplementing the standard monitoring.

Hydrographic data analysis

The much-used RV of EBC is defined as the water volume with salinity ≥ 11 and oxygen content > 2 ml O₂/l, based on the assumption that these conditions are necessary for successful fertilization and egg development in EBC (e.g. Vallin *et al.*, 1999 and references therein). In addition to this traditional way of estimating RV (Table S1), we also calculated a RV accounting for that EBC eggs, on average, are floating on water with higher salinity than 14.5 (Table S1; Nissling *et al.*, 1994). The advantage of taking the upper salinity limit into account is that it filters out water masses that are not containing EBC eggs from the time series. In practice, this excludes the occasional inflows of very salty oxygen-rich waters that occur periodically in the Arkona and Bornholm Basins but do not contribute to the RV because of the high salinity. For comparison reasons, we also evaluated our RVs estimates in different basins (SD 25, 26, and 28) in relation to the recent estimations made at WKCONGA (ICES, 2018).

We reconstructed annually averaged three-dimensional gridded fields of salinity and oxygen concentration from the observations using the interpolation algorithm developed for the Data Assimilations System (DAS, Sokolov *et al.*, 1997) and described in detail in many implementations (e.g. Conley *et al.*, 2002; Savchuk, 2018). The regular fields were used to delineate and compute areas and volumes confined by prescribed isohaline and iso-oxygen surfaces.

Furthermore, we used the three-dimensional oxygen fields to estimate the basin-wide extent of well-oxygenated seafloor, where a healthy benthic community is anticipated to occur, as well as hypoxic areas, where the benthic community is likely to be negatively affected (Table S2). We account for practice for routinely measuring the oxygen content above the bottom boundary layer, while the oxygen content may decline sharply within this layer close to the seafloor by defining well-oxygenated seafloor as no less than 5 ml O₂/l for SD 24–25. For SD 26 and SD 28–29, the limit for well-oxygenated seafloor is set at no less than 4 ml O₂/l since the near-bottom salinity gradient is expected to be weaker in the north according to the general stratification gradient. It is expected that lower oxygen levels will cause hypoxic/anoxic conditions at the seafloor. On the other hand, hypoxia on the seafloor was defined, as routinely made, from observations of water just above the seafloor containing less than 2 ml O₂/l (Table S2).

To study the frequency of hypoxia events at different depth strata, we extracted observations between 1957 and 2017, where oxygen content at 10 m depth intervals has been

measured nearly every month at three fixed stations (Figure 1) in the SD 24 (BY2), SD 25 (BY5), and SD 28 (BY15). We calculated the occurrence of events not satisfying the condition for well-oxygenated as the annual proportion of monthly oxygen concentration measurements below the basin-wise thresholds as given above, in essence, no less than 5 ml O₂/l for SD 24–25, and 4 ml O₂/l for SD 28.

Indices on stock productivity

Landings-per-recruit (LPR_{*i*}) in year *I* was estimated by dividing EBC landings in tonnes by the estimated number of age zero recruits (*REC*) taken from ICES latest assessment (ICES, 2021) in year *i*-4, i.e. assuming that recruitment preceding the recorded year of landings was by four years for the period 1946–2020 (Figure 2c):

$$LPR_i = \frac{\text{Landings}}{REC_{i-4}}$$

As proxy on stock productivity, biomass of commercial sized cod (≥ 35 cm in length), *TSB* _{≥ 35} in the beginning of the year was used for the period 1946–2020 (ICES, 2021).

Compilation of benthic data

To describe spatial and temporal variation in benthos as a food source for cod, we compiled data on benthic macrofaunal biomass from SD 24–26 to SD 28 (Figure 1, Table S3) from national and international databases, i.e. the HERTTA database at the Finnish Environment Institute (<https://www.syke.fi/avoointieto>), the SHARK database at the Swedish Meteorological and Hydrological Institute (<https://www.smhi.se/data/oceanografi/datavardskap-oceanografi-och-marinbiologi/sharkweb>), and the ICES data portal (www.ices.dk). We retrieved data from sites deeper than 10 m (Figure S4) between 1990 and 2018 to match the period of the assumed decline in EBC growth/survival rates. In total, data on benthic biomass were obtained from 364 stations (Figure S4), encompassing over 1900 sampling occasions from all included subdivisions (SD 24–28; Table S4). The majority of the samples (95.5%) had been collected during spring (May and June), while just a few in summer (July; 1%) and autumn (3.5%). We, therefore, have not explored the data for any seasonal variation. All samples had been collected using comparable methods and performed with a van Veen grab (one replicate, 0.1 m²) and sieved on a 1.0 mm mesh before preservation. Benthic biomass is represented as blotted wet weight (g m⁻²).

Statistical analysis

Changes in hydrography

Since auto-correlations were assumed to be present in all the hydrographic time series, we applied a modified version of the non-parametric Mann–Kendall test for evaluating unidirectional trends (available in the r-script `bbsmk()`, “modifiedmk” package version 1.6; Patakamuri and O’Brian, 2021). Block length was predetermined to three years, as longer periods were considered of less population dynamic/hydrographic importance. We followed the recommendation of 2000 bootstrap replicates (Patakamuri and O’Brian, 2021, and the references therein).

Since the time series on the productivity proxy LPR indicated a breakpoint about 1995 (Figure 2c), a segmented

regression analysis was applied by using r-script segmented(), “segmented” package version 1.3–4 (Muggeo, 2021). Correlations between studied time series were tested by using the non-parametric Spearman rho statistic, available in the r-script package “Hmisc version 4.6” (Harrell and Dupont, 2021).

Analysis of benthic communities

The benthic biomass composition describes the biomass contribution of each species to the total biomass of the community. We used multivariate methods to explore the differences in benthic community biomass composition between two depth strata (shallow and deep) and two periods for each subdivision. The subdivisions were separated in the analyses as they are known to differ in benthic biodiversity, which is reduced northwards along the gradient of decreasing salinity (Villnäs and Norkko, 2011; Zettler *et al.*, 2014; Törnroos *et al.*, 2015). We arranged the border between depth strata to represent the presence and non-presence of hypoxia and it was hence situated close to the halocline. This limit was set when the proportion of hypoxia events exceeded the value of 0.2 of the annual observations at a given depth stratum at three fixed stations in the ICES subdivision (Figure 1) SD 24 (BY2), SD 25 (BY5), and SD 28 (BY15): for SD 24: 40 m, SD 25: 60 m, SD 26: 60 m, and SD 28: 70 m. Recurring hypoxia gradually degrades the tolerance of the benthic communities towards future hypoxic stress (Villnäs *et al.*, 2013), and the legacy of oxygen deficiency can often still be observed after a longer period of time, as community recovery is not linear to the degradation (Diaz and Rosenberg, 2008). The depth strata were, therefore, left unchanged between years. The time comparisons 1990–2004 and 2005–2018 were based on the observations when the feeding rate in EBC significantly increased (Svedäng *et al.*, 2020), and the hepatosomatic index (HSI) and Fulton’s condition factor, as indicators of condition, sharply fell (Eero *et al.*, 2012), i.e. around 2005.

Prior to the analyses of benthic fauna, we examined the depth distribution of benthic sampling occasions between time periods with the non-parametric Kruskal-Wallis test (Table S4). In addition, principal component analysis (PCA) was used to explore spatial variation (by using coordinates) in sampling points between the two periods. The results were confirmed with a one-way analysis of similarities (ANOSIM), run on Euclidean distances. ANOSIM is a non-parametric permutation procedure that compares rank similarities among samples within and between periods and depths based on the underlying similarity matrix. The test statistic, R , represents well separated comparisons when $R > 0.75$, overlapping but clearly different comparisons $0.75 > R > 0.5$, while $R < 0.25$ represents comparisons that are barely separable at all (Clarke and Gorley, 2001). The significance level is obtained by referring the observed value of R to its permutation distribution, and therefore it is strongly affected by sampling size. Thus, the R -values have been considered more useful for interpreting existing differences than the p -values (Clarke and Gorley, 2015).

Although the benthic data are highly variable in time and space (Table S3), a significant difference in the median station depth between the two periods was only found for SD 28 in shallow areas ($p < 0.05$), where the median sampling depth had changed from 48 to 39 m. In the deeper parts of the study areas, significant differences were found for SD 24 and 26. However, the deeper stations were all beneath the halocline. Likewise, ANOSIM confirmed the pattern observed

with PCA, i.e. that there were no obvious differences in the geographic locations of sampling stations in SD 24, 25, and 26 between the two periods ($R < 0.165$, $p < 0.02$). However, in SD 28, more shallower stations were sampled during 2005–2018, especially around Gotland, resulting in a clear spatial difference between the periods ($R = 0.407$, $p = 0.0001$). It should be noted that the temporal and spatial comparisons for SD 24 should be interpreted with caution, as data available from this subdivision were restricted.

Non-parametric multidimensional scaling (nMDS) was used to explore changes in community biomass patterns visually. These changes were further analysed with 2-way crossed analyses of similarities (ANOSIM), illustrating the differences between periods (i.e. 1990–2004 and 2005–2018) and depths (i.e. above and below 40 m for SD 24, 60 m SD 25, 60 m SD 26, and 70 m SD 28). Additionally, one-way ANOSIM was used to explore differences between periods for the different depths. The analyses were based on the Bray–Curtis similarity measure, calculated on fourth-root transformed biomass data. The SIMPER procedure was used to identify the species contributing to (dis)similarities between and within depth strata (Clarke *et al.*, 2014). All multivariate analyses were performed with the PRIMER 7 software, developed for community ecology analyses where the underlying data do not fulfil multivariate normality requirements as required by classical statistical methods (Clarke *et al.*, 2014; Clarke and Gorley, 2015).

In addition to the community analyses (above), we also explored temporal trends in benthic species groups. First, we examined the total biomass of benthic polychaetes and crustaceans, bivalves, and priapulids. Benthic polychaetes and crustaceans are documented to be important food items for cod, especially for smaller size classes (e.g. Bagge *et al.*, 1994; Uzars, 1994; Dziaduch, 2011; Pachur and Horbowy, 2013; Haase *et al.*, 2020). Bivalves and priapulids encompass large and long-lived species and were therefore included as indicators of a more stable benthic community that has not been subjected to frequent disturbances such as hypoxia (Norkko *et al.*, 2013). In 87% of the sampling occasions, these four benthic groups contributed $\geq 90\%$ of the total community biomass. Second, we studied the total biomass of the dominant food items for cod, i.e. benthic polychaetes and crustaceans. Trends were analysed by fitting loess smoothing to their biomass pattern per subdivision and depth strata (using SPSS Statistics 25). We chose a Gaussian kernel type with 25% point to fit to give weight to sampling occasions with benthic biomass. Third, we separately analysed temporal variation in biomass of the isopod *Saduria entomon*, as it is known to be a dominant food item for cod of all size classes (Pachur and Horbowy, 2013; Kulatska *et al.*, 2019).

Results

Hydrographic influence on reproduction, cod reproductive volume

To illustrate the typical locations of the RVs in the Baltic Sea, maps of the thickness of the reproductive layer are shown for twelve selected years linked to the major saltwater inflows of 1976, 1993, 2003 and 2014 (Figure 3). These maps provide a qualitative understanding of how the intruding salty, oxygen-rich water spread into the Arkona Basin, Bornholm Basin, Stolpe Furrow, Gdansk basin and to the southernmost part of the Gotland Basin, and create conditions where cod eggs can

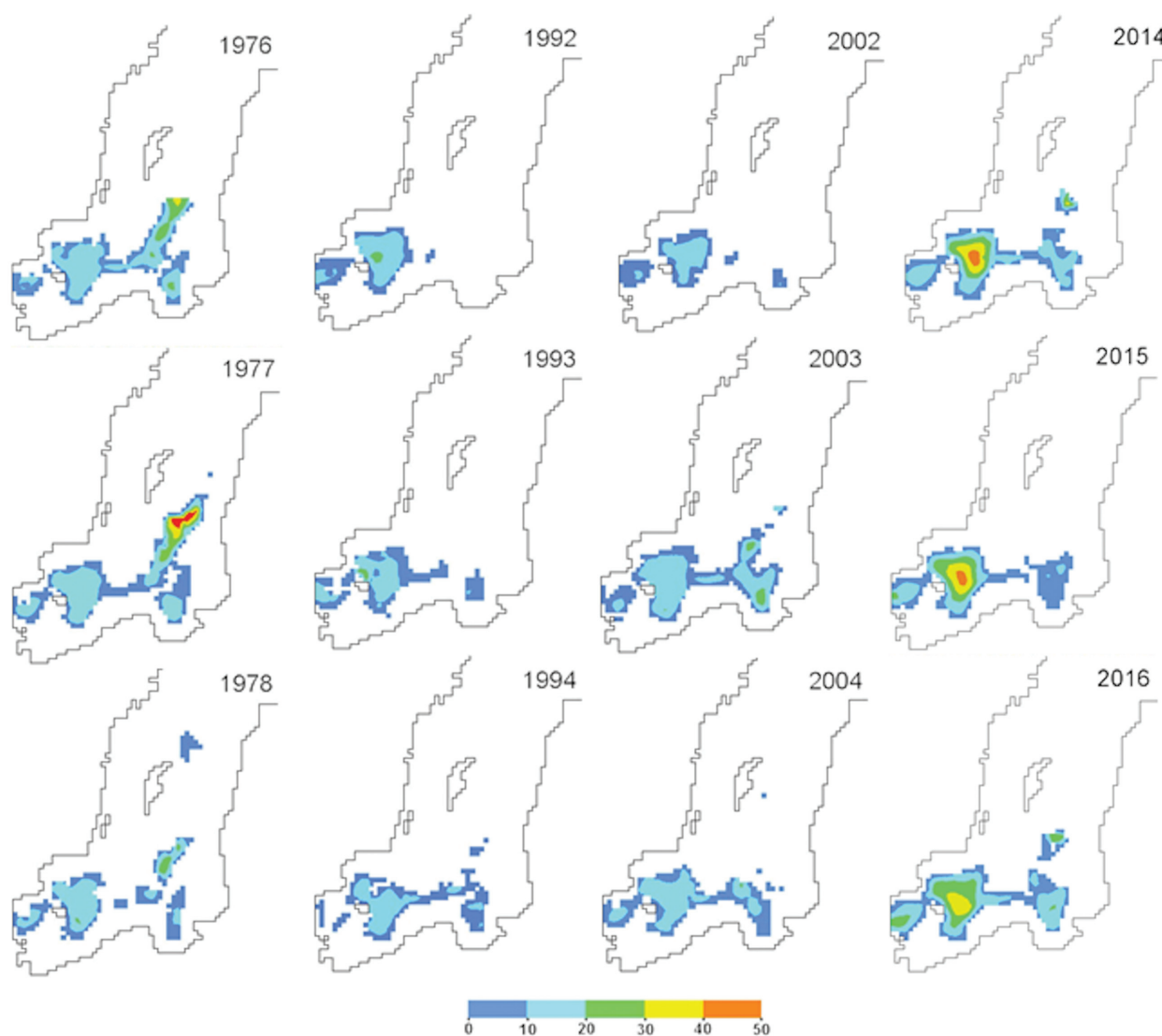


Figure 3. Depiction of the geographical extent and thickness (in meter) of the RVs $RV_{\geq 11}$ (defined by the salinity ≥ 11 PSU and >2 ml O_2/l) in the Baltic Sea. Top to bottom: the left column: the years 1976, 1977, and 1978; the middle left column: 1992, 1993, and 1994; the middle right column: 2002, 2003, and 2004, the right column: 2014, 2015, and 2016. Maps are built with the DAS tool (Sokolov *et al.*, 1997) from oceanographic data contained in the Baltic Environmental Database (<http://nest.su.se/bed>). The explanations on the data and tools are given in Savchuk (2018 and references therein). The thickness of $RV_{\geq 11}$ is indicated by colours: dark blue 0–10 m; light blue 10–20 m; green 20–30 m; yellow 30–40 m; red 40–50 m.

float in oxygenated waters. The conditions prior to the inflow events, as well as the characteristics of the inflows themselves, were quite different, resulting in varying RVs in the basins. For example, prior to the 1993 inflow, the overall salinities were relatively low, so the intruding water penetrated deep and was effectively diluted. Since the major inflows rapidly transition through the Arkona and Bornholm basins, Figure 3 shows the weak influence of these inflows on thicknesses of the reproductive layers in these basins.

The physical variations of the deep-water dynamics are reflected by $WV_{11-14.5}$, driven by the amount of salt brought into the Baltic Sea by inflows of Atlantic water masses (Figure 4). Total $RV_{11-14.5}$ and $WV_{11-14.5}$ were quite similar until the mid-20th century, but after that the $RV_{11-14.5}$ has generally been significantly smaller. This implies that since the 1950s, oxygen concentration has replaced salinity as the main determinant of the RV in the Baltic Sea, since a large part of

the water mass with sufficient salinity has become hypoxic, primarily due to eutrophication.

Despite considerable variation between years, $RV_{11-14.5}$ shows no clear trend in the Arkona Basin (*SD* 24) or the Bornholm Basin (*SD* 25) (Figure 4). $RV_{11-14.5}$ is situated at or above the halocline in the Arkona and Bornholm Basins, while hypoxia occurs below the halocline (Figure S1).

In the Gotland Deep (*SD* 28), there have only been a few years with significant $RV_{11-14.5}$ since the 1950s and none since the mid-1980s. In the Gdansk Deep (*SD* 26), $RV_{11-14.5}$ almost disappeared in the 1980s and 1990s, i.e. during the stagnation period when salinity decreased, while recovering since the 2000s. Comparison $RV_{11-14.5}$ and estimates of $RV_{>11}$ produced at WKCONGA (ICES, 2018), similar to those presented in Köster *et al.* (2017), shows that $RV_{11-14.5}$ reduced variability in the time-series in primarily Arkona and Bornholm basin (Figure S5). By eliminating short periods of high salinity and

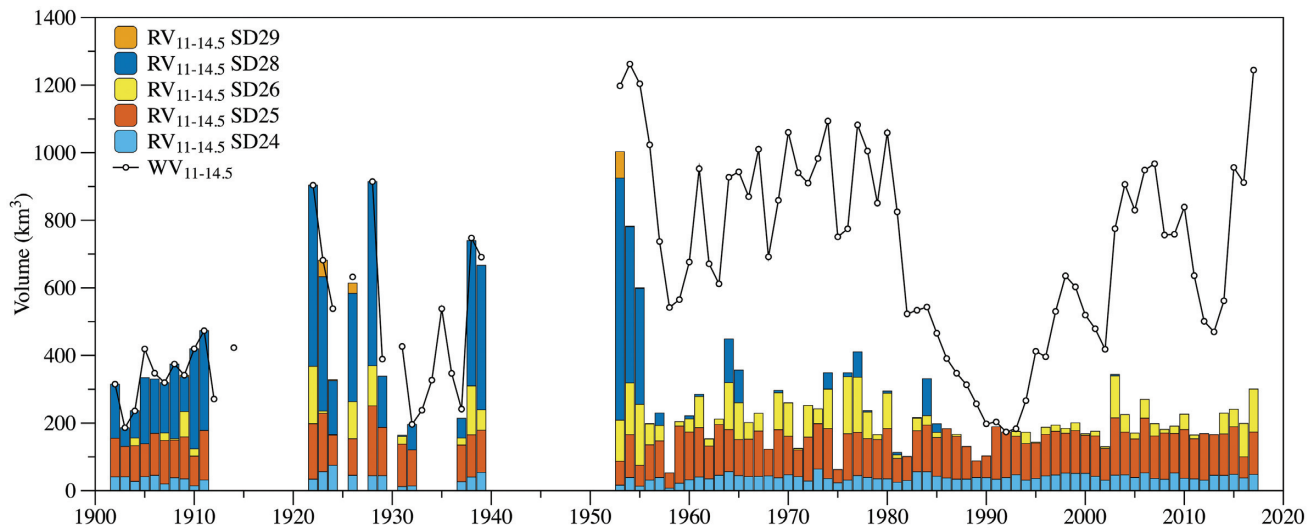


Figure 4. The temporal development of RVs in the Baltic Sea: $RV_{11-14.5}$ (represented by the salinity interval between ≥ 11 and ≤ 14.5 PSU and > 2 ml O_2/l) in different subdivisions. The development of water volume $WV_{11-14.5}$ (defined by the salinity interval between ≥ 11 and ≤ 14.5 PSU) is also displayed. All volumes are in km^3 and estimated as annual values.

oxygen associated with inflows that are not expected to include any eggs, the quality of the annual time series may improve.

The extent of well-oxygenated benthic habitats

The temporal development of well-oxygenated seafloor area (> 5 ml O_2/l for SD 24–25 and > 4 ml O_2/l for SD 26 and SD 28–29) differs between the sub-basins (Figure 5). In area SD 24, the size of well-oxygenated seafloor areas has been stable since 1953, and there was no significant trend over the period 1990–2017 (Mann–Kendall test: results are not shown). In SD 25, there was no significant trend over the period 1990–2017 (Mann–Kendall test: results are not shown), i.e. when condition (Fulton’s condition and HSI) and growth declined in EBC.

Because the seafloor is permanently oxygenated at depths shallower than 50 m in all basins, except for SD 24, it is worthwhile comparing the ratio between the extent of shallow (< 50 m) bottom area and the total bottom area (Figure 6). For the entire BP, this ratio is 0.46, while more than half the EBC core area, SD 25, is shallower than 50 m.

In SD 28, for which a more extended time series exists, the range of oxygenated area was lower already in the 1950s than at the beginning of the century, indicating oxygen depletion (Figure 5). In SD 26 and SD 28–29, the well-oxygenated seafloor area temporarily increased due to the weakening of the stratification during the stagnant period (no major inflows) in the 1980s and early 1990s (Figure S2 and S3). However, SD 26 and SD 28–29 became rapidly depleted of oxygen due to the strong vertical density gradient as the stagnation was broken with the new, major inflows starting in 1993 (Kendall’s Tau = -0.59 ; p -value < 0.0001 ; Kendall’s Tau = -0.68 ; p -value < 0.00001 ; Kendall’s Tau = -0.61 ; p -value < 0.00001 , respectively). It should be noted that the oxygenated areas in SD 26 and SD 28–29 are similar in size compared to the 1970s and early 1980s.

Frequency of hypoxia in the pelagic habitat

We studied the frequency of hypoxia events at different depth strata since 1957 at fixed stations in three areas: SD 24–25

and SD 28. The frequency of hypoxia was measured as the annual proportion of events with less than 5 ml O_2/l for SD 24–25 and less than 4 ml O_2/l for SD 28 (Figure 7). Hypoxic events were found at shallower depths in SD 24, with no trend at 30 and 50 m depth since 1990, while weakly increasing at 40 m (Kendall’s Tau = 0.28; p -value = 0.035). In SD 25, frequent hypoxic events occurred from 60 to 70 m depth. A weak increasing trend can be noted at 60 m from 1990 and on (Kendall’s Tau = 0.28; p -value = 0.038). In contrast, the oxygen conditions temporally improved at 70 and 80 m depth in SD 28 in the late 1980s, only to return in the late 1990s to similar hypoxic levels that had prevailed before.

We also explored the oxygen content development (ml O_2/l) at different depth strata at the fixed stations in SD 24–25 and SD 28 (Figure 8). For the period 1991–2017, decreasing trends were found in oxygen content over time in SD 24 at 30 and 40 m depth (Kendall’s Tau = -0.095 , p -value = 0.010; and Kendall’s Tau = -0.10 , p -value = 0.006, respectively), and in SD 25 at 50 and 60 m depth (Kendall’s Tau = -0.19 , p -value < 0.0001 ; and Kendall’s Tau = -0.13 , p -value < 0.001 , respectively). In SD 28, oxygen content at 60 and 70 m depth showed a parabolic pattern over time, where oxygen content increased during the stagnant period in the 1980s and the beginning of the 1990s and was at the lowest levels at the beginning and the end of the time series. At 50 m depth, the oxygen content showed a decreasing trend since 1990 (Kendall’s Tau = -0.15 , p -value < 0.001).

Relationship between productivity proxies and the extent of the hypoxic area

The segmented regression indicated a breakpoint in the time series on the proxy on productivity and LPR in 1998 (Table S5). Consequently, as to achieve stationarity in the time series, i.e. a study period without a monotonic trend, a correlation study was restricted for the years from 1946 to 1998 for the proxies on productivity, LPR, and the biomass of commercial-sized cod at ≥ 35 cm in length, $TSB_{\geq 35}$, and the extent of the hypoxic area in the Baltic Sea (Table 1). LPR was neither correlated to $TSB_{\geq 35}$ nor the extent of the hypoxic area. $TSB_{\geq 35}$

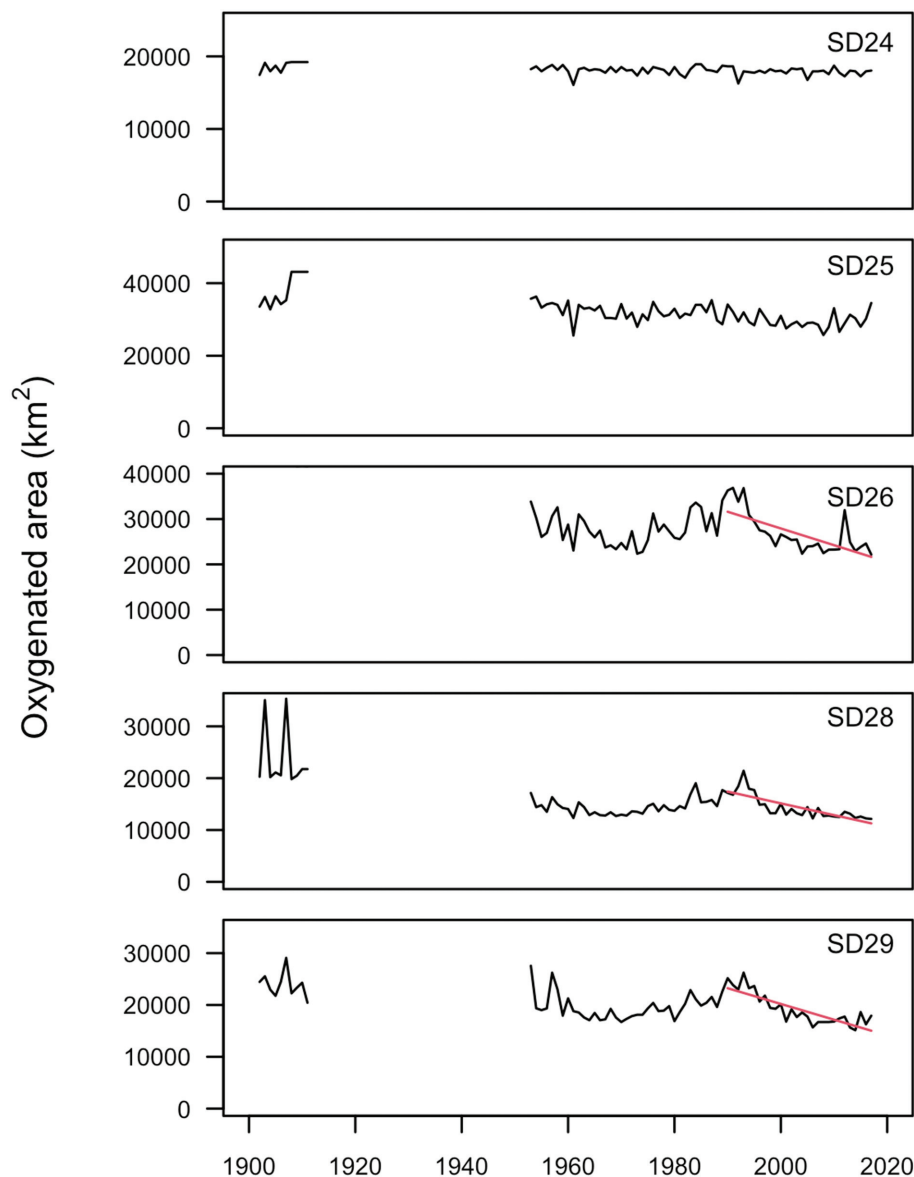


Figure 5. The extent of well-oxygenated areas over time is shown for ICES SD 24–26 and SD 28. Oxygen limit: >5 ml O_2/l for SD 24–25; >4 ml O_2/l for SD 26 and SD 28–29. All areas are in km^2 and estimated as annual values. Significant trends (tested by the non-parametric Mann–Kendall test for evaluating unidirectional trends) for the period 1990–2017 are shown as red lines: Note the different scales on the y-axis.

and the size of the hypoxic area showed a weak, positive correlation for the studied period, i.e. the biomass of fish above 35 cm in length increased in parallel with the expansion of the hypoxic area.

The development of benthos at different depth strata

The benthic community biomass composition differed between deep and shallow stations in all studied subdivisions (Figure 9, Table 2), suggesting that our independent characterization of frequent hypoxia by depth was relevant (Figure 7). In deeper areas, the benthic community was often dominated by a single polychaete species, *Byligides sarsi* (Table 3). In the shallower areas, bivalves, polychaetes, crustaceans, and priapulids contributed to similarities in benthic community biomass between basins. In SD 24, the community composition between shallow and deep seafloor areas was partly

overlapping (Table 2), while the average community dissimilarity was still high ($>70\%$; Table 3).

In contrast to the vertical gradient, the benthic community showed similar biomass composition between the two periods representing different phases in the development of the cod feeding rate and metabolism (Svedäng *et al.*, 2020), based on a HSI, used as a proxy on condition (Eero *et al.*, 2012; i.e. 1990–2004, and 2005–2018). ANOSIM comparisons showed low R-values in each of the subdivisions (Table 2), with an exception in SD 28, where 1990–2004 separates from 2005–2018 ($R = 0.308$, $p < 0.0001$). Accordingly, the total biomass of bivalves, crustaceans, polychaetes, and priapulids was not reduced over time, as indicated by the loess smoothing curves for different depth strata in each subdivision (Figure 10). Exceptionally, the improved oxygen conditions during the 1990s coincided with minor biomass increases at some of the deeper stations, which disappeared rapidly as the bottom water oxygen content declined.

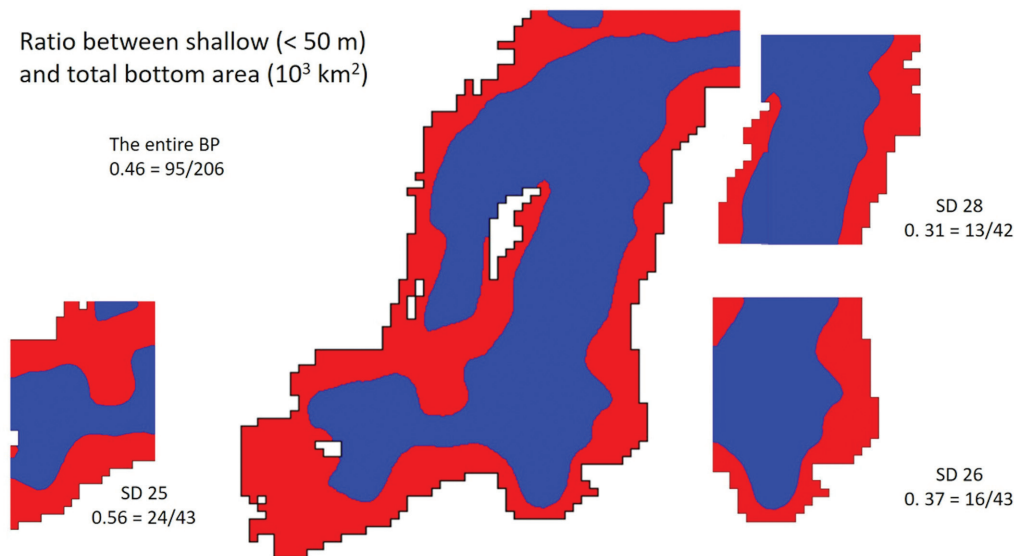


Figure 6. The red area shows the extent of shallow (< 50 m) bottom area, i.e. mostly oxygenated, in the entire BP and in SD 25, 26, and 28. The blue area shows the extent of deeper (>50 m) bottom area. Numbers show the ratio between the bottom area shallower than 50 m and the total bottom area.

Crustaceans and polychaetes, important for feeding of EBC, constituted a relatively small part of the total benthic biomass (c.f. Figures 10 and 11) and showed no clear temporal trend in SD 24–25 (Figure 12). In SD 26, a potential increase was indicated at depths < 60 m since 2005 (Figure 11), caused by *Marenzelleria* spp. and *Hediste diversicolor*, and frequent occurrences of the isopod *Saduria entomon* (Figure 12). In SD 28, the biomass of polychaetes and crustaceans tended to decrease over time (Figure 10) due to the decline in the biomass of the amphipods *Monoporeia affinis* and *Pontoporeia femorata* (Pearson $r = -0.47$, $p < 0.001$). *Saduria entomon* often dominated total crustacean biomass in shallower areas in SD 25–26 and SD 28 (Pearson $r > 0.81$, $p < 0.0001$), while it often was absent from the deeper areas of all investigated subdivisions (Figure 11). In SD 24, *Saduria entomon* was present only to a limited extent (found in just 17% of the samples <40m depth).

Discussion

The relationship between hydrography and EBC RV

The effect of the increasing oxygen demand due to eutrophication has resulted in quite different developments of the salinity-oxygen environment in the Baltic basins. There was no significant trend in $RV_{11-14.5}$ in the Arkona Basin (SD 24) and Bornholm Basin (SD 25) since the 1960s while differing between years due to varying hydrographic conditions (Köster *et al.*, 2017; Figure S1). These basins usually contain high saline waters, and residence times are relatively short, so the effect of increasing oxygen consumption due to eutrophication is less prominent.

The requirements for cod reproduction are still satisfactory in the Bornholm Basin because RV is located above or in the halocline (Stigebrandt, 2017). Further, the Bornholm Basin is well-ventilated, especially during winter, with a frequent water transfer with higher salinity from the Danish straits than the subdivisions in the east and north (SD 26 and 28). Hence, we suggest that the resilience of the cod spawning area in the

Bornholm Basin is much higher than in the Gotland Deep and Gdansk Deep.

In the Gdansk Deep (SD 26), the development has been different, and, at present, we only identify the occurrence of RV as a consequence of inflow events (c.f. Mohrholz, 2018), enabling a period of high saline and oxygen conditions to occur, e.g. in 2003, 2014–2017 (Figure 4).

RV in the Eastern Gotland Deep (SD 28) only occurred sporadically after the 1950s and was then completely absent since oxygen became depleted below the halocline (c.f. Savchuk, 2018). Thus, this is an even more pessimistic estimate of RV than Köster *et al.* (2017), who found at least occasional RV in recent decades. Here, there are no signs that RV will return yet, although the deepwater salinities increased to relatively high levels, as depicted by the development of $WV_{11-14.5}$ (see Figure 4 and Figure S3). Most probably, a lower oxygen demand has to be obtained first before this formerly important area for EBC reproduction can be contributing again (Carstensen *et al.*, 2014; Andersen *et al.*, 2017). It has been higher temperatures in the deepwater and RVs since the 1990s (e.g. Carstensen *et al.*, 2014; Köster *et al.*, 2017; Schmidt *et al.*, 2021), most probably because inflows on average occurred at warmer seasons. Since the oxygen concentration of the inflowing water most commonly is close to saturation at the sills, warmer water implies lower oxygen concentrations in the deeper parts of the basins as the inflowing water masses stream through the Baltic Sea. Consequently, the higher temperature of the inflowing water has contributed to a reduction of oxygen concentration in all basins, in addition to already existing oxygen demand. We found that weak decreasing trends in oxygen concentration occurred in SD 24 at 30 and 40 m depth and in SD 25 at 50 and 60 m depth (Figure 8).

Our documentation of the development of EBC RV and hydrography shows, in addition to previous studies (MacKenzie *et al.*, 2000; Köster *et al.*, 2005; 2009; 2017), that a shift occurred in the mid-20th century from salinity to oxygen content as the prime factor limiting RV in the Baltic Sea. The new parameter on the water volume with sufficient salinity to ensure

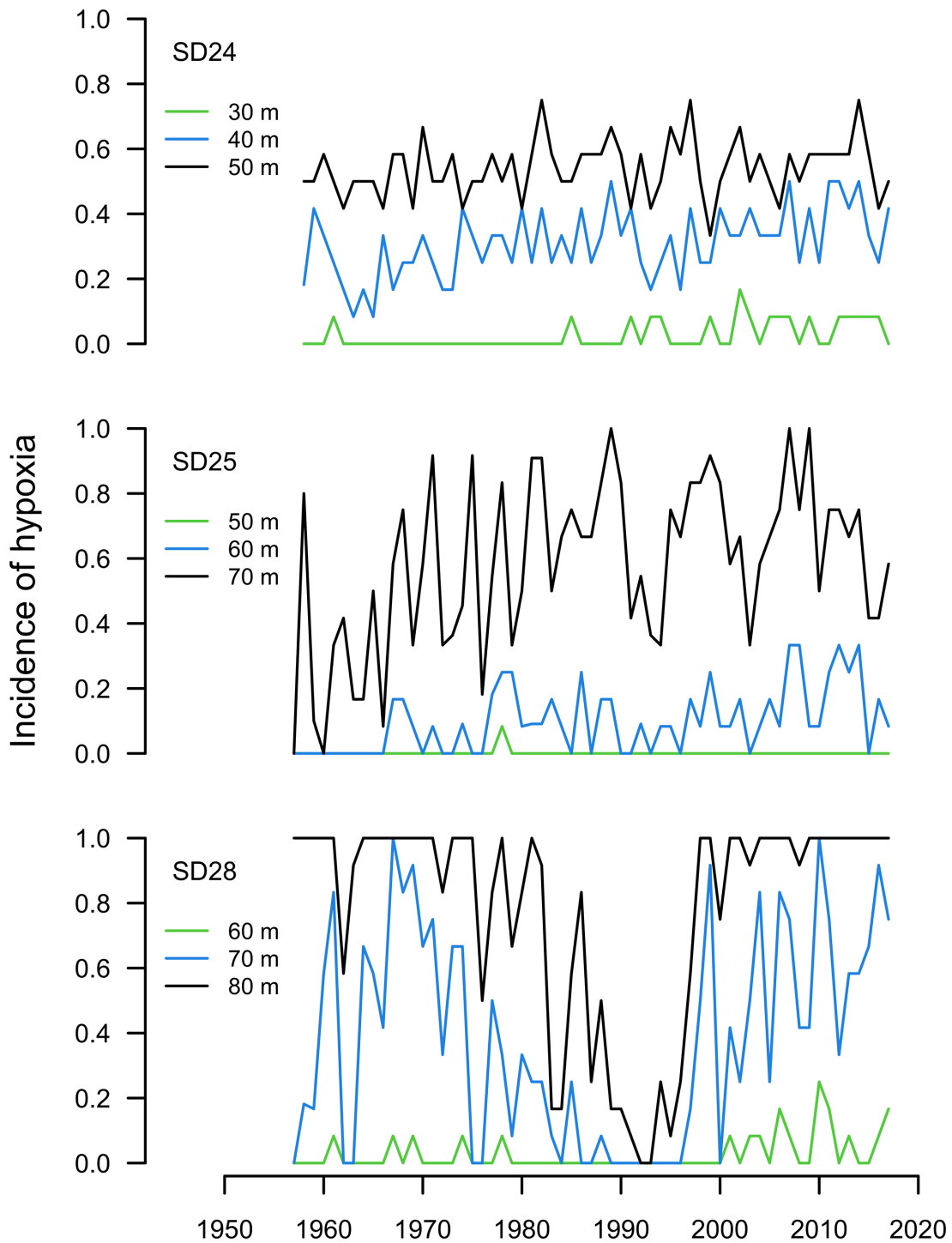


Figure 7. The incidence of hypoxic events by depth, shown as the proportion of the monthly observations per year with hypoxic conditions. Hypoxia is defined as $<5 \text{ ml O}_2/\text{l}$ in SD 24–25; $<4 \text{ ml O}_2/\text{l}$ in SD 28. It is expected that lower oxygen levels will cause anoxic conditions at the seafloor. The time series are based on thousands of measurements (see Figures S1-S3) extracted with the tools from the Nest, which is a decision support system for management of the Baltic Sea (<http://nest.su.se/next>). The explanations on the data and tool are given in Savchuk (2018 and the references therein).

neutral buoyancy for at least 50% of the laid eggs, $WV_{11-14.5}$, irrespectively of oxygen content, shows that in the first half of the 20th century, most of the RV was found in the Gotland Deep and varied in correspondence with $WV_{11-14.5}$, i.e. oxygen was not then a limiting factor. Also, a large proportion of the laid eggs is regularly lost due to sedimentation (c.f. Pacariz *et al.*, 2014).

The temporary RV’s disappearance in the Gdansk Deep corresponds with the stagnant period from the mid-1980s to the mid-1990s when the salinity decreased substantially in the deepwater. While Köster *et al.* (2017) acknowledge the relatively good spawning conditions usually observed in the Słupsk Furrow (connecting the Bornholm and the Gdansk basins), we also find that RV occurs in the Gdansk Deep since

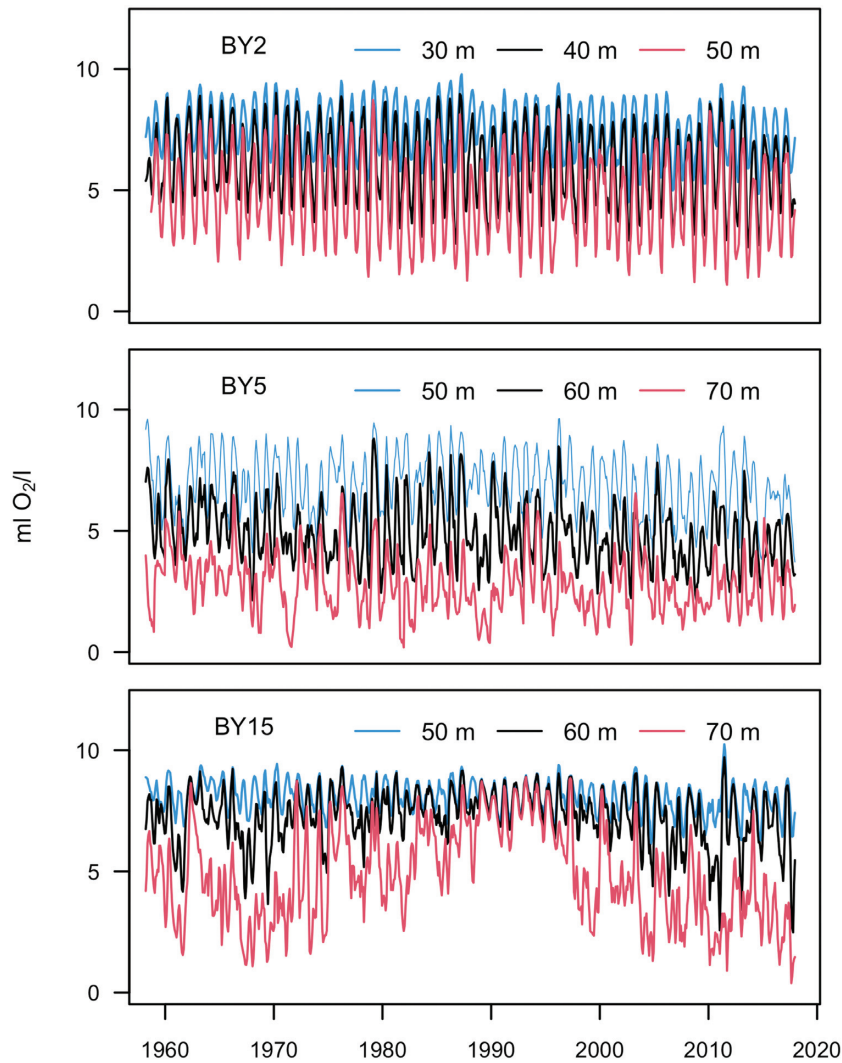


Figure 8. The monthly development of oxygen content at different depth strata from 1957 to 2017 at (a) BY2 (SD 24), (b) BY5 (SD 25), (c) BY15 (SD 28).

Table 1. Spearman ρ correlation matrix of studied parameters (spearman ρ is shown above the diagonal, p -value below) LPR and EBC biomass ≥ 35 cm in total length ($TSB_{\geq 35}$), the extent of hypoxic area in the Baltic Sea between 1946 and 1998.

| | LPR | $TSB_{\geq 35}$ | Hypoxic area |
|-----------------|-------|-----------------|--------------|
| LPR | 1 | -0.21 | -0.13 |
| $TSB_{\geq 35}$ | 0.218 | 1 | 0.39 |
| Hypoxic area | 0.442 | 0.021 | 1 |

All comparisons are balanced ($n = 35$).

the late 1990s. However, the subsequent reestablishment of a water body suitable for cod reproduction has not led to recovered cod reproduction in the Gdansk Deep (Köster *et al.*, 2017), i.e. the number of cod larvae as an index on cod spawning activity has remained low in spite that adult cod are present (c.f. Eero *et al.*, 2012). This lack of correspondence between physical conditions suitable for EBC reproduction and actual reproduction points to a biological interference that has been ignored hitherto. We suggest that the loss of the spawning unit in the Gdansk Deep in the early 1990s also meant a loss of homing behavioural traits, whether phenotypically or

genetically imprinted (c.f. De Luca *et al.*, 2014), which may impede recovery (André *et al.*, 2016).

The extent of hypoxia at the sea floor and in the water column

Since the beginning of the 1900s, eutrophication, i.e. higher production of organic matter, has resulted in the spread of hypoxia in deeper water layers and less oxygenated areas in the Baltic Sea (Fonselius, 1972; Carstensen *et al.*, 2014). The cyclic variation in the frequency of inflows of water of oceanic origin also affects the extent of hypoxia in the Baltic Sea (Savchuk, 2018). However, the temporal development of oxygen conditions and the extent of hypoxia differ considerably between the studied areas.

Stagnant periods that lead to lower salinity, also increase oxygen content (Savchuk, 2018). Periods with a well-stratified water column, leading to hypoxic conditions at the seafloor over large parts of the Baltic Sea, occurred during the 1960–1970s and have returned since the mid-1990s. In the intermitting period from the mid-1980s to the mid-1990s, fewer and weaker inflows led to stagnation, causing a freshening of the Baltic Sea deepwater and more turbulent conditions with a

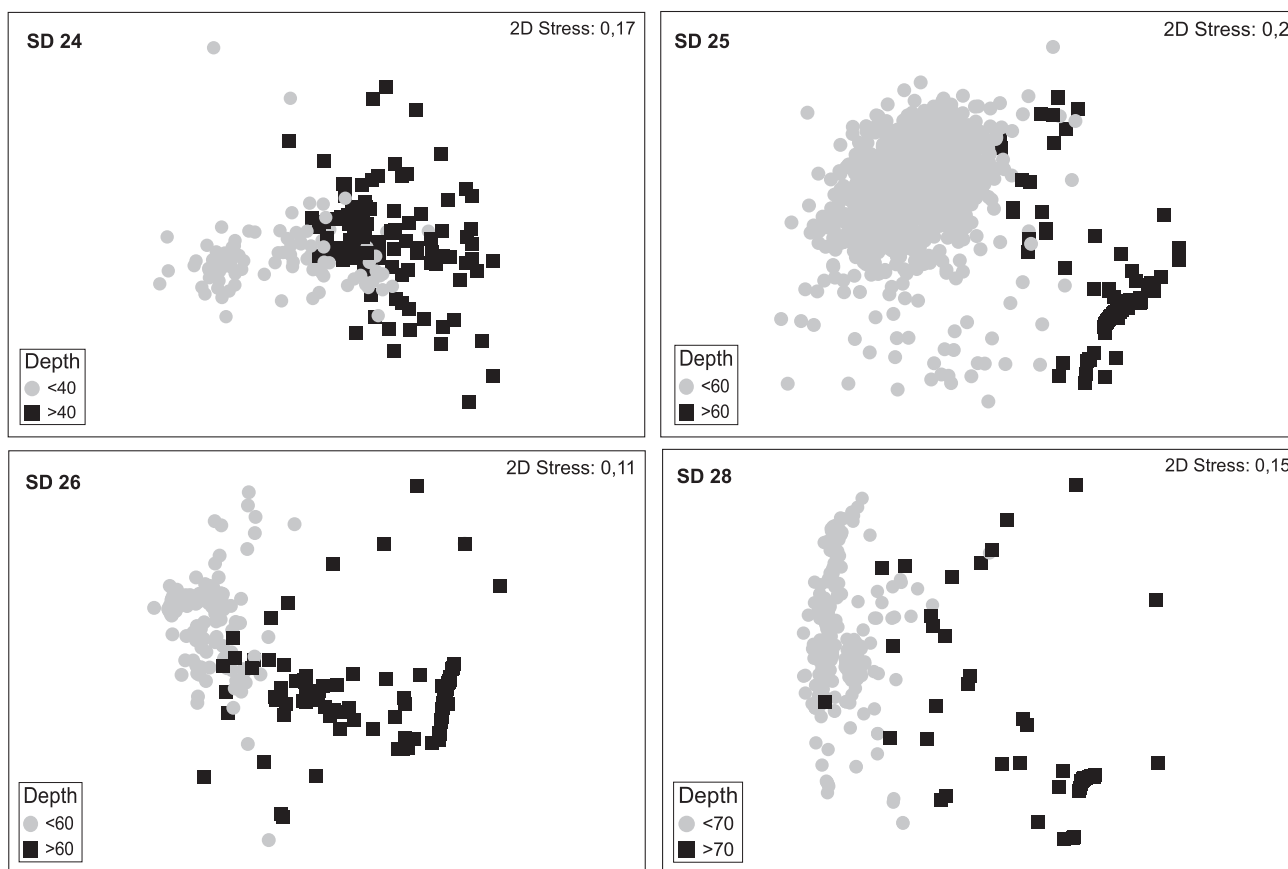


Figure 9. The general pattern in total benthic community biomass (g ww_w m⁻²) between shallow and deep areas, the latter having a higher frequency of hypoxic events (c.f. Figure 7), as illustrated with non-metric multidimensional scaling. The configurations present the pairwise distances among samples (based on ranked similarities), hence samples that have more similar benthic biomass composition will be placed closer to one another on the plot.

Table 2. Two-way crossed (*) analyses of similarities (ANOSIM) regarding differences in benthic community biomass composition between depths (SD 25: 10–60 m vs >60 m, SD 26: 10–60 m vs >60 m and SD 28 10–70 m vs >70 m) and time periods (1990–2004 and 2005–2018).

| ANOSIM | | SD 24 | SD 25 | SD 26 | SD 28 |
|------------------|---|-------|-------|-------|-------|
| Depth* | R | 0412 | 0876 | 0695 | 0884 |
| | p | 0000 | 0000 | 0000 | 0000 |
| Period* | R | 0157 | 0046 | 0135 | 0218 |
| | p | 0000 | 0000 | 0001 | 0000 |
| Period (deep) | R | 0228 | 0080 | 0048 | |
| | p | 0001 | 0000 | 0035 | ns |
| Period (shallow) | R | 0177 | 0043 | 0248 | 0308 |
| | p | 0000 | 0000 | 0002 | 0001 |

One-way ANOSIM was further run to explore differences between periods within depths (deep and shallow). The R test statistics of this non-parametric permutation procedure represents well-separated differences when $R > 0.75$, overlapping but clearly different $0.75 > R > 0.5$, while $R < 0.25$ represents comparisons that are barely separable at all.

downward erosion of the halocline, which eventually reduced the extent of deepwater and seafloor hypoxia (e.g. Conley *et al.*, 2002; Stigebrandt, 2017).

In the Gotland Deep and Gdansk Deep, where hypoxia was already wide-spread in the deep layers in the 1950s, we can confirm that oxygen levels have remained low for more than 60 years except for the stagnant years from the 1980s to the beginning of the 1990s, as mentioned, when freshening improved the oxygen conditions temporarily. The extent

of the oxygenated seafloor area has been on the same level in the Arkona since the 1950s. In the Bornholm Basin, the present core area of EBC, the oxygenated area was reduced between the 1950s and the 1980s. However, it has been stable during the “critical” period since the 1990s, when the growth/survival of EBC declined, as also shown by other studies (e.g. Svedäng and Hornborg, 2014; 2017; Mion *et al.*, 2020; ICES, 2021). The stability of oxygen condition in the Bornholm Basin differs from the development in the Gotland and Gdansk Deep, where the reversal of the temporary decline in the hypoxic area resulted in a strong expansion of the hypoxic area since the mid-1990s. In addition, our proxies on productivity, LPR, and $TSB_{\geq 35}$, showed either no, or a positive, correlation to the extent of the hypoxic area during the period 1946–1998.

In contrast to our finding of a stable oxygen situation in Bornholm since the 1980s, Brander (2020) identified a declining trend in oxygen concentration at 50–65 m depth from 1960 to 2020. While Casini *et al.* (2021) suggested a shallowing of the depth of the 4.3 ml/l oxygen concentration level in the Bornholm Basin in October–November from 60 to 50 m, and in SDs 26–28 from 80 to 60m since the early 1990s. Unfortunately, these studies suffer from inconsistent data analysis, which makes their conclusions questionable. There is no visual shallowing of the 4.3 ml/l level, merely seasonal variations (Figure S6). Ignoring sharp vertical gradients and averaging oxygen dynamics in the water layer 50–65 m, Brander (2020) gives an impression of almost detrimental deep-water

Table 3. SIMPER analyses, based on benthic community biomass, present the average dissimilarity (%) of sampling occasions between depth strata, as well as the average similarity between sampling occasions within a depth strata per subdivision.

| SD | Depth (m) | Avg. dissim. | Avg. sim. | Species contributing to similarity |
|----|-----------|--------------|-----------|--|
| 24 | <40 | 71.21% | 44.32% | <i>Limecola balthica</i> (35%), <i>Mya arenaria</i> (12%), <i>Pygospio elegans</i> (8%), Hydrobiidae (7%), <i>Mytilus</i> spp. (7%), <i>Marenzelleria</i> spp. (5%), <i>Halicryptus spinulosus</i> (4%), <i>Diastylis rathkei</i> (4%), <i>Hediste diversicolor</i> (4%), <i>Cerastoderma glaucum</i> (4%) |
| | >40 | | 40.90% | <i>Limecola balthica</i> (40%), <i>Halicryptus spinulosus</i> (14%), <i>Scoloplos armiger</i> (13%), <i>Bylgides sarsi</i> (11%), <i>Diastylis rathkei</i> (9%), <i>Pontoporeia affinis</i> (4%) |
| 25 | <60 | 93.03% | 45.64% | <i>Limecola balthica</i> (53%), <i>Halicryptus spinulosus</i> (6%), <i>Pygospio elegans</i> (6%), <i>Mytilus</i> spp. (6%), <i>Monoporeia affinis</i> (5%), <i>Oligochaeta</i> (4%), <i>Marenzelleria</i> spp. (4%), <i>Saduria entomon</i> (4%), <i>Mya arenaria</i> (2%) |
| | >60 | | 30.98% | <i>Bylgides sarsi</i> (89%), <i>Scoloplos armiger</i> (7%) |
| 26 | <60 | 91.51% | 48.34% | <i>Limecola balthica</i> (40%), <i>Marenzelleria</i> spp. (15%), <i>Hediste diversicolor</i> (11%), <i>Mya arenaria</i> (10%), <i>Oligochaeta</i> (7%), Hydrobiidae (6%), <i>Pygospio elegans</i> (5%) |
| | >60 | | 21.28% | <i>Bylgides sarsi</i> (82%), <i>Limecola balthica</i> (11%) |
| 28 | <70 | 94.90% | 47.76% | <i>Limecola balthica</i> (38%), <i>Marenzelleria</i> spp. (15%), <i>Monoporeia affinis</i> (15%), <i>Saduria entomon</i> (13%), <i>Halicryptus spinulosus</i> (7%), <i>Pygospio elegans</i> (4%) |
| | >70 | | 9.71% | <i>Bylgides sarsi</i> (82%), <i>Pontoporeia femorata</i> (8%) |

Species that are important contributors to similarity within biomass per depth strata are added to the table.

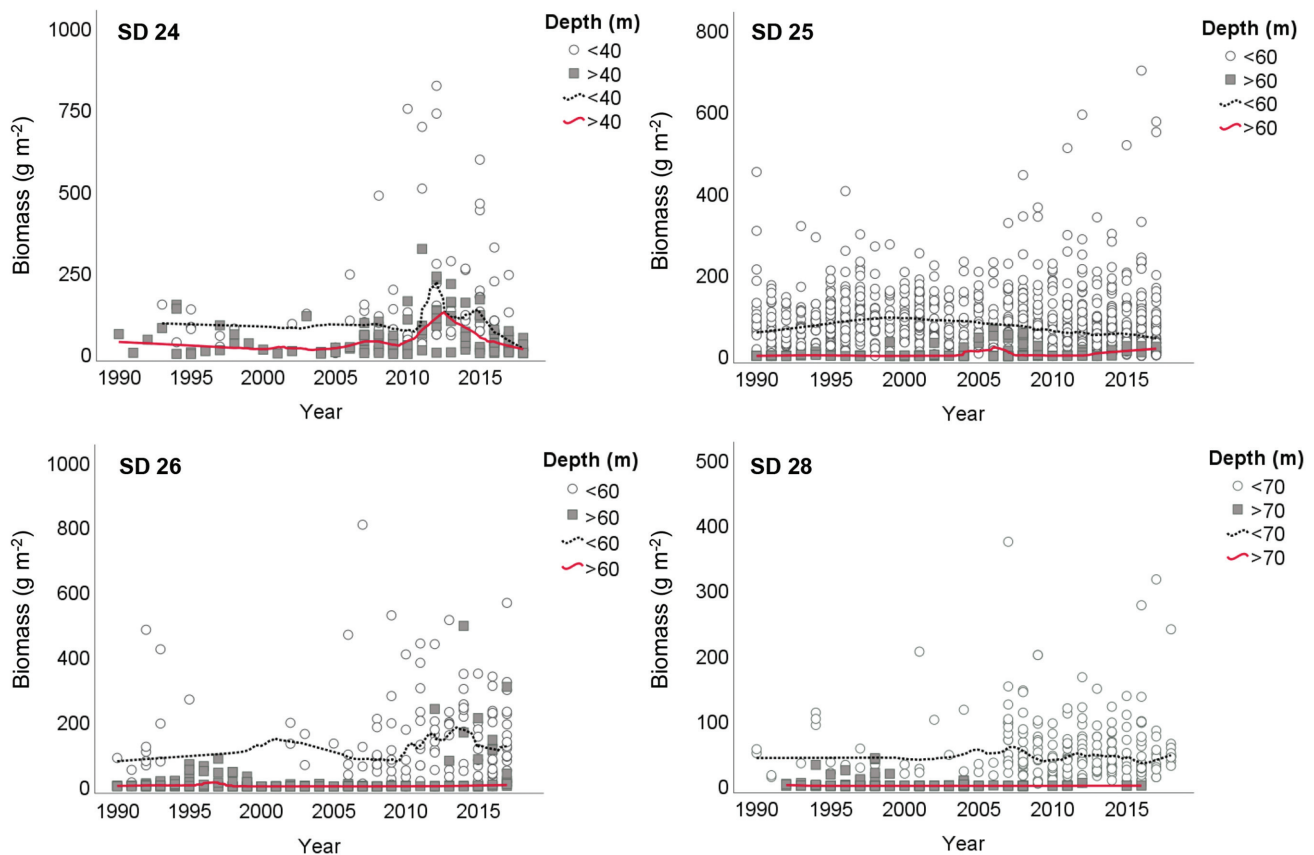


Figure 10. Temporal trends (1990–2018) in the total biomass (g wwet m^{-2}) of benthic polychaetes and crustaceans, bivalves, and priapulids per ICES subdivision and depth strata. Bivalves and priapulids encompass large and long-lived species and were therefore included as indicators of a stable benthic community. A loess smoothing was fitted to the plotted data. Note the different scales on the y-axes.

oxygen concentrations (op.cit. Figure 2), fluctuating in the recent decades between about 4 and 5 ml/l, i.e. about 50–60% of the oxygen saturation. Meanwhile, in the appropriately depth-wise differentiated approach (Figure 8), the oxygen concentration of about 6–7 ml/l (70–80% saturation) is typical for 50 m depth and is certainly higher at the shallower depths. In other words, vast bottom areas in SD 25 (c.f. Figure 6) are populated by the abundant benthic animals suitable as cod feed, as indicated in this study (Figures 10–12 and Table 3).

Furthermore, the variability of oxygen concentration within these depth ranges is exceedingly large (see Figure 8 and Stigebrandt, 2017) in relation to these small changes in mean oxygen content, as found by Brander (2020) and Casini *et al.* (2021). It suggests that periodic hypoxia exposures occurred before the current deterioration of the cod stock. Alternatively, it has been proposed that the exposure to low-oxygen conditions has increased during the last decades due to behavioural changes causing cod to spend more time in

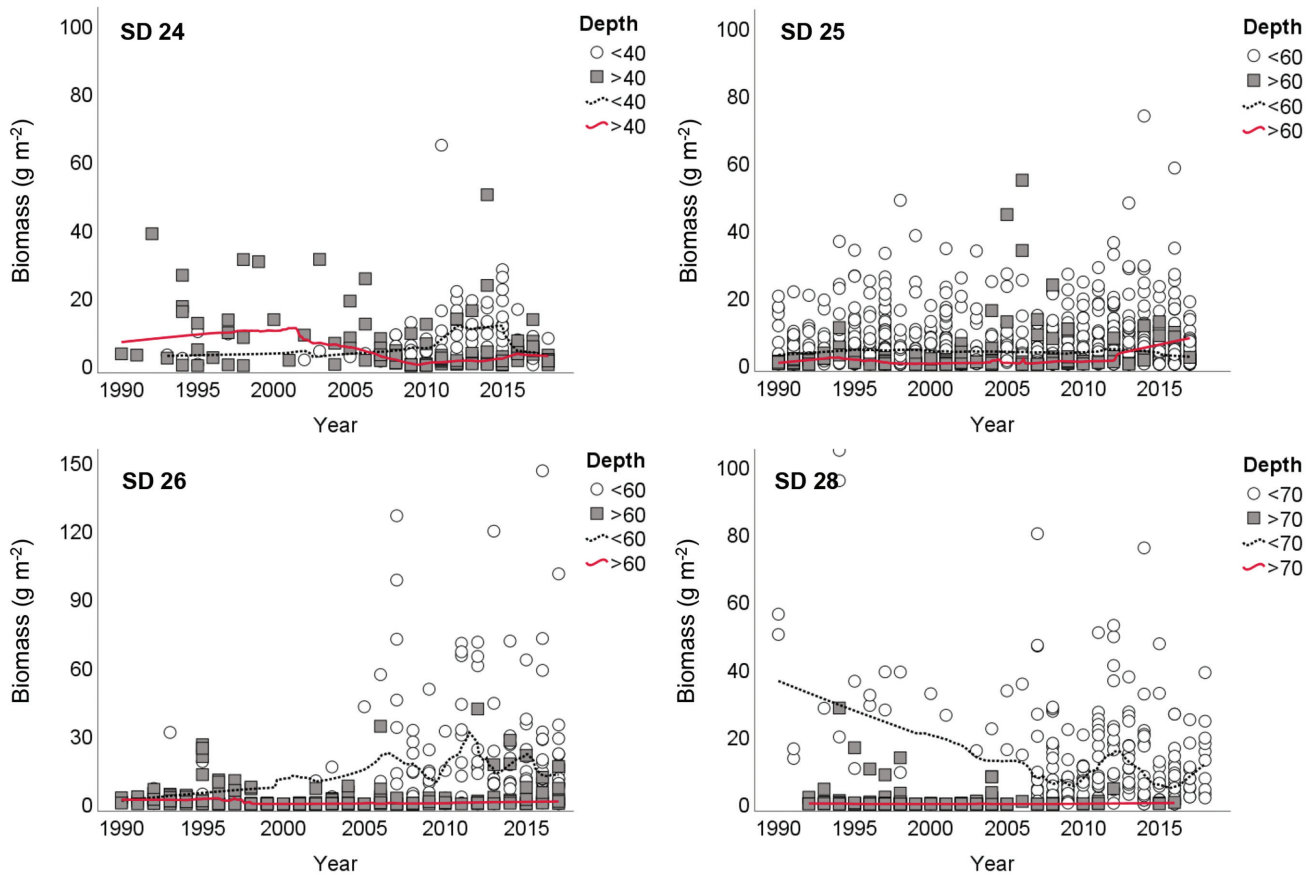


Figure 11. Temporal trends (1990–2018) in the total biomass (g wwvt m^{-2}) of crustaceans and polychaetes, documented to be the main food sources for cod, per ICES subdivision and depth strata. A loess smoothing was fitted to the plotted data. Note the different scales on the y-axes.

deeper water (Casini *et al.*, 2021). Information on changes in EBC semi-pelagic, active daily vertical swimming behaviour is scarce. Still, we know that the overall most common migratory behaviour in cod is vertical movements, either along the bottom slope or, mainly, through vertical migrations in the water column (Righton *et al.*, 2010). In other words, such behavioural change would require that cod willingly stay in water with unsuitable oxygen conditions, which seems implausible.

The role of hypoxia for the benthic community

The data on zoobenthic communities showed that the deep areas in all basins (SDs) deviated sharply from well-oxygenated, shallower areas due to their low biomass and different community composition. Notably, the main invertebrate food item for cod, *Saduria entomon*, was absent in the deeper areas of all subdivisions. These observations suggest that the benthic communities are strongly affected by frequent hypoxia events in the deepwater, as emphasized in previous studies (Norkko *et al.*, 2015). During the last century, oxygen deficiency has severely affected benthic community composition and biomass in the deeper open areas of the Baltic Sea (Hessle, 1924; Karlson *et al.*, 2002; Carstensen *et al.*, 2014). A deteriorated benthic biomass below the halocline has been reported in the central parts of the BP (SD 26–29) since the 1960s (Laine *et al.*, 1997; Olenin, 1997; Karlson *et al.*, 2002).

However, intermittent recoveries of these communities, have been observed in response to improved bottom water oxygen conditions as during the early 1990s. Interestingly, in the more species-rich areas of the Arkona and Bornholm Basins, benthic community composition co-varies with the saltwater inflows. These southern Baltic basins have experienced an overall reduction in salinity during the 20th century, which has resulted in a replacement of marine species with brackish-water species (Norkko and Jaale, 2008; HELCOM, 2009; Villnäs and Norkko, 2011), and a shift towards more polychaete-dominated communities (Karlson *et al.*, 2002).

In contrast, our data show little sign of disturbance to benthic communities in shallow areas over the last three decades. Frequently occurring disturbances are likely to disrupt ecosystem stability by reducing the presence of large, long-lived species (Norkko *et al.*, 2013; Villnäs *et al.*, 2013). In this study, such species (e.g. the bivalves *Limecola balthica* and *Mya arenaria*) dominated benthic community biomass in shallower areas of all investigated subdivisions, indicating no major perturbations during 1990–2018. Overall, we found no evident decline in the biomass of crustaceans or polychaetes over time (c.f. Figure 11). An exception, however, was observed for the amphipods *Monoporeia affinis* and *Pontoporeia femorata* in SD 28. Although this trend is based on a limited number of observations, it is following the collapse noted for these amphipod populations in the northern parts of the Baltic

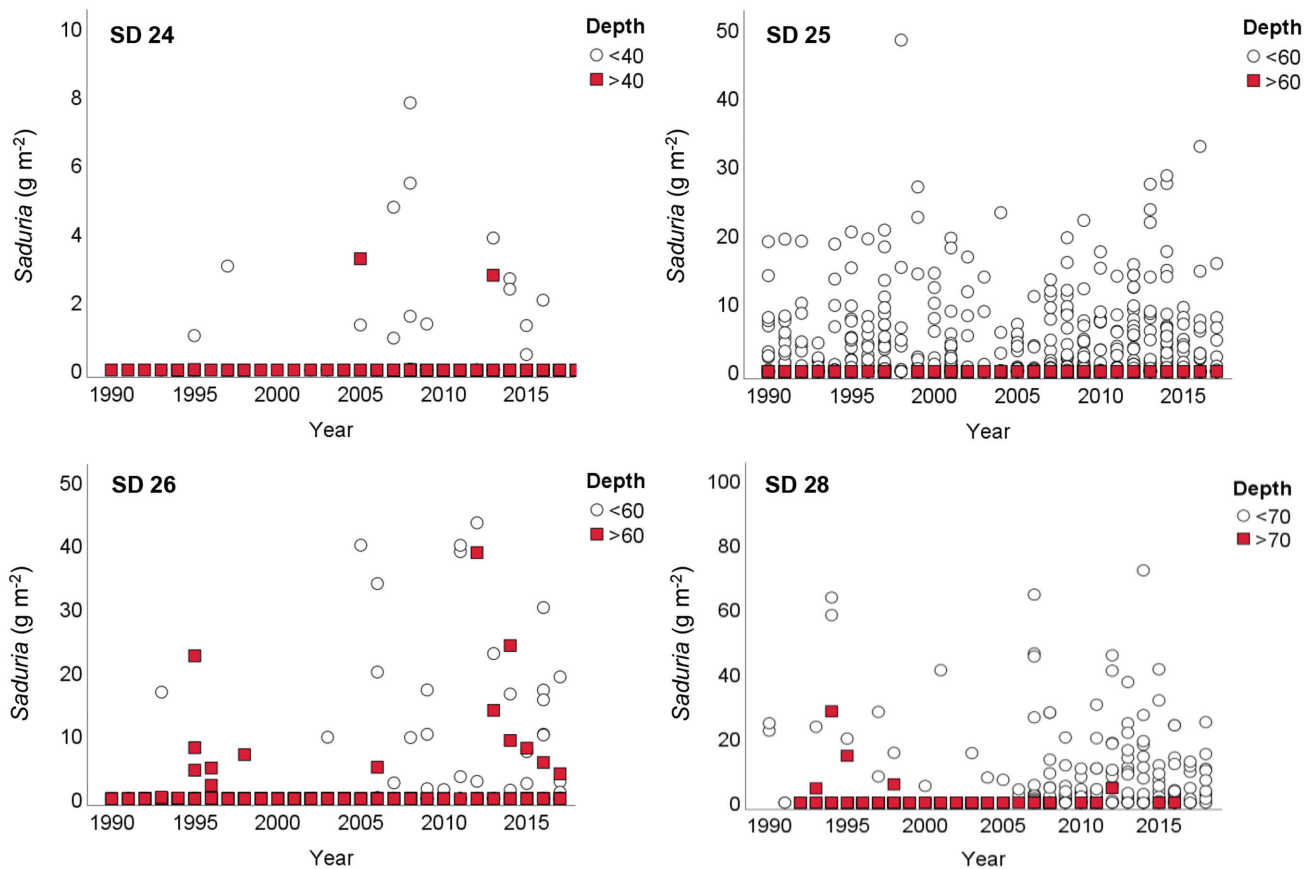


Figure 12. Temporal trends (1990–2018) in the biomass (g wwwt m^{-2}) of the isopod *Saduria entomon* per ICES subdivision and depth strata. Note the different scales on the y-axes.

Sea, which has been explained by several factors, such as the decrease in primary production during the spring bloom (Eriksson-Wiklund and Andersson, 2014), changes in temperature and salinity (Rousi *et al.*, 2013) or top-down control (Karlsson *et al.*, 2019).

In general, the community biomass values reported by this study are in accordance with earlier values reported by Gogina *et al.* (2016) for the investigated areas. These authors performed a wide-scale inventory of benthic faunal communities and biomass over the entire Baltic Sea, based on data from 2000 to 2013, but did not explore temporal variation. Carman and Cederwall (2001) reported a similar range of benthic biomass for areas < 70 in the BP (i.e. SD 24, 25, 26, and 28) based on data from ca 1970 to 2000 (Gogina *et al.*, 2016). The lack of temporal trend in benthic data is in line with recent modelling work suggesting that benthic biomass has not decreased in the BP (SD 27, 28) during 1970–2012 (Ehrnsten *et al.*, 2020). Thus, our results indicate that the standing biomass of benthic food in shallow areas had not changed markedly from 1990 to 2018, when the survival or growth of EBC deteriorated (Svedäng and Hornborg, 2014; 2017; Mion *et al.*, 2020; Neuenfeldt *et al.*, 2020). Hence, our results do not provide any evidence of a major change, or a severe reduction, in benthic food sources for EBC, which has been suggested as one constraining factor for EBC condition or growth (e.g. Casini *et al.*, 2016; ICES, 2019; Kulatska *et al.*, 2019) or survival (Neuenfeldt *et al.*, 2020).

Comparison over time in EBC production in relation to hydrography and benthos

Our findings suggest that declining growth and survival in EBC, leading to reduced productivity, cannot altogether be attributed to an increased extent of hypoxia at the seafloor or in the water column since the mid-1990s, affecting food supply (e.g. Casini *et al.*, 2016; Karlsson *et al.*, 2019; Neuenfeldt *et al.*, 2020), or the physiological status of cod (Brander, 2020; Casini *et al.*, 2021). In comparison, the extent of hypoxia in SD 26, SD 28–29 was at similar levels in the 1970s as they are at present. In other words, between the 1960s and the 1980s, high and increasing levels of CPUE and landings (ICES, 2019) coincided with *increasing* hypoxia. Since the mid-1990s, higher salinity has led to stronger stratification and, consequently, an increased extent of hypoxia. Though seeing a marked recovery in CPUE in the southern Baltic Sea in the late 2000s (c.f. Svedäng and Hornborg, 2014), cod landings, however, continued to fall even further.

Moreover, in SD 25, the present core area of EBC, neither oxygen content in the water column, the frequency of hypoxia events, the extent of hypoxia at the seafloor, nor the oxygenated seafloor area have changed. Importantly, our results on benthos biomass also underscore the fact that there is no indication of decreasing benthic food supply. Conclusively, the recent decline in individual growth and health status strongly deviates from the previous stratification period.

The parsimonious explanation of why landings were not amplified at increasing EBC abundance in the years around 2010 is that individual growth (Eero *et al.*, 2012; Svedäng and Hornborg, 2014; ICES, 2019; Mion *et al.*, 2020) or survival (Neuenfeldt *et al.*, 2020) of EBC have declined in size groups above 30 cm since the mid-1990s (Svedäng and Hornborg, 2017). We find no support for that this is driven by a decreased abundance of benthic prey, explaining the decline in benthic feeding as observed by Kulatska *et al.* (2019). In other words, low growth does not necessarily imply low feeding rates; it could also depend on the quality of the food (Litzow *et al.*, 2006). Food quality changes may affect EBC throughout a whole area, such as the southern Baltic Sea (c.f. Gorokhova, 2019, and the references therein). This conclusion is also in line with the observed *increased feeding rates* since around 2005, as indicated by the increased otolith nitrogen content (Svedäng *et al.*, 2020).

Conclusion

The decline in EBC production and productivity is related to two phenomena: (i) lower recruitment due to the loss of two out of three major spawning locations in the 1980s, and (ii) recent reductions in individual growth or increases in natural mortality.

We investigate the conditions for recruitment and growth/survival in EBC production by using the most comprehensive hydrographic data set for a longer time than previously available, combined, and modern 3D field modelling. Further, we add a unique compilation of studies on benthic fauna and biomass.

First, we find that the decline in spawning conditions started in the 1950s in the Gotland Deep due to oxygen depletion during stratified hydrographic conditions. We also find that during periods of a low rate of inflows, the RV disappeared temporarily in the Gdansk Deep in the 1980s due to lower salinity (freshening). We conclude that conditions suitable for reproduction have prevailed in the Bornholm Basin while only intermittently reoccurring in the Gdansk Deep. Further, we cannot expect EBC reproduction in the Gotland Deep before oxygen conditions have improved in the deepwater.

Second, this study shows no consistent connection between the extent of well-oxygenated/hypoxic area and the productivity or condition of EBC. In the stock's core distribution area in SD 25, the extent of well-oxygenated area/water column and benthos have remained unchanged over the last three decades when the productivity declined.

Supplementary Data

Supplementary material is available at the *ICESJMS* online version of the manuscript.

Author contribution

Authors' contributions. H.S. coordinated the study, H.S., C.H., O.S., B.G., S.A.W., A.N. and A.V. designed the research; O.S., C.H. and B.G. acquired the hydrographic data; A.N. and A.V. acquired the benthic data; H.S., O.S., A.N., and A.V. analysed the data, H.S., A.N., A.V., O.S., S.A.W., B.G., and C.H. wrote the paper. All authors gave their final approval for publication.

Data availability statement

Fishery data have been collected from referenced publications. Benthic data have been collected at the HERTTA database at the Finnish Environment Institute (<https://www.syke.fi/avoointieto>), the SHARK database at the Swedish Meteorological and Hydrological Institute (<https://www.smhi.se/data/oceanografi/datavardskap-oceanografi-och-marinbiologi/sharkweb>), and the ICES data portal (www.ices.dk). Salinity and oxygen data have been retrieved from the Baltic Environmental Database (BED, <http://nest.su.se/bed>) with DAS (<http://nest.su.se/das/>) and Nest (<http://nest.su.se/nest/>) tools; these data can also be retrieved online via distributed databases (<http://nest.su.se/dataPortal>) hosted by various Baltic Sea riparian countries. Presented hydrographical data are available in its online supplementary material.

Competing Interests

The authors declare that they have no conflict of interest.

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