

Evaluating drivers of spatiotemporal changes in the condition of Eastern Baltic cod

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Le Cren's condition index, Weight at length, Spatial analysis, Spatio-temporal models, Density dependence, Predator-prey overlap, Deoxygenation

Abstract

The body condition of a fish describes the weight given its length and is often positively associated with fitness. Atlantic cod (*Gadus morhua*) in the south-eastern Baltic Sea has experienced a drastic deterioration of its physiological status since the early 1990s to levels that compromise the growth of the population. Several hypotheses have been proposed in the literature (competition, hypoxia, lack of prey), however, despite operating on small spatial scales, these variables have only been evaluated temporally on large spatial scales (basin- or population level). By applying a geostatistical model that includes spatially and spatiotemporally correlated random effects using Gaussian Markov random fields, we analyze changes in cod condition in relation to biotic and abiotic covariates at different scales and their spatiotemporal distribution. We find that the body condition declined in the whole domain until 2008, after which a plateau was reached. The decline occurred for cod of all sizes, and upper and lower quantiles of the distribution of Le Cren's condition indices declined at the same rate. Oxygen, sprat biomass (at the sub-division level), temperature and saduria biomass (to a lesser extent) were positively related to condition, whereas density of cod and depth-at-catch were negatively associated with condition. However, even though the biomass-weighted overlap with sprat and have decreased over time, and cod are now on average at deeper and less oxygenated waters, the effects sizes of these variables were small, and could not alone explain the steep decline that occurred between 1993–2008. In fact, residual spatial and spatiotemporal variation were several times larger in magnitude than any single covariate's coefficient, suggesting there is still considerable variation unexplained by covariates. Understanding the drivers of spatiotemporal variation in body condition, which affects mortality and reproduction, is important for understanding the impacts of environmental change and for the management of marine fishes.

Introduction

The body condition is a morphometric index that describes the “plumpness” of an organism, or its weight relative to its length. Body condition is related to food intake rates and metabolic activity, and often positively associated with fitness (Morgan *et al.*, 2010; Thorson, 2015). In fishes, individuals with high condition have greater reproductive potential and success (Hislop *et al.*, 1978; Marshall and Frank, 1999), and poor condition increases the likelihood of skipped spawning (Jørgensen *et al.*, 2006; Mion *et al.*, 2018) and can lower chances of survival (Dutil and Lambert, 2000; Casini *et al.*, 2016b). Hence, body condition constitutes a valuable index for evaluating changes in productivity of fish stocks from ecosystem changes (Thorson, 2015; Grüss *et al.*, 2020).

Because of the link to food consumption, interannual variation in condition is often associated with changes in the strength of competition for food, via changes in density of the population, competitors, or prey species (Cardinale and Arrhenius, 2000; Casini *et al.*, 2006; Thorson, 2015; Grüss *et al.*, 2020). It has also been linked to environmental conditions, (e.g., temperature, salinity) affecting ecosystem productivity and local habitat quality (Möllmann *et al.*, 2003; Morgan *et al.*, 2010; Thorson, 2015; Grüss *et al.*, 2020). More recently, studies have found a link between declining body condition and deoxygenation (expansion of dead zones causing habitat degradation and compression) (Casini *et al.*, 2016a, 2021), fueled by warming and nutrient enrichment (Diaz, 2001; Breitburg, 2002; Diaz and Rosenberg, 2008; Carstensen *et al.*, 2014). However, reduced oxygen concentrations also cause lower food intake rates due to lower metabolic rates, which can occur even during milder hypoxia (Kramer, 1987; Chabot and Dutil, 1999; Claireaux *et al.*, 2000; Hrycik *et al.*, 2017; Brander, 2020; Sampaio *et al.*, 2021). As both environmental and biological variables can affect condition, it is important to study their relative contribution to variation in condition in a common framework.

Modelling fine-scale ecological data tends to result in correlated residuals, as these data are spatially and temporally correlated. Recently, spatiotemporal models been applied to study variation in fish condition (Thorson, 2015; Grüss *et al.*, 2020). In these studies, spatially correlated residual variation was accounted for with spatial random effects through Gaussian random fields in a GLMM (generalized linear mixed-effects model) framework. This approach to model spatiotemporal data is an increasingly popular method for explicitly accounting for spatial and spatiotemporal variation — likely due to its ability to improve predictions of fish density (Thorson *et al.*, 2015a) and range shifts (Thorson *et al.*, 2015b), and its availability in standard open source software such as the R-packages ‘INLA’, ‘VAST’ (Thorson, 2019) or ‘sdmTMB’ (Anderson and Ward, 2019; Anderson *et al.*, 2021; Barnett *et al.*, 2021). In the first such application to body condition, Thorson (2015) found that spatial processes (spatial variation in condition that is constant in time) and spatiotemporal processes (spatial variation that varies among years) explained more variation than demersal CPUE and temperature covariates, respectively, in the California current ecosystem. Studies such as these reveal the importance of accounting for latent spatial and spatiotemporal variation beyond measured covariates (e.g., depth, temperature) when examining sources of variation in condition.

The Baltic Sea constitutes an interesting case study for disentangling ecosystem drivers affecting body condition (Reusch *et al.*, 2018). First, in the Eastern Baltic Sea cod stock, the average body growth and body condition has declined in the time post the collapse of the stock in the early 1990s (Casini *et al.*, 2016a; Mion *et al.*, 2021). This has compromised the stock productivity to the extent that population biomass is expected to remain below safe limits despite the ban of targeted cod fisheries in 2019 (ICES, 2021a, 2021b). Second, the Baltic ecosystem has seen a major change in the abundance of both cod and its potential competitors for the important prey the isopod *Saduria entomon* (Neuenfeldt *et al.*, 2020) the

flounder complex (European flounder *Platichthys flesus* and Baltic Flounder *Platichthys solemdali*) (Orio *et al.*, 2017), and in the distribution of its main pelagic prey species (sprat *Sprattus sprattus* and herring *Clupea harengus*) (Casini *et al.*, 2011; Eero *et al.*, 2012; ICES, 2021a). Lastly, the irregular inflows of saline and oxygenated water from the North Sea together with a long residence time (25–30 years) are features that have contributed to making the Baltic Sea the largest anthropogenically induced hypoxic area in the world (Carstensen *et al.*, 2014), and it is also one of the fastest warming regional seas (Belkin, 2009; Reusch *et al.*, 2018). However, it remains unknown what the relative importance of these variables are, since they have not been analyzed directly in a single framework, and not on different spatial scales.

In this study, we apply spatiotemporal predictive-process GLMMs to characterize spatiotemporal variation in body condition of cod in the south-eastern Baltic Sea, as well as their spatiotemporal distribution. We use data from the Baltic International Trawl Survey between 1993–2019, which corresponds to a period of initially high but deteriorating condition (Casini *et al.*, 2016a). We then seek to (1) identify which set of covariates (biomass densities of saduria, flounder and cod, biomass of pelagic prey (sprat and herring), as well as depth, oxygen concentration and temperature) can explain variation in weight given length and (2) explore the role of changes in the spatiotemporal distribution for the trends in body condition.

Materials and methods

Data

To model the spatiotemporal development of cod condition and distribution, we acquired weight and length data, as well as catch per unit effort data (CPUE, numbers/hour) of cod by 10-mm length class from the Baltic International Trawl Survey (BITS) between the years 1993–2019 and in ICES sub-divisions 24–28 (*SI Appendix*, Fig. S1). CPUE data were standardized based on gear dimensions and towing speed following Orio *et al.* (2017) to the unit kg/km²

using a TVL trawl with 75 m sweeps (note that compared to Orio *et al.* (2017), we further express density in kg/km² instead of kg in 1 h trawling sweeping an area of 0.45 km² by dividing by 0.45). Abundance density was converted to biomass density by fitting annual weight-length regressions. We used only data from the fourth quarter, which corresponds to the main growing and feeding season (Aro, 1989) and also the quarter in which the Baltic International Acoustic Survey (BIAS) is conducted, meaning sprat and herring abundance can be used as covariates. The BITS data can be downloaded from <https://www.ices.dk/data/data-portals/Pages/DATRAS.aspx>.

Estimating spatiotemporal development of body condition and biomass density

Condition model

We modelled condition by assuming weight is related to length as $w = al^b$, where w is weight in grams, l is length in cm, b is the allometric length exponent and a is the condition factor in unit $\frac{g}{l^b}$ (Froese *et al.*, 2014). In addition to estimating the log condition factor, we used this relationship to calculate Le Cren's relative condition index for each individual fish i ($\frac{w_i}{al^b}$). Unlike Fulton's K , this relative condition index does not rely on the assumption that growth is isometric ($b = 3$), which if violated leads to bias when comparing condition of different lengths as the condition index scales in proportion to L^{b-3} (Le Cren, 1951).

To acquire a spatiotemporal condition factor and to assess the ability of covariates to explain variation in condition, we fit a geostatistical GLMM to the weight-length relationship on log-log scale, assuming Student-t distributed residuals (with 5 degrees of freedom) due to the presence of extreme values:

$$\log(w_{s,t}) \sim \text{Student-t}(\mu_{s,t}, \phi, \nu) \quad (1)$$

$$\mu_{s,t} = \alpha_t + \beta_l \log(l) + \sum_{k=1}^{n_k} \beta_k x + \omega_s + \epsilon_{s,t} \quad (2)$$

$$\alpha_{t=1} \sim \text{Uniform}(-\infty, \infty) \quad (3)$$

$$\alpha_{t>1} \sim \text{Normal}(\alpha_{t-1}, \sigma_\alpha^2) \quad (4)$$

$$\boldsymbol{\omega} \sim \text{MVNormal}(\mathbf{0}, \boldsymbol{\Sigma}_\omega) \quad (5)$$

$$\boldsymbol{\epsilon}_t \sim \text{MVNormal}(\mathbf{0}, \boldsymbol{\Sigma}_\epsilon) \quad (6)$$

where $w_{s,t}$ represents the weight at space \mathbf{s} (a vector of two UTM zone 33 coordinates) and time t , μ represents the mean weight and ϕ represents the scale parameter. The parameter α_t was modelled as a time-varying intercept following a random walk with a uniform prior for the initial value and a normal prior with standard deviation σ_α^2 for subsequent values. The parameter β_l represents the length-coefficient (corresponding to the allometric exponent b), and x_k represents a vector of the k -th additional covariate and β_k is its effect. The parameters $\boldsymbol{\omega}_s$ and $\boldsymbol{\epsilon}_{s,t}$ represent spatial and spatiotemporal random effects, respectively. These were assumed to be drawn from Gaussian Markov random fields (Lindgren *et al.*, 2011; Cressie and Wikle, 2015) with covariance matrices $\boldsymbol{\Sigma}_\omega$ and $\boldsymbol{\Sigma}_\epsilon$. The covariance ($\Phi(s, s')$) between spatial points s and s' in all random fields is given by a Matérn function:

$$\Phi(s, s') = \frac{\tau^2}{\Gamma(\nu)2^{\nu-1} \left(K_\nu(\kappa d_{s,s'}) \right)} \quad (7)$$

where kappa controls the spatial scale, tau controls the variance, and nu is fixed at nu = 1 to use the Stochastic Partial Differential Equation (SPDE) approximation to the GMRF (Lindgren *et al.*, 2011). Lastly, we assumed the spatiotemporal random effects to follow a stationary AR1 process:

$$\boldsymbol{\delta}_{t=1} \sim \text{MVNormal}(\mathbf{0}, \boldsymbol{\Sigma}_\epsilon) \quad (8)$$

$$\boldsymbol{\delta}_{t>1} = \rho \boldsymbol{\delta}_{t-1} + \sqrt{1 - \rho^2} \boldsymbol{\epsilon}_t, \boldsymbol{\epsilon}_t \sim \text{MVNormal}(\mathbf{0}, \boldsymbol{\Sigma}_\epsilon) \quad (9)$$

where ρ represents the correlation between subsequent spatiotemporal random fields. In summary, a log spatiotemporal condition factor can be defined as: $\log(a) = \alpha_t + \sum_{k=1}^{n_k} \beta_k x +$

$\omega_s + \epsilon_{s,t}$, i.e., Eq. 2 with $\log(\text{length}) = 0$. When calculating Le Cren's condition index over time, we use β_l and the average α_t across all t (1993 to 2019) to calculate the predicted weight, from which Le Cren's condition index are the residuals on log scale.

Density models

We fit spatiotemporal models to biomass density data in a similar fashion as for condition for two reasons: 1) to evaluate how the depth distribution, temperature and oxygen conditions experienced by cod have changed of the Baltic cod and 2) to use predicted local densities of cod and flounder as covariates in the condition model. For the first task, we used the predicted density at space \mathbf{s} and time t as weights when calculating the annual average depth, temperature, and oxygen concentration.

We modelled densities using a Tweedie distribution, as density is both continuous and contains 0 values (Tweedie, 1984; Shono, 2008; Anderson *et al.*, 2019):

$$y_{s,t} \sim \text{Tweedie}(\mu_{s,t}, p, \phi), 1 < p < 2 \quad (10)$$

$$\mu_{s,t} = \exp\left(\alpha_t + \sum_{k=1}^{n_k} f_k(x_k) + \omega_s + \epsilon_{s,t}\right) \quad (11)$$

where $y_{s,t}$ represents density [kg/km^2] at space \mathbf{s} and time t , μ is the mean density, p and ϕ represents the power and dispersion parameters, respectively. The parameters α_t represent independent means for each year, f_k is a smooth function for covariate x_k and ω_s and $\epsilon_{s,t}$ represent spatial and spatiotemporal random effects and have the same definition as in the condition model (Eqns. 5–6).

Model fitting

For computational efficiency, we fit the model in a “predictive process” modelling framework (Latimer *et al.*, 2009; Anderson and Ward, 2019), where spatial and spatiotemporal random

fields are approximated using a triangulated mesh and the SPDE approximation (Lindgren *et al.*, 2011) (*SI Appendix*, Fig. S3, S13), created using the R-package ‘R-INLA’ (Rue *et al.*, 2009). The random effects are estimated at the vertices (“knots”) of this mesh. The locations of the knots were chosen using a *k*-means clustering algorithm (with a fixed seed for reproducibility), which minimizes the total distance between data points and knots. As the knot random effects are projected to the locations of the observations, more knots generally increase accuracy at the cost of computational time, up to a threshold (REF). After initial exploration, we chose 200 knots for this application. The models were fit using ‘TMB’ (Kristensen *et al.*, 2016) via the R-package ‘sdmTMB’ (version sdmTMB_0.0.20.9, sim2 branch) (Anderson *et al.*, 2019, 2021). We checked the models were consistent with convergence by confirming the maximum absolute gradient was < 0.005 and that the Hessian matrix was positive-definitive. We used packages in the ‘tidyverse’ (Wickham *et al.*, 2019) for data processing and plotting.

Covariates

For both models (condition and density model), covariates were chosen to reflect hypothesized drivers based on published literature. For the condition model, we included covariates at different spatial scales that roughly reflect the habitats cod would have been exposed to during the build-up of energy reserves. Recent tagging studies suggest cod are either stationary or mobile over the course of a year moving between feeding and spawning habitats. However, within the feeding season, cod move roughly over an area corresponding to an ICES rectangle (1° by 30') (Hüssy *et al.*, 2020). Therefore, we included environmental and demersal covariates (temperature, oxygen, depth, cod, flounder and saduria) at the haul and the median over the ICES rectangle-level, and the pelagic covariates at the ICES rectangle- and sub division-level (not including haul-level densities as pelagic species are highly mobile). Biomass of sprat and herring (tonnes) were extracted from the ICES WGBIFS database for the BIAS survey data

(<https://www.ices.dk/community/groups/pages/WGBIFS.aspx>). Sea bottom temperature (°C) and sea bottom concentration of dissolved oxygen (ml/L) in the fourth quarter were extracted from the ocean model NEMO-Nordic-SCOBI (Eilola *et al.*, 2009; Almroth-Rosell *et al.*, 2011; Hordoir *et al.*, 2019). Depth (m) raster files were made available by the EMODnet Bathymetry project, <https://www.emodnet.eu/en/bathymetry>, funded by the European Commission Directorate General for Maritime Affairs and Fisheries. Biomass densities of *Saduria entomon* (g/m²) were extracted from a habitat distribution forced to a regional coupled ocean biogeochemical model (Gogina *et al.*, 2020; Neumann *et al.*, 2021). Biomass densities of cod and flounder (kg/km²) were taken from the same scientific survey as the condition data (BITS). We used predicted densities from GLMMs (described below) fitted to cod and flounder density as covariates, since not all hauls in the CPUE (density) data could be standardized and joined with the condition data. For the cod density models, we used depth, temperature, and oxygen as covariates, and only depth as a covariate for the cod and flounder models that were used to predict covariates for the condition model.

Following (Thorson, 2015; Grüss *et al.*, 2020), we rescaled all covariates to have a mean of 0 and a standard deviation of 1. This facilitates comparison between covariates of different units and allows for comparison between the estimated coefficients and the standard deviation of spatial (σ_O) and spatiotemporal (σ_E) variation. We did not conduct any model selection after our a priori selection of covariates to avoid statistical issues with inference stepwise selection (e.g., Whittingham *et al.*, 2006) and because initial analyses suggested the model was not overfit. This was evaluated by fitting a minimal and a full model to 80% of the data, calculating the mean squared error (MSE) for the same 80% as well as the withheld 20%. Since the MSE was not considerably worse on the withheld 20% for the full model, we proceeded with it. The importance of the covariates was judged by the effect size and confidence interval of the standardized variable.

Results

The spatiotemporal condition model revealed a decline in the log condition factor (i.e., the spatiotemporal prediction when $\log(\text{length}) = 0$) of 3.6% [2.6%, 4.2%] (values in brackets are the 2.5% and 97.5% quantiles from 500 draws from the joint precision matrix). It declined from approximately -4.50 to -4.66 between 1993 and 2019 (the decline leveled in around 2008) (Fig. 1A). This corresponds to a 15% [17%, 11%] decline in weight for cod of median length (35 cm) (see Fig. S10 for changes in weight-at-length on the arithmetic and log scale given β_l and the estimated α_t for years 1993 and 2019). Calculating change over time in Le Cren's condition index for discrete 10 cm length classes using the spatiotemporal length-weight model shows that the condition index declined for size-classes 20-70 cm (upper boundary) with approximately -0.007 annually. The decline for cod in the size-class 10-20 cm was more modest (-0.015 annual decline) (Fig. 1C). The median Le Cren's condition index declined at the same rate as the 1st and 9th decile, meaning the decline in the condition factor was not solely driven by a decrease of fish in good condition or a worsening of condition of cod already in poor condition, but a more general decline.

Predictions from the condition model illustrate the presence of consistent “low spots” of body condition in deep and low-oxygen areas (east of Bornholm, south of Gotland and between Öland and Gotland) (Fig. 2, *SI Appendix*, Fig. S1), and that the condition factor declines in the whole area over time (Fig. 2, *SI Appendix*, Fig. S9).

The covariates with the largest positive standardized effect sizes are temperature at the haul (0.009 [0.004, 0.014]) (values in brackets indicate 95% confidence interval), median depth (0.01 [0.004, 0.02]) and oxygen concentration at the ICES rectangle level (0.01 [0.002, 0.016]), and biomass of sprat in the ICES sub-division (Fig. 3). Depth at the haul is negatively associated with condition (-0.023 [-0.028, -0.02]) (weight) (Fig. 3) (see *SI Appendix*, Fig. S11,

for marginal effects plots). The biomass density of cod, flounder and the biomass of herring did not affect the weight of cod at any scale (Fig. 3). The magnitude of single covariate effect size is generally small. In fact, several times smaller than residual spatiotemporal and spatial variation. To ensure that this was not due covariates not being matched properly (i.e., the scale, or the use of the entire cod population even though feeding interactions and competition are size-dependent), we conducted sensitivity by fitting the condition model to different parts of the data (e.g., only juvenile or adult cod, omitting the mixing zone with western Baltic cod, etc. (Fig. S12). However, the model coefficients were similar across all models. This suggests there is considerable variation in space, and variation in space that changes through time, that the covariates cannot explain.

The median depth and oxygen (depth and oxygen in the environment weighted by the predicted biomass density of cod, Fig. 4) got deeper or declined throughout the time period (Fig. 5), though the population again occupied slightly shallowed waters in the last 3 years of the time series. However, their contribution to the decline over time is likely quite minor. For instance, the standardized effect size for oxygen is 0.0034 [95% confidence interval: -0.0002, 0.0070], meaning that for each unit increase in the standardized oxygen variable (i.e., 1 standard deviation or 1.85 ml/L), log weight increases by 0.34% (corresponding to a 1.2% increase in weight for a cod of median length (35cm). As a comparison, the average oxygen concentration in the environment declined by approximately 0.65 ml/L between 1993 and the lowest in 2006 (Fig. 6C-D. The biomass-weighted oxygen concentration declined more steadily (approximately 1 ml/L between 1993 and 2019), but still, the contribution to the 3.6% decline in the log condition factor is likely minor, as the change in experienced oxygen only corresponds to a change that is slightly larger than half a standard deviation in change, and oxygen trends vary in space whereas condition declined everywhere (*SI Appendix*, Fig. S9, S11).

Discussion

The body condition of fish depends on the recent energy accumulation and is therefore largely shaped by the local habitat quality. By using a fine-scale spatiotemporal condition model, we can link the condition of cod to local covariates. Our model reveals that the weight of a cod of median length declined by 15%, primarily between the years 1993–2019, and the decline occurred mostly between 1993–2008. Moreover, while there are persistent low-spots of body condition (deep and low-oxygen areas), the condition declined in the whole area, suggesting several factors are responsible for the decline in condition. While we identify changes in the spatiotemporal distribution of cod that could have led to poorer environments for condition (deeper areas with less oxygen), effect sizes of single covariates are overall small and residual spatial and spatiotemporal variation is several times larger in magnitude.

Previous studies have suggested both direct (Limburg and Casini, 2019; Brander, 2020) and indirect (Neuenfeldt *et al.*, 2020; Orio *et al.*, 2020) effects of oxygen as a cause for the declining body condition of cod. Direct effects here refer to mild hypoxia reducing the appetite and food consumption (Chabot and Dutil, 1999) and by extension also their condition, as they are not able to accumulate as large energy reserves. First, we find that the Baltic cod are currently experiencing oxygen concentrations at around 6.3 ml/L on average (1st and 9th decile are 3.6 and 7.5). In sub division 25 we estimate it to be around 6.4 (Fig. S20). This is higher than a recent estimate of 4–4.5 ml/L as the average oxygen concentration in recent years based on oxygen levels at the mean depth (Brander, 2020; Casini *et al.*, 2021). 4.3 ml/L has been proposed as a threshold for negative but sub-lethal physiological impacts, including, but not limited to, reduced feeding rates (Chabot and Dutil, 1999; Hrycik *et al.*, 2017). The difference in the estimated average oxygen concentration could be because we estimate the average oxygen by weighted the average sea bottom oxygen concentration from the ocean model

NEMO-Nordic-SCOBİ by the predicted densities from the density model. This approach overcomes the issue that oxygen concentrations span a large range for any given depth. Moreover, we see that the 1st decile of the density-weighted oxygen concentration reached an all-time low (approximately 3.5 ml/L in 2010), and then steadily increased, suggesting the average decline in oxygen concentration is not driven by a decline in the lowest oxygen concentrations. Interestingly, despite the median oxygen the population experiences being above proposed thresholds, we still find a positive effect of oxygen, in line with previous studies showing that exposure to low-oxygen areas is associated with low condition (Limburg and Casini, 2019; Casini *et al.*, 2021). However, we can only speculate if this is due to oxygen being correlated with richer habitats or if there are direct physiological impacts at lower threshold in the wild. Either way, the current trend of declining oxygen will likely contribute to further deteriorating body condition of cod.

An indirect effect of declining oxygen is a potentially intensified competition with other cod and/or flounder for shared benthic prey species, such as the isopod *Saduria entomon*, due to the habitat contraction caused by the expansion of “dead zones” (Casini *et al.*, 2016a; Orio *et al.*, 2019; Haase *et al.*, 2020). We did not include the extent of hypoxic areas as a covariate representing suitable habitat area. Instead, we use predicted density of flounder and cod at the haul and at the ICES rectangle-level as a direct density effects. Population-level density has previously been linked to fishery-induced size truncation causing higher intraspecific competition among smaller sized fished who primarily feed on benthic prey (Svedäng and Hornborg, 2014). We detected a very weak negative effect of haul-level density of cod, but not for flounder at any scale. However, biomass density is not a direct measure of competition; areas with higher densities of cod and flounder could simply also have more food. That said, we did not find strong effects of saduria density on condition. Even if we do not detect strong evidence of benthic competition as a driver of the decline in

condition, it could still be important on local scales, i.e. in habitats with saduria and flounder. Further studies are needed to investigate the effect of benthic competition for local differences in condition, potentially in combination with benthic prey biomass.

A reduced availability of sprat (either changes in their size-distribution or shifting distributions and thus reduced spatial overlap) has also been linked to poor growth and condition at the population level (Gårdmark *et al.*, 2015; Casini *et al.*, 2016a). We found positive effects of sprat abundance at the ICES subdivision level, but not for herring. It is however unclear if the decline in sprat drove the decline in condition. Even though the spawning stock biomass of sprat declined from 1.9 million tonnes in the whole Baltic in 1994 to 1.05 million tonnes in 2006, most of the decline occurred in subdivision 26-28 where cod densities are low (Fig. 4, Fig. S21) whereas the condition of cod on the other hand has declined in the whole Baltic.

The last piece of evidence (although indirect) against a general shortage of a specific prey for the decline in condition is that our model predicts a decline in condition for cod of all sizes and in all areas, even though prey densities vary geographically as well (e.g., saduria). Hence, for the decline to still be related to competition or food availability, all food sources used by cod over ontogeny ought to have declined in synchrony, or that poor condition starts early in life due a shortage of a specific resource and that cod cannot compensate for that later in life. Even if that is possible, Neuenfeldt *et al.*, (2020) showed that the feeding levels of cod between 21-30 cm were relatively high in the period 1995-2004 when the decline in condition was the most rapid, and the growth rates had not yet declined to the lowest in seven decades (Mion *et al.*, 2021). That low feeding levels was not limiting cod in the mid 90's in the midst of the steep decline in condition is in line with a recent finding that feeding rates may actually have increased, based on the N-content of otoliths (Svedäng *et al.*, 2020). Increased feeding rates

could be an attempt to compensate for declines in the quality rather than quantity of food (Svedäng *et al.*, 2020).

In conclusion, our study illustrates the fine-scale spatiotemporal development of body condition in the eastern Baltic cod, and the population-level changes in depth distribution and oxygen concentrations. We show, in line with Casini *et al.*, (2016a) that the decline in body condition started in the early 1990's and reached a bottom in the mid 2000s, and that condition has declined for all sizes and in all areas. These two features, together with small effect sizes of covariates in relation to several times larger magnitude of residual spatiotemporal and spatial variation, suggest that multiple factors have caused the decline. It is also possible that the mechanisms that caused the decline in body condition may not be the ones that have kept cod in a poor physiological state in the last 15 years. More research is needed to understand the role of fine-scale food availability for condition, e.g., by evaluating factors associated with hotspots in condition in recent years. The Eastern Baltic cod stock are not predicted to grow even in the absence of fishing mortality (ICES, 2021a). This makes it crucial to understand the role of environment and species interactions for the body condition of cod (Eero *et al.*, 2020), as body condition is a key biological trait determining mortality and reproductive output.

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395 **Author Contributions**

396 All authors contributed to the manuscript. Specifically, M.C. coordinated the study, M.L.
397 prepared the raw data, M.G. provided saduria data, M.L. led the design and conducted the
398 statistical analyses with critical contribution from S.C.A and input from M.C. M.L. wrote the
399 first draft. All authors contributed to revisions and gave final approval for publication.

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401 **Data and code availability**

402 All code and data are publicly available at https://github.com/maxlindmark/cod_condition and
403 will be deposited on Zenodo upon publication.

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641 **Figures**

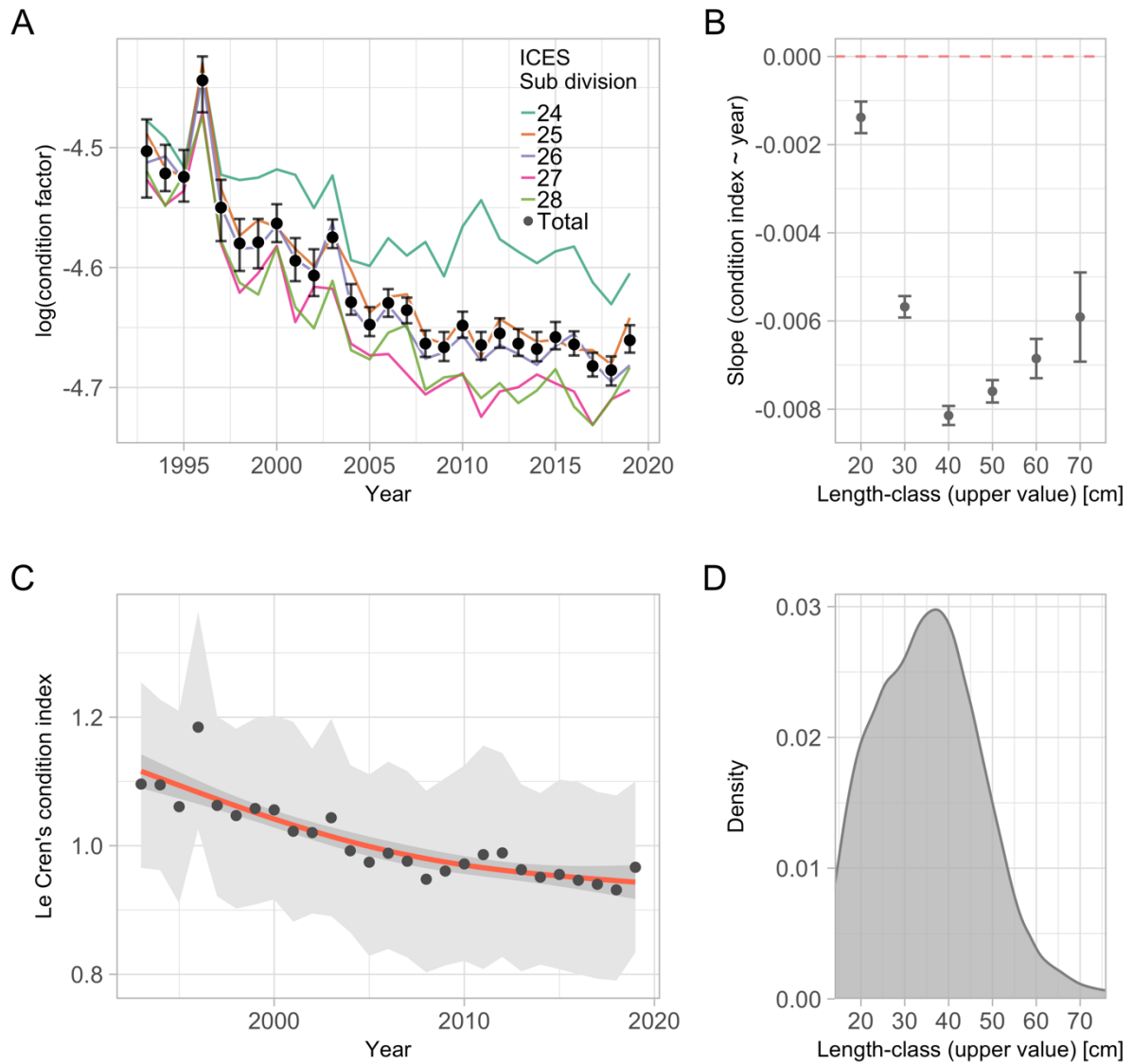
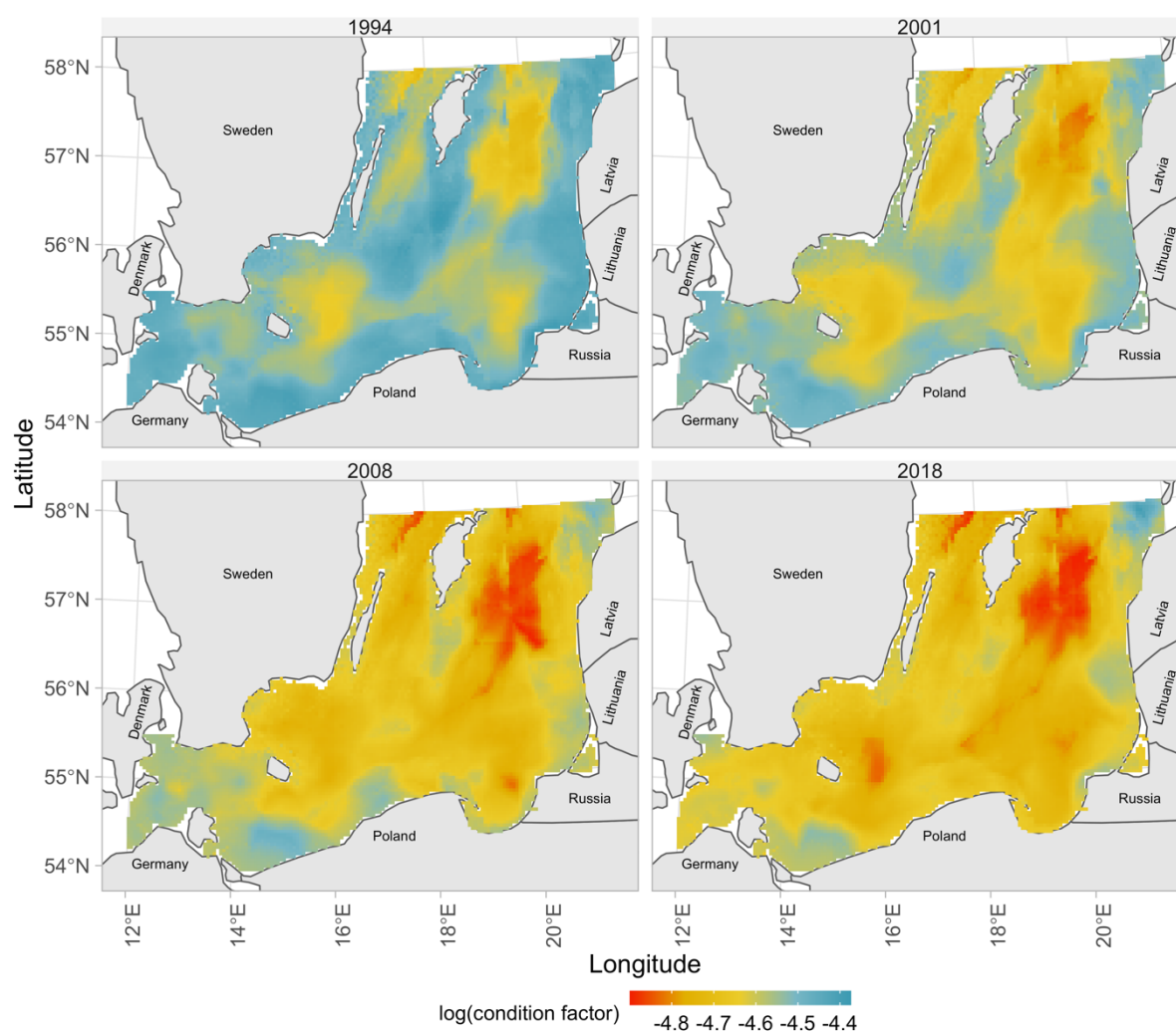


Fig. 1. A) Logarithm of the condition factor survey domain for years 1993-2019, total and by ICES sub division, acquired by predicting from the spatiotemporal condition model over a grid with spatially-varying covariates set to their true values (ICES rectangles with missing pelagic data were given the sub division mean, see *SI Appendix*, Fig. S22). Vertical lines depict the 95% confidence interval. B) Slope of the linear regression relating Le Cren's condition index and year by 10 cm length-classes (vertical lines depict the 95% confidence interval). C) Le Cren condition index as a function of year (points indicate median, large shaded area the range of the 10th and 90th percentile). Lines depict GAM fits ($k=4$) fits and the narrow shaded band corresponds to the 95% confidence interval of the median) and D) Density-plot of the size-distribution (all years pooled) of cod (note it has the same x-axis as panel B).



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655 **Fig. 2.** Predicted log condition factor with spatially varying covariates set to their true values
 656 (ICES rectangles with missing pelagic data were given the sub division mean, see *SI Appendix*,
 657 Fig. S22). Included in the plot are years 1994, 2001, 2008, 2018. For all years in the series, see
 658 *SI Appendix*, Fig. S9.

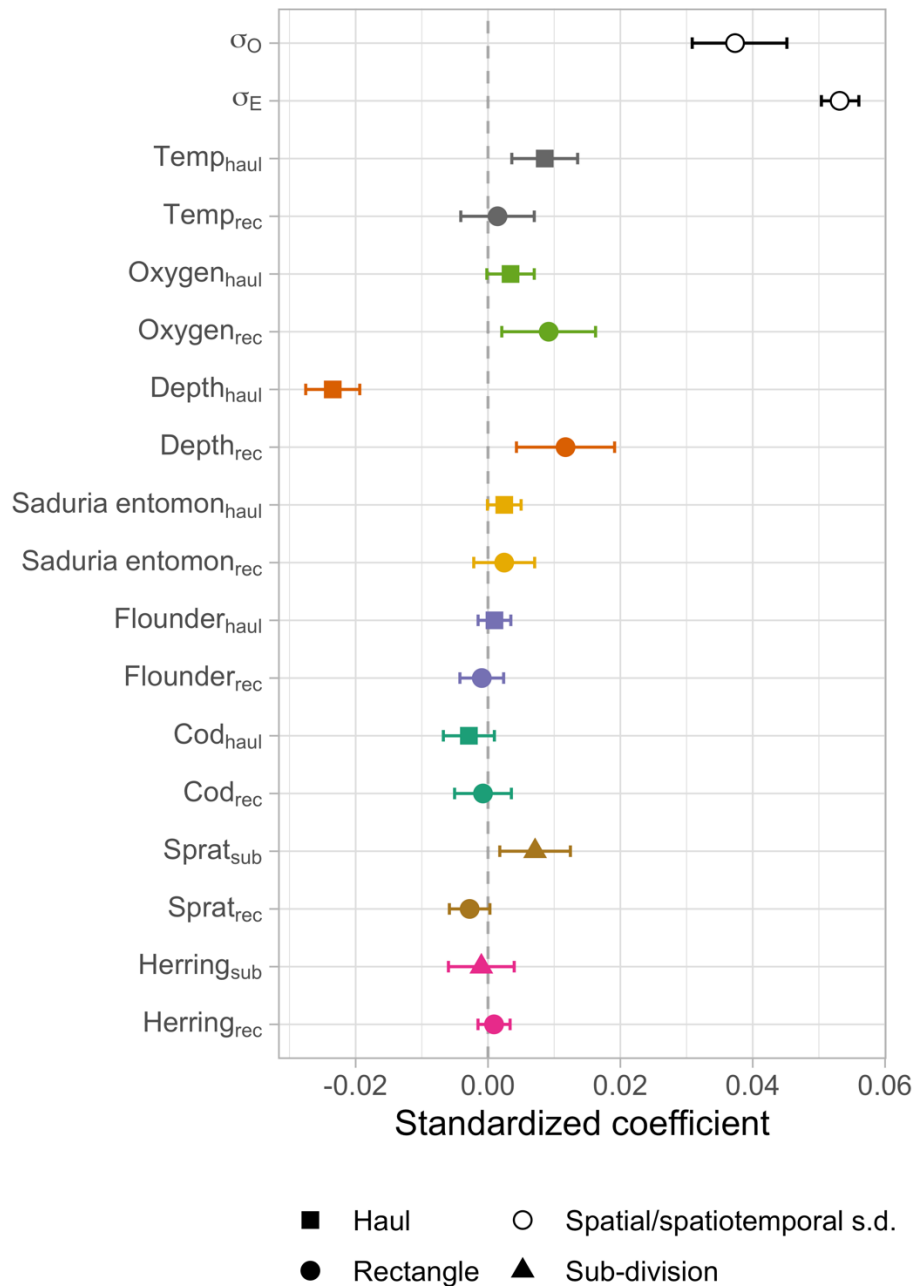


Fig. 3. Mean and 95% confidence interval of the standardized coefficients and the spatial and spatiotemporal standard deviation (σ_E and σ_O , respectively) in the condition model. The subscript *haul* refers to a covariate estimated at the location of the haul, *rec* refers to a covariate at the ICES statistical rectangle and *sub* refers to a covariate at the over ICES subdivision (*SI Appendix*, Fig. S1). Colors indicate covariate-groups and shapes indicate scale.

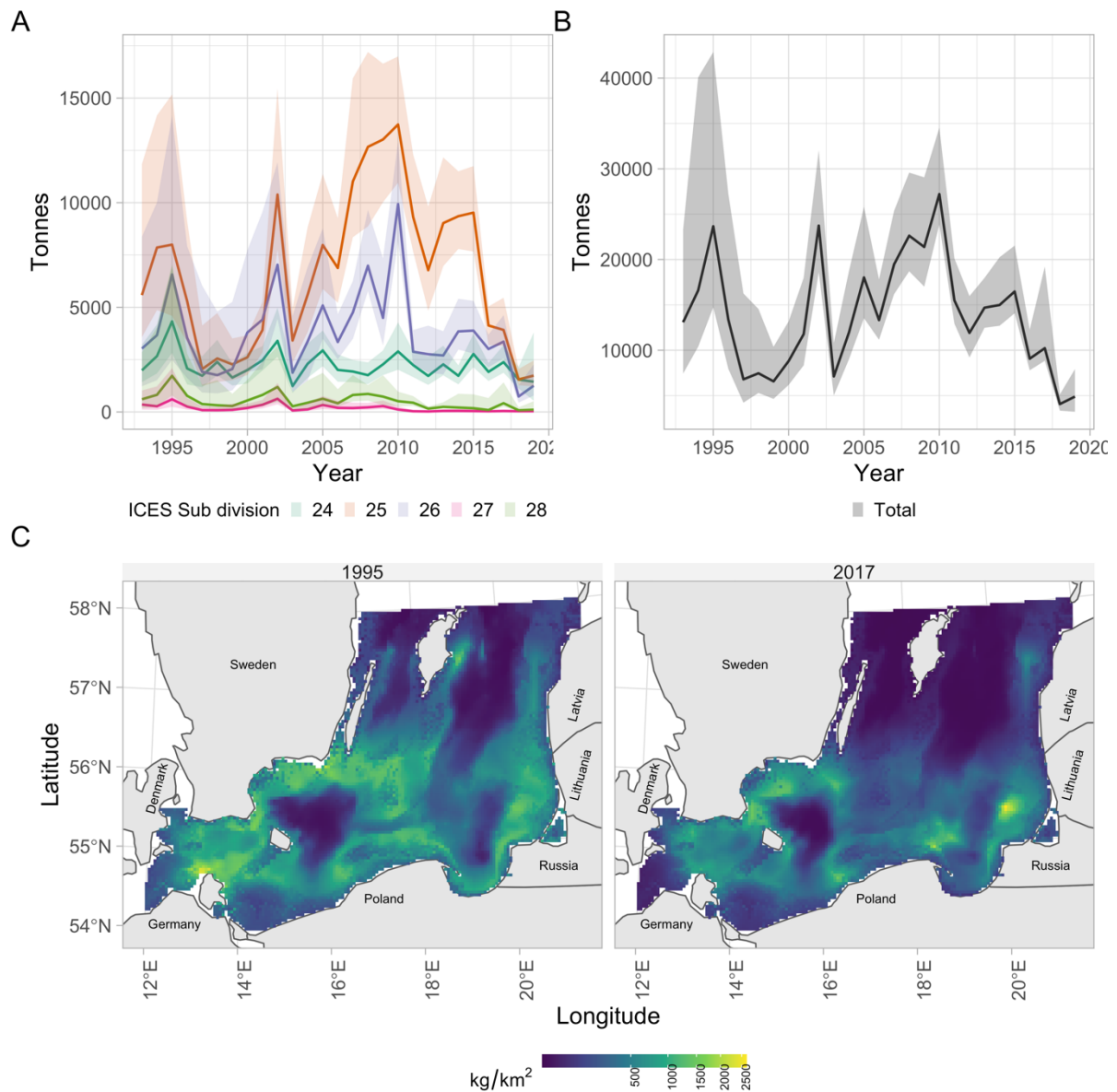


Fig. 4. A) Predicted biomass (tonnes) from the spatiotemporal CPUE model (Eq. 10-11) by ICES sub division (B) and total across all sub divisions. C) Predicted density [kg/km^2] in select years (1995 and 2017) (for all years in the series, see *SI Appendix*, Fig. S18).

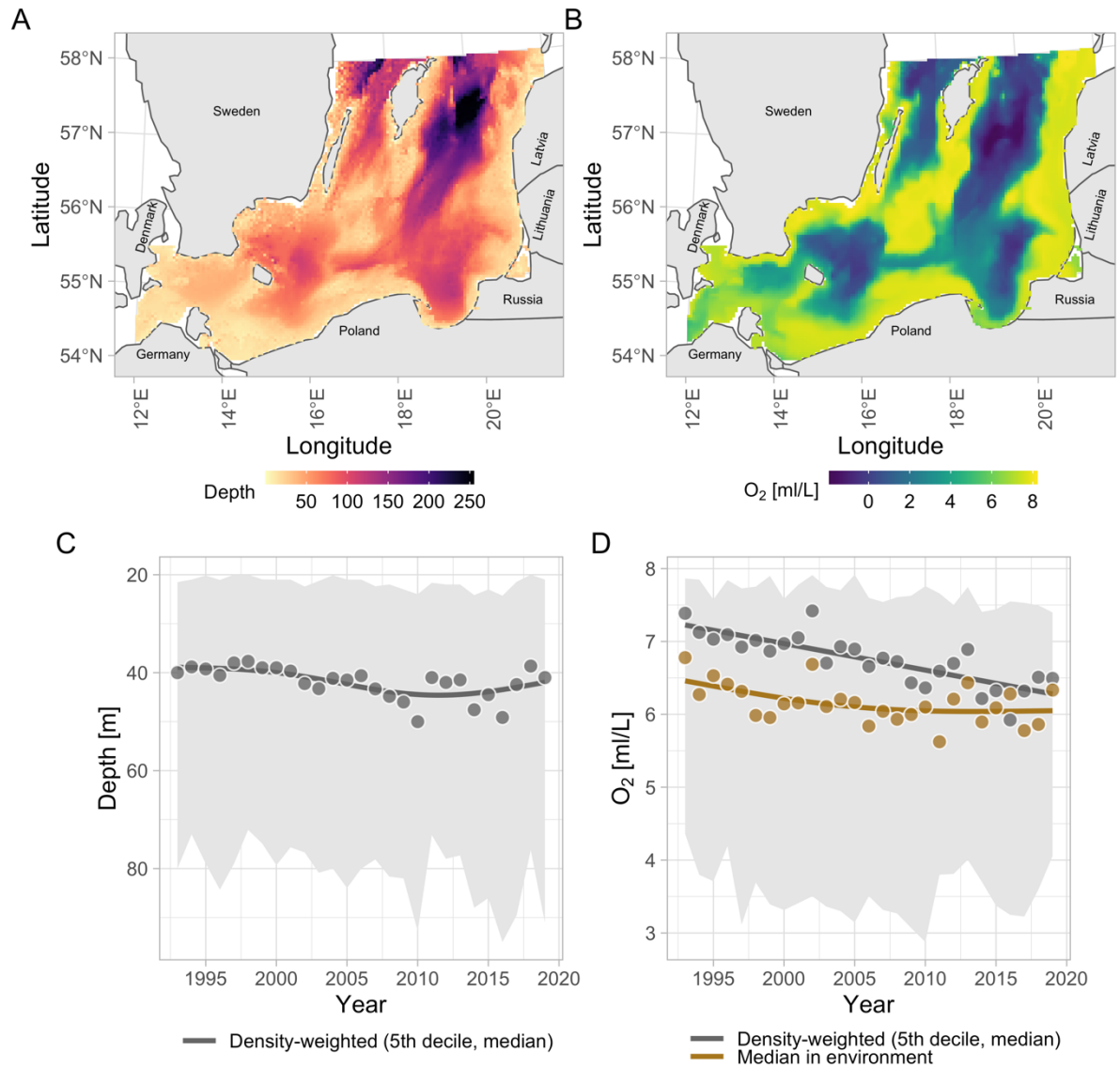


Fig. 5. (A) Bathymetry and (B) oxygen concentration (exemplified using year 1999) in the study area. Panels (C) and (D) illustrate depth and oxygen weighted by predicted cod density, respectively. The shaded areas correspond to the range of weighted depths and oxygen concentrations (1st and 9th deciles). Lines depict GAM fits ($k=4$) fits.