Changes in population depth distribution and oxygen stratification are involved in the current low condition of the Eastern Baltic Sea cod (*Gadus morhua*)

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Abstract

During the past twenty years, hypoxic areas have expanded rapidly in the Baltic Sea, which has become one of the largest marine "dead zones" in the world. At the same time, the most important commercial fish population of the region, the Eastern Baltic cod, has experienced a drastic reduction in mean body condition, but the processes behind the relation between deoxygenation and condition remain elusive. Here we use extensive long-term monitoring data on cod biology and distribution as well as on hydrological variations, to investigate the processes that relate deoxygenation and cod condition during the autumn season. Our results show that the depth distribution of cod has increased during the past four decades at the same time of the expansion, and shallowing, of waters with oxygen concentrations detrimental to cod performance. This has resulted in a progressively increasing spatial overlap between the cod population and low-oxygenated waters after the mid-1990s. This spatial overlap and the actual oxygen concentration experienced by cod therein statistically explained a large proportion of the changes in cod condition over the years. These results complement previous analyses on fish otolith microchemistry that also revealed that since the mid-1990s, cod individuals with low condition were exposed to low-oxygen waters during their life. This study helps to shed light on the processes that have led to a decline of the Eastern Baltic cod body condition, which can aid the management of this population currently in distress. Further studies should focus on understanding why the cod population has moved to deeper waters in autumn and on analysing the overlap with low-oxygen waters in other seasons to quantify the potential effects of the variations in physical properties on cod biology throughout the year.

Keywords: hypoxia, fish body condition, direct exposure, depth distribution, cod *Gadus morhua*

1. Introduction

The oceans and marine coastal areas are experiencing dramatic deoxygenation worldwide (Breitburg et al., 2018). Declining oxygen can have multiple direct and indirect effects on aquatic organisms and entire ecosystems (Breitburg, 2002; Rabalais et al. 2002; Wu, 2002; Diaz and Rosenberg, 2008; Levin et al., 2009). In particular, studies undertaken both in the wild and within experimental set-ups have revealed large effects of hypoxia on basic metabolism, behavior, ecology, distribution and life-history traits of fish (Chabot and Dutil, 1999; Pichavant et al., 2001; Eby et al., 2005; Herbert and Steffensen, 2005; Domenici et al., 2007; Stramma et al., 2012).

The Baltic Sea (Fig. 1) is one of the largest brackish areas in the world where the oxygenated, yet scarce and irregular saline water inflows from the adjacent North Sea, combined with a water residence time of about 25–30 years, make the system particularly prone to hypoxia (Carstensen et al., 2014; Reusch et al., 2018). As a consequence, and in combination with global warming and eutrophication, the Baltic Sea has become one of the largest anthropogenic "dead zones" in the world (Breitburg et al., 2018), with degradation or elimination of benthic communities and disruption of benthic food webs over vast areas (Conley et al., 2009). In particular, since the early 1990s the anoxic and hypoxic areas have increased rapidly in the southern and central Baltic Sea (Carstensen et al., 2014) (Fig. 2).

In this degraded demersal and benthic environment, body condition (a morphometric index of fish fatness and well-being) of the dominant demersal fish population, the Eastern Baltic cod *Gadus morhua* (hereafter simply referred to as Baltic cod), has declined since the mid-1990s (Casini et al., 2016a). This decline was also stressed by the fishery that suffered from an increasingly high proportion of catches of lean cod with low economic value. Low condition has a negative effect on reproductive potential (Mion et al., 2018), mortality (Casini et al., 2016b) and potentially also movements (Mehner and Kasprzak, 2011) with indirect effects on prey and therefore food-web structure and ecosystem functioning as shown in other systems (e.g. Ekau et al., 2010). Therefore, it is very important to understand the ultimate factors leading to low cod condition.

The decline in the Baltic cod condition has been related to a decrease in the main pelagic prey abundance in the main distribution area of cod (Eero et al., 2012; Casini et al., 2016a) and increased parasite infestation (Horbowy et al., 2016), but also to the increased extent of hypoxic and anoxic areas (Casini et al., 2016a). The mechanistic processes linking hypoxia and cod conditions could be various and not mutually exclusive, including stress due to direct hypoxia exposure, suitable habitat contraction and consequent change in cod spatial distribution, and change in the surrounding biota such as reduction of important benthic prey (Casini et al., 2016a). Limburg and Casini (2019), using otolith microchemistry, showed that fish in low condition at capture were exposed during their lives to lower oxygen levels than those in good condition (at least from the mid-1990s), suggesting that direct exposure to low-oxygen waters could constitute a key factor. However, Limburg and Casini (2019) did not analyse the spatial distribution of the cod population in relation to low-oxygen layers, and therefore whether or not a large part of the population indeed experienced stressful circumstances, which could explain the decline in mean population condition found by Casini et al. (2016a).

In this study, we fill this gap and specifically analyse the temporal changes in the depth distribution of cod, from long-term monitoring data, in relation to the actual oxygen levels experienced by the cod population and the oxygen levels acknowledged in literature to affect cod behavior and performance.

2. Materials and methods

2.1 Biological data and estimation of cod condition

Biological data on Eastern Baltic cod individuals (n = 124 165) were collected during the Baltic International Trawl Survey, BITS, between 1991 and 2018 (retrieved from the DATRAS database of the International Council for the Exploration of the Sea, ICES; www.ices.dk; downloaded 28 January 2020) and previous Swedish and Latvian bottom trawl surveys performed in 1979-1990 in the Baltic Sea (Casini et al., 2016a). Cod individual body condition (Fulton's K) was estimated as $K = W/L^3 * 100$, where W is the total weight (g) and L the total length (cm, typically measured from the tip of the snout to the tip of the longer lobe of the caudal fin) of the fish. Mean condition was estimated for ICES

Subdivision (SD) 25 (corresponding to the main distribution area for Eastern Baltic cod since the early 1990s, Orio et al., 2017) and SDs 26-28 separately, updating the time-series in Casini et al. (2016a). More northern SDs were not included due to their low and inconsistent survey coverage through the years. Condition for small fish (represented here by the size-class 20-29 cm) and large fish (represented here by the size-class 40-49 cm) were used in the analyses, as cod change diet during its ontogeny and these two size-classes differ in feeding habits (Neuenfeldt et al., 2020). We could not use smaller and larger size-classes because of their scarcity in the BITS survey catches. The small size-class could also be considered as representing juvenile fish (Eero et al., 2015; ICES, 2017a) although, from around 2005, the mean length at first maturity has decreased below 30 cm (Köster et al., 2017). Years with < 25 observations for the respective length-classes and areas were excluded from the analyses. We focused on cod condition in autumn (quarter 4 BITS survey, from mid-October to mid-December), corresponding to the cod main growth season after spawning in spring-summer (Mion et al., 2020). Moreover, for the autumn season, long time-series of oxygen levels and extent of hypoxic areas are also available (Casini et al., 2016a).

2.2 Estimation of cod depth distribution

Indices of cod biomass (calculated as catch-per-unit-effort, CPUE, kg/h, herein referred to as biomass) and depth distribution (i.e. mean depth and interquartile range of predicted depth distribution) from the BITS and historical bottom trawl surveys in SDs 25-28 from 1979 to 2018 were estimated for large (≥ 30 cm) and small cod (< 30 cm) using a modelling procedure similar to the one used in Orio et al. (2019). However, in the current study rather than including environmental variables in the models, quarter was included in interactions with latitude and longitude, and with depth. To estimate the changes in cod depth distribution in SDs 26-28 that account for the changes in the spatial distribution of the cod population, the SD-specific depth distributions were weighted by the annual SD-specific cod CPUEs from the bottom trawl surveys in quarter 4, estimated from the same model, for large and small cod.

2.3 Depth of hypoxic layers

Baltic cod has been shown to avoid oxygen concentrations below 1 ml/l (approximately 1.4 mg/l) (Schaber et al., 2012). Therefore, time-series of the depth at which 1 ml/l oxygen concentration was encountered by SD were obtained from the Swedish Meteorological and Hydrological Institute (SMHI, www.smhi.se).

Time-series of depth at which 4.3 ml/l oxygen concentration (approximately 6 mg/l) was encountered by SD were also obtained from SMHI. This oxygen concentration, on average, has been found to affect the performance of fish (Vaquer-Sunyer and Duarte, 2008). Specifically for cod, 4.3 ml/l has been found as threshold from which an effect on condition and growth starts to be observable (Chabot and Dutil, 1999). Therefore, we expected that the occurrence of cod in areas and depths with an oxygen concentration ≤ 4.3 ml/l would lead to an increase in the proportion of cod individuals with very low condition ($K < 0.8$; Eero et al., 2012) and a decrease in mean condition in the population. To relate the depths at which 1 ml/l and 4.3 ml/l oxygen concentrations were encountered to cod depth of occurrence in SDs 26-28, the oxygen depths in each SD were weighted with the annual SD-specific cod CPUEs from the bottom trawl surveys in quarter 4, for large and small cod. In this way, the oxygen circumstances in the SDs where cod was more abundant were weighted the most.

2.4 Depth overlap between cod and hypoxic layers, and oxygen experienced by cod

We estimated the overlap (% meters) between the cod depth range of distribution and the water layer with oxygen concentration ≤ 4.3 ml/l, as estimated above, in both SD 25 and SDs 26-28. We also reconstructed the time-series of the oxygen concentrations at the mean depth and interquartile range of the cod depth distribution in each SD (data from SMHI). Also in this case, for SDs 26-28 the oxygen concentrations in each SD were weighted with the annual SD-specific cod CPUEs from the bottom trawl surveys in quarter 4, for large and small cod.

2.5 Modelling of cod condition versus oxygen

To formally analyse the effect of the depth overlap and oxygen concentrations experienced by cod on cod condition, we used generalized additive models (GAMs; Hastie and Tibshirani, 1990). The following additive formulation was used:

Condition ~ s (*Depth overlap*) + s (*Oxygen experienced*) + ε

where *Depth overlap* is the overlap between the cod depth range of distribution and the water layer with an oxygen concentration ≤ 4.3 and *Oxygen experienced* is the actual oxygen level corresponding to the cod depth distribution (we used for this the oxygen corresponding to the deeper interquartile of the cod depth range of distribution). *s* is the thin plate smoothing spline function and *ε* is random error. We limited the maximum degrees of freedom acceptable for each term to k=4, which retains model flexibility and allows at the same time an ecological interpretability of the results. A Gamma distribution with an identity function was used. Residuals were inspected for deviation from the assumption of normality and no autocorrelation using graphical methods (Cleveland, 1993). The statistical analyses were performed using the mgcv library of R v. 4.0.2 (www.r-project.org). The significance level was set to α =0.05 for all tests.

3. Results

3.1 Cod condition

Cod condition increased slightly between the mid-1970s and mid-1990s but declined abruptly thereafter. This pattern was similar in SD 25 and SDs 26-28 for both large and small cod (Fig. 3), but after the mid-1990s condition dropped more for large cod (~30% for large cod and 20-25% for small cod). The percentage of large fish with very low condition (< 0.8, see Eero et al., 2012) increased from the end of the 1990s in both SD 25 and SDs 26-28 reaching in recent years 30-40%. The percentage of small fish with low condition also increased, but lagged temporally behind the large cod, and at 10-20% of observations was lower than the high incidences of large cod in poor condition (Fig. 3). In general, in SD 25 condition declined slightly more (and the percentage of fish with very low condition increased more) than in SDs 26-28 after the mid-1990s.

3.2 Cod depth distribution

Large cod in SD 25 were distributed between 35 and 50 m depth (average 43 m) at the beginning of the time-series, but have been found in somewhat deeper waters (down to 40-60 m, average 50 m) from the early 2000s (Fig. 4a). In SDs 26-28 large cod were distributed between 35 and 55 m depth (average 45 m) at the beginning of the time-series, whereas after the mid-1990s they became distributed between 50 and 75 m depth (average 62 m) (Fig. 4c). Along with the change in mean depth, large cod in SDs 26-28 have shown a contraction of the range of depth distribution in the past 20 years. Small cod were distributed somewhat shallower than the large fish, but also moved into deeper waters during the time period investigated. In SD 25, small cod shifted distribution from between 30 and 50 m depth (average 40 m) to 45-60 m depth (average 53 m) (Fig. 5a). In SDs 26-28 small cod moved deeper with time as well, from 30-50 m depth (average 40 m) to 45-65 m depth (average 55 m), and experienced a contraction of the range of depth distribution similar to what occurred for the large fish in this area (Fig. 5c).

3.3 Depth of hypoxic layers

The depth at which 1 ml/l was encountered remained fairly constant at around 70 m in SD 25, while in SDs 26-28, it decreased from below 120 m to around 80 m over the past 20 years (Fig. 4a,c and 5a,c). Over the same time period, the depth at which 4.3 ml/l was encountered diminished in SD 25 from ~ 60 m to ~ 50m, and in SDs 26-28 the 4.3 ml/l threshold shifted from ~ 80 m to ~ 60 m since the early 1990s (Fig. 4a,c and 5a,c). The oxygen depths in SDs 26-28, accounting for the SD-specific distribution of the cod, did not differ much between large and small cod (note the slightly different patterns in the oxygen depths between Fig. 4c and Fig. 5c, which is due to the different distribution of small and large cod among these three SDs).

3.4 Depth overlap between cod and hypoxic layers, and oxygen experienced by cod

Large cod depth distribution never overlapped with the depth of oxygen ≤ 1 ml/l along the time period analysed, except in the very last year in SD 25 (Fig. 4a,c). On the other hand, large cod distribution heavily overlapped with the depth with oxygen ≤ 4.3 ml/l since the mid-1990s (Fig. 4a,c) and the overlap, although oscillating, increased in the past twenty years reaching values higher than 90% in SD 25 and higher than 80% in SDs 26-28 (Fig. 4b,d).

Also small cod distribution never overlapped with depth with oxygen ≤ 1 ml/l along the time period analysed, except in the very last year in SD 25 (Fig. 5a,c). On the other hand, small cod distribution overlapped with the depth with oxygen ≤ 4.3 ml/l since early-2000s (Fig. 5a,c) and the overlap, although oscillating, increased in the past fifteen years reaching values higher than 90% in SD 25 and up to 50% in SDs 26-28 (Fig. 5b,d).

The actual oxygen concentrations experienced by cod changed extensively during the study period. Large cod in SD 25 experienced oxygen concentrations of 5-7 ml/l (average ~ 6.5 ml/l) during the late 1970s and early 1980s, while especially from the mid-1990s a decline, paralleled by a widening of the experienced oxygen range, occurred until reaching values of 2.5-5.5 ml/l (average ~ 4 ml/l). Similar patterns occurred also in SDs 26-28 although the oxygen at the lower interquartile range of the cod depth distribution declined further down to be close to 1 ml/l (Fig. 4b,d).

Small cod in SD 25 experienced oxygen concentrations of 6-7.5 ml/l (average ~ 7 ml/l) during the late 1970s and early 1980s, while especially from the late-1990s a decline, paralleled by a widening of the experienced oxygen range, occurred until reaching values of 3-6 ml/l (average ~ 4 ml/l). Similar patterns occurred also in SDs 26-28 although the oxygen experienced in the latest years was relatively better than in SD 25, being 3.5-6.5 ml/l (average ~ 5 ml/l) (Fig. 5b,d).

3.5 Modelling of cod condition versus oxygen

The GAMs explained 68.3 % and 61.8 % of the total deviance, for large and small cod, respectively (see the caption of Fig. 6 for more statistics). For both models, *Oxygen experienced* by cod was the most important predictor of condition, while *Depth overlap* explained a minor part of the model deviance. For large cod, the effect of *Oxygen experienced* was positive and seemed to reach an asymptote at around 5 ml/l (Fig. 6a), while for the small cod this was not the case with a positive effect over the whole range of the experienced oxygen (Fig. 6b). *Depth overlap* was negatively correlated to condition, although this effect was much stronger for the large cod (Fig. 6a,b). The residuals of the models did not strongly violate the normality and homogeneity assumptions and were not autocorrelated (Fig. S1). The use of GAMs with an interactive formulation (i.e. *Depth overlap* and *Oxygen experienced* used in interaction) explained a similar amount of deviance (69.4 % and 62.1 %, for large and small cod, respectively).

4. Discussion

In this paper, we analysed the potential mechanisms relating Baltic Sea deoxygenation with changes in Eastern Baltic cod body condition during the past four decades. To this end, we investigated the changes in depth distribution of the cod population and the vertical changes in oxygen gradients based on long-term biological and hydrological monitoring data. Moreover, we related the results of these analyses with proxies for hypoxia exposure from individual fish otolith microchemistry recently published in literature.

4.1 Cod depth distribution and overlap with hypoxic layers

Our analyses show an increase in the areas with an oxygen level below cod tolerance (i.e. oxygen concentration ≤ 1 ml/l; Schaber et al., 2012). Moreover, this oxygen threshold has also shifted with time towards shallower depths, determining an overall contraction of the potentially suitable habitat for cod (Casini et al., 2016a). Declines in oxygen concentrations have caused a contraction of the habitat and the distribution of fish in other systems (Eby and Crowder, 2002; Stramma et al., 2012; Breitburg et al., 2018) with measurable effects on, for example, individual growth (e.g. Campbell and Rice, 2014). In the Baltic Sea, however, this change seems not to have affected the cod depth distribution in autumn, since the latter has been always above 70-75 m, a depth only almost never reached by the waters with oxygen concentration ≤ 1 ml/l. On the other hand, it could be hypothesized that during the latest decade the cod population was unable to occupy even deeper habitats because of the vertical rise of this oxygen layer. This hypothesis seems to be supported by the decline in the range of depth distribution (i.e. a squeeze of the cod habitat occupation) shown by both large and small cod in SDs 26-28 during the past twenty years. Explaining the temporal changes in the depth distribution of cod is beyond the scope of this paper, but a potential reason could be that cod seek deeper layers to avoid too warm waters, which could be detrimental when resources are scarce. In fact, pelagic prey have declined after the mid-1990s in the southern and central Baltic Sea (Casini et al., 2016a) and therefore cod might go deeper to optimize metabolism. Small cod, moreover, could seek deeper waters to escape from the predation of the increased seals and aquatic birds (Orio et al., 2019). The temporal patterns revealed by our study for quarter 4 generally conform to what found by Orio et al. (2019) for quarter 1. However, the increased depth distribution of large cod in SDs 26-28 found in our study in quarter 4 contrasts with findings in the same areas in quarter 1, where a shallowing has instead been observed since the mid-1990s after an initial deepening (Orio et al., 2019). In quarter 1 cod is in general distributed deeper than in quarter 4 (Orio et al., 2019 and this study, respectively) and it could be that in quarter 1, when the water is also less stratified, large cod were able to dwell in exceptionally deep layers in the mid-1990s because of the good oxygen circumstances during that period (Carstensen et al. 2014; this study). A different requirements that the large mature fish have for their maturation and successful reproduction when they approach spawning in late spring (Røjbek et al., 2012) could potentially also contribute to the difference in the temporal patterns of distribution between the quarters.

The depth where oxygen concentration falls to ≤ 4.3 ml/l (“sub-lethal” level, i.e. level that has been shown in previous studies to affect cod performance; Chabot and Dutil, 1999; Vaquer-Sunyer and Duarte, 2008) has shallowed during the past four decades, as a consequence of deoxygenation. Our analysis revealed that this vertical rise, together with the deepening of the cod depth distribution, has resulted in that cod has started to dwell more and more in these hostile low-oxygen waters. The depths at which cod has been dwelling during the past two decades correspond to the depths of the Baltic Sea permanent stratification where the oxygen drops quickly, explaining the wider range of oxygen concentrations that cod has experienced during this period. Moreover, our analysis reveals that the oxygen concentrations that the cod population indeed experienced has progressively decreased until approaching the 1 ml/l at the lowest boundary of its distribution (tolerance level, i.e. level that has been shown in previous studies to be avoided by cod; Schaber et al., 2012). The overlap between cod depth distribution and “sub-lethal” oxygen layers occurred mainly after the mid-1990s, concomitant with the drop in cod condition, while in earlier years the cod population was occurring mostly above those layers. The progressively higher proportion of the cod population in “sub-lethal” oxygen layers after the mid-1990s, as revealed by our study, conforms also to the increasingly higher proportion of individuals in extremely low condition (< 0.8 Fulton’s K), which include starving fish and fish close to the condition mortality threshold (Eero et al., 2012; Casini et al., 2016b).

4.2 Relation to otolith microchemistry from literature

Limburg and Casini (2019) using otolith microchemistry recently found that Baltic cod with low condition at capture experienced during their lives lower oxygen levels than cod with high condition. However, Limburg and Casini (2019) did not analyse to what extent the cod population indeed experienced low-oxygen levels, and therefore whether the exposure to low-oxygen waters could explain the decline in the mean condition of the cod population. Our study did this, showing that a large part of the population has dwelled in sub-lethal low-oxygen levels after the mid-1990s in quarter 4. Together, the individual-based study by Limburg and Casini (2019) and the population-level present study provide consistent and robust indications that the decline in mean cod condition of the population from the mid-1990s is due to an increased overlap with low-oxygen layers. This suggests that currently condition may carry over from chronic exposure to low oxygen concentrations, which weakens fish and produces a cascade of effects, from reduced metabolic scope leading to lower activity and slower digestion (Claireaux and Chabot, 2016), to greater susceptibility to disease and parasites (e.g., Sokolova et al., 2018). Both Limburg and Casini (2019) and the present study also revealed that the exposure to hypoxic waetrs was lower in the period before the mid-1990s, and was unrelated to cod condition confirming that, before the mid-1990s, factors other than direct low-oxygen exposure played a greater role in shaping cod condition as concluded also by Casini et al. (2016a).

4.3 Mechanisms shaping cod condition

We have confirmed here, using population-level monitoring data, that direct oxygen exposure is likely a key factor shaping cod condition after the mid-1990s (Limburg and Casini, 2019). Low-oxygen exposure has been shown in laboratory experiments to reduce cod appetite with consequent significant decline in body condition and growth (Chabot and Dutil, 1999). This seems to conform to the observation of a decline in Eastern Baltic cod feeding level from stomach content analyses (Neuenfeldt et al., 2020) that has been put earlier in relation with cod growth by Brander (2000). Therefore, a lower appetite due to an increased direct exposure to low-oxygen waters seems to be a sound explanation to both the decline in growth (Brander 2000) and condition (this study). In our estimations of cod overlap with sub-lethal waters we considered the oxygen thresholds affecting cod performance as found in laboratory experiments performed on relatively large fish (~ 45 cm, Chabot and Dutil, 1999). Interestingly, in our statistical analysis the inflection of the curve relating the actual oxygen experienced and condition for large cod (40-49 cm in our study) started to occur at ~ 4.5-5 ml/l, corresponding well to the threshold found experimentally in Chabot and Dutil (1999). The threshold for small fish could be however higher, although a size-dependent hypoxia tolerance in fish is still debated (Vaquer-Sunyer and Duarte, 2008; Nilsson and Östlund-Nilsson, 2008). This could however explain why in our statistical analysis the effect of oxygen experienced on small cod condition was linear without reaching an asymptote at high oxygen concentrations. In this case our assumption of a 4.3 ml/l sub-lethal threshold for small cod could be considered very conservative.

Beside direct exposure to sub-lethal oxygen levels, other factors, not mutually exclusive, might contribute to explain the decline in condition as well (Casini et al., 2016a). For example deoxygenation, by deteriorating the benthic communities, has likely affected important benthic prey for cod in negative ways, and therefore also influenced indirectly cod condition and growth (Neuenfeldt et al., 2020). Moreover, the more severe decline in condition in SD 25 compared to SDs 26-28, for example, could be due to the higher density of cod in the southern Baltic Sea during the past twenty years (Orio et al., 2017) leading to density-dependent effects, and the lower abundance of sprat, the main pelagic fish prey for cod, in this area (Casini et al., 2014). Additional potential reasons of the decline in cod condition after the early 1990s are constituted by the increased biomass of flounder that could have deprived cod of important benthic food resources (Haase et al., 2020) and increased parasite infestation (Horbowy et al., 2016). All these factors could have acted, singularly or in combination, on cod together with direct low-oxygen exposure shaping the decline in its condition observed in the past three decades. Moreover, cod condition was relatively low also in the 1970s-1980s (although not showing individuals with very low condition, Fig. 2), when the cod population did not seem to spend time in low-oxygen waters, confirming that the main drivers of mean condition can vary in time.

4.4 Conclusions

We have shown here the potential mechanisms linking deoxygenation to cod condition in the Baltic Sea. A combination of increased depth distribution of the cod population and a vertical rise of the "sub-lethal" oxygen layers has led cod dwelling progressively more in hostile low-oxygen waters, contributing to explain the reduction in cod condition in the past two decades. Further analyses should focus on revealing the reasons of the shift of cod distribution to deeper and less-oxygenated waters. We stress that our depth analyses were focused on the autumn season, when cod growth is maximised for the accumulation of energy reserves to be utilized for spawning the following spring-summer (Mion et al., 2020). The changes in cod depth distribution are different in other seasons, especially those before and during spawning (Orio et al., 2019), when cod could have different environment requirements for reproduction. Therefore, further analyses should be performed to investigate the changes in cod population depth distribution in relation to oxygen stratification in other seasons to better understand the biotic and abiotic spatio-temporal dynamics, and their effects on cod performance, over the entire year.

Data availability

Time-series used in this study are available upon request to the corresponding author.

Author contribution

MC designed and coordinated the study. MC, MH, AO and KL prepared the raw data. MC estimated cod condition, MH performed the hydrographic modelling, and AO performed the cod distribution modelling. MC prepared the first draft of the manuscript and all authors contributed to the final version.

Competing interests

The authors declare that they have no conflict of interest.

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Figure captions

Figure 1. Bathymetric Map of the Baltic Sea divided into ICES Subdivisions (SDs). The study area includes the SDs 25–28 (i.e. the Central Baltic Sea).

Figure 2. Maps of the Baltic Sea with superimposed the areas with oxygen concentration ≤ 1 ml/l (black, avoided by cod) and ≤ 4.3 ml/l (grey, sub-lethal level, producing negative effects on cod performance) in (**a**) 1990 and (**b**) 2018. Time-series of the total area (km^2) with oxygen concentration ≤ 1 ml/l and ≤ 4.3 ml/l in the Subdivisions 25-28 (**c**). Data were from the Swedish Meteorological and Hydrological Institute (SMHI, www.smhi.se) (see also Casini et al., 2016a).

Figure 3. Temporal developments of mean cod condition (± 1 s.d.) in Subdivision (SD) 25 and SDs 26-28 for (**a, c**) large cod (40–49 cm) and (**b, d**) small cod (20-29 cm). Superimposed (grey bars) the temporal developments of the percentage of cod with very low condition (< 0.8) for the respective areas and length classes.

Figure 4. Time-series of large cod (≥ 30 cm) depth distribution (mean and interquartile range of each predicted depth distribution; see Orio et al., 2019) as well as depths of oxygen concentration 1 ml/l and 4.3 ml/l, for (**a**) Subdivision (SD) 25 and (**c**) SDs 26-28. Time-series of the depth overlap (i.e. overlap between large cod depth range of distribution and the depth of the water layer with oxygen concentration ≤ 4.3 ml/l) (grey bars), and oxygen at the mean depth and interquartile range of large cod distribution (solid line and dotted lines), in (**b**) SD 25 and (**d**) SDs 26-28.

Figure 5. Time-series of small cod (< 30 cm) depth distribution (mean and interquartile range of each predicted depth distribution; see Orio et al., 2019) as well as depth of oxygen concentration 1 ml/l and 4.3 ml/l, for (**a**) Subdivision (SD) 25 and (**c**) SDs 26-28. Time-series of the depth overlap (i.e. overlap between small cod depth range of distribution and the depth of the water layer with oxygen concentration ≤ 4.3 ml/l) (grey bars), and oxygen at the mean depth and interquartile range of small cod distribution (solid line and dotted lines), in (**b**) SD 25 and (**d**) SDs 26-28.

Figure 6. Results of the General Additive Models (GAMs). The plots show the partial effects of the depth overlap (i.e. overlap between cod depth range of distribution and the depth of the water layer with

oxygen concentration ≤ 4.3 ml/l) and of the actual oxygen experienced (at the lowest interquartile of the cod depth range of distribution) on cod condition, for (**a**) large cod and (**b**) small cod. Blue and red dots represent Subdivision (SD) 25 and SDs 26-28, respectively. Statistics for large cod (**a**): *Depth overlap* (edf = 1.00; F = 6.46; p = 0.01), *Oxygen experienced* (edf = 2.86; F = 10.88; p < 0.00001). Statistics for small cod (**b**): *Depth overlap* (edf = 1.30; F = 0.82; p = 0.55), *Oxygen experienced* (edf = 1.51; F = 17.60; p < 0.00001). See Fig. S1 and S2 for the analysis of the residuals.

Figure 1

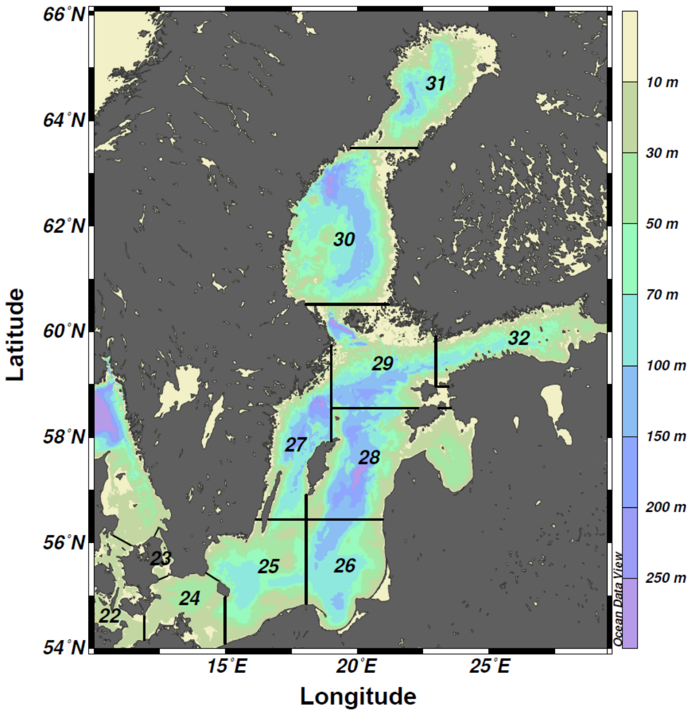

66°N
64°N
62°N
60°N
58°N
56°N
54°N
Latitude
15°E
20°E
25°E
Longitude
31
30
32
29
27
28
23
25
26
24
22
10 m
30 m
50 m
70 m
100 m
150 m
200 m
250 m
Ocean Data View

Figure 2

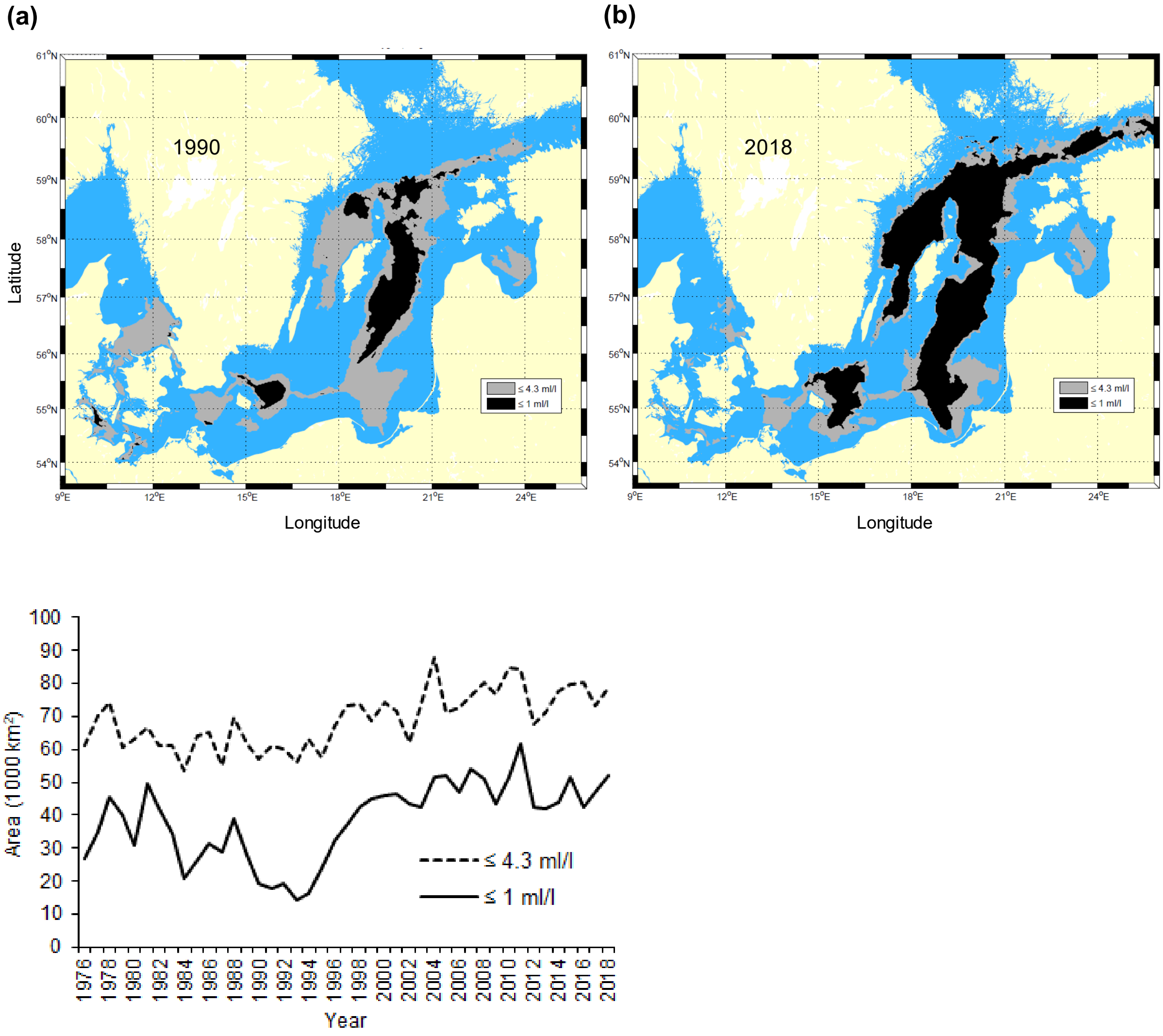

(a)
(b)
1990
2018
61°N
60°N
59°N
58°N
57°N
56°N
55°N
54°N
9°E
12°E
15°E
18°E
21°E
24°E
Latitude
Longitude
≤ 4.3 ml/l
≤ 1 ml/l
100
90
80
70
60
50
40
30
20
10
0
Area (1000 km²)
1976
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
2016
2018
Year
≤ 4.3 ml/l
≤ 1 ml/l

Figure 3

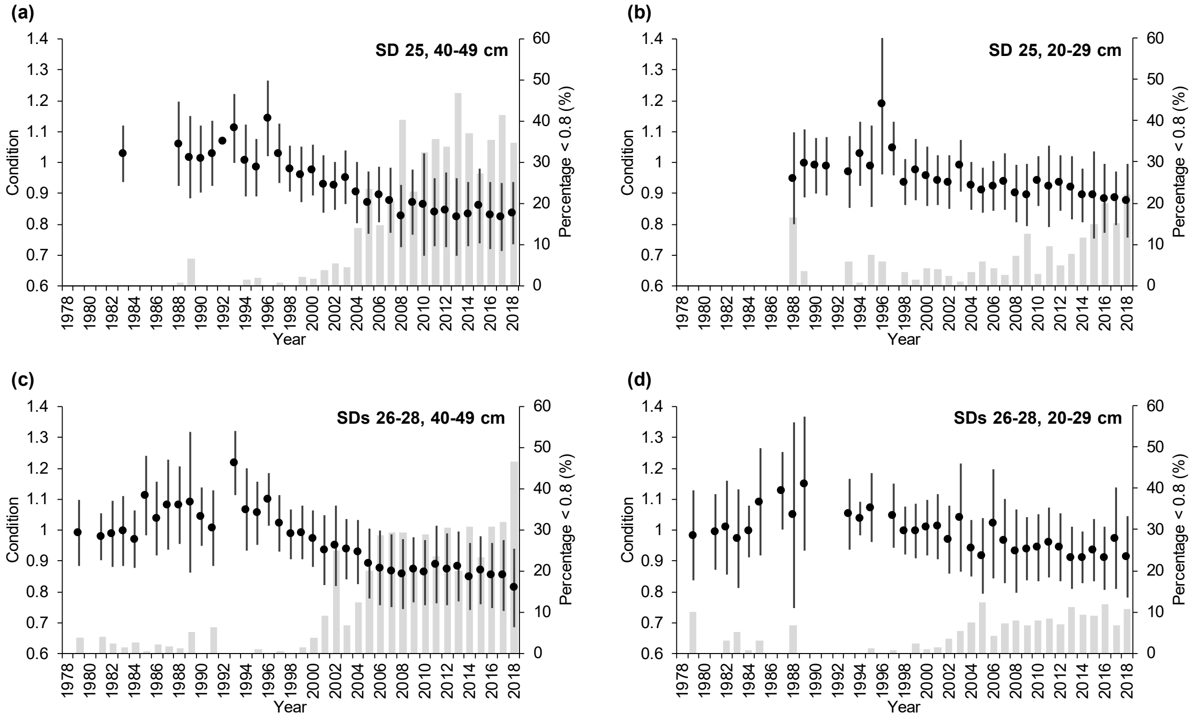

(a)
SD 25, 40-49 cm
(b)
SD 25, 20-29 cm
(c)
SDs 26-28, 40-49 cm
(d)
SDs 26-28, 20-29 cm
Condition
Percentage < 0.8 (%)
Year
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
60
50
40
30
20
10
0
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
2016
2018

Figure 4

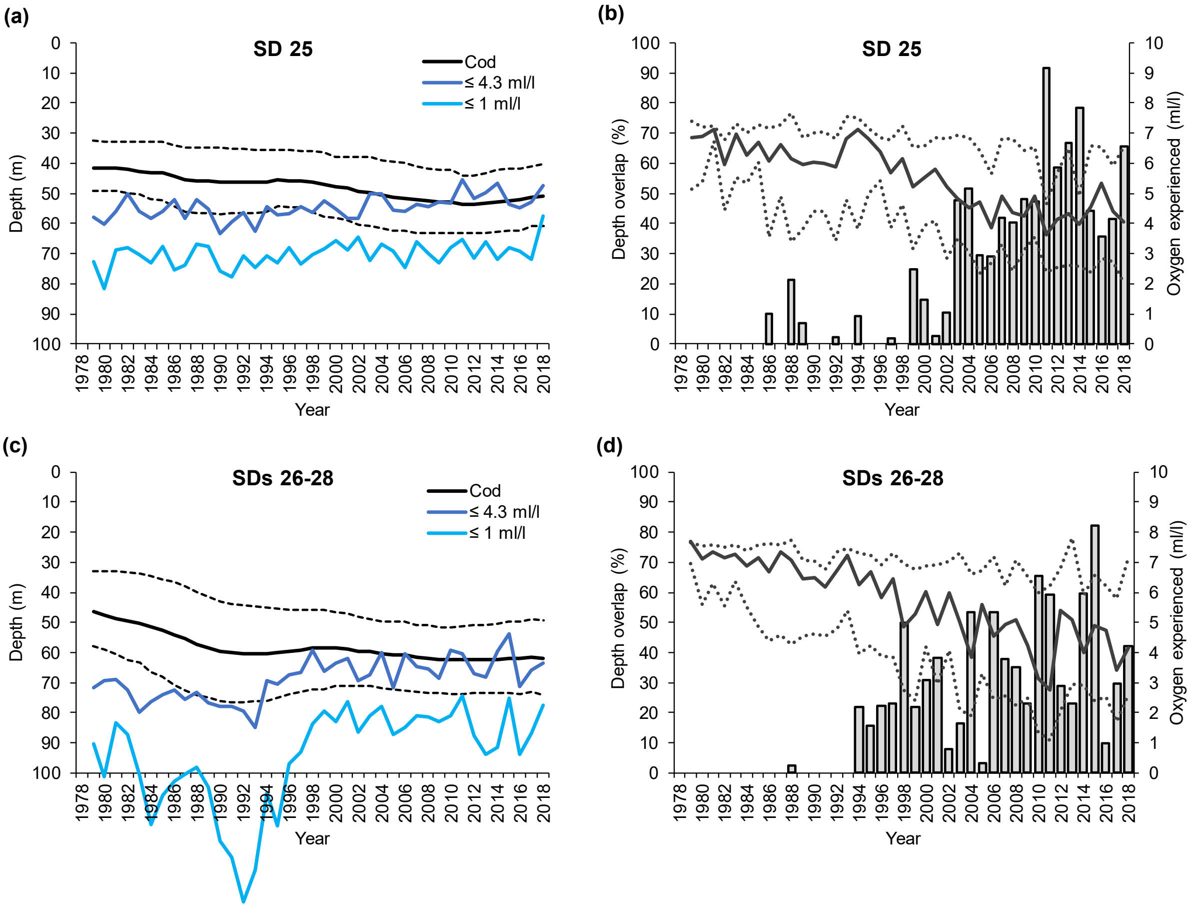

(a)
SD 25
Cod
≤ 4.3 ml/l
≤ 1 ml/l
Depth (m)
0
10
20
30
40
50
60
70
80
90
100
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
2016
2018
Year
(b)
SD 25
Depth overlap (%)
Oxygen experienced (ml/l)
Year
(c)
SDs 26-28
Cod
≤ 4.3 ml/l
≤ 1 ml/l
Depth (m)
Year
(d)
SDs 26-28
Depth overlap (%)
Oxygen experienced (ml/l)
Year

Figure 5

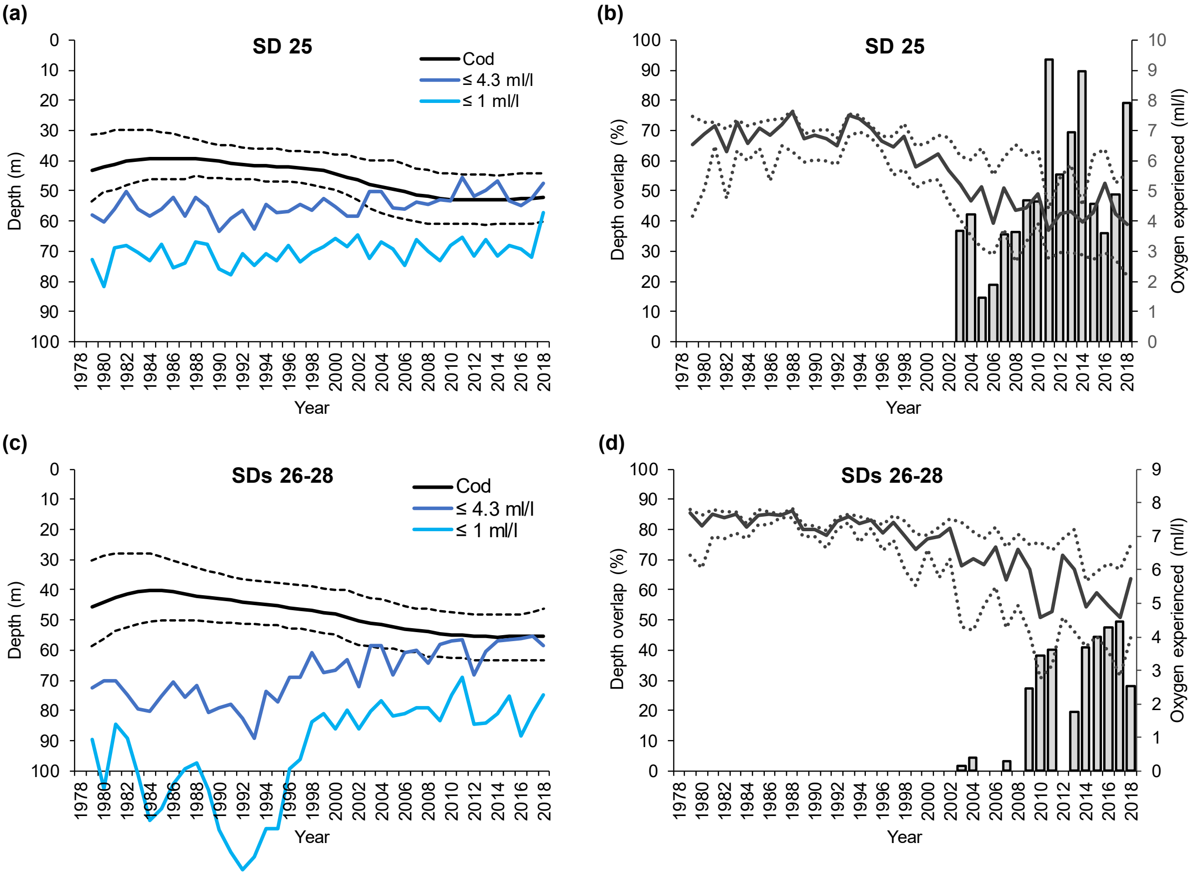
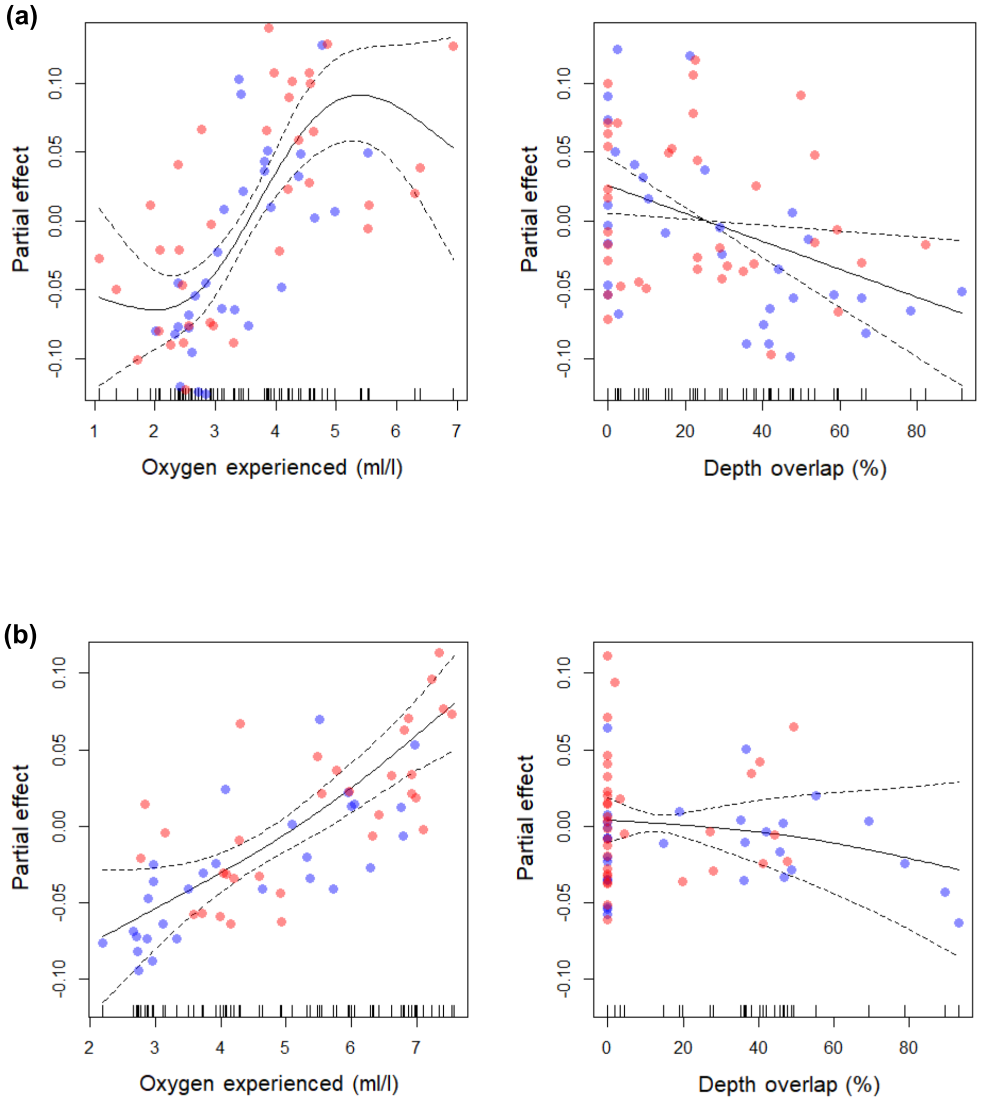

(a)
SD 25
Cod
≤ 4.3 ml/l
≤ 1 ml/l
Depth (m)
0
10
20
30
40
50
60
70
80
90
100
Year
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
2006
2008
2010
2012
2014
2016
2018
(b)
SD 25
Depth overlap (%)
Oxygen experienced (ml/l)
0
1
2
3
4
5
6
7
8
9
10
Year
(c)
SDs 26-28
Cod
≤ 4.3 ml/l
≤ 1 ml/l
Depth (m)
Year
(d)
SDs 26-28
Depth overlap (%)
Oxygen experienced (ml/l)
Year

Figure 6


(a)
Partial effect
-0.10
-0.05
0.00
0.05
0.10
1
2
3
4
5
6
7
Oxygen experienced (ml/l)
Partial effect
0
20
40
60
80
Depth overlap (%)
(b)
Partial effect
2
3
4
5
6
7
Oxygen experienced (ml/l)
Partial effect
0
20
40
60
80
Depth overlap (%)